This dissertation has been
microfilmed exactly as received 66-697

OSGOOD, Jr., Richard Grosvenor, 1936-
TRACE FOSSILS OF THE CINCINNATI AREA.

University of Cincinnati, Ph.D., 1965
Geology

University Microfilms, Inc., Ann Arbor, Michigan

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

TRACE FOSSILS OF THE CINCINNATI AREA

A dissertation submitted to

The Graduate School
of the University of Cincinnati

in partial fulfillment of the
requirements for the degree of

DOCTOR OF PHILOSOPHY

1965

by

Richard Grosvenor Osgood, Jr.

A.B. Princeton University, 1959

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

UNIVERSITY OF CINCINNATI

August 2 19 65

I hereby recommend that the thesis prepared under my supervision by Richard G. Osgood Jr.

entitled Trace Fossils of the Cincinnati Area

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

Approved by:

Form 668—Grad. Sch.—1M—7-63

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

Please Note
Some figure pages have paper
prints which tend to curl.
Filmed as received.
University Microfilms, Inc.

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

Table of Contents

	Page
Acknowledgements	vi
Abstract	viii
Introduction	1
Difficulty and Value of Trace Fossil Studies	6
Stratigraphy of the Cincinnati Section	10
Chapter I - History of Invertebrate Palichnology	15
A. Age of "Fucoids"	16
B. Period of Reaction	18
C. Development of Ethological and Paleoecological Approaches	26
Chapter II - Preservation of Trace Fossils	33
A. Types of Preservation	33
B. Mechanics of Preservation of Boundary Relief Traces	36
Chapter III - Nomenclature of Trace Fossils	41
A. Classification at the Generic and Specific Levels	41
B. Suprageneric Classification of Trace Fossils	50
Chapter IV - History of the Study of Cincinnatian "Fucoids" and Trace Fossils	57
Chapter V - Cubichnia	69
Rusophycus	69
Lockeia	91

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

Asteriacites 103
Chapter VI - Domichnia 111
Introduction to Spreite-bearing U-tubes 111
Corophioides 113
?Skolithos 152
Chapter VII - Fodinichnia 162
Chondrites 162
Fascifodina 205
Phycodes 209
Dactylophycus 223
Trichophycus 230
Chapter VIII - Repichnia 244
General Introduction to Arthropod Tracks 244
Synopsis of the Ventral Morphology of Cincinnatian Trilobites 256
Asaphoidichnus 261
Allocotichnus 268
Petalichnus 276
Trachomatichnus 284
Teratichnus 292
Rhabdoglyphus 296
Tylichnus 304
Ormathichnus 308
Palaeophycus 310
Walcottia 327a
Fucusopsis 333

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

?Mollusk Trails 338
Chapter IX - ?Pascichnia 344
?Paleodictyon 344
Chapter X - Body Fossils Described as Plants 356
Chapter XI - "Fucoids" of Inorganic Origin 362
"Chloephycus" 362
"Blastophycus" 366
"Dystactophycus" 370
"Scolithus dispar" 376
"Palaeophycus flexuosum" 379
Chapter XII - Incertae sedis 383
Sphenophyllum primaevum 383
Protostigma 385
Palaeoscia 387
Aristophycus 395
Cyathophycus silurianum 400
Walcottia sulcata 402
Saccophycus 403
Chapter XIII - Invalid Species 406
Chapter XIV - Comparative Palichnology and Suggestions for Further Study 407
Comparative Palichnology 407
Comments on Cincinnatian Paleoecology and Suggestions for Additional Studies 418
Appendix - Various Classifications of Trace Fossils ... 422

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

Bibliography 426
Text Figures 1-44 446
Plates 1-27 481

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

Acknowledgements

The author wishes to express his gratitude to the many people who have contributed to the successful completion of this work. Especial thanks go to Dr. Kenneth E. Caster under whose direction this manuscript was prepared. He gave generously of his time and was a constant source of inspiration. Thanks are also due Dr. Hans Hofmann for many helpful discussions on Cincinnatian trace fossils and stratigraphy and Dr. Warren Huff for X-ray analysis and advice on the interpretation of X-ray data employed herein.

I am grateful to the following for loan of study materials: Drs. H. B. Whittington and B. H. Kummel, Museum of Comparative Zoology, Harvard University; Dr. E. S. Barghoorn, Harvard Botanical Museum; Drs. G. A. Cooper and R. S. Boardman, United States National Museum; Dr. R. L. Batten, American Museum of Natural History; Dr. C. F. Kilfoyle, New York State Museum; Mr. J. K. Pope and Dr. R. Rinehart, Miami University, Oxford, Ohio; Dr. W. D. I. Rolfe, Hunterian Museum, Glasgow; Dr. Zapfe, Natural History Museum of Vienna; Dr. F. Westphal, Tübingen University; Dr. R. H. Flower, Socorro, New Mexico.

The writer is deeply indebted to Dr. Adolf Seilacher of Tübingen University and Dr. Walter Häntzschel of the Geologische Staatsinstitut, Hamburg. Dr. Seilacher made several trips to Cincinnati to discuss the material under consideration and was most helpful in answering numerous questions.

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

Dr. Häntzschel repeatedly provided information on obscure European forms and placed his then unpublished manuscript of Fossilium Catalogus (1965) at the writer's disposal.

I would also like to thank Dr. Roland Goldring of Reading University, Reading, England, and Dr. Scott Simpson of Essex University, Essex England, for helpful correspondence, and Mrs. Elizabeth Dalvé, who so ably draughted many of the illustrations in this text. Heartfelt thanks also go to my wife, Joanne, for the thankless task of typing and proof-reading the entire manuscript more than once.

The cost of the illustrations was supported in part by the Nevin M. Fenneman Fund and necessary travel connected with the study in part from the Walter H. Bucher Fund, both of the University of Cincinnati. The author also wishes to acknowledge the support of the National Science Foundation through two Summer Fellowships for Graduate Teaching Assistants and a Cooperative Graduate Fellowship.

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

Abstract

All previously described "fucoids" (fossil seaweeds) from the North American standard section for the Upper Ordovician are discussed and evaluated. A restudy of type materials reveals that approximately one-fourth of these are inorganic sedimentary markings, while the remainder are trace fossils (tracks, trails, burrows). Extensive treatment is given to the early history of trace fossil studies, generic and suprageneric classification, and preservation of trace fossils. Thirty genera and 44 species of Cincinnatian traces are illustrated and interpreted. These are grouped in the five categories proposed by Seilacher (1953b). New genera proposed include Allocotichnus, the trail of a large arthropod; Fascifodina, a bundled feeding burrow; and Tylichnus, a trail of unknown origin. In addition, a new species of the trilobite burrow Rusophycus is established under the name R. cryptolithi. It represents the first known burrow of a trinucleid. A comparison of the entire Cincinnatian trace fossil community with assemblages from different ages and locations reveals a correlation between the types of trace fossils and the general environmental setting.

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

Introduction

This study has a two-fold purpose; first to discuss all of the "fucoids," or supposed marine algae, reputed to be present in the rocks of the Cincinnatian Series in the vicinity of Cincinnati, Ohio. Aside from being noted for its excellent, well preserved invertebrate fossils, the Cincinnatian contains an abundance of these problematics. Since 1873 some 37 species have been recognized. Most were described by three local amateur paleontologists, Uriah P. James, Samuel A. Miller, and Charles B. Dyer, over a period extending from 1874-1885. A restudy of these forms was undertaken by still another amateur, Joseph F. James (1884, 1885); however, he lacked the type specimens and was forced to work almost entirely from the literature and his own observations. Nevertheless, many of his interpretations appear to have been correct. Fortunately most of the type specimens have been located and were made available for the present study. With a few exceptions Miller and Dyer's (1878) and Miller's (1880) types were found in the Dyer collection at the Museum of Comparative Zoology and the Botanical Museum of Harvard University. While topotype material of some of U. P. James' species is present in the University of Cincinnati collections, the actual James types (if indeed type specimens were designated) are most likely with the James collection (formerly at the Walker Museum, University of Chicago) now at the Chicago Natural

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

History Museum. At the time of writing these specimens were not available. In addition, the type specimens of several species, originally described by James Hall (1847, 1852), from the Lower Paleozoic strata of New York State, and reported by local authors to be present in the Cincinnatian, were obtained from the New York State Museum and the United States National Museum. None of these "fucoids" is now believed to be marine algae. Most of them are trace fossils and the remainder are of physical origin.

The second and most important part of this study deals with the description, illustration, and interpretation of Cincinnatian trace fossils. This includes all named forms, as well as previously undescribed material.

Trace fossils include fossil tracks, trails, coprolites, and burrows as opposed to body fossils which are the actual remains, casts, or molds of organisms. Admittedly there is no rigid separation of tracks and molds, hence tracks are one aspect of body fossils. A trace fossil may be formally defined as: evidence of the activity of an organism in or on the sediment, produced by some voluntary action of that organism. The term trace fossil was proposed by Simpson (1957) and is synonomous, at least in part, with "hieroglyph" (Fuchs, 1895), Lebensspur (Abel, 1912), trace d'activité (Lessertisseur, 1955), vestigiofossil (Moore, 1936), Bioglyph (Vassoevich, 1953), Ichnofossil (German-Spurenfossil-Seilacher, 1953b), and Problematica (Caster, 1938, 1957, and others). The study of such structures

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

may be referred to as ichnology (Buckland, c. 1830), which is subdivided into palichnology, the study of fossil traces and neoichnology, the study of Recent forms. Other terms will be defined as they are encountered in the text.

The material used in this study consists of the type specimens (when obtainable) of all named forms, supplemented by additional material from the Dyer collection, the collections of the University of Cincinnati and Miami University, as well as specimens collected by the author. Unfortunately, precise locality data for many specimens are lacking, and in most instances it was not possible to recollect the type localities. The following abbreviations for repositories are used herein:

American Museum of Natural History
New York, New York..... AMNH
Harvard University Botanical Museum
Cambridge, Massachusetts..... HBM
Museum of Comparative Zoology
Harvard University..... MCZ
Miami University
Oxford, Ohio..... MU
Hunterian Museum
Glasgow, Scotland..... HM
University of Cincinnati Museum
Cincinnati, Ohio..... UCM

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

New York State Museum

Albany, New York..... NYSM

United States National Museum

Washington, D. C. ..... USNM

The body of the paper contains a rather lengthy introductory section, giving the history of the development of invertebrate palichnology, the nature of the preservation of trace fossils, and the generic and suprageneric classification of trace fossils. This extended treatment is justified, since much of this material has never been synthesized, and several of the more important works are in foreign languages, chiefly German. The generic descriptions of trace fossils (and other forms) have been arranged by employing a combination of the ecological classification proposed by Seilacher (1953a) (see Chapter IIIB herein) and the format used by Häntzschel (1962) in the Treatise on Invertebrate Paleontology, Part W. The trace fossils are separated into Seilacher's five groups: Cubichnia (traces of repose), Domichnia (dwelling traces), Fodinichnia (feeding traces), Pascichnia (grazing traces), and Repichnia (crawling or walking traces). It has also been necessary to consider other kinds of "fucoids." Some of these are of physical origin; some are body fossils originally described as land plants. Unfortunately, there must also be a section on Incertae sedis and unrecognizable genera. The final chapter is devoted to a comparison of the entire

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

spectrum of Cincinnatian trace fossils with suites from different ages in different parts of the world. Throughout this survey there are abundant suggestions for additional studies which are necessary before many of these forms are clearly understood.

Because of the large number of forms discussed (some 59 species), the coverage is uneven and admittedly superficial in spots. This applies especially to the larger "genera,"[1/] such as Rusophycus, Chondrites, and Paleodictyon. Likewise, synonomies for these larger genera are not complete. Only those forms are included which there has been an opportunity to study or of which the descriptions and figures are sufficiently clear and accurate to permit a meaningful diagnosis. The reader is referred to Häntzschel (1962, 1965) for extensive synonomies and a comprehensive bibliography. Since all synonomies are largely subjective, the only ones the author can vouch for are his own.

1/ There is some question as to whether trace fossil names constitute valid zoological taxa. However, throughout this work the taxa are treated as if they were valid, and the rules of zoological nomenclature (rule of priority, etc.) are applied. A further discussion of this problem is given in Chapter III.

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

Difficulty and Value of Trace Fossil Studies

Only recently have trace fossils been recognized as useful tools in the paleoecological analysis of sediments. In large part this has been due to the work of Rudolf Richter, Häntzschel, Seilacher, Schäfer, and the other German workers at the Senckenberg Marine Station. Since the value of trace fossil studies has been discussed at some length in English by Seilacher (1964), it needs only to be dealt with briefly.

As Seilacher (1964a) pointed out, trace fossils have certain advantages over body fossils. First, they are virtually always biocoenosic, i.e., they occur "in place," while body fossils are most often thanatocoenosic. Second, trace fossils are most frequently encountered in rock types (silts and sands), where body fossils are not overly common and often are poorly preserved. Third, whereas diagenesis tends to destroy the detailed structure of body fossils, it appears to enhance the visibility of trace fossils. Processes such as pyritization and minor additions of iron oxides tend to make many trace fossil structures (e.g., U-tubes) stand out more clearly than their Recent counterparts.

It has been successfully demonstrated that trace fossils can add to our knowledge in diverse ways. Broadly speaking, the information gained can be subdivided into two categories: A) Biological-morphology and ethology of the producer and B) Physical-water depth, amount of oxygen, facies analysis, etc.

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

A) Biological- Trace fossils are our sole evidence of numerous soft-bodied organisms. While in most cases they provide little insight into the detailed morphology of the producer, some imprints (e.g., Walcottia rugosa Miller, pl. 13, fig. 5) are sufficiently clear to permit diagnosis. Arthropod tracks are particularly valuable in revealing the nature of the seldom preserved distal portions of the walking legs. For example, the tracks of Asaphoidichnus trifidum Miller (pl. 15, fig. 7) indicate that the originator, which most probably was Isotelus, possessed trifid dactyls. Similar examples are given by Seilacher (1962b).

The only direct evidence of the behavioral patterns (i.e., ethology) of fossil life is furnished by traces. Seilacher (1955), through a study of trilobite morphology and the configuration of the trails, was able to hypothesize on the mechanics of movement in this extinct group. Caster (1938) has done the same for fossil xiphosurans, with the advantage of being able to observe the locomotion of the existing Limulus. Unfortunately, in most instances it is impossible to determine the originator of the well documented patterns (e.g., Phycodes Reinhard Richter, Helminthoida Schafhäutl).

It is fundamentally important to separate trace fossils of invertebrate origin from vertebrate tracks and from imprints of true marine algae (fucoids s. s.). Prior to the work of Nathorst (1881), the great mass of "fucoids" gave an erroneous impression of early plant evolution. Such false evidence has however not been restricted to the

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

vegetable realm. Willard (1935) established the "Order Icthyopoda" for a supposedly very primitive group of Devonian amphibians, based solely on the tracks of his lone genus Paramphibius. Through neoichnological studies Caster (1938) was able to show that Paramphibius represents the trails of a xiphosuran similar to the Recent Limulus. In a more positive vein Seilacher (1956) employed trace fossils to support an argument for accelerated evolution at the beginning of Cambrian time. He found that the small number of Precambrian traces were of relatively simple morphology, whereas the numerous Cambrian forms were much more complex.

B) Physical- It is generally acknowledged that the greatest potential value of fossil traces lies in their contribution to paleoecology. They have been used as indices of various physical factors. Trace fossils can document the rate of sedimentation and the presence of subaqueous erosion in a way that most body fossils can not. R. Goldring (1962) demonstrated that rapid sedimentation in the Devonian Baggy Beds of Great Britain forced a U-tube dweller (Diplocraterion yoyo) to elevate the level of its burrow. In contrast, truncated burrows (see Lockeia and Corophioides herein) are proof of subaqueous erosion. The presence of trace fossils indicates a non-toxic, oxygenated environment. Thus Rudolf Richter (1931), through the discovery of burrows (mainly Chondrites) in some beds of the Devonian Hunsrück Shale of the Rhineland, was able to demonstrate the presence of oxygen in one of the classic black shale sequences. Seilacher (1964b)

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

believes that certain traces can be used as depth indicators. Although his arguments are convincing, the hypothesis requires Recent confirmation.

Trace fossils have been utilized in facies analyses. Seilacher (1964b) reported that the Carboniferous cyclothems of the Ruhr Basin can be further subdivided on the basis of traces. Weimer and Hoyt (1964) were able to plot Pleistocene shorelines in Georgia using the burrows of the arthropod Callianassa; and Caster (1938), using Paramphibius, demonstrated a marine influence in the Devonian of the Penn-York embayment in horizons where before only terrestrial conditions has been postulated.

In spite of the knowledge that can be gained from the investigation of fossil traces, several difficulties are encountered in the course of such studies. Perhaps the greatest problem is the inability at the present time to apply fully the concept of Uniformitarianism to trace fossils. This is due solely to our vast lack of knowledge on the traces of Recent organisms. The sedimentologist is more interested in the physical characters of the sediment and tends to ignore the organisms, while the ecologist or zoologist ignores the sediment and concentrates on the organism. The study of traces lies midway between these two fields; and the prospective worker must be well versed in sedimentology, paleontology, zoology, and ecology. Also, the trace fossil nomenclature has been, and still remains, in a state of confusion; only recently has Häntzschel (1962, 1965) attempted to clarify

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

the situation at the generic level. However, restudies of specimens, as well as the literature, are required before Häntzschel's work can be tested in full. In addition to the lack of a stable classification, the absence of an established descriptive terminology has led to many conflicting terms. It is hopeful to note that recent reattention to traces has partly alleviated some of these problems.

Stratigraphy of the Cincinnatian Section

The strata of the North American standard section for the Upper Ordovician crop out on the axis and along the flanks of the Cincinnati Arch in Ohio, Indiana, and Kentucky. Basically, the section is composed of a more or less monotonous interstratification of lutites, calcisiltites, and calcarenites, whose aggregate thickness is some 270 meters.[2]

---

[2] As used herein lutite refers to rocks having grains less than 1/256 mm in diameter, siltites to rocks having grains whose diameter is between 1/256-1/16 mm, and arenites to rocks the grains of which have a diameter in excess of 1/16 mm.

The individual beds are thin (1 cm-2 meters), and the contacts between various lithologies are normally quite sharp. Most of the beds pinch and swell, and only rarely can they be traced for more than a few hundred feet.

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

The blue-gray Cincinnatian lutites ("shales") lack prominent fissility and probably are better termed mudstones. According to Scotford (1965, p. 219), "the mean size distribution is clay 38 per cent, silt 59 per cent and sand 3 per cent. The mean mineral composition is quartz 24 per cent, calcite 6 per cent, dolomite 9 per cent, illite 47 per cent, mixed-layer illite 4.4 per cent, chlorite 7.7 per cent [and] mixed-layer chlorite 2 per cent." Trace amounts of feldspar, kaolinite, and pyrite are also present. Scotford (1965, p. 219) also pointed out that the lutites "...show a persistent vertical and lateral textural, mineralogical, and chemical uniformity." However, his conclusions were based on a relatively small number of samples. Neither body fossils nor trace fossils are common in the lutites, although brachiopods, trilobites, trilobite tracks, and irregular structureless burrows are sometimes encountered.

The calcisiltites ("siltstones") are normally thin (1-10 cm) and frequently exhibit cross-lamination. They are primarily composed of fine-grained fossil fragments, although according to Weiss and Norman (1960) the insoluble residue content may be as high as 50 per cent. The calcisiltites are well sorted and individual laminae stand out in polished sections. Although well preserved body fossils are not common, trace fossils and inorganic sole markings are abundant.

Cincinnatian calcarenites ("limestones") are composed dominantly of whole fossils or fossil fragments.

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

According to Weiss and Norman (1960) they make up some 70 per cent of the volume of the rock. The fine-grained calcarenites may show cross-laminations; sorting is good. As with the calcisiltites, trace fossils are common, and the upper surface may show oscillation or interference ripple marks. The very coarse-grained calcarenites, commonly used for building stone, are composed almost entirely of fossils and fossil fragments. Sorting and stratification generally are poor, although shells may exhibit a parallel arrangement. Many of these beds are marked by large para-ripples (see Bucher, 1919). Owing to the grain size, any trace fossils found lack detail and are difficult to diagnose. Weiss and Norman (1960) have studied the Cincinnatian calcisiltites and calcarenites in some detail, and Scotford has analyzed the mineralogical composition of Cincinnatian lutites. Recently Weiss et al (1965) have given an excellent analysis of the lithology of the Eden rocks. The reader is referred to the above works for more detailed lithologic descriptions.

Most of the original work on Cincinnatian stratigraphy was done by Orton (1873), Nickles (1902, 1903), Foerste (1903), Cumings (1908), and Fenneman (1916). Because of the apparent difficulties involved in delimiting homogeneous lithologic units, most boundaries were drawn primarily on the basis of fossils. According to the North American Code of Stratigraphic Nomenclature (1961), such designations do not constitute valid rock-stratigraphic

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

units. For this reason several individual workers, as well as the federal and state geological surveys, are currently in the process of re-evaluating the Cincinnatian section.

Sweet and Weiss (1964) have proposed the name Kope Formation for rocks formerly included in the Eden or Latonia "Group" (from Kope Hollow, Levanna, Brown County, Ohio). According to Ford (1965, unpublished Ph.D. dissertation, The Ohio State University) and Dr. Hofmann of Cincinnati (1964, personal communication), the name Kope can be applied to Eden rocks in the Cincinnati area. However, the upper 2.5 meters of the traditional Eden "Formation," as seen at the reference section on Clifton Avenue in Cincinnati, are now included in the redefined Fairview Formation. Neither Ford nor Hofmann recognized the traditional members of the Eden and Maysville "Groups" as being valid rock-stratigraphic units. Likewise, Weiss et al (1965) have rejected the "members" of the Eden.

The Richmond "Group" of southeastern Indiana was restudied by Fox (1962). Employing mainly lithologic criteria, he established the Tanner's Creek Formation to embrace the Arnheim "Formation" of Foerste (1903) and the Waynesville and Liberty "Formations" of Nickles (1903). He did not accept the traditional members of the three formations as rock-stratigraphic units.

While recognizing its contemporary inadequacies, the author has chosen to employ the traditional section as given by Caster, Dalvé, and Pope (1955) (see fig. 1 herein).

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

This course was followed for two reasons. First, many of the specimens included in this study bear labels of the traditional formations and members, and it would be both awkward and confusing to fit them into the new terminology at this time. Second, and more important, the nomenclature of the Cincinnatian is currently in a state of flux. Until the works of Ford, Hofmann, and the various survey groups are published, it would be premature to employ their terminology. However, it is acknowledged that the rock-stratigraphic units used herein are not valid according to the most recent Stratigraphic Code.

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

Chapter I

History of Invertebrate Palichnology

The history of invertebrate palichnology has never been adequately covered. This is especially true of the controversy which raged during the 1880's over the nature of "fucoids." No attempt will be made to present a complete survey, as this would require a volume in itself.

For convenience this account is divided into three parts. It is acknowledged that the divisional boundaries are somewhat arbitrary, because it is difficult to subdivide the continuium of history into artifactual bundles. The first period extends from 1828 to 1881 and covers the "Age of Fucoids;" it was during this period that dozens of genera and hundreds of species of fossils, supposedly marine algae ("fucoids"), were described. The second period, the "Period of Reaction," extends from 1881 to the 1920's. 1881 was the year of the classic work of Alfred Nathorst, who was the first to really question the "fucoid" myth. Although establishment of "fucoid" genera and species continued at a rapid rate, this 40-year interval marks the time when several authors of varying backgrounds began to question the algal nature of these forms. The 1920's saw the birth of invertebrate palichnology. It was during this decade that Rudolf Richter initiated his important studies at the Senckenberg-am-Meer Institute. This final period, spanning the last 45 years, is entitled "The Development of the Ethological and

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

Paleoecological Approaches."

A) The Age of "Fucoids"

Perhaps as Maillard (1887) says, the "Age of Fucoids" began in 1828 when Brogniart erected the genus Fucoides and placed it within the algae. As the years passed, this genus became the receptacle for many species until it rivaled "Orthoceras" in its nomenclatoral complexity. Certainly one of the highpoints of the period was the work of James Hall on the Paleozoic section of New York State. He proposed several new genera (e.g., Palaeophycus, Rusophycus) which later authors (e.g., Billings, Miller) extended to other parts of North America. However, it was in Europe where most of the work was being done by Schimper, Heer, Saporta, Delgado, etc. The results of these 50 years of labor can best be seen in Schimper in Zittel (1889), where the "Algae Incertae sedis" cover 25 pages and are subdivided into 16 groups. The brief discussions of the different genera are accompanied by elaborate reconstructions which illustrate the supposed resemblance to modern seaweeds. It should be pointed out that there were some contemporary authors who attacked the overzealous taxonomy of the "paleobotanists." For example, Dawson (1865) correctly exposed Rusophycus, one of the most sacred of all "fucoids," as a product of the burrowing activity of trilobites; however, his work was largely ignored until years later.

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

Several factors seem to have contributed to the proliferation of "fucoids" in the latter part of the 19th Century, but none more than the spirit of the times which was overwhelmingly descriptive. The broad outlines of the taxonomy of hard-part fossils (mollusca, brachiopods, trilobites) were already described, and the problematic fringe still remained for naming. Both professionals and publishing amateurs (especially of the "Cincinnati school") zealously engaged in wholesale description of these supposed seaweed traces. The orientation of most fossil-students (mainly geologists) was non-biologic (even largely non-evolutionary, e.g., James Hall, Joaquim Barrande, and Louis Agassiz) and non-ecologic. Paleontology was a study of thanatocoenoses, and paleobiology was yet a generation in the future. Moreover, sedimentology and allied aspects of stratigraphic geology were in their infancy. Thus many purely physical phenomena of sedimentary rocks (e.g., rill marks, ripple marks, as well as dendrites), which create "pseudofossils," were misinterpreted, and the most obvious interpretation became first choice--with a binomial name to tie it down! In the later phase of the "fucoid" period, the impact of Darwin's evolutionary works may have served as a stimulus; some of the "fucoids" seemed to be links in the evolutionary chain. By the 1880's there was a great body of "fucoid" species arranged with varying confidence into higher taxa. Only today are we beginning to emerge from the nomenclatoral snarl which resulted from this misdirected energy.

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

However, not all forms, which are recognized today as trace fossils, were once described as "fucoids." One of the most enigmatic of all trace fossils, Climactichnites, from the Upper Cambrian Potsdam Sandstone of New York State and Quebec, was described by Logan in 1860 and recognized as non-algal. Likewise, Owen established Protichnites in 1852 for trilobite tracks occurring in the Potsdam. Other works, such as Miller's (1880) study on "Silurian Ichnolites" of the Cincinnatian, can be mentioned as examples of early trace fossil studies, but these works were in the minority.

B) The Period of Reaction

The first comprehensive attack against "fucoids," and in the final analysis the most divestating, was delivered by the Swedish paleobotanist, A. G. Nathorst, in 1881. His long article, published first in Swedish and then somewhat abridged and translated into French, was accompanied by several plates based on neoichnological studies on the coast of Sweden. He made plaster-of-paris molds of Recent traces which were illustrated in the plates and by line drawings. Therefrom he proceeded systematically to demolish many "fucoids."

Nathorst pointed out that "fucoids" almost always are found on the surface of beds, usually on the under surface of a layer, but never in their interior, where genuine

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

plant remains commonly occur. Certainly for the kinds of "fucoids" with which Nathorst was concerned this observation was valid. He also found it puzzling that "fucoids," in contrast to genuine plant fossils, never show carbonaceous or other normal organic substances.

Two of the most famous and controversial "fucoids" are the traces known as Cruziana (see Seilacher, 1959, fig. 5D) and Rusophycus (pl. 2). Nathorst chose them as a special focus of his reanalysis. He noted that both forms occur as casts on the under surface of a stratum or as depressions originally made in the subjacent bed. These original depressions may be several centimeters deep, and he questioned the mechanism by which such a small object sinking to the bottom could impress itself so deeply in the underlying mud. He said (1881, p. 62) that this "...would necessitate a weight and consistency...which is found in no present-day plants." Nathorst also mentioned that Cruziana is never composed of a substance which differs from the host rock. Likewise, when two cruzianids come in contact, one eradicates the other. If they represented branches of plants, this certainly would not be the case.

Following Nathorst's challenge there shortly appeared several attempts at rebuttal, especially centering on the proper assignment of Cruziana. Lebesconte (1883) in an appendix to "Oeuvres Posthumes de Marie Rouault" attempted to re-establish Cruziana as an alga. The Marquis de Saport (1884) presented a 100-page attempt at free-wheeling

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

rebuttal in his monograph "Les Organismes Problematiques des Anciennes Mers." Lebesconte (1886) renewed his argument, and in the same year Delgado, working with the beautifully preserved cruzianids of the Silurian of Portugal, argued for the plant nature of Cruziana. In 1886 Nathorst answered all three authors in a monograph in which he described how he was able to reproduce many of the "fucoids" by mechanical means. In 1886 and 1887 Saporta published two long articles, mostly concerned with Cruziana and conceding nothing. Thus the years 1881-1887 mark the period of the great controversy.

Since most of the arguments employed by the "algal" proponents (Saporta, Lebesconte, Delgado) are the same, little would be gained by discussing each of the papers in turn; rather the major points of the controversy are synthesized below. While this is concerned mainly with Cruziana, many of the arguments hold for other "fucoids."

1) Nathorst (1881) had claimed that "fucoids" were almost invariably preserved only on the soles of beds. Lebesconte (1883, 1886) remarked that he possessed specimens which gave the appearance of arching up into the host rock. Nathorst replied that such examples could be produced by trilobites burrowing along the sand-mud interface. Likewise, a false impression of post-depositional origin could be given by a trilobite which changed from crawling to swimming.

2) Saporta (1881, 1882, 1884) recognized that most "fucoids" are preserved as casts on the bottom surface of sandstones or siltstones which overlie shales. To explain

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

this unusual mode of preservation, he postulated a special process of fossilization entitled "fossilization in demi-relief." In essence, Saporta's theory holds that a plant falls to the bottom and when covered by overlying sand is driven down into the mud. Decay is initiated on the upper surface of the plant and proceeds downward with the sand filling in behind it. The final portion to decompose is that in contact with the mud; thus only the lower surface of the plant is faithfully preserved.

Nathorst (1886) attacked this hypothesis on several fronts. Why, he reasoned, should decomposition always begin on the upper surface and proceed downward? Is it not more natural to assume that those organs most sensitive to decay and most accessible to bacteria would be the first to undergo putrifaction? As mentioned above, he also questioned the source of the great amount of pressure required to force the object in some cases several centimeters into the underlying mud. Since Cruziana is always convex downward, there must have been a pressure differential. Why was the greatest amount of pressure always exerted on the central portion? A highly damaging point of Nathorst's argument is that if this process works for supposedly soft-bodied plants, why does it not operate for the preservation of soft-bodied animals as well? Why are not similarly originating casts of holothuroids and worms found in the geologic record? Nathorst rejected Saporta's explanation of the process of fossilization of "fucoids" and maintained that "fossilization

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

in demi-relief" occurred only on very rare occasions.

3) Just as Lebesconte claimed to have forms which were found within the interior of the host rock, Saporta asserted that he possessed specimens which occurred on the upper surface as well as on the lower. Nathorst (1886) referred to these as "false cruzianids" and explained them as burrows which were formed slightly below the surface and caused a bulging up of the overlying sand.

4) The presence or absence of organic matter in "fucoids" was long a subject of dispute. Although this argument was more critical in other genera (e.g., Chondrites), it also found its way into the Rusophycus controversy. Whereas Nathorst (1881) maintained that Rusophycus and Cruziana contain not the slightest vestige of organic structures or organic material, both Saporta (1884) and Lebesconte (1883, 1886) believed that the subparallel striae on the lobes of Cruziana represented a network of fibrous material of plant origin. Moreover, Lebesconte (1886) claimed to have seen a meshwork of unknown composition and origin lying below the striae. This so impressed him that he altered his opinion and considered Rusophycus and Cruziana to be sponges rather than plants. Nathorst rejected Lebesconte's network and declared that it represented the sagging of the bedding within the Cruziana cast (see Nathorst, 1886, fig. 23).

5) Lebesconte (1883) stated that some bilobed traces gradually converted into unilobed forms. Nathorst

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

(1886, fig. 12) explained that this could be due to a simple lateral tilting of the trilobite's body.

6) Not infrequently cruzianids appear to branch. Whereas the algal adherents believed this to be a case of simple vegetable branching, Nathorst maintained that it was truncation. A study of Delgado's (1910) illustrations of the Portuguese cruzianids confirms Nathorst's explanation.

7) Many of Nathorst's cruzianid examples were from the Cambrian beds of Lugnås, Sweden. Here cruzianids are found throughout the section, while trilobites occur only in the upper part. Lebesconte (1886) was quick to point this out, although Nathorst had offered an explanation in 1881, remarking that trilobites were active throughout the entire section but did not possess hard exoskeletons until they actually appear preserved as fossils. Delgado (1886) went one step farther and argued that trilobites were never found in the beds containing Cruziana but, instead, were found in the immediate adjacent beds. Nathorst (1886) replied that the lithological nature of the Cruziana beds did not provide optimum conditions for trilobite preservation. More recent work certainly upholds Nathorst's view; one of the main values of trace fossils is that they commonly occur where body fossils do not.

8) Saporta (1884) argued that Cruziana is frequently preserved as short, disconnected fragments which appear to represent parts of plants broken up and scattered about by storms. Nathorst (1886) explained that

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

such forms were created by trilobites which settled down, crawled along the bottom for a short distance, and then proceeded to swim, thus losing contact with the substrate.

9) A common "argument" offered by many "fucoid" adherents expresses their skepticism as to how such surface traces could possibly have been preserved. This was one of the major reasons for their reluctance even to consider an animal origin for the many "fucoids." The problem is still with us today and is considered at greater length below.

Nathorst was fighting the entire corps of "fucoid" adherents pretty much alone. The arguments became extremely heated, and at one point Albert Gaudry (1883) in essence accused Nathorst of not believing in Darwinian evolution, as the latter was unwilling to accept "fucoids" as the documentation of algal life which assuredly must have been present from very early times.

In answering Gaudry, Nathorst (1883) delivered a stinging reply to Saporta (1882), who had accused Nathorst of discarding all of the forms placed by Schimper (1879) in the algae. Nathorst retorted that he too was a strong adherent of the Darwinian theory and believed that there were definite examples of true marine algae in the fossil record. He was attacking only those forms placed by Schimper (1879) in the "Algae Incertae sedis." He could not understand why Saporta did not realize this, and he mused, "On pourrait presque croire que c'est seulement par suite de son ignorance de la langue suédoise" (Nathorst, 1883, p. 453).

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

Despite these concentrated attacks, other workers began to accept Nathorst's arguments.[3] J. F. James (1884, 1885), working independently and in ignorance of Nathorst and certainly much less ambitiously, used many of the same criteria as Nathorst had to criticize Miller and Dyer's (1878) Cincinnatian "fucoids." As Häntzschel (1962) remarked, James' work has long been ignored by more recent authors. Likewise, Maillard (1887) and Dawson (1895) agreed with Nathorst's conclusions on the majority of "fucoids" but still considered the chondritids to be "true fucoids." In 1895 Fuchs published a lengthy treatment of "fucoids" which is second in importance only to Nathorst's works of this period. This was the first major paper in German attacking "fucoids." Fuch's covered several genera and largely echoed Nathorst's beliefs.

---

[3] Later work on Rusophycus and Cruziana have vindicated Nathorst's views on these two forms. Numerous examples (many from the Cincinnatian) show the impressions of the genal spines and pleurae. In Cincinnati alone three specimens are known which show the trilobite in place, thus "caught in the act" of forming the Rusophycus burrow. These discoveries, now not uncommon from many ages and areas, are "proof positive" of the animal origin of this long-debated trace fossil.

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

By 1900 the arguments had died down, and most "fucoids" were generally accepted as being inorganic or traces of animal activity. Understandably few new forms were named during the next two or three decades, and the general disillusionment with respect to "fucoids" militated against their study or discussion.

C) The Development of the Ethological and Paleoecological Approaches

By 1900 the "fucoid" ranks had been badly depleted, and most of the organic forms were recognized as trace fossils. However, the realization that they might be useful, meaningful fossils was slow to gain acceptance; no doubt the nomenclatoral problems discouraged many. Moreover, paleontology was still in the descriptive stage (as it still is in the main today), and these "works" of organisms lent themselves less conveniently to morphology-based analysis. Nathorst had stressed the Uniformitarian principles in his 1881 paper. He demonstrated that Recent traces, both physical and organic, are the key to most "fucoid" forms; but it was not until the 1920's that Rudolf Richter broadened and refined Nathorst's techniques. Actually Nathorst's objective was not so much the interpretation of fossil forms in the light of present phenomena as an endeavor to prove the non-algal nature of "fucoids." Thus there was a slightly greater "destructive" element in his studies than a

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

"constructive" one. In 1925 Richter and his associates established the Forschungsanstalt für Meeresgeologie und Meerespaläontologie der Senckenbergischen Naturforschenden Gesellschaft zu Frankfurt am Main, better known as Senckenberg-am-Meer. The purpose was to exploit the vast Wattenmeer mudflats of the North Sea for what they might teach with respect to geologic phenomena. This was the first careful systematic study of Recent ecology, with the principal emphasis on invertebrate traces. Much of Richter's work is contained in three articles which were issued in sections over a period of years: "Flachseebeobachtungen zur Paläontologie und Geologie" (1922-1926), "Marken und Spuren aus allen Zeiten" (1937-1939), and "Marken und Spuren im Hunsrückschiefer" (1931-1941). The last stands as the single most important contribution of trace fossil study to the general field of paleoecology. The black Lower Devonian Hunsrück Shale of the Rhineland has long been noted for its beautifully preserved echinoderms and other organisms of great delicacy. It had long been assumed that the Hunsrück represented a classic euxinic environment and that all the fossils had been washed in. The bottom of the Hunsrück basin itself was thought to have been barren of life. Through careful studies, Richter (1931, 1935, 1936, 1941) was able to show a well developed suite of trace fossils. The most significant form was Chondrites, whose branching pattern extended down several centimeters into the substrate. This genus had survived longer than any other

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

"fucoid." Richter (1927) was able to demonstrate that it is the mining record of a feeding animal, and, as Simpson (1957) says, its correct interpretation was the final death knell of the "fucoids." The discovery of Chondrites and other trace fossils in the Hunsrück proved the presence of an amount of oxygen sufficient to sustain life at the depositional interface, and Richter was able to show that reduction took place a few centimeters below the surface. This of course means that the pyritized fauna was more biocoenosic than had been realized.

Richter did not confine his labors to general paleoecologic studies, for he contributed much to the understanding of individual genera. His studies (1924, 1926) of "Spreitebau" are the most comprehensive treatment of these forms. Likewise, he was able to demonstrate that the regularly meandering traces in the European Flysch (see fig. 42, no. 64-76) were Weidespuren or browsing traces of benthonic vermiform organisms. Richter's work stimulated others (e.g., Schindewolf, Häntzschel); and Senckenberg-am-Meer became, and still remains, the headquarters for research on fossil and Recent traces. (See, for example, Schäfer's (1962) Aktuo-Paläontologie which is the most detailed study of the traces of a Recent environment to date.)

In 1935 Othenio Abel summarized the scattered literature on trace fossils, together with many astute observations of his own, in his Vorzeitliche Lebensspuren. Until Häntzschel's recent (1962, 1965) work on The Treatise

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

on Invertebrate Paleontology, this was the standard reference for all trace fossil studies.

By 1950 a large number of trace fossils had been redescribed and redefined by a variety of workers. Many authors were utilizing the terms defined by Krejci-Graf (1932) (see Appendix 1), and thus there was introduced a measure of stability and universality. However, the study of trace fossils was still considered largely as an avocational pursuit. There was too little in the way of a unifying force, and the nomenclatoral problem was a pressing one. In the last 15 years two workers, Walter Häntzschel and Adolf Seilacher, have made very great contributions to unity and nomenclature. The former has almost singlehandedly put the nomenclature in a workable condition at the generic level in his publication in Part W, Miscellanea, of the Treatise on Invertebrate Paleontology. Even more significant is his volume of Fossilium Catalogus (1965) which attempts complete indices of each ichnogenus and contains the most comprehensive bibliography to date.

Through numerous publications Seilacher has contributed greatly to the interpretation of trace fossils and has demonstrated their broad geologic value. His works have established a pattern for future analyses. In 1953 he initiated his Studien zur Palichnologie and proposed an ecological classification for trace fossils which has found acceptance among many workers. He subdivided traces into five groups: grazing, resting, dwelling, movement, and

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

feeding.[4] Although suprageneric classifications had been

---

[4] See Chapter III for a more detailed analysis of Seilacher's classification.

---

proposed before, Seilacher's proved to be the most workable. In the same year he published Part II of the same study which contained an analysis of Cubichnia or resting traces. The remainder of the series has yet to be published, but when complete it will presumably consist of a comprehensive analysis of all five ecologic groups. Seilacher (1955) was the first to systematically study trilobite tracks. His work on the redlichiid tracks of the Pakistan Salt Range serves as a strong foundation for others to build on. What may prove to be his greatest contribution has yet to be fully realized. In 1955 he began a study of comparative palichnology through an examination of the trace fossil suites of the Lower Cambrian of the Salt Range, the Lower Paleozoic of Portugal, the Schlif Sandstone of Württemberg, the Lias and Dogger of Württemberg, the Miocene marine Molasse of Europe, and the Cretaceous and Tertiary Alpine Flysch (see fig. 42). The preliminary results of the comparison indicate that broad ecologic correlations are involved. Seilacher found that grazing traces (Pascichnia) dominate the Lower Paleozoic of Portugal and the European Flysch, while resting traces (Cubichnia) are almost totally lacking. The reverse is true for the other three localities,

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

where Cubichnia are numerous and the intricate grazing traces virtually nonexistant. Seilacher concluded that the suite dominated by Cubichnia is indicative of shallow, well lighted water, whereas the Pascichnia suites formed below the euphotic zone. In 1964 Seilacher expanded this study to include several more localities. Although the evidence looks good and results very significant, it would be premature to accept this interpretation without additional studies of both ancient and Recent materials. Seilacher has already placed invertebrate palichnology on a firm foundation by carrying on the work of Rudolf Richter; he has shown that the greatest value of trace fossils is in paleoecological work. The mere correlation of organism with trace fossil is but the first stage in research of considerable scope.

The reader should not be left with the impression that all recent work on trace fossils is of German origin. As mentioned previously, Caster (1938) produced what is still today the most detailed analysis of a single trace fossil genus (Paramphibius Willard). This work was the first modern study on arthropod tracks. Lessertisseur (1955) published a comprehensive monograph covering both invertebrate and vertebrate traces. Because of its scope it is understandably superficial in places but is still the most extensive work in the French language. It is hopeful to note that Ager's (1963) text on paleoecology and Approaches to Paleoecology (ed., Imbrie and Newell, 1964) contain chapters on trace fossils.

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

Thus the study of trace fossils is gradually being recognized as a valid and productive field of scientific inquiry. Yet in a sense it is still in its infancy, for Recent traces have been virtually untouched. Such work as has been done has centered mostly on tidal flats, for we have very little knowledge of the neritic, let alone the bathyl and abyssal zones. However, with the current impetus in oceanographic science, this void is about to be filled. Underwater photography is proving to be a great boon, but what is really required is a method of sampling that will allow for study of non-surface traces. Cores are helpful but provide only a small sample. Several means of impregnating unconcolidated materials have been devised, and these should be utilized in trace fossil studies. The more we learn of Recent traces, the more meaningful becomes our interpretation of fossil forms.

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

Chapter II

Preservation of Trace Fossils

A) Types of Preservation

The most complete dissertation so far on the types of preservation of trace fossils is given by Seilacher (1953a, 1964a, 1964b). As shown by Seilacher (1964a, fig. 1) and illustrated in fig. 4, there are two principal varieties of preservation. The first of these is full relief (Vollform of Seilacher, 1953a), where the entire structure is preserved. These arise when an animal burrows at some depth below the surface through a homogeneous sediment. The burrow may then be packed with fecal material or passively filled by overlying sediment and/or by sediment sifting into the burrow. Generally, forms preserved in this manner do not exhibit delicate morphological details, e.g., scratch marks of appendages. Two such examples of full relief preservation are the U-tube Corophioides (pl. 4, fig. 5,8), and Chondrites (pl. 23, fig. 4).

The second and more important type of preservation is semirelief (Halbform of Seilacher, 1953a; demi-relief of Saporta, 1882). Records of this type are incomplete, only the top half or bottom half being preserved. Semirelief preservation is further subdivided into cleavage relief (Spaltrelief of Seilacher, 1953a) and boundary relief (Grenzrelief of Seilacher, 1953a).

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

In the first, Seilacher recognized the fact that the walking or crawling action is reflected in the bedding planes beneath the surface--on the sedimentary cleavage planes--of thinly laminated sediments. He also noted that these subsurface records progressively deviate from the surface semirelief expression with depth and can be quite misleading if misconstrued as surface records (see fig. 19). Cleavage relief preservation is a common expression of arthropod tracks. The great majority of Cincinnatian trilobite tracks commonly encountered are of the cleavage relief type, and both nomenclatoral and interpretational confusion has resulted from failure to recognize the multiform subsurface expressions of the same track.

Certainly the most common trace expression is the form which Seilacher called boundary relief. By this he refers to the record on a stratum (usually clastic, e.g., silt, fine sand) surface, either superior or inferior, and where the adjacent stratum is of different lithology (e.g., lutite). These two expressions of a trace are essentially like conventional molds (superior surface imprints) and casts (inferior surface fillings) of traces originally made on the surface of the subjacent stratum. When they were preserved on the upper surface of a stratum, Seilacher termed them epireliefs; when on the bottom, hyporeliefs. These are purely descriptive terms. Although the most common expression of epireliefs is concave imprints and of hyporeliefs, convex fillings, either may occur as bas-reliefs or intaglios on the

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

stratum surface. So far the discussion has dealt with exogene boundary reliefs originating on the depositional interface. However, they may also originate as endogene reliefs made below the depositional interface.

Seilacher's usage (1953a, 1964a, 1964b) of the dynamic terms endogene and exogene is somewhat confusing, because the reader forgets that Seilacher is employing endogene only in reference to the track, not the organism. Assume, for example, that a 10 cm bed of mud is overlain by 2 mm of silt. According to Seilacher a trilobite walking on the silt surface would exert enough force to penetrate into the underlying mud. As the foot is withdrawn the thin silt layer immediately fills in the depression, and the resulting trilobite tracks is preserved as a convex hyporelief of endogenous origin. To avoid this ambiguity it seems best to adopt the neoecologic terms epifaunal and infaunal (see Johnson,(1964), Petersen (1913), and Thorson (1957)). Seilacher's original meaning of endogene and exogene are retained, and the two ecologic terms refer to the epistratal or endostratal position of the organism while making the track or trace. Epifaunal applies to an organism which was moving on the surface, infaunal to an animal moving below the surface. In the example of the trilobite track given above, the track is of both endogenous and epifaunal origin. It may appear at first that this is mere duplication of terminology, but if one remembers that one set of terms refers

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

to the organism and the other to the track, the difference becomes apparent.

Although it has not yet been seen in the Cincinnatian rocks, an additional type of preservation, termed pseudoexogene, has been described by Seilacher (1962; 1964b, p. 297) from the Eocene flysch deposits of Spain. Here an endogenous fecal-filled burrow has been exposed by erosion so that the roof of the burrow and fecal filling were removed. When the remainder of the burrow was filled and covered by subsequent deposition, the resultant spoor resembles an exogenous trace.

When the terminology discussed above is combined with Seilacher's ecological classification of trace fossils, it is possible to give an accurate, concise definition of any form.

B) Mechanics of Preservation of Boundary Relief Traces

The mechanics of trace fossil preservation has long troubled students in this field. As mentioned previously, it was just this that prevented many early workers from even considering "fucoids" as representing the work of animals. The problem centers mainly around exogenous imprints; why were they not destroyed in the normal processes of sedimentation? Since endogenous traces are already covered by sediment, they present less of a problem.

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

Both Kuenen (1957, p. 251) and Dzułynski and Sanders (1962, p. 84-85) agree that the condition of the bottom is a most important factor in preserving either sedimentary markings or traces of organic origin. Sand and silt lack the cohesiveness of mud, and the grains move independently, while mud acts as a unit. It is obvious that the mud presented just the right degree of consistency for track-making. Had it been too firm, faint records would be left; if too soft, flowage would have obliterated the finer details. The grain size of the overlying sediment is also critical. It must be coarser than the substrate in order to present a contrast in grain size and a sharp parting plane; yet if it is too coarse, the fine detail of the trace may be lost. This explains why the best preserved trace fossils generally occur as convex hyporeliefs in sediment of silt size which is underlain by a lutite. This is the usual condition in the Cincinnatian rocks where traces are abundant. These are generally accepted facts; the great question is how can delicate imprints escape erosion from the currents and scouring inherent in the transportation of the supradjacent coarser stratum?

Nathorst recognized this problem and attempted to answer it in 1881 and 1886. While discussing Cruziana from the Swedish Amoricain Sandstone, he (1881, p. 35) postulated that these traces were formed "at the bottom of the sea" (deep water?) and later covered by sand. Delgado (1886) countered by pointing out that the Amoricain Sandstone was a

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

shallow water deposit. The currents, indicated by the presence of ripple marks, should have certainly eradicated such traces. In 1886 Nathorst presented a more elaborate hypothesis, suggesting that the traces originated in the intertidal zone. They were formed below water; and then as the tide ebbed, the mud, by exposure to the air, was to a certain degree indurated. The imprints were then covered by both wind-blown sand and by the sand driven forward by the rising tide. While this explanation may hold for certain isolated examples of trace fossils, it is too specialized to serve as a general method of preservation.

Very little interest was exhibited in this problem until the publication of Kuenen and Migliorini's studies of turbidite flows in 1950. Following this, many sedimentologists took an interest in the origin and preservation of the numerous primary sedimentary features and trace fossils found in turbidite sequences. Dzułynski and Sanders (1959, 1962) have devised an ingenious hypothesis to explain preservation of sedimentary markings and trace fossils under such circumstances. Utilizing observations of Gilbert (1914) and Bagnold (1956), they pointed out that in traction carpets[5/]

5/ Dzułynski and Sanders (1962, p. 88) define a traction carpet as the zone "...which is not invaded by turbulent eddies of any size from the overlying turbulent flow."

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

grains expend their energy laterally, and as a result there is no turbulence and hence no scouring (see Dzułinski and Sanders, 1962, fig. 7). Instead, several varieties of tool marks (i.e., markings caused by the gouging of the bottom by shell fragments, etc.) are produced. These markings are almost immediately covered by gravity settling and thus preserved from future scouring. In contrast, when the entire load is carried in suspension and no traction carpet is present, scouring occurs and all surface markings are obliterated. This hypothesis was proposed to explain the method of preservation of surface markings in sequence characterized by graded-bedding. As yet unexplained is how similar markings can be preserved in other environments. The clarity of detail present in Cincinnatian tool marks certainly rivals that found in the finest turbidite sequences.

Seilacher (1962) sidestepped the problem of preservation by maintaining that most arthropod traces, as well as some others, are of endogenous origin. He envisioned the very thin layer of silt mentioned previously in the example of the trilobite track. However, it is difficult to picture such a thin blanket consistently covering wide areas. Likewise, it must be explained how light objects such as crinoid stems could penetrate through this layer to leave such clear imprints and why there is never any mixing of the silt and mud, especially where large tool marks are concerned. Seilacher's hypothesis may hold in rare instances; however, it would seem that there is some other, more common mechanism.

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

Cincinnatian materials were examined in the hope of shedding some light on the problem. First, an attempt was made to determine if the traction carpet and graded-bedding of Dzułkinski and Sanders could be extended to cover non-turbidite sequences. It was thought that graded-bedding on a much smaller scale might be found directly overlying the sole markings. However, thin-sectioning of a dozen or so of the best preserved specimens revealed no trace of graded-bedding. It is now believed that cross-bedding provides the key, for approximately 75 per cent of all specimens bearing traces or inorganic sole markings show cross-lamination. Such currents quite possibly could deposit the silt without scouring the mud surface. This theory has not been tested experimentally, but it is proposed here as a working hypothesis. The shape and angle of the cross-laminations should be studied in detail and experimental stream table investigations might also prove fruitful.

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

Chapter III

Nomenclature of Trace Fossils

A) Classification at the Generic and Specific Level

Until recently the nomenclatural complexity of trace fossils was sufficient to frustrate even the most conscientious worker. Due in large part to the efforts of Häntzschel (1962, 1965), some degree of order has been attained at the generic level. Unraveling the great number of species, of course, will require more time.

The reason for the complexity of the nomenclature is due in large part to two factors: 1) the early history of trace fossils when nearly all forms were thought to be plants--hence a great number of taxa were based on minute morphologic details; and 2) the International Code of Zoological Nomenclature (ICZN) has provided no clear guide lines--thus, different workers have employed different methods and philosophies of taxonomy. These methods have ranged from strict adherence to the rules governing zoological taxa to the opposite extreme of not naming the forms at all.

The most recent Code (1961) is inconsistent with regard to the legality of trace fossils. Article 24b states that the Law of Priority applies "when, before 1931, a name is founded on the work of an animal before one is founded on the animal itself." This implies that trace fossil taxa

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

proposed prior to 1931 are valid, whereas subsequent names are not. This is an unacceptable situation.

It has been accepted by most modern workers in palichnology that a form must be named if it is not to be "lost" in the literature. Such an example is found among Cincinnatian trace fossils. In a penetrating and well thought out discussion, Flower (1955) described what he considered to be tentacle imprints and resting traces of nautiloids. These were described in some detail but never named. Neither Flower's paper nor the described forms appear in the section dealing with trace fossils in the Treatise on Invertebrate Paleontology or in Häntzschel's (1965) volume of Fossilium Catalogus. Although Flower's conclusions are not accepted by the present writer, there is certainly no reason why the paper should be lost to posterity, but such is generally the price of failing to name the described forms.[6/]

6/ This, of course, is not to imply that even the most poorly preserved trace fossils should be named. Only those forms which are well preserved and which have distinct morphology are deserving of names.

Thus, it can be declared at the outset of this discussion that, regardless of the individual worker's taxonomic philosophy, trace fossils must be named to survive. Also eliminated are informal names such as "crawling traces

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

of a gastropod" or "U-tube of an annelid," for such designations are awkward to deal with in faunal lists. Witness that neither James Hall's (1852) nor Charles Walcott's (1918) arthropod tracks appear in the body of the text of Häntzschel's two compilative works. Likewise, it is not sufficient to consider a trace fossil as a junior synonym of the body fossil it represents, if indeed the latter can be ascertained at all. The two should bear separate generic and specific names. For example, the Cincinnatian representatives of Rusophycus pudicum Hall can be considered with certainty to represent the burrow of Flexicalymene meeki (Foerste), since the maker of the trace fossil has been found in situ (pl. 2, fig. 4-5). Technically R. pudicum is regarded as the junior synonym, but, for reasons which will be justified below, the two are retained as separate taxa.

While there is little disagreement today that trace fossils must be named, there is a diversity of opinion on the actual system to be employed.

Rudolf Richter (1941, p. 86; 1948, p. 163) has used "nomenclatura describens," such as Ichnia catenaria and Ichnia diserta, latinized but not proposed as "formal" zoological taxa. Many workers have employed what Seilacher (1953, p. 444) referred to as "semizoological nomenclature." The name appears to conform to zoological nomenclature, but it may have affixed to it such a designation as "new form;" thus, according to Seilacher, losing the protection of the ICZN. The latter procedure has been followed by Schmidtgen

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

(1927), Desio (1940), and Caster (1944). Other similar methods would be placing the name itself or the word "genus" in quotes or using the terms "ichnogenus" and "ichnospecies."

A more elaborate and even more unorthodox method of nomenclature was employed by Faul (1951) for tetrapod traces. His "species" is designated by a capital letter, followed by a numeral indicating the "greatest number of feet clearly impressed." The last numeral indicates the number of toe imprints in each track. For example, a four-toed bipedal track would be A 2.4. If the same author erected another similar species, it would be B 2.4. Such a designation may suffice for one's personal use, but it would be impossible to handle large numbers of such keys, and, as Seilacher (1953a, p. 444) noted, most invertebrate traces would be "A 0.0."

Desio (1950) has gone so far as to suggest giving uninomial names to inorganic sedimentary markings, such as flow casts and ripple marks and binomial names to trace fossils. The main problem here is that this system removes trace fossils from the biologic domain and considers them as sedimentary markings instead of traces of life.

Since it appears that trace fossils are not recognized as formal zoological taxa, and thus not protected by the rules, one may employ any system of nomenclature one desires. However, for the sake of stability it is best to follow some set pattern, and the best possible choice seems to be the rules of zoological nomenclature. There are two

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

reasons for this choice. First, most trace fossil workers are paleontologists and are familiar to varying degrees with the rules. Second, at some future date the ICZN may accept trace fossils as valid zoological taxa or possibly even as valid parataxa. If until then diverse schemes of nomenclature are followed, a massive reshuffling will be necessary. This does not mean that the suggestions of Seilacher (1953a) and Häntzschel (1962) of adding the suffix "ichnus" or "ichnum" to generic names may not be followed. This is an excellent proposal, for it allows the reader to quickly realize that he is dealing with a trace fossil.

What has been discussed above is in essence a practical problem. The deeper and more complex problem is of a philosophical nature and deals with the principals of taxonomy to be employed in the study of trace fossils. At present there are two opposing schools. One holds the more traditional zoologically oriented view that we are dealing with the remains of an organism as shown by its activity, and we are naming the organism as mirrored by the trace rather than the trace itself. The latter has no intrinsic value. Howell (1957) probably provides the best example, for even his title, "New Cretaceous Scoleciform Annelid from Colorado," belies his philosophy. He is discussing an annelid rather than the U-tube. Within the text he places his form (Polyupsilon coloradoense) in proper taxonomic order from phylum through the specific level. However, there is no vestige of the remains of the maker, only its tube.

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

A number of workers would agree with Howell's procedure. There is excellent reason for this; paleontologists have long been aware of the heterogenous nature of their material. Introductory paleontology texts list several different varieties of fossils grading from the finest, such as a mammoth preserved in Pleistocene ice, down to the most poorly preserved mold. We realize that the fossil record is highly incomplete both in regard to numbers and preservation, yet we must work with what is available. Trace fossils are not merely a side branch of fossils, for there is an imperceptible gradation between body fossils and trace fossils. Plate 1, fig. 1 illustrates a specimen of Rusophycus carleyi J. F. James, which combines the features of the mold of a body fossil with the attributes of a trace fossil. It is the ventral mold of a trilobite in that the imprints of the hypostome, genal spines, cephalic doublure, and walking legs are present, yet the lateral lobes of a typical Rusophycus are also visible. By our definition this is a trace fossil because it shows a trace of voluntary movement; however, it could just as easily be considered a ventral mold of an isotelid (a true biocoenosic fossil, in fact). If one recognizes this intergradation between molds and trace fossils, it is perfectly reasonable to follow the zoological philosophy embodied by Howell. It may also be argued that many trace fossils have resulted from the activity of soft-bodied forms of which there is only a minute statistical chance of discovering.

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

In this sense the main value of trace fossils would be their contribution to our knowledge of body fossils; all else would be secondary.

Recently an opposing point of view has arisen, championed mainly by Seilacher but having its roots in the studies of Rudolf Richter. This school considers that the main value of trace fossils is ecological rather than morphologic. Seilacher, Richter, and Häntzschel all point out that it is a mistake to place the major emphasis on the biologic systematics of the originator of the trace. The reason that palichnology is still considered by some today as an avocation rather than a valid scientific pursuit is undoubtedly due at least in part to this overemphasis. Seilacher (1953a, p. 445) remarked, "we name the trace-fossil as an independent manifestation, i.e. not as a proxy for the originator." To Seilacher the trace fossil does possess intrinsic value. If one is to orient trace fossils toward paleoecology, the procedure of taxonomy must change correspondingly. Traditionally genera and species have been based primarily on morphological not ecological interpretation; yet where the ecologic difference between two trace fossils is marked, taxonomic separation is justified to emphasize this difference. For example, Seilacher (1955) separated Rusophycus from Cruziana because the former was interpreted as a trilobite resting trace, the latter a feeding trace. However, it is entirely possible that the two traces were made by the same species of trilobite. A

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

similar example can be given from Cincinnatian trace fossils. While it is probable that both Asaphoidichnus trifidum Miller (pl. 15, fig. 7) and Allocotichnus dyeri n. gen. (pl. 16, fig. 1) are trails of Isotelus, they exhibit two different varieties of movement. A. trifidum (fig. 32-1) is indicative of straight-ahead movement, while in A. dyeri (fig. 33-2) the body axis was oriented to the right of the direction of movement, and only the first four or five pairs of walking legs were used. This difference of behavior is judged sufficient to justify separate generic designations.

One might believe that such a procedure would lead to a vast proliferation of names. In actuality the opposite is true, for modern palichnologists realize that slight changes in behavior and preservation can lead to an apparent difference in morphology. Miller (1880) established Petalichnus multipartitum (pl. 19, fig. 4), Trachomatichnus permultum (pl. 17, fig. 5), and Trachomatichnus cincinnatiensis (pl. 18, fig. 2) for trails of cephalopods. As will be shown, these are trilobite tracks, and there is no evidence to indicate that the trails were made by different species. The difference in morphology between P. multipartitum and T. permultum is due solely to the orientation of the body during movement (see fig. 34). In the former the body was oriented to the right of the axis of movement, while the latter shows a conversion from straight-ahead to oblique movement. T. cincinnatiensis differs because it is preserved as a cleavage relief and the body was parallel to the axis of

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

movement. Since none of these variations are judged to be as significant as those separating A. trifidum from A. dyeri, Miller's three species are combined under P. multipartitum. At the same time care must be taken to avoid excessive "lumping." The results of such action are genera which contain such a wide range of variation as to render them virtually meaningless.

It has been clearly indicated by several studies, e.g., Seilacher (1957), that trace fossils vary more with ecologic setting than with age. There is no reason, a priori, why a Cambrian form should not be combined in the same genus with one from the Tertiary if the two are morphologically identical. In traditional taxonomy such practice is frowned upon; in palichnological studies it is the rule rather than the exception. However, "identity" here, as in all taxonomy, is a matter of "expert opinion."

We thus have two apparently irreconcilable schools, but it is believed that a middle ground exists which combines the best of both views. It recognizes the fact that trace fossils grade imperceptibly into body fossils, and there is a philosophical basis for treating them as valid zoological taxa. However, it also recognizes that an important value of trace fossils lies in what they can contribute to the paleoecologic setting, and the taxonomy must be geared to it. In this paper trace fossils are recognized as the manifestation of organisms (thus contributing to our knowledge of morphology), but they also are recognized as possessing

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

intrinsic value (thus contributing to our knowledge of paleoethology and paleoecology in a way that a body fossil can not). Usually, morphologic criteria are employed in differentiating forms and constitute the underlying philosophical nomenclatural basis. However, in certain cases the activities of the once living creature are taken into consideration and used as a taxobase. The study of trace fossils requires this kind of treatment, for if the paleoecological importance of trace fossils is not acknowledged and accepted as a basis for taxonomic treatment of them, the science will not progress as it should.

B) Suprageneric Classification of Trace Fossils

Although there may be room for argument as to whether trace fossils constitute valid zoological taxa, it is obvious that they do not fit easily into the zoological heirarchy. Some authors, e.g., Rudolf Richter (1926), have erected "families;" however, there was never a pretext that these constituted valid taxa in the zoological sense. Several authors have attempted other means of classification.

Hundt (1931)[7/] separated trace fossils into two

7/ See Appendix 1 for the classifications of Hundt (1931), Krejci-Graf (1932), and Lessertisseur (1955).

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

major groups--those which originated on the surface and those which formed at depth. These two categories were further subdivided according to the geometric pattern of the trace (e.g., stellate, pocket-like, ramified, etc.).

Krejci-Graf (1932) presented a much more elaborate classification based mainly on the various life activities of organisms. He proposed three major headings: traces of existence (coprolites, etc.), traces of repose, and traces of movement. Minor categories were based on life activities such as crawling, swimming, eating, etc. This classification, although more comprehensive, is so elaborate that it tends to be cumbersome.

Seilacher (1953a) proposed a classification similar in essence to Krejci-Graf's but greatly simplified. His scheme is shown diagramatically in fig. 2. By employing a "pie" diagram, he stressed the inseparability of trace fossils from body fossils. The traces are subdivided into five ethological categories, and for each he coined a new latin name with the -ichnia suffix. Seilacher's categories are as follows:

1) Pascichnia (grazing trace=Weidespur of Seilacher, 1953a) Normally two dimensional, these traces are usually tightly coiled or appear as closely packed meanders which are only very rarely branched. In a sense they follow the principals of strip-mining, i.e., systematically covering the greatest area with the least possible expenditure of energy. Rudolf Richter (1928) was the first to conclude that such

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

traces are the feeding trails of vagile benthos. While Seilacher (1962a) maintained that Pascichnia are of infaunal origin, there is no strong evidence to support his conclusion. The present author has observed Recent examples in photographs taken in 12,000' of water on the Mid-Atlantic Ridge by vessels of the Woods Hole Oceanographic Institution. Other Recent forms are illustrated by Schäfer (1962, fig. 155, 171). With one possible exception (Paleodictyon), Pascichnia are not present in the Cincinnatian strata.

2) Fodinichnia (feeding structures=Fressbauten of Seilacher, 1953a) Traces of this variety are the three dimensional analogues of Pascichnia, for they too show maximum space utilization. Whereas Pascichnia exhibit the characteristics of strip-mining, Fodinichnia, which are infaunal, embody the principles of mining at depth. They commonly follow nutrient-rich layers of sediment. They may be branched and illustrate phobotaxis as in Chondrites (pl. 23, fig. 6), bundled as in Phycodes (pl. 13, fig. 4), or possibly U-shaped as in Rhizocorallium (fig. 40-52). Fodinichnia differ because they also serve as a permanent or semi-permanent dwelling structure for the organism producing them. The U-tube of Arenicola marina (see Wells, 1945) is a Recent example, as are the burrows of Heteromastus filiformis illustrated by Schäfer (1962, fig. 215). Fodinichnia are abundant in the Cincinnatian, both in kind and numbers (see fig. 44).

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

3) Repichnia (crawling trace=Kriechspur of Seilacher, 1953a) Repichnia are simple, branched or unbranched trails, burrows, or tunnels of vagile benthos which originate either on the surface or at depth. This category also includes tracks of arthropods. These are simple traces of movement made as the organism moved from one location to another, and thus they lack the characteristic morphologic patterns of Pascichnia. To use Seilacher's comparison, Repichnia are similar to modern highway systems, for they lack numerous sharp curves and instead are linear or gently arcuate. Recent examples are easily seen in a variety of settings--ponds, streams, seafloors, etc. Repichnia are common in the Cincinnatian and consist of arthropod tracks and gently arcuate trails and burrows.

4) Domichnia (dwelling structure=Wohnbauten of Seilacher, 1953a) Domichnia serve as dwelling structures for sessile or hemisessile benthos. Generally they are simple unbranched vertical tubes, U-tubes, or in some cases W-tubes. The inhabitants are filter feeders, scavengers, or predators; and since the structure is utilized as a more or less permanent domicile, the walls may be coated with mucus to prevent collapse. Recent counterparts are the straight, unbranched tubes of phoronids, as well as the U-tubes of numerous polychaetes. Cincinnatian representatives consist primarily of U-tubes.

5) Cubichnia (resting trace=Ruhespur of Seilacher, 1953a) Cubichnia are shallow burrows which mirror the

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

outline of the producer in varying degrees of clarity (pl. 2). They are unbranched but may show some signs of rotary movement and are epifaunal in origin. The purpose of such burrows, e.g., Rusophycus (pl. 2) and Asteriacites (pl. 6, fig. 5), in the fossil record is not clear. Based on experimental observations on Recent materials, Seilacher (1953b) has surmised that these might well have provided temporary shelter and safety for vagile benthos. In contrast Fenton and Fenton (1937) have suggested that some Cubichnia, e.g., Rusophycus, may represent egg depositories, while Caster (1938) proposed that such burrows could be employed as a device to keep the gills moist when the organism was exposed. The latter's hypothesis was based on studies of the Recent Limulus. Recent examples are difficult to recognize unless the producer is "caught in the act," for once the organism has departed of is buried, only a disturbed area remains as evidence. Illustrations of Recent asteroid and xiphosuran Cubichnia are given by Seilacher (1953b, pl. 11, fig. d) and Caster (1938, pl. 12, fig. 2). Cubichnia constitute one of the more common varieties of Cincinnatian traces.

The boundaries between Seilacher's categories are not sharp and therein lies the major weakness of his classification. For example, both Domichnia and Fodinichnia serve as dwellings, and it is difficult in practice to separate linear Repichnia from the burrows of vagile selective feeders or predators. To this extent the classification is somewhat subjective but is still workable, especially when

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

combined with his "classification" of the preservation of trace fossils.

Lessertisseur (1955) utilized a modified form of Seilacher's classification combined with the general configuration of the trace. He subdivided traces into endogenous and exogenous, and each of these in turn is subdivided into traces of locomotion, nutrition, and repose, with the endogenous forms having the additional category of dwelling trace. Each of these is again separated into units based on shape, e.g., spiral, helminthoid, etc.

In the most recent classification, Müller (1962, fig. 3 herein) has greatly expanded Seilacher's scheme. He recognized four major categories: traces of movement, bioreaction (sickness, parasitism, death struggles), resting, and eating. These are divided into the groups employed by Seilacher with the addition of such categories as swimming, flying, gnawing and biting, and running. This is a much more comprehensive classification which follows the general format used by Abel (1935) in treating Vorzeitliche Lebensspuren.

All of the attempts at classification of traces recognize geometry and/or ethology as fundamental criteria. There seems little point in classifying trace fossils merely according to general shape. As Seilacher (1953a) has shown, the same morphology is created in many instances by quite different creatures, and at the same time dissimilar traces can be made by the same organism. An ethological classifi-

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

cation is judged to be the most workable and also the most meaningful. Seilacher's (1953a) scheme best serves current needs. It is possible to fit all but the most unusual traces into his groups, and his units also provide an excellent framework for comparison of suites of ichnofossils as are discussed in Chapter XIII.

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

Chapter IV

History of the Study of Cincinnatian "Fucoids" and Trace Fossils

The first reference to "fucoids" in the Cincinnatian section was made by Orton (1873) in a report on the geology of southern Ohio. He briefly referred to the "plants of the Blue Limestone" and the "dumb-bell fucoid" (Corophioides biclavata (Miller), herein pl. 5, fig. 1), also reporting (1873, p. 268) that "stems and roots apparently referable to the genera Palaeophycus and Buthotrephis of Hall are common." At the same time Orton described one new form which he provisionally named Palaeophycus radiata. It is evident from his short discussion that "fucoids" had been known to local collectors for many years. It is also apparent that Hall's work (1847, 1852) on the "fucoids" of New York State was regarded as the general reference on North American forms. Nearly all workers on Cincinnatian material refer to this study at one time or another.

In 1874 Leo Lesquereux, who is better known for his work on the Pennsylvanian coal flora of Ohio, made what he thought was the momentous discovery of the oldest remains of land plants in North America. From a section six miles east of Lebanon, Ohio, he described two specimens which he believed represented small stems or branches of Sigillaria. Such a find could not long escape notice or further study; and in the same year Newberry (1874, p. 111) cast doubt on

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

Lesquereux's interpretation, reasoning that if these were indeed land plants, they would show "...more distinctness and regularity of surface markings, some coating of carbonaceous matter and some traces of organic structure." He also reminded Lesquereux that the Cincinnati area, during Silurian (Ordovician) time, was so far from land that it would be difficult to explain the presence of land plants even by floating. Lesquereux was apparently not convinced, for in 1878 he formally erected three new species of Cincinnatian "land plants" based on the discovery of new material. These were sent to Dana, Eaton, and Verrill and he reported that they concurred with his opinion. The only subsequent reference to these forms in the local literature was by Miller (1889) and J. F. James (1891), who both questioned Lesquereux's interpretation.

The description of Cincinnatian "fucoids" began in earnest in 1878. In a three year period (1878-1881), U. P. James, a Cincinnati bookdealer and printer, described seven species in his own short-lived journal, The Paleontologist. Most of these species were referred to Hall's Clinton genera and none were figured. Also in 1878 the most extensive work on local "fucoids" was published by Miller and Dyer, who, in two papers, proposed 15 new species distributed among eight new genera. In reading these papers, one gets the idea that the work was mostly Miller's and that Dyer's contribution was to supply the specimens. In contrast to the work of U. P. James, most of the forms described by

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

Miller and Dyer were accompanied by excellent lithographic reproductions.

It is ironic that Miller, who adhered so strongly to the "fucoid" notion, was the first to describe tracks as such from the local rocks. In 1880 he created four new genera and seven new track species. Because of associated body fossils, most of the forms were assigned to cephalopods and the remainder to trilobites.

Up to this point no one had questioned the vegetable nature of the many "fucoid" forms described, and the Cincinnatian strata had become second only to the New York State section in the number of North American species. In 1884 and 1885 J. F. James, another Cincinnati amateur and the son of U. P. James, attacked all of Miller and Dyer's forms as well as those of his father. He made no mention of Miller's paper on the tracks and trails. James concluded that all Cincinnatian "fucoids" were either inorganic sedimentary markings or tracks, trails, burrows, etc. It is interesting to note that James used the same tools as Nathorst (1881), although he clearly stated that he had no knowledge of Nathorst's work until his own paper was near completion. In fact, James' paper closely resembles Nathorst's, though on a much smaller scale. Whereas Nathorst made extensive observations in intertidal areas, employing plaster-of-paris molds and photographs to support his conclusions, James confined himself to the local ponds and streams. The main deficiency of his work is that all the illustrations are

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

highly schematic. This however is not to detract from the importance or quality of his paper, for he was laboring under most difficult conditions. Although he probably studied some of his father's types, it is apparent that he never saw any of Miller's specimens. As an amateur he was writing in an age when the plant nature of "fucoids" was still widely accepted by professionals. James was to North America what Nathorst and Fuchs were to Europe, although regrettably his work has been commonly overlooked or ignored.

Miller's North American Geology and Paleontology for the Use of Amateurs, Students and Scientists (1889) shows that James' publications had little effect on him, for he still persisted in listing all but two of his forms as "fucoids." However, it is true that in both his 1877 compilation and his work of 1889, he made no effort to arrange the "fucoids" in families. He specifically indicated in the prologue to Plantae in the first work (1877, p. 21) that because of the controversial nature of "fucoids," he was making no attempt at suprageneric classification. It is apparent that there was little love lost between Miller and James, for the latter's writings show only contempt for Miller's work. In rejecting the "fucoid" assignment of Miller's Walcottia, James (1885, p. 162) says, "it is safe to consign the genus with its species to the limbo of the improbable and wipe from the catalogues three more useless names."

James' works of 1884 and 1885 represent the last major publication on Cincinnatian trace fossils. From the

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

period 1891-1897 James undertook an extensive summary of Cincinnatian paleontology, and in the preface to this work he listed all those forms which he believed to represent the activity of annelids, trilobites, etc. Unfortunately the body of the text which he had promised was never completed due to his untimely death. The only other mention of Cincinnatian traces was by Caster (1938), who made a brief reference to some arthropod tracks but gave them no extended treatment, and by Flower (1955), who discussed what he interpreted as tentacle imprints and resting traces of Nautiloids. Häntzschel (1962) included Cincinnatian "fucoid" genera in the Miscellanea volume of the Treatise on Invertebrate Paleontology, but, lacking the type specimens and without a first-hand knowledge of the forms, he could add little except for limited first-hand observations of Seilacher which were made available to him.

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

Trace Fossils and "Fucoids" Reported From The Cincinnatian

The following chart portrays the synoptic history of "fucoids" and trace fossils reported to be present in the local Cincinnatian section. Column "1" represents the interpretation of the original author, column "2" the interpretation of J. F. James (1884, 1885, 1891, 1892), column "3" the interpretation of Häntzschel (1962, 1965), column "4" the interpretation given in the present work. With regard to the taxonomic treatment of individual forms, the first name given is the valid name. Names placed in parentheses represent the assignments of the original author. A key to the symbols employed in the chart is given below.

A - alga

I - inorganic

T - trace fossil

P - Pascichnia

D - Domichnia

R - Repichnia

F - Fodinichnia

C - Cubichnia

? - Incertae sedis

L - land plant

B - body fossil

\- - author did not discuss species

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

Name	1	2	3	4	Comments
Allocotichnus (Asaphoidichnus) dyeri (Miller), 1880	R	R	R	R	n. gen.
Aristophycus ramosum Miller and Dyer, 1878	A	I	I?	?	
Aristophycus ramosum var. germanum Miller and Dyer, 1878 (=A. ramosum)					
Asaphoidichnus trifidum Miller, 1880	R	R	R	R	
Asteriacites (Heliophycus) stelliforme Miller and Dyer, 1878	A	B	C	C	
Blastophycus diadematum Miller and Dyer, 1878	A	T	T	I	
Buthotrephis filciformis U. P. James, 1878	A	I	-	I	?=Chloephycus
Chloephycus plumosum Miller and Dyer, 1878	A	I	I	I	
Chondrites (Buthotrephis) gracilis Hall, 1843	A	B	D/F	F	not present
Chondrites (Buthotrephis) gracilis var. crassa Hall, 1852	A	B	D/F	F	not present
Chondrites (Buthotrephis) ramulosa Miller, 1874	A	T	-	F?	no specimens seen

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

Name	1	2	3	4	Comments
Chondrites (Buthotrephis) succulosa Hall, 1847	A	T	D/F	F	not present
Chondrites, type-A	-	-	-	F	
Chondrites, type-B	-	-	-	F	
Chondrites, type-C	-	-	-	F	
Conostichnus truncatum Ulrich, 1880	A	-	-	-	nomen nudum
Corophioides (Arthraria) biclavata (Miller), 1875	A	I	T	D	
Corophioides cincinnatiensis n. sp.	-	-	-	D	new report
Corophioides cf. luniformis	-	-	-	D	new report
Cyathophycus silurianum J. F. James, 1891	T	-	-	I	?Trichophycus venosum
Cyclophycus laterale Ulrich, 1880	A	-	-	-	nomen nudum
Dactylophycus tridigitatum Miller and Dyer, 1878	A	T/I	T/I	F	
Dactylophycus quadripartitum Miller and Dyer, 1878	A	T/I	T/I	F	probably = D. tridigitatum
Dystactophycus mamillanum Miller and Dyer, 1878	A	B	?	I	
Fascifodina floweri n. gen., n. sp.	-	-	-	F	interpreted by Flower, 1955, as Cephalopod tentacle imprint

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

Name	1	2	3	4	Comments
Fucusopsis (Trichophycus) sulcatum Miller and Dyer, 1878	A	I	T	R	
Lockeia siliquaria U. P. James, 1879	A	B	C	C	
Mastigograptus (Psilophytum) gracillimum Lesquereux, 1878	L	L	-	B	
Ormatichnus moniliformis Miller, 1880	R	I	R	R	one cotype specimen inorganic
Palaeophycus flexuosum U. P. James, 1879	A	I	-	I	
Palaeophycus ornatum Ulrich, 1880	A	-	-	-	nomen nudum
Palaeophycus radiata Orton, 1873	A	T	-	T	?=Phycodes or Dactylophycus
Palaeophycus rugosum Hall, 1847	A	T	T	R	not present
Palaeophycus sculptum Ulrich, 1880	A	-	-	-	nomen nudum
Palaeophycus tubulare Hall, 1847	A	T	T	R	not present
Palaeophycus virgatum Hall 1847	A	B	-	F/D	Cincinnatian forms=Trichophycus venosum

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

Name	1	2	3	4	Comments
Palaeophycus, type-A	-	-	-	R	new report
Palaeophycus, type-B	-	-	-	R	new report
Palaeophycus, type-C	-	-	-	R	new report
Palaeoscia floweri Caster, 1942	B	-	-	T/I	
?Paleodictyon sp. Savi and Meneghini, 1850	A	-	T	I/P	new report
Petalichnus multipartitum Miller, 1880	R	-	R	R	
Phycodes (Licrophycus) flabellum (Miller and Dyer), 1878	A	B	F	F/D	
Protostigma sigillaroides Lesquereux, 1878	L	L	-	?	not seen
Rhabdoglyphus sp. Wassojewitsch, 1951	T	-	T	R	new report
Rusophycus bilobatum (Vanuxum), 1842	A	T	C	C	not present
Rusophycus (Cruziana) carleyi (J. F. James), 1885	T	-	C	C	
Rusophycus cryptolithi n. sp.	-	-	-	C	new report
Rusophycus pudicum Hall, 1852	A	T	C	C	
Rusophycus subangulatum Hall, 1852	A	T	C	C/R	not present

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

Name	1	2	3	4	Comments
Saccophycus intortum U. P. James, 1879	A	T?	?	?	not seen
Skolithos (Scolithus) delicatulus U. P. James, 1881	A	T	-	D	
Skolithos (Scolithus) dispar J. F. James, 1892	I	-	-	I	
Skolithos (Scolithus) tuberosus Miller and Dyer, 1878	T	T	-	F?	
Sphenophyllum primaevum Lesquereux, 1878	L	L	-	?	not seen
Teratichnus confertum Miller, 1880	R	-	R	R	
Trachomatichnus cincinnatiensis Miller, 1880 (=Retalichnus multipartitum)					
Trachomatichnus permultum Miller, 1880 (=Retalichnus multipartum)					
Trachomatichnus numerosum Miller, 1880	R	-	R	R	
Trichophycus lanosum Miller and Dyer, 1878	A	T	T	R	
Trichophycus venosum Miller, 1879	A	I	T	F/D	

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

Name	1	2	3	4	Comments
Tylichnus (Rusophycus) asperum (Miller and Dyer), 1878	A	T	-	R	n. gen.
Walcottia rugosa Miller and Dyer, 1878	A/T	B	?	R	
?Walcottia cookana Miller and Dyer, 1878	T	I/T	?	?	not seen
Walcottia sulcata U. P. James, 1881	-	T	?	?	not seen

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

Chapter V

Cubichnia

Rusophycus Hall, 1852

(pl. 1, fig. 1,5,6; pl. 2, fig. 1-10; pl. 3, fig. 4-6; pl. 4, fig. 3; pl. 10, fig. 3; pl. 15, fig. 1; pl. 26, fig. 9; text fig. 5-6)

1823 (non) Fucoides Brongniart, A., Soc. Nat. Hist. Paris, Mem. 1, p. 308, pl. 19, fig. 2.

1831 (non) Bilobites Rafinesque, C. S., Enumeration and Account of Some Remarkable Natural Objects in the Cabinet of Prof. Rafinesque in Philadelphia, p. 2.

1839 (non) Bilobites d'Orbigny, A., Voyage dans l'Amérique meridional, Atlas, pl. 1.

1842 (non) Cruziana d'Orbigny, A., Voyage dans l'Amérique meridional, vol. 3-4, p. 30.

1842 (in partim) Fucoides, Vanuxem, L., Nat. Hist. New York, Geol. New York, pt. 3, p. 79, fig. 11-1.

1852 (in partim) Rusophycus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 2, p. 23, pl. 9, fig. 1-3; pl. 8, fig. 6a,b.

1864 Rusichnites Dawson, C., Canadian Natur., n.s., vol. 1, p. 367.

1879 Rhysophycus Schimper, W., in Zittel, K., Handbuch der Paläont., 2nd ed., p. 54.

1885 Cruziana, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 153-157, pl. 8, fig. 1.

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

1935 Cruziana, Abel, O., Vorzeitliche Lebensspuren, p. 253-255, fig. 224.

1953 Cruziana, Seilacher, A., Neues Jahrb. Geologie u. Paläont., Abh., Bd. 98, p. 107-115, fig. 4-5.

1955 Rusophycus, Seilacher, A., in Schindewolf, O., and Seilacher, A., Akad. Wiss. Lit. Mainz, Math.-nat. Kl., Abh., no. 10, p. 368, pl. 20, fig. 1,3,4; pl. 19, fig. 1; pl. 16, fig. 2.

1955 (in partim) Cruziana, Seilacher, A., in Schindewolf, O., and Seilacher, A., Akad. Wiss. Lit. Mainz, Math.-nat. Kl., Abh., no. 10, p. 368, pl. 16, fig. 2; pl. 19, fig. 1; pl. 20.

1955 Rhysophycus, Lessertisseur, J., Soc. Géol. de France, Mem., n.s., vol. 74, p. 44-47, fig. 25-27,39; pl. 6, fig. 4.

1959 Rusophycus, Seilacher, A., Die Naturwissenschaften, vol. 12, p. 292-293, fig. 4.

Type Species: Fucoides biloba Vanuxem (1842) from the Silurian (Clinton) of New York State.

Diagnosis: Short bilobate Cubichnia of trilobites. The lobes are commonly covered by anterolaterally directed striae. Imprints of cephalic and/or pygidial doublures, genal spines, and thoracic pleurae may be present.

Discussion: Probably the most famous of all the "fucoids," Rusophycus served as the principal example in the "fucoid-" trace fossil controversy of the 1880's and has been

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

the subject of numerous nomenclatural arguments.

Rusophycus, which is typically preserved as a convex hyporelief in silt or sand-sized material, is a common Paleozoic genus with a widespread geographical representation. Broadly speaking the body consists of two parallel lobes separated by a median furrow. Beyond this it is difficult to generalize, for the genus shows a wide range of morphologic variation. The length varies from 1 cm in the Cambrian R. didyma Salter to over 25 cm in some Cincinnatian forms. In most specimens the width is equal to one-half the length. The height of Rusophycus is independent of width and length; while most forms are only moderately convex (pl. 2, fig. 8), in some specimens (fig. 6I-L) the height is nearly equal to the length. In contrast some forms (pl. 1, fig. 1), which may be as much as 20 cm long, have a height of only 2-3 cm. Although the general outline is elliptical, it may vary considerably. The lobes may part slightly at one end to give a cordate appearance (fig. 6E), or they may be so deeply notched that the resulting outline resembles a "V" (fig. 6D). On rare occasions the lobes may be separate throughout their entire length (fig. 6C). Even in ellipsoid specimens the median furrow can take on various expressions. In most forms it is a simple V-shaped cleft, but occasionally the lobes may part to expose two rows of node-like bodies (pl. 2, fig. 8). A more extreme case is where the lobes are poorly developed and the median area has become highly complex. Specimens of Rusophycus with such well developed median areas

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

are thus far known only from the Upper Cambrian of Poland and the Cincinnatian.

One of the most diagnostic features of Rusophycus are the striae which cover the lobes. As shown in fig. 6B the striae are normally directed anterolaterally, although in some forms, e.g., R. bilobatum Hall (1852, pl. 9, fig. 3), they may be nearly normal to the longitudinal axis.

Striae vary in size from extremely coarse, as in R. bilobatum Hall and R. grenvillensis Dawson, to very fine as in R. didyma Salter. Although Seilacher (1960) generalized that the larger the specimen, the better developed are the striae, Cincinnatian forms do not confirm this statement. Some large forms (pl. 15, fig. 1) may have almost smooth lobes, while much smaller specimens have well developed striae (pl. 4, fig. 2).

There has been considerable disagreement regarding the nomenclatural status of these buckle-like burrows. The problem revolves mainly around the usage of four names: Bilobites Rafinesque (1831), Rusophycus Hall (1852), Crossochorda Schimper (1879), and Cruziana d'Orbigny (1842). D'Orbigny (1839) proposed the name Bilobites for a "fucoid" which was illustrated in the plates of his South American work. By the time the text was published (1842), he realized that this name was apparently preoccupied by Bilobites DeKay (1824), a pelecypod; in its stead he proposed Cruziana. Unaware of d'Orbigny's work, Hall (1852) erected the genus Rusophycus for a form from the Clinton (Silurian) beds of

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

New York State, figured by Vanuxem (1842) under the name Fucoides biloba. At the same time Hall described several new Clinton species. For the next 100 years confusion reigned and Bilobites, Rusophycus, and Cruziana were used interchangeably. To add to the confusion several authors altered (illegally) the spelling of Rusophycus, e.g., Rusichnites Dawson (1864), Rhysophycus Schimper (1879). Sinclair (1951) has summarized the problems surrounding the usage of Bilobites, finding that the name has been employed at various times for a pelecypod, trace fossil, brachiopod, and trilobite. He concluded that Bilobites Rafinesque (1831), for an unrecognizable trilobite, has priority. The reader is referred to Sinclair for a more complete discussion of the Bilobites problem.

Seilacher (1953b) restricted Cruziana to the short bilobate buckle-like imprints, i.e., Rusophycus in the usage of Hall. The longer band-like bilobate forms, such as those described by Delgado (1886), he referred to Crossochorda Schimper (1879). At the same time he placed Isopodichnus Bornemann (1889) in synonomy with Cruziana. Isopodichnus is morphologically quite similar to Cruziana (in the sense of Seilacher, 1953b) but has been employed mainly for Triassic and later forms. In 1955 Seilacher completely reversed himself. He now considered Rusophycus as the short, buckle-imprints and in part restricted the longer bands to Cruziana. He likewise separated Cruziana from Crossochorda. The reason for this sudden shift was his ethological interpretation of

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

the various forms. Rusophycus was thought to represent a resting trace (Cubichnia), while Cruziana was interpreted as a grazing trace (Pascichnia). Crossochorda, which he interpreted as a crawling trace (Repichnia), was considered to be an intermediate stage between Rusophycus and Cruziana. Häntzschel (1962) largely agreed with Seilacher's treatment of 1955, although he separated Isopodichnus from Rusophycus. To further confuse matters, Seilacher (1964) did not employ the generic designation Crossochorda. Forms which had been included under this name in 1955 now came under Cruziana.

It seems best in this case to keep paleoethological interpretation apart from nomenclatural philosophy and base the names strictly on morphology. The following usage will be employed in this work: Rusophycus is restricted to the short bilobate coffee-bean-like imprints of trilobite origin. This includes all forms described by Seilacher (1953b) under the name Cruziana, as well as what Seilacher (1955, fig. 5, no. 7-8) referred to as Cruziana. Cruziana is restricted to the longer bilobate forms also of trilobite origin, such as those described by Delgado (1886). It is obvious that it is difficult to draw a dividing line between these two genera. Forms such as those on pl. 10, fig. 3 illustrate this point. However, the situation is not clarified by establishing an intermediate genus, i.e., Crossochorda, for this only compounds the problem. A complete study of Crossochorda has not been undertaken, but it apparently lies within the limits of Cruziana as defined herein. In this work

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

Isopodichnus is restricted to short Rusophycus-like imprints of non-trilobite origin. Both Seilacher (1960) and Glaessner (1957) are agreed that Isopodichnus is most probably of phyllopod origin.

Interpretation: Since Rusophycus was used as an illustration for the "fucoid-"trace fossil controversy, there is no need to give an extensive treatment of the history of the genus here. For many years it was interpreted as a "fucoid" possessing a wrinkled bilobate stem, and Hall (1852, pl. 9, fig. 1) even illustrated one form with a "stipe" attached. As early as 1864 Dawson challenged the "fucoid" assignment, regarding the genus as a trace fossil representing the burrowing activity of trilobites. His arguments were similar to those used later by Nathorst, but in addition he appointed out the similarity of Rusophycus to the Recent burrows of Limulus. Dawson's writings made little impression, and not until after Nathorst's work of the 1880's was it generally accepted that Rusophycus was the cast of a trilobite burrow.

However, studies of Recent burrows have demonstrated that not all short, bilobate, Rusophycus-like bodies were produced by trilobites. Seilacher (1960) maintained that there are at least three other groups of organisms capable of excavating burrows similar to those of trilobites. Figure 5a shows the shallow burrow of the marine polychaete Aphrodite. Although no fossil representatives are known, Seilacher (1960) has observed Recent examples on the tidal flats at Wilhelmshaven.

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

According to Seilacher (1960) several fossil bilobitids can be assigned to gastropods (e.g., those described by Barrois (1882) from the Upper Cretaceous of the Ardennes). Recent counterparts produced by Bullia have been studied by Abel (1935) and Götzinger and Becker (1932). The actual mechanics of burrow excavation are unknown (see fig. 5b). Seilacher (1960, p. 42) stated that these may be differentiated from trilobite-produced burrows by the orientation of the striae. In gastropod burrows the striae are directed posterolaterally from the midline; in Rusophycus they are directed anterolaterally. Although a generic designation has not been established for short bilobed burrows of supposed gastropod origin, longer band-like forms have been placed in Scolicia Quatrefages (1849) by Seilacher (1955) and Häntzschel (1962).

As mentioned previously, the genus Isopodichnus Bornemann (1889) has been used for bilobate forms of presumed phyllopod origin. Isopodichnus has been applied to many post-Paleozoic specimens, especially those from the Triassic of Germany, but Glaessner (1957, p. 106) has mentioned several possible Paleozoic representatives. Some forms are from marine environments, others from brackish and fresh water settings. Recent examples (fig. 5c) have not been extensively studied. The only mention of such phyllopod activity is by Krejci-Graf (1932, p. 31), who made a brief reference to the bilobed burrows of Artemisia salina observed in brine pools in Romania. According to

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

Seilacher (1960) phyllopod burrows can be distinquished by their extremely small width (± 1 mm).

Several authors, e.g., Dawson (1864), Caster (1938), have mentioned bilobate burrows of Recent Limulus. Caster found that by sprinkling stranded young limuloids with water, they could be induced to burrow vertically (see Caster, 1938, pl. 12, fig. 2). It should be possible to distinquish well developed deep limuloid burrows by their general outline; however, initially the excavation is very reminiscent of Rusophycus.

As illustrated, several organisms can produce Rusophycus-like burrows, and great care must be taken in interpreting them. Unfortunately with a few exceptions, e.g., Limulus, Recent perpetrators have not received extensive study, and more work is required before positive identification of fossil forms can be confidently made. This is especially true in attempting to distinquish between alleged phyllopod and trilobite burrows. The only apparent difference is size, and this is no sure criterion (e.g., see Ormatichnus herein).

Nevertheless many times it is possible to assign such burrows to specific trilobites. Imprints of the cephalic and pygidial doublures (pl. 1, fig. 1), genal spines (pl. 2, fig. 1), and thoracic pleurae (pl. 3, fig. 6) are not uncommon. Moreover, three specimens are known where the trilobite has been found in situ (pl. 2, fig. 4-5; pl. 1, fig. 6). All three forms are Flexicalymene meeki and were

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

collected from the Corryville section at Stonelick Creek, Clermont County, Ohio. Such specimens are important not only because they offer proof of trilobite origin, but also because they provide a guide for anterior-posterior orientation. They confirm that the striae are directed anterolaterally from the midline.

Seilacher (1955) noted that there is never a trace of the excavated sediment. Rusophycus is not found with the raised rims one would expect if the sediment were pushed out to the sides of the burrow. He theorized that the legs dug toward the median line and to the rear (fig. 6B) and that the comb-shaped pre-epipodites might have set up currents which would aid in swirling away excavated material. On the other hand, Caster (1938) noted that the simple up and down digging movement was sufficient to carry away the sediment.

Seilacher (1955, 1959) has discussed two additional variations of burrow excavation. He described one specimen from the Lower Cambrian of Sweden where the striae are directed anterolaterally as well as posterolaterally. Seilacher envisioned a trilobite with a strongly arched back in which the first few pairs of appendages pushed the sediment to the median line and forward. The remaining pairs behaved in the more conventional manner, moving the material posterolaterally to the midline.

Normally the cephalon and genal spines took no active part in the digging process. However, Fenton and Fenton (1937)

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

have described a burrow (fig. 6F-H herein), R. Jenningsi, from the Lower Cambrian of Alberta in which the cephalon played more than a passive role. Both the Fentons (1937) and Seilacher (1955, 1959) believed that the trilobite (most likely an olenellid) used the cephalon as a shovel and scooped the sediment from the anterior portion of the burrow. Three distinct impressions of the cephalon may be seen on the sides of the specimen.

Opinions on the ethological significance of Rusophycus have differed. Seilacher (1953b, 1955, 1959) believed that the majority of specimens represent Cubichnia, where the originator burrowed for concealment. However, he labeled R. jenningsi a Bau, implying that it was something more than a simple Cubichnia. Glaessner (1957) maintained that all Rusophycus, as well as the longer cruzianids, were feeding structures where the movement of the legs set up a "feeding current." Finally, Fenton and Fenton (1937) suggested that Rusophycus might represent an egg depository. While all three explanations are possible, the Cubichnia assignment appears the most logical, for trilobites are known to have had vulnerable ventral surfaces. One defense mechanism developed by many species was that of enrollment, and it is not illogical to assume that Rusophycus represents another. In most cases the trilobite burrowed just deep enough to cover the dorsum with a thin layer of sediment; and, based on observation of Recent arthropods, e.g., the sand crab Emerita, it is probable that the organism

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

could completely conceal itself in a few seconds.

Cincinnatian Representatives

Most of the work on Cincinnatian representatives of Rusophycus was done by J. F. James (1885), who undertook a general survey of all North American species and correctly interpreted them as trilobite burrows. James concluded that two of Hall's (1852) Clinton species, R. bilobatum and R. pudicum, were present locally; and in addition he erected one new species, Cruziana carleyi.[8/] At the same

---

8/ James was of the opinion that Cruziana d'Orbigny had priority over Rusophycus Vanuxem and employed the former name.

---

time he stated that R. subangulatum Hall (1852), which he considered to be the senior synonym of R. clavatum Hall (1852), was not of trilobite origin, representing instead the trail of a gastropod similar to that produced by the Recent Melania. According to James such trails are present in the Cincinnatian, but since there was no accompanying figure, it is difficult to visualize what he had in mind. Observation of the types of R. subangulatum (pl. 3, fig. 3) and R. clavatum (pl. 11, fig. 5) shows that they are almost certainly of arthropod origin. James also dismissed R.

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

asperum Miller and Dyer (1878) as the trail of an annelid. Although it is not clear what this latter form represents, it is certainly not a Rusophycus and is discussed under Tylichnus.

A restudy of Hall's types necessitates some rearrangement of James' nomenclatural assignments. Although the type specimen of R. bilobatum has not been located, topotype material and the original description indicate that this species is not present in the Cincinnatian. R. bilobatum is a large (15 cm long) form with extremely coarse striae which actually are better termed rugae. Here again it is difficult to determine what James envisioned when he discussed Cincinnatian forms of R. bilobatum. He may have been thinking either of large isotelid-produced specimens or perhaps of much smaller non-isotelid forms in which the median furrow extends nearly the entire length of the specimen. Hall had mentioned this latter feature in his original description. In R. bilobatum the median furrow extends the length of the specimen, while in R. pudicum it is confined to the central area.

