INFORMATION TO USERS

This reproduction was made from a copy of a document sent to us for microfilming. While the most advanced technology has been used to photograph and reproduce this document, the quality of the reproduction is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help clarify markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure complete continuity.

2. When an image on the film is obliterated with a round black mark, it is an indication of either blurred copy because of movement during exposure, duplicate copy, or copyrighted materials that should not have been filmed. For blurred pages, a good image of the page can be found in the adjacent frame. If copyrighted materials were deleted, a target note will appear listing the pages in the adjacent frame.

3. When a map, drawing or chart, etc., is part of the material being photographed, a definite method of "sectioning" the material has been followed. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again–beginning below the first row and continuing on until complete.

4. For illustrations that cannot be satisfactorily reproduced by xerographic means, photographic prints can be purchased at additional cost and inserted into your xerographic copy. These prints are available upon request from the Dissertations Customer Services Department.

5. Some pages in any document may have indistinct print. In all cases the best available copy has been filmed.

University Microfilms International
300 N. Zeeb Road
Ann Arbor, MI 48106

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

8512631

Wahlman, Gregory Paul

MIDDLE AND UPPER ORDOVICIAN MONOPLACOPHORA AND BELLEROPHONTACEAN GASTROPODA OF THE CINCINNATI ARCH REGION

University of Cincinnati PH.D. 1985

University Microfilms International 300 N. Zeeb Road, Ann Arbor, MI 48106

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLEASE NOTE:

In all cases this material has been filmed in the best possible way from the available copy. Problems encountered with this document have been identified here with a check mark ✓.

1. Glossy photographs or pages ✓
2. Colored illustrations, paper or print _____
3. Photographs with dark background ✓
4. Illustrations are poor copy _____
5. Pages with black marks, not original copy _____
6. Print shows through as there is text on both sides of page _____
7. Indistinct, broken or small print on several pages ✓
8. Print exceeds margin requirements ✓
9. Tightly bound copy with print lost in spine _____
10. Computer printout pages with indistinct print _____
11. Page(s) _____ lacking when material received, and not available from school or author.
12. Page(s) _____ seem to be missing in numbering only as text follows.
13. Two pages numbered _____. Text follows.
14. Curling and wrinkled pages _____
15. Other _____

University
Microfilms
International

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MIDDLE AND UPPER ORDOVICIAN MONOPLACOPHORA AND BELLEROPHONTACEAN GASTROPODA OF THE CINCINNATI ARCH REGION

A dissertation submitted to the

Division of Graduate Studies and Research
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

in the Department of Geology
of the College of Arts and Sciences

1985

by

Gregory Paul Wahlman

A. B., Indiana University, 1972

M. A., Indiana University, 1974

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UNIVERSITY OF CINCINNATI

May 12 19 84

I hereby recommend that the thesis prepared under my supervision by Gregory Paul Wahlman

entitled Middle and Upper Ordovician Monoplacophora and Bellerophontacean Gastropoda of the Cincinnati Arch Region

be accepted as fulfilling this part of the requirements for the degree of Doctor of Philosophy

Approved by:

Douglas E. Caster

John Pojeta

David L. Meyer

Wayne A. Pryor

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLE OF CONTENTS

	Page No.
ABSTRACT	14
INTRODUCTION	18
ACKNOWLEDGMENTS	22
STRATIGRAPHY AND GEOLOGIC SETTING	24
Biostratigraphic Classification	24
Structural - Paleogeographic History	26
Ordovician Lithostrigraphy of Central Tennessee	29
Middle Ordovician Lithostratigraphy of Central Kentucky	49
Upper Ordovician Lithostratigraphy of Kentucky, southwestern Ohio, and southeastern Indiana: Introduction	64
Upper Ordovician Lithostratigraphy of south-central Kentucky.	70
Upper Ordovician Lithostratigraphy of north-central Kentucky and southwestern Ohio	78
Upper Ordovician Lithostratigraphy of southeastern Indiana	87
MATERIAL AND PRESERVATION	92
MEASUREMENTS	96
STRATIGRAPHIC DISTRIBUTION OF SPECIES OF ORDOVICIAN MONOPLACOPHORA AND BELLEROPHONTACEAN GASTROPODA IN THE CINCINNATI ARCH REGION	97
PALEOECOLOGY OF MONOPLACOPHORANS AND BELLEROPHONTACEAN GASTROPODS	98
Introduction	98
Autecology of Monoplacophorans	98
Autecology of Bellerophontacean Gastropods	102
Previous Ordovician Paleoecological Studies	112
Ordovician Clastic Paleoecological Studies	112
Ordovician Carbonate Paleoenvironments	117
Post-Ordovician Paleoecological Studies of Note	119
Monoplacophoran - Bellerophontacean Paleocology of the Tyrone Limestone and the Lexington Limestone of central Kentucky	125
Comments on the Paleoecology of the Stones River Group of central Tennessee	131
Comments on the Paleoecology of the Nashville Group of central Tennessee	132
Comments on the Paleoecology of Upper Ordovician Faunas	135
Shell Sculpturing and Encrustation as Defenses against Predation	139

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FUNCTIONAL MORPHOLOGY 143

Introduction 143
Monoplacophora 144
Tryblidiida 144
Cyrtonellida 146
Bellerophontacean Gastropoda 151
Shell Coiling 151
Functional Aspects of Selected Bellerophontacean Shell Forms 158
The Pallial System and the Labral Emargination 163
Parietal Deposits 169
Muscle Scars and their Functional Significance 172

PHYLOGENY AND CLASSIFICATION 178

The Bellerophont Conundrum 178
Classification and Phylogeny of the Monoplacophora 196
Suprageneric classification and phylogeny of the Bellerophontacean Gastropoda 205

SYSTEMATIC PALEONTOLOGY 217

Class Monoplacophora 217
Order Tryblidiida 218
Superfamily Tryblidiacea 219
Family Tryblidiidae 219
Genus Helcionopsis 220
H. striata 222
Family Propilinidae 228
Genus Vallathotheca 230
V. manitoulini 233
V. unguiformis 236
Superfamily Kirengellacea 239
Family Archaeophialidae 240
Genus Micropileus 242
M. variabilis new species 244
Superfamily Archinacellacea 247
Family Archinacellidae 252
Genus Archinacella 253
A. simulatrix 258
A. valida 262
A. cingulata 264
A. cf. A. depressa 266
A. alta new species 268
?A. davisi new species 270
A. cf. A. pulaskiensis 272
A. rugatina 275

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

A. arca new species 277
A. indianensis 280
Order Cyrtonellida 287
Superfamily Cyrtolitacea 288
Family Cyrtolitidae 288
Genus Cyrtolites 288
Subgenus Cyrtolites (Cyrtolites) new subgenus 306
C. (C.) ornatus 307
C. (C.) retrorsus 312
C. (C.) claysferryensis new species 324
C. (C.) minor 329
C. (C.) hornyi new species 333
C. (C.) disjunctus 337
Subgenus Cyrtolites (Paracyrtolites) new subgenus 340
C. (P.) subplanus 341
C. (P.) carinatus 345
C. (P.) parvus 349
Family Sinuitidae 351
Genus Sinuites 352
S. pervoluta 355
S. cancellatus 356
S. obesus 361
S. planodorsatus 364
S. granistriatus 366
S. globularis 369
S. subcompressus 371
Class Gastropoda 371
Order Archaeogastropoda 372
Suborder Bellerophontina 374
Superfamily Bellerophontacea 375
Family Tropidodiscidae 380
Subfamily Tropidodiscinae 380
Genus Tropidodiscus 383
T. subacutus 385
T. cristatus 388
T. magnus 389
Genus Phragmolites 391
P. compressus 393
P. grandis 396
P. cellulosus 398
P. bellulus 401
P. elegans 402
P. dyeri 405
Genus Temnodiscus 408
T. nitidula 411
Family Bucaniidae 413
Subfamily Bucaniinae 415
Genus Bucania 416

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

B. emmonsi 422
B. halli 424
B. subangulata 428
B. lindsleyi 432
B. nashvillensis 435
B. frankfortensis 440
B. peracuta 442
B. sublata 445
B. micronema 448
B. rugatina 449
B. singularis 452
B. pojetai new species 454
B. simulatrix 458
B. crassa 460
Genus Kokenospira 462
K. costalis 464
Subfamily Undulabucaniinae new subfamily 466
Genus Undulabucania new genus 467
U. gorbyi 469
U. punctifrons 472
Subfamily Plectonotinae 475
Genus Tetranota 477
T. bidorsata 481
T. obseleta 487
T. sexcarinata 489
T. wisconsinensis 492
Subfamily Salpingostomatinae 495
Genus Salpingostoma 498
S. buelli 502
S. kentuckyense 505
S. richmondensis 512
Family Bellerophontidae 520
Subfamily Bellerophontinae 521
Genus Bellerophon 523
Subgenus Bellerophone (Bellerophon) 525
B. (B.) subglobulus 526
B. (B.) bilineatus 527
B. (B.) nana 529
B. (B.) subpatula 532
Subfamily Bucanopsinae new subfamily 533
Genus Bucanopsis 535
B. carinifera 538
B. diabloensis new species 543
Genus Sphenosphaera 546
S. clausus 550
S. troosti 556
S. burginensis 560
S. recurvus 562

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. subangularis 564
S. capax 566
S. mohri 568
Family Carinaropsidae 574
Subfamily Carinaropsinae 576
Genus Carinaropsis 578
C. acuta 583
C. cunulae 585
C. cymbula 588
C. explanata 595
Subfamily Pterothecinae 597
Genus Pterotheca 597
P. saffordi 603
P. expansa 607
P. angusta 614
P. harviei 616

BIBLIOGRAPHY 619

APPENDIX I - LOCALITY REGISTER 660

PLATES . . . . . .

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

LIST OF ILLUSTRATIONS

Figure 1: Outcrop areas of Ordovician sedimentary deposits in eastern North America and area of present study.

Figure 2: Late Middle and Late Ordovician Series and Stages in eastern North America.

Figure 3: Cincinnati Arch, Appalachian Basin, and associated orogenic belt.

Figure 4: General paleogeographic settings in eastern North America during Middle and Late Ordovician time.

Figure 5: Ordovician lithofacies relationships in the Cincinnati Arch Region.

Figure 6: Champlainian lithostratigraphic units in central Kentucky and central Tennessee.

Figure 7: Idealized paleogeographic setting in central Tenneesee during deposition of the Bigby-Cannon Limestone.

Figure 8: Depositional facies of the Bigby-Cannon Limestone in central Tennessee.

Figure 9: Facies relationships of the members of the Bigby-Cannon Limestone.

Figure 10: Facies relationships of the members of the Hermitage Formation.

Figure 11: Facies relationships of the major members of the Lexington Limestone and the Clays Ferry Formation in central Kentucky.

Figure 12: Cincinnatian lithostratigraphic units.

Figure 13: Common measurements on fossil specimens.

Figure 14: Paths of water currents through the shells and mantle cavities of monoplacophorans.

Figure 15: Morphological and corresponding ecological trends in Middle Ordovician bellerophontaceans.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 16: Paths of water currents through the shells and mantle cavities of bellerophontaceans.

Figure 17: Four primary models for the phylogenetic relationships between monoplacophorans, bellerophontaceans, and pleurotomariaceans.

Figure 18: Four general morphotypes of monoplacophorans representing four superfamilies.

Figure 19: Phylogenetic relationships of bellerophontacean slit-bearing subfamilies during the Late Cambrian-Middle Ordovician.

Figure 20: Graph illustrating apparent growth rate of the holotype of Helcionopsis striata.

Figure 21: Bivariate plots of measurements made on Vallatotheca unguiformis.

Figure 22: Bivariate plots of measurements on Archinacella simulatrix.

Figure 23: Bivariate plots of measurements on Archinacella indianensis.

Figure 24: Stratigraphic range chart for species of Cyrtolites (Cyrtolites) and C. (Paracyrtolites) in the Ordovician of the Cincinnati Arch region.

Figure 25: Bivariate plots of measurements on C. (Cyrtolites) ornatus.

Figure 26: Bivariate plots of measurements on C. (Cyrtolites) retrorsus from the Logana Member of the Lexington Limestone.

Figure 27: Bivariate plots of measurements on C. (Cyrtolites) retrorsus from the Grier Limestone Member of the Lexington Limestone.

Figure 28: Bivariate plots for measurements on C. (Cyrtolites) claysferryensis.

Figure 29: Bivariate plots for measurements on C. (Cyrtolites) minor.

Figure 30: Bivariate plots for measurements on C. (Cyrtolites) hornyi.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 31: Bivariate plots for measurements on Salpingostoma buelli and S. kentuckyense.

Figure 32: Bivariate plots for measurements on Salpingostoma richmondensis.

Figure 33: Bivariate plots for measurements on Bucanopsis carinifera and B. diabloensis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TABLES

Table 1: Distribution of species in Stones River Group of central Tennessee.

Table 2: Distribution of species in the Nashville Group of central Tennessee.

Table 3: Distribution of species in the Tyrone Limestone, Lexington Limestone, and Clays Ferry Formation in central Kentucky.

Table 4: Distribution of species in Upper Ordovician stratigraphic units of the Cincinnati Arch Region.

Table 5: Species relative abundances in U.S.G.S. silicified samples from the Tyrone Limestone.

Table 6: Species relative abundances in U.S.G.S. silicified samples from the Curdsville Limestone Member of the Lexington Limestone.

Table 7: Species relative abundances in U.S.G.S. silicified samples from the Logana Member of the Lexington Limestone.

Table 8: Species relative abundances in the U.S.G.S. silicified samples from the Grier Limestone Member of the Lexington Limestone.

Table 9: Species relative abundances in U.S.G.S. silicified samples from the Perryville Limestone Member of the Lexington Limestone.

Table 10: Species relative abundances in U.S.G.S. silicified samples from the Devil's Hollow Member of the Lexington Limestone.

Table 11: Species relative abundances in U.S.G.S. silicified samples from the Millersburg Member of the Lexington Limestone.

Table 12: Species relative abundances in U.S.G.S. silicified samples from Tanglewood Limestone Member of the Lexington Limestone.

Table 13: Species relative abundances in U.S.G.S. silicified samples from the Clays Ferry Formation.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 14: Species relative abundances in U.S.G.S. silicified samples from the Dillsboro Formation in Indiana.

Table 15: Examples of post-Cambrian bellerophontiform molluscan univalves from which muscle scars have been described.

Table 16: Familial classification of the class Monoplacophora.

Table 17: Familial and subfamilial classification of the Bellerophontacea and a synposis of taxonomic criteria.

Table 18: Measurements for Helcionopsis striata.

Table 19: Measurements of the growth lines of the holotype of Helcionopsis striata.

Table 20: Measurements for Vallatotheca unguiformis.

Table 21: Measurements for Micropileus variabilis.

Table 22: Measurements for Archinacella simulatrix.

Table 23: Measurements for Archinacella cingulata.

Table 24: Measurements for Archinacella indianensis.

Table 25: Measurements for C. (Cyrtolites) ornatus.

Table 26: Measurements for C. (Cyrtolites) retrorsus.

Table 27: Measurements for C. (Cyrtolites) claysferryensis.

Table 28: Measurements for C. (Cyrtolites) minor.

Table 29: Measurements for C. (Cyrtolites) hornyi.

Table 30: Measurements for C. (Cyrtolites) disjunctus.

Table 31: Measurements for C. (Paracyrtolites) subplanus.

Table 32: Measurements for C. (Paracyrtolites) carinatus.

Table 33: Measurements for Sinuites cancellatus.

Table 34: Measurements for Sinuites obesus.

Table 35: Measurements for Sinuites granistriatus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 36: Measurements for Sinuites globularis.

Table 37: Measurements for Tropidodiscus subacutus.

Table 38: Measurements for Tropidodiscus cristatus.

Table 39: Measurements for Tropidodiscus magnus.

Table 40: Measurements for Phragmolites compressus.

Table 41: Measurements for Phragmolites grandis.

Table 42: Measurements for Phragmolites cellulosus.

Table 43: Measurements for Phragmolites bellulus.

Table 44: Measurements for Phragmolites elegans.

Table 45: Measurements for Phragmolites dyeri.

Table 46: Measurements for Temnodiscus nitidula.

Table 47: Measurements for Bucania emmonsi.

Table 48: Measurements for Bucania halli.

Table 49: Measurements for Bacania subangulata.

Table 50: Measurements for Bucania lindsleyi.

Table 51: Measurements for Bucania nashvillensis.

Table 52: Measurements for Bucania frankfortensis.

Table 53: Measurements for Bucania peracuta.

Table 54: Measurements for Bucania sublata.

Table 55: Measurements for Bucania micronema.

Table 56: Measurements for Bucania rugatina.

Table 57: Measurements for Bucania singularis.

Table 58: Measurements for Bucania pojetai.

Table 59: Measurements for Bucania simulatrix.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 60: Measurements for Bucania crassa.

Table 61: Measurements for Kokenospira costalis.

Table 62: Measurements for Undulabucania gorbyi.

Table 63: Measurements for Undulabucania punctifrons.

Table 64: Measurements for Tetranota bidorsata.

Table 65: Measurements for Tetranota obseleta.

Table 66: Measurements for Tetranota sexcarinata.

Table 67: Measurements for Tetranota wisconsinensis.

Table 68: Measurements for Salpingostoma buelli.

Table 69: Measurements for Salpingostomas kentuckyense.

Table 70: Measurements for Salpingostoma richmondensis.

Table 71: Measurements for B. (Bellerophon) subglobulus.

Table 72: Measurements for B. (Bellerophon) bilineatus.

Table 73: Measurements for B. (Bellerophon) nana.

Table 74: Measurements for B. (Bellerophon) subpatula.

Table 75: Measurements for Bucanopsis carinifera.

Table 76: Measurements for Bucanopsis diabloensis.

Table 77: Measurements for Sphenosphaera clausus.

Table 78: Measurements for Sphenosphaera troosti.

Table 79: Measurements for Sphenosphaera burginensis.

Table 80: Measurements for Sphenosphaera recurvus.

Table 81: Measurements for Sphenosphaera subangularis.

Table 82: Measurements for Sphenosphaera capax.

Table 83: Measurements for Sphenosphaera mohri.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 84: Measurements for Carinaropsis acuta.

Table 85: Measurements for Carinaropsis cunulae.

Table 86: Measurements for Carinaropsis cymbula.

Table 87: Measurements for Pterotheca saffordi.

Table 88: Measurements for Pterotheca expansa.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ABSTRACT

The taxonomy, phylogenetic relationships, biostratigraphy, functional morphology and paleoecology of Middle and Upper Ordovician (Blackriveran-Richmondian) Monoplacophora and bellerophontacean Gastropoda of the Cincinnati Arch Region are discussed. Six genera and 29 species of monoplacophorans, and 13 genera and 56 species of bellerophontaceans are evaluated. The study is centered around extensive new collections of silicified fossils made by the U.S. Geological Survey during a geologic mapping program of the State of Kentucky, but museum collections, including the type specimens for most species discussed, were also examined.

Recent sedimentological and structural studies show that a proto-Cincinnati Arch existed during Middle and Late Ordovician time as a discontinuous positive platform running NW-SE, paralleling the continental margin. This proto-Cincinnati Arch apparently resulted from the continental convergence of North America with Europe and possibly Africa, and it reflects upward movement along a hinge line between the miogeocline to the east and the craton to the west. During Middle Ordovician time, carbonate deposition was more dominant on this platform than in the adjacent lower lying areas, which were dominated by shale deposition. Shale deposition increased on the platform during Late Ordovician time as a result of the erosion of tectonic lands to the east.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Paleozoic monoplacophorans and bellerophontacean gastropods are found throughout the spectrum of shallow marine shelf paleoenvironments. Bellerophontacean faunas of low diversity often dominate very shallow, restricted marine paleoenvironments. However, while numbers of individuals are less abundant, a greater diversity of taxa is seen in normal marine shelf paleoenvironments. Ordovician monoplacophorans and bellerophontaceans must have led a variety of modes of life, and could inhabit both firm and soft bottom environments. Different taxa were probably algal mat grazers, algal foliage dwellers and feeders, deposit feeders, scavengers, and possibly even predators, feeding on such sedentary benthos as sponges and bryozoans. Paleoecological analyses of the faunas of the individual members of the Lexington Limestone in central Kentucky does not show any clear trends in the distribution of most taxa. Possibly future synecological analyses will reveal trends.

In the Cincinnati Arch symmetrical molluscan univalve fauna, all limpetform taxa and all sinuate planispiral taxa are assigned to the Monoplacophora. Assignment of planispiral taxa to the Monoplacophora is based on known muscle scar patterns (multiple discrete pairs), and the possible functional significance of diamond-shaped apertures and umbilical reentrants, both of which may have channeled water currents to a posterior mantle cavity. Assignment of planispiral taxa to the bellerophontacean Gastropoda is based on known muscle scar patterns (single circumumbilical pair), the presence of a median labral slit (especially a deep slit), a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

trilobate aperture, massive parietal deposits, or an inner apertural parietal platform. It is concluded that in some cases the functional analysis of shell morphology is more reliable than muscle scar patterns in distinguishing monoplacophorans and bellerophontacean gastropods among planispiral taxa.

Four models for the phylogenetic relationships of monoplacophorans, bellerophontaceans, and pleurotomariacean archaeogastropods are considered. One model considers bellerophontaceans to be monoplacophorans and not ancestral to the pleurotomariaceans. The other three consider bellerophontaceans to be gastropods, and to be either an independent group, or ancestral to or descended from the pleurotomariaceans. However, before any of these models is accepted, a great deal more morphological and phylogenetic analyses are needed. Primarily because of the common possession of a median labral slit in many taxa, I believe that the bellerophontaceans and pleurotomariaceans are closely related phylogenetically.

Within the Bellerophontacea, there is a clear trend during the Late Cambrian and Ordovician toward the tighter coiling of the shell and an increased rate of whorl expansion, both of which acted to make the shell more compact and mobile. This increased mobility allowed bellerophontaceans to occupy higher energy environments and a greater variety of niches. This greater adaptability, along with the environmental heterogeneity resulting from the tectonism of the period, the radiation of marine algal groups, and the general diversification of marine biota, were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

responsible for the radiation of the Bellerophontacea during the Middle and Late Ordovician.

Classifications are proposed for the Monoplacophora and Bellerophontacea that are morphologically and phylogenetically based. Within the Monoplacophora, two orders are recognized - the Tryblidiida and Cyrtonellida. The more primitive order Tryblidiida contains three superfamilies - the Kirengellacea, Tryblidiacea, and Archinacellacea. The Cyrtonellida contains the superfamily Cyrtolitacea. The slit-bearing families of the superfamily Bellerophontacea are, in order of increasing phylogenetic advancement, the Tropidodiscidae, Bucaniidae, Bellerophontidae, and Carinaropsidae. Tentatively recognized within the Bellerophontacea, although none were present in the fauna under consideration, are the sinuate planispiral families Bucanellidae, Grandostomatidae, Tremanotidae, and Euphemitidae.

New taxa of Monoplacophora named herein are: Micropileus variabilis; Archinacella alta, ?Archinacella davisi, Archinacella arca; Cyrtolites (Cyrtolites) claysferryensis, Cyrtolites (Cyrtolites) hornyi. New taxa of Bellerophontacea named herein are: subfamily Undulabucaniinae, genus Undulabucania; subfamily Bucanopsinae, Bucanopsis diabloensis; Bucania pojetai; subfamily Pedasiolinae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

INTRODUCTION

The purpose of the present work is to discuss the taxonomy, functional morphology, paleoecology, biostratigraphy, and phylogenetic relationships of the Middle and Upper Ordovician Monoplacophora and bellerophontacean Gastropoda of the Cincinnati Arch Region in central Kentucky and Tennessee, southwestern Ohio, and southeastern Indiana. The last comprehensive and critical treatment of these faunas was the monograph by Ulrich and Scofield in 1897. Although fossil monoplacophorans and gastropods can be locally common elements of North American Ordovician faunas, they have undergone almost no modern study. The lack of attention of these faunas is due primarily to the scarcity of well-preserved specimens. The originally aragonitic skeletons of these mollusks were generally dissolved in early diagenesis, and therefore the preponderance of known specimens are preserved as internal molds. Fortunately, the silicification of fossils is widespread in the Middle Ordovician limestones of central Kentucky and Tennessee. Many of the specimens described by Ulrich and Scofield (1897) were silicified specimens that had weathered out of these limestones. However, silicified fossils are much less common in the Upper Ordovician strata of the Cincinnati Arch Region, and so most mollusk taxa from these rocks are known mainly from internal molds and from scarce calcitic replicas.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The present work is centered around extensive new silicified fossil collections made by the U.S. Geological Survey between 1962 and 1971 during a geologic mapping program of the State of Kentucky conducted in cooperation with the Kentucky State Geological Survey (see Pojeta, 1979). Field samples were taken as bulk limestone blocks, which were later etched in acid baths in the laboratories of the Smithsonian Institution, Washington, D.C., to release a residue of abundant silicified fossils. These new collections provide numerous additional specimens of many heretofore poorly known species. Moreover, the field samples were precisely located both stratigraphically and geographically, unlike many earlier collections, which often have vague and outdated locality and horizon data. Therefore, these new collections comprise a superior new data base for taxonomic, paleoecologic, and biostratigraphic studies. Because of the abundance of new material, and the high diversity of the Cincinnati Arch fauna, only the symmetrical molluscan univalves are covered herein. The large collections of asymmetrical conispiral gastropods in the new U.S. Geological Survey silicified collections must await study at some future date. Previous reports on other invertebrate fossils groups from the new collections have dealt with the trilobites (Ross, 1967, 1979), brachiopods (Neuman, 1967; Alberstadt, 1979; Howe, 1979), edrioasteroids (Bell, 1979), and asteroids (Branstrator, 1979).

The Cincinnati Arch fauna contains 19 genera and 85 species of monoplacophorans and bellerophontacean gastropods. In addition to the new

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

silicifield collections, many museum collections were also examined, including the type specimens for most of the species discussed. Photographs of many of these type specimens are presented for the first time here.

Middle and Upper Ordovician symmetrical molluscan univalves have important bearing on the current controversy in molluscan phylogenetic studies concerning the class level assignment of the Bellerophontida and their evolutionary role, if any, in the origin of the class Gastropoda. One group of paleontologists thinks that the Bellerophontida were evolutionary intermediates between the monoplacophorans and the archaeogastropods, while another group thinks that the Bellerophontida were monoplacophorans and were not ancestral to the archaeogastropods. Early and Middle Cambrian symmetrical molluscan univalve faunas, which are all minute in size, have recently been found to be diverse and widespread, but their relationships to later Paleozoic faunas is still a matter of active debate (Yochelson, 1978, 1979; Berg-Madsen and Peel, 1978; Runnegar, 1983). During the Late Cambrian and Early Ordovician, there appeared relatively larger molluscan univalves which have clear relationship to later Paleozoic taxa, but these faunas are uncommon and apparently of low diversity. Therefore, the diverse Middle and Late Ordovician symmetrical molluscan univalve faunas are particularly significant, as they represent the first true radiation of bellerophontiform taxa which persisted throughout the Paleozoic. These faunas provide the first adequate sample of typical

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Paleozoic morphotypes on which to base a range of functional morphological interpretations and taxonomic conclusions.

From analyses of functional morphology, I conclude that the bellerophontaceans are archaeogastropods, but that some sinuate planispiral taxa can be interpreted to be monoplacophorans.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ACKNOWLEDGMENTS

I would like to express my sincere gratitude to Drs. Kenneth E. Caster, Wayne A. Pryor, and David L. Meyer of the Department of Geology, University of Cincinnati, and to Dr. John Pojeta, Jr., of the United States Geological Survey, Washington, D.C., who offered their advice and encouragement throughout the course of this work. Special thanks are due Drs. Caster and Pojeta, whose detailed reviews of the manuscript at various stages contributed greatly to the final form. I would like to thank Dr. Ellis Yochelson, U.S. Geological Survey, Washington, D.C. for advice during the early part of the study.

For the generous loan of museum specimens, I thank the curatorial staffs of the Smithsonian Institution, Washington, D.C.; the American Museum of Natural History, New York, New York; the Field Museum of Natural History, Chicago, Illinois; the Geology Museum at the University of Cincinnati, Cincinnati, Ohio; and the Geology Museum at the University of Miami, Oxford, Ohio. Thanks also to Mr. Steve Felton of Cincinnati, Ohio, for the loan of specimens from his personal collections and for many enjoyable and informative discussions.

I appreciate the many courtesies of the U.S. Geological Survey geologists of the geologic mapping program of the State of Kentucky, particularly Drs. Earl R. Cressman and Gordon W. Wier. Many thanks are also due to Dr. George Sanderson of the Amoco Research Center, Tulsa, Oklahoma, who provided facilities for typing of the manuscript.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

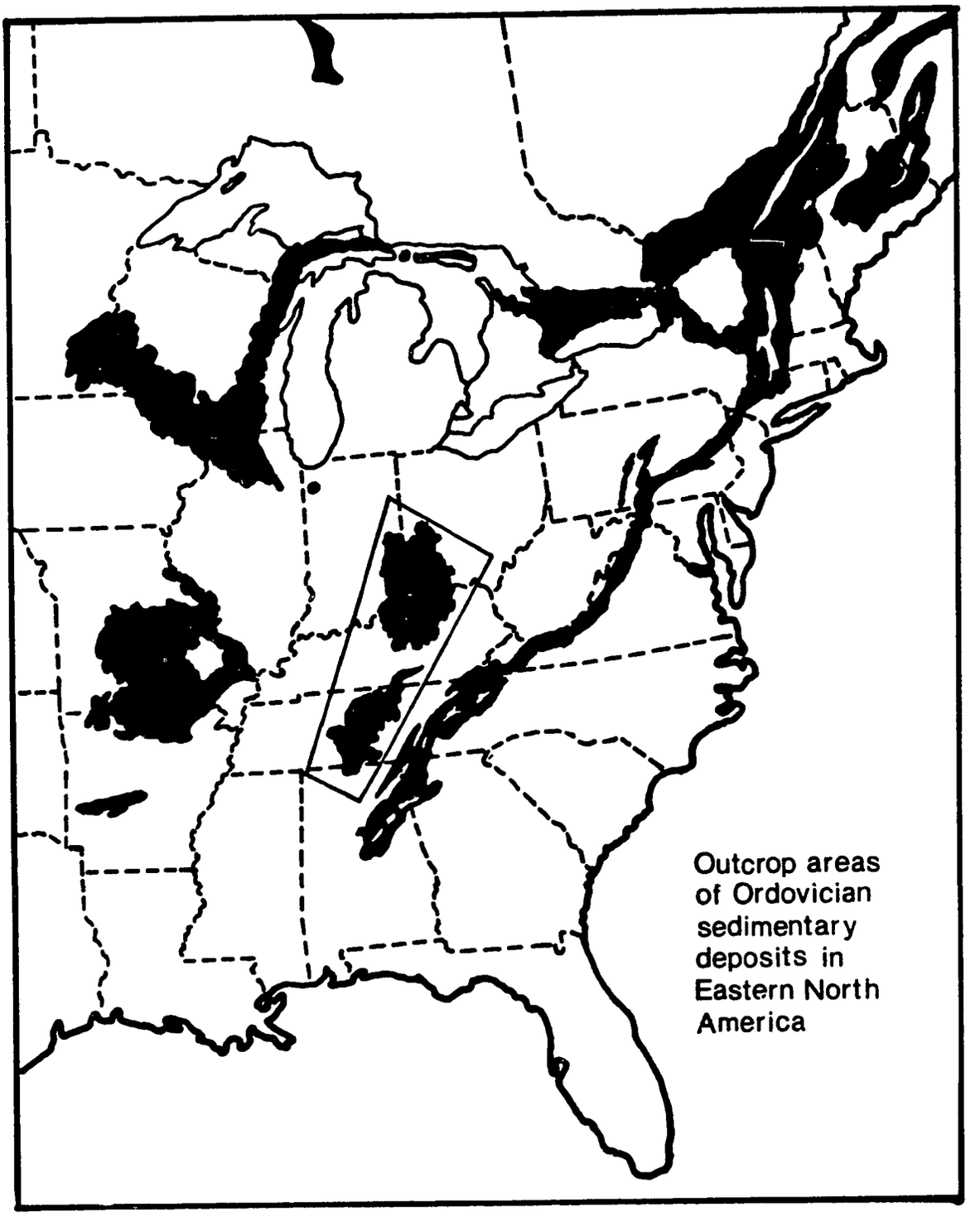
This research was financially supported by the Department of Geology, University of Cincinnati, and by the United States Geological Survey.

Finally, I offer may deepest gratitude to my family and friends for their continuing support and encouragement. In particular, I thank my wife, Joan Knoblich Wahlman, who contributed to this research in innumerable ways.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 1: Outcrop Areas of sedimentary deposits in eastern North America. Area of present study (enclosed within solid lines) includes outcrop areas around Cincinnati Arch in southeastern Indiana, southwestern Ohio, central Kentucky and central Tennessee.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

STRATIGRAPHY AND GEOLOGIC SETTING

BIOSTRATIGRAPHIC CLASSIFICATION

The Middle and Upper Ordovician time-stratigraphic units adopted here were defined by Sweet and Bergstrom (1971, p. 624, fig. 10; 1976, figs. 2-3) and Sweet (1979, fig. 3) based on conodont zonations (Figure 2). They recognized the traditional separation of Middle and Upper Ordovician rocks into the Champlainian and Cincinnatian Series, respectively, but proposed a partially new stadial classification, which was recently accepted by the U.S. Geological Survey (Pojeta, 1979, pp. A14-15).

Sweet and Bergstrom (1971, p. 624) accepted the long-standing tripartite subdivision of the Cincinnatian Series into the (ascending) Edenian, Maysvillian, and Richmondian Stages. These three divisions had historically been used dually as lithostratigraphic (Groups) and time-stratigraphic (Stages) units (Orton, 1872; Foerste, 1903; Cummings, 1908). Their restriction to stadial usage was facilitated by a complete revision of the lithostratigraphic nomenclature of the Cincinnatian strata of the type area, which is discussed in a following section.

The standard Upper Champlainian section for North America is in the Black River and Mohawk Valleys of New York. Traditionally these rocks have been divided into the Black River Group below and the Trenton Group

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

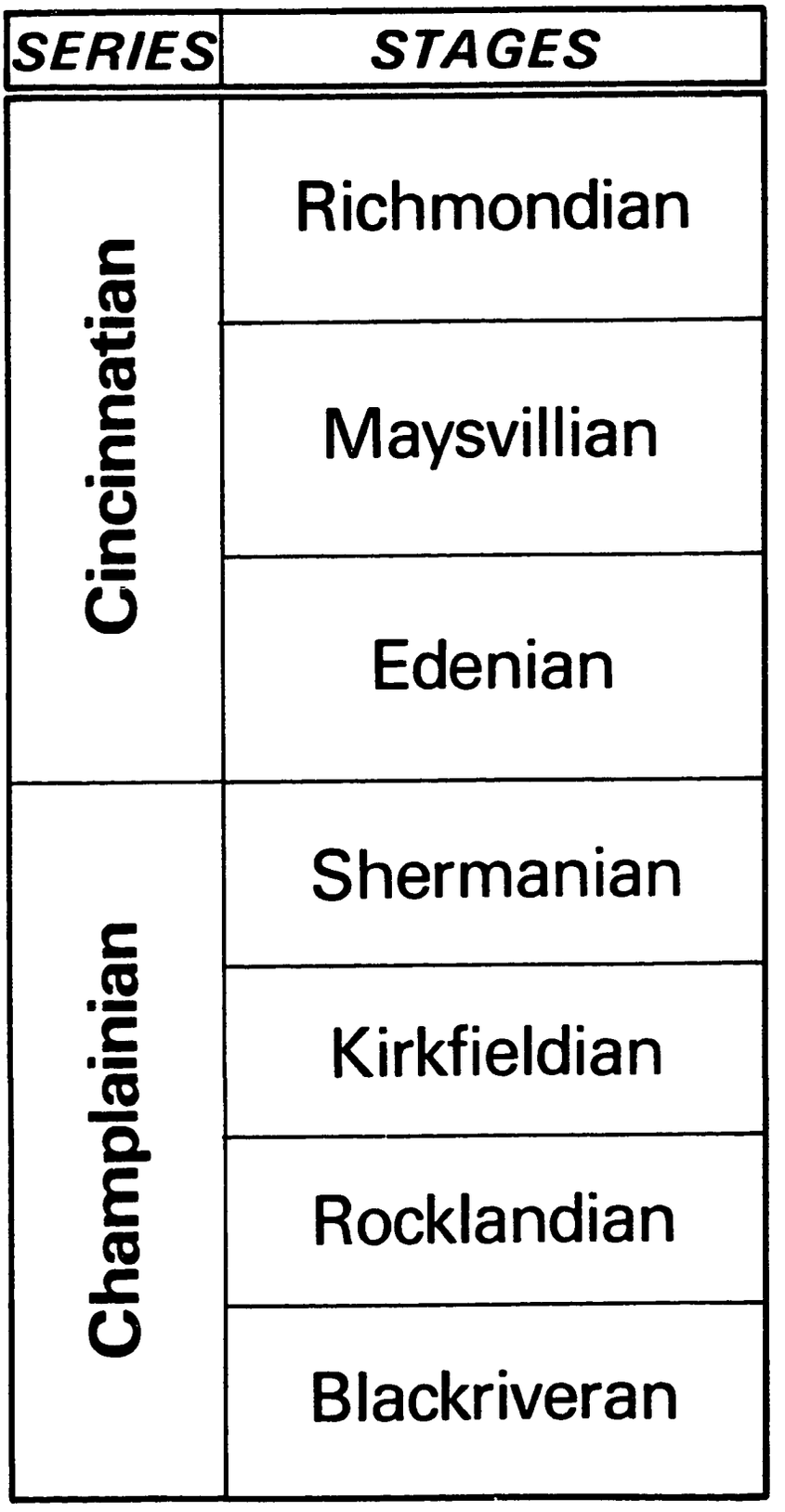


Figure 2 : Late Middle and Late Ordovician Series and Stages in eastern North America.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 3: Major structural features of the Cincinnati Arch and locations of Appalachian Basin and the associated orogenic belt during Ordovician continental convergence.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

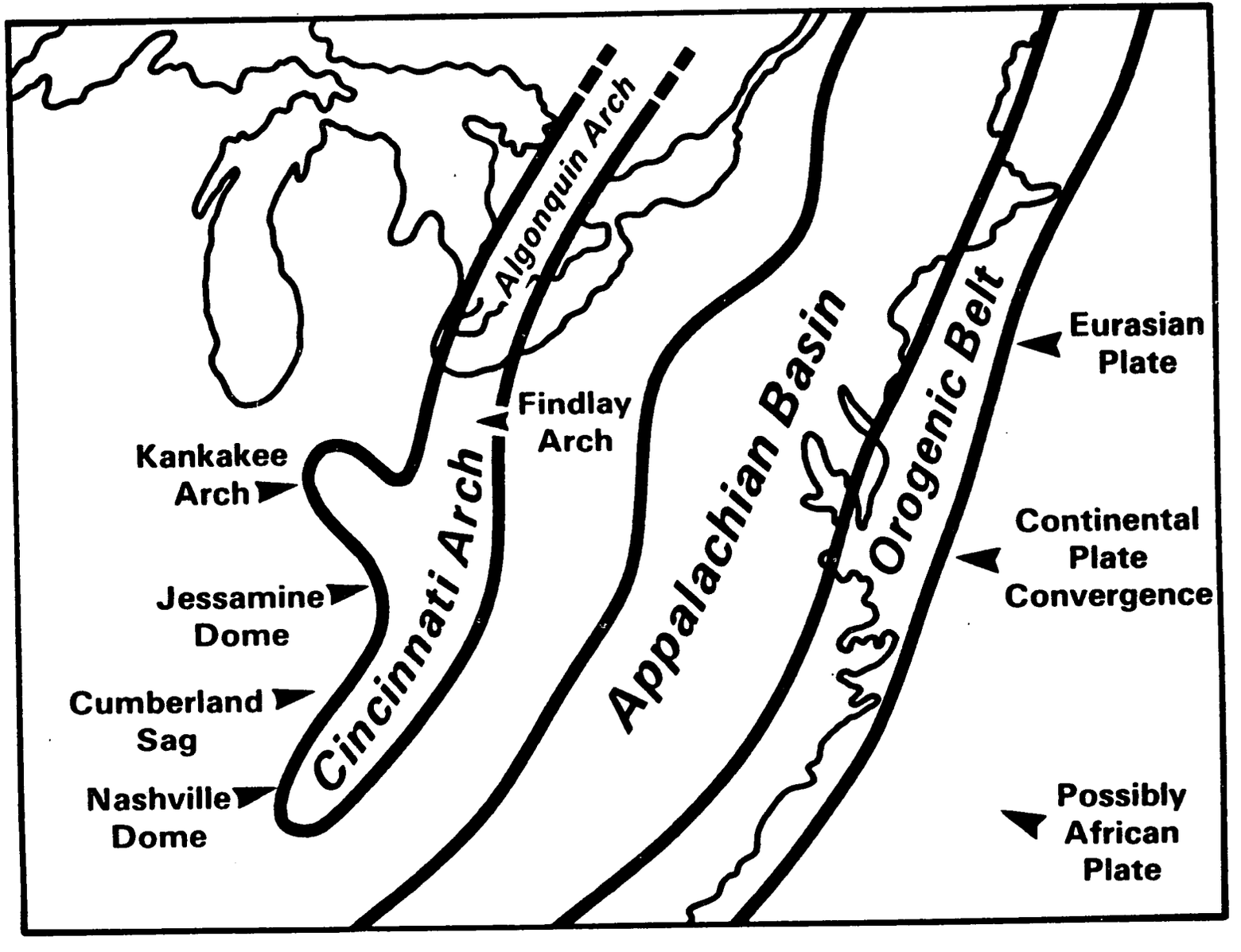
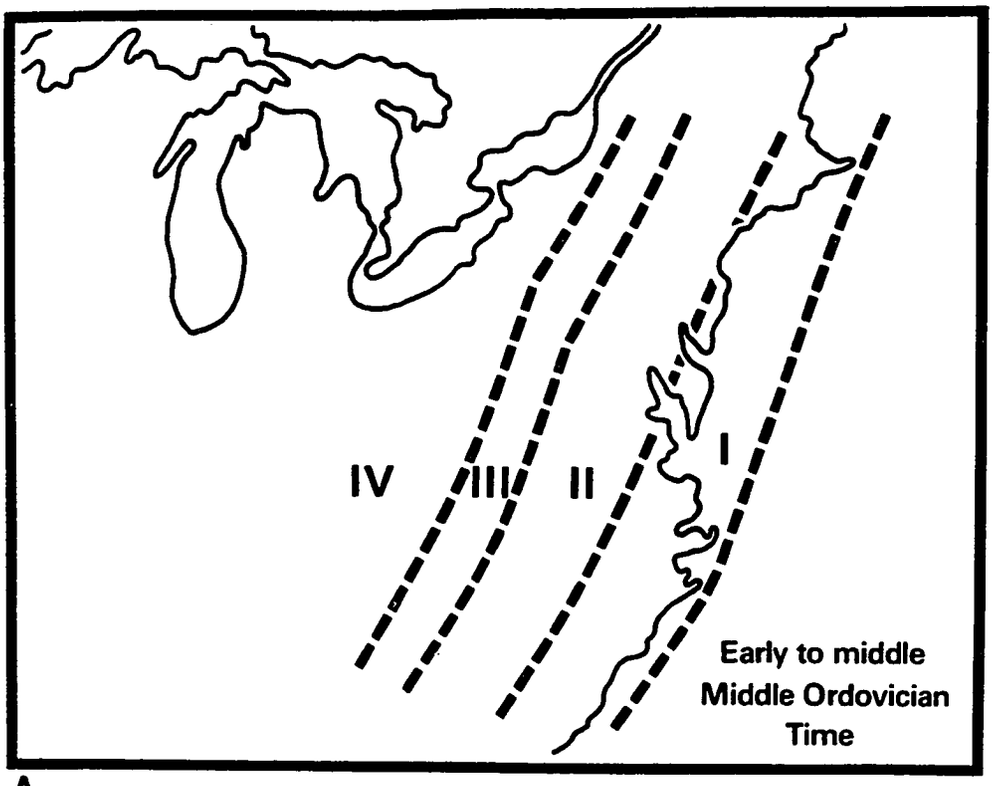


Figure 4: General paleogeographic settings in the eastern United States during Middle and Late Ordovician time.

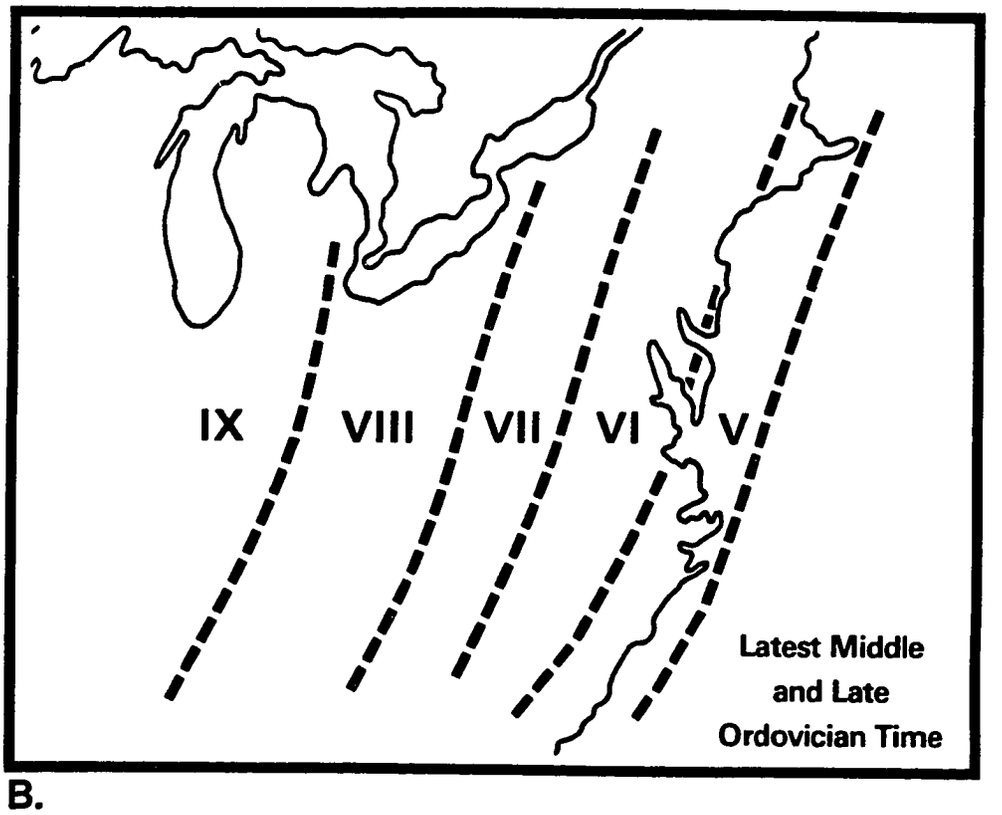
A. Early Middle to middle Middle Ordovician time.
   I. Tectonic Land.
   II. Foreland Basin (Eugeosyncline).
   III. Shelf (Miogeocline).
   IV. Cratonic interior.

B. Latest Middle and Late Ordovician time.
   V. Tectonic Land (eroding and shedding sediments westward).
   VI. Fluvial-deltaic systems transporting sediment westward.
   VII. Shallow to deep marine shelf (site of deposition of shales of Martinsburg Formation
   VIII. Carbonate platform (proto-Cincinnati Arch).
   IX. Cratonic interior basin (site of deposition of Maquoketa Group).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



A.



B.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

above. Kay (1948, p. 1401) proposed the term Trentonian as a series name, and since it has sometimes been used as a stadial term. Twenty years later, Kay (1968) reverted back to using the Trenton Group purely as a lithic term, and proposed entirely new lithic subdivisions to replace the traditional formations, which he had concluded were actually faunal-based units. Kay (1968) then proposed the older geographically-named, faunal-based subdivisions be converted to time-stratigraphic units. These were, in ascending order, the Rocklandian, Kirkfieldian, Shermanian, and Cobourgian Stages. Sweet and Bergstrom (1971, p. 624) accepted Kay's (1968) stadial classification for the most part. However, they concluded from conodont studies that the top of the Shermanian Stage in New York was at the same stratigraphic level as the base of the Edenian Stage in the Cincinnati area. Because the name Edenian had priority over Cobourgian, the latter term was rejected. Sweet and Bergstrom (1979, fig. 5; 1976, fig. 3) maintained the term Blackriveran for the stage below the Rocklandian.

The resulting stadial classification for upper Middle (Upper Champlainian) and (Upper Cincinnatian) Ordovician rocks of North America, which has been accepted by the U.S. Geological Survey (Pojeta, 1979, pp. A13-A15), is, in ascending order, the Blackriveran, Rocklandian, Kirkfieldian, Shermanian, Edenian, Maysvillian, and Richmondian Stages (fig. 2).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

STRUCTURAL-PALEOGEOGRAPHIC HISTORY

The Middle and Upper Ordovician was a period of continental convergence. The Iaepetus (proto-Atlantic) Ocean was being closed by convergence of the North American Plate with the plates of Eurasia and Africa. As these three plates approached one another in the Middle Ordovician, a subduction zone and island-arc system formed along the orogenic belt running approximately parallel to the present eastern coast of North America (Figure 3) (Bird and Dewey, 1970; Hatcher, 1972).

Landward of this orogenic belt, the Appalachian geosynˣcline became a composite foreland basin in the Middle Ordovician, with a miogeocline plunging seaward toward the subduction zone (Figure 4A) (Dickenson, 1981). During this time, deposition on the craton and upper miogeoclinal shelf was primarily carbonate, while deep marine shales were being deposited in the eugeosyncline, or foredeep basin, directly adjacent to the arc (Kay 1951, p. 15; Shanmugam and Lash, 1982; Read, 1980; Shanmugam and Walker, 1980).

As convergence continued, the orogenic belt apparently built into a continuous linear tectonic landmass. This tectonic landmass shed great amounts of sediment into the foreland basin, eventually nearly filling it. By Late Ordovician time, great deltas, most notably the Queenston Delta, built out across the basin landward (Figure 4B).

This sequence of events is reflected in the Middle and Upper Ordovician sediments of the Cincinnati Arch region. There is a marked increase

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the clastic portion in the section in latest Middle Ordovician time. The Upper Ordovician strata of the area is characterized by the interbedding in varying proportions of limestone and shale.

The Cincinnati Arch runs roughly parallel to the Appalachian Basin, basically forming a geanticline (Kay, 1951, p. 17) between it and the cratonic interior (Figure 3). A major matter of controversy since the original description of the Cincinnati "geanticline" (Locke, 1838) has been the timing of the first expression of an arch. Schuchert (1943, p. 539-545) summarizes the history of that controversy to the time of his writing. Borella and Osborne (1978) more recently addressed the problem bringing to bear new stratigraphic evidence resulting from Wilson's (1949, 1962) work around the Nashville Dome of Tennessee, and work done by numerous geologists during the U.S. Geological Survey mapping project around the Lexington Dome of Kentucky.

The Cincinnati Arch is composed of five primary structural elements. These are, from north to south: the Kankakee Arch of Indiana, and the Findlay Arch of Ohio, which merge near Cincinnati; the Jessamine Dome of central Kentucky; the Cumberland Sag (or Saddle) at the Kentucky-Tennessee border; and the Nashville Dome of central Tennessee (Figure 3). Of primary concern herein are the Jessamine and Nashville Domes, as they are primarily responsible for the fine exposures of Ordovician strata in the study area.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Wilson (1962, p. 494, fig. 16) suggested that the Nashville Dome was initiated as a mild bulging in Kirkfieldian time during deposition of the Hermitage Formation. He referred to this proto-Nashville Dome as the Central Tennessee Bank or High. He further suggested that the same period of crustal movement produced the much more prominent Ozark Dome to the west and the tectonic lands (Appalachia) to the east, both of which were high enough to yield to erosion and provide fine clastic sediments to the intervening low area.

Ervin and McGinnis (1975, p. 1290) also considered the Ozark Dome to have been initiated in the Ordovician, and agreed the origin of Nashville Dome was related.

Borella and Osborne (1978) summarized the continuing controversy over the origins of the Jessamine Dome. Using facies distribution maps for the Kirkfieldian-Shermanian-aged Lexington Limestone and sedimentologic-stratigraphic data from other authors, they concluded that the Jessamine and Nashville Domes, or precussors to these domes, were present during late Middle and early Late Ordovician time. However, they claimed that there was no continuous Cincinnati Arch at that time, this being created by renewed activation in the Late Devonian during the final closing of the proto-Atlantic Ocean.

Elias (1982, text-fig. 4) and Meyer and Tobin (1981, fig. 3) showed that during the Late Ordovician, carbonate sedimentation was concentrated along the Algonquin-Cincinnati line (see Kay, 1951, p. 21) with fine clas-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 5: Lithofacies relationships of Middle and Upper Ordovician stratigraphic units in the Cincinnati Arch Region of southeastern Indiana, southwestern Ohio, central Kentucky and central Tennessee. (Modified from Sweet, 1979).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

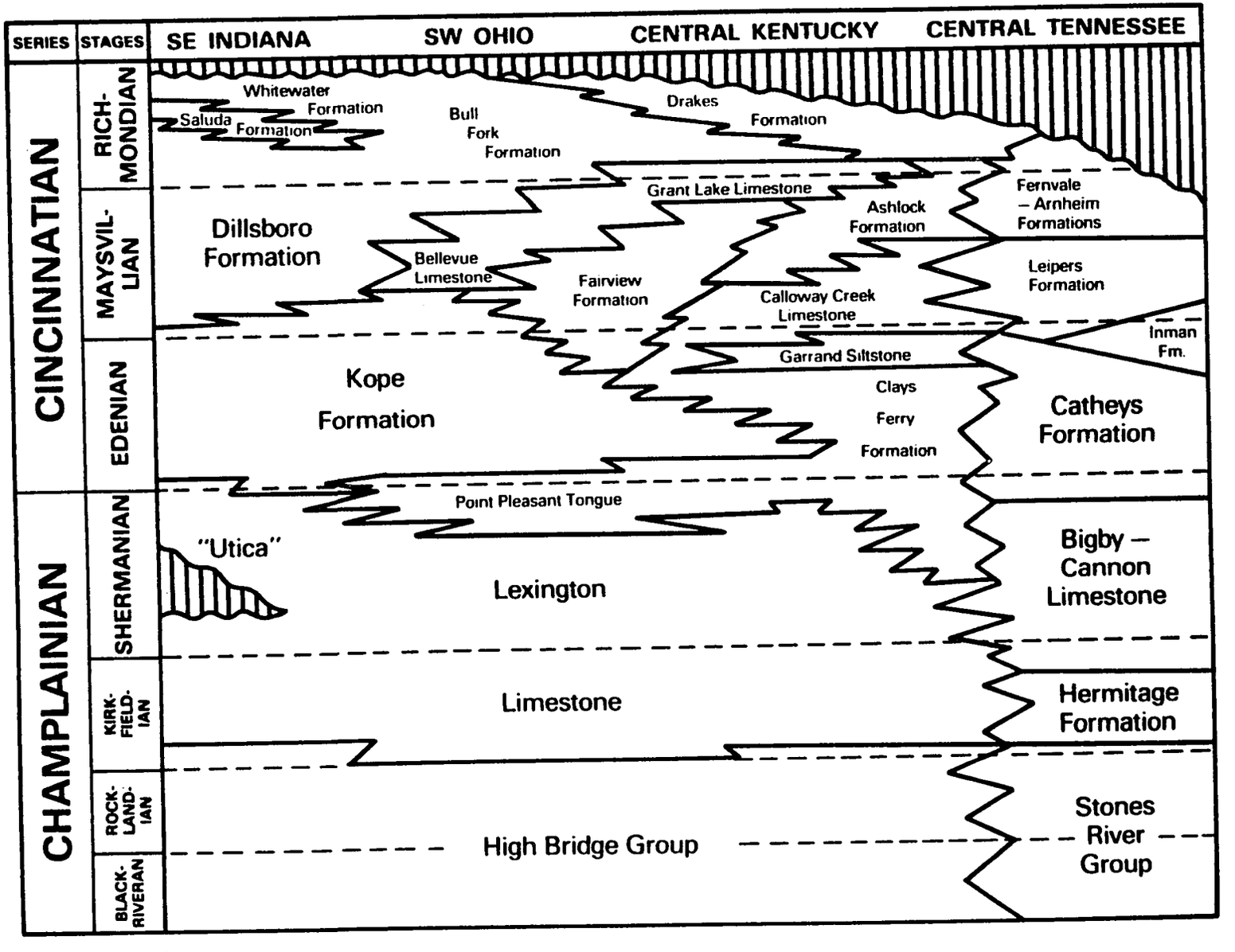


Figure 6: Champlainian lithostratigraphic units in central Kentucky and central Tennessee.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CHAMPLAINIAN LITHOSTRATIGRAPHIC UNITS		
SERIES	CENTRAL KENTUCKY	CENTRAL TENNESSEE
CHAMPLAINIAN		
Stages		
Shermanian	Clays Ferry Formation	Catheys Formation
Kirkfieldian	Lexington Limestone	Bigby-Cannon Limestone
Rocklandian	High Bridge Group	Nashville Group
Blackriveran	Tyrone Limestone	Hermitage Formation
	Oregon Formation	Carters Limestone
	Camp Nelson Limestone	Stones River Group
		Lebanon Limestone
		Ridley Limestone
		Pierce Limestone
		Murfreesboro Limestone

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tics of the Maquoketa group to the west and the Martinsburg Formation to the east. They referred to this area of carbonate deposition as a carbonate platform, not really addressing the structural controversy. However, the insinuation is obvious - it was paleotopographically high.

It is concluded here that the Cincinnati Arch formed a hinge line between the Appalachian foreland basin and the cratonic interior. As such, its origin, degree of expression, areal extent, and orientation were directly related to continental margin tectonic activity. Stratigraphic evidence strongly supports the contention that while the arch did not exist as presently known until the Middle Paleozoic, it was initiated in the Middle Ordovician and must have been a low, broad, discontinuous, linear, paleotopographic high extending from southern Ontario (Algonquin Arch) to central Tennessee (Nashville Dome).

ORDOVICIAN LITHOSTRATIGRAPHY OF CENTRAL TENNESSEE

The following discussion concerns only the Middle and Upper Ordovician stratigraphy of the Central Basin of Tennessee, and does not cover the strata of eastern Tennessee. Nearly all of the information related here was drawn directly from the works of Charles W. Wilson, Jr. (1949, 1962). The Central Basin Ordovician section consists of, in ascending order, the Stones River, Nashville, Eden, Maysville, and Richmond Groups.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stones River Group

The Stones River Group is Blackriveran and Rocklandian in age, and correlates with the High Bridge Group of central Kentucky (Sweet and Bergstrom, 1974, text-fig. 3) (Figures 5 and 6). The group consists of, in ascending order, the Murfreesboro Limestone, Pierce Limestone, Ridley Limestone, Lebanon Limestone, and Carters Limestone (Figure 6).

Murfressboro Limestone

The Murfreesboro is the oldest Ordovician-aged formation exposed in the Central Basin of Tennessee. The base of the formation is not exposed, but the maximum known thickness is 70 ft. It is overlain conformably by the Pierce Limestone.

The Murfreesboro limestone is mainly dark gray, very fine grained, and massively-bedded. Locally, it has laminations, mud cracks, intraformational conglomerate, and selectively dolomitized burrows. Chert is common. The fauna is dominantly molluscs, particularly gastropods.

Evidence indicates that the Murfreesboro was deposited in a shallow, probably restricted marine environment, most likely inner shelf lagoons and associated tidal flats.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Pierce Limestone

The Pierce is 23-28 ft of dense, very fine grained, gray, blue-gray, or dove-colored limestone. It is essentially a thin-bedded unit separating the more massive-bedded overlying Ridley and underlying Murfreesboro Limestones. The thin beds (ave. 2 in. thick) are separated by partings of gray calcareous shale. The fauna is abundant and concentrated on the bedding surfaces, consisting mainly of a diverse brachiopod-bryozoan assemblage.

This unit represents a fairly quite subtidal, normal marine environment.

Ridley Limestone

The Ridley consists of about 90 to 115 ft of massive-bedded (up to 4 ft thick), gray to bluish-gray to tan limestone. It is chiefly fine grained, but medium to coarse textures are common. Selectively dolomitized burrows and chert are both common. A widespread thin-bedded clay-rich member occurs 25-30 ft above the base of the formation. The Ridley fauna is dominated by a diverse assemblage of brachiopods and bryozoans.

This formation was deposited in a normal marine subtidal environment. The thin-bedded member seems to reflect a temporary return to conditions similar to those under which the Pierce Limestone was deposited.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lebanon Limestone

The Lebanon is 74-118 ft of gray, bluish-gray, or tan, dense, fine grained limestone, with interbeds of coarser grained limestones. The 1 to 6 inch limestone beds are separated by thin calcareous shale partings. Very characteristic of this unit are dolomitic and and clayey burrows that differentially weather giving the limestone a "worm-eaten" appearance.

The Lebanon Limestone is conformable with the underlying Ridley, but is overlain unconformably by the Carters Limestone. Similar to the Pierce Limestone, the Lebanon is also a thin-bedded unit separating two more massive-bedded units.

The Lebanon fauna is diverse and is concentrated on the platy bedding surfaces. It is dominated by a bryozoan-brachiopod assemblage.

The environment of deposition was quiet subtidal and normal marine.

Carters Limestone

The Carters Limestone is divided into two informal members.

Lower Member - This member ranges from 27 to 65 ft in thickness. Beds are 1 to 4 ft thick, though some thinner beds occur. Limestone lithologies vary from fine grained and dense, through medium to coarse grained, and even coquinoid.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Alberstadt, Walker, and Zurawski (1974) described patch reefs in southern Tennessee from the Lower Carters Limestone built primarily by stromatoporoids, corals, and algae. Wilson (1949, p. 56) cited colonial corals such as Columnaria and Tetradium as being the most characteristic fossils in the Lower Member.

Upper Member - This member reaches 28 ft in thickness, and consists mainly of dense, fine grained, laminated, argillaceous, gray to tan limestone. The most characteristic fossils are ribbon-like bryozoans and the colonial coral Tetradium cellulosum, but there is also a moderately diverse assemblage of gastropods, ostracods, and brachiopods.

The Lower and Upper Members are conformable, but the Upper Member is overlain unconformably by the Hermitage Formation of the Nashville Group.

Summary of Stones River Group Facies

As is apparent from the preceding descriptions, there are two basic facies in the Stones River Group. The first facies, Wilson's (1949, p. 67) Facies A, consists of pure, massive-bedded limestone, which commonly has dolomitized burrows, chert, and fauna of corals, stromatoporoids, brachiopods, bryozoans, molluscs, and others. The second facies, Wilson's (1949) Facies B, consists of thin limestone beds separated by shale partings, and bears a faunal characterized by fragile ramose and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ribbon-like bryozoans, brachiopods, and some molluscs and ostracods. The alternation of these two facies defines the succession of formations in the Stones River Group.

Wilson (1949) believed that the presence or absence of silt and clay was the primary control over facies (including faunal) distributions within the Stones River Group. He suggested that the alternation of the two facies in the group was the result of periodic uplifting and erosion of surrounding positive areas.

It should be noted that sedimentary features characteristic of tidal flat conditions (e.g., lamination, fenestral fabric, etc.) occur locally throughout the Stones River Group, but only characterize the basal formation, the Murfreesboro Limestone. Furthermore, the only widespread unconformities recognized in this group of rocks are at the base of the Murfreesboro, and the top of the Carters Limestone.

Nashville Group

The Nashville Group is Kirkfieldian, Shermanian, and early Edenian in age (Figure 5 and 6). It correlates with the Lexington Limestone, Clays Ferry Formation, and lower Kope Formation of Kentucky. The included formations are, in ascending order, the Hermitage Formation, Bigby-Cannon Limestone, and Catheys Formation (Figure 6).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hermitage Formation

The Hermitage Formation thickens westward across the Central Basin from 70 to 180 ft maximum. Wilson (1949, p. 82-3) subdivided the formation into numerous members, including the basal Curdsville Member, which onlaps the Carters Limestone on the flanks of the Nashville Dome island; two tongues, the Laminated Argillaceous Member that thickens westward, and the Silty Nodular Limestone Member that thickens eastward in complement; and four lentils, the Dalmanella Coquina Member, the Granular Phosphatic Member, the Ctenodonta Member, and the Blue Clay-shale Member (Figure 10). These lentils rise diagonally northwestward through the formation between the two tongues (Wilson, 1949, fig. 15).

Curdsville Limestone Member - This thin to medium bedded, coarsely crystalline limestone onlaps the Nashville Dome island, lying unconformably on the Carters Limestone. The member is only 7 ft thick on the western flank, and 10 to 15 ft thick on the eastern flank. It is absent over the top of the island.

The limestone is blue to gray in color and coarsely crystalline. Beds are 1 to 10 inches thick, averaging 2 to 3 inches, and are separated by thin gray shale partings. Fossils are abundant. Brachiopods and bryozoans predominate, but molluscs, trilobites, corals, crinoids, and ostracods also occur.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Curdsville is interpreted as a shallow subtidal, normal marine, transgressive unit.

Laminated Argillaceous Member - This member thickens westward across the Central Basin from 20 to 70 ft, but has been reported as thick as 180 ft in the subsurface. It is conformable with the underlying Curdsville and with the various overlying lentils of the Hermitage Formation.

The limestone is bluish-gray and argillaceous, and often is evenly laminated. Fossils are sparse, but those species found are typical of the entire formation. Beds are 2 to 10 inches thick, and are separated by shale partings or thin shale beds. Penecontemporaneous bedding deformation is common, with contorted and rolled-up beds being interbedded with beds consisting of rounded cobbles and boulders of the same lithology.

The perfection of the lamination and the sparse fauna suggest a relatively deep, stagnant depositional environment.

Dalmanella Coquina Member - This lentil occurs in a north-south belt and attains a thickness of 30 feet. It is a massive-bedded, grayish-blue, silty limestone with a great profusion of Dalmanella shells contributing to a coquinoid character. The lentil grades westward into the Laminated Argillaceous Member and eastward into the Silty Nodular Member. The Bigby-Cannon Limestone overlies the lentil across a local minor unconformity.

The abundant Dalmanella shells are generally unbroken, but they are shingled. Wilson (1962, p. 485-86) suggested that the environment of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

deposition was relatively deep and quiet, where the currents were strong enough to stack the rather thin delicate shells, but not strong enough to break them.

Granular Phosphatic Member - This member is probably actually a series of several lentils, rather than one continuous lentil. It ranges from 5 to 30 ft thick in any single exposure. The limestone is coarse grained, crossbedded, and contains varying amounts of phosphate. Bedding is massive to irregular. The lentils are surrounded by, and grade into, the Laminated Argillaceous Member and Silty Nodular Member.

The fauna is mostly worn and broken, and usually the only well-preserved fossils are sturdy equidimensional brachiopods and massive bryozoans.

This member represents shoaling areas that were acted upon by intense waves and currents. Wilson (1962, p. 486) suggested that the lentils formed in a north-south shoal belt.

Ctenodonta Member - This single lentil is nearly circular in outline, and reaches a maximum thickness of about 20 feet. The limestone is thin-bedded, laminated, argillaceous, and fine to medium grained. Beds are separated by shale partings. The blue-gray limestone weathers to yellowish-brown due to the oxidation of disseminated iron. The fauna is dominated by the pelecypod Cyrtodonta hermitagensis and other molluscs, which often cover the surfaces of slabs.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The lentil grades westward into the Laminated Argillaceous Member, and eastward into the Silty Nodular Member.

Blue Clay-shale Member - This lentil consists of calcareous blue clay-shale. It grades into the Laminated Argillaceous Member to the west. It reaches a thickness of 30 feet toward the southeast. Fossils are very sparse.

Silty Nodular Limestone Member - This tongue thickens eastward across the Central Basin to a thickness of about 30 feet, and grades westward into the Dalmanella Coquina, Granular Phosphatic, Ctenodonta, and Blue Clay-shale Members. It consists of nodular beds of limestone from 3 to 8 inches thick, and separated by irregular clay-shale partings. The fauna is moderately diverse and common, the most characteristic elements being bryozoans and corals, but also with other normal marine fossils.

This unit contains less clastic silt than any other member of the Hermitage. Wilson (1949) suggests this reflects a western to southwestern source for the clastics within the formation.

Bigby-Cannon Limestone

The Bigby-Cannon Limestone is Kirkfieldian-Shermanian in age, and correlates directly with the Lexington Limestone of Central Kentucky (Figure 6). The formation ranges from about 60 to 100 ft in thickness, and consists of three major lithofacies, which are distributed in north-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

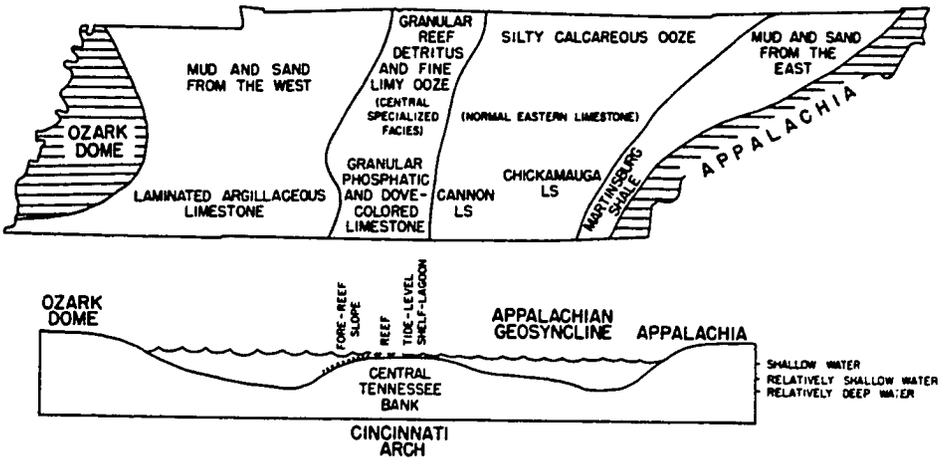


Figure 7: Idealized paleogeographic setting in central Tennessee during deposition of the Bigby-Canon Limestone (from Wilson, 1949).

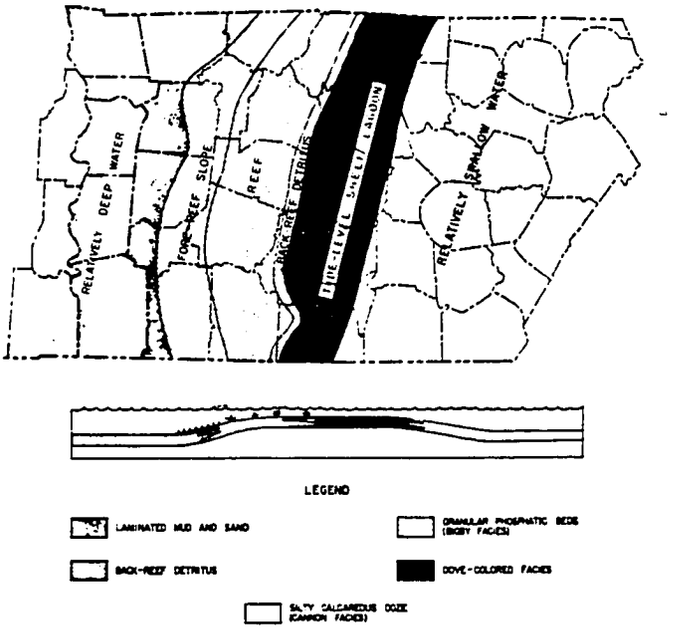


Figure 8: Depositional facies of the Bigby-Canon Limestone in central Tennessee (from Wilson, 1949).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

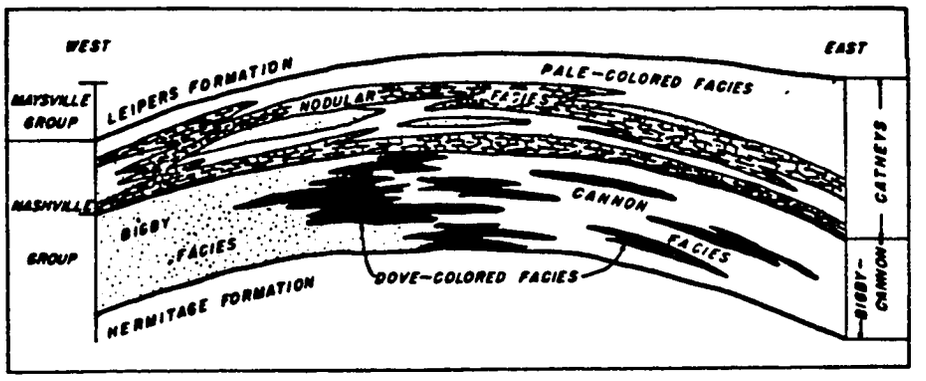


Figure 9: Facies relationships of the members of the Bigby-Canon Limestone across the Central Tennessee High (from Wilson, 1949).

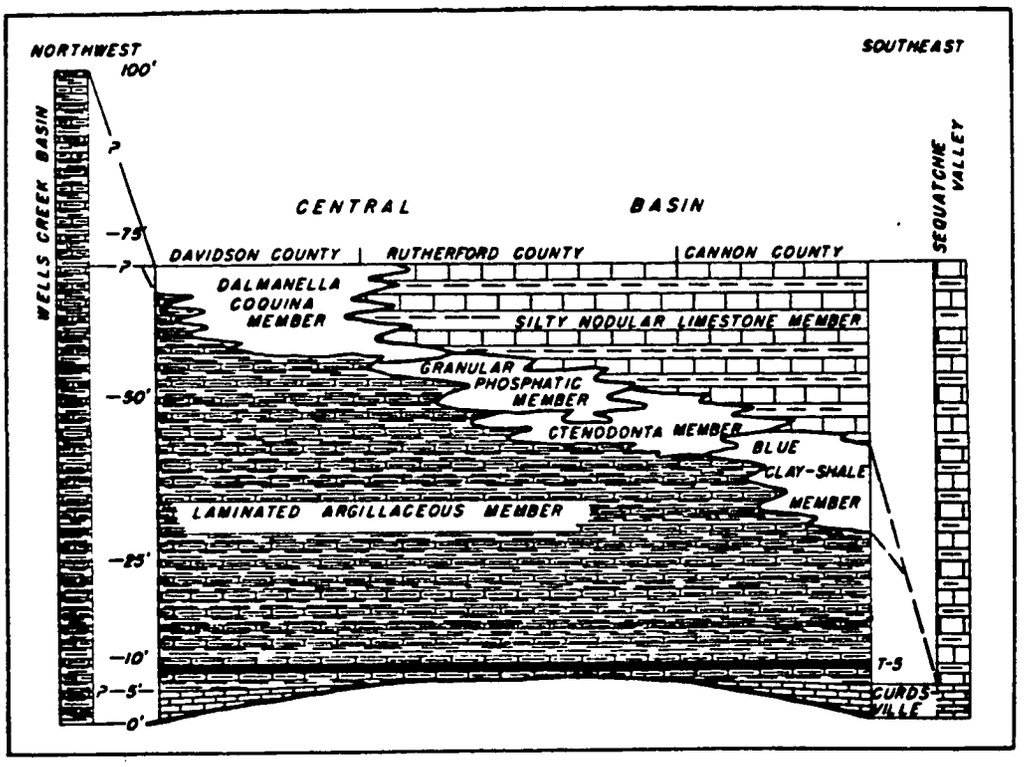


Figure 10: Facies relationships of the members of the Hermitage Formation in central Tennessee (from Wilson, 1949).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

south trending belts through the Central Basin. From west to east, these lithofacies are the Bigby facies, the Dove-colored facies, and the Cannon facies (Figures 7-9).

The contact between the Bigby-Cannon Limestone and the underlying Hermitage Formation is locally unconformable. In apparent paleotopographic high areas the Hermitage shows thinning due to erosion. However, in other areas, lithologies of the two formations clearly intertongue demonstrating continuous deposition.

Other than the papers of Wilson (1949, 1962) and Alberstadt (1973), very little has been written about this interesting and important unit in the modern literature.

Bigby facies - This facies makes up the westernmost facies belt in the formation. It rarely exceeds 60 ft in composite thickness, and its facies belt has a maximum width of 40 miles.

The Bigby limestone is coarse grained and crossbedded, and the constituent grains are mainly thoroughly broken and abraded skeletal fragments. The fauna has been so damaged by the intense wave action under which it was deposited that it is generally poorly preserved. Fossils do become better preserved eastward, and a diverse fauna is known, the most prominent members being brachiopods, bryozoans, gastropods, pelecypods, and corals. Locally within the Bigby, there are lentils of massive, coarse grained, gray limestone that have long been referred to as the Cyrtodonta beds or member. Its fauna consists almost entirely of the pelecypods Cyr-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

todonta and Vanuxemia, and the gastropods Lophospira, Bucania, and Bellerophon.

The Bigby facies represents the limits of Wilson's (1949) Central Tennessee Bank, which he interpeted as a topographically high, broad shoaling area where the water never exceeded 30 ft in depth (Figure 7). Westward off this bank, the water deepened rapidly and a laminated argillaceous limestone facies was deposited, which is now exposed only in the Western Highland Rim of the Central Basin. Eastward off the bank, the Bigby grades into the Dove-colored facies, which represents shallow lagoonal and tidal flat conditions (Figure 9).

Dove-colored Facies - This facies consists of lentils occurring in a north-south belt between the Bigby and Cannon facies belts (Figure 9). Its maximum composite thickness is 60 to 70 feet. The bases of these lentils often show evidence of scouring prior to deposition.

The facies is so-named because of its light-gray color on fresh surfaces, but it becomes chalky white upon weathering. The limestone is very fine grained, dense, and brittle. Beds vary in thickness from 2 inches to 3 feet, averaging about 1 foot. The beds are characteristically laminated, and fenestral fabric and mudcracks are common. Fossils are rare, and are generally restricted to ostracods and high-spired gastropods, with occassionally common small vertical burrows. Sometimes beds of corals, brachiopods, and other normal marine fauna occur, but Wilson (1949, 1962) interpeted these as detritus washed back off the Bigby bank during storms.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Cannon Facies - This easternmost facies of the formation thickens eastward from its intertongueing with the Dove-colored facies to a maximum thickness of 100 ft in the eastern Central Basin and the Sequatchie Valley of southeastern Tennessee (Figures 7-9).

The Cannon limestone is dark gray, fine to medium grained, moderately fossiliferous, and evenly bedded. Beds average about 1 ft thick and often have silty partings, though silt is nearly absent within the limestone itself.

Fossils are moderately abundant and well-preserved in the Cannon, consisting mainly of brachiopods, gastropods, corals, and other normal marine fauna (Wilson, 1949). Alberstadt (1973, p. 630) cited work demonstrating that most Cannon communities were dominated by bellerophontid and lophospired gastropods, and leperditid ostracods, which might indicate somewhat restricted conditions. Alberstadt further reported incrusting and boring blue-green algae, green algae, and the red alga Solenopora in the Cannon facies.

Because of the algal-gastropod-ostracod assemblage and the predominance of carbonate mud matrix, Alberstadt (1973) concluded that the Cannon was deposited in relatively quiet lagoonal conditions. The salinity of the environment was probably normal marine to slightly restricted. Since stenohaline taxa do occur commonly, the predominantly "restricted fauna" may reflect quiet, nearly stagnant conditions more than hypersalinity.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bassler (1932) had made a comprehensive study of the "Cannon" fauna, but Wilson (1949) stated that his reinterpetation of the formational contact between the Cannon and overlying Catheys Formation was so different as to put the current stratigraphic placement of many species in some doubt. Most specimens described herein from this section were collected in the late 19th century, before Bassler's or Wilson's work, so stratigraphic placement of many type specimens is a problem.

Catheys Formation

The Catheys Formation is Shermanian-Edenian in age, correlating with the Clays Ferry Formation and Kope Formation in Kentucky (Figure 5). Wilson (1949, 1962) claimed that the Catheys was unconformable with the underlying Bigby-Cannon Limestone over the Central Tennessee High, but that the hiatus was of short duration and the two formations are conformable to the east and west.

The Catheys thickens eastward across Central Tennessee from about 25 ft in the eastern Central Basin to nearly 250 ft in the Sequatchie Valley of southeastern Tennessee. The formation consists of six interbedded and intertongueing facies, which are described below (Figure 9).

Granular phosphatic facies - This facies is essentially identical to the like units in the Hermitage and Bigby-Cannon Formations. The massive-bedded, coarse grained, blue-gray limestone occurs in 5 to 10 ft

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

thick lentils. These lentils are most common in the lower half of the formation, and are most prominent in the westernmost Central Basin. Fossils are mainly badly worn and fragmented.

Dove-colored facies - This facies occurs as less than 5 ft thick lentils in the basal 25 ft of the formation. The limestone is light-gray, fine grained, dense, and brittle. It differs from the like-named facies of the Bigby-Cannon Limestone mainly by its appreciably higher clay and glauconite content. Ostracods are the most common element of a very sparse fauna.

Pale-colored facies - Nearly half the formation is made up of this blue limestone that weathers to characteristically pale hues. The facies thickens eastward, along with the total formation, from 10 to 125 ft in composite thickness.

The limestone is dark blue in color on fresh surfaces, fine grained, and dense. Beds range from 3 to 24 inches in thickness, have wavy surfaces, and are separated by blue-gray shale partings that sometimes thicken to several inches. The fauna is moderately diverse, and is dominated by brachiopods and bryozoans.

Shaly facies - This blue-gray shale facies is very irregular in its occurrence within the formation and in its thickness. It commonly occurs in about 5 ft thick shale beds, but can reach 20 ft in thickness. It varies from soft, crumbly, clay shale to fissile, compact, calcareous shale that breaks into flakes.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The most typical fossils in these shales are slender branching bryozoans, particularly Constellaria, which is often crowded into beds. Other fossils also occur including brachiopods, and lophospirid and bellerophontid gastropods, as well as Cyclonema.

Nodular facies - This facies makes up about one-third of the formation. It is distributed throughout the unit and throughout the Central Basin, and it interbeds with all the other facies. It thickens from west to east, attaining a maximum composite thickness of 75 feet.

This blue-gray limestone contains the most well-preserved fossils of any facies of the formation. The fauna is mainly composed of a brachiopod-bryozoan assemblage. The beds are 3 to 8 inches thick, have irregular knobby surfaces, and are separated by thin shale partings.

Laminated siltstone facies - This facies consists of thin laminae of fine grained, blue-gray limestone uniformly interlaminated with laminae of silt and clay. It occurs as a 5 to 10 ft unit near the base of the formation, and grades laterally and vertically into the Shaly facies. It is nearly barren of fauna.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Eden Group

Inman Formation

The Edenian-aged Inman Formation is bounded by unconformities. It varies from 40 to 70 ft in thickness, and has a rather limited area of exposure.

The formation consists of greenish-gray calcareous shale, with zones of red shale interbedded with uniformly-bedded, greenish-gray to light-gray, fine grained, dense limestone having fenestral fabric. The fauna is neither abundant nor diverse, and consists of mainly brachiopods and bryozoans. It seems to represent a quiet, shallow, subtidal to intertidal environment of deposition. The red shales might represent the first incursion of the Queenston Delta red bed facies into the area.

Maysville Group

Leipers Formation

The Maysvillian-aged Leipers Formation is also bounded by unconformities, like the underlying Inman Formation. It is generally less than 75 ft thick, but reaches 175 ft in thickness in northernmost Central Tennessee. Wilson (1949, p. 182-190) described the following facies.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Argillaceous facies - This variable facies consists of: (1) thin-bedded nodular limestone with shale partings, (2) slabby-bedded argillaceous to rather pure blue-gray limestone, (3) massive-bedded argillaceous to silty limestone, (4) blue-gray calcareous shale, and (5) light-gray to bluish-gray mudstone and siltstone. All subfacies except the last bear an abundant brachiopod-bryozoan assemblage.

Granular facies - This massive-bedded, coarse grained, dark blue limestone is usually crossbedded or irregularly bedded with local lenses of gray calcareous shale. Fossils are generally badly broken and abraded.

The facies thickens westware, just like the similar facies of Bigby-Cannon Limestone and Catheys Formation, to a maximum composite thickness of 75 feet.

Pale-colored facies - This fine grained dense limestone is dark blue in color when fresh, but weathers to a pale blue color. The beds are 2 to 24 inches thick and are separated by shale partings. The unit may be 25 to 50 ft in composite thickness.

Fossils are not as abundant in this facies as the previous two, but they are still common. The most representative members of the fauna are the brachiopod Platystrophia ponderosa and several species of gastropods.

Summary of Leipers Formation - The Granular facies dominates the formation in the western outcrop area, the Argillaceous facies dominates in the lower formation to the east, and the pale-colored facies dominates the upper formation in the east. The pattern is interpreted as a western

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

shoaling area or bank, with a broad lagoon to the east which probably shallowed upward through time.

Richmond Group

This group of rocks has not been well-studied and is rather poorly understood. Its precise relationship with the Richmondian-aged strata to the north has not been worked out.

The group is bounded by unconformities, and contains 2 main formations, the Arnheim Formation and Fernvale Limestone, with tongues of the Sequatchie Formation entering the section from the east.

The Nashville Dome was a positive feature during Richmondian time, and the Arnheim and Fernvale were apparently deposited only around the western and northern flanks of the dome.

Arnheim Formation

This unit probably does not correlate with the type Arnheim Formation of the Cincinnati area. Sparse faunal evidence may indicate a somewhat younger Richmondian age for the Tennessee unit (see McFarlan, 1943, p. 29; Bassler, 1932, p. 122, 124; Elias, 1982, p. 27-28), correlating with the Waynesville or Liberty biofacies of the type Cincinnatian section.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Tennessee Arnheim varies from 10 to 20 ft thickness around the northern and western flanks of the Nashville Dome. It consists of four facies, which intergrade laterally and vertically. These are: (1) massive-bedded, argillaceous, rubbly limestone, (2) thin-bedded, nodular, blue-gray limestone, (3) cherty, argillaceous, blue-gray limestone, and (4) gray shale. The unit is very fossiliferous, the fauna being dominated by brachiopods.

In most places the lowermost Arnheim is a basal conglomerate lying on a ferruginous contact with the underlying Leipers Formation. In some areas the Arnheim is overlain by a massive-bedded calcareous mudstone tongue of the Sequatchie Formation, rather than by the Fernvale Limestone.

Fernvale Limestone

The Fernvale Limestone typically consists of massive or irregularly-bedded, very coarsely crystalline, gray limestone with varicolored grains. Sometimes thin wavy lenticular beds can be discerned within the massive beds. In some areas, the unit becomes ferruginous or phosphatic.

The Fernvale generally overlies either the Arnheim or Leipers unconformably, but overlies a tongue of the Sequatchie Formation when present. The formation grades eastward into the Sequatchie Formation.

Again, brachiopods dominate the moderately common fossil assemblage, particularly Rhynchotrema capax.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MIDDLE ORDOVICIAN LITHOSTRATIGRAPHY OF KENTUCKY

The Middle Ordovician strata of Kentucky are exposed around the flanks of the Jessamine Dome. The section includes the High Bridge Group (Blackriveran-Kirkfieldian) and the Lexington Limestone (Kirkfieldian-Shermanian). In different areas, the Clays Ferry Formation, Kope Formation, and Lexington Limestone straddle the Middle-Upper Ordovician boundary (Pojeta, 1979, p. A14) (Figure 5).

High Bridge Group

The carbonate rocks of the High Bridge Group range from 550-700 ft in thickness. The High Bridge Group is divided into three formations, which are, in ascending order, the Camp Nelson Limestone, Oregon Formation, and Tyrone Limestone. These are the oldest strata exposed in Kentucky. They outcrop in the gorge carved by the Kentucky River across the Jessamine Dome. The thickest exposed section of the High Bridge Group is in this gorge, and measures 440 ft in thickness. The lower part of the Camp Nelson Limestone is known only from drill cores.

Cressman and Noger (1976) and Kuhuhenn, Grabowski, and Dever (1981) have described the carbonate rocks of the High Bridge Group. They have interpreted the depositional environments of the group as being analogous to the shallow subtidal, intertidal, and supratidal facies of the modern

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bahama Islands. Peritidal carbonates dominate in series of shallowing-upward cycles resulting from constantly migrating environments on a stable cratonic platform. Cressman and Noger (1976, pp. 9-13) compared the High Bridge Group with other correlative carbonate sequences in Alabama, Arkansas, New York, and Ontario. They concluded that the High Bridge Group was part of a vast complex of tidal flats and associated environments that extended over much of the craton of eastern North America during Blackriveran-Rocklandian time. The High Bridge Group of central Kentucky is directly correlative with the Stones River Group of Central Tennessee (Sweet and Bergstrom, 1976, text-fig. 3) (Figures 5 & 6).

Camp Nelson Limestone

The Camp Nelson Limestone is the lowermost formation in the High Bridge Group. It unconformably overlies the Whiterockian-aged Wells Creek Dolomite in the subsurface (Sweet and Bergstrom, 1976, text-fig. 3), and is conformable with the overlying Oregon Formation.

The formation is composed of micrite, pelmicrite, and biopelmicrite (Cressman and Noger, 1976, p. 1). Burrows are common throughout most of the unit, and are often selectively dolomitized.

Most of the Camp Nelson represents shallow subtidal environments, with subordinate peritidal deposits. Some biomicrites have a diverse fauna of ostracodes, trilobites, brachiopods, corals (Tetradium), bryo-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

zoans, pelecypods, and nautiloids. The peritidal carbonates display algal laminae, fenestral fabric, intraformational conglomerates, and mudcracks. The two types of carbonates are arranged in shallowing-upward cycles. These cycles are thicker than those in the overlying two formations.

Oregon Formation

The Oregon Formation ranges from 6 to 65 ft in thickness. It is dominantly composed of a finely crystalline dolomite that is interbedded with micritic limestone. The contacts with the adjacent limestone formations are placed at the base of the lowest dolomite bed and the top of the highest dolomite bed.

Peritidal depositional environments in repeated shallowing-upward cycles characterize the formation. Biopelsparites contain fragments of crinoids, bryozoans, brachiopods, ostracodes, and tabulate corals. Biomicrites have a more restricted fauna of ostracodes, gastropods, and some trilobites and tabulate corals. Peritidal carbonates, which predominate, have cryptalgalaminated and thin-bedded dolostones with desiccation features and some intraclastic layers (Kuhnhenn, Grabowski, and Dever, 1981).

Dolomite is much more abundant in the Oregon than the Camp Nelson or Tyrone Limestones. Kuhnhenn, Grabowski, and Dever (1981, p. 9) suggested that perhaps the Oregon sediments were more exposed as parts of low broad islands. The dolomite is believed to be diagenetic in origin by these

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

authors, as lithologies in the Oregon do not significantly differ from those of the Tyrone Limestone.

Tyrone Limestone

The Tyrone Limestone is 55 to 155 ft in thickness, and its thickness varies in compliment with the thinning of the Oregon Formation. The Tyrone is conformable with the underlying Oregon, but is disconformable with the overlying Lexington Limestone (Cressman, 1973, p. 12-13). The limestones of the Tryone are biopelsparites, biomicrites, and peritidal micrites, similar to the rocks of the underlying Oregon Formation, but with less dolomite. Just as in the lower High Bridge strata, the Tyrone carbonates are arranged in shallowing-upward cycles. These cycles become shorter and simpler in the upper portion of the Tyrone (Kuhnhenn, Grabowski, and Dever, 1981, p. 5). Greene (1966) lists a mainly molluscan fauna dominated by gastropod species.

Lexington Limestone

The Lexington Limestone is a complex 3-dimensional facies mosaic of mostly bioclastic and fossiliferous limestones outcropping around the Jessamine Dome in Central Kentucky (Figure 11). Sweet and Bergstrom (1976, text-fig. 3) and Sweet (1979, p. G13) assigned a Kirkfieldian-Edenian-age to the unit (Figure 5).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

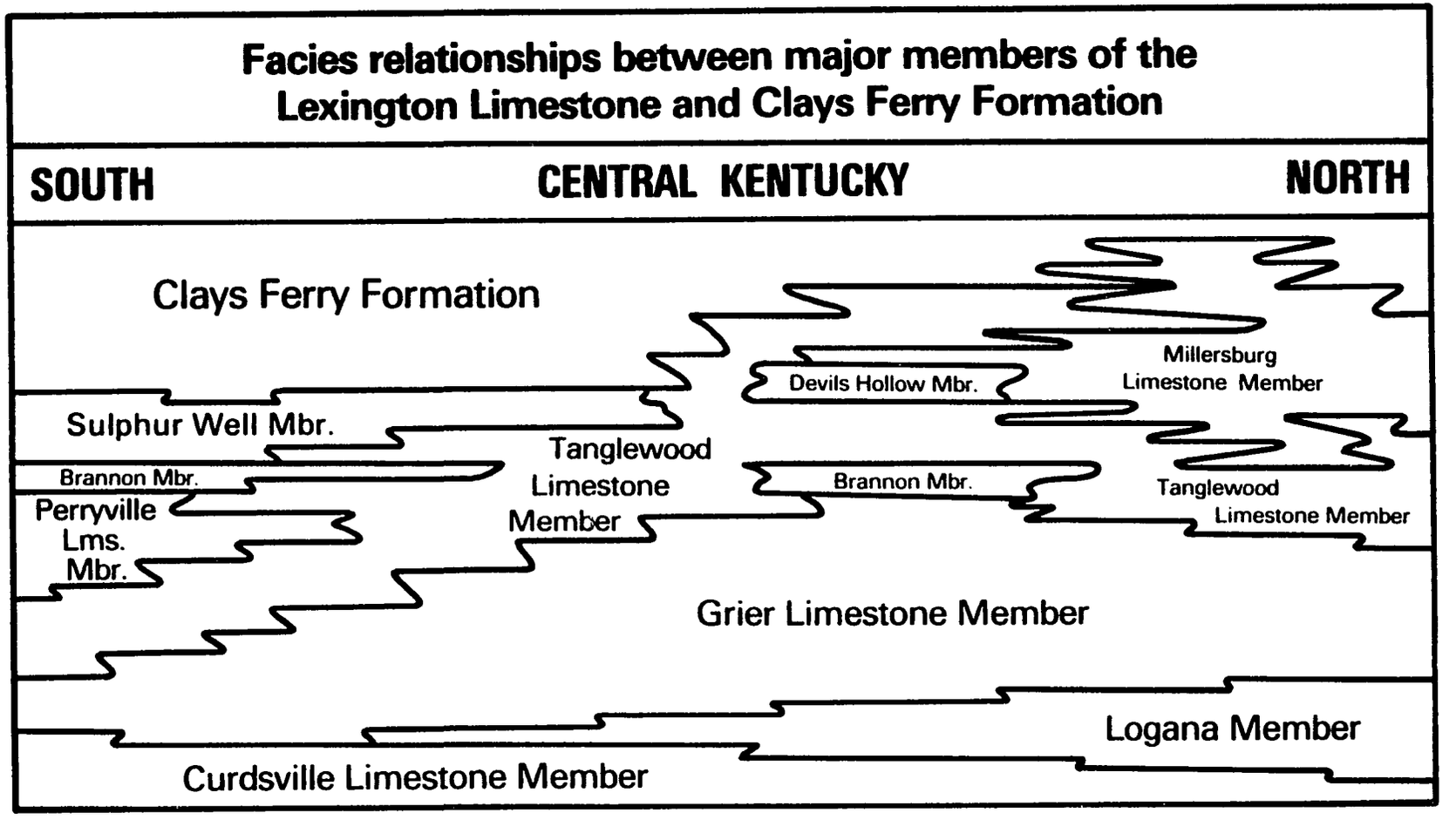


Figure 11: Facies relationships between the major members of the Lexington Limestone and the Clays Ferry Formation in central Kentucky (modified from Cressman, 1973, and unpublished figure).

Black, Cressman, and MacQuown (1965) redefined the formation to include all strata formerly assigned to the Lexington Limestone and the Cynthiana Formation (McFarlan, 1943; McFarlan and White, 1948; Nosow and McFarlan, 1960), with the exception of those Cynthiana beds placed in the Clays Ferry Formation by Wier, Green, and Simmons (1965). The mainly bioclastic and fossiliferous limestones of the Lexington contrast strongly to the mainly micritic Tyrone limestones below and the interbedded shales and limestones of the Clays Ferry Formation above.

The Lexington Limestone unconformably overlies the Tyrone Limestone. Cressman (1973, pp. 12-13) demonstrated at least 10 ft of erosional relief on the Tyrone Limestone, over which the Curdsville Limestone Member of the Lexington Limestone transgressed, but he felt that the time gap represented was small.

The contact between the Lexington Limestone and the overlying Clays Ferry Formation is conformable and diachronous because of intertongueing (Figures 5 and 11). The Lexington is up to 320 ft thick in its central outcrop area, but thins to less than 200 ft to the north and south because of intertongueing of the upper members of the Lexington Limestone with the shale and limestone of the Clays Ferry Formation. Silicified fossil horizons are common in the Lexington Limestone, and the majority of silicified fossils studied here were collected from this unit by the U.S. Geological Survey. Cressman (1973) presented an excellent detailed lithostratigraphic study of the Lexington Limestone. The following descriptions of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the members of the Lexington Limestone are taken primarily from that report.

Curdsville Limestone Member

The Curdsville Limestone Member is the basal unit within the Lexington Limestone (Figure 11). The contact with the underlying Tyrone Limestone is an erosional unconformity. The member ranges from about 20 to 40 ft in thickness, thinning westward due to facies gradation into the Logana Member. The Curdsville is overlain by the Logana Member in the central and northern outcrop areas, and by the Grier Limestone Member to the south.

Macquown (1967) divided the Curdsville into three informal units, which are gradational at their contacts. The lower 10 ft thick unit is light-colored bioclastic limestone that consists of calcirudites, and crossbedded and ripple-marked calcarenites. This unit is composed of well-sorted, abraded skeletal debris, and about 5 to 10 percent quartz sand. The middle unit occurs for 10 to 20 ft above the base of the member, and consists of bioclastic calcarenite and calcirudite that is interbedded with calcisiltite and shale. The upper unit consists of medium-gray, irregularly bedded, fossiliferous limestone and bioclastic calcarenite. Cressman (1973, p. 14) interpreted this sequence as recording a marine transgression, with higher energy, shallow-water depo-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

sits grading upward into lower energy deposits. The close interbedding between calcirudite, calcarenite, calcisiltite, and minor shales probably represents small migrating bars separated by intervening low areas.

Logana Member

The Logana Member reaches 50 ft in thickness in the northern outcrop area, and thins southward where it intertongues with the underly ing Curdsville and overlying Grier Limestone Members (Figure 11). The member consists of interbedded dark calcisiltite and shale in nearly equal proportions. The calcisiltite is generally argillaceous, is in broad lensing beds about 0.2 to 0.3 ft thick, and often has a petroliferous odor. The interbedded shales are brownish-gray, fissile, calcareous, and partly dolomitic.

Most beds are unfossiliferous, but silicified molluscs and brachiopods are sometimes common. Dalmanellid brachiopods can occur as coquinas, or can coat upper and lower bed surfaces with closely packed pelecypods between in the bed interior. Cressman (1973, p. 17) believed that the Logana was deposited at the height of the initial Lexington transgression, and that its facies relationship with the Curdsville and Grier Limestone Members reflects a deepening of water to the north. The dark color, even tabular bedding, and general sparcity of fossils or burrows in the Logana suggests deeper water, quiet conditions with poor oxygenation.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Grier Limestone Member

The Grier Limstone Member consists predominantly of thin and irregularly bedded to nodular bedded, poorly sorted, fossiliferous limestone. It ranges in thickness from 100 to 180 ft resulting mainly from intertongueing of the lower part with the Logana Member and the upper part with the Tanglewood Limestone Member (Figure 11).

Through the northern outcrop area the Grier conformably overlies the Logana Member, and in the southern area it has a gradational contact through 10 to 15 ft with the Curdsville Limestone Member. Through most of central Kentucky, the Grier is overlain by the calcarenites of the Tanglewood Limestone Member, the two members complexly intertongueing, but in the south-central outcrop area it is overlain by the calcisiltite and shale of the generally unfossiliferous Brannon Member (Figure 11).

The most common bedding assemblage in the Grier Limestone Member is about 0.5 ft thick sets of nodular bedded, fossiliferous calcisiltite to very poorly sorted, fossiliferous calcarenite with minor shale partings, alternating with slightly irregular, 0.4 ft thick beds of poorly sorted fossiliferous calcarenite. Brachiopods and bryozoans are the most conspicuous fossils, but gastropods are common in some calcisiltites, and ostracodes, crinoids, pelecypods, and trilobites are also present. This member was apparently deposited in shallow, well-aerated, moderately agitated water of normal salinily. The nodular bedding is probably due to the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

activity of burrowing organisms. Cressman (1973, p. 19) estimated the member was deposited in water depths of 15 meters or less.

Perryville Limestone Member

Cressman (1973, p. 23) defined the Perryville Limestone Member as the beds lying between the calcarenite of the Tanglewood Limestone Member below and the interbedded calcisiltite and shale of the Brannon Member above, in the southwest part of the Lexington Limestone outcrop area (Figure 11).

The Perryville has been divided into three units. The basal unit is called the Faulconer bed, and consists of 40 ft of brownish-gray fossiliferous micritic limestone. Beds are about 0.5 ft thick, have rough surfaces, and show nodular internal structure upon weathering. The fauna of the Faulconer bed consists of ostracodes, pelecypods, gastropods, brachiopods, bryozoans, crinoids, colonial corals, and stromatoporoids. The fossils show little breakage or abrasion, no obvious sorting or orientation, and are often coated by encrusting algae (probably Girvanella).

The middle unit in the Perryville is called the Salvisa bed. It consists of 10 to 15 ft of interbedded light-gray to light olive-gray micritic limestone and brownish-gray micritic limestone. Fossils are usually sparse, but may be locally abundant (e.g., USGS 5015-CO) with ostracods being most common and gastropods being scattered. The matrix is largely pelletal and often burrowed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The upper unit is the Cornishville bed. It is 2 to 10 ft thick, and consists of mostly nodular bedded calcisiltite and fine grained calcarenite containing abundant brachiopods and some bryozoans. This unit resembles the Grier Limestone Member and may be a tongue of that unit (Cressman, 1973, p. 28).

The Faulconer bed was deposited in shallow quiet water of normal marine salinity. The Salvisa bed was deposited in quiet, perhaps more hypersaline conditions as indicated by its restricted fauna. The Cornishville bed was deposited in a depositional environment similar to that of the Grier Limestone Member (Cressman, 1973).

Tanglewood Limestone Member

The Tanglewood Limestone Member is an extensive irregular body of bioclastic calcarenite, which completely intertongues with other members of the upper Lexington Limestone and the Clays Ferry Formation (Figure 11). It is typically a cross-bedded, phosphatic, pinkish-gray, medium grained, well-sorted, bioclastic calcarenite, in which whole fossils or large fossil fragments are rather uncommon. The unit ranges in thickness from 60 to 100 ft because of intertongueing with other members. The calcarenite consists largely of bryozoan, brachiopod, and crinoid fragments that are thought to have been transported from adjacent cites of accumulation of the Grier Limestone and Millersburg Members.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Crossbedding is common in the Tanglewood calcarenites. Harbar, Cressman, and Potter (1971) found these crossbeds to be bimodal, and interpreted them to be the result of tidal currents. Cressman (1973, pp. 31-32) interpreted the Tanglewood calcarenite body as a bank that stood above surrounding areas of the sea floor, with tidal currents producing migrating sand bars.

Brannon Member

The Brannon Member consists of about 30 ft of interbedded calcisiltite and shale. Throughout most of its area of exposure, it is both overlain and underlain by the Tanglewood Limestone Member. In other areas, the Brannon lies on the Grier or Perryville Limestone Members, and can be overlain by the Sulphur Well Member (Figure 11).

The interbedded calcisiltite and shale of the Brannon occur in nearly equal proportions, so that the member closely resembles the Logana Member. The calcisiltite is medium to light gray in color and generally occurs in smooth surfaced, tabular beds about 0.2 to 0.3 ft thick. The shale is calcareous and medium to dark gray. Fossils are sparse in the unit, but thin-shelled brachiopods are present on some bedding surfaces.

The Brannon weathers to a clayey soil containing abundant chert. Campbell (1898) placed the Brannon beds in what he called the Flanagan Chert because of this characteristic. McFarlan and White (1948, p. 1636)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

stated that the Flanagan Chert was mainly included in the Brannon Member. Recognizing what was meant by the term Flanagan Chert in the modern stratigraphic scheme is important because numerous type specimens of bellerophontids described by Ulrich and Scofield (1897) were cited as coming from that unit. Apparently, silicified beds at many different stratigraphic levels were erroneously called the Flanagan Chert. No monoplacophorans or bellerophontaceans occurred in USGS silicified samples from the Brannon Member.

The Brannon was apparently deposited in an environment similar to that of the Logana Member; that is, quiet water, below wave base, where bottom conditions were generally inhospitable for life (Cressman, 1973, p. 37).

Sulphur Well Member

The Sulphur Well Member consists of about 35 ft of mostly poorly-sorted bryozoan calcirudite having a clay and silt-rich, calcitic to dolomitic matrix. Beds are lenticular and irregular, a few inches thick generally, and are separated by thin shale partings. Bryozoans are found throughout the unit, but are most abundant on bedding surfaces. Brachiopods can be fairly common.

The Sulphur Well Member always has a sharp planar contact with underlying units, which may be the Brannon, Tanglewood Limestone, or Grier

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Limestone Members (Figure 11). It is overlain by the Clays Ferry Formation, with the contact being either sharp or gradational. Cressman (1973, p. 37) stated that the Sulphur Well and Grier Limestone Members were deposited under similar invironmental conditions; that is, moderately agitated, normal marine waters, slightly below wave base.

Stamping Ground Member

This member consists of about 15 ft of fossiliferous nodular limestone that is apparently entirely surrounded by the Tanglewood Limestone Member. The brachiopod Rhynchotrema, which is commonly silicified, is the most conspicuous fossil in the unit. At many localities, stromatoporoids are present directly above the Stamping Ground Member in the basal Tanglewood Limestone Member. Cressman (1973, p. 39) suggested that the environment of deposition was similar to that of the Millersburg Member; that is , shallow, moderately turbulent, normal marine water.

Greendale Lentil

This unit is a 10 to 15 ft thick lentil surrounded entirely by the Tanglewood Limestone Member. It consists of 75 percent limestone and 25 percent shale. Bedding sets of 0.2 to 1.5 ft thickness consist of olive-gray to light-gray, fossiliferous, argillaceous calcisiltite in nodular

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

beds separated by irregular shale partings and thin shale beds, which alternate with 0.2 to 0.5 ft thick irregular beds of light-gray, coarse grained, fossiliferous calcarenite. This lentil is restricted to parts of the Georgetown and Lexington West quadrangles, in the area immediately northwest of Lexington, Kentucky.

Devils Hollow Member

The Devils Hollow Member was described by McFarlan and White (1948, p. 1640) at its type locality as consisting of 15 ft of coarse grained, gastropod coquina overlain by 10 ft of micritic limestone containing ostracods (resembling the Tyrone Limestone). These two rock types intertongue, and some localities contain only one of the two types. The member is underlain conformably by the Tanglewood Limestone Member, and is overlain either by the Tanglewood calcarenites or by the nodular, fossiliferous, shaly limestone of the Millersburg Member (Figure 11).

The gastropod coquina is a coarse biosparite crowded with specimens of such species as Sphenosphaera troosti, Tropidodiscus subacutus, and Lophospira medialis (McFarlan and White, 1948, p. 1637). Locally, the coquina may be composed of brachiopods rather than gastropods. In either case, the fossils are sometimes silicified. The micritic limestone contains only ostracodes and sparse gastropods.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Devils Hollow Member seems to represent very shallow subtidal to intertidal environments of deposition. As sedimentary structures characteristic of tidal flats (i.e., mudcracks, intraformational breccia) are lacking in the micritic limestones. Cressman (1973, p. 41) suggested that these beds were deposited in shallow restricted lagoons of higher than normal salinity. The gastropod coquinas were bar and/or beach deposits directly associated with these lagoons.

Millersburg Member

The Millersburg Member is at 0 to 90 ft thick body of nodular and irregularly bedded, fossiliferous limestone and shale that completely intertongues with the Tanglewold Limestone Member and the overlying Clays Ferry Formation (Figure 11). The Millersburg limestone is gray to brownish-gray and nodular bedded. It consists of whole and broken fossils in a silt to clay-sized carbonate matrix. Shale makes up about one-third of the member. Characteristically, the Millersburg appears as limestone nodules several inches in diameter aligned along bedding and set in a matrix of calcareous shale, which alternate with irregular beds of poorly sorted calcarenite. Both fragments and whole fossils of bryozoans, brachiopods, molluscs, and trilobites are abundant, and scattered stromatoporoids and colonial corals occur at several horizons.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Millersburg is similar in lithology, bedding, and fossil content to the Grier Limestone Member, but contains a greater proportion of shale. Both were deposited in shallow, well-aerated, moderately agitated, normal marine waters probably less than 15 meters deep (Cressman, 1973, p. 43). The nodular bedding is probably due to active burrowing. The high shale content of the Millersburg is the result of the increased supply of terrigenous sediment to the area in latest Middle Ordovician time, which is also reflected in the composition of the intertongueing Clays Ferry Formation.

UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF KENTUCKY, SOUTHWESTERN OHIO, AND SOUTHEASTERN INDIANA: INTRODUCTION

The tri-state area surrounding Cincinnati, Ohio (Ohio-Indiana-Kentucky) exposes the type section for the Upper Ordovician (Cincinnatian Series) of North America. Traditionally the Cincinnatian Series has been divided into three groups, which are now considered stages (Figure 12). These are, in ascending order, the Edenian, Maysvillian, and Richmondian stages. The history of lighostratigraphic nomenclature for this region is extremely complex. Excellent summaries of this history are given by Gutstadt (1958) and Weiss and Norman (1960).

Throughout much of this century the basic stratigraphic scheme outlined by Patton, Perry, and Wayne (1953) and Caster, Dalve, and Pope

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

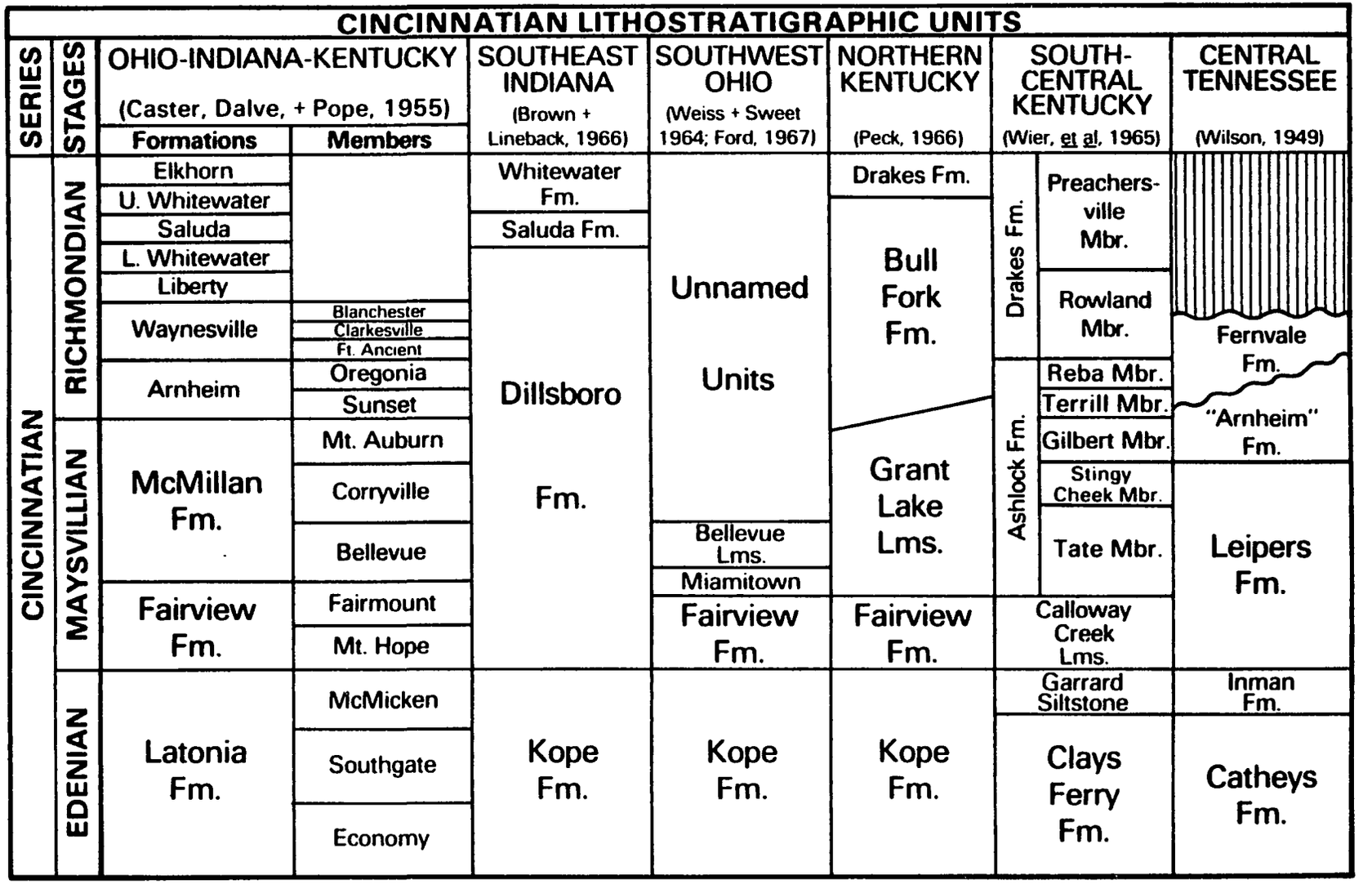


Figure 12: Cincinnatian lithostratigraphic units in Ohio, Indiana, Kentucky, and central Tennessee.

(1955) has been used throughout the tri-state region (Figure 12). However, more recent work has demonstrated that many of these traditional units were based more on paleontologic parameters than on lithologic ones. Therefore, numerous new lithostratigraphic names have been proposed. These new classifications apply more or less to the three adjacent geographic areas: central Kentucky, southeastern Indiana, and southwestern Ohio-northern Kentucky (Figure 12). The change in nomenclature from central Kentucky to northern Kentucky and southwestern Ohio seems well warranted because of facies changes. The change in nomenclature into southeastern Indiana is due more to the crossing of state borders than to any change in the character of the strata. The application of some names coined for strata in northern Kentucky to strata in southwestern Ohio has not been satisfactorily confirmed by mapping in Ohio, but the general scheme seems to work (Gordon Wier, pers. comm., 1977). As will be discussed below, some workers do not agree with this extension of the Kentucky nomenclature.

In the central Kentucky area, Upper Ordovician strata outcrop around the perimeter of the Jessamine Dome, outlining the Middle Ordovician strata previously discussed. Nearly all of the Ordovician strata to the north in the tri-state area are Late Ordovician in age, except for some exposures of Lexington Limestone and the Point Pleasant Member of the Clays Ferry Formation along the Ohio River Valley.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The revision of stratigraphic nomenclature in these areas began in the early 1960's. Weiss and Sweet (1964) renamed the Eden shale of northern Kentucky and southwestern Ohio, calling it the Kope Formation (Figure 12). They argued that the term Eden had a stadial connotation.

In south-central Kentucky, Wier and Greene (1965) named the Clays Ferry Formation to replace Edenian faunally-based units such as the Cynthiana Formation, and retained usage of the Late Edenian Garrard Siltstone. In the same area, Wier, Greene, and Simmons (1965) named the Calloway Creek Limestone, Ashlock Formation, and Drakes Formation for traditional Maysvillian and Richmondian units previously extended from the Cincinnati area on faunal bases (Figure 12).

Peck (1966) studied the Upper Ordovician strata in northern Kentucky along the eastern flank of the Cincinnati Arch. He found it difficult to trace rock units above the Fairview Formation (early Maysvillian) from the type sections in the Cincinnati area to the Maysville, Kentucky area. He concluded that these post-Fairview units had been previously identified on faunal bases in the Maysville area, and rejected the traditional units. He assigned strata previously called Bellevue, Corryville, and Mt. Auburn Members of the McMillan Formation to the Grant Lake Limestone. Also, he assigned strata previously called the Arnheim, Waynesville, Liberty, and Whitewater Formations in that area to the new Bull Fork Formation. Finally, Peck extended Preacherville Member of the Drakes Formation (Wier, Green, and Simmons, 1965) from south-central Kentucky to the Maysville

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

area for the uppermost Ordovician strata, which had previously been assigned to the Whitewater and Elkhorn Formations.

Ford (1967) mapped Ordovician strata in the southwest corner of Ohio, on the west side of Cincinnati. He recognized the Kope Formation, Fairview Formation, Miamitown Shale, and Bellevue Limestone as mappable units in the area (Figure 12). He did not address stratigraphy above the Bellevue Limestone. Pojeta (1979, fig. 2) extended the use of the Bull Fork Formation for post-Bellevue units in southwestern Ohio.

Brown and Lineback (1966) revised the Upper Ordovician lithostratigraphy of southeastern Indiana (Figure 12). They recognized the Kope Formation and proposed the name Dillsboro Formation for "the sequence of highly fossiliferous argillaceous limestones and calcareous shales that lie between the shale of the Kope Formation and the dolomitic limestone of the Saluda Formation" (p. 1020). Finally, they continued recognition of the Saluda Formation and the Whitewater Formation for the latest Richmondian-aged strata of the area. Shaver and others (1970) supported this classification, as did Gray (1972), who placed all the Cincinnation units in Indiana in the Maquoketa Group.

Recently, Hay, Pope, and Frey (1981) and Tobin (1982) have proposed Upper Ordovician lithostratigraphic classifications that would apply to southwestern Ohio, southeastern Indiana, and adjacent northermost Kentucky. Both classifications accept the Kope and Fairview Formations, and the Bellevue Limestone and Miamitown Shale as used by Ford (1967). How-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ever, the later Maysvillian and Richmondian-aged strata are classified quite differently.

Hay, Pope, and Frey (1981) introduced the Brookville Formation for limestone and shale wedges between the Bellevue Limestone and Whitewater Formation. They recognized four new members, as well as the Waynesville shale and Liberty limestone of the traditional classification. However, this classification has only been outlined in a guidebook, and is not valid according to the rules of the Code of Stratigraphic Nomenclature.

Likewise, Tobin's (1982) classification has not yet been published properly. However, its approach is so different, and its contribution so significant, that it warrants some discussion here.

Tobin (1982) disagreed with the approach of most recent workers, who have chosen to combine the traditional stratigraphic units, which they believed to be faunally-based, into larger units (e.g., Brown and Lineback, 1966; Peck, 1966; Hay, Pope, and Frey, 1981). Through reference to original descriptions of the traditional stratigraphic units and extensive field work, Tobin concluded that many of the traditional units were indeed valid.

Tobin (1982) recognized three shallowing-upward carbonate sequences in the Cincinnatian Series. These sequences are described below in ascending order.

Kope to Bellevue Sequence - In this sequence, the Kope represents an offshore facies, the Fairview a transitional facies, and the Bellevue a shoreface facies.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Corryville to Oregonia Sequence - In this sequence, the Corryville is an offshore facies, the Sunset is the transitional facies, which contains the Mt. Auburn offshore bar facies, and the Oregonia is the shoreface facies.

Waynesville to Saluda Sequence - In this sequence, the Waynesville shales represent an offshore facies, the Liberty limestone is a transitional facies, the Whitewater is the shoreface facies, and the Saluda dolomite represents restricted lagoonal, intertidal and supratidal facies.

Tobin (1982) recognized all of these facies as formations. He stated that these facies built eastward down paleoslope toward the Appalachian Basin. The diachronous nature of the Cincinnatian units has been previously demonstrated by conodont studies (Sweet, 1979, fig. 3). Viewing the Cincinnatian Series in this way is a significant step toward the understanding of this important type section.

The most modern recognized stratigraphic classifications are used here (Figure 12). The lithostratigraphy of Wier and Green (1965) and Wier, Green, and Simmons (1965) are used for south-central Kentucky. The units of Peck (1966) are used for north-central Kentucky. The units of Ford (1967) and Peck (1966) are used for southwestern Ohio and adjacent northernmost Kentucky. The classification of Brown and Lineback (1966) is used for southeastern Indiana. The distribution of these stratigraphic units through the tri-state area is shown in Figure 5.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The revision of the traditional Cincinnatian lithostratigraphic classification seems to have been warranted in most cases. However, the complete abandonment of the traditional units seems unwise. The paleontological and paleoecological knowledge accumulated through years of work in this type section is based on the traditional classification. If this wealth of data is to be retained and used effectively in both the understanding of the type section and in extrapolation to other areas, the traditional units must be retained in some form. Therefore, these traditional units are used here as informal biofacies units. For example, in this work, Cyrtolites (Cyrtolites) hornyi n. sp. is described from the Liberty biofacies of the Dillsboro Formation in southeastern Indiana.

The lithostratigraphy of the tri-state region will be described in three sections: South-central Kentucky, Northern Kentucky and Southwestern Ohio, and Southeastern Indiana. Formations are considered in ascending order for each area within the region.

UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF SOUTH-CENTRAL KENTUCKY

As a result of the joint U.S. Geological Survey - Kentucky Geological Survey mapping program of the State of Kentucky, Wier and Green (1965) and Wier, Green and Simmons (1965) completely revised the Upper Ordovician lithostratigraphic classification for south-central Kentucky (Figure 12). Except where noted, the descriptions given below are drawn from those works.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Clays Ferry Formation

The Clays Ferry Formation was named by Wier and Greene (1965) to encompass strata previously included in the Cynthiana Formation, Fulton Shale, and Million Shale as used by Foerste (1906) and Palmquist and Hall (1961). The 120 to 220 feet of interbedded limestone and shale straddles the Middle-Upper Ordovician boundary (Figure 5). To the south it intertongues with the upper members of the Lexington Limestone, but it becomes younger northward, and intertongues with the shales of the Kope Formation in north-central Kentucky (Figures 5 and 11).

Limestone makes up 30 to 60 percent of the Clays Ferry Formation. Beds are even and 1 to 6 inches thick. The limestone varies from medium to dark gray, argillaceous calcisiltite, to medium gray brachiopodal limestone, to medium gray crinoidal calcarenite. The calcisiltite is sparsely fossiliferous, and contains mainly crinoidal fragments and some gastropods. The brachiopodal limestone is characterized by abundant Rafinesquina, which are sometimes shingled, as well as Sowerbyella and Dalmanella, all packed in a mud matrix. Bryozoans are also common.

Shale makes up 30 to 60 percent of the formation. It is generally greenish to olive-gray, and occurs in distinctly laminated sets 1 to 12 inches thick. Fossils are generally sparse in these shales, though bryozoans are occassionally common.

Siltstone makes up 5 to 10 percent of the unit, occurring mainly in the upper part. It is mostly in 1 to 3 inch even beds, in which fossils

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

are sparse. This lithology resembles the Garrard Siltstone, which overlies the Clays Ferry in south-central Kentucky.

Point Pleasant Tongue - Eastward from Cincinnati along the Ohio River Valley, the Lexington Limestone and Kope Formation are separated by 100 ft of limestone and shale interbedded in near equal proportions (Figure 5). This unit's even bedding and regular interbedding of limestone and shale are reminiscent of typical Clays Ferry Formation, but in the upper part are beds as thick as 10 ft that consist of crossbedded calcarenite.

This unit has a complex nomenclatural history. Until recently it had been assigned to the Cynthiana Formation, but the U.S. Geological Survey mapped it as the Point Pleasant Formation (Weiss et al, 1965; Cressman, 1973). Now the unit is considered the Point Pleasant Member (or Tongue) of the Clays Ferry Formation (Swadley, 1975), and is correlated to the upper Lexington Limestone and lower Clays Ferry (Cressman, 1973; Sweet, 1979, fig. 3). It is overlain by the Kope Formation.

Cressman (1973, p. 45) suggested that the finer grained, less fossiliferous portions of the Clays Ferry Formation were deposited in quiet water at least 25 meters deep, similar to the environments of the Logana and Brannon Members of the Lexington Limestone. The more fossiliferous portions of the formation were probably deposited in shallower depths, but currents were never strong enough to remove fine clastics or to break up the skeletal material effectively. The Point Pleasant Tongue was, at

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

least in its upper portion, a much shallower facies, with thick cross-bedded units demonstrating rather high energy conditions. It is noteworthy that these upper Point Pleasant beds are directly overlain by Kope shales characterized by a trilobite- crinoid fauna. This situation apparently reflects a rapid transgression at the end of Point Pleasant deposition.

Garrard Siltstone

The Garrard Siltstone is a 10 to 100 ft thick unit of chiefly limy siltstone with minor thin lenses of mudstone and limestone. Most beds are 6 to 24 inches thick, and many are laminated. Fossils are scarce except for brachiopods in the thin limestone lenses.

The Garrard is Late Edenian in age, correlating with the upper Kope Formation to the north (Figures 5 and 12). It is conformable with the underlying Clays Ferry Formation and overlying Calloway Creek Limestone. Ford (1968, p. 1784) suggested that the northward decrease in grain size from the Garrard to the Kope implied tectonic control of sedimentation from a southerly source area.

Calloway Creek Limestone

This early Maysvillian-aged unit ranges from 80 to 130 ft in thickness in south-central Kentucky. It consists of 70 to 80 percent fine to medium grained, thin bedded, gray limestone; 15 to 25 percent greenish-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

gray calcareous shale; and about 5 percent calcareous siltstone. Fossils are abundant, with brachiopods and bryzoans being most conspicuous.

The Calloway Creek Limestone is transitional with both the underlying Garrard Siltstone and overlying Ashlock Formation (Figures 5 and 12). It grades northward into the Fairview Formation, which is similar in its lithologic and faunal character but is much thicker bedded.

Ashlock Formation

The Ashlock Formation is a 125 to 145 ft thick unit of late Maysvillian and early Richmondian age in south-central Kentucky (Figures 5 and 12). Wier, Green, and Simmons (1965) divided the formation into five members, which are described in ascending order below.

Tate Member - The Tate was originally described as a member of the McMillan Formation by Foerste (1912). This 30 to 80 ft thick unit consists of greenish-gray, laminated to thin bedded, sparsely glauconitic, calcareous to dolomitic mudstone, which commonly grades into an argillaceous limestone at the top. Fossils are uncommon, except for a silicified brachiopod-bryozoan assemblage in the Back Bed, a coarse grained silty limestone occurring at 5 to 15 ft above the base of the member.

This member belongs to Wier and Peck's (1968, p. 168) dolomitic mudstone lithofacies, which was thought to have been deposited in very shallow quiet subtidal to tidal flat environments.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Gilbert Member - The Gilbert was also recognized as a member of the McMillan Formation by Foerste (1912). It consists of bluish to olive-gray, fine to medium grained limestone, occurring in thin wavy beds. A brachiopod-bryozoan fauna is common and well-preserved. The unit is 10 to 20 ft thick. The few inch thick limestone beds are generally separated by less than one inch thick gray limy siltstone partings.

This member belongs to Wier and Peck's (1964) micrograined limestone lithofacies, which was deposited in shallow, quiet lagoons.

Stingy Creek Member - This term replaces the name Mt. Auburn member in south-central Kentucky. It is a 5 to 15 ft thick unit of gray limy siltstone and silty limestone that is obscurely thin bedded and has an abundance of brachiopods and bryozoans. This member belongs to Wier and Peck's (1968) nodular-bedded fossiliferous limestone and mudstone lithofacies, which was deposited in somewhat higher energy conditions than the Gilbert Member, possibly wave-agitated shoals on a sloping shelf.

Terrill Member - This unit replaced a designation of Sunset Member of the Arnheim Formation. It consists mainly of greenish-gray, laminated, limy or dolomitic mudstone. Bedding surfaces characteristically display ripple marks and mudcracks, and fossils are rare. However, the basal few feet of the 5 to 15 ft thick member commonly has a good brachiopod-bryozoan fauna.

This member belongs to Wier and Peck's (1968) dolomitic mudstone lithofacies, which was probably deposited mainly on broad tidal flats.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reba Member - This unit was previously known as the Oregonia Member of the Arnheim Formation in south-central Kentucky. The 10 to 25 ft thick member has a basal micrograined limestone overlain by medium grained limestones that become more silty and argillaceous near the top. The basal unit is essentially barren of fossils, except for some ostracodes and trace fossils. The overlying thin bedded limestones contain a fairly abundant brachiopod-bryozoan fauna.

This member belongs to the same lithofacies as the Stingy Creek Member.

Drakes Formation

Wier, Green, and Simmons (1965, p. 16) named the Drakes Formation for Richmondian-aged strata in south-central Kentucky formerly called the Waynesville, Liberty, and Whitewater beds (Figure 12). The formation consists of 120 to 150 ft of grayish-green, dolomitic or calcareous, silty mudstone to argillaceous, finely crystallive dolomite or dolomitic limestone.

On the south and east sides of the Lexington Dome in central Kentucky, the formation is divisible into the Rowland and overlying Preachersville Members. On the west side of the dome, the formation is divisible into (ascending) the Rowland, Bardstown, and Saluda Dolomite Members.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Rowland Member - This member encompasses mainly strata assigned earlier to the Waynesville Limestone. The 40 to 60 ft thick member consists chiefly of grayish-green, sparsely galuconitic, dolomitic or calcareous, silty mudstone. The mudstone is obscurely bedded, and many of the bedding surfaces are covered by ripple marks and mud cracks. Fossils are rare to absent.

This member belongs to Wier and Peck's (1968) dolomitic mudstone facies, and is thought to have been deposited on extensive tidal flats.

Preachersville Member - Strata included in this member had previously been assigned to the Liberty and Whitewater limestones. The 55 to 95 ft thick unit is similar to the underlying Rowland Member, but contains 10 to 20 percent argillaceous, finely crystalline dolomite or dolomitic limestone. Locally, the basal 6 ft is a limestone rich in colonial corals and stromatoporoids known as the Otter Creek Coral Bed. Petersen (1970) correlated these beds with coral-rich layers in the Bardstown Member on the west side of the Cincinnati Arch.

Bardstown Member - This 12 to 40 ft thick member overlies the Rowland Member and underlies the Saluda Dolomite Member on the western side of the Cincinnati Arch in Kentucky. It consists of about 90 percent gray to greenish-gray, fine to medium grained limestone containing abundant whole or fragmented fossils. These beds are 1 to 8 inches thick. About 10 percent of the member is bioclastic to coquinoid limestone. Petersen (1970) described 2 to 4 layers with concentrations of colonial corals in the middle two-thirds of the member.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Saluda Dolomite Member - This member reaches a maximum thickness of 25 ft in Kentucky on the west side of the Cincinnati Arch. Northward in Indiana, it expands to as much as 60 ft in thickness and is recognized as a formation. The Saluda is a dolomite or calcareous dolomite, and is distinguished from the underlying Bardstown Member by the abrupt change from the fossiliferous limestone of the latter to a mainly unfossiliferous dolomite.

Hatfield (1968) described the Saluda in detail in Indiana. His work is discussed here in the section on Indiana Upper Ordivician lithostratigraphy.

UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF NORTH-CENTRAL KENTUCKY AND SOUTHWESTERN OHIO

It was in this area that the stratigraphic units of the traditional classification were mainly originally described, particularly in the vicinity of Cincinnati (Caster, Dalve, and Pope, 1961) (Figure 12). The stratigraphic revisions of Peck (1966), Ford (1967), and Pojeta (1979) are used here (Figure 12).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kope Formation

The Kope Formation is Edenian and early Maysvillian in age (Figure 12). It grades southward into the Clays Ferry Formation (Figure 5). It lies conformably upon the Point Pleasant Member of the Clays Ferry Formation east of Cincinnati, and lies with conformity upon the Lexington Limestone in extreme southeastern Indiana, but this contact becomes unconformable northwestward. The Kope is overlain conformably by the Fairview Formation in Ohio and Kentucky, and the two intertongue in some areas (see Sweet, 1979, fig 3). The Kope ranges in thickness from 150 to 280 ft over the Indiana-Ohio-Kentucky tri-state outcrop area.

The Kope Formation is 70 to 80 percent shale, with some shales being over 3 ft thick. The shales are interbedded with limestones and minor siltstone beds. Kope limestones are thin to medium bedded and generally contain whole or broken fossils in varying amounts. The shales also are often fossiliferous. The fauna is dominated by brachiopods and bryozoans, but crinoids, trilobites, and molluscs are characteristic of some parts of the section (Weiss and others, 1965).

The name Kope Formation was proposed by Weiss and Sweet (1964) to replace the term Eden shales, as Eden has stadial connotations. The traditional 4-part subdivision of the Eden shales (Nickles, 1902) was rejected by Weiss and others (1965) because the four "members" were based largely on biofacies exposed in the immediate vicinity of Cincinnati, and could

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

not be traced consistently into surrounding areas. In this 4-part scheme, the basal Fulton beds, consisted of 5 ft of dark shales characterized by the presence of the trilobite Triarthus eatoni. The overlying Economy shale was characterized by the trilobite Cryptolithus, and by crinoids and delicate brachiopods. The upper southgate and McMicken "members" contained more and thicker bedded limestones, some being characterized by ripple marks and by robust brachiopods and bryozoans. This sequence reflects the shallowing upward toward higher energy Fairview conditions.

Weiss and others (1965, pp. 49-50) concluded that the Kope and Clays Ferry shales and siltstones were derived from the southeast and east, based on percent clastics, grain size increase, and paleogeography. Ford (1968) suggested a southerly source area.

Weiss and others (1965) postulated that clastic mud accumulated in depressed areas on a sea floor of low broad relief, while limestones were deposited on the tops and flanks of topographically higher areas, with skeletal debris occassionally being swept into adjacent lows. They estimated an average depth of accumulation at 25 meters.

Anstey and Fowler (1969) also studied Kope depositional environments. They estimated that water depths averaged over 20 meters based on bryozoan growth forms. They claimed that the Kope limestone formed by the growth of benthonic communities, dominated by bryozoans, on slightly elevated areas of the sea floor. They also outlined an upward shallowing of water depth based on an upward increase of limestone content and fauna abun-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

dance, an upward decrease in the wave-length of megaripples, and the presence of oncolites and mud cracks in the overlying Dillsboro Formation in Indiana.

Fairview Formation

The early Maysvillian-aged Fairview Formation ranges from 70 to 110 ft in thickness over southwestern Ohio and northern Kentucky (Figure 12). The formation consists of interbedded limestone, shale, and minor silt stones. Limestone makes up 50 to 60 percent of the unit, consisting of medium to course grained skeletal limestone in the lower part, and fine grained, silty, sparsely fossiliferous limestone in the upper part. Shale makes up 35 to 40 percent of the formation, occurring as thin beds or partings between the limestones. Siltstone makes up 5 to 15 percent of the unit, occurring as thin to medium beds that become more abundant upward (Peck, 1966).

The Fairview was originally referred to as the "Hill quarry beds" in the vicinity of Cincinnati, where it was extensively quarried. Nickles (1902) named the Fairmount (Dekayia aspera) beds and the underlying Mount Hope (Amplexopora septosa) beds, which were later combined as members of the Fairview Formation by Bassler (1906). Ford (1966, p. B5) felt that these 2 members were based more on faunal than lithologic characters, and did not favor their usage outside the immediate type area.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ford (1967, p. 935) postulated that the coarse fragmental limestones of the Fairview were formed around submarine swells. He envisioned a situation where waves and currents broke and sorted skeletal material on the swells, and deposited progressively finer skeletal debris in progressively deeper surrounding areas where fine clastics were also settling. The positions of these swells and intervening depressions migrated laterally through time.

The Fairview Formation lies conformably on and intertongues with the Kope Formation (Figure 5). In the Cincinnati area, it is conformably overlain by two local units, the Miamitown Shale and Bellevue Limestone. Elsewhere, it is conformably overlain by the Grant Lake Limestone. The Fairview grades westward into the Kope and Dillsboro Formations of Indiana, and southward into the Ashlock Formation of Kentucky.

Bellevue Limestone

Ford (1967, p. 932-4) redefined the Bellevue Limestone as a sequence of medium to thin bedded coquinoid limestones with minor interbedded shales occurring in the vicinity of Cincinnati (Figure 12). Its maximum known thickness is 25 ft at the type locality.

Ford (1967) noted that the formation had a limited areal extent, and that it thickened to the south and southeast of Cincinnati. He suggested that the Bellevue might be a northwestward tongue of the Grant Lake Limestone, and Luft (1971) mapped it as such (Figure 5). Tobin (1982) consid-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ered the Bellevue to be the top unit of a shallowing-upward carbonate sequence which began with Kope deposition.

Miamitown Shale

Ford (1967) proposed the Miamitown Shale for 5 to 35 ft of shale and mudstone with widely spaced limestone interbeds that conformably overlies the Fairview Formation in the vicinity of Cincinnati (Figure 12). The limestones within this unit are commonly nodular bedded and contain a characteristic gastropod-pelecypod assemblage that includes Lophospira, Cyclonema, and Byssonychia.

Ford (1967) suggested that the Miamitown Shale reflected a return to conditions of Kope deposition. Considering the Miamitown's, relatively small areal extent, situation between the rather high-energy Fairview and Bellevue limestones, and the presence of a predominantly molluscan fauna, it seems improbable that the Miamitown was deposited in water as deep as Kope sediments. Possibly, the Miamitown reflects a period of increased fine clastic influx into a protected lagoonal setting.

Grant Lake Limestone

The Grant Lake Limestone is Maysvillian-Richmondian in age and is distributed through northern Kentucky and portions of adjacent south western Ohio (Figure 12). The Bellevue Limestone of the Cincinnati area is thought to be a northern tongue of the Grant Lake (Figure 5) (Ford,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1967; Luft, 1981). The formation is conformable with the underlying Fairview Formation and overlying Bull Fork Formation. It grades westward into the Dillsboro Formation of Indiana, and southward into the Calloway Creek Limestone and Ashlock Formation (Figure 5).

Peck (1966) created the Grant Lake Formation for strata in the Maysville, Kentucky area that had previously been assigned to the Bellevue, Corryville, and Mt. Auburn Members of the McMillan Formation. He described the Grant Lake as chiefly irregularly-bedded argillaceous limestone and minor interbedded calcareous shale. Limestone comprises 70 to 90 percent of the unit, and is mainly gray with olive-gray mottling, micrograined to medium grained, argillaceous, and very fossiliferous. Some well-sorted, fine to coarse grained bioclastic limestones occur locally. The fauna is dominated by brachiopods and bryozoans, but gastropods, cephalopods, pelecypods, crinoids, trilobites, and ostracods can be common locally.

The formation belongs to Wier and Peck's (1968) nodular bedded fossiliferous limestone and mudstone lithofacies, which they regarded as representing a relatively high energy shelf environment, such as wave-agitated shoals (Pojeta, 1979).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bull Fork Formation

Peck (1966) created the Bull Fork Formation for strata previously called Arnheim, Waynesville, Liberty, and Whitewater Formations in the Maysville, Kentucky area. The unit was mapped in north-central Kentucky on the east side of the Cincinnati Arch (Figure 12). Pojeta (1979, fig. 2) extended its use into southwestern Ohio for strata above the Bellevue Limestone that Ford (1967) had left unnamed.

The Bull Fork Formation is 200 ft thick in its type area. It consists of interbedded limestone and shale. The shale content gradually increases from 20 percent near the base to about 80 percent in the upper part, and is mainly calcareous, medium gray to greenish gray, and fissile to poorly fissile. There are three main types of limestone in the formation. The most common type, which composes 50 to 70 percent of the total limestone, is gray, with some olive-gray mottling, and has fine to medium grained matrix encasing medium to very coarse grained fossil fragments. This type of limestone is even to irregular bedded, with beds 1 to 8 inches thick, and sometimes has large ripple marks on upper bed surfaces. The second limestone type, which makes up 5 to 40 percent of the limestone, consists of 1 to 8 inch thick even beds composed of olive-gray, microgranular limestone with sparse fossil fragments. The third limestone type, which makes up 5 to 30 percent of the limestone, is medium to bluish-gray, fine to coarse grained, well-sorted, bioclasitc limestone. This limestone type occurs in 2 to 18 inch thick even beds that often display crossbedding.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Brachiopods and bryozoans are the dominant faunal elements, but solitary and colonial corals, gastropods, cephalopods, pelecypods, crinoids, trilobites, and ostracods are locally common.

The Bull Fork belongs to Wier and Peck's (1968) planar-bedded fossiliferous limestone and mudstone lithofacies. This lithofacies is believed to represent a deeper, more protected environment than the nodular-bedded limestone and mudstone lithofacies (Pojeta, 1979, p. A6).

Drakes Formation

The only part of the Drakes Formation present in this area is 25 to 30 ft of the Preachersville Member (Figure 12). The unit thickens southward toward its type area in south-central Kentucky (Wier, Green, and Simmons, 1965).

The Preachersville Member in northern Kentucky consists of calcareous to dolomitic mudstone and minor interbedded dolomitic limestone and dolomite. The mudstone makes up about 90 percent of the unit. It is mainly grayish-green, but becomes reddish purple locally near the top. It is thin bedded, fissile to blocky, and locally silty. The dolomitic limestone and dolomite are gray to brown, fine to medium grained, argillaceous to silty, and occur as thin lenses and irregular beds. Megafossils are sparse and poorly preserved (Peck, 1966, p. B22).

The Preachersville is generally overlain unconformably by the Early Silurian Brassfield Formation, or by even younger units, in different areas.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UPPER ORDOVICIAN LITHOSTRATIGRAPHY OF SOUTHEASTERN INDIANA

The Lexington Limestone is exposed at a couple localities along the Ohio River in southeastern Indiana (Brown and Anstey, 1968), where it is directly overlain by the Kope Formation. The contact is well-defined by the change from mud-free bioclastic limestone of the Lexington to the argillaceous limestones and shales of the Kope.

Rooney (1966) described an erosional unconformity at the top of the "Trenton" in all but extreme southwestern Indiana. He delineated a northeast-southwest hinge-line that ran from the Findlay Arch in Ohio to the Ozark Dome of Missouri. Uplift of the area northwest of this hinge line at the end of "Trenton" deposition culminated in the emergence of a broad plateau, while deposition remained continuous southeast of the hinge line (Rooney, 1966, figs. 1-9). The plateau was transgressed in Edenian time by Kope muds. The unconformable contact is marked by truncation of "Trenton" beds, karst solution features, and concentrations of pyrite, angular chert, phosphatic grains, and carbonate breccia.

The Kope Formation was discussed previously, so a detailed description is not necessary here. However some local features are pointed out below.

Discussed in more detail are the younger Ordovician units recognized in Indiana: the Dillsboro, Saluda, and Whitewater Formations.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Kope Formation (Indiana)

Brown and Lineback (1966, p. 1020) extended the use of this formational name into Indiana from the type area in the Maysville area of Kentucky and Ohio, which was described by Weiss and Sweet (1964) (Figure 12).

The Kope thickens northward in southeastern Indiana from 220 ft in outcrop to 550 ft thick in the subsurface of Wayne County. The Kope overlies the Lexington Limestone conformably in extreme southeastern Indiana, where the Lexington thins northward in concert with the Kope thickening (Figure 5). Brown and Lineback (1966) suggested this might reflect a facies relationship. Northwestward, the Lexington is not present, and the Kope unconformably overlies the "Trenton Limestone" of Indiana usage (Rooney, 1966, figs 1, 9; Shaver and others, 1970, p. 85-6).

In Indiana, the Kope Formation consists of mainly bluish to brownish-gray clay shale, with only 5 percent limestone, most of which occurs in the upper one-third of the unit. These are generally rather discontinuous beds of fossiliferous limestone.

The Kope is overlain conformably by the Dillsboro Formation in Indiana. The contact is marked by much lower percentage of limestone in the Kope.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Dillsboro Formation

Brown and Lineback (1966, p. 1020) named the Dillsboro Formation for "the sequence of highly fossiliferous argillaceous limestones and calcareous shales that lie between the shales of the Kope Formation and the dolomitic limestone of the Saluda Formation" in southeastern Indiana (Figure 12). The formation is Maysvillian and early Richmondian in age. It was proposed to take the place of the biofacies units of traditional usage (Patton, Perry, and Wayne, 1953). The replaced units were, in ascending order, the Mount Hope, Fairmount, Bellevue, Corryville, Mount Auburn, Arnheim, Waynesville, and Liberty Formations. It is recommended here that these units continue to be cited as informal biofacies units within the Dillsboro, in order to retain the extensive paleontological information for paleoecological and biostratigraphic purposes.

The Dillsboro contains about 30 percent limestone and 70 percent shale. Shale becomes more predominant southward in the lower part of the formation. Limestone are variable, but are mainly argillaceous and contain an abundant fossil fauna. Brachiopods and bryozoans are most conspicuous, but locally various molluscs, arthropods, and echinoderms are common.

Pojeta (1979, p. A7) noted that much of the Dillsboro is lithologically and faunally similar to the Bull Fork Formation. The Bull Fork is a direct lateral equivalent to the upper Dillsboro (see Sweet and Bergstrom, 1979, fig. 3), but the name changes going across state borders from Ohio-Kentucky to Indiana (Figure 5).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Saluda Formation

The Richmondian-aged Saluda Formation is a broad lens-shaped unit distributed through southeastern Indiana and extending into adjacent southwestern Ohio and northern Kentucky (Figure 5 and 12). In Indiana it lies conformably between the Dillsboro and Whitewater Formations, although where the Whitewater has been removed by erosion the Lower Silurian Brassfield Formation lies on it unconformably. In Ohio the Saluda has generally been considered a thin member (6 ft thick) of the Whitewater Formation, separating upper and lower members (Caster, Dalve and Pope, 1961). In Kentucky, Wier, Green, and Simmons (1965) made the Saluda a member of the Drakes Formation along the western flank of the Cincinnati Arch (see discussion under Central Kentucky).

The Saluda Formation of Indiana has been described in detail by Hatfield (1968). The formation is mainly composed of dolomitic mudstone, but also has a coral rich zone at the base and a coral-stromotoporoid-rich zone just above the top of the formation.

The basal coral zone is composed of large heads of the colonial corals Tetradium and Favistella in a matrix of dolomitic limestone, skeletal-micritic limestone, or calcareous shale. The zone ranges from 2 to 12 ft in thickness and can occur within either, or overlap the boundary between, the Saluda and Dillsboro Formations.

The upper Tetradium stromatoporoid zone lies just above the Saluda in the lowermost Whitewater Formation.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Saluda itself is mainly calcitic dolomite, which often has laminations, mudcracks, and small ripple marks. Ostracods are the only common fossil. Beds of more bioclastic limestone or shales occur locally.

Hatfield (1968) concluded that the Saluda was deposited in a broad shallow lagoon enclosed by broad low banks of corals. Dolomite content increases toward the interior of this lagoon. Bioclastic limestones and shales were interpreted as storm deposits washed into the lagoon. Evidence suggests that water depth was mainly a few inches to a few feet within the lagoon, and that salinities were above normal.

Whitewater Formation

The Whitewater Formation was originally named by Nickles (1903). As presently recognized, the formation includes the Elkhorn Formation of earlier classifications (Utgaard and Perry, 1964; Brown and Lineback, 1966; Shaver and others, 1970).

The Whitewater is the youngest Richmondian-aged formation in the Cincinnatian type section (Figure 12). It overlies the Saluda Formation conformably, as is unconformably overlain by either the Lower Silurian Brassfield Formation or the Middle Silurian Osgood Formation. In general, the Whitewater contains a higher percentage of limestone than the strata beneath the Saluda.

The Whitewater consists of various types of limestone interbedded with calcareous shales. The limestones include thin-bedded argillaceous

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fossiliferous limestone, thin-bedded ostracodal limestone, medium-bedded relatively unfossiliferous limestone, medium-bedded limestone with burrows, and rubbly-weathering argillaceous limestone (Brown and Lineback, 1966, p. 1022). As the Whitewater thickens in concert with Saluda thinning, the two are thought to be facies of one another. The Whitewater is generally believed to reflect the shallowing upward associated with the Ordovician-Silurian unconformity.

The fauna of the Whitewater is dominated by a brachiopod-bryozoan assemblage.

MATERIAL AND PRESERVATION

The new silicified collections that make up the core of this study were made between 1961 and 1972 during a joint geologic mapping project of the State of Kentucky undertaken by the U.S. Geological Survey and the Kentucky State Geological Survey. Nearly 1,100 fossil collections were made during the mapping project, of which over 200 contained silicified fossils. Altogether, nearly 36,000 pounds of limestone containing silicified fossils were collected. The Lexington limestone was found to have the most widespread silicification, both stratigraphically and geographically, and that unit accounts for 116 of the silicified fossils collections. Twenty-five silicified collections were made from the High Bridge Group, and 64 silicified fossil collections were made from rock units above the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lexington limestone. Pojeta (1979, pp. A15-A19) described these collections and the methods by which the silicified fossils were etched from the bulk limestone samples.

Other specimens described herein were primarily from museum collections. Collections from the U.S. National Museum (Smithsonian Institution), the American Museum of Natural History, the Chicago Field Museum of Natural History, and the Geology Museums at the University of Cincinnati and Miami University, Oxford, Ohio, were examined. The type material for most of the species described herein were examined and many were photographed for the first time. Finally, a small proportion of specimens studied were new collections made by the author.

The symmetrical molluscan univalves described herein occur in five different modes of preservation: (1) internal molds, (2) external molds, (3) composite molds (McAlester, 1962), (4) calcitic casts or replicas, some apparently being coated by micrite envelopes (Bathurst, 1966), and (5) silicified casts or replicas. The first four of these modes of preservation are prevalent in the interbedded shales and limestones of the Cincinnatian Series. However, the vast majority of specimens known from the limestones of the Lexington Limestone and High Bridge Groups in central Kentucky and the Stones River and Nashville Groups of central Tennessee are silicified replicas.

Generally, the aragonitic shells of mollusks are dissolved soon after burial, leaving only internal and/or external molds. Therefore, calcitic

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

replicas were the least common preservational type encountered here. However, occasionally these aragonitic shells are replaced by calcite. Probably more common are calcitic specimens preserved by micrite envelopes (Bathurst, 1966) produced by algal borings into the mollusk shells after the death of the inhabitant. After the algal filaments died and decayed, micritic aragonite filled the borings, forming a micrite envelope that preserved the outer form of the original shell.

Many internal molds of mollusk fossils also retain the markings of the shell exterior. McAlester (1962) proposed that such composite molds resulted from the early dissolution of the aragonitic mollusk shells while the enclosing matrix was still in a plastic state. After dissolution, compaction of the sediment imprinted the external mold onto the surface of the internal mold. The interpretation of internal and composite molds should be done with care. Often they are distorted by compaction, and their size is generally much smaller than the original shell, with shrinkage known up to 40% of original size (McAlester, 1962; Basan and Frey, 1982).

As noted above, nearly all mollusk fossils described here from the Middle Ordovician strata of the Cincinnati Arch Province are silicified. The source of silica for these silicified fossil horizons was probably bentonites within the section. Bentonite seams have been reported in the Middle Ordovician strata of the Cincinnati Arch outcrop area by Nelson (1922), Fox and Grant (1944), Fetzer (1973), and Cressman (1973). These

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

bentonites can be correlated across eastern North America and even to northern Europe (Fetzer, 1973; Bergstrom and Nilsson, 1974).

