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COMPARATIVE MORPHOLOGY AND SHELL HISTOLOGY OF THE ORDOVICIAN STROPHOMENACEA (BRACHIOPODA)

A dissertation submitted to

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requirements for the degree of

DOCTOR OF PHILOSOPHY

1966

by

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I hereby recommend that the thesis prepared under my supervision by JOHN KEYLER POPE

entitled Comparative Morphology and Histology of Ordovician Strophomenacea (Brachiopoda).

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

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TABLE OF CONTENTS

Text-Figures

Charts and Tables

ABSTRACT

The forty-four genera of the Superfamily Strophomenacea (Brachiopoda) may be arranged into a phylogeny of four families. The Family Oepikinidae, which contains the oldest species of the superfamily, possesses archaic characters including fine pseudopunctae, subrectangular to prolate shape, plano-convex to concavo-convex profile and prominent dorsal septa. The Family Leptaenidae diverges from the oldest oepikinids by acquisition of coarse pseudopunctae, prominent geniculation and rugae. The Leptaenidae subsumes the Subfamilies Murinellinae, nov., with prominent dorsal septa, Leptaeninae, without prominent dorsal septa, and Leptaenoideinae, with cemented habit. The Family Rafinesquinidae originates from early oepikinids by loss of dorsal septa and acquisition of coarse pseudopunctae. The Family Strophomenidae arises from the oepikinids with the development of a biconvex, flattened or resupinate profile. The Strophomenidae subsumes the Subfamilies Furcitellinae, with evident dorsal septa and unusual shell shapes and profiles, and Strophomeninae, with strong resupination and obscure dorsal septa.

Many morphological structures undergo modification throughout the history of the Strophomenacea. The shape and profile of the valves, size of pseudopunctae and form

of the teeth and diductor muscle scars are taxonomic differentia at the familial level. The pseudodeltidium, chilidium, pedicle foramen and dorsal septa undergo parallel evolution in the various families. The cardinal process displays poorly defined taxonomic differentiation and parallel evolution. The profile of the valves, dental lamellae, muscle bounding ridges and socket buttresses undergo collateral changes which are indicative of interrelationship. The adductor muscle scars, posterior platform, meso-cardinal ridge, vasculae, radial prosopon and size of species have little taxonomic or evolutionary significance.

A revised shell-layer nomenclature for brachiopods is proposed to replace standard terminology which is either inappropriate or ambiguous. The shell-layers are, from external to internal surface, the periostracum, the outer carbonate layer (primary layer of authors), inner initial layer (secondary layer of authors) and secondary deposits. Microstructural designations may be substituted for these layer-names in reference to specific brachiopod groups.

Strophomenaceans do not possess evidence of periostracum. The outer carbonate layer is a dark lamellar layer on the disk of the valves and a thick microcrystalline layer on the palintrope. The pseudodeltidium and chilidium are continuations of the microcrystalline layers of the palintropes. The microcrystalline layers of the palintropes are folded complexly along the sides of the denticular plates and into the sockets. The inner initial layer is pseudopunctate lamellar tissue which forms most of the bulk and morphological features of the valves. The denticular plates and socket plates are composed of specialized inner initial tissue. The inner initial tissue of the dental lamellae is not separated from the palintrope or floor of the valve by sutures. The pedicle conduit penetrates the inner initial tissue at the apex of the ventral valve. The secondary deposits are limited generally to the muscle scars and cardinal regions of the valves. The structure of the secondary deposits of the muscle scars is complex. The myophores of the cardinal process are formed of cancellus secondary deposits. A spondylium triplex and a hemisyrinx are formed of secondary deposits in the apex of the delthyrial cavity of a few species.

All strophomenaceans are pseudopunctate; most bear taleolae. Fine pseudopunctae are randomly dispersed in oepikinids and strophomenids and coarse pseudopunctae are geometrically positioned in rafinesquinids and leptaenids.

In general, there is an inverse relationship between the diameter and packing density (number per unit area) of taleolae.

Evidence suggests that those strophomenaceans which possess a sealed pedicle foramen in adulthood probably rested upon the concave valve during life.

INTRODUCTION

The articulate brachiopods of the Order Strophomenida Öpik flourished from Lower Ordovician time throughout the rest of the Paleozoic Era. The order diminished in early Mesozoic time and reached extinction in the Jurassic if the taxonomically perplexing thecideoids (Triassic to Recent) are excluded. The order as it is understood today subsumes more genera than any other order of the Brachiopoda. No other order of brachiopods exceeds the Strophomenida in morphological diversity or ecological adaptations.

The four suborders and nine superfamilies of the Strophomenida form a related continuum but their extreme diversification precludes the possibility of a succinct, unequivocal diagnosis for the entire group. Most of the strophomenides possess pseudopunctate shell structure. The valves generally have wide hinge-lines and concavo-convex, less commonly resupinate or biconvex, profiles. Generally, a supra-apical pedicle foramen in the juvenile shell, a pseudodeltidium and a chilidium are present. The cardinal process is rarely absent but this structure may be varied in form. There is rarely a prominent or elevated structure for support of the lophophore. The Order Strophomenida differs from all other orders by the combination of these characters but not one character is unique to the order or invariably present.

The Order Strophomenida is divided into the Suborders Strophomenidina Öpik, Chonetidina Muir-Wood, Productidina Waagen and Oldhaminidina Williams. The Strophomenidina (Ordovician to Triassic) includes the oldest and least specialized species of the order. There is no single unique and ubiquitous character which distinguishes the Strophomenidina from the related suborders. The Strophomenidina has the characters of the order but lacks the hinge spines of the Chonetidina, the excessively concavo-convex or conical profile and the hollow spines of the Productidina and the slotted internal plate and oyster-like shape of the Oldhaminidina.

This study concerns the Superfamily Strophomenacea King which is one of five superfamilies of the Strophomenidina. The other superfamilies are the Plectambonitacea Jones, the Christianiacea Williams, the Stropheodontacea Caster and the Davidsoniacea King (=Orthotetacea Waagen). The oldest species of the Strophomenacea are early Middle Ordovician in age. Strophomenaceans occur in great number and diversity in rocks of Middle and Upper Ordovician age. Of the four families of strophomenaceans, the Oepikinidae Sokolskaya becomes extinct in the Upper Ordovician, the Rafinesquinidae Schuchert and Strophomenidae King continue in reduced numbers into the Silurian where they become extinct and the Leptaenidae

Hall and Clarke ranges into the Mississippian.

The Plectambonitacea (Lower Ordovician to Devonian) incorporates the oldest species of the Strophomenidina and in many respects possesses the fundamental morphological characteristics of the suborder. As is the case in many ancestral stocks, certain structures of the Plectambonitacea are so diversely formed that if the variations were present in later stocks the variations would constitute major taxonomic differentia. For example, the cardinal process of the plectambonitaceans is either absent, a single blade or trifid, that is, a set of three blades. The cardinal process of the other superfamilies is bifid, *i.e.* a pair of blades.

The Strophomenacea is an evolutionary derivative from the Plectambonitacea. Unfortunately, the Plectambonitacea is not known in sufficient detail to permit a more specific judgment of the source of the Strophomenacea. The Stropheodontacea and Davidsoniacea are derived from the Strophomenacea; the origin of the Christianiacea is unresolved. The Strophomenacea is differentiated from the Plectambonitacea by the character of the cardinal process. The simple teeth of the Strophomenacea are absent from the Stropheodontacea and in their place occur rows of denticles along the hinge-line. The Strophomenacea and Christianiacea are differentiated most readily by the shape, profile and prosopon of the valves. The valves of the Strophomenacea have the shape of a shield. The profile of the valves is flattened to moderately concavo-convex or resupinate. The prosopon of the external surfaces is distinctly costellate. The valves of the Christianiacea are much longer than wide and are deeply concavo-convex. The Christianiacea has only faint traces of external prosopon. The Davidsoniacea is not as easily differentiated from the Strophomenacea as are the other superfamilies. Few species of strophomenaceans lived cemented to an object on the sea-floor. The posterior platform in the dorsal valve is a prominent structure of the Strophomenacea. The simple teeth generally are supported by dental lamellae. The lobes of the cardinal process are disjunct or barely fused (conjunct) at the posterior. In contrast, most species of the Davidsoniacea lived cemented to an object on the sea-floor. A posterior platform and dental lamellae generally are absent and the lobes of the cardinal process commonly are completely ankylosed to form a shelf-like structure. A more detailed justification for the novel superfamilies Christianiacea and Stropheodontacea is presented in the introduction to the section on Systematic Paleontology.

The object of this study has been to document and clarify the morphology and shell histology of the Ordovician strophomenaceans. No comprehensive analysis of the entire superfamily has been published. Those works which treat taxonomically, stratigraphically or geographically restricted portions of the superfamily contain some unresolved discrepancies in observation, interpretation and terminology. In the course of the work, over 1300 peel sections and 1400 photographs have been made. The extensive collection of Ordovician strophomenaceans in the United States National Museum as well as collections and specimens from other museums have been studied. It is hoped that this work may be useful in consolidating and expanding the understanding of strophomenacean morphology and histology.

Early in the course of study it became apparent that the taxonomy of the Strophomenacea required revision. Neither morphological or histological studies could be rationally pursued without a detailed taxonomic framework to guide the investigation. The sections on Systematic Paleontology and Phylogeny are the result. Taxonomy has not been a goal of this study but a necessary and hopefully significant adjunct to the study.

Genera are not diagnosed or described in the section on Systematic Paleontology. The genera are clearly diagnosed and illustrated in the recently published (November, 1965) _Treatise on Invertebrate Paleontology, Part H, Brachiopoda_, hereafter called the _Treatise_. Additional excellent contemporary descriptions and illustrations of most strophomenacean genera appear in Cooper (1956) and Spjeldnaes (1957). Fortunately, these works permit the laborious and voluminous descriptions and illustrations to be omitted. Several new genera have been recognized in the course of the study. These do not add significantly to the descriptions or ranges of the families of the Strophomenacea nor do they evidence new taxa of familial rank. Inasmuch as manuscript names do not have formal status or protection under the International Code of Zoological Nomenclature and these genera do not add significantly to this study, the newly recognized genera are neither named nor described.

Most of the taxa within the Order Strophomenida have been the subjects of contemporary, comprehensive studies. The catalogue includes the works of Williams (1953) on the Stropheodontacea and Oldhaminidina, Elliot (1958) on the enigmatic Thecideidina, Muir-Wood and Cooper (1960) on the Productidina and Muir-Wood (1962) on the Chonetidina. Only the Plectambonitacea, Strophomenacea and Orthotetacea have not received a detailed comprehensive study in recent years. It is hoped that this investigation to some extent will contribute to our understanding of the Strophomenacea.

Techniques.- The nature of strophomenacean brachiopods has required development of several novel preparation techniques. These include techniques for the study of pseudopunctae, for preparation of thin sections and peel sections and for removing matrix from brachiopods.

Pseudopunctae may be observed on the external and internal surfaces of strophomenacean valves. The number and arrangement of pseudopunctae near the internal surface is controlled and obscured by secondary deposits. It is more practical to count pseudopunctae on the external surface of the valve for an accurate determination of their packing density in the inner initial layer. Not all pseudopunctae, however, reach the external surface of the inner initial layer. Moreover, some areas of the external surface of the valves may be covered by outer carbonate layer, which is not penetrated by pseudopunctae, or by matrix and some areas may be bruised or abraded.

The packing density of pseudopunctae may be computed easily from counts made upon tangential peels. The planar tangential peels can pass through only one small area of a curved brachiopod shell. Brief etching of the entire external surface of a valve is more practical than fabrication of tangential peels. Complete etching permits packing densities to be computed for several regions of a valve for comparison.

Brief etching in acid causes pseudopunctae to become prominent pits in the shell surface. Etching also removes the outer carbonate layer, thin matrix deposits and obliterates bruises and scratches. The surface of the valve is cleaned and polished after etching. Counts of pseudopunctae may be made directly from the shell surface under a microscope with a calibrated grid reticle. Valves are etched satisfactorily in 0.85N[1/] acetic acid for 10 to 20 minutes depending upon shell thickness. This technique is not recommended for rare or exceptional specimens and, of course, renders specimens unsuitable for photography or display.

Tangential peels are useful for measuring the diameter of taleolae. Details of the preparation of peels are furnished in the paragraphs on serial sectioning to follow. The center of the external surface of the ventral valve is ground to a flat surface for preparation of a tangential peel. The surface is ground until the visceral cavity is reached. The taleolae to be measured occur about halfway between the center and the edge of the ground surface, that is, taleolae diameters are measured at approximately the middle of the inner initial layer. Taleolae diameters are measured with an accurately calibrated, finely divided reticle at high magnifica-

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[1/] 0.85N acetic acid may be made by mixing 1 part 17N C.P. glacial acetic acid (from the bottle) with 19 parts water.

tion (X100).

Only longitudinal thin sections of strophomenaceans may be made by conventional techniques. Transverse and sagittal sections require special preparation. The shell material flakes away if a sagittal or transverse edge of a specimen is ground in the conventional manner upon a rotary lap or a glass plate. Shell material is too impermeable to impregnate with Canada balsam or Lakeside 70. Specimens have been invested in plaster compounds with hope that the plaster would prevent spalling of tissue. Plaster is brittle and does not adhere well to the surface of the specimens. Specimens have been invested in polyester resin plastics[2/] with limited success. Polyester resins bond tightly to specimens, are strong and may be ground with ease. Unfortunately, polyester plastic warps and becomes flexible at the temperature needed to cement the ground surface to a glass slide with Lakeside 70 (145° C.). Several brands of epoxy cement have been used for bonding the lapped surface to glass microscope slides. The epoxy bond is satisfactory but all epoxy cements that have been tried have bubbles and fibrous structure or objectionable flow-structures after

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2/ Polylite (8237), Reichhold Chemicals, Inc., White Plains, New York. E-Z Cast, Clear Polyester Casting Resin, Industrial Arts Supply Co., Minneapolis, Minnesota.

polymerization. The cover glass is mounted with cold setting Permount[3/]. Slides made by this method are satisfactory for study but are not adequate for published illustrations.

Closely spaced, serial thin sections of brachiopod shell cannot be made with commonly available equipment. Closely spaced, serial peel sections may be made quickly and easily with parallel grinding instruments as those described in the Treatise (p. H253). Peel sections are well suited for studies of brachiopods in which it is necessary to follow changes of morphology and histology of structures.

Peel sections are prepared by grinding a surface into a specimen with fine abrasive, etching the ground surface in acid and replicating the etched surface in transparent plastic. The process works because a crystal of calcite (and other anisotropic crystals) etches at different velocities in different crystallographic directions. A ground and etched surface through a brachiopod shell has topographic relief which is determined by the crystallographic orientation of the calcite plates, fibers and granules of which the shell is constructed. The plastic replica has a frosted, translucent appearance except in areas where the plastic incorporates insoluble

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3/ Fisher Scientific Co., Fair Lawn, New Jersey.

grains of opaque matrix which have been liberated by etching. The peel section of the fossil has the appearance of a thin section in phase contrast illumination because the surface of the plastic acts as a fine diffraction grating. Histological differences in the shell are more apparent in peel sections than in thin sections.

Transverse peel sections of brachiopods are most useful because every structure in a transverse peel section is symmetrical or paired. It is easy to locate the position of a transverse section on a whole specimen to which it is compared.

Serial sections for this study were ground with a modified Simpson serial section machine[4/]. A Simpson serial sectioning machine permits faster but less accurate grinding than a Croft parallel grinder. Nevertheless, grinding error with a Simpson serial sectioner is ±0.002 inches which is less than the depth of etching.

Preparation of peel sections is outlined by Boardman and Utgaard (1964). Their procedure is unnecessarily complicated for brachiopod studies and is modified as follows:

(1) Make a carefully oriented, transverse cut with a

4/ G. G. Simpson, A simplified serial sectioning technique for the study of fossils. Am. Mus. Novitates 634, June 10, 1933.

diamond saw through the anterior end of a brachiopod specimen. Cut several specimens of the same species. Stand the specimens on the cut surface in a square metal mold or a glass ring[5]. Very small specimens may be held in a small pyramid of modeling clay. Leave at least 1/4 inch (about 5 mm.) space between the specimens. Be careful to orient all specimens in the same way for convenience in later study. Stand several automatic pencil graphite "leads" in modeling clay pyramids near the edges of the mold. The spots made by the "leads" will serve as indicator marks in the finished series of peels.

(2) Invest the specimens in polyester resin[6]. Remove the plastic block from the mold.

(3) Grind the top of the plastic block to a flat surface and cement the top with epoxy resin to a holder of the serial section machine.

5/ Glass rings may be made by cutting small vials with a diamond saw. Place the glass ring on a sheet of glass and seal the edge with modeling clay. Metal molds are available from Ward's Natural Science Establishment, Inc., Rochester, New York.

6/ Polylite (8237) Reichhold Chemicals, Inc., White Plains, New York, has been found to be excellent. Unlike other plastics, Polylite (8237) has a Mohs hardness of 3, is acetone and acid resistant and does not smear when ground.

(4) Affix the holder and plastic block to the serial section machine. Grind with coarse abrasive on a rotary lap to a desired surface in the brachiopod specimens. Grinding should proceed from anterior to posterior.

(5) Record the setting of the serial section machine. Remove the holder and plastic block and finish the surface on a glass plate with number 600 grit abrasive. It is not necessary to polish the surface with tin oxide as Boardman and Utgaard indicate because etching polishes the surfaces of the specimens and removes the scratches produced by the fine grinding.

(6) Etch the finished surface for 20 seconds in 0.6N hydrochloric acid. Comparative tests show that hydrochloric acid produces a finer surface than acetic or formic acid. During etching, agitate the specimen to dislodge bubbles and to prevent unequal etching. Let the plastic block and specimens dry thoroughly. Do not touch the etched surface.

(7) The peel is made in 0.06 inch thick cellulose acetate sheet stock7/. Cut the cellulose acetate sheets into pieces twice as large as the ground surface of the plastic block. A large border around the peel sections minimizes warping of the plastic sheet.

7/ Obtainable from the Transilwrap Company of Cleveland, Inc., Cleveland, Ohio.

(8) Immerse the ground surface of the plastic block in acetone. Drip acetone onto the cellulose acetate slide to form a puddle larger than the ground surface of the plastic block. Acetone must not flow onto the underside of the cellulose acetate sheet. Press the ground surface of the plastic block into the cellulose acetate sheet and place a small weight (3 lbs. is satisfactory) on the plastic block. This step <u>of</u> the process must be done quickly because acetone evaporates rapidly. Both surfaces must be wet with acetone or bubbles will occur in the peel. Too much weight on the plastic block will cause the cellulose acetate sheet to warp. Contrary to Boardman and Utgaard, some weight on the plastic block seems to be necessary unless the specimen holder is quite heavy.

(9) Allow the acetone to evaporate for at least 30 minutes. Long periods of drying (overnight) do not cause damage.

(10) Snap the plastic block from the cellulose acetate sheet. Rub one border of the slide with a coarse typing eraser. Label the slide in this area with drawing ink and cover the label with clear lacquer.

(11) Replace the plastic block and holder in the serial section machine. Adjust the serial section machine to the desired depth of grinding. Grind a new surface. Repeat the entire operation.

Conventional methods of cleaning brachiopod specimens with steel needles and potassium hydroxide pellets may injure specimens. Hard matrix may require these cleaning methods as a last resort. Matrices which contain clay may be removed by immersing the specimen in 30% hydrogen peroxide. The hydrogen peroxide will cause the clays to oxidize, expand and soften. Transfer the specimen to an ultrasonic cleaner[8/]. The ultrasonic cleaner will remove most clay deposits but leave sand grains upon the surface of the specimen. The sand grains may be removed under a microscope with a needle or brush. The procedure may be repeated as many times as necessary. Use 30% hydrogen peroxide with caution; it is extremely caustic and potentially explosive.

All photographs for this study, except those taken by the Audio-Visual Service, Miami University, Oxford, Ohio, have been made with a 35 mm., single-lens reflex camera, equipped with a 55 mm. lens. Photographs were made on Eastman Kodak, High Contrast Copy film, developed in Dektol and printed on Polycontrast paper. All specimens were coated with ammonium chloride sublimate for photography. Specimens were backlighted with a portable

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[8/] The ultrasonic cleaner that has been used successfully has a maximum output of 100 watts at 40 kilocycles frequency.

light table to obviate close cropping of each photograph. Dark field illumination is advantageous for photography of peel sections.

Acknowledgments.- The work for this dissertation was conducted during graduate study at the University of Cincinnati, Department of Geology, 1956-1960, and while an Instructor of Geology at Miami University, Oxford, Ohio, 1960-1966. The support, encouragement and facilities offered by the faculties and administrations of both institutions is sincerely appreciated. Professor Kenneth E. Caster has supervised this study. His guidance and interest is acknowledged with deep gratitude and respect. Dr. G. Arthur Cooper, Director of Paleobiology, United States National Museum, has provided generous counsel and has made available for study the extensive brachiopod collections of the National Museum.

I am indebted to the following persons for valuable advice and specimens for this investigation: Dr. G. Winston Sinclair, Geological Survey of Canada; Dr. Alwyn Williams, Queens University of Belfast; Dr. Nils Spjeldnaes, Paleontological Institute, University of Oslo; Dr. Arthur J. Boucot, California Institute of Technology; and Dr. Robert B. Neuman, United States Geological Survey. Additional specimens were loaned by the curatorial staffs of the American Museum of Natural History, New York State Museum and Science Service, and the Walker Museum of the

University of Chicago. Mr. Jess Merida of the National Museum provided helpful instruction in the preparation of peel sections.

The staff of the Audio-Visual Service of Miami University has given valuable guidance in the preparation of illustrations. Their prompt, proficient photographic assistance is appreciated. This manuscript has been proofread and typed by my wife, Gracia T. Pope. My continuing thanks go to her for her encouragement and help.

In the explanations to illustrations, the abbreviations U.S.N.M. and M.U. signify the United States National Museum and the geology museum of Miami University.

ORIENTATION AND GENERAL MORPHOLOGY

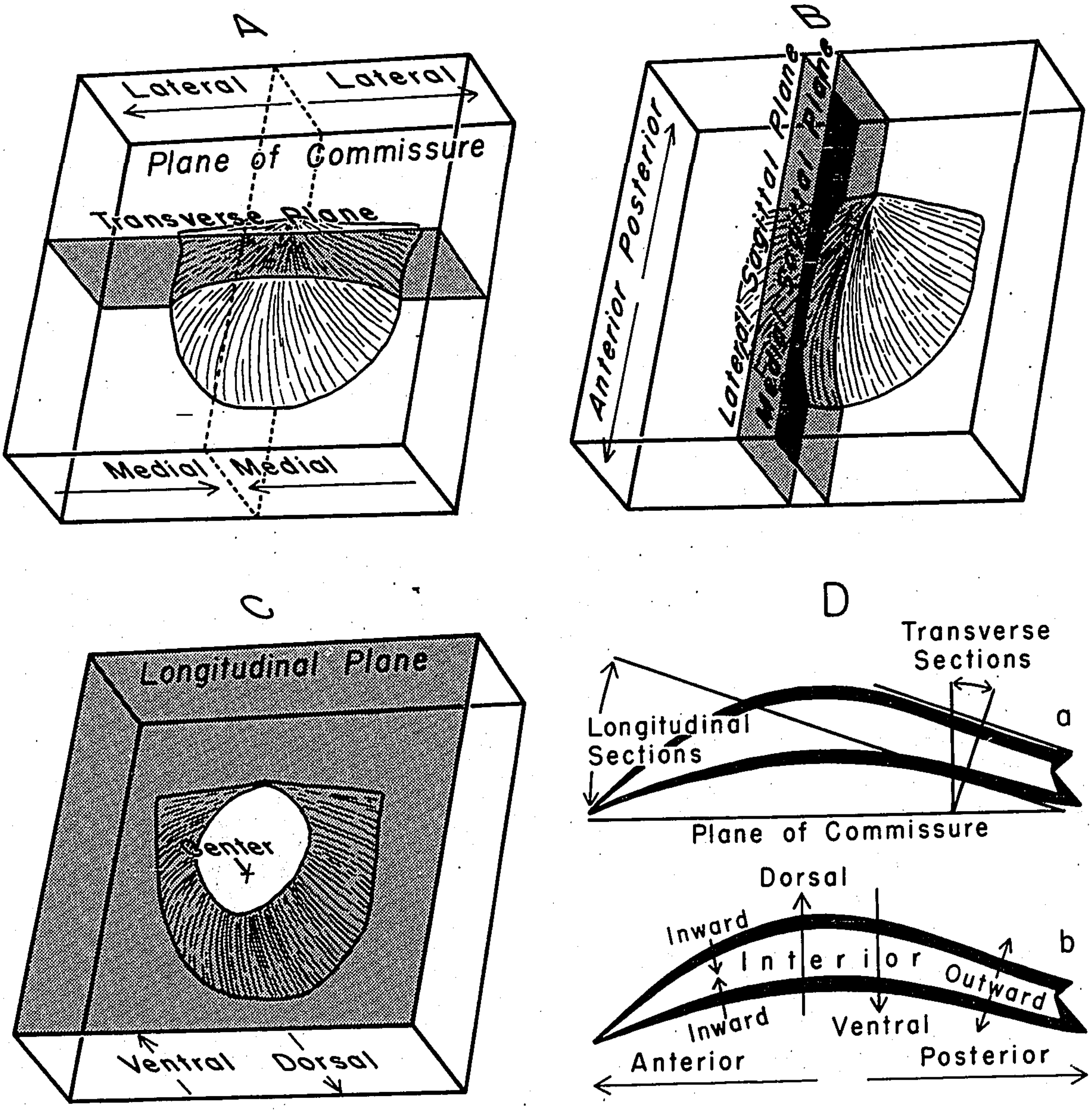
Terminology of orientation and direction.- The general terminology of orientation of articulate brachiopods, as anterior, posterior, dorsal and ventral, is adequately understood and will not be reviewed. It should be noted that the description by Percival (1960) of orientation during the larval development of *Notosaria nigricans* (Sowerby) reverses his earlier observations (1944) of orientation during the larval development of *Terebratella inconspicua* (Sowerby). Consequently, descriptions of brachiopods may again include reference to dorsal and ventral valves without explanation and the cumbersome and commonly inappropriate terms, pedicle valve and brachial valve, may be retired.

There is a definite need for a more rigid discipline of terminology concerned with directions in brachiopods, especially the directional terminology applied to structures on the internal surfaces of the valves. Even in published descriptions of recent date, it is not uncommon to find directional terms so ambiquously employed that authors' meanings are clear only by reference to illustrations. Text-Figure 1 illustrates some of the recommendations which follow. For brevity, only those terms which are new in this study or commonly subject to misuse or ambiguous application are discussed.

Text-Figure 1.- Planes, sections and directions in brachiopods. A and B, Transverse and sagittal planes. C, The clear area in the center of the brachiopod marks the surface of intersection of the longitudinal plane (top surface of block) and the brachiopod. The center is an arbitrary point along the medial axis about mid-way between the anterior and posterior extremes of the brachiopod. D-a, The direction of longitudinal sections may vary from parallel to the plane of commissure to parallel to the external, posterior surface of a valve. The upper limb of the angle of longitudinal sections is parallel to the line above the external, posterior surface of the dorsal valve. Transverse sections are normal to longitudinal sections.

It is convenient to imagine a brachiopod set into a rectangular prism, as in Text-Figure 1, A, B, C, for definition of directions. It may be seen in the text-figure that "anterior", "posterior", "dorsal" and "ventral" may be used as positional terms (the anterior, etc.), and as directional terms (toward the anterior, etc.).

Another set of directional terms is needed in addi-



Text-Figure 1.- Planes, sections and directions in brachiopods.

tion to anterior, posterior, dorsal and ventral. This set of directional terms is "medial" and "lateral". The plane of bilateral symmetry is a sagittal plane which divides the brachiopod into mirror-image halves. The plane of bilateral symmetry corresponds to the medial sagittal plane. "Medial" is preferred to "median", although the latter is customary, because of the established usage of "median" in statistics and because the adjective "medial" combines more euphoniously with most nouns. Structures included in the medial sagittal plane have a medial position. Structures which face or are directed toward the medial sagittal plane have a medial direction. "Lateral" is used to indicate the direction or position away from the medial sagittal plane. "Dorsad", "ventrad", "mediad" and "laterad" are convenient adverbial forms of these terms.

Most structures of brachiopods are oriented at an angle to the anterior-posterior, dorsal-ventral and medial-lateral directions. It is necessary commonly to combine directional terms to describe the orientation of oblique structures. For example, the surfaces of muscle bounding ridges which converge toward the posterior may be called the anterior-medial surfaces and the posterior-lateral surfaces. If structures converge or diverge, as in the example, the direction of convergence or divergence must be specified or clearly understood.

A brachiopod valve has an "internal surface" and an "external surface". The space between articulated valves is the "interior". There is no "interior surface" and no "exterior surface". The internal surface is called the "floor" of the valve by some authors. Use of "floor" in this manner should be suppressed because if one imagines articulated valves the floors face one another. "Floor" may be used for restricted areas of the internal surfaces of valves, as the "floor" of the delthyrial cavity or the "floor" of the umbonal chamber, because there is no satisfactory substitute term.

The words "in", "out", "inner", "outer", "inside" and "outside" should be avoided in description of orientation and direction of structures. These words are difficult to apply without ambiguously meaning either the medial to lateral direction or the dorsal to ventral direction. "Inward" and "outward" may be used with caution, as shown in Text-Figure 1, D-b, to indicate direction across the thickness of one valve.

"Middle" is a meaningless term with respect to brachiopods. "Middle" may mean medial, the interior, the surface of the visceral cavity of a valve or a position midway between the posterior and anterior along the medial plane. "Center" may be used for the position midway between anterior and posterior along the medial sagittal plane as shown in Text-Figure 1, C.

By convention, the "plane of commissure", Text-Figure 1, D-a, is misused in this work and elsewhere with reference to the orientation of longitudinal and transverse sections of strongly curved concavo-convex and resupinate brachiopods. The line marked "plane of commissure" in Text-Figure 1, D-a, is parallel to the plane which includes the line of commissure of a curved brachiopod as shown. It is customary to say that longitudinal sections are ground parallel to the plane of commissure and that transverse sections are ground normal to the plane of commissure. In reality, longitudinal sections are ground parallel to a plane tangential to the medial-posterior region of the external surface of the disk of the valve (see glossary for "disk of the valve") and transverse sections are ground normal to longitudinal sections. These orientations provide the most intelligible sections through structures of the internal surfaces of the valves.

<u>General morphological terminology of strophomenacean valves</u>.- The general morphological terminology of brachiopods is well known and does not need discussion here. Some of the general and specialized terms required for taxonomic description and discussion of the comparative

morphology of the Strophomenacea are illustrated in Text-Figures 2 through 6. The many standard and commonly used

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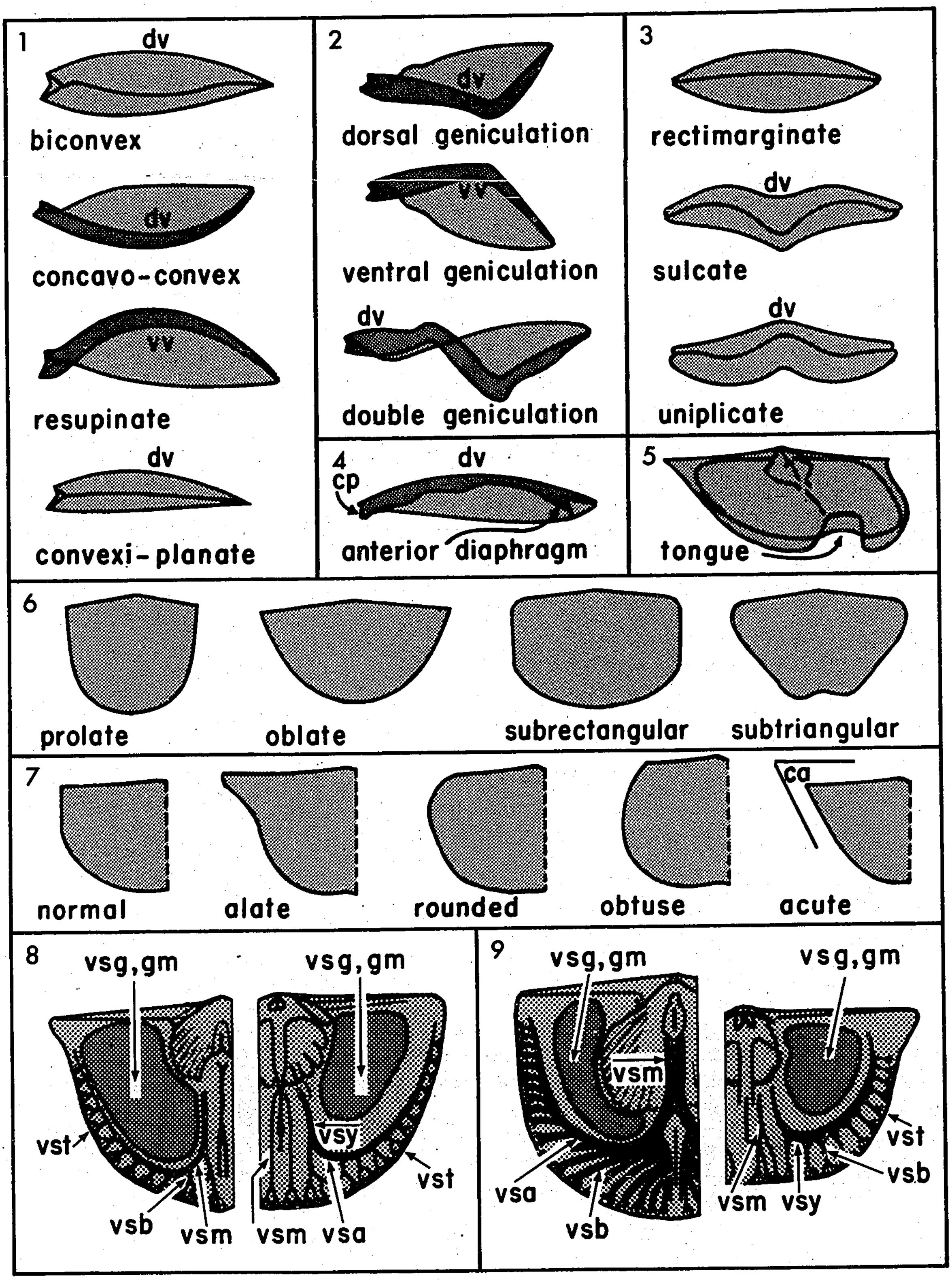
Text-Figure 2.- Morphological terms applicable to strophomenoid brachiopods. ca - cardinal angle, cp - cardinal process, dv - dorsal valve, gm - genital markings, vsa - *vascula arcuata*, vsb - *vascula bifurcata*, vsg - *vascula genitalia*, vsm - *vascula media*, vst - *vascula terminalia*, vsy - *vascula myaria*, vv - ventral valve.

1. The shape of the profiles of some brachiopods. The dorsal valve is directed toward the top of the page.
2. The shape of the geniculation of some brachiopods as seen in profile. Note that geniculation of the ventral valve results in geniculation in the dorsal direction, *i.e.* dorsal geniculation.
3. The shape of the anterior margin of some brachiopods.
4. A profile view of the anterior diaphragm of the dorsal valve, as found in species of *Murinella*.
5. A sharply geniculated flap or tongue on the anterior-medial margin of the ventral valve of *Notoleptaena* and *Rugoleptaena* fits against a complementary tongue of the dorsal valve.
6. The shape of brachiopod valves in plan-view.
7. Variation of the shape of the alae or cardinal angles of brachiopods.

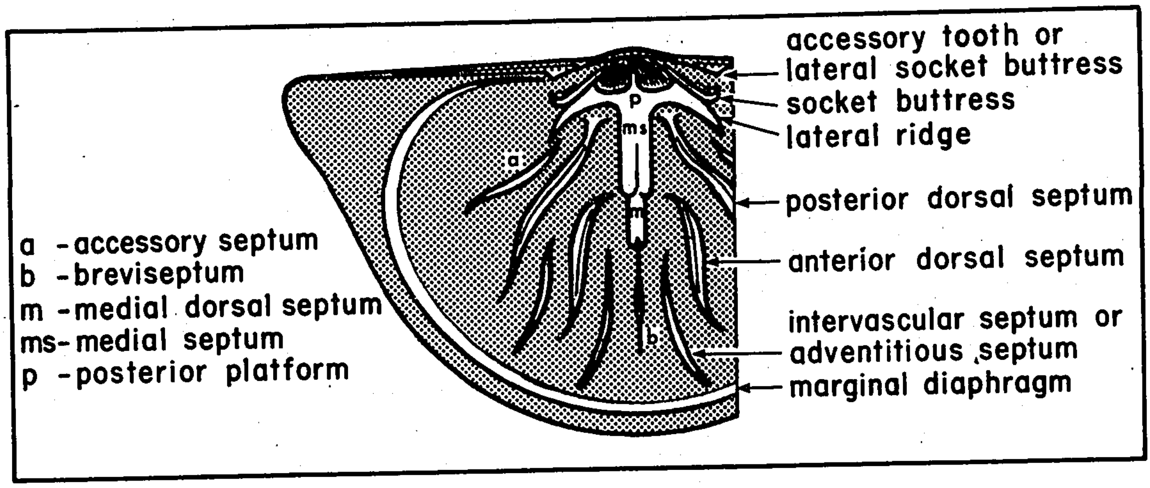


Text-Figure 2

8. Vascular markings on the internal surfaces of resupinate strophomenacean brachiopods. The vascular markings are reconstructed from traces on valves of several species of *Strophomena*. The ventral valve is on the left; the dorsal valve is on the right.

9. Vascular markings on the internal surfaces of concavo-convex strophomenacean brachiopods. A ventral valve is shown on the left, a dorsal valve on the right. The ventral valve (left) is reconstructed from several specimens of *Macrocoelia expansa*, see Text-Figure 6, number 13. The dorsal valve (right) is reconstructed from published illustrations and several specimens of species of *Leptaena* and *Kiaeromena*.

terms which appear in this work and which are satisfactorily defined in the glossary of the *Treatise on Invertebrate Paleontology*, *Part H*, *Brachiopoda*, pp. 138-155, do not require redefinition. The authors of the *Treatise* apparently believe that their glossary is complete. They state (p. H3) that they hope to have achieved "...a consistent terminology of manageable proportions that will act as a deterrent to any further maintenance of elaborate private vocabularies". Notwithstanding, detailed



<u>Text-Figure 3</u>.- The ridges on the internal surface of the dorsal valve of a generalized strophomenacean brachiopod. These structures may be called either ridges or septa depending upon their shape in various species. The lateral socket buttress may be called an accessory tooth if this structure has an articulatory function. The lateral ridge and medial septum or ridge are parts of the posterior platform. Intervascular septa may be called adventitious septa if their form is irregular. The accessory septa are intervascular septa which are not to be related to the five transmuscle dorsal septa. The medial dorsal septum is the medial member of the five transmuscle dorsal septa (that is, it is a breviseptum overlain by secondary deposits) whereas the medial septum is the anterior projection of the posterior platform.

investigation of any group of organisms, fossil or living, is certain to uncover features and concepts which have not been recognized previously. New terms are necessary for these features and concepts to avoid awkward descriptive phrases and to avoid unfortunate implication of homology where none exists. Consequently, it has been necessary to assemble a "private vocabulary" of terms which are necessary for taxonomic description and morphological discussion of the Strophomenacea.

All entries in the glossary to follow are either new terms, rarely used terms not included in the glossary of the *Treatise*, terms defined in an unconventional manner for specific application to strophomenaceans or terms of disputed definition for which a preferred definition has been selected.

Key to abbreviations on Text-Figures 4, 5 and 6.-

adm, adductor muscle scars. Fig. 4: 2,3,4,5,6; Fig. 5: 4,5,6a.

ajm, adjustor muscle scars. Fig. 4: 3; Fig. 5: 4,5.

al, ala. Fig. 3: 2; Fig. 6: 14.

anm, anterior margin. Fig. 6: 14.

ant, anterior. Fig. 4: 4.

apv, apex of the valve. Fig. 5: 4; Fig. 6: 14.

aso, accessory socket. Fig. 5: 4.

ath, accessory tooth. Fig. 4: 1,5; Fig. 5: 6c.

avs,	adventitious septa. Fig. 4: 1.
bcp,	bifid cardinal process. Fig. 4: 1,2; Fig. 5: 6a.
br,	beak ridge. Fig. 6: 11.
bvs,	breviseptum. Fig. 4: 1,5.
ca,	cardinal angle. Fig. 4: 3,4.
cft,	cleft. Fig. 4: 6.
ch,	chilidium.. Fig. 4: 5; Fig. 5: 6a,6b; Fig. 6: 11,12.
cpl,	cardinal process lobe. Fig. 4: 5,6; Fig. 5: 6a,6c.
dc,	delthyrial cavity. Fig. 4: 3,4.
ddm,	diductor muscle scar. Fig. 4: 3,4; Fig. 5: 4,5; Fig. 6: 13.
df,	dorsal foramen. Fig. 5: 6a.
dkv,	disk of the valve. Fig. 6: 14.
dl,	dental lamella. Fig. 5: 5.
dn,	dorsal node or protegular node. Fig. 6: 12.
dp,	denticular plate. Fig. 5: 5; Fig. 6: 8,11.
dsa,	anterior dorsal septum. Fig. 4: 2,5,6.
dsm,	medial dorsal septum. Fig. 4: 2,6.
dsp,	posterior dorsal septum. Fig. 4: 2,6
es,	endospines. Fig. 4: 1,3.
fln,	flange. Fig. 6: 8.
gm,	genital markings. Fig. 5: 1; Fig. 6: 13.
gn,	geniculation. Fig. 6: 14.
h,	hemisyrinx. Fig. 6: 10.
hn,	hinge nick. Fig. 4: 3; Fig. 5: 1.
ia,	interarea. Fig. 4: 1,3,4,5; Fig. 5: 4; Fig. 6: 11.

lr,	lateral ridge. Fig. 4: 5; Fig. 5: 6a,6b,6c.
mbr,	muscle bounding ridge. Fig. 5: 4; Fig. 6: 10.
mcr,	meso-cardinal ridge. Fig. 5: 6b.
md,	marginal diaphragm. Fig. 4: 1,2,3,6; Fig. 5: 1,2.
mdr,	medial ridge. Fig. 4: 3,5,6; Fig. 5: 4,6b,6c.
mgb,	marginal beads. Fig. 4: 2; Fig. 5: 2.
myr,	myophore ridges. Fig. 5: 4,5,6c.
pc,	pedicle conduit. Fig. 6: 10.
pd,	pseudodeltidium. Fig. 4: 3,4; Fig. 5: 4,5; Fig. 6: 11,12.
pdc,	pedicle callist. Fig. 5: 5; Fig. 6: 9.
pll,	papillae. Fig. 4: 4.
ppl,	posterior platform. Fig. 4: 1,5,6; Fig. 5: 6c.
prc,	primary costa. Fig. 6: 1,4.
psm,	posterior margin. Fig. 6: 14.
rg,	ruga. Fig. 6: 6,14.
s,	socket. Fig. 4: 1,2,5,6; Fig. 5: 6a,6b,6c.
sb,	socket buttress. Fig. 4: 1,2,5,6; Fig. 5: 6a,6b.
scs,	secondary costa. Fig. 6: 1,4.
spn,	septal node. Fig. 4: 2.
st,	spondylium triplex. Fig. 5: 4; Fig. 6: 10.
t,	tooth. Fig. 4: 3,4; Fig. 5: 4,5; Fig. 6: 8,9.
tr,	trail. Fig. 6: 14.
uc,	umbonal cavity. Fig. 4: 4; Fig. 5: 2,4.
vs,	vascular markings. Fig. 4: 1.

vsa, vascula arcuata. Fig. 4: 3; Fig. 5: 1,2.

vsb, vascula bifurcata. Fig. 5: 2; Fig. 6: 13.

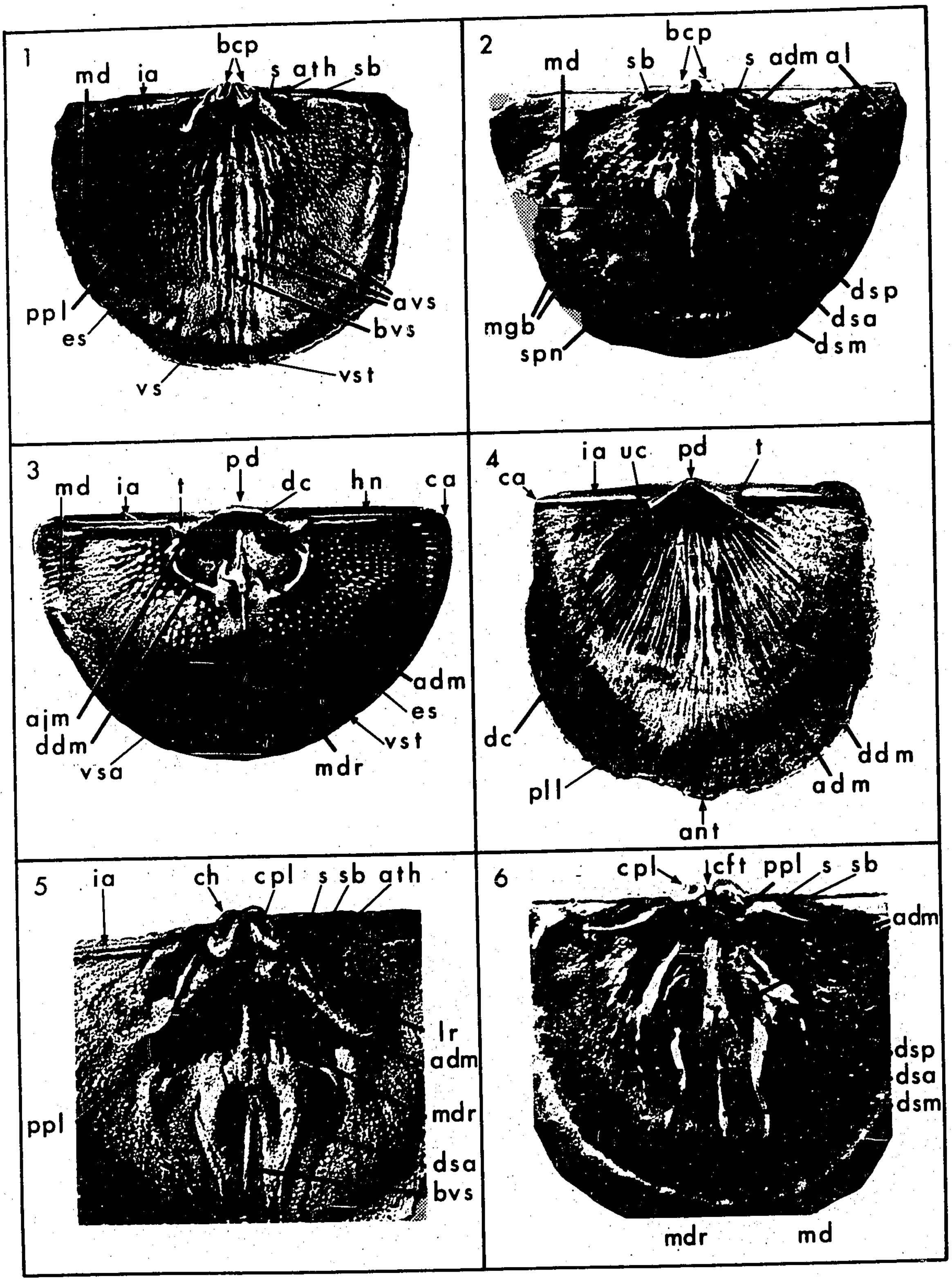
vsg, vascula genitalia. Fig. 5: 1.

vsm, vascula media. Fig. 5: 1; Fig. 6: 13.

vst, vascula terminalia. Fig. 4: 1,3; Fig. 5: 3; Fig. 6: 13.

Text-Figure 4.- General features of the internal surfaces of valves of strophomenacean brachiopods.

1. Internal surface of the dorsal valve of Strophomena vetusta (James). The cardinal process lobes are slightly abraded. Note the irregular form of the adventitious septa. Whitewater Formation. Paint Creek, one mile west of Camden, Ohio. M.U. 130-T. X1.5.
2. Internal surface of the dorsal valve of Oepikina septata Salmon. Lebanon Formation. Smith Co., Tennessee. Hypotype, U.S.N.M. 117830. X2.7.
3. Internal surface of the ventral valve of Strophomena planumbona elongata (James). Waynesville Formation. Clarksville, Ohio. M.U. 131-T. X2.6.
4. Internal surface of the ventral valve of Rafinesquina ponderosa Ulrich. An enlargement of the cardinal area is shown in Fig. 4, number 5. Waynesville Formation. Southwest corner of Boudinot Avenue and



Text-Figure 4

Westwood-Northern Boulevard, Cincinnati, Ohio. M.U. 132-T. X1.35.