It is concluded that there are three species of Rusophycus present in the local section. These are R. pudicum Hall (1852), R. carleyi J. F. James (1885), and R. cryptolithi n. sp. Justification for these assignments will be given below.

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

Rusophycus pudicum Hall

(pl. 1, fig. 6; pl. 2, fig. 3-5,7,9-10; pl. 3, fig. 5; pl. 4, fig. 2; pl. 10, fig. 3; pl. 25, fig. 9)

1852 Rusophycus pudicus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 2, p. 24, pl. 8, fig. 6a,b.

1885 ?Cruziana biloba James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 154-157.

1885 ?Cruziana pudica James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 154-157.

Type Locality: Clinton (Silurian) beds of New York State. Type specimens: pl. 2, fig. 7; USNM 41113; latex mold UCM 37581; pl. 3, fig. 5, USNM 41115.

Diagnosis: Medium-sized bilobed Cubichnia of trilobites (probably calymenids). The median furrow is only moderately expanded and the striae may be weak or well defined.

Discussion: Hall figured two specimens of R. pudicum. The first (pl. 2, fig. 7 herein), measuring 3.2 cm by 2.0 cm, is strongly bilobate, and the median furrow runs nearly the entire length of the specimen. Striae are present on the lobes but are only weakly developed. The second specimen (pl. 3, fig. 5 herein) is similar to the first in dimensions (3.9 cm by 1.8 cm) but differs in that the median furrow is less well developed and is confined to the central portion of the specimen. Both specimens are preserved as convex hyporeliefs on a coarse-grained quartz arenite, the bottom

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

of which is covered by a thin micaceous film, apparently indicating that the burrow was excavated in mud.

All Cincinnatian representatives of R. pudicum occur as convex hyporeliefs in sediments ranging from fine silt to coarse sand. The species is relatively common and ranges throughout the section. Although it does not normally occur in association with other trace fossils, it is not unusual to find more than one specimen of R. pudicum on a given slab, and occasionally it may occur in great numbers (pl. 2, fig. 9). Morphologically it is difficult to distinquish Hall's specimens from the majority of those found in the Cincinnatian. Measurement of 33 Cincinnatian specimens reveals that the dimensions (mean length of 3.46 cm, mean width of 1.65 cm) compare favorably with those of Hall's types. Although the lobes vary in their development, normally they are widest anteriorly and taper gently to the rear. This is in contrast to some forms of Rusophycus, e.g., Seilacher (1955, fig. 5, no. 4-5), where the lobes are constant in width or may even taper slightly anteriorly. The median furrow extends the entire length of the lobes and does not show any marked expansion. The striae covering the lobes are normally poorly developed just as they are in the cotypes. In some forms (pl. 4, fig. 2) they appear to be unevenly concentrated over the lobes, thus giving the lobes an almost annulate appearance.

Interpretation: There can be little doubt that the producer of the Cincinnatian R. pudicum was Flexicalymene.

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

The general size and shape of the trilobite conform to the morphology of the burrow, and impressions of the cephalic doublure and thoracic pleurae are sometimes encountered (pl. 25, fig. 9). As mentioned previously, three specimens of R. pudicum have been found with the specimen of Flexicalymene meeki still in place. It is indeed rare when a trace fossil is found in direct association with the organism that produced it, and these are the first confirmed occurrences of a trilobite found with a Rusophycus-Cruziana trace.[9/]

9/ Abel (1935, fig. 224) illustrated a form from the Upper Devonian sandstones of South Africa in which the striae are very faithfully preserved. He believed that removal of the matrix would reveal the producer in situ.

As is true of many Cubichnia, R. pudicum not infrequently exhibits horizontal repetition (i.e., repetition of the burrow in a horizontal plane). In the example seen on pl. 10, fig. 3, the trilobite burrowed, moved forward a short distance, and then burrowed again. Specimens such as this are similar to Cruziana but there is a basic behavioral difference. The surface of the long band-like furrows of Cruziana is always even, demonstrating that the organism was moving horizontally across the substrate. In contrast the specimen of Rusophycus under discussion shows an alternation

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

of vertical and horizontal movement.

R. pudicum, as well as other Cincinnatian representatives of the genus, appear to confirm Seilacher's statement (1955) that tracks are rarely associated with Rusophycus. The reason for this is not clear. Although Seilacher believed that most Rusophycus were of endogenous origin, no such examples have been found in the local section. The lack of tracks is probably due to a variety of factors. Some specimens of Rusophycus may well be of endogenous origin; however, it is also possible that the currents sweeping the bottom were of sufficient velocity to eradicate the tracks, yet were not strong enough to obliterate the burrow. It is not unlikely that some examples of Rusophycus are the burrows of nektonic trilobites, where the organism settled to the bottom, burrowed, and then swam out of the excavation.

It is probable that Hall's cotypes were made by calymenids, for Fisher (1960) lists both Calymene niagarensis Hall and C. clintoni (Vanuxem) as index fossils for the New York Clinton. Presumably European calymenids, e.g., C. blumenbachii Green, would leave similar traces.

Rusophycus carleyi (J. F. James)

(pl. 1, fig. 1; pl. 2, fig. 6,8; pl. 3, fig. 6; pl. 15, fig. 1)

1885 Cruziana carleyi James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 155, pl. 8, fig. 1.

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

Type Locality: "Cincinnatian Group near Bantam, Clermont County, Ohio" (James, 1885, p. 155). Presumed type specimen: pl. 15, fig. 1; UCM 37604.

Diagnosis: Large bilobate Cubichnia of trilobites. In some specimens the lobes part mesially to reveal two longitudinal series of nodes.

Discussion: James (1885, p. 155) proposed R. carleyi for specimens which differ from all other Rusophycus "in being entire at one end and separated into two lobes at the other; and also, and especially, in having seven or more pairs of elevations and depressions arranged in an oval in the center of the longitudinal groove." He interpreted it as an isotelid burrow.

What is most likely the holotype is now in the University of Cincinnati collections.(pl. 15, fig. 1). Although the specimen bears no label, the dimensions are similar to those given by James. He also mentioned a sudden "flaring out" just anterior to the median furrow. This is clearly shown in his figure (James, 1885, pl. 8, fig. 1) and is present on the specimen in question. The presumed holotype measures 13 cm by 7.5 cm and the depth is approximately 3.5 cm. The median furrow is 2.0 cm wide in R. carleyi, and within this area are the small ridges or nodes mentioned by James. Close observation reveals that there are nine such pairs. James neglected to mention one additional feature which differentiates this species from all others--the over-all shape. R. carleyi is ellipsoidal,

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

while most other species have a cordate or slightly lacrimal outline. Normally such an outline would make orientation difficult, but the cast of one of the genal spines eliminates this problem. With the exception of the extreme anterior area, the lobes are remarkably free of striations.

Additional specimens of the same species are even more revealing. One form (pl. 1, fig. 1) from the rich trace fossil locality at Stonelick Creek (Corryville beds) shows the cast of 11 pairs of walking legs, the hypostome, genal spines, and cephalic and pygidial doublures! Were it not for the presence of the poorly developed lateral lobes, this specimen could easily be mistaken for an actual cast, i.e., a body fossil. (Compare this form with Isotelus maximus (Locke) (pl. 1, fig. 5; USNM 33458) from the Richmond beds near Oxford, Ohio, where the actual appendages are present.)

The morphology of the Corryville specimens is quite similar to Rusophycus sp. illustrated by Radwanski and Roniewicz (1963) from the Upper Cambrian of the Holy Cross Mountains of Poland. Although the Polish forms are smaller (3-7 cm long), the lobes are weakly developed, and the series of nodes are present in the median area. Since Isotelus is unknown in the Upper Cambrian of Poland, the producer most likely was a different genus.

Also included in R. carleyi are a few large specimens from unknown localities where the lobes do not part mesially. Plate 3, fig. 6 illustrates one form which has a

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

length of 25 cm. This is the largest Rusophycus ever reported and approaches the upper limits of isotelid dimensions. In contrast to the other members of the species, the lobes bear extremely strong striae. The casts of one of the genal spines and the thoracic pleurae are also preserved.

Interpretation: Because of their large size it is apparent that the Cincinnatian representatives of R. carleyi are the products of the burrowing activity of Isotelus, the only local trilobite large enough to produce such a burrow. The series of nodes seen in the specimens represent casts of the proximal portions of the walking legs, probably the coxae or coxal gnathobasic extensions. It is interesting to note that these impressions on the Stonelick specimen (pl. 1, fig. 1) differ somewhat from the coxae of the Oxford specimen of I. maximus. Both the specimen and Raymond's (1920), fig. 9) reconstruction of it show exceptionally long coxae. The coxae of the Stonelick specimen are much shorter, and in the posterior portion of the specimen, there is a V-shaped joint. Although these impressions are distorted by the movement of the legs, the joint which moved was shorter than the gnathobasic appendages shown by Raymond. Since the Oxford specimen is composed of coarse crystalline calcite (there is no original carapace material remaining), it is entirely possible that a joint could have been masked during replacement.

Those forms bearing the nodes appear to illustrate

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

a type of digging which differs from that found in most Rusophycus (e.g., R. pudicum) where nodes are not present. Excavation of the burrow might have been achieved by a broad sweeping motion of the appendages much like a swimmer doing the breaststroke. This would account for the weak development of the lobes and striae and would also make possible preservation of some of the features of the ventral surface. It is equally possible that the digging movement was similar to that in R. pudicum but that some of the sediment became clogged along the mid-ventral axis.

Rusophycus cryptolithi n. sp.

(pl. 2, fig. 1-2; pl. 3, fig. 4)

Type Locality: The specimen figured on pl. 2, fig. 2; UCM 37587 is designated as the type specimen. The type locality is the Economy beds of Humphrey's Branch of Twelve Mile Creek on Washington Trace Road, 350 meters southeast of the intersection with Twelve Mile Creek Road, Campbell County, Kentucky.

Diagnosis: Small, ovoid, button-like Rusophycus. The striated lobes are subdivided into a coarser outer zone and cordate more finely striated inner zone. Imprints of genal spines are commonly present. This species differs from all others in the genus by having a width which is equal to or slightly greater than the length.

Discussion: To date 15 specimens of the species

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

are known, 11 are from the type locality, three are from the Economy strata of Duck Creek, 1,000 meters southwest of the intersection of Duck Creek Road and Kentucky Route 8, Campbell County, Kentucky. The remaining specimen is from the McMicken beds of West Fork Creek, approximately 30 meters upstream from the ?mollusk trails locality (see p.338). All are preserved as convex hyporeliefs in a 2 cm thick cross-laminated calcisiltite which overlies a thick calcilutite. In contrast to other Cincinnatian Rusophycus, R. cryptolithi shows positive rheotaxic orientation.

These button-like specimens average 17 mm in width and 15 mm in length. A slightly raised rim commonly subscribing an arc of 180° is preserved on some forms. A median furrow is present in all forms but is less well developed than in the other two species. The morphology varies with the depth of the burrow. The deeper forms, such as those seen in pl. 2, fig. 1-2, exhibit the greatest detail. In these two forms the anterior wall of the burrow is slightly undercut, and the genal spines are plainly evident. In contrast shallower "incipient" burrows, such as that one the right in pl. 3, fig. 4, show only the two lobes.

As the specific name implies, R. cryptolithi represents the burrowing activities of Cryptolithus. The ovoid shape, size range, and the imprints of the genal spines all point to this genus. The rocks in which the specimens were found abound in Cryptolithus fragments, while other trilobites are comparatively rare. Only two small specimens of

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

R. pudicum (probably made by Flexicalymene callicephala Green) were found at the first two localities mentioned above.

Traditionally the blind Cryptolithus has been considered a burrower, yet it appears that it was not as successful in excavating resting traces as other trilobites were. The oval burrow would serve only to conceal the cephalic area, for in some of the burrows where the anterior wall is much deeper than the posterior, the thorax and genal spines must certainly have been exposed. This is somewhat analogous to an ostrich burying its head in the sand. Likewise, the undercut anterior wall must have presented some problems when the organism desired to leave the burrow. Perhaps the cordate inner area of the lobes was made as the animal backed out of the burrow, for it is best developed on those forms in which the wall is undercut.

Lockeia U. P. James, 1879

(pl. 1, fig. 7; pl. 2, fig. 10; pl. 3, fig. 1,7; pl. 7, fig. 6; text fig. 27)

1873 (non) Dawsonia Nicholson, A., Monograph of British Graptolitidae, p. 70.

1879 Lockeia James, U. P., The Paleontologist, vol. 1, p. 17.

1885 Dawsonia, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 161-162, pl. 9, fig. 7.

1892 Dawsonia, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 162-163, fig. 7.

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

1953 ?Pelcypodichnus amygdaloides Seilacher, A., Neues Jahrb. Geologie u. Paläont., Abh., Bd. 98, p. 105-107, pl. 10, fig. 1; pl. 12, fig. 1-2.

Type Species: Lockeia siliquaria U. P. James (1879) from the bank of the Ohio River "halfway between high and low water" at Ludlow, Kentucky (most probably Upper Trenton).

Diagnosis: Small oblong bodies pointed at both ends, which resemble the end of an almond projecting above a surface. Preservation as convex hyporelief. Surface of specimens normally smooth, although a longitudinal crest or furrow may be present in some. Vertical sectioning reveals a shaft of disturbed bedding conforming to the measurements of the specimen overlying most forms.

Discussion: U. P. James (1879, p. 17) proposed Lockeia siliquaria for "elongated, convex fossil sea-plants, rounding and tapering to sharp or obtuse points, seed-like in appearance, with or without slight longitudinal depressions, attached to the surface of rocks."

Unfortunately the type locality is now permanently covered by damming of the Ohio River, and recollecting is no longer possible. However, several slabs of topotype material (pl. 1, fig. 7; UCM 37597) are present in the University of Cincinnati collections. Additional material includes a single slab bearing about 15 specimens from the Economy beds of Twelve Mile Creek, Kentucky (pl. 3, fig. 7), and a single

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

slab with three specimens (pl. 2, fig. 10) from the Corryville strata of Stonelick Creek.

As shown by the association with Rusophycus and assorted tool marks (pl. 2, fig. 10), Lockeia is preserved as convex hyporeliefs on calcisiltites. Specimens from the topotype locality show a high "population density--"as many as 215 individuals occur on a surface of 150 square cm! Individuals may occur singly or in groups of three or four, and truncation is not uncommon. There is no preferred orientation, although up to six individuals may be aligned one behind the other, thus presenting a sort of pseudo-preferred orientation. Usually a faint ridge connects the aligned forms, although it is not always present. Plate 1, fig. 7 shows a variation of the above, where several specimens are arranged in an en-echelon pattern.

The individual specimens occur as oblong bodies which are pointed at both ends. Forms from the topotype locality occurring on the same slab show a wide size variation. The length may vary from 2-9 mm, while the height ranges from a fraction of a millimeter up to 4 mm; the width is 1-2 mm. The surface of most specimens is smooth, although some may bear a faint longitudinal ridge or furrow. While the majority of the forms are symmetrical, a few are tilted to one side or are slightly irregular in outline.

The Twelve Mile Creek specimens (pl. 3, fig. 7) are larger than the topotype forms, as they average 1.2 cm in length and 3 mm in width and height. Some of these are

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

irregular in outline, and many appear to have been broken off, possibly by Recent stream erosion. The Stonelick Creek specimens (pl. 2, fig. 10) resemble the topotype material in their regular outline but are somewhat plumper.

Both longitudinal and cross-sections were prepared of specimens from Twelve Mile Creek and the topotype locality. These sections clearly reveal that there is a disturbance of the bedding directly above the markings in the material from the first locality. This disturbed area conforms to the dimensions of the fossil and extends to the top of the bed. It is noteworthy that the contiguous bedding is bent as if something had been forced down through the sediment. One section (pl. 7, fig. 6) shows what appears to be the outline of a rounded object near the base of the bed. That the disturbed bedding overlying the hyporeliefs is arranged in an arcuate pattern is noteworthy.

Sectioning of the topotype material presents a more complex picture. Of the 32 specimens of Lockeia that were studied in this manner, 27 showed no disturbed bedding over the specimen such as was found in those from Twelve Mile Creek. The remaining five did show the disturbance. Where there was no disturbed bedding, it was found that the silt forming the almond-shaped bodies was both darker and more coarse-grained than that of the overlying bed, and the line of contact was exactly flush with the base of the calcisiltite bed. This is best seen in vertical section (pl. 3, fig. 1) but is also apparent from close

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

observation on the surface of the slab itself.

J. F. James (1885, 1892) compared Lockeia to certain forms from the Llandeilo beds (Ordovician) of Scotland which were described by Nicholson (1873) under the name Dawsonia. Since James' comparison rested more on interpretation than on a similarity of morphology, it will be discussed later.

Lockeia closely resembles Pelecypodichnus Seilacher (1953b) from the Braun-Jura Beta beds of Württemberg (see Seilacher, 1953b, pl. 10, fig. 1; pl. 12, fig. 1; plastotype UCM 37688). Seilacher's forms are preserved as convex hyporeliefs and are associated with Asteriacites quinquefolias. Although their length is close to that of the Cincinnatian topotype specimens, their width is consistently greater (4 mm). In this sense they are more like the Corryville specimens. As in the Cincinnatian topotype material, individuals may occur in groups, and truncation is not infrequent. It is not known whether disturbed bedding is found overlying the forms, as apparently Seilacher did not have a sufficient number of specimens to permit sectioning.

Lastly, Lockeia resembles Linck's (1949, pl. 8, fig. 1-2) "Reihenhöcker-Spur" from the Schilf Sandstone (Triassic: Keuper) of Württemberg. The most striking feature of Linck's forms is the degree of alignment found. The longest observed specimen was 26 cm in length and consisted of 14 individuals connected by low ridges. Occasionally one form will protrude out of line to break the symmetry. These too are preserved as convex hyporeliefs and their size

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

range compares favorably with Lockeia.

Interpretation: J. F. James (1885) discarded his father's algal hypothesis and instead compared Lockeia to "reproductive bodies" or "ovarian capsules" of graptolites similar to those described by Nicholson (1866, 1873). Nicholson (1873, p. 139) had characterized Dawsonia as "horny or chitinous capsules...furnished in most cases with a small spine or mucro, and having a marginal filament exactly resembling the solid axis of a graptolite." James admitted that local workers had questioned his interpretation because Lockeia is not associated with graptolites. However, since he erroneously believed that "Buthotrephis" gracilis Hall represented a graptolite and since it occurs with Lockeia, this seemed to him convincing. Although Dawsonia[10/] is a problematicum (Bulman (1955), in his grapto-

---

10/ Dawsonia Nicholson (1873) is preoccupied by Dawsonia Hartt in Dawson (1868), an agnostid trilobite.

---

lite monograph, places it under "unrecognizable genera"), Nicholson's description indicates that it is really quite different from Lockeia. None of the Cincinnatian specimens possess an organic covering, a "mucro," or a "marginal filament." Likewise, there is no evidence to support James' conclusion that we are dealing with "ovarian capsules" of graptolites. As shown elsewhere in this paper, "Buthotrephis" gracilis is not a graptolite but a chondritid burrow. Moreover,

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

James was reasoning from the philosophy that graptolites were hydrozoans and thus would possess large reproductive bodies. There is no evidence that they did. The disturbed bedding overlying the specimens and the truncation of some forms by others indicates that Lockeia is a trace fossil.

Neoichnological studies conducted by Seilacher (1953b) and used by him to explain the origin of Pelecypodichnus likewise provide insight into the origin of Lockeia. Seilacher's interpretation is based on experiments conducted with Tivela ponderosa (Koch), a burrowing marine pelecypod of the Pakistan sand flats. Seilacher (1953b, pl. 12, fig. 3a) shows a vertical section in which the anterior portion of the shell is imbedded in mud, while the bulk of it is encased in the overlying silt bed. His pl. 12, fig. 3b is a plaster cast of the impression left in the mud after the pelecypod and the overlying silt bed have been removed. This cast is morphologically very similar to both Pelecypodichnus and Lockeia. Seilacher classified the former among the Cubichnia, as he believed that the organism burrowed for protection and then extended its siphons to the surface to feed. Although he did not elaborate, he considered Linck's forms as Pelecypodichnus and regarded them both to be Repichnia.

It is entirely possible that Lockeia too was made by burrowing pelecypods. Dalvé (1948) lists nine bivalves as being present in the Fulton strata.[11] Four of these,

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

11/ Even though the type locality of Lockeia is most probably Trenton in age, it is not invalid to include Lower Cincinnatian fossils in a discussion of the probable originators of the topotype burrows. As Weiss et al (1965, p. 17) point out, the Cynthiana and Lower Eden faunas intergrade.

Byssonchia vera (Ulrich), Modiolopsis sp., Pterinea demissa (Conrad), and Pterinea mucronata (Ulrich), are byssate pelecypods and need not be considered here. Of the remaining five, two forms, Cleidophora fabula (Hall) and Ctenodonta obliquata (Hall), measure only a few millimeters in length and thus are too small to have produced the burrow. The other three, Orthodesma nasutum (Conrad), Cleidophorus planulatus (Conrad), and Psiloconcha tenuistriata Ulrich, are larger and have the relatively smooth elongated body indicative of burrowers. Although the local representatives of Orthodesma nasutum (Conrad) have never been described, Foerste (1914, pl. 3, fig. 5A,B) has discussed coeval forms from the Cincinnatian of New York State. One described specimen has a length of 44 cm, while the greatest height is 1.55 cm and the convexity is 4 mm. Foerste (1914, p. 287) mentioned that "the most striking feature of the shell...is the distinct dropping of the cardinal margin anterior to the beak." Cleidophorus planulatus (Conrad) is listed by Bassler (1915) and Shimer and Shrock (1944) as being present

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

in the local strata, but, like O. nasutum, the Cincinnati specimens are undescribed. Shimer and Shrock (1944, p. 377; pl. 146, fig. 17) said that the species is "characterized by prominent umbonal ridge extending from beak to posterior extremity, and by conspicuous flattening of shell hingeward from this ridge." Foerste (1914, p. 302) mentioned that forms from New York State attained a length of 2.0 cm. The greatest height is 9 mm and the convexity 1.6 mm. The third form, Psiloconcha tenuistrata, was established by Ulrich (1893, p. 668; pl. 52, fig. 10) for forms "near the low water mark of the Ohio River at Covington, Kentucky." The specimens are rather small, having a length of about 1.1 cm and a height of 4.5 mm. The distinguishing features are the "narrowly rounded anterior end, and the exceeding fineness of the concentric surface markings" (Ulrich, 1893, p. 668).

While it must be admitted that there is no conclusive proof that Lockeia represents the burrowing activity of clams, the evidence is suggestive. Seilacher has shown that burrowing pelecypods such as Tivela can produce Lockeia-like bodies, and there are three pelecypods present in the Fulton strata which appear, from their shell configuration, to have been burrowers. Moreover, the consistent symmetry of most specimens of Lockeia indicates that they were made by some rigid or semi-rigid body. (Several ostracods are present in the Fulton rocks, but the ornamentation found on most forms demonstrates that they were surface

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

dwellers. Those species with smooth carapaces are far too small to have produced the structure. The only other known burrowing form in the Fulton beds is Lingula, but as seen in Moore, Lalicker, and Fischer (1952, fig. 6-1), the structure of the burrow is different.) Thus it is concluded that Lockeia most likely represents the burrowing activity of pelecypods. Based on the different size of the specimens from the three Cincinnatian localities, it is unlikely that all the forms were made by one species. Seilacher's Pelecypodichnus is probably synonomous with Lockeia, but since conclusive proof is lacking, the two are retained as separate genera. Not enough is known about Linck's forms to make an interpretation meaningful. He thought that they might be casts of imprints of amphibian or fish pectoral appendages. Vertical sectioning should be sufficient to test his theory.

It is unusual that the remains of the maker of Lockeia are not found at the bottom of some of the structures, for such a covering of silt greatly increases the chances of fossilization. However, the fact that Lockeia occurs in small clusters and shows horizontal repetition indicates that the organism probably changed the location of its burrow from time to time. Also, changes in the salinity or in the oxygen content of the water will cause hemi-sessile forms to move to the surface (personal observation made at Pacific Marine Station, Dillon Beach, California, during the summer of 1962). Moreover, the fact that the Fulton pelecypods do not have a well developed pallial sinus indicates that they

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

did not possess long retractile siphons. This means that the posterior end of the shell was probably located at or just below the depositional interface. In times of rapid sedimentation the organism would be forced to elevate its burrow in order to maintain this relationship. The arcuate nature of the disturbed bedding in some of the Twelve Mile Creek specimens does suggest that the animal moved up in the burrow.

Most probably some of the almond-shaped bodies represent casts of the foot, while others are casts of the shell itself. Normally when a pelecypod burrows, the foot is out ahead of the shell, but the longitudinal ridges and depressions found on some specimens lead one to believe that these specimens are casts of the shell. It is also probable that as the foot was retracted, gravity would cause the shell to settle down into the resulting depression.

A more complete analysis of the topotype material is now possible. As mentioned above, 27 of the 32 forms studied do not penetrate up into the silt bed bearing them. The remaining five show clear evidence of extending from the base of the bed to the top. The following sequence of events is hypothesized to explain these facts and is illustrated in fig. 27. First, several pelecypods burrowed through the silt until they encountered the underlying mud[12] (fig. 27A).

12/ Many specimens have trapped lutite fragments along their

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

margins.

At this point the organism withdrew, and the overlying silt filled in the depression. The silt bed was then completely stripped off by current action down to (but not into) the surface of the mud (fig. 27B). This is not as implausible as it may seem at first, for once deposition has taken place, a great deal more energy is required to move mud than is necessary for the erosion of silt (Hjulström, 1939). If there was no increase in current velocity, a given current might be able to move silt yet be incapable of eroding mud. Since the molds of the original burrows were already filled with silt and were below the surface of the mud, they were not obliterated. Following this erosive period, another silt bed, slightly finer grained and lighter in color than the previous one, was deposited over the mud. Finally, a few pelecypods burrowed through this silt and nicked the surface of the mud (fig. 27C). They then withdrew, the overlying silt filled in the depression, and the disturbed bedding remained as evidence of their activity. During diagenesis the silt bed underwent cementation, and the casts of the first group of burrowing pelecypods were cemented to the bottom of the new silt bed. However, there is a difference in the strength of bonding, for J. F. James (1885, p. 162) remarked that many of the Lockeia specimens could be easily removed from the rock, much like grains of wheat.

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

This indicates that the bonding of the original casts to the siltstone was weak. On the other hand, the later casts, which form an integral part of the new siltstone bed, are not so easily removed; here cementation was more perfect.

Asteriacites Schlotheim, 1820

(pl. 1, fig. 2; pl. 3, fig. 2; pl. 6, fig. 5)

1820 Asteriacites Schlotheim, E. F. v., Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier--und Pflanzenreichs der Vorwelt erläutert, p. 324.

1878 Heliophycus Miller, S. A., and Dyer, C. B., Contributions to Palaeontology no. 2 (Cincinnati, Ohio, private publication), p. 2, pl. 3, fig. 3.

1885 Heliophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 163.

1953 Asteriacites, Seilacher, A., Neues Jahrb. Geologie u. Paläont., Abh., Bd. 98, p. 93-105, pl. 7-10.

Type Species: Asteriacites lumbricalis Schlotheim (1820) from Lias of Coburg, Germany. Lectotype, Seilacher (1953b).

Diagnosis: Stellate Cubichnia of starfish which may be preserved as both concave epireliefs and convex hyporeliefs.

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

Vertical repetition is not uncommon and some evidence of the activity of tube feet is normally present.

Discussion: Seilacher (1953b), who has monographed the genus, recognized two species of Asteriacites: A. lumbricalis Schlotheim (1820) and A. quinquefolius Quenstedt (1876). The former is known from several localities, ranging in age from Upper Silurian through the Dogger. When preserved as a convex hyporelief, it consists of a small well defined central disc and five long thin arms which may be striate. In some examples (Seilacher, 1953b, fig. 2-2b) the disc may be poorly defined and the proximal portion of the arms greatly expanded. When A. lumbricalis is found as a concave epirelief, the morphology is far different (Seilacher, 1953b, fig. 2-1b)--the central disc is indistinct and the arms taper gradually. The delicate striae which mark the arms in the convex hyporeliefs are not evident.

A. quinquefolius Quenstedt (1876) is known only from two specimens, both from the Dogger Beta Sandstone near Zürich. One form is preserved as both a concave epirelief and a convex hyporelief, the other only as a concave epirelief. The convex hyporelief differs from A. lumbricalis in being somewhat larger and having a shaggy appearance. Likewise, the central disc is not as well defined. The concave epireliefs have the same stellate outline as the convex hyporelief, but the details are blurred. As Seilacher noted, it is difficult to distinquish the two species solely from the concave epireliefs (compare Seilacher, 1953b,

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

fig. 2-1a,b with pl. 10, fig. 2; pl. 11, fig. 3).

Seilacher has undertaken an extensive study of the literature and has worked out a detailed synonomy, especially for A. lumbricalis. No attempt will be made here to judge his conclusions on this matter.

Interpretation: Asteriacites has most frequently been regarded as a cast of the ventral surface of asteroids. This was the interpretation of Schlotheim (1820), and many workers have since echoed this belief. Although Richter (1927, pl. 1, fig. 3) concluded that Asteriacitid-like forms from the Ordovician of Bohemia were the fillings of stellate burrows, it is not possible to support his interpretation on the basis of his illustration.

The major problem is to determine whether a given form is a trace of body fossil. Seilacher listed several criteria in support of his trace fossil assignment. In the specimens he studied there was never a vestige of organic material and neighboring individuals may intersect. Moreover, the striae marking the arms do not resemble a plate pattern but instead show the imprints made by the tube feet during digging. The most convincing evidence is provided by vertical repetition. Seilacher (1953b, fig. 3; 1964, fig. 3) illustrated a slab from the Lower Triassic of the Tyrol which demonstrates the reaction of eight individuals to rapid sedimentation. As sand washed over the organisms, they struggled to reach the surface, and their upward path may be traced on the cleavage planes (hence the origin of

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

the term vertical repetition). Another type of vertical repetition involves a rotation of the body during digging (Seilacher, 1953b, pl. 7, fig. 2). Such behavior results in several partial imprints.

Aquarium studies conducted by Seilacher employing an asteroid and ophiuroid have been most illuminating. A mud surface was covered with sand and the organisms were allowed to burrow. The results show that ophiuroids or ophiuroid-like forms may leave imprints which closely resemble those of asteroids (see Seilacher, 1953b, fig. 2). Likewise, by moving the distal portion of the arms, an ophiuroid with unbranched arms can leave an impression which could erroneously lead one to select a form with branching arms (e.g., Euryale) as the probable originator of the trace.

Seilacher reserved A. lumbricalis for traces made by ophiuroids or ophiuroid-like stelleroids and A. quinquefolius for traces of asteroids. However, based on the results of his aquarium studies, it is apparent that one must exercise extreme caution in making specific assignments.

He placed Asteriacites within the Cubichnia, basing his conclusion on the known fact that many Recent stelleroids burrow just deep enough to cover the body with a thin layer of sediment. The most obvious explanation for this behavior is that the shallow burrow serves as a temporary place of refuge.

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

Cincinnatian Representatives

Asteriacites stelliforme (Miller and Dyer)

(pl. 1, fig. 1; pl. 3, fig. 2; pl. 6, fig. 5)

1878 Heliophycus stelliforme Miller, S. A., and Dyer, C. B., Contributions to Palaeontology no. 2 (Cincinnati, Ohio, private publication), p. 2, pl. 2, fig. 3.

1885 Heliophycus stelliforme, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 163.

1953 (in partim) Asteriacites lumbricalis, Seilacher, A., Neues Jahrb. Geologie u. Paläont., Abh., Bd. 98, p. 95.

Type Locality: "about the middle of the Cincinnati Group" (probably Fairview?), Cincinnati, Ohio.

Diagnosis: Cubichnia of moderate-sized stelleroids, the radii of which bear fine chevron-shaped striae.

Discussion: Only three specimens are available for study--the type (pl. 3, fig. 3; HBM 3175), a specimen from the Corryville of Stonelick Creek (pl. 1, fig. 2), and a third form from an unknown locality and horizon (pl. 6, fig. 5). All are preserved as convex hyporeliefs in calcisiltites. There is no trace of the associated concave epirelief preservation found in Seilacher's forms. The dimensions of the forms are identical; the length of each arm is 2.0 cm, while

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

the greatest width is 8 mm. The most noteworthy feature is the presence of the "rugosites" on the arms mentioned by Miller and Dyer. In the type specimen (pl. 3, fig. 2) and the Corryville specimen (pl. 1, fig. 2), these striae form a "V," the apex of which is directed proximally. In the other specimen (pl. 6, fig. 5) there is no well developed "V," and instead the striae are nearly normal to the main axis of the arm. Such sculpturing is also present in some of Seilacher's forms and the orientation of the "V" is the same in both cases. The Corryville specimen shows clear evidence of the vertical repeition noted by Seilacher in some of the European forms. The other two specimens have a simple stellate outline.

Although Seilacher (1953b) placed A. stelliforme in synonomy with A. lumbricalis, it is believed that there is sufficient basis for retaining Miller and Dyer's specific designation. A. stelliforme differs from A. lumbricalis in having wider arms and chevron-shaped striae and from A. quinquefolius in having thinner arms and lacking the shaggy appearance.

Interpretation: Miller and Dyer (1878b, p. 2) believed that A. stelliforme was a "...starlike plant without any stem," while J. F. James (1885, p. 163) interpreted the form as the mold of an asteroid, possibly Palaeaster. He explained the "rugosities" on the arms as "caused by arrangement of the plates on the underside of the body, but the surface of the mud not taking the impression perfectly and the

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

plates were not preserved."

Both Seilacher (1953b) and Häntzschel (1962) considered Heliophycus to be the junior synonym of Asteriacites and considered it a trace fossil.

Although sometimes it may be difficult to distinguish Asteriacites from bona fide ventral casts of body fossils, such is not the case here. All three specimens clearly show the activity of the tube feet. The striae are analogous but not directly comparable to the V-shaped striae found on the lobes of Rusophycus. In the latter the digging motion was directed toward the median line and to the rear. It is probable that in A. stelliforme digging was directed away from the median line. If the opposite were true, it is difficult to visualize how the organism could burrow at all, for the sediment would soon become clogged in the proximal region of the arms. The imprints seen on the specimen most likely reflect the final movement of the tube feet as the animal left the burrow.

Further support for the trace fossil assignment of A. stelliforme is offered by the vertical repetition seen in the Corryville specimen. The imprints of only four arms can be sharply distinguished in this form; perhaps the organism had lost one of its arms as the result of an accident. The resulting asymmetry of the body might well provide the explanation for the rotary movement during burrowing.

In conclusion, A. stelliforme is interpreted as

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

the resting trace of an asteroid, possibly Promopalaeaster Schuchert (1914), which is a Maysville and Richmond form and is of the same general size and shape as A. stelliforme. As Seilacher surmised, it is most probable that Asteriacites falls within the Cubichnia and is the stelleroid analogue of Rusophycus.

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

Chapter VI

Domichnia

Introduction to Spreite-bearing U-tubes

One of the more common marine burrows (domiciles) from the Cambrian to Recent has a U-shape in profile. Some show a transverse zone of disturbed sediment (the Spreite) between the limbs of the "U," whereas others do not. The makers of the Spreite-bearing U-tubes here under discussion are probably responsible for most, if not all, of the enigmatic "dumbbell" markings of ancient sediments.

Before undertaking a discussion of U-tubes, it is necessary to define certain terms, for although U-tubes have received a great deal of study, there has been little uniformity of terminology. Most of the terms discussed below are illustrated in fig. 7.

arms - the lateral cylindrical portions or limbs of the "U."

aperture - the openings of the "U" on the depositional interface.

U-plane section - a vertical section which passes through the apertures of the "U" (fig. 7A).

median section - a vertical section taken at

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

right angles to a U-plane section at a point midway between the apertures (fig. 7B-C).

transverse section - a section taken parallel to the bedding (fig. 7D), i.e., normal to the U-plane and median section.

depth - in complete forms, the distance from the depositional interface to the base of the "U." In incomplete forms, where the upper part of the tube is missing, the depth is the distance from the highest point of the "U" (as seen in U-plane section) to the base of the "U."

length - the distance as measured from the outside of one arm to the outside of the other arm.

breadth - a measurement taken across the Spreite normal to the length. In some European forms the breadth increases with depth (see fig. 7D).

Spreite - arcuate relics of U-tube excavation. As seen in U-plane section Spreite appear as a series of arcs connecting the arms of the "U" and generally parallel to the base of the "U."

descending Spreite (=protrusive, Goldring, 1962)- a series of arcs indicating a deepening of the tube. As viewed in a median section (fig. 7B), the breadth of the Spreite may increase with depth and the arcs are convex upward. As viewed in a transverse section (fig. 7D1-3), the arcs have their convex face directed

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

away from the arms of the "U." As seen in U-plane section (fig. 7A), the arcs extend only to the inner margin of the arms.

ascending Spreite (=retrusive, Goldring, 1962) - a series of arcs which indicate an elevation of the bottom of the "U." As viewed in a median section (fig. 7C, dashed lines), the arcs are convex downward. As viewed in a transverse section (fig. 7D-4), the arcs have their convex face directed toward the arms of the "U." As seen in U-plane section, the arcs extend to the outer margin of the arms. Figure 7A,C shows ascending Spreite superimposed over decending Spreite.

free tube - the portion of the arm as measured from the aperture to the first evidence of a Spreite.

Corophioides John Smith, 1893

(pl. 4, fig. 1-6,8; pl. 5, fig. 1-8; pl. 6, fig. 1-4,6; pl. 10, fig. 5; pl. 13, fig. 3; pl. 14, fig. 5; pl. 15, fig. 5; pl. 21, fig. 8; text fig. 7-9)

1874 ?Arthraria Billings, E., Canadian Natur., n.s., vol. 6, p. 467, fig. 2.

1875 Arthraria, Miller, S. A., Cincinnati Quart. Jour. Sci., vol. 2, p. 354, fig. 26.

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

1893 Corophioides Smith, J., Geol. Soc. Glasgow, Trans., vol. 9, p. 289-292, pl. 10.

1916 Arenicoloides Blanckenhorn, M., Ges. z. Beförderg. ges. Naturwiss. Marburg, 1916, Sitz. Ber. p. 21-43.

1921 Arenicoloides, Kolesch, K., Preussen Geol. Landes. Anst., Jb., Bd. 40, Teil III (for 1919), p. 356-366, fig. 8-15.

1924 Corophioides, Blanckenhorn, M., Preussen Geol. Landes. Anst., Jb., Bd. 44 (for 1923), p. 31.

1924 Corophioides, Richter, Rud., Senckenbergiana, Bd. 6, p. 119-165.

1924 Arenicoloides, Sörgel, G., Neues Jahrb. Geologie u. Paläont., Beil-Bd. 44, p. 510-549, fig. 1-7, pl. 19-20.

1926 Corophioides, Richter, Rud., Senckenbergiana, Bd. 8, p. 185-219, pl.3.

1927 Arenicoloides, Andree, K., Paläontol. Zeitschr., Bd. 8, p. 120-128.

1929 Corophioides Öpik, A., Acta Comment. Univers. Tartuensis, A., XV, 2, p. 31-38, fig. 3-4.

1931 Corophioides, Westergård, A. H., Sverige geol. Unders., Ser. C, Arh. och Upps., no. 372 (=Årsbok 25, no. 5), p. 3-9.

1935 Corophioides, Abel, O., Vorzeitliche Lebensspuren, p. 452-456, fig. 378-379.

1940 ?Bifungites Desio, A., Museo. Libico Storia Naturele, vol. 2, p. 78, pl. 8, fig. 3.

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

1955 Corophioides, Seilacher, A., in Schindewolf, O., and Seilacher, A., Akad. Wiss. Lit. Mainz, Math.-nat. Kl., Abh., no. 10, p. 377.

Type Species: Corophioides polyupsilon John Smith (1893) from the Upper Carboniferous sandstones of the Gowkha Quarry near Kilwinning, Scotland.

Diagnosis: Vertical U-tubes with Spreite. The arms of the "U" are parallel or diverge with depth. Spreiten are mainly of the descending variety, although forms with ascending Spreiten have been reported. The walls of the arms are without striations; the apertures of the tube are not flared into funnels.

Discussion: The genus Corophioides was established by John Smith (1893, p. 291) for structures which begin "as a simple U-shaped tube of about 1½ inches wide by the same in height, the animal appears to have enlarged its tube or habitation to accommodate its increasing circumstances till it reached as much as 4 inches wide and five inches high, these being the largest measurements I have taken. Between these extremes they are to be met with all sizes....They resemble a lot of distorted and crushed up U's of different sizes, placed one within the other." Smith's figure of the form (pl. 10, top) indeed shows that he visualized Corophioides to be a series of several complete "U's" placed one inside the other. Smith noted that some of the sandstone beds contain several such forms. Judging from his

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

diagram (Smith, 1893, pl. 10, bottom), they occur in the ?basal sands associated with cyclothems. Through the kindness of Dr. W. D. I. Rolfe of the Hunterian Museum in Glasgow, the type specimen (pl. 4, fig. 6; HM X.59) was made available for study. The host rock is a poorly sorted, coarse-grained micaceous quartz arenite. There is no well defined bedding, although carbonaceous stringers give an incipient stratification. The U-tube, which is vertical throughout its length, has a depth of 8 cm and a length of 6.5-7 cm. The tube is slightly longer at the base than near the top. The breadth is not clearly shown, but the diameter of the arms of the "U" is 1-1.2 cm. The specimen shows that what Smith interpreted as a "U in U" structure is actually a Spreite, where the arcs abut against the arms of the "U." Although the Spreiten are slightly irregular, they are plainly visible. The dark carbonaceous material filling the "U" and incorporated into the Spreite makes the fossil stand out against the lighter gray of the host rock.

Although Corophioides has been reported from the Devonian of Scandinavia (Richter, 1926) and Germany (Dahmer, 1937) and from the Lower Cambrian of Estonia (Öpik, 1929) and Pakistan (Seilacher, 1955), it is best developed in the Triassic Bunter Sandstone of Southern Germany. It occurs in large numbers in the middle and upper members and has also been reported from the Lower Bunter by Schindewolf (1928). Although U-tubes had been noted as early as 1869

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

by Platz, not until several years later were they named Arenicoloides luniformis by Blanckenhorn (1916). Rud. Richter (1924) placed Arenicoloides in synonomy with Corophioides in spite of the fact that he had had no opportunity to study the type specimen and realized that Smith had described a "U in U" structure. Although some authors, e.g., Andree (1927), Bather (1925), Westergård (1931), have reserved opinion because of the uncertainty regarding the morphology of Corophioides polyupsilon, most workers, e.g., Schindewolf (1928), Abel (1935), Häntzschel (1962), have followed Richter. Even Blanckenhorn (1924) admitted that Richter was correct in reducing Arenicoloides to synonomy. As will be explained below, Richter's conclusion is accepted herein.[13]

---

[13] Sörgel (1924), who conducted extensive studies on the Bunter forms, recognized Arenicoloides as valid; however, his conclusion was based on his ethological interpretation and not on morphology.

C. luniformis are found in such large numbers in the Bunter that Blanckenhorn (1916) was able to count 36 individuals in an area of 90 square cm. According to him the tubes occur in a strong, medium-grained, quartz sandstone which has a "siliceous mud cement." C. luniformis has several expression in the Bunter. As described by Blanckenhorn (1916, 1924) and Sörgel (1924), some may occur as shallow,

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

vertical, semi-lunar depression (see Sörgel, 1924, pl. 19, fig. 1); while others appear as dumbbells. There is no preferred orientation and the forms frequently interpenetrate; occasionally three will converge to form a Hühnertrappe-like (chicken track) imprint. The forms are best seen in U-plane section (see Sörgel, 1924, pl. 20, fig. 2-3 and Abel, 1935, fig. 379). The specimens are normal to the bedding plane and appear as gently rounded "U's." There is no increase in length as the tube deepens as there is in C. polyupsilon. Even though the coarse grain size obscures the finer details, the Spreite is plainly visible. Richter (1924, p. 211) described the Spreite as being slightly irregular in a U-plane section, and Sörgel (1924, fig. 2) mentioned that the breadth of the Spreite may widen with depth, as shown herein in fig. 7B. Although no specific mention is made as to whether the Spreite is of the ascending or descending variety, judging from the interpretations of the various workers, the Spreite is descending.[14] There is

---

[14] However, Seilacher tentatively placed his Salt Range forms in C. rosei instead of C. luniformis, because the latter "...offenbar einen abweichenden (retrusive) Bauplan verkörpert" (Seilacher, 1955, p. 377).

---

no mention of scratch marks on the arms or the presence of an apertural funnel. As will be shown below, both these

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

features serve to differentiate Corophioides from other U-tube genera. Measurements on the dimensions of the Bunter forms vary and are in part given in tabular form by Sörgel (1924, p. 545). The length varies from 1-5 cm, the depth from 1-130 mm., and the breadth from 1-5 mm. Large and small individuals can occur on the same slab. Although Sörgel believed that many forms were incomplete and once extended into the overlying muds, he was unable to confirm this by direct observation.

Several other examples of U-tubes are known in the fossil record, and in 1926 Rudolf Richter established two "families." The "Rhizocorallidae" was reserved for forms with a Spreite and the "Arenicolitidae" for genera lacking a Spreite. Three of the better known genera, Diplocraterion Torell (1870), Rhizocorallium Zenker (1836), and Arenicolites Salter (1857), will be briefly compared and contrasted with Corophioides. The problematic dumbbell genera, Arthraria Billings (1874) and Bifungites Desio (1940), will be discussed later.

Diplocraterion was erected by Torell (1870) for forms from the Cambrian sandstones at Lugnås, Sweden. Torell's description was rather vague and the genus was not figured. The one key point he mentioned was that the apertures of the tube were funnel-like. Richter (1926), working solely from the literature, believed that Diplocraterion lacked Spreite and placed it in the "Arenicolitidae."

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

The true nature of the genus was revealed by Westergård (1931), who was able to locate what he believed to be three specimens of Torell's original material. Combining this with additional material from the Swedish section, he was able to give an accurate diagnosis of Diplocraterion. Westergård found that the tubes are vertical and the arms normally parallel, although some may diverge or converge slightly with increasing depth. Tubes of all sizes occur together, and the depth and length are mutually independent. Occasionally the base of the tube is straight instead of U-shaped. The breadth varies from 2-15 mm, the length from 2-7 cm, and the depth from 2-32 cm. Funnels are definitely present as is shown in Westergård (1931, pl. 4-7), albeit Westergård remarked that weathering tends to exaggerate them and most unweathered specimens did not possess funnels. Westergård was also able to clearly illustrate the presence of Spreiten in Diplocraterion, thereby correcting Richter's earlier error.

The most recent work on Diplocraterion is by Goldring (1962), who described D. yoyo as it occurred in the Upper Devonian Baggy Beds of Great Britain. The depth of the tubes ranges from 1-10.5 cm, although most have been truncated by subaqueous erosion. By studying the various levels of the tubes, Goldring was able to work out several stages of erosion. His uneroded forms show a remarkable development of the funnels (see Goldring, 1962, pl. 3,

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

fig 3 and text fig. 2). A transverse section through the funnels reveals "a series of concentric laminae composed of fecal pellets, mudstone and sandstone surrounding each core. The distance across the rings may be 3-8 times the diameter [of the arm]..." (Goldring, 1962, p. 240). Goldring was also able to illustrate the presence of ascending and descending Spreiten in D. yoyo. In one case both varieties of Spreiten were found in the same specimen (Goldring, 1962, p. 240).

In summary, the only major difference between Diplocraterion and Corophioides is the presence of funnels in the former. Although these are not especially well developed in many of the Swedish forms, they were present in two of Torell's three specimens located by Westergård, and they are very well developed in Goldring's material. Although Seilacher (1963) has discounted funnels and placed Corophioides in synonomy with Diplocraterion, it is believed herein that they are of sufficient importance to permit maintaining the two as separate genera.

Rhizocorallium Zenker (1836), originally described from the Muschelkalk (Triassic) of Germany, is a common form and is known from the Cambrian, ?Devonian, Permian, Triassic, Jurassic, Cretaceous, and Tertiary and has been reported from Europe, North America, Asia, and Australia. Rhizocorallium differs from the genera discussed above, as the greater portion of the "U" may be oblique or even parallel to the bedding plane. The burrow is initially vertical but it then undergoes a 90° bend. Rhizocorallium may be quite

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

large; Abel (1935, fig. 375-376) illustrates two forms which have a depth of nearly 12 cm. Moreover, the breadth of the arms may exceed 1 cm. The genus also differs from all other U-tubes in that both the Spreiten and the arms are marked by numerous short striae (see Abel, 1935, fig. 376). According to Goldring (1962) no forms with ascending Spreite are known. The striated arms and the curvature of the "U" suffice to separate Rhizocorallium from all other U-tubes. The reader is referred to Abel (1935) and Häntzschel (1962) for a more complete discussion of the morphology and relationships of Rhizocorallium.

Arenicolites Salter (1857) was first described from the Carboniferous sandstones of Lancashire, England. More recently it has been described from the Upper Jurassic of the Juras (Rieth, 1931), Jurassic of England (Bather, 1925), Ordovician of Thuringia (Zimmermann, 1914), and Lower Cretaceous of Colorado (MacKenzie, 1963). Arenicolites differs from other U-tube genera, because it clearly lacks Spreite and thus is merely a simple U-tube. There have been no reports of striae or apertural funnels. The forms described by Bather had a depth of 20-30 cm and a length of 4-6 cm. It is worthy of note that even though there is no Spreite in Arenicolites, the apertures, when viewed on the bedding plane, may be connected by a bar. This is a feature which is normally restricted to the Spreite-bearing genera. Bather (1925, p. 188) was able to show that this was due to

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

a sagging of the bedding between the arms of the "U" following the death or departure of the inhabitant. He was able to trace the bedding across the entire structure and this interpretation was confirmed by Richter (1926). Bather (1927) attempted to extend this explanation to the Spreite of "Arenicoloides," but in an appendix to the paper he admitted that direct field observations of "Arenicoloides" failed to confirm his hypothesis and that the Spreite of "Arenicoloides" formed an integral part of the "U."

It should be mentioned that Arenicolites may be more common than is supposed. Spreite-bearing U-tubes are usually easy to recognize on bedding plane surface because of their dumbbell shape. Unless sagging had occurred, Arenicolites (as well as Spreitebau with long free tubes--see fig. 7D) would appear only as two circular openings and might well be overlooked. Moreover, the Spreiten tend to form vertical planes of weakness, and thus jointing commonly reveals the U-plane section. This would not be as likely to occur in Arenicolites. Nevertheless, it must be admitted that this realization has not yet led to the discovery of arenicolitid structures in the Cincinnatian section.

Interpretation: Smith (1893) believed that Corophioides was made by an animal similar to the Recent filter-feeding amphipod, Corophium, which is a common member of the infauna of tidal flats in many parts of the world. He maintained that the organism enlarged its burrow to compensate

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

for an increase in body size by breaking "through the outer and under sides of its tube and [reforming] its habitation, in some cases as many as eight times. It is therefore only the last dwelling-place or the largest outer U that is preserved in an entire state..." (Smith, 1893, p. 291). The U-tubes of the Recent Corophium volutator (Pallas) have been studied by Häntzschel (1939, 1955), Seilacher (1953a, 1957), and Schäfer (1962). These amphipods construct a U-shaped burrow in sand or mud which may attain a depth of 4 cm. The arms of the "U" are close together but may diverge slightly with depth. The walls of the "U" are smooth. Häntzschel (1955, fig. 1f) illustrated an occurrence of Corophium U-tubes where the upper portion of the tubes had been eroded away and only the base remained. As he pointed out, this closely resembles Corophioides luniformis, as it frequently occurs in the Bunter as well as in some Cincinnatian specimens (pl. 5, fig. 5). In well aerated sand the animal may construct a single vertical shaft instead of a "U" (compare Seilacher, 1953a, fig. 4, left with fig. 4, right). The aperture of the shaft is marked by a characteristic stellate pattern of markings which are apparently a result of feeding. Originally Häntzschel (1939) described the burrow of C. volutator as a simple "U" lacking Spreite. However, Seilacher (1957, pl. 22, fig. 1-2) was able to show that, although difficult to see, descending Spreiten are definitely present. This observation was confirmed by Schäfer

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

(1962, fig. 178-180). Schäfer remarked that the Spreiten were easiest to see where there is an interbedding of sand and mud. He also pointed out that the Spreiten are not closely packed and that the "U" is not always vertical. His fig. 180 shows one form which is initially vertical but then undergoes several "zig-zags" as the depth of the tube increases. The reason behind the construction of the descending Spreite is not clear. The animals are quite small, and it is doubtful that the sole purpose was to compensate for an increase in body length.

The only other organism known which constructs a Spreitebau is a small sphionid polychaete, Polydora ciliata. The burrows are most commonly made in pelecypod shells, and the Spreite is not destructional but constructional. As shown by Schäfer (1962, fig. 177), the organism first excavates a pocket-shaped burrow (not a U-tube!) (Schäfer, 1962, fig. 177, left). It then proceeds to construct a U-tube while filling in the center of the pocket with agglutinated sand grains. The resulting structure closely resembles a U-tube with descending Spreiten (see Schäfer, 1962, fig. 177, right). As will be shown below, all fossil Spreitebauten are believed to be of the destructional variety.

In marked contrast to Smith's interpretation of Corophioides polyupsilon, Blanckenhorn (1902, 1916)

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

originally regarded the shallow U-shaped depressions of Corophioides luniformis as the tracks of a three-toed dinosaur, probably Cheirotherium, which occurs in the Bunter beds. Later Blanckenhorn (1916) studied U-plane sections and recognized his mistake. As his choice of a generic name indicates, he believed that the genus was the U-tubes of a polychaete similar to that of the Recent lug worm Arenicola marina (Lamarck), which occurs in large numbers on tidal flats. Sörgel (1924) echoed this opinion. However, Richter (1924, 1926) was quick to point out that for the most part Arenicola does not construct a well defined U-tube.[15] As Wells has illustrated, in loose sand

---

15/ The tube of the lug worm has received considerable study; and the reader is referred to Richter (1924), Wells (1945), and Schäfer (1962) for a complete discussion.

Arenicola marina excavates a J-shaped burrow which is strengthened by a coating of mucus. The animal lies with its anterior end at the closed end of the "J" and moves upwards, disturbing the overlying sand. The worm then withdraws into the closed portion of the "J," and gravity causes subsidence of the disturbed sand which the organism then ingests. The sediment is passed through the gut where the nutrients are removed, and the undigested sediment is passed out of the open end of the "J," where it forms long rope-like

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

fecal strings. The resulting structure, which is well illustrated by Schäfer (1962, fig. 174), thus resembles a U-tube with a conical column of disturbed sand lying above the closed end of the "J." As viewed on the depositional interface, the burrow appears as a small circular opening surrounded by fecal strings and a much larger saucer-shaped depression marking the location of the column of disturbed sand. This is probably what led earlier workers to believe that it was a simple U-tube. In hard-packed sand it is necessary for the animal to lengthen the closed portion of the burrow, with the result that the cone-like column of disturbed sand is much smaller (see Schäfer, 1962, fig. 175). In neither of the above-discussed examples is there a Spreite developed. In contrast, when dwelling in highly cohesive mud, Arenicola does construct a Spreite-like structure. Schäfer (1962, fig. 216-217) has shown that the worm forms a U-shaped burrow, then withdraws to the base of the "U" and excavates a new shaft, feeding on some of the removed mud and plastering the remainder in the old shaft. This process may be repeated several times, with the result being one permanent shaft and several bundled feeding shafts. It is interesting to note that this explanation is similar to the one given by Sörgel (1924, fig. 4) as an explanation for the Spreiten of Corophioides luniformis. While this may be a valid explanation for some of the Bunter forms, it was completely rejected by Richter (1924). In most of the Bunter

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

specimens the Spreiten are not asymmetric or crowded against one arm, and there is no mention of multiple openings on the depostional interface. Instead there are only two openings to the burrow, and the Spreiten are parallel to the last-formed base of the "U." In other words, the deepest part of the Spreite (see fig. 7A) lies midway between the arms. Moreover, the Bunter forms occur in a sandstone; and, as shown by Wells (1945) and Schäfer (1962), Arenicola builds J-tubes in sand. It is more likely that Richter (1924, 1926) was correct when he concluded that Corophioides was the Domichnia of a filter-feeding organism and that the descending Spreiten represent movements by the organism to lengthen its burrow to compensate for an increase in body size. The sediment removed from the floor of the burrow was packed on the roof probably with the aid of a mucus cement. This is not offered as a general explanation for all Spreitebauten but applies only to C. polyupsilon, C. luniformis, and the Swedish examples of Diplocraterion. Goldring's study of D. yoyo has shown that some Spreiten are a response to sedimentation or erosion. Moreover, the fact that a major part of the Rhizocorallium structure lies parallel to the bedding suggests that these are feeding structures where the organism has mined a particularly rich area.

Öpik (1929) believed that the irregular Spreiten of C. helmerseni might represent the fillings of a pocket-like burrow (i.e., similar to the burrow of Polydora

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

illustrated by Schäfer (1962, fig. 177, left)) which was filled by sediment following the departure of the inhabitant. More will be said regarding the origin of the Spreite in the discussion of the Cincinnatian forms.

Likewise, it is impossible to assign Corophioides or fossil U-tubes in general to a given group of organisms. As already shown, both amphipods and polychaetes construct Spreiten-like structures, and simple U-tubes lacking Spreiten are formed by the echiuroid Urechis caupo, freshwater insect larvae, several polychaetes, and the hemichordate Balanoglossus. With the possible exception of Balanoglossus, the animals are filter-feeders which remain stationary in their burrows. By movement of the parapodia and/or other mechanisms, they set up currents which draw organic detritus into the burrow. (See Barnes, 1963, p. 184-186, for a discussion of the feeding habits of Chaetopterus and Rickets and Calvin, 1962, p. 304-306, for Urechis caupo.)

Richter (1926) concluded that fossil Spreitebauten occurring in large numbers are indicative of marine environments. Although he believed that this is the only environment which could supply a sufficient amount of plankton, the theory has not been adequately tested.

Cincinnatian Representatives

Over the past 70 years Corophioides has accumulated from all over the world a total of seven species, ranging in

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

age from Cambrian through Triassic. Without a detailed restudy their validity can not be assured. There does not appear to be any significant difference between C. polyupsilon Smith (Scotland: Upper Carboniferous) and C. luniformis (Blanckenhorn) (Germany: Lower Triassic) as restudied by Sörgel (1924). The only apparent morphologic difference is that in the former the transverse section lengthens slightly with the depth of the "U," whereas the arms of C. luniformis remain parallel.

Rudolf Richter (1926) proposed C. erraticus for a single specimen occurring in a glacial erratic boulder found in Prussia but apparently originally derived from the Cambrian sandstones of Sweden. He differentiated it from C. luniformis because the Spreiten of C. erraticus are crowded against one of the arms. Yet, one of Sörgel's (1924, pl. 20, fig. 3) illustrations of C. luniformis appears to show this same phenomenon. Richter separated C. erraticus from C. polyupsilon because the former lacked the "U in U" structure of the Spreite in Smith's species. It has been shown above, however, that Smith's description was a misinterpretation. Aside from the fact that C. erraticus was based on a single specimen, both of Richter's differentia appear to rest on shaky ground. Westergård (1931) placed Richter's species in synonomy with Diplocraterion parallelum Torell (1870) (Sweden: Lower Cambrian).

Öpik (1929) proposed C. helmerseni for a form from

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

the Lower Cambrian of Estonia. This differs from other species in being slightly expanded (transverse section lengthens) at the base and in having a few irregularly spaced Spreiten. Nevertheless, Westergård (1931) considered it synonomous with the Swedish Diplocraterion parallelum.

In 1930 Hecker erected Rhizocorallium devonicus for a U-tube from the Devonian of Russia. Without explanation Abel (1935) placed the species in Corophioides. Judging from Abel's (1935, fig. 381) illustration, the arms have the distinctive deflection of the U-plane of Rhizocorallium; and there appears to be no basis for placing it in Corophioides. (Perhaps it was age rather than morphology that influenced Abel.)

The morphologic distinctiveness of C. balticus Andree (1927, from the Devonian of Prussia, and C. rosei Dahmer (1937), from the Taunus Quartzite (Lower Devonian) of the Rhineland is questionable. The former was never figured nor diagnosed, and the latter was figured but only briefly discussed. One gets the impression that the sole reason for proposing the species was because they were found in areas where U-tubes had not previously been reported.

Kolesch (1922) described one U-tube species from the Middle Bunter Sandstone (Upper Triassic) of Germany under the name of Arenicolites zimmermanni. However, as

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

Andree (1927) and Häntzschel (1965) have pointed out, the species possesses Spreiten and belongs in Corophioides. Kolesch (1922, fig. 7) differentiated it from C. luniformis because the Spreiten are bowed out to one side, and thus the transverse section takes on an arcuate shape. The species has never been restudied and it is not known how consistent this pattern is.

Three varieties of U-tube traces are present in the Cincinnatian section, and their relationship to the forms in the world literature is necessarily somewhat doubtful. One of the Cincinnatian forms closely resembles most of the forms discussed above, i.e., it is a simple U-tube with Spreiten, but without any marked characteristics which would set it apart from the other "species." It is the least common of the three varieties and will be discussed as Corophioides cf. luniformis. The other two forms differ sufficiently from each other and from all other species of Corophioides seemingly to merit specific designations. C. cincinnatiensis n. sp. is characterized by a bilateral expansion of the base of the "U." It is somewhat similar to C. helmerseni Öpik (Lower Cambrian: Estonia) but differs in that the Spreite is more regular and the basal expansion more abrupt in the Cincinnatian form. C. biclavata (Miller) (1875) was originally described as Arthraria biclavata, the "dumbbell fucoid." It can now be shown that this type of dumbbell represents a modification of the base of C.

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

cincinnatiensis, where the arms of the "U" have been extended below the arcuate base of the "U."

Median sections reveal that the *Spreiten* of all three types of *Corophioides* of the Cincinnatian are of the descending variety and are composed of reworked host rock. In contrast to the Bunter specimens described by Sörgel (1924), the Cincinnatian *Spreiten* do not broaden with depth but instead remain constant. The arms and the base of the "U" are filled with a finer grained material which readily weathers out or is easily removed. Presumably it represents sediment washed into the tube after the inhabitant had departed.

Corophioides is one of the most common Cincinnatian trace fossils. It ranges throughout the entire section and, when found, normally occurs in large numbers. The individual U-tubes commonly intersect one another, and there is no preferred orientation other than vertical to the bedding. The genus is most frequently encountered in hard, cross-laminated, fine-grained calcarenites but has also been found in platy calcisiltites. As will be shown below, there is indirect evidence to show that it occurs in lutites as well. It has never been found in the extremely coarse-grained calcarenites.

It is noteworthy that at one locality all three species have been found in the same bed, while in another locality *C. cincinnatiensis* and *C. cf. luniformis* have been

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

found together. This suggests the possibility that these three "ichnospecies" represent different expressions of the burrow of the same organism.

Corophioides cf. *luniformis*

(pl. 5, fig. 5; pl. 6, fig. 1-2; pl. 13, fig. 3)

The forms included under *C.* cf. *luniformis* are *Spreite*-bearing U-tubes which have a gently rounded base and thus lack the marked basal expansion of *C. cincinnatiensis*. As nearly as can be determined from the literature (no specimens were available for study), these tubes are morphologically similar to many of the European "species." However, since *C. luniformis* is the best known of the European forms, the Cincinnatian specimens are tentatively allied with it. Nevertheless, it should be pointed out that a direct detailed comparison of the Bunter forms with those from the Cincinnatian might well reveal characteristics that would set them apart, for it is quite possible that they were made by totally unrelated organisms.

Three specimens of *C.* cf. *luniformis* showing U-plane sections are known. Two of these (pl. 13, fig. 3) were found only a few centimeters apart in the McMicken beds in West Fork Creek (Cincinnati, Ohio) at the type locality of *C. cincinnatiensis*. The host rock is a fine-grained, cross-laminated calcarenite, which has a thickness

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

of 7.5-12 cm. The overlying and subjacent lutites are barren of U-tubes. The two specimens are nearly identical in measurements, as both have a depth of 2.3 cm and a breadth of 5 mm. The transverse length of one specimen is 3.3 cm, that of the other 3.2 cm. No free tubes are visible, as the Spreiten extend to the upper limit of the calcarenite, and attempts to trace the tubes into the overlying lutite were unsuccessful. Also available for study was a slab from an unknown locality bearing a single specimen of C. cf. luniformis (pl. 6, fig. 1), as well as several examples of C. cincinnatiensis. The tube has a transverse length of 4 cm, a breadth of 2.5 cm, and a depth of 3.8 cm. The Spreiten are evenly spaced and extend to the top of the bed.

Broad arcuate impressions, which are believed to represent "molds" of the base of C. cf. luniformis, have been found in the Corryville and Richmond rocks. The Corryville specimens has a breadth of 8 mm and a depth of 1 cm; the transverse length is 10 cm. The Richmond specimen, which has an area of 91 square cm., contains 55 individuals, many of which intersect. The breadth (2 mm) is the only consistent measurement, for the transverse length varies from 6-15 mm and the depth ranges from 1 to 3 mm. These impressions closely resemble Blanckenhorn's (1902, fig. 1) illustration and discussion (1924) of the lower portions of some of the Bunter specimens of C. luniformis.

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

While admittedly there is no direct proof, the Cincinnatian specimens are believed to represent the bases of C. cf. luniformis where the upper portions of the tube have been stripped away by erosion. The fact that no Spreiten are found suggests that the main body of the tube lay within a lutite and that the tubes bottomed in the calcarenite. Unfortunately this can not be confirmed, as none of the specimens were found in place.

Interpretation: Based on the discussion of Recent U-tube dwellers given elsewhere, the specimens grouped under C. cf. luniformis are thought to represent the Domichnia of sessile filter-feeding organisms. Although it has never been demonstrated, there may well be an optimum set of tube dimensions for maximum efficiency in filter feeding. If the tube is too long (as measured along the "U"), it might be difficult for the organism to set up sufficient current. On the other hand, if the tube is too short, the inhabitant might be too close to the apertures. The descending Spreite might represent an attempt by the organism proportionately to lengthen the tube as the body length increases with age. In addition, erosion of the upper part of the U-arms could force the inhabitant to deepen the tube. The fact that the Spreite extends to the top of the bed suggests that erosion was operative. A third possibility would be a combination of these two factors.

The zoological affinities of the producer of C. cf. luniformis are unknown. U-tubes are constructed by

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

representatives of so many different phyla that it is unwise to speculate too extensively. While the lack of striae on the arms and Spreiten would seem to rule out arthropods, C. cf. luniformis could be the tube of any one of a number of soft-bodied organisms. Of course, the annelids are a favorite in such speculation.

Corophioides cincinnatiensis n. sp.
(pl. 4, fig. 1,5,8; pl. 5, fig. 4,6,8; pl. 6, fig. 3,4,6; pl. 7, fig. 4; text fig. 9)

Type Locality: The specimen illustrated on pl. 5, fig. 4 (UCM 37590) from the McMicken beds of West Fork Creek, Cincinnati, Ohio, is designated as the type specimen for C. cincinnatiensis. The type locality is 303 meters east of the intersection of Shepherds Road and West Fork Road, Mt. Airy Forest, Hamilton County, Ohio. The bed containing the specimen crops out on the south bank some 50 cm above the water level and 2-3 meters downstream from a dam.

Diagnosis: Vertical Spreite-bearing U-tubes which increase in transverse length with depth. Most specimens are marked by an abrupt flaring of the base of the "U." The upper part of the arms is approximately parallel but in many cases exhibits numerous minor irregularities. Free tubes unknown. The Spreiten are quite regular and parallel in most cases but may show some overlapping.

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

Discussion: C. cincinnatiensis is more common than C. cf. luniformis and is especially abundant in the upper part of the McMicken, where it is associated with Chondrites and Trichophycus venosum. Two of the best exposures are the type locality and a long outcrop on U. S. Route 27, 1.4 miles south of Newport Shopping Center, Newport, Kentucky. At the latter locality the species is best seen on the east side of the road at the top of the talus slope.

At the type locality the tubes occur in the well bedded calcisiltite which contains C. cf. luniformis. The basal 1-2 cm of the bed is composed of a more coarse-grained fossil hash. While a few of the tubes penetrate to the base of the bed (fig. 9), the majority terminate at the upper limit of the fossil hash. The contact between the host rock and the subjacent lutite is sharp, but the upper calcisiltite-lutite contact is more gradational, the distance of transition being 2-3 cm.

The type specimen (pl. 5, fig. 4) has a depth of 6.8 cm and a breadth of 3 mm. The arms are approximately parallel throughout most of their length, although irregularities do exist, especially in the upper portion of the right arm. The transverse length of the specimen down to the expanded base varies between 2.3-2.8 cm, and the Spreiten, which extend to the upper limit of the tube, are parallel and quite regular. At a depth of 5.1 cm both arms diverge outward at an angle of 40° off the vertical axis to

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

produce the flared base so characteristic of the species. The transverse length of the tube then increases to a maximum of 3.9 cm before terminating in a gently rounded base 1 cm above the bottom of the bed. Although the Spreiten are evenly spaced, those of the expanded portion of the tube are more strongly bowed (i.e., more strongly convex downward) than the Spreiten of the unexpanded portion.

Figure 9 illustrates three additional topotype specimens which, owing to the size of the slab, could not be removed from the outcrop. Figure 9-1 shows a tube which extends through the shell hash to the base of the bed. It differs from the type specimen in that the arms gradually diverge with depth, the basal expansion is not as pronounced, and the base of the tube is slightly flattened. Forms similar to this were seen to extend as much as 1 cm into the subjacent lutite. Another variety of C. cincinnatiensis is shown in fig. 9-2. Here the arms continue to diverge with depth, and although the base of the tube is flattened, there is no sudden expansion. The specimen shown in fig. 9-3 quite closely resembles the type specimen, except that the upper portion of the arms is more regular. Several other forms similar to the three discussed above occur in the same bed, along with representatives of C. cf. luniformis and C. biclavata.

At the Kentucky locality mentioned above, C. cincinnatiensis occurs in large numbers in two cross-laminated calcisiltites separated by some 60 cm of barren

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

lutite. The specimens do not differ greatly from those just discussed, except that in all observed cases the U-tubes reach to the base of the calcisiltites and many times extend up to 5 mm into the subjacent lutite. None of the specimens in either bed could be traced into the overlying lutite, yet in all cases the Spreiten extended to the upper limit of the calcisiltite. Most of the tubes are characterized by a marked basal expansion. The most extreme example is seen on pl. 5, fig. 6, where the length as measured across the upper part of the specimens is 2.4 cm, while the length at the base of the calcisiltite is 6.2 cm. As in the specimens from the type locality, the transverse length of the tubes varies considerably. In some (pl. 5, fig. 4) the average length is only one-third the depth, while in others (pl. 4, fig. 5) the length may exceed the depth. Several specimens showing intermediate stages have been observed.

Although the arms of most of the tubes from both localities are smooth or covered with secondary calcite encrustations, two specimens are known where the last-formed "U" bears annulations. Plate 6, fig. 4 shows the base of a "U" from the Kentucky locality which has 12 annulations per centimeter. The other specimens (pl. 4, fig. 1), from the type locality, shows an unweathered filling of one of the arms where the annuli are larger, averaging 8/cm. This latter specimen also shows the angular irregularity of

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

the arms which is encountered in many forms.

Interpretation: As mentioned elsewhere, C. cincinnatiensis may well be a behavioral variant of C. cf. luniformis, where the major deviations are the irregularity of the arms and the basal expansion of the tube. As in C. cf. luniformis the Spreiten are thought to represent older relics of the base of the "U" where the organism deepened the tube: a) to compensate for an increase in body length, b) to compensate for erosion of the upper part of the tube, or c) a combination of the above. If the inhabitant of the tube was a filter-feeder, a steady even flow of water through the tube was a necessity. Since neither the irregularity of the arms nor the angular expansion of the base would seem to increase the efficiency of the tube, they must represent a reaction of the organism to some obstacle encountered in burrowing. In fine-grained material irregularities in the symmetry of the tube could arise through uneven compaction or slippage, but in the forms under consideration here only the arms are distorted. The Spreiten are quite even and show no trace of any disturbance. Perhaps the organism was forced to detour around slightly indurated or more compact patches of sediment.

The basal expansion of the "U" is thought to represent the reaction of the organism to a physical or chemical change in the sediment. Note that at both localities the tubes terminate either at a silt-mud or silt-fossil hash interface. At the type locality only a few of the individuals

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

(fig. 9-1) were able to penetrate through the fossil hash and into the underlying mud. Instead most forms were forced to lengthen the tube by moving laterally. At the Kentucky locality the organism apparently had an aversion to mud. Perhaps it was too hard, tended to clog the respiratory apparatus, or was chemically distasteful.[16]

---

[16] It is interesting to note that the animal could lengthen the tube by either expanding the length, as the Cincinnatian forms did, or by directing the "U" either oblique or parallel to the bedding. It is unusual that the latter variant is not found in at least a few Cincinnatian specimens. It would also be worthwhile to re-evaluate Rhizocorallium in this light. Perhaps it too is a response to a change in lithology and not a feeding structure as Seilacher (1955) and others have postulated. Likewise, Corophioides helmerseni Öpik should be restudied to see if the flared base can be explained in the same manner. Öpik (1929) attributed it solely to the growth of the animal.

However, it must be admitted that a change in the texture of the sediment does not provide the answer for all such expanded U-tubes. U-plane sections of C. biclavata (see pl. 21, fig. 8) occur with C. cincinnatiensis at the West Fork Creek locality and alone in the Mt. Hope in a creek adjacent to Sheed Road, 200 meters northeast of the

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

intersection with Gaines Road, Hamilton County, Ohio. As will be shown, C. biclavata also expands at the base, and the only apparent difference between it and C. cincinnatiensis is that the arms extend below the level of the Spreite. Specimens of C. biclavata have been found at these two localities where the tube ends well within the silt bed and not at a lithologic contact. Perhaps here the animal encountered a chemical change which is not reflected in the sediment.

As noted in the discussion of C. cf. luniformis, it is difficult to assign U-tubes to a given group of organisms. However, annuli found in two specimens of C. cincinnatiensis suggest a segmented vermiform body. If C. cf. luniformis is only a behavioral variant, this means that it too was inhabited by a metameric vermiform organism.

Corophioides biclavata (Miller)

(pl. 4, fig. 3-4; pl. 5, fig. 1,3,7; pl. 9, fig. 6; pl. 10, fig. 5; pl. 14, fig. 5; pl. 21, fig. 8; text fig. 8)

1872 ?Arthraria antiquata Billings, E., Canadian Natur., n.s., vol. 6, p. 467, fig. 2.

1875 Arthraria biclavata Miller, S. A., Cincinnati Quart. Jour. Sci., vol. 2, p. 354, fig. 26.

1879 Arthraria biclavata, James, U. P., Supplement to a Catalogue of Lower Silurian Fossils of the Cincinnati Group, Cincinnati, Ohio, p. 29.

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

1884 Arthraria biclavata, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 8-9, pl. 6, fig. 6.

1940 ?Bifungites fezzanensis Desio, A., Museo Libico Storia. Nat., Ann., vol. 2, p. 78-79, pl. 8, fig. 3.

1940 ?Bifungites halli Desio, A., Museo Libico Storia. Nat., Ann., vol. 2, p. 78-79,

Type Locality: Miller's figured specimen was from "one of the numerous impressions in the slabs that make up the sidewalk, on Torrence Road near Forest Avenue" (Miller, 1875, p. 374). The genus is relatively common throughout the Cincinnatian section. The "type sidewalk" has long since been replaced by concrete.

Diagnosis: Vertical Spreite-bearing U-tubes in which the arms are extended below the base of the deepest "U" to form blind pouches. The species is most frequently preserved as concave epireliefs with a dumbbell shape, i.e., two kettle-like depressions connected by a bar. The connecting bar resembles a very shallow vertical "U," and it may or may not be directly connected to the kettles.

Discussion: The Cincinnatian dumbbells were placed in Billings' (1872) genus, Arthraria, first described from the Upper Cambrian rocks of Newfoundland. As will be shown later, there is some doubt as to whether the Newfoundland forms are the same as those from the Cincinnatian. Miller (1875, p. 354) established Arthraria biclavata for a "fucoid [which] consists of a straight cylindrical stem,

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

with an enlargement at each end, nearly as round as a ball. It has some resemblance in shape to dumb-bells. It shows no structure. It usually consists of the impression, only.... sometimes, the cylindrical stem, between the balls, is found in tolerably good condition, but it is quite rare to find even part of a ball in the matrix, and I have never seen a specimen free from a slab." His highly schematic figure moved U. P. James (1879, p. 29) to remark that "the published figure of this species appears much as if copied from a specimen just from the turning lathe--a remarkable growth for a sea plant."

The dumbbell impressions referred to by Miller are common in the local section and occur as concave epireliefs in calcisiltites or calcarenites. Forms of varying size may be found on the same slab and they frequently intersect. The length (the greatest distance as measured along the bar) varies from 5-14.5 cm. The kettle-like depressions at either end may be round (pl. 10, fig. 5), reniform (pl. 5, fig. 3), or cordate (pl. 5, fig. 1). In addition, J. F. James (1884, fig. 6c) figures one form shaped like an arrowhead. Although the kettle-like depressions on a given specimen are normally similar in size and shape, one may be smaller than the other or even missing entirely (pl. 9, fig. 6). The diameter of the depressions ranges from 1-3 cm, and they are invariably deeper than the bar connecting them. For example, in a specimen from the Corryville of Stonelick Creek (pl. 5, fig. 1), the cordate depressions have a depth of 1.4 cm,

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

while the deepest point of the connecting bar is only 6 mm below the surface of the slab. Although the bottom of most depressions is gently rounded, in some the center of the depression is not the deepest point. In the specimen seen in pl. 5, fig. 3, the floor of the depressions slope toward the connecting bar and the inner wall is undercut.

Likewise, the morphology of the connecting bar may vary. The bar may actually connect the two depressions or it may terminate some 5 mm from the depressions (pl. 5, fig. 1,3). The width of the bar average 4-7 mm and is independant of the diameter of the depressions. In cross-section the base of the bar is gently rounded. In almost all cases the bar resembles a very shallow vertical "U," where the greatest depth is attained at the midpoint, while in some examples the bar may be filled with sediment and rise above the surface of the slab as seen in pl. 4, fig. 3. This filling is most significant in the interpretation of the species. Sectioning of several specimens shows that neither the depressions nor the connecting bar extend down into the host rock. The entire structure is visible as a concave epirelief.

Similar dumbbell-shaped forms have been described from other geological horizons, but a discussion of them is withheld until an interpretation of C. biclavata is given. The difficulties of a direct comparison will then be apparent.

Interpretation: Miller (1875) interpreted the species as a "fucoid," while J. F. James (1884) believed that

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

it may be a concretion. There were no further attempts to interpret the species until Fenton and Fenton (1934, pl. 28, fig. 2) studied the movements of the gastropod Illyanassa obsoleta (Say) on the tidal flats of San Francisco Bay. They observed that the snail plows along the surface leaving a trail which resembles a gently rounded trough; then, for no apparent reason, it twists and digs a shallow hemicylindrical pit. The organism may remain in the pit for several hours before again proceeding on its way. This same behavior may be repeated several times, and the final result is several pit-like depressions connected by rounded troughs. However, several features of the Cincinnatian dumbbells fail to support this conclusion. The connecting bar is straight and does not show the irregularities seen in the Fentons' illustration of the trail of I. obsoleta. Moreover, the bar is U-shaped, and in many cases does not actually connect the depressions. As already noted and shown in pl. 4, fig. 3, the bar may be filled and stand above the surface of the host rock.

Several lines of evidence indicate that what Miller described as A. biclavata actually represents the base of a Spreite-bearing U-tube, where the arms have been secondarily deepened below the base of the Spreite (see fig. 8). The connecting bar is U-shaped, and the filling of the bar seen in pl. 4, fig. 3 is actually the remnants of a descending Spreite (compare pl. 4, fig. 3 with fig. 7D-4). Moreover, some specimens of Corophioides with expanded bases show

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

that one or both of the arms have been extended. One specimen (pl. 5, fig. 7) from the Fulton beds of Union Levee, Cincinnati, Ohio, is most significant. It is preserved as a hyporelief in calcisiltite and shows the Spreite and the filling of the expanded arm. A latex mold of this specimen is quite similar to the specimen seen in pl. 4, fig. 3. U-plane sections of tubes with modified bases have been found both at the type locality for C. cincinnatiensis and also at the Sheed Road locality. Note that a transverse section taken 2 mm above the base of the specimen seen on pl. 21, fig. 8 would resemble the reconstruction given in fig. 8.

As already noted, the dumbbells occur on calcisiltites or fine-grained calcarenites which are overlain by lutites. No examples have yet been located where a U-tube has been found overlying the dumbbell, and apparently in all observed examples the upper parts of the tube have been stripped away. It is believed that the organism burrowed down through the lutite and halted excavation when the subjacent silt or sand was encountered. This would be the opposite of the Newport examples of C. cincinnatiensis, where the subjacent mud was apparently in some way distasteful to the burrower. This might suggest that the maker of C. biclavata and C. cincinnatiensis were different organisms, the former being primarily a mud-dweller, the latter an inhabitant of silts and sands. Unfortunately this can not

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

be accepted as a firm conclusion, since both varieties have been found together in the silts of West Fork Creek.

Why the arms were extended below the Spreite is not at all clear; perhaps another organism used the arms as a domicile after the death or departure of the original inhabitant. In this case two animals could live in the tube, one in one arm, one in the other. Also several U-tube dwellers are known to have commensals living with them. For example, the tube of the polychaete Chaetopterus provides refuge for the small crab Pinnixa, and, according to Ricketts and Calvin (1962), the large tube of the echiuroid Urechis caupo is also inhabited by the scale worm Hesperonoë adventor, a small crab, Scleroplax granulata, and a fish, Clevelandia ios. These organisms feed on detritus pumped into the tube by the echiuroid. Although the Recent commensals do not modify the architecture of the tube, it is possible that the extended arms of C. biclavata are outpocketings inhabited by Ordovician commensals.

Other dumbbell-shaped bodies have been found in the Cincinnatian rocks. All are preserved as convex hyporeliefs and none extend up into the host rock. In some the terminal enlargements are rounded (pl. 5, fig. 2), in others they are shaped like arrowheads (pl. 15, fig. 5). The total length of the specimens ranges from 2.7-4.8 cm. Since they do not extend up into the host rock, they can not be the actual bases of C. biclavata. Transverse sections of the Cincinnatian Corophioides taken at any depth reveal a

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

dumbbell outline. As mentioned, the Spreiten do not broaden with depth, indicating that while the animal may have grown in length, the diameter of the body did not correspondingly expand. However, the arms of the "U" were used throughout the life of the tube, and constant movement of the inhabitant would lead to an increase in their diameter. For this reason the dumbbells preserved as convex hyporeliefs could be the casts of the base of C. biclavata or casts of any portion of the tube of any of the three Cincinnatian species.

This uncertainty makes it difficult to compare C. biclavata with Arthraria antiquata Billings, the holotype of the genus Arthraria. Billings' (1872, fig. 2) illustration of the type specimen shows that it is a convex body, not a depression as is normally the case with C. biclavata. While there is no direct proof, A. antiquata is probably the cast of some portion of a U-tube, but it is not known whether the tube is a Corophioides, Rhizocorallium, or Diplocraterion. It may even be a tube similar to Arenicolites in which sagging of the bedding has produced a connecting arch. Unfortunately the type specimen of A. antiquata has been lost and no topotype material is available. Until such material can be studied, the species will have to remain Incertae sedis.

The same is true for Bifungites fezzanensis Desio (1940) from the Devonian of North Africa and B. halli Desio (1940) from the Clinton (Silurian) beds of New York State. B. fezzanensis, which apparently is preserved as a convex

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

hyporelief in a quartz sandstone, bears a close resemblance to the convex dumbbells discussed above. While it may be similar to C. biclavata, Desio makes no mention of U-tubes associated with Bifungites. He believed that it was a "fucoid" or "colonial animal." B. halli is based on a specimen figured but not named by James Hall (1852, pl. 10, fig. 6) from the Clinton of New York. Hall believed that this was a "fucoid" or possibly even a bone. Without a study of the topotype locality, a meaningful conclusion can not be given at the present time.

Finally Ruedemann (1925) established Arthraria magna for dumbbells from the Upper Ordovician strata of Pulaski, New York. They are preserved "by the hundreds" as concave epireliefs in "dark-gray mud" which forms a film over the subjacent sandstone. U-plane sections (Ruedemann, 1925, fig. 65) reveal that these are the upper expressions of U-tubes and thus are not similar to C. biclavata. Ruedemann maintains that settling of the Spreite has led to the origin of a connecting bar between the two apertures. However, Richter (1926) said that the connecting bar of A. magna was entirely straight and thus could not be due to sagging. He believed that the bar marked the path of the organism as it slid across the surface from one aperture to the other. Examination of U-plane sections of Ruedemann's material should provide the answer.

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

?Skolithos Haldemann, 1840

(pl. 6, fig. 7-8)

1840 ?Skolithos Haldemann, S. T., A Monograph of the Limniades, or freshwater univalve shells of North America, containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in Paludina and Anculosa, no. 1, suppl., p. 3.

1847 ?Scolithus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 2, pl. 1, fig. 1a-c.

1881 (in partim) Scolithus, James, U. P., The Paleontologist, no. 5, p. 33.

1892 (in partim) Scolithus, James, J. F., Geol. Soc. America, Bull., vol. 3, p. 32-44, fig. 1-15.

1920 (?in partim) Sabellarites Richter, Rud., Senckenbergiana, Bd. 2, p. 226, pl. 1,3,4.

1921 (?in partim) Sabellarifex Richter, Rud., Senckenbergiana, Bd. 3, p. 50.

1931 ?Scolithus, Westergård, A. H., Sverige geol., Unders., ser. C, Avh. och upps., no. 372 (=Årsbok, vol. 25, no. 5), p. 14-16, pl. 7-11.

1943 ?Skolithos, Howell, B. F., Wagner Free Inst. Sci., Public., vol. 3, p. 6-16.

Type Species: Skolithos linearis Haldemann (1840)

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

from the Lower Cambrian Chickies Quartzite between Reading and Columbia, Pennsylvania.

Diagnosis: Closely packed, unbranched, vertical tubular penetrations which occur most frequently in arenaceous sediments. The diameter varies from 1-10 mm; the length from a few centimeters up to 30 cm.

Discussion: Since these tubular forms are rare in the Cincinnatian and can only very tentatively be assigned to Skolithos, the genus will not be covered in detail here. For a complete treatment the reader is referred to J. F. James (1892), Rudolf Richter (1920, 1921), and Howell (1943). Skolithos has received extensive coverage and is fairly common in the Lower Paleozoic rocks of eastern North America and Europe. Specimens have been described from nearly every continent; and it is so numerous in some localities, e.g., Lower Cambrian of northwest Scotland, that the beds have been called "pipe rocks."

Skolithos was proposed by Haldemann (1840, p. 3), who characterized it as "stem simple (never branched), rectilinear, surface nearly even, diameter 1/4 - 1/8 inch, length several feet, cylindrical or compressed." The genus was not figured and the precise type locality is unknown. Howell (1943) reported that he searched in vain for a type specimen and that probably Haldemann never selected one. Therefore, Howell designated a neotype (PU 3625a) from Mt. Penn, a locality which is presumably close to that of Haldemann's original find.

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

At the Mt. Penn locality S. linearis occurs in a light-gray, poorly bedded quartz sandstone. The material filling the tubes is either lighter or darker than the host rock and tends to weather more rapidly, leaving pits up to 1 cm in depth on bedding plane surfaces. The individual tubes range from 3-7 mm in diameter and incomplete specimens attain a length of 9 cm. All forms are normal to the bedding plane and most are quite straight. Howell observed that the straight forms occur in a fine-grained sand and that as the grain size of the host rock increased, so did the irregularity of the tube. Occasionally specimens appeared to branch, but Howell believed that this was due to the intersection of two separate individuals. The fossils are extremely close-packed, sometimes being separated by as little as 5 mm.

Skolithos is quite common in the Upper Cambrian rocks of eastern North America and has been studied by Hall (1847), Billings (1865), and Dawson (1890). Hall changed Haldemann's original spelling and described his New York forms (Potsdam Sandstone) as Scolithus linearis. Most subsequent authors erroneously have believed that this is the correct spelling; some workers, e.g., U. P. James (1881), have even credited the species S. linearis to Hall. However, as Howell (1943) and Häntzschel (1962) point out, Haldemann's initial designation prevails.

As with many fossils, the early descriptions of the genus were so vague that Skolithos rapidly accumulated

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

several species; James (1892) lists 11 species from North America alone. Rudolf Richter (1920) undertook a revision and clarification of the genus. He restricted Skolithos to straight, closely packed vertical forms best typified by the specimens from the Cambrian of Sweden (see Richter, 1920, fig. 6). The irregular, loosely packed specimens, which included most forms previously described under Skolithos, were placed in a new genus, Sabéllarites. The type species was S. eifliensis from the Lower Devonian Koblenz Quartzite of Germany. In 1921 Richter changed the name to Sabellarifex, when he realized that the earlier name was preoccupied by Sabellarites Dawson (1890), an annelid. Richter's treatment of the genus has not gained wide acceptance. Westergård (1931) pointed out that the Swedish specimens from the Lower Cambrian "Scolithus" Sandstone fail to support Richter's conclusions. He found that some scattered tubes were straight and some closely packed tubes were wavy. Westergård (1931, p. 14-15) said, "as these different Scolithus forms [Skolithos and Sabellarifex of Richter] are connected by intermediate forms and occur associated, they can hardly be distinguished...."

At present the genus still remains in a state of confusion. Like so many of the larger trace fossil genera, it is badly in need of a monographic study.

Interpretation: Most early workers, such as Haldemann (1840) and Hall (1847, 1852), believed that Skolithos represented the stems of marine plants preserved

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

in situ. However, shortly after the genus was proposed some authors, e.g., MacCulloch (1848) and Logan (1852), suggested an annelid origin, and it was not long before the "fucoid" theory was generally discarded. The tubes show neither rootlets nor any trace of organic matter. Nevertheless, over the years there have been several different hypotheses on the origin of the genus. Perry (1872) believed that the shorter tubes might represent brachiopod pedicle perforations, while Billings (1865) claimed to have found sponge spicules in the filling of some tubes from the Potsdam Sandstone of eastern Canada. Billings' discovery has never been confirmed and Howell (1943) was inclined to dismiss it. Polychaetes have been frequently mentioned as possible originators. Some authors, e.g., Richter (1920, 1921), believed that Skolithos was the tubes of filter-feeding annelids, such as Sabellaria, the fan worm. Others, such as McNair and Reid (1929), thought that the genus was a burrow similar to that of the Recent lug worm Arenicola. For many years the structure of the Arenicola burrow was not clearly understood, and not until the work of Rudolf Richter (1924) and Wells (1945) was it realized that Arenicola makes J- or L-shaped burrows, not simple vertical shafts. In a convincing piece of work, Fenton and Fenton (1934) postulated that many Skolithos burrows could be the tubes of phoronids. They compared the fossil forms to the closely packed vertical tubes of Phoronopsis viridis observed on the tidal flats at Elkhorn Slough, California. The author

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

has seen these same tubes in Tomales Bay, California, and can confirm the Fentons' observations. The thin, unbranched tubes are over 30 cm long and are so closely packed that they serve to bind the sediment, producing a topographic high. They closely resemble some illustrations of Skolithos (e.g., see Westergård, 1931, pl. 8, fig. 1)

Some authors, for example, Högbom (1915) and Geinitz (1915), have concluded that Skolithos is inorganic and that the vertical tubes mark the passage of air which was forced to the surface when the incoming tide covered a dry sand flat. Such phenomena are discussed at some length by Cloud (1960).

Even though Skolithos-like forms probably have a variety of origins, there is general agreement that the Upper Cambrian forms, e.g., S. linearis, are organic. They are too straight and in many cases too closely packed to be otherwise.. Nevertheless, some forms of inorganic origin have been assigned to the genus. One of these is Skolithos linearis as described from the Cincinnatian by U. P. James (1881). As shown elsewhere, this is a groove cast.

Cincinnatian Representatives

?Skolithos delicatulus U. P. James

(pl. 6, fig. 7-8)

1881 Scolithus delicatulus James, U. P., The Paleontologist,

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

no. 5, p. 33.

1892 Scolithus delicatulus, James, J. F., Geol. Soc. America, Bull., vol. 3, p. 40, fig. 15.

Type Locality: Richmond strata of Dearborn County, Indiana. The only figure of the species is given by J. F. James (1892, fig. 15).

Diagnosis: Small, short vertical tubes occurring in medium-grained clacarenites which are seen on the bottom of the slab as raised "pimples." The "pimples," which are composed entirely of coarse crystalline calcite, are frequently surrounded by a circular depression.

Discussion: U. P. James (1881, p. 33) described S. delicatulus as "small cylindrical stems from half a line [1/24 inch] to one line in diameter, passing vertically through the strata irregularly arranged from 1/8 to 1/4 of an inch apart...." The author remarked that these occurred in slabs which varied from 0.12 to over 0.5 inches in thickness. He went on to say that "on the underside the plants are broken off even with the surface, or leaving small, shallow pits; on the upper side they are elevated from half a line to over one line. Other markings on the upper surface, resemble Annelid trails" (U. P. James, 1881, p. 34). James never figured the species, but his son (J. F. James, 1892, fig. 15) did in his paper on the nature of Skolithos.

A specimen (pl. 6, fig. 7-8; UCM 37673) is present in the University of Cincinnati collections which may well be

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

the form illustrated by J. F. James. It is identified as "Scolithus delicatulus James, Cincinnati Group, Indiana" and bears the label of the Cincinnati Society of Natural History. The number "15" appears on one surface, and this corresponds to the figure number in J. F. James' paper. Although the specimen does not exactly match James' lithograph, it is so similar that it probably is the figured specimen. Judging from the associated markings, it appears that U. P. James oriented the slab incorrectly. The raised ridges, which are fillings of trails, show that the "pimple-" like elevations occur as convex hyporeliefs, not convex epireliefs as he believed. The opposite surface represents a cleavage plane and bears the label, "Typical character not shown on this side. Specimen split." Thus the upper surface expression of S. delicatulus is unknown.

Viewed as a convex hyporelief, the specimen, which has a surface area of 72 square centimeters, consists of over 190 raised "pimples." The "pimples" have a diameter of 1.5 mm and are approximately 1 mm in height. They resemble irregular or truncated cones surrounded by a shallow doughnut-shaped depression which may be filled with a soft, fine-grained material. The "pimples" themselves are composed entirely of coarse calcite, and these same calcite blebs can be seen on the upper surface of the specimen. Observation of the edge of the slab shows that the "pimples" are actually vertical rods of calcite which completely pierce the specimen.

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

Interpretation: U. P. James (1881, p. 34) believed that S. delicatulus were plants and gave the appearance "...as if soft mud, forming the strata, had deposited gently around the plants without disturbing their erect position." J. F. James (1892, p. 40) dismissed this with "...there can be no question about its being a worm burrow."

With only one small incomplete specimen from an unknown locality to work with, it is difficult to reach a confident decision on the nature of S. delicatulus. It is unlikely that they represent the passageways of gas moving up through the calcisiltite. According to Shrock (1948, p. 138) the diameter of S. delicatulus would be on the extreme lower range of gas passageways. Although Twenhofel (1921) found experimentally that gas continuously rising through mud could maintain open tubes which resemble those produced by worms, it is unlikely that they would remain open long enough to be filled by calcite. Moreover, gas tubes illustrated by Cloud (1960, pl. 3) are somewhat irregular in outline.

It is probable that S. delicatulus is the filling of a portion of a slender polychaete or phoronid tube. Many tubiculous polychaetes either secrete parchment-like tubes or construct agglutinated tubes which are cemented by mucus. Phoronids employ the latter method. Such a tube would prevent collapse of the walls after the death or departure of the organism. If the opening of the tube were plugged with sediment, the void could later be filled by calcite. In all

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

probability the specimen at hand was underlain by mud and represents only a portion of a much longer tube. Since the base of the tube is missing, it is not possible to definitely assign the species to Skolithos. It is impossible to determine whether we are dealing with unbranched vertical tubes, U-tubes, or even a portion of Chondrites. The latter appears to be unlikely, for as shown in pl. 8, fig. 6, Chondrites tunnels many times occur in groups and are never filled with calcite. Even Perry's (1872) suggestion that short vertical shafts might be perforations made by brachiopod pedicles can not be dismissed.

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

Chapter VII

Fodinichnia

Chondrites Sternberg, 1833

(pl. 7, fig. 2-5; pl. 8, fig. 2-8; pl. 9, fig. 8; pl. 11, fig. 4; pl. 13, fig. 1,8; pl. 23, fig. 5-6; pl. 26, fig. 4; pl. 27, fig. 2; text fig. 14-17,22,25)

1823 (in partim) Fucoides Brongniart, A., Soc. Hist. Nat. Paris, Mém., vol. 1, p. 308, pl. 19, fig. 2.

1833 Chondrites Sternberg, K. M. Graf v., Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, Bd. 7-8, p. 25.

1833 (in partim) Sphaerococcites Sternberg, K. M. Graf v., Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, Bd. 7-8, p. 28, pl. 4, fig. 1.

1833 (in partim) Caulerpites Sternberg, K. M. Graf v., Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt, Bd. 7-8, p. 20.

1840 (non) Skolithos Haldemann, S. T., A Monograph of the Limniades, or freshwater univalve shells of North America, containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in Paludina and Anculosa, vol. 1, supp., p. 3.

1847 (in partim) Buthotrephis Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 8, pl. 2, fig. 6.

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

1849 ?Phymatoderma Brongniart, A., Végétaux fossiles, p. 59.

1852 (in partim) Buthotrephis Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 2, p. 18, pl. 5, fig. 1a-d.

1858 (non) Dendrograptus Hall, J., Geol. Surv. for Canada 1857, Report Progr., 1858, p. 143; Report fig. a,b,c.

1873 (non) Planolites Nicholson, H. A., Roy. Soc. London, Proc., vol. 21, p. 289.

1874 Buthotrephis, Miller, S. A., Cincinnati Quart. Jour. Sci., vol. 1, p. 235, fig. 29.

1878 ?Scolithus, Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 4, pl. 4, fig. 4.

1885 (in partim) Dendrograptus, James, J. F. Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 159-161.

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 17.