Laufeld and Jeppsson (1976) made conclusions of broad application in their study of bentonites and silicified fossil horizons in the Silurian strata of Gotland. They reported that the Gotland silicified fossil horizons were generally restricted to fairly thin stratiform levels and are often found in limestone beds directly beneath bentonite seams. In most silicified horizons, they found that only the skeletal material was silicified, not the matrix. They noted that many of these silicified fossil horizons are almost certainly correlative to bentonite layers that were deposited adjacent quieter water depositional environments. Finally, they cited a general agreement with other studies of silicified faunas on the sequence of silicification by taxa groups and shell mineralogy (see also Newell and others, 1953; Cooper and Grant, 1972; Dapples, 1967; Hintze, 1953). The low-Mg calcite skeletons of bryozoans, brachiopods and corals are most susceptible to replacement by silica, followed by high-Mg groups, such as crinoids and ostracods, and aragonitic groups, such as gastropods and pelecypods.

The distribution, taphonomy and diagenesis of the Cincinnati Arch Middle Ordovician silicified fossil horizons have not yet been analyzed in detail, but some generalizations and observations are possible. As noted for many other such occurrences (Laufeld and Jeppsson, 1976), the Kentucky silicified fossil horizons appear to be restricted to fairly thin strati-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

form levels. However, most silicified fossil horizons are not known to be associated with bentonite seams. There are various grades of silicification in the Kentucky specimens. Some are hard and durable, particularly those that have weathered out of the limestones naturally, others are brittle and fragile, and still others are coarsely crystalline and friable. No correlation between taxa and grade of preservation was observed, and it is concluded the preservational differences are strictly diagenetic. Occasionally, specimens seem to have layers of silicification which peel away like an onion skin. Possibly this might reflect differential silicification of shell layers. Detailed analyses of these different patterns of silicification are needed, such as those done on Permian silicified fossil assemblages from Wyoming by Boyd and Newell (1972) and Schmitt and Boyd (1981).

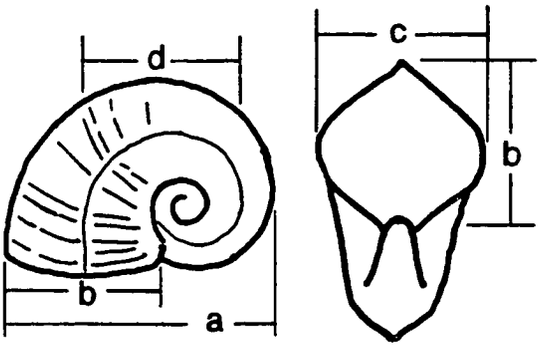
MEASUREMENTS

When sufficient material was available, series of measurements were made. These measurements are listed with the descriptions of the individual species under Systematic Paleontology. The orientation of the most common measurements made are shown in Figure 13. These measurements were shell length, apertural length, aperture width, and umbilical diameter. Other common measurements were ventral width, posterior width, and dorsal width. These measurements simply measured the width of the body whorl at

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 13: Common measurements made on fossil specimens herein.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



a – Shell Length
b – Aperture Length
c – Aperture Width
d – Umbilical Diameter

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

evenly spaced points around the coiled shell in order to assess rate of whorl expansion.

It should be realized that there is bound to be some amount of error in many of the measurements given because of the nature of the fossil material. Many of the specimens measured were fragmented or embedded and it was often difficult to determine the accuracy of measurements. Nevertheless, I am confident that the measurements listed will at the very least give the reader an appreciation for the sizes and relative dimensions of the individual species. When measurements were sufficiently accurate and had important bearing on the differentiation of species, bivariate plots were drawn and regression analyses carried out.

STRATIGRAPHIC DISTRIBUTION OF ORDOVICIAN MONOPLACOPHORA AND BELLEROPHONTACEAN GASTROPODA IN THE CINCINNATI ARCH REGION

In the accompanying tables (Tables 1-4) are listed the stratigraphic distributions of monoplacophoran and bellerophontacean gastropods in the Middle and Upper Ordovician lithostratigraphic units of the Cincinnati Arch region.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 1 : Distribution of bellerophontaceans in the Stones River Group of central Tennessee. Data based on museum collections and species lists in Wilson (1949). MF = Murfreesboro Limestone; PL = Pierce Limestone; RL = Ridley Limestone; LL = Lebanon Limestone; CL = Carters Limestone.

	MF	PL	RL	LL	CL
Bucania emmonsi	X				
Phragmolites grandis				X	
Pterotheca expansa	X				
Pterotheca saffordi				X	
Pterotheca undulata					X
Tetranota bidorsata	X	X	X	X	
Tetranota sexcarinata				X	

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 2 : Distribution of monoplacophorans and bellerophontaceans in the Nashville Group of central Tennessee. Data are based on museum collections and species lists in Wilson (1949).

	Hermitage Formation	Bigby-Cannon Limestone			Catheys Formation
		Bigby	Cannon	Dove-colored	
Archinacella depressa			X		
Archinacella patelliformis		X			
Archinacella valida	X				
C. (Cyrtolites) retrorsus	X	X		X	
Bucania frankfortensis					X
Bucania lindsleyi			X		X
Bucania nashvillensis		X	X	X	
Bucania peracuta			X		
Bucania singularis					X
Bucania sp.		X			
Bucanopsis carinifera			X		
Carinaropsis cunulae			X		
Phragmolites cellulosa	X				
Sphenosphaera clausus		X	X	X	
Sphenosphaera troosti			X	X	
Sphenosphaera sp.					X
Tropidodiscus cristatus			X	X	
Tropidodiscus subacutus				X	
Undulabucania punctifrons	X				

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 3 : Distribution of species of monoplacophorans and bellerophontacean gastropods in the Tyrone Limestone of the High Bridge Group, the members of the Lexington Limestone, and the Clays Ferry Formation of central Kentucky. Data are based on the new U.S. Geological Survey silicified collections and on museum collections. Note that Middle Ordovician stratigraphic units in the central Kentucky area from which no taxa are known are not included in the table. TY = Tyrone Limestone; CF = Clays Ferry Formation; members of the Lexington Limestone are designated: CL = Curdsville Limestone; LO = Logana; GL = Grier Limestone; PL = Perryville Limestone; DH = Devils Hollow; TL = Tanglewood Limestone; and ML = Millersburg.

Species	TY	CL	LO	GL	PL	DH	TL	ML	CF
Micropileus variabilis		X							
Vallatotheca unguiformis		X			X				
Archinacella simulatrix	X	X	X	X					
A. cingulata		X							X
A. alta									X
C. (Cyrtolites) retrorsus		X	X	X	X			X	?
C. (Cyrtolites) claysferryensis									X
C. (Paracyrtolites) subplanus			X	?					
C. (Paracyrtolites) parvus									X
Sinuites pervoluta	X	X							
S. obesus		X	X						
S. cancellatus		X	——	——	?	——	——	——	X
Tropidodiscus subacutus	X	?	?		X	X			
Phragmolites compressus	——	?	——						
Temnodiscus nitidula									X
Bucania halli		X		X					
B. subangulata		X		X					
B. nashvillensis				X	X				
B. frankfortensis						X			
B. sublata				X	X	X			
B. micronema					?				
B. rugatina									X
Tetranota obseleta		X							
Salpingostoma kentuckyense	X	X							
Bucanopsis carinifera				X	X		X		
B. diabolensis						X			
Sphenosphaera clausus			X	X	X	X	X	X	X
S. sp. indet.		X							
S. troosti				X	X				
S. subglobulus	?								
S. bilineatus						X			
Carinaropsis acuta		X	X						
C. cymbula			X	X	X		X		
C. explanata									X
Pterotheca saffordi	X								
P. expansa	X	X							
P. angusta		X							

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 4 : Distribution of species of monoplacophorans and bellerophontacean gastropods in the Upper Ordovician stratigraphic units of the Cincinnati Arch Region. Stratigraphic units in southeastern Indiana are designated: KO = Kope Formation, DO = Dillsboro Formation, SA = Saluda Formation, and WW = Whitewater Formation. Units in southwestern Ohio and north-central Kentucky are designated: KO = Kope Formation, FV =Fairview Limestone, BL = Bellevue Limestone, GL = Grant Lake Limestone, BF = Bull Fork Formation, and DR = Drakes Formation. Units in south-central Kentucky are designated: GS = Garrard Siltstone, CC = Calloway Creek Limestone, AS = Ashlock Formation, and DR = Drakes Formation. Units in central Tennessee are designated: IF = Inman Formation, LP = Liepers Formation, AR = Arnheim Limestone, and FN = Fernvale Limestone.

Species	SE Indiana				SW Ohio - N Ky.						S Ky.				Tennessee			
	KO	DO	SA	WW	KO	FV	BE	GL	BF	DR	GS	CC	AS	DR	IF	LP	AR	FN
Vallatotheca manitoulini									X									
Helcionopsis striata																	X	
?Archinacella davisi					?													
Archinacella cf. patelliformis						X												
A. rugatina									X									
A. arca									X									
A. indianensis		X		X					X	X								
C. (Cyrtolites) ornatus		X	X	X		X	X	X	X	X								
C. (Cyrtolites) cf. C. (C.) retrorsus					X													
C. (Cyrtolites) claysferryensis					X													
C. (Cyrtolites) minor					X	X												
C. (Cyrtolites) hornyi		X																
C. (Paracyrtolites) carinatus	X				X													
Sinuites cancellatus	?																	
S. planodorsata					X													
S. granistriata					X													
S. globularis					X													
S. subcompressus		X																
Tropidodiscus magnus				X														
Phragmolites bellulus						X												
P. elegans									X									
P. dyeri		X	X	X					X	X								
														X				

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 4 : (continued)

Species	SE Indiana				SW Ohio - N Ky.						S Ky.				Tennessee			
	KO	DO	SA	WW	KO	FV	BL	GL	BF	DR	GS	CC	AS	DR	IF	LP	AR	FN
Undulabucania gorbyi		X																
Bucania pojetai																X		
B. simulatrix				X					X	X								
B. crassa				X														
Kokenospira costalis					X													
Tetranota bidorsata					X													
Salpingostoma richmondensis				X					X	X								
Sphenosphaera recurvus								X										
S. subangularis				X														
S. capax						X							X					
S. mohri		X	X	X					X	X								
Pterotheca harviei					X													

THE PALEOECOLOGY OF MONOPLACOPHORANS AND BELLEROPHONTACEANS

INTRODUCTION

Paleontologists have generally regarded bellerophontacean archaeogastropods, and those Paleozoic taxa now recognized as monoplacophorans, as algal grazers that inhabited mainly nearshore shallow subtidal and intertidal marine environments. This general conclusion has been based on common paleoenvironmental occurrences and faunal associations in the fossil record, as well as on comparison with some modern archaeogastropods (mainly limpets). However, data on fossil archaeogastropods and monoplacophorans show this conclusion to be a clear oversimplification.

AUTECOLOGY OF MONOPLACOPHORANS

Modern monoplacophorans, such as Neopilina, all live at 200 meters or more water depths, all are limpet-shaped, and, as far as is known, all are deposit feeders (Cesari and Guidastri, 1976). On the other hand, Paleozoic taxa interpreted to be monoplacophorans were relatively shallow subtidal shelf inhabitants, and included limpet-shaped (Pls. 1-4), convolute (Pl. 9, figs. 1-4), involute (Pl. 5, figs. 5-7) and evolute (Pl. 6, figs. 19-22) isostrophically coiled shell forms. Detailed paleoecological data on these Paleozoic monoplacophorans are scarce, and therefore their

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

life habits can presently only be speculated upon. Lemche and Wingstrand (1959, p. 63) stated that the modern monoplacophoran Neopilina was taken from abyssal dark muddy clay sediment were there were no suitable objects for the animal to creep on. However, Lowenstam (1978) reported that specimens of Vema, another modern monoplacophoran, were found clinging to phosphate pebbles in dredge samples from bathyl depths. He observed tehse living monoplacophorans in a tank for nearly a month, and noted a maximum linear movement of only 10 cm. Similarly, many Paleozoic limpet-shaped monoplacophorans were probably also clingers.

The cap-shaped to conical tryblidiid monoplacophorans in the Ordovician strata of the Cincinnati Arch are distributed throughout a spectrum of depositional environments (Tables 1-4). In the U.S.G.S. silicified collections Archinacella simulatrix occurred in such varied facies as the Tyrone Limestone, and the lowermost Curdsville Limestone and Grier Limestone Members of the Lexington Limestone. One common factor in these occurrences is that all of these facies were deposited in less than 15 meters of water (Cressman, 1973).

Other species of Archinacella cited herein are found in various Middle and Upper Ordovician formations, many of which contain multiple facies of different depositional origins. Most of these occurrences are known from museum specimens and the sedimentological and faunal associations are generally unknown. Therefore, at present correlation between taxa or morphotypes and depositional environments is not possible.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

There are some consistent environmental distributions for other tryblidiid genera in the U.S.G.S. silicified collections. Vallatotheca unguiformis and Micropileus variabilis are both known from only very shallow water facies. V. unguiformis is known only from the Salvisa bed of the Perryville Limestone Member and the basal meter of the Curdsville Limestone Member of the Lexington Limestone. The fine-grained limestones of the Salvisa bed were deposited in 2 meters or less water depth and are characterized by an ostracod fauna and some mollusk shell beds (Cressman, 1973, p. 30). The lower part of the Curdsville Limestone Member consists of crossbedded bioclastic limestone deposited above wave base in a transgressive sea (Cressman, 1973, p. 14). V. unguiformis was most likely an algal grazer. Micropilleus variabilis was found only in the basal 2 feet of the Curdsville Limestone Member of the Lexington Limestone. Its unsculptured low conical shell, and its apparent possession of a continuous muscle ring, suggest that it led a limpet-like existence, clinging to and rasping algae from exposed lithified surface of the Tyrone Limestone along the shoreline of the transgressing Curdsville sea.

The common bryozoan encrustation of tryblidiid shells in the present fauna suggests that these molluscs lived exposed lives in firm-bottom depositional environments. Such encrustations are known on the shells of Archinacella simulatrix (Pl. 2, figs. 7-8), A. indianensis (Pl. 3, figs. 16-18), Helcionopsis striata (Pl. 2, figs. 1-5), Vallatotheca unguiformis (Pl. 1, figs. 30-31), and V. manitoulini (Pl. 1, figs. 8-11).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Also, the highly sculptured dorsal shells of genera such as Vallatotheca and Helcionopsis might speak against the deposit-feeding habit, in which the shell is often at lease partially submerged in soft sediment. All of these taxa were probably algal grazers in shallow water habitats.

Some smooth-shelled tryblidiids occur in more shale-rich facies, such as Archinacella arca from the Bull Fork Formation and A. alta from the Clays Ferry Formation. Hurst (1979) cited Archinacella sp. and indeterminate monoplacophorans from offshore shale facies in the British Caradoc Series. These monoplacophorans may have been deposit-feeders. However, it is curious that archinacellids possess continuous muscle rings, which are generally though to be characteristic of clinging molluscan univalves.

Species of the cyrtonellid monoplacopharan genera Cyrtolites and Sinuites were were highly successful during the Middle and Late Ordovician and are found in most Ordovician formations in the Cincinnati Arch region (Tables 1-4). Both were probably sluggish vargrant benthos. They often occur together, but one genus is usually clearly dominant over the other in any single collection. They are often found in shaly and silty rocks. In fact, they are the dominant symmetrical molluscan univalves in both the Logana Member (Kirkfieldian) of the Lexington Limestone and the Kope Formation (Edenian), the deepest water units in the Kentucky- Indiana-Ohio Ordovician section. However, Cyrtolites retrorsus is also common throughout shallow water facies of the Lexington Limestone, and C. ornatus is common through most of the Cincinnatian section. Cyrtolites ornatus is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

commonly encrusted by bryozoans, and the encrustations can be shown to have occurred both during the life of the animal and after death (see section on encrustation below). Such encrustation suggests that the animal lived exposed on firm substrates in normal marine conditions. On the other hand, specimen of Sinuites are rarely ever encrusted, which may be attributable to their smoother shell surfaces, their occupation of more turbid environments, some aspect of their mode of life, or a combination of these factors. Sinuites seems to be more dominant in deeper water facies than Crytolites. The highly irregular aperture margin of Sinuites also seems more adapted for the efficient channelling of water through the shell than clamping onto a firm surface (see Functional Morphology section). It appears that Sinuites may have been a deposit-feeder on soft-bottoms, while Cyrtolites was more likely an algal-feeder in predominantly firm-bottom areas.

AUTECOLOGY OF BELLEROPHONTACEANS

Bellerophontacean archaeogastropods are commonly allied closely with the pleurotomariaceans because of their common possession of a median labral emargination along the apertural margin (Knight, 1952), as well as their common association in Paleozoic fossil assemblages. Unfortunately, ecological comparison of bellerophontaceans to modern pleurotomariaceans is nearly fruitless, as the latter group is mainly represented today by

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

only a small number of relict species living in deeper-water environments (Vermeij, 1978, p. 221). A more fruitful ecological comparison can be made between bellerophontaceans and those modern archaeogastropods that occupy the same shallow subtidal environmental regime. These modern groups are mainly algal grazers. They either rasp algae (mainly blue-green) from hard surfaces, like many patellaceans, or feed on the thalli of erect green algae, like other patellaceans and most trochaceans (Morton, 1967, pp. 96-98).

Steneck and Watling (1982) and Steneck (1983) have discussed the morphological limitations on the feeding capabilities in herbivorous mollusks. They concluded that bellerophontaceans and monoplacophorans were probably restricted to feeding on delicate filamentous and microscopic algae (browsing habit), as are most recent non-limpet archaeogastropods. These modern archaeogastropods, and modern monoplacophorans (as known from Neopilina), possess radulae with chitinous teeth which are too soft to excavate calcareous substrata. This morphological feature is thought to have restricted their feeding on calcareous algae. However, it should be noted that patellacean archaeogastropods have strong buccal muscles and uniquely designed radular teeth that are strengthened by silicate and iron mineral coatings, which allow them to excavate calcareous substrata effectively and even to feed on crustose red algae (Steneck and Watling, 1982; Steneck, 1983).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

As pointed out by Peel (1977, p. 41-43), there are some notable exceptions to the algal feeding habit in modern archaeogastropods. Some fissurellids feed on sponges (Morton, 1967), and the deep-water pleurotomariacean Mikadotrochus includes sponges in its microphagous scavenging habit (Fretter, 1964). Fretter (1964) also found foraminifers, diatoms, algal fragments, and organic detritus in the stomach of Mikadotrochus. Woodward (1901), Matsumato and others (1972), Yonge (1973) and Hickman (1976, 1984) have inferred or actually observed carnivory (particularly on sponges) by modern pleurotomariaceans. Fretter (1975) has even observed ciliary suspension feeding in the modern trochid Umbonium. Morton (1967) has discussed the minor anatomical modifications needed for the adaptation of archaeogastropods to these more sophisticated feeding habits. Surely, if the necessary anatomical conversions to allow the carnivorous, the microphagous deposit feeding (scavenging), and the ciliary suspension feeding habits have taken place in modern archaeogastropods, then there is no reason to assume such adaptations did not also occur in Paleozoic forms.

Some exceptions to the algal browsing habit in Paleozoic archaeogastropods have been demonstrated. For example, Bowsher (1955) showed that many platycerids were coprophagous on crinoids. The common Upper Ordovician platycerid genus Cyclonema is commonly associated with camerate crinoids (Thompson, 1970, pp. 222-22). McKerrow (1978, pp. 80-82) claimed that Ordovician bellerophontaceans, which he considered to be monoplaco-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

phorans, were bottom-dwelling detritus-feeders and scavengers, but offered no evidence to support the contention. Yochelson (1971) and Peel (1975) have interpreted open-coiled Paleozoic gastropods as sedentary ciliary suspension feeders based on comparisons with modern forms. Runnegar (1983, p. 128) has also suggested that macluritid and euomphalid archaeogastropods were suspension-feeders from analysis of the "living fossil" Neomphalus, a modern filter-feeding limpet interpreted to be a euomphalid. Peel (1977, p. 47) suggested that explanate bellerophontaceans were epifaunal deposit feeders on soft substrates, micromorphic bellerophontaceans were grazers amongst algal foliage, and other shell forms led one or the other of these life styles. He stressed, however, that although other life habits have been demonstrated for modern archeogastropods (as cited above), sufficient evidence of such habits is usually lacking in the fossil record.

Batten (1958) noted the common association of pleurotomariaceans and sponges in shallow muddy bottom paleoenvironments in the Permian strata of the southwestern United States. More significantly, Batten (1958) and Finks (1960) have cited four instances when one or more specimens of the pleurotomariacean G. (Glyptotomaria) marginata have been found within the cloaca of the demosponge Heliospongia vokesi. Batten (1958) has suggested the gastropods may have fed on algal material collected on the cloacal walls. However, since some modern fissurellids (Morton, 1967) and possibly some pleurotomariaceans (Fretter, 1964) feed on sponges, it is possible that some Paleozoic archaeogastropods also did so.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Yonge (1947) claimed that archaeogastropods were restricted to firm substrates in relatively clean water environments because their bipectinate aspidobranch gills are prone to clogging by fine sediment particles. However, evidence from the fossil record amply demonstrates the common occurrence of archaeogastropods, and particularly bellerophontaceans, in muddy sediments. Peel (1977, pp. 41-46) has discussed this problem at some length, initially recognizing two important points. First, the general absence of modern archaeogastropods adapted to life on a soft-bottom may be a result of post-Paleozoic competition with the more advanced caenogastropods, whose monopectinate ctenidia and anterior siphon enabled them to cope more easily with soft-bottom conditions. And second, it is possible that some Paleozoic forms presently included in the Archaeogastropoda may actually be caenogastropods, or may even be of an now extinct organizational grade.

Assuming Yonge's (1947) assessment of the bipectinate gill is correct, there are three ways to explain the presence of archaeogastropods in muddy sediment deposits. First, the gastropods might have been supported on algal films which bind and cover the muddy sediment surface. Gebelein (1969) cited gelatinous films of algal mucilage from modern carbonate environments in Bermuda, where they stabilized substrates and passively trapped carbonate muds. Peel (1977, p. 45) cited examples of modern caenogastropods living on such films and pointed out that these films would also furnish an abundant food source. Ferguson (1962) described an assem-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

blage of small bellerophontaceans (generally less than 10 mm. in diameter) from British Mississippian shales of intertidal to shallow subtidal environments in a transgressive sequence. He postulated that the small snails could survive on the muddy bottom because the rate of sedimentation was very slow and the sediment surface may have been loosely bound by organic slime.

The second possibility is that the snails lived on drifting masses of algae comparable to the modern Sargassum (Peel, 1977, p. 44). Ruedemann (1934) explained the occurrence of benthic faunas in Paleozoic black shales in this way. However, it is unlikely this is an important mechanism in explaining the widespread occurrences of archeogastropods in normal marine shales deposited in shallow aerobic settings.

The third and most common explanation is that the snails were algal foliage-dwellers, living above the turbid mud bottoms in stands of erect algae (Peel, 1977; Gromaczakiewicz-Lomnicka, 1972; Goldring and Langerstrassen, 1979; Bowen and others, 1974; Johnson, 1962, 1964; Chronic, 1952). Johnson (1961, p. 5-6) claimed that Ordovician seas supported a rich algal flora of noncalcareous and weakly calcified marine algae. The mild climates and widespread areas of shallow marine carbonate deposition of the Ordovician were an ideal setting for the development of calcareous marine algae. Johnson believed that the floors of Ordovician shallow shelf areas were covered by an algal flora as populous and diverse as those of modern seas, and he envisioned these algae as the basic food supply for the teeming marine invertebrate communities of the period.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The late Middle Ordovician radiation of archaeogastropods could be linked to the early Middle Ordovician radiation of marine algae. Blue-green algae, in the form of stromatolites and oncolitic encrustations, dominate pre-Middle Ordovician marine algal floras, but during the Middle Ordovician, a radiation of green (Codiaceae and Dasycladaceae) and red (Solenoparaceae) algae occurred (Johnson, 1961; Wray, 1977, Fig. 161). Moore (1977, p. 18) reported an abundant and diverse marine algal flora composed of both calcareous and noncalcareous components from the early Middle Ordovician (Chazyan) limestones of eastern Tennessee, and described an algal ecologic zonation comparable to that of recent shallow marine environments. Moore found green and red algae to be most abundant in the broad shelf-lagoon environment and its contained patch reefs, but absent in shelf margin shoal and reef environments. Tidal flats and associated environments showed the influences of stromatolite growth.

There are also some fairly well-preserved erect noncalcareous algae known from Ordovician strata. Arbey and Koeniguer (1979) reported casts of small seaweeds from the Ordovician of the Sahara Desert which are similar to the well-known Devonian-aged Protaxites (see Koeniguer, 1974; Jonker, 1979). Also, Fry (1969, 1983) described collections of noncalcareous marine algae made by G. Winston Sinclair from the dolomites of the Late Ordovician (Richmondian) Red River Formation of Manitoba. He recognized numerous erect morphotypes that most closely resemble modern red, green and brown algae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Numerous authors discussing Paleozoic marine benthic communities have cited bellerophontaceans as common inhabitants of nearshore delta front shales and siltstones (Bretsky, 1969, 1970; Johnson, 1962; Bowen and others, 1974; Sutton and others, 1970; Thayer, 1974; Goldring and Langerstrassen, 1979; Linsley, 1979; West, 1972; Rollins and others, 1979; Sturgeon, 1964, MacLeod, 1982). Sutton and others, (1974) suggested that their Bellerophon Community from the Devonian of New York was located near delta channel mouths during periods of active progradation when outflowing nutrients would provide for the most prolific growth of marine plants. Johnson (1962) likewise associated Pennsylvanian gastropod assemblages in the Illinois Basin with areas of prolific plant growth in delta front areas. Likewise, MacLeod (1982, p. 172) cited a bellerophontid community in delta front environments in the Upper Pennsylvanian of north-central Texas and suggested they fed on benthic algae. It should be noted that these prodelta areas must have also been sites of active fine clastic sedimentation and accordingly would have been particularly turbid.

Peel (1977, pp. 43-46) has pointed out some possible shortcomings of the algal foliage-dweller hypothesis. In modern seas, the dominant types of vegetation on soft sediment in shallow water are sea grasses, whereas algal stands are more characteristic of modern rocky shoreline areas. However, sea grasses did not appear in the fossil record until the Tertiary (Brazier, 1975), and therefore it would be necessary to suggest that algae dominated marine areas in the Paleozoic in which they are now subordinate.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Peel (1977, p. 44) further pointed out that the supporting ability of algal foliage restricts the size of gastropods that can live on it. Most modern algal foliage-dwelling gastropods are quite small. Warmke and Almodovar (1963) found 99% of the molluscs associated with algae in Puerto Rico were gastropods, but they were mainly less than 2 mm. in diameter. Brazier (1975) cited small gastropod faunas as a possible criterion for the recognition of former grass beds in the Tertiary fossil record. Johnson (1964, p. 123) claimed that a modern gastropod assemblage dominated by a few species in fine-grained sediments generally indicates the presence of plants. Diverse diminutive molluscan faunas have also been interpreted as algal foliage-dwelling faunas in the Upper Ordovician Maquoketa Formation (Bretsky and Bermingham, 1970) and the Lower Silurian Brassfield Formation (Harrison and Harrison, 1975). Peel (1978, p. 302) suggested, in his study of the gastropod faunas of the Silurian Arisaig Group in Nova Scotia, that many of the smaller forms of 5 mm. or less in diameter were probably algal foliage-dwellers, and those in the 10-15 mm. size range may also have been. However, he doubted that the high proportion of Arisaig gastropods attaining 20 mm or more in size could have lived in algal foliage. However, large and small species of archeogastropods are commonly found together in Paleozoic fine-grained deposits. Sturgeon (1964, p. 193) stressed the co-occurrence of gastropods in the Pennsylvanian shales of Ohio ranging in size from 5.5 mm to 35 mm Chronic (1952, pp. 109-111) claimed small, finely ornamented, delicate snails of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the fine-grained Permian Kaibab Limestone of Arizona lived in "seaweed forests" above the calcareous mud substrates, while contemporary thick-and smooth-shelled large forms lived on the sea floor beneath. Heuer (1973, p. 527-528) suggested that bellerophontaceans lived on soft muddy bottoms in Late Pennsylvanian prodelta settings in Texas, while most associated pleurotomareaceans lived above the sea floor on erect algae, crinoids, bryozoans and sponges. Peel (1977, p. 43) cited examples of modern stratified gastropod faunas in algal foliage habitats, and noted that upon death ecologically mixed assemblages containing forms from different levels within the foliage, as well as forms living amongst the holdfasts and at the sediment surface, would result.

It therefore appears that the algal foliage-dwelling habit may be a partial answer for small Paleozoic archaeogastropods in muddy sediments, but they are generally associated with other species thought to be too large to have been supported by algal foliage. Apparently, at least some Paleozoic archaeogastropods had adaptations which allowed them to cope with soft substrates, and it is likely that feeding habits were much more varied than generally supposed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PREVIOUS ORDOVICIAN PALEOECOLOGICAL STUDIES

There are very few published studies focusing on Ordovician bellerophontacean-monoplacophoran paleoecology. However, a small number of genera are commonly cited in more general Ordovician community studies. These studies can be conveniently divided into those concerned with clastic and carbonate depositional environments. A brief review of these studies documents that monoplacophorans and bellerophontaceans occupied a wide variety of Paleozoic habitats.

Ordovician Clastic Environments

Bretsky (1969, 1970) studied marine benthic communities in Upper Ordovician clastic depositional environments along the Queenston delta front in the Central Appalachians. He reported Plectonotus sp. and Bucania sp. from shall subtidal and intertidal silt and fine sand bottom environments. They occur in Bretsky's Orthorhynchula-Ambonychia assemblage, and are associated with rhynchonellid and linguloid brachiopods, and modiomorphid, ambonychiid, and nuculoid bivalves. Although the bellerophontaceans are found in sediments of the same textures as pleurotomariaceans, the two groups do not commonly co-occur, the bellerophontaceans occupying more nearshore areas adjacent to crossbedded sand and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

organic-rich mud depositional environments. Plectonotus sp. was by far the more abundant of the two bellerophontaceans, and was commonly found in clumps of numerous specimens in sediment stained with more organic-matter than surrounding sediments. These specimens were most likely concentrated around a common food source, probably algal.

Brenchley and Cocks (1983) recognized ten faunal associations in the latest Ordovician regressive sequence in Norway. Unidentified bellerophontaceans occurred in three of these associations. All three occurrences were in mudstones, but the three associations were found in deep shelf, midshelf, and inner shelf environments, respectively. None were reported from nearshore or onshore facies.

Pickerill and Brenchley (1979) described benthic marine communities in the clastic rocks of the Caradocian Series in North Wales. They recognized four communities, all of which were believed to have been deposited in offshore shelf areas of 30 meters or less depth. Cyrtolites sp., Sinuites sp., Bucania sp., Bucanopsis sp. and indeterminate bellerophontaceans were found in fine sand, silt, and mud bottom environments of 25 meters or less in depth. Cyrtolites sp. was also found in coarse sands deposited in less than 10 meters, and Sinuites was also found in brachiopod-bryozoan-trilobite assemblages originating in greater than 25 meters water depth.

Hurst (1979) described the succession of benthic marine faunas of the type Upper Caradocian Series of England, a transgressive clastic sequence

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ranging from coarse onshore sands to deep water organic-rich laminated shales. Bellerophontaceans were rare in nearshore sand and silt facies, but composed up to 8.1% of the total fauna in stable offshore silt facies, and were locally common in deeper mud environments. In a gradient of 14 depositional facies (1 = onshore sands, 14 = deep offshore bioturbated and laminated muds) and faunal assemblages, bellerophontaceans and monoplacophorans were common faunal elements (2 to 8% of total fauna) only in facies 10 through 13 (offshore silts to muds). Taxa cited were indeterminate bellerophontaceans (facies 6-13), Sinuites sp. (facies 8-13), Cyrtolites sp. (facies 11), Temnodiscus sp. (facies 10-12), Cymbularia sp. (facies 11-13), Archinacella sp. (facies 12-13), and indeterminate monoplacophorans (facies 12-13). It is noteworthy that Archinacella sp. and indeterminate monoplacopharans were found in only the deepest water assemblages. Sinuites was the most wide ranging taxon in the sequence, while Cyrtolites and recognizable bellerophontaceans were concentrated in assemblages 10 through 12, all of which occurred in offshore silt bottom environments. Hurst (1979, p. 239) noted that as in the successional faunal stages described by Bretsky and Bretsky (1975) from the Upper Ordovician of Quebec, Temnodiscus sp. and Sinuites sp. are characteristic of early diversification faunas succeeding a Nuculites-trilobite fauna that colonized barren fine mud bottoms. It seems likely that these molluscs were dependent on the establishment of some member or members of the pioneer community which may have acted as a food source and/or a supporting structure above the mud bottom.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Horny (1963) described Middle and Upper Ordovician bellerophontaceans from Bohemia and briefly discussed their paleoecology. The Bohemian Ordovician section consists predominantly of shales, siltstones, and sandstones, with scattered limestones. His data showed that bellerophontacean genera are generally distributed through two or more facies, but individual species are restricted to a single facies. He observed that while clay shales rarely contained any bellerophontaceans, calcareous shales often had abundant specimens. He further observed that while some explanate bellerophontacean species (Grandostoma grande, Pterotheca consobrina) were found only in shaly sediments, other explanate morphotypes (Grandostoma bohemicum, Bucanopsis calypso) were found in both shales and sandstones, and still others (Cyclotheca bohemica, Tremanotus tuboides) occurred only in coarse-grained bioclastic-tufaceous limestones around volcanic islands. His data suggests that the explanate shell form was not adapted to any special substrate conditions.

McKerrow (1978, pp. 78, 83, 89) cited undetermined bellerophontaceans from three Ordovician communities: the Dinorthis Community of shallow shelf, coarse clastic bottoms; the Diverse Brachiopod Community of the middle to deep shelf environment; and the Christiania-Sampo Community of the deep shelf.

In summary, Ordovician bellerophontaceans living on clastic sediment substrates seem to be most common in siltstones, somewhat less common in calcareous shales, and are only found occasionally in sandstones. How-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ever, the environmental settings of these substrate types can be quite variable. Bretsky (1969, 1970) cited bellerophontaceans as nearshore silt-bottom inhabitants in a progradational delta front setting, similar to occurrences in Devonian and Pennsylvanian strata cited above. Conversely, Pickerill and Brenchley (1979) and Hurst (1979) cited their silt-bottom dwelling bellerophontaceans and monoplacophorans from relatively deep offshore environments in a transgressive setting. This apparent discrepancy is clarified when the character and composition of the faunas from the two settings are considered. Bretsky's delta front fauna contained only two species, with Plectonotus sp. being clearly dominant. That species may have been an opportunist, capable of surving the relatively unstable delta front conditions with eurytopism and a high rate of fecundity (see Levinton, 1970). Moreover, trilobation of the shell, as in Plectonotus sp. has been convincingly interpreted as a modification of the entrance to the mantle cavity to increase the efficiency of water circulation (Peel, 1974, p. 249), and would thereby serve to assist in keeping the gills unfouled in turbid delta-front conditions. On the other hand, the monoplacophoran-bellerophontacean assemblages cited from the British Caradocian Series are much more diverse (at least 10 genera), as is expected in more stable offshore environmental settings (see Sanders, 1968). Moreover, a diversity of general shell forms is present in the Caradocian, including cap-shaped, involute, convolute, and explanate morphotypes, probably representing the occupation of a variety of niches.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ordovician Carbonate Environments

Berry (1974, p. 159) cited nautiloid cephalopods and bellerophontacean and macluritacean archaeogastropods as the dominant fauna of the extensive tidal flat environments of the Late Cambrian-Early Ordovician carbonate platforms in North America. He interpreted all three groups as algal grazers. He (1974, p. 161) claimed that this nautiloid-bellerophontacean-macluritacean fauna continued to dominate intertidal and adjacent shallow subtidal carbonate environments through the end of the Ordovician, while orthid-strophomenid brachiopod faunas came to dominate essentially all other subtidal carbonate environments.

Walker (1972), who studied the community ecology of the Black River Group (Blackriveran) of New York State, cited only one bellerophont, Plectonotus sp., that being from his wave-baffle margin community. This community occupied the front and back flanks of Tetradium coral banks and was dominated (80% of total biovolume) by the byssate pelecypod Cyrtodonta and the high-spired gastropod Loxoplocus.

There was a distinct increase in abundance and diversity of molluscan univalves in post-Blackriveran strata in eastern North America. In their work on communities of the Lower Trenton Group (Rocklandian-Shermanian) of New York State, Titus and Cameron (1976) cited Phragmolites compressus, Sinuites bilobatus corrugatus, Sinuites cancellatus, and Sinuites cancellatus acutus as common elements in the Triplesia community of the lagoonal

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

facies and in the Liospira community of the nearshore shoal facies. Phragmolites compressus was also a member of the Encrinurus community of the foreshoal shallow shelf facies. Titus (1982) continued this work on the communities of the middle Trenton Group (Shermanian) of New York State. He reported Sinuites cancellatus liratus from the Liospira community in the nearshore shoal facies, Sinuites cancellatus from the Encrinurus community in the foreshoal shallow shelf facies, and Sinuites bilobatus corrugatus from the Trematis community in the offshore open shelf facies.

Byers and Galvin (1979) studied two contemporaneous communities from normal marine shallow subtidal deposits of the Platteville Formation (Rocklandian) in Wisconsin. Sinuites sp. and Phragmolites sp. were found to make up 11% and 2% of the first community, respectively. The second which contained the same common taxa, but in different percentages, had Sinuites sp. and Phragmolites sp. making up 26% and 1% of the community, with Sinuites sp. being the most abundant fossil in the total assemblage. Sinuites sp., which was considered to be an algal-browsing archaeogastropod, was often found alone covering bedding planes, and the authors suggested that it might have been an opportunistic species.

The scant data on molluscan univalves from community studies on carbonate strata of the Champlainian Series give a deceptive impression of low diversities. The monoplacophoran-bellerophontacean faunas of the Lexington Limestone covered herein show that these mollusks could be abundant

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and diverse. The apparent abundances of species of Sinuites and Phragmolites in Middle Ordovician studies from New York and Wisconsin cannot be readily explained, as these genera are not dominant in the Middle Ordovician strata of the intervening Cincinnati Arch Region, but they are more common in the more shale-rich Late Ordovician strata of that area.

In summary, it appears from an examination of Middle and Upper Ordovician benthic marine community studies that only a small number of bellerophontacean and monoplacophoran taxa were associated with onshore environments, but rather, most were distributed through nearshore and offshore normal marine shelf environments.

POST-ORDOVICIAN PALEOECOLOGICAL STUDIES OF NOTE

In a general study on Siluro-Devonian communities, Boucot (1975, pp. 13-18) charted six benthic assemblages. His only mention of bellerophontaceans was his Homolonotid-Plectonotus community, which characterizes the most nearshore assemblage zone (Benthic Assemblage 1). Berry (1975, p. 49, fig. 15) interpreted his community as occupying a quiet-water, high intertidal environment.

Peel (1975, 1977, 1978) contributed greatly to the understanding of the paleoecology of Paleozoic gastropods through his studies on the faunas of the Silurian Arisaig Group of Nova Scotia. The morphotypic compositions of these Silurian monoplacophoran-bellerophontacean faunas are

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

similar to those of Middle and Late Ordovician faunas, so Peel's observations apply to the present investigation. The Arisaig Group is a 1300 meter thick siltstone-dominated sequence that provides a nearly continuous faunal record of shallow marine communities throughout the Silurian and Early Devonian Periods. Watkins and Boucot (1975) and Bambach (1969) have studied the brachiopods and pelecypods of the Arisaig Group, respectively. Watkins and Boucot (1975) concluded that most of the Arisaig could be referred to nearshore Benthic Assemblage 2 of Boucot (1975), with offshore Benthic Assemblages 3 and 4 in some parts of the group. Peel's (1977, 1978) observations on bellerophontacean paleoenvironmental distributions are summarized below.

(1) The hard-bottom shallow marine platform fauna was characterized by trochiform pleurotomariaceans, with the small globose bellerophontacean Bucanopsis sp. making up 12% of the gastropod fauna.

(2) The soft-bottom shallow marine platform fauna was dominated by high-spired murchisoniids and loxonomataceans, with the trilobed Tritonophon trilobata and the explanate Phragmosphaera globata making up 14-25% and 12% of the gastropod fauna, respectively.

(3) The soft-bottom open lagoon fauna was heavily dominated by trochiform holopeids in its typical development. With a decrease in water depth, the holopeids were replaced by a fauna of small bellerophontaceans, including trilobed plectonotinids, and by lenticular pleurotomariaceans, and some high-spired gastropods.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Peel (1975, 1978) suggested that explanate bellerophontaceans in the Arisaig, such as Phragmosphaera globata, were adapted to life on soft substrata, the broadly expanded apertures serving to support the shell on top of the sediment. He further reasoned (1978, pp. 302-303) that gastropods ranging up to 10-15 mm in diameter could have been algal foliage-dwellers, including species of Tritonophon, Tropidodiscus, Pharetrolites, and Cymbularia.

Heuer (1973, p. 510-541) discussed the paleoecology of Upper Pennsylvanian gastropods from the Wolf Mountain Shale (Canyon Group - Missourian Series) of north-central Texas. The Wolf Mountain Shale was deposited in a prodeltaic shallow shelf setting. The formation contains a diverse gastropod fauna, including 13 genera and 24 species of pleurotomariaceans, and 3 genera and 4 species of bellerophontaceans, as well as less common euomphalaceans, murchisoniaceans, and subulitaceans. Heuer (1973, p. 527-530) concluded that the bellerophontaceans were deposit feeders that lived directly on the sea floor, while the pleurotomariaceans mostly dwelled above the sea floor on erect organisms such as algae, crinoids, bryozoans and sponges. He proposed that the pleurotomariaceans either fed directly on their supporting hosts or fed on epizoans and organic detritus on the surfaces of the hosts. Heuer claimed that the morphology of the bellerophontaceans was better adapted to life on soft substrates as indicated by: (1) generally shorter labral slits than in the cooccurring pleurotomariaceans, reflecting shallower mantle cavities that could be

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

more easily flushed of fouling detritus by rapid contraction of the shell muscles; (2) a symmetrical shell with a low center of mass due to the weighting of thick parietal deposits, which would give greater stability during movement through soft sediments; and (3) the presence of broad to explanate apertural margins in 3 of 4 bellerophontacean species (i.e., B. (Bellerophon) sp., B. (Pharkidonotus) percarinatus, and Knightites (Cymatospira) montfortianus) in the fauna, which reflect a broad foot that would prevent sinking into soft sediment.

A survey of a complete spectrum of Paleozoic community studies gives the impression that bellerophontaceans were most abundant during the Devonian and Pennsylvanian Periods, and most commonly occurred in communities associated with delta front environments (as previously discussed). It should be noted that in such occurrences a single species is usually dominant and probably represents opportunistic situations. More significantly, most bellerophontacean genera have been cited from Paleozoic communities throughout the marine environmental spectrum. Linsley (1968, p. 360) found bellerophonts in environments associated with Devonian coral - stromatoporoid biostromes. Moore (1964, p. 339-341) cited bellerophontaceans as being scattered throughout most marine facies in Kansas Pennsylvanian-Lower Permian cyclothems, but they were most abundant in nearshore limestones containing algal (Osagia) - molluscan assemblages. Stevens (1965, 1966) and Yancey and Stevens (1981) cited bellerophontaceans (Euphemitid community) as characterizing Middle Pennsylvanian to

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lower Permian communities inhabiting the subtidal to lower intertidal zone of large bays or sounds, where sedimentation was rapid and the salinity was variable, though generally normal. Yochleson (1969) and Imbrie and others (1964) cited bellerophontaceans from firm-substrate "shelly facies" from Mississippian and Pennsylvanian carbonates, respectively. Finally, Ausich and others (1979, p. 1191-3) who studied Mississippian Borden delta communities in Indiana and Kentucky, noted bellerophontaceans in prodelta slope and basin siltstones and shales deposited in up to 500 feet water depth. They speculated that these patchy basinal communities, which were dominated by gastropods, survived in these depths by feeding on plant debris channeled down submarine canyons. Interestingly, some modern pleurotomariaceans lead a similar mode of life in deep western Atlantic waters (Abbott, 1968, p. 52).

Monoplacophorans are generally so rare in Paleozoic communities that they are not even cited in paleoecological studies. Notable exceptions are species of the isostrophically coiled Ordovician genera Sinuites and Cyrtolites, which are both found in local abundance in Ordovician mollusk-dominated assemblages discussed in the following sections.

In summary, from this review it appears that Paleozoic monoplacophorans and bellerophontaceans were not uniformly nearshore algal grazers as generally assumed, but occupied a wide range of depositional environments and probably led a number of different modes of life. Most probably fed on marine algae and therefore occupied those shallow water depositional

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

environments where plant growth was most prolific. Some must have grazed on algal mats and rasped algal coatings from hard surfaces. Others, particularly those taxa characterized by small light-weight shells, dwelled within and fed upon the foliage of erect benthic algae. Those taxa occurring in deeper soft-bottom facies, as well as many of those that were so abundant in turbid delta front areas, were most likely detritus feeders and scavengers. Some taxa with disjunct coils, or other features which seem to indicate an essentially immobile existence, may have been suspension feeders. The common occurrence of bellerophontaceans in fine-grained soft-bottom facies does not lend support to Yonge's (1947) conclusion that the presumed aspidobranch gill of primitive mollusks is intolerant of turbid conditions. Bellerophontaceans thought to be too large and heavy to have been supported in algal foliage are commonly found in muddy rocks, and probably dwelled on the soft-bottoms. Many bellerophontaceans were euryhaline and were able to build large populations in such unstable environments as delta fronts, bays, and restricted lagoons. In fact, low-diversity bellerophontacean assemblages often dominate the faunas of such depositional environments, particularly in Devonian though Permian strata. However, at least in Ordovician strata, higher diversity assemblages of bellerophontaceans and monoplacophorans occur in more normal marine settings, but are much less abundant in number of specimens.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MONOPLACOPHORAN - BELLEROPHONTACEAN PALEOECOLOGY OF THE TYRONE LIMESTONE AND THE LEXINGTON LIMESTONE

The U.S. Geological Survey silicified fossil collections from the Middle Ordovician limestones of Kentucky were taken as bulk samples that were precisely located both stratigraphically and geographically. Such collections afford a potential for paleoecological analyses never before available. Previously existing collections of fossils from these strata were mostly made around the turn of the century and generally have vague locality data, which are difficult to use because of changes in stratigraphic nomenclature and geographic markers.

Of the 1,100 silicified collections made from the Ordovician strata of Kentucky and adjacent states (Pojeta, 1979), 81 samples contained approximately 2,700 specimens of recognizable taxa of monoplacophorans and bellerophontacean gastropods. In attempting to analyze the paleoenvironmental distributions of these data, it was found that mere presence-absence data in the various stratigraphic units show little of paleoecological significance (Table 3). Many taxa were distributed through numerous stratigraphic units, and therefore through many depositional environments. However, upon constructing histograms of relative abundances of taxa by percentage of the total monoplacophoran-bellerophontacean fauna in a stratigraphic unit, the dominance of certain species in different paleoenvironmental settings became obvious. Tables 5-12 display the distribution

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and relative abundance of individual species in the U.S.G.S. silicified collections from the Tyrone Limestone and the various members of the Lexington Limestone.

Tyrone Limestone

Three silicified samples from the Tyrone Limestone contained 40 specimens of monoplacophorans and bellerophontaceans. Two of these samples, each contained only a single specimen of two species Tropidodiscus cf. T. subacutus and Archinacella cf. A. simulatrix. The third sample (6034-CO) contributed 96% of the Tyrone specimens (Figure 1), and consisted of two explanate species, Salpingostoma kentuckyense and Pterotheca expansa. The low diversity of the Tyrone fauna may be partly the result of the small number of samples. The apparent abundance of the two above species might demonstrate support for Peel's (1978) hypothesis that explanate shell forms were an adaptation for soft substrates, as the Tyrone is characterized by very fine grained limestone lithologies representing mainly shallow lagoon and tidal flat environments. However, collection 6034-CO is from a shell bed within a calcarenite.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 5 : Species relative abundances in U.S.G.S. silicified samples from the Tyrone Limestone. Total number of samples = 3; total number of specimens = 40.

Species	% of fauna	No. samples
Salpingostoma kentuckyense	68	1
Pterotheca expansa	28	1
Tropidodiscus cf. T. subacutus	2	1
Archinacella cf. A. simulatrix	2	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 6 : Species relative abundances in U.S.G.S. silicified samples from the Curdsville Limestone Member of the Lexington Limestone. Total nunber of samples = 13; total number of specimens = 263.

Species	% of fauna	no. samples
Sinuites obesus	41	9
Cyrtolites cf. C. (Cyrtolites) retrorsus	24	3
Salpingostoma kentuckyense	9	2
Carinaropsis acuta	6	5
Salpingostoma sp. indet.	4	2
Pterotheca expansa	4	2
Micropileus variabilis	3	2
Sphenosphaera sp. indet.	2	2
Bucania cf. B. halli	1.5	2
Tropidodiscus sp. indet.	1.5	2
Archinacella cf. A. simulatrix	1	1
Bucania sp. indet.	1	4
Cyrtolites sp. indet.	1	2
Tetranota cf. T. obseleta	1	1
Vallatotheca cf. V. unguiformis	1	1
Pterotheca angusta	1	1
Bucania subangulata	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 7 : Species relative abundance in U.S.G.S. silicified samples from the Logana Member of the Lexington Limestone. Total number of samples = 8; total number of specimens = 534.

Species	% of fauna	No. samples
Sinuites obesus	77	6
Cyrtolites (*Cyrtolites*) *retrorsus*	11	4
Cyrtolites cf. *C.* (*C.*) *retrorsus*	11	5
Carinaropsis cymbula	1	1
Cyrtolites (*Paracyrtolites*) *subplanus*	1	1
Carinaropsis cf. *C. acuta*	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 8 : Species relative abundance in the U.S.G.S. silicified samples from the Grier Limestone Member of the Lexington Limestone. Total number of samples = 18; total number of specimens = 541.

Species	% of fauna	no. samples
Carinaropsis cymbula	25	11
Sphenosphaeara clausus	19	6
Bucanopsis carinifera	13	6
Cyrtolites (Cyrtolites) retrorsus	9	6
Sphenosphaera cf. S. burginensis	8	3
Sphenosphaera cf. S. troosti	7	3
Cyrtolites (Paracyrtolites) subplanus	4	1
Archinacella simulatrix	3	4
Bucania cf. B. nashvillensis	3	2
Bucania sp. indet.	2	4
Bucania subangulata	1	2
Cyrtolites sp. indet.	1	3
Sphenoshaera cf. S. clausus	1	2
Sphenosphaera sp. indet.	1	2
Carinaropsis sp. indet.	1	2
Bucania cf. B. sublata	1	1
Tropidodiscus sp. indet.	1	1
Sinuites sp. indet.	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 9: Species relative abundance in the U.S.G.S. silicified samples from the Peryville Limestone Member of the Lexington Limestone. Total number of samples = 5; total number of specimens = 217.

Species	% of fauna	No. samples
Sphenosphaera clausus	47	4
Bucanopsis carinifera	12	4
Bucania cf. B. sublata	7	2
Vallatotheca unguiformis	6	3
Carinaropsis cymbula	6	1
Bucania cf. B. nashvillensis	5	3
Sphenosphaera cf. S. burginensis	4	1
Sphenosphaera sp. indet.	4	2
Tropidodiscus subacutus	3	3
Cyrtolites (Cyrtolites) retrorsus	2	1
Sphenosphaera cf. S. bilineatus	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 10 : Species relative abundance in the U.S.G.S. silicified samples from the Devils Hollow Member of the Lexington Limestone. Total number of samples = 4; total number of specimens = 187.

Species	% of fauna	No. samples
Tropidodiscus subacutus	70	2
Bucania cf. *B. frankfortensis*	11	1
Bucanopsis diabloensis	7	2
Sphenosphaera sp. indet.	5	1
Tropidodiscus sp. indet.	4	2
Sphenosphaera cf. *S. clausus*	2	1
Bucania cf. *B. sublata*	1	2
Sphenosphaera clausus	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 11: Species relative abundance in the U.S.G.S. silicified samples from the Millersburg Member of the Lexington Limestone. Total number of samples = 5; total number of specimens = 80.

Species	% of fauna	No. samples
Sphenosphaera clausus	68	5
Cyrtolites (*Cyrtolites*) *retrorsus*	19	2
Archinacella sp. indet.	9	1
Cyrtolites sp. indet.	4	2
Sphenosphaera sp. indet.	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 12 : Species relative abundance in U.S.G.S. silicified samples from the Tanglewood Limestone Member of the Lexington Limestone. Total number of samples = 5; total number of specimens = 89.

Species	% of fauna	no. samples
Sphenosphaera cf. *S. clausus*	65	3
Sphenosphaera clausus	15	1
Bucanopsis carinifera	13	1
Sphenosphaera sp. indet.	5	1
Carinaropsis cymbula	1	1
Carinaropsis sp. indet.	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 13 : Species relative abundance in U.S.G.S. silicified samples from the Clays Ferry Formation. Total number of samples = 12; total numer of specimens = 419.

Species	% of fauna	No. samples
Sphenosphaera clausus	73	7
Cyrtolites (Cyrtolites) claysferryensis	16	10
Sphenosphaera cf. S. clausus	8	3
Sphenosphaera sp. indet.	2	3
Bucania rugatina	1	2
Bucania sp. indet.	1	2

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lexington Limestone

The distribution of monoplacophoran-bellerophontacean assemblages in the members of the Lexington Limestone seems to reflect three stages of faunal dominance. Different taxa groups dominate: (1) the Curdsville Limestone and Logana Members (Figures 2-3), (2) The Grier Limestone Member (Figure 4), and (3) the Upper Lexington Limestone Members and the intertongueing Clays Ferry Formation (Figures 5-9). It should be noted that these three stages are stratigraphically distributed through the lower, middle, and upper parts of the Lexington Limestone.

The lowest members of the Lexington, the Curdsville Limestone and Logana Members, were both dominated by two species, these being in decreasing order of abundance, Sinuites obesus and Cyrtolites retrorsus, with Salpingostoma kentuckyense continuing to be a common element from the Tyrone Limestone into the transgressive deposits of the lower portion of Curdsville Limestone Member (Figures 2-3). The Curdsville has a high species diversity (16 species), probably reflecting the variety of depositional environments represented within the unit, ranging from shallow transgressive bar and interbar deposits in the lower part to deeper subtidal environments in the upper part where it intertongues with the Logana Member. The three species cited above constitute 74% of the Curdsville fauna. The Logana member represents the height of the initial Lexington transgression, and may represent the deepest water environments in the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

formation. Although the Logana is a much more homogeneous lithologic unit of deeper water origin than the Curdsville Limestone, it is dominated by two of the same species. Sinuites obesus makes up 77% of the low diversity Logana fauna, and occurs in six of eight silicified samples. The Cyrtolites retrorsus group makes up 22% of the Logana fauna (Figure 3). It is noteworthy that the monoplacophoran-bellerophontacean fauna of the Edenian Kope Formation, which consists of relatively deep water shales at the base of the Cincinnatian Series, is also dominated by species of Sinuites and Cyrtolites. The Logana fauna is low in diversity, having only 5 species in 3 genera, and 3 of those species accounting for only about 1% of the fauna.

The Grier Limestone Member represents the most enduring, widespread, and uniform environmental conditions during Lexington deposition. It smonoplacophoran-bellerophontacean fauna is somewhat transitional in its composition, and its moderately high diversity (16 species) and its even distribution of species relative abundances (Figure 4) apparently reflect the stability of the Grier environment. The nodular wackestones of the Grier indicate a soft bottom environment with shell beds, and the abundance and variety of a normal marine fauna indicate a very favorable habitat. The three dominant molluscan univalve species in the Grier are, in descending order of abundance, Carinaropsis cymbula (25%), Sphenosphaera clausus (19%), and Bucanopsis carinifera (13%). All have rapidly expanding shell forms, but only the first can be truely considered expla-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

nate. The abundance of morphotypes with broadly expanded apertures is comparable to Peel's (1977, 1978) soft-bottom shallow marine platform fauna from the Silurian Arisaig Group discussed above. It should be noted that the intrageneric species diversities are higher than any other member of the Lexington Limestone. Cyrtolites, Bucania, and Sphenosphaera all have more than one species in the Grier, probably attesting to environmental stability and greater partitioning of niches.

The Upper Lexington Limestone is a complex facies mosaic of interfingering carbonate depositional environments which intertongues upward with the more shaly deposits of the Clays Ferry Formation. Except for the Devils Hollow Member, all members of the Upper Lexington Limestone, as well as the intertongueing Clays Ferry Formation, are dominated by Sphenosphaera clausus, with species of Bucanopsis, Cyrtolites, and Carinaropsis distributed throughout. Whereas the Sphenosphaera clausus group makes up nearly 70% of the Upper Lexington monoplacophoran-bellerophontacean fauna, it is nearly absent in the Devils Hollow Member, which is dominated by 70% Tropidodiscus subacutus, a species that is rare in the other members. This discrepancy might be explained by the small number of samples from the Devils Hollow Member. Only one sample accounts for the apparent dominance by T. subacutus in the unit, but if this sample is ignored, Sphenosphaera spp. is still subordinate to other species in the Devils Hollow. Cressman (1973, p. 41) suggested that the Devils Hollow represented very shallow restricted lagoon and bar deposits. Most other Upper Lexington

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

members represent more normal shallow marine conditions, possibly accounting for the faunal differences.

The marked dominance of Sphenosphaera clausus through such varied depositional environments as the Perryville Limestone, Millersburg, and Tanglewood Limestone Members of the Upper Lexington Limestone, as well as the relatively shale-rich Clays Ferry Formation, is difficult to explain. It can only be assumed that there was some unifying environmental factor, such as a food source, in these varied environments which allowed the species to flourish during this period of time. In any case, S. clausus must have been somewhat of an ecological generalist. Possibly when the paleosynecology of the entire Lexington fauna is analyzed, explanations for the distribution of individual taxa will become more clear. It is interesting that while most of the members in the Upper Lexington Limestone are moderately shallow water facies and would seem to be adequate habitats for symmetrical molluscan univalves, diversities are generally relatively low. The Perryville Limestone Member is most diverse with 10 species; next is the Devil's Hollow Member with 7 species. The Millersburg and Tanglewood Limestone Members, as well as the Clays Ferry Formation, have only 3 species each. The Millersburg, which is similar to the Grier Limestone Member in lithology, bedding style, and overall fauna (Cressman, 1973, p. 43), would especially be expected to have a more diverse fauna. This apparent anomaly can probably be explained by there being only 5 samples from the Millersburg and 18 samples from the Grier Limestone Member.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

COMMENTS ON THE PALEOECOLOGY OF THE STONES RIVER GROUP OF CENTRAL TENNESSEE

The monoplacophorans and bellerophontaceans from the Blackriveran-Rocklandian-aged Stones River Group of Central Tennessee are listed in Table 1. Data are derived from Wilson (1949) and museum specimens examined in the present study. No relative abundance data or any other significant paleoecological data are available on the fauna, and except for a few observations made below, the present data do not permit any detailed analysis.

The apparent low diversity of the Stones River fauna may be the result of a scarcity of collections. Only four genera and seven species are known (Table 1). However, the Blackriveran-Rocklandian-aged Stones River and High Bridge Groups both represent shallow subtidal-intertidal environmens that are generally conceived as ideal habitats for the animals under discussion, and the low diversity assemblages might truly reflect a paucity of species during that time.

Tetranota bidorsata is distributed throughout the Stones River Group. Pterotheca expansa and Pterothetca saffordi both occur in thin-bedded limestones in association with abundant leperditicopid ostracodes, suggesting that these species were adapted to tidal flat and restricted lagoonal environments (Pl. 39, figs. 5, 12, 13; pl. 40, figs. 8-9). Such occurrences are also known from the correlative Tyrone Limestone of Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

COMMENTS ON THE PALEOECOLOGY OF THE NASHVILLE GROUP IN CENTRAL TENNESSEE

The occurrences of monoplacophoran and bellerophontacean taxa in the Nashville Group are listed in Table 2. Data are from museum specimens examined in this study and from faunal lists by Wilson (1949). No relative abundance data are available.

Hermitage Formation

The monoplacophoran-bellerophontacean fauna of the Hermitage Formation is apparently of low diversity and abundance. Wilson (1949) reported species from only two members, Phragmolites cellulosum from the Curdsville Member, and that species with Cyrtolites retrorsus in the "Ctenodonta Member". Other species identified from museum collections in this study were Archinacella valida and Undulabucania punctifrons. Museum labels on these specimens do not allow more precise placement within the members of the formation. One noteworthy point is that both of the above species listed by Wilson (1949) were reported from the two shallowest subtidal facies of the Hermitage Formation.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bigby-Canon Limestone

It is unfortunate that presently only presence-absence data are available on species of the Bigby-Canon Limestone. That formation seems to be an ideal unit for paleoecological analysis, consisting of a high-energy subtidal shoaling facies (Bigby facies), a low-energy shelf lagoon facies (Cannon facies), and a restricted lagoon--tidal flat facies (Dove-colored facies). Nevertheless, some trends are discernible. Table 2 shows the distribution of monoplacophoran-bellerophontacean taxa in these three facies, as well as in the overlying Catheys Formation. Data are derived from both Wilson's (1949) species lists and specimens found in museum collections during the present study.

The Cannon facies contain 10 monoplacophoran-bellerophontacean species, twice the number reported from either of othe other facies. Alberstadt (1973, p. 630) cited preliminary work that found most Cannon communities were dominated by bellerophontid and lophospirid gastropods and leperditicopid ostracodes. He suggested that the dark organic-rich muddy wackestone-packstones of the Cannon indicate quiet, nearly stagnant lagoonal conditions. Alberstadt (1973, p. 626) attributed much of the organic material in the Cannon to marine algae. Blue-green algal encrustations are common, but the rock also contains an appreciable amount of crushed, dark orange and brown fragments of unidentifiable organic fossils apparently of algal origin. On such fragment illustrated by Alberstadt

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(1973, fig. 5D) resembles a small plumose growth of blue-green algae. It seems likely that the abundant gastropods and other fauna lived above the fetid mud bottom on such algal masses. Considering the moderately large shells of some of the Cannon bellerophontaceans (e.g., Bucania sp. and Sphenosphaera spp.), if the animals were indeed algal foliage-dwellers, the algae may have formed low thick bushes ormats capable of supporting their weight. It seems the algae would have not only been a food source for the gastropods, but possibly would have baffled and stabilized the muddy sediment, effectively reducing the turbidity. If the Cannon bellerophontaceans were not algal foliage-dwellers, they must have been able to cope with muddy substrate conditions much better than predicted by Yonge (1947) and others. In fact, the abundance of bellerophontaceans in such organic-rich fine sediments might lend support to the interpretation that they were bottom-dwelling detritus feeders and scavengers.

Each facies of the Bigby-Cannon Limestone contains a variety of general bellerophontacean morphotypes, and without relative abundance data no patterns are obvious. The high-energy shoals of the Bigby facies and the lagoonal-tidal flat muds of the Dove-colored facies each supported five monoplacophoran-bellerophontacean species, three of which are common to both facies. Four of the species in the Dove-colored facies are also found in the Cannon facies, but only two of the five Bigby species also occur in the Cannon.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

COMMENTS ON THE PALEOECOLOGY OF UPPER ORDOVICIAN FAUNAS

Data on the paleoecology of the molluscan univalve taxa in the Upper Ordovician of the tri-state area are scant. Previous paleoecological studies have focused on the prolific brachiopod and bryozoan faunas of these strata, and gastropods are generally mentioned only as a general grouping (Fox, 1962, 1968; Hatfield, 1968; Richards, 1972; Richards and Bambach, 1975; Harris and Martin, 1979). Mollusks are usually abundant only in sparse mollusk-rich beds scattered through the section. Pojeta (1971) has discussed the autecology of Upper Ordovician pelecypods, but the synecology and environmental distributions of the entire molluscan communities remain unstudied.

Silicified beds and fossils are uncommon in the Upper Ordovician of the tri-state area, and only a few collections were made by the U.S. Geological Survey. Most specimens examined here were from existing museum collections. The current data base does not allow detailed paleoecological analysis. The U.S.G.S silicified samples from the Liberty biofacies of the Dillsboro Formation (Richmondian) of southeastern Indiana (6139-CO, 6140-CO) were the only Upper Ordovician U.S.G.S. collections containing abundant well-preserved specimens. These samples contained specimens of Cyrtolites hornyi, Sphenosphaeramohri, and Archinacella indianensis. The only other common genera in Upper Ordovician rocks of the area are Sinuites and Salpingostoma.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 14 : Species relative abundance in U.S.G.S. silicified samples from the Dillsboro Formation of Indiana. Total number of samples = 2; total number of specimens = 337.

Species	% of fauna	No. samples
Sphenosphaera mohri	74	2
Cyrtolites (Cyrtolites) hornyi	13	1
Archinacella indianensis	12	1
Bellerophontacean sp. indet.	1	1

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

By far the most abundant taxa in the Cincinnatian section are species of Sinuites and Cyrtolites. Specimens of these two genera are locally abundant in mollusk-dominated beds, often occurring together, but one or the other generally clearly dominant. Such mollusk beds are generally thin limestone beds or lenses in interbedded limestone and shale sections. Adjacent strata are commonly dominated by brachiopod-bryozoan assemblages. The mollusk beds are generally considered to represent special environmental conditions, such as nearshore areas with abnormal marine salinities, but at present there are few sedimentological data to support such interpretations. Before interpretations can be made with confidence, detailed sedimentological and paleoecological analyses are needed of thick stratigraphic sections. One such section is Locality KY-1, near Carrollton, Kentucky, where the well-exposed Kope Formation contains a number of such isolated mollusk beds. The small slab shown in Plate 8, Figure 20, is from this locality, and demonstrates the diversity of mollusks that can be contained in such beds.

At locality OH-1 (Bear Creek Quarry), an argillaceous mollusk-rich limestone lens surrounded by gray shale was found in the lower Kope Formation, about 10 feet above the Point Pleasant member of the Clays Ferry Formation. This small lens was only a few feet across and about 3 inches maximum thickness. The surrounding shales and overlying and underlying limestone beds were dominated by trilobite-crinoid-brachiopod assemblages. Excavation of about 4 square feet of the lens produced over 100 well-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

preserved specimens of Sinuites planodorsata, five specimens of Tetranota bidorsata, one specimen of Cyrtolites claysferryensis, and sparse othoconic nautiloids, lingulid brachiopods, small loxonometacean gastropods, crinoid ossicles and Cryptolithus trilobite fragments (Pl. 4, fig. 17; Pl. 21, fig. 1). This great concentration of symmetrical molluscan univalves is puzzling, as the surrounding strata are apparently barren of the taxa, but mostly likely it can be attributed to a localized food source. Petrographic analysis has not yielded any significant clues as to the nature of this possible food source. Another possible interpretation is that the molluscs were not the feeders, but rather the meal. Could such a concentration of shells be the "nest" of predatory nautiloids? It should be noted that the monoplacophoran and bellerophontacean shells were exceedingly well-preserved and showed no breakage. But then there is no evidence for the presence of an operculum in these early forms which would have required forced entry by predators. Other such occurrences should be watched for in hopes that clues to their origin might be found.

A third field occurrence, from the Clays Ferry Formation of north-central Kentucky, was a mollusk bed dominated by Cyrtolites claysferryensis with lophospirid gastropods and sparse pelecypods (Pl. 4, figs. 15-16). Of particular interest is a specimen of C. (Cyrtolites) claysferryensis with an apparent borehole through its dorsum (Pl. 4, fig. 15). Fenton and Fenton (1931), Carriker and Yochelson (1968), and Sohl (1969) have reviewed the occurrence of Paleozoic borings, which are most common

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in brachiopods in the Upper Ordovician. Although Fenton and Fenton (1931) and most other early authors assumed these borings were made by predatory gastropods, the reviews of the more recent authors have concluded that there is little evidence to support this contention. Sohl (1969) believed that the predatory boring habit common to many recent snails did not arise until Late Cretaceous time. He further agreed with Carriker and Yochelson (1968) that Paleozoic borers were probably mainly unknown soft-bodied organisms, which employed a purely chemical means of boring. The boring shown here is believed to be the first reported in a shell of a monoplacophoran. It is interesting that this boring is in the approximate position of the shell muscles.

The possible sources of nutrition and modes of feeding for primitive gastropods and monoplacophorans were discussed above, and it was stressed that evidence in the fossil record is scarce indeed. However, a possible approach is to draw conclusions from repeated associations. For example, the repeated occurrence of species of Pterotheca with leperditid ostracods in restricted lagoonal to intertidal environments in the Stones River and High Bridge Groups might be brought to bear as evidence for an algal grazing habit (Pl. 30, figs. 3-5, 12, 13; Pl. 40, figs. 8-9).

Another association which has been repeatedly observed in Upper Ordovician strata is the occurrence of species of Phragmolites with small stick-like bryozoans. Phragmolites was never observed in mollusk beds, but was seen only in predominantly bryozoan-brachiopod assemblages. P.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

dyeri is shown on Pl. 45, fig. 11, with abundant stick-like bryozoans. And specimens in the original type suite of P. elegans (Pl. 45, fig. 10) are preserved with aperture attached to stick-like bryozoans. The evidence is far from conclusive, but it is suggested that Phragmolites may have grazed on these bryozoans. Surely, the shells of most species of Phragmolites are small and thin enough to have been supported in bryozoan thickets. Note also the specimen of the related species Undulabucania punctifrons preserved with its aperture clamped over a massive bryozoan colony (Pl. 23, figs. 2-3).

Sphenosphaeramohri and Salpingostoma richmondensis have been observed in the rubbly, higher-energy deposits in the Richmondian-aged Whitewater Formation of southeastern Indiana. These relatively large massive-shelled species are commonly associated with massive bryozoans and brachiopods in transported shell debris deposits, where much of the skeletal material is broken and worn. S. mohri is commonly found encrusted by massive bryozoans. Apparently these taxa inhabited higher energy environments either on or surrounding shoaling areas.

SHELL SCULPTURING AND ENCRUSTATION AS DEFENSES AGAINST PREDATION

As noted, in the Systematic Paleontology section under the appropriate ate species' shell sculpturing might be an adaptation for camoul-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

flage against predators. Most notable examples are the reticulate patterns on the shells of species of C. (Cyrtolites) (Pls. 4-7), and the fine wavy patterns on the shells of species of Undulabucania (Pl. 23, figs. 1-15).

Of even greater advantage for camouflage is encrustation by epizoans. Carrier shells (gastropods which cement skeletal debris to their surface for camouflage) are known from the Devonian (Linsley and Yochelson, 1973) to the Recent. McNamara (1978) has discussed the encrustation of Late Ordovician gastropods by bryozoans, and suggested a symbiotic relationship. The gastropod was afforded protection from predators, while the bryozoan benefitted by having a perch from which to suspension feed. Benefit to the bryozoan was enhanced by currents created by movement of the gastropod, as well as by the movement of currents through the shell of the gastropod itself.

Bryozoan-encrusted shell debris of all kinds abounds in many Upper Ordovician beds of the tri-state area, and is usually easily attributable to post-postem encrustation. Many of the shells illustrated on the plates here have bryozoan encrustations. By virtue of the positions of the encrustations on the shells, or their extremely massive character, most of these encrustations obviously took place on dead shells (Pl. 1, figs. 9-11; Pl. 30, fig. 10; Pl. 32, figs. 6-9; Pl. 37, Figs. 18-19; Pl. 41, figs. 4-5; Pl. 34, figs. 4, 6). However, other encrustations thinly cover both sides of a coiled shell, but not the outer aperture lip.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Such cases are particularly common in species of Cyrtolites (Pl. 6, figs. 1, 12-13, 14-16; Pl. 7, figs. 5-7). Morris and Rollins (1971, Figs. 4-5) illustrated another such specimen of Cyrtolites cf. C. ornatus that is completely encrusted by bryozoans, but also has further encrustation by Cornulites worm tubes. Of particular significance is the symmetrical attachment of these Cornulites on the upper umbilical regions of both sides of the shell, and the mutual adapertural orientation of the worm tubes. This occurrence is strong evidence for encrustation of the Cyrtolites shell while still occupied by a living animal. These encrustations would not only serve to camoulflage the shell, but also would strengthen it against crushing, and thicken it so as to make entry by drilling more difficult. We do not know of any Ordovician predators capable of crushing shells, as do modern crabs (Vermeij, 1978), but the borehole in a shell of C. (Cyrtolites) claysferryensis (Pl. 4, fig. 15) demonstrates the presence of drilling predators.

Signor and Brett (1984) have proposed that bellerophontaceans and other invertebrate groups showed an increase in the frequency of predation-resistant morphologic features during the mid-Paleozoic in response to the rapid radiation of durophagous (shell-crushing) predators (primarily crustaceans and fishes). They pointed out that among mid-Paleozoic bellerophontaceans, there is a decrease in the frequency of phaneromphalous genera and an increase in the frequency of genera with sculptured shells. Vermeij (1975, 1978) has demonstrated that modern gas-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tropods with phaneromphalous shells or unsculptured shells are more susceptible to durophagous predation. It should be noted that a trend toward reduction of the umbilicus in Ordovician bellerophontaceans is thought here to have facilitated the transport of the bellerophontiform shell, but apparently this more mobile shell form was also preadapted to deal with later durophagous predators (see Functional Morphology section).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

FUNCTIONAL MORPHOLOGY

INTRODUCTION

The primary functions of the shell in molluscan univalves is to house and protect the animal from the dangers of its external environment and to provide sites for muscle attachment. The ancestral monoplacophoran univalve is generally assumed to have had a simple low conical shell reflecting the form of the animal's visceral hump (Stasek, 1972). As evolution progressed and the visceral mass and its containing shell enlarged and became more elongate, the shell coiled in order to maintain balance. The factors which seem to have had the greatest control over coiled shell morphology are the balancing of the shell itself, and the efficient channelling of water currents through the shell for respiration and sometimes feeding.

In a symmetrically coiled monoplacophoran, which has not undergone the larval process of torsion, the head of the animal is under the coil (exogastric). In a symmetrically coiled bellerophontacean gastropod, which has undergone torsion, the head is toward the outer apertural margin, and the shell coils posteriorly away from the head (endogastric). These opposite orientations should be reflected in the functional aspects of shell morphology. Herein, morphological evidence for each orientation in bellerophontiform shells is discussed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Raup (1966) presented four parameters which can be used in the description and functional analysis of coiled shells: the shape of the generating curve (whorl shape), the rate of whorl expansion (W), the distance of the generating curve from the axis (D), and the movement of the generating curve along the axis (whorl translation = T). In planispiral shells T always equals zero. Raup (1967, text-fig. 3), illustrated cephalopod shell forms under a continuum of varying W and D values. This approach is also useful in picturing the effects of these parameters on bellerophontacean-monoplacophoran shell forms. These W and D values are referred to repeatedly in the following functional analyses.

MONOPLACOPHORA

Tryblidiida

The shells of monoplacophorans of the order Tryblidiida grade from cap-shaped to conical in form, and are generally considered more primitive morphotypes than the coiled shells of the Cyrtonellida. However, Pojeta and Runnegar (1976, p. 29) pointed out that relatively tall shells are the first to appear in the Tommotian fossil record, and the limpet-shaped shells seem to have developed from them. They suggested that the limpet-form shells may not represent the ancestral stock, but rather were secondarily adapted for benthic grazing. Indeed, the morphological similari-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ties of the typical cap-shaped tryblidiid shell and that of the patelliform gastropods, which are secondarily adapted for clinging and grazing, suggest a common mode of life for the two groups. In fact, Lowenstam (1978, p. 231) has reported the modern monoplacophoran Vema clinging to phosphorite nodules in dredge samples and noted a nearly stationary existence for the animals under a month of laboratory observation. On the other hand, Lemche and Wingstrand (1959, p. 63) cited Neopilina, whose shell is essentially identical to that of Vema, as a deposit feeder from abyssal dark muddy sediment where they claimed there was an absence of suitable hard substrata for clinging. It remains uncertain whether the monoplacophoran cap-shaped shell is adapted secondarily to a clinging mode of life, like that of the patellacean gastropods, or if it simply reflects the primitive condition. The latter possibility is favored here.

The common encrustation of many Ordovician tryblidiid shells by bryozoans suggests that the animals led an exposed life, such as that of an algal grazer, rather than the often partially covered life of a bottom-dwelling deposit-feeder. Furthermore, the highly sculptured shells of some genera, such as Helcionopsis (Pl. 2, figs. 1-3) and Vallatotheca (Pl. 1, figs. 8-31), seem to speak against a deposit-feeding habit. Vermeij (1978, p. 33) pointed out that gastropods living under wave-energy stress generally have lower shells, often with smoother surfaces, and a relatively larger aperture and foot than those animals living in more sheltered surroundings. These observations probably also hold true for

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Paleozoic monoplacophorans occurring in shallow water habitats. However, detailed paleoecological data on the distributions of tryblidiid taxa are presently insufficient to test this prediction.

Through the studies on the anatomy of Neopilina galathaea by Lemche and Wingstrand (1959), tryblidiid monoplacophorans are known to have a poorly developed head, and to have numerous pedal muscles and 5 or 6 pairs of gills distributed around the lateral and postero-lateral shell margins. Pojeta and Runnegar (1976, Fig. 10) confidently adapted this morphology to the Cambrian genus Scenella. They traced the probable path of water flow through the shell as entering anterolaterally, running along the lateral mantle cavity and exiting posterolaterally (Figure 14). In side view, the lateral margins of Ordovician trybilidiid shells can be straight (Pl. 2, figs. 3, 7, 20), convex (Pl. 1, figs. 27-28), or concave (Pl. 3, figs. 9, 22). It seems likely that these different lateral aperture margin profiles were designed to channel currents more efficiently through the mantle cavity. However, presently it is impossible to say what significance these different lateral aperture profiles had to possibly varied modes of life.

Cyrtonellida

The Cyrtonellida is generally believed to be the more advanced of the two monoplacophoran orders. Because of the mechanical requirements of a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

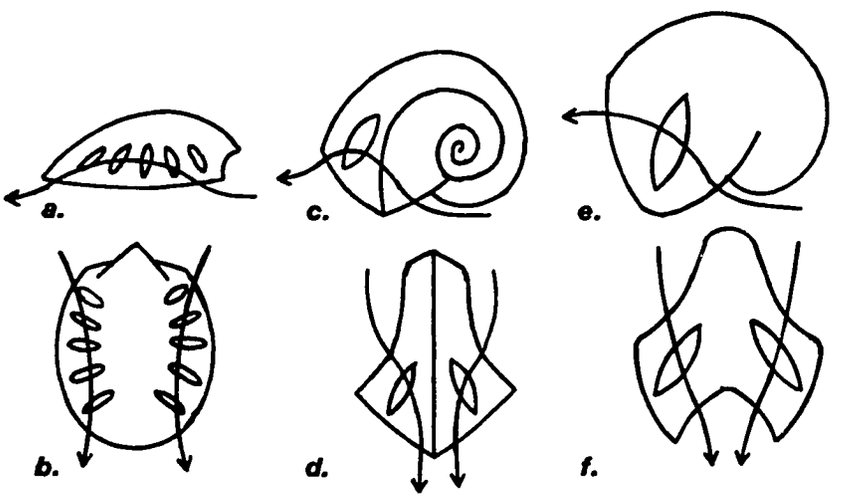


Figure 14: Paths of water currents through the shells and mantle cavities of monoplacophorans.
a-b.) Dorsal and right-lateral views of a tryblidiid, which has multiple pairs of gills in a lateral to postero-lateral mantle cavity.
c-d.) Right-lateral and dorsal views of Cyrtolites, which has a single pair of gills in a posterior mantle cavity. Water currents enter around the lateral angulations of the diamond-shaped aperture and exit through the dorsal angulation, which is sinuate in some species.
e-f.) Right-lateral and dorsal views of Sinuites, which has a single pair of gills in a posterior mantle cavity. Water currents enter through apertural reentrants in the lobate aperture and exit through a deep dorsal sinus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

coiled shell, the isostrophic cyrtonellids possessed a smaller number of muscle scars than the tryblidiids. These scars typically form anterior, posterior, and lateral pairs arranged in a ring well up within the aperture (Rollins, 1969). Stasek (1972, p. 21) proposed that this migration of the muscle insertions deeper into the shell suggests the concomitant development of a larger posterior mantle cavity and the ability of the animal to draw into it. Peel (1980) also suggested that circumumbilical muscle attachment in sinuitids represents the ability to retract into the shell and reflects a monoplacophoran morphological grade which may have first undergone torsion. Stasek (1972) further claimed that the enlarged mantle cavity was accompanied by a reduction in the number of the gills, but an increase in their size. Finally, Stasek claimed that the steep anterior slope of the coiled shell might indicate the development of a distinct head in the organisms.

Such anatomical modifications could explain the success of the cyrtonellid genera Cyrtolites and Sinuites during the Middle and Late Ordovician. Features of the shell morphology of these two successful Ordovician genera demonstrate adaptations in the exogastric shell for more efficient water flow through the mantle cavity. Linsley (1978) pointed out that the obstruction of anterior inhalent passages into the shell by the coil and the fleshy stalk leading from the foot to the visceral mass necessitated that the inhalent ducts to the posterior mantle cavity would be concentrated laterally. Typically, species of Cyrtolites have diamond-shaped

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

apertures (Pl. 5, figs. 11, 14; Pl. 8, figs. 1, 5, 8; Figure 14). Starabogatov (1970, p. 295) and Linsley (1978, p. 437) have interpreted the lateral angulations of these apertures as inhalent canals, and the dorsal angulation, which is sinuate in Middle Ordovician species of Cyrtolites, as the exhalent canal. It should be noted that not all species of Cyrtolites have such angulated apertures. C. (Cyrtolites) retrorsus shows a complete gradational series in aperture outlines from diamond-shaped to nearly circular (Pl. 5, figs. 3, 5, 8, 11, 14, 18, 22). However, the marked lateral angulations of the apertures in C. (C.) claysferryensis (Pl. 8, figs. 11, 15) and C. (P.) carinatus (Pl. 7, figs. 18-25), which occupied the clay-rich environments of the Clays Ferry and Kope Formations, might indicate the necessity for more efficient channelling of currents, and thereby support Linsley's conclusions.

Starabogotov (1970, p. 295) noted grooves along the sides of the final whorl in the Devonian cyrtonellid Sinuitopsis that he interpreted as inhalent channels, with the posterior sinus acting as an exhalent canal. He claimed that the narrow streams of water which would be channelled through these lateral grooves into the posterior mantle cavity could probably bathe only one pair of posterolateral gills efficiently. This sinuitid hydrodynamic design is also demonstrated well by Ordovician species of Sinuites illustrated here (Figure 14). Water would be drawn into the shell anterolaterally through umbilical re-entrants along the inner apertural margin (Figure Pl. 9, figs. 3-4, 12; Pl. 11, figs. 3, 7, 9).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

After passing over the gills, the deoxygenated water and waste products would be expelled through the posterior apertural sinus (Figure; Pl. 9, figs. 1-2, 6, 10-11). The lateral apertural lobes of Sinuites, which project downward to varying degrees in different species, probably protected the single pair of large gills. Possibly these lobes could have also acted as struts, supporting the shell while the animal was inactive, yet still allowing the movement of water through the shell. Such supportive struts are known in the shells of living and fossil gastropods (Linsley, Yochelson, and Rohr, 1978).

Although the aperture margins of the above two genera have been modified for the same purpose, the general shell morphologies of Sinuites and Cyrtolites are quite different. Species of Cyrtolites are loosely coiled and widely umbilicate (Pl. 5, figs. 6, 9, 12; Pl. 6, figs. 1, 6, 18) (high D value of Raup, 1966), and even become disjunctly coiled in C. (C.) disjunctus (Pl. 6, figs. 19-22). The plane of the aperture in Cyrtolites is tangential to the coil, enabling the animal to clamp down onto hard substrata. Middle Ordovician species, such as C. (C.) retrorsus, had a shallow apertural sinus that would have prevented a complete seal around the clamped aperture, but would have enabled more efficient expulsion of water from the mantle cavity (Pl. 5, figs. 7, 13). This apertural sinus was lost in Late Ordovician species, such as C. (C.) ornatus (Pl. 6, figs. 7, 10), so that the entire aperture margin was in the same plane, and the clamped shell would be more completely sealed off. Perhaps such

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

protection was of more benefit to the survival of species of Cyrtolites than the sinus and its exhalent function.

On the other hand, species of Sinuites have more tightly coiled shells (Pl. 9, figs. 4, 8; Pl. 11, figs. 3, 8) (low D value), which are nonumbilicate, or nearly so, have rounded whorls, and have very irregular aperture margins. As discussed above, the inhalent umbilical re-entrants, the jutting posterolateral lobes, and the pronounced posteromedian sinus (Pl. 11, figs. 6-11) are all clear adaptations for efficient channelling of water through the shell, but such irregularities of the apertural margin would surely preclude efficient clamping on firm substrates. In the faunas studied here, species of Sinuites are most common and diverse from deeper water muddy environments of the Logana Member of the Lexington Limestone and the Kope Formation. Living in these soft-substrate environments must have made efficient channelling of water through the shell (in order to prevent fouling of the bipectinate gills by fine sediment) more important to survival than the ability to clamp down. Also, the tightly coiled shell of Sinuites most likely indicates a more vagrant mode of life than in Cyrtolites. Of possible significance to this point is the fact that specimens of Cyrtolites are commonly encrusted by epizoans, whereas specimens of Sinuites are rarely encrusted.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BELLEROPHONTACEAN GASTROPODA

Shell Coiling

Linsley (1977, 1978) capably discussed the benefits and problems resultant from the coiling of the shell in the Gastropoda. Shell coiling lowers the center of gravity and the pressure point, reduces the total surface area of the shell subject to fluid drag, reduces the shearing effect, and thus reduces the energy necessary to move the shell forward. In other words, shell coiling enables the animal to be more mobile, which has obvious advantages in feeding and self-protection.

The anisostrophically coiled shell, such as possessed by the vast majority of gastropods, is naturally imbalanced. Shell balance must be restored by positioning the center of gravity over the midline of the foot (Linsley, 1977). This is done through the tipping up of the shell (inclination) and the twisting of the coil toward the rear so that torsion is effectively reduced (regulatory detorsion). On the other hand, the isostropically coiled gastropod shell, such as possessed by a bellerophontacean, is naturally balanced. Its axis of coiling is parallel to the substrate and its center of gravity is positioned over the midline of the foot automatically. Nevertheless, a loosely coiled isostrophic shell can also be difficult to balance, as it affords broad areas of resistance from all sides. Just as in an anisostrophically coiled form, a loose coil hin-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ders movement, makes the animal more prone to predation, and probably restricts it to either algal grazing or sedentary suspension feeding in a quiet water environment. Bellerophontaceans adopted three adaptive strategies to reduce resistance of their planispiral shells to movement and/or currents: (1) lateral compression of the whorl shape; (2) a tightening of the coiling radius (decrease in D), which increased whorl overlap and reduced the size of the umbilicus; and (3) an increase in the rate of whorl expansion (W) (Linsley, 1977).

In the early evolution of the Bellerophontacea, there is a clear trend from primitive loose shell coiling toward tighter shell coiling (decrease in D value) or reduction of the coil altogether (Figure 15). All of the earliest bellerophontaceans are loosely coiled (high D value). The Upper Cambrian Chalarostrepsis is actually disjunctly coiled in adulthood (see Knight and others, 1960, Fig. 94). Yochelson (1971) and Peel (1975) have interpreted disjunct coiling in gastropods as representing a sedentary suspension feeding mode of life. The descendents of Chalarostrepsis, the Ordovician genera Tropidodiscus (Pl. 41, figs. 6-13) and Phragmolites (Pl. 44, figs. 1, 5, 8), have loose but contiguous coils, leaving a wide open umbilicus. Their laterally compressed shells are generally thin and light, probably in order to make balancing easier. These forms must have inhabited only quiet water areas (Linsley, 1978) and were probably algal grazers or algal foliage-dwellers.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The progressive trend toward tighter coiling is exemplified within the genus Bucania (Figure 15). The earliest appearing and more morphologically primitive members of the genus, those species in Ulrich and Scofield's (1897) B. sulcatina group (Pl. 12, figs. 1-9), possess wide umbilici (high D values) and deep narrow slits like the tropidodiscids, but have broad depressed whorls (with low W values). Members of the new genus Undulabucania (Pl. 23, figs. 1-15) are of the same morphological grade. From this level, there is a complete morphological gradation within the genus Bucania to the more advanced B. nashvillensis group (Pl. 14, figs. 1-12), which is characterized by tighter coiling (lower D values), smaller umbilici, longer apertures (higher W values), more rounded whorls, and often thicker shells. These features lowered the center of gravity of the shell, reduced its surface area, and streamlined its form, thus making it easier to balance and transport. The thickening of the shell suggests migration of some specimens into new higher energy environments. The lengthening of the aperture and presumably the foot, indicate a trend toward faster movement. And the rounding of the whorls served to streamline the shell, reducing resistance against movement. These modifications apparently demonstrate an increase in the mobility of species of Bucania during the Middle Ordovician. The broad bulky shells of the B. sulcatina group probably represent sluggish grazers. The more compact and streamlined shells of the B. nashvillensis group must have allowed a greater variety of life habits. Most species of both of these groups have moder-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 15: Morphological and corresponding ecological trends in Middle Ordovician bellerophontaceans. Five general levels of development are recognized.

Level 1 - a,b: Left-lateral and ventral views of Bucania sulcatina. Typical of this level of development are a wide open umbilicus and a deep labral slit as much as a half whorl deep. Species of Bucania and Undulabucania in this group have broad depressed whorl forms, but the tropidodiscids, most of which have high narrow laterally-compressed whorl forms, also belong in this group. Probably sluggish vagrant benthos.

Level 2 - c,d: Left-lateral and ventral views of Bucania nashvillensis. Note the increase in the rate whorl expansion (W), the decrease in the coiling radius (D), the lengthening of the whorl form, and the shortening of the labral slit. Similar shell forms such as those of Tetranota bidorsata would also belong to this group. Moderately mobile vagrant benthos.

Level 3 - e,f,g: Left-lateral, antero-dorsal, and ventral views of Spheno-sphaera clausus. Note the closing of the umbilicus through continued increase in the rate of whorl expansion (W) and decrease in the radius of coiling (D). Note also the increase in the flairing of the aperture lips and the incipient outbuilding of an inner aperture platform. Species of Bellerophon and Bucanopsis also belong to this group, which is thought to be the most mobile of the Ordovician bellerophonataceans.

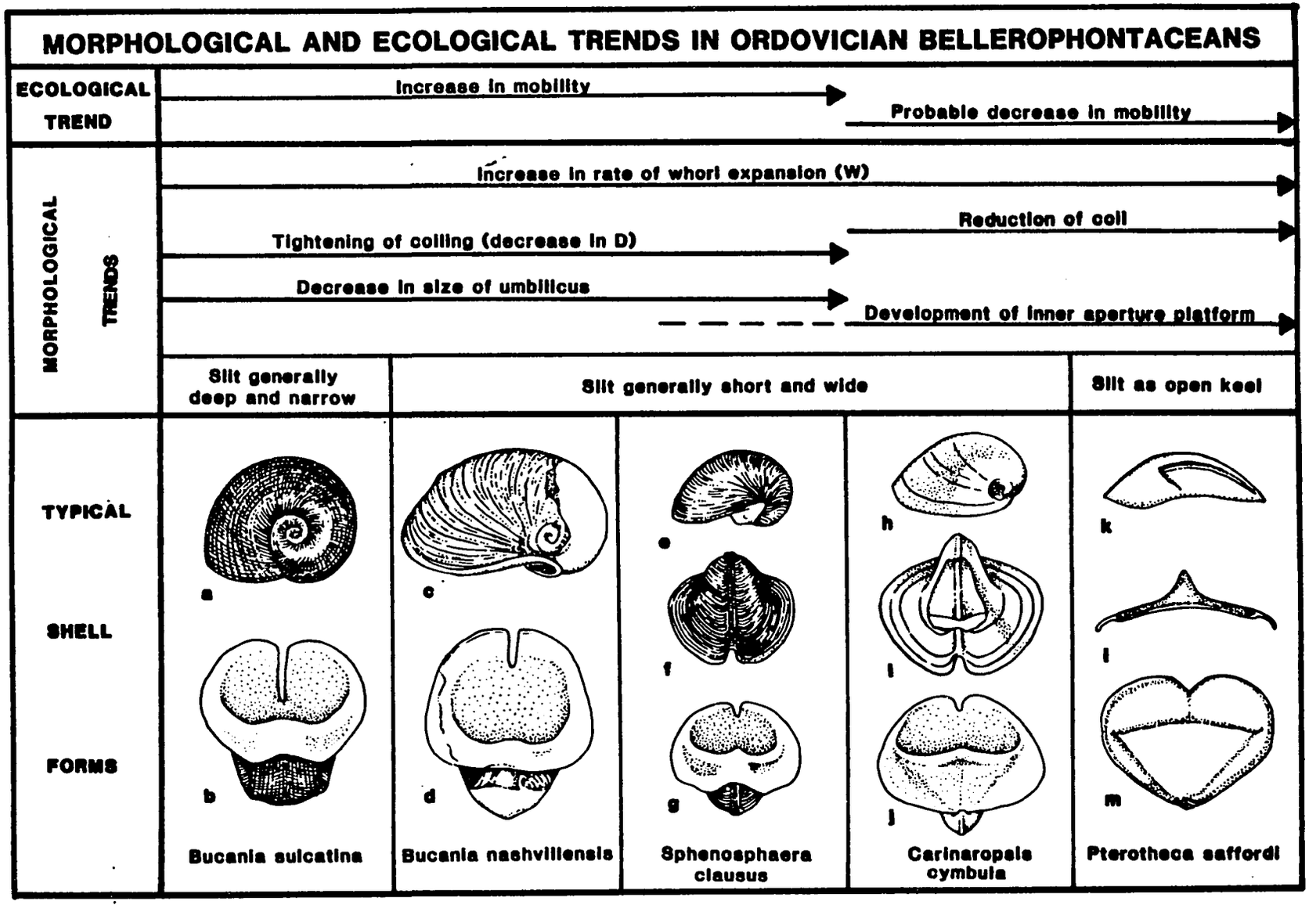
Level 4 - h,i,j: Left-lateral, antero-dorsal (with dorsum partly cut-out to show apertural platform), and ventral views of Carinaropsis cymbula. At this level the rate of whorl expansion has increased to the point where the coil is nearly completely reduced in the adult animal. Because the coil can no longer support the visceral mass in the adult animal, and inner apertural platform was developed to serve that function. Probably sluggish vagrant benthos.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 15 (continued):
Level 5 - k,l,m: Left-lateral cross-sectional, transverse cross-sectional, and ventral views of Pterotheca saffordi. At this specialized level of development, the coil is completely reduced, and the apertural platform grows to cover approximately two-thirds of the aperture. These were probably very sluggish, nearly sedentary animals.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



ately large to large shells, and must represent bottom-dwelling animals. Bucania micronema (Pl. 19, figs. 1-6) may have been small and light-weight enough to have been an algal foliage-dweller.

This progression was taken still further in more advanced Middle Ordovician bellerophontaceans. The bucanopsids and bellerophontids have still more tightly coiled shells (low D values), with most species completely closing the umbilicus, or nearly so. The rate of whorl expansion (W) in the shells also increases, resulting in a more compact coil. The compact rounded shells of this level of development are thought to represent the most mobile of the Ordovician bellerophontaceans. This interpretation could partially account for the wide distribution and large numbers of species such as Sphenosphaera clausus (Pl. 30, figs. 1-23, Pl. 31, figs. 1-13) and Bucanopsis carinifera (Pl. 27, figs. 1-15) in the Middle Ordovician deposits of Kentucky and Tennessee (see Paleoecology Section). These species apparently occupied a variety of depositional environments and may have had a wide range of life habits.

The next step in this progression was toward specialization, through reduction of the coil and development of a broadly expanded aperture (very high W values), as seen in the carinaropsids and pterothecids. Sphenosphaera showed the incipient stages of apertural platform evolution in the lineage (Pl. 30, figs. 2, 9, 17). In Carinaropsis, the apertural platform evolved to cover approximately one-third the aperture opening (Pl. 37, figs. 3-4, 18-19). Its function must have been to support the animal's

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

visceral mass, a function the reduced coil could no longer serve in the adult animal. This specialized shell form probably represents a mobile, but sluggish creature. The epitome of the trend is seen in Pterotheca and its relatives. They completely reduced the vestigial coil and developed an interior apertural platform that covered more than one-half the aperture opening (Pl. 40, figs. 4, 6). This more highly specialized animal was probably nearly sedentary, living in shallow nearshore areas and possibly suspension feeding, like the morphologically similar Crepidula of modern seas, or sluggishly grazing on algal mats.

In summary, there was a clear trend toward the tighter coiling of the shell and the reduction of the umbilicus (decreasing D values) in Ordovician bellerophontaceans. This trend was often accompanied by an increase in the rate of whorl expansion (W). These trends allowed easier balance and transport of the shell, and thereby permitted greater mobility. This greater mobility enabled the bellerophontaceans to live in higher energy habitats and to adopt new modes of life. This trend was therefore an important factor in the Middle Ordovician radiation of the bellerophontaceans.

These conclusions are at slight variance with those of Rollins (1967, pp. 54-64), who postulated three modes of life for Bellerophontaceans: clingers, creepers, and ploughers. Clinging forms were thought to be sluggish in their habits and to have clamped their shells vertically down over the foot against firm substrate in a limpet-like fashion for protec-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tion. Typically, Rollins' clingers had rapidly expanding, even explanate apertures with flat margins. Ordovician genera which I would agree with Rollins to include in this group are Carinaropsis, Pterotheca, and possibly Salpingostoma. However, only the last of these genera has been found associated with firm substrates in the present study. Salpingostoma kentuckyense occurs in bioclastic beds of the lower Curdsville Limestone Member of the Lexington Limestone, and S. richmondensis occurs in Upper Ordovician bioclastic beds. Carinaropsis and Pterotheca are more common in fine-grained limestones in the Middle Ordovician rocks of Kentucky and Tennessee. Peel (1977, p. 47) has proposed that low explanate shell forms were adapted to life on soft substrates where their broad shells would act like snowshoes to prevent the animal from sinking into the soft sediment. "Clinger" is probably a poor term for this group, as they were more likely sluggish vagrant benthonic animals. Horny (1963) reported explanate shells of similar morphology from both soft muddy paleoenvironments as well as firm bioclastic ones. It may be that the explanate shell form was not adapted to any specific substrate conditions.

Rollins' (1967) second group, the creepers, were thought to be more mobile types and to be capable of total retraction of the head-foot mass into the shell like most conispiral gastropods. He included such Ordovician genera as Bellerophon (Pl. 18, figs. 10-17), Kokenospira (Pl. 20, figs. 9-12), Tetranota (Pls. 21-22), Tropidodiscus (Pl. 41, figs. 6-13), Phragmolites (Pls. 43-44), and Temnodiscus (Pl. 42, figs. 3-6). I would

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

add to this group the genera Sphenosphaera (Pls. 29-36), Bucanopsis (Pl. 27, figs. 1-20), and Bucania (Pls. 12-20), which Rollins had considered clingers. The relative mobility of individual species in this group was probably quite variable. Mobility should have increased with an increase in the whorl overlap (decrease in D), a decrease in the size of the umbilicus, and an increase in the rate of whorl expansion (W) to a point where the coil was small and light in weight but still large enough to continue support of the visceral mass. Other important considerations in estimating relative mobility are the shell thickness and the whorl cross-sectional area and shape.

Rollins' (1967) third group, the ploughers, included only such Late Paleozoic forms as Euphemites, which has extensive inductural deposits over much of the body whorl. They were believed to have ploughed through soft sediment in search of food much like the modern gastropod Polinices. Presumably such forms must have been either deposit feeders or predators, like Polinices.

Linsley (1978a) attempted to estimate bellerophontacean locomotion rates from shell forms and used generic morphotypes for examples. He concluded that low explanate shells belonged to sluggish grazers or deposit feeders. He regarded the laterally compressed whorl form of Tropidodiscus to indicate considerable mobility, but he thought that its high center of gravity must have restricted it to quiet water environments. He considered the tightly coiled Bellerophon and Euphemites morphotypes to be the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

most mobile of the bellerophonts. Finally, he considered Knightites, which is a moderate sized shell with a small umbilicus and a slightly flairing aperture, as a sluggish grazing animal because of its high development of ornamentation. I generally agree with Linsley's conclusions cited above, but tend to disagree with this last. I doubt that the shell ornamentation of Knightites would have hindered its mobility. In fact, that general shell form is believed here to have the potential of at least moderate locomotory capability. The same general morphotype also characterizes many other taxa, the most notable here being the Bucania nashvillensis group and species of Tetranota, such as T. bidorsata and T. wisconsinensis.

Functional Aspects of Selected Bellerophontacean Shell Forms

Explanate shells - An explanate shell is one in which the rate of whorl expansion increases markedly in maturity, so that the aperture becomes broadly expanded and oriented tangential to the coil and the substratum. Many unrelated bellerophonetacean genera are characterized by this adult expansion of the shell. Notable examples in the present fauna are Salpingostoma (Pls. 24-5) and Carinaroposis (Pls. 37-38).

Before expansion, the shell of Salpingostoma (Pl. 24, figs. 8, 14) closely resembles members of the Bucania sulcatina group, except that it apparently possesses a nearly radial aperture. Linsley (1977, p. 197)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

defined radial apertures as those whose apertural plane passes through the axis of coiling, rather than being tangential to the body whorl. Linsley claimed that modern gastropods with radial apertures typically are nearly sedentary and live with the apertural plane perpendicular to the substrate, rather than parallel to substrate as in tangential forms. The adult expanded aperture of Salpingostoma is tangential to the coil. Therefore, it seems that the juvenile Salpingostoma may have led an essentially sedentary existence, like most gastropods with radial apertures (Linsley, 1977, p. 198), but became more capable of mobility with the development of tangential aperture in maturity. Furthermore, the expanded bell-shaped aperture of the adult is often quite thickened, and of course, has the long open slit characteristic of the genus. Possibly, the apparently sedentary juvenile lived through suspension feeding in more sheltered microhabitats. The adult with its tangential thickened aperture could sluggishly move its broadly umbilicate shell into more current swept areas where its expanded foot would cling to firm substrata. The long adult slit probably served an enlarged single pair of gills and furnished a large exhalent area, making it possible to move a larger amount of water through the mantle cavity. This would have been of particular advantage if the animal was a suspension filter-feeder. The modern suspension-feeding caenogastropod Siliquaria possesses a long open slit to serve a single large food-collecting gill.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

In Carinaropsis the coil is nearly reduced, and in Pterotheca it is completely reduced. In both genera, the shell is thin and light-weight. In these forms, the visceral mass is supported within a broadly expanded body whorl by an internal platform, similar to that of the modern slipper limpet, Crepidula fornicata, which is a nearly sedentary suspension feeder.

Explanate shells have often been interpreted as being adapted for a clinging mode of life. Concomitant with the development of an expanded explanate aperture is the expansion of the foot. Vermeij (1978, p. 33) has reported that modern marine gastropods living in higher energy settings generally have lower shells and a relatively larger aperture and foot than those gastropods living in adjacent more sheltered settings. Of course, the expanded foot would give a broader, more powerful base for clinging. On the other hand, Peel (1975, 1977, 1978) has suggested that the expanded aperture and foot of explanate bellerophontaceans was an adaptation for life on soft substrates, acting like snowshoes to prevent submergence of the animal into the sediment, as in the modern deposit-feeding gastropod Aporrhais. He supported this conclusion by citing occurrences of the explanate bellerophontacean genera Anapetopsis and Phragmosphaera in soft-bottom environments in the Silurian Arisaig Group of Nova Scotia. A comparable association was reported by Gromczakiewicz-Lomnicka (1972) from a Carboniferous black shale in Poland, where the explanate bellerophontacean Patellilabia is the only large gastropod in a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fauna of otherwise diminutive algal-foliage dwelling gastropods. However, Horny (1963, p. 66-67) cited bellerophontaceans with explanate apertures and similar shell morphologies from soft- bottom muddy facies and from firm-bottom facies of tuffaceous and skeletal debris in the Ordovician-Silurian of Bohemia.

Perhaps the broadly explanate aperture in bellerophontaceans was an adaptation that could serve different functions. Other morphological characters of the shells must also be taken into account in functional analyses, such as shell size and thickness. For example, Carinaropsis generally has a very thin light-weight shell, and among the faunas described here was most common in the the Grier Limestone Member of the Lexington Limestone, an apparently soft-bottom facies. Conversely, those explanate shells adapted for powerful clinging in higher energy conditions would be expected to be thicker and heavier. One such example might be Salpingostoma richmondensis, which is commonly found in deposits of broken and worn skeletal debris in the Richmondian Whitewater Formation of Indiana and Ohio.

Trilobed shells - Peel (1974) reported at least five genera of bellerophontaceans with trilobate shells in Lower Ordovician through Devonian strata. The appearance of the trilobed whorl form in unrelated stocks can be explained through its functional attributes. Peel (1974, pp. 248-249) interpreted the trilobate dorsum as a modification of the shape of the mantle cavity and its openings to separate inhalent streams of clean water

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

from the exhalent current of fouled and deoxygenated water. Such a modified design would increase the efficiency of water flow through the mantle cavity and would therefore be a likely functional adaptation in unrelated stocks.

Peel (1977, 1978) has noted the common occurrence of trilobate bellerophonts in nearshore fine-grained sediments in Ordovician and Siluro-Devonian deposits. He cited Tritonophon as a common element of soft-bottom shallow marine platform facies in the Arisaig Group of Nova Scotia, while being absent in contemporary firm-bottom faunas. He considered the genus to be a likely algal foliage-dweller. Likewise, Bretsky (1970) cited the trilobate Plectonotus sp. from delta front silts and shales of the Upper Ordovician Queenston Delta of the central Appalachian region. He also speculated that this form was an algal foliage-dweller.

In the fauna studied here, Tetranota is the only trilobed bellerophontacean. In the Middle Ordovician Stones River Group of Tennessee, the genus occurs in fine-grained limestones. The genus also occurs in the offshore shales of the Upper Ordovician Kope Formation in Kentucky and Ohio. Both occurrences reflect soft-bottom environments. It may be that the increased efficiency of water flow through the mantle cavity of the trilobate shell allowed these animals to inhabit fine-sediment soft-bottom facies.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

THE PALLIAL SYSTEM AND THE LABRAL EMARGINATION

The mantle cavity is one of the most characteristic features of the Mollusca. In gastropods, it is primarily a respiratory chamber housing the ctenidia (gills) and the associated osphradia and hypobranchial glands, which together form a functional unit (Yonge, 1947). The osphradia lie near the entrance to the cavity and estimate the sediment influx. The hypobranchial glands secrete mucus to consolidate the invading sediment particles, so that they do not foul the ctenidia and are easier to expel. The ctenidia are cilia-covered feather-like structures that absorb oxygen and sometimes collect food from currents passing through the mantle cavity. Also, in gastropods, the alimentary, renal, and reproductive systems open into the upper exhalent portion of the mantle cavity, so that their discharged materials can be carried outward by the exhalent pallial currents.

Yonge (1947) thoroughly described and analyzed the structure and function of the pallial organs in aspidobranch Gastropoda. The term aspidobranch refers to the presence of bipectinate ctenidia which characterize the Archaeogastropoda and are considered the most primitive of known molluscan gill types. Yonge (1947) recognized four aspidobranch arrangements in modern archaeogastropods: (1) asymmetrical shell with two asymmetrical ctenidia (all Zeugobranchia except the Fissurellacea); (2) secondarily

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

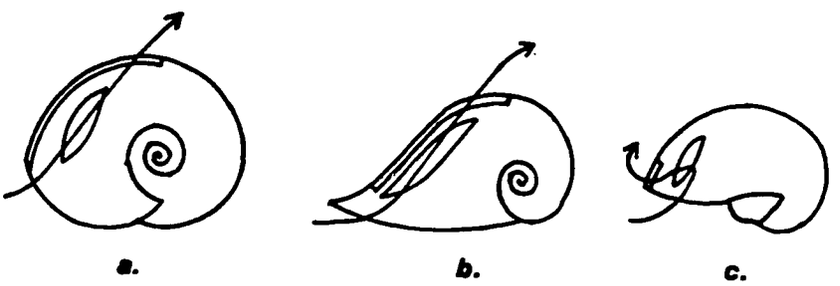


Figure 16: Paths of water currents through the shells and mantle cavities of some Ordovician bellerophontacean gastropods. a.) Tropidodiscus, left-lateral view; water currents enter anteriorly and exit through the deep slit postero-dorsally. b.) Salpingostoma, left-lateral view; water currents enter broad aperture antero-laterally, pass over a hypothetical enlargened pair of gills, and exit postero-dorsally through the deep slit. c.) Spheno-sphaera, left-lateral view; water currents enter shell antero-laterally and curve around to exit dorsally through a short slit. This is the path also seen in pleurotomariaceans.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

symmetrical shell with two symmetrical ctenidia (Fissurellacea); (3) asymmetrical shell with loss of one ctenidium (Neritacea, Valvatacea, Trochacea); and (4) secondarily symmetrical shell with loss of one or both ctenidia (Patellacea, Cocculinacea, some Neritacea).

In the zeugobranchiate molluscs (Nos. 1 and 2 above), Yonge (1947) reported that inhalent currents, created by ctenidial cilia, are drawn into the mantle cavity on both sides and above the animal's head. After passing over the ctenidia, the deoxygenated currents pass upward and out of the cavity through a dorsal labral slit (as in the Pleurotomariidae, Scissurellidae, and some Fissurellidae, e.g., Emarginula), or through a single apical trema (as in some Fissurellidae, e.g., Diodora (Fissurella)), or through a series of tremata (as in the Haliotidae, e.g., Haliotis). Such shell emarginations as these are morphological adaptations to prevent the mixing of fresh incoming currents and deoxygenated and fouled exiting currents in zeugobranchiate forms. In gastropods with only one ctenidium, such as the more advanced archaeogastropods and the caenogastropods, inhalent currents enter the mantle cavity on one side of the head and exhalent currents are expelled on the other side of the head. Therefore, there is no need for a labral emargination. Rarely, highly specialized caenogastropods do bear labral slits, such as the Siliquariidae, which are sessile suspension feeders with a single enlarged food-gathering ctenidium.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

In 1843, de Konnick noted the similarity between the labral emargination of Bellerophon and that of the modern fissurellid Emarginula. Meek (1866) supported this comparison and further noted the similarity of the tremata of the Silurian bellerophont Tremanotus. These comparisons convinced these early authors, and most subsequent authors, of the close phylogenetic relationship between the pleurotomariacean archaeogastropods and the bellerophontaceans. Knight (1952) used Yonge's (1947) analysis of the zeugobranchiate pallial system to reconstruct the soft anatomy of bellerophonts. He diagramed bellerophonts as having a zeugobranchiate pallial system, with a pair of bipectinate ctenidia receiving anterolateral inhalent currents from either side of the head, these currents moving upward and inward through the mantle cavity, converging near the top and being expelled through a dorsal slit. Such a reconstruction is also supported here.

It should be noted that some genera formerly considered bellerophontaceans, but currently being interpreted as monoplacophorans because of their muscle scar patterns (e.g., Sinuites, Sinuitopsis, Cyrtolites), may also possess a distinct labral sinus. This is not surprising, as these forms are also believed to possess one or more pairs of bipectinate gills arranged on either side of the body. Even though the path of currents through the posterior mantle cavities of these forms would be quite different from that of a gastropod, with inhalent currents entering at the opposite end, the zeugobranchiate condition would still be served by an

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

exhalent sinus. Thus far no species with a well-defined slit-selenizone complex has been accepted as a monoplacophoran, but such homeomorphy would not be impossible.

In the Pleurotomariacea and the Bellerophontacea the characteristic labral emargination can be in the form of a sinus or a slit. A sinus is a simple U-shaped to V-shaped re-entrant of the aperture margin. The slit is a parallel-sided re-entrant varying from a short notch (Pl. 14, fig. 14; Pl 38, fig. 16) to a deep fissure as much as a half whorl in extent (Pl. 23, figs. 10-13; Pl. 44, figs. 3, 6). A slit is generally located at the apex of a shallow sinus, and generates a slitband or selenizone. A selenizone (Pl. 16, fig. 15; Pl. 18, fig. 5; Pl. 28, fig. 5; Pl. 30, fig. 6; Pl. 31, fig. 6) is a spiral band tracing the path of the slit around the shell, and is best expressed when marked by a series of concentric growth lines (lunulae) bordered by a pair of spiral threads. If the selenizone is not well-defined by lunulae and bordering threads, it may be expressed as a simple, generally slightly elevated, band, often referred to as a pseudoselenizone. Horny (1963, p. 68) has pointed out that there seems to be a complete morphological gradation from the U-shaped sinus to the narrow channel-like slit. Regardless of its form, a median labral emargination, with few exceptions, indicates the presence of a dibranchiate pallial system.

The labral emargination can occur in 5 general forms in Paleozoic symmetrical molluscan univalves: (1) a V-shaped to U-shaped sinus, as in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Sinuites (Pl. 11, figs. 1, 6, 11); (2) a short, relatively broad, notch or slit, as in advanced bucaniids, bucanopsids, and bellerophontids (Pl. 38, fig. 16); (3) a deep, narrow slit, which may extend up to one-half a whorl back from the aperture margin, as in tropidodiscids and primitive bucaniids (Pl. 44, figs. 3, 6, 12; Pl. 23, fig. 10); (4) a long open slit closed off at the anterior margin, such as in Salpingostoma (Pl. 24, figs. 1-3); (5) one or a series of discrete openings, such as the tremata of Tremanotus, which according to Peel (1972) are repeated closings of a deep labral sinus.

Linsley (1978a, pp. 438-439) concluded that broad shallow slits were generally associated with broad shell forms, such as Bellerophon (Figure 16c). The breadth of the outer lip of the shell allowed inhalent currents to be spread to the anterolateral extremities. In these forms, he envisioned a shallow mantle cavity where anterolateral inhalent currents were effectively separated by virtue of the shell's width from the exhalent currents exiting through the dorsomedian slit. In contrast, in narrow shell forms, such as Tropidodiscus, Linsley (1978a) pointed out that the separation of inhalent and exhalent currents would be difficult. The solution was a greatly deepened slit and mantle cavity. In such a form, currents could enter anteriorly into the mantle cavity, bathe the ctenidia, and continue on in nearly the same line to exit posteriorly at the back of the deep slit (Figure 16a). This arrangement in effect created a posteriorly placed anus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

There are some exceptions to Linsley's astute observations concerning the association of a deep slit with only narrow shell forms. Some bellerophonts with broad depressed whorls, such as species of the Bucania sulcatina group (Pl. 12, figs. 1-3) and Undulabucania spp. (Pl. 23, figs. 5, 11), also apparently possessed deep slits. As discussed elsewhere, all of these broadly umbilicate forms with deep slits, regardless of the whorl shape, are considered morphologically primitive. None of the more advanced genera possess deep slits, and therefore, the structure's functional advantages for respiration must have been overshadowed by some disadvantages, such as weakening of the shell and making the animal more open to predation.

The homeomorphic explanate genera Salpingostoma (Pl. 24, figs. 1-3; Pl 25, fig. 1; Figure 16b) and Tremanotus also bear deeply inset shell openings in the form of a deep slit closed-off anteriorly and a line of open tremata, respectively. It is suggested here under the discussion of explanate shell forms that these genera may have been suspension-feeders. The deep emarginations would be useful in allowing more water to move through an enlarged set of ctenidia. As noted, such a situation is known in the modern caenogastropod family Siliquariidae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PARIETAL DEPOSITS

Knight (1952) and Rollins and Batten (1968) argued that parietal deposits and long trails on the concave side of the curved or coiled shell would impede the maneuverability of a protracted head in a monoplacophoran, and therefore, one would not expect to find these features in that class of molluscs. Pojeta and Runnegar (1976, p. 32) disagreed, pointing out cowries and other gastropods secrete secondary shell layers over the entire shell, and that there was no valid reason why parietal deposits could not be secreted by epithelium near the head. This point is well taken; however, I must agree with Harper and Rollins (1982, p. 228) that the crux of the problem is not the capability of secreting secondary deposits in any certain region of the shell, but rather the functional utility of secreting massive secondary deposits in the parietal region.

Sinuites granistriata and related species are generally accepted as monoplacophorans, and are known to possess a thin swash of secondary deposits in the parietal region and over the ventral coil (Pl. 45, figs. 1-2). But these deposits are so thin so as not to even slightly mask the original morphology of the covered areas.

On the other hand, many bellerophontaceans possess strongly thickened inner aperture margins and parietal areas. Rollins (1966) has described thick pad-like parietal deposits in Ptomatis, and explanate Devonian genus. Salpingostoma kentuckyense (Pl. 25, figs. 11-12), Bucania nashvil-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lensis (Pl. 13, fig. 19; Pl. 14, figs. 1-5), Bucania peracuta (Pl. 16, figs. 5-8), Bucania crassa (Pl. 19, figs. 7-10), and other species in the present study clearly demonstrate the common thickening of the parietal lip in bellerophontaceans. Specimens of Sphenosphaera clausus show the marked thickening of the entire parietal region by secretion of rather massive secondary shell layers over the medial region (Pl. 29, figs. 4, 13, 30; Pl. 30, figs. 2-9; Pl. 31, fig. 3).

Thickened parietal regions in bellerophontacean gastropods seem to serve two functions. First, such deposits add considerable weight to the part of the shell that lies on the central portion of the foot, thereby creating a fulcrum for balancing the shell. The added weight would also serve to stabilize the shell under higher energy conditions. Considering the difficulting in balancing such large umbilicate shells as some of those cited above, the added weight in a low central position would be of obvious advantage. Secondly, thickened parietal deposits may modify the design of the parietal region. This is particularly noticeable in S. clausus (same figures as above). Such modification of the parietal region in S. clausus would provide a broader, more stable area for the shell to rest on when the foot was extended.

The incipient outbuilding of the parietal region evident in the figures cited above for S. clausus was taken to its maximum development in species of Carinaropsis (Pl. 37, figs. 3-4, 18-19). In Carinaropsis, the coil has been reduced to the point of no longer being able to support the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

visceral mass of the animal in maturity. The extensive outbuilding of the parietal region in this specialized case was for the support of the visceral mass. The apertural platform of the modern gastropod Crepidula is clearly analogous in its morphology and function.

In summary, it is concluded here that thickened parietal regions furnish greater weight over the central area of the gastropod for better balance and stabilization of the shell. It is further concluded that such deposits may assist in supporting the shell on the extended foot, and even to provide a better surface over which to move the foot in and out of the shell. Such thickened deposits would overlie the head region in an untorted monoplacophoran, and would not seem to serve any reasonable function. In fact, massive deposits in such a position would seem to be impractical and would probably hinder the balancing of the shell in a monoplacophoran. Therefore, it is here considered highly dubious that monoplacophorans would secrete thickened secondary parietal deposits. Harper and Rollins (1982) even went so far as to claim that the development of a thickened parietal inductura is the single most reliable criterion for distinguishing fossil gastropods among Paleozoic isostrophic shell forms.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MUSCLE SCARS AND THEIR FUNCTIONAL SIGNIFICANCE

Muscle patterns in fossil univalved mollusks are central to the continuing controversy over the class level affinities of Paleozoic bilaterally symmetrical isostrophic shell forms. These muscle patterns are occasionally discovered under fortuitous preservation of muscle scars. Over the sites of muscle attachment on the shell interior, the calcification of the shell material is inhibited, and as a result, there develops a slight depression - the muscle scar (Fretter and Graham, 1962, p. 142). In fossil specimens, these muscle scars are occasionally preserved as raised fillings of the original scar depression on an internal mold of the shell.

The modern monoplacophoran Neopilina has six pairs of discrete muscle scars arranged around the interior periphery of the shell (Lemche and Wingstrand, 1959). A number of Early to Middle Paleozoic limpet-like shells, the Tryblidiida, also possess five to eight pairs of discrete scars of similar form and arrangement, and therefore, have been interpreted as monoplacophorans (Wenz, 1940; Knight, 1952). Pojeta and Runnegar (1976, p. 29) have convincingly reconstructed the musculature of the Middle Cambrian Scenella using Neopilina as a model.

Pairs of discrete dorsal muscle scars have also been found in some isostrophically coiled Early Paleozoic genera. Wenz (1940) first described such a muscle scar pattern in Cyrtonella from the Devonian of Michigan, and using that single occurrence, he proposed that all bilater-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ally symmetrical isostrophic Paleozoic molluscan univalves were not gastropods as generally believed, but rather were untorted forms. A number years later, Horny (1963) described symmetrical pairs of muscle scars in the Late Ordovician Cyrtolites ornatus. Rollins and Batten (1968) then found monoplacophoran-like muscle scars in the Middle Devonian Sinuitopsis acutilira, and more recently Runnegar (1981) and Peel (1980) have recognized similar scars in two other sinuitid species, the Late Ordovician Sinuites cancellatus and the Late Silurian Sylvestrosphaera lemchei, respectively.

The muscle scars in limpet-form monoplacophorans, as well as in some isostrophically coiled taxa, are located in a ring just inside the aperture margin. Such an arrangement indicates that the animal could not retract into the shell, but rather must have clamped the shell down over the body for protection. On the other hand, muscle scars in the sinuitids are inset more deeply into the shell opening and sometimes are even located at the umbilical shoulder a half whorl back, suggesting that these forms were probably capable of retracting into the shell (Peel, 1980, p. 95-96). Considering the widespread use and success of retractability in the gastropods, it is not surprising that the Monoplacophora also adopted it as a protective strategy.

The shell, or columellar, muscles in coiled gastropods attach to the inner surface of the shell at the columella. The majority of prosobranch gastropods have only a single columellar muscle as the result of larval

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

reduction of a second retractor muscle. However, numerous archaeogastropods, including the Haliotidae, Scissurellidae, and some Neritacea, as well as some mesogastropods, possess a pair of columellar muscles (Fretter and Graham, 1962, p. 140; Knight, 1952, p. 12). All of these taxa have asymmetrically coiled shells, and the posttorsional right muscle is always larger than the one on the left side. Symmetrical paired columellar muscle scars have been described on the internal molds of a number of bellerophontaceans (Table 15).

In the bilaterally symmetrical patellacean gastropods, the shell muscles form a horseshoe-shaped ring around the inner shell margin, the open anterior end marking the position of the mantle cavity. The continuous horseshoe-shaped muscle is the product of a pair of lateral muscles, one on either side of the torted visceral mass, that increased in size and gradually extended their insertions in a backward direction through ontogeny until coalescing (Fretter and Graham, 1962, p. 140; Bandel, 1982, p. 32-33). All of these patelliform gastropods are thought to be descended from asymmetrically coiled ancestors which presumably had two asymmetrical shell muscles. Therefore, the bilateral symmetry of the shell muscles in patelliform gastropods is an adaptation to the secondary symmetry of their shells.

Just as in the Monoplacophora, the arrangement of muscle scars around the inner periphery of the shell opening in patelliform gastropods indicates a clamping mechanism for protection, while a circumumbilical muscle

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

position demonstrates the ability to retract the body into the shell. Linsley (1978) and Peel (1980) have suggested that the location of muscle scars half a whorl back from the aperture in sinuitid monoplacophorans, as well as their fusion into fewer attachment sites, were adaptations favorable to development of torsion. Peel (1980) proposed that these sinuitid muscles may represent a similar morphological grade in terms of retraction to possible gastropod ancestors.

Peel (1980) and Harper and Rollins (1982) stressed how muscle arrangements in bellerophontiform mollusks are controlled by the mechanical requirements of shell form and by the functional requirements of the animal's mode of life. Both monoplacophorans and gastropods can have muscles arranged in a ring around the aperture. Further, the discreteness of these muscle scars is not significant, as the supposedly continuous horseshoe-shaped muscle scar of diotocardian limpets actually represents a series of discrete bundles of muscle fibers, which may leave discrete scars in some cases (Fretter and Graham, 1962; Harper and Rollins, 1982). Moreover, muscle scars positioned in the circumumbilical region in retractile monoplacophorans can appear quite similar to the columellar scars of gastropods (Peel, 1980).

I must agree with Peel (1980) and Harper and Rollins (1982) in their conclusion that muscle scars are not a reliable criterion for assessing class level affinities of molluscan univalves. The genera Cyrtolites and Sinuites are assigned to the Monoplacophora in this study because of their

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

multiple sets of discrete muscle scars, and because their apertural forms can be rationalized as serving an exogastric animal. However, much work on modern gastropod muscle patterns is required before confident transfers of taxa to the Monoplacophora can be made. Studies such as that of Gundrum (1981) are heading in the right direction, but tangible data remain rather scarce. Another factor that should be realized is that muscle scars on internal molds are quite difficult to see. For instance, Runnegar (1981, p. 315), Knight (1952), and Peel (1980) have all observed different numbers and forms of muscle scars on a single specimen of Sinuites cancellatus.

Runnegar (1981, p. 315) described a single pair of muscle scars that cross the edges of the umbilici in a specimen of ?Bucania christianae (Koken). It should be noted that this species was described by Koken (1925) as a species of Bucaniella, a sinuate genus. Even Runnegar stated that the specimen was sinuate, and did not possess a slit-selenizone complex, and thus it is questionable why he referred the specimen to the slit-bearing genus ?Bucania. Runnegar (1981, p. 315) agreed with Peel (1980) and Harper and Rollins (1982) that positions of muscle scars can be directly correlated with shell form, and he illustrated an evolutionary sequence in these two characters in monoplacophorans that matches another sequence of opposite polarity in living trochacean gastropods (Runnegar, 1981, fig. 4). Based on these two sequences, he concluded that bellerophonts were probably all monoplacophorans. Frankly, I do not follow Run-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

negar's reasoning. If anything, Runnegar's figure seems to show what Peel (1980) and Harper and Rollins (1982) claimed; that is, muscle patterns in gastropods and monoplacophorans can be essentially identical, and therefore, cannot be used exclusively as a reliable criterion in determining the class level assignment of bilaterally symmetrical molluscan univalves. Muscle patterns are controlled by the mechanical requirements of shell form and by functional aspects related to the animal's mode of life.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PHYLOGENY AND CLASSIFICATION

THE BELLEROPHONT CONUNDRUM

The class level assignment of Paleozoic bellerophontiform mollusks has been debated since the early 19th century (Yochelson, 1967). The current controversy over the classification of the Bellerophontacea centers around whether or not these mollusks had undergone torsion, the larval process which defines the class Gastropoda. Torsion is the process by which the larval shell and visceral mass of the veliger are rotated 180 degrees with respect to the head-foot mass. According to Croft (1937, 1955), torsion results from the differential development and growth of the larval left and right retractor muscles. However, Bandel (1982, p. 27-28) has recently observed that torsion is caused by the differential growth of epithelial cells and is not related to muscle activities. As a result of torsion, the originally posterior mantle cavity, and its respiratory, sensory, reproduction, and renal organs, are brought into an anterior position above the head, and the shell coils backwards away from the head (endogastrically). Monoplacophorans, which are believed to be the ancestral group to the gastropods, do not undergo torsion, and therefore their mantle cavity remains posteriorly positioned and the shell coils forward over the head (exogastrically). The debate over classification of the bellerophontaceans has been rekindled in recent years by the discovery of multiple symmetrical pairs of discrete muscle scars in some bellerophonti-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

form taxa, and by the description of diverse Lower and Middle Cambrian mollusk faunas. One group of paleontologists claims that this new evidence from the fossil record indicates that the Paleozoic bellerophontiform univalves were untorted exogastrically-oriented molluscs assignable to the class Monoplacophora (Wenz, 1940; Moore, 1952; Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Runnegar, 1981, 1983; Salvini-Plawen, 1980). However, most Paleozoic gastropod specialists consider such fossils to represent torted endogastrically-oriented archaeogastropods (Knight, 1947, 1952; Knight and others, 1960; Yochelson, 1967, 1978; Berg-Madsen and Peel, 1978; Peel, 1980; Linsley, 1978a, b; Harper and Rollins, 1982). This latter viewpoint is taken herein. Below, evidence will be reviewed which suggests that the slit-bearing bellerophontaceans, and many of the morphologically similar sinuate taxa, were gastropods and were closely related to the pleurotomariaceans.

In the early nineteenth century, Bellerophon and its allies were generally considered nautiloid cephalopods (Yochelson, 1967). This opinion persisted even after Defrance (1824) demonstrated that bellerophonts lacked both a siphuncle and septation. Some other authors of that period considered bellerophonts to be heteropods, prosobranch gastropods adapted to a pelagic mode of life (Yochelson, 1967). De Konnick (1843) and Meek (1866) first linked bellerophonts to the archaeogastropods by comparing their labral emarginations to that of Emarginula, the modern keyhole limpet. Meek (1866) also argued that the shells of most bellerophonts

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

seemed to be much too thick and heavy for the animals to have led a pelagic mode of life.

Since Meek's (1866) paper, the association of the bellerophonts with the archaeogastropods has been widely accepted, but with some notable exceptions. Simroth (1906) proposed a separate class of mollusks for the bellerophonts, which he termed Amphigastropoda. This class was later also used by Thiel (1935) in his mollusk classification. Also, Naef (1911) taxonomically isolated the bellerophonts by placing them in a division that he termed the Planospiralia. All of these authors considered the bellerophonts to be pelagic swimming animals, an impression which Yochelson (1967, p.149) claimed must have influenced their views on classification. Moore (1952, p. 289), who also used Amphigastropoda and allied the group with the tryblidiids, did not consider them to be pelagic.

The present period of controversy was initiated by Wenz's (1938) observation that the symmetrical paired muscle scars of the Silurian patelliform genus Tryblidium seemed to indicate that the animal's soft parts were symmetrical and untorted. He proposed that Tryblidium and its allies be transferred from the Patellacea to a new superfamily, the Tryblidiacea. Wenz (1940) then also found multiple pairs of muscle scars on an internal mold of the Devonian species Cyrtonella mitella (Hall), an incompletely coiled isostrophic form. Based on this evidence, Wenz (1940) concluded that all Paleozoic bellerophontiform taxa represented primitive

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

untorted mollusks. He placed all such taxa in the subclass Amphigastropoda, and all anisostrophic gastropods in the subclass Prosobranchia.

Knight (1947, 1952) strongly contested Wenz's (1940) conclusion that the bellerophonts had not undergone torsion. In rebuttal, Knight (1947) described single pairs of gastropod-like columellar muscle scars in two species of Bellerophon and in Sinuites cancellatus. However, additional muscle scar pairs have been recently recognized in Knight's specimen of S. cancellatus, thus apparently demonstrating its monoplacopharan affinities (Runnegar, 1981; Peel, 1980). Knight (1952, fig. 10) also reconstructed the soft anatomy of a bellerophontacean based on the pleurotomariacean gastropod design. He claimed that the median labral slit in these two groups was a homologous structure and therefore indicated that bellerophontaceans had undergone torsion. He envisioned the bellerophontacean animal to have an anterior dibranchiate mantle cavity. As known from pleurotomariaceans with this arrangement, fresh water currents enter the mantle cavity anteriorly, pass over the gills, and the deoxygenated water, and waste products from a dorsal anal tube, are then expelled through the dorsal labral emargination (Yonge, 1947). This reconstruction is accepted herein. Knight (1952, p. 52) argued that three common morphological characters demonstrated a close relationship between the bellerophontaceans and pleurotomariaceans: (1) a deeply, hollow, usually closely-coiled shell, (2) a sinus or a slit (and selenizone), and (3) a single pair of columellar retractor muscles. As will be seen below, it now seems likely that monoplacophorans could also have a coiled shell and a labral sinus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Horny (1963a) reported multiple pairs of discrete muscle scars in the Upper Ordovician isostrophic species Cyrtolites ornatus, and Rollins and Batten (1968) also described such scars in the Middle Devonian sinuitid Sinuitopsis acutilira (Table 1). S. acutilira bears a deep labral sinus, and Middle Ordovician species of Cyrtolites sometimes bear a shallow labral sinus. Recently monoplacophoran-like muscle scars have also been reported in the sinuitids Sinuites and Sylvestrosphaera (Runnegar, 1981; Peel, 1980). So far, all isostrophic species reported to possess multiple pairs of monoplacophoran-like muscle scars have been cyrtolitids and sinuitids, except for a single specimen of questionable taxonomic affinity cited by Runnegar (1981) as ?Bucania christianae (Table 1). Bellerophont genera reported to possess a single pair of gastropod-like columellar muscle scars include Bellerophon, Pharkidonotus, Tremanotus, Salpingostoma, Sinuitina, and Megalomphala (Table 1).

The reliability of muscle scars as a primary taxobase on which to base the class level assignments of bellerophontiform fossils may be questionable. First of all, the muscle scar patterns of most extinct or extant gastropods have not been assessed, and therefore, the range of variability for this feature is unknown. Secondly, muscle scars are rarely preserved, and when they supposedly are, their recognition and interpretation is quite subjective. A case in point is the specimen of Sinuites cancellatus on which Knight (1947) saw a single pair of columellar scars, but on which Runnegar (1981) has recognized a second pair, and Peel (1980)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

has recognized yet a third pair (see Runnegar, 1981, p. 315). In another case, Runnegar and Jell (1976, p. 127) recognized monoplacophoran-like muscle insertions on illustrations of species of Sinuitina and Tremanotus by Horny' (1963, Pl. 8, fig. 9; Pl. 19, figs. 3-5, respectively), but Berg-Madsen and Peel (1978, p. 123) criticized these observations. These latter authors claimed that in the specimen of Sinuitina, the supposed scar might be no more than a spurious mark. Regarding the specimen of Tremanotus, Berg-Madsen and Peel (1978, p. 123) claimed that Runnegar and Jell's (1976) supposed muscle scars were actually umbilical nodes which are commonly present in tremanotids. Moreover, gastropod-like columellar scars have also been reported in other species of Sinuitina and Tremanotus by Rollins and others (1971) and Peel (1972), respectively.

Recently, evidence from comparative and functional morphological observations has been cited to suggest further hazards in the total reliance on muscle scars as class discriminators in bellerophontiform fossils (Linsley, 1978a, p. 437-438; Peel, 1980, p. 95-96; Harper and Rollins, 1982, p. 228-230). Many authors have concluded that the number and position of muscle scars are primarily related to shell form and mode of life, and therefore, the muscle scars in some monoplacophorans and gastropods could appear identical. For example, tryblidiid and some cyrtonellid monoplacophorans have numerous pairs of muscle scars or a muscle band arranged around the aperture opening. Similarly, patellacean gastropods have a horseshoe-shaped muscle scar around their aperture openings. It

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

should be noted that although the muscle band of patellacean gastropods usually appears continuous, it actually consists of separate bundles of muscle fibers, a condition which is occassionally reflected in the muscle scars (Fretter and Graham, 1962; Harper and Rollins, 1982). All of these arrangements reflect a clinging animal which could not retract into its shell for protection, but rather clamped the shell opening down onto firm substrata. Starabogatov (1970, p. 297) has argued that the Archinacellacea, which are assigned to the Monoplacophora here, were actually limpetform gastropods, because their continuous muscle band would leave no room for a head if exogastrically oriented. It appears, therefore, that a ring of muscles, whether a continuous band or consisting of multiple discrete pairs, may be either functional or phylogenetic in origin. Detailed analyses of muscle scars are needed, but even then, as in the Archinacellacea, interpretations are open to question.

Isostrophic taxa that are capable of retracting into the shell for protection typically have muscle insertions set deep into the shell. Bellerophontaceans and some coiled monoplacophorans, such as Sinuites and Sylvestrosphaera, have deeply inset circumumbilical muscle scars (Peel, 1980, pp. 95-96). While Sinuites also possesses one or more dorsal pairs of muscle scars, Sylvestrophaera apparently has no dorsal scars (Peel, 1980). The fusion of muscle scars into more localized lateral positions improved the ability to retract into the shell, and it is probable that some coiled monoplacophorans with only a single pair of circumumbilical

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

muscles occur in the fossil record. In such a case, it would be virtually impossible to distinguish isostrophic gastropods and monoplacophorans using only muscle scars (Peel, 1980, p. 96).

Linsley (1978a, b), Peel (1980), and Harper and Rollins (1982) have suggested that morphological features other than muscle scars, such as the form of the aperture opening, may be more reliable taxobases for class level assignments of bellerophontiform taxa. As discussed here in the Functional Morphology section, an endogastric versus an exogastric orientation for bellerophontiform shells should be discernible from the functional analysis of shell morphologies. For example, Peel (1974) has demonstrated that the trilobate isostrophic shell is an adaptive strategy by which to separate incoming and outgoing mantle cavity currents in an endogastric gastropod. Linsley (1978b, p. 440) has shown that the deep slit of the narrow tropidodiscid shell (Pl. 44, figs. 3, 6) effectively provides a posterior exhalent area in a presumed endogastric gastropod. The same effect would be had in broader shell forms with deep slits, such as in Undulabucania (Pl. 23, figs. 5, 10) and the Bucania sulcatina group (Pl. 12, figs. 1-9) (see Functional Morphology). Harper and Rollins (1982, p. 228) concluded that massive secondary parietal deposits may be the most reliable criterion for recognizing gastropods among Paleozoic isostrophic shells. I agree with the importance of this character (see Functional Morphology). Whereas the massive parietal deposits of bellerophontaceans such as Sphenosphaera clausus would clearly serve as a stabi-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lizing structure in an endogastric gastropod, they would seem to be more of a hinderance to an exogastric monoplacophoran. Of particular note are the large parietal platforms of the specialized Ordovician bellerophontaceans Carinaropsis and Pterotheca, which are analogous in position, and presumably function, to the parietal platform of the modern gastropod Crepidula. The presence of a slit that generates a selenizone is strong evidence of a close affinity between the bellerophontaceans and pleurotomariacean gastropods.

Functional morphological interpretations have also been used to support an exogastric orientation for some bellerophontiform taxa (see Functional Morphology). For example, Starabogatov (1970, p. 295) interpreted the lateral angles of the typically diamond-shaped aperture of Cyrtolites as inhalent ducts to a posterior mantle cavity. Subsequently, Linsely (1978b, p. 437) suggested that such diamond-shaped apertures could serve to distinguish untorted monoplacophorans in bellerophontiform genera where muscle scars were unknown. Starabogatov (1970, p. 295) also noted narrow umbilical grooves on Sinuitopsis which he interpreted as inhalent channels to a posterior mantle cavity. Peel (1975) has since noted similar umbilical grooves in two species of Pharetrolites, and Berg-Madsen and Peel (1978, p. 120-121) have observed such channels in the minute Middle Cambrian Protowenella.

The other body of evidence used to suggest that all Paleozoic bellerophontiform taxa were monoplocophorans are the recently described diverse

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Early and Middle Cambrian mollusk faunas, such as those from the Tommotian Series of the Siberian Platform (Rozanov and others, 1969; Matthews and Missarzhevsky, 1975; Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Runnegar and Jell, 1976; Runnegar, 1981, 1983). These Early and Middle Cambrian mollusks are all minute in size and are often preserved as phosphatized internal molds (Runnegar, 1983). The univalved mollusks occur as both isostrophic and anisostrophic forms. The higher taxonomic assignment of many of these minute fossils, such as the low-spired pellagiellaceans, is a matter of some debate (Knight, 1952; Yochelson, 1967, 1975, 1978; Golubev, 1976; Berg-Madsen and Peel, 1978; Runnegar, 1983). Rozanov and others (1969) regarded all the Tommotian molluscan univalves to be gastropods, but Runnegar and Pojeta (1974) have interpreted them all as monoplacophorans and have used them as ground work for a new viewpoint on molluscan phylogeny. Runnegar and Pojeta (1974, pp. 313-314) have proposed that the pellagiellaceans were anisostrophic monoplacophorans, which were ancestral to the pleurotomariacean gastropods through an intermediate primitive gastropod form such as the Cambrian genus Aldanella. They preferred Ghiseln's (1966) theory for the origin or torsion, which states that torsion is a necessary consequence of helical coiling. They suggested that the larval shell of the anisostrophic pellagiellacean was awkward to balance upon settling from the plankton, and so the animal adopted a functional torsion in order to move the shell into a more manageable position. Subsequently, torsion was selected for because of its advan-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tages to the larval animal. Runnegar (1983) has elaborated on pellagiellaceans and the adult animals' ability to cope with torsion.

Knight (1952) had previously proposed that torsion in isostrophic monoplacophorans gave rise to the bellerophontacean gastropods, which in turn gave rise to the anisostrophic pleurotomariaceans gastropods. In support of this model, Morton (1958) suggested that torsion was of obvious benefit to the adult animal, as well as to the larva, by moving the mantle cavity into an anterior position, where the gills and pallial sense organs were put in a more advantageous situation from which to sample the environment into which the animal was moving. In further support of this model, Batten, Rollins, and Gould (1967) concluded that an exogastric isotrophic shell would be as difficult to balance as an exogastric anisostrophic shell for both the larval and adult monoplacophoran, and therefore it would be beneficial to both morphotypes to move the coil around 180 degrees to rest on the foot. Linsley (1978) and Peel (1980) have attempted to demonstrate that there was a trend in isostrophically coiled monoplacophorans to fuse and localize muscle insertions into lateral areas deep in the shell, which resulted in a morphological grade favorable to the development of torsion. They claimed that the development of an isostrophically coiled monoplacophoran shell was accompanied by the development of a narrow neck between the visceral and head-foot masses, which would have facilitated the torsional rotation of the visceral mass and shell.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

In Knight's (1952) model, it is assumed that there are both monoplacophorans and gastropods among the Paleozoic bellerophontiform taxa. However, in Runnegar and Pojeta's (1974) model, no torted isostrophic intermediate form is required in the evolution of the Pleurotomariacea from the Monoplacophora. Because of this viewpoint, and the fact that some bellerophontiform taxa have been found to possess multiple pairs of discrete muscle scars, Runnegar and Pojeta (1974) have concluded that all bellerophontiform taxa were untorted monoplacophorans. Peel (in press) has pointed out that there is no evidence that torsion was a unique event, as both the above models assume. Rather, possibly the Gastropoda represent a grade of evolution, and torsion may have occurred in both the above ways, and even several times in different lineages. Rollins and Batten (1968, p. 134) have suggested that possibly the bellerophontaceans themselves may be polyphyletic, evolving from monoplacophoran ancestors as many as three different times in the Early to Middle Paleozoic.

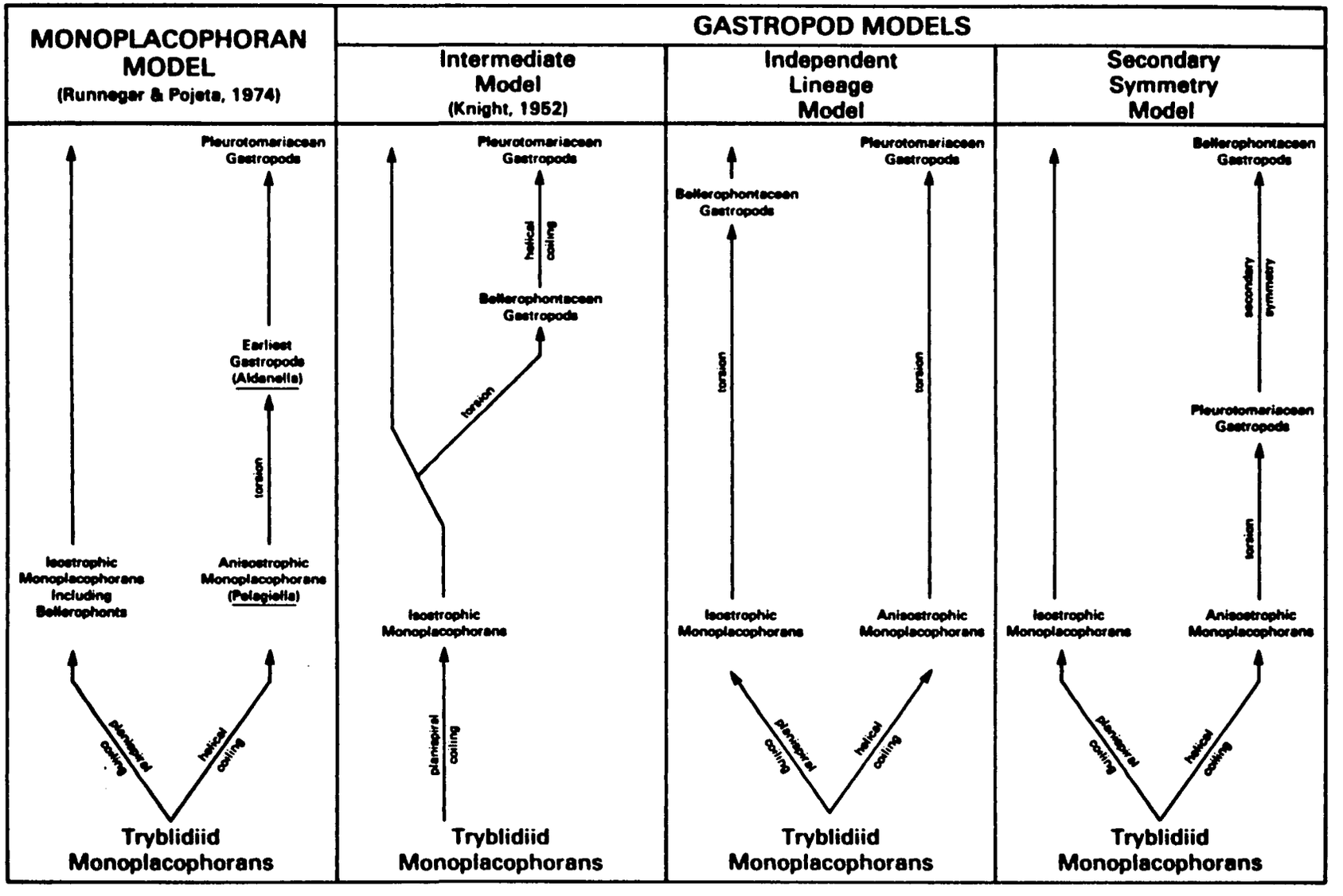
Regardless of how torsion may have originated, for reasons of comparative and functional morphology, the Bellerophontacea (as used herein) are considered here to be archaeogastropods related to the pleurotomariaceans. If this viewpoint is accepted, then there are three main phylogenetic models to consider (Figure 17). First, as Knight (1952) proposed, the Bellerophontacea were evolutionary intermediates between the isostrophic monoplacophorans and the pleurotomariacean gastropods (Figure 17). Second, the bellerophontaceans may represent one or more independent line-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 17: Four primary models for the phylogenetic relationships between monoplacophorans, bellerophontaceans, and pleurotomariaceans. The first model considers bellerophontaceans to be isostrophic monoplacophorans and suggests that pleurotomariacean gastropods are descended from anisostrophic monoplacophorans. All of the other models consider bellerophontaceans to be gastropods. The intermediate model suggests that bellerophontaceans are phylogenetically intermediate between isostrophic monoplacophorans and pleurotomariacean gastropods. The independent lineage model suggests that bellerophontaceans and pleurotomariaceans developed independently from different monoplacophoran ancestors. The secondary symmetry model suggests that pleurotomariaceans are derived from anisostrophic monoplacophorans, and that bellerophontaceans are secondarily symmetrical pleurotomariaceans.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



ages of gastropods which evolved from isostrophic monoplacophorans but did not give rise to any descendant groups (Figure 17). Such a scenario could accept multiple origins of torsion. It would also deny the homology between the slit-selenizone complexes of the bellerophontaceans and pleurotomariaceans, unless a common ancestral slit-bearing monoplacophoran group existed. The third possible phylogenetic model has not been adequately considered, in my opinion (Figure 17). Possibly the bellerophontaceans were secondarily symmetrical and descended from the pleurotomariaceans. Yochelson (1967, p. 154; 1978, p. 177; 1984, p. 262) has repeatedly expressed this opinion, but has unfortunately never attempted to document it. Such a model has ample precedent. Secondary symmetry is known in at least nine stocks of Tertiary and modern archaeogastropods (Eales, 1950, p. 191; Vermeij, 1975, p. 419).

The derivation of the bellerophontaceans from the pleurotomariaceans can be supported by both comparative morphology and by the biostratigraphic development of the two groups. The pleurotomariaceans first appeared during the Late Cambrian and rapidly diversified into three families: the Sinuopeidae, Eotomariidae, and Raphistomatidae (Knight and others, 1960). Slit-bearing bellerophontaceans also first appeared in the Late Cambrian, but are presently known from only the single tropidodiscid genus Chalarostrepsis Knight. A number of sinuate bellerophontiform genera also appeared in the Late Cambrian, but many of these taxa are still poorly understood and the group probably contains both monoplacopho-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

rans and gastropods. Bellerophontacean diversity appears to have remained low through the Early Ordovician, with only Eobucania Kobayashi known from that time. It was not until the late Middle Ordovician (Blackriveran-Shermanian) that the bellerophontaceans radiated into a diversity of forms.

Many of the early pleurotomariaceans (Late Cambrian-Early Ordovician) had very low spired shells with wide open umbilici. Of particular interest is the raphistomatid subfamily Ophiletinae (see Knight and others, 1960, p. I 200, Fig. 113), which contains such genera as Dirachopea Ulrich and Bridge, and Calaurops Whitfield. These genera are characterized by very low spires (low rate of whorl translation), large open umbilici, lanceolate whorl shapes, slits with selenizones, and disjunct coiling in adulthood. Such forms could have been ancestral to the Late Cambrian tropidodiscid Chalarostrepsis, which varies from the above features only in its possession of a planispiral coil. The Late Cambrian sinuate genus Strepsodiscus Knight, which was placed in the Cyrtolitidae by Knight, and others (1960, p. I 174), also agrees fairly well with the above morphological features, and it is even slightly anisostrophically coiled. Schizopea Butts represents a Ophiletinae morphotype that has a broader whorl shape and a greater rate of whorl expansion, and it could similarly represent an ancestor for a bellerophontacean like Eobucania. The low-spired, widely umbilicate shells of the Ophiletinae would apparently have been quite awkward to carry. Secondary symmetry would have

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

allowed the shell to be more easily carried in a vertical position on the foot.

Salvini-Plawen (1980, p. 254) pointed out that the apparent absence of a helically coiled protoconch in bellerophontaceans speaks against a secondarily symmetrical origin for the group. Salvini-Plawen may be correct in this observation, but it should be noted that bellerophontacean protoconchs have never really been investigated. Moreover, Bandel (1982, p. 32-33) has asserted that some patellaceans and other related archaeogastropod limpets do not have a trochospiral shell stage in early ontogeny. He has observed that the bilateral symmetry of the adult secondary shell may be carried into the early development of the embryonic (primary) shell, so that the trochospiral twist of the larval shell may be lost completely. Also, it is of interest to note that Lemche (1957, p. 414) reported a dextrally coiled helical protoconch on the modern monoplacophoran Neopilina galatheae, although other modern monoplacophorans have been reported to only have bulbous protoconchs (Pojeta and Runnegar, 1976, p. 30).

