Review of Ordovician Pelecypods

GEOLOGICAL SURVEY PROFESSIONAL PAPER 695

U.S. DEPARTMENT OF THE INTERIOR

March 3, 1849

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By JOHN POJETA, JR.

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*Summary of morphological, taxonomic,
phylogenetic, and paleoecological data
for Ordovician pelecypods*

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REVIEW OF ORDOVICIAN PELECYPODS

By John Pojeta, Jr.

ABSTRACT

The study of Ordovician pelecypods has lagged because of the impression that adequate material for detailed investigations was not available. Silicified specimens from the Cincinnati arch area have provided much of the material for the present study. These specimens show the entire shell morphology of many Ordovician species and have helped resolve a number of morphological and systematic questions which have previously hindered the understanding of early pelecypod phylogeny and modes of life.

Ordovician pelecypods are taxonomically and morphologically more diverse than has heretofore been generally recognized. The hard-part morphology of each of the major families of Ordovician pelecypods is described herein, and the families are united into six major phylogenetic groups; almost all other Paleozoic pelecypods can be derived from one or another of these six groups. Because the groups represent the primary radiation of the class, it is proposed that the Pelecypoda be divided into six subclasses: (1) Rostroconchida Cox (Conocardiacea), (2) Palaeotaxodonta Korobkov (Nuculoidea and Solemyoida), (3) Isofilibranchia Iredale (Mytilacea), (4) Pteriomorphia Beurlen (Cyrtodontacea, Arcacea, Limopsacea, Pteriacea, Pinnacea, Ambonychiacea, Pectinacea, Anomiacea, Limacea, and Ostreacea), (5) Heteroconchia Hertwig (Actinodontoida, Babinkidae, Unionoida, Trigonioida, Veneroida, Myoida, and Hippuritoida), and (6) Anomalodesmata Dall (Edmondiidae, Sanguinolitidae=Solenomorphidae, Pholadomyacea, Pandoracea, Megadesmatidae, and ?Septibranchoidea). Five of the six subclasses continue to the present, with only the problematic Rostroconchida becoming extinct.

Mode of life reconstructions for the various epochs of the Ordovician suggest that pelecypods were originally infaunal and point up the diversification of epifaunal forms through Ordovician time.

INTRODUCTION

Ordovician pelecypods are the first undoubted representatives of an important biological group, and of necessity are the forms upon which the phylogenetic speculations of the origin of younger pelecypod taxa are based. Early Paleozoic pelecypods in general, and Ordovician pelecypods in particular, are heirs to several generalizations which at best are only partly correct. Chief among these misunderstandings are the belief that adequate material for detailed studies is not available and the belief that Ordovician pelecypods are a homogeneous group showing little morphologic, ecologic, and phyletic variation. Mainly because of these generalizations, the study of Ordovician pelecypods has lagged far behind that of other Ordovician invertebrates. In the 19th century there was a great deal of descriptive work dealing with Ordovician pelecypods. However, since that time, taxonomic studies have continued on a diminished scale, and little has been added to the knowledge of the detailed stratigraphic distribution of these animals.

In recent years there has been renewed interest in the study of early Paleozoic pelecypods. The silicified specimens that are being obtained from the Ordovician deposits of North America show that adequate material for detailed study is available and that Ordovician pelecypods are not a homogeneous group. It is now possible to document each of the major groups of Ordovician pelecypods morphologically and to use these data to draw ecologic and phylogenetic conclusions.

Phylogenetically, I have grouped Ordovician pelecypods into six major lineages from which almost all other Paleozoic pelecypod groups can be derived. Because the six lineages represent the primary radiation of the class, I propose that the Pelecypoda (Bivalvia) be divided into six subclasses: (1) Rostroconchida Cox (Conocardiacea), Early Ordovician–Permian; (2) Palaeotaxodonta Korobkov (Nuculoidea and Solemyoida), Early Ordovician–Holocene; (3) Isofilibranchia Iredale (Mytilacea), Early Ordovician–Holocene; (4) Pteriomorphia Beurlen (Cyrtodontacea, Arcacea, Limopsacea, Pteriacea, Pinnacea, Ambonychiacea, Pectinacea, Anomiacea, Limacea, and Ostreacea), Middle Ordovician–Holocene; (5) Heteroconchia Hertwig (Actinodontoida, Babinkidae, Unionoida, Trigonioida, Veneroida, Myoida, and Hippuritoida), Early Ordovician–Holocene; (6) Anomalodesmata Dall (Edmondiidae, Sanguinolitidae=Solenomorphidae, Pholadomyacea, Pandoracea, Megadesmatidae, and ?Septibranchoidea), Middle Ordovician–Holocene.

Early Ordovician pelecypod faunas are dominated by infaunal deposit (nuculoid) and suspension (conocardiids, babinkids, redoniids, cycloconchids, and lyrodesmatids) feeders; at this time probably only some of the modiomorphids (and perhaps some conocardiids) were epifaunal suspension feeders. The fact that the earliest pelecypod faunas are dominated by infaunal forms suggests that the ancestral mode of life of the class is infaunal. In the Middle Ordovician there was a diversification of epifaunal suspension feeders with the appearance of the pteriaceans and ambonychiids. However, infaunal forms remain prominent, and are supplemented by the appearance of the edmondiids, sanguinolitids, and some cyrtodontids; other cyrtodontids probably were semi-infaunal in their mode of life.

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MATERIALS AND METHODS

Many museum specimens of Ordovician pelecypods are poor molds and casts. This is partly an artifact of collecting, partly because previous workers did not take advantage of silicified material, partly the result of no one having a long continuing interest in working with these animals, and only partly the result of poor preservation.

Molds and casts preserved on the exposed surfaces of limestone ledges are generally weathered and show little morphological detail other than shell shape (pl. 15, fig. 4). However, "crack-out" specimens from limestone blocks commonly preserve some muscle scars (pl. 14, fig. 6; pl. 15, fig. 7). Such specimens may be internal or composite molds, although in some specimens the recrystallized shell is preserved (pl. 18, fig. 9). Specimens obtained from the splitting of shales commonly preserve the shell sculpture which is commonly superimposed on the internal mold (pl. 13, figs. 16, 17). Unfortunately many of the early workers, on whose reconnaissance studies a large part of our knowledge of Ordovician pelecypods rests, described specimens preserved on the exposed surfaces of limestone ledges or else described inferior molds and casts of various sorts. This approach is understandable in an historical context, as these men were interested in describing large unknown faunas as fast as possible. However, it has created difficulties for later systematists who attempt to use these early names, as well as for workers who wish to summarize data dealing with Ordovician pelecypods.

There is a great deal of silicified Ordovician fossil material in North America. My work since 1965 on the Ordovician faunas of the tristate area of Ohio, Indiana, and Kentucky has resulted in the collecting of 17 tons of rock, which is yielding an abundant and varied silicified pelecypod fauna. In addition, I have smaller collections of silicified Ordovician pelecypods from 10 other American States and one Canadian province.

Silicified material is unrivaled in the information it provides about early Paleozoic pelecypods in that it allows one to observe most of the hard-part morphology of the species concerned (pl. 13, fig. 6). These species are generally preserved as various types of molds and casts (pl. 13, fig. 15) which seldom show hinge-line features, although it is not uncommon for them to show some of the muscle scars. One must crack a great deal of limestone to obtain a relatively few reasonably well-preserved specimens which usually do not provide as much information as does silicified material. Thus, when available, silicified material is preferable for observing shell morphology in Ordovician pelecypods.

The early describers of Ordovician pelecypods seldom took advantage of silicified specimens; when they did use such material it generally consisted of individual specimens weathered free of the matrix and stained a red-brown color. No concentrated efforts were made to etch large quantities of this material in hydrochloric acid. For many years, Dr. G. A. Cooper, U.S. National Museum, has been etching large quantities of Permian limestone and assembling an exquisite collection of silicified Permian invertebrates. I am now attempting to do the same with North American Ordovician faunas, beginning with the classic Cincinnati arch section.

The belief that Ordovician pelecypods show little morphologic variation has been expressed to me on several occasions by colleagues working with younger molluscan faunas. This is categorically not so. From the Middle Ordovician onward, pelecypods form a highly varied and highly successful group that is abundantly represented in the Ordovician platform deposits of North America. Furthermore, most of the higher level Ordovician pelecypod taxa are known from the Early Ordovician onward (figs. 5, 6).

The variability and abundance of Ordovician pelecypods have been masked by several historical and fortuitous factors including: (1) The widespread use of a few common generic names such as *Ctenodonta* for most Ordovician nuculoids and *Modiolopsis* for most modioliform shells. These names have become nearly synonymous with family-level taxa and convey such broad concepts that they hide the fact the animals themselves are much more varied. (2) The literature is highly scattered in a large number of faunal studies and small monographs which have been published in a great many periodicals; until someone compiled this literature no adequate idea of the morphological diversity of the group could be formed. (3) The fact that most describers of Ordovician pelecypods dealt with them as side issues has resulted in a series of confusing, contradictory, and generally vague taxon concepts, which in turn has resulted either in indiscriminate use of generic names or in the lumping of all more or less similar shapes under a few broadly defined names. Many workers have been involved in the description of Ordovician pelecypod species. Most species were described as a part of more general faunal studies, or monographs on the group were prepared between other studies; no one developed a long-term continuing interest in working with these animals, and workers interested in comparing younger pelecypod faunas to Ordovician ones can develop only vague concepts about Ordovician faunas from the available literature. In general the concepts of Ordovician pelecypod taxa are at a stage where the family-level and generic-level categories are poorly defined or are mere lumpings of species under one heading, and most species-level taxa are defined on slight differences in the shape of molds or on geographic or stratigraphic bases.

The seemingly widespread opinion that Ordovician pelecypods were rare faunal elements is again an example of overgeneralization. There is, of course, no comparison between the variety of Ordovician brachiopods and pelecypods when the sum total of genera and species are compared. However, in some areas, pelecypods are known to be as varied as brachiopods. Identified in the Cincinnati arch area, on the basis of specimens obtained from 4 tons of etched limestone in a stratigraphic interval about 400 feet thick (upper Camp Nelson Limestone through Devils Hollow Member of Lexington Limestone) were: 29 species of pelecypods placed in 17 genera, 23 species of brachiopods placed in 21 genera (identified by R. B. Neuman), and 32 species of gastropods placed in 19 genera (identified by E. L. Yochelson). These identifications are all preliminary pending further study and the obtaining of additional specimens; nonetheless, the figures show the order of magnitude of the species present in the three groups studied.

In the Middle Ordovician rocks of central Kentucky (where my collecting has been the most extensive), pelecypods and brachiopods are not necessarily mutually exclusive. They occur together in all combinations from approximately equal numbers of individuals of each group to combinations where one group occurs almost to the total exclusion of the other. I have many collections that have yielded hundreds of individuals of various species of pelecypods. My single largest collection (USGS 6034–CO) is from the Tyrone Limestone. It consisted of 1,468 pounds of limestone, which yielded about 12,500 silicified specimens. Of these about 10,000 were mollusks, whereas only six were brachiopods; 2,200 of the mollusks were pelecypods, 3,200 were gastropods, 4,300 were cephalopods, and there were 95 chiton plates. USGS collection 6134–CO from the Curdsville Limestone Member of the Lexington Limestone consisted of 632 pounds of limestone. Upon etching, this yielded a silicified fauna having 779 pelecypods and 927 brachiopods. USGS collection 6145–CO from the Point Pleasant Limestone consisted of 114 pounds of limestone. Upon etching, this yielded a silicified fauna having 18 pelecypods and 500 brachiopods. Many more examples could be given, but those given above show that in these Middle Ordovician rocks, brachiopods and pelecypods occur together in varying proportions. USGS collection 6034–CO illustrates another point, that at least in the Cincinnati arch area, Ordovician pelecypod species may be represented by large numbers of individuals that may form a significant part of the rock in which they occur.

As the first undoubted representatives of their class, Ordovician pelecypods are often referred to by persons working on younger faunas and are sometimes incorporated into elaborate phylogenetic diagrams. For much of their data, these workers must refer to 19th century authors whose works are subject to the inherent difficulties of the period, especially to the highly interpretive hand-drawn figures which they often published (*Allodesma*, fig. 1*F*, *G*; pl. 2, figs. 1–5; *Plethocardia*, fig. 1*H*; pl. 14, fig. 9). Many of these early drawings are really reconstructions and the specimens from which they were made show various features in an equivocal manner or not at all (Pojeta, 1966, pl. 46, figs. 1–5).

Many of the phylogenetic diagrams of pelecypods show a broad Ordovician base from which a number of branches arise. These diagrams give the general appearance of a bush and imply that in Ordovician time there was some sort of broad, homogeneous, but "plastic" ancestral pelecypod stock. I do not think that this picture is a reasonable approximation of early pelecypod phylogeny. Rather it is a picture that is produced because of a lack of knowledge of many of these early forms. I think that it is possible to document at least six distinct Ordovician pelecypod lineages (figs. 5, 6); four of these lineages are distinct from the Early Ordovician onward, and two are known from the Middle Ordovician onward. In addition there are probably a few more lineages which at present are too poorly known to document adequately. Already by the Early Ordovician, pelecypods had differentiated into several stocks, which suggests that the ancestors of these stocks should be sought in the Cambrian.

Because so much of the knowledge of Ordovician pelecypods still rests upon early reconnaissance studies, the stratigraphic occurrences of generic- and specific-level taxa are known only in a general way, and the group has not been used for the biostratigrahic zonation of the Ordovician. The Cincinnati arch material is providing a beginning for an evaluation of the usefulness of pelecypods for detailed Ordovician biostratigraphic studies; once the vertical succession of the pelecypods is understood in this area it can then be used as a standard of comparison for other late Middle and Late Ordovician sequences.

In the subdivision of the Ordovician into Lower, Middle, and Upper units I have followed Cooper (1956) in placing the Whiterock Stage at the base of the Middle Ordovician, in a position older than the Chazy. Also I have used the traditional Middle–Upper Ordovician boundary as drawn in the Ohio Valley, which places Eden age rocks in the Upper Ordovician. Bergström and Sweet (1966) presented evidence suggesting that Eden age rocks in the Ohio Valley overlap with Barneveld (Trenton) age rocks in New York and that the Eden is not younger but partly or wholly of the same age as the Barneveld. This latter stratigraphic consideration has little effect in figures 5 and 6 as there are only a few pelecypods known from Eden age rocks, and no new higher taxa or phylogenetic groups originate in these rocks.

This report has required the accumulation of specimens from a number of museums, the names of which are subsequently abbreviated as follows: AM, American Museum of Natural History; GSC, Geological Survey of Canada; LGB, Laboratoire de Géologie, Brest; MU, Miami University, Oxford, Ohio; NYSM, New York State Museum; UCM, University of Cincinnati Museum; USGS, U.S. Geological Survey; USNM, U.S. National Museum, Department of Paleobiology; USNMDM, U.S. National Museum, Division of Mollusks; WM, Walker Museum collection at the Field Museum of Natural History, Chicago; YPM, Yale Peabody Museum.

HISTORICAL RÉSUMÉ

The study of Ordovician pelecypods began with Goldfuss' 1836 description of *Pterinea carinata* (fig. 1*I*) from the Ordovician rocks of New York. This species is now recognized as an ambonychiid, probably some species of *Ambonychia* Hall. North American descriptive studies were continued by Conrad, Hall, and a few others in the early reports of the New York Survey, so that by 1850 a few dozen names had been proposed for Ordovician pelecypods. In 1868, Bigsby listed about 300 species names that had been proposed for this group; his compilation was on a worldwide basis, but was largely made up of names proposed for western European and eastern North American forms. In the latter part of the 19th century, a large number of species names were proposed for North American species in many different journals; fortunately this scattered literature was brought together by Miller (1877, 1889–97) and Bassler (1915) in their bibliographies. Bassler (1915) listed about 550 names that had been proposed for North American species to that date.

Miller (1874) was the first worker to attempt anything like a monograph of the group, when he treated all Ordovician pelecypods that had been described from the Cincinnati, Ohio, area. However, it was not until Ulrich began a systematic study of the group in the 1890's that Ordovician pelecypods received any intensive monographic treatment. Between 1890 and 1895 Ulrich published a series of smaller papers (1890a, b, c, 1892a, b) and two lengthy monographs (1893 [1895], 1894); these papers are still the standard references for American species.

Ulrich revised the nomenclature of the group to his satisfaction, although some of his nomenclatural decisions are unusual by 1970 standards. He published his last major paper about Ordovician pelecypods in 1895, although an earlier paper was reprinted in 1897. Occasionally thereafter, Ulrich described a few new species in the works of other authors, but published nothing else dealing with Ordovician pelecypods. However, he was not inactive in the field as his opinion was often solicited by others when they had to deal with these animals, and he was responsible for many of the pelecypod identifications appearing in American Ordovician faunal lists between 1900–40. Toward the end of his life he apparently planned a major paper or papers dealing with Ordovician pelecypods as there are bits and pieces of manuscripts written in a shaky hand and dated in the late 1930's scattered throughout the Ordovician collections of the U.S. Geological Survey and the U.S. National Museum. These manuscripts contain many new names which also often appear on museum labels; however, to my knowledge none of these names were ever published.

Twentieth century American literature dealing with Ordovician pelecypods is not extensive; a number of new names have been proposed, however, as in the 19th century, pelecypods were usually described in more general faunal studies, and only a few papers deal mainly with pelecypods.

Most of the knowledge of North American Ordovician pelecypods is based upon faunas described from the northeastern part of the United States and adjacent parts of Canada. Forms from the southeastern United States are poorly known as are Appalachian and Arctic species; western North American pelecypod faunas are almost unknown, although we are now beginning to accumulate materials from the Ordovician of Nevada and Utah.