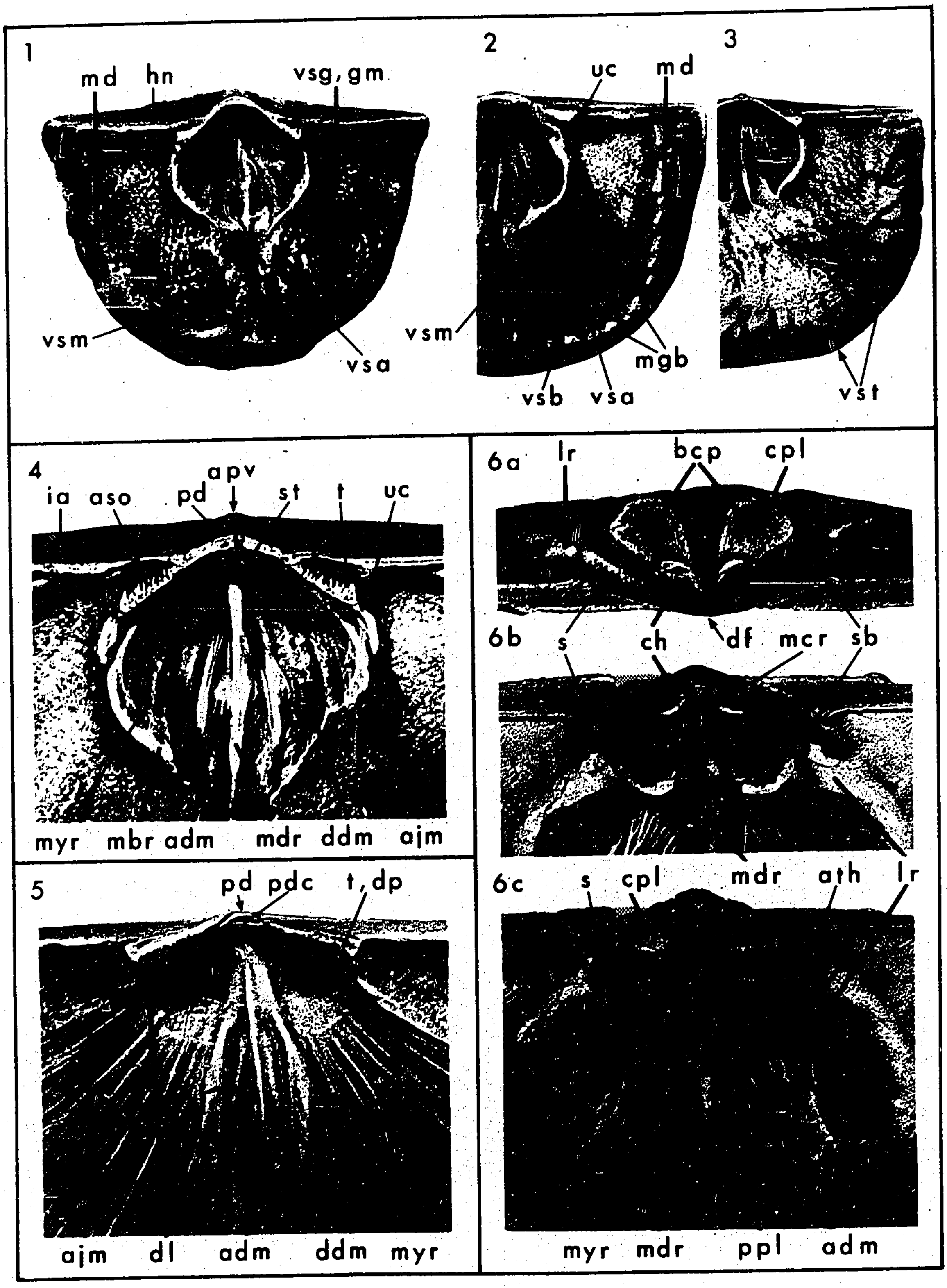
5. Posterior-medial region of the internal surface of a dorsal valve of Holtedahlina sulcata (Verneuil). The specimen is gerontic. Whitewater Formation. Richmond, Indiana. M.U. 133-T. X4.5.

6. Enlargement of the central region of the internal surface of a dorsal valve of Oepikina formosa Cooper. Note that the right cardinal process lobe of this specimen has been lost since the specimen was illustrated by Cooper (1956, Pl. 243, 24-26). Bromide Formation. Rock Crossing of Hickory Creek, Carter Co., Oklahoma. Paratype, U.S.N.M. 117808. X3.75.

Text-Figure 5.- Features of the cardinal regions and vascular markings of strophomenacean brachiopods.

1-3. Internal surfaces of three ventral valves of Strophomena planumbona (Hall) showing the vascular markings. (1) Liberty Formation. Crossing of Mixerville Road and Indian Creek, Butler Co., Ohio. M.U. 134-T. X2.5. (2) Liberty Formation. Oxford, Ohio. M.U. 135-T. X2.75. (3) Liberty Formation. Oxford, Ohio. M.U. 136-T. X2.7.

4. Internal surface of the posterior-medial region of the ventral valve of Strophomena vetusta (James). The hemisyrinx is obscured by the pseudodeltidium.



Text-Figure 5

Waynesville Formation. Collins Run, Oxford, Ohio. M.U. 137-T. X3.65.

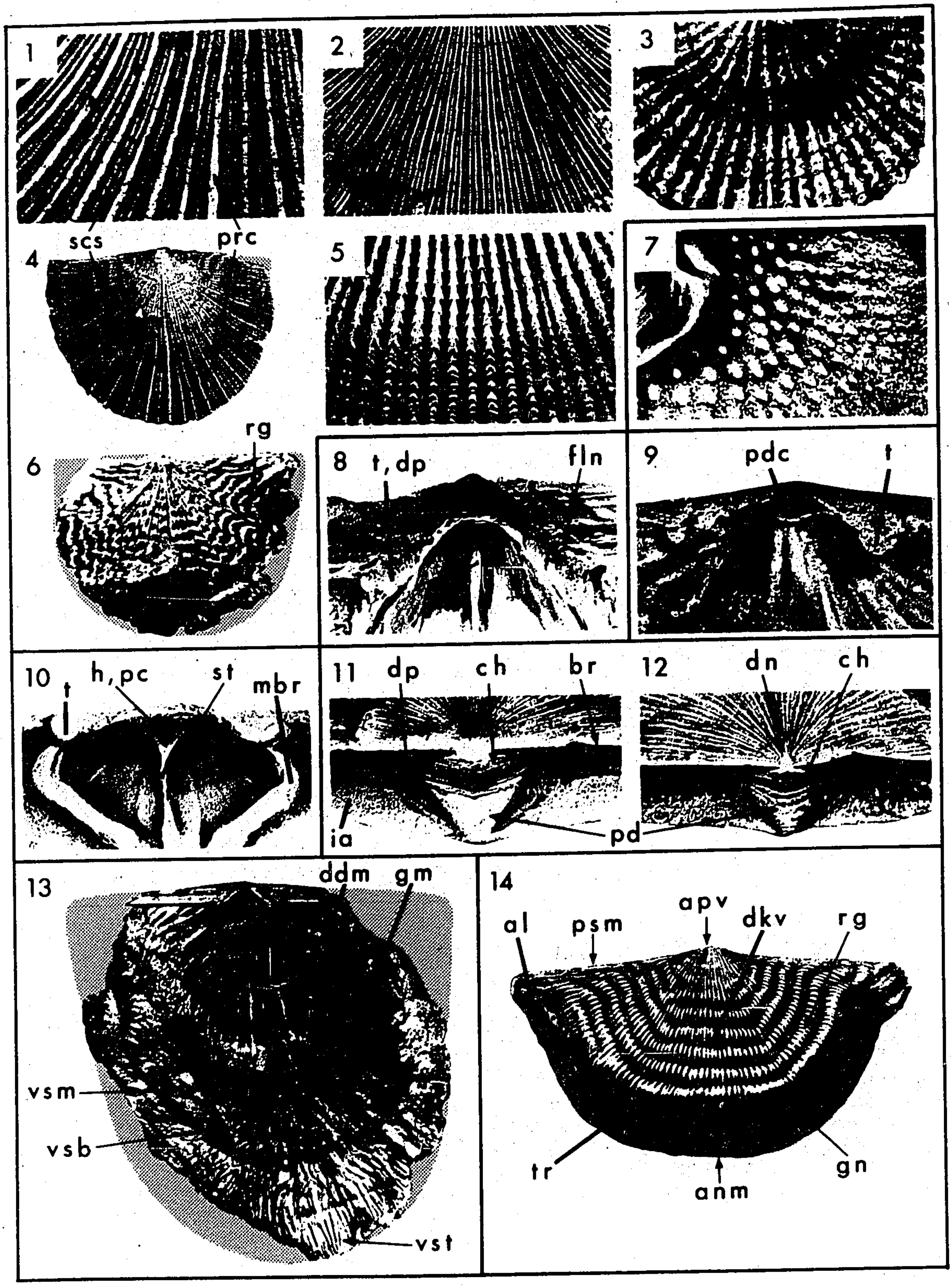
5. Internal surface of the posterior-medial region of the ventral valve of _Rafinesquina ponderosa_ Ulrich. Note the denticles on the denticular plate. Same specimen as shown in Fig. 4, number 4. X3.6.

6. Three views of the internal surface of the posterior-medial region of the dorsal valve of _Rafinesquina ponderosa_ Ulrich. (6a) View parallel to the plane of commissure. (6b) Specimen rotated about 60 degrees from the horizontal. (6c) View normal to the plane of commissure. Arnheim Formation. Martindells Creek, a tributary of Four Mile Creek, Butler Co., Ohio. M.U. 138-T. X3.8.

Text-Figure 6.- Prosopon and miscellaneous features of strophomenacean brachiopods.

1. Rafinesquinoid prosopon with alternate costae on the external surface of the ventral valve of _Rafinesquina fracta_ [?] (Meek). Waynesville Formation. Collins Run, Oxford, Ohio. M.U. 139-T. X4.

2. Strophomenoid prosopon with uniform costae on the external surface of the dorsal valve of _Strophomena planumbona subtenta_ (Hall). Formation and locality unknown. Charles Dyche Collection at Miami University. M.U. 140-T. X4.5.



Text-Figure 6

3. Scoticoid prosopon on external surface of ventral valve of an immature specimen of Strophomena [?] scotica Bancroft. Gasworks Mudstone, Lower Llandovery. Haverfordwest, Wales. U.S.N.M., no number. X3.5.
4. Glyptomenoid prosopon with kjaerinoid medial costa on the external surface of the ventral valve of Kjaerina squamula (James). Latonia Formation. Newport, Kentucky. M.U. 141-T. X3.
5. Glyptorthoid prosopon showing accentuated varices on external surface of the ventral valve of Glyptorthis insculpta (Hall). Waynesville Formation. Addison's Creek, 3 miles north of Oxford, Ohio. M.U. 142-T. X5.
6. Ptychoglyptoid prosopon on external surface of dorsal valve of Bellimurina subquadrata Cooper. Bromide Formation. Springer, Carter Co., Oklahoma. Paratype, U.S.N.M. 117655c. X4.9.
7. Endospines on the internal surface of the ventral valve of Strophomena planumbona elongata (James). Same specimen as shown in Fig. 4, number 3. X7.
8. Internal surface of the posterior-medial region of the ventral valve of Strophomena vetusta (James). The interarea of this gerontic specimen is eroded and exposes the flange of the microcrystalline layer of the palintrope underlying the denticular plate.

Formation unknown. From the area of Oxford, Ohio. M.U. 143-T. X3.

9. A latex cast of the internal surface of the posterior-medial region of the ventral valve of Macrocoelia expansa (Sowerby). The pedicle callist extends between the dorsal-medial edges of the teeth and is draped into the delthyrial cavity. Caradoc Sandstone (C_4 of King, 1928), Soudleyan. West side of Gallty Aner., Meiford District, Montgomeryshire, Wales. U.S.N.M. 105890; latex cast, M.U. 144-T. X3.1.

10. A specimen of Strophomena planumbona (Hall) tilted to show the hemisyrinx and spondylium triplex in the delthyrial cavity of the ventral valve. Liberty Formation. One mile south of Camden, Ohio. M.U. 145-T. X4.

11-12. Medial region of the interareas of two specimens of Strophomena planumbona subtenta (Hall). The specimens are inclined for maximum view of the pseudodeltidium and chilidium; the dorsal valve is toward the top of the page. The ventral interarea of number 11 is slightly eroded. Formation and locality unknown. Both specimens from the Charles Dyche Collection at Miami University, number De280D. (11) M.U. 146-T; (12) M.U. 147-T. X4.7.

13. Latex cast showing the vascular markings of the internal surface of the ventral valve of *Macrocoelia expansa* (Sowerby). The approximate valve outline is reconstructed. Caradoc Sandstone (C_4 beds of King, 1928), Soudleyan. Allt Fawr, Meiford District, Montgomeryshire, Wales. U.S.N.M., no number. Latex cast, M.U. 148-T. X1.4.

14. Leptaenoid prosopon on the external surface of the ventral valve of *Kiaeromena richmondensis* (Foerste). The trail (tr) is the deflected part of the valve between the geniculation (gn) and the anterior and lateral margins of the valve. The disk of the valve (dkv) is the valve including the trail minus the palintrope. Waynesville Formation. Collins Run, near Oxford, Ohio. M.U. 149-T. X1.75.

Glossary.-

accessory septa. See dorsal septa.

accessory socket. A shallow groove or pit in the palintrope of the ventral valve lateral to the denticular plate. The accessory socket accommodates the accessory tooth or lateral socket buttress of the dorsal valve.

accessory tooth. A ventrally directed projection from along the posterior-lateral margin of the socket of the dorsal valve (lateral socket buttress) which articulates with a groove or pit (accessory socket) lateral to the denticular plate in the palintrope of the ventral valve.

adventitious septa or ridges. Septa of the internal surface of the dorsal or ventral valve exclusive of the true dorsal septa accessory septa and medial septum. Adventitious septa correspond to intervascular septa but adventitious septa have irregular form and commonly are not bilaterally arranged.

alternate costae. Costae which alternate large and small, that is, primary and secondary.

anderidium (a). The pair of septa or ridges which flank the medial septum or ridge on the internal surface of the dorsal valve of chonetoids and plectambonitoids. The anderidia of plectambonitoids possibly correspond to the anterior-dorsal ridges of the Strophomenacea.

anterior diaphragm. A high septum on the internal surface of the dorsal valve which is concentric to the anterior margin of the valve. The anterior diaphragm is a modification of the marginal diaphragm in the anterior region. The anterior diaphragm bridges the space between the two valves and may cause a complementary groove in the ventral valve. The anterior diaphragm is most pronounced in species of *Murinella*.

anterior dorsal septa or *ridges*. See dorsal septa.

apex of the valve. The posterior-most point of a brachiopod valve where the protegulum is situated. Radially disposed features of brachiopods, *e.g.* costae, converge toward the apex of the valves. Strophomenaceans do not have elongated "beaks" as have other groups of brachiopods. The apex of the valve has been called the "umbo" but authors have used umbo with conflicting meanings.

bimuroid prosopon. External aspect caused by the anterior extension of the edges of coarse varices (comae) at regular intervals along the length of the valve. The comae commonly are deformed and chipped and impart a rough and ragged appearance to the valve. The bimuroid aspect is well developed on the dorsal valve of *Bimuria buttsi* Cooper.

<u>brachial ridges</u>. A synonym of dorsal ridges.

<u>breviseptum</u>. A thin septum which extends anteriorly from the anterior end of the medial ridge of the posterior platform of the dorsal valve. The breviseptum of strophomenaceans appears to correspond to the breviseptum of chonetoids and productoids. The breviseptum is composed of coarsely granular calcite in contrast to the lamellar calcite of adjacent shell tissue.

<u>cancellus tissue</u>. A microstructural type of shell tissue which has a cellular character. In the Strophomenacea, the cancellus structure seems to be confined to the muscle attachment sites on the cardinal process lobes.

<u>cardinal process</u>. A process or processes which project inward from the internal, medial-posterior surface of the dorsal valve and which serve for attachment of the diductor muscles. The cardinal process of the Strophomenacea is bifid, that is, divided into two lobes. Descriptive terms applied to cardinal process lobes are: blade (tabular, elongated in anterior-posterior direction), shaft (short, cylindrical, erect), cylindrical (tall, erect, round in cross section), lobate (irregular, short, obese), petaloid (top flattened and overhanging, as a mushroom, flattened top generally wider at anterior end than posterior end), hooked (ventral end curved in posterior direction).

cardinal process lobe. One process of the pair of processes which together constitute the bifid cardinal process of the Strophomenacea.

chilidium. By conventional definition, the flat or convex plate which partly or completely closes the notothyrium. The dorsal interarea of strophomenaceans is so narrow that a posterior-medial notch, the notothyrium, is obscure. For the Strophomenacea, the chilidium must be defined as continuation of the microcrystalline tissue of the interarea which extends from socket to socket across the posterior faces of the cardinal process lobes. The chilidium covers that part of the posterior base of the cardinal process which would be exposed by the delthyrium. No evidence of paired chilidial plates occurs in the Strophomenacea.

christianioid prosopon. The external aspect of a valve which is smooth. The surface of the valves of most species of Christiania bear, at most, only the faintest traces of capillae and fila.

clear lamellar tissue. A type of secondary deposit which is lamellar and which is brighter or clearer than other lamellar tissue when observed in peel sections.

cleft. The space between the lobes of a bifid cardinal process.

compound prosopon pattern. The external surface of valves of some species may bear two superimposed prosopon patterns. This condition is called a compound pattern. Prosopon patterns are listed under "prosopon".

<u>conjunct cardinal process</u>. A type of bifid cardinal process in which the posterior ends of the lobes are pressed together or ankylosed. The posterior ends of conjunct cardinal process lobes are covered commonly by the chilidium.

<u>cupped myophore</u>. A myophore surface on a cardinal process lobe that is cupped or folded.

<u>cymostrophioid prosopon</u>. A type of external prosopon in which the valve has the appearance of seersucker fabric. The surface of the valve bears widely spaced primary costa separated by fields of secondary costa. Each field between primary costa is rugose. The rugae of adjacent fields are alternate, that is, an outward projecting ruga lies next to an inward projecting ruga. The alternating rugae of many species are not so regular as to produce a definite geometric pattern. The rugae of a few species do form geometric patterns resembling a checkerboard made of rhombs. The cymostrophioid aspect is named for the stropheodontid genus <u>Cymostrophia</u>.

<u>dark lamellar tissue</u>. A type of secondary deposit which is lamellar and which is darker than other lamellar tissue when observed in peel sections.

dental lamella (ae). Tabular, vertical structures which unite the teeth and delthyrial margin of the palintrope of the ventral valve with the posterior-internal surface of the ventral valve. The tissue of the dental lamellae is confluent with the tissue of the palintrope and the internal surface of the valve, that is, dental lamellae are not bounded by sutures. Structures with similar position which are sutured to the floor of the valve and to the palintrope should be called dental plates. Dental plates are not found in the Strophomenacea.

denticular plate. A plate in the tooth of strophomenoid brachiopods which is sutured along the ventral edge or surface to the dental lamella and along the lateral surface to the palintrope. The denticular plate is the principal articulatory projection. The denticular plate is composed of lamellar tissue formed into tabular pseudopunctae in the Strophomenacea.

dictyostrophioid prosopon. An external prosopon pattern formed by the crossing of varices and secondary costae of equal prominence. Stronger primary costae divide the reticulate pattern into fields. The compound pattern resembles the surface of some fossil hyalosponges, e.g. Dictyospongia. The pattern is named for the strophеodontid brachiopod Dictyostrophia.

disjunct cardinal process. A type of bifid cardinal process in which the lobes are distinctly separated.

disk of the valve. A valve minus the palintrope.

dorsal foramen. The dorsal foramen is a questionable perforation near the apex of the dorsal valve of juvenile strophomenaceans. Thin sections through the apex of the dorsal valve of adult strophomenaceans show a point of very thin shell at the apex of the notothyrial cavity and the posterior edge (juvenile edge) of the chilidium. This thin spot in the shell separates the bulbous base of the chilidium from the long, thin plate of the adult chilidium. Probably the dorsal foramen is always closed by secondary deposits in adult strophomenaceans. Rupture of the thin filling of secondary tissue may give rise to an apparent dorsal foramen in adults at the site of the original dorsal foramen (Text-Figure 5, 6a). The function of the dorsal foramen is not definitely established. Spjeldnaes (1957) has suggested that the dorsal foramen may be a juvenile pedicle foramen.

dorsal geniculation. Dorsal geniculation refers to an angular bend in the valves, concentric to the margin, such that the trail is flexed in the dorsal direction.

dorsal node. A node or facette on the apex of the dorsal valve. According to Kemežys (1965, p. 505) the dorsal node of Spjeldnaes (1957, p. 50-52) is equivalent to the dorsal protegular fold. The dorsal node is also called the protegular node.

dorsal septa or ridges. A set of five ridges or septa which are found on the internal surface of the dorsal valve of many species of strophomenaceans. The five ridges include the medial dorsal septum, a pair of anterior dorsal septa and a pair of posterior dorsal septa. The medial dorsal septum may be the breviseptum or may be a breviseptum covered by secondary shell deposits. The medial dorsal septum is a projection of the medial ridge of the posterior platform anterior to the adductor muscle scars. The medial ridge of the posterior platform commonly is wider than the medial dorsal septum because of addition of secondary tissue along the medial borders of the muscle scars. The anterior dorsal septa may correspond to the anderidia of the plectambonitaceans. The posterior dorsal septa arise in the boundary between the anterior and posterior adductor muscle scars.

Synonyms for the dorsal septa include transmuscle septa and brachial septa. Synonyms for the anterior and posterior pairs of dorsal septa include anterior and posterior lateral septa, floor plates, standing plates and submedian septa.

Other septa or ridges may be found on the interior of the dorsal valve which may be confused with the true dorsal septa. These are the intervascular septa or ridges which border or overlie the vascular channels in the shell. Adventitious septa are irregularly formed intervascular septa. The pair of accessory septa may lie between the posterior dorsal septa and the lateral ridges of the posterior platform. The accessory septa may resemble the true dorsal septa but the accessory septa are intervascular (*i.e.* adjacent to the *vasculae cruralia*).

drape. The fold of the chilidium into the cleft of the bifid cardinal process.

endospines. Short, sharp, elevated spines on the internal surface of either valve. An endospine generally encases the end of a taleola. There is little difference between endospines and papillae except that endospines are sharp and erect and papillae are blunt, lobate or pimple-like and very short or recumbent.

flange. The flange is a structure encased entirely within the shell material of the ventral palintrope. The flange has no expression on either the external or internal surface of the palintrope or valve. The flange is a ridge on the ventral surface (underside) of the microcrystalline layer of the ventral palintrope which projects between the lateral surface of the denticular plate and lamellar tissue at the junction of the dental lamella and the palintrope. See Text-Figure 6, number 8, and Text-Figure 25.

floor plates. Synonym for the anterior and posterior dorsal septa.

fulcral plates. Concave plates of lamellar tissue which constitute the lateral part of the socket plates. The fulcral plates line the inner surface of the socket of the Strophomenacea and brace the socket buttress. Accessory teeth seem to be formed from the fulcral plates. The fulcral plates of Strophomenacea should be called "recumbent fulcral plates" because they are fused into the floor of the socket.

glyptomenoid prosopon. The external prosopon pattern shown by Glyptomena in which there are wide fields of uniform secondary costellae separated by primary costa.

glyptorthoid prosopon. The external prosopon pattern shown by species of Glyptorthis, an orthoid, and some species of Kierulfina, a strophomenacean, in which the varices extend a short distance outward from the shell surface, but not as far outward as the comae of the bimuroid pattern. The glyptorthoid pattern has the appearance and the feel of a mill file.

granular tissue. See microcrystalline tissue.

hinge nick. A groove on the interarea parallel and near to the free, anterior edge of the palintrope. The hinge nick may mark the site of attachment of a ligament or the site of abrasion by the edge of the opposing interarea.

initial layers.- The layers of the brachiopod shell which are secreted at the margin of the mantle. These include the periostracum, outer carbonate layer and inner initial layer. The boundary of the initial layers and the secondary deposits is indistinct.

inner initial layer.- The mineral shell layer which underlies the outer carbonate layer. The inner initial layer is secreted by the margin of the mantle. In the Strophomenacea, the inner initial layer is lamellar and pseudopunctate. For synonyms, see Table 2.

intervascular septa.- Septa situated between or upon the main branches of the vascular channels in the shell. Intervascular septa which are irregular in form are called adventitious septa.

kjaerinoid costa.- One exceptionally prominent costa along the midline of the valve, usually the ventral valve. This common feature is prominently displayed by species of the genera Kjaerina, Megamyonia and Kjerulfina.

lateral.- The direction opposite to medial, that is, toward the sides of the valve.

lateral ridge.- The ridge which extends laterally from the base of the cardinal process or from the posterior end of the medial ridge of the dorsal valve. The lateral ridges form the blades of the anchor-shaped posterior platform. The posterior margin of the lateral ridges may merge with the socket buttresses. The lateral ends of the lateral ridges may merge with the posterior-medial ends of the marginal diaphragm. The adductor muscle scars lie in the crotches between the lateral ridges and the medial ridge. "Lateral ridge" as defined corresponds to the lateral ridge of productoids as used by Muir-Wood and Cooper (1960) but not to "lateral septa" (=anderidia) of chonetoids as used by Muir-Wood (1962).

leptaenoid prosopon. The external pattern of prosopon in which uniform or alternate costae are crossed by regularly spaced concentric rugae, as shown on species of *Leptaena* and *Kiaeromena*.

marginal beads. Rounded nodes along the course of the marginal diaphragm. The marginal beads are commonly best developed near the anterior-medial margin of the dorsal valve. Marginal beads are formed by interruption of the marginal diaphragm by vascular canals.

marginal chamber or marginal tunnel. A tunnel or chamber around the lateral and anterior margins of articulated valves between the marginal diaphragms of both valves and the edges of the valves. The vascula terminalia are found on the surface of the marginal chamber.

marginal diaphragm. A low ridge on the internal surface of a valve which is concentric to the margin of the valve. The marginal diaphragm arises in the umbonal cavity or at the lateral ends of the lateral ridges. The marginal diaphragm may be interrupted in the medial-anterior region for passage of the vascula media. The marginal diaphragm separates the surface of the visceral cavity from the surface of the marginal chamber upon which are found the channels of the vascula terminalia. The marginal diaphragm may be a low ridge or a high septum as in species of Murinella. Marginal diaphragm of the strophomenacea is equivalent to the marginal ridge of the Productoidea.

medial. The posterior to anterior line or plane which divides the valve (or articulated valves) into equal, mirror-image halves. Also used to mean toward the medial line or plane. The direction opposite to medial is "lateral".

medial ridge. The medial-anterior projection of the posterior platform of the dorsal valve or a medial ridge which separates the diductor and adductor muscle scars of the ventral valve.

meso-cardinal ridge. A ridge or septum in the cleft between the lobes of a bifid cardinal process. Also called the "undifferentiated process".

microcrystalline tissue. Microscopically granular shell tissue associated with the surface of the palintrope or with muscle scars. This is the fibrous tissue of authors. In strophomenoids the crystalloid units of this tissue tend to be more equidimensional than elongated.

myophore ridges. The low ridges on muscle scar areas. The myophore ridges usually are radially oriented. They are most pronounced on the diductor muscle scars.

nervose prosopon. The external prosopon pattern found on _Nervostrophia_ in which the primary costae, and to a lesser extent, the secondary costae, vary in height along their length from apex to margin. The interruptions of the costae are random in position and impart to the surface a rough appearance.

notothyrial platform. In strophomenoid brachiopods the notothyrial platform is called the posterior platform. Notothyrial platform should not be used in reference to strophomenoids because the posterior platform is not situated near the notothyrium. A notothyrial cavity may be designated in strophomenoids as the space between the chilidium and the posterior surface of the bases of the cardinal process lobes.

outer carbonate tissue. The thin, external layer of mineral shell tissue in brachiopods. The outer carbonate layer underlies the periostracum. The outer carbonate layer on the disk of the valves of the Strophomenacea is finely lamellar; the layer may be finely granular in other brachiopod groups. For synonyms, see Table 2.

palintrope. The posterior, flexed part of a brachiopod valve. The external surface of the palintrope is the interarea. Palintrope is here defined in the sense of Thomson (1927, p. 49, not p. 64), Shrock and Twenhofel (1953, p. 293), Moore, Lalicker and Fischer (1952, p. 210) and Schuchert and Cooper (1932, p. 9). Cloud's definition of palintrope (1942, p. 14) which is based upon Thomson's definition (1927, p. 64, not pp. 49-50 which Cloud cites) restricts palintrope to a synonym of false cardinal area. Cloud's definition must be rejected by convention and because Cloud's definition leaves the prominent and important reflexed part of the valve without a suitable name.

papillae. Short or recumbent, blunt, lobate, or pimple-like projections on the internal surface of either valve. Papillae may or may not encase taleolae.

pedicle conduit. The conduit within the shell material of the apex of the ventral valve which served for protrusion of the pedicle. The external expression of the pedicle conduit is the pedicle foramen.

pedicle tube or sheath. A tube on the external, medial-posterior surface of the ventral valve of juvenile strophomenoid brachiopods through which the pedicle extended.

plate. A discrete structure joined to the rest of the shell by sutures. The tissue of a plate is not confluent with the tissue of the rest of the valve. The only plates of Strophomenacea are the socket plates and the denticular plates. "Dental plate" is inappropriate in reference to the Strophomenacea.

posterior-dorsal septa or ridges. See dorsal septa.

posterior platform. An anchor-shaped thickening in the medial-posterior region of the dorsal valve from which arises the cardinal process. The posterior platform is composed of the medial septum and the lateral ridges. "Posterior platform", Muir-Wood (1960, p. 7), replaces "notothyrial platform" in reference to strophomenoids because the platform is not located under the notothyrium and because the platform may extend a considerable distance anterior to the base of the cardinal process.

posterior rugae. Localized rugae near the posterior margin and cardinal extremities of brachiopod valves.

The posterior rugae commonly are oblique, that is, not concentric to varices and fila.

<u>prosopon</u>. Prosopon signifies those generally repetitive surface features of fossils which are judged to have minor taxonomic importance. Among brachiopods, prosopon includes features as costae, rugae and papillae. Prosopon replaces the term "ornament" because prosopon carries no asthetic connotation.

Different patterns and combinations of prosopon on the external surfaces of brachiopods may be named for genera or species which typically carry the pattern. For strophomenaceans, it is convenient to recognize the following patterns: bimuroid, christianioid, cymostrophioid, dictyostrophioid, glyptomenoid, glyptorthoid, nervose, leptaenoid, ptychoglyptoid, rafinesquinoid, scoticoid, sowerbyelloid and strophomenoid. These patterns are indexed separately in this glossary.

<u>protegular fold</u>. A medial node or fold on the dorsal protegulum of strophomenide brachiopods. Equivalent to the dorsal node.

<u>pseudodeltidium</u>. A flat to convex structure of the ventral valve which extends across part of the delthyrium between the medial-dorsal edges of the dental lamellae. The pseudodeltidium is confluent with the microcrystalline tissue on the surface of the palintrope; the

pseudodeltidium does not possess a medial suture. The microcrystalline tissue of the pseudodeltidium may have a backing of secondary tissue. Pseudodeltidium is used in preference to "deltidium" of Shrock and Twenhofel (1953, p. 285) and "xenidium" of Cloud (1942, p. 20).

ptychoglyptoid prosopon.- The external prosopon pattern exhibited by Ptychoglyptus and Bellimurina in which rugae between adjacent or nearly adjacent primary costa are chevron-shaped, with the apex of the chevrons pointed toward the apex of the valve.

rafinesquinoid prosopon.- The common prosopon pattern, as found on Rafinesquina, which is composed of primary costae which separate narrow fields of secondary and tertiary costae. The rafinesquinoid pattern differs from the glyptomenoid pattern in the narrowness of the fields between the primary costae and differentiation of costae therein.

scoticoid prosopon.- External prosopon in which the intersection of each major costa and varix is accentuated by a node. Commonly, the node is comma-shaped, with the tail of the comma lying along the varix. The tails of the commas may point alternately to either side along the length of a costa. This alternation gives the costa a zig-zag appearance. This aspect is named for *Strophomena scotica* Bancroft; this pattern is well developed also on *S. scabrosa* (Davidson).

secondary deposits. Mineral shell tissue deposited on the internal surface of the inner initial layer posterior to the margin of the mantle. Secondary deposits in the Strophomenacea are composed of lamellar or granular tissue and are rarely taleolate or pseudopunctate. For synonyms, see Table 2.

semidenticles. The irregular denticles on the dorsal and medial surfaces of the denticular plate of strophomenaceans.

septal nodes or *septal bosses*. Elevated nodes near the anterior ends of the dorsal septa.

shaft buttresses. Vertical lamellae which are oriented parallel to the medial sagittal plane and which buttress the anterior bases of the cardinal process lobes.

size. Species of Strophomenacea are described arbitrarily according to the following size classes for adults: small, specimens generally less than 20 mm. (3/4 in.) wide; medium, specimens generally between 20 mm. and 40 mm. (1½ in.) wide; large, specimens generally larger than 40 mm. wide.

socket buttress. A ridge which extends along the medial margin of the socket. The socket buttress contains the granular blade or rod of the socket plate. "Socket buttress" is preferred to "socket ridge" because socket ridge has been used for structures of several brachiopod groups which are not closely related to strophomenoids. See Muir-Wood (1962, p. 21).

socket ridge. See socket buttress.

socket plate. A plate which lines the sockets of the Strophomenacea. The socket plate is formed of two pieces, a granular blade or rod located along the medial margin of the socket and a concave plate of dark, finely lamellar tissue in the base of the socket. The granular blade or rod may be homologous to the brachiophore of the orthoids, at least they have the same microstructure and position. The concave plate of dark lamellar tissue may be a homologue of the fulcral plate of orthoids. Williams (1953) calls the socket buttress a socket plate.

sowerbyelloid prosopon. The pattern of prosopon found on species of Sowerbyella in which the secondary costae and, to a lesser extent, the primary costae are rows of tiny beads formed at the intersection of the costae and varices. The sowerbyelloid pattern resembles the scoticoid pattern except that the nodes of the scoticoid pattern occur only on primary costae, are large and tend to cause the costae to zig zag, whereas the beads of the sowerbyelloid pattern are small and uniformly distributed.

standing plates. Thin, high, anterior dorsal septa which partition the internal cavity between the valves into chambers. Standing plates may extend across the entire thickness of the internal cavity between the valves. The exaggerated standing plates of some specimens of *Teratelasma neumani* Cooper perforate the ventral valve.

strophomenoid prosopon. The common external pattern of prosopon exhibited by many species of *Strophomena*, in which fine, uniform costae are crossed by faint varices.

tongue. A flap of shell at the anterior-medial margin of a valve which bears a sulcus. The tongue fits into the complementary space provided by the fold along the anterior-medial margin of the opposing valve.

uniform costa. Costae of regular size which cannot be divided into primary and secondary ranks by reference to size.

varix (varices). A growth line. Minor varices, fila, are the fine, regularly spaced concentric lines on the external surfaces of valves. Major varices are the coarse, randomly spaced concentric grooves on the external surface of a valve which are evidence of a major interruption of growth.

vascular canals, channels or markings. Branching canals produced by the impression of vascular sinuses (=pallial sinuses) upon the internal surfaces of valves. "Vascular sinuses" or "pallial sinuses" properly refer to elongated cavities within the flesh of the brachiopod and consequently should not be applied to the marks which they produce in the shell.

ventral geniculation. Geniculation of the valves such that the trail is bent in the ventral direction. This is opposite to dorsal geniculation in which the trail is bent in the dorsal direction.

visceral cavity. The central-medial region of the internal surface of the valves to which was attached the visceral mass of the living animal including the muscles.

visceral disk. The portion of the disk of the valve which overlies the visceral cavity on the internal surface of the valve upon which was situated the principal organs and muscle attachment areas of the living animal.

SYSTEMATIC PALEONTOLOGY

The principal aim of this work is to document the comparative morphology of selected features and the shell histology of the Ordovician Strophomenacea. In such work, it becomes necessary to refer to taxa, most generally of generic or familial rank. This systematic review of the Strophomenacea is presented to permit the cited genera and families to be placed in their proper context within the superfamily. The concept of the Superfamily Strophomenacea has had a long and complex history in paleontology. The evolution of the strophomenacean concept, from 1846 when King proposed the Family Strophomenidae to Muir-Wood's comprehensive classification in 1960, is summarized in Chart 5, in the pocket at the end of this manuscript.

The recently published <u>Treatise on Invertebrate Paleontology, Part H</u> (1965) contains diagnoses of the families and genera, notation of the type species of genera, geographic and stratigraphic range of genera and illustrations of the type species of genera of the Strophomenacea (pp. H383-H395). The familial assignments and diagnoses of some genera presented in the <u>Treatise</u> are not acceptable to this writer whose classification of the group was constructed by phylogenetic analysis prior to publication of the <u>Treatise</u>. The differences between the classifications of the Treatise and this manuscript are minor and should not be stressed. They are largely differences of opinion as to where familial boundaries should be constructed with respect to transitional genera and differences of opinion concerning the rank of suprageneric taxa. The writer was surprised and pleased to review the classification in the Treatise because the Treatise supported so many of the systematic conclusions concerning the Strophomenacea which had been independently derived, even to the creation of several identical suprageneric taxa names.

There is a movement in paleontology today to standardize the endings of suprageneric taxonomic names. The International Code of Zoological Nomenclature specifies endings for familial-rank taxa only. These endings are "ini" for tribe, "inae" for subfamily, "idae" for family and "acea" for superfamily. Standardized endings for suprafamilial taxa of brachiopods have been adopted in the Treatise although such endings are not required by the International Code. The standardized endings are "idina" for suborder and "ida" for order. It is convenient and conventional to modify suprageneric taxonomic names to form vernacular nouns and adjectives. A recommendation is made in Footnote 1 of the Treatise, p. H12, that the endings of vernacular nouns formed from proper taxonomic names be constructed as follows: "ins" from subfamily names, "ids" from family names, "aceans" from superfamily names, "idines" from suborder names and "ides" from order names. The adjectival form of each vernacular noun is constructed by deleting the final "s". Most of this manuscript was written before publication of the _Treatise_. The recommended endings have been adopted herein with the exception that the more conventional termination "oids" is employed for the vernacular form of subordinal taxa, _e.g._ the Suborder Strophomenidina, the strophomenoids.

An outline of the suprageneric classification is given below to assist in the correlation of the present classification with that of the _Treatise on Invertebrate Paleontology_, _Part H_, _Brachiopoda_ (1965). Illustrations of the type species of most genera of the Strophomenacea may be seen in the _Treatise_ (pp. H383-H395). Additional illustrations of many species may be found in Cooper (1956, plates 208, 212-267) and Spjeldnaes (1957, plates 6-14).

A comparison of the strophomenacean classification of the Treatise and that employed in this study.-

Classification of the Treatise

- Superfamily Strophomenacea King, 1846
  - Family Strophomenidae King, 1846
    - Subfamily Strophomeninae King, 1846
    - Subfamily Furcitellinae Williams, 1965
    - Subfamily Rafinesquininae Schuchert, 1893
    - Subfamily Glyptomeninae Williams, 1965
    - Subfamily Oepikinae Sokolskaya, 1960
    - Subfamily Leptaenoideinae Williams, 1953
  - Family Foliomenidae Williams, 1965
  - Family Christianiidae Williams, 1953
  - Family Leptaenidae Hall and Clarke, 1894
  - Family Stropheodontidae Caster, 1939
    - Subfamily Stropheodontinae Caster, 1939
    - Subfamily Leptostrophiinae Caster, 1939
    - Subfamily Douvillininae Caster, 1939
    - Subfamily Pholidostrophiinae Stainbrook, 1943
    - Subfamily Shaleriinae Williams, 1965
    - Subfamily Leptodontellinae Williams, 1965
    - Subfamily Liljevalliinae Williams, 1953

Classification in this work

- Superfamily Strophomenacea King, 1846
  - Family Oepikinidae Sokolskaya, 1960
  - Family Rafinesquinidae Schuchert, 1893
  - Family Leptaenidae Hall and Clarke, 1894
    - Subfamily Murinellinae, nov.
    - Subfamily Leptaeninae Hall and Clarke, 1894
    - Subfamily Leptaenoideinae Williams, 1953
  - Family Strophomenidae King, 1846
    - Subfamily Furcitellinae Williams, 1965
      - Tribe Furcitellini Williams, 1965
      - Tribe Glyptomenini Williams, 1965
      - Tribe Teratelasmini, nov.
    - Subfamily Strophomeninae King, 1846
- Superfamily Christianiacea Williams, 1953
- Superfamily Stropheodontacea Caster, 1939

Phylum BRACHIOPODA Duméril, 1806
Class ARTICULATA Huxley, 1869
Order STROPHOMENIDA Öpik, 1934
Suborder STROPHOMENIDINA Öpik, 1934
Superfamily STROPHOMENACEA King, 1846

Diagnosis.- Pseudopunctate and generally taleolate, finely costate strophomenoids, with concavo-convex, resupinate, biconvex or rarely plano-convex profile, wide hinge line, relatively narrow interarea, bifid cardinal process and a supra-apical pedicle foramen.

Description.- In addition to the diagnostic features, all strophomenaceans bear a pseudodeltidium and chilidium. The pseudodeltidium or chilidium may be reduced in certain species with complementary enlargement of the opposing structure. The teeth are distinct and bear a semidenticulate denticular plate. Socket buttresses, lateral to the base of the cardinal process, are fixed along their length to the internal surface of the valve. The socket buttresses are reinforced by a socket plate. The lateral, free edge of the socket buttresses is corrugated to compliment the semidenticles of the teeth. Dental lamellae commonly are present. They are histologically confluent with the palintrope, internal surface of the valve and, if present, muscle bounding ridges. The dental lamellae may recede under the palintrope or may be encased in secondary deposits. Prominent dorsal septa are present in older species; they are reduced, modified or absent in younger species. The diductor muscle scars are large and flabellate in most concavo-convex species and small and restricted by a muscle bounding ridge in most plano-convex, biconvex and resupinate species. The pedicle foramen of adults may be open or sealed. According to authors, the lophophore was spirolophous.

Age.- Ordovician (Lower Chazy, Whiterock) into Mississippian.

Remarks.- The origin of the Strophomenacea lies most certainly within the Plectambonitacea but a convincing progenitor has not been discovered. The meso-cardinal ridge between the lobes of the cardinal process of some strophomenaceans is a superficial appendage. The Strophomenacea may not be related to these plectambonitaceans which bear a trifid cardinal process on the basis of the meso-cardinal ridge. Pseudopunctation of certain clitambonitoids can be regarded only as coincidental. There is no evidence of evolutionary relationship between these clitambonitoids and the Strophomenacea.

The Treatise incorporates the Superfamily Stropheodontacea Caster into the Strophomenacea as the Family Stropheodontidae. The number of stropheodontacean genera (38) rivals the number of strophomenacean genera (42).

The morphological diversification, geographic distribution and stratigraphic range of the Stropheodontacea is as great as that of the Strophomenacea. The astonishing homeomorphy of genera indicates only that the groups are closely related. In fact, the earliest genera of the Stropheodontacea, Eostropheodonta, Protomegastrophia and Eostrophonella, are not clearly differentiated from some strophomenaceans. All strophomenaceans possess a denticular plate in each tooth which is the homologue of the attenuated denticular plate along the free edge of the palintrope of stropheodontaceans. It is the loss of true teeth and the elongation of the denticular plate along the hinge, not just the possession of a denticular plate, which is the true differentium of the Stropheodontacea.

The evidence suggests that a greater degree of difference exists between the stropheodontid group and the families of the Strophomenacea, s.s. than between any of the families of the Strophomenacea, s.s.. The rank of the stropheodontid group is clear; it is a superfamily derived from the Strophomenacea. The Superfamily Orthotetacea (Davidsoniacea of the Treatise) is collateral with the Stropheodontacea in having been derived from the Strophomenacea.

The Stropheodontacea and Strophomenacea do not display heterochronous parallel evolution as would seem to be indicated upon first consideration of the groups. The sequence of evolutionary stages through which some of the features of the Stropheodontacea progress is the inverse of the evolutionary sequence for these features in the Strophomenacea. For example, the stropheodontaceans show enlargement of the pseudodeltidium and reduction of the chilidium with evolutionary advance whereas the strophomenaceans show reduction of the pseudodeltidium and enlargement of the chilidium. The stropheodontacean cardinal process progresses from the conjunct condition to the disjunct condition whereas the strophomenacean cardinal process progresses from disjunct to conjunct. The earliest stropheodontaceans, mentioned above, have closest affinities to moderately advanced strophomenaceans, for example, <u>Kjaerina</u> and <u>Hedstroemina</u>. Thus, it is not strange that advanced strophomenaceans should have heterochronous homeomorphs in primitive and moderately advanced stropheodontaceans.

<u>Christiania</u> cannot be placed in the phylogeny of the Strophomenacea. The genus does possess a bifid cardinal process which is the only diagnostic feature of the Strophomenacea also possessed by <u>Christiania</u>. The cardinal process of <u>Christiania</u> does not resemble in shape the cardinal process of any true strophomenacean. In fact, the cardinal process of <u>Christiania</u> most closely resembles the bilobed, shelf-like cardinal process of the

thecideoids (Thecidella), some of the advanced orthotetids (Streptorhynchus) and the thecospirids (Thecospira). Other features, for example, the pseudopuncta, socket buttresses and pseudodeltidium require inclusion of Christiania into the strophomenid complex but not necessarily into the Strophomenacea. The shape of Christiania, the form of the ventral muscle field, the unique dorsal septa and the digitate vascular markings are completely foreign to the Strophomenacea. Spjeldnaes (1957) makes a strong case for inclusion of Christiania into the Plectambonitacea. On the basis of non-plectambonitacean shape, cardinal process and dorsal septa of Christiania, this genus is regarded as typifying a new superfamily, the Christianiacea. The Christianiacea is probably a derivative of the plectambonitacean complex. The new superfamily mimics the Strophomenacea in possession of a bifid cardinal process but in all other respects is a unique strophomenoid.

Williams (1965, pp. H368-H369) discusses the forms of the lophophores borne by strophomenid brachiopods. He tentatively proposes that certain of the Plectambonitacea were schizolophous or ptycholophous, that Christiania was schizolophous and that the rest of the strophomenid brachiopods, including the Strophomenacea, Davidsoniacea, Productidina and certain plectambonitaceans, were spirolophous. Williams' suppositions would seem appropriate considering the rather lowly evolutionary position generally assigned to the strophomenids among the orders of brachiopods. Moreover, the unquestionable spire of the orthotetacean *Thecospira*, the spiral ramp in the ventral valves of the orthotetacean *Davidsonia verneuili* Bouchard and the plectambonitacean *Leptaenisca jukesi* (Davidson), support the supposed spirolophe of the Strophomenidina. Unfortunately, the form of the lophophore with specific reference to the Strophomenacea and Productidina is not certain.

The internal surface of the dorsal valve of *Leptaenisca concava* Hall bears paired serpentine ridges and the same surface of many productoids and strophomenaceans bear asymmetrical paired ridges or septa, the brachial ridges or dorsal septa. These ridges may be regarded either as "pads" which served for support of the lophophore or as "spacers" which separated the various segments of the lophophore and which may have channeled water into the lophophore apparatus. If hypothetical lophophores are drawn upon the serpentine ridges of *Leptaenisca*, the brachial ridges of a productoid or the dorsal septa of a strophomenacean, a spirolophe is not formed regardless of whether the ridges are considered "pads" or "spacers". Hypothetical lophophores constructed upon the serpentine ridges of Leptaenisca are either schizolophous or plectolophous. Hypothetical lophophores constructed upon the brachial ridges and dorsal septa of productoids and strophomenaceans are either ptycholophous or plectolophous. These strophomenids probably possessed the simpler lophophore systems, that is, they probably were schizolophous or ptycholophous.

The marginal diaphragm of the Strophomenacea does not seem to be homologous to the concentric dorsal ridge of the Plectambonitacea. Kozłowski (1929) and Öpik (1930) have proposed that the concentric dorsal ridge of plectambonitaceans supported a schizolophe. Sagittal thin sections show that the marginal diaphragm of strophomenaceans could not have been a lophophore support; there was not enough space between the valves at this position. In all probability, the marginal diaphragm was a strainer device, as in the productoids, and may have been a posterior and medial retaining wall for the marginal coelomic canal in the marginal chamber.

Family OEPIKINIDAE Sokolskaya, 1960

Diagnosis.- Finely pseudopunctate strophomenaceans with concavo-convex profiles, prolate to subrectangular shape and prominent dorsal septa or standing plates.

Description.- The cardinal process lobes are low, generally posteriorly curved shafts or hemicylinders with a cupped myophore on the posterior faces. The teeth are stout and semidenticulate. The socket buttresses generally are straight and possess deeply corrugated lateral margins. The pseudodeltidium and chilidium are variable in size. Older species bear large pseudodeltidia and small chilidia; younger species bear small pseudodeltidia and large chilidia. The chilidium commonly possesses a drape which unites with the meso-cardinal ridge. The posterior platform is strongly developed. A breviseptum is present but may be buried in secondary shell tissue. The diductor muscle scars are flabellate and generally lack muscle bounding ridges. The marginal diaphragm is prominent on the internal surface of the dorsal valve. The pedicle foramen is open in older genera, sealed in younger genera.

Age.- Ordovician (lower Chazyan, Whiterock to Richmondian).

Generic content.- *Oepikina* Salmon, 1942; *Kirkina* Salmon, 1942; *Dactylogonia* Ulrich and Cooper, 1942; *Hesperinia* Cooper, 1956; *Macrocoelia* Cooper, 1956; *Maakina* Andreeva, 1961.