The secondary symmetry model for the origin of bellerophontacean gastropods deserves further investigation. More detailed comparisons of early pleurotomaricacean and bellerophontacean morphologies are needed before the model can become a viable alternative. One possibly attractive aspect of the model is that it allows acceptance of Runnegar and Pojeta's (1974) theory for the evolution of the Gastropoda, but also accepts

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Knight's (1952) premise that the bellerophontaceans were archaeogastropods. The apparent absence of an anisostrophic protoconch in bellerophontaceans (Salvini-Plawen, 1980) does not necessarily exclude the hypothesis from further consideration.

In summary, there is good evidence from functional morphological analyses and muscle scar patterns to indicate that there are both monoplacophorans and gastropods among the Paleozoic bellerophontiform taxa. So far, only sinuate bellerophontiform taxa have been proven to be monoplacophorans. The slit-bearing bellerophontaceans, and many similar sinuate forms, are thought to be archaeogastropods and closely related to the pleurotomariaceans. It is my opinion that those paleontologists insisting that all Paleozoic bellerophontiform taxa were untorted monoplacophorans have over extended their interpretation of new fossil data and are insufficiently familiar with post-Cambrian bellerophontiform taxa. The diverse minute molluscan faunas of the Early and Middle Cambrian are not typical bellerophontaceans, and conclusions derived from such forms cannot be automatically applied to all planisprial molluscan univalves. Many conclusions drawn from those minute faunas are based on an unproven theory on the origin of torsion and on highly interpretive functional morphology. On the other hand, the comparative and functional morphological evidence supporting the assignment of most bellerophontaceans to the Gastropoda is much more tangible and relies on direct comparisons to living animals. Clearly a great deal more detailed morphological analysis is needed before

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the phylogenetic role of bellerophontaceans is clarified. There are at least four possible phylogentic models which bear close scrutiny (Figure 17). Hopefully, continued concentrated and cooperative research will eventually result in the resolution of the problem, or at least a consensus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 15: Examples of post-Cambrian bellerophontiform molluscan univalves from which muscle scars have been described.

Monoplacophoran-type muscle scars - multiple discrete pairs.

Species	Age	Area	Author(s)
Cyrtonella mitella	Devonian	Michigan	Wenz (1940
Cyrtolites ornatus	Ordovician	New York	Horny' (1965)
Sinuitopsis acutilira	Devonian	New York	Rollins & Batten (1968)
Sinuites cancellatus	Ordovician	New York	Runnegar (1981)
Sylvestrosphaera lemchei	Silurian	Britain	Peel (1980)
?Bucania christianae	Ordovician	Norway	Runnegar (1981)

Gastropod-type muscle scars - single symmetrical pair, columellar, circumumbilical.

Species	Age	Area	Author(s)
Bellerophon gibsoni	Mississippian	Indiana	Knight (1947)
Bellerophon sp.	Pennsylvanian	Indiana	Knight (1947)
Bellerophon cf. B. gibsoni	Mississippian	Indiana	Rollins (1967)
Bellerophon sp.	Pennsylvanian	Missouri	Rollins (1967)
Pharkidonotus labioreflexus	Pennsylvanian	Ohio	Rollins (1967)
Sinuitina brevilineata	Devonian	New York	Rollins (1967) and Rollins and others (1971)
Tremanotus alphaeus	Silurian	Illinois	Peel (1972)
Salpingostomia buelli	Ordovician	Wisconsin	Peel (1972)
Bellerophon sp.	Pennsylvanian	U.S.A.	Peel (1972)
	Carboniferous	Ireland	
Megalomphala taenia	Silurian	Gotland	Peel (1976)
Bellerophon recticostatus	Carboniferous	Ireland	Peel (1982)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CLASSIFICATION AND PHYLOGENY OF THE MONOPLACOPHORA

Knight (1952) proposed the Monoplacophora as an order of the gastropod subclass Isopleura. However, he credited the concept of the taxon to Wenz (1938, 1940), who had originally recognized that the presence of multiple pairs of discrete muscle scars in Paleozoic symmetrical molluscan univalves, such as Tryblidium and Cyrtonella, suggested that they had not undergone the larval process of torsion. Wenz (1940) had concluded that all symmetrical molluscan univalves were untorted, and he assigned them to Simroth's (1906) subclass Amphigastropoda. Knight (1952, p.5) disagreed with this conclusion and restricted the Monoplacophora to three families - the Tryblidiidae, Hypseloconidae, and Archinacellidae. A few years later, Lemche (1957) described the living monoplacopharan Neopilina galatheae and elevated the Monoplacophora to the class level. Knight and Yochelson (1958, p. 37-39) recognized this new class and modified Knight's (1952) classification accordingly. Also at that time, Knight and Yochelson (1958, p.38) developed the modern concept of the class Gastropoda as mollusks that undergo larval torsion, the process by which the visceral mass and shell are rotated 180 degrees with respect to the headfoot mass. Knight and Yochelson (1958, p. 38-40) included three orders within the Monoplacophora - the Tryblidoidea, Archinacelloidea, and ?Cambridioidea. The Tryblidoidea was considered the "heart of the class" and included

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

those symmetrical forms with discrete paired muscle scars assigned to the superfamilies Tryblidiacea and Cyrtonellacea. The Archinacelloidea was considered an artificial grouping of forms which did not fit conveniently in the Tryblidioidea, but some of which were known to possess completely or nearly completely fused muscle scar bands. The single superfamily Archinacellacea included the families Archinacellidae and Hypseloconidae. The order Cambridioidea were considered questionable monoplacophorans and consisted of elongate, slightly asymmetrical shells in which the muscle scars were unknown. Knight and Yochelson (1960, p. I77-83) continued to follow this classification in the Treatise on Invertebrate Paleontology.

Horny' (1965, p. 10) outlined a revised higher classification of the Monoplacophora in which he presented two new subclasses - the Tergomya and Cyclomya. The Tergomya included limpet-like genera having several pairs of discrete muscle scars arranged in a ring, and with the anterior apex of the shell located outside that ring. The Cyclomya included limpet-like, cone-shaped, and planispiral genera having discrete paired or fused muscle scars arranged in a ring, and with the apex of the shell located inside that ring. The Tergomya included the order Tryblidiida, and the Cyclomya included the orders Archinacellida and Cyrtonellida. Horny' (1963) had erected the order Cyrtonellida for incompletely or completely coiled forms that had the muscle scars reduced in number and often specialized. In the Cyrtonellida, Horny' (1965, p.10) included the family Cyrtolitidae with the subfamilies Cyrtolitinae, Cyrtonellinae, and Cyrtonellopsinae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Starabogatov (1970) proposed another revision of the classification of the Monoplacophora based on his functional analyses of shell features and muscle scars. First, he (p. 296) excluded the family Palaeacmeidae (including Scenella) and the Cambridioidea from the class, because he claimed that the scars reported from genera of both groups were not really muscle scars. However, more recently Runnegar and Pojeta (1974, fig. 2) convincingly reconstructed the musculature of Scenella using the modern monoplacophoran Neopilina as a model. Starabogatov (1970, p. 296) also removed the Archinacellida from the Monoplacophora and suggested that they were a specialized order of the Gastropoda. He argued that the circular muscle of Archinacella approached so near the apical end of the shell that there was no room left for the animal's head, and he reinterpreted the pair of discrete muscle scars at the contra-apical end of the muscle ring in Archinacelliopsis as radular muscle scars. Starabogatov (1970, p. 298-302) recognized three monoplacophoran orders - the Tryblidiida, Cyrtonellida, and the new order Sinuitopsida. He redefined the Cyrtonellida as those planispiral shells with few whorls and 2-3 pairs of shell muscles inserted on the periphery of the final whorl, and he concluded that such forms retained multiple pairs of gills. Only the family Cyrtonellidae was included in this order. He (p. 300) proposed the order Sinuitopsida for planispiral forms with several whorls and only one pair of shell muscles. He concluded that other muscle scars described in Cyrtolities by Horny' (1963) and in Sinuitopsis by Rollins and Batten (1968) were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

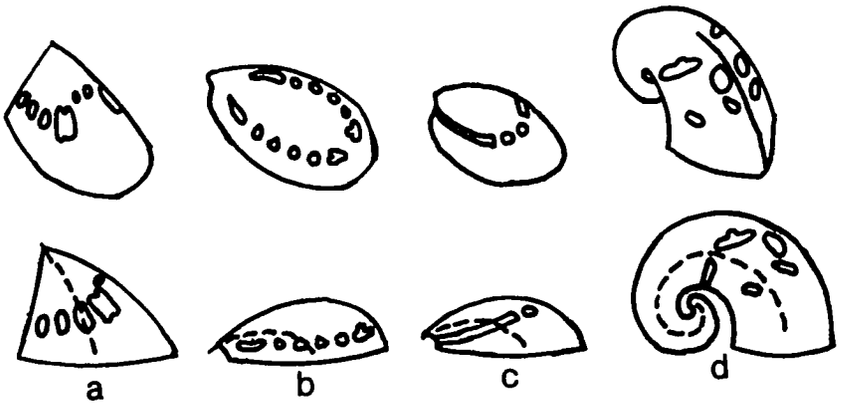
muscle scars of the radula and genitalia. He interpreted apertural features of these genera as indicating narrow inhalent channels to a posterior mantle cavity, and concluded that these forms must have had only a single pair of enlarged posterior gills. In the Sinuitopsida, he placed the families Cyrtolitidae, Bucanellidae, and Cyclocyrtonellidae. In the order Tryblidiida, he included the superfamilies Tryblidioidea, Neopilinoidea, and Kirengelloidea.

Bjaly (1973, p. 326) proposed the order Multifariida to the class Monoplacophora, which was based on the single species Multifariites lenaensis Bjaly from the Lower Ordovician of the Siberian Platform. The Multifariida was said to be similar to the Sinuitopsida in its number of whorls, but was distinguished by its four pairs of identical muscle scars. The new order was considered unique in its duplication of the muscles during the growth of the shell.

Rosov (1975, p. 39) elevated the superfamily Kirengelloidea to the order Kirengellida and included three families - the Kirengellidae (including Scenella and Moyerkania), the Romaniellidae (including Romaniella and Hypseloconus), and the Archaeophialidae (including Archaeophiala). He (p. 39) defined the new order as having conical shells, with the apex generally being antecentrally located, but varying from anterior to central to postcentral, and sometimes having a tendency to coil, but for no more than one-third of a whorl (Figure 18a). Muscle scars in the group occurred in 6-8 pairs arranged around the apex. Rosov (1975, p. 39)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 18: Four general morphotypes of monoplacophorans representing four superfamilies. a.) Kirengellacean - simple conical shells with discrete to fused muscle scars. b.) Tryblidiacean - low limpetform shell with discrete muscle scars. c.) Archinacellacean - low to high limpetform shell with fused muscle scars. d.) Cyrtonellacean - coiled shell with multiple discrete muscle scars. According to Rosov (1975), the kirengellaceans gave rise to the tryblidiaceans and archinacellaceans through forward displacement of the shell apex and simultaneous flattening of the shell, and to the cyrtonellaceans through progressive coiling of the conical shell (from Rosov, 1975).



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

suggested that the Kirengenllida were the most primitive monoplacophoran group known and that they gave rise to the Tryblidiida and Archinacellida through forward displacement of the apex and simultaneous flattening of the shell, and to the Cyrtonellida by further coiling of the shell (Figure 18). He claimed that muscle scars evolved toward fusion to some degree in all four orders.

Runnegar and Jell (1976) proposed a new classification of the Monoplacophora based on the theory of molluscan evolution proposed by Runnegar and Pojeta (1974) and Pojeta and Runnegar (1976). Their concept of the Monoplacophora closely approximated that of Wenz (1940), in which all Paleozoic symmetrical univalves were considered to be untorted. Unlike other modern classifications of the Monoplacophora, Runnegar and Jell (1976) emphasized shell morphology in their ordinal diagnoses, not mentioning muscle scar patterns. They recognized three orders - the Tryblidiida, Cyrtonellida, and Bellerophontida. They defined the Tryblidiida as limpet-shaped forms with an anteriorly placed protoconch; the Cyrtonellida as orthoconic, cyrtoconic, laterally compressed, and evolute planispiral forms that lack a well-formed apertural sinus or slit; and the Bellerophonitida as involute to evolute planispiral forms which have an apertural sinus or slit. They included in the order Bellerophontida the families Bellerophontidae, Sinuitidae (= Sinuitopsida Starabogatov, 1970), and Multifariidae (= Multifariida Bjaly, 1973).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The classificaton of Runnegar and Jell (1976) cannot be accepted here primarily because I consider the taxa those forms in their family Bellerophontidae to be archaeogastropods rather than monoplacophorans. Also, Runnegar and Jell's (1976) concept of the Cyrtonellida does not seem acceptable. Their diagnosis of that order departs greatly from the original meaning of the taxon given by Horny' (1963, 1965), and they would have been well-advised to have coined a new ordinal name rather than distorting an already well-known and widely used one. Moreover, Runnegar and Jell (1976, p. 116) stated that Horny's (1965) subclass Cyclomya is an alternative taxon to Cyrtonellida, but was not appropriately named. However, Horny' (1965) cited the Cyrtonellida as one of two orders in the subclass Cyclomya, and therefore the two taxa should not be considered alternative to one another. Finally, Runnegar and Jell's (1976) use of the presence of absence of a labral emargination as an ordinal taxabase is placed in doubt here by the demonstration that Middle Ordovician species of Cyrtolites bear a labral sinus (Pl. 5, figs. 7, 10, 13), whereas similar Upper Ordovician species of Cyrtolites lack a labral sinus (Pl. 6, figs. 7, 10, 17).

As previously discussed, Berg-Madsen and Peel (1978), Linsley (1977, 1978) and Peel (1980) have refuted the claim that all bellerophontiform mollusks are monoplacophorans. Based on analyses of functional morphology, those authors have concluded that both gastropods and monoplacophorans are present in that group. That opinion is shared here. On the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

hand, Harper and Rollins (1982) have concluded that muscle scar patterns reflect life habits and shell form rather than phylogenetic origins, and proposed that cyrtonellid monoplacophorans and bellerophontaceans were all gastropods. They accepted only the Tryblidiida as true monoplacophorans. The higher classification of the class Monoplacophora adopted here is shown in Table 16. This classification is considered conservative and tentative, but workable. The classification is based on the author's experience with mainly Ordovician taxa and on a survey of the literature.

At the present I consider the Monoplacophora to consist of two orders - the Tryblidiida and the Cyrtonellida.

The order Tryblidiida sensu Starabagatov (1970) is accepted here with some important modifications. The Archinacellacea is retained within the Monoplacophora as a superfamily of the Tryblidiida. Certainly Staraborgatov's (1970) arguments for returning the Archinacellacea to the Gastropoda warrant further investigation, but, at the present time, the bulk of evidence more strongly suggests that the group evolved from the Kirengellacea, as proposed by Rosov (1975), and should remain within the Monoplacophora. Also, the superfamily Kirengellacea Starabagatov, 1970, is recognized here in the sense of Rosov's (1975) order Kirengellida, consisting of the three families Kirengellidae, Romaniellidae, and Archaeophialidae. Rosov's (1975) order Kirengellida is quite similar in concept and composition to the family Scenellidae Wenz, 1938, sensu Runnegar and Jell (1976, p. 117). Noting the similarities in muscle scar patterns in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the Cambrian Scenella, the Silurian Tryblidium and Pilina, and the modern Neopilina, Runnegar and Jell (1976, p. 119) suggested that these taxa represent a conservative lineage of monoplacophorans which survived from the Cambrian to the present day. I agree with this statement by Runnegar and Jell (1976), and with the views of Rosov (1975), and support the proposal that the simple conical kirengellaceans seem to be to the most morphologically primitive group of monoplacophorans, and that they probably gave rise to the tryblidiaceans and archinacellaceans through forward displacement of the apex with simultaneous flattening of the shell, and to the cyrtonellaceans by progressive coiling of the lengthening conical tube.

The order Cyrtonellida here includes both the orders Cyrtonellida and Sinuitopsida sensu Starabogatov (1970). As pointed out by Peel (1980, p. 92), the order Sinuitopsida was inappropriately defined in terms of interpreted muscle functions and numbers of supposed gills. Furthermore, Rollins (1969) has shown that the muscle scar patterns of Cyrtonella and Sinutopsis are more alike than previously thought, and Peel (1980) has demonstrated that the musculature of sinuitids can vary considerably.

The superfamily Helcionellacea and some other problematical taxa are assigned to the Monoplacophora here, but their affinities within that group remain unclear.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 16: Classification of the class Monoplacophara to family level adopted here.

Class MONOPLACOPHORA Wenz in Knight, 1952
- Order CYRTONELLIDA Horny, 1963
  - Superfamily CYRTONELLACEA Miller, 1889
    - Family Cyrtonellidae Knight and Yochelson, 1958
    - Family Cyclocyrtonellidae Horny, 1962
    - Family Cyrtolitidae Miller, 1889
    - Family Sinuitidae Dall in Zittel-Eastman, 1913
    - Family Multifariidae Bjaly, 1973
- Order TRYBLIDIIDA Lemche, 1957
  - Superfamily TRYBLIDIACEA Pilsbry in Zittel-Eastman, 1899
    - Family Propilinidae Knight and Yochelson, 1958
    - Family Bipulvinidae Starabogatov, 1970
    - Family Tryblidiidae Pilsbry in Zittel-Eastman, 1899
    - Family Drahomiridae Knight and Yochelson, 1958
    - Family Neopilinidae Knight and Yochelson, 1958
  - Superfamily Kirengellacea Starabogatov, 1970
    - Family Kirengellidae Starabogatov, 1970
    - Family Romaniellidae Rosov, 1975
    - Family Archaeophialidae Knight and Yochelson, 1958.
    - Family Hypseloconidae Knight, 1956
  - Superfamily ARCHINACELLACEA Knight, 1956
    - Family Archinacellidae Knight, 1956
- Order Uncertain
  - Superfamily HELCIONELLACEA Wenz, 1930
    - Family Helcionellidae Wenz, 1930 (sensu Runnegar and Jell, 1976)
    - Family Yochelsioniellidae Runnegar and Jell, 1976
  - Superfamily Uncertain
    - Family Palaeacmaeidae Grabau and Shimer, 1909

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SUPRAGENERIC CLASSIFICATION AND PHYLOGENY OF THE BELLEROPHONTACEAN GASTROPODA

In the above discussion of the conundrum of the class level assignment of the Bellerophontacea, it was concluded that the group belongs to the class Gastropoda and is closely related to the pleurotomariacean Archaeogastropoda. In this chapter, the suprageneric classificaton of the Bellerophontacea is reviewed, and a classification is proposed which satisfies both morphological similarities and inferred phylogenetic relationships. The families and subfamilies of the Bellerophontacea are discussed individually and in more detail in the Systematic Paleontology Section.

The monograph by Ulrich and Scofield (1897) on the Ordovician gastropods from the Cincinnati Arch and Upper Mississippi Valley regions of North America laid the groundwork for subsequent classifications of the Bellerophontacea. They recognized five bellerophontacean families - the Cyrtolitidae, Protowarthiidae (= Sinuitidae), Bucaniidae, Bellerophontidae, and Carinaropsidae. As previously discussed, the Cyrtolitidae Miller, 1889, and the Sinuitidae Dall, 1913, are both now considered to be families of the class Monoplacophora. The Bucaniidae Ulrich and Scofield, 1897, was established to house planispiral genera which were involute, relatively loosely coiled, with a wide open umbilicus, a slit and selenizone, collabral and revolving ornament that always cross at or near right angles, and commonly with expanded apertures. Ulrich and Scofield (1897,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

p. 849-852) included in the Bucanniidae the genera Bucania, Tetranota, Kokenia (= Kokenospira), Megalomphala, Salpingostoma, Tremanotus, Conradella (= Phragmolites), and Oxydiscus (= Tropidodiscus). Ulrich and Scofield (1897, p. 852-857) considered the family Bellerophontidae to encompass planispiral shells which were involute, rapidly expanding and relatively tightly coiled, with a small or closed umbilicus, a slit and selenizone, and generally with only collabral ornament. When revolving ornament was present in a bellerophontid, it was said to always parallel the longitudinal axis of the shell whorls, and not to curve to maintain right angles with curving collabral ornament, as it does in the Bucaninae. Within the Bellerophontidae, they placed the genera Bellerophon, Bucanopsis, Patellostium, Euphemites, Warthia, Mogulia, and Stachella. While concept of this family has remained essentially unchanged to the present day, the generic composition has changed greatly. Euphemites, Warthia, and Stachella have been found to lack a true slit and selenizone and were transferred to sinuate families, Mogulia has been placed in synonomy with B. (Bellerophon) by Knight and others, (1960, p. I 182), and Patellostium is considered problematical and may possibly contain heterogeneous taxa. More recently a number of new genera have been added to the Bellerophontidae (see Knight and others, 1960, and Horny', 1963b). The Carinaropsidae Ulrich and Scofield, 1897, was established for planispiral shells with greatly expanded apertures and a small or completely reduced coil, with a slit, and with a well-developed inner aperture platform.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ulrich and Scofield (1897, p. 857-858) included the genera Carinaropsis and Pterotheca in this family.

Koken (1925) recognized the single family Bellerophontidae, but he divided it into four subfamilies - the Bellerophontinae, Cyrtolitinae, Bucaniinae, and the new Salpingostomatinae, which housed the single genus Salpingostoma.

Wenz (1938, p. 93-112) recognized the same five families as Ulrich and Scofield (1897), but added the families Pterothecidae and ?Procarinariidae. Procarinaria is now considered to be a pelecypod (Horny', 1963b, p. 69). Wenz (1938) retained Salpingostoma within the family Bucaniidae.

In the Treatise on Invertebrate Paleontology, Knight and others (1960, p. I 171-184) constructed a familial classification for the Bellerophontacea based primarily on the character of the labral emargination. This classification was the first to arrange bellerophontacean suprageneric taxa in such a way as to suggest phylogenetic relationships within the group. The Cyrtolitidae were defined by a shallow, commonly angular, labral sinus, with no slit. The Sinuitidae were defined by an open U-shaped labral sinus, with no slit. Three subfamilies were recognized within the Sinuitidae - the Sinuitinae, Bucanellinae, and Euphemitinae. It was said that in some advanced Euphemitinae, the sinus could become a broad slit. All of the slit-bearing bellerophontaceans were placed in the family Bellerophontidae and divided amongst the subfamilies Tropidodis-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

cinae, Bucaniinae (tribes Bucaniides and Salpingostomatides), Carinaropsinae, Pterothecinae, Bellerophontinae, and Knightitinae. The Tropidodiscinae Knight, 1956, were separated from the Bucaniinae because of their narrow coil, broad umbilicus, deep slit, and posterior labral train (Knight and others, 1960, p. I 179). The Knightitinae Knight, 1956, was distinguished from the Bellerophontinae by the possession of strong spiral ornament. It should be noted that Knight and others (1960, p. I 172), included the superfamily Helcionellacea Wenz, 1938, in the suborder Bellerophontina. The class level assignment of the Helcionellacea has also been a matter of debate in recent years (Knight, 1952; Knight and others, 1960; Yochelson, 1967; Pojeta and Runnegar, 1976; Runnegar and Jell, 1976). They are assigned to the Monoplacophara here, but their relationships within that class are considered unresolved.

Horny' (1963b, p. 69) proposed a number of amendments to the classification of Knight and others (1960). First, based on the discovery of multiple pairs of discrete muscle scars in Cyrtolites ornatus by Horny' (1963a), he transferred the family Cyrtolitidae to the class Monoplacophora. He (1963b, p. 69) elevated the Euphemitinae to the family Euphemitidae because of the unique development of the apertural region and anal emargination, and the peculiar development of inductural deposits over much of the shell. He also reestablished the family Pterothecidae because the existence of a true selenizone has not been confirmed in the group, and because of the lack of shell coiling and the presence of a large par-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ietal platform. He reestablished the family Salpingostomatidae, including Salpingostoma, Tremanotus, and Boiotremus, all of which have either a deep slit or a series of open tremata across the dorsum of an expanded aperture. He (1963b, p. 69) erected the new subfamily Grandostomatinae of the family Sinuitidae for sinuate taxa having greatly laterally expanded apertures. He also erected the new subfamily Temnodiscinae of the family Sinuitidae for those taxa in which the sinus became a parallel-sided notch similar to a true slit. Finally, he (1963b, p. 69) erected the new subfamily Cymbulariinae of the family Bellerophontidae for taxa having the slit diverging into a V-shaped sinus rather than meeting the anterior margin of the shell aperture at nearly right angles.

Boucot and Yochelson (1966, p. A7) cited evidence confirming the presence of a true slit in the trilobate genus Plectonotus, which had been previously assigned to the sinuate subfamily Bucanellinae of the Sinuitidae by Knight and others (1960). Because of this new evidence, they transferred Plectonotus to the family Bellerophontidae and proposed the subfamily Plectonotinae for bellerophontids having a trilobate cross-section.

Peel (1972, p. 419) demonstrated that Tremanotus was sinuate and that its series of open tremata were the result of successive closings of a deep sinus. Therefore, he separated the genera Tremanotus and Boiotremus into the new subfamily Tremanotinae of the family Sinuitidae, and returned Salpingostoma to the subfamily Bucaniinae of the Bellerophontidae, thereby eliminating the family Salpingostomatidae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Golikov and Starabogatov (1975) preferred to recognize most suprageneric taxa within the Bellerophontacea as distinct families. They listed the Sinuitidae, Grandostomatidae, Temnodiscidae, Tropidodiscidae, Bucaniidae, Salpingostamatidae, Carinaropsidae, Pterothecidae, Bellerophontidae, Cymbulariidae, Knightitidae, and Euphemitidae.

Because of the discovery of monoplacophoran-liked muscle scars in Sinuites and the morphologically similar Sinuitopsis and Sylvestrosphaera, the family Sinuitidae has recently been transferred to the Monoplacophora. Strangulites Horny', 1962, almost certainly belongs in this family also. Other genera included in the Sinuitidae by Knight and others (1960) have little in common with the true sinuitids except for a rounded sinuate aperture and have been variously assigned to the Monoplacophora or Gastropoda.

Runnegar and Jell (1976, p. 121) assigned the superfamily Bellerophontacea to the Monoplacophora, as previously discussed. They placed all sinuate bellerophontiform taxa in the Sinuitidae and all slit-bearing taxa in the Bellerophontidae. They did not give any subfamily groupings. As previously stated, their classification is disagreed with here.

The suprageneric classification of the Bellerophontacea adopted here is shown in Table 17. It is based mainly on my experience with Ordovician taxa, and conclusions regarding the placement of post-Ordovician taxa are based primarily on the current literature. This classification attempts to show phylogenetic relationships within the Bellerophontacea by the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

grouping of related subfamilies within more broadly based and traditional families.

The sinuate families Bucanellidae Koken, 1925; Grandostomatidae Horny', 1963; and Tremanotidae Peel, 1972, are tentatively recognized here. However, the relationships between these sinuate families, and between them and the slit-bearing families, are still unresolved. No taxa from these sinuate families are present in the fauna under consideration here. The class level assignment of many sinuate bellerophontiform genera is not yet resolved. Some genera are still two poorly known to classify with confidence, however, others have morphological features indicative of gastropod affinities (Peel, 1974, p. 232-234). Sinuitina (of the Bucanellidae here) has been shown to possess gastropod-like columellar muscle scars (Rollins and others, 1971). Ptomatis and related genera of the Grandostomatinae are quite different morphologically from the sinuitids, and Ptomatis has been functionally interpreted to be a gastropod (Rollins, 1966). The euphemitids are considered to be gastropods here primarily because of their extensive inductural deposits. Finally, the tremanotids, which Peel (1972) showed to be sinuate, are considered to be gastropods here because their series of open tremata appear to be homeomorphic with the long open slit of the salpingostomatids. Much work needs to be done on these groups in order to determine whether sinuate forms and morphologically similar slit-bearing forms are phylogenetically related or are homeomophic. It should be noted that Bandel (1982, p. 37) concluded from

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

his studies on the development of modern fissurellids and scissurellids that the presence or absence of a slit is of questionable value in assessing systematic assignments.

All of the slit-bearing families, and many of their subfamilies are represented in the fauna under consideration. Four slit-bearing families are recognized here - the Tropidodiscidae, Bucaniidae, Bellerophontidae, and Carinaropsidae. Each of these families represents a morphological grade of development. The Tropidodiscidae is the most primitive slit-bearing family, and its genera are characterized by narrow, loosely coiled, widely phaneromphalous shells with slits as deep as one-half whorl back from the aperture margin. The Bucaniidae developed from tropidodiscid ancestors. Primitive members of the subfamilies Bucaniinae (such as the Bucania sulcatina group of Ulrich and Scofield, 1897) and Undulabucaniinae are also widely phaneromphalous and have deep slits like the tropidodiscids, but their whorls are wider and more depressed. The Salpingostomatinae, with their deep closed-off slit, probably developed from primitive Bucaniinae. Juvenile specimens of Salpingostoma, prior to the adult expansion of the aperture, closely resemble members of the Bucania sulcatina group.

In more advanced Bucaniinae (such as species of the Bucania lindsleyi group of Ulrich and Scofield, 1897) the shell becomes more tightly coiled, reducing the size of the umbilicus, the whorls become more rapidly expanding and more rounded, and the slit becomes shorter. A similar trend can be seen in the genus Tetranota of the Plectonotinae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

In the family Bellerophontidae, the shells have become still more tightly coiled, so that the umbilicus is closed, or nearly so, and the whorls are generally quite rapidly expanded and rounded, resulting in a more compact shell. The subfamily Bucanopsinae is probably the most primitive in the family. Within that subfamily is seen the incipient building of a parietal platform in the genus Sphenosphaera, which is thought to be ancestral to the Casinaropsidae. In the Carinaropsidae, the rate of whorl expansion has increased to the point where the coil is nearly or completely reduced in the adult, and a large parietal platform has developed to support the visceral mass within the shell. This development reached its peak in the genus Pterotheca.

The morphological trends summarized in the above paragraphs are treated in more detail in the section on Functional Morphology. This morphological progression can also be traced upward stratigraphically from the Upper Cambrian through the Middle Ordovician. The tropidodiscid Chalarostrepsis appeared in the Late Cambrian, followed by the somewhat transitional genus Eobucania in the Early Ordovician. The primitive bucaniids of the Bucania sulcatina group appeared in the early Middle Ordovician (Chazyan-Blackriveran). The more advanced Bucaniinae, the Salpingostomatinae, and the Plectonotinae appeared near the beginning of the late Middle Ordovician (Blackriveran-Rocklandian). The Bucanopsinae, as well as the Carinaropsidae, appeared in the latest Middle Ordovician (Rocklandian-Shermanian).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

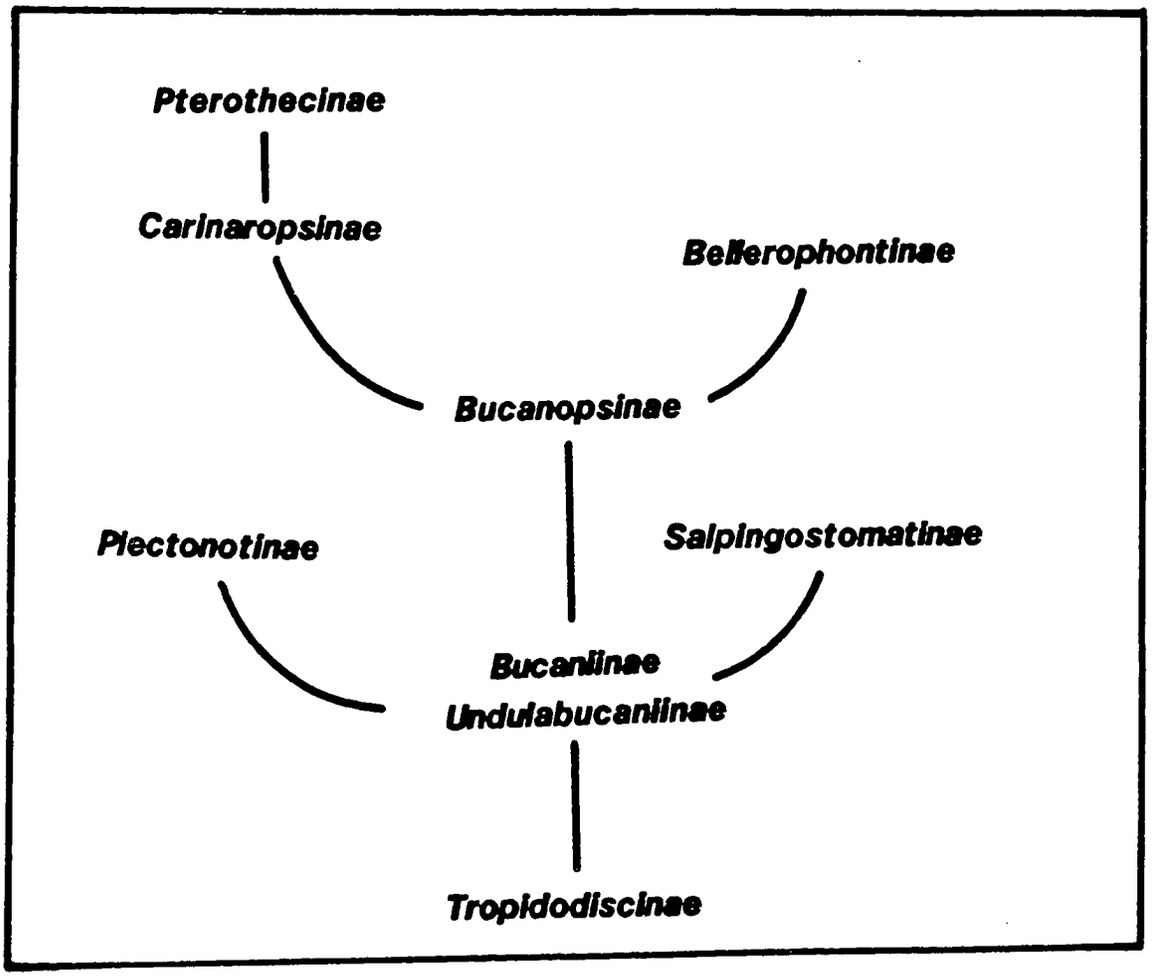


Figure 19: Phylogenetic relationships of bellerophontacean slit-bearing subfamilies during the Late Cambrian-Middle Ordovician in eastern North America. Note that on the familial level, the progression would be Tropidodiscidae - Bucaniidae - Bellerophontidae - Carinaropsidae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The broad epicontinental seas of the Middle Ordovician transgression apparently provided an ideal environment for the radiation of the bellerophontaceans, as well as many other invertebrate groups. The Middle Ordovician radiation of the bellerophontaceans probably had internal and external driving forces. The beginning of continental convergence during that time may have played a part by creating depositional topography over the cratonic sea floor (such as the proto-Lexington and - Nashville Domes - see Stratigraphy Section) which provided heterogeneous, and even somewhat isolated, environmental settings. As mentioned in the Paleoecology Section here, there was also a radiation of calcareous algal groups during the early Middle Ordovician, which would have offered a greater variety of food resources, and thus niches, to the predominantly algal-feeding archaeogastropods. The contemporaneous diversification of other invertebrate groups during the Middle Ordovician would have also encouraged bellerophontacean radiation as entire new communities evolved. Finally, the trend toward more rapid whorl expansion and tighter coiling in the bellerophontaceans produced more mobile shell forms, which must have enabled the group to occupy new, particularly higher energy, environments and additional niches.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 17: A synopsis of the suprageneric classification of the Bellerophontacean Gastropoda adopted herein, with a summary of higher taxonomic criteria.

Class GASTROPODA
 Subclass PROSOBRANCHIA
  Order ARCHAEOGASTOPODA
   Suborder BELLEROPHONTINA
    Superfamily BELLEROPHONTACEA

     Family BUCANELLIDAE - Shell sinuate, phaneromphalous, broad dorsally transverse and radial ornament.

     Family GRANDOSTOMATIDAE - Shell explanate, phaneromphalous, sinuate; transverse and radial lines.

     Family TREMONOTIDAE - Shell gradually expanded, phaneromphalous, with bell-shaped aperture; sinuate, with tremata developed.

     Family EUPHEMITIDAE - Shell somewhat inflated, anomphalous; inductural deposits over most or all of shell, sinus narrow to slit-like.

     Family TROPIDODISCIDAE - Shell laterally compressed, phaneromphalous; slit deep.
       Subfamily TROPIDODISCINAE - As for family.

     Family BUCANIIDAE - Shell gradually expanded, widely phaneromphalous; whorls depressed to evenly rounded; aperture margins tending to flair; usually collabral and radial lines; slit short to deep.
       Subfamily BUCANIINAE - Slit short to deep open at aperture margin, dorsum rounded.
       Subfamily SALPINGOSTOMATINAE - Slit deep, closed off at aperture margin in adult.
       Subfamily PLECTONOTINAE - Whorls trilobate in cross-section, slit short.
       Subfamily UNDULABUCANIINAE - Slit deep; ornament of closely-spaced, regularly-wavy, fine collabral threads only.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Family BELLEROPHONTIDAE - Shell rounded with narrow to closed umbilicus; aperture margins tend to flair; parietal lip generally reflexed; slit short.

Subfamily BELLEROPHONTINAE - Shell convolute or nearly so, whorls rounded to globose; growth lines only.

Subfamily BUCANOPSINAE - Shell anomphalous or nearly so; median ridge on whorl floor; selenizone often slightly elevated.

Family CARINAROPSIDAE - Shell greatly expanded, aperture explanate, with coil nearly or completely reduced; posteromedian platform developed within aperture.

Subfamily CARINAROPSINAE - Shell with small coil, then rapidly and broadly expanded; slit as short notch, generating a selenizone.

Subfamily PTEROTHECINAE - Coil completely reduced, apex marginal and low.

Subfamily PEDASIOLINAE - Coil completely reduced, apex submarginal and elevated.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SYSTEMATIC PALEONTOLOGY

In the following taxonomic descriptions of species, the type species of a genus is described first, if present, and all other species are arranged in ascending stratigraphic order.

The following abbreviations for museum depositories are used.

AMNH American Museum of Natural History, New York, N.Y.

MU Miami University Geology Museum, Oxford, Ohio.

UC Field Museum of Natural History, Chicago, Illinois.

UCGM University of Cincinnati Geology Museum, Cincinnati, Ohio.

USNM United States National Museum of Natural History, Smithsonian Institution, Washington, D.C.

The United States Geological Survey field samples cited in the following text are denoted by a four digit number with a -CO suffix (i.e., 6134-CO). The collecting localities for these and other field samples are listed in the Locality Register (Appendix I).

Phylum MOLLUSCA Cuvier, 1797

Subphylum CYRTOSOMA Runnegar and Pojeta, 1974

Class MONOPLACOPHORA Wenz in Knight, 1952

Diagnosis. - Molluscs with a single, bilaterally symmetrical, cap-shaped, orthoconic, cyrtoconic, or planispiral shell, the apex generally

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

being anteriorly situated, with symmetrical muscle scars arranged in discrete pairs or a partially to completely fused ring around the aperture.

Stratigraphic Range. - Earliest Cambrian (Tommotian) - Holocene.

Discussion. - The above diagnosis is conchological. The Class Monoplacophora can be further defined in biological terms based on the limited knowledge provided by the few known living species as untorted mollusks with an anterior mouth, a posteromedian anus, a lateral to posterior mantle cavity, pseudometamerically arranged organ systems, a radula, and a gastropod-like creeping foot.

Order TRYBLIDIIDA Lemche, 1957

Diagnosis. - Shells cap-shaped to cone-shaped; apex may be central, but is generally anteriorly situated, being subcentral, submarginal, marginal, or supramarginal, and often incurved to varying degrees; muscle scars arranged nearly or completely around inner margin of shell, either as discrete pairs or as partially to completely fused ring.

Stratigraphic range. - Lower Cambrian - Holocene.

Discussion. - This order was erected by Lemche (1957), who described it in primarily biological terms based on the then newly discovered modern monoplacophoran Neopilina. His definition is difficult to apply to a study of fossils, and in reality is probably too limited even for the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

group of genera Lemche recognized as members. The definition given above is paleontological in its applications and is most similar to that of Starabogatov (1970), but with significant changes in the composition of the order. Herein the superfamily Archinacellacea is included in this order; the order Archinacellida is rejected. Also, the superfamily Kirengellacea is included in the Tryblidiida, but has the same composition as Rosov's (1975) order Kirengellida. The superfamily Tryblidiacea is included nearly as conceived by Starabogatov (1970), except for the transfer of the family Archaeophialidae to the superfamily Kirengellacea. For further discussion of these actions, the reader is referred to the introductory section on Phylogeny and Classification and Table 16.

Superfamily TRYBLIDIACEA Pilsbry, 1899

Diagnosis. - Shell cap-shaped, apex marginal or supramarginal; muscle scars of discrete separate pairs.

Stratigraphic range. - Lower Cambrian - Holocene.

Family TRYBLIDIIDAE Pilsbry, 1899

Diagnosis. - Shell more or less cap-shaped, being broadly rounded posteriorly, narrowing rapidly near anterior end; convexity low; apex marginal or slightly supramarginal; comarginal growth lines distinct, some-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

times lamellose, often accompanied by radial lines; muscle scars in 5-8 discrete pairs, commonly more complex anteriorly.

Stratigraphic range. - The family contains species from the Upper Cambrian (Propilina Kobayashi, 1933) to the Holocene (Neopilina Lemche, 1957), but members are most common in Middle Ordovician to Middle Silurian strata.

Discussion. - The original concept of the family Tryblidiidae by Pilsbry (in Zittel-Eastman) (1899) was as follows: "Limpets with muscle scars broken into numerous separate impressions". This definition would now more closely fit the order Tryblidiida. As muscle scars were found in more genera, a considerable diversity was discovered and the concept of the family was restricted to fit the Ordovician-Silurian genus Tryblidium and closely related forms.

Subfamily TRYBLIDIINAE Pilsbry, 1899

Diagnosis. - Same as for family.

Genus HELCIONOPSIS Ulrich and Scofield, 1897

Pl. 2

Diagnosis. - Shell with slightly supramarginal apex, and distinct widely-spaced growth lines crossed by prominent radiating threads.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell cap-shaped, moderate in size, low convexity; aperture outline subovate; posteriorly broadly rounded, narrow anteriorly to small beak area; apex protruding slightly beyond anterior aperture margin; comarginal growth lines distinct, widely and irregularly spaced; radial threads prominent, bifurcating posteriorly. Muscle scars unknown.

Type species. - Helcionopsis fissicostata Ulrich and Scofield, 1897, by original designation; lapsus calami for Helcionopsis striata Ulrich and Scofield, 1897 (Knight, 1941, p. 142).

Distribution. - Middle Cambrian (Ordian stage of Australia) - Middle Silurian (Wenlockian) of Gotland (Sweden). In North America the genus is known only from the Ordovician (Shermanian? - Richmondian).

Discussion. - Runnegar and Jell (1976) reported Helcionopsis sp. from the Middle Cambrian of Australia based on small internal molds having the shell form and radial markings characteristic of this genus. This identification appears to be correct. Easton (1943) described Helcionopsis? reticulatus from the Upper Mississippian Pitkin Formation of Arkansas, but this occurrence requires reexamination.

When Ulrich and Scofield (1897, pp. 826-827) named the genus Helcionopsis, they included three species - H. striata Ulrich and Scofield, H. subcarinata Ulrich and Scofield, and H. radiata (Lindstrom). H. striata, from the Maysvillian and Richmondian strata of the Cincinnati Province, is a well-known, distinctive species. H. subcarinata is known only from a few internal molds from the Prosser Formation (Shemanian-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Edenian) of Minnesota. Its placement in this genus is questionable. From Ulrich and Scofield's (1897, Pl. 61, fig. 28) figure of the species, it appears to have the shell outline of an archinacellid, and its radial ornament is very poorly defined. The third species, H. radiatum, was described by Lindstrom (1884, p. 58) as ?Tryblidium radiatum from the Silurian "crystalline limestone of Wialmsudd near Farosund", and it appears to be a valid member of the genus.

The muscle scars of this genus are unknown, and its higher systematic position is difficult to determine. Knight and Yochelson (1960) placed a question-mark prefix before the genus and associated it with Pilina because of similarities in shell forms and the common possession of radial ornament. These two genera are closely related, but Helcionopsis seems to be distinct in its possession of heavy radiating threads, rather than faint radiating grooves as in Pilina.

HELCIONOPSIS STRIATA Ulrich and Scofield, 1897

Pl. 2, figs. 1-6

Helcionopsis striata ULRICH & SCOFIELD, 1897, p. 827, Pl. 61, figs. 29-30; KNIGHT, 1941, pp. 142-43, Pl. 3, fig. 5; KNIGHT & YOCHELSON, 1960, p. 179, figs. 46, 7.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Tryblidium striatum (Ulrich and Scofield), SHIMER & SHROCK, 1944, p. 437, Pl. 174, fig. 3.

Diagnosis. - Shell elongate subovate, broadly rounded posteriorly, with narrow anterior beak area; apex slightly supramarginal, pointing horizontally to slightly downcurved in later growth.

Description. - Shell elongate subovate in outline, broadly rounded posteriorly, narrowing rapidly to small beak area at anterior end; lateral apertural margin horizontal; dorsally low and broadly convex, becoming more gently convex on posterior slope; anterior slope tightly concave; apex extending slightly beyond anterior apertural margin, pointing essentially horizontally in immature specimens, becoming increasingly downcurved in mature growth stages. Protoconch small smooth cone. Shell thin with surface marked by widely, mostly irregularly-spaced comarginal growth lines of varying prominence; radial threads slightly rounded, bifurcate posteriorly, with secondary ribs intercalated in maturity; radiating costellae vary in spacing over length of shell (4/mm near beak, 3/mm at 5-6mm from apex, and 2/mm at 20mm from apex).

Measurements. - Measurements of this species are listed in Table 18. Table 19 lists the measurements of the distances between growth lines of the holotype (USNM 45827), and Figure 20 graphically displays the apparent growth rate of the specimen.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 18: Measurements of Helcionopsis striata in mm.

Museum Number	Shell Length	Aperture Length	Shell Width	Shell Height	Height of Apex
USNM					
45827	23.25	22.90	17.40	6.1	1.5
263785	14.20	13.70	11.85	5.2	3.5
47494	14.00	13.55	11.15	4.3	2.0

Table 19: Measurements of the growth lines of the holotype, USNM 45827, of Helcionopsis striata in mm. Row A contains the numbers assigned to each growth line moving from anterior to posterior. Row B designates the relative strength of each growth line (s is strong, m is medium, and w is weak). Row C contains the measurements from one growth line to the next, the first measurement being taken from the apex to the first distinct growth line.

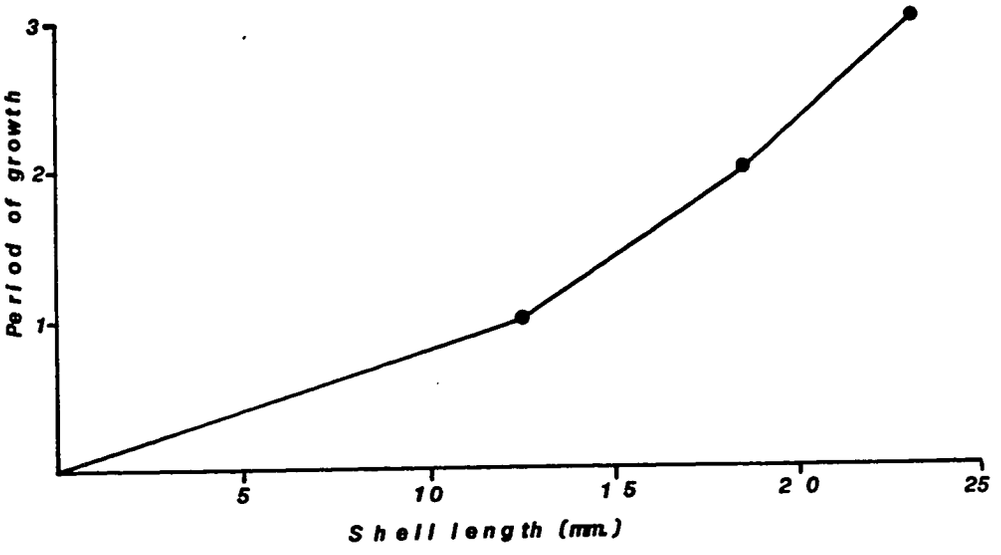
A	1	2	3	4	5	6	7	8	9	10	11	12
B	s	w	m	w	w	s	s	s	m	w	s	m
C	3.4	1.7	2.8	0.5	1.0	1.0	1.9	6.0	1.0	1.4	1.3	1.0

Material. - No new specimens of this species were found in the USGS silicified collections from the Cincinnati Arch region. Only 3 specimens were located and examined. The holotype, USNM 45827, is an external mold in the base of a bryozoan colony (Pl. 2, figs. 1-3 are latex molds made from holotype), as is specimen USNM 47494 (Pl. 1, fig. 4, and fig. 5 is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 20: Graph illustrating apparent growth rate of the holotype (USNM 45827) of Helcionopsis striata. The strongest growth lines were measured from the apex to the posterior shell margin assuming that these lines marked annual growth increments. Three periods of growth were recognized, and an apparent decrease in growth rate with age is evident.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

latex mold). The third specimen, USNM 263785, retains the shell and protoconch (Pl. 2, fig. 6).

Distribution. - The holotype, USNM 45827, is from the Richmondian-age strate in Marion County, Kentucky; no further stratigraphic or locality data are given with the specimen. Specimen USNM 263785 is also Richmondian in age, but is from the "Arnheim" Formation at Clifton, Tennessee. Specimen USNM 47494 comes from the Maysvillian age Bellevue Tongue of the Grant Lake Limestone at Cincinnati, Ohio. Therefore, the species is known only from the middle and upper Upper Ordovician (Maysvillian-Richmondian) of the Cincinnati Arch Province (Table 4).

Comparisons. - Helcionopsis striata is the only species of monoplacophoran in the Cincinnati Arch Province to possess prominent radial ribs that cross growth increments (Pl. 2, figs. 1-6). Vallatotheca unguiformis (Ulrich, 1897) (Kirkfieldian-Shemanian) (Pl. 1, figs. 12-31) and V. manitoulini Foerste, 1914 (Richmondian) (Pl. 1, figs. 8-11) have regular, closely-spaced, sublamellose growth lines, and fine radiating threads that are restricted to individual growth increments.

Discussion. - The two specimens preserved as external molds in the bases of calcitic bryozoan colonies (Pl. 2, figs. 1-3 and 4-5) strongly suggest that the shell of H. striata was aragonitic in composition, having been preferentially dissolved away. The specimen from Tennessee (Pl. 2, fig. 6) is the only known specimen of the species preserving the shell.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The shell is somewhat worn, but it is clear that it was very thin and probably quite delicate. This in part accounts for the rareness of H. striata.

The protoconch preserved in the Tennessee specimen (Pl. 2, fig. 6) is very small, apparently smooth, and symmetrically cone-shaped. It is nothing like the supposed protoconch of Neopilina galatheae described by Lemche and Wingstrand (1959), which was said to be coiled. All other monoplacophorans have shown noncoiled bulbous protoconchs. In any case, the pointed cone-shaped protoconch of H. striata is neither coiled nor bulbous.

The bifurcation and intercalation of the radial ribbing in this species is striking reminiscent of brachiopod costallae patterns (Pl. 2, fig. 1). If other species of Helcionopsis are found, these patterns might prove useful for specific differentiation.

The unusual cone-shaped protoconch, the bifurcation and intercalation of growth lines, and the absence of data on musculature cause some hesitation in the higher systematic assignment of this taxon.

Of considerable interest is the periodicity of the concentric growth lines in the holotype of H. striata (Pl. 2, figs. 1-3). Table 19 lists the spacing distances and the relative strengths of these lines. The pattern shown by the growth lines in Figure 20 could be interpreted as representing seasonal or annual growth increments. The first possible period (lines 1-7) shows a general decrease in the width of the growth incre-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ments. It should be noted that there were two very faint lines between lines 2 and 3 which were about 1.0 from each other and from stronger adjacent lines. The second period (lines 7-8) shows more continuous growth over a relatively large distance, with only very faint cessations of growth. The third period is again more punctuated (lines 9-12), similar to the first. These period boundaries were subjectively selected, but they appear to form a pattern. When the length of each growth period is plotted, the general decrease in growth rate is obvious (Figure 20).

The holotype and its encrusting bryozoan occur in a matrix of fairly coarse biosparite, containing fragments of brachiopods, bryozoans, and trilobites. Because of the quality of the preservation of this specimen's shell markings, and considering the rather high energy conditions indicated by the matrix, it seems that the animal might have been encrusted while it was still alive. The encrusting bryozoan itself is not very thick, so the animal could have probably supported it easily. As in the case with Cyrtolites (Cyrtolites) ornatus, such encrustation may have furnished camouflage and protection from predation. On the other hand, the second encrusted specimen (Pl. 2, figs. 4-5) was probably encrusted after the death of the animal. The bryozoan is well-preserved, but the external mold of the shell in its base is somewhat worn. Furthermore, the bryozoan colony is quite large relative to the monoplacophoran shell, and most likely would have been too massive for the animal to have supported in life.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The Tennessee specimen (Pl. 2, fig. 6) also occurs in a rather coarse fragmental biosparite matrix, but it must have been buried quickly in order for the thin shell to have been preserved. It is difficult to determine whether the slight breakage and wear of the shell came about prior to burial, or by weathering on the outcrop. The latter seems more likely, because the shell retains the protoconch, which would have been readily broken off during transport.

Evidence suggests that H. striata lived in normal marine waters of moderate to high energy, but well offshore in a bryozoan-brachiopod community.

Family PROPILINIDAE Knight and Yochelson, 1958

Diagnosis. - Shell elongate, more or less cap-shaped, wider posteriorly, quite narrow anteriorly, moderately to strongly convex; apex distinctly extending past anterior shell margin; six pairs of elongate muscle scars situated normal to margin of aperture, posterior pair particularly elongate and continuing well into interior of shell.

Stratigraphic range. - Upper Cambrian-Upper Ordovician.

Discussion. - Knight and Yochelson (1958, 1960) recognized this group as a subfamily of the Family Trybilidiidae, including in it Proplina Kobayashi, 1933 and ?Vallatotheca Foerste, 1914.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Starabogatov (1970) used the grouping at the family level and added 3 genera - Kotysium Horny, 1961; Litavina Horny, 1963; and ?Pilinopsis Horny, 1961. Horny (1961) had originally placed both Kotysium and Pilinopsis in the subfamily Trybliniinae. Kotysium resembles Propilina in its shell form, but Horny claimed that its five known pairs of muscle scars are quite different from the latter's. Pilinopsis resembles Pilina in its shell form, but its muscle scars are unknown. The genus Pilinopsis is based on Helcionopsis eminens Perner, and bears closely-spaced comarginal growth lines with short radiating lines restricted to the spaces between these lines (Perner, 1903, figs. 10c), resulting in an ornament pattern which is very similar to that of the genus Vallatotheca. The shell form of Pilinopsis (according to Perner, 1903, Fig. 10a, b) is very similar to that of Helcionopsis, or even to that of some archinacellids. Clearly, the assignment of these genera to higher taxonomic groupings is difficult because of the inconsistent levels of knowledge of their rather simple morphologies.

Vallatotheca, the only genus of the family studied here, is a distinctive taxon that is included in the Proplinidae because its general shell form and its distinctly supramarginal apex, both of which resemble Proplina. Unfortunately, its muscle scars are unknown.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus VALLATOTHECA Foerste, 1914

Pl. 1

Diagnosis. - Shell distinctly convex; apex curved downward, growth lines closely and regularly spaced, sublamellose, with fine radial threads restricted to growth increments between sublamellose growth lines.

Description. - Shell distinctly convex dorsally, broadly rounded in posterior two-thirds, anterior third narrowing rapidly to blunt beak area; apex blunt, downcurved, becoming more so with growth, and extending far beyond aperture margin; aperture outline elongate-oval; lateral aperture margin horizontal; growth lines closely and regularly-spaced, sublamellose; radial threads fine, closely-spaced, restricted to growth increments between sublamellose growth lines. Shell moderately thick.

Type species. - V. manitoulini Foerste, 1914, by original designation, reported from the "Cape Smyth or Waynesville Member of the Richmond, at Clay Cliffs on the eastern side of Cape Smyth, three miles north of Wekmemikongsing, on the eastern shore of Manitoulin Island" (Ontario, Canada) (Foerste, 1914).

Distribution. - The genus is known with certainty from the Lexington Limestone (Kirkfieldian-Shemanian; upper Middle Ordovician) of central Kentucky; and from the Richmondian (upper Upper Ordovician) strata of southwestern Ohio and of Manitoulin Island, Ontario, Canada. Runnegar and Jell (1976) assigned some Middle Cambrian specimens from Australia to the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

genus, but for reasons given below, this assignment is not accepted. Talent (1959) has described specimens from the Lower Devonian of Australia that appear to represent a valid species of Vallatotheca. Therefore, the genus is presently known from the late Middle Ordovidian to the Early Devonian.

Comparisons. - The shell form of Vallatotheca is similar to that of Proplina Kobayashi, 1933, but its sublamellose growth lines with their enclosed fine radial threads distinguish it from that genus.

Vallatotheca is similar to Helcionopsis, as both have radial ornament. However, the close regular spacing of the growth lines, the fine character of the radial threads, and particularly their restriction to individual growth increments, and the general shell form of Vallatotheca easily distinguish it from that genus.

Discussion. - Foerste (1914) originally placed two species in the genus - V. manitoulini Foerste, 1914, and V. unguiformis (Ulrich, 1897). The latter species was described from the Middle Ordovician Lexington Limestone of central Kentucky as Stenotheca unguiformis. The former species was described as the type species of the genus (Foerste, 1914, p. 482, Pl. 4, figs. 4a,b): "Genotype differing from the congeneric Stenotheca unguiformis Ulrich, in its much larger size, and the greater curvature of the beak. The concentric markings are not due to transverse folds, but are successive lamellose outgrowths of the shell, striated only on their apical sides."

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Miller (1897) felt that Stenotheca unguiformis should be included in the genus Tryblidium Lindstrom, 1880. Shimer and Shrock (1944, p. 437) placed this same species in the genus Proplina, and assigned V. manitoulini to the genus Tryblidium. The present investigation reveals no basis to justify the separation of the two species originally placed in Vallatotheca by Foerste (1914). On the contrary, the new silicified material from the Ordovician of Kentucky shows that the two species are morphologically closer than originally believed. Knight and Yochelson (1958, 1960) were influenced by the lack of confidence shown by these previous authors in the validity of the genus Vallatotheca when they placed a question-mark before the genus.

Runnegar and Jell (1976, pp. 131-132, fig. 9A, 1-5) referred four small specimens from the Middle Cambrian of Australia to Vallatotheca sp., but this assignment seems unwarranted because the Australian Cambrian specimens have very coarse comarginal and radial shell markings. Runnegar and Jell referred to the coarse comarginal rings as "plicae", and it is clear from their fine photographs that this is the appropriate terminology. Furthermore, their fig. 9A, 2, clearly shows that the radial ribs cross over and between the plicae. On the other hand, the American Ordovician species have fine radial threads that are restricted to individual concentric lamellae. It therefore appears that the Australian Cambrian specimens are only superficially similar to Vallatotheca, differing significantly in the basic mode of growth of the shell. Runnegar and Jell's

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

specimens bear much closer resemblance to some species of the comarginally plicate genera Latouchella and Helcionella which are also illustrated in their fig. 9. However, the occurrence of radial ribbing on their specimens may give a clue to the ancestry of Ordovician genera which also possess radial ornament, including Vallatotheca, Helcionopsis, Cyrtolites, and others. Radial ornament seems to be more common in the Monoplacophora and Bellerophontida than is generally realized. Most of these genera show basic differences in their types of radial ornament. The types of comarginal and radial ornament in Vallatotheca and Cyrtolites (Cyrtolites), may indicate a common origin for the genera.

VALLATOTHECA MANITOULINI Foerste, 1914

Pl. 1, figs. 8-11

Vallatotheca manitoulini FOERSTE, 1914, p. 482, Pl. 4, figs. 4a,b.

Tryblidium manitoulini (Foerste) SHIMER & SHROCK, 1944, p. 437, Pl. 174, fig. 2.

Diagnosis. - Shell relatively broad (shell L/W = 1.30), somewhat inflated.

Description. - Shell broadly teardrop-shaped in outline, quite broad posteriorly, narrowing in anterior third to blunt beak; shell length/width ratio 1.30; dorsally and posteriorly broad and somewhat inflated; apex bluntly pointed, markedly downcurved to near level of aperture, extending

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

well beyond anterior aperture margin; growth lines closely and regularly spaced, sublamellose; radial threads fine, closely-spaced, restricted to individual growth increments.

Measurements. - The specimens examined were not sufficiently exposed to allow reliable measurements. Foerste's (1914, Pl. 4, figs. 4a,b) figure of the holotype was measured, resulting in a shell length/width ratio of 1.30.

Material. - Only 2 specimens of this species were available for examination, MU 244T (Pl. 5, figs. 8-9) and MU 245T (Pl. 5, figs. 10-11), both calcitic replacements. The holotype, No. 8448 in the collections of Geological Survey of Canada, in Victoria Memorial Museum, Ottawa, Canada, was not examined, but Foerste (1914, Pl. 4, figs. 4a,b) and Knight (1941, Pl. 3, figs. 4a,b) both adequately illustrated this specimen.

Distribution. - Foerste (1914, p. 482) described the species from "The Cape Smyth or Waynesville Member of the Richmond, at Clay Cliffs on the eastern side of Cape Smyth, three miles north of Wekmemikongsing, on the eastern shore of Manitoulin Island", Ontario, Canada. The two specimens examined here come from correlative strata in southwestern Ohio. Specimen MU 244T comes from the Elkhorn biofacies of the Bull Fork Formation (Richmondian), just south or Morning Sun, Ohio. MU 245T comes from the Whitewater Formation (Richmondian) near Camden, Ohio.

Comparisons. - Foerste (1914, p. 482) stated that =V=. =manitoulini= differed from V. unguiformis "...in its much larger size and the greater

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

curvature of the beak". The new silicified material from Kentucky shows that V. unguiformis attains a larger size than previously known (up to 22 mm in shell length), and that the beak increases in its downward curvature in later adult growth so that it nearly reaches the apertural plane (Pl. 1, figs. 27-28). Nevertheless, the 2 species can be separated on the basis of their convexity, V. manitoulini being more inflated, and on their relative shell length/width ratios. V. manitoulini has a ratio of 1.30, and V. unguiformis of 1.40, showing the former species is somewhat wider.

Discussion. - The new specimens of V. manitoulini described here are the first reported since the original description of the species from Manitoulin Island (Foerste, 1914). It is likely that the species is more widespread than presently realized, and its rarity may in part be the result of the poor preservation of small aragonitic shells. Also, as is speculated for Cyrtolites (Cyrtolites) ornatus below, bryozoan encrustation may have played a part in camouflaging the shells from detection by Ordovician predators, as well as Holocene collectors. V. manitoulini and C. (C.) ornatus have very similar shell sculpturing, which in both cases may have been preferred by settling bryozoan larvae (see discussion of C. (C.) ornatus. Lending some support to this speculation is specimen MU 245T of V. unguiformis (Pl. 1, figs. 14-15), which was revealed only after an encrusting bryozoan was partially removed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

VALLATOTHECA UNGUIFORMIS (Ulrich, 1897)

Pl. 1, figs. 12-31

Stenotheca unguiformis ULRICH in ULRICH & SCOFIELD, 1897, p. 843, Pl. 61, figs. 42-44.

Tryblidium unguiforme (Ulrich) MILLER, 1897, p. 771.

Vallatotheca unguiformis (Ulrich) FOERSTE, 1914, p. 482.

Proplina unguiformis (Ulrich) SHIMER & SHROCK, 1944, p. 397, Pl. 174, figs. 7-8.

Diagnosis. - Shell narrowly teardrop-shaped in dorsal outline (Shell L/W = 1.4), moderately convex.

Description. - Shell narrowly teardrop-shaped in dorsal outline, broadly rounded posteriorly, tapering rapidly in anterior third to blunt beak; shell length/width ratio 1.40; apex bluntly pointed, extending well beyond anterior apertural margin, curving downward, the curvature increasing in later growth so that apex may reach to plane of aperture margin; dorsal shell surface broadly and gently convex, increasing in convexity over beak area; growth lines closely and regularly spaced, sublamellose; radiating threads fine, closely spaced, restricted to individual growth increments.

Measurements. - Measurements for V. unguiformis are listed in Table 20 and accompanying graphs are shown in Figure 21.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 20: Measurements for Vallatotheca unguiformis in mm.

Museum Number	Shell Length	Aperture Length	Shell Width	Shell Height	Height of Beak	No. growth lines in 1 mm
USNM						
45990	12.65	10.9	9.05	4.85	0.5	3
265930	13.45	11.1	9.40	5.50	0.9	-
265931	7.50	6.9	6.30	3.50	-	5
265932	7.10	-	6.15	3.20	_	-
265933	9.55	-	6.85	3.35	_	-
387030	6.60	-	5.05	3.10	_	-
	5.80	-	4.55	2.20	_	-
265934	9.80	9.2	7.55	3.80	_	2
265935	10.30	-	7.30	3.50	_	-
265936	21.60	18.4	13.50	7.85	_	2
387031	9.20	-	6.60	4.30	_	2
	-	-	9.20	5.45	_	-
387032	22.50	-	15.00	10.00	_	-

Material. - The type suite consists of 3 silicified syntypes catalogued under the number USNM 45990. The specimen shown here on Pl. 1, figs. 12-15, is designated the lectotype and retains the original number USNM 45990. The other two type syntypes shown in Pl. 1, figs. 21-22 and 23-24 are designated paralectotypes, with the numbers USNM 265930 and 265931, respectively.

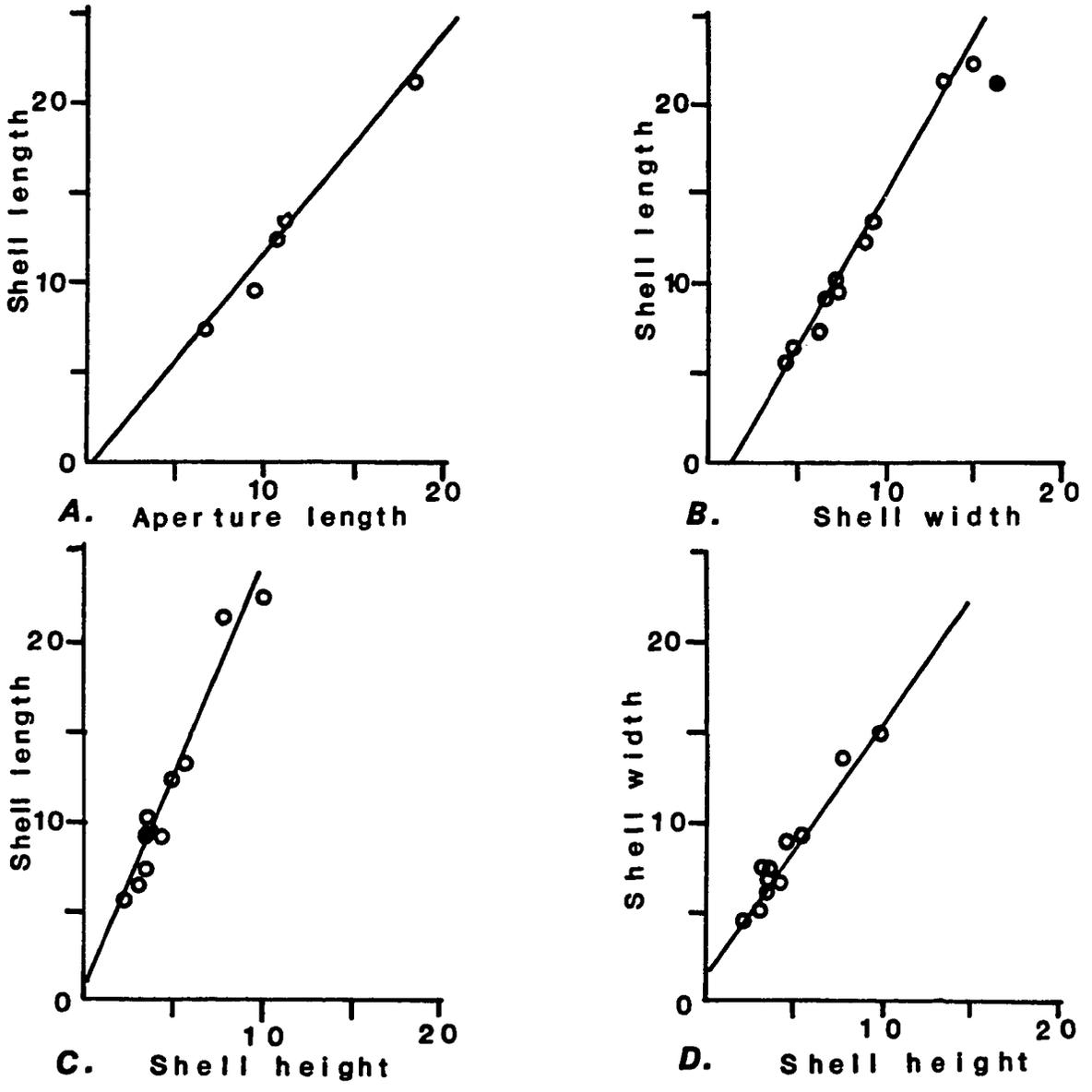
Fifteen specimens of this species were found in the new silicified collections from samples 7784-CO, 6916-CO, 6915-CO, and 5015-CO. Specimens USNM 265932 (Pl. 1, figs. 18-20), USNM 265933 (Pl. 1, figs. 30-31), and USNM 387030 are from sample 5015-CO. Specimens USNM 265934-6 (Pl. 1, figs. 16-17, 29, and 25-28, respectively) and USNM 387031 are all from sample 6915-CO. Collections 5015-CO, 6915-CO, and 6916-CO are all from

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 21: Bivariate plots of measurements made on specimens of Vallatotheca unguiformis. The solid dot in graph B. represents Vallatotheca manitouiini, which is slightly wider than V. unguiformis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Vallatotheca unguiformis



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the Salvisa bed, Perryville Limestone Member, Lexington Limestone, Perryville Quadrangle, Kentucky. Collection 7784-CO is from the Curdsville Limestone Member, Lexington Limestone, Little Hickman Quadrangle, Kentucky.

Distribution. - The museum label with the type suite (USNM 45990, 265930, 265931) reads: "Upper Trenton" at "Harrodsburg Junction, Cincinnati and Southern Railroad, Kentucky." Ulrich (in Ulrich and Scofield, 1897) listed the locality for the types as "Upper beds of the Trenton Group, between Burgin and Danville, Kentucky". The Geologic Map of the Danville Quadrangle, Boyle and Mercer Counties, Kentucky (USGS GQ-985 - Cressman, 1972), shows that the tracks of the Southern Railroad between Burgin and Danville, pass mainly through exposures of the Curdsville Limestone and Grier Limestone Members of the Lexington Limestone, but they also cut across exposures of the Perryville Limestone Member of the same formation just south of Burgin and just north of Danville.

In the USGS silicified collections, one questionable specimen of the species was found in sample 7784-CO from the Curdsville Limestone Member (Kirkfieldian), Lexington Limestone. All other specimens were found in samples 6915-CO, 6916-CO, and 5015-CO, all from the Salvisa bed of the Perryville Limestone Member (Shermanian) of the Lexington Limestone near Perryville, Kentucky.

Comparisons. - V. manitoulini is distinguished by its wider, more convex shell form.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - V. unguiformis is known with certainty only from the Salvisa bed of the Perryville Limestone Member of the Lexington Limestone in central Kentucky. The Salvisa bed is a calcilutite containing ostracods, gastropods and other shelly megafossils, and has been interpreted to represent shallow, quiet marine conditions of greater than normal salinity, such as tidal lagoons (Cressman, 1973). It therefore appears that V. unguiformis occupied nearshore to onshore depositional environments. It might be inferred that the species was an algal grazer.

Superfamily KIRENGELLACEA Starabogatov, 1970

Diagnosis. - Shell conical, occasionally with tendency to coil for 1/4-1/3 whorl; apex high, usually located in a slightly anterocentral to marginal position, but may be central or even posterocentral in position; muscle scars in 6-8 discrete pairs placed about halfway between shell margin and apex.

Stratigraphic range. - Lower Cambrian-Lower Devonian.

Discussion. - Starabogatov (1970) proposed this superfamily for the single genus Kirengella Rosov, 1968. Rosov (1975) erected the order Kirengellida, including three families - Kirengellidae Starabogatov, 1970 (genera Scenella Billings, 1872; Kirengella Rosov, 1968; Moyerokania Rosov, 1970); Romaniellidae n. fam. (Romaniella Doguzhaeva, 1972; Hyseloconus Berkey, 1898; Nyuella Rosov, 1975); and Archaeophialidae Knight and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Yochelson, 1958 (Archaeophiala Koken in Perner, 1903). Concerning this new order Rosov (1975, p. 39) stated: "We have combined the oldest monoplacophorans into a new order with a stratigraphic range extending from the Lower Cambrian to the Middle Ordovician inclusive. They are apparently the most primitive members of the class, ones that gave rise to other branches: to the orders Tryblidiida Lemche, 1957, Archinacellida Knight and Yochelson, 1958, and Cyrtonellida Horny, 1963. Evolution proceeded in the direction of further curling of the shell (order Cyrtonellida) or farther forward displacement of the apex with simultaneous flattening of the shell (orders Tryblidiida and Archinacellida); the muscle scars evolved toward fusion of adjacent pairs of scars, which is to be seen to some degree in members of all four orders" (Figure 18). Rosov's (1975) concept of the Kirengellida is considered useful, but is used here as a superfamily, the Kirengellacea, of the order Tryblidiida.

Family ARCHAEOPHIALIDAE Knight and Yochelson, 1958

Diagnosis. - Shell broadly conical, with subcircular to oval aperture outline; apex high, slightly antecentral to nearly marginal; muscle scars 6-8 discrete pairs, the anterior pairs more complex.

Stratigraphic range. - Middle Ordovician-Lower Devonian.

Discussion. - Knight and Yochelson (1958, 1960) included three genera in this group - Archaeophiala Perner, 1903; ?Micropileus Wilson,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1951; and ?Calloconus Perner, 1903 - but used the taxon as a subfamily (Archaeophialinae) of the family Tryblidiidae. Starabogatov (1970) elevated the taxon to the family level in the superfamily Tryblidiacea. Then Rosov (1975) transferred the family to his new order Kirengellida. The muscle scars of Micropileus and Calloconus are unknown, but because of similarities in shell form, they are generally classified with Archaeophiala, whose muscle scars are well known. Starabogatov (1970) included a fourth genus, Platypilina Horny, 1961, whose type species is Scenella? tardissima Perner, 1903. This species, as figured by Perner (1903, figs. 23a-c, and Pl. 117, figs. 1-3) has radial ornament crossed by growth lines on a shell with a slightly curled anterocentral apex. Platypilina tardissima seems to be close to Macroscenella Wilson, 1951, which was proposed to include many of the Ordovician species assigned to Scenella by Ulrich and Scofield, 1897. The subcentral apex and closely similar shell sculpturing suggests a close relationship between Platypilina and Macroscenella. They seem better accommodated in the superfamily Kirengellacea, and provisionally in the family Archaeophialidae, or because of their Scenella-like markings, possibly in the family Kirengellidae.

Rosov (1975) included the genera Romaniella Doguzhaeva, 1972, Nyuella Rosov, 1975, and Hypseloconus Berkey, 1898, in the then newly proposed family Romaniellidae. Rosov pointed out that the similar shell forms and ranges of Romaniella and Hypseloconus indicate that they are synonyms. This group of genera is characterized in part by the fusion of some pairs

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of muscle scars. Hypseloconus was once placed in the Archinacellacea by Knight and Yochelson (1958, 1960) because it was thought to possess fused scars. Stinchcomb (1980, pp. 45-47) recently described separate discrete paired muscle scars in specimens of Hypseloconus, as well as one or more continuous rings which have previously been interpreted as muscle bands. The classification of Hypseloconus in the superfamily Kirengellacea seems valid, however, its familial affinities remain questionable. The species Nyuella bjalyi Roxov, 1975, has a shell form that is quite comparable to that of some archinacellids. For example, compare the species (Rosov, 1975, figs. 2a-d) with Archinacella arca n. sp. (herein, Pl. 3, figs. 7-10); dorsally there is a resemblance, but the former species has a convex lateral aperture margin, whereas in A. arca the aperture margin is distinctly concave. It seems that the Romaniellidae may be the ancestors of the archinacellids, through flattening of the shell and fusion of the shell muscles, as suggested by Rosov (1975).

Genus MICROPILEUS Wilson, 1951

Pl. 1, figs. 1-7

Diagnosis. - Shells with blunt, elevated, submarginal apex; shell slopes smooth to slightly wrinkled, with no distinct ornament; aperture outline subcircular to subovate.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell high, cap-shaped; aperture outline subcircular to subovate; apex blunt, elevated, located slightly within, or nearly over, anterior shell margin; anterior shell slope slightly concave (particularly in immature shells), flat, or slightly convex; posterior slope broadly convex; comarginal striae and/or weak undulations; muscle scars unknown.

Type species. - M. obesus Wilson, 1951, by original designation; reported from the Lowville-Leray beds (Blackriveran) of eastern Canada.

Distribution. - Wilson (1951) described 2 species from the Lowville-Leray beds (late Blackriveran) of the Ottawa-St. Lawrence Lowland, Canada. The new species described below was found in the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). On the basis of the figures and description given by Hussey (1926, p. 171, Pl. 6, fig. 1), his Archinacella simmonsi from the Stonington beds (Richmondian) of Michigan is herein transferred to Micropileus. Therefore, the genus is known from the upper Middle Ordovician (Blackriveran) to the upper Upper Ordovician (Richmondian).

Discussion. - Wilson (1951) proposed 2 new genera, Micropileus and Macroscenella, for Ordovician cap-shaped shells originally assigned to the genus Scenella, which is presently considered to be restricted to the Cambrian Period. Macroscenella differs from Micropileus in its more subcentral apex, the presence of a supposed labral emargination, and a reticulate type of shell ornament formed by comarginal growth lines and radial

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

striae (rather than only concentric growth lines and/or undulations as in Micropileus). Wilson assigned a number of Middle Ordovician species of "Scenella" described by Ulrich and Scofield (1897), and others, to Macroscenella, but did not assign any previously described species to Micropileus, although she believed many Ordovician species that had been assigned to Scenella would eventually be transferred to Micropileus when better known. Herein the following North American species are placed in Micropileus: M. obesus Wilson; M. ottawaensis Wilson; M. simmonsi (Hussey); and M. variabilis n. sp.

Although Wilson (1951) was uncertain of the heirarchal level at which to place Micropileus, it now seems best to recognize it as a genus closely related to the European Ordovician genus Archaeophiala based on the similar shell form. Macroscenella seems to be more closely related to Scenella than Micropileus, as indicated by its more central apex and reticulate ornament.

MICROPILEUS VARIABILIS n. sp.

Pl. 1, figs. 1-7

Diagnosis. - Shell with submarginal apex and slightly concave to nearly flat anterior slope; aperture outline subcircular; shell exterior sometimes with irregular comarginal undulations.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell medium-sized (up to 12.7 mm in length), high cap-shaped; aperture outline subcircular to broadly subovate, length equals about 1.15 times the width, and about 1.60 times the shell height; apex position somewhat variable, but always submarginal, and generally located about halfway between center of shell and anterior shell margin; apex bluntly pointed, elevated; anterior slope steep, slightly concave to flat; posterior slope more gently sloped and broadly convex; shell essentially smooth, but commonly with one or more concentric undulations; fine radial striae faintly visible near aperture of some specimens; shell fairly thin.

Measurements. - Measurements of M. variabilis n. sp. are listed in Table 21.

Table 21: Measurements for Micropileus variabilis n. sp. in mm.

Museum Number	Shell Length	Shell Width	Shell Height
USNM			
265926	12.7	11.4	7.25
265927	-	12.4	10.65
265928	13.5	11.6	7.60
265929	12.45	10.6	8.25

Material. - This species is known from about 15 silicified specimens from USGS sample 7784-CO, and from 1 silicified specimen from USGS sample 7817-CO. This latter specimen (Pl. 1, figs. 1-4) is here designated the holotype (USNM 265926). Three paratypes from USGS 7784-CO are figured -

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

USNM 265927 (Pl. 1, fig. 7); USNM 265928 (Pl. 1, fig. 5); and USNM 265929 (Pl. 1, fig. 6). The other paratypes are combined under the number USNM 265956, most of these being fragments.

Distribution. - M. variabilis is known only from the lower 6 feet of the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). It was found at USGS localities 7784-CO and 7817-CO in the Little Hickman Quadrangle, Jessamine County, Kentucky. The holotype (USNM 265926) is from 6 inches above the Curdsville-Tyrone contact at a roadcut on Kentucky Rt. 39, 0.3 miles southeast of Black Bridge, which crosses Hickman Creek (USGS 7817-CO). The paratypes come from the basal 2 feet of the Curdsville Limestone, at an exposure 0.3 miles southeast of a bridge crossing the Kentucky River on Kentucky Rt. 27 (7784-CO).

Comparisons. - M. variabilis n. sp. differs from the type species M. obesus Wilson in its slightly smaller size and centrally located apex.

Discussion. - Two specimens of M. variabilis, USNM 265926 (Pl. 1, figs. 1-4) and USNM 265927 (Pl. 1, fig. 7), show a comarginal undulation in the shell about halfway between the apertural margin and the apex. These band-like comarginal undulations are suggestive of a muscle scar in their appearance and location. It is possible that at maturity, the muscles caused an undulation in these thin-shelled animals. Considering the fact that the basal Lexington Limestone is transgressive in nature, it may be that the animal occupied a higher-energy environment where strength of attachment to the substrate would have been of paramount importance. Pos-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

sibly M. variabilis led a limpet-like existence, clinging to protruding irregularities of the lithified surface of the Tyrone Limestone which was being transgressed during Curdsville deposition. The nature of this disconformable contact was described by Cressman (1973, pp. 12-13).

Superfamily ARCHINACELLACEA Knight, 1956

Diagnosis. - Shells cap-shaped, height variable, generally widest anteriorly; apex located distinctly anteriorly, submarginal, marginal, or supramarginal. Muscle scars fused completely into ring-like band, or incompletely into a horseshoe-shaped scar which is open posteriorly; accessory scars sometimes located along the band itself or in opening of horseshoe-shaped scar.

Stratigraphic range. - Chazyan (middle Middle Ordovician) - Richmondian (upper Upper Ordovician). It should be noted that Knight and Yochelson (1960) listed the range for the order as Upper Cambrian to Lower Silurian, but with the transfer of Hypseloconus to the Kiringellacea (Rosov, 1975), all Upper Cambrian and Lower Ordovician taxa are eliminated from the superfamily. This author knows of no Silurian archinacellaceans. Horny (1965b, p. 63) also listed the superfamily as Upper Cambrian to ?Lower Silurian, but noted the group is probably not known above the uppermost Ordovician. He did, however, suggest that Silurian genus Archaeopraga might be a possible descendant of this line.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Knight and Yochelson (1958) defined the order Archinacelloidea as containing the families Archinacellidae Knight, 1956 and ?Hypseloconidae Knight, 1956. This classification was continued in the Treatise on Invertebrate Paleontology (Knight and Yochelson, 1960). In 1958, these authors noted that this order was an unsatisfactory and artificial grouping of forms which did not fit within the concept of the order Tryblidioidea. They defined the Archinacelloidea as: (1958, p. 39) "Shell shape variable, but always bilaterally symmetrical and with distinct apex, presumed to be anterior; muscle scars, where known, forming an incomplete to complete ring".

Horny (1965b, p. 10) corrected the ordinal name to Archinacellida, and defined it as follows: "Shell never coiled, scars often fused to form a complete ring; apex anterior or central". He did not elaborate on subordinal classification.

Knight (1952, p. 52) included molluscan univalves having a continuous muscle scar, such as Archinacella Ulrich and Scofield, 1897, with those having discrete paired scars in the Monoplacophora. He pointed out that in both types the scars have elements that close or nearly close the circlet anteriorly. He proposed that these forms, like the Polyplacophora, did not have an anterior pallial cavity and had not undergone torsion. He suggested that the scars narrowed anteriorly because the muscles attached in that area were extensions from the pedal muscles at each side arching over the head.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

However, Starabogatov (1970, p. 296-7) has argued in favor of the return of the Archinacellida to the class Gastropoda based on the interpretation of the muscle scar patterns in Archinacella, Archinacelliopsis, Archinacellina, and Archaeopraga. It should be noted that Archinacellina and Archinacelliopsis are not present as such in the Treatise on Invertebrate Paleontology (Knight and Yochelson, 1960). Archincellina was erected by Horny (1961) for those species originally assigned to Archinacella which have two pairs of nearly isolated, triangular scars posterolaterally on the inner side of the ring-shaped principal scar. Archinacelliopsis was erected by Horny (1963) for those archincellids possessing an open contra-apical end on the main muscle band, with a pair of discrete scars located in the gap; this genus is represented in Knight and Yochelson (1960, fig. 50,4) by Archinacella patelliformis. Starabogatow (1970, p. 296-7) argued that the cicular muscle of Archinacella approaches slightly too close to the shell margin at the apical end, leaving no room for the head. Conversely, at the contra-apical end it is sufficiently removed, and is even open in Archinacelliopsis. Starabogatov interpreted the pair of discrete scars in the gap at the contra-apical end of Archinacelliopsis as radular muscle scars similar to those of the cap-shaped Monoplacophora and Docoglossa. He believed that the loop-like thickenings of the circular muscle located along the sides of the apex of both genera indicate the original point of insertion of the shell muscles. He compared the position of the pair of muscles scars or the Silurian patellid

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

gastropod Archaeopraga (Horny, 1963d), which converge at the apical end and separate at the contra-apical end, with the positioning of the circular muscle in Archinacella, Archinacelliopsis, and Archinacellina. Based on this comparison, Starabogatov concluded that the contra-apical rather than the apical end was anterior in the archinacellids, and therefore, the Archinacellida should be an order within the Gastropoda.

Starabogatov's arguments (1970) are impressive, but his conclusions require more documentation. Other authors (Horny, 1965; Rosov, 1975) have shown how archinacellid scars fit well into the monoplacophoran picture, and their conclusions are generally accepted. Therefore, the burden of proof lies on Starabogatov (1970) to demonstrate his point of view with greater detail and clarity. His interpretation concerning the placement of the discrete scars in the open contra-apical end of the muscle scar of Archinacelliopsis is particularly interesting. It is not understood why this monoplacophoran would preferentially segregate muscles posteriorly. But then the problem can be looked at in an opposite manner - possibly these discrete scars indicate a more primitive condition than seen in Archinacella, where the muscle band has not yet completely fused. Rosov (1975) suggested that the evolution toward fusion of adjacent pairs of muscle scars is to be seen to some degree in members of all the orders of the Monoplacophora, the trend reaching completion in the Archinacellida. Also, Starabogatov's (1970) argument that there is not sufficient space for the head of the animal beneath the beak of Archinacella does not seem

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

conclusive. The head region of Neopilina seems quite small. For the present, the Archinacellida should continue to be classified as monoplacophorans.

Rosov (1975) recognized the order Archinacellida, but rejected the family Hypseloconidae from that order, rather placing the genus Hypseloconus Berkey, 1898, in his new family Romaniellidae of his order Kirengellida.

Runnegar and Jell (1976) placed the family Hypseloconidae in their order Cyrtonellida and superfamily Helcionellacea, noting the group's possible ancestry to the Cephalopoda, as proposed by Yochelson, Flower, and Webers (1973). These authors further rejected the order Archinacellida, not considering the fusion of muscle scars a significant higher level taxobase, and placed the archinacellids in the family Tryblidiidae. While agreeing with these authors that the archinacellids should not be considered a separate order of monoplacophorans, it is not agreed that they should be included with the Tryblidiidae. Rather, the placement of the superfamily Archinacellacea within the order Tryblidiida is supported. The Tryblidiacea should be reserved for those cap-shaped shells with an anteriorly placed apex and discrete muscle scars. As demonstrated by the emplacement of a pair of discrete muscle scars in the posterior gap of a fused horseshoe-shaped muscle scar in Archinacelliopsis, it appears that the Archinacellacea developed from ancestors with discrete paired scars by progressive fusion of such scars. Possible ancestors of the Archinacel-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lacea might be found within the Family Romaniellidae of the superfamily Kirengellacea. Nyuella bjyali Rosov (1975, p. 40-42) of that family exhibits fusion of the anterior scars of its muscle ring. Probably fusion of muscle scars progressed posteriorly, resulting in forms such as Archinacelliopsis, and finally in the completely fused ring seen in Archinacella.

Family ARCHINACELLIDAE Knight, 1956

Diagnosis and Stratigraphic Range. - As for superfamily.

Discussion. - Knight and Yochelson (1958) recognized two genera in this family - Archinacella and ?Ptychopeltis. The latter genus is a poorly understood form from the Middle Ordovician of eastern Europe (Perner, 1903) that was placed in the Archinacellidae because its shell shape has some resemblance to Archinacella. The muscle scars of Ptychopeltis are unknown and its placement in this family is doubted.

Three genera are presently recognized in the family Archinacellidae - Archinacella Ulrich and Scofield, Archinacellina Horny, and Archinacelliopsis Horny. Until fairly recently, Archinacella included all Ordovician cap-shaped species possessing horseshoe-shaped or circular muscle bands, as well as those species sharing the general shell characteristics of forms in which the muscle scars are known. Horny (1963a) created the genus Archincelliopsis for species such as A. patelliformis (Hall), which possesses an incomplete muscle ring with a pair of discrete scars situated

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in the open posterior end of the ring. In 1961, Horny (1961) also proposed the genus Archinacellina for species such as A. modesta (Perner, 1903), which have two pairs of nearly isolated, triangular muscle scars located on the inner posterolateral margins of a complete muscle ring. The validity of these two genera is questionable, because the muscle scars of very few species of archinacellids have been described, and therefore the variation in the scar patterns within the group is virtually unknown.

Genus ARCHINACELLA Ulrich and Scofield, 1897

Pl. 2-5

Diagnosis. - Shell patelliform, ovate to subcircular, generally widest anteriorly; position of apex variable; lateral apertural margin horizontal and straight to arched; only comarginal shell ornament. Muscle scar a continuous band around the interior periphery of shell.

Description. - Shell low to fairly high, cap-shaped, ovate to subcircular in dorsal profile, usually widest anteriorly; apex distinct, may be situated up to one-third the shell length from anterior shell margin, over that margin, or slightly overhanging it, but shows little or no incurving; lateral apertural profile horizontal and straight to markedly arched. Shell ornament generally weak, only consisting of regular to irregular, comarginal growth lines. Muscle scars form continuous band just inside periphery of shell.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Type species. - A. powersi Ulrich and Scofield, 1897, by original designation.

Distribution. - Chazyan (middle Middle Ordovician) - Richmondian (upper Upper Ordovician). Knight and Yochelson (1960) reported the genus as extending into the Lower Silurian, but without documentation of any Silurian species.

Comparisons. - Archinacella includes a rather heterogeneous assemblage of shell forms. Some have the apex being situated well posterior to the anterior shell margin (Pl. 3, figs. 11-24) to slightly past the anterior margin (Pl. 3, fig. 9). The lateral aperture margin is horizontal and straight (Pl. 4, fig. 7) to distinctly arched (Pl. 3, fig. 9). The shell ranges from low and streamlined (Pl. 2, figs. 8, 10, 11) to high and somewhat inflated (Pl. 3, figs. 5 and 9). The genus is usually identified by its ovate dorsal shell profile, its elevated, anteriorly located, non-incurved to slightly incurved apex, and the presence of only comarginal growth lines. The genus is easily distinguished from other cap-shaped genera in the present study by its lack of radial ornament, its straight or nearly straight apex, and usually by general shell form. Archinacella is separated from its relatives Archinacellina and Archinacelliopsis by the form of the muscle band; the two latter genera have discrete separate accessory muscles posteriorly.

Discussion. - Ulrich and Scofield (1897) proposed the genus Archinacella for species previously assigned in part to Metoptoma Phillips by

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Billings (1965), and in part to Trybliidium Lindstrom by Whiteaves (1884) and Whitfield (1886-1869). In addition, Ulrich and Scofield (1897) described a number of new species. Their original generic description was (1897, p. 821): "Shell patelliform, ovate to subcircular, usually widest anteriorly, forming a low cone with the apex in front of the center and often submarginal. Muscle scars forming a continuous band. Surface markings concentric only". When preserved muscle scars were lacking in specimens, they distinguished Archinacella from Tryblidium by the characteristic wider and more rounded anterior end of the former genus.

Ulrich and Scofield (1897) considered the continuous muscle band of Archinacella to show close affinity to the patellacean gastropods, which have a continuous horseshoe-shaped scar that opens anteriorly. In A. powersi, they described a discrete pair of rostral scars on the band beneath the apex, a narrow pair of scars just within the band on either side of the beak, an anterolateral pair of scars outside the band, a pair of loops extending outward from the band at about midlength, and numerous loop-like irregularities along the outer band around the posterior end (Ulrich and Scofield, 1897, p. 829, Pl. 61, fig. 5). However, Knight (1941, p. 44-45, Pl. 1, figs. a-g) disagreed with their interpretation of the form of the muscle ring in A. powersi. He stated: "These authors interpret what I regard as the sharply impressed inner margin of the principal horseshoe-shaped scar as the principal scar itself wholly ignoring the outer margin of the scar. The evidence for what they regard as ros-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tral scars is almost nonexistent. What they interpret as a narrow pair of scars lying close to the principal scar just within its forward ends I interpret simply as local thickenings of the secondary deposits within the circle of the principal scar. It must be remembered that molluscan muscle scars are commonly produced by resorption of shell material, not by piling up of secondary deposits. Their 'faint impressions of a larger anterior pair without the band' are simply slight spots of seemingly fortuitous ferruginous stain within the area of what I regard as the principal muscle scar".

Knight and Yochelson (1958, p. 43-44) reaffirmed Knight's (1941) interpretation of an "unbroken ring-shaped muscle scar" in A. powersi, but further noted the new discovery of a specimen of A. patelliformis (Hall) from the Blackriveran strata of New York State which shows instead of a continuous ring, an incomplete ring with a pair of scars at the posterior of the exposed continuous ring (Knight and Yochelson, 1958, Pl. 5, fig. 4). They (1960, fig. 50, 1b and 4) later illustrated both types of archinacellid muscle scars. As previously pointed out, Horny (1963) erected Archinacelliopsis for A. patelliformis.

Thirty-two species of Archinacella have been proposed from North America; all are from Ordovician strata in the eastern half of the continent. The large number of species in a genus with such a simple shell form and ornament seem unlikely. The conceptualization of species is aggravated by the high degree of intraspecific variability in the shell

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

form of many monoplacophorans. Unfortunately, many species of Archinacella are known from only a few specimens that are often poorly preserved. In the present state of knowledge of the species of Archinacella, there is no alternative to proposing new species names for distinctive morphologies. Even the new silicified collections described here do not have adequate numbers of specimens of Archinacella for variability analyses, and in general, the quality of preservation is not good. The archinacellids were generally too badly fragmented to allow reliable measurements. However, these samples are sufficient to have given a better impression of intraspecific variability on a qualitative level than any other collections known, largely because it is known whether or not all of the specimens actually came from a single bed.

Many species of Archinacella are known only from internal molds, and thus are unsatisfactory for diagnosis and comparison. The preservation of A. richmondensis Ulrich and Scofield as external molds in the bases of calcitic bryozoan colonies (Pl. 3, fig. 16; Pl. 4, figs. 8-9) suggests that the shell of Archinacella was probably aragonitic, and thus easily dissolved. Also, where known, the shells of Archinacella seem to be fairly thin (Pl. 2, figs. 13-14, Pl. 3, figs. 19-20). These facts suggest why well-preserved specimens are rare. Collections of any one species generally consist of only a few specimens, which may simply be a product of poor preservation, or it may be partly related to the population dynamics of the species. It is possible that these animals maintained

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

small populations, or had widely spaced population distributions. Still another factor may be the apparent ecology of these animals. Their continuous muscle bands suggest that the archinacellids led a limpet-like existence, clinging to solid objects in environments or even micro-environments where rapid burial was unlikely.

Specific differences are based on 5 main criteria: (1) position of the apex relative to the anterior apertural margin; (2) relative convexity and height of the shell; (3) the horizontal or arched character of the lateral apertural margin; (4) the shape of the shell aperture; and (5) shell length/width ratios. In most specimens examined, the shell margins are fragmented and incomplete so that criteria 3 and 4 were often difficult to evaluate. The species of Archinacella recognized here are based on small samples and some may be synonymized when better material becomes known.

ARCHINACELLA SIMULATRIX Ulrich and Scofield, 1897

Pl. 2, figs. 7-12

Archinacella simulatrix ULRICH & SCOFIELD, 1897, p. 833, Pl. 61, figs. 10-11; GRABAU & SHIMER, 1909, p. 606, figs. 805f,i.

Diagnosis. - Shell small (length ≦ 15 mm), subovate, wider anteriorly, with narrowly rounded dorsomedian crest; aperture horizontal; apex sharp, scarcely incurved, extends to nearly over anterior shell margin.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell small for genus (length ≤ 15 mm); subovate, slightly wider anteriorly, convexity low; narrowly rounded dorsomedian crest runs most of length of shell, crest sharpest toward apex; lateral slopes splay outward slightly in larger specimens; apex sharply pointed in dorsal view, scarcely incurved with gently concave anterior shell slope, extends to just over or scarcely beyond anterior shell margin; comarginal growth lines faint.

Measurements. - Measurements of A. simulatrix are listed in Table 22 below. Note that measurements were often made on imcomplete specimens and thereby are open to some amount of error.

Table 22: Measurements for Archinacella simulatrix in mm.

Museum Number	Shell Length	Shell Width	Shell Height	Height of apex
USNM				
45695	10.5	8.3	3.3	2.1
47471	14.88	13.0	5.5	2.8
265944	11.55	10.0	4.6	-
265945	12.60	9.6	4.6	-
387033	9.90	7.3	4.5	-
	8.4	6.8	3.4	-
	6.1	4.2	2.15	-
387034	10.15	8.5	-	-
387035	10.2	8.0	4.5	-
	11.2	8.3	5.0	-
387036	7.7	6.6	2.85	-

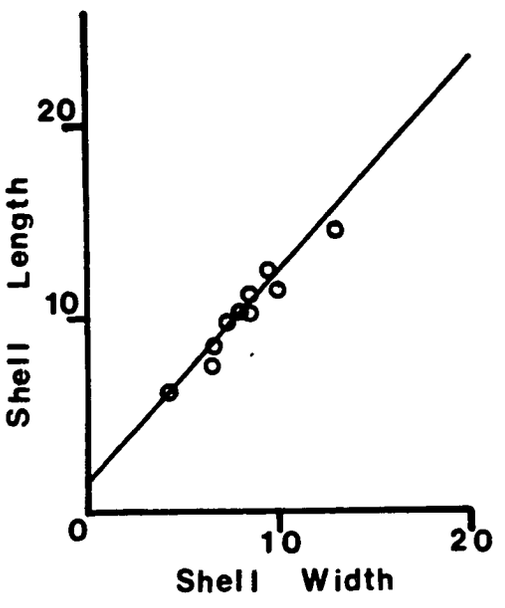
Material. - The holotype of A. simulatrix (USNM 45695) is an external mold in the base of a bryozoan colony from the Decorah Formation (Rocklandian-Kirkfieldian) at St. Paul, Minnesota. A latex replica is

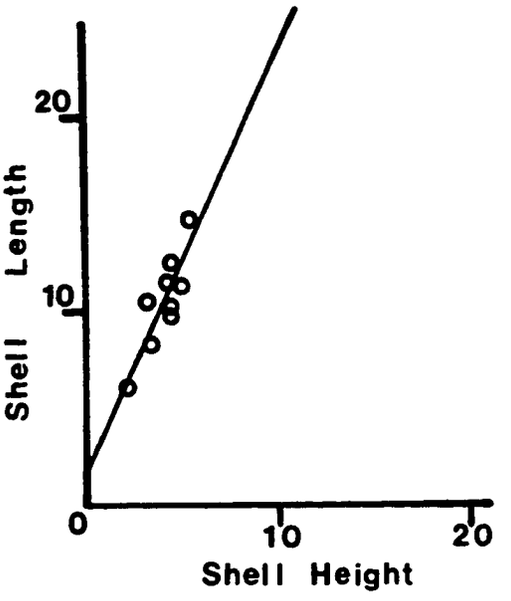
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

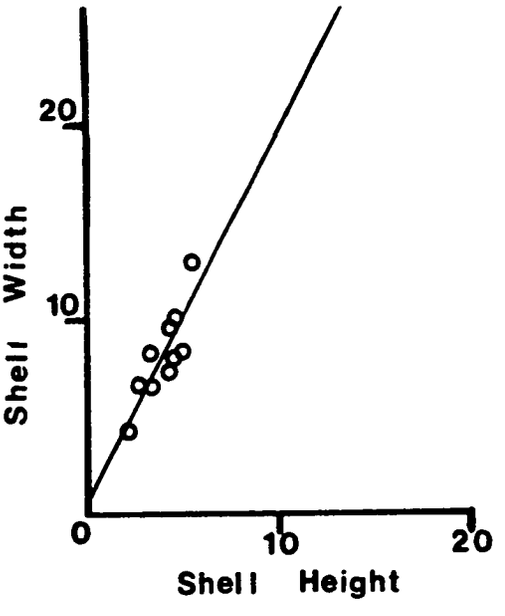
Figure 22: Bivariate graphs of measurements made on specimens of *Archinacella simulatrix*.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Archinanella simulatrix







Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

shown on Pl. 2, figs. 7-8. The best preserved specimen examined was USNM 47471 (Pl. 2, fig. 12), a calcitic cast which the museum label says is from the "Modiolodon beds of the Hermitage member" of the Lexington Limestone. These beds are now included in the upper Logana Member of the Lexington Limestone.

The new silicified collections contain mostly fragmented specimens of A. simulatrix. Poorly preserved specimens, here termed A. cf. A. simulatrix, were recognized from the Tyrone Limestone (1 specimen from 6035-CO; USNM 387034); and from the Curdsville Limestone (7784-CO; USNM 387035), Grier Limestone (4874-CO and 4959-CO; USNM 387036) Members of the Lexington Limestone. A number of fairly well-preserved specimens of A. simulatrix were found in sample 4073-CO (USNM 387033) from the Grier Limestone Member, and 2 of these, USNM 265944 (Pl. 2, fig. 11) and USNM 265945 (Pl. 2, fig. 10) are figured here.

Distribution. - Ulrich and Scofield (1897, p. 833) listed A. simulatrix from the "Black River Group, Phylloporina bed, St. Paul, Minnesota; Trenton Group, Modiolodon bed, Frankfort, Kentucky". According to Weiss (1957) the Phylloporina-Fucoid bed in Minnesota would presently be considered the upper Decorah Formation, which would be Kirkfieldian rather than Blackriveran. The Modiolodon bed of Kentucky would now be placed in the Logana Member of the Lexington Limestone, which is also Kirkfieldian in age.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The new silicified collections contain probable specimens of this species from the Tyrone Limestone (Rocklandian) and the Curdsville and Grier Limestone Members of the Lexington Limestone (Kirkfieldian-Shermanian). Specimen USNM 47471 confirms the occurrence of the species in the Logana Member of the Lexington Limestone. Therefore, A. simulatrix may occur in the Rocklandian strata of Kentucky, and it does occur in the Kirkfieldian age rocks of Kentucky and Minnesota, and the Shermanian rocks of Kentucky.

Comparisons. - A. simulatrix is generally easily recognized by its small size, wide anterior end, and its relatively sharp dorsomedian crest leading to its marginal apex.

Ulrich and Scofield (1897) stated: "This species is distinguished from A. deleta, A. valida, A. semicarinata, and A. patelliformis in having a less regularly elliptical outline, the anterior half being wider. In this particular it is like the much larger A. cingulata."

Discussion. - This is the most common species of Archinacella in the upper Middle Ordovician of Kentucky. The fact that it is known in Kirkfieldian strata of Kentucky and Minnesota suggests that it is useful for midcontinent correlation.

The preservation of the holotype as an external mold in the base of a calcitic bryozoan colony suggests the shell was aragonitic. The specimen was apparently encrusted after the animal had died. The shell was somewhat worn before encrustation, as the surface of the latex replica (Pl. 2, figs. 7-8) is somewhat irregular.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The specimens from sample 4073-CO (Pl. 2, figs. 10, 11) from the Grier Limestone Member occur with the pelecypod Cyrtodonta sp. Specimens from the Logana Member of the Lexington Limestone (Pl. 2, fig. 12) occur with the pelecypod Modiolodon sp. It is therefore inferred that A. simulatrix was a common member of molluscan communities.

ARCHINACELLA VALIDA (Sardeson, 1892)

Pl. 2, figs. 15-16

Tryblidium validum SARDESON, 1892, p. 337, Pl. 6, figs. 1-2.

Archinacella valida (Sardeson) ULRICH & SCOFIELD, 1897, p. 832, Pl. 61, figs. 14-15.

Diagnosis. - Moderate-sized shell (16-18 mm length), with ovate outline; aperture margin horizontal; apex small, submarginal, slightly incurved.

Description. - Shell moderate in size, regularly ovate in outline, length/width ratio about 1.2; aperture margin horizontal; apex laterally compressed, dorsally narrowly rounded, broadening posteriorly, located just within shell margin, slightly incurved so that anterior shell slope is distinctly concave; growth lines faint but distinct, closely and fairly regularly spaced.

Measurements. - Measurements of USNM 47467 are: length from apex to posterior margin 17.2 mm; aperture length 18.2 mm; aperture width 15.4 mm;

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

shell height 6.0 mm; height of apex over anterior shell margin 3.3 mm Ulrich and Scofield (1897) gave measurements of a small specimen as: "Length 16.5 mm; width 15.4 mm; height nearly 7 mm".

Material. - Only one specimen was examined (USNM 47467); it is labelled "Archinacella patelliformis, from the Trenton (Ctenodonta horizon), Mt. Parnassus, Columbia, Tennessee". This specimen is not A. patelliformis Hall, because it is larger, relatively broader, it's dorsum is not as carinate, and its apex is submarginal. The specimen is a calcitic cast embedded in a buff biosparite matrix; most associated skeletal debris are brachiopod fragments, but there is also a small bellerophontid, possibly Bucanopsis.

Distribution. - Ulrich and Scofield (1897, p. 833) listed A. valida as from the "Trenton Group, Clitambonites bed, near Canyon Falls and Kenyon, Minnesota". According to Weiss (1957, fig. 1), the Clitambonites bed, which was basal "Trenton" in Winchell and Ulrich's stratigraphic classification, is now considered the Cummingsville Member of the Galena Formation (Kirkfieldian-Shemanian). Specimen USNM 47467 came from the Ctenodonta Member of the Hermitage Formation of Tennessee (Kirkfieldian). A. valida is therefore known from Kirkfieldian-Shemanian aged strata in Minnesota and Tennessee.

Comparisons. - Ulrich and Scofield (1897, p. 832) stated: "Specifically A. valida is nearer A. (Carinaropsis) patelliformis Hall from the Trenton of New York, than any other form known to us. The lateral profile

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

especially is nearly or quite the same in the two species. The New York species, however, is smaller, has more distinct surface markings, and is obtusely carinated on the back. It should be noted further that the apex of A. patelliformis is more incurved and extends past the anterior shell margin slightly".

In dorsal view A. valida is similar to A. powersi Ulrich and Scofield (see Ulrich and Scofield, 1897, Pl. 61, figs. 4 and 14), but the two species can be easily distinguished in lateral view, the former being higher and having a horizontal lateral apertural margin, the latter being lower and having an arched apertural margin.

Discussion. - The single well-preserved specimen (USNM 47467) studied here agrees with every essential aspect of A. valida described by Ulrich and Scofield (1897). The only notable difference is that the specimen from Tennessee is not as inflated as the specimens they described from Minnesota.

ARCHINACELLA CINGULATA Ulrich, 1897

Pl. 2, figs. 22-26

Archinacella cingulata ULRICH in ULRICH & SCOFIELD, 1897, p. 829-830, Pl. 61, figs. 1-2.

Diagnosis. - Shell large (up to 44 mm in length), with broadly convex lateral profile; apex blunt, slightly downcurved, projecting

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

slightly beyond aperture margin; growth lines distinct, sublamellose, with close regular spacing.

Description. - Shell relatively large for genus, outline subovate, wider anteriorly, narrowing posteriorly gradually; lateral profile broadly convex with greatest shell height about one-third shell length back from anterior shell margin; lateral apertural margin nearly horizontal, scarcely arched; apex blunt, curved downwards slightly to about one-half the shell height, and projecting just barely beyond anterior apertural margin. Growth lines distinct, sublamellose fine ridges with close regular spacing; over most of shell there is nearly consistent 1 mm spacing of growth lines.

Measurements. - Measurements for A. cingulata are listed below in Table 23.

Table 23: Measurements for A. cingulata in mm.

Museum Number	Length - apex to post. margin	Aperture Length	Aperture Width	Shell Height	Height of Apex
USNM 45686	30.4	29.0	23.85	11.5	4.5
MU 249T	44.1	43.6	34.5	12.1	6.8

Material. - The holotype of the species (USNM 45686) (Pl. 2, figs. 22-24) is a worn silicified replica from the "Amygdalocystites bed" of the Curdsville Limestone Member of the Lexington Limestone. The only other known specimen is in the Miami University Collections (MU 249T)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Pl. 2, figs. 25-26); that specimen is a large internal mold from the Clays Ferry Formation, collected near Owenton, Kentucky, about 2 miles east of the intersection of U.S. Rt. 127 and Ky. Rt. 35.

Distribution. - Kirkfieldian (upper Middle Ordovician) to Edenian (lower Upper Ordovician) of Kentucky.

Comparisons. - Ulrich and Scofield (1897) noted that A. powersi differs from A. cingulata by its strongly arched aperture. A. simulatrix resembles A. cingulata somewhat in general shell form, but the latter species is much larger and has much more distinct growth markings.

Discussion. - Ulrich and Scofield (1897) described the aperture of A. cingulata as horizontal, but in both specimens examined here, the lateral apertural profile is slightly arched. There also seems to be faint traces of radiating lines between the growth lines in this species, but this observation cannot be confirmed without more specimens. If so, the species should be removed from the Archinacella, and possibly be placed in Helcionopsis or Vallatocheca because of the similarity in their regular sublamellose growth lines.

ARCHINACELLA cf. A. DEPRESSA Ulrich and Scofield, 1897

Pl. 2, figs. 13-14

Archinacella depressa ULRICH & SCOFIELD, 1897, p. 830, Pl. 61, figs. 8-9.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell medium-sized for genus (16-17 mm in length), outline broadly oval, convexity low; anterior slope gently concave, posterior slope gently convex; apex located distinctly within anterior shell margin; lateral apertural margin slightly arched; growth lines faint and closely spaced through most of shell, becoming strong and lamellose near outer shell margin.

Measurements. - Measurements for the single specimen examined are as follows: length from beak to posterior margin 15.0 mm; aperture length 16.8 mm; aperture width 15.2 mm; shell height 5.2 mm; height of apex ~3.6 mm.

Material. - The single specimen identified here as A. cf. A. depressa (USNM 59295) is a siliceous cast embedded in a wackestone matrix containing fragments of bryozoans and brachiopods.

Distribution. - Ulrich and Scofield (1897) reported A. depressa from the "Stones River Group, Vaunexemia bed, Minneapolis, Minnesota". According to Weiss (1957, fig. 1), this would be in the middle part of the Platteville Formation (Rocklandian). The specimen described here (USNM 59295) comes from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shemanian) at Hartsville, Trousdale County, Tennessee.

Comparisons. - Ulrich and Scofield (1897) emphasized the similarity between A. depressa and A. perovalis (Whitfield) from the Platteville Formation (Rocklandian) of the Minnesota-Wisconsin area, saying that the only difference of any consequence between the two species is the greater width of A. depressa.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

A. subrotunda Ulrich and Scofield from the Decorah Formation (Rocklandian-Kirkfieldian) of Minnesota is also somewhat similar to A. depressa, but the former is higher and more convex based on Ulrich and Scofield's (1897, Pl. 61, figs. 26-27) illustration. Wilson (1951, p. 18, Pl. 1, figs. 9-10) described A. subrotunda from the Cobourg beds (Edenian?) of Ontario, but her figures look more like A. depressa, having a shell with low convexity.

Discussion. - The single specimen from the Cannon facies of Tennessee compares favorably with the description of A. depressa given by Ulrich and Scofield (1897). Points in which it agrees are its broad ovate outline, its low convexity, its submarginal apex, and its slightly arched lateral apertural marring. Measurements given for the species by Ulrich and Scofield (1897, p. 830) are length 20.5 mm and width 15.2 mm, which gives a L/W ratio of 1.13. The Tennessee specimen has a L/W ratio of 1.10 showing close agreement. The species is known from Rocklandian aged strata in Minnesota and from Kirkfieldian-Shemanian aged strata in the Cincinnati Arch Province.

ARCHINACELLA ALTA new species

Pl. 3, figs. 4-6

Diagnosis. - Shell medium-sized, high, and inflated; outline ovate; lateral aperture margin horizontal; apex blunt, slightly downcurved, situated over shell margin.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell medium-sized for genus (about 15 mm in length), high, somewhat inflated, with highly convex dorsal and posterior slopes; highest point on shell about one-third the shell length back from anterior margin; anterior slope distinctly concave; shell outline regularly oval; beak area narrowly rounded medially in dorsal view, becoming broader gradually toward posterior; apex blunt, slightly downcurved about three-eights the shell height, situated above anterior shell margin; lateral aperture margin horizontal to very slightly arched; growth lines barely discernible.

Measurements. - Measurements on the holotype (MU 248T), are: shell length at aperture or apex 14.75 mm; aperture width 13.2 mm; shell height 8.1 mm; and height of apex 4.9 mm (L/W 1.12; L/H 1.82; W/H 1.63).

Material. - The holotype (MU 248T) is the only known specimen. It appears to be a highly recrystallized calcitic cast, and was collected from the Clays Ferry Formation in northern Kentucky. The locality No. OC3 with the specimen could not be traced. The Miami University museum label states that the late Prof. Shideler suggested the specific name of "alta" for the new species, referring to its high shell, and so that name is used here. The specimen is partially embedded in a limestone matrix.

Distribution. - The new species is known only from the Edenian-aged part of the Clays Ferry Formation of Kentucky.

Comparisons. - The new species bears some resemblance to A. laevis Foerste (1924, p. 202, Pl. 30, figs. 3a-d) from the Richmondian of Snake

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Island, Ontario, but the former has a much higher shell. It also resembles A. subrotunda Ulrich and Scofield (1897, p. 834, Pl. 61, figs. 6-7) in having a marginal apex and a horizontal aperture margin. However, when the proportionate measurements are compared, the difference is striking. For example, the shell length/shell height ratios for A. alta, A. subrotund, and A. laevis are 1.8, 2.5, and 3.1, respectively (measurements for latter two species taken from illustrations of holotypes).

ARCHINACELLA? DAVISI new species

Pl. 3, figs. 1-3

Diagnosis. - Shell very large, with broad subovate outline; beak long and fairly narrow, with apex slightly downcurved and apparently extending well beyond the anterior shell margin; lateral apertural margin straight.

Description. - Shell very large for genus (70 mm in length) outline broadly subovate; dorso-lateral profile broadly convex; lateral aperture profile apparently horizontal; beak area long and narrow, ending in pointed apex which is slightly downcurved and apparently extends well past anterior aperture margin; anterior slope distinctly concave. Shell thickness and markings unknown.

Measurements. - The holotype and only known specimen measures: length from apex to posterior margin 70 mm; aperture length 63 mm; aperture width 54 mm; shell height 23 mm. The specimen is poorly preserved (Pl. 3, figs. 1-3) and all these measurements are only approximations.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - The holotype (CMNH P2) is the only known specimen of the new species. The specimen is a large internal mold in rather fissile gray shale and the actual shell boundaries are difficult to pinpoint. The lines which appear to be possible concentric growth lines are actually shale laminae (Pl. 3, figs. 1-3).

Distribution. - The holotype was found in the Cincinnati Museum of Natural History Collections with only locality data. It comes from the Gallatin, Kentucky area. The character of the matrix and the stratigraphy of the type area strongly suggest that the specimen came from the Kope Formation (Edenian).

Derivation of specific name. - The specific name for the new species is named for Richard Davis of the Cincinnati Museum of Natural History, through whose courtesy the specimen was made available for study.

Comparisons. - Because of the poor preservation of the holotype, its generic placement is open to question. The only other possible generic assignment is Carinaropsis, which also has a long extended beak area (the coil could be missing in the internal mold). However, the dorsal beak of A.? davisi shows no evidence of a carina, it is quite rounded, and there is no evidence of an anteromedian slit or a trailing slit-band; also, the aperture outline appears too regularly ovate for Carinaropsis. If the generic assignment is correct, this is the largest known species of Archinacella.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ARCHINACELLA cf. A. PULASKIENSIS Foerste, 1914

Pl. 2, figs. 17-18

Carinaropsis patelliformis (in part) HALL, 1847, p. 306, Pl. 83, figs 7a,b.

Carinaropsis patelliformis Hall, MILLER, 1874, p. 314; (in part) 1889, p. 400.

Archinacella pulaskiensis FOERSTE, 1914, p. 309, Pl. 3, figs. 3a-d; 1924, p. 203, Pl. 31, figs. 3a,b, and Pl. 29, fig. 1.

Description. - Shell fairly small for genus (about 8 mm in length), subovate, broader anteriorly than posteriorly; convexity low; lateral aperture margin horizontal; beak area sharply angular dorsomedially, rapidly becoming broadly convex postero-medially; apex sharply pointed, slightly incurved, situated over anterior aperture margin; concentric growth lines fairly distinct.

Measurements. - The measurements for the single specimen available are as follows: shell length 8.4 mm; shell width 6.4 mm; shell height 2.2 mm; widest point on shell (from apex) 3.5 mm.

Material. - The only specimen available was UC 19640 from Maysvillian strata, probably of the Cincinnati area (no locality data were included with the specimen). This specimen is small with poorly preserved margins. The type specimens were not examined except from the illustrataions of the author (Foerste, 1914, Pl. 3, figs. 3a-d).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - The single specimen UC 19640 was labelled as coming from the "Maysville", but no further stratigraphic or locality data were given. The specimen most likely comes from the Cincinnati, Ohio area. Miller (1874, p. 314) reported finding Carinaropsis patelliformis (Hall) (the Cincinnatian forms of this species described by Hall, 1847, are now considered A. pulaskiensis) from "the quarries back of Cincinnati". These quarries were in the Fairview Formation (Maysvillian).

Comparisons. - This species is similar to A. simulatrix, but loses the angularity of the beak posteriorly. Without more and better material no further comparisons are possible, but the possibility of synonymy between the two species should be kept in mind.

Hall (1847, p. 183) remarked about Carinaropsis patelliformis: "There are one or two other species in the Hudson River Group [as the Upper Ordovician was then called], and a single more elevated one in the Trenton limestone, which has not been satisfactorily determined". Miller (1874, p. 314) identified the same species in the Maysvillian strata at Cincinnati, Ohio, reaffirming the species presence there in 1889 (p. 400). In their discussion of Archinacella deleta, Ulrich and Scofield (1897, p. 831) stated: "This is the first of a group of species that seems to be related to A. (Carinaropsis) patelliformis Hall. One or the other of these forms occurs in, or in the equivalent of, every one of the principal beds between the base of the Black River Group and the top of the Cincinnati formation. None of the western or northwestern species however seem

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to be strictly identical with the New York types of patelliformis, all of them having a nearly smooth surface, while Hall's species according to his figures and description has the surface marked by regular concentric, sub-lamelliform striae". They then compared the following species to A. patelliformis: A. deleta, A. valida, A. semicarinata, and A. simulatrix.

Foerste (1914, p. 309) described A. pulaskiensis from the late Maysvillian Pulaski Formation of New York and Quebec, starting his description as follows: "The form figured by Hall from the Lorraine at Pulaski, New York, as Archinacella patelliformis, differs in outline from his Trenton types... This shell [A. pulaskiensis] is broader and more convex along the middle and the outline, therefore, rather broadly ovate than ovate oblong. Otherwise the shells are closely similar". Foerste (1924, p. 203) also cited this species from the Cryptolithus zone of New York and Quebec, which he correlated with the "Southgate member of the Eden" in the Cincinnati area.

The species in the Maysvillian strata of the Cincinnati area reported by Miller (1874, 1889) is here placed in A. pulaskiensis Foerste because it agrees with that species in its small size, low convexity, and sharply pointed, marginal apex. The exact apertural outline of the shell of the present specimen is not shown, and unfortunately this character of the species is stressed by Foerste in comparing it with A. patelliformis. The present assignment is supported by the correlative stratigraphic occur-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

rence of the New York - Quebec and the Cincinnati area specimens. However, a review of all species which are directly comparable to A. patelliformis is needed. Unfortunately, sufficient collections are not presently available.

ARCHINACELLA RUGATINA Ulrich, 1897

Pl. 2, figs. 19-21

Archinacella rugatina ULRICH in ULRICH & SCOFIELD, 1897, p. 835, Pl. 82, figs. 5-6.

Diagnosis. - Shell medium-sized, nearly circular in outline, moderately high and convex in lateral profile; apex inset from shell margin; aperture margin nearly horizontal; strong sublamellose growth lines in later adult growth.

Description. - Shell medium-sized for genus (about 20 mm in length), outline nearly circular, lateral profile moderately high and convex; highest point on shell near apex; apex distinct, fairly blunt, slightly curved anteriorly, situated distinctly just within anterior shell margin; anterior slope convex near shell margin, becoming concave beneath apex; lateral aperture margin nearly horizontal, but arches slightly; growth lines strong and apparently sublamellose in later growth stages.

Measurements. - Measurements on the holotype are: length from apex to posterior margin 19.5 mm; aperture length 20.85 mm; aperture width

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

20.4 mm; shell height 7.0 mm; height of apex 5.7 mm; width between outer growth lines 1.5-2.0 mm.

Material. - Only the holotype of the species was examined (USNM 45693), it is an internal mold with some highly recrystallized and weathered shell material around the posterior margin. One other specimen of the species was located. It is an unnumbered specimen on display in the Geology Museum at Miami University.

Distribution. - The holotype (USNM 45693) comes from the "Arnheim Formation", now placed in the Bull Fork Formation (earliest Richmondian - upper Upper Ordovician) at Middletown, Ohio. Nickles (1902) listed the species as part of the "Lower Richmond Fauna".

Comparisons. - Ulrich (1897) described A. rugatina with only the following comparison: "This species agrees closely with A. richmondensis [A. indianensis] Ulrich, but may be distinguished by its more distinct and slightly incurved apex, somewhat arched aperture, and stronger surface markings. The latter are coarsely lamelliform in the outer third". Herein, A. richmondensis is placed in subjective synonomy with A. indianensis Miller. This comparison can be somewhat expanded. First of all, A. richmondensis apparently can have a horizontal or slightly arched aperture (Pl. 4, figs. 7; Pl. 3, figs. 21 and 22), so this morphological feature is not a reliable basis for comparison. Most distinctive are the character of the apex, it being more curved in A. rugatina (Pl. 2, figs. 20-21), and the general form of the shell, which in A. rugatina is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

much broader in outline and more convex in lateral profile (Pl. 2, figs. 19-21), as well as the sublamellose growth lines in A. rugatina.

Discussion. - A. rugatina is known only from the lower Richmondian strata of Ohio, whereas A. indianensis occurs in the middle and upper Richmondian strata of the same area. The two species are quite similar morphologically, and it is likely that A. indianensis was descended from A. rugatina; alternativley the two species may have had a common ancestor.

On the left posterolateral slope of the holotype of A. rugatina (Pl. 2, figs. 19-21) there is a prominent concentric protuberance. Although I have concluded that this feature is probably a product of weathering, the possibility exists that it may represent the position of a muscle scar.

ARCHINACELLA ARCA new species

Pl. 3, figs. 7-10

Diagnosis. - Shell medium-sized, highly convex, nearly circular in outline; apex bluntly pointed, situated high over, and slightly past, anterior aperture margin; lateral aperture margin strongly arched.

Description. - Shell medium-sized for genus (about 19 mm in length), nearly circular in outline, quite high and strongly convex dorsally and posteriorly; lateral slopes nearly flat, anterior slope broadly concave; apex distinct, bluntly pointed, slightly curved anteriorly, situated high

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

over, and slightly past, anterior aperture margin, which is slightly convex; posterior aperture margin broadly convex; lateral aperture margin strongly arched, increasingly so posteriorly. Growth lines fairly widely spaced until mature shell, where they become more closely spaced and slightly irregular, even showing mild wrinkling near base of anterior slope.

Measurements. - The measurements for the holotype (USNM 40615) are as follows: length from apex to posterior margin 19.5 mm; aperture length 17.85 mm; shell width 20.5 mm; shell height 9.3 mm; height of apex 7.7 mm; distance between growth lines 1.0 to 1.5 mm.

Material. - Only the holotype (USNM 40615) of the species is known, which is apparently a partial composite mold. No shell material seems to be present, but rather the surface of the specimen is coated by a hard, dense, dark, outer layer, as is often the case with composite molds. The specimen is embedded in a matrix of gray micrite, the only other skeletal material visible being a brachiopod fragment.

Distribution. - The single known specimen, the holotype (USNM 40615), is labelled as coming from the "Waynesville Formation (Richmond)" at Waynesville, Ohio. This unit is now part of the Bull Fork Formation (Richmondian - upper Upper Ordovician).

Comparisons. - There can be no doubt concerning the distinctiveness of this species. The only similar species is A. powersi Ulrich and Scofield, the type species of Archinacella. It too has a strongly arcuate

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lateral aperture margin, a broad shell, and its apex is similarly positioned and formed (Ulrich and Scofield, 1897, p. 829, Pl. 61, figs. 3-5). But A. arca is higher and more convex, and is proportionately wider, even being slightly wider than long.

A. arca cannot be confused with other Richmondian species of the study area, all of which have submarginal apices, straighter lateral aperture margins, and less convex shells.

Discussion. - The only comparable species to A. arca is A. powersi, which is listed as coming from the "Stones River Group" at Beloit, Wisconsin, by Ulrich and Scofield. In modern terms, this probably translates into the Platteville Formation, which is Rocklandian (upper Middle Ordovician) in age (Weiss, 1957; Sweet and Bergstrom, 1976). These two species both have a strongly arcuate lateral aperture, which results in a broad posterior apron (Pl. 8, figs. 11 and 13). The arched lateral margins probably allowed better flowage of oxygenated water to the pairs of lateral gills. The broad posterior apron does not seem to provide an efficient exit for waters circulating through the mantle cavity, but it must have provided protection for a broad foot.

As seen particularly well in Pl. 3, figs. 9 and 10, there seems to be a wide smooth band over the posterodorsal slope of A. arca which angles slightly downward and narrows anteriorly and runs beneath the apex. This band does not seem to be a positive relief feature, but it might still represent a broad muscle band insertion. It appears to be identical in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

position to the muscle band of A. powersi (Ulrich and Scofield, 1897, Pl. 61, fig. 5; Knight and Yochelson, 1960, fig. 50,1b), although it seems to be extraordinarily wide. On the other hand, it is possible that the borders of this band are simply growth lines. If it does represent a remnant of a muscle band like that in A. powersi, then these species might be interpreted as strong clingers, where the apron protected the large muscular foot posteriorly, and the fused muscle band furnished strong even pulling force for adherence. Morphology suggests that A. arca is a descendant of A. powersi.

ARCHINACELLA INDIANENSIS (Miller, 1892)

Pl. 3, figs. 13-24; Pl. 4, figs. 1-14; Pl. 5, figs. 27-28

Tryblidium indianense MILLER, 1892, p. 695, Pl. 14, fig. 14; CUMINGS, 1908, p. 977, Pl. 39, fig. 11.

Archinacella richmondensis ULRICH in ULRICH & SCOFIELD, 1897, p. 834, Pl. 61, figs. 6-7; FOERSTE, 1924, pp. 201-202, Pl. 34, figs. 1a,b.

Archinacella kagawongensis FOERSTE, 1924, p. 202, Pl. 35, figs. 2a-d; HUSSEY, 1926, p. 171, Pl. 6, figs. 2,3,4,9,10.

Diagnosis. - Shell medium sized, with subovate outline and fairly low convexity; apex distinct, elevated, not incurved, located directly within shell margin; lateral aperture margin horizontal to slightly arched.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell medium-sized for genus (length up to about 20 mm), subovate in outline, fairly low convexity; anterior slope gently concave and sloped anteriorly, posterior slope broadly convex to nearly flat, particularly in later growth; lateral slopes flat to slightly concave near margins; apex distinct, elevated, not incurved, located well within the shell margin at about one-sixth the shell length from the anterior end; lateral aperture margin generally horizontal, but occasionally slightly arched; concentric growth lines distinct in outer half of shell, sometimes somewhat irregular.

Measurements. - Measurements for the species are listed in Table 24 below.

Table 24: Measurements of Archinacella indianensis in mm.

Museum Number	Apex to Posterior Length	Aperture Length	Shell Width	Shell Height	Height of Beak
USNM					
45691	20.5	24.4	20.2	6.0	5.5
47468	13.4	16.3	14.1	4.4	3.6
70467	20.3	21.2	16.5	6.0	4.2
265946	-	16.2	12.2	6.15	-
265950	-	13.5	10.2	5.65	-
265951	-	16.7	12.55	6.1	-
265954	12.75	9.45	4.4	-	-
265954	12.85	-	-	-	-
265954	13.5	10.2	5.3	-	-
265954	9.5	8.1	3.7	-	-
265954	11.15	8.3	4.3		-
265954	10.7	7.7	3.7	-	-
265954	7.8	5.8	3.0	-	-
265954	19.0	16.4	6.8	-	-
265954	18.46	10.25	-	-	-
265954	10.95	8.9	4.25	-	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UCGM					
10048	16.0	20.0	15.4	4.6	-
10048	-	13.9	10.7	-	-
19642	19.6	22.6	20.3	6.1	-
19642	6.6	8.2	7.0	5.0	-
MU					
247T	17.0	20.0	15.7	6.55	-
15541	17.1	18.15	14.2	6.2	-
15542	15.5	16.5	11.8	5.9	-
246T	14.3	17.0	14.2	5.3	-
15540	-	18.4	15.5	-	-
15540	11.1	12.5	11.15	5.0	-
250T	24.0	26.55	21.5	6.9	-
15545	18.2	20.45	17.6	6.2	-

Material. - The holotype of A. richmondensis (USNM 45691) (Pl. 3, figs. 16-18) is an external mold in the base of a bryozoan colony, as is specimen USNM 47468 (Pl. 4, figs. 8-12), the two specimens coming from the Whitewater Formation at Richmond, Indiana, and the Bull Fork Formation (Waynesville biofacies) at Oregonia, Ohio, respectively. Specimen 70467 from Richmondian strata at Oakland, Ohio, preserves the shell and the irregular nature of the growth lines to be found in some specimens (Pl. 4, figs. 1-2).

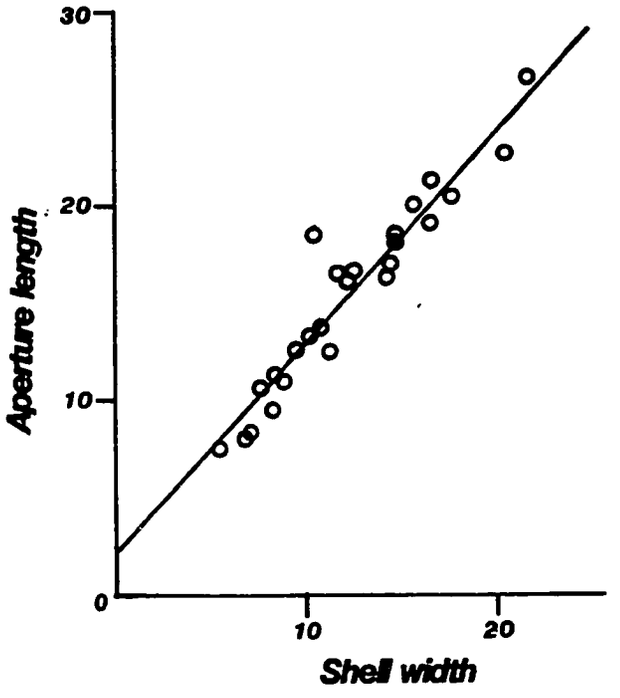
The holotype of A. indianenses (UC 6065) (Pl. 3, figs. 13-15) is an internal mold, but preserves the outline and form of the shell quite well. Specimens MU 247T (Pl. 3, figs. 23-24), MU 246T (Pl. 3, fig. 21), MU 250T (Pl. 3, fig. 22), MU 15540-15545, UC 10048, all from the Drakes Formation (Elkhorn biofacies) just south of Morning Sun, Ohio, and UC 19642 from the Drakes at Whitewater, Indiana (totaling 15 specimens) were also examined.

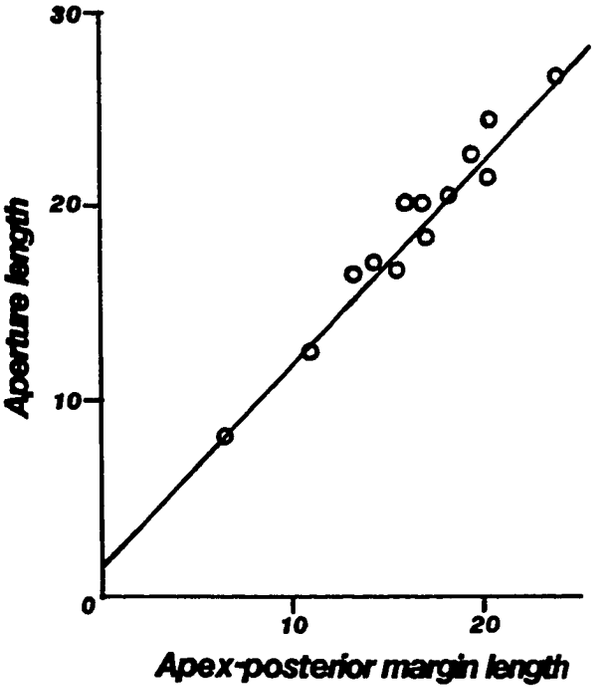
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

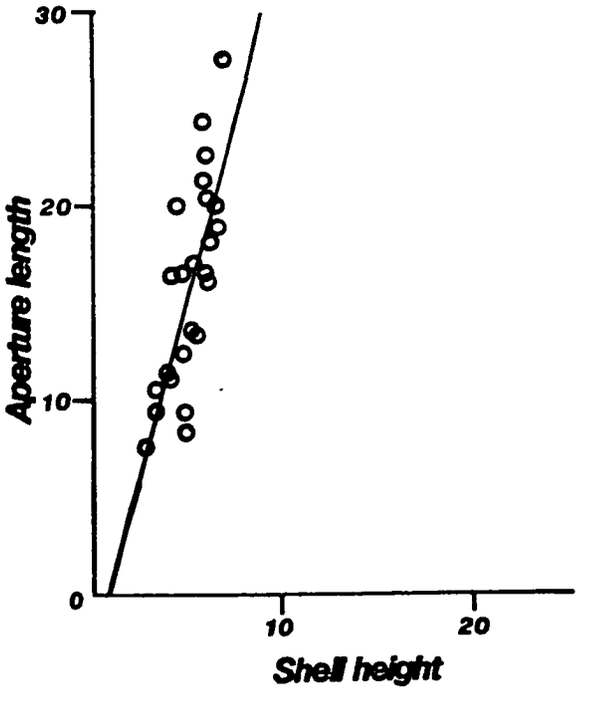
Figure 23: Bivariate plots from measurements made on specimens of *Archinacella indianensis*.

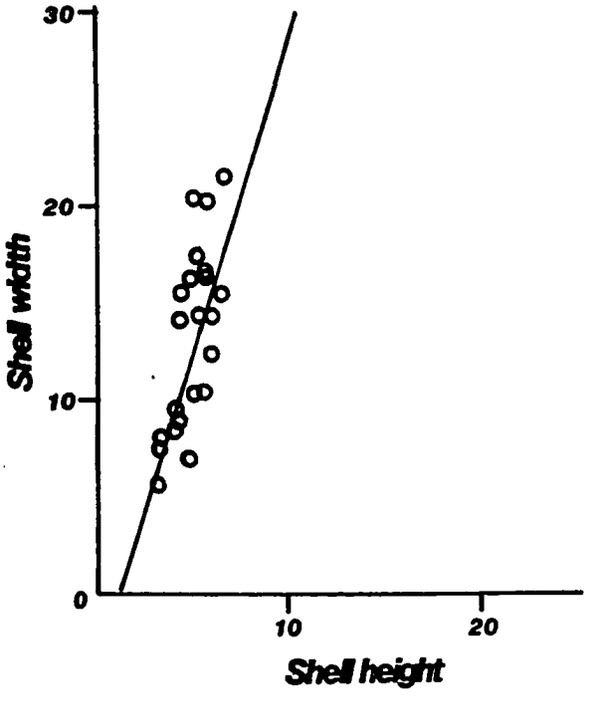
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Archinacella indianensis









Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

New material from the USGS silicified collections consists of about 45 specimens and fragments from the Dillsboro Formation (Liberty biofacies) from the New Point Quadrangle of southeastern Indiana (loc. 6139-CO). Specimens USNM 265946 (Pl. 3, figs. 19-20), USNM 265949 (Pl. 4, figs. 13-14), USNM 265950 (Pl. 5, figs. 27-28), and USNM 265951 (Pl. 4, figs. 3-7) of this collection are figured; all unfigured specimens are placed under the number USNM 265954.

Distribution. - Archinacella indianensis is known from Richmondian age strata in southeastern Indiana and southwestern Ohio. It is likely that it occurs in correlative strata in central Kentucky. The subjective synonym A. kagawongensis extends the species geographic range to the Upper Peninsula of Michigan and Manitoulin Island, Ontario, where it also occurs in Richmondian age rocks.

Comparisons. - A. indianensis Miller has been considered as possibly conspecific with A. richmondensis ever since the original description of the latter species. Ulrich and Scofield (1897, p. 834) closed their discussion of A. richmondensis stating: "We could come to no positive conclusion respecting Miller's Tryblidium indianese, but if his description is reliable it is certainly distinct". Bassler (1915) advised comparison of the two. Foerste (1924) noted only that Miller's figure of the species showed it to be shorter, relatively narrower anteriorly, and broader posteriorly and A. richmondensis. The holotypes of A. indianensis and A. richmondensis are very close in their shell form, having submarginal

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

apices, gently curved posterior slopes, rather steeply concave anterior slopes, and broad ovate aperture outlines. They seem to be conspecific, and Miller's (1892) specific name has priority.

Foerste (1924) described A. kagawongensis with the beginning line, "Specimens similar to Archinacella richmondensis; one specimen being 20 mm long, 16 mm wide, and 7 mm high...". When these measurements are plotted on the graphs for A. indianenses in text-fig. __, they are found to agree quite well. Foerste (1924) went on to say that his new species from the Richmondian strata of Manitoulin Island, Ontario, differed from A. richmondensis by having the apex curved downward farther, by being somewhat smaller, and by having less distinct growth lines. Hussey (1926, p. 171) began his description of A. kagawongensis from the Richmondian strata of the Upper Peninsula of Michigan stating: "This is a variable species". He figured two specimens, the first (Hussey, 1926, Pl. 1, figs. 3-9) appearing to be quite similar to Foerste's (1924) figured specimens; the second (Hussey, 1926, Pl. 6, figs. 4-10), however, looks like a specimen of a typical A. indianensis from the Cincinnati Arch area, and he pointed out that this latter specimen was "more like the typical form".

Examination of a good number of specimens of A. indianensis shows clearly that there is a wide range of variation in shape. Foerste's (1924) and Hussey's (1926) descriptions and figures of A. kagawongensis show that it clearly falls within the range of variability for A. indianensis. Specimens from the study area in the Miami University

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

collections labelled A. kagawongensis or A. richmondensis were indistinguishable, and many were from the same locality at Morning Sun, Ohio. This morphological variation, as well as the exact stratigraphic correlation of the two species, argues for the suppression of the name A. kagawongensis.

Ulrich and Scofield (1897, p. 834) compared A. richmondensis to the geologically older species A. depressa Ulrich and Scofield (see herein, Pl. 2, figs. 13-14), but stated the latter species' "arched aperture, lesser convexity and somewhat different outline" distinguish it from the former. They further stated a belief that "A. richmondensis is probably more nearly related to A. subrotunda, but do not elaborate. A. indianensis shows a closer morphological similarity to A. depressa, the two both having rather low shells with distinctly submarginal apices.

Specimen USNM 265955 should be noted here (Pl. 3, figs. 11-12). This single specimen from the Grier Limestone Member of the Lexington Limestone appears to be an Archinacella, but is too poorly preserved to allow a specific designation. It is a rather high shell with slightly convex slopes and a distinctly submarginal apex. It bears some resemblance to A. indianensis in its general form and the positioning of its apex, and could be related to this species.

Discussion. - The fact that the holotype of A. richmondensis (USNM 45961) and specimen USNM 47468 are both preserved as external molds in the bases of calcitic bryozoan colonies, but come from different stra-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tigraphic levels and localities, strongly suggests that Archinacella had an aragonitic shell. However, a fair number of specimens of Archinacella are also known to retain a recrystallized calcitic shell. Considerable insight into shell compositions would be gained if in future collecting, the nature of the preservation of associated molluscs were noted.

The graphs in Figure 23 show high correlation values for plots of shell length and width, but correlation values for plots dealing with shell height are much lower. The shell height was the most difficult measurement to make, because many specimens had fragmented margins or broken apices, and many specimens had shell margins embedded in matrix.

Ulrich and Scofield (1897) were under the impression that the lateral aperture margin of this species is "nearly or quite horizontal". Examination of type and new material reveals considerable variation in this character. While most specimens had essentially horizontal aperture margins (Pl. 3, figs. 16, 18, 21, 24; Pl. 4, fig. 7), a few specimens have obviously arched lateral margins (Pl. 3, fig. 22). If both of these forms are accepted as conspecific, as confluent variation suggests, then the use of shape of the lateral aperture margin (as often employed by Ulrich and Scofield) as a specific taxobasis is questionable. If the members of Archinacella were clinging animals, as their limpet-like form and fused ring-like muscle scar suggest, then the shape of their lateral aperture margins may reflect ontogenetic deformation by the shape of the substrate.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Order CYRTONELLIDA Horny, 1963

Diagnosis. - Shells planispirally coiled, with symmetrical paired muscle scars which are generally discrete, but a tendency toward fusion is apparent. Aperture may be non-sinuate or sinus-bearing, but no slits are known.

Stratigraphic range. - Members of this order certainly range from the Upper Cambrian to the Lower Silurian. Some Lower and Middle Cambrian taxa may also be cyrtonellids.

Discussion. - The above diagnosis for the Cyrtonellida follows the concept of Horny (1963) rather than that of Runnegar and Jell (1976). The latter authors defined the order as essentially including all monoplacophorans that lack a labral emargination. They included many genera whose taxonomic placement is debated, such as the helcionellids, hypseloconids, and yochelcionellids, and others that are assigned by this author to the Tryblidiida, such as the scenellids. It should also be noted that they included Cyrtolites in their concept of the Cyrtonellida, however, the present investigation shows that several species of Cyrtolites bear a labral sinus. Runnegar and Jell's ordinal concept needs to be restructured, as its composition, and therefore its definition, is questionable. Much more morphologic and phylogenetic analysis of the Monoplacophora is needed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Superfamily CYRTOLITACEA S. A. Miller, 1889

Diagnosis. - Same as for order.

Family CYRTOLITIDAE S. A. Miller, 1889

Diagnosis. - Shell evolute to involute with open umbilicus; whorls often angular or narrowly rounded dorsally and laterally; may or may not possess an apertural sinus.

Stratigraphic range. - Lower Ordovician-Middle Devonian.

Genus CYRTOLITES Conrad, 1838

Pls. 4-8

Diagnosis, - Shell rather loosely coiled, umbilicus widely open, aperture shape generally quadrangular, but may be rounded; aperture often sinuate; growth lines raised, often with intervening fine revolving threads; collabral rugae often present.

Description. - Shell planispiral, consisting of about 3 whorls as adult, with wide open umbilicus; coils contiguous, but barely touching, and disjunct in one known species. Aperture generally quadrangular to rhomboidal; may be rounded to sharply angular laterally, dorsal crest usually angular, can be carinate. Whorls generally expand gradually and show

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

only slight tendency toward flaring in gerontic stages. Aperture with dorsomedian sinus in some species, but always lacks silt and selenizone. External markings always consist of distinctly raised thin growth lines, these passing straight over the dorsal crest or swinging abaperturally to varying degrees forming a sinus; growth lines often connected by short revolving threads forming a reticulate pattern; some species have collabral rugae developed at fairly regular intervals along dorsal and dorsolateral flanks of whorls. Shell thin.

Muscle scars in 5 discrete symmetrical pairs arranged in main and secondary rings. The main ring consists of 3 pairs, the first lying near the dorsal crest, the second on the lower dorsal slope, and the third on the ventral slope. The secondary ring consists of 2 pairs of small scars on upper and lower slopes, respectively, that lie just anterior (abaperturally) to the main ring.

Type species. - C. ornatus Conrad, 1838, by monotypy.

Distribution. - Middle Ordovician (Blackriveran) to Lower Silurian (Llandoverian) of North America and Europe. The genus occurs throughout Eastern North America.

Comparisons to similar genera. - Cyrtolites is generally easily distinguished from similarly-shaped genera, such as Cloudia Knight (1947), by its quadrangular whorl shape and distinctly raised growth lines, as well as by the fine revolving threads (forming a reticulate pattern) and rugae marking many species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion, - The genus Cyrtolites was described by Conrad (1838, p. 118) in the following brief statement: "Shell with general form of Cyrtoceras, but destitute of septa". Conrad's (1838) original illustration of C. ornatus is a disjunct internal mold. For many years afterward a variety of fossil shells were assigned to this genus (Bassler, 1915, p. 365-368). Ulrich and Scofield (1897, p. 858) recognized this vague usage of the genus for symmetrically evolute shells, having a carinate or angular dorsum and a broad umbilicus. They noted: "These characters pertain to several widely distinct genera, and to use them as characteristic of a single genus is to bring together a most heterogeneous assemblage of forms.... We must return to the original type C. ornatus, and restrict the genus to species possessing essentially the same generic peculiarities".

Reed (1920-21, p. 23) criticized Ulrich and Scofield's generic definition saying that it was too broad and included species probably referable to Temnodiscus Koken. However, comparison of Reed's definition with that of Ulrich and Scofield shows no greater morphological restriction of the genus. It should be noted that Ulrich and Scofield stressed their removal of shells with slits from the genus Cyrtolites. They assigned shells with deep slits to a new genus, Cyrtolitina, which Knight (1941) cited as an objective synonym of Temnodiscus Koken, 1896, as both genera had Cyrtolites lamellifer Lindstrom, 1884, designated as their type species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Prior to 1965 Cyrtolites had generally been considered a bellerophontid gastropod. However, Horny (1965b) described several specimens of C. ornatus Conrad from the Upper Ordovician of Canada (located in the British Museum of Natural History) which show 5 pairs of discrete symmetrical muscle scars arranged in main and secondary rings. He placed Cyrtolites in the class Monoplacophora.

Horny (1965b, p. 62) argued that Cyrtolites differed from the Bellerophontacea in the following features: (1) absence of a sinus; (2) no parietal inductura; and (3) the presence of symmetrical multiple pairs of discrete muscle scars. The latter two differences are still valid. However, concerning the absence of a sinus, present work shows the presence of a shallow posterior apertural sinus in several species of Cyrtolites from the Middle and early Late Ordovician (Pl. 5, figs. 7, 9-10, 13; Pl. 7, figs. 11, 14, 23, 34, 35; Pl. 8, figs. 13, 17), because the growth lines turn conspicuously abaperturally over the dorsal crests of the shells. In his discussion, Horny conceded that there appeared to be some evidence of sinus development in American Cyrtolites, but he suggested that if any emargination were present, these species could be regarded as true bellerophontaceans (which he considered to be gastropods). I regard such a separation of forms to be contrary to the generic unity of Cyrtolites expressed by other morphological features. It should be noted that Horny's study was prior to Rollins and Batten's (1968) description of symmetrical pairs of discrete muscle scars in the sinuate monoplacophoran Sinuitopsis acutilira (Hall).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Horny (1965b) recognized the necessity for a revision of the North American species of Cyrtolites, and predicted that they would prove to be rather variable with regard to the coiling and external ornamentation. He also expected there would emerge a continuous gradational series between C. disjunctus Ulrich and Scofield, 1897, and C. ornatus Conrad, 1838. He was correct about the variation in external ornamentation in the American species of Cyrtolites, which is expressed mainly in the strength of the rugae, growth lines, and revolving threads at the interspecific level. The most striking intraspecific variation is in the actual cross-sectional shape of the whorls themselves. C. retrorsus Ulrich and Scofield can have a variety of aperture outlines in any one population ranging from quadrangular (Pl. 5, fig. 14) to dorsally arched (Pl. 5, fig. 18) to nearly circular (Pl. 5, fig. 22). C. ornatus is also quite variable in cross-sectional shape, but not to the extent of C. retrorsus. There is no gradational series showing any progressive uncoiling in C. ornatus. Many internal molds of this species have been examined in the course of this study, and when the inner coils are sufficiently visible, all specimens appear disjunct (Pl. 6, fig. 18; Pl. 3, fig. 1). When C. ornatus is compared to C. disjunctus Ulrich and Scofield (Pl. 6, figs. 19-22), the difference in the rate of whorl expansion and increase in coiling radius are clearly very different in the two species.

Discussion of subgenera. - The two subgenera of the genus Cyrtolites recognized in the Cincinnati Arch Province, C. (Cyrtolites) Conrad and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C. (Paracyrtolites) n. subgen., are separated on the basis of differences in shell sculpture. C. (Cyrtolites) exhibits a distinct reticulate ornament pattern formed by short revolving threads between coarser raised growth lines (Pl. 5, fig. 26; Pl. 8, fig. 18), as well as regularly-spaced collabral swellings along the slopes of the whorls, here termed rugae (Pl. 5, figs. 7, 12, 26; Pl. 6, figs. 6, 19; Pl. 8, figs. 2, 14). This subgenus contains those species most closely fitting the traditional concept of the genus, and includes the type species of the genus C. ornatus Conrad. C. (Paracyrtolites), on the other hand, is composed of those species which lack development of rugae and have only faint revolving threads (Pl. 7, figs. 23, 27, 30, 32, 34, 35), in contrast to the distinct threads that give the strong reticulate ornament pattern seen in C. (Cyrtolites).