1895 Chondrites, Fuchs, T., Akad. Wiss. Wien, math.-nat. Kl., Denkschr., Bd. 62, p. 407-410, fig. 10-12, pl. 9, fig. 3.

1910 Chondrites, Reis, O., K. K. geol. Reichsanst., Jahrb., Bd. 59, p. 615-638, pl. 17.

1948 Clematischnia Wilson, A., Canada Dept. Mines Resourc., Geol. Survey Bull., vol. 11, p. 10.

1949 Chondrites, Tauber, A., Geol. Bundesanst., Jahrb., Bd. 93, p. 141-154, 3 fig.

1951 Chondrites, Seilacher, A., "Zur Einteilung und Deutung fossilen Lebensspuren" (unpublished Ph.D. dissertation,

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

Tübingen University, West Germany).

1957 Chondrites, Simpson, S., Geol. Soc. London, Quart. Jour., vol. 112, p. 475-500, pl. 21-24.

Type Species: Fucoides targionii Brongniart (1828) from the Eocene Flysch of Switzerland. Lectotype, Andrews (1955).

Diagnosis: Tunnel systems possessing a small number of master shafts open to the surface which ramify with depth to form a dendritic network. The individual branches may or may not cross over and interpentrate.

Discussion: Chondrites is one of the most common and notable of all the "fucoids." It ranges from the Ordovician through the Tertiary and has been found at numerous localities in North America, Europe, and Asia. The genus is probably best developed in the Devonian and Jurassic of western Germany and the Tertiary Flysch of the Alps, and several forms have been described by Hall (1847, 1852) from the Lower Paleozoic of New York State. Although Chondrites has received extensive coverage by a number of authors, most notably Richter (1927, 1931), Tauber (1949), and Simpson (1957), unanswered questions still remain. At present the genus contains such a wide variety of morphologic expressions that a detailed analysis would probably result in the establishment of several genera.

Chondrites occurs in sediments ranging from fine-grained lutites to medium-grained arenites, and, as Seilacher

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

(1964, fig. 7) has shown, it is a fossil which is common to several different environments. It has been found in such diverse settings as the black Hunsrück Shale of the Rhineland Devonian and the Carboniferous calcarenites of Great Britain. Although Chondrites can occur individually, more frequently it is encountered in great numbers where it forms dendritic patterns on bedding plane surfaces or riddles the sediment at depth with a large number of tunnels (Simpson, 1957, pl. 21, fig. 1-2).

The tunnel system is normally either oblique or parallel to planes of stratification, and Seilacher (unpublished manuscript) remarked that both varieties may be found in the same bed. Simpson (1957) mentioned that a system may proceed obliquely for a distance and then flatten out along a bedding plane. He added that even in forms which are oblique throughout their entire length, the distal portions tend to be more nearly parallel to the bedding planes.

The diameter of the tunnels varies from 0.5 mm in C. intracatus (Brongniart) (Austria: Eocene) to nearly 5 mm in C. gracilis var. crassa (Hall) (New York: Silurian). As illustrated by forms occurring in medium-grained sediments, the original cross-section of the tunnels was circular. However, specimens which are found in finer grained materials are often depressed and present an ellipsoidal outline. The most extreme examples are to be seen in C. bollensis (Zieten) (Württemberg: Jurassic) (pl. 23, fig. 6), where the tunnels are almost paper thin. In contrast Seilacher (unpublished

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

manuscript) mentioned a specimen of C. hechingensis (Quenstedt) (Germany: Jurassic), where the bedding is deflected around the tunnel filling. In nearly all forms the diameter tends to remain constant throughout the entire length of the tunnel system; however, unconnected systems of differing diameters can occur in close proximity (see Rothpletz, 1896).

The branching pattern of Chondrites could best be termed random or alternating. Regular patterns, e.g., sympodial, dichotomous, are unknown. Normally branching proceeds to the second or third order, although Rudolf Richter (1927, fig. 7) shows a form with fifth or sixth order branching. As seen in the specimen of C. bollensis illustrated on pl. 23, fig. 6, the branching tends to be alternating, and the angle of bifurcation varies from 25-40°. Based on a study of several European species, Simpson (1957) found that the angle was consistently 35-45°. Although Simpson (1957, p. 483) reported that the "tunnels are straight [giving] a characteristic rigid appearance to the pattern" (as seen in pl. 9, fig. 8 and noted by Simpson, 1957, pl. 23, fig. 3), some of the tunnels are gently arcuate. A remarkable fact and one most significant in the interpretation of the genus is that in many forms the branches rarely interpenetrate. This was first demonstrated by Richter (1927) and later confirmed by Derichs (1928), Simpson (1957), and Seilacher (unpublished manuscript). If two branches are headed on a "collision course," one will terminate before contact is made.[17] In addition, the authors mentioned above have shown

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

17/ Richter (1927) has employed the term phobotaxis (fear of touching) to describe the avoidance of contact in these chondritids. The meaning of them term as used in trace fossil studies is discussed in greater detail below.

that the proximal branches of the system consistently abut against the distal branches. This variety of phobotaxis is best developed in specimens preserved on bedding planes in the Lias of southwestern Germany (pl. 23, fig. 6) and the Devonian Hunsrück Shale (see Richter, 1931, fig. 2-5). The variety of phobotaxis described above refers to forms occurring on one plane only. Another type of phobotaxis is present in three dimensional forms, where two branches cross over but do not interpenetrate. An example is shown on the front and side face of Richter's block diagram (herein fig. 15). However, when Chondrites occurs in fine-grained sediments, compaction might well close the small gap separating the two tunnels and give the impression of "pseudopenetration." Thus in practice it is difficult to distinguish between crossing over and actual interpenetration.

Phobotaxis is not found in all representatives of the genus. Some forms, described by Hall (1852, pl. 5a, fig. 1; pl. 5, fig. 2B,3C) under the name Buthotrephis from the Silurian of New York State and observed by the present author, exhibit interpenetration. Simpson (1957, p. 492) mentioned that in

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

specimens from the Lias of Great Britain, "separate systems may intersect one another but when this happens the two systems are never of the same colour." As will be shown, Cincinnatian forms exhibit only an incipient phobotaxis, and interpenetration is relatively common. A search of the literature was undertaken to determine if the two varieties of phobotaxis were somehow restricted by time or geography. While the possibility of "pseudopenetration" and the highly schematic diagrams of the earlier workers makes such a determination difficult, there does not appear to be any pattern. The phenomenon of phobotaxis is not restricted to a certain horizon or location.

The controversy regarding the origin of Chondrites has in large part revolved around the nature of the material filling the tunnels. In some forms, e.g., those from the Holzmaden Jurassic section (pl. 23, fig. 6), the filling is much lighter than the host rock, whereas in others, e.g., C. paleozoicus Richter from the Hunsrück (see Rudolf Richter, 1931, fig. 2-5), the filling is darker and stands out in bold relief against the lighter color of the host. However, Seilacher (unpublished manuscript) reported that the color can vary with a single specimen. In Cincinnatian forms the filling is normally lighter than the rock enclosing it. For many years it was assumed that the black material filling the tunnels of many European species was carbonaceous in nature as simple tests for carbon gave positive results. Some early authors even claimed to be able to distinguish

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

"cells" or "traces of parenchymal tissue."[18] Several workers,

---

[18] The quotes are those of Lessertisseur (1955, p. 66), who did not identify the original author of the statements.

---

e.g., Rothpletz (1897) and Gümbel (1897), conducted more careful chemical analyses and found that only 2-4 per cent carbon was present, and most of this was bound up in silicates. The most detailed analysis is that of Tauber (1949), who analyzed the fillings of Chondrites furcatus (Brongniart) as it occurred in fine sands, limestones, and marls. His results are shown in Table II.

As evident in Table II, Tauber found that the material filling the tunnels differed considerably from that comprising the host rock. The tunnels were poor in calcium carbonate and showed only a trace of carbon. Tauber attributed the black color to an enrichment in iron sulfide. In contrast, Rothpletz (1896) found that specimens of C. furcatus from the Jurassic Posidonien Shales would effervesce, whereas the host rock would not. Seilacher (unpublished manuscript) reported that in general the fillings of Jurassic forms of C. furcatus tend to reflect the lithology of the host.

The only species of Chondrites possessing a filling which shows any trace of structure is C. granulatus (Schlotheim) (Württemberg and Great Britain: Lias; Alps:

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

Table II

Composition of Chondrites furcatus

	Limestone	
	Filling	Host Rock
Carbonate as $CaCO_3$	2.50	83.03
Iron sulfide as FeS	16.58	2.81
Clay minerals, quartz, mica	80.92	14.16
Coal flakes	trace	trace
	100.00	100.00

	Marl	
	Filling	Host Rock
Carbonate as $CaCO_3$	2.73	36.66
Iron sulfide as FeS	14.54	4.83
Clay minerals, quartz, mica	72.72	58.51
Coal flakes	trace	trace
	99.99	100.00

	Fine Sandstones	
	Filling	Host Rock
Carbonate as $CaCO_3$	0.37	4.88
Iron sulfide as FeS	18.63	5.90
Clay minerals, quartz, mica	80.99	89.22
Coal flakes	trace	trace
	100.00	100.00

(from Tauber, 1949, Table 1)

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

Eocene Flysch), and even this is questioned by Simpson (1957). Since the argument is based largely on interpretation, it will be discussed below.

Reconstructions of the over-all pattern formed by the tunnel systems of Chondrites vary considerably. Simpson (1957, fig. 2) illustrated an idealized form of Chondrites (herein fig. 14) in which he envisioned six or seven master shafts which are bundled together proximally. These diverge with depth and give rise to secondary, tertiary, and quaternary branches. The main branching pattern is slightly oblique to the bedding plane and as viewed from above, is radial in outline. In contrast, Tauber (1949, fig. 1) (herein fig. 16) in a reconstruction of C. furcatus (Austria: Tertiary) portrayed a single master shaft which branches repeatedly to produce an antler-like pattern. Going one step further, Tauber (1949, fig. 3) (herein fig. 17) showed a series of such patterns arranged in tiers. This latter configuration is similar to a figure of C. bollensis (West Germany: Lias) given by Rudolf Richter (1931, fig. 1) (herein fig. 15). Richter (1931, fig. 10) figured one specimen of Chondrites sp. from the Eocene of Austria which shows 14-16 such tiers, each separated by 1.5 mm.

Fuchs (1895, fig. 11) illustrated an unnamed form from the Cretaceous flysch of Rignano which is unusual in that it possesses a crude bilateral symmetry. When viewed from above, it resembles a lyre with numerous secondary branches. Finally, Liberman (1900, pl. 2) and Papp (1941,

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

fig. 2) show figures of Chondrites which are arranged in a stellate pattern.

Since the orientation of many specimens is oblique to the bedding planes, it is difficult to accurately establish the dimensions of an entire network. The longest branch found by Simpson (1957) was 15 cm, and he estimated that the ratio between the length of a branch and the diameter of a tunnel was 40:1. It would not be surprising to find single specimens which cover an area as great as one square meter.

As shown above, Chondrites contains such a wide range of morphologic variations that at present it is a form genus in the widest possible sense. However, a complete restudy of the genus will be an undertaking of some magnitude, since it contains more "species" than any other "fucoid." Bassler (1915) lists 29 for the North American Ordovician and Silurian alone, and the number of species described from Europe is much greater. As accepted by recent authors, Chondrites is in part synonomous with Fucoides Brongniart (1823). In 1828 Brongniart described and figured 36 species of Fucoides, 11 of which appear to be chondritids. The remaining 25 fall into several diverse groups, and today the "genus" Fucoides has very little meaning. As nearly as can be determined from the schematic figures, Chondrites is also partly synonomous with Caulerpites Sternberg (1833) and Sphaerococcites Sternberg (1833). The former genus, as originally recognized by Sternberg, contains chondritids, various trails, and possibly even conifers (Häntzschel,

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

1962, p. 187). Likewise, Chondrites is partly synonomous with Buthotrephis Hall (1843), originally described from the Clinton beds (Silurian) of New York State. Hall's type specimens are quite fragmentary and reveal only portions of what were undoubtedly much larger systems. However, a restudy of some of his types shows that Buthotrephis gracilis (pl. 13, fig. 8), as well as B. gracilis var. crassa (pl. 7, fig. 5; USNM 41134), are chondritids.[19] As

---

[19] Over a period of nine years Hall proposed nine species and varieties of Buthotrephis. With the exception of the forms mentioned above, these are not considered in the present study, since they were not listed as being present in the Cincinnatian. Judging from Hall's illustrations, many of them appear to be chondritids.

---

discussed herein under Phycodes, B. palmata (pl. 11, fig. 7; USNM 41079) is not a chondritid but a bundled burrow similar to a form described by Seilacher as Phycodes palmata (1955, p. 383) from the Cambrian of the Salt Range. Buthotrephis is discussed more completely below.

Interpretation: More than any other genus Chondrites is the embodiment of the term "fucoid." Its dendritic pattern so closely resembles some Recent algae (e.g., Delesseria) and higher plants that it is not surprising that it was the "last of the fucoids." As late as the middle of

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

the present century, Wilson (1948) and Maubeuge (1950) still accepted an algal origin. Nathorst (1881) was one of the first authors to offer a non-algal hypothesis. Basing his conclusion mainly on forms from the Alpine Flysch, he reasoned that it was unlikely that plants would grow in such deep water where even body fossils are rare. In addition he remarked that there was no vestige of organic material, and the genus occurred in rock types which could offer no firm foundation for attachment. Nathorst (1881, p. 96) interpreted the genus as the "casts of the ramified conduits of worms" but did not elaborate. Likewise, Fuchs (1895) believed that all chondritids were non-algal. He interpreted them as brood chambers which were later filled by sediment sifting into the tunnel system from above. One of his strongest arguments was that the fillings lack the high carbon content which one would expect to find in plant fossils. According to Fuchs the black color of the fillings was caused by coal particles washed in from above. Rothpletz (1896) criticized Fuchs' views and, after conducting chemical analyses on some forms, concluded that the Flysch specimens were true algae, while the Jurassic forms from Württemberg were sponges. A sponge origin has also been postulated by Maillard (1884) and Walther (1904). Reis (1910), working with Cretaceous forms from the Appenine flysch, for the most part confirmed Fuchs' observations. He pointed out the lithologic similarity between the fillings and the beds overlying the host rock and concluded that Chondrites was a burrow. The coup de

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

grace was delivered by Richter (1927), who was able to demonstrate the presence of phobotaxis in C. bollensis (pl. 23, fig. 6) as it occurs on bedding planes in the Württemberg Lias. As mentioned above, phobotaxis was later confirmed by Derichs (1928), Simpson (1957), and Seilacher (unpublished manuscript).

Although Chondrites is now generally accepted as a trace fossil, there is still considerable disagreement concerning its ethological interpretation. Rudolf Richter (1927, 1931) concluded that it was the burrow system of a Sedimentfresser which was later filled by sediment sifting in from above. Phobotaxis, presumably due to some variety of chemoreceptor, enabled the animal to achieve maximum efficiency by avoiding areas which had already been worked. To Richter the fact that some networks were arranged in tiers demonstrated that the nutrients were concentrated in thin layers rather than spread evenly throughout the host rock.

In contrast to Richter's theory, Tauber (1949) maintained that Chondrites was the burrow of a filter-feeding annelid and that the fillings represented a combination of fecal packings and collapse of the lining of the tube. He believed that the tier-like arrangement was a response to increased sedimentation which forced the organism to elevate the entire system. He cited the branched burrows of the Recent annelids Pygospio and Nereis as evidence for his interpretation. Both these organisms employ iron oxides to cement

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

the slime covered walls of the burrow. Tauber concluded that the iron was extracted from plankton ingested by the organism. However, Tauber's explanation fails to explain several facts. If, as Tauber maintained, Chondrites was the Domichnia of a filter-feeder, why was it necessary for the organism to construct such an elaborate system which in many specimens follows the bedding planes and exhibits phobotaxis? Moreover, Tauber's explanation of the tier-like arrangement of some chondritids is not very convincing. The burrows of neither Nereis nor Pygospio appear to resemble Chondrites. According to Schäfer (1962), Nereis normally lies in a long (up to 40 cm) unbranched burrow with its head near the depositional interface. Only if the water is low in oxygen does the worm construct several accessory shafts which open on the surface to increase free circulation of water through the burrow. As illustrated by Schäfer (1962, fig. 166), this does not have the organization of the Chondrites network. Pygospio is an annelid which feeds either by extending its tentacles over the substrate or by constructing a slime net to catch plankton. Schäfer (1962, p. 388) reported that the organism dwells in a small tube which may reach a depth of 9 cm. According to Linck (1939), the burrow is branched only when it has been partly plucked out by current action and is torn. The animal then constructs a secondary branch at the site of the tear and, depending on the location of the tear, the auxillary branch may either be a blind shaft or open to the surface. This certainly is not

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

homologous with Chondrites.

Seilacher (unpublished manuscript) agreed with Richter that Chondrites is the burrow of a Sedimentfresser, but he implied that the burrow was packed with fecal material rather than passively filled at some later time. Small ovoid bodies have been found in the filling of C. granulatus (Brongniart) in the Lias of both Württemberg and Great Britain, and Seilacher interpreted them as fecal pellets. He also noted that when the fillings are washed out, the interior of the walls are marked by small concave ellipsoidal depressions. Seilacher was the first to demonstrate that the proximal branches of Chondrites abut against the distal branches; thus, he was able to show that the organism first moved to the distal portions of the network and then worked back toward the main shaft. The concept of Chondrites representing a stuffed burrow was questioned by Simpson (1957). In the British examples of C. granulatus, he was able to prove that the pellets were derived from the overlying bed. He was less certain regarding the origin of the pellets in the Württemberg forms, although he tentatively suggested that the markings on the walls may represent impressions of egg cases. The major weakness of Seilacher's interpretation lies in the mechanics of the burrow formation. In order for Chondrites to be a burrow packed with fecal material, it means that the organism must have moved backwards to the distal portions of the system and then "fed" his way out, stuffing the burrow with fecal pellets. Conversely, if the

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

animal had burrowed head first, feeding as it moved, it would have to back out through its own feces. Neither of these alternatives appear to be the work of an organism which employed phobotaxis as a means of maximum efficiency.

Simpson's (1957) interpretation was similar to that of Richter (1927, 1931), the major difference being the meaning of phobotaxis. Simpson (1957, p. 485) believed that "the key to the problem lies in the fact that the animal was working from a fixed point on the surface. By first exploring outwards to the maximum distance permitted to it, and then working sideways and backwards, the animal was able to ensure that the unexploited territory lay always on the near side of the last sideways exploration. Thus the phobotactic reaction was not employed so much in preventing the animal [from] penetrating into already exploited territory as in enabling it to keep contact with the near limit of such territory." Simpson was the first to suggest that Chondrites might be the burrows of sipunculids, although he admitted that his belief could not be confirmed by Recent examples. While such a hypothesis requires an organism of considerable length, Hyman (1959) reported that some sipunculids attain lengths of 30 cm and enteropneusts range from 10-50 cm. Barnes (1963) stated that most annelids are 5-10 cm long, although forms up to 3 meters in length are known.

Recent examples which even approximately approach Chondrites are unknown. As mentioned above, the burrows of

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

Pygospio and Nereis are quite different, as are those of other Sedimentfressers such as Heteromastus (see Schäfer, 1962, fig. 159) and Balanoglossus. This seems unusual since Chondrites is so abundant in the fossil record and occurs in such a wide range of depositional environments. It is unlikely that our lack of knowledge concerning Recent environments provides the entire answer. Perhaps Seilacher (1957) was correct in his belief that many trace fossils become clearly visible only after they have undergone diagenetic alteration.

Cincinnatian Representatives

There are at least three distinct types of Chondrites present in the Cincinnatian. However, none of the three can be confidently placed in the trace fossil or "fucoid" taxa discussed by any of the local authors. A search of the literature reveals that the local strata contain two genera and five species which either resemble chondritids or were actually assigned to taxa today considered synonomous with Chondrites. J. F. James (1885) maintained that three of Hall's species of "Buthotrephis," originally described from the Lower Paleozoic of New York State, could be identified in the Cincinnatian. These were "B." gracilis Hall (1843), "B." gracilis var. crassa Hall (1852), and "B." succulens Hall (1852).

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

Although it was not possible to locate the type specimen of "B." gracilis Hall (1843, p. 69, fig. 14), four hypotypes (Hall, 1852, pl. 5, fig. 1a-d) from the Clinton beds of New Hartford, Oneida County, New York, were available for study. The specimens are so similar that only one form is illustrated herein (pl. 13, fig. 8; USNM 41125; latex mold UCM 37676).[20] "B." gracilis is preserved as an epirelief on a fine-grained, iron-stained micaceous quartz arenite. The most striking feature of the species is its small size; the branches have a diameter of only 0.5 mm and the length of the longest branch is but 4 cm. Branching proceeds to the fourth order and the angle of bifurcation varies between 40-55°. Interpenetration of the branches is present but is not common, and contrary to Hall's illustrations, the branches do not taper distally. The species agrees with Simpson's observation of European chondritids as the branches are straight and give the arborescent pattern a rigid appear-

---

[20] Hall first used the specific name "gracilis" in 1843 for Fucoides gracilis from the Clinton strata of New York. In 1847 (pl. 21, fig. 1) he employed the same species name for "Buthotrephis" gracilis from the Trenton beds of Herkimer County, New York. However, in 1852 he changed the specific name of the Trenton specimens to "B." tenuis and retained "B." gracilis for the Clinton forms only.

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

ance. The material filling the tunnels is both darker and finer grained than the host rock. There is no evidence of fecal pellets or other internal structures. As in all chondritids the contact between the filling and the host rock is sharply defined.

"B." gracilis var. crassa Hall (1852), also from the Clinton beds of New Hartford, New York, is poorly known. Although Hall (1852, pl. 5, fig. 3a-d) figured what appear to be complete forms, the actual specimens (pl. 7, fig. 5; USNM 41134) are incomplete. The specimens of "B." gracilis var. crassa observed by the present author are preserved as epireliefs on a platy, micaceous, fine-grained quartz arenite. The irregular main branch has a diameter of 5 mm and the angle of bifurcation varies from 35-60°. In some cases the secondary branches have a diameter which is slightly less (4 mm) than that of the main branch. The filling is slightly darker and finer grained than the host rock, and although Hall described the surface of the branches as nodose, the surface of all observed forms was smooth. There is no trace of granules or pellets similar to those described in Chondrites granulatus by Simpson (1957) and Seilacher (unpublished manuscript). The type specimens are so fragmentary that the over-all pattern of "B." gracilis var. crassa can not be determined. Hall (1852, p. 19) remarked that "...it varies in form so much that scarcely two specimens are precisely alike."

Hall (1852, p. 18-19) believed that "B." gracilis and "B." gracilis var. crassa represented the end members of

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

a completely intergraded series of Clinton "fucoids." Based solely on a study of the type material, it is impossible to support his conclusion. "B." gracilis is small and has a rigid arborescent pattern, while "B." gracilis var. crassa is much larger and more irregular. The former closely resembles on a smaller scale the pattern of the "typical" European chondritids. The latter has the general appearance of a chondritid, but its over-all pattern can be revealed only through a study of topotype material. As will become evident later, neither of these two "species" closely resembles the Cincinnatian chondritids.

It is apparent from J. F. James' (1885, p. 159) discussion that he never saw Hall's specimens of "B." gracilis or "B." gracilis var. crassa. He concluded that the two forms were conspecific with Psilophyton gracillimum Lesquereux which he placed in Dendrograptus Hall, believing them to be graptolites. James was mislead by Hall's figures of "B." gracilis which indeed do resemble Lesquereux's (1878, pl. 1, fig. 2) illustration of P. gracillimum. As the above discussion of "B." gracilis and "B." gracilis var. crassa shows, there is nothing to support a graptolite assignment for the species. On the other hand, P. gracillimum is judged to be a graptolite and is discussed herein under Mastigograptus Ruedemann.

Whereas J. F. James (1885) believed that "B." succulens Hall (1847, pl. 22, fig. 2a,b) could be identified in the local Cincinnatian section, an examination of the

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

more complete of the two cotypes shows that it can not be. The specimen (pl. 13, fig. 1; USNM 41133; latex mold UCM 37639) from the Trenton Limestone of Glens Falls, New York, is preserved as an epirelief on a black lithographic limestone. The basal portion of the host rock is a coarse-grained calcarenite. The specimen is quite large and subscribes an arc of almost 180°; the length of the longest observed branch is 12 cm. The nearly cylindrical individual branches are slightly sinuous and have a diameter of 4-5 mm. Fourth order branching was observed and the angle of bifurcation is between 30-45°. Interpenetration of the branches is not common. Although the fillings are also composed of dark, fine-grained lithographic limestone, the contact between the fossil and the host rock is well defined. Where the filling has been removed, a thin sheath of limonite is exposed. "B." succulens is best characterized by periodic swellings which occur at 2-4 mm intervals and give the branches an irregular nodose appearance. Since the filling reveals no trace of spherical bodies, the swellings are thought to be of prior origin.

Wilson (1948) selected "B." succulens as the type species for her monotypic genus Clematischnia. She redescribed Hall's figured specimens as well as additional material from the Cobourg (Middle Ordovician) beds of Ontario. She concluded that the genus was a "fucoid" and cited the "...solid, slender stems and...undulating ridges" as the diagnostic features (Wilson, 1948, p. 11). Other

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

than the arborescent pattern, the present author sees no evidence to support a vegetable origin. Instead the form is thought to be chondritid-like burrows, and the limonite sheath probably represents the vestiges of a mucus-coated wall. The origin of the nodular wall structure is problematic, for the swellings would seem to be too widely spaced and irregular to be attributed to peristaltic movements of a vermiform body. In general appearance the species lies midway between "Buthotrephis" gracilis Hall and "B." palmata Hall.[21] Whether the nodose walls of "B." succulens are of

---

21/ See Phycodes herein for a discussion of "B." palmata.

---

generic or specific importance can only be determined through a monographic study of Chondrites. In its present state Chondrites has sufficient latitude to permit inclusion of "B." succulens within the genus. In any event the form is unknown in the Cincinnatian, for the walls of Cincinnatian chondritids are either smooth or bear faint longitudinal striae.

Miller (1874, p. 235-236, fig. 29) proposed "Buthotrephis" ramulosus for a form which he described as "fossil ramose; stems branching; branches bifurcating, with very little change in size. Diameter of stems and branches from 1/16th to 1/10th inch. Structure not distinct, but has a granular appearance, as if from some change in its character."

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

The specimens occurred in "clay nodules, or indurated marl stones, [and] form entire layers of strata for hundreds of feet in length, between six and twelve feet above low water-mark, under the bank of the Ohio River." He interpreted it as a "fucoid."

J. F. James (1885) believed that the species was a burrow, but from the manner of his discussion, it is apparent that he never actually saw an identified specimen.

Both Fuchs (1895) and Reis (1910) discussed "B." ramulosus and compared it to the tubes of the Recent annelid Lanice conchilega. Reis remarked that "B." ramulosus had a tunic of pelecypod shell fragments, and Seilacher (1955) has shown that L. conchilega does construct a U- or W-tube composed of mucus-cemented shell fragments.

Unfortunately the three localities mentioned by Miller, which are probably Lower Eden and Upper Cynthiana, are now permanently covered by a rise in the level of the Ohio River due to the installation of navigation dams. Identified specimens are not present in Miller's collections at Harvard or the Chicago Natural History Museum, nor could they be found in the University of Cincinnati collections. His description and figure do resemble Cincinnatian chondritids with the exception that none of the local chondritids possesses a "granular appearance." Moreover, Miller remarked that the species is restricted to the one horizon. Each of the Cincinnatian chondritids here discussed is known from various localities and horizons. It is probable that Reis

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

(1910) based his interpretation on Miller's figures. No burrows with a lining of shell fragments have yet been discovered in the local rocks. In conclusion, while it is possible that "B." ramulosus is a chondritid which is restricted to basal Cincinnatian, it is also possible that it is a chondritid similar to those discussed below, except that it is filled with a coarse-grained sediment.

Scolithus tuberosus Miller and Dyer (1878) is also possibly a chondritid. They described the species as "the holes (sometimes called stems) are curved or winding, and pass through the rock, in an irregular course, sometimes uniting or branching, but never passing vertically through the strata as in S. linearis from the Potsdam Group [Upper Cambrian]. Upon the upper surface of the rock, the tubes are prolonged into crateriform elevations which are rarely at right angles to the surface of the rock" (Miller and Dyer, 1878b, p. 5). They went on to say that the diameter of the holes varies from 4-7 mm but remains constant in a given form. According to the authors, while the form is more abundant in the lower part of the Cincinnatian, it occurs throughout the section. They interpreted it as a burrow and stated that any comparison with Scolithus linearis was fallacious. J. F. James (1892, p. 38-39), in his monographic study of Skolithos, pointed out that S. tuberosus differed considerably from the accepted concept of the genus. He suggested that it be proposed as the basis of a new genus.

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

Identified material of S. tuberosus has not been located, and Miller and Dyer's illustration shows only the "crateriform elevations" which they likened to "the mud elevations, thrown up around the holes, made by the common crawfish [sic] [Cambarus diogenes] on our fresh-water streams" (Miller and Dyer, 1878, p. 5). While their description of the species resembles what will be discussed below as Chondrites, type-B, the diameter of the branches of S. tuberosus is nearly twice as great, and no "crateriform elevations" have ever been found associated with Cincinnatian chondritids. Thus, while it is possible that S. tuberosus is a chondritid, it is just as likely some variety of Palaeophycus. (See p. 310 for a discussion of Palaeophycus.) Little more can be said until identified material is located.

U. P. James (1878, p. 9) proposed Buthotrephis filciformis for specimens from "near Lebanon, Ohio, middle beds of Cincinnati Group." The species was never figured, but it is clear from his description that this is not a chondritid. Instead it is though to be synonomous with "Chloephycus plumosum" Miller and Dyer (1878) and is discussed thereunder.

The above discussion indicates that earlier authors did recognize the presence of Chondrites in the local section. However, the original descriptions and illustrations are inadequate and prohibit a meaningful comparison with the material at hand. It is equally as difficult to place the Cincinnatian specimens studied by the author in any of the myriad

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

European species. It is concluded that under the present circumstances little would be gained from establishing yet additional species of Chondrites. Therefore, the three Cincinnatian varieties are considered below as Chondrites, types A,B, and C. Of these three, C., type-A appears the most likely to stand up under a detailed comparison with other chondritids.

Chondrites, type-A

(pl. 8, fig. 6; pl. 11, fig. 4; pl. 27, fig. 2; text fig. 22)

Discussion: The forms included in Chondrites, type-A are abundant in the fine-grained calcarenites of the upper part of the McMicken member on U. S. Route 27, 1.4 miles south of Newport Shopping Center, in Taylor Creek where crossed by Wesselman Road, Hamilton County, Ohio, and also at the type locality of Corophioides cincinnatiensis.[22]

---

[22] See the discussion of Corophioides cincinnatiensis for detailed locality data on these occurrences.

They have also been recovered from the platy, fine-grained calcisiltites in the Southgate beds at Newport Shopping Center. Chondrites, type-A has not been encountered elsewhere in the Cincinnatian section. At the three McMicken localities mentioned above, the specimens are associated

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

with Trichophycus venosum, Corophioides cincinnatiensis, C. cf. luniformis, and Chondrites, type-B. Chondrites, type-A differs from all other Cincinnatian chondritids in that the entire system is quite small and compact, having its greatest dimension directed vertically rather than horizontally. As seen in vertical section (pl. 11, fig. 4; pl. 27, fig. 2), the system resembles a series of rootlets. Frequently the specimens extend through the entire thickness of the bed and into the subjacent lutite, although others terminate before reaching the base of the host rock. The longest (7 cm) form encountered was incomplete. The individual branches, which are only slightly depressed, have an average diameter of 0.8 mm. As in the chondritids studied by Simpson (1957), the diameter of the branches does not change within a system. As seen in vertical sections the tunnels vary considerably in their attitude. The angle formed by the branches and the ill-defined central axis ranges from 20-50°. While some branches continue at this attitude for their entire length, others flatten out and proceed parallel to the bedding planes. In contrast other branches (pl. 27, fig. 2) are deflected even more strongly downwards. The highest order of branches observed was secondary. There is no evidence of phobotaxis and the tunnels occasionally interpenetrate.

When viewed on bedding plane surfaces, Chondrites, type-A appears as a series of numerous, closely spaced holes arranged in a circular pattern. Plate 8, fig. 6 illustrates one slab from the Southgate strata of Newport Shopping Center

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

which bears seven separate systems on an area of 105 square cm. These can be readily distinguished from the other chondritids which occur in the same bed by the close spacing and small size of the tunnels. Serial sections taken parallel to the bedding plane demonstrate that there is no marked increase in the over-all diameter of the system with depth as is found in most chondritids. The diameter of one representative form measured 8 mm at the top of the bed and had expanded to only 1.5 cm at a depth of 4.5 cm. Serial sections also show that there is no well defined central axis, although the perforations may be more closely spaced in this area. As seen in fig. 22 it appears that first one branch then another served as the axis.

The sediment filling the tunnels is both finer grained and lighter in color than that of the host rock. As can be seen in pl. 11, fig. 4, the fillings frequently weather out when exposed to the elements; the contact between the tunnel wall and the host rock is always sharply defined. X-ray defraction analysis of fresh samples of host rock and filling shows significant mineralogical differences discussed in detail below.

The nature of the upper limits of the burrow are unknown, for in all observed cases the surface of the host rock bore patterns similar to that seen in pl. 8, fig. 6, and the tunnels could not be traced into the overlying lutite. The fact that both Corophioides and Trichophycus venosum are also incomplete strongly suggests that the upper portion of

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

the host rock was stripped away before the deposition of the lutite. Presumably, as shown in the reconstruction in fig. 22, Chondrites, type-A had one central opening.

Interpretation: As noted in the generic discussion, the ethological interpretation of Chondrites is still an open question. The most critical feature is the origin of the tunnel fillings. Richter (1931) and Simpson (1957) considered it to be sediment which sifted into the galleries; Tauber (1949) interpreted it as a combination of fecal material and collapsed lining of the burrow; and Seilacher (unpublished manuscript) has described it as fecal stuffings.

It has already been pointed out that there are obvious physical differences between the fillings and the host rock that contains them. In order to ascertain if these physical differences reflected a mineralogical variation, X-ray defraction analyses were conducted on the filling, host rock, and overlying lutite from the Route 27 locality. The results reveal that the filling is composed of 75-80 per cent quartz, 10 per cent illite, and minor amounts of chlorite, calcite, and mixed-layer clays in decreasing order of abundance. In contrast, the host rock contains 60 per cent calcite, 30 per cent quartz, and minor amounts of illite, chlorite, and mixed-layer clays. The mineralogical composition of the overlying lutite is nearly identical with that of the filling, the only difference being that the lutite contains even less calcite. Moreover, the data indicate that the clay minerals of the filling and overlying lutite

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

are well crystallized, whereas those of the host rock are not.

These facts would seem to indicate that neither Seilacher's nor Tauber's interpretation of the European chondritids apply to this Cincinnatian form. While it is true that the organic acids of the digestive system of an annelid or annelid-like form might account for the low calcite content of the filling, it is difficult to explain the increase in the quartz content in this manner. Also digestive enzymes would tend to reduce rather than increase the degree of crystallinity of the clay minerals. This, combined with the mechanical difficulties involved in stuffing the burrow discussed elsewhere, leads to the conclusion that Chondrites, type-A is not a stuffed burrow. It is also difficult to reconcile the texture and mineralogical composition of the filling with Tauber's hypothesis regarding C. furcatus. In addition, agglutinated tubes are normally composed of relatively large particles (see Seilacher's 1951 discussion of tube formation in Lanice conchilega).

Chondrites, type-A would seem to be the burrow of an organism which fed by ingesting the sediment of the host rock, extracting the nutrients, and excreting the waste products at the burrow's aperture, where they were swept away by currents. No trace of fecal pellets has been found in the overlying lutite. The animal probably lay with its anus near the burrow aperture and extended the body and/or proboscis into the substrate. When the limit of reach was attained, the organism partly contracted and excavated a new

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

tunnel. The same process was repeated several times until the entire network was formed. Due to the lack of phobotaxis in the burrow, it has not been possible to determine the exact mode of burrow formation as Seilacher and Simpson have done for some chondritids. If, however, the burrow was inhabited throughout the life of the dweller, it is likely that the upper branches were excavated first, and as the body increased in length, the animal burrowed progressively deeper. After the death or departure of the inhabitant, the open system was filled by the same mud which now forms the overlying lutite. The sharp contact between the fillings and the tunnel walls probably indicates that the walls were coated with mucus which inhibited collapse.

The major unanswered question is how could sediment completely fill such a large system without leaving voids which would later be filled by calcite or other minerals? Simpson (1957, p. 497) was questioned on this point and was unable to offer an explanation. This problem is considered in detail below.

Chondrites, type-B

(pl. 7, fig. 3; pl. 8, fig. 3,7,8; pl. 9, fig. 8; pl. 23, fig. 5; text fig. 25)

Discussion: The forms grouped under Chondrites, type-B constitute the most common, yet the most poorly understood of the Cincinnatian chondritids. They occur throughout

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

the Cincinnatian section in rocks ranging from fine-grained calcisiltites to medium-grained calcarenites. They are frequently associated with Trichophycus venosum and Corophioides. The reason that the morphology of the form is poorly known is that most frequently the entire system is oriented obliquely to the bedding planes and is thus difficult to observe. Normally Chondrites, type-B is seen only as a loose grouping of tunnels piercing the bedding planes (pl. 8, fig. 8). At some localities these tunnels are so numerous that they weaken the resistance of the host rock to erosion.

In spite of the difficulties involved, it is possible to piece together a rough outline of the geometry of the network through fragments which are found on bedding and joint planes. However, a complete analysis can be made only by detailed serial section studies.[23] When this is accom-

---

[23] As a senior thesis project Miss Beverly Barrow (1965) of this department attempted to establish the most feasible method for serial section study of Chondrites. She has found that the tunnels are so numerous in some areas that vertical sections taken at 7 mm intervals are not sufficient to reveal the pattern of the burrow. She has concluded that serial grinding is required.

---

plished, it may well be discovered that a number of valid species are contained in what is herein considered as

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

Chondrites, type-B.

As viewed in vertical section, Chondrites, type-B is seen as a series of tunnels intersecting the vertical plane at various attitudes. The diameter of the branches varies from 1-4 mm, and, as in the smaller chondritids discussed above, the contact between the filling and the host rock is always clearly defined. The form is especially well developed at the type locality of Corophioides cincinnatiensis, where the chondritids occur in the same bed as the U-tubes (pl. 23, fig. 5). One vertical section from this locality, covering an area of 171 square cm, revealed cross-sections of 239 tunnels which can be separated into two varieties. As seen in pl. 23, fig. 5, the lower half of the host rock contains branches averaging 1.5-2.0 cm in diameter. These are filled with a sediment both lighter in color and finer grained than that of the host rock. The tunnels are loosely grouped and do not show any preferred arrangement. In contrast the branches in the upper half of the specimen have a smaller diameter (0.5-1 mm), are more closely crowded, and are darker than the host rock. While they do not show the well developed stratification illustrated by Richter (1931) (herein fig. 15), some degree of linear arrangement is present. Observation of the upper surface of the host rock shows that only the lower portions of the systems are preserved in the calcisiltite. Either the upper part of the network lies concealed in the friable lutites or has been stripped away by subaqueous erosion.

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

A remarkable vertical section (pl. 8, fig. 3), from the uppermost Richmond beds of Blue Bank, Kentucky, on State Route 32, six miles southeast of Flemingsburg, provides insight into what appears to be the main axis of a Chondrites, type-B system. The host rock is a medium-grained, iron-stained calcarenite which bears large amplitude interference ripples on its upper surface. The fillings have been washed out and the walls of the branches can be seen to be perfectly smooth. This main axis is nearly vertical and has a diameter of 1-2 mm. As can be deduced from the truncated branches, both the upper and lower limits of the axis are incomplete. The secondary branches measure 1.0-1.5 mm in diameter and bifurcate from the main axis at an angle which varies from 35-75° off a horizontal plane. While the axis is well defined throughout most of its length, it apparently loses its individuality in the lower portion of the illustration. Another side of the same slab (pl. 7, fig. 3) gives additional information on the nature of the secondary branches. While most of the secondary branches proceed obliquely downward, some are recurved toward the upper surface of the bed. Close observation shows that they are following the bedding planes of the host rock. Miss Barrow has noted the same phenomena in some of the specimens from West Fork Creek, although the recurvature appears to be independent of the bedding. It is apparent from the discussion of these vertical sections that this variety of Chondrites differs markedly from Chondrites, type-A. The dimensions of the

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

individual branches and the system as a whole greatly exceed those found in C., type-A. Moreover, the branches of the Blue Bank specimens are gently arcuate and do not show the sinuosity of the smaller chondritids.

Thus far Chondrites, type-B has been discussed only as seen in vertical sections. Bedding plane surfaces bearing small segments of C., type-B branches are not uncommon. Occasionally exceptional specimens are found which reveal the nature of the branching as it occurs in the horizontal plane. The specimen from the Corryville strata of Stonelick Creek illustrated on pl. 9, fig. 8 is similar to the representatives of Chondrites described by Simpson (1957), as the branches are rigid and the angle of bifurcation varies within a small range. The tunnels have a diameter of 2.5 mm and the angle formed by any two branches is between 30-40°. While the branches do not cross over or interpenetrate, neither do they demonstrate the well developed phobotaxis seen in the Holzmaden specimens of C. bollensis.

The largest and most complete specimen of a Chondrites, type-B network discovered to date in the Cincinnatian rocks is also from the Corryville beds at Stonelick Creek. It is preserved as a concave epirelief on a calcisiltite and is superimposed over interference ripples. The network covers an area of 289 square cm and as seen in fig. 25 appears to be composed of five "main" branches arranged in a radial pattern. The walls of the tunnels are smooth and their diameter varies from 2.5-4 mm. Bifurcation

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

proceeds to the fifth order, and while it follows no set pattern, many of the branches are forked distally. The angle of branching ranges between 20-40°. As in the other Stonelick specimens the branches do not interpenetrate but only in a few isolated instances do they show anything which even approaches phobotaxis.

In contrast to the above forms, specimens are known where interpenetration is the rule rather than the exception. Plate 8, fig. 7 illustrates one such form from the Blue Bank which occurs as an epirelief on the same bed bearing the specimens shown on pl. 7, fig. 3. The branches interpenetrate to such a degree that they form a bewildering cross-hatched pattern. Generally the interpenetration appears to be between branches of different systems. The dimensions of the tunnels are similar to those seen in vertical section on the same slab.

Interpretation: The origin of the Chondrites, type-B network is thought to be similar to that discussed for C., type-A, i.e., the empty burrow of a Sedimentfresser which was later filled by sediment. None of the fillings contain fecal pellets nor is there anything that could be interpreted as the lining of an agglutinated tube. The consistently larger size of the C., type-B system suggests that C., type-B and C., type-A were made by different organisms. The fact that some C., type-B networks are oblique throughout their entire length, while others tend to flatten out on bedding planes, is probably indicative of the food distribution in the

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

substrate. Planar networks indicate a high concentration of nutrients in some beds, whereas the oblique forms show that the food was rather evenly distributed throughout the host rock.

As mentioned above, a most critical factor is whether it is possible to fill such a large system solely with sediment sifting in from above. In order to test this hypothesis, a glass model of a portion of a Chondrites network was constructed (fig. 36). Glass tubing with an internal diameter of 4 mm was used, and the various sections were connected by plastic sleeves. The greatest length of the system (A-G) measured 51 cm, far in excess of the longest known chondritid branch. The distal ends of the system (C-G) lay on a horizontal plane, and the vertical distance from the top of the funnel (A) to the plane on which the distal ends lay was 17 cm.

Three types of sediment were used: 1) highly angular silt-sized quartz, 2) a fine silt composed of pumice, and 3) Pleistocene lake clays. Corks were placed in all the endings (B-G), and the system was completely filled with fresh water; care was taken to see that no air bubbles remained. The sediment was then mixed with 200 ml of fresh water and stirred until it was in suspension. The suspension was then placed in the mouth of the funnel with an eyedropper, the volume of suspended solution introduced at any given time varying from 2-5 cc. In order to accelerate the process, the amount of sediment entering the system was in

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

excess of that which might be expected to occur under normal geological processes.[24] It must be admitted that the above

---

[24] It was noted that when a large volume of sediment was introduced at one time, the result was quite prominent graded bedding. It might be fruitful to check some of the more coarse chondritid fillings for graded bedding which would be proof of passive filling.

---

apparatus represents a rather crude attempt to simulate actual conditions, and, therefore, the obtained results can be accepted only as suggestive rather than conclusive.

It was found that the angular sand grains would fill a maximum of only 53 per cent of the volume of the network. The results achieved with the finer grained pumice were no better. The apparent reason for this is that we are dealing with a completely closed system and that a point was reached where the water pressure in the distal ends of the system prohibited further flow. It was found that once the sediment stopped moving, no amount of sediment added would start the process again.

Even though the chondritid network was coated with mucus, it was probably not a closed system, and in order to better approximate actual conditions, the entire apparatus was submerged in water, the corks being replaced by fiberglass wool packings. It was found that under these conditions the angular sand would fill 62 per cent of the

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

system, and the lake clays filled 74 per cent. One additional experiment was attempted. In order to simulate bottom currents moving over the mouth of the burrow, an electric fan was allowed to blow across the tank. It was found that the clays filled 87 per cent of the entire system, and the sediment completely filled a segment of the tube 44 cm in length. This is nearly three times the length of the longest chondritid branch noted by Simpson (1957).

Under actual geological processes it might be even easier to fill the burrow. The rate of sediment inflow into the burrow would almost certainly be less than that used in the experiment, and intermittent and continuous currents moving across the mouth of the burrow could alter the currents sufficiently to allow the sediment to move to the ends of the system before more sediment was introduced. Likewise, wave shock or similar phenomena might be sufficient to jar loose any sediment which had become clogged. Possibly most important of all is the role that diagenetic compaction could play. Most of the Cincinnatian chondritids are generally overlain by lutites. During compaction the host rock, being a silt or sand, would remain relatively unchanged, but the finer grained lutites, which would be greatly affected, could literally be intruded into the open network. This would explain how arcuate chondritids, such as those seen on pl. 7, fig. 3, could be filled by such a process. Thus, while it is not possible to prove that Cincinnatian chondritids are open burrows which are later

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

filled by sediment, there may well be sufficient mechanisms by which such a process could be achieved. Additional studies should be conducted employing a more refined model of Chondrites. Moreover, X-ray analysis of the larger C., type-B networks would be worthwhile. This is especially true for the forms from West Fork Creek which show two different types of fillings.

Since the above hypothesis requires inspection of the overlying beds, host rock, and fillings, the author is not in a position to extend this hypothesis to cover chondritids in general. The thesis can be tested only by direct field observations and laboratory analysis of the actual materials in question.

Chondrites, type-C

(pl. 7, fig. 2; pl. 8, fig. 2,4,5; pl. 25, fig. 4)

Discussion: Chondrites, type-C appears to differ from all other Cincinnatian chondritids because the branches of the system form a dense interwoven network, the surface of which is marked by delicate longitudinal striae. Since all specimens at hand are preserved as concave epireliefs on fine- and medium-grained calcarenites, the composition of the filling and the nature of the upper limits of the network are unknown. All of the specimens are from Richmond age rocks, and most are from the Whitewater beds of Short Creek where crossed by Indiana Route 227, three miles southeast of Rich-

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

mond, Indiana. The locality was recollected without success, as the bed containing the specimens could not be located.

The most striking feature of these forms is the density of the network. Some areas have been so thoroughly mined that the interburrow areas occur as isolated knife-like ridges (pl. 7, fig. 2).[25] The density of the system is

---

[25] It was found that the network can best be seen in latex molds, and with the exception of pl. 7, fig. 2 and pl. 25, fig. 4, all illustrations are of latex molds rather than the actual specimen.

---

best shown by the form illustrated on pl. 7, fig. 7, where the burrows in the lower half of the specimen cover an area of 49 square cm. However, this is accomplished at the expense of considerable interpenetration, and one set of branches appears to be superimposed over another. Sixth order branching can be observed in at least one segment of the system illustrated on pl. 8, fig. 2, and while the angle of bifurcation varies, it tends to be quite acute (20-30°). The branches irregularly pinch and swell, and the diameter varies from 1.5-3 mm.

Based solely on the specimens discussed above, one would have great difficulty in justifying a chondritid assignment for the Short Creek material. Yet, other specimens from the same locality reveal a more typical chondritid pattern. One specimen (pl. 8, fig. 4) possesses a bilateral

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

symmetry slightly reminiscent of the form illustrated by Fuchs (1895, fig. 11). However, this may only be a fortuitous arrangement of two branches from different systems. Note that the branches do not show the extremely close packing of those discussed previously. Another slab (pl. 8, fig. 5) bears two specimens, one of which (lower left) shows five tunnels which are bundled proximally but branch distally to form the characteristic anastomosing network. The diameter of the branches is slightly in excess of 1 mm. The other specimen on the slab differs as it is obliquely oriented and only portions of the system are visible. It gives the impression of possessing a radial outline. What is perhaps the most significant specimen is illustrated on pl. 8, fig. 2. At the proximal end of the large flabellate branch are nine holes arrayed in a circular pattern. This indicates that the master plan of C., type-C might be a relatively small number of vertically directed shafts which flatten out with depth and bifurcate repeatedly. If this is the case, the specimens seen on pl. 8, fig. 2,4,5 represent small segments of a much larger pattern.

The branches of all specimens are marked by faint longitudinal striae which do not form a well defined pattern. Usually the larger the diameter of the branches, the more apparent are the striae.

Interpretation: The origin of the Chondrites, type-C network is thought to be similar to that of the two types of chondritids discussed previously. The fact that

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

the branches are oriented horizontally indicates a high concentration of organic material in thin layers. Presumably the host rock was overlain by a lutite, and the tunnels were filled with fine-grained material which has since been removed by erosion. The presence of striae suggests that the originator of the burrow may have been different from those that excavated the other Cincinnatian chondritids. Although the striae recall arthropods, it is equally possible that they are the impressions of setae borne by a vermiform organism.

Fascifodina n. gen.

(pl. 10, fig. 6; pl. 25, fig. 8; text fig. 18,21)

Type Species: The specimen illustrated on pl. 10, fig. 6 (UCM 37632), from the Corryville beds of Second Creek where crossed by Cozzadale Road, Warren County, Ohio, is designated as the type specimen for the monotypic species Fascifodina floweri n. sp.

Diagnosis: Vertical bundled tunnel systems of infaunal origin which are arranged in a semi-elliptical pattern and are preserved principally as short vermiform concave epireliefs on calcisiltites.

Discussion: The genus was first described by Flower (1955) from the Corryville beds at Stonelick Creek. He characterized it as "...short curved or vermicular markings...arranged consistently in groups, each group showing a

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

crescentic or horseshoe-shaped pattern" (Flower, 1955, p. 862). Flower remarked that although the markings occur as shallow concave epireliefs on only one bed, they are so numerous that they frequently overlap.[26] In nearly all

---

[26] Stream action has covered Flower's original locality which was some 20 meters below the Ohio Route 131 bridge. At the same time a second, slightly higher exposure has been uncovered 50 meters above the bridge.

---

cases the crescentic markings are oriented with their concave face to the median line of the horseshoe (herein fig. 21A,B). He maintained that there is a definite bilateral symmetry, although the total number of individual markings comprising the horseshoe varies from 6-13. Two forms (Flower, 1955, fig. 3A,B) were figured.[27] One is nearly equidimensional,

---

[27] These two specimens are in Dr. Flower's private collection.

---

measuring 6.0 cm by 6.5 cm, while the other is shorter (4.0 cm) and broader (7.0 cm). Both forms show a faintly defined raised area in the center of each horseshoe, and in one (fig. 21A) a series of linear markings leads from the vicinity of the vermiform imprints to the raised central area.

Additional specimens have been collected from the Corryville beds of Second Creek, which is 10.4 miles north

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

of the Stonelick Creek occurrence. For the most part these have the same horseshoe pattern described by Flower, although some are irregular and poorly developed. The Second Creek specimens provide a clearer insight into the morphology of the genus in that the raised area between the open ends of the horseshoe is much better developed. Upon close examination this structure appears as a group of eight or nine curved cylinders, 2-3 mm in diameter, which are bundled together at their apex but radiate out in the direction of the imprints at the base. One of these cylinders (pl. 10, fig. 6, center right) leads directly into one of the vermiform markings. Serial sections of these specimens reveal that the vermiform markings extend in a highly sinuous course to a depth of 2-3 cm and are filled with a sediment which is lighter in color and more fine grained than the host rock. In contrast, vertical section of the Stonelick Creek specimens show that they extend only a few millimeters into the substrate.

Interpretation: Flower (1955) believed that the markings were made by the appendages of some animal grasping the bottom. He maintained that the pattern is consistently too regular to be a "chance arrangement of individual vermicular markings made by individual worm-like animals" (Flower, 1955, p. 862). He mentioned holothuroids as a possibility but doubted that they would be able to produce such a regular pattern. Instead he selected an orthoconic nautiloid, Orthonybyoceras Shimizu and Obata, whose remains are common

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

in the Corryville. Flower went on to describe in some detail how the tentacles might have produced such markings (see fig. 21C-F herein). Since parallel alignment and other current indicators are lacking, he believed that the animals grasped the bottom in order to temporarily anchor themselves against wave-produced turbidity.

Flower's interpretation fails to explain both the bundled cylinders and the fillings found beneath the markings. Even if the tentacles probed to a depth of 2-3 cm, how could the holes remain open long enough to be filled with the finer grained material? The Second Creek specimens occur in a calcarenite, and any opening formed would certainly collapse as soon as the tentacles were withdrawn.

Instead it is concluded that the structure represents a portion of a bundled feeding burrow. Unfortunately the morphology of the entire burrow is unknown. At the Stonelick Creek locality the surface bearing the markings is overlain by a 2.5 cm bed of lutite which bears no trace of any allied structure. It is probable that the upper portions of the original burrow were stripped away prior to the lutitic deposition. The specimens from Second Creek were found in Corryville float, and it was not possible to locate material in place. As shown in the reconstruction (fig. 18), it is believed that the organism burrowed down throught an unknown thickness of lutite and laced the subjacent calcarenite with a series of bundled burrows arranged in a semi-elliptical pattern. This differs from Phycodes and other bundled burrows

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

not only in the orientation (vertical as compared to horizontal) but in the highly irregular nature of the portion of the tunnels found in the calcarenite bed. The vermiform markings seen on the surface are attributed partly to the actual mining activity of the organism and partly to the collapse of the tunnel system. The material filling the tunnels is probably composed of a mixture of the overlying lutite and the sediment worked by the organism. There is no evidence of fecal pellets or strings. The raised bundles found between the open ends of the horseshoe in the Second Creek forms represent material dragged up the tube, thus the bundles form a mold of that portion of the network.

The walls of the burrow are not annulated as in Phycodes or scratched as in Trichophycus venosum, hence there is no direct evidence which would point to the zoological affinities of the producer.

Phycodes Reinhard Richter, 1850

(pl. 1, fig. 4; pl. 9, fig. 1-5; pl. 10, fig. 2,4; pl. 12, fig. 9; pl. 13, fig. 4; pl. 14, fig. 6; text fig. 12-13)

1850 Phycodes Richter, Reinhard, Deutsche Geol. Gesell., Zeitschr., Bd. 2, p. 205.

1851 (non) Inocaulis Hall, J., American Jour. Sci. and Arts, Second Ser., vol. 11, p. 401.

1862 Licrophycus Billings, E., Palaeozoic Fossils, vol. 1, Geol. Surv. Canada, Public., p. 99, fig. 87.

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

1878 Licrophycus, Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 2-3, pl. 2, fig 4.

1885 Inocaulis, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 164, fig. 8.

1934 Phycodes, Magdefrau, K., Neues Jahrb. Mineral., Geol., u. Paläont., Beil-Bd. 72, p. 259-282, fig. 1-6, pl. 10-11.

1955 (in partim) Phycodes, Seilacher, A., Akad. Wiss. Lit. Mainz, math.-nat. Kl.., Abh., no. 10, p. 383-388, fig. 3.

Type Species: Phycodes circinatum Reinhard Richter (1850) from the Ordovician "Phycodes beds" of Thuringia.

Diagnosis: Horizontal bundled burrows of infaunal origin preserved outwardly as convex hyporeliefs. Over-all pattern flabellate, broom-like, or occasionally circular. Some forms consist of a few main branches showing a Spreite-like structure which distally gives rise to numerous free branches. In other forms the Spreiten are lacking and branching tends to be more random. Individual branches are terete and finely annulate or smooth. Length of entire burrow 2.5-15 cm; diameter of branches 1.5 cm.

Discussion: Phycodes, or comparable forms, have been the subject of three excellent studies; Sarle (1906), Magdefrau (1934), and Seilacher (1955) all have added to the knowledge of these bundled structures, which are found

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

in the Lower Paleozoic of North America, Europe, and Asia.

Magdefrau (1934) has restudied topotype material (pl. 9, fig. 5) and has found that Phycodes circinatum is preserved as convex hyporeliefs in quartzites. Most specimens are 10-15 cm long, although individuals as small as 2-4 cm long are known. The depth (taken from deepest branch to base of quartzite bed) is 2.5 cm (see fig. 12b). Although branching occurs at very acute angles, the branches first proceed parallel for a distance and then fan out, some doubling back so that they again run parallel to the main axis. Specimens exhibit no apparent preferred orientation, as the main axes of the various forms proceed in every conceivable direction. The free branches, which have an average diameter of 1.3 mm, are marked by delicate annulations which were originally noted by Richter. These average 20-25/cm, the greatest number being 38/cm. According to Magdefrau (1934, fig. 4), the annulations are exposed only when a smooth, thin (0.25-0.5 mm) outer covering is eroded.

Serial sectioning undertaken by Seilacher (1955) has clearly revealed the Bauplan of P. circinatum (fig. 12b). The proximal portion of the structure consists of a few main tunnels with retrusive Spreiten. Distally each tunnel divides into numerous free branches which angle back up into the host rock. Beyond this there is no set pattern, as the free branches may swing first one way then another.

There is some disagreement regarding the morphological limits of Phycodes. Seilacher (1955) has greatly expanded the

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

genus, while Häntzschel (1962) has been more conservative. Seilacher (1955) considered Arthrophycus Hall (1852) to be a junior synonym of Phycodes and also placed Buthotrephis palmata Hall (1852) (herein pl. 11, fig. 3,7) within the genus. At the same time he proposed a new species, P. pedum, from the Lower Cambrian of the Salt Range.

Although there is an apparent similarity in general pattern between Arthrophycus and Phycodes, the former differs in that it is quite large (branches up to 60 cm long, according to Häntzschel, 1962), bears prominent annulations, and has bilobate branches which can be as much as 1 cm in diameter. Moreover, Sarle (1906) has shown that the bundled structure of Arthrophycus, as it occurs in the Silurian Medina Sandstone of western New York, is a response to sedimentation (fig. 23 herein). The organism was forced to raise the level of the burrow as sand repeatedly buried the aperture. Whether this explanation applies to Arthrophycus from other localities is not known. As will be shown below, the bundled structure of Phycodes is of different origin. Häntzschel (1962) considered Arthrophycus a separate genus, and, based on the differences cited above, his decision is accepted here.

Seilacher (1955) also considered Buthotrephis palmata Hall (1852) (see pl. 11, fig. 3,7 herein) to be a species of Phycodes. B. palmata Hall is not common. It was originally described from the Clinton (Silurian) beds of New York and has been identified by Seilacher (1955) in the Lower Cambrian of the Salt Range. While B. palmata is

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

certainly not similar to the other species of Buthotrephis figured by Hall (1847, 1852) (they are clearly chondritids; see pl. 13, fig. 8 herein), it is highly doubtful that it should be assigned to Phycodes. Seilacher's sectioning of his Salt Range forms (fig. 12a) shows that the branching pattern is slightly different and that there is only an incipient Spreite developed. More important is the fact that Hall's forms have far fewer branches than P. circinatum, and these branches are smooth and much larger (up to 2 cm in diameter). Hall's material has never been sectioned or adequately studied. When such a study has been completed, it will most likely be found that B. palmata merits a new generic designation.

The specimens from the Lower Cambrian of the Salt Range described by Seilacher (1955, fig. 4a,b) as P. pedum differ considerably from all forms discussed above. A gently sloping master tunnel which is open to the outside bifurcates at depth to give rise to horizontal sickle-shaped galleries. In turn numerous short vertical shafts branch off the galleries. Although the form is known only from a few specimens, it should be established as a separate genus.

Phycodes is judged to be the senior synonym of Licrophycus Billings (1862). Although none of Billings' many species from the Middle and Upper Ordovician of Ontario has ever been sectioned, Licrophycus is externally similar to Phycodes (compare Magdefrau, 1934, pl. 10-11 with Billings, 1862, fig. 87 and Wilson, 1948, pl. 4, fig. 1; pl. 5, fig. 4).

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

Based on Billings' figures and descriptions, the only apparent differences are that Licrophycus has smooth branches and these lack the recurvature seen in some of Magdefrau's material. The forms are similar in the diameter of the branches and the size of the structure as a whole.

Interpretation: There have been several interpretations as the the origin of Phycodes-like structures.[28]

---

[28] The reader is referred to Magdefrau (1934) for a more complete discussion of the early history of the genus and its interpretation.

Most early workers, e.g., Reinhard Richter (1850) and Billings (1862), held them to be "fucoids," and this notion persisted with at least two authors (Hundt, 1931, and Wilson, 1948) well into the present century. Others (e.g., Potonié, 1899) thought Phycodes to be of inorganic origin (rill marks), while Abel (1935) considered Arthrophycus as the casts of worm tubes thrown together during a storm. Although Abel never mentioned Phycodes specifically, he may well have believed that the origins of the two were similar. However, more careful studies by later authors have shown conclusively that it is a branching burrow. As has proved true with so many "fucoids," sectioning of the specimens provided the key. This reveals (fig. 12b) that both ends

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

the hyporelief structure extend up into the bed bearing them. Magdefrau reflected that this concave-upward orientation is strange preservation for algae.

The most detailed ethological analysis of P. circinatum was given by Seilacher (1955). He considered it a Fodinichnia where the organism more or less systematically mined a nutrient-rich layer along a silt-mud interface (see fig. 12b herein). The animal first burrowed down through the silt, then moved horizontally along the interface before once again angling up into the silt bed. The resulting structure resembles a "U" in which one limb is steeper than the other. Following this, the organism withdrew from the distal portion of the burrow and proceeded to excavate a new tunnel adjacent to the old one. Periodically the unbranched proximal portion of the burrow was elevated by removing sediment from the ceiling and packing it, along with waste material, on the floor.[29] This activity

---

[29] Neither Magdefrau (1934) nor Seilacher (1955) reported finding fecal pellets in the tunnel.

---

gave rise to the retrusive Spreite-like structure seen in fig. 12b. When a given area was mined out, a new "master" tunnel was formed in another location, and the entire process repeated again.

Although Seilacher (1955) drew an analogy between

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

the bundled feeding shafts of Arenicola marina and those of Phycodes, directly comparable Recent structures are unknown. The annulate branches of P. circinatum suggest an organism with an annelid-like body, but the fact remains that we are dealing with a basic pattern which could have been made by any one of a number of organisms.

Cincinnatian Representatives

Phycodes flabellum (Miller and Dyer)

(pl. 1, fig. 4; pl. 9, fig. 1-4; pl. 10, fig. 2,4; pl. 12, fig. 9; pl. 13, fig. 4; pl. 14, fig. 6; text fig. 13)

1878 Licrophycus flabellum Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 2-3, pl. 2, fig. 4.

1885 Inocaulis flabellum, James, J. F., Cincinnati Soc. Nat. Nat. Hist., Jour., vol. 7, p. 164.

Type Locality: Licrophycus flabellum Miller and Dyer (1878) from the "upper part of the Cincinnati Group" (Richmond) of Lebanon, Ohio. Type specimen: pl. 9, fig. 1; HBM 3178.

Diagnosis: Bundled burrows generally arranged in a flabellate pattern. Individual branches cylindrical and annulate. Sectioning reveals no evidence of Spreite-like structure or fecal material.

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

Discussion: Although P. flabellum is known from several localities in the upper two-thirds of the Cincinnatian section (Maysville-Richmond), it is not a common form, and only 25 specimens have been available for study. However, when the species is encountered, it is not unusual to find more than one specimen on a slab, e.g., an area in the Corryville beds of Stonelick Creek, measuring 45 cm by 27 cm, contained five specimens. All Cincinnatian specimens are preserved outwardly as convex hyporeliefs in calcisiltites or fine-grained calcarenites. There is no marked difference between the lithology of the host rock and that of the branching structure.

It is difficult to generalize on the over-all pattern of P. flabellum, because the species shows a good deal of variation. However, as Miller and Dyer indicated in their choice of a specific name, many Cincinnatian specimens are flabellate. This condition is best typified by a portion of the type specimen (pl. 9, fig. 1) and the specimen illustrated on pl. 14, fig. 6. The latter form possesses 98 separate branches which cover an area of 41 square cm, while in the flabellate portion of the type specimen, 23 branches cover an area of 3.75 square cm. This fan-like arrangement points up one difference between P. flabellum and P. circinatum. The European species is more fasciular, closely resembling a broom-shaped bundle, where the height[30/]

30/ Height is here defined as the height of the entire

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

structure. It is equal to the height as used by Magdefrau (lowest branch to base of bed) plus the added height shown by sectioning. As viewed in fig. 13C it would be the distance from the lowest branch to the dashed line.

---

is nearly equal to the width. In many Cincinnatian forms the width of the structure greatly exceeds the height. A vertical section of the form seen on pl. 14, fig. 6 reveals that only the basal 2 mm of the bed is disturbed. Thus this specimen has a width of 13 cm and a height of only 2+ mm. A variation of the flabellate pattern (pl. 10, fig. 4) consists of five or six bundles which radiate out from a central point in such a manner that they nearly cover a complete circle.

Not all Cincinnatian forms show such a definite Bauplan. In such specimens (pl. 10, fig. 2) the branches are bundled together, but the over-all arrangement appears to be rather haphazard, and the various bundles cross over and interpenetrate.

The individual branches are terete in cross-section and range from 1-3 mm in diameter; the diameter remains constant throughout their length. Some branches give the appearance of possessing a median furrow, but if the branches are traced far enough,, they are seen to bifurcate. All branches are marked by delicate annulations which average 6-8/cm. There is no trace of a smooth outer sheath like that described by Magdefrau in P. circinatum.

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

In hopes of presenting a reconstruction of P. flabellum as Seilacher did for P. circinatum and Buthotrephis palmata, serial sections of several specimens were prepared. When it became apparent that polished, etched, and stained sections would not suffice, thin sections were cut. All these reveal that with one lone exception there is no Spreite-like structure present in P. flabellum. One encounters only a general area of disturbed bedding (pl. 9, fig. 3). Moreover, the contact between this area and the undisturbed bedding of the host rock is not sharp but gradational. The one exception mentioned above is the presence of a protrusive Spreite in a small area of one form (pl. 9, fig. 2). As will be shown below, this lack of a definitive internal structure is significant in the ethological interpretation of the species.

While the internal structure of most of the burrow is not known, it is possible for the first time to shed some light on the nature of the main shaft. Neither Seilacher nor Magdefrau made any mention of the extreme proximal (unbranched) ends of Phycodes. Two specimens of P. flabellum (pl. 1, fig. 4; pl. 9, fig. 4) show a wide (up to 1 cm) vertical shaft along which the bedding planes are bowed down. The original diameter of the shaft was undoubtedly smaller, for the dark L-shaped body seen in pl. 9, fig. 4 shows that collapse of the walls has led to some enlargement. A most interesting point is that the main shaft is vertical. In both specimens it extends nearly to the base

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

of the calcisiltite bed, where it geniculates at 90° to run parallel to the base of the bed before fanning out in multiple burrows along the interface (see fig. 13).

In gross morphology P. flabellum is not unlike P. circinatum or the many species described by Billings. However, it differs sufficiently to justify the retention of Miller and Dyer's specific designation. The diagnostic features are the flabellate pattern, the lack of a smooth outer sheath, and the general absence of Spreiten. Billings' specimens have never been restudied, but it is likely that further work on them will reduce the number of Canadian species in the genus.

Interpretation: Miller and Dyer (1878) followed the lead of earlier workers on Phycodes and assigned P. flabellum to the "fucoids."

The species reminded J. F. James (1885, p. 164) "...of the appearance that would be made in mud by the expanded tentacles of a crinoid." He believed, however, that it was a graptolite and placed it in Inocaulis Hall (1852), noting that it differed greatly from I. plumosum but was "quite similar" to I. walkeri Spencer (1884).

As Ruedemann (1908) has shown, Inocaulis plumosum and I. walkeri (=Acanthograptus walkeri) are graptolites in which the usual graptolite integument is preserved. Clearly such forms have no genetic bearing on P. flabellum. Ruedemann (1908, p. 191) succinctly dismissed I. flabellum with "this is no graptolite."

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

The serial sections confirm that neither Miller and Dyer nor James made a correct interpretation. The internal structure and the interpenetration of the branches leave no doubt that P. flabellum is a trace fossil. However, the exact ethological meaning of P. flabellum is unclear and three alternate hypotheses will be presented below.

As Seilacher has suggested, the inhabitant of the burrow may have been a Sedimentfresser similar to the Recent Arenicola marina. However, Schäfer (1962) has shown that Arenicola constructs bundled feeding shafts only in highly cohesive mud. In sand the burrow more closely resembles a J- or U-tube. Likewise, there is no trace of cone-shaped areas of disturbed sediment associated with the numerous branches. Moreover, if the organism has mined out the burrow and the filling represents a collapse structure, one would expect to find slumping in the overlying beds of the host rock. The serial sections show very little evidence of any slumping.

It is also possible that the inhabitant was a selective feeder, i.e., a form which was able to selectively glean the nutrients from the sediment without ingesting a large volume of inorganic material. It may be that the organism lay with its anus near the mouth of the burrow and systematically extended its anterior end and/or tentacles through the sediment, selectively removing the nutrients. The animal was thus disturbing and displacing the sediment rather than removing it. After the animal had extended

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

itself to the maximum length, it withdrew and the sediment filled in the cavity. Since there was little net loss of sediment, one would not expect to find extensive slumping. As evidenced by the bundled nature of the burrow, this process was repeated several times. When a given area was mined out, the organism changed directions and again proceeded to feed. Since the Spreiten are generally conspicuous by their absence, there is little evidence that the animal made a practice of packing waste material on either the floor or the roof of the burrow. Following the demise or departure of the organism, a combination of collapse and sediment sifting in from outside filled the proximal portion of the burrow (i.e., the main shaft). It must be admitted that the feeding habits of Recent organisms do not provide strong support for this argument. All known selective feeders (e.g., terebellids) live in vertical shafts and extend their tentacles over the depositional interface. It is somewhat difficult to visualize how this might be accomplished at depth.

The third possibility is that P. flabellum represents the Domichnia of a hemisessile organism in which only the upper part of the burrow was coated with mucus. When the animal periodically departed from the burrow, the lower, unsupported portion collapsed. Thus, the inhabitant was obliged to reconstruct the distal portions of the structure each time it re-entered the burrow. Although this theory explains the gradational contact between the burrow filling

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

Filmed as received

without page(s) 223.

UNIVERSITY MICROFILMS, INC.

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

and the host rock, it too is unsupported by Recent observations. In addition, it does not seem logical that the organism should repeatedly have to reconstruct a portion of the burrow. Such behavior would indicate that there was a defect in the general Bauplan.

Dactylophycus Miller and Dyer, 1878

(pl. 1, fig. 3; pl. 7, fig. 7; pl. 13, fig. 2; pl. 18, fig. 3)

1847 (non) Palaeophycus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 7, pl. 2, fig. 1,2,4,5.

1873 ?Palaeophycus, Orton, E., Geol. Ohio, vol. 1, p. 387.

1873 (non) Planolites Nicholson, A., Roy. Soc. London, Proc., vol. 21, p. 289.

1878 Dactylophycus Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 2-3, pl. 3, fig. 1-2.

1885 (in partim) Palaeophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 164.

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Species: Dactylophycus tridigitatum Miller and Dyer (1878) from the Eden beds of Cincinnati, Ohio.

Diagnosis: Small, branching, annulate, bilobed burrows of infaunal origin which are preserved outwardly as convex hyporeliefs. Branching pattern may be radiate or random.

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

Discussion: Dactylophycus was proposed for forms with "a single stem, which divides, at one or both ends, into three or more buds or short branches, each of which terminates more or less abruptly in a point. The stem and branches may be smooth or rugose" (Miller and Dyer, 1878b, p. 1). Two species, D. tridigitatum and D. quadripartitum, were established with the former being designated the type species. Figured specimens of both species are listed in the catalogue of the paleobotanical collection of Harvard University, but only D. quadripartitum was located. Therefore, judgment on the nature of D. tridigitatum must be based solely on Miller and Dyer's description and their highly schematic illustration.

As James (1885) stated, it is possible that Palaeophycus radiata Orton (1873) belongs here. The species, from "Morris' Hill, Warren County, Ohio," was never figured and Orton's description is vague. He characterized it as "five or six cylindrical stems radiating from a common center. The stems are from two to three inches long, and agree in form with some that Hall has figured as Palaeophycus" (Orton, 1873, p. 387). While it is possible that P. radiata is synonomous with Dactylophycus, it is just as likely that it is a specimen of Phycodes flabellum. The only form described by Hall under Palaeophycus which resembles either of the above is ?Palaeophycus sp. Hall (1852, pl. 10, fig. 3).

Miller (1889) pointed out the close similarity between Dactylophycus and Ichnophycus tridigitatum Hall (1852),

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

pl. 10, fig. 7a,b), described from the Clinton (Silurian) beds of New York State. The present author has had the opportunity to study the type specimen of Ichnophycus and must disagree with Miller's conclusion. Ichnophycus is preserved as a concave epirelief in the thin micaceous bed which overlies a coarse-grained quartz sandstone. It possesses three completely smooth non-bilobate branches and closely resembles a "bird's foot" in outline. While it is probably a portion of a burrow, there is no real basis for comparison with Dactylophycus.

Dactylophycus quadripartitum Miller and Dyer
(pl. 1, fig. 3; pl. 7, fig. 7; pl. 13, fig. 2; pl. 18, fig. 3)

1873 ?Palaeophycus radiata Orton, E., Geol. Ohio, vol. 1, p. 387.

1878 Dactylophycus quadripartitum Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 2-3, pl. 3, fig. 1.

1885 Palaeophycus radiata, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 164.

1891 Planolites radiata, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Locality: Eden beds, Cincinnati, Ohio. Type specimens: pl. 1, fig. 3 (HBM 3174; latex mold UCM 37600)

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

and pl. 13, fig. 2 (HBM 3174; latex mold UCM 37608).

Discussion: Miller and Dyer (1878b, p. 2) characterized D. quadripartitum as a "plant [with] a stem, which is divided, at one end, into four finger-like prongs or branches, the other end is unknown....Each branch has a slight longitudinal depression, in the middle, and shows some evidence of rugose markings. The specimen illustrated, however, is nearly smooth."

Only six specimens of D. quadripartitum are known, all are from the Eden and occur outwardly as convex hyporeliefs in platy calcisiltites. The individual branches have an average diameter of 2-4 mm and a length of 15 mm. The number of branches varies from specimen to specimen and is not a critical factor as Miller and Dyer believed. Each branch possesses a well developed median furrow which in some specimens is more like a flat median trough, taking up one-third to one-half the width of the branch (pl. 18, fig. 3; USNM 40027). Well preserved specimens[31] possess

---

[31] Miller and Dyer claimed the branches were smooth or annulate. However, their smooth branches are the results of Recent erosion.

---

delicate annulations which average 15/cm. In the specimens just mentioned the annuli are confined to the lateral ridges and are not found in the trough.

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

The pattern of branching is variable. Two specimens show a flabellate pattern. One of these (pl. 7, fig. 7) possesses 10 branches which cover an arc of nearly 180°; the other (pl. 1, fig. 3) has only four branches which do not overlap. One other specimen (pl. 18, fig. 3) is slightly flabellate, while in another the branching is random.

D. quadripartitum differs from other bundled structures (e.g., Phycodes, Arthrophycus), as it shows a marked relief off the sole of the host rock. The branches are not seen as hemicylinders but instead are exposed as almost complete cylinders. Many of the branches have trapped fragments of lutite along their lateral margins. In the three specimens discussed above what appears to have been the main shaft (i.e., the trunk which connects the numerous branches) has broken off, indicating that it once lay wholly within the lutite and has since been lost. Sectioning confirms that there are no "hidden" tunnels lying completely within the calcisiltite, thus with the exception of the main shaft and the extreme distal portions of the branches, the entire network is visible as a convex hyporelief.

In appearance Dactylophycus is most closely related to Phycodes and Arthrophycus. It differs from Phycodes in possessing a smaller number of branches which are bilobate. The smaller diameter and less prominent annulations of the branches of Dactylophycus differentiate this genus from Arthrophycus. Moreover, it lacks the bundled structure described by Sarle (1906).

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

Two species of Dactylophycus are probably not required. The descriptions of D. tridigitatum and D. quadripartitum are quite similar, the only difference (as the specific name indicates) being the mode of branching. However, the authors did state the D. tridigitatum branched at both ends. If this is actually the case, D. tridigitatum may be something entirely different. For this reason it seems wise to retain the two species until the type specimen of D. tridigitatum can be located.

Interpretation: James (1885) considered Dactylophycus to be the fragments of burrows; the same conclusion is reached here. As mentioned previously, the ethological meaning of Phycodes is in doubt. Although the general Bauplan of Dactylophycus is similar to that of Phycodes, the ethological interpretation is more clear-cut. The fact that the greater volume of the burrow once lay within the subjacent lutite indicates that Dactylophycus is the excavation of a Sedimentfresser.

Presumably the organism burrowed down through the calcisiltite into the subjacent calcilutite and then proceeded to feed along the interface. As the animal withdrew from the tunnels, the overlying calcisiltite sifted in to insure preservation of at least the distal portions of the burrow. The main shaft, i.e., master tunnel, is not present in any of the specimens at hand. It has either been broken off or was composed of lutite and thus not preserved.

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

Trichophycus Miller and Dyer, 1878

(pl. 4, fig. 7; pl. 12, fig. 1-8; pl. 14, fig. 4; text fig. 10-11)

1847 (?in partim) Palaeophycus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 263, pl. 70, fig. 1.

1873 (non) Planolites Nicholson, A., Roy. Soc. London, Proc., vol. 21, p. 288-290.

1878 (non) Blastophycus Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 24, pl. 1, fig. 1-2.

1878 Trichophycus Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 1-3.

1879 Trichophycus, Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 112, pl. 9, fig. 5,5a.

1884 (in partim) Blastophycus James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 158-159.

1885 Palaeophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 158.

1885 (in partim) Trichophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 131.

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Species: Trichophycus lanosum Miller and Dyer (1878) from the "upper part of the Cincinnati Group" (Richmond) of Warren County, Ohio.

Diagnosis: Cylindrical, gently U-shaped Fodinichnia

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

or Domichnia of moderate size. A small number of vertically directed secondary branches may be present. The ventral surface of the burrow is marked by a series of delicate striae.

Discussion: The authors established Trichophycus for "simple branches or stems having diagonal or longitudinal markings, as if made by the folding down of hair-like filaments" (Miller and Dyer, 1878a, p. 3).

Initially only a single species, T. lanosum, was proposed, although in the same year and in Part 2 of the same paper, the authors proposed another species, T. sulcatum, and with some doubts placed it within the genus. In 1879 Miller added a third species, T. venosum.

J. F. James (1884, 1885) considered T. sulcatum and T. venosum to be synonomous, while he placed T. lanosum in synonomy with Blastophycus Miller and Dyer (1878).

It is unfortunate that T. lanosum was selected as the type species, as it does not best express the nature of the genus. It is known only from the cotypes and appears to be an aberrant variety of T. venosum, which is an extremely common form. T. sulcatum is entirely different and is discussed under Fucusopsis sp.

Interpretation: Miller and Dyer interpreted all three species as "fucoids," while J. F. James (1884, 1885) considered both T. sulcatum and T. venosum to be casts of rill marks and T. lanosum an annelid burrow. Häntzschel (1962, p. 219) characterized the genus as "burrows with delicately scraped walls," noting that Seilacher too had

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

reached this conclusion (Seilacher, 1955, personal communication to Häntzschel).

As will be shown, T. venosum is a branching burrow of infaunal origin. Although T. lanosum is not thoroughly understood, it may be a behavioral variant of the same organism that produced T. venosum.

Trichophycus venosum Miller

(pl. 4, fig. 7; pl. 12, fig. 1,3,4-7; pl. 14, fig. 4; text fig. 10-11)

1847 ?Palaeophycus virgatus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 263, pl. 70, fig. 1.

1879 Trichophycus venosum Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 9-10, pl. 9, fig. 5,5a.

1884 Trichophycus venosum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 131.

1885 Palaeophycus virgatus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 158.

1891 Planolites virgatum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

1891 Trichophycus venosum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Locality: "Hudson River Group, Cincinnati, Ohio." The species is common throughout the Cincinnatian.

Diagnosis: Vertically branched, gently U-shaped

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

structures of infaunal origin. Floor of burrow marked by numerous fine striae which radiate out posterolaterally from midline.

Discussion: Miller (1879, p. 9-10) described T. venosum as a "half cylindrical stem, covered upon the cylindrical surface with irregular and inconsistent elevated lines, varying in their course from longitudinal with the stem to diagonally radiating from a central line." He believed that the stem originally may have been cylindrical in shape but that half of it has been lost.

Although it was not possible to locate the actual specimens figured by Miller, several similar ones are available for study. These are not strictly hemicylinders (i.e., "planoconvex" to borrow from brachiopod terminology) as Miller described but instead are "concavo-convex." The convex face bears the delicate striae of the original description. Plate 12, fig. 7 shows one such form in which the striae radiate back from at least two central points. These in turn are superimposed over other such markings. The shallow concave surface shows no sculpturing.

Striated hemicylinders have been recovered from the Economy beds of Humphrey's Branch of Twelve Mile Creek, Kentucky (type locality of Rusophycus cryptolithi). Field studies carried out in this area reveal that the lamellae occur in what local collectors for many years have referred to as "turkey tracks." "Turkey tracks" are shallow hemicylindrical depressions with no apparent preferred orienta-

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

tion which are deepest in the middle and rounded at both ends (pl. 4, fig. 7). They are either straight or gently arcuate in outline, and although the surface may be slightly irregular, they are normally devoid of sculpturing. They have never been observed to branch laterally, yet truncation is common. The width varies from 2.5-3.5 cm, and the length from 8.5-33 cm.[32/]

32/ The earliest known reference to such "turkey track" depressions in the local section was by J. F. James (1885, p. 158), who placed the Cincinnatian forms in Palaeophycus virgatum Hall. Indeed the shallow depressions do resemble Hall's (1847, pl. 70, fig. 1) figure of P. virgatum from the Upper Ordovician (Utica) of Union County, New York. However, until the type specimen of P. virgatum is studied, it is not possible to reach a conclusion regarding the nature of the New York form. If it is found that the Cincinnatian and the New York forms are conspecific, the trivial name virgatum would have priority. As shown elsewhere in this work, P. virgatum is unlike the other species of Palaeophycus proposed by Hall.

Although beds containing large numbers of "turkey tracks" occur throughout the Cincinnatian section, the form is especially well developed at the locality mentioned above and in the Corryville section at Stonelick Creek,

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

some 90 meters downstream from where State Route 131 crosses the creek. At these two localities approximately 25 per cent of the depressions are filled with the lamellae (pl. 14, fig. 4). When the fillings are carefully removed with a knife, the resulting depression exactly resembles the "turkey tracks." Because the lamellae are normally softer and finer grained than the host rock, it is apparent that most of them have been eroded out by Recent stream action.

When the lamellae are either similar to or slightly finer grained than the enclosing rock (the usual case), there is no evidence of the sculpturing described by Miller. If, however, the fillings are composed of a material which is more coarse than the host rock (e.g., coarse silt), striae are present. When the lamellae are found in place, they commonly rise above the general level of the bedding plane. Closer investigation reveals that these are not just simple fillings but instead represent several packings stacked on top of each other (pl. 4, fig. 7; pl. 14, fig. 4). Sectioning confirms that they do have a definite Spreite-like form. This leads one to believe that Miller has described only a small portion of a much larger and more complex structure.

Attempts to follow the forms into overlying beds have met with little success. Normally the beds containing them are overlain by lutites which bear no vestige of any structure, and only at one locality (Twelve Mile Creek) was it possible to trace the lamellae into the lutites and then only for a few centimeters. At most localities T. venosum

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

is associated with Chondrites and Corophioides, and almost invariably none of the three can be followed across lithologic boundaries. The most obvious interpretation is that the upper portion of the silt and/or lutite has undergone subaqueous erosion. However, it is possible that in some instances structures are actually present in lutites but are masked by diagenetic compaction and Recent desiccation.

A few unlabeled specimens in the University of Cincinnati collections indicate that T. venosum is indeed a more complex structure than Miller's description would indicate. The specimens in question are in the form of long cylinders composed of calcisiltite. The length varies from 15-25 cm, the diameter from 1.5-3 cm. Since they show the same pattern of delicate striae on the ventral face, there can be no doubt that these are a more complete expression of Miller's hemicylinders. In contrast, the dorsal surface reveals a series of long, parallel, discontinuous striae arranged in groups (pl. 12, fig. 4). Two of the cylinders possess short vertically directed secondary branches. A lateral view (pl. 12, fig. 1) shows that the secondary branches remain bundled to the main cylinder for some distance beyond the actual point of bifurcation. A cross-section of such a structure somewhat resembles the retrusive Spreite of a U-tube.

Interpretation: The earlier interpretations have already been noted and need not be repeated here. Flower (1955), unaware of the genetic relationship between T.

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

venosum and "turkey tracks," described the latter as resting traces of a nautiloid, probably Orthonybyoceras Shimizu and Obata (see fig. 10C-E). His conclusions were based on observations at the Stonelick Creek locality. He found four or five examples where the aperture of the shell lies beyond the end of the depression (fig. 10A). He felt that while one such specimen could be dismissed as accidental, four or five could not. He maintained that the organism came in contact with the bottom, made the imprint and then died. Another form (fig. 10B) shows where a shell has swung laterally partly blurring the outlines of the trace. In addition, Flower found a number of "turkey tracks" grouped around a mass of shell debris. To him this indicated several nautiloids feeding on an unfortunate group of organisms concentrated by swirling currents.

It is difficult to refute the evidence cited above, but the fact remains that at least 25 per cent of the "turkey tracks" at Stonelick Creek contain the lamellae described by Miller. When these lamellae are removed, the depression is an exact replica of the average "turkey track." For this reason Flower's hypothesis is not accepted as a general explanation for the origin of "turkey tracks."[33/]

33/ Flower is most probably correct in assuming that nautiloid resting traces should be found more frequently in the geologic record. To date, however, only one possible example has been found by the author in the Cincinnatian.

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

The specimen is form the Eden beds, U. S. Route 50, five miles west of Aurora, Indiana, and is illustrated on pl. 27, fig. 3. The surface of the depression is perfectly smooth, and the edges have raised rims as if something had pushed down into the mud.

Instead, it is concluded that T. venosum is a burrow, although the exact nature of the entire structure is unknown. It is believed that the organism burrowed down through an unknown thickness of mud until it encountered a subjacent silt bed. At this point the tunnel angled back up into the mud. Since most of the "turkey tracks" have the same shallow depth, it is probable that the organism was a mud dweller; and when it encountered silt in its burrowing activity, it changed direction in order to remain in a pelitic environment.

It appears then that the first-formed structure was in the shape of a gentle "U" or a flattened "U" lacking the upper portion of one of the arms. It is not known whether the tube was open to the surface at both ends (fig. 11A) or was a blind gallery (fig. 11B). Following excavation of this first tunnel, the organism backed up and initiated the construction of a second higher tunnel, partially truncating the upper portion of the first. The sediment removed from the roof of the second tunnel was packed on the floor of the first, giving rise to the retrusive Spreite. After following the course of the first-formed

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

tunnel for some distance, the new tunnel lost contact and angled obliquely upwards. How far it proceeded is unknown, as the distal portions are truncated. None of the branches show the button-like endings so characteristic of T. lanosum. Presumably this process of excavating and filling could have been repeated several times, although the greatest number of secondary tunnels found thus far is two.

T. venosum is thus far limited to the Cincinnatian. The closest relatives appear to be Teichichnus Seilacher (1955) and Pennatulites de Stefani (1885). Teichichnus was erected for Cambrian forms which resemble a stacking of very flat "U's." They are 1 cm wide and attain a height of 5 cm. In plan view (see Seilacher, 1955, pl. XXIV, fig. 1), they closely resemble the truncated lamellae found in the Cincinnatian "turkey tracks," although there are significant differences. Teichichnus lacks the vertical branching and striae of T. venosum, and some examples exhibit a lateral branching which is unknown in T. venosum. Pennatulites, from the Cretaceous and Tertiary of Europe and Trinidad, could also be generally classified as a branching Spreitebau. Its most diagnostic feature is the knobby prosopon found on the lower face of the lamellae (see Häntzschel, 1962, fig. 127, 1a,b).

The branching and Spreite-like nature of Pennatulites and Teichichnus indicates that they are most likely Fressbauten. This may be the case with T. venosum also, but on the other hand, it may be a Domichnia. The Spreite could

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

be a reaction to sediment sifting in and partially filling the burrow. Perhaps the organism first constructed a simple shallow U-tube or blind "U" in mud. Silt then sifted in from above, forcing the animal to raise the general level of the burrow. This would result in Spreiten and possibly secondary branching.

The peculiar striae found on both the upper and lower faces of the burrow could have been made by either the dactyls of arthropods or the chaetae of annelids. Trilobites come to mind, but all known trilobite burrows possess a distinct bilobate pattern which is lacking here. Whatever the nature of the organism, they must have been extremely abundant and gregarious. One rarely finds only a single or even a few examples of T. venosum. When this form occurs, it covers the bedding planes. A distant analogy may be drawn with the Recent decapod crustacean Callianassa, which excavates irregularly branching burrows. In these burrows, which may be as much as one meter below the depositional interface, the organism sifts through the sediment feeding on microscopic material. Weimer and Hoyt (1964) have estimated that the density of individuals is as much as three per square foot, and this would be in line with the occurrence of T. venosum observed in the Cincinnatian.

Trichophycus lanosum Miller and Dyer

(pl. 12, fig. 2,8)

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

1878 (non) Blastophycus diadematum Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 24, pl. 1, fig. 1-2.

1878 Trichophycus lanosus Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 2, pl. 1, fig. 3-4.

1884 (in partim) Blastophycus diadematum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 158-159.

1891 (in partim) Planolites diadematum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Locality: "Upper part of Cincinnati Group" (Richmond), Warren County, Ohio. Type specimens: pl. 12, fig. 2 (HBM 3185; latex mold UCM 37595) and pl. 12, fig. 8 (HBM 3183; latex mold UCM 37594).

Diagnosis: Striate vermiform trails of moderate size with a button-like anterior(?) end.

Discussion: The species is known only from the two specimens figured by Miller and Dyer. The larger of the two (pl. 12, fig. 8), which is shaped like a series of "S" curves, is preserved as a convex hyporelief. The hemicylindrical body is entirely covered by a series of striae which give it a shaggy appearance, and at one end there is a small button-like depression from which the striae radiate. Truncation prohibits observation of the entire form. The smaller specimen (pl. 12, fig. 2), also a convex hyporelief,

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

possesses the same button-like depression and radiating striae but ends abruptly in a hemispherical "bud."

James (1885) considered T. lanosum to be synonomous with Blastophycus. He based his decision on the button-like ending, which he homologized with the "bud" of Blastophycus. In 1891 he placed Blastophycus, along with several other genera, in synonomy with Planolites. Unfortunately his reasons for this action were never explained.

Interpretation: Miller and Dyer (1878) assigned T. lanosum to the "fucoids," while James (1885) explained it merely as an "annelid trail." James is correct in his interpretation that T. lanosum is a trail or burrow; however, it has nothing to do with Blastophycus. As shown elsewhere, Blastophycus is a cast of an enrolled trilobite with associated scour marks.

The exact nature of T. lanosum is not clear. The small depression with radiating striae is tentatively suggested as the anterior end. Perhaps the striae represent the impressions of a circlet of appendages or extensions surrounding the mouth. The sinuous nature of the trace suggests a highly flexible vermiform body. For the present these two features serve to separate T. lanosum from T. venosum. As mentioned previously T. lanosum may only be a behavioral variation of T. venosum. The former is most likely a variety of Repichnia, the latter a Fodinichnia or Domichnia. On the other hand, T. lanosum may be something

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

entirely different. Until additional material of T. lanosum can be collected, the two are retained as separate species; however, it should be repeated that the genus Trichophycus is best typified by T. venosum, even though T. lanosum is technically the type species.

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

Chapter VIII

Repichnia

General Introduction to Arthropod Tracks

Arthropod tracks have been known for many years and are figured by several authors, most notably by Hall (1852, pl. 15-16) and Walcott (1912, 1918). Yet with the exception of Caster's (1938) study on limuloid tracks, this group of trace fossils has not received serious notice until relatively recently. This is unfortunate because study of such tracks increases our knowledge of both arthropod anatomy and behavior.

Naturally any investigation of trilobite tracks must be conducted indirectly. Seilacher (1955, 1959) suggested that trilobites walked employing a wave of motion which proceeded from the rear end of the body toward the front. The pygidial appendages were the first to make contact with the substrate, the wave moved forward along the body and as it reached the cephalic area, a new wave was initiated at the pygidium. The result of this would be a constant wave of motion not unlike that seen in Recent millipedes. The tracks produced by such movement resemble a series of "V's" in which the two limbs do not quite join (compare fig. 26B and 26C). There is reason to believe that the open end of the "V" is directed anteriorly. The general shape of the trilobite body (excluding agnostids

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

and some bizarre forms) points to this, and studies of preserved appendages show, as one might expect, that in the pygidial area the distance between pairs is not as great as in the thoracic region. This holds true even for such forms as Isotelus and Cryptolithus, which have ovate or ellipsoidal body outlines. Seilacher (1955) also presented evidence to support his theory that the wave proceeded anteriorly. If the movement had been in the opposite direction, the distance between the first and last impression in a wave measured along the axis of movement would be quite short, and the angle formed by the limbs of the "V" would be well over 90°. This is not supported by the fossil record, for the series are drawn out and the acute angle of the "V" is less than 90°.

It should be stressed that while Seilacher's hypothesis regarding trilobite movement is logical, it is nevertheless only a theory. Unfortunately trilobite remains have never been found at the end of a trail. This is in contrast to the xiphosurids at Solnhofen where several corpses have been preserved at the end of their "death march" (Walther, 1904).

It is noteworthy that in xiphosurid trails the point of the "V" is directed anteriorly as Caster (1938) has shown (fig. 26D). At first this is a disquieting discovery, since xiphosurids are presumably the trilobites' closest living relatives. However, even early limuloids were highly specialized, having undergone fusion of the thoracic area

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

and modification and reduction of the walking legs which are restricted to the prosoma (cephalic shield). Moreover, unlike trilobites, xiphosurids possess differentiated walking legs. Just as their anatomy has become specialized, so has the method of walking. Caster (1938, fig. 5) has shown that by doubling up on the cephalic-buckler joint and alternating the placement of the last pair of walking legs (pushers) with the remaining pairs, the animal tends to move forward in a series of lurches. Even though it is conceded that xiphosurids and trilobites probably walked in somewhat different ways, some of what has been learned from the study of xiphosurid movements can be applied to the analysis of trilobite trails.

Before a more detailed discussion can be attempted, it is necessary to define certain terms. Unfortunately this has not previously been done in English and Seilacher's German terms defy translation. For these reasons most of the terms illustrated in fig. 24 and discussed below are new. Since most trilobite tracks are preserved, or at least collected, as convex hyporeliefs and are best studied this way, all further discussions are given as if the viewer were looking up at a trilobite walking on a glass table top. Thus, when we speak of right-hand side or left-hand side, the reader must bear in mind that anatomically speaking these terms are reversed. The following terms are useful in the discussion:

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

trail - the whole record of one walk. It is normally composed of many complete sets.

complete set (=Trittsatz of Seilacher, 1955) - the tracks formed by a single wave of movement. A complete set is in the shape of an open-ended "V" directed posteriorly.

series (=Trittseries of Seilacher, 1955) - either the right- or left-hand limb of the "V ('s)" as seen by the viewer. These do not conform to right and left in the anatomical sense.

track - an essentially undeformed mold (or cast) of a leg or foot, not a scratch or other ethologic expressions of an appendage.

imprint (=Trittsiegel of Seilacher, 1955) - a single leg record of any sort, deformed or undeformed. The proximal portion of an imprint is closest to the axis of movement; the distal portion farthest from the axis. Proximal and distal refer only to the imprint, not to the leg itself.

pair - two imprints or tracks, one on each limb of the "V," which are judged to represent the trace of a pair of legs.

length of set - the length of each set is measured along the axis of movement.

width of set (=Trittabstand of Seilacher, 1955) - the width is the distance from the distal termination of one imprint of a pair to the distal

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

end of the corresponding imprint. Where the width varies in a set, two measurements, indicating the range of variability, are given.

withdrawal markings - semi-lunar welts (depressions on casts) marking the withdrawal of the legs from the sediment. These are normally found at the proximal end of the imprints.

Trilobite tracks fall into three intergradational groups: A) those in which the direction of movement was coincidental to the body axis, B) those in which the direction of movement was slightly oblique ($\pm 30^{\circ}$) to the body axis, and C) those in which the direction of movement was almost at right angles to the body axis, which might be termed "crab-walking."

A) Movement parallel to body axis

As Seilacher (1955) remarked, it is indeed fortunate that trilobites did not choose to walk by this method all of the time, or we would know very little about their tracks, for in this manner of locomotion the various sets become superimposed; and it is nearly impossible to determine the number of imprints in a series (see fig. 28a-c and pl. 17, fig. 3). Seilacher felt that this was particularly true when the trilobites were moving rapidly, apparently using only the stronger anterior legs, while the rest of the body was dragged along with the possibility that the cerci or pygidial

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

spine (s) (when present) acted as skids. It is quite likely that straight-forward walking at any rate of speed gave a superimposed and indistinct record, no matter how few or how many legs were employed. At any rate, virtually no traces of straight-forward locomotion are known in which sets are clearly decipherable. Moreover, this mode of locomotion would not appear to have been preferred by the trilobites in general.

Such tracks have been described from several horizons and under such a bewildering variety of names that a monographic study is necessary to sort them out. Two of the more frequently mentioned names are Diplichnites Dawson (1873) and Protichnites Owen (1852).