Remarks.- The Oepikinidae is the primitive family of the Strophomenacea from which other families have been derived. The Leptaenidae differs from the Oepikinidae by gradual deletion of the dorsal septa, coarse pseudopuncta, development of various elaborations of geniculation and rugation and restriction of the diductor muscle field. The Rafinesquinidae and Strophomenidae share a common derivation from the Oepikinidae. The Rafinesquinidae retains the concavo-convex shape of the Oepikinidae but deletes the dorsal septa and acquires coarse pseudopuncta. The Strophomenidae are little more than plano-convex to resupinate oepikinids with mechanical modifications, as muscle bounding ridges and receding dental lamellae, required by their profile.

The Oepikinidae of this study and the Oepikinae of the Treatise differ in inclusion (here) of Dactylogonia and Hesperinia and exclusion (here) of Colaptomena. Dactylogonia and Hesperinia are closely related if not synonymous. Specimens of Hesperinia, the oldest strophomenacean, are too poorly preserved to permit complete analysis. Hesperinia is not related to the glyptomenid complex as indicated in the Treatise. Apparently Hesperinia has been compared to Glyptomena parvula Cooper [=Cyphomena ? parvula (Cooper)], a leptaenid, not to Glyptomena sculpturata Cooper, type species. Dactylogonia and Hesperinia are transitional between the Oepikinidae and the Leptaenidae. Their inclusion in one family or the other is largely arbitrary provided they both receive the same allocation. These genera are placed in the Oepikinidae because of the finely pseudopunctate structure of Dactylogonia and the prominent dorsal septa or standing plates of both genera.

Colaptomena and Macrocoelia are closely related genera which are transitional between the Oepikinidae and the Rafinesquinidae. Macrocoelia is judged to be an oepikinid because it possesses fine pseudopuncta and small dorsal ridges. Colaptomena is placed in the Rafinesquinidae because the genus is coarsely pseudopunctate, bears no stronger dorsal ridges than any rafinesquinid and has a large diductor muscle field. The diductor muscle field of the archaic oepikinids tends to be small and restricted by lateral bounding ridges in the fashion of the leptaenids. Advanced oepikinid genera, e.g. Oepikina and Macrocoelia, have larger diductor muscle fields which tend to completely surround the adductor muscle scars. Nevertheless, the diductor fields of these advanced oepikinids are smaller and more deeply impressed than the diductor muscle field of the Rafinesquinidae.

Kirkina, the second oldest strophomenacean, is known from only one poorly preserved specimen of the internal surface of the dorsal valve and several specimens of external surfaces. Kirkina, as Macrocoelia, lies along the lineage connecting the Oepikinidae and Rafinesquinidae. Kirkina has fine pseudopuncta and reduced dorsal septa and consequently is a phylogenetically advanced oepikinid. Kirkina indicates that either the age of the Oil Creek Shale of Millard Co., Utah, is younger than lower Chazyan (Whiterock) or that the base of the strophomenacean phylogeny is older and more complex than can be documented at this time.

Family LEPTAENIDAE Hall and Clarke, 1894

Diagnosis.- Coarsely pseudopunctate, coarsely taleolate strophomenaceans with biconvex or concavo-convex, subrectangular, oblate, rarely prolate valves, variously developed geniculation and rugation, modified, reduced or absent dorsal septa, open pedicle foramen and pronounced pseudodeltidium present in older species and small restricted diductor muscle field with adductor muscle scars open to the anterior.

Description.- In addition to the diagnostic features, the cardinal process lobes of the leptaenids are low, stout nodes or shafts in older genera to blades with petaloid or cupped, posteriorly facing myophores in younger genera. Older genera lack a meso-cardinal ridge, younger genera possess a meso-cardinal ridge which may be united to the chilidium. The chilidium of older genera is small; the chilidium of younger genera is large commonly domed and protrusive. A pedicle callist commonly occurs in place of a pseudodeltidium among younger species. The teeth are semidenticulate. The socket buttresses are straight and corrugated along their lateral margins. Dental lamellae are recessive immediately under the teeth but merge with the muscle bounding ridge of the diductor muscle scar. The diductor muscle scar is generally small. The muscle bounding ridge of the diductor muscle scar is weakly to strongly developed and commonly present only along the lateral margins of the muscle scars. If the muscle bounding ridge occurs along the anterior margin of the muscle scars, the muscle bounding ridge is drawn out toward the anterior to produce a lanceolate or petaloid shape. The posterior platform is strongly developed. The adductor muscle scars of the dorsal valve of older genera which bear weak dorsal ridges are obscure. Younger genera which lack dorsal ridges have circular adductor muscle scars in the dorsal valve. The circular adductor muscle scars are formed by the lateral and anterior curvature of the lateral ridges of the posterior platform. The medial ridge of the posterior platform of younger genera bifurcates anterior to the anterior edge of the adductor muscle scars to form a circular depression or low platform. Prominent endospines and dorsal marginal diaphragm generally are present.

Age.- Ordovician (lower Champlainian, Ashby) into Mississippian.

Remarks.- The Leptaenidae may be divided into three subfamilies, the Leptaeninae with dorsal geniculation and concentric rugae, the Leptaenoideinae with a cemented habit and the Murinellinae with elaborate prosopon, unusual geniculation and reduced or modified dorsal ridges. The Leptaenidae of this classification differs from the Leptaenidae of the Treatise by division of the family into subfamilies, incorporation of the Leptaenoideinae which the Treatise places in the Strophomenidae, and incorporation of Murinella and Megamyonia.

Subfamily MURINELLINAE, nov.

Diagnosis.- Primitive leptaenids possessing reduced or modified dorsal septa, elaborate prosopon and unusual geniculation.

Description.- The murinellins possess glyptomenoid, ptychoglyptoid, nervose or rarely rafinesquinoid prosopon which is commonly combined with weak concentric to oblique rugae. The profile varies from biconvex to planoconvex with dorsal geniculation or multiple geniculation. If dorsal ridges are present, they appear to be smeared or flattened against the internal surface of the valve. A prominent marginal diaphragm occurs in the dorsal valve.

Age.- Ordovician (Champlainian, Ashby into Trentonian).

Generic content.- Murinella Cooper, 1956; Cyphomena Cooper, 1956; Bellimurina Cooper, 1956; Limbimurina

Cooper, 1956; questionably *Oslomena* Spjeldnaes, 1957.

Remarks.- The Murinellinae is the ancestral group of the Leptaenidae. *Murinella* is related structurally to *Dactylogonia* and *Hesperinia*, thus *Murinella* is one of the least advanced of all strophomenaceans. All specimens of *Murinella* examined by the writer are silicified with the consequence that details of the pseudopuncta are not known. If *Murinella* should prove to be finely taleolate, the genus should be placed in the Oepikinidae. *Murinella* is placed in the Furcitellinae in the *Treatise*. Except for the biconvex to plano-convex profile of *Murinella*, this allocation cannot be supported.

The familial assignment of *Oslomena* cannot be determined satisfactorily. *Oslomena* may be closely related to *Cyphomena* of the Murinellinae or synonymous with *Glyptomena* of the Furcitellinae. Williams' discussion (1962) does not solve the position of *Oslomena* because he does not indicate whether he compares *Oslomena osloensis* Spjeldnaes, type species, to *Glyptomena sculpturata* Cooper, type species, or to *Glyptomena parvula* Cooper [=*Cyphomena* ? *parvula* (Cooper)]. The internal surface of the dorsal valve of *O. papilio* Spjeldnaes resembles that surface of *Bellimurina charlottae* (Winchell and Schuchert), and supports the murinelline assignment of *Oslomena*.

Subfamily LEPTAENINAE Hall and Clarke, 1894

Diagnosis.- Leptaenids with subrectangular to subtriangular shape, dorsal or rarely ventral geniculation, concavo-convex or rarely biconvex profile, weak to strong concentric rugae, poorly defined or no true dorsal ridges.

Description.- All older leptaenids have subrectangular to subtriangular shapes with pronounced alae; younger species may be oblate or prolate. All older species possess simple dorsal geniculation; younger species may be biconvex or ventrally geniculate, with or without a tongue. Most species bear regularly spaced, concentric rugae on the visceral disk but not on the trail. The fine prosopon of the external surface is rafinesquinoid, nervose or dictyostrophioid. The pseudodeltidium is commonly small to obsolete, rarely large and prominent. The chilidium is protrusive, thin and united with the posterior base of the meso-cardinal ridge. The cardinal process lobes are blades with cupped or petaloid myophores directed toward the posterior. The lobes of the cardinal process of young species (Devonian and Mississippian) may be so conjunct as to form a shelf-like structure. The socket buttresses are low, straight and short. True dorsal ridges are obscure or absent but there may be adventitious ridges or erratic ridges formed by the coalescence of recumbent endospines. The dental lamellae are low, receding and commonly obscured by filling of the umbonal cavities with secondary shell tissue. A pedicle callist is present at the apex of the delthyrial cavity of young species which do not possess an open pedicle foramen. The diductor muscle scars are enclosed, laterally or completely, by muscle bounding ridges. The muscle bounding ridges commonly are drawn-out toward the anterior. The internal surfaces of the valves bear recumbent endospines and pronounced marginal diaphragms. The pedicle foramen is open or sealed.

Age.- Ordovician (Champlainian, Porterfield) into Mississippian.

Generic content.- Leptaena Dalman, 1828; Kiaeromena Spjeldnaes, 1957; Leptagonia McCoy, 1844; Leptaenella Frederiks, 1917; Bekkeromena Rōōmusoks, 1963; Notoleptaena Gill, 1951; Rugoleptaena Havlíček, 1956; Megamyonia, Wang, 1949, Kjerfulfina Bancroft, 1929.

Remarks.- The Subfamily Leptaeninae contains all of the well known species associated with the family. The group has had a long and complex history in brachiopod taxonomy. In older classifications, the names Leptaenidae and Rafinesquinidae signified identical groups of genera. The genera of these two families, as they are now differentiated, have many similar attributes, for example, the reduced pseudodeltidium, petaloid cardinal process lobes, large taleolae and lack of dorsal septa. These similarities are isophenes in parallel evolving lineages. Because of the parallelism, the familial assignments of several genera are uncertain.

The relationship of Bekkeromena to the Leptaeninae is not certain. The shape and curvature of the valves, the posterior platform and the adductor muscle scars of the dorsal valve relate this genus to the Rafinesquinidae. The protrusive chilidium, pedicle callist, attenuated muscle bounding ridges lateral to the diductor muscles and low, obscure dental lamellae are leptaenid features. The leptaenid features are judged to be more strongly developed and of greater significance than the rafinesquinid features.

Megamyonia is placed in the Rafinesquinidae in the Treatise. The subtriangular to oblate shape, dorsal geniculation, recumbent teeth and round adductor muscle scars in the dorsal valve indicate relationship to the Leptaenidae. The large diductor muscle scars which lack muscle bounding ridges and absence of rugae are rafinesquinid characters.

Kierulfina is a most unusual leptaenid. Externally, Kierulfina is a rugose, ventrally geniculate homeomorph of the rugose, dorsally geniculated rafinesquinid Kjaerina. Despite the rugae and geniculation which in this case have no significance, *Kjerulfina* is a leptaenid and not a rafinesquinid because the genus has leptaenoid diductor and adductor muscle scars in the ventral valve, receding dental lamellae, a pedicle callist, circular adductor muscle scars in the dorsal valve and short socket buttresses. Internally, *Kjerulfina* closely resembles *Actinomena* of the Furcitellinae but *Kjerulfina* bears coarse pseudopunctae. The kjaerinoid costa of *Kjerulfina* and *Megamyonia* seems to have no taxonomic significance. In spite of all observations, the taxonomic position of *Kjerulfina* is not settled.

Subfamily LEPTAENOIDEINAE Williams, 1953

Diagnosis.- Small, subrectangular, concavo-convex leptaenids with dorsal geniculation, which cemented the medial-posterior region of the ventral valve to a foreign object.

Description.- The Leptaenoideinae includes very small strophomenaceans with leptaenid shape and a cemented habit. The pseudopuncta are coarse and widely spaced. The prosopon is rafinesquinoid to glyptomenoid, with faint rugae, many major varices and distortion caused by the cemented habit. The cardinal process lobes are low, irregular nodes without a distinct myophore. There is no meso-cardinal ridge. The socket buttresses are short, straight, thick ridges which are directed anterior-laterally from the lateral margin of the cardinal process nodes. The posterior platform does not bear distinct lateral ridges. The medial ridge of the posterior platform is medially grooved and bears an alveolus at its anterior termination. A breviseptum extends toward the anterior from the alveolus. A serpentine coiled ridge extends laterally from the medial ridge of the posterior platform. The semidenticulate teeth are supported by low, receding to obsolete dental lamellae. The faint dental lamellae merge with muscle bounding ridges along the lateral margins of the diductor muscle scars. A prominent medial ridge bisects the diductor muscle scars and the delthyrial cavity. The pseudodeltidium is small, thick and crudely formed. The interior of the ventral valve bears many bead-like papillae. There is a pedicle foramen in juvenile specimens.

Age.- Upper Silurian into Lower Devonian.

Generic content.- *Leptaenoidea* Hedström, 1917; *Leptaenisca* Beecher, 1890.

Remarks.- The name of this subfamily is poorly chosen because the interior of the dorsal valve of *Leptaenoidea* is unknown. The Subfamily Leptaenoideinae is placed in the Family Strophomenidae by the *Treatise*. This assignment cannot be supported by any feature or structure. The leptaenoideins are leptaenids by virtue of their shape and profile, coarse pseudopunctae, teeth, obscure dental lamellae and muscle bounding ridges. The interior of the dorsal valve of Leptaenisca does not resemble that of any known strophomenacean. When more is known about this curious group, it probably will be necessary to place it in a separate superfamily.

The coiled ridges of the brachial valve may have been callosities for support of a spirolophous lophophore as has been suggested by Muir-Wood (1960, p. 20). If this is true, these ridges are the only indication of the shape of the strophomenacean lophophore. The coiled ridges do no seem to be homologues of the dorsal septa of the oepikinids. The microstructure of the coiled ridges is not known.

The stropheodontacean Liljevalia gotlandica Hedström has been placed by authors in the Leptaenoideinae. L. gotlandica is a true stropheodontacean. The curious perforations of the ventral interarea of this species are caused by accidental rupture of thin shell at the apices of the umbonal cavities and not by perforation of the pseudodeltidium by the cardinal process lobes.

Family RAFINESQUINIDAE Schuchert, 1893

Diagnosis.- Coarsely pseudopunctate strophomenaceans with concavo-convex, non-geniculate or dorsally geniculate profile, prolate to subtriangular shape, distinct dental lamellae, adductor muscle scars encircled by large diductor muscle scars in the ventral valve, no dorsal septa and no muscle bounding ridges marginal to the diductor muscle scars.

Description.- The rafinesquinids bear rather coarse, regularly spaced pseudopunctae. The prosopon is rafinesquinoid or glyptomenoid, with or without oblique or concentric rugae and a kjaerinoid costa. The profile is concavo-convex and smoothly curved to indecisively geniculate. The pseudodeltidium is greatly reduced; the chilidium is large, thin and recumbent upon the posterior bases of the cardinal process lobes. The cardinal process lobes are blade-like in older species and juveniles to massive and petaloid in young species. There is no meso-cardinal ridge in juveniles and older species. The socket buttresses are long, straight and deeply corrugated along the free edge. The posterior platform is anchor-shaped to arrowhead-shaped. The medial ridge of the posterior platform does not extend far anterior of the adductor muscle scars and does not bifurcate. A breviseptum is rarely present. The adductor muscle scars of the dorsal valve are not circular. The semidenticulate teeth are supported upon distinct, thin, non-receding dental lamellae. The dental lamellae rarely are prolonged to the anterior to form weak muscle bounding ridges on the posterior-lateral margin of the diductor muscle scars.

The diductor muscle scars are large and flabellate. The adductor muscle scars of the ventral valve are situated near the center of the diductor muscle scar area. The pedicle foramen is generally sealed, rarely minute and supra-apical. Endospines and a marginal diaphragm are weakly to strongly developed.

Age.- Ordovician (upper Chazy, Ashby) into Lower Silurian.

Generic content.- *Rafinesquina* Hall and Clarke, 1892; *Colaptomena* Cooper, 1956; *Pionomena* Cooper, 1956; *Kjaerina* Bancroft, 1929; *Hedstroemina* Bancroft, 1929.

Remarks.- The Rafinesquinidae is a distinctive family which arose from a *Macrocoelia*-like ancestor by deletion of the dorsal septa and enlargement of the pseudopuncta. *Rhipidomena* of the Furcitellinae is so closely related to *Macrocoelia* that *Rhipidomena* could be considered a rafinesquinid if it were not finely pseudopunctate and gently resupinate. As noted, *Colaptomena* possesses coarse pseudopuncta and lacks dorsal septa. In other respects, *Colaptomena* closely resembles *Macrocoelia*. This would indicate that the coarsely pseudopunctate condition arose abruptly and without related structural change.

The type species of *Kjaerina* and *Hedstroemina* are distinct. Other species of these genera seem to be intergradational. Whether these genera are distinct but partly homeomorphic or truly intergradational has not been established.

The generic assignment of the late Ordovician species of Rafinesquina has been questioned by Salmon (1942). The late Ordovician species have no relationship to Longvillia, contrary to her suggestion. The number of species of Rafinesquina is so great that there are no prominent discontinuities in the morphogenesis of the genus. If the record of this genus were incomplete, the early Trentonian species and the Cincinnatian species would probably be placed in separate genera.

Pionomena is known from several casts of the external surface of the valves and one poorly preserved internal surface of the posterior region of the ventral valve. Pionomena is tentatively placed in the Rafinesquinidae on the basis of external appearance, prominent tetth, well developed dental lamellae and coarse pseudopunctae.

Family STROPHOMENIDAE King, 1846

Diagnosis.- Finely pseudopunctate, resupinate, biconvex or rarely plano-convex or concavo-convex strophomenaceans with recurved socket buttresses, commonly with receding dental lamellae, restricted diductor muscle scars, true but reduced dorsal ridges or adventitious ridges and a breviseptum from the bifurcate anterior end of the medial ridge of the posterior platform.

Description.- The Strophomenidae includes species with every possible strophomenacean shape. The profile commonly is resupinate or biconvex but may be biplanate, plano-convex or concavo-convex in atypical species. The valves have either smoothly curved profiles or ventral geniculation. The anterior margin may be rectimarginate, sulcate or uniplicate. The prosopon generally is strophomenoid or glyptomenoid but every other variety of prosopon known in the Strophomenacea is found. The pseudodeltidium and chilidium are present in all species. The size of the pseudodeltidium varies from large to small; the chilidium is small. The cardinal process lobes are erect cylinders or nodes. The cardinal process myophores of advanced species are cupped or petaloid. Few species have a mesocardinal ridge which, if present, is hidden under the chilidium. The socket buttresses are recurved in the shape of a hunting bow. The posterior-medial ends of the socket buttresses are widely divergent. The lateral ends of the socket buttresses generally merge into the palintrope lateral to the socket. The floor of the socket may be elevated above the nearby region of the internal surface of the valve. The free edges of the socket buttresses are corrugated. The posterior platform is small. The lateral ridges of the posterior platform are short and not sharply curved toward the anterior. The medial ridge of the posterior platform generally is bifurcate. The breviseptum arises in the split end of the medial ridge. The adductor muscle scars of the dorsal valve are indistinct. The internal surface of the dorsal valve may or may not possess true dorsal ridges or adventitious ridges. The teeth are stout. The blunt, semidenticulate anterior end of the denticular plate projects toward the anterior from the free edge of the palintrope. An accessory socket for reception of the lateral socket buttress (=accessory tooth) may occur in the free edge of the palintrope lateral to the denticular plate. The dental lamellae commonly recede under the teeth. The dental lamellae merge into muscle bounding ridges. The muscle bounding ridges vary from short ridges along the lateral-posterior margin of the small diductor muscle scars to ridges which almost surround the diductor muscle scars. The adductor muscle scars are situated near the anterior margin of the diductor muscle field. The adductor muscle scars are not enclosed to the anterior by the diductor muscle scars. Prominent adjustor muscle scars may interrupt the posterior-lateral segments of the muscle bounding ridges. The interior surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm is weakly to strongly developed. The pedicle foramen is open or sealed.

Age.- Ordovician (lower Champlainian, Ashby) to Upper Silurian.

Remarks.- The Family Strophomenidae is the largest, most complex and most diverse family of the Strophomenacea. There is no absolute differentia for the Strophomenidae but combinations of features permit their recognition. The Strophomenidae arises from a Macrocoelia-like oepikinid. The earliest strophomenid, Rhipidomena, is a gently resupinate Macrocoelia. The Orthotetacea surely arise from the Subfamily Furcitellinae.

Other descriptions of strophomenids specify that the muscle bounding ridges arise from the medial surfaces of the dental lamellae and, by inference, are not anterior continuations of the dental lamellae. This interpretation is not correct. The muscle bounding ridges and the dental lamellae are histologically continuous structures. The adjustor muscle scars are impressed into the site where the dental lamellae become ridges. The effect is shown in Text-Figure 5, number 4.

Subfamily FURCITELLINAE Williams, 1965

Diagnosis.- Biconvex, biplanate, resupinate or rarely concavo-convex strophomenids with incomplete muscle bounding ridges, slightly reduced or modified dorsal septa, large pseudodeltidium and an open or sealed pedicle foramen.

Description.- The shape, profile, nature of the anterior commissure, and prosopon may be any of the various forms listed for the family. The profile is rarely concavo-convex, geniculate or strongly resupinate. The chilidium is small; the pseudodeltidium generally is large. The cardinal process lobes are nodes in older species. In younger species, the cardinal process lobes are posteriorly bent, low cylinders with cupped myophores in the posterior face. The socket buttresses and posterior platform are those described for the family. True dorsal ridges or standing plates occur in all but the most advanced species. The teeth are more delicate and more pointed than the teeth of the Strophomeninae. The dental lamellae may or may not recede. The diductor muscle field is small and restricted by lateral muscle bounding ridges. The diductor muscle field is not elevated above nearby regions of the internal surface of the valve. The pedicle foramen is open in all but the most advanced species. The internal surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm is weakly developed.

Age.- Ordovician (lower Champlainian, Ashby, to upper Cincinnatian, Richmondian).

Remarks.- The Furcitellinae includes the primitive strophomenids as indicated by the presence of true dorsal septa, an open foramen, large pseudodeltidium and great variability of shape, profile and anterior commissure.

Tribe GLYPTOMENINI Williams, 1965

Diagnosis.- Weakly plano-convex, biplanate, resupinate or concavo-convex furcitellines with prolate shape, a rectimarginate anterior commissure, weak to absent posterior platform, strong to absent true dorsal septa, incomplete muscle bounding ridges and cylindrical or minute, bead-like cardinal process lobes.

Age.- Ordovician (lower Champlainian, Ashby, into Cincinnatian, Maysvillian).

Generic content.- *Rhipidomena* Cooper, 1956; *Glyptomena* Cooper, 1956; *Platymena* Cooper, 1956; *Actinomena* Öpik, 1930; *Mjoesina* Spjeldnaes, 1957.

Remarks.- The principal distinguishing features of the Glyptomenini are the flat profile and the prolate shape.

The Glyptomenini are the least advanced tribe of the Furcitellinae. There is a major gap in the phyletic record between *Rhipidomena*, the most primitive genus of the tribe, and the succeeding genera, *Glyptomena* and *Platymena*. *Rhipidomena* is not typical of the tribe by possession of strong, true dorsal septa, cylindrical cardinal process lobes, a large posterior platform, no muscle bounding ridges, and stout teeth. *Rhipidomena* could be considered to typify a monogeneric tribe. *Rhipidomena* is weakly resupinate to biplanate and prolate. Consequently, *Rhipidomena* fits into the Glyptomenini if a hiatus is accepted.

The Glyptomenini are ancestral to the Furcitellini and to the Strophomeninae.

Tribe FURCITELLINI Williams, 1965

Diagnosis.- Biconvex, oblate or subtriangular, rectimarginate or uniplicate, coarsely costate furcitellines with strongly to weakly developed true dorsal ridges, incomplete muscle bounding ridges and cardinal process lobes bent toward the posterior.

Age.- Ordovician (lower Trenton into upper Cincinnatian, Richmondian).

Generic content.- *Furcitella* Cooper, 1956; *Holtedahlina* Foerste, 1924.

Remarks.- The most characteristic features of the Furcitellini are the biconvex profile and oblate shape.

Furcitella and *Holtedahlina* are quite similar in all features except for the stronger dorsal ridges of *Furcitella* and the fold of *Holtedahlina*. When middle Trenton species are found, the two genera probably will not be differentiable.

The Teratelasmini probably arises from pre-*Furcitella* species of the Furcitellini.

Tribe TERATELASMINI nov.

Diagnosis.- Small, very oblate, weakly biconvex or concavo-convex furcitellines with very prominent anterior dorsal septa, with or without a medial dorsal septum, with widely divergent socket buttresses, uniformly capillate or smooth external surfaces, without muscle bounding ridges, with bead-like or no cardinal process lobes.

Age.- Ordovician (middle Champlainian, Porterfield, and upper Cincinnatian, lower Ashgill).

Generic content.- Teratelasma Cooper, 1956; Foliomena Havlíček, 1952.

Remarks.- These two strange, minute furcitellin genera differ by the presence of a high medial dorsal septum in Teratelasma and the smooth external surfaces of Foliomena. The prominent anterior dorsal septa of Teratelasma seem to be formed by the fusion of both the anterior and the posterior dorsal septa. There do not seem to be cardinal process lobes on Foliomena. This may be an accident of preservation. The differences between Teratelasma and Foliomena may be explained by the long interval, middle Champlainian to middle Cincinnatian, which separates them.

Subfamily STROPHOMENINAE King, 1846

Diagnosis.- Resupinate strophomenids with muscle bounding ridges extended around the anterior margin of the diductor muscle field, true dorsal septa weakly developed to absent, adventitious septa strongly developed to absent.

Description.- The Strophomeninae includes strophomenids which generally are strongly resupinate, with or without ventral geniculation. The shape of the valves is prolate, subtriangular, subrectangular or rarely oblate. The prosopon commonly is strophomenoid but may be rafinesquinoid or glyptomenoid. Unusual species have nervose, cymostrophoid or ptychoglyptoid prosopon. Weak concentric or oblique rugae may be combined with any of the common patterns of prosopon. The pseudodeltidium is large, rarely small; the chilidium is small. The cardinal process lobes are slender to stout cylinders which bear a posteriorly directed petaloid or cupped myophore. A meso-cardinal ridge is rarely present. The socket buttresses are recurved toward the interarea on the lateral-posterior side of the socket. Both the socket buttress and the lateral socket buttress are generally corrugated. The posterior platform is small but highly elevated. The medial ridge of the posterior platform generally is bifurcate. A breviseptum may arise in the split end of the medial ridge. True but reduced dorsal ridges transect the adductor muscle field of some species. Thick adventitious or intervascular ridges may occur in the region anterior and anterior-lateral to the adductor muscle scars. Those species with prominent adventitious ridges commonly have breviseptum-like ridges or narrow grooves in the positions of the true anterior dorsal septa and posterior dorsal septa. Some species lack all traces of dorsal septa or adventitious septa. The teeth are stout and semidenticulate on the dorsal surface. A transverse muscle bounding ridge may occur along the anterior margin of the adductor muscle field of the dorsal valve. The dental lamellae commonly recede. The muscle bounding ridges of the ventral valve almost encircle the anterior ends of the small diductor muscle scars. The adductor muscle scars of the ventral valve generally are not enclosed toward the anterior by the muscle bounding ridges. There may be a small spondylium triplex and hemisyrinx in the apex of the delthyrial cavity. The pedicle foramen is sealed but commonly apparent because of differential erosion. The internal surfaces of the valves may be smooth or may bear papillae or endospines. The marginal diaphragm commonly is well developed in the ventral valve.

Age.- Ordovician (middle Champlainian, Porterfield) into Upper Silurian.

Generic content.- *Strophomena* Rafinesque, in deBlainville, 1825; *Tetraphalerella* Wang, 1949; *Longvillia* Bancroft, 1933; *Gunnarella* Spjeldnaes, 1957; *Pentlandia* Bancroft, in Lamont, 1949; *Trigrammaria* Wilson, 1945; *Microtrypa* Wilson, 1945; *Luhaia* Rōōmusoks, 1956.

Remarks.- The nomenclatural validity of *Strophomena* is not established. The type species of *Strophomena* is *S. rugosa* Rafinesque, in deBlainville, 1825. Illustrations of *S. rugosa* are unrecognizable; the type specimens apparently are lost. A strict interpretation of the International Code of Zoological Nomenclature would require that *Strophomena* be declared unrecognizable and invalid. Hall and Clarke (1892) and Nickles (1903) have reviewed the status of *Strophomena* and the history of the name. Nickles suggests that *Leptaena planumbona* Hall, 1847 [=*S. planumbona* (Hall)] is probably not conspecific with *S. rugosa* Rafinesque as Hall and Clarke (1892) claim it to be. Nickles concludes, in substance, that this is not significant inasmuch as authors, "King, Davidson, Hall and Clarke, Winchell and Schuchert", have understood the type of *Strophomena* to be *S. planumbona* (Hall). Authors subsequent to Nickles, *e.g.* Cooper and Williams, also have based *Strophomena* upon *S. planumbona* (Hall). The status of *Strophomena* has not been ruled upon by the International Commission on Zoological Nomenclature. The type should be fixed as *Strophomena planumbona* (Hall) by appeal to the commission so that no uncertainty continues.

Unfortunately, the *Treatise* compounds the *Strophomena*-problem. The internal surface of a dorsal valve shown in Fig. 246, 3c (p. H385) which is identified as

S. planumbona (Hall) is actually *S. vetusta* (James).

True dorsal ridges do occur in the Strophomeninae. These are not the thick, adventitious ridges which may be so apparent on the internal surface of the dorsal valve. The true dorsal ridges are slender ridges or faint grooves located between the adventitious ridges. Both the adventitious ridges and the true dorsal ridges may arise in the adductor muscle field. Generally only the medial dorsal ridge, *i.e.* breviseptum, and the anterior lateral dorsal ridges are present. The true dorsal septa are most apparent on slightly eroded or naturally etched calcite specimens because the inner initial tissue which forms the true dorsal ridges is slightly darker in color than the secondary tissue which forms the adventitious ridges.

The nomenclatural validity of *Longvillia* Bancroft and *Pentlandia* Bancroft has been questioned. The obscure publications in which these genera are described, by the fact of their obscurity, have attracted the attention of brachiopod specialists. Consequently, these names must be judged to be acceptably published. *Longvillia* Bancroft is not a synonym of *Strophomena*, as shown in the *Treatise*, if the type species of *Strophomena* is *S. planumbona* (Hall). *Longvillia grandis* (Sowerby), type species, has a flattened resupinate profile, delicate teeth, a weakly developed muscle bounding ridge and no dorsal septa.

The differentiation of Microtrypa from Strophomena is uncertain. The type specimens of M. altilis Wilson, type species, are too poorly preserved to permit an adequate diagnosis of this genus.

OTHER GENERA

The genera of the following list have been at one time assigned to the Strophomenacea. The reason for rejection of each name is indicated.

Bekkerella Reed, 1936. - Inadequately known and probably a stropheodontacean.

Brynella Bancroft, 1933. - nomen nudum

Christiania Hall and Clarke, 1892. - Placed in a new superfamily, the Christianiacea.

Coolinia Bancroft, in Lamont, 1949. - Probably an orthotetacean.

Drummuckina Bancroft, in Lamont, 1949. - Probably a stropheodontacean.

Goniotrema Ulrich and Cooper, 1936. - A plectambonitacean.

Lamanskya Moberg and Segerberg, 1906. - Unrecognizable.

Leptaenella Sarycheva and Sokolskaya, 1952. - A synonym of Leptagonia McCoy, 1844; a homonym of Leptaenella Frederiks, 1917.

Leptaenulopsis Haupt, 1878. - A synonym of Leptaena.

Oepikinella Wilson, 1945. - Probably a synonym of Strophomena.

Playfairia Reed, 1917. - An unrecognizable subgenus of Rafinesquina.

Pseudoleptaena Miloradovich, 1947. - A synonym of Leptagonia.

Saughina Bancroft, in Lamont, 1949. - Probably an orthotetacean.

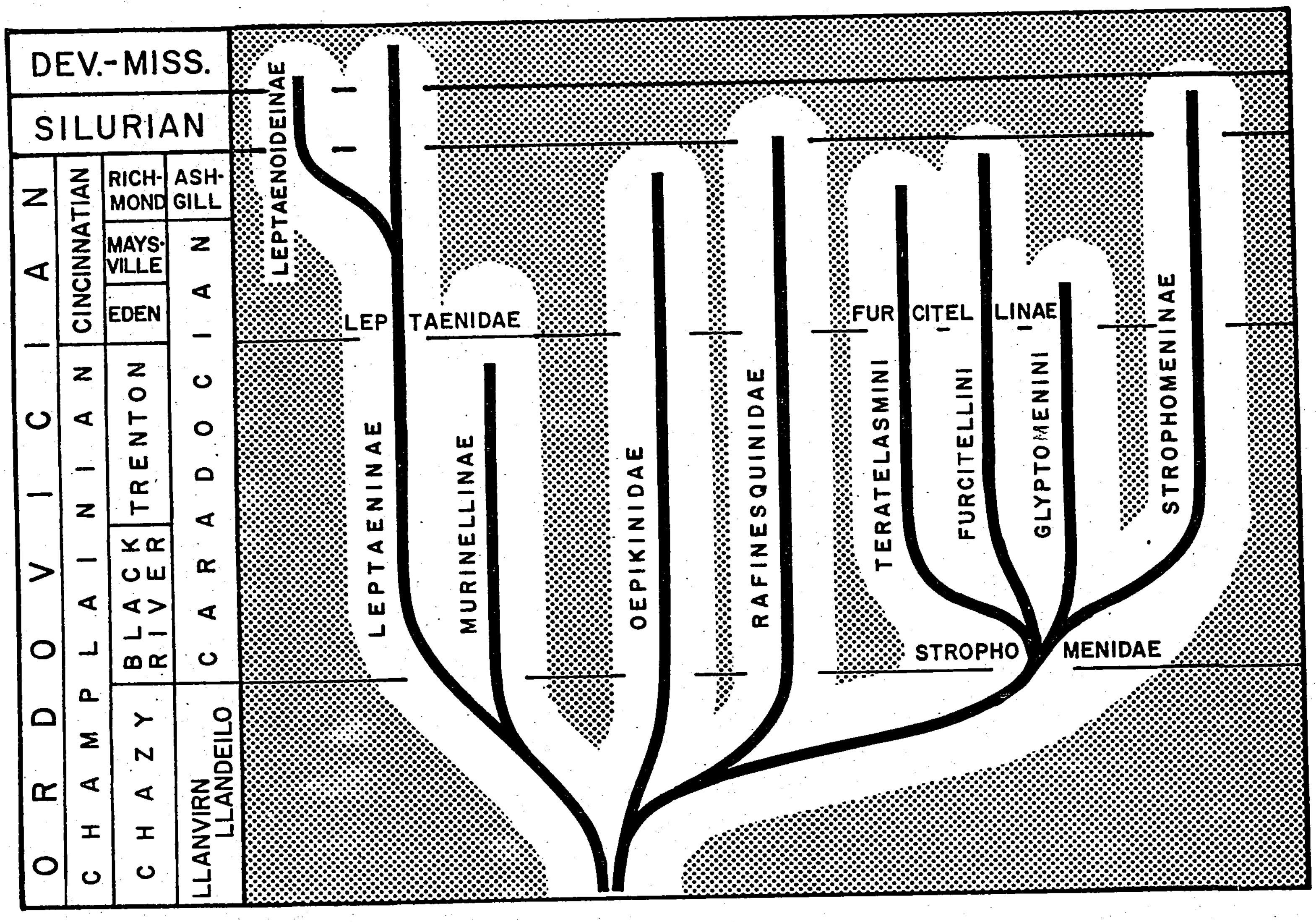
PHYLOGENY

A phylogeny of the Strophomenacea of the Ordovician may be postulated from the morphological characteristics of the groups which have been described in the last section. The postulated phylogeny is shown in Text-Figure 7.

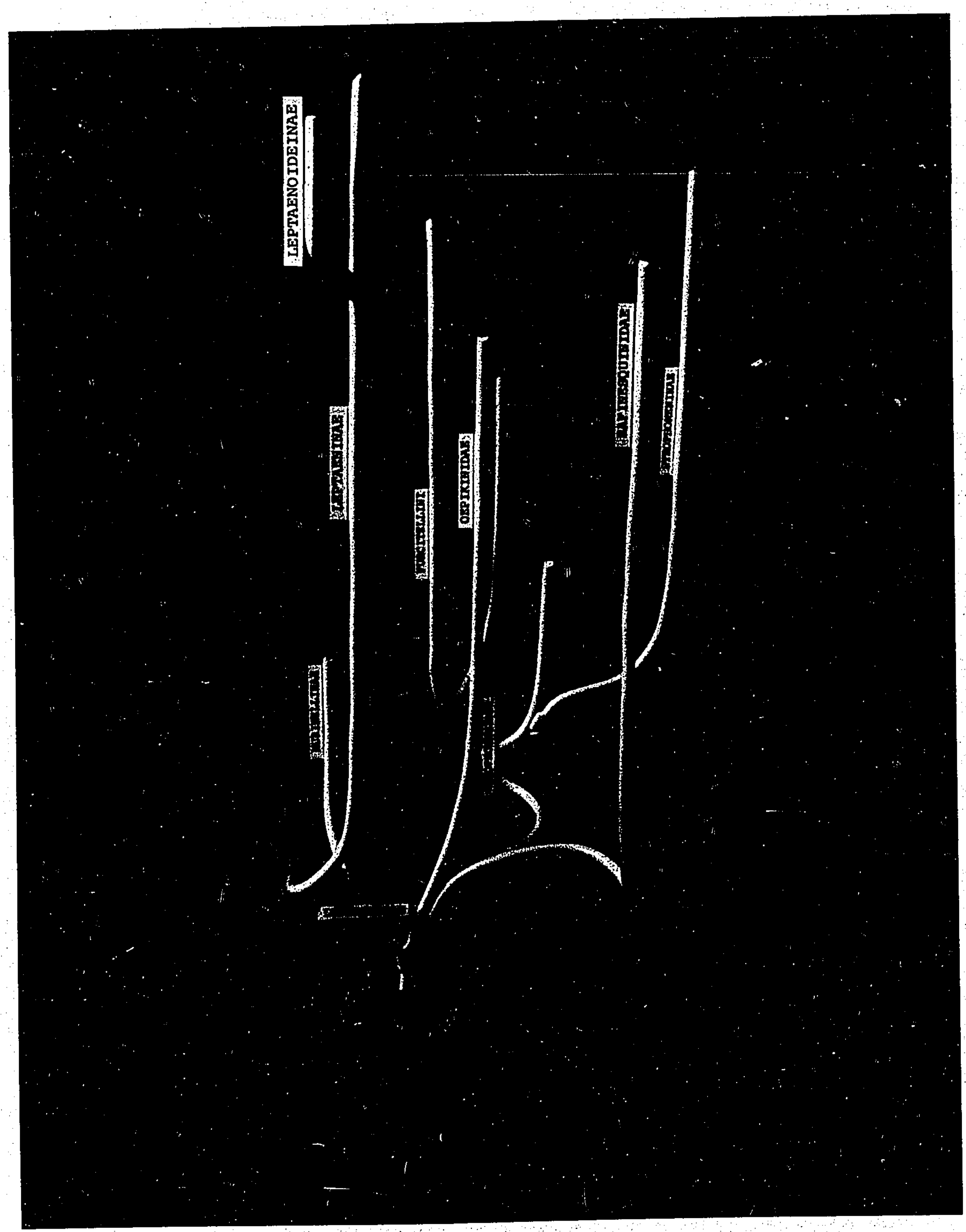
Text-Figure 7.- The postulated phylogeny of the families of the Strophomenacea.

Many dendrograms of the Strophomenacea have been constructed in the course of this study. None are entirely satisfactory. Two-dimensional dendrograms can show only the divergence of the various groups. The two-dimensional dendrograms cannot show the relative degree of divergence of the groups involved nor can they show convergence. Every possible juxtaposition of families and subfamilies, within the limits of their relationships, has been drawn. There is separation of closely related or convergent families in every possible combination. The phylogeny of the Strophomenacea properly should be viewed in three dimensions, as shown in Text-Figure 8.

Text-Figure 8.- Phylogeny of the families of the Strophomenacea shown in three dimensions.



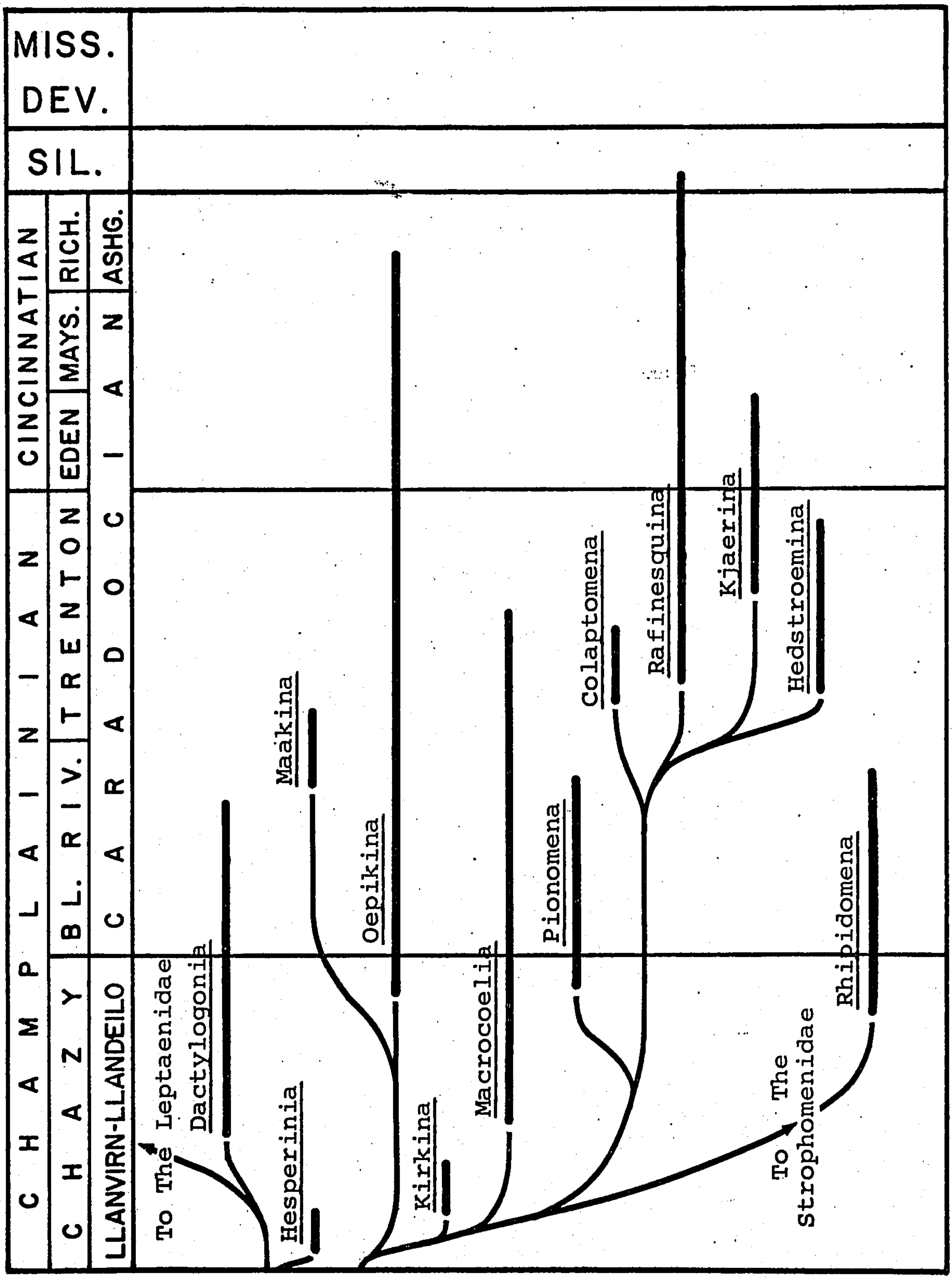
Text-Figure 7.- The postulated phylogeny of the families of the Strophomenacea.



Text-Figure 8.- Phylogeny of the families of the Strophomenacea shown in three dimensions.

The Oepikinidae contains the fundamental characteristics of the Strophomenacea. These basic strophomenacean traits include fine pseudopuncta, the bifid cardinal process with shaft-like lobes bearing myophores on the posterior face, concavo-convex profile, prolate to subrectangular shape, a large pseudodeltidium with an open, supra-apical pedicle foramen, distinct dental lamellae, unrestricted diductor muscle scars, straight socket buttresses and true dorsal septa. The diagnostic characteristics of the other families occur by modification or loss of one or more of these fundamental characters. In a three-dimensional view of strophomenacean phylogeny, the Oepikinidae has an axial or central position. The most primitive oepikinids, Hesperinia and Dactylogonia, most closely resemble the leptaenids, whereas the advanced oepikinids, Kirkina, Macrocoelia and Oepikina, closely resemble the rafinesquinids and the earliest strophomenids. Consequently, graphic illustration of the Oepikinidae must show the family situated between the Leptaenidae and the Rafinesquinidae. The basal portion of the oepikinid lineage must be near the Leptaenidae and the upper portion of the oepikinid lineage must be bent toward the Rafinesquinidae. Text-Figure 9 shows the relationship of genera of the Oepikinidae and Rafinesquinidae.

The Leptaenidae diverges from the Oepikinidae in early Chazyan time by the acquisition of coarse pseudo-



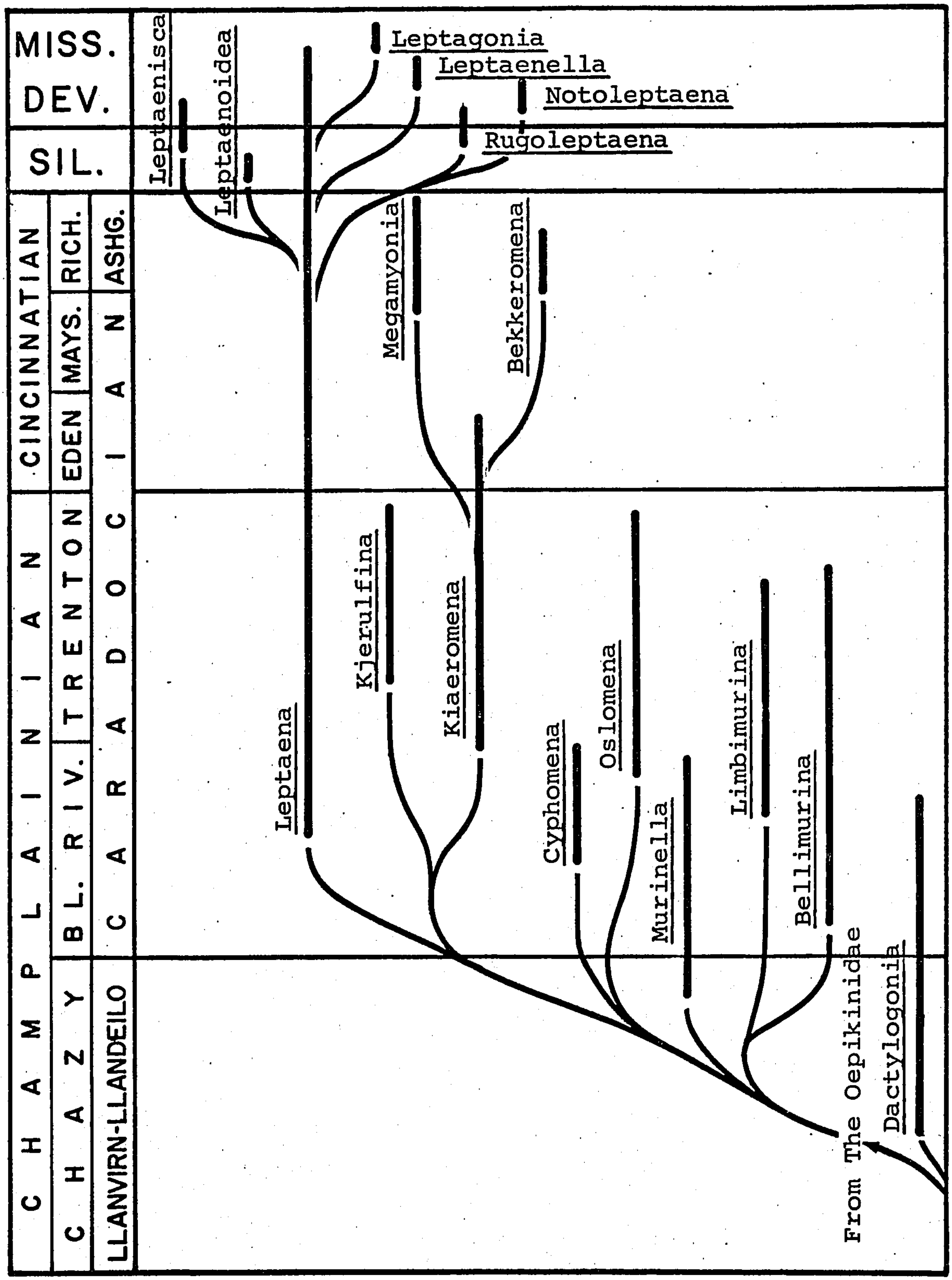
Text-Figure 9.- The relationship and stratigraphic distribution of genera of the Oepikinidae and Rafinesquinidae.