The oldest species in each of these two subgenera, C. (C.) retrorsus Ulrich and Scofield and C. (P.) subplanus Ulrich in Ulrich and Scofield, both have V-shaped growth lines deflected abaperturally on the dorsal slopes, showing that each had a sinuate aperture (Pl. 5, fig. 7; Pl. 7, figs. 34-35). Both of these species are found in the Kirkfieldian-Shermanian strata of Kentucky and Tennessee. The probable descendants of C. (P.) subplanus in the study area are C. (P.) carinatus Miller (Pl. 7, figs. 18-25) and C. (P.) parvus Ulrich (Pl. 7, fig. 17). Both of these species retain a sinuate aperture and are known from only the Edenian (lower Upper Ordovician) portion of the Kope Formation of northern Kentucky and southwestern Ohio. The longer-lived, more diverse lineage stem-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ming from C. (C.) retrorsus loses the labral sinus after Edenian time. C. (C.) claysferryensis (latest Shermanian and Edenian; Pl. 8, figs. 12-20) and C. (C) cf. retrorsus (Edenian; Pl. 5, figs. 6-7, 9-10, 13, 19, 23, 26) both retain the shallow sinus. C. (C.) minor Ulrich and Scofield (Kirkfieldian - early Maysvillian) has growth lines which pass essentially at right angles over the dorsal crest with little or no deflection (Pl. 7, figs. 2, 5, 8). All subsequent species of the lineage in the Cincinnatian have nondeflected growth lines passing straight over the dorsal crest, and thus possessed a nonsinuate aperture.

The reasons for the loss of the sinus in C. (Cyrtolites) in the Late Ordovician is unclear, but it may be related to the changing depositional systems from the Champlainian to the Cincinnatian Series in the study area. The Champlainian was much more free of clastic sedimentation than the Cincinnatian sea. Toward the end of Middle Ordovician time fine clastic sediments began to be fed into the system in large quantities, so that the Cincinnatian Series is characterized by alternating shale and limestone deposition. The loss of the sinus, therefore, may have been an adaptation to protect the mantle cavity from fouling by clay-sized sediment. Other general morphologic trends in the subgenus C. (Cyrtolites) are: (1) a slight increase in some species of the width of the aperture relative to the height, (2) a slightly looser coiling with a more open umbilicus, and (3) in the post-Edenian rocks, a general size increase.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The distinct external sculpturing of Cyrtolites is of some interest. Hall (1847), Meek (1873), and Ulrich and Scofield (1897) all included magnified illustrations of the reticulate sculpturing pattern seen in C. (Cyrtolites). It can be seen on C. (C.) retrorsus (Pl. 5, fig. 26) that each raised growth line is the termination of a sublamellate increment of growth, and that each growth increment between the growth lines bears a series of slightly finer revolving threads which are raised to or nearly to the same height as the lines they intersect. These short revolving threads generally alternate from one increment to the next, so that they appear as bricks in a wall (Pl. 5, figs. 15 and 26). The strength of the connecting threads varies between species of Cyrtolites, but preservation usually affects their expression.

The revolving threads between the growth lines are indistinct and faint in C. (Paracyrtolites), and therefore, so is the reticulate ornamentation. C. (P.) subplanus Ulrich in Ulrich and Scofield has finer growth lines than any species of C. (Cyrtolites) (Pl. 7, figs. 27 and 35, 30 and 34), and its weak connecting threads are revealed only by very close examination. The descendants of C. (P.) subplanus retain this faint type of ornamentation (Pl. 7, figs. 18, 23, and 24). Miller (1874) did not recognize a reticulate pattern in the original description of C. (P.) carinatus Miller, but Ulrich and Scofield (1897, p. 863) observed that only the best-preserved material retained the delicate revolving threads, and that just short exposure to weathering could remove them entirely. The

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

same authors claimed that C. (P.) parvus Ulrich in Ulrich and Scofield has a strong ornament, but the holotype (Pl. 7, fig. 17) does not support this contention.

It is important to note that the ornament of C. (P.) carinatus appears to decrease in strength during growth, in contrast to the strengthening of ornament seen during the growth of C. (C.) retrorsus. The presence of distinct reticulate ornament in juveniles of C. (P.) carinatus suggests that C. (Paracyrtolites) had a common origin with, or possibly descended from C. (Cyrtolites). While the weakly reticulate subgenus C. (Paracyrtolites) is not known from rocks younger than Edenian (lower Upper Ordovician), the strongly reticulate C. (Cyrtolites) persisted throughout the remainder of Cincinnatian time.

C. (C.) ornatus Conrad is commonly found encrusted by bryozoans in the Maysvillian and Richmondian strata of the study area (Pl. 6, figs. 12-16), and one specimen of C. (C.) minor Ulrich and Scofield from the Edenian Kope Formation is known to be similarly encrusted (Pl. 7, figs. 6-8). No other species of the genus are known to be encrusted. The encrusting bryozoans may have preferred the distinctly reticulate surface of these species as a base for larval settlement and colony growth. Many of these specimens appear to have been encrusted while alive. The aperture rim is generally not encrusted in otherwise completely encrusted shells, and the bryozoans rarely ever attain a thickness where it would appear their weight might interfere with the mollusks' locomotion (Pl. 6,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

figs. 12-13, 15-16). Morris and Rollins (1971, p. 162, figs. 4-5) also assumed a symbiotic bryozoan encrustation of a specimen of C. (C.) ornatus from the study area because of additional encrustation by oriented cornulitid tubes. Such a symbiotic relationship would have been mutually beneficial to both the monoplacophoran and the bryozoan colony. The monoplacophoran would acquire greater shell strength and a camouflage cover to assist in protection against predation, and the bryozoan was assured an elevated attachment site. The suspension feeding bryozoans might have further benefitted from the molluscan feeding scraps and fecal products, or the microorganisms attracted thereto. McNamara (1978) reached similar conclusions from the study of gastropods encrusted by trepostome bryozoans from the Upper Ordovician of England. He pointed out that the bryozoans might have benefited from increased water flow over the colony caused by the gastropod's movement. Also, Vermeij (1978, p. 64) suggested that "complex shell topography" might promote encrustation of modern gastropods by calcareous algae and other epizoans, and this might increase predator resistance.

Evolution and Speciation. - Horny (1965b, p. 63-64) proposed that the Cyrtolitidae were descended form the Archinacellacea (Upper Cambrian - Richmondian). He claimed that the muscle scars of Cyrtolites resemble the complete muscle ring of the archinacellids, and that the "decomposition of the continuous archinacellan band-like scar" and the addition of the anterior scars are caused by the coiling of the shell of Cyrtolites and its

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 24: Stratigraphic ranges of species of Cyrtolites (Cyrtolites) and C. (Paracyrtolites) in the Middle and Upper Ordovician of the Cincinnati Arch region. C. (C.) retrorsus is known from the Black-riveran only in the Upper Mississippi Valley (Ulrich and Scofield, 1897).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Series	Stage	Range
Cincinnatian	Richmondian	C.(C.) hornyi; C. (C.) ornatus; C. (C.) disjunctus
	Maysvillian	C. (C.) ornatus; C. (C.) disjunctus
	Edenian	C. (C.) claysferryensis; C. (C.) minor
Champlainian	Shermanian	C. (C.) claysferryensis; C. (P.) subplanus; C. (P.) carinatus; C. (P.) parvus
	Kirkfieldian	C. (P.) subplanus; C. (P.) carinatus; C. (P.) parvus
	Rocklandian	C. (C.) retrorsus
	Blackriveran	C. (C.) retrorsus

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

relatives. He also proposed that Cyrtolites was the ancestor of the Silurian genera Yochelsonia and Cyclocyrtonella and the Devonian genera Cyrtonella and Neocyrtolites. Horny did not believe that Cyrtolites and its allies were an important stem stock for any subsequent major taxa, and hence did not give rise to any groups of the Gastropoda. He believed, rather, that they represented a "highly specialized group of molluscs", but he did not say exactly how, or for what, they were specialized.

C. (Cyrtolites) and C. (Paracyrtolites) are closely related to one another because both possess: (1) a common general shell form, (2) shallow sinuate apertures in the oldest species of both groups, and (3) reticulate surface sculpturing, although this is only weakly developed in C. (Paracyrtolites). C. (C.) retrorsus fillmorensis from the Blackriveran strata of Minnesota was named by Ulrich and Scofield (1897, p. 862) as the oldest member of that species and the genus (this name is herein placed in synonymy with C. (C.) retrorsus Ulrich and Scofield because of the lack of sufficient knowledge of the taxon to distinguish it from the C. (C.) retrorsus retrorsus. The oldest known species of C. (Paracyrtolites) is C. (P.) subplanus Ulrich from the Kirkfieldian-Shermanian Lexington and Bigby-Cannon Limestones of Kentucky and Tennessee, respectively. C. (C.) retrorsus occurs in the same strata. It is likely that C. (P.) subplanus had a common ancestor with C. (C.) retrorsus.

C. (Paracyrtolites) is a relatively short-lived taxon, and is rare in collections relative to members of the subgenus C. (Cyrtolites). C. (P.)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

subplanus apparently gave rise to C. (P.) carinatus and C. (P.) parvus near the beginning of Edenian deposition. C. (Cyrtolites) was a relatively long-lived taxon, including some highly successful species, such as C. (C.) retrorsus and C. (C.) ornatus, which are abundant throughout much of their stratigraphic range in the Cincinnati Arch region. C. (C.) ornatus is particularly abundant and widespread, being known essentially everywhere in eastern North America where Upper Ordovician carbonates are exposed. Like C. (P.) subplanus, C. (C.) retrorsus also gave rise to two descendants near the Champlainian-Cincinnatian boundary in the study area. C. (C.) claysferryensis n. sp. appears in the late Shermanian - Edenian Clays Ferry and Kope Formations of Kentucky and Ohio. C. (C.) minor Ulrich and Scofield first appears in the Edenian portion of the Kope Formation of the study area, although it has been reported from the uppermost Champlainian of Minnesota (Ulrich and Scofield, 1897) and possibly New Jersey (Weller, 1903).

Four new species of Cyrtolites appeared near the Champlainian-Cincinnatian (Middle Ordovician-Upper Ordovician) boundary. This correlates with a marked change in sedimentological conditions throughout the region, with predominantly carbonate deposition giving way to intermittent shale and carbonate deposition. C. (C.) claysferryensis is similar to the more angular forms of C. (C.) retrorsus, the former inhabiting a somewhat more muddy environment. The other 3 species - C. (C.) minor, C. (P.) carinatus, and C. (P.) parvus - are found in the dominantly shaley Kope

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

environments which are thought to reflect somewhat deeper water. These three small species (shell lengths generally less than 15 mm) probably led rather similar modes of life. Their small sizes may have kept them from sinking into the soft bottoms of the Kope environments. Peel (1978, p. 301-304) has suggested that small gastropod species from the Lower Silurian Arisaig Group were algal-foliage dwellers. Such minute gastropod faunas are well known in the modern seas living on seagrasses and various algae (Warmke and Almodovar, 1963; Brasier, 1975). As in modern seagrass communities, the Ordovician algae would have provided a protective habitat with abundant food above a possibly turbid sediment-water interface. Johnson (1959, 1961) has demonstrated a prolific calcareous algal flora in the Ordovician and Silurian, and so noncalcified algae must have also been abundant (see Paleoecology section). Although the mode of feeding of Paleozoic monoplacophorans is not known, most previous workers have assumed an algal-feeding habit similar to that of gastropods. The common association of gastropods and monoplacophorans in fossil assemblages provides some support for this concept.

C. (C.) minor was the only one of these small cyrtolitids to survive into Maysvillian time (Fairview Formation of southwestern Ohio). This species most likely was ancestral to C. (C.) ornatus, as indicated by their very similar morphologic characters, except for size. C. (C.) minor was originally described by Ulrich and Scofield (1897) as a subspecies of C. (C.) ornatus, the main difference being the small size of C. (C.)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

minor. The smaller species is not known from strata younger than the Fairview Formation, and it is in that same unit that C. (C.) ornatus first appears in the study area. The Fairview Formation is distinguished from the underlying Kope Formation by a marked increase in carbonate deposition relative to shale deposition, and it may be that this specific turnover correlates with changing environmental conditions.

C. (C.) ornatus is believed to have given rise to C. (C.) disjunctus in Richmondian time, as the two are quite similar, with the coiling of the latter species being disjunct. C. (C.) disjunctus is known only from the Richmondian strata of Minnesota, but is treated in this study because of the possibility of confusing it with internal molds of C. (C.) ornatus. It may be that this rare disjunct form is not a valid species, but rather a morphological variant of C. (C.) ornatus.

C. (C.) hornyi n. sp. is known only from the USGS silicified sample 6139-CO taken at a single locality in southeastern Indiana. It comes from the upper Dillsboro Formation, from strata formerly designated as the Liberty Formation or Strophomena planumbona Bed (see Shaver, et al., 1970, p. 45-58), which consist of interbedded shales and limestones. This species morphologically resembles C. (C.) claysferryensis n. sp. from the Clays Ferry Formation of Kentucky, which is also a unit of interbedded shale and limestone characterized at many horizons by the strophomenacean brachiopod Rafinesquina (see Wier and Green, 1965, p. B11). The presence of large, flat strophomenid brachiopods such as

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Strophomena and Rafinesquina is generally considered to indicate level, soft-bottom conditions (Fox, 1968; Richards, 1972; Walker and Parker, 1976).

C. (C.) retrorsus and C. (C.) ornatus have much in common. They are the longest-lived and most abundant of any of the species of Cyrtolites considered here; they both show a high degree of intraspecific variability; and they both inhabited depositional systems which were complex facies mosaics. In both species, different morphotypes co-occur, suggesting a genetic rather than an ecophenotypic origin for their variable morphologies. These species were probably ecological generalists which maintained genetic flexibility in their populations in order to permit them to readily adapt to constantly shifting sedimentologic-environmental conditions. In contrast to the above two species, the other species of Cyrtolites in the study area, particularly the three small species of the Kope Formation, may have been ecologic specialists. Their relatively short stratigraphic ranges and small populations suggest that they were more finely tuned to certain environmental conditions and less able to adapt to environment fluctuations.

Modes of speciation employed by Cyrtolites are difficult to discern because of the nature of cratonic stratigraphic sequences, which are characterized by shifting environments and diastemic breaks in sedimentation. Speciation events seem to happen rather quickly across boundaries of marked environmental change, such as the Champlainian-Cincinnatian boun-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

dary. However, abundant species such as C. (C.) retrorsus, which show a high degree of intraspecific variability and cross many environmental boundaries, give an impression of phyletic gradualism that is very difficult, if not impossible, to interpret. It can be discerned that C. (C.) retrorsus was able to maintain large populations in a variety of dominantly carbonate environments from Rocklandian to Shermanian time, apparently without any species turnover. This success may be partly the result of a regional consistency in carbonate deposition. C. (C.) ornatus behaved similarly during the extended period of alternating carbonate and shale deposition during Maysvillian and Richmondian times, where again an overall regional consistency in deposition conditions existed, even though of a fluctuating character. The greatest apparent proliferation of species took place when there was a rather drastic change in regional depositional conditions, that is, during the flood of clay-sized sediments in latest Shermanian and Edenian times. The speciation of the genus Cyrtolites therefore seems to be linked to regional environmental conditions and species distribution shows a correlation with the percentage of clay shale deposition.

Notes on British species of Cyrtolites. - Reed (1920-21) described 5 species of Cyrtolites from the Ordovician and Lower Silurian of the British Isles. These species are listed below with comments.

(1) C. budleighensis Reed - This species is known only from internal molds occurring in Ordovician pebbles found in Triassic conglomerates.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reed cited resemblance of this species to C. subplanus and C. retrorsus. Based on his figures of the species, it most resembles C. ornatus in both general shape and the development of strong rugae.

(2) C. craigensis Reed - This species from the Stinchar Limestone (Caradocian) is known only from poor internal molds whose morphology is comparable to that of C. subplanus.

(3) C. nodosus (Salter) - This species comes from the Bala Series (Caradocian-Ashgillian) of Wales, and is characterized by growth lines which are deflected abaperturally over the dorsal crest of the shell, a distinct reticulate ornament, and rugae that are distinct, rounded slightly, and extend about three-fourths of the way up the width of the dorsal whorl slope. C. nodosus seems to be nearly identical the the North American species C. retrorsus, and is probably a synonym of that species.

(4) C. nodosus llandoveria Reed - This supposed "variety" of C. nodosus was found in Lower Llandoverian rocks, and differs from the type subspecies in having sharper rugae that extend all the way up the dorsal whorl slope to the dorsal carina, and in having straight growth lines that are not deflected abaperturally. Although Reed believed that this form resembled C. retrorsus more than C. ornatus, it now seems that both the longer rugae and the non-deflected growth lines rather suggest a relationship to C. ornatus.

(5) C. thraivensis Reed - This species was collected from the Drummuck Group (Ashgillian), Scotland, and is very similar in general form and style of ornamentation to C. ornatus, which Reed called an allied species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Although it is beyond the scope of this study to evaluate the British species of Cyrtolites, some insight into their taxonomy may be obtained from comparison with American species. Only 3 of the British species names can be confidently used (numbers 3-5 above) because of adequate preservation and stratigraphic location. The oldest of these three is C. nodosus nodosus (Caradocian-Ashgillian), which is very similar to the North American species C. retrorsus (Kirkfieldian-Shermanian) in the development of its rugae and the abapertural curvature of its growth lines. The other two recognizable British species, C. nodosus llandoveria (Lower Llandoverian) and C. thraivensis (Ashgillian) compare quite favorably with the American species C. ornatus in the lengthening of their rugae and the straightening of their growth lines dorsally. Although stratigraphic correlation between the two faunas is rather broad, it is obvious that the same morphologic trends toward the accentuation of rugae and loss of an apertural sinus were essentially concommitantly proceeding during late Middle and Late Ordovician times in North America and Great Britain. In fact, the British and American species names are probably synonyms, the two associations seem to have been given different specific names because of their present-day wide geographic separation. In any case, there can be little doubt about their derivation from a common ancestral stock, and their similar paths of evolution at least strongly suggest some contact between the two faunas.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Subgenus CYRTOLITES (CYRTOLITES) Conrad, 1838

Pls. 4-8

Diagnosis. - Shell with rugae developed on the dorsal slopes of the whorls, and having distinct, short, revolving threads between raised growth lines to form a strong reticulate external shell sculpture. Apertural sinus and abaperturally deflected growth lines present in stratigraphically older species; younger species are nonsinuate with growth lines passing straight over the dorsal crest of the shell.

Type species. - C. (C.) ornatus Conrad, 1838, by monotypy.

Distribution. - Blackriveran (Middle Ordovician) - Richmondian (Latest Ordovician) of eastern North American, and Caradocian (Middle Ordovician) - Lower Llandoverian (Lower Silurian) of Great Britain.

North American species. - C. (C.) retrorsus Ulrich and Scofield, C. (C.) claysferryensis n. sp., C. (C.) minor Ulrich and Scofield, C. (C.) ornatus Conrad, C. (C.) hornyi n. sp., C. (C.) disjunctus Ulrich and Scofield.

British species. - C. (C.) nodosus (Salter), C. (C.) nodosus llandoveria Reed, C. (C.) traivensis Reed. The other two British species assigned to Cyrtolites by Reed (1921) are at present known only from internal molds and cannot be assigned to a subgenus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES (CRYTOLITES) ORNATUS Conrad, 1838

Pl. 6, figs. 1-18; Pl. 7, fig. 1

Cyrtolites ornatus CONRAD, 1838, p. 118; CONRAD, 1839, p. 63; CONRAD, 1841, p. 37; HALL, 1847, p. 308, Pl. 84, figs. 1a-g; ROGERS, 1858, p. 820, fig. 619; BILLINGS, 1863, p. 217, fig. 226; MEEK, 1873, p. 148, Pl. 13, figs. 3a-b; MILLER, 1874, p. 308; LESLEY, 1889, p. 182, figs. ; MILLER, 1889, p. 402, fig. 669; ULRICH & SCOFIELD, 1897, p. 860, Pl. 62, figs. 27-29; CUMINGS, 1908, p. 962, Pl. 40, figs. 8-8a; GRABAU & SHIMER, 1909, p. 609, figs. 815a-b; FOERSTE, 1924, p. 203-4, Pl. 34, fig. 3; KNIGHT, 1941, p. 94, Pl. 5, figs. 5a-d; SHIMER & SHROCK, 1944, p. 439, Pl. 175, figs. 24-25; KNIGHT et al., 1960, p. I175, fig. 90,4; CASTER, DALVE, & POPE, 1961, p. 41, Pl. 5, fig. 11.

Porcelia ornata Sharpe, EMMONS, 1860, p. 102, fig. 7. (See also possible British synonyms in generic discussion.)

Diagnosis. - Shell large, with subquadrangular aperture, angular dorsally and narrowly rounded at umbilical shoulders; rugae well-developed, generally rounded; growth lines not deflected abaperturally, passing straight over dorsal crest.

Description. - Shell relative large (length up to 33 mm); umbilici large and open; whorls loosely coiled. Aperture subquadrangular, dorsum sharply angular to distinctly carinate, dorsal slopes convex, umbilical

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

shoulders narrowly rounded to angular, ventral slopes flat to slightly concave. Rugae well-developed, usually broadly rounded, but sometimes as narrow ridges; extend from umbilical shoulders to dorsal crest; sometimes rugae weakly developed on upper ventral slopes of larger specimens. Growth lines not deflected abaperturally, passing straight over dorsal crest of shell; reticulate ornament formed by somewhat weaker revolving threads.

Measurements. - Very few specimens were available upon which reliable measurements could be made; these are shown in Table 25 below with accompanying plots in Figure 25. The poor quality of the measurements is reflected in the values of the statistics.

Table 25: Measurements for C. (C.) ornatus in mm.

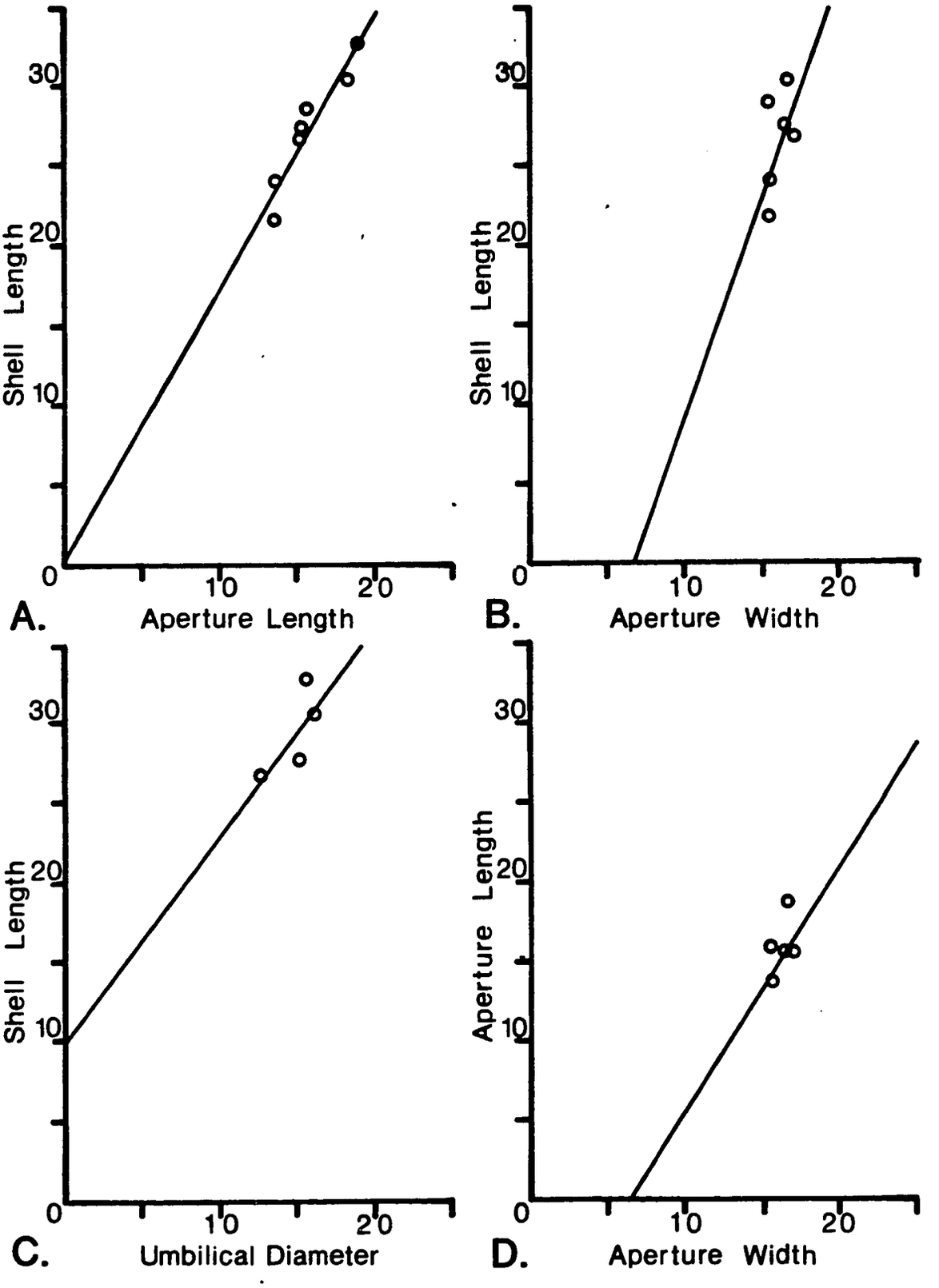
Museum Number	Shell Length	Aperture Length	Aperture Width	Maximum Umbilical Diameter	Width at base of Aperture	Wavelength of Rugae
USNM						
45786	27.6	14.5	16.7	15.3	4.9	2-3
265906	30.4	18.5	16.8	16.2	6.2	3-4
265907	26.9	15.4	17.1	12.9	5.7	2-3
265908	32.9	19.0	-	15.7	-	2.7-4.5
UCGM						
3097	21.8	13.9	15.8	-	-	-
19671	24.1	13.9	15.8	-	-	-
SF						
2008	29.0	15.8	15.8	-	-	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 25: Bivariate plots of measurements made on specimens of *Cyrtolites* (*Cyrtolites*) *ornatus*.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES ORNATUS



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Note: USNM 45786, 265906, and 265097 are fairly reliable measurements, but USNM 265908 is a large internal mold. Specimens UCGM 3097, 19671, and SF 2008 are all totally encrusted by bryozoans, so that apertural and length measurements only were possible.

Material. - No new specimens of this species were found in the USGS silicified collections. Collections were examined at the U.S. National Museum, the University of Cincinnati, Miami University, and the Cincinnati Museum of Natural History. All of these collections were greatly dominated by specimens from the Cincinnati Arch region and all were predominantly internal molds, composite molds, and bryozoan encrusted specimens. SF 2008 is from the private collection of Mr. Steve Felton of Cincinnati, Ohio.

Knight (1941, p. 94) designated the specimen illustrated by Hall (1862, Pl. 11, fig. 19) as the holotype of the species, but its whereabouts is uncertain. Hall maintained that this was one of Conrad's original specimens. Knight suggested that a collection of specimens in the Academy of Natural Sciences of Philadelphia (No. 13307) might be Conrad's original syntypes. The only previously figured specimen examined by me is a hypotype (USNM 45786) which was figured by Ulrich and Scofield (1897, Pl. 62, fig. 27). That specimen is photographed for the first time here (Pl. 6, figs. 1-3). A collection of specimens bearing the same USNM number as this hypotype, but found in a separate box and drawer, was also examined, and 3 more specimens from the collection are figured here

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Pl. 6, figs. 6-8 and 9-11; Pl. 7, fig. 1; these new hypotypes are here assigned the museum numbers USNM 265906, 265907, and 265908, respectively). All of these specimens (originally with suite number USNM 45786) are labelled as coming from the "Corryville member of the McMillan Formation (Maysvillian) at Cincinnati, Ohio" (equivalent to Grant Lake Formation or a tongue of the Bull Fork Formation).

Distribution. - Maysvillian (middle Upper Ordovician) and Richmondian (upper Upper Ordovician) of eastern North America. The species is usually common in all formations of the middle to upper Upper Ordovician in the Cincinnati Arch area, and according to the comments of other authors, it is often common throughout its geographic range.

Comparisons. - The Mayvillian-aged C. (C.) minor is similar in shell form and ornament (Pl. 7, figs. 2-10) to C. (C.) ornatus, but is much smaller. The only other Richmondian-aged species presently recognized in North America are C. (C.) hornyi n. sp. and C. (C.) disjunctus. C. (C.) hornyi (Pl. 8, figs. 1-10) is more angular in its form and has flatter whorl slopes than C. (C.) ornatus. C. (C.) disjunctus (Pl. 6, figs. 19-22) is disjunctly coiled, being distinguished from disjunct internal molds of C. (C.) ornatus by the rate of whorl expansion and the rate of increase in the radius of coiling.

Discussion. - C. (C.) ornatus Conrad, 1838, is the type species of the genus Cyrtolites, and is the species in which Horny (1963) discovered symmetrical discrete pairs of muscle scars leading to the transfer of the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

genus to the class Monoplacophora. The species is distinguished from other species by its relatively large size (Pl. 6, figs. 6-8), its usually broadly rounded rugae that extend from the umbilical shoulders to the dorsal crest of the shell (Pl. 6, figs. 1, 6, 17), and its straight growth lines (Pl. 6, figs. 7 and 10), which cross the dorsum at right angles to the dorsal crest.

Horny (1965b) believed that there would be a continuous gradational series of forms between C. (C.) ornatus and C. (C.) disjunctus. This idea is not supported by this study, although rarely a gerontic specimen of the C. (C.) ornatus is found which appears to have a slight tendency to uncoil near the end of the body whorl.

C. (C.) ornatus shows a high degree of intraspecific variability in the shape of its whorls and the expression of its rugae. Plate 6 shows a representative collection of forms, the specimens in figures 1-3, 6-8, and 9-11, as well as the disjunct internal mold figured on Pl. 7, fig. 1, are from one collection from Maysvillian strata at Cincinnati, Ohio. Contributing significantly to the difficulty of clearly defining the species is the variety of preservational states in which it is commonly found. Most common are internal molds (Pl. 7, fig. 1), which can be quite variable in appearance. Composite molds are not uncommon, where the external mold is impressed upon the internal mold as a result of early dissolution of the shell material while the enclosing sediment was still in a plastic state (Pl. 6, figs. 6-8, 9-11). These composite molds, and even some internal

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

molds, often have a thin, hard, resistant coating over their surfaces. This coating may be the remains of the organic content of the shell, or possibly could be the remnants of a micritized layer, as discussed by Bathurst (1966). Molds are commonly compressed and distorted so that their preserved morphology can vary greatly. Some calcitic casts are known (Pl. 6, fig. 17); most specimens with intact shells preserved are encrusted by bryozoans (Pl. 6, figs. 12-14 and 15-16, showing Maysvillian and Richmondian specimens, respectively).

The New York specimens of the species that I have examined (Conrad originally based the species on New York material) (Pl. 6, figs. 4-5) generally are somewhat smaller, narrower, and more carinate dorsally than specimens of C. (C.) ornatus from the Cincinnati Arch region. A comprehensive examination of material from the different areas of eastern North America where the species has been recognized could possibly result in the subdivision of this well-known species into subspecies, or even into discrete species. However, there is a great deal of variation observed in the Cincinnati Arch material, which is best interpreted as intraspecific variation.

CYRTOLITES (CYRTOLITES) RETRORSUS Ulrich in Ulrich & Scofield, 1897

Pl. 5, figs. 1-25; Pl. 7, figs. 17-22

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Cyrtolites retrorsus ULRICH in ULRICH & SCOFIELD, 1897, p. 861, Pl. 62, figs. 32-37; BASSLER, 1932, Pl. 20, figs. 6-7; SHIMER & SHROCK, 1944, p. 439, Pl. 175, figs. 24-25.

Cyrtolites retrorsus fillmorensis ULRICH & SCOFIELD, 1897, p. 862, Pl. 62, figs. 38-39.

Diagnosis. - Shell moderate-sized (up to 21 mm in length), relatively tightly coiled; apertural shape varying from quadrangular to rounded; rugae as narrow sharply rounded ridges extending from umbilical shoulders to near dorsal crest; curved growth lines and revolving threads of near equal strength form a distinct reticulate ornament pattern; median labral sinus broad and shallow.

Description. - Shell moderately-sized for genus, broad in dorsal view, relatively tightly coiled, with a fairly wide umbilicus. Aperture generally quadrangular to subquadrangular, but can be quite rounded; average length/width ratio 0.85-0.90; dorsum carinate in juveniles, becoming angular to sharply rounded in adults; dorsal whorl slopes broadly convex, except near dorsal carina where they may become concave briefly; umbilical shoulders angular to sharply rounded in juveniles, becoming sharply to broadly rounded in adults; ventral slopes generally flat to slightly concave, but can be slightly convex in inflated forms. Rugae well-developed as low, narrow, rather sharply rounded, regularly-spaced ridges which extend from the umbilical shoulders to near the dorsal crest, generally weakening dorsally, and sometimes extending slightly onto the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

uppermost ventral slope; rugae generally lacking in juveniles. Distinct reticulate shell sculpture formed by coarse transverse raised growth lines that swing gently abaperturally across the dorsal crest, and short revolving connecting threads of nearly equal strength that alternate from one growth increment to the next. Labral sinus broad and shallow. Shell fairly thin; rugae can be very weakly expressed on the shell interior.

Measurements. - Measurements are given in Table 26 below, arranged by stratigraphic unit and type samples. Figures 26 and 27 show graphs and statistics for all measured specimens, Logana specimens, and Grier specimens, respectively.

The Logana Member yielded the best preserved and most abundant samples of C. (C.) retrorsus in the USGS silicified collections. In total, 87 Logana specimens from 4 samples were measured for at least one parameter, depending on the quality and completeness of the preservation (USGS collections 7791-CO, 6419-CO, 5092-CO, and D-1196). Other Logana samples containing this species were USGS collections 5086-CO, 5073-CO, 4865-CO, and 5091-CO (see Figure 26).

Nine samples from the Grier Limestone Member contained this species: USGS collections 4073-CO, 5067-CO, 4852-CO, 4883-CO, 4876-CO, and 4879-CO, which contained measurable specimens, and 4929-CO, 4880-CO, and 4874-CO, which contained only poor material (see Figure 27).

It should be noted that correlation coefficients in Figures 26 and 27 are high (over 0.90) and that the ratios and slopes of graphs for the two

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

different stratigraphic collections are in close agreement with one another.

Table 26: Measurements for C. (C.) retrorsus Ulrich in mm.

USNM Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
Types							
USNM							
45789	23.2	13.1	18.4	10.15	4.4	3.0	6
265902	205.	14.7	17.0	9.8	4.3	2.5	-
465901	22.45	14.3	19.6	9.2	3.7	2.0	5
265899	16.05	10.5	10.7	7.3	3.1	-	5-6
265900	21.0	11.8	14.25	11.3	3.3	-	5
265938	12.95	8.4	8.05	6.8	2.3	2.0	-
45790	12.2	6.8	7.85	6.2	2.0	-	-
Lexington Limestone							
Curdsville Member							
387024	13.1	-	-	8.8	2.7	2.0	7
387024	14.2	-	-	-	2.2	-	-
265939	14.7	9.7	11.3	8.4	2.7	-	-
265939	-	-	-	-	-	2.0	4
265940	17.7	11.95	15.7	-	3.5	-	5
Logana Member							
265942	17.1	14.4	14.9	10.0	5.2	1.5	4
	-	7.1	7.0	-	-	1.5	3-4
	-	12.7	14.35	-	-	2.0	2-3
	-	-	-	-	-	2.0	3
	-	-	-	-	-	1.75	3-4
	9.2	6.0	6.9	5.0	1.0	-	4
	11.0	-	-	6.05	-	-	-
	-	8.9	10.1	-	-	-	3
	-	12.0	12.9	-	-	-	4
	11.9	8.3	-	5.5	-	-	5
	8.8	5.5	7.0	5.0	-	1.5	-
	-	-	-	-	-	2	4
	11.0	6.5	8.8	4.5	-	2	3-4
	-	5.2	6.2	-	-	-	4
	12.4	7.5	7.0	6.5	2.0	-	5
265943	15.4	11.0	11.3	8.1	3.1	1-1.5	4

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

USNM Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
	14.6	10.9	11.95	8.05	3.1	1-2.0	4-5
	-	-	13.1	8.1	3.0	1-1.5	5
	13.9	9.4	-	7.9	2.8	-	4-5
	11.6	9.0	10.5	8.3	2.5	-	4-5
	9.0	6.0	8.55	5.55	-	-	4
	-	-	-	10.0	-	2.0	4-5
	-	-	-	7.6	-	-	4
	11.1	-	-	6.6	-	-	3-4
	7.95	5.0	5.0	4.7	-	-	4
	20.1	12.8	12.8	9.35	3.7	1.5-2.3	5
	17.2	10.4	12.5	-	-	2.0	5
	18.4	12.4	13.7	9.1	3.65	-	5
	20.6	13.1	14.6	10.5	3.85	2.0	5-6
	-	11.35	12.6	-	-	-	4
	-	14.5	16.35	-	-	1.5-2.0	4
	-	11.5	15.2	-	-	2.0	3-4
	18.4	12.5	14.0	9.4	-	2.0	5
	16.8	11.4	12.75	8.95	3.4	-	-
	-	14.15	16.9	-	-	-	5
	-	12.95	15.7	-	-	1-2	5-6
	18.45	-	-	10.1	-	1.5-2.0	-
	18.00	12.4	14.2	9.4	-	2.0	5
	16.75	12.1	13.1	9.2	2.5	2.0	4-5
	-	12.1	12.7	-	-	-	-
	15.75	10.2	11.9	9.0	2.7	1.5-2.0	4-5
	17.9	11.9	14.2	8.8	-	-	-
	16.8	11.95	11.95	-	-	-	4-5
	-	-	11.7	7.7	3.2	-	-
	-	10.75	12.5	-	-	-	-
	19.5	12.7	13.6	9.3	3.9	-	5
	18.0	11.6	12.4	9.0	3.4	-	5
	16.9	11.65	13.5	9.4	2.5	-	3
	16.0	11.0	12.2	7.7	2.9	-	4-5
	12.1	8.2	8.4	7.3	1.8	-	5
	13.6	8.45	9.65	6.6	2.4	2.0	4-5
	-	-	12.9	8.9	3.0	-	-
	17.75	11.2	11.75	8.8	3.8	-	5
	13.1	8.1	8.9	6.5	2.4	1.5	5
	10.45	6.5	7.4	6.2	-	-	5
	-	10.2	12.1	8.2	-	-	4
	-	-	11.3	7.9	2.5	-	-
	16.1	10.5	12.3	-	-	-	4

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

USNM Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
	-	-	10.4	8.8	2.7	-	-
	-	-	7.4	5.5	2.0	-	3-4
	-	8.05	9.25	-	-	-	4-5
	15.0	10.7	12.45	-	-	-	5
	18.3	13.5	13.55	9.4	3.5	-	4
	15.6	10.75	11.4	-	3.2	-	6
	14.8	10.45	11.4	8.1	3.4	1.5-2.0	4
	18.5	13.2	14.0	8.8	4.5	2.0	4
	17.5	11.2	12.9	9.0	3.4	1.5-2.0	5
	19.6	13.45	13.5	-	-	-	4
	15.35	9.65	10.95	7.4	3.1	-	5
	-	10.4	11.4	-	-	-	-
	7.95	5.2	6.15	3.8	-	-	4
387025	17.6	10.4	12.9	9.05	-	2.0	4
	-	4.75	5.0	4.8	-	-	-
	18.2	11.25	12.8	9.2	3.5	2.0	3
	13.4	8.3	8.4	6.4	3.0	-	4
	-	10.4	11.2	-	-	-	3-4
	17.75	11.1	14.1	10.2	-	-	-
	15.0	9.55	12.4	7.95	3.0	1.5-2.0	4
265953	12.7	8.5	9.2	5.8	2.8	1-1.5	-
	14.8	9.5	9.8	8.05	-	1.5-2.0	4-5
	8.3	5.25	5.8	3.9	1.4	-	-
	9.3	5.4	6.9	4.0	2.6	-	-
Grier Member							
387026	12.2	7.0	8.8	7.0	3.0	-	-
	7.3	5.0	7.0	4.5	-	-	-
387027	7.0	4.3	4.4	4.2	-	-	5
	11.2	5.5	8.6	5.5	-	1.5	-
265958	9.35	4.9	7.1	5.35	2.2	-	-
	14.6	-	12.4	7.6	-	-	-
	13.1	8.5	11.2	6.1	2.6	-	-
	11.8	7.4	9.4	-	-	-	-
	-	4.7	8.0	-	-	-	-
	-	4.5	6.5	-	-	-	-
	9.7	6.1	8.2	5.1	-	-	4
	11.7	6.7	8.7	5.8	-	2.0	3-4
387028	4.0	2.3	2.9	2.0	1.0	-	-
	-	3.7	3.7	-	-	-	-
387029	7.0	4.4	5.1	3.7	-	-	-
	-	5.5	7.6	-	-	-	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

USNM Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
265973	15.8	10.6	11.9	8.5	3.15	1.5-2.0	4-5
	17.0	10.3	12.6	8.1	3.9	-	5
	16.2	11.4	12.0	8.4	3.8	1.5-2.0	4-5
	13.3	9.0	10.4	7.1	2.4	1.5-2.0	5-6
	6.0	3.5	3.6	3.8	-	-	5
	11.0	7.3	9.0	5.6	2.2	1.5-2.0	5
Millersburg Member							
265968	18.8	11.5	14.7	11.1	3.8	2.0	4-5
	9.9	5.9	7.9	5.9	2.0	-	4
	-	-	14.0	11.0	-	-	-
	-	-	7.8	5.3	-	-	-
Perryville Member							
265969	6.2	4.0	4.0	3.7	1.6	-	-
	17.8	12.8	15.0	8.0	3.8	-	4

Material. - Tennessee samples - The only Tennessee specimens of this species examined were 4 of Ulrich and Scofield's (1897) syntypes (USNM 45798) which are all large silicified casts, ranging from well-preserved to rather worn, and labelled "Trenton, near Nashville, Tennessee". One of these specimens is here designated the lectotype of the species and retains the museum number USNM 45798 (Pl. 5, figs. 5-7). The other three specimens from the syntype suite are designated paralectotpyes with the museum numbers USNM 265901 (Pl. 5, figs. 8-10), USNM 265902 (Pl. 5, figs. 11-12), and USNM 265937 (not figured).

Kentucky samples - Ulrich and Scofield's (1897) syntypes included 7 silicified casts and 1 internal mold labelled "Trenton (Flanagan), about

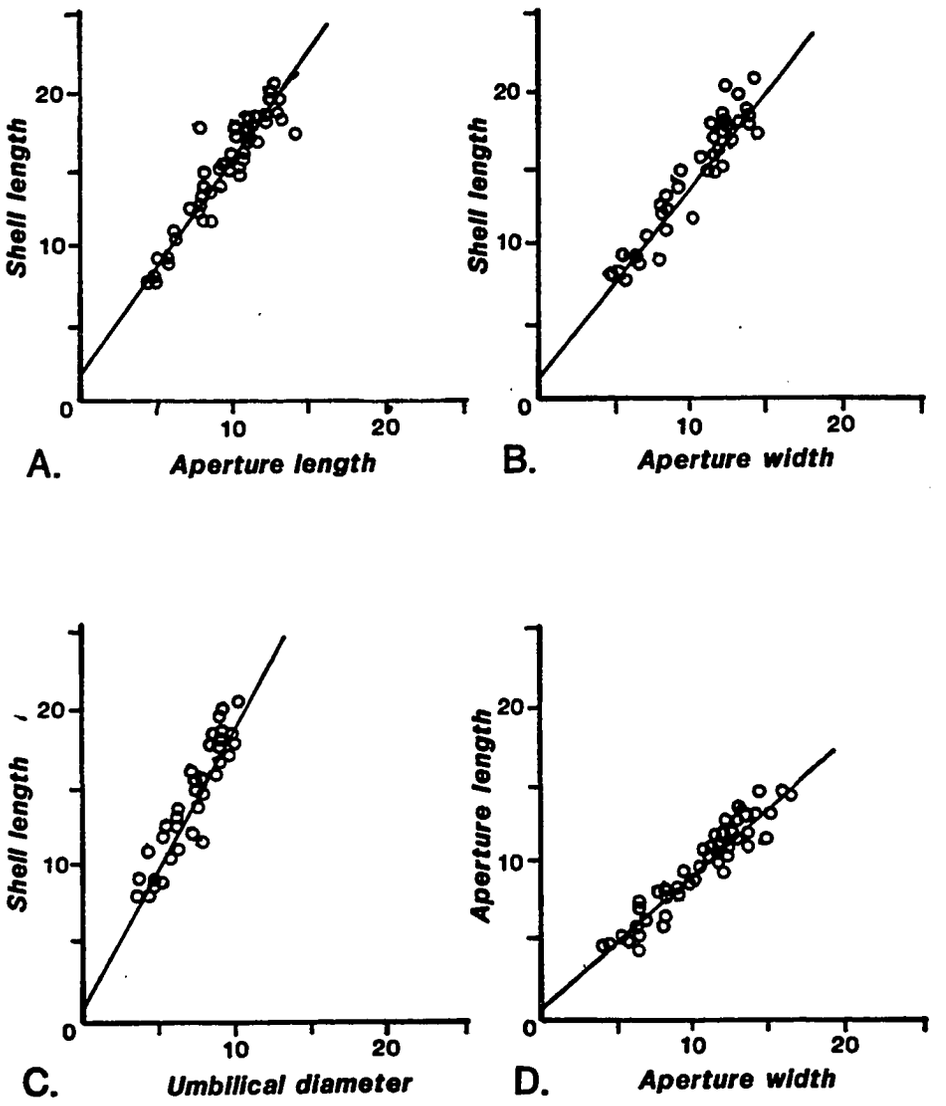
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 26: Bivariate plots of measurements made on specimens of Cyrtolites (Cyrtolites) retrorsus from the Logana Member of the Lexington Limestone in central Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C. (Cyrtolites) retrorsus

Logana member - Lexington Limestone



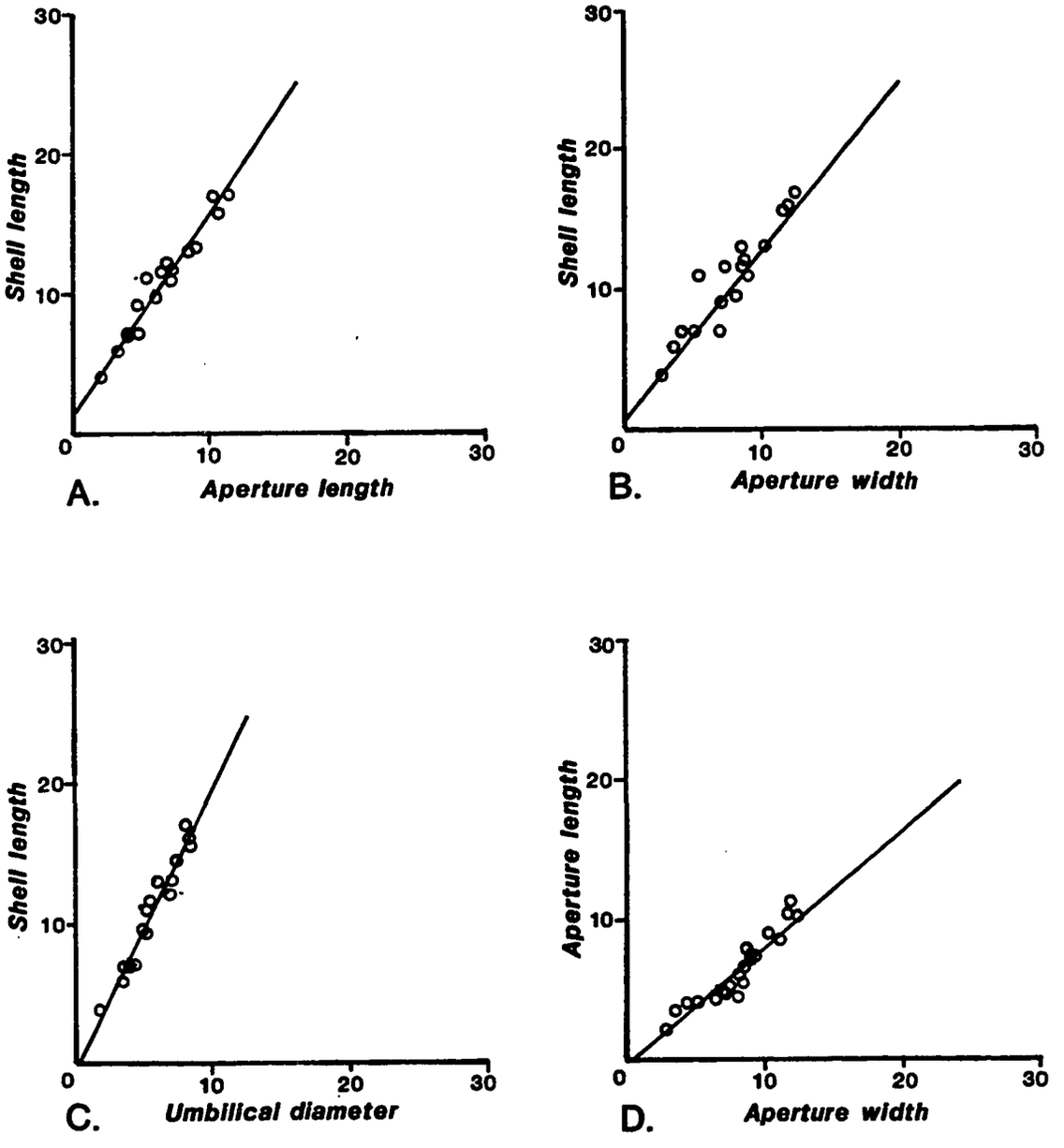
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 27: Bivariate plots of measurements made on specimens of Cyrtolites (Cyrtolites) retrorsus from the Grier Limestone Member of the Lexington Limestone in central Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C. (Cyrtolites) retrorsus

Grier limestone member - Lexington Limestone



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

1 mile south of Burgin, Kentucky". The stratigraphic units "Flanagan" is no longer in use as it was found to include different units in different areas, but the USGS map of the Danville Quadrangle (Cressman, 1972) shows the designated area as exposing the Curdsville, Grier, and Perryville Limestone Members of the Lexington Limestone. All of these specimens are designated here as paralectotypes. The 5 paralectotypes not figured in this study remain under the original museum number USNM 45790, but the other 3 are figured here and are given the new numbers USNM 265938 (Pl. 5, figs. 1-2), USNM 265899 (Pl. 5, figs. 3-4), and USNM 265900 (Pl. 5, fig. 13).

In the USGS silicified collections, C. (C.) retrorsus was recognized in the Curdsville Limestone (5022-CO, 5023-CO, 5072-CO, 5080-CO, 5100-CO), Logana (D-1196, 4865-CO, 5073-CO, 5086-CO, 5091-CO, 5092-CO, 6419-CO, 7791-CO), Grier Limestone (4073-CO, 4852-CO, 4876-CO 4879-CO, 4880-CO, 4883-CO, 5067-CO), Millersburg (7344-CO, 7353-CO, 7455-CO), and Perryville (5015-CO) Members of the Lexington Limestone. The best preserved and most abundant samples came from the Logana Member; fairly good samples came from the Grier Limestone Member; and the samples from the other members of the Lexington Limestone were fair to poor in preservation and did not contain many specimens.

Two calcitic specimens of C. (C.) retrorsus (USNM 265909 and 265910 - Pl. 7, figs. 11-13 and 14-16, respectively), which are well-preserved but with variable form, came from the Edenian portion of the Kope Formation at Covington, Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution . - C. (C.) retrorsus is known from the study area in the Lexington Limestone (Kirkfieldian-Shermanian) to the Kope Formation (Edenian). A supposed subspecies (C. retrorsus fillmorensis) was described by Ulrich and Scofield (1897) from Blackriveran strata of Minnesota. Because this supposed "subspecies" is very poorly known and does not seem clearly distinct from the stock as known in the type area, and because C. (C.) retrorsus is shown here to have a variable shell morphology, the Minnesota "subspecies" is synonymized with C. (C.) retrorsus. The species is known in Kirkfieldian-Shermanian strata from the Curdsville Limestone, Logana, Grier Limestone, Millersburg, and Perryville Limestone (Salvisa bed) Members of the Lexington Limestone of Kentucky. Specimens assigned to C. (C.) retrorsus are known from the Edenian Kope Formation of Kentucky (Pl. 7, figs. 11-16).

In Tennessee, Bassler (1932) and Wilson (1949) reported the species from the Bigby, Cannon, and Dove-colored facies of the Bigby-Cannon Limestone; from the Ctenodonta member of the Hermitage Formation; and from the upper Catheys Formation. The first two occurrences are Kirkfieldian-Shermanian in age, and the third is either Shermanian or Edenian in age, probably the latter (Sweet and Bergstrom, 1976, text-fig. 3).

Comparisons. - C. (C.) retrorsus is quite variable in its shape, but as shown in Figures 26 and 27, its whorl dimensions are notably consistent. The only other Kirkfieldian-Shermanian species presently recognized in North America is C. (P.) subplanus (Pl. 7, figs. 26-35), which can be

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

readily distinguished by its noncarinate dorsal crest, lack of rugae, and its much weaker growth lines, with revolving threads absent or only barely discernible, so that no reticulate sculpturing is obvious.

The latest Shermanian-Edenian species C. (C.) claysferryensis n. sp. (Pl. 8, figs. 11-20) is very similar to C. (C.) retrorsus, but the former species has a slightly wider aperture and always has sharply angular umbilical shoulders. In the Edenian, juveniles of C. (C.) retrorsus might easily be confused with C. (P.) carinatus (Pl. 7, figs. 18-25), which is a small species; these two should be distinguishable by the difference in the number of whorls present in the juveniles of the former versus the adults of C. (P.) carinatus.

Specimens of C. (C.) retrorsus (Pl. 7, figs. 11-16) from the Edenian portion of the Kope Formation vary in shell form, but the character of their surface markings suggests that they are conspecific with the specimens from Kirkfieldian-Shermanian aged strata.

Discussion. - In the discussion of the species C. retrorsus, Ulrich and Scofield (1897, p. 861-862) were confident of its specific distinctiveness, but showed concern for the inclusion of some specimens, particularly those from the basal beds of their Trenton Group in Kentucky and Tennessee. They stated: "So far as the form of the shell and the volutions are concerned, the specimens in question certainly agree very closely with C. retrorsus, and if appearances are not deceptive, they are like it also in the backward swing of the surface markings. The evidence

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

at hand, therefore, seems to indicate that all of the Tennessee and Kentucky Trenton specimens hitherto referred to C. ornatus really belong to C. retrorsus".

It is not surprising that Ulrich and Scofield showed apprehension in their remarks concerning this species, as it demonstrates a high degree of intraspecific variability in shape. It is recognized mainly on the basis of its distinct reticulate ornament pattern (in adult shells), the gentle curving of its growth lines over the dorsal crest of the shell, and its aperture height/width ratio regardless of the apertural outline. As shown in Plate 5, figures 14, 18, and 22, the apertural shape of C. (C.) retrorsus can vary from quadrangular to nearly circular in a single population. All three of these figured specimens are from a single sample from the Logana Member of the Lexington Limestone (USGS sample 6419-CO) in central Kentucky. This sample is considered to represent a single population because of: (1) occurrence in a single sampled bed, (2) the presence of a gradational growth series, and (3) the quality of preservation, which suggests very little transport. It appears that this intraspecific variability in whorl shape is largely genetic in origin, rather than ecophenotypic. There is also, however, what appears to be ecophenotypic variation expressed between populations from different stratigraphic units. For example, when some of the more rounded, inflated forms from the Logana Member of the Lexington Limestone (Pl. 5, figs. 18-25) are compared directly to more angular forms, such as Ulrich and Scofield's (1897) type

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

specimens from Tennessee (Pl. 5, figs. 5-12), there appears to be two possible species. However, Ulrich and Scofield's type specimens from Kentucky (Pl. 5, figs. 1-4, 13) are intermediate in form, as are many other specimens, including some of the Logana specimens (Pl. 5, figs. 14-17). Such marked variation makes the formulation of a concise description of the species difficult. Possibly equally frustrating are ontogenetic changes in shell form. Juvenile specimens are usually quite angular, some even being carinate dorsally and laterally, and the dorsal slopes can be slightly concave. These small, smooth, angular specimens while resembling C. (P.) carinatus, can be distinguished by their narrower form and fewer whorls. This situation is not uncommon when dealing with isotropic molluscan univalves. Ulrich and Scofield (1897) claimed that immature specimens of Cyrtolites and Carinaropsis are virtually indistinguishable. Thein and Nitecki (1974, p. 55) encountered a similar problem with Chesterian bellerophontids, finding that the differentiation of three subgenera of Knightites was impossible from immature specimens.

During adult and gerontic growth, shell form often continually changes. Some shells retain some of the angularity of youth (Pl. 5, fig. 11), but the aperture broadens and the dorsal whorl slopes become convex. Others lose their angularity complete in the final volution, with the dorsal crest becoming almost rounded, so that a more inflated form results (Pl. 5, figs. 22-25).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Also, the coarseness of the rugae can be quite variable, and does not vary in concert with the degree of angularity or roundness of the shell. For example, the lectotype (Pl. 5, figs. 5-7) and a paralectotype (Pl. 5, figs. 8-10) from the same collection from Tennessee are very similar in their general form, but the former specimen has more distinct ridge-like rugae, similar to some of the inflated Logana forms (Pl. 5, figs. 22-25). Regardless of shell form, all adult specimens of the species have distinct reticulate shell sculpturing, with abaperturally curved growth lines reflecting a broad, shallow, dorsal labral sinus.

C. (C.) retrorsus apparently gave rise to a fairly diverse group of Late Ordovician descendants. The two specimens of C. (C.) cf. retrorsus from the Edenian Kope Formation (Pl. 7, figs. 11-13 and 14-16) previously discussed, may represent the last surviving populations of C. (C.) retrorsus in the study area, possibly struggling for existence under the more turbid conditions of the early Cincinnatian seas.

CYRTOLITES (CYRTOLITES) CLAYSFERRYENSIS new species

Pl. 4, figs. 15-17, Pl. 8, figs. 11-20

Diagnosis. - Shell moderate-sized (up to 19 mm in shell length), angular; aperture wide and subquadrangular, dorsal crest and umbilical shoulders sharply angular, dorsal slopes convex, ventral slopes concave; reticulate ornament distinct; sinus shallow.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell of moderate size for genus, with broad angular shell; coiling moderately loose; umbilicus wide and rather deep. Aperture shape subquadrangular and broad, aperture height/width ratio 0.76; dorsum carinate in juveniles, becoming sharply angular in adults; dorsal slopes broadly convex, sometimes draping slightly at umbilical shoulders in large specimens; umbilical shoulders sharply angular; ventral slopes distinctly concave. Rugae distinct, thin, regularly-spaced, forming small nodes at umbilical shoulder and extending dorsally for about three-fourths the width of the dorsal slope; rugae do not influence ventral slopes at all. Growth lines swing quite gently abaperturally over dorsal crest of shell reflecting a broad, shallow, dorsomedian labral sinus; short, alternating, revolving threads of near equal prominence, resulting in distinct reticulate surface sculpturing.

Measurements. - The measurements for C. (C.) claysferryensis are listed in the Table 27 below, and accompanying plots are in Figure 28.

Growth appears to be highly coordinated on all parameters plotted, having correlation coefficients of 0.97-0.98, and all regression lines approach the graph origins quite closely.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 27: Measurements for C. (cyrtolites) claysferryensis n. sp. in mm.

Museum No.	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	No. Growth Lines per mm
USNM							
265923	16.9	9.75	13.0	9.1	3.4	1.5-2.0	4
265924	15.0	9.0	12.7	8.6	3.0	1.5	5-6
265925	19.0	12.8	16.2	9.5	4.5	2.0-3.0	4
265973	16.1	10.4	14.4	8.1	3.6	1.5-2.0	-
265973	-	10.4	14.6	-	-	2.0	5
265973	-	12.2	13.8	11.2	-	-	-
265973	14.1	10.7	12.5	-	-	-	-
265973	16.9	11.5	16.4	8.0	3.5	-	-
265970	17.3	13.1	17.1	10.1	4.7	-	5-6
265970	16.7	10.9	15.8	8.0	3.7	2.0	-
265970	15.8	10.7	13.0	8.9	2.8	2.0	4
265970	15.1	-	13.2	9.1	3.0	2.0	4-5
265972	13.5	7.6	10.5	7.7	3.0	1.5	4
265976	15.2	-	-	6.9	3.6	1.5-2.0	5-6

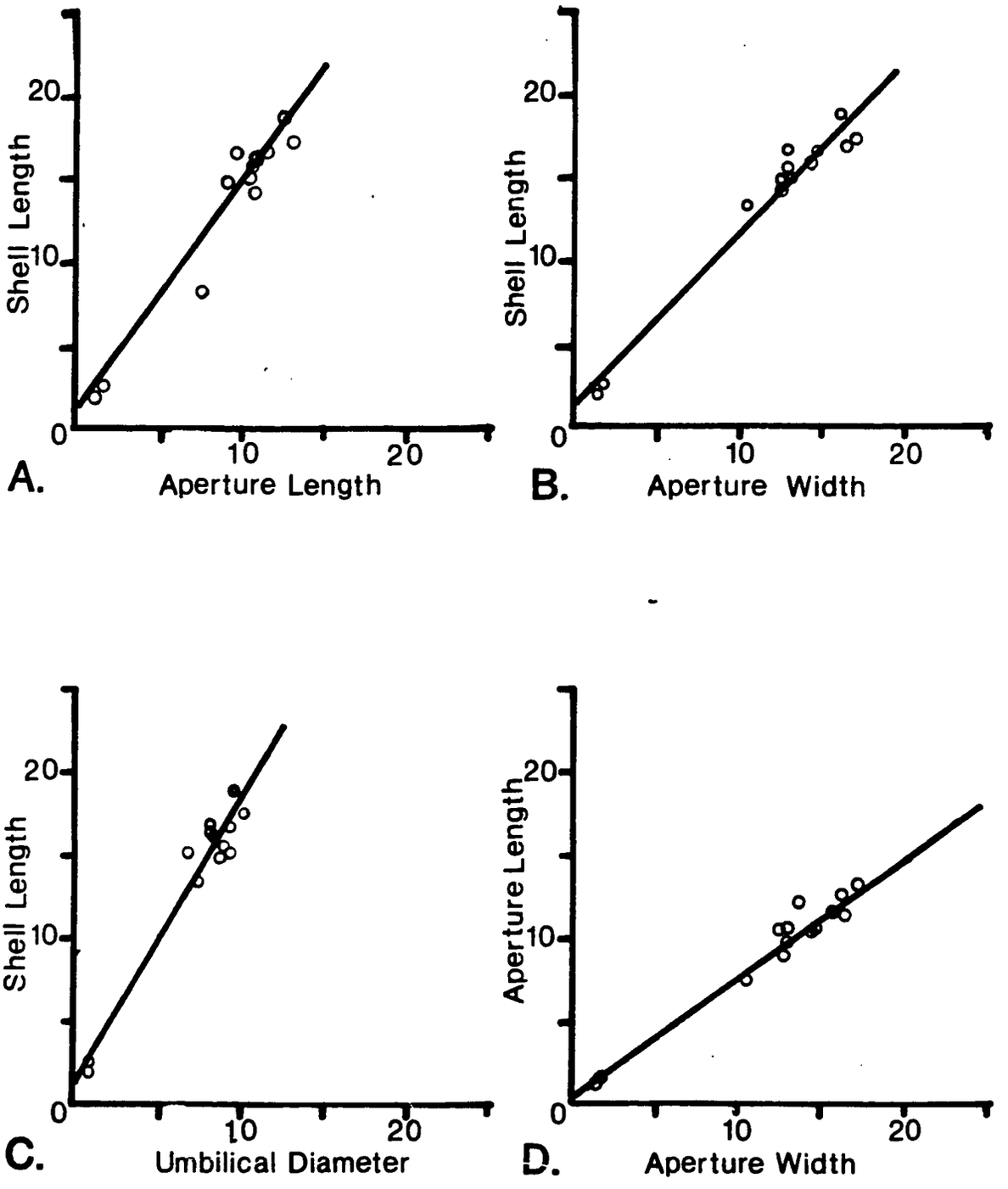
Types. - The new species was found in the following USGS silicified samples from the Clays Ferry Formation: 6143-CO, 6990-CO, 7343-CO, 7348-CO, 7349-CO, 7350-CO, 7458-CO, 7461-CO, and 7812-CO. The specimen designated here as the holotype for the new species is USNM 265924 (Pl. 8, figs. 14-18) (shell length = 15.0 mm, aperture length = 9.0 mm, aperture width = 12.7 mm) from USGS sample 6143-CO, from the upper tongue of the Clays Ferry Formation in a road exposure on the east side of Kentucky Route 982, 0.4 miles south of the junction of Kentucky Routes 32, 36, and 982 in Cynthiana, Kentucky. Two silicified paratypes are also figured, USNM 265923 (Pl. 8, figs. 19-20) from the same collection as the holotype, and USNM 265925 (Pl. 8, figs. 11-13) from USGS sample 6990-CO. About

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 28: Bivariate plots of measurements made on specimens of Cyrtolites (Cyrtolites) claysferryensis from the Clays Ferry Formation of north-central Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES CLAYSFERRYENSIS



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

60-70 specimens and fragment are present in the silicified collections, but only 14 were of sufficient preservation to be usable for measurements.

Two calcitic specimens collected by the author are designated paratypes with the above silicified material. Paratype USNM 265959 (Pl. 4, figs. 15-16) was found in a mollusk bed composed predominantly of small pelecypods and gastropods, in the Clays Ferry Formation at the Sadieville, Kentucky Exit on Interstate Highway I-75. Paratype USNM 315609 (Pl. 4, fig. 17) was found in a mollusk bed dominated by Sinuites granistriatus in the lower Kope Formation, about 10 feet above the contact with the Point Pleasant Member of the Clays Ferry Formation, just north of Ohio Route 52 along the north shore of the Ohio River, at Bear Creek Quarry, between Neville and Chilo, Ohio.

Distribution. - The new species is known from the Clays Ferry Formation (latest Shermanian - early Edenian), and the lower Kope Formation (Edenian) in Kentucky and southwestern Ohio.

Comparisons. - C. (C.) claysferryensis is very similar to some of the more angular forms of C. (C.) retrorsus, but its aperture height/width ratio is lower, reflecting its relatively broader aperture; its umbilical shoulders are consistently more sharply angular, this impression being accentuated by the concave slopes of the broad umbilicus; its growth lines generally do not swing abaperturally as deeply (reflecting a shallower sinus) (Pl. 8, fig. 18); and its rugae are generally thinner and sharper (Pl. 8, fig. 14), and never extend onto the upper ventral slopes. C. (C.)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

claysferryensis is also quite similar in some respects to C. (C.) hornyi n. sp. from the Richmondian Dillsboro Formation of southeastern Indiana, but the latter species has flatter whorl slopes (Pl. 8, fig. 1), straight growth lines (Pl. 8, fig. 2), and attains a somewhat larger size (Pl. 8, figs. 1-4).

Discussion. - It is clear that C. (C.) claysferryensis evolved directly from C. (C.) retrorsus, which not only closely resembles the former species in many morphological features, but also immediately precedes and partially overlaps with it stratigraphically. C. (C.) retrorsus thrived in the dominantly carbonate environments of the upper Middle Ordovician Lexington Limestone, and apparently only barely survived into the overlying Edenian Kope Formation. C. (C.) claysferryensis first appears in the Clays Ferry Formation, which straddles the Middle-Upper Ordovician boundary, and is an adjacent facies to both the upper Lexington Limestone and the lower Kope Formation, having more shale than the former and less than the latter. The new species is also recognized in the Kope Formation. Apparently, the development of a wider, more angular aperture, with a shallower dorsomedian sinus, helped C. (C.) claysferryensis to survive the more turbid conditions of the early Cincinnatian seas. Possibly this apertural modification created better channeling of currents through the mantle cavity and thus prevented clogging of the ctenidia by fine sediments, or possibly it assisted in the support of the shell on softer substrates.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

It should be noted that whereas C. (C.) retrorsus has a relatively well-developed dorsal sinus, that of C. (C.) claysferryensis is somewhat shallower, and later species lose the sinus altogether. It is difficult to see why this lineage shows this trend toward the reduction of a labral sinus, because an emargination is known to be highly efficient as an exhalent canal in pleurotomariacean gastropods, and it would seem to be likewise useful in monoplacophorans. Possibly, its loss allowed a tighter seal when the animal champed down onto substrate for protection.

As noted above, C. (C.) claysferryensis shows similarity to C. (C.) hornyi from the Richmondian Dillsboro Formation of Indiana. Both species inhabited similar depositional environments of alternating carbonate and shale sedimentation, and C. (C.) hornyi is likely the end product of slow intrafacies evolution, but at present intermediate forms are not known.

CYRTOLITES (CYRTOLITES) MINOR Ulrich, 1897

Pl. 7, figs. 2-10

Cyrtolites ornatus minor ULRICH in ULRICH & SCOFIELD, 1897, p. 860, Pl. 62, figs. 30-31; WELLER, 1903, p. 174-175, Pl. 12, figs. 6-7

Diagnosis. - Shell small (up to 13.5 mm shell length), narrow; dorsal carina high and sharp, umbilical shoulders rounded to narrowly rounded; rugae distinct; growth lines pass over dorsal carina with little or no deflection; reticulate ornament distinct.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell small and narrow in form, umbilicus fairly wide. Aperture subquadrangular; dorsal carina well-developed, high and sharp; dorsal slopes concave for short distance near dorsal carina, becoming convex through most of their extent; umbilical shoulders rounded to narrowly rounded; ventral slopes flat to slightly concave. Rugae well-developed, particularly at umbilical shoulder, over which they extend onto the upper ventral slope; rugae thick and rounded at umbilical shoulder, becoming weaker dorsally to near the dorsal carina. Growth lines generally at right angle to dorsal carina, but may be slightly deflected abaperturally; revolving threads of near equal strength to growth lines, together forming a distinct reticulate shell sculpture.

Measurements. - The measurement of three specimens, including the holotype, are listed in Table 28 below, and accompanying plots are shown in Figure 29. A fourth set of measurements listed were taken from Weller's (1903, Pl. 12, figs. 6-7) figure of the species from New Jersey. Although only a small number of specimens were available for measurement, growth appears highly coordinated, with correlation values being high, but the regression lines do not approach the graph origins very closely. It is likely that this picture would change greatly with the measurement of more specimens.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 28: Measurements of C. (Cyrtolites) minor in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae
USNM 45787	9.8	6.4	6.2	4.7	1.4	1.0
UC 19668	13.5	8.0	7.0	6.2	2.0	2.0
UC 44275	12.0	7.0	6.5	6.5	2.0	2.0
Weller (1903)	11.5	-	8.5	-	-	-

Material. - Only three specimens of C. (C.) minor are known from the study area, the holotype (USNM 45787), a specimen from the Kope Formation (UC 19668), and a specimen collected by Mr. Steve Felton of Cincinnati from the Fairview Formation (UC 44275). All three specimens are calcitic casts, and the Kope specimen is encrusted by bryozoans.

Distribution. - The holotype (USNM 45787) is from the Clitambonites bed of the Prosser Formation at Cannon Falls, Minnesota, which Winchell and Ulrich (1897) considered to be the base of the "Trenton Series", and which Templeton and Willman (1963, figs. 19A-b) considered the basal beds and formation of the Galena Group. Weiss (1957) split off the base of the Prosser into a new unit, the Cumingsville Formation, which Sweet and Bergstrom (1976, text-fig. 3) designated as Kirkfieldian-Shermanian in age. Weller (1903) reported the species from the "Trenton Series" of New Jersey.

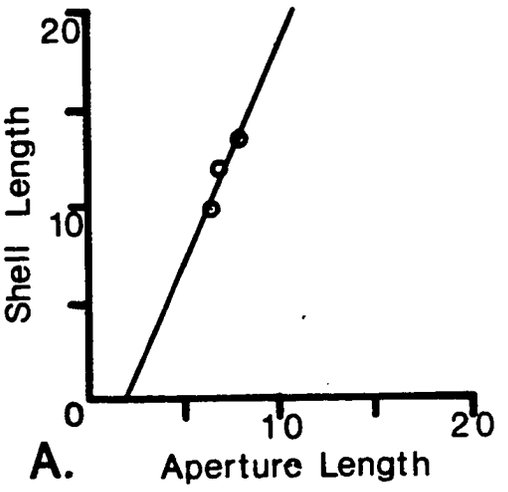
Comparisons. - C. (C.) minor is quite similar in form to C. (C.) ornatus, of which it was originally considered a "variety" by Ulrich and Scofield (1897). However, C. (C.) minor is much smaller than C. (C.)

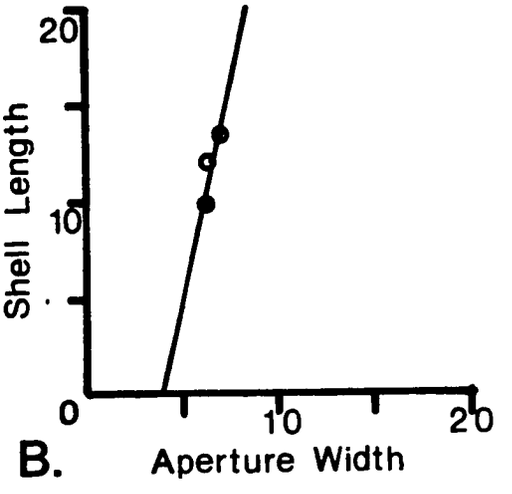
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

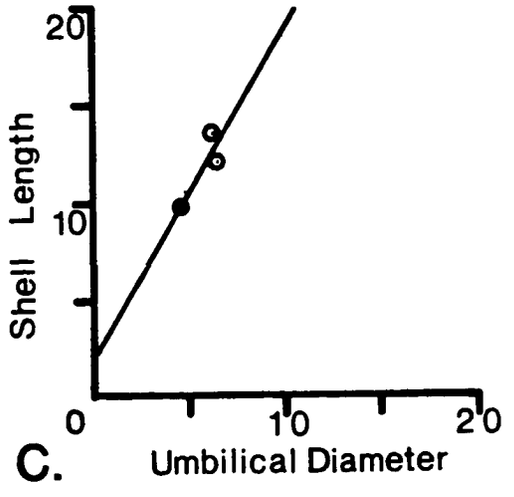
Figure 29: Bivariate plots of measurements made on specimens of Cyrtolites (Cyrtolites) minor.

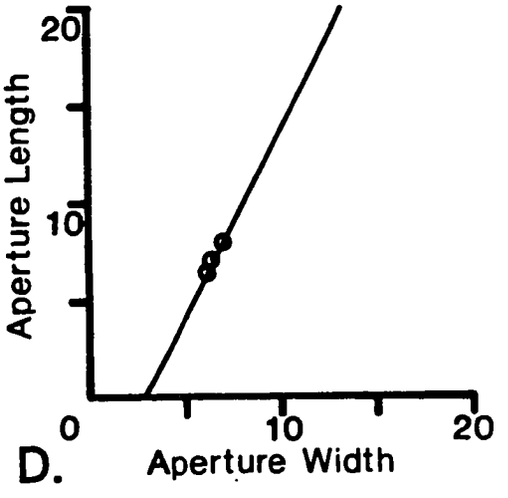
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES MINOR









Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ornatus, and there can be no doubt that the specimens assigned to the C. (C.) minor are adults and not juveniles of the C. (C.) ornatus, as they possess at least 2 whorls and have well-developed rugae and reticulate shell sculpturing. Two reasons have prompted me to regard C. (C.) minor as a distinct species. First, it is consistent in its form over a wide geographic area (Minnesota to Kentucky to New Jersey) and through a distinct stratigraphic range (Kirkfieldian - lower Maysvillian). Second, besides its smaller size, it differs from C. (C.) ornatus in its slightly narrower shell form, and by having the growth lines slightly deflected abaperturally over the dorsal crest (at least in the geologically older forms of the species), showing a possible transitional relationship with C. (C.) retrorsus.

It is easy to confuse C. (C.) minor with C. (P.) carinatus (Pl. 7, figs. 18-25), as the general shell form of the two species can be quite similar. Both are small species with distinct dorsal carinae, and the two occur in the same stratigraphic interval (Edenian) in the study area. C. (P.) carinatus differs in lacking rugae and a distinct reticulate ornament, as well as in having sharply angular to carinate umbilical shoulders.

Discussion. - C. (C.) minor may be an intermediate species between C. (C.) retrorsus and C. (C.) ornatus. Not only does the stratigraphic range of C. (C.) minor overlap with the upper part of that of C. (C.) retrorsus and the lowest part of that of C. (C.) ornatus, but the curva-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ture of the growth lines of C. (C.) minor is also intermediate between these two other species. The holotype (Pl. 7, figs. 2-4) of C. (C.) minor from the uppermost Champlainian strata (Prosser Formation) of Minnesota has surface markings that are essentially identical with those of C. (C.) ornatus, "except the transverse striae in crossing the dorsal carina are sometimes bent slightly backward" (Ulrich and Scofield, 1897, p. 861). Weller (1903, p. 174) in the description of his specimens from the "Trenton" of New Jersey, noted that the growth lines ran "almost straight across the volutions". The Cincinnatian (Edenian and lower Maysvillian) specimens from the present study area appear to show no abapertural deflection of the growth lines dorsally (Pl. 7, figs. 5-7 and 8-10). Therefore, there appears to be a gradualistic evolutionary trend within the species C. (C.) minor toward the final and complete reduction of an apertural sinus in the C. (Cyrtolites) lineage.

CYRTOLITES (CRYTOLITES) HORNYI new species

Pl. 8, figs. 1-10

Diagnosis. - Shell large (up to 27 mm shell length), with broad angular shell form and relatively rapid rate of whorl expansion; aperture diamond-shaped, dorsally and laterally sharply angular, dorsal and ventral slopes nearly flat; rugae thin, growth lines not deflected anteriorly over dorsum, revolving lines weaker.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell relatively large for genus, with broad, angular shell form; relatively rapid rate of whorl expansion, whorls barely contiguous, even showing slight tendency toward uncoiling in largest specimens; adult shell with 2-3 whorls. Aperture quadrangular and diamond-shaped; dorsal and ventral slopes slightly concave in juveniles, becoming nearly flat in adults; dorsum and umbilical shoulders slightly carinate in juveniles, becoming sharply angular in adults. Rugae are thin, distinct, regularly-spaced ridges, often forming nodes along the umbilical shoulders, and extending to near the dorsal crest. Growth lines directed straight over dorsal crest of shell without any abapertural deflection, stronger than revolving connecting threads, so that reticulate surface sculpturing is not conspicuous.

Measurements. - Measurements for C. (C.) hornyi are shown in Table 29 below, and accompanying graphs are displayed in Figure 30. All parameters plotted for this species have very high correlation coefficients (being nearly perfect), and the regression lines approach the graph origins closely. Although only 4 specimens were measurable, the species appears to have nearly isometric growth, as the ratios between plotted parameters stay constant throughout growth.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 29: Measurements of C. (Cyrtolites) hornyi in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
USNM 265920	26.9	17.9	21.9	14.5	2.4	3.0	4
265921	22.7	14.5	17.2	11.35	2.7	3.0	4-5
265922	22.9	15.0	18.1	13.0	-	2-3	4
265978	12.8	8.65	10.4	7.0	-	-	-

Type material. - C. (C.) hornyi n. sp. is known from about 16 specimens, most of which are fragmentary, from the USGS silicified collection 6139-CO taken from the upper Dillsboro Formation along the south bank of Salt Creek, 900 feet upstream from the covered bridge on Enochsburg-Oldenburg Road, in New Point Quadrangle, Indiana. The holotype (USNM 265920) (shell length = 26.9 mm, aperture length = 17.9 mm, aperture width = 21.9 mm) is here designated as the specimen shown on Pl. 8, figs. 1-4. Two paratypes are also figured (USNM 265921 and 265922 on Pl. 8, figs. 5-7 and 8-10, respectively). All other paratypes are placed together under the number USNM 265978.

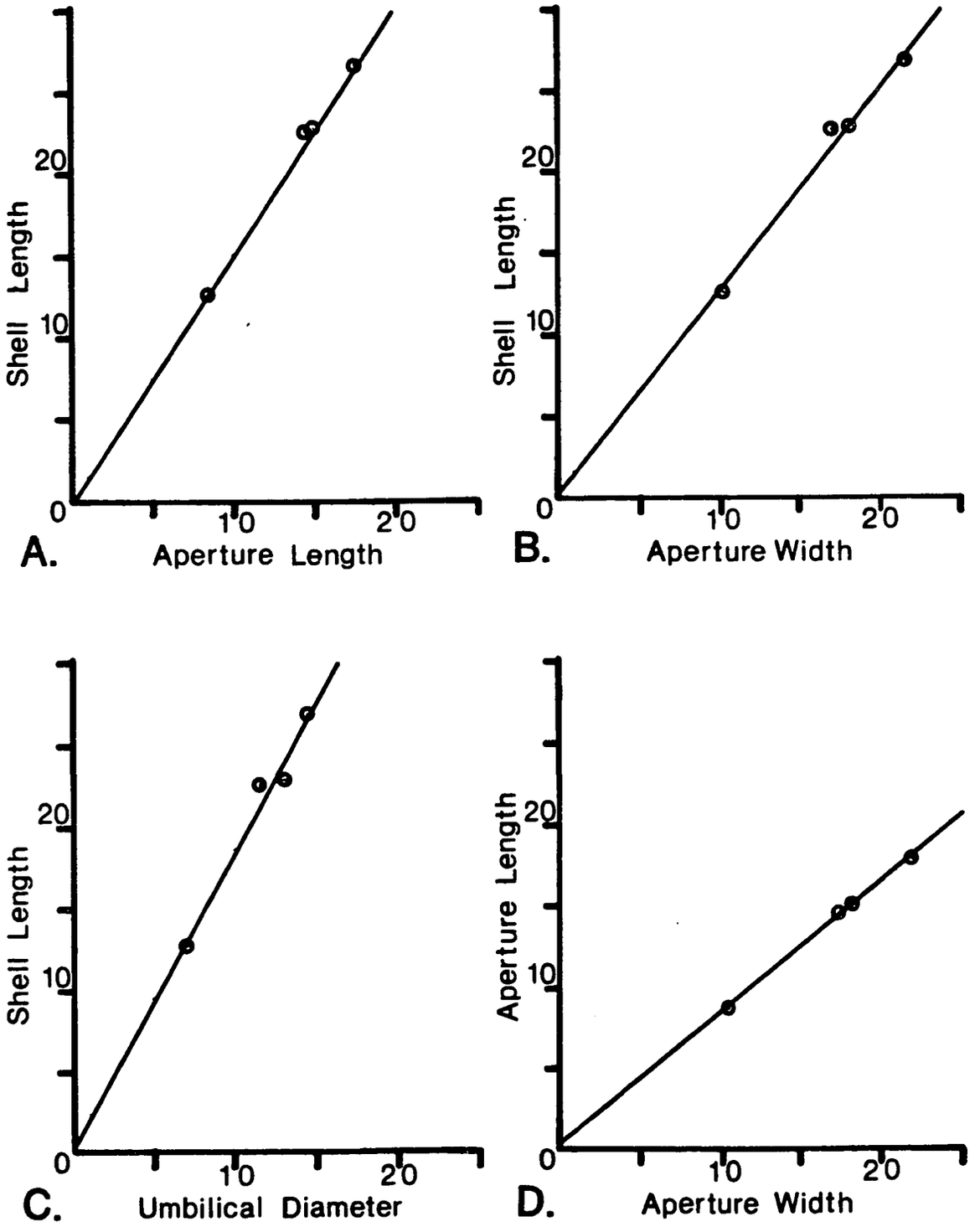
Distribution. - The new species is only known from the single locality given above in the Richmondian (upper Upper Ordovician) Dillsboro Formation of southeastern Indiana. The single sample came from that part of the Dillsboro Formation previously termed the Liberty Formation (and even earlier was termed "the Strophomena beds"). This portion of the formation is referred to here as the Liberty biofacies.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 30: Bivariate plots of measurements made on specimens of *Cyrtolites* (*Cyrtolites*) *hornyi* new species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES HORNYI



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - C. (C.) hornyi is clearly distinguishable from all other Richmondian Cyrtolites. C. (C.) ornatus has somewhat narrower, more rounded shell form, and its rugae are much more strongly expressed (Pl. 6, figs. 1-18). C. (C.) disjunctus is even more distinct in being disjunctly coiled and even more rounded than C. (C.) ornatus (Pl. 6, figs. 19-22). C. (C.) hornyi (Pl. 8, figs. 1-10) most closely resembles C. (C.) claysferryensis (Pl. 8, figs. 11-20). However, the whorl slopes of C. (C.) hornyi are much flatter, giving a distinctly diamond-shaped aperture, and its growth lines are straight rather than deflected abaperturally over the dorsal crest, demonstrating the lack of an apertural sinus as was clearly present in C. (C.) claysferryensis. Figures 28 and 30 show that the modes of growth in the two species is also very similar, the most striking difference being in the larger size attained by the Richmondian species.

Discussion. - C. (C.) hornyi almost certainly is descended from C. (C.) claysferryensis. Not only are they quite similar morphologically, but they apparently inhabited similar depositional environments (see discussion of subgenera) characterized by intermittent carbonate and shale deposition. Both stratigraphic units in which the respective species are found are characterized in part by the presence of large flat strophomenid brachiopods. Although it is not known whether either species inhabited these brachiopod communities, the widespread presence of these environments indicates a similar depositional system operating during the deposition of the formations. I collected C. (C.) claysferryensis from

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

two localities, one in the Clays Ferry Formation and one in the lower Kope Formation, and in both cases the species was restricted to thin horizons characterized by almost entirely molluscan assemblages. At the present state of knowledge, considering the apparent rarity of C. (C.) hornyi, and the lack of known intermediate Maysvillian forms, it is inferred that this species was more specialized in its habits than the more abundant Maysvillian-Richmondian aged species C. (C.) ornatus.

CYRTOLITES (CRYTOLITES) DISJUNCTUS Ulrich and Scofield, 1897

Pl. 6, figs. 19-22

Cyrtolites disjunctus ULRICH & SCOFIELD, 1897, p. 864, Pl. 62, figs. 48-49; WILSON, 1951, p. 23, Pl. 2, figs. 3-4

Diagnosis. - Shell with disjunct coiling; aperture ovoid; rugae well-developed as rounded ridges; growth lines not deflected over dorsal crest, revolving threads of near equal strength with growth lines and the two forming a distinct reticulate surface sculpture.

Description. - Shell of moderate size for genus (up to 23 mm shell length), disjunctly coiled, whorls rapidly expanding in size; narrow in dorsal view. Aperture broadly ovoid, narrowing dorsally to a low dorsal carina; dorsal slopes convex; umbilical shoulders broadly rounded; ventral slopes convex and shorter than dorsal ones. Ventral side of whorl bears a revolving, elevated, tapering band, with squared-off raised margins bord-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ering a depressed central furrow. Rugae strongly developed as broadly rounded ridges, which extend from the lower ventral slopes to near the dorsal carina. Distinct reticulate shell ornament formed by straight growth lines, which are not deflected abaperturally over the dorsal crest, and revolving connecting threads of equal strength. Shell thin.

Measurements. - Measurements on the holotype only are listed in Table 30.

Table 30: Measurements for C. (Cyrtolites) disjunctus in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width	Wavelength of Rugae	Number growth lines per mm
USNM 45785	23.0	12.1	11.0	11.2	-	2-3	4-5

Material. - The only specimen known of this species is the holotype (USNM 45785), but that single specimen preserves the shell and its markings excellently.

Distribution. - The holotype comes from Richmondian strata near Spring Valley, Minnesota. Wilson (1951) reported Cyrtolites cf. disjunctus from the Rockland beds (Rocklandian - upper Middle Ordovician) of the Ottawa-St. Lawrence Lowland, Canada, but emphasized: "The specimens at hand are too poorly preserved for certain identification, but they show the free final whorl". She figured only a copy of the drawing given by

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ulrich and Scofield (1897, Pl. 62, figs. 48-49) of the holotype, and did not show any of her material. I doubt very strongly that Wilson's specimens belong to C. (C.) disjunctus mainly because of their much lower stratigraphic position. I suspect that she might have had internal molds of another species of Cyrtolites, which because of the loose coiling of the genus, often are disjunct (see Pl. 7, fig. 1 for examples of disjunct internal molds of C. (C.) ornatus).

Comparisons. - Even though C. (C.) disjunctus is not known from the Cincinnati Arch Province, it is treated herein so that it could be compared to the disjunct internal molds of C. (C.) ornatus which are quite common in the Upper Ordovician of the study area (Pl. 6, fig. 18; Pl. 7, fig. 1). The whorls of C. (C.) disjunctus expand at a different rate (somewhat more rapidly) and the volutions increase their distance from the axis of coiling at a much higher rate. This mode of coiling results in a shell with a relatively small initial whorl and a relatively large adult whorl that is exposed on all sides, including the venter. Moreover, the ovoid whorl shape of C. (C.) disjunctus is much more rounded.

Discussion. - It is important to note that C. (C.) disjunctus retains the ventral "saddle" on the venter of the whorl which would fit over the dorsal crest of the preceding whorl in conjunctly coiled species (Pl. 6, figs. 20 and 22). This would seem to indicate that this species had developed directly from a conjunct species. C. (C.) ornatus is the most likely ancestor. The two species have similar whorl shapes, although

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C. (C.) disjunctus has more rounded umbilical shoulders. Their external sculpturing is especially similar. Both have well-developed, thick, ridge-like rugae and a distinct reticulate sculpture pattern, with near equally strong straight growth lines and revolving threads. Furthermore, some gerontic specimens of C. (C.) ornatus show a tendency to uncoil in the last quarter whorl, or so.

Disjunct coiling is generally considered an adaptation to a more sessile mode of life in the Gastropoda, and this may also apply to the Monoplacophora also. Such shells would seem to be rather awkward to move about.

Subgenus CYRTOLITES (PARACYRTOLITES) new subgenus

Pl. 7, figs. 17-35; Pl. 8, figs. 21-27

Description. - Shell having no rugae developed on whorl slopes, and having no or only weakly developed reticulate ornament. Aperture sinuate, with V-shaped growth lines deflected abaperturally over dorsal crest of shell.

Distribution. - Kirkfieldian (upper Middle Ordovician) - Edenian (lower Upper Ordovician) of eastern North America.

Type species. - C. (P.) subplanus Ulrich in Ulrich and Scofield, 1897.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

North American species. - C. (P.) subplanus Ulrich in Ulrich and Scofield, C. (P.) carinatus Miller, and C. (P.) parvus Ulrich in Ulrich and Scofield.

CYRTOLITES (PARACYRTOLITES) SUBPLANUS Ulrich, 1897

Pl. 7, figs. 26-35; Pl. 8, figs. 22-27

Cyrtolites subplanus ULRICH in ULRICH & SCOFIELD, 1897, Pl. 62, figs. 40-44; (non) FOERSTE, 1924, p. 204, Pl. 34, fig. 5; BASSLER, 1932, Pl. 20, figs. 8-9; (non) WILSON, 1951, p. 23, Pl. 2, figs. 5-6.

Diagnosis. - Shell medium-sized (up to 12.4 mm shell length), narrow, rounded; umbilicus small and nearly circular; aperture subquadrangular, dorsum sharply rounded, dorsal slopes and umbilical shoulders rounded, ventral slopes flat to slightly concave; no distinct rugae developed; growth lines fine, deflected strongly abaperturally over dorsum, revolving threads weak or lacking.

Description. - Shell medium-sized for genus, narrow in dorsal view, rather tightly coiled; umbilicus relatively small, nearly circular. Aperture rounded subquadrangular, height and width nearly equal; dorsum sharply rounded with no carina developed, dorsal slopes gently convex, umbilical shoulders rounded, ventral slopes flat to slightly concave. Dorsal slopes smooth, lacking distinct rugae, but may have some gentle wrinkling, particularly near aperture of larger specimens. Growth lines

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fine but distinct, becoming slightly stronger with growth; lines turn rather sharply abaperturally over dorsum, increasing in angle near crest, reflecting relatively deep labral sinus. Very faint revolving connecting threads, barely visible on adult specimens, not being distinct enough to create reticulate pattern, but can give a faint impression of pitting. Shell thin.

Measurements. - Measurements of the types are given in Table 31. Because the species is relatively thin-shelled and therefore is not generally completely preserved, the measurements are open to greater error than those of thicker shelled species. Although it is difficult to determine actual proportions of the species and their variation, the measurements should be accurate enough to give a general impression of size and trends.

Table 31: Measurements of C. (Paracyrtolites) subplanus in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter
USNM				
45792	-	13.3	12.1	-
265914	12.4	-	7.5	6.3

Material. - Ulrich and Scofield's (1897) types include two silicified specimens (USNM 45792), collected from the Bigby-Cannon Formation at Snow's Hill, 4 miles east of Liberty, Tennessee. A note in the box containing the two types indicates that the specimens came from the Lophospira sumnerensis zone of the "Upper Trenton". Wilson (1949, p. 129) lists

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

L. sumnerensis as a typical fossil of the Cannon facies of the Bigby-Cannon Formation. The larger of these two types is here designated the lectotype (USNM 45792) (Pl. 7, fig. 26-27), the other is designated a paralectotype (USNM 265914) (Pl. 7, figs. 28-29). It should be noted that Ulrich and Scofield (1897, Pl. 62, figs. 40-43) showed a partial reconstruction of the lectotype.

The species was recognized for the first time in Kentucky from USGS silicified collections D-1196 from the Logana Member and 4852-CO from the Grier Limestone Member of the Lexington Limestone. The best of these specimens comes from the Logana collection (Pl. 7, figs. 30-32, 34) (USNM 265915) and it preserves the aperture shape and surface ornament very well. Specimen USNM 265917 (Pl. 8, fig. 27) also comes from this collection. The collection from the Grier Limestone Member includes forms which compare favorably, but uncertainly, with C. (P.) subplanus. Specimens USNM 265918 (Pl. 7, fig. 33) and USNM 265916 (Pl. 8, figs. 22-24) are fragmented and their shells seem a bit too broad for the species. Specimen USNM 265919 (Pl. 8, figs. 25-26) has the same problems, but is also worn nearly smooth and is bored.

Distribution. - The species is known from strata of the Kirkfieldian-Shermanian stages (upper Middle Ordovician) in Tennessee and Kentucky. In Tennessee the species is known from the Cannon facies of the Bigby-Cannon Formation according to the label with the types and Wilson (1949). Bassler (1915) listed the species from the Catheys Formation

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Shermanian-Edenian). Foerste (1924, p. 204) affirmed the occurrence of the species in the Catheys, and he further cited a possible specimen from Edenian strata of Manitoulin Island. He does not figure this specimen, but from his description, it is more like C. (P.) carinatus, having angular umbilical shoulders. In Kentucky the species is known for certain from the Logana Member (Kirkfieldian) of the Lexington Limestone, and possibly also from the Grier Limestone Member (Kirkfieldian and possibly early Shermanian) of the same formation.

Comparisons. - This distinctive species is separable from the co-occurring C. (C.) retrorsus (Pl. 4, figs. 1-26) in that it is narrower in dorsal view (Pl. 7, figs. 27, 29, 30); it has a nearly smooth, rounded (but not inflated form, lacking rugae (Pl. 7, figs. 26, 38, 32); its growth lines are finer and swing abaperturally more sharply over the dorsal crest of the shell (Pl. 7, figs. 34, 35), reflecting a more deeply cut V-shaped sinus; and the short, revolving connecting threads between the growth lines are so weak that there is no apparent reticulate sculpture.

Discussion. - Bassler (1915, p. 386) listed a page number in Ulrich and Scofield's (1897) monograph where the original description of the species is supposed to be found, and the latter authors give the same page reference on their plate description for the species. However, there is no description for Cyrtolites subplanus on that or any other page in Ulrich and Scofield (1897), so that the new species was only figured by

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

them. Therefore, the description given here is the first published for the species. This is the oldest species known for C. (Paracyrtolites) and is the type species for the subgenus. It is believed to be ancestral to the Edenian species C. (P.) carinatus and C. (P.) parvus.

The ecological requirements of the C. (P.) subplanus species appear to have been the same as for C. (C.) retrorsus with which it co-occurs in USGS silicified samples D-1196 from the Logana Member and 4852-CO from the Grier Limestone Member of the Lexington Limestone.

CYRTOLITES (PARACYRTOLITES) CARINATUS Miller, 1874

Pl. 7, figs. 18-25; Pl. 4, fig. 21

Cyrtolites carinatus MILLER, 1874, p. 311, fig. 32; MILLER, 1889, p. 401, text-fig. 67; ULRICH & SCOFIELD, 1897, p. 862, Pl. 62, figs. 50-51; GRABAU & SHIMER, 1909, p. 610, figs. 815e-g; FOERSTE, 1924, p. 205, Pl. 34, figs. 2a-c, Pl. 35, figs. 5a,b

Diagnosis. - Shell moderate in size (up to 22 mm shell length), angular, narrow; aperture quadrangular and nearly equidimensional; dorsal carina high and sharp, lateral carinae not as prominent, dorsal and ventral whorl slopes essentially flat; distinct rugae lacking; growth lines very fine and swing abaperturally over dorsum; revolving threads very faint.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderate-sized; form angular and narrow, tightly coiled; umbilici large, open, and nearly circular. Aperture quadrangular; dorsum with high, sharp carina; lateral angles with low, sharp carinae; dorsal whorl slopes nearly flat, but can be slightly convex or concave; ventral whorl slopes flat to slightly concave. Distinct rugae lacking, but sometimes weak wrinkling of shell visible on dorsal slopes, particularly in gerontic specimens. Growth lines very fine and closely-spaced, swinging gently abaperturally over dorsum; revolving threads lacking or very faintly developed, particularly in immature specimens.

Measurements. - Measurements for C. (P.) carinatus are listed in Table 32.

Table 32: Measurements of C. (Paracyrtolites) carinatus in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Umbilical Diameter	Ventral Width
USNM					
49993	22.0	14.3	11.6	11.0	3.0
265913	17.95	10.25	12.2	8.75	3.5
265912	13.05	7.0	7.6	7.5	2.15
265911	8.2	5.6	6.05	5.0	1.1
45499	12.9	-	7.2	7.3	-
45783	13.8	9.25	8.7	6.9	2.5
45783	11.25	-	-	-	-
45783	11.1	-	-	6.7	-
UCGM					
44277	12.5	7.3	7.0	6.9	2.1
44278	12.8	7.4	7.4	6.2	2.5
44279	13.1	-	-	7.2	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - No specimens of this species were recognized in the new USGS silicified collections. Twelve specimens listed under only three museum numbers (USNM 47499, 49993, 45783) and labelled as Ulrich and Scofield's (1897) "plesiotypes" were examined. From this suite, specimen USNM 265913 is numbered here and shown on Plate 7, figures 24-25, it being a fairly large specimen with part of the shell preserved. The largest specimen, USNM 49993, is not figured. The specimen in Plate 7, figure 21 has been numbered USNM 265912, that on Plate 7, figure 23 as USNM 265911, and the specimen in Plate 7, figure 22 as USNM 47499. All the other specimens of this lot are placed under one number, USNM 45783. This collection of specimens was labelled as being collected from the Kope Formation (Edenian) at Newport, Kentucky.

A few specimens of the species were found in the University of Cincinnati Geological Museum under the number UCGM 19658.

Mr. Steve Felton of Cincinnati made a number of specimens available to me from his private collections from the Kope Formation near Carrolton, Kentucky. These specimens were collected from a thin bed made up almost entirely of a molluscan assemblage (Pl. 8, fig. 21). These calcitic specimens are designated UCGM 44277 (Pl. 7, figs. 20), UCGM 44278, and UCGM 44279 (Pl. 8, figs. 21). These specimens were more well-preserved than any others examined.

Distribution. - Ulrich and Scofield (1897) stated that the species was to be found in the lower shales of the Cincinnatian in the Cincinnati,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ohio area, as well as probably in Wisconsin, Iowa, and Minnesota. More recent collections affirm that the species appears restricted to the Kope Formation (Edenian) of the study area. Foerste's (1924) reported of the species from the Edenian Sheguiandah Formation on Manitoulin Island, Ontario.

Comparisons. - This species can be distinguished from all other species of C. (Paracyrtolites) by its possession of both dorsal and lateral carinae. It does resemble C. (C.) claysferryensis, but it: (1) does not attain as large a size, (2) lacks distinct rugae on the whorl slopes, (3) has finer growth lines, and (4) has such fine revolving lines that they are generally not even discernible.

Discussion. - Miller (1874) did not mention any revolving connecting threads in his original description of the species, but Ulrich and Scofield (1897, p. 863) observed a faint but distinct reticulate pattern on the inner volutions of some well-preserved specimens. They claimed that the connecting threads are present in young growth stages, but become weaker through growth, and are removed by even minimal abrasion.

To my knowledge, C. (P.) carinatus always occurs in a molluscan assemblage in thin limestone beds of the Kope Formation (Pl. 8, fig. 21). The molluscan association recalls the usual occurrence of C. (C.) claysferryensis and C. (C.) ornatus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

CYRTOLITES (?PARACYRTOLITES) PARVUS Ulrich, 1897

Pl. 7, fig. 16

Cyrtolites parvus ULRICH in ULRICH & SCOFIELD, 1897, p. 846, Pl. 62, figs. 45-47; FOERSTE, 1924, p. 204-5, Pl. 34, figs. 4a,b.

Description. - Shell small (up to 8.5 mm shell length), tightly coiled; umbilicus relatively small. Aperture subquadrangular; dorsum with low carina; dorsal slopes gently convex; umbilical shoulders rounded; ventral slopes nearly flat. Rugae totally absent. Growth lines fine but distinct, swinging abaperturally over dorsum; no revolving threads known.

Measurements. - The only measurements possible on the single specimen examined were the shell height (8.55 mm) and the maximum umbilical diameter (3.75 mm).

Material. The only specimen known is the holotype, USNM 45788, which is a small, rather poorly preserved calcitic cast (Pl. 7, fig. 16).

Distribution. - The holotype, USNM 45788, is from "near the top of the Trenton group at Covington, Kentucky", according to the museum label. The specimen was most likely collected before the submergence of sub-Kope (Edenian) outcrops along the Ohio River Valley near Cincinnati by the damming of the Ohio River. In present-day stratigraphic nomenclature, these beds would probably be assigned to the Point Pleasant Tongue of the Clays Ferry Formation of latest Shermanian age. Foerste (1924, p. 204) cited the species from the "Cynthiana Formation", now included in the Clays

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ferry Formation, at Covington, Kentucky. He also noted specimens "resembling this species" in the Maysvillian strata of Manitoulin Island, Ontario.

Comparisons. - Ulrich and Scofield (1897) claimed that this species was characterized by stronger surface markings than any other member of the genus. The holotype does not support this contention (Pl. 7, fig. 16). The holotype bears some resemblance to small specimens of C. (C.) retrorsus (Pl. 5, figs. 1-2), but the single known specimen is less carinate dorsally and laterally than juveniles of that species (Pl. 7, fig. 16). The same point holds true when the species is compared to C. (P.) carinatus in the same respect.

Discussion. - The single specimen of this species examined does not support the contention made in the original description that the species bears stronger surface markings than any other species of the genus. Because the holotype does not support the details of the original description, I am compelled to suspect the validity of the species. Nevertheless, the single, rather poorly preserved specimen does not fit readily into any other known species, so the "species" is maintained here with strong reservations.

Based on the faint ornament of the holotype, the species is tentatively placed in the subgenus C. (Paracyrtolites).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Family SINUITIDAE Dall in Zittel-Eastman, 1913

Diagnosis. - Shell tightly involute to convolute; umbilicus moderately small to lacking; whorls rounded to globose; sinus relatively wide, U-shaped to rounded V-shaped; lateral aperture margins rounded to distinctly lobate; surface markings generally very fine collabral lines; thin inductural deposits sometimes extending slightly beyond parietal area.

Stratigraphic distributsion. - As presently defined, the family is restricted to strata of Ordovician age. It is certainly known from Blackriveran - Richmond-aged strata in Eastern North America, and may extend into the Lower Ordovician (see Bassler, 1915, p. 1159-1161).

Genera included. - Sinuites Koken, 1896; Sinuitopsis Perner, 1903; Strangulites Horny, 1962; Sylvestrosphaera Peel, 1980.

Discussion. - As defined herein, the family Sinuitidae is more restricted than ever before, consisting of only four closely related genera. Previously, authors such as Knight and others (1960) included many genera that had little more in common with Sinuites and its true allies than a similarly shaped sinus. With the discovery of discrete paired muscle scars in Sinuitopsis, Sinuites and Sylvestrosphaera by Rollins and Batten (1968), Peel (1980), and Runnegar (1982), these genera were transferred to the Monoplacophora. Muscle scars are not yet known in Strangulites. The other genera previously placed in the Sinuitidae by Knight and others (1960) and Horny (1963) are tentatively assigned to the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bucanellidae of the superfamily the Bellerophontacea. Runnegar and Jell (1976, p. 121) included such genera as Cloudia and Strepsodiscus in the Sinuitidae, but I do not think these genera are closely related to the sinuitid genera cited herein.

Genus SINUITES Koken, 1896

Pls. 9-11, 21, 45

Diagnosis. - Shell tightly coiled, convolute, umbilicus closed or very small; dorsum generally rounded, occasionally flattened somewhat, rarely with dorso-median ridge; aperture large, generally longer than wide, with deep, rounded, median sinus, and lateral margins projecting downward as rounded or subangular lobes; parietal deposits thin, often ornamental; growth lines fine, closely spaced, often intersected by faint revolving lines.

Types species. - Bellerophon bilobatus Sowerby, 1839, by subsequent designation of Bassler (1915, p. 1159).

Distribution. - Middle and Upper Ordovician of North America, Europe, and North Africa.

Comparisons. - The species placed in the genus Sinuites are usually quite distinctive, and confusion with other genera is likely only when poorly preserved internal molds are encountered. In that case, there may be confusion with species of Sphenosphaesa Knight or Bellerophan Montfort.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Knight and others (1960, p. I177) placed Sinuitopsis Perner as a subgenus of Sinuites, but Horny (1963, p. 76-7) strongly contested the assignment. He claimed that their Figures 93/7a-b (Knight and others, 1960, p. I176) misinterpreted the lateral lobes of Sinuitopsis, and show a circumumbilical structure not present in the type, or related, species. Important points distinguishing Sinuitopsis are the higher, rounder shell shape on lateral view, the distinctly open umbilicus, the rounded, but not lobate, lateral aperture margins, and the narrower aperture sinus.

Horny (1962, p. 473; 1963, p. 75) proposed the genus Strangulites stating that it differs from Sinuites by more rounded, closely involuted whorls with characteristic deep constrictions of the adult body whorl. He noted (1963) that a number of the British Upper Ordovician species of Sinuites described by Reed (1920) also bear body whorl constrictions, but that these species are laterally compressed and have lobate lateral aperture margins. The type species, Strangulites strangulatus (Perner) is certainly globose, but no more so than the Kentucky species Sinuites obesus (Ulrich) (compare Horny, 1963, Pl. 6, figs. 1-3, and, here, Pl. 9, figs. 1-12). Furthermore, Horny's (1963, Pl. 6, fig. 2, and Pl. 5, fig. 4) figures seem to show that the lateral lips of S. strangulatus actually are mildly lobate (note growth lines). Horny admitted that Strangulites might be considered a subgenus of Sinuites. It is concluded here that the two are most likely synonymous.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Species of Sinuites described prior to 1896-97 were generally assigned to Bellerophon. Koken (1896, p. 392) erected the new genus Sinuites to contain European Ordovician species. Unaware of this new genus, Ulrich and Scofield (1897, p. 848) proposed the genus Protowarthia for American species. Bassler (1915, p. 1159) recognized the synonymy, and the priority of Sinuites Koken, and formally designated Bellerophon bilobatus Sowerby, as the type species of Sinuites. Reed (1920, p. 5) pointed out that: "Unfortunately, the species B. bilobatus has been made to comprise a somewhat miscellaneous assortment of forms, and the cumstomary usage of the specific name has become loose and unsatisfactory." Therefore, he subdivided B. bilobatus into three new species, and restricted the definition of the original taxon.

The American species Sinuites cancellatus (Hall) may be plagued by the same problem pointed out by Reed for S. bilobatus. Specimens of Sinuites are fairly common in the Upper Ordovician of the Cincinnati Arch region, but just as in other areas of occurrence, these specimens are nearly always internal molds. S. cancellatus has become the usual receptacle for these specimens. At least three subspecies have been named (Bassler, 1915, p. 1159) but the validity of these is questionable (see discussion of species below).

The genus Sinuites is greatly in need of a comprehensive specific review. It is an important taxon not only because of its broad geographic and stratigraphic distribution, and its relative abundance in some strata,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

but also because of its phylogenetic significance (see sections on Functional Morphology and Phylogeny).

SINUITES PERVOLUTA (Ulrich and Scofield, 1897)

Protowarthia pervoluta ULRICH & SCOFIELD, 1987, p. 871, Pl. 63, figs. 21-27; GRABAU & SHIMER, 1909, p. 611, figs. 817d-f.

Sinuites pervolutus (Ulrich and Scofield). BASSLER, 1915, p. 1160.

Diagnosis. - Shell small (<15mm in length), tightly enrolled, rather globose; dorsum uniformly rounded, without ridge or flattening; aperture wider than long; parietal deposits granistriate; growth and revolving lines exceedingly fine.

Material. - The type material (USNM 45968-45970) was adequately illustrated by Ulrich and Scofield (1897, Pl. 63, figs. 21-27) and is not figured herein. No new material is known.

Distribution. - Ulrich and Scofield (1897, p. 871) listed the species from the "Black River group and in the lowest bed (Orthis or Modiolodon bed) of the Trenton group" in Kentucky and equivalent strata in Minnesota (Decorah Fm.). In modern terms, the Kentucky occurrences are in the Tyrone Limestone (Rocklandian) and the Logana Member of the Lexington Limestone (Kirkfieldian).

Comparisons. - Ulrich and Scofield (1897, p. 871) noted that S. pervoluta might be a "variety" of S. granistriata (Ulrich). However,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. pervoluta is constantly smaller (the shell generally being less than 15mm in length), more tightly coiled, more globose, and with a wider aperture than in S. granistriata. S. pervoluta also lacks a dorsal ridge or a flattening of the dorsum.

In the discussion of S. obesus (Ulrich), Ulrich and Scofield (1897, p. 875) stated: "Very young specimens may look much like the largest of P. pervoluta, but the adult form, which is all we have seen is certainly quite distinct." A number of small specimens of a globose species of Sinuites were found in USGS silicified samples 5023-CO, 5084-CO, and 5100-CO from the Curdsville Limestone Member of the Lexington Limestone. These small poorly preserved silicified specimens are probably not S. pervoluta, because some show a small umbilicus, as cited for S. obesus, and so they were placed in that species. Unless well preserved material is available, juveniles of S. obesus and adults of S. pervoluta are extremely difficult to distinguish.

SINUITES CANCELLATUS (Hall)

Pl. 11, figs. 6-12

Bellerophon bilobatus EMMONS (not Sowerby), 1842, p. 392, fig. 6; HALL, 1847, p. 184, Pl. 40, figs. 3a-d; MILLER, 1874, p. 306; LESLEY, 1889, p. 81, figs.; MILLER 1899, p. 396, fig. 652.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Cyrtolites bilobatus EMMONS, 1855, p. 166, figs. 2-3, 22, 24, and, Pl. 17, fig. 10c.

Bellerophon cancellatus Hall, 1847, p. 307, Pl. 83, figs. 10a-c.

Protowarthia cancellata (Hall), ULRICH & SCOFIELD, 1897, p. 872, Pl. 63, figs. 1-14; WELLER, 1903, p. 175, Pl. 12, figs. 3-5; CUMINGS, 1908, p. 971, Pl. 39, figs. 6a-b; GRABAU & SHIMER, 1909, p. 611, figs. 817g-i; KNIGHT, 1941, p. 279, Pl. 6, figs. 3a-b.

Sinuites cancellatus (Hall) BASSLER, 1915; p. 1159; BASSLER, 1919, p. 313, Pl. 50, figs. 37-39, and, Pl. 55, figs. 12-21; FOERSTE, 1924, p. 205, Pl. 34, fig. 6; RUEDEMANN, 1926, p. 62, Pl. 8, fig. 6; BASSLER, 1932, Pl. 21, figs. 16-18; SHIMER & SHROCK, 1944, p. 441, Pl. 176, figs. 24-25; WILSON, 1951, p. 25, Pl. 2, figs. 11-12; CASTER ET AL, 1961, Pl. 1, figs. 16-17; POPE & MARTIN, 1977, Pl. 1, figs. 16-17.

Diagnosis. - Shell of medium size, smoothly rounded dorsally and laterally, subglobose; involute, umbilicus closed; sinus moderately shallow, lateral aperture lobes well rounded; growth lines fine, revolving lines even finer.

Description. - Shell of medium size (adult about 25mm shell length), involute with closed umbilicus, generally subglobose, smoothly rounded dorsally and laterally, degree of convexity variable. Sinus moderately shallow, V-shaped, with well rounded apex; lateral aperture margins merge into well rounded lobes. Aperture distinctly wider than long. Parietal inductura thin, folding over venter of coil onto umbilical region, marked

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

by fine wavy revolving lines. Shell ornament of fine closely spaced growth lines, crossed by even finer revolving lines giving a faint cancellated appearance.

Measurements. - Measurements for Sinuites cancellatus are listed in Table 33.

Table 33: Measurements of Sinuites cancellatus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Sinus Depth	Sinus Width
UCGM 44304	24.4	16.3	16.3	21.9	14.4	11.8	9.7	10.8	14.2
44307	24.6	16.5	17.4	21.0	16.0	13.7	-	9.8	9.9

Material. - The holotype was adequately figured by Knight (1941, P. 6, fig. 3a). Specimens preserving the shell examined here are UCGM 44304 and UCGM 44307. Numerous internal molds of the species, most of which are unnumbered, were examined in UCGM and MU collections.

Distribution. - The species has been reported from "Trenton through Richmond groups" (Kirkfieldian-Shermanian to Richmondian) throughout the eastern half of the United States and Canada (Ulrich and Scofield, 1897; Bassler, 1915; Shimer and Shrock, 1944). Here, the species were recognized from Shermanian through Richmondian-aged strata in the Cincinnati Arch region.

Comparisons. - S. cancellatus is distinguished from S. planodorsatus (Ulrich) and S. granistriatus (Ulrich) by its smoothly rounded dorsum,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

being neither flattened nor bearing a ridge. It is further distinguished from these, as well as from S. rectangularis (Ulrich and Scofield), by its more broadly rounded lateral aperture lobes and its shallower apertural sinus.

Discussion. - S. cancellatus is stratigraphically long-ranging and widely distributed geographically for this group of fossils. It is difficult to properly evaluate the species without examining specimens from its entire distribution. All specimens examined here were from the Shermanian through Richmondian-aged strata of the Cincinatian Arch Province. Nearly all of these were internal molds, and none of the few specimens retaining the shell preserved the shell ornament satisfactorily. Furthermore, many of the internal molds were badly compressed, apparently owing to the animal's thin, probably aragonitic shell, which must have dissolved away prior to compaction of the generally fine-grained encasing sediment. Such specimens are particularly common weathering out of Cincinnatian shales.

Even dealing only with Cincinnati Arch material, and with mainly internal molds, the morphological variation of specimens included in this species was quite apparent. However, no consistent pattern could be discerned which could form a confident basis for subdividing S. cancellatus. A number of subspecies have been named by previous authors. Bassler (1915, p. 1159) recognized S. cancellatus acutus (Hall, 1847) and S. cancellatus corrugatus (Hall, 1847). These were originally named as subspecies of S. bilobatus Emmons, which was placed in synonymy with

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. cancellatus by Bassler. Ulrich and Scofield (1897, p. 872) named S. cancellatus trentonensis for specimens from the "Trenton group" which "are almost constantly a trifle more narrowly rounded dorsally than is the geologically higher typical form of the species." It should be noted that the species was originally described from the Trenton Group of New York, so that the Trenton material is actually "typical". Wilson (1951) persisted in using S. bilobatus corrugatus (Hall), and named two new subspecies, S cancellatus angularis and S. cancellatus liratus (the latter being equivalent to S. cancellatus acutus). I do not believe any specimens bearing a dorsal ridge should be included in S. cancellatus, and therefore S. liratus Wilson is regarded as a distinct species here. However, based on her illustration, the specimen's placement in Sinuites is uncertain.

In the Cincinnati Arch material, three general variants of S. cancellatus are recognized as end members in a maze of morphological gradations. The first end member would be placed in S. cancellatus corrugatus (Hall) of some authors. However, the distal corrugations of this variant are variable in strength and number (1-3) and were seen only in internal molds. Furthermore, corrugated specimens occur in collections in which most of the internal molds lacked corrugations, and I strongly suspect that the corrugations are the result of compaction. The other two variants have more narrowly (S. cancellatus acutus) or more broadly rounded (S. cancellatus cancellatus) dorsal shell forms (Pl. 11,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

figs. 10-12 and 6-9, respectively). Even though these two general forms were seen in specimens preserving the shell as well as in internal molds, there was much gradation between the two end members, and such a feature can be influenced by compaction. Therefore, at present it is not possible to subdivide S. cancellatus from the Cincinatti Arch region into subspecies.

Note the specimens shown here (Pl. 11, figs. 6-12) are slightly worn and preserve only a trace of the growth lines. Knight (1941, Pl. 6, fig. 3a) illustrated the holotype, which although unfortunately distorted by crushing, preserves the cancellate shell ornament very well. Knight's (1941, Pl. 6, fig. 3b) hypotype is more typical in preservation.

SINUITES OBESUS (Ulrich, 1897)

Pl 9, figs. 1-12

Protowarthia obesus ULRICH in ULRICH & SCOFIELD, 1897, p. 874-75, Pl. 63, figs. 45-47.

Sinuites obesus (Ulrich). BASSLER, 1915, p. 1160.

Diagnosis. - Shell large (up to 31 mm shell length), obsese; umbilicus closed; sinus broad and shallow, lateral lobes rounded.

Description. - Shell large, involute, with umbilicus closed; whorl form obese, broadly and uniformly rounded; dorsum smooth. Aperture distinctly wider than long, fairly semicircular in outline around outer mar-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

gins, inner margins angling inward. Aperture lip thickened near contact with coil, thinning outward around periphery. Parietal deposits quite thin, and their ornamentation unknown. Sinus broad, moderately shallow; lateral lobes broadly rounded. Growth lines very fine. Internal molds often with two or three broad transverse furrows across outer body whorl of adult.

Measurements. - As seen on Plate 9, figures 1-12, specimens of this species are generally too badly fragmented for many reliable measurements. Those measurements given in Table 34 are meant only to give general relative dimensions.

Table 34: Measurements of Sinuites obesus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
USNM							
315658	23.4	17.0	10.5	--	--	--	--
315634	31.2	21.5	17.7	30.7	20.5	17.3	14.0
315659	28.5	20.3	17.1	26.0	--	--	11.1
315659	--	8.7	5.8	12.1	8.4	6.9	5.2
315659	16.1	--	9.4	20.6	--	--	7.4
315659	--	--	12.7	22.2	--	--	10.0
315660	10.4	--	6.2	10.6	--	--	--
315661	9.9	8.0	5.0	10.8	--	--	--
315635	11.6	9.0	7.1	10.9	7.5	6.3	4.6
315635	36.1	--	22.1	36.3	23.0	17.4	14.4
315667	29.0	--	17.5	27.7	--	--	--
315663	--	--	--	19.4	13.7	10.9	--
315663	26.0	18.2	16.0	25.4	18.8	15.4	11.6
315663	16.9	11.6	9.2	16.8	11.2	9.5	8.1
315663	15.9	--	9.5	16.4	11.9	--	--
315664	12.9	13.4	10.5	18.4	12.3	10.1	8.1
315664	--	--	--	29.1	18.9	16.3	11.9
315664	17.0	--	9.4	16.0	11.6	9.8	8.2
315664	13.4	10.1	8.1	12.9	--	--	6.3

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Ulrich and Scofield's (1897, p. 874-5, Pl. 63, figs. 45-47) type specimens (USNM 45961, 45962) were internal molds from the Curdsville Limestone Member of the Lexington Limestone.

New USGS silicified material from Kentucky comes from the Curdsville Limestone Member (4940-CO, 5022-CO, 5023-CO, 5084-CO, 5100-CO, 5072-CO, and 7785-CO), and the Logana Member (4865-CO, 5073-CO, 5086-CO, 5092-CO, 6419-CO, and 7791-CO) of the Lexington Limestone. Essentially all silicified specimens were fragmented, so that accurate counts were not possible, but the most prolific samples contained over 100 specimens and fragments (5092-CO, 6419-CO, 7791-CO). Specimens catalogued under USNM 315634, 315635, 315636, and 315637 were selected for illustration herein (Pl. 9, figs. 1-12).

Distribution. - The species occurs in the Curdsville Limestone and Logana Members of the Lexington Limestone (Kirkfieldian), and is presently known only from Central Kentucky.

Comparisons. - In the smooth roundness of the whorls, S. obesus matches S. cancellatus, but S. obesus is much larger and more obese. As discussed under S. pervoluta, adults of that species might be confused with juveniles of S. obesus.

Discussion. - Ulrich and Scofield (1897, p. 875) cited a shallow sinus as characteristic of this species, but that conclusion is the result of having poor material. USNM 315635 (Pl. 9, fig. 5) clearly shows by its growth lines that the sinus is at least moderately deep. This growth line

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

evidence further points out that even new silicified material, which appears to have a nearly complete aperture margin (Pl. 9, figs. 1-4, 6-12), actually has had the thin outer aperture margin completely broken away.

Another distinctive feature of S. obesus are the transverse furrows on the outer whorls of internal molds. These are much like the furrows in the so-called "S. cancellatus corrugatus" (Hall). No such furrows were seen on the silicified material, neither externally nor internally. As in S. cancellatus corrugatus, such wrinkles in S. obesus internal molds may be a response in local populations to some environmental stress, may be a gerontic feature, may reflect actual internal soft parts such as band-like muscles, or may be due to deformation from compaction of the encasing sediments. In any case, its use as a diagnostic species level taxobasis is unlikely. Finally, Ulrich and Scofield (1897) also noted a faint dorso-median ridge on internal molds. Like the wrinkles on internal molds, this observation is not seen on silicified replicas of the shells.

SINUITES PLANODORSATUS (Ulrich)

Protowarthia planodorsata ULRICH in ULRICH AND SCOFIELD, 1897, p. 871, Pl. 63, figs. 31-35.

Sinuites planodorsatus (Ulrich), BASSLER, 1915, p. 1160; RUEDEMANN, 1926, p. 61, pl. 8, fig. 5.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Diagnosis. - Shell of medium size; dorsum narrowly and smoothly rounded in submaturity, becoming broad and flattened in maturity.

Material. - Ulrich and Scofield's (1897) type suite (USNM 45960) consisted of six specimens, three of which they illustrated (Pl. 63, figs. 31-35). Their illustrations are adequate and the species is not illustrated here. No definite new material was found, though some unnumbered internal molds in the UCGM collections from the Kope Formation may be assignable to this species.

Distribution. - The type material comes from the Southgate biofacies of the Kope Formation (middle Edenian) at Covington, Kentucky (Ulrich and Scofield, 1897; Bassler, 1915). Ruedemann (1926, p. 61) reported the species from Edenian strata in New York State.

Comparisons. - Ulrich and Scofield (1897, p. 871) stated that this species might be a "variety" of S. granistriatus (Ulrich), the two agreeing in general shell form and ornamentation, but S. planodorsatus differs in having a much more emphasized dorsal flattening and a total lack of a dorsal ridge.

Discussion. - This species seems to be valid and is distinct from S. granistriatus, though the two are certainly closely related. Ruedemann (1926, p. 61) noted that S. planodorsatus "fills a thin band" at one stratigraphic section he studied. Such an occurrence is typical of other species of Sinuites this author has collected from Edenian strata (S. cancellatus and S. granistriatus).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SINUITES GRANISTRIATUS (Ulrich, 1897)

Pl. 11, figs. 1-5; Pl. 21, fig. 1; Pl. 45, figs. 1-9

Protowarthia granistriata ULRICH in ULRICH & SCOFIELD, 1897, p. 870, Pl. 63, figs. 28-30.

Sinuites granistriatus (Ulrich), BASSLER, 1915, p. 1160; 1919, p. 314, Pl. 50, figs. 40-41, and, Pl. 55, figs. 9-11; RUEDEMANN, 1926, p. 63, Pl. 8, figs. 7-8.

Diagnosis. - Shell of medium size (up to 30 mm in length), involute; dorsomedian ridge distinct through submaturity, weakening or disappearing in maturity.

Description. - Shell of medium size, rather tightly involute; umbilicus closed. Whorls relatively narrow in early growth, broadening dorsally and inflating somewhat laterally toward maturity. Dorsomedian ridge distinct, rounded, marked by faint revolving striae in submaturity; in maturity, dorsum flattens, dorsomedian ridge becomes continually lower and broader, often eventually disappearing completely. Dorsomedian ridge occasionally bordered by shallow furrows in compressed specimens. Aperture width and length (from inner lateral lip contact with whorl) nearly equal, or width slightly greater. Labral sinus moderately deep; lateral aperture lobes distinctly projecting, the lobe margins apparently rounded but bending rather sharply inward in adults at contact with flattened dorsum. Shell thin, except at inner aperture margins; parietal deposits

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fairly thin, with fine pitting. Shell surface marked by fine growth lines, and very delicate revolving lines.

Measurements. - The measurements presented below in Table 35 were taken on three of the largest and best preserved specimens from Locality OH-1 (Bear Creek Quarry), but because of the consistently fragmented aperture lip, the first four measurements are only approximations. Ulrich and Scofield (1897, p. 870) presented a series of average measurements apparently from smaller specimens (average shell length equals 19mm). Note that their aperture length was taken from a median point, whereas measurements made here are relatively longer, being taken at the lateral extremity, where the lip reaches the coil.

Table 35: Measurements of Sinuites granistriatus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
UCGM							
44295	30.0	20.2	22.0	22.0	16.7	13.0	10.3
44296	29.5	--	21.3	21.7	15.3	12.2	10.2
44297	27.0	19.0	--	--	--	11.3	9.5

Material. - Ulrich and Scofield's (1897) type suite is under USNM 45959. The new specimens described here are UCGM 44295, 44296, 44297, 44298 (Pls. 11, 21, and 45), and a number of unfigured specimens catalogued under UCGM 44299. Almost all of these specimens retain at least part of the shell, but none is complete. All were collected from a single limestone lens at Bear Creek Quarry (Locality OH-1), Clermont Co., Ohio.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

UCGM 44306 (PL. 45, figs. 5-7), another specimen retaining the shell, was collected from Locality KY-1, Carroll Co., Kentucky.

Distribution. - The species is presently known only from the Edenian portion of the Kope Formation in southwestern Ohio and northern Kentucky.

Comparisons.- S. granistriata resembles S. planodorsata in shell size and form, particularly in the flattening of the dorsum in maturity, but can be easily distinguished from that species, as well as S. cancellatus, by its submature dorsomedian ridge. Sinuites globularis (Miller and Faber) is smaller, broader, and differs in having a flattened dorsum with a median ridge and two diverging lateral ridges throughout growth.

Discussion. - Ulrich and Scofield (1897, p. 870) described the dorsomedian ridge of S. granistriatus as continuing to the aperture margin and as being bounded by wide furrows. Their specimens averaged only 19mm in shell length. Larger adult specimens described here show that the dorsomedian ridge becomes lower and broader, and often even disappears completely, in maturity (Pl. 11, figs. 1-5; Pl. 45, figs. 3-9). These same specimens also show that the dorsomedian ridge is not bounded by true furrows, but rather furrows commonly result from vertical compression due to the thinner shell material on either side of the thickened ridge.

A collection of over 100 specimens of this species was found in a lenticular argillaceous limestone bed enclosed by shale in the lower Kope Formation at Locality OH-1. Tetranota bidorsata is associated with Sinuites granistriatus, but occurs in small numbers. Other associated

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

skeletal fragments include sparse trilobite and crinoid debris (Pl. 21, fig. 1). The shale encasement may have been responsibile for the preservation of the thin delicate shells, but even such an ideal circumstance did not allow preservation of any perfect specimens. This case demonstrates why well preserved speciments of this species, and of other species of Sinuites, are so rare.

SINUITES GLOBULARIS (Miller and Faber, 1894)

Pl. 10, figs. 1-13

Bellerophon globularis MILLER & FABER, 1894, p. 28, Pl. 1, figs. 21-22.
Sinuites globularis (Miller and Faber), BASSLER, 1915, p. 1160.

Diagnosis. - Shell moderately small, umbilicus closed; dorsum broad; rounded dorsomedian ridge and 2 lateral, low, diverging ridges present throughout growth.

Description. - Shell moderatly small in size (up to 20 mm shell length), tightly coiled; umbilicus closed. Whorls broad, inflated; dorsum with distinct, round dorsomedian ridge, bounded by shallow widening furrows, which in turn are bordered by low, rounded, diverging ridges. Aperture broad, semicircular in general outline; parietal deposits unknown; sinus deep, lateral aperture lobes well-rounded. Growth lines fine, closely-spaced; revolving lines not known.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - Measurements for S. globularis are listed below in Table 36.

Table 36: Measurements of Sinuites globularis in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
UC8811a	19.6	12.0	12.8	17.6	11.2	8.4	--
UC8811b	20.0	14.0	--	18.4	12.0	8.8	--
UCGM 44305	16.5	11.1	9.8	14.3	9.9	8.7	6.4

Material. - The lectotype (UC 8811a) and paralectotype (UC 8811b) (Pl. 10, figs. 1-7 and 11-13, respectively) are calcareous replicas. One other similar specimen, UCGM 44305 (Pl. 10, figs. 8-10), was collected during the course of this study from Locality KY-1.

Distribution. - The type specimens are from the Edenian portion of the Kope Formation at Cincinnati, Ohio. The new specimen cited above comes from the same horizon at Locality KY-1, near Carrollton, Kentucky.

Comparisons. - The dorsomedian ridge of this species is broader than that of S. granistriatus. The latter species also can occasionally appear to also have lateral furrows, but this seems to be simply a result of vertical compaction of the thin shell adjacent to the thickened median ridge. Furthermore, S. globularis is broader and more globular than S. granistriatus, and possesses true dorsolateral ridges.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SINUITES SUBCOMPRESSUS (Ulrich, 1897)

Protowarthia subcompressa ULRICH in ULRICH & SCOFIELD, 1897, p. 873, Pl. 63, figs. 40-44; CUMINGS, 1908, p. 972, Pl. 39, figs. 5-56. Sinuites subcompressus (Ulrich), BASSLER, 1915, p. 1161.

Diagnosis. - Shell large, well-rounded dorsally, somewhat laterally compressed, umbilicus closed; aperture semi-ovate, sinus width and depth near equal, lateral lobes gently rounded; growth lines fine, revolving lines not known.

Material. - Ulrich's types are USNM 45973 and 45974. No additional material is known. The original illustrations are adequate and the species is not refigured here.

Distribution. - The species is known only from the Waynesville biofacies of the Dillsboro Formation (Richmondian) in Butler County, Ohio, and near Versailles, Indiana (Bassler, 1915).

Comparisons. - S. subcompressus differs from S. cancellatus (Hall) in its greater size, narrower and flatter sides, and in its apparent lack of revolving shell ornament.

Class GASTROPODA Cuvier, 1797

Diagnosis. - Mollusks with a distinct head, a radula, a sole-like foot adapted for creeping, and a visceral mass which has been rotated 180

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

degrees with respect to the head-foot, so that the gut becomes twisted, the left and right gills come to lie, respectively, on the right and left sides of the body, and the nervous system forms a figure eight (Runnegar and Pojeta, 1974).

Subclass PROSOBRANCHIA Milne-Edwards, 1848

Diagnosis. - Gastropods displaying the full effects of torsion as defined by Knights and others (1960, p. I171).

Order ARCHAEOGASTROPODA Thiel, 1925

Diagnosis. - Prosobranchia with aspidobranch ctenidia (i.e., bipectinate, with filaments alternating on two sides of axis) that are free at one end; organs of pallial complex, including ctenidia, paired primitively, the right set generally partially or completely reduced; no siphon or proboscis, and thus no siphonal canal at the shell margin.

Discussion. - Knight and others (1960, p. I155-156) preferred the term Archaeogastropoda over earlier used names (i.e., Scutibranchia, Aspidobranchia, Streptoneura, and Diotocardia) because of inconsistency in the use of those names and because the present term embraces the desired groups of fossil snails without the restriction of implying the existence of certain anatomical conditions. The Archaeogastropods is a fairly

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

diverse assemblage of taxa that possess the primitive features attributed to the hypothetical newly torted ancestral form to varying degrees (Knight and others, 1960).

The above morphological characters are largely anatomical, but have direct bearing on the form of the shell containing them. Yonge (1947) described the features of the aspidobranch condition in detail. He noted that the possession of paired gills is reflected by a labral emargination in the pleurotomariaceans. This labral emargination, in the form of a sinus or slit, acts as an exhalent passage midway between the pair of gills, affecting the more efficient expulsion of deoxygenated water (which has passed over the gills), fecal wastes, and sediment contaminants. Knight (1952) strongly supported homology between the pleurotomariaceans and the bellerophontaceans in this regard. Yonge (1947) cited four aspidobranch conditions in living prosobranches: (1) Assymetrical shell with two assymetrical ctenidia (Zeugobranchia); (2) Secondarily symmetrical shell with two symmetrical ctenidia (Fisurellidae); (3) Assymmetrical shell with loss of one or both ctenidia (Neritacea, Valvatacea, Trochacea); and (4) Secondarily symmetrical shell with loss of one or both ctenidia (Patellacea, Cocculinacea, some Neritacea).

Knight (1952) envisioned the Bellerophontacea as evolutionary intermediates between untorted mollusks and the asymmetrically coiled Pleurotomariacea. Recent observations made on Early and Middle Cambrian molluscan univalves place some doubt on this interpretation, suggesting that torsion

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

was a slow adaptive process resulting from the asymmetrical coiling of primitive untorted mollusks (Runnegar and Pojeta, 1974; Pojeta and Runnegar, 1976; Runnegar, 1983). However, even if this view is excepted, it does not mean that the Bellerophontacea were untorted, as secondary symmetry is a common condition in the Archaeogastropoda. Pojeta and Runnegar (1976, p. 32) noted that the earliest pleurotomariaceans were low spired shell forms, such as the sinuopeids, raphistomenids, and eotomariids of the Late Cambrian. The nearly synchronous appearance of the belleophontaceans and these low spired pleurotomariaceans in the Late Cambrian might also be significant in this matter. In any case, the homology of the labral emargination and other features of the shell are considered here to support a close relationship between the pleurotomariaceans and bellerophontaceans. Therefore, the Bellerophontacea is assigned to the Archaeogastropods, and not to the Monoplacophora. (See section on Phylogeny and Classification for complete discussion.)

Suborder BELLEROPHONTINA Ulrich and Scofield, 1897

Diagnosis. - Shell isostrophic, bilaterally symmetrical; coiling generally contiguous, involute to convolute, but disjunct coiling is known; aperture margin with median sinus or slit, the latter generating a selenizone, and the former occasionally resulting in the development of trematа; no opercula known; presence of paired aspidobranch ctenidia

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

implied by presence of labral emargination; circumumbilical muscle scars infer single pair of retractor muscles.

Distribution. - Upper Cambrian - Lower Triassic.

Superfamily BELLEROPHONTACEA McCoy, 1851.

Diagnosis. - Same as for order.

Distribution. - Same as for order.

Discussion. - Table 17 presents a synopsis of the higher taxonomic classification within the Bellerophontacea. It should be immediately noted that the first four families recognized are sinus-bearing, but do not possess a slit, as do the following four families. However, aside from their lack of a slit, their shell morphologies are quite comparable to the slit-bearing families. Two families, the Cyrtolitidae and Sinuitidae, which are sinuate families included in the Bellerophontacea by Knight and others (1960), are now generally considered Monoplacophora because of the discovery of dordally-disposed discrete paired muscle scars in species of Cyrtolites and Sinuitopsis. It is considered premature and unwise, however, to transfer all sinuate groups to the Monoplacophora on the basis of the discovery of such muscle scars in a few genera. Moreover, the interpretation of such muscle scars as monoplacophoran is not considered to be infallible. (See discussion under Functional Morphology.)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The family Bucanellidae Koken, 1925, is characterized by a relatively broad, phaneromphalous shell with a sinuate aperture, and with fairly fine collabral, and sometime spiral, threads. It is known from the Upper Cambrian to the Middle Permian. As used here, the Bucanellidae may be a rather unnatural grouping, including some genera previously considered to be of the Sinuitidae and Cyrtolitidae by Knight and others (1960). The discovery of discrete paired muscle scars in Cyrtolites ornatus and Sinuitopsis acutilira by Horny (1963) and Rollins and Batten (1968), respectively, suggested that these genera should be interpreted as monoplacophorans. Runnegar (1982) has also reported monoplacophoran-like muscle scars in Sinuites, contrary to Knight's (1947) claim of columellar scars in the genus. This last discovery is not too surprising considering the strong morphological similarity between Sinuites and Sinuitopsis, the two even having been subgenera by Knight and others (1960). Horny (1962) has described a third genus Strangulites that might be considered synonymous with the subgeneric to Sinuites. These genera are quite distinct from most other genera placed in the family Sinuitidae by Knight and others (1960), except for the common possession of a sinuate aperture. Therefore, it is difficult to judge whether the rest of the family also deserves transfer to the Monoplacophora. Starabogatov (1970) assigned the subfamily Bucanellinae (sensu Knight and others, 1960) to the Monoplacophora, but subsequently Rollins and others (1971) described apparent columellar muscle scars in one of the included genera, Sinuitina. As sug-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

gested by Horny (1963), there seems to be a gradation between the sinus and the slit, and it is possible that this morphologic feature does not have the taxonomic significance generally accorded to it. Knight and others (1960) even used the character of the labral emargination as the basis for the dichotomous split of the Bellerophontacea into the Sinuitidae and Bellerophontidae.

As described here in the Functional Morphology section, the genus Sinuites and its close relatives can be reasonably interpreted as exogastric monoplacophorans, with tightly coiled shells, making them easier to manipulate in the exogastric position, and lobate lateral aperture margins on either side of the sinus, which appear to be efficiently designed for the free flow of water through a posterior mantle cavity. However, other members of the Sinuitidae (sensu Knight and others, 1960) vary greatly from this morphologic plan. Bucanella, for example, is widely phaneromphalous and is trilobate dorsally. Peel (1974) has presented a convincing functional analysis of trilobed symmetrically-coiled shells as being endogastric. Furthermore, the Grandostomatidae are explanate, and somewhat convergent morphologically with slit-bearing genera such as Carinaropsis. Sinuitina, which bears a notable resemblance to Cyrtolites, has been described to have gastropod-like columellar muscle scars (Rollins and others, 1971). All of this would seem to indicate that even though Sinuites and its allies may prove to be monoplacophorans, certainly there is an adequate basis for demurring at the wholesale transfer of all sin-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

uate bellerophontaceans to the Monoplacophora. Until new evidence is brought to bear, or until new bases for familial differentiation are settled upon, four sinus-bearing families should be recognized within the Bellerophontacea: Bucanellidae, Grandostomatidae, Tremanotidae, and Euphemitidae. Sinuites and its close allies, and Cyrtolites and its close allies, should each be treated as representatives of two families of the monoplacophoran order Cyrtonellida.

Genera included in the Sinutinae by Knight and others (1960), that have not been demonstrated to possess discrete paired muscle scars, should be placed in one of the above sinuate bellerophontacean superfamilies, at least temporarily. Horny (1963) has already reassigned Ptomatis to his Grandostomatinae (here a family). Anconochilus and Crenistriella are tentatively placed in the Bucanellinae, because both are phaneromphalous and sinuate, and the latter is subtrilobed. The Bucanellidae as here used would tentatively include the genera Bucanella, Owenella, and Sinuitina, and also Trigyra, Anconochilus, and Crenistriella with question.

The family Euphemitidae is characterized by a shell entirely covered by inductural layers, with a narrow sinus that nearly becomes a slit in some species. The family is known from the Mississippian to the Permian, with questionable members in the Devonian. The family consists of the genera Euphemites, Paleuphemites, Euphemitopsis, Warthia, and ?Stachella. The exact position of this family in the phylogeny of the bellerophontaceans is uncertain, and its relationships to other sinuate and slit-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

bearing families needs to be carefully evaluated. Rollins (1967) interpreted this group as being "ploughers", which ploughed through the surface sediments in search for food similar to the modern moon snail Polinices.

The family Grandostomatidae is characterized by an explanate adult shell which is phaneromphalous and sinuate, and has transverse and spiral ornament. The family ranges from the Middle Ordovician to the Devonian, and consists of the genera Grandostoma, Ptomatis, and ?Patellostium. Horny (1962) proposed this grouping as a subfamily of the Sinuitidae in order to distinguish those sinuate forms with a strongly expanded body whorl. This shell form seems convergent with some slit-bearing bellerophontaceans, such as members of the Carinaropsidae. Peel (1977) has interpreted such expanded shell forms as adaptations to life on soft substrates, the broad surface area inhibiting sinking into the mud.

The Tremanotidae includes sinuate shells having dorsal tremata developed in association with an expanded aperture. The family is represented by the Middle Silurian and Lower Devonian genera Tremanotus and Boiotremus, respectively. Peel (1972, p. 419) erected the subfamily Tremanotinae of the family Sinuitidae, demonstrating that the previous close association of these genera to Salpingostoma was due to homeomorphy. He showed that the tremata of the above genera were formed by the periodic expansion of the aperture and closing off of a deep sinus, and that no slit was present. Peel pointed out that the periodic expansions of the shell aperture in Tremanotus commenced only in later ontogenetic stages,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

whereas in Boiotremus they occurred throughout ontogeny. He presumed that the successive flaired apertures were resorbed with continuation of growth.

It is important to note that there are no sinuate bellerophontaceans in the fauna under consideration here because the genera Cyrtolites and Sinuites have been reassigned to the Monoplacophora. The sinuate forms appeared during the Late Cambrian along with the slit-bearing bellerophontaceans, but in greater diversity and abundance. Both groups maintained low diversities through the Early Ordovician. But the Middle Ordovician was a time of great radiation for the slit-bearing group. The only sinus-bearing group to reach a true level of abundance and diversity seems to be the Late Paleozoic euphemitids; their success may be related to their specialized morphology. The slit-bearing families are all present in the faunas under consideration, as are most of the subfamilies. All are treated in some detail below.

Family TROPIDODISCIDAE Knight, 1956

Diagnosis. - Shell small to moderate in size, whorls laterally compressed and narrow, though occasionally somewhat expanded; umbilicus wide; slit deep, extending as much as one-half whorl from the aperture margin; parietal callosity not developed; posterior train rarely present.

Distribution. - Upper Cambrian - Lower Devonian.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Most American species of Tropidodiscus Meek and Worthen (1866) and Phragmolites Conrad (1838) were described under the synonymous names Oxydiscus DeKonnick, 1882, and Conradella Ulrich and Scofield (1897), respectively. Ulrich and Scofield (1897, pp. 851-852) assigned these two genera (under the names Oxydiscus and Conradella) to the family Bucaniidae, believing they were allied to Bucania through the common possession of a deep slit, a wide umbilicus, and the lack of a parietal callosity. Dall in Zittel (1927) and Wenz (1938) continued this practice.

Knight (1956, p. 42) erected the new subfamily Tropidodiscinae, and Knight and others (1960) placed it in the family Bellerophontidae (adjacent to the Bucaniinae), and included the genera Tropidodiscus, Phragmolites, Temnodiscus Koken, 1896, and Chalarostrepsis Knight, 1948. All but the last of these genera occurs in the Ordovician faunas of the Cincinnati Arch region.

Horny (1963, p. 70) supported the classification of Knight and others (1960), but Golikov and Starabogatov (1975, p. 207) elevated the Tropidodiscinae to the family level, a change that is supported here.

The familial assignment of the genus Temnodiscus is a matter of some controversy. Koken had associated the genus with sinuate forms, as did Horny (1962), who claimed the genus did not bear a true slit. However, I must agree with the classification of Knight and others (1960), as Knight's (1941, Pl. 10, figs. 3a-d) figures clearly show a true slit and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

selenizone in the type species of the genus Temnodiscus lamellifer (Lindstrom, 1884).

The tropidodiscids seem to have played a significant role in the ancestry of other Early Paleozoic bellerophontaceans. Chalarostrepsis praecursor Knight, 1947, from the Upper Cambrian of Quebec, and ?Tropidodiscus sp. from the Middle or Upper Cambrian of Bolivia are the earliest known bellerophontaceans (Curry and Morris, 1967, p. 426). Chalarostrepsis is exemplary of the primitive morphological traits of the Bellerophontacea: a loose style of coiling, a wide open umbilicus, and a deep antero-median apertural slit (see Functional Morphology Section). Chalarostrepsis is apparently ancestral to the other genera of the family, with a trend toward tighter involute coiling. The Lower Ordovician Eobucania Kobayashi, 1955, seems to have descended from the tropidodiscids, or at least from the same stock, both having deep slits and well-defined selenizones. Also, like Chalarostrepsis and Tropidodiscus, Eobucania has only collabral shell ornament, except for threads bordering the selenizone. The more primitive members of the genus Bucania (the B. sulcatina group of Ulrich and Scofield, 1897) are also characterized by a wide open umbilicus and a deep slit, as are species of the new genus Undulabucania, these forms differing from the tropidodiscids mainly by their more broadly rounded depressed whorl forms. Clearly, the tropidodiscids are likely ancestors of the bucaniids.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Such traits as the narrow whorl form and the occasional presence of a posterior train in the tropidodiscids could conceivably suggest a link to the Early and Middle Cambrian helcionellaceans, but such a connection is not actively supported here. At the present time, relationships between Upper Cambrian molluscan univalves and those earlier forms remain a matter of some controversy and require a great deal more study.

TROPIDODISCUS Meek and Worthen, 1866

Pl. 41, figs. 6-13; Pl. 42, figs. 1-2

Diagnosis. - Shell laterally compressed, whorls gradually expanding, barely contiguous; umbilicus large; slit deep, selenizone as thin keel, with or without lunulae; growth lines only.

Description. - Shell small to moderate in size, strongly compressed laterally; whorls gradually expanding throughout growth, barely contiguous, resulting in large open umbilicus exposing all previous volutions. Aperture outline subtriangular to lanceolate; parietal callosity not developed; sinus broadly curved, rather deep; slit deep, narrow; selenizone on high, thin keel, which may be sharp or slightly truncated and with lunulae. Growth lines as fine threads or fine imbricating lamellae. No revolving ornament.

Type species. - Bellerophon curvilineatus (Conrad, 1842), by original designation (Knight, 1941, p. 360-61).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - The genus is known from the Early Ordovician (Canadian) to the Late Devonian Period. Species are present in upper Middle Ordovician (Kirkfieldian-Shermanian) and Late Ordovician (Richmondian) strata in the Cincinnati Arch Region.

Comparisons. - Tropidodiscus could only be confused with species of Phragmolites, the latter differing mainly in the consistent strong, wavy lamellae which do not curve over the surface of the shell, thus reflecting the absence of an apertural sinus.

Discussion. - Knight (1941, p. 360-361) wrote a detailed review and opinion on the complex nomenclatural history of this genus. The genus was originally named Tropidiscus Meek (1866) but this was an invalid homonym. Meek and Worthen (1866, p. 160) emended the name to Tropidodiscus (whether purposely or not is a matter of question). Koninck (1882, p. 81) erected the genus Tropidocyclus as an objective synonym of Tropidiscus, designating Bellerophon curvilineatus Conrad, 1842, as type species. Koken (1889, p. 390) erected the genus Oxydiscus to replace the homonym Tropidiscus, and its emendation, and Tropidocyclus, which he rejected because it encompassed unrelated species. Knight (1941, p. 361) strongly disagreed with Koken's action, and favored the adoption of Tropidocyclus as the valid genus name, but reluctantly accepted the principles of the International Commission of Zoological Nomenclature which dictate the retention of the emended name Tropidodiscus Meek and Worthen (1866).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Tropidodiscus shows relationship to the Bucaniidae in its large umbilicus, lack of a parietal callosity, and deep slit, but this evidence is offset by its lack of any spiral ornament. Nevertheless, the genus is a likely representative of a primitive stock of bellerophontaceans which gave rise to the Bellerophontidae and Bucaniidae. The earliest known bucaniid genus, Eobucania Kobayashi (1955) agrees with Tropidodiscus in its open umbilicus and deep apertural slit, and significantly, its spiral ornament consisting of only two threads bordering the selenizone.

TROPIDODISCUS SUBACUTUS Ulrich, 1897

Pl. 41, figs. 9-13

Oxydiscus subacutus ULRICH in ULRICH & SCOFIELD, 1897, p. 913, Pl. 62, figs. 62-65, and, Pl. 82, figs. 23-25; WELLER, 1903, p. 179, Pl. 12, figs. 8-9; GRABAU & SHIMER, 1909, p. 616, p. 826; BASSLER, 1932, p. 222, Pl. 20, figs. 11-12.

Cyrtolites subacutus MILLER, 1897, p. 767.

Tropidodiscus subacutus (Ulrich), SHIMER & SHROCK, 1944, p. 443, Pl. 178, figs. 8-9.

Diagnosis. - Shell moderately small (up to 13 mm in length), lenticular, with 3.5-4.5 volutions, each embracing one-third to one-half the preceding one; whorl floor keel distinct, narrow, sharply rounded.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderately small, lenticular, the greatest width about one-half the shell height; 3.5-4.5 volutions in adult, each volution embracing one-third to one-half the preceding one. Shell width and thickness greatest at narrowly rounded umbilical shoulder; dorsal slopes slightly concave to flat; dorsum acutely carinate, but with narrow truncation at crest for selenizone. Umbilici wide, all earlier volutions visible; umbilical slopes cut inward essentially horizontally. Whorl floor keel distinct, narrow, sharply rounded. Slit deep, narrow; sinus narrow V-shaped, relatively deep. Growth lines fine, closely spaced, and fairly regularly spaced.

Measurements. - Measurements of Tropidodiscus subacutus are in Table 37.

Table 37: Measurements of Tropidodiscus subacutus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Umbilical Diameter
USNM 387021	12.95	9.9	6.4	5.2	3.8

Distribution. - Ulrich and Scofield (1897) reported this species from the upper beds of the "Trenton Group" near Danville, Kentucky, and their 21 type specimens are labeled as coming from the "Flanagan" beds of that vicinity, which would now be considered in the Lexington Limestone. The name "Flanagan chert beds" was abandoned after finding that it was used for different silicified limestone horizons at various stratigraphic

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

levels within the Lexington Limestone. They also claimed possible recognition of the species "in Tennessee and in the Fusispira bed in Minnesota". Weller (1903, p. 46) reported this species from talus blocks from "the upper Black River and the lower Trenton beds" of New Jersey.

In the USGS silicified collections, T. subacutus was identified from the Salvisa bed of the Perryville Limestone Member (6915-CO, 6916-CO) and the upper Devils Hollow Member (5087-CO, 5095-CO) of the Lexington Limestone. Fragmented specimens assigned to T. cf. T. subacutus were found in the Tyrone Limestone (5075-CO), and the Faulconer bed of the Perryville Limestone Member (6136-CO) of the Lexington Limestone. More fragmented specimens referrable to only T. sp. indet., but which probably belong to this species occurred in the Curdsville Limestone Member (6134-CO, 7784-CO), the Grier Limestone Member (4880-CO), and the Devils Hollow Member (5036-CO, 7789-CO) of the Lexington Limestone.