Dawson's (1873, p. 20, fig. 3) illustration of the type species of Diplichnites is so schematic that it is impossible to determine if it is a trilobite track. Dawson himself suggested that the form might represent imprints of the pectoral spines of fish. Moreover, since the genus occurs in flagstones associated with coals, there is some doubt that it is even of marine origin. Ignoring these uncertainties, Seilacher (1955) has used the name for trilobite trails from the Lower Cambrian of the Salt Range.

Protichnites Owen (1852), originally described from the Upper Cambrian Potsdam Sandstone of eastern North America, has been used by both Seilacher (1955, pl. XVI, fig. 2) and Öpik (1959, fig. 2-6) for trilobite tracks showing straight-forward movement. In both cases there is a

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

median groove separating the right and left series. The nature of the Potsdam Protichnites is even more enigmatic than Diplichnites. Dawson (1873) suggested xiphosurids, while Billings (1870) questionably assigned the tracks to either trilobites or aglaspids. Raymond (1920) accepted a trilobite origin, but Burling (1917, p. 387) suggested a "short low-lying, more or less heavy set, approximately 12-legged, crab-like animal." Caster (1938, p. 28) maintained that Protichnites is probably of gastropod origin.

Finally, Walcott (1918, pl. 38, fig. 1-2) has illustrated tracks from the Tonto Shale of the Grand Canyon, Arizona, which show straight-forward movement. He neither named nor discussed them.

The above discussion illustrates that while straight-forward tracks are known from various horizons and locations, there is no uniformity of opinion as to the interpretation or the application of names. The treatment has been limited to tracks of probable trilobite origin. For a discussion of possible xiphosurid tracks, see Caster (1938, p. 26-36).

B) Movement slightly oblique to body axis

Generally, trilobites moved in a slightly oblique manner much as modern crabs, and frequently this variety of movement was combined in the same trail with that just discussed. A trilobite can be observed to have started with

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

straight-ahead movement then switched to slightly oblique movement before changing back to straight-ahead movement, thus leaving an alternating record. This oblique locomotion produced a characteristic track morphology. Such a record is seen in fig. 28e,f, where the body was angled slightly to the right. Note that the left-hand series forms a line of superimposed imprints, making it impossible to sort them out into separate series. In contrast, the nine imprints of the right-hand series are plainly defined. If the number of imprints or tracks in a set are known, one has a better chance of determinating the originator of the trail.

Trilobite tracks showing oblique movement are known from at least three different localities. Rudolf Richter (1941, fig. 13) illustrated one such form from the Devonian Hunsrück Shale of Germany, and Abel (1935, fig. 222) figured another from the Silurian Clinton beds of New York State. Seilacher (1955) has described tracks of this variety from the Salt Range Cambrian under Diplichnites.

There are additional explanations for dimorphic tracks than the one discussed above. Caster (1944) has described a xiphosurid trail from the Newspaper Rock member of the Chinle formation (Triassic) of Arizona, where the right-hand series is more deeply impressed than the left. He theorized that the organism was struggling to keep its balance on a sloping beach. In the same manner a slippery mud slope on the sea floor could affect a trilobite and lead

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

to a dimorphism of the tracks. Likewise, a moderate current on a level surface could drive the trilobite sideways or momentarily upset its balance so that it might lash out in an attempt to regain its equilibrium. Here again the result would be a dimorphism of the imprints. It is thus evident that not all dimorphic tracks were the result of simple oblique "crab-walking." When current indicators are present, they should be studied to see if they might have had some bearing on the morphology of the trail.

C) Movement strongly oblique to body axis

Trilobite trails in which the direction of movement was nearly at right angles to the body axis are thus far known only from the Lower Cambrian of Pakistan and Sweden. In such specimens (fig. 28g) there is a marked dimorphism in the configuration of the right- and left-hand series, which suggested to Seilacher (1955) the generic designation Dimorphichnus. In the track illustrated in fig. 28g, the body was oriented far to the right of the direction of movement. The imprints of the right-hand series indicate a long raking motion. If these are long enough, they resemble a sine curve, this type of curve being the result of two vectors, one directed in the line of movement, the other normal to the line of movement. Combining this information with the "rule of the V'," it is possible to determine the direction of movement, in this case (fig. 28g)

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

from bottom to top. Markings such as those seen in the right-hand series may be called "raking imprints" (=Harksiegel of Seilacher). Seilacher believed that raking imprints were the result of the legs being passively dragged over the substrate. If this were true, they would offer little support for the body, and it remained for the left-hand appendages to provide such support. This appears to be the case, as the imprints of the left-hand series show no such raking movement and instead are quite short and stumpy and commonly impressed more deeply than the raking imprints. Such imprints are termed "support imprints" (=Stemmsiegel of Seilacher). Seilacher maintained that Dimorphichnus has definite paleoecologic significance. It was his thesis that this was not merely another variety of Repichnia but instead represented a grazing (scavenging) trace and should be classified among the Pascichnia. This hypothesis was based on studies of a large slab from the Salt Range (see fig. 30A herein), which measured 165 cm in length and bore 23 complete sets and over 360 individual imprints. Two lines of evidence led Seilacher to his conclusion. First, as the trilobite was employing the strongly oblique movement, it encountered the tracks of an earlier Redlichiid (fig. 30B). At this point the organism turned around and proceeded back in the direction from which it came, being careful to avoid crossing over its own track. Eventually it reached a point where it must cross over, but it did so without utilizing the raking motion. The

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

raking motion ceased as it crossed the track and picked up again on the other side. Finally, near the edge of the slab the strong raking motion converted to moderate oblique movement. As Rudolf Richter (1938, 1941) has shown, vermiform grazing trails rarely cover the same area twice. The tightly packed meanders of Helminthoida and other such forms from the European Flysch never come in contact. This is a principle of economy; there is no point in "regrazing" an area once it has already been picked clean. Seilacher felt that the same is true here. This would explain why the "grazing" trilobite turned around when it encountered another track, and it also explains why the trilobite moved so quickly over its own track. The little that is known of trilobite feeding habits does nothing to discredit Seilacher's thesis, for the fossil record indicates that trilobites possessed neither strong mandibles nor gnathobases; apparently they were not predators. Størmer (1951) mentioned that the flabellate pre-epipodites, whose main function was to serve as ctenidea, may have also acted as sieves on which food could be collected. Employing this idea, Seilacher pictured the nutrient-rich sediment moving up the leg, where, due to the curvature of the telopodite, it came in contact with the pre-epipodite. From here it moved to the mouth.

Although Seilacher's hypothesis is an ingenious one, he is perhaps reading too much into the record. The trail could just as easily have been caused by an oscillatory current (e.g, wave action) which first drove the trilobite

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

one way and then carried him back again. Moreover, it is not clear how the food was carried from the legs to the mouth. If Seilacher's hypothesis is correct, the method he describes must have been an early experiment in feeding which proved ineffective and was abandoned by later forms. As mentioned, Dimorphichnus is known only from a few specimens from the Lower Cambrian of Pakistan and Sweden. There is no evidence that Cincinnatian trilobites fed in the manner described by Seilacher.

While trilobite tracks tell us something about behavioral patterns, they also contribute to our knowledge of the morphology of the walking legs, especially the distal portions. Due to the imperfections of the fossil record, we have relatively little direct evidence in this field. What is known has been summarized by Raymond (1920) and Størmer (1939).

Even if it is possible to assign a set of tracks to a given form, many times it is difficult to determine the exact nature of the dactyls. Some forms, such as that illustrated in pl. 17, fig. 1, present a bewildering variety of imprints. Note that trifid, bifid, and unifid imprints are all present in the same trail. There are several possible explanations for such discrepancies. It is likely that the manner in which the leg was placed on the substrate could effect the morphology of the imprint. An appendage might strike the substrate in such a way that all three dactyls make contact, resulting in a trifid track, but if

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

the leg is rotated slightly to one side or the other, only two dactyls may leave imprints. Conceivably unifid impressions could be explained in the same manner. The curved outline of the imprints in pl. 17, fig. 1 support this view.

As shown in fig. 18 preservation may play a key role in the appearance of any arthropod track. Occasionally tracks are preserved as convex hyporeliefs in calcisiltites which overlie clay-sized material (pl. 18, fig. 1). This method of preservation usually provides us with the greatest clarity of detail. More frequently, however, the tracks are found as clevage reliefs in fine-grained calcisiltites. Here the fine details are lost and, depending on how far below the surface the imprint is found, the morphology may vary considerably. An imprint found 2 mm below the surface may deviate greatly from that found 4 mm below the surface. Sometimes the vagaries of preservation make it difficult to recognize that apparently different forms are in reality the same thing.

Lastly, it is possible that trilobites exercised some degree of voluntary control over the movement of the dactyls. There is no direct evidence to indicate that such was the case. However, other arthropods, e.g., xiphosurans and crabs, possess musculature control extending to the distal ends of the walking legs.

Synopsis of The Ventral Morphology of Cincinnatian Trilobites

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

Something is known of the ventral surface of the more common Cincinnatian trilobite genera. Specimens recovered from the Middle Ordovician black shales of Trenton Falls, New York, have been the subject of studies by Walcott (1881, 1884, 1918), Beecher (1893-1902), Raymond (1920), and Størmer (1939). Unfortunately with regard to the terminal digit, setae, etc., Walcott, Beecher, and Raymond employed the artist's license; and their reconstructions must be used with extreme caution. In discussing the appendages of each of the genera, emphasis is placed on those structures which may have left their imprints on the substrate.

1) Isotelus

The best preserved specimen of Isotelus showing appendages is from Oxford, Ohio (pl. 1, fig. 5), and has been discussed previously. Twenty-six pairs of appendages have been reported; 10 on the thorax and 16 on the pygidium. Judging from their size, the thoracic appendages must have been quite powerful. Nothing is known of the nature of either the pre-epipodite or the terminal segment of the walking legs. Walcott (1884) figured setiferous legs, but Raymond (1920) could find no evidence to support this conclusion.

2) Cryptolithus

The exact number of appendages in Cryptolithus is unknown. Raymond's reconstruction (fig. 20) shows 22 with the last 10 or so being quite small. Størmer (1939, p. 211) noted that "the telopodites are strongly curved in the distal

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

portion and the position in preserved state indicates that this part was directed downwards and slightly backwards in the thorax and pygidium during life." Although the pre-epipodite is not well known, it appears to have resembled a large fan (Størmer, 1939, fig. 25). The morphology of the dactyls is clearly shown by Raymond (1920, pl. 7, fig. 3-4). They resemble a tuft of bristles, although Beecher's reconstruction (Raymond, 1920, fig. 45) shows a large terminal spine surrounded by slightly smaller spines. Although both Raymond (1920, fig. 20) and Størmer (1939, fig. 25) show a grouping of proximally directed spines on each segment of the telopodite, it is not possible to confirm this from Raymond's illustrations.

3) Ceraurus

Raymond's reconstruction of Ceraurus (fig. 16) shows 26 pairs of appendages, 18 of which are quite large. The nature of the dactyls is problematic. Walcott (1881) illustrated a single long terminal spine. Raymond (1920) agreed that while there probably was a terminal spine, it was not as well developed as Walcott had shown. In a later paper (1918, pl. 34, fig. 1-2), Walcott clearly showed three spines, and Størmer (1939, pl. 11, fig. B) dotted in three spines, illustrating that the true nature of the dactyls is really not known. Størmer (1939, pl. 11a) has done extensive work on the pre-epipodites and found that the unicorn-like spirals of Walcott (1918) and Raymond (1920) are due to preservation. Instead he pictures a small fan-like member.

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

4) Flexicalymene

Størmer (1939) remarked that although he has not studied Flexicalymene in detail, sections appear to reveal appendages similar to those of Ceraurus. Raymond (1920, p. 56) admitted that nothing is known of the telopodites and that any conclusion must be based on analogies with other forms.

5) Triarthrus

Raymond's reconstruction of Triarthrus (fig. 10) indicates 24 pairs of appendages. He reported that one specimen possessed a terminal segment which consisted of two or three short hair-like spines with a ball and socket joint. In addition, Raymond illustrated the legs as possessing long setae and bearing a grouping of spines on the segments much like those of Cryptolithus. Størmer (1939, p. 204-205) stated that he had not studied the distal portion of the telopodite, but he believed that Raymond's conclusions appeared to be valid. In addition he pictured a large flabellate pre-epipodite similar to that of Cryptolithus.

Cincinnatian Representatives

Although arthropod tracks are not uncommon in the Cincinnatian section, they have never received adequate study, and this was the one field which J. F. James neglected entirely. Miller (1880) established the genus Asaphoidichnus for two species of asaphid tracks, and Caster (1938) figured

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

and briefly discussed four specimens, placing three of them in Asaphoidichnus, while referring to the other as Merostomchnites sp. In spite of this small amount of work, there is an abundance of names, for Miller (1880) unwittingly erected three additional genera and five species of arthropod tracks. These were collected from the ?Southgate beds of "Walker Mill Road" (now State Avenue) in Cincinnati, and because of their association with molluscan body fossils, Miller considered them to be cephalopod tracks. However, as will be shown, these are clearly tracks of arthropods and most probably were made by trilobites.

As pointed out previously, there is considerable doubt as to the true affinities of the two most commonly mentioned genera of supposed trilobite tracks, Protichnites Owen and Diplichnites Dawson. Because of this uncertainty, the Cincinnatian tracks will be discussed within the framework of Cincinnatian nomenclature.

Five genera, all monotypic, are recognized in this study. One of these, Asaphoidichnus trifidum Miller (1880), was correctly interpreted by Miller as the tracks of an isotelid. However, what Miller (1880) established as Asaphoidichnus dyeri becomes the type species of a new genus, Allocotichnus. As Miller originally indicated, this too is probably an isotelid track, but it illustrates a type of movement not previously seen in trilobite tracks. Three other Miller species, Trachomatichnus permultum, T. cincinnatiensis, and Petalichnus multipartitum, as well as what

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

Caster (1938, pl. 10, fig. 1) described as "Merostomichnites sp (cf. Petalichnus multipartitus)," are all considered to be Petalichnus multipartitum. These are most likely tracks of Flexicalymene, but since the nature of the dactyls of most Cincinnatian trilobites is unknown, there is no way of corroborating this. Trachomatichnus numerosum Miller (1880) appears to be generically valid and may well represent the tracks of the brush-like dactyls of Cryptolithus. Teratichnus confertum Miller (1880) is retained; there is some evidence that is may be the track of an aglaspid.

In order better to illustrate the number of imprints in a series and to show the direction of movement, tracings were prepared of some of the specimens (see fig. 32-35). In some areas the imprints are so indistinct or crowded together that they tend to defeat the purpose of the illustrations, and they were therefore omitted. The overlays represent the author's interpretation of the trails. The different markings are used to differentiate the opposing rows of the various series. The trilobite outlines superimposed over the drawings indicate the orientation of the body and the direction of movement.

Asaphoidichnus Miller, 1880

(pl. 9, fig. 2; pl. 15, fig. 6; pl. 16, fig. 3; pl. 17, fig. 1-2; text fig. 32-1,33-1)

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

1880 (in partim) Asaphoidichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 217-219 (refers to unnamed specimen figured by author in Cincinnati Quart. Jour. Sci., vol. 1, p. 136, fig. 11).

1938 Asaphoidichnus, Caster, K. E., Jour. Paleont., pl. 10, fig. 2-4.

Type Species: Asaphoidichnus trifidum Miller (1880) (pl. 15, fig. 6; MCZ 540; latex mold UCM 37704) from "less than 100' above low water on Walker Mill Road, Cincinnati, Ohio" (?Southgate of State Avenue, Cincinnati, Ohio). Monotypic.

Diagnosis: Large, trifid arthropod tracks, exhibiting both straight-ahead and oblique movement. Width of track varies from 6.0-15.5 cm; number of imprints per set averages nine.

Discussion: Miller (1880, p. 217) said of Asaphoidichnus that "the tracks are separate and distinct, showing that the animal lifted its feet to advance, and appearing as if made by an articulated animal, but not by one holding its feet in an inflexible position." Two species, A. trifidum and A. dyeri, were named; the latter was placed in the genus with some misgivings, which appear to be justified, as its morphology varies greatly from any known trilobite track. It is here removed from Asaphoidichnus and is made the type species for the new genus Allocotichnus.

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

Miller (1880, p. 218) erected A. trifidum for tracks where "the anterior third of each track is trifid, the outer toe usually branching from the main stem of the track first, and the middle being a little longer than either the outer or inner one." He also maintained that one paratype specimen shows "a small toe thrown off from the posterior elevation on the inner side of the track, having a length about equal to the inner anterior toe" (ibid).

Although Miller remarked that several specimens of A. trifidum were in the Dyer collection, only the type could be located. The trail (pl. 15, fig. 6), 3.5 cm long and 6.0 cm wide, consists of 14 impressions on the right-hand side and six on the left. The individual impressions vary in their morphology; the best preserved ones show an oblong raised welt from which radiate three thin lines. At their point of termination the trifid imprints, whose length varies from 1.5-2.0 cm, may be separated from each other by as much as 3 mm (see pl. 16, fig. 3).

Examination of the right side of the trail reveals that not all the tracks belong to one series. As shown in fig. 32-1, six of the tracks are from one series, six from another. The left-hand side of the trail can likewise be differentiated into two series, although the imprints are not as clearly defined. None of these are judged to represent a complete set.

Interpretation: The width of the trail (6.0 cm) eliminates all known Cincinnatian arthropods except Isotelus,

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

eurypterids, and possibly aglaspids. The morphology of the best known Cincinnatian eurypterid, Megalograptus, has been studied in detail by Caster and Waering (1964). They have shown that the four pairs of "walking legs" are strongly differentiated. The first pair is short, bears numerous spines, and was probably used more for grasping than for walking. The second pair is greatly enlarged and armed with many long slender spines; it probably did not play an active role in walking. The third pair of "walking legs" is rather short and possesses a great number of spines, while the fourth pair is slightly long than the third, and except for trifid dactyls, is devoid of spines. The fifth and final pair of legs is modified for swimming, as both the fourth and seventh joints are enlarged. Even though the fourth pair of "walking legs" is trifid, it is extremely difficult to imagine the type specimen of A. trifidum as an eurypterid track. Other eurypterids were present in the Cincinnatian seas, for scraps of their integument are found scattered throughout the section. These fragments more closely resemble Eurypterus than they do Megalograptus, but there is not sufficient material available to undertake a morphological study. In any event it is likely that eurypterid tracks would more closely resemble the tracks of Recent scorpions (fig. 26C) than those now under consideration.

Neostrabops Caster and Macke (1952), the only known non-Cambrian American aglaspid, was described from the Corryville section at Stonelick Creek. Although the

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

unique specimen is too small (3.5 cm x 2.8 cm) to have made the trail, Raasch (1939) has described Upper Cambrian aglaspids from Wisconsin which attained a length of 18.6 cm. Since the appendages of Neostrabops are unknown, their morphology must be inferred from Raasch's Cambrian forms. Aglaspis spinifer Raasch (1939) possesses 12 and possibly 14 pairs of "walking legs" which do not extend beyond the body margins. Each leg has a single terminal dactyl, and Raasch was unable to find any evidence of setae. It seems improbable therefore that A. trifidum represents the tracks of an aglaspid. The Crustacea of the Cincinnatian are so inadequately known that no generalizations are possible.

This leaves Isotelus as the most likely candidate to have produced the track. Even though it can not be unequivocally stated that A. trifidum is an isotelid track, it is probable that Isotelus possessed three long slender dactyls which, when the need arose, could spread to provide a flabellate "snowshoe-like" support. In this sense the dactyls may have been analogous to the blades of the fifth pair of "walking legs" of Limulus.[34]

34/ The meaning of "the small toe" mentioned by Miller is not clear. There is no trace of any such structure on the specimen under discussion. It most likely represents one track partially superimposed over another.

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

Since there is no marked dimorphism in the right and left series, the track is indicative of straight-ahead movement. However, the morphology of this specimen differs from many trilobite trails in showing vertical emplacement of the legs without any appreciable movement toward the median line. In most trails after initial contact with the substrate, the leg moved toward the median line, leaving a scar with a small raised pimple marking the point of withdrawal (fig. 24). Thus, A. trifidum represents relatively undisturbed tracks. Moreover, the method of walking is probably responsible for the unusual type of preservation which was noted by Miller (1880). The posterior oblong welts mark the highest point of the track. Near the welt the trifid imprints are preserved as thin raised ridges (i.e., "convex"), but as they are followed distally, the ridges grade into shallow depressions (i.e., "concave"). Thus, the trail shows the characteristics of both convex hyporelief and concave epirelief preservation. It is concluded that the trail is preserved as an epirelief and that the mud was drawn up by the proximal portion of the dactyls as the weight was shifted distally. This would be analogous to a man drawing up mud with his heel as he shifted his weight to the ball of the foot. This might indicate that the tracks were made subaerially. It is difficult to perceive how mud would behave in this manner when covered by water.

Miller (1880) also believed that the trail was

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

preserved as an epirelief. However, he remarked that the feet might have been webbed to aid in swimming. While this might explain the peculiar preservation, there is no evidence that the organism was "web-footed."

Caster (1938, pl. 10, fig. 2-4) has figured portions of additional trails which, because of their size, were most probably made by Isotelus. All are preserved as convex hyporeliefs and are from the Fulton beds of the Union Levee, Cincinnati. One of these (herein pl. 17, fig. 2) shows marked dimorphism. The five right-hand series consist of long, slightly sigmoidal raking imprints, while the left-hand series are made up of superimposed support imprints. The trail width ranges from 2.2-4.0 cm. As noted elsewhere, the markings vary in their appearance; some are unifid, while others are bifid or trifid. Only nine imprints can be counted in any given series, but none of the series appear to be complete, and most likely the total number was greater than this.

Plate 19, fig. 2 illustrates another specimen from the Fulton beds which, judging from the width (15.5 cm), is probably the trail of an isotelid. The right-hand series consist of eight to ten long sigmoidal raking imprints, and in contrast to the form just discussed, they show no evidence of being bifid or trifid. The support imprints of the left-hand series also show some slight sigmoidal development. A more detailed analysis of this form is given in fig. 33-1.

Both of these dimorphic trails are indicative of

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

oblique movement. In both cases movement was from bottom to top as viewed by the reader. Either the animal was "crab-walking" with the body angled slightly to the right of the axis of movement, or it was being swept to the left by current. However, the former appears the more likely as neither of the specimens bear any current indicators.

Allocotichnus n. gen.

(pl. 16, fig. 1-2; pl. 17, fig. 7; pl. 18, fig. 6-7; pl. 25, fig. 7; text fig. 33-2,3)

1880 (in partim) Asaphoidichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 219, pl. 13, fig. 1.

Type Species: Asaphoidichnus dyeri Miller (1880) (pl. 16, fig. 1; MCZ 543; latex mold UCM 37693) from ?Southgate beds of "Walker Mill Road," (State Avenue) Cincinnati, Ohio. Monotypic.

Diagnosis: Bifid, dimorphic trails of arthropod origin. Each complete set apparently composed of four pairs of imprints, one side being preserved as long subparallel raking imprints, the other arranged as en-echelon support imprints.

Discussion: Miller (1880, p. 219) established A. dyeri for a trail with four toes "...which do not come together as in A. trifidus but spring from a wider foot."

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

The type specimen (pl. 16, fig. 1), which has a length of 23 cm, consists of 10 separate groups of markings and is preserved as a convex hyporelief in a platy fine-grained calcisiltite. The five complete groups each possess four long subparallel imprints, as well as four shorter imprints which are arranged in an en-echelon pattern. For purposes of discussion the long imprints are labeled A,B, C,D; the shorter ones A',B',C',D' (see pl. 16, fig. 1). As viewed in pl. 16, fig. 1, the longer imprints fade out on the bottom but terminate rather abruptly on the top, and in some cases withdrawal markings can be seen. The length of these imprints decreases from left to right; the average length of A is 6.75 mm, while the length of D is 14 mm. In contrast, the shorter imprints increase in length from bottom to top. Whereas A' is quite small and may be preserved only as a wart-like body, D' has an average length of 7.2 mm. The average length of the complete sets is 1.6 cm.

Below and to the right of A' in many of the groups is a series of two to four rounded parallel markings which give the appearance of being slightly arcuate. These have a length of 6 mm and are not as sharply defined as the imprints described above.

Another specimen from the Dyer collection, evidently from the same locality as the type, clarifies some of the features mentioned above. As viewed in pl. 18, fig. 7, all of the imprints end abruptly on the right but fade out

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

gradually to the left. The most striking feature of the topotype specimen is the parallel markings above and to the left of each group of imprints. Whereas only three or four of these markings were present in the type specimen, as many as nine can be counted in this form. They gradually decrease in length and prominence away from the track. As in the type they are quite broad and not as sharply impressed as the other markings. Instead of being arcuate as in the type, they take somewhat of a cuneiform appearance, both the lower and right-hand slopes (as viewed in pl. 18, fig. 7) being steeper than their counterparts. It is apparent that the markings form an integral part of the trail and that any hypothesis regarding the origin of the trail must somehow account for these markings.

Through the kindness of Dr. George Walker of the Dry Dredgers, several additional specimens are available for study. These were collected from the Eden beds of an intermittent tributary of Mud Lick Creek where crossed by Kentucky Route 14. The locality is 1,650 meters southeast of the intersection of U. S. Route 42-127 and Kentucky Route 14, Boone County, Kentucky. Aside from being slightly smaller and lacking the cuneiform markings, they are similar to the specimens described above. They confirm the existence of eight imprints in each group, although, as in the type, A,A', and B' may be weakly impressed, and in a few specimens they are lacking entirely (pl. 17, fig. 7). One Mud Lick specimen (pl. 18, fig. 6) plainly shows that the longer

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

imprints are bifid, a feature which is not present on the forms from the State Avenue locality.

Examination of all the specimens discussed to this point indicates that they are preserved as cleavage reliefs. None of the specimens present the sharpness of detail that is characteristic of boundary relief. As shown in fig. 18 cleavage relief preservation can mask details and lead to an erroneous interpretation of the track or trail. To some degree this is true here, for one specimen (pl. 18, fig. 1), associated with Trachomatichnus numerosum and preserved as a boundary relief, illustrates that the longer imprints (A,B,C,D) are not as simple as they appear. The trail is incomplete and contains only 13 imprints which are arranged in four groups. One of the imprints shows a peculiar "feather-stitch" (zig-zag) pattern in which long spine-like projections on one side alternate with shorter projections on the other. The distance between each of the longer projections is 2 mm. Another form (pl. 25, fig. 7) in a different group lacks the "feather-stitch" pattern and instead possesses six long projections which are visible on only one side of the imprint. The other imprints are variations of the patterns described above. It is not surprising that the detailed morphology should vary; a slight rotation of the leg can greatly affect the over-all appearance of the resulting track or imprint. Miller also noticed the spur-like projections, remarking "some of the toe-tracks are more or less fringed, which I attribute to the action of the

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

water, though Mr. Dyer is impressed with the idea that it may indicate hairy or spinous feet" (Miller, 1880, p. 219).

Interpretation: Allocotichnus dyeri is unlike any other known arthropod track, yet the fact that some 15-20 specimens are known from two localities 30 miles apart indicates that it is a recurrent phenomenon, not an accidental expression of some other common form. The most fundamental question is whether the specimens under consideration represent the entire track or only one side of it. Miller (1880) believed that each group of four long imprints represented the essentially undisturbed track of a quadridigitate foot, while the shorter en-echelon imprints were the indistinct impressions of the opposite foot. However, the track would appear to be much too narrow to support such a conclusion. If the four imprints represent the marking of a quadridigitate foot, the organism must have been extremely large, and the trail should have a width of 15-20 cm. Moreover, none of the many specimens found from Mud Lick Creek show two sets of quadridigitate imprints. It seems more likely that Allocotichnus is a strongly dimorphic track where A,B,C,D represent raking imprints and A',B',C', D', support imprints. This impression is confirmed by a specimen from Mud Lick Creek which shows a lesser degree of dimorphism. As viewed in pl. 16, fig. 2, the imprints on the right would seem to be homologous with B,C,D, while those on the left represent B',C',D'. Note that if all the imprints are rotated clockwise approximately 45°, the re-

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

sulting configuration resembles the other Mud Lick specimens of Allocotichnus. The direction of the "V" formed by the two series of imprints, as well as the withdrawal markings at the proximal end of each imprint, indicates that the direction of movement was from bottom to top (as viewed in fig. 33-3). It follows that movement in both the type (pl. 16, fig. 1) and topotype specimen (pl. 18, fig. 7) was from left to right, and the body axis was angled to the right of the direction of movement (see fig. 33-2). If the above reasoning is correct, then each complete set consists of a maximum of four pairs of imprints. In many sets three and sometimes only two pairs of imprints are present.

While the producer of the trail is unknown, the small number of imprints in each series leads one to search for an arthropod with a relatively small number of walking legs. The only known possibilities in the Cincinnatian rocks are Cryptolithus, Megalograptus, and Neostrabops. Of course, there is always the additional possibility that we are dealing with the trail of some yet undescribed arthropod form.

The appendages of Megalograptus have already been discussed, and it is difficult to homologize the morphology of the walking legs with that of the tracks. Moreover, the little that is known of eurypterid tracks in general (see Sharpe, 1912) gives reason to believe that Allocotichnus dyeri is not such a trail. It is equally as difficult to make a direct comparision between aglaspids and Allocotichnus dyeri. While there is no evidence to indicate that it is not

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

an aglaspid trail, there is certainly nothing to indicate that it is. The stratigraphic position of the specimens (Eden) and the small number of appendages involved in producing the track make Cryptolithus an attractive choice. Nevertheless, measurements show that Cryptolithus is too small to have made the trail. Since the trail is strongly dimorphic, the width varies. The least width, measured from the distal end of A to the distal end of A', ranges from 1.5-2.5 cm, while the greatest width, measured from the distal end of D to the distal end of D', is 4-5 cm. Raymond's (1920, pl. 7, fig. 4) illustration of Cryptolithus shows that the appendages even when spread-eagled--which is unlikely--cover only three-quarters the width of the cephalon. Thirty-five specimens of Cryptolithus were measured; it was found that the mean "three-quarters width" was 1.59 cm, while the largest form observed had a width of only 2.3 cm. These figures indicate that Cryptolithus must be eliminated as a possible originator of the trail.

The only remaining arthropods capable of leaving such a wide trail are the multisegmented trilobites, such as Flexicalymene and Isotelus. However, it is doubtful that even the larger flexicalymenids would be able to produce the tracks, for they rarely attain a length over 6.0 cm or a width in access of 3.0-3.5 cm. This leaves Isotelus as the most likely producer. Nevertheless, it should be repeated that Allocotichnus dyeri is unlike any known trilobite track, and the choice of Isotelus as the producer is by no

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

means certain. Note that Asaphoidichnus trifidum, which is also attributed to Isotelus, bears little resemblance to Allocotichnus.

Judging from the Oxford specimen of the ventral side of Isotelus (pl. 1, fig. 5), the first 8-10 pairs of walking legs were probably quite strong, and it is possible that the first three or four pairs of legs could propel the animal fast enough to keep the pygidium off the substrate. While the smooth platter-like streamlined body of Isotelus would not produce as great a drag as the bodies of other trilobites, it is believed that the cuneiform markings of the State Avenue specimens (pl. 16, fig. 1; pl. 18, fig. 7) show where the pleurae occasionally nicked the bottom. In addition the imprints seen on pl. 18, fig. 1 indicate that sometimes nearly the entire leg was placed on the substrate, for the spur-like bodies associated with the markings most likely represent spines on the distal ends of each leg segment. If three or four joints of the leg made contact with the substrate, it follows that the eight blunt pleurae of the right side of the body were extremely close to the bottom and could have gouged the sediment in the rhythm of movement. It is unlikely, however, that the leg was always placed flat on the substrate; the bifid markings of some specimens (pl. 18, fig. 6) show that sometimes only the dactyls made contact with the bottom.

In summary then, it is believed that Allocotichnus dyeri probably represents the strongly dimorphic trail of

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

Isotelus in which only the stronger anterior appendages were employed. In some instances nearly the entire length of the leg was placed on the substrate and the thoracic pleurae gouged the bottom. On the other hand, the bifid markings of some specimens (pl. 18, fig. 7) illustrate that in a few cases only the dactyls made contact with the substrate. The reason behind such movement is problematic. Perhaps Isotelus (if indeed this was the producer of the trail) under some circumstances made use only of its stronger anterior legs.

Petalichnus Miller, 1880)

(pl. 17, fig. 5-6; pl. 18, fig. 2,4,5; pl. 19, fig. 4; text fig. 34)

1880 Petalichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 219-221, pl. 13, fig. 5; pl. 14, fig. 3.

1880 (in partim) Trachomatichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 219-221, pl. 14, fig. 2.

1938 Merostomichnites, Caster, K. E., Jour. Paleont., vol. 12, p. 34, pl. 10, fig. 1.

Type Species: Petalichnus multipartitum Miller (1880) (pl. 19, fig. 4; MCZ 546; latex mold UCM 37697) from the ?Southgate beds of "Walker Mill Road," (State Avenue)

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

Cincinnati, Ohio. Monotypic.

Diagnosis: ?Trilobite tracks showing straight-ahead or slightly oblique movement. Each series consists of 9-12 unifid or bifid imprints. Generic designation of producer unknown.

Discussion: As explained previously, recent studies on arthropod tracks (Caster, 1938; Seilacher, 1955) have shown that a slight rotation of the body during walking can result in tracks which differ greatly from those produced by straight-ahead movement. Such slight modifications must be taken into consideration when making taxonomic assignments, otherwise the result will be a different name for every track. It is believed that the best taxobases for arthropod trails are: 1) a consistent pattern of imprints which is found in several specimens and sets that trail apart from others, e.g., the unique dimorphism of Allocotichnus dyeri, and 2) a known producer--can the originator of the track be determined with a reasonable degree of confidence? For example, the width of Asaphoidichnus trifidum shows that it is most likely the trail of an isotelid; therefore, it merits separate taxonomic treatment. Regrettably Petalichnus does not really come under either heading. The genus contains trails showing a wide range of morphology, and these can not be assigned to a given trilobite. Included in Petalichnus are forms which in Miller's work constituted two genera and three species. Justification for placing them in synonomy with Petalichnus will be given as

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

each is discussed below. Also included in the genus is a form which Caster (1938, pl. 10, fig. 1) referred to as "Merostomichnites sp. (cf. Petalichnus multipartitus)." It is acknowledged that Petalichnus as defined herein is a form genus and more than likely contains trails made by more than one genus of trilobite and conceivably may even include tracks of other classes of arthropods.

Petalichnus multipartitum Miller

(pl. 17, fig. 5,6; pl. 18, fig. 2,4,5; pl. 19, fig. 4; text fig. 34)

1880 Petalichnus multipartitus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 222, pl. 14, fig. 2.

1880 Trachomatichnus permultus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 220, pl. 13, fig. 5.

1880 Trachomatichnus cincinnatiensis Miller, S. A., Cincinnati Soc. Nat.,Hist., Jour., vol. 2, p. 220-221, pl. 14, fig. 3.

1938 Merostomichnites sp. Caster, K. E., Jour. Paleont., vol. 12, p. 34, pl. 10, fig. 1.

Discussion: The type specimen (pl. 19, fig. 4) is a highly complex trail. It is preserved as a convex hyporelief and has a length of 11.3 cm and a width of 2.2 cm. The clearest portion of the trail is on the right (as viewed in pl. 19, fig. 4). Here it is possible to make out five

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

series of unified raking imprints with plainly defined withdrawal markings at their proximal ends. The number of imprints in each complete series varies from 10-12. The shorter cuneiform imprints in the central part of the trail are judged to be support imprints. These stand out in bold relief when compared to the more shallow raking imprints. In the upper part of the trail, the imprints become so superimposed that it is not possible to make a detailed analysis. Therefore, only a partial reconstruction of the trail is given in fig. 34-3. The position of the raking imprints relative to that of the support imprints shows that, as viewed in pl. 19, fig. 4 and text fig. 34-3, movement was from bottom to top, and the body was angled slightly to the right of the axis of movement.

"Trachomatichnus permultum" (pl. 17, fig. 5; MCZ 548; latex mold UCM 37696): In contrast to the type specimen of P. multipartitum, the form designated by Miller (1880) as "Trachomatichnus permultum" is a picture of simplicity. Miller (1880, p. 220) separated "T. permultum" from T. numerosum, because the imprints of the former "are not so numerous, they are destitute of the beaded appearance, they are subtriangular instead of somewhat uniformally rounded and the rows are proportionately farther apart." In this case the last two criteria are insignificant as taxobases, but the first two, i.e., the number of imprints and the beaded appearance, are judged to be important. As will be shown, there is a good possibility that T. numerosum is the

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

trail of Cryptolithus, "T. permultum" has a length of 8.5 cm and consists of five separate sets. The three complete sets contain 10, 10, and 11 imprints. The trail width measured in the lower part of the trail, as viewed in pl. 17, fig. 5, is 1 cm. The specimen is noteworthy because it shows a transition from straight-ahead movement. Midway through the trail the imprints on the right side become longer and slightly sigmoidal in outline, while in the upper part of the trail they are strongly sigmoidal, indicating that the animal was oriented to the right of the axis of movement. Note that the imprints on the left side show little change and that it is difficult to distinguish between the various series. As illustrated by the sigmoidal outline and the orientation of the "V" formed by the opposing series, movement was from bottom to top as seen in fig. 34-2.

Outwardly this specimen differs greatly from the type specimen of P. multipartitum, yet basically they are the same. The track widths are similar as are the number of imprints in a series. There is no consistent morphological difference on which the two could be separated.

"Trachomatichnus cincinnatiensis" (pl. 18, fig. 2; MCZ 542; latex mold UCM 37571): Miller (1880, p. 220-221) separated "T. cincinnatiensis" from "T. permultum" "...by the smaller and more ill-defined form of the tracks, by the greater number in each series, and by the greater distance between the two series." He differentiated it from T. numerosum "...by the greater distance between the two series,

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

by the [fewer] number of impressions in each series, and by the simple character of the tracks instead of the compound or beaded form" (Miller, 1880, p. 221).

The trail, which has a total length of 16 cm and a width of 1.8 cm, is preserved as a convex hyporelief and is quite indistinct. This obscurity suggests that the trail actually is preserved as a cleavage relief and not as a boundary relief (compare with pl. 18, fig. 1). If this is the case, the more complete set of tracks lies beneath the surface. There are no clearly defined sets, and the individual imprints are small and show no evidence of raking motion. The linear arrangement of the opposing rows suggests straight-ahead movement; however, the criteria normally used for determining the direction of movement are lacking. The only hint of a "V" is seen in the middle of the trail; if this actually represents one-half of a "V," movement would be from bottom to top, as seen in pl. 18, fig. 2. The width of the trail is similar to that of the type specimen, and there are no distinct features that would serve to set it apart as a separate taxon.

"Merostomichnites sp. (cf. Petalichnus multipartitus)" (pl. 18, fig. 4; UCM 22033): Caster (1938, pl. 10, fig. 1) illustrated a trail from the Fulton beds of the Union Levee, Cincinnati, Ohio, which he compared to Merostomichnites as figured by Størmer (1934). The trail is preserved as a convex hyporelief in a calcisiltite and has a total length of 5.7 cm and a width of 1.8 cm. The

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

specimen, which is incomplete, consists of a portion of six obliquely-directed series of raking imprints on the left and a continuous row of support imprints on the right. The greatest number of impressions seen in any series is 10. The trail is unusual in that nearly all of the imprints are simple scallop-like markings. However, a short, faintly-defined ridge can be seen leading from some of the imprints on the left. These ridges are oriented normal to the trend of the row of support imprints.

Although the trail bears some resemblance to Størmer's (1934, pl. 2, fig. 7) illustration of Merostomichnites strandi from the Downtonian (Devonian) beds of Spitzbergen, there are significant differences. As Størmer (1934, p. 22) noted, each of the imprints in the Norwegian specimen consistently contains three or four markings grouped together. This demonstrates that the trail was made by an organism with quadridigitate walking legs. In contrast, in the right-hand row of the Cincinnatian form, neither the spacing between the imprints nor the number of imprints is as consistent as it is in Størmer's specimen. It is instead concluded that the Cincinnatian specimen is a trilobite trail where the body was oriented to the left of the axis of movement; thus, the superposition of the support imprints in the right-hand row give a false impression of a polydactylous leg. Størmer believed that M. strandi was probably the trail of an eurypterid, and his conclusion is not questioned herein. The present author agrees with

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

Caster (1938) that the Cincinnatian specimen is a trilobite trail. The scallop shape of the imprints indicates that the legs probably struck the substrate in a slicing motion. The weak preservation of the raking imprints demonstrates that the specimen is preserved as a cleavage relief.

Two other previously undiscussed specimens which are assigned to P. multipartitum are shown on pl. 17, fig. 6 and pl. 18, fig. 5. One of these (pl. 18, fig. 5) is an excellent example of oblique movement. While the imprints of the left side are superimposed, the obliquely-directed imprints on the right are clearly defined, and it is possible to count 10-12 imprints in the various series (see fig. 34-1). The width of the trail is 9 mm, while the length of each series averages 2.5 cm. The specimen differs from most forms showing oblique movement as there are no well developed raking imprints; however, this may be more a factor of preservation than of behavior.

The other specimen (pl. 17, fig. 6) was illustrated by Caster, Dalvé, and Pope (1955, pl. 2, fig. 35). The trail has a width of 2.6 cm and the length of each series is 3.4 cm. The individual imprints, which average 8/series, are bifid distally and show well developed withdrawal markings at their proximal extremity. As viewed in pl. 17, fig. 6, movement was from bottom to top.

Interpretation: As indicated above, the forms grouped under P. multipartitum, although interpretated by

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

Miller (1880) as cephalopod tracks, are herein thought to be the trails of moderate-sized trilobites. Unfortunately it is not possible to assign them to a given genus. Based on the percentage of trilobites found in the Cincinnatian rocks, most of the trails should be those of Flexicalymene; however, Petalichnus almost certainly contains tracks of other trilobites. Until a trilobite is found at the end of a trail or body fossils are found with the dactyls well preserved as in Cryptolithus, P. multipartitum must remain a form genus for unifid or bifid tracks of moderate-sized trilobites.

Trachomatichnus Miller, 1880

(pl. 9, fig. 7; pl. 17, fig. 3-4; pl. 18, fig. 1; pl. 19, fig. 1; pl. 27, fig. 5; text fig. 32-2)

1880 (in partim) Trachomatichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 219-220, pl. 13, fig. 2-4.

Type Species: Trachomatichnus numerosum Miller (1880) from the ?Southgate beds of State Avenue, Cincinnati, Ohio. Monotypic. The specimen (MCZ 539; latex mold UCM 37583) illustrated by Miller (1880, pl. 13, fig. 3; herein pl. 18, fig. 1) is designated as the type specimen.

Diagnosis: Straight-ahead trails consisting of crowded, poorly defined imprints made by a polydactylous leg.

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

As best can be determined, the number of imprints per set ranges from 9-11.

Discussion: As noted elsewhere, Miller (1880) established three species of Trachomatichnus. Since no holotype was named by the author, Häntzschel (1962) designated T. numerosum as the type species. This was a fortunate choice for, as shown previously, the specimens referred to "T. permultum" and "T. cincinnatiensis" lack sufficient diagnostic features to justify their retention as separate taxa. On the other hand, the three specimens of T. numerosum illustrated by Miller differ from all others discussed by the author in his 1880 paper. According to Miller (1880, p. 219-220), the species is characterized by tracks which are "...composed of four or five parts, which present a beaded appearance."

The specimen herein designated as the type specimen (pl. 18, fig. 1) occurs as a convex hyporelief on a cross-laminated calcisiltite. In contrast to most Cincinnatian arthropod trails which are found on cleavage planes, the clarity of detail indicates that this form is preserved as a boundary relief. The length of the trail is 10.5 cm and the width ranges from 1.3-1.5 cm. While there is no dimorphism in the two rows, the morphology of the specimen varies along its length.[35/] Three different expressions are

---

35/ For purposes of discussion the left side of the specimen,

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

as viewed in pl. 18, fig. 1, is referred to as posterior; the right side as anterior.

---

present, each occupying roughly one-third of the total trail length.

The imprints of the posterior third of the trail resemble cuneiform wedges which taper and fade out anteriorly. The posterior portion of the wedge has a denticulate margin, thus differentiating it from all other imprints so far discussed. The better preserved forms show three to six denticles. The various imprints are so irregularly placed that it is impossible to determine the number of imprints in a set. In the center portion of the trail, the imprints flow together to form two parallel continuous fasciculate ridges, although some individual imprints can be seen to the interior of each ridge. In the anterior third of the trail, it is possible to discern separate sets, albeit the number of imprints comprising a set is unknown. The open end of the "V" formed by the opposing arms is directed anteriorly. Note that at one point the rows merge briefly to form a short bilobed Rusophycus-like body.

As indicated by the orientation of the "V's," movement was from left to right, as viewed in pl. 18, fig. 1. The variations in the morphology of the trail reflect different types of movement, which were probably caused at least in part by the uneven surface of the bottom upon which the organism was walking. The surface of most of

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

the slab slopes gently to the left, while in the anterior third of the trail, the slope is more precipitous. The cuneiform nature of the imprints indicates that the dactyls were not placed flat on the substrate as in the type specimen of Asaphoidichnus trifidum nor were they moved toward the median line to form raking imprints. Instead the animal inserted the dactyls obliquely to the rear, as if it were slipping and struggled to gain more traction. The fasciculate ridges in the eenter portion of the trail would seem to confirm this. The lack of dimorphism indicates that the body was parallel to the axis of movement.

Another specimen (MCZ 547; latex mold UCM 37695) of T. numerosum figured by Miller (1880, pl. 13, fig. 2) is illustrated herein on pl. 17, fig. 3. The trail is preserved as a convex hyporelief, and the lack of detail indicates that it is a cleavage relief. The trail length is 12 cm and the width is less than 1 cm. Miller's illustration is slightly deceptive, as it shows cuneiform imprints similar to those of the type specimen. In contrast, the specimen reveals that the imprints were made by straight downward movment. As in the type specimen the imprints are denticulate, although the 3-4 denticles are not as well preserved. A small degree of dimorphism, evident in the lower part of the trail, indicates that the direction of movement was from bottom to top, as seen on pl. 17, fig. 3. For the most part the body was parallel to the axis of movement.

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

The final specimen (MCZ 544; latex mold UCM 37671) figured by Miller (1880, pl. 13, fig. 4) is shown on pl. 17, fig. 4. In contrast to the others, it is preserved as a concave epirelief. A latex mold was made in an attempt to determine if the cavities concealed any details not visible from the surface. However, the mold reveals imprints similar to those in the specimen just discussed. The trail has a length of 6 cm and a width of 4-7 mm. Some of the imprints in the right row (see fig. 32-2) can be differentiated into sets, while those of the left row are superimposed. This demonstrates that the direction of movement was from bottom to top, as viewed in pl. 17, fig. 4, and that the body was oriented slightly to the right of the axis of movement.

Interpretation: There is evidence to indicate that T. numerosum is the trail of Cryptolithus. As shown in the introduction to this section, Cryptolithus is the only Cincinnatian trilobite in which the morphology of the dactyls is known from preserved material. Beecher's (1895) illustrations of the genus plainly show that the terminal joint consists of several bristle-like digits. This type of structure is capable of producing the multidigitate imprints of the trail. Moreover, the dimensions of the track are well within the range of the average Cryptolithus. As mentioned previously in the discussion of Allocotichnus, the mean "three-quarter width" of Cincinnatian Cryptolithus is 1.59 cm. The greatest width of the trail is 1.5 cm and normally it is less than a centimeter. Also the crowding

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

of the imprints suggests the closely spaced legs seen in Cryptolithus. However, it is puzzling that no evidence of the long genal spines is preserved with the trail. One might expect that the long spines would leave linear imprints on either side of the track. It may be that some of the markings near the trail on the type specimen represent the intermittent contact of the genal spines with the substrate, but it is not possible definitely to distinguish them.

Two other trails thought to be made by Cryptolithus were found in the University of Cincinnati collections. Unfortunately locality data is lacking, but Cryptolithus fragments found in the slab bearing the specimens probably indicates Eden rocks. These are not assigned to T. numerosum and are informally discussed below. In reality they lie closer to the band-like Cruziana burrows than they do to trilobite surface-walking trails. Both are preserved as convex hyporeliefs in calcisiltites. At first glance the form illustrated on pl. 19, fig. 1 appears to be a single discontinuous trail, but as will be shown, the gently curving arc on the upper right is not connected with the serpent-like complex on the left.

The main body of the trail consists of a series of discontinuous chevron-shaped ridges which average 6-8/cm. In places (pl. 27, fig. 5) the chevrons are so closely spaced that they resemble the continuous bilobate ridges of Cruziana. Close observation shows that the ridges are

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

covered by delicate bundled striae. On either side of the trail are two thin ridges which are separated from the chevrons by a distance of 2-5 mm. These are discontinuous and may be present on one side of the trail and lacking on the other. The width of the entire trail, including the ridges, varies from 0.9-1.2 cm. The other specimen (pl. 9, fig. 7) is similar to that described above except that the chevron bodies merge to form a continuous bilobate trail. Likewise, the thin ridges flanking the trail are better developed, and in one area the bilobate ridges actually rest on a small terrace, as shown in fig. 40.

Both specimens are judged to be the Cruziana-like trails of Cryptolithus. The bundled striae on the chevron-shaped bodies resemble the imprints that could have been made by brush-like dactyls of the walking legs seen on Beecher's illustration of Cryptolithus. Moreover, the narrow width of the trail places it well within the range of most Cincinnatian specimens of Cryptolithus. The V-shaped ridges demonstrate that the legs operated in a manner similar to that used when excavating a Rusophycus-like burrow, i.e., the digging movement was directed toward the median axis and to the rear. Thus, the animal was ploughing over the surface instead of using merely the distal portions of the legs. As in Rusophycus the open end of the "V" formed by the striae of the opposing lobes is directed anteriorly. This indicates that movement in the serpentine trail, shown on the left side of pl. 19, fig. 1, was from top to bottom.

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

On the other hand, the direction of movement in the arcuate trail, seen on the right side of pl. 19, fig. 1, was from left to right. Movement in the specimen on pl. 9, fig. 7 was from left to right. The smaller secondary ridges represent places where the genal spines gouged the surface. In the one specimen the "terrace" on which the ridges occur reveals that at times the cephalon acted as a shovel and skimmed off the upper millimeter or so of the substrate.

This type of trail is quite similar to the classic band-like Cruziana which is especially well developed in the Silurian of Portugal and has been figured by Delgado (1910). The only difference between the two is that the Silurian representatives form even, bilobate ridges with continuous secondary ridges on either side. The Cincinnati forms vary because the trail was shallower; thus, the markings produced by the legs generally appear as individual chevron-shaped markings instead of continuous bilobate ridges. The broad cephalon of Cryptolithus, combined with the relatively small legs, may well have impeded digging in all but the softest sediments.

The ethological significance of these Cruziana-like trails is unknown. Perhaps, as Seilacher (1959) suggested, they are feeding trails, where the organism stirred up the mud and filtered out the nutrients. On the other hand, they may be a variety of Repichnia.

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

Teratichnus Miller, 1880

(pl. 19, fig. 3; text fig. 35)

1880 Teratichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 221, pl. 14, fig. 1.

Type Species: Teratichnus confertum Miller (1880) (pl. 19, fig. 3; MCZ 540; latex mold UCM 37570) from the ?Southgate beds of State Avenue, Cincinnati, Ohio. Monotypic.

Diagnosis: An arthropod track, consisting of nine bifid imprints per set, which is marked by a median groove located midway between the right and left series.

Discussion: The genus is known only from the type specimen and is preserved as a faintly impressed concave epirelief on a gently undulating calcisiltite. Because of the difficulty of photographing the actual type specimen, a latex mold was used for illustrative purposes. The trail, which is incomplete at both ends, is sickle-shaped and has a total length of 26 cm. The trail width does not exceed 1.7 cm. In the lower part of the specimen, as viewed in pl. 19, fig. 3, the imprints are irregular and there are no well defined sets. The first discernible set of imprints is located 2 cm from the bottom of the slab and is marked by the letter A. These imprints do not form a "V" or modified "V," as in most trilobite tracks, but instead are arranged in an elliptical pattern. This suggests that the animal lay in this spot and moved the legs toward the

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

median axis as if to momentarily anchor itself to the substrate. Extending from one end of the ellipsoid is a long (1.5 cm), sharply defined groove (C). Note that similar grooves are located at positions B and D. These grooves may well be significant in assigning a maker to the trail. In the center of the slab the imprints become highly confused, and as will be shown, it is believed that in this area there was considerable rotation of the body. In the remainder of the trail it is possible to distinguish at least portions of individual sets. As illustrated in fig. 35, there is an average of nine imprints per set, and the open end of the "V" is directed toward the top of the slab. Withdrawal markings are plainly defined at the proximal end of many of the imprints, and one set shows four imprints which are bifid distally and unifid proximally (pl. 19, fig. 3).

Interpretation: Although Miller (1880) interpreted Teratichnus as the trail of a cephalopod, it is evident that it is of arthropod origin. The basic direction of movement, as viewed in pl. 19, fig. 3, was from bottom to top. This is indicated by three lines of evidence. 1) The ellipsoidal series of imprints (pl. 19, fig. 3B) truncate those imprints near the lower margin of the slab. 2) In the confused area in the center of the slab, the imprints leading directly into the long sweeping arc are superimposed over the earlier formed imprints, indicating that the movement here was from right to left. 3) In the arcuate portion of the trail, the

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

open end of the "V" formed by the sets is directed toward the top of the slab (see fig. 35). It is believed that as the organism entered from the bottom, as seen in fig. 35, the direction of movement was nearly at right angles to the body axis. As noted above, the animal then briefly anchored itself to the substrate. After progressing forward for a few centimeters, the orientation of the imprints shows that the organism apparently moved obliquely backwards. Finally the animal moved in a tight arc, pivoting on the walking legs of the right side and lashing out at the bottom with the legs of the left side. As shown in fig. 35, the body was oriented to the left of the axis of movement. Thus, the imprints of the left side are well defined, while those of the right side are superimposed and form a continuous line. Whether this unusual movement was voluntary or whether the animal was being driven by current is difficult to determine. There is no clear evidence of current action on the slab.

It is possible that Teratichnus is the trail of a trilobite similar to those discussed under Petalichnus multipartitum. However, the three grooves (pl. 19, fig. 3BCD) are an integral part of the trail, and these appear to be imprints of a median posteriorly directed spine or appendage. No known Cincinnatian trilobite possesses a single well developed pygidial spine. Seilacher (1955) has attributed twin grooves in redlichiid trails to imprints of caudal cerci. However, according to Moore, Harrington, and

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

Stubblefield (1959, p. 118), such cerci are found only in the Cambrian species Olenoides serratus; and is is not known whether they were common to all trilobites. The only other arthropod known to be present in the Cincinnatian which has a posterior spine and is similar in size to the track is the aglaspid Neostrabops Caster and Macke (1952). Although the telson of this genus is unknown, most Cambrian aglaspids possessed a narrow lanceolate telson. The dimensions of the sole specimen of Neostrabops compare favorably with those of the track. Neostrabops has a maximum width of 2.8 cm, while the track width is 1.8 cm. The length of the sets, which because of the dimorphism is difficult to measure, is 4.9 cm. The length of Neostrabops, which is incomplete and measured only to the end of the 10th segment, is 3.5 cm. The nine imprints present in the sets of T. confertum correlate well with the 11 thoracic segments of the aglaspid. The only apparent difference is that, as Raasch (1939, p. 62) demonstrated, aglaspids had but a single dactyl; as noted above, the trail shows the imprints of bifid dactyls.

In summary, it is concluded that T. confertum was made by a relatively small arthropod which possessed bifid dactyls and a median posterior spine or fleshy appendage (cercus). At present it is not possible to give a more precise assignment. No known Cincinnatian arthropod exactly matches the morphology of the track. None of the trilobites has a single pygidial spine, and the nature of

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

the cerci, if present, is unknown. On the other hand, aglaspids have a telson, but the walking legs apparently have but a single dactyl. It must also be noted that Neostrabops is known only from a single specimen.

Rhabdoglyphus Vassoevich, 1951

(pl. 22, fig. 4-9)

1951 Rhabdoglyphus Vassoevich, N. B., Les Conditions de la Formation du Flysch, p. 61, pl. 5, fig. 3; pl. 6, fig. 3-4.

1962 Rhabdoglyphus, Bouček, B., and Elias, M. K., Geol. Práce Zprávy, vol. 25-26, p. 145-151, pl. 7-8.

Type Species: Rhabdoglyphus grossheimi Vassoevich (1951) from the Cenomanian of the Caucasus, Czechoslovakia. Monotypic.

Diagnosis: Rosary-like trails and/or tunnel fillings of varying length, preserved either as convex hyporeliefs or concave epireliefs.

Discussion: Although Vassoevich proposed Rhabdoglyphus for what he referred to as a "bioglyph," his genus was invalid due to the lack of a formal diagnosis. Recognizing this, Bouček and Elias (1962) formally described and diagnosed the form, studying the original type material, as well as additional specimens from the Paleogene flysch of the Czechoslovakian Carpathians. The facts related below

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

are taken from the plates and a short German summary.

R. grossheimi is preserved as a convex hyporelief and consists of cylindrical tunnel fillings with periodic well defined swellings or "knots" (herein pl. 22, fig. 8-9). The diameter of the cylindrical fillings is 4 mm, that of the swellings is 7 mm. The latter are not evenly spaced, as the distance between them varies from 1.8-3.0 cm, and in one form illustrated by the authors, two swellings occur together. Judging from the specimen illustrated on pl. 22, fig. 8, it seems that we are not dealing with just a simple convex hyporelief, for at both ends the hemicylinder appears to extend up into the bed.

Rhabdoglyphus resembles Hormosiroidea florentina F. X. Schaffer (1928) from the Pietraforte Limestones (Upper Cretaceous) near Florence, Italy. Through the kindness of Dr. Zapfe of the Natural History Museum of Vienna, a plaster case of Hormosiroidea was made available for study (pl. 22, fig. 7). The specimen, 9 cm long and shaped as an open "S" curve, consists of a series of raised hemispherical bodies connected by thin, short hemicylindrical rods. The diameter of the hemisphere ranges from 6-9 mm; the diameter of the connecting rods is 1 mm. Near the larger specimen is a slightly shorter form consisting of only two hemispheres. Associated with these two specimens are small raised vermiform-like markings whose diameter is the same as the connecting links between hemispheres. The attitude of the latter indicates that Hormosiroidea is most

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

probably a convex hyporelief rather than a concave epirelief as Schaffer believed.

It is entirely possible that Rhabdoglyphus is synonomous with Hormosiroidea. Although the general morphology of the two is similar, a decision can not be made without additional study. Both forms should be sectioned to determine if they are exclusively surface features or whether they actually extend into the host rock as they appear to.

Interpretation: Schaffer interpreted Hormosiroidea as an alga comparable to the Recent Hormosira and regarded the swellings as spore cases. Boucek and Elias suggested that Rhabdoglyphus may represent the workings of an amphipod, a gastropod, e.g., Bulla, or even possibly a holothuroid similar to Leptosynapta. They rejected a possible annelid origin. In the German summary they give no explanation for the periodic swellings nor do they give any reason for mentioning Bulla and Leptosynapta as possible originators.

Cincinnatian Representatives

Rhabdoglyphus sp.

(pl. 22, fig. 4-6)

Discussion: Rhabdoglyphus-like forms are present, though uncommon, in the Cincinnatian. Only 10 specimens

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

have been collected, eight from the Richmond and one each from the Eden and Maysville. Unfortunately material has never been observed in place. In contrast to the European forms discussed above, all Cincinnatian representatives are preserved in calcisiltites and calcarenites as concave epireliefs, i.e., as hemispherical depressions normally connected by hemicylindrical troughs. The entire pattern, whose length ranges from 9-30 cm, is either straight or gently curved. Both the size and shape of the hemispherical depressions vary greatly. They may be round (pl. 22, fig. 4), cordate (pl. 22, fig. 5), bottle-like (pl. 22, fig. 5), or rectangular (pl. 22, fig. 6). When only four or five depressions are present, they are normally of the same size, but when the number is greater, there is a definite gradation from smaller to larger. One example noted in the field consisted of 12 depressions. The first and largest measured 8 mm in diameter, the last only 2 mm. The depth varied from 0.5-1.0 mm and generally speaking the larger the diameter, the greater the depth. As in European specimens of Rhabdoglyphus, the distance between the depressions varies. The actual measurements are present in Table III.

The shallow connecting troughs are only one-third or one-half as wide as the depressions. In some cases the troughs are deeper adjacent to the depressions and appear to bend down into them. Where there is a definite gradation in the size of the depressions, there is an associated trend in the development of the connecting troughs. The larger

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

Table III

Distance Between Hemispheres in Millimeters

-Hemisphere Number-

Specimen Number	1	2	3	4	5	6	7	8	9	10	11	12
1)	9	18	20	13	30	-	-	-	-	-	-	
2)	8	8	7	7	9	-	-	-	-	-	-	
3)	15	6	16	9	3	11	8	7	-	-	-	
4)	11	8	9	20	18	-	-	-	-	-	-	
5)	8	11	-	-	-	-	-	-	-	-	-	
6)	8	7	8	5	-	-	-	-	-	-	-	
7)	5	7	12	11	-	-	-	-	-	-	-	
8)	7	10	12	17	17	7	-	-	-	-	-	
9)	9	7	10	?	6	9	6	-	-	-	-	
10)	9	10	10	14	10	8	11	9	7	6	17	

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

and deeper the depression, the better developed the connecting trough; on the other hand, where the depressions are small and shallow, there may be no connecting trough present (pl. 22, fig. 6). Normally the connecting troughs appear to be simple impressions, but one specimen (pl. 22, fig. 6) shows raised boaders, and apparently there has been movement along this trough from left to right. No evidence of sculpturing was found on any of the specimens, as both the connecting troughs and the hemispherical depressions are smooth.

A comparison of the morphology of the Cincinnatian forms with that of Rhabdoglyphus shows that both can be safely placed within a single genus. The Cincinnatian specimens are judged to represent molds of the same trace described from casts in Europe. This is a difference in preservation rather than morphology, and for the present there seems no good reason for not assigning the Cincinnatian representatives to Rhabdoglyphus.

Interpretation: The origin of these bead-like forms is not readily apparent. Other than bearing a superficial resemblance to the Recent algal genus Hormosira (see Schaffer, 1928, fig. 1-2), there is no indication that it is a plant. The general form does recall prod marks such as those figured by Dzułinski and Sanders (1962, pl. XII, fig. B). The authors illustrate a sole-marking from the Polish flysch which shows a series of hemispheres produced by a fragment of a fish vertebra skipping along the bottom. The problem in extending this kind of explanation to at least the

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

Cincinnatian representatives of Rhabdoglyphus is that there is no evidence of linear current action; in fact one specimen (pl. 22, fig. 5) is superimposed over interference ripples. Moreover, the hemispherical depressions of Rhabdoglyphus do not show the distortion one would expect if an object had gouged the bottom at a shallow angle. For these reasons Rhabdoglyphus is not thought to be of physical origin.

Although the behavioral pattern reflected by its morphology is not understood, there is reason to believe that Rhabdoglyphus is a trace fossil, most probably a variety of Repichnia or Fodinichnia. As mentioned previously, one specimen illustrated by Bouček and Elias appears to extend up into the host rock, and one Cincinnatian specimen (pl. 22, fig. 6) does show evidence of movement. If we assume that these fossil-bearing calcisiltites and calcarenites were overlain by lutite[36] and that the form represents infaunal

---

[36] One specimen shows a finer grained mud filling the hemispheres.

---

activity, it is relatively easy to explain why troughs are not found between all the hemispheres. It is believed that the organism burrowed down through an unknown thickness of lutite, periodically altering its behavior to produce the "knots" or swellings. Only where it was burrowing horizontally along the shale-silt interface would we find both the

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

swellings and connecting depressions. If the animal veered up ever so slightly into the mud, the connecting depressions would be the first feature to be lost, since they are not as deeply impressed as the "knots." However, one would expect the swellings to be smaller and shallower than when there is a connecting link between them. This is exactly the case. The same would hold for the specimens described by Boucek and Elias, except here the calcarenite which contains the specimen was probably underlain by lutite. The organism burrowed down through the calcarenite and along the interface. The overlying calcarenite filled in the depression as the animal moved along, thus producing the type of preservation so commonly encountered in trace fossils, i.e., convex hyporelief. Still unexplained is the nature of the organism which produced the trace and the meaning of the periodic swellings.

One Recent trace has been described which may possibly offer a basis for comparison with fossil forms. In attempting to explain the origin of Arthraria, Fenton and Fenton (1934, pl. XXVIII, fig. 2) described the peculiar actions of the gastropod Illyanassa obsoleta (Say) on the mud flats of San Francisco Bay. Illyanassa ploughs along the surface, leaving a trail much like the connecting depressions found in Cincinnatian Rhabdoglyphus, then it abruptly twists and digs a shallow conical pit before once again proceeding on its way. The authors give no reason for this behavior.

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

The meaning of periodic swellings in Rhabdoglyphus is uncertain. Perhaps they are infaunal analogues of the conical pits of Illyanassa. It is also possible that Rhabdoglyphus is the burrow of a Sedimentfresser and that the swellings represent periodic (peristaltic) anal constrictions and expansions. Likewise, they might be the results of localized muscle knotting, possibly for the eversion of a proboscus.

Rhabdoglyphus bears a superficial resemblance to some moniliform sponges, e.g. Girtyocoelia; however, there is no evidence to indicate that Rhabdoglyphus is the mold of a sponge or sponge-like body.

Tylichnus n. gen.

(pl. 10, fig. 7; pl. 15, fig. 2; text fig. 38)

1842 (non) Cruziana d'Orbigny, A., Voyage dans l'Amérique meridionale, T. 3, p. 30, pl. 1, fig. 1.

1852 (non) Rusophycus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 2, p. 23, pl. 9, fig. 1a-c.

1873 (non) Planolites Nicholson, A., Roy. Soc. London, Proc., vol. 21, p. 389.

1878 Rusophycus, Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 2, pl. 1, fig. 5-5a.

1885 (in partim) Cruziana, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 156, pl. 8, fig. 3.

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

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Species: Rusophycus asperum Miller and Dyer (1878) (pl. 15, fig. 2; HBM 3179; latex mold UCM 37588) from the Eden beds, Cincinnati, Ohio. Monotypic. The form is not common and is known from only four specimens. Regrettably precise locality data are lacking.

Diagnosis: Faintly bilobate trails preserved as convex hyporeliefs; surface of trail characterized by nine parallel rows of nodes which are offset so as to form a "zipper-like" pattern.

Discussion: Miller and Dyer (1878a, p. 2) characterized "Rusophycus" asperum as consisting "...of long stems, flattened on the upper side, or having a longitudinal depression, which gives to them a subangular outline. The surface is made very rough by numerous papillae, many of which are transversely elongated." While they remarked that "...it is separated by generic differences from such forms as R. pudicum and R. bilobatum" (ibid, p. 2), they declined to establish a new genus. As will be shown below, the unusual papillose prosopon serves to differentiate this form from all known trace fossils. Accordingly the new genus Tylichnus is proposed for "Rusophycus" asperum.

The type specimen of Tylichnus asperum (pl. 15, fig. 2) is preserved as a convex hyporelief on a fine-grained, cross-laminated calcarenite. The slab bears short

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

fragments of several specimens which interpenetrate but do not branch. Vertical sectioning reveals that the forms extend up into the host rock and are subquadrate in cross-section, the width of the burrow being 3.5 mm; the height, 1.5 mm. The contact between the burrow filling and the host rock is not sharply defined, and there is no apparent difference in lithology. As viewed in pl. 15, fig. 2, the surface of the burrow is flattened, although one portion (upper left) is faintly bilobate. The pustulose prosopon varies in its arrangement. As shown in fig. 38, the basic pattern consists of nine parallel rows of transversely elongate nodes. The rows are offset so as to give the overall pattern a "zipper-like" appearance. In contrast, some segments of the burrow show no preferred arrangement, and the closely packed nodes are distributed randomly over the surface.

Plate 10, fig. 7 shows another slab bearing six short specimens. The burrow width is 2.5-3.0 mm, and the largest form has a length of only 1 cm. The nodose surface of these specimens differs somewhat from that seen in the type. In one form the nodes are arranged in three parallel rows which are slightly oblique to the longitudinal axis of the burrow. The lateral rows consist of a single moniliform chain of nodes. In opposition, the median row is slightly wider, and along most of its length the nodes exhibit no preferred grouping. However, in one small segment the nodes are arranged in an alternating 1-2-1-2 pattern. The remaining

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

specimens on the slab are weakly bilobate, and the nodes do not show a linear arrangement; however, the lateral nodes are slightly larger than the median. On one of the specimens the side of the burrow adjacent to the host rock is partly exposed, and the same nodose prosopon can be seen, suggesting that the entire burrow may be characterized by a pustulose surface. Vertical sections reveal that, like the type specimens, the burrows are of infaunal origin.

The additional specimens available for study add little to the knowledge of the prosopon. However, they do show that the burrow may attain a length of up to 8.5 cm.

Interpretation: Miller and Dyer (1878) believed that "Rusophycus" asperum was a "fucoid," while J. F. James (1885) concluded that it was an annelid burrow. In 1891 James placed the form in Planolites, but as shown elsewhere, his concept of Planolites embraced such a variety of forms that it is virtually meaningless. It is also clear from the above discussion that Tylichnus bears no resemblance to either Rusophycus or Cruziana. The nodose prosopon of Tylichnus is totally unlike the striae which cover the lobes of the trilobite burrows.

The nodose surface does recall forms such as Ophiomorpha Lundgren (1891) from the Upper Cretaceous and Tertiary of North America, Europe, and Japan and Pennatulites de Stefani (1885) from the Tertiary of Europe and the West Indies. However, as illustrated by Häntzschel (1952, pl. 13-14), Ophiomorpha is oriented either normal to or only

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

slightly oblique to the bedding and may attain a diameter of 2 cm. Moreover, the nodes of Ophiomorpha are much larger and show no preferred grouping. Pennatulites is a bilobate bundled burrow and is briefly discussed herein under Trichophycus venosum. The specimen of Pennatulites illustrated by Häntzschel (1962, fig. 127-1a,b) has a diameter of 4 cm, and while the nodes are smaller than those of Ophiomorpha, they are arranged in parallel rows much like kernels of corn.

Since there are no known Recent counterparts of Tylichnus, little can be said of the originator of the burrow. The subquadrate cross-section and the possibility that the nodes encircle the entire burrow suggest a vermiform body ringed by some type of papillae. Perhaps the nodes represent the impressions of a feeding apparatus surrounding the mouth of an organism working along the lutite-calcisiltite interface. There is no evidence of a genetic relationship between T. asperum and the moniliform ?fecal string seen on pl. 10, fig. 7 (center bottom).

Ormathichnus Miller, 1880

(pl. 22, fig. 1-3)

1880 (in partim) Ormathichnus Miller, S. A., Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 222, pl. 14, fig. 4-5.

1886 (in partim) Ormathichnus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 160-161.

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

Type Species: Ormathichnus moniliformis Miller (1880) from "Walker Mill Road [State Avenue, Cincinnati, Ohio], less than 100' above low water" (probably Southgate). Monotypic.

Diagnosis: A very small trail resembling a series of minute disconnected Rusophycus which grade into the continuous ridges of Cruziana.

Discussion: Miller (1880, p. 222) described the genus as "a single continuous beaded track or trail." Two specimens were figured and discussed. The first (Miller, 1880, pl. 14, fig. 4) he likened to a cast of the stem of Heterocrinus simplex; the second (pl. 14, fig. 5) differed in that it possessed "a longitudinal furrow in the middle."

An analysis of the cotypes reveals that we are dealing with two entirely different things. The form illustrated by Miller on pl. 14, fig. 4 (herein pl. 22, fig. 3) is preserved as a convex hyporelief and consists of a row of 30 moniliform welts whose aggregate length is 25 mm. It fades out in one direction and is incomplete at the other end. It is associated with groove casts and a few scour marks, as well as a series of parallel striae which resemble a cast of the markings made by a rolling crinoid stem.

The other specimen (Miller, 1880, pl. 14, fig. 5; herein pl. 22, fig. 1-2), 1 mm wide and 6.0 cm long, is semicircular in outline. The morphology of the form varies along its length. In the upper left-hand corner, as viewed on

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

pl. 22, fig. 2, it consists of three long grooves separated by two raised ridges. These ridges are so small that it is impossible to determine whether they are striate or smooth. The remaining 4.0 cm of the specimen resemble a series of minute unconnected Rusophycus (pl. 22, fig. 1). These recall on a much smaller scale Seilacher's (1955, fig. 4a-b and 5a) illustration of Rusophycus didymus.

Interpretation: Although Miller stated that Ormathichnus was probably a gastropod trail, he gave no supporting evidence other than the fact that gastropods were found in the same bed. J. F. James (1886) regarded the genus as a cast of the impression of a rolling crinoid stem, and this probably is a correct interpretation for one of the specimens (pl. 22, fig. 3). The length of the raised segments (1 mm) is equal to the spacing between the parallel striae on the same surface. The only problem is that "Ormathichnus" is oriented parallel to the current direction. Normally casts of the impressions of rolling crinoid stems are either at right angles or oblique to the current. An alternate hypothesis is that the specimen is somehow related to "skip casts" in the sense of Dzułynski and Sanders (1962). In any event it apparently is not a trace fossil but some variety of an inorganic tool mark.

The other specimen (pl. 22, fig. 1-2) is judged to be the trail of a very small arthropod, possibly a trilobite. Based on the orientation of the Rusophycus-like imprints, movement was from left to right as viewed in

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

pl. 22, fig. 2. In reality the trail is a combination of Cruziana and Rusophycus. The organism initially ploughed along producing a "micro-Cruziana" consisting of three grooves and two ridges. It then altered its method of movement to give rise to a series of unconnected Rusophycus. Because of its extremely small size, Miller's original generic designation is retained; however, the form is not a common Cincinnatian track fossi, and no subsequent specimens have been found.

Palaeophycus Hall, 1847

(pl. 20, fig. 1-9; pl. 21, fig. 1,4-7; pl. 27, fig. 1,4)

1847 Palaeophycus Hall, J., Nat. Hist. New York, Paleont. New York, vol. 1, p. 7-8,63, pl. 2, fig. 1-5; pl. 21, fig. 2; pl. 22, fig. 1.

1852 Palaeophycus Hall, J., Nat. Hist. New York, Paleont. New York, vol. 2, p. 6,22, pl. 3, fig. 2a-b; pl. 22, fig. 10.

1873 (non) Planolites Nicholson, H. A., Roy. Soc. London, Proc., vol. 2, p. 289.

1885 Palaeophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 155-157.

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

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

Type Species: Palaeophycus tubulare Hall (1847) from the "Calciferous Sandstone" (Beekmantown; Lower Ordovician, marine) from the Mohawk Valley of New York State (NYSM 241/1, 241/2, 241/3, 241/4). Lectotype, Wilson (1948).

Diagnosis: Slightly irregular cylindrical burrows of varying length which are oriented obliquely to the bedding plane. Most forms are unbranched, although a few bifurcate infrequently in no apparent pattern. The genus is most commonly found as hemicylinders which are preserved either as convex hyporeliefs or concave epireliefs. The surface of the hemicylinder may be smooth, striate, or annulate. Specimens vary from 3-15 mm in diameter and have a length of 5-20 cm.

Discussion: Hall (1847, p. 7) defined Palaeophycus as "stem terete, simple or branched, cylindric or subcylindric surface nearly smooth, without transverse ridges, apparently hollow." Four specimens of the type species were figured and each of these will be discussed below.

1) P. tubulare Hall (1847, p. 7, pl. 2, fig. 5; herein pl. 21, fig. 4; NYSM 241/2; latex mold UCM 37700). This specimen, which is preserved as a convex hyporelief in a blue, medium-grained calcarenite, contains several terete or hemicylindrical tubes which vary in diameter from 3-7 mm. Apart from one form which has a median longitudinal furrow, the surface of the tube is smooth. None of them show any clear evidence of branching, although interpenetration is common; and where the tubes intersect the side of the slab,

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

the bedding is disturbed. Thus, these are not mere surface features but are instead of infaunal origin. There is no marked difference between the composition of the tubes and that of the host rock.

2) P. tubulare Hall (1847, pl. 2, fig. 2; herein pl. 21, fig. 7; NYSM 241/2; latex mold UCM 37701). In essence this specimen is similar to the one just described. It is preserved as a convex hyporelief in a calcarenite, and the hemicylinders with their smooth surface have a diameter which ranges from 3-10 mm. Only one form is seen to bifurcate; the others cross over and interpenetrate. Observation of the margins of the slab reveals that the burrows penetrate the host rock and disturb the bedding. The fillings of the tube are slightly more fine grained than the surrounding calcarenite. Presumably serial sectioning of the specimen would show that those hemicylinders which appear to fade out on the surface in reality extend up into the host rock.

3) P. tubulare Hall (1847, pl. 2, fig. 4; herein pl. 21, fig. 1; NYSM 241/3; latex mold UCM 37699). This form is so poorly preserved that it adds little to the knowledge of the genus. The host rock is a dense, blue, limonite-encrusted calcarenite. The single smooth terete tube, which is 8 mm in diameter, appears to give off three small branches. It is not possible to determine whether the tube is preserved as a convex hyporelief or convex epirelief. Likewise, it is so encrusted with limonite that its composition is unknown.

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

4) P. tubulare Hall (1847, pl. 2, fig. 1; herein pl. 20, fig. 8; NYSM 241/1; latex mold UCM 37698). Remnants of bedding indicate that the host rock originally consisted of thick beds of blue calcarenite interstratified with thinner layers of pink calcarenite. However, the bedding has been so disturbed by bioturbation that the pink calcarenite now appears only as lenses. The numerous tubes possess the same basic patterns as those in the specimens described above, for there is no branching but interpenetration is common. They differ only in that they are slightly larger (diameter of largest form is 1.7 cm), and their surface bears faint irregular longitudinal striae. Vertical sections show that only about one-third of the surface of the tube is visible; thus, here again we are dealing with cylindrical bodies which extend up into the host rock.

In summary then, a restudy of the cotypes of P. tubulare demonstrates that the type species consists of generally unbranched cylindrical tunnels of varying diameters which extend up into the host rock. Aside from the exceptions noted above, the surface of the cylinders is smooth, and the fillings have a composition similar to that of the host.

Hall (1847, 1852) proposed six additional species of Palaeophycus. In order to illustrate the wide range of morphology occurring in the genus, these will be briefly discussed below.

1) P. rugosum Hall (1847, p. 63, pl. 21, fig. 2; NYSM 240/1) was described from the marine Trenton (Middle

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

Ordovician) beds of Middleville, New York. The species (herein pl. 20, fig. 1) is characterized by coarse irregular rugosites which are oriented approximately parallel to the axis of the branch. The main branch has a diameter of nearly 3 cm and is forked at one end. As the margin of the slab shows, the specimen is preserved as a convex hyporelief where the composition of the filling is the same as that of the host (coarse-grained calcarenite).

2) P. tortuosum Hall (1852, p. 6, pl. 3, fig. 2a-b; USNM 41102) was proposed for forms from the red Queenston (Upper Ordovician) strata of Irondequoit Bay, New York. The smooth subcylindrical fragments (pl. 20, fig. 2-4) are composed of an ferruginous silt and have a diameter of 1 cm. As Hall noted, two of the specimens are helicoid. Since the specimens are completely disassociated from the host rock, it is impossible to determine the lithology of the latter.

3) ?P. striatum Hall (1852, p. 22, pl. 10, fig. 1-2) from the Clinton (Middle Silurian) of Oneida County, New York, was placed in the genus with some hesitation. Only two of the five specimens figured by Hall were studied.[37]

---

[37] ?P. striatum Hall, 1852, pl. 10, fig. 1a; USNM 41108; latex mold UCM 37585; herein pl. 20, fig. 6 and ?P. striatum Hall, 1852, pl. 10 fig. 1c; USNM 41111; herein pl. 20, fig. 7.

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

The specimens are preserved as convex hyporeliefs in poorly sorted silts and can be seen to extend up into the host. The form illustrated on pl. 20, fig. 6 consists of two subcylindrical burrows which have a width of 1 cm. Both are marked by numerous faint longitudinal striae, and the longer burrow is characterized by a narrow longitudinal crest. The other slab (pl. 20, fig. 7) bears four unbranched subcylindrical fillings. The width of the burrows ranges from 6-8 mm, and only one form possesses the faint striae which characterize the species.[38]

---

[38] The remaining three species proposed by Hall were not studied; therefore, the description is taken from the original work.

---

4) P. irregularis Hall (1847, p. 8, pl. 2, fig. 3) from the Beekmantown (Lower Ordovician) beds of northeastern New York is an irregularly branched, smooth form which covers "the entire surface of large slabs of sandstone." Hall related that it is much smaller than P. tubulare, but other than that the species is so nondescript that it is difficult to diagnose or compare.

5) P. simplex Hall (1847, p. 63, pl. 22, fig. 1a-d) from the Trenton (Middle Ordovician) Limestone of Middleville, New York, normally occurs as fragments which have a diameter of 1 cm and a length of 15 cm. Hall remarked that he has

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

several hundred fragments and that "...the interior is filled with fragments of shells, crinoidal columns, etc." (Hall, 1847, p. 63). He went on to say (ibid, p. 63) that the species "...appears to have grown only during the shaly deposition, and is imbedded in this portion of the mass; consequently it is absent or obscure where such material is wanting as a component part of the rock."

6) P. virgatum Hall (1847, p. 263, pl. 70, fig. 1) was described from the "Hudson River Group" (Upper Ordovician) of Washington County, New York. Hall (1847, p. 263) remarked that "this species is only seen in fragments of long rigid stems, of nearly equal diameter....Fractured or weathered surfaces of arenaceous shales often present great numbers of these fragments, imbedded in great confusion." Hall said that the species was similar to P. simplex but that "it is impossible to indicate characters either to assimilate or distinguqish them" (ibid, p. 263).

In the years following Hall's work, 15 additional species of Palaeophycus were proposed by various authors from the Cambrian, Ordovician, and Pennsylvanian rocks of North America and from a variety of depositional environments. These were differentiated from Hall's species by the number, size, and rigidity of the branches, as well as the size of the entire pattern.

In view of the wide range of forms included in Palaeophycus, it is not surprising that the validity of the genus has been questioned. Most frequently Palaeophycus has

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

been compared with Planolites Nicholson (1873), which was originally described from the Guelph (Lower Silurian) section of Ontario. Howell (1943) placed Palaeophycus incipiens Billings (1861) and Palaeophycus congregatus Billings (1861), from the Upper Cambrian Potsdam Sandstone of Vermont, in Planolites. J. F. James (1885) discussed several species under Palaeophycus, but in 1892 he considered these, and still additional forms, under the heading of Planolites. Recognizing the confusion, Howell (1943, p. 18) suggested restricting Planolites to "...all those usually more or less horizontal but sometimes diagonal or vertical burrows having diameters of approximately 8-12 mm that are not marked by such prominent cross ridges as are characteristic of the species of Arthrophycus..." However, as seen by the above discussion of Hall's forms, this diagnosis does not really serve to differentiate Planolites from Palaeophycus. It is instead believed that Nicholson's original discussion (1873) as augmented by Nicholson and Hinde (1875) may provide the key. Nicholson (1873, p. 309-310) described Planolites as "...burrows [which] run more or less horizontally as compared with the laminae of deposition, or they penetrate the strata obliquely....[These] are preserved to us...not [as] the actual burrows themselves, but the burrows filled up with sand or mud which the worm has passed through its alimentary canal." Nicholson and Hinde (1875, p. 3) expanded the definition, stating "they appear usually in the form of cylindri-

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

cal or flattened stem-like bodies, which are often more or less matted together and which may cross one another in every imaginable direction." Although the type species, P. vulgaris, was not figured, Nicholson (1873) stated that the diameter varies from 1-4 mm; and the burrow may be irregularly thickened. There was no mention of branching. Although they did not elaborate, both Nicholson (1873) and Nicholson and Hinde (1875) remarked that some of Hall's species of Palaeophycus should probably be placed in Planolites.

Although neither Nicholson nor Nicholson and Hinde flatly states that there is a difference between the lithology of the cylindrical tubes and that of the host rock, they certainly imply it. In addition, their description has been followed by Rudolf Richter (1937) and Reineck (1955). Richter (1937) established Planolites montanus for irregular compressed cylinders from the Carboniferous (coal swamp) of the Ruhr. The cylinders are 4 mm in diameter and can be traced for 1-4 cm; there is no over-all pattern. However, there is a marked difference in the lithology of the tunnel fillings (see Richter, 1937, fig. 2-4), and in some cases the bedding bends around these fillings (see Richter, 1937, fig. 5). Reineck (1955) proposed Planolites rugulosus for specimens from the nonmarine Wadener beds (Permian) of Germany. These are cylindrical bodies over 1 cm in diameter which are marked externally by annulations and longitudinal striae. They lie obliquely to the bedding planes, are unbranched, and follow an irregular course. Internally P. rugulosus

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

consists of material which is either coarser or finer grained than the host rock. A cross-section of the cylinder reveals a series of "growth rings," while a longitudinal sections shows that these are hemispherical packings (see Reineck, 1955, fig. 2).

Based on the above discussions, there may be clear grounds for separating Palaeophycus and Planolites. The key factor is the lithology of the burrow filling as compared to that of the host rock. As best can be determined from a restudy of some of Hall's type material, there is no marked lithological difference between the fillings and the host. In contrast, on the basis of Nicholson's description, Planolites appears to show a distinct difference.

Interpretation: Hall (1847, 1852), Billings (1862), and other earlier authors considered Palaeophycus to be fragments of stems of once larger "fucoids." J. F. James (1885) was one of the first to point out that Palaeophycus was a burrow, and he compared the genus to Recent annelid trails observed on the banks of the Little Miami River in Ohio. Most subsequent authors, e.g., Bassler (1915), Häntzschel (1962), have accepted the burrow interpretation. Although no one has studied the genus in detail, other interpretations have been offered. Wilckens (1947) applied Abel's (1935) interpretation of Arthrophycus to Palaeophycus and thought that both were fragments of worm tubes uprooted and scattered about during storms. On the other hand, Wilson (1948) has held to the "fucoid" hypothesis.

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

The fact that the tubes of *Palaeophycus* interpenetrate and extend up or down into the host rocks indicates that they are burrows and not "fucoids" or portions of agglutinated tubes. It is concluded that they are of infaunal origin and represent the unorganized pathways of errant organisms which were progressing through the sediment, quite possibly in search of food. As the animal moved along at depth, the sediment was pushed aside only to collapse again as the organism moved past, although in some cases mucus may have given the walls a temporary rigidity. There is no evidence in any of the Hall specimens studied by the author that we are dealing with a structure which was either packed by a *Sedimentfresser* or mined out and filled by sediment sifting in from outside. There is no significant difference between the grain size or composition of the filling and that of the host rock.

Recent counterparts of *Palaeophycus* are made by predaceous polychaetes (*e.g.*, *Glycera*), gastropods (*e.g.*, *Polynices*), and presumably could be made by some pelecypods. The difference in the sculpturing seen on some of Hall's species would seem to indicate that the genus includes forms made by several different organisms. In its present state *Palaeophycus* contains too wide a range of morphological characteristics, and the type specimens alone do not provide sufficient material to permit a meaningful restudy of the genus; they are far too fragmentary. It will be necessary to recollect original localities, noting such characteristics as branching patterns, if any, and the continuity of

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

sculpturing on a given form. This will undoubtedly result in a reduction of the number of species, and if a given form is sufficiently distinctive and persistent, it may well be possible to establish new genera. Moreover, "species" of Palaeophycus have been described from such diverse environments as the marine Trenton beds of New York, the Queenston "red beds" of New York, and the Pennsylvanian coal swamps of Indiana.

An additional problem is how to distinguish Planolites from Palaeophycus, since the morphology of the two is quite similar. Both genera are cylindrical, irregular, unbranched, and penetrate obliquely through the strata. The only significant difference lies in the nature of the filling. It may well be that Nicholson (1873), Richter (1937), Howell (1943), and Reineck (1955) were correct in believing that Planolites is the stuffed burrow of a Sedimentfresser and that the filling is host rock that has been passed through the animal's gut. Thus, if a restudy of Nicholson's type specimens confirms this, Planolites may be restricted to the stuffed burrows of Sedimentfressers, while Palaeophycus is the passageways of errant predaceous or selective feeders. However, it must be admitted that in some cases it may be difficult to distinguish between these two categories. Very little work has been done on the effect that organisms have on the mineralogical and textural properties of ingested sediment. Presumably soft particles could be reduced by abrasion, and it is possible that organic acids could alter both the

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

grain size and composition of carbonate particles. Enzymes might also produce a color change. Obviously the most positive evidence for a fecal-stuffed burrow is the presence of fecal pellets.

Cincinnatian Representatives

Palaeophycus sp.

(pl. 20, fig. 5,9; pl. 21, fig. 5-6; pl. 27, fig. 1,4)

Discussion: J. F. James (1885) reported that five "species" of *Palaeophycus* could be identified in the local Cincinnatian section. As he recognized, *Palaeophycus flexuosum* U. P. James (1879) is of inorganic origin and is not comparable to the species of *Palaeophycus* figured by Hall. This form is discussed herein under "Fucoids of Inorganic Origin." Likewise, what J. F. James (1885) presented as *Palaeophycus virgatum* Hall does not appear to belong in the genus. He remarked that they were "...about an inch wide, and about eight inches long, of the same width [throughout] their whole length...and overlying one another in various directions" (James, 1885, p. 158). These were tentatively interpreted by James as the molds of large *Solen* (which are unknown in the Cincinnatian). The descriptions recalls the "turkey tracks" which have been shown elsewhere in this work to be portions of the burrow of *Trichophycus venosum*.

The remaining three "species" are *P. tubulare* Hall,

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

P. rugosum Hall, and P. simplex Hall. J. F. James considered the latter two as synonomous and believed that P. tubulare and P. rugosum were two different expressions of the same burrow. To James (1885, p. 158) P. rugosum represented the entire burrow with "the rugose surface...caused by the irregularly thrown up mud; the flexuous stem and the branching, by the windings of the worm." He mentioned that he had seen similar burrows on the banks of the Little Miami River. P. tubulare was merely a P. rugosum with the roof of the burrow removed (i.e., a concave epirelief or hyporelief). However, the restudy of the type specimens of the two species indicates that they are both preserved as convex hyporeliefs, and thus James' explanation is incorrect. In 1891 J. F. James listed P. virgatum, P. tubulare, and P. rugosum under the generic heading Planolites, but gave no explanation. Since J. F. James never figured any of these species, it is difficult to correlate his names and brief descriptions with the specimens which actually occur in the Cincinnatian section. Moreover, as shown above, the various "species" of Palaeophycus have little meaning at this time, and nothing would be gained from assigning Cincinnatian forms to previously existing species of the genus. For this reason Cincinnatian material is informally discussed below as P., types A, B, and C. Possible affinities with various "species" of Palaeophycus are drawn where possible.

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

Palaeophycus, type-A

(pl. 20, fig. 5)

Discussion: *Palaeophycus*, type-A (pl. 20, fig. 5) is known only from the Corryville beds of O'Bannion Creek, Clermont County, Ohio. The form occurs as a convex hyporelief in a well-bedded, medium-grained calcarenite and consists of cylindrical tunnel fillings which are both parallel and oblique to the planes of stratification. The cylinders are 3-6 mm in diameter and attain lengths up to 19 cm. The tunnels are distinctly annulate and bear 3-5 annuli/cm; they show no other surface markings. The forms are unbranched but interpenetration and crossing over are common. *P.*, type-A is either straight or gently curved in outline, and in places the tunnels appear to dip below the surface of the host rock, sometimes rising again after a few centimeters. They are not found preserved as either convex or concave epireliefs. Vertical sections reveal a disturbance of the bedding where the tunnels penetrate the host rock, and the composition and grain size of the tunnel filling is no different from that of the host. *P.*, type-A appears to differ from all known species of *Palaeophycus* in the possession of annuli. In general appearance it resembles the illustrations of *Planolites annularius* Walcott (1889) (see Walcott, 1890, pl. 60, fig. 5) from the Lower Cambrian near Greenwich, New York, and *Planolites corrugatus* Walcott (1899, pl. 24, fig. 8) from the Precambrian Greyson Shale near Neihart,

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

Montana. However, examination of the type specimen reveals that P. corrugatus (herein pl. 21, fig. 2; USNM 33796) is not annulate as Walcott believed, and the "annuli" probably represent the cleavage planes of the slate. P. annularius (herein pl. 21, fig. 3; USNM 18360) is badly weathered but does appear to be annulate. As nearly as can be determined, both specimens are stuffed burrows, and thus according to the definition employed herein are planolitids.

Palaeophycus, type-B

(pl. 20, fig. 9; pl. 21, fig. 6)

Discussion: The forms grouped under P., type-B are not common; single specimens are known from the Mt. Hope beds on U. S. Route 50, 0.5 miles west of Aurora, Indiana, and the Corryville beds at Stonelick Creek. P., type-B combines the longitudinal striae of Palaeophycus striatus Hall with the annulations of P., type-A. These cylindrical forms are gently curved and are preserved outwardly as convex hyporeliefs. The diameter varies from 5-10 mm; the longest form is 21 cm in length. There are 4-5 annuli/cm and the striae appear as fine wavy lines. As seen in pl. 21, fig. 6, the annuli may be better developed in one area than in another. In both specimens where this is true, the weakly annulate portion of the cylinder has a greater diameter than the strongly annulate section. All four specimens extend up into the host rock with a resulting

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

disturbance of the bedding. As in P., type-A the grain size and composition of the tunnel filling is similar to that of the host rock.

Palaeophycus, type-C

(pl. 21, fig. 5; pl. 27, fig. 1,4)

Discussion: P., type-C is the most common, yet the most nondescript variety of Palaeophycus. It occurs in great numbers in calcarenites whose coarse grains do not permit the preservation of fine details. If the grain size were smaller, it is possible that some sculpturing might be evident. P., type-C is common in Eden strata but relatively rare higher in the Cincinnatian section. It is especially well developed in the Lower Eden near the mouth of Brierley Creek, 3.5 meters downstream from its crossing by Taylor Creek Road, Hamilton County, Ohio.

The diameter of the tunnels varies from 5-12 mm, and incomplete forms have a length of 10 cm. In the same bed P., type-C can be preserved both as a convex hyporelief (pl. 21, fig. 5) and a more poorly defined convex or concave epirelief (pl. 27, fig. 4). None of the specimens were observed to branch, although they frequently interpenetrate. At the Brierley Creek locality the specimens occur in a coarse-grained calcarenite that is 2-5 cm thick. A parallel arrangement of shell fragments gives the rock a poorly defined bedding. There is a sharp boundary separating the

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

calcarenite from the overlying lutite, and inspection of this lutite revealed several obliquely-directed, cylindrical tunnels which angled down toward the calcarenite. Although none of these tunnels could be traced directly into the tunnels of the calcarenite, the evidence is suggestive. As in the other varieties of Palaeophycus discussed herein, cross-sections of P., type-C indicate that the bedding of the host rock is disturbed where penetrated by the tunnels.

When preserved as an epirelief, P., type-C closely resembles trails found in the McMicken beds at West Fork Creek, Cincinnati, Ohio. The difference is largely one of interpretation and is discussed herein under "?Mollusk Trails."

Interpretation: The ethological interpretation of Palaeophycus has already been discussed and will only be briefly repeated here. As shown by the disturbance of the bedding in the host rock, all three varieties discussed above are of infaunal origin. Most likely they are the burrows of either selective feeders or predators. The fact that there is no "master plan" or pattern to the structures suggests the latter, but this is no sure criterion. There is no evidence that they are the stuffed burrows of Sediment-fressers. The annulate nature of Palaeophycus, types A and B suggest the peristaltic movements of an elongated annelid-like body, while the longitudinal striae of P., type-B could be the impressions of setae which occur on the ventral surfaces of many polychaetes and other vermiform organisms.

Although such forms are difficult to study and

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

characterize because they are obliquely oriented and cut across bedding planes in addition to occurring in coarse-grained sediment, their importance should not be underestimated. In reality they were probably more important members of the infauna than were the more definitive and impressive forms, such as Phycodes.

Walcottia Miller and Dyer, 1878

(pl. 11, fig. 6; pl. 13, fig. 5)

1878 Walcottia Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 39, pl. 2, fig. 11-11a.

1878 ?Walcottia Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 11, pl. 3, fig. 12-12a.

1881 ?Walcottia, James, U. P., The Paleontologist, no. 5, p. 44.

1886 (in partim) Walcottia, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 161-162.

Type Species: Walcottia rugosa Miller and Dyer (1878) (pl. 11, fig. 6; pl. 13, fig. 5; MCZ 545; latex mold UCM 37677) from "near the top of the hills at Cincinnati" (?Corryville).

Diagnosis: Slender vermiform bodies preserved as convex hyporeliefs which possess obliquely directed paired lobes. The closely spaced lobes are ridge-like and tend to

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

obscure the body. The form tapers at one end and terminates at the other in a structureless ovoid mass. Other forms of the genus are reputedly marked by a shell-like covering composed of small plates or rings, or by a longitudinal groove from which issue five oblique striae.

Discussion: Miller and Dyer (1878, p. 16) established Walcottia for "...long, tapering, rugose, flexuous bodies, worm-like in form... [which] come to a point at one end and are enlarged at the other...." Originally only a type species, W. rugosa, was proposed; although in the second part of the same paper, they questionably assigned an additional species, W. cookana, to the genus. In 1881 U. P. James added yet another, W. sulcata. The cotypes of of W. rugosa were located in the collections of the Museum of Comparative Zoology at Harvard and will be discussed below. While Miller and Dyer remarked that the type specimen of ?W. cookana was also in the Dyer collection, the form could not be found at Harvard, nor is it with the Miller collection at the University of Chicago. Unfortunately the type specimen must be regarded as lost, and any discussion will have to be based on Miller and Dyer's description and figure. Although U. P. James never figured W. sulcata, identified material may be present in the James collection at the University of Chicago. However, the collections are inaccessible at this time. The latter species is discussed under Incertae sedis.

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

Walcottia rugosa Miller and Dyer

(pl. 11, fig. 6; pl. 13, fig. 5)

1878 Walcottia rugosa Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 39, pl. 2, fig. 11-11a.

1886 Walcottia rugosa, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 161-162.

Type Locality: The species is known only from the two cotype specimens, which presumably are from the McMillan formation.

Diagnosis: Slender vermiform bodies preserved as convex hyporeliefs which possess obliquely directed parallel lobes. The closely spaced lobes are ridge-like and, where present, tend to obscure the body. The form tapers at one end and terminates at the other in a structureless ovoid mass.