Text-Figure 9.- The relationship and stratigraphic distribution of genera of the Oepikinidae and Rafinesquinidae.

puncta and modification of the dorsal septa. Later in the history of the leptaenid lineage, the divergence is reinforced by the development of strong geniculation, rugae and incomplete muscle bounding ridges, the reduction of dental lamellae and the pseudodeltidium, and further modification or loss of the dorsal septa. The relationship and stratigraphic distribution of genera in the Leptaenidae is shown in Text-Figure 10.

Text-Figure 10.- The relationship and stratigraphic distribution of genera of the Leptaenidae.

The Leptaenidae divides into two subfamilies in Chazyan time. The Murinellinae is distinguished by elaborate geniculation and prosopon and by retention of a foramen, large pseudodeltidium and modified dorsal septa through much of its history. The Murinellinae is a more primitive lineage than the Leptaeninae by reason of these characters and consequently occupies a position between the Oepikinidae and the Leptaeninae. Moreover, the prosopon, posterior platform, socket buttresses and dorsal septa of the Murinellinae resemble those features in the



Text-Figure 10.- The relationship and stratigraphic distribution of genera of the Leptaenidae.

Furcitellinae. A three-dimensional model shows the Murinellinae closer to the Oepikinidae than the Leptaeninae and bent into convergence with the Furcitellinae.

The Leptaeninae diverges further from the Oepikinidae than does the Murinellinae by complete loss of the dorsal septa and reduction of the pseudodeltidium. The Leptaeninae shows some convergence toward the Rafinesquinidae by development of bladed cardinal process lobes which become petaloid, loss of the dorsal septa, reduction of the pseudodeltidium, and in some genera, the shape of the posterior platform, the loss of rugae, geniculation, subrectangular shape and muscle bounding ridges.

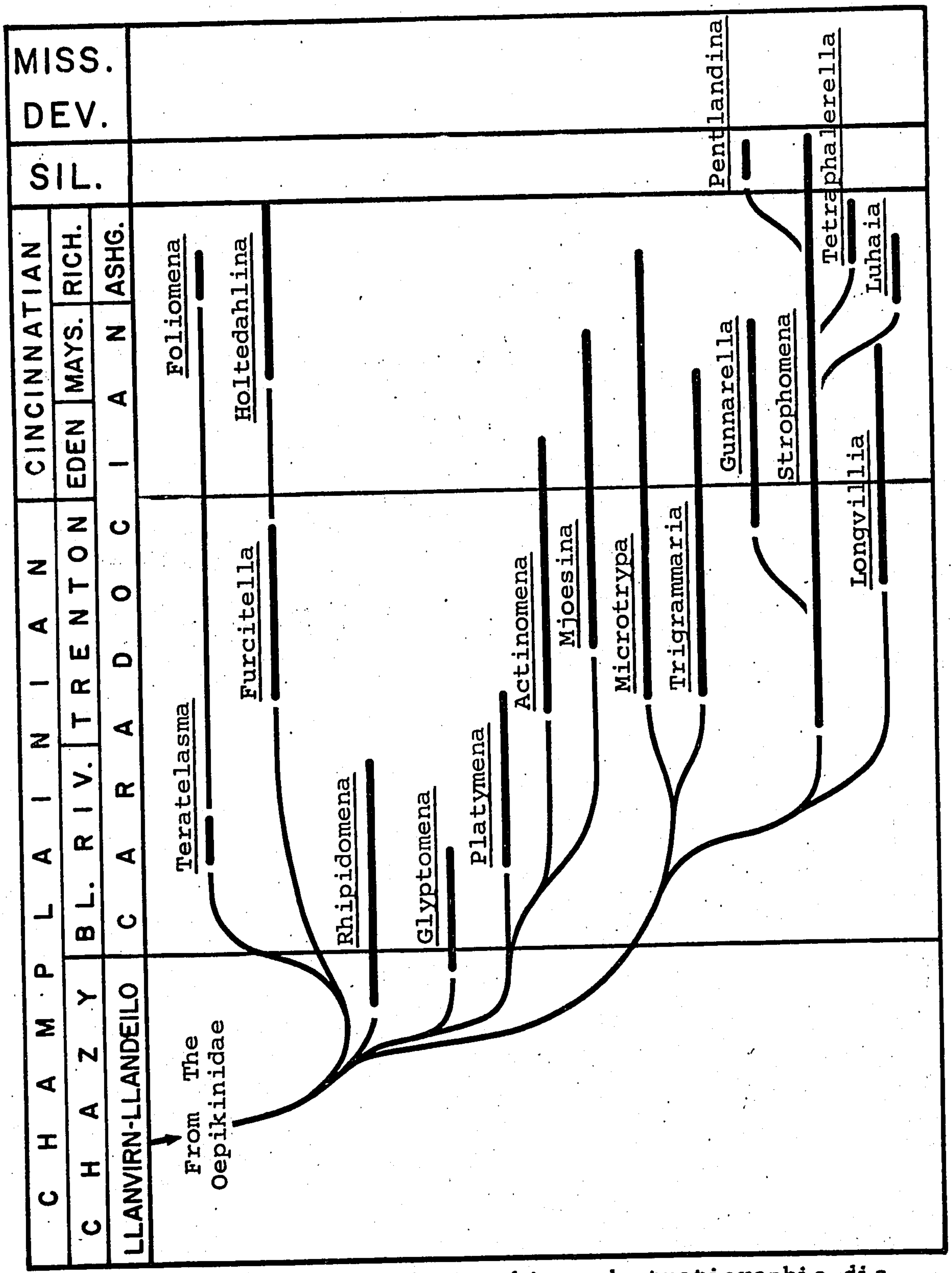
The Leptaenoideinae diverges from the Leptaeninae in late Ordovician or early Silurian time. The cemented habit of these minute leptaenids does not occur elsewhere in the Strophomenacea. The Leptaenoideinae, thus, must be imagined to diverge centripetally from the strophomenacean complex.

The Rafinesquinidae diverges from an advanced oepikinid by development of coarse pseudopuncta, loss of the dorsal septa and increase in the size of the diductor muscle field. Also, the petaloid myophores of the most advanced rafinesquinids face in the posterior-dorsal direction unlike the myophores of all oepikinids. In all other characters, the Rafinesquinidae resembles advanced genera of the Oepikinidae which have prolate shape, a sealed pedicle foramen and a reduced pseudodeltidium. As noted, the Rafinesquinidae and the Leptaenidae show some convergent characteristics. A three-dimensional illustration of the Strophomenacea would show these families bent toward each other.

The Strophomenidae arises from the same advanced oepikinid stock as do the Rafinesquinidae. The stratigraphic distribution and relationship of genera of the Strophomenidae is shown in Text-Figure 11. The earliest strophomenid, Rhipidomena, is so nearly intermediate that only the gentle resupination and obsolete dental lamellae require that the genus be rejected from the Oepikinidae. Moreover, the morphology of Rhipidomena places this genus at the bifurcation of the Furcitellinae and the Strophomeninae. Rhipidomena is assigned to the Furcitellinae, Tribe Glyptomenini, only because the Furcitellinae collectively displays more primitive features than does the Strophomeninae.

Text-Figure 11.- The relationship and stratigraphic distribution of genera of the Strophomenidae.

The Furcitellinae encompasses the primitive but experimental strophomenids. The primitive attributes of



Text-Figure 11.- The relationship and stratigraphic distribution of genera of the Strophomenidae.

the group are internal and include features as the prominent dorsal septa, the node or shaft-like cardinal process lobes and the incomplete muscle bounding ridges. The shape, profile and prosopon of the Furcitellinae are experimental features. They include the flattened profile of the Glyptomenini, the oblate shape of the Furcitellini and Teratelasmini, the biconvex profile of the Furcitellini and Teratelasma and the concavo-convex profile of Foliomena.

In a phylogenetic reconstruction, the Furcitellinae must be shown closer to the Oepikinidae than the Strophomeninae. In addition, the Glyptomenini and Furcitellini are convergent with the Murinellinae. A three-dimensional view of the strophomenacea shows the Glyptomenini and Furcitellini near the origin of the Strophomenidae and bent in the direction of the Murinellinae. The Teratelasmini do not resemble any other strophomenaceans. This tribe must be imagined to diverge from the Furcitellini in a direction away from the oepikinids.

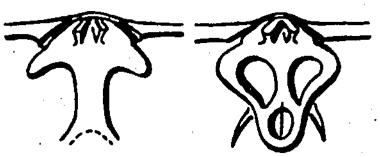
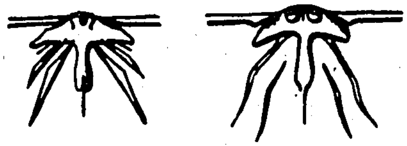
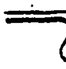
The Strophomeninae is the progressive subfamily of the Strophomenidae. The fundamental structures retained by this subfamily from the oepikinid origin are fine pseudopuncta, prolate shape and, in less advanced species, the dorsal septa, the cylindrical cardinal process lobes with the myophore on the posterior face and a large pseudodeltidium. The progressive features of the subfamily include the extreme resupination, strong muscle bounding ridges and adventitious septa of many species. The Strophomeninae is divergent from the base of the Glyptomenini in a direction away from the Oepikinidae.

COMPARATIVE MORPHOLOGY

Many of the morphological and microstructural characteristics of the Strophomenacea change throughout the history of the superfamily. Morphological variation in the Strophomenacea is summarized in Table 1. Some of the changes seem to be related to changes in the profile of the valves; other changes seem to be independent of the profile. The features which seemingly undergo change without relationship to profile include the size and shape of the valves, pseudopunctae, teeth, diductor muscle scars, prosopon, the cardinal process lobes, the pseudodeltidium, the chilidium, the pedicle foramen, the dorsal septa and the meso-cardinal ridge. Characters which may change collateral to changes of profile include the dental lamellae, the muscle bounding ridges and the socket buttresses. It is convenient to discuss the modifications of these characters in respect to variations of the profile of the valves. The selection of profile as the standard of reference is arbitrary. The characters, including profile, change collaterally. No character has precedence over another; changes of profile are not necessarily a cause which produce an effect in the other characters.

The structures which change without relationship to profile of the valves may be divided into three catego-

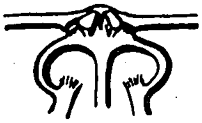
TABLE 1.- SUMMARY OF MORPHOLOGICA

TAXONOMIC DIFFERENTIA	LEPTAENIDAE LEPTAENINAE	MURINELLINAE	OEPIKINIDAE	RA
PSEUDOPUNCTAE	COARSE		FINE	
SHAPE	SUBRECTANGULAR OR SUBTRIANGULAR RARELY OBLATE OR PROLATE		PROLA ARCHAIC SUBRECTANGULAR	
PROFILE	PLANO-CONVEX, CONCAVO-CONVEX, BICONVEX DORSAL, RARELY VENTRAL OR MULTIPLE GENICULATION		CONCAVO-CON ARCHAIC GENICULATION	WEAK
DENTAL LAM.	RECEDING TO ABSENT	COMPLETE		
TEETH	DELICATE, POINTED COMMONLY CURVED	LARGE, BLUNT, STRAIGHT ROUNDED ANTERIOR PROJECTION COMMON		DEL
CARDINAL PROCESS	DISJUNCT BLADES TO CONJUNCT PETALOID BLADES	DISJUNCT BLADES, SHAFTS OR NODES	HEMICYLINDERS	CON
MUSCLE BOUND. RIDGES	LATERAL TO COMPLETE COMMONLY LANCEOLATE			NO
DIDUCTOR MUSCLE SCARS	SMALL, RARELY LARGE FLABELLATE	POSTERIOR	LARGE F	
SOCKET BUTTRESSES	STRAIGHT, SHORT, LOW SMALL ANGLE	STRAIGHT TO CURVED, SHORT TO LONG, LOW TO HIGH, LOW TO MEDIUM ANGLE	STRAIGHT, MEDIUM A SHORT, HIGH	LONG
POSTERIOR PLATFORM				
HABIT	LEPTAENOIDEINAE (FAMILY LEPTAENIDAE) CEMENTED BY VENTRAL VALVE TO SUBSTRATE.			

STRUCTURES WHICH UNDERGO PARALLEL EVOLUTION		DORSAL RIDGES OR SEPTA	CARDINAL PROCESS	
	ADVANCED	TRUE DORSAL RIDGES OR SEPTA ABSENT	LOBES FUSED	LARGE, PETA MYOPHORE
	↑	STRONGLY REDUCED OR MODIFIED RIDGES	LOBES CONJUNCT	↑
		SLIGHTLY REDUCED OR MODIFIED RIDGES	↑	
		FIVE PROMINENT SEPTA OR RIDGES		
	PRIMITIVE	FIVE PROMINENT STANDING PLATES	LOBES DISJUNCT	SMALL MYOPH

FEATURES OF LITTLE SIGNIFICANCE	SIZE.- NOT TAXONOMICALLY DISTINCTIVE. GENERAL INCREASE FROM OLDER TO YOUNGER GENERA WITH MANY EXCEPTIONS.	PROSOPON.- NOT DISTINCTIVE FOR FAMILY RANK TAXA. MUCH HOMEOMORPHY. NO EVOLUTIONARY TRENDS.	ADDU SI NO

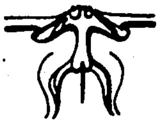
OF MORPHOLOGICAL VARIATION IN THE STROPHOMENACEA

DAE	RAFINESQUINIDAE	STROPHOMENID			
		FURCITELLINAE			S
		TERATELASMINI	FURCITELLINI	GLYPTOMENINI	
E	COARSE	FINE			
PROLATE TANGULAR		OBLATE SULCATE	UNIPLICATE	PR	
CAVO-CONVEX CULATION	WEAK DORSAL GENICULATION	BICONVEX CONCAVO-CONVEX		FLATTENED	
LETE		NONE	COMPLETE TO RECEDING	NONE	RE
	DELICATE, POINTED, STRAIGHT	POINTED CURVED	LARGE, POINTED, STRAIGHT		
YLINDERS	DISJUNCT BLADES TO CONJUNCT PETALOID BLADES	POORLY KNOWN	SHAFTS	MINUTE NODES	
NONE	RARELY LATERAL RIDGES	SHORT LATERAL RIDGES	RARELY LONG		
LARGE FLABELLATE	RARELY SMALL	SMALL, POST		RARELY LARGE	
TRAIGHT, MEDIUM ANGLE T, HIGH	LONG, MEDIUM HIGH	STRAIGHT, HIGH LONG, LARGE ANG.	CURVED, GENERA MEDIUM TO L		
	 				
UBSTRATE.	ALL OTHERS LIVED FREE UPON SEA FLOOR OR TETHERED BY PEDICLE.				

INAL PROCESS	PSEUDODELTIDIUM	CHILIDIUM	VENTRAL INTERAREA	
CT LARGE, PETALOID MYOPHORES ↑ CT SMALL MYOPHORES	ABSENT ↑ MINUTE QUOIN | SMALL, CONVEX → PEDICLE CALLIST | LARGE, CONVEX	LARGE ↑ SMALL	NARROW ↑ WIDE	SEALED ↑ SMALL | LARGE

E FOR HOMEO- Y TRENDS.	ADDUCTOR MUSCLE SCARS.- POSITION AND SIZE NOT TAXONOMICALLY DISTINCTIVE. NO EVOLUTIONARY TREND OBSERVED.	MESO-CARDINAL RIDGE.- A GERONTIC STRUCTURE. NO EVOLUTIONARY OR TAXONOMIC SIGNIFICANCE.	VASC TO

ACEA

STROPHOMENIDAE					
FURCITELLINAE					STROPHOMENINAE
TERATELASMINI		FURCITELLINI	GLYPTOMENINI		
FINE					
OBLATE			PROLATE		
SULCATE		UNIPLICATE			
BICONVEX			FLATTENED		RESUPINATE
CONCAVO-CONVEX					
NONE	COMPLETE TO RECEDING		NONE	RECEDING, RARELY COMPLETE	
POINTED CURVED		LARGE, POINTED, STRAIGHT			LARGE, POINTED TO BLUNT STRAIGHT TO SLI. CURVED
POORLY KNOWN		SHAFTS	MINUTE NODES		CONJUNCT SHAFTS TO HEMICYLINDERS
SHORT LATERAL RIDGES					GENERALLY COMPLETE RIDGES CIRCULAR
		RARELY LONG			
SMALL, POSTERIOR					
			RARELY LARGE		
STRAIGHT, HIGH LONG, LARGE ANG.		CURVED, GENERALLY LONG, HIGH MEDIUM TO LARGE ANGLE			
					
EA FLOOR OR TETHERED BY PEDICLE.					

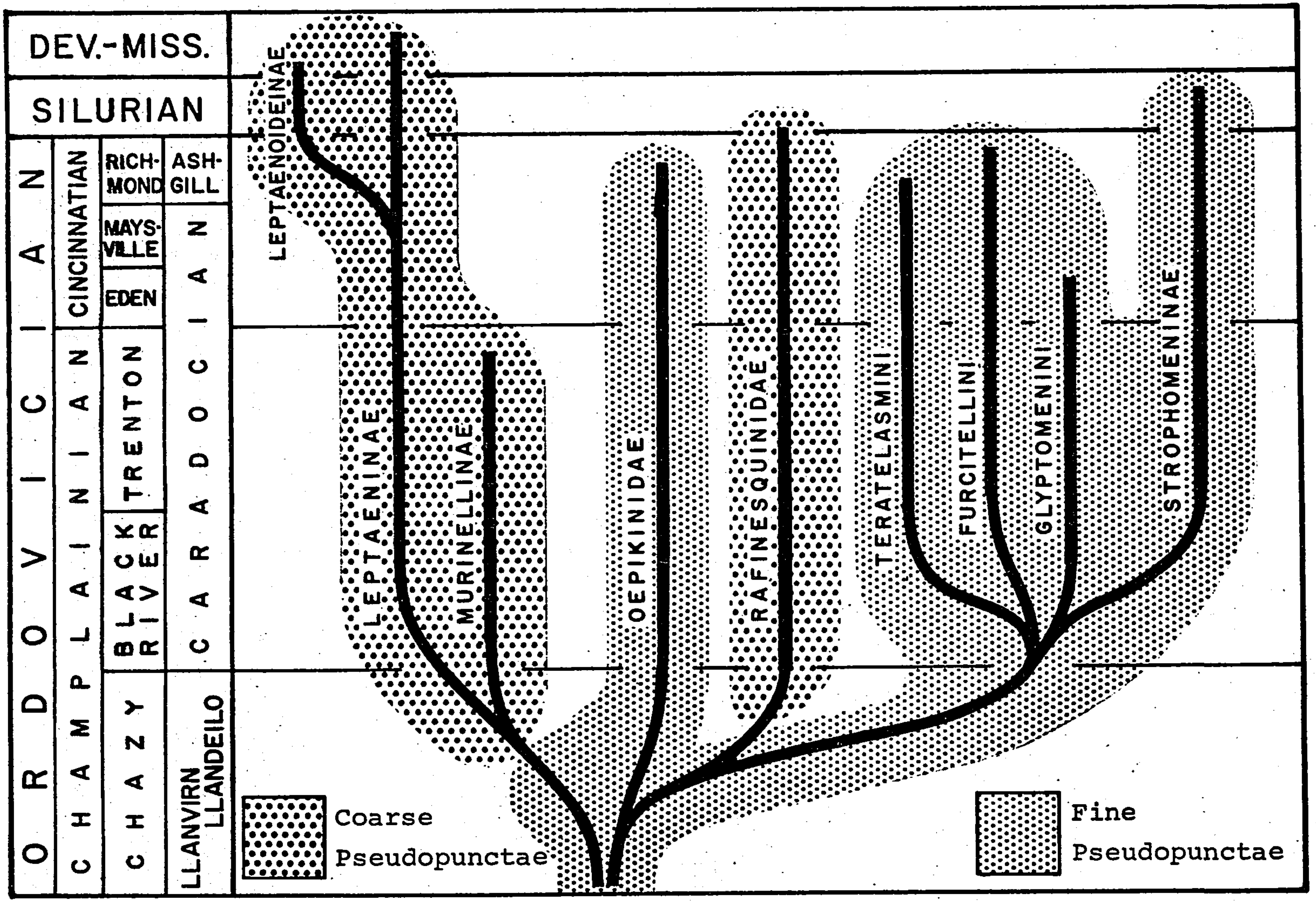
ICLE LIST	**CHILIDIUM** LARGE ↑ SMALL	**VENTRAL INTERAREA** NARROW ↑ WIDE	**PEDICLE FORAMEN** SEALED ↑ SMALL LARGE DELTHYRIAL APERTURE WITH PEDICLE CALLIST

AND TIVE. .	MESO-CARDINAL RIDGE.- A GERONTIC STRUCTURE. NO EVOLUTIONARY OR TAXONOMIC SIGNIFICANCE.	VASCULAR MARKINGS.- TOO OBSCURE TO BE EVALUATED.

ries. The shape and profile of the valves, nature of the pseudopuncta, teeth, and diductor muscle scars, in general, are taxonomic differentiae at the familial level. These features do not change through a sequence of evolutionary stages within the superfamily, nor do the variations of these features, in general, occur at random within the superfamily. Changes which occur in the pseudodeltidium, interarea of the ventral valve, chilidium, foramen and dorsal septa are the result of evolutionary parallelism in the various lineages. The cardinal process shows poorly defined taxonomic differentiation and evolutionary progression. Size, nature of the prosopon, adductor muscle scars, and occurrence of a meso-cardinal ridge do not seem to have much taxonomic or evolutionary significance above the generic level. Vascular markings are too obscure to be evaluated.

Pseudopunctae.- The size and density of distribution of the pseudopunctae sharply divide the Strophomenacea into two groups as shown on Text-Figure 12. All members of the Oepikinidae and the Strophomenidae bear fine pseudopunctae which are densely packed together without geometric ar-

Text-Figure 12.- The distribution of coarse and fine pseudopunctae within the Strophomenacea.



Text-Figure 12.- The distribution of coarse and fine pseudopunctae within the Strophomenacea.

rangement. The Rafinesquinidae and Leptaenidae, in contrast, bear coarse pseudopunctae which are widely and geometrically spaced in the shell. These pseudopunctae occur along the intercostal grooves in the leptaenids and at the intersection of the intercostal grooves and the fila in the rafinesquinids. The pseudopunctae of the rafinesquinids are bimodal in size. Smaller, but still coarse, pseudopunctae are scattered at random among the geometrically placed larger pseudopunctae. The rafinesquinids and leptaenids bear taleolae along the axes of the pseudopunctae. Most of the oepikinids and strophomenids seem to be taleolate as well but the extremely small size of the pseudopunctae of some species makes detection of taleolae very difficult.

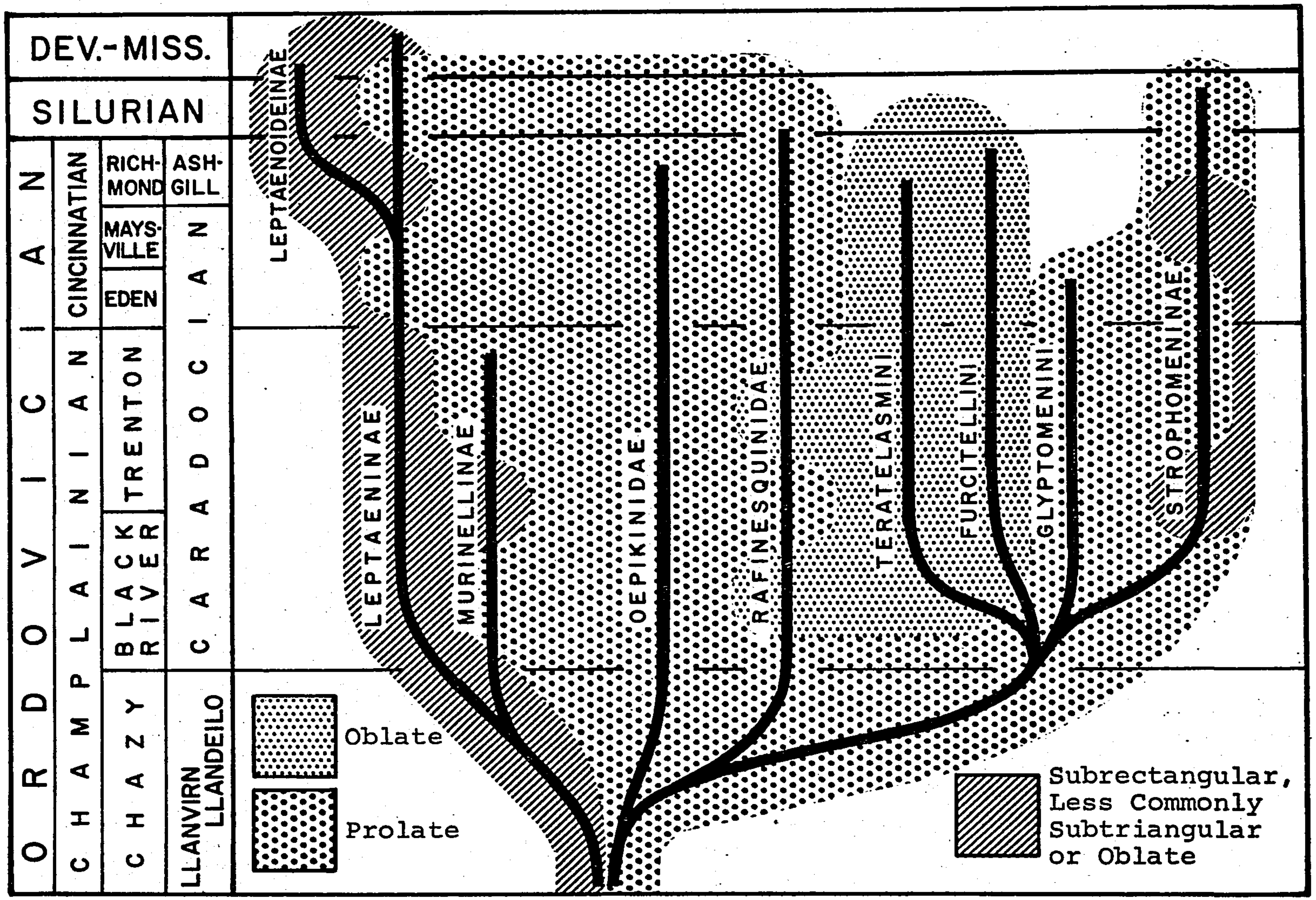
"Fine" and "dense" are relative terms. Some measurements of the size of pseudopunctae and the density of packing are presented in the section on histology of the shell. In general, the size of the pseudopunctae is inversely related to the number of pseudopunctae per unit area of shell.

The character of the pseudopunctae of _Maakina_, _Luhaia_ and _Foliomena_ is not known. Contrary to the descriptions of the _Treatise_ the pseudopunctae of _Tetraphalerella_, _Kirkina_ and _Macrocoelia_ are fine and the pseudopunctae of _Pionomena_ are coarse. The size of the pseudopunctae of _Hesperinia_ cannot be determined from direct examination and the specimens of this genus are too rare to etch or section. The coarse endospines of the internal surfaces of the valves cause the specimens to appear coarsely pseudopunctate. The closely related *Dactylogonia* bears large endospines but sections reveal fine pseudopunctae.

Shape of the valves.- The Strophomenacea are fundamentally subrectangular or prolate, slightly alate brachiopods. The earliest genera exhibit pronounced differentiation of shape in the strongly subrectangular form of *Hesperinia* and *Dactylogonia* and the prolate form of *Kirkina*. Inasmuch as most of the genera of the Plectambonitacea are oblate to subrectangular, the prolate form of *Kirkina* probably represents a divergence of shape within the Strophomenacea prior to the known fossil record. The distribution of variations of the shape of the valves within the Strophomenacea is plotted in Text-Figure 13.

Text-Figure 13.- The distribution of the various shapes of the valves within the Strophomenacea.

Shape is not an absolutely consistent feature within each lineage of the Strophomenacea. The Oepikinidae, Rafinesquinidae, Glyptomenini and Strophomeninae generally are prolate. There are unusual species within each of these lineages which are subrectangular, subtriangular or

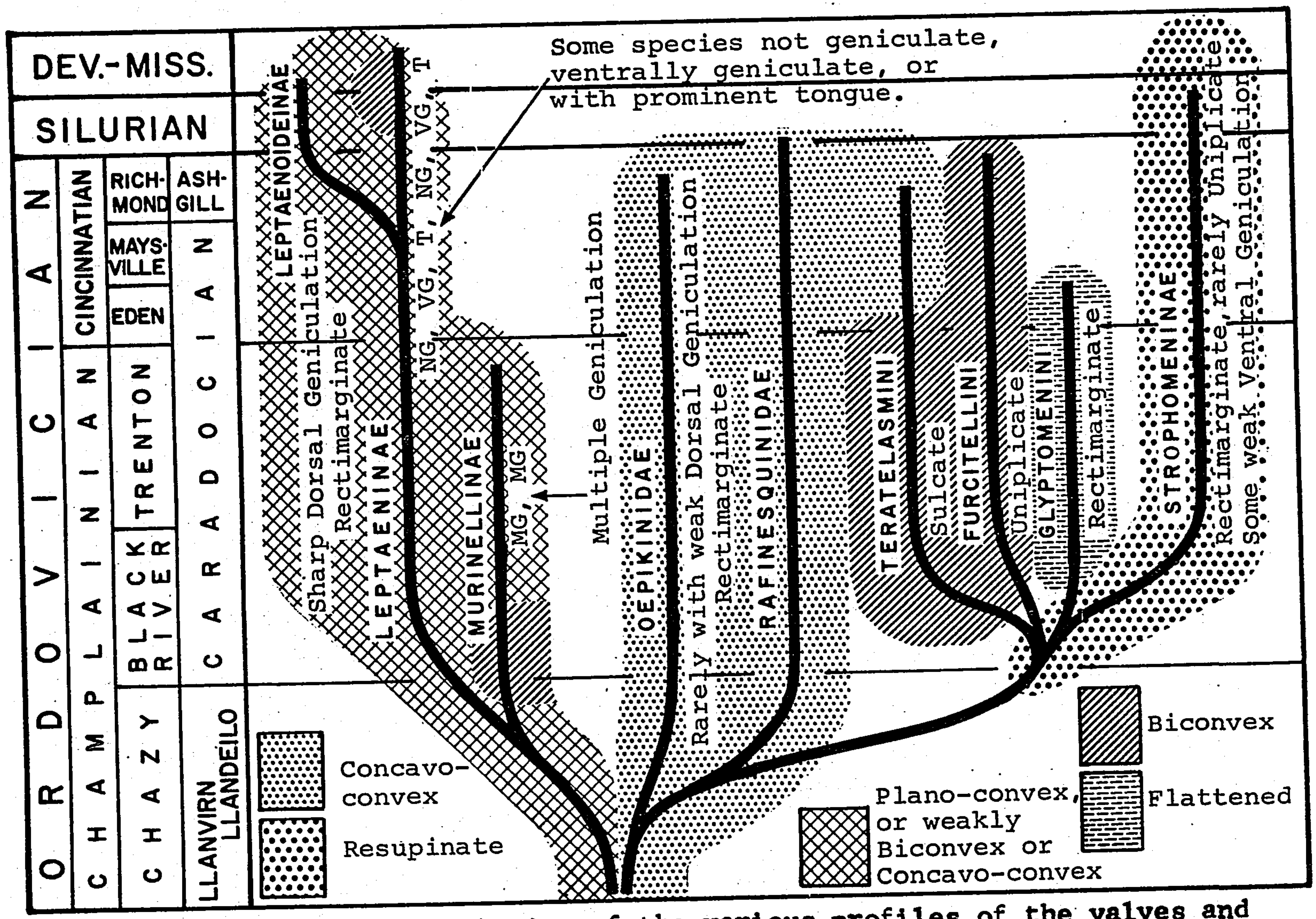


Text-Figure 13.- The distribution of the various shapes of the valves within the Strophomenacea.

oblate. These unusual shapes are regarded as independent divergences from prolate ancestors. Other characteristics indicate that the species with unusual shapes are not anachronistic. The Murinellinae incorporates species without stabilized shape. _Murinella_ is oblate to prolate; _Cyphomena_ is oblate to subrectangular; _Bellimurina_ and _Limbimurina_ are prolate. The Leptaenidae in general are strongly subrectangular and alate. Exceptional species of _Leptaena_ may be subtriangular or oblate and unusual genera may be prolate, _e.g._ _Kjerulfina_, _Bekkeromena_ and _Leptagonia_. The Furcitellini and the Teratelasmini are oblate in form.

There seems to be an association of the subrectangular and oblate shapes with geniculation. Commonly these characters are accompanied by concentric rugation of the valves. If there is an interrelationship of these characters, the independent character cannot be distinguished from the dependent characters. Neither subrectangular shape, geniculation or rugae occur always in association with either of the other two characters.

Profile of the valves.- The Strophomenacea are fundamentally plano-convex or slightly concavo-convex brachiopods. Text-Figure 14 illustrates the distribution of the various profiles of the valves and shapes of the anterior commissure within the Strophomenacea. The earliest oepikinids,



Text-Figure 14.- The distribution of the various profiles of the valves and shapes of the anterior commissure in the Strophomenacea.

Text-Figure 14.- The distribution of the various profiles of the valves and shapes of the anterior commissure in the Strophomenacea.

Hesperinia and Dactylogonia, have basically plano-convex or faintly concavo-convex profiles with a dorsally geniculated short trail. Kirkina has a weakly concavo-convex, smoothly curved profile. The basic profile of Hesperinia and Dactylogonia persists throughout the history of the Leptaeninae. The only general modification which occurs in this subfamily involves lengthening of the trail. Exceptions to the general profile of the Leptaeninae are found in Kiaeromena and Bekkeromena which are not sharply geniculate, Kjerulfina which is ventrally geniculate and Leptagonia which is biconvex.

There is no consistent profile in the Murinellinae. Murinella is biconvex or plano-convex. Cyphomena and Bellimurina are plano-convex or concavo-convex with short, dorsally geniculated trails. The multiple geniculation of Limbimurina is unique.

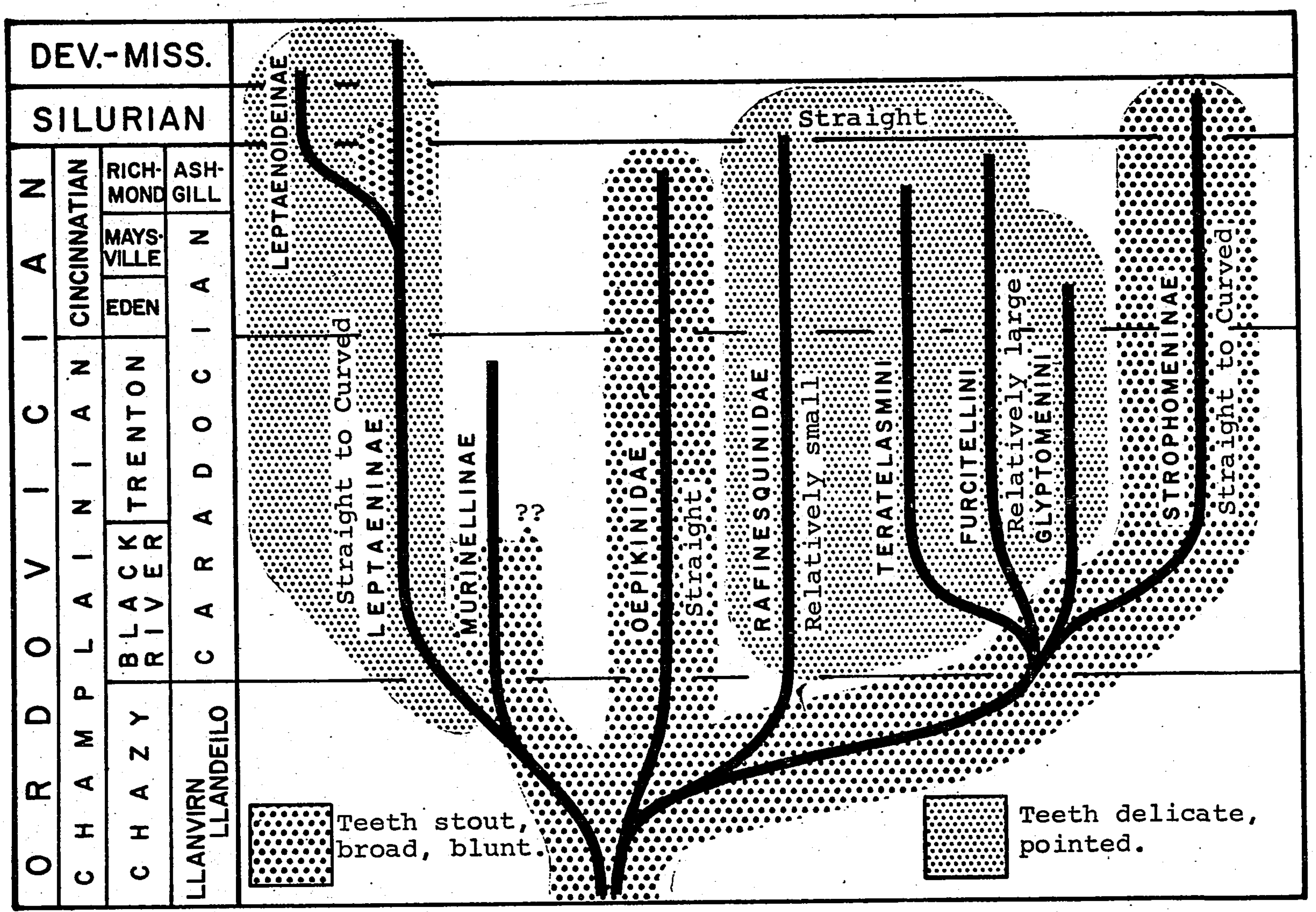
The younger genera of the Oepikinidae, the Rafinesquinidae and the Strophomenidae have smoothly curved profiles. Sharp geniculation as found in the Leptaenidae is rare. Weak geniculation is relatively common among the younger species of each family. The Oepikinidae and the

Rafinesquinidae are composed entirely of concavo-convex species. The Strophomenidae begins with the weakly resupinate, weakly concavo-convex or biplanate genera of the Glyptomenini. The strongly resupinate Strophomeninae and the biconvex, uniplicate or sulcate Furcitellini and Teratelasmini diverge from the flattened Glyptomenini. Only concavo-convex Foliomena is an exception to this sequence.

Teeth.- The teeth are the principal articulatory edges, surfaces and projections of the ventral valve. The taxonomic significance of the teeth of the Strophomenacea is difficult to evaluate. The teeth are delicate structures which project into the cavity of the ventral valve in, or even slightly dorsal to, the plane of commissure. Consequently, it is unusual to find teeth preserved without abrasion or fracture. Moreover, the taxonomic significance of variations of the teeth is difficult to evaluate because the variations probably are related to the profile of the valves and to the form of the dental lamellae. The character of the teeth of the Strophomenacea is plotted in Text-Figure 15.

Text-Figure 15.- The shape of the teeth of the Strophomenacea.

The teeth are formed by confluence of the shell tis-



Text-Figure 15.- The shape of the teeth of the Strophomenacea.

sue along the delthyrial edge of the palintrope with the narrow or receding dental lamellae. This angular confluence of shell tissue is penetrated by the cuneiform denticular plate, see Text-Figure 25. The denticular plate is emergent from the tissue of the palintrope and dental lamellae along the dorsal margin of the delthyrium. The denticular plate projects a short distance anterior to the anterior edge, *i.e.* the free edge, of the palintrope.

The teeth of the oepikinids are relatively stout structures. The anterior end of the denticular plate is broadly rounded. Judging from the sites of semidenticulation and abrasion, the principal articulatory contact with the socket buttress occurs on the medial surface and the medial-dorsal edge of the anterior projection of the denticular plate. Neither the dorsal surface of the anterior projection of the denticular plate nor the dorsal margin of the delthyrium show pronounced evidence of articulatory contact. The teeth of the Oepikinidae, Strophomeninae, *Murinella* and *Rhipidomena* are similar in shape and in abrupt demarkation of the denticular plate from the palintrope on the dorsal surface of the tooth. Details of the teeth of *Hesperinia* and *Kirkina* are not known.

Only *Murinella* of the several genera of the Murinellinae has teeth well enough preserved for some detailed examination. Unfortunately, many of the specimens are silicified and the size of the irregularities of silicification approximately equal the size of semidenticles. The general size and shape of the teeth of *Murinella* correspond to the teeth of the Oepikinidae. The dental lamellae of *Murinella* are flared in a lateral direction at their base. As a result, the teeth tend to overhang the delthyrial cavity. The surfaces of articulatory contact seem to be under the overhanging medial edges of the teeth and on the flat dorsal surfaces of the anterior projections of the denticular plates.

The teeth of the Leptaeninae are curious structures if species of *Leptaena* and *Megamyonia* are adequate representatives. The teeth of *Leptaena* are delicate. The denticular plates are emergent along the margin of the delthyrium. The denticular plates project only a short distance anterior to the free edge of the palintrope where they terminate in narrow, sharp points, not blunt knobs as in *Oepikina*. The dental lamellae of *Leptaena* are receding or obsolescent. The poorly supported teeth tend to curve in a lateral direction. Curvature of the teeth also is observed in some strophomenids and may be related to obsolescence of the dental lamellae in both families. The articulatory surfaces are on the ventral sides, *i.e.* undersides, of the denticular plates of *Leptaena*. The teeth of *Megamyonia* resemble the teeth of *Oepikina* except that the teeth are not supported on dental lamellae. Details of the articulatory surfaces of <u>Megamyonia</u> are not known.

The teeth of the Rafinesquinidae tend to be delicate and sharply pointed as the teeth of <u>Leptaena</u>. The teeth of the rafinesquinids do not resemble the stout, bluntly terminated teeth of the oepikinids. Unlike the teeth of <u>Leptaena</u>, the teeth of the Rafinesquinidae are straight and are borne on thin, vertical dental lamellae. The denticular plate is emergent along the margin of the delthyrium. The denticular plate projects as a short, sharp or angular point from the anterior edge of the palintrope. Articulatory contact occurs on the medial surface and delthyrial edge of the denticular plate. There is no evidence to indicate extensive articulatory contact on the dorsal or ventral surface of the anterior projection of the denticular plate.

The shape of the teeth of the Furcitellinae, except for <u>Rhipidomena</u> and <u>Foliomena</u>, resemble the teeth of the Rafinesquinidae by being straight and sharply pointed at the anterior. The teeth of the Furcitellinae are relatively larger in proportion to the size of the valves than are the teeth of the Rafinesquinidae. Both the medial and the dorsal surfaces of the anterior projection of the tooth serve for articulatory contact in the furcitellines. Only <u>Teratelasma</u> shows evidence of articulatory contact along the edge of the delthyrium. The teeth of <u>Foliomena</u>

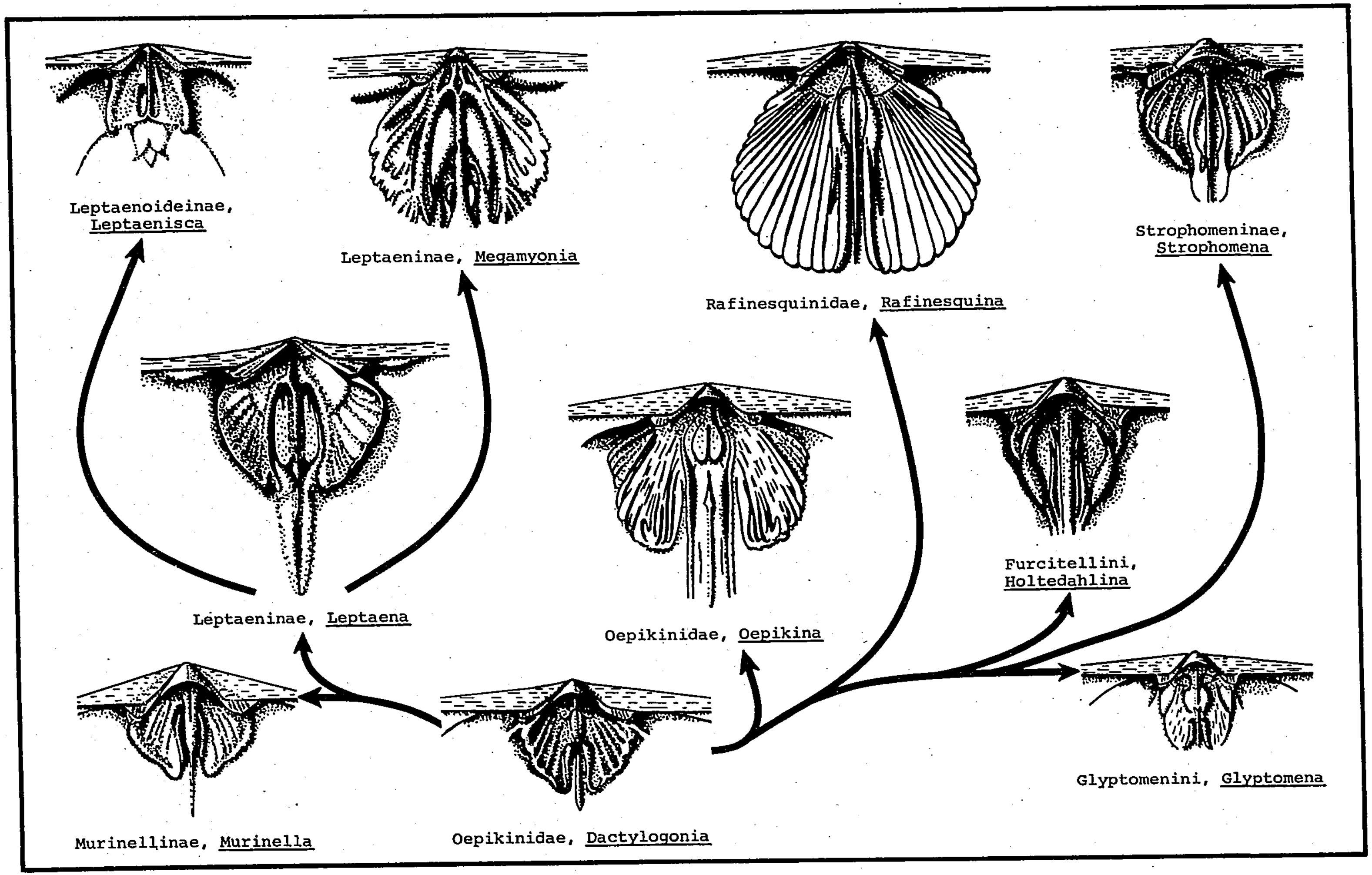
are not known in detail. The teeth of Rhipidomena resemble the teeth of the Strophomeninae.

The teeth of the Strophomeninae are similar in shape to the teeth of the Oepikinidae. The anterior terminations of the teeth are broad and blunt. The principal sites of articulatory contact are the dorsal surface and medial edge of the anterior projection of the denticular plate. As noted, the teeth of the Strophomeninae may be curved. An accessory socket commonly is formed in the surface of the palintrope on the posterior-lateral side of the tooth of the Strophomeninae. The lateral socket buttress functions as an accessory tooth in this family.

The shape of the teeth, diductor muscle scars, pseudodeltidium and delthyrial cavity of several genera of strophomenaceans is illustrated in Text-Figure 16.

Text-Figure 16.- The ventral cardinalia of several genera of the Strophomenacea.

Dorsal septa.- The dorsal septa undergo parallel evolution in the lineages of the Strophomenacea. Four distinct evolutionary stages, i.e. isophenes, may be defined in the sequence of gradual reduction or modification and eventual loss of the dorsal septa. The distribution of the four stages is shown in Text-Figure 17.



Text-Figure 16.- The ventral cardinalia of several genera of the Strophomenacea.

Text-Figure 17.- The stages of development of the dorsal septa of the Strophomenacea. The division of the Leptaenidae, Oepikinidae and Strophomenidae into stages is not related to any specific epoch.