Therefore, T. subacutus is certainly recognized from the Upper Lexington Limestone (Shermanian), but may occur also in the Tyrone Limestone (Rocklandian), and in the lower Lexigton Limestone (Kirkfieldian).

Material. - The lectotype is selected from the original type suite (USNM 45952) and is herein designated USNM 387021 (Pl. 41, figs. 11-13). It and 20 paralectotypes (USNM 45952), as well as all of the new USGS collections cited above, are silicified. No complete specimens are known, all having at least the anteromedian, slit-bearing, area broken away. As in Salpingostoma, the shell adjacent to the deep slit must have been thinnest and weakest, and thereby most easily broken away.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - The only other species in the fauna warranting comparison is T. cristatus (Safford), which differs in its somewhat larger size, its more rapid expansion and fewer number of volutions at maturity, its looser coiling (volutions embrace only about one-sixth the height of the preceding whorl) resulting in a larger umbilicus, and its more rounded whorl floor keel (Ulrich and Scofield, 1897, p. 914).

Discussion. - T. subacutus appears to have been a geographically widespread, and possibly stratigraphically long-ranging species. Its rather thin, delicate, small shell makes its preservation and recognition difficult. It appears to have inhabited a wide range of normal marine shallow water carbonate environments.

TROPIDODISCUS CRISTATUS (Safford, 1869)

Pl. 41, figs. 6-8

Cyrtolites cristatus SAFFORD, 1869, p. 289.

Oxydiscus cristatus ULRICH & SCOFIELD, 1897, p. 914, Pl. 82, figs. 26-28.

Diagnosis. - Shell moderately large (up to 23 mm in length), with 3.0-3.5 volutions in adult, each embracing about one-sixth the previous one; whorl floor keel relatively low and rounded.

Measurements. - Measurements for T. cristatus are listed below in Table 38.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 38: Measurements of Tropidodiscus cristatus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Umbilical Diameter
USNM 45950	21.9	17.0	8.7	8.0	6.5
45950	22.8	20.2	8.8	9.1	8.4

Material. - Only the two type specimens (USNM 45950) are known. Both of these are silicified and have the last one-third whorl broken away.

Distribution. - The type specimens are from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) in Jackson County, Tennessee.

Comparisons. - The most similar species is T. subacutus, and for comparisons between the two, the reader is referred to this section under that species. (See also Ulrich and Scofield, 1897, p. 814).

TROPIDODISCUS MAGNUS (Miller, 1878)

Pl. 42, figs. 1-2

Cyrtolites magnus MILLER, 1878, p. 103, Pl. 3, fig. 10.

Oxydiscus magnus ULRICH & SCOFIELD, 1897, p. 859; Cumings, 1908, p. 970, Pl. 41, fig. 5.

Diagnosis. - Shell large (up to 27 mm in length), narrow, lenticular, dorsal slopes gently convex, dorsum rounded; volutions three or

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

more, each embracing about one-third of previous one; sinus narrow and deep.

Measurements. - Measurements for the holotype of T. magnus are listed below in Table 39.

Table 39: Measurements for Tropidodiscus magnus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Umbilical Diameter
UC10838	27.0	24.0	18.5	10.0	8.0

Material. - The holotype (UC 10838; Pl. 42, figs. 1-2) is a badly weathered calcitic specimen. A few other unnumbered specimens are in the UCGM collections.

Distribution. - The holotype is from Richmondian-aged strata near Richmond, Indiana (Miller, 1878). Unnumbered specimens in the UCGM collections are labeled as coming from the Saluda Formation at Madison, Indiana.

Comparisons. - The convex dorsal slopes and rounded dorsum of T. magnus distinguish it from any other known species of the genus.

Discussion. - Although T. magnus is known from only a small number of specimens, no other species possesses such a rounded (rather than carinate) dorsum (Pl. 42, figs. 1-2). T. magnus is the only species of Tropidodiscus recognized from the Upper Ordovician of the Cincinnati Arch region. However, it should be noted that 16 poorly preserved silicified

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fragments assignable only to T. sp. indet. were recognized in 4 USGS samples (6411-CO, 6412-CO, 6414-CO, 7843-CO) from the Gilbert Member of the Ashlock Formation (Maysvillian) in Kentucky.

Genus PHRAGMOLITES Conrad, 1838

Pls. 42-45

Diagnosis. - Shell generally rather small (usually less than 10 mm shell length); sinus lacking, slit half of a volution deep; growth increments lamellose, corrugated, scalloped; fine revolving threads present.

Description. - Shell rather small, generally narrow and gradually expanding, but rarely broad and rapidly expanding; whorl slopes gently convex; umbilici wide; aperture outline elliptical, subchordate to subtriangular; parietal deposits lacking. Sinus lacking; slit half of a volution deep; selenizone narrow, lunulate, bordered by revolving threads, often elevated on a carina. Growth lines fine, straight; periodic growth increments lamellose, corrugated, scalloped, evenly spaced; fine revolving threads generally present.

Type species. - Phragmolites compressus Conrad, 1838, by monoytypy.

Distribution. - Middle and Upper Ordovician (Blackriveran-Richmondian) in North America and Europe.

Comparisons. - The lamellose, corrugated, scalloped, and uncurved (nonsinuate) growth increments readily distinguish Phragmolites from Tro-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

pidodiscus, which has a similar shell form and deep slit. Temnodiscus can have many lamellose growth increments similar to those of Phragmolites, but it differs by having a sinus and a relatively shallow slit.

Discussion. - Conrad (1838) thought P. compressus to be a chambered shell, hence the generic name, translating "partitioned stone." Hall (1847) asserted that the species was non-chambered and placed it in the genus Cyrtolites (Conrad, 1838). Ulrich and Scofield (1897, p. 905) recognized the species' generic distinctiveness, but chose not to revive Conrad's (1838) Phragmolites as it gave "an incorrect idea of the fossil." They concluded: "Had the name (Phragmolites) ever attained currency, we would feel ourselves bound to revive it, on the score of priority, despite its inappropriateness, but as no one, so far as we can learn ever adopted it, we thought it best to view the name as one that has failed of being established because of incorrect and insufficient definition." Hence, they renamed the genus Conradella, but curiously made C. obliqua Ulrich and Scofield the type species, even though Conrad's original type species was recognized as a member of the new genus. Bassler (1915) used the name Phragmolites rather than Conradella, but numerous other authors, including Koken (1898, 1925) and Reed (1921), used Conradella. Wenz (1938, p. 102) placed Conradella in synonymy with Phragmolites. Knight (1941) described the type species of both genera, and Knight and others (1960, p. I179) followed suit with Wenz (1938). All modern authors agree with the priority of Phragmolites.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ulrich and Scofield (1897, p. 905) proposed that Phragmolites and Bucania Hall were derived from the same stock, citing a long apertural slit, large umbilicus, generally gradually expanding whorls, and surface sculpture as comparative morphological characters. This viewpoint is heartily supported here. Of the Tropidodiscidae Phragmolites shows the closest connection to the Bucaniidae. Specially comparable to Phragmolites is Undulabucania n. gen., which includes species whose general form resembles that of the Bucania sulcatina group, but who have very deep slits, and distinctly wavy, intersecting or nearly intersecting, growth lines. In these latter two characters, Undulabucania shows common morphologic traits with Phragmolites.

PHRAGMOLITES COMPRESSUS Conrad, 1838

Pl. 42, fig. 14; Pl. 44, figs. 1-4.

Phragmolites compressus CONRAD, 1838, p. 119; WELLER, 1903, p. 178, Pl. 12, figs. 16-17; KNIGHT, 1941, p. 242, Pl. 9, fig. 2; SHIMER & SHROCK, 1944, p. 443, Pl. 178, fig. 5; WILSON, 1951, p. 29, Pl. 2, figs. 17-18.

Cyrtolites compressus (Conrad) HALL, 1847, p. 188, Pl. 40A, figs. 2a-f; 1862, p. 40, fig. 4; CHAMBERLAIN, 1883, p. 158, fig. ; LESLEY, 1889, p. 182, fig.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Conradella compressa (Conrad), ULRICH & SCOFIELD, 1897, p. 906, no description or figures.

Conradella similis ULRICH in ULRICH & SCOFIELD, 1897, p. 906, not figured.

Diagnosis. - Shell narrow, very gradually expanding; whorls barely contiguous, lanceolate-shaped, longer than wide; corrugated growth lamellae widely spaced, with 5-6 re-entrants per side.

Description. - Shell small (up to 13 mm in length), narrow, very gradually expanding; whorls barely contiguous, embracing only the dorsal carina of the preceding whorl. Dorsal carina prominent, slightly rounded, with faint lumulae; dorsal slopes briefly concave near carina, then becoming evenly convex; umbilical shoulders sharply rounded; ventral slopes slightly convex to nearly flat. Aperture outline lanceolate, higher than wide. Umbilici wide. Slit deep, apparently about one-half of a volution. Growth lines fine, closely spaced; very fine revolving lines sometimes visible. Periodic corrugated growth lamellae rather widely spaced, with 5-6 square re-entrants from shoulder to carina.

Measurements. - Note that the measurements of Phragmolites compressus in Table 40 are estimates based on fragmented material (Pl. 44, figs. 1-4).

Table 40: Measurements of Phragmolites compressus in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Lamellae Spacing
387019	]12.7	--	5.5	4.7	1.0
387020	9.0	7.3	4.8	--	0.7-1.0

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Three specimens from Kentucky were examined. The holotype of P. similis (USNM 47568; Pl. 42, fig. 14) is a fragmentary silicified specimen. USNM 387020 is a broken silicified shell with a well preserved exterior (Pl. 44, figs. 2-4). USNM 387019 (Pl. 44, fig. 1) is calcitic specimen embedded in a limestone with brachiopod and bryozoan fragments.

The whereabouts of Conrad's (1838) type is unknown, but Knight (1941, p. 242, Pl. 9, fig. 2) described and figured Hall's (1847, Pl. 40A, figs. 2a-b) hypotype. Knight assumed that because Conrad was a colleague of Hall, Hall was familiar with the species, and his description might well be based on the type material. Knight speculated that Hall's figured specimen may have been part of Conrad's type suite.

Distribution. - This species has been reported from the "Trenton Group" of New York State, New Jersey, Pennsylvania, and Ontario. The label included with the Kentucky specimens (Pl. 44, figs. 1-4) described here says: "Lower part of Trenton and perhaps Black River, Mercer Co., Kentucky, 2 and 4 miles north of Burgin." The species is therefore Kirkfieldian-Shermanian in age, and probably Rocklandian or even Blackriveran in age.

Comparisons. - P. compressus has a lanceolate aperture outline which is longer than wide, whereas P. obliqua has a nearly circular aperture, and P. grandis and P. triangularis have apertures that are wider than long.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Conradella similis Ulrich is put in synonymy with this species. The holotype (USNM 47568) for C. similis is a poorly preserved fragment (Pl. 42, fig. 14) that is closest to P. compressus and no other specimens were located. A label with the holotype's museum box initialed by Ulrich notes: "2 other specimens formerly in this box are of C. compressa and have been removed." The single remaining specimen resembles P. compressa in its size, general shell form, and by the obliquity of its corrugated growth lamellae and the number of reentrants on those lamellae. This specimen is from the High Bridge Group (Blackriveran) of Kentucky.

PHRAGMOLITES GRANDIS (ULRICH, 1897)

Pl. 42, figs. 7-13; Pl. 43, figs. 1-4

Conradella grandis ULRICH in ULRICH & SCOFIELD, 1897, p. 908, Pl. 62, fig. 67, and Pl. 67, figs. 16-18.

Phragmolites grandis (Ulrich) BASSLER, 1932, p. 194, Pl. 6, figs. 11-12.

Diagnosis. - Shell relatively large (up to 30.5 mm shell length) and rapidly expanding; aperture subtriangular, wider than long; corrugated lamellae with 5-6 re-entrants per side.

Description. - Shell large and rapidly expanding for genus, lateral flaring of aperture increases in adulthood. Dorsal slopes gently convex, umbilical shoulders sharply rounded, umbilical slopes nearly flat and hor-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

izontal; umbilici moderate in size and deep. Aperture outline subtriangular, width becoming increasingly greater than length through growth. Slit about one-half of a volution deep, rather wide; selenizone on truncated dorsum, bordered by revolving threads. Growth lines fine, closely spaced, crossed by fine, widely spaced revolving lines; periodic corrugated growth lamellae distinct, with 5-6 re-entrants from whorl crest to shoulder.

Measurements. - Measurements on the lectotype and a paralectotype are listed below in Table 41.

Table 41: Measurements of Phragmolites grandis in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter	Wavelength of Lamellae
315667	30.5	23.0	16.0	--	8.8	9.8	1.5-2.0
315668	20.0	13.7	11.4	19.0	7.2	5.4	1.5

Material. - Five calcitic specimens are in the original type suite (USNM 45756). The specimen shown on Pl. 42, figs. 7-9 is here selected as the lectotype, because it was Ulrich's (1897, Pl. 67, figs. 16-18) figured specimen, and it is given the number USNM 315667. The paralectotypes figured here (Pl. 42, figs. 10-13, and Pl. 43, figs. 1-3) are given USNM numbers 315668 and 387018, respectively. The remaining two paralectotypes are left under USNM 45756.

Distribution. - The species is known only from the Lebanon Limestone (Blackriveran) in the vicinity of Lebanon, Tennessee.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - P. grandis is similar to P. triangularis Ulrich and Scofield from Blackriveran strata of the Upper Mississippi Valley, but is larger, more rapidly expanding, and has more convex dorsal slopes, a relatively wider aperture, fewer corrugated lamellae folds, and more distinct revolving lines (Ulrich and Scofield, 1897, p. 908-9).

Discussion. - The smaller, submature specimens of this species, as shown by the paralectotype USNM 315669 (Pl. 43, figs. 1-3), are proportionately narrower. The increase in whorl expansion rate was apparently an adult occurrence. The two adult specimens figured here (Pl. 42, figs. 7-9 and 10-13) initially appear different, but this seems to be a result of preservation. The lectotype (Pl. 42, figs. 7-9) has the expanded aperture broken away, its right side is an internal mold, and the preserved shell material on the left side is worn. The paralectotype USNM 315668 (Pl. 42, figs. 10-13) preserves the aperture and shell sculpturing much better. The broad expanded aperture of this species is uncharacteristic of the genus and suggests a generic relationship to Bucania and Undulabucania.

PHRAGMOLITES CELLULOSUS (Ulrich and Scofield, 1897)

Pl.43, figs. 4-12

Conradella dyeri var. cellulosa ULRICH & SCOFIELD, 1897, p. 910, Pl. 67, figs. 27-29; CUMINGS, 1908, Pl. 39, fig. 9.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Phragmolites dyeri cellullosus (Ulrich and Scofield), BASSLER, 1915, p. 972.

Diagnosis. - Shell small, gradually expanding, whorls somewhat inflated in adults; aperture subcordate; corrugated lamellae closely spaced, spiral threads weak.

Description. - Shell small (up to 11.5 mm in length), gradually expanding, narrow; whorls becoming somewhat inflated in adulthood. Dorsal slopes moderately convex; umbilical shoulders rather narrowly rounded; ventral slopes slightly convex, angled downward. Aperture outline subcordate. Slit deep; selenizone on prominent, elevated, rounded dorsomedian keel; lunulae faint. Corrugated growth lamellae very closely spaced (4 per 1mm), scalloping generally not distinctly squared; revolving threads moderately distinct on well preserved surface, generally 3 per 1mm.

Measurements. - Measurements of P. cellulosus are listed in Table 42.

Table 42: Measurements of Phragmolites cellulosus in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter
47562	8.5	7.3	3.6	4.3	1.9	3.5
79250	10.0	--	4.1	5.5	1.9	--
61029	11.5	9.25	6.5	6.0	3.0	4.6

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Three specimens were examined. USNM 47562 is a complete calcitic shell with a worn surface (Pl. 43, figs. 7-9). USNM 61029 is a calcitic specimen with a well preserved surface (Pl. 43, figs. 4-6). USNM 79250 is a calcitic specimen with the ventral whorl broken away (Pl. 43, figs. 10-12).

Distribution. - The specimens examined here are all from the Hermitage Formation (Kirkfieldian) of central Tennessee. Ulrich and Scofield (1897, p. 910) reported this species from the "Clitambonites bed" at St. Paul and Cannon Falls, Minnesota, which was their basal "Trenton" unit. Bassler (1915, p. 972) stated the species occurred in the Prosser Formation at the same localities, which, according to Sweet and Bergstrom (1976, text-dif. 3), is Shermanian-Edenian in age.

Comparisons. - Ulrich and Scofield (1897, p. 910) distinguished P. dyeri var. cellulosus from the P. dyeri dyeri by having much less of a dorsal keel and by differences in the surface markings. I recognize P. cellullosus as a distinct species based on these characters. The Tennessee specimens assigned to P. cellulosus have a very strong dorsal keel, but their surface markings are subtly different from P. dyeri. The lamellae of P. cellullosus are more strongly scalloped and not quite as closely spaced as in P. dyeri. The Tennessee specimens also attain a slightly larger size, and their whorls become more inflated, in comparison to typical Richmondian P. dyeri.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - As implied above, the differences between P. cellulosa and P. dyeri are subtle, but they are recognizable. Confusion between the two similar species should not be a problem, and their stratigraphic ranges are not known to overlap.

P. cellulosus occurs in Safford's (1869) "Orthis bed" (Hermitage Formation) in Tennessee and in Ulrich and Scofield's (1897) "Clitambonites bed" (Prosser Formation) in Minnesota, each being considered the base of the "Trenton" by those authors. Both formations are interbedded shales and argillaceous limestones with abundant brachiopod faunas.

PHRAGMOLITES BELLULUS (Ulrich, 1897)

Pl. 44, figs. 5-7

Conradella bellulus ULRICH in ULRICH AND SCOFIELD, 1897, p. 910, Pl. 67, figs. 23-26.

Phragmolites bellulus (Ulrich), BASSLER, 1915, p. 971.

Diagnosis. - Shell small (up to 11 mm in length), narrow; slit only one-quarter whorl deep; selenizone with distinct lunulae; corrugated growth lamellae moderately closely spaced, with 8-9 saddles per side.

Description. - Shell small, very gradually expanding, narrow throughout. Dorsal slopes broadly convex, umbilical shoulders rather well rounded, umbilical slopes gently convex; aperture outline subovate to subchordate. Dorsal carina elevated, truncate, with distinct lunulae. Slit

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

apparently open only one-quarter whorl. Corrugated growth lamellae moderately closely spaced (3 per 1mm), with 8-9 saddles from shoulder to crest, but losing corrugations within the umbilicus. Revolving lines fairly distinct, about 6 from shoulder to crest (2 lines per 1mm).

Measurements. - Measurements of the holotype P. bellulus are listed below in Table 43.

Table 43: Measurements of the holotype of P. bellulus in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width
45751	10.75	9.1	4.5	4.0	1.9

Material. - The holotype (USNM 45751) (Pl. 44, figs. 5-7) and only known specimen of P. bellulus is a well preserved calcitic specimen.

Distribution. - The holotype came from the Fairmount member of the Fairview Formation at Covington, Kentucky (Maysvillian).

Comparisons. - Ulrich and Scofield (1897) placed P. bellulus in an intermediate position between P. elegans Miller and P. dyeri Hall. It differs from P. elegans by its "more slender whorls and less coarsely marked surface," and from P. dyeri by its narrower shell, less crowded corrugated lamellae, and in having distinct lunulae on the slitband.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PHRAGMOLITES ELEGANS (Miller, 1874)

Pl. 44, figs. 11-15; Pl. 45, fig. 10

Cyrtolites dyeri Hall (part), MEEK, 1873, p. 149, Pl. 13, figs. 2d-e.

Cyrtolites elegans MILLER, 1874, p. 310, fig. 31, 1889, p. 402, fig. 668.

Conradella elegans (Miller) ULRICH & SCOFIELD, 1897, p. 911, Pl. 67, figs. 12-15.

Phragmolites elegans (Miller), BASSLER, 1915, p. 972.

Diagnosis. - Shell small (up to 11.4 mm in length); aperture outline lanceolate with angular shoulders; selenizone with distinct lunulae; corrugated growth lamellae moderately spaced, with 5-6 shallow saddles per side.

Description. - Shell small, gradually expanding, relatively tightly enrolled with each volution embracing one-third to one-half the previous one, consisting of about 3 whorls. Dorsal slopes very gently convex and quite acute to one another; umbilical shoulders subangular; ventral slopes nearly flat and sloping inward; aperture outline lanceolate. Slit one-half whorl deep; selenizone on moderately elevated dorsomedian keel, flat-topped, with bordering threads and distinct closely spaced lunulae. Corrugated growth lamellae moderately spaced with 5-6 shallow saddles per side. Growth lines very fine; revolving threads apparently lacking.

Measurements. - Four Ulrich and Scofield (1897) hypotypes were measured (Table 44).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 44: Measurements of P. elegans in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter
315569	8.0	6.6	4.5	4.0	1.7	3.3
315571	11.4	8.2	5.6	25.6	2.0	4.5
315570	6.0	5.3	--	3.3	--	2.7
315572	4.4	3.8	2.5	2.2	0.8	1.8

Material. - Four of twelve calcitic specimens in Ulrich and Scofield's (1897) holotype suite (USNM 45754) are figured here: USNM 315669 (Pl. 44, figs. 11-13); USNM 315670, Pl. 44, fig. 14; USNM 315671 (Pl. 44, fig. 15); USNM 315672 (Pl. 45, fig. 10). Other calcitic specimens examined were UCGM 19819 and 19820.

Distribution. - The species is known only from the Corryville biofacies of the Grant Lake or Bull Fork Formations (late Maysvillian) in the vicinity of Cincinnati, Ohio.

Comparisons. - P. grandis Ulrich and P. triangularis Ulrich and Scofield possess similar shell forms to P. elegans, but both of these Blackriveran species attain much greater size and have coarser ornament. The early Maysvillian species P. bellulus Ulrich differs in its more rounded whorl form and generally more closely spaced and more scalloped lamellae. The Richmondian species P. dyeri (Hall) differs similarly, but also lacks distinct lunulae, and bears distinct revolving threads.

Discussion. - P. elegans is a distinctive species related to both P. bellulus and P. dyeri. P. bellulus is apparently ancestral to P. dyeri and P. elegans seems to have evolved separately, as shown by the different

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

character of its shell lamellae. Possibly P. elegans is descended from P. grandis, which, while larger, had a similar whorl form and corrugated lamellae.

Meek (1873) thought that this species bore revolving threads, but Miller (1874, p. 310-311) claimed what Meek described "were merely the rows formed by the flexures of the transverse lamellae." Miller's point is demonstrated in specimen USNM 315669 (Pl. 44, fig. 11) in the last few visible corrugated lamellae near the aperture margin.

It is to be noted that like other Cincinnatian species of the genus, P. elegans is associated with ramose bryozoa. Plate 45, figure 10, is only one of three of Ulrich and Scofield's specimens found "attached" at the aperture to a ramose bryozoan fragment. Two possibilities other than chance could explain this repeated association and position. The bellerophant could have used the elevated position for a site from which to suspension feed, or it may have been actually feeding at the surface of contact, either preying on the bryozoan itself, or possibly grazing on algae growing on a dead colony. In any case, it is probable that such occurrences reflect essentially instantaneous burial, in which the bellerophont clamped down, clinging to the bryozoan branch, and was entombed.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PHRAGMOLITES DYERI (Hall, 1872)

Pl. 44, figs. 8-10, Pl. 45, fig. 11

Cyrtolites dyeri HALL, 1872, p. 230, Pl. 8, figs. 7-8; MEEK, 1873, p. 149, Pl. 13, figs. 2a-c, [non] figs. 2d-e; MILLER, 1874, p. 309.

Conradella dyeri (Hall) ULRICH & SCOFIELD, 1897, p. 909, Pl. 67, figs. 30-33; CUMINGS, 1908, p. 957, Pl. 39, figs. 8a-c.

Phragmolithes dyeri (Hall) GRABAU & SHIMER, 1909, p. 618, fig. 823e-f.

Phragmolites dyeri (Hall) BASSLER, 1915, p. 972.

Diagnosis. - Shell small (up to 9.0 mm in length); aperture outline cordate; dorsal carina elevated, rounded, lacking distinct lunulae; corrugated growth lamellae very closely spaced, with about 10 saddles per side; revolving threads prominent.

Description. - Shell small, rarely greater than 10mm in diameter, gradually expanding, each whorl embracing about one-third of the previous one. Aperture outline cordate; dorsal slopes broadly rounded, becoming more tightly enrolled at umbilical shoulders, ventral slopes convex, angled downward. Slit depth uncertain, but apparently less than one-half whorl; selenizone on elevated dorsomedian carina, crest rounded, lunulae lacking. Corrugated growth lamellae very closely spaced (4 to 5 per 1mm), notched at contact with prominent spiral threads (about 3 per 1mm), straight to round or square between threads, about 10 notches from whorl shoulder to crest.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - Measurements of P. dyeri are listed below in Table 45.

Table 45: Measurements of P. dyeri in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter
315573	8.0	6.5	4.0	4.5	1.6	3.0
45752	9.0	7.6	4.3	4.4	1.8	3.0
45752	5.7	--	2.5	2.8	--	2.0

Material. - Ulrich and Scofield's (1897) hypotype material (USNM 45752) consists of four calcitic specimens and a small slab containing two more specimens. USNM 315573 (Pl. 44, figs. 8-10) and USNM 315574 (Pl. 45, figs. 11) were selected from the USNM 45752 suite for illustration of the species here. Numerous unnumbered specimens were examined in UCGM and MU collections.

Distribution. - Ulrich and Scofield (1897, p. 910) reported this species from the "Richmond Group" in southeastern Indiana, southwestern Ohio, north-central Kentucky, and near Spring Valley, Minnesota. Specimens examined here came from the Arnheim, Waynesville, and Liberty biofacies of the Bull Fork Formation (Richmondian) in the Indiana-Ohio-Kentucky area.

Comparisons. - P. dyeri is readily distinguished from P. bellulus and P. elegans by its more cordate-shaped aperture, its more closely spaced lamellae, its prominent spiral threads, and by the lack of lunulae on its selenizone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - This species is rather uncommon, probably largely due to being overlooked because of its small size, but when found, it is never abundant. It is often quite well preserved, and it is generally found in association with a brachiopod-ramose bryozoan-trilobite assemblage. The small slab (USNM 315574) shown in Pl. 45, fig. 11, is typical. The implications of the association between Cincinnatian species of Phragmolites and ramose bryozoans are presented in the discussion of P. elegans.

Ulrich and Scofield (1897, p. 910) claimed the revolving threads of P. dyeri were "as a rule not ridges at all, but only an appearance due to the elevation and longitudinal arrangement of the closely following loops of the transverse lamellae." Contrary to this claim, and in agreement with other descriptions, specimens examined here, including those of the Ulrich and Scofield collection (Pl. 44, figs. 8-9), appear to have distinct revolving ridges independent of the scalloping of the lamellae.

Although lunulae generally appear to be lacking on the selenizone of this species, there is a suggestion of lunulae on the specimen shown in Pl. 44, figure 9.

From material examined, it appears P. dyeri has a slit which is much shorter than the general depth of one-half whorl, but at present an exact slit depth for the species cannot be given. It should be noted that the most closely related species, P. bellulus (Maysvillian), has a slit of only one-quarter whorl depth. It seems a reduction of slit depth may be characteristic of this latest Ordovocian lineage of Phragmolites.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TEMNODISCUS Koken, 1896

Pl.42. figs. 3-6

Diagnosis. - Shell small, disjunct to loosely coiled, relatively rapidly expanding; whorl slopes convex; aperture sinuate, with shallow slit; selenizone generally on truncated dorsum, narrow to broad, with lunulae, without distinct borders, can be ridge-like in submaturity; growth lines sublamellose to distinctly lamellose, sometimes finely crenulated, with fine revolving threads between growth lines.

Type species. - Cyrtolites lamellifer Lindstrom, 1884, by subsequent designation of Reed (1921, p. 47).

Distribution. - Temnodiscus is known from the Silurian of Sweden (Lindstrom, 1884) and Great Britain (Reed, 1920), and possibly from the Late Ordovician and Silurian of Bohemia (Horny, 1963). The single North American species is from late Middle Ordovician (Shermanian) strata near Cincinnati, Ohio.

Comparisons. - Temnodiscus is distinguished from Tropidodiscus by its lamellose growth increments and revolving threads, from Phragmolites by its curved (sinuate), more finely crenulated lamellae, and from both by its generally more rapid rate of whorl expansion, its occasionally disjunct coiling, and its relatively shallow slit.

Discussion. - Koken (1896, p. 100) erected the genus Temnodiscus for five species placed in Cyrtolites described by Lindstrom (1884) from the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Silurian of Sweden. Unaware of Koken's genus, Ulrich and Scofield (1897) proposed the genus Cyrtolitina for a single American species C. nitidula and the same five species assigned by Koken to Temnodiscus; they also designated Cyrtolites lamellifer Lindstrom as the type species. Reed (1921, p. 47) correctly recognized the validity of Temnodiscus, indicating C. lamellifer as type species (Knight, 1941, p. 345).

The familial placement of Temnodiscus is a subject of some controversy. Lindstrom (1884) and Ulrich and Scofield (1897) clearly described and figured slit-bands in the species they described. Koken (1896) agreed with these descriptions, but then in 1897 he gave a new description of the genus in which he stated no slit-band was present (Reed, 1921, p. 47). Horny (1963, p. 90), after describing three new species of Temnodiscus from the Ordovician-Silurian of Bohemia and upon examination of Knight's (1941, Pl. 10, figs. 3a-d) photographs of the type species, concluded that there was no real selenizone in T. lamellifer and congeneric species. He stated (p. 90): "The apparent selenizone originates from the very narrow and deep true sinus with nearly parallel sides." I have also examined Knight's (1941) figures, and believe that the species does possess a true selenizone with distinct lunulae. However, Horny's species do not appear to have true selenizones, but rather have sharp dorsal carinae. Reed's (1921) species are stated to have narrow slit-bands (with lunulae) mounted on flat-topped carinae; in one case (T. monilifer), the slit-band is flattened in maturity, but becomes "narrower and completely (?) closed to form an acute keel in proximal part of shell" (p. 48).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

T. nitidula Ulrich and Scofield is also problematical. Its truncate dorsum has distinct "lunulae", but some of these appear continuous with growth lines, whereas others do not (Pl. 42, figs. 4, 6). There are no distinct bordering threads separating the selenizone from the dorsal slopes of the shell, and the emargination present is not nearly as deep as in species of Tropidodiscus and Phragmolites. This pseudoselenizone is similar to those of some other bellerophontacean species, such as Tetranota bidorsata (Hall) or T. sexicarinata (Ulrich and Scofield) (Pls. 21-22). Furthermore, it is relatively well defined in comparison to species such as Sphenosphaera troosti (D'Orbigny) (Pl. 29), which bears only a dorso-median ridge, but which is clearly closely related to S. clausus (Ulrich), which has an excellently defined slit-band with lunulae.

In light of these observations, Temnodiscus is retained in the Tropidodiscidae. Direct comparison of specimens of species from the various areas is needed in order to determine the uniformity and validity of composition of the genus Temnodiscus.

TEMNODISCUS NITIDULA (Ulrich, 1897)

Pl. 42, figs. 3-6

Cyrtolites nitidula ULRICH, 1879, p. 12, Pl. 7, figs. 7-7a.

Cyrtolitina nitidula ULRICH in ULRICH & SCOFIELD, 1897, p. 866, Pl. 62, figs. 53-55.

Temnodiscus nitidula KNIGHT, 1941, p. 345.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Diagnosis. - Shell small (up to 9 mm in length), rapidly expanding, relatively tightly coiled; dorsum broadly truncated, selenizone broad, with distinct lunulae; growth lines sublamellose; revolving threads fine.

Description. - Shell small, expanding rather rapidly to about two volutions; relatively tightly coiled for genus, the outer volution embracing about half of the inner one; umbilici moderate in size, with rounded shoulders. Dorsal slopes entirely gently convex; dorsum broadly truncated; parietal deposits not apparent; aperture outline subcordate. Selenizone broad, borderless, with distinct lunulae. Sinus deep, slit relatively shallow. Growth lines strong, apparently sublamellose, closely and evenly spaced, strongly curved. Fine revolving threads.

Measurements. - Measurements for T. nitidula are listed below in Table 46.

Table 46: Measurements of Temnodiscus nitidula in mm.

USNM No.	Shell Length	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter	Selenizone Width
315542	9.0	5.5	5.4	2.0	5.0	1.1
315543	7.8	5.1	4.9	1.5	4.0	1.1

Material. - The four specimens located were Ulrich's type specimens, all catalogued under USNM 45793. Shell material is apparently lacking in all, but external ornament is well preserved, and thus they are apparently composite molds. From this suite, USNM 315542 (Pl. 42, figs. 3-4) is designated the lectotype, and USNM 315543 (Pl. 42, figs. 5-6) and the other two specimens (left under the original number) are paralectotypes.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - Ulrich and Scofield (1897, p. 867) cited the species as occurring in the "Upper part of the Trenton Group, in the river quarries just west of Covington, Kentucky." These beds would be presently assigned to the Point Pleasant Tongue of the Clays Ferry Formation (Shermanian).

Comparisons. - Probably the species most easily confused with T. nitidula would be the monoplacophorans Cyrtolites (Paracyrtolites) carinatus and C. (P.) parvus. Both can be readily distinguished from T. nitidula by their carinate, rather than distinctly truncate, dorsal sides.

Discussion. - This species is rare. This may be the result of its small size and the apparent difficulty of the preservation of its shell. It cannot be confirmed, but the uniform preservation of Ulrich's type suite suggests collection from a single bed.

Family BUCANIIDAE Ulrich and Scofield, 1897

Diagnosis. - Shell with numerous volutions which are barely contiguous to slightly overlapping, with early volutions visible in moderately narrow to wide umbilicus; generally having a shallow labral slit which generates a selenizone; shell surface with collabral growth lines or lamellae, which are generally crossed by revolving lines varying from angular ridges to threads.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stratigraphic distribution. - Lower Ordovician?, Middle Ordovician - Devonian.

Discussion. - Ulrich and Scofield (1897) erected this family and included some genera which have since been removed. Knight (1956) recognized the distinctiveness of some genera which he separated in the Tropidodiscidae, and Peel (1972) placed Tremanotus in the Tremanotidae, demonstrating that the genus was only sinuate, and did not possess a true slit.

There has never been any significant disagreement over the distinctiveness of this family, only over how this should be expressed in the classification scheme within the Bellerophontacea. Koken (1925), Knight, et al. (1960), and Horny (1963) considered the group to be a subfamily of the Bellerophontidae. Ulrich and Scofield (1897), Dall in Zittel-Eastman (1913), Wenz (1938), and Golibkov and Starabogatov (1975) have considered the group to be an independent family, as is done here. The separation of the Bucaniidae from the Bellerophontidae expresses more clearly that the former group is a distinct and more primitive phylogenetic entity.

Within the Bucaniidae, there are four known subfamilies - Bucaniinae (Ulrich and Scofield, 1897), Salpingostomatinae (Koken, 1925), Plectonotinae Boucot and Yochelson (1968), and Undulabucaniinae new subfamily.

As is obvious from its name, the Lower Ordovician genus Eobucania Kobayashi, 1955, was considered to be closely related to Bucania from its inception. Knight, et al. (1960) placed Eobucania in the Bucaniinae, supporting such a relationship. However, it is felt here that Eobucania

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

bears as much, or more, resemblance to the Tropidodiscidae as to the Bucaniidae. Like Tropidodiscus, Eobucania has a deep slit and has only fine, closely-spaced collabral shell markings. The aperture in Eobucania does flair and expand like that of a bucaniid, but its whorl form is quite distinct. Eobucania seems to be somewhat intermediate in morphology between Tropidodiscus and Bucania, and might very well represent a group of early bellerophontaceans that gave rise to Bucania and its relatives.

Subfamily BUCANIINAE Ulrich and Scofield, 1897

Diagnosis. - Shell with aperture margins tending to flair, mainly laterally; slit relatively short, open at aperture margin; collabral growth lines often crossed by revolving threads.

Stratigraphic distribution. - Middle Ordovician - Devonian.

Genera included. - Bucania Hall, 1847; Kokenospira Bassler, 1915; ?Megalomphala Ulrich and Scofield, 1897, and Eobucania Kobayashi, 1955, are members of this subfamily. Horny (1963) removed Coelocyclus Perner, 1903, from the Bucaniinae, where it had been placed by Knight and others (1960), and assigned it to his new subfamily Cymbularinae Horny of the Bellerophontidae. However, the open umbilicus and depressed whorls of this genus suggest that it should remain with the bucaniids.

Genera considered here. - Bucania, Kokenospira.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - This is the central group of the family Bucaniidae, and is nearly the same grouping of genera considered as the tribe Bucanides by Knight and others (1960). This group apparently descended from the tropidodiscids through such an intermediate stock as represented by the Lower Ordovician genus Eobucania. It would seem that the other subfamilies of the Bucaniidae, as well as possibly the subfamily Bucanopsinae of the Bellerophontidae, evolved from the Bucaniinae during the Early to Middle Ordovician radiation of the bellerophontaceans.

Genus BUCANIA Hall, 1847

Pls. 12-20

Diagnosis. - Shell with medium to large umbilici; revolving ornamentation running normal to, and generally interrupted by, growth lines or lamellae.

Description. - Shell size from small to large, the whorls rounded or depressed and generally gradually expanding; umbilici medium to large in size. Outer aperture lip thin, with broad V-shaped sinus and central slit; slit shallow to quite deep; selenizone generally narrow, being slightly elevated, flat, or channel-like; inner aperture of lip often thickened. Shell surface marked by transverse growth lines or lamellae and revolving threads; revolving threads run normal to, and are generally interrupted by, the growth lines; growth lines often become lamellose in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

maturity, accompanied by a general thickening of the whorl laterally and posterolaterally.

Type species. - Bellerophon sulcatinus Emmons, 1842, by subsequent designation of Waagen (1880, p. 130).

Distribution. - Lower Middle Ordovician (Chazyan) to Middle Silurian (Niagaran) in eastern North America (Bassler, 1915), and in Middle Ordovician to Silurian rocks in Europe and northeast Asia (Knight and others, 1960).

Comparisons. - Salpingostoma Roemer, 1876, differs from Bucania in having abrupt expansion of the adult whorls and a long, closed-off slit. Tetranota Ulrich and Scofield, 1897, differs in having the selenizone mounted on a broad, elevated dorso-median band, often with one or two lateral ridges. Members of the new genus Undulabucania resemble species of the Bucania sulcatina group (see discussion below) in shell form, but differs in lacking revolving threads, and having the more Phragmolites-like features of a deep slit and regularly wavy growth lines.

Discussion. - Hall (1847, p. 32) erected the genus Bucania for those species previously assigned to Bellerophon Montfort (1808) which have an umbilicus of sufficient size to reveal the earlier volutions. In the following years, most authors found it impossible to mark a proper boundary between Bucania and Bellerophon based solely on umbilical size, and, therefore, they generally considered the two names to be synonyms. Nevertheless, Hall (1861, p. 93) reaffirmed his contention that Bucania

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

was a valid genus, but unfortunately offered no further supportive evidence.

Waagen (1880, p. 150) asserted that the primary taxobasis of the genus Bucania was its spiral ornamentation. He noted that the umbilicus was generally larger in species of Bucania than in those of Bellerophon, but the overlap between the two genera excluded that character as the primary taxobasis. Waagen also emphasized the presence of distinct transverse growth lines crossing the revolving threads, and the general thinness of the shell, except for the massive thickening of the inner lip in many species.

Ulrich and Scofield (1897, p. 883-84) commended Waagen's definition of the genus, but showed that it was too broad, encompassing a variety of distinct forms which also bear revolving ornament (such as Salpingostoma, Kokenospira, and Bucanopsis). Ulrich and Scofield's review and redefinition of the genus remains the most definitive statement on Bucania. They stated that Bucania should be restricted to species which have fairly large umbilici, a broad V-shaped sinus with a central slit, and the characteristic shell markings. They emphasized that these shell markings differed from other genera with revolving lines, in that both the revolving and transverse markings in Bucania were oblique to the direction of coiling. Other comparable genera all are characterized by revolving lines parallel to the direction of coiling.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ulrich and Scofield (1897, p. 851) recognized two informal "groups" of species. The first, their "typical section" (the B. sulcatina group herein), was characterized by a thin shell, a broad umbilicus, broad whorls with a slow expansion rate, no massive parietal thickening, and a long slit. The second group, referred to both as the "B. nashvillensis section" (p. 851), or the "B. lindsleyi section" (p. 884), was described as having a thicker shell, smaller umbilicus, more rapidly expanding whorls with a relatively longer aperture, often with massive parietal thickening, and a shorter slit. These two groups are left informal here because although the two end members, B. sulcatina and B. lindsleyi, are quite distinct, some species are gradational between them and have characters of both groups. For example, B. rugatina resembles B. lindsleyi in its smaller umbilicus and its surface markings, but was placed in the B. sulcatina group by the Ulrich and Scofield (1897) because of its gradual whorl expansion and thin shell.

The B. sulcatina group is more primitive than, and ancestral to, the B. lindsleyi group. The former group is mainly Chazyan and Blackriveran in age, with only two known Kirkfieldian-Shermanian species. The B. lindsleyi group first appeared during Kirkfieldian time and continued into the Silurian Period.

At one time, Knight (1942, p. 487) advocated the placement of the B. lindsleyi group in the genus Loxobucania Knight, which he claimed was essentially the genus Bucania as conceived by Ulrich and Scofield (1897,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

p. 850). They had largely characterized Bucania by the possession of revolving ornament that runs normal to the aperture margin (and thus the growth lines), converges inward upon the slit and selenizone, and is generally interrupted by the growth lines or lamellae (Pl. 14, fig. 14; Pl. 17, fig. 2; Pl. 18, fig. 7). Knight (1942) pointed out that B. sulcatina, the type species of Bucania, differs from that definition by the possession of revolving ornament that meets the aperture margin at a slight angle, runs parllel to the selenizone, and continues uninterrupted by the growth lines (Pl. 12, figs. 1-5). Examination of Knight's (1941, Pl. 11, figs. 1a-b) figures of the holotype of B. sulcatina confirm these observations. However, Knight and others (1960, p. I180) placed Loxobucania in synonymy with Bucania. I have found no explanation for this reversal in judgment. However, it might be explained in the following manner. The members of the B. sulcatina group do not have a deep V-shaped sinus with broadly rounded anterolateral aperture margins, as do members of the B. lindsleyi group. Rather, the B. sulcatina group have nearly straight anterior aperture margins (as reflected by their straight dorsal growth lines), that angle back slightly to form a very broadly obtuse, shallow, anteromedian sinus (Pl. 12, fig. 5). The revolving ornament seems to be nearly normal to this straight aperture margin. It appears that the revolving threads came to converge on the selenizone at a higher angle in the more advanced group by the curving of the anterior aperture margin and development of a deep V-shaped sinus (Pl. 18, fig. 7).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

B. sulcatina and its allies probably did not require a deep sinus to assist in the efficient circulation of water through the mantle cavity because of the possession of a deep slit. As pointed out elsewhere in this study, the broken dorsal shells in numerous specimens of other deep slit-bearing genera such as Salpingostoma and Tropidodiscus suggest a structural weakness of the shell in that area. Possibly the shortening of the slit and development of a deeper V-shaped sinus were apertural modifications in more advanced species of the genus Bucania which allowed the maintenance of efficient water circulation through the mantle cavity as well as strengthening of the shell dorsum. Because of the gradational morphologic progression between the end-member species of these two groups, the genus Loxobucania is not used herein.

The B. sulcatina group is thought here to have descended from the Phragmolites stock of the tropidodiscids. The two groups both possess wide umbilici, long slits, and revolving ornament. The new genus Undulabucania also appears to have developed from that common stock. U. punctifrons was included in the "B. sulcatina group" by Ulrich and Scofield, but differs significantly from the other species in that group by lacking spiral ornament, and by having wavy growth lines reminiscent of the corrugated shell markings of Phragmolites.

The genus Salpingostoma is undoubtedly closely related to, and probably derived from, Bucania. Juveniles of species of Salpingostoma are very similar to the "B. sulcatina group" in their large umbilici,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

depressed whorls, thin shell and deep slit; whereas, upon adult expansion, these species take on a shell form similar to members of the "B. lindsleyi group", with a longer aperture and thickened parietal lip. Also, the two genera have very similar shell markings.

BUCANIA EMMONSI Ulrich and Scofield, 1897

Pl. 12, figs. 1-4

Bucania emmonsi ULRICH & SCOFIELD, 1897, p. 887, Pl. 66, figs. 1-3

Diagnosis. - Shell widely umbilicate, umbilical slopes gently convex, sutures deep with wavy indentations; shell width increases by 2.8 times in one volution; revolving threads strongly angled inward over dorsum.

Description. - Shell relatively small (up to 18 mm in length), thin, and consists of 3-4 volutions; rate of whorl expansion fairly rapid, the shell width increasing by about 2.8 times in one volution. Umbilici widely open, so that all earlier whorls are clearly visible; umbilical slopes gently convex, causing the whorl sutures to be quite deep. Ventral whorl surface, as visible along the suture lines, has numerous gentle, wavy indentations. Shell dorsum gently and evenly convex, and umbilical shoulders sharply to narrowly rounded, giving the aperture a rounded subtrapezoidal outline. Slit is unknown, but selenizone narrow and channel-like.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Shell ornament dominated by revolving threads, which are equal in strength, but widen slightly in their spacing outward from the dorso-median line numbering about 12 on either side; revolving threads pass over shell dorsum with an obvious obliqueness to direction of coiling, angling inward at about 10 degrees toward the selinizone, and angle outward on the ventral shell slopes, thus always remaining perpendicular to the curved growth lines and the growing shell margin; growth lines only faintly visible, reflecting a rather straight sided, slightly convex, V-shaped apertural sinus.

Measurements. - Measurements of B. emmonsi are listed in Table 47.

Table 47: Measurements of the lectotype (UNSM 46049) of B. emmonsi in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Post-erior Width	Ventral Width	Seleni-zone Width	Umbilical Diameter
18.4	14.25	10.0	17.0	11.45	7.85	6.1	0.5	12.15

Material. - The lectotype of B. emmonsi is here designated as specimen USNM 46049, which is a silicified replica that was figured by Ulrich and Scofield (1897, Pl. 66, figs. 1-3).

Stratigraphic distribution. - The lectotype, USNM 46049, was collected from the Murfressboro Limestone (Blackriveran) at Murfreesboro, Tennessee. Ulrich and Scofield (1897, p. 888) also cite the species from the Vaunexemia and Ctenodonta beds of Minnesota, which Weiss (1957, fig. 1) considered to be parts of the Platteville (Rockfieldian) and Decorah (Kirkfieldian) Formations, respectively.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - This species is distinguished from B. halli by its smaller size, more rapid whorl expansion, and more revolving threads that are more obtuse to the midline. B. emmonsi also resembles B. intexta Hall (Middle Ordovician, New York), but differs from that species, and all others by the wavy indentations on the deep suture lines.

BUCANIA HALLI Ulrich and Scofield, 1897

Pl. 12, figs. 5-18

Bucania halli ULRICH & SCOFIELD, 1897, p. 886, Pl. 66, figs. 4-8; GRABAU & SHIMER, 1909, p. 614, fig. 822; WILSON, 1951, p. 27, Pl. 2, figs. 15-16.

Diagnosis. - Shell widely umbilicate, umbilical shoulders subangular, umbilical slopes nearly flat; shell width increases by about 2.25 times in one volution; revolving ribs equal in strength and spacing, angled very slightly toward the selenizone.

Description. - Shell of moderate size (20-30mm in length); volutions numbering 3 or 4; depressed whorls increase in size gradually, the shell width increasing by about 2.25 times in one volution; umbilici widely open, the umbilical shoulders being subangular to sharply rounded, and the umbilical slopes nearly flat. Shell dorsum broadly and evenly convex, the ventral whorl being gently concave reflecting the opposing shape of the previous whorl; aperture shape subtrapezoidal, the L/W ratio equaling 6.2.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Revolving threads dominate shell ornament, consisting of about 12 dorsal threads on either side of the selenizone that angle very slightly toward the midline; weaker growth lines interrupt revolving threads only slightly, and are only slightly curved across the drosal slopes, reflecting a broad shallow V-shaped sinus. Slit is unknown; selenizone slightly elevated, but concave.

Measurements. - Measurements for B. halli are listed in Table 48.

Table 48: Measurements of Bucania halli in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
45717	21.3	15.0	10.5	16.9	13.2	10.0	7.5	13.8	0.8
315582	37.0	23.1	23.7	30.0	16.75	14.8	12.3	14.9	--

Material. - The lectotype designated herein is specimen USNM 45717 (Pl. 12, figs. 5-9), which is apparently a composite mold dorsally and internal mold in the umbilical areas. This specimen from Minnesota was illustrated by Ulrich and Scofield (1897, Pl. 66, figs. 4-5).

The remainder of the type suite is from the Curdsville Limestone Member of the Lexington Limestone in Mercer County, Kentucky, and consists of seven specimens under the number USNM 45718. Six of these are poorly preserved internal molds, and are here designated paralectotypes under the original number. The seventh paralectotype (USNM 315582) is a badly weathered silicified specimen retaining some aspect of the shell on the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

posterior coil and around the aperture (Pl. 12, figs. 10-14) and it may be the specimen outlined by Ulrich and Scofield (1897, Pl. 66, fig. 8).

Two specimens of B. halli were found in the USGS silicified collections from Kentucky. The first, USNM 315544 (Pl. 12, figs. 15-16), is from the Grier Limestone Member (4073-CO), and the second, USNM 315545 (Pl. 12, fig. 17-18), is from the lower Curdsville Limestone Member (5100-CO), both of the Lexington Limestone. The first is referred to B. halli with confidence. The second, however, is referred to B. cf. B. halli, consisting of an internal mold, apparently with a very thick shell remnant. This latter specimen's shell form (depressed whorls, wide umbilicus) agree well with B. halli, but the apparently thick shell may reflect expansion during silicification.

Distribution. - The lectotype (USNM 45717) is from the Decorah Formation (Rocklandian) (Black River Group of Ulrich and Winchell, 1897) at Cannon Falls, Minnesota. The paralectotypes, USNM 45718 and 315582, are from the Curdsville Limestone Member of the Lexington Limestone in Mercer County, Kentucky. USNM 315544 is from USGS Sample 4073-CO, Grier Limestone Member of the Lexington Limestone, and USNM 315545 is from USGS sample 5100-CO, Curdsville Limestone Member of the same formation (Kirkfieldian). Wilson (1951, p. 27) reported B. halli from the Lowville and Leray beds (Blackriveran) of eastern Canada.

Comparisons. - B. halli resembles B. emmonsi, both having the broad umbilici and depressed whorls of the B. sulcatina group. However, the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

whorls of B. halli expand more slowly (the width increasing by about 2.25 times in one volution, as compared to a 2.8 times increase in B. emmonsi). The umbilical shoulders of B. halli are more angular, its umbilical slopes are flatter, and its revolving threads approach the dorsomedian selenizone at a lesser angle.

Discussion. - Specimen USNM 315544 (Pl. 12, figs. 15-16) confirms the occurrence of B. halli in the Ordovician of Kentucky. The internal molds of the type suite (USNM 45718) are somewhat questionable in their species assignment. The figured paralectotype (Pl. 12, figs. 10-14), USNM 315582, is also questionably referred to B. halli. It may be the specimen shown in Ulrich and Scofield's Plate 66, figure 8, which they say is only doubtfully referred to the species, "the back being unusually convex and the sides too blunt." If one examines the photographs of this specimen (Pl. 12, figs. 10-14), it appears that the whorls were depressed and less convex in the early portion of the last whorl, but about one-third through that volution the whorl begins to expand toward the anterior, making the whorl much more convex dorsally. The umbilical form of this specimen (Pl. 12, figs. 12-13) is comparable to that of the lectotype (Pl. 12, fig. 9), both having subangular shoulders and flat slopes, but the former's appears slightly deeper. It should be noted that in the last one-third volution of the lectotype, the shell shows a tendency toward increased anterior expansion of the whorl. Finally, the specimen USNM 315582 shows strong lamellose growth lines on the expanded aperture

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Pl. 12, figs. 13-14), whereas the lectotype (which is a composite mold) shows only weak evidence of growth lines. However, it is common in bucaniids for growth lines to become stronger, and even lamellose, in maturity. Therefore, the specimen is tentatively left in B. halli. In doing so, it is shown that the B. sulcatina group may have undergone a similar expansion and thickening of the shell to that of the B. lindsleyi group in maturity. It might also be noted that the mature B. halli, as shown by the specimen USNM 315582, shows some resemblance to the Richmondian species B. crassa (Pl. 19, figs. 7-10) by its highly convex dorsum and angular, deep umbilicus. However, B. crassa is somewhat more globose.

BUCANIA SUBANGULATA Ulrich

Pl. 14, figs. 15-19; Pl. 15, figs. 8-24, Pl. 38, figs. 11-12.

Bucania subangulata ULRICH in ULRICH & SCOFIELD, 1897, p. 891, Pl. 66, figs. 20-23.

Diagnosis. - Shell small (up to 25 mm in length), rapidly expanding; umbilici moderately wide; whorl shape cordate to subtriangular; aperture slightly flared in maturity; selenizone elevated, flat; growth lines sublamellose, scalloped.

Description. - Shell small, but rapidly expanding, consisting of about 3-1/2 volutions at maturity; umbilici moderately wide, clearly exposing earlier whorls; dorsum rounded in juveniles, but becomes increas-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ingly angular with a greater rate of aperture length growth, resulting in a prominent dorsomedian angle with steep, gently convex dorsolateral slopes; umbilical shoulders narrowly rounded to angular, and umbilical slopes cut inward sharply and nearly flat. Adult aperture outline cordate to subtriangular. Selenizone moderately wide and nearly flat-topped, occasionally showing distinct lunulae. Growth lines broadly sweeping, and become sublamellose with scalloped margins in maturity; revolving threads fine and closely spaced.

Measurements. - Measurements for B. subangulata are listed below in Table 49.

Table 49: Measurements of Bucania subangulata in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
315559	25.55	19.0	19.5	30.0	11.5	7.1	6.3	11.5	--
315560	22.3	14.5	14.5	--	10.5	7.5	--	10.5	1.4
315575	13.35	9.2	6.4	10.2	7.05	5.4	3.3	6.1	--
315578	--	--	--	21.7	12.8	--	6.85	--	--
265989	9.6	6.3	6.4	7.8	5.5	4.0	--	4.5	0.6
315576	14.3	8.9	9.0	10.9	6.8	4.7	2.8	6.5	0.9
315577	--	--	--	16.8	10.7	--	--	--	--
315596	--	--	--	13.2	7.9	5.9	3.8	--	--

Material. - The original type suite, USNM 45731, consists of eight silicified syntypes. Six of these are small and too poorly preserved to yield much data, but they are designated paralectotypes and catalogued under the type suite number. The seventh syntype here (paralectotype

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

herein) is figured under the number USNM 315560 (Pl. 14, fig. 19). The eighth syntype is here designated the lectotype, USNM 315559 (Pl. 14, figs. 15-18). It should be cautioned that the anteromedian portion of the lectotype was reconstructed with plaster by the original author, but the reconstruction appears correct.

A number of specimens belonging to this species were found in the USGS silicified collections. USGS Sample 7785-CO yielded four specimens which appear to be silicified internal molds; one is figured as USNM 315575 (Pl. 15, figs. 8-12). USGS Sample 5094-CO contained six specimens, including USNM 265989 (Pl. 38, figs. 11-12), 315576 (Pl. 15, figs. 13-15), 315577 (Pl. 15, figs. 16-20), and 315596. USGS Sample 5096-CO contained two fragments, including USNM 315578 (Pl. 15, figs. 21-24.)

Distribution. - The type material was collected from the "Flanagan beds," an outdated unit in the upper Lexington Limestone (Shermanian) subsequently found to represent multiple silicified horizons, from 1-1/2 miles south of Burgin, Kentucky. The type suite may be from the Grier or Perryville Limestone members of the Lexington Limestone.

The species is recognized here from the Curdsville Limestone Member (7785-CO) and Grier Limestone Member (5094-CO, 5096-CO) of the lower part of the Lexington Limestone (Kirkfieldian).

Comparisons- Ulrich and Scofield (1897, p. 891) stated that B. subangulata could be distinguished from the associated B. rugatina by its subtriangular aperture outline. The more similar B. frankfortensis

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

and B. nashvillensis, which also have an angular dorsum (though to somewhat different degrees), can be readily distinguished from B. subangulata by their greater shell sizes and smaller umbilici.

Another feature which helps recognizing this species is the sublamellose, scalloped growth lines on the adult dorsolateral slopes. The scalloping may be accentuated by the weathering of the fine revolving threads along the margin of the sublamellose growth line. However, the feature is present in both the lectotype (Pl. 14, figs. 15-18) and the USGS material (Pl. 15, figs. 14-15, 21, 24), and was not seen to be so clearly developed in any other species.

Discussion. - The rapidly expanding shell and dorsomedian angulation of B. subangulata indicate a relation to B. frankfortensis and B. nashvillensis. The larger umbilici of B. subangulata may indicate that it is more primitive than these other species, because large umbilici are more characteristic of the B. sulcatina group.

The lectotype USNM 315559 (Pl. 14, figs. 15-18), shows the overall morphology of the species better than any other known specimen. The paralectotype specimen USNM 315560 (Pl. 14, fig. 19) shows two critical morphological features not clearly visible on the lectotype, the truncated slit band with lunulae, and the fine revolving lines (on right dorsolateral slope). A number of the USGS specimens exhibit the scalloping of the growth lines (Pl. 15, figs. 14-15) as seen in the lectotype (Pl. 14, fig. 17). Specimen USGS 315577 (Pl. 15, figs. 16-20) preserves the slit band, which is unusual for such a small specimen.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Ulrich and Scofield (1897, p. 891) stated that this species was associated with B. rugatina in the upper Lexington Limestone. Specimen USNM 265989 (Pl. 38, figs. 11-12) shows the species also occurs in association with Carinaropsis cymbula.

BUCANIA LINDSLEYI (Safford, 1869)

Pl. 18, figs. 1-9

Bellerophon lindsleyi SAFFORD, 1869, Pl. 3(G), figs. 3a, b, d, e.

Bucania lindsleyi Safford, ULRICH & SCOFIELD, 1897, p. 889, Pl. 66, figs. 24-25; BASSLER, 1932, Pl. 20, fig. 28.

Diagnosis. - Shell rapidly expanding, broadly and evenly convex dorsally; selenizone concave, lunulae strong; revolving threads and growth lines strong, latter becoming lamellose in adulthood.

Description.. - Shell moderately large (up to 36mm in length), consisting of three to four fairly rapidly expanding whorls which are rather closely coiled; umbilici of moderate size and deep with rather narrowly rounded shoulders, and steeply cut, slightly convex umbilical slopes; dorsum of shell broadly convex, becoming broader and more evenly convex through growth, becoming nearly semicircular; whorl outline distinctly wider than long, and rather flat ventrally. Aperture lips remain thin, even on the inner side, and even in adulthood. Selenizone distinct, bordered by thin ridges, wide, broadly concave, and marked by strong lunulae;

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

slit unknown. Revolving threads strongly developed over entire shell, including umbilical slopes; growth lines also distinct, being broadly curved, reflecting a rather deep apertural sinus, becoming very lamellose in adulthood, and being very regularly spaced throughout growth.

Measurements. - Measurements of the lectotype and a paralectotype of Bucania lindsleyi are listed in Table 50.

Table 50: Measurements of Bucania lindsleyi in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
315550	~36.0	22.2	*/*21.8	30.5	21.0	17.0	14.7	13.0	2.0
315551	19.8	14.3	10.6	18.0	13.2	11.0	8.0	7.6	1.5

Material. - The three syntypes of the species examined are catalogued as USNM 45719. No other specimens were found. Two of the syntypes are figured here, the first, now USNM 315550, is designated lectotype (Pl. 18, figs. 1-6), and the other, now USNM 315551, a paralectotype (Pl. 18, figs. 7-9). The third unfigured syntype remains catalogued under the original museum number. All three are brown, weathered, silicified replicas. The lectotype is quite well preserved, probably because it was largely encrusted by bryozoans, most of which are now broken away to reveal the shell.

Distribution. - Ulrich and Scofield (1897, p. 890) and Bassler (1915, p. 136) cited B. lindsleyi from the Catheys Formation of Dekalb

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

County, Tennessee, and possibly from the Prosser Formation near Cannon Falls, Minnesota. Both occurrences are in Shermanian-Edenian aged strata.

Bassler (1932) listed the species from the Stromatacerium pustulosum bed of the Catheys Formation, and the Cannon Limestone (Kirkfieldian-Shermanian) of central Tennessee.

Comparisons. - B. lindsleyi differs from the closely related B. nashvillensis in being somewhat less tightly coiled, resulting in a larger umbilicus, in having a broadly rounded whorl dorsum rather than an angled one, in having a depressed channel-like selenizone rather than an elevated one, in having a thinner shell, and in having stronger shell markings.

B. micronema is similar to B. lindsleyi, but the former is much smaller in size, and its revolving threads are finer and slightly wavy.

B. lindsleyi differs from B. rugatina in being larger, less tightly coiled, less expanded, and in having a concave selenizone.

Discussion. - B. lindsleyi and B. nashvillensis are closely related species. These two species are representative of the more advanced group of bucaniids, as designated informally by Ulrich and Scofield (1897, pp. 851, 844, 886). They are the earliest known members of this informal group of species and gave rise to a number of late Middle and Upper Ordovician species. Apparently, B. lindsleyi evolved from the B. sulcatina group by the lengthening of the whorl outline and the development of a tighter coil, which was probably an adaptation for facilitating the carrying and balancing of the shell.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BUCANIA NASHVILLENSIS, Ulrich, 1897

Pl. 13, figs. 15-21; Pl. 14, figs. 1-14;

Pl. 15, figs. 1-7; Pl. 27, figs. 21-22.

Bucania nashvillensis ULRICH in ULRICH & SCOFIELD, 1897, p. 890-91, Pl. 66, figs. 36-40; BASSLER, 1932, Pl. 20, figs. 19-20.

Diagnosis. - Shell with somewhat flattened dorsolateral slopes and subangular dorsum; umbilici relatively small; transverse and radial ornament distinct.

Description. - Shell moderately large (up to 36mm in length), consisting of about three rapidly expanding volutions; coiling rather tight, umbilici relatively small and deep. Dorsolateral whorl slopes slightly flattened making the dorsal crest subangular; umbilical shoulders tightly rounded; ventral whorl only slightly concave, with low broad hump on the parietal floor reflecting the adjacent subangular dorsum. Aperture outline broad and roughly subtriangular. Shell becomes quite thick in mature growth, particularly along the posterolateral (inner) whorl slopes. Slit fairly deep, about one-fourth the aperture length, and situated in broad rounded sinus; selenizone moderately wide, forming a flattened to slightly elevated crest to the subangular dorsum. Growth lines evenly and closely spaced, becoming coarsely lamellose in later growth; revolving threads closely spaced, and although distinct, are weaker than the growth lines, and appear much stronger dorsally than within the umbilicus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - Measurements of B. nashvillensis are listed in Table 51.

Table 51: Measurements of Bucania nashvillensis in mm

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width	Slit Length	Umbilical Diameter
315557	25.8	15.3	18.1	26.0	14.4	11.4	~7.8	1.4	~5.3	9.2
315558	--	21.1	26.1	27.8	--	--	--	1.8	~6.6	--
45724	~36.0	21.75	~27.0	~33.0	19.3	14.4	10.1	1.5	--	~12.9
315566	--	~11.1	--	~16.2	10.0	7.3	--	--	--	~6.1
315567	--	~15.9	--	~19.8	~11.3	~8.3	~6.3	~0.7	--	~9.5
315569	--	16.2	--	~20.0	--	--	--	1.3	--	8.1

Material. - Ulrich's (1897) type suite consists of five silicified syntypes under the number USNM 45725 and one under USNM 45724. Three of these syntypes are figured here; USNM 315557 (from suite 45725) (Pl. 14, figs. 10-14) is here designated the lectotype; USNM 315558 (from suite 45725) (Pl. 14, figs. 6-9) and USNM 45724 (Pl. 13, figs. 1-5) are designated paralectotypes, as are the three unfigured specimens left under USNM 45725.

Numerous specimens in the USGS silicified collections from the Lexington Limestone of Kentucky were assigned to this species. Those figured here are designated USNM 315566 (Pl. 13, figs. 15-16), 315567 (Pl. 13, figs. 17-18), 315568 (Pl. 13, fig. 19), 315569 (Pl. 13, figs. 20-22), 315572 (Pl. 15, figs. 1-2), 315573 (Pl. 15, figs. 3-5), and 315574 (Pl. 15, figs. 6-7). Another new silicifed spcimen from Tennessee, UCGM

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

44284, is shown in Pl. 27, figs. 21-22. In all, about 32 new specimens and fragments were identified.

Distribution. - Ulrich and Scofield's (1897) type specimens were labeled as coming from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) in Nashville and Dekalb Counties, Tennessee. Specimen UCGM 44284 comes from the same unit at a "Hill north of Well No. 1, Smith County, Tennessee."

Specimens assigned to B. nashvillensis in the USGS silicified collections from Kentucky came from the Grier Limestone Member (4959-CO, 4073-CO) and the Salvisa (5015-CO, 6915-CO, 6916-CO) and Faulconer (6136-CO) beds of the Perryville Limestone Member of the Lexington Limestone (Kirkfieldian-Shermanian).

Comparisons. - The six type specimens of this species is based were originally assigned to Bucania lindsleyi (Safford) by Safford, but Ulrich and Scofield (1897, p. 890) concluded that they were a distinct species. B. nashvillensis has a slightly more rapid rate of whorl expansion and is more tightly coiled, resulting in a slightly smaller and deeper umbilicus (Pl. 14, figs. 3 and 12; Pl. 27, fig. 22) than in B. lindsleyi (Pl. 18, fig. 3). The dorsum of B. nashvillensis is slightly angled medially and has somewhat flattened dorsolateral slopes (Pl. 14, figs. 1-5, 6 and 9, 11 and 13), whereas that of B. lindsleyi is broadly rounded (Pl. 18, figs. 1 and 7). The slit band of B. nashvillensis is slightly elevated (Pl. 14, figs. 2, 6, 13) instead of channel-like (Pl. 18, figs. 1,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

5 and 7), and the lunulae are not so strongly developed as in B. lindsleyi (Pl. 18, figs. 5 and 7). Differences in shell sculpture between the two species cited by Ulrich and Scofield (1897, p. 890) are difficult to evaluate because of generally poor preservation, but one point seems certain, that is, the revolving threads in B. nashvillensis (Pl. 14, figs. 3, 7, 13-14) are much weaker than those of B. lindsleyi (Pl. 18, figs. 3-4 and 6, and 7). Finally, the shell is thicker in B. nashvillensis.

Discussion. - Previously B. nashvillensis had been reported only from the Bigby-Cannon Formation of Tennessee. Ulrich and Scofield (1897, p. 891) cited the species from the "Trenton group, Dekalb County, and Nashville, Tennessee." Bassler (1932, p. 106, Pl. 20, figs. 19-20) reported the species from the "Cannon limestone," which is in agreement with the labeling of the type suite. Wilson (1949, p. 118 and 125), on the other hand, reported the species from only the Bigby and Dove-colored facies of the Bigby-Cannon Limestone. Specimen UCGM 44284 (Pl. 27, figs. 21-22) was in a collection of gastropods from the Cannon facies in Smith County, Tennessee.

Numerous fragmented specimens from the USGS silicified material from Kentucky are smaller than the large specimens of the type suite (Pl. 14, figs. 1-14); however, they bear resemblance to these type specimens in their angular whorl forms. The characteristic revolving threads of Bucania are not clearly preserved on any of these specimens from the Lexington Limestone of Kentucky, but neither are they preserved in the para-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

lectotype USNM 45724 (Pl. 14, figs. 1-5). It should be noted that many other bellerophontaceans described here that are known to possess shell markings, also lack preserved ornament markings in some of the silicified collections from Kentucky (for example, see Bucanopsis carinifera, on Pl. 27, figs. 5-19).

The small specimens from the Grier Limestone Member (Pl. 15, figs. 1-7) appear to have the correct umbilical size and whorl form, and show a tendency toward slight dorsal angulation. It must be noted that, as seen in the earlier volutions of the type specimens of B. nashvillensis (Pl. 14, figs. 5 and 6), the dorsomedian angulation was an adult feature, and submature specimens have a more evenly rounded dorsum (as in the small Grier specimens). Similarly, the specimens from the Perryville Limestone Member that are assigned to B. nashvillensis, such as specimen USNM 315569 (Pl. 13, figs. 20-21), is somewhat larger than the Grier specimens and shows a greater dorsomedian angulation, as does the lower dorsal fragment of USNM 315566 (Pl. 13, figs. 15-16) and USNM 315568 (Pl. 13, fig. 19), which also shows a thickened parietal lip as seen in the type specimens (Pl. 14, figs. 3, 5, and 7). Although different collections of Kentucky specimens differ in small points from the type suite, I believe they are all so similar in overall morphology that they are best assigned to B. nashvillensis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BUCANIA FRANKFORTENSIS Ulrich, 1897

Pl. 13, figs. 22-24; Pl. 16, figs. 1-4.

Bucania frankfortensis ULRICH in ULRICH & SCOFIELD, 1897, p. 891, Pl. 66, figs. 30-33; BASSLER, 1932, Pl. 21, figs. 11-12.

Diagnosis. - Shell aperture with distinctly triangular outline; whorls high, relatively narrow, with subangular dorsal crest.

Description. - Shell moderately large (up to 40.5mm in length), consisting of about 3-4 volutions; umbilicus moderately wide and deep; juvenile whorls somewhat depressed, subreniform in shape, and only slightly, if at all, angled dorsally; whorls expand more rapidly anteriorly in later growth so that the dorsum becomes increasingly angular; adult dorsal slopes gently convex and steeply inclined, umbilical shoulders rather tightly rounded, and umbilical slopes are steep but broadly convex, all resulting in a gently rounded, but distinctly triangular aperture outline. Inner aperture lip thickened and folded back to form a posterior shelf to the aperture; aperture margins continually thin around lateral rims to a broad, fairly deep, anterior sinus; slit unknown; selenizone slightly elevated and rounded. Shell markings known only on adult thickened aperture flanks, consisting of rather regularly spaced, wrinkled, lamellose growth lines; revolving threads very weak.

Measurements. - Measurements for the holotype of B. frankfortensis are listed in Table 52.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 52: Measurements of the holotype of Bucania frankfortensis in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter
45716	40.5	25.5	26.8	29.8	16.9	14.0	11.5	14.0

Material. - The holotype, USNM 45716 (Pl. 16, figs. 1-4), is a silicified replica in which the anteromedian portion of the shell has been rebuilt with plaster. The reconstruction appears to be quite faithful to the form of the actual shell. The species was identified here from silicified fragments, mainly of the thickened posterior aperture, from USGS sample 5036-CO.

Distribution. - The museum label states that the holotype, USNM 45716, is from the "Trenton (Cynthiana) at Frankfort, Kentucky." Writing on the specimen itself states: "Top of Trenton, Gastropoda beds, Frankfort, Kentucky." The highest gastropodal beds in the interval previously referred to as the Cynthiana Formation in the vicinity of Frankfort, Kentucky, are those of the Devils Hollow Member of the Lexington Limestone (Shermanian) (Pomeroy, 1968), which in part is characterized by a profusion of gastropods, most conspicuously species of the genus Lophospira, this facies being interpreted as very shallow bank deposits (Cressman, 1973, p. 40-41). B. frankfortensis occurs in the USGS silicified Sample 5036-CO from the Devils Hollow Member of the Lexington Limestone (Shermanian) in Coletown quadrangle, Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bassler (1932, pp. 113-114, Pl. 21, figs. 11-12) cited this species as being characteristic of the Cathys Formation (Shermanian) of the Central Basin of Tennessee.

Comparisons. - This species most resembles B. nashvillensis which also has an angular dorsum, but the dorsum of B. frankfortensis is higher, its dorsal whorl slopes are steeper, and its aperture is much more triangular. The coarse wrinkle-like growth lamellae on the thickened posterior portion of the adult whorl of B. frankfortensis, as well as the weakeness of the revolving threads, also serve to distinguish the species.

Discussion. - By virtue of their similar shell forms, most particularly the angular dorsal whorl, B. frankfortensis and B. nashvillensis should be considered closely related, but distinct, species.

BUCANIA PERACUTA Ulrich, 1897

Pl. 16, figs. 5-8

Bucania peracuta ULRICH in ULRICH & SCOFIELD, 1897, p. 896, Pl. 66, figs. 34-35; BASSLER, 1932, Pl. 20, fig. 29

Diagnosis. - Shell large, thick; aperture broadly subtriangular, angular dorsally and laterally; umbilici wide; dorsolateral slopes with rugae.

Description. - Shell large (up to 29 mm in length) and thick, the adult parietal lip being particularly massive. Aperture outline broadly

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

subtriangular, the width being more than twice the length; whorl dorsum angular, dorsolateral slopes broadly spread and gently convex; umbilical shoulders angular; umbilical slopes deeply cut and slightly concave to nearly flat; base of the whorl nearly flat, except for a low ridge over the previous dorsal angle. Slit unknown, but selenizone rather narrow for such a large shell, being slightly elevated and truncated. Dorsolateral slopes marked by low, but rather sharp and distinct rugae, which angle straight back from the umbilical shoulder to the selenizone, reflecting a very straight-sided, V-shaped aperture sinus; rugae form nodes at the umbilical shoulder, but do not pass over it. Growth lines indistinct and revolving threads unknown.

Measurements. - Measurements on the holotype of B. peracuta (USNM 45726) are listed in Table 53. Figures 5-8 on Pl. 21 should be examined in order to understand the difficulties with these measurements.

Table 53: Measurement on holotype of Bucania peracuta in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter
29.1	20.0	16.3	34.8	21.0	15.3	--	15.5

Material. - Only one specimen of B. peracuta was located, the holotype (USNM 45726). This specimen is a large, thick, brown, weathered, silicified fragment.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - The museum label states that the holotype, USNM 45726, is from the "Trenton (Cannon), Dekalb Co., Tennessee." Bassler (1915, p. 137) cited the species from the Catheys Formation, this is probably a mistake, as Bassler (1932, p. 106) later confirmed the occurrence only in the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) of central Tennessee.

Comparisons. - Because of the rugae developed on the dorsolateral slopes of this species, it is reminiscent of the genus Cyrtolites, but its extremely thick shell and possession of a slit band show that this resemblance is only superficial. Its rapid rate of expansion and angular dorsum led Ulrich and Scofield (1897, p. 897) to suggest a possible relation to B. nashvillensis.

The common possession of rugae and a rather narrow, slightly elevated selenizone may show a close relationship between B. peracuta and B. singularis (Pl. 19, fig. 15-18) of the Catheys Formation (Shermanian-Edenian) of Tennessee.

Discussion. - As suggested above, B. peracuta is seemingly a member of the B. lindsleyi group of species, but its thick, angular shell set it apart from the typically more rounded species. It may represent a branch of this group, or, as indicated by its wide angular umbilicus, may be an independent outgrowth from the ancestral B. sulcatina group.

Although placed in the genus Bucania, it must be pointed out that revolving lines are not confirmed on the holotype. However, the specimen

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

is worn. Likewise, the possible descendant species, B. singularis is too poorly preserved to retain any ornament other than its rugae (Pl. 19, fig. 15-18). In my opinion, both species possessed rather fine shell markings.

BUCANIA SUBLATA Ulrich and Scofield, 1897

Pl. 13, figs. 1-14

Bucania sublata ULRICH & SCOFIELD, 1897, p. 888-89, Pl. 66, figs. 16-19

Diagnosis. - Shell small (up to about 12 mm in length), umbilici moderately wide, whorls very broad, globose; selenizone wide, flush, bordered by distinct thin ridges; slit short, sinus shallow or absent.

Description. - Shell small, rate of whorl expansion gradual; umbilici moderately wide, exposing earlier volutions; umbilical shoulders sharply rounded in early growth, becoming more rounded in adult growth; umbilical slopes nearly flat. Dorsum very broad and somewhat globose; aperture outline acutely subelliptical, becoming less angular with growth; whorl floor has low, broad, median ridge. Selenizone wide, flush with adjacent whorl slopes, and bordered by distinct thin ridges; slit short, and as shown by growth lines which run nearly straight over the dorsal slopes, the sinus was either very shallow or possibly lacking. Growth lines are weak, evenly spaced, and essentially straight; revolving threads even weaker, being fine and closely spaced.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - Measurements of the lectotype of B. sublata are listed in Table 64.

Table 54: Measurements of the lectotype of Bucania sublata in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter
315561	11.8	9.5	7.1	11.5	9.4	6.4	5.0	6.7

Material. - The type suite consisted of three silicified syntypes under the museum number USNM 45733. Of these, the specimen in Pl. 13, figs. 1-4, is designated the lectotype for B. sublata, with the new number USNM 315561. Specimen USNM 315562 (Pl. 13, fig. 5-8) and the unfigured third syntype (retained under USNM 45733) are paralectotypes.

Specimens from the USGS collections identified as B. cf. B. sublata are USNM 315563 (Pl. 13, figs. 9-10), 315564 (Pl. 13, fig. 11), and 315565 (Pl. 13, figs. 12-14).

Distribution. - The type suite was collected from the so-called "Flanagan beds," a name that erroneously recognized silicified beds at different horizons in the Upper Lexington Limestone (Shermanian) as the same bed, near Burgin, Kentucky.

Specimens of B. cf. B. sublata from the Lexington Limestone (Kirkfieldian-Shermanian) were found as fragments in USGS silicified samples from the Grier Limestone Member (4879-CO) (Pl. 13, figs. 9-10), the Faulconer bed of the Perryville Limestone Member (6136-CO) (Pl. 13,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

fig. 11), and the Devils Hollow Member (5095-CO) (Pl. 13, figs. 12-14) of the Lexington Limestone.

Comparisons. - B. sublata can be distinguished from related species such as B. halli and B. emmonsi by its broader, more globose whorls, its slightly smaller umbilicus, its essentially straight growth lines, very weak revolving lines, and its wide, flush, bordered selenizone.

Discussion. - B. sublata is a member of the B. sulcatina group, as indicated by its large open umbilici and depressed whorls, and is therefore related to B. halli and B. emmonsi, which are present in the Cincinnati Arch area in slightly older strata. B. sublata demonstrates a more advanced condition by its more globose dorsal whorls and its smaller umbilici, both traits pointing toward the more advanced B. lindsleyi group.

The specimens identified here as B. cf. B. sublata are done so cautiously. None are well preserved, all being fragments in which silicification has destroyed any traces of shell ornament. USNM 315563 (Pl. 13, figs. 9-10) compares well in its small shell size, its umbilical size, and aperture lip shape, to the paralectotype, USNM 315562 (Pl. 13, figs. 5-8). The other fragments from the USGS collections are somewhat larger, and their whorl breadth and umbilical size suggest that they may belong to this species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BUCANIA MICRONEMA Ulrich, 1897

Pl. 19, figs. 1-6

Bucania micronema ULRICH in ULRICH & SCOFIELD, 1897, p. 892, Pl. 66, figs. 26-29.

Diagnosis. - Shell small (up to about 10 mm in length), rapidly expanded, umbilici of moderate size, with narrowly rounded shoulders; aperture broadly rounded subtriangular; revolving lines fine (5 in 1mm), continuous, slightly wavy, selenizone slightly elevated, flat-topped, bordered by very fine ridges, with distinct lunulae.

Material. - The holotype (USNM 45720) is a small silicified replica and is the only specimen of the species located and examined.

Measurements. - Measurements on the holotype (USNM 45720) of B. micronema are listed in Table 55.

Table 55: Measurements on the holotype of Bucania micronema in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
9.8	7.2	6.0	10.2	6.5	4.0	3.0	4.7	0.7

Distribution. - The holotype is labelled as coming from the so-called "Flanagan Chert," a name which erroneously recognized silicified beds at different horizons in the Upper Lexington Limestone (Shermanian) of central Kentucky as the same bed. The specimen was collected at "Danville, Kentucky".

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - This species is quite similar to the B. lindsleyi (Pl. 18, figs. 1-9), but is much smaller, and its revolving threads are finer, more continuous across growth lines, and slightly wavy (Pl. 19, fig. 6).

Discussion. - B. micronema is known only from the holotype, but it appears to be a valid taxon, as that specimen preserves sufficient detail to demonstrate its distinctiveness. Its relation to B. lindsleyi is obvious, and it is likely descended from that species. Its small size may have enabled it to dwell within erect marine algal foliage.

BUCANIA RUGATINA Ulrich, 1897

Pl. 16, figs. 9-15; Pl. 17, figs. 1-12

Bucania rugatina ULRICH in ULRICH & SCOFIELD, 1897, p. 890, Pl. 66, figs. 13-15.

Diagnosis. - Shell moderately small (up to 26 mm in length), rapidly expanding and tightly enrolled; umbilici small; selenizone flush with dorsum; growth lines evenly and closely spaced, gently wrinkled to sublamelose; revolving threads subordinate to growth lines, but distinct.

Description. - Shell moderately small, reaching a maximum length of about 26mm as known; whorls expand rapidly and are relatively tightly enrolled, resulting in rather small, deep umbilici. Dorsum broad and very convex, umbilical shoulders well rounded. Adult aperture nearly semicir-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

cular and somewhat explanate laterally, never much thickened; thin inner parietal lip blankets previous dorsal whorl, resulting in a broad ridge at the base of the aperture; outer parietal lip folds back over the coil slightly beyond the plane of the aperture. Selenizone of moderate width, bordered by fine ridges, flush with dorsolateral slopes. Growth lines evenly and closely spaced, and may be developed as weak wrinkles or weak lamellae, the latter becoming stronger in maturity; these lines strongly developed onto umbilical slopes. Revolving threads slightly subordinate to growth lines, but are still quite distinct, as fairly coarse ridges which appear increasingly restricted to single growth increments as the growth lines become more lamellose.

Measurements. - Measurements of B. rugatina are listed in Table 56.

Table 56: Measurements of Bucania rugatina in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
315555	--	~12.6	~10.6	14.65	11.6	8.5	6.6	7.1	--
315556	--	10.9	~6.0	10.8	9.0	7.0	--	6.5	1.4
315580	~26.3	18.0	~16.0	21.6	15.8	--	~9.4	8.2	0.9
315579	~21.3	11.95	~13.2	23.2	12.5	~8.3	6.7	~7.1	--
315597	--	~7.6	--	~10.7	~5.9	~4.5	~3.3	5.0	--

Material. - Ulrich's (1897) type suite (USNM 45728) consisted of five silicified syntypes. From this suite, USNM 315555 (Pl. 16, figs. 9-12) is here designated lectotype, USNM 315556 (Pl. 16, figs. 13-15) is figured, and the other three paralectotypes remain under the original museum number, USNM 45728.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Four specimens have been identified as B. rugatina from the USGS silicified collections: USNM 315579 (Pl. 17, figs. 1-6), 315580 (Pl. 17, figs. 7-11), 315581 (Pl. 17, fig. 12), and 315597 (not figured).

Distribution. - Ulrich's (1897) type specimens are labeled as coming from the "Trenton (Flanagan), 1-1/2 miles south of Burgin, Kentucky." According to McFarlan (1943, p. 14), the Flanagan is an obsolete unit in the upper Lexington Limestone (Shermanian). It probably included different silicified beds in the Grier and/or Perryville Limestone Members of the Lexington Limestone.

The species is known from two USGS silicified samples from Kentucky, 6143-CO and 7348-CO, both being from the lower tongue of the Clays Ferry Formation (Shermanian), which is overlain by the Tanglewood Member and underlain by the Millersburg Member of the Lexington Limestone.

Comparisons. - B. rugatina is generally similar to B. lindsleyi, but differs in its smaller size, its more explanate aperture, its flush (rather than concave) selenizone, and its more closely spaced, wrinkled growth lines. Ulrich and Scofield (1897, p. 890) claimed that the umbilicus of B. rugatina was smaller than that of B. lindlsyei. Measurements show that the ratio of shell length/umbilical diameter equals about 3.1 in B. rugatina and 2.7 in B. lindsleyi, supporting their claim. A difference is also reflected in the ratio of dorsal width/ventral width, which equals 1.77 B. rugatina and 1.46 for B. lindsleyi. Combined, these two ratios show that B. rugatina expands its shell width at a greater rate, while

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

coiling more tightly, which supports Ulrich and Scofield's (1897) qualitative observations. B. rugatina also might be confused with B. nashvillensis, but the former's more globose dorsum, flush selenizone, and distinctive sculpturing should serve to distinguish it.

Discussion. - This species is obviously closely related to B. lindsleyi and B. nashvillensis, and may have been derived from the former.

BUCANIA SINGULARIS Ulrich

Pl. 19, figs. 15-18

Bucania singularis ULRICH in ULRICH & SCOFIELD, 1897, p. 894, Pl. 66, fig. 47.

Diagnosis. - Shell moderate in size (up to 27 mm in length), whorls depressed, broadly convex dorsally, with narrowly rounded umbilical shoulders; dorsolateral slopes with prominent rugae, forming nodes at shoulders; selenizone elevated, flat-topped, widens notably over last half-whorl; adult aperture laterally expanded and more or less square in outline.

Measurements. - Measurements on the poorly preserved lectotype of B. singularis are listed in Table 57.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 57: Measurements on lectotype of Bucania singularis in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
315549	27.0	20.2	18.3	20.2	17.0	14.2	11.1

Material. - The specimen shown in Pl. 19, figs. 15-18 is here designated lectotype under USNM 315549. It was separated from another syntype, which is now a paralectotype, and which remains under the original suite number USNM 45730. The lectotype retains very little shell material; its umbilici and ventral aperture are covered by matrix, its dorsum is largely covered by an encrusting bryozoan, and the entire specimen is weathered.

Distribution. - The museum label on the type specimens states that they came from the Catheys Formation (Shermanian-Edenian) at Nashville, Tennessee. No other occurrences are known.

Comparisons. - Ulrich and Scofield (1897, p. 894) were in doubt of the specific relations of this species, but believed it to be nearest to B. crassa and B. lindsleyi. They did not state their reasons for this conclusion, and I can see no reason for the comparison.

The broad depressed whorls are more reminiscent of the B. sulcatina group, as is the squared-off adult aperture. The only other species of Bucania which displays the dorsal rugae of the shell is B. peracuta, but that species is larger and has a highly angular dorsum resulting in a more triangular aperture outline.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - After first examining the poorly preserved type specimens of B. singularis, I was uncertain about the validity of this species. However, after further examination, and comparison with Ulrich and Scofield's (1897, Pl. 66, fig. 47) interpretive, but accurate, reconstruction it was concluded that the specimens do actually represent a distinct species of Bucania. Its more or less square aperture outline, prominent rugae, and distinctly elevated selenizone distinguish it from all other species.

It is possible that the common possession of distinct rugae on the dorsolateral slopes of this species and B. peracuta indicates a genetic relationship. As stated under the discussion of B. peracuta, that species may represent a separate branch of the genus Bucania distinct from the B. lindsleyi group. If so, B. singularis also appears to be a part of this group, and might indicate by its depressed whorl form the connection to ancestors in the more ancient B. sulcatina group.

BUCANIA POJETAI n. sp.

Pl. 20, figs. 1-8

Diagnosis. - Shell moderately large (up to 43 mm in length), gradually expanding; umbilici large; whorl shape reniform in submaturity, cordate in maturity; growth lines wrinkled in maturity.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderately large, rate of whorl expansion gradual. Umbilici large and circular in appearance, showing a relatively loose style of coiling. Submature whorls depressed and reniform in outline, being broadly and evenly rounded dorsally, with well rounded umbilical shoulders, and a gently concave ventral side covering only the dorsum of the previous whorl; with growth toward maturity, the length of the aperture increases at a greater rate than the width, so that that the dorsum becomes jutting and angular, and the aperture outline becomes subtriangular to cordate. Thickness of shell unknown, but parietal lip became moderately thick in adulthood. Slit unknown; selenizone a low rounded ridge showing only faint lunulae. Growth lines preserved as low wrinkles (almost rugose) fairly closely spaced, swing back over the dorsum very gently reflecting only a shallow anteromedian apertural sinus; these wrinkled growth lines become stronger with growth. No revolving ornament known.

Measurements. - Measurements of B. pojetai are listed in Table 58.

Table 58: Measurements of Bucania pojetai in mm.

UCGM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
44285	40.4	26.5	22.0	31.7	19.4	16.5	12.8	17.2	--
44286	42.9	26.5	27.5	29.1	18.4	15.2	14.0	17.0	--
44287	32.5	21.9	17.0	25.5	17.4	12.6	10.6	14.2	--
44288	28.3	--	11.6	22.0	17.6	14.0	--	--	2.1
44288	24.5	19.4	11.9	17.5	15.2	13.5	--	11.7	1.6
44289	28.6	19.8	14.9	19.6	--	--	--	--	2.3

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Twelve specimens of this new species are known. Figured specimens are the holotype, UCGM 44285 (Pl. 20, figs. 3-4), and the paratypes UCGM 44286 (Pl. 20, figs. 1-2), and 44287 (Pl. 20, figs. 5-8). Eight paratypes are placed under one number, UCGM 44288, and the eleventh paratype is catalogued under UCGM 44289. Most of these specimens have some calcitic shell material preserved (see discussion).

Distribution. - All known specimens are from a collection made by R. Flower and W. Shideler from the Liepers Formation (Maysvillian) at Rowena Ferry, Russell County, Kentucky. Note that this locality is in southern Kentucky near the Tennessee border where the Central Basin facies persist and its stratigraphic names are used.

Comparisons. - B. potejai is quite similar to B. simulatrix (Pl. 19, figs. 11-14) and Salpingostoma richmondensis (Pl.26, figs. 1-8). Problems with the separation and validity of these two latter species are covered under their respective discussion sections. Briefly, the two are nearly identical in overall shell form, but S. richmondensis shows evidence of possessing a long open slit which was closed off anteriorly, as is characteristic of the genus. As in B. simulatrix (Pl. 19, figs. 11-14), B. pojetai (Pl. 20, figs. 1, 3, and 6) appears to have had the slit covered by a selenizone to near the aperture margin. B. pojetai differs from B. simulatrix in having a broader whorl form, a less elevated selenizone, and wrinkle-like growth lines.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - The marked similarity between the Maysvillian B. pojetai and the Richmondian B. simulatrix must indicate a close genetic relationship. B. pojetai is almost certainly ancestral to B. simulatrix.

The mode of preservation of B. pojetai is quite similar to that of B. simulatrix and Salpingostoma richmondensis. Although specimens of B. pojetai have some remnant of the original shell, the only ornament preserved is the wrinkle-like (almost rugose) growth lines in one specimen (Pl. 20, figs. 5-8). Where the shell is broken away, the deep-brown calcitic shell material can be seen to be quite thin dorsally (Pl. 20, figs. 1 and 6); however, the parietal lip was clearly progressively thickened in mature growth as seen by coarse crystalline calcite remnants in the umbilici of adult specimens (Pl. 20, figs. 2 and 4). B. simulatrix possesses a similar thin, dorsal, poorly preserved calcitic, shell remnant, and the holotype possesses a parietal gap (which may have been widened through vertical compaction), which probably reflects a similar thickened adult parietal region (Pl. 19, fig. 13). It is difficult to determine whether these similar conditions of preservation are due to similar original shell structure and mineralogy or similar diagenetic histories, or both. The shell of known specimens of B. pojetai has apparently been so totally recrystallized, or acted upon by surface dissolution, as to mask details of ornamentation. What remains may be a single more stable layer of the shell.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BUCANIA SIMULATRIX Ulrich, 1897

Pl. 19, figs. 11-14

Bucania simulatrix ULRICH in ULRICH & SCOFIELD, 1897, p. 892, Pl. 63, figs. 48-49, and Pl. 67, fig. 45; CUMINGS, 1908, p. 955, Pl. 42, figs. 9-9a.

Diagnosis. - Shell large (up to 45.6 mm in length), loosely coiled, with large open umbilici; submature whorls subreniform, adult aperture greatly expanded anteriorly with an elongate subtriangular outline.

Description. - Shell large, consisting of about three volutions, loosely coiled so as to create a wide, open umbilicus. Submature whorls rather narrow and depressed, subreniform in outline; dorsum gently convex, lateral angles well rounded, venter concave; throughout growth length gradually increases at greater rate than width, but at adulthood aperture expands anteriorly at even a greater rate, resulting in an elongate subtriangular outline. Posterolateral lip of adult aperture is slightly reflexed; anterior lip curved upward into a fairly deep V-shaped sinus; parietal lip apparently thickened centrally. Dorsomedian ridge over expanded portion of whorl on internal molds reflects an elevated, hollow slit band. No surface markings known.

Measurements. - Measurements of the lectotype of B. simulatrix are given in Table 59. The mode of preservation and fragmentation affected the measurements.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 59: Measurements of lectotype of Bucania simulatrix in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter
315548	45.6	26.8	24.7	31.7	17.6	12.9	9.6	~23.0

Material. - Specimen USNM 315548 (Pl. 19, figs. 11-14) is here designated the lectotype. Its companion syntype remains catalogued under the museum number USNM 45729, which was originally used for both syntypes; it is now a paralectotype. Numerous other unnumbered specimens were also examined in the USNM and MU collections. Two types of preservation were observed. The first type consisted of specimens which were generally micritic, compressed and distorted internal molds. The second type of preservation is nearly as common, and is very similar, consisting of internal molds being coated by a hard glossy resistant layer, most likely representing some portion of the original shell. The type specimens are preserved in this second manner (Pl. 19, figs. 11-14). The lectotype shows a gap between the coil and parietal lip of the expanded aperture, representing a thickened area of the shell now dissolved away (Pl. 19, fig. 13). Possibly some layer of the shell was of a different mineralogy and is retained preferentially, thus accounting for the glossy, thin, calcitic coating on such specimens.

Distribution. - The species is known only from the Whitewater Formation (Richmondian) in the vicinity of Richmond, Indiana.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - A detailed comparison between this species and Salpingostoma richmondensis is presented under the latter species. The primary reason for distinguishing B. simulatrix from that species is the apparent continuation of the dorsomedian ridge, which represents the path of the slit, to the outer margin of the aperture lip in B. simulatrix (Pl. 19, figs. 11-13). B. simulatrix differs from B. pojetai in having a more narrow whorl form and a more elevated selenizone, and in lacking the wrinkle-like growth lines of B. pojetai.

Discussion. - Present evidence supports Ulrich's original claim for distinction of this species from Salpingostoma richmondensis, as the dorsomedian ridge of B. simulatrix (Pl. 19, fig. 11-13) apparently represents the path of a raised, hollow selenizone. However, better preserved material will be required before the differentiation of these species is confirmed.

BUCANIA CRASSA Ulrich, 1897

Pl. 19, figs. 7-10

Bucania crassa ULRICH in ULRICH & SCOFIELD, 1897, p. 893, Pl. 67, figs. 46-48; CUMINGS, 1908, p. 955, Pl. 39, figs. 4-46.

Diagnosis. - Shell large (up to 36 mm in length) dorsal whorl inflated, nearly semicircular, uniformly convex; umbilici moderately small, with sharply rounded shoulders; shell very thick and massive.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell large, thick and massive, rather tightly coiled. Umbilici deep, moderately small, circular in appearance, with sharply rounded umbilical shoulders, and nearly horizontal umbilical slopes. Dorsal whorl inflated, nearly semicircular and evenly convex. Outer aperture lip has broad V-shaped sinus and becomes slightly upturned in maturity; inner and posterolateral aperture lip is massively thickened. Selenizone slightly elevated and moderately wide. Growth lines broadly curved and rather evenly spaced. Revolving threads finer, closely spaced, always intersecting the growth lines at right angles.

Measurements. - Measurements on the lectotype of B. crassa (USNM 315547) are listed in Table 60.

Table 60: Measurements of Bucania crassa (USNM 315547) in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter
~35.8	23.9	19.7	29.2	18.0	15.2	12.9	11.65

Material. - Only Ulrich's two syntypes are known; both are calcitic replicas and were catalogued under USNM 45714. The specimen figured here (Pl. 19, figs. 7-10) is the same one illustrated by Ulrich (1897, Pl. 67, figs. 46-48) and is here designated the lectotype, USNM 315547. The second specimen is designated a paralectotype and left under the number USNM 45714.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - The species is known only from Elkhorn Falls, near Richmond, Indiana, from the Elkhorn biofacies of the Dillsboro Formation (Richmondian), at the top of the Cincinnatian Series.

Comparisons. - There can be no doubt of the distinctiveness of this species. Ulrich (1897) pointed out that its evenly convex, inflated dorsum, as well as its smaller and more abrupt umbilici, readily distinguish it from species such as B. frankfortensis and B. nashvillensis, which each have a more subangular dorsum. He also noted a resemblance between B. crassa (Pl. 19, fig. 9) and B. lindsleyi (Pl. 18, figs. 1-7). B. crassa is closely related to B. lindsleyi, which has both comparable shell markings and a similarly evenly rounded dorsum (Pl. 18, figs. 1-7), but B. crassa has deeper umbilici and a much thicker, more massive shell.

Discussion. - Uppermost Cincinatian rocks represent the last deposition of a regressing Ordovician sea on the Cincinnati Arch Region, and are characterized by coarse grainstones made up of broken and worn skeletal fragments. The strata are further often characterized by thick shelled invertebrates and massive bryozoan colonies, all indicating rather high energy environmental conditions. The massive shell of B. crassa seems to fit well into this picture.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

GENUS KOKENOSPIRA Bassler, 1915

Pl. 20, figs. 9-12

[pro] Kokenia Ulrich and Scofield, 1897, p. 849.

[non] Kokenia Holzapfel, 1895.

Diagnosis. - Shell phaneromphalous, expands gradually; selenizone elevated, flat-topped; shell surface with numerous uninterrupted revolving threads.

Description. - Shell expands gradually and evenly; umbilici moderately wide. Selenizone elevated, flat-topped; adjacent dorsolateral slopes on either side concave; outer dorsolateral slopes and umbilical shoulders convex; umbilical slopes convex to flat. Shell surface is marked by numerous, uninterrupted revolving threads; growth lines very weak, often not visible.

Type species. - Bucaniella esthona, Koken (1889, p. 389), by original designation.

Stratigraphic distribution. - The type species of the genus is known only from Ordovician float in Pleistocene glacial drift at Berlin, Germany. The only other known species, K. costalis, was described by Ulrich and Scofield (1897, p. 883) from the Prosser Formation (Shermanian-Edenian) near Cannon Falls, Minnesota, and was reported from the Ordovician of Frobisher Bay, Baffin Land, by Schuchert (1904). The species is reported here for the first time from the Kope Formation (Edenian) at Cincinnati, Ohio.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - As pointed out by Ulrich and Scofield (1897, p. 882), Kokenospira differs from Tetranota in two significant ways: first, the aperture is much less expanded laterally than it is in Tetranota; and second, the revolving surface lines continue to the aperture, are more numerous, and are more thread-like and less angular than in Tetranota.

The type species, K. esthona (Koken, 1889), was originally placed in Bucanella, but was distinguished from that sinus-bearing genus by its possession of a slit by Ulrich and Scofield (1897).

Discussion. - By its shell form, elevated slit band, and dominant revolving threads, Kokenospira shows a close relationship to Tetranota, the two most likely having evolved from a common ancestral stock. Bucania also had a common ancestry with these two genera. All three genera evolved in the Middle Ordovician.

KOKENOSPIRA COSTALIS (Ulrich and Scofield, 1897)

Pl. 20, figs. 9-12

Kokenia costalis ULRICH & SCOFIELD, 1897, p. 882, Pl. 64, figs. 46-49.

Diagnosis. - Shell moderately small (up to 13.5 mm in length); slit band elevated, flat-topped; six or seven revolving threads on each dorsolateral slope.

Description. - Shell moderately small and apparently rather thin; expands gradually. Umbilici rather large and open. Selenizone distinctly

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

elevated and flat-topped, with fine, sharp, bordering threads. Dorsolateral slopes are concave immediately adjacent to slit band, but rapidly become convex, continuing to be rounded over umbilical shoulders. Whorls reniform in section, aperture length/width ratio being about .60-.65. Growth lines indistinct; each dorsolateral slope with six or seven thin, uninterrupted, revolving threads which continue to aperture margin; first revolving thread adjacent to the slit band weaker than others on dorsal whorl slope, as are additional threads within the umbilicus.

Measurements. - Measurements of K. costalis (UCGM 26519) are listed in Table 61.

Table 61: Measurements of Kokenospira costali (UCGM 26519) in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Umbilical Diameter
13.5	12.0	8.0	12.4	12.5

Material. - Only one specimen of this species was examined, UCGM 26519, a worn and fragmented calcitic replica (Pl. 20, f. 9-12), collected by Leigh Van Valen. The holotype is catalogued under USNM 45868.

Distribution. - Ulrich and Scofield (1897, p. 883) described the species on a single specimen from the Clitambonites bed, Prosser Formation (Shermanian-Edenian), near Cannon Falls, Minnesota. Schuchert (1900, p. 164) reported the species from the "Trenton" of Frobisher Bay, Baffin Land.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The specimen described here comes from the Southgate biofacies of the Kope Formation (Edenian), from a "Pit on Beekman Street, Cincinnati, Ohio."

Comparison. - K. costalis differs from K. esthona (Koken) in having a less prominent slit band and a more rounded shell form. K. costalis may be distinguished from similar species of the genus Tetranota by its more numerous revolving threads which remain distinct to the aperture margin.

Discussion. - This rare species appears to be quite widespread geographically. The specimen described here (UCGM 26519) (Pl. 20, figs. 9-12), compares well with Ulrich and Scofield's (1897) single specimen which was stated to be about 10mm in length. Measurements of the aperture dimensions in the figures of their specimen (Pl. 63, fig. 48) give an aperture length/width ratio of 0.61, closely comparable to the ratio of 0.64 in the Cincinnati specimen. UCGM 26519 clearly shows the centralmost revolving thread to be weaker than the others, but it is difficult to say for certain whether six or seven threads are present on each side.

Subfamily UNDULABUCANIINAE new subfamily

Diagnosis. - Whorls subtrapezoidal to rounded in cross-section; slit long, narrow, generates selenizone; shell surface marked only by closely-spaced, regularly wavy, fine collabral threads, which may or may not intersect.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stratigraphic distribution. - Middle Ordovician (Kirkfieldian) - Upper Ordovician (Maysvillian).

Type genus. - The genus Undulabucania n. gen. is the type and only known genus of the subfamily.

Discussion. - The subfamily Undulabucaniinae is unique in its possession of a deep slit, a characteristic ornament of closely-spaced wavy threads, and a shell form similar to that of the primitive Bucania sulcatina group, with broad-topped, depressed whorls and wide umbilici. The long slit and wavy shell markings suggest descent from the Tropidodiscidae, and most likely from Phragmolites.

GENUS UNDULABUCANIA n. gen.

Pl. 23

Diagnosis. - Shell gradually expanding, with wide, open umbilici; slit very deep; shell ornament of fine, closely spaced, undulating collabral threads, which may or may not intersect.

Description. - Shell of moderate size (about 15-20mm in length), expands gradually and evenly; umbilici wide open. Whorl shape generally subtrapezoidal, but may be much more uniformly rounded. Slit very deep, usually generates channel-like selenizone. Surface sculpturing of fine, closely spaced, undulating collabral threads, which when intersecting form a netlike meshwork. No revolving ornament known, except for threads bordering the selenizone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Type species. - Bellerophon gorbyi Miller, 1982, p. 649, is here designated the type species of the new genus Undulabucania.

Other species placed in Undulabucania. - In addition to the type species, Bellerophon punctifrons Emmons (1842) and Bucania punctifrons primaeva Bradley (1930) are here assigned to Undulabucania n. gen.

Distribution. - Species of the new genus are known from strata ranging in age from the Kirkfieldian (Upper Middle Ordovician) to Maysvillian (Middle Upper Ordovician) stages in eastern North America.

Discussion. - Of the three species included in Undulabucania, U. punctifrons (Emmons, 1842) and U. gorbyi (Miller, 1897) were both originally described as members of the genus Bellerophon, although Hall (1847) transferred U. punctifrons to Bucania. The third species, U. primaeva, was described from the Kimmswick Limestone (Kirkfieldian-Edenian) near Butchtown, Illinois, as Bucania punctifrons primaeva by Bradley (1930, p. 236, Pl. 25, figs. 23-24). This taxon is here regarded to be a distinct species based on its more narrow, somewhat circular whorl form. All three of the above species, but most particularly U. punctifrons and U. gorbyi, have a shell form closely resembling that of species belonging to the Bucania sulcatina group. They have thin shells, broad umbilici, gradually enlarging depressed whorls, a wide, yet not expanded, aperture with thin lips, and a long slit. Although the species of Undulabucania agree well with all of these traits, they differ in one very significant aspect. By definition, species of the genus Bucania possess revolving threads

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

which intersect the growth lines at right angles. The species here included in Undulabucania lack any revolving ornament, except for threads bordering the selenizone; they do have the common presence of fine, undulating growth lines, which intersect, or nearly do so.

The similarity in all characters but shell sculpturing suggests Undulabucania had a common ancestry with the Bucania sulcatina group. As discussed previously, it is likely that Undulabucania and Bucania had a common ancestral connection with the tropidodiscids. That family contains the oldest know slit-bearing bellerophont, Chalarostrepsis Knight, 1948, from the Upper Cambrian of Canada. It is assumed that this genus was of the stock which gave rise to Phragmolites Conrad (1838) and Tropidodiscus Meek and Worthen (1866) in the Ordovician. Undulabucania and Phragmolites have a great deal in common, such as their wide umbilici, long slits, and particularly their wavy growth lines. However, Undulabucania differs from Phragmolites in its lack of any spiral ornament and in its shell form, which closely resembles that of the Bucania sulcatina group. At the present state of knowledge, it seems possible that Undulabucania evolved from a Phragmolites-like tropidodiscid.

UNDULABUCANIA GORBYI (Miller, 1892)

Pl. 23, figs. 10-15

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bellerophon gorbyi MILLER, 1892, p. 694, Pl. 14, figs. 7-9; CUMINGS, 1908, p. 953, Pl. 39, figs. 1-16.

Diagnosis. - Shell with broad, dorsally rounded, subtrapezoidal whorl outline; slit deep and narrow; growth lines fine, wavy, closely spaced but not intersecting.

Description. - Shell moderate in size (about 20mm in length), increasing in size gradually and evenly. Umbilici fairly wide; dorsum of shell evenly and highly convex; umbilicial shoulders narrowly, but well rounded; umbilical slopes flat to slightly convex, and angle rather gently from the shoulders to the lower dorsolateral slope of the previous whorl; ventral whorl is deeply concave as it closely covers the dorsum of the previous whorl. Slit long and narrow, bordered by a fine ridge on either side; selenizone slightly depressed, with fine lunulae. Shell ornament of very fine, closely spaced, nearly equidistant, wavy growth lines which never intersect; growth lines bend back over dorsum reflecting a broad, moderately deep apertural sinus. Only revolving ornament known is the ridges bordering the selenizone. Aperture lips tend to flare laterally slightly in maturity.

Measurements. - Measurements on the holotype of U. gorbyi (UC 6138) are listed in Table 63.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 63: Measurements of holotype of Undulabucania gorbyi (UC 6138) in mm.

Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Slit Length	Selenizone Width
20.5	14.3	12.4	13.5	11.7	9.5	8.8	10.0	15.0	<0.8

Material. - Only one specimen of this species was located, UC 6138, which is the holotype. This well-preserved calcitic replica was collected by S. S. Gorby, after whom it was named, and is deposited in the Gurley Collection at the Field Museum of Natural History, Chicago, Illinois.

Stratigraphic range. - The holotype was collected from Maysvillian (Middle Upper Ordovician) strata in Dearborn County, Indiana. No more specific horizon or locality is given by the original author on the museum label. Maysvillian-aged strata in southeastern Indiana are presently included in the Dillsboro Formation.

Comparisons. - This species is obviously closely related to U. punctifrons, but its whorls are much broader (Pl. 23, fig. 11-12), and its wavy growth lines never intersect, but rather they remain nearly equidistant (Pl. 23, fig. 10).

Discussion. - Superficially, the shell ornament of U. gorbyi appears much like that of U. punctifrons, but on closer examination the wavy growth lines can be seen to remain separate and to never touch one another. Nevertheless, the camouflage effect of the ornament would be the same as in U. punctifrons, which was probably directly ancestral to this species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The slit is very long in U. gorbyi (15mm in length) (Pl. 23, figs. 10-11 and 13-14). As the shell of the holotype is so well preserved, it is doubtful that this impression is false, particularly because lunulae are visible dorsally where the slit was covered by the selenizone, and there the dorsomedian line is barely depressed, whereas anteriorly it is excavated as a deep channel. It should also be noted that the small bump situated about a third of a whorl back on the right side of the slit (Pl. 23, fig. 10) is a small bryozoan colony. This colony may have been so situated on the living gastropod to take advantage of exhalent currents being emitted from the deep slit.

UNDULABUCANIA PUNCTIFRONS (Emmons, 1842).

Pl. 23, figs. 1-9

Bellerophon punctifrons EMMONS, 1842, p. 392, figure 5; LESLEY, 1889, p. 87, figs.

Bucania punctifrons (Emmons) HALL, 1847, p. 187, Pl. 40A, figs. a-e; ULRICH & SCOFIELD, 1897, p. 894, Pl. 67, figs. 41-44; RAYMOND, 1902, Pl. 19, figs. 9-10; WELLER, 1903, p. 177, Pl. 12, figs. 10-12; GRABAU & SHIMER, 1909, p. 614; BASSLER, 1932, Pl. 13, figs. 16-17; WILSON, 1951, p. 27, Pl. 2, figs. 21-23.

Diagnosis. - Shell with relatively large umbilici; aperture outline rounded subtrapezoidal; undulating growth lines intersect to form net-like meshwork.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell of moderate size (up to 20 mm in length), consisting of about three volutions; expands gradually and evenly throughout growth. Umbilici relatively wide for the genus; whorls rounded subtrapezoidal in outline, with evenly and rather deeply convex dorsum and sharply rounded umbilical shoulders, flat and broad umbilical slopes that angle gently inward to shoulder of previous whorl, and a concave ventrum covering the surface of the previous whorl. A aperture shows only very slight flaring as an adult, and has wide, fairly deep anterior sinus; slit quite deep, generating a channel-like selenizone bordered by a thin, sharp ridge on either side. Shell surface covered by evenly undulating, wavy growth lines which intersect to form a fine, slightly raised net-like meshwork; this sculpturing also evident in juvenile whorls visible in umbilicus. Growth becomes coarsely lamellose in later growth.

Measurements. - Measurements of U. punctifrons are listed in Table 62.

Table 62: Measurements of Undulabucania punctifrons in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width	Umbilical Diameter
45727	19.75	14.35	10.35	13.25	10.4	8.65	6.7	0.7	10.8
315547	17.4	12.5	9.0	12.25	10.0	8.15	6.6	0.6	10.3

Material. - Only Ulrich and Scofield's (1897, pl. 67, figs. 41-44) two hypotypes from the Hermitage Formation at Nashville, Tennessee were

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

examined. The first retains the original museum number, USNM 45727 (Pl. 23, figs. 1-4). This well preserved calcitic specimen has a massive bryozoan colony plugging the aperture (probably a post mortem association) and is missing only some of the dorsal shell. The second specimen, here designated USNM 315546 (Pl. 23, figs. 5-9), is very similarly preserved, also missing a small portion of the dorsal shell. Emmon's (1842) original type material was not located and is probably lost.

Distribution. - This species is known from Rocklandian to Edenian rocks throughout eastern North America. Emmons (1842), Hall (1847), Lesley (1889), and Ulrich and Scofield (1897) reported the species from the Trenton group in New York and Canda, Pennsylvania, and Tennessee. Wilson (1951, p. 27) reported it from the Rockland, Sherman Falls, and Cobourg beds (Rocklandian-Edenian) of the Ottawa Formation in the Ottawa-St. Lawrence Lowland, Ontario, Canada. Weller (1903) cited the species from the Trenton Group in New Jersey. Bassler (1932, Pl. 13, figs. 16-17) reported the species from the Hermitage Formation (Kirkfieldian) of central Tennessee, which are the horizon and area where the specimens figured here (Pl. 23, figs. 1-9) were collected.

Comparisons. - The shell form of U. punctifrons is similar to that of members of the B. sulcatina group, particularly B. halli, but its mesh-like shell sculpturing easily distinguishes it. U. punctifrons can be distinguished from U. gorbyi by the intersection of its wavy collabral threads, whereas those of U. gorbyi remain separated.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Hall (1847, Pl. 40A, fig. 1e), and Ulrich and Scofield (1897, Pl. 67, fig. 44), among other authors, have illustrated the shell markings of U. punctifrons as being a regular pitting of the shell surface. As shown here in Pl. 23, fig. 4, this sculpturing is in reality a rather regular netlike meshwork of raised, wavy, intersecting, collabral threads. It may be that this shell pattern served as camouflage for the animal, mingling with the intersecting patterns of light in a shallow subaqueous environment, much like a fishnet. Such an adaptation would be an important protective cover to hide from predators.

Subfamily PLECTONOTINAE Boucot and Yochelson, 1966

Diagnosis. - Shell with raised dorsomedian lobe giving the whorls a trilobed cross-section.

Stratigraphic distribution. - Middle Ordovician - Devonian.

Genera included. - Tetranota Ulrich and Scofield, 1897; Plectonotus Clarke, 1899; Tritonophon Opik, 1953.

Genera covered here. - Tetranota.

Discussion. - Plectonotus was described by Clarke (1899) as possessing a slit generating a selenizone. Knight (1941) redescribed the type material noting only a V-shaped sinus in the aperture margin. Therefore, Knight and others (1960) placed Plectonotus as a subgenus of Bucanella Meek (1871) in the Sinuitidae. Boucot and Saul (in Boucot, Saul, and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Finks, 1963) discovered new material from the Devonian of Ghana which confirmed Clarke's original observation of a slit in the genus. In light of this discovery, Horny (1963) placed Plectonotus near Tetranota in the subfamily Bucaniinae of the Bellerophontidae. Boucot and Yochelson (1966) proposed the subfamily Plectonotinae of the Bellerophontidae, including only the genus Plectonotus. Peel (1974) summarized the information about trilobed bellerophontaceans and analyzed their functional morphology. He accepted the subfamily Plectonotinae and added the genus Tritonophon, placing Nylanderina Boucot (1967) in synonymy with it. Herein, Tetranota is also placed in the Plectonotinae.

The Plectonotinae is transferred to the family Bucaniidae because of their somewhat depressed whorl forms, open umbilici, flairing lateral apertural margins, and common possession of spiral ornamentation.

Tetranota is the earliest known member of the subfamily and therefore may be ancestral to the later genera. Bretsky (1970) reported Plectonotus? from the Upper Ordovician of the Central Appalachians, but these internal molds may actually belong to the widespread Ordovician genus Tetranota. Peel (1974) suggested that Bucanella might also possess a slit, rather than merely a sinus, but presently known material is too poorly preserved to resolve the matter. If it is found that Bucanella is slit-bearing, then it should also be placed in the Plectonotinae. It would thereby be the earliest member of the subfamily, being Early Ordovician in age.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus TETRANOTA Ulrich and Scofield, 1897

Pls. 20-22, 38

Diagnosis. - Shell with selenizone lying on broad, elevated, dorsomedian band often bordered by a pair of revolving threads, with one or two pairs of dorsolateral revolving angular ridges; aperture lip chiefly expanded laterally.

Description. - Shell variable in size, and thin. Umbilici moderate to large in size, deep. Whorls broad and depressed, aperture wider than long throughout growth. In maturity, aperture lips tend to flare, chiefly in the lateral directions. Parietal lip without thickened collosity. Selenizone on broad, elevated, gently convex to nearly flat-topped, dorsomedian band, which generally has revolving threads along its edges; lunulae usually faint. Outward from dorsal band, shell briefly concave to dorsolateral pair of angular revolving ridges; occasionally a second outer pair of dorsolateral ridges also present; pairs of dorsolateral ridges best developed in youth, often gradually becoming indistinguishable in the mature shells. Apertural sinus broad and moderately deep, terminating in wide short slit. Growth lines fine, closely spaced.

Type species. - Bucania bidorsata Hall, 1847, by original designation.

Other North American Ordovician species. - T. sexcarinata Ulrich and Scofield, 1897; T. macra Ulrich and Scofield, 1897; T. obseleta Ulrich and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Scofield, 1897, T. wisconsinensis (Whitfield, 1878), T. charon (Billings, 1860), T. rugosa (Emmons).

Stratigraphic distribution. - In eastern North America, the genus is widely known from strata of latest Chazyan or early Blackriveran to Maysvillian age. Walcott (1884) also reported the type species from the upper Pogonip Group (Blackriveran?) of Nevada.

In Europe, the genus is known only from the British Isles. Reed (1920-21, p. 41) described a possible species from the Lower Ordovician Arenigian Series of England, and three "varieties" of a species from the Stinchar Limestone (Llanvirnian-Llandelian), the Balclatchie Group (Caradocian), and the Drummock Group (Ashgillian) of Girvan. These occurrences are discussed further below.

Discussion. - Of the species presently included in the genus Tetranota, T. bidorsata (Hall, 1847) was originally assigned to Bucania, and T. charon (Billings, 1860), T. rugosa (Emmons), and T. wisconsinensis (Whitfield, 1889) were first placed in Bellerophon. Koken (1889, p. 389) incorrectly placed T. bidorsata with unrelated Silurian-Devonian European species in the sinuate genus Bucanella (for discussion, see Ulrich and Scofield, 1897, p. 876).

Ulrich and Scofield (1897, p. 875) proposed the genus Tetranota for those Ordovician species which are phaneromorphalous, slit-bearing, and possess four revolving ridges on the shell, two bordering an elevated slit band and two dorsolaterally. The lines bordering the slit band are often

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

not well preserved, but when they are (Pl. 21, figures 2-9, and 14), they appear to be quite thread-like. The dorsolateral lines are not thread-like, but rather they are like angled ridges or carinas. In this respect, these dorsolateral revolving ridges are more similar to the revolving ornament of Kokenospira than to the ornament of genera such as Bucania or Bucanopsis. In its gradually expanding, depressed whorls, and in its possession of revolving ornament, Tetranota shows relationship to Bucania and Kokenospira. Besides the difference in the character of the revolving ornament, Tetranota also differs from Bucania in expanding at maturity chiefly only in the lateral directions, rather than anteriorly. In addition to the similarity in the character of the revolving lines, Kokenospira costalis (Pl. 20, figs. 9-12) also bears an elevated, nearly flat-topped, dorsomedian band, similar to that of Tetranota. Therefore Kokenospira and Tetranota may be closely related bucaniid genera, even though they are placed in separate subfamilies.

The earliest occurrences of Tetranota in North America are those of T. bidorsata by Wolcott (1884) from the U. Pogonip Group (Chazyan-Blackriveran) of Nevada, and by Raymond (1908) from Chazyan strata in New York, and Butts' (1926) report of T. cf. T. obseleta from the Little Oak Limestone north of Pelham, Alabama (see here, Pl. 22, figs. 16-18). Drahovzal and Neathery (1971, Table 1) date the Little Oak at late Chazyan to early Blackriveran in age. Reed (1920-21, p. 43) reported T. hippapus (Salter) from the Lower Ordovician Arenigian Series of England, but noted

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(p. 44) that the two known specimens are poorly preserved. Restudy of these specimens is needed for confirmation of this earliest reported occurrence of the genus. Reed also described three "varieties" of T. carrickensis Reed, the earliest being from the Stinchar Limestone, which, interestingly, Bergstrom (1971, p. 114) correlated with the Upper Lenoir Limestone (Porterfieldian) of eastern Tennessee. As shown by Drahovzal and Neathery (1971, Table 1), the upper Lenoir and Little Oak Limestones are time equivalent, therefore correlating the probable confirmed occurrences of Tetranota in Great Britain and North America. Comparisons are difficult with Reed's illustrations, but British species of Tetranota do not appear significantly different from the American species, and upon direct comparison could possibly be found to be synonymous.

As pointed out by Ulrich and Scofield (1897, p. 877), some species of Tetranota are quite long-ranging relative to most other bellerophontaceans. For example, T. bidorsata ranges from Blackriveran through Edenian strata. As far as preservation and present collections allow, specimens of T. bidorsata from widely different stratigraphic levels and geographic localities appear essentially morphologically identical (compare Pl. 22, figs. 1 and 5). Scheltema (1977, p. 105) pointed out that there may be a relationship between larvae dispersal potential, geographic range, and longevity of species. Geographically widespread and stratigraphically wide-ranging species are generally eurytopic and have a greater genetic diversity. Following this line of reasoning, most bellerophontacean spe-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

cies, which are usually quite short-ranging and local, may have been stenotopic, being too narrowly specialized to survive long periods in a constantly fluctuating epicontinental environmental situation. Tetranota bidorsata may be an exception to this scenario, because of its broad geographic and stratigraphic distribution.

TETRANOTA BIDORSATA (Hall, 1847)

Pl. 21, figs. 1-14; Pl. 22, figs. 1-10.

Bucania bidorsata HALL, 1847, p. 186, Pl. 40, figs. 8a-g; 1862, p. 39, fig. 6; CHAMBERLIN, 1883, p. 158, fig. ; WALCOTT, 1884, Pl. 1, figs. 13a-c; LESLEY, 1889, p. 96, figs.

Tetranota bidorsata (Hall) ULRICH & SCOFIELD, 1897, p. 877, Pl. 65, figs. 10-18; WELLER, 1903, p. 176, Pl. 12, figs. 18, 19; RAYMOND, 1908, p. 197, Pl. 50, fig. 5; GRABAU & SHIMER, 1909, p. 612, figs. 819a-d; KNIGHT, 1941, p. 347, Pl. 8, fig. 4; SHIMER & SHROCK, 1944, p. 441, Pl. 177, fig. 119; ?WILSON, 1951, p. 30, Pl. 4, figs. 1-2; STEELE & SINCLAIR, 1971;, p. 19, Pl. 10, figs. 4 and 15.

Diagnosis. - Shell with prominently elevated, broad dorsomedian band with distinct bordering threads and carrying a slightly concave selenizone; dorsolateral slopes with centrolateral grooves between median band and single pair of distinct lateral revolving ridges.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell of moderate size, with maximum known shell length about 22mm. Whorls depressed and subreniform in outline, being more than twice as wide as long, this ratio increasing in maturity where aperture flares laterally somewhat. Umbilici wide and deep; shoulders squared-off and angular in specimens retaining the shell, appearing tightly rounded in internal molds. Dorsum with prominently elevated, broad, median band, which carries slightly concave selenizone with fine but distinct lunulae, bordered by two angular revolving threads; occasionally, median line visible down axis of selenizone. Median band appears as broad flat-topped to rounded ridge in molds. Outward from the dorsomedian band is a pair of centrolateral concave grooves, followed by a pair of angular, slightly elevated ridges; lateral ridges distinct in small to moderate sized shells, but as known from molds only, tend to disappear in maturity, the dorsal slopes flattening and flaring laterally; outer dorsal slope nearly flat to the angular umbilical shoulder. Growth lines very fine, closely spaced, and quite distinct, being nearly straight, though angled slightly toward the posterior on the outer slopes, then increasing in their curvature from the dorsolateral ridges to the median band; fine collabral threads pass over the dorsolateral ridges uninterrupted.

Measurements. - Measurements of T. bidorsata are listed in Table 64.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 64: Measurements of Tetranota bidorsata in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width	Width of Lateral Ridges
AMNH Fl										
29592	~20.0	~16.5	--	--	--	--	--	--	--	--
787	--	--	--	--	--	--	--	--	2.2	~7.2
29594	18.0	~14.0	14.5	16.7	~14.0	~9.3	~8.5	11.6	~2.8	~8.9
29593	~21.0	--	~13.1	24.1	15.2	13.3	--	12.0	~4.0	--
USNM										
17301	20.5	14.9	9.3	23.6	~13.0	--	8.2	6.4	3.0	--
47545	22.0	--	12.25	34.9	16.3	14.5	--	9.8	3.0	--
UCGM										
44291a	--	--	--	--	--	--	--	--	1.8	8.1
44291b	--	--	--	--	--	--	--	--	2.1	8.4
44292	~16.1	~13.0	~8.5	~18.0	--	11.4	--	8.5	2.0	9.0
44293	--	--	--	--	--	--	--	--	1.9	~10.0
44294	--	--	--	~12.1	--	--	--	--	1.4	6.5

Material. - Hall's (1847) type suite was examined. Specimen AMNH Fl 29592 (Pl. 21, figs. 12-13) (Hall, 1847, Pl. 40, figs. 8c, d) was designated the lectotype by Knight (1941, p. 347, Pl. 8, fig. 4). That specimen retains part of the shell, but all the paralectotypes, AMNH Fl 29593 (Pl. 22, fig. 1), AMNH Fl 29594 (Pl. 22, figs. 2-4), AMNH Fl 29595, and AMNH Fl 787 (Pl. 21, fig. 14), are all black, micritic, internal molds. Walcott's (1860, Pl. 1, fig. 13) specimen from Nevada is also largely an internal mold, but retains some shell on the left antero-dorsal slope (Pl. 22, figs. 5-10).

Ulrich and Scofield (1897, Pl. 65, fig. 24) illustrated a specimen they identified as T. sp. indet. from Edenian strata at Cincinnati. They favored an identification as T. obsoleta rather than T. bidorsata because

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of the "obsolescence of the latero-dorsal ridges." This specimen, USNM 47545 (Pl. 21, figs. 9-11), is here identified as T. bidorsata, and is discussed further below. Some small, partially crushed specimens of the species, UCGM 44308 and 8695, were found in other collections from Edenian strata of the Cincinnati area.

Five well preserved specimens retaining the shell, UCGM 44291a, 44291b, 44292, 44293, and 44294 (Pl. 21, figs. 1-8), were collected by me, John Pojeta, Jr., and William Harrison from a mollusk bed in Edenian strata east of Cincinnati (Locality OH-1 - Bear Creek Quarry). To my knowledge, these are the best preserved specimens of T. bidorsata available, and they clarify features poorly shown in the lectotype.

Stratigraphic distribution. - Ulrich and Scofield (1897, p. 878) listed T. bidorsata from Blackriveran to Edenian strata throughout eastern North America, including New York and adjacent Canada, West Virginia, Kentucky, Tennessee, Ohio, and Minnesota. Weller (1903) reported the species from numerous horizons in the "Trenton limestone" of New Jersey. Raymond (1908, p. 197) tentatively identified specimens from Chazyan strata on Valcour Island, New York as T. bidorsata. Walcott (1884) reported the species from the Upper Pogonip Group (Whiterockian-Blackriveran) in the White Pine District of Nevada. Wilson (1951) and Steele and Sinclair (1971) reported the species from Blackriveran and Rocklandian strata in eastern Canada.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

The new specimens shown here are five well preserved calcitic replicas from the Kope Formation (Edenian) at Bear Creek quarry (Locality OH-1), located in the bluffs on the north side of the Ohio River, on the northeast corner of the junction of Ohio Route 52 and Bear Creek Road, between Neville and Chilo, Ohio. The specimens came from a lenticular mollusk bed about 10 feet above the Point Pleasant tongue of the Clays Ferry Formation (Shermanian), where they were associated with abundant specimens of Sinuites granistriatus, as well as sparse specimens of C. (Cyrtolites) claysferryensis, small lophospirids, and orthoconic nautiloids.

Comparisons. - T. bidorsata may be distinguished from T. wisconsinensis (Pl. 38, figs. 13-16) by its prominent dorsolateral revolving ridges (Pl. 21, figs. 1-14, Pl. 22, figs. 1-10). Otherwise, the two species are quite similar. T. sexcarinata is somewhat more globose than T. bidorsata and has a second pair of lateral ridges.

Discussion. - T. bidorsata is unusually long-ranging stratigraphically and widespread geographically for a bellerophontacean. This situation may be a result of the similar appearance of internal molds of a group of closely related species. Most known specimens are internal molds. Comparing steinkerns from New York (Pl. 22, figs. 1-4), Ohio (Pl. 21, figs. 9-11), and Nevada (Pl. 22, figs. 5-10), all appear to have the same depressed, laterally spreading whorls, the same broad, elevated dorsomedian band, and the same low rounded lateral ridges. The last two

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of these specimens retain some remnant of the shell, and both show fine closely spaced growth lines. Besides the lectotype of the species (Pl. 21, figs. 1-13), the only specimens preserving a significant portion of the shell are five new specimens collected from the Edenian portion of the Kope Formation in southern Ohio (Pl. 21, figs. 1-8). These specimens are mostly deeply embedded in fairly compact mudstone, but they nevertheless show, for the first time, the true form of the shell and nature of the ornament. They show that the lateral revolving lines are not cords, but angular ridges over which the growth lines pass essentially uninterrupted. They also confirm the presence of a dark median line along the selenizone (Pl. 21, figs. 2-3), which is also visible in the lectotype (Pl. 21, fig. 13). This median line is of unknown origin.

Specimen USNM 47545 (Pl. 21, figs. 9-11), an internal mold, was identified as T. obseleta? by which Ulrich and Scofield (1897, Pl. 65, fig. 24) because of the "obselescence of the latero-dorsal ridges," but, as shown here (Pl. 21, figs. 9-11), there are faint low ridges over the dorsal slopes of the specimen, and the form of the shell, flaring of the adult aperture, and large umbilicus, clearly show that the specimen is T. bidorsata.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

TETRANOTA OBSELETA Ulrich and Scofield, 1897

Pl. 20, figs. 13-15; Pl. 22, figs. 16-21

Tetranota obseleta ULRICH & SCOFIELD, 1897, p. 880, Pl. 65, figs. 19-23; GRABAU & SHIMER, 1909, p. 613, figs. 819i-k; BASSLER, 1919, p. 310, Pl. 55, figs. 22-24; BUTTS, 1926, Pl. 26, figs. 12-13; SHIMER & SHROCK, 1944, p. 441, Pl. 177, figs. 20-21.

Diagnosis. - Shell relatively tightly coiled, umbilici relatively small; dorsum evenly rounded, nearly semicircular, with a low broad median band, and a single pair of weak dorsolateral ridges which disappear by adulthood.

Description. - Shell small (up to about 14 mm in length), thin, and rather tightly coiled; umbilici small and deep for the genus. Aperture shape subelliptical to nearly semicircular; umbilical slopes flat, slightly sloped to nearly horizontal; umbilical shoulders tightly rounded; dorsum evenly rounded. No distinct parietal lip over previous whorl surface at base of aperture. Dorsomedian band slightly elevated, slightly concave, and bordered by distinct revolving threads; band gradually widens with growth. Low angular dorsolateral ridges present on juvenile whorls, but disappear toward maturity. No lunulae or growth lines well preserved.

Measurements. - Measurements on T. obseleta are listed in Table 65.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 65: Measurements of Tetranota obseleta in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Umbilical Diameter	Selenizone Width	Posterior Width
46014	13.8	11.0	7.8	16.2	4.4	2.4	7.2
71496	11.7	10.2	5.35	11.35	4.3	1.5	--
315541	9.5	--	4.2	9.9	4.0	1.2	--

Material. - Three specimens were examined, all of which are silicified. Specimen USNM 46014 (Pl. 22, figs. 19-21) is here designated the lectotype. Specimen USNM 71496 was previously figured by Butts (1926, Pl. 22, figs. 16-18) as T. cf. T. obseleta, and is accepted as a valid member of the species here. Specimen USNM 315541 (Pl. 20, figs. 13-15) is a fragment of a little more than a half-whorl here referred to T. cf. T. obseleta.

Distribution. - Ulrich and Scofield (1897, p. 880) cited T. obseleta from Blackriveran and Shermanian-aged strata in Minnesota and Wisconsin, from Blackriveran-aged strata in Mercer Co., Kentucky, and Edenian-aged strata in the vicinity of Cincinnati, Ohio. Bassler (1919, p. 310-311) reported it from the Edenian-aged portion of the Martinsburg Shale in Maryland. Butts (1926, Pl. 26, figs. 12-13) found the species in the Little Oak Limestone north of Pelham, Albama, which Drahovzal and Neathery (1971, Table 1) date as latest Chazyan to early Blackriveran in age.

One specimen of T. cf T. obseleta, USNM 315541, was found in USGS silicified collection 6131-CO from the Upper Curdsville Member of the Lexington Limestone (Kirkfieldian) of Central Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - Specimens of this species examined here are smaller than average specimens of T. bidorsata, T. sexcarinata, or T. wisconsinensis, but Ulrich and Scofield (1897, p. 880) cited specimens up to 30mm in length. T. obseleta differs from T. bidorsata and T. sexcarinata in lacking any lateral revolving ridges in adulthood, and having only a weak pair as a juvenile. T. wisconsinensis, which is known only from dolomitic steinkerns, also seems to lack dorsolateral revolving ridges in adulthood, but it is easily distinguished by its smaller umbilicus and by the form of its adult whorl, which is more similar to that of T. bidorsata in its lateral flaring and its flattened anterior slope.

Discussion. - T. obseleta is regarded as a species the genus Tetronata because of the presence of a pair of dorsolateral ridges on the juvenile whorls of the lectotype (Pl. 22, figs. 19-21), and on the small specimen USNM 315541 (Pl. 20., figs. 13-14). Similar to T. bidorsata and T. sexcarinata, this species is widely distributed geographically and stratigraphically.

TETRANOTA SEXCARINATA Ulrich and Scofield, 1897

Pl. 22, figs. 11-15

Tetronata sexcarinata ULRICH & SCOFIELD, 1897, p. 878-9, Pl. 65, figs. 3-9; GRABAU & SHIMER, 1909, p. 613, figs. 819, figs. 819e-h, 1; SHIMER & SHROCK, 1944, p. 441, Pl. 177, figs. 9-11; WILSON, 1951, p. 31, Pl. 4, figs. 10-11.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Diagnosis. - Shell relatively large (up to 22.6 mm in length) dorsum broad; two pairs of dorsolateral ridges on either side of elevated dorsomedian selenizone.

Description. - Shell relatively large and inflated for the genus, broader over dorsum than other species; umbilici wide and open. Dorsomedian band wide, distinctly elevated, and only slightly concave; bordering ridges somewhat indistinct. Two pairs of angular dorsolateral ridges present, with broad grooves between each; area between outer dorsolateral ridge and angular umbilical shoulder narrower and only slightly concave to flat. Lunulae of selenizone are poorly known, but appear to have been straight. Growth lines are raised threads, rather widely spaced for genus, and distinct on the umbilical slopes as well as dorsally, where they increase in their backward deflection across each dorsolateral ridge; these lines reflect a broad sinus, narrowing to a rather deeply set squared-off slit.

Measurements. - Measurements of T. sexcarinata are listed in Table 66.

Table 66: Measurements of Tetranota sexcarinata in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter	Selenizone Width	1st Ridge Width	2nd Ridge Width
46018	23.6	22.6	13.3	25.3	16.9	12.7	3.9	11.75	18.73
47712	18.8	15.0	7.7	7.9	8.5	8.9	2.6	7.2	11.35

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - No new specimens of T. sexcarinata are described here. Ulrich and Scofield's (1897) type specimens (USNM 46016-46018) are all from the Minnesota-Illinois area. USNM 46018 is here designated the lectotype (Pl. 22, figs. 14-15). This specimen appears to be a recrystallized calcitic replica. The only other specimen figured for this study (USNM 47712) (Pl. 22, figs. 11-13), is an internal mold from Tennessee that clearly shows the outer pair of lateral ridges.

Distribution. - The lectotype, USNM 46018, is from the Fusispira bed of the Prosser Formation (Shermanian) at Wykoff, Minnesota. The paralectotypes are from the Platteville Formation (Rocklandian); USNM 46017 from the Vanuxemia bed at Minneapolis, Minnesota, and USNM 46016 is from Dixon, Illinois. USNM 47712 comes from the Lebanon Formation (Blackriveran) at Lavergne, Tennessee. Wilson (1951, p. 31) reported the species from numerous localities in the Ottawa-St. Lawrence Lowland of eastern Canada, from beds ranging from Blackriveran to at least Edenian in age. In summary, T. sexcarinata has been reported from Blackriveran to Edenian-aged strata throughout eastern North America.

Comparisons. - T. sexcarinata is similar to T. bidorsata (Hall), but differs in being larger and broader, in having six rather than four revolving lines of ornament, and in having slightly coarser and more widely spaced growth lines.

Discussion. - With the discovery of the new specimens of T. bidorsata from the Kope Formation of Ohio (Pl. 21, figs. 1-8), it is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

possible for the first time to make clear side-by-side comparisons between that species and T. sexcarinata (Pl. 22, figs. 14-15). Although the differences stated above are clear, there can be little doubt that the two species are closely related. It is interesting that they share a very similar stratigraphic distribution, being known over most of eastern North America from Blackriveran to Edenian strata. The main differences in their distributions is that T. bidorsata is apparently more common, and has also been reported from western North America.

TETRANOTA WISCONSINENSIS (Whitfield, 1878)

Pl. 38, figs. 13-16

Bellerophon wisconsinensis WHITFIELD, 1878, p. 7y; 1882, p. 223, Pl. 26, figs. 15-16.

Tetranota wisconsinensis (Whitfield) ULRICH & SCOFIELD, 1897, p. 881, Pl. 65, figs. 26-29; SHROCK & RAASCH, 1937, p. 558-9, Pl. 8, figs. 1-9.

Diagnosis. - Shell rather large (up to 21.4 mm in length), whorls broad and depressed; adult aperture lip expanded, mainly laterally; dorsolateral ridges present in juveniles, lacking in adults.

Description. - Shell large, tightly coiled, consisting of 2-1/2 to 3 whorls in adult. Whorls broad and depressed. Dorsomedian band wide and distinctly elevated; selenizone as a groove between two prominent, rather

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

thick cords. Dorsal slopes broad showing low dorsolateral ridges in juvenile whorls, these gradually disappearing during ontogeny; umbilical shoulders tightly rounded; umbilical slopes cut steeply inward; umbilici moderately small and deep. At maturity, aperture expands laterally and anterior slope flattens somewhat; expanded aperture has broad sinus which ends in wide slit having nearly parallel sides, and an arch-shaped termination. Ornament unknown.

Measurements. - Measurements of T. wisconsinensis are listed in Table 67.

Table 67: Measurements of Tetranota wisconsinsensis in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Ventral Width	Umbilical Diameter	Selenizone Width
158279	21.4	14.75	12.4	23.95	8.15	7.4	3.5

Material. - The holotype was not located, but Shrock and Raasch's (1937, Pl. 8, fig. 1) hypotype (USNM 158279) was examined and is shown here in Pl. 38, figs. 13-15.

Small collections of unnumbered specimens of the species were also examined at the University of Cincinnati and Miami University Geology Museums. One specimen, MU 251T, is shown here because of its excellent preservation of the slit (Pl. 38, fig. 16). All known specimens of the species are dolomitized steinkerns.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - Ulrich and Scofield (1897, p. 881-82) reported the species from the Blackriveran strata of Minnesota and Wisconsin. Bassler (1915, p. 1271) specified these occurrences as being from the Plattville Formation. Shrock and Raasch (1937, p. 558-59) also cited the species as occurring in the Platteville Formation at McCray quarry, Kentland, Indiana. While the Platteville has traditionally been considered Blackriveran in age, Sweet and Bergstrom (1976, text-Fig. 3) indicated that it is Rocklandian in age.

Comparisons. - T. wisconsinensis is distinguished from T. obseleta by its laterally expanded adult aperture and its more prominent dorsal band, but shares with that species the loss of the dorsolateral ridges in maturity.

The depressed whorls, prominent dorsal band, and laterally expanding adult aperture allies T. wisconsinensis with T. bidorsata, but I. wisconsinensis lacks the adult dorsolateral ridges generally so prominent (even in steinkerns) of T. bidorata. For example, compare Plate 38, figs. 13-15, and Plate 22, figures 5-10. The possibility exists that T. wisconsinensis might eventually be placed in synonomy with T. bidorsata if specimens retaining the shell are found to retain dorsolateral ridges in adulthood.

Discussion. - Although T. wisconsinensis is from just outside the present area of study, and actually from an adjacent faunal province, T. wisconsinensis is briefly considered here because of its morphological

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

similarity to T. bidorsata. These two species are without a doubt closely related and might both have evolved from an earlier simpler stock represented by T. obseleta. If the pattern of continuing accentuation of the dorsal ridges in Tetranota is substantiated as new material accumulates, then T. sexcarinata could be considered a more advanced species. It is then likely that Tetranota developed from an early bucaniid such as Eobucania Kobayashi, which had revolving lines only along the borders of the selenizone. However, the tendency toward reduction of the dorsolateral ridges during ontogeny in T. obseleta, T. wisconinensis, and to some extent in gerontic specimens of T. bidorsata, suggest an opposite evolutionary trend. This problem can only be resolved when more specimens of all North American species of Tetranota are available.

Subfamily SALPINGOSTOMATINAE Koken, 1925

Diagnosis. - Shell with wide umbilici; submature whorls depressed and gradually expanding, aperture greatly expanded at maturity; slit long and open on adult whorl, being closed off anteriorly; selenizone generated over submature whorls.

Stratigraphic distribution. - Middle Ordovician - Middle Silurian.

Genera includes. - The only genus included in this subfamily at the present is Salpingostoma Roemer, 1876, which is considered below.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Koken (1925) erected the subfamily Salpingostomatinae of the family Bellerophontidae McCoy, 1851, including only Salpingostoma itself. Knight and others (1960, p. 180) made this taxon into the tribe Salpingostomatides of the subfamily Bucaniinae, family Bellerophontidae, including the genera Salpingostoma and Tremanotus, and defining the group based on the presence of an exhalent orifice consisting of one or more tremata. Horny (1962), on the other hand, elevated the subfamily to the family rank, including the genera Salpingostoma, Tremanotus, and a new genus Boiotremus Horny from the Upper Silurian and Lower Devonian of Bohemia. Boiotremus included species previously assigned to Tremanotus, but which developed tremata throughout ontogeny, rather than merely during adulthood. Boiotremus seems to have evolved directly from the Lower Silurian Tremanotus. The generic turnover may have been paedomorphic in nature, that is, involving maturation at the juvenile stage of development. Sprinkle and Bell (1978, p. 82) have pointed out that: "Organisms entering new niches or colonizing new environments different from or marginal to their ancestral range often show large and rapid evolutionary changes in their morphology, life history, and mode of reproduction". Horny (1962, p. 65, fig. 6) showed that Tremanotus occurs in a largely clastic sequence of strata, and occupied (p. 67) "a hard bottom of tuffaceous and organic debris" in shallow seas near volcanic islands; whereas Boiotremus occurs in an immediately overlying carbonate sequence of bituminous limestones in the Upper Silurian and biohermal facies in the Lower

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Devonian. This regional change in sedimentologic conditions may have encouraged the proliferation of forms developing tremata at early growth stages.

Peel (1972) was of the opinion that Salpingostoma was only homeomorphic with Tremanotus and Boiotremus, pointing out that while Salpingostoma possessed a slit throughout its ontogeny, the other two genera were merely sinuate, and that their tremata were formed by repeated expansion of the aperture and concommitant closing off of all but the deepest portion of the sinus. He therefore rejected Horny's (1962) familial grouping, transferring Salpingostoma back to the subfamily Bucaniinae (as in Knight and others, 1960), and erected the new subfamily Tremanotinae of the family Sinuitidae for the other two closely related genera.

Peel's (1972) emendation seems valid as the basic difference in the development of the shells of Salpingostoma and Tremanotus-Boiotremus would seem to indicate quite different origins. The separation of the Salpingostomatinae into a separate subfamily of the Bucaniidae expresses the close resemblance of Salpingostoma to some species of Bucania in most characters save the morphology of the long closed-off slit.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus SALPINGOSTOMA Roemer, 1876

Pls. 24-26

Diagnosis. - Adult shell having expanded, trumpet-like aperture, and a long open slit extending from dorsum to slightly inside the outer lip where it is closed-off.

Description. - Shell generally large, involute, with wide open umbilici revealing numerous earlier volutions; submature whorls often vertically depressed, subreniform, and submature aperture plane level with ventral umbilical shoulder; at maturity, aperture abruptly expands to trumpet-like form and becomes tangentially oriented toward coil; submature whorls with selenizone; mature expanded whorl with long open slit extending from dorsum to near outer sinuate aperture margin where it is closed off; shell surface often marked by transverse and radial ornament.

Type species. - Bellerophon megalostoma Eichwald, 1840, by monotypy.

Distribution. - Middle Ordovician (Blackriveran) - Middle Silurian (Niagaran) of North America. In Europe, the genus supposedly appears lower in the Middle Ordovician (Koken, 1925) and continues at least to the end of the Ordovician.

North American species. - S. billingsi Wilson; S. buelli (Whitfield); S. kentuckyense Ulrich and Scofield (formerly S. buelli kentuckyense); S. canadense (Billings); S. expansa (Hall); S. fraternus (Billings); S. imbricata Ulrich and Scofield; S.(?) lata Foerste;

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. richmondensis Ulrich and Scofield; and S. sculptilis Ulrich and Scofield are all Ordovician species. Peel (1972, p. 420) listed 4 North American Silurian species of Salpingostoma; S. boreale Whiteaves; S. dilatus (Sowerby); S. inornatum Northrop; S. orientalis Twenhofel; all coming from Canada.

Discussion. - The genus Salpingostoma was proposed by Roemer (1876) for Bellerophon megalostoma Eichwald, 1840, from the Ordovician of Estonia. Koken (1925) later listed 15 species from the Orodvician of the Baltic area. However, Koken's generic assignments and species should be reevaluated, as he recognized cephalopod-like chambers in one supposed species, S. locator (Eichwald) (Koken, 1925, p. 26).

Adult specimens of Salpingostoma are easily recognized by their expanded trumpet-like aperture and long open slit. The slit is recognizable on internal molds as a long dorsal ridge that ends rather abruptly just inside the apertural lip (Pl. 24, figs. 1-3; Pl. 26, figs. 1-3, 6). But in immaturity before the above morphological features are developed, the genus is not nearly so distinctive. Ulrich and Scofield (1897, p. 897) believed that juvenile specimens "correspond in nearly every respect with the whole adult shell of the most typical species of Bucania". They proposed that there was a progressive development from one genus to another in a series Bucania - Salpingostoma - Tremanotus. They stated (p. 900): "In the first the aperture is never greatly expanded, in the second it flares abruptly at maturity, while in the third the expanded

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

mouth is developed at more or less frequent intervals". They further suggested that the resemblance of the external sculpturing of these three genera demonstrated their close generic relationship.

Koken (1925) disagreed with Ulrich and Scofield's (1897) interpretations concerning not only their progressive evolutionary sequence, but even their generic identification of the American species. Koken apparently believed that the American species assigned to the genus Salpingostoma by Ulrich and Scofield should actually be placed in his Bucania cornu group, which he asserted to have had a different derivation from that of the true Salpingostoma group. Koken claimed that the style of ornament of S. buelli (Whitfield) from the Middle Ordovician of Minnesota was more like that of a Bucania and that its slit was situated too far anterior. He further pointed to S. sculptilis Ulrich and Scofield as clearly being derived from a Bucania, as shown by its ornament, slit, and selenizone. Koken noted Ulrich and Scofield's (1897) claim that Salpingostoma should include shells where the inner volutions resemble the adult shell of Bucania sulcatina (Emmons), and it is only in the fully mature specimens that the peculiarities of the genus are apparent. Koken stated that this claim further demonstrated that the American species differed from the type species of the genus. Koken did not believe juvenile specimens of the type species resembled Bucania, and that the type species was distinct throughout growth. In Koken's generic description he claims that in many specimens, and particularly juveniles, the shell is characteristically

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

wrinkled, the wrinkling being independent of the thread-like growth lines, and also distinct from the wrinkled spiral lines of Bucania. Some of his figures of species of Salpingostoma (Koken, 1925, Pls. 19-21) show this transverse wrinkling, others do not. It should be noted that some of Reed's (1921, Pl. 12, figs. 1-2) species from the Ordovician of Great Britain also show rather strong transverse wrinkling. However, the American species illustrated by Ulrich and Scofield (1897, Pls. 67 and 82) do not. Koken (1925, p. 27-28) concluded that Salpingostoma and Bucania are completely unrelated, but that several species of Bucania in the submature state are misleadingly similar to the true Salpingostoma. He further concluded that Tremanotus and Salpingostoma are not directly related because of the differences in the production of the expanded aperture in the two genera, being abrupt and occurring only once (at maturity) in Salpingostoma, but occurring periodically in Tremanotus.

Although American species of Salpingostoma lack the marked transverse wrinkling of the shell present in many of the European species, this does not seem to be adequate justification for generic differentiation. The common features shown by both the American and European species (expanded aperture, long closed-off slit, shell markings) are too numerous and seem to indicate a close relationship.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SALPINGOSTOMA BUELLI (Whitfield, 1878)

Pl. 24, figs. 1-9

Bucania buelli WHITFIELD, 1878, p. 76; CHAMBERLAIN, 1883, p. 158, fig. 33f.

Bucania (Tremanotus?) buelli WHITFIELD, 1882, p. 224, Pl. 6, figs. 12-14.

Salpingostoma buelli (Whitfield) WHITEAVES, 1897, p. 189; ULRICH & SCOFIELD, 1897, p. 900, Pl. 67, figs. 34-37; GRABAU & SHIMER, 1909, p. 614, figs. 823a-c; SHIMER & SHROCK, 1944, p. 443, Pl. 177, figs. 14-16; KNIGHT and others, 1960, figs. 96-6a,b.

Diagnosis. - Moderately large Salpingostoma (up to 48.5 mm in length) with expanded adult aperture extended anteriorly into a long, slightly recurved apron; shell surface entirely sculptured by curving transverse growth lines and thin, nodular, revolving threads, the latter increasing in strength on expanded aperture with a smaller set being interpolated between, giving an alternating pattern; adult shell length/umbilical diameter is 2.17.

Measurements. - Measurements for S. buelli are listed in Table 68.