Discussion: Both specimens of W. rugosa occur on a single slab of fine-grained calcisiltite. The numerous tool marks associated with them indicate that they are preserved as convex hyporeliefs. The form which probably best typifies the species (pl. 13, fig. 5) is shaped like an open "S" and has a length of 4 cm and a width of 3 mm. The most striking feature is the presence of 21 paired lobes. The lobes are wides proximally and taper to a point distally. All are obliquely directed toward the tapering end of the

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

specimen, and the spacing between them is less than a millimeter. The lobes do not extend the entire length of the specimen but instead terminate 1 cm from the tapering end. In this area the specimen is marked by a thin ridge which bears a faintly impressed longitudinal groove. To one side of the ridge are markings which may be poorly developed lobes. The other end of the specimen is characterized by an ovoid body, 6 mm long and 4 mm wide. It is free of lobes and bears no trace of any markings. Both sides of the specimen are marked by a shallow groove which in latex molds appears as a ridge. As will be shown later, these are important for the interpretation of the species.

The second specimen (pl. 11, fig. 6), 3 mm wide and 1.4 cm long, is located 2.5 cm from the first and is oriented at right angles to it. There is no evidence of a connection between the two. At one end is the same ovoid mass described in the specimen above. The rest of the body consists of six paired lobes which differ slightly from those in the other form. Instead of joining the body at the sides, the lobes join at the midpoint and thus give the appearance of being imbricate chevron-shaped structures. As in the first specimen the apex of the "V" formed by the juncture of the lobes is directed toward the ovoid mass.

Interpretation: Although Miller and Dyer (1878, p. 16) were uncertain whether W. rugosa was a "fucoid" or was of animal origin, they were inclined to believe that it was "the long lost borer of Silurian age, which has left so

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

many holes in the corals and the rocks." They briefly described another specimen from Miller's collection which "represents a track from one worm hole to another, 1½ inches apart. The track curves from one side to the other, and has every appearance of having been made by such an object as fig. 11 [herein pl. 13, fig. 5] represents" (ibid, p. 16). J. F. James (1886, p. 162) rejected Miller and Dyer's interpretation and instead believed that W. rugosa was "the impression of the under side of the flexible arm of a starfish."

It appears that this time Miller and Dyer's explanation is more plausible than that of James. One of the specimens (pl. 13, fig. 5) closely resembles (and in fact may be) the cast of an errant polychaete. The body proportions are similar, and the paired lobes are quite reminiscent of the parapodia seen on the Recent Nereis. Vertical sections cut adjacent to both ends of the longer form and near the enlarged end of the other show that there is no disturbance of the bedding. Therefore, W. rugosa is regarded as being of epifaunal origin. Since the lobes are so well preserved, it is unlikely that there was much lateral movement involved. It is believed that a swimming annelid or annelid-like form settled to the bottom and left its imprint. The depressions on either side of the body represent sediment that was squeezed up as the organism came to rest. The animal then arched its body off the substrate and began to burrow into the subjacent bed. The ovoid mass would thus represent the

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

point of penetration. In the shorter of the two forms it appears that only the anterior portions of the body came in contact with the bottom and that most of the body remained off the substrate.

?Walcottia cookana Miller and Dyer

1878 ?Walcottia cookana Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 11, pl. 3, fig. 12-12a.

1886 ?Walcottia cookana, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 161-162.

Type Locality: Fairview and McMillan formations at Cincinnati, Ohio. The only known figure of the species is that given by Miller and Dyer (1878b, pl. 3, fig. 12-12a).

Discussion: Miller and Dyer (1878b, p. 11) proposed ?W. cookana for "...a small, nearly round, flexuous body, having a shell-like covering, upon the outer side, which is composed of plates or rings. A distinct longitudinal depression marks the back of the specimen so as to give a section a somewhat quadrate form." The specimen, which they believed to be incomplete, measured 1.8 cm in length and had a width slightly in excess of 1 mm. The plates were quite small, averaging only 2/mm. One end of the specimen was larger than the other, and this was regarded by the authors as the anterior end. The lines separating the rings

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

or plates are directed adapically. Miller and Dyer also believed that the rings were imbricate, thus allowing the organism freedom of movement.

The type specimen could not be located with the Dyer collection at Harvard, nor is it with Miller's material at the University of Chicago. In all probability the type is lost.

Interpretation: Miller and Dyer believed that the species was a fossil annelid, but only questionably assigned it to Walcottia. J. F. James (1886, p. 162) evidently never saw the specimen but thought that it was "...the impression of some portion of a crinoid, either a part of the stem or one of the fingers."

With no specimens available for study, it is impossible to make any interpretation of the species. Perhaps it is similar to W. rugosa and thus possibly is of annelid origin. Miller and Dyer's description is also reminiscent of Lepidocoleus Faber, a machaeridian which occurs in the local Cincinnatian rocks. However, Lepidocoleus is normally a little larger than the specimen of ?W. cookana described by the authors.

Fucusopsis Vassoevich, 1932

(pl. 8, fig. 1; pl. 14, fig. 1; pl. 15, fig. 5)

1878 (in partim) Trichophycus Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati,

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

Ohio, private publication), p. 4, pl. 4, fig. 2.

1932 Fucusopsis Vassoevich, N. B., Akad., Nauk, USSR, Trudy, Geol. Inst., T. 2, p. 51, pl. 2, fig. 2,6.

1959 Fucusopsis, Seilacher, A., Eclog. Geol. Helvetiae, Bd. 51, p. 1070, Table 2, fig. 30.

Type Species: Fucusopsis angulatus Vassoevich (1932) from the Senonian beds (Cretaceous) of Caucasus, U.S.S.R.

Diagnosis: Palaeophycus or Planolites-like burrows of infaunal origin which lie close enough to the basal surface of the silt beds containing them to produce a characteristic stretching of the sole of the bed.

Discussion: Fucusopsis was established by Vassoevich (1932) for "hieroglyphs in the form of tubes." An illustration given by Häntzschel (1962, fig. 120-4) shows that the genus consists of long cylindrical structures which have a diameter of approximately 1 cm. These penetrate the bedding of the host rock and commonly cross over and interpenetrate. According to Seilacher (personal communication), when the genus is preserved as a convex hyporelief, it has various modes of expression. It may be visible only as a series of thin cracks in the sole of the host rock (pl. 14, fig. 1), or it may be preserved as a hemicylindrical swelling marked by longitudinal striae (pl. 8, fig. 1). These two forms occur together and can be intergradational.

Interpretation: According to Seilacher (1959 and

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

personal communication), Fucusopsis is a burrow of infaunal origin. As the organism burrowed a few millimeters above the bottom of the silt bed, the pressure of the body produced sufficient tension in the sole of the bed to cause a series of faults. Ethologically this is of little significance, but it does show that the host sediment was strong enough to fault rather than flow. On the other hand, when the organism worked along the contact of the host silt and the subjacent mud, the specimens are characterized by a complex series of longitudinal striae which probably are indicative of the digging action of bristles or dactyls. It may be argued that Fucusopsis should not be retained as a separate genus, since ethologically it differs little from Palaeophycus and Planolites. However, Palaeophycus is badly in need of restudy, and little would be gained by placing Fucusopsis in synonomy with Palaeophycus at the present time. Moreover, the fact remains that Fucusopsis does tell us something of the properties of the host sediment.

It is doubtful that the forms described by Birkenmajer (1959) from the Danian-Paleocene flysch of the central Carpathians belong in Fucusopsis. In the English summary the author makes no mention of the faulting pattern which distinguishes the genus. Birkenmajer concluded that the Polish specimens were the burrows of sediment-eating annelids working along the sand-mud interface which were filled by the overlying sand. This interpretation would place them in Planolites.

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

Cincinnatian Representatives

Fucusopsis sulcatum (Miller and Dyer)

(pl. 8, fig. 1; pl. 14, fig. 1; pl. 15, fig. 5)

1878 Trichophycus sulcatum Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 4, pl. 4, fig. 2.

1884 (in partim) Trichophycus sulcatum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 131, pl. 6, fig. 5.

Type Locality: The type specimen (pl. 15, fig. 5; HBM 3182; latex mold UCM 37705) is from the Economy beds, Cincinnati, Ohio.

Diagnosis: A Palaeophycus-like burrow of infaunal origin which produces tension faulting in the sole of calcisiltite beds.

Discussion: Miller and Dyer (1878b, p. 4-5) described F. sulcatum as a "fucoid" which "...consists of a long, round, flexuous stem, which has not been noticed to divide or bifurcate. The surface is longitudinally furrowed [and] ...are not regular in their size, nor in their course.... The ridges or elevated lines, which separate the furrows anostomoze in places, thus suddenly cutting short the furrows." They placed the species within Trichophycus with some reservations.

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

The type specimen of F. sulcatum, from "the lower part of the Cincinnati Group, Cincinnati, Ohio," is preserved both as a cleavage relief and a convex hyporelief. Viewed as a cleavage relief, the form appears as a shallow concave furrow which completely traverses the slab and has a diameter of 6 mm. On the sole of the slab (pl. 15, fig. 5) is what Miller and Dyer (1878b, pl. 4, fig. 5) illustrated as the type. The specimen is 7 mm wide at the edge of the slab and appears to gradually taper to a point at its other extremity. However, under favorable lighting a faint linear bulge in the bedding can be traced from the pointed end of the fossil to the opposite edge of the slab. The striated hemicylinder and this convex bulge are located directly below the concave furrow on the opposite face of the slab. The central portion of the hemicylinder is marked by a series of short, sharply defined, approximately parallel ridges. The basal lamina of the host rock "laps up" on the sides of the hemicylinder, and this feature alone differentiates F. sulcatum from Palaeophycus. A vertical section through the specimen shows that the bedding is not completely obliterated as it is in Palaeophycus but instead is bowed down, forming a "microsyncline."

Two other well developed forms, as well as six or seven fragmentary specimens of F. sulcatum, have been found in the Cincinnatian beds. One of these specimens, from the Bellevue beds exposed in Hall's Creek near Morrow, Ohio, has a length of 16.9 cm and a width of 6 mm. As viewed in

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

pl. 14, fig. 1, the upper part of the form is hemicylindrical and bears the longitudinal striae of the type specimen. The path of the burrow may be traced across the slab by the series of ragged faults occurring in the basal lamina of the host rock. The other specimen, from an unknown locality, (pl. 8, fig. 1) more closely resembles the type specimen. It has a length of 13.5 cm and a width of 6 mm and plainly shows the knife-like anastomosing ridges. As in the type specimen the basal lamina of the host rock laps up on the sides of the hemicylinder.

Interpretation: J. F. James (1884) believed that both Trichophycus (Fucusopsis) sulcatum and Trichophycus lanosum were the casts of rill marks. As shown elsewhere, T. lanosum is a sinuous burrow marked by a button-like ending from which radiate fine striae. On the other hand, F. sulcatum is a Palaeophycus-like burrow which was excavated extremely close to the base of the calcisiltitic host rock. The pressure of the body produced a series of faults in the basal lamina of the host rock, although occasionally the organism broke through the base of the bed to give rise to the longitudinal striae.

?Mollusk Trails

(pl. 23, fig. 4; text fig. 37, 41)

Discussion: This section is concerned with a number of long, gently arcuate trails which are preserved

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

as convex and concave epireliefs in coarse-grained calcarenites. The single exposure occurs in the lower part of the McMillan beds in West Fork Creek, approximately 25 meters east (downstream) of the intersection of Shepherds Road and West Fork Road. A dam in the stream has left a surface of about 25 square meters relatively free of debris, and the trails are remarkably well exposed. The host rock is a thick coarse-grained calcarenite composed of fossil fragments.[39] The upper 2 mm of the bed is slightly finer

---

[39] The calcarenite was so thick that it was not possible to collect any specimens.

---

grained and tends to spall off. There is a sharp contact between the calcarenite and the thin bed (1-2 cm) of overlying lutite. Approximately 40 per cent of the surface of the calcarenite bed is marked by a series of irregular pararipples which have a maximum amplitude of 9 cm. The remainder of the bed, where most of the trails occur, has a gently undulating surface, and the relief does not exceed 3-4 cm. The trails do not appear to be affected by the irregularity of the surface. Upon encountering a depression, the trail does not deviate or end abruptly but instead proceeds down one side of the depresssion and up the other; the same is true for high areas.

To take maximum advantage of this excellent

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

exposure, a grid was prepared, and some 17 square meters of the surface were mapped, employing a scale of 1/20 (see fig. 41). As can be seen from the map, most of the trails are gently curved and their length varies considerably. While some extend for only a few centimeters before fading out, others are much longer. The longest trail (fig. 41, center left) is in the form of a "U" and has a length of nearly 2 meters. Although there is no over-all preferred orientation, the trails do exhibit some degree of parallel alignment in small areas. The trails frequently cross over one another and some branch, generally at an acute angle.

The pattern seen in the map is not thought to be a complete reconstruction of the trail network. Many of the trails appear to dip into the surface of the slab and thus are lost to view. In addition, several others are quite faint and have been affected by Recent stream erosion. These two factors account for the numerous discontinuities which will be discussed in greater detail below.

The width of the trails ranges from 5-10 mm but remains constant in a single trail. Several different varieties are visible on the calcarenite surface and are best studied in cross-section. Some of the trails exhibit a change in morphology along their length. One form (pl. 23, fig. 4; text fig. 37A) begins as a hemicylindrical depression, only a few millimeters deep and flanked by a pair of longitudinal ridges which in turn are flanked by

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

two shallow depressions. After proceeding in this manner for 10 cm, the trail gradually converts into a ridge the crest of which is marked by a small V-shaped longitudinal rift (fig. 37B). On either side of the ridge are the two shallow depressions described above. This type of structure can be followed for approximately 20 cm, and then the trail reverts to the hemicylindrical depression (see fig. 37A). Another variety is similar to the combination discussed above except that the ridge lacks the median rift; several of these were observed. The most common trail is either a hemicylindrical depression with a ridge on either side (fig. 37E) or a ridge with a shallow depression on either side (fig. 37D). One last type, which is not common, differs from the others as it is a shallow flat trough with two small ridges on either side.

Interpretation: Undoubtedly these are trace fossils. The branching, crossing over, and lack of a definite pattern rule out a vegetable or inorganic origin. They somewhat resemble Archaeonassa Fenton and Fenton (1937) which are preserved as concave epireliefs in the Lower Cambrian of British Columbia. These forms, which were interpreted as gastropod trails, differ from the Cincinnatian specimens in that they possess "rounded to subangular wrinkles which are convex in the anterior direction" (Fenton and Fenton, 1937, p. 454). Likewise, the West Fork Creek specimens are quite similar to Palaeophycus, type-C, and the difference is largely one of interpretation. As shown elsewhere, Palaeophycus is

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

thought to be of infaunal origin, i.e., made at some depth below the depositional interface. In contrast, it is concluded that these trails were made on or just below the depositional interface. Many of them are quite long, and, as mentioned, they follow the irregular contours of the surface. Two trails were observed to progress down into the trough of a pararipple, a vertical distance of about 9 cm.

The variation in the morphology of the trails suggests a difference in the type of movement. It is believed that in some cases (fig. 37A,E) the animals ploughed along the surface forcing the sediment to either side. On the other hand, the hemicylindrical ridges (fig. 37B,C,D) suggest that the organism burrowed in a mole-like fashion parallel to and just below the depositional interface. The depressions flanking the ridges may represent the areas where sediment had been drawn to the ridge.

Since no organisms have been found directly associated with the trails, the selection of the trail-maker is speculative. However, a comparison with the trails of the Recent sand snail Littorina littorea, illustrated by Häntzschel (1941, pl. 1-2), strongly suggests gastropods. Moreover, a number of different species occur in the McMicken. Such forms as Archinacella patelliforme, Hormotoma gracilis, Lophospira bicincta, L. tropidophora, Sinuites cancellatus, and S. globularis could have produced the trail. Pelecypods are another possibility, but the McMicken pelecypods are the same as those that occur in the Economy beds, and it has

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

already been shown (see Lockeia) that these were most likely burrowers. Of course, there is always the possibility that we are dealing with the trail of an unknown soft-bodied form.

Häntzschel's (1941) observations on the behavior of Littorina on the German Wattenmeer offer a possible explanation for the branching in the West Fork Creek trails. He found that as many as seven gastropods would move along in a single track, one behind the other. Apparently the leader was "breaking trail," and the others found it easier to move in a pre-existing track. However, at times they would strike off one their own, thus giving rise to a branching trail. It is not unreasonable to tentatively extend this explanation to the Cincinnatian forms.

Since the trails are long, gently curved, and lack any peculiar geometric pattern, they are classified under Repichnia. However, it should be pointed out that they might well represent feeding trails where the organism was feeding on surface detritus.

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

Chapter IX

?Pascichnia

?Paleodictyon Savi and Meneghini, 1850

(pl. 10, fig. 1; pl. 11, fig. 1; pl. 13, fig. 6-7; pl. 25, fig. 2; text fig. 29,31)

1850 ?Paleodictyon Savi, P., and Meneghini, G., in appendix to Murchison: Memoria sulla Structura geologia del Alpi, p. 484.

1863 ?Glenodictyum Marck, W. v. d., Palaeontog., Bd. 11, p. 1-8 (fide Häntzschel, 1962).

1865 (non) Palaeodictyon Heer, O., Die Urwelt der Schweiz, p. 245, pl. 10, fig. 10.

1895 ?Pleurodictyon Fuchs, T., Akad. Wiss. Wien, math.-nat. Kl., Denkschr., Bd. 62, p. 394, 396, pl. 6, fig. 1.

1935 ?Palaeodictyon, Abel, O., Vorzeitliche Lebensspuren, p. 24, fig. 11-13, 261B, 263, 264.

1939 (in partim) ?Palaeodictyon, Sacco, F., Roy. Accad. Torino, Mem., vol. 69, p. 267-285, pl. 1-2.

1954 ?Palaeodictyon, Seilacher, A., Deutsch geol. Gesell., Zeitschr., Bd. 105, p. 217, fig. 2, no. 16.

1959 ?Palaeodictyum, Nowak, W., Kwartalnik Geol., T. 3, p. 103-125, pl. 1-6.

1960 ?Paleodictyon, Vialov, O., and Golev, B., Akad. Nauk USSR, Doklad., T. 134, p. 175-178.

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

1964 ?Paleodictyon, Vialov. O., Jour. Sed. Petrology, vol. 34, p. 664-666, fig. 1.

Type Species: Paleodictyon strozzii Savi and Meneghini from the Lower Tertiary flysch of Tuscany, Italy.

Diagnosis: Honeycomb-like networks generally composed of hexagonal polygons which are preserved as convex hyporeliefs, i.e., a series of ridges arranged in a polygonal pattern. The diameter of the polygons varies from 1-50 mm but remains constant in a given specimen.

Discussion: Paleodictyon is one of the most unusual fossil forms and could be properly labeled as a "problematicum." The genus was originally established by Savi and Meneghini (1850) for what was considered to be a hexagonal algal network from the Lower Tertiary of Italy. Since its original discovery the genus has been reported from every period except the Cambrian and has been found in Alaska, Oklahoma, Italy, Spain, Russia, Germany, Iraq, Wales, Albania, and Japan. A recent study by Nowak (1959) on forms from the Cretaceous and Tertiary of the Carpathian flysch of Poland has contributed much toward the understanding of this most difficult genus.

The genus is most frequently encountered in fine-grained clastics, and no marked compositional or textural differences between the fossil and the host rock have been observed. However, Seilacher (1962, pl. 2, fig. 4) figures one form where the network is much darker than the matrix.

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

Nowak (1959) reported that while most forms have a hexagonal network, individuals with quadrangular, pentagonal, or septagonal polygons are not uncommon. Superficially these polygons appear to be nearly geometrically perfect, but upon close examination Nowak (1959, fig. 6) was able to reveal several minor irregularities. In some specimens the polygons may be systematically distorted, e.g., elongated parallel to the current direction.

The diameter of the polygons in the Carpathian specimens varies from 1-50 mm, and while it remains constant within a given specimen, forms having different diameters may be found in close proximity. According to Nowak there appears to be no correlation between the diameter of the polygons and the geologic age of the specimen. Likewise, the width of the polygon walls can vary from specimen to specimen. Normally the width is 1-2 mm, but von der Marck (1876) (see Nowak, 1959, fig. 1) and Koriba and Miki (1939, pl. 5, fig. 5) illustrate forms where the thickness of the sides overshadows the polygonal outlines of the network. Nowak also noted that many of the polygons are incomplete. These incomplete individuals most frequently occur along the margins but can also be seen within the body of the specimen, as shown by Nowak (1959, fig. 1), Vialov and Golev (1960, pl. 3, fig. 3) and Abel (1935, fig. 12).

Present in the University of Cincinnati collections are two specimens from the Eocene beds near Trieste, Italy, which illustrate many of the features noted above. Both

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

forms occur as convex hyporeliefs in a massive, medium-grained micaceous quartz arenite. One of the specimens (pl. 13, fig. 7) has large hexagonal polygons which are elongated parallel to the current direction. The length of the individual sides varies from 0.4-1.0 cm. The length of the polygons varies from 1.4-1.7 cm, while the width is 1 cm. The outline and dimensions remain constant within the specimen, and the major variation is that some of the polygons rise as much as 1.5 mm off the face of the host rock, while others are barely visible. Associated with Paleodictyon are irregularly winding hemicylindrical trails which have the same diameter (1.5 mm) as the sides of the polygon. These trails and the hexagonal network are composed of a material which is only slightly darker than the host rock.

The polygons in the other specimen (pl. 10, fig. 1) are much smaller and have a diameter of only 4-5 mm. The width of the walls is 0.8 mm. While the hexagons are not notably distorted, the walls are not straight and several minor irregularities can be seen. However, none of the features illustrated by Nowak (1959, fig. 6) were noted in either of the two specimens. The regular pattern of this second specimen is broken by large gaps, and in some places isolated stringers extend out from the complex. As in the larger specimen, the network is only slightly darker in color than the host rock.

Forms similar to those above have been described

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

under a variety of names. Several authors have changed Meneghini's original spelling to Palaeodictyon or Palaeodictyum. The specimen, illustrated by Fuchs (1895, pl. 6, fig. 1) from the Eocene of Austria and referred to Pleurodictyon, differs in that it possesses "interrupted nodose walls" (Vialov, 1964, p. 666), while as mentiond above, Glenodictyum von der Marck (1863) differs in that the walls are quite thick. Häntzschel (1962) considered both of these to be junior synonyms of Paleodictyon, while Vialov and Golev (1960) recognized Pleurodictyon as a separate genus and considered Glenodictyum to be a subgenus of Paleodictyon. It is not known how consistent or important the supposed differentiating features are. As Häntzschel (1962, p. 210) pointed out, Palaeodictyon Heer (1865) from the flysch of Switzerland is not synonomous with Paleodictyon Meneghini. The former is a burrow consisting of several branched loops which are connected by Spreite-like arcs (see Häntzschel, 1962, fig. 129-6a) and is placed by Häntzschel in Phycosiphon Fischer-Ooster (1858). It certainly bears no similarity to Paleodictyon.

At the specific level the picture is one of confusion, as over 30 species have been named. Nowak (1959, p. 125) employed a quasi-zoological nomenclature and recommended delimiting "species" on the size and configuration of the polygons. He designated six "species" based on size (P. minimum-up to 2.0 mm, P. minus-from 2.0-5.0 mm, etc.). At the same time he also proposed three "subspecific" desig-

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

nations. If the polygons vary in shape but not in size, "poliformis" is affixed. If the polygons are constant but the size shows a progressive increase or decrease, the "subspecific" name is "crescens." Lastly, if the polygons are constant and the size varies indiscriminately, "inconstans" is used. While such terms may be useful for descriptive purposes, they hardly conform to the principals of zoological taxonomy.

Interpretation: The enigmatic nature of Paleodictyon is reflected in the variety of interpretations that have been applied to it.[40] It has been variously interpreted as mudcracks, raindrop imprints, and the result of gas percolated up through the sediment. Sacco (1939), who studied the genus at various times over a 50-year period, finally concluded that it represented interference ripple marks. Earlier he had been an algal adherent. The organic interpretations also have run the full gamut. It has been believed to represent fossil honeycombs, sponges or corals, algae, strings of eggs, gastropod larvae, tadpole nests, and traces of invertebrate activity. Those holding to a trace fossil origin are Fuchs (1895), Abel (1935), Seilacher (1954, 1955, 1962), Nowak (1959), and Vialov and Golev (1960).

---

[40] See Sacco (1939) and Vialov (1964) for a more complete discussion.

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

Nowak (1959) based his trace fossil assignment on three features: the irregularities of the polygons, the number of unclosed polygons, and the fact that polygons with varying numbers of sides may occur in the same specimen. Nowak (1959) and others have pointed out that Paleodictyon may have developed from a Beloraphe-like trail. Beloraphe Fuchs (1895) (herein fig. 31, right), a Mesozoic form, resembles a series of zig-zags with short projections at the angles. As shown in fig. 31, left, two of these placed side by side give the polygonal appearance of Paleodictyon. Further evidence is that Beloraphe and Paleodictyon do occur together, although they have not been found in direct association. Figure 29 shows two interpretations by Nowak (1959, fig. 9) of how a Beloraphe-type trail might give rise to Paleodictyon. In fig. 29, left the trail is organized into linear series, while in fig. 29, right the arrangement is cyclic. Although Seilacher has not conducted a detailed study of the genus, he (1955) has placed Paleodictyon within the Pascichnia. Likewise, Nowak (1959) concluded that the form was the feeding trace of an annelid.

There is disagreement as to whether the trail is of epifaunal or infaunal origin. Seilacher (1962) held Paleodictyon to be infaunal, while Vialov and Golev (1960) concluded that most formswere epifaunal. Nowak (1959) believed that both conclusions were valid.

Silvestri (1911) and Koriba and Miki (1939) have pointed out the similarity between Paleodictyon and the Recent

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

fresh water alga Hydrodictyon utriculatum (Roth). The cenobiae of this species form a net of pentagonal, hexagonal, or septagonal polygons. Koriba and Miki (1939, p. 61) report that triangular and octagonal forms are also known. Moreover, they maintained that while the plant may attain a length of one meter in which the polygons are several centimeters wide, most forms have measurements which conform to those of Paleodictyon.

Cincinnatian Representatives

?Paleodictyon sp.

(pl. 11, fig. 1; pl. 25, fig. 2)

Only two small fragmentary specimens with a hexagonal network similar to that of the European Paleodictyon have been found in the Cincinnati strata. These are placed in Paleodictyon with some hesitation, since there is a possibility that both specimens are of inorganic origin.

One specimen is from the Economy beds of Duck Creek, near Silver Grove, Kentucky, 1,010 meters southwest of the intersection of Duck Creek Road and Kentucky Route 8. The outcrop is located on the southeast bank, 20 meters below the bridge crossing the creek. The other form is from the McMillan beds on Ravine Street in Cincinnati. Both localities have been recollected without success. The two specimens are preserved as convex hyporeliefs in calcisiltites.

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

The Duck Creek form (pl. 25, fig. 2) is poorly preserved and consists of nine incomplete hexagons which have an internal diameter of 3 mm. The greatest thickness of the walls of the polygon is 1 mm. As indicated by the numerous tool marks, the specimen is elongated parallel to the current directions. The relationship between the network and the tool marks is unclear, but the former does not seem to be truncated. There is no apparent difference in composition between the network and the host rock.

The Ravine Street specimen (pl. 11, fig. 1) is better developed. It is composed of 25 polygons with an internal diameter of 2 mm. Although the pattern is more regular than most specimens of Palaeodictyon, the network varies in its clarity. As viewed in pl. 11, fig. 1, the polygons in the center stand out in bold relief, while those on the right- and left-hand margins are barely visible. Likewise, all of the polygons along the lower margin are incomplete. As in the specimen from Duck Creek the network is elongated parallel to the current direction. There is a consistent variation in the thickness of the polygon walls; the walls normal to the current are thicker (0.6 mm) than those parallel to the current (0.3 mm). This specimen differs from the two Trieste forms (pl. 10, fig. 1; pl. 13, fig. 7), as the network of the Cincinnatian specimen blends into the background of the host. This is due in part to the lithologic similarity of the host rock and the network.

Interpretation: It is not possible to determine

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

whether the two specimens under consideration actually represent Paleodictyon or instead are of physical origin. While it is clear that the forms are not interference ripple marks or fillings of mud cracks, as some authors have suggested for Paleodictyon, it is possible that they are tool marks. As noted above, both forms are elongated parallel to the current direction and are associated with tool marks (groove casts). Moreover, there is at least one fossil present in the Cincinnatian strata which could produce such imprints as it rolled over the bottom. This is the problematic genus Pasceolus Billings which is most frequently placed in the receptaculitids. Pasceolus darwini Miller (1874), described from the Bellevue beds near Maysville, Kentucky, approximately 60 miles southeast of Cincinnati, has a discoid or globular body which measures up to 4 cm in diameter. The surface is marked by hexagonal cups whose dimensions conform to those of the polygons of the two ?Paleodictyon networks. Specimens of Pasceolus were rolled over a plaster-of-paris surface to test the validity of this hypothesis. The results (pl. 13, fig. 6) demonstrate that under proper conditions a globular specimen of Pasceolus being tumbled along the bottom can produce the "tire-tread" imprints here under discussion. However, to form such markings it is necessary that the rolling specimen just nick the surface of the substrate. If the sediment is too soft or the specimen too deeply impressed, the polygons are superimposed on a shallow ellipsoidal depression which is not present in the Cincinnatian

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

specimens. This hypothesis also explains the unequal development of the walls in the Ravine Street specimen, since the walls of Pasceolus, oriented normal to the current, would cut a wider marking than those parallel to the current.

The major problem with this explanation is that, although Pasceolus darwini occurs in large numbers at the type locality in Maysville, it is quite rare in the Cincinnati area. It has not been found at either of the two localities where ?Paleodictyon occurs and has never been reported from the Eden strata. It is thus possible that at least the Duck Creek specimen is a valid Paleodictyon.

While the biological affinities of Paleodictyon must still be considered an open questions, the bulk of the evidence favors either a vegetable or trace fossil origin. The over-all regularity in the pattern and size of the polygons in a given form does suggest an algal network similar to the Recent Hydrodictyon. However, no organic material has ever been found in Paleodictyon, and the type of preservation (convex hyporelief) is the one must frequently exhibited by trace fossils. Also Paleodictyon is not uncommonly associated with trace fossils which show unusual geometric patterns, e.g., Beloraphe and Spirodictyon (see Abel, 1935, fig. 263-264). Moreover, one of the specimens from Trieste figured herein (pl. 13, fig. 7) is judged to be most significant, since it bears gently arcuate trails which have the same diameter as the hexagonal network. This suggests two behavioral variations of the same organism.

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

This evidence indicates that Paleodictyon is a trace fossil, probably a Pascichnia. It exhibits the same characteristics as the spiral forms with which it is associated, e.g., a maximum coverage of area. Admittedly it is difficult to visualize how a burrowing organism could evolve such an intricate pattern, but perhaps this is not so surprising when one recalls such unusual forms as Daimonhelix and Helminthoida (see Häntzschel, 1962, fig. 121-9 and 122-5).

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

Chapter X

Body Fossils Described as Plants

Mastigograptus Ruedemann, 1908

(pl. 23, fig. 3)

1858 (non) Dendrograptus Hall, J., Geol. Survey Canada for 1857, Rept. Prog., p. 143.

1878 (in partim) Psilophyton, Lesquereux, L., American Phil. Soc., Proc., vol. 17, p. 164, pl. 1, fig. 2.

1883 (in partim) Dendrograptus, Walcott, C., Albany Inst., Trans., vol. 10, p. 21.

1885 (in partim) Dendrograptus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 160-161.

1908 Mastigograptus Ruedemann, R., New York State Museum, Mem., no. 11, p. 210-223, fig. 116-118.

Type Species: Dendrograptus tenuiramosum Walcott (1883) from the "Utica Slate" (Upper Ordovician), Trenton, Oneida County, New York.

Diagnosis: Dendroid rhabdosomes which may attain a length of over 20 cm. Individual branches quite slender (0.1-0.8 mm). Well preserved specimens possess irregularly placed conical thecae, while in more poorly preserved forms the thecae are detached and the branches appear to be smooth.

Discussion: Mastigograptus is most commonly found as relatively small "monopodial" branching fragments whose

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

black color makes them stand out against the lighter color of the host rock. Usually the slender branches bear no trace of any structures, although some may show a series of depressed conical pits (see Ruedemann, 1908, pl. 12, fig. 1-6). In addition, one specimen of M. gracillimum (Lesquereux) was seen "...to contract and expand regularly about eight times in 10 mm from 2 mm to 2.5 mm, producing an apparent jointed structure" (Ruedemann, 1908, p. 221). The only specimens showing the rather long conical thecae are those of the type species M. tenuiramosum (Walcott, 1883). Thecal-bearing specimens have been recovered both from the type locality and from the Eden beds of Covington, Kentucky. Ruedemann believed that the point of juncture of the thecae and the branch was extremely fragile and that in most cases the thecae have become detached. He remarked that "great numbers of such bodies have been [found loose] on the Covinton slabs" (ibid, p. 212).

The purpose here is not to completely discuss the graptolite genus and its relationships. Instead attention will be focused on one species which is most probably conspecific with what Lesquereux (1878) described as a "Silurian Land Plant." Therefore, the reader is referred to Ruedemann (1908, p. 210-223) for a more complete treatment of Mastigograptus and of the Lesquereux error.

Mastigograptus gracillimum (Lesquereux)

(pl. 23, fig. 3)

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

1878 Psilophytum gracillimum Lesquereux, L., American Phil. Soc., Proc., vol. 17, p. 164.

1883 Dendrograptus gracillimum, Walcott, C. D., Albany Inst., Trans., vol. 10, p. 21.

1885 (in partim) Dendrograptus gracillimum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 160-161.

1908 Mastigograptus gracillimus, Ruedemann, R., New York State Museum, Mem., no. 11, p. 219-221, fig. 116-118.

Type Locality: The type specimen, which was unavailable for study, may be in the collections of the University of Chicago; it was taken from Eden strata in the bed of the Licking River, Covington, Kentucky.

Diagnosis: Moderate-sized dendroid rhabdosomes with thin (0.8 mm) branches. Surface normally smooth, but one specimen shows an apparent jointed structure. Nature of thecae unknown.

Discussion: Lesquereux (1878, p. 164) characterized M. gracillimum as "stem very slender, dichotomously branching, smooth or naked half round, slightly channeled in the length; branches numerous, of various length, filiform. The stem is scarcely one millimeter thick at the base; the upper branches curved as from a spiral unfolding, are slender, gradually attenuated and capilliform, or of the thickness of thin thread at their extremities."

In the course of his research on the fossils of

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

the "Utica Slate," Walcott (1883) studied specimens from Cincinnati which had been identified by Miller as Psilophyton gracillimum. Walcott placed them in Dendrograptus Hall but did not describe the species in detail.

J. F. James (1885, p. 160) also placed the forms in Dendrograptus, and at the same time he declared that M. gracillimum "precisely resembles in its essential features the figure of Buthotrephis gracilis given by Hall." For this reason he likewise referred Buthotrephis gracilis to Dendrograptus. Although he gave no specific reference to any of Hall's plates, he was most likely comparing Lesquereux's figure to that of Hall (1852, pl. 5, fig. 1a-c). As shown elsewhere in this work, B. gracilis is not comparable to Dendrograptus or Mastigograptus and instead is a chondritid. There is no evidence to indicate that James ever saw Lesquereux's type specimen; most probably he was working entirely from the literature.

Ruedemann (1908) studied two specimens of topotype material obtained from Ulrich. He also mentioned that the type specimen of M. gracillimum, which was collected by Ulrich, was loaned to a Reverend Herzer of Cincinnati, who in turn loaned it to Lesquereux. Apparently the type was then sold with the Herzer collection to James Hall. Ruedemann further remarked that the specimen was probably sold again, this time to the University of Chicago with a portion of the Hall collection. He too was unable to obtain it for study.

Ruedemann (1908) described the "stems," which have

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

a diameter of 0.8+ mm, as being solid and showing few effects of compression. The "stem" of one specimen was smooth, that of the other regularly expanded and contracted to give the jointed appearance mentioned above. He said that the species was closely allied to M. tenuiramosum (Walcott), although it differed in that the secondary branches were a little thicker and "the branches of a higher order are here arranged a little closer than in M. tenuiramosum" (Ruedemann, 1908, p. 221). He mentioned that more complete collections of the two species might result in synonomy.

Unfortunately if the type specimen of M. gracillimum is in the collections of the University of Chicago, it is still unaccessible; however, unlabeled material (pl. 23, fig. 3) has been found in the collections of the University of Cincinnati which closely resembles the descriptions given by Lesquereux and Ruedemann. The blue lutite contains several black fragments, the longest of which is 2.5 cm. The main "stem" is 0.7 mm in diameter, while the secondary and tertiary branches have a diameter of 0.5 mm. The specimens appear to be solid, and the only signs of compaction are faint longitudinal wrinkles which may be analogous to the longitudinal channels of Lesquereux. None of the specimens possess the jointed structure noted by Ruedemann, and no thecae were found associated with them.

Interpretation: Although Lesquereux (1878) originally placed M. gracillimum in the Lycopodes, i.e., land plants, there has been general agreement since then

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

that the species is a graptolite. If the specimens described by Walcott and Ruedemann are actually the same material as Lesquereux's type specimen, it appears that their graptolite assignment was correct. In general appearance M. gracillimum is extremely close to M. tenuiramosum (Walcott), where thecae are found on the branches (see Ruedemann, 1908, pl. 11, fig 1). Although Ruedemann (1908, p. 221) stated that the jointed structures of M. gracillimum might represent thecae, it was more likely that they were "internodes between the bases of branches of the third order which are all broken off." The finding of undoubted thecae on the branches of M. gracillimum would affirm its graptolite assignment.

Walcott (1883, p. 21) concluded that "the resemblance of these two species of Dendrograptus [Mastigograptus] to Lycopodiaceous plants of the genus Psilophyton is very striking and apt to mislead the observer. Their occurrence with algae, graptolites, trilobites and brachiopods in the same layers of shale, in a position indicating their growth in situ, taken with their graptolite structure, precludes the idea of their being other than of marine origin."

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

Chapter XI

"Fucoids" of Inorganic Origin[41]

---

[41] The forms included in this chapter are judged to be inorganic. Correspondingly, the names are not valid and are placed in quotation marks.

"Chloephycus" Miller and Dyer, 1878

(pl. 24, fig. 1,6)

1847 (non) Buthotrephis Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 8, pl. 2, fig. 6.

1878 Buthotrephis, James, U. P., The Paleontologist, vol. 2, p. 9.

1878 Chloephycus Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 3, pl. 4, fig. 1.

1884 Chloephycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 130, pl. 6, fig. 3.

1885 (in partim) Buthotrephis, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 159.

1889 Chloephycus Miller, S. A., North American Geol. and Palaeont., p. 113.

"Type Species:" Chloephycus plumosum Miller and

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

Dyer (pl. 24, fig. 1; HBM 3154; latex mold UCM 37617) from the Eden beds of Cincinnati, Ohio

Discussion: Miller and Dyer (1878, p. 3) described "Chloephycus" as "simple, slender stems which throw off, upon each side, numerous fine filaments." According to the authors bifurcation is never present; and while a single "stem" resembles a feather, several of them together suggest grass. They differentiated it from Trichophycus by the spreading of the "filaments" and by the rigidity and delicate nature of the "stem."

Such forms are rare in the Cincinnatian section, as indicated by the fact that only the type and one other previously undescribed specimen located on the reverse of the slab bearing Trachomatichnus numerosum (pl. 17, fig. 4) are available for study. Both occur on calcisiltites and cross-laminations in both specimens and load or flute casts on the second one indicate that they are preserved as convex hyporeliefs. The type (pl. 24, fig. 1) consists of approximately 24 parallel separate "specimens." The "stems," which are mostly incomplete, range from a fraction of a millimeter to 5 mm in width. The fine "filaments," which issue from the "stem" at an angle of 20°-30°, range up to 1 mm in diameter. Distally the "filaments" grade imperceptibly into the surface of the bed. The angle of branching is constant, and in all cases the orientation of the "Y" formed by the intersection of two branches is the same. In almost all examples the "filaments" are better developed in

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

the upper part of the specimen, thus obscuring the "stem." In the lower portion of the specimen, where the "filaments" are not as well developed, the "stem" stands out in bold relief.

The specimen on the reverse of Trachomatichnus numerosum is similar to the type, except that the "filaments" are best developed in the mid-portion and fade out in either direction. Associated with this form are what are interpreted as load or flute casts (pl. 24, fig. 6, right) and an area of flowage-produced stress patterns (pl. 24, fig. 6, left).

In all probability "Chloephycus" is synonomous with Buthotrephis filciformis U. P. James (1878). James described B. filciformis as having a slightly sinuous stem less than 1/12 inch in width, and every 1/12 - 1/6 inch the stem gives off slender branches at a 45° angle. This form, which was collected from the Maysville beds near Lebanon, Ohio, was never figured. The type may be with the James collection at the University of Chicago. Nevertheless, due to the similarity of the two descriptions, B. filciformis is considered synonmous to "Chloephycus." J. F. James (1885, 1891) was of the same opinion.

Interpretation: Miller and Dyer (1878) assigned "Chloephycus" to the "fucoids," while J. F. James (1884, p. 7) dismissed the genus with "...it is nothing more than a mark or series of marks produced...by the running of water down a sloping bank into a stream." Miller (1889) was evidently convinced by James' arguments, for although he listed

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

"Chloephycus" among the algae, he admitted that it was probably of inorganic origin.

Evidently "Chloephycus" is not common in the geologic record or at any rate has not been reported. Certain traces from the Lower Devonian Hunsrück Shale bear a superficial resemblance. One such form was illustrated by Rudolf Richter (1941, fig. 15), who interpreted it as the cast of the drag marks of a xiphosurid telson. Since the marking is flanked by tracks, Richter's interpretation appears to be plausible. The other specimen is mentioned by Seilacher (1960, pl. 12, fig. 2-3), who attributed it to "fillings of pinnatulated drag-marks" (Scheifrillen), probably originating from the dragging of a starfish arm along the bottom. According to Seilacher the acute angle would point downcurrent.

There is no evidence which would point to an algal or trace fossil origin for the Cincinnatian forms, which are thought to be modified groove casts originally made on a mud surface. It is possible that original markings resembled "Scolithus dispar" and that the feather-like pattern resulted from penecontemporaneous flowage of mud into the linear depression. An alternate hypothesis is that the structure originated during compaction after the mud surface had been covered by the calcisiltite bed. The area to the left of the specimen seen on pl. 24, fig. 6 does show evidence of deformation and flowage, and this may well have been post-depositional. In either case the direction of flowage was

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

toward the closed end of the "V." Whatever the exact origin, "Chloephycus plumosum" and "Buthotrephis filciformis" are believed to be nothing more than modified groove casts.

"Blastophycus" Miller and Dyer, 1878
(pl. 11, fig. 2; pl. 24, fig. 2; pl. 25, fig. 1,3,5,10)

1873 (non) Planolites Nicholson, H. A., Roy. Soc. London, Proc., vol. 2, p. 289.

1878 Blastophycus Miller, S. A., and Dyer, C. B., Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 24, pl. 1, fig. 1-2.

1885 (in partim) Blastophycus James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 158-159.

1891 (in partim) Planolites diadematum James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

"Type Species:" Blastophycus diadematum Miller and Dyer (1878) (pl. 24, fig. 2; HBM 3181; latex mold UCM 37618; pl. 25, fig. 10; HBM 3181; latex mold UCM 37703) from the Eden beds, Cincinnati, Ohio.

Description: "Blastophycus" was described by Miller and Dyer (1878a, p. 1) as a bilobate "fucoid" "... with a protuberance or bud-like attachment at the junction of the branches." They noted that the protuberance may be smooth or rugose and believed it to be either a bud, shoot, frond, or "spore."

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

J. F. James (1885) compared the "bud-like protuberance" with the "enlarged end" of Trichophycus lanosum Miller and Dyer (1878) and placed the two in synonomy. In his listing of 1891 he renamed the form in question Planolites diadematum and considered it as synonomous with T. lanosum and Saccophycus intortum U. P. James.

Fortunately several specimens of "Blastophycus," including those figured by Miller and Dyer, were located in the paleobotanical collections of Harvard University. These are preserved as convex hyporeliefs (as indicated by cross-bedding and associated sole markings) on conspicuously cross-bedded, iron-stained calcisiltites. All of the specimens appear to be from the same bed; although, due to the lack of data, the type locality has not been rediscovered.

Interpretation: Miller and Dyer (1878a) interpreted "Blastophycus" as a "fucoid," while J. F. James (1885) believed it to be a burrow but did not elaborate.

Häntzschel (1962) listed "Blastophycus" under trace fossils and cited Seilacher (personal communication to Häntzschel) as stating that the "genus" represented "worm burrows projecting above surface of sediment" (Häntzschel, 1962, p. 187)

A study of the cotypes (pl. 24, fig. 2; pl. 25, fig. 10) and other specimens shows that the "bud-like protuberances" are in actuality casts of an enrolled trilobite, apparently Flexicalymene. In many forms the outlines of the thoracic segments and the cephalic border are plainly evident. With this in mind, the origin of the two "branches" is not

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

difficult to perceive. Groove casts and the cross-laminations reveal that the branches lie in the downstream sector. What Miller and Dyer referred to as "branches" are the casts of scour markings around an enrolled trilobite. Potter and Pettijohn (1964, pl. 91B-93B) have termed such markings "current crescent casts."

In testing the hypothesis, "Blastophycus" has been produced experimentally in the laboratory. A tray was filled with fine-grained, water-saturated silt, and several enrolled Flexicalymene specimens were then dropped onto the surface. The tray was tilted at an angle of 10° and a moderately strong current of water was introduced at the upper end. The flow of the water around the trilobites produced settling and also led to the formation of two scour channels on the downcurrent side (pl. 25, fig. 1-2). The trilobites were then removed and plaster casts made (pl. 11, fig. 2; pl. 25, fig. 5); these casts compare favorably with the original "Blastophycus." The scour marks of the original were undoubtedly made on a mud surface, as the channels are much deeper than those produced experimentally. As soon as the flow of water was terminated in the experimental model, caving began which ultimately produced a wider, shallower channel than was the case in the original.

Enrolled trilobites are relatively common in the Cincinnatian lutites and can occur in large numbers.[42] Pre-

---

[42] At the corner of Boudinot and Montana Avenues in Cincinnati,

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

a low angle exposure slope (area of 1,000 square meters) in the "butter layers" of the Waynesville beds yielded over 3,000 specimens of Flexicalymene meeki.

---

sumably enrollment reflects a life-reaction, and the lutite occurrence, a record of rapid entombment. It is postulated that the trilobites were freed from the lutite by erosion and rolled along the sea floor until they temporarily came to rest again. Currents moving past them produced settling and scouring as described above and ultimately succeeded in dislodging the trilobites and washing them farther downstream. The mud surface was then covered by a calcisiltite bed. Another possibility is that the current eroded down to the level of the enrolled trilobites, produced the scour marks, and finally washed the fossils away but left the scour marks intact. This latter suggestion is somewhat analogous to the "pseudoexogenous preservation" hypothesized by Seilacher (1962) for forms from the Spanish flysch, where burrows were unroofed, the filling material washed out, and the mold filled anew with a coarser sediment.

Although Miller and Dyer remarked that "Blastophycus occurs in the Eden beds, it is more likely that the form will be encountered higher in the section (Corryville to Waynesville), where enrolled trilobites are common. However, these beds are the favorite focal point of local collectors, and the fact that no additional specimens of "Blastophycus" have been reported would seem to indicate that the

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

"genus" is rare. This is unfortunate for crescent scour casts are valuable in the determination of paleocurrent velocity and direction.

"Dystactophycus" Miller and Dyer, 1878
(pl. 14, fig. 2-3; pl. 24, fig. 3-4; pl. 25, fig. 6)

1878 Dystactophycus Miller, S. A., and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 2-3, pl. 3, fig. 4.

1885 Dystactophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 163.

"Type Species:" Dystactophycus mamillanum Miller and Dyer (1878) (pl. 24, fig. 4, HBM 3177; latex mold UCM 37691) from the Richmond strata near Milford, Ohio. Monotypic.

Discussion: Miller and Dyer (1878, p. 2-3) characterized the "genus" as a "Rhizoma or frond, mammiform, or depressed conical, and much expanded at the base. Surface marked by numerous closely-arranged, concentric ridges or wrinkles. Some species may be marked, also, by radiating lines."

The type specimen of "D. mamillanum" (pl. 24, fig. 4) resembles a small truncated cone, having a diameter of 3.5 cm at the base and a height of 1.5 cm. The entire structure is composed of 15 flattened rings which subscribe an arc of 220°. The remaining 140° is either covered by

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

sediment or has been destroyed. Likewise, the apex of the cone is missing. As seen in lateral view the specimen is not a perfect cone but instead is shaped like a "liberty cap." On the attenulated slope the rings are 1.5 mm wide and well preserved, although they are offset by a small fault. Most of the rings on this slope are arranged in an imbricate pattern where the larger rings overlap the smaller ones. On casual inspecition the rings are smooth, but careful study reveals a series of faint parallel ridges on one small section of one of the rings near the apex. On the shortened slope of the cone, the rings are thinner (1 mm), more indistinct, and give the appearance of having been compressed. Evidently the authors attempted to clean this area of the specimen, and it is difficult to determine to what degree it has been altered. The imbricate arrangement of the rings is not as noticeable here as it is on the attenulated slope. There is no trace of crystalline or organic material anywhere on the form; it is composed entirely of calcisiltite. Likewise, there is no trace of the "radial lines" which Miller and Dyer mentioned were present on some specimens.

A specimen (pl. 24, fig. 3) labeled "D. mamillanum" from the Richmond (Arnheim) near Hamilton, Ohio, has been found in the collections of the United States National Museum. Like the type it is a conical body which has a diameter of 9.0 cm at the base and a height of 3.0 cm. The specimen is composed entirely of thinly laminated calcisiltite

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

which is bowed down toward the apex; the surface opposite the apex resembles a saucer-shaped depression. The concentric rings vary in their morphology. The flattened rings near the base are 1.5 mm wide. There is no evidence of imbrication, and the faint parallel lines found in the type specimen are plainly seen. In contrast, the rings near the apex show the same imbricate pattern of the type specimen with the difference that here the smaller rings appear to overlap the larger.

Interpretation: Miller and Dyer (1878b) interpreted "Dystactophycus" as an unbranched "fucoid" and believed that the broken apex represented an injury to the plant. However, there is no evidence that would point to a vegetable origin.

J. F. James (1885) compared "Dystactophycus" with the cryptostome bryozoan Lichenalia concentrica Hall (1852, pl. 40E, fig. 5a), originally described from the Clinton (Silurian) beds of New York State. He related that "it can now be conclusively shown that certain species of Monticulipora[43/] have bases which are marked by concentric lines very

---

43/ James' concept of Monticulipora embraced what today are considered to be several different genera.

---

similar to those of Lichenalia concentrica, and there can hardly be a doubt but that they are the same. A figure of Hall's species is given in Palaeontology of New York, Vol. II,

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

pl. 40E, which exactly resembles the markings of Dystactophycus. This "fucoid," then, has resulted from the impression of the base of a coral [sic] resting on a mud-bank and leaving its mark in the concentric rings. The elevated portion is the part extending up into the base of the coral stem, and the outer rings mark the extent of the expanded base. Comparison of Hall's figure and the specimens of Dystactophycus leave little doubt as to this fact" (James, 1885, p. 163).

A study of the type specimen (herein pl. 24, fig, 5; AMNH 1487/1) shows that it differs from Hall's figure. The form is composed of dark calcite and is preserved as a shallow saucer-shaped depression, i.e., concave epirelief. The flattened rings are much smaller (5/mm) and more numerous than Hall's figure would indicate. In addition, the margins of the rings are not smooth as shown by Hall but instead are crenulate. Both Hall's figure and the specimen show that several of the rings either pinch out or are truncated by others. Where they are not covered by foreign material, most of the rings of "D. mamillanum" appear to be complete. It is judged that James was misled by Hall's figure and that L. concentrica bears only a superficial resemblance to the type specimen of "D. mamillanum." While certain Cincinnatian bryozoa may have bases which are similar to Lichenalia and "Dystactophycus," James gave no specific examples to support his argument, and his voluminous works on the genus contain no mention of any. Moreover, Drs. Richard Boardman and John

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

Utgaard of the United States National Museum remark (personal communication) that they have never seen a bryozoan base that resembles "Dystactophycus."

It instead is concluded that the type specimen, as well as the other specimen of "Dystactophycus" described above, represent casts of the rotational sweepings of crinoid stems. The attitude of the bedding in the Hamilton specimen (pl. 24, fig. 3) shows that the correct orientation of the cone is "apex down," and the faint parallel ridges on a portion of one of the rings of the type specimen could easily represent casts of the secondary ridges found on many columnals. It is believed that the stem was first buried by mud to a depth equal to the height of the cone, i.e., 1.5 cm in the type and 3.0 cm in the other specimen. Swirling currents caused the stem to rotate in circular patterns, producing a cone-shaped cavity. Since there is no remnant of the stem or its impression on either specimen, it must have been plucked out at this time. Where the walls of the cone were steepest, minor flowage of the mud occurred, resulting in the imbricate pattern. Finally, silt-size material was swept into the cavity thus insuring preservation. The imbricate pattern also could have resulted from diagenetic compaction after burial. The asymmetry and the faulting seen in the type specimen show that some movement has taken place.

Such imbricate patterns can arise by other means. Some crinoids possess columnals which are shaped like

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

truncated cones, i.e., the diameter of the bottom of the columnal is less than that of the top or vice-versa. Although columnals of this variety are found locally in Ectenocrinus Miller (1889), the genus is not known to occur in Richmond rocks, and in Ectenocrinus the columnals described above alternate with cylindrical ones. Thus, it is not possible to explain the origin of "Dystactophycus" in this manner.

As mentioned in the discussion of Palaeoscia, there are concentric patterns which can be shown to be the marks made by crinoid stems. Plate 14, fig. 2-3 illustrates one such form from an unknown Richmond locality. This form is unusual because it is preserved both as a concave epirelief (pl. 14, fig. 3) and a convex hyporelief (pl. 14, fig. 2). The irregular concentric markings on the lower side have a diameter of 16.0 cm. The markings on the upper surface have a smaller diameter (10 cm) and show a more regular concentric pattern. Vertical sectioning through the center of the specimens not only indicates that the bedding is undisturbed but also reveals three or four columnals. It is concluded that the stem first swept over the bottom probably dragging shell fragments with it. These could account for the irregularity of the markings. The stem was then buried by 1.5 cm of silt, and before breaking off it again scoured the substrate, this time leaving a more regular concentric pattern.

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

"Scolithus dispar" J. F. James

(pl. 24, fig. 7)

1840 (non) Skolithos linearis Haldemann, S. T., "A Monograph of the Limnidades, or freshwater univalve shells of North America, containing descriptions of apparently new animals in different classes, and the names and characters of the subgenera in Paludina and Anculosa," Supp. to no. 1.

1881 Scolithus linearis, James, U. P., The Paleontologist, no. 5, p. 33.

1881 (nom. nud.) Scolithus dispar James, U. P., The Paleontologist, no. 5, p. 33

1892 Scolithus dispar James, J. F., Geol. Soc. America Bull., vol. 3, p. 41, fig. 14.

"Type Locality:" From the "bed of Crawfish Run, eastern part of Cincinnati, 80 feet or so above low-water mark of the Ohio River" (most probably Economy).

Discussion: U. P. James (1881, p. 33) described the Cincinnatian representatives of "S. linearis" as "... strong, raised lines, from 1/24th to over 1/2 an inch or so wide, generally straight, and parallel to each other.... All of the forms here referred to are found on the under side of the bedded shale, resting on a bed of fine, soft blue clay...." He went on to say that "if, owing to the different Geological horizon, or otherwise, these forms

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

shall prove to be distinct from S. linearis, I propose the name dispar for the species" (ibid, p. 33). Since U. P. James never formally proposed "S. dispar," he does not receive credit for the species. Technically, the specific designation "dispar" goes to J. F. James (1892), who figured the "species" and was the first to use the name without reservation.

Several specimens of identified topotype material are present in the University of Cincinnati collections (pl. 24, fig. 7). These closely resemble the figure of the Crawfish Creek material illustrated by J. F. James (1892, fig. 16). The host rock is a cross-laminated calcisiltite which bears several linear markings preserved as convex hyporeliefs. As viewed in pl. 24, fig. 7, there are two sets of markings, one proceeding from left to right, the other from lower left to upper right. The markings specifically referred to "S. linearis" by U. P. James (=S. dispar J. F. James) are thin (1.5 mm), straight ridges, some of which have a longitudinal furrow. A few proceed the entire breadth of the slab, others fade out before reaching the margin. Associated with "S. linearis" are other raised markings. Some are shaped like an open "S," others resemble small drumlins, gradually sloping at one end and sharply rounded at the other. Also found on the slab are moniliform ridges and closely spaced parallel striae. One additional structure varies from all others for it is preserved as a concave hyporelief. These form a branching vermiform-

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

like network, which cuts through both sets of ridges.

Interpretation: U. P. James (1881) agreed with Hall that "S. linearis" was a "fucoid," and J. F. James (1892, p. 40) considered it as "...the passage of some organism over the surface of the mud." There is nothing to indicate that either of these interpretations is correct. As discussed elsewhere, S. linearis, as described by Haldemann (1840) and Hall (1847), is the vertical tube of a phoronid or sessile polychaete. However, "S. linearis" as employed by U. P. James is a groove cast. The ridges are too straight and parallel to be otherwise. Similar forms are illustrated by Dzułinski and Sanders (1962, pl. 11, fig. B and pl. 14) from the Oligocene Krosno beds of southeastern Poland. As shown by Dzułinski and Sanders (1962, p. 74) and Potter and Pettijohn (1964, pl. 61, 66), the orientation of the drumlin-like prod marks shows that current movement was from left to right on the photograph. The tools which made "S. linearis" were probably fragments of brachipod shells. The S-shaped ridges show where shell fragments tore into the bottom, twisted, and were pulled out. The parallel striae and moniliform markings are the casts of crinoid stems which were dragged or rolled over the substrate. The vermiform markings are the only organic feature on the slab and apparently are molds of fecal strings of Sedimentfressers which moved along the silt-mud interface.

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

"Palaeophycus flexuosum" U. P. James

(pl. 23, fig. 1-2)

1879 Palaeophycus flexuosus James, U. P., The Paleontologist, no. 3, p. 18.

1884 Palaeophycus flexuous James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 6, pl. 6, fig. 1.

"Type Locality:" "Cincinnati Group, Hamilton County, Ohio, near Milford, at a hillside cut of the Little Miami Railroad."

Discussion: U. P. James (1879, p. 18) characterized "P. flexuosum" as a "fucoid" consisting "...of a regular series of slightly rounded or flattened stems, which may have been cylindrical and become flattened by pressure. The stems lie nearly parallel to each other in their flexuous course across the slabs of blue shale, sometimes anastomosing (very seldom bifurcating) and are of nearly uniform size from end to end, about one line [1/12 inch] in width and the same distance apart." He mentioned that thin slabs gave the appearance of being composed entirely of "P. flexuosum" specimens. The largest specimen observed by him had an area of over 600 square cm. The species was not figured, and the type specimen (if designated) is in the presently inaccessible collections of the Chicago Natural Museum. The only known illustration is a highly schematic drawing given by J. F. James (1884, pl. 6, fig. 1).

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

Two specimens from the University of Cincinnati collections closely resemble U. P. James' description and J. F. James' illustration. One form (pl. 23, fig. 2) occurs on a thinly laminated micaceous siltite which has a thickness of 5 mm. The host rock has fractured in such a way as to reveal portions of several bedding planes and each plane is marked by the "P. flexuosum" structure. The markings resemble a pattern of small, flattened, parallel ripple marks having a "wave length" of 5 mm and an "amplitude" of 0.1 mm. The material forming the crests is darker, more micaceous, and slightly coarser grained than the sediment found in the troughs. The markings are wavy and infrequently bifurcate to form two parallel branches.

The other specimen (pl. 23, fig. 1) was collected from the Economy beds of Twelve Mile Creek, Campbell County, Kentucky, some 20 meters downstream from the type locality of Rusophycus cryptolithi. In general pattern it is similar to the specimen just discussed. It differs in that the markings are smaller ("wave length" of 3 mm, "amplitude" of 0.1-0.2 mm), more wavy, and anastomose more frequently. The structure covers an area of 700 square cm on the upper surface of a fine-grained calcisiltite. The "ripples," which have a width of but 1.7 mm, are obliterated by trails. However, it is not possible to determine whether the trails are infaunal or exofaunal in origin.

Apparently similar structures have been described by Walcott (1914) from the Precambrian Belt Series of Montana

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

under the name Kinneyia (see Häntzschel, 1962, fig. 146-3). Walcott (1914, p. 107) described Kinneyia as having a "body built up of thin, subparallel layers separated by narrow intervals that are not much greater than the thickness of the layers forming the body." Desio (1940) has assigned forms from the Silurian of North Africa to Kinneyia, and Fuchs (1895) mentioned but did not name similar forms from the Lias Alpha of southern Germany.

Interpretation: U. P. James (1879, p. 18) interpreted "P. flexuosum" as a "fucoid," although he admitted "how [the stems] came to be laid down so evenly laminated and with so little disturbance of arrangement is not apparent." J. F. James (1884, p. 6) believed that "P. flexuosum" represented swash marks, remarking that "the washing of water against the bank of a stream often produces ripple marks which extend along the shores for some distance in regular, undulating lines." He went on to say that U. P. James agreed with this inorganic explanation. Fuchs (1895, p. 444) interpreted the Lias forms as corrosive markings etched on bedrock by the organic acids of algae or the trails of larvae feeding on algal networks. Desio (1940) was somewhat more cautious regarding the origin of the North African forms. He tentatively compared them to the tubulate coral Cladopora reticulata Hall (1851) (jun, syn. of Coenites Eichwald) from the Niagaran (Silurian) of New York State. He also pointed out what he believed to be a similarity between Kinneyia and Paleodictyon.

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

The morphology of the two Cincinnatian specimens recalls depressed ripple marks; however, according to Dr. Paul Potter (personal communication), the smaller specimen (pl. 23, fig. 1) has a "wave length" which is less than that of the smallest undoubted ripple mark. Nevertheless, Shrock (1948, fig. 79) illustrated a form equal in dimensions to the Cincinnatian specimen from the Lower Ordovician New Richmond Sandstone of Wisconsin which he referred to as "eroded symmetrical ripple marks." While it is possible that "P. flexuosum" represents some diagenetic phenomenon, such structures have not been reproduced in laboratory studies.

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

Chapter XII

Incertae sedis

Sphenophyllum primaevum Lesquereux

1878 Sphenophyllum primaevum Lesquereux, L., American Phil. Soc., Proc., vol. 17, p. 167-169, pl. 1, fig. 3-5.

1889 Sphenophyllum primaevum, Miller, S. A., North American Geol. and Palaeont., p. 141.

1892 Sphenophyllum primaevum, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 48.

Type Locality: "Covington, opposite Cincinnati;" Limekiln Run, about 370' above low water, Cincinnati, Ohio. (The first locality could be either Eden, Fairview, or McMillan; the latter is probably McMillan.) No specimens have been available for examination, the types not being known.

Discussion: Lesquereux (1878, p. 167) described the species as "stems or branches slender, articulations close, equidistant; leaves in whorls of four or five leaflets connected towards the base and joined by slightly obtuse sinuses; leaflets either truncate and crenulate at the top, or sometimes deeply slit or lobate; nerves simple at the base, sparingly dichotomous, forking mostly once, even simple." The only known figures of the species are given by Lesquereux (1878, pl. 4, fig. 4-5). The form illustrated

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

by Lesquereux on pl. 4, fig. 3 was also thought to be Sphenophyllum, but he could not identify it as conspecific with S. primaevum. The specimens were found in place "imbedded in the clay or attached to pieces of hardened clay of the same compound as the Cincinnati blue marl" (ibid, p. 169).

Interpretation: Lesquereux (1878) considered S. primaevum, along with Psilophytum gracillimum Lesquereux and Protostigma sigillarioides Lesquereux, to be the oldest land plants yet discovered in North America. He allied S. primaevum with S. sclotheimii Brongniart (1828) and S. oblongifolium Germar (1844) which he had identified in the coal flora of Pennsylvania. Although J. F. James (1892) accepted Lesquereux's interpretation without question, Miller (1899, p. 141) was more skeptical and remarked, "I think this is not a plant." Although Lesquereux's description and figures of S. primaevum resemble the generally accepted concept of Sphenophyllum, it is unlikely that we are dealing with a land plant. The first known true Sphenophyllum is from the Upper Devonian beds of New York State and the Gaspé region of Canada. It would be remarkable if one of the earliest known land plants were found in marine deposits hundreds of miles from the nearest shore. However, at present the form remains a problematicum. Despite the fact that the present study has turned up no new specimens nor are any in the collections studied, it was Lesquereux's impression that it was not rare. He mentioned that he had heard of several specimens and that local collectors had thought

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

it to be "the work of insects...fucoidal or coralline productions like Oldhamia" (Lesquereux, 1878, p. 169). Oldhamia Forbes (1849) is now generally reocgnized to be a stellate burrow, and while it is possible that S. primaevum is a comparable burrow, Oldhamia-like forms are not known to occur in the Cincinnatian. The fact that it occurs "attached to pieces of hardened clay" makes it more likely that this is some sort of organic encrustation, perhaps a sponge or crinoid rootlet system. Until an actual specimen is found, there is little more that can be done.

Protostigma Lesquereux, 1878

1878 Protostigma Lesquereux, L., American Phil. Soc., Proc., vol. 17, p. 169-173, pl. 1, fig. 7-8.

1889 Protostigma, Miller,, S. A., North American Geol. and Palaeont., p. 135.

1892 Protostigma, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 48-49.

Type Species: Protostigma sigillarioides Lesquereux (1878) from the "Cincinnati Group" in Longstreet Creek, six miles east of Lebanon, Ohio (probably Richmond beds). Monotypic.

Discussion: P. sigillarioides was described by Lesquereux (1878, p. 169) as "branches or stems cylindrical, scarcely flattened by compression; surface marked by

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

rhomboidal cicatrices, enlarged on the sides, contiguous and in spiral order, with indistinct impressions of oval scars in the middle." The form was figured by Lesquereux (1878, pl. 4, fig. 7-8). One specimen which was not figured "...is larger, seven centimeters in diameter, nine centimeters long, nearly exactly cylindrical, with irregular more or less distinct ribs, marked crosswise by large wrinkles or irregular protuberances, which do not show any distinct relation of form and position between them" (ibid, p. 169-170). The specimens consist of a "hard bluish clay or marl mixed with grains of coarse sand" (ibid, p. 173).

Lesquereux had mentioned the form in 1874 (without naming it), and this prompted an immediate reply from Newberry (1874), who had the specimens in his possession before Lesquereux described them. Newberry (1874, fig. 1-2) gave two figures which are far less schematic than those of Lesquereux (1878). He failed to find any trace of oval scars in the center of the cicatrices.

Interpretation: Lesquereux (1874, 1878) considered Protostigma to be the oldest of the lycopods. Newberry (1874) regarded them as the stems of large "fucoids," as did Miller (1889). Newberry pointed out that there was no carbonaceous material anywhere on the specimens. J. F. James (1892) questioningly placed the genus in the lycopods.

Newberry's discussion and figures case some doubt on Lesquereux's interpretation. The first undoubted lycopods occur in the Lower Devonian of Australia. While it is

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

not possible to refute Lesquereux's hypothesis, it is equally probable that Protostigma is the cast of a large burrow, the internal mold of a large nautiloid, or even possibly a specimen of Beatricea, the problematic stromatoporoid; however, the latter does possess internal structure. Until identified material is located, Protostigma must remain Incertae sedis.

Palaeoscia Caster, 1942

(pl. 15, fig. 3; pl. 26, fig. 1-6; text fig. 20)

1879 ?Laevicyclus Quenstedt, F. v., Petrefactenkunde Deutschlands, pt. 1, vol. 6, Korallen, Die Röhren und Sternkorallen, p. 577, pl. 164, fig. 35.

1912 ?Cyclozoon Wurm, A., Deutsche geol. Gesell., Zeitschr., Bd. 63, p. 128, pl. 7, fig. 11.

1942 Palaeoscia floweri Caster, K. E., Palaeontographica Americana, vol. 3, p. 26-29, pl. 5, fig. 1-4.

1955 ?Laevicyclus Seilacher, A., in Schindewolf, O., and Seilacher, A., Akad. Wiss. Lit. Mainz, math.-nat. Kl., Abh., no. 10, p. 389-390, pl. 18, fig. 1.

Type Species: Palaeoscia floweri Caster (1942) (pl. 26, fig. 1; UCM 24079) from the Corryville beds of Stonelick Creek, Clermont County, Ohio. Monotypic.

Diagnosis: A series of regular or irregular

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

concentric circles marked by a central "pore." In some forms a series of faintly impressed grooves radiates out from the "pore."

Discussion: At the time of Caster's study only two specimens were known, both from the Corryville beds of Stonelick Creek, some 290 meters downstream from where the creek is crossed by Ohio Route 131. Both specimens are preserved as concave epireliefs in a thin calcisiltite which grades down into a coarse-grained calcarenite. The type specimen (pl. 26, fig. 1) is composed a a series of irregular concentric circles 7.5 cm in diameter. Many of the circles are incomplete and some of them intersect. The center of the specimen is marked by a small well developed "pore" from which radiate 16 grooves (pl. 26, fig. 3). These were interpreted by Caster as representing eight pairs of radial canals. The larger paratype (Caster, 1942, pl. 5, fig. 4) is not as well preserved and covers an arc of 160°. The concentric lines are faintly impressed but appear to be more regular. There is no trace of radial grooves or a central "pore."

Since the original description additional specimens have been recovered from the same locality which shed more light on the nature of the genus. The most revealing are two overlapping specimens neither of which is complete (pl. 26, fig. 5). The larger form, 6.4 cm in diameter, consists of two strongly impressed concentric arcs as well as four very faint ones. Radiating from the central "pore" are

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

numerous grooves which cover an arc of 180°. They are too faint to count accurately but the number appears to be about 25. There is no hint of a regular paired arrangement. The smaller specimen truncates the larger and has a diameter of 4.6 cm. It lacks the concentric appearance of the other specimen, as only a single arc is present. Likewise, there are no radial grooves. The "pores" of both forms are similar; each is cone-shaped and possesses a raised rim. Also the outer arcs are similar in that the outer wall is much steeper than the inner. In some areas the inner wall give the appearance of having been planed off.

Three additional specimens from the type locality should be noted. The first (pl. 26, fig. 2) differs from those described above in that it consists of 8-10 faint but regularly spaced, nearly perfect circles. The outer circle is the most plainly defined, and in cross-section the specimen resembles a very shallow dish. There is no well defined central "pore" nor is there any hint of radial grooves. Another specimen (pl. 26, fig. 6), which has a diameter of 5.4 cm, is characterized by a marked contrast in the appearance of the circles. The circle, whose outer margin lies 9 mm from the central "pore," is incised 2 mm below the general level of the specimen. The central "pore" has a diamter of 3 mm and thus exceeds the dimensions of the "pores" of other specimens. It is uncertain whether the third specimen (pl. 15, fig. 3) represents topotype material. In opposition to the other Stonelick forms, it is preserved

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

as a convex hyporelief, and the clarity of preservation indicates that the subjacent bed was a lutite. All other Stonelick forms are found as concave epireliefs in calcisiltites. It may be that the difference in preservation is due to a lateral facies change in the same bed. On the other hand, the specimen may be from a different bed entirely. The form in question is ellipsoidal in outline; the long axis measures 5.5 cm, the short axis, 5.0 cm. This variation in dimensions can be ascribed to the difference in the development of the four quadrants. The outer margins of the opposing quadrants on the long axis are raised 3 mm off the surface of the host rock. In contrast, the margins of the quadrants on the shorter axis are nearly flush with the surface of the host. Proceeding from the central "pore" to the margin of the specimen is a shallow U-shaped trough which has a width of 2 mm.

Similar concentric markings have been found at other Cincinnatian localities. Mr. Joseph Stocker, a local amateur, has collected a half dozen specimens from the Corryville beds of Hall's Creek, some 10 miles from the Stonelick Creek locality. These forms possess anywhere from 8-26 concentric rings which are more regular both in outline and spacing than most of the previously described specimens. All are preserved as concave epireliefs and have a dish-shaped cross-section. There is no evidence of planation, radial mrakings, or a central "pore" on any of the specimens.

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

Palaeoscia-like forms have also been collected from the Economy beds of Duck Creek, Kentucky. A single slab (pl. 26, fig. 4), having an area of 33.6 square cm, yielded 23 specimens which are preserved as convex hypo-reliefs. Instead of being complete or nearly complete circles, markings are found in only one quadrant. Casts of scour marks associated with the "pore" (here a small conical pimple) reveal that the arcs are developed only in the downcurrent quadrant. The number of arcs varies from 4-8; they are very sharply defined but not evenly spaced. There is no evidence of planation.

Forms like those described above are by no means confined to the local Cincinnatian section. Quenstedt (1879) proposed Laevicyclus for one such form from the Angulaten Sandstone (Jurassic) of Württemberg. It is preserved as a concave epirelief and consists of several concentric circles with a central "pore." Wurm (1912) has described others from the Triassic of Aragon, as has Philipp (1904) from the Upper Triassic of northern Italy. Wurm's specimens, which he named Cyclozoon philippi, have a diameter of 34 mm and possess only two concentric circles. His figure (Wurm, 1912, pl. VII, fig. 11) shows a central "pore" but no radial grooves. Philipp's form, which was unnamed, differs in that it has only a single circular impression. The specimens occur as concave epireliefs on a ripple-marked surface. Instead of being a depression, the central "pore" appears to be a raised area (see

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

Häntzschel, 1962, fig. 123-3a).

Seilacher (1955, pl. 18, fig. 1) described additional specimens of Laevicyclus from the Lower Cambrian of the Salt Range. Preserved as convex hyporeliefs, the small (diameter of 1 cm) Salt Range forms have concentric arcs developed only in two opposing quadrants. In one specimen the best preserved specimen has three arcs in one quadrant, two in the other.

Interpretation: Theories on the origin of these circular structures are as varied as the morphology of the forms themselves. Quenstedt (1879) assigned Laevicyclus to the corals, while both Philipp (1904) and Wurm (1912) considered their forms to be body fossils of unknown affinities. Schmidt (1934) and Lessertisseur (1955) maintained that such circular structures arise from gas bubbles being driven upward during diagenesis.

Seilacher (1953b, fig. 5) believed that Quenstedt's Laevicyclus was a trace fossil. He based his conclusion on the feeding methods of the polychaete Scolecolepis squamata Söderström, which lies vertically in sand with only its head and tentacles protruding above the surface (fig. 20). In calm water (fig. 20, left) the tentacles rotate in a circular pattern, gleaning the nutrients from the substrate; however, when currents are present (fig. 20, right), such actions are not necessary, and the organism merely grasps food particles as they are washed within its reach. As Seilacher shows, the only markings left on the substrate are small scour channels on either side of the tube. Seilacher

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

(1955) mentioned that mollusca and arthropods, as well as polychaetes, might have produced the Salt Range specimens. The smaller diameter and the fact that the markings were developed in only two quadrants indicated to him that the tentacles were not as mobile as they are in Scolecolepis.

Caster (1942) interpreted the two Stonelick specimens, then available to him, as molds of porpitid siphonosphores, comparing them to the Recent Porpalia prunella Haeckel. Admittedly the Cincinnatian forms do bear some resemblance to undoubted soft-bodied coelenterate fossils. Sprigg (1947, 1949) has described several such forms from the ?Precambrian Ediacara beds of Australia. There can be little doubt that these are bona fide "jelly-fish." The radial canals are regularly disposed and encircle the entire specimen, and the forms are associated with numerous other soft-bodied fossils (see Glaessner, 1959).

In spite of the resemblance to the Australian forms, there is reason to believe that the Stonelick specimens are not siphonophores. The raised rims of the central "pore," the numerous radial grooves, the irregularity of the concentric arcs in some forms, and the planed-off appearance of the outer arcs all indicate that the Stonelick Creek specimens represent the markings made by some swirling object. The holotype of the type specimen and the two overlapping specimens illustrated on pl. 26, fig. 5 come the closest to resembling the pattern which might have been made by an Ordovician Scolecolepis-like polychaete. There

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

is evidence of planation, the arcs are uneven, and the radial grooves could well be the imprints of the tentacles. However, the other specimens from the same locality do not support this conclusion; the arcs are too regular. Moreover, sectioning of one specimen revealed a brachiopod shell immediately underlying the center of the circle. We must thus consider the possibility that these circular patterns are the markings of a partly uncovered agglutinated tube as it was being swept around by the currents. The brachiopod shell offers no real problem as the tube could have been anchored to it and have been partly uncovered by erosion. There is no evidence of crinoid holdfasts or stems in any of the specimens, thus that group is ruled out.

Even though some of the specimens resemble Scolecolepis feeding traces while others resemble sweep marks, it is highly improbable that the specimens, all from the same bed, have two different origins. However, at this point it is not clear which of the two explanations is the correct one; therefore, Palaeoscia is assigned to the Incertae sedis. The origin of the Hall's Creek forms is even more problematic. The circular markings are too perfect in outline to represent either a trace fossil or a siphonophore. While it is believed that these are probably sweep marks of an eroded tube, it must be admitted that careful sectioning failed to reveal any trace of a tube or similar structure. This may not be as critical as it first appears. The "pores" are so small (1 mm) that such a tube might not even be

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

visible in vertical sections, unless it were filled with a material different from that of the host rock.

Since the Duck Creek specimens (pl. 26, fig. 4) are preserved as convex hyporeliefs, vertical sections are irrelevant. The scour marks on either side of the pimple-like raised area in the center show that these most probably are sweep marks. There seems little reason why such regular arcs should be developed in only the downstream quadrant if this were the feeding trace of a Scolecolepis-like organism. Yet it is unusual that no evidence of the tube or stem is found in any of the 23 specimens.

In summary, the generic designation Palaeoscia is applied only to specimens from Stonelick Creek. These may be either feeding traces or the sweep marks of an agglutinated tube. The specimens from Hall's Creek and Duck Creek are thought to be sweep marks and they are not assigned to Palaeoscia. Not all such markings are so enigmatic, for some can definitely be shown to be sweep marks of crinoid stems. These are discussed under "Dystactophycus."

Aristophycus Miller and Dyer, 1878

(pl. 27, fig. 6-8; text fig. 39)

1878 Aristophycus Miller, S. A. and Dyer, C. B., Contributions to Palaeontology, no. 2 (Cincinnati, Ohio, private publication), p. 3, pl. 4, fig. 2-3.

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

1885 Aristophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 130.

Type Species: Aristophycus ramosum Miller and Dyer (1878) (pl. 27, fig. 7; HBM 3173; latex mold UCM 37580; pl. 27, fig. 8; HBM 3172; latex mold UCM 37668) from the Fairview or McMillan Formation, Cincinnati, Ohio.

Diagnosis: Pulmonate, branching structures of moderate size which are preserved as convex epireliefs. As viewed in cross-section, the smaller secondary branches join the terete main branch from beneath, forming an angle of 30-45° with the horizontal. The tertiary and quaternary branches inosculate to form an anastomosing pattern.

Discussion: Aristophycus was described by Miller and Dyer (1878, p. 3-4) as a "fucoid" with a "stem which divides into branches or fibres; these again divide and subdivide, until they become exceedingly numerous. The ramifications are sent off like the roots of a tree or shrub without any determinate order, while many of the smaller fibres inosculate like the veins in the leaf of a tree."

One species, A. ramosum, and the variety A. ramosum var. germanum were proposed. The latter differed in that "small fibres are thrown off from the main stem between the branches... [these] are finer and more completely interwoven than they are in A. ramosum" (Miller and Dyer, 1878, p. 4).

On the whole Miller and Dyer's description is accurate, but the authors neglected to mention the unusual

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

mode of branching. As seen in fig. 39, the secondary branches do not join the main trunks of the system on a horizontal plane but instead from beneath. The angle of juncture varies between 30-60° off the horizontal. The same generally holds for the relationship between the small secondary and tertiary branches; beyond this the branches become so small that observation is difficult.

The type specimen of A. ramosum (pl. 27, fig. 7), which is 17 cm long and 13 cm wide, consists of seven irregularly winding main branches which vary from 2-6 mm in diameter along their length. Distally these give rise to numerous short secondary branches which have a diameter of 0.5-1.5 mm. These in turn branch to produce a capillary-like system which crosses over and interpenetrates the "capillaries" of a neighboring branch. The unusual method of branching mentioned above is best seen in the distal portions of the system. The type specimens of A. ramosum var. germanum (pl. 27, fig. 8) is slightly smaller, having a length of 9.5 cm and width of 5 cm. The main trunk has a diameter slightly in excess of 1 mm. Unlike the type of A. ramosum where the anastomosing pattern is confined to the distal regions, A. ramosum var. germanum shows this arrangement along most of its length, although it is best developed distally. The small branches wind about in interpenetrate to form a system which is even more complex than that of A. ramosum.

In the A. ramosum var. germanum type, there is no

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

difference in lithology between the host rock and the fossil. Conversely the A. ramosum type appears to be finer grained than the host rock, for it flakes off with comparative ease.

In spite of these minor differences, it is concluded that there is no need for separate taxa for the two specimens. The more important features, e.g., the anastomosing pattern and the mode of branching, are common to both; therefore, A. ramosum var. germanum is placed in synonomy with A. ramosum.

Similar structures have been reported from Europe and were called "figures de viscosité" by Issel (1889). Fuchs (1895, pl. 9, fig. 4) illustrates one specimen from the Braun-Jura Beta of Württemberg. As nearly as can be determined from his figure, it is congeneric with Aristophycus. The form measures 9 cm by 2.2 cm, and the main trunk has a diameter of less than a millimeter. The exact nature of the branching is undeterminable.

Interpretation: James (1885) interpreted Aristophycus as casts of rill marks; and apparently Miller (1889, p. 107) was convinced, for he conceded that the genus might well be inorganic in origin, or if it were a "fucoid," it was too poorly known to be retained as a separate genus. Häntzschel (1965, p. 10) reported that Seilacher (personal communication to Häntzschel) considered Aristophycus to be a "figure de viscosité."

Upon casual inspection, James' rill mark interpretation certainly appears plausible. However, closer examin-

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

ation reveals that Aristophycus occurs as convex epireliefs, i.e., raised patterns, on the upper surface of the beds. There can be no question of this, as the side of the slab bearing A. ramosum contains a portion of a Corophioides, in which the bottom of the "U" is 180° to the surface bearing Aristophycus. The presence of channel fillings in the other specimen confirms this orientation.

Seen in this light, the origin of such a form becomes problematic. In fact it is not possible to entirely disregard a possible algal origin, but the mode of preservation, i.e., convex epirelief, makes it more likely that Aristophycus is either a burrow or some physical phenomenon.

Fuchs likened it to the anastomosing pattern which results when a knife blade is raised off a slab of butter. Anyone who has ever polished rock sections has seen the same effect. Fuchs pictures a shell-less gastropod or a large Planaria rising vertically off the bottom with the resulting suction producing the pattern. However, it is difficult to see how suction could produce such a regular hierarchic and interlocking pattern where the secondary branches consistently join the main trunk from below.

Because of the unique preservation it is most probable that Aristophycus originated below the depositional interface along a bedding plane surface. The clarity of preservation indicates that the overlying sediment was undoubtedly a lutite. It is possible that Aristophycus is a branching feeding burrow, where the organism moved along

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

the main branch and extended a slender proboscis or tentacles down along the mud-silt interface. The terete cross-section of the branches and the variations in the diameter of the main trunk support such a hypothesis. However, Aristophycus differs in many respects from all known burrows. It is difficult to explain why the angle of branching is consistently 30-60° off the horizontal and why the branches become progressively smaller distally. Likewise, the mode of preservation is exactly the opposite from that found in many burrows. In most burrows, which are preserved as boundary reliefs, e.g., Phycodes, the overlying sediment fills the cavity made by the organism. The burrow hypothesis would be more attractive if Aristophycus were preserved as a convex hyporelief or a concave epirelief.

Because of these difficulties it is equally as probable that Aristophycus is of physical origin. Perhaps it represents some variety of diagenetic flow pattern. However, just as Aristophycus resembles no known burrow, neither does it resemble any known diagenetic phenomenon. Moreover, the anastomosing pattern of the branches is in opposition to the characteristics of flowing, percolating water.

It must be concluded that for the time being Aristophycus remains a problematicum.

Cyathophycus silurianum J. F. James

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

1891 Cyathophycus siluriana James, J. F. Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 64, fig. 5a-c.

Type Locality: Corryville beds, Cincinnati, Ohio. The only illustrations of the species are those given by James.

Discussion: James (1891, p. 64) proposed C. silurianum for "rounded or flattened cylindrical bodies, varying from one to two and one-half inches in length, and about one inch in width; outer surface marked by longitudinal lines starting from a common point at one end, and radiating in the form of a cup; numerous transverse lines crossing the longitudinal ones and so forming an irregular net work. The internal structure seems to be entirely lacking, the center being filled with clay, and only a portion of the framework remains."

James admitted that the Cincinnatian forms could only tentatively be allied with the other species of Cyathophycus (a problematic sponge) proposed by Walcott (1883) from the "Utica Slate" (Upper Ordovician) of New York State. He postulated that preservation might account for the morphological differences. He also remarked that C. silurianum resembled the specimens of Rauffellia Ulrich figured by Ulrich (1889, fig. 1,2,4) from the Ordovician of Minnesota.

Interpretation: James believed that C. silurianum was a sponge. Unfortunately identified material was not

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

available for the present study. If a type specimen was designated, it is in the inaccessible collections of the Chicago Natural History Museum. Nevertheless, James' description, figures, and the illustrations of Rauffellia given by Ulrich would seem to indicate that C. silurianum is synonomous with Trichophycus venosum. Bassler (1915, p. 1289) reached the same conclusion. However, if this is the case, it is strange that James himself did not recognize the similarity. Miller's (1879, pl. 9, fig. 5-5a) lithographs of the Trichophycus venosum fillings are quite accurate and James had discussed T. venosum in his 1885 paper. This suggests that C. silurianum may be something entirely different. Little more can be done until the James collection is available for study.

Walcottia sulcata U. P. James

1881 Walcottia sulcata James, U. P., The Paleontologist, no. 5, p. 44.

1886 Walcottia sulcata, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 162.

Type Locality: Economy beds of the eastern part of Cincinnati. There is no known illustration of the species.

Discussion: U. P. James (1881, p. 44) created W. sulcata for "...sub-cylindrical, slightly tortuous forms,

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

with a longitudinal groove along the center of the exposed part; a series of fine, closely arranged transverse or gently oblique striae, commencing, apparently, at the bottom of the groove, and passing over the higher rounded surface to the embedded portion on each side." He remarked that the species had a length of 2 inches and a width of 1/12 inch and "differed materially" from W. rugosa Miller and Dyer (1878) in "...the features of the longitudinal groove, the uniform width and the transverse striae" (ibid, p. 44).

Interpretation: U. P. James offered no interpretation for W. sulcata and J. F. James (1886) merely referred to the form as"a burrow." While identified material may be with the James collection at the Chicago Natural History Museum, none is at hand for the present study. The original description recalls small, striate, bilobed Cruziana-like trails. Thus, it is possible that the species is a trail similar to Ormathichnus Miller (1880).

Saccophycus U. P. James, 1879

1847 ?Sphenothallus Hall, J., Nat. Hist. New York, Palaeont. New York, vol. 1, p. 268, pl. 68, fig. 1.

1878 Sphenothallus, James, U. P., The Paleontologist, no. 2, p. 9.

1879 Saccophycus James, U. P., The Paleontologist, no. 3, p. 17.

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

1885 Saccophycus, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 157.

1891 (in partim) Planolites, James, J. F., Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 47.

Type Species: Saccophycus intortum U. P. James (1879) from the "Cincinnati Group, near Lebanon, Ohio." Monotypic.

Discussion: U. P. James (1879, p. 17) characterized Saccophycus as resembling "...a long tortuous bag or sack, with the ends drawn in; undulating, wavy surface, finely striated longitudinally; sides and ends rounded in and under." He further mentioned that the type (the only known specimen!) was approximately three inches long and had a breadth of one inch at one end and one-half inch at the other. The specimen was "partly imbedded in a fragment of limestone." There is no known figure of the genus. U. P. James (1878) had mentioned the specimen previously, tentatively assigning it to Sphenothallus latifolius Hall (1847) (Upper Ordovician: New York). He remarked that it resembled the specimen illustrated by Hall (1847, pl. 68, fig. 2e) and that the Cincinnatian form might be the stem of S. latifolius. Hall's figure shows a smooth truncated cone having a height of 4.5 cm and a diameter of 2.5 cm at the base and 1.5 cm at the apex. The specimen figured by Hall does not resemble any Cincinnatian fossil or pseudofossil.

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

The sole specimen of Saccophycus may be with the James collection at the Chicago Natural History Museum. Regrettably the collection was not available for the present study. A search of the literature reveals that no subsequent author has enlarged upon the original description.

Interpretation: U. P. James interpreted Saccophycus as a "fucoid," while J. F. James (1885, p. 157) believed it to be "the burrow of an annelid." J. F. James (1891) considered Saccophycus to be synonomous with Blastophycus diadematum and Trichophycus venosum. Although there is nothing to indicate that Saccophycus is synonomous with Blastophycus, U. P. James' original description is reminiscent of Trichophycus venosum. Until the type specimen of Saccophycus is located, the matter must rest.

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

Chapter XIII

Invalid Species

Ulrich (1880) in his *Catalogue of Fossils Occurring in the Cincinnati Group* listed four species of previously undescribed "fucoids." *Palaeophycus ornatum*, *Palaeophycus sculptum*, *Conostichnus truncatus*, and *Cyclophycus laterale*. He mentioned in the preface that "many of the new species recorded in the list, have as yet not been published." A search of his subsequent works reveals that he never formally proposed nor described the above species and that they are thus *nomen nudum*. A comparison of the names with any forms actually occurring in the Cincinnatian would be pure speculation.

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

Chapter XIV

Comparative Palichnology and Suggestions for Further Study

Comparative Palichnology

Until quite recently most study of trace fossils has been concerned primarily with description and interpretation of individual forms, i.e., paleoautoecological investigations. Assemblages of traces and their mass economy and ecology have only sporadically received attention. Richter's (1931) analysis of trace fossils in the Hunsrück Shale (Devonian: Rhineland) and Linck's (1949) study on the Schilf Sandstone (Triassic: Württemberg) are notable pioneer works of synthesis, i.e., paleosynecological analysis.

However, the broader aspect of the paleosynecology of traces, an attempted integrated investigation of the entire trace fossil spectrum and subdivisions, is very new indeed. Seilacher (1954) initiated the comprehensive work in his comparison of the trace fossils of the Alpine Flysch and Molasse. More complete documentation of his 1954 conclusions came in his 1955 paper on trace fossils of the Cambrian section in the Salt Range of Pakistan. Here he compared the trace community of the Salt Range with five other trace communities: the Triassic Schilf Sandstone, the Lias and Dogger (Jurassic) Sandstones of Württemberg, the Swiss Miocene Molasse of the Alps, the Cretaceous and Tertiary Flysch of the same area, and the Ordovician-Devonian

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

Nereites beds of Portugal (see fig. 42 herein).

Seilacher found that the trace assemblages of the Alpine Flysch and the Portuguese section were characterized by abundant Pascichnia which exhibited intricate geometric patterns. While Fodinichnia and Repichnia were also numerous, there was a complete lack of Cubichnia.

On the other hand, in the remaining four sections Cubichnia formed the dominant group and Pascichnia were virtually nonexistant. The Weidespuren were represented only by Dimorphichnus (fig. 42-8) in the Salt Range and Helminthoida (fig. 42-96) in the Molasse, and both of these are questionable. As shown elsewhere herein, Dimorphichnus may be a variety of trilobite trail which exhibits strongly oblique movement. The Molasse representative of Helminthoida is poorly organized and lacks the tight meanders of its Flysch counterpart (fig. 42-64). The Repichnia are well represented in these same four sections, and while several different varieties of Fodinichnia were present in the Salt Range and Lias and Dogger section, the latter were not well developed in the Schilf and marine Molasse strata.

The dichotomy in the trace fossil assemblages is reflected by a marked difference in lithology and paleoecologic setting. A capsule summary of the stratigraphy of each unit is given below.

The Cambrian section of the Salt Range is composed of nearly 360 meters of dominantly clastic sediments. The basal 80-100 meters of alternating beds of fine-grained

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

sandstones and shales are marked by imprints of salt casts, mud cracks, and ripple marks. These are overlain by a 10 meter thick, well rounded quartz conglomerate which grades upward into a micaceous, glauconitic quartz sandstone containing a good marine fauna. Overlying this are dolomite beds interstratified with thin shales. The uppermost units are thin bedded sands and shales bearing salt pseudomorphs. Schindewolf and Seilacher (1955) believed that the column reflected a shallow water marine environment which became terrestrial in the upper portion.

The Schilf Sandstone (Triassic: Württemberg) varies from 3-42 meters in thickness and is composed of well sorted, fine-grained micaceous sands and shales which are ripple-marked and bear other evidence of current activity. Locally some of the sands have a high iron content. Although plant fossils are common, invertebrate body fossils are almost entirely absent. Linck (1949) interpreted the Schilf as representing a shallow water deltaic environment which was predominately marine but contained some brackish water units.

According to Brinkmann (1960) the Lias of the Württemberg area contains 70 meters of fossiliferous limestones and marls. Most of the trace fossils occur in the thin (6 meters) Angulaten Sandstone (Lias Alpha-2). The Dogger of Württemberg is composed of over 100 meters of feruginous sandstones, limestones, and marls. The trace fossils are encountered in the clastics of the Dogger Beta. The Lias and Dogger are interpreted as shallow water deposits which thicken to the north and grade into the fine-

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

grained deep water clastics of northwestern Germany.

The Tertiary Alpine Molasse exhibits such a wide lithologic range that it is difficult to characterize in a few brief phrases. Generally speaking, the section is made up of interbedded bituminous slates, conglomerates, sandstones, and shales. Vertical and lateral facies changes are numerous, and cross-lamination and channel fillings are common. Current indicators, even in local areas, present a bewildering variety of directions. According to Kuenen and Carozzi (1953) the strata are irregular in thickness and distribution, and the contacts between the various units are not sharp. Graded bedding within individual units is generally absent. The Molasse is thought to indicate sediments deposited in shallow neritic and non-marine environments; the fauna is well developed and is composed of marine, brackish, and lacustrine forms. As noted above, Seilacher confined his study to the marine beds.

While the four sections discussed above vary in details (as do their respective trace fossil communities), they are all regarded as being shallow water (neritic) deposits. In contrast, the sediments of the Alpine Flysch and the Nereites beds of Portugal are thought to reflect a far different environment.

Recently the Cretaceous and Tertiary Flysch of the Alps has received considerable attention. The sequence, whose thickness is measured in thousands of meters, includes a monotonous succession of micaceous sandstones and shales.

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

The sandstones are normally graded and the contact with the subjacent shale is sharply defined. Convolute bedding is not uncommon, and the soles of the sandstones bear numerous sedimentary markings (flute casts, tool marks, etc.). In opposition to the Molasse, these markings indicate a uniform current direction. Ripple marks, scour channels, and cross-lamination are generally absent. Body fossils are rare, and any fossils found are fragmentary and poorly preserved; in many areas trace fossils are the only evidence of autochthonous life. Although the origin of the Flysch was for many years in doubt, the work of Kuenen, Migliorini, and others on turbidity flows has shown that the alpine sequence is most probably of deep water origin and that the sediments are derived from periodic submarine slides.

The Nereites beds of Portugal, as described in part by Delgado (1908), include over 4,700 meters of interbedded graywackes, shales, and quartzites. Some carbonates and sedimentary breccias are also present. While the micaceous shales do contain graptolites, other body fossils are not common. Like the Alpine Flysch, the Nereites beds are thought to be deep water geosynclinal deposits.

Seilacher (1954, p. 223) pointed out that the basic differences in the two assemblages can not be explained by the different ages of the units. With a few exceptions trace fossils make very poor index fossils (see Seilacher, 1960). Pascichnia are as well developed in the Lower Paleozoic of Portugal as they are in the Mesozoic and

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

Cenozoic; likewise, Cubichnia range from the Cambrian through the Tertiary. Seilacher (1954, p. 223) also maintained that the lithology of the host rock was not important. Even though the gross aspects of the sequences may differ, most of the trace fossils occur in similar rock types, e.g., silts or fine-grained sands. Seilacher concluded that water depth was the controlling factor. He believed that Cubichnia represented burrows of concealment, and while in shallow, well lighted water such burrows were an important means of protection, they were unnecessary in the dark, deep water basins. Although Seilacher judged that Pascichnia reflected the concentration of organic material in thin layers of sediment, he was unable to explain why Pascichnia were not found in shallow water environments.

In 1964 Seilacher greatly expanded his previous comparison to include 42 sections of varying ages and geographic locations (see fig. 43 herein). He renamed the community typified by Pascichia the "Nereites facies," while the Cubichnia suite became the "Cruziana facies." In addition he recognized a third suite, the "Zoophycos facies." He reiterated his earlier belief that the "Cruziana facies" represented a shallow water environment, while the "Nereites facies" was indicative of deep water. The "Zoophycos facies" was intermediate between the two.[44/]

44/ Seilacher did not define what he meant by deep or shallow

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

water. However, for our usage, shallow water refers to environments within the zone of effective light penetration, while deep water refers to environments below the depth of light penetration. By the nature of his discussion Seilacher implied that shallow water is in the neighborhood of 0-100 meters, while deep water would be 350 meters+.

In the Ordovician of norther Iraq, Seilacher (1964, p. 314, fig. 8) was able to demonstrate a succession of all three facies in a single vertical section. The lower unit, the Khabour Quartzite, is typified by Cruziana, Diplocraterion, Daedalus, and Phycodes. This is overlain by Dershish Sandstone which carries Zoophycos, Teichichnus, and Chondrites. In contrast, the uppermost unit, the Sinat Shale, contains the Pascichnia Helminthoida, Paleodictyon, and Neonereites, as well as Chondrites. To him this indicated a transition from shallow to deep water environment. Seilacher (1964) also remarked that a lateral transition between the "Nereites facies" and "Zoophycos facies" can be found in the Upper Paleozoic of the Ouachitas, where what he interpreted as the deep water Johns Valley turbidites grade north into the more shallow water Atoka Sandstones which carry Zoophycos. Seilacher (1964, p. 314) concluded that "there is no doubt that still further toward the craton this Zoophycos facies would eventually grade into the Cruziana facies including littoral deposits."