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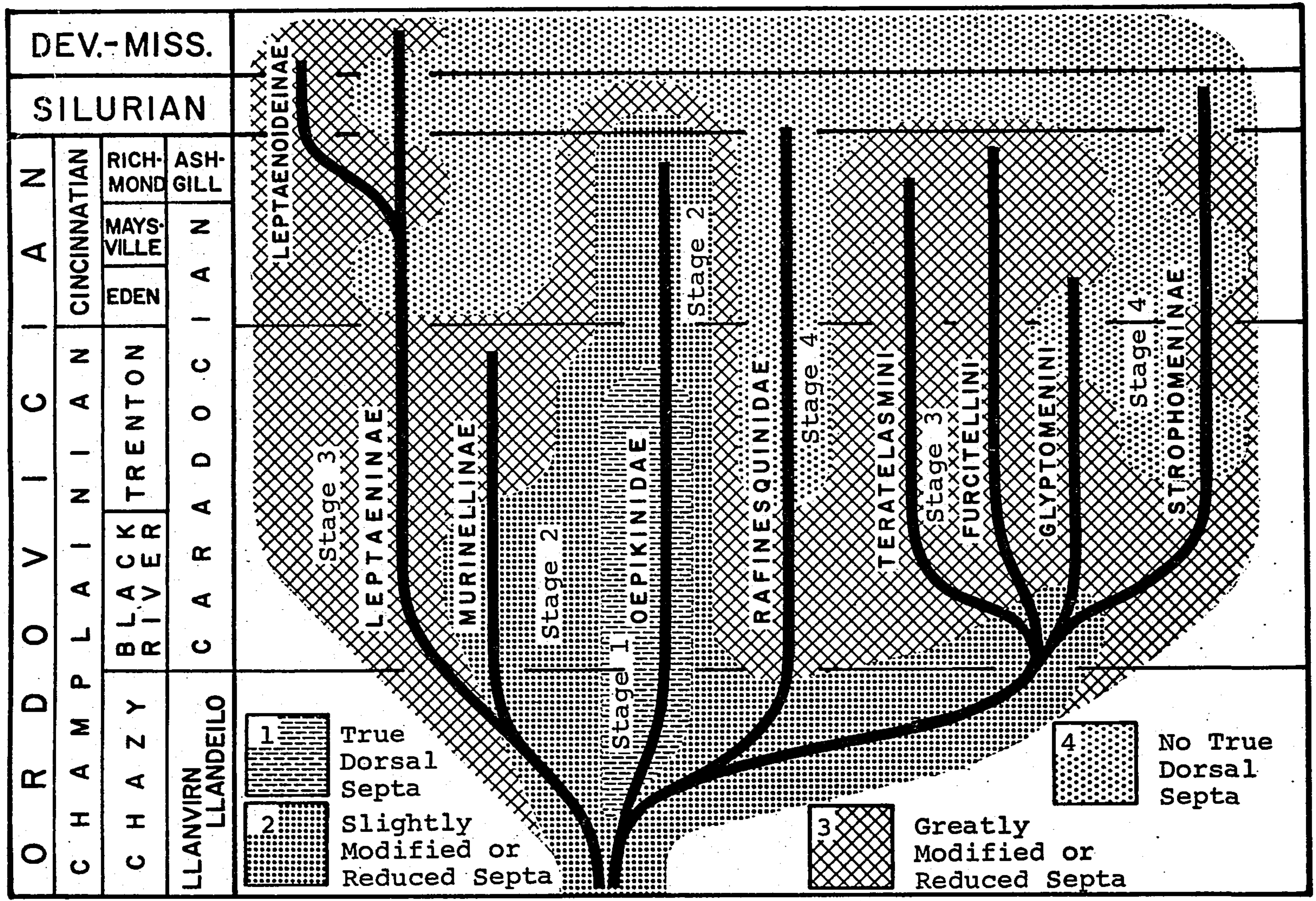
(1) The septa may be long, rather high, sharply defined ridges which are not submerged in secondary shell tissue or interrupted by endospines. Some species of *Dactylogonia* and *Oepikina* possess unmodified, full developed dorsal septa. For example, the specimen of *O. formosa* Cooper shown in Text-Figure 4, number 6, belongs in this category. Possibly those species of *Dactylogonia* which possess standing plates, *e.g. D. geniculata* Ulrich and Cooper, deserve a separate category preceding this one. The standing plates of *D. geniculata* and related species more closely resemble the septa of the plectambonitaceans than the septa of *Oepikina*. These standing plates are not duplicated elsewhere among the strophomenaceans. Thus, it is not known at this time if these standing plates belong to a separate evolutionary stage or are a unique innovation of *Dactylogonia*. The plectambonitacean character of the standing plates of *Dactylogonia*, among other characters, support the belief that this genus is the most archaic, but not the oldest, strophomenacean.

(2) The dorsal septa may show some reduction of length



Text-Figure 17.- The stages of development of the dorsal septa of the Strophomenacea.

or height, slight submergence in secondary tissue or overlap by endospines. The septa in this second category may be easily recognized and all five septa are present. A few species of *Oepikina* which have reduced septa, *e.g.* *O. bellula* Cooper, and *Dactylogonia incrassata* (Hall) which shows interference of the septa by endospines may be placed in this second stage. *Kirkina*, *Macrocoelia*, *Rhipidomena*, *Hesperinia*, *Murinella*, *Cyphomena* and *Maakina* belong in this second stage of septal development.

(3) The third stage of septal development includes species in which the dorsal septa are very short, low or indistinct, or in which the septa are extensively modified by additions of secondary shell tissue or conflict with adventitious septa. Commonly the five true dorsal septa cannot be identified. The most persistent of the five septa is the medial dorsal septum which appears as a breviseptum in almost all genera of this category and category four. The anterior dorsal septa are more commonly absent than the medial dorsal septum but more commonly present than the posterior dorsal septa. The third stage of septal development includes species of *Leptaena*, *Kiaeromena*, questionably *Leptaenisca*, *Bellimurina*, *Limbimurina*, *Oslomena*, questionably *Colaptomena*, *Glyptomena*, *Platymena*, *Actinomena*, *Furcitella*, *Holtedahlina*, *Teratelasma*, *Foliomena*, *Microtrypa*, *Trigrammaria*, *Pentlandina* and species of *Strophomena*.

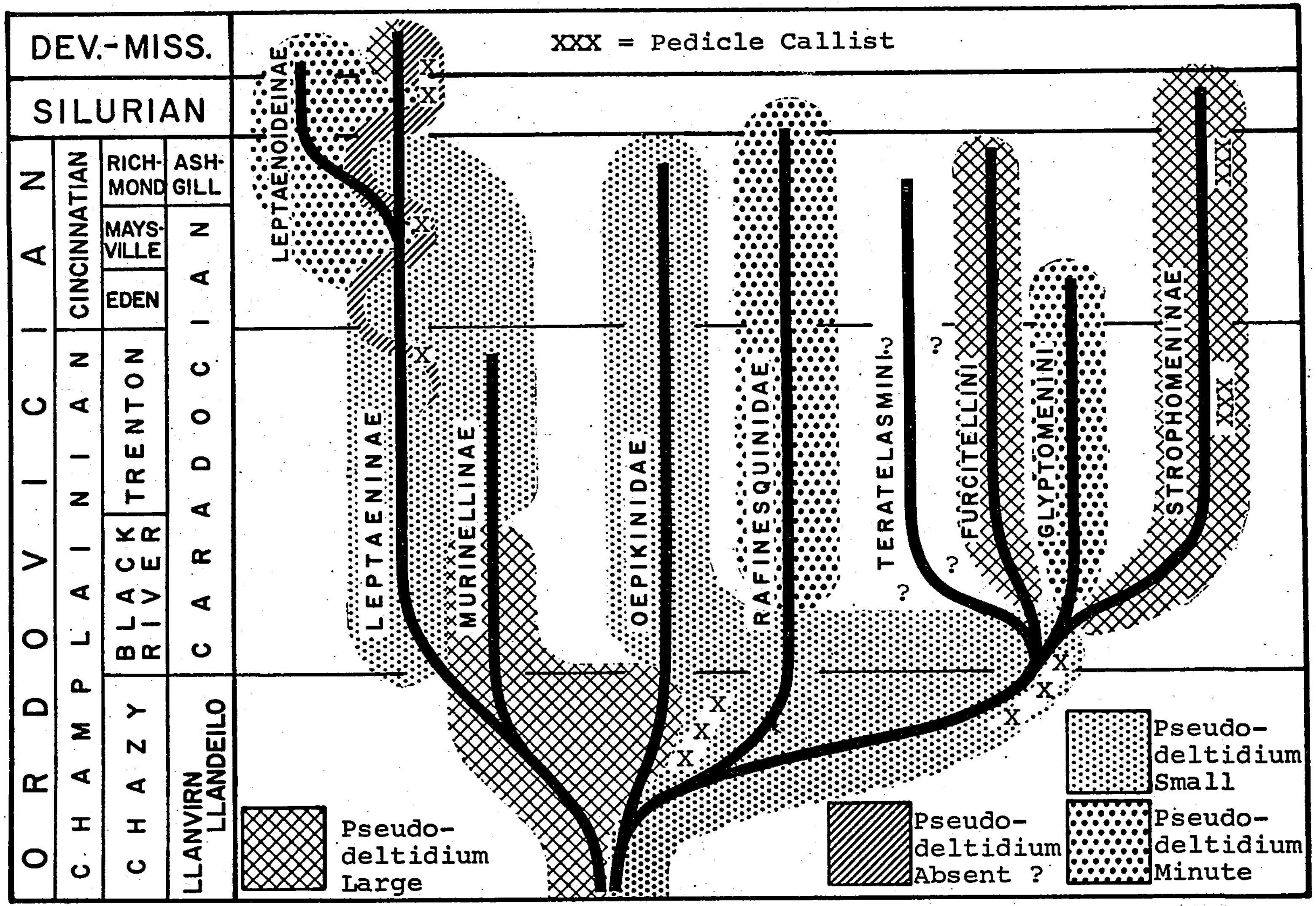
(4) The final stage is defined by the absence of the posterior and anterior pairs of dorsal septa. The medial dorsal septum or breviseptum generally is present in the species of the fourth category. This final stage of the parallel evolution of the septa includes most of the species of *Leptaena*, *Kierulfina*, *Megamyonia*, *Bekkeromena*, *Leptagonia*, *Leptaenella*, *Notoleptaena*, *Rafinesquina*, *Kjaerina*, *Hedstroemina*, *Mjoesina*, *Longvillia*, *Gunnarella*, *Tetraphalerella* and some of the species of *Strophomena*. The stage of septal development of *Luhaia*, *Pionomena*, *Leptaenoidea* and *Rugoleptaena* is not known.

Pseudodeltidium, chilidium and pedicle foramen.- The comparative morphology of the pseudodeltidium, chilidium and pedicle foramen cannot be considered independently. Distinct isophenous stages cannot be defined readily in the progressive parallel evolution of the pseudodeltidium and chilidium of the lineages of the Strophomenacea. Modification of these two structures form a continuum. Any apparent discontinuities in development of these structures may be related to deficiencies in the fossil record. Development of the pedicle foramen does progress through isophenes if adult individuals of the various species are considered. The isophenes of the pedicle foramen are defined by the states of being open and large, open and small, or sealed. The condition of the pedicle foramen is significant only in respect to adult individuals because it is probable that the foramen of all juvenile strophomenaceans was open. Text-Figures 18 and 19 illustrate the conditions of the pseudodeltidium and pedicle foramen in the Strophomenacea.

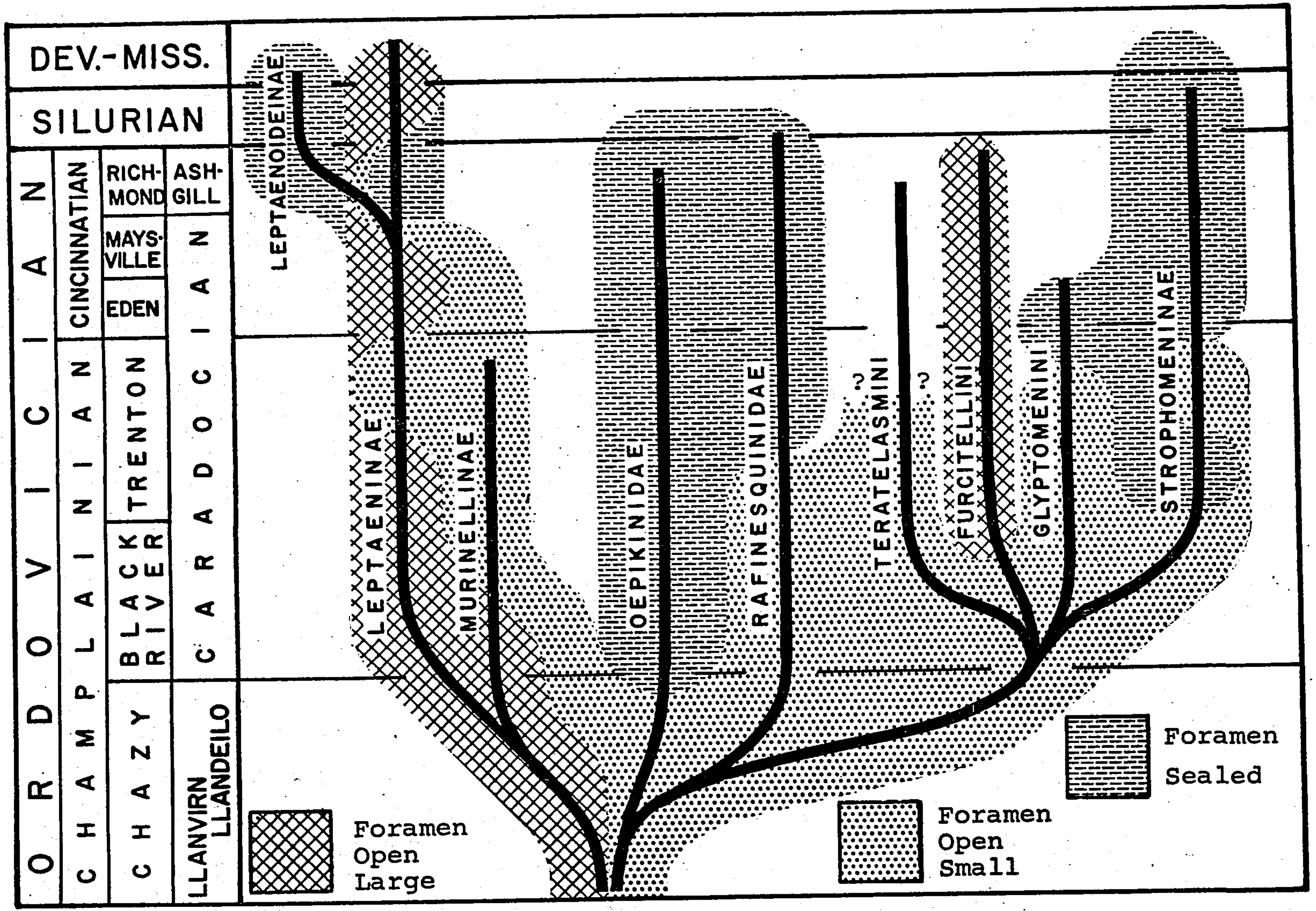
Text-Figure 18.- The approximate size of the pseudodeltidium of strophomenaceans relative to the general size of the valves.

Text-Figure 19.- The condition of the pedicle foramen in adult strophomenaceans.

The pseudodeltidium of several early strophomenacean genera is a large, highly arched structure which covers most of the delthyrial cavity. The ventral interarea of these early genera is quite long (posterior to anterior) in comparison to the ventral interareas of other strophomenaceans. The large size of the pseudodeltidium of early genera is not attributable entirely to the length of the interarea because the chilidium is relatively short. *Dactylogonia*, *Hesperinia*, *Murinella* and *Cyphomena* possess this combination of posterior structures as well as a large, supra-apical pedicle foramen. From this beginning, there is a general and gradual decrease of the relative size of the pseudodeltidium and length of the ventral



Text-Figure 18.- The approximate size of the pseudodeltidium of strophomenaceans relative to the general size of the valves.



Text-Figure 19.- The condition of the pedicle foramen in adult strophomenaceans.

interarea, and a relative increase of the size of the chilidium. Accompanying these changes, the pedicle foramen of adult strophomenaceans becomes smaller and eventually is sealed by secondary shell tissue.

The pseudodeltidium and chilidium of the Leptaeninae and the younger Murinellinae are considerably smaller than these structures of the older strophomenaceans. The pseudodeltidium of the younger leptaenids is a small pyramidal block set into the apex of the delthyrial cavity. Deposits of secondary shell tissue commonly cover the anterior surface of the pseudodeltidium within the delthyrial cavity. The pseudodeltidium of some species cannot be distinguished from the surrounding shell tissue. In particular, species which possess a pedicle callist rarely have a pseudodeltidium that can be recognized on the surface of the shell.

The chilidium of all species of the younger leptaenids is a distinct but thin sheet of wrinkled shell tissue which is molded onto the posterior bases of the cardinal process lobes. A large chamber may exist between the chilidium and the lateral bases of the cardinal process lobes. A similar condition is found in species of Oepikina. The chilidium is either fused to the posterior edge of the meso-cardinal ridge or deeply folded into the cleft between the cardinal process lobes. The chilidium appears to be protrusive because of the narrowness of the dorsal interarea and because, in many species, there is not an emergent pseudodeltidium but an introverted pedicle callist for comparison. The small size of the pseudodeltidium and chilidium of the advanced leptaenids is directly correlated to their exceedingly short interareas. These structures cannot be larger; there would not be enough room for them.

The advanced leptaenids generally have an open pedicle foramen in contrast to other strophomenaceans which have a small pseudodeltidium. Older species of Leptaena have a relatively large foramen. Kiaeromena and some of the younger species of Leptaena have a small foramen. The foramen of Megamyonia, some species of Leptaena, Bekkeromena, and the Leptaenoideinae is sealed. The pedicle foramen of the leptaenids lies on the external surface of the ventral valve. Commonly a thin yoke of shell tissue separates the foramen from the apex of the pseudodeltidium, hence, the foramen is supra-apical. The foramen seems to have increased in size by resorption of shell tissue because the rim commonly is polished or calloused and the foramen interrupts costae. Species of Leptaena, Macrocoelia and Rhipidomena which have a pedicle callist do not have a pedicle foramen. Apparently the pedicle protruded through the open delthyrium. A curious slot commonly is found which seems to be eroded into the posterior-medial region of the ventral valve of those species of Leptaena and *Rhipidomena* which have a pedicle callist. Apparently, the pedicle passed through the open delthyrium, curved over the apex of the ventral valve where it left no impression, and abraded or was cemented to the midline of the ventral valve anterior to the apex. Species of *Macrocoelia*, *e.g.* *M. expansa* (Sowerby), which have a pedicle callist do not have a slot in the ventral valve. However, some specimens of *Macrocoelia* have a small, circular facet at the apex of the ventral valve which may have been a site of pedicle attachment. *Leptagonia* appears to have both a pedicle callist and an open foramen on first inspection. The "pedicle callist" of *Leptagonia* is smooth and thick. It is probably a filling of the posterior region of the delthyrial chamber inasmuch as the large pseudodeltidium of this genus would not have permitted passage of the pedicle through the delthyrium.

Leptagonia demonstrates an interesting reversal of the evolutionary changes which effect the pseudodeltidium, chilidium and pedicle foramen. The pseudodeltidium and chilidium of this genus are large; the interareas are long; there is an open pedicle foramen. *Leptagonia* is Mississippian in age, yet the character of these posterior structures belong to a leptaenid from the Lower or Middle Ordovician. It is not likely that *Leptagonia* arose from an unknown lineage of primitive leptaenids which survived from Middle Ordovician to Mississippian time. Probably

Leptaena or Leptaenella is ancestral to Leptagonia. The posterior structures of Leptagonia are conservative or atavistic. Less pronounced atavism of the pseudodeltidium and chilidium is found also in the Furcitellini and Strophomeninae.

The pseudodeltidium and chilidium of the Oepikinidae, excluding Dactylogonia and Hesperinia, are in a moderately advanced state of development. The pseudodeltidium is smaller, thicker and shorter than the archaic pseudodeltidium. It is not a pyramidal block as in the leptaenids because the apex of the delthyrial cavity may extend under the slightly arched pseudodeltidium. Secondary shell tissue commonly fills the extension of the delthyrial cavity under the pseudodeltidium of Oepikina. This secondary tissue is drawn-out toward the anterior to form ridges on the lateral margins of the adductor muscle scars. The pseudodeltidium is replaced by a pedicle callist in a few species of Macrocoelia.

The chilidium of the advanced oepikinids is relatively large. It may be tightly pressed against the posterior bases of the cardinal process lobes. The chilidium may be draped into the cleft between the cardinal process lobes, fused to the edge of the meso-cardinal ridge or, rarely, the chilidium may bridge the cleft between the lobes to produce a small notothyrial cavity. The increase of size of the chilidium in the Oepikinidae parallels the increase of size in the Rafinesquinidae.

The pedicle foramen of the advanced oepikinids is minute or sealed.

The pseudodeltidium, chilidium and pedicle foramen of the Rafinesquinidae are very similar in form to those structures of the Oepikinidae. The interareas of the Rafinesquinidae are slightly narrower than those of the Oepikinidae with the result that the pseudodeltidium and chilidium are slightly smaller in proportion to valve size. The only outstanding difference in the pseudodeltidium and chilidium of these two families is found in the most advanced species of Rafinesquina. The pseudodeltidium of the Upper Ordovician species of Rafinesquina is a very small quoin in the apex of the delthyrium. In detail, the quoin has the form of a regular trapezoid except that the opposite sides are concave arcs rather than straight parallel lines. The pseudodeltidium is buttressed by a secondary deposit. The childium of these advanced species is very large. The pedicle foramen of the Rafinesquinidae is minute, possibly open in Hedstroemina and Colaptomena, and sealed in Kjaerina and Rafinesquina.

The pseudodeltidium, chilidium and pedicle foramen of Rhipidomena, excepting species with a pedicle callist, are similar to these structures in Oepikina. That is, these structures in the oldest and most primitive genus of the Strophomenidae are in a moderately advanced state.

The advanced Glyptomenini, Platymena, Glyptomena and Mioesina, show simple, progressive reduction of these structures. The pseudodeltidium becomes very small so that it resembles the pseudodeltidium of Rafinesquina. The chilidium becomes minute because the dorsal interarea and the cardinal process lobes become minute. There is a minute pedicle foramen in all of the genera of the Glyptomenini.

The Furcitellini show conservatism, or perhaps atavism, of the pseudodeltidium, chilidium and pedicle foramen. The interareas are long relative to the size of the valves and the pseudodeltidium, chilidium and foramen are large. The condition of these features is compatible with that of Dactylogonia and Cyphomena but there is no phylogenetic relationship involved.

Teratelasma and Foliomena have a pseudodeltidium and chilidium but details concerning these structures are not known. There is an open pedicle foramen in Teratelasma but the condition of the pedicle foramen of Foliomena is not known.

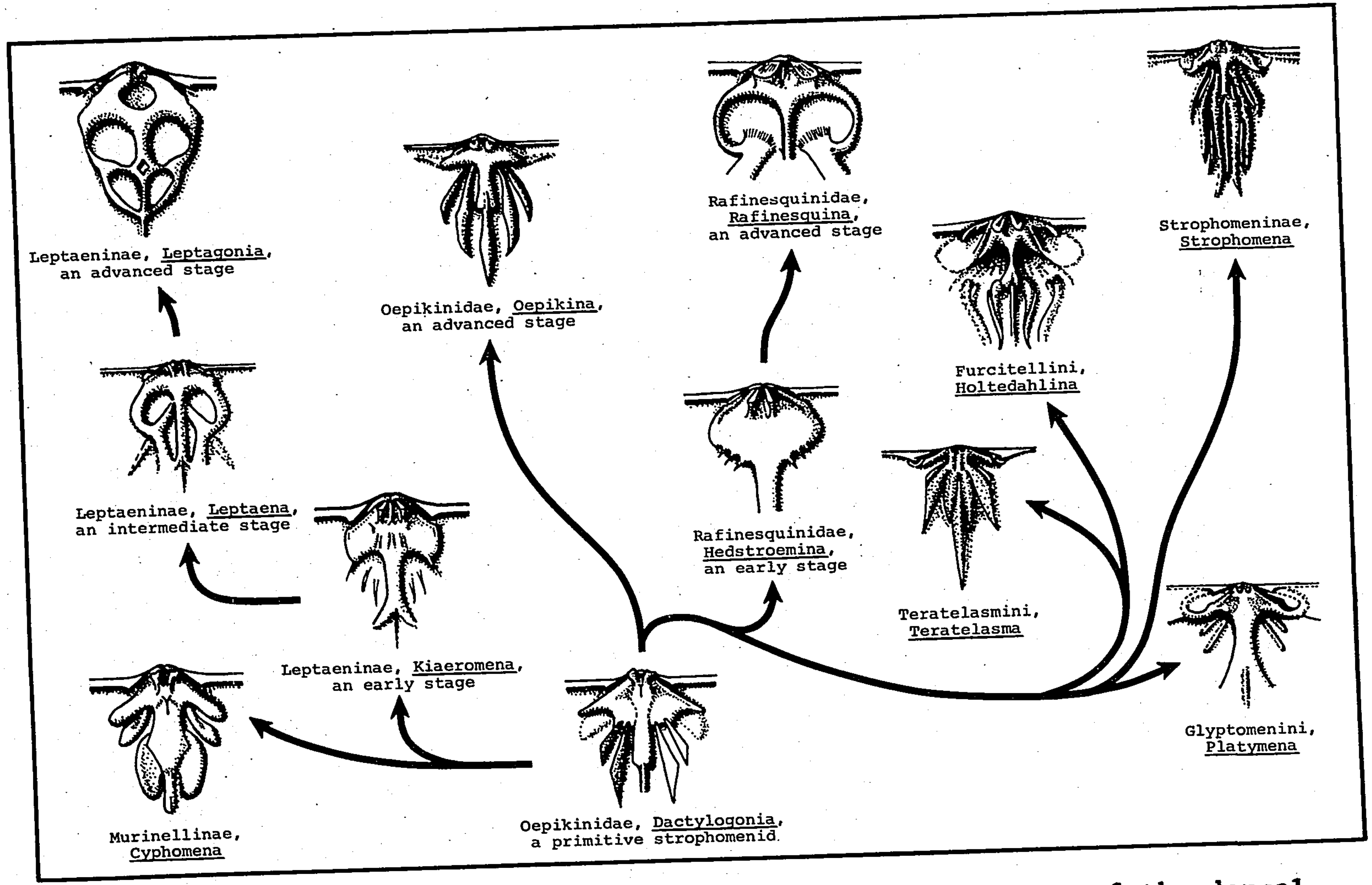
The Strophomeninae also shows conservatism or atavism of the pseudodeltidium and chilidium. The ventral interarea of species in this subfamily is moderately long. The pseudodeltidium is long and highly arched. Unlike other genera which have a large pseudodeltidium, most of the species of Strophomena and allied genera have a sealed foramen. The chilidium is relatively small. It adheres to the posterior and lateral bases of the cardinal process lobes. A meso-cardinal ridge is rarely present in the strophomenids. The meso-cardinal ridge, if present, lies on the posterior-medial base of the cardinal process under the chilidium. As a consequence, well preserved specimens of strophomenids have a distinct notothyrial cavity.

No measurements have been taken of dental angles throughout the Strophomenacea. The dental angle is the angular divergence of the edges of the delthyrium in the plane of the interarea. Bancroft (1929) has shown that the dental angle of species of *Kiaerina* and *Hedstroemina* is variable. Moreover, the dental angle is not constant throughout the ontogeny of those species with curved teeth, *e.g.* species of *Leptaena* and *Strophomena*. The general appearance of the dental angle of the various genera suggests that the dental angle is inversely related to the length of the interarea and to the size of the pseudodeltidium. The shorter the interarea and the smaller the pseudodeltidium, the greater is the dental angle. This relationship seems plausable in respect to the mechanics of the cardinal process and articulation.

Cardinal process.- The form of the cardinal process and the shape of the cardinal process lobes are highly variable qualities in the Strophomenacea. The cardinal process in general and the lobes in particular show little in the way of orderly evolutionary progression or taxonomic differentiation. It is probable that the poor organization of these structures in respect to evolutionary progression and taxonomic differentiation is caused by the interplay of at least four independent variables. These are, taxonomic lineage, evolutionary stage of development within each lineage, the ontogenetic stage of individuals examined and the effects of weathering, natural abrasion and preparation upon the individuals examined. If perfectly preserved individuals of the same ontogenetic stage were available for all genera, probably a more meaningful and orderly arrangement of cardinal process types could be found. Text-Figure 20 shows sketches of the dorsal cardinalia of selected strophomenacean genera. The cardinal processes are shown.

Text-Figure 20.- The cardinal process and related structures of the dorsal valve of selected strophomenacean genera.

The cardinal process lobes show some slight taxonomic differentiation in the shape of the base of the lobes, the amount of space between the bases of the lobes and the direction in which the myophore faces. Unfortunately, the



Text-Figure 20.- The cardinal process and related structures of the dorsal valve of selected strophomenacean genera.

cardinal processes of the oldest strophomenaceans, *Hesperinia* and *Kirkina*, which are quite rare, are too abraded to yield much information. The bases of the cardinal process lobes of *Kirkina* are very small in respect to the size of the valve, elongated in the anterior-posterior direction and closely spaced together. The narrow cleft has parallel sides. The bases of the lobes of *Hesperinia* are like those of *Kirkina* but are larger in respect to the size of the valves. Specimens of *Dactylogonia* and *Cyphomena* are better preserved and more numerous than *Hesperinia* and *Kirkina*. The form of the bases of the lobes of *Dactylogonia* and *Cyphomena* resembles the bases of the older genera. The distal terminations of the lobes of *Dactylogonia* and *Cyphomena* are irregular knobs or shafts with narrowly cupped myophores directed toward the posterior. Some individuals of *Dactylogonia* have a small fillet added between the anterior base of the lobe and the posterior platform. The archaic cardinal process lobes may be described as shafts or irregular knobs, with posteriorly directed myophores, elongate bases and a narrow, parallel sided cleft.

The parallel sides of the cleft of these archaic genera, as well as the older Leptaeninae and Rafinesquinidae, would seem to indicate a disjunct condition of the cardinal process lobes. The posterior ends of the cardinal process lobes of advanced genera of all lineages tend to merge together, *i.e.* they become conjunct. It is strange that the disjunct to conjunct evolution of the cardinal process and the relative increase of size and importance of the chilidium of the Strophomenacea are opposite to the evolution of these structures in the Stropheodontacea.

The cardinal process of *Murinella* has approximately the same shape as that described for the other early genera. The width and height of the lobes in respect to shell size is much greater than that of the earlier genera. The myophore faces are rotated in the posterior direction, more than 90° from the plane of commissure. The myophores are deep, narrow slots in the posterior edge of the lobes.

Bellimurina and *Oslomena* have cardinal process lobes quite different from those of *Murinella*. They resemble the knob-like lobes of some species of *Dactylogonia* but they are minute. The lobes of *Limbimurina* are known from one specimen. They are similar to the elongated, cupped lobes of some species of *Dactylogonia* and *Cyphomena*.

The cardinal process lobes of the Leptaeninae are subject to evolutionary modification throughout the long history and the many genera and species of the subfamily. The earliest species of the Leptaeninae, *Leptaena rugosa* Dalman and *L. ordovicica* Cooper, have parallel, blade-shaped lobes with a wide cleft. The myophore is located on the dorsally inclined, posterior edge of the lobe. If younger species and genera are observed several progressive effects may be noted. The anterior end of the cleft remains wide, but the posterior end of the cleft becomes narrow until in Devonian varieties of Leptaena rhomboidalis [?] (Wilckens) and the Mississippian species Leptagonia analoga (Phillips) the posterior ends of the lobes are fused together in the manner of some orthotetids. The distal ends of the lobes tend to converge over the cleft in younger species. The result is a broad shallow chamber in place of the anterior end of the cleft. Also, in younger species, there is a tendency for broadly petaloid or cupped myophores to develop. The petaloid myophore may be very large and gently inclined on L. richmondensis Foerste, Kiaeromena kjerulfi (Holtedahl), Megamyonia unicostata (Meek and Worthen) and some varieties of Leptaena rhomboidalis (Wilckens).

The irregular, knob-like lobes of Leptaenisca are exceptional. They may be associated with the cemented habit of the Leptaenoideinae.

The cardinal process lobes of advanced genera of the Oepikinidae and Rhipidomena are distinctly different from those of the archaic oepikinids and murinellines. The lobes of Oepikina, Macrocoelia and Rhipidomena are short (posterior to anterior), broad (medial to lateral), tall hemicylinders. They stand normal to the plane of commissure and flush with the posterior margin of the valve. These cylinders generally bear deeply folded or cupped myophores on the posterior surface. The cleft is narrow and tends to converge to a very thin slit between the posterior bases of the lobes. The myophore surfaces on the posterior faces of the lobes are convergent toward the apex of the dorsal valve. The cardinal process lobes of Macrocoelia and Rhipidomena differ from the description, which applies to Oepikina, only by being slightly more elongated in a posterior to anterior direction than the lobes of Oepikina. The right cardinal process lobe of Oepikina commonly is distorted. Deformation of a cardinal process lobe is not common in other genera.

The cardinal process of the Rafinesquinidae has a great range of size through the various species. The cardinal process of Pionomena is unknown. The only known cardinal process of Colaptomena is broken. The one incomplete lobe seems to more closely resemble the lobes of Oepikina than any rafinesquinoid species. The lobes of Kjaerina, Hedstroemina and older species of Rafinesquina are elongated, erect, delicate blades. The blades of Hedstroemina are widely separated and nearly parallel. The blades of Kjaerina and older species of Rafinesquina are widely separated to the anterior. They converge but do not unite toward the posterior. The myophores are situated on the steeply inclined posterior edges of the lobes. These delicate blades resemble the juvenile cardinal process blades of advanced species of Rafinesquina. The bases of the cardinal process lobes of advanced species of Rafinesquina are elongated and strongly convergent toward the posterior; some bases may be overgrown with secondary shell tissue. The distal terminations of the blades are greatly expanded petaloid or flat-iron shaped platforms. The myophore surfaces are inclined so as to face in the posterior-dorsal direction. The posterior bases of the myophores converge toward the apex of the valve under the chilidium. These are the largest cardinal process lobes in the Strophomenacea. There is an interesting parallelism of the blade-like lobes of the older species of leptaenids and rafinesquinids and the petaloid lobes of the younger species of leptaenids and rafinesquinids.

As noted, the earliest strophomenid, Rhipidomena, has a cardinal process resembling the advanced oepikinids. From this beginning, the strophomenid groups, Glyptomenini, Furcitellini and Strophomeninae diverge strongly in the character of the cardinal process. The cardinal process lobes of the advanced Glyptomenini and Teratelasma are minute in relation to shell size. They are tiny nodes or hemispheres at the medial-posterior ends of the socket buttresses. The nodes are flush with the posterior margin of the valve. The myophores are shallow excavations in the posterior faces of the nodes. The cardinal process lobes of Foliomena either are absent or submerged in secondary shell tissue. Species of the Furcitellini possess cardinal process lobes which bear a strong resemblance to that structure in Dactylogonia and Cyphomena. This is another example of the striking convergence of this group and the archaic leptaenids.

The cardinal process of the Strophomeninae is reminiscent of this structure in Oepikina. The lobes are hemicylindrical and broader than they are long. They bear deeply folded or cupped myophores. The lobes of the Strophomeninae differ from the lobes of the Oepikinidae by being slightly smaller and more delicate relative to shell size, more closely spaced together, and slightly inclined. The myophore face of gerontic specimens of younger species may be petaloid or grossly enlarged and the bases of the lobes may be overgrown with secondary shell tissue.

The general evolutionary trends of the cardinal process lobes of the Strophomenacea seem to be toward increased size, shortening in the posterior-anterior direction, increased area of the myophore and inclination of the myophore. The Glyptomenini and advanced Murinellinae are the principal exceptions to this generality. The changes which accompany the growth of individuals approximately duplicate the phylogenetic trends. The tendency of gerontic individuals to bear elaborately expanded or cupped myophores which are less steeply inclined than those of juveniles is particularly noticeable.

Socket buttress.- The shape of the socket buttress, the profile of the valve and the dental angle undergo collateral changes in the evolution of the Strophomenacea. As has been noted, the dental angle is inversely related to the length of the interareas and the size of the pseudodeltidium. The socket buttresses mate with the teeth, consequently the dental angle controls the angle formed by the socket buttresses. As there is a general tendency for the dental angle to increase throughout the phyletic history of the Strophomenacea, the angle formed by the socket buttresses also increases with phyletic advance. This general tendency is partly obscured by the variable amount by which the socket buttress may overhang the cavity of the socket. In those groups with greatly projecting teeth or receding dental lamellae, as the Oepikinidae and the Strophomeninae, the socket buttresses hook further under the teeth then in the groups with pronounced dental lamellae or delicate teeth. For the purpose of description, the angles between the lateral-posterior edges of the socket buttresses may be small (up to 100°), moderate (100 to 120°) or large (greater than 120°).

The archaic oepikinids and leptaenids have rather long socket buttresses that are set at a moderate to large angle. The buttresses are long because the teeth are long and prominent. The lateral-posterior edge of the socket buttresses may or may not project strongly above the internal surface of the valve. If the profile of the valves is biconvex, the socket buttress is a prominent ridge, but if the profile of the valves is concavo-convex, the socket buttresses are low ridges which may be almost flush with the internal surface of the valve.

The advance leptaenids have very short, obscure socket buttresses that are set at a small angle. The socket buttresses are scarcely longer than the length of the ventral interarea. Apparently the posterior end of the socket buttress hooks under the posterior end of the tooth into the space occupied by the fully developed dental lamellae of other groups. In this way, the angle formed by the lateral edges of the socket buttresses is quite small.

The socket buttresses of the advanced oepikinids and the rafinesquinids are set at a moderate angle. Among the advanced oepikinids, the buttresses are short and very prominent. This form is the result of articulation of the buttress with only the thick, blunt anterior projection of the tooth. The rafinesquinids have moderately long, projecting socket buttresses. The length of the buttress results from its mating with the long edge of the tooth along the dorsal margin of the delthyrial chamber. The buttress projects into the delthyrial chamber and consequently is a high ridge.

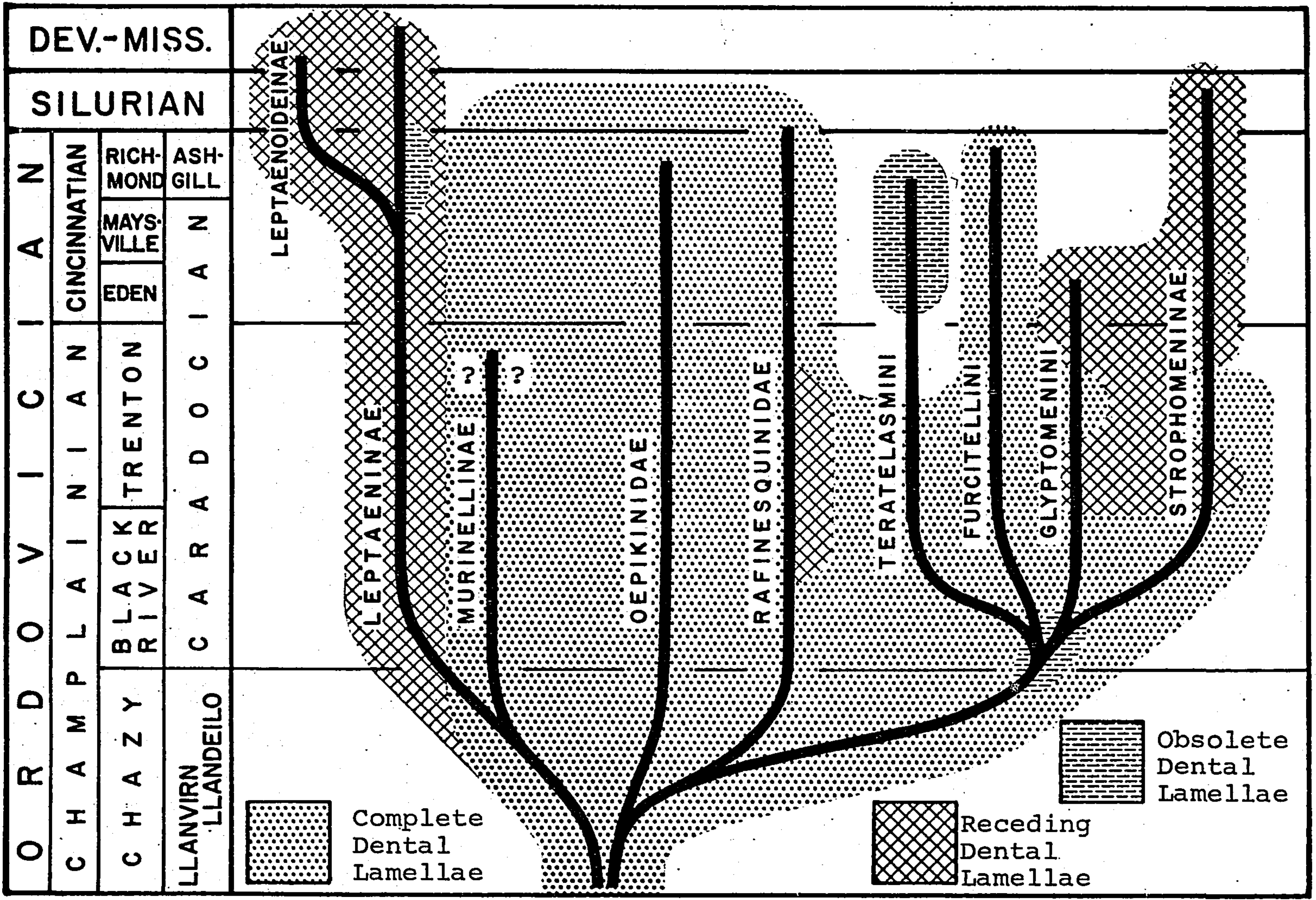
The socket buttresses of the Strophomenidae, in general, are long, curved and prominent. They are set at a small to large angle depending upon the length of the ventral interarea, which is quite variable in this family. The posterior end of the buttress may completely overhang the socket so that the lateral-posterior edge of the buttress directly overlies the lateral socket buttress. The lateral-anterior end of the socket buttresses are reflexed toward the interarea. The reflexed curvature of the buttress in many species is accompanied by elevation of the surface of the fulcral plate plus secondary deposits across the entire floor of the socket. The entire socket and buttress is thus set apart from the rest of the internal surface of the valve.

The curvature of the socket buttress and the elevation of the surface of the fulcral plate plus secondary deposits in the socket are characteristic of strophomenoids which have plano-convex, biconvex and resupinate profiles. These features are not restricted to the Strophomenidae but also occur in biconvex Murinella and some of the other leptaenids which tend to have biplanate or biconvex valves posterior to the geniculation. That is, these features are found only in those strophomenaceans in which the dorsal valve tends to be flat or arched away from the plane of commissure. Apparently the curvature of the buttresses and the layer of secondary tissue is required to lift the socket into the plane of commissure.

Dental lamellae.- Changes in the form of the dental lamellae are antithetic to changes in the socket buttresses with respect to variation in the profile of the valves. The fulcral point of the tooth-socket articulation must lie on the hinge line of the valves. The plane of commissure, which is defined by the line of contact of the two valves around their periphery, passes through the hinge line. If the arch of the ventral valve is directed toward the plane of commissure, that is, if the ventral valve is concave, or if the ventral valve is flat, the height of the teeth above the internal surface of the ventral valve must be very small to maintain the fulcrum on the hinge line. Reduction of the height of the teeth apparently is accomplished in strophomenoid evolution by reduction or obsolescence of the dental lamellae which support the teeth and possibly also by the curvature of the teeth. This hypothesis correlates well with the condition of the dental lamellae throughout the strophomenacea. The genera which have convex ventral valves, whether the entire profile be biconvex or concavo-convex, generally have completely formed dental lamellae. This is the condition in the Oepikinidae, Murinellinae, Rafinesquinidae and Furcitellini. The Leptaenidae with largely planate ventral valves and the Strophomeninae and Rhipidomena with concave ventral valves all have receding or obsolescent dental lamellae. The advanced Glyptomenini present an exception to this hypothesis. The profile of all of the genera of this tribe is very flat, either biplanate, or weakly concavo-convex or resupinate. The interareas of genera in this tribe are very narrow. All of the members of the Glyptomenini have fully formed or very slightly receding, very short dental lamellae. Apparently if both valves are flat and the interareas are narrow, the fulcrum of articulation has to lie on the hinge line and there is no mechanical necessity for evolutionary recession of the dental lamellae. The distribution of variations upon the dental lamellae is show in Text-Figure 21.

Text-Figure 21.- The nature of the dental lamellae throughout the Strophomenacea.

Muscle bounding ridges.- The Leptaenidae, excluding some murinellines, and the Strophomenidae, excluding the Teratelasmini, possess ridges along the margins of the diductor muscle scars in the ventral valve. The Oepikinidae

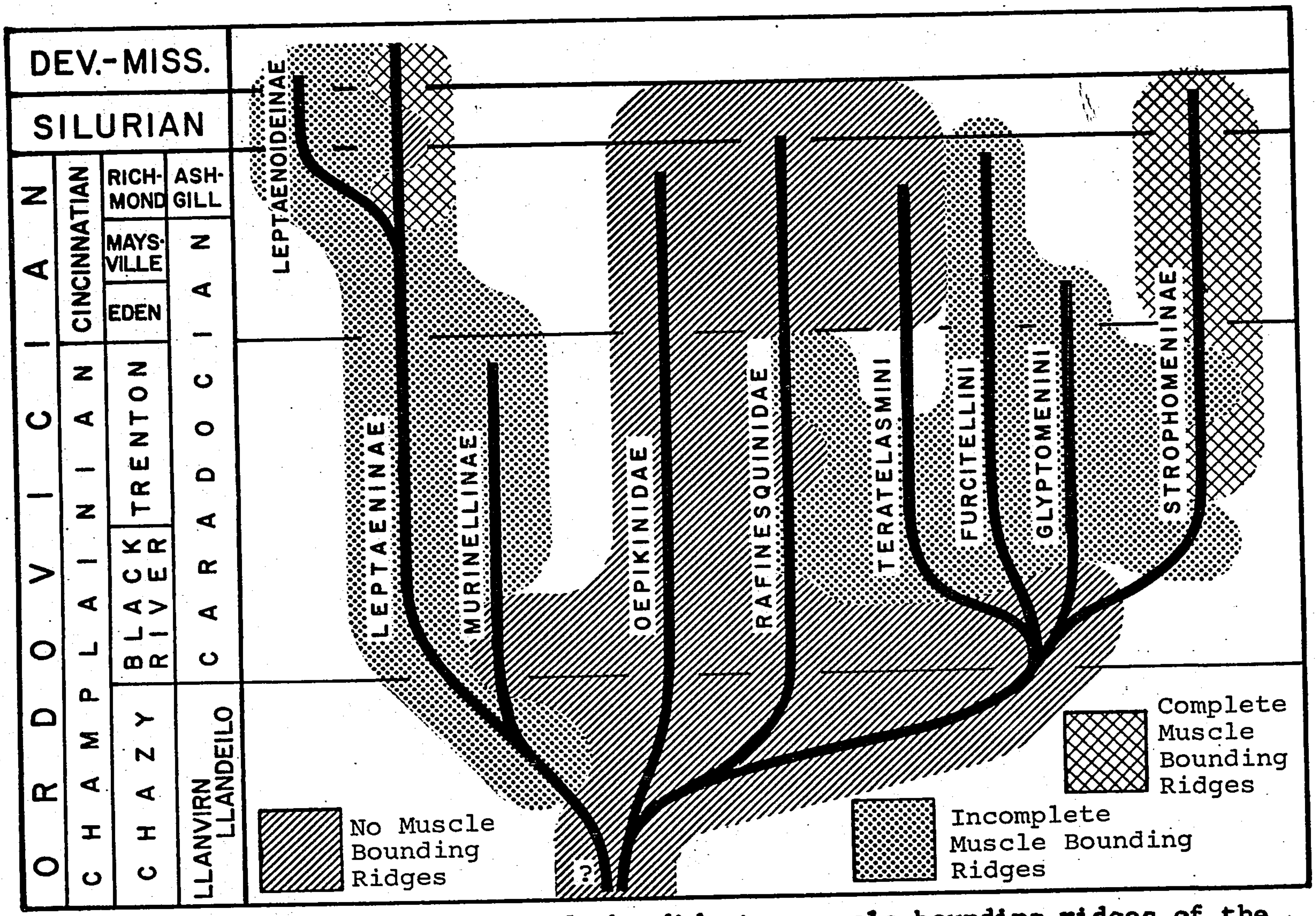


Text-Figure 21.- The nature of the dental lamellae throughout the Strophomenacea.

and the Rafinesquinidae largely are devoid of muscle bounding ridges. As has been noted, these muscle bounding ridges are histologically continuous with the dental lamellae. There is a physical discontinuity between these structures only in genera which have obsolescent dental lamellae. Text-Figure 22 shows the distribution of muscle bounding ridges in the Strophomenacea.

Text-Figure 22.- The condition of the diductor muscle bounding ridges of the Strophomenacea.