In Europe, Ordovician pelecypod studies have been carried out by a number of workers in a series of regional papers which deal with most of the important Ordovician outcrop areas. Here too, many of these studies are now old and many of them were parts of more general faunal studies. Some of the more important works include: Barrande (1881) and Pfab (1934) in Bohemia; Barrois (1891), Thoral (1935), and Babin (1966) in France; Hind (1910), Reed (1944, 1946, and 1952), Lamont (1946), and Harper (1947) in the British Isles; Maillieux (1939) in Belgium; Isberg (1934), Soot-Ryen (1969) and Soot-Ryen and Soot-Ryen (1960) in Scandinavia; Sharpe (1853), Verneuil and Barrande (1855), and Born (1918) in Iberia; Vinassa de Regny (1927) in Sardinia; and Eichwald (1860), Bekker (1921), and Öpik (1930) in Estonia.

Except for a relatively recent monograph on the Middle Ordovician pelecypods of Kazakhstan (Khalfin, 1958), Ordovician pelecypods from other parts of the world have been described as incidental to more general faunal studies, and only a handful of species is known. In Asia, Reed (1912, 1915) described a few species from the Himalayas and Burma, Kobayashi (1934) and Endo (1935) described some species from Korea and Manchuria, and Reed (1917) and Grabau (1922) made some of the Chinese forms known. What little is known about South American Ordovician pelecypods is largely based upon the works of Kobayashi (1937), Harrington (1938), and Rusconi (1954, 1955). Termier and Termier (1950) and Gigout (1951) have described a few shells from the North African Ordovician. Little has been published about Australian, Tasmanian, and New Zealand Ordovician pelecypods, but a few species were described by Johnston (1888), Tate (1896), and Hill, Playford, and Woods (1969).

Since the first Ordovician pelecypod was described in the middle 1830's, about 200 different generic names have been used for pelecypods of this period. About 125 of these names are based upon Ordovician type species; approximately 100 of these latter names are useful or potentially useful, the other 25 being objective synonyms, obvious subjective synonyms, or based upon such poor material that their concepts may never be tied down. As an estimate, based on what is presently known about Ordovician pelecypods, about 150 generic-level taxa would accommodate the morphological variability. This estimate is largely based on North American and western European faunas; how the extensive Ordovician faunas of Asia, South America, and Australia will alter this number when they become better known is of course uncertain. As a basis of comparison, Branson (1948) listed about 160 generic names which had been used for Permian pelecypods; in the past 20 years, Permian mollusks have been investigated far more intensively than Ordovician ones, and a number of new generic names have been proposed for the pelecypods.

On the species level, I know of about 1,400 names which have been used for Ordovician pelecypods (table 1). Unfortunately, most of these names are based upon molds and casts which have been little studied since the names were proposed, and there is no way to predict how many of them will prove to be meaningful conceptual designations. The general impression one obtains from the literature is that Ordovician pelecypods have been split too finely at the species level. Variation studies on Ordovician pelecypods are in their infancy (McAlester, 1963a), but on the basis of the Cincinnati arch silicified material such studies can now be carried out for several species. Branson (1948) listed about 1,500 species level names which had been used for Permian pelecypods; there may be as many as 10,000 names available for Cretaceous pelecypods (E. G. Kauffman, oral commun., 1968), and the estimates of the number of Holocene species are from 10,000 to 20,000.

Of the 1,400 Ordovician species names which I have indexed so far, almost one-third of these are placed in only three genera: *Ctenodonta*, 183 species; *Cyrtodonta*, 116 species; and *Modiolopsis*, 163 species; more than half of all the species names are placed in only 16 generic-level taxa (table 1).

At one time or another, Ordovician pelecypods have been placed in at least 50 different family-level taxa, although all 50 names were not applied to the group at any one time. Recent work suggests that about 15–20 would be sufficient, with approximately half of these families having Ordovician type genera. Vokes' (1967) classification included Ordovician pelecypods in 15 of 51 superfamilies, 10 of 15 orders, and five of six subclasses.

TABLE 1.—*Alphabetic listing of the 223 generic names used for Ordovician pelecypods with the approximate number of species presently assigned to each genus*

[Author names for each genus can be found in Vokes (1967). The generic names listed include all those in which anyone has ever placed an Ordovician species. The species counts per genus are based on the most recent work(s) which deals with the species concerned; as some species have not been revised for a long time, some are still assigned to genera which obviously do not occur in the Ordovician. Of the 223 generic names listed, 18 belong to bivalved animals which also have been placed in the Conocardiacea, Ribeiriidae, or Conchostraca; some of these may be pelecypods, whereas others may be arthropods or distinct bivalved mollusks. Six of the 223 generic names are Ulrich's (1894) informal taxonomic groups of the genus *Ctenodonta*. If these 24 generic names are deleted there remain 199 generic names which have been used for Ordovician pelecypods. Of the 143 genera which have Ordovician type species, 18 belong to bivalved animals which may not be pelecypods and 13 are objective synonyms. Of the 1,487 species, 68 belong to bivalves which may not be pelecypods leaving 1,419 names that have been applied to pelecypods]

Genus	*Type species Ordovician in age*	*Approximate number of Ordovician species presently assigned to each genus*
Actinodonta	Yes	12
Actinomya	Objective synonym *Whiteavesia.*	
Actinopterella	No	1
Actinopteria	No	1
Actinopterinia	Yes	1
Adranaria	Yes	2
Ahtioconcha	Yes	1
Allodesma	Yes	3
Allonychia	Yes	5
Alnifia	Yes	1
Ambonychia	Yes	40
Ambonychinia	Yes	30
Ambonychiopsis	Yes	14
Amita	Objective synonym *Tetinka.*	
Amphicoelia	No	1
Ancilla	Objective synonym *Sluzka.*	
Anderkenia	Yes	3
Angellum	Yes	1
Anodontopsis	No	None
Anomalocoelia	Yes	1
Anomalodonta	Yes	2
Anoptera	Yes	2
Anuscula	Objective synonym *Babinka.*	
Arca	No	4
Aristerella	Yes	2
Astarte	No	2
Avicula	No	11
Aviculopecten	No	1
Babinka	Yes	2
Bodmania	Yes	2
Boucekia	Yes	1
Byssodesma	Yes	1
Byssonychia	Objective synonym *Ambonychia.*	
Cadomia	Yes	2
Callodonta	Yes	1
Cardiola	No	11
Cardiolaria	Yes	1
Cardiomorpha	No	1
Cardium	No	None
Caritodens	Yes	1
Ceromyopsis	Yes	1
Chaenodomus	Objective synonym *Cymatonota.*	
Cleidophorus [*Clidophorus*]	Yes	26
Cleionychia [*Clionychia*]	Yes	24
Clionopistha	No	1
Colpomya	Yes	7
Conocardium	No	13
Corallidomus	Yes	1
Cornellites	No	None
Cosmogoniophorina	Yes	3
Coxiconchia	Yes	2
Ctenodonta	Yes	183
nasuta group	Yes	
gibberula group	Yes	
levata group	Yes	
pectunculoides group	Yes	
recurva group	Yes	
logani group	Yes	
Cucullea	No	1
Cucullella	Yes	3
Cuneamya	Yes	22
Cycloconcha	Yes	4
Cymatonota	Yes	10
Cypricardia	No	4
Cypricardinia	No	4
Cypricardites	Yes	5
Cyrtodonta	Yes	116
Cyrtodontula	Yes	49
Davidia	Yes	2
Dceruska	Yes	2
Dipleurodonta	Yes	2
Disteira	Yes	1
Dolabra	No	1
Dualina	No	1
Ectenocardiomorpha	Yes	5
Ectenoptera	Objective synonym *Opisthoptera.*	
Edmondia	No	10
Elasmodophora	Yes	1
Endodesma	Yes	11
Eoasmussia	Yes	1

Genus	*Type species Ordovician in age*	*Approximate number of Ordovician species presently assigned to each genus*
Eoischyrina	Yes	1
Eopteria	Yes	7
Eridonychia	Yes	None
Euchasma	Yes	2
Euchasmella	Yes	1
Eurymya	Yes	4
Eurymyella	No	2
Filiola	Objective synonym *Dceruska*.	----------
Filius	Objective synonym *Synek*.	----------
Gloria	Objective synonym *Slava*.	----------
Glyptarca	Yes	3
Goniophora	No	7
Goniophorina	Yes	5
Gosseletia	No	1
Grammysia	No	3
Heikea	Yes	26
Hemicardium	No	None
Hippomya	Yes	2
Ischyrinia	Yes	2
Ischyrodonta	Yes	10
Isoarca	No	8
Isocardia	No	2
Leda	No	4
Leptodesma	No	3
Lithobia	Yes	1
Lunulacardium	No	3
Lyonsia	No	None
Lyrodesma	Yes	26
Lyronucula	Yes	1
Macrodesma	Yes	2
Maminka	No	2
Maryonychia	Yes	1
Matercula	Objective synonym *Maminka*.	----------
Matheria	Yes	5
Megalodus	No	1
Megambonia	No	None
Megaptera	Objective synonym *Opisthoptera*.	----------
Modiodesma	Objective synonym *Modiolopsis*.	----------
Modiola	No	None
Modiolodon	Yes	19
Modiolopsis	Yes	163
Modiomorpha	No	6
Myalina	No	5
Myophoria	No	1
Myoplusia	Yes	9
Mytilarca	No	13
Mytilops	No	1
Mytilus	No	3
Nucula	No	35
Nuculana	No	5
Nuculites	No	6
Opistholoba	Yes	None
Opisthoptera	Yes	5
Orthodesma	Yes	32
Orthodontiscus	Yes	None
Orthonota	No	9
Orthonotella	Yes	1
Ortonella	Yes	3
Palaearca	Yes	9
Palaeoconcha	Yes	2
Palaeoneilo	No	9
Palaeopteria	Yes	1
Palaeosolen	No	3
Paracyclas	No	1
Parallelodon	No	2
Parallelodus	Yes	1
Paramodiola	Yes	2
Paramytilarca	Yes	7
Paraphtonia	Yes	4
Patrocardia	Yes	2
Periploma	No	None
Pholadomorpha	Yes	8
Physetomya	Yes	1
Plethocardia	Yes	5
Plethomytilus	No	1
Pleurorhynchus	No	None
Posidonomya	No	4
Praeanomalodonta	Yes	3
Praearca	Yes	3
Praecardium	No	1
Praeleda	Yes	4
Praelucina	No	2
Praemyophoria	Yes	1
Praenucula	Yes	2
Prolobella	Yes	8
Prothyris	No	None
Pseudarca	Yes	3
Pseudaxinus	Yes	1
Pseudocyrtodonta	Yes	2
Pseudoeuchasma	Yes	1
Pseudotechnophorus	Yes	1
Psiloconcha	Yes	13
Psilonychia	Yes	2
Pteria	No	None
Pterinea	No	31
Pteronites	No	1
Pteronitina	Yes	2
Ptychopterinia	Yes	1
Pyanomya	Yes	2
Pyrenomoeus	No	1
Redonia	Yes	7
Rhombopteria	No	1
Rhynchotropsis	Yes	1
Rhytimya	Yes	23
Ribeirella	No	1
Ribeiria	No	15
Ribeirina	Yes	1
Saffordia	Yes	6
Sanguinolites	No	2
Sedgwickia	No	2
Semicorallidomus	Yes	3
Servitor	Objective synonym *Sluha*.	----------
Shanina	Yes	1
Shaninopsis	Yes	18
Siliquarca	Yes	1
Similodonta	Yes	1
Slava	No	7
Sluha	Yes	1
Sluzka	No	2
Solen	No	1
Solenomorpha	No	1
Solenomya	No	1
Sowteria	Yes	1
Spathella	No	1
Sphenolium	Yes	5
Synek	Yes	3
Tancrediopsis	Yes	2
Technophorus	Yes	15
Tellinites	No	1
Tellinomya	Objective synonym *Ctenodonta*.	----------
Tenka	No	1
Tenuis	Objective synonym *Tenka*.	----------
Tetinka	No	1
Thorslundia	Yes	1
Tolmachovia	Yes	1

Genus	*Type species Ordovician in age*	*Approximate number of Ordovician species presently assigned to each genus*
Vanuxemia	Yes	50
Vlasta	No	1
Wanwanella	Yes	1
Wanwania	No	2
Wanwanoidea	Yes	2
Warburgia	Yes	5
Whiteavesia	Yes	20
Whitella	Objective synonym *Cyrtodontula.*	---------

CAMBRIAN BIVALVES

Undoubted pelecypods are documented in the fossil record from the beginning of the Ordovician onward (Tremadoc–Holocene; figs. 5, 6). Early Ordovician pelecypods have been identified from France (Barrois, 1891; Thoral, 1935; Babin, 1966), Malaysia (Pojeta, herein), Manchuria (Kobayashi, 1933), North America (Billings, 1865; Butts, 1941; Cloud and Barnes, 1948), South America (Harrington, 1938), Sweden (Soot-Ryen, 1969), and Wales (Hicks, 1873).

Because pelecypods are well represented in the Early Ordovician, it is reasonable to infer that there must have been some Cambrian (pre-Tremadoc) ancestor(s) of the group. However, the problem of what Cambrian animals can reasonably be assigned to the Pelecypoda is still a vexing one. The various Cambrian bivalves which have been placed in the Pelecypoda are all suspect for one reason or another, and there have been long debates as to whether these Cambrian bivalves are pelecypods, arthropods, or unique bivalved animals.

A group of Cambrian (pre-Tremadoc) bivalves which has sometimes been placed in the Pelecypoda (but which may be a unique group of bivalved animals), is represented by the genera *Bagenovia*, *Cambridium*, (Horný, 1957; Sytchev, 1960), and *Stenothecoides* (Rasetti, 1954; Robison, 1964). These three genera have a peculiar muscle pattern and are not known to have had a ligament. Yochelson (1969) has described bivalved articulated specimens of *Stenothecoides* from the Lower Cambrian of Alaska and Siberia; his reconstruction of the soft tissues of this genus is not pelecypodlike, and he proposed a new class of mollusks, the Stenothecoida, for the three genera.

Of the various Cambrian bivalves the Early to Middle Cambrian genus *Fordilla* Barrande is probably the most pelecypodlike in external appearance (Barrande, 1881; Lochman, 1956). Ulrich and Bassler (1931) placed *Fordilla* in the Conchostraca; Raymond (1946) regarded *Fordilla* as an arthropod of uncertain position; Kobayashi (1954) felt it to be an open question as to whether *Fordilla* is a pelecypod or a conchostracan; and Poulsen (1932, 1967) regarded *Fordilla* as a pelecypod. Arguments as to whether or not *Fordilla* is a pelecypod are based largely upon shell shape, thickness, and composition; little is known about the internal features of the genus, although Barrande (1881) figured a specimen showing some muscle scars and a structure resembling a pallial line.

Morris (1967) placed the Early Cambrian-Late Ordovician group Ribeirioida in the Pelecypoda. However, he documents this placement only with the following statement (1967, p. 469):

> The Bivalvia [Pelecypoda] may have separated as a distinct group of Mollusca by lateral compression as an adaptation to burrowing or ploughing through a soft substrate, i.e., originally infaunal. Primitive forms including the Ribeiroida [sic] attain this having a simple folded shell with a gape along the anterior, ventral and posterior margins; but more advanced groups develop an elastic ligament dorsally joining two calcified shells.

It would seem likely that early bivalved arthropods would also have a simple folded shell. Kobayashi (1933, 1954) in his studies of the ribeirids was impressed by their lack of pelecypod features and considered them to be arthropods. Both Morris and Kobayashi included some Ordovician genera in the ribeirioids which I feel are better allied to the concardiids, for example, *Eopteria* Billings and *Euchasma* Billings; these genera are further discussed on page 22.

Vogel (1962) described the species *Lamellodonta simplex* from the Middle Cambrian of Spain; he classified the species as a pelecypod. The specimens upon which *L. simplex* is based are deformed and all the features which Vogel indicated on his reconstructions are not readily seen on his plate figures. However, some of the figures do show what appear to be elongate teeth; the presence of these apparent teeth suggest that the form may be a pelecypod. Better illustrations and more specimens of *L. simplex* are needed before its pelecypod nature can be unequivocally established.

At one time or another, about 34 species of Cambrian animals have been placed in the Pelecypoda (table 2). In my opinion, none of these species can be unequivocally regarded as a Cambrian pelecypod, although some of them show some features found in pelecypods.

TABLE 2.—*The 17 generic names that have been applied to Cambrian animals which at one time or another were thought to be pelecypods*

Genus	*Approximate number of Cambrian species which have been placed in each genus*
Ambonychia	1
Bagenovia	3
Cambridium	2
Ctenodonta	5
Cypricardia	1
Davidia	3
Fordilla	2
Lamellodonta	1
Modioloides	1
Modiolopsis	4
Ozomia	1
Palaeoneilo	1
Posidonomya	1
Ribeiria	1
Stenothecoides	5
Synek	1
Wanwania	1

ORDOVICIAN PELECYPODS

ACTINODONTOIDA

Three Ordovician families (Cycloconchidae, Lyrodesmatidae, and Redoniidae) seem to be related to one another on the basis of a common dental pattern and can be united in an upper level taxon. There is a serious problem as to what to call this taxon. Douvillé (1912, 1913) placed *Actinodonta*, *Lyrodesma*, *Modiolopsis*, *Redonia*, and others in his higher taxon Actinodonta, based on what he regarded as a common dental pattern among these genera. Dechaseaux (1952) placed *Actinodonta*, *Lyrodesma*, and the families Ambonychiidae, Anthracosiidae, and Cyrtodontidae in a suborder Actinodonta of the order Taxodonta. These groupings are extremely broad, and unite diverse stocks under one heading on a presumed relationship between diverse dental patterns.