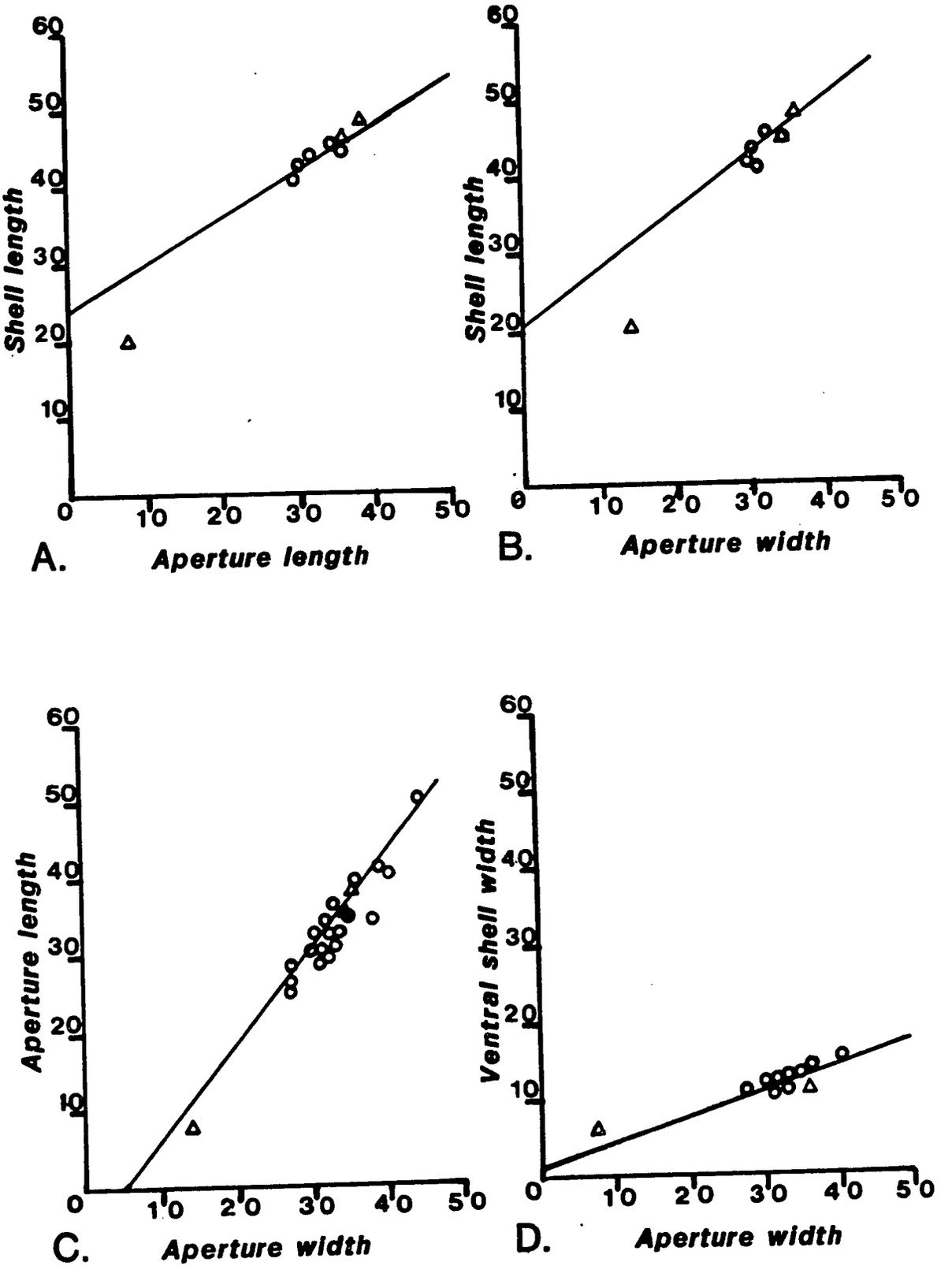
Table 68: Measurements of Salpingostoma buelli in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Shell Height	Umb. Diam.	Dorsal Width	Post. Width	Ventral Width
USNM								
265957	20.55	7.4	13.95	22.0	8.0	11.85	8.85	5.85
45980	46.3	35.4	34.3	22.0	21.3	15.5	13.2	-
47590	48.5	38.4	36.0	-	-	-	-	11.09

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 31: Bivariate plots of measurements made on specimens of *Salpingostoma kentuckyense* and *S. buelli*.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Two dolomitized specimens from a set of 5 of Ulrich and Scofield's (1897) hypotypes (USNM 45980) have been selected for illustration here. USNM 265957 (new no.) (Pl. 24, figs. 6-8) is a submature internal mold; USNM 265960 (new no.) (Pl. 24, figs. 1-5) is an adult specimen which preserves part of the shell around the expanded aperture margin, the remainder of the specimen being a composite mold retaining an impression of the shell ornament pattern. These specimens come from the Platteville Formation (Rocklandian) at Beloit, Wisconsin. USNM 45790 (Pl. 24, fig. 9) is a dark gray calcitic (partly carbonaceous?) replica which is embedded in gray, finely crystalline biosparite from the Platteville Formation of Minnesota.

Distribution. - Ulrich and Scofield (1897, p. 901) reported S. buelli from the "Stones River Group" of Minnesota and the "Black River Group" of Wisconsin, which translate into the presently recognized Platteville and Decorah Formations (Rocklandian-Kirkfieldian) (Weiss, 1957; Sweet and Bergstrom, 1976). Weiss (1957, fig. 1) reported Salpingostoma sp. from the Cummingsville member of the Galena Formation (Kirkfieldian-Shermanian) of Minnesota, and this probably also represents S. buelli. Bassler (1915) cited the species from Wisconsin, Minnesota, Illinois, and Manitoba.

Comparisons. - See this heading under S. kentuckyense (Ulrich and Scofield).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - This species is not represented in the fauna of the Cincinnati Arch region, but is considered here for comparison with S. kentuckyense (Ulrich and Scofield), which was originally designated a subspecies of S. buelli.

Specimen USNM 265957 (Pl. 24, figs. 6-8) is apparently a specimen on the verge of maturity, just before the aperture began its abrupt expansion, because the shell height of this specimen is equal to that of an expanded adult specimen (USNM 265960, Pl. 24, figs. 1-5). Note that this submature specimen of S. buelli is nearly identical with a submature specimen of the stratigraphically younger species S. richmondensis Ulrich and Scofield (Pl. 24, figs. 13-16), although the relative proportions are slightly different. All submature specimens of the genus examined here have the plane of the aperture at a level with the ventral umbilical shoulder. This nearly radial orientation of the apertural plane of juveniles may indicate a much less mobile life style than led by the adult, which possesses a tangential aperture. This interpretation is in accordance with Linsley's (1978) observations of modern conispiral gastropods, whose shells with radial apertures are generally very sluggish or even sedentary. Also note the depressed form of the juvenile whorls (Pl. 24, fig. 8), which would seem to make the shell rather awkward to balance in a highly active organism. As pointed out in the discussion of S. kentuckyense, the earlier whorls of the submature coil are quite thin-shelled, which may have alleviated this awkwardness to some degree.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Specimen USNM 265960 (Pl. 24, figs. 1-5) is an adult of S. buelli. The shell around the aperture margin shows how the lip was expanded far to the anterior as an apron. On the portion of the specimen where the shell is lacking, there is a prominent dorsomedian ridge over the anterior slope. This ridge is the reflection of the long open slit of the shell. Lateral to this ridge, the mold becomes composite and the external sculpturing is preserved (Pl. 24, figs. 1-3). The sculpture consists of growth lines that curved back toward the slit, and thin parallel revolving threads. Specimen USNM 47590 (Pl. 24, fig. 9) was photographed without whitening for better definition. This specimen shows the shape of the aperture, with its anterior sinus and wide anterior marginal apron.

SALPINGOSTOMA KENTUCKYENSE (Ulrich and Scofield, 1897)

Pl. 24, figs. 10-12; Pl. 25, figs. 1-14; Pl. 26, figs. 11-12

Salpingostoma buelli var. kentuckyense ULRICH & SCOFIELD, 1897, p. 901.

Diagnosis. - Shell moderately sized (up to 45.5 mm in length) expanded aperture rim thickened and massive, not strongly reflexed anteriorly; shell markings restricted to external rim of expanded aperture, consisting of coarse spiral ribs and growth lines; adult shell length/umbilical diameter ratio is 2.70.

Description. - Shell moderately large, relatively thin on submature portion, becoming thick and massive on mature expanded aperture; volutions

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

numerous, visible in wide open umbilici; sutures deeply impressed; submature whorls depressed, subreniform, with dorsum broadly convex, umbilical shoulders narrowly rounded, venter slightly concave; whorl size increases quite gradually until maturity, where aperture abruptly expands and thickens; shell length/umbilical diameter ratio in adults averages 2.70; expanded aperture may slope anteriorly to margin, or may reflex slightly to form short apron; anteromedian sinus quite shallow; dorsomedian slit extends from dorsum down the anterior slope where it is closed well within the anterior apertural margin; selenizone distinct, narrow, appears as rounded cord; posterior expanded aperture with broad re-entrant around previous whorl; outer parietal rim of expanded aperture where coil rests often bears coarse chevron-like wrinkles angling outward and downward; submature shell surface smooth; mature expanded shell surface marked by coarse radiating ribs and fine to lamellose growth lines.

Measurements. - Measurements of S. kentuckyense are listed in Table 69 below and accompanying plots are shown in Figure 31.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 69: Measurements of Salpingostoma kentuckyense in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Dorsal Width	Ventral Width	Shell Height	Umb. Length	Umb. Height
USNM								
265961	43.5	32.4	31.0	-	-	28.7	-	-
265964	42.4	30.7	30.2	18.8	11.65	23.3	19.15	13.95
265965	41.2	29.75	31.5	18.25	10.9	22.5	15.0	13.6
265966	-	30.1	31.3	-	-	-	-	-
265979	-	32.8	32.85	-	11.45	-	-	-
265980	45.25	35.05	35.00	17.25	13.05	-	16.5	14.5
265980	-	49.75	45.00	-	-	-	-	-
265980	45.3	36.6	33.0	19.8	12.5	22.5	17.3	15.0
265980	-	32.85	33.7	-	-	-	-	-
265980	-	31.6	33.4	-	12.8	-	-	-
265980	-	40.3	40.5	-	14.85	-	-	-
265980	-	26.2	27.7	-	10.7	-	-	-
265980	-	28.0	27.8	-	-	-	-	-
265980	-	25.55	27.4	-	-	-	-	-
265980	-	34.3	38.25	-	-	-	-	-
265980	-	32.3	31.6	-	-	-	-	-
265980	-	29.8	32.4	-	12.2	-	-	-
265980	-	39.4	36.0	-	13.85	-	-	-
265981	-	33.9	32.5	-	-	-	-	-
265981	-	41.3	39.3	-	-	-	-	-

Material. - Ulrich and Scofield (1897) designated 8 "cotypes" under the number USNM 45981. All of these are fragmented, badly weathered silicified casts from the Curdsville Limestone Member of the Lexington Limestone. Two specimens have been extracted from this set of types; USNM 265961 (Pl. 24, figs. 11-12) is here designated the lectotype for the species, and USNM 265962 (Pl. 24, fig. 10) and the other 6 specimens (these are being left as USNM 45981) are designated paralectotypes.

The USGS silicified collections from Kentucky yielded numerous new specimens which are far better preserved than the type suite.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Sample 6034-CO is from the Tyrone Limestone and includes USNM 265964 (Pl. 25, figs. 1-8), USNM 265965 (Pl. 25, figs. 9-13), USNM 265966 (Pl. 26, figs. 11-12), USNM 265979 (Pl. 25, fig. 14), and USNM 265980, which is used for a set of about 40 specimens and fragments. All of the specimens from sample 6034-CO are firmly silicified. All other new specimens were in samples 7784-CO and 7785-CO, and all were coarsely silicified fragments of columellas and apertural rims.

Distribution. - S. kentuckyense is known from the Tyrone Limestone of the High Bridge Group (Rocklandian), and the Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian). The species was found in the Tyrone Limestone (6034-CO) in the Little Hickman Quadrangle, Jessamine County, Kentucky; at 1-2 ft (7784-CO) and 11-12 ft (7785-CO) above the base of the Curdsville Limestone Member in the same quadrangle and county, and also at 23 ft above the base of that unit (6131-CO) in the Danville quadrangle, Boyle County, Kentucky.

Comparisons. - Ulrich and Scofield (1897, p. 902) briefly described S. buelli var. kentuckyensis from silicified fragments from the "Black River Limestone of Kentucky" stating that it differed from S. buelli "in having a thicker shell, coarser surface markings, and smaller inner volutions when compared with the expanded aperture which is fully as large as S. buelli". Like S. expansa, the aperture is not so abruptly turned outward as in S. buelli; but S. kentuckyense is smaller than S. expansa and it is rounded over the dorsum rather than subangular. Two of Ulrich and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Scofield's (1897) type specimens are shown herein on Plate 24, figures 10 and 11-12. Ulrich and Scofield (1897) did not illustrate the species. The new and much better preserved USGS silicified material confirms many of Ulrich and Scofield's (1897) interpretations, but has revealed more detail, enabling the recognition of the Kentucky specimens as a distinct species.

The mature expanded aperture of the Kentucky specimens is greatly thickened and much more massive than that of S. buelli (Pl. 25, figs. 10-12). In the Kentucky specimens, this expanded aperture is sculptured with rather thick radiating ribs and often lamellose growth lines (Pl. 24, figs. 1-8 and 9-11); the submature portion of the shell seems to lack any ornament. On the other hand, S. buelli has relatively fine transverse and spiral threads which seem to cover the entire shell (Pl. 24, figs. 1-3).

Ulrich and Scofield (1897) stated that the Kentucky specimens had a smaller coil in proportion to the size of the expanded aperture. Comparison of the umbilical diameter to shell length in the two species shows S. buelli (USNM 265960) to have a ratio of 2.17 in these dimensions, whereas 3 specimens of S. kentuckyense show an average ratio of 2.70, thus demonstrating the latter has a relatively smaller coil. Although the aperture length/width ratios of the two species do not differ significantly on the average, the form of the extended anterior margin does differ. S. buelli has a steeper anterior slope, the anterior lip then

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

flattening outward into a relatively broad apron. Many specimens of S. kentuckyense show no tendency whatsoever to form an anterior apron (Pl. 25, figs. 4-5), but a few specimens do reflex the aperture margin to form a relatively small apron (Pl. 25, fig. 11). S. buelli and S. kentuckyense were contemporaries during the Rocklandian and Kirkfieldian Stages. There can be little doubt that the two are closely related, but subtle differences in morphology, as well as different paleogeographic distributions, suggests that they are geographic variants and distinct species.

Another species which should be considered closely related to the two above is S. billingsi Wilson (1951, p. 28) from the Blackriveran and Rocklandian strata of the Ottawa-St. Lawrence Lowland, Canada. According to Wilson, "The species differs from both S. buelli (Whitfield) and S. expansum (Hall) in its smaller size, more rapidly increasing and more tightly coiled whorls, and in its less abrupt aperture". The size of the species is very near that of S. kentuckyense, and it also possesses a thickened expanded aperture with lamellose growth increments (Wilson, 1951, Pl. 3, figs. 1-3). The only obvious differences between S. billingsi and S. kentuckyense is that the former bears S. buelli-like sculpturing on the entire shell, and apparently has a more highly raised anteromedian sinus. S. buelli, S. kentuckyense, and S. billingsi seem to form a closely related group. S. billingsi appears first, in the Blackriveran, and may have given rise to the other two.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - The expanded aperture of S. kentuckyense is much thicker than the submature portion of the shell. As a result of this condition, the great majority of the specimens in Ulrich and Scofield's (1897) type suite and in the USGS silicified collections are only the apertural rims of the shells (Pl. 24, fig. 10; Pl. 26, fig. 11; Pl. 25, fig. 14). The more complete specimens of the species (Pl. 25, figs. 1-8 and 9-13) all are missing the anterior slope of the expanded aperture, presumably because of the structural weakness caused by the long open slit. Ulrich and Scofield (1897, p. 898) pointed out that the anterior closing of the slit may have been a "necessity of overcoming the liability of fracture to which the aperture would have been subject had the slit been allowed to continue to the outer margin". The only known specimen which preserves any portion of the slit is specimen USNM 265964 (Pl. 25, figs. 1-8), which shows the uppermost part. In that specimen, however, the slit was closed well back from the aperture. Specimen USNM 265965 (Pl. 25, figs. 9-10) shows the slit in the process of being closed anteriorly, with only a crack remaining dorsally and being entirely closed ventrally. As known from the aperture rims only, adults of all sizes had the slit closed anteriorly. When most of these specimens are held up to a light, the median closed-off slit area is slightly transluscent, showing that it is distinctly thinner than the lateral portions of the rim. The shell along this anteromedian line must have been originally secreted thinner than the adjacent shell rim. It seems that as the expanding aper-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ture grew anteriorly along its outer edge, the slit must have been lengthened anteriorly by resorption of the thin shell along the median line. When the animal reached a certain age in later ontogeny, it essentially halted further outward growth, and only thickened the aperture rim, apparently also filling in the already closed-off anterior part of the slit with interior shell layers (Pl. 25, figs. 9-10).

SALPINGOSTOMA RICHMONDENSIS Ulrich, 1897

Pl. 24, figs. 13-16; Pl. 26, figs. 1-8

Salpingostoma richmondensis ULRICH in ULRICH & SCOFIELD, 1897, p. 903, Pl. 67, figs. 39-40; CUMINGS, 1908, p. 974, Pl. 39, figs. 7-7a; GRABAU & SHIMER, 1909, p. 614, figs. 823d-e; SHIMER & SHROCK, 1944, p. 443, Pl. 177, figs. 17-18; FOERSTE, 1924, p. 206, Pl. 34, fig. 8.

Diagnosis. - Shell moderately large (up to 50 mm in length); submature whorls depressed, reniform, width about twice length; coiling loose; at maturity, aperture abruptly expands, extending anteriorly at much greater rate than laterally, so that aperture becomes longer than wide, anterior slope steep, lateral margins slightly explanate.

Description. - Shell moderately large for genus, with about 3 loosely coiled volutions and wide-open umbilici; submature whorls depressed, reniform, width about twice length (L/W = 0.55), broadly convex dorsally, umbilical shoulders narrowly rounded, venter concave where con-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tiguous with preceding whorl; at about 15-20 mm shell length, aperture expands abruptly, mainly anteriorly, so that in fully mature specimens aperture length slightly exceeds width (L/W = 1.11); expanded aperture widest posteriorly, reaching back to about even with posterior umbilical shoulder, lateral and posterolateral apertural margins flare slightly but do not recurve upward; anterior slope of expanded aperture steeply convex to or nearly to margin, generally flaring very little, anterior margin raised above level of lateral margins in broad shallow sinus; slit open from dorsum to just inside anterior aperture margin, the anteromedian closure being marked by shallow linear indentation; selenizone apparently developed on submature whorls; no shell markings known.

Measurements. - Measurements of S. richmondensis are listed in Table 70.

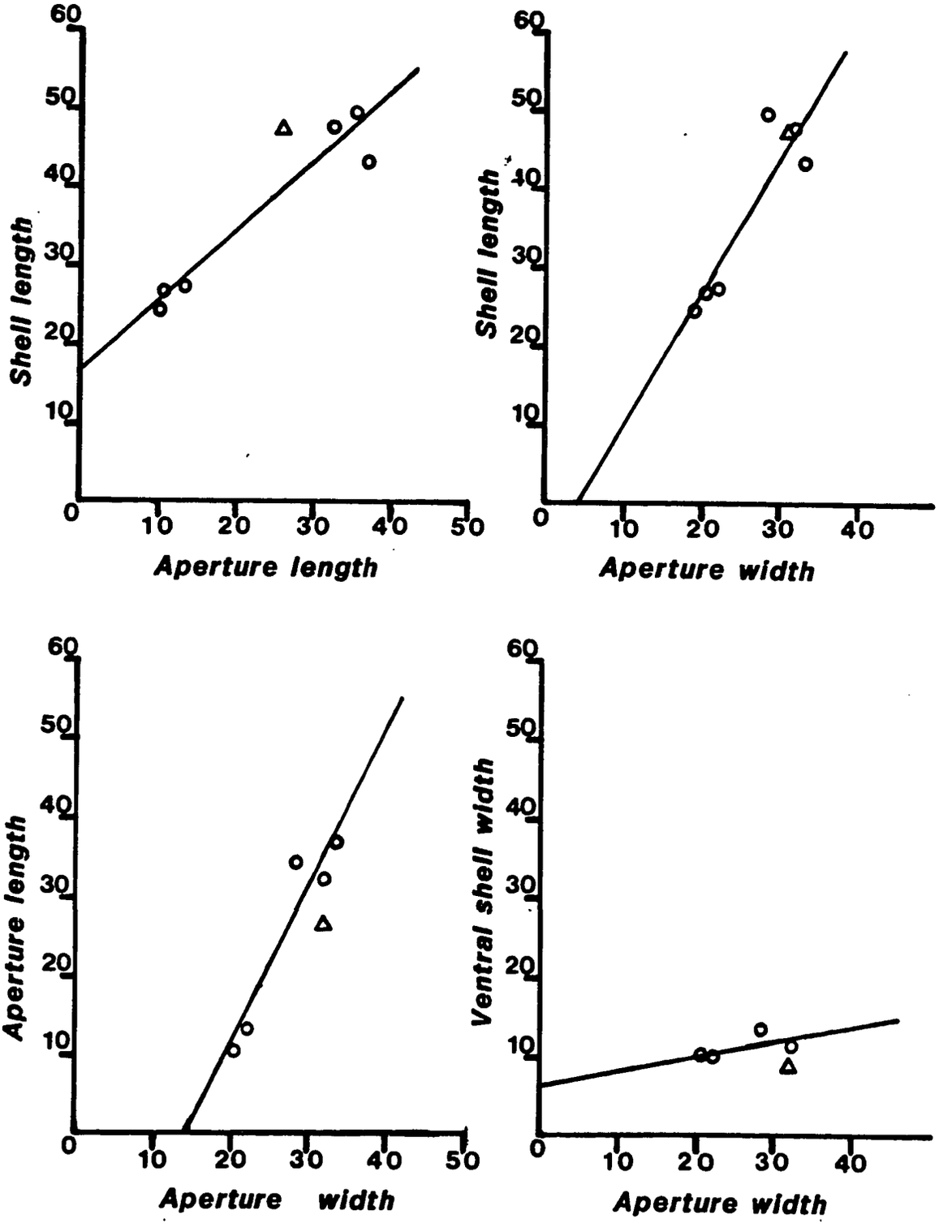
Table 70: Measurements of Salpingostoma richmondensis in mm.

Museum Number	Shell Length	Aperture Length	Aperture Width	Shell Height	Umb. Diam.	Dorsal Width	Post. Width	Ventral Width
USNM								
45983	43.3	37.0	33.6	25.0	13.4	16.8	-	11.9
UCGM								
28660	27.3	13.5	22.2	20.3	13.7	17.5	14.1	10.5
44281	47.6	32.5	32.2	28.6	19.9	18.15	15.0	12.0
44280	24.6	10.1	19.2	19.2	13.6	16.5	13.25	10.5
38549	26.9	10.85	20.7	19.9	14.2	17.0	14.0	10.5
38549	49.6	34.75	28.8	25.3	23.6	19.85	16.7	13.6

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 32: Bivariate plots of measurements made on specimens of *Salpingostoma richmondensis* and *Bucania simulatrix*.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - The holotype (USNM 45963) which preserves some shell around the margin of the expanded aperture (Pl. 26, figs. 1-5); UCGM 44281 (Pl. 26, figs. 6-8), UCGM 44280 (Pl. 24, figs. 13-16) are both hypotypes; UCGM 28660 and UCGM 38549 were used in measurements, but are not figured; all of these specimens are internal molds. Numerous other collections of internal molds were examined in the USNM, UCGM, and MU.

Distribution. - The species is known only from the Richmondian (upper Upper Ordovician) of southeastern Indiana and southwestern Ohio. Most collections examined came from the Whitewater Formation (Richmondian), near Richmond, Indiana, or Camden, Ohio. Other collections are only labelled "Richmond". Cumings' (1908, p. 975) specimens are all from the Whitewater Formation near Richmond Indiana, being most abundant near the top of that unit. Cumings (1908, p. 662-63) noted the species as common in "lumpy limestones" associated with abundant Rhynchotrema dentatum, several species of gastropods, and Strophomena sulcata. He cited S. richmondensis as occurring in a typical Whitewater biofacies of brachiopods and bryozoans.

Comparisons. - As noted by Ulrich and Scofield (1897, p. 904), many specimens of this species in old collections are labelled Bucania expansa Hall, a species from the Middle Ordovician of New York which is now placed in Salpingostoma. The two species are easily distinguished on morphological grounds. S. richmondensis differs from the S. expansa in having one less volution for the same sized shell, and S. expansa has a subtriangular

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

whorl which is in sharp contrast to the broader reniform shape of S. richmondensis.

It is much more difficult to distinguish between S. richmondensis and Bucania simulatrix Ulrich. The two species are homeomorphic, and thus have closely similar shell forms. Both species are known mainly or completely from internal molds, and both are found in the Richmondian Whitewater Formation in the vicinity of Richmond, Indiana. Preliminary examination gave me the impression that the two species were synonymous, but on close scrutiny they appear to be truly distinct. Many museum collections having either species label commonly contain both species. In well-preserved specimens, the slit of B. simulatrix can be observed to extend to the anterior apertural margin, readily distinguishing it from S. richmondensis.

Comparison of the holotype of Bucania simulatrix (USNM 45729, Pl. 19, figs. 11-14) with the holotype of S. richmondensis (USNM 45983, Pl. 26, figs. 1-5) shows the distinctiveness of the two species. Figure 32 shows the lateral expansion rates of 6 (3 immature and 3 mature) specimens of S. richmondensis and the holotype of Bucania simulatrix, using width measurements taken at every quarter volution on the last whorl. These measurements reveal that the last whorl of B. simulatrix is a good deal narrower than in Salpingostoma richmondensis. Moreover, in Bucania simulatrix the anterior width gradually and constantly increases throughout ontogeny. Conversely, Salpingostoma richmondensis shows

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

gradual size increase until maturity, then abruptly expanding, reaching the same width as Bucania simultrix, but over a shorter longitudinal distance, and after a much briefer period of increased expansion.

Figure 32 shows scattergrams for the 6 specimens of Salpingostoma richmondensis listed in Table 70, as well as for the holotype of Bucania simulatrix. The regression line and the statistics were calculated only for the measurements on Salpingostoma richmondensis. Bucania simulatrix stands slightly away from the other points in 3 of the 4 graphs, agreeing best on the plot of shell length vs. aperture width.

Although there is no known complete specimen of Salpingostoma richmondensis retaining the shell, there can be little doubt about its generic placement. In the anteromedian area of the holotype, where some shell is preserved, there is a shallow linear indentation (Pl. 26, fig. 1) just as in Salpingostoma buelli (Pl. 25, figs. 9), which reflects the thinness of the shell there. This thin strip of shell was apparently easily resorbed in the lengthening of the slit as the anterior margin of the aperture was extended. Posterior to this indentation, there is a low, weathered median ridge (Pl. 26, figs. 1-3) reflecting the long open slit on the internal mold. This ridge is better preserved on the internal mold UCGM 44281 (Pl. 26, figs. 6-7). Furthermore, the anteromedian apertural margin is raised above the level of the lateral margins (Pl. 26, fig. 8), but only slightly, and there is apparently only a broad shallow sinus.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Although the general shell form of Bucania simulatrix (Pl. 19, figs. 11-14) is very similar to that of Salpingostoma richmondensis (Pl. 26, figs. 1-5), the anteromedian expanded aperture of B. simulatrix shows a deeply-cut V-shaped sinus in the anteromedian lip which reaches to about the level of the dorsal umbilical shoulder on the coil (Pl. 19, figs. 11 and 14). Posterior to this deep sinus is a long median ridge in the internal mold (Pl. 19, figs. 11-12) as was seen in S. richmondensis; however, in B. simulatrix the ridge reaches all the way to the tip of the sinus. It is doubtful that this ridge reflects a long open slit, but more likely represents a selenizone on an elevated dorsal carina which formed an internal channel along the interior median crest of the shell. If this interpretation of the dorsal ridge in the holotype of B. simulatrix is incorrect, and it is found that the structure does reflect a long open slit, then the species should be transferred to the genus Salpingostoma. However, even in that case, it should still be considered distinct from S. richmondensis because of its different rate of expansion at maturity.

Discussion. - Ulrich and Scofield (1897) observed revolving ribs and transverse growth lines preserved on the dorsum of a single specimen of S. richmondensis, but no ornament was seen on any specimens examined during this study. Therefore, it has not been included in the specific description given here. I could not locate Ulrich and Scofield's specimen.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Because all known species of Salpingostoma bear a sinuate aperture, it would be surprising if this species did not. However, none of the specimens of S. richmondensis examined had the anterior portion of the expanded aperture well enough preserved to confirm the presence of a distinct anteromedian sinus. The absence of growth lines in any specimens further masks the exact nature of this region, but the raised anterolateral margins of the expanded aperture seen in some specimens (Pl. 26, fig. 8) seems to support the presence of a broad shallow sinus. It should be recalled that the sinus in S. kentuckyense is known to be fairly shallow.

The most similar species of Salpingostoma seems to be the Middle Ordovician S. expansa from New York, and that species might be ancestral to S. richmondensis. However, this similarity may be superficial, and the result of similar preservation of both species as internal molds. Such preservation suggests that these were fairly thin-shelled species in comparison to S. buelli, S. kentuckyense, and S. billingsi, which have thickened apertures. In further support of this contention is the fact that molds of S. richmondensis are commonly strongly compressed. A similar situation exists with some species of Sinuites (i.e., S. cancellatus) in the Cincinnatian rocks of the study area, and it is known that these species were quite thin-shelled.

As previously noted, Cumings (1908, p. 662-3) cited S. richmondensis as characteristic of the Rhynchotrema dentatum beds near the top of the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Whitewater Formation, where it occurred in "lumpy limestone" beds with several species of gastropods, R. dentata and Stromphomena sulcata. Although most internal molds of S. richmondensis are composed of fine carbonate mudstone or wackestone, the matrix in which it occurs is generally packstone to grainstone. Putting this information together, it seems that S. richmondensis probably inhabited a quiet environment in a typical molluscan-brachiopod community. Commonly shells were transported into adjacent higher energy environments (probably during storms) and deposited in adjacent banks of shell debris, being associated there with a more typical bryozoan-brachiopod assemblage. This reasoning is in keeping with the regressive nature of the Whitewater Formation, which records the last stage of Ordovician deposition in the northwestern part of the area. Scattered low shelly banks with intervening quieter lagoons would fit this picture. Moreover, this interpretation agrees with Peel's (1977) conclusion that explanate bellerophontaceans are adapted for life on fine substrates.

I collected badly fragmented specimens of S. richmondensis at Thistlewaite Falls along the Whitewater River at Richmond, Indiana. The specimens occurred in nodular limestone beds composed of the fragmented skeletal debris of brachiopods, bryozoans, and mollusks. The fragmented, worn skeletal debris was neither sorted nor oriented, but gave the impression of debris transported and deposited by storms.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Family BELLEROPHONTIDAE McCoy, 1851

Diagnosis. - Shell rounded, often inflated; aperture margins often flairing or even somewhat explanate, parietal lip generally reflexed; anteromedian slit generated distinct selenizone; umbilicus narrow or closed.

Stratigraphic distribution. - Middle Ordovician - Lower Triassic.

Discussion. - This family encompasses most Late Paleozoic bellerophonts. Golikov and Starabogatov (1975) preferred to recognize the below subfamilies as distinct families. The problem is how to best represent the phylogenetic relationships between these taxa in the systematic heirarchy. It is believed here that the common morphological features of the taxa represent a phylogenetic grade of shell development which is best expressed under one family.

Four subfamilies are recognized within the family Bellerophontidae - Bellerophontinae McCoy, 1851; Bucanopsinae new subfamily; Knightitinae Knight, 1956; and Cymbularinae Horny, 1962.

As discussed under the family Carinaropsidae, Bucanopsis and Sphenosphaera are quite distinct from Carinaropsis and are not included in that family; here they are placed in the new subfamily Bucanopsinae of the Bellerophontidae. The strong revolving ornament of Bucanopsis is believed to indicate an ancestry with the Bucaniinae of the Bucaniidae. Sphenosphaera has a very similar shell form to Bucanopsis, and both bear a keel

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

along the median whorl floor. Sphenosphaera also bears a striking resemblance to Bellerophon in general shell form. Sphenosphaera was extracted from Bellerophon because of subtle differences in the form of the parietal lip and presence of the median whorl floor keel (Knight, 1945, p. 334). It is likely that the Bellerophontinae evolved from the Bucanopsinae through Sphenosphaera. It may be that the Knightitinae also evolved from the Bucanopsinae through Bucanopsis or closely related forms. This view is supported by the common possession of strong radial ornament by Bucanopsis and genera of the Knightintinae, and by the presence of a whorl floor keel in at least one species of Knightites, as reported by Rollins (1967), who also proposed Bucanopsis as the ancestor to the Knightitinae.

The Cymbularinae was proposed by Horny (1962) for globose shells with a distince V-shaped sinus preceding the slit. Its ancestry is questionable, as is its placement within the Bellerophontidae. If the genus Coelocyclus is a valid member of this subfamily, as Horny thought, then the Cymbularinae may have evolved from the Bucaniinae of the Bucaniidae. This is subfamily to which Coelocyclus was assigned by Knight and others (1960).

Subfamily BELLEROPHONTINAE McCoy, 1851

Diagnosis. - Shell convolute or nearly so, umbilici narrow or lacking; whorls usually broadly rounded, somewhat globose; slit fairly short, generating selenizone; shell surface with growth lines only.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stratigraphic distribution. - Middle Ordovician - Lower Tirassic.

Genera included. - B. (Bellerophon) Monfort, 1808; B. (Aglaoglypta) Knight, 1942; B. (Pharkidonotus) Girty, 1912; Liljevallospira, Knight, 1945; ?Ptychobellerophon Delpey, 1941. Horny (1962) assigned two rather unusual genera to the Bellerophontinae, Bubovicus Horny and Kodymites Horny. Both genera probably belong within the Bellerophontidae, but they do not appear to conform to the morphobases of the subfamily Bellerophontinae. Kodymites has umbilici filled with the inductural deposits, and may represent a new subfamily, as suggested by Horny (1962, p. 122). Bubovicus is here left in the Bellerophontinae for the time being, but its high narrow whorls and moderately small open umbilicus are somewhat atypical of the subfamily. Because of some spiral ornamentation, Horny (1963, p. 121) suggested a possible relationship to Kokenospira, but concluded that the development of the selenizone and the general shape of the growth lines are typical of the Bellerophontinae. Thus far only one species of Bubovicus has been described, and more data are needed before its higher level placement can be confidently made.

Discussion. - With Horny's (1963) removal of the Cymbularinae from this subfamily (3 or 4 genera), the Bellerophontinae is now a very homogeneous grouping of genera. Because of the close morphologic similarity between these genera and Sphenosphaera, there can be little doubt that the Bellerophontinae evolved from the Bucanopsinae through some such form as Sphenosphaera.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus BELLEROPHON Montfort, 1808

Pls. 18, 28, 33

Diagnosis. - Shells with broadly rounded whorls, but some may have subdued dorsal crest; umbilici small or closed; median whorl floor ridge lacking.

Type species. - Bellerophon vasulites Montfort, 1808, by original designation.

Distribution. - Middle Ordovician to Lower Triassic. Cosmopolitan.

Discussion. - Throughout most of the 19th century, the genus Bellerophon encompassed nearly all described bellerophontaceans. Late in that century, subtle differences in different groups within the genus were recognized and new genera were segregated and erected.

Knight (1945, p. 334) proposed the genus Sphenosphaera to include American Ordovician species assigned to Bellerophon by Ulrich and Scofield (1897), and related species. The primary taxobase distinguishing the new genus was the presence of a median whorl floor ridge. Rollins (1967) has contested the collective assignment of the American Ordovician species to Sphenosphaera, pointing out that some of these species lack a whorl floor ridge, and in many others the whorl floor is not known. He believed that all such species should be returned to B. (Bellerophon). It should be noted that the whorl floor ridge dies out at the parietal callosity in Sphenosphaera, not extending outside the aperture, so any filling of the aperture prevents the visibility of the structure.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

In the fauna discussed here, three species are confirmed as members of B. (Bellerophon) (lacking a whorl floor ridge), five species are confirmed as members of Sphenosphaera (possessing a whorl floor ridge), and three species are of uncertain generic assignment (specimens not exposing the whorl floor). For the generic placement of the uncertain group of species, other comparative morphological features are used to determine to which genus they belong. Two of these species, S. recurvus Ulrich (Pl. 33, figs. 1-4) and S. subangularis Ulrich (Pl. 33, figs. 10-15), have comparatively angled, nonglobose shell forms and nearly closed umbilici, and seem to be related to S. clausus Ulrich. The third species of uncertain affinity, Bellerophon subglobulus Ulrich (Pl. 33, figs. 7-9), is poorly preserved and its assignment is most troublesome, particularly because it is the earliest known species of the two genera in the Cincinnati Arch faunas (Blackriveran in age). This species is similar to Sphenosphaera troosti in the size of its umbilici and its thin ridge-like selenizone, but because of the globosity of its shell and the lack of evidence of a whorl floor keel, the species is tentatively assigned B. (Bellerophon).

With the confirmation of the assignment of the three species, B. (B) bilineatus, B. (B.) nana, and B. (B) subpatula to the genus Bellerophon (Bellerophon), the range of the genus is once again extended back to the Middle Ordovician. This is at variance with Knight and others (1960), who claimed a Silurian origin for B. (Bellerophon).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Subgenus BELLEROPHON (BELLEROPHON) Montfort, 1808

Diagnosis. - Shell rounded to commonly globose; selenizone distinct, sometimes on dorsal crest; aperture lips flairing slightly near small umbilici; inductura thin to slightly thickened but always smooth, and extending only a short distance out of the plane of the aperture; ornament predominantly collabral.

Type species. - Same as for genus.

Distribution. - Same as for genus.

Discussion. - Three subgenera are currently recognized within the genus Bellerophon. B. (Aglaoglypta) Knight, 1942, is like B. (Bellerophon), but is ornamented with quincuncially arranged pustules (Knight and others, 1960). B. (Pharkidonotus) differs from the other two subgenera by having strongly thickened inductural deposits that are often padlike in shape, an ornament of collabral undulations, a crested selenizone, and no umbilicus (Knight and others, 1960). The subgenera B. (Aglaoglypta) and B. (Pharkidonotus) are Middle and Late Paleozoic in age. B. (Bellerophon) is the oldest subgenus of the three (appearing in the Middle Ordovician), and was almost certainly ancestral to the other two more specialized subgenera.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BELLEROPHON (BELLEROPHON) SUBGLOBULUS Ulrich, 1897

Pl. 33, figs. 7-9

Bellerophon subglobulus ULRICH in ULRICH & SCOFIELD, 1897, p. 917, Pl. 64, figs. 17-18.

Diagnosis. - Shell moderately small (up to 19.4 mm in length), subglobose; umbilici small, circular; selenizone thin, elevated, ridge-like, with lunulae.

Description. - Shell moderately small, subglobose in form; dorsal slopes uniformly well rounded; umbilici small, circular, with slightly reflexed parietal lip passing just beneath them. Aperture rounded; whorl floor not visible due to filling by matrix. Growth lines broadly rounded over dorsum, sharp, evenly and closely spaced. Selenizone thin, elevated, ridge-like, with lunulae present.

Measurements. - The measurements of B. (B.) subglobulus given in Table 71 are only approximations due to the poor preservation of the specimens.

Table 71: Measurements of B. (Bellerophon) subglobulus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
USNM								
45709	19.4	13.8	(14.6)	16.0	11.8	--	--	0.85
387022	11.8	8.6	8.4	10.5	7.5	5.3	3.6	0.60

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Only two specimens were located, both catalogued under USNM 45709. The lectotype designated herein (Pl. 33, figs. 7-9) retains that number, and the paralectotype is assigned USNM 387022.

Distribution. - Ulrich and Scofield (1897) stated only "Black River limestone, Mercer County, Kentucky." The species probably occurs in the High Bridge Group (Blackriveran-Rocklandian) of central Kentucky.

Comparisons. - Although poorly preserved, the type specimens of B. (Bellerophon) subglobulus can be distinguished from Sphenosphaera troosti by lacking distinct continuous whorl-floor ridges and by their more globose form, more broadly curved and thread-like growth lines, narrower ridge-like selenizone, and probably by a smaller parietal callosity. S. clausus shows the same differences and also has a channel-like selenizone and lacks umbilici. B. (Bellerophon) bilineatus has larger umbilici and a channel-like selenizone.

BELLEROPHON (BELLEROPHON) BILINEATUS Ulrich, 1897

Pl. 28, figs. 1-9

Bellerophon bilineatus ULRICH in ULRICH & SCOFIELD, 1897, p. 917, Pl. 64, figs. 19-21.

Diagnosis. - Shell moderately small (up to 13 mm in length); umbilici relatively large; whorl floor keel very low or lacking; selenizone concave, bordered and lunulate.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderately small, expanding rather slowly. Whorl slopes cutting downward sharply, forming a rounded dorsolateral shoulder and giving the shell a squarer appearance than in other species. Umbilici relatively large for genus. Parietal lip not much thickened centrally; posterolateral lips folded back just beneath umbilici. Low rounded whorl floor keel occasionally present. Selenizone nearly flush with dorsal whorl slopes, slightly concave, bordered by a distinct revolving thread on either side, lunulae well developed. Growth lines fine, thread-like, very closely and evenly spaced, gently curved.

Measurements. - Measurements on B. (B.) (bilineatus) are listed in Table 72.

Table 72: Measurements of B. (Bellerophon) bilineatus in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
USNM 45697	12.9	10.9	5.0	14.0	8.6	6.5	5.4	0.9
"	--	8.75	--	13.6	7.3	5.9	4.9	0.9
315612	--	14.6	--	20.2	--	--	--	--

Material. - The holotype (USNM 45697) (Pl. 28, figs. 1-5) and paratype (USNM 387023) are both silicified and fragmented. One possible new specimen of B. (B.) cf. bilineatus was identified from USGS silicified sample 6136-CO (USNM 315612) (Pl. 28, figs. 6-9).

Distribution. - The type specimens are listed as coming from the "Upper portion of the Trenton Group, near Danville, Kentucky" (Ulrich and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Scofield, 1897), this corresponding to the Upper Lexington Limestone (Shermanian) of modern usage. The possible new specimen cited above is from the Faulconer bed of the Perryville Limestone Member of the Lexington Limestone (Shermanian) in central Kentucky.

Comparisons. - This species is most similar to Sphenosphaera troosti and S. burginensis, but is distinguished by its larger umbilicus, its squarer whorl form, its lack of a distinct whorl floor keel, and its concave, bordered, lunulate selenizone.

Discussion. - As pointed out by Rollins (1967, p. 118), the holotype of this species apparently lacks a true whorl floor ridge, and therefore does not fit the definition of the genus Sphenosphaera. In every other character, the holotype seems closely related to contemporaneous species of that genus, but it must be assigned to Bellerophon (Bellerophon). The relatively large umbilicus of the species is a primitive morphological feature.

BELLEROPHON (BELLEROPHON) NANA (Ulrich, 1897)

Pl. 18, figs. 13-17

Bucania nana ULRICH in ULRICH & SCOFIELD, 1897, p. 895, Pl. 66, figs. 41-44.

Sphenosphaera nana (Ulrich) ROLLINS, 1967, p. 119, Pl. 4, figs. 2-3.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Diagnosis. - Shell small (up to 9.5 mm in length), whorls rounded but relatively narrow; selenizone channel-like and bordered by thin ridges; growth lines broadly curved.

Description. - Shell small; whorls rounded dorsally and laterally, but relatively narrow rather than globose; umbilici of moderate size for genus; aperture outline subreniform, lips not known to flair laterally. Sinus moderately shallow; selenizone concave, channel-like, with distinct lunulae and bordering threads. Growth lines broadly curved over dorsum, thread-like, closely-spaced and quite evenly-spaced.

Measurements. - Measurements of the lectotype and a paralectotype of B. (Bellerophon) nana are listed in Table 73.

Table 73: Measurements of B. (Bellerophon) nana in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
USNM							
315553	6.4	4.8	4.0	5.5	4.5	3.5	3.0
315554	9.5	7.0	5.0	8.0	5.0	3.8	3.2

Material. - The lectotype USNM 315553 (Pl. 18, figs. 10-12) and the paralectotype USNM 315554 (Pl. 18, figs. 15-17) were extracted from Ulrich's (1897) syntype suite of 11 small silicified specimens. The remaining 9 paralectotypes remain catalogued under USNM 45722. No new material is known.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - The museum label with the type material lists the collection from the "Flanagan beds of the Trenton, one and a half miles south of Burgin, Kentucky". The Flanagan is an outdated stratigraphic name for silicified beds in the upper Lexington Limestone that were at different horizons, but were probably in the Perryville Limestone Member of the Lexington Limestone (Shermanian).

Comparisons. - This species can be differentiated from B. (B.) bilineatus by its smaller umbilici and narrower whorl form. See also comparison to B. (B.) subpatula under that species.

Discussion. - Ulrich and Scofield (1897, p. 896) assigned this species and its supposed subspecies B. nana subpatula to the genus Bucania because they believed the former to possess faint revolving threads. But they qualified this assignment by saying that they were not satisfied that either was a "true Bucania", as their umbilici were too small, and their sculpturing was "not what it should be".

Rollins (1967, p. 119) suggested that both of the above forms might actually be juveniles of Sphenosphaera troosti or S. clausus, because of similarities in the character of the collabral ornament and the presence of strong bordering threads bordering the selenizone. However, he decided to recognize the present species as Sphenosphaera nana.

It appears here that this species is distinct, particularly by virtue of its rounded but narrow whorls. It shows no evidence of a whorl floor ridge (Pl. 18, figs. 14 and 17), and therefore is recognized here as a species of B. (Bellerophon).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BELLEROPHON (BELLEROPHON) SUBPATULA (Ulrich, 1897)

Pl. 18, figs. 10-12.

Bucania nana var. subpatula ULRICH in ULRICH & SCOFIELD, 1897, p. 896, Pl. 66, figs. 45-46.

Diagnosis. - Shell small (up to 7.1 mm in length); whorls broadly rounded over dorsum; umbilici moderately small; selenizone narrow, slightly concave, with fine bordering threads; growth lines fine, thread-like, only slightly curved over dorsum reflecting a very shallow apertural sinus.

Measurements. - Measurements of the lectotype of B. (Bellerophon) subpatula are listed in Table 74.

Table 74: Measurements of B. (Bellerophon) subpatula in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width
USNM 315552	7.1	4.5	4.0	7.0	4.7	3.3	2.8

Material. - The lectotype USNM 315552 (Pl. 18, figs. 10-12) is here designated from the syntype suite USNM 45723, which consisted of 3 small silicified specimens. No new material is known.

Distribution. - The museum label with the type suite reads: "Trenton, 1.5 miles south of Burgin, Kentucky". The specimens are most likely from the upper Lexington Limestone (Shermanian).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - This species can be distinguished from B. (B.) nana by its wider aperture and whorl form, its slightly smaller umbilici, its narrower and less concave selenizone, and its nearly straight growth lines.

Discussion. - See the discussion under B. (B.) nana for the history of B. (B.) subpatula. The species is included in B. (Bellerophon) because the lectotype shows no evidence of bearing a whorl floor ridge (Pl. 18, fig. 11).

Subfamily BUCANOPSINAE new subfamily

Diagnosis. - Shell anomphalous, or very nearly so; median keel or ridge on whorl floor; selenizone generally slightly elevated.

Stratigraphic distribution. - Middle Ordovician - Silurian.

Genera included. - Bucanopsis Ulrich in Ulrich and Scofield, 1897; and Sphenosphaera Knight, 1945.

Discussion. - The revolving ornament of Bucanopsis suggests that the genus may be ancestral to the Knightitinae. Rollin's (1967) observation of the presence of a median whorl floor ridge in a species of Knightites further supports this idea.

The Bucanopsinae is thought to be ancestral to the Bellerophontinae. Knight (1945) proposed the genus Sphenosphaera for Ordovician species previously assigned to Bellerophon. The two genera are almost indistingui-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

shable except for the presence of a prominent whorl floor keel in Spheno-sphaera. The median whorl floor keel in the tropidodiscids, the earliest appearing family of the slit-bearing Bellerophontacea, is simply the result of the wrapping of a subsequent whorl coiling over the carinate dorsum of the previous whorl. However, in the Bucanopsinae, this whorl floor keel even persists in forms without a dorsomedian prominence. Possibly the whorl floor keel served an unknown function, such as being a muscle attachment site. Such a function would explain the continued presence of a whorl floor keel when no dorsomedian prominence is present. On the other hand, it may be that the whorl floor keel of the bucanopsids is a vestigial structure.

Knight and others (1960, p. I180) placed Bucanopsis and Sphenosphaera in the Carinaropsinae because of their rapidly expanding shells and their possession of whorl floor keels. However, these two genera do not have the parietal lip developed into a platform that extends well into the aperture opening, nor do they show true reduction of the coil. It is reckoned here that Carinaropsis and its relatives, who do show these features, are a distinct, specialized group that is deserving of a separate family within the bellerophontacean taxonomic scheme. However, it is quite likely that the Carinaropsidae and Bucanopsinae have a common ancestry, or that the Carinaropsidae evolved from a bucanopsid such as Sphenosphaera.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus BUCANOPSIS Ulrich and Scofield, 1897

Pl. 27, figs. 1-20

Diagnosis. - Shell rapidly expanding selenizone elevated; parietal lip broad, shelf-like, with sharp median keel developed over ventral whorl floor; ornament of fine straight, parallel, revolving threads and fine growth lines.

Description. - Shell small to moderate in size, rapidly expanding; umbilici of moderate size. Selenizone generally elevated on dorsomedian ridge. Aperture broadly expanded; parietal lip reflexed over the coil and spread laterally to form a ventral shelf posterior to the aperture opening; whorl floor and parietal shelf with median keel caused by covering of dorsomedian elevation by thin parietal lip. Shell surface marked by fine, unwrinkled, uninterrupted, revolving threads which run parallel to the direction of coiling. Occasionally, faint growth lines are of sufficient strength to give a weak reticulate pattern to the shell.

Type species. - Bucanopsis carinifera Ulrich and Scofield, 1897, by original designation.

Distribution.- In the Ordovician of North America, Bucanopsis is known from the species B. carinifera and B. diabloensis n. sp., which are found in the Lexington Limestone of Kentucky and the Bigby-Cannon Limestone of Tennessee, both formations being Kirkfieldian-Shermanian in age.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Reed (1920-21, p. 58-62) reported four species of Bucanopsis from the Caradocian, Ashgillian and Wenlockian-aged (M. Ord.-U. Sil.) strata of Great Britain. Horny (1963, 113-116) described four species of Bucanopsis from the Llandeilian, Caradocian, and Ashgillian strata of Bohemia. Three species of Bellerophon named by Lindstrom (1884) from the Middle Silurian of Scotland have been referred to Bucanopsis by Rollins (1967, p. 116-117). Therefore, Bucanopsis is known from the Middle Ordovician to Upper Silurian in North America and Europe.

Discussion. - Ulrich and Scofield (1897, p. 922-924) proposed the genus Bucanopsis for species resembling Bellerophon, but possessing straight, non-wrinkled, revolving lines which run parallel with the direction of coiling. They discussed the previous history of these species in some detail and only a brief synopsis is presented here. Paleontologists prior to 1880 classified species placed by Ulrich and Scofield (1897) in Bucanopsis in the genus Bellerophon. Waagen (1880) separated such species from Bellerophon on the basis of their spiral sculpture, and placed them in Bucania Hall. Koken (1884, p. 379) adopted this approach. Ulrich and Scofield (1897) believed the shell form of species they placed in Bucanopsis was more similar to that of Bellerophon than Bucania, and emphasized differences in the characters of the revolving ornament between Bucania and Bucanopsis. Species of Bucania are characterized by oblique revolving lines which are wrinkled and generally interrupted regularly by growth lines; however, the revolving threads of species of Bucanopsis are

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

straight and parallel to the direction of coiling, and are never wrinkled or broken by stronger growth lines. Knight (1945 p. 335) proposed the genus Retispira and placed therein all Devonian through Permian aged species previously placed in Bucanopsis, stating that Retispira differs from Bucanopsis "by its simple, inductural inner lip and its lack of the sharp ridge on the floor of the interior of the whorl." Knight and others (1960) treated Retispira as a subgenus of Knightites in the Bellerophontidae, and placed Bucanopsis in the Carinasopsinae, stating that the presence of a whorl floor keel and expanded aperture allied Bucanopsis with Sphenosphaera and Carinaropsis (see also Knight, 1945, pp. 334-5).

As noted by Rollins (1968, p. 112), it is here recognized that the nature of the whorl floor keel in Bucanopsis is quite different from those of Sphenosphaera and Carinaropsis. Bucanopsis is partially characterized by a selenizone carried upon a highly prominent dorsal carina, as exmplified by the type species Bucanopsis carinifera (pl. 27, figs. 1, 16). The whorl floor keel in that species is the result of the covering of this dorsal carina by the parietal lip of the subsequent whorl. This is also shown by the presence of the keel ventrally over the entire parietal lip (Pl. 27, figs. 4, 11, 14, 20). Species of Sphenosphaera and Carinaropsis, on the other hand, do not generally possess a prominent dorsal carina (although there are exceptions), but they still develop a whorl floor keel. Furthermore, the whorl floor keel in these genera does not continue ventrally over the extended parietal lip (Pls. 28-38).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bucanopsis may represent a more primitive condition. Sphenosphaera and Carinaropsis may represent intermediate and advanced forms, respectively, that evolved from Bucanopsis. Sphenosphaera and Carinaropsis apparently have lost distinct revolving ornament, except for the threads commonly bordering their selenizones. However, faint revolving threads have been found here in a single silicified specimen of Carinaropsis cymbula (Hall) (Pl. 38, fig. 8). The selenizones of Sphenosphaera and Carinaropsis are generally either flat or on low ridges, but both genera retain a sharp whorl floor keel. This may be because it has assumed some functional significance, such as a muscle attachment site.

Rollins (1968, pp. 131-2, 249) suggested that Bucanopsis was ancestral to the subfamily Knightitinae because of similarities in their ornament patterns, parietal lips, and the presence of a low parietal keel in at least one species of Knightites.

BUCANOPSIS CARINIFERA Ulrich, 1897

Pl. 27, figs. 1-16

Bucanopsis carinifera ULRICH in ULRICH & SCOFIELD, 1897, p. 925, Pl. 62, figs. 56-61; GRABAU & SHIMER, 1909, p. 622, fig. 836; SHIMER & SHROCK, 1944, p. 443, Pl. 178, figs. 24-25.

Diagnosis. - Shell small (up to nearly 11 mm in length), with moderate sized umbilici; aperture cordate in outline, the width being nearly

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

twice the length; sides of whorls somewhat square; high dorsomedian carina becoming increasing flat-topped in maturity.

Description. - Shell small, compact, rapidly expanding, and tightly coiled, so that parietal lip is reflexed and coils about the umbilical shoulder. Whorls are broad and appear somewhat square at the shoulders in dorsal view. Selenizone only clearly visible in adulthood where prominent dorsal carina gradually becomes less angular and more flat-topped. Dorsal slopes briefly concave adjacent to carina, then becoming gently convex; umbilical shoulders narrowly rounded, the change of slope being abrupt and giving an angular impression; umbilici moderate in size and deep. Aperture broadly cordate, the width being nearly twice the length; parietal lip folds back over coil to form a rather broad ventral shelf posterior to the aperture opening; parietal lip thickens laterally from the median whorl floor carina that results from the covering of the dorsal carina by the thin parietal lip; whorl floor carina extends length of reflexed parietal lip. Shell sculpturing of numerous thin revolving threads which run parallel to direction of coiling, and seem restricted to dorsal slopes of whorls. Occasionally, transverse growth lines, which reflect broadly curved aperture sinus, become strong enough in maturity to create a reticulate pattern on the shell.

Measurements. - Measurements of B. carinifera are listed in Table 75.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

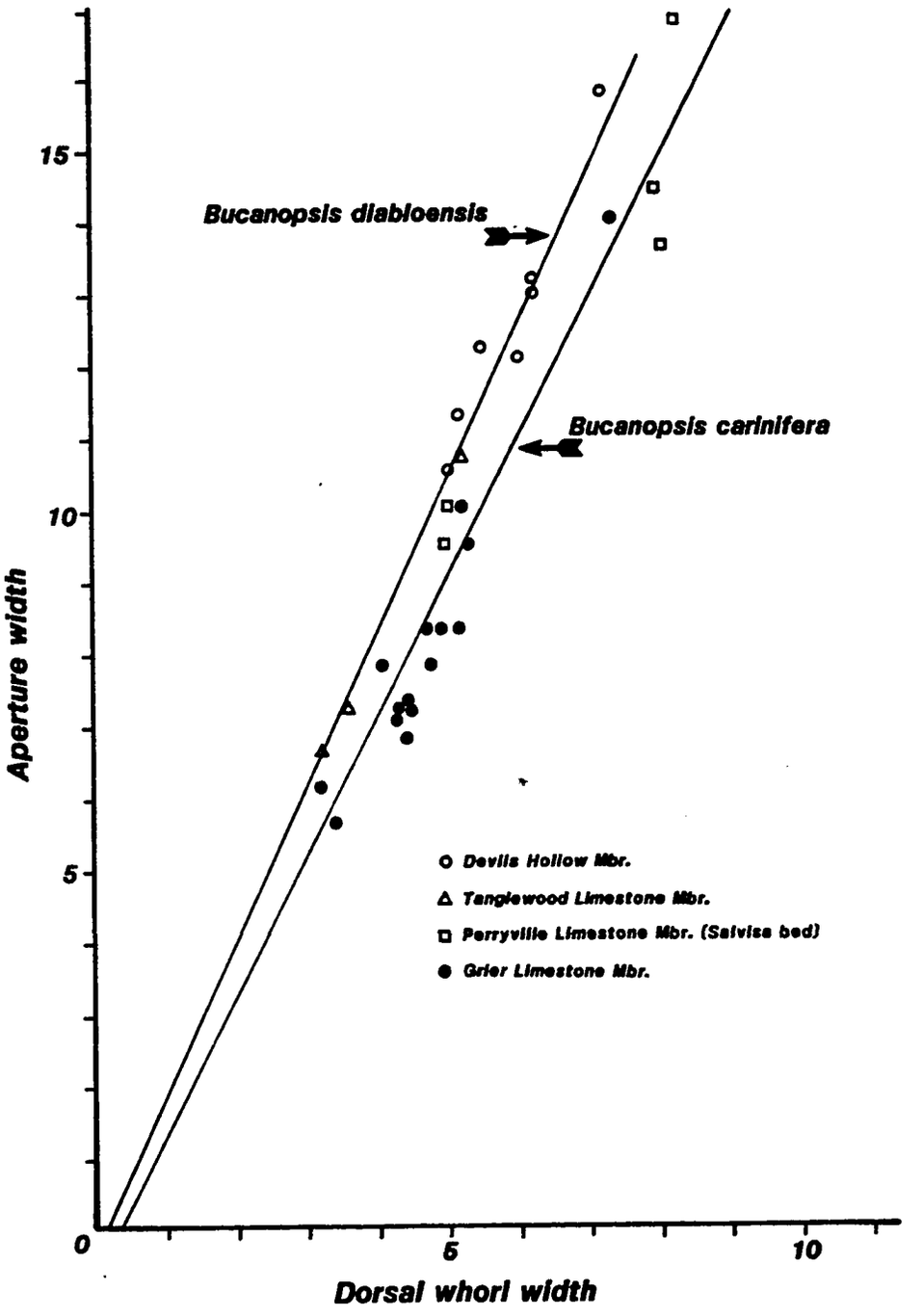
Table 75: Measurements of Bucanopsis carinifera in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Umbilical Diameter	Selenizone Width
USNM									
315583	--	9.2	--	13.5	7.6	5.4	--	4.5	0.9
45734	~8.7	~6.0	~6.0	8.1	--	--	--	3.2	0.9
"	9.0	7.0	6.9	9.6	--	--	--	3.4	--
"	9.4	7.15	7.05	8.7	--	--	--	3.5	--
"	5.7	4.5	4.5	6.2	--	--	--	2.3	--
"	5.9	5.0	4.5	5.8	--	--	--	2.2	--
"	7.0	5.7	--	7.9	--	--	--	3.0	--
"	--	3.9	--	5.2	--	--	--	2.1	--
315592	8.8	6.0	7.5	8.3	5.15	--	--	--	--
"	7.0	5.2	6.5	7.4	--	--	--	--	--
"	7.7	5.3	6.6	7.3	4.4	--	--	--	--
"	8.0	5.6	6.5	7.2	4.45	--	--	--	--
"	4.3	3.5	3.0	4.2	--	--	--	--	--
"	6.4	4.8	5.5	7.0	--	--	--	--	--
"	3.7	3.0	2.9	3.8	--	--	--	--	--
"	7.3	4.5	5.8	7.8	4.05	--	--	--	--
"	8.2	6.0	7.5	9.5	5.3	--	--	--	--
"	5.7	4.0	4.3	6.1	3.2	--	--	--	--
"	5.5	4.2	4.5	5.5	--	--	--	--	--
"	8.2	6.0	6.3	8.3	4.7	--	--	--	--
"	8.3	6.05	--	8.3	4.9	--	--	--	--
"	--	--	--	6.8	4.4	--	--	--	--
"	7.9	6.0	6.25	7.8	4.75	--	--	--	--
"	7.25	5.9	5.4	7.1	4.3	--	--	--	--
"	7.85	5.3	5.2	7.2	4.3	--	--	--	--
"	5.35	4.2	4.35	5.6	3.4	--	--	--	--
315586	--	--	--	14.0	7.3	--	--	--	--
315593	--	--	--	10.0	5.2	--	--	--	--
315589	10.8	8.0	8.35	10.0	6.1	5.5	--	--	--
315594	--	--	--	13.6	8.0	--	--	--	--
"	--	--	--	17.0	8.05	--	--	--	--
"	--	--	--	14.4	7.95	--	--	--	--
"	--	--	--	10.0	4.9	--	--	--	--
"	--	--	--	9.5	4.9	--	--	--	--
"	--	--	--	7.8	5.0	--	--	--	--
"	--	--	--	10.4	6.3	--	--	--	--
"	--	--	--	17.9	9.8	--	--	--	--
"	--	--	--	12.2	6.4	--	--	--	--
315595	--	--	--	10.7	5.2	--	--	--	--
"	--	--	--	6.6	3.2	--	--	--	--
"	--	--	--	7.2	3.6	--	--	--	--

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Figure 33: Bivariate plots of measurements made on specimens of *Bucanopsis carinifera* and *B. diabloensis* new species.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - All specimens known are silicified replicas. The lectotype was designated by Knight (1943, p. 60, Pl. 14, figs. 3a,b), and was catalogued under the same number as the rest of the original syntypes. It is here designated USNM 315583 (Pl. 27, figs. 1-2). The paralectotypes remain catalogued under USNM 45734, except for two specimens figured here, USNM 315584 (Pl. 27, fig. 3) and USNM 315585 (Pl. 27, fig. 4). Other Kentucky specimens in the USGS silicified collections are from USGS samples 4073-CO (USNM 315592), 4883-CO, 4928-CO (including USNM 315586), 4959-CO (including USNM 315593), 5096-CO, 5099-CO, 6136-CO (including USNM 315589), 5015-CO (including USNM 315587, 315588, 315594), 6915-CO (including USNM 315598), 6916-CO, and 7796-CO (including USNM 315595). One specimen from Tennessee is numbered UCGM 44283.

Distribution. - The type specimens of Ulrich and Scofield (1897) are labeled as being collected from the "Flanagan chert, near Danville, Kentucky". The Flanagan chert is an outdated term used formerly for different silicified horizons in the upper Lexington Limestone (Kirkfieldian-Shermanian). Ulrich and Scofield (1897, p. 925) also reported the species from Maysvillian strata in the Cincinnati, Ohio, area, but no specimens from Cincinnatian beds were located during this study, and such an occurrence cannot be confirmed.

The species was found in the USGS silicified collections from Kentucky in the Grier Limestone Member (4073-CO, 4883-CO, 4928-CO, 4959-CO, 5096-CO, 5099-CO), the Salvisa (5015-CO, 6915-CO, 6916-CO) and Faulconer

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(6136-CO) beds of the Perryville Limestone Member, and the lower tongue of the Tanglewood Member (7796-CO) of the Lexington Limestone (Kirkfieldian-Shermanian). Specimens were most abundant in the Grier Limestone Member, particularly sample 4073-CO, which contains nearly 50 specimens.

One specimen (UCGM 44283) (Pl. 27, figs. 5-7) was found in a collection from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) in Smith County, Tennessee, which is the first report of the species in that state.

Comparisons. - Bucanopsis carinifera could be confused with species of Sphenosphaera, if the revolving threads are not preserved. However, even when these are not present, the whorl outline of Bucanopsis carinifera is not as evenly rounded as most species of Sphenosphaera, it having a more abrupt change in angle at the umbilical shoulder. Also, the dorsomedian carina of B. carinifera is more prominent and its whorl floor keel runs ventrally over the entire length of the parietal lip, which forms a broader shelf posterior to the aperture opening.

Discussion. - The specimens of Bucanopsis carinifera show well the problems encountered when working with silicifed material. Because all specimens examined here were silicifed, it is difficult to completely assess the impact of silicification on the shell. The lectotype, USNM 315583 (Pl. 27, figs. 1-2), preserves the revolving threads better than any other specimen seen here, as well as showing how the carina widens into a flat-topped, elevated selenizone in adulthood. Note the fineness

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of these revolving threads and how they are not visible when the lighting is parallel to them (Pl. 27, fig. 2). Most specimens do not preserve these threads at all (Pl. 27, figs. 3-10). Some specimens show them very weakly (Pl. 27, figs. 13, 15-16). Some specimens show up to three different shell layers which peel away like layers in an onion (Pl. 27, fig. 13). Such circumstances of preservation make it impossible to always rely on the presence of the revolving threads to distinguish the species, or even the genus, although this character is a primary generic taxabasis.

Bucanopsis carinifera is found in a variety of facies in the Lexington Limestone and was apparently a broadly adapted species.

BUCANOPSIS DIABOLENSIS n. sp.

Pl. 27, figs. 17-20

Diagnosis. - Shell small (up to 15.8 mm in length), rapidly expanding; aperture broad, nearly semi-circular posteriorly; coil relatively small, rounded, narrow.

Description. - Shell small, compactly coiled, and rapidly expanding, so that coil is relatively small in comparison to the broad aperture; dorsum has distinct median carina and well rounded slopes; umbilical shoulders well rounded, and umbilici of moderate size and depth. Aperture broad, apparently subelliptical in outline, and broadly rounded, nearly semi-circular in its posterior portion; parietal lip somewhat reflexed,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

folding back over ventral coil to form a wide shelf posterior and postero-lateral to the aperture opening; whorl floor has distinct, sharp median carina which continues over parietal shelf. Shell ornament unknown.

Measurements. - Because of the preservation of available specimens, only 2 measurements are consistently reliable. These are listed in Table 76. Generally only the coil and posterior aperture were preserved.

Table 76: Measurements of Bucanopsis diabloensis in mm.

Museum No.	Aperture Width	Dorsal Width
USNM		
315590	15.8	7.15
315591	13.2	6.2
"	12.2	5.45
"	10.5	5.0
"	13.0	6.2
"	11.3	5.15
"	12.1	6.0
315599	11.5	5.65

Material. - All known specimens are from the USGS silicified collections from Kentucky. Selected from USGS sample 5095-CO, USNM 315590 (Pl. 27, figs. 17-20) is designated the holotype. Eleven specimens catalogued under 315591 are also from USGS 5095-CO and are designated paratypes, as are two specimens catalogued under USNM 315599 from USGS sample 5087-CO.

Distribution. - B. diabolensis is known only from the Devils Hollow Member of the Lexington Limestone (Shermanian) of central Kentucky (USGS samples 5095-CO and 5087-CO).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - B. diabolensis is distinguished from B. carinifera, which is also found in the upper Lexington Limestone, by its more rapidly expanding shell, its relatively smaller, more rounded, narrower coil, and its more broadly rounded parietal shelf (Pl. 27, figs. 17-20).

Discussion. - None of the available specimens of B. diabloensis preserves any surface ornament; however, as stated previously, very few specimens of B. carinifera, which is also known only from silicified material, have the revolving threads preserved. Therefore, it is possible that the B. diabloensis could actually belong to the genus Sphenoshpaera. I placed the species in the genus Bucanopsis because of similarity with B. carinifera, specifically, the tight coiling, the size of the umbilici, the dorsomedian carina, and the especially broad parietal shelf over which the whorl floor carina continues.

The difference in the rate of whorl expansion between B. carinifera and B. diabolensis is displayed in a crossplot of aperture width versus dorsal coil width (Figure 33). In successive samples from the Grier Limestone, Perryville Limestone, and Tanglewood Limestone Members, the aperture width/dorsal width ratios for B. carinifera are 1.74, 1.82, and 2.04, respectively; the equivalent ratio for B. diabolensis from the Devils Hollow Member is 2.14. B. diabolensis was apparently an offshoot (or a culmination) of a phyletic trend in B. carinifera of increasing the rate of whorl expansion.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus SPHENOSPHAERA Knight, 1945

Pls. 28-36,41

Diagnosis. - Shell moderately rapidly expanding, aperture flaring posteriorly and laterally; whorl floor with distinct median ridge, ridge not present on parietal shelf; shell markings colabral only.

Description. - Shell small to moderate in size, rather rapidly expanding, rounded but generally not globose in form; umbilici small or closed. Aperture broader than long; margins flared laterally and posteriorly, producing flat to slightly excavated posterolateral shelves; parietal lip reflexed over venter of previous whorl; whorl floor always with narrowly to well rounded median ridge, ridge not extending over onto ventral parietal lip. Slit shallow to moderately deep, housed in broad sinus; selenizone distinct, either a rounded to flat-topped ridge or a concave channel, often with distinct lunulae and a thin revolving thread bordering on each side. Shell surface marked only by fine, generally closely spaced growth lines.

Type species. - Bellerophon clausus Ulrich, 1897, by original designation of Knight (1945).

Distribution. - Sphenosphaera is known from Middle Ordovician (Blackriveran?-Rocklandian) to Upper Ordovician (Richmondian) strata in eastern and central North America (Rollins, 1967).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - Sphenosphaera differs from Bellerophon Montfort in its generally less globose whorl form, its more flared aperture margins, which form prominent posterolateral shelves (Pl. 30, figs. 9-10), and most particularly in the possession of a distinct median ridge on the whorl floor (Pl. 30, figs. 2, 9, 17).

Carinaropsis Hall has a median whorl floor ridge, but it is sharp rather than rounded (Pl. 38, figs. 9, 11). It also differs from Sphenosphaera in having a reduced coil, a much greater rate of whorl expansion, and a parietal platform extending well into the apertural cavity (Pl. 38, figs. 3-5).

Bucanopsis Ulrich also has a sharp median whorl floor ridge as in Carinaropsis, but its ridge continues over the ventral parietal shelf. Bucanopsis is further distinguished by revolving shell markings. Rollins (1967) noted that some species of Knightites bear a low, rounded, whorl floor ridge, but that genus is also characterized by revolving shell ornament. In the fauna under consideration, species of Bucania with small umbilici can closely resemble Sphenosphaera in their general shell form. Bucaniids can be readily distinguished, however, by their revolving ornament and their lack of any median whorl floor keel.

Discussion. - Knight (1945, p. 334) erected the genus Sphenosphaera for the Ordovician species assigned to Bellerophon by Ulrich and Scofield (1897) and other related species. He believed that the median whorl floor ridge and the posterolaterally flaring aperture margins allied these spe-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

cies more closely to the Ordovician genera Carinaropsis and Bucanopsis. Knight and others (1960, p. 1180) placed these three genera together in the subfamily Carinaropsinae Ulrich and Scofield, 1897.

Rollins (1967, p. 117-121) recognized only three species to Sphenophaera: S. clausus, S. troosti, and tentatively S. mohri. He claimed that the median floor ridge which largely defines the genus is not present, or at least is not known to be present (due to preservation) in other Ordovician species which he returned to B. (Bellerophon). In this study, the presence of a median whorl floor ridge is illustrated in S. clausus (Pl. 30, figs. 2, 9, 17; Pl. 31, fig. 3; Pl. 32, fig. 4), S. troosti (Pl. 29, figs. 4, 9, 13, and 15), and is confirmed in S. mohri (Pl. 41, figs. 1, 3).

The presence of a whorl floor ridge is also shown in two more species here. The type specimens of Bellerophon troosti burginensis Ulrich (=Sphenosphaera burginensis, herein) do not expose the whorl floor, but fragmented silicified specimens of the species from USGS Sample 4883-CO show a distinct, narrowly rounded, whorl floor ridge. The situation is the same with Sphenosphaera capax Ulrich, with new silicified material from USGS Sample 6412-CO (Pl. 34, figs. 10-13) of that species revealing a distinct, rounded, whorl floor ridge. Therefore, both species are assigned to the genus Sphenosphaera.

Three of Ulrich's (1897) species are assigned to B. (Bellerophon), as done by Rollins (1967), because of the apparent absence of a median whorl

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

floor keel, these being B. (B.) bilineatus Ulrich, B. (B.) nana Ulrich, B. (B.) subpatula Ulrich.

Three other species in the fauna under discussion unquestionably belong to either B. (Bellerophon) or Sphenosphaera and are tentatively assigned to the Sphenosphaera in this paper. The known specimens of S. recurvus Ulrich (Pl. 33, figs. 1-6), S. subangularis Ulrich (Pl. 33, figs. 10-15), and ?S. subglobulus Ulrich (Pl. 33, figs. 7-9) do not expose the whorl floor; however, because of greater similarity of shell morphology with species of Sphenosphaera, they were believed better placed in that genus (see discussion under B. (Bellerophon)).

The whorl floor keel ends within the aperture at the parietal callosity in Sphenosphaera, as it also does in Carinaropsis; however, the keel extends onto the parietal lip in Bucanopsis, Phragmolites, and Tropidodiscus, where it is the result of the blanketing of a dorsal carina by the parietal lip. The whorl floor keel in Sphenosphaera and Carinaropsis may be a vestigial structure, possibly being retained in the more advanced genera as a muscle attachment site.

Contrary to Knight and others (1960), who placed Sphenosphaera in the Carinaropsinae, the genus is here allied with Bellerophon in the Bellerophontinae. There is almost certainly a relationship between Sphenosphaera and Carinaropsis, the two either arising from the same stock, or more likely the latter being a specialized derivative of the former. The reduction of the coil and the marked growth of a platform into the aper-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tural cavity distinguish the Carinaropsinae. Sphenosphaera could easily be considered a subgenus of Bellerophon, the only major distinguishing feature being the whorl floor ridge. This whorl floor ridge is rounded, rather than sharp as in Carinaropsis, and Rollins (1967) notes low rounded whorl floor ridges in some members of the Knightinae, so that the significance of that character as a supragenetic taxobasis is rather dubious.

Two previously named species are placed in synonomy: Bellerophon rogersensis Foerste, 1914, with S. clausus Ulrich, 1897, and Bellerophon cincinnatiensis Miller and Faber, 1894, with S. mohri Miller, 1874.

SPHENOSPHAERA CLAUSUS Ulrich, 1897

Pl. 30, figs. 1-23; Pl. 31, figs 1-13; Pl. 32, figs. 1-15

Bellerophon clausus ULRICH in ULRICH & SCOFIELD, 1897, p. 916, Pl. 64, figs. 7-10; BASSLER, 1932, Pl. 20, figs. 17-18; KNIGHT AND OTHERS, 1960, Fig. 98, 2a-c

Bellerophon rogersensis FOERSTE, 1914, p. 141, Pl. 2, figs. 4a-c.

Diagnosis. - Shell moderate in size (up to 26.5 mm in length), umbilici closed; parietal lip thickened in central area, reflexed posterolaterally forming excavated shelves; selenizone elevated, with distinct bordering threads and lunulae.

Description. - Shell moderate in size and in its rate of expansion; umbilici completely closed by reflexed parietal lip; dorsal whorl slopes

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

broadly convex, angle of their slope becoming more obtuse with growth. Selenizone on elevated flat-topped median carina, bordered by fine revolving thread on either side, lunulae distinct. Aperture outline sub-triangular, flared posteriorly to form concave posterolateral shelves; median parietal area thickened; median whorl floor ridge well rounded, not extending onto parietal callosity. Growth lines as thin threads, closely spaced and regular, becoming less so in maturity, broadly curved over dorsal slopes reflecting broad shallow sinus; slit shallow.

Measurements. - Measurements of S. clausus are listed in Table 77.

Table 77: Measurements of Sphenosphaera clausus in mm.

MUSEUM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
USNM								
45701	~22.0	15.3	16.5	~21.9	12.75	10.3	8.2	1.0
45700	~18.0	12.1	~11.6	~17.6	~10.0	9.6	7.0	1.1
315618	~16.0	13.0	7.5	18.95	9.8	9.1	6.7	0.6
315640	--	7.8	--	11.7	6.75	5.0	3.4	0.6
"	--	--	--	12.5	--	6.1	4.8	--
"								
"	--	11.6	--	19.0	--	10.0	7.7	--
"	--	10.1	--	18.0	9.5	7.1	6.3	--
315645	12.6	9.3	9.0	13.75	7.0	--	--	0.6
"	--	7.2	--	10.6	6.1	4.5	3.1	0.75
"	12.3	8.6	9.7	11.7	--	--	4.25	--
"	--	--	--	11.4	--	5.2	4.35	--
"	--	--	--	13.8	--	--	4.6	--
"	--	--	--	--	7.2	--	4.4	0.7
"	--	--	--	10.9	5.9	--	3.6	--
"	--	--	--	9.1	5.3	--	--	--
"	--	--	--	8.5	4.9	--	--	0.55
"	--	--	--	9.9	6.4	--	--	0.7
315647	--	7.2	--	10.7	5.7	5.0	3.7	0.65
"	--	--	--	9.75	--	--	--	0.60
"	--	11.8	--	19.0	11.15	8.0	6.7	1.3
"	--	9.4	--	14.6	9.15	6.9	5.5	0.8
"	--	--	--	18.8	--	--	6.4	--
"	--	--	--	16.4	--	--	5.8	--
"	--	12.8	--	19.6	--	9.6	7.7	--

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

MUSEUM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
"	--	--	--	16.2	7.1	6.6	5.0	--
"	--	--	--	19.5	--	9.2	7.35	--
"	--	--	--	23.5	--	--	10.75	--
"	12.8	9.3	9.4	13.7	7.9	7.0	4.9	--
315649	--	14.6	--	20.2	--	--	--	--
315648	--	--	--	17.0	--	--	--	--
"	--	--	--	17.0	11.2	--	--	--
"	--	11.0	--	15.7	10.1	9.2	6.7	1.1
315622	10.6	8.1	7.3	12.4	7.7	6.4	5.1	0.5
315623	--	--	--	20.9	--	--	7.8	1.0
315651	18.0	--	--	20.8	--	--	--	--
315624	18.55	13.5	14.75	21.05	12.75	8.2	7.1	1.3
315652	26.55	--	19.15	26.0	--	--	--	1.25
"	23.5	--	18.4	28.0	14.8	11.7	--	--
"	21.0	14.8	16.7	26.0	12.2	9.7	7.0	--
"	--	--	--	20.8	11.0	--	6.2	1.2
"	--	--	--	20.2	9.1	7.3	6.2	1.0
315653	--	10.4	--	19.0	9.4	8.2	6.0	--
315626	23.0	17.7	10.7	22.7	--	--	--	--
315627	--	12.0	--	21.0	10.7	8.8	6.5	1.5
315628	--	14.0	--	24.5	13.0	10.0	7.8	--
315654	18.5	14.8	15.8	22.5	10.7	9.4	7.8	1.4
"	20.2	14.1	16.0	23.0	12.1	10.6	7.7	1.1
"	22.5	14.7	17.8	24.0	--	--	--	--
"	--	--	--	23.1	13.7	9.5	8.0	--
"	--	--	--	24.5	--	--	--	--
"	--	--	--	24.6	--	--	--	--
"	13.8	9.4	8.2	16.1	8.9	6.5	5.5	--
"	13.6	9.4	9.8	15.5	--	7.0	5.6	0.9
"	16.55	11.1	12.9	17.1	9.3	7.7	6.8	1.2
"	--	13.6	--	22.9	11.0	9.1	8.4	1.5
"	--	12.5	--	19.0	9.7	8.25	7.5	1.3
"	--	12.1	--	17.3	9.4	8.0	6.4	1.25
"	--	12.8	--	18.5	9.9	7.5	6.5	1.1
"	--	12.5	--	20.2	9.6	--	7.2	1.2
"	--	--	--	22.2	--	--	8.1	--
"	--	12.3	--	22.8	--	--	--	--
"	--	--	--	17.0	10.2	8.1	6.4	1.3
"	--	12.7	--	19.0	--	--	--	--
"	--	10.4	--	16.9	9.6	7.3	6.5	1.15
"	--	10.5	--	15.8	--	--	--	1.2
"	--	--	--	17.0	--	--	--	1.4
"	12.15	9.4	9.0	13.6	7.6	--	--	.08
"	--	8.9	--	13.3	7.7	6.5	5.3	0.9

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - The holotype, USNM 45701 (Pl. 30, figs. 1-6), is a brown, silicified specimen from the Bigby-Cannon Limestone of Tennessee. An Ulrich and Scofield (1897, Pl. 64, fig. 9) hypotype from Kentucky (USNM 45700, Pl. 30, figs. 7-8), was the only calcitic specimen examined here.

The species is common in the new silicified samples from Kentucky. It was recognized in the Grier Limestone Member (4879-CO, 4880-CO, 4928-CO, 5067-CO, 5094-CO, 5096-CO, 5107-CO, 7782-CO); the Salvisa bed of the Perryville Limestone Member (5015-CO, 6915-CO, 6916-CO), the Tanglewood Member (7783-CO, 7787-CO, 7796-CO), the Devils Hollow Member (5087-CO, 5095-CO), and the Millersburg Member (7344-CO, 7353-CO) of the Lexington Limestone, and the Clays Ferry Formation (6128-CO, 6142-CO, 6143-CO, 7343-CO, 7345-CO, 7348-CO, 7349-CO, 7350-CO, 7450-CO, 7458-CO, 7812-CO).

Two weathered slabs (UCGM 44301 and 44302) from the Cannon Facies of the Bigby-Cannon Limestone of Smith County, Tennessee show well preserved silicified specimens associated with other mollusk debris and tabulates (Pl. 31, figs. 11, 12-13).

Distribution. - The species is known from both the Cannon and Bigby facies of the Bigby-Cannon Limestone in central Tennessee (Bassler, 1932; Wilson, 1949). In Kentucky, it is known throughout the Lexington Limestone above the Logana Member (see Material heading above), and from the Clays Ferry Formation, mainly where this unit intertongues with the Lexington Limestone. S. clausus is apparently restricted to strata of Kirkfieldian-Shermanian age.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. clausus was the most abundant species in the USGS silicified collections from the Upper Lexington Limestone of central Kentucky (see Paleoecology section).

Comparisons. - S. clausus is very similar in form to S. troosti (D'Orbigny), but the former's umbilici are entirely closed, its selenizone is more clearly defined by bordering threads and distinct lunulae, and its parietal lip has a more thickened central callosity which is bordered by shallow concavities on the posteriorly flared aperture shelves. The closed umbilicus and the much thickened parietal area also distinguish S. clausus from other congeneric species in the Cincinnati Arch fauna.

Discussion. - S. clausus is by far the most common species of the genus Sphenosphaera in the Cincinnati Arch fauna. It is undoubtedly closely related to S. troosti, and with imperfect material it may be difficult to distinguish the two species from one another. It is believed here that the closure of the umbilicus is an advanced character, and therefore S. clausus is derived from S. troosti or some earlier umbilicate species such as S. subglobulus (Ulrich). Late Ordovician species with closed umbilici, such as S. recurvus, S. subangularis, and S. mohri, were most likely descended from S. clausus. The extremely well marked selenizone of S. clausus is also thought to be an advanced feature.

S. clausus, more than any other species of Sphenosphaera, shows similarity to Carinaropsis cymbula (Pls. 37, figs. 1-11), and it is possible that the Carinaropsis is derived from Sphenosphaera. Like Carinaropsis

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

cymbula, S. clausus has a similarly well-defined selenizone, and, more importantly, has a similar inner aperture region. Both species have a median whorl floor ridge, an enlarged parietal area, and posterolateral excavations on the parietal shelf. However, the whorl floor ridge is broadly rounded in S. clausus (Pl. 30, figs. 2, 9, 14, 17), rather than narrow and sharp as in Carinaropsis (Pl. 38, figs. 9, 11). The parietal area of S. clausus is thickened and slightly extended (Pl. 30, figs. 9-10), but does not protrude well into the apertural cavity as it does in Carinaropsis (Pl. 38, figs. 1-2, 4-5). The posterolateral excavation of the parietal shelf in both species is the result of the median parietal thickening and the flaring and draping of the aperture margins. It is likely that these excavations had similar functions in both species, but they do not seem to have been effective channels for currents, as they are not linear, nor do they open to the shell interior. It is probable that the concavities housed the posterior foot when the animal clamped down against the substrate.

Bellerophon rogersensis Foerste, 1914, was described from compressed internal molds and a single shell fragment collected from the Clays Ferry Formation just above Millersburg Member of Lexington Limestone in central Kentucky. It was reported from a "gastropod horizon" which also contained specimens of Tetranota, Liospira, and Lophospira, and which was bounded above and below by strata containing brachiopod-bryozoan-trilobite assemblages. Foerste (1914, p. 141) compared the species to Sphenosphaera

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

recurvus, each having a relatively elongate aperture. It is believed here that compressed internal molds give this mistaken impression (Pl. 32, figs. 13-15), and that these specimens most likely belong to S. clausus, which is also reported from the Clays Ferry Formation here (see Pl. 30, figs. 17-21). The general shell form and the wavy parietal lip curled back closing the umbilicus (or nearly so) support this conclusion. Further support is given by Foerste's single shell fragment which shows a slightly elevated selenizone which is concave and bordered by thin threads, just as in S. clausus.

SPHENOSPHAERA TROOSTI (D'Orbigny, 1840)

Pl. 29, figs. 1-22

Bellerophon troosti D'ORBIGNY, 1840, p. 206; SAFFORD, 1869, p. 289, Pl. 3G, figs. 4a-d; ULRICH & SCOFIELD, 1897, p. 915, Pl. 64, figs. 1-5; GRABAU & SHIMER, 1909, p. 618, fig. 829a-c; BASSLER, 1909, p. 183, figs. 20, 9-10; BASSLER, 1932, Pl. 20, figs. 14-16; McFARLAN, 1931, Pl. 4, fig. 8; SHIMER & SHROCK, 1944, p. 443, Pl. 178, figs. 12-14; WILSON, 1948, Pl. 10, figs. 7-9; WILSON, 1949, Pl. 10, figs. 7-9.

Diagnosis. - Shell moderately small (up to 19.5 mm in length); whorls broad, somewhat inflated; umbilici narrowly open, small; selenizone a rounded dorsomedian ridge, lunulae faint.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderately small; whorls somewhat inflated, dorsal slopes broadly convex, width greatest at base, outline subtriangular. Umbilici open, small, sometimes partly covered by reflexed parietal lip. Aperture margin flared posteriorly and laterally forming shelves with slight excavations; parietal thickening moderate; whorl floor ridge low, well rounded. Selenizone a prominent, rounded, dorsomedian ridge, with lunulae faint or lacking. Growth lines fine, closely spaced, becoming coarser and even slightly wrinkled on lateral whorl slopes in maturity; growth lines curve gently showing broad shallow sinus.

Measurements. - Measurements of S. troosti are listed in Table 78.

Table 78: Measurements of Sphenosphaera troosti in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
315602	19.5	14.75	8.0	22.5	11.7	9.3	7.5	1.1
315665	17.8	13.9	7.5	20.8	10.7	7.8	6.9	1.0
315603	--	12.8	--	19.6	10.4	7.8	6.9	1.25
315604	9.5	7.65	4.1	9.8	5.85	4.6	3.9	0.5
45711	--	--	--	18.2	10.15	7.8	6.6	1.1
"	14.0	11.0	6.0	16.5	8.75	6.25	5.7	0.8
"	14.1	10.8	6.15	15.9	8.5	7.8	6.1	0.8
"	--	9.0	--	14.4	7.2	5.35	4.75	0.7
"	--	7.5	--	9.8	5.85	4.6	3.9	0.5
"	7.2	5.3	3.15	7.3	4.35	3.7	2.7	0.5
315613	--	9.5	--	17.0	8.6	7.1	5.4	--

Material. - Two collections of type material were examined. USNM 45710 consisted of six silicified specimens from the Cannon facies of the Bigby-Cannon Limestone at Nashville, Tennessee, and USNM 45711 consisted

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

of 17 silicified specimens "Flanagan Chert" near Danville, Kentucky. Ulrich and Scofield (1897, p. 916) state these collections were made by J. M. Safford and by E. O. Ulrich, respectively. The Tennessee specimens are probably those on which Safford based his original figures of the species; from this collection, USNM 315602 (Pl. 29, figs. 1-4) is here designated the lectotype of the species, and USNM 315665 (Pl. 29, figs. 5-9) and the four specimens remaining under USNM 45710 are designated paralectotypes. The hypotypes USNM 315603 (Pl. 29, figs. 10-13), USNM 315604 (Pl. 29, figs. 14-16) were selected from Ulrich's Kentucky collection (USNM 45711) for illustration. New specimens from the USGS silicified collections were recognized in samples from the Grier Limestone Member (4073-CO, 4959-CO, 5067-CO) of the Lexington Limestone.

Distribution. - In Tennessee, S. troosti is known from the Cannon and Dove-colored facies of the Bigby-Cannon Limestone (Bassler, 1932; Wilson, 1949). In Kentucky, the species was recognized here in the Grier Limestone Member of the Lexington Limestone. McFarlan (1931, Pl. 20) reported the species from the Faulconer bed of the Perryville Limestone Member of the Lexington Limestone. The type collections made by E. O. Ulrich are from the "Flanagan Chert" of the upper Lexington Limestone, an outdated term found to represent various silicified horizons.

Some poor fragments of small specimens of Sphenosphaera sp. indet. were found in USGS silicified samples 5022-CO and 6131-CO from the Curdsville Limestone Member of the Lexington Limestone. These specimens have

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

an angular dorsum and small open umbilici; therefore, they may be related to S. troosti.

Comparisons. - The most distinctive features of S. troosti, which serve to distinguish it from contemporaneous species, are its small but distinctly open umbilicus, and its prominent, rounded, ridge-like selenizone.

Discussion. - Although similar to S. clausus, S. troosti is easily recognized when sufficiently well-preserved material is available. S. troosti is thought to be descended from S. subglobulus and closely related to S. clausus, being somewhat intermediate in form between these two species, because of its slightly inflated whorls and its small umbilicus.

It is interesting that Wilson (1949) listed S. clausus from the Bigby and Cannon facies, and S. troosti from the Cannon and Dove-colored facies of Bigby-Cannon Limestone. The two species overlapped in the normal marine shelf environment (Cannon), but S. troosti also inhabited quiet nearshore lagoons and mudflats (Dove-colored facies), whereas S. clausus also dwelt in the high energy shoaling environment (Bigby facies). The tighter coiled, nonumbilicate shell of S. clausus may have been streamlined for life in higher energy environments. The two species were not found to co-occur in the USGS Kentucky samples.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SPHENOSPHAERA BURGINENSIS (Ulrich, 1897)

Pl. 28, figs. 10-23

Bellerophon troosti burginensis ULRICH in ULRICH & SCOFIELD, 1897, p. 916, Pl. 4, fig. 6.

Diagnosis. - Shell moderate in size (up to 21.5 mm in length); whorls relatively narrow; umbilici narrowly open; posterolateral aperture margins horizontal; selenizone thin, elevated, concave, with bordering threads and lunulae.

Description. - Shell moderate in size; expanding rather slowly so that whorls are relatively narrow; whorl slopes evenly convex. Umbilici moderate in size. Posterolateral aperture margins reflexed horizontally, not curling over umbilicus, but passing straight beneath it. Whorl floor ridge narrow, sharply rounded. Selenizone elevated on thin dorsomedian carina, concave, bordered by thin revolving threads; lunulae present. Growth lines thin, threadlike, evenly and closely spaced, curving back rather strongly toward selenizone reflecting moderately deep sinus.

Measurements. - Measurements of S. burginensis are listed in Table 79.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 79: Measurements of Sphenosphaera burginensis in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
45712	21.5	15.3	(16.45)	22.4	11.5	9.8	--	1.1
47595	19.15	13.8	(14.5)	21.0	9.9	7.6	--	1.2
315615	14.3	11.0	(10.2)	15.0	8.7	6.2	4.4	--
315641	--	--	--	13.2	--	5.0	3.5	--
315616	17.4	9.8	(11.8)	15.5	8.25	6.0	5.3	0.75

Material. - The holotype, USNM 45712 (Pl. 28, figs. 10-12), is a brown, worn, silicified specimen. The single paratype, USNM 47595 (Pl. 28, figs. 13-15) is also silicified. S. burginensis was found in the new USGS silicified collections (Pl. 28, figs. 16-23) from the Grier Limestone Member (4883-CO, 5094-CO, 5096-CO) and Perryville Limestome Member (S. cf. burginensis) (6915-CO) of the Lexington Limestone.

Distribution. - Both type specimens cited above are labeled from the "Flanagan Chert" near Burgin, Kentucky, this being an archaic name used for silicified beds at different horizons in the upper Lexington Limestone. New material comes from the Grier Limestone and Perryville Limestone Members of the Lexington Limestone (Kirkfieldian-Shermanian).

Comparisons. - This species can be separated from all others by its narrow whorl form, resulting from a slower whorl expansion rate and less flaring of the aperture margins. Like S. troosti, it has a small open umbilicus.

Discussion. - S. burginensis was originally described as a "variety" of S. troosti by Ulrich (1897) with some reservations. Considering the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

subtle differences used to define the species of Sphenosphaera, S. burginensis is distinct enough to warrant an independent specific designation, having a distinctly narrower whorl profile.

SPHENOSPHAERA RECURVUS (Ulrich, 1897)

Pl. 33, figs. 1-6

Bellerophon recurvus ULRICH in ULRICH & SCOFIELD, 1897, p. 920, Pl. 64, figs. 11-13.

Diagnosis. - Shell moderately small (16.8 mm in length), rather narrow; umbilici closed; selenizone elevated, rounded; growth lines strongly curved back.

Description. - Shell moderately small in size, rather narrow in dorsal view, gradually expanding. Umbilici completely closed by thin parietal lip curled back over ventral coil. Aperture seemingly elongate, probably subtriangular, not expanded laterally. Selenizone elevated, truncated but rounded, with no lunulae visible. Growth lines wrinkled-sublamellose, broadly curved, becoming strongly curved backward dorsally to reflect relatively deep sinus, not evenly spaced.

Measurements. - Measurements of S. recurvus are listed in Table 80.

Table 80: Measurements of Sphenosphaera recurvus in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
45705	16.8	11.6	12.7	--	9.4	7.8	5.6	1.2

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Ulrich (1897) reported only a few specimens were known. Only one was located here, the holotype (USNM 45705) a calcitic specimen with a broken aperture and with a fairly well preserved shell surface (Pl. 33, figs. 1-4).

Distribution. - The holotype is labelled as coming from the Corryville biofacies of the Grant Lake Limestone or Bull Fork Formation (Maysvillian) in the Mt. Auburn area of Cincinnati, Ohio.

Comparisons. - S. recurvus resembles S. clausus, but is narrower in form, with a more elongate aperture. Also S. recurvus has a rounded selenizone with no bordering threads nor lunulae, sublamellose rather than thread-like growth lines, a deeper apertural sinus, and a lesser parietal callosity. S. subangularis is even higher and narrower than S. recurvus, and has thin thread-like, closely and evenly spaced growth lines.

Discussion. - This species was returned to B. (Bellerophon) Montfort by Rollins (1968) because no specimen is sufficiently well-preserved to prove the presence of a median whorl floor ridge. The species is here tentatively placed in Sphenosphaera Knight, as Knight (1945) intended, and is thought to have been descended from S. clausus.

The wrinkled sublamellose growth lines in this species are unique when compared to related species in the fauna under consideration.

A few highly recrystallized, fragmentary specimens from the Maysvillian Leipers Formation, Rowena Ferry, Russell County, Kentucky, are here identified as S. aff. S. recurvus. The specimens have closed umbilici,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

rather narrow coils, and seem to have wrinkled growth lines. The specimen figured here (Pl. 33, figs. 5-6; UCGM 44282) shows moderate lateral expansion of the aperture, a feature which is not preserved in the holotype of the species.

SPHENOSPHAERA SUBANGULARIS (Ulrich, 1897)

Pl. 33, figs. 10-15.

Bellerophon subangularis ULRICH in ULRICH & SCOFIELD, 1897, p. 920, Pl. 64, figs. 14-16.

Diagnosis. - Shell moderate in size (up to 21 mm in length), with high angular dorsum; umbilici closed; aperture longer than wide.

Description. - Shell moderate in size; whorl expansion rather rapid; umbilici closed by thin reflexed parietal lip. Median parietal callosity poorly developed. Whorls very high, increasingly so in maturity, the dorsal slopes being gently convex and forming an acute angle with one another. Aperture outline subtriangular, lateral expansion apparently slight so that aperture longer than wide. Selenizone low and rounded in early growth, becoming more prominent in maturity; no lunulae or bordering threads known. Growth lines fine, thread-like, evenly and closely spaced, broadly curved.

Measurements. - Measurements of S. subangularis are listed in Table 81.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 81: Measurements of Sphenosphaera subangularis in mm.

USNM No.	Shell Length	Shell Length	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
45708	~21.0	15.4	~16.5	~16.2	10.1	8.6	6.8	0.9
315666	~13.0	9.8	--	--	--	--	--	0.7

Material. - Two worn calcitic specimens were catalogued as "holotype(s)" under USNM 45708. The specimen here left catalogued with that number (Pl. 33, figs. 11-15) is designated the lectotype. The second specimen (Pl. 33, fig. 10) is designated a paralectotype, and is here catalogued under USNM 315666.

Distribution. - The type specimens are labled as coming from the "Richmond Group" (Richmondian) at Richmond, Indiana.

Comparisons. - The extremely high dorsum of this species separates it from S. clausus and S. recurvus, which are otherwise closest to it morphologically.

Discussion. - No specimen reveals the whorl floor, so it is not known if a whorl floor ridge is present or absent. However, because the species appears to be descended from S. clausus, it is placed in Sphenosphaera. S. recurvus is morphologicaly, and thus probably phylogentically, intermediate between S. clausus and S. subangularis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

SPHENOSPHAERA CAPAX (Ulrich, 1897)

Pl. 34, figs. 1-13

Bellerophon capax ULRICH in ULRICH & SCOFIELD, 1897, p. 921, Pl. 63, figs. 50, 51, and Pl. 64, figs. 40-43.

Diagnosis. - Shell moderately large (up to 38.2 mm in length), rapidly expanding; whorls somewhat inflated; umbilici open; whorl floor keel large and broadly rounded.

Description. - Shell moderately large, whorls rather rapidly expanding throughout growth, abruptly expanded laterally in maturity. Aperture outline nearly semicircular, broadening to more semielliptical in maturity. In relation to this, whorls somewhat inflated, becoming less so in maturity. Umbilici moderate in size, often partially covered by reflexed parietal lip. Selenizone a low rounded ridge, no lunulae known. Whorl floor keel large, broadly rounded; little or no parietal callosity; parietal lip thin, folded back and over coil and reflexed postero-laterally. Shell moderately thin, expanded adult aperture somewhat thicker. Growth lines poorly known, apparently fine, gently curved, becoming more sharply curved dorsally reflecting a rather deep, narrow sinus.

Measurements. - Note that the measurements of S. capax in Table 82 were made on poorly preserved specimens.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 82: Measurements of Sphenosphaera capax in mm.

USNM No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
315606	33.0	18.0	26.4	33.2	15.95	13.5	11.0	--
315607	38.2	26.3	28.0	35.6	21.3	17.4	14.0	1.3
315608	--	--	24.8	38.3	--	--	--	--
45699	37.3	--	27.5	45.7	--	--	--	--

Material. - Eight poorly preserved calcitic specimens were catalogued as "cotypes" under USNM 45698, and a ninth as USNM 45699. From this group a lectotype was selected (USNM 315606, Pl. 34, figs. 1-3). All others are paralectotypes, three of which are also figured here (Pl. 34, 4-9): USNM 315607 and 315608, both formerly in 45698 group, and USNM 45699. A small number of fragmented specimens in USGS silicified collections 6411-CO, 6412-CO, and 6414-CO, are here placed in S. capax, including USNM 387016 (Pl. 34, fig. 10) and USNM 387017 (Pl. 34, figs. 11-13).

Distribution. - Ulrich and Scofield (1897, p. 922) cited the species as occurring in the "Lower part of the Loraine group and upper part of the Utica group....in the vicinity of Cincinnati, Ohio," the old stratigraphic names being quivalent to strata of late Edenian and early Maysvillian age. The type suite is from the Maysvillian-aged Fairmount biofacies of the Fairview Formation at Covington, Kentucky. The new silicified material comes from the Gilbert Member of the Ashlock Formation (late Maysvillian) in central Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - S. capax is quite similar in general shell form to S. mohri Miller, but can be distinguished by its open umbilicus, its much less prominent selenizone, and its more prominent whorl floor ridge. S. capax is also easily distinguished from S. recurvus by its open umbilicus, as well as by its more inflated and more greatly expanded and inflated whorl form.

Discussion. - Comments on S. capax are made in the discussion of S. mohri.

SPHENOSPHAERA MOHRI (Miller, 1874)

Pl. 35, figs. 1-16; Pl. 36, figs. 1-15; Pl. 41, figs. 1-5

Bellerophon mohri MILLER, 1874, p. 306, fig. 30; 1889, p. 397, fig. 653; ULRICH & SCOFIELD, 1897, p. 920, Pl. 64, figs. 44-45; CUMINGS, 1908, p. 954, Pl. 39, figs. 2-2a; FOERSTE, 1924, p. 208, Pl. 34, fig. 9.

Bellerophon cincinnatiensis MILLER & FABER, 1894, p. 29, Pl. 1, figs. 23-24.

Bellerophon parksi FOERSTE, p. 208, Pl. 35, figs. 4a-d.

Diagnosis. - Shell large (up to 36.4 mm in length), umbilici closed; whorls rapidly expanding, somewhat inflated; aperture broad, nearly semicircular; selenizone a prominent ridge.

Description. - Shell large; whorls somewhat inflated, expanding rather rapidly throughout growth, but abruptly expanding laterally in

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

adulthood; umbilici closed. Aperture broad, anterior and lateral margins thin and nearly semicircular in outline; posterolateral margins form rounded corners; inner lip nearly straight and parallel to axis of coiling, thickening inward toward well developed median parietal callosity, and reflexed over coil to close umbilicus. Whorl floor ridge prominent, narrowly rounded to rounded. Selenizone elevated, nearly flat-topped, becoming more prominent through growth; lunulae faint. Sinus moderately narrow and deep; slit apparently rather wide and deep. Growth lines distinct fine threads, very closely spaced throughout growth, broadly curved over whorl slopes, turning abruptly backward only in immediate proximity of selenizone.

Measurements. - Measurements of S. mohri are listed in Table 83.

Table 83: Measurements of Sphenosphaera mohri in mm.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
UC8796	36.4	16.8	30.4	--	13.2	11.3	8.0	1.65
UC8793a	--	--	--	~32.1	16.0	10.3	--	1.9
USNM								
315629	30.0	18.9	22.4	37.25	16.4	13.0	9.8	1.5
315630	--	--	--	41.1	18.4	14.4	12.8	--
315631	--	19.0	--	37.0	17.5	14.3	11.7	1.6
315632	--	7.5	--	11.6	5.7	4.5	--	0.5
315633	--	12.0	--	21.0	9.4	7.85	6.0	1.0
315656	--	18.6	--	39.3	15.4	13.3	10.7	--
"	--	--	--	46.3	18.7	14.3	12.2	--
"	--	15.8	--	33.4	14.2	--	--	1.4
"	--	--	--	30.8	13.9	11.1	--	--
"	--	15.5	--	29.0	13.1	8.0	6.8	--
"	--	19.1	--	32.3	15.2	12.2	11.0	--
"	--	17.5	--	--	14.0	11.7	9.3	--
"	--	--	--	30.2	--	12.4	--	--
"	--	--	--	22.4	13.5	--	--	--
"	--	--	--	30.0	14.5	9.3	7.4	--

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Museum No.	Shell Length	Shell Height	Aperture Length	Aperture Width	Dorsal Width	Posterior Width	Ventral Width	Selenizone Width
"	--	14.0	--	26.7	12.0	10.2	7.2	--
"	--	13.9	--	25.3	11.5	8.0	6.4	--
"	--	--	--	34.0	15.1	13.7	11.0	--
"	--	--	--	27.5	13.3	11.0	8.2	--
"	--	--	--	27.7	--	12.5	9.5	--
"	--	13.2	--	20.7	10.7	9.25	6.7	--
"	--	--	--	20.0	9.2	7.2	5.2	--
"	--	--	--	23.4	10.4	8.1	6.3	--
"	--	--	--	17.9	9.75	7.55	5.5	--
"	--	9.5	--	15.3	8.6	7.0	5.0	0.6
"	--	6.1	--	10.4	5.1	4.4	3.4	--
"	--	--	--	9.75	5.2	4.15	--	--

Material. - The original syntypes are in the Faber Collection at the Field Museum of Natural History, Chicago, Illinois; they consist of three calcitic specimens. UC8793a is designated the lectotype (Pl. 35, figs. 1-4). UC8793b and UC8793c, which are both crushed and distorted by compression, are paralectotypes (Pl 35, figs. 5-8).

The holotype (UC8796), and only known specimen, of Bellerophon cincinnatiensis Miller and Faber (1894) is illustrated here (Pl. 35, figs. 15-16), and that species is placed in synonymy with S. mohri. Bellerophon parksi Foerste is also placed in synonymy with Sphenosphaera mohri.

Ulrich's (1897) hypotypes (USNM 45702) are nine calcitic casts and internal molds, some of which probably do not belong in this species or genus. Two of the better specimens which do belong to S. mohri have been extracted from this collection, and are now catalogued under USNM 315610 (Pl. 35, figs. 12-14) and USNM 315611 (Pl. 35, figs. 9-11).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Numerous specimens were found in the collections of the University of Cincinnati, and Miami University. Specimens used here are UCGM 44303, an internal mold, MU 14539, apparently an external mold but seeming to retain some aspect of the shell, and MU 252T, a calcitic cast.

New silicified material is from USGS Collections 6139-CO, which contained over 200 specimens and fragments, and 6140-CO, containing about 30 poor fragments. From the 6139-CO collection, five specimens were selected for illustration (USNM 315629-315633) (see Pls. 36 and 41), and 19 other specimens were measured (USNM 315656).

Distribution. - S. mohri is distributed throughout Richmondian-aged strata in the Indiana-Ohio-Kentucky tri-state area. It is best known from the Whitewater Formation in the vicinity of Richmond, Indiana, but has also been recognized in the Saluda Formation, and the Liberty and Waynesville biofacies of the Dillsboro Formation.

The holotype of Bellerophon cincinnatiensis, (= S. mohri) is from the Maysvillian Fairview Formation at Cincinnati, Ohio. Bellerophon parksi Foerste, 1924, (= S. mohri) is from Richmondian-aged strata of Ontario, Canada.

Comparisons. - S. mohri differs from S. capax in having closed umbilici, a more rapidly expanded shell, a more prominent selenizone, and a smaller, narrower whorl floor ridge. S. recurvus, which also has a closed umbilicus, is less inflated and expanded than S. mohri, and does not have as prominent a selenizone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - Miller (1874) referred to S. mohri as involute, implying the presence of umbilici, but his type specimens, particularly UC8793c (Pl. 35, figs. 6-8), clearly show the umbilici are closed by the parietal lip. Likewise, Ulrich and Scofield (1897, p. 920) mentioned small umbilici, but the two specimens from their collections shown here (Pl. 35, figs. 9-11 and 12-14) also show the umbilici closed. Foerste (1924, p. 208) named Bellerophon parksi from the Richmondian-aged strata of Ontario saying that it differed from S. mohri in its closed umbilici. As it is clear that the umbilici of S. mohri are closed, then Foerste's "species" appears essentially identical to S. mohri.

S. A. Miller and Faber (1894) named Bellerophon cincinnatiensis for rare specimens from the Maysvillian Fairview Formation at Cincinnati, Ohio, 20 years after S. A. Miller named the Richmondian B. mohri. The holotype, and only specimen of B. cincinnatiensis located here, is a vertically compressed specimen comparing favorably with S. mohri in its closed umbilicus, high selenizone, and distinct closely spaced growth lines, as well as in its general shell form. Miller and Faber (1894) described the aperture as expanded, probably wider than long, but their specimen is not well enough preserved that the shape or size could be accurately ascertained. Because in the present state of knowledge, B. cincinnatiensis has no distinctive morphological traits to readily distinguish it from S. mohri, the two species must be considered synonyms. This extends the range of S. mohri from the late Richmondian down to the early Maysvillian.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S. mohri is undoubtedly the most common member of the genus Sphenosphaera Knight in the Cincinnatian series, being most abundant in the late Richmondian Whitewater Formation in southeastern Indiana. Specimens from this area, while being locally common, are generally poorly preserved. They are often internal molds (Pl. 36, figs. 14-15), encrusted by bryozoan colonies, badly recrystallized (Pl. 35, frigs. 9-11), and many times crushed and distorted by compression (Pl. 35, figs. 5, 6-8). A similar situation plagues other bellerophontaceans and gastropods in that fauna (see Salpingostoma richmondensis, Bucania simulatrix, Cyrtolites ornatus). On the other hand, groups such as the articulate brachiopods and horn corals are often well preserved in these beds. These circumstances support the contention that these bellerophontaceans and gastropods had predominantly aragonitic shells. This aspect of preservation compounds the problem of dealing with rather simple, subtly changing morphologies. Consider the subtle differences in the whorl forms of USNM 315631 and 315629 (Pl. 36, figs. 1-3 and 4-7, respectively), the former being more inflated and robust--and these two specimens are from a single sample. The bryozoan encrusted paralectotypes of S. capax (Pl. 34, figs. 4-5, 6-7) are quite difficult to distinguish from S. mohri. The two species were probably closely related, but may have simply been convergent homeomorphs. Both are larger than their Middle Ordovician ancestors, both are rapidly expanding shells with marked lateral expansion in adulthood, and both occur in rubbly, bioclastic limestone sequences associated with a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

diverse fauna, often where complete encrustation of living or dead shells by bryozoans was common. The expanded, thickened adult apertures of these species suggests that they were sluggish vagrant benthos living in moderately high energy environments, probably grazing on benthic algae.

Family CARINAROPSIDAE Ulrich and Scofield, 1897

Diagnosis. - Shell greatly expanded, coil nearly or completely reduced; interior posteromedian septum developed within aperture; slit as short notch with selenizone, or as a raised hollow keel.

Stratigraphic distribution. - Middle Ordovician - Middle Devonian.

Genera included. - Carinaropsis Hall, 1847; Gyrospira Boucot, 1956; Pterotheca Salter, 1853; Cyclotheca Teichert, 1935; Aspidotheca Teichert, 1935; and Pedasiola Spriestersbach, 1919.

Discussion. - Ulrich and Scofield (1897) placed Carinaropsis and Pterotheca in the Carinaropsidae. Teichert (1928, 1930, 1935) also concluded the two genera were closely related after a series of studies on Pterotheca. Wenz (1938) and Golikov and Starabogatov (1975) recognized two distinct families, the Carinaropsidae and Pterothecidae, but placed the two in close association with one another.

Knight and others (1960) included the Carinaropsinae and Pterothecinae as subfamilies of the Bellerophontidae. In the Carinaropsinae, they included a number of genera showing a tendency toward rapid expansion of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

whorls, reduction of coiling, and generally development of the parietal lip into a plate-like extension, with a whorl floor keep, and a selenizone on a moderately developed dorsal crest. As demonstrated below in the discussion of Carinaropsis cymbula (Hall), the internal septum of the genus is not simply a reflexed parietal lip, as in Bucanopsis and Sphenosphaera, but a greatly extended outgrowth of the parietal region which protrudes into the aperture opening as a separate structural element. Rollins (1967) came to a similar conclusion regarding the Carinaropsinae (sensu Knight and others, 1960). He stated (p. 149): "The Carinaropsinae reflect an unnatural grouping of genera. Gyrospira and Carinaropsis are quite distinct, by virtue of an incipient aperture plate, from Bucanopsis and Sphenosphaera. The former genera reflect a trend that culminated in the Pterothecidae, with the development of a Crepidula-like platform." Rollins (1967) considered Phragmosphaera a subgenus of Patellilabia of the family Knightitinae. However, Rollins (1967) did not formally proposed redefinition of the Carinaropsinae (sensu Knight and others, 1960). That step is taken here, with Bucanopsis and Sphenosphaera transferred to the new subfamily Bucanopsinae of the Bellerophontidae, and Carinaropsis and Gyrospira only left in the Carinaropsinae.

The Carinaropsidae is here treated as a family, and is considered to contain the three distinct but closely related subfamilies Carinaropsinae, Pterothecinae, and Pedasiolinae. It is believed that the Carinaropsinae was ancestral to the other two subfamilies, which include the genera

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

assigned to the Pterothecinae by Knight and others (1960). The Carinaropsinae are characterized by the possession of a small coil and the development of an apertural platform. The Pterothecinae is restricted to genera with a completely reduced coil and a marginal apex, and includes the genera Pterotheca Salter, 1853, and Cyclotheca, Teichert, 1935.

The Pedasiolinae is proposed here as a new subfamily of the Carinaropsidae. This group is characterized by a completely reduced coil, a submarginal elevated apex, and a slit developed as a raised median keel. It contains the genera Pedasiola Spriestersbach, 1919, and Aspidotheca Teichert, 1935, which are distributed through the Middle and Lower Devonian, respectively. The stratigraphic position of these genera suggests that they developed from the Pterothecinae. However, their elevated submarginal apex would seem to be a less advanced condition, being morphologically intermediate between the shell forms in the Carinaropsinae and Pterthecinae. It is believed that the Pedasiolinae probably evolved from the Carinaropsinae separately from the Pterothecinae, which also evolved from the Carinaropsinae.

Subfamily CARINAROPSINAE Ulrich and Scofield, 1897

Diagnosis. - Shell with small but distinct phaneromphalous coil, then broadly expanding rapidly; posteromedian septum well-developed within aperture, but relatively small; slit as short notch, generating a distinct selenizone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Stratigraphic distribution. - Middle Ordovician - ?Devonian.

Genera included. - Carinaropsis Hall, 1847, which occurs in the Middle and Upper Ordovician of North America and Europe. Gyrospira Boucot, 1956, whose occurrence in South America is questionably Devonian (Knight and others, 1960).

Discussion. - The retention of a small coil and a distinct selenizone, and the relatively small apertural septum, show the Carinaropsinae to be the most morphologically primitive grouping within the family. Phylogenetic roots for the family depend on comparisons with Carinaropsis. A genus that may fit the role of ancestor is the Lower Ordovician Eobucania Kobayashi (1955) which has a small involute coil, with a moderately expanded adult aperture, and a distinct selenizone with bordering threads. With partial reduction of the coil and greater expansion of the aperture of an eobucanid type, a Carinaropsis-like shell results. This appears to be the direction of the general morphologic trend within the Carinaropsidae. The Bucanopsinae appear to have a common ancestry with the Carinaropsinae, but in the Carinaropsinae the morphologic trends of coil reduction and rapid shell expansion developed much further. Sphenosphaera shows incipient outbuilding of the parietal area, as well as a tendency toward an increasing rate of whorl expansion, and is considered here to be the most likely ancestor to Carinaropsis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus CARINAROPSIS Hall, 1947

Pls. 4, 37, 38, and 40

Diagnosis. - Shell with small, carinate coil, followed by greatly expanded adult whorl; slit short; selenizone moderately wide, bordered by small ridges; posteromedian platform in apertural cavity, bearing dorsomedian keel.

Description. - Shell having small juvenile coil with carinate dorsum, convex lateral slopes, and open umbilicus; followed at maturity by rapid, broad expansion of whorl producing a patelliform appearance, with broadly convex dorsum; expanded aperture wider posteriorly; slit as short notch; selenizone moderately wide, with lunulae; posteromedian platform protruding into apertural cavity, the anterior margin being straight to concave-upward, with sharp keel dorsomedially; parietal lip excavated to varying degrees; shell thin; growth lines broadly sweeping.

Type species. - C. carinata Hall, 1847, by subsequent designation of Fischer (1885).

Stratigraphic distribution. - Middle (Rocklandian) to Upper Ordovician (Edenian?) of eastern North America (New York, Kentucky, Tennessee, Minnesota) and Great Britain.

North American species. - C. acuta Ulrich and Scofield, 1897; C. carinata Hall, 1847; C. cunulae Hall, 1861; C. cymbula Hall, 1861; C. explanata Ulrich, 1897; C. minima Ulrich and Scofield, 1897; C. phalera (Sardeson, 1892).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

European species. - C. gracilis Reed, 1921; C. moccoyi Reed, 1921.

Discussion. - Hall (1847, p 183) described the genus Carinaropsis as: "Symmetrical, subconical, patelliform, subangulated or carinated on the dorsal line; apex incurved or convolute; aperture oval, narrowed posteriorly". In modern terms, the coil would be considered involute. Also, it is now known that the aperture is broader posteriorly. Hall (1847) named two species, C. carinata and C. patelliformis, the latter of which is now the type species for the Ordovician monoplacophoran genus Archinacelliopsis Horny, 1963.

Hall (1861, p. 93-95) described two more species from the Ordovician of Kentucky and Tennessee which he said resembled Carinaropsis externally, but also showed "a kind of septum as in Crepidula, extending from the posterior side one-third the distance across the cavity". Concerning this feature, Hall commented: "Should this prove to be identical with those which I have designated as Carinaropsis, that generic term will have precedence; but should this important character not be found in those forms, I propose for those now under consideration the generic name of Phragmostoma, from the septum within the aperture". These two species tentatively described as Phragmostoma are now Carinaropsis cunulae and C. cymbula.

Ulrich and Scofield (1897, p. 926-27) briefly discussed the possible relationships of Carinaropsis to Bellerophon (by which they meant the Ordovician species now assigned to Sphenosphaera). They pointed out that

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

both genera possess an expanded aperture with a parietal plate, a carinate dorsum, and a selenizone. However, they concluded that these features had an outward resemblance, but differed greatly in their development. Therefore, they believed Carinaropsis to represent a distinct family. They further proposed that Pterotheca, a genus which most authors of that time believed to be a pteropod, to belong to the same family as Carinaropsis based on their common possession of greatly expanded adult shell, a well-developed parietal platform, a reduced coil, and a carinate dorsum.

Teichert (1935), after studying Pterotheca in detail, also concluded that Carinaropsis and Pterotheca were closely related phylogenetically. Wenz (1938) supported this conclusion placing the families Carinaropsidae and Pterothecidae in close association. Wenz placed Pedasiola with Carinaropsis in the Carinaropsidae. Pedasiola was placed with Pterotheca in the Pterothecinae by Knight and others (1960). Herein, Pedasiola is placed with Aspidotheca Teichert, 1935, in the new subfamily Pedasiolinae of the Carinaropsidae.

Knight and others (1960) allied Carinaropsis with Bucanopsis, Sphenosphaera, Gyrospira, and Phragmosphaera in the subfamily Carinaropsisinae. This interpretation stressed the reflected parietal lips and whorl-floor keel common to these genera. Their Figure 98, 3a is misleading, making the parietal lip of Carinaropsis appear as a simple reflected aperture margin, as in Bucanopsis and Sphenosphaera, when actually the parietal platform of Carinaropsis seems to be developed quite differently. This

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

parietal platform, or septum as it is commonly called, does not simply reflex around the ventral coil, but grows anteriorly into the apertureal cavity through ontogeny. As seen in C. cymbula (Hall) (Pl. 38, figs. 1-2), the septum is developed from the parietal lip, but apparently as a separate structural element. The dorsolateral septal surface attaches to the interior shell roof, sloping downward convexly; it then folds back tightly upon itself, sloping posteriorly as a concave surface to meet the shell wall, and lining that wall to the parietal shell margin. As shown in Pl. 38, figs. 1-2, there appears to be a cavity within the septum. Whether this cavity was actually open is uncertain, as it may be a product of silicification, but the open cavity was seen on other silicified specimens also. Sections through well-preserved calcitic material, which were not available for this study, are needed to confirm the presence of this cavity. If the cavity was actually open, it might be construed as indicating a buoyancy device for a possible pelagic mode of life. However, from the occurrence of the genus and related genera, such an ecologic interpretation is highly unlikely. It is obvious, however, that the septum in Carinaropsis is quite distinct from the reflexed parietal lips in Bucanopsis and Sphenosphaera, and is similar to the interior platform of Pterotheca, as illustrated by Teichert (1935). It is conceivable that Carinaropsis is intermediate in form between forms such as Sphenosphaera and Pterotheca. Supporting this notion is the presence of a keel on the dorsal septal floor in Carinaropsis.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparison between the septa of Crepidula and those of Carinaropsis and Pterotheca has been made ever since Hall's (1861) descriptions and comparisons of Carinaropsis cymbula and C. cunulae. Hoagland (1977, p. 358), in his review of the Calyptraeidae, stated: "The septum of Crepidula is homologous to the columnella. Migration of the point of muscle insertion to the junction of the septum and the shell proper, or onto the shell, is a specialization for sedentary limpet-like existence, as is the derivation of new muscles for shell attachment. The presence of an insertion on either side of the septum as shown by the presence of two muscle scars is a third solution to the problem of attachment of body to shell and substrate". He further explained: "The septum supports the viscera and provides for muscle attachment. It divides the body into three parts: the foot, the viscera, and the head and brood chamber regions.... The disc-like foot covers the area of the septum and no more; thus the larger the septum proportional to the size of the shell, the greater will be the area of the foot. Also, the deeper the septum is inserted into the shell, the thicker may be the foot". Hoagland was able to use the morphology of the septum (median ridge, notches and curves in the margin, positions of muscle attachment) for the differentiation of species. However, he noted that the depth of insertions and the depth of the notches show some intraspecific variation, and that changes in septal area to apertural area in ontogeny must be carefully distinguished from interspecific differences. Many of his observations probably show direct application to the

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Carinaropsidae. It seems likely that the carinaropsids were adapted to a largely sedentary existence, and the morphology of the carinaropsid septum can be used in specific differentiation. Moreover, the increase in the size of the septum from Carinaropsis to Pterotheca probably indicates a concommittant increase in the size of the foot, and possibly denotes an increased specialization to a purely limpet-like existence with stronger clamping power. However, it should be realized that although the septa of Crepidula and Carinaropsis seem to have analogous functional significance, the septum of Carinaropsis is not columellar (as suggested for Crepidula), and the two structures have quite different origins.

CARINAROPSIS ACUTA Ulrich and Scofield, 1897

Pl. 4, figs. 18-25

Carinaropsis acuta ULRICH & SCOFIELD, 1897, p. 928, Pl. 62, figs. 6-9.

Diagnosis. - Shell small (up to 13 mm in length), submature coil greatly compressed laterally and having a sharply angular dorsum; adult shell rapidly expanded; aperture outline becomes subcircular; septum short.

Description. - Shell relatively small for genus, thin, and smooth; submature whorls greatly compressed laterally, producing a relatively high narrow coil with a sharply angular dorsal crest; umbilici subcircular and deep; with rapid expansion of adult whorl, aperture outline changes from

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

triangular to subcircular, dorsal angle becomes less acute quickly and broadens to accommodate a moderately wide selenizone; anterior slope of shell rather steep; posterior lip not reflected strongly, but rather explanate; septum short.

Measurements. Measurements of C. acuta are listed in Table 84. Because of the fragmentary nature of the specimens, these measurements are coarse approximations.

Table 84: Measurements of Carinaropsis acuta in mm.

Museum Number	Shell Length	Shell Width	Shell Height	Coil Width	Septum Length	Septum Width
USNM						
265992	13.05	15.15	8.35	-	6.0	6.3
265993	-	17.15	8.00	3.6	-	-
265994	-	10.10	-	3.5	-	-

Material. - C. acuta was recognized in USGS silicified samples 7784-CO, 5100-CO, 5101-CO, 5023-CO, and possibly (C. cf. C. acuta) in 6134-CO and 6419-CO; the total number of fragmentary specimens was 15. Figured specimens are USNM 265992, 265993, 265994, and 265995 (Pl. 4, figs. 18-25). The types of the species are not figured herein.

Distribution. - Ulrich and Scofield (1897) described C. acuta from the Decorah Formation (middle Rocklandian-middle Kirkfieldian) of Minnesota. In Kentucky the species was recognized in 5 samples from the Curdsville Limestone Member (5023-CO, 5100-CO, 5101-CO, 6134-CO, 7784-CO) and a single possible specimen from the Logana Member (6419-CO) of the Lexington Limestone (both members are Kirkfieldian in age).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - The consistently small size of all the specimens of Carinaropsis in the Curdsville Limestone samples suggested that these forms might be taxonomically distinct from the larger C. cymbula from the Grier Limestone Member. Closer examination confirmed that the Curdsville specimens have a more laterally compressed submature coil that C. cymbula, with a more prominent dorsal carina (Pl. 4, figs. 20 and 24); and their expanded whorl is relatively higher and has a subcircular outline (Pl. 4, figs. 18-19).

Ulrich and Scofield (1897) differentiated C. acuta differed from C. phalera (Sardeson) by its narrower coil and shorter septum. The septum in the Kentucky specimens of C. acuta is always poorly preserved, but where visible, is quite short.

Discussion. - This is the first identification of C. acuta outside of Minnesota. The species is distinguished from juveniles of C. cymbula and C. cunulae mainly by its narrow, sharply crested submature coil. For its small size, C. acuta possessed a rather wide selenizone (Pl. 4, figs. 18 and 24), which broadens rapidly as the mature whorl expanded rapidly into its steep, subcircular form (Pl. 4, fig. 18-19).

CARINAROPSIS CUNULAE (Hall, 1861)

Pl. 37, figs. 12-14

Phragmostoma cunulae HALL, 1861, p. 95; MILLER, 1889, p. 415.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Carinaropsis cunulae (Hall) ULRICH & SCOFIELD, 1897, p. 927, Pl. 62, figs. 10-13; GRABAU & SHIMER, 1909, p. 626, Pl. 845a-c.

Diagnosis. - Shell with relatively large initial coil; septum relatively small and flat, with shallow excavation posteroventrally; posterior aperture margin broad and straight.

Description. - Shell of moderate size (up to 20 mm in length); submature coil relatively large, with sharp dorsal crest and rounded lateral whorl slopes, umbilici small but deep; coil projects distinctly beyond broad straight posterior aperture margin; dorsum of rapidly expanded adult whorl broadly convex; median selenizone distinct and moderately wide; septum relatively short, dorsally nearly flat with slightly concave-upward anterior margin and sharp median keel, ventrally with shallow posteroventral excavation. Ornament unknown.

Measurements. - Measurements of C. cunulae are listed in Table 85. Note that all shell length measurements are minimum values, as the anterior shell margin was not preserved in any available specimen.

Table 85: Measurements of Carinaropsis cunulae in mm.

Museum Number	Shell Length	Shell Width	Shell Height	Septum Width	Septum Length	Coil Width	Selenizone Width
USNM							
45738	20.5	22.4	9.2	13.5	9.85	5.1	2.0
45738	18.9	22.5	8.9	-	10.0	4.95	2.0
45738	16.2	17.75	8.1	10.5	7.9	5.2	2.0
45738	15.2	18.8	-	11.3	9.05	4.5	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - The original Hall types are not present at the American Museum of Natural History and have not been located in any other museum register. Ulrich and Scofield's (1897) hypotypes, USNM 45738, were the only specimens of the species located and examined. This suite consisted of 4 silicified specimens, none of which was complete. Three specimens (USNM 45738) preserved the expanded dorsum and the septum. The fourth specimen which has the dorsum missing, revealing the dorsal septum, was also the only one to retain the submature coil (Pl. 37, figs. 12-14); this specimen is separated from the type suite and catalogued under the new number USNM 265998.

Distribution. - Ulrich and Scofield's (1897) hypotypes (USNM 45738 and 265998) came from the Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) at Nashville, Tennessee. Those authors cited the species from the "Upper Trenton group, Nashville, Tennessee, and Boyle County, Kentucky".

Comparisons. - C. cunulae differs from C. cymbula (Hall) subtly but significantly, having a more inflated submature coil, a septum which is shorter and flatter, and a shallower posteroventral excavation. The last difference is the most distinctive distinguishing morphological feature (compare Pl. 37, figs. 9-11 and 12-14). Ulrich and Scofield (1897, p. 928) compared C. cunnulae to C. phalera (Sardeson) from the Decorah Formation of Minnesota. They stated that C. phalera differs in a less reflected aperture margin which is scarcely truncated posteriorly, a more circular outline, and a greater depth to the concavity of the septum.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Discussion. - C. cunulae appears to be less advanced than C. cymbula when the major morphological trends of the family Carinaropsidae are considered. These trends are mainly the reduction of the coil and the increased development of the septum. C. cunulae has a more inflated coil and a smaller septum. Carinaropsis probably evolved from Sphenosphaera of the Bucanopsinae, which shows rapid whorl expansion, incipient outbuilding of the parietal area, and a median keel on the whorl floor (Pls. 29-36).

CARINAROPSIS CYMBULA (Hall, 1861)

Pl. 37, figs. 1-11 and 15-23; Pl. 38, figs. 1-12

Phragmostoma cymbula HALL, 1861, p. 94.

Phragmostoma natator HALL (in error for cymbula), 1862, Pl. 6, figs. 12-14.

Phragmostoma cymbula Hall, MILLER, 1889, p. 415, fig. 693.

Carinaropsis cymbula (Hall) ULRICH & SCOFIELD, 1897, p. 927, Pl. 62, figs. 1-4; GRABAU & SHIMER, 1909, p. 626, fig. 845d-g; BASSLER, 1932, p. 222, Pl. 20, figs. 21-22.

Diagnosis. - Shell with relatively narrow initial coil; septum relatively large, angled downward toward anterior, anterior margin slightly concave upward; deeply excavated posteroventrally to rear of septum; posterior shell margin convex.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Description. - Shell moderately large (up to about 30 mm in length); submature coil relatively small and narrow, with sharp dorsum, convex (but not inflated) lateral whorl slopes, umbilici small and deep; coil protruding slightly beyond slightly convex posterior shell margin; dorsum of rapidly expanded adult whorl broadly convex, but with median crest upon which slightly raised selenizone rests, the crest becoming increasing rounded through growth; selenizone moderately wide, bordered by low sharp ridges, with median groove, lunulae sometimes distinct; septum relatively large, angled strongly downward toward anterior, dorsally convex in side view, anterior margin nearly straight to strongly concave-upward, dorsomedian keel; posteroventral excavation deep; growth lines broadly sweeping, showing greatest width of shell to be posterolateral, and curve strongly backward near selenizone reflecting rather broad shallow sinus housing short slit; growth lines sometimes as low broad wrinkles; radiating threads sometimes visible; posterior shell margin occasionally slightly arched; shell thin.

Measurements. - Measurements of C. cymbula are listed in Table 86. Although a number of specimens were available, most were not measured because of the fragmentary conditions of the shell margins.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Table 86: Measurements of Carinaropsis cymbula in mm.

Museum Number	Shell Length	Shell Width	Shell Height	Septum Width	Coil Width
USNM					
45739	27.8	21.3	10.8	-	-
45739	-	-	-	9.55	4.4
45739	-	-	8.8	9.5	4.6
265997	-	13.4	-	9.4	4.55
265996	-	-	-	6.8	3.55
265984	-	42.6	-	22.3	3.9
265986	-	47.0	-	21.5	4.0
265987	-	39.3	-	19.3	4.2
265990	-	-	-	-	-
265988	-	31.0	-	14.4	4.35
265985	-	31.9	-	15.1	3.6
4959-CO	-	27.7	-	14.8	-
5015-CO	-	38.2	-	17.9	-
5015-CO	-	36.2	-	16.4	-
7783-CO	-	30.7	-	17.6	-

Material. - Type specimens examined were Hall's (1861) holotype (Pl. 37, figs. 1-4; AMNH 37723) and paratypes (AMNH 37724, 37725a-c), and Ulrich and Scofield's (1897) hypotypes (USNM 45739). Two specimens from the latter suite figured here are given the new catalog numbers USNM 265996 (Pl. 37, figs. 7-8) and USNM 265997 (Pl. 37, figs. 9-11). All of these types are silicified specimens. USNM 87778 is also figured (Pl. 37, fig. 23).

A number of excellent specimens were found in the following USGS silicified collections from Kentucky: D-1196, 5096-CO (USNM 265984, 265986, 265991), 4879-CO (USNM 265987, 265985, 265988, 265990), 4880-CO, 4852-CO, 4876-CO, 4883-CO, 5107-CO, 4073-CO, 5094-CO, 5074-CO, 5099-CO, 5067-CO, 4959-CO, 5015-CO, 7783-CO, ?7809-CO (See Pls. 37 and 38).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Distribution. - Hall's (1861) types are labelled as coming from the "Trenton Limestone at Allen's Bluff, Tennessee". Ulrich and Scofield's (1897) hypotypes are labelled "Trenton Group, near Danville, Kentucky". It should be noted that Hall (1861) had originally mistakenly recorded the species from the "Hudson River Group", which was the equivalent to the Cincinnatian. The so-called "Trenton Group" in Tennessee would be the Nashville Group of modern usage, and in Kentucky would be the Lexington Limestone.

In the USGS silicified collections from Kentucky, C. cymbula was recognized from the Logana Member (D-1196), the Grier Limestone Member (4073-CO, 4852-CO, 4876-CO, 4879-CO, 4880-CO, 4883-CO, 4959-CO, 5067-CO, 5074-CO, 5094-CO, 5096-CO, 5099-CO, 5107-CO), the Salvisa bed of the Perryville Limestone Member (5015-CO), and the Tanglewood Limestone Member (7783-CO and possibly 7809-CO) of the Lexington Limestone. All occurrences of the species are Kirkfieldian-Shermanian in age.

Comparisons. - The only species in the study area which bears any close resemblance to C. cymbula is C. cunulae. The primary basis for distinguishing these two species is the deep excavation of the posteroventral septum (Pl. 37, figs. 3-4, 11, 18-19; Pl. 38, fig. 4-5) of C. cymbula, as compared to the shallow indentation of the posteromedian septum in C. cunulae (Pl. 37, figs. 14). The septum of C. cymbula is larger, protruding farther into the apertural cavity, and is more convex, sloping strongly anteriorly. The submature coil of C. cymbula is slightly smaller and distinctly narrower than that of C. cunulae.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C. phalera (Sardeson) was originally described as possessing indistinct radial folds on the dorsal surface of the shell, but Ulrich and Scofield (1897) did not find any such markings on their specimens. However, a single specimen of C. cymbula from USGS sample 5096-CO (Grier Limestone Member) does show radial markings, these being in the form of faint, widely-spaced threads (Pl. 38, fig. 8). Ulrich and Scofield (1897, p. 928) stated that C. phalera is very similar to C. cunulae, which in turn is very similar to C. cymbula. These species apparently form a closely related group. If new material of C. phalera becomes available, it should be closely compared to the Cincinnati Arch species, as it could be a synonym of one of them.

Discussion. - C. cymbula seems to be more advanced than C. cunulae as shown by the former's smaller coil and larger septum. Hoagland (1977) correlated the size of the septum in the modern Crepidula with the size of the foot. This relationship may hold true for the analogous carinaropsin septum. Possibly the deep posteroventral excavation of the septum in C. cymbula helped to house an enlarged foot when the animal clamped down its shell to the substrate.

Although a few specimens of C. cymbula were found in samples from the Logana, Perryville Limestone, and Tanglewood Members of the Lexington Limestone, the species is most abundant and often fairly well-preserved in samples from the Grier Limestone Member. This would suggest that the species inhabited a wide range of environments, but thrived in shallow, only

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

moderately agitated, normal marine environments, such as represented in the Grier Limestone.

All specimens examined were readily placed in C. cymbula if the ventral septum was visible with its deep excavation. As pointed out by Ulrich and Scofield (1897), the excavation is the main distinguishing feature of the species. The dorsal shell of the species is thin and easily fragmented. Not one specimen is known with a complete shell. The most commonly preserved portion of the shell is the septum, which is thickened by the recumbent folding of the shell layers that construct it. Through most of the breadth of the septum two shell layers are sandwiched together; as the species grew larger, apparently the lateral areas of the septum opened into a small cavity (Pl. 38, figs. 1-2). The double-walled septum and parietal lip of the shell is all that is usually preserved intact. Therefore, the dimensions of the shells and the actual characteristics of the shell margins are poorly known, and variability within the species is difficult to assess with any confidence.

The septum of C. cymbula does show a good deal of variation in size and form, even within a single population. If these animals led a clinging mode of life, as proposed by Rollins (1967), the host object or the energy of the environment may have at least partially governed the morphology of the septum. This would have been particularly true if the septum was the attachment base for the shell muscles. For example, compare specimens USNM 265984 (Pl. 37, figs. 15-21) and USNM 265988 (Pl. 38,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

figs. 3-6), both being from the Grier Limestone Member of the Lexington Limestone but from different samples. The general form of the septa in the two specimens is quite similar, but that of the first is noticeably larger. The anteromedian part of the septum is generally protuberant, as in the above two specimens, but this "nose" is sometimes lacking, particularly in younger specimens (Pl. 37, figs. 3, 9 and 11; Pl. 38, figs. 11-12). Also, the anterior margin of the septum apparently increases in concavity (from an anterior view) during growth.

The submature coil does not appear to have a selenizone, but because of its size it is difficult to tell. The selenizone develops quickly with the rapid expansion of the shell to a certain width, and then remains essentially the same width through the remainder of growth (Pl. 37, fig. 1). There is a median groove on the selenizone, the origin of which is unknown here (Pl. 37, fig. 1; Pl. 38, fig. 10).

The growth lines in the species vary somewhat. Usually they are only fine varices, giving the surface of ths shell a rather smooth appearance (Pl. 37, figs. 15-16 and 20; Pl. 38, figs. 3 and 10). But sometimes they are developed as low wrinkles (Pl. 37, figs. 1-2; Pl. 38, figs. 7-8), which lend a slightly wavy appearance.

Except for the sharp, low ridges bordering the selenizone (Pl. 37, fig. 1), few specimens preserve the radial ornament in Carinaropsis. Contrary to the opinion of Ulrich and Scofield (1897), and confirming that of Sardeson that there are indistinct radial wrinkles in C. phalera

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(Sardeson), one USGS silicified specimen from the Grier Limestone Member (USNM 265991) shows faint, but distinct, widely-spaced, radial threads (Pl. 38, figs. 6-8). This confirmation of radial ornament in the genus supports the opinion that the Carinaropsinae had a common origin with the Bucanopsinae, both most likely arising from early members of the Bucaniinae.

CARINAROPSIS EXPLANATA Ulrich, 1897

Pl. 40, figs. 10-14

Carinaropsis explanata ULRICH in ULRICH & SCOFIELD, 1897, p. 929, Pl. 62, fig. 5.

Diagnosis. - Shell having a large, prominent, triangular beak area with a sharp dorsal crest and steep slopes, and apparently a small coil; lateral shell slopes gently convex and outward sloping.

Description. - Shell moderately large for genus (minimum of 32 mm in length), known only from a fragmentary internal mold; beak area large, prominently elevated, triangular in dorsal view, with sharp dorsal crest and steep lateral slopes, and although this crest broadens with growth, the median axis of the shell remains elevated above the lateral slopes of the shell; broadly, but strongly convex in side view; contact between beak area and lateral shell slopes marked by a sharp break in slope, lateral shell slopes very gently convex and sloping at a much gentler angle outward; character of shell and septum unknown.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - The lectotype (USNM 45740) is a minimum of 32 mm in length, 41.2 mm in width, and 14.4 mm in height. These are the measurements on the single fragmentary internal mold.

Material. - Only 2 specimens are known of this species, both originally catalogued under the number USNM 45740. The specimen shown in Pl. 40, figs. 10-14 is here designated the lectotype (USNM 45740); the other is a paralectotype (USNM 315531). Both specimens are internal molds.

Distribution. - Ulrich and Scofield (1897, p. 929) cited the species as occurring in the "Upper part of the Trenton Group, Covington, Kentucky". These beds are now covered by the Ohio River and its tributaries due to damming of the Ohio River, but would be assigned today to the Point Pleasant Tongue of the Clays Ferry Formation, which is latest Shermanian in age.

Comparisons. - The large triangular beak area distinguishes the species from all others known.

Discussion. - As far as can be told from examination of the type material, Ulrich's (1897) description of the species is highly interpretive, as is his illustration, Pl. 62, fig. 5. The types are fragmentary and do not retain the growth lines, so that the actual outline of the species is unknown. Likewise, the nature of the septum is unknown. Nevertheless, the form of the shell strongly supports the assignment to Carinaropsis. Its coil must have been very small (Pl. 40, figs. 13-14).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Subfamily PTEROTHECINAE Wenz, 1938

Diagnosis. - Shell with coil completely reduced, apex marginal and curved downward; slit developed as a raised hollow keel.

Stratigraphic distribution. - Middle Ordovician - Upper Silurian.

Genera included. - Pterotheca Salter, 1853; Cyclotheca Teichert, 1935.

Discussion. - This is the most advanced subfamily in the Carinaropsidae, completely reducing any vestige of the coil. The broad explanate shells and large parietal platforms of genera in the Pterothecinae are analogous to the morphology of the modern slipper limpet Crepidula, which leads a nearly sedentary mode of life. This analogy infers that species in the Pterothecinae were also sedentary, or nearly so. Species of Pterotheca are commonly associated with abundant leperditiid ostracods (discussed further below), and they probably inhabited shallow lagoons and tidal flats. Considering their paleoenvironmental occurrence and their shell form, it is generally believed that these animals were algal grazers.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Genus PTEROTHECA Salter, 1853

Pls. 26, 39-40

Diagnosis. - Shell broadly expanded, outline ovate to subtriangular to subquadrangular; coil completely reduced, apex marginal and incurved to varying degrees; slit in elevated dorsomedian keel; septum triangular, with 2 short, diverging, ridgelike partitions on upper surface at apex.

Description. - Shell often large (up to 50 mm in length and width), broadly expanded, generally wider than long, outline varying from ovate to subtriangular to subquadrangular; coil completely absent; apex marginal, incurved to varying degrees, often hook-like; slit developed more or less vertical, generating a prominent elevated dorsomedian keel from the apex to the anteromedian aperture margin, which is generally sinuate; lateral shell surfaces convex with comarginal growth lines, lamellae, or undulations, and sometimes with radial markings on either side diverging from the apex along the lines of attachment between the ventral septum and the ventral shell surface, thus defining a slightly elevated triangular area of the dorsal shell overlying the septum; radial treads or cords unknown; septum triangular, proportionate size and angles variable, flat to convex upward, with 2 short, diverging, ridge-like supports or partitions at apical end in narrow space between septum and ventral shell surface; space between shell dorsum and septum very narrow.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Type species. - Atrypa transvera Portlock, 1843, by subsequent designation of Miller (1889, p. 392).

Distribution. - Middle Ordovician (Chazyan) to Upper Ordovician (Richmondian) of Eastern North America and Europe (Great Britain, Czechoslovakia, Germany, Estonia).

Comparisons. - Pterotheca is easily distinguished from similar genera by its prominent dorsomedian keel, its lack of a coil, its marginal incurved apex, and its large triangular septum with its short apical supports.

Discussion. - Species of Pterotheca have been erroneously described as brachiopods (e.g., Atrypa transversa Portlock, 1843) and pelecypods (e.g., Tellinomya anatiformis Hall, 1847), and the genus itself has often been classified with the Pteropoda or Heteropoda.

Hall (1861, p. 96-98), not knowing of Salter's (1853) genus Pterotheca, described a number of North American species under the generic name of Clioderma. Hall (1861) did note that his species were related to Carinaropsis, and that they were more distantly related to Bellerophon (Sphenosphaera of modern usage), thus recognizing the ancestry and relations of the genus. Ulrich and Scofield (1897) also regarded Pterotheca as being related to the bellerophontids, placing it with Carinaropsis in their family Carinaropsidae. Notwithstanding these views, the genus was still often regarded as a pteropod or heteropod by their contemporaries. For example, such influential workers as Miller (1889) and Dall in Zittel-Eastman (1913) both assigned the genus to the Pteropoda.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Teichert (1928), in his initial study of the genus, considered Pterotheca to be a heteropod. However, upon examination of better material (Teichert, 1935), he concluded the genus was actually closely related to Carinaropsis, as proposed by Ulrich and Scofield (1897), and was therefore a bellerophont gastropod. Teichert (1935) suggested that Pterotheca had descended from Carinaropsis and had given rise to the genera Cyclotheca Teichert (1935) and Aspidotheca Teichert (1935) (Silurian and Devonian, respectively). I agree with Teichert's opinion on the ancestry of Pterotheca, and that Cyclotheca was derived from that genus; however, the genera Aspidotheca and Pedasiola Spriestersbach (1919) seem to have developed along a separate line of evolution from the Carinaropsinae. Pterotheca and Cyclotheca are characterized by shells with a marginal incurved apex, whereas Aspidotheca and Pedasiola are characterized by a distinctly submarginal elevated apex.

Teichert (1935, fig. 1b) showed a transverse cross-section of a Pterotheca shell, with the caption (translated from German by author): "The cross-section goes through the shell and septum, and shows how the shell rests in a cavity of the septum". If I understand Teichert's diagram and caption correctly, then I must disagree with his interpretation. The line which Teichert apparently regarded as separating the shell from the septum is simply the line along which the septum attached to the ventral surface of the shell. Hall (1861, p. 98) pictured this structure correctly when he stated in his description of P. anatiformis (Hall): "The divergent

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

grooves are apparently caused by the thickening at the junction of the ventral partition with the outer shell". In internal molds, these lines of attachment are represented by narrow grooves which look like sutures. As shown in Pl. 26, figs. 9-10, these suture-like grooves do not reach to the shell margin, but only the length of the septum.

Pterotheca is a genus in great need of complete restudy. Most species were named in the mid to late 19th century (many by Hall, 1861), and their sketchy descriptions and poor illustrations make identifications and comparisons very difficult. Wilson (1951) also noted this problem, as well as pointing out the problem of general poor preservation.

Foerste (1924, p. 218-220) made some instructive observations and comparisons concerning American and European species of Pterotheca. He informally divided the genus into 2 groups. The first consisted of ovate to subtriangular species, including P. attenuata (Hall), P. saffordi (Hall) (Pl. 39, figs. 1-5, 13), and P. harviei Foerste (Pl. 26, figs. 9-10). The second group consisted of more subquadrate forms, whose lateral angles were sharper and lateral margins were more or less parallel. In this latter group he included P. clochensis Foerste, P. canaliculata (Hall), P. expansa (Emmons) (Pl. 39, figs. 10-11), P. anatiformis (Hall), P. undulata (Hall), P. angusta Raymond (Pl. 12, figs. 8-9), and P. transversa Salter (as identified by Billings, 1866, from the Richmondian strata of Anticosti Island). Some of the species in this latter group are probably more ovate (such as P. expansa) and would be better placed in the former grouping.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Foerste (1924) employed a taxobasis which shows great promise in specific differentiation within Pterotheca; that is, the angle by which the lateral septal margins diverge from the apex. He also used the angle made by the posterior shell margins, but this angle is less commonly preserved as the shell margins of most species are usually incomplete. However, if growth lines are preserved, they can be used. The septal angle seems to be the most fruitful approach to species differentation because it can be measured when only the dorsal shell is preserved or exposed, by noting the radial markings made along the line of septal attachment; when only the septum is preserved or exposed; and even when only internal molds are available, because of the suture-like grooves left along lines of septal attachment. This character is quite useful when employed in conjunction with other morphological evidence. It should be noted that in the present work comparisons were made partly from measurements taken from drawings, which may be highly subjective. Before the septal angle can be effectively used, a restudy of the types of all species is necessary so that both interspecific and intraspecific variability can be assessed.

Four "species" have been distinguished herein. P. saffordi (Hall) (Blackriveran-Rocklandian) has been distinguished from P. expansa (Emmons) (Blackriveran-Kirkfieldian) mainly on the angularity and abruptness of the dorsal keel and on differences in ornament features; both species have a septal angle of about 80 degrees. P. angusta Raymond, which occurs with P. expansa in the USGS silicified collections from Kentucky, was easily

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

distinguished by its low septal angle of about 60 degrees. P. harviei Foerste bears a low angular keel, broad shell form, and septal angle of about 85 degrees. It occurs in the uppermost Shermanian beds of Kentucky.

By analogy with Crepidula, it is likely that Pterotheca led a largely sedentary life. Hoagland (1978) noted that juvenile Crepidula are somewhat mobile, but adults are sedentary clingers that filter-feed. Possibly the high keel of Pterotheca with its more or less vertical slit was an adaptation to a filter-feeding a mode of life. However, it seems more likely that Pterotheca was an algal grazer. Pterotheca appears to be consistently associated with the ostracods Leperditia and Leperditella (identified by Jean Berdan of USGS) (Pl. 39, figs. 5, 12, 13; Pl. 40, figs. 8, 9) in the Middle Ordovician of Tennessee and Kentucky. This common association suggests that Pterotheca inhabited intertidal to shallow nearshore subtidal environments, possibly in waters of abnormal salinities (Berdan, 1984). Gastropods living in such restricted environments are mostly algal grazers.

PTEROTHECA SAFFORDI (Hall, 1861)

Pl. 39, figs. 1-5, 13; Pl. 40, Figs. 8-9

Clioderma saffordi HALL, 1861, p. 96, Pl. 6, figs. 15-17.

Pterotheca (Clioderma) saffordi (Hall) LESLEY, 1889, p. 821, figs.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Pterotheca saffordi (Hall), SHIMER & SHROCK, 1944, p. 445, Pl. 180, figs. 17-18.

Diagnosis. - Shell ovate-subtriangular in outline; dorsomedian keel high, rising abruptly from lateral shell slopes, subangular crest becoming rounded through ontogeny; septum large, extending two-thirds the shell length; shell surface lamellose-striate.

Description. - Shell moderately large (up to 49.5 mm in length), outline ovate-triangular, length and width more or less equal; posterior shell margins slightly concave, extending into slightly protuberant beak area, diverging from apex at about 114 degrees; anterolateral shell margins broadly rounded, with anteromedian sinus; dorsolateral slopes moderately arched; dorsomedian keel high, rising abruptly from lateral slopes, subangular crest becoming rounded through ontogeny; septum large and triangular, convex upward, extending from apex to two-thirds the shell length, the lateral margins diverging from apex at angle of 80-85 degrees; shell surface with strongly comarginal lamellose growth lines.

Measurements. - Hall (1861, p. 96) stated that the species had a shell length of about 1.5 inches (3.8 cm), with the width being nearly the same.

Measurements are usually approximate on specimens of Pterotheca because the thin shell margins are generally broken. Probably the most reliable measurement is the septal angle, this being most easily taken from photographs. The measurements of P. saffordi are listed in Table 87.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

As most of these measurements are approximations, only figured specimens are included so that the reader can assess their reliability. The row marked "Hall (1861)"includes measurements taken on his Plate 6, figure 15. It is obvious from these measurements that Hall's (1861) original figures do not agree well with the specimens figured here in their length-width proportions. However, all measured specimens and Hall's figure have nearly the same septal angle. It should be noted that USNM 79262 is a plaster cast of the holotype, and it agrees favorably with other specimens measured.

Table 87: Measurements of Pterotheca saffordi in mm.