Spjeldnaes (1957, pp. 42-49) has presented a lucid account of the mechanics of the diductor muscles, cardinal process and muscle bounding ridges. With reference to Dr. Spjeldnaes' discussion of the muscular system, pp. 42-49, it should be noted that Fig. 13, p. 43, does not correspond to his discussion. Dr. Spjeldnaes has told me that the plate for Fig. 13 was disassembled accidently during the printing process and reassembled incorrectly without his knowledge. The substance of his discussion is that the mechanical advantage of the diductor muscles is greatest when the vector of pull of the muscles is along the midline of the valves and at 90° to the valve being rotated. If this is the case, the lifting of the muscle scars above the general level of the internal surface of the ventral valve by the muscle bounding ridge



Text-Figure 22.- The condition of the diductor muscle bounding ridges of the Strophomenacea.

and the thick secondary deposits within the muscle field impares the mechanical efficiency of the muscles. This is true, but other attributes imparted by the muscle bounding ridges outweigh the mechanical disadvantage of elevation of the muscle scars. The muscle bounding ridges along the lateral margins found in the Leptaenidae and Furcitellinae confine the muscle attachment sites to near the midline of the valves where efficiency is greatest. It is curious that the Oepikinidae and Rafinesquinidae lack lateral ridges, not that the Leptaenidae and the Furcitellinae have them. The anterior margin of the muscle bounding ridge confines the muscle attachment to the posterior medial region of the valve where efficiency is greatest, *i.e.* where the vector of pull is nearest to 90° to the valve being rotated. Moreover, the measure of a muscle's power is not proportional to the area of the muscle scar but rather to the cross sectional area of the muscle. The anterior elevation of the diductor muscle scars of the Strophomeninae and some of the Leptaenidae by the muscle bounding ridges permitted the muscles to be ovoid in cross section. If these genera had lacked muscle bounding ridges, the muscles would have been flattened sheets with very small cross sectional area. Also, if a strophomenacean with highly arched, resupinate profile, as found in species of *Strophomena*, had flabellate diductor muscles as found in *Rafinesquina*, the portion of the muscle attached in the anterior region of the muscle field could not follow a straight line to the cardinal process. Elevation of the muscle field by the ridges permits all parts of the muscle scars to lie along straight lines from the cardinal process. Hence, the principal attributes of the anterior segments of the muscle bounding ridges were to confine the muscles to the posterior-medial region of the valves, to increase the cross sectional area of the muscle and to place all parts of the muscle field within "view" of the cardinal process.

Posterior platform.- The shape and height of the posterior platform is interrelated with the profile of the valves, angle of divergence of the socket buttresses and shape and position of the adductor muscle scars. The posterior-lateral boundaries of the lateral ridges of the posterior platform are the socket buttresses. Hence, those genera which have a small angle of divergence between the socket buttresses, i.e. which have long ventral interareas and complete dental lamellae, have a small angle of divergence between the lateral ridges of the posterior platform. The opposite condition holds, as well. The height of the posterior platform is related to profile, just as is the height of the socket ridges. Lineages of resupinate and biconvex genera, i.e. the Strophomeninae, Furcitellinae, and archaic murinellines, tend to have high posterior platforms. The Oepikinidae, Rafinesquinidae, Leptaeninae, Glyptomenini and Teratelasmini which have flattened, weakly biconvex or concavo-convex profiles tend to have low to slightly elevated posterior platforms. The anterior-lateral margin of the posterior platform is controlled by the shape of the adductor muscle scars. The anterior-lateral tip of the lateral ridge is curved in genera with circular or subcircular adductor muscle scars and straight among genera with subquadrate adductor muscle scars. Thus, the older oepikinids, rafinesquinids and all strophomenids have relatively straight lateral ridges and the leptaenids, advanced oepikinids and rafinesquinids have curved lateral ridges. The width (posterior to anterior) of the lateral ridges is governed by the distance between the posterior margin of the adductor muscle scars and the cardinal process. The primitive rafinesquinids and Kirkina have very wide lateral ridges, the strongly resupinate strophomenins have very narrow lateral ridges and the remaining genera have lateral ridges of intermediate width. The length of the medial ridge of the posterior platform depends upon the length of the adductor muscle scars. The medial ridge tends to bifurcate at the anterior end for emission of the breviseptum in the Oepikinidae, Murinellinae, Strophomeninae and Furcitellini. The Glyptomenini have a reduced to absent medial ridge from the posterior platform.

The interplay of all these variables prevents simple description of the changes which occur in the shape of the posterior platform in the evolving lineages of the Strophomenacea. Text-Figure 20 illustrates the characteristic shape of the posterior platform of the various lineages.

Muscle scars.- The taxonomic importance of the shape of the diductor muscle scars and pattern of the myophore ridges has been stressed by Spjeldnaes (1957) and other authors. Inasmuch as the size and shape of the diductor muscle scars are related to the muscle bounding ridges, discussed in a previous section, which in turn are related to profile, the diductor muscle scars have some taxonomic importance. Text-Figure 16 shows the shape of the diductor muscle scars of a few strophomenacean genera. An evolutionary sequence of the diductor muscle scar size and shape, except as related to evolution of profile, cannot be established. The myophore ridges of the diductor muscle scars do not seem to have any taxonomic or evolutionary importance. In general, large, flabellate diductor muscle scars are found in families with concavo-convex, not strongly geniculated valves, as the Oepikinidae and Rafinesquinidae. The groups with biconvex, weakly concavo-convex or weakly resupinate profiles, Furcitellinae, primitive rafinesquinids and most leptaenids, have incomplete muscle bounding ridges and consequently long, subparallel sided diductor muscle scars. The strongly resupinate genera of the Strophomeninae have small, rounded posteriorly confined muscle scars. The only important exceptions occur among genera of the Leptaeninae, archaic Murinellinae and archaic Oepikinidae which are not resupinate but have posteriorly confined diductor muscle scars.

Very little of taxonomic or evolutionary importance may be adduced from the size, shape and position of the adductor muscle scars. Nowhere in the Strophomenacea are the adductor muscle scars surrounded entirely by the diductor muscle scars. There tends to be a wider and more prominent adductor muscle track leading to the anterior-medial border of the diductor muscle scar in the Leptaenidae and Strophomenidae than in the Oepikinidae or Rafinesquinidae. This seems to be related simply to the larger, flabellate diductor scars of the latter two families relative to the small, posteriorly restricted diductor scars of the former two families. The adductor muscle scars in the ventral valve of a few leptaenids, _e.g._ _Megamyonia_, may be set far to the posterior, even into the delthyrial cavity. The position of the adductor muscle scars in the ventral valve of all other groups seems to be comparable relative to the apex of the valve. This means, therefore, that the adductor muscle scars are situated a relatively greater distance posterior to the anterior margin of diductor muscle scars in the Oepikinidae and Rafinesquinidae than in the Leptaenidae or Strophomenidae.

The adductor muscle scars of the dorsal valve have negligible taxonomic or evolutionary significance, also. The posterior dorsal septum of the Oepikinidae clearly divides the anterior and posterior pairs of adductor muscle scars. Genera which lack well defined posterior dorsal septa also lack clear separation of the muscle scar pairs. The anterior dorsal septa are not transmuscle septa.

The archaic oepikinids, some murinellines and all of the strophomenids tend to have subquadrate to subtriangular dorsal adductor muscle scars which commonly are split by the posterior dorsal septa. The posterior margin of these muscle scars seems generally to be straight and perpendicular to the medial ridge of the posterior platform. In the Leptaenidae and Rafinesquinidae, and to a lesser extent in the advanced Oepikinidae, there is a strong tendency for the adductor muscle scars to be subcircular.

Size.- The mean size of species does not seem to have any great taxonomic or evolutionary significance above the generic level in the Strophomenacea. There does seem to be a vague tendency in the Strophomenacea for increase of size throughout the history of the superfamily. For example, species of *Rafinesquina* and *Strophomena* of Cincinnatian age generally are larger than species of these genera of Trenton age; most species of *Oepikina* are larger than species of *Dactylogonia* or *Hesperinia*; *Leptaena rhomboidalis* Wilckens from the Devonian is larger than *L. richmondensis* Foerste or *L. ordovicica* Cooper from the Ordovician. Species of the Strophomenacea are so numerous and exceptions to this trend are so common that statistical confirmation would be most difficult to establish. Moreover, exceptions to the tendency for increased size are so numerous that size could not be useful either as an indicator of geological time or evolutionary position of a species within the superfamily.

The mean size of adult individuals is a useful feature for diagnoses of species but not for genera or families. Many genera include species of greatly differing size. For example, an adult specimen of *Rafinesquina mucronata* Foerste measures 19 mm. wide whereas an adult specimen of *R. loxorhytis* (Meek) measures 76 mm. wide, a gerontic specimen of *Strophomena parvula* Foerste is 14 mm. wide whereas an adult specimen of *S. vetusta* (James) is 46 mm. wide. Reference to size in generic or familial descriptions applies only to known species and should not bias the allocation of future discoveries.

Prosopon.- The distribution of patterns of prosopon in the strophomenacea does not seem to follow any evolutionary progression. Moreover, the patterns of prosopon show little restriction to suprageneric taxa. All attempts to base phylogeny upon pattern of prosopon have led to aggregations of species that are incompatible in internal characteristics. This is a curious situation because the fine costation, but not rugae, would seem to have the least adaptive value of all strophomenacean features. At best, some genera may be distinguished by prosopon, for example, the cymostrophioid pattern which distinguishes *Gunnarella* and the ptychoglyptoid pattern which marks *Bellimurina*. Other genera may incorporate species with dissimilar prosopon patterns, for example, the rafinesquinoid pattern of *Oepikina speciosa* Cooper and the strophomenoid pattern of *O. gregaria* Cooper.

If the many exceptions are ignored, the various families do show ill-defined differentiation by radial prosopon patterns. The earlier oepikinids are coarsely and uniformly costate (*Hesperinia*), glyptomenoid (*Dactylogonia*) or rafinesquinoid (*Kirkina*). Other oepikinids are either rafinesquinoid or strophomenoid. The murinellines are nervose (*Murinella*), coarsely and uniformly costate (*Murinella* and *Cyphomena*) or ptychoglyptoid. The Leptaeninae is all coarsely and regularly costate with a few exceptional occurrences of the rafinesquinoid pattern. The

Rafinesquinidae are all rafinesquinoid. The Glyptomenini are glyptomenoid. The Furcitellinae and *Teratelasma* are uniformly costate. *Foliomena* is smooth. The Strophomeninae includes species which are strophomenoid, rafinesquinoid or scoticoid.

The poor correlation of prosopon patterns and families is disturbing. Possibly the prosopon patterns have not been correctly defined or possibly the prosopon patterns have not been differentiated in sufficient detail.

The occurrence of rugae is not taxonomically restricted. Most genera of the Leptaeninae are rugose but rugation also occurs in species of *Oepikina*, *Rafinesquina*, *Kjaerina*, *Actinomena*, *Luhaia* and *Strophomena*. Concentric rugation seems to be correlated with strongly oblate or subrectangular shape and geniculation. Possibly these characters are somewhat interdependent. Oblique rugae, however, seem to occur on resupinate or concavo-convex species which are prolate and highly arched but not geniculate.

A kjaerinoid costa is found most commonly on early species and juvenile individuals of the Rafinesquinidae. In addition, a kjaerinoid costa occurs on some species of *Kierulfina* and *Megamyonia*. Both of these genera have some rafinesquinid characteristics. Because the costa does not occur on all species of these genera, its presence is considered to be homeomorphic and not indicative of relationship.

Meso-cardinal ridge.- The meso-cardinal ridge is a gerontic feature of strophomenaceans (Text-Figure 28). Consequently, the occurrence of this feature is not consistent among the individuals of a species. It is common to find that all of the individuals in a collection of a species will possess a meso-cardinal ridge. The larger size, thicker shells and more prominent features of gerontic individuals cause them to be more resistant to fracture and more attractive to collectors. Not all specimens of young individuals of the same species will show the meso-cardinal ridge. The meso-cardinal ridge is a more prominent feature of the Leptaenidae, Oepikinidae and Rafinesquinidae than of the Strophomenidae. This structure in the Strophomenidae is located on the medial-posterior base of the cardinal process under the chilidium. It may be observed in this family only in sections or in exceptionally preserved specimens.

Vasculae.- The vascular channels of the Strophomenacea rarely are well preserved. Specimens commonly possess ill-defined vascular markings which are too faint to permit analysis of the complete pattern. The few relatively complete patterns which have been observed seem to be saccate, inequidistributate in both valves. The lemniscate pattern figured by Williams (1956, p. 274) for the ventral valve of Strophomena cannot be supported. If the vascular pattern of Foliomena is digitate, as tentatively proposed by Williams (1965, p. H391), the genus is unique in the superfamily in respect to vasculae.

European specimens more commonly show well preserved vascular markings than specimens from North America. It is tempting when first noticed to attribute this situation to special taxonomic lineages or special environmental conditions as water temperature or quantity of available oxygen. Such is not the explanation. The European specimens commonly are preserved in the form of molds and illustrated as such. A natural mold characteristically shows a more complete vascular pattern than the complementary shell. The internal surfaces of dried specimens of terebratuloids generally show the vascular patterns as granular, brown crusts, possibly of coagulated coelomic fluid. If these crusts are brushed or scraped away, there are no vascular channels evident in the shell. Apparently, the vascular sinuses influenced the deposition of sediment adjacent to the internal surfaces of the valves of a strophomenacean shortly after its death.

HISTOLOGY

__Composition__.- The shell material of unaltered fossil articulate brachiopods is composed largely of calcium carbonate in the form of calcite. Quantitative chemical analyses and optical mineralogical analysis of articulate brachiopod shell have been presented by Clarke and Wheeler (1915, 1917) and Hobbs and Cloud (1942). Clarke and Wheeler report that modern articulate brachiopods contain from 52% to 55% CaO, 44% to 45% organic combustibles and less than 0.5% each of SiO_2, $(AlFe)_2O_3$, MgO, SO_3 and P_2O_5. Recalculation of oxide percentages to carbonate percentages with omission of the organic combustibles, by Clarke and Wheeler, reveals that the inorganic fraction of modern articulate brachiopod shells is 97% to 99% $CaCO_3$.

There are no published chemical or optical analyses of strophomenoid brachiopod shells. Mr. John Shade, Miami University, Department of Geology, has performed x-ray fluorescence analysis of __Strophomena__ __planumbona__ (Hall). Analysis was made with a chromium tube and sodium chloride analyzer crystal. Unweathered specimens of single valves of exceptional initial cleanliness were selected for analysis. The surfaces were scraped with a steel blade to remove all clay and silt particles. No preparatory reagent other than hydrogen peroxide was used to loosen clay and silt. The K_α and K_β maxima of calcium were the only strong maxima of the spectrogram. Other maxima not attributable to the tube and columnator include the $K_{\alpha 1}$, $K_{\alpha 2}$ and $K_{\beta 1}$ maxima of iron, the K_{α} maximum of strontium, questionably the K_{β} maximum of rubidium and an unidentified maximum at about 6.8° 2θ. There are no maxima to indicate the presence of silicon, phosphorus or aluminum. Magnesium and sulphur are too light to be detected conveniently by this technique.

Samples of crushed strophomenacean brachiopod shells have been examined with a petrographic microscope. The individual crystalline bodies of which the lamina of the shell are composed are too small to be resolved clearly and, consequently, are too small for positive optical identification. Hobbs and Cloud conclude that the shell material is calcite because its refractive index is within the calcite range which is less than the refractive index range of aragonite. They note, also, that cleavages of the crystalline bodies are oriented as would be expected in calcite and not as in fibrous aragonite. Hobbs and Cloud could not present conclusive optical identification because the grains they observed gave biaxial interference figures, although calcite is uniaxial. They postulate that the biaxial character of the calcite originated from strains generated in the process of grinding sections. Sass, Monroe and Gerace (1965) illustrate the crystalline bodies by electron photomicrographs of sections of the shell of *Pictothyris picta* (Dillwyn) and *Gryphus stearnsi* (Dall and Pilsbry). Sass *et al* state that the crystalline bodies are calcite but do not support their identification.

X-ray diffractograms of crushed shells of *Rafinesquina ponderosa* Ulrich and *Strophomena planumbona* (Hall) have been made by Dr. Taki Negas, The Ohio State University, Department of Mineralogy. Specimens were prepared for analysis as described above. Both diffractograms show that the only important compound in the samples is calcite. A trace of quartz is recorded in both diffractograms. No other mineral constituents are present. Compositional variation cannot be used to explain the color differentiation of the characteristically dark *Leptaena*-*Rafinesquina* group and the light *Holtedahlina*-*Strophomena* group.

Nomenclature of articulate brachiopod shell layers.- General descriptions of the microscopic structure of brachiopod shells appear in many texts, *e.g.* Shrock and Twenhofel (1953). Descriptions of microscopic structure of strophomenacean shell have been published by Kozłowski (1929), Öpik (1930), Williams (1953, 1956) and Spjeldnaes (1957). All accounts of brachiopod microstructure convey confusion by (1) the lack of uniformity of nomenclature used to designate the four layers of the brachiopod shell,

(2) oversimplification of the character and homogeneity of each of the four layers and (3) oversimplification of the differentiation of the shell layers. Variance in the nomenclature of shell layers is summarized in Table 2.

Inspection of Table 2 demonstrates the general lack of agreement for shell-layer nomenclature. Disagreement stems from variations in shell structure of different brachiopod groups studied by authors and from different methods of preparation of specimens for observation. Each of the three shell layers formed by the edge of the articulate brachiopod mantle and the "secondary deposits" formed posterior to the mantle edge are assumed to be homologous throughout the class. This assumption is made on the basis of gross microstructural similarity, relative thickness, compositional uniformity, and disposition in important macroscopic structures of each of the layers in representatives of different suborders. Lack of homology of the four shell layers of extinct suborders of articulate brachiopods would be difficult to establish because the character of secretory cells and mantle-edge grooves and lobes cannot be studied. Consequently, it is considered prudent to adopt a shell layer nomenclature related to the position of the layer within the entire shell, not to microstructure.

The nomenclature of Hobbs and Cloud (1942), Shrock and Twenhofel (1953), Williams (1953, 1956) and Spjeldnaes

Table 2.- Nomenclature of the shell layers of articulate brachiopods

AUTHOR	← EXTERNAL SURFACE OF VALVE		INTERNAL SURFACE OF VALVE →	
Shrock and Twenhofel (1953)	Periostracum	Outer carbonate layer Lamellar or Lamellate layer middle layer nonfibrous layer	Inner carbonate layer Prismatic layer fibrous layer	secondary deposits
Schuchert and Cooper (1932)	Periostracum Epidermis	outer, first, primary, nonfibrous, lamellar	fibrous	extra shell matter
Miloradovitsch (1937), <u>fide</u>, Ager and Riggs (1964)			Fibrous layer	
Hobbs and Cloud (1942)	Periostracum	Outer carbonate layer	Inner carbonate layer	
Salmon (1942)			intermediate layers	
Alexander (1948)		Outer shell layer	Prismatic layer	Inner shell layer

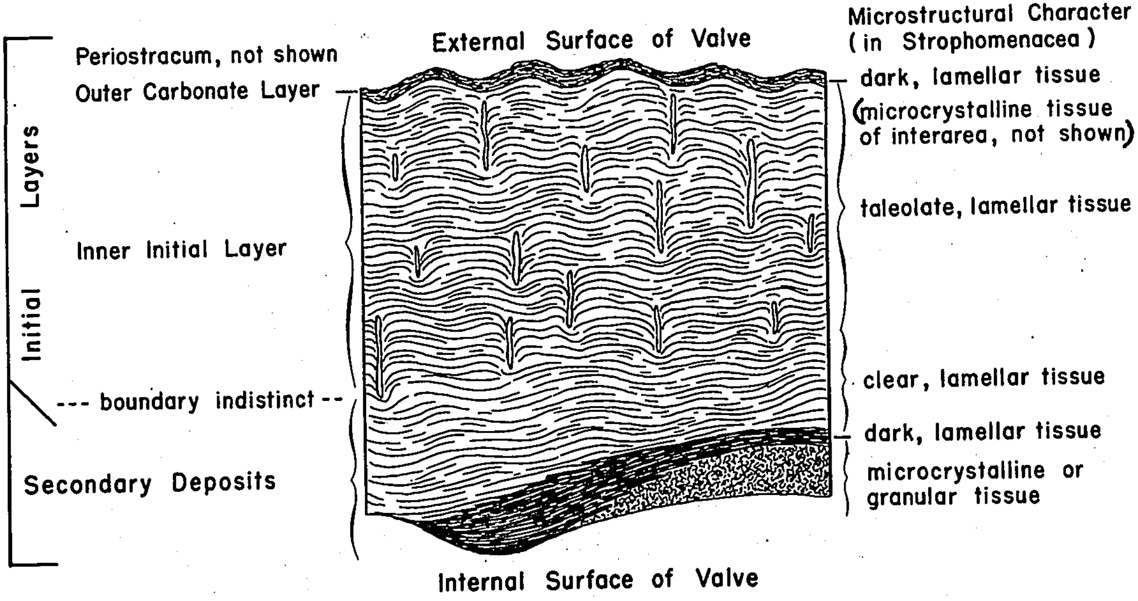
Williams (1953)	Periostracum	Outer layer	Internal layer	
		Lamellar layer nonfibrous layer	Inner fibrous layer	Impunctate fibrous material (of muscle attachment sites) Cryptocrystalline material (of tendenous patches).
Williams (1956)	Periostracum	Primary layer	Secondary layer, in part, Prismatic layer	
Vandercammen (1956-1959) *fide*, Ager and Riggs (1964)		Fibrotest	Prismotest	Callotest
Spjeldnaes (1957)		Primary layer, external layer	Secondary layer, inner layer	
Muir-Wood and Cooper (1960), Muir-Wood (1962)		Lamellar layer	Fibrous layer	granular material

Capitalization indicates author(s) used name in formal sense; other names used by author(s) in descriptive sense.

(1957) are non-structural. Shrock and Twenhofel's system is inappropriate because the "secondary deposits" are carbonate and lie on the inner surface of the "inner carbonate layer". Williams' and Spjeldnaes' classifications are not suitable because the inner-most deposits (Shrock and Twenhofel's "secondary deposits") are formed later than the adjacent "secondary layer" and because the "periostracum", "primary layer", and "secondary layer" are all primary in that they are initiated at the growing margin of the mantle. The words "primary" and "secondary", in this context, should be discarded from shell-layer terminology because of ambiguity.

An emended system of shell-layer nomenclature is illustrated in Text-Figure 23. The inner initial layer is initiated at the mantle margin but may be thickened by continued deposition posterior to the margin. The boundary between the initial layers and the secondary deposits consequently is indistinct. The general names of the shell layers in the emended system may be applied to all articulate brachiopods. Names based upon microstructural characteristics may be substituted for the general names in

<u>Text-Figure 23</u>.- A revised nomenclature for the shell layers of strophomenacean brachiopods.



Text-Figure 23.- A revised nomenclature for the shell layers of strophomenacean brachiopods.

descriptions of specific brachiopod groups. The emended shell-layer nomenclature is employed in the sections which follow.

In cases where only part of a layer is being described, the shell material will be called "tissue", as inner initial tissue and outer carbonate tissue. Zoologists have disapproved of this usage of "tissue". However, this paleontological usage is defensible on the following grounds: (1) Structural parts of a shell are called tissue by convention. (2) Shells, although not made entirely of living cells, have the function of an organ in that they provide an animal with a specific service. The structural units of a fleshy organ are tissues; the structural units of a shell should be called tissues also. (3) Shells are products of a distinct organ, in brachiopods, the mantle. Shell tissues are the product of separate mantle tissues.

Microstructure of the strophomenacean shell.- The observations to follow have been made from study of sagittal, transverse and longitudinal thin sections and peel sections of strophomenoid brachiopods. Transverse peel sections have been most informative, hence have been made in greatest number. The species which have been studied, the number of specimens sectioned and the number of sections are shown in Table 3.

Table 3.- Species Sectioned

No. of Specimens	Species	Sections	
		Thin	Peel
3	*Dactylogonia alternata* Cooper. Lenoire Lst.; Friendshipville, Virginia.		44
3	*Oepikina minnesotensis* (Winchell). Edinburgh Fm.; Rye Cove, Virginia.		66
3	*O. gregaria* Cooper. Bromide Fm.; Fittstown, Oklahoma.		68
6	*Leptaena richmondensis* Foerste. Liberty Fm.; Camden, Ohio.	5	103
1	*L. precursor* Foerste. Arnheim Fm.; Cox Creek, Bardstown, Kentucky.		24
4	*Megamyonia unicostata* (Meek and Worthen). Elkhorn Fm.; Hamburg, Indiana.		96
10	*Rafinesquina ponderosa* Ulrich. Blanchester Mem., Waynesville Fm.; Bull Run, Oxford, Ohio.	7	205
10	*Holtedahlina sulcata* (Verneuil). Whitewater Fm.; Blanchester, Ohio.	6	116

13	*Strophomena planumbona* (Hall). Base of Liberty Fm.; Tallawanda Creek at crossing of Butler and Preble Co. boundary, Ohio.	4	116
3	*S. nutans* Meek. Base of Liberty Fm.; west end of Collins Run, Oxford, Ohio.		32
4	*S. vetusta* (James). Liberty Fm.; Devil's Backbone, Camden, Ohio.		58
3	*S. planoconvexa* (Hall). Fairmount Fm.; Muddy Creek, Cheviot, Hamilton Co., Ohio.		59
2	*S. concordensis* Foerste. Arnheim Fm.; Hill's Fork, Adams Co., Ohio.		60
2	*Tetraphalerella neglecta* (James). Blanchester Mem., Waynesville Fm.; Collins Run, Oxford, Ohio.		56
5	*Thaerodonta rugosa* (Meek). Liberty Fm.; Rt. 127, 2 miles south of Camden, Ohio.		60
1	*Fardenia subplana* (Conrad). Waldron Shale; Hartsville, Indiana.		13

1	*Schuchertella sp.* Arkona Shale; Arkona, Ontario, Canada.	27
1	*Derbyia* cf. *hooserensis* Dunbar and Condra. Camp Creek Shale; Pueblo, McCullock Co., Texas.	33
5	*Stropheodonta extenuata* Imbrie. Alpena Lst.; 2 miles west of Alpena, Michigan.	79
1	*S. demissa* (Conrad). Silica Shale; Sylvania, Ohio.	20
1	*S. heteromys Imbrie*. Bell Shale; Rogers City, Michigan.	17

Periostracum.- The periostracum is a thin layer of organic material which covers the external surface of modern brachiopod shells. Williams (1956, p. 249) has observed that the periostracum "has never been found in fossils" (brachiopods). No definite periostracum has been observed in thin sections or peel sections of Ordovician strophomenaceans. The surface of specimens is rarely covered with a carbonaceous film which might be attributed to the periostracum, as occurs upon molds of associated pelecypods. Black material in grooves in the interareas of _Rafinesquina_ may be a carbonaceous residue of periostracum. Thin sections of articulated specimens, _i.e._ specimens with minimal time between death and burial, with thin bryozoan and coral incrustations were expected to show indication of periostracum between the outer carbonate layer and the incrustation. Either periostracum was absent from Ordovician strophomenaceans, exceedingly thin, or composed of an unstable organic compound not analogous to conchiolin or chitin.

Williams (1956, p. 249) and Spjeldnaes (1957, p. 14) suggest independently the presence of a periostracal "pad" or "ligament" which bridged the hinge line along the interareas of strophomenoids. Their suggestions are based upon the presence of grooves in the interareas which are parallel to the hinge line and upon the convergent attitude of lamellae in the pseudodeltidium and chilidium of strophomenoids. These features may be seen without question, and, as noted, the grooves may be filled with black, carbonaceous-appearing material. Williams (1956, p. 257) reports that the modern thecideoid Lacazella possesses a periostracal pad along the hinge line. Spjeldnaes (1957, p. 14) claims to have observed "a brownish-yellow substance in the frontal [?] part of the pseudodeltidium and chilidium" which he interprets as remains of a ligament. The outer carbonate layer of the interarea is thick, finely microcrystalline and invariably present in contrast to the thin, discontinuous, lamellar, outer carbonate layer of the rest of the external surface. The "outer carbonate layer" of the interarea is comparable in structure to the finely granular secondary deposits associated with sites of muscle attachment on the internal surfaces of the valves. In the process of making thin sections, it has been noted that the microcrystalline tissue of the interareas is less likely to flake than lamellar shell tissue. The microcrystalline tissue possibly possesses greater tensile strength. These observations plus lack of conflicting evidence direct tentative acceptance of Williams' and Spjeldnaes' hypothetical ligament.

Outer carbonate layer.- The outer carbonate layer is evident as a thin, granular, fibrous or lamellar, relatively dark layer in sections of modern articulate brachiopods and representatives of some extinct suborders (spiriferoids, pentameroids). Williams (1956, p. 250) states, "the primary layer in its typical form is also found sporadically on the shell surface of orthoids and strophomenoids." The present study confirms this observation; the presence of the outer carbonate layer on the disc of the valves is a rare occurrence.

Sections through articulated specimens with bryozoan incrustations reveal the outer carbonate layer under the bryozoan. Outer carbonate layer is not found under all incrustations. Areas of shell surface not protected by bryozoa rarely show the layer. Patches of outer carbonate layer seem to occur most commonly toward the margin of the concave valve; that is, the dorsal valve of _Rafinesquina_, the ventral valve of _Strophomena_ and _Tetraphalerella_. The protegulum of _Strophomena planumbona_ (Hall), and probably of other species, is composed of outer carbonate tissue.

The outer carbonate layer is difficult to discriminate from the inner initial layer; there is no sharply defined boundary separating the two. Both layers are lamellar in strophomenaceans. The outer carbonate layer tends to be relatively darker than the inner initial layer as observed in peel sections because the lamellae of the outer carbonate layer are consistently thinner than the lamellae of the inner initial layer and the lines separating the lamellae thicker and darker than those of the inner initial layer. The outer carbonate layer is not penetrated by taleolae. Lamellae of the outer carbonate layer tend to be concentric to the costellae of the valve surface and hence are undulatory. Near the margin of the valve, adjacent to the marginal diaphragm and outward to the edge of the valve, the lamellae of the outer carbonate layer and inner initial layer tend to be turbulent. Turbulence is caused by interference from the *vascula terminalia*, marginal thickening of the valve, and the relatively small angle between the plane of transverse section and the direction of costellae.

The valves of *Derbyia hooserensis* Dunbar and Condra, *Fardenia subplana* (Conrad) and *Schuchertella sp.* (all orthotetaceans) seem to be made entirely of outer carbonate layer in the region anterior to the muscle scar areas. *Stropheodonta heteromys* Imbrie (a stropheodontacean) has scattered patches of outer carbonate layer between costae in the central region of the valves. The entire thickness of the central region of the ventral valve of *Thaerodonta rugosa* (Meek) (a plectambonitacean) is coarsely crystalline, outer carbonate tissue.

The thickest outer carbonate layer observed on an Ordovician strophomenacean occurs on the central area of a ventral valve of *Rafinesquina ponderosa* Ulrich. The layer is approximately 0.09 mm. thick. Undulations of the layer prevent more precise measurement. The layer is slightly thinner in *Leptaena richmondensis* Foerste. and *Megamyonia unicostata* (Meek and Worthen). The thinnest observed section of outer carbonate layer, about 0.04 mm. thick, occurs in a specimen of *Strophomena planumbona* (Hall). The extra thickness, persistence and optical density of the outer carbonate layer of rafinesquinids and leptaenids may account partly for the characteristically darker color of specimens belonging to these families than specimens of oepikinids and strophomenids.

Silica preferentially replaces the inner initial layer and leaves unaltered the outer carbonate layer of *Oepikina gregaria* Cooper. The crests of costellae of *Holtedahlina sulcata* (Verneuil) seem to be outer carbonate layer as the crests lack pseudopunctae. Other species of strophomenaceans show patches of outer carbonate layer in the rugae and major varices around the margin of the valves, especially the concave valve. It is curious that even a clean, well preserved strophomenoid with finely sculptured, sharp surface detail, does not present an original surface.

A low chamber or tunnel, called here the marginal chamber, leads around the lateral and anterior periphery of the valves. This marginal chamber is formed between the marginal diaphragm and the edge of the valves. The internal surface of valves of Strophomena at the site of the marginal chamber is composed of material resembling the outer carbonate layer. A section of one specimen of Strophomena planumbona (Hall) which had an unabraded shell edge suggests that this internal peripheral coating is a continuation of the outer carbonate layer from the external surface of the valve. If this is true, it means that the mantle of Strophomena was retractile and that dark laminae in the inner initial layer are outer carbonate layer.

Williams (1953, p. 3) has stated that the outer carbonate layer is found upon stropheodontid interareas and is the material of which the pseudodeltidium and chilidium are composed. His observation applies equally to Ordovician strophomenaceans.

The surface layer of strophomenacean palintropes, the pseudodeltidium, and the chilidium, corresponds to outer carbonate layer in position only. The "outer carbonate layer" of these structures overlies inner initial tissue and is not penetrated by taleolae. The "outer carbonate layer" of the palintrope is thick in comparison to the layer observed on the disc of the valves. The layer is microcrystalline, not finely lamellar. These latter characteristics and lack of evidence of continuity between the outer carbonate layer of the disc and the palintrope suggest that the "outer carbonate layer" of the two regions may not be homologous. Sections of some specimens of Strophomena reveal a finely lamellar, non-taleolate layer under the microcrystalline "outer carbonate layer" of the palintrope. This finely lamellar layer is sharply differentiated from the microcrystalline layer but merges without a well defined boundary into the underlying inner initial tissue. From a microstructural standpoint, this finely lamellar layer is probably the homologue of the outer carbonate layer of the disc of the valves.

The microcrystalline "outer carbonate layer" of the palintrope extends over the length and width of the interarea. Sections parallel to the medial sagittal section (plane of symmetry) but lateral to the teeth and sockets show the cross sectional shape of the microcrystalline layer (Text-Figure 24, section D). The microcrystalline layer

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Text-Figure 24.- Parallel sagittal sections through the posterior region of Strophomena planumbona (Hall). Outline drawings below, dorsal valve left and ventral valve right, show the course of the sections. Section A does not pass through the apex of the valves but includes the medial side of a cardinal process lobe. The margin of the chilidium of Section B rests against the posterior edge of a cardinal process lobe, leaving a pocket, the notothyrial cavity (open area). The base of the chilidium of Section B is bulbous and convoluted. A small piece of the denticular plate occurs above the umbonal cavity of Section B. The "fold" in Section B marks the posterior margin of the pseudodeltidium. Specimen from Liberty Formation, Camden, Ohio. Magnification of sections, X9.5.

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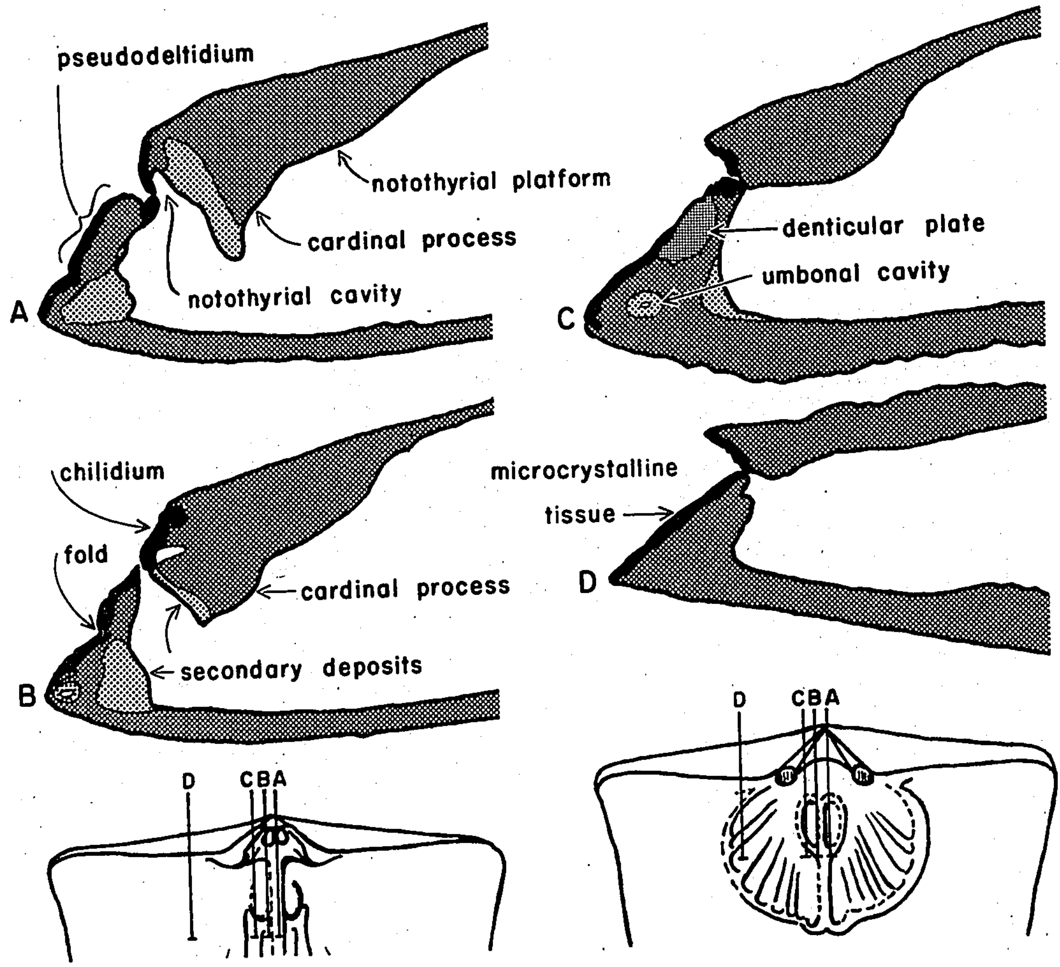
of the ventral palintrope of *Leptaena richmondensis* Foerste is obtusely triangular in section. The hypotenuse is the interarea; the longer of the two adjacent sides is sutured in an intertonguing fashion to the inner initial layer of the palintrope; the shortest side forms the internal margin of the palintrope. The microcrystalline layer of the dorsal palintrope is a flattened sheet in sectional shape. Microcrystalline tissue forms a parallel-sided layer upon the surface of both interareas of *Rafinesquina ponderosa* Ulrich, *Strophomena planumbona* (Hall) and *Strophomena nutans* Meek. The microcrystalline layer may be joined to the inner initial tissue of the palintrope by a convoluted suture.

External grooves of the palintrope appear as notches in sagittal sections of the microcrystalline layer. Faint



Text-Figure 24.- Parallel sagittal sections through the posterior region of Strophomena planumbona (Hall). Outline drawings below, dorsal valve left and ventral valve right, show the course of the sections. Section A does not pass through the apex of the valves but includes the medial side of a cardinal process lobe. The margin of the chilidium of Section B rests against the posterior edge of a cardinal process lobe, leaving a pocket, the notothyrial cavity (open area). The base of the chilidium of Section B is bulbous and convoluted. A small piece of the denticular plate occurs above the umbonal cavity of Section B. The "fold" in Section B marks the posterior margin of the pseudodeltidium. Specimen from Liberty Formation, Camden, Ohio. Magnification of sections, X9.5.

variations in the optical density of the microcrystalline tissue correlate with the grooves. These bands are too poorly defined and too faint to be called lamellae. The bands are visible only in sagittal sections.

The microcrystalline tissue of the pseudodeltidium and chilidium is more coarsely crystalline than the microcrystalline tissue of the palintrope. The microcrystalline tissue of the pseudodeltidium and chilidium is obscurely lamellar in sagittal section; the lamellae are thicker and less distinct than lamellae of the inner initial layer. The lamellae correspond to the imbricated rugae on the surface of the pseudodeltidium and chilidium. The medial sagittal groove of the external surface of the pseudodeltidium and chilidium has no microstructural expression. There is no evidence to indicate that the pseudodeltidium originates phylogenetically or ontogenetically from a pair of deltidial plates. The microcrystalline tissue of the pseudodeltidium and chilidium overlies inner initial tissue of the apex of the valves and secondary deposits of the delthyrial and notothyrial cavities.

The pseudodeltidium is irregular to slightly triangular in sagittal section, Text-Figure 24, sections A and B. The boundary between microcrystalline tissue of the pseudodeltidium and inner initial tissue is difficult to detect but appears to be an irregular, intertonguing suture. The center of the dorsal margin of the pseudodeltidium of Strophomena planumbona (Hall), Text-Figure 24, section A, and some other species, e.g. S. auburnensis Fenton, bears a dorsally concave plate which is directed anteriorly into the delthyrial cavity. This concave plate appears to be a receptacle into which was fit the ventral margin of the chilidium when the valves were opened. This concave plate has the same microstructure as the microcrystalline tissue of the pseudodeltidium.

The chilidium resembles the pseudodeltidium in microstructure. Chilidia have the form of thin, flattened sheets obscurely sutured into the inner initial tissue of the dorsal apex. The dorsal surface of the chilidium is not supported by inner initial tissue in central sagittal sections. The cavity beneath the central region of the chilidium is the notothyrial cavity. Inner initial tissue forms a backing to the microcrystalline tissue of the chilidia in lateral sagittal sections. Also, the chilidium may rest upon secondary deposits of the posterior surfaces of the cardinal process lobes. The base of the chilidium tends to be bulbous and convoluted, that is, thicker than the unsupported ventral edge. This indicates that the chilidium became thinner as growth proceeded.

The microcrystalline tissue of the pseudodeltidium and chilidium is a continuation of the microcrystalline, "outer carbonate layer" of the palintrope. This may be demonstrated only in transverse or longitudinal sections of perfectly preserved specimens.

The microcrystalline "outer carbonate layer" of the palintrope along the lateral margins of the pseudodeltidium is exceedingly thin. At this position, the microcrystalline layer passes over the denticular plate of the teeth. The conical or cuneate denticular plate is ankylosed to the medial, dorsal margin of the dental lamella. The dorsal surface of the denticular plate tends to be arched slightly. Consequently, the microcrystalline tissue overlying the denticular plate is slightly arched or reduced in thickness. At this position, the microcrystalline tissue is commonly missing, *e.g.* on *Strophomena planumbona* (Hall), and permits the ridged denticular plate to be seen as a part of the surface of the interarea. As a consequence, not all transverse sections show continuity of the pseudodeltidium and the microcrystalline layer of the palintrope.

The form of the microcrystalline layer of the palintrope in the region marginal to the pseudodeltidium is complex, as shown in Text-Figure 25. Evidence of the

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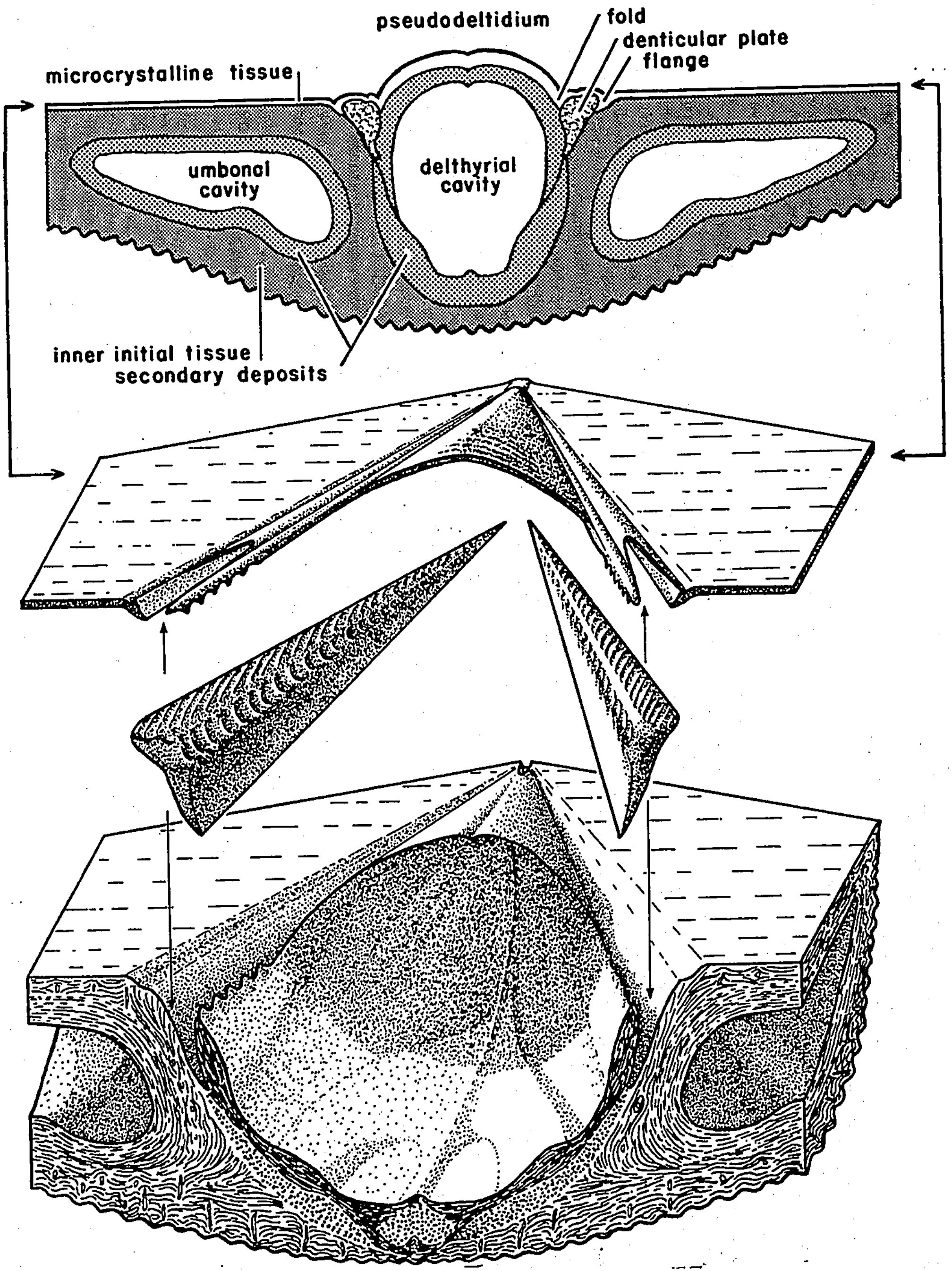
Text-Figure 25.- Transverse section and exploded block diagram of the posterior-medial region of the ventral valve of an idealized strophomenacean brachiopod. Parts of the diagram are, from top to bottom: idealized transverse section, microcrystalline layer of palintrope and pseudodeltidium, two denticular plates, the remaining inner initial tissue and secondary deposits of the posterior-medial region.

morphology about to be described has been found in all of the Ordovician strophomenaceans that have been sectioned. Tissue differentiation is sufficiently obscure that the following description of the morphology of the microcrystalline layer cannot be followed in any single set of transverse serial sections.

The base of the microcrystalline layer of the palintrope lateral to the denticular plate gives rise to a ridge or flange. This flange penetrates into the boundary between the lateral face of the denticular plate and its supporting dental lamella. The flange tends to be a curved triangle in cross section in specimens of _Oepikina_, _Rafinesquina_, _Kiaeromena_, _Strophomena_ and _Tetraphalerella_. _Tetraphalerella_ possesses the largest and most sharply defined flange of the genera mentioned. _Holtedahlina sulcata_ possesses a thickening in the ventral (fixed) surface of the microcrystalline layer which is less regular, shorter and wider than the flange of other species.

The flange does not occur along the entire anterior to posterior margin of the denticular plate. The flange,

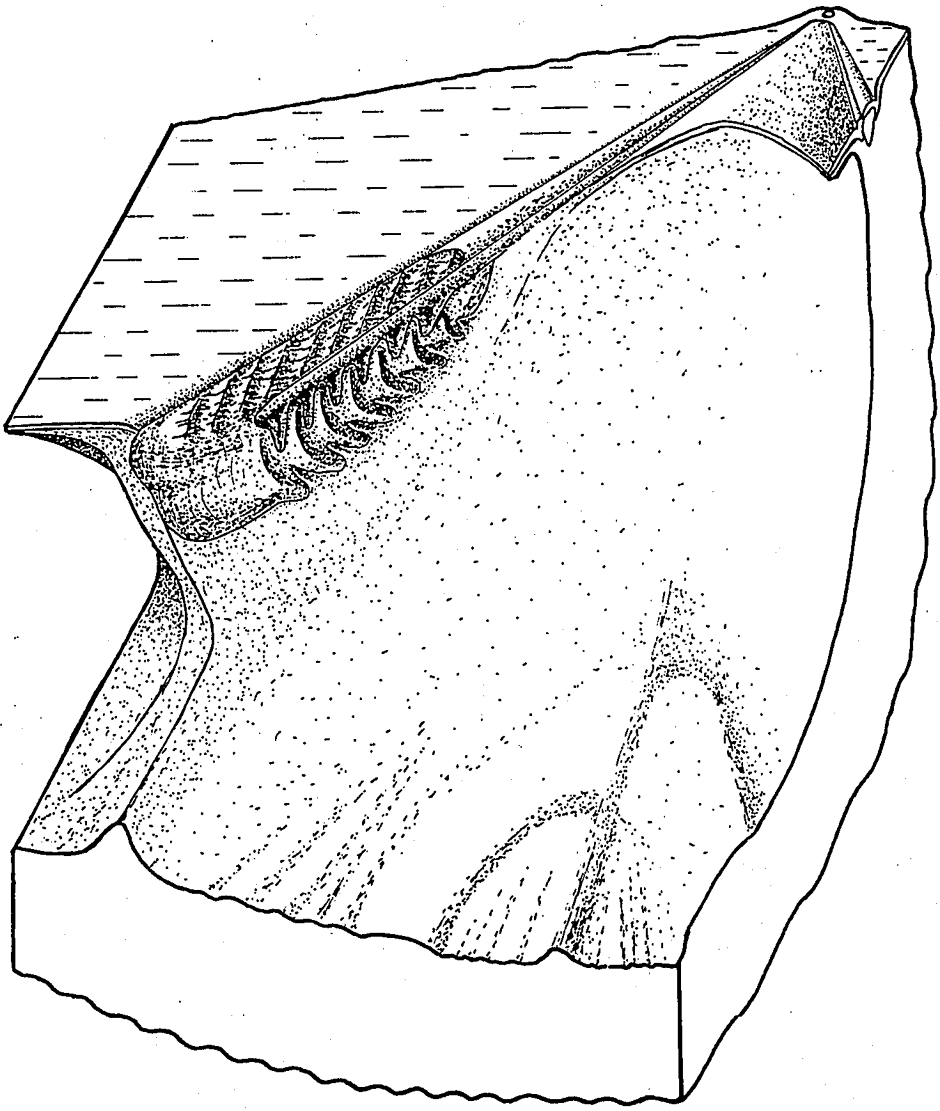


Text-Figure 25.- Transverse section and exploded block diagram of the posterior-medial region of the ventral valve of an idealized strophomenacean brachiopod.

also, is absent along the lateral margin of the denticular plate to the anterior of the free edge (anterior edge) of the palintrope. The denticular plate is not apparent in sections less than approximately 0.8 mm. from the apex of the valve. Between the posterior end of the denticular plate and the apex of the valve, the flange, if actually present, merges with the microcrystalline tissue of the palintrope and pseudodeltidium.