Newell (1965) placed the Carydiidae, Cycloconchidae, Lamellodontidae, and Modiomorphidae in the order Actinodontoida; at the same time he allied the Lyrodesmatidae questionably to the order Trigonioida, and placed the Actinodontoida, Trigonioida, and Unionoida in the subclass Palaeoheterodonta.

As an ordinal-level taxon, the Actinodontoida (Actinodonta) has at one time or another included most Ordovician, nonnuculoid, dentate pelecypods. It has been a convenient wastebasket grouping that was either vaguely defined or else defined on the basis of features which were equivocally possessed by a number of forms placed in the order.

Cox (1960) proposed that Dall's (1900) name Pantodontida be used for a taxon which included: *Actinodonta*, *Allodesma*, *Cycloconcha*, *Ischyrodonta*, *Lyrodesma*, and *Redonia*. This proposal has the advantages of eliminating the confusing term Antinodonta (Actinodontoida) as an ordinal-level taxon and of not allying the modiomorphids to the other included groups. However, Cox's concept of the Pantodontida was significantly broader than Dall's which included only *Allodesma* and *Cycloconcha*, and the name Pantodontida is little known.

Further, *Allodesma* is founded on poor material (pl. 2, figs. 1–5). Ulrich's (1894) reconstruction of the hinge needs to be corroborated (fig. 1*F*, *G*) and based on what is presently known of the genus it cannot be allied to *Actinodonta*, *Cycloconcha*, *Lyrodesma*, and *Redonia*. *Ischyrodonta* is a problematic form, some species of which may possess a duplivincular ligament (pl. 1, fig. 6); if this is so, these species might better be allied to the Cyrtodontidae as suggested by Ulrich (1893 [1895]).

In spite of its obvious drawbacks, it seems best to use the name Actinodonta, as Actinodontoida, for a grouping including the Cycloconchidae, Lyrodesmatidae, and Redoniidae. Actinodontoida is widespread in the literature, and at one time or another has included all of the groups which I would place in it. Short of proposing a new name it is a matter of redefining Pantodontida which has not been widely used or redefining Actinodontoida which often appears in the literature. What the latter has lacked is an adequate conceptual base; my definition of Actinodontoida follows.

Phylum MOLLUSCA Cuvier, 1797
Class PELECYPODA Goldfuss, 1820
Subclass HETEROCONCHIA Hertwig, 1895

Order ACTINODONTOIDA Douvillé, 1912

Shell equivalved, inequilateral; beaks prosogyral or opisthogyral; nonbyssate; sculpture usually of concentric growth lines, sometimes with a few radial ribs; ligament opisthodetic, elongated, and parivincular.

Pallial line continuous in attachment, integropalliate or sinupalliate; dimyarian, adductors subequal, anterior adductor supported by a myophoric buttress on its posterior face; pedal muscles, two or more pairs; dentition flaring, ventrally divergent, with all of the teeth reaching or nearly reaching the beaks; at least primitively, the posterior teeth extend the full length of the dorsal margin posterior to the beaks and extend under the ligament.

The Ordovician range of the Actinodontoida is Arenig-Richmond (late Early Ordovician-late Late Ordovician).

This definition is sufficiently broad to include non-Ordovician forms such as the Carydiidae Haffer (1959) which may be late surviving actinodontoids; it is framed so as to exclude forms with a duplivincular ligament and all byssate groups.

Babin (1966) used the ordinal name Pantodontida for essentially what I have called Actinodontoida. He defined the Pantodontida as being inequivalved; this is probably a misprint as each of the genera concerned is equivalved, and Babin defined them as such.

CYCLOCONCHIDAE

Two genera are herein included in the Cycloconchidae. *Cycloconcha* Miller (pl. 2, figs. 6–21; pl. 3, figs. 1–4) is known from about 200 specimens from Middle and Upper Ordovician rocks from the tristate area of Ohio, Indiana, and Kentucky. The genus presently includes four named species all of which are small, the largest known specimen being 30 mm long. *Cycloconcha* possesses well-defined cardinal, anterior lateral, and posterior lateral teeth (pl. 2, figs. 14–17); the teeth are numerous and all reach or nearly reach the beaks. In addition, the genus is elongate in an anterior-posterior direction (pl. 2, figs. 6, 7) and has an external, elongate ligament posterior to the prosogyral beaks (pl. 2, figs. 12, 18, 21), an integropalliate pallial line (pl. 3, figs. 1, 2), and multiple pedal scars extending between the adductors (pl. 2, figs. 8, 9; pl. 3, fig. 3).

Actinodonta Phillips (pl. 1, figs. 3–5) has been reported from the lower Middle Ordovician rocks of Great Britain and Morocco (Llanvirn and Llandeilo), but it is best known from the Armoricain Sandstone of Arenig age (Early Ordovician) of Brittany. It too is a small shell, generally less than 50 mm long. Although the details of the morphology of *Actinodonta* are poorly known, many of the published figures of species of the genus show a hinge line with numerous well-developed diverging teeth all of which reach or almost reach the beaks (pl. 1, fig. 3). Commonly the teeth can be divided into cardinal, anterior lateral, and posterior lateral elements; as in *Cycloconcha* the posterior lateral teeth run the length of the hinge line posterior to the beaks (pl. 1, fig. 5). Babin (1966, p. 230) illustrated the hinge lines of several species of *Actinodonta*.

Based upon the similarity of dentition a close phylogenetic relationship is indicated between *Cycloconcha* and *Actinodonta*.

LYRODESMATIDAE

The Lyrodesmatidae is presently regarded as a monotypic family, although *Lyrodesma* Conrad will probably be subdivided when it is studied in more detail; Fischer (1886) and Stewart (1920) suggested bases for subdividing the genus. Babin (1966) placed *Siliquarca* Tromelin and Lebesconte [*Pseudarca* Tromelin and Lebesconte] in the family. *Siliquarca* is usually considered to be a nuculoid (McAlester, 1968); however, it is so poorly known that its affinities are uncertain.

Lyrodesma as presently recognized is primarily a Middle and Late Ordovician genus occurring in North America and Great Britain (pl. 3, figs. 5–23); it may range into the Silurian as noted by Ziegler, Cocks, and Bambach (1968). However, at least two species of similar animals (*L. armoricana* Tromelin and Lebesconte and *L. acuminata* (Barrois)) are known from the Lower Ordovician (Arenig) rocks of Brittany (pl. 3, fig. 11; fig. 1*A*–*E*). *L. acuminata* was originally placed in *Nuculites* by Barrois (1891), however, as figured by him and by Babin (1966) it is most probably a species of *Lyrodesma.*

The Middle and Late Ordovician species of *Lyrodesma* have a prominent dentition which flares outward from, but is concentrated immediately below, the beaks (pl. 3, figs. 10, 15, 20, 23). At first glance this appears to be distinct from the dentition of the Cycloconchidae. However, in some species of Middle and Late Ordovician Lyrodesmas the posterior teeth are significantly longer than the other teeth (pl. 3, figs. 9, 23); further, Barrois (1891) figured specimens of *L. armoricana* (Early Ordovician) which have prominent posterior lateral teeth that extend the length of the dorsal margin posterior to the beaks (fig. 1*A*–*C*). I have made a very serious attempt to locate Barrois' specimens of *L. armoricana* but have been unable to find them. However, Dr. Claude Babin has sent me a specimen of this species which shows the dentition (pl. 3, fig. 11). It is a shell with *Lyrodesma* shape and prominent posterior lateral teeth and sockets which run the length of the posterior dorsal margin.

Thus, the oldest known members of the Lyrodesmatidae have a dentition similar to that of the Cycloconchidae. In some of the Middle and Late Ordovician Lyrodesmas the posterior teeth are still significantly longer than the other teeth (pl. 3, figs. 9, 23), although they no longer occupy the entire dorsal margin posterior to the beaks; in other Middle and Late Ordovician Lyrodesmas (pl. 3, figs. 10, 15, 20) the posterior teeth are not appreciably different in size from the other teeth. This reduction in the length of the posterior lateral teeth is the most obvious trend in the evolution of lyrodesmatids; it is a trend not seen in the Ordovician cycloconchids.

Lyrodesma is unique in that it is the earliest known siphonate pelecypod which possesses a pallial sinus (pl. 3, figs. 16–18). This feature must be strongly emphasized for it indicates that infaunal siphonate pelecypods originated early in the history of the class and not in the middle or late Paleozoic as is sometimes suggested.

REDONIIDAE

Babin (1966) proposed the family Redoniidae for the Early and Middle Ordovician genus *Redonia* Rouault. *Redonia* is not known to occur in North America, and I have seen few specimens of the genus; therefore, the following discussion is based largely upon the literature, especially upon the recent review of the group by Babin.

The dentition of *Redonia* (pl. 1, fig. 7; fig. 2*A–C*) differs from that of other actinodontoids in that the number of teeth per valve is reduced. In lyrodesmatids (pl. 3, figs. 10, 15, 20, 23) and cycloconchids (pl. 2, figs. 14, 15) it is common to have five or six teeth per valve, and there may be as many as seven or eight (pl. 3, fig. 12); rarely there are as few as four teeth per valve (Babin, 1966, p. 230, fig. 1). According to Babin (1966, p. 243), redoniids have one or two long posterior lateral teeth and one or two short anterior teeth (pl. 1, fig. 7; fig. 2*A–C*). Especially important in relating the redoniids to the cycloconchids and lyrodesmatids are the observations that all the teeth reach or nearly reach the beaks, and that the posterior lateral teeth extend the length of the dorsal margin posterior to the beaks. *Redonia* shows such other actinodontoid features as a myophoric buttress supporting the posterior face of the anterior adductor muscle and an external ligament.

At one time or another, *Redonia* has been allied to several other pelecypod groups. Most recently Chavan (1954, 1966a, b, 1967) regarded it as being a carditacean belonging to the family Permophoridae [Kalenteridae]

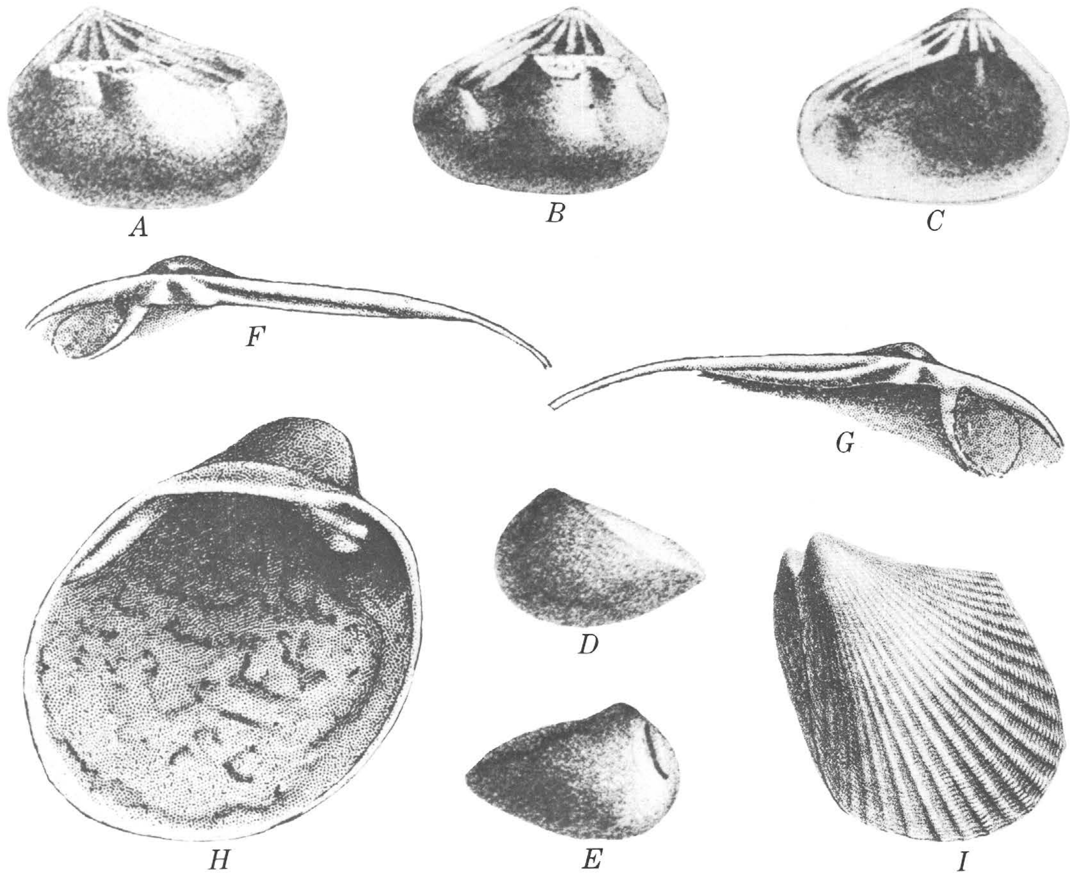

FIGURE 1.—*Lyrodesma, Allodesma, Plethocardia,* and *Ambonychia* from various authors. *A–C, Lyrodesma amoricana* from Barrois (1891). *D, E, Lyrodesma acuminata* from Barrois (1891). *F, G, Allodesma subellipticum,* reconstruction of hinge line from Ulrich (1894). See also plate 2, figures 2 and 5; *H, Plethocardia umbonata,* reconstruction of hinge line from Ulrich (1894). See also plate 14, figure 9. *I, Ambonychia carinata* from Goldfuss (1836). *A–H* are × 2; *I* is natural size.

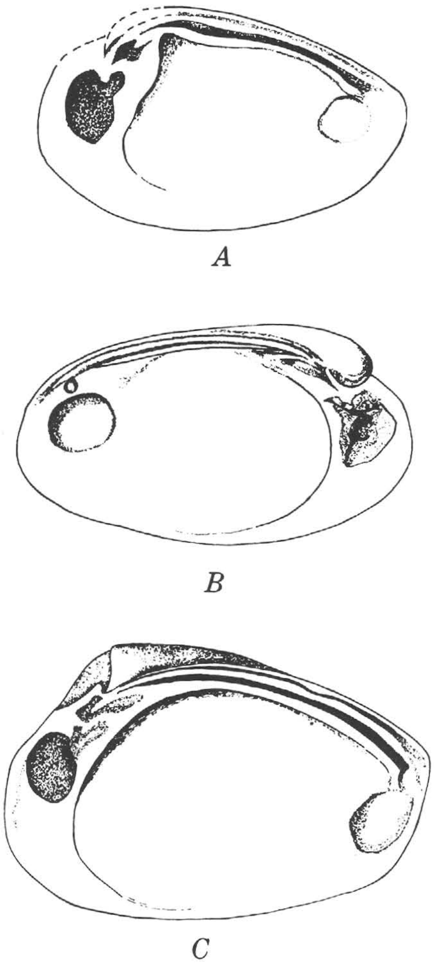

FIGURE 2.—*Redonia deshayesi* Rouault. Drawings of casts from Babin (1966). *A*, × 5. *B*, *C*, × 3. Reproduced with permission of the author.

on the basis of his interpretation of the homologies of the teeth of *Redonia* using Bernard's notation.

Newell (1957) included *Redonia* in the mytiliform family Modiomorphidae [Modiolopsidae] on the basis that at least some modiomorphids have posterior lateral teeth extending backward from the beaks under the ligament. This does not seem to be the so among Ordovician modiomorphids; species in which the hinge line is well known are either edentulous (pl. 17, figs. 1, 3, 11, 13, 15) or possess only cardinal teeth (pl. 13, figs. 6, 8). This topic will be further discussed below in the section entitled Modiomorphidae.

The oldest known specimens of *Redonia* are from the Arenig rocks of Brittany (Barrois, 1891; Babin, 1966) and south-central France (Thoral, 1935).

BABINKIDAE

The Babinkidae is a monotypic taxon represented by the now well-known genus *Babinka* Barrande which contains the two species *B. prima* Barranda, 1881 (pl. 1, figs. 12–14) and *B. oelandensis* Soot-Ryen, 1969.

At the time the concept of the Monoplacophora was being constructed, in the early and middle 1950's, Vokes (1954) briefly reviewed a few species of early Paleozoic pelecypods which possess multiple pedal scars. The species reviewed included *B. prima*, and Vokes felt that the multiple pedal scars indicated a phylogenetic relationship between monoplacophorans and early pelecypods.

Horný (1960) considered monoplacophorans and multiple-muscled hypothetical pelecypods as having arisen independently from an annelid ancestor. He regarded *Babinka* as being the closest known pelecypod to the hypothetical diplacophoran pelecypod ancestor. He placed *Babinka* in a separate order of pelecypods—the Diplacophora—and felt that all pelecypods were descended from this type of ancestor.

McAlester (1964, 1965, 1966) described the shell morphology of *Babinka* in detail, discussed its taxonomic position within the Pelecypoda, and speculated on its relationship to the Monoplacophora.

Babinka prima is known from about 136 specimens from rocks which range in age from late Tremadoc to about Llanvirn (early Early Ordovician to early Middle Ordovician) in south-central France (Thoral, 1935; Dean, 1966) and Bohemia (McAlester, 1964, 1965, 1966), and thus it is one of the earliest known undoubted pelecypods. McAlester did not regard *Babinka* as the stem stock from which all other pelecypods arose. Rather he presented convincing documentation that *Babinka* is the earliest known lucinoid pelecypod; previously lucinoids had not been reported from rocks older than Middle Silurian, and none are presently known between the early Middle Ordovician and the Middle Silurian.