The Cincinnatian ichnospectrum is illustrated in

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

fig. 44. As can be seen the Cubichnia, Fodinichnia, Domichnia, and Repichnia are well represented, while the only Pascichnia are two specimens questionably assigned to Paleodictyon. A comparison of the Cincinnatian forms with those suites illustrated by Seilacher clearly reveals that the Cincinnatian is a member of the "Cruziana facies," i.e., shallow water.[45/] This shallow water assignment of the

---

45/ This is not to imply that the Cincinnatian trace fossil assemblage is identical to any previously described suite; as one would expect each assemblage is unique. In this chapter we are comparing the relative development of Cubichnia, Pascichnia, etc.

Cincinnatian is independently confirmed by several factors. Hofmann (1964) has reported mud cracks from the Corryville beds at Stonelick Creek, as has Fox (1962) from the Richmond of southeastern Indiana. In addition large amplitude pararipples are not uncommon in the Cincinnatian (see Bucher, 1919), and these are generally considered to be indicators of shallow water. The Cincinnatian is noted for the tremendous numbers and variety of body fossils which, of course, represent only a fraction of the original populations. Such diversity and numbers are encountered today only in shallow seas. It is the author's belief that the Cincinnatian sea was less than 35 meters deep, and at times the bottom may have been exposed to brief periods of subaerial erosion.

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

The author is in basic agreement with Seilacher's interpretation of the "Cruziana" and "Nereites facies." Cubichnia most probably are burrows of concealment, and these would be more numerous in shallow, well lighted water than in the abyssal deeps. Conversely Pascichnia are indicators of organic material concentrated in thin layers. It is reasonable to assume that thin layers of organic material would be more likely to accumulate in deep water where current and wave action is less apt to be as constant than in shallow water. The lack of Pascichnia in the Cincinnatian probably demonstrates that wave and current agitation distributed the organic material evenly through the sediment. This would explain why most Cincinnatian chondritids and several others forms do not follow depositional interfaces.

The author does not believe that the differences between the "Cruziana" and "Nereites facies" is as clear-cut as they appear in Seilacher's chart (fig. 43). It is felt that additional work on both fossil and Recent sediments will cloud some of these sharp boundaries. For example, Zenkevich and Birstein (1956) reported that investigations of the Kuril Trench revealed that the relative importance of plankton predators and detritus feeders increases with depth, while the importance of larger predators decreases. They found that below 10,000 meters predators are lacking entirely. However, there is no mention of a sharp transition, and instead their diagram of the number of various organisms (Zenkevich and Birstein, 1956, fig. 4) shows that

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

the change in feeding habits is gradational. Thus, it is reasonable to assume that Pascichnia and Cubichnia can occur together at some intermediate depth. It is also possible that they can coexist in either very shallow or very deep water. Indeed, Seilacher's chart (fig. 43 herein) shows that Taphrhelminthopsis Sacco, a meandering gastropod trail (Pascichnia), is present in the Devonian Taunus Quartzite of Germany, even though the majority of the Taunus trace fossils belong to the "Cruziana facies." Also, questionable specimens of Paleodictyon are present in the Cincinnatian. Confirming the coexistence of Pascichnia and Cubichnia in Recent sediments will not be easy, since it is difficult to recognize Cubichnia as such on the depositional interface (see Seilacher, 1953b, pl. 11, fig. D). It is likely that only through careful analysis of undisturbed bottom samples can any conclusions be reached.

In spite of the evidence provided by the Iraqian section discussed above, the author questions whether the Zoophycos suite represents a true intermediate facies. It is difficult to comprehend why the trace fossils found at intermediate depths should be so markedly different from the shallow and deep water assemblages. It is more reasonable to expect a mixture of the shallow and deep water communities. Moreover, at least two sections in North America bearing numerous Zoophycos are considered shallow water deposits. Concerning the Chemung (Devonian) strata of New York State, Cooper (1957, p. 271) wrote, "the peculiar worm burrow

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

Taonurus [Zoophycos] is abundant in all the argillaceous sandstones and coarse siltstones, especially in central and eastcentral New York and parts of the Appalachians. The burrows are characteristic of the shallow-water epineritic environment." Likewise, the regional setting of the Buena Vista Sandstone of Kentucky (Lower Mississippian) which contains numerous Zoophycos bespeaks a shallow water origin. Note that Seilacher himself (herein fig. 43) reported Zoophycos from three deep water deposits. Thus, the validity of Zoophycos as an accurate depth indicator is questionable.

It is also probable that additional studies of the "Nereites" and "Cruziana facies" will result in the establishment of subassociations, i.e., trace fossils suites dominated by a few genera. In the Cincinnatian Trichophycus venosum, Corophioides, and Chondrites are very common, and they frequently occur together in the same bed. Although Trichophycus is thus far limited to the Cincinnatian, it has a Bauplan similar to that of Teichichnus Seilacher. According to Seilacher (1964) Teichichnus, Corophioides, and Chondrites occur in the Upper Malm Sandstone (Jurassic: northern France) and in the Lias Alpha Sandstone (Jurassic: southern Germany). It would be interesting to know how abundant the three genera are and whether they occur together in the same bed as they do in the Cincinnatian. It might well be that these forms represent a subassociation within the "Cruziana facies."

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

Throughout this work the lack of information on Recent traces has been stressed. While this deficiency makes interpretation of individual fossil forms difficult, it is even more apparent in a study of Spuren communities. It is ironic that we have more data on fossil suites than Recent associations. Nevertheless, the true meaning of fossil communities can be learned only through an examination of Recent environments. For obvious reasons the bulk of Recent studies to date have dealt with the littoral environment, one which is rarely preserved in the fossil record. More research should be conducted on the physical and biological aspects of the sediments of the neritic zone. It is thus clear that while Seilacher has made an excellent beginning, any conclusions regarding trace fossil associations must be considered as tentative and subject to revision.

Comments on Cincinnatian Paleoecology and Suggestions for Additional Studies

The value of trace fossils as paleoecological indicators is most striking in sequences where other organic evidence is lacking (e.g., Alpine Flysch). As mentioned previously, the Cincinnatian has an abundance of evidence, and it all points to a shallow water, open marine environment. The trace fossils confirm both this and the recurrent nature of the Cincinnatian fauna. As seen in Caster, Dalvé, and Pope (1955), several species of body

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

fossils reappear higher in the local section, and much of the Corryville fauna is again encountered in the Sunset beds. The most outstanding recurrence in trace fossils is the Trichophycus-Corophioides-Chondrites complex which is found in the Economy of Twelve Mile Creek, the Southgate of Newport Shopping Center, the Upper McMicken of Route 27 south of Newport, West Fork Creek and Wesselman Road, the Corryville of Stonelick Creek, the Sunset of Four Mile Creek (3.7 miles south of Oxford, Ohio), and the Liberty of Lick Run. This indicates a repetition of bottom conditions and preservation favorable to these three forms.

The author has also been impressed by the amount of subaqueous erosion as evidenced by truncated burrows. Free tubes have never been found in any specimens of Corophioides; and Trichophycus venosum most frequently occurs as "turkey tracks," i.e., only the basal portion of the burrow. Several other examples (e.g., Lockeia, Fascifodina) could also be cited. The evidence provided by trace fossils, coupled with the many scour channels, indicates frequent periods of erosive activity.

Additional research on Cincinnatian traces should prove most rewarding. An attempt should be made to determine if there is any vertical variation in the suite. To date the most notable change is that Palaeophycus, type-C is more common in the calcarenites of the Eden and is less frequently encountered higher in the section. Weiss et al (1965) and Ford (1965) have shown that the Eden rocks in the vicinity

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

of Cincinnati contain a greater percentage of lutite (75 per cent+) than the Maysville strata (40-65 per cent). Conversely calcarenites are thicker and more important in the Maysville. Although no exact data are yet available for the Richmond, the upper part of the Cincinnatian section is generally considered to contain a greater percentage of calcarenites than does the lower portion. It would be interesting to know if this lithologic change is reflected by a variation in the number and kinds of traces.

Just as Seilacher (1964) has traced Spuren communites laterally in the Upper Paleozoic of Oklahoma, the local Cincinnatian suite should be compared with the trace fossils of its lateral equivalents. The most fruitful field of investigation should be the Martinsburg Shale of the Appalachian Geosyncline. The Martinsburg represents a muddier, more unstable environment, and there may well be significant differences between the two communities.

A considerable amount of work still remains to be done on individual species. Although the local traces are useful as guide fossils only for very short distances, additional studies may indicate that some forms can be employed for long distance correlation. The Trichophycus-Corophioides-Chondrites association has been found just below the top of the McMicken at three widely separated localities. Further work would reveal whether this is merely a coincidence or whether a single bed covers a wide area. Likewise, Fascifodina has been found only in the Corryville beds of two

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

localities 10 miles apart. Perhaps the lateral range of this genus can be extended by careful collecting of the Middle Corryville. Such work will also provide greater insight into facies relations within the Cincinnatian.

As mentioned previously, the magnitude of the present study has resulted in a superficial coverage of some genera. The morphology of forms such as Chondrites, type-B, Trichophycus, and Tylichnus is not completely understood. It would be well to test techniques which have not yet been used in palichnological studies, i.e., radiography and amino acid analyses. X-ray defractions analysis (the first ever attempted on trace fossils) proved valuable in the interpretation of Chondrites, type-A, and this method should be used on other forms as well. Only through the employment of a wide spectrum of geologic and paleontologic tools can this difficult group be understood.

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

Appendix

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

Classification of Hundt (1932, p. 17)

I. Surface tracks and traces

- A. thigmotaxic tracks and traces
  - 1. free meanders
  - 2. free spirals
- B. homostrophic tracks and traces
  - 1. oriented meanders
  - 2. oriented spirals
- C. phobotaxic tracks and traces
  - 1. stellate
  - 2. corymbiform
  - 3. pseudo-corymbiform
  - 4. chondritiform
- D. linear smooth tracks and traces
  - 1. simple
  - 2. ramified

II. Deep traces and imprints

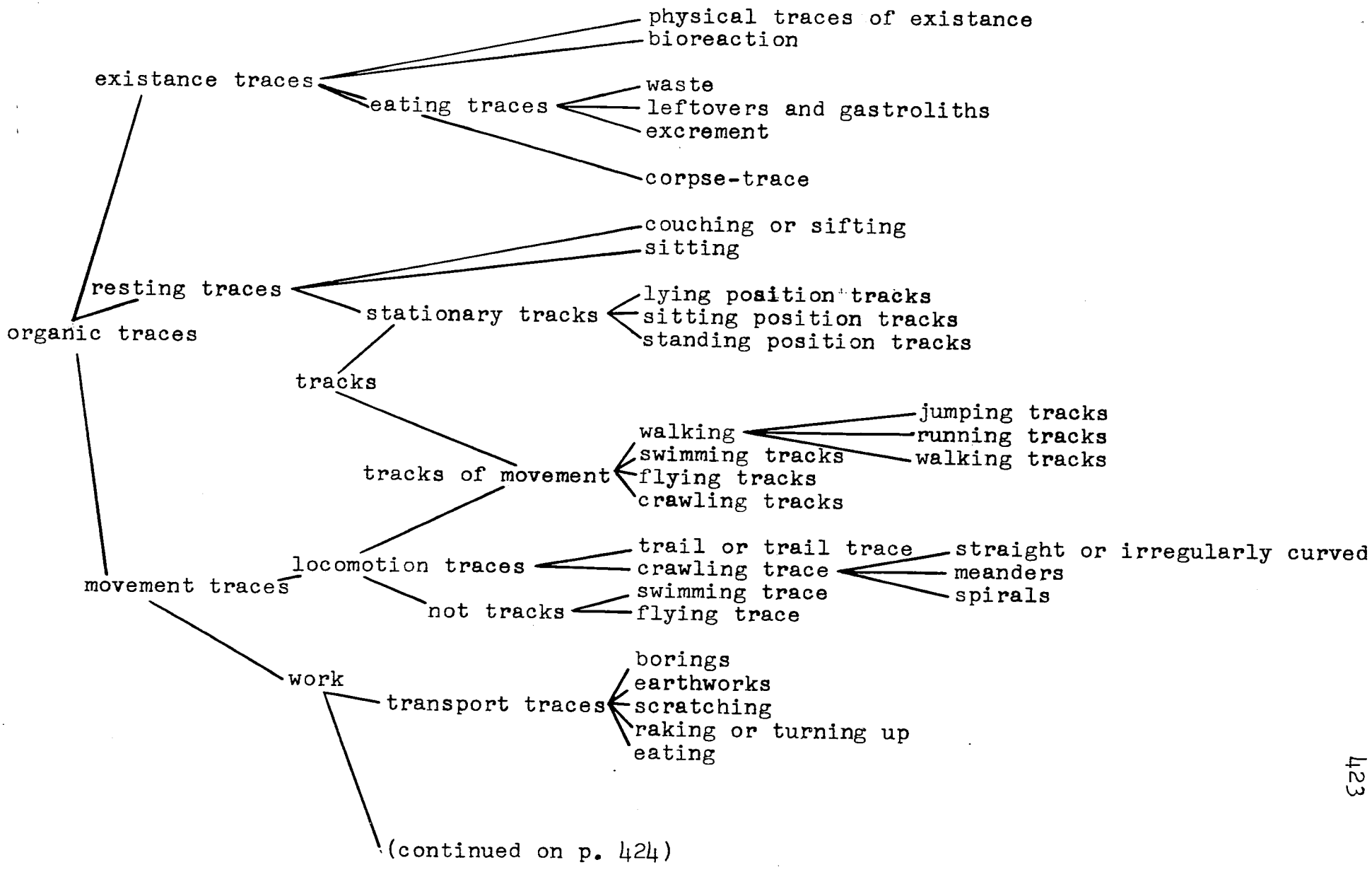
- A. tube-shaped
- B. U-shaped
- C. pocket-shaped
- D. irregular

(after Desio, 1940, p. 51)

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

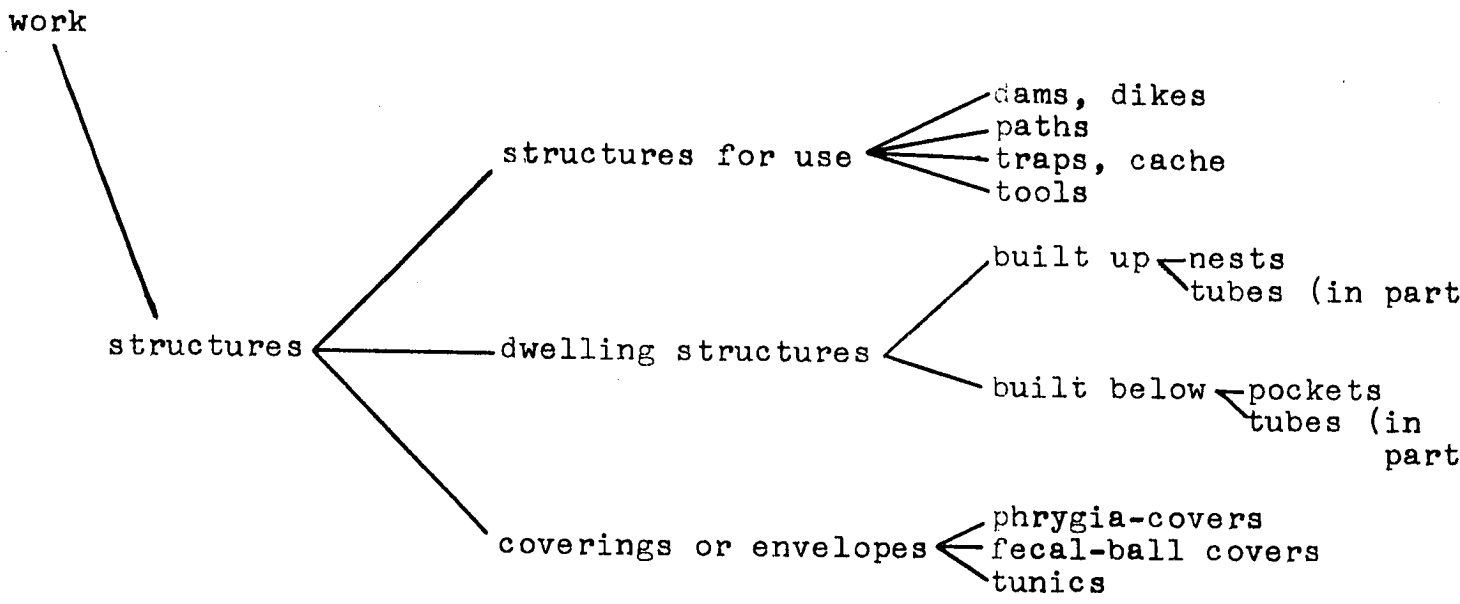
Reproduced with permission of the copyright owner. Further reproduction prohibited without permission.

Classification of Organic Traces (Krejci-Graf, 1932, p. 29)

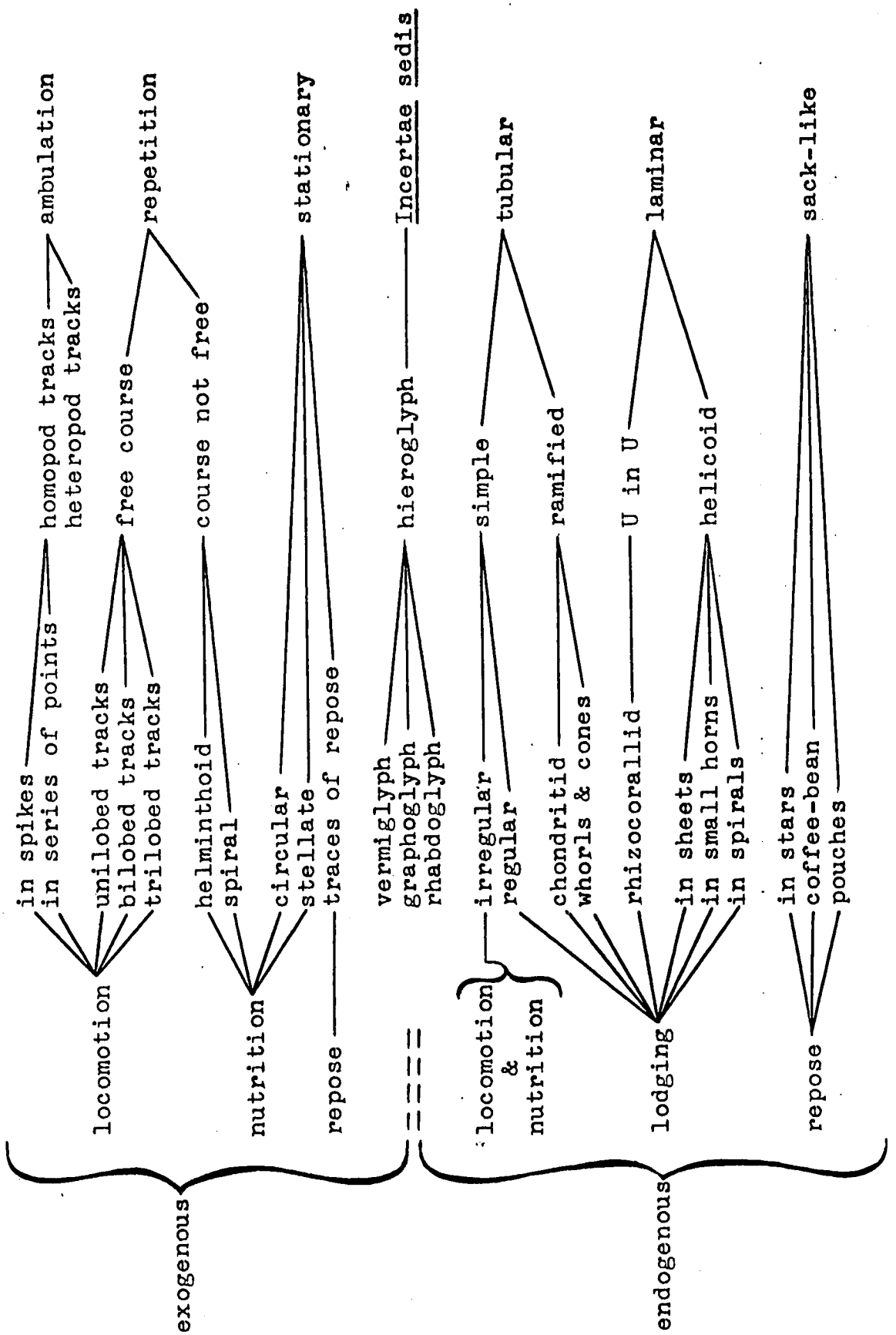


(continued on p. 424)

Classification of Organic Traces (Krejci-Graf, continued)



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



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

NOTE: The following list of references is not complete. Only the more important sources are included. Works to which casual reference is made in the text will be found in Lessertisseur (1955) or Häntzschel (1965).

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

Bibliography

Abel, O. (1935), Vorzeitliche Lebensspuren: Jena, Kramer, 644 p., 530 fig.

Ager, D. (1963), Principles of Paleoecology: New York, McGraw-Hill, 371 p., 145 fig., 6 pl.

Andree, K. (1927), Bedeutung und zeitlich Verbreitung von Arenicoloides BLANCKENHORN und verwandte Formen: Paläont. Zeitschr., vol. 8, p. 120-128.

Bagnold, R. A. (1956), The flow of cohesionless grains in fluids: Roy. Soc. London Philos. Trans., ser. A, vol. 249, p. 235-297.

Barnes, R. D. (1963), Invertebrate Zoology: Philadelphia, W. B. Saunders, 632 p., 490 fig.

Bassler, R. S. (1915), Bibliographic index of American Ordovician and Silurian fossils: United States Nat. Mus., Bull. 92, 718 p.

Bather, F. (1925), U-shaped markings on estuarine sandstone near Bleawyke: Yorkshire Geol. Soc. Proc., n.s., vol. 20, p. 185-199, pl. 14-16.

_____ (1927), Arenicoloides, a suggestion: Paläont. Zeitschr., Bd. 8, p. 128-130.

Billings, E. (1865), Paleozoic Fossils, vol. 1: Geol. Survey of Canada, 426 p., 401 fig.

_____ (1870), Are Protichnites and Climactichnites the tracks of trilobites?: Geol. Soc. London, Quart. Jour., vol. 26, p. 484-486.

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

_____ (1872), On some fossils from the primordial rocks of Newfoundland: Canadian Natur., n.s., vol. 6, p. 465-479, 14 fig.

Blanckenhorn, J. (1924), Über Fossil und Fährtenhorizonte im Buntsandstein Deutschlands: Deutsche Geol. Gesell., Zeit., Bd. 76, p. 269-279.

Bouček, B., and Eliáš, M. (1962), Über eine interessante Lebensspur aus dem Paläogen der tschechoslowakischen Flysch-Karpathen: Geol. Práce, Zprávy, vol 25-26, p. 145-151, pl. 7-8.

Brinkmann, R. (1960), Geologic Evolution of Europe (translated from the German by J. E. Sanders): New York, Hafner, 161 p., 64 fig., 19 pl.

Caster, K. E. (1938), A restudy of the tracks of Paramphibius: Jour. Paleont., vol 12, p. 3-60, 9 fig., 13 pl.

_____ (1942), Two siphonophores from the Paleozoic: Palaeontographica Americana, vol. 3, 34 p., 6 fig., 2 pl.

_____ (1944), Limuloid trails from the Upper Triassic (Chinle) of the Petrified Forest National Monument, Arizona: American Jour. Sci., vol. 242, p. 74-84, 2 fig., 1 pl.

_____ (1957), Problematica: in Treatise on Marine Ecology and Paleoecology, vol. 2, Paleoecology, Ladd, H. S. (ed.), Geol. Soc. America Mem. 67, p. 1025-1032.

_____ and Macke, W. B. (1952), An aglaspid merostome from the Upper Ordovician of Ohio: Jour. Paleont., vol 26, p. 753-757, 1 fig., 1 pl.

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

_____ Dalvé, E., and Pope, J. K. (1955), Elementary Guide to the Fossils and Strata of the Ordovician in the Vicinity of Cincinnati, Ohio: Cincinnati Soc. Nat. Hist., 47 p., 8 pl.

_____ and Waering, E. N. K. (1964), Upper Ordovician Eurypterids of Ohio: Palaeontographica Americana, vol. 4, p..301-358, 34 fig., pl. 43-53.

Cloud, P. E. (1960), Gas as a sedimentary and diagenetic agent: American Jour. Sci., vol. 258-A (Bradley volume), p. 35-45, 1 fig., 3 pl.

Cooper, G. A. (1957), Paleoecology of Middle Devonian of eastern and central United States: in Treatise on Marine Ecology and Paleoecology, vol. 2, Paleoecology, Ladd, H. S. (ed.), Geol. Soc. America Mem. 67, p. 249-279, 2 fig.

Cumings, E. R. (1908), The stratigraphy and paleontology of the Ordovician rocks of Indiana: Indiana Dept. Geol. and Nat. Res., Ann. Rept. 33, 401 p., 55 pl.

Dalvé, E. (1948), The Fossil Fauna of the Ordovician in the Cincinnati Region: Cincinnati, Ohio, University Museum, University of Cincinnati, 55 p.

Dawson, J. W. (1862), On the footprints of Limulus as compared to Protichnites of the Potsdam Sandstone: Canadian Natur., n.s., vol. 7, p. 271-277.

_____ (1864), On the fossils of the genus Rusophycus: Canadian Natur., n.s., vol. 1, p. 363-367, 4 fig.

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

_____ (1865), On the structure of certain organic remains in the Laurentian Limestones of Canada: Geol. Soc. London, Quart. Jour., vol. 21, p. 51-59, pl. 6-7.

_____ (1890), On burrows and tracks of invertebrate animals in Palaeozoic rocks, and other markings: Geol. Soc. London, Quart. Jour., vol. 46, p. 595-617, 19 fig.

Delgado, J. F. N. (1908), Système Silurique du Portugal. Étude de stratigraphie paléontologique: Serv. Geol. Portugal, Mem., ser. 4, 245 p., 8 pl.

_____ (1910) (ouvrage posthume), Terrains paléozoiques du Portugal. Et de sur les fossiles des schistes à Néréites de San Domingos et des schistes à Néréites et à Graptolites de Barrancos: Serv. Geol. Portugal, vol. 56, 68 p., 51 pl.

Desio, A. (1940), Vestigia problematiche paleozoiche della Libia: Mus. Libico Storia Naturele, Ann., vol. 2, p. 47-92, 13 pl.

_____ (1950), Sulla nomenclatura della vestigia problematische fossili: Italiano Pal. e. Strat., Riv., vol. 56, p. 1-5.

Dzulinski, S., and Sanders, J. E. (1959), Bottom marks on firm lutite substratum underlying turbidite beds (abs.): Geol. Soc. America Bull., vol. 70, p. 1594.

_____ (1962), Current marks on firm mud bottoms: Connecticut Acad. of Arts and Sci., Trans., vol. 42, p. 57-96, 7 fig., 22 pl.

Faul, H. (1951), The naming of fossil footprints "species": Jour. Paleont., vol. 25, p. 409.

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

Fenneman, N. M. (1916), Geology of Cincinnati and vicinity: Ohio Geol. Survey, ser. 4, bull. 19, 207 p., 59 fig., 12 pl.

Fenton, C. L., and Fenton, M. A. (1934a), Arthraria-like markings made by annelids and snails: Pan-American Geol., vol. 61, p. 264-266, 1 fig.

_____ (1934b), Scolithus as a fossil phoronid: Pan-American Geol., vol. 61, p. 341-348, 1 fig., 1 pl.

_____ (1937a), Archaeonassa, Cambrian snail trails and burrows: American Midland Natur., vol. 18, p. 454-456, 1 fig., 1 pl.

_____ (1937b), Trilobite nests and feeding burrows: American Midland Natur., vol. 18, p. 446-451, 6 fig.

Fisher, D. W. (1960), Correlation of the Silurian rocks in New York State: New York State Mus. and Sci. Geol. Survey Map and Chart Ser., no. 1.

Flower, R. H. (1955), Trails and tentacular impressions of orthoconic cephalopods: Jour. Paleont., vol. 29, p. 857-867, 4 fig.

Foerste, A. F. (1903), The Richmond Group along the west side of the Cincinnati Anticline in Indiana and Kentucky: American Geol., vol. 31, p. 333-335, pl. 20-22.

_____ (1914), Notes on the Lorraine faunas of New York and the Province of Quebec: Denison Univ. Sci. Lab., Bull., vol. 17, p. 247-339, pl. 1-5.

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

Ford, J. (1965), Bedrock Geology of Southwestern Hamilton County, Ohio: (unpublished Ph.D. dissertation, Ohio State University).

Fox, W. T. (1962), Stratigraphy and paleoecology of the Richmond Group in southeastern Indiana: Geol. Soc. America Bull., vol. 73, p. 621-642, 10 fig.

Fuchs, T. (1895), Studien über Fucoiden und Hieroglyphen: Akad. Wiss. Wien, math.-nat. Kl., Denkschr., Bd. 62, p. 369-448, 9 pl.

Gilbert, G. K. (1914), The transportation of debris by running water: United States Geol. Survey Prof. Paper 86, 263 p., 83 tables, 89 fig.

Glaessner, M. F. (1957), Palaeozoic arthropod trails from Australia: Paläont. Zeitschr., Bd. 31, p. 103-109, pl. 10-11.

Goldring, R. (1962), The trace fossils of the Baggy Beds (Upper Devonian) of North Devon, England: Paläont. Zeitschr., Bd. 36, p. 232-251, 5 fig.

Hall, J. (1847), Nat. Hist. New York, Palaeont. New York: Albany, vol. 1, 338 p., 88 pl.

____ (1851), New genera of fossil corals: American Jour. Sci., ser. 2, vol. 11, p. 398-401.

____ (1852), Nat. Hist. New York, Palaeont. New York: Albany, vol. 2, 362 p., 85 pl.

Häntzschel, W. (1939), Die Lebensspuren von Corophium volutator (PALLAS) und ihre paläontologische Bedeutung: Senckenbergiana, Bd. 21, p. 215-227, 7 fig.

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

_____ (1941), Gleichlauf und Verzweigung von Fährten der Strandschnecke (Littorina): Nat. und Volk, Bd. 71, p. 117-120, fig. 1-2.

_____ (1962), Trace-fossils and Problematica: in Treatise on Invertebrate Paleont., Moore, R. C. (ed.), pt. W, Miscellanea, Lawrence, Kansas, University of Kansas Press, p. 177-245, fig. 109-149.

_____ (1965), Vestigia invertebratorum et Problematica: Fossilium Catalogus, 1. Animalia, s'Gravenhage, Junk, 142 p.

Hjulstrom, F. (1939), Transportation of detritus by moving water: in Recent Marine Sediments, Trask, P. D. (ed.), Tulsa, American Assoc. Pet. Geol., p. 5-31.

Hofmann, H. J. (1964), Mud cracks in the Ordovician Maysville Group: Jour. Geol., vol. 72, p. 638-641, 1 fig., 1 pl.

_____ (1965, in press), Deformational structures near Cincinnati, Ohio: Geol. Soc. America Bull.

Howell, B. F. (1943), Burrows of Skolithos and Planolites in the Cambrian Hardyston Sandstone at Reading, Pennsylvania: Wagner Free Inst. Sci., Public., vol. 3, p. 3-33, pl. 1-8.

_____ (1957), New Cretaceous scoleciform annelid from Colorado: Palaeont. Soc. India, Jour., vol. 2, p. 149-152, pl. 16.

Hundt, R. (1931), Eine Monographie der Lebensspuren des Unteren Mitteldevons Thüringens: Leipzig, 68 p., 128 fig.

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

Hyde, D. (1959), A structural and stratigraphic study of the Fairview-McMillan formational contact in the Cincinnati area: Compass, vol. 36, p. 161-172, 4 fig.

Imbrie, J., and Newell, N. (ed.) (1964), Approaches to Paleoecology: New York, John Wiley and Sons, 432 p.

James, J. F. (1884), The fucoids of the Cincinnati Group, pt. 1: Cincinnati Soc. Nat. Hist., Jour., vol 7, p. 124-132, pl. 5-6.

_____ (1885), The fucoids of the Cincinnati group, pt. 2: Cincinnati Soc. Nat. Hist., Jour., vol. 7, p. 151-166, pl. 8-9.

_____ (1886), Remarks on some markings on the rocks of the Cincinnatian Group, described under the names of Ormathichnus and Walcottia: Cincinnati Soc. Nat. Hist., Jour., vol. 8, p. 160-163.

_____ (1891), Manual of the paleontology of the Cincinnati Group, pt. 1: Cincinnati Soc. Nat. Hist., Jour., vol. 14, p. 45-72, 6 fig.

_____ (1892), Studies in problematic organisms, the genus Scolithus: Geol. Soc. America Bull., vol. 3, p. 32-44, 15 fig.

James, U. P. (1878), Descriptions of newly discovered species of fossils and remarks on others from the Lower and Upper Silurian rocks of Ohio: The Paleontologist, no. 2, p. 9-16.

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

_____ (1879), Description of new species of fossils and remarks on some others from the Lower and Upper Silurian rocks of Ohio: The Paleontologist, no. 3, p. 17-24.

_____ (1881), Contributions to paleontology; fossils of the Lower Silurian formation; Ohio, Indiana and Kentucky: The Paleontologist, no. 5, p. 33-44.

Johnson, R. G. (1964), The community approach to paleoecology: in Approaches to Paleoecology, Imbrie, J., and Newell, N. (ed.), New York, John Wiley and Sons, p. 107-134, 6 tables.

Kolesch, K. (1921), Beitrag zur Stratigraphie des mittleren Buntsandsteins im Gebiete des Blattes Kohla (S.-A.): Preussen geol. Landesanst., Bd. 40, p. 307-382, 15 fig.

Krejci-Graf, K. (1932), Definition der Begriffe Marken, Spuren, Fährten, Bauten, Hieroglyphen und Fucoiden: Senckenbergiana, Bd. 14, p. 19-39.

Kuenen, P. H. (1957), Sole markings of graded graywacke beds: Jour. Geol., vol. 65, p. 231-258, 22 fig., 3 pl.

_____ and Carozzi, A. (1953), Turbidity currents and sliding in the geosynclinal basins of the Alps: Jour. Geol., vol. 61, p. 363-373, 3 fig., 2 pl.

Lebesconte, P. (1883), Présentation à la société des oeuvres posthumes de Marie Rouault par P. Lebesconte, suivies d'une note sur les Cruziana et Rhysophycus: Soc. Geol. France, Bull., ser. 3, vol. 11, p. 466-472.

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

_____ (1886), Constitution générale du massif breton comparée à celle du Finisterre: Soc. Geol. France, Bull., ser. 3, vol. 14, p. 776-820, pl. 34-36.

Lesquereux, L. (1874), On the remains of land plants in the Lower Silurian: American Jour. Sci., ser. 3, vol. 7, p. 31-34.

_____ (1878), Land plants, recently discovered in the Silurian rocks of the United States: American Philos. Soc., Proc., vol. 17, p. 163-173, pl. 4.

Lessertisseur, J. (1955), Traces fossiles d'activité animale et leur significance paléobiologique: Soc. Geol. France, Mem. 74, 150 p., 68 fig., 11 pl.

Linck, O. (1949), Lebens-Spuren aus dem Schilfsandstein (Mittl. Keuper km 2) NW-Württembergs und ihre Bedeutung für die Bildungsgeschichte der Stufe: Ver. vaterl. Naturkd. Württemberg, Jahresh., Bd. 97-101, p. 1-100, 5 fig., 8 pl.

Magdefrau, K. (1932), Über Phycodes circinatum Reinh. Richter aus dem Thüringischen Ordovicium: Neues Jahrb. Mineral., Geologie, u. Paläont., Beil-Bd. 72, p. 259-282, 6 fig., pl. 10-11.

Miller, S. A. (1874), [Notes and descriptions of Cincinnatian fossils]: Cincinnati Quart. Jour. Sci., vol. 1, p. 4-7, 3 fig.

_____ (1875), Some new species of fossils from the Cincinnati Group and remarks upon some described forms: Cincinnati Quart. Jour. Sci., vol. 2, p. 349-355, 3 fig.

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

_____ (1879), Description of twelve new fossil species and remarks upon others: Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 104-118, pl. 9-10.

_____ (1880), Silurian ichnolites, with definitions of new genera and species. Note on the habit of some fossil annelids: Cincinnati Soc. Nat. Hist., Jour., vol. 2, p. 217-229, 2 pl.

_____ and Dyer, C. B. (1878a), Contributions to palaeontolgy, no. 1: Cincinnati Soc. Nat. Hist., Jour., vol. 1, p. 24-39, 2 pl.

_____ (1878b), Contributions to palaeontology, no. 2: Cincinnati, Ohio, private publication, 11 p., 2 pl.

Moore, R. C., Lalicker, C. G., and Fischer, A. G. (1952), Invertebrate Fossils: New York, McGraw-Hill, 766 p., 451 fig.

_____ Harrington, H. J., and Stubblefield, C. J. (1959), Morphological terms applied to trilobites: in Treatise on Invertebrate Paleontology, Moore, R. C. (ed.), pt. O, Arthropoda, Lawrence, Kansas, University of Kansas Press, p. 117-127.

Müller, A. H. (1962), Zur Ichnologie, Taxiologie und Ökologie fossiler Tiere: Freiberger Forschungsh., Bd. 151, p. 5-49, 21 fig.

Nathorst, A. G. (1881), Om spar af nagra evertebrerade djur M.M. och deras paleontologiska betydelse. (Mémoire sur quelques traces d'animaux sans vertèbres etc. et de leur portée paléontologique.): Kgl. Svenska Vetensk. Akad. Handl., vol. 18, 104 p., 11 pl.

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

_____ (1883), Quelques remarques concernant les algues fossiles: Soc. Geol. France, Bull., ser. 3, vol. 11, p. 452-455.

_____ (1886), Nouvelles observations sur des traces d'animaux et autres phénomenes d'origine purement mécanique décrits comme "Algues fossiles": Kgl. Svenska Vetensk. Akad. Handl., vol. 21, 58 p., 14 fig., 5 pl.

Newberry, J. S. (1874), On the so-called land plants from the Lower Silurian of Ohio: American Jour. Sci., ser. 3, vol. 8, p. 110-113, 2 fig.

Nickles, J. M. (1902), The geology of Cincinnati: Cincinnati Soc. Nat. Hist., Jour., vol. 20, p. 49-100,

_____ (1903), The Richmond Group in Ohio and Indiana and its subdivisions, with a note on the genus Strophomena and its type: American Geol., vol. 32, p. 202-218.

Nowak, W. (1959), Palaeodictyum in the Flysch Carpathians: Kwartaln. Geolog., vol. 3, p. 103-125, 9 fig., 6 pl.

Öpik, A. (1929), Studien über das estonische Unterkambrium, pt. 1-4: Geol. Inst. Univ. Tartu, Public. 15, 56 p., 7 fig., 4 pl.

____ (1959), Tumblagooda Sandstone trails and their age: Commonwealth Australia, Dept. Nat. Devel., Bur. Mines, Geol., Geophy., rept. 38, p. 3-20, 19 fig.

Orton, E. (1873), Fossils of the Cincinnati Group: in Meek, F. B., Geol. Survey of Ohio, Rept., vol. 1, Geol. and Paleont., pt. 2, Paleont., p. 1-175, 14 pl.

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

Owen, R. (1852), Description of the impressions and footprints of the Protichnites from the Potsdam Sandstone of Canada: Geol. Soc. London, Quart. Jour., vol. 8, p. 214-225.

Petersen, C. G. J. (1913), Valuation of the sea, pt. 2, The animal communities of the sea bottom and their importance for marine zoogeography: Danish Biol. Stat., Rept., vol. 21, 44 p., 6 pl., 3 charts.

Raasch, G. O. (1939), Cambrian Merostomata: Geol. Soc. America Spec. Paper, no. 19, 146 p., 21 pl.

Radwański, A., and Roniewicz, P. (1963), Upper Cambrian trilobite ichnocoenosis from Wielka Wiśiówka (Holy Cross Mountains, Poland): Acta Pal. Polonica, vol. 8, p. 259-280, pl. 1-10.

Raymond, P. E. (1920), The appendages, anatomy and relationships of trilobites: Connecticut Acad. Arts Sci., Mem. 7, 169 p., 11 pl.

Reineck, H. -E. (1955), Marken, Spuren und Fährten in den Waderner Schichten (ro) bei Martinstein (Nahe): Neues Jahrb. Geologie u. Paläont., Abh., Bd. 101, p. 75-90, pl. 7-11.

Reis, O. M. (1910), Zur Fukoidenfrage: k. k. geol. Reichsanst., Bd. 59, p. 615-638, pl. 17.

Richter, R. (1920), Ein devonischer "Pfeifenquarzit" verglichen mit der heutigen "Sandkoralle" (Sabellaria, Annelidae): Senckenbergiana, Bd. 2, p. 215-235, 6 fig.

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

_____ (1921), Scolithus, Sabellarifex und Geflechtquarzite: Senckenbergiana, Bd. 3, p. 49-52

_____ (1924), Flachseebeobachtungen zur Paläontologie und Geologie, VII-XI: Senckenbergiana, Bd. 6, p. 119-165, 8 fig.

_____ (1926), Flachseebeobachtungen zur Paläontologie und Geologie, XII-XIV: Senckenbergiana, Bd. 8, p. 200-240 pl. 3.

_____ (1927), Die fossilen Fährten und Bauten der Würmer, ein Überblick über ihre biologischen Grundforman und deren geologische Bedeuntung: Paläont. Zeitschr., Bd. 9, p. 193-240, pl. 1-4.

_____ (1931), Tierwelt und Umwelt im Hunsrückschiefer zur Entstehung eins schwarzen Schlammsteins: Senckenbergiana, Bd. 13, p. 299-342, 13 fig.

_____ (1937), Marken und Spuren aus allen Zeiten, pt. 1, Wühl-Gefüge durch kot-gefüllte Tunnel (Planolites montanus n. sp.) aus dem Ober-Karbon der Rhur: Senckenbergiana, Bd. 19, p. 151-159, 5 fig.

_____ (1941), Marken und Spuren im Hunsrückschiefer, pt. 3, Fährten als Zeugnisse des Lebens auf dem Meeres-Grunde: Senckenbergiana, Bd. 23, p. 218-260, 17 fig.

Ricketts, E. F., and Calvin, J. (1952), Between Pacific Tides (revised by Hedgpeth, J. W.): Stanford, California, Stanford University Press, 502 p., 134 fig., 46 pl.

Ruedemann, R. (1908), Graptolites of New York, pt. 2: New York State Mus. Mem., no. 11, 583 p., 482 fig., 31 pl.

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

Sacco, F. (1939), Paleodictyon: Roy. Accad. Sci. Torino, Mem. 69, p. 267-285, pl. 1-2.

Saporta, G. de (1881), L'évolution du règne végétal, Les Cryptogames: Paris, Masson.

_____ (1882), A propos des algues fossiles: Paris, Masson, 82 p., 9 pl.

_____ (1884), Les organismes problématiques des anciennes mers: Paris, Masson, 100 p., 13 pl.

_____ (1886), Nouveaux documents relatifs à des fossiles végétaux et à des traces d'invertébrés associés dans les anciennes mers: Soc. Geol. France, Bull., ser. 3, vol. 14, p. 407-430, pl. 18-22.

Sarle, C. J. (1906), Arthrophycus and Daedalus of burrow origin: Rochester Acad. Sci., Proc., vol. 4, p. 203-210, 4 fig.

Schäfer, W. (1962), Aktuo-Paläontologie: Frankfurt, Kramer, 666 p., 277 fig., 36 pl.

Schaffer, F. X. (1928), Hormosiroidea florentina n.g. n.sp., ein Fucus aus der Kreide der Umgebung von Florenz: Paläont. Zeitschr., Bd. 10, p. 212-215, 3 fig.

Scotford, D. M. (1965), Petrology of the Cincinnatian Series shales and environmental implications: Geol. Soc. America Bull., vol. 76, p. 193-222, 7 fig., 14 tables.

Seilacher, A. (1951), Zur Einteilung und Deutung fossiler Lebensspuren: (unpublished Ph.D. dissertation, Tübingen University).

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

_____ (1951), Der Rohrenbau von Lanice conchilega. Ein Beitrag zur Deutung fossiler Lebensspuren: Senckenbergiana, Bd. 32,, p. 267-280, 7 fig.

_____ (1953a), Über die Methoden der Palichnologie, Studien zur Palichnologie, no. 1: Neues Jahrb. Geologie u. Paläont., Abh., Bd. 96, p. 421-452, 10 fig. 1 pl.

_____ (1953b), Über die Methoden der Palichnologie, Die fossilien Ruhespuren (Cubichnia): Neues Jahrb. Geologie u. Paläont., Abh., Bd. 98, p. 87-124, 5 fig., 5 pl.

_____ (1954), Die geologische Bedeutung fossiler Lebensspuren: Deutsche Geol. Gesell. Zeitschr., Bd. 105, p. 214-227, 3 fig., pl. 7-8.

_____ (1955), Spuren und Lebensweise der Trilobiten; Spuren und Fazies im Unterkambrium: in Schindewolf, O. H., and Seilacher, A., Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan): Akad. Wiss. Lit. Mainz, math.-nat. Kl., Abh., no. 10, p. 86-143, fig. 1-11, pl. 16-27.

_____ (1957), An-aktualistisches Wattenmeer?: Paläont. Zeitschr., Bd. 31, p. 198-206, 2 fig., pl. 22-23.

_____ (1958), Zur ökologischen Charakteristik von Flysch und Molasse: Eclogae Geologica Helvetiae, vol. 51, p. 1062-1078, 1 fig.

_____ (1959), Vom Leben der Trilobiten: Die Naturwissenschaften, Hft. 12, p. 389-393, 5 fig.

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

_____ (1960), Lebensspuren als Leitfossilien: Geol. Rundschau, Bd. 49, p. 41-50, 3 fig. 2 pl.

_____ (1962a), Paleontological studies on turbidite sedimentation and erosion: Jour. Geol., vol. 70, p. 228-234, 1 fig., 2 pl.

_____ (1962b), Form und Funktion des Trilobiten-Daktylus: Paläont. Zeitschr. (Hermann Schmidt-Festband), p. 218-227, 2 fig., pl. 24-25.

_____ (1964a), Biogenic sedimentary structures: in Approaches to Paleoecology, Imbrie, J., and Newell, N. (ed.), New York, John Wiley and Sons, p. 296-316, 7 fig.

_____ (1964b), Sedimentological classification and nomenclature of trace fossils: Sedimentology, vol. 3, p. 253-256.

Shimer, H. W., and Shrock, R. R. (1944), Index Fossils of North America: New York, John Wiley and Sons, 837 p., 303 pl.

Shrock, R. R., (1948), Sequence in Layered Rocks: New York, McGraw-Hill, 507 p., 397 fig.

Simpson, S. (1957), On the trace fossil Chondrites: Geol. Soc. London, Quart. Jour., vol. 112, p. 475-499, 2 fig., pl. 21-24.

Smith, J. (1893), Peculiar U-shaped tubes in sandstone near Crawfurdland Castle and in Gowkha Quarry, near Kilwinning: Geol. Soc. Glasgow, Trans., vol. 9, p. 289-292, pl. 10.

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

Sörgel, W. (1924), Beiträge zur Geologie von Thüringen, Teil 2, Spuren mariner Würmer im mittleren Buntsandstein (Bausandstein) und im unteren Muschelkalk Thüringens: Neues Jahrb. Geologie u. Paläont., Beil-Bd. 44, p. 510-549, 7 fig., pl. 19-20.

Størmer, L. (1939), Studies on trilobite morphology, pt. 1, The thoracic appendages and their phylogenetic significance: Norsk geol. tidsskr., vol. 19, p. 143-273, fig. 1-35, pl. 1-12.

_____ (1951), Studies on trilobite morphology, pt. 3, The ventral cephalic structures with remarks on the zoological position of the trilobites: Norsk geol. tidsskr., vol. 29, p. 108-158, 14 fig., pl. 1-4.

Tauber, A. F. (1949), Paläobiologische Analyse von Chondrites furcatus Sternberg: Geol. Bundesanst., Jahrb., Bd. 93, p. 141-154, 3 fig.

Thorson, G. (1957), Bottom communities: in Treatise on Marine Ecology and Paleoecology, vol. 1, Ecology, Hedgpeth, J. W. (ed.), Geol. Soc. America Mem. 67, p. 461-534, 20 fig.

Ulrich, E. O. (1880), Catalogue of Fossils occurring in the Cincinnati Group of Ohio, Indiana, and Kentucky: Cincinnati, Barclay, 26 p.

_____ (1893), New and little known Lamellibranchiata from the Lower Silurian rocks of Ohio and adjacent states: in Geol. Survey Ohio, Rept., vol. 7, p. 626-693, pl. 45-56.

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

Vialov, O. S. (1964), Network structures similar to those made by tadpoles: Jour. Sed. Petrology, vol. 34, p. 664-666, 1 fig.

_____ and Golev, B. T. (1960), Zur Systematike von Paleodictyon: Akad. Nauk USSR, Doklad., vol. 134, p. 175-178, 1 fig.

Walcott, C. D. (1881), The trilobite: New and old evidence relating to its organization: Mus. Comp. Zool., Bull., vol. 8, p. 192-224, pl. 1-6.

_____ (1883), Fossils of the Utica Slate: Albany Inst. Trans., vol. 10, p. 18-38, pl. 1-2.

_____ (1884), The appendages of the trilobite: Science, vol. 3, p. 276-279, fig. 1-3.

_____ (1889), Descriptive notes of new genera and species from the Lower Cambrian or Olenellus zone of North America: United States Nat. Mus., Proc., vol. 12, p. 33-46.

_____ (1899), Pre-Cambrian fossiliferous formations: Geol. Soc. America Bull., vol. 10, p. 199-244, 7 fig., pl. 22-28.

_____ (1918), Appendages of trilobites: Smithson. Misc. Coll., vol. 67, p. 115-216, pl. 14-42.

Wells, G. P. (1945), The mode of life of Arenicola marina: Marine Biol. Assoc., Jour., vol. 26, p. 170-207.

Weimer, R. J., and Hoyt, J. H. (1964), Burrows of Callianassa major Say, geologic indicators of littoral and shallow neritic environments: Jour. Paleont., vol. 38, p. 761-767, 2 fig., 2 pl.

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

Weiss, M. P., and Norman, C. E. (1960), The American Ordovician standard, pt. 2, Development of stratigraphic classification of Ordovician rocks in the Cincinnati region: Geol. Survey Ohio Information Circ., no. 26, 14 p., 1 fig., 1 chart.

_____ and Sweet, W. C. (1964), Kope Formation (Upper Ordovician) Ohio and Kentucky: Science, vol. 145, p. 1296-1302, 1 table, 1 fig.

_____ Edwards, W. R., Norman, C. E., and Sharp, E. R. (1965), The American Upper Ordovician standard, pt. 7, Stratigraphy and petrology of the Cynthiana and Eden Formations of the Ohio Valley: Geol. Soc. American Spec. Paper, no. 81, 76 p., 5 fig., 7 tables, 8 pl.

Westergård, A. H. (1931), Diplocraterion, Monocraterion and Scolithus from the Lower Cambrian of Sweden: Sverige geol. Unders., ser. C, Avh. och upps., no. 372 (=Årsbok, vol. 25, no. 5), 25 p., 10 pl.

Willard, B. (1935), Chemung tracks and trails from Pennsylvania: Jour. Paleont., vol. 9, p. 43-56, pl. 10-11.

Wilson, A. E. (1948), Miscellaneous classes of fossils, Ottawa Formation, Ottawa-St. Lawrence Valley: Canada Dept. Mines Resourc., Geol. Survey Bull., vol. 11, 116 p., 4 fig., 28 pl.

Zenkevitch, L. A., and Birstein, J. A. (1956), Studies of the deep water fauna and related problems: Deep-Sea Research, vol. 4, p. 54-64, 8 tables, 4 fig.

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

Text Figures

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

Explanation of Text Figure 1

Figure

1. Columnar section of the Upper Ordovician strata exposed near Cincinnati, Ohio . . . . . p. 10

This section portrays the "traditional" nomenclature applied in the Cincinnati area. It is acknowledged that the members are not recognized as valid lithostratigraphic by the most recent North American Code of Stratigraphic Nomenclature.

(from Caster, Dalvé, and Pope, 1955, fig. 3)

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

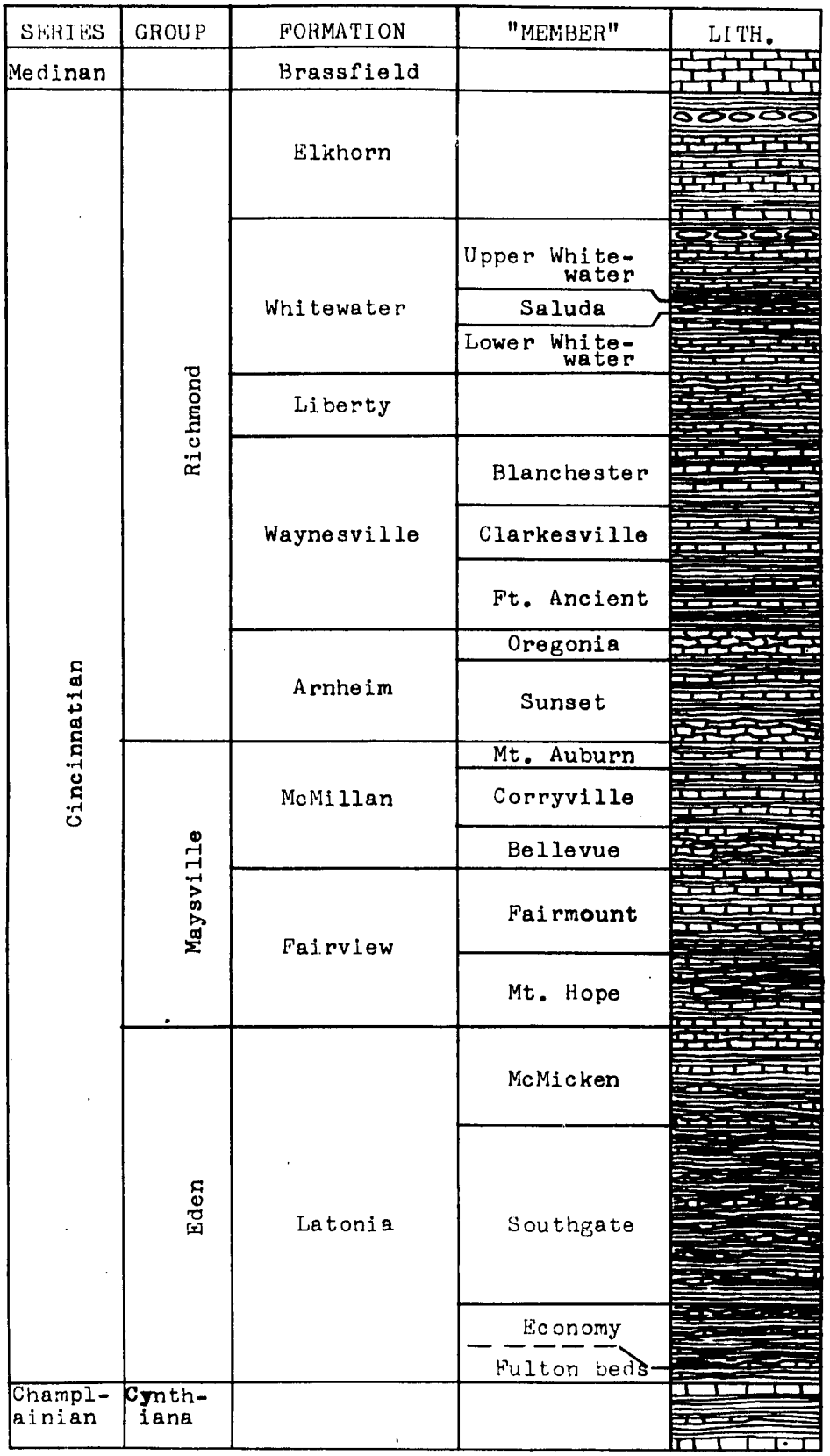


Figure 1

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

Explanation of Text Figures 2,3

Figure

2. Ethologic classification of organic traces proposed by Seilacher (1953). . . . . p. 50

The outside circle contains the five major ethologic catagories (Cubichnia, Pascichnia, etc.) which are based primarily on the type of behavior exhibited by the organism. This behavior is in turn reflected in the geometry of the trace. However, in practice it is difficult to place some traces in this classification. (See the discussion of Palaeophycus). The term "Body Fossils" in the center of the diagram demonstrates that trace fossils can not be separated from molds, casts, and other hard part remains of organisms. (translated from Seilacher, 1953, fig. 6)

3. Ethologic classification of organic traces proposed by Müller (1962). . . . . p. 50

The classification is basically similar to that of Seilacher's but is more comprehensive. Like Seilacher's this classification can be applied to both fossil and Recent traces. (translated from Müller, 1962, pl. 21)

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

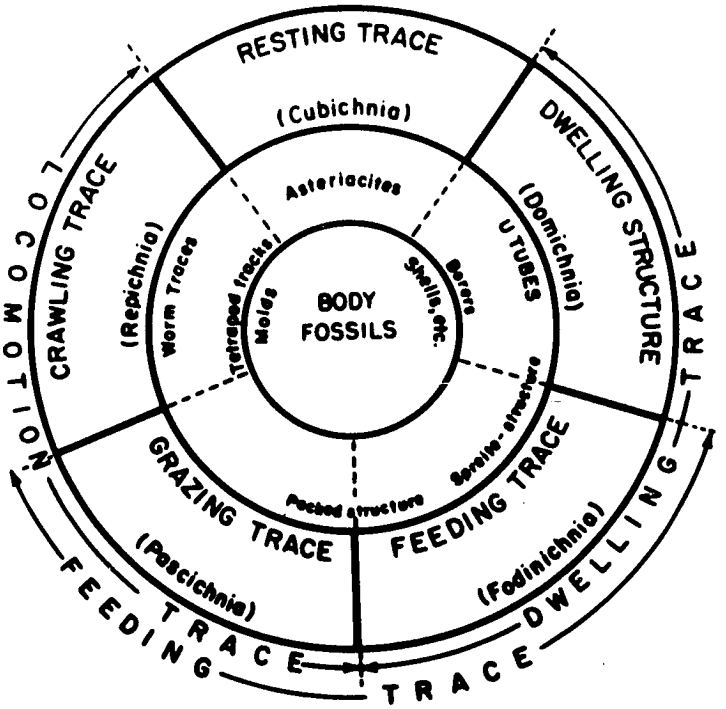


Figure 2

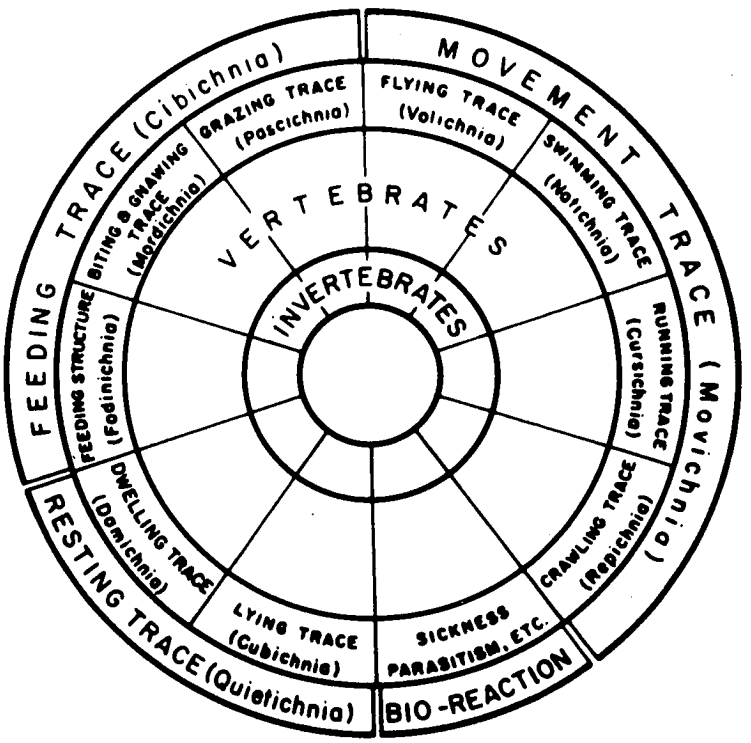


Figure 3

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

Explanation of Text Figure 4

Figure

1. Various types of preservation of trace fossils

. . . . . p. 33

The dark stippling indicates mud; the light stippling sand. The most common type of preservation encountered is convex hyporelief. Secondary casts are unknown in the Cincinnatian section.

(from Seilacher, 1964, fig. 1; reproduced with the permission of John Wiley and Sons, New York)

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

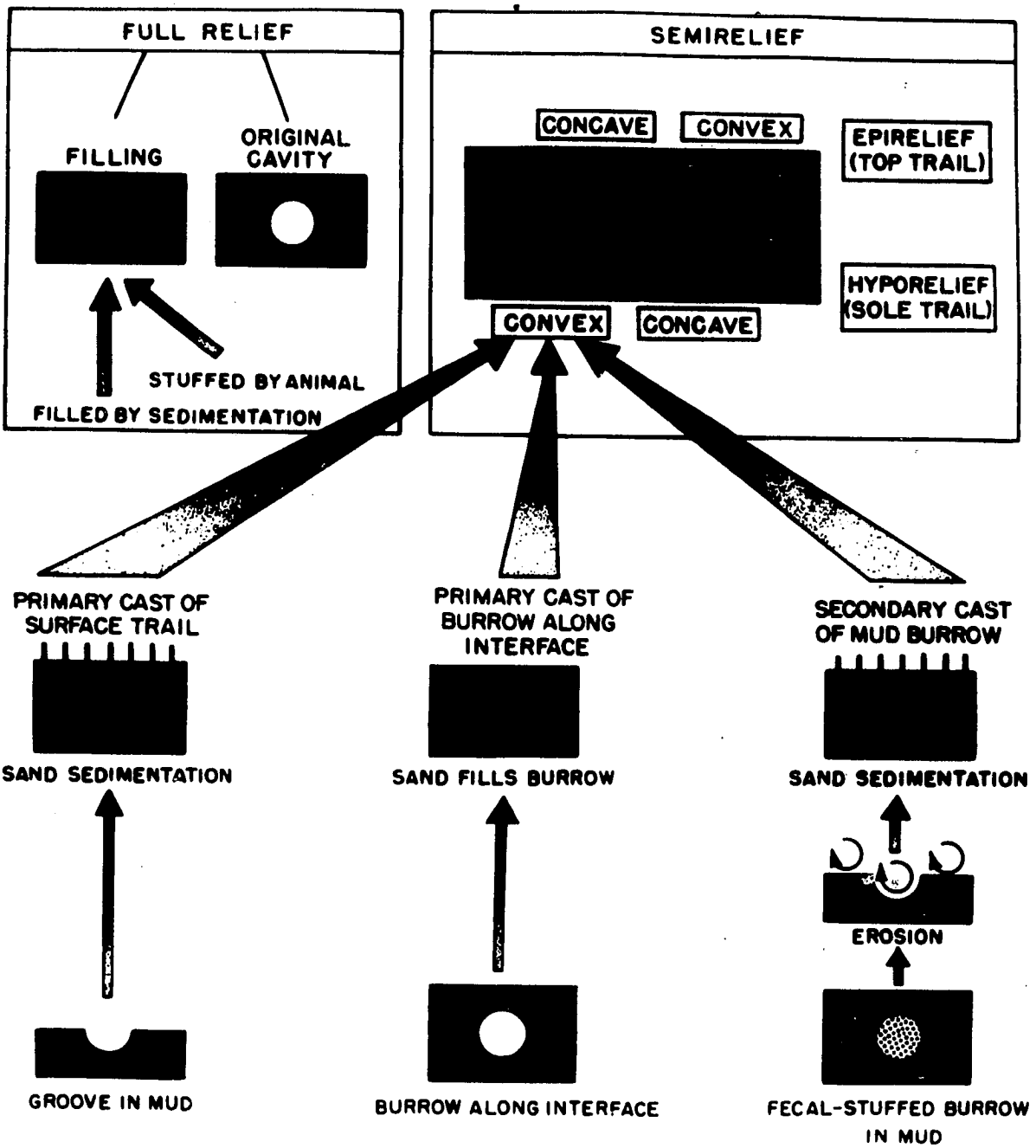


Figure 4

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

Explanation of Text Figures 5,6

Figure

5. Recent Rusophycus-like resting traces. . . . . p. 69

a. Cubichnia of the Recent polychaete Aphrodite. Note that the apex of the "V" formed by the striae is directed anteriorly.

b. Cubichnia of a nassid gastropod showing the apex also directed anteriorly.

c. Cubichnia of a Recent phyllopod. The apex of the "V" is directed posteriorly making it difficult to separate these forms from the Cubichnia of trilobites seen in fig. 5d below.

d. Cubichnia of a trilobite showing that the apex of the "V" is directed posteriorly.

(from Seilacher, 1960, fig. 1)

6. Diverse Cambrian examples of Rusophycus. . . . p. 69

A. Reconstruction of a trilobite excavating a shallow burrow.

B. Diagram showing the direction of movement of the legs in the formation of the burrow illustrated in fig. A above.

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

Explanation of Text Figure 6 continued

C. Shallow burrow where the lobes are separate throughout their entire length. X 1.5.

D. Burrow with a V-shaped outline. X 1.5.

E. Deeper, more typical, cordate burrow. X 0.5.

F. Interpretation of R. jenningsi (Fenton and Fenton, 1937) showing that the cephalon was used as a shovel.

G. R. jenningsi showing delicate striae.

H. Lateral view of fig. 6 above showing the imprints made by the cephalon (right) and the walking legs (left). X 0.5.

I. Reconstruction of a burrow from the Lower Cambrian rocks of Lugnås, Sweden.

K. Diagram of fig. I above showing that some of the walking legs moved the excavated material anteriorly whereas the remaining legs moved it posteriorly.

L. Lateral view of fig. I, K above. X 0.5.

(from Seilacher, 1959, fig. 4)

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

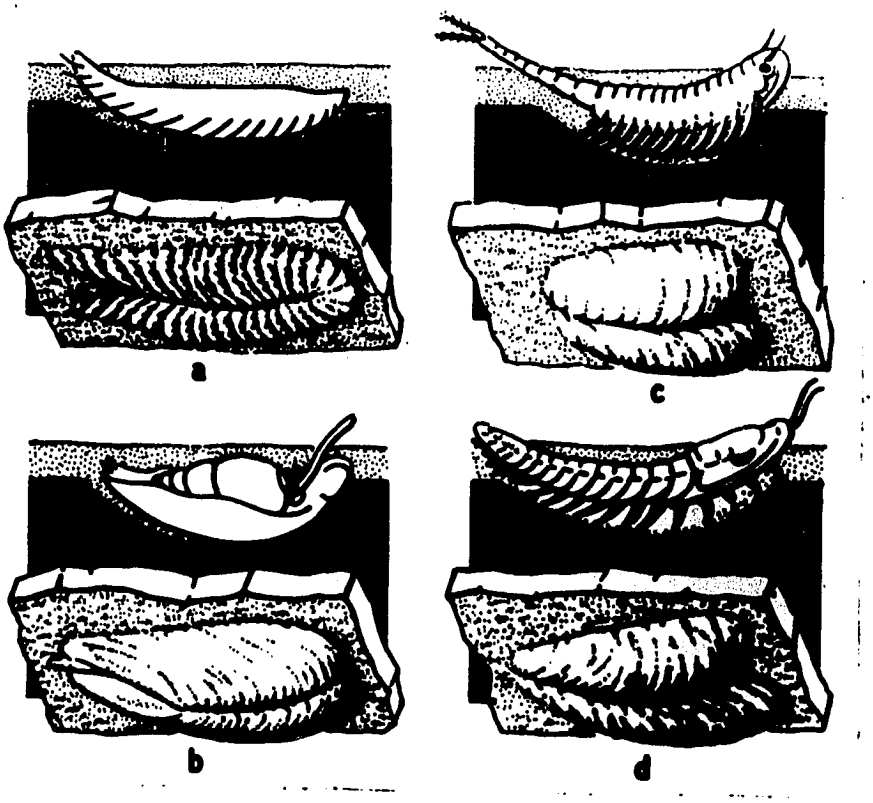


Figure 5

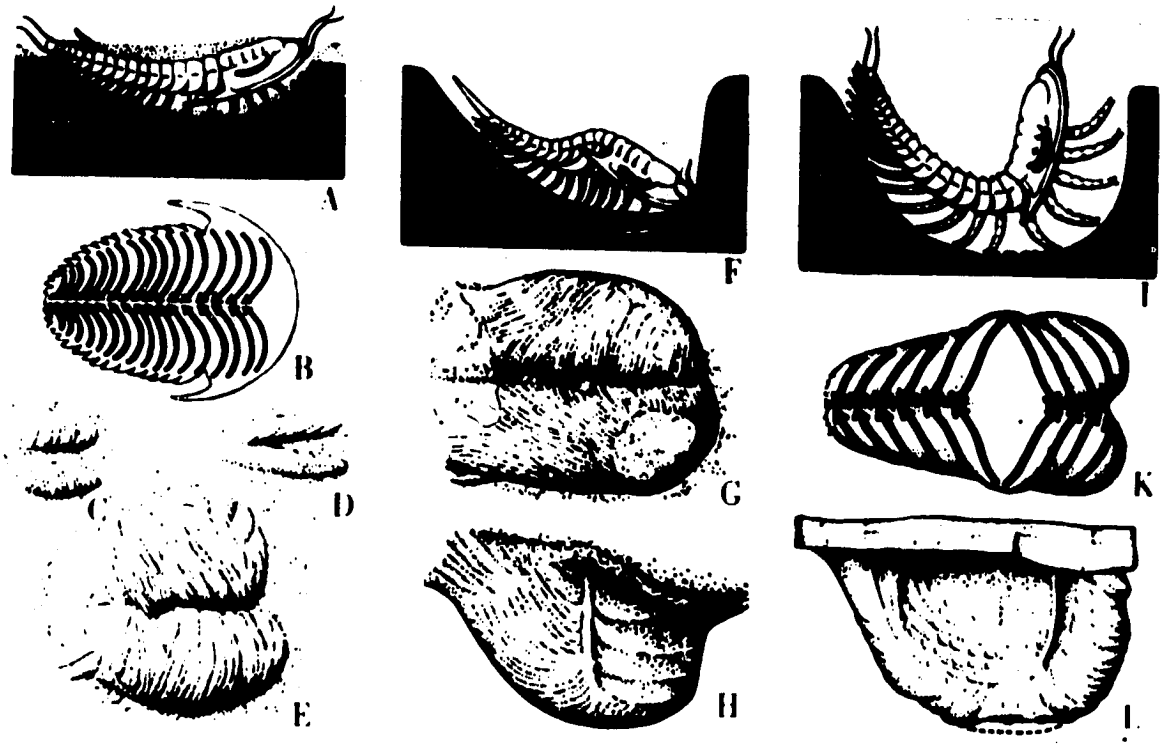


Figure 6

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

Explanation of Text Figure 7

Generalized U-tube Morphology. . . . . p. 111

A. U-plane section of a Spreite-bearing tube with a combination of descending and ascending Spreiten. Note that the descending Spreiten (solid lines) extend only to the inner margin of the arm of the U whereas the ascending Spreiten (dashed lines) extend to the outer margin.

B. Median section taken through points a-b on fig. A showing descending Spreiten only. The arcs are convex upward. If the Spreiten reflect the organisms attempt to lengthen the tube to compensate for an increase in body size one might expect the diameter of the tube to increase accordingly, as illustrated herein. However, the diameter of the Cincinnatian tubes remains constant.

C. Median section taken through points a-b on fig. A showing the superposition of ascending Spreiten over descending Spreiten. Specimens with ascending Spreiten are unknown in the Cincinnatian section.

D. Four transverse sections taken at corresponding points on fig. A. Note that the arcs of the descending Spreiten (2-3) are convex inward whereas the

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

Explanation of Text Figure 7 continued

ascending Spreiten are convex outward. A transverse section taken at the mouth of the "U" (1) reveals no trace of the Spreiten.

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

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

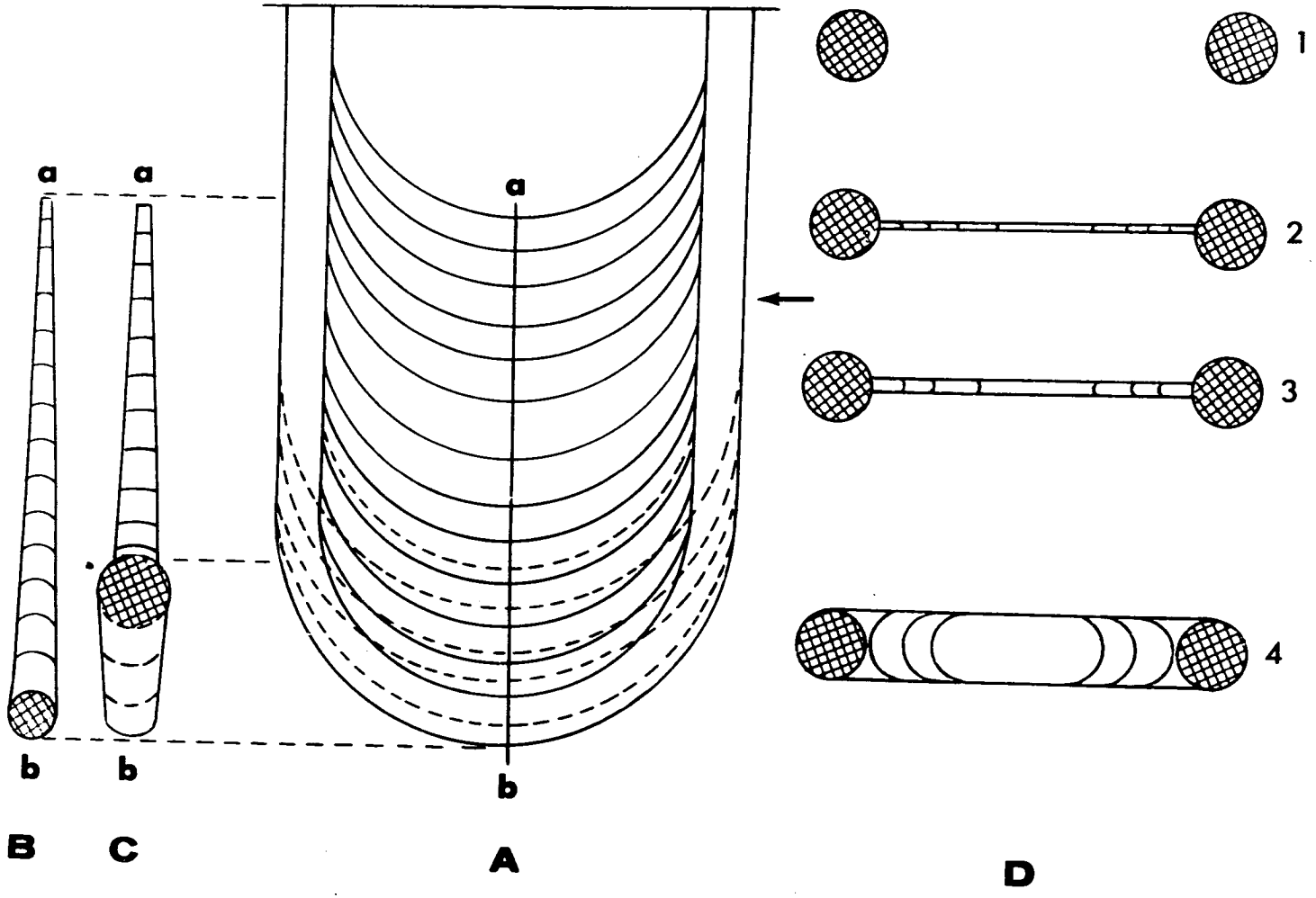


Figure 7

Explanation of Text Figures 8,9

Figure

8. Reconstruction of *Corophioides biclavata* (Miller)

. . . . . p. 143

The major portion of the tube lies within the lutite (light shading) and only the base of the "U" and the extended arm lie in the calcisiltite (dark shading). When the lutite is stripped away by erosion, only a dumbbell-shaped depression remains.

9. *Corophioides cincinnatiensis* n. gen., n. sp.

. . . . . p. 137

Three specimens from the type locality, West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio, showing various types of basal expansions. Tubes 2 and 3 terminate at the upper limit of a coarse-grained fossil hash. X 0.75.

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

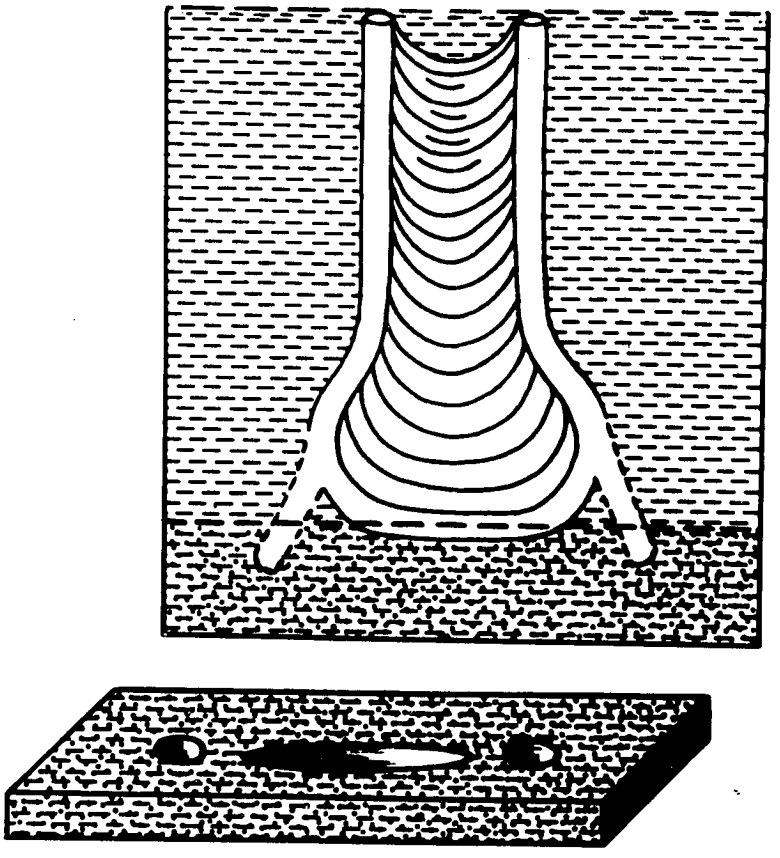


Figure 8

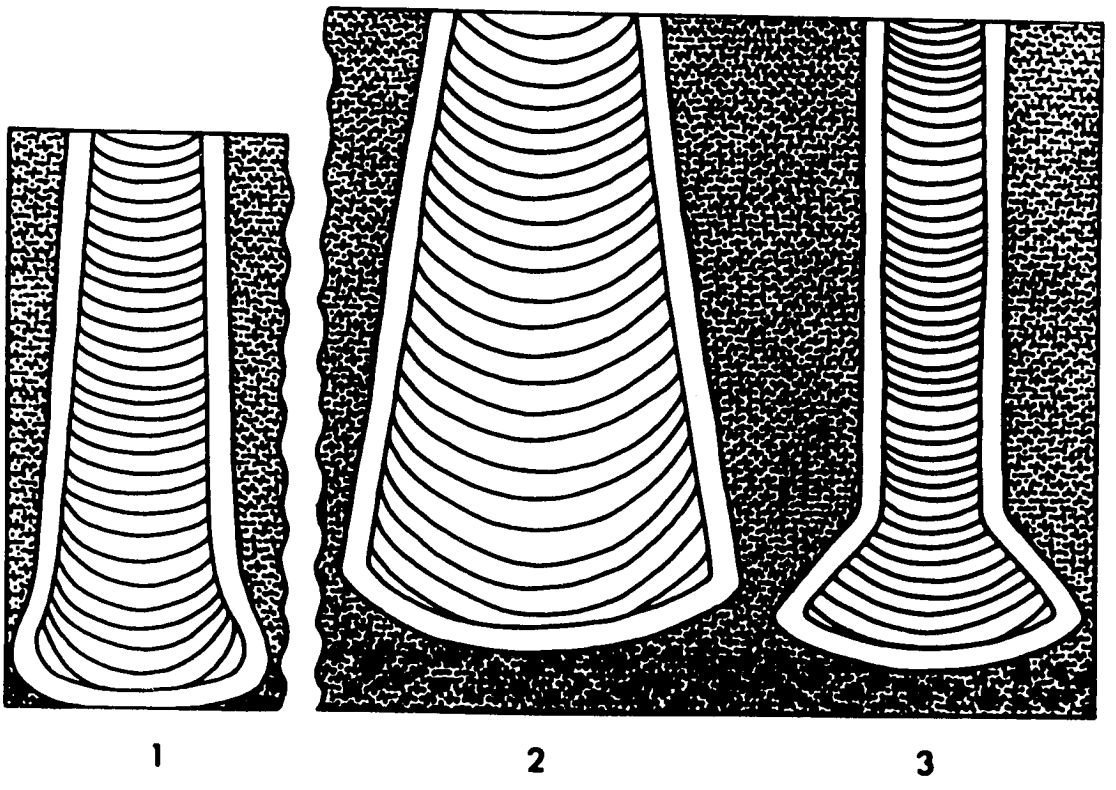


Figure 9

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

Explanation of Text Figures 10,11

Figure

10. Flower's (1955) interpretation of *Trichophycus venosum* depressions. . . . . p. 232

A. The remains of a nautiloid shell found at the end of a depression. Flower reported finding five such specimens in the Corryville beds at Stone-lick Creek.

B. A depression which Flower attributed to the lateral swinging of a nautiloid shell.

C-E. Flower's interpretation of the origin of the depression. A nautiloid, using its tentacles as a prow skims over the bottom (A), comes to rest (B), and by using its hyponome, leaves without disturbing the trace (C).

(from Flower, 1955, fig. 1)

11. Interpretation of *Trichophycus venosum* . . . . p. 232

A. Reconstruction showing a burrow with all branches open to the surface. The numbers (1-3) indicate the order of formation. X 0.5.

B. Alternate interpretation showing a main shaft open to the surface and three blind-ending branches. X 0.5.

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

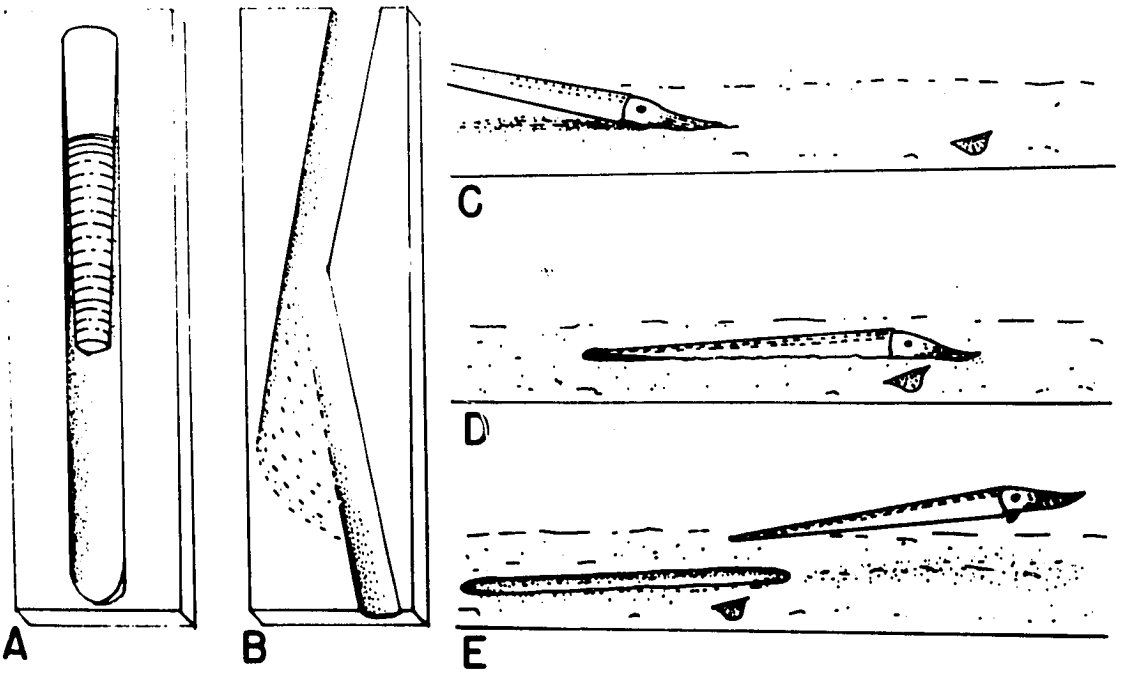


Figure 10

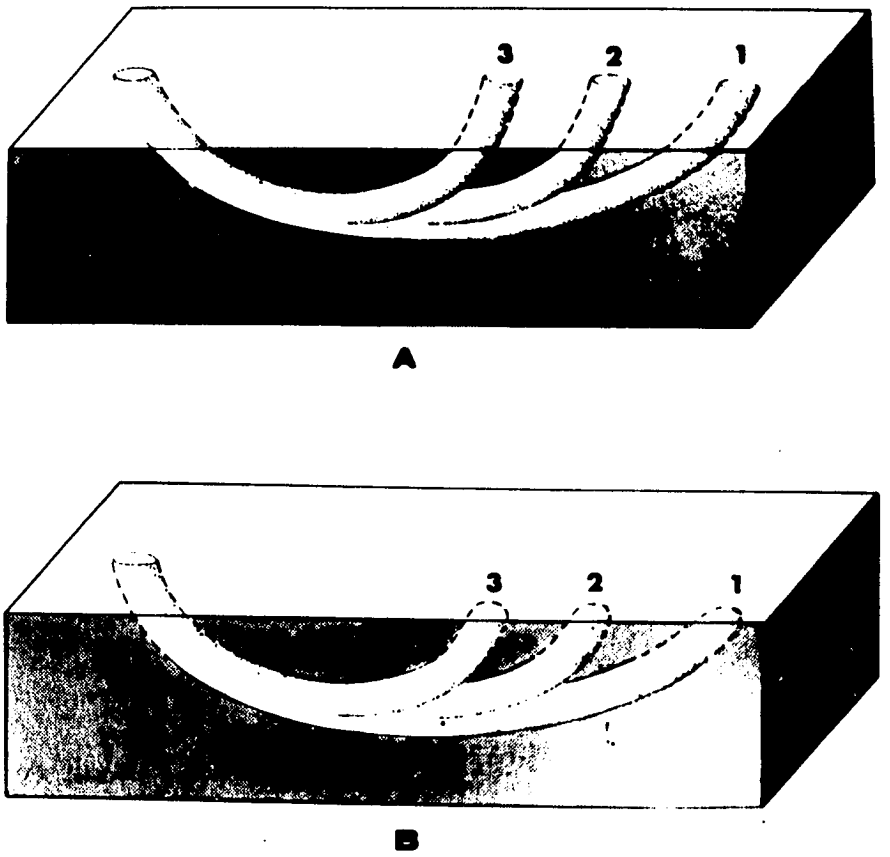


Figure 11

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

Explanation of Text Figure 12, 13

Figure

12. a. Seilacher's reconstruction of Buthotrephis palmata Hall . . . . . p. 209

The reconstruction is based on specimens from the Lower Cambrian of the Salt Range, Pakistan. A relatively small number of master shafts (left) branch to give a broom-like pattern. The master shafts show a crude Spreiten-like arrangement. X 0.75.

b. Seilacher's reconstruction of Phycodes circinatum Reinhard Richter . . . . . p. 209

The interpretation is based on material from the Salt Range. Note that the master shafts (left) have a well-developed Spreiten-like arrangement and that the free branches are smaller and more numerous than in Buthotrephis palmata. X 1.5. (from Seilacher, 1955, fig. 3)

13. Reconstruction of Phycodes flabellum (Miller and Dyer) from the Cincinnatian. . . . . p. 216

Block A shows the master shaft as seen in vertical section. Blocks B and C show that there is no

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

Explanation of Text Figure 13 continued

Spreiten structure in the Cincinnatian. Careful study has revealed only an area of disturbed sediment whose contacts are gradational with the host rock. X 1.

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

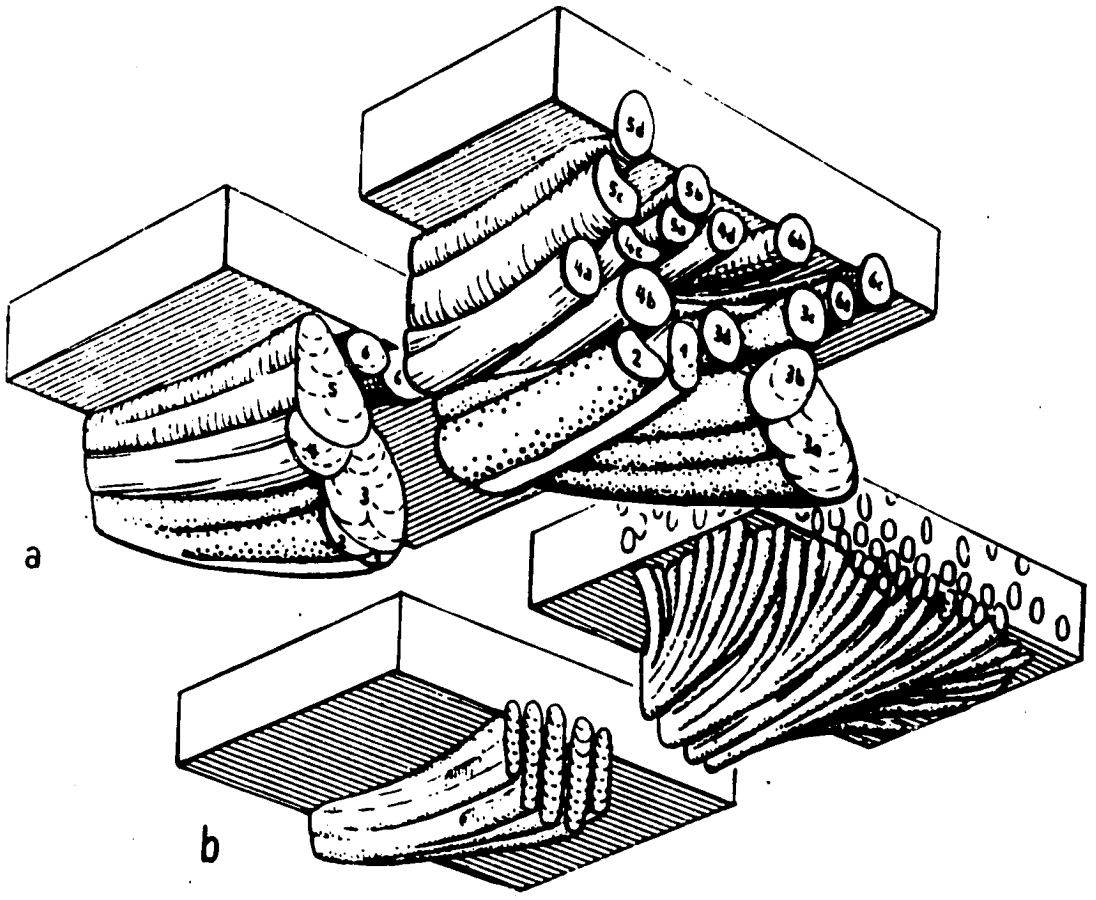


Figure 12

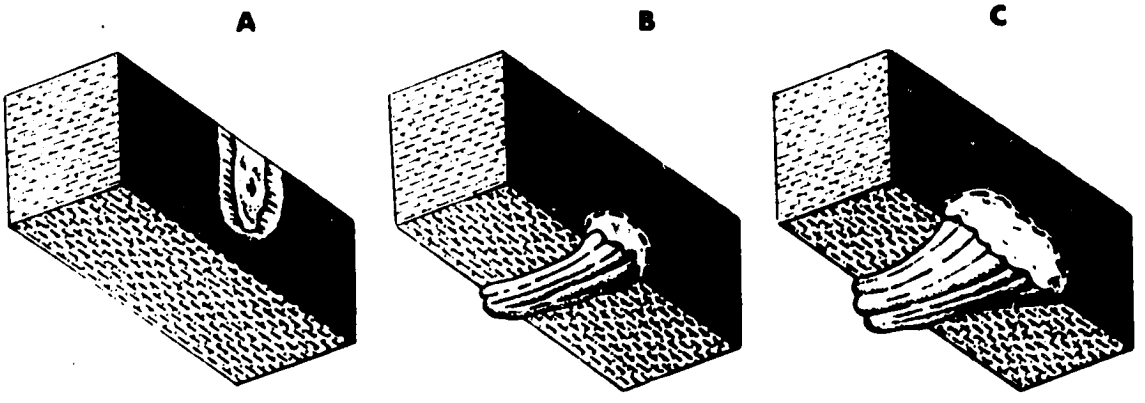


Figure 13

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

Explanation of Text Figures 14-17

Figure

14. Simpson's reconstruction of a Chondrites network... p. 162

The generalized reconstruction is based on fragmentary specimens from several localities and ages and the morphology was confirmed by serial sections. Note that the system displays phobotaxis indicating that the distal branches were the first formed.

(from Simpson, 1957, fig. 2)

15. Rudolf Richter's reconstruction of a Chondrites bollensis network. . . . . p. 162

The reconstruction is based on specimens from Holzmaden, West Germany. The network consists of several tiers which show phobotaxis. Both Richter and Simpson interpreted Chondrites as the mined out network of a sediment-feeder.

(from Melendez, 1951, fig. 3; after Rud. Richter, 1931, fig. 1)

16. Tauber's reconstruction of Chondrites furcatus... p. 162

Reconstruction of a simple network based on materials from the Alpine Flysch. Unlike Richter and Simpson, Tauber believed that Chondrites was the tunnel system of a plankton feeder.

(from Melendez, 1951, fig. 4; after Tauber, 1949, fig. 2)

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

Explanation of Text Figures 14-17 continued

Figure

17. Tauber's reconstruction of Chondrites furcatus. . . p. 162

Reconstruction of a more complex network arranged in tiers. Tauber believed that the tiers could be explained by erosion which forced the organism to deepen the network.

(from Melendez, 1951, fig. 5; after Tauber, 1949, fig. 3)

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

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

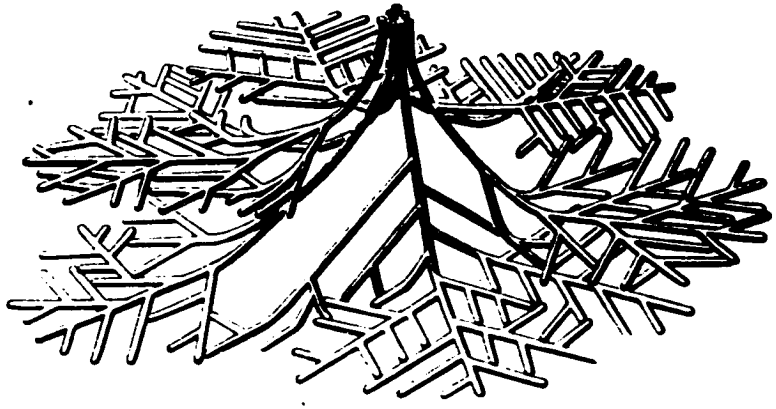


Figure 14

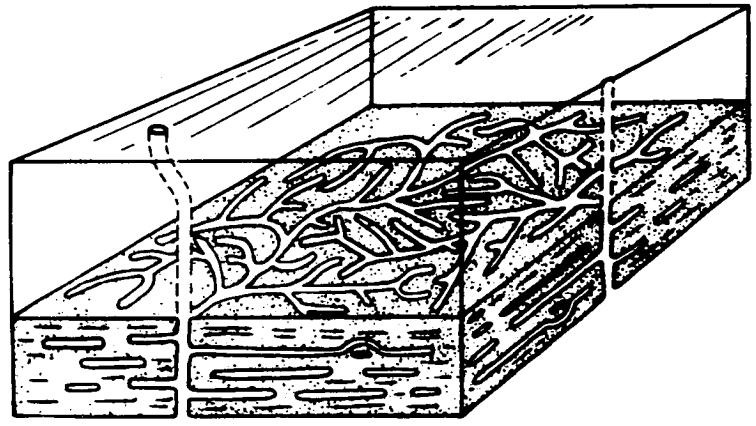


Figure 15

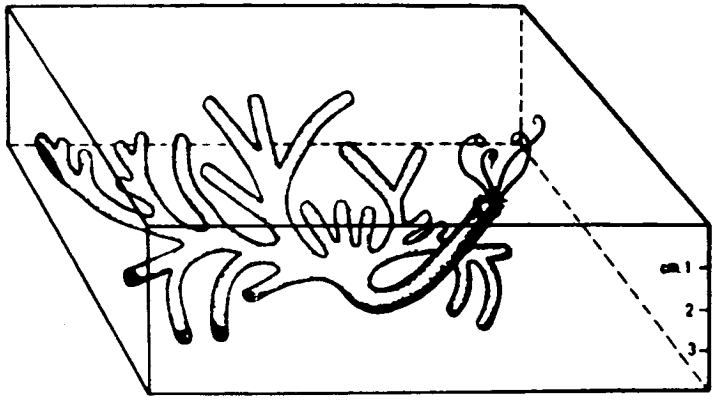


Figure 16



Figure 17

Explanation of Text Figures 18-22

Figure

18. Interpretation of *Fascifodina floweri* n. gen., n. sp. . . . . p. 205

Block diagram showing that the major volume of the burrow lies within the silt (dark pattern). Only the upper part of the bundled structure and the ?master shaft lies within the lutite (dashed pattern). In all Cincinnatian specimens the master shaft has been stripped away by penecontemporaneous erosion. Compare with fig. 21 below. X 0.25.

19. Effect of preservation on arthropod track morphology. . . . . p. 244

If the worker is not aware of the effects that preservation can have on track morphology misinterpretation will follow. The track illustrated is hypothetical; each block is 1 mm thick.

Top. The imprint is impressed as a concave epirelief on the depositional interface. The track is quadrifid and has an arcuate posterior fringe.

Center. The imprint is preserved as a cleavage relief 1 mm below the depositional interface.

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

Explanation of Text Figures 18-22 continued

Figure

19.continued. The arcuate fringe is not preserved.

Bottom. The imprint is preserved as cleavage relief 2 mm below the depositional interface. Only the two interior imprints are preserved.

20. Feeding trace of the Recent polychaete Scolecolepis. p. 387

Top. In quiet water the worm lies with only its head and tentacles projecting above the depositional interface. The tentacles sweep in a circular pattern, removing the nutrients from the substrate. It is possible that Palaeoscia Caster and Laevicyclus Quenstedt are fossil counterparts.