A shallow groove may be found on the interarea above the flange of microcrystalline tissue, as shown in Text-Figure 26. The groove seems to be caused by folding of the microcrystalline layer downward between the denticular plate and the dental lamella. A groove has been observed in specimens of _Rafinesquina ponderosa_ Ulrich, _Rafinesquina loxorhytis_ (Meek), _Oepikina speciosa_ Cooper, _Rhipidomena tennesseensis_ (Willard), _Dactylogonia sculpturata_ Cooper, _Dactylogonia alternata_ Cooper and _Stropho-_

Text-Figure 26.- The tooth, pseudodeltidium and adjacent structures of an idealized strophomenacean brachiopod. The dorsal and medial surfaces of the tooth are ridged by semidenticles. Microcrystalline and secondary tissues lap into the depressions between the semidenticles on the medial face of the tooth.



Text-Figure 26.- The tooth, pseudodeltidium and adjacent structures of an idealized strophomenacean brachiopod. The dorsal and medial surfaces of the tooth are ridged by semidenticles. Microcrystalline and secondary tissues lap into the depressions between the semidenticles on the medial face of the tooth.

mena grandimusculosa Cooper. Observation of a groove in so many species suggests that the flange is a persistent feature of Ordovician strophomenaceans, though poorly developed in some species. Extension of the groove to the apex of the valve suggests that the flange does extend posterior to the extremity of the denticular plate.

As noted, the microcrystalline layer of the palintrope may be arched over the denticular plate. Along the medial-dorsal edge of the denticular plate, the microcrystalline layer may project a short distance downward (ventrally) into tissue on the side of the delthyrial cavity. The microcrystalline layer folds back upon itself, returns to the surface where it arches over to form the pseudodeltidium, as shown in Text-Figures 25 and 26. The isoclinal folding of the microcrystalline layer along the margin of the pseudodeltidium produces an optical effect in some peel sections in which there appears to be a sharply defined boundary between the pseudodeltidium and the microcrystalline layer of the palintrope. Hasty inspection of such sections may lead to the false conclusion that the microcrystalline layer of the palintrope and the pseudodeltidium are separate structures.

The boundary between the pseudodeltidium and palintrope commonly is marked by a shallow groove where the microcrystalline tissue is depressed down into the fold along the medial-dorsal edge of the denticular plate.

Less commonly, a narrow ridge is the external expression of the fold. The latter condition is observed on species of Rafinesquina. The fold may be traced along the medial-dorsal edge of the denticular plate beyond the anterior margin (free margin) of the pseudodeltidium. The fold anterior to the free margin of the pseudodeltidium is set onto a chamfer along the medial-dorsal edge of the denticular plate. In this position, the fold has the form of a ridge along the edge of the denticular plate. This anterior extension of the fold continues as a ridge almost to the anterior end of the tooth, as shown in Text-Figure 26.

The ridge of microcrystalline tissue along the chamfered edge of the denticular plate overhangs the delthyrial cavity further than any other part of the tooth. The ridge occupies the undercut cavity of the sockets. This ridge acts as the pin of a hinge to positively lock the valves together. The ridged or semidenticulate dorsal-anterior and medial faces of the denticular plate are the bearing surfaces of the tooth which are in actual contact with the socket. The microcrystalline ridge along the dorsal-medial edge of the denticular plate has no bearing function. Scallops from the margin of the microcrystalline ridge may lie in the depressions between the semidenticles of the denticular plate, as shown in Text-

Figure 26.

The region of the interarea of Ordovician strophomenaceans which overlies the denticular plate is not homologous to the perideltidial area of orthotetaceans. The region is not as evident as the perideltidial area of orthotetids; it is topographically less distinct, narrower and not distinguished by features of prosopon. Sections of Derbyia hooserensis Dunbar and Condra show that the perideltidial area overlies the entire dental lamella and tooth-plate assembly and that the perideltidial area is simply a region of thinner microcrystalline tissue than that which covers the rest of the palintrope. The tooth-plate of Derbyia is taleolate, but denticles are not present along its surface. Consequently, this structure cannot be called a denticular plate. The denticular plates of strophomenaceans and the tooth-plate of orthotetaceans are similar in other respects and are probably homologous structures.

The chilidium is a continuation of the microcrystalline tissue of the palintrope. The chilidium is not backed by secondary deposit except at its base. For this reason, the chilidium is less resistant to mechanical abrasion and fracture than the pseudodeltidium.

Observation of the chilidia of entire specimens of many species of Ordovician strophomenaceans leads to an ambiguous opinion of the histological affinity of the chilidium. The chilidium of some specimens arises from a sheet which is attached to the inner margin of the sockets. Other specimens show unmistakable continuity of tissue from the interarea to the chilidium posterior to the sockets. Still other specimens possess a low ridge or groove along the margin of the chilidium posterior to the sockets which separate the chilidium from the interarea.

Serial transverse peel-sections permit a unified explanation for the conflicting observations. The socket is basically a groove in the inner initial tissue. A concave socket plate stretches across the floor and the medial margin of the socket, Text-Figure 27. Flanges of microcrystalline tissue of the palintrope are inserted into the suture along the lateral and medial margins of

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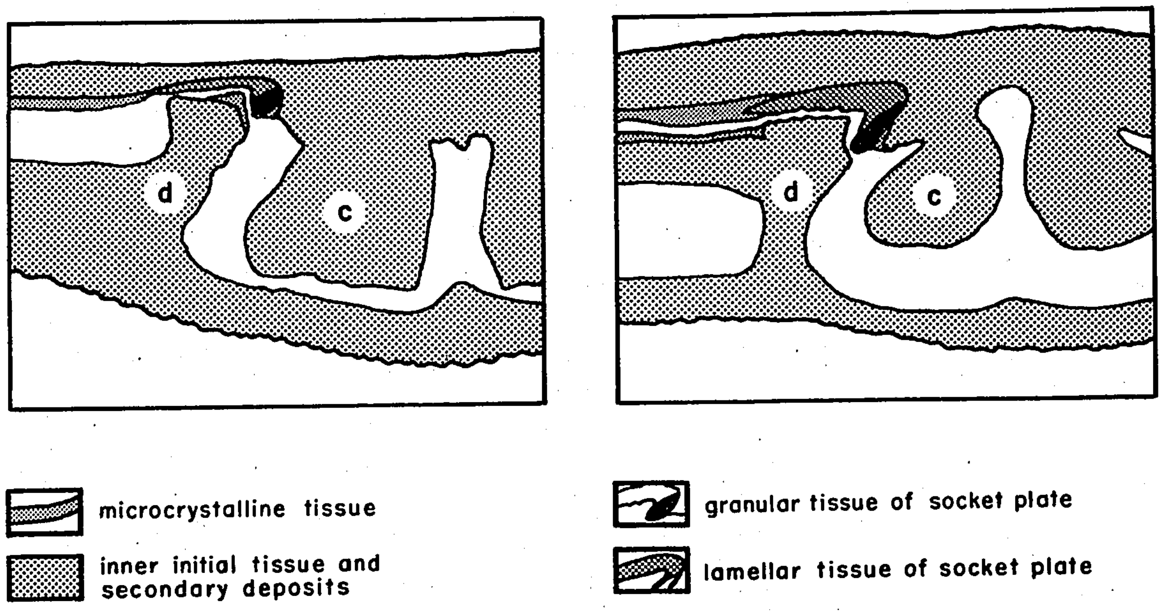
Text-Figure 27.- Transverse sections through the tooth and socket of *Rafinesquina ponderosa* Ulrich (left) and *Strophomena planumbona* (Hall) (right) to show the structure of the socket plate. Inner initial tissue, secondary deposits, and denticular plate tissue are not differentiated. c - cardinal process, d - dental lamella and denticular plate.



Text-Figure 27.- Transverse sections through the tooth and socket of *Rafinesquina ponderosa* Ulrich (left) and *Strophomena planumbona* (Hall) (right) to show the structure of the socket plate. Inner initial tissue, secondary deposits, and denticular plate tissue are not differentiated. c - cardinal process, d - dental lamella and denticular plate.

the socket plate. The socket plate is covered by microcrystalline tissue posterior to the area where the socket is functional. Hence, the anterior margin of the chilidium nearest the sockets does arise from tissue of the medial margin of the sockets; the posterior apex of the chilidium does arise from microcrystalline tissue of the palintrope. The ridge or groove in the interarea along the margin of the chilidium posterior to the sockets marks the position of the microcrystalline tissue which fills in the posterior extremity of the socket. Microcrystalline tissue may extend from the medial margin of the sockets to the lateral bases of the cardinal process lobes.

The pedicle tube or collar of the juvenile Rafinesquina and Strophomena is found imbedded in inner initial tissue in the apex of the ventral valve of adult specimens. The pedicle tube is microstructurally identical to the pseudodeltidium. The thin, juvenile foramen of these genera is blocked with coarsely crystalline calcite which may be secondary.

The apex of the conical notothyrial cavity beneath the chilidium is formed entirely in inner initial tissue. The chilidium may be unusually thin at the apex of the notothyrial cavity. Where observed, this thin point lies just ventral to the basal bulb of the chilidium. In specimens of an undescribed species of Rafinesquina from the Cynthiana Formation of Kentucky, this thin point in the childium is an open foramen, probably secondarily opened by abrasion, weathering and preparation. These observations support Spjeldnaes' (1957, p. 51) contention of a juvenile dorsal foramen of unknown function. The basal bulb of the chilidium represents a dorsal pad associated with the dorsal foramen in the juvenile. No microcrystalline tissue is incorporated into the inner initial tissue of the dorsal apex, that is, no inwardly directed tube or collar was associated with the dorsal foramen. The dorsal foramen was not functional in adults. The inner initial tissue which internally closes the dorsal foramen is a later deposit. The dorsal foramen has not been found in transverse sections through the chilidium.

The medial sagittal grooves in the pseudodeltidium and chilidium possibly originate from folding of these structures into the dorsal and ventral foramina in a juvenile stage. The groove of the chilidium may rest upon the posterior edge of the meso-cardinal ridge between the cardinal process lobes. As a consequence, the medial groove of the chilidium may simply be attributed to draping of the chilidium into the cleft between the lobes. There is no microstructural discontinuity across the groove of the pseudodeltidium, nor does the groove provide any support to the pseudodeltidium.

Inner initial layer.- Most of the shell of strophomenoid brachiopods is composed of the inner initial layer. The external surface of the disc of the valves generally is formed in inner initial tissue; all of the important structures of the internal surface of the valves are composed of inner initial tissue or have their origin in inner initial tissue. The inner initial layer is composed of coarse and fine lamellae penetrated by pseudopunctae and taleolae. The lamellae are oriented obliquely at a low angle to the surface of the valves. If a lamella is traced in a sagittal section, the posterior edge of the lamella is nearest the external surface of the valve, the anterior edge is nearest the internal surface of the valve. Viewed in transverse section, the severed ends of lamellae are lenticular, curved or wavey and roughly concentric to the surfaces of the valve. Hobbs and Cloud (1942, p. 24) describe this aspect of the lamellae as having "the appearance of 'cut and fill structure' in stream sands."

The inner initial layer of strophomenaceans is not composed of flattened, elongated fibers, as Hobbs and Cloud (1942) and others have described for other groups of brachiopods. The lamellae are sheet-like or fan-like in form, that is, the lamellae are too broad to be called fibers. Contrary to the observations of Blockman (1908), Jackson (1912, 1918) and Leidhold (1922), reported in Hobbs and Cloud (1942, p. 24), details of the size, thickness, number and inclination of the lamellae seem to have little taxonomic significance in reference to Ordovician strophomenaceans. The only characters of potential taxonomic significance ascribable to lamellae are the color and sheen of the valves. The dark gray color common to many Rafinesquina, Leptaena and their allies has been tentatively related to the outer carbonate layer of these forms. It is possible, also, that the dark color is caused by the thicker, more translucent, and more steeply inclined fine lamellae possessed by these genera relative to the lamellae of Oepikina, Furcitella and Strophomena which are light colored. The nacreous sheen of some species of the Furcitellini and Glyptomenini, e.g. Mjoesina higginsportensis (Foerste) (formerly Strophomena higginsportensis Foerste), approaches the sheen of the Devonian stropheodontacean Pholidostrophia. The fine lamellae of Mjoesina and Holtedahlina are extremely thin and lie nearly parallel to the external surface of the valves.

The external surfaces of strophomenoid brachiopods do not possess true varices inasmuch as the external surfaces are formed of inner initial tissue. The "varices", properly fila, that are observed are molds of the actual varices of the outer carbonate layer or the truncated edges of the lamellae of the inner initial tissue. These two types of fila may be difficult to differentiate on eroded or abraded specimens. Molds of the true varices generally cross costae without deflection; laminae are deflected as they cross the costa in the manner of truncated plunging anticlines and synclines.

The coarse lamellae vary in number from 5 to 20 across the thickness of a valve. They appear as alternately darker and lighter bands across the shell's thickness. They vary in number in different regions of one valve; they differ in number in the same region of two valves of one species. The coarse lamellae are observed in both thin sections and peel sections. Peel sections do not show large quantities of opaque grains in the darker, coarse lamellae. Consequently, the coarse lamellae are caused probably by preferred orientations of the submicroscopic crystalline bodies of which the valves are constructed. Williams (1956, p. 249) has provided a possible explanation for the coarse lamellae in his discussion of the growth of <u>Mucrospirifer</u> (Devonian), where he notes that "the lamellae ... were built up by slight shifts in the direction of growth ... of the mantle edge ....." Shifting of the direction of growth would cause changes of the preferred crystallographic orientation of the submicroscopic grains of which the lamellae are composed. This could cause different gray-values of adjacent coarse lamellae. The coarse lamellae resemble and are to be compared optically to the banding of moiré silk.

Each coarse lamella is composed of many fine lamellae. The fine lamellae are so thin that they may be clearly resolved only at magnifications of X50 and greater. The fine lamellae in a transverse section near the center of a dorsal valve of <u>Rafinesquina</u> <u>ponderosa</u> Ulrich number about 285 per mm. The fine lamellae are alternating bands of thin, dark material and thicker, clear calcite. The thin, dark bands contain opaque or darkly colored bodies which are too small to identify. Williams (1956, p. 249) contends that these darker bands are composed of chitin, <u>i.e.</u> periostracum, incorporated onto the surface of each lamella at the time of its secretion at the margin of the mantle. As noted previously, the dark lamellae may be outer carbonate tissue.

The inner initial layer grew in thickness throughout the life of the strophomenacean. Very young strophomenoids lack most internal structures except the cardinal process, teeth and sockets. Valves of very young strophomenoids apparently lack the inner initial layer. Large, gerontic specimens possess valves which are much thicker and which have more accentuated internal features than smaller ephebic specimens. Thus, the inner initial layer is initial only at its base. No means have been discovered for differentiating original from secondary "inner initial tissue" in those regions where the entire layer is penetrated by pseudopunctae.

Selected regions, for example, most of the material of the cardinal process lobes, do not possess pseudopunctae and are considered to be constructed of secondary tissue. Otherwise, the microstructure of these regions resembles inner initial tissue. The cardinal process lobes of all strophomenaceans develop from thin, vertical blades in the juvenile. The several types of adult cardinal processes are all secondary modifications. The dorsal septa of Oepikina, Dactylogonia and Strophomena develop from ridges of the inner initial layer. The dorsal septa may be modified and heightened by secondary deposits. Some, but not all, sections show a distinct dark line or fracture situated under the diductor muscle scars. This dark line is parallel to laminae and may differentiate original and secondary inner initial tissue in the ventral valve.

The marginal diaphragm is composed of inner initial tissue penetrated throughout its entire thickness by prominent pseudopunctae. The fine lamellae of the marginal diaphragm are thicker than elsewhere in the valves.

The fine lamellae of the marginal diaphragm and the diductor muscle bounding ridges tend to be turbulent. The marginal diaphragm and muscle bounding ridges differ in that the fine lamellae terminate on the anterior and lateral surfaces of the marginal diaphragm and upon the posterior and medial facing surfaces of the muscle ridges.

The denticular plate of the tooth is composed of turbulent inner initial tissue with coarse, tabular pseudopunctae. The suture between the denticular plate and the microcrystalline layer of the palintrope is unmistakable. Large, tabular pseudopunctae which project from the dorsal surface of the denticular plate may penetrate as pegs into the microcrystalline tissue. A suture separates the denticular plate from the dental lamella. The suture may be obscured in sections because both structures are composed of lamellar tissue and the suture is deeply crenulated. Crenulations of the suture between the denticular plate and dental lamella have a dorsal-ventral direction. Thus, the crenulations are seen in longitudinal sections only. The suture between the inner initial layer and microcrystalline layer of the palintrope lateral to the denticular plate may be crenulated, also. These crenulations cause the parallel, anterior to posterior grooves of the interareas. The microcrystalline flange lateral to the denticular plate, discontinuity of lamellae between the denticular plate and the dental lamella and differences of color and texture of the denticular plate in whole specimens of the ventral valve indicate that the denticular plate is a separate part.

The dental lamellae are continuous with the inner initial tissue of the floor of the valves and with the palintrope. No suture is evident at either junction. The fine lamellae of the inner initial tissue may be sharply flexed but not discontinuous at these two positions. The sharp flexure of the lamellae produces in transverse sections a line along the axis of the flexure as may be seen on the edge of a sharply folded magazine or booklet. This line in the flexure may be misinterpreted as suture. Similar lines of flexure may be found at the cardinal extremities, where the inner initial tissue of the palintrope and floor of the valve meets, and under the lateral margins of the cardinal process lobes.

The socket is a groove in the inner initial tissue occupied by the compound socket plate. The socket plate is less distinctly delineated than the denticular plate. Some sections of a specimen may show a socket plate while adjacent sections may not. Thus, the reality of a socket plate is not positively confirmed.

The socket plate seems to be composed of a granular blade or rod along the medial margin of the socket, and a concave plate of dark, finely lamellar, coarsely pseudopunctate tissue on the floor of the socket, as shown in Text-Figure 27. Lamellae of the concave plate may be either smooth or turbulent. Spjeldnaes (1957, text-figure 3) calls only the granular blade the socket plate. As both pieces of the assembly are set apart from the inner initial tissue by a suture and the margins of the assembly are underlain by flanges of microcrystalline tissue of the palintrope, the granular blades and concave plate together constitute a compound socket plate.

The coarse pseudopunctae of the concave plate form endospines which mesh with the semidenticles of the dorsal surface of the denticular plate. The granular blade or rod is scalloped along the medial-ventral margin of the socket. The scallops, which do not seem to be formed by pseudopunctae, mesh with the ridges of the medial face of the denticular plate. The socket plate is thicker and better delineated in resupinate strophomenaceans, e.g. Strophomena, than in concavo-convex forms, e.g. Rafinesquina, Kiaeromena and Oepikina. In the latter forms, the concave plate is thin and the granular blade is a terete rod. The principal articulatory contact of concavo-convex species lies between the granular rod of the socket and the medial face of the denticular plate. The major articulatory contact of resupinate species is between the dorsal surface of the denticular plate and the floor of the socket. This may explain why the largest ridges of denticular plates are on the dorsal surface in resupinate forms and the medial surface in concavo-convex forms; why the denticular plate is exposed commonly on the interarea of resupinate forms but exposed rarely on the interarea of concavo-convex forms; and why the sockets of resupinate forms are wider than the sockets of concavo-convex forms.

The edges of the compound socket plate are underlain by flanges of microcrystalline tissue of the palintrope. In this respect, the socket plate and denticular plate have a similar relationship to the microcrystalline layer. Transverse sections through the sockets of the orthoid brachiopods, Plaesiomys subquadrata (Hall) and Hebertella sinuata (Hall) show structures comparable to the structures of the sockets of strophomenaceans. The bases of the brachiophores are granular rods inserted along the medial margins of the sockets. The floor of the socket is underlain by a concave lamellar plate, a recumbent fulcral plate. Possibly the strophomenacean socket buttress is a homologue of the orthoid brachiophore. Öpik (1933) has advocated this conclusion with respect to the plectambonitaceans.

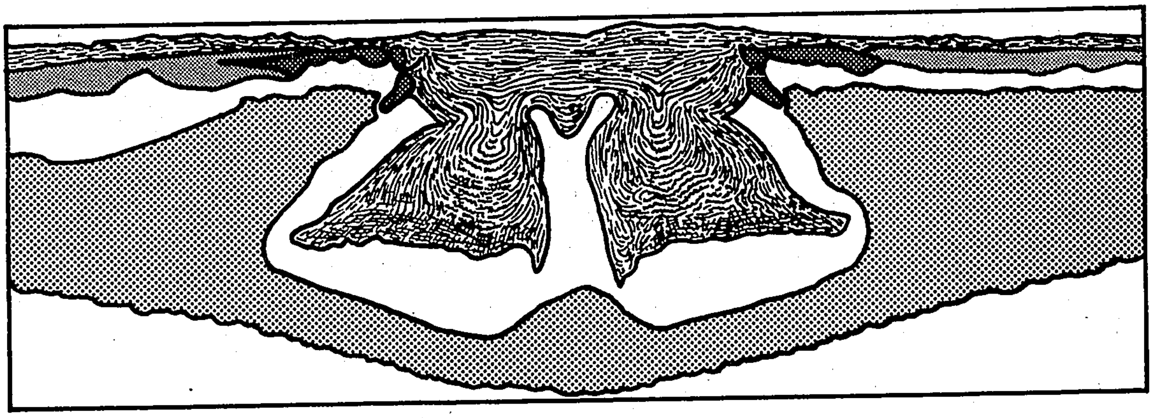
Secondary deposits.- Secondary deposits within strophomenacean brachiopods are concentrated toward the central-posterior region of the valves. Secondary deposits are associated with the following structures: the muscle bounding ridges, the medial and lateral dorsal ridges, the surface of the muscle scar areas, the posterior platform, the cardinal process lobes and meso-cardinal ridge, the lateral umbonal cavities and the delthyrial and notothyrial cavities. Secondary deposits are constructed of three distinct tissues which are morphologically segregated and which may have served different functions.

The first variety of secondary tissue resembles inner initial tissue except that pseudopunctae are rare to absent. This variety of secondary deposit is quite translucent in peel sections. It possesses fine laminae which may be continuations of the laminae of the inner initial layer. The second variety of secondary tissue has a microcrystalline structure. This type of tissue incorrectly has been called cryptocrystalline. The grains may be clearly resolved at X50 magnification and, thus, are larger than the grains of the microcrystalline tissue of the palintrope. The result is that the microcrystalline secondary deposits are more translucent than the microcrystalline layer of the palintrope. The microcrystalline secondary tissue is associated mainly with sites of muscle attachment. The third variety of secondary tissue resembles the outer carbonate layer of the disc of the valves. This tissue is formed of very thin lamellae with thick, dark boundaries. The tissue appears darker and denser than inner initial tissue or secondary lamellar tissue in peel sections. This dark lamellar secondary tissue is not pseudopunctate. This dark tissue is associated mainly with the muscle scar regions of the valves.

The relatively clear, lamellar secondary deposits are found in association with the muscle bounding ridges, the posterior platform, the cardinal process lobes, the lateral umbonal cavities and the delthyrial and notothyrial cavities. The lamellar secondary tissue is rarely pseudopunctate in the muscle bounding ridges, never pseudopunctate in other regions. In the muscle bounding ridges, the lamellae curve into the ridges such that the free ends of the lamellae are exposed on the posteriorly and medially directed surfaces of the ridges. This condition causes the muscle bounding ridges of transverse sections to resemble a breaking wave.

The laminae are parallel to the surfaces of the umbonal cavities in transverse sections so that the umbonal cavities appear as sets of concentric triangles. The ventral surface of the umbonal cavities may be interrupted by posterior extensions of the marginal diaphragm. These swellings of secondary tissue tend to divide each lateral umbonal cavity into two chambers. The internal surfaces of the pseudodeltidium and chilidium and the medially directed surfaces of the dental lamellae are coated with lamellar secondary tissue. The lamellae of the tissue are parallel to the internal surface of the inner initial layer or microcrystalline layer. Transverse sections through the delthyrial cavity and pseudodeltidium reveal the lamellae of the secondary tissue as a set of concentric circles or ovals. The pedicle conduit of *Leptaena richmondensis* Foerste lies in the center of the concentric lamellae. The pedicle conduit itself appears to be a thin microcrystalline tube. The pedicle conduit of species of strophomenaceans without a functional pedicle in adulthood, including species of *Oepikina*, *Rafinesquina*, *Strophomena* and *Tetraphalerella*, is a microcrystalline tube with a coarsely crystalline plug of secondary tissue.

The posterior platform, the cardinal process lobes and the meso-cardinal ridge are constructed of clear lamellar secondary tissue. These lie upon a gently swollen area of inner initial tissue in the posterior central region of the dorsal valve. There is a low swelling of inner initial tissue under each cardinal process lobe. The swellings do not have the shape, the angularity or the topographic relief of the cardinal process lobes as shown in Text-Figure 28.



Text-Figure 28.- The microstructure of the cardinal process lobes and meso-cardinal ridge of Rafinesquina ponderosa Ulrich. The configuration of the lamellae of the secondary tissue of the cardinal process lobes and meso-cardinal ridge suggests that the meso-cardinal ridge develops later in ontogeny than do the lobes. Other tissues of the dorsal valve include the cancellus tissue of the myophores of the cardinal process lobes (cross-hatched), the socket plates (coarse stipple) and the microcrystalline layer of the palintrope (fine stipple). The ventral valve is shown for reference only; its tissues are not differentiated. Magnification about X8.5.

The tissue of the posterior platform, cardinal process lobes and meso-cardinal ridge, viewed in peel section, is the clearest encountered anywhere in the brachiopod. The fine lamellae are thicker than usual and the dark planes separating the fine lamellae are very thin. There are no pseudopunctae in the secondary tissue of the notothyrial platform or cardinal process lobes. Nevertheless, there is no distinct line of demarkation between the inner initial tissue and these structures.

The posterior surfaces of the cardinal process lobes are the sites of insertion of the diductor muscles. These myophore surfaces bear deep grooves which are arranged as radii from the apex of the valve. The radial grooves seem to correspond to radially arranged planes within the tissue of the cardinal process lobes. The radial planes cross and interrupt the turbulent lamellae of the secondary tissue. This condition imparts a cellular or cancellus appearance to sections through the tissues of the myophore regions. The structure of the cancellus tissue of the myophores resembles bone. The cancellus appearance of the myophores is shown in Text-Figure 28.

A meso-cardinal ridge or septum occurs in most strophomenacean species, Text-Figure 28. The meso-cardinal ridge may be evident on the internal surface or may be buried in overhanging or confluent tissue of the medial sides of the cardinal process lobes. The meso-cardinal ridge has been the subject of considerable speculation. If the meso-cardinal ridge and the cardinal process lobes have the same origin, the bifid cardinal process of the Strophomenacea then could be compared with confidence to the trifid cardinal process of the Plectambonitacea.

The meso-cardinal ridge overlies the posterior extension of the medial ridge from the visceral cavity surface of the dorsal valve. The medial ridge may project under the posterior platform and between the bases of the cardinal process lobes. The meso-cardinal ridge and underlying medial ridge are separated commonly by a zone of lamellar secondary tissue comparable in thickness to the thickness of the posterior platform. The lamellae of this zone of secondary tissue are not folded into the base of the meso-cardinal ridge but they are folded into the bases of the cardinal process lobes. The meso-cardinal ridge is a gerontic feature; it is not present in the ephebic brachiopod. The meso-cardinal ridge is a superficial structure of minor phylogenetic significance.

The clear, lamellar secondary tissue which is found in many other regions of the valves seems to be a filling substance with little function other than to strengthen the valves by increasing thickness, to fill in pockets and holes and to buttress ridges.

The secondary deposits of the muscle scar areas of the dorsal and ventral valves are constructed of layers of microcrystalline and dark lamellar tissue. Specimens of all species of strophomenaceans that have been sectioned, except _Dactylogonia alternata_ Cooper, show layers of the microcrystalline and dark lamellar secondary deposits in the same sequence and of generally similar shape.

The microcrystalline and dark lamellar secondary deposits of the posterior-central region of the ventral valve of _Rafinesquina ponderosa_ Ulrich and of the dorsal valve of _Tetraphalerella neglecta_ (James) are shown in Text-Figure 29. In the anterior-central region of the

Text-Figure 29.- Assembled transverse serial sections of the posterior-central region of the ventral valve of _Rafinesquina ponderosa_ Ulrich (left) and of the posterior-central region of the dorsal valve of _Tetraphalerella neglecta_ (James) (right). Tissues shown: black - dark, finely lamellar secondary tissue; white - microcrystalline tissue; stippled - inner initial tissue and clear secondary tissue. The curved lines along the sides of the blocks are a projection of the curvature of the mid-line of the valves. Interval between sections: _R. ponderosa_ (left), 1/16 inch between the first six sections, 1/32 inch between sections six and seven, 1/64 inch between remaining sections; _T. neglecta_ (right), 1/32 inch between all sections except sections three and four which are 3/64 inch apart. Magnification: left X5, right X6.

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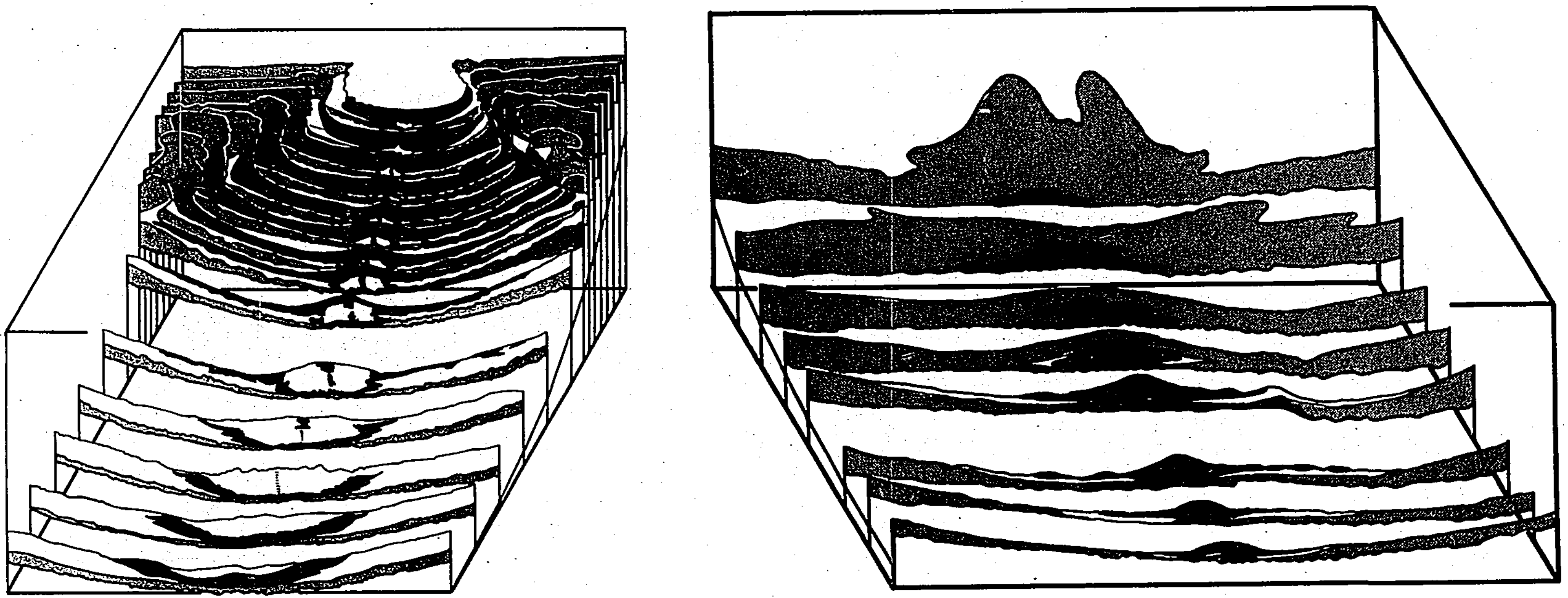
ventral valve of _Rafinesquina ponderosa_ Ulrich (see first section of the text-figure), the inner initial tissue is overlain by a broad expanse of microcrystalline secondary tissue (unpatterned zone of diagram). The central region of the microcrystalline tissue is depressed and replaced by a transversely curved plate of dark lamellar tissue (black plate). The central region of the curved plate of dark lamellar tissue is overlain by microcrystalline tissue (unpatterned area). These three layers are interpreted as follows: the lower layer of microcrystalline tissue is the site of diductor muscle attachment; the upper layer of microcrystalline tissue is the site of adductor muscle attachment; the dark plate marks the position of attachment of connective tissue. As the brachiopod grew in length and width, the area of attachment of the adductor muscles became wider and migrated toward the anterior. The tendons on the surface of the adductor muscles spread laterally with growth and increased shell thickness with the result that tissue marking the site of tendon attachment forms a curved plate. Succeeding sections toward the posterior (sections 4 to 11) show intro-



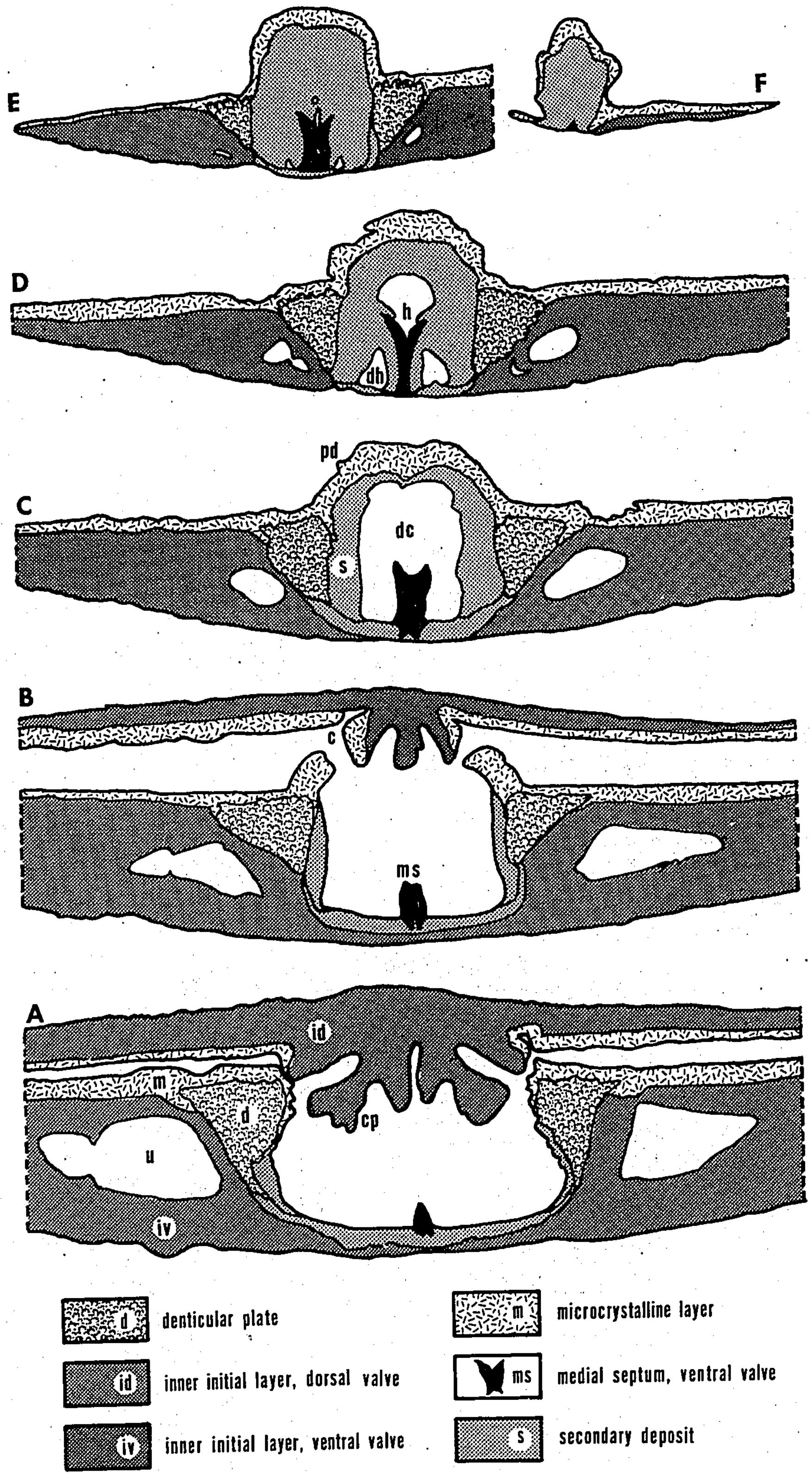
<u>Text-Figure 29</u>.- Assembled transverse serial sections of the posterior-central region of the ventral valve of <u>Rafinesquina ponderosa</u> Ulrich (left) and of the posterior-central region of the dorsal valve of <u>Tetraphalerella neglecta</u> (James) (right). Tissues shown: black - dark, finely lamellar secondary tissue; white - microcrystalline tissue; stippled - inner initial tissue and clear secondary tissue. The curved lines along the sides of the blocks are a projection of the curvature of the mid-line of the valves. Interval between sections: <u>R. ponderosa</u> (left), 1/16 inch between the first six sections, 1/32 inch between sections six and seven, 1/64 inch between remaining sections; <u>T. neglecta</u> (right), 1/32 inch between all sections except sections three and four which are 3/64 inch apart. Magnification: left X5, right X6.

duction of a partition of dark lamellar tissue into the center of the microcrystalline tissue underlying the adductor scars. This partition is evidence of separation of the adductor muscles and insertion of a tendinous strip between them. Toward the posterior, the dark lamellar tissue spreads laterally across the microcrystalline tissue of the diductor muscle scars, fifth section, and centrally across the microcrystalline tissue of the adductor muscle scars, sixth section. The lateral and central spreading of the dark lamellar tissue marks the posterior margin of the diductor and adductor muscles at the time of death of the brachiopod. The spreading of the dark lamellar layer over the adductor muscle scars occurs directly beneath the anterior edge of the cardinal process lobes. Posterior extensions of the microcrystalline layers under dark lamellar tissue mark former positions of diductor and adductor muscle attachment. These posterior sites of attachment were abandoned during growth as the posterior margin of the muscles migrated toward the anterior.

The microcrystalline and dark lamellar secondary tissues from the muscle scars may be traced into the delthyrial cavity. The medial body of microcrystalline tissue from the adductor muscle scars disappears under the delthyrial cavity. The microcrystalline layer from the diductor muscle scars becomes a thin plate in the floor of the delthyrial cavity. The lateral edges of this plate curve up the sides of the dental lamellae and contact the basal edge (ventral edge) of the denticular plate. In a few sections, the entire denticular plate seems to be bedded in this tissue. Further toward the delthyrial apex, this layer becomes thinner and finally disappears. In Text-Figure 30, the plate of secondary tissue in the floor of the delthyrial cavity is this microcrystalline tissue. Note that the plate thins in sections A to E and is absent from section F, possibly because of abrasion.

Text-Figure 30.- Transverse serial sections of the posterior-central region of Strophomena vetusta (James). c - chilidium, cp - cardinal process, dc - delthyrial cavity, dh - cavity in secondary tissue which fills apex of delthyrial cavity, h - hemisyrinx, pd - pseudodeltidium, u - umbonal cavity. Interval between sections: A to B, 1/32 inch; remaining sections, 1/64 inch; section F less than 1/64 inch from posterior end of valve. Magnification X6.67.

The dark lamellar secondary tissue may be traced into the delthyrial cavity. At the anterior end of the delthyrial cavity, the dark lamellar secondary tissue curves



Text-Figure 30.- Transverse serial sections of the posterior-central region of *Strophomena vetusta* (James).

up the sides of the dental lamellae. Toward the apex of the delthyrial cavity, the dark lamellar secondary tissue is restricted to a medial position and either gradually disappears, as in *Rafinesquina ponderosa* Ulrich, or becomes compressed into a medial septum, as in *Strophomena vetusta* (James), Text-Figures 29 and 30.

The microcrystalline and dark lamellar secondary tissues are submerged under a layer of clear lamellar secondary tissue in the delthyrial cavity. This clear lamellar layer begins on the sides of the dental lamellae below the exposed medial faces of the denticular plate. It is not known whether clear lamellar tissue or dark lamellar tissue flows into the depressions between the semidenticles of the medial face of the denticular plate as shown in Text-Figure 26. The clear, lamellar secondary deposit becomes thicker toward the delthyrial apex. Under the pseudodeltidium, this tissue covers all surfaces of the delthyrial cavity. Horizontal or vertical transverse flanges in the surface of this tissue at the delthyrial apex of some species, *e.g.* *Strophomena concordensis* Foerste, may mark the site of attachment of adjustor or pedicle muscles.

The delthyrial regions of *Strophomena vetusta* (James) and *S. planumbona* (Hall) differ from the delthyrial regions of all other strophomenaceans that have been sectioned, including other species of *Strophomena*. In these two species, the dark lamellar secondary tissue of the delthyrial region becomes concentrated into a thin, sharp septum. The septum has a rounded top in *S. planumbona* (Hall) and a flattened or trough-like top in *S. vetusta* (James), see Text-Figure 30. The septum is found to the tip of the delthyrial cavity. There is a hole in the clear, lamellar secondary tissue on either side of the septum. The holes are directed into the apex of the ventral valve. These holes are filled with coarsely granular, sparry calcite which was deposited after death. *Tetraphalerella neglecta* (James) has a pair of cavities in the floor of the delthyrial cavity which receive the posterior ends of the cardinal process lobes when the valves are closed. This is not the function of the pair of cavities in *S. vetusta* (James) or *S. planumbona* (Hall). No other strophomenacean species that has been sectioned has a pair of cavities in the floor of the delthyrial cavity, however, sections of the delthyrial region of *Thaerodonta rugosa* (Meek), a plectambonitacean, reveal a pair of holes in the secondary tissue. The pairs of holes in the delthyrial regions of *Thaerodonta* and *Strophomena* have no taxonomic significance, but they may indicate the presence of an unknown fleshy structure. The pair of apically directed holes flanking a septum with a trough-shaped top, as borne by Strophomena vetusta (James), has an interesting similarity to the spondylium triplex and hemisyrinx of the pseudopunctate clitambonitoids of the Superfamily Gonambonitacea.

The secondary deposits associated with the muscle scars of the dorsal valve are not as complex as those of the ventral valve, as shown in Text-Figure 29. The regions of adductor muscle attachment are underlain by coarsely microcrystalline tissue. A ridge of dark inner initial tissue, which is the medial ridge of the dorsal valve, divides the microcrystalline tissue. The microcrystalline tissue of the central region of most species is spread across the medial ridge. Posterior to the center of the valves, just anterior to the anterior margin of the posterior platform, a ridge of dark, lamellar secondary tissue appears on top of the medial ridge. The two superimposed ridges are commonly separated by a thin zone of clear, lamellar inner initial tissue. At the anterior margin of the notothyrial platform, the dark lamellar ridge of secondary tissue spreads laterally over the microcrystalline layer. This region of lateral spreading corresponds to the posterior margin of the dorsal adductor muscle scars. The microcrystalline and dark, lamellar secondary tissues can be traced under the cardinal process. Under the cardinal process, lamellae of the dark, lamellar tissue gradually become thicker and clearer. The medial ridge grades into clear lamellar tissue in the posterior region of the notothyrial platform.

Specimens of *Stropheodonta* (Devonian) that have been sectioned possess secondary tissue deposits in the muscle scar regions that strongly resemble those of *Rafinesquina*. In fact, sections of these two genera cannot be differentiated easily without reference to the teeth and cardinal processes. The plectambonitacean *Thaerodonta rugosa* (Meek) possesses a layer of microcrystalline tissue overlain by a curved plate of dark lamellar tissue in the ventral valve. There is no differentiation of secondary deposits in the muscle scar regions of the dorsal valve. The orthotetaceans *Fardenia subplana* (Conrad) (Silurian) and *Schuchertella sp*. (Devonian) do not show differentiation of secondary tissue in the muscle scar region. *Derbyia hooserensis* Dunbar and Condra shows a differentiation of microgranular and dark lamellar secondary tissue in the muscle scar regions of the ventral valve. The high medial septum is constructed of dark lamellar tissue. The adductor muscle scar areas of the dorsal valve do not show secondary deposits. Transverse sections of the orthoid species *Plaesiomys subquadrata* (Hall), *Hebertella sinuata* (Hall) and *Platystrophia acutilirata* (Conrad) show microstructurally differentiable tissue associated with the muscle scars of the ventral valve. The tissues of the muscle scar areas of these orthoids have not been examined in detail. Nevertheless, the tissue layers seem to have the same general form and sequence as found in strophomenaceans.

Microstructure of the dorsal ridges.- The ridges of the internal surface of the dorsal valves of strophomenaceans are not conspicuous features in thin or peel sections. The ridges are most evident on specimens of the older genera, for example, *Dactylogonia* and *Oepikina*. The ridges appear in modified form in *Strophomena*, *Holtedahlina* and allied genera and are greatly reduced to absent in *Leptaena*, *Rafinesquina* and related genera. The dorsal ridges are significant in the evolutionary history of the Superfamily Strophomenacea and may become important structures for determination of the ancestry of the strophomenaceans within the Superfamily Plectambonitacea.

Specimens of the plectambonitacean species *Thaerodonta rugosa* (Meek) have been sectioned for comparison to strophomenacean sections. The inner surface of the dorsal valve of *Thaerodonta rugosa* (Meek) possesses seven septa (a medial septum and three pairs of lateral septa) which invite comparison to the five dorsal ridges of strophomenaceans. The shell material of the dorsal valve of *Thaerodonta rugosa* (Meek) does not resemble the shell material of strophomenaceans. The inner initial layer is thin, poorly lamellar and has a cellular or prismatic appearance in peel sections. The difference in appearance of the tissue is not caused by preservation. The specimens of Thaerodonta came from the same outcrop as several of the specimens of Strophomena which were sectioned. The medial septum is composed of dark, prismatic to poorly lamellar inner initial tissue. The anterior pair of lateral dorsal septa, the anderidia, are thin and high. They possess a thin axial plate of inner initial tissue of prismatic appearance. The axial plate expands and contracts in transverse section, which imparts to it a beaded appearance. The lateral flanks of each axial plate are covered by a fillet of prismatic secondary tissue. The two pairs of low, posterior septa are composed of relatively clear prismatic tissue without axial structures.

The microstructure of the dorsal ridges of Oepikina gregaria Cooper, O. minnesotensis (Winchell) and Dactylogonia alternata Cooper cannot be compared in all aspects to the septa of Thaerodonta rugosa (Meek). Oepikina and Dactylogonia do not possess any tissue with a cellular or prismatic appearance except in the cardinal processes. The medial and anterior pair of dorsal ridges of Oepikina and Dactylogonia are linear welts of dark, finely lamellar inner initial tissue containing pseudopunctae. There is no indication in the ridges of either genus of an axial plate but there is a cylindrical core of granular tissue at the anterior ends of the medial ridge and anterior-lateral ridges. The core of granular tissue in the anterior pair of ridges of Oepikina and Dactylogonia may be homologous to the axial plates in the anterior pair of septa of Thaerodonta. This comparison leaves the granular core in the medial ridge of Oepikina and Dactylogonia without a comparable feature in Thaerodonta. The medial septum of Thaerodonta disappears anterior to the posterior platform. The axial plates of the anterior pair of septa of Thaerodonta converge and unite at the anterior margin of the posterior platform. This union produces a "U" shaped plate filled with secondary tissue. The medial and anterior pair of ridges of Oepikina coalesce into a single medial ridge near the anterior margin of the posterior platform. The pair of posterior-lateral ridges of Oepikina and Dactylogonia differ from the other ridges by being composed of clearer, more coarsely lamellar tissue identical to normal inner initial tissue. As noted, the posterior pair of dorsal ridges are less persistent in the phylogeny of the Strophomenacea than either the anterior pair of dorsal ridges or the medial ridge. The single pair of posterior-lateral ridges of Oepikina and Dactylogonia and the dual pairs of posterior-lateral septa of *Thaerodonta* are simple muscle bounding ridges, *i.e.* transmuscle ridges.

Specimens of all genera of strophomenaceans that have been sectioned possess a medial ridge composed of dark, finely lamellar inner initial tissue. In this character, all genera resemble *Oepikina* and *Dactylogonia*. *Holtedahlina* and *Oepikina* possess a medial ridge with a cylindrical core of granular tissue, but *Strophomena*, *Tetraphalerella*, *Rafinesquina* and *Kiaeromena* do not. The cylindrical core of granular tissue probably forms the breviseptum.