Museum Number	Figure Pl.	Figure Fig.	Septal Angle	Shell Length	Shell Width	Kell Height	Keel Width
Hall (1861)	(6)	(15)	85	35.0	44.7	6.5	6.4
USNM 79262	40	3	77-80	37.5	34.7	11.9	7.2
79268	39	5	85	49.5	50.4	9.8	6.6
50093	39	2	78	14.0	14.5	-	-

Material. - The holotype was not examined, but Shimer and Shrock (1944, Pl. 180, figs. 17-18) do show good photographs of the specimen. However, a plaster cast of it (USNM 79262, Pl. 39, figs. 1-2) is shown here.

A fine calcitic specimen (USNM 79268; Pl. 39, figs. 3-4) from the Tyrone Limestone at High Bridge, Kentucky, was found in the U.S. National Museum collections. It is embedded in the upper few millimeters of a

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

small slab in a matrix of gray micrite, while a few millimeters beneath the specimen (on the other side of the slab) is an ostracodal biomicrite (packstone) (Pl. 39, fig. 5). According to the museum label, specimen USNM 59903 (Pl. 39, fig. 13) is from the "top of the Tyrone - just beneath the lower bentonite beds" at High Bridge, Kentucky. This small slab is mainly micrite, but the surface is covered by a densely packed layer of leperditicopid ostracodes, a few brachiopod fragments, and a fragment of a small P. saffordi, all being silicified. Specimen USNM 50099 (Pl. 40, figs. 8-9) is also from the Tyrone Limestone at High Bridge, and occurs associated with ostracodes. Some of the specimens identified here as P. cf. P. expansa (Emmons) may actually be P. saffordi. For further comments see the discussion of P. cf. P. expansa.

Distribution. - P. saffordi was originally described from the Lebanon Limestone (late Blackriveran - early Rocklandian) at Lebanon, Tennessee. The species is recognized here from the Tyrone Limestone (Rocklandian) of central Kentucky.

Comparisons. - P. saffordi is distinguished mainly on the basis of its high, rounded dorsomedian keel, its ovate shell outline, and its lamellose growth lines. Wilson (1951, p. 33) stressed the narrow keel of P. expansa in distinguishing it from P. saffordi.

Foerste (1924) grouped P. saffordi with P. attenuata (Hall) and P. harviei Foerste on the basis of their relatively ovate shells in comparison with other American species, which he claimed were subquadrangular

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

in outline. From Chamberlain's (1883, fig. 33g) figure of P. attenuata, it appears that that species is in reality more triangular, and relatively longer than P. saffordi, as well as possessing a smaller septum. Foerste (1924) further stated: "P. harviei resembles P. saffordi most nearly in outline, but it is a much larger species, of less convexity, and the median carina is relatively narrower and less strongly elevated".

Discussion. - The specimen USNM 79268 (Pl. 39, figs. 3-4) confirms the presence of P. saffordi in Kentucky. Specimen USNM 50093 (Pl. 39, fig. 13) was just one of five such small slabs in a collection from the same locality. All of these specimens are associated with ostracods, strongly suggesting a very shallow, onshore to nearshore, habitat for the species.

PTEROTHECA EXPANSA (Emmons, 1842)

PL. 39, figs. 6-7, 10, 11, 12; Pl. 40, fig. 1-5.

Delthyris expansus EMMONS, 1842, p. 397, fig. 109,2; OWEN, 1844a, p. 368, fig. 2; 1844b, p. 84, Pl. 17, fig. 14.

Clioderma expansa (Emmons), HALL, 1861, p. 98.

Pterotheca expansa (Emmons), LESLEY, 1889, p. 821, fig.; RAYMOND, 1902, p. 306, p. 19, fig. 12; WELLER, 1903, p. 179, Pl. 12, fig. 35; BRANSON, 1909, p. 45, Pl. 7, fig. 14; SHROCK & RAASCH, 1937, p. 570-1, Pl. 5, figs. 8, 9, 13; SHIMER & SHROCK, 1944, p. 445,

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

pl. 180, figs. 15, 16; WILSON, 1951, p. 33, Pl. 2, figs. 19-20; STEELE & SINCLAIR, 1971, p. 20, Pl. 10, figs. 5-8.

Diagnosis. - Shell moderately large (up to 50 mm in length), with broad, subovate outline; dorsomedian carina high, subangular at crest, basal slopes of keel gently concave; septum large, convex upward, septal angle about 80 degrees.

Description. Shell relatively large, subovate in outline, anterior broadly rounded, posterior margins somewhat straighter; dorsum broadly convex; dorsomedian keel highly elevated, having gently concave basal slopes, crest subangular; septum large, extending from apex to more than half the shell length, the sides diverging from the apex at about 80 degrees, dorsally convex; growth lines fine, very closely-spaced.

Measurements. - Because of the fragmented condition of available specimens of P. expansa, measurements are approximate. Examination of the figures (Pls. 39-40) of measured specimens will aid assessing the reliability of measurements listed in Table 88.

Table 88: Measurements of Pterotheca expansa in mm.

Museum Number	Figure Pl.	Figure Fig.	Septal Angle	Shell Length	Shell Width	Kell Height	Keel Width
USNM							
79283	39	6-7	-	23-27	31-32	7.0	4.7
315534	40	6-7	82	-	-	-	-
315536	40	1-3	80	50-51	58-59	13.0	11.0
315537	40	4	80	40-44	51-52	-	-
(from Steele and Sinclair, 1971)							
GSC 22372	10	5	83	-	-	-	-
GSC 22375	10	8	80	-	-	-	-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Material. - Emmon's type invertebrate fossils have been mostly lost (Pojeta, written comm., Dec. 1983), and P. expansa has no known types. The best preserved specimen known, which shows the greatest number of morphological taxobases, was illustrated by Steele and Sinclair (1971, Pl. 10, figs. 5-7) and is catalogued by the Geological Survey of Canada under GSC No. 22372. That specimen is herein designated the neotype.

All material studied here comes from the USNM collections and the new USGS silicified collections. Specimens assigned to P. expansa include those in USGS sample 6034-CO, such as USNM 315532 (Pl. 40, fig. 5), USNM 315533 (Pl. 39, fig. 11), and USNM 315534 (Pl. 40, figs. 6-7); and a fragment from 6134-CO (USNM 315535, Pl. 39, fig. 10). Specimens designated P. cf. P. expansa were found in USGS sample 7784-CO, and include USNM 315536 (Pl. 40, figs. 1-3) and 315537 (Pl. 40, fig. 4). Other specimens designated P. cf. P. expansa include USNM 50100 (Pl. 39, fig. 12) and 79283 (Pl. 40, figs. 6-7).

Distribution. - P. expansa has been reported from Blackriveran to Kirkfieldian aged strata in New York, Ontario, Wisconsin, Illinois, Missouri, New Jersey, and herein from Kentucky. The Kentucky material comes from the Tyrone Limestone (6034-CO) (Rocklandian), and from the lowest 3 feet of the Curdsville Limestone Member of the Lexington Limestone (7784-CO and 6134-CO) (earliest Kirkfieldian). Specimen USNM 50100 (Pl. 39, fig. 12) is from the Murfreesboro Limestone (Blackriveran) at Murfreesboro, Tennessee. Specimen USNM 79283 is from the Curdsville Member of the Lexington Limestone at Curdsville, Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Comparisons. - P. expansa is the earliest described species of the genus Pterotheca in North America. Emmons (1842, p. 397, fig. 109,2) figured a drawing of an internal mold without a description, placing the new species in the brachiopod genus Delthyris. Hall (1861) placed the species in his new genus Clioderma as a gastropod, but did not include a figure, and stated only that the species had a "great lateral expansion and a very strong dorsal carina" with a shell "length of more than an inch and three-fourths on the carina". Lesley (1889, p. 821) was the first to publish the species under the generic name Pterotheca, but did not include a description and used only Emmons' original figure. It should be noted that this original illustration shows a broad specimen with a septal angle of about 85-90 degrees. Raymond (1902) presented a new figure of the species which showed a septal angle of about 81 degrees, stating only: "This obscure fossil is figured here in hope that the attention of other workers will be called to it. Its affinities seem to be rather doubtfully understood". Weller (1903) figured a single fragment with a sharp carina and a septal angle of about 83 degrees.

The first detailed description of P. expansa by Shrock and Raasch (1937, p. 571) was not made from the type specimens (Emmon's type specimens are apparently lost), but from new material from Wisconsin and the quarries at Kentland, Indiana. They said that their specimens had an average width of 42 mm, an average length of 32 mm, and a septal angle of 78-82 degrees. They described the two, short, diverging, ridge-like sup-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

ports between the apices of the shell and the septum in P. expansa, which had previously been described in P. attanuata (Hall, 1861). These authors also used the distance between the lateral edge of the septum and the posterolateral shell margin as a taxobasis. The distance was said to be 7-9 mm in P. expansa, only 5 mm in P. attenuata, and 10 mm or more in their new species P. intermedia Shrock. These authors concluded: "The angle made by the lateral edges of the septum, the distance from the anterior and lateral margins of the shell to the anterior and lateral edges of the septum, the distance the septum reaches into the cavity, the general outline of the shell, and the convexity of the carinate exterior surface are the features which are of most value in the identification of this form".

Wilson (1951, p. 33) remarked that all known Pterotheca have been inadequately described and figured due to poor preservation. She stated: "Pterotheca expansa, however, is more explanate than other forms. The sides of the platform make a greater angle than that of Pterotheca transversa. The sharp surface ridge seems narrower than that of Pterotheca saffordi, and the sides of the interior platform do not seem to be so close to the shell margin". Shrock and Raasch (1937) worked from internal and external molds, but Wilson (1951) had silicified shell material similar to that studied here.

Steele and Sinclair (1971) also described P. expansa from Wilson's (1951) study area in Ontario, and recognized the species sensu Wilson

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

(1951). Their material, as seen in their Plate 10, figures 5-8, was silicified and appears to conform exactly to specimens figured here as P. expansa. The form of the dorsal keels, the septa, and the septal angles, the presence of the apical supports, and shell markings are essentially identical in the Ontario and Kentucky specimens. There can be no doubt that the Kentucky specimens are P. expansa sensu Wilson, but it is uncertain if they are P. expansa sensu Emmons. Emmons types of invertebrate fossils are mostly lost (Pojeta, written comm., December, 1983). Direct comparison between the internal molds of Emmons (1842) and Shrock and Raasch (1937) must be made to the shelled material of Wilson (1951), Steele and Sinclair (1971), and this study before this species' wide geographic and stratigraphic range can be accepted. The species seems to have become the most popular label to affix on partial specimens, whereas its original concept remains quite unclear.

P. expansa (sensu Wilson, 1951) differs from P. attenuata (Hall), P. transversa Salter, and P. angusta Raymond by having a septal angle of about 80 degrees, this being 13-20 degrees greater than in the other species. P. canaliculata (Hall) and P. undulata have apparently never been figured and no comparison can be made. From Hall's (1847, Pl. 34, fig. 7) illustration of P. anatiformis (Hall), that species appears to be quite broad and possibly closely related or a synonym of P. expansa (Emmons). P. clochensis Foerste is quite distinct in its small size and different outline. P. harviei has a much lower and more angular keel.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

P. saffordi (Hall) appears to be more equidimensional than P. expansa, but both have a septal angle of about 80-85 degrees, and both have high, subangular to rounded keels. It appears that the keel of P. saffordi arises more abruptly from the lateral slopes (Pl. 39, figs. 3-4), while the basal keel slopes of P. expansa are more gently concave (Pl. 39, figs. 10-11). Whereas P. saffordi seems to have a rather broaded rounded, abrupt keel throughout growth, the keel of P. expansa is subangular through most of its ontogeny. However, as seen in specimen USNM 315536 (Pl. 40, figs. 1-3), in large mature specimens of P. expansa the keel appears to become much broader, similar to that of P. saffordi, but still retains the gently concave basal slopes. The surface markings of P. saffordi were described by Hall (1861) as "lamellose-striate" (Pl. 39, figs. 3-4), but the shell markings of P. expansa are fine closely-spaced growth lines (herein, Pl. 40, fig. 5; see Steel and Sinclair, 1971, Pl. 10, figs. 5 and 8). Although P. expansa and P. saffordi are very similar morphologically, there are recognizable differences and I continue to interpret them as distinct species.

Discussion. - If all of the specimens identified as P. expansa or P. cf. P. expansa are truly a single species, then this species was quite successful, ranging throughout eastern North America from the Blackriveran to the Kirkfieldian stages. Throughout this stratigraphic range in the present study area, "Pterotheca expansa" is repeatedly associated with leperditiid ostracod assemblages, as is P. saffordi. If such an associa-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

tion can be demonstrated to carry on through the entire genus, it could have important bearing on the paleoautecologic interpretations of the taxon.

PTEROTHECA ANGUSTA Raymond, 1921

Pl. 39, figs. 8-9

Pterotheca angusta RAYMOND, 1921, p. 29, Pl. 8, figs. 8.

Diagnosis. - Shell relatively small (up to 24 mm in length), with sharply angular, moderately high dorsal keel; septal angle about 60 degrees.

Description. - Shell relatively small for genus, ovate-subquadrangular in outline, anterolateral margins broadly rounded, posterior margins imperfectly known but appear to be quite obtuse; anteromedian sinus shallow; dorsomedian keel moderately high, with sharply angular crest and steep flat to concave slopes, having an inverted V-shape; septum long but narrow, the sides diverging from the apex at about 60 degrees; dorsolateral shell surface generally of low convexity, the greatest arching over the ventral septum, so that the margins of the septum are deflected dorsally by a distinct radial undulation on either side of the shell; shell surface with rather widely-spaced, weakly undulating, concentric growth lines.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Measurements. - Raymond (1921) gave the length of the holotype (GSC No. 3266) as 16 mm, with a nearly equal width, and the septal angle as about 60 degrees. The single specimen identified here as P. angusta, USNM 315538, measures: shell length 24 mm, shell width 24.9 mm, maximum keel height above lateral shell slopes 4.5 mm, and septal angle 60 degrees.

Material. - Only one specimen was examined, USNM 315538 (Pl. 39, figs. 8-9) from USGS silicified sample 7784-CO from Kentucky.

Distribution. - Raymond (1921) reported the holotype from "the highest layers of the Cobourg at Collingwood", Ontario. Sweet and Bergstrom (1971) correlate the Coburgian strata of New York with the Edenian and earliest Maysvillian aged strata of the type Cincinnatian section of the present study area. The single specimen found in the USGS silicified samples from Kentucky comes from the basal 2 feet of the Curdsville Limestone Member of the Lexington Limestone (earliest Kirkfieldian) (7784-CO).

Comparison. - This species is immediately separable from other species of the study area by its narrow septal angle of only about 60 degrees, and its very narrow, sharply angular dorsomedian keel (Pl. 39, figs. 8-9).

The only other species of Pterotheca which has a comparatively low septal angle is P. attenuata, that also being about 60 degrees. Hall (1861), in discussing P. attenuata, stated: "This species closely resembles P. canaliculata in form, but has no depressions of the shell parallel

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

to the sides, and the surface is apparently less distinctly striated". There are no known illustrations of P. canaliculata (Hall) for comparison with P. attenuata, but the differences stated by Hall are probably due to preservation and the two species names may be synonyms. In any case, P. attenuata is probably closely related to P. angusta, as shown by their common possession of extremely acute septal angles.

Discussion. - This report of P. angusta from the Kirkfieldian strata of Kentucky is only the second occurrence of the species known. The two occurrences are widely separated stratigraphically, the first being in the latest Edenian or earliest Maysvillian of Ontario, but the diagnostic morphologic features of the two specimens are in close agreement.

PTEROTHECA HARVIEI Foerste, 1924

Pl. 26, figs. 9-10

Pterotheca harviei FOERSTE, 1924, p. 219, Pl. 26, fig. 6.

Diagnosis. - Shell large (up to 60 mm in shell length), broadly ovate in outline; dorsomedian keel of moderate height, with sharply angular crest and flat slopes; septal angle about 85 degrees; shell surface marked by broadly rounded, gently undulating rugose growth lines.

Description. - Shell relatively large, broadly ovate-subtriangular in outline, with moderately low convexity; anterolateral margins broadly rounded, posterolateral margins nearly straight but slightly convex; beak

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

area not particularly protruberant but moderately incurved; median sinus fairly deep; dorsomedian keel of moderate height, but rather low in comparison to width of shell, with sharply angular crest and flat slopes; septum large, lateral margins diverging from apex at about 85 degrees and curving outward slightly; shell surface marked by low but distinct, broad, comarginal rugae.

Measurements. - Foerste (1924) gave the approximate measurements for the species as: shell length 60 mm, shell width 75 mm, length of lateral margins of septum 40 mm, and septal angle 98 degrees. This measurement of the septal angle appears to be in error, as the septal angle on the holotype in his Plate 26, figure 6 measures about 85 degrees.

The single specimen examined here can also yield only approximate measurements: shell length 31 mm, shell width 50 mm, length of the lateral septum margins 28 mm, and septal angle 85 degrees.

Material. - The specimen identified here as P. harviei, USNM 50092 (Pl. 26, figs. 9-10), is a composite mold, possibly retaining some shell, but coated by a thin, resistant, glossy layer, probably consisting mainly of residual organic matter. As Wilson (1951) pointed out, the line of attachment of the septum with the shell is a thickening of the shell, which leaves a narrow groove on internal molds, such as seen in this specimen. The specimen is embedded in gray micrite.

Distribution. - Foerste (1924) originally described P. harviei from "Two miles northwest of St. Hughes on Yamaska, in the Cryptolithus zone of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

the Lorraine Formation", in Ontario, Canada. The present specimen is from the Kope Formation at Covington, Kentucky. Both occurrences are Edenian in age (lower Upper Ordovician).

Comparisons. - The Kentucky specimen appears to agree well with the holotype of P. harviei (as figured by Foerste, 1924, Pl. 26, fig. 6), the two having shell length/width ratios of 1.29 and 1.25, respectively, septal angles of about 85 degrees, and similar shell outlines and keel forms. Foerste (1924) stated: "P. harviei resembles P. saffordi most nearly in outline, but it is a much larger species, of less convexity, and the median carina is relativley narrower and less strongly elevated".

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

BIBLIOGRAPHY

Abbot, R. T. 1968. Seashells of North America: Golden Press, New York, 280 pp.

Alberstadt, L. P. 1973. Depositional environments and the origin of the fine-grained limestones of the Bigby-Cannon Formation (Middle Ordovician), Central Basin, Tennessee: J. Sed. Petrology, 43(3):621-633.

_____. 1979. The brachiopod genus Platystrophia: U.S. Geol. Surv. Prof. Paper 1066-B, 20 pp., 7 pls.

_____, K. R. Walker, and R. P. Zurawski. 1974. Patch reefs in the Carters Limestone (Middle Ordovician) in Tennessee, and vertical zonation in Ordovician reefs: Geol. Soc. America Bull., 85:1171-1182.

Anstey, R. L. and M. L. Fowler. 1969. Lithostratigraphy and depositional environment of the Eden Shale (Ordovician) in the tri-state area of Indiana, Kentucky and Ohio: Jour. Geology, 77:668-682.

Arbey, F. and J. C. Koeniguer. 1979. Les Nematophytes et les alqueraies de l'Ordovician et du Devonien saharien: Bull. Cent. Rech. Explor.-Prod. Elf-Aquitain, 3(2):409-418.

Ausich, W. I., T. W. Kammer, and N. G. Lane. 1979. Fossil communities of the Borden (Mississippian) delta in Indiana and northern Kentucky: J. Paleontol., 53(5):1182-1196.

Bambach, R. K. 1969. Bivalvia of the Siluro-Devonian Arisaig Group, Nova Scotia: Unpub. Ph.D. Thesis, Yale Univ., New Haven.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Bandel, Klaus. 1982. Morphologie und Bildung der frühontogenetischen Gehäuse bei conchiferen Mollusken: Facies, 7:1-198.

Basan, P. B. and R. W. Frey. 1982. Size reduction with dessication of modern internal molds of the mussel Geukensia demissa: J. Paleontol., 56(4):970-972.

Bassler, R. S. 1909. The cement resources of Virginia west of the Blue Ridge: Virginia Geol. Surv. Bull. 2-A, 309 pp.

_____. 1915. Bibliographic index of American Ordovician and Silurian fossils: U.S. Nat. Mus. Bull. 92, 1521 pp.

_____. 1919. The Cambrian and Ordovician deposits of Maryland: Maryland Geol. Surv., 7, 424 pp., 58 pls.

_____. 1932. The stratigraphy of the Central Basin of Tennessee: Tenn. Div. Geol. Bull. 38, 268 pp.

Bathurst, R. G. C. 1966. Boring algae, micrite envelopes, and lithification of molluscan biosparites: Geol. Journal, 5(1):15-32.

Batten, R. L. 1958. Permian Gastropoda of the southwestern United States. 2. Pleurotomariacea: Portlockiellidae, Phymatopleuridae, and Eotomariidae: Bull. Amer. Mus. Nat. Hist., 114:153-246.

_____, H. B. Rollins, and S. J. Gould. 1967. Comments on "The adaptive significance of gastropod torsion": Evolution, 21(2):405-406.

Bell, B. M. 1979. Edrioasteroids (Echinodermata): U.S. Geol. Surv. Prof. Paper 1066-E, 7pp., 2pls.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Berdan, J. 1984. Leperditicopid ostracodes from Ordovician rocks of Kentucky and nearby states and characteristic features of the order Leperditicopida: U.S. Geol. Surv. Prof. Paper 1066-J, 143 pp.

Berg-Madsen, V. and J. S. Peel. 1978. Middle Cambrian Monoplacophorans from Bornholm and Australia, and the systematic position of the bellerophontiform molluscs: Lethaia, 11(2):113-126.

Bergstrom, S. M. 1971. Conodont biostratigraphy of the Middle and Upper Ordovician of Europe and eastern North America: In, Sweet, W. C. and S. M. Bergstrom (Eds.), Symposium on conodont biostratigraphy: Geol. Soc. America, Mem. 127, p. 83-157.

_____ and R. Nilsson. 1974. Age and correlation of the Middle Ordovician bentonites on Bornholm: Bull. Geol. Soc. Denmark, 23:27-48.

Berry, W. B. N. 1974. Facies distribution patterns of some marine benthic faunas in Early Paleozoic platform environments: Paleogeogr., Paleoclim., Paleoecol., 15:153-168.

Billings, E. 1865. Paleozoic Fossils: Geol. Surv. Canada, Vol. 1.

Bird, J. M. and J. F. Dewey. 1970. Lithosphere plate - continental margin tectonics and the evolution of the Appalachian orogen: Geol. Soc. America Bull., 81:1031-1060.

Bjaly, V. I. 1973. New Early Ordovician monoplacophorans of Siberia: Paleont. Jour. 7(3):326-330.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Black, D. F., E. R. Cressman, and W. C. MacQuown. 1965. The Lexington Limestone (Middle Ordovician) of central Kentucky: U.S. Geol. Survey Bull. 1224-C, 29pp., 5 figs.

Borella, P. E. and R. H. Osborne. 1978. Late Middle and early Late Ordovician history of the Cincinnati Arch Province, central Kentucky to central Tennessee: Geol. Soc. America Bull., 89:1559-1573.

Boucot, A. J. 1975. Evolution and extinction rate controls: Developments in Paleontology and Stratigraphy 1. Elsevier, Amsterdam. 427 pp.

_____ and E. L. Yochelson. 1966. Paleozoic Gastropoda from the Moose River Synclinorium, northern Maine - Contributions to Paleontology: U.S. Geol. Surv. Prof. Paper 503-A, 20 pp.

Bowen, Z. P., D. C. Rhoads, and A. L. McAlester. 1974. Marine benthic communities in the Upper Devonian of New York: Lethaia, 7:93-120.

Bowsher, A. L. 1955. Origin and adaption of platycerid gastropods: Kansas Univ. Paleont. Contr., no. 17, Mollusca, art 5, p. 1-11.

Boyd, D. W. and N. D. Newell. 1972. Taphonomy and diagenesis of a Permian fossil assemblage from Wyoming: J. Paleontol., 46(1):1-14.

Bradley, J. H., Jr. 1930. Fauna of the Kimmswick Limestone of Missouri and Illinois: Contrib. Walker Mus., 2(6):219-290.

Branson, E. B. 1909. The fauna of the residuary Auburn chert of Lincoln County, Missouri: Trans. Acad. Sci. St. Louis, 18:39-52.

Branstrator, J. W. 1979. Asteroidea (Echinodermata): U.S. Geol. Surv. Prof. Paper 1066-F, 7 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Brazier, M. D. 1975. An outline history of seagrass communities: Palaeontology, 18:681-702.

Brenchley, P. J., and L. R. M. Cocks. 1979. Ecological associations in a regressive sequence: the latest Ordovician of the Oslo-Asker district, Norway: Palaeontology, 25(4):782-815.

Bretsky, P. W. 1969. Central Appalachian Late Ordovician Communities: Geol. Soc. America Bull. 80:193-212.

_____. 1970. Late Ordovician benthic marine communities in north-central New York: New York State Mus. Sci. Serv., Bull., No. 414, 32 pp.

_____. 1970. Upper Ordovician ecology of Central Appalachians: Peabody Mus. Nat. Hist. Bull., 34:1-150.

_____ and J. J. Bermingham, 1970. Ecology of the Paleozoic scaphopod genus Plagioglypta with special reference to the Ordovician of eastern Iowa: J. Paleontol., 44:908-924.

_____ and S. S. Bretsky. 1975. Succession and repetition of Late Ordovician assemblages from the Nicolet River Valley, Quebec: Paleobiology, 1:225-237.

Brown, G. D. and R. L. Anstey. 1968. Lexington Limestone - Kope Formation contact (Ordovician) in southeastern Indiana: Amer. Assoc. Petr. Geol., Bull., 52(3):488-300.

_____ and J. A. Lineback. 1966. Lithostratigraphy of Cincinnatian Series (Upper Ordovician) in southwestern Indiana: Amer. Assoc. Petrol. Geol., Bull., 50:1018-1032.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Butts, Charles. 1926. The Paleozoic Rocks, in Geology of Alabama: Geol. Surv. Alabama, Spec. Rept. 14, p. 41-230.

Byers, C. W. and S. Galvin, 1979. Two contemporaneous equilibrium communities in the Ordovician of Wisconsin: Lethaia, 12:297-305.

Campbell, M. R. 1898. Description of the Richmond Quandrangle, Kentucky: U.S. Geol. Surv. Geol. Atlas, Folio 46.

Carriker, M. R. and E. L. Yochelson. 1968. Recent gastropod boreholes and Ordovician cylindrical borings: U.S. Geol. Surv. Prof. Paper 593-B, 26 pp.

Caster, K. E., E. A. Dalve, and J. K. Pope. 1955. (reprinted 1961). Elementary guide to the fossils and strata of the Ordovician in the vicinity of Cincinnati, Ohio: Cincinnati Mus. Nat. Hist., 47 pp., 8 pls., 6 figs.

Cesari, P. and R. Guidastri. 1976. Contributo alla conoscenza dei Monoplacophori recenti: Conchiglie, 12:223-250.

Chamberlin, T. C. 1883. Geology of Wisconsin: Wisconsin Geol. Surv., Vol. 1, 300 pp.

Chronic, H. 1952. Molluscan fauna from Permian Kaibab Formation, Walnut Canyon, Arizona: Geol. Soc. America Bull., 63:95-166.

Clarke, J. M. 1899. Molluscos devonianos do Estado do Parå: Archos. Musc. nac., Rio de Janiero, 10:49-174.

Conrad, T. A. 1838. Report on the paleontological department of the Survey: New York Geol. Surv., Ann. Rept. 2, p. 107-119.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1842. Observations on the Silurian and Devonian Systems of the United States, with descriptions of new organic remains: Jour. Acad. Nat. Sci. Philadelphia, 8(2):228-280.

Cooper, G. A. and R. E. Grant. 1972. Permian Brachiopods of West Texas, II: Smithsonian Contr. Paleobiology, 14:1-231.

Cressman, E. R. 1972. Geologic map of the Danville Quadrangle, Mercer and Boyle Counties, Kentucky: U.S. Geol. Surv. Geol. Quad. Map GQ-985.

_____. 1973. Lithostratigraphy and depositional environments of the Lexington Limestone (Ordovician) of central Kentucky: U.S. Geol. Surv. Prof. Paper 768, 61 pp.

Crofts, D. R. 1937. The development of Haliotis tuberculata, with special reference to organogensis during torsion: Phil. Trans. (B), 228:219-268.

_____. 1955. Muscle morphogenesis in primitive gastropods and its relation to torsion: Proc. Zool. Soc. London, 125(3-4):711-750.

Cumings, E. R. 1980. The Stratigraphy and Paleontology of the Ordovician Rocks of Indiana: Indiana Dept. Nat. Res., 32nd Ann. Rept.

Curry, D. and N. J. Morris, 1967. Mollusca: Amphineura Monoplacophora and Gastropoda, Chapter 13: In, The Fossil Record, Geol. Soc. London, p. 423-430.

Dall, W. H. 1913. Gastropoda: In, Eastman, C. R. (ed.), Textbook of Paleontology, 2nd Edition, (adapted from German of Karl A. von Zittel), Vol. 1, 839 pp. MacMillan and Co., London. (Reprinted 1927).

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Dapples, E. C. 1967. Silica as an agent in diagenesis: In, Larsen, G. and V. Chilingar (eds.), Diagenesis in Sediments, p. 323-342. Elsevier, Amsterdam.

Defrance, M. J. L. 1824. Rectification des caracteres du genre Bellerophe, etabli dans le Conchyliologie de Denys de Montfort: Ann. sci. naturelles, 1:264-265.

Dickenson, W. R. 1981. Plate tectonic evolution of sedimentary basins: In, Plate Tectonics and Hydrocarbon Accumulation, Amer. Assoc, Petr. Geol., Ed. Course Note Series No. 1, p. 1-62.

Dietz, R. S. and J. C. Holden. 1966. Miogeoclines (miogeosynclines) in space and time: J. Geology, 74:566-583.

Drahovzal, J. A. and T. L. Neatherly. 1971. The Middle and Upper Ordovician of the Alabama Appalachians: Alabama Geol. Soc., 9th Ann. Fld. Trip Gdbk., 240 pp.

Eales, N. B. 1950. Secondary symmetry in gastropods: Malac. Soc. London, 28:185-196.

Easton, W. H. 1943. The fauna of the Pitkin Formation: J. Paleontol., 17:125-154.

Elias, R. J. 1982. Latest Ordovician solitary rugose corals of eastern North America: Bull. Amer. Paleontology, 81(314):1-116.

Emmons, E. 1842. Geology of New York, Pt. 2, comprising the survey of the second geological district: New York St. Geol. Surv., Albany.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1855. American geology, containing a statement of the principles of the science with full illustrations of characteristic American fossils. Albany.

_____. 1860. Manual of Geology, p. 103, 93 figs.

Ervin, C. P. and L. D. McGinnis. 1975. Reelfoot Rift: reactivated precursor of the Mississippi Embayment: Geol. Soc. America Bull., 86:1287-1295.

Fenton, C. L. and M. A. Fenton. 1931. Some snail borings of Paleozoic age: Amer. Mid Nat., 12:521-528.

Ferguson, L. 1962. The paleoecology of a Lower Carboniferous marine transgression: J. Paleontol., 36:1090-1107.

Fetzer, J. A. 1973. Biostratigraphic evaluation of some Middle Ordovician bentonite complexes in eastern North America: Unpubl. Masters Thesis, Ohio State Univ., Columbus. 164 pp.

Finks, R. M. 1960. Late Paleozoic sponge faunas of the Texas Region - Siliceous sponges: Bull. Amer. Mus. Nat. Hist., 120(1):1-160, 50 pls.

Foerste, A. F. 1903. The Cincinnati Group of Western Tennessee, between the Tennessee River and the Central Basin: Jour. Geol., 11:29-45.

_____. 1906. The Silurian, Devonian, and Irvine Formations of east-central Kentucky, with an account of their clays and limestones: Kentucky Geol. Surv., ser. 3, Bull. 7, 369 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1912. Strophomena and other fossils from Cincinnatian and Mohawkian horizons, chiefly in Ohio, Indiana, Kentucky: Bull. Sci. Lab. Denison Univ., 17:17-174.

_____. 1914a. Notes on Agelacrinidae and Lepadocystinae, with descriptions of Thresherodiscus and Brockocystites: Bull. Sci. Lab Denison Univ., 17:399-487.

_____. 1914b. Notes on Lorraine faunas of New York and Quebec: Bull. Sci. Lab. Denison Univ., 17:274-340.

_____. 1914c. The Rogers Gap fauna of central Kentucky: J. Cincinnati Soc. Nat. Hist., 21:109-156.

_____. 1924. Upper Ordovician faunas of Ontario and Quebec: Geol. Surv. Canada, Mem. 138, 255 pp.

Ford, J. P. 1967. Cincinnatian geology in south west Hamilton Co., Ohio: Amer. Assoc. Petr. Geol. Bull., 51:918-936.

_____. 1968. Upper Ordovician stratigraphic relations between Covington and Clays Ferry, Kentucky: Amer. Assoc. Petr. Geol. Bull., 52:1779-1791.

Fox, P. P. and L. F. Grant. 1944. Ordovician bentonites in Tennessee and adjacent states: J. Geology, 52:319-332.

_____. 1962. Stratigraphy and paleoecology of the Richmond Group in southeastern Indiana: Geol. Soc. America Bull., 73:621-642.

_____. 1968. Quantitative paleoecologic analysis of fossil communities in the Richmond Group: J. Geology, 76(6):613-640.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Fretter, V. 1964. Observations on the anatomy of Mikadotrochus amabilis Bayer: Bull. Marine Science, 14:172-184.

_____. 1975. Umbonium vestiarium, a filter feeding trochid: J. Zoology, 17:541-552.

_____ and Graham. 1962. British Prosobranch Molluscs - Their Functional Anatomy and Ecology: Ray Society, No. 144, 755 pp. London.

Fry, W. L. 1969. Noncalcareous marine algae from the Upper Ordovician of the Lake Winnepeg region, Manitoba: Geol. Soc. Amer. Bull., 71(12):1868 (Abstract).

_____. 1983. An algal flora from the Upper Ordovician of the Lake Winnepeg region, Manitoba, Canada: Rev. Paleobot. Palynology, 39:313-341.

Gebelein, C. D. 1969. Distribution, morphology, and accretion rates of Recent subtidal algal stromatolites: J. Sed. Petrology, 39:49-69.

Ghiselin, M. T. 1966. The adaptive significance of gastropod torsion: Evolution, 20(3):337-348.

Goldring, R. and F. Langenstrassen. 1979. Open shelf and nearshore clastic facies in the Devonian: Palaeontological Assoc., Sp. Papers in Paleontology, 23:81-97.

Golikov, A. N. and Y. I. Starabogatov. 1975. Systematics of prosobranch gastropods: Malacologia, 15(1):185-232.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Grabau, A. W. and H. W. Shimer. 1909. North American Index Fossils, Invertebrates, Vol. I: New York.

Gray, H. H. 1972. Lithostratigraphy of the Maquoketa Group (Ordovician) in Indiana: Indiana Geol. Surv., Spec. Rept. 7, 31 pp.

Green, R. C. 1966. Geologic map of the Valley View Quandrangle, central Kentucky: U.S. Geol. Surv. Quad. Map G.Q. 470.

Gromczakiewicz-Lomnicka. 1972. Visean gastropods from Orlej near Cracow: Pr. Muz. Ziemi, 20:3043.

Gundrum, L. E. 1981. Position of muscle attachment, shell geometry and depth of withdrawal in conispiral marine prosobranch gastropods: Paleontol. Assoc., Ann. Conf. Abstracts, p. 5.

Gutstadt, A. M. 1958. Cambrian and Ordovician stratigraphy and oil and gas possibilities in Indiana: Indiana Geol. Surv. Bull. 14, 103 pp.

Hall, James. 1847. Paleontology of New York, Vol. 1, containing descriptions of the organic remains of the lower division of the New York System: Albany.

_____. 1861. Notes on the genera Bellerophon, Bucania, Carinaropsis, and Cyrtolites: 14th Rept. New York St. Cab. Nat. Hist., p. 93-98.

_____. 1872. Descriptions of new species of fossils from the Hudson River Group, in the vicinity of Cincinnati, Ohio: 24th Rept. New York State Cab. Nat. Hist., p. 225-232.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Harper, J. A. and H. B. Rollins. 1982. Recognition of Monoplacophora and Gastropoda in the fossil record: a functional morphological look at the bellerophont controversy: 3rd North Amer. Paleontol. Conv., Proc., 1:227-232.

Harris, F. W. and W. D. Martin. 1979. Benthic community development in the limestone beds of the Waynesville (upper Dillsboro) Formation (Cincinnatian Series) of southeastern Indiana: J. Sed. Petrology, 49(4):1295-1306.

Harrison, W. B. and L. K. Harrison. 1975. A Maquoketa-like molluscan community in the Brassfield Formation (Early Silurian) of Adams Co., Ohio: Bull. Amer. Paleontology, 67(287):193-234.

Hatcher, R. D., Jr. 1972. Developmental work for the Southern Appalachians: Geol. Soc. America Bull., 83:2735-2760.

Hatfield, C. B. 1968. Stratigraphy and paleoecology of the Saluda Formation (Cincinnatian) in Indiana, Ohio, and Kentucky: Geol. Soc. America, Sp. Paper 95, 34 pp.

Hay, H. B., J. K. Pope, and R. C. Frey. 1981. Lithostratigraphy, cyclic sedimentation, and paleoecology of the Cincinnatian Series in southwestern Ohio and southeastern Indiana: In, Roberts, T. G. (ed.), Geol. Soc. America Ann. Mtg. Fld. Trip Bdbk., 1:73-86.

Heuer, E. 1973. The paleoautecology of the megafauna of the Pennsylvanian Wolf Mt. Shale: Ph.D. thesis, Univ. Wisconsin, Madison (Univ. Microfilms Interm.), 736 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Hickman, C. S. 1976. Pleurotomaria (Archaeogastropoda) in the Eocene of the northeastern Pacific: A review of Cenozoic biogeography and ecology of the genus; J. Paleontol., 50(6):1090-1102.

_____. 1984. Composition, structure, ecology, and evolution of six Cenozoic deep-water mollusc communities: J. Paleontol., 58(5):1215-1234.

Hintze, L. F. 1983. Silicification of Ordovician fossils in Utah and Nevada: Geol. Soc. America Bull., 64:1508 (Abstract).

Hoagland, K. E. 1977. Systematic review of fossil and Recent Crepidula and discussion of evolution of the Calyptraeidae: Malacologia, 16(2):353-420.

Holzapfel, E. 1889. Die Cephalopoden-fuhrenden Kalke des unteren Carbon von Erdbach-Breitscheid bei Herborn: Palaeontologisches Abhandlungen (Dames-Kayser), Band 5, (Neue Folge Bd. 1), Heft. 1. Jena.

Horny, R. 1961. New genera of Bohemian Paleozoic Monoplacophora and patellid Gastropoda: Vestnik Ustred. ust. geol., 36:299-302.

_____. 1962. New genera of Bohemian Lower Paleozoic Bellerophontina: Vest. Ustred. ust. geol., 37:473-476.

_____. 1963a. On the systematic position of Cyrtonelloids (Mollusca): Cas. narod. Muz. prirod., 132(2):90-94.

_____. 1963b. Lower Paleozoic Bellerophontina (Gastropoda) of Bohemia: Sb. geol. Vid. Paleontologie, 2:57-164.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1963c. New finds of Silurian Drahomirinae (Monoplacophora) in Bohemia and notes on their ontogeny and bionomy: Gas. narod. Muz. prirod., 132(2):79-89.

_____. 1965a. On the systematic position of Cyrtolites Conrad, 1838 (Mollusca): Sb. geol. Vid. Paleontologie, 134(1):8-10.

_____. 1965b. Cyrolites Conrad, 1838, and its systematic position among the Monoplacophora (Mollusca): Prague Narod. Mus. Sbornik, Rada B (Pridodni vedy), 21:57-70.

Howe, H. J. 1979. Middle and Late Ordovician plectambonitacean, rhynchonellacean, syntrophiacean, trimerellacean, and atrypacean brachiopods: U.S. Geol. Surv. Prof. Paper 1066-C, 18 pp.

Hrabar, S. V., E. R. Cressman, and P. E. Potter, 1971. Crossbedding of the Tanglewood Limestone Member of the Lexington Limestone (Ordovician) of the Blue Grass region of Kentucky: Brigham Young Univ. Geol. Studies, 18:99-114, 11 figs.

Hurst, J. M. 1979. Evolution, succession and replacement in the type Upper Caradoc (Ordovician) benthic faunas of England: Paleogeogr., Paleoclim., Paleoecol., 27:189-246.

Hussey, R. C. 1926. The Richmond Formation of Michigan: Univ. Mich. Contr. Mus. Geol., 2(8):113-187.

Imbrie, J., L. F. Laporte, and D. F. Merriam, 1964. Beattie Limestone facies (Lower Permian) of the northern midcontinent: In, Merriam, D. F. (ed.), Symposium on Cyclic Sedimentation: Kansas Geol. Surv., Bull. 169, pp. 219-238.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Johnson, J. H. 1961. Review of Ordovician algae: Colorado School of Mines Quarterly, 56(2):1-101.

Johnson, R. G. 1962. Interspecific associations in Pennsylvanian fossil assemblages: J. Geology, 70:32-55.

_____. 1964. The community approach to paleoecology: In, Imbrie, J. and N. D. Newell (Eds.), Approaches to Paleoecology, p. 107-134, John Wiley and Sons, New York.

Jonker, F. P. 1979. Protaxites in the Lower Devonian: Palaeontographica, Abt. B, 171:39-56.

Kay, M. 1948. Summary of Middle Ordovician bordering Allegheny synclinorium: Amer. Assoc. Petrol. Geol. Bull., 32:1397-1416.

_____. 1951. North American geosynclines: Geol. Soc. America, Mem. 148, 143 pp.

_____. 1968. Ordovician formations in northwestern New York: Naturaliste Canadien, 95:1373-1378.

Knight, J. B. 1941. Paleozoic gastropod genotypes: Geol. Soc. America, Sp. Paper 32, 510 p.

_____. 1942. Four new genera of Paleozoic Gastropoda: J. Paleontol., 16(4):487-88.

_____. 1945. Some new genera of the Bellerophontacea: J. Paleontol., 19(4): 333-340.

_____. 1945. Some new genera of Paleozoic Gastropoda: J. Paleontol., 19(6):573-587.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1947. Bellerophont muscle scars: J. Paleontol., 21(3):264-267.

_____. 1947. Some new Cambrian bellerophont gastropods: Smithsonian Inst. Misc. Coll., 106(17):1-11.

_____. 1948. Further new Cambrian bellerophont gastropods (cont. from 1947): Smithsonian Inst. Misc. Coll., 111(3):264-267.

_____. 1952. Primitive fossil gastropods and their bearing on gastropod classification: Smithsonian Misc. Coll., 117(3):1-56.

_____. 1956. New families of Gastropoda: Washington Acad. Sci. J., 46(2):41-42.

_____, L. R. Cox, A. M. Keen, R. L. Batten, E. L. Yochelson, and R. Robertson. 1960. Systematic Descriptions (Archaeogastropoda): In, Moore, R. C. (ed.), Mollusca 1, Part I, Treatise on Invertebrate Paleontology, p. I169-I331. Univ. Kansas Press, Lawrence.

_____ and E. L. Yochelson. 1958. A reconsideration of the Monoplacophora and the primitive Gastropoda: Malacolog. Soc. London Proc., 33(1):37-48.

_____ and E. L. Yochelson. 1960. Monoplacophora: In, Moore, R. C. (ed.), Mollusca I, Part I, Treatise on Invertebrate Paleontology, p. I77-I84. Univ. Kansas Press, Lawrence.

Koeniguer, J. C. 1974. Les Protaxites (Nematophytes) Ordoviciens et Devoniens du Sahara Central: Actes du 99e Congre national des Societes savantes, Besancon, Sciences, fasc. II, pp. 383-388.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Koken, E. 1889. Ueber die Entwicklung der Gastropoden von Cambrium bis zur Trias: Neues Jahrbuch fur Mineralogie, Geologie und Palaeontologie, Beilageband 6, pp. 305-484, pls. 10-14. Stuttgart.

_____. 1896. Die Leitfossilien: Leipzig.

_____. 1897. Die Gastropoden des baltischen Untersilurs: Bull. de l'Academie Imperiale des Sciences de St. Petersbourg, t. 7, no. 2, pp. 97-214.

_____ and J. Perner. 1925. Die Gastropoden des baltischen Untersilurs: Acad. Sci. Russie Mem., 8er Ser., Class Phys.-Math., v. 37, no. 1, 322 pp., 51 pls.

Koninck, L. G., de. 1843. Description des animaux fossiles qui se trovent dans le terrain carbonifere de Belgique: Liege, text, 649 pp., atlas, 69 pls (1842-1844).

_____. 1822. Notice sur le famille des Bellerophontidae suiviede ls description d'un nouveau genre de cette famille: Annales Societe geologique de Belgique, 9:72-90.

Kuhnhenn, G. L., G. J. Grabowski, and G. R. Dever, Jr. 1981. Paleoenvironmental interpretation of the Middle Ordovician High Bridge Group in central Kentucky: In, Roberts, T. G. (ed.), Geol. Soc. America, 1981 Ann. Mtg. Fld. Trip Gdbk., 1:1-30.

Laufeld, S. and L. Jeppson. 1976. Silicification and bentonites in the Silurian of Gotland: Geologiska Foreningens i Stockholm Forhandlingar, 98:31-44.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Lemche, H. 1957: A new living deep-sea mollusc of the Cambro-Devonian class Monoplacophora: Nature, 179:413-416.

_____ and K. G. Wingstrand. 1959. The anatomy of Neopilina galatheae Lemche, 1957. Galathaea Rept., 3:9-71.

Lesley, J. P. 1889. A dictionary of the fossils of Pennsylvania and neighboring states: Pennsylvania 2nd Geol. Surv. Rept. P-4 (3 Vols.).

Levington, J. S. 1970. The paleoecological significance of opportunistic species: Lethaia, 3:69-78.

Lindstrom, G. 1884. On the Silurian Gastropoda and Pteropoda of Gotland: Kongl. Svenska Vetenskaps-Akademiens Handlingar, 19(6):1-250.

Linsley, R. M. 1968. Gastropods of the Middle Devonian Andernon Limestone: Bull. Amer. Paleontology, 54(244):333-465.

_____. 1977. Some "laws" of gastropod and shell form: Paleobiology, 3(2):196-206.

_____. 1978a. Locomotion rates and shell form in the Gastropoda: Malacologia, 17(2):193-206.

_____. 1978b. Shell form and the evolution of the gastropods: American Scientist, 66(4):432-441.

_____. 1979. Gastropods of the Devonian: Palaeontol. Assoc., Sp. Papers in Palaeont., 23:249-253.

_____, and W. M. Kier, 1984. The Paragastropoda: a proposal for a new class of Paleozoic Mollusca: Malacologia, 25(1):241-254.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____, and E. L. Yochleson. 1973. Devonian carrier shells (Euomphalidae) from North America and Germany: U.S. Geol. Surv. Prof. Paper 824, 26 pp.

_____, E. L. Yochleson, and D. M. Rohr. 1978. A reinterpretation of the mode of life of some Paleozoic frilled gastropods: Lethaia, 11(2):105-112.

Locke, John. 1838. Geological Report: In, W. W. Mather and others, 2nd Ann. Rept. on geological survey of the State of Ohio, p. 201-274.

Lowenstam, H. 1978. Recovery, behavior and evolutionary implications of live Monoplacophora: Nature, 273(5659):231-232.

Luft, S. J. 1971. Geologic map of part of the Covington Quadrangle, northern Kentucky: U.S. Geol. Surv. Quad. Map GQ-955.

MacLeod, N. 1982. Upper Pennsylvanian peri-tidal benthic marine communities from the Wolf Mountain Formation (Canyon Group), north-central Texas: Soc. Econ. Paleon. Min., Permian Basin Sect., Publ. No. 82-21, pp. 167-178.

MacQuown, W. C., Jr. 1967. Factors controlling porosity and permeability in the Curdsville Limestone Member of the Lexington Limestone: Kentucky Univ. Water Res. Inst. Res. Rept. 7, 80 pp.

McAlester, A. L. 1962. Mode of preservation in Early Paleozoic pelecypods and its morphologic and ecologic significance: J. Paleontol., 36(1):69-73.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

McFarlan, A. C. 1931. The Ordovician fauna of Kentucky: In, Jillson, W. R. (ed.), The Paleontology of Kentucky: Kentucky Geol. Surv., Frankfort.

_____. 1943. Geology of Kentucky: Univ. Kentucky, Lexington, 531 pp.

_____ and W. H. White. 1948. Trenton and pre-Trenton of Kentucky: Amer. Ass. Petrol. Geol. Bull., 32(8):1627-1646.

McKerrow, W. S. 1978. The Ecology of Fossils - an illustrated guide: The MIT Press, Cambridge, 395 pp.

McLean, J. H. 1981. The Galapagos Rift limpet Neomphalus: relevance to understanding the evolution of a major Paleozoic-Mesozoic radiation: Malacologia, 21:291-336.

McNamara, K. J. 1978. Symbiosis between gastropods and bryozoans in the Late Ordovician of Cumbria, England: Lethaia, 11(1):25-40.

Matsumato, Y. T., T. Kataoka, and M. Sekido. 1972. On the behavior of Beyrich's slit shell, Mikadotrachus beyrichii (Hilgendorf) kept in aquarium: Venus, 30:147-152.

Matthews, S. C. and V. V. Missarzhevsky. 1975. Small shelly fossils of the Late Precambrian and Early Cambrian age: a review of recent work: J. Geol. Soc., London, 131:289-304.

Meek, F. B. 1866. Note on the affinities of the Bellerophontidae: Chicago Acad. Sci. Proc., 1:9-11.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1873. Descriptions of the Invertebrate fossils of the Silurian and Devonian Systems: Paleontology, Geol. Surv. Ohio, v. 1, pt. 2, 399 pp.

_____ and A. H. Worthen, 1866. Descriptions of invertebrates: Illinois Geol. Surv., Paleontology, v. 2.

Meyer, D. L., R. C. Tobin, W. A. Pryor, W. A. Harrison, and R. G. Osgood. 1981. Stratigraphy, sedimentology, and paleoecology of the Cincinnatian Series (Upper Ordovician) in the vicinity of Cincinnati, Ohio: In, Roberts, T. G. (ed.), Geol. Soc. America, 1981 Ann. Mtg. Fld. Trip Gdbk., v. 1, pp. 31-71.

Miller, S. A. 1874. Monograph of the Gasteropoda of the Cincinnati Group: Cincinnati Quart. J. Sci., 1(4):302-320.

_____. 1878. Description of a new genus and eleven new species: J. Cincinnati Soc. Nat. Hist., 1:100-108.

_____. 1889. North American Geology and Paleontology for the use of amateurs, students, and scientists: Cincinnati.

_____. 1892. First appendix to North American Geology and Paleontology for the use of amateurs, students and scientists: Cincinnati.

_____. 1897. Second appendix to North American Geology and Paleontology for the use of amateurs, students, and scientists: Cincinnati.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____ and C. L. Faber. 1894. New species of fossils from the Hudson River Group, and remarks upon others: J. Cincinnati Soc. Nat. Hist., 17(1):22-33.

Montfort, P. H. de. 1908. Conchylioge systematique, et classification méthodique des coquilles, offrant leurs figures, leur arrangement generique, leurs descriptions caracteristiques, leurs noms; ainsi que leur synonymie en plusieurs langues. Tome 1, Coquilles univalves, cloisonees. Paris.

Moore, N. K. 1977. Distribution of the benthic algae flora in Middle Ordovician carbonate environmental units of the Southern Appalachians: In, Ruppel, S. C. and K. R. Walker (eds.), The Ecostratigraphy of the Middle Ordovician of the Southern Appalachian (Kentucky, Tennessee, and Virginia), U.S.A.: A Field Excursion, p. 18-29: Int. Symp. Ordovician System, Columbus, Ohio.

Moore, R. C. 1964. Paleoecological aspects of Kansas Pennsylvanian and Permian cyclothems: In, Merriam, D. F. (ed.), Symposium on Cyclic Sedimentation, Kansas Geol. Surv., Bull. 169, 1:287-380.

_____, C. G. Lalicker, and A. G. Fisher. 1952. Invertebrate Fossils: McGraw-Hill Book Co., New York, 766 pp.

Morris, R. W. and H. B. Rollins, 1971. The distribution and paleoecological interpretation of Cornulites in the Waynesville Formation (Upper Ordovician) of southwestern Ohio: Ohio Jour. Sci., 71(3):159-169.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Morton, J. E. 1958. Torsion and the adult snail: a reevaluation: Proc. Malacological Soc. London, 33:2-10.

_____. 1967. Molluscs: Hutchinson and Co., London, 244 pp.

Naef, A. 1911. Studien zur generellen Morphologie der Mollusca. Teil 1:Uber Torsion and Asymmetrie der Gastropoden: Ergebnisse U. Fortschr. Zool., ed., Spengel, v. 3, p. 73-164. Jena.

Nelson, W. R. 1922. Volcanic ash beds in the Ordovician of Tennessee, Kentucky and Alabama: Geol. Soc. America Bull., 33:605-616.

Neuman, R. B. 1967. Some silicified Middle Ordovician brachiopods from Kentucky: U.S. Geol. Surv. Prof. Paper 583-A, 14 pp., 2 pls.

Newell, N. D., J. K. Rigby, A. J. Fisher, A. J. Whiteman, J. E. Hickox, and J. S. Bradley. 1953. The Permian Reef Complex of the Guadalupe Mountain Region, Texas and New Mexico: Hafner Publ. Co., New York, 236 pp.

Nickles, J. M. 1902. The Geology of Cincinnati, Ohio: Cinc. Soc. Nat. Hist., Jour., V. 20, 53 pp.

_____. 1903. The Richmond Group in Indiana and Ohio and it subdivision, with a note on the genus Strophomena and its type: Amer. Geologist, 32:202-218.

Nosow, E. and A. C. McFarlan. 1960. Geology of the central Bluegrass area: Geol. Soc. Amer., Southeastern section, 1960 Field Trip Gdbk., No. 1, 56 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Orton, Edward. 1873. Report on the geological district; geology of the Cincinnati Group, Hamilton, Clermont, and Clarke Counties: Ohio Geol. Surv. Rept., v. 1, pt. 1, p. 365-480.

Osborne, R. H. 1968. American Upper Ordovician Standard. lX. Bedrock geology of eastern Hamilton Co., Ohio: Amer. Assoc. Petr. Geol. Bull., 52:2137-52.

Palmquist, W. N., Jr. and F. R. Hall. 1961. Reconnaissance of groundwater resources in the Bluegrass region, Kentucky: U.S. Geol. Surv. Water-Supply Paper 1533, 39 pp.

Patton, J. B., T. G. Perry, and W. J. Wayne. 1953. Ordovician stratigraphy and physiography of part of southeastern Indiana: Indiana Geol. Surv. Fld. Conf. Gdbk. 6, 29 pp.

Peck, J. H. 1966. Upper Ordovician formations in the Maysville area, Kentucky: U.S. Geol. Surv. Bull. 1244-B. 30 p., 8 figs.

Peel, J. S. 1972. Observations on some lower Paleozoic tremanotiform Bellerphontacea (Gastropoda) from North America: Palaeontology, 15(3):412-422.

_____. 1974. Systematics, ontogeny, and functional morphology of Silurian trilobed bellerophontacean gastropods: Bull. Geol. Soc. Denmark, 23(3-4):231-264.

_____. 1975a. Anapetopsis, a new Late Silurian gastropod from Nova Scotia: Can. J. Earth Sci., 12:509-513.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1975b. New Silurian Gastropods from Nova Scotia and Britain: Can. J. Earth Sci., 12:1524-1533.

_____. 1975c. A new Silurian gastropod from Wisconsin and the ecology of uncoiling in Paleozoic gastropods: Bull. Geol. Soc. Denmark, 24:211-221.

_____. 1976. Musculature and systematic position of Megalomphala taenia (Bellerophontacea, Gastropoda) from the Silurian of Gotland: Geol. Soc. Denmark Bull., 25:49-55.

_____. 1977a. Relationship and internal structure of a new Pilina (Monoplacophora) from the Late Ordovician of Oklahoma: J. Paleontol., 51(1):116-122.

_____. 1977b. Systematics and Paleoecology of the Silurian Gastropods of the Arisaig Group, Nova Scotia: Kougelige Dauske Videnskabernes Selskab, Biologiske Skrifter, 21(2):1-89.

_____. 1978. Faunal succession and mode of life of Silurian gastropods in the Arisaig Group, Nova Scotia: Palaeontology, 21(2):285-306.

_____. 1980. A new Silurian retractile monoplacophoran and the origin of the gastropods: Proc. Geol. Assoc., 91(1-2):91-97.

_____. 1982. Muscle scars in Bellerophon recticostatus (Mollusca) from the Carboniferous of Ireland: J. Paleontol., 56(5):1307-1310.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. (in press). Class Gastropoda (Part II): In, Boardman, R. S., A. H. Cheetam, and A. J. Rowell (eds.), Textbook of Invertebrate Paleontology, Blackwell and Co., San Francisco.

Perner, J. 1903. In, Barrande, J.: Susteme silurian du centre de la Boheme, v. 4, Gasteropodes. Tome 1. Texte (Patellidae et Bellerophontida), pls. 1-89, Prague.

Peterson, W. L. 1970. Bardstown Member of the Drakes Formation in central Kentucky: U.S. Geol. Surv. Bull. 1294-A, p. A36-A41.

Pickerill, R. K. and P. J. Brenchley. 1979. Caradoc marine benthic communities of the South Berwyn Hills, North Wales. Palaeontology, 22(1):229-264.

Pojeta, J., Jr. 1971. Review of Ordovician Pelecypods: U.S. Geol. Surv., Prof. Paper 695, 46 pp., 20 pls.

_____. 1979. The Ordovician paleontology of Kentucky and nearby states - Introduction: U.S. Geol. Surv. Prof. Paper 1066-A, pp. A1-A48, 3 figs.

_____ and B. Runnegar. 1976. The Paleontology of Rostrocouch Molluscs and the Early History of the Phylum Mollusca: U.S. Geol. Surv. Prof. Paper 968, 88p., 54 pls.

Pomeroy, J. S. 1968. Geology map of the Frankfort East Quadrangle, Franklin and Woodford Counties, Kentucky: U.S. Geol. Surv. Geol. Quad. Map GQ-707.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Pope, J. K. and W. D. Martin (eds.) 1977. Biostratigraphy and paleoenvironments of the Cincinnatian Series of Southeastern Indiana: Fld. Gdbk., 7th Ann. Fld. Conf. Great Lakes Sect., Soc. Econ. Paleont. and Min.

Raup, D. M. 1966. Geometric analysis of shell coiling: general problems: J. Paleontol., 40:1178-1190.

_____. 1967. Geometric analysis of shell coiling: coiling in ammonoids: J. Paleontol., 41:43-65.

Raymond, P. E. 1902. The Crown Point Section: Bull. Amer. Paleontology, 3(14):1-44.

_____. 1908. The Gastropoda of the Chazy Formation: Annals of the Carnegie Museum, 4(3):168-225. Pittsburg.

_____. 1921. A contribution to the description of the fauna of the Trenton Group: Dept. of Mines and Geol. Surv. Canada, Mus. Bull. 31 (Geol. Ser. 38), 64 p.

_____. 1922. Trenton of central Tennessee and Kentucky: Geol. Soc. Amer., Bull., 33:571-585.

Reed, F. R. C. 1921. British Silurian and Ordovician Bellerophontacea: Paleontographical Soc. Monograph for 1919, p. 1-92, 13 pls.

Reed, J. F. 1980. Carbonate ramp-to-basin evolution, Middle Ordovician, Virginia Appalachians: Amer. Assoc. Petr. Geol. Bull., 64:1575-1612.

Richards, R. P. 1972. Autecology of Richmondian brachiopods (Late Ordovician) of Indiana and Ohio: J. Paleontol., 46(3):386-405.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1974. Ecology of the Cornulitidae: J. Paleontol., 48(3):514-523.

_____. and R .K. Bambach. 1975. Population dynamics of some Paleozoic brachiopods and their paleoecologic significance: J. Paleontol., 49(5):775-798.

Roemer, C. F. von. 1876. Lethaea geognostica oder Beshreibung und Abbildung oder fur die Gebirgs-Formationen bezeichenendsten Versteinerungen: 1. Theil. Lethaea paleozoica. Atlas. Stuttgart.

Rogers, H. D. 1858. The Geology of Pennsylvania: 2 Vols., 1044 pp. J. P. Lippinincott and Co., Philadelphia.

Rollins, H. D. 1966. Morphological observations on the bellerophont Ptomatis patulus (Hall) (Gastropoda, Bellerophontacea): Amer. Mus. Nat. Hist., Novitates, 2242:1-7.

_____. 1967. The phylogeny and functional morphology of the Knightitinae, Carinaropsinae, and Praematuratropidae (Gastropoda, Bellerophontacea): Ph.D. Dissertation, Columbia University, 187 pp., 10 pls.

_____. 1969. The taxonomic position of Cyrtonella mitella Hall (Mollusca, Monoplacophora): J. Paleontol., 43(1):136-140.

_____ and R. L. Batten. 1968. A sinus-bearing monoplacophoran and its role in the classification of primitive molluscs: Palaeontology, 11(1):132-140.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____, M. Carothers, and J. Donahue. 1979. Transgression, regression, and fossil community succession: Lethaia, 12:89-104.

_____, N. Eldridge, and J. Spiller. 1971. Gastropods and Monoplacophora of the Solsville member (Middle Devonian, Marcellus Fm.) in the Chenango Valley, New York State: Am. Mus. Nat. Hist., Bull., 144(2):133-170.

Rooney, L. F. 1966. Evidence of unconformity at top of Trenton Limestone in Indiana and adjacent states: Amer. Assoc. Petrol. Geol. Bull. 50-533-546.

Rosov, S. N. 1975. A new order of Monoplacophora: Paleont. Jour., 9(2):193-203.

Ross, R. J., Jr. 1967. Calymenid and other Ordovician trilobites from Kentucky and Ohio: U.S Geological Survey Prof. Paper 583-B, 19 pp., pls. 35-37.

_____. 1979. Additional trilobites from the Ordovician of Kentucky: U.S. Geol. Surv. Prof. Paper 1066-D, 13 pp, 6 pls.

Rozanov, A. Yu., V. V. Missarzhevskiy, N. A. Volkova, L. G., Voronova, I. N., Krylov, B. M. Keller, I. K. Korolyuk, K. Lenozion, R. Mikhnyak, N. G. Pykhova, and A. D. Sidorov. 1969. Tommotian Stage and the Cambrian lower boundary problem: Trudy geol. Inst. Leningr., 206, 379 pp.

Ruedemann. R. 1926. The Utica and Lorraine Formations of New York: Pt. 2, Systematic paleontology, Mollusca, crustaceans, and eurypturids: New York State Mus. Bull. 272, 227 pp.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1934. Paleozoic Plankton of North America: Geol. Soc. America. Mem. 2.

Runnegar, B. 1981. Muscle scars, shell form and torsion in Cambrian and Ordovician univalved molluscs: Lethaia, 14:311-322.

_____. 1983. Molluscan phylogeny revisted: Mem. Assoc. Australas. Paleontols., 1:121-144.

_____ and P. A. Jell. 1976. Australian Middle Cambrian Molluscs and their bearing on early molluscan evolution: Alcheringa 1(2):109-138.

_____ and J. Pojeta, Jr. 1974. Molluscan phylogeny: the paleontological viewpoint: Science, 186:311-317.

Safford, J. M. 1869. Geology of Tennessee: S. C. Mercer, printer of the State, Nashville, Tenn.

Salvini-Plawen, L. V. 1980. A reconsideration of systematics in the Mollusca (phylogeny and higher classification): Malacologia, 19:249-278.

Sanders, H. L. 1968. Marine benthic diversity: a comparative study: The American Naturalist, 102(925):243-532.

Sardeson, F. W. 1892. The range and distribution of the Lower Silurian fauna of Minnesota with descriptions of some new species: Minnesota Acad. Nat. Sci. Bull., 3:326-343.

Saul, J. M., A. J. Boucot, and R. M. Finks. 1963. Fauna of the Accraian Series (Devonian of Ghana) including a revision of the gastropod Plectonotus: J. Paleontol., 37(5):1042-1053.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Scheltema, R. S. 1977. Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications: In, Kauffman, E. G. and J. E. Hazel (eds.), Concepts and Methods of Biostratigraphy. Hutchinson and Ross, Inc., Stroudsburg, Pa.

Schmitt, J. G. and D. W. Boyd. 1981. Patterns of silicification in Permian pelecypods and brachiopods from Wyoming: J. Sed. Petrology, 51(4):1297-1308.

Schuchert, C. 1900. Lower Silurian (Trenton) fauna of Baffinland: U.S. Nat. Mus. Proc., 22:143-177.

_____. 1943. Stratigraphy of the eastern and central United States: John Wiley and Sons, New York.

Shanmugam, G. and G. G. Lash, 1982. Analogous tectonic evolution of the Ordovician foredeeps, southern and central Appalachians: Geology, 10:562-66.

_____ and K. P. Walker, 1980. Sedimentation, subsidence, and evolution of a foredeep basin in the Middle Ordovician, southern Appalachians: Amer. Jour. Sci., 280(6):479-596.

Shaver, R. H. and others. 1970. Compendium of rock-unit stratigraphy in Indiana: Indiana Geol. Surv. Bull. 43, 229 pp.

Shimer, H. W. and R. R. Shrock, 1944. Index Fossils of North America: John Wiley and Sons, New York.

Shrock, R. R. 1937. Stratigraphy and structure of the area of disturbed Ordovician rocks near Kentland, Indiana: Amer. Midland Naturalist, 18:471-531.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____ and G. O. Raasch. 1937. Paleontology of the disturbed Ordovician rocks near Kentland, Indiana: Amer. Midland Naturalist, 18:532-607.

Signor, P. W. III, and C. E. Brett. 1984. The mid-Paleozoic precursor to the Mesozoic marine revolution: Paleobiology, 10(2):229-245.

Simroth, H. 1906. Mollusca (Weichtiere): In, Bronn, H. G., Klassen und Ordnungen des Tier-Reichs, Dritter Band. Abt. II. Gastropoda, Prosobranchia: Leipzig, Akademische Verlagsgeschellschaff m.b.H., p. 809-888 (1896-1907).

Sohl, N. F. 1969. The fossil record of shell boring by snails: In, Penetration of calcium carbonate by lower plants and invertebrates: Am. Assoc. Adv. Sci. Symp., Dallas, Texas, 1968: American Zoologist, 9(3):725-734.

Sprinkle, J. and B. M. Bell. 1978. Paedomorphosis in edrioasteroid echinoderms: Paleobiology, 4:82-88.

Starabogatov, Ya. I. 1970. K systematike rannepaleozoyskikh Monoplacophora (Systematics of Early Paleozoic Monoplacophora): Paleont. Zhur. 1970, no. 3, p. 6-17. (English translation in Paleont. Jour. 1970, no. 3, p. 293-302).

Stasek, C. R. 1972. The molluscan framework: In, Florkin, M. and B. T. Scheer (eds.), Chemical Zoology, Vol. VII, Mollusca, p. 1-43. Academic Press, New York.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Steele, H. M. and G. W. Sinclair. 1971. A Middle Ordovician fauna from Braeside, Ottawa Valley, Ontario: Geol. Surv. Canada, Bull. 211, 96 pp., 23 pls.

Steneck, R. S. 1983. Escalating herbivory and resulting adaptive trends: Paleobiology, 9(1):44-61.

_____ and L. Watling. 1982. Feeding capabilities and limitations of herbiverous molluscs: a functional group approach: Marine Biology, 68:299-319.

Stevens, C. H. 1965. Faunal trends in nearshore Pennsylvanian deposits near McCoy, Colorado: Mtn. Geologist, 2:71-77.

_____ 1966. Paleoecological implications of Early Permian fossil communities in eastern Nevada and western Utah: Geol. Soc. America Bull., 77:1121-1130.

Stinchcomb, B. L. 1980. New information on Late Cambrian Monoplacophora Hypseloconus and Shelbyoceras (Mollusca): J. Paleontol., 54(1):45-49, 2 text-figs.

Sturgeon, M. T. 1964. Allgeheny fossil invertebrates from eastern Ohio - Gastropoda: J. Paleontol., 38(2):189-212.

Sutton, R. G., Z. P. Bowen, and A. L. McAlester. 1970. Marine shelf environments of the Upper Devonian Sonyea Group of New York: Geol. Soc. America Bull., 81:2975-2992.

Swadley, W. C. 1975. Geologic map of the Lawrenceville Quadrangle, Grant and Owen Counties, Kentucky: U.S. Geol. Surv. Quad. Map GQ-1204.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Sweet, W. C. 1979. Conodonts and conodont biostratigraphy of post-Tyrone Ordovician rocks of the Cincinnati Arch region: U.S. Geol. Surv. Prof. Paper 1066-G, 26 p., 3 figs.

_____ and S. M. Bergstrom. 1971. The American Upper Ordovician Standard, XIII. A revised time-stratigraphic classification of North American upper Middle and Upper Ordovician rocks: Geol. Soc. America Bull., 82:613-628.

_____ and S. M. Bergstrom. 1974. Provincialism exhibited by Ordovician conodont faunas: Soc. Econ. Paleontol. Mineral., Sp. Publ. 21, pp. 189-202.

_____ and S. M. Bergstrom. 1976. Conodont biostratigraphy of the Middle and Upper Ordovician of the United States Midcontinent: In, Bassett, M. G. (ed.), The Ordovician System: proceedings of a Paleontological Association Symposium (1974). Univ. Wales Press and Nat. Mus. Wales, Cardiff.

Talent, J. A. 1959. Vallatotheca (Monoplacophora) in the Lower Permian of Victoria: Min. Geol. J., 6(3):33-34.

Teichert, Curt. 1928. Die silurische Familie Pterothecidae Walcott, nov. emend. (Gastrop. Heterop.): Senckenbergiana 10:136-157.

_____. 1930. Neues über die Gattung Pterotheca Salter: Senckenbergiana, 12:66-71.

_____. 1935 Uber Pterotheca Salter und verwandte Bellerophontacean: Palaeontologische Zeitschrift, 17:167-177.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Templeton, J. S. and William, H. B. 1963. Champlainian Series (Middle Ordovician) in Illinois: Illinois State Geol. Surv. Bull. 39, 260 pp.

Thayer, C. W. 1974. Marine paleoecology in the Upper Devonian of New York: Lethaia, 7:121-155.

Thein, M. L. and M. H. Nitecki. 1974. Chesterian (Upper Mississippian) Gastropoda of the Illinois Basin: Fieldiana, Geol., v. 34, 238 pp.

Thiele, J. 1935. Handbuch der systematischen Weichtierkunde, Teil 4: Jena, Gustav Fisher, p. 1023-1154.

Thompson, E. H. 1970. Morphology and taxonomy of Cyclonema Hall (Gastropoda), Upper Ordovician Cincinnatian Province: Bull. Amer. Paleont., 58(261):219-284.

Titus, R. 1982. Fossil communities of the Middle Trenton Group (Ordovician) of New York State: J. Paleontol., 56(2):477-485.

_____ and B. Cameron. 1976. Fossil communities of the lower Trenton Group (Middle Ordovician) of central and northwestern New York State: J. Paleontol., 50:1209-1255.

Tobin, R. C. 1982. A model for cyclic deposition in the Cincinnatian Series of southwestern Ohio, northern Kentucky, and southeastern Indiana: Ph.D. Thesis, Univ. Cincinnati, Cincinnati, Ohio, 483 pp.

Ulrich, E. O. 1911. Revision of the Paleozoic systems: Geol. Soc. America, 22:281-680.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____ and W. H. Scofield. 1897. The Lower Silurian Gastropoda of Minnesota: Minnesota Geological Survey, v. 3, pt. 2, pp. 812-1801, pls. 61-82.

Utgaard, J. and T. G. Perry. 1964. Trepostomatous bryozoan fauna of the upper part of the Whitewater Formation (Cincinnatian) of eastern Indiana and western Ohio: Indiana Geol. Surv. Bull. 33, 111 pp.

Vermeij, G. J. 1975. Evolution and distribution of left-handed and planispiral coiling in snails: Nature, 254(5499):419-420.

_____. 1978. Biogeography and Adaptation: Patterns of Marine Life: Harvard Univ. Press, Cambridge, Mass., 332 pp.

Waagen, W. H. 1980. Productus Limestone Fossils: Geol. Surv. of India, Mem., Paleont. Indica, ser. 13, Salt Range Fossils, pt. 2, v. 1, p. 73-183.

Walker, K. R. 1972. Community ecology of the Middle Ordovician Black River Group of New York State: Geol. Soc. America, Bull. 83:2499-2524.

_____ and W. C. Parker. 1976. Population structure of a pioneer and a later stage species in an Ordovician ecological succession: Paleobiology, 2(3):191-201.

Warmke, G. L. and L. R. Almodovar. 1963. Some associations of marine mollusks and algae in Puerto Rico: Malacologia, 1:163-177.

Watkins, R. and A. J. Boucot. 1975. Evolution of Silurian brachiopod communities along the southeastern part coast of Acadia: Geol. Soc. America Bull., 86:243-254.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Weir, G. W. and R. C. Greene. 1965. Clays Ferry Formation (Ordovician)-a new map unit in south-central Kentucky: U.S. Geol. Surv. Bull. 1224-B, 18 p., 17 figs.

_____, R. C. Green, and G. C. Simmons. 1965. Calloway Creek Limestone and Ashlock and Drakes Formations (Upper Ordovician) in south-central Kentucky: U.S. Geol. Surv. Bull. 1224-D, 36 pp., 12 figs.

_____ and J. H. Peck, Jr. 1968. Lithofacies of the Upper Ordovician rocks exposed between Maysville and Stanford, Kentucky: U.S. Geol. Prof. Paper 600-D, p. 162-168.

Weiss, M. P. 1957. Upper Middle Ordovician Stratigraphy of Fillmore Co., Minnesota: Geol. Soc. America Bull., 68:1027-1062.

_____, W. R. Edwards, C. E. Norman, and E. R. Sharp. 1965. The American Upper Ordovician Standard VII. Stratigraphy and petrology of the Cynthiana and Eden Formations of the Ohio Valley: Geol. Soc. America, Sp. Paper 81, 76 p., 8 pls.

_____ and C. E. Norman. 1960. The American Upper Ordovician Standard II. Developments of stratigraphic classification of Ordovician rocks in the Cincinnati region: Ohio Geol. Surv. Info. Circ. 26, 14 p.

_____ and W. C. Sweet. 1964. Kope Formation (Upper Ordovician): Ohio and Kentucky: Science, 145-1296-1302.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Weller, S. 1903. A report on the Paleozoic paleontology of New Jersey: Geol. Surv. New Jersey, Report on Paleontology, Vol. 3. Trenton, New Jersey.

Wenz, W. 1938. Handbuch der Palaozoologie Bd. 6, Gastropoda, Teil. 1 und 2, Allgemeiner Teil and Prosbranchia. Berlin.

_____ 1940. Ursprung and frühe Stammesgeschichte der Gastropoden: Arch. Molluskenkunde, 72:1-10.

West, R. R. 1972. Relationship between community analysis and depositional environments: an example from the North America Carboniferous: 24th Int. Geol. Congr., Sect. 7, p. 130-146.

Whiteaves, J. F. 1884. Paleozoic Fossils: Geol. Surv. Canada, 3(1):1-43.

_____ 1897. Galena-Trenton and Black River formations of Lake Winnepeg and its vicinity: Geol. Surv. Canada, Pal. Fossils, pt. 3.

Whitfield, R. P. 1878. Preliminary descriptions of new species of fossils from the lower geological formations of Wisconsin: Ann. Rept. Wisconsin Geol. Surv. for 1877, p. 50-89.

_____. 1882. Geology of Wisconsin: Wisconsin Geol. Surv., 1873-1879, vol. 4, pp. 163-363, pls. 1-27.

_____. 1886. Notice of geological investigations along the eastern shores of Lake Champlain, with descriptions of the new fossils discovered: Amer. Mus. Nat. Hist. Bull., 1:293-345.

Wilson, A. E. 1951. Gastropoda and Conularida of the Ottawa Formation of the Ottawa-St. Lawrence Lowland: Geol. Surv. Canada, Bull. 17, 149 pp., 19 pl.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Wilson, C. W. Jr. 1948. Geology of Nashville: Tenn. Div. of Geology, Bull. 53, 172 pp.

_____. 1949. Pre-Chatanooga Stratigraphy in Central Tennessee: Tenn. Div. Geol., Bull. 56, 407 pp.

_____. 1962. Stratigraphy and geologic history of Middle Ordovician rocks of central Tennessee: Geol. Soc. America, Bull., 73:481-504.

Woodward, M. F. 1901. The anatomy of Pleurotomaria beyrichii Hilgendorf: Quart J. Microscop. Sci., 44:215-268.

Wray, J. L. 1977. Calcareous algae: Elsevier, Amsterdam, 185 pp.

Yancey, T. E. and C. H. Stevens. 1981. Early Permian fossil communities in northeastern Nevada and northwestern Utah: In, Gary, J., and A. J. Boucot and W. B. N. Berry (eds.), Communities of the Past, Hutchinson Ross Publ. Co., Stroudsburg, Pa.

Yochelson, E. L. 1967. Quo Vadis, Bellerophon?: p. 141-161, In, C. Teichert and E. L. Yochelson (eds.), Essays in Paleontology and Stratigraphy, Univ. Kansas Press, Lawrence.

_____. 1971. A new Late Devonian gastropod and its bearing on problems of open coiling and septation: In, Paleozoic perspectives, a tribute to G. Arthur Cooper, Smithsonian Contr. Paleobiol., 3:231-241.

_____. 1978. An alternative approach fo the interpretation of the phylogeny of ancient Molluscs: Malacologia, 17(2):165-191.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

_____. 1979. Early radiation of Mollusca and Mollusc-like groups: p. 323-358, In, M. R. House (ed.), The Origin of Major Invertebrate Groups: Systematics Assoc. Sp. Vol. 12, Academic Press, London and New York.

_____. 1984. Historic and current considerations for revision of Paleozoic gastropod classification: J. Paleontol., 58(1):259-269.

_____, R. H. Flower, and G. L. Webers, 1973. The bearing of the new Late Cambrian monoplacophoran genus Knightoconus upon the origin of the Cephalopoda: Lethaia, 6(3):275-309.

Yonge, C. M. 1947. The pallial organs in aspidobranch Gastropoda and their evolution throughout the Mollusca: Phil. Trans. Royal Soc. London, Series B233, p. 433-518.

_____. 1973. Observation of the pleurotomarid Entemnotrochus adansoniana in its natural habitat: Nature, 241(5384):66-68.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

APPENDIX I

LOCALITY REGISTER

During the geologic mapping of the State of Kentucky by the United States Geological Survey, nearly 1,100 localities were collected for fossils. Pojeta (1979, pp. A19-A46) lists 317 of these localities from which Ordovician fossils were collected and studied.

Below is a listing of the USGS localities from which the fossils studied in this report were collected. The localities are arranged sequentially by collection number assigned to each in the USGS register of Cambrian and Ordovician localities (- CO). The following abbreviations are used in this listing for convenience.

C.n. ----- Collection Number

G.l. ----- Geographic location

C. ----- Coordinates

F. ----- Formation

S.p. ----- Stratigraphic position

Q.n. ----- Quadrangle name

S.n. ----- Section name

S.no. ----- Section number

U.S. Geological Survey Localities

C.n. ----- 4073 - CO.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

G.l. ----- Proceed east from Milner, Ky., 0.75 mi. and turn right (southwest) on Shryock Ferry Road. Continue down Shryock Ferry Road about 1 mile to top of section.
C. ----- 153 mm east, 99 mm north (base of section at 134 mm east; 87 mm north).
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 148 ft above the base of the Curdsville Limestone Member, Lexington Limestone.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone A.
S.no. ----- 89.

C.n. ----- 4852 - CO.
G.l. ----- Section along Interstate Route 75, 1.4 mi. south of Georgetown, Ky., exit.
C. ----- 364 mm east, 321 mm north.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 25 ft below top of the Grier Limestone Member.
Q.n. ----- Georgetown, Ky.
S.n. ----- Georgetown A.
S.no. ----- 151.

C.n. ----- 4865 - CO.
G.l. ----- U.S. Route 62 at crossing of Kentucky River from east side Blackburn Memorial Bridge, take side road north 0.1 mi. to railroad roadcut exposure.
C. ----- N. Zone - 198, 450' north; 1,828, 300' east.
F. ----- Logana Member, Lexington Limestone.
S.p. ----- Lower 12 ft of Logana.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone C or KY Utilities Plant.
S.no. ----- 174.

C.n. ----- 4874 - CO.
G.l. ----- Road exposures between Trinity Church and Antioch Church, southwest quadrant, Valley View Quadrangle, Ky.
C. ----- Base of section at 19 mm east; 176 mm north.
F. ----- Grier Limestone Member, Lexington Limestone
S.p. ----- 30 ft above the base of the section.
Q.n. ----- Valley View, Ky.
S.n. ----- Valley View C (Antioch Church Road).
S.no. ----- 180.

C.n. ----- 4876 - CO.
G.l. ----- The same as for 4874 - CO.
C. ----- Do.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 35 ft above the base of the section.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Q.n. ----- Valley View, Ky.
S.n. ----- Valley View C (Antioch Church Road).
S.no. ----- 180.

C.n. ----- 4879 - CO.
G.l. ----- The same as for 4874 - CO.
C. ----- Do.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 43-45 ft above the base of section.
Q.n. ----- Valley View, Ky.
S.n. ----- Valley View C (Antioch Church Road).
S.no. ----- 180.

C.n. ----- 4880 - CO.
G.l. ----- The same as for 4874 - CO.
C. ----- Do.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 47 ft above the base of the section.
Q.n. ----- Valley View, Ky.
S.n. ----- Valley View C (Antioch Church Road).
S.no. ----- 180.

C.n. ----- 4883 - CO.
G.l. ----- Roadcut in southwest quarter of quadrangle running from Trinity Church to Antioch Church - 1 mi. southwest of the northern termination of Ky. Route 595 at the Kentucky River.
C. ----- 2,363, 125'; 532, 175', S zone base section.
F. ----- Grier Member, Lexington Limestone.
S.p. ----- 60-1/2 ft above base section.
Q.n. ----- Valley View.
S.n. ----- Antioch Church Road.
S.no. ----- 180.

C.n. ----- 4928 - CO.
G.l. ----- Ky. Route 513 east of McBrayer, Ky.
C. ----- N zone 1, 821, 500'; 174, 550'.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 22 ft below base Brannon Member.
Q.n. ----- Salvisa
S.n. ----- Salvisa A.
S.no. ----- 175.

C.n. ----- 4929 - CO.
G.l. ----- Road exposures 0.5 mi. east and 1.6 mi. south of northwest corner of Salvisa Quadrangle, Ky.
C. ----- 32 mm east, 467 mm north.
F. ----- Grier Limestone Member, Lexington Limestone.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S.p. ----- 8 ft below base of the Brannon Member, Lexington Limestone.
Q.n. ----- Salvisa, Ky.
S.n. ----- Salvisa A.
S.no. ----- 175.

C.n. ----- 4940 - CO.
G.l. ----- Road exposure on west side of Kentucky River at bridge crossing of Central Kentucky Parkway on north side of parkway.
C. ----- Base of section at 186 mm east; 508 mm north.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- 7 ft above the top of the Tyrone Limestone.
Q.n. ----- Salvisa, Ky.
S.n. ----- Salvisa B.
S.no. ----- 176.

C.n. ----- 4959 - CO.
G.l. ----- The same as for 4940 - CO.
C. ----- Do.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 149-152 ft above the top of the Tyrone Limestone.
Q.n. ----- Salvisa, Ky.
S.n. ----- Salvisa B.
S.no. ----- 176.

C.n. ----- 5015 - CO.
G.l. ----- Quarry exposure 0.4 mi. south of Perryville, Ky., on east side of Mitchellsburg Road, east side of Chaplin River.
C. ----- 191 mm east; 92 mm north.
F. ----- Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
S.p. ----- 5 ft above base of Salvisa Bed.
Q.n. ----- Perryville, Ky
S.n. ----- Perryville B (Perryville South)
S.no. ----- 30 B.

C.n. ----- 5016 - CO.
G.l. ----- The same as for 5015 - CO.
C. ----- Do.
F. ----- Cornishville Bed, Perryville Limestone Member, Lexington Limestone.
S.p. ----- 14 ft above the base of the Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
Q.n. ----- Perryville, Ky.
S.n. ----- Perryville B (Perryville S).
S.no. ----- 30 B.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 5022 - CO.
G.l. ----- Section in quarry and road exposures near Clear Creek, 0.2 mi. east and 2.6 mi. south of the northwest corner of the Keene Quadrangle, Ky.
C. ----- Do.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- Float from the lower 22 ft of the Curdsville Limestone Member.
Q.n. ----- Keene, Ky.
S.n. ----- Keene A.
S.no. ----- 150.

C.n. ----- 5023 - CO.
G.l. ----- The same as for 5022 - CO.
C. ----- Base of section at 21 mm east; 326 mm north.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- 30 ft above the base of the Curdsville Limestone Member.
Q.n. ----- Keene, Ky.
S.n. ----- Keene A.
S.no. ----- 150.

C.n. ----- 5024 - CO.
G.l. ----- Quarry and roadcut - 1st outcrop southeast of crossing Ky. Route 35 (Fordsmill Road) and Clear Creek.
C. ----- North zone 1, 857,000' east, 162,000' north.
F. ----- Logana Member, Lexington Limestone.
S.p. ----- Float from lower Logana Member.
Q.n. ----- Keene, Ky.
S.n. ----- Keene A.
S.no. ----- 150.

C.n. ----- 5036 - CO.
G.l. ----- Small stream exposure on Squires Road, 1.8 mi. southwest of intersection with U.S. Route 421 (upstream 0.1 mi.).
C. ----- 151 mm east; 494 mm north.
F. ----- Devils Hollow Member, Lexington Limestone.
S.p. ----- 60 ft. above base of the Brannon Member, Lexington Limestone.
Q.n. ----- Coletown, Ky.

C.n. ----- 5067 - CO.
G.l. ----- Hillside pasture exposure on west side of U.S. Route 227, 0.4 mi. south of intersection of Ford-Hampton Road and U.S. 227, north of Ford, Ky.
C. ----- 423 mm east, 187 mm north.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 140 ft above top of Tyrone Limestone.
Q.n. ----- Ford, Ky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 5072 - CO.
G.l. ----- Immediately behind Old Crow Distillery, north bluff of Glenns Creek Road, 0.7 mi. west of intersection with Hanley Lane.
C. ----- 107 mm east; 102 mm north.
F. ----- Lower Lexington Limestone; mostly basal Curdsville Limestone Member, but with some float blocks of the Logana Member included in the sample.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East B.
S.no. ----- 87

C.n. ----- 5073 - CO.
G.l. ----- Northwest of Old Crow Distillery on first sharp north bend of Glenns Creek Road, 0.9 mi. west of intersection with Hanley Lane.
C. ----- 82 mm east, 111 mm north.
F. ----- Upper Logana Member, Lexington Limestone.
S.p. ----- Just below 4 ft thick dalmanellid coquina.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East B.
S.no. ----- 87

C.n. ----- 5075 - CO.
G.l. ----- 2nd Quarry, Jessamine Creek, southeast of Wilmore, Ky.
C. ----- South zone - 2,318, 150' east; 551, 100' north.
F. ----- Tyrone Limestone.
S.p. ----- Tyrone Limestone.
Q.n. ----- Wilmore, Ky.

C.n. ----- 5080 - CO.
G.l. ----- First crossing of Southern Railroad tracks by unnamed road running due south from 2 right angle turns in Kentucky Route 342, 1.2 mi. west of Herrington Lake Spillway.
C. ----- 88 mm east, 158 mm north.
F. ----- Upper part of Curdsville Limestone Member, Lexington Limestone.
Q.n. ----- Wilmore, Ky

C.n. ----- 5084 - CO.
G.l. ----- From east side of Blackburn Memorial Bridge crossing Kentucky River take first road north toward Kentucky Utilities Plant; section in railroad and road exposures.
C. ----- 108 mm east; 214 mm north (railroad exposures).
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- 5 ft above base of Curdsville Limestone Member.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone C.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S.no. ----- 174.

C.n. ----- 5085 - CO.
G.l. ----- The same as for 5084 - CO.
C. ----- Do.
F. ----- Curdsville Member, Lexington Limestone.
S.p. ----- 16 ft above Tyrone - Lexington contact.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone Co. Kentucky Utilities Plant.
S.no. ----- 174.

C.n. ----- 5086 - CO.
G.l. ----- The same as for 5084 - CO.
C. ----- Do.
F. ----- Logana Member, Lexington Limestone.
S.p. ----- 18-20 ft above the base of the Logana Member.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone C.
S.no. ----- 174

C.n. ----- 5087 - CO.
G.l. ----- Small road exposure on U.S. Route 421, 0.5 mi. east of the U.S. Routes 60 and 421 junction.
C. ----- 242 mm east; 287 mm north.
F. ----- Upper part of Devils Hollow Member, Lexington Limestone.
Q.n. ----- Frankfort East, Ky.

C.n. ----- 5091 - CO.
G.l. ----- Behind old Stagg Distillery.
C. ----- Zone 1, 820, 750 E; 262, 600 N.
F. ----- Logana Member, Lexington Limestone.
S.p. ----- 20 ft above base Logana Member.
Q.n. ----- Frankfort East, Kentucky.
S.n. ----- Stagg Distillery.

C.n. ----- 5092 - CO.
G.l. ----- From east side of Blackburn Memorial Bridge crossing of Kentucky River take 1st road north toward Kentucky Utilities Plant; section in railroad and road exposures.
C. ----- 108 mm east, 197 mm north.
F. ----- Logana Member, Lexington Limestone.
S.p. ----- 10-12 ft above base of Logana Member.
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone C.
S.no. ----- 174.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 5094 - CO.
G.l. ----- Devils Hollow Road south of Buttlmer Hill about 0.7 mi.
C. ----- North zone 1, 816, 700' east; 253, 275' north.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- Float 45' above Macedonia Bed.
Q.n. ----- Frankfort West, Kentucky.
S.n. ----- Devils Hollow Road section.

C.n. ----- 5095 - CO.
G.l. ----- Road exposure on north side of westbound lanes of Interstate Route 64, 0.5 mi. east of bridge over Kentucky River.
C. ----- 123 mm east, 195 mm north.
F. ----- Devils Hollow Member, Lexington Limestone.
S.p. ----- 6-8 ft above base of Devils Hollow Member.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East A.
S.no. ----- 86

C.n. ----- 5096 - CO.
G.l. ----- Just before ferry crossing of Tates Creek Road and Kentucky River, take road west toward Daniel Boone YMCA Camp; collection from near top of north bluff Kentucky River, 0.4 mi. southeast of YMCA Camp in abandoned railroad bed.
C. ----- 151 mm east; 432 mm north.
F. ----- Grier Limestone Member, Lexington Limestone.
Q.n. ----- Valley View, Ky.

C.n. ----- 5099 - CO.
G.l. ----- Roadcut along stream immediately across Kentucky River, Kentucky, Route 595.
C. ----- Base section 1, 932, 350' east, 110, 30' north.
F. ----- Grier Limestone Member, Lexington Limestone.
S.p. ----- 78-80' above base section.
Q.n. ----- Valley View, Kentucky
S.n. ----- Hunters Ferry Road.
S.no. ----- 34

C.n. ----- 5100 - CO.
G.l. ----- Crisman Mill Road, 0.2 mi. west of Hickman Creek crossing.
C. ----- 411 mm east; 451 mm north.
F. ----- Lower part of Curdsville Limestone Member, Lexington Limestone.
Q.n. ----- Little Hickman, Ky.
S.n. ----- Little Hickman B.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 5101 - CO.
G.l. ----- Kentucky Route 169 just west of Hickman Creek crossing.
C. ----- North zone 1, 923, 225' east; 143, 075' north.
F. ----- Lower part of Curdsville Limestone Member, Lexington Limestone.
Q.n. ----- Nicholasville, Ky.

C.n. ----- 5107 - CO.
G.l. ----- Hillside exposure in farm road leading south from U.S. Route 60, west of Keeneland Racetrack; collected at 900 ft contour.
C. ----- 43 mm east; 194 mm north.
F. ----- Grier Limestone Member, Lexington Limestone.
Q.n. ----- Lexington West, Ky.

C.n. ----- 6034 - CO.
G.l. ----- Section on New Matte Mill road, 0.1 mi. southwest intersection with Kentucky Route 39.
C. ----- N. zone 1, 911, 400' east; 117, 700' north.
F. ----- Tyrone Limestone
S.p. ----- 112 ft above base section.
Q.n. ----- Little Hickman, Kentucky
S.n. ----- Little Hickman A.

C.n. ----- 6035 - CO.
G.l. ----- The same as for 6034 - CO.
C. ----- Do.
F. ----- Tyrone Limestone.
S.p. ----- 89-94 ft above base section.
Q.n. ----- Little Hickman, Kentucky.
S.n. ----- Little Hickman A.
S.no. ----- None given here.

C.n. ----- 6127 - CO.
G.l. ----- Southernmost tributary of Landing Run, 2000 ft east of intersection of U.S. Route 31E and Kentucky Route 46, between Balltown and Culvertown, Ky.
C. ----- 381 mm east; 436 mm north.
F. ----- Rowland Member, Drakes Formation.
Q.n. ----- New Haven, Ky.

C.n. ----- 6128 - CO.
G.l. ----- Outcrop at farm pond 2000 ft west of intersection of Mt. Horeb and Carrick Roads, 1000 ft north of Carrick Road.
C. ----- 183 mm east; 387 mm north.
F. ----- Clays Ferry Formation tongue between Millersburg Member, Lexington Limestone, below and Tanglewood Limestone Member, Lexington Limestone, above.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

S.p.	-----	5-10 ft above base Clays Ferry Formation tongue, 15-20 ft above Allonychia flanaganensis zone in the Millersburg Member, Lexington Limestone.
Q.n.	-----	Centerville, Ky.
C.n.	-----	6131 - CO.
G.l.	-----	Section on Kentucky Route 33 north of bridge crossing of Mocks Branch, 2.5 mi. north of Danville, Kentucky.
C.	-----	405 mm east; 307 mm north.
F.	-----	Upper part of Curdsville Limestone Member, Lexington Limestone.
S.p.	-----	23 ft above the Tyrone Limestone - Lexington Limestone contact.
Q.n.	-----	Danville, Ky.
C.n.	-----	6134 - CO.
G.l.	-----	Road exposures 0.2 mi. west of Dix River crossing of Kentucky Route 52.
C.	-----	315 mm east; 78 mm north.
F.	-----	Curdsville Limestone Member, Lexington Limestone.
S.p.	-----	Lower 3 ft of Curdsville Limestone Member.
Q.n.	-----	Bryantsville, Ky.
S.n.	-----	Bryantsville D.
C.n.	-----	6136 - CO.
G.l.	-----	Roadcut on Kentucky Route 52, 1.45 mi. east junction with U.S. Route 150; 0.15 mi. east of crossing of Kentucky Route 52 and Balls Branch Run.
C.	-----	74 mm east, 35 mm north.
F.	-----	Faulconer Bed, Perryville Limestone Member, Lexington Limestone.
S.p.	-----	Basal 3-4 ft of Perryville Limestone Member, immediately above Tanglewood Limestone Member, Lexington Limestone.
Q.n.	-----	Bryantsville, Ky.
S.n.	-----	Bryantsville B.
C.n.	-----	6138 - CO.
G.l.	-----	The same as for 6136 - CO.
C.	-----	74 mm east; 35 mm north.
F.	-----	Cornishville Bed, Perryville Limestone Member, Lexington Limestone.
S.p.	-----	16 ft above the Perryville Limestone Member - Tanglewood Limestone Member contact.
Q.n.	-----	Bryantsville, Ky.
S.n.	-----	Bryantsville B.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 6139 - CO.
G.l. ----- South bank Salt Creek, 900 ft upstream from covered bridge on Enochsburg-Oldenburg (Indiana) Road.
C. ----- 328 mm east; 378 mm north.
F. ----- Upper part of Dillsboro Formation.
Q.n. ----- New Point, Indiana

C.n. ----- 6140 - CO.
G.l. ----- North bank Salt Creek, 0.4 mi. upstream from covered bridge on Enochsburg-Oldenburg (Indiana) Road.
C. ----- 315 mm east; 380 mm north.
F. ----- Upper part of Dillsboro Formation.
Q.n. ----- New Point, Indiana.

C.n. ----- 6142 - CO.
G.l. ----- Road exposure on east side on Kentucky Route 982, 0.4 mi. south of junction of Kentucky Routes 32, 36 and 982 in Cynthiana, Ky. (across from River View Mission and Liggett and Meyers tobacco warehouse).
C. ----- 290 mm east; 39 mm north.
F. ----- Lower tongue Clays Ferry Formation.
S.p. ----- 18-20 ft above the base of the section.
Q.n. ----- Cynthiana, Ky.

C.n. ----- 6143 - CO.
G.l. ----- The same as for 6142 - CO.
C. ----- Do.
F. ----- Upper tongue of Clays Ferry Formation.
S.p. ----- 30-35 ft above the base of the section.
Q.n. ----- Cynthiana, Ky.

C.n. ----- 6144 - CO.
G.l. ----- The same as for 6142 - CO.
C. ----- Do.
F. ----- Base of upper tongue Millersburg Member, Lexington Limestone.
S.p. ----- 24 ft above the base of the section.
Q.n. ----- Cynthiana, Ky.

C.n. ----- 6145 - CO.
G.l. ----- Kentucky Route 8, 1 mi. south of Carntown, Ky.
C. ----- 28 mm east; 326 mm north.
F. ----- Point Pleasant tongue, Clays Ferry.
S.p. ----- About 50 ft below the base of the Kope Formation.
Q.n. ----- Moscow, Ohio - Kentucky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 6411 - CO.
G.l. ----- U.S. Route 27, 0.1 mi. northeast of crossing of Dix River.
C. ----- 42.5 mm east; 342 mm north.
F. ----- Gilbert Member, Ashlock Formation.
S.p. ----- 5 ft above base of the Gilbert Member.
Q.n. ----- Lancaster, Ky.
S.n. ----- Ashlock Cemetary.
S.no. ----- 21 B.

C.n. ----- 6412 - CO.
G.l. ----- The same as for 6411 - CO.
C. ----- Do.
F. ----- Gilbert Member, Ashlock Formation.
S.p. ----- 11.5 ft above the base of the Gilbert Member.
Q.n. ----- Lancaster, Ky.
S.n. ----- Ashlock Cemetary.
S.no. ----- 21 B.

C.n. ----- 6414 - CO.
G.l. ----- Exposures of Kentucky Route 21, 0.9 mi. south of the junction of Walnut Meadow Branch and Paint Lick Creek.
C. ----- 18 mm east; 372 mm north.
F. ----- Gilbert Member; Ashlock Formation.
S.p. ----- 1-2 ft silicified zone at top of Gilbert Member.
Q.n. ----- Berea, Ky.

C.n. ----- 6419 - CO.
G.l. ----- 1.4 mi. east of Wilmore, Ky., 500 ft north of main road.
C. ----- 420 mm east; 534 mm north.
F. ----- Lower part of Logana Member, Lexington Limestone.
Q.n. ----- Wilmore, Ky.

C.n. ----- 6915 - CO.
G.l. ----- Boyle County Quarry, west side of U.S. Route 68, 1.3 mi. northeast of Perryville, Ky.
C. ----- 217 mm east, 176 mm north.
F. ----- Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
S.p. ----- Basal 2 ft of Salvisa bed; northwest wall of quarry.
Q.n. ----- Perryville, Ky.
S.n. ----- Perryville A (Perryville north).
S.no. ----- 30 A.

C.n. ----- 6916 - CO.
G.l. ----- Same as 6915-CO.
C. ----- Do.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

F. ----- Salvisa Bed, Perryville Limestone Member, Lexington Limestone.
S.p. ----- Same as for 6915-CO, but collected from east wall of quarry.
Q.n. ----- Perryville, Ky.
S.n. ----- Perryville A (Perryville north).
S.no. ----- 30 A.

C.n. ----- 6990 - CO.
G.l. ----- West side of U.S. Route 27, 1,700 ft from highway, 0.9 mi. south of Lair, Ky.
C. ----- 245 mm east; 369 mm north.
F. ----- Top of Tongue of Clays Ferry Formation which lies between a lower Millersburg Member tongue, Lexington Limestone, and an upper tongue of the Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- 60 ft above the top of the Grier Limestone Member, Lexington Limestone.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7044 - CO.
G.l. ----- 0.7 mi. southwest of junction of Kentucky Route 974 and Dry Fork Road on Dry Fork Road. Section begins in valley of East Fork of Fourmile Creek in the Tanglewood Limestone Member, Lexington Limestone, just below the Allonychia flanaganesis zone of the Millersburg Member, Lexington Limestone. The main part of the section is north of East Fork, along Dry Fork Road above the 823 ft elevation mark.
C. ----- Base of section at 394 mm east; 268 mm north.
F. ----- Tongue of the Clays Ferry Formation
S.p. ----- 25 ft above Allonychia flanaganesis horizon.
Q.n. ----- Winchester, Ky.
S.n. ----- Winchester A (Dry Fork Road).
S.no. ----- 1004

C.n. ----- 7343 - CO.
G.l. ----- West side of U.S. Route 27, 1,700 ft from highway, 0.9 mi. south of Lair, Ky.
C. ----- 245 mm east; 369 mm north.
F. ----- Top of Tongue of Clays Ferry Formation which lies between a lower Millersburg Member Tongue, Lexington Limestone, and an upper tongue of the Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- 60 ft above the top of the Grier Limestone Member, Lexington Limestone.
Q.n. ----- Shawhan, Ky.
S.n. ----- Section at White Farm.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 7344 - CO.
G.l. ----- East side of U.S. Route 27, 900 ft from highway, 0.4 mi. north of Lair, Ky.
C. ----- 246 mm east; 439 mm north.
F. ----- Near top of the lower tongue of the Millersburg Member, Lexington Limestone.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7345 - CO.
G.l. ----- The same as far 6142 - CO.
C. ----- Do.
F. ----- Lower tongue Clays Ferry Formation.
S.p. ----- 20-22 ft above the base of section.
Q.n. ----- Cynthiana, Ky.

C.n. ----- 7348 - CO.
G.l. ----- 4300 ft east, 6300 ft south of the northwest corner of the Shawhan Quadrangle.
C. ----- 54 mm east, 493 mm north.
F. ----- Tongue of Clays Ferry Formation underlain by a tongue of the Millersburg Member, Lexington Limestone and overlain by a tongue of the Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- Float, 4 ft above 810 foot contour.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7349 - CO.
G.l. ----- The same as for 7348 - CO.
C. ----- Do.
F. ----- Do.
S.p. ----- Float, 5 ft above 810 foot contour.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7350 - CO.
G.l. ----- The same as for 7348 - CO.
C. ----- Do.
F. ----- Do.
S.p. ----- Float, 6 ft above the 810 foot contour.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7353 - CO.
G.l. ----- 1 mi. east northeast junction of Cook Road and Lair Road in stock pond.
C. ----- 428 mm east; 471 mm north.
F. ----- Lower tongue of Millersburg Member, Lexington Limestone.
Q.n. ----- Shawhan, Ky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 7450 - CO.
G.l. ----- Section along road to U.S. Route 25, 0.4 mi. west of Sadieville, Ky.
C. ----- Base of section at 295 mm east; 63 mm north.
F. ----- Clays Ferry Formation tongue.
S.p. ----- 5 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville B.
S.no. ----- 192.

C.n. ----- 7452 - CO.
G.l. ----- The same as for 7450 - CO.
C. ----- Do.
F. ----- Clays Ferry Formation tongue.
S.p. ----- 10 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

C.n. ----- 7454 - CO.
G.l. ----- The same as for 7450 - CO.
C. ----- Do.
F. ----- Millersburg Member, Lexington Limestone.
S.p. ----- 20 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

C.n. ----- 7455 - CO.
G.l. ----- The same as for 7450 - CO.
C. ----- Do.
F. ----- Millersburg Member, Lexington Limestone.
S.p. ----- 22 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

C.n. ----- 7457 - CO.
G.l. ----- The same as for 7450 - CO.
C. ----- Do.
F. ----- Millersburg Member, Lexington Limestone.
S.p. ----- 32 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 7458 - CO.
G.l. ----- Same as for 7450-CO.
C. ----- Do.
F. ----- Clays Ferry Formation tongue.
S.p. ----- 35 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

C.n. ----- 7461 - CO.
G.l. ----- The same as for 7450 - CO.
C. ----- Do.
F. ----- Clays Ferry Formation tongue.
S.p. ----- 50-55 ft above the base of the section.
Q.n. ----- Sadieville, Ky.
S.n. ----- Sadieville C.
S.no. ----- 192.

C.n. ----- 7782 - CO.
G.l. ----- The same as for 5084 - CO.
C. ----- Do.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- Lower 5 ft of Curdsville Limestone Member
Q.n. ----- Tyrone, Ky.
S.n. ----- Tyrone C.
S.no. ----- 174

C.n. ----- 7783 - CO.
G.l. ----- South side of westbound lanes of Interstate Route 64, 0.5 mi. south of bridge across Kentucky River.
C. ----- East 1, 27, 150'; north 241, 350'.
F. ----- Top bed Tanglewood upper tongue.
S.p. ----- Top bed upper tongue Tanglewood, below Devil Hollow.
Q.n. ----- Frankfort East.
S.n. ----- Frankfort East A.
S.no. ----- 86.

C.n. ----- 7784 - CO.
G.l. ----- U.S. Route 27, 0.3 mi. southeast of crossing of Kentucky River bridge on south side of road.
C. ----- 41 mm east; 75 mm north.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- Basal 2 ft of the Curdsville Limestone Member.
Q.n. ----- Little Hickman, Ky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 7785 - CO.
G.l. ----- The same as for 7784 - CO.
C. ----- Do.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- 11-12 ft above base of Curdsville Limestone Member.
Q.n. ----- Little Hickman, Ky.

C.n. ----- 7787 - CO.
G.l. ----- South side westbound lanes I-64 about 0.8 mi. east bridge over Kentucky River.
C. ----- East 1, 827, 150'; north 241, 350'.
F. ----- Top bed of upper tongue of Tanglewood Limestone Member, Lexington Limestone.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East.
S.no. ----- 86.

C.n. ----- 7789 - CO.
G.l. ----- Eastbound lanes of Interstate Route 64 (north and south sides), 0.8 mi. east of Kentucky River.
C. ----- 123 mm east, 195 mm north
F. ----- Upper part of Devil's Hollow Member, Lexington Limestone.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East A.
S.no. ----- 86.

C.n. ----- 7791 - CO.
G.l. ----- The same as for 4940 - CO.
C. ----- Do.
F. ----- Lower part of Logana Member, Lexington Limestone.
S.p. ----- 35 ft above Tyrone-Lexington Limestones contact.
Q.n. ----- Salvisa, Ky.
S.n. ----- Salvisa B.
S.no. ----- 176.

C.n. ----- 7796 - CO.
G.l. ----- Exposures on Interstate Route I-75, 1.3 mi. south exit to Kentucky Route 418.
C. ----- North zone 1, 962, 100' east; 161, 250' north.
F. ----- Lower Tongue of Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- 3-9 ft above base of Cane Run Bed.
Q.n. ----- Coletown, Ky.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- 7809 - CO.
G.l. ----- 75 ft south of junction Kentucky Route 388 and U.S. Route 227.
C. ----- 384 mm east, 113 mm north.
F. ----- Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- First bed above Brannon-Tanglewood contact.
Q.n. ----- Ford, Ky.
S.n. ----- Boonesboro Beach.

C.n. ----- 7812 - CO.
G.l. ----- Farm pond 250 ft west of U.S. Route 27, 500 ft south of junction of U.S. Routes 27 and 62.
C. ----- 220 mm east; 548 mm north.
F. ----- Clays Ferry Formation.
Q.n. ----- Shawhan, Ky.

C.n. ----- 7817 - CO.
G.l. ----- Section Kentucky Route 39, 0.3 mi. southeast of Black Bridge crossing over Hickman Creek.
C. ----- North zone 1, 912, 950' east; 113, 250' north.
F. ----- Curdsville Limestone Member, Lexington Limestone.
S.p. ----- 6 inches above contact of Tyrone Limestone and Curdsville Member, Lexington Limestone.
Q.n. ----- Little Hickman, Ky
S.n. ----- Little Hickman A.

C.n. ----- 7843 - CO.
G.l. ----- Exposures on Kentucky Route 35, north of Moreland about 2.5 miles.
C. ----- 2,274, 225' east; 439, 950' north.
F. ----- Ashlock Formation
Q.n. ----- Junction City, Ky.

C.n. ----- D-1172 - CO.
G.l. ----- 45 ft above old Clays Ferry Road, section beginning about 1750 ft west of high bridge piers for the Interstate Route 75 bridge crossing the Kentucky River.
C. ----- Base of section at 132 mm east, 31 mm north.
F. ----- Clays Ferry Formation.
S.p. ----- 25 ft above top of Lexington Limestone.
Q.n. ----- Ford, Ky.
S.n. ----- Clays Ferry (lower part); Ford A.
S.no. ----- 22 B.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

C.n. ----- D-1196
G.l. ----- Eastbound lanes of Interstate Route 64 from Kentucky River bridge crossing to end of exposure.
C. ----- Base of section at 88 mm east; 164 mm north.
F. ----- Top of Logana Member, Lexington Limestone.
S.p. ----- 50 ft above the top of the Tyrone Limestone.
Q.n. ----- Frankfort East, Ky.
S.n. ----- Frankfort East A.
S.no. ----- 86.

C.n. ----- D-1206
G.l. ----- South side westbound lanes I-64, 0.5 mi. south of bridge across Kentucky River.
C. ----- East 1, 27, 150'; north 241, 330'.
F. ----- Top of upper tongue of Tanglewood Limestone Member, Lexington Limestone.
S.p. ----- Just below 7783 - CO.
Q.n. ----- Frankfort E.
S.n. ----- Frankfort East A.
S.no. ----- 86.

Other Sample Localities

C.n. ----- OH-1.
G.l. ----- Bear Creek Quarry, an abandoned quarry along the bluffs on the north side of the Ohio River, at the intersection of Bear Creek Road and U.S. Route 52, 3 mi. east of Neville and 1.1 mi. west of Chilo, Washington Co., Ohio.
F. ----- Kope Formation
S.p. ----- 10-15 ft above contact of Kope Formation and the Point Pleasant Tongue of the Clays Ferry Formation.
Q.n. ----- Moscow, Ohio-Kentucky Quad.

C.n. ----- KY-1.
G.l. ----- Roadcut on west side of Interstate Highway I-75, at the Sadieville, Kentucky, exit.
F. ----- Clays Ferry Formation
S.P. ----- Mollusc-rich lens along bench in roadcut.
Q.n. ----- Sadieville, Kentucky, Quad.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATES 1-45

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 1

FIGURES 1-7. *Micropileus variabilis* n. sp.

1-4. Dorsal, ventral, left and right-lateral views of holotype (X3). Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian), USGS 7817-CO. USNM 265926.

5. Left-lateral view of a paratype (X3). Curdsville Limestone Member of the Lexington Limestone (Kirkfieldian), USGS 7784-CO. USNM 265928.

6. Left-lateral view of a paratype (X3). Same sample as Figure 5 above. USNM 265929.

7. Left-lateral view of a paratype (X3). Same sample as Figure 5 above. USNM 265927.

8-11. *Vallatotheca manitoulini* Foerste, 1924.

8-9. Left-lateral oblique and dorsal views of a calcitic cast (X3). Elkhorn biofacies of Preachersville Member of Drakes Formation, from creek just south of Morning Sun, Ohio. MU 244T.

10-11. Right dorsolateral and dorsal views of calcitic cast (X3). Upper Whitewater Formation from tributary of Paint Creek near Camden, Ohio.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 1 (Cont'd)

12-31. Vallatotheca unguiformis (Ulrich in Ulrich and Scofield, 1897).

12-15. Dorsal, ventral, left and right-lateral views of lectotype (X3). The museum label give the horizon and locality as: "Upper Trenton, Harrodsburg Junction, C. S. Railroad, Kentucky. USNM 45990.

16-17. Right-lateral and dorsal views of a silicified specimen (X4). Perryville Limestone Member of the Lexington Limestone (Salvisa bed), USGS 6915-CO. USNM 265934.

18-20. Dorsal, right- and left-lateral views of a silicified specimen (X3). Salvisa bed, Perryville Limestone Member of the Lexington Limestone, USGS 5015-CO. USNM 265932.

21-22. Right-lateral and dorsal views of a paralectotype (X3). Same sample as Figures 12-15 above. USNM 265930.

23-24. Dorsal and right-lateral views of a paralectotype (X3). Same sample as Figures 12-15 above. USNM 265931.

25-28. Dorsal, ventral, left- and right-lateral views of a large silicified specimen (X3). Note the apex is

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 1 (Cont'd)

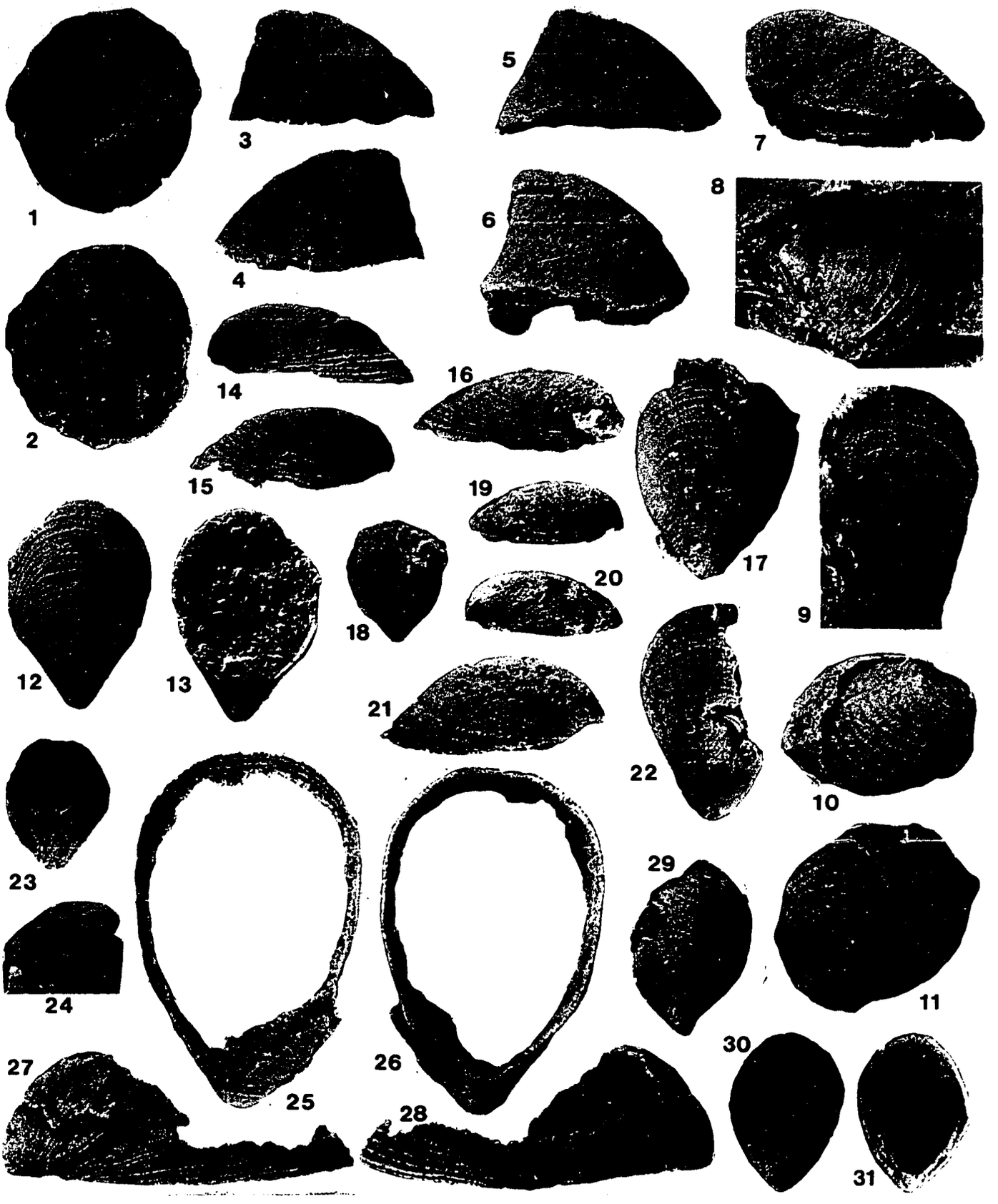
nearly level with the apertural plane. Same sample as Figures 16-17 above. USNM 265936.

29. Dorsal view of silicified specimen; slightly curved beak probably a preservational feature (X3). Same sample as Figures 16-17 above. USNM 265935.

30-31. Dorsal and ventral views of a bryozoan-encrusted silicified specimen (X3). Same sample as Figures 18-20 above. USNM 265933.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 1



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 2

FIGURES 1-6. *Helcionopsis striata* Ulrich and Scofield, 1897.

1-3. Dorsal, dorsolateral, and left-lateral views of latex rubber mold of holotype, which is an external mold in the base of a bryozoan colony (X2). Museum label gives horizon and locality as "Richmond Group, Marion County, Kentucky." USNM 45827.

4-5. Ventrolateral view (X2) of external mold in base of bryozoan colony, and dorsal view (X3.25) of latex rubber mold of same. Bellevue biofacies of Grant Lake Limestone (Maysvillian), at Cincinnati, Ohio. USNM 47494.

6. Dorsal view of calcitic cast showing thin shell of species as well as a small cone-shaped protoconch (X2). Arnheim "Formation" (Richmondian), at Clifton, Tennessee. USNM 263785.

7-12. *Archinacella simulatrix* Ulrich and Scofield, 1897.

7-8. Dorsal and left-lateral views of latex rubber mold of holotype, which is an external mold in the base of a bryozoan colony (X3). Decorah Formation (Rocklandian-Kirkfieldian), at St. Paul, Minnesota. USNM 45695.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 2 (Cont'd)

9. Dorsal view of silicified specimen embedded in matrix (X3). Grier Limestone Member of the Lexington Limestone, USGS 5094-CO. USNM 265941.

10. Right-lateral view of silicified specimen (X2.5). Grier Limestone Member of the Lexington Limestone, USGS 4073-CO. USNM 265945.

11. Right-lateral view of a silicified specimen (X2.5). Same sample as Figure 10 above. USNM 265944.

12. Dorsal view of silicified specimen embedded in matrix. (X2.5). The museum label gives the horizon and locality as: "Trenton (Hermitage), Frankfort, Kentucky," USNM 47471.

13-14. Archinacella cf. A. depressa Ulrich and Scofield, 1897. Dorsolateral and dorsal views of silicified specimen (X2.5). The museum label gives the horizon and locality as: "Mohawkian (Cannon), Hartsville, Tennessee." USNM 59295.

15-16. Archinacella valida (Sardeson, 1892). Dorsal and dorsolateral views of calcitic specimen (X2). Museum label gives horizon and locality as "Trenton

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 2 (Cont'd)

(Ctenodonta horizon), Mt. Parnassus, Columbia, Tennessee. USNM 47467.

17-18 Archinacella cf. A. pulaskiensis Foerste, 1914.
Dorsal and right-lateral views of fragmentary calcitic case. Specimen oriented opposite to specimens on rest of plate so that apex is more visible. The museum label gave only the horizon as "Maysville," but specimen most likely from Cincinnati, Ohio, area. UCGM 19640.

19-21. Archinalcella rugatina Ulrich in Ulrich and Scofield, 1897.
Dorsal, lateral, and dorsolateral views of the holotype (X2). Arnheim biofacies of the Bull Fork Formation (Richmondian), at Middleton, Ohio. USNM 45965.

22-26. Archinacella cingulata Ulrich in Ulrich and Scofield, 1897.
22-24. Dorsal, right- and left-lateral views of holotype, a weathered silicified specimen (X2). Curdsville Limestone Member of the Lexington Limestone, Mercer County, Kentucky. USNM 45666.

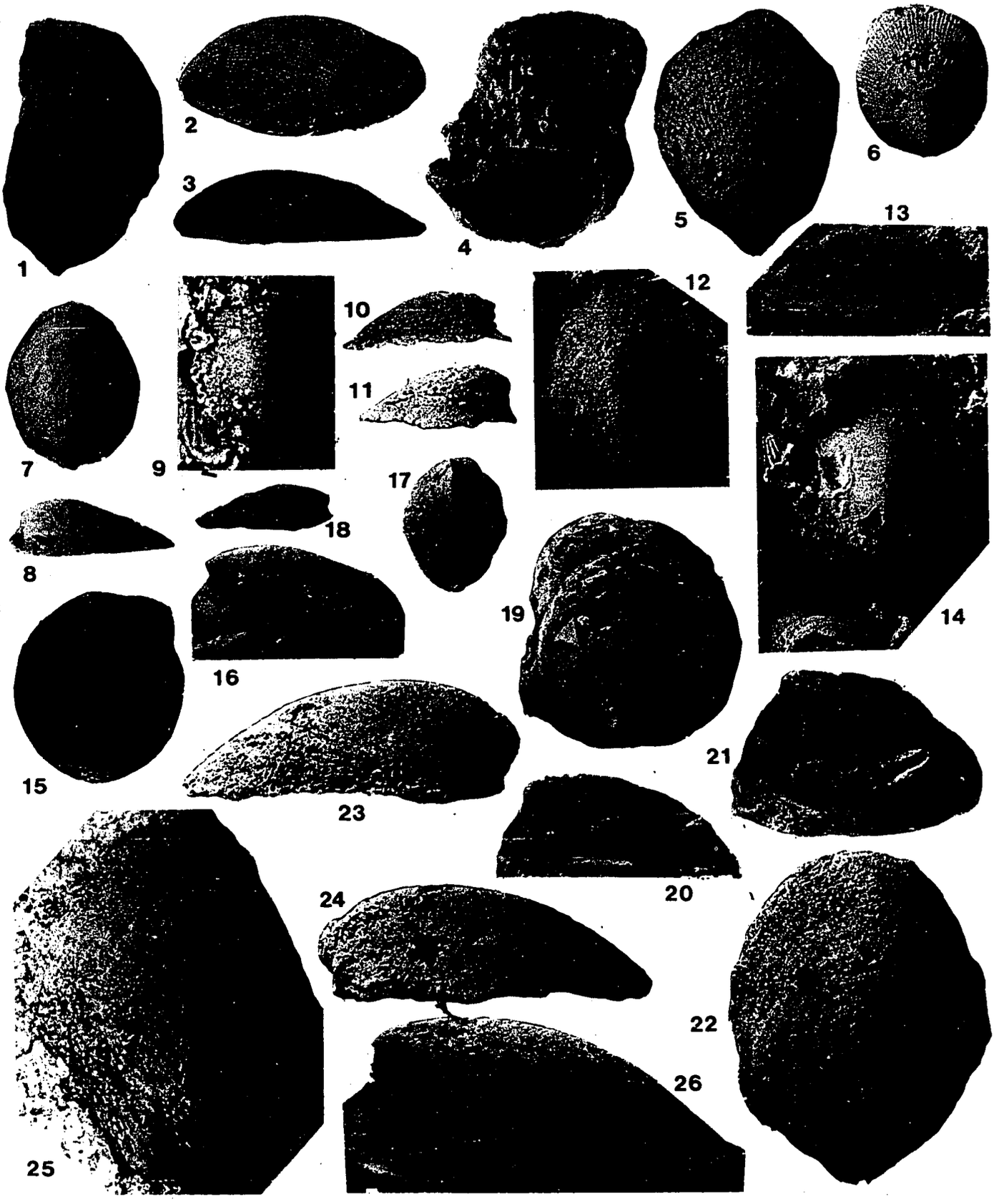
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 2 (Cont'd)

25-26. Dorsal and left-lateral views of internal mold (X1.5). Clays Ferry Formation, at Owenton, Kentucky. MU 249T.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 2



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 3

FIGURES 1-3. *Archinacella*? *davisi* n. sp.
Dorsal, right- and left-lateral views of holotype, an internal mold (X1.0). Kope? Formation (Edenian), near Glencoe, Kentucky. CMNH P2.

4-6. *Archinacella alta* n. sp.
Dorsal, lateral, and dorsolateral views of holotype (X2). Clays Ferry Formation (Edenian), northern Kentucky. MU 248T.

7-10 *Archinacella arca* n. sp.
Dorsal, posterior, right-lateral, and anterior views of holotype (X2). Waynesville biofacies of Bull Fork Formation (Richmondian), at Waynesville, Ohio. USNM 40615.

11-12. *Archinacella* sp. Right-lateral and dorsal views of coarsely silicified specimen (X2). Grier Limestone Member of the Lexington Limestone, USGS 4073-CO. USNM 265955.

13-24. *Archinacella indianensis* (Miller, 1892).
13-15. Dorsal, right- and left-lateral views of holotype, a badly weathered calcitic specimen (X1.5). The museum label gives the horizon and locality as: "Richmond, Fayette County, Indiana." UC 6065.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 3 (Cont'd)

16-18. A ventral view of an external mold in the base of a bryozoan colony, and dorsal and right-lateral views of a latex rubber cast of that mold. Holotype of Archinacella richmondensis Ulrich and Scofield (1897) (X2). Whitewater Formation (Richmondian), at Richmond, Indiana. USNM 45961.

19-20. Dorsal and dorsolateral views of silicified specimen (X2). USNM 265946. Dillsboro Formation (Liberty biofacies) (Richmondian), USGS 6139-CO, New Point Quadrangle, Indiana.

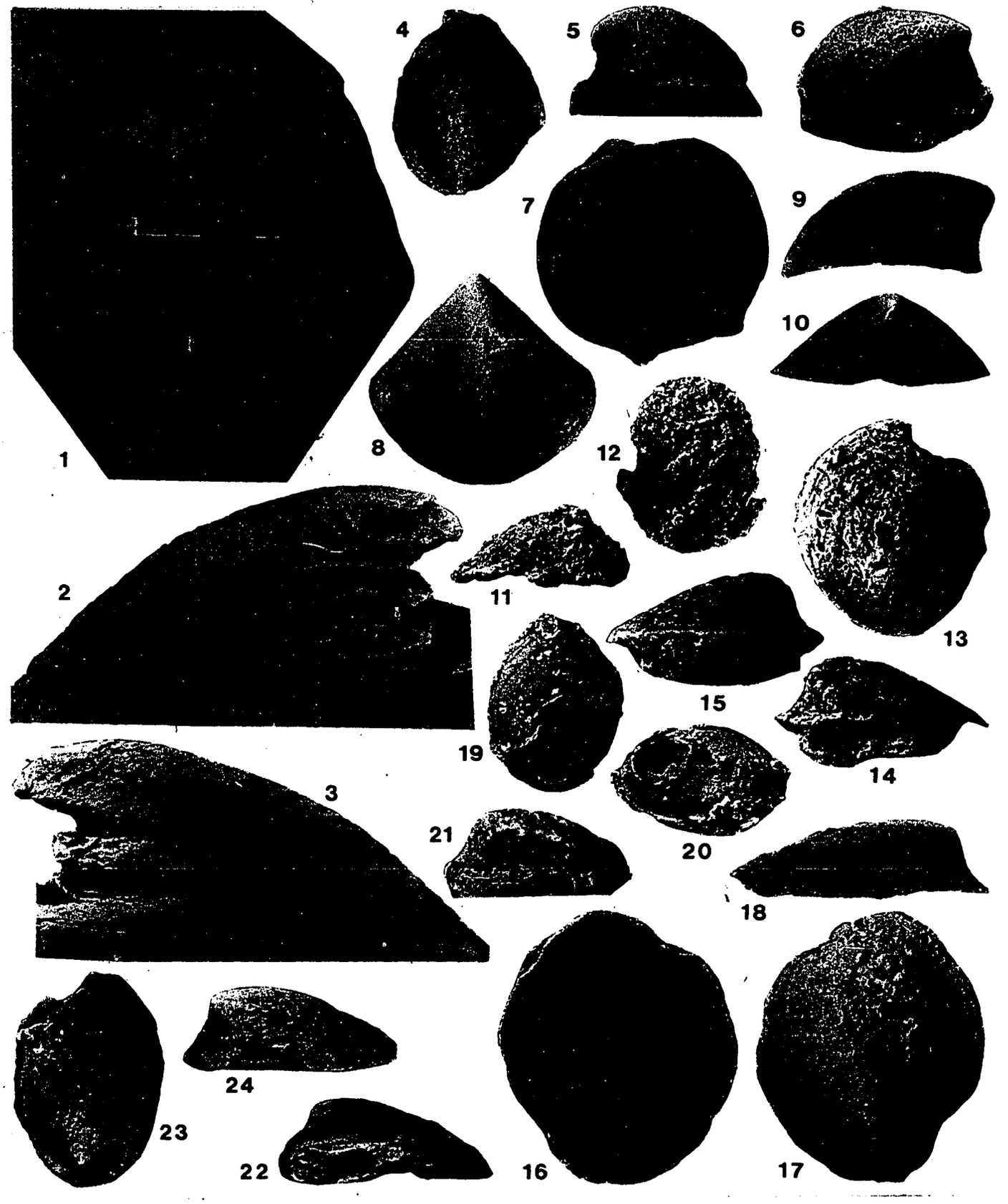
21. Left-lateral view of a calcitic cast (X2). Elkhorn biofacies, Drakes Formation, from creek just south of Morning Sun, Ohio. MR 246T.

22. Left-lateral view of a calcitic cast (X1.5). Note arched lateral aperture margin. Same horizon and locality as Figure 21 above. MU 250T.

23-24. Dorsal and left-lateral views of calcitic cast (X2). No data, but certainly from Richmondian strata of southwestern Ohio or southeastern Indiana. MU247T.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 3



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 4

FIGURES 1-14. Archinacella indianensis (Miller, 1892).

1-2. Dorsal and left-dorsolateral views of calcitic cast showing rather irregular growth lines (X2). White-water biofacies, Drakes Formation, at Oakland, Ohio. USNM 70467.

3-7. Dorsal, anterodorsal, laterodorsal, left- and right-lateral views of a silicified specimen (X2). Liberty biofacies, Dillsboro Formation, USGS 6139-CO. USNM 265951.

8-12. Ventrolateral and ventral views of external mold in base of bryozoan colony, and dorsal, dorsolateral, and right-lateral views of latex rubber cast made from that mold (X2). Waynesville biofacies, Bull Fork Formation (Richmondian), at Oregonia, Ohio. USNM 47468.

13-14. Left-lateral and dorsal views of anterior portion of fragmented silicified specimen (X2). Same sample as Figures 3-7 above. USNM 265949.

15-17. Cyrtolites (Cyrtolites) claysferryensis n. sp.

15-16. Both sides of small slab from mollusc bed containing gastropods, clams, and rarely cephalopods

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 4 (Cont'd)

and small unrecognizable bellerophontaceans, as well as typical non-mollusc Edenian fossils such as Cryptolithus (trilobite) and brachiopod fragments. Note circular hole in dorsal slope of paratype in Figure 15, which could be a boring (X2). Clays Ferry Formation (Edenian), from north end of bench of roadcut on northwest side of Sadieville, Kentucky Exit from Interstate I-75. USNM 265937.

17. Lower side of slab from a lenticular mollusc bed containing Sinuites, Sphenosphaera, Tetranota, Cyrtolites, small conispiral gastropods, and cephalopods, in that order of abundance. Lower Kope Formation (Edenian), about 10 feet above contact with Point Pleasant Tongue of Clays Ferry Formation, at Bear Creek Quarry, just north of Ohio River between Neville and Chilo, Ohio (X1.5). USNM 265938. Paratype.

18-25. Carinaropsis actua Ulrich and Scofield, 1897.

18-19. Dorsal and left-lateral views of silicified specimen (X2). Note subcircular outline and rather wide selenizone in Figure 18. Basal 2 feet of

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 4 (Cont'd)

Curdsville Limestone Member of Lexington Limestone, USGS 7784-CO. USNM 265992.

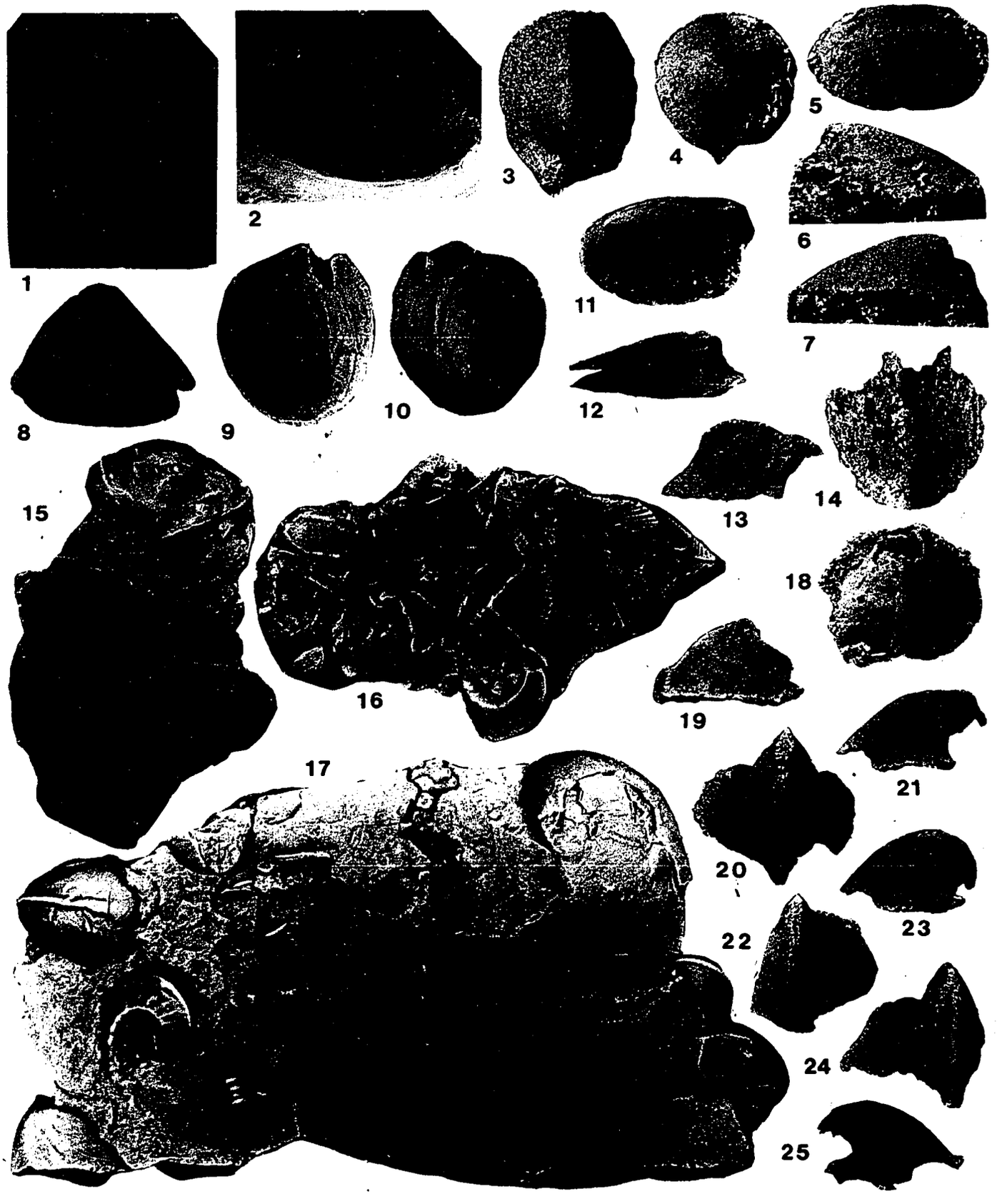
20-21. Dorsal and left-lateral views of silicified specimen (X2). Curdsville Limestone Member of Lexington Limestone, USGS 7784-CO. USNM 265993.

22-23. Dorsal and left-lateral views of silicified specimen (X3). Curdsville Limestone Member of Lexington Limestone, USGS 5100-CO. USNM 265994.

24-25. Dorsal and right-lateral views of a silicified specimen (X3). Curdsville Limestone Member of Lexington Limestone, USGS 5023-CO. USNM 265995.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 4



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 5

FIGURES 1-26. *Cyrtolites* (*Cyrtolites*) *retrorsus* Ulrich in Ulrich and Scofield, 1897.

1-2. Aperture and left lateral views of paralectotype (X2). Lower Lexington Limestone (Kirkfieldian), about 1 mile south of Burgin, Kentucky. USNM 265938.

3-4. Aperture and right-lateral views of paralectotype (X2). Lower Lexington Limestone (Kirkfieldian), about 1 mile south of Burgin, Kentucky. USNM 265899.

5-7. Aperture, right-lateral, and dorsal views of lectotype (X2). "Trenton" (Kirkfieldian-Shermanian) near Nashville, Tennessee. USNM 45789.

8-10. Aperture, left-lateral, and dorsal views of paralectotype (X2). "Trenton" (Kirkfieldian-Shermanian), near Nashville, Tennessee. USNM 265901.

11-12. Aperture and left-lateral views of paralectotype (X2). "Trenton" (Kirkfieldian-Shermanian), near Nashville, Tennessee. USNM 265902.

13. Dorsal view of paralectotype (X2). Lower Lexington Limestone (Kirkfieldian), about 1 mile south of Burgin, Kentucky. USNM 265900.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 5 (Cont'd)

14-17. Aperture, dorsal, left and right-lateral views (X2). Lower Logana Member of Lexington Limestone, USGS 6419-CO. USNM 265903.

18-21. Aperture, dorsal, left and right-lateral views (X2). Same sample as Figures 14-17 above. USNM 265904.

22-25. Aperture, dorsal, left and right-lateral views (X2). Same sample as Figures 14-17 above. USNM 265905.

26. Dorsal view illustrating shell sculpturing of specimen USNM 265903 of Figures 14-17 above (X5).

27-28. Archinacella indianensis (Miller, 1892)
Dorsal and right-lateral views (X3). Liberty biofacies of Dillsboro Formation, USGS 6139-CO. USNM 265950.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 5

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 6

FIGURES 1-18. Cyrtolites (Cyrtolites) ornatus Conrad, 1838.

1-3. Left-lateral (X2), aperture (X1.5), and dorsal (X1.5) views of an Ulrich and Scofield (1897) hypotype. Corryville biofacies of Bull Fork Formation (Maysvillian), at Cincinnati, Ohio. USNM 45786.

4-5. Dorsal and left-lateral views of internal mold (X2). The museum label gives the locality and horizon as: "Hudson River Group, northern New York." UCGM 44270.

6-8. Left-lateral, dorsal and aperture views of composite mold (X2). Same locality and horizon as Figures 1-3 above. USNM 265906.

9-11. Left-lateral, dorsal and aperture views of composite mold (X2). Same locality and horizon as Figures 1-3 above. USNM 265907.

12-14. Right-lateral (X2), dorsal (X2), and aperture (X1.5) views of bryozoan encrusted specimen. Museum label states horizon as "Maysville", giving no locality, but almost certainly from vicinity of Cincinnati, Ohio. UCGM 44273.

15-16. Dorsal and aperture views of bryozoan encrusted specimen (X1.5). Museum label states horizon as

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 6 (Cont'd)

"Richmond", giving no locality, but almost certainly from southwestern Ohio. UCGM 44272.

17. Dorsal view of vertically compressed specimen preserving calcitic shell (X1.5). Same sample as Figures 15-16 above. UCGM 44271.

18. Right-lateral view of disjunct internal mold (X2). Waynesville biofacies, Rowland Member, Drakes Formation (Richmondian), southwestern Ohio. UCGM 44274.

19-22. Cyrtolites (Cyrtolites) disjunctus Ulrich and Scofield, 1897.

Dorsal, aperture, left-lateral, and oblique left-lateral views of holotype, which is a calcitic specimen (X2). Museum label gives horizon and locality as: "Richmond Group, near Spring Valley, Minnesota." USNM 45785.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 6

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 7

FIGURES 1. *Cyrtolites* (*Cyrtolites*) *ornatus* Conrad, 1838.

Right-lateral view of disjunct internal mold (X2). Same sample as USNM 45786, 265906, 265907 - Corryville biofacies of Bull Fork Formation (Maysvillian), at Cincinnati, Ohio. USNM 265908.

2-10. *Cyrtolites* (*Cyrtolites*) *minor* Ulrich *in* Ulrich and Scofield, 1897.

2-4. Dorsal, aperture, and right-lateral views of holotype (X3). Museum label gives horizon and locality as: "Clitambonites bed, Trenton (Prosser), Cannon Falls, Minnesota." USNM 45787.

5-7. Dorsal, aperture, and right-lateral views of a bryozoan encrusted specimen from the McMicken biofacies of the Kope Formation (Edenian); no locality given, but certainly from Cincinnati, Ohio, area. UCGM 19668.

8-10. Dorsal, aperture, and right-lateral views of calcitic cast (X2). Contact of Fairview Formation and Miamitown shale (Maysvillian). Hamilton-Butler County line, Ohio. USNM 44275.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 7 (Cont'd)

11-16. Cyrtolites (Cyrtolites) retrorsus Ulrich in Ulrich and Scofield, 1897).

11-13. Dorsal, aperture, and right-lateral views of calcitic cast (X3). Kope Formation (Edenian), at Covington, Kentucky. USNM 265909.

14-16. Dorsal, aperture and left-lateral views of calcitic cast (X3). Same sample as Figures 11-13. USNM 265910.

17. Cyrtolites (Paracyrtolites) parvus Ulrich in Ulrich and Scofield, 1897.

Right-lateral view of holotype (X4). The museum label gives horizon and locality as: "Upper Trenton, Covington, Kentucky." USNM 45788.

18-25. Cyrtolites (Paracyrtolites) carinatus Miller, 1874.

18-19. Left-lateral and dorsal views of holotype (UC8895) (X3). Kope Formation (Edenian), the locality being given on the museum label as "within two hundred feet of low water-mark, at Bold Face Creek, opposite Fifth Street, and at the excavation for Columbia Avenue." (Note that Fifth Street is in Covington, Kentucky, and Columbia Avenue is now

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 7 (Cont'd)

named Columbia Parkway in Cincinnati, Ohio, the two cities being located across from one another on the Ohio River.

20. Aperture view of calcitic cast from Steven Felton collection (UCGM 44277) (X3). Kope Formation (Edenian), from mollusc bed in lower part of large exposure just southeast of the Carrollton, Kentucky, exit (U.S. Hwy 227) from Interstate Hwy. 71, Carroll County, Kentucky. (See also Plate 4, Figure 21).

21. Left-lateral view of composite mold which is an Ulrich and Scofield (1897) hypotype (X2). Southgate biofacies of Kope Formation at Newport, Kentucky. USNM 265912.

22. Left-lateral view of another Ulrich and Scofield (1897) hypotype (X2). Same sample as Figure 21 above. USNM 47499.

23. Dorsal view of another Ulrich and Scofield (1897) hypotype which retains the shell and its fine growth lines (X3). Same sample as Figure 21 above. USNM 265911.

24-25. Left-lateral and aperture views of another Ulrich and Scofield (1897) hypotype (X3) from same sample

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 7 (Cont'd)

as Figure 21 above, showing fine growth lines. USNM 265913.

26-35. Cyrtolites (Paracyrtolites) subplanus Ulrich in Ulrich and Scofield, 1897.

26-27, 35. Right-lateral (X1.5), dorsal (1.5), and dorsal close-up (about X4.5) of lectotype, a slightly weathered silicified cast. Note the strong deflection of the growth lines reflecting a relatively deep sinus, and the faint trace of revolving threads along some growth lines. Cannon facies of the Bigby-Cannon Limestone (Kirkfieldian-Shermanian) at Snow's Hill, 4 miles east of Liberty, Tennessee. USNM 45792.

28-29. Left-lateral and dorsal views of paralectotype (X2). Same samples as Figures 26-27 above. USNM 265914.

30-32, 34. Dorsal, aperture, left-lateral (all X2), and a dorsal close-up showing the detail of the shell sculpturing (about X5). Note the weak revolving threads which give the surface of faint pitted appearance. Logana Member of the Lexington Limestone (Kirkfieldian), USGS D-1196. USNM 265915.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

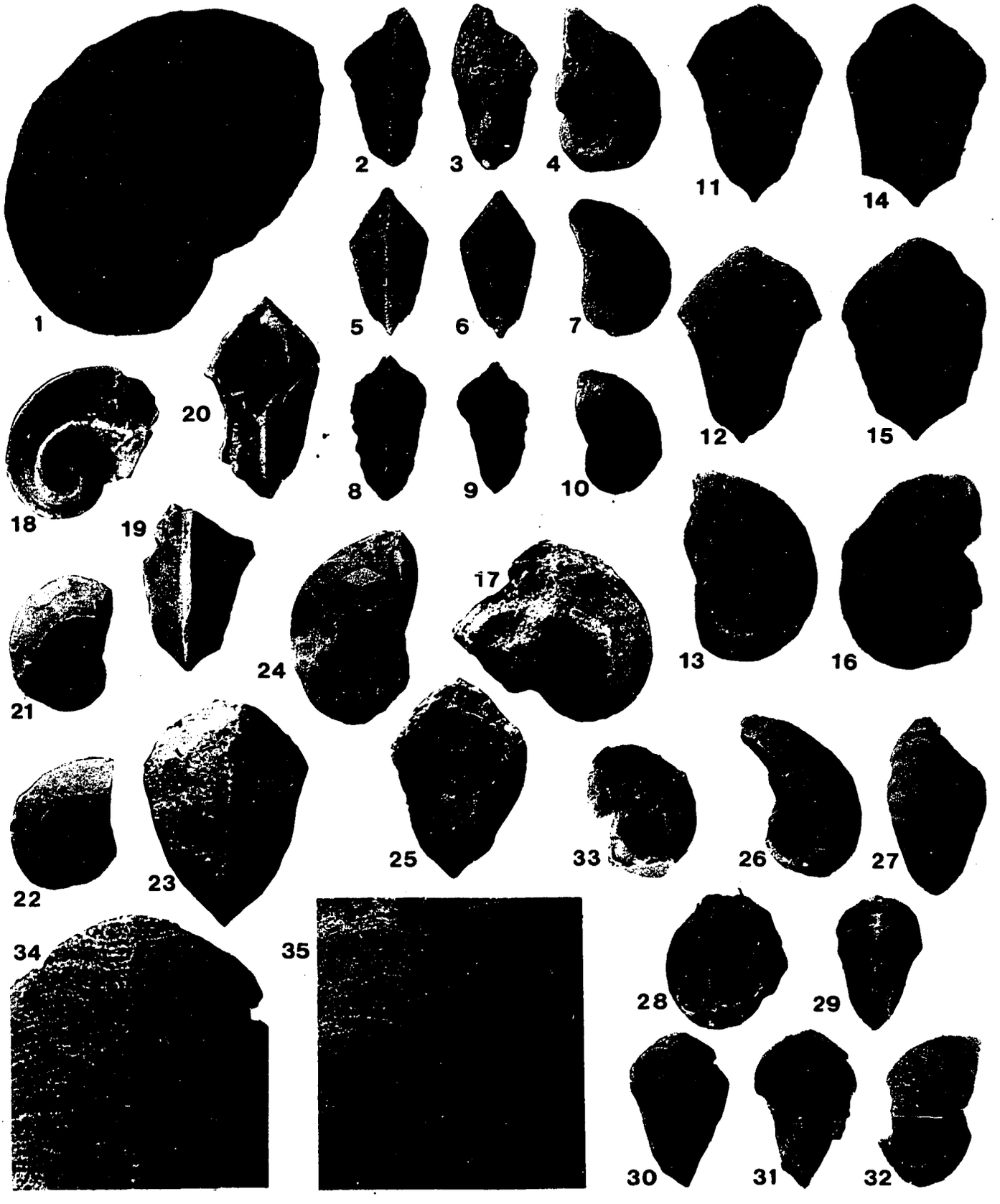
PLATE 7 (Cont'd)

33. Cyrtolites (Paracyrtolites) cf. subplanus Ulrich in Ulrich and Scofield, 1897.

33. Right-lateral view of silicified specimen (X2). Grier Limestone Member of the Lexington Limestone (Kirkfieldian), USGS 4852-CO. USNM 265918.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 7



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 8

FIGURES 1-10. Cyrtolites (Cyrtolites) hornyi n. sp.

1-4. Aperture, dorsal, left- and right-lateral views of holotype (X2). Liberty biofacies of Dillsboro Formation (Richmondian), USGS 6139-CO. USNM 265920.

5-7. Aperture, dorsal, and right-lateral views of paratype. Same sample as Figures 1-4 above. USNM 265921.

8-10. Aperture, dorsal, and left-lateral views of another paratype. Same sample as Figures 1-4 above. USNM 265922.

11-20. Cyrtolites (Cyrtolites) claysferryensis n. sp.

11-13. Aperture, dorsal, and left-lateral views of paratype (X2). Clays Ferry Formation (Edenian), USGS 6990-CO. USNM 265925.

14-18. Dorsal, aperture, left- and right-lateral views (all X2), and dorsal close-up of shell sculpturing of holotype (about X6). Upper Tongue of Clays Ferry Formation, 6143-CO. USNM 265924.

19-20. Left-lateral and dorsal views of paratype (X2). Same sample as Figures 14-18 above. USNM 265923.

21. Cyrtolites (Paracyrtolites) carinatus Miller, 1892.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 8 (Cont'd)

Small slab from mollusc bed from same locality and horizon as Plate 7, figure 20, Kope Formation (Edenian) near Carrollton, Kentucky. Contains Lophospira, Liospira, Sinuites, an ambonychiid, and cephalopod fragments. From Steven Felton collection. UCGM 44279.

22-27. Cyrtolites (Paracyrtolites) cf. C. (P.) subplanus Ulrich in Ulrich and Scofield, 1897.