Bottom. In moving water (current from left to right). Actions such as those described above are not necessary since currents wash the food particles over the tentacles.

(from Seilacher, 1953a, fig. 5)

21. Flower's interpretation of Fascifodina floweri. p.205

A,B. Diagram shows the burrow preserved as short arcuate concave epireliefs.

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

Explanation of Text Figures 18-22 continued

Figure

21 continued. C-F. Nautiloids with tentacles flexed in such a way so as to produce the patterns seen in A,B above. X 0.25. (from Flower, 1955, fig. 4)

22. Chondrites, type-A . . . . . p. 188

Reconstruction showing a complete network. Note that there is no well-defined central axis. X 2.

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

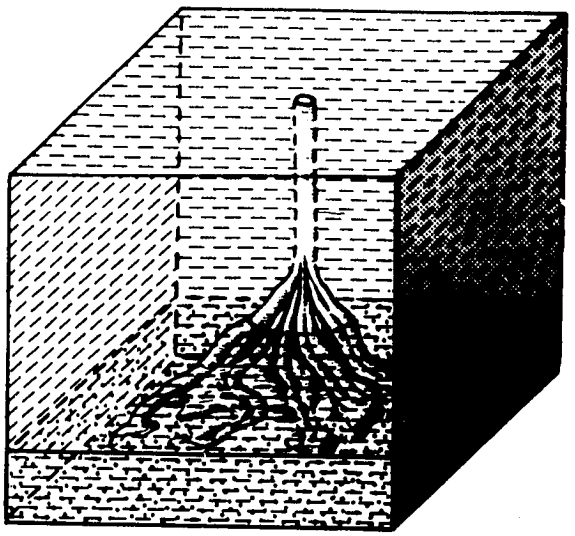


Figure 18

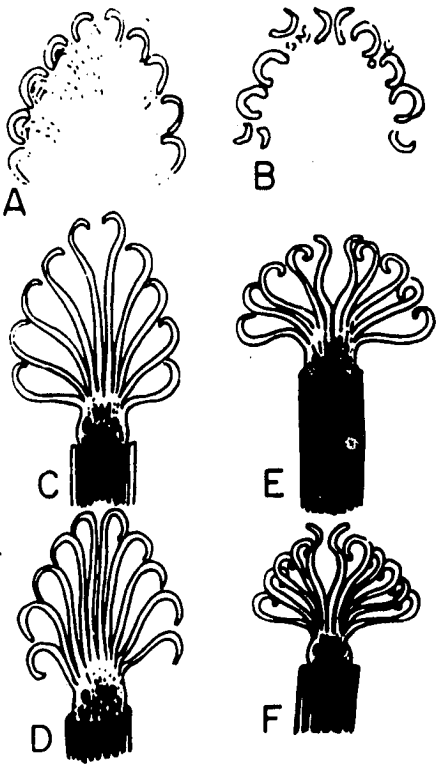


Figure 21

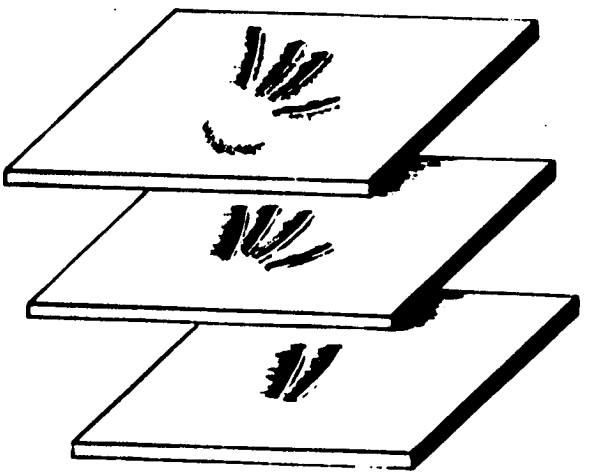


Figure 19

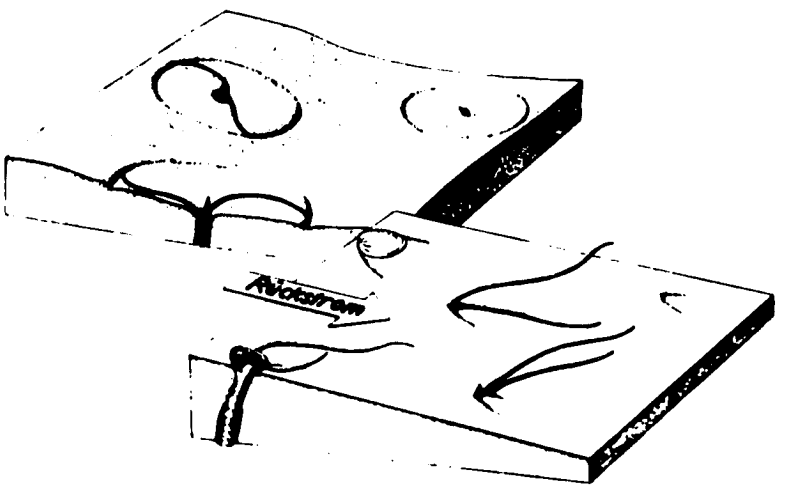


Figure 20

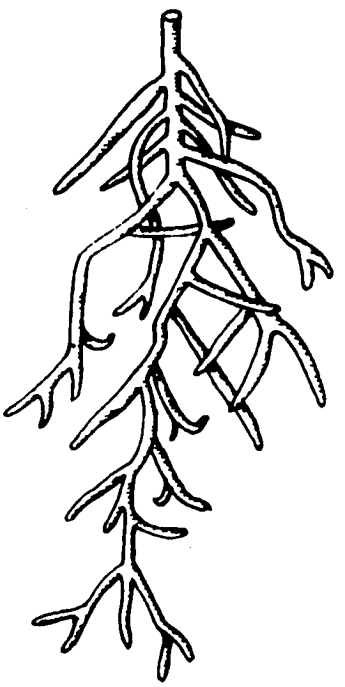


Figure 22

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

Explanation of Text Figures 23-27

Figure

23. Sarle's interpretation of the origin of Arthrophycus . . . . . p. 209

According to Sarle the bundled burrows of Arthrophycus were a response to sediment covering the mouth of the burrow. As sediment (dashed lines - C) covered the burrow, the organism correspondingly elevated the aperture (B). A bedding plane section taken along X-Y shows a Spreiten-like structure (S).

(from Sarle, 1906, fig. 4)

24. Morphology of trilobite tracks . . . . . p. 246

See the text for definition and discussion of the terms employed.

25. Chondrites, type-B . . . . . p. 193

The most complete C., type-B system thus far found in the local Cincinnatian section. The overall pattern appears to exhibit radial symmetry. Corryville beds, Stonelick Creek. UCM 37623.

26. Various types of arthropod tracks. . . . . p. 244

A. Trilobite (Phacops) showing oblique movement. Note that the imprints of the right series are

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

Explanation of Text Figures 23-27 continued

Figure

26 continued. superimposed while those of the left series are clearly definable.

B. Trilobite showing straight ahead movement. The parallel striae are markings made by the caudal cerci.

C. Tracks of a Recent scorpion. Note that the right and left series are offset. The tracks of eurypterids probably would more closely resemble scorpion tracks than they would those of trilobites.

D. Tracks of a Recent Limulus. Even though limuloids are the trilobites closest living relatives the tracks of the two are quite different. The apex of the "V" is directed anteriorly while in trilobite tracks it points posteriorly.

(from Seilacher, 1959, fig. 2)

27. Interpretation of Lockeia siliquaria . . . . . p. 91

Reconstruction showing the origin of specimens from the type locality.

A. Three pelecypods burrow through silt (dark pattern) and just nick the subjacent mud (dashed

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

Explanation of Text Figures 23-27 continued

Figure

27 continued. lines) with their foot or the anterior portion of the valves.

B. Subaqueous erosion strips away the silt down to the silt-mud interface. The dark ovoid imprints of the valves and/or foot have been filled with silt and are protected.

C. Following deposition of more silt (dark pattern) the sequence of events described in A above is repeated. Observation of the mud surface now reveals six ovoid imprints, however, cross-sections show that only three are overlain by a disturbed column of silt.

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

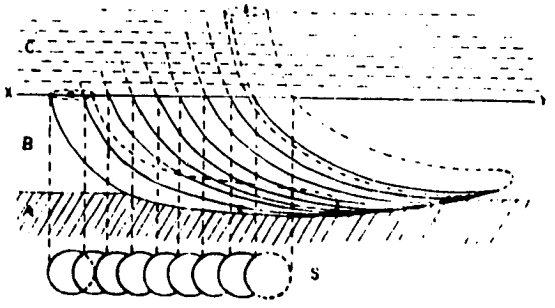


Figure 23

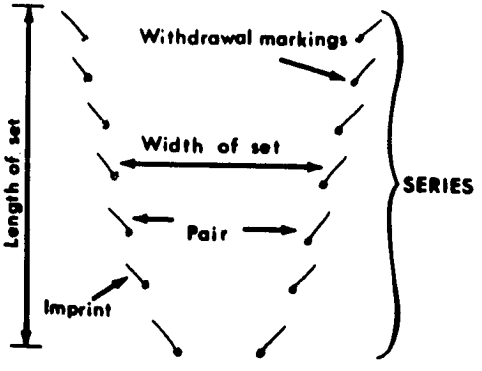


Figure 24

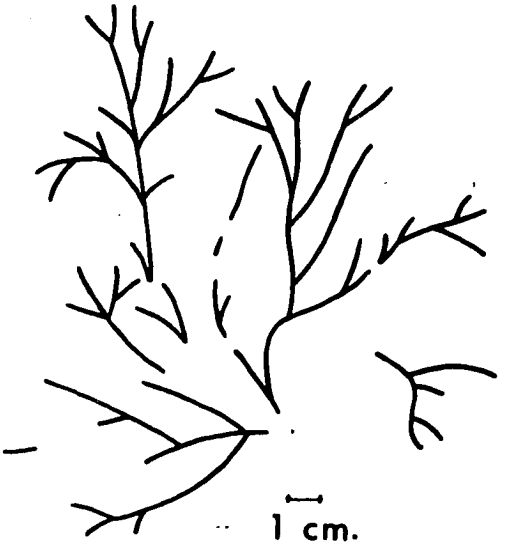


Figure 25

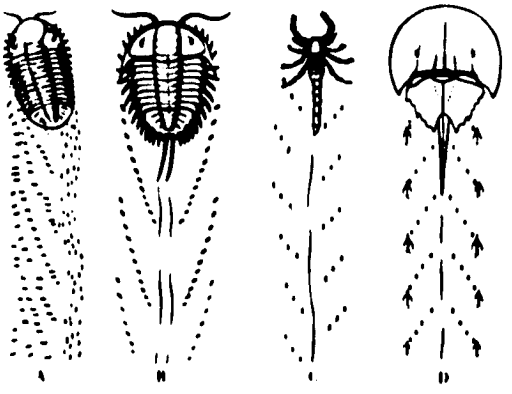
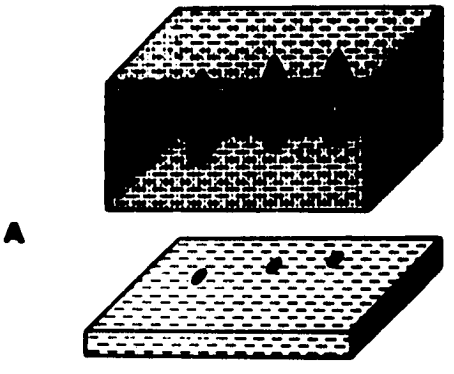
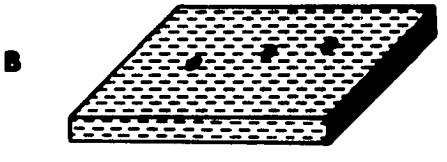


Figure 26





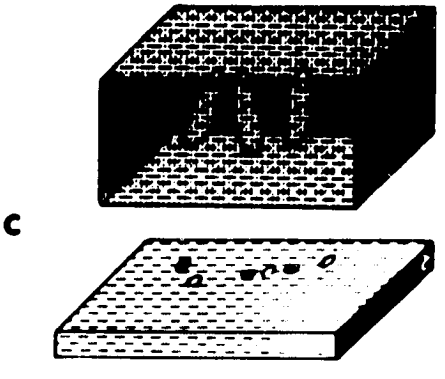


Figure 27

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

Explanation of Text Figures 28-31

Figure

28. Morphology of trilobite tracks . . . . . p. 246

a. The order of emplacement of the legs on the substrate as viewed from below.

b-d. Tracks indicative of straight-ahead movement from the Cambrian beds of the Salt Range, Pakistan. The imprints are superimposed and difficult to separate into series.

e. A trilobite "crab-walking" and giving rise to dimorphic tracks.

f. Dimorphic tracks from the Cambrian of the Salt Range.

g. Strongly dimorphic tracks. Seilacher (1955) believed that these were grazing or browsing trails (Weidespur). See text figure 30.

(from Seilacher, 1955, fig. 1, X 0.7.)

29. Nowak's interpretation of the origin of Paleodictyon . . . . . p. 344

Nowak believed that Paleodictyon was a Pascichnia where the organism systematically mined a nutrient-rich horizon. On the left the pattern is arranged

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

Explanation of Text Figures 28-31 continued

Figure

29 continued. in series. As the arrows indicate, the basic movement resembles a series of closely spaced meanders. In the figure on the right the pattern is arranged in cycles.

(from Nowak, 1959, fig. 9)

30. Dimorphichnus obliquum Seilacher, 1955 . . . . p. 252

Diagram shows the morphology of a large specimen from the Cambrian of the Salt Range. Seilacher believed that the trilobite (A) moved laterally with the body axis far to the left of the direction of movement. When the organism encountered the tracks of another trilobite (B) it reversed its direction and moved laterally, again employing strongly oblique movement. Note that this type of movement was temporarily discontinued as the trilobite crossed over its own tracks. Near the margin of the slab the strongly oblique movement converted into moderately oblique movement. Although Seilacher (1955) maintained that Dimorphichnus was a Pascichnia it is possible that oscillatory currents could produce the same type of trail by driving the trilobite laterally. C shows a trilobite making a strongly oblique trail

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

Explanation of Text Figures 28-31 continued

Figure

30 continued. as viewed from beneath. The raking imprints are elongated whereas the support imprints are cuneiform.

(from Seilacher, 1955, fig. 3; A=X 0.2; C=X 0.6)

31. Beloraphe Fuchs, 1895. . . . . p. 344

Right. Beloraphe showing the "zig-zag" pattern and projections characteristic of the trail.

Left. A hypothetical arrangement of five Beloraphe to produce a Paleodictyon-like pattern.

(from Nowak, 1959, fig. 4)

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

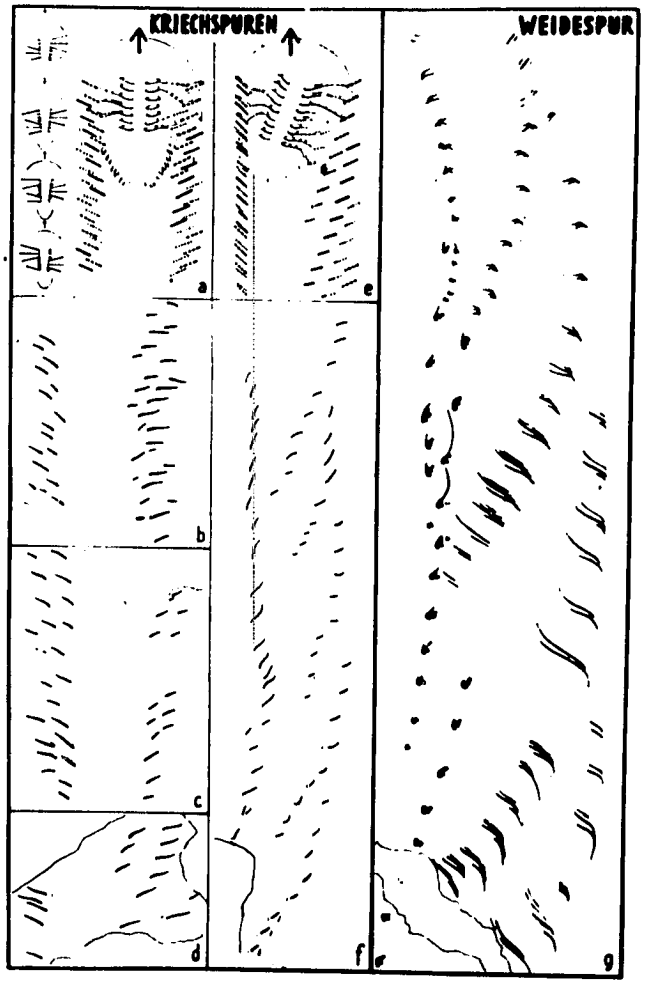


Figure 28

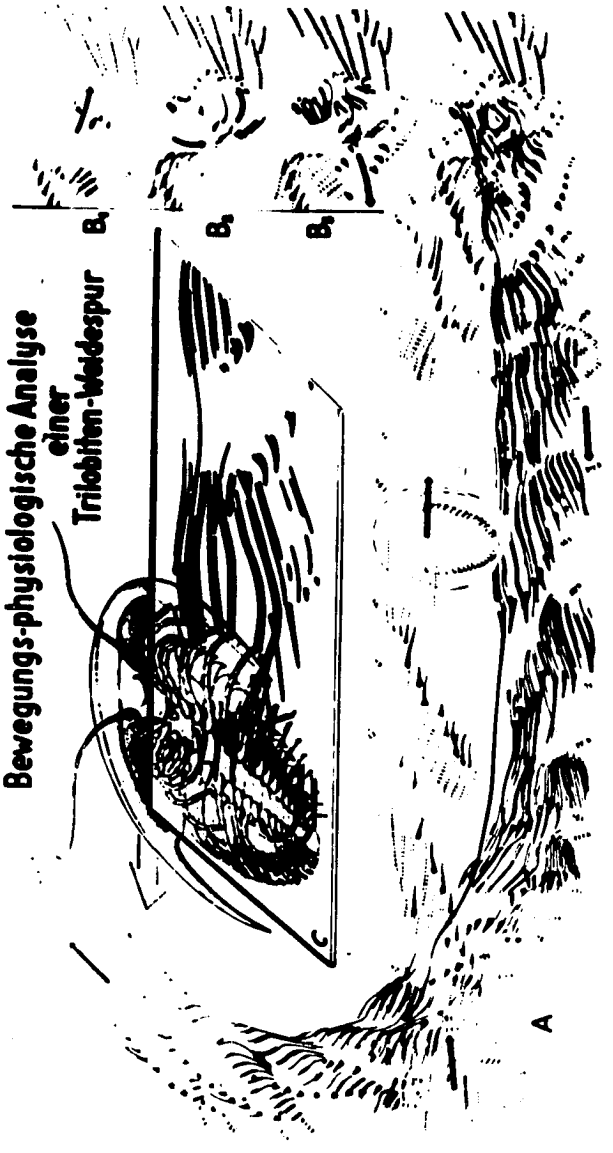


Figure 30

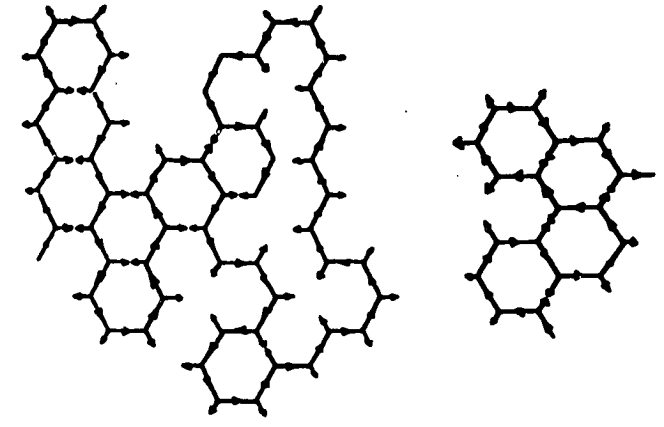


Figure 29

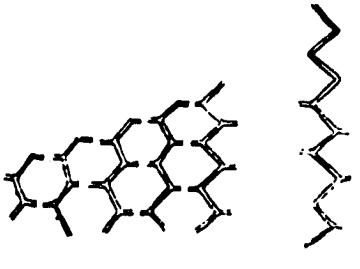


Figure 31

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

Explanation of Text Figure 32

NOTE: Text Figures 32-35 represent the authors interpretation of several arthropod trails. The organisms superimposed over the tracks indicate the direction and method of movement. In the acetate overlays different symbols are used to portray imprints in different series. In all cases the trails are viewed from below, i.e. as if the viewer were looking up at the trails through a glass table top.

Figure

1. Asaphoidichnus trifidum Miller, 1880 . . . . . p. 261

   Repichnia of Isotelus; interpretation of the trail illustrated on Pl. 15, fig. 6. Holotype. MCZ 540; latex mold UCM 37694, X 1.2.

2. Trachomatichnus numerosum Miller, 1880 . . . . p. 284

   Repichnia of Cryptolithus; interpretation of the trail shown on Pl. 17, fig. 4. Note that it is difficult to separate the imprints into series. MCZ 544; latex mold UCM 37671, X 3.2.

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



Figure 32

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

Explanation of Text Figure 33

Figure

1. *Asapheidichnus trifidum* Miller, 1880 . . . . . p. 261

   Repichnia of *Isotelus*; interpretation of the trail illustrated on Pl. 19, fig. 3. UCM 37569, X 0.75.

2,3 *Allocotichnus dyeri* (Miller), 1880 . . . . . p. 268

   2. Repichnia of *Isotelus*; interpretation of the trail illustrated on Pl. 16, fig. 1. Holotype. MCZ 543; latex mold UCM 37693, X 1.

   3. Repichnia of *Isotelus*; interpretation of the trail illustrated on Pl. 16, fig. 2. Note that the dimorphism of the series is not as marked as it is in fig. 2 above. UCM 37627, X 1.

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

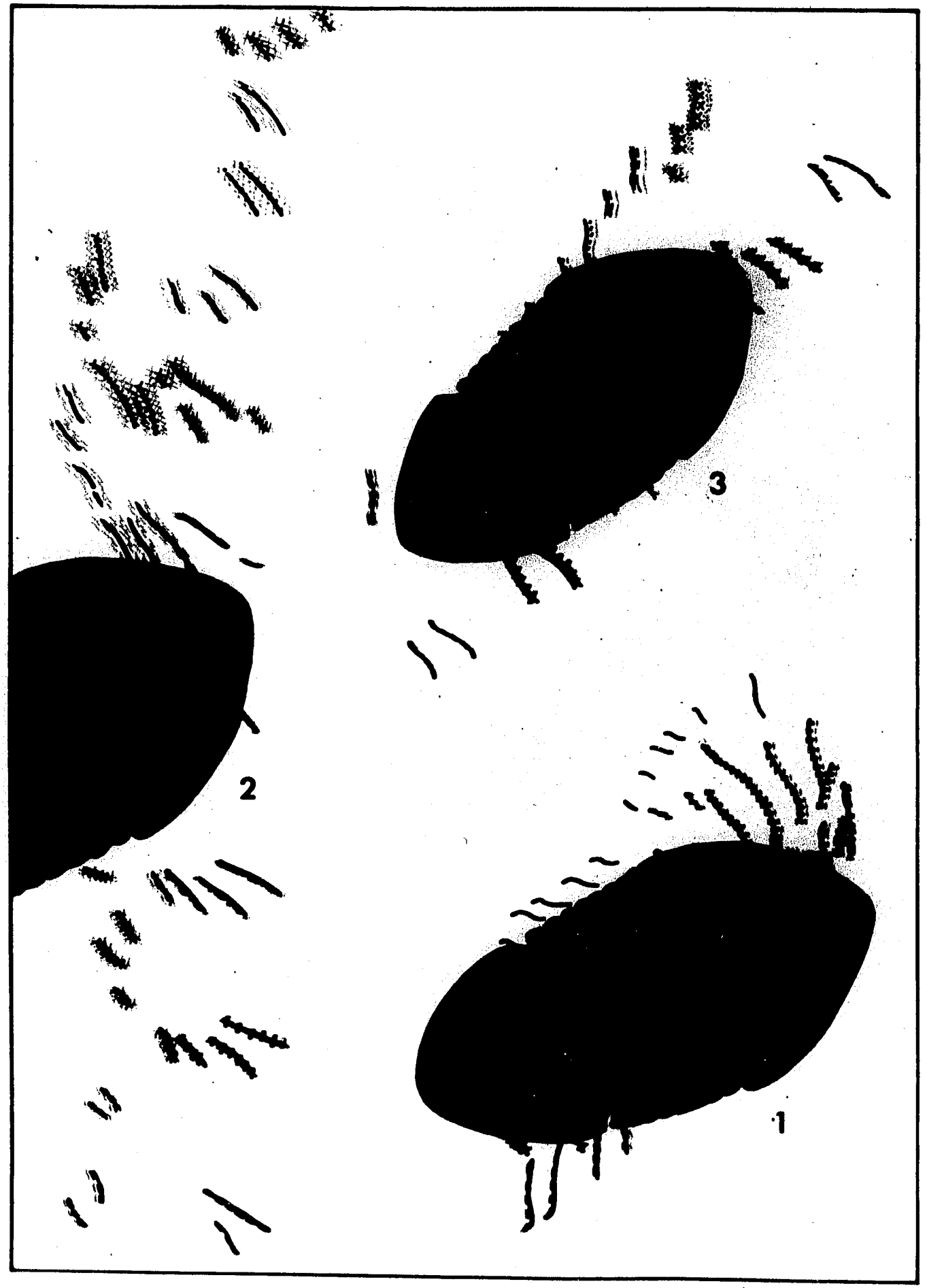


Figure 33

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

Explanation of Text Figure 34

Figure

1-3 Petalichnus multipartitum Miller, 1880 . . . . p. 276

1. Repichnia of a medium sized trilobite; interpretation of the trail illustrated on Pl. 18, fig. 5. MU T86; latex mold UCM 37707, X 1.7.

2. Repichnia of a medium sized trilobite; interpretation of the trail illustrated on Pl. 17, fig. 5. MCZ 548; latex mold UCM 37696, X 1.4.

3. Repichnia of a medium sized trilobite; interpretation of the trail illustrated on Pl. 19, fig. 4. The trail is so complex that it is not possible to place all imprints in their proper series. Holotype. MCZ 546; latex mold UCM 37697, X 1.5.

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

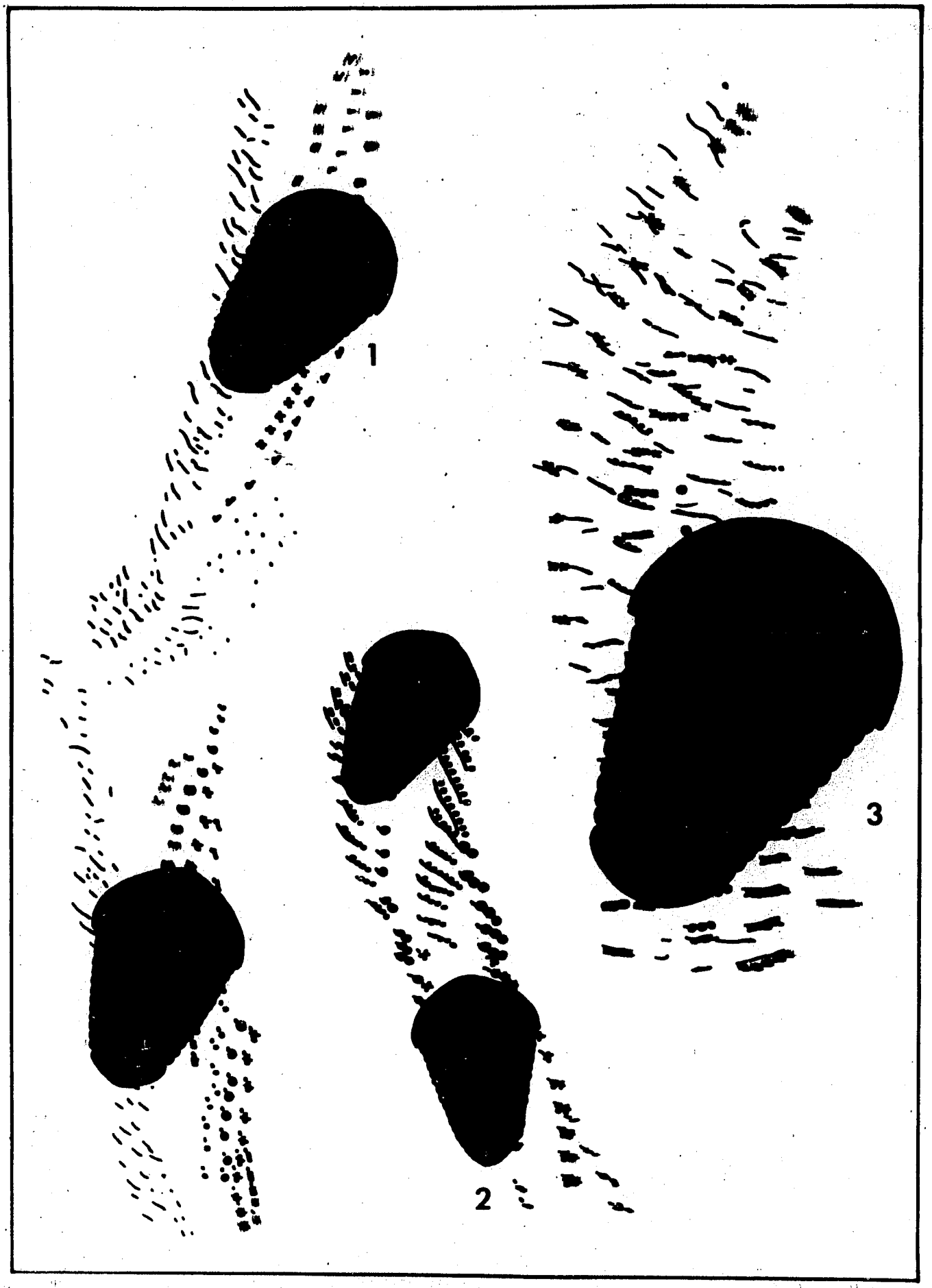


Figure 34

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

Explanation of Text Figure 35

Figure

1. Teratichnus confertum Miller, 1880 . . . . . p. 292

Repichnia of a medium sized trilobite or aglaspid; interpretation of the trail illustrated on Pl. 19, fig. 3. The trail is highly complex and only a partial interpretation is given. Holotype. MCZ 540; latex mold UCM 37570, X 1.4.

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

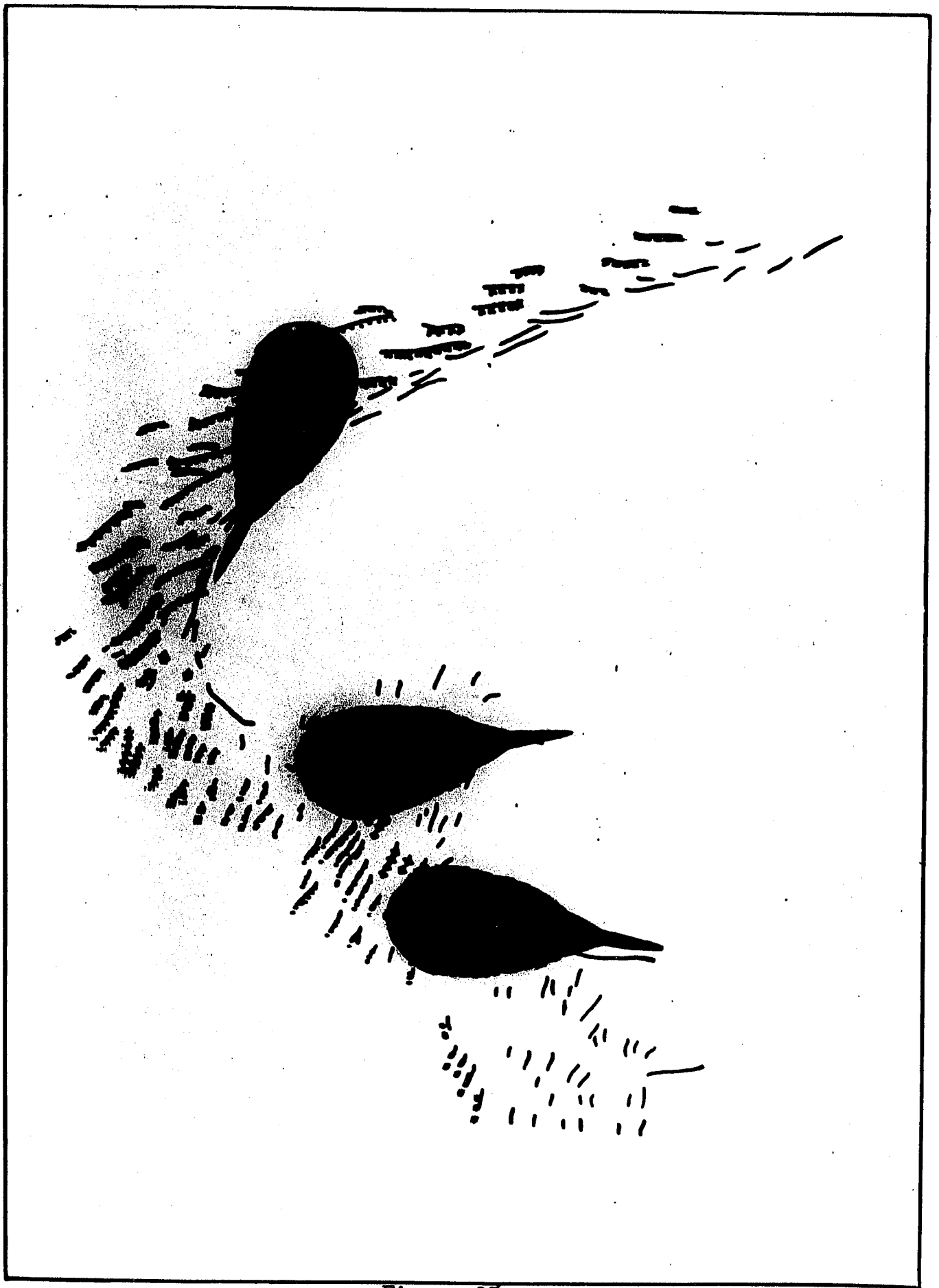


Figure 35

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

Explanation of Text Figures 36-40

Figure

36. Chondrites "apparatus" . . . . . p. 193

The illustrated apparatus was used to determine if sediment could passively fill a Chondrites system. The system was constructed of glass tubing with an internal diameter of 4 mm. The tube endings, which lay on a horizontal plane, were plugged with corks or fiberglass wool packing and the network was filled with water. Sediment was introduced at the funnel mouth (A).

37. ?mollusk trails. . . . . p. 338

The diagrams (A-E) illustrate cross-sections of the trails from the McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. The trails resemble those forms placed in Palaeophycus, however the trails here under discussion were made on or just below the depositional interface. X 1.

38. Enlargement of Tylichnus asperum (Miller and Dyer), 1878. . . . . p. 304

The prosopon of the holotype consists of alternating rows of nodes arranged in a 5-4-5-4- pattern. In

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

Explanation of Text Figures 36-40 continued

Figure

38 continued. other members of the species the arrangement is not as regular. X 7.5.

39. Schematic cross-section of Aristophycus ramosum Miller and Dyer, 1878 . . . . . p. 395

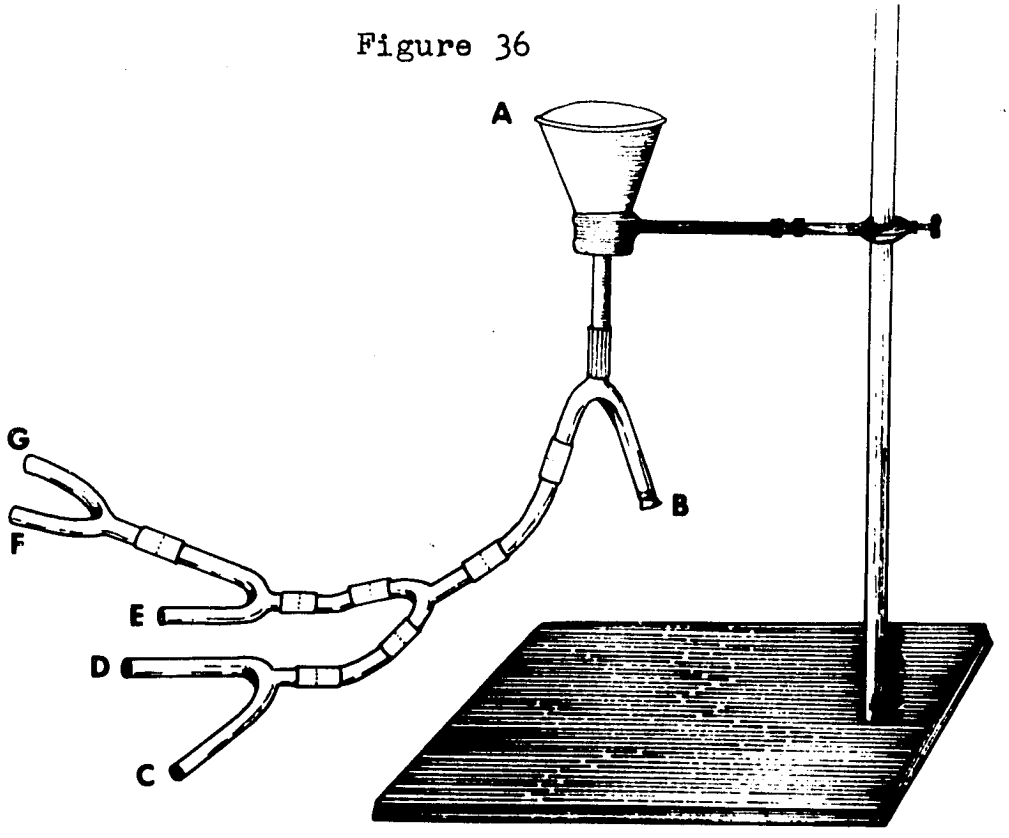
The diagram shows that the secondary branches bifurcate from the main branch from below rather than at right angles (i.e., below a horizontal plane bisecting the main branch). X 5.

40. Schematic cross-section of Trachomatichnus numerosum Miller, 1880. . . . . p. 284

The hook-like casts of markings made by the walking legs rest on a "terrace" which was gouged out by the cephalon. X 1.25.

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

Figure 36




A


B


C


D


E

Figure 37

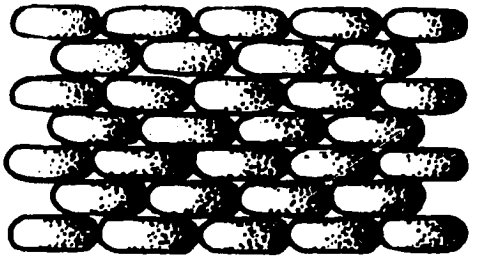


Figure 38

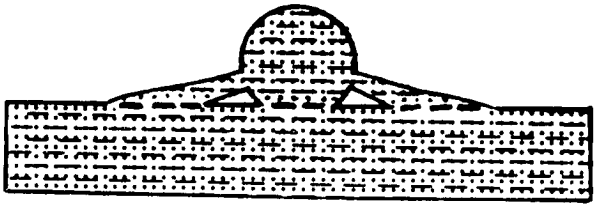


Figure 39

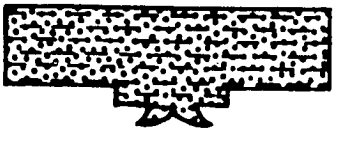


Figure 40

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

Explanation of Text Figure 41

Figure

1. ?Mollusk trails. . . . . p. 338

Map of trails exposed in the McMillan beds of West Fork Creek, Cincinnati, Ohio. Many of the trails dip below the surface giving the overall pattern a disjointed appearance. The dark, irregular patches within the map area represent eroded areas.

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

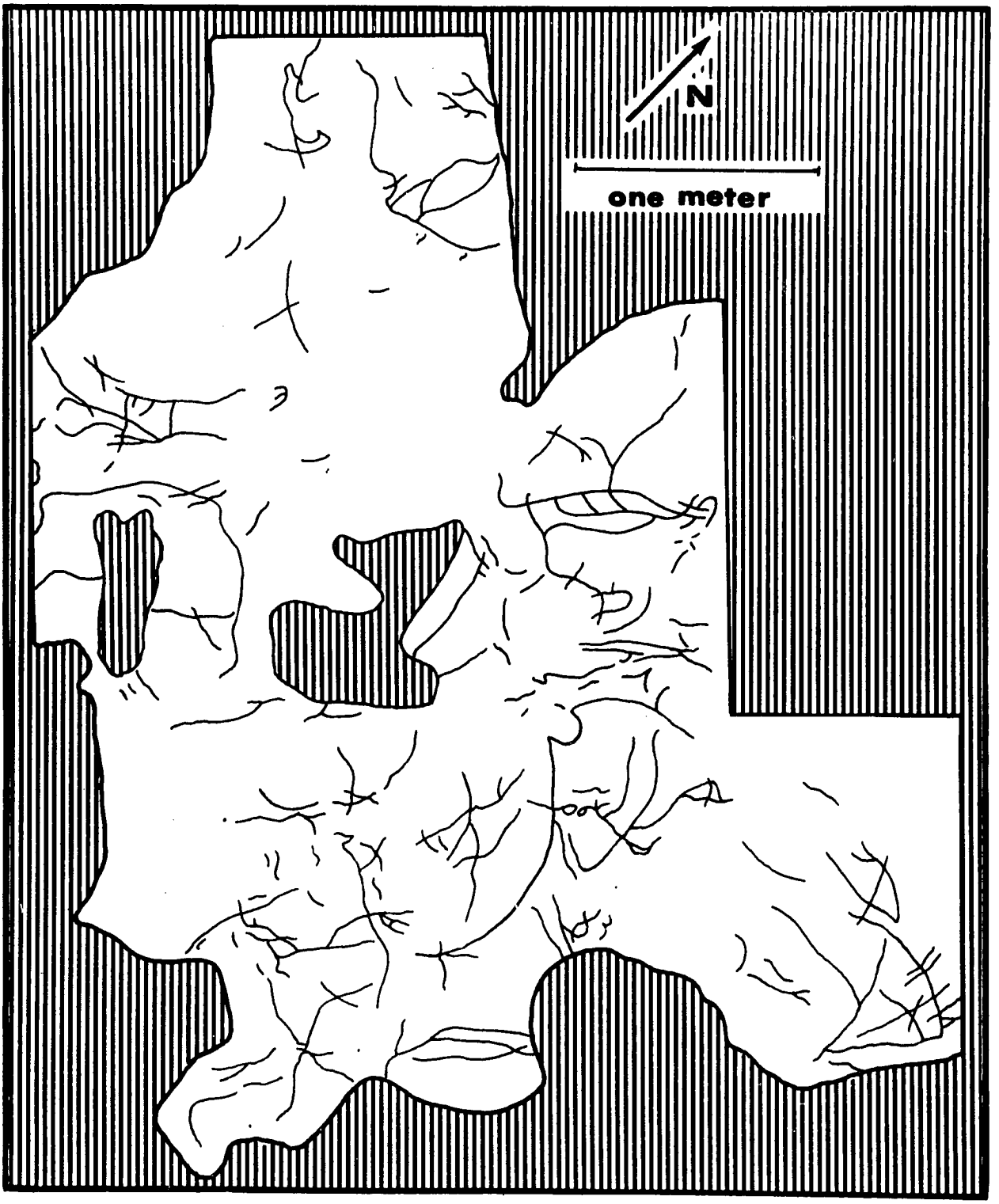


Figure 41

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

Explanation of Text Figure 42

Figure

1. Comparative Palichnology (Seilacher, 1955) . . p. 407

Seilacher's comparison of trace fossil suites from six localities. The Nereites beds of Portugal and the Cretaceous-Tertiary Flysch of Europe are characterized by an abundance of Pascichnia and a complete lack of Cubichnia. In the marine Molasse of Switzerland, the Lias and Dogger sandstones of Württemberg, the Lower Cambrian of the Salt Range, Pakistan, and the Schilf Sandstone of Württemberg the opposite is true; Cubichnia are common and Pascichina are wanting.

(from Seilacher, 1955, fig. 5)

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



Abb. 5. Vorzeitliche Spurengemeinschaft

Neobolus Beds und Magnesian Sandstone (epikontinentales Unterkambrium). Salt Range.

Ruhespuren:

1. *Rusophycus bilobatus* HALL. *Neobolus* Beds; Khewra (Ic 1071/4). 1/3.
2. *Rusophycus didymus* (SALTER). Magnesian Sandst.; (Ic 1071/5 u. 6). 3/4.

Kriechspuren:

3. *Protichnites* sp. B. Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 4). 3/4.
4. *Protichnites* sp. A. Magnesian Sandst.; Kusak (vgl. Taf. 16, Bild 2). 3/4.
5. *Diplichnites* sp. Magnesian Sandst.; Khewra (vgl. Teil IV, Abb. 1). 3/4.
6. *Crossochorda* sp. Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 5). 3/4.
7. *Scolicia* cf. *sardoa* (MGH.). Modelle nach Stücken aus dem Magnesian Sandst. von Khewra und Kusak. a) Oberseitenform (negativ exogenes Epirelief). b) Endogene Vollform, von unten gesehen.

Weidespur eines Trilobiten:

8. *Dimorphichnus obliquus* n. g. n. sp., Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 3). 1/3.

Freßbauten:

9. *Dictyodora simplex* n. sp., Schichtflächen-Schnitt. *Neobolus* Beds; Khân Zamân Nala bei Chhidru (Ic 1071/7). 1/3.
10. *Teichichnus rectus* n. g. n. sp.; Modell nach Stücken aus den *Neobolus* Beds von Khewra und Kusak. Etwa 1/3.
11. *Corophioides* cf. *rosei* DAHMER; Modell nach Stücken aus den *Neobolus* Beds von Khewra.

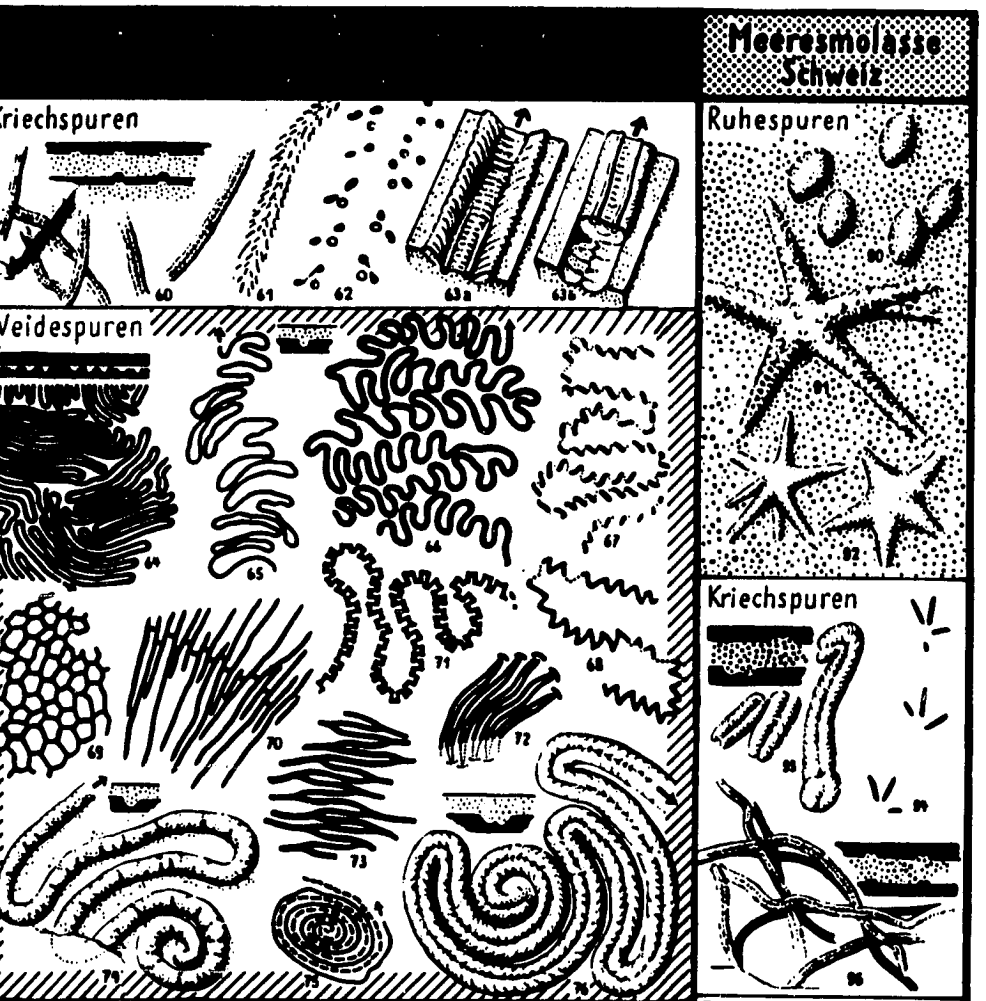
gelegentlich in derselben Ebene durchs
ist also nur eine oberflächliche.

19. *Palaeodictyon* sp. (= *Retiphycus*; vgl
Geologischen Staatsinstitut, Hamburg
Wissens noch nicht gefunden.
20. *Nereites* sp. (eine von mehreren, zum
stimmten Arten). Obersilur oder Unter
21. *Myrianites*? (vielleicht auch zu *Dict*
Taf. 32, Fig. 4). 1/3.
22. *Crossopodia* aff. *henrici* GEIN. (= mäa
oder Unterdevon; Malhadinha, Aljustr

Freßbauten:

23. *Phycosiphon* cf. *incertum* FISCHER-OOST
56 und 78). Obersilur oder Unterdev
ergänzt). 3/4.
24. *Lophoctenium comosum* RICHT. (vgl. 86
DEGLADO, ergänzt nach thüringischen
25. Noch unbeschriebener Freßbau ähnlich
Fig. 2). 1/1.
26. *Chondrites* sp., Obersilur oder Unterde
Fig. 1). 1/2.

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



rschiedener Habitate.

chorda (Abb. 2)

d (Original im
e Form meines

Myrianites be-
11, Fig. 1). 1/3.
rancos (DELG.,

n 76). Obersilur

teri DELG.; vgl.
, Fig. 3; etwas

rtola (Abb. von

DELG., Taf. 40,

DELG., Taf. 18,

35. *Cylindricum antiquum* (PLIEN.) (= *C. gregarium* LINCK). Schilfsandst.; Stuttgart (PLIENINGER 1845, Taf. 2, Fig. 5). 1/2.

Schwäbischer Lias- und Dogger-Sandstein (Zopfplatten-Fazies; epikontinental)

Ruhespuren:

36. *Asteriacites lumbricalis* SCHLOTH. (horizontal-repetierte Ruhespur eines Ophiuren). Lias α2; Hochberg bei Lorch (Ic 1047/3). 3/4.
37. *Asteriacites quinquefoliae* (QUENST.) (Ruhespur eines Asteroiden). Dogger β; Weilheim/Teck (SEILACHER 1953b, Taf. 10, Fig. 1; Ic 1009/8). 1/3.
38. *Ichnocumulus radiatus* SEILACHER. Lias α2; Hochberg bei Lorch (SEILACHER 1955, Abb. 4; Ic 1047/3). 3/4.
39. *Ichnocumulus pexus* SEIL. Dogger β; Weilheim T. (SEILACHER 1955, Abb. 5; Ic 1047/4). 3/4.
40. *Pelecypodichnus amygdaloides* SEIL. (Ruhespuren sandliegender Muscheln). Dogger β; Weilheim/T. (SEILACHER 1953b, Taf. 10, Fig. 1; Ic 1009/8). 3/4.

Kriechspuren:

41. Einzelnes Trittsiegel eines riesigen Limuliden (vgl. Nr. 30!). Lias α2; Wernau a. N. (Ic 1071/9). 1/3.
42. *Sinusites* sp. (Schlängelspur eines Wurmes). Lias α2; Hüttlingen (Original im Staatl.

50. *Rhizocorallium jenense* ZENKER. Söhlig-protrusiver Spreitenl aus dem Lias α2; Helmstedt (ähnliches auch in Württemberg).
51. cf. *Rouaultia*. Zwiebel-schaliger Versatzbau. Dogger β; Weilh schematisiert). 1/8.
52. *Phycodes* sp. Verzweigte U-Röhre mit gebüschelten Freß-Stu aus dem Lias α2 von Plochingen, Nürtingen und Möhringen. E
53. *Gyrophyllites geryonides* (v. HUENE). Schacht mit sternförm Freß-Stollen; früher als Meduse gedeutet. Rekonstruktion württembergischen Dogger β. 1/3.
54. *Laericyclus* QUENST. Schacht mit Scharrkreis um die Münd nach Hyporeliefs aus dem Lias α2 von Hüttlingen. 3/4.
55. Unbestimmter Freß-Stern eines Röhrenbewohners. Nach einer α2 von Hüttlingen (Ic 1071/14). 1/1.
56. *Phycosiphon incertum* FISCHER-OOSTER (vgl. Nr. 23 u. 78!). 1071/15; auch in Württemberg häufig). 1/1.
57. *Spongites suevicus* QUENST. Ausfüllung eines dreistrahlig verz α2; Hüttlingen (Ic 1071/16). 1/6.
58. „Feather stitch trail" (WILSON 1948). Nach Art des Gräten- verzweigtes Gangsystem. Lias α2; Frickenhofen (Ic 1071/17).
59. *Chondrites hechingensis* (QUENST.). Pflanzen-artig verzweig Hüttlingen (Ic 1009/29). 1/1.

Alpiner Kreide-Tertiär-Flysch (geosyn

Kriechspuren:

60. *Gyrochorda comosa* HEER (vgl. Nr. 47 u. 94!) mit der bezeich Vertikal-Repetition (die linke obere Ecke der Zeichnung stellt dar). Eozän; Greifenstein b. Wien (Ic 1071/18). 1/2.
61. Unbestimmte Artikulaten-Fährte. Oberkreide; Wien (GÖT Abb. 13). 1/5.
62. Große Schreitfährte; nach MIGLIORINI 1947 von Tetrapoden stu auf einen riesigen Arthropoden zu beziehen. Calcare alberese (b. Florenz (nach einer Photographie). 1/20.
63. *Scolicia prisca* QUATREF. Kriechspuren grabender Schnecken (seiten-Ausbildung (= *Palaeobullia* G. & B.). b) Unterseiten G. & B.). Modelle nach italienischen und österreichischen Stü

Weidespuren:

64. *Helminthoida labyrinthica* HEER. Als Vollform (Querschni endogene Weidespur mit vollkommenster Parkettierung. Ober Institut, Pisa). 1/2.
65. *„Helminthoida" crassa* SCHAFHÄUTL. Diese und die folgenden, glypten" sind stets als positiv endogene Hyporeliefs erhalten u offenbar grundsätzlich verschieden. Oberkreide (?); Marnia (1/4.
66. *Cosmorhaphe* FUCHS. Oberkreide (?); Seranza (Geolog. Institut
67. *Helicolithus sampelayoi* AZPEITIA. Oberkreide (?); Seranza (Geol
68. *Belorhaphe* FUCHS (ohne nähere Bezeichnung in der Sammlung
69. *Palaeodictyon* sp. Unetikettiert in der Sammlung HOSNIASKI, P
70. *Desmograpton* sp. Oberkreide (?); Altomena (Geolog. Institut,
71. *Palaeomaeandron elegans* PERUZZI. Flysch; Toscana (nach P Taf. 5, Fig. 7). 3/4.
72. Unbenannte Form. Flysch; Melosa (Geolog. Institut, Florenz).
73. *Helminthoida appendiculata* HEER (= *Hercorhaphe* FUCHS). Ob TIA 1932, Taf. 5). 1/4.
74. *Ceratophycus* sp., mit Querschnitts-Schema. Eozän; Pallers Institut, Wien). 1/3.
75. *Spirorhaphe spiralis* (ULRICH). Yakutat-Formation (Eozän); 1904, Taf. 18, Fig. 2; gleiche Formen auch in Europa). 1/3.
76. *Taphrhelminthopsis auricularis* SACCO. Mäandrierende Gast Nr. 22. Flysch; Spazzarento (Geolog. Institut, Pisa). 1/6.

Freßbauten:

77. *Zoophycos* sp. Spiralig-protrusiver Spreitenbau. Modell nach S Etwa 1/4.
78. *Phycosiphon incertum* FISCHER-OOSTER (vgl. Nr. 23 u. 56!). Ob (Sammlung THENIUS, Wien). 3/4.
79. *Pennatulites* sp. (= „Schuppenkerne"; vgl. auch Nr. 14 u. 21!). und österreichischen Stücken. Etwa 1/10.
80. *„Gyrophyllites" doblhoffi* v. LIBURNAU. Stopfbau mit spiralig Gegensatz zur quiriligen Anordnung bei echten Gyrophylliten!). stücken aus der Oberkreide von Bergheim (Haus der Natur, Sa
81. *Zonarites alcicornis* FISCHER-OOSTER (= *Caulerpa arcuata* SC zweigte Freßbauten mit quer eingestopften Kotpillen. Im Gegens die Stollen nicht nach unten, sondern nach oben auseinander. Florenz (FUCHS 1895, Taf. 9, Fig. 1). 1/4.
82. *Hydrancylus oosteri* FISCHER-OOSTER. Oberkreide; Exelberg b. 1/2.
83. *Taenidium fischeri* HEER. Stopfbau ähnlich *Chondrites* mit rege (Stopf-Portionen!). Oberkreide; Salzburg (v. LIBURNAU 1900, T
84. *Chondrites* sp. (vgl. Nr. 53!). Oberkreide; San Sebastian (Go Taf. 4, Fig. 19). 1/3.
85. Unbenannte Form. Oberkreide; Montefiesole (Geolog. Institut, vorkommend). 1/3.
86. *Lophoctenium ramosum* (TOULA). Freßbau ähnlich Nr. 24 Eozä (Ic 1071/18). 1/2.
87. *Gyrophyllites* sp. (vgl. Nr. 53!). Rekonstruktion nach Stücken a fenstein (Paläontolog. Institut, Wien). 1/3.
88. *Lorenzinia apenninica*. Flysch; Porretta (nach dem Original zu Institut, Bologna). 1/3.
89. Unbenannter sternförmiger Freßbau. Flysch; Karpathen (gesa 1071/19). 1/6.

Meeresmolasse (paralisches Miozän), Sch

Ruhespuren:

90. *Pelecypodichnus amygdaloides* SEIL. (vgl. Nr. 29 u. 40!). We 1071/20). 3/4.

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



Abb. 5. Vorzeitliche Spurengemeinschafte

Neobolus Beds und Magnesian Sandstone (epikontinentales Unterkambrium), Salt Range.

Ruhespuren:

1. *Rusophycus bilobatus* HALL. *Neobolus* Beds; Khewra (Ic 1071/4). 1/3.
2. *Rusophycus didymus* (SALTER). Magnesian Sandst.; (Ic 1071/5 u. 6). 3/4.

Kriechspuren:

3. *Protichnites* sp. B. Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 4). 3/4.
4. *Protichnites* sp. A. Magnesian Sandst.; Kusak (vgl. Taf. 16, Bild 2). 3/4.
5. *Diplichnites* sp. Magnesian Sandst.; Khewra (vgl. Teil IV, Abb. 1). 3/4.
6. *Crossochorda* sp. Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 5). 3/4.
7. *Scolicia* cf. *sardoa* (MGH.). Modelle nach Stücken aus dem Magnesian Sandst. von Khewra und Kusak. a) Oberseitenform (negativ exogenes Epirelief). b) Endogene Vollform, von unten gesehen.

Weidespur eines Trilobiten:

8. *Dimorphichnus obliquus* n. g. n. sp., Magnesian Sandst.; Kusak (vgl. Teil IV, Abb. 3). 1/3.

Freßbauten:

9. *Dictyodora simplex* n. sp., Schichtflächen-Schnitt. *Neobolus* Beds; Khân Zamân Nala bei Chhidru (Ic 1071/7). 1/3.
10. *Teichichnus rectus* n. g. n. sp.; Modell nach Stücken aus den *Neobolus* Beds von Khewra und Kusak. Etwa 1/3.
11. *Corophioides* cf. *rosei* DAHMER; Modell nach Stücken aus den *Neobolus* Beds von Khewra. Etwa 1/3.
12. *Rhizocorallium jenense* ZENKER. Modell nach Stücken aus den *Neobolus* Beds von Khewra. Etwa 1/3.
13. *Phycodes pedum* n. sp., Modell nach Stücken aus den *Neobolus* Beds der Khân Zamân Nala. Etwa 2/3.
14. *Phycodes palmatum* (HALL). Modell nach Stücken aus den *Neobolus* Beds von Khewra. Etwa 1/3.
15. *Bifungites* sp., Magnesian Sandst.; Kusak (Ic 1071/8). 3/4.
16. *Laericyclus* sp., Rekonstruktion nach Stücken aus dem Magnesian Sandst. von Tobra (vgl. Taf. 18, Bild 1). 4/3.

Nereiten-Schichten (geosynklinales Ordovizium bis Devon), Portugal (nach DELGADO 1910)

Kriechspuren:

17. Trilobiten-Fährten verschiedener Größe, zum Teil im Schräggang entstanden. Untersilur; Barrancos (DELG., Taf. 43, Fig. 4). 1/3.

Weidespuren:

18. In unregelmäßigen Zirkeln parkettierende Doppelschnur. Untersilur; Barrancos (DELG., Taf. 46, Fig. 2). 1/2. — Wie ich mich durch Vermittlung von Herrn Dr. L. SCHLEICHER am Original überzeugen konnte, handelt es sich um vollkörperliche Schnüre, die sich gelegentlich in derselben Ebene durchsch ist also nur eine oberflächliche.
19. *Palaeodictyon* sp. (= *Retiphycus*; vgl. Geologischen Staatsinstitut, Hamburg) Wissens noch nicht gefunden.
20. *Nereites* sp. (eine von mehreren, zum stimmten Arten). Obersilur oder Unterde
21. *Myrianites*? (vielleicht auch zu *Dicty* Taf. 32, Fig. 4). 1/3.
22. *Crossopodia* aff. *henrici* GEIN. (= mäan oder Unterdevon; Malhadinha, Aljustrel

Freßbauten:

23. *Phycosiphon* cf. *incertum* FISCHER-OOST 56 und 78). Obersilur oder Unterdevon ergänzt). 3/4.
24. *Lophoctenium comosum* RICHT. (vgl. 86!) DEGLADO, ergänzt nach thüringischen St
25. Noch unbeschriebener Freßbau ähnlich (Fig. 2). 1/1.
26. *Chondrites* sp., Obersilur oder Unterdev Fig. 1). 1/2.

Schilfsandstein (kontinentale Ober LINC

Ruhespuren:

27. *Rusophycus didymus* (SALTER). Ähnlich stammend. Ob. Schilfsandstein; Mühlbac
28. *Sagittichnus linckі* SEIL. Schilfsandstein
29. *Pelecypodichnus amygdaloides* SEIL. (vgl (Original Sammlung LINCK, Güglingen).

Kriechspuren:

30. *Limuludichnulus gracilis* LINCK. Ob. S
31. Unbenannte Kriechspur einer Muschel Sternenfels (LINCK, Taf. 8, Fig. 1). 1/3.
32. Doppelwulstige Kriechspur eines wurmar Relief unterschieden!). Ob. Schilfsandst.

Freßbauten?

33. Nicht näher bestimmbares Tunnel-Ge Fig. 1). 1/3.

Wohnbauten:

34. *Biformites insolitus* LINCK. Schilfsandst.

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

Explanation of Text Figure 43

Comparative Palichnology (Seilacher 1964). . . . . p. 407

The chart compares suites from 42 different localities having a wide geologic and geographic range. Seilacher recognised three distinct "facies"; the "Nereites facies" characterised by Pascichnia, the "Cruziana facies" characterised by Cubichnia, and the "Zoophycos facies" dominated by Zoophycos. For a more complete portrayal of the Cincinnatian suite see fig. 44. A key to the numbered specimens is given below.

1. Nereites
2. Dictyodora
3. Helminthoida
4. Cosmoraphe
5. Urohelminthoida
6. Paleomaendron
7. Taphrhelminthopsis
8. Ceratophycus, Spirodesmos
9. Spirorhaphe
10. Lophoctenium
11. Oldhamia
12. Paleodictyon
13. Zoophycos
14. tracks of trilobites (left), Limulids (right) and other arthropods
15. Cruziana, Rusophycus

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

Explanation of Text Figure 43

Comparative Palichnology (Seilacher 1964). . . . . p. 407

The chart compares suites from 42 different localities having a wide geologic and geographic range. Seilacher recognized three distinct "facies"; the "Nereites facies" characterized by Pascichnia, the "Cruziana facies" characterized by Cubichnia, and the "Zoophycos facies" dominated by Zoophycos. For a more complete portrayal of the Cincinnatian suite see fig. 44. A key to the numbered specimens is given below.

1. Nereites
2. Dictyodora
3. Helminthoida
4. Cosmoraphe
5. Urohelminthoida
6. Paleomaendron
7. Taphrhelminthopsis
8. Ceratophycus, Spirodesmos
9. Spirorhaphe
10. Lophoctenium
11. Oldhamia
12. Paleodictyon
13. Zoophycos
14. tracks of trilobites (left), Limulids (right) and other arthropods
15. Cruziana, Rusophycus

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

Explanation of Text Figure 43 continued

16. Thalassinoides
17. Rhizocorallium
18. Asteriacites
19. Bergaueria (left), Solicyclus (right)
20. Pelecypodichnus
21. Corophioides
22. Teichichnus
23. Phycodes
24. Chondrites
25. Phycosiphon
26. Scolicia
27. Muensteria
28. Fucusopsis
29. Gyrochorte
30. Scalarituba (=Neonereites)

(from Seilacher, 1964, fig. 7, reproduced with the permission of John Wiley and Sons, New York)

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

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

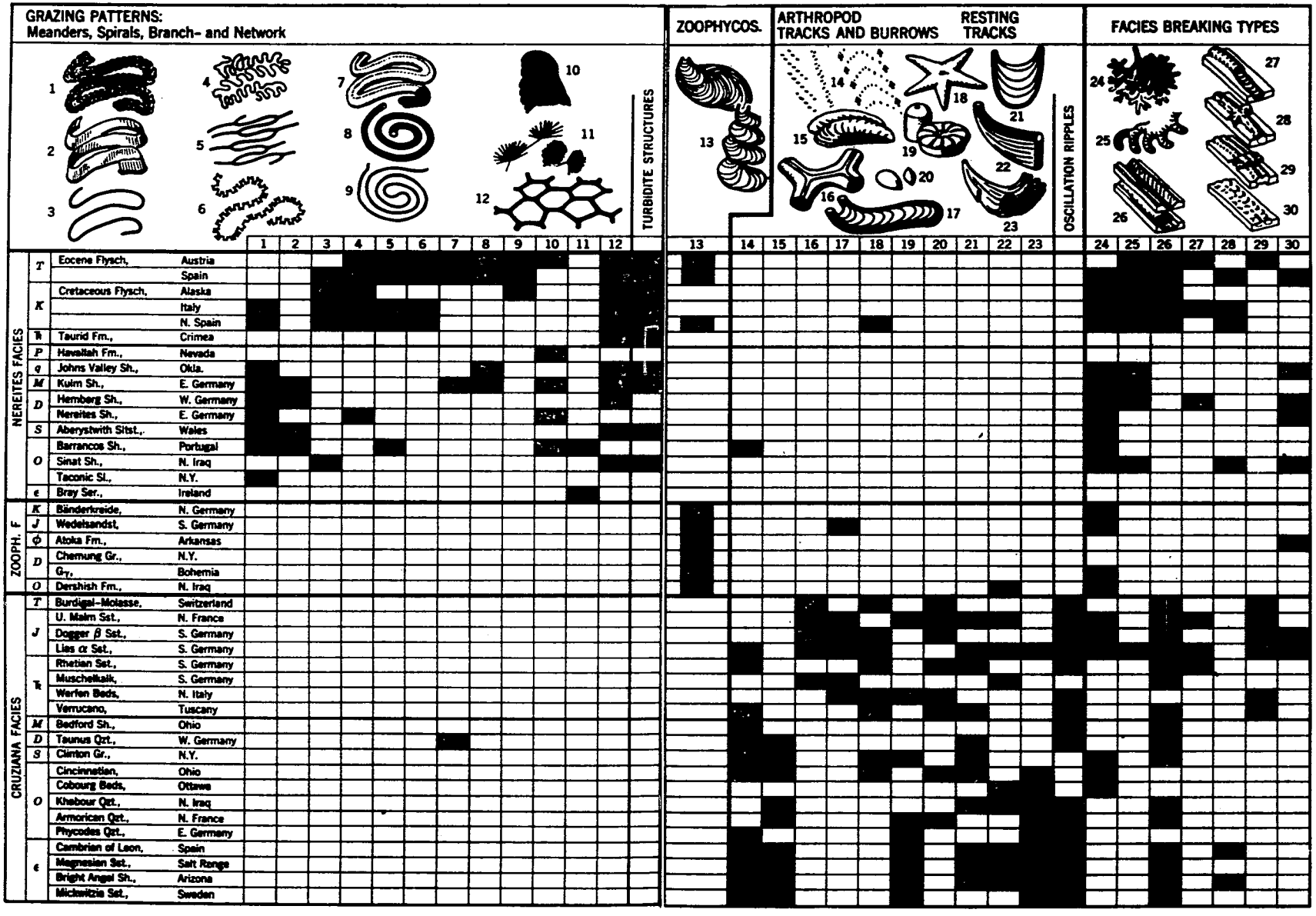


Figure 43

Explanation of Text Figure 44

Cincinnatian Trace Fossil Suite. . . . . p. 407

The chart shows reconstruction of Cincinnatian trace fossils placed in their ethologic catagories. Cubichnia are numerous both in kind and numbers whereas the only Pascichnia are two specimens tentatively assigned to Paleodictyon. This distribution places the Cincinnatian suite within Seilacher's "Cruziana facies", i.e., a shallow water, marine environment.

a. Rusophycus carleyi (X 0.25)
b. Rusophycus pudicum (X 0.5)
c. Rusophycus cryptolithi (X 1)
d. Lockeia siliquaria (X 0.5)
e. Asteriacites stelliforme (X 0.3)
f. Asaphoidichnus trifidum (X 0.25)
g. Trachomatichnus numerosum (X 0.25)
h. Allocotichnus dyeri (X 0.3)
i. cf. Petalichnus multipartitum; oblique movement (X 0.5)
j. cf. Petalichnus multipartitum; straight-ahead movement (X 0.5)
k. Palaeophycus sp.; plan and cross-section views (X 0.3)
l. Rhabdoglyphus sp. (X 0.5)
m. Tylichnus asperum (X 4)
n. ?Paleodictyon sp. (X 1)
o. Corophioides cf. luniformis (X 0.2)

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

Explanation of Text Figure 44 continued

p. Corophioides cincinnatiensis (X 0.2)

q. Corophioides biclavata (X 0.2)

r. Skolithos delicatulus (X 0.5)

s. Chondrites, type-B (X 0.2)

t. Chondrites, type-C (X 0.25)

u. Chondrites, type-A (X 0.25)

v. Fascifodina floweri (X 0.2)

w. Trichophycus venosum (X 0.15)

x. Phycodes flabellum (X 0.25)

y. Dactylophycus quadripartitum (X 0.25)

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

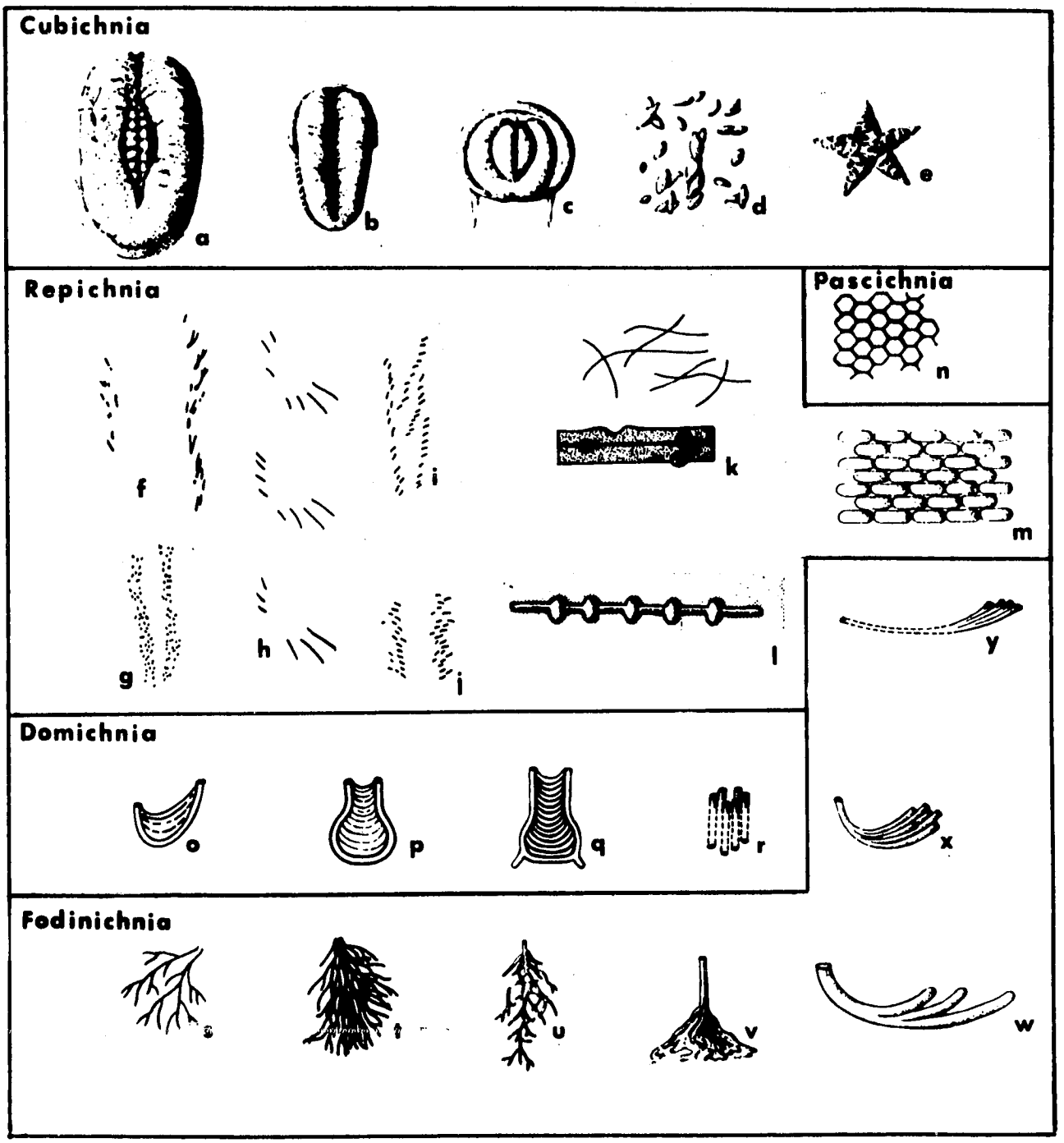


Figure 44

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

Plates

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

Explanation of Plate 1

Figure

1. Rusophycus carleyi (J.F. James), 1885. . . . . p. 85
Cubichnia of Isotelus; convex hyporelief which demonstrates the inseparability of body fossils and trace fossils. Casts of the genal spines, cephalic and pygidial doublures, hypostome and proximal portions of the walking legs as well as the lateral lobes are imprinted. Gift of Dr. George Walker. Corryville beds, Stonelick, Clermont County, Ohio. UCM 37598, X 0.75.

2. Asteriacites stelliforme (Miller and Dyer), 1878
. . . . . p. 103
Cubichnia of asteroid; convex hyporelief showing vertical repetition. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37599, X 1.

3. Dactylophycus quadripartitum Miller and Dyer, 1878
. . . . . p. 226
Fodinichnia; convex hyporelief showing bilobation and faintly defined annuli. Cotype. Eden beds, Cincinnati, Ohio. HBM 3174; latex mold UCM 37600, X 1.

4. Phycodes flabellum (Miller and Dyer), 1878 . . p. 216
Fodinichnia or Domichnia; cross-section showing filling of the proximal portion of the burrow, i.e.

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

Explanation of Plate 1 continued

Figure

4 continued. the master shaft. Locality unknown. UCM 37667, X 1.

5. Isotelus maximus Locke, 1838 . . . . . p. 85
View of ventral surface showing preserved appendages. Note that coxae are much longer than those seen in Rusophycus carleyi (fig. 1 above). Hypotype. Richmond beds, Oxford, Ohio. USNM 33458, X 0.75.

6. Rusophycus pudicum Hall, 1852. . . . . p. 82
Cubichnia of Flexicalymene meeki; one of three specimens known from the Cincinnatian where the producer of the burrow (Flexicalymene meeki) is preserved in situ. Corryville beds of Stonelick Creek, Clermont County, Ohio. Specimen in private collection of Mr. William White, Jr., Milford, Ohio; latex mold UCM 37641, X 1.5.

7. Lockeia siliquaria U.P. James, 1879. . . . . p. 91
Cubichnia of pelecypod. Note linear alignment of some forms. Paratype. Uppermost Trenton or lowermost Cincinnatian, Ludlow, Kentucky. UCM 37597, X 1.

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.

Explanation of Plate 2

Figure

1,2 Rusophycus cryptolithi, n. sp. . . . . p. 89

1. Cubichnia of Cryptolithus; convex hyporelief showing a specimen with an undercut forward wall (top). Note the casts of the impressions of the genal spines. Economy beds, Humphrey's Branch, Twelve Mile Creek, Campbell County, Kentucky. Specimen in private collection of Mr. William White, Jr., Milford, Ohio; latex mold UCM 37601, X 1.

2. Convex hyporelief showing coarsely striate outer lobes and finely striate inner lobes. Holotype. Locality same as fig. 1 above. UCM 37587, X 1.25.

3-6 Rusophycus pudicum Hall, 1852. . . . . p. 82

3. Cubichnia of Flexicalymene; convex hyporelief showing horizontal repetition. Corryville beds, Taylor Creek between Miamitown and Dent, Ohio. MU T88; latex mold UCM 37709, X 1.75.

4. Convex hyporelief of fig. 5 below, X 1.1.

5. This remarkable specimen reveals the originator of the trace, Flexicalymene meeki, in situ.

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

Explanation of Plate 2 continued

Figure

5 continued. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37574, X 1.1.

6. Cubichnia of ?Calymene; convex hyporelief of Cotype. Note that this specimen closely resembles those seen in fig. 9-10 below. Clinton beds, Oneida County, New York. USNM 41113; latex mold UCM 37581, X 0.7.

7,8 Rusophycus carleyi (J.F. James), 1885. . . . . p. 85

7. Cubichnia of Isotelus; convex hyporelief showing a well-preserved cephalic or pygidial doublure. Corryville beds, Stonelick Creek, Clermont County, Ohio. Specimen in private collection of Mr. William White, Jr., Milford, Ohio; latex mold UCM 37710, X 0.7.

8. Convex hyporelief showing nodes attributable to the coxae of Isotelus. Locality unknown. MCZ 551; latex mold UCM 37596, X 0.75.

9,10 Rusophycus pudicum Hall, 1852. . . . . p. 82

9. Convex hyporelief which shows a dense grouping of the resting traces. It is impossible to

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

Explanation of Plate 2 continued

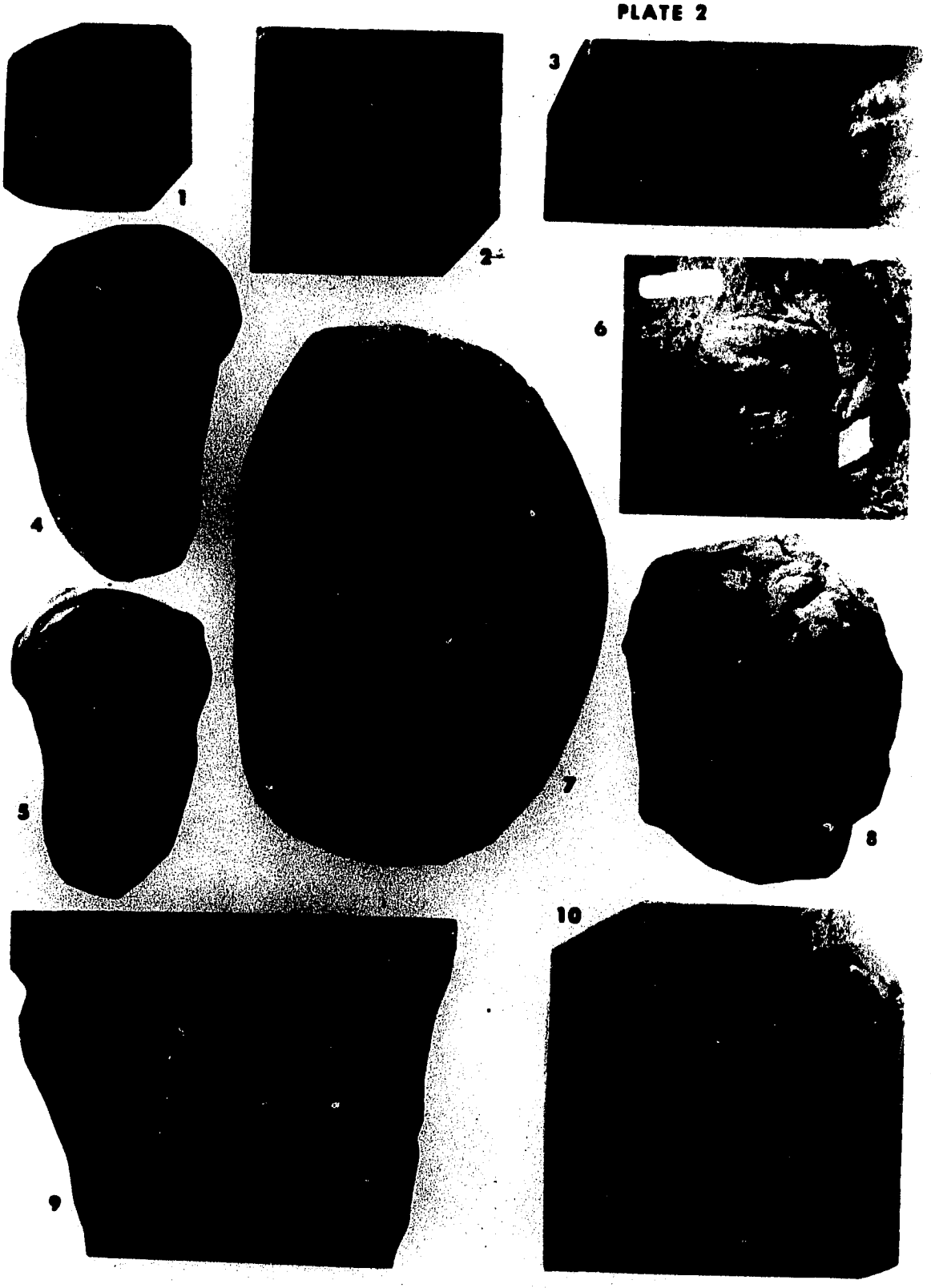
Figure

9 continued. determine how many trilobites were involved. Locality unknown. MU T87; latex mold UCM 37641, X 0.6.

10. Convex hyporelief associated with six specimens of Lockeia siliquaria. The traces occur at the bottom of a channel filling. Mt. Hope beds, Stonelick Creek, Clermont County, Ohio. UCM 37642, X 0.9.

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.

Explanation of Plate 3

Figure

1. Lockeia siliquaria U.P. James, 1879. . . . . p. 91
Cubichnia of pelecypods; etched cross-section showing that the burrow is truncated and does not extend up into the host rock. Uppermost Trenton or lowermost Eden, Ludlow, Kentucky. UCM 37675, X 4.5.

2. Asteriacites stelliforme (Miller and Dyer), 1878
. . . . . p. 103
Cubichnia of asteroid; showing striae made by the tube feet. Holotype. Maysville beds, Cincinnati, Ohio. HBM 3175; latex mold UCM 37568, X 1.25.

3. "Rusophycus" subangulatum Hall, 1852 . . . . . p. 80
Repichnia of trilobite; convex hyporelief. Such elongated burrows are not common in the Cincinnatian. Cotype (Hall, 1852, pl. 8, fig. 2b). Clinton beds, Oneida County, New York. USNM 41112, X 0.67.

4. Rusophycus cryptolithi n. sp. . . . . p. 89
Cubichnia of Cryptolithus; convex hyporelief showing groupings of casts of four shallow burrows showing vertical repetition. Paratype. Economy beds of Duck Creek, Campbell County, Kentucky. UCM 37567, X 1.

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

Explanation of Plate 3 continued

Figure

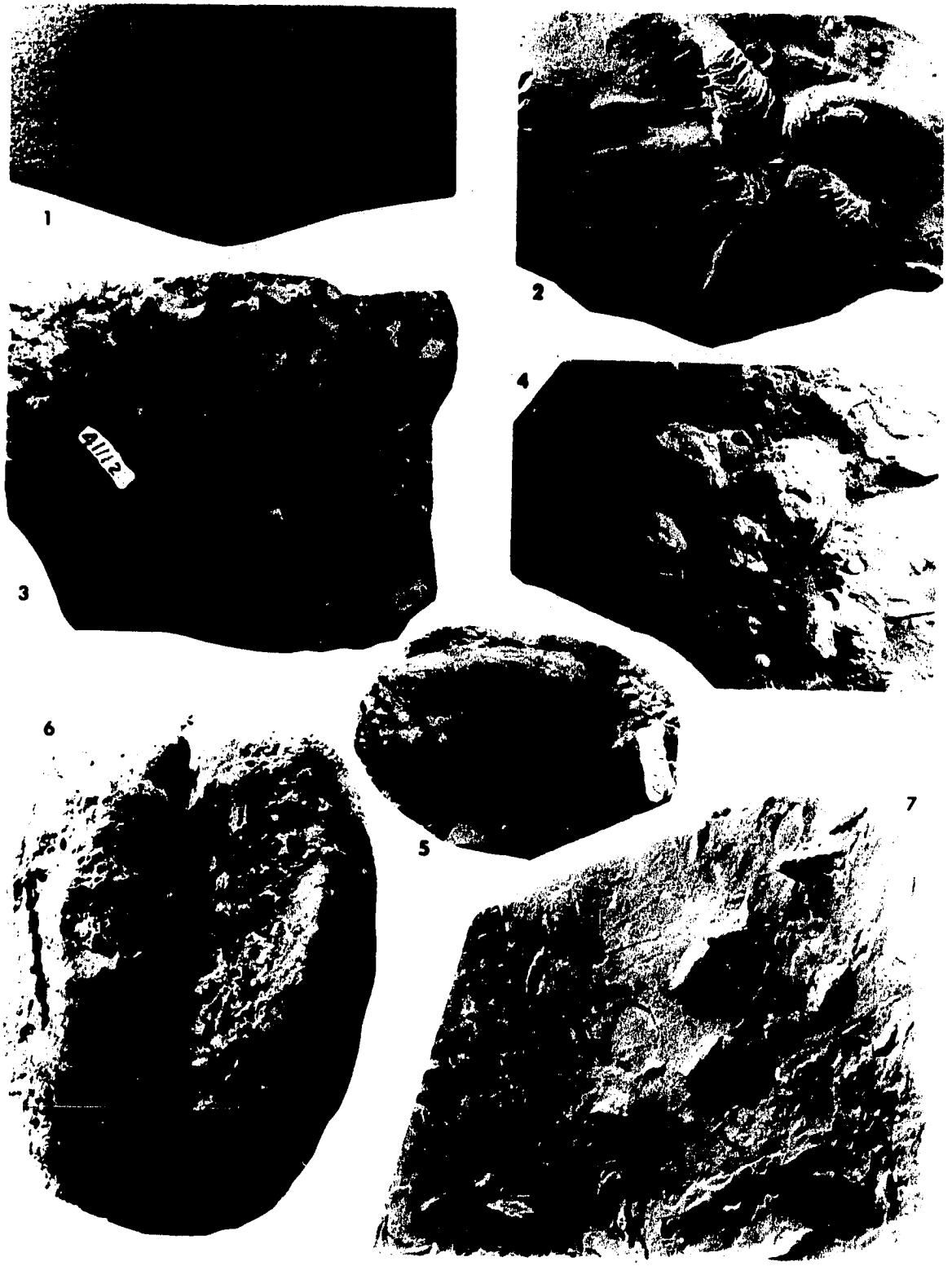
5. Rusophycus pudicum Hall, 1852. . . . . p. 82
Cubichnia of ?calymenid; convex hyporelief. Cotype. Clinton beds, Oneida County, New York. USNM 41115, X 1.

6. Rusophycus carleyi (J.F. James), 1885. . . . . p. 85
Cubichnia of Isotelus; convex hyporelief showing largest Rusophycus known. Note the well-defined genal spine and pleural imprints. ?Maysville beds, near Bantam, Clermont County, Ohio. UCM 37566, X 0.4.

7. Lockeia siliquaria U.P. James, 1879. . . . . p. 91
Cubichnia of pelecypod; convex hyporelief. ?Economy beds of Twelve Mile Creek, Campbell County, Kentucky. UCM 37577, X 1.

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.

Explanation of Plate 4

Figure

1. Corophioides cincinnatiensis n. sp. . . . . p. 137
Domichnia; U-plane section showing an annulate irregular arm. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37602, X 1.

2. Rusophycus pudicum Hall, 1852. . . . . p. 82
Cubichnia of trilobite; convex hyporelief showing horizontal repetition. Southgate strata of Rapid Run, Hamilton County, Ohio. UCM 16448, X 0.6.

3,4 Corophioides biclavata (Miller), 1875 . . . . . p. 143

3. Domichnia; epirelief showing a modified arm and the remnants of the Spreiten. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37659, X 0.75.

4. Hyporelief showing modified arms and Spreite. Locality unknown. UCM 37658, X 1.

5. Corophioides cincinnatiensis n. sp. . . . . p. 137
U-plane section. McMicken beds, U.S. Route 27, 1.4 miles south of Newport Shopping Center, Southgate, Kentucky. UCM 37592, X 0.8.

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

Explanation of Plate 4 continued

Figure

6. Corophioides polyupsilon John Smith, 1893. . . p. 113
Domichnia; U-plane section of holotype demonstrating that the Spreiten abut against the arms instead of forming a "U in U" structure as Smith believed. Upper Carboniferous beds near Kilwinning, Scotland. HM X59; latex mold UCM 37572, X 0.75.

7. Trichophycus venosum Miller, 1879. . . . . p. 232
Fodinichnia or Domichnia. A "turkey track" truncating another individual still containing remnants of the burrow filling. Humphrey's Branch of Twelve Mile Creek, Campbell County, Kentucky, some 30 meters upstream from the type locality of Rusophycus cryptolithi. UCM 37575, X 0.5.

8. Corophioides cincinnatiensis n. sp. . . . . p. 137
U-plane section showing marked basal expansion. Locality same as fig. 5 above. Specimen destroyed by subsequent sectioning. X 1.5.

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.

Explanation of Plate 5

Figure

1-3 Corophioides biclavata (Miller), 1875. . . . . p. 143

1. Domichnia; concave epirelief showing that the connecting bar does not extend to the terminal depressions. Locality unknown. UCM 37656, X 0.8.

2. Convex hyporelief. Locality unknown. UCM 37655, X 1.

3. Concave epirelief. The inner wall of the large terminal depressions is undercut. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37657, X 0.75.

4. Corophioides cincinnatiensis n. sp . . . . . p. 137
Domichnia; U-plane section of holotype showing the irregular course of the arms. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37590, X 1.

5. Corophioides cf. luniformis . . . . . p. 134
Domichnia; concave epirelief showing numerous closely spaced U-shaped depressions. Waynesville beds, Flat Fork of Caesar's Creek, Harveysburg, Warren County, Ohio. MU T89; latex mold UCM 37711, X 0.75.

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

Explanation of Plate 5 continued

Figure

6. Corophioides cincinnatiensis n. sp. . . . . p. 137
U-plane section showing marked basal expansion. McMicken beds, U.S. Route 27, 1.4 miles south of Newport Shopping Center, Southgate, Kentucky. UCM 37589, X 1.

7. Corophioides biclavata (Miller), 1875. . . . . p. 148
Convex hyporelief showing filling of the dumbbell and remnants of the Spreiten. Fulton beds, Union Levee, Cincinnati, Ohio. UCM 16566, X 1.

8. Corophioides cincinnatiensis n. sp. . . . . p. 137
U-plane section. Locality same as fig. 6 above. UCM 37591, X 0.9.

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.

Explanation of Plate 6

Figure

1,2 *Corophioides* cf. *luniformis*. . . . . p. 134

1. Domichnia; U-plane section. Locality unknown. UCM 37611, X 1.

2. Concave epirelief; probable mold of the base of the "U." Locality unknown. UCM 37654, X 1.

3,4 *Corophioides cincinnatiensis* n. sp. . . . . p. 137

3. Domichnia; U-plane section showing details of the *Spreite* structure. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37624, X 1.25.

4. Latex mold of the basal portion of the U showing close-spaced annuli. McMicken beds, U.S. Route 27, 1.4 miles south of Newport Shopping Center, Southgate, Kentucky. UCM 37589, X 1.

5. *Asteriacites stelliforme* (Miller and Dyer), 1878 . . . . . p. 107

Cubichnia of asteroid; convex hyporelief. Locality unknown. UCM 37674, X 1.

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

Explanation of Plate 6 continued

Figure

6. Corophioides cincinnatiensis n. sp. . . . . p. 137
U-plane section of incomplete specimen. Locality same as fig. 4 above. UCM 37625, X 1.

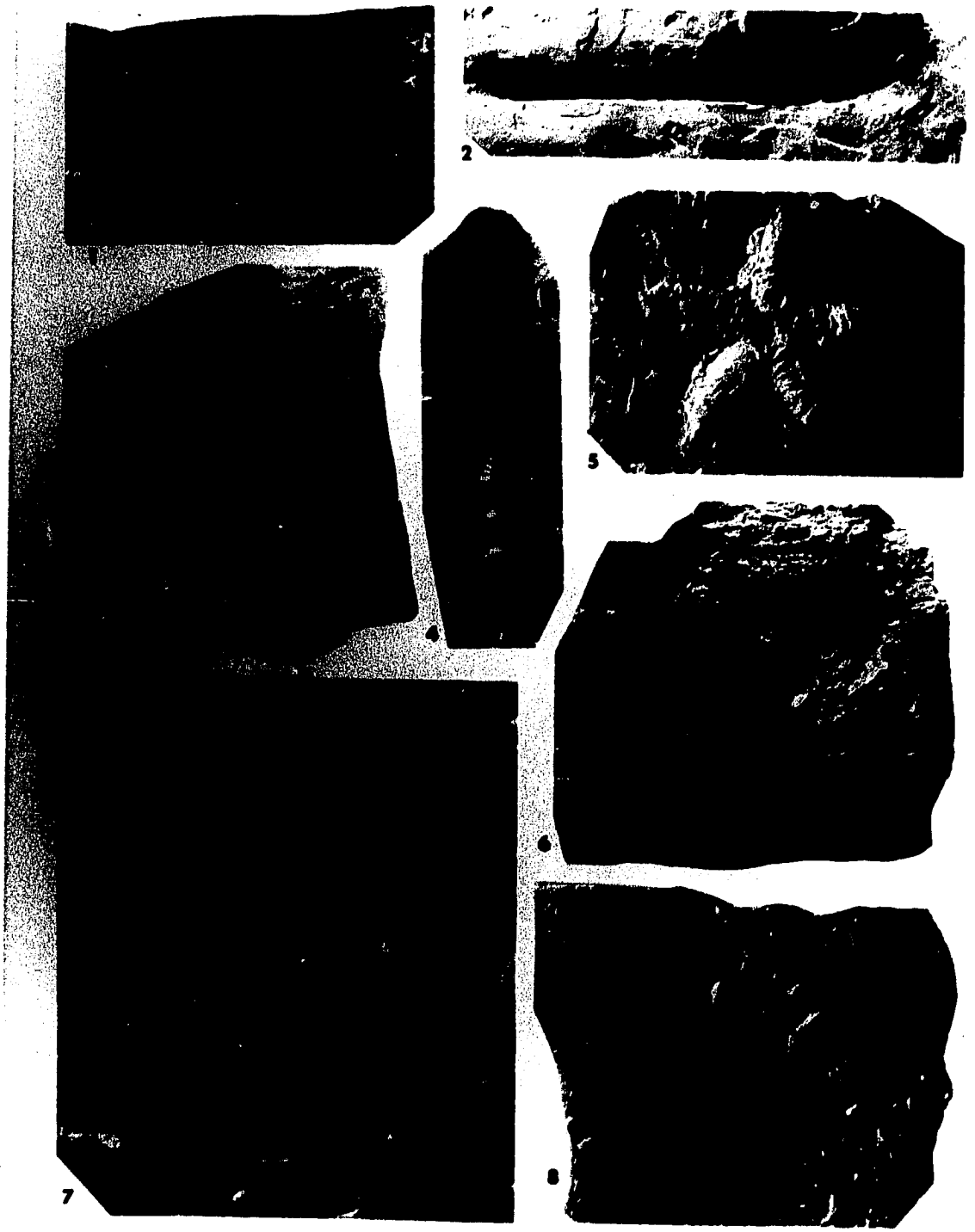
7,8 Skolithos delicatulus U.P. James, 1881 . . . . p. 157

7. ?Domichnia; view of lower (hyporelief) surface of hypotype (J.F. James, 1892, fig. 15). Richmond beds of Dearborn County, Indiana. UCM 37673, X 0.75.

8. Enlarged view of a portion of above showing calcite fillings and encircling depressions. X 3.

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.

Explanation of Plate 7

Figure

1. cf. Palaeophycus Hall, 1847. . . . . p. 322
Repichnia; concave epirelief showing the sinuous nature of the trail. Southgate beds of Newport Shopping Center, Newport, Kentucky. UCM 37637, X 0.75.

2. Chondrites, type-C . . . . . p. 202
Fodinichnia; concave epirelief. Whitewater beds of Short Creek, three miles southeast of Richmond, Indiana. MU T93; latex mold UCM 37636, X 1.

3. Chondrites, type-B . . . . . p. 193
Fodinichnia; vertical section showing a portion of the network. Note upward curvature of some of the branches. Upper Richmond beds, State Route 32, six miles southwest of Flemingsburg, Kentucky. UCM 37665, X 0.8.

4. Corophioides cincinnatiensis n. sp. . . . . p. 137
Domichnia; U-plane section showing association of C. cincinnatiensis and Chondrites, type-A. McMicken beds, U.S. Route 27, 1.4 miles south of Newport Shopping Center, Kentucky. UCM 37680, X 0.6.