Lucinoids are infaunal suspension feeders; they differ from other pelecypods having this mode of life by lack of a posterior inhalent siphon, although they have both anterior and posterior inhalent currents and some have a posterior exhalent siphon (Allen, 1958). In all lucinoids, the anterior inhalent current is the main feeding and respiratory current. Such an anterior inhalent current is regarded as a phylogenetically primitive feature in various taxodonts and solemyids. However, Allen (1958, p. 480) considered the anterior inhalent current of lucinoids to be a secondary specialization on the basis of the observation that living forms have the posterior inhalent and exhalent apertures of typical pelecypods.

Lucinoids use the foot for burrowing and locomotion and also for the construction of a mucous-lined anterior inhalent tube which connects the front edge of the mantle cavity with the water-sediment interface. The posterior exhalent current discharges either directly into the sediment or to the surface through a retractable posterior siphon. Correlated with this specialized mode of life is a characteristically elongated anterior adductor muscle which has a complex ciliary sorting mechanism for directing food to the mouth. Commonly, especially in the family Lucinidae, the anterior end of the shell is prominently expanded.

Babinka has an anteriorly expanded shell; the anterior adductor muscle scar is somewhat larger than the posterior one, but it is not nearly so elongated as in later lucinoids (pl. 1, fig. 14). McAlester (1965) also described a vague elongated impression below the anterior adductor scar in *Babinka* which he felt suggested that the ciliary sorting mechanism might have been developing. In general external physiognomy, *Babinka* is lucinoid, and the bulk of its other shell features fall within the range of variation expressed by later lucinoids. One would not expect the earliest members of a group to exhibit all the complex of characters which the later members of the group possess. At the very least, *Babinka* shows some lucinoid features, it is the only Ordovician form known to exhibit these tendencies, and it is a fair appraisal of our present knowledge to regard *Babinka* as the earliest lucinoid related to members of the group which became prominent in Silurian time.

The chief critic of the lucinoid assignment of *Babinka* is Chavan (1966a). He has pointed out that *Babinka* is morphologically further removed from Silurian lucinoids than the latter are from post-Paleozoic members of the group. This is especially true in the elongation and digitation of the anterior adductor scar which is prominent in the Silurian lucinoid *Ilionia* Billings but almost absent in *Babinka*. Chavan felt that the dentition of *Babinka* is not comparable to lucinoids, and that such features as anterior shell elongation and lack of a pallial sinus are too widespread among many groups to have significance in placing *Babinka* in the lucinoids.

Chavan did not derive the lucinoids from *Babinka* and he placed the genus in the Actinodontoida. *Babinka* does not have actinodontoid dentition, as least not in the sense that I have defined this feature (p. 9). Unfortunately, the dentition of *Babinka* is known only from the youngest (early Middle Ordovician) representatives of the genus. If the older representatives of the genus are found to have the elongate posterior teeth of actinodontoids, then *Babinka* can be placed in the Actinodontoida. If *Babinka* never had such teeth, then it and the younger lucinoids probably form a lineage distinct from the other heteroconchians and should be placed in a separate subclass.

At the same time that McAlester related *Babinka* to the lucinoids, he postulated that *Babinka* was a direct descendant of monoplacophoran (or monoplacophoranlike) mollusks and that *Babinka* (and therefore the lucinoids) arose independently of other pelecypods indicating that the pelecypods are "polyphyletic" and that for these reasons the lucinoids should be taxonomically separated from other pelecypods at a high taxon level. His arguments on these latter points are based upon a series of comparisons of the muscle scars of *Babinka prima* to the musculature of *Neopilina galatheae* Lemche. McAlester rightly placed only secondary emphasis on the multiple pedal scars of *Babinka* as indicating a relationship to the Monoplacophora; rather he based his arguments on a set of small accessory muscle scars and the total muscle scar pattern of *Babinka* which he regarded as being close to that of *Neopilina galatheae*.

Many groups of pelecypods, both living and fossil, are known to possess multiple pedal or multiple byssal muscles; these muscles are used for movements of the foot or for adjustment on the byssal anchorage. Two pairs of pedal muscles are the common situation in living heteroconchian pelecypods. However, some living nuculoids, cardiids, pteriids, and mactrids have from three to five pairs of pedal muscles (McAlester, 1965, p. 234; Newell, 1937 [1938], p. 21). Among Paleozoic pelecypods, multiple pedal or byssal scars are known in several groups including: nuculoids (Driscoll, 1964, p. 62), modiomorphids (pl. 13, figs. 7, 11), ambonychiids (pl. 10, fig. 17), myalinids (Newell, 1942, p. 30), cycloconchids (pl. 2, figs. 8, 9; pl. 3, fig. 3), and babinkids (pl. 1, figs. 12–14); if anything, the condition seems to be more widespread in the Paleozoic. Because multiple pedal or byssal scars occur in a number of unrelated and variously specialized recent and fossil pelecypods, this feature by itself does not indicate an especial relationship of any one stock to the Monoplacophora.

Babinka has eight pairs of pedal scars running between and over the adductor scars, and ventral to the pedal scars are numerous pairs of smaller accessory scars (pl. 1, figs. 12–14). *Neopilina galatheae* also has eight pairs of pedal muscles and has numerous pairs of smaller muscles laterad the pedal muscles (fig. 3*A*); these smaller muscles serve as pallial, ctenidial, and visceral muscles.

Neopilina galatheae has five pairs of ctenidial retractors on each side of the body, and these are situated between the third and seventh pedal muscles (fig. 3*A*); the numerous smaller accessory muscle scars of *Babinka* are situated approximately between the third and seventh pairs of pedal muscles (although they almost reach the second pair of pedal muscles) and have been

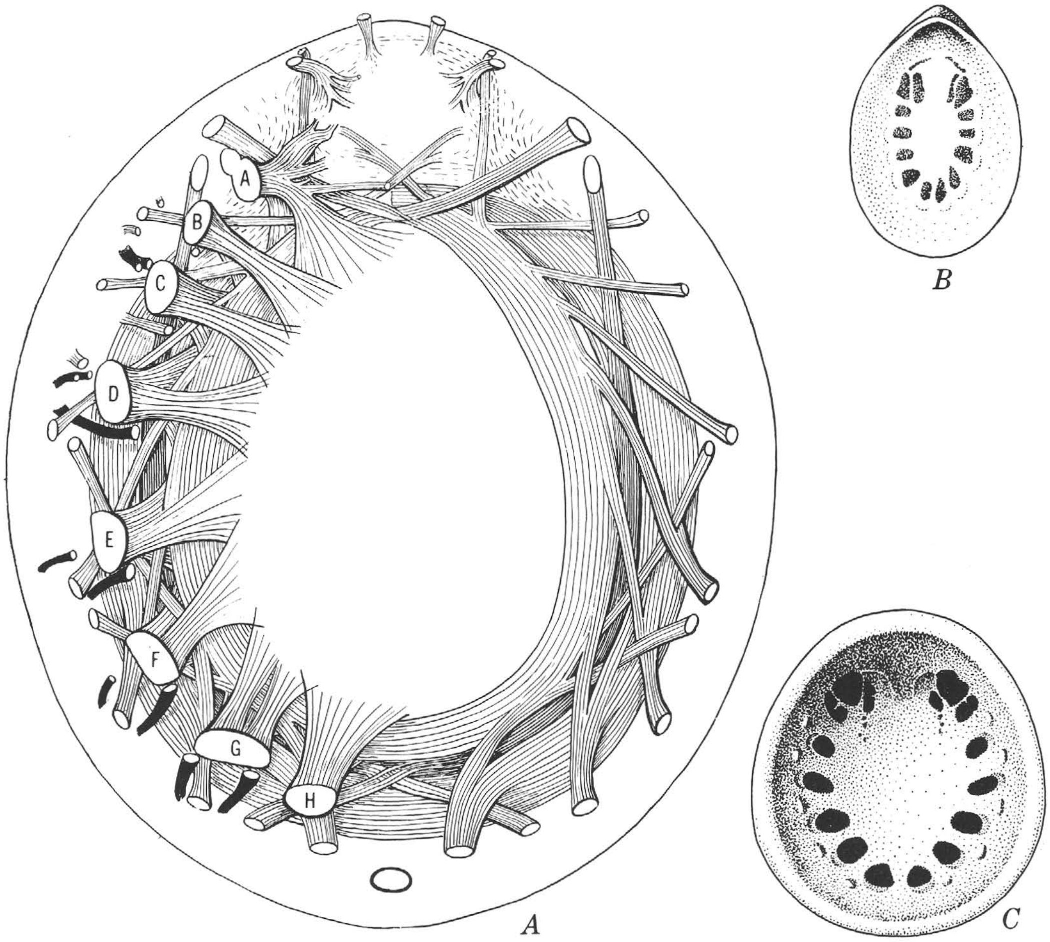

FIGURE 3.—Monoplacophorans. *A*, Reconstruction of body musculature of *Neopilina galatheae* modified from Lemche and Wingstrand (1959, pl. 35, fig. 121). × ⅔ of their figure. Lettered muscles are the pedal retractors, and blackened muscles are the ctenidial retractors. Reproduced with permission of the authors. *B*, Pedal retractor muscle scars of *Pilina* from Knight and Yochelson (1960). *C*, Pedal retractor muscle scars of *Archacophiala* from Knight and Yochelson (1960). *B* and *C* are natural size and are from the Treatise on Invertebrate Paleontology, courtesy of The Geological Society of America and The University of Kansas.

called ctenidial retractors (pl. 1, figs. 12–14). The proposed relationship of *Babinka* to the Monoplacophora is based upon the similarity in the number of pedal scars and, more importantly, upon the positioning of the smaller gill retractors of *Neopilina galatheae* and more or less similar scars of *Babinka prima* between the third and seventh pedal scars in the former species, and approximately between the third and seventh pedal scars in the latter species.

McAlester (1965) also pointed out that the Silurian monoplacophoran *Pilina* Koken has eight pairs of pedal retractors, and he showed that this number also occurs in early Paleozoic forms. However, the distribution of the pedal retractors in *Pilina* (fig. 3*B*) is quite different from that of *Neopilina galatheae* (fig. 3*A*). The three anteriormost scars of *Pilina* may represent multiple origins of only one muscle; this is the interpretation given by Knight and Yochelson (1960) for a more or less similar arrangement of pedal scars in the Ordovician monoplacophoran *Archaeophiala* Perner (fig. 3*C*). The number of pedal retractors in early Paleozoic monoplacophorans ranges widely from the possible eight pairs in *Pilina* to two pairs in *Cyrtonella* Hall. Eight pairs of linearly arranged pedal retractors, which represent the known maximum for monoplacophorans, occurs unequivocally only in one species of the Holocene genus *Neopilina* and at best is not a common condition in early Paleozoic monoplacophorans. Thus, to extrapolate from a living monoplacophoran to an Ordovician pelecypod on this basis leaves a strong element of uncertainty.

The numerous smaller scars of *Babinka* are known from only one specimen of that genus; their positioning approximately between the third and seventh pedal retractors, though similar to the positioning of ctenidial retractors in *Neopilina galatheae*, may be fortuitous as the variation or lack of variation of this positioning in *Babinka* cannot be established at the present time. Furthermore, additional living species of *Neopilina* have been described which have a different number of gills than *N. galatheae*. *N. ewingi* Clarke and Menzies (1959) is known to have six pairs of gills; although the details of the anatomy of this species are not yet available, it presumably has six pairs of gill retractors on each side. It is not known if all of these are positioned between the third and seventh pair of pedal retractors.

In some groups of pelecypods, such as the astartids, a variable number of small muscles originate high in the umbonal cavity (pl. 1, figs. 1, 2) and insert into various organs in the visceral mass. In some of the Miocene Astartes from Chesapeake Bay there are from one to seven pairs of such muscle scars in a single species. These muscles, rather than the branchial retractors of *Neopilina galatheae*, may be the homologues of the numerous small accessory muscles of *Babinka*.

Proponents of the monoplacophoran-*Babinka* relationship feel that the muscle patterns in *Babinka prima* and *Neopilina galatheae* are too similar to be entirely the result of chance and that it is reasonable to infer that the pedal and small accessory scars of *Babinka* represent and inheritance from some sort of monoplacophoran ancestor. I feel that the gaps in knowledge of the variation in the small accessory scars of *Babinka* and the gill retractors of *Neopilina*, the lack of demonstration of the occurrence of eight linearly arranged pairs of pedal retractors in early Paleozoic monoplacophorans, and the presence of possible homologues of the small accessory muscles of *Babinka* in other groups of pelecypods weigh heavily against the probability of a *Babinka*-monoplacophoran relationship exclusive of all other pelecypods. At the present time there is no need to separate the lucinoids from all other pelecypods at the subclass level for reason of a possible relationship of this group to the Monoplacophora. However, as discussed above, Babinka and the lucinoids should perhaps be separated at the subclass level for other reasons.

The probable lucinoid relationship of *Babinka* is one of the links in the chain which points up the diverse origins of various later pelecypod taxa in Ordovician ancestors. Ordovician pelecypods do not form some sort of undifferentiated "plastic" stock which from time to time gave rise to later groups; already by Ordovician time, pelecypods had differentiated into several major phyletic lines which are not readily related to one another, or to another molluscan group, on the basis of the known fossils.

NUCULOIDS

Until recently, most Ordovician nuculoids were placed in the single family Ctenodontidae; this arrangement is now being questioned, and the family-level taxa of the group are in a state of flux.

To date no Ordovician nuculoids with a resilifer have been discovered; all have a continuous tooth row with no ligament pit interrupting it (pl. 4, figs. 13, 17, 18, 20; pl. 5, figs. 3, 20; pl. 6, fig. 9). Ulrich (1894) noted that Late Ordovician species of what he called the *Ctenodonta levata* group have a small undefined pit beneath the beak, whereas Middle Ordovician species of this group do not, I have examined Ulrich's Late Ordovician specimens of the species concerned (pl. 5, figs. 14–16), and in my opinion the material is not well enough preserved to establish the presence of such a pit. In most Ordovician nuculoids the teeth below the beaks are very small, and it is only on the best of specimens that they can be seen. Pfab (1934) indicated the presence of a ligament pit in some of the Bohemian Ordovician nuculoids; this structure is clearly indicated on his text figures but is not obvious on his photographs. Thus, on the basis of what is presently known, the evolution of a resilifer in nuculoids seems to have been a post-Ordovician development.

Ordovician nuculoids are a highly varied and successful group, although this fact has been hidden to a large extent by the placement of most of them in one of two genera. *Cleidophorus* Hall has been used for those species having a prominent anterior myophoric buttress (pl. 6, figs. 1, 2) which leaves a slit-like impression in molds, and *Ctenodonta* Salter has been used for those forms supposedly lacking a prominent anterior buttress. It is now generally felt that *Cleidophorus* is a synonym of *Nuculites* Conrad, a name long used for similar Silurian-Devonian shells, and indeed there is relatively little morphologic diversity in this stock.

On the other hand, *Ctenodonta* means many things to many people; the name has been used so widely for so many different nuculoids that the only information it now conveys is that a nuculoid is being described. Small *Nucula*-like shells (pl. 5, figs. 1–6), large *Nuculana*-like shells (pl. 4, figs. 6, 7), and a host of intermediate shell shapes (pl. 1, figs. 8–11; pl. 5, figs. 7, 8; pl. 6, figs. 9–15) have all been placed in *Ctenodonta*. At least 180 Ordovician nuculoid species have been placed in *Ctenodonta*, and the name has been used for some nuculoids in every Paleozoic system.

Ulrich (1894) divided *Ctenodonta* into a series of informal taxa, each of which was named after a "typical" species and called a group. His informal nomenclature has been used by a few workers but has not gained widespread acceptance; some of his groups are clearly generic-level taxa. A few workers have proposed additional generic-level taxa for Ordovician nuculoids; however, for the most part these names have not been widely used. In some taxa this was due to poor initial conceptualization; a few names were consciously avoided (for example, *Palaeoconcha* Miller; Ulrich, 1894, p. 580), and in North America in particular almost all names except *Ctenodonta* and *Cleidophorus* were simply neglected.

North American Ordovician nuculoids as known at the present time belong to a minimum of eight generic-level taxa: *Ctenodonta* Salter (pl. 4, figs. 1–24), *Deceptrix* Fuchs (pl. 5, figs. 7–20), *Myoplusia* Neumayr (pl. 6, figs. 3–5), *Nuculites* Conrad (pl. 6, figs. 1, 2), *Palaeoconcha* Miller pl. 6, figs. 6–8), *Palaeoneilo* Hall and Whitfield (pl. 1, figs. 8–11), *Similodonta* Soot-Ryen (pl. 5, figs. 1–6), and *Tancrediopsis* Beuhausen (pl. 6, figs. 9–15). Further, some authors recognize *Praenucula* Pfab as being distinct from *Deceptrix*, and the known material suggests that at least three new genera have not been named. There may be as many as 12 genera of North American nuculoids where previously only two genera were usually recognized. In Europe at least two additional Ordovician genera are recognized: *Cardiolaria* Munier-Chalmas and *Cadomia* Tromelin; *Pseudarca* Tromelin and Lebesconte is a European genus which is usually classified as a nuculoid, however, its affinities are uncertain.

The name *Ctenodonta* was originally proposed for large opisthogyrate *Nuculana*-form shells, *Tellinomya nasuta* Hall being the type species (pl. 4, figs. 1–3). The name should be restricted to this general type of shell. In eastern North America this type of shell is known to range from the Murfreesboro Limestone (Porterfield Age) (pl. 4, figs. 11, 12) to the Waynesville Shale and Kagawong beds (Richmond Age) (pl. 4, figs. 8, 9). In western North America, shells assignable to *Ctenodonta* are known from the Antelope Valley Limestone of Nevada (pl. 4, figs. 16, 17) and from the Ordovician of the Seward Peninsula of Alaska (pl. 4, figs. 14, 15). Elsewhere in the world, *Ctenodonta* s. s. has been reported from the Ordovician Gordon Limestone of Tasmania (Johnston, 1888, pl. 5). Recently acquired shells from the Ordovician part of the Setul Formation of Malaya (probably latest Early Ordovician, Yochelson and Jones, 1968) are the oldest known specimens of the genus (pl. 4, figs. 20–22).