The lateral pairs of dorsal ridges of *Holtedahlina* and *Oepikina* are similar in microstructure. Species of *Strophomena* show three types of ridges in the dorsal valve. The anterior pair of ridges of *S. nutans* Meek resemble the dorsal ridges of *Oepikina* by being linear welts of inner initial tissue. These ridges of *S. nutans* Meek are wider and are composed of clearer, more coarsely lamellar tissue than the dorsal ridges of *Oepikina*. The lateral ridges of *S. nutans* Meek are buried beneath secondary tissue in the posterior platform region. *S. planumbona* (Hall) possesses lateral ridges composed of dark, lamellar secondary tissue resembling the tissue adjacent to the muscle scars of the ventral valve. The dark tissue of the lateral ridges overlies clear, pseudopunctate, inner initial tissue and, hence, must be a secondary deposit. S. vetusta (James) possesses many irregularly formed lateral dorsal ridges. These are constructed of coarsely lamellar, coarsely taleolate, clear inner initial tissue. The ridges of S. vetusta (James) have topographic relief but are not microstructurally differentiated. Tetraphalerella neglecta (James), Rafinesquina ponderosa Ulrich, Leptaena richmondensis Foerste and Megamyonia unicostata (Meek and Worthen) do not possess lateral ridges on the internal surface of their valves or in the microstructure tissue of their valves. The ridges of Strophomena which are composed of secondary tissue are not related to the ridges of Oepikina which are composed of inner initial tissue. The ridges of Strophomena should be called adventitious ridges because of their irregular form, inconsistent occurrence and secondary character.

There is no consistency of construction of the dorsal ridges throughout the Superfamily Strophomenacea except for the ubiquitous medial ridge. The pairs of lateral dorsal ridges are a phylogenetically primitive feature which are suppressed and even deleted in advanced lineages.

Pseudopunctae and taleolae.- The most convenient unifying character of the strophomenoid brachiopods is the pseudopunctate condition of the shell material. Williams (1956, p. 251) proposed the term "taleolae" for the slender rods of granular calcite which occur along the axes of localized deflections of the lamellae of the shell material, the pseudopunctae. His definitions of that date left unclear the difference between a pseudopuncta and a taleola. The distinction between these structures has been resolved in the Treatise on Invertebrate Paleontology, Part H, 1965, p. 151. The present observations largely support Williams' (1956, p. 251 and 1953, p. 3) descriptions of pseudopunctae and taleolae without serious conflict.

Taleolae are thin unbranched rods of granular calcite which arise from an indistinct, expanded base at, or just below, the outer surface of the inner initial layer. The taleolae are crossed by dark lines which suggest the presence of cleavages or grain boundaries. Taleolae commonly penetrate to the interior surface of the inner initial layer. They may project into the visceral cavity as short spines called endospines. Some taleolae do not seem to penetrate the entire inner initial layer but this trait cannot be established without question because sections may cut obliquely through taleolae.

Taleolae may be straight or gently curved in sagittal section. They most commonly curve or slope slightly to the anterior of a line perpendicular to the shell surface when they are traced from exterior to interior. Some taleolae may be oriented at random angles to the shell surface and may even curve in a vermicular fashion. Randomly oriented and vermicular taleolae are found only in thickened regions of the inner initial layer where the lamellae are turbulent, as in the muscle bounding ridge and the marginal diaphragm.

The lamellae of the inner initial layer adjacent to taleolae are curved toward the internal surface of the valve. This curvature produces the illusion that the taleolae have been pressed through the inner initial tissue as pins might be pressed through a magazine. The width of the zone of curvature of the lamellae around a taleola is about one to one and a half times the diameter of the taleola. Curvature of the lamellae to form a pseudopuncta amounts to approximately 45 degrees rotation. There is slightly more than 45 degrees curvature of lamellae along the anterior margin of a taleola and from 30 to 45 degrees curvature along the posterior margin. Variation of curvature is caused by the anterior slope of the taleolae. The set of stacked cones of lamellae, *i.e.* a pseudopuncta, may occur without an axial taleola, but a taleola never occurs without deflected lamellae around its margin.

The margin of a taleola may be deeply indented by the edges of the lamellae. The indentations may be so deep as to cause a taleola to have a beaded appearance in thin sections. Rarely, lamellae pass through a taleola without interruption. Cleavages or grain boundaries in taleolae commonly correspond to adjacent lamellae, hence, may not be crystallographically controlled. Some taleolae have smooth, uninterrupted margins. Those with uninterrupted margins have a thin, dark layer which separates the taleola from the edges of adjacent lamellae. This layer has the same appearance as the thin dark layers which separate lamellae. The dark, marginal layer of taleolae is not visible in peel sections. Williams (1956) described "two or more layers" around the central axis of some taleolae and Muir-Wood (1965) reported a central cavity within taleolae. Two layers may be observed in cross sections of large taleolae of _Leptaena richmondensis_ Foerste and _Megamyonia unicostata_ (Meek and Worthen). The outer layer is probably the upturned edge of a lamella and not a layer of the granular rod of a taleola. No evidence of a central cavity can be found in the taleolae of strophomenaceans.

No evidence has been found to support Spjeldnaes' (1957) belief that taleolae were puncta during the life of the brachiopod and were filled by post-depositional precipitation of sparry calcite. Spjeldnaes bases his theory upon the presence of "possible traces of clay material" (1957, p. 10) in taleolae of one sectioned specimen of *Leptaena depressa* (Sowerby) and upon depressions in the crests of endospines. In 1929, Kozłowski presented convincing evidence that pseudopunctae are structures of the original shell material.

Foreign matter is commonly observed in sections of brachiopods. Some enters by inadequate cleaning of sections prior to mounting; some enters along natural fractures in shells. "Pearls" formed by deposition of secondary shell tissue over pockets of clay and fossil fragments have been observed. A specimen of *Rafinesquina* incrusted by *Lichenocrinus* (a crinoid radix) shows deep erosion and entrapment of foreign matter under the margin of the crinoid base. The canals of *Rhopalonaria* (a bryozoan) on a sectioned specimen are filled with clay. Sections of *Leptaena* and *Rafinesquina* usually show tiny vermicular tubes in the inner initial layer. These have the dimensions of dalmanelloid endopunctae. They do not appear to be true punctae because they have an erratic distribution within the shell material, some specimens lack tubes, the tubes are randomly curved and branched, the tubes seem to emerge at both the exterior and interior surfaces of the shell and no brush can be found at the external end of the tubes, as occurs at the external end of endopunctae. These tubes are filled with an opaque substance which makes them conspicuous. One tube penetrates diagonally through a taleola. The tubes are probably caused by an epizooic (or epiphytic) microorganism. Regardless of the origin of the tubes, they do introduce foreign matter into the shells. Specimens of the dalmanelloid Onniella meeki (Miller) from the Waynesville Formation, Upper Ordovician, Ohio, commonly show euhedral crystals of pyrite in the endopuncta. Associated specimens of Rafinesquina ponderosa Ulrich and R. loxorhytis (Meek) do not have pyrite along the axes of the pseudopunctae.

Pits rarely occur on the crests of unweathered endospines. Etching by acid proceeds more rapidly in granular tissue of a taleola than in the surrounding lamellar tissue of the pseudopuncta. The result is a pit in the crest of endospines that have been subjected to gentle, natural or laboratory etching.

No taleolae resembling the "hemispherical humps" described by Williams (1956, p. 251) have been observed. Toward the margins of shells, especially in the marginal diaphragm, there commonly are broad, hemispherical swellings in the lamellar tissue which have the appearance of being adjacent to hemispherical taleolae, but no hemispherical taleolae have been observed in association with these.

The microstructure of the denticular plate is unique. The denticular plate has been described as being pseudopunctate for convenience only. The ventral region of the denticular plate is composed of exceedingly turbulent lamellar tissue. Toward the dorsal surface of the plate, the curled lamellae gradually become marshalled into parallel, discontinuous isoclinal folds. The crests of the isoclinal folds form the parallel ridges (semidenticles) of the dorsal surface of the plate. The axial planes of the isoclinal folds are oriented perpendicular to the hinge line and interarea, not parallel to the margin of the delthyrium. Because the isoclinal folds are oblique to the denticular plate, they crop out along the medial face of the denticular plate where they produce ridges. The axial region of each fold tends to be granular tissue without distinct boundaries. If these granular axes may be called taleolae, they are taleolae with a tabular shape. The folds and tabular taleolae are visible only in transverse and longitudinal sections. Sagittal sections are parallel to the axial planes of the folds with the result that the denticular plate is difficult to distinguish in sagittal section.

The function of pseudopunctae and taleolae is unknown. Williams (1956, p. 252) postulates that they were the "seat of attachment for tendons (tonofibrils) permeating the connective tissue of the mantle". If this be the case, it is difficult to understand why taleolae and pseudopunctae do not penetrate the secondary tissue of the shell. It would seem reasonable to assume that the visceral mass of the brachiopod animal would have been as securely fixed to the shell as the mantle. Williams suggests, also, that they had the function of pegs which riveted together the fissile lamellae of the shell. It might be suggested that taleolae are "pearls" caused by inclusion of exotic grains under the margin of the mantle or in the mantle groove. This idea is unacceptable because there are no foreign grains at the base of the taleolae, pseudopunctae may occur in a regular pattern in the shell material and the size of taleolae tends to be uniform within a species.

There tends to be a regular variation of size and distributional density of taleolae within a strophomenacean valve. Taleolae are more closely packed toward the center of the valves than toward the lateral or anterior margins of the valves. The packing is especially close in the regions of the dorsal ridges and under muscle scar areas and especially open in the muscle bounding ridges and marginal diaphragm. Text-Figure 31 shows the number of taleolae per square millimeter in different regions of

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Text-Figure 31.- The number of taleolae per square millimeter in different regions of the valves of *Rafinesquina ponderosa* Ulrich (above) and *Leptaena richmondensis* Foerste (below). The stippled squares show the areas where taleolae were counted.

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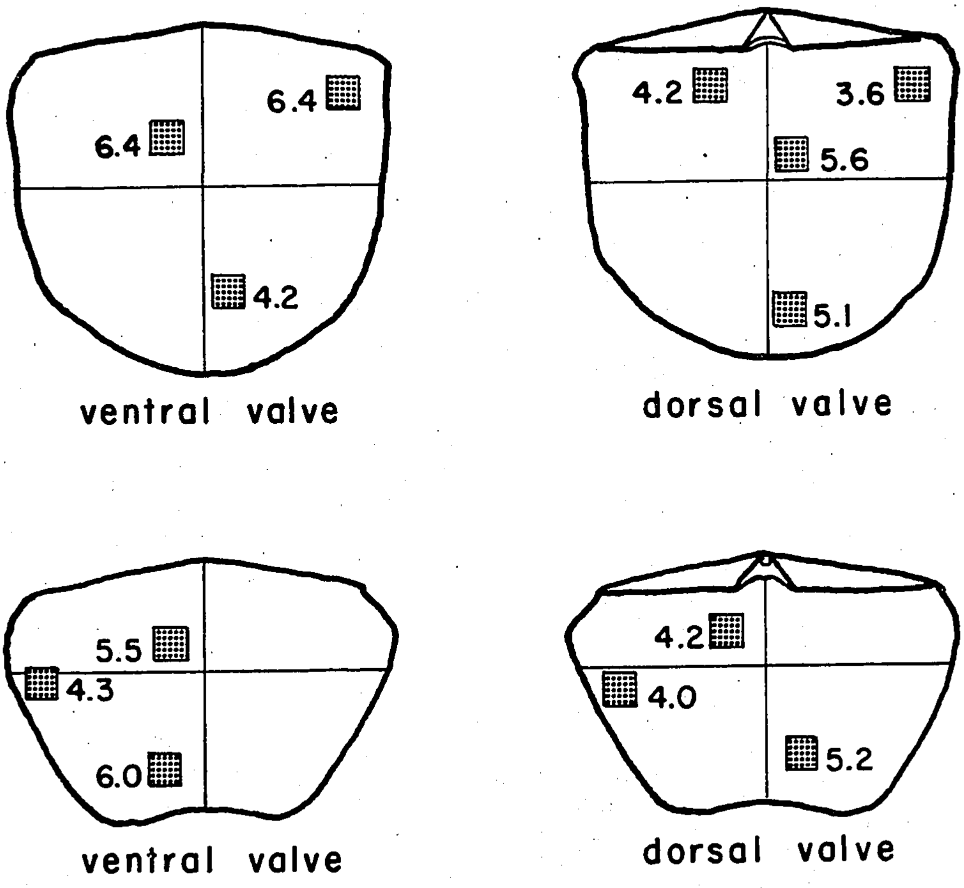
the disc of the valves of *Rafinesquina ponderosa* Ulrich and *Leptaena richmondensis* Foerste. Taleolae and pseudopunctae were counted on external surfaces of etched valves. The taleolae of the etched, external surfaces do not reflect variations of packing associated with internal structures. There does not seem to be an important difference in the packing density of taleolae in the exterior tissue of ventral valves compared to dorsal valves in *Rafinesquina ponderosa* Ulrich and *Leptaena richmondensis* Foerste.

The diameter of taleolae in a specimen is inversely related to the density of packing of the taleolae. Taleolae are thicker in regions of the shell where they are widely spaced than in regions where they are crowded together.

The relative size of taleolae, the density of their packing and their pattern of occurrence in shell material may be familial differentia. These characters of the taleolae are not useful differentia because other mor-



Text-Figure 31.- The number of taleolae per square millimeter in different regions of the valves of *Rafinesquina ponderosa* Ulrich (above) and *Leptaena richmondensis* Foerste (below). The stippled squares show the areas where taleolae were counted.

phological features are more evident, detailed analysis of taleolae requires destruction of the shell, and characters of the taleolae are difficult to determine in silicified and recrystallized specimens and molds. Specimens assigned to some strophomenacean genera are very rare and should not be destroyed. For example, *Hesperinia kirki* Cooper, monospecific, is represented by eight specimens; *Kirkina millardensis* Salmon, monospecific, ten specimens; *Colaptomena leptostrophoidea* Cooper, monospecific, nine specimens; *Pionomena*, three species; total of twenty-four specimens. *Teratelasma neumani* Cooper, monospecific, is known only from molds. All available specimens of the type species of *Kjerulfina*, *K. trigonalis* Bancroft, of the type species of *Kjaerina*, *K. typa* Bancroft, and of the type species of *Hedstroemina*, *H. fragilis* Bancroft are molds in siltstone. Most of the known specimens assigned to *Murinella*, *Platymena* and *Glyptomena* are silicified.

The number of taleolae per square millimeter has been computed for several species to demonstrate the range of packing densities. Table 4 shows the species analyzed, the number of taleolae per square millimeter and the total surface area of the shell on which the count was made. All counts were made on an etched, external surface near the center of the ventral valve.

The diameter of taleolae is variable, also, among species of strophomenaceans. Table 4 shows the mean diameter of taleolae in several species. All taleolae were measured on longitudinal peel sections from near the center of ventral valves. Measurements were made of the minimum diameter of the taleolae because taleolae may be circular, ovoid, irregularly ovoid or angular in cross-sectional shape. Moreover, the planes of the longitudinal sections are not perpendicular to all of the taleolae which were measured. The minimum diameter corresponds to the minor axis of the ellipse formed by intersection of a cylinder and an oblique plane, which is the diameter of the cylinder. Consequently, the minimum diameter is the best approximation of the true diameter of the taleolae. The measurements and the statistics derived from them are approximate because the boundaries of the taleolae are diffuse and the diameter of taleolae is known to be variable along their length.

Table 4 shows that the diameter of taleolae may vary by a factor of X5 from species to species. The species of Table 4 are arranged in order of increasing packing density of taleolae. Inspection of the "$\bar{x}$" column shows that the mean diameter of taleolae tends to decrease as packing density increases. Column "V", coefficient of variation, shows that the standard deviation of taleolae

Table 4.- Measurements of the packing density and diameter of taleolae

	Packing density of taleolae		Diameter of taleolae			
Species	#/sq. mm.	area counted in sq. mm.	N	$\overline{x}$	s	V
Megamyonia unicostata	4.9	11.1	20	.052	.0152	29.3
Leptaena richmondensis	5.5	11.1	20	.044	.0146	33.1
Rafinesquina ponderosa	6.4	11.1	18	.051	.0192	38.0
Tetraphalerella neglecta	34.0	11.1	21	.038	.0084	22.0
Oepikina minnesotensis	43.0	1.34	17	.011	.0026	23.1
Holtedahlina sulcata	78.5	0.67	20	.011	.0046	41.5
Strophomena planumbona	94.0	0.67	15	.019	.0046	23.9

N = number of taleolae measured

x = value of any measurement

$\overline{x}$ = the mean diameter of taleolae in mm. = $\frac{\sum (x)}{N}$

d = the difference between a measurement and the mean, $(x - \overline{x})$ or $(\overline{x} - x)$

s = standard deviation of taleolae diameters = $\left(\frac{\sum (d^2)}{N - 1}\right)^{\frac{1}{2}}$

V = coefficient of variation = $\frac{100s}{\overline{x}}$

diameters relative to mean diameters for all seven species is about the same. Holtedahlina sulcata (Verneuil) has the largest coefficient of variation. There seems to be no regular pattern in the position of unusually small taleolae and unusually large taleolae within this species.

Rafinesquina ponderosa Ulrich and Leptaena richmondensis Foerste, also, show large coefficients of variation of taleolae size. The taleolae of these two species are set in the shell in a definite pattern according to size. The thicker taleolae of Leptaena richmondensis Foerste occur in the striae between costellae. In longitudinal sections, the thicker taleolae are aligned along radii from the apex of the valve. Small taleolae occur at random positions between the rows of large taleolae. The taleolae of Rafinesquina ponderosa Ulrich tend to be set in a grid-like pattern. The larger taleolae of Rafinesquina lie along the deeper striae between costellae at the intersection of the varices. Smaller taleolae are set at random between the larger taleolae. In both species, the long axis of the oval cross section of taleolae is parallel to the costellae.

HABITAT AND HABITUS

Ordovician strophomenacean brachiopods are best known from rocks of marine neritic origin of North America, northern Europe and European Russia. Species from the Southern Hemisphere, eastern Asia, southern Europe, and western and northern North America are poorly known. Representatives of the entire superfamily are not restricted to any specific lithotope but generally are absent from black shales and littoral sandstones. Species may show environmental selectivity by accompanying recurrent faunas.

Variation of size and thickness of Ordovician species does not support or contradict Flower's (1942, 1946, 1957) and Spjeldnaes' (1957) delineation of Ordovician climatic zones. There is a general evolutionary tendency for increase of size and thickness in all generic lineages through Ordovician time which masks potential provincial differences. Apparent correlation of size and thickness of species and geographic province is related to the age of faunas known from each province.

Strophomenacean brachiopods were part of the Ordovician benthonic fauna. Contrary to Sardeson (1929), probably no species led a planktonic existence. Ephebic individuals of most leptaenid species and older oepikinid and strophomenid species probably were attached to the substrate by a thin pedicle. At least, adults of these groups have an open pedicle foramen. Ephebic individuals of all other species have a plugged pedicle conduit from which may be inferred a functional pedicle and a tethered existence during nepionic development.

A problem which has never been successfully resolved concerns the preferred orientation of strophomenaceans during life. They may have stood upon the cardinal margin, hung pendent from floating objects, or they may have been recumbent upon the sea-floor. Sardeson (1929) suggests that species of Strophomena and resupinate allies hung pendent from floating objects and that species of Oepikina cemented themselves in an upright position to the substrate. Sardeson's conclusions are based upon the attitude of specimens within a bentonitic stratum. There is no structure of the resupinate group which could be concerned with suspension, as, for example, the spines of chonetoids and linoproductids. Moreover, if individuals lived suspended, it is difficult to explain restriction of species to (and from) specific lithologies. It is most unlikely that concavo-convex forms, such as Oepikina, lived in an erect position. The umbo of concavo-convex species is not deformed to indicate cementation as found among orthotetids. Uncemented to the substrate, a flattened concavo-convex individual could not stand upon its narrow cardinal margin in the slightest water current unless many individuals were imbricated together, as in the shingling of Rafinesquina fracta (Meek) in the Fairmount Formation of Cincinnati, Ohio. In reality, the shingling of Rafinesquina is probably a thanatocoenosic condition inasmuch as the imbricated valves generally occur in current-scoured channels.

It is assumed generally that strophomenaceans rested upon the convex valve to elevate the anterior commissure away from the muddy substrate. Undoubtedly, untethered strophomenaceans lived in any position in which they could perform all of their body functions. Evidence tends to indicate that unattached strophomenaceans rested upon the concave or planate valve. The evidence is circumstantial and subject to contradiction. Nevertheless, the following observations support this hypothesis.

It is unusual to find the thin outer carbonate layer preserved on the surface of strophomenaceans. The outer carbonate layer is usually abraded from the surface except where it is preserved under incrustations. The rare occurrences of unprotected outer carbonate layer are most commonly found near the margin of the concave valve. The occurrence is marginal because the margin is the last-formed part of the valves and had the least time of abrasion before burial. The valve upon which the brachiopod rested was subjected to less abrasion than the overlying valve.

Two specimens of the ventral valve of Rafinesquina cf. ponderosa in the collections of the University of Cincinnati bear massive, discoidal bryozoan zoaria on the external surface. The bounding ridges around the diductor muscle scars, the radial ridges of the diductor muscle scars, and the medial ridges of each valve are enlarged grotesquely. The diductor muscles must have lifted the bryozoan colony as well as the ventral valve when the valves were opened.

The suggested life-position negates the problem of hydrodynamic instability, discussed by Menard and Boucot (1951), that would have been present if the convex valve were downward during life. Also, it is most common to find the exterior of convex valves exposed on the upper surface of strata and the exterior of concave or planate valves exposed on the underside of strata. It has been argued that the attitude of valves in strata is caused by post mortem turning of valves by water currents. Untethered species probably had little control of their attitude during life and would also have been subject to turning by water currents.

It is more common to find argillitic matrix than sparry calcite in contact with the inner surface of the concave valve in thin sections. The sparry calcite probably represents post-depositional filling of gas pockets within the valves.

A census has been made of epizoic organisms on valves of species of Rafinesquina from two lenses in the Waynesville Formation of Butler County, Ohio, and Franklin County, Indiana. Only clean, articulated specimens were selected for the census. Of the 358 specimens considered, 28% have epizoic organisms on the convex valve only, 13% have epizoic organisms on the concave valve only, 30% have no epizoic organisms, 9% have epizoic organisms equally developed on both valves, 14% have larger epizoic incrustations on the convex valve than on the concave valve, and 6% have larger epizoic incrustations on the concave valve than on the convex valve. Sixteen individuals have fossil fragments piercing the concave valve or incorporated into the concave valve during growth. Only two individuals show fossil fragments which project into the ventral valve. The epizoic organisms which were noted include bryozoa, inarticulate brachiopods, crinoid bases, dendroid bases and annelid tubes.

Hyman (1958, p. 585) stated that modern brachiopods, except lingulids, usually take a horizontal position, with the larger ventral valve uppermost "but may erect to a vertical position by manipulating the adjustor muscles of the pedicle". Tethered shells would naturally rest upon the concave valve because of current action.

Consideration of water circulation within strophomenaceans conflicts with this hypothesis. Water circulation is assumed to have been in the same direction as occurs among living articulates, i.e. incurrent areas lateral, excurrent areas antero-medial. Authors have presumed that the commissure was elevated to avoid suffocation, that is, that the living animal rested upon the convex valve. Possibly the curling of the cardinal angles in the direction of the convex valve, ventrally in Oepikina and dorsally in Strophomena and Tetraphalerella, served for ingress of water from above the sediment interface at the posterior-lateral corner of the valves. The marginal diaphragm, which is well developed in Murinella, Oepikina, Leptaena, Cyphomena and Strophomena may have restricted ingress of sediment when the valves were parted and may have directed the flow of water within the animal. A posterior-lateral depression in the marginal diaphragm, which is observed in many species, may be the site of water ingress. The biconvex, folded species of the Furcitellini, including Holtedahlina sulcata (Verneuil), commonly lack a marginal diaphragm. Possibly folding of the valves permitted ingress of water without the necessity of a sediment barrier or a channel way to conduct water into the mantle cavity.

There are no published measurements of the possible anterior gape of strophomenacean brachiopods. Sagittal sections show that the valves might have opened until the ventral edge of the chilidium came into contact with the dorsal edge of the pseudodeltidium, as shown in Text-Figure 24, section A. Sagittal sections through the chilidium and pseudodeltidium do not show the axis of rotation of the valves, but sagittal sections lateral to the teeth do show the axis of rotation of the valves, Text-Figure 24, section D. An enlarged outline of a lateral sagittal section of _Strophomena_ _planumbona_ (Hall) was accurately positioned upon an outline of an exact medial sagittal section of the same specimen. Graphic analysis shows that one valve was capable of 5° of rotation with respect to the other valve. The specimen studied was neither unusually large or small. It was 20.5 mm. long from the axis of rotation to the antero-central commissure along a straight line. The individual was capable of a maximum of 2 mm. gape at the anterior margin. If thick diductor muscles overlay the ventral ends of the cardinal process lobes, or if a periostracal pad existed along the hinge-line, the actual possible gape may have been less than 2 mm.

In addition to the epizoic organisms mentioned, strophomenaceans were subject to parasitism by boring sponges and predation by gastropods. Fragments of both Rafinesquina and Strophomena that were drilled presumably by gastropods, of unestablished species, have been found in Richmondian rocks. No earlier examples are known. Many species of strophomenaceans from throughout the Ordovician show predation by creatures which attacked the margin of the mantle and shell. Attack upon the mantle margin produced deformation of later costellae and varices without discontinuity of these features. Many specimens show evidence that pieces of the shell margin were broken or bitten-off during ontogeny. These accidents or depredations produced great deformation of the shell and discontinuity of the prosopon. Evidence of removal of pieces of shell is more common on convex valves than on concave valves. Rafinesquina winchesterensis Foerste from a lens in the Cynthiana Formation, Carntown, Kentucky, and R. ponderosa from a lens in the Waynesville Formation, along Indian Creek, Butler County, Ohio, show a high frequency of breakage or predation by removal of shell pieces during mid-life of the individuals. The predator, if such it was, probably invaded the shell-bank, attacked many brachiopods, and left. Orthoconic nautiloid cephalopods are common in both localities. No evidence can be offered for predation by trilobites, as suggested by Sardeson (1929). Their manducatory apparatus would appear to have been quite unsuited to such habits.

The interior of strophomenoid specimens that have sectioned for study are commonly packed with ovoid, argillitic pellets. The pellets are probably coprolites of scavenging organisms.

No information has been found concerning the nutrition, excretion or reproduction of strophomenacean brachiopods. Evidence of sexual dimorphism has not been found. There is no evidence to suggest that the untethered strophomenaceans could move in the manner of pectens.

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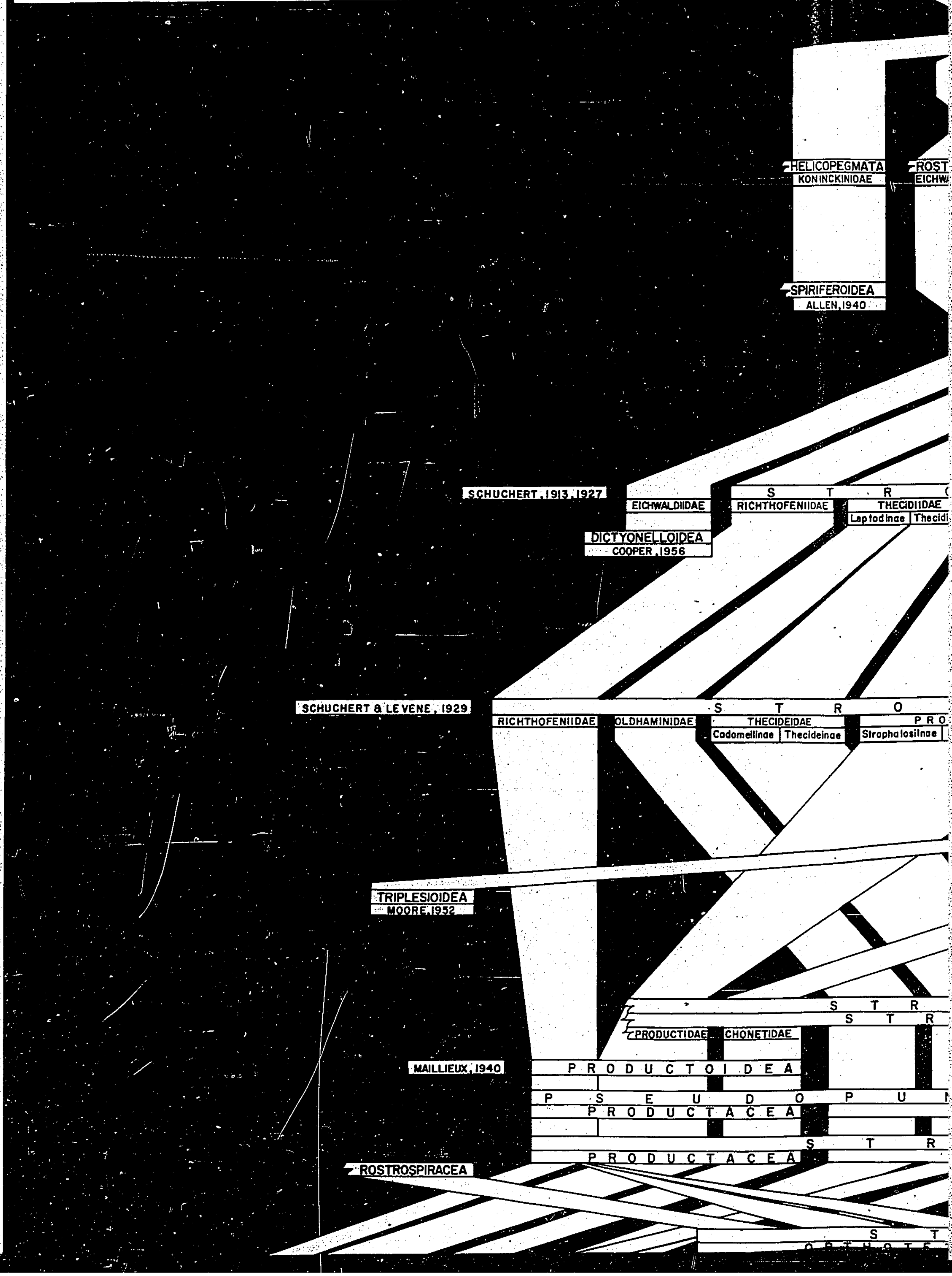
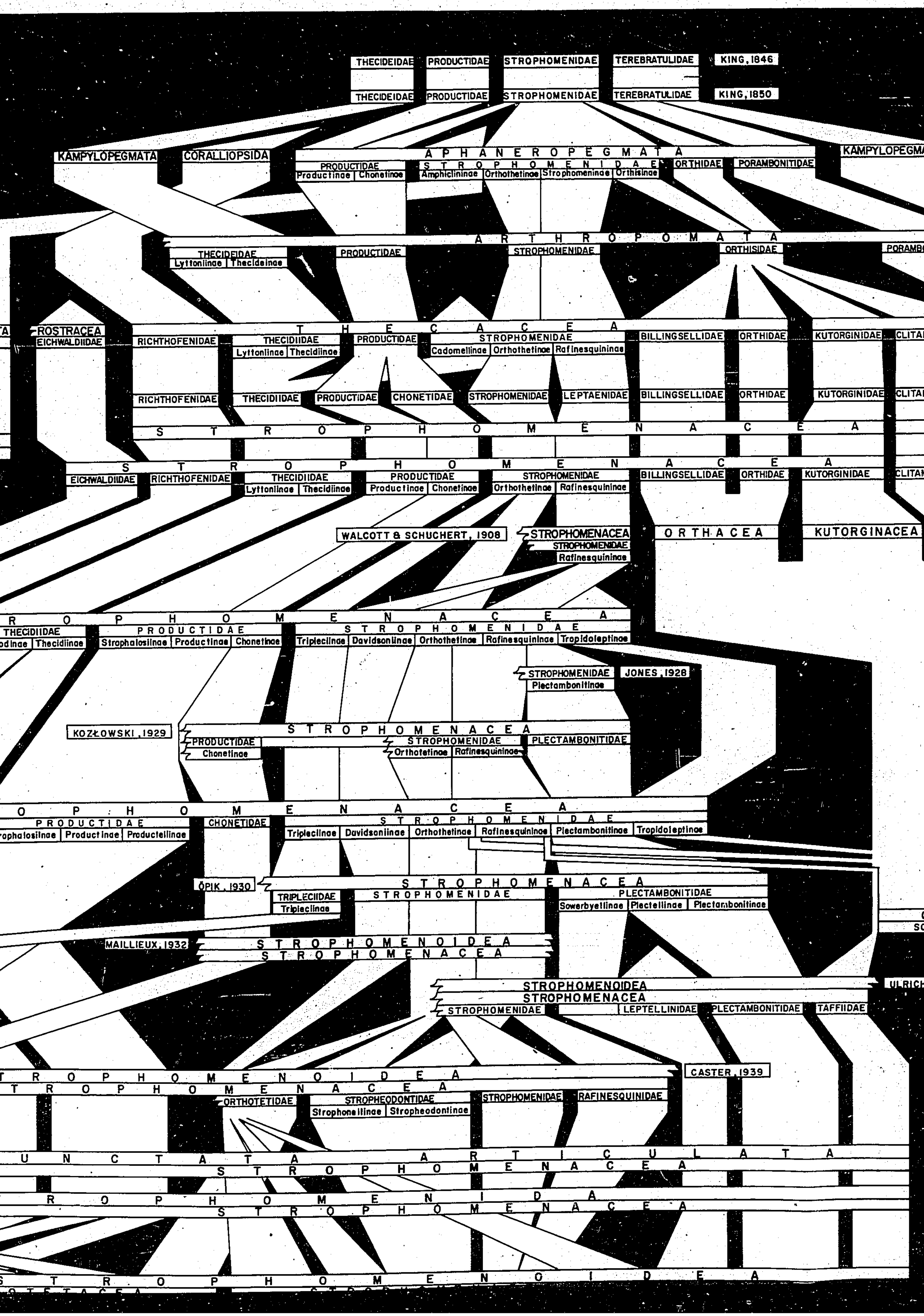
CHART 5

CHRONOLOGICAL SUCCESSION OF BRACHIOPOD CLASSIFICATIONS PERTINENT TO THE DEVELOPMENT OF THE SUPERFAMILY STROPHOMENACEA

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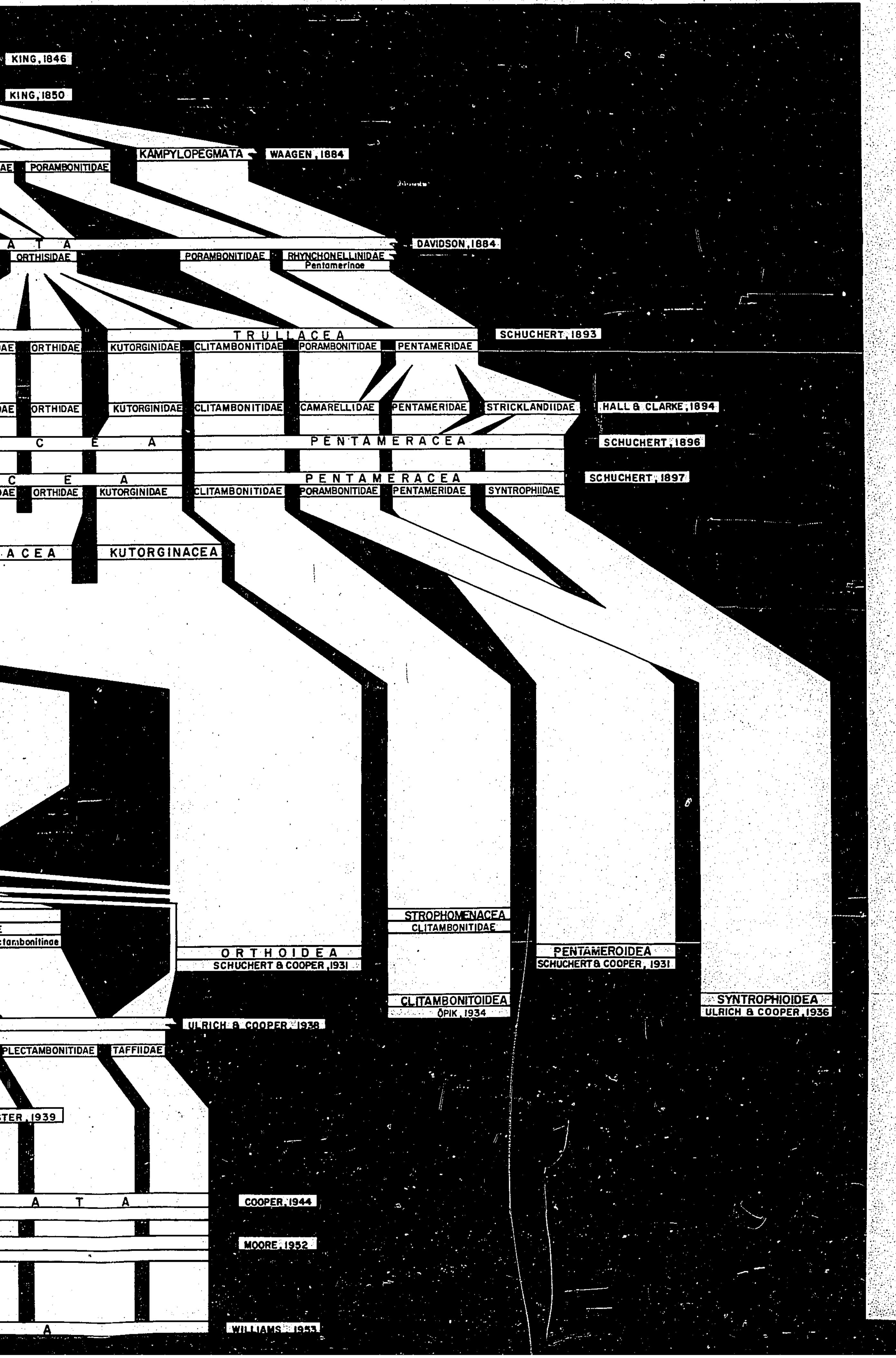
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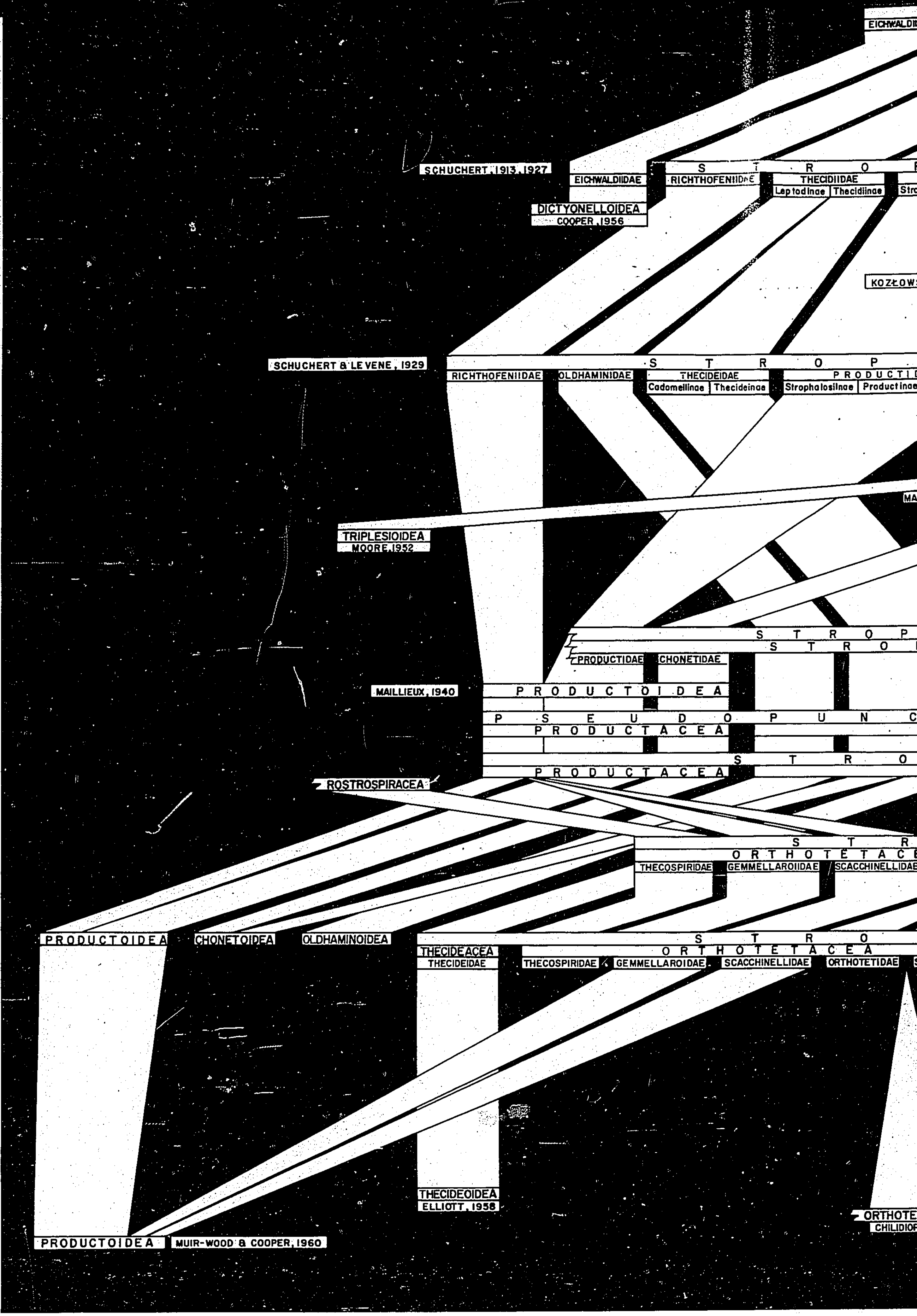
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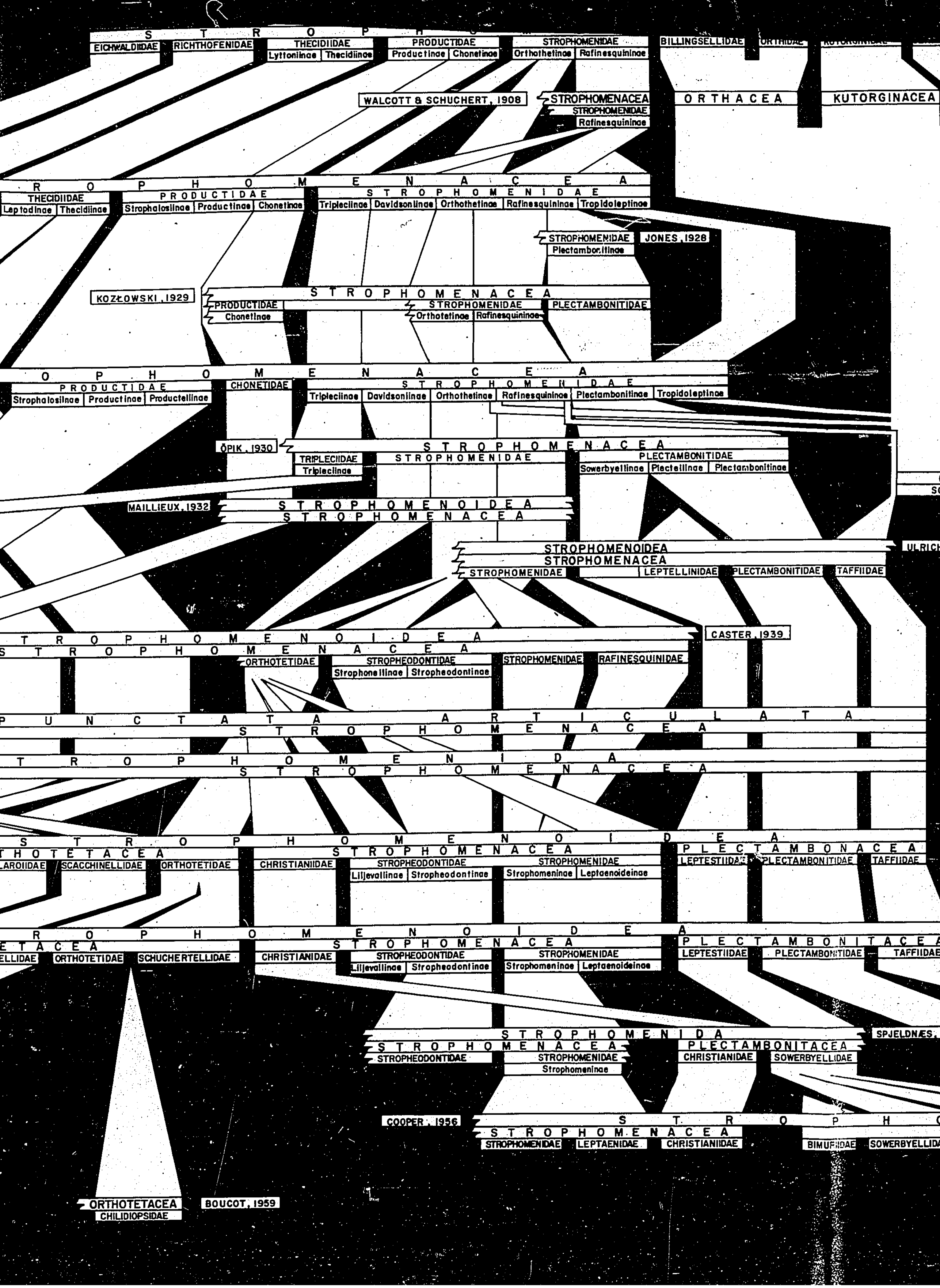
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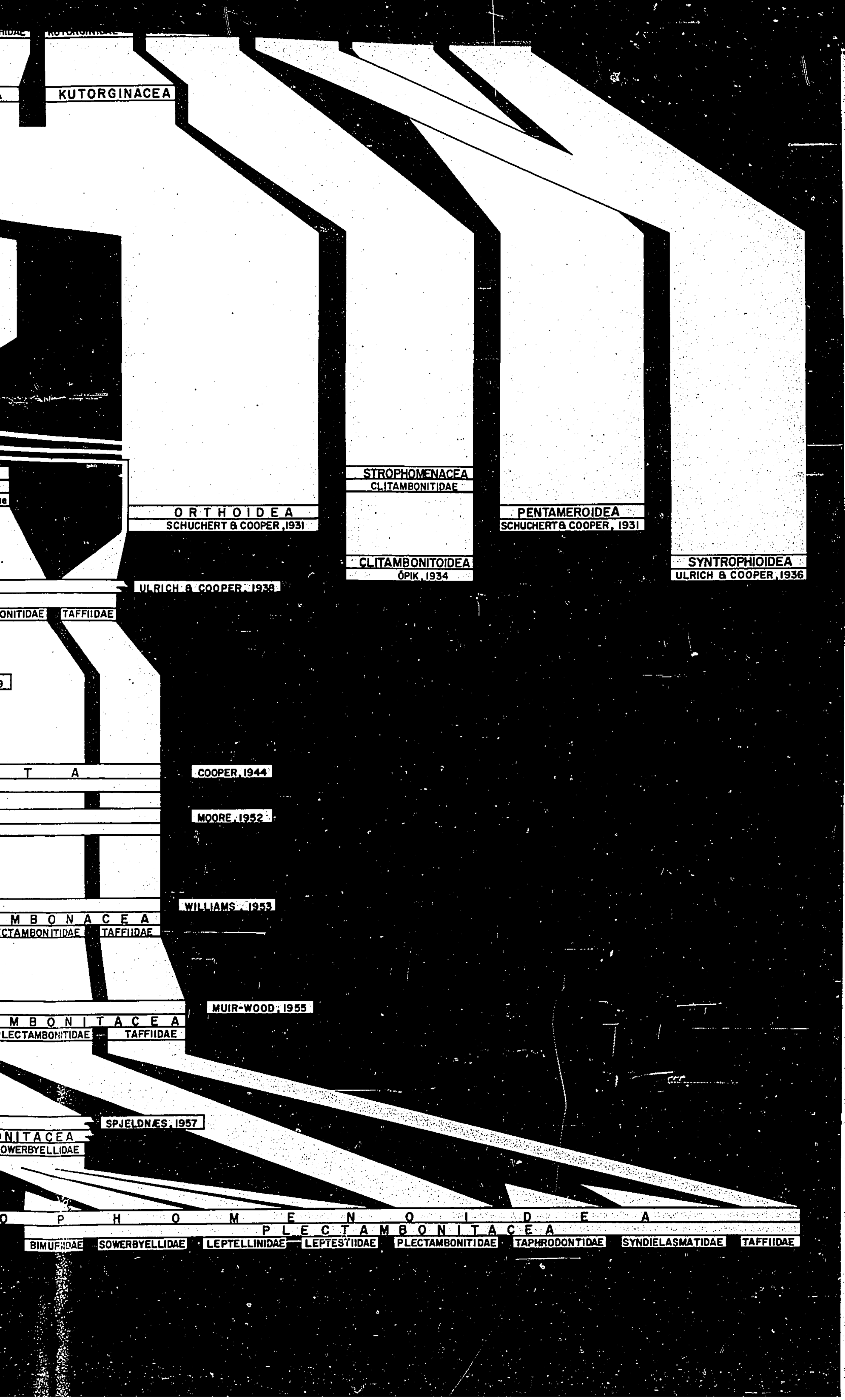
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