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

Explanation of Plate 7 continued

Figure

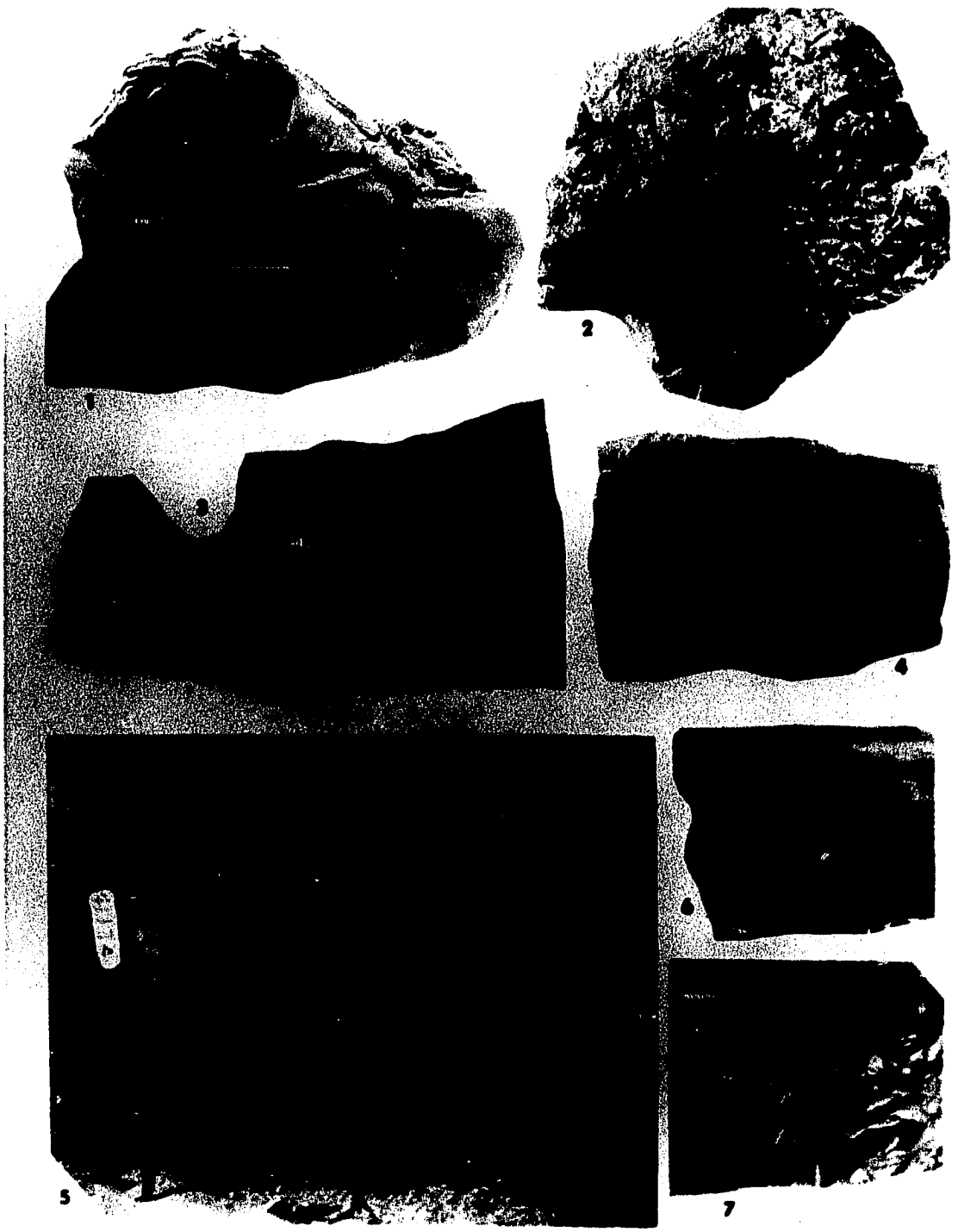
5. Chondrites gracilis var. crassa Hall, 1852 . . p. 179
Fodinichnia; slab shows only a portion of the network. Cotype (Hall, 1852, Pl. 5, fig. 3c). Clinton beds, Oneida County, New York. USNM 41134, X 1.

6. Lockeia siliquaria U.P. James, 1879. . . . . p. 91
Domichnia of pelecypod; vertical section showing disturbed column of sediment overlying the almond-shaped burrow filling. ?Economy beds of Twelve Mile Creek, Campbell County, Kentucky. UCM 37679, X 1.3.

7. Dactylophycus quadripartitum Miller and Dyer, 1878
. . . . . p. 223
Fodinichnia; convex hyporelief. The master shaft presumably extended to the upper left. Economy beds, West Covington, Kentucky. USNM 40027; latex mold UCM 37712, X 1.

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.

Explanation of Plate 8

Figure

1. *Fucusopsis sulcatum* (Miller and Dyer), 1878. . p. 336
Repichnia; convex hyporelief. Locality unknown. UCM 37616, X 1.

2. *Chondrites*, type-C . . . . . p. 202
Fodinichnia; latex mold of a concave epirelief. Note the circular grouping of the burrows in the lower left. Whitewater beds, Short Creek, three miles southeast of Richmond, Indiana. MU T92; latex mold UCM 37615, X 1.25.

3. *Chondrites*, type-B . . . . . p. 193
Fodinichnia; vertical section showing what is interpreted as a portion of the main shaft of the burrow. Upper Richmond beds, State Route 32, six miles southeast of Flemingsburg, Kentucky. UCM 37665, X 1.

4,5 *Chondrites*, type-C . . . . . p. 202

4. Latex mold of epirelief showing some degree of bilateral symmetry. Locality same as fig. 2 above. MU T91; latex mold UCM 37614, X 0.85.

5. Latex mold of epirelief. One system of burrows (upper left) is oriented parallel to the bedding

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

Explanation of Plate 8 continued

Figure

5 continued. plane; the other system (lower right) obliquely to the bedding plane. Locality same as fig. 2 above. MU T90; latex mold UCM 37678, X 0.6.

6. Chondrites, type-A . . . . . p. 188
Fodinichnia; epirelief showing a compact group of vertical burrows. Southgate beds, Newport Shopping Center, Newport, Kentucky. UCM 37612, X 1.

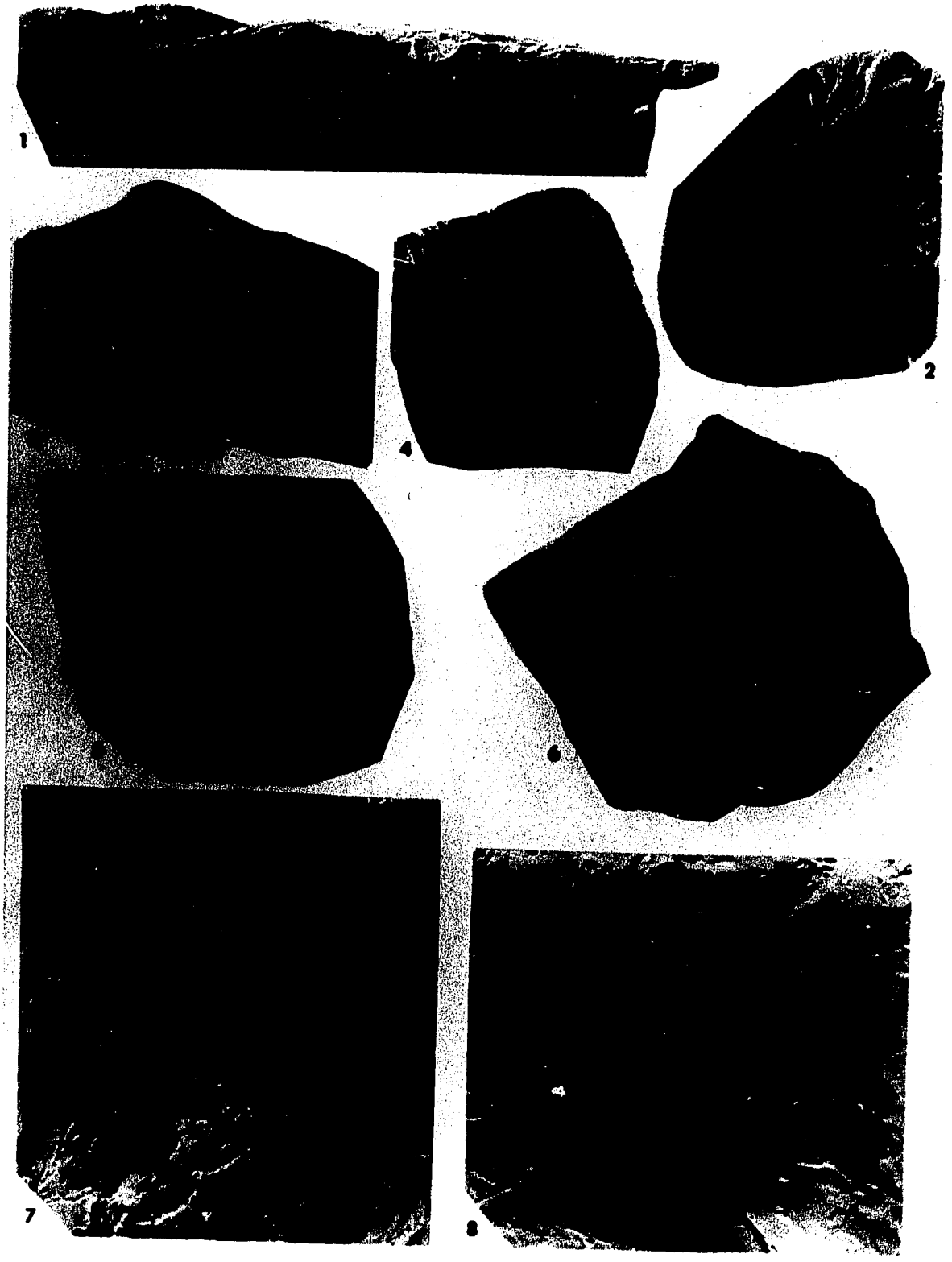
7,8 Chondrites, type-B . . . . . p. 193

7. Epirelief showing a dense grouping of burrow systems. Locality same as fig. 3 above. UCM 37613, X 0.4.

8. Typical arrangement of C., type-B structure. Locality unknown. UCM 37666, X 0.85.

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.

Explanation of Plate 9

Figure

1-4 Phycodes flabellum (Miller and Dyer), 1878 . . p. 216

1. Fodinichnia or Domichnia; convex hyporelief showing portions of more than one burrow system. Holotype. Richmond beds near Lebanon, Ohio. HBM 3178; latex mold UCM 37621, X 0.85.

2. Vertical cross-section showing "ascending Spreiten". Note that the burrow truncates the clay inclusions. Locality unknown. UCM 37684, X 2.3.

3. Vertical cross-section; disturbance of the bedding caused by burrow penetration (center bottom). Corryville beds, Stonelick Creek, Clermont County, Ohio. Specimen destroyed by subsequent grinding. X 0.85.

4. Vertical cross-section showing master shaft extending nearly to the base of the host rock. Locality unknown. UCM 37672, X 1.1.

5. Phycodes circinatum Reinhard Richter, 1850 . . p. 209 Convex hyporelief of a sparsely branching specimen. "Phycodes beds" (Ordovician), Saalfeld, Thuringia. UCM 37526, X 1.1.

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

Explanation of Plate 9 continued

Figure

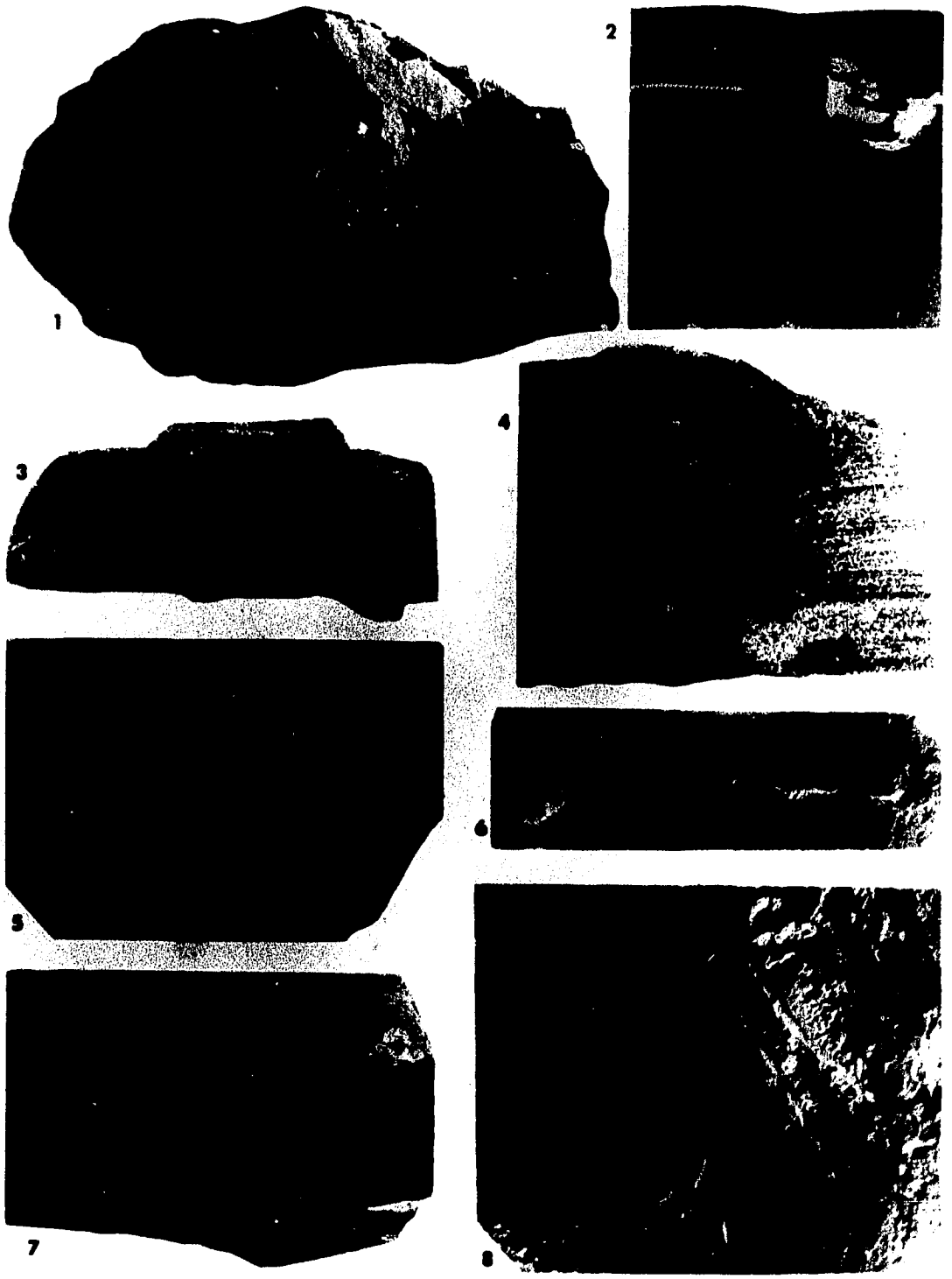
6. Corophioides biclavata (Miller), 1875. . . . . p. 143
Domichnia; concave epirelief. Note that only the left end of the structure has been modified. Locality unknown. UCM 37648, X 0.5.

7. Trachomatichnus numerosum Miller, 1880 . . . . p. 281
Repichnia; convex hyporelief interpreted as the Cruziana-like trail of Cryptolithus; also see text figure 40. Location unknown. UCM 37622, X 0.85.

8. Chondrites, type-B . . . . . p. 198
Fodinichnia; latex mold showing the characteristic rigidity of the branches noted by Simpson (1957). Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37623, X 0.85.

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.

Explanation of Plate 10

Figure

1. Paleodictyon sp. Savi and Meneghini, 1850. . . p. 344
Pascichnia; convex hyporelief showing a well-preserved network. Eocene beds near Trieste, Italy. UCM 37507, X 0.7.

2. Phycodes flabellum (Miller and Dyer), 1878 . . p. 209
Fodinichnia or Domichnia; convex hyporelief showing a poorly organized system. Note that the flabellate pattern characteristic of most Cincinnatian representatives of the genus is lacking. Corryville beds, Stonelick Creek, Clermont County, Ohio. UCM 37635, X 0.85.

3. Rusophycus pudicum Hall, 1852. . . . . p. 82
Cubichnia of moderate sized trilobite; convex hyporelief. The morphology exhibited by this specimen is intermediate between Rusophycus and Cruziana. Such elongated forms are not common in the Cincinnatian. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 37633, X 0.85.

4. Phycodes flabellum (Miller and Dyer), 1878. . . p. 209
Fodinichnia or Domichnia; convex hyporelief showing a system with radial symmetry. The large protuberance marking the center of the system is not thought

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

Explanation of Plate 10 continued

Figure

4 continued. to be genetically related to the Phycodes burrow. Locality unknown. UCM 37631, X 0.75.

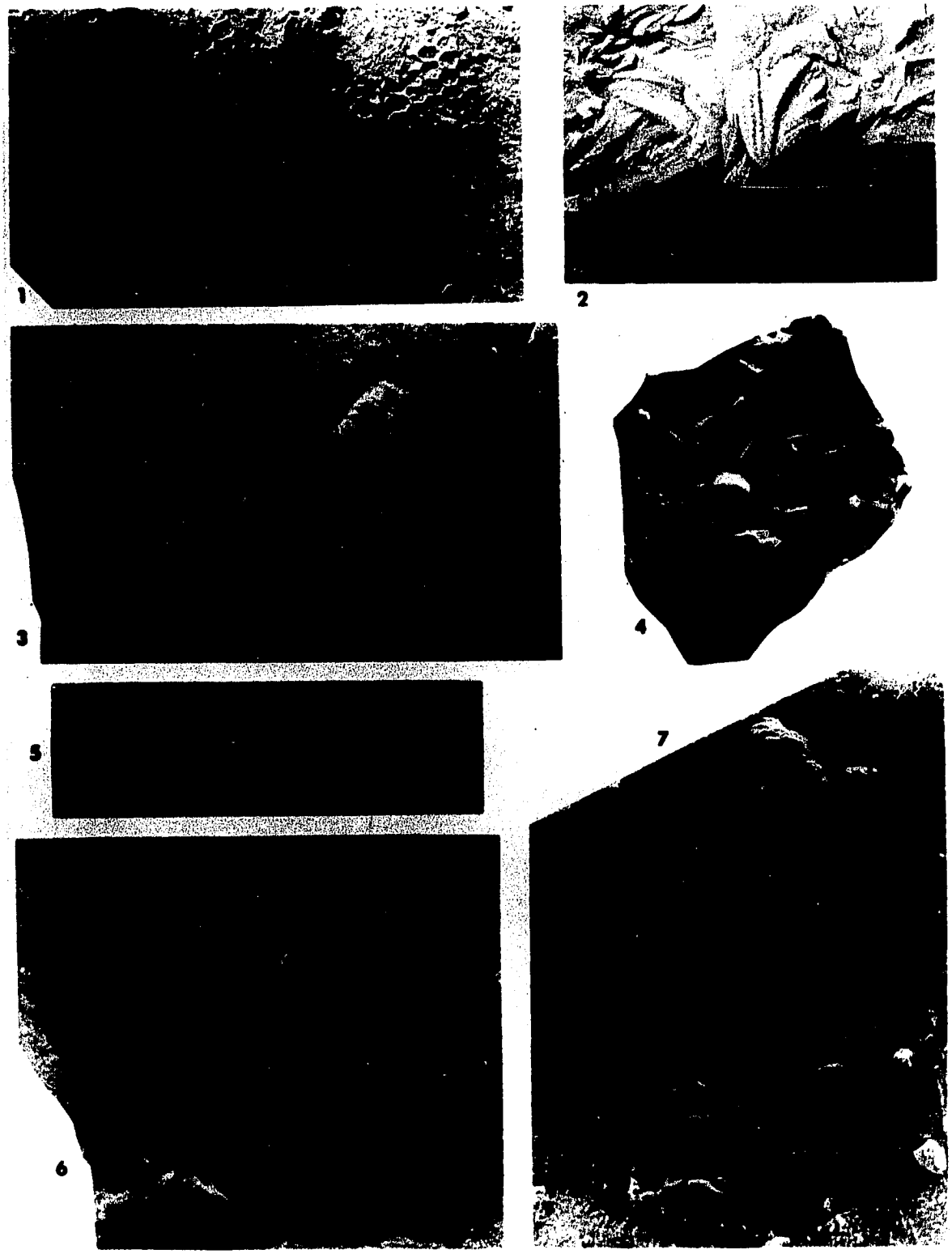
5. Corophioides biclavata (Miller), 1875. . . . . p. 143
Domichnia; concave epirelief. Corryville beds of Stonelick, Clermont County, Ohio. UCM 37634, X 1.

6. Fascifodina floweri n. gen., n. sp. . . . . p. 205
Fodinichnia; epirelief showing concave vermiform markings surrounding the convex bundled shafts. Note that one of the branches (lower right) leads directly into one of the concave markings. Holotype. Corryville beds of Second Creek where crossed by Cozzadale Road, Clermont County, Ohio. UCM 37632, X 1.1.

7. Tylichnus asperum (Miller and Dyer), 1878. . . p. 304
Repichnia; convex hyporelief showing several superimposed trails. Note moniliform casts of ?fecal strings in bottom center. Locality unknown. MCZ 1054; latex mold UCM 37687, X 2.3.

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

PLATE 10



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

Explanation of Plate 11

Figure

1. ?*Paleodictyon* sp. Savi and Meneghini, 1850 . . p. 344
Pascichnia; convex hyporelief showing unequal development in the thickness of the walls. McMillan beds of Ravine Street, Cincinnati, Ohio. UCM 17431, X 1.5.

2. "*Blastophycus diadematum*" Miller and Dyer, 1878
. . . . . p. 366
Plaster cast showing scour marks associated with an enrolled trilobite, *Flexicalymene meeki*. Experimentally produced. UCM 37640, X 0.85.

3. *Buthotrephis palmata* Hall, 1852. . . . . p. 162
?Fodinichnia; convex hyporelief. View of cotype illustrated by Hall (1852, pl. 7, fig. 1b). The specimen differs considerably from the other species of *Buthotrephis* proposed by Hall. Clinton (Silurian) beds of New Hartford, New York. USNM 41083, X 0.85.

4. *Chondrites*, type-A . . . . . p. 188
Fodinichnia; vertical section showing that there is no well-defined central axis. McMicken beds, West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37607, X 0.85.

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

Explanation of Plate 11 continued

Figure

5. Rusophycus clavatum Hall, 1852 . . . . . p. 80
Repichnia; convex hyporelief. The pod-like outline of the burrow is attributable to a "back and forth" movement by the originator. In reality the specimen lies closer to Cruziana than Rusophycus. Cotype. (Hall, 1852, pl. 8, fig. 1a). Clinton (Silurian) beds of Oneida County, New York. USNM 41114, X 0.85.

6. Walcottia rugosa Miller and Dyer, 1878 . . . . p. 329
Repichnia; convex hyporelief showing chevron-shaped bodies probably made by parapodia-like appendages. Ovoid body is believed to represent the anterior end of the "body". Maysville beds, Cincinnati, Ohio. Cotype. MCZ 545; latex mold UCM 37677, X 2.5.

7. Buthotrephia palmata Hall, 1852. . . . . p. 179
?Fodinichnia ; convex hyporelief. This species is not present in the local Cincinnatian strata. Cotype. Clinton (Silurian) beds of New Hartford, New York. USNM 41079, X 0.4.

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

PLATE 11



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

Explanation of Plate 12

Figure

1. Trichophycus venosum Miller, 1879. . . . . p. 232
Fodinichnia or Domichnia; lateral view of burrow filling showing coarse striae. Upper surface of the burrow is to the right. Fulton beds of Twelve Mile Creek, Campbell County, Kentucky. UCM 16574, X 1.7.

2. Trichophycus lanosum Miller and Dyer, 1878 . . p. 240
?Repichnia; convex hyporelief. View of cotype showing bulb-like expansion which led J.F. James (1885, 1891) to compare the species with Blastophycus diadematum. Eden beds, Cincinnati, Ohio. HBM 3185; latex mold UCM 37595, X 0.25.

3-7 Trichophycus venosum Miller, 1879. . . . . p. 232

3. Convex hyporelief showing delicate striae. Locality unknown. UCM 37681, X 0.8.

4. View of the upper surface of figure 1 above showing parallel discontinuous striae. Note the slight constrictions in the diameter of the burrow. X 0.8.

5. Convex hyporelief showing a nearly complete burrow filling. Locality unknown. UCM 37629, X 0.7.

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

Explanation of Plate 12 continued

Figure

6. Lateral view of burrow cast showing two secondary branches. Locality unknown. UCM 37593, X 0.85.

7. Ventral view of burrow filling showing at least two well-developed sets of striae. Locality unknown. UCM 37628, X 1.1.

8. Trichophycus lanosum Miller and Dyer, 1878 . . p. 240 ?Repichnia; convex hyporelief. View of cotype showing highly sinuous burrow and button-like ?anterior end. Eden beds, Cincinnati, Ohio. HBM 3183; latex mold UCM 37594, X 1.7.

9. Phycodes flabellum (Miller and Dyer), 1878 . . p. 216 Fodinichnia or Domichnia; convex hyporelief showing the typical flabellate pattern. Locality unknown. UCM 37670, X 0.85.

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.

Explanation of Plate 13

Figure

1. Chondrites succulens (Hall), 1847. . . . . p. 162
Fodinichnia; convex hyporelief of cotype (Hall, 1847 pl. 22, fig. 2a) showing nodose structure of branches (upper left). Trenton beds, Glens Falls, New York, USNM 41133; latex mold UCM 37639, X 0.5.

2. Dactylophycus quadripartitum Miller and Dyer, 1878 . . . . . p. 226
Fodinichnia; convex hyporelief. View of cotype showing the bilobate, annulate nature of the burrow. Eden beds, Cincinnati, Ohio. HBM 3174; latex mold UCM 37608, X 1.1.

3. Corophioides cf. luniformis. . . . . p. 134
Domichnia; U-plane section of two specimens. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37661, X 0.75.

4. Phycodes flabellum (Miller and Dyer), 1878 . . p. 216
Fodinichnia or Domichnia; convex hyporelief. Locality unknown. UCM 37609, X 0.85.

5. Walcottia rugosa Miller and Dyer, 1878 . . . . p. 329
Repichnia; convex hyporelief. Note that the burrow closely resembles the impression that might be made

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

Explanation of Plate 13 continued

Figure

5 continued. by a Nereis-like annelid. Anterior end is believed to be to the left. McMillan beds, Cincinnati, Ohio. MCZ 545; latex mold UCM 37677, X 2.7.

6,7 Paleodictyon sp. Savi and Meneghini, 1850. . . p. 344

6. Latex mold of impression achieved by rolling a specimen of Pasceolus darwini over wet plaster. Compare with Cincinnatian representatives of ?Paleodictyon (see pl. 25, fig. 2 and pl. 11, fig. 1). UCM 37610, X 1.9.

7. ?Pascichnia; convex hyporelief showing that hexagons are elongated parallel to the current direction. Note arcuate trails of similar dimensions in upper left. Eocene beds near Trieste, Italy. UCM 37505, X 0.7.

8. Chondrites gracilis (Hall), 1852 . . . . . p. 179 Fodinichnia; latex mold of cotype showing rigidity of the branches. This form is not directly comparable to any of the varieties of Cincinnatian chondritids. Clinton (Silurian) beds, New Hartford, New York. USNM 41125; latex mold UCM 37676, X 1.7.

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.

Explanation of Plate 14

Figure

1. *Fucusopsis sulcatum* (Miller and Dyer), 1878. . p. 336
Repichnia; convex hyporelief showing tension cracks produced by the pressure of the burrow on the sole of the bed. Bellevue beds, Hall's Creek, Morrow, Ohio. UCM 37606, X 0.6.

2,3 "*Dystactophycus mamillanum*" Miller and Dyer, 1878
. . . . . p. 370

2. Inorganic; convex hyporelief. The irregularity of the arcs was probably caused by shell fragments which were swept around with the stem. Richmond beds, locality unknown. UCM 37605, X 0.85.

3. Concave epirelief of fig. 2 above showing a more regular series of markings. A vertical section taken through the center of the specimen revealed the partially disarticulated columnals. X 0.85.

4. *Trichophycus venosum* Miller, 1879. . . . . p. 232
Fodinichnia or Domichnia; epirelief showing burrow packings in a "turkey track" depression. Field photograph. Corryville beds, Stonelick Creek, Clermont County, Ohio. X 0.2. (silver coin is a quarter).

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

Explanation of Plate 14 continued

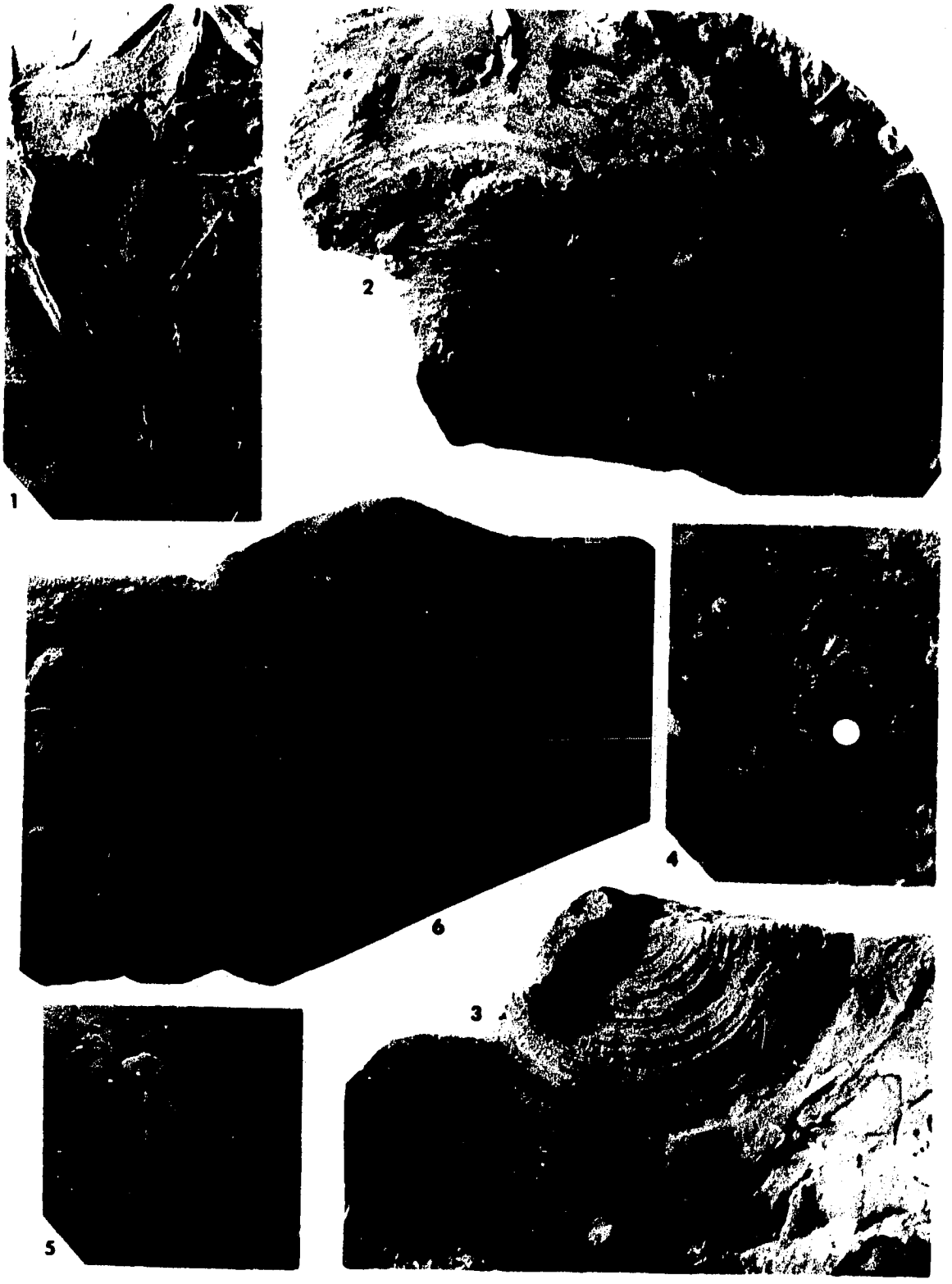
Figure

5. Corophioides biclavata (Miller), 1875. . . . . p. 143
Domichnia; convex hyporelief showing the base of the U and the fillings of the extended U-arms. Mt. Hope beds of Rapid Run, Hamilton County, Ohio. UCM 37662, X 1.

6. Phycodes flabellum (Miller and Dyer), 1878 . . p. 216
Fodinichnia or Domichnia; convex hyporelief showing a flabellate specimen. Liberty beds of Talawanda Creek where it enters Four Mile Creek just above the Butler-Preble County line, north of Oxford, Ohio. MU T95; latex mold UCM 37686, X 0.85.

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

PLATE 14



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

Explanation of Plate 15

Figure

1. Rusophycus carleyi (J.F. James), 1885. . . . . p. 85
Cubichnia of Isotelus; convex hyporelief. Presumed holotype showing nodes revealed by a mesial parting of the lateral lobes. Anterior end at top. ?Maysville beds near Bantam, Clermont County, Ohio. UCM 37604, X 0.6.

2. Tylichnus asperum (Miller and Dyer), 1878. . . p. 304
Repichnia; convex hyporelief showing segments of several burrows. For an enlargement of the nodose prosopon see text figure 39. Holotype. Eden beds, Cincinnati, Ohio. HBM 3179; latex mold UCM 37588, X 1.7.

3. Palaeoscia floweri Caster, 1942. . . . . p. 387
Fodinichnia or inorganic; convex hyporelief of a slightly ellipsoid specimen. The furrow leading from the center of the specimen to the lower margin may represent the mold of an agglutinated tube. Corryville beds, Stonelick Creek, Clermont County, Ohio. UCM 37586, X 1.1.

4. ?Corophioides biclavata (Miller), 1875 . . . . p. 143
Domichnia; convex hyporelief. This specimen may represent a cast of the modified base of Corophioides

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

Explanation of Plate 15 continued

Figure

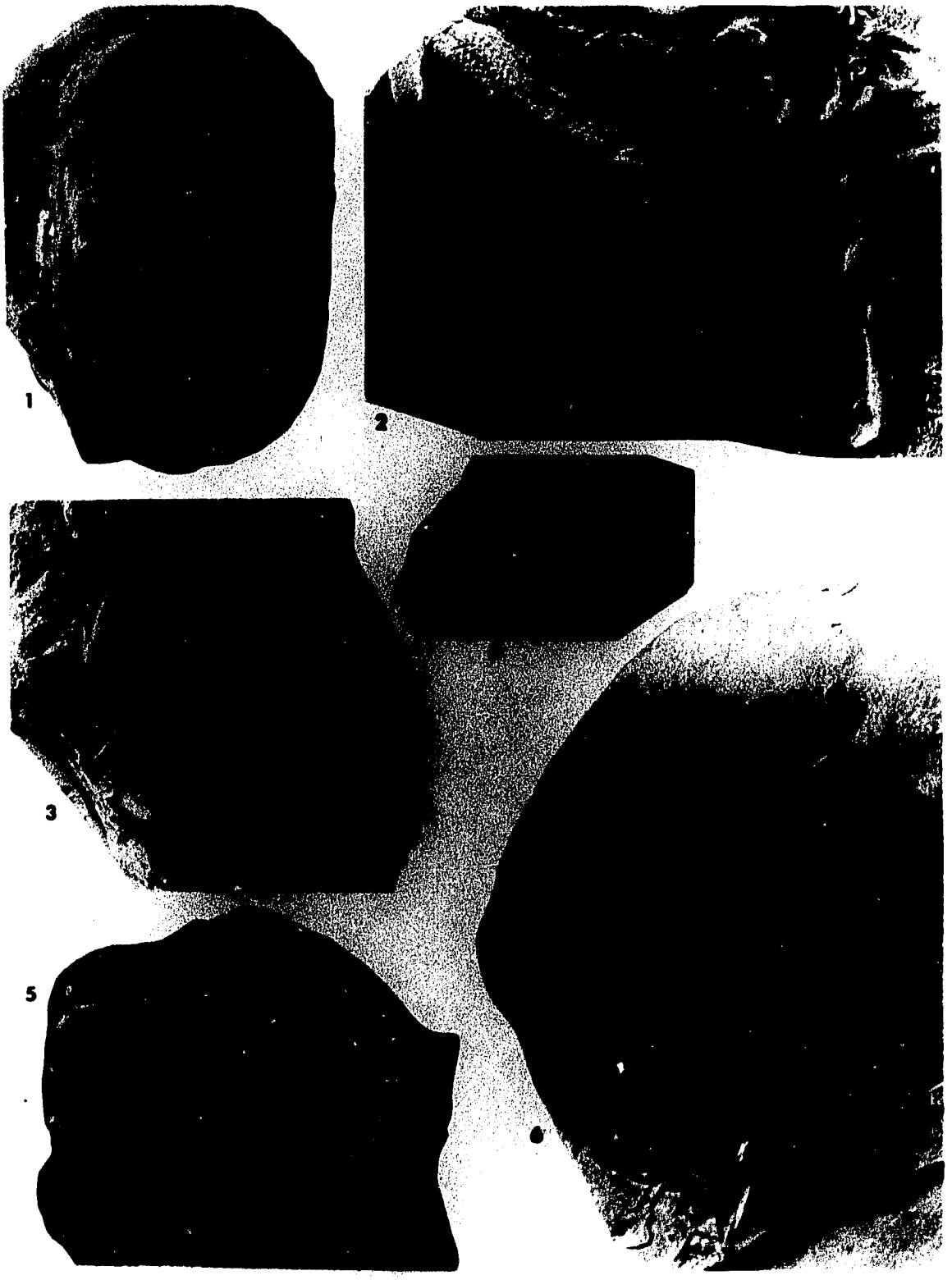
4 continued. cincinnatiensis or it may be the cast of the upper portion of the tube. Locality unknown. UCM 37660, X 0.95.

5. Fucusopsis sulcatum (Miller and Dyer), 1878. . p. 336 Repichnia; convex hyporelief. Holotype of Trichophycus sulcatum. Note that the basal lamina of the host rock "laps up" on the side of the burrow. Eden beds, Cincinnati, Ohio. HBM 3182; latex mold UCM 37705, X 0.85.

6. Asaphoidichnus trifidum Miller, 1880 . . . . . p. 261 Repichnia of Isotelus; epirelief showing well-developed trifid imprints of the right series. Holotype. Compare with plate 16, fig. 3. Right-hand series was illustrated by Miller (1874, p. 136, fig. 11). Eden beds of State Avenue, Cincinnati, Ohio. MCZ 540; latex mold UCM 37704, X 0.7.

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.

Explanation of Plate 16

Figure

1,2 Allocotichnus dyeri (Miller) 1880. . . . . p. 268

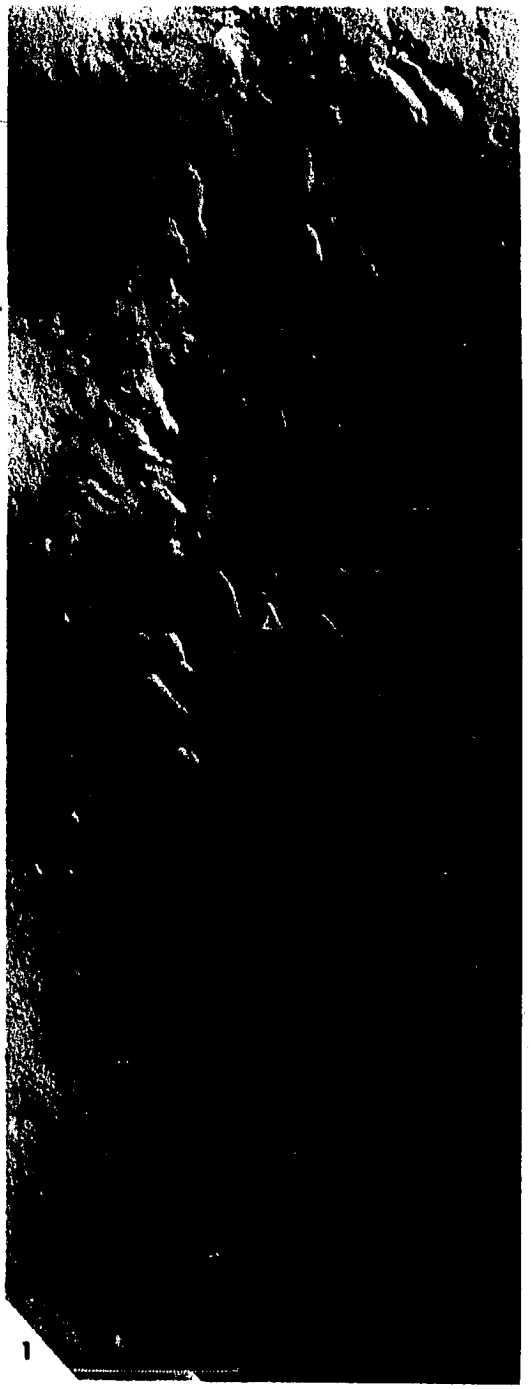
1. Repichnia of ?Isotelus; convex hyporelief. Holotype. Movement was from bottom to top and the body was angled to the right of the axis of movement. Eden beds, State Avnue, Cincinnati, Ohio. MCZ 543; latex mold UCM 37693, X 1.

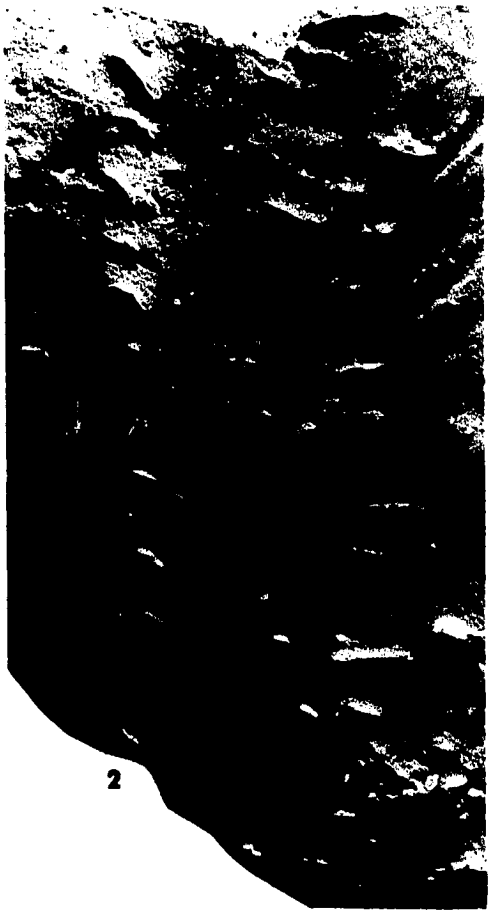
2. Convex hyporelief showing only three pairs of imprints in each set. Note that if the imprints are rotated 45° clockwise, the resulting configuration resembles Figure 1 above. Eden beds of Mud Lick Creek near Walton, Kentucky. UCM 37627, X 1.

3. Asaphoidichnus trifidum Miller, 1880. . . . . p. 261
Enlargement of portion of holotype (see plate 15, fig. 6) showing trifid imprints. X 1.7.

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

PLATE 16


1


2

3



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

Explanation of Plate 17

Figure

1,2 Asaphoidichnus trifidum Miller, 1880 . . . . . p. 261

1. Repichnia of Isotelus; convex hyporelief showing a combination of unifid, bifid, and trifid imprints. Locality unknown. MCZ 1055; latex mold UCM 37694, X 0.85.

2. Repichnia of Isotelus; covex hyporelief. Hypotype (Caster, 1938, pl. 10, fig. 2). Movement was from bottom to top and the body was oriented to the right of the axis of movement. Fulton beds, Union levee, Cincinnati, Ohio. UCM 22034, X 0.7.

3,4 Trachomatichnus numerosum Miller, 1880 . . . . p. 284

3. Repichnia of Cryptolithus; convex hyporelief showing closely spaced casts of the impressions of the multifid legs of Cryptolithus. Movement was from bottom to top. Cotype. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 547; latex mold UCM 37695, X 0.85.

4. Repichnia of Cryptolithus; concave epirelief. Movement was from top to bottom. Cotype. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 544; latex mold UCM 37671, X 1.25.

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

Explanation of Plate 17 continued

Figure

5,6 Petalichnus multipartitum Miller, 1880 . . . . . p. 276

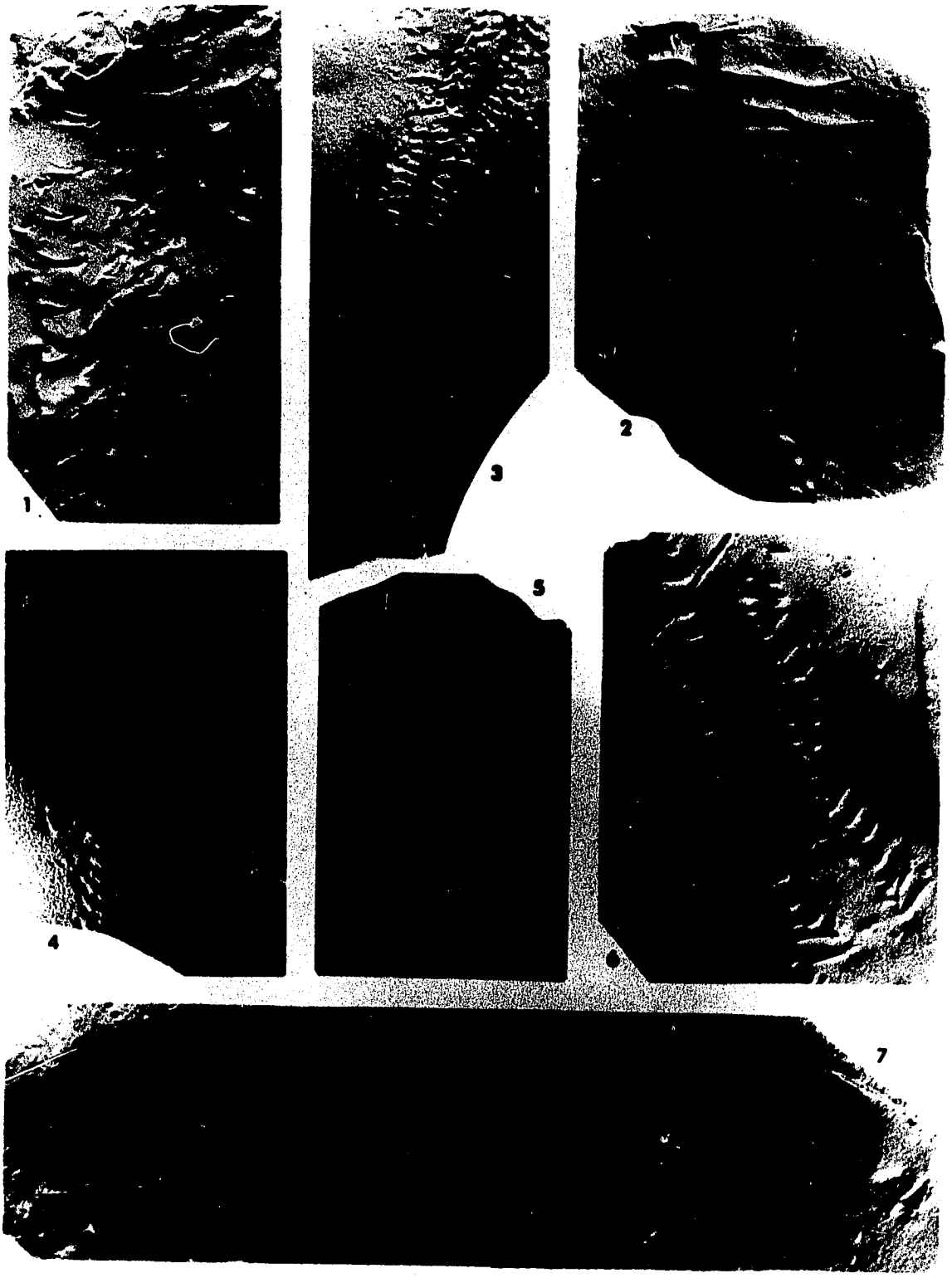
5. Repichnia; convex hyporelief showing conversion from straight-ahead to oblique. Movement was from bottom to top. Specimen placed by Miller (1880) in Trachomatichnus permultum. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 548; latex mold UCM 37696, X 0.85.

6. Repichnia; concave cleavage relief showing withdrawal markings at the proximal termination of each imprint. Movement was from bottom to top. Locality unknown. UCM 37579, X 0.85.

7. Allocotichnus dyeri (Miller), 1880 . . . . . p. 268
Repichnia of ?Isotelus; convex hyporelief. Movement was from right to left and the body was oriented to the right of the axis of movement. Eden beds of Mud Lick Creek near Walton, Kentucky. UCM 37630, X 0.85.

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.

Explanation of Plate 18

Figure

1. Trachomatichnus numerosum Miller, 1880 . . . . p. 284
Repichnia of Cryptolithus; convex hyporelief. The clarity of preservation indicates that the trail is preserved as a boundary relief. Note the tracks of Allocotichnus dyeri which occur near the upper margin of the specimen. Direction of movement from left to right. Lectoholotype. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 539; latex mold UCM 37583, X 0.85.

2. Petalichnus multipartitum Miller, 1880 . . . . p. 276
Repichnia of a medium sized trilobite; convex hyporelief. The trail is poorly defined and is most likely preserved as a cleavage relief. Presumably a more complete set of imprints lies just below the surface. This specimen was designated by Miller as the holotype of Trachomatichnus cincinnatiensis. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 542; latex mold UCM 37571, X 0.8.

3. Dactylophycus quadripartitum Miller and Dyer, 1878
. . . . . p. 223
Fodinichnia; convex hyporelief showing a flabellate specimen where the median groove of the branches has

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

Explanation of Plate 18 continued

Figure

4,5 Petalichnus multipartitum Miller, 1880 . . . . p. 276

4. Specimen was assigned by Caster (1938, pl. 10, fig. 4) to Merostomichnites sp. Note the scallop-like nature of the imprints. Movement was from lower left to upper right and the body was oriented to the left of the axis of movement. Fulton beds, Union Levee, Cincinnati, Ohio. UCM 22033, X 1.

5. Convex hyporelief showing an excellent example of dimorphic imprints. The imprints of the left series are superimposed while those of the right series are clearly defined. Southgate beds below the east end of the Beechmont Levee, Hamilton County, Ohio. MU T86; latex mold UCM 37707, X 0.85.

6,7 Allocotichnus dyeri (Miller), 1880 . . . . . p. 268

6. Repichnia of Isotelus; convex hyporelief showing bifid imprints. Eden beds of Mud Lick Creek near Walton, Kentucky. UCM 37626, X 0.85.

7. Convex hyporelief showing deeply impressed raking imprints. Note the series of imprints

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

Explanation of Plate 18 continued

Figure

7 continued. to the upper left of each series which probably represent casts of gouge marks made by the pleurae of Isotelus. Movement was from left to right and the body was oriented far to the left of the axis of movement. ?Eden beds of State Avenue, Cincinnati, Ohio. MCZ 1053; UCM 37708, X 0.7.

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

PLATE 18



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

Explanation of Plate 19

Figure

1. Trachomatichnus numerosum (Miller), 1880 . . . p. 284
Repichnia of Cryptolithus; convex hyporelief of two Cruziana-like trails. Note the imprints of the genal spines flanking the trail on either side. Locality unknown. UCM 37603, X 0.8.

2. Asaphoidichnus trifidum Miller, 1880 . . . . . p. 261
Repichnia of Isotelus; convex hyporelief showing sigmoidal imprints in both series. Movement was from bottom to top and the body was oriented to the right of the axis of movement. Fulton beds, Union Levee, Cincinnati, Ohio. UCM 37569; X 0.8.

3. Teratichnus confertum Miller, 1880.. . . . . p. 292
Repichnia of aglaspid or medium sized trilobite; concave epirelief. Latex mold of holotype. B,C,D, mark the locations of long striae produced by a caudal cercum or terminal spine. The letter A marks the locality of an ellipsoid grouping of imprints. General direction of movement was from bottom to top. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 540; latex mold UCM 37570, X 0.95.

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

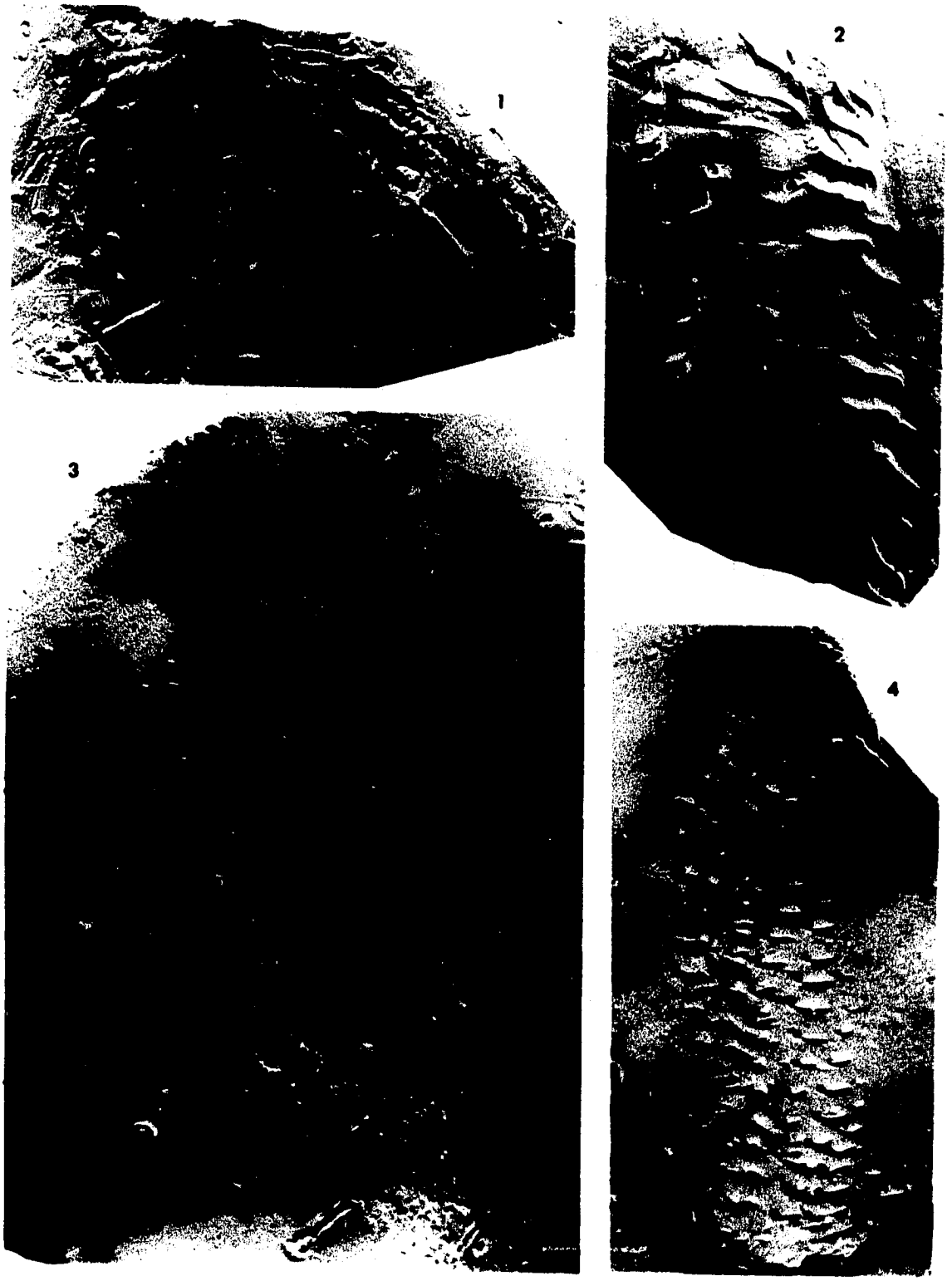
Explanation of Plate 19 continued

Figure

4. Petalichnus multipartitum Miller, 1880 . . . . p. 276
Repichnia of medium sized trilobite; convex hypo-relief showing a complex superposition of imprints. A few cuneiform support imprints can be seen in the center of the trail. Holotype. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 546; latex mold UCM 37697, X 0.85.

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.

Explanation of Plate 20

Figure

1. Palaeophycus rugosum Hall, 1847. . . . . p. 310
Repichnia; convex hyporelief showing the coarse rugosities which characterize the species. Holotype. Trenton (Ordovician) beds of Middleville, New York. NYSM 240/1, X 0.65.

2-4 Palaeophycus tortuosum Hall, 1852. . . . . p. 310

2. A small cylindrical segment of the burrow filling. Cotype. Queenston (Ordovician) beds of Irondequoit Bay, New York. USNM 41106, X 0.6.

3. Burrow filling shaped like a depressed, helicoid cylinder. Cotype. Locality same as fig. 2 above. USNM 41102, X 0.6.

4. Faintly striate, arcuate burrow filling. Cross-section depressed cylindrical. Cotype. Locality same as fig. 2 above. USNM 41107, X 0.6.

5. Palaeophycus, type-A. p.324
Repichnia; convex hyporelief of cylindrical burrows with well developed annuli. Corryville beds of O'Bannion Creek, Clermont County, Ohio. UCM 37646, X 0.85.

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

Explanation of Plate 20 continued

Figure

6,7 ?Palaeophycus striatum Hall, 1852. . . . . p. 310

6. Repichnia; convex hyporelief showing hemicylindrical burrow filling marked by a narrow linear crest. Hypotype. Clinton (Silurian) beds, Oneida County, New York. USNM 41108; latex mold UCM 37585, X 0.7.

7. Repichnia; convex hyporelief showing three intersecting burrows. Hypotype. Locality same as fig. 6 above. USNM 41111, X 0.85.

8. Palaeophycus tubulare Hall, 1847 . . . . . p. 310
Repichnia; convex hyporelief showing several intersecting burrow fillings, some of which are striate. Cotype. Beekmantown (Ordovician) beds of Amsterdam, New York. NYSM 241/1; latex mold UCM 37698, X 0.4.

9. Palaeophycus, type-B . . . . . p. 325
Repichnia; convex hyporelief showing hemicylindrical burrow filling marked by longitudinal striae and annuli. Locality unknown. UCM 37584, X 0.85.

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.

Explanation of Plate 21

Figure

1. *Palaeophycus tubulare* Hall, 1847 . . . . . p. 310
Repichnia. View of a cotype which is heavily encrusted with limonite. Beekmantown (Ordovician) beds of Fort Plain, New York. NYSM 241/3; latex mold UCM 37699, X 0.5.

2. *Planolites corrugatus* Walcott, 1899. . . . . p. 324
Repichnia. What Walcott described as corrugations are actually cleavage planes deflected by the burrow. Holotype. Greyson Shale (Precambrian) near Neihart, Montana. USNM 33796, X 0.85.

3. *Planolites annularis*, Walcott, 1889. . . . . p. 324
Repichnia. A weathered specimen bearing annuli. Holotype. Lower Cambrian beds near Greenwich, New York. USNM 18360, X 0.85.

4. *Palaeophycus tubulare* Hall, 1847 . . . . . p. 310
Repichnia; convex hyporelief showing several cylindrical burrow fillings. Note that one of the forms is bilobate. Cotype. Locality same as Fig. 1 above. NYSM 241/4; latex mold UCM 37700, X 0.35.

5. *Palaeophycus*, type-C . . . . . p. 326
Repichnia; convex hyporelief showing burrow fillings

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

Explanation of Plate 21 continued

Figure

5.continued. preserved in a coarse-grained calcarenite. McMicken beds of Brierly Creek, Hamilton County, Ohio. UCM 37647, X 0.4.

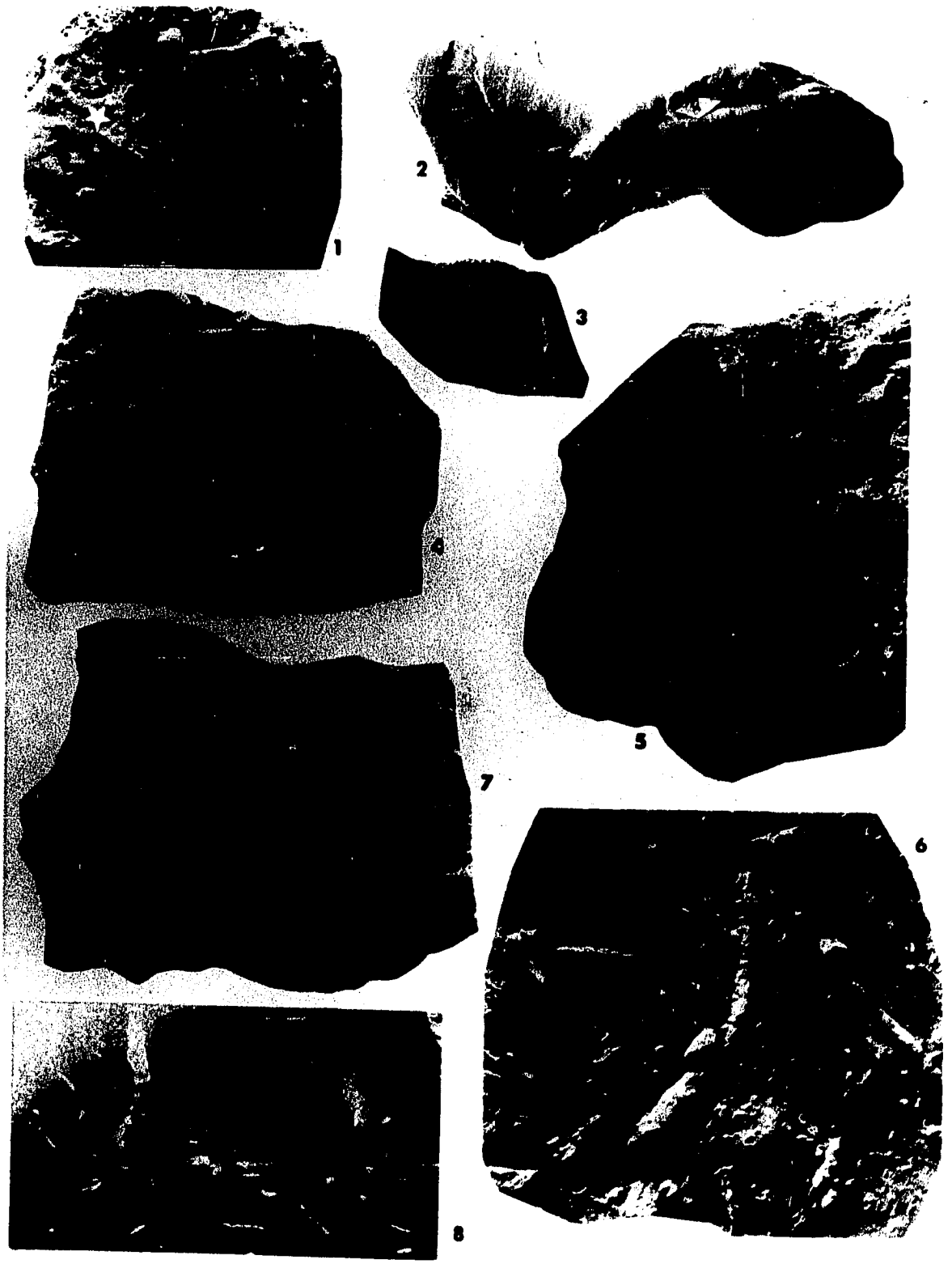
6. Palaeophycus, type-B . . . . . p. 325
Repichnia; convex hyporelief showing annuli and longitudinal striae. Note bulbous expansion. Sunset beds, Four Mile Creek, 10 miles south of Oxford, Ohio. UCM 37682, X 0.8.

7. Palaeophycus tubulare, Hall, 1847. . . . . p. 310
Repichnia; convex hyporelief with several flattened hemicylindrical burrow fillings. Cotype. Locality same as Fig. 1 above. NYSM 241/2; latex mold UCM 37701, X 0.35.

8. Corophioides biclavata (Miller), 1880. . . . . p. 143
Domichnia; U-plane section showing that the arms have been extended below the level of the Spreite. The smaller, lighter colored burrows are Chondrites, type-C. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37649, X 0.85.

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

PLATE 21



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

Explanation of Plate 22

Figure

1-3 Ormathichnus monilliformis Miller, 1880 . . . .p. 308

1. Enlarged view of fig. 2 showing a series of small disconnected Rusophycus-like bodies. X 4.3.

2. Repichnia of a small arthropod; convex hyporelief. Cotype. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 549; latex mold UCM 37689, X 2.6.

3. Inorganic; convex hyporelief. The monilliform casts are interpreted as markings of a crinoid stem. Cotype. Locality same as fig. 2 above. MCZ 541; latex mold UCM 37690, X 2.1.

4-6 Rhabdoglyphus sp. Vassoevich, 1951 . . . . . p. 298

4. Repichnia; concave hyporelief. Locality unknown. MU T96; latex mold UCM 37702, X 1.

5. Concave epirelief showing the variation in the morphology of the hemispherical depressions. UCM 37683, X 0.85.

6. Concave epirelief showing raised rims of the connecting troughs. Sunset beds of Four Mile Creek 10 miles south of Oxford, Ohio. UCM 37653, X 0.85.

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

Explanation of Plate 22 continued

Figure

7. Hormosiroidea florentina Schaffer, 1928. . . . p. 296
Repichnia; ?convex hyporelief showing closely spaced hemicylinders. Note small vermiform trails. Holotype. Upper Cretaceous of Italy. Plastotype UCM 37652, X 0.85.

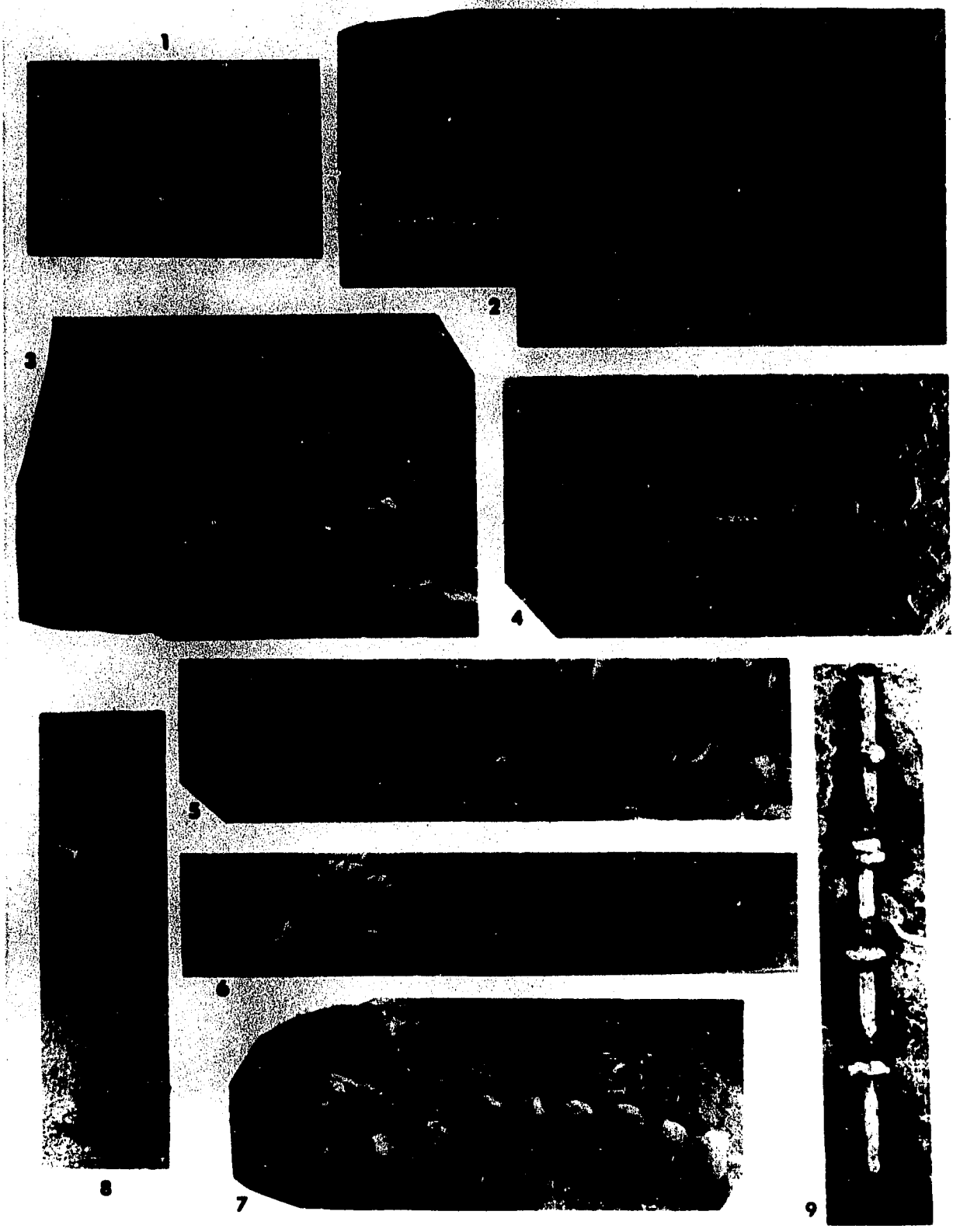
8,9 Rhabdoglyphus grossheimi Vasseovich, 1951. . . p. 296

8. Repichnia; convex hyporelief. Vertical sections would probably reveal the connecting bar just below the surface. Hypotype. Tertiary flysch of Czechoslovakia, X 1 (from Bouček and Elias, 1962, pl. 8, fig. 2).

9. ?Convex hyporelief showing ellipsoidal swellings. Note that two of the swellings occur together. Locality same as fig. 8 above. X 1 (from Bouček and Elias, 1962, pl. 8, fig. 2).

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.

Explanation of Plate 23

Figure

1,2 "*Palaeophycus flexuosum*" U.P. James, 1879. . . p. 379

1. Inorganic; epirelief showing the numerous anastomosing ridges. Humphrey's Branch of Twelve Mile Creek, Campbell County, Kentucky. UCM 37645; X 0.85.

2. Inorganic; specimen reveals several layers marked by the flattened ridges. Locality unknown. UCM 37650, X 0.6.

3. *Mastigograptus gracillimum* (Lesquereux), 1878. p. 357 The form was interpreted by Ruedemann (1908) as a graptolite. This specimen bears no trace of thecae. Locality unknown. UCM 37651, X 1.3.

4. ?Mollusk trails. . . . . p. 338 Note that trails change from a median furrow flanked by two ridges into a raised ridge marked by a median rift. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio.

5. *Chondrites*, type-B . . . . . p. 193 Vertical cross-section showing a concentration of burrows in lower half of the host rock. Note that one branch angles upwards. McMicken beds of West

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

Explanation of Plate 23 continued

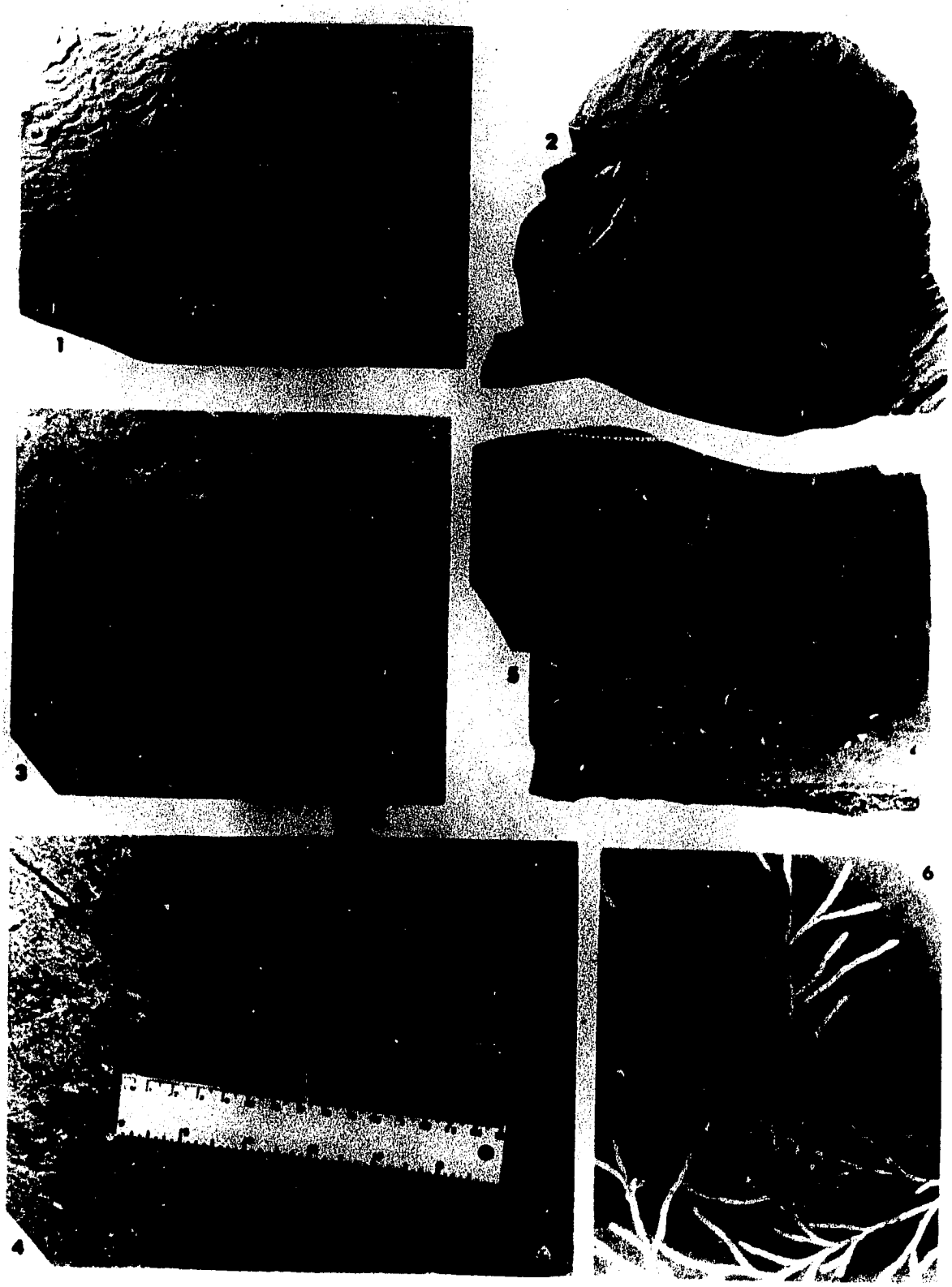
Figure

5 continued. Fork Creek, Mt. Airy Forest, Cincinnati, Ohio (type locality of Corophioides cincinnatiensis). UCM 37669, X 0.5.

6. Chondrites bollensis Zieten, 1839. . . . . p. 162 Fodinichnia; bedding plane surface showing a specimen which exhibits phobotaxis. Such specimens marked the "death knell" of the "fucoids". Jurassic Posidion beds of Württemberg, West Germany. UCM 37538, X 0.7.

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.

Explanation of Plate 24

Figure

1. "Chloephycus plumosum" Miller and Dyer, 1878 . p. 362
Inorganic; convex hyporelief of holotype showing numerous parallel specimens. Current flow was from top to bottom. Eden beds, Cincinnati, Ohio. HBM 3154; latex mold UCM 37617, X 1.1.

2. "Blastophycus diadematum" Miller and Dyer, 1878 . . . . . p. 366
Inorganic; convex hyporelief showing cast of enrolled trilobite with casts of scour markings. Current flow was from top to bottom. Compare with forms on plate 25, fig. 1-3. Paratype. Eden beds, Cincinnati, Ohio. HMB 3181; latex mold UCM 37618, X 1.3.

3,4 "Dystactophycus mamillanum" Miller and Dyer, 1878 . . . . . p. 370

3. Inorganic; convex hyporelief representing the cast of markings made by a sweeping crinoid stem. Richmond beds, Hamilton, Ohio. USNM 40043; latex mold UCM 37620, X 0.85.

4. Inorganic; convex hyporelief showing the apparent imbrication of the rings. The left side of the specimen has been altered by preparation.

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

Explanation of Plate 24 continued

Figure

4 continued. Holotype. Richmond beds near Morrow, Ohio. HBM 3177; latex mold UCM 37691, X 0.85.

5. Lichenalia concentrica Hall, 1852. . . . . p. 370
Bryozoa; latex mold bearing a vague resemblance to "Dystactophycus". J.F. James (1885) believed that the two were synonomous. Cotype. Niagaran (Silurian) beds near Rochester, New York. AMNH 1487/1; latex mold UCM 37685, X 2.1.

6. "Chloephycus plumosum" Miller and Dyer, 1878 . p. 362
Inorganic; convex hyporelief showing a single specimen. Note flute casts to the right of "Chloephycus". Eden beds of State Avenue, Cincinnati, Ohio. Specimen on reverse of Trachomatichnus numerosum, MCZ 544; latex mold UCM 37692, X 1.1.

7. "Scolithus dispar" J.F. James, 1892. . . . . p. 376
Inorganic; convex hyporelief. U.P. James (1881) assigned the long linear markings to "Scolithus linearis". Also present on the slab are casts of rolling crinoid stems, and groove casts made by twisting brachiopod shell fragments. Current flow was from upper left to lower right and top to

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

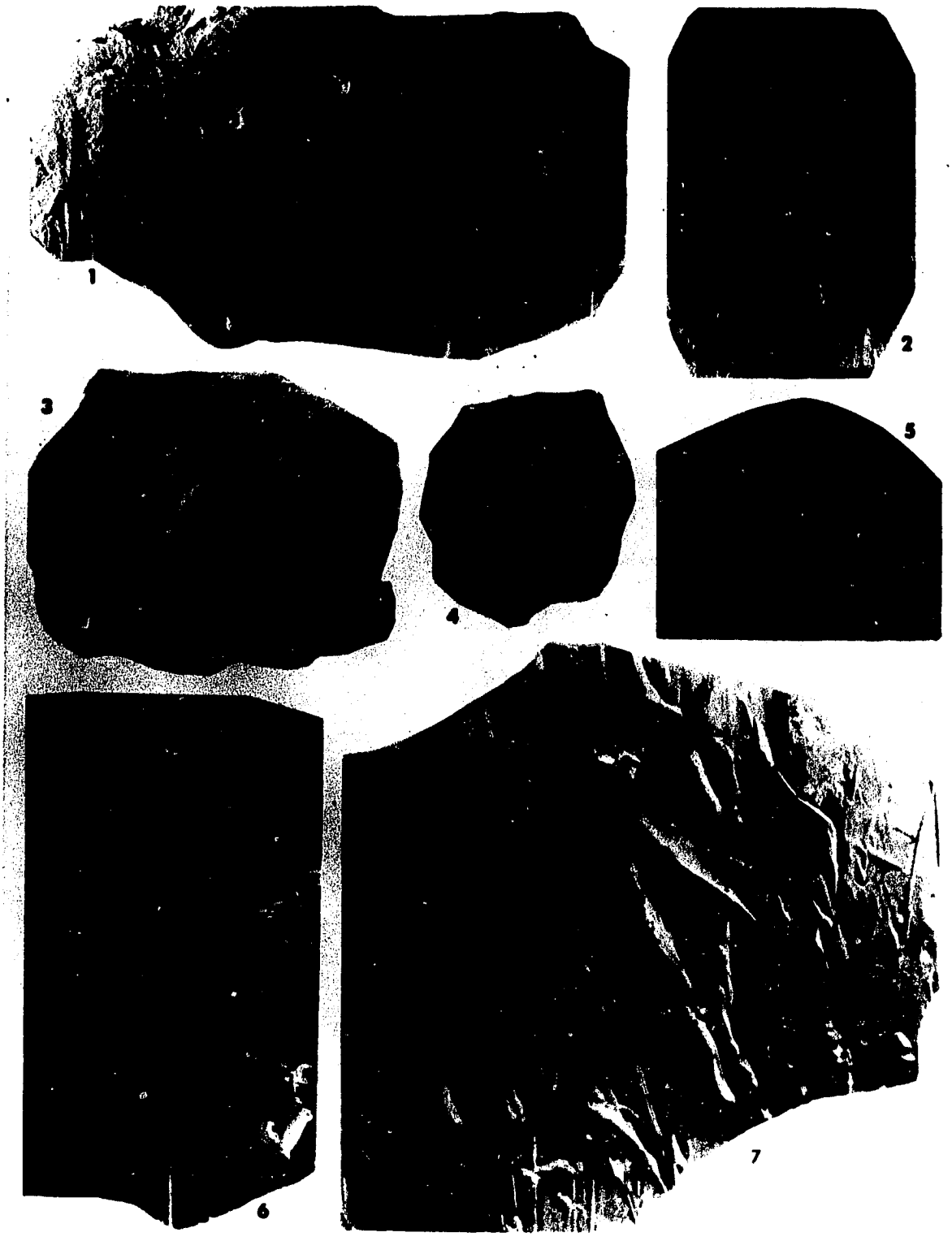
Explanation of Plate 24 continued

Figure

7 continued. bottom. Paratype. Eden beds, "Crawfish Creek". UCM 37619, X 0.5.

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.

Explanation of Plate 25

Figure

1. "Blastophycus diadematum" Miller and Dyer, 1878 . . . . . p. 366
Inorganic; scour marks around an enrolled trilobite. Current flow from upper right to lower left. Compare with fig. 5, 10 below. Experimentally produced. X 0.85.

2. ?Paleodictyon sp. Savi and Meneghini, 1850 . . p. 344
?Pascichnia; convex hyporelief showing a poorly developed specimen. Note that the network is oriented parallel to the current direction. Economy beds of Duck Creek, Campbell County, Kentucky. UCM 37638, X 1.

3. "Blastophycus diadematum" Miller and Dyer, 1878 . . . . . p. 366
Inorganic; same as fig. 1 above. Rill marks are attributable to subaerial erosion. Current flow from lower right to upper left. X 0.6.

4. Chondrites, type-C . . . . . p. 202
Fodinichnia; concave epirelief showing two systems, one oriented parallel, the other oblique to the bedding plane. A latex mold of this specimen is illustrated on pl. 8, fig. 5. Whitewater beds, Short

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

Explanation of Plate 25 continued

Figure

4 continued. Creek, three miles southeast of Richmond, Indiana. MU T90; latex mold UCM 37678, X 0.5.

5. "Blastophycus diadematum" Miller and Dyer, 1878 . . . . . p. 366
Inorganic; plaster cast of experimentally produced scour marks around an enrolled trilobite. Current flow from top to bottom. UCM 37664, X 0.4.

6. "Dystactophycus mamillanum" Miller and Dyer, 1878 . . . . . p. 370
Inorganic; convex hyporelief clearly showing the casts of markings made by a sweeping crinoid stem. Arnheim beds, Hamilton, Ohio. USNM 40044; latex mold UCM 37687, X 0.7.

7. Allocotichnus dyeri (Miller), 1880 . . . . . p. 268
Repichnia; convex hyporelief. An enlargement of a portion of the trail shown on pl. 18, fig. 1. The small parallel markings were probably made by spinose projections on the distal ends of the segments of the walking legs. Eden beds of State Avenue, Cincinnati, Ohio. MCZ 539; latex mold UCM 37583, X 3.4.

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

Explanation of Plate 25 continued

Figure

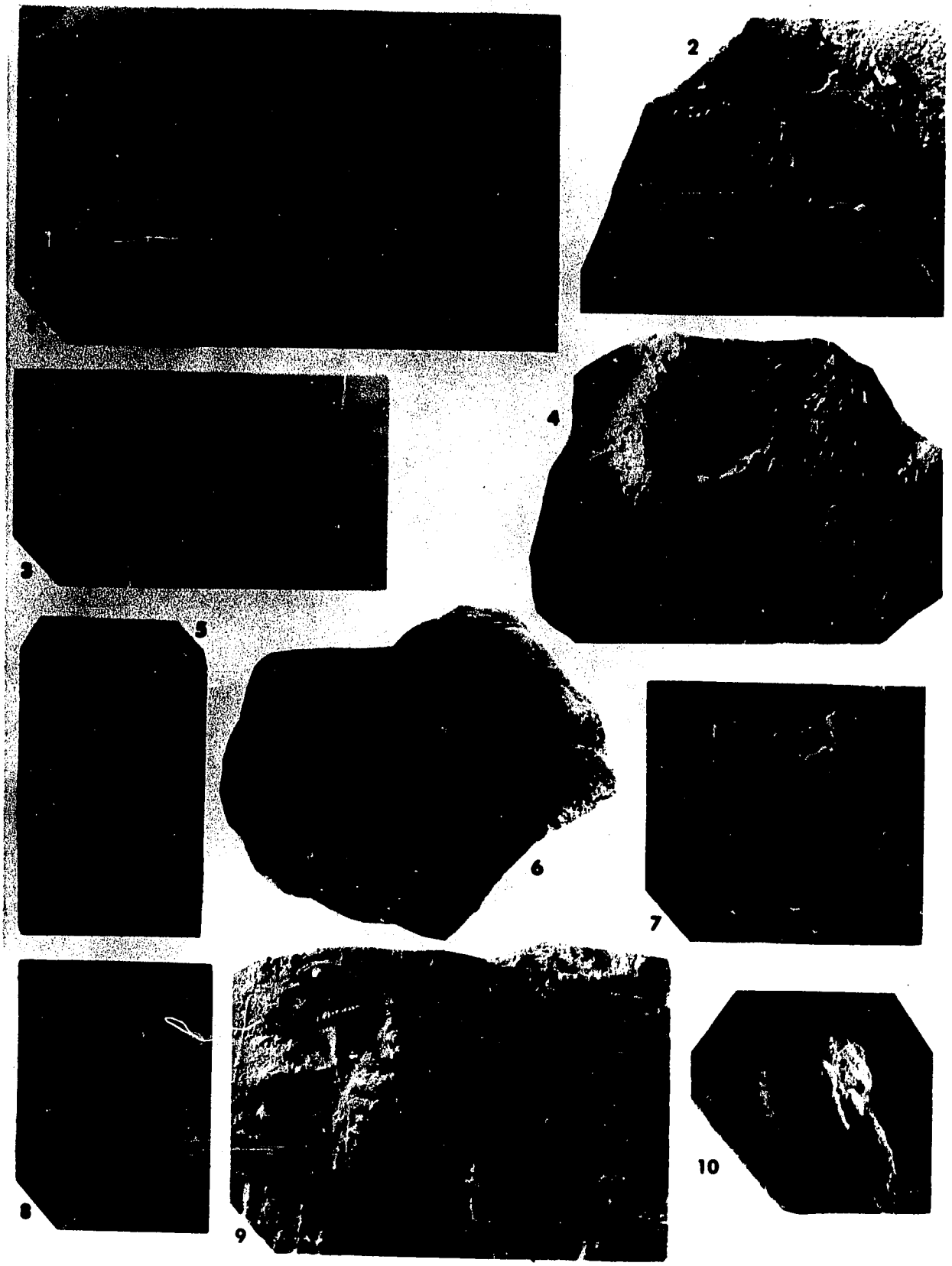
8. Fascifodina floweri n. gen., n. sp. . . . . p. 205
Fodinichnia; epirelief. A small individual showing the concave imprint and the convex, lower portion of the master shaft. Corryville beds of Second Creek where crossed by Cozzadale Road, Clermont County, Ohio. UCM 37632, X 0.85.

9. Rusophycus pudicum Hall, 1852. . . . . p. 82
Cubichnia of Flexicalymene; convex hyporelief showing a trail leading away from the resting trace. Note the well-preserved casts of the pleurae on the Rusophycus body. Corryville beds, Stonelick Creek, Clermont County, Ohio. MU T94; latex mold 37663, X 0.6.

10. "Blastophycus diadematum" Miller and Dyer, 1878
. . . . . p. 361
Inorganic; convex hyporelief showing the "bud" which clearly reveals its trilobite origin. Cotype. Eden beds, Cincinnati, Ohio. HBM 3181; latex mold UCM 37703, X 1.5.

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.

Explanation of Plate 26

Figure

1-6 Palaeoscia floweri Caster, 1942. . . . . p. 387

1. Fodinichnia or Inorganic; concave epirelief showing a well developed central pore, "radial canals" and concentric markings. Holotype. Corryville beds of Stonelick Creek, Clermont County, Ohio. UCM 24079, X 1.

2. Concave epirelief of a shallow very regular specimen. Locality same as fig. 1 above. UCM 24389, X 0.6.

3. Concave epirelief. An enlargement of a portion of the holotype showing the central pore and "radical canals". X 2.6.

4. Convex hyporelief showing several specimens. The concentric arcs are developed only in the downcurrent quadrant. Economy beds of Duck Creek, Campbell County, Kentucky. UCM 37578, X 1.1.

5. Concave epirelief showing two overlapping specimens. Note that the central pore has a raised rim and the inner wall of the arcs appears to

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

Explanation of Plate 26 continued

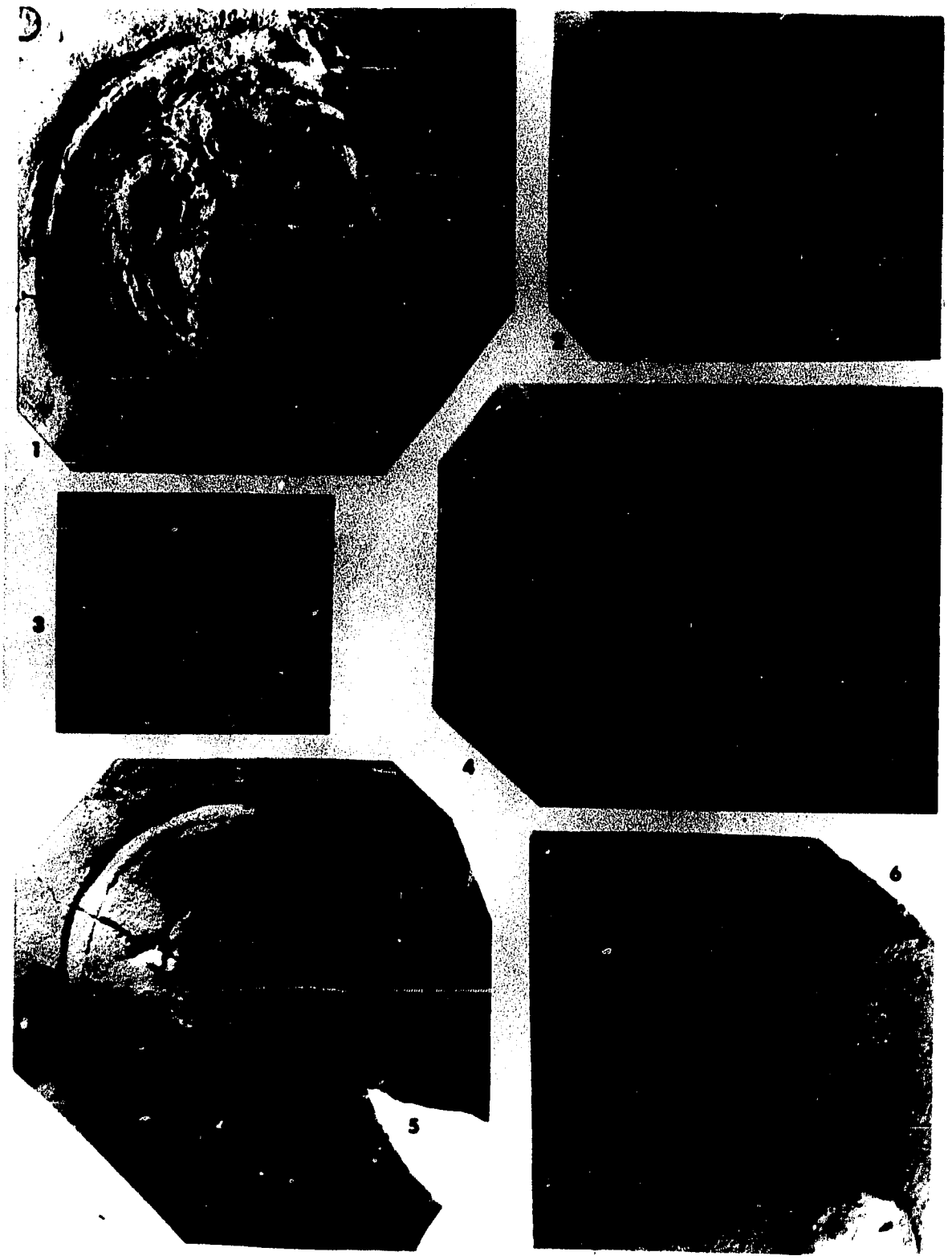
Figure

5 continued. have been planed off. Locality same as fig. 1 above. UCM 37575, X 0.85.

6. Concave epirelief showing a portion of a larger specimen. Note the comparatively large diameter of the central pore. Locality same as fig. 1 above. UCM 37576, X 1.1.

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.

Explanation of Plate 27

Figure

1. Palaeophycus, type-C . . . . . p. 326
Repichnia; convex hyporelief showing several interpenetrating burrows. The coarse grain size of the host rock obscures the finer details of the burrows. Locality unknown. UCM 37582, X 1.7.

2. Chondrites, type-A . . . . . p. 188
Fodinichnia; vertical section. Note downward deflection of some of the secondary branches. McMicken beds of West Fork Creek, Mt. Airy Forest, Cincinnati, Ohio. UCM 37680, X 1.2.

3. ?Resting trace of a nautiloid cephalopod . . . p. 232
Concave epirelief. This specimen differs from the "turkey track" depressions which Flower (1955) believed to be nautiloid resting traces. The two critical features are the raised borders and the smooth floor of the depression. Mt. Hope beds on U.S. Route 50, 0.4 miles west of Aurora, Indiana.

4. Palaeophycus, type-C . . . . . p. 326
Repichnia; note that trails are preserved as both concave and convex epireliefs. Eden beds of Brierly Creek. UCM 37644, X 0.4.

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

Explanation of Plate 27 continued

Figure

5. Trachomatichnus numerosum Miller, 1880 . . . . p. 284
Enlargement of a portion of the trail shown on pl. 19, fig. 1 illustrating two Cruziana-like ridges. The delicate striae are attributed to the brush-like terminal segment of the Cryptolithus walking leg. X 1.3.

6-8 Aristophycus ramosum Miller and Dyer, 1878 . . p. 395

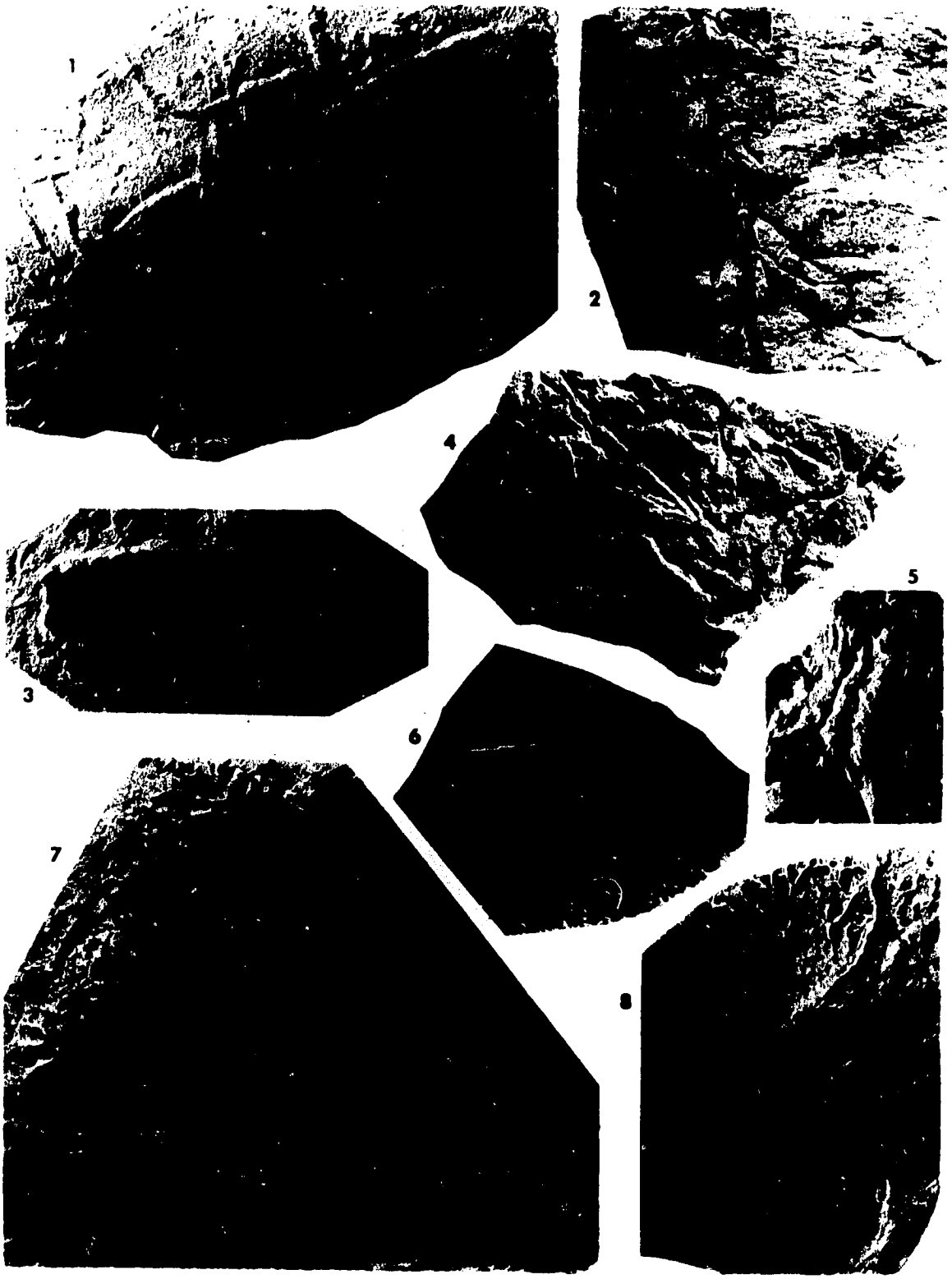
6. Incertae sedis; latex mold of fig. 8 below showing the anastomosing pattern of the secondary and tertiary branches. X 0.7.

7. Convex epirelief. Note that the secondary branches extend down into the host rock much like Ivy tendrils. Compare with text figure 38. Holotype. Maysville beds, Cincinnati, Ohio. HBM 3173; latex mold UCM 37580, X 0.65.

8. Convex epirelief showing a single main branch. This specimen was assigned to A. ramosum var. germanum by Miller and Dyer (1878). Maysville beds, Cincinnati, Ohio. HBM 3172; latex mold UCM 37668, X 1.

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.