The name *Tancrediopsis*, proposed about 70 years ago, was little used for Ordovician shells until recently (McAlester, 1963a). It is used for small triangular shells whose stratigraphic distribution is not well known (pl. 6, figs. 9–15), but which are found in the Middle and Upper Ordovician rocks of North America. Among the oldest specimens assignable to this genus are those from the Antelope Valley Limestone of Nevada (pl. 6, fig. 14). Some of the shells figured by Endo (1935) under the name *Ctenodonta takahashii* from the Kangyao Formation of Manchuria may belong to *Tancrediopsis*.

Many posteriorly auriculate and anteriorly elongate North American nuculoids have long been referred to *Ctenodonta* (pl. 5, figs. 7–22). Ulrich (1894) assigned these shells to his *Ctenodonta levata* group and subsequent to his work at least three generic names were proposed for shells of this general character: *Deceptrix* Fuchs (1919), *Praeleda* Pfab (1934), and *Praenucula* Pfab (1934). (See McAlester, 1968, for figures of the type specimens of the type species of each of the genera.) When shell shape is used as the major generic criterion, these names appear to be synonyms. Because *Deceptrix* is the oldest of the three names, it is used herein; *Praenucula* is sometimes distinguished from *Deceptrix* on the basis of the number and size of the teeth in the tooth rows anterior and posterior to the beaks. The teeth in each tooth row of *Praenucula* are of approximately the same size and number, whereas, in *Deceptrix* the teeth in the posterior tooth row are similar and more numerous than those in the anterior tooth row.

Shells of the *Deceptrix* type are known from rocks as old as the Antelope Valley Limestone of Nevada (pl. 5, figs. 11, 12) and range upward into rocks of Devonian age. *Deceptrix* is widely distributed in the Ordovician rocks of North America being known from the Arctic (pl. 5, fig. 21) to Tennessee (pl. 5, fig. 13) and from Nevada (pl. 5, figs. 11, 12) to New York (pl. 5, fig. 22).

The names *Palaeoconcha* (pl. 6, figs. 6–8) and *Similodonta* (pl. 5, figs. 1–6) are applied to more or less similar small shells which are triangular dorsally, rounded ventrally, and *Nucula*-like in general aspect. However, *Palaeoconcha* is used for extremely small shells which possess a posterodorsal auricle that is lacking in *Similodonta*. The oldest Ordovician shells of the *Similodonta* type known to me are Wilderness Age and they range upward into the Silurian. Endo (1935) described shells which may belong to *Similodonta* under the name *Ctenodonta manchuriensis* from the Kangyao Formation of Manchuria.

Small nuculoids which are probably best placed in the genus *Palaeoneilo* are known from many parts of the Ordovician and are at least as old as late Wilderness (pl. 1, figs. 8–11); they range upward into the Jurassic (Cox, 1937).

Although *Myoplusia* is not well known in the American Ordovician, at least one arctic species, *Ctenodonta* *carpenderi* Schuchert (1900), seems to belong here (pl. 6, figs. 3–5); several species from European rocks have been placed in the genus (Neumayr, 1884).

The oldest known nuculoids are those reported by Thoral (1935) from the lower Arenig and perhaps upper Tremadoc rocks of south-central France. Harrington (1938) reported some nuculoids from the lower Tremadoc of Argentina; based on external features these forms seem to be properly assigned; however, they have not yet been shown to have taxodont dentition. One of the specimens Harrington assigned to *Cosmogoniophorina tenuicostata* (1938, pl. 3, fig. 4) seems to show taxodont dentition; it is from the lower Tremadoc of Argentina and may be the oldest known nuculoid pelecypod. Other Early Ordovician nuculoids have been reported from the Arenig rocks of Argentina (Harrington, 1938), France (Barrois, 1891; Babin, 1966), Wales (Hicks, 1873), and Malaysia (herein, pl. 4, figs. 20–22).

In the past, the diversity of Ordovician nuculoids has been masked by an extremely conservative taxonomic approach which resulted in excessive lumping at the generic level. This was especially true in North America where even as new names became available they were not used. Generic-level splitting of *Ctenodonta* is constructive from the biological point of view as it is a means of indicating the diversity of Ordovician nuculoids and from the stratigraphic point of view as the restricted taxa are more useful age indicators than was the older more broadly defined *Ctenodonta*.

PTERIOMORPHIANS

Ordovician species of three families Cyrtodontidae, Ambonychiidae, and Pterineidae possess the highly characteristic and distinctive duplivincular ligament (pl. 7, fig. 10; pl. 10, figs. 6, 8; pl. 11, fig. 11), a primitive feature among pteriomorphian pelecypods. This type of ligament leaves a series of parallel grooves and ridges on the ligament area. (See Newell, 1937 [1938] and 1942, for detailed discussions of this ligament type.) In living forms the duplivincular ligament is present only in arcoids; however, in the Paleozoic it was more widespread. In addition to the Ordovician groups mentioned above, the duplivincular ligament is found in Paleozoic arcaceans, myalinids, the older pteriaceans and pectinaceans, and perhaps in the limaceans. Thus, the duplivincular type of ligament is a primitive feature among most groups of anisomyarian pelecypods.

I think of these various groups as being phylogenetically related (1) on the basis of the common possession of the morphologically and physiologically complex duplivincular ligament, (2) on the tendency of most members of the group to reduce the anterior end through byssal attachment, and (3) on the maintenance of the byssus during the adult stage with a consequent epifaunal life habit as the main mode of life. Newell (1954) on the basis of his studies of late Paleozoic pelecypods felt that this duplivincular ligament group probably gave rise to the Mytilacea, a widespread byssally attached superfamily. He (1965) united the mytilaceans and duplivincular ligament forms in the subclass Pteriomorphia, but placed Ordovician mytilaceanlike shells in the subclass Palaeoheterodonta as part of the order Actinodontoida.

Ordovician mytilaceanlike shells lack a duplivincular ligament (pl. 15, figs. 5, 6; pl. 13, figs. 6, 8), have a distinctive shell shape (pl. 12, figs. 5, 13; pl. 15, figs. 2, 3) often much like living species of *Arcuatula* Lamy (pl. 11, fig. 32), *Modiolus* Lamarck (pl. 11, fig. 31; Soot-Ryen, 1955, pl. 7), and *Mytella* Soot-Ryen (1955, pl. 5, fig. 22), and probably should be classified with the Mytilacea and not the Actinodontoida. Paleozoic modioliform shells do not seem to be allied to forms having a duplivincular ligament, and the two groups are distinctive throughout their stratigraphic range. I feel that Ordovician modioliform shells were probably ancestral to the later mytilaceans, and I think that the Mytilacea should form a separate high-level taxon equal in rank to, and distinct from, the other byssally attached anisomyarian groups; Ordovican modioliform mytilaceans are further discussed on page 20.

CYRTODONTIDAE

Kobayashi (1934), Hicks (1873), and Barrois (1891) placed several Arenig (Early Ordovician) species in genera assigned to the Cyrtodontidae. Kobayashi's placement of a species from Korea in *Cyrtodonta* was cited as a questionable identification by him. Hicks' figures are generalized, but the specimens he illustrated do not seem to be cyrtodontids. Barrois' figures of *C. lata* (1891, pl. 3, figs. 5a–b) and one of his figures of *C. obtusa* (1891, pl. 3, fig. 4a) resemble younger cyrtodontids in general outline, however, Babin (1966) felt that these species might belong to *Actinodonta* and questionably placed them in that genus.

Barrois (1891) illustrated two other possible arcoids, *Arca? naranjoana?* and *Parallelodon antiquus*. Babin (1966) illustrated the hinge of the former species and showed that it has actinodont dentition and that in shell shape it is similar to *Cyrtodonta lata*. *Parallelodon antiquus* is an enigmatic form whose generic placement can only be correctly established when additional specimens of the species are found. As figured by Barrois (1891), this species has a dentition similar to that of middle and late Paleozoic parallelodontids which are generally regarded as descended from early Paleozoic cyrtodontids. It was Barrois' figure of *P. antiquus* which led Cox (1960) to suggest that *Cyrtodonta* and *Parallelodon* arose from some common Ordovician ancestor.

In 1966, when Babin restudied *P. antiquus* he could locate only one specimen of the species, and he felt that this was probably the one used by Barrois to illustrate the dentition. Babin noted that the specimen showed the dentition illustrated by Barrois in an equivocal manner (1966, p. 146): "* * *; cette denture est d'ailleurs d'analyse délicate et beaucoup moins demonstrative que ne laisse supposer la figure donnée par Barrois." Babin regarded a second specimen which he thought Barrois might have had as probably being lost. Babin did not figure *P. antiquus;* however, based on Barrois' figures of the species the shape is highly reminescent of *Pseudarca* [*Siliquarca*] *and* therefore *Parallelodon antiquus* may belong to this genus.

Be that as it may, the point is obvious that few, if any, cyrtodontids or other arcoids are known from Lower Ordovician rocks. In North America, cyrtodontids probably occur in the Chazy Limestone of New York (Raymond, 1916) and are probably the oldest known representatives of the group. Somewhat younger are possible species of cyrtodontids from the St. Peter Sandstone of Minnesota (Sardeson, 1896) and the Llandeilo of Scotland (Hind, 1910). However, cyrtodontids are not well represented in the Ordovician record until Wilderness-Barneveld time (late Middle Ordovician) when they are among the most varied, abundant, and geographically widespread pelecypods (fig. 6). The family continued on into Devonian time.

Cyrtodontids are especially conspicuous elements of later Middle Ordovician pelecypod faunas, and it is on the basis of shells of this age that the group is best known. Cyrtodontids have a prominent duplivincular ligament (pl. 7, fig. 10; pl. 9, fig. 1), are equivalved (pl. 6, figs. 16, 17, 21–23; pl. 8, figs. 3, 12), and have well-developed dentition of cardinal and posterior lateral teeth (pl. 7, figs. 1–4, 7–10; pl. 8, figs. 1, 5, 6, 8, 13; pl. 9, figs. 1–3). They show a great deal of variation in the number, position, shape, and direction of growth of the cardinal teeth (pl. 7, figs. 1–4, 7, 8, 10; pl. 8, figs. 1, 5, 6, 8); on some specimens these teeth do not reach the beaks but are positioned more like anterior lateral than cardinal teeth (pl. 7, figs. 1, 2, 7). The posterior lateral teeth are all confined to the posterior end of the hinge area, never cross the ligament area, and never reach the beaks (pl. 7, figs. 2, 10; pl. 8, fig. 8).

It is generally agreed that crytodontids are the most probable ancestors of the arcaceans (Douvillé, 1913; Newell, 1954 and 1965; Cox, 1960) on the basis of comparisons of the dentition of early Paleozoic crytodontids and younger arcaceans. However, the mode of life of cyrtodontids is difficult to evaluate. Some cyrtodontids are *Glycymeris*-like in their shell form (pl. 6, figs. 21–23) and probably lived as shallow infauna. However, most show some reduction of the anterior end of the shell (pl. 7, fig. 3; pl. 9, figs. 4–7), a feature of byssally attached pelecypods, and some show the anterior aductor muscle mounted on an umbonal shelf or shell thickening (pl. 7, fig. 10; pl. 8, figs. 1, 2, 5), a feature known only in byssally attached pelecypods. Cyrtodontid phylogenetic relationships and the modes of life of members of the group are discussed further on page 35.

In the Middle Ordovician rocks of the Jessamine dome area of central Kentucky, cyrtodontids are common elements of the Tyrone Limestone and the lower Lexington Limestone; here the group is most abundant in biogenic calcarenites and comes and goes up the section as this lithofacies comes and goes. In this type of rock, cyrtodontid species are represented by large numbers of individuals of varied sizes, and probably lived in this habitat. The robust nature of the shells of most cyrtodontids suggests that they could have lived in higher energy zones where sands were being deposited.

The Tyrone Limestone is largely a fine-grained (sublithographic) unit which contains a few small biogenic calcarenite bodies. Numerous cyrtodontids occur in these sands; they also occur in the enclosing cryptograined limestone, but are smaller, much less numerous, and not as well silicified.

AMBONYCHIIDAE

Ambonychiids are the best known of the three Ordovician pteriomorphian families (Pojeta, 1962, 1966, 1968). They are equivalved (pl. 10, fig. 17), strongly inequilateral shells (pl. 10, fig. 1), which have a highly variable dentition (pl. 10, figs. 6–11) and are known to have had a prominent byssus (pl. 10, figs. 4, 12). Where posterior lateral teeth are present in ambonychiids, they are confined to the posterior part of the hinge line and do not cross the ligament area or reach the beaks (pl. 10, figs. 7, 9–11); cardinal teeth, where present, are ventral to the duplivincular ligament in the region of the beaks (pl. 10, fig. 8).

For the most part, ambonychiids are relatively large animals that lived epifaunally. Some species were obviously gregarious, and large numbers of articulated shells are found together in some places on a bedding plane or forming the bulk of a single thin bed. Forms which are herein interpreted as nestling are found surrounded by erect branching bryozoans.

The entire hard-part morphology of several Ordovician ambonychiid genera is known. These are ribbed monomyarian forms that had lost the entire anterior end of the shell and had already undergone a recurring theme of pelecypod phylogeny. The oldest known members of the family have been found in Chazy Limestone of New York (Raymond, 1916); the family ranges into the late Late Devonian and probably gave rise to the late Paleozoic and early Mesozoic Myalinidae.

An interesting sidelight about Ordovician ambonychiids is that some individuals served as attachment sites for edrioasteroids (pl. 10, figs. 13, 16). The few specimens I have seen with edrioasteroids attached have them near the ventral and posterior edges—or those parts of the shell closest to the inhalent and exhalent currents. Attachment is also on the broadest part of the shell, and it may be that attachment on this site was related more to the space available than to currents set up by the pelecypod.

PTERINEIDAE

Paleozoic pteriaceans have been little studied and are poorly known. *Ahtioconcha* Öpik from the Baltic Kukruse stage (C_2–early Caradoc) is the oldest known probable pteriacean (fig. 4). In North America a few undoubted pteriaceans are known from upper Middle Ordovician (Barneveld) rocks (pl. 11, fig. 9); the group underwent a slight expansion in the Late Ordovician (fig. 6), but its evolution is primarily a post-Ordovician one.

Ordovician pteriaceans are largely placed in the single family Pterineidae, and most undoubted pteriacean species are placed in the single genus *Pterinea* Goldfuss. In the Ordovician, this genus is most abundant in rocks of Cincinnati age (Late Ordovician), and as known from Ohio Valley and New York species is strongly inequilateral (pl. 11, figs. 7, 14) and inequivalved (pl. 11, figs. 3–6). The left valve is convex, and the right valve is almost flat to concave (pl. 11, figs. 4, 6); the sculpture of the two valves differs, with that of the left valve being more accentuated (pl. 11, figs. 1, 7) than that of the right valve (pl. 11, figs. 2, 8). The shell is strongly dentate and has both cardinal and posterior lateral teeth which do not cross the ligament nor reach the beaks (pl. 11, figs. 10, 11), the ligament is duplivincular (pl. 11, fig. 11), and there are anterior and posterior alations of the dorsal margin (pl. 11, figs. 10–13). Commonly in Ohio Valley specimens the outer ostracum is preserved whereas the inner ostracum is dissolved away (pl. 11, fig. 12); this suggests that the inner ostracum was aragonitic whereas the outer was calcitic. *Pterinea* was an epifaunal element and probably was similar to the living genera *Pteria* and *Pinctada* in its mode of life.

The oldest known undoubted North American pterineids are from the upper Lexington Limestone (upper Middle Ordovician) of Kentucky; they are known only from left valves which are convex (pl. 11, fig. 9) and are probably assignable to the genus *Palaeopteria* Whiteaves on the basis of the teeth being nearly parallel to the dorsal margin and being arranged as anterior and posterior laterals. Whiteaves (1897) figured a right valve of *Palaeopteria* which was also convex, but less convex than the left valve.

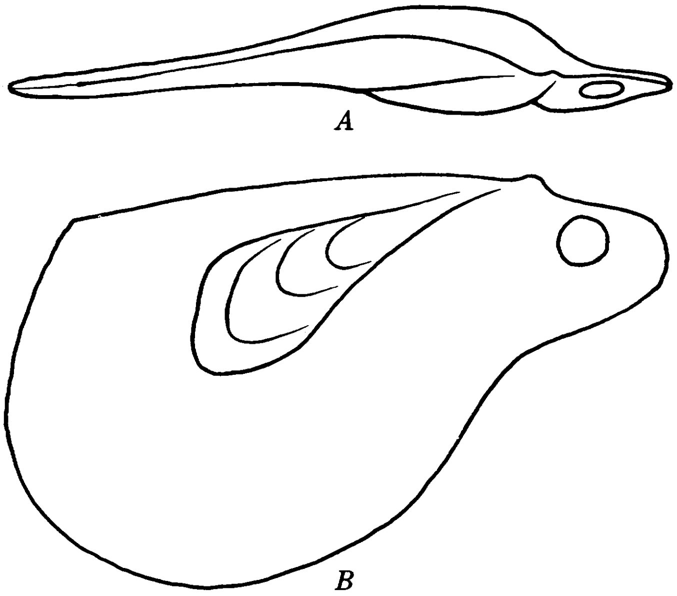

FIGURE 4.—*Ahtioconcha auris. A*, dorsal view. *B*, right valve. Reproduced from Öpik (1930). × 2/3.

Except for *Ahtioconcha* Öpik (1930), older species placed in the Pteriacea are not well documented and some such as Thoral's (1935) ?*Pterinea crassa* belong to other taxa (in this example, *Eopteria*). *Ahtioconcha* (fig. 4) is an inequivalved shell from the Middle Ordovician of Estonia; it has a convex left valve and a flat to concave right valve, it is strongly anisomyarian, but lacks a posterior alation. Eberzin (1960) placed the genus in a separate family Ahtioconchidae.

Several other pteriacean generic names usually applied to younger species have been used for Ordovician forms including: "*Avicula*" (Barrande, 1881), *Rhombopteria* (Jackson, 1890), and *Leptodesma* (Soot-Ryen and Soot-Ryen, 1960); a few Ordovician genera including *Alnifia* Termier and Termier and *Anderkenia* Khalfin have been questionably placed in the Pteriacea.

Other Ordovician pelecypods which have been described as being inequivalved are *Aristerella* Ulrich (pl. 11, figs. 15–24) and *Heikea* Isberg. Ulrich (1894) described *Aristerella* as having the left valve smaller than the right (pl. 11, fig. 20). His specimens of the type species of the genus (*A. nitidula* Ulrich) include individuals which are right convex (pl. 11, fig. 20), left convex (pl. 11, fig. 23), and equivalved (pl. 11, fig. 15). The specimens are all small molds and could easily have been distorted; *Aristerella* may be a distinct generic-level taxon, but it is doubtful that it was inequivalved.

As pointed out by Nicol (1958), right-convex inequivalved shells are known from the Ordovician. Two fairly large specimens in the U.S. National Museum collections from the Ordovician of Estonia are markedly right convex (pl. 11, figs. 25–30). These molds are labeled *Aristerella*, but it is doubtful that they can be assigned to that genus, and it is uncertain to what higher level taxon they belong.

Heikea Isberg (1934) was described as being inequivalved. Based on Isberg's figures this inequality is at best slight and may be the result of distortion during preservation.

Some Ordovician pterineids, like ambonychiids, served as attachment sites for edrioasteroids (pl. 10, figs. 14, 15).

MODIOMORPHIDAE [MODIOLOPSIDAE]

The family Modiomorphidae is perhaps the most perplexing of Ordovician pelecypod groups. Pelecypods which range in age from Early Ordovician to Late Permian have been placed in the Modiomorphidae, but the concept summed up by the name is vague and uncertain, and probably more than one family-level taxon is included in the Modiomorphidae as presently recognized. Many of the genera in the family have a modioliform shape (pl. 12, figs. 5, 9; pl. 13, figs. 1–6; pl. 15, figs. 1–3, 6; pl. 17, figs. 2, 4, 6–9); however, other aspects of the hard-part morphology, especially the hinge-line features, are unknown in the majority of genera. Because of this situation the phylogenetic position of these animals has long been moot, and they have been allied to the mytilaceans (Cox, 1960; Soot-Ryen, 1955), carditaceans (Newell, 1957), and actinodontoids (Douvillé, 1913; Newell, 1965).

In the Ordovician, *Modiolopsis* Hall is the most widely used modiomorphid generic name. In the years before family-level priority, the family name for this group of shells was Modiolopsidae; Modiomorphidae Miller (1877) has 10 years priority over Modiolopsidae Fischer (1887). As the modern study of these animals develops, it may prove useful to resurrect the name Modiolopsidae. *Modiolopsis* was proposed by Hall (1847) with the type species being *Pterinea modiolaris* Conrad (1838) by original designation. Ulrich (1924) using a tortured nomenclatural and taxonomic logic removed *P. modiolaris* from the genus *Modiolopsis*, substituted *Cypricardites ovata* Conrad (1841) as the type species of *Modiolopsis*, and made *Pterinea modiolaris* the type species of a new genus *Modiodesma* Ulrich. This procedure made *Modiolopsis* and *Modiodesma* objective synonyms as both names have the same type species.

Fortunately, Conrad's holotype of *Modiolopsis modiolaris* has been preserved (fide Hall, 1847, p. 295 and Ulrich, 1924, pl. 32 explanation), and it is figured herein on plate 15, figures 1–3. It is a composite mold of a distinctly modioliform shell with anisomyarian musculature and concentric sculpture. The museum label accompanying the holotype gives the locality as "Pulaski beds [Late Ordovician], Rome, N.Y." (this differs somewhat from the locality as given by Conrad, 1838). In general form and musculature, *M. modiolaris* is distinctly mytilacean. Nothing definite is known about the dentition of this species, although Ulrich (1924) regarded *Modiodesma* (type species *Modiolopsis modiolaris*) as being edentulous. Specimens similar to *M. modiolaris* from the Pulaski Shale of New York and elsewhere show that the species has multiple accessory muscle scars anterior to the beaks (probably anterior pedal-byssal retractors) (pl. 16, figs. 1, 2), an integropalliate pallial line (pl. 16, figs. 1, 2), and an elongate opisthodetic ligament (pl. 15, figs. 5, 6). The ligament is only rarely preserved and then only as a dark stain connecting the two valves.

Based on the type species, the name *Modiolopsis* is applicable to modioliform shells which expand noticeably posteriorly so that the maximum height of the shell is significantly more than the height measured down from the beaks and which also have concentric sculpture, an entire pallial line, anisomyarian musculature, and multiple accessory muscle scars in front of the beaks.

Ulrich (1894, p. 521) illustrated the hinge lines of two species of *Modiolopsis* which generally fit the definition of the genus based on the type species. Although the hinges of Ulrich's specimen's are not so well preserved as indicated on his figures, they do suggest that the genus was edentulous (pl .14, fig. 1). Other specimens not previously figured (pl. 14, figs. 2–5) also suggest that *Modiolopsis* was edentulous.

The hinges of three species of Ordovician pelecypods which are placed in the Modiomorphidae in most classifications are now reasonably well known on the basis of silicified specimens from the Lexington Limestone of central Kentucky. *Modiolodon oviformis* Ulrich possesses only cardinal teeth (pl. 13, figs. 6, 8, 9), *Whiteavesia cincinnatiensis* (Hall and Whitfield) is entirely edentulous (pl. 17, figs. 1, 3, 5, 11, 13, 15; pl. 19, figs. 16–18), and *Colpomya constricta* Ulrich possesses a large bosslike cardinal tooth below the beak of each valve (pl. 12, figs. 2, 3).

Modiolodon oviformis possesses multiple byssal retractor muscle scars posterior to the beaks (pl. 13, figs.

7, 11) and has the shell shape, pallial line, and anisomyarian musculature of byssally attached mytilaceans (pl. 13, figs. 1–6). Details of the shell musculature are not so well known in *Whiteavesia* and *Colpomya*, however, in shell shape they suggest byssally attached mytilaceans.

Based on shell shape and general hard-part morphology such Ordovician modiomorphids as *Modiolopsis* (pl. 15, figs. 1–6), *Modiolodon* (pl. 13, figs. 1–15), *Whiteavesia* (pl. 17), and less well known genera such as *Pholadomorpha* Foerste (pl. 12, figs. 5–9) are strongly reminiscent of the geologically younger modioliform mytilaceans. Soot-Ryen (1955) in his summary paper on American west coast Mytilacea regarded this group as having descended from middle Paleozoic modiomorphids. Indeed, Ordovican modiomorphids are so mytilaceanlike in shell shape that it is difficult to entertain thoughts of other possible relationships for the group.

In comparing the hinge of mytilaceans and Ordovician modiomorphids, little is known of the modiomorphid ligament. As mentioned above, on some molds it is preserved as a dark stain connecting the two valves (pl. 15, figs. 5, 6), and it is opisthodetic and elongate.

Trueman (1950) and Soot-Ryen (1955) discussed the opisthodetic elongate mytilid ligament. Trueman noted that the inner fibrous part of the ligament of *Mytilus edulis* Linné is attached to the flat surfaces (nymphae) of ligamental ridges composed of nacreous vacuolated shell material (pl. 13, fig. 18). To the unaided eye these ligamental ridges are white and of an obviously different consistency from the rest of the shell (pl. 13, figs. 18–20). Because these ridges support the ventral, fibrous, compressional (resilial) part of the ligament, Soot-Ryen named them the resilial ridges, and he regarded them as one of the most characteristic features of the family Mytilidae (pl. 13, figs. 18–20). No such resilial ridges have been observed on any of the silicified Ordovician modiomorphid shells discussed above (pl. 12, fig. 2; pl. 13, figs. 6–8; pl. 17, figs. 1, 3, 11, 13).

The modiomorphid ligament may not have been entirely composed of tensional elements acting only in C-spring fashion. It is normal in pelecypods for the ligament to contain both tensional and compressional parts although these are developed to differing degrees in different taxa. Ulrich (1924) described the ligament of *Modiolopsis* [*Modiodesma*] as having both inner and outer parts, the inner part being supported by a longitudinal rib which left a slitlike mark on molds (pl. 12, fig. 4). The ventromedial edge of the resilial ridge of some living mytilaceans leaves a more or less similar mark on rubber molds. However, as the silicified specimens of Ordovician modiomorphids show no sign of an internal longitudinal rib supporting the ligament, it is doubtful that such a structure was present. Probably Ulrich's "longitudinal slit" was made by the dorsal margin of the shell.

As far as known, American Ordovician modiomorphids either are edentulous (pl. 14, figs. 1–5; pl. 17, figs. 1, 3, 5, 10, 11, 13, 15; pl. 19, figs. 16–18) or have only cardinal teeth (pl. 12, figs. 2, 3; pl. 13, figs. 6, 8, 9). The latter when present are mounted on a hinge plate and are strong obvious teeth (pl. 12, fig. 3; pl. 13, fig. 8).

Mytilids, too, either are edentulous (pl. 13, fig. 19) or have only cardinal teeth (pl. 13, figs. 18, 20). In the latter, the teeth may be derived from provincular teeth, or they may be related to shell sculpture (dysodont). Cardinal teeth in the Mytilidae may be small and not mounted on a hinge plate as in *Mytilus edulis* (pl. 13, fig. 18), or they may be large and supported on a hinge plate as in some species of *Perna* (pl. 13, fig. 20). It is not possible to draw an absolute homologous parallel between mytilid dentition and that of the Ordovician modioliform modiomorphids. However, the two groups are similar in showing several dental types which vary in more or less the same way.

The various phylogenetic relationships postulated for the Modiomorphidae result, at least in part, from the uncertainty of the concept implied by the name. Several distinct groups of Ordovician shells have been united in the Modiomorphidae including: (1) the modioliform byssate forms discussed above, (2) *Redonia* (pl. 1, fig. 7) which is herein regarded as an actinodontoid (p. 11) and (3) burrowing forms such as *Cymatonota* (pl. 18, figs. 10–13).

Newell (1942, 1954) in his work on late Paleozoic mytilaceans felt that it was most likely that they came from cyrtodontids through an ambonychiacean intermediary rather than from the Modiomorphidae. He also based much of his interpretation on shell shape and musculature, some of the late Paleozoic myalinids being remarkably like mytilaceans in these respects. However, mytilacean shell shape is known from the Early Ordovician onward, and if for no other reason than the principle of parsimony it would seem best to regard late Paleozoic undoubted mytilaceans as having descended from similarly shaped early Paleozoic forms. The reasons advanced for not coming to this conclusion are to me less likely than those given for regarding mytilaceans as descended from modiomorphids.

Ordovician modioliform modiomorphids are like late Paleozoic mytilaceans in shell shape, musculature, byssal attachment, and, in a more general way, ligament type and dentition. They differ by specifics of dentition and by lack of a resilial ridge. My interpretation of these data is that the early Paleozoic modioliform modiomorphids are ancestral mytilaceans. I regard the late Paleozoic modioliform myalinids as being convergent to the Mytilacea. The myalinids have a duplivincular ligament which is unknown in either the mytilaceans or the modiomorphids. I am aware that the duplivincular ligament was lost in the phylogeny of the pectinaceans and pteriaceans and there is no reason why it could not be lost in the phylogeny of other groups. However, both the pectinaceans and the pteriaceans are regarded as having descended from the first occurring similarly shaped Paleozoic shells, and none of the modioliform early Paleozoic shells are known to have had a duplivincular ligament.

Newell (1957) allied the modioliform modiomorphids and *Redonia* to the Carditacea on the basis that these were the earliest known forms to have posterior lateral teeth extending under the ligament to the beaks and on general body form. *Redonia* does have such teeth, but as noted above is probably better classified with the actinodontoids than with the modiomorphids. *Redonia* was considered to be the ancestral carditacean by Chavan (1966a, b). None of the Ordovician modioliform modiomorphids in which the hinge line is known have posterior lateral teeth (although younger forms placed in the same group have been described as having such teeth). As noted previously, they are either edentulous or possess only cardinal teeth, and on this basis their postulated relationship to the Carditacea is weakened.

Newell (1965) placed the Modiomorphidae in the order Actinodontoida along with the Cycloconchidae, Lamellodontidae, and Carydiidae. For reasons similar to those cited above that deal with a possible modiomorphid-carditacean relationship, it seems doubtful that the modioliform modiomorphids can be allied to the actinodontoids. Modioliform modiomorphids have a complex of characters similar to those of the Mytilacea, and the former are herein regarded as the ancestors of the latter.

The earliest modioliform modiomorphids seem to be Arenig Age (fig. 6) and were figured by Hicks (1873, pl. 5, fig. 18), Barrois (1891, pl. 3, fig. 9), and Babin (1966, pl. 7, fig. 13). The specimens placed in the Modiomorphidae by Harrington (1938) from the lower Tremadoc and lower Arenig of Argentina cannot be readily allied to the modioliform modiomorphids. In North America, modioliform modiomorphids are known from rocks as old as the lower Lehman Formation of Utah (pl. 15, fig. 8) and the upper Pogonip Group of Nevada (Walcott, 1884).

The Mytilacea has long been recognized as a distinctive high-level taxon, and Iredale (1939), Cox (1960), and Newell (1965) have placed the group in its own order. For the most part, however, the Mytilacea have consistently been classified with the other Anisomyaria. The concept of the Anisomyaria is an old one to which in recent years the arcoids have been added and for which the name Pteriomorphia Beurlen (1944) has been adopted. As long as the early history of the Mytilacea was not well known, their placement with the anisomyarians was acceptable on the basis of the musculature and the byssal mode of life of the adults. However, mytilaceans from the Early Ordovician onward are not known to have had a duplivincular ligament, and they are distinct from the pteriomorphians from the begining of the known fossil record of the two groups. If the two groups have had a separate history from the Ordovician onward this should be reflected in their taxonomy; I think that this can best be done by treating them as separate subclasses. Cox (1960, p. 78) briefly summarized the malacological data indicating that the Mytilacea are distinct from the other anisomyarians; although he did not place the mytilaceans in a separate subclass he was thinking along these lines: "Their [mytilaceans] recognition as a distinct order seems justified, but at present I hesitate to place them in a different subclass from that to which the remaining dysodonts of Neumayr belong, and so include them in the Pteriomorphia."

LESS WELL KNOWN ORDOVICIAN PELECYPOD GROUPS

The remaining groups of Ordovician pelecypods are not well known largely because of the lack of well-preserved specimens. So far my etching program has shed little light on these families; it is hoped that expansion of the program into geographic areas other than the tristate area of Ohio, Indiana, and Kentucky will improve knowledge of these animals.

CONOCARDIIDAE

About three-dozen species names are presently available for Ordovician *Conocardium*-like animals. These species are distributed among several genera, the best known being: *Eopteria* Billings (pl. 19, figs. 1–14), *Euchasma* Billings (pl. 20, figs. 6–21), and *Conocardium* Bronn (pl. 20, figs. 1–5). At one time or another most of these forms have been allied to the Crustacea, although their calcareous shells with growth lines suggest they are mollusks. Animals with conocardiid shell shape are persistent Paleozoic faunal elements and range in age from Early Ordovician to Late Permian; they are an enigmatic group and their pelecypod affinities are not well established.

The oldest known possible conocardiids are species placed in *Eopteria* and *Euchasma* by Kobayashi (1933) from the Wanwaukou Dolomite (lower Canadian) of

Manchuria; the species which Thoral (1935) called *?Pterinea crassa* from the Arenig rocks of south-central France probably belongs to *Eopteria;* and species of *Euchasma* (pl. 20, figs. 18–21) are known from the Setul Formation of Malaysia in rocks which are probably latest Canadian in age (Yochelson and Jones, 1968). In North America, *Eopteria* and *Euchasma* are known from rocks of Canadian age (Early Ordovician) in Newfoundland (Schuchert and Dunbar, 1934), the Ozarks (pl. 19, figs. 5–14), Quebec (pl. 19, figs. 1–3; pl. 20, figs. 6–11), Texas (Cloud and Barnes, 1948), Vermont (pl. 20, figs. 16, 17), Virginia (pl. 20, figs. 12, 13), and elsewhere (pls. 19, 20). In Canadian (Lower Ordovician) rocks, conocardiids are widely distributed. In post-Canadian Ordovician rocks, conocardiids are known from fewer specimens and places. However, conocardiids are as distinct from other pelecypods in the Ordovician as they are in the Permian.

Ordovician representatives of the Conocardiidae are known from a relatively few specimens which show little beyond external features. They are small, are known from a variety of rock types, do not have so pronounced a posterior (?) tube as do later forms, and probably had a burrowing mode of life. Recently, silicified specimens of *Euchasma* have been obtained which promise to provide some data on the internal features of the group (pl. 20, figs. 18–21).

During the Paleozoic, the conocardiids underwent a complex radiation which is not well documented in the available literature. The biological diversity of the group is not at present well understood because of the inclusion of all species within a relatively few genera and families, and the group is badly in need of modern monographic treatment.

VLASTIDAE

In the Ordovician of North America the family Vlastidae is represented by the single species *Vlasta americana* Fritz, 1951, (pl. 20, fig. 22) from the Dundas Formation (Upper Ordovician) of Ontario; this is a large species with prominent concentric undulations, but about which little else is known.

The Vlastidae is largely a Silurian family known primarily from material described by Barrande (1881) from Bohemia. Reed (1915) placed the genus *Shanina* from the Middle Ordovician of Burma in this family, Isberg (1934) placed *Shaninopsis* from the Upper Ordovician of Sweden in the Vlastidae, and Vokes (1967) added *Hippomya* Salter to the Vlastidae. The last three mentioned genera are all diagramed as having unusually large shell (byssal?) gapes.

ANOMALODESMATA

This section deals with a series of forms which are or have been regarded as burrowing pelecypods ("desmodonts") and which cannot be assigned to any of the infaunal groups discussed previously.

Douvillé (1907, 1912, 1913) using Neumayr's terminology (1884, 1891) developed the concept of a primary radiation of pelecypods into three major modes of life: (1) normal infaunal forms—taxodonts, preheterodonts, and heterodonts; (2) epifaunal forms fixed in some manner to the substrate—dysodonts; and (3) burrowing or boring infaunal form—desmodonts. The phylogenetic validity of Douvillé's burrowing branch has not been generally accepted, although Cox (1960) and Runnegar (1966) felt that there was probably a core group among his desmodonts which had an early Paleozoic origin and continues to the present.

For various reasons, several Ordovician genera have been considered to be burrowing forms including: *Cymatonota* Ulrich (pl. 18, figs. 10–13), *Psiloconcha* Ulrich (pl. 18, figs. 1–6), *Orthodesma* Hall and Whitfield (pl. 18, figs. 7–9), *Rhytimya* Ulrich (pl. 16, figs. 10, 11), and *Cuneamya* Hall and Whitfield (pl. 15, figs. 9–14). Vokes (1967) listed these genera in five different families: Modiomorphidae, Solemyidae, Orthonotidae, Pholadellidae, and Edmondiidae, respectively. Four of the five families concerned are placed by Newell (1965) and Vokes (1967) in the subclass Cryptodonta. This taxon is a sort of pelecypods *imperfecti* and is admittedly one of convenience for poorly understood Paleozoic pelecypods.

Of the genera listed above, *Cymatonota* is the best documented as an undoubted burrower. Nothing is known of the hinge or pallial line of this genus, and little is known of its musculature. However, it has a distinctly soleniform shape, with subparallel dorsal and ventral margins (pl. 18, figs. 12, 13) and it has both anterior and posterior shell gapes (pl. 18, figs. 10, 11). In shell shape and gapes, *Cymatonota* is much like the later Paleozoic genera *Palaeosolen* Hall, *Prothyris* Meek, and *Solenomorpha* Cockerell (see Driscoll, 1965, for figures of the latter genera) and should probably be allied to these forms. *Cymatonota* has traditionally been placed in the Modiomorphidae; however, its shell shape and gapes make it distinct from the byssate modioliform modiomorphids. Shells of the *Cymatonota* type seem to form a separate pelecypod lineage distinct from the Ordovician onward throughout the Paleozoic.

Psiloconcha (pl. 18, figs. 1–6) is another burrowing Ordovician form which is probably related to *Cymatonota*. The former genus is not so strongly soleniform as *Cymatonota;* however, it does have anterior and posterior shell gapes (pl. 18, figs. 5, 6) and a general burrowing aspect to the shell. Unfortunately in preparing the best preserved of the known specimens of *Psiloconcha*, Ulrich accentuated the posterior gape unduly (pl. 18, fig. 5). Nothing is known of the hinge or pallial line of *Psiloconcha;* however, on one specimen the adductor muscle scars are known (pl. 18, fig. 1).

Orthodesma (pl. 18, figs. 7–9) as defined by Ulrich (1894) was supposed to have anterior and posterior shell gapes. None of the specimens of this genus seen by me show this in an unequivocal manner, and some species placed in the genus have a modioliform aspect. However, most species of *Orthodesma* have a general soleniform shell shape, and Bayer (1967, p. 420) noted having found: "One hundred and fifty pelecypods of the burrowing type (*Orthodesma*) * * * in growth position." It may be that *Orthodesma* as presently defined includes both burrowing and nonburrowing forms.

Runnegar (1966) felt that pholadomyids and edmondiids constitute a major division of the class Pelecypoda; a division which has been distinct since the Ordovician, having descended from such genera as *Rhytimya* (pl. 16, figs. 10, 11). His suggested relationship of *Rhytimya* to the pholadomyaceans is based largely upon shell sculpture, the Ordovician genus having the radially arranged granules and concentric undulations of many younger members of the group (pl. 16, fig. 11). Unfortunately nothing is known of the hinge or pallial line of *Rhytimya.* Runnegar placed a number of genera in this lineage including such widely used names as *Edmondia* Koninck (Wilson, 1959, 1960), *Chaenomya* Meek, *Myonia* Dana, and tentatively *Wilkingia* Wilson [*Allorisma*]. Ulrich (1894) suggested that *Rhytimya* was related to *Wilkingia* on the basis of criteria similar to those suggested by Runnegar (1966). Cox (1960), Dickens (1963), and Runnegar (1966) considered the Devonian genus *Grammysia* as being related to the pholadomyacean lineage. Also probably allied to this complex is the genus *Cuneamya* (pl. 15, figs. 9–14), a primarily Middle and Late Ordovician form which has a shell sculpture consisting of concentric undulations. As early as 1894, Ulrich related *Cuneamya* to *Grammysia.*

Ulrich (1893 [1895], 1894), allied *Sphenolium* Miller, *Physetomya* Ulrich, and *Saffordia* Ulrich to either *Rhytimya* or *Cuneamya.* Of the species of *Sphenolium* illustrated by Ulrich, only *S. palallelum* was figured with concentric undulations; I have not been able to locate his material of this species nor his specimens of *Physetomya. Sphenolium striatum* (pl. 12, fig. 14) was also illustrated by Ulrich, but it does not show concentric undulations. Ulrich's specimens of *Saffordia ventralis* (pl. 12, figs. 10–12), the type species of the genus, show a shell with a prominent escutcheon (pl. 12, fig. 10) and a single cardinal tooth in the left valve (pl. 12, fig. 11). *Saffordia* is in most respects similar to *Heikea* Isberg (1934), and the two names may be synonyms.

As a working hypothesis I propose that Ordovician anomalodesmatans be divided into two groups: (1) those forms with gaping soleniform shells such as *Cymatonota* and *Psiloconcha*, which are probably related to such younger genera as *Solenomorpha*, *Prothyris*, and *Palaeosolen*, and (2) those forms which have a shell sculpture of prominent concentric undulations such as *Rhytimya* and *Cuneamya* and which are probably related to such younger genera as *Grammysia*, *Edmondia*, and *Wilkingia.* How these two groups are related to each other is not clear although Cox (1960, p. 80) placed both of them in the order Eudesmodontida. It should be mentioned that Ordovician infaunal pelecypods also occur in the following groups: nuculoids, actinodontoids, abinkids, conocardiids, and probably some cyrtodontids.

ORDOVICIAN PELECYPODS OF UNCERTAIN HIGHER TAXONOMIC POSITION

There remain a few problematic Ordovician genera which have been allied to groups that are well represented in younger rocks: *Plethocardia* Ulrich (pl. 14, figs. 7–12) has been placed in the Megalodontidae (Ulrich, 1894; Vokes, 1967), *Matheria* Billings (pl. 16, figs. 6–9) has been placed in the Astartidae (Chavan, 1966a, b; Vokes, 1967), and *Tenka* Barrande, *Tetinka* Barrande, and *Patrocardia* Fischer have been placed in the Lunulacardiidae (Fischer, 1887; Vokes, 1967).

Ulrich (1894) questionably placed *Plethocardia* in the family Megalodontidae, and in his discussion was hesitant about including the genus in that family. Ulrich had two specimens of *Plethocardia* on which he based his analysis of the hinge line. A figured syntype of *P. umbonata* Ulrich (pl. 14, figs. 9–12), type species of the genus, does not preserve the dentition nearly so well as indicated in Ulrich's drawing (fig. 1*A*); there are remnants of cardinal and lateral teeth that suggest a cyrtodontid hinge (pl. 14, fig. 9), and the general shell shape and enrolled beaks are also suggestive of the Cyrtodontidae (pl. 14, figs. 11, 12). Ulrich (1894) also discussed the dentition of a specimen of *P. umbonata* from Kentucky (pl. 14, figs. 7, 8) which he did not figure. Much of the hinge line of this shell has been weathered away, and the rest is covered with adventitious silica (pl. 14, fig. 8), and little can be determined of the teeth.

Based on what is presently known of *Plethocardia* it would be better to ally the genus to the Cyrtodontidae than to the Megalodontidae. There is a resemblance of the shell shape of *Plethocardia* to *Megalodon* and cyrtodontids, but *Plethocardia* does not show the large hinge plate and complex dentition of megalodontids.

Chavan (1966a, b) felt that he could establish the presence of three heterodont groups in the Ordovician. Using Bernard's method of tooth notation he regarded *Redonia* as a carditacean, and felt that he could relate the two crassatellacean families Cardiniidae and Astartidae to the genera *Cypricardinia* and *Matheria*, respectively.

Redonia has been discussed above in the sections dealing with the actinodontoids and modiomorphids. *Cypricardinia* is a generic name little used for Ordovician pelecypods, and it would be necessary to know to which species Chavan was referring before discussing any possible relationships. *Matheria* is a small shell with cardinal teeth (pl. 16, figs. 6, 9) and a duplivincular ligament; the latter structure is unknown in heterodonts. On general morphological grounds it would seem that the late Paleozoic crassatellaceans (Newell, 1958; Boyd and Newell, 1968) should be related to such forms as *Cycloconcha* rather than *Matheria*.

Barrande (1881) described four Ordovician species placed in the genera *Tenka*, *Tetinka*, and *Patrocardia* (originally placed in *Hemicardium*). These genera are usually placed in the Lunulacardiidae, a family allied to the Ambonychiacea in most classifications (Clarke, 1904; Newell, 1965; Vokes, 1967). Clarke (1904) discussed *Lunulacardium* Muenster at some length, but the genera placed in the family are all poorly understood, and at best the family is not well represented in the Ordovician.

PHYLOGENETIC SUMMARY

Based on the preceding interpretations, Ordovician pelecypods can be arranged in six major lineages: (1) Rostroconchida (Conocardiacea); (2) Palaeotaxodonta (Nuculoidea and Solemyoida); (3) Isofilibranchia (Mytilacea); (4) Pteriomorphia (Cyrtodontacea, Arcacea, Limopsacea, Pteriacea, Pinnacea, Ambonychiacea, Pectinacea, Anomiacea, Limacea, and Ostreacea); (5) Heteroconchia (Actinodontoida, Babinkidae, Unionoida, Trigonioida, Veneroida, Myoida, and Hippuritoida); and (6) Anomalodesmata (Edmondiidae, Sanguinolitidae=Solenomorphidae, Pholadomyacea, Pandoracea, Megadesmatidae, and ?Septibranchoidea). These lineages are distinct from the Early Ordovician or early Middle Ordovician onward; eventually it may prove necessary to add additional lineages when such groups as the vlastids and older babinkids become better known and to divide the anomalodesmatans into two evolutionary lines. At the present time it is possible to relate most post-Ordovician pelecypod stocks to one or another of the six Ordovician lineages recognized herein (fig. 5).

ROSTROCONCHIDA

Conocardiaceans (pls. 19, 20) are a highly distinctive Paleozoic group. There has long been a lingering doubt about their pelecypod nature; however, they seem to be mollusks, and they are generally regarded as aberrent Paleozoic pelecypods which gave rise to no other stock. The group appears in the Early Ordovician and continues to the Late Permian.

PALAEOTAXODONTA

From the Early Ordovician onward, nuculoids are important constituents of pelecypod faunas, and by Middle Ordovician time they are highly diversified (fig. 6). The major features of their post-Ordovician evolution seem to have been the development of a resilifer and in some groups a pallial sinus. Like the conocardiids, nuculoids are as distinctive in the Ordovician as in younger rocks and are not readily related to other Ordovician pelecypod stocks.

ISOFILIBRANCHIA

The modioliform modiomorphids form a third distinctive Ordovician pelecypod stock. As mentioned previously, it is doubtful if all the genera placed in the Modiomorphidae form a single family unit, but the modioliform genera form a compact unit from the Early Ordovician onward, and I regard them as ancestral to the Mytilidae. The mytilids cannot be readily related to the rest of the anisomyarians, all of which have a duplivincular ligament somewhere in their ancestry, and it would be best to place the mytilaceans in a subclass of their own, separate from the rest of the Anisomyaria.

PTERIOMORPHIA

A fourth Ordovician pelecypod lineage is formed by the three families which possess a duplivincular ligament: Ambonychiidae, Cyrtodontidae, and Pterineidae. As interpreted herein, this group gave rise to the arcoids and to all later anisomyarians except the Mytilacea. This general viewpoint was suggested by Newell (1954), except that he regarded mytilaceans as having descended from forms possessing a duplivincular ligament.

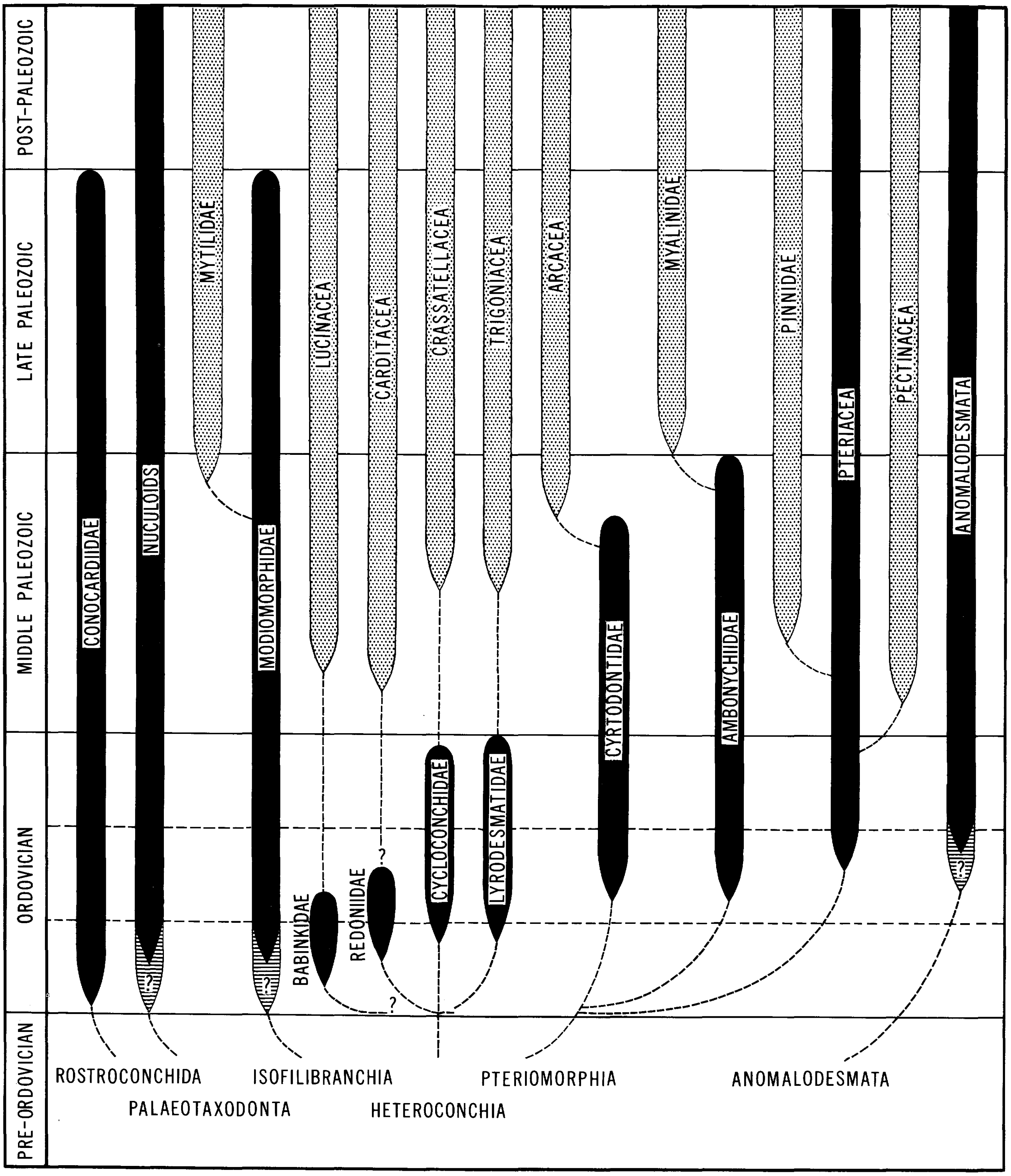

FIGURE 5.—Proposed phylogenetic relationships of most groups of Paleozoic pelecypods. Black lineages are those which originate in the Ordovician; stippled lineages are those which have post-Ordovician origins.

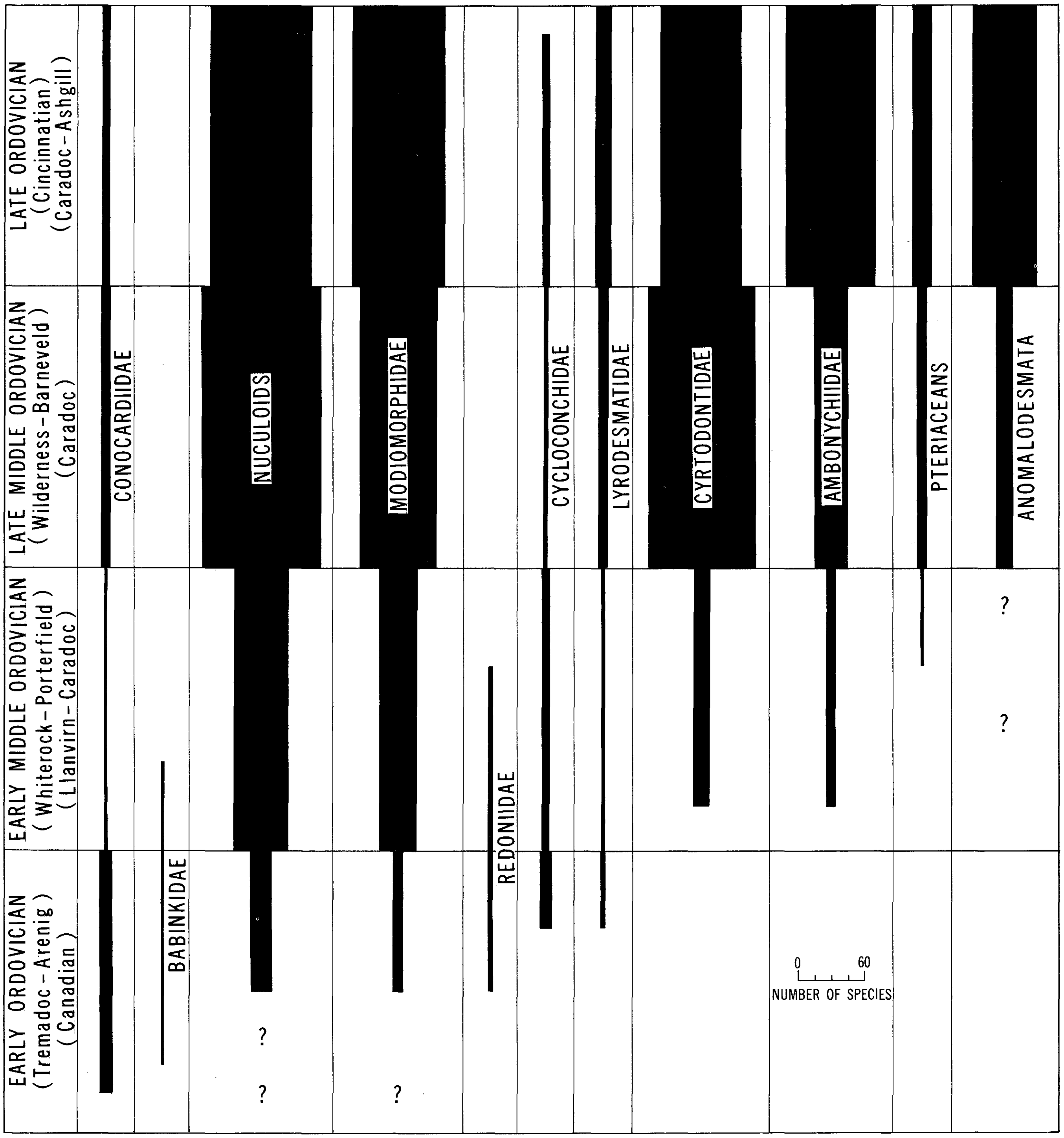

FIGURE 6.—Chart showing range and relative abundance of various Ordovician pelecypod groups. Figures are based on approximately 1,000 species which could be assigned both to the taxon and stratigraphic interval concerned. Species in any one of the stratigraphic intervals used are treated as though they occur throughout that interval, hence the effect of a histogram.

The descent of arcaceans from cyrtodontids has been widely accepted for many years and was documented by Douvillé (1913), Newell (1954), and Cox (1959). These authors showed how in successive stages the cyrtodontid type of dentition could give rise to the parallelodont dentition of middle and late Paleozoic arcaceans, and how this in turn could give rise to the arcacean dentition typical of Mesozoic and Cenozoic forms. In this process, the horizontal and oblique teeth of cyrtodontids and parallelodontids eventually came to be almost at right angles to the dorsal margin, which makes the arcaceans secondarily taxodont. In their dentition, arcaceans are convergent to the nuculoids, but as indicated by the stratigraphic succession and the presence of the duplivincular ligament in living arcoids, they are related to the pteriomorphians and not to the nuculoids. This line of reasoning is also supported by ontogenetic data (Jackson, 1890, p. 365) which show that in at least some living arcaceans the earliest teeth are oblique to the dorsal margin and perpendicular teeth form later in the growth of the animal.

Duplivincular-ligament forms first appear in the fossil record somewhat later in Ordovician time than the first three lineages discussed above, and relationships among the three duplivincular-ligament families are difficult to evaluate. The pterineids are the most specialized in that they have an inequivalved shell, a feature unknown in any Early Ordovician pelecypods. The ambonychiids and the cyrtodontids have retained the primitive equivalved shell. The ambonychiids show a tendency toward the loss of the anterior end of the shell and the development of a monomyarian condition, although some ambonychiids retain an anterior lobe and maintain a heteromyarian condition. The cyrtodontids are the most generalized of the three families in that as a group they show the least reduction of the anterior end, some species being almost *Glycymeris*-like in shell shape (pl. 6, figs. 21–23). Most cyrtodontids show some reduction of the anterior end (pl. 7, fig. 3; pl. 9, figs. 4–7); however, this is usually not as pronounced as in the ambonychiids (pl. 10, figs. 1, 3, 6, 8). Even in the cyrtodontid genus *Vanuxemia* where the beaks are almost terminal (pl. 7, fig. 10; pl. 8, fig. 1), the anterior adductor is not lost, rather it is raised and originates on an umbonal shelf.

As a working hypothesis it is suggested that the cyrtodontids are the most primitive of the duplivincular-ligament forms and that this family gave rise independently to the pterineids and ambonychiids; presumably the pterineids arose first as they are the most specialized (fig. 5). Later in the Paleozoic the cyrtodontids gave rise to the arcaceans, the ambonychiids gave rise to the myalinids, and the pterineids gave rise to the rest of the pteriaceans, the pectinaceans, and the pinnids.

HETEROCONCHIA

The actinodontoids form a fifth Ordovician pelecypod lineage. As herein defined, three, possibly four, Ordovician families belong to this stock: Cycloconchidae, Lyrodesmatidae, Redoniidae, and possibly Babinkidae. It seems probable that most of the later heterodont and palaeoheterodont groups are descended from the actinodontoids. On the basis of what is presently known, only the actinodontoids have a dentition which could have given rise to various heterodont and palaeoheterodont dental types. This general viewpoint has previously been suggested by Douvillé (1913) and Cox (1960).

Cox (1960) placed the heterodonts and the palaeoheterodonts (actinodontoids, unionoids, and trigonioids) in a single subclass—the Heteroconchia Hertwig. If the actinodontoids did give rise to the other palaeoheterodonts and to the heterodonts, it would seem that the taxonomy would better reflect the phylogeny of the groups if they were placed in a single subclass (Heteroconchia); there seems to be no need for a subclass Palaeoheterodonta. In Ordovician time, heteroconchians (actinodontoids) were subordinate pelecypod faunal elements (fig. 6); it was in the post-Ordovician that this group became so important and eventually in the Mesozoic and Cenozoic became the dominant pelecypod group.

In spite of some morphological differences from younger lucinoids, *Babinka* shows more lucinoid features than any other known pre-Silurian pelecypod, and it probably should be classified as a lucinoid. Lucinoids form an ancient pelecypod lineage which solved the problems of infaunal living in an unique way. If *Babinka* cannot be related to the actinodontoids then the lucinoids have an ancestry different from that of the heteroconchians and should be placed in a subclass of their own. Herein *Babinka* is tentatively allied to the actinodontoids.

Cycloconcha is similar in general morphology and especially in hinge features to such late Paleozoic crassatellaceans as *Oriocrassatella* (Newell, 1958; Boyd and Newell, 1968), and it seems likely that the crassatellaceans are descended from the cycloconchids. Likewise, *Lyrodesma* in its general morphology, but especially in its hinge features is so similar to younger trigoniaceans that it seems likely the Lyrodesmatidae gave rise to the Trigoniacea.

Chavan (1966a, b) felt that by using Bernard's method of establishing tooth homologies he could relate *Redonia* to what he considered to be middle and late

Paleozoic carditaceans. However, Cox (1960, p. 69) and Boyd and Newell (1969) cautioned that care should be taken in the application of Bernard's system. The hinge similarities between *Redonia* and the Permophoridae [Kalenteridae] are not as striking as those between other actinodontoids and their presumed descendants.

ANOMALODESMATA

Anomalodesmatans, the sixth lineage, became prominent in the latter part of the Ordovician (fig. 6), and most species placed in the genera *Cuneamya*, *Cymatonota*, *Psiloconcha*, and *Rhytimya* are Late Ordovician in age. The soleniform anomalodesmatans may date from the lower Middle Ordovician rocks of Europe (Llandeilo) where species now placed in the genus *Coxiconchia* (Babin, 1966) were regarded as desmodonts by Douvillé (1913). The earliest known anomalodesmatans with concentric undulations are early Wilderness Age and have been placed in the genus *Cuneamya* (Wilson, 1956). It may be that the seemingly late appearance of the anomalodesmatans is based upon the difficulty of identifying such structures as shell gapes and concentric undulations in inadequately preserved molds and casts; as the group becomes better known its range may be extended downward.

RELATIONSHIPS OF THE VARIOUS LINEAGES TO ONE ANOTHER

The fact that the six lineages are so distinct from the time when pelecypods first became abundant in the fossil record makes it exceptionally difficult to relate them to one another; it also suggests a more or less long pre-Ordovician evolution of the group, or alternatively, an exceedingly rapid Early Ordovician evolution similar to that of mammals in the Paleocene. Presumably all pelecypods had a common pre-Ordovician ancestor, and Vogel (1962) has postulated that the Middle Cambrian animal *Lamellodonta* fulfilled this role. Horny (1960) proposed that some *Babinka*-like pelecypod would be most suitable as the common ancestor of all pelecypods, and that *Babinka* was the least modified descendant of this common ancestor. Neither of these proposals is entirely satisfactory; *Lamellodonta* needs to be better documented before it can be cast in the role of the ancestral pelecypod, and *Babinka* seems to be no more or less primitive morphologically than *Cycloconcha* or various of the nuculoids which also show multiple accessory muscle scars and a more or less generalized type of shell.

The concept that all pelecypods are descended from nuculoid taxodonts (Jackson, 1890) is not well supported by the stratigraphic sequence which shows that conocardiids, babinkids, nuculoids, modioliform modiomorphids, and actinodontoids all appear in the fossil record at about the same time (figs. 5, 6); in addition, it is difficult to see how taxodont dentition could have given rise to the other Ordovician dental types. Allen and Sanders (1969) described the solemyid protobranch *Nucinella serrei* Lamy which has a dentition that they regarded as reminiscent of Ordovician actinodontoids. If *Nucinella* can be shown to possess actinodontoid dentition this raises the attractive possibility that the earliest pelecypods were all protobranch, but not taxodont. However, if Allen and Sander's interpretation is correct, *Nucinella* is unique among pelecypods in that it is a monomyarian which maintains the anterior adductor muscle and not the posterior one; normally this is a characteristic of early ontogenetic stages in pelecypods.

In the past few years a number of authors, both paleontologists and malacologists, have speculated on the early phylogeny of the Pelecypoda including: Babin (1966), Cox (1960), Dechaseaux (1952), Newell (1965), Purcheon (1959, 1960, 1963), Stasek (1963), and Vogel (1962). These speculations generally fall into one of two categories: (1) Those which place the nuculoid taxodonts at the base of pelecypod phylogeny, and (2) those which treat actinodontoids as the ancestral stock. This is a serious difference, although if Allen and Sanders (1969) are correct, many of the difficulties presented by this dichotomy will be obviated. However, even among those who regard actinodontoids as the basal stock there is strong disagreement as to how the other groups are related to the actinodontoids. For example, Vogel suggested that taxodonts were derived from cyrtodontids, whereas, Babin suggested that they were derived from a hypothetical archetypic pelecypod ancestor. Add these conclusions to those of persons who would place taxodonts at the base of the pelecypod phylogenetic tree and one quickly sees that speculations on the interrelationships of early pelecypod groups are based on exceedingly scanty data which can be interpreted in various logical ways with one interpretation being as likely as another.

The question of the relationships of the various Ordovician pelecypod lineages to one another is still wide open; because of the scantiness of the available data on this point I have made no attempt herein to relate these lineages to one another (fig. 5); presumably they are related somewhere in the pre-Ordovician. Only the finding of additional specimens which provide documentation that one proposed phylogeny is more likely than another will resolve the difficulties.

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ORDOVICIAN LINEAGES AND HIGHER LEVEL PELECYPOD TAXONOMY

If the Ordovician pelecypod lineages documented above reasonably approximate pelecypod phyletic lines, as I believe they do, then this information should be reflected in the taxonomic hierarchy of the class at the subclass level.

Both Cox (1960) and Newell (1965) regarded the nuculoids and the duplivincular-ligament forms and their descendants as pelecypod subclasses, and this much of the picture drawn above is already incorporated into the formal taxonomy of the class. The rest of this picture should be reflected in the pelecypod taxonomic hierarchy and the conocardiids, mytilaceans, heteroconchians, and anomalodesmatans should also be placed in separate subclasses. Ordovician pelecypods show what the primary radiation of the group was like, and they are the ancestors of all later forms. If phylogenetic data should be incorporated into classification, then the taxonomy of pelecypods should be revised along the lines suggested below.

Based on the relationships postulated herein I propose that the subclass level taxonomy of the Pelecypoda should be arranged as follows:

Subclass Rostroconchida Cox.—The conocardiids are an enigmatic, highly distinctive, Paleozoic, bivalved group which is usually allied to the Pelecypoda; they originated in the Early Ordovician and died out in the Late Permian. For this subclass the name Rostroconchida Cox (1960) is available.

Subclass Palaeotaxodonta Korobkov.—Nuculoids are a distinct pelecypod lineage from the Early Ordovician to the present and already in Ordovician time they were a highly varied and highly successful group. Most recent authors have placed nuculoids in a separate high-level taxon for which the name Palaeotaxodonta Korobkov is available.

Subclass Isofilibranchia Iredale.—Mytilacean-like shells are known from the Early Ordovician to the present; the older species all have a more or less *Modiolus* shape and are probably ancestral to the younger Mytilidae. Mytilaceans are like the pteriomorphians in being byssally attached anisomyarians; however, throughout their stratigraphic ranges the two groups are distinct from each other, and the mytilaceans never possessed the duplivincular type of ligament. These data suggest that the two groups are separate lineages of about equal antiquity which should have the same taxonomic rank. For this subclass the name Isofilibranchia Iredale (1939) is available.

Subclass Pteriomorphia Beurlen.—Duplivincular ligament forms are a distinctive pelecypod stock from the early Middle Ordovician onward, although the primitive duplivincular ligament was eventually lost in all members of the group except the arcoids. The taxon includes most of the living anisomyarians as well as the arcoids and the ambonychiaceans. For this subclass the name Pteriomorphia Beurlen (1944) is available.

Subclass Heteroconchia Hertwig.—Ordovician actinodontoids are probably ancestral to the heterodonts, unionaceans, and trigoniaceans. For this group, Hertwig's (1895; Cox, 1960) name Heteroconchia is available. Cox included the forms here called anomalodesmatans in this subclass; I think that this group forms a subclass of its own.

Subclass Anomalodesmata Dall.—Certain Ordovician burrowing forms and their probable descendants, such as *Edmondia*, *Solenomorpha*, *Wilkingia*, and *Pholadomya*, are herein placed in a separate subclass; two distinct stocks may at present be combined in this taxon. Newell (1965) placed the Paleozoic members of this subclass in the subclass Cryptodonta, and the younger forms in the subclass Anomalodesmata. Runnegar (1966) placed both the Paleozoic and younger forms in the Anomalodesmata; this procedure is followed herein. For this taxon the name Anomalodesmata Dall (1889) is available.

LIFE HABITS

By Late Ordovician time, pelecypods had undergone an adaptive radiation by which they had already explored most of the major modes of life utilized by younger forms except for the cementing of the shell to the substrate and swimming, although the degree of exploration of some of the modes of life was not as advanced as it was to become.

Ordovician infaunal burrowing pelecypods are represented by babinkids, cycloconchids, anomalodesmatans, lyrodesmatids, nuculoids, probably some cyrtodontids and modioliform modiomorphids, and possibly some ambonychiids. Epifaunal forms include the pterineids, most ambonychiids, and some modioliform modiomorphids and cyrtodontids. Epifaunal nestlers on bryozoan colonies are found among the modioliform modiomorphids, probably among the ambonychiids, and perhaps among the pterineids. Boring infaunal pelecypods are not undoubtedly known in the Ordovician; however, Whitfield (1893 [1895]) described the boring modioliform modiomorphid *Corallidomus* and figured (pl. 13) specimens of this genus embedded in burrows on the underside of a coral; unfortunately I have not been able to locate his material. Although conocardiids bear at least superficial resemblances to some younger boring pelecypods there is to date nothing to suggest that they lived like them.

A review of the introduction of the various ecological types into the known fossil record is instructive. At approximately the same time in the early Early Ordovician (Tremadoc