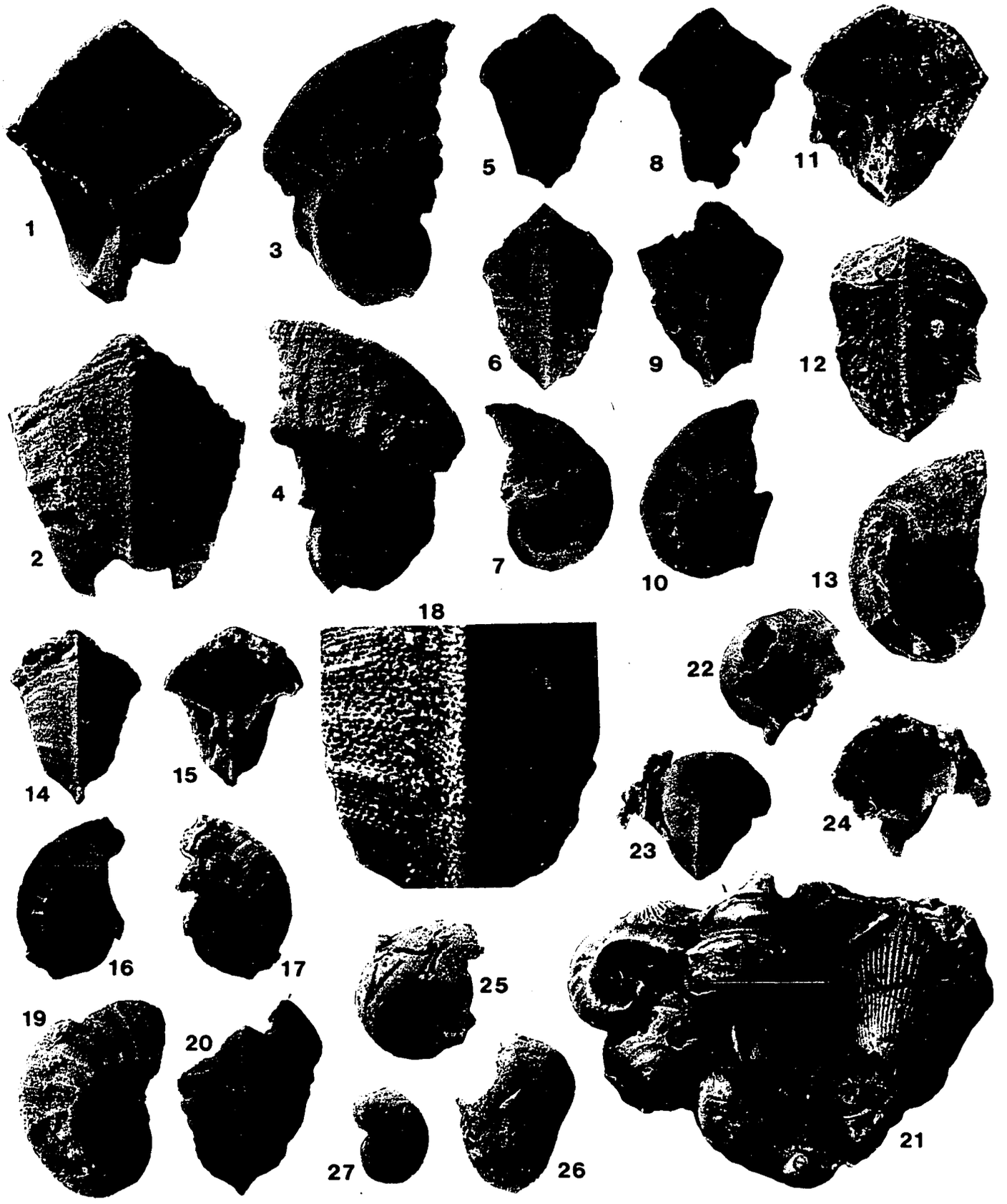
22-24. Left-lateral, dorsal, and aperture views of silicified specimen (X2). Grier Limestone Member of the Lexington Limestone, USGS 4852-CO. USNM 265916.

25-26. Left-lateral and dorsal views of worn silicified specimen which appears to have been bored. Same sample as Figures 22-24 above. (X2). USNM 265919.

27. Right-lateral view of small silicified specimen (X2). Logana Member of the Lexington Limestone. USGS D-1196. USNM 265917.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 8



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 9

FIGURES 1-12. *Sinuites obesus* (Ulrich)

1-4. Dorsal, ventral, anterior, and left-lateral views (X1.5) of silicified specimen. Curdsville Limestone Member, Lexington Limestone, USGS 5022-CO. USNM 315634.

5. Dorsal view (X1.5) of silicified specimen preserving trace of growth lines. Logana Member, Lexington Limestone, 5092-CO. USNM 315636.

6-9. Dorsal, ventral, right-lateral and anterior views (X1.5) of fragmented silicified specimen. Same sample as No. 5 above. USNM 315635.

10-12. Dorsal, ventral, and posterior views (X2.0) of silicifed specimen. Same sample as No. 5 above. USNM 315637.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 9

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 10

FIGURES 1-13. *Sinuites globularis* (Miller and Faber)

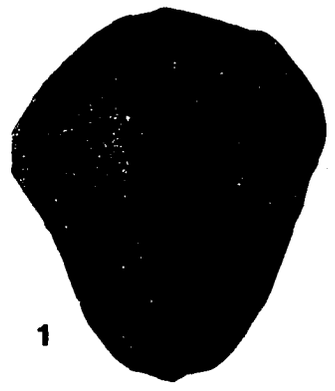
1-7. Dorsal, ventral, left-lateral, anterior, right anterolateral, and right dorsolateral views (X2.5) and a close-up dorsal view (X6.75) of the lectotype. Kope Formation, Cincinnati, Ohio. UC 8811a.

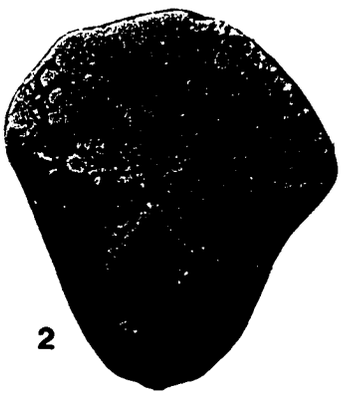
8-10. Dorsal, anterior, and left-lateral views (X3.0) of another calcitic specimen. Kope Formation, Carrollton, Kentucky. UCGM 44305.

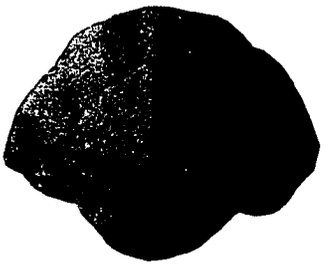
11-13. Dorsal, left dorsolateral, and left-lateral views (X2.5) of paralectotype. Same locality as Nos. 1-7 above. UC 8811b.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

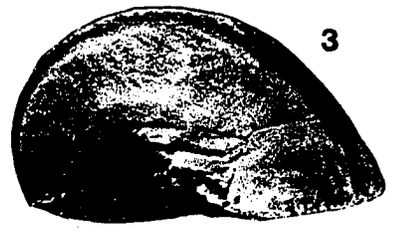
PLATE 10

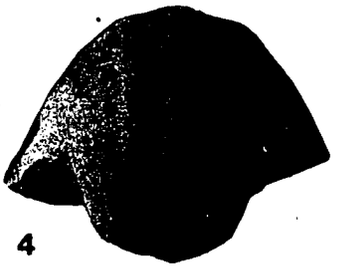

1

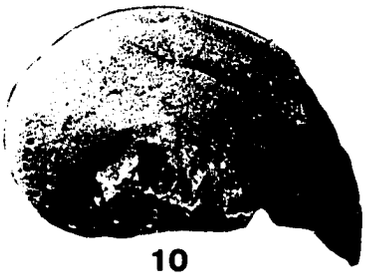

2


9

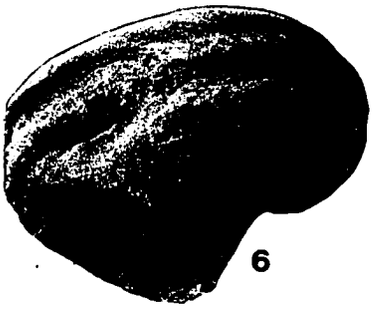
8

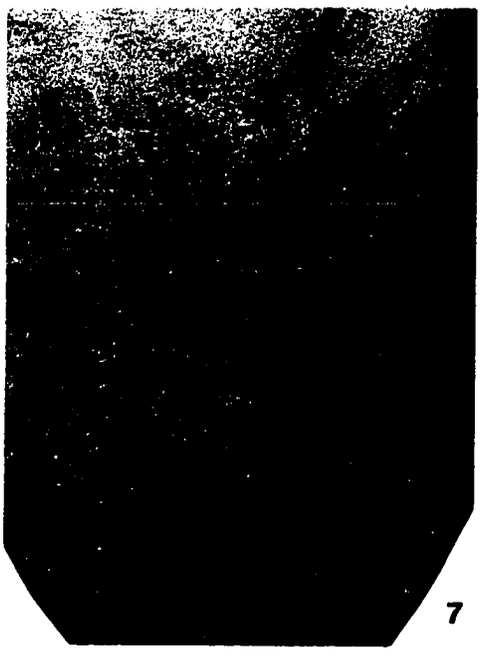

3

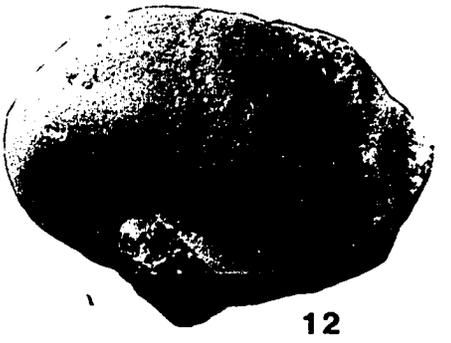

4


10

5


6


7


12

11

13

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 11

FIGURES 1-5. Sinuites granistriatus (Ulrich)

1-5. Dorsal, right dorsolateral, right lateral, and ventral views (X2.0) and close-up dorsal view (X4.5) of calcitic specimen preserving the growth lines. Kope Formation, Locality OH-1, Clermont Co., Ohio. UCGM 44295.

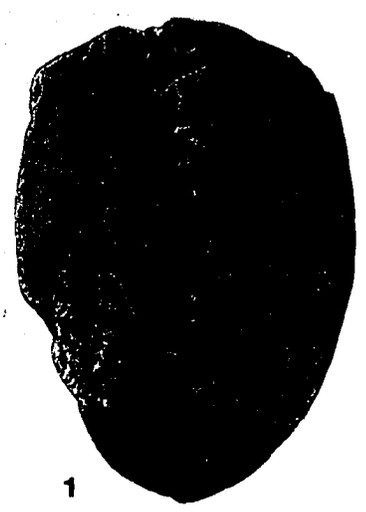
6-12. Sinuites cancellatus (Hall)

6-9. Dorsal, anterior, right-lateral, and left anterolateral views (X2.0) of calcitic specimen with shell weathered away dorsally. Museum lable specifies only "Cincinnatian", Cincinnati, Ohio. UCGM 44304.

10-12. Dorsal, posterior, and left-lateral views of calcitic specimen. Kope Formation, Cincinnati, Ohio. UCGM 44307.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 11



1

2

5

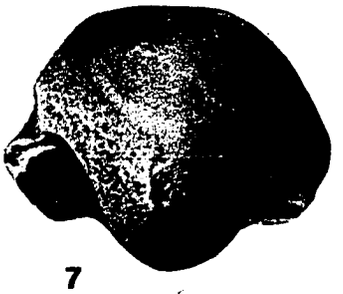
4

3

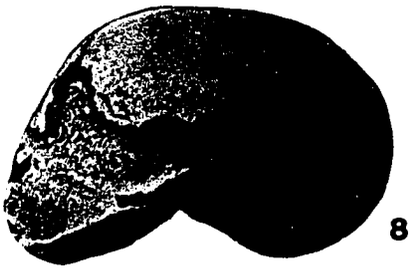
10

11

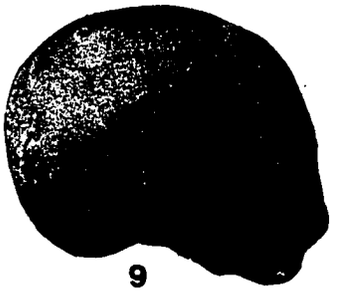
6



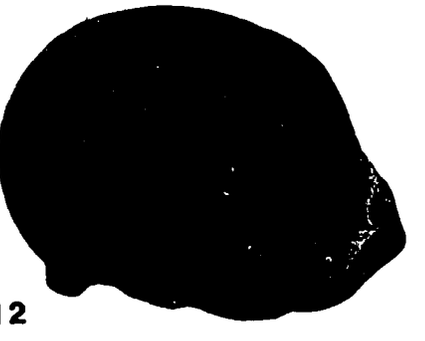
7



8



9



12

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 12

FIGURES 1-4. *Bucania emmonsi* Ulrich and Scofield

1-4. Dorsal, posterior, left posterolateral, and left-lateral views (X3.0) of silicified holotype. Stones River Group, Murfreesboro Formation, Murfreesboro, Tennessee. USNM 46049.

5-16. *Bucania halli* Ulrich and Scofield

5-9. Dorsal (X3.0), right-lateral anterodorsal, right-lateral, ventral, and posterior views (X2.0) of lectotype. Museum label says only: "Black River Group," Cannon Falls, Minnesota. USNM 45717.

10-14. Dorsal, ventral, left-lateral, and right-lateral views (X1.5) and right-lateral close-up view (X6.0) showing shell markings of paralectotype. Apparently a fully mature specimen. Curdsville Limestone Member, Lexington Limestone, Mercer County, Kentucky, USNM 315582.

15-16. Posterior and right-lateral views (X3.0) of fragmented silicified specimen. Grier Limestone Member, Lexington Limestone, 4073-CO. USNM 315544.

17-18. *Bucania* cf. *B. halli* Ulrich and Scofield

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 12 (Cont'd)

17-18. Right-lateral and dorsal views (X2.0) of silicified specimen. Lower Curdsville Limestone Member of Lexington Limestone, USGS 5100-CO. USNM 315545.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 12

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 13

FIGURES 1-8. Bucania sublata Ulrich and Scofield

1-4. Dorsal (X5.0), posterior, left dorsolateral, and left-lateral views (X3.0) of silicified lectotype. Lexington Limestone, near Burgin, Kentucky. USNM 315561.

5-8. Right posterolateral, right-lateral, dorsal, and posterior views (X2.0) of silicified fragment showing large umbilicus, reflexed parietal lip, and broad median parietal ridge. Same collection as Nos. 1-4 above. Paralectotype, USNM 315562.

9-14. Bucania cf. B. sublata Ulrich and Scofield

9-10. Right-lateral and dorsal viws (X3.0) of silicified fragment from Grier Limestone Member, Lexington Limestone, USNM 4879-CO. USNM 315563.

11. Left-lateral view (X2.0) of silicified fragment from the Faulconer bed, Perryville Limestone Member, Lexington Limestone, USGS 6136-CO. USNM 315564.

12-14. Right-lateral, posterior, and dorsal views (X1.5) of large silicified fragment from Devil's Hollow Member, Lexington Limestone, USGS 5095-CO. USNM 315565.

15-21. Bucania nashvillensis Ulrich

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 13 (Cont'd)

15-16. Two views of 2 silicified specimens cemented together with other skeletal debris, showing the characteristic small umbilicus and narrowly rounded dorsum. Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315566.

17-18. Posterior (X3.0) and right-lateral (X2.0) views of partial specimen. Same sample as Nos. 15-16 above. USNM 315567.

19. Right posterolateral view (X2.0) of silicified fragment showing small umbilicus, angular dorsum, and thickened parital lip. Same sample as Nos. 15-16 above. USNM 315568.

20-21. Left-lateral, right-lateral, and dorsal views (X2.0) of silicified specimen from Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 6915-CO. USNM 315569.

22-24. Bucania frankfortensis Ulrich

22. Right-lateral view (X2.0) of silicified fragment showing characteristic wrinkled lateral aperture slope. Devil's Hollow Member, Lexington Limestone, USGS 5036-CO. USNM 315571.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 13 (Cont'd)

23-24. Ventral and right-lateral views (2.0) of silicified fragment showing subtriangular aperture outline and wrinkled lateral aperture slope. Same sample as No. 22 above. USNM 315570.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 13

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 14

FIGURES 1-14. *Bucania nashvillensis* Ulrich

1-5. Anterior, posterior, left-lateral, dorsal, and ventral views (X1.5) of silicified paralectotype. Cannon facies of Bigby-Cannon Limestone, at Nashville, Tennessee. USNM 45724.

6-9. Posterodorsal, left-lateral, ventral, and anterior views (X1.5) of bryozoan-encrusted, silicified paralectotype, showing deep slit and mature lamellose growth lines. Cannon facies of Bigby-Cannon Limestone, Dekalb Co., Tennessee. USNM 315558.

10-14. Oblique anterolateral, dorsal, right-lateral, and anterodorsal views (X2.0) and close-up of slit and shell ornament (X5.0). Same collection as Nos. 6-9 above. USNM 315557.

15-19. *Bucania subangulata* Ulrich

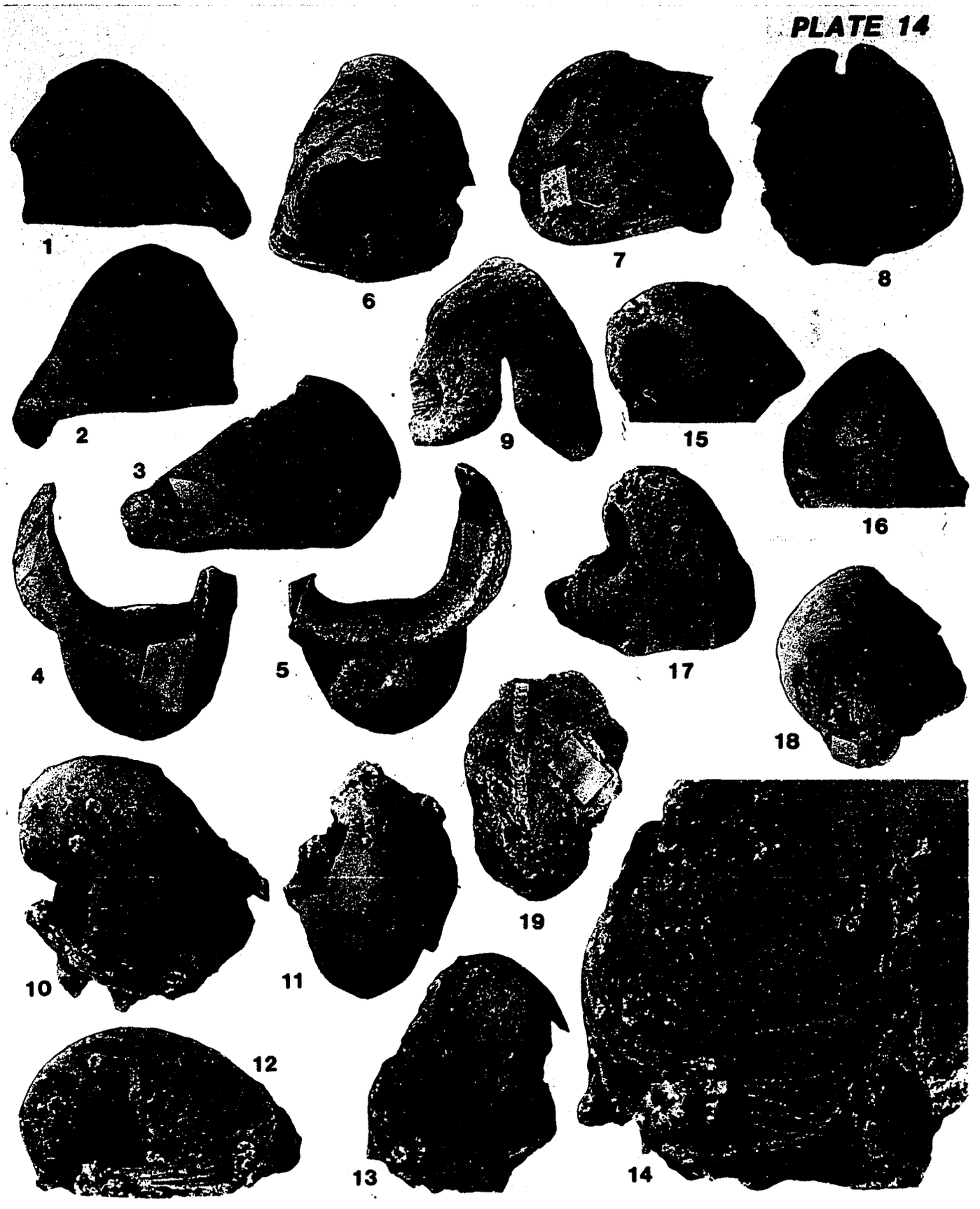
15-18. Right-lateral, posterior, anterolateral, and posterodorsal views (X1.5) of silicified lectotype, in which the anterodorsal shell area has been reconstructed with plaster (lighter-colored area). Lexington Limestone, 1.5 miles south of Burgin, Kentucky. USNM 315559.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 14 (Cont'd)

19. Dorsal view (X2.0) of silicified paralectotype, showing lunulae of selenizone and shell markings. Same collection as Nos. 15-18 above. USNM 315560.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 15

FIGURES 1-7. *Bucania nashvillensis* Ulrich

1-2. Right-lateral and anterior views (X2.0) of fragmented silicified specimen from Grier Limestone Member of Lexington Limestone, USGS 4959-CO. USNM 315572.

3-5. Dorsal, ventral, and left-lateral views (X3.0) of fragmented specimen from same sample as Nos. 1-2 above. USNM 315573.

6-7. Left-lateral and dorsal views (X2.5) of silicified specimen from Grier Limestone Member of Lexington Limestone. USGS 4073-CO. USNM 315574.

8-24. *Bucania subangulata* Ulrich

8-12. Posterior, dorsal, left-posterior, ventral, and left-lateral views (X3.0) of a silicified internal mold. Curdsville Limestone Member, Lexington Limestone, USGS 7785-CO. USNM 315575. (For a similar specimen from the Grier Limestone Member, USGS 5094-CO, see Pl. 38, figs. 11-12).

13-15. Dorsal, right-posterior, and right-lateral views (X2.5) of a relatively large fragment of a silicified specimen. Grier Limestone Member, Lexington Limestone, 5094-CO. USNM 315576.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

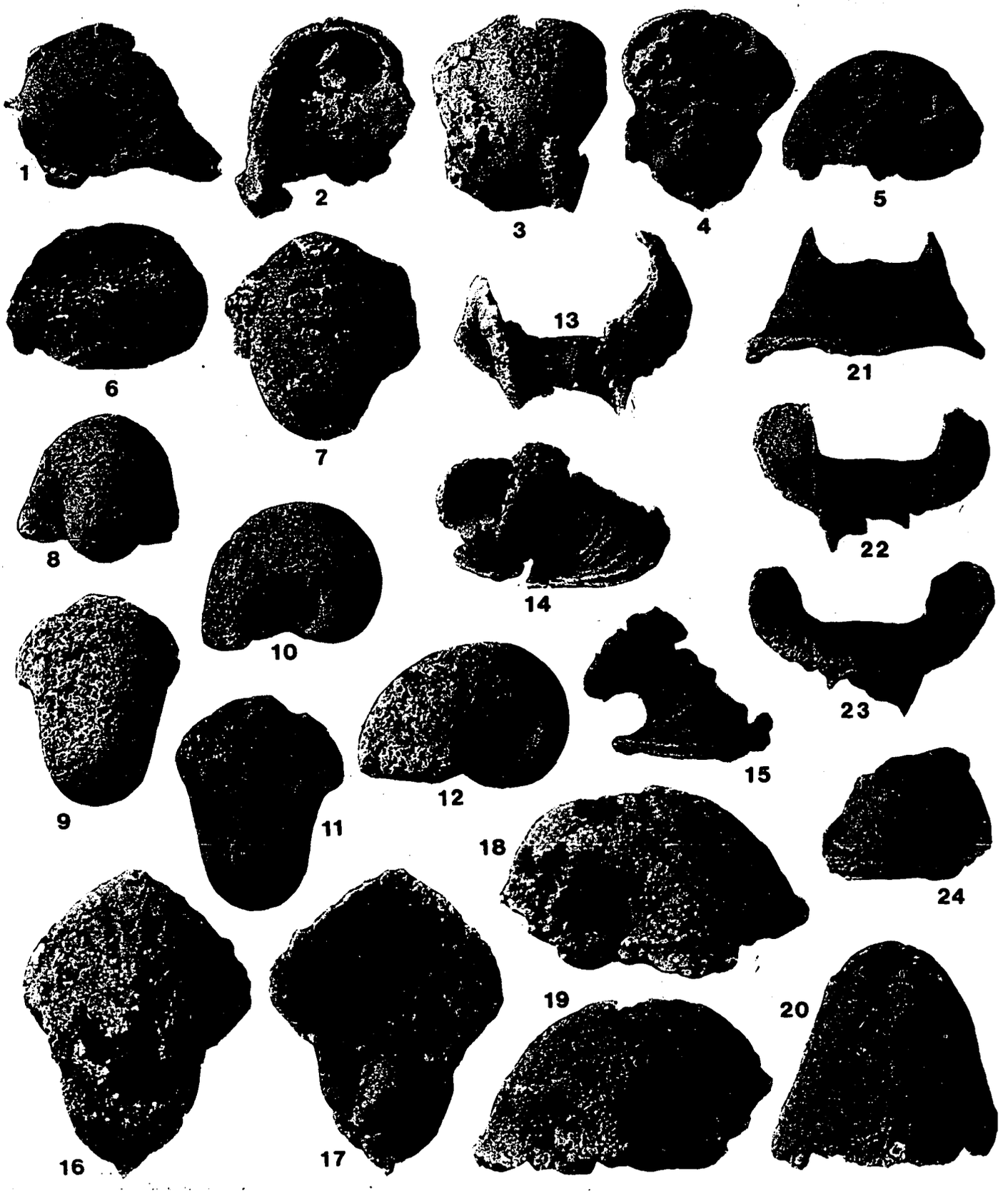
PLATE 15 (Cont'd)

16-20. Dorsal, ventral, right-lateral, left-lateral, and anterior views (X4.0) of a small silicified specimen preserving the selenizone. Same sample as Nos. 13-15 above. USNM 315577.

21-24. Posterior, dorsal, ventral, and left-lateral views (X2.0) of fragment of silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 315578.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 15



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 16

FIGURES 1-4. Bucania frankfortensis Ulrich

1-4. Dorsal, ventral, left dorsolateral, and left-lateral views (X1.5) of the silicified holotype, in which much of the dorsum and essentially all of the anteromedian shell have been reconstructed with plaster (the smoother, less granular surfaces). Clays Ferry Formation, at Frankfort, Kentucky. USNM 45716.

5-8. Bucania peracuta Ulrich

5-8. Posterior, left-lateral, dorsal, and aperture views (X1.5) of silicified holotype, in which the anterior portion of the shell has been broken away. Cannon facies of Bigby-Cannon Limestone, Dekalb Co., Tennessee. USNM 45726.

9-15. Bucania rugatina Ulrich

9-12. Left posterolateral view (X3.0) with a close-up view (X6.0) of the shell markings, and left-lateral and dorsal views (X3.0) of a lectotype. Lexington Limestone, 1.5 miles south of Burgin, Kentucky. USNM 315555.

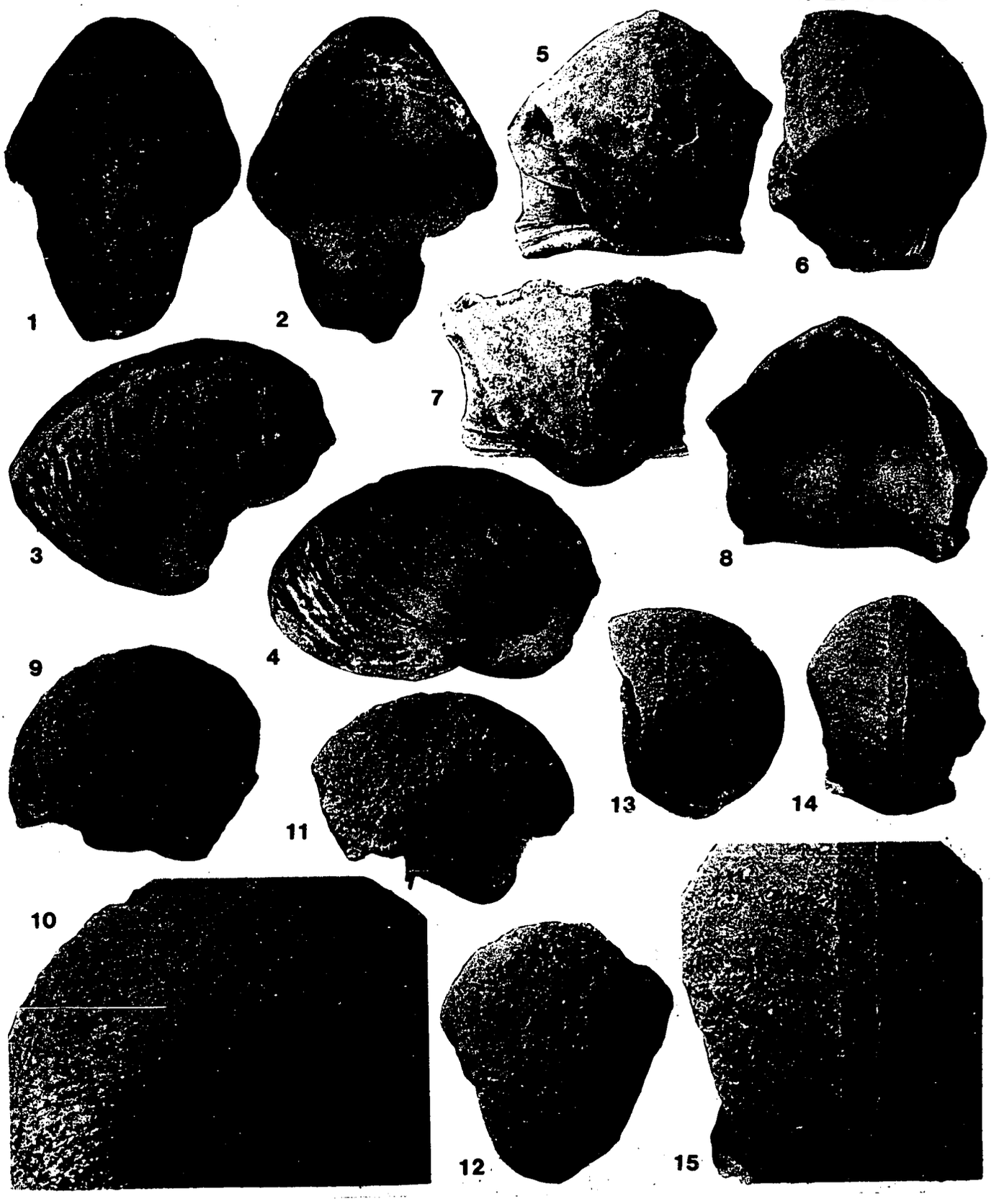
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 16 (Cont'd)

13-15. Left-lateral and dorsal views (X3.0) and a close-up of the selenizone and growth lines (approximately X6.0) of silicified paralectotype. Same collection as Nos. 9-12 above. USNM 315556.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 16



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 17

FIGURES 1-12. *Bucania rugatina* Ulrich

1-6. Left posterolateral views (X2.0 and X6.0), and dorsal, ventral, left-lateral, and posterior views (X2.0) of silicified specimen preserving the shell markings. Upper tongue of Clays Ferry Formation, USGS 6143-CO. USNM 315579.

7-11. Dorsal, ventral, right-lateral, left-lateral, and left anterodorsal views of a silicified specimen encrusted by a bryozoan colony. The chimney-like growth of the bryozoan colony in two directions apparently resulted from partial burial of the shell, exhumation, and reburial at a different orientation. Tongue of Clays Ferry Formation between tongues of the underlying Millersburg Member and overlying Tanglewood Member of the Lexington Limestone, USGS 7348-CO. USNM 315580.

12. Left-lateral view (X3.0) of worn fragment showing characteristic shell markings of the species. Same sample as Nos. 7-11 above. USNM 315581.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 17

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 18

FIGURES 1-9. Bucania lindsleyi (Safford)

1-6. Dorsal, ventral, left-lateral, and left dorsolateral views (X1.5) and close-up views (X5.0) of the selenizone and of the shell markings on the left-anterior aperture of the silicified lectotype. Cannon facies of Bigby-Cannon Limestone, Dekalb County, Tennessee. USNM 315550.

7-9. Dorsal view (X3.5), and left-lateral and ventral views (X2.0) of silicified paralectotype. Note that this specimen is smaller than Nos. 1-6 above, and has not yet developed the lamellose growth lines. Same collection as Nos. 1-6 above. USNM 315551.

10-12. Bellerophon subpatula (Ulrich)

10-12. Dorsal, ventral, and right-lateral views (X4.0) of silicified lectotype. Lexington Limestone, 1.5 miles south of Burgin, Kentucky. USNM 315552.

13-17. Bellerophon nana (Ulrich)

13-14. Dorsal and ventral views (X4.0) of silicified lectotype. Upper Lexington Limestone, 1.5 miles south of Burgin, Kentucky. USNM 315553.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

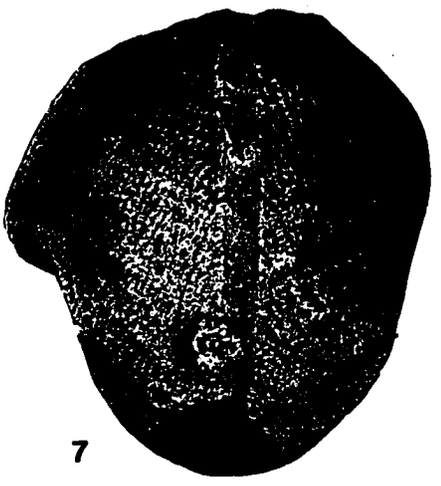
PLATE 18 (Cont'd)

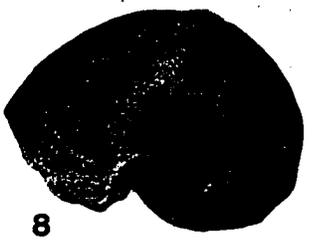
15-17. Left-lateral, dorsal, and ventral views (X4.0) of silicified paralectotype. Same collection as Nos. 13-14 above. USNM 315554.

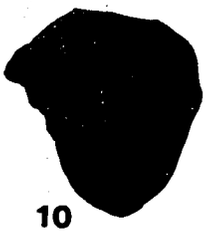
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 18

1


7

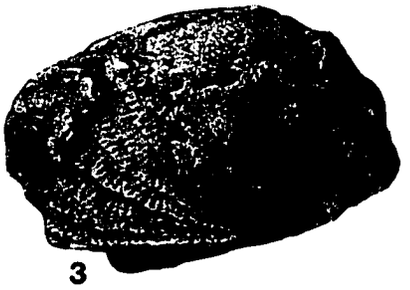

8


10

9

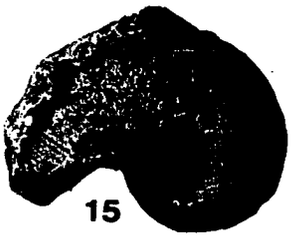
11

2

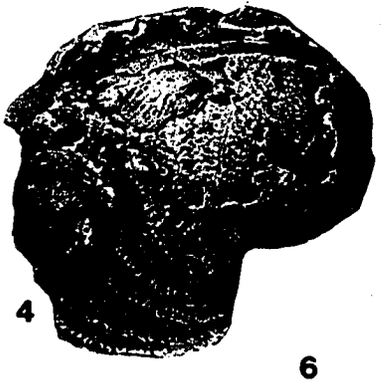

3

12

13


15

5


4

14

16

6

17

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 19

FIGURES 1-6. Bucania micronema Ulrich

1-6. Dorsal, ventral, left-lateral, posterior, and left anterodorsal views (X3.0), and close-up of the last (X6.0) to show shell markings of the silicified holotype. Note that in Figure 2 there is an extraneous shell fragment blocking the aperture opening. Upper Lexington Limestone, at Danville, Kentucky. USNM 45720.

7-10. Bucania crassa Ulrich

7-10. Dorsal, ventral, right anterolateral, and right lateral views (X1.5) of the calcitic lectotype. The museum label states: "Richmond (Elkhorn Formation), near Richmond, Indiana." USNM 315547.

11-14. Bucania simulatrix Ulrich

11-14. Anterodorsal, dorsal, right-lateral, and right anterolateral views (X1.5) of calcitic lectotype. Whitewater Formation, at Richmond, Indiana. USNM 315548.

15-18. Bucania singularis Ulrich

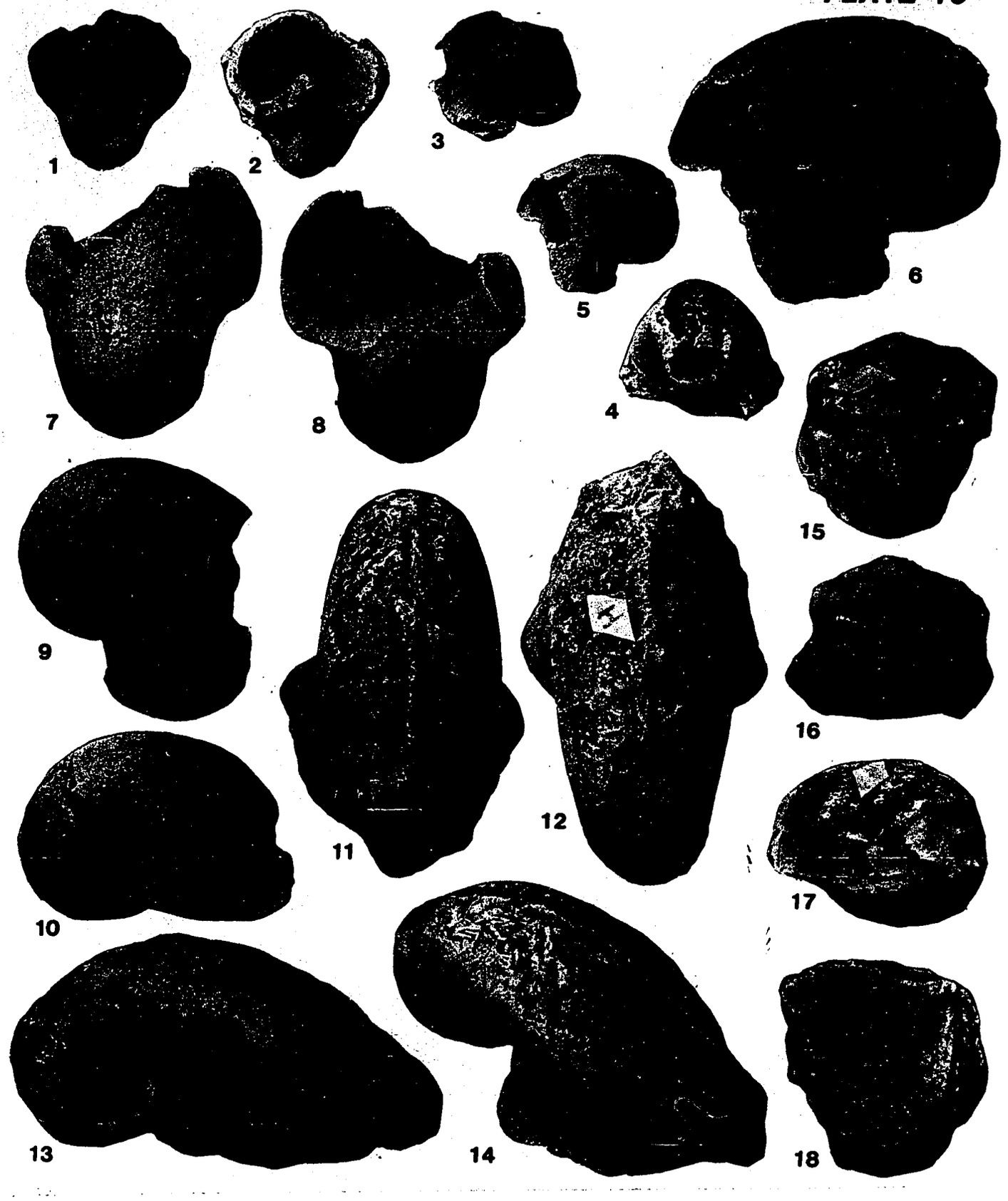
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 19 (Cont'd)

15-18. Dorsal, posterior, left-lateral, and ventral views (X1.5) of lectotype. Catheys Formation, at Nashville, Tennessee. USNM 315549.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 19



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 20

FIGURES 1-8. *Bucania pojetai* new species

1-2. Dorsal and right-lateral views (X1.5) of calcitic specimen preserving some remnant of the shell, and showing the internal mold of the dorsum as lacking a ridge-like slit filling such as would be expected in species of *Salpingostoma*, which has a similar shell form. Leipers Formation, at Rowena Ferry, Russell Co., Kentucky. Paratype, UCGM 44286.

3-4. Dorsal and left-lateral views (X1.5) of calcitic specimen with apparently highly recrystallized shell, showing the selenizone as a low rounded ridge. Same collection as Nos. 1-2 above. Holotype, UCGM 44285.

5-8. Posterior, dorsal, and left-lateral views (X1.5) of calcitic paratype, showing wrinkle-like growth lines. Same collection as Nos. 1-2 above. UCGM 44287.

9-12. *Kokenospira costalis* (Ulrich and Scofield)

9-12. Left-lateral, left posterolateral, and dorsal views (X2.5), and dorsolateral close-up (X6.0) of calcitic specimen. Southgate biofacies of Kope Formation, Cincinnati, Ohio. UCGM 26519.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 20 (Cont'd)

13-15. *Tetranota* cf. *T. obseleta* Ulrich and Scofield

13-15. Right posterodorsal, and ventral views (X4.0) of small silicified specimen. Upper Curdsville Member, Lexington Limestone, USGS 6131-CO. USNM 315541.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 20

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 21

FIGURES 1-14. *Tetranota bidorsata* (Hall)

1-4. *Tetranota bidorsata* with *Sinuites granistriatus* (Ulrich) in small slab of limestone (X1.5), and two close-ups (X3.0 and X6.0) emphasizing the lateral ridges and selenizone of the upper specimen, and a close-up (X3.0) of the lower specimen showing the growth lines. From lens-like mollusc bed in Economy biofacies of lower Kope Formation, Locality OH-1, Clermont Co., Ohio. UCGM 44291.

5-7. Posterior, anterior, and dorsolateral views (X2.0) of calcitic specimen from same bed as Nos. 1-4 above. UCGM 44292.

8. Dorsal view (X2.0) of specimen in association with fragments of a crinoid column and the trilobite *Cryptolithus* sp., a typical assemblage of the Kope Formation. Note the gastropod is somewhat crushed. Same bed as Nos. 1-4 above. UCGM 44293.

9-11. Anterodorsal, right-lateral, and right anterodorsal views (X2.0) calcitic specimen preserving the lateral aperture expansion of maturity. Economy biofacies of Kope Formation, from Bloody Run, Cincinnati, Ohio. USNM 47545.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 21 (Cont'd)

12-13. Left-lateral and ventral views (X2.0) of lectotype. Trenton Group, Watertown, New York. AMNH Fl 29592 (James Hall Collection).

14. Dorsal view (X2.0) of paralectotype. Trenton Group, Middleville, New York. AMNH Fl 787 (James Hall Collection).

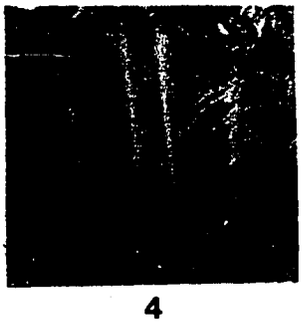
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 21

1

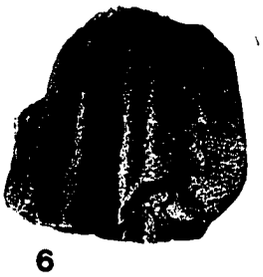
2

3



4

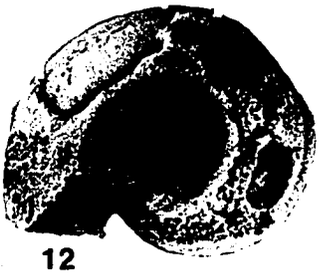
5



6

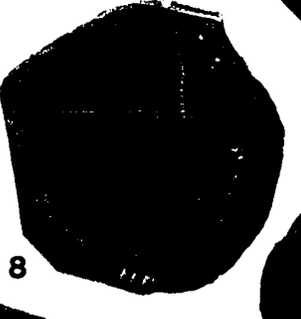
7

14

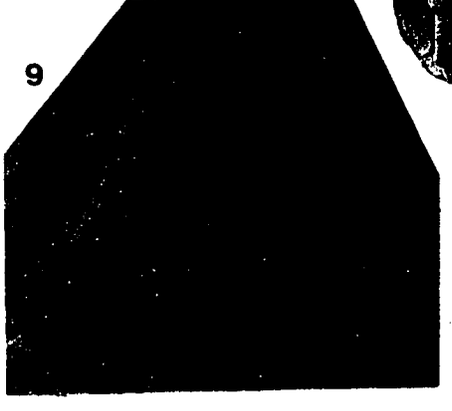


12

13

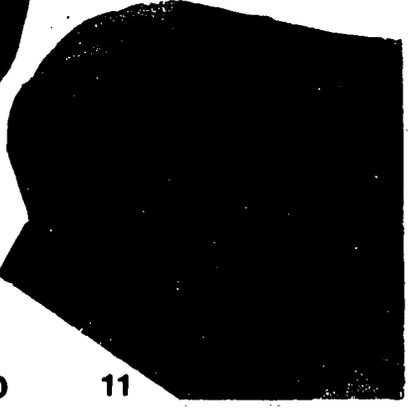


8



9

10



11

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 22

FIGURES 1-10. Tetranota bidorsata (Hall)

1. Dorsal view of large internal mold (X2.0). Trenton Group, Watertown, Jefferson Co., New York. AMNH Fl 29593, paralectotype.

2-4. Dorsal, ventral, and right-lateral views (X2.0) of internal mold. Trenton Group, Watertown, New York. Paralectotype, AMNH Fl 29594.

5-10. Dorsal, posterior, ventral, left anterodorsal, left-lateral, and right-lateral views (X2.0) of internal mold with some shell preserved dorsally. Pogonip Group, White Pine District, Nevada. USNM 17301.

11-15. Tetranota sexcarinata Ulrich and Scofield

11-13. Dorsal, left and right dorsolateral views (X2.0) of internal mold. Lebanon Formation, at Lavergne, Tennessee. USNM 47712.

14-15. Right dorsolateral (X2.0) and dorsal close-up (X6.0) of selenizone, growth lines, and first lateral ridges. Fusispira bed, Prosser Formation, at Wykoff, Minnesota. Lectotype, USNM 46018.

16-21. Tetranota obseleta Ulrich and Scofield

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 22 (Cont'd)

16-18. Dorsal, ventral, and left-lateral views (X2.0) of small silicified specimen. Holotype of Butts (1926). Little Oak Formation, from north of Pelham, Alabama. USNM 71496.

19-21. Dorsal, ventral, and left-lateral views (X2.0) of silicified lectotype. Ctenodonta bed, Decorah Formation, at Chatfield, Minnesota. USNM 46014.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 22

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 23

FIGURES 1-9. Undulabucania punctifrons (Emmons)

1-4. Dorsal, right-lateral, and right anterodorsal views (X3.0), and a close-up (X6.0) of the last to show the shell sculpturing. Base of Hermitage Formation, at Nashville, Tennessee. USNM 45727.

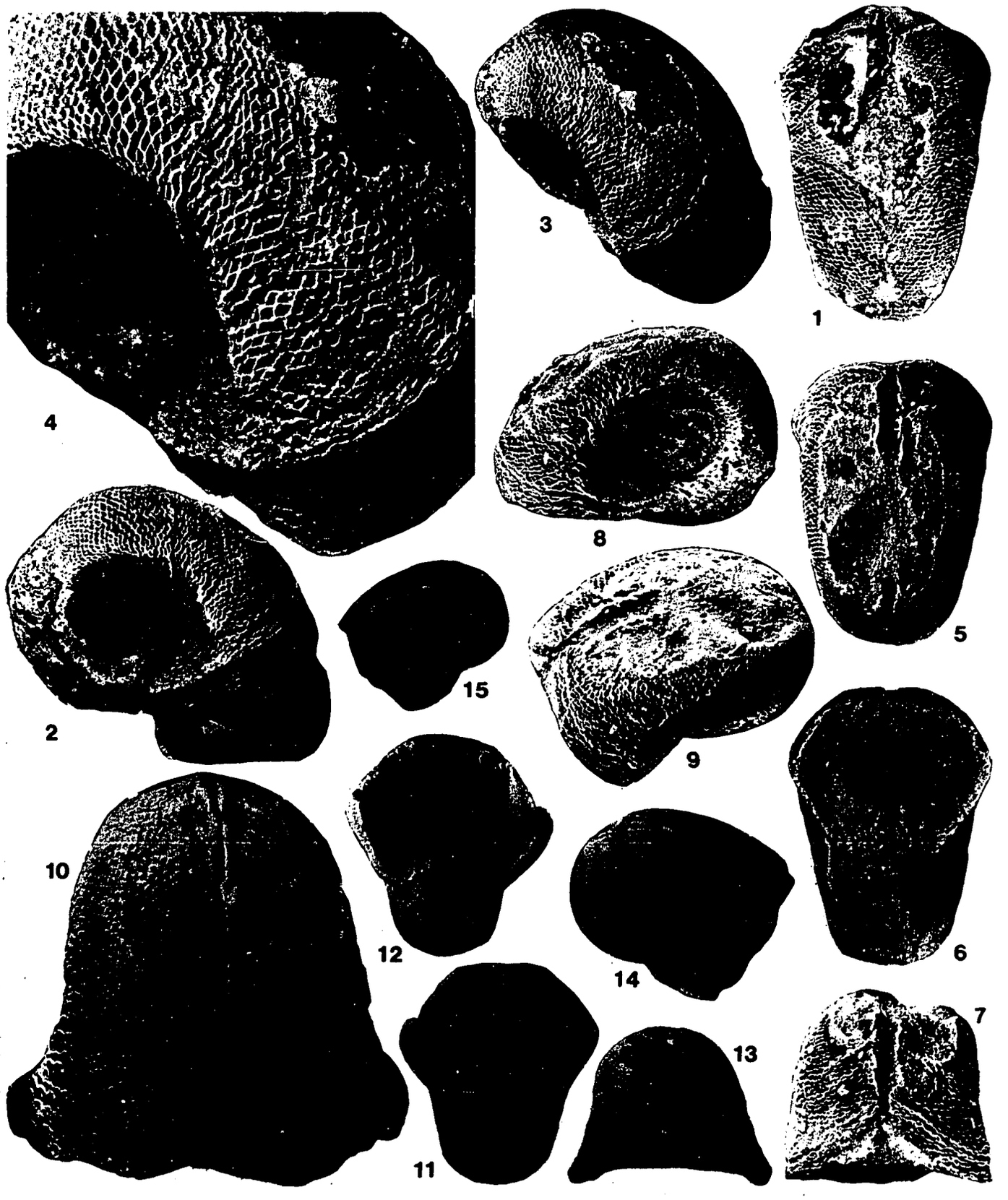
5-9. Dorsal, ventral, anterior, left-lateral, and left anterodorsal views (X3.0) of another calcitic specimen from the same collection as Nos. 1-4 above. USNM 315546.

10-15. Undulabucania gorbyi (Miller)

10-15. Anterodorsal view (X4.0), dorsal, ventral, anterior, right anterodorsal views (X2.0), and left anterodorsal view (X1.5) of calcitic holotype. Maysvillian-aged strata of Dearborn Co., Indiana. UC 6138.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 23



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 24

FIGURES 1-9. Salpingostoma buelli (Whitfield, 1878)

1-5. Left and right anterolateral, dorsal, and left and right lateral views of an Ulrich and Scofield (1897) hypotype, which is a composite mold dorsally, but retains some dolomitized shell material around expanded aperture (X1.5). Platteville Formation (Rocklandian), Beloit, Wisconsin. USNM 265960.

6-8. Dorsal, aperture, and right-lateral views of a dolomitized internal mold of a submature specimen (X2). Same horizon and locality as Figures 1-5 above. USNM 265957.

9. Aperture view of dark gray calcitic cast showing the outline of the aperture and its anterior sinus (X1.5). Specimen not whitened for photograph. Platteville Formation (Rocklandian), Old Concord, Minnesota. USNM 47590.

10-12. Salpingostoma kentuckyensis (Ulrich and Scofield, 1897).

10. Dorsolateral view of weathered silicified fragment of expanded, thickened aperture rim, showing trace of coarse radiating ribs. Paralectotype (X1.5). Curdsville Member of the Lexington Limestone (Kirkfieldian), Mercer County, Kentucky. USNM 265962.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 24 (Cont'd)

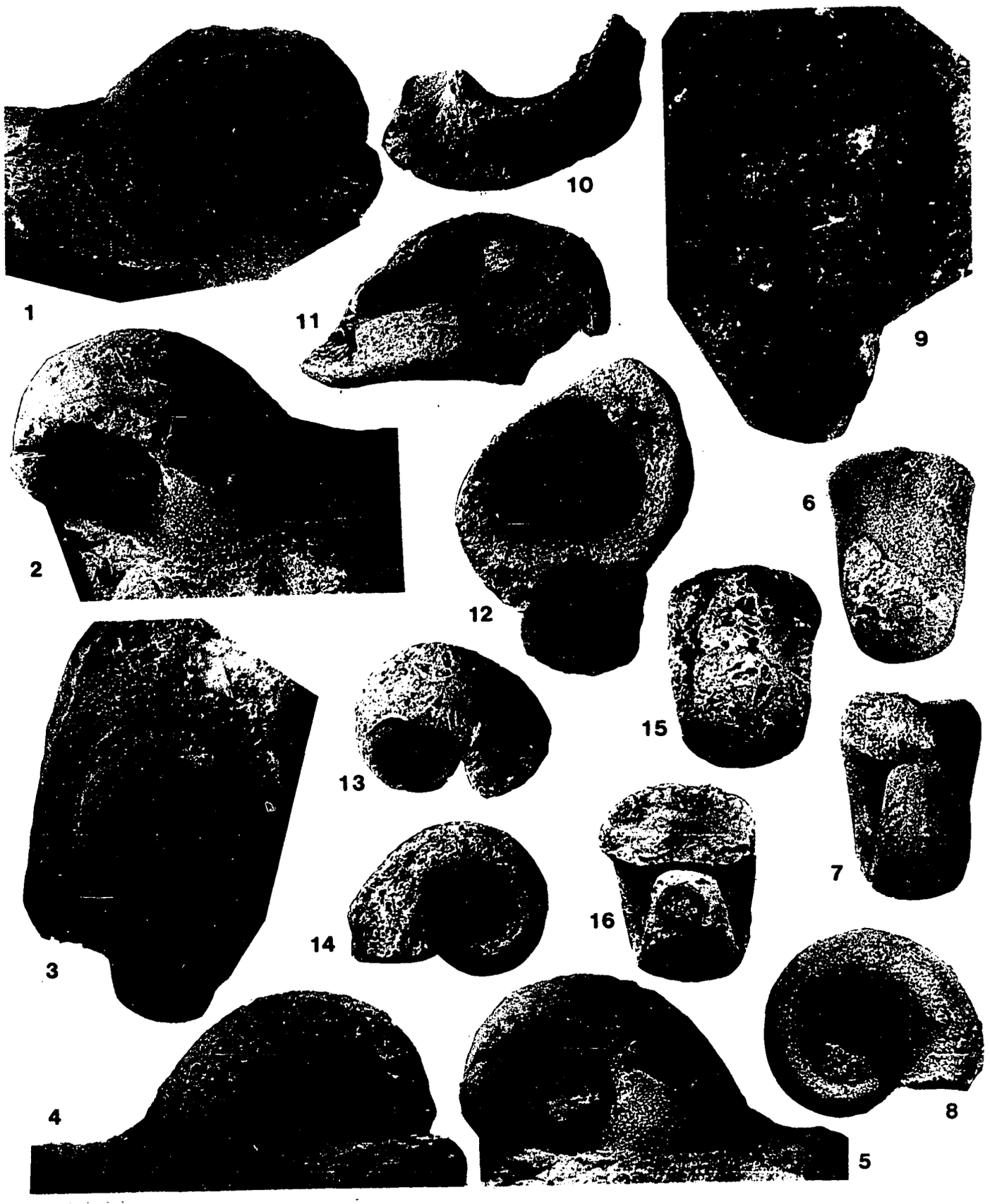
11-12. Left-lateral and ventral views of a weathered silicified specimen. Lectotype (X1.5). USNM 265961.

13-16. Salpingostoma richmondensis Ulrich in Ulrich and Scofield, 1897.

13-16. Right dorsolateral, left-lateral, dorsal, and aperture views of an internal mold of an immature specimen (X1.5). Museum label gives horizon and locality as: "Richmond Group, Richmond, Indiana." UCGM 44280.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 24



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 25

FIGURES 1-14. Salpingostoma kentuckyense Ulrich and Scofield, 1897.

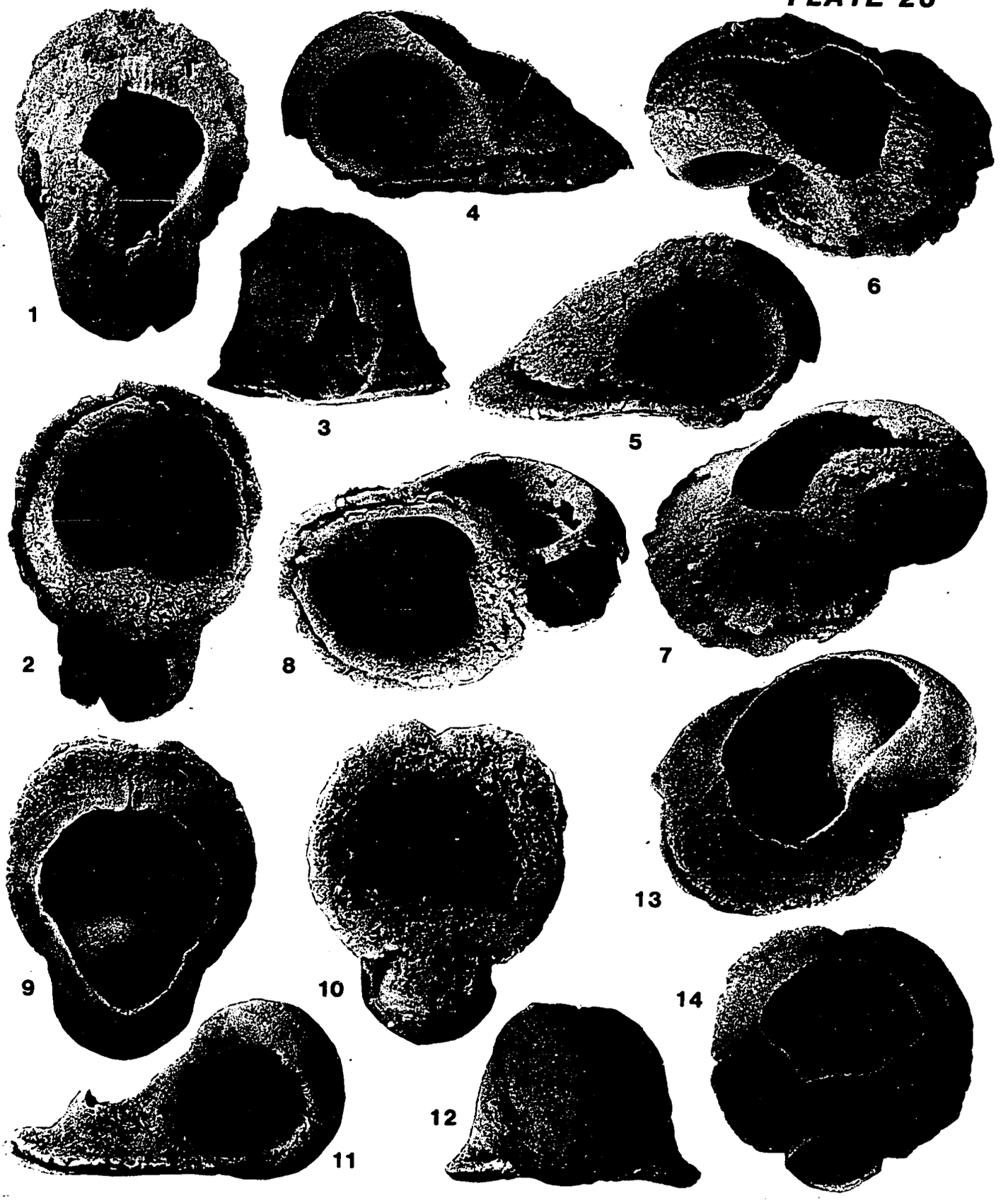
1-8. Dorsal, aperture, posterior, right- and left-lateral, right and left oblique dorsolateral, and ventrolateral views of silcified specimen (X1.5). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 265964.

9-13. Dorsal, aperture, left-lateral, posterior, and left oblique dorsolateral views of silicified specimen (X1.5). Same sample as Figures 1-8 above. USNM 265965.

14. Dorsal view of silicified specimen, showing chevron wrinkling beneath coil (X1.5). Same sample as Figures 1-13 above. USNM 265979.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 25



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 26

FIGURES 1-8. *Salpingostoma richmondensis* Ulrich *in* Ulrich and Scofield, 1897.

1-5. Anterodorsal, right and left oblique dorsolateral, and left- and right-lateral views of internal mold preserving some shell around expanded aperture rim. Holotype (X1.5). Whitewater Formation (Richmondian), Richmond, Indiana. USNM 45983.

6-8. Oblique anterodorsal, anterior, and left lateral views of internal mold (X1.5). Museum label gives horizon and locality as: "Whitewater Formation, Camden, Ohio." UCGM 44281.

9-10. *Pterotheca harviei* Foerste, 1924.

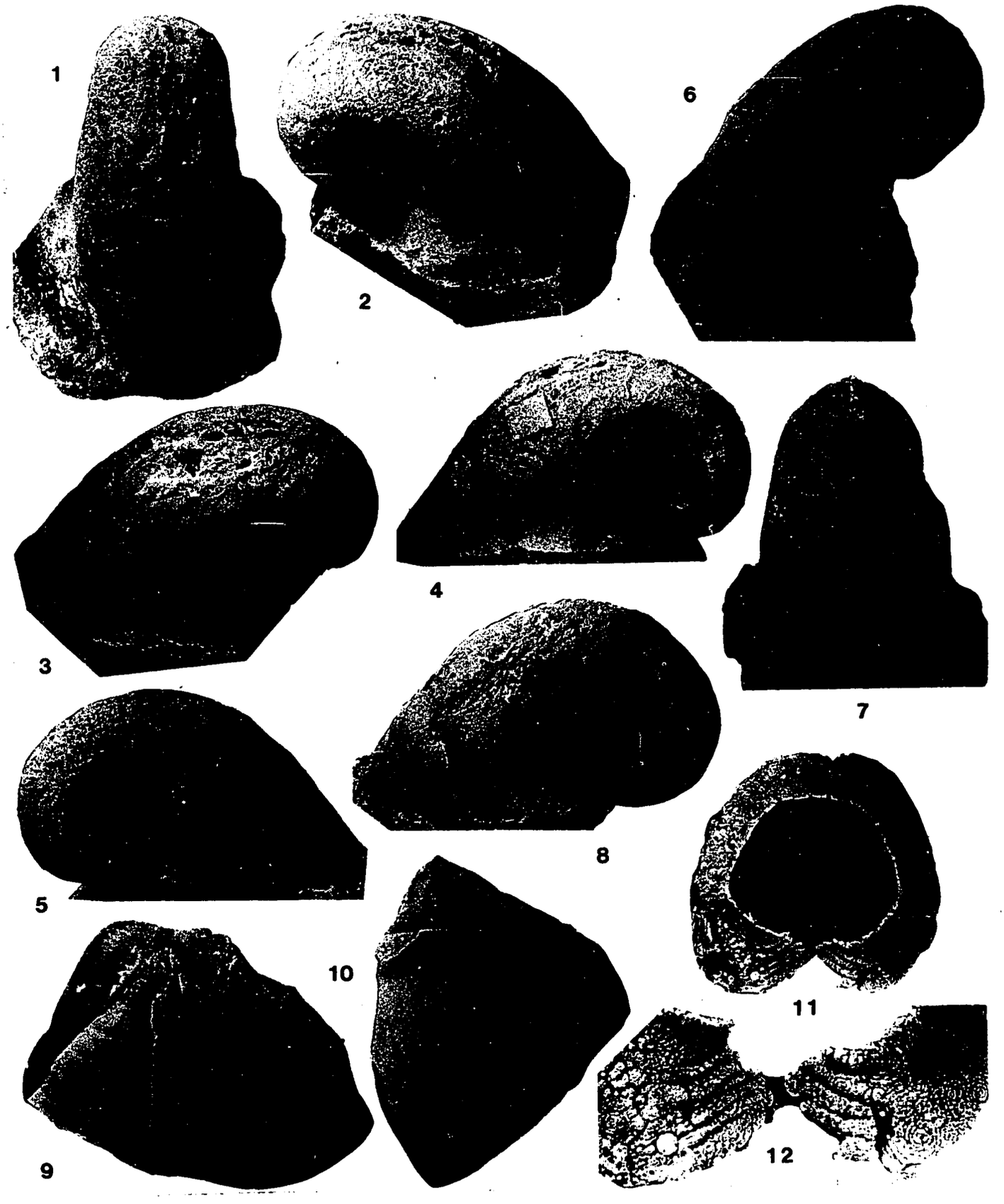
9-10. Dorsal and left dorsolateral views of a specimen that appears to be a composite mold (X1.5). Southgate biofacies of Kope Formation (Edenian), Covington, Kentucky. USNM 50092.

11-12. *Salpingostoma kentuckyensis* Ulrich and Scofield, 1897.

11-12. Dorsal view (X1.5) and close-up of posterior area (X3) of silicified aperture rim showing chevron wrinkling beneath coil. Same sample as Plate 25, figures 1-14. USNM 265966.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 26



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 27

FIGURES 1-15. Bucanopsis carinifera Ulrich

1-2. Dorsal and left-lateral views (X6.0) of silicified lectotype showing the revolving threads. The museum label states: "Trenton (Flanagan), near Danville, Kentucky." USNM 315583.

3. Left-lateral view (X6.0) of a silicified paralectotype. Same collection as Nos. 1-2. USNM 315584.

4. Ventral view (X6.0) of another silicified paratype showing sharp whorl floor keel. Same collection as Nos. 1-2 above. USNM 315585.

5-7. Dorsal, right-lateral, and posterior views of a silicified specimen. Cannon facies of Bigby-Cannon Limestone, from "Hill north of Well No. 1, Smith County, Tennessee," UCGM 44283.

8-12. Dorsal, left-lateral, posterior, ventral, and anterior views (X2.5) of silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 4928-CO. USNM 315586.

13. Dorsal view (X3.0) of a small silicified specimen apparently showing outer shell layers peeling away. Faulconer bed, Perryville Limestone Member, Lexington Limestone, USGS 6136-CO. USNM 315589.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 27 (Cont'd)

14. Two silicified specimens cemented together showing the aperture form and whorl floor keel (X3.0). Salvisa bed, Perryville Limestone Member, Lexington Limestone. USGS 5015-CO, USNM 315587.

15-16. Dorsal view (X3.0) and left anterodorsal close-up (X9.0) showing faint revolving threads on a weathered silicified specimen. Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315588.

17-20. Bucanopsis diabolensis n. sp.

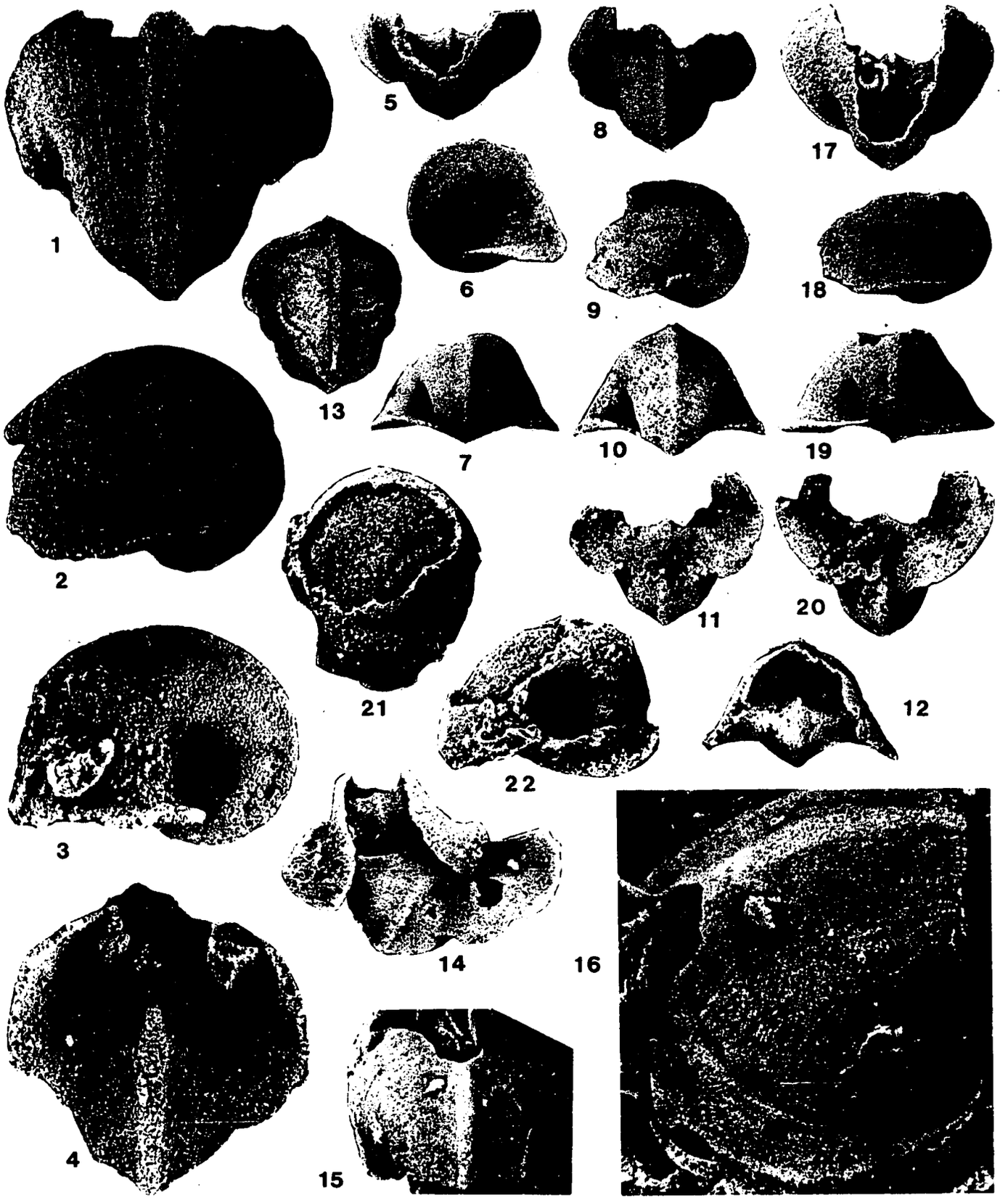
17-20. Dorsal, left-lateral, posterior, and ventral views (2.5) of a silicified specimen. Devil's Hollow Member, Lexington Limestone, USGS 5095-CO. USNM 315590. Note the narrower coil and relatively wider and more rounded aperture in comparison to Bucanopsis carinifera.

21-22. Bucania nashvillensis Ulrich

21-22. Dorsal and left-lateral views (X2.5) of a fragmented silicified specimen. Cannon facies of Bigby-Cannon Limestone, from "Hill north of Well No. 1, Smith Co., Tennessee." UCGM 44284.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 27



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 28

FIGURES 1-5. Bellerophon (Bellerophon) bilineatus Ulrich

1-5. Dorsal, posterior, left-lateral, and ventral views (X3.0), and dorsal close-up (X6.5) of selenizone and growth lines, of the silicified holotype. Labelled as coming from the "Trenton Group," near Danville, Kentucky. USNM 45697.

6-9. Bellerophon (Bellerophon) cf. B. (B.) bilineatus Ulrich

6-9. Posterior, ventral, dorsal, and right-lateral views (X2.5) of a silicified specimen. Faulconer bed, Perryville Limestone Member, Lexington Limetone, USGS 6136-CO. USNM 315612.

10-23. Sphenosphaera burginensis (Ulrich)

10-12. Right-lateral, posterior, and dorsal views (X2.0) of silicified holotype; Upper Lexington Limestone, 3 miles north of Burgin, Kentucky. USNM 45712.

13-15. Dorsal (X2.5), right anterodorsal views (X2.0), and anterodorsal close-up (X6.0) of selenizone, of silicified paratype. Upper Lexington Limestone, 1.5 miles south of Burgin, Kentucky. USNM 47595.

16-18. Dorsal and left-lateral views (X2.0), and dorsal close-up (X10.0) of selenizone, of a silicified spe-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 28 (Cont'd)

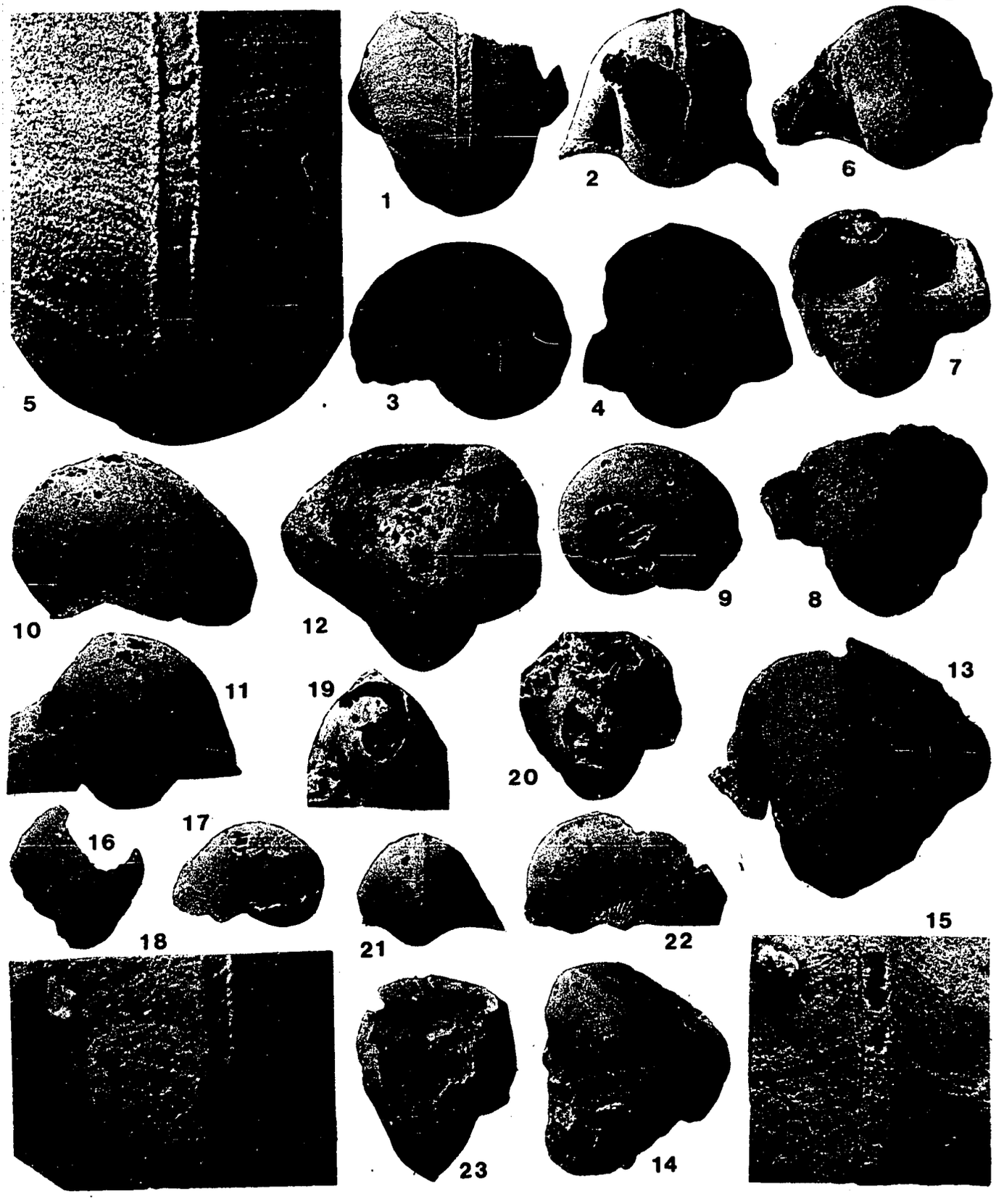
cimen. Grier Limestone Member, Lexington Limestone, USGS 5096-CO. USNM 315617.

19-20. Posterior and dorsal views (X2.0) of a silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 4883-CO. USNM 315615.

21-23. Posterior, right-lateral, and dorsal views (X2.0) of a silicified specimen. Same sample as Nos. 16-18 above. USNM 315616.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 28



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 29

FIGURES 1-16. Sphenosphaera troosti (D'Orgigny)

1-4. Dorsal close-up (X5.0), and right-lateral, ventral, and anteroventral views (X2.0) of silicified lectotype. Cannon facies of Bigby-Cannon Limestone, at Nashville, Tennessee. USNM 315602.

5-9. Left-lateral, right-lateral, dorsal, ventral, and anteroventral views (X2.0) of a silicified paralectotype figured by Ulrich and Scofield (1897). Same horizon and locality as Nos. 1-4 above. USNM 315665.

10-13. Posterior (X2.0), dorsal, right-lateral, and anterior views (X2.5) of another silicified paralectotype from the Ulrich and Scofield (1897) collection. Labeled as coming from the "Flanagan chert" (Lexington Limestone), near Danville, Kentucky. USNM 315603.

14-16. Dorsal, anterior, and right-lateral views (X3.0) of another Ulrich and Scofield (1897) silicified paralectotype from the same collection as Nos. 10-13 above. USNM 315604.

17-22. Sphenosphaera cf. S. troosti (D'Orbigny)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

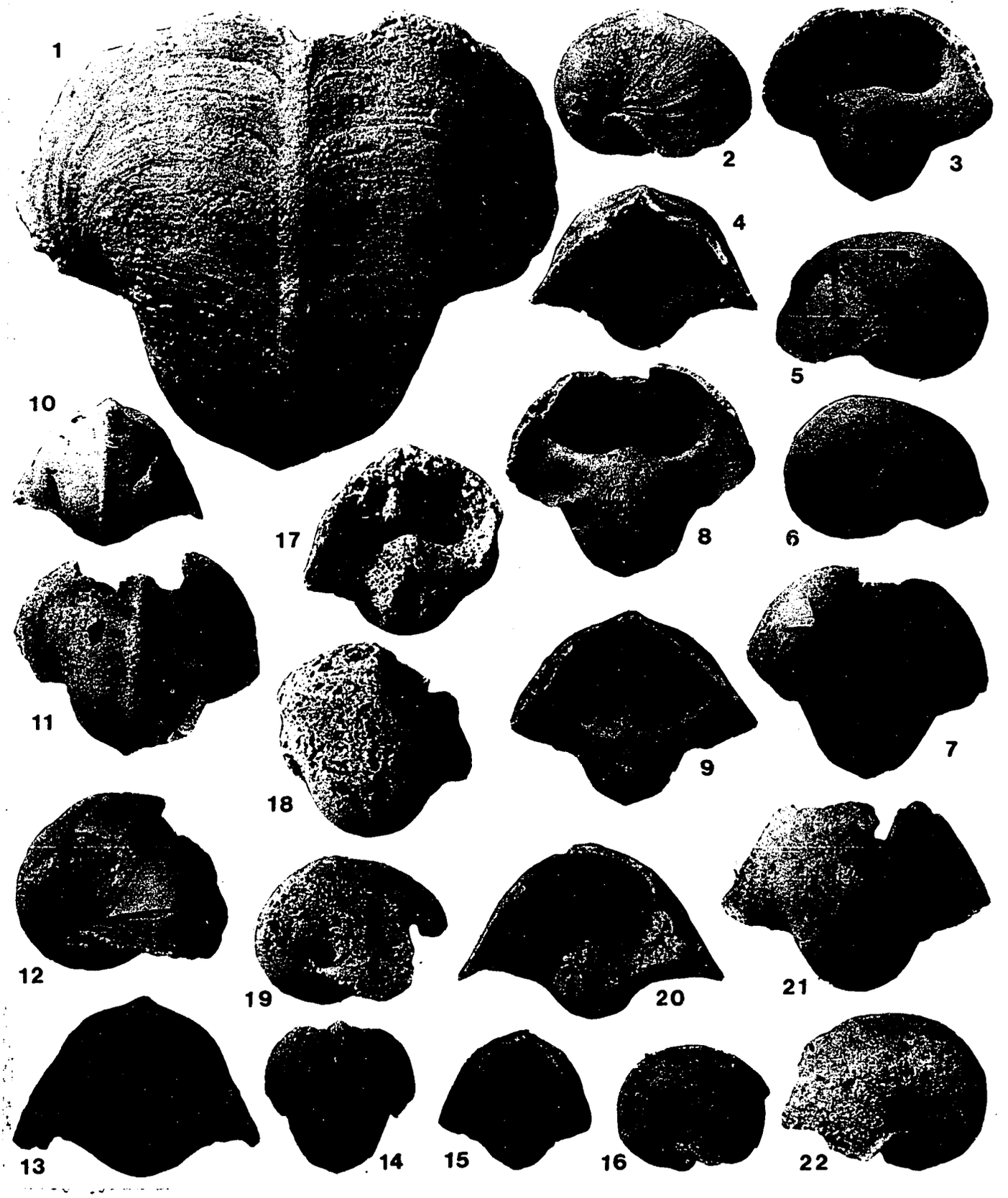
PLATE 29 (Cont'd)

17-19. Anteroventral, dorsal, and right-lateral views (X3.0) of a coarsely silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 4073-CO. USNM 315614.

20-22. Anterior, dorsal, and left-lateral views (X3.0) of silicified specimen. Grier Limestone Member, Lexington Limestone, USGS 4959-CO. USNM 315613.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 29



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 30

FIGURES 1-23. Sphenosphaera clausus (Ulrich)

1-6. Dorsal, anterior, ventral, right-lateral, and left posterolateral views (X2.0), and posterodorsal close-up (X6.0) of silicified holotype. Cannon facies of Bigby-Cannon Limestone, from central Tennessee. USNM 45701.

7-8. Dorsal and left-lateral views (X2.0) of slightly compressed calcitic paralectotype. Lexington Limestone, at Frankfort, Kentucky. USNM 45700.

9-10. Anteroventral and ventral views (X3.0) of silicified specimen. Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 5015-CO. USNM 315621.

11-14. Dorsal, right-lateral, ventral, and anteroventral views (X2.0) of a silicified specimen from same sample as Nos. 9-10 above. USNM 315620.

15-16. Posterodorsal and right-lateral views (X2.0) of a silicified specimen apparently showing an outer shell layer peeling away. Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 6916-CO. USNM 315619.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 30 (Cont'd)

17-18. Anteroventral and left-lateral views (X2.0) of a silicified specimen. Clays Ferry Formation, USGS 7812-CO. USNM 315628.

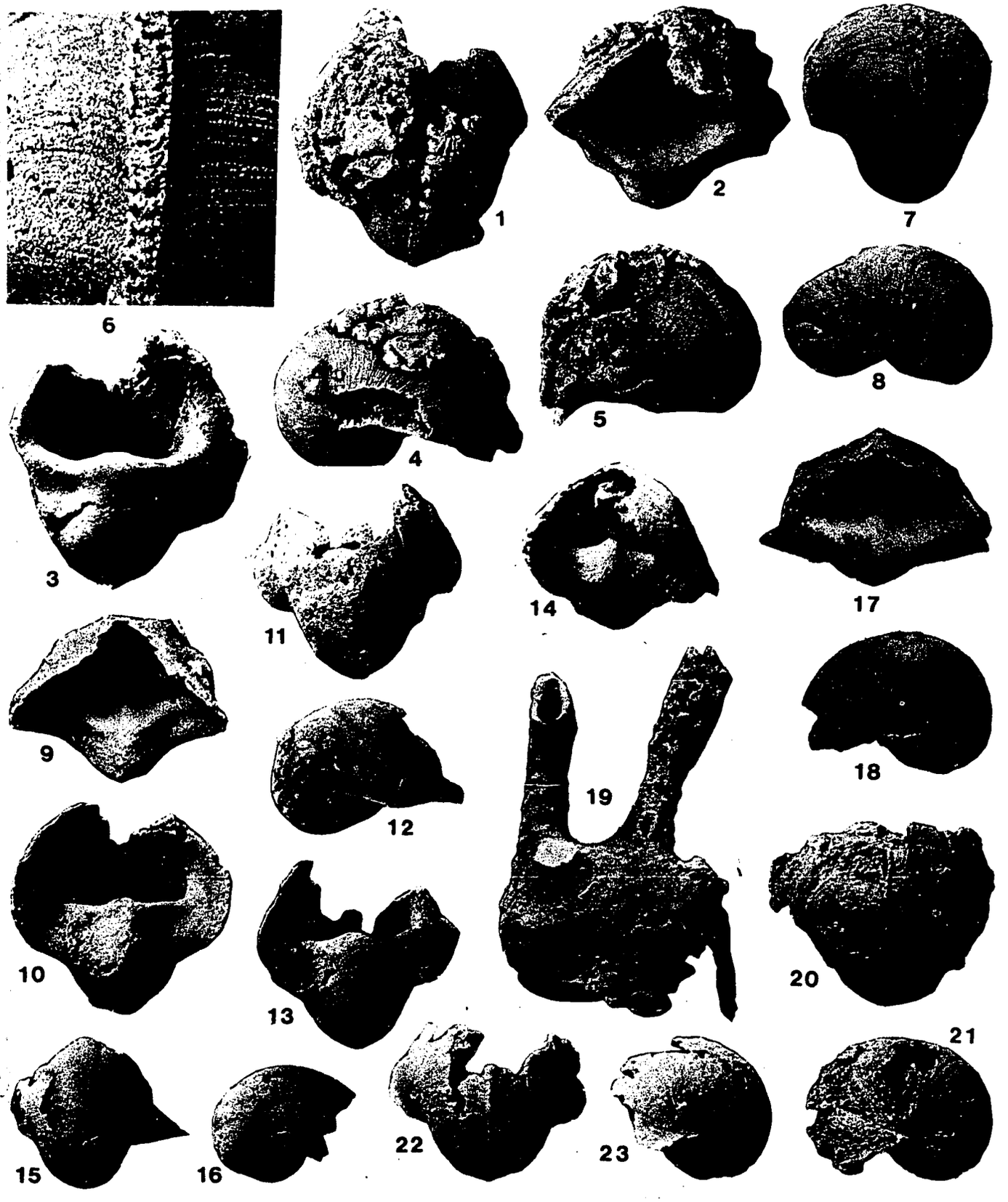
19. Right-lateral view (X2.0) of silicified specimen encrusted by a digitate bryozoan colony. Same sample as Nos. 17-18 above. USNM 315626.

20-21. Dorsal and left-lateral views (X2.0) of a silicified specimen. Same sample as Nos. 17-18 above. USNM 315627.

22-23. Dorsal and left-lateral views (X3.0) of a silicified specimen. Devil's Hollow Member, Lexington Limestone, USGS 5087-CO. USNM 315622.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 30



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 31

FIGURES 1-13. Sphenosphaera clausus Ulrich

1-6. Dorsal, ventral, anteroventral, posterior, left-lateral views (X2.0), and dorsal close-up of selenizone (X8.0), of a silicified specimen. Millersburg Limestone Member, Lexington Limestone, USGS 7353-CO. USNM 315624.

7-10. Dorsal, ventral, left-lateral, and posterior views (X2.0) of silicified specimen. Grier Limetone Member, Lexington Limestone, USGS 4879-CO. USNM 315618.

11. Small slab (X1.0) showing ventral view of a specimen associated with other silicified skeletal debris in gray, dense wackestone-packstone. Cannon facies of Bigby-Cannon Limestone, "Hill north of Well No. 1, Smith Co., Tennessee." UCGM 44301.

12-13. Another small slab (X1.5) from same collection as No. 11 above (and probably from same bed?), showing a posterolateral view of a silicified specimen, and a dorsal view (X2.0) of the same specimen. Other silicified skeletal material includes lophospirid gastropod and nautiloid cephalopd fragments, and a portion of a colonial coral colony. UCGM 44302.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 31

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 32

FIGURES 1-15. Sphenosphaera clausus (Ulrich)

1-3. Dorsal and ventral views (X2.0) and a close-up of the selenizone of a silicified specimen encrusted by a bryozoan colony. Millersburg Limestone Member, Lexington Limestone, USGS 7353-CO. USNM 315665.

4-5. Anterodorsal and anterior views (X2.0) of fragmented silicified specimen clearly showing the whorl floor ridge. Same sample as Nos. 1-3 above. USNM 315625.

6-10. Dorsal, right anterodorsal, ventral, and right lateral views (X2.0), and dorsal close-up (X10.0) of a silicified specimen encrusted on one side by a digitate bryozoan colony. Millersburg Limestone Member, Lexington Limestone, USGS 7344-CO. USNM 315623.

11-12. Left-lateral and posterior views (X2.5) of a calcareous specimen. The museum label states that the specimen comes from the "Top of the Bromley Shale" (now included in the Clays Ferry Formation), 1.5 miles east of Sadieville, Kentucky. MU 235T.

13-15. Dorsal, right-lateral, and left-lateral views (X2.0) of an internal mold, the lectotype of Belle-

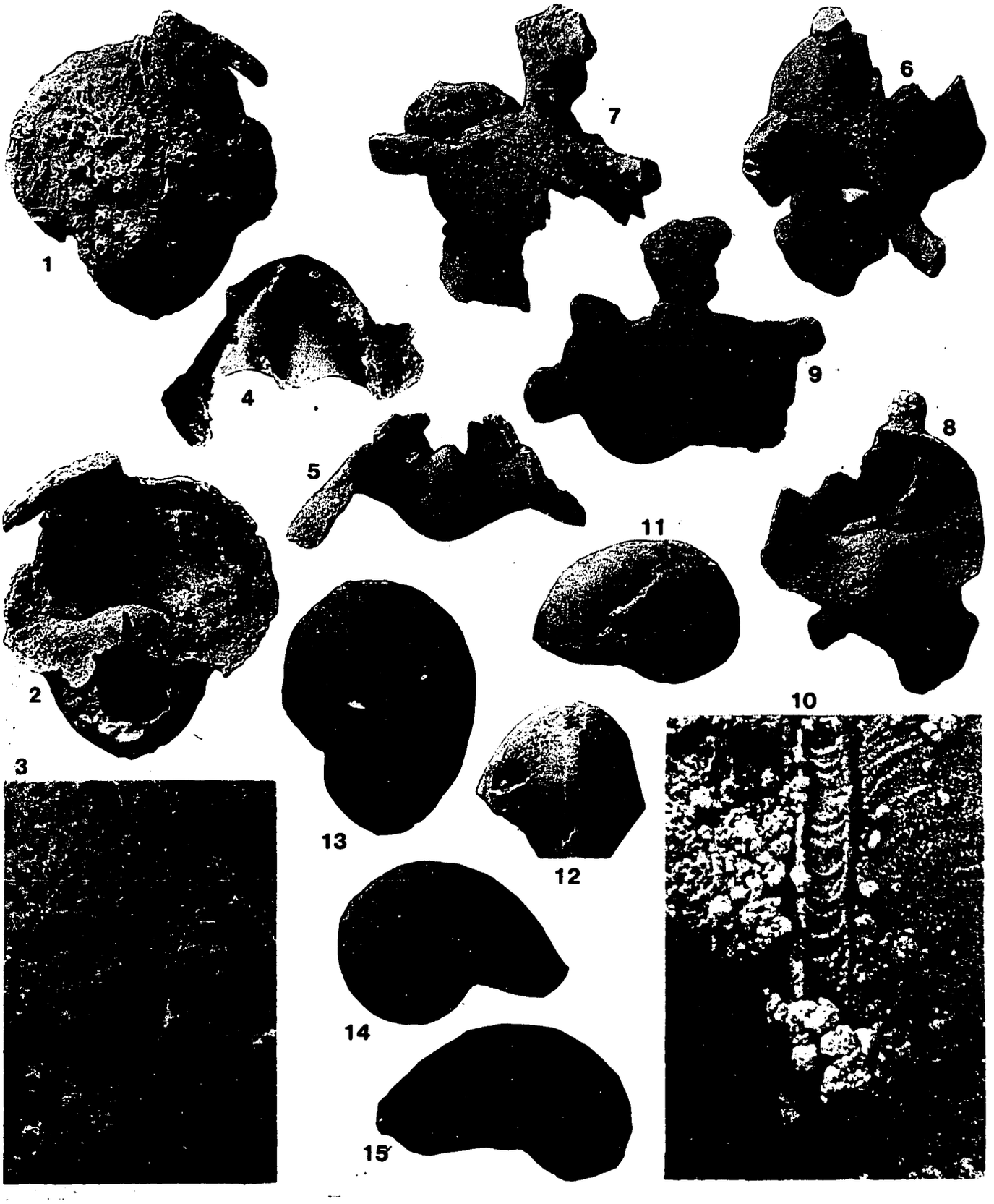
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 32 (Cont'd)

rophon rogersensis Foerste, which is here placed in synonymy with S. clausus. Note that the specimen is slightly compressed. Clays Ferry Formation, at Rogers Gap, Kentucky. USNM 315601.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 32



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 33

FIGURES 1-4. *Sphenosphaera recurvus* (Ulrich)

1-4. Dorsal (X2.0), dorsal close-up (X8.0), right-lateral, and right posterolateral views (X3.0) of calcareous holotype. Corryville biofacies, Grant Lake Formation, at Cincinnati, Ohio. USNM 45705.

5-6. *Sphenosphaera* aff. *S. recurvus* (Ulrich)

5-6. Right dorsolateral and anterior views (X2.0) of a badly recrystallized calcareous specimen partially embedded in limestone. Leipers Formation, at Rowena Ferry, Russell Co., Kentucky. UCGM 44282.

7-9. *Bellerophon* (*Bellerophon*) *subglobulus* Ulrich

7-9. Dorsal, right-lateral, and left-lateral views (X2.0) of silicified lectotype. The museum label states only "Black River Group," Mercer Co., Kentucky. USNM 45709.

10-15. *Sphenosphaera subangularis* (Ulrich)

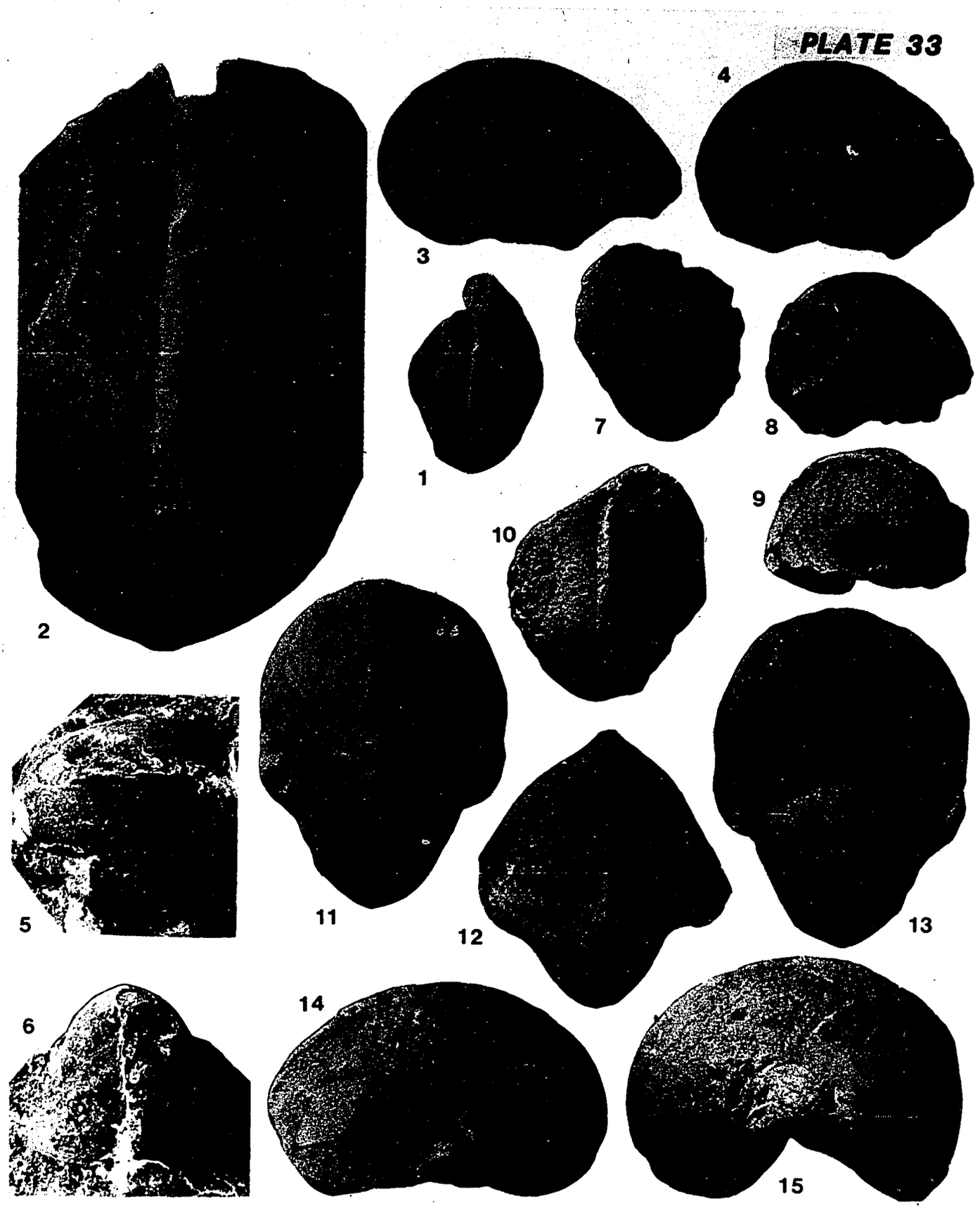
10. Dorsal view (X3.0) of a paralectotype. The museum label states only "Richmond Group," at Richmond, Indiana. USNM 315666.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 33 (Cont'd)

11-15. Dorsal, posterior, ventral, left-lateral, and right-lateral views (X3.0) of the calcareous lectotype. Same sample and locality as No. 10 above. USNM 45708.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 34

FIGURES 1-13. Sphenosphaera capax (Ulrich)

1-3. Dorsal, left-lateral, and ventral views (X1.5) of calcareous lectotype. Fairmount biofacies of Fairview Formation, at Covington, Kentucky. USNM 315606.

4-5. Dorsal and ventral views (X2.0) of a bryozoan encrusted, calcareous paralectotype. Same collection as Nos. 1-3 above. USNM 45699. (Note that specimen is vertically compressed.)

6-7. Dorsal and ventral views (X1.5) of another bryozoan encrusted, calcareous paralectotype. This specimen is also compressed. Same collected as Nos. 1-3 above. USNM 315608.

8-9. Dorsal and left-lateral views (X1.5) of calcareous paralectotype. Same collection as Nos. 1-3 above. USNM 315607.

10. Posterior view (X1.5) of silicified specimen with shell broken away to expose the whorl interior and whorl floor ridge. Gilbert Member, Ashlock Formation, USGS 6412-CO. USNM 387016.

11-13. Dorsal, posterior, and right-lateral views (X1.5) of silcified specimen with dorsal shell broken away

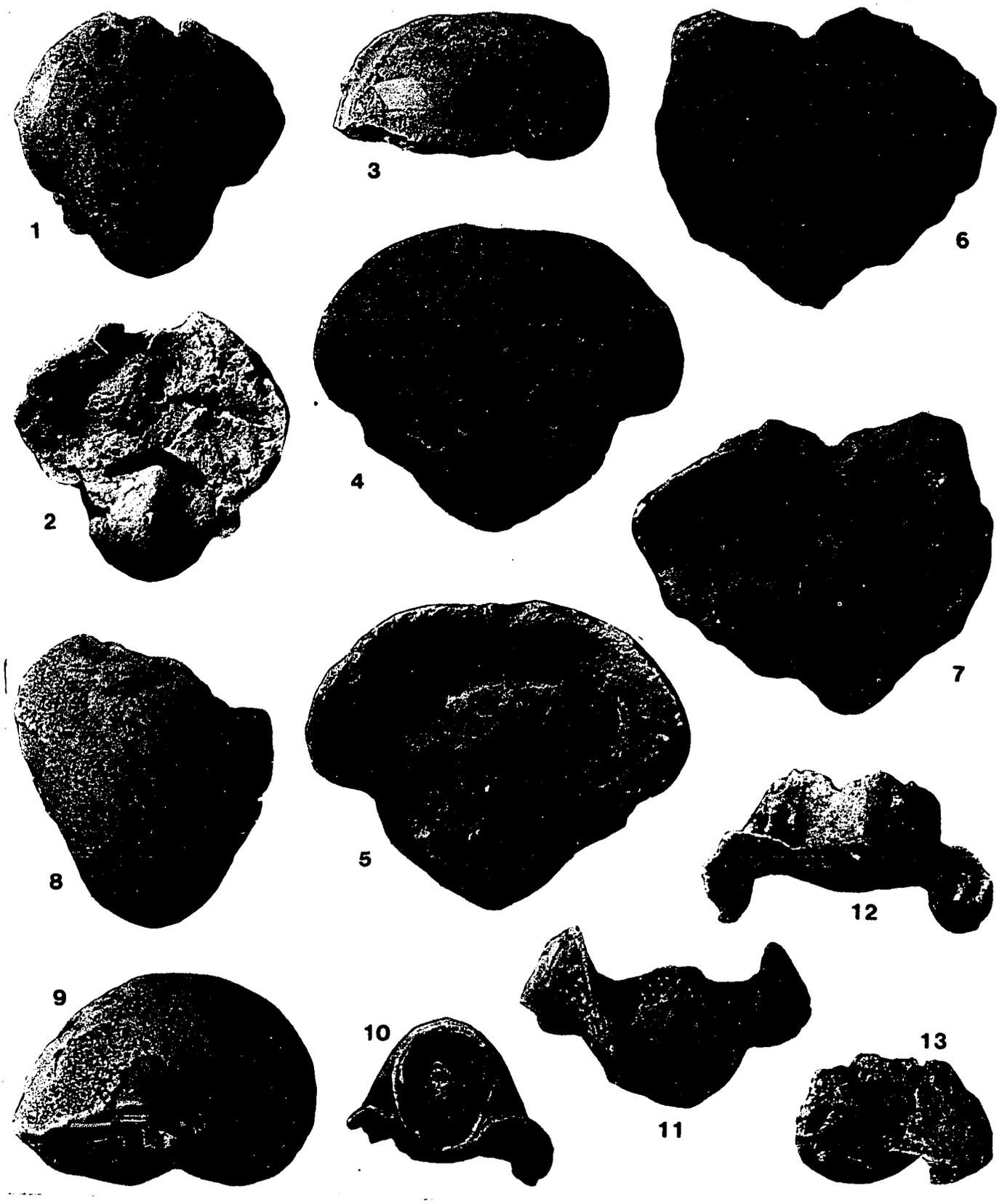
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 34 (Cont'd)

showing whorl floor ridge. Same sample as No. 10 above. USNM 387017.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 34



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 35

FIGURES 1-14. Sphenosphaera mohri Miller

1-4. Dorsal, posterior, and right-lateral views (X1.5), and right dorsolateral close-up (X4.0), of the calcareous lectotype. Whitewater Formation, at Richmond, Indiana. UC 8793a.

5. Dorsal view (X1.5) of large, broken, and vertically compressed, calcareous paralectotype. Same collection as Nos. 1-4 above. UC 8793b.

6-8. Ventral, right dorsolateral, and right-lateral views (X1.5) of broken calcareous paralectotype that has been distorted by compression. Same collection as Nos. 1-4 above. UC 8793c.

9-11. Dorsal, right-lateral, and posterior views (X2.0) of calcareous specimen figured by Ulrich and Scofield (1897). Whitewater Formation, at Richmond, Indiana. USNM 315611.

12-14. Dorsal, ventral, and left-lateral views (X2.0) of another specimen figured by Ulrich and Scofield (1897). Same collection as Nos. 9-11 above. USNM 315610.

15-16. Dorsal and left-lateral views (X1.5) of calcareous holotype of Bellerophon cincinnatiensis Miller

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 35 (Cont'd)

and Faber, 1894, which is placed in synonymy with S. mohri. The museum label states: "Maysville, at quarries in Cincinnati, Ohio" UC 8796.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 35

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 36

FIGURES 1-15. *Sphenosphaera mohri* Miller

1-3. Dorsal, posterior, and right-lateral views (X1.5) of silicified specimen. Dillsboro Formation, USGS 6139-CO. USNM 315631.

4-7. Dorsal, posterior, left-lateral, and ventral views (X1.5) of silicified specimen. Same sample as Nos. 1-3 above. USNM 315629.

8-9. Dorsal and ventral views (X3.0) of silicified specimen. Same sample as Nos. 1-3 above. USNM 315633.

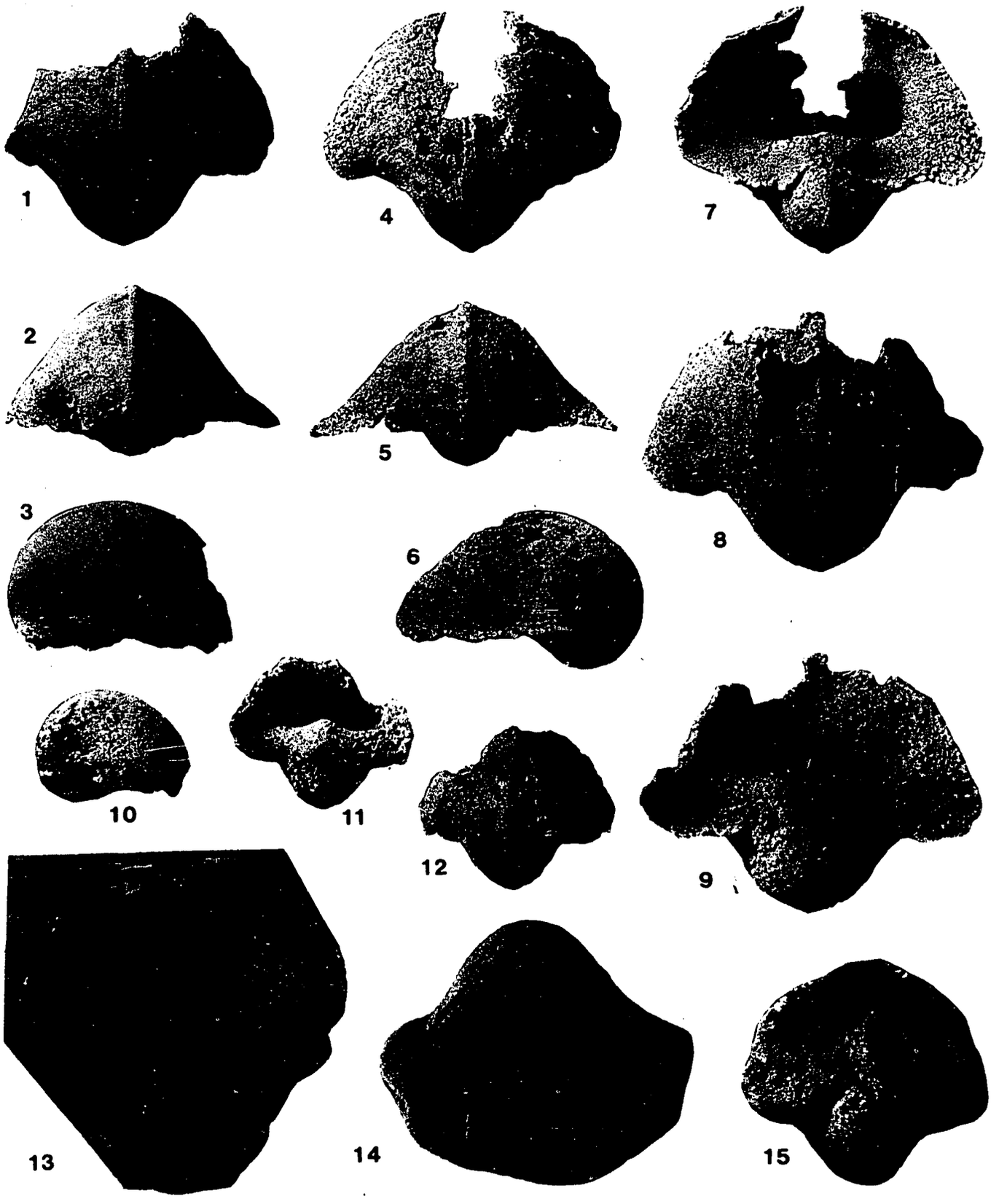
10-12. Right-lateral, ventral, and dorsal views (X3.0) of a juvenile silicified specimen. Same sample as Nos. 1-3 above. USNM 315632.

13. View of concave impression of shell (X1.5) of a fragmented dorsum showing the dorsal slit and growth lines. Whitewater Formation, locality unknown, but certainly from southwestern Ohio or southeastern Indiana. MU 14539.

14-15. Anterodorsal view (X2.0) showing the slit, and ventral view (X1.5), of an internal mold. Labelled as from the Waynesville Formation, but with no locality given; probably from same area as cited for No. 13 above. UCGM 44303.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 36



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 37

FIGURES 1-11, 15-23.

Carinaropsis cymbula (Hall, 1861).

1-4. Dorsal, left anterodorsal, ventral, and anteroventral views of holotype (X2.0). Note median groove in selenizone. Museum label gives horizon and locality as: "Trenton Limestone, Allen's Bluff, Tennessee." AMNH 37725a.

5-6. Dorsal and right-lateral views of a paratype (X2.0). Same sample as Figures 1-4 above. AMNH 37725b.

7-8. Dorsal and right-lateral views of a hypotype from Ulrich and Scofield's (1897) suite USNM 45739 (X3.0). Museum label gives horizon and locality as: "Trenton Group, near Danville, Kentucky." USNM 265996.

9-11. Dorsal, left-lateral, and ventral views of another Ulrich and Scofield (1897) hypotype (USNM 45739 suite) (X1.5). Same sample as Figures 7-8 above. USNM 265997.

15-21. Dorsal, left-lateral and close-up of coil of same, ventral, anteroventral, left dorsoventral, and

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 37 (Cont'd)

posterior views of silicified specimen (X1.5). Grier Limestone Member of the Lexington Limestone, USGS 5906-CO. USNM 265984.

22. Dorsal view of specimen showing dorsal septum (X1.5). Grier Limestone Member of Lexington Limestone, USGS 4879-CO. USNM 265985.

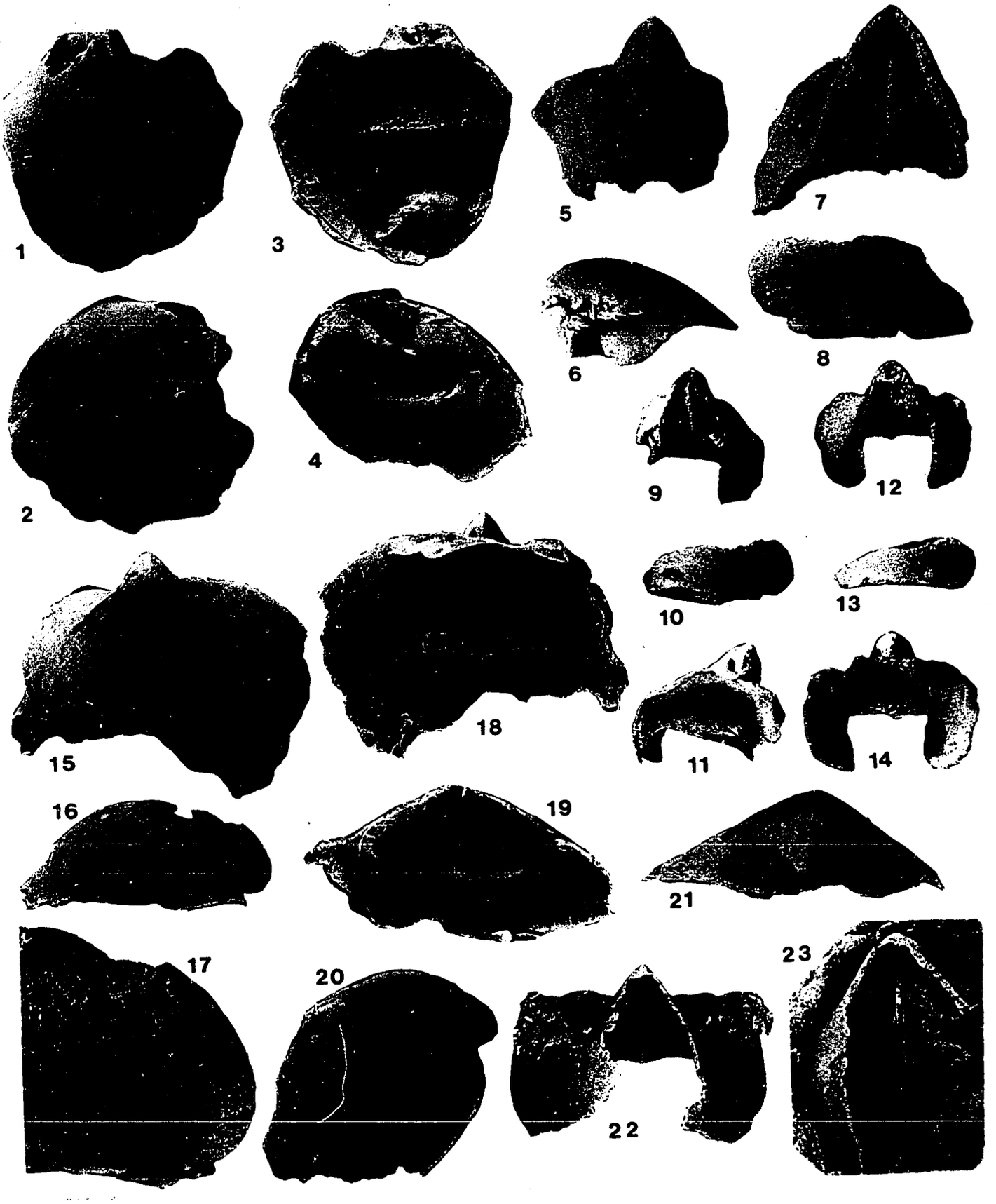
23. Dorsal view of specimen showing dorsal septum (X2.0). Museum label says: "Siliceous layer below Perryville bed, 2 miles north of Danville, Kentucky. USNM 87778.

12-14. Carinaropsis cunulae (Hall, 1861)

12-14. Dorsal, left-lateral and ventral views of an Ulrich and Scofield (1897) hypotype from USNM 45738 suite (X1.5). Museum label gives horizon and locality as: "Trenton (Cannon Limestone), Nashville, Tennessee. USNM 265998.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 37



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 38

FIGURES 1-12 *Carinaropsis cymbula* (Hall, 1861).

1-2. Anterolateral view (X1.5) and close-up of same (about X6.0) of broken silicified specimen showing structure of septum and parietal lip. Grier Limestone Member of the Lexington Limestone, USGS 5096-CO. USNM 265986.

3-6. Dorsolateral, ventral, anteroventral, and right-lateral views of a silicified specimen (X2.0). Grier Limestone Member of Lexington Limestone, USGS 4879-CO. USNM 265988.

7-8. Posterior and left posterolateral views of a silicified specimen, the latter showing fine radial threads (X1.5). Same sample as Figures 1-12 above. USNM 265991.

9. Dorsal view of silicified specimen showing coil and septum (X1.5). Same sample as Figures 3-6 above. USNM 265987.

10. Dorsal view of silicified specimen showing selenizone with median groove (X2.0). Same sample as Figures 3-6 above. USNM 265990.

11-12. Dorsal and anteroventral views (X2.0) of silicified specimen with *Bucania subangulata*. Note ante-

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 38 (Cont'd)

rior margin of septum nearly straight. Grier Limestone Member of the Lexington Limestone, USGS 5094-CO. USNM 265989.

FIGURES 13-16. Tetranota wisconsinensis (Whitfield, 1878).

13-15. Dorsal, right oblique anterodorsal, and posterior views of the hypotype of Shrock and Raasch (1937) (X2.0). Museum label gives horizon and locality as: "Platteville Formation, Dir. 4-6, McCray Quarry, 3 miles east of Kentland, Indiana. USNM 158279.

16. Anterior view of another dolomitized internal mold, showing the deep median slit (X2.0). No locality or horizon data given, but from mode of preservation, probably from same sequence of strata in northeast-central U.S.A. MU251T.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 38

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 39

FIGURES 1-5,13. *Pterotheca saffordi* (Hall, 1861).

1-2. Dorsal and dorsolateral views of a plastotype of the holotype (X1.5). Museum label gives horizon and locality as: "Stones River (Lebanon Limestone), Lebanon, Tennessee." USNM 79262.

3-5. Dorsal, anterolateral, and dorsal (X1.0) views of calcitic specimen, and view of counter side of small slab showing association with ostracods (X1.5). Tyrone Limestone (Rocklandian), High Bridge, Kentucky. USNM 79268.

13. Dorsal view of small specimen on slab with abundant leperditiid ostracods (X1.0). Museum label give horizon and locality as: "Top of Tyrone Limestone just beneath lower bentonite beds, High Bridge, Kentucky. USNM 50093.

6-7,12. *Pterotheca* cf. *P. expansa* (Emmons, 1842).

6-7. Dorsal and anterodorsal views of weathered silicified specimen (X1.5). Curdsville Limestone Member of the Lexington Limestone, at Curdsville, Kentucky. USNM 79283.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 39 (Cont'd)

12. Dorsal view of fragment in small slab with abundant leperditiid ostracods (X1.0). Murfressboro Formation (Blackriverian), at Murfressboro, Tennessee. USNM 50100.

FIGURES 8-9. Pterotheca angusta Raymond, 1921

8-9. Dorsal and anterolateral oblique views of a silicified specimen (X1.5). Note narrow septal angle. Basal 2 feet of Curdsville Limestone Member of Lexington Limestone, USGS 7784-CO. USNM 315538.

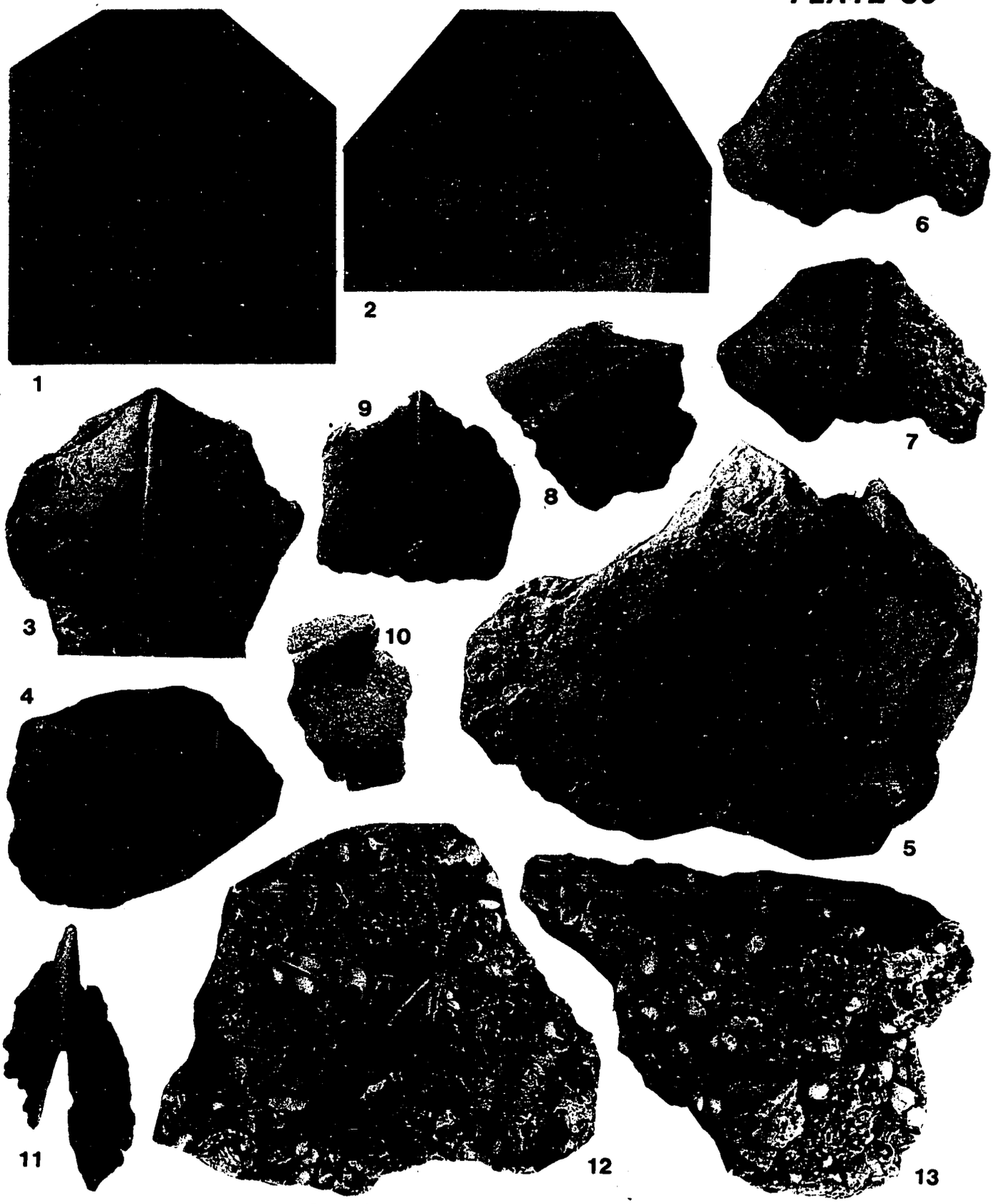
10-11. Pterotheca expansa (Emmons, 1842).

10. Anterolateral oblique view of a dorsal fragment showing high, narrowing keel (X2). Lower Curdsville Member of the Lexington Limestone, USGS 6134-CO. USNM 315535.

11. Dorsal view of fragment of dorsal keel (X1.5). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 315533.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 39



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 40

FIGURES 1-4. *Pterotheca* cf. *P. expansa* (Emmons, 1842).

1-3. Dorsal, anterolateral, and left-lateral views of a silicified specimen (X1.0). Basal 2 feet of Curdsville Limestone Member of Lexington Limestone (Kirkfieldian), USGS 7784-CO. USNM 315536.

4. Dorsal view of silicified specimen showing septum (X1.5). Note there is no trace of the divergent apical ridges in this specimen. Same sample as Figures 1-3 above. USNM 315537.

5-7. *Pterotheca expansa* (Emmons, 1842).

5. Dorsolateral view of fragmented silicified specimen showing fine, closely-spaced growth lines (X1.5). Tyrone Limestone (Rocklandian), USGS 6034-CO. USNM 315532.

6-7. Dorsal view (X2.0) of fragmented specimen, and close-up of apical area (X5.0), showing convex septum and divergent apical ridges. Same sample as Figure 5 above. USNM 315534.

8-9. *Pterotheca* cf. *P. saffordi* (Hall, 1861).

Both sides of small slab showing association with ostracods (X1.5). Tyrone Limestone (Rocklandian), High Bridge, Kentucky. USNM 50099.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

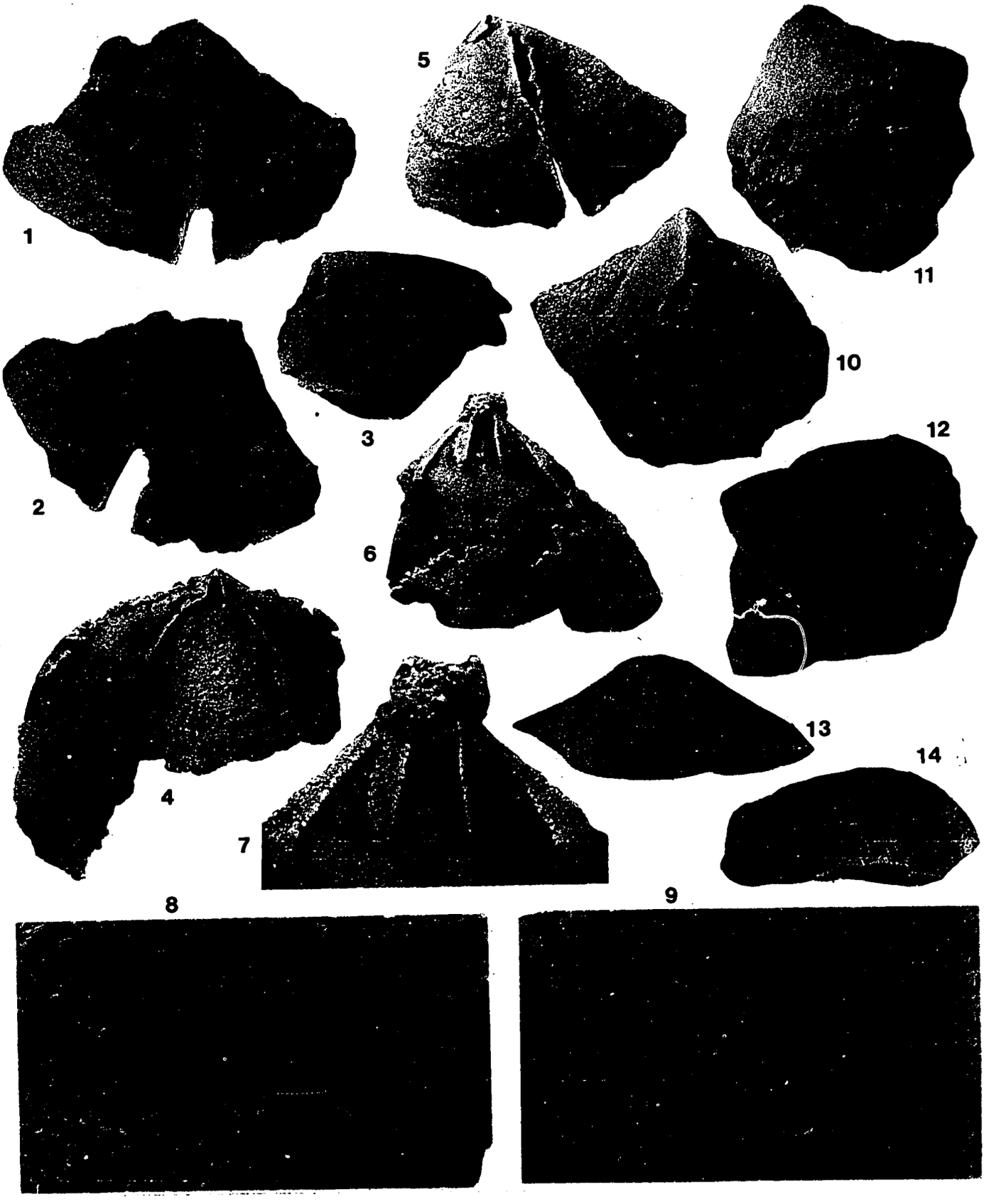
PLATE 40 (Cont'd)

10-14. Carinaropsis explanata Ulrich in Ulrich and Scofield, 1897.

10-14. Dorsal, left and right anterolateral oblique, posterior, and left-lateral views of the lectotype (X1.5). Museum label gives horizon and locality as: "Upper Trenton, Covington, Kentucky." USNM 45740.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 40



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 41

FIGURES 1-5. *Sphenosphaera mohri* (Miller)

1-2. Anterodorsal and ventral views (X1.5) of silicified specimen with dorsum broken away to show the whorl floor ridge. Liberty biofacies, Dillsboro Formation, USGS 6139-CO. USNM 315630.

3-5. Dorsal and ventral views (X1.5) and close-up of parietal lip showing bryozoan encrustation (about X5.0), of an embedded calcitic specimen. Saluda Formation, "Roadside exposure above upper part of Crooked Creek, Madison Indiana." MU 252T.

6-8. *Tropidodiscus cristatus* (Safford)

6-8. Left-lateral, anterior, and dorsal views (X3.0) of the silicified lectotype with the anterodorsal portion of the shell broken away. Cannon facies of the Bigby-Cannon Limestone, Jackson Co., Tennessee. USNM 45950.

9-13. *Tropidodiscus subacutus* (Ulrich)

9-10. Anterior and right-lateral views (X3.0) of a silicified specimen with the anterodorsal shell broken away. Salvisa bed, Perryville Limestone Member, Lexington Limestone, USGS 6915-CO. USNM 315638.

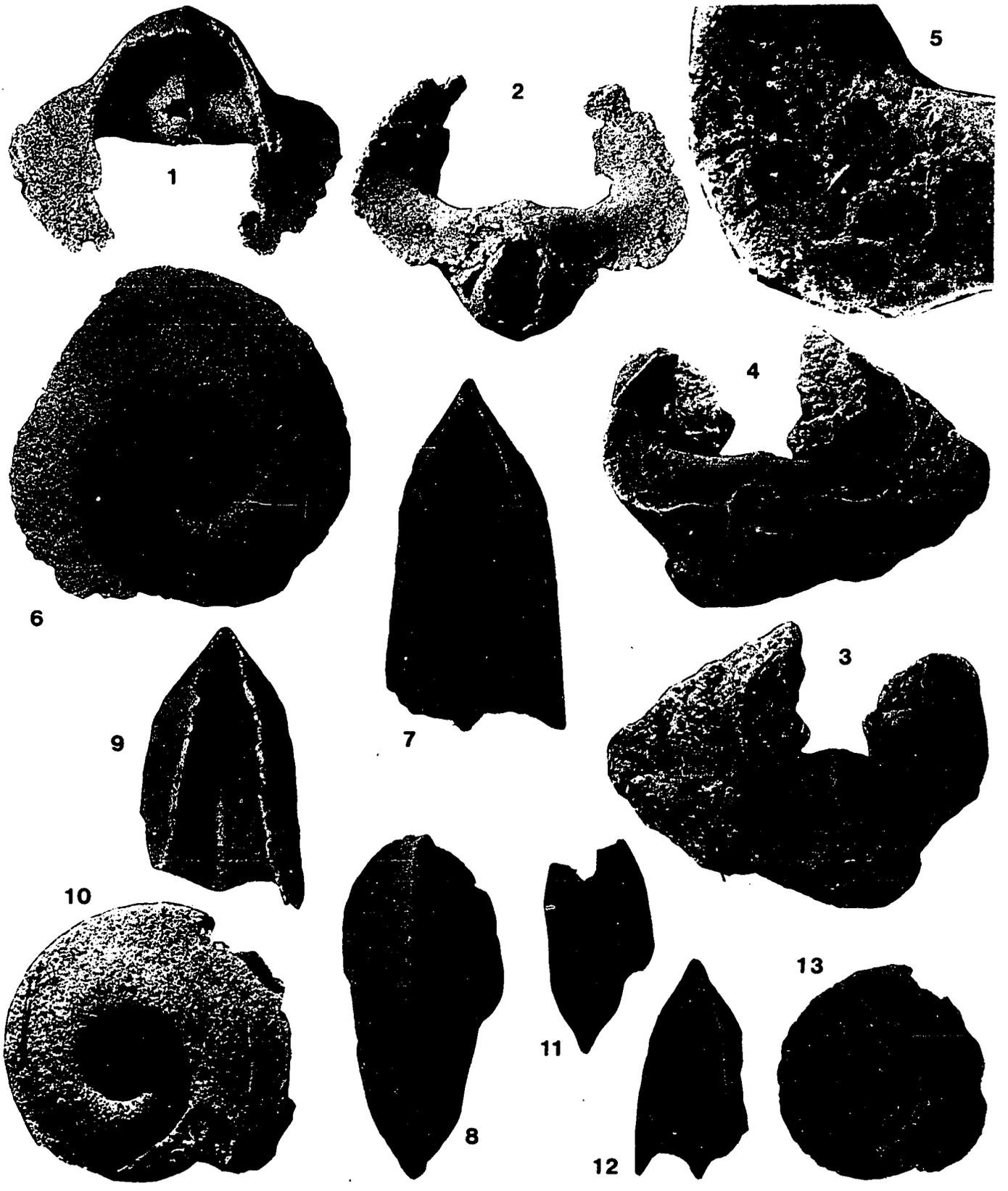
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 41 (Cont'd)

11-13. Dorsal, anterior, and right-lateral views (X3.0) of silicified lectotype with anterodorsal shell broken away. Lexington Limestone, at Danville, Kentucky. USNM 387021.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 41



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 42

FIGURES 1-2. *Tropidodiscus magnus* (Miller)

1-2. Left-lateral and ventral views (X2.0) of calcitic holotype. "Richmond Group" (Richmondian), at Richmond, Indiana. UC 10838.

3-6. *Temnodiscus nitidula* (Ulrich)

3-4. Left-lateral and dorsal views (X5.0) of calcitic lectotype. "Upper Trenton" (Shermanian), at Covington, Kentucky. USNM 315542.

5-6. Right-lateral and dorsal views (X5.0) of calcitic paralectotype. Same collection as Nos. 1-2 above. USNM 315543.

7-13. *Phragmolites grandis* (Ulrich)

7-9. Left-lateral, dorsal, and ventral views (X2.0) of silicified paralectotype. Lebanon Formation, at Lebanon, Tennessee. USNM 315668.

10-13. Dorsal, left anterolateral, left lateral and ventral views (X2.0) of silicified lectotype embedded in fine-grained limestone. Same collection as Nos. 7-9 above. USNM 315667.

14. *Phragmolites compressus* (Ulrich)

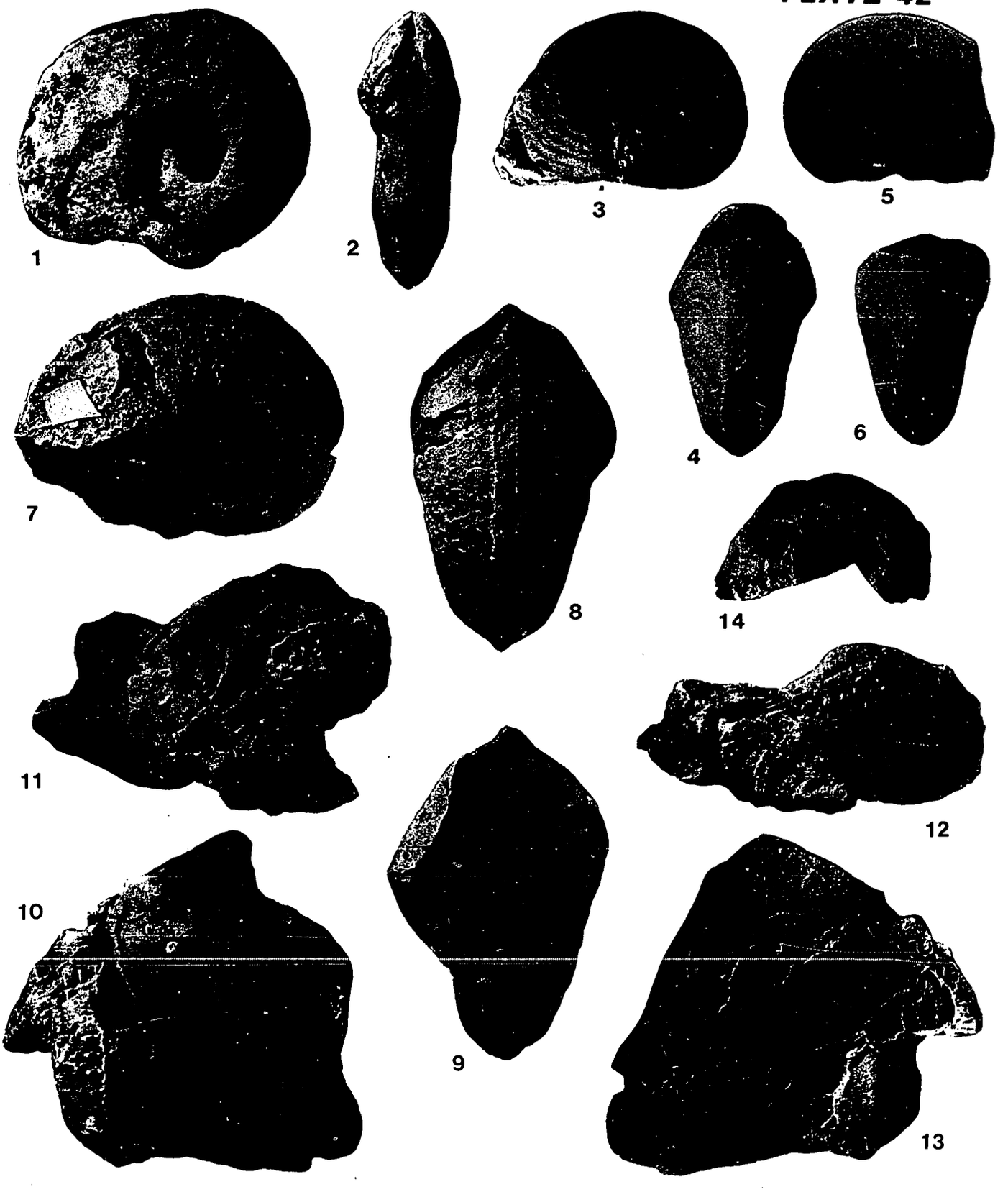
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 42 (Cont'd)

14. Left-lateral view (X2.0) of silicified holotype of P. similis (Ulrich), which is placed in synonymy wtith the above species herein. "Lowville beds, Black River Group, near High Bridge, Mercer Co., Kentucky."

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 42



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 43

FIGURES 1-3. Phragmolites grandis (Ulrich)

1-3. Left-lateral, dorsal, and ventral views (X6.0) of silicified paralectotype, a juvenile. Lebanon Formation, at Lebanon, Tennessee. USNM 387018.

4-12. Phragmolites cellulosus (Ulrich and Scofield)

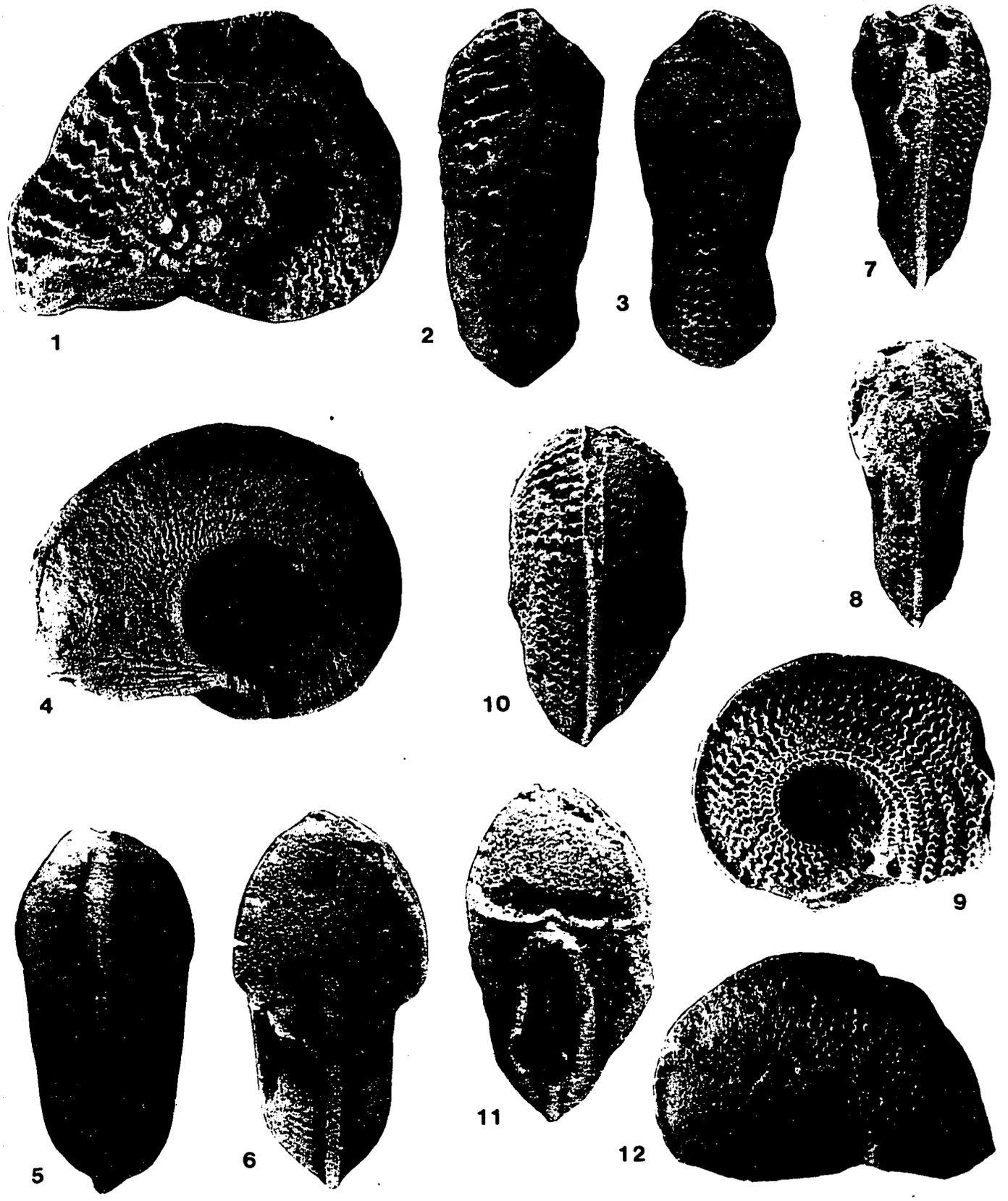
4-6. Left-lateral, dorsal and ventral views (X6.0) of silicified specimen. "Orthis bed of Trenton Group" (Hermitage Formation), "central Tennessee". USNM 61029. Note that specimen is quite worn.

7-9. Dorsal, ventral, and right-lateral views (X6.0) of silicified specimen. "Bed 1, Trenton Group" (Hermitage Formation ?), "2 miles south of Belfast, Tennessee." USNM 47562.

10-12. Dorsal, ventral, and right-lateral views (X6.0) of silicified specimen from the "pelecypod beds" of Hermitage Formation, 1.5 miles south of Woodbury, Tennessee. USNM 79250.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 43



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 44

FIGURES 1-4. *Phragmolites compressus* (Conrad)

1. Left-lateral view (X5.75) of a calcitic specimen embedded in limestone. "Lower part of Trenton and perhaps Black River, 2-4 miles north of Burgin, Mercer Co., Kentucky." USNM 387019.

2-4. Left-lateral, dorsal and ventral views (X5.75) of silicified specimen with ventral half of shell broken away. Same collection as above (probably different samples). USNM 387020.

5-7. *Phragmolites bellulus* (Ulrich)

5-7. Left-lateral, dorsal and ventral views (X6.0) of calcitic holotype. Fairmount member of Fairview Formation, at Covington, Kentucky. USNM 45751.

8-10. *Phragmolites dyeri* (Hall)

8-10. Right-lateral, dorsal and ventral views (X6.0) of an Ulrich and Scofield (1897) calcitic hypotype. Waynesville biofacies, Butler Co., Ohio. USNM 315673.

11-15. *Phragmolites elegans* (Miller)

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 44 (Cont'd)

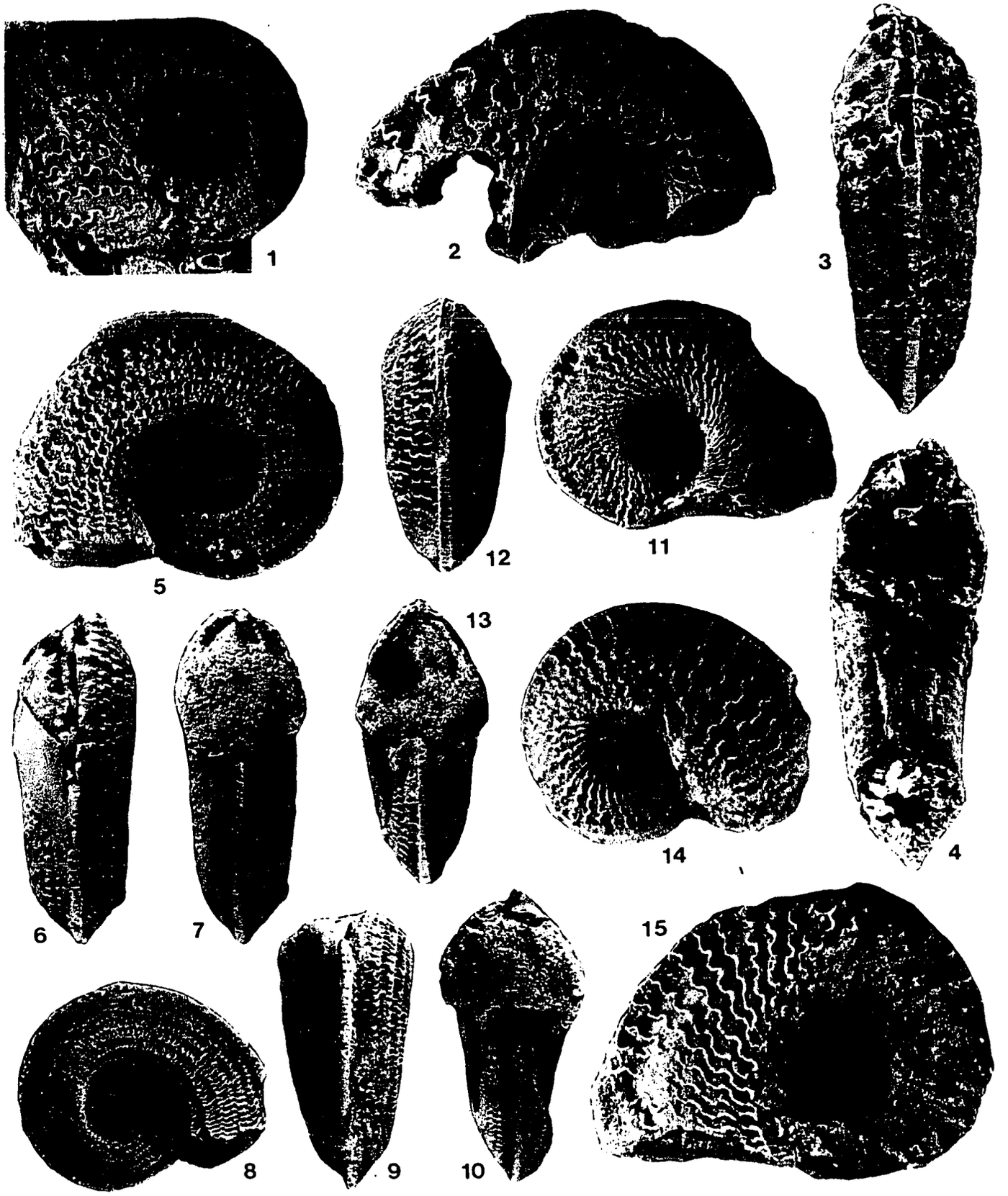
11-13. Right-lateral, dorsal and ventral views (X6.0) of an Ulrich and Scofield (1897) calcitic hypotype. Corryville biofacies, at Cincinnati, Ohio. USNM 315669.

14. Right-lateral view (about X8.0) of a calcitic specimen from same collection as Nos. 11-13 above. USNM 315670.

15. Left-lateral view of large calcitic specimen (X6.5) from same collection as Nos. 11-13 above. USNM 315671.

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 44



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 45

FIGURES 1-9. *Sinuites granistriatus* (Ulrich)

1-2. Ventral views (X2.0 and X7.0) of calcitic specimen showing pitting on ventral coil and aperture rim. Kope Formation. Locality OH-1, Clermont Co., Ohio. UCGM 44298.

3-4. Dorsal and ventral views (X2.0) of calcitic specimen. Same sample as Nos. 1-2 above. UCGM 44296.

5-7. Dorsal, anteroventral, and left-lateral views (X2.0) of calcitic specimen. Kope Formation, Locality KY-1, Carroll Co., Kentucky. UCGM 44306.

8-9. Dorsal and anterior views (X2.0) of calcitic specimen. Same sample as Nos. 1-2 above. UCGM 44297.

10. *Phragmolites elegans* (Miller)

10. Left-lateral view (about X8.0) of small calcitic specimen showing common association of the species with ramose bryozoans. Corryville biofacies, at Cincinnati, Ohio. USNM 315672.

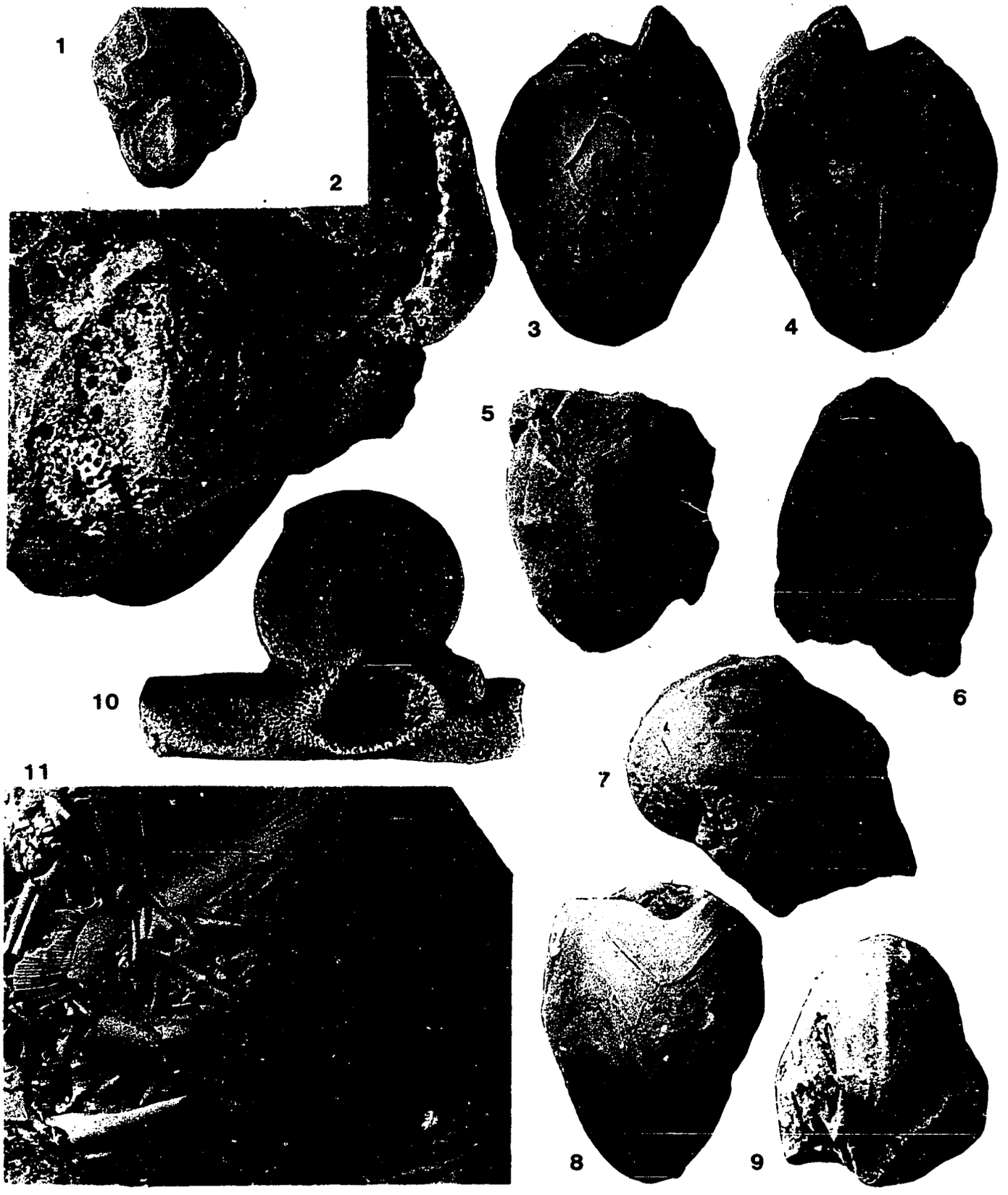
11. *Phragmolites dyeri* (Hall)

11. Small slab (X1.5) showing the species associated with diverse assemblage of ramose bryozoans, brachiopods, and trilobites. Waynesville biofacies, Butler Co., Ohio. USNM 315674.

GAS:lmw
84300ART0058

Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

PLATE 45



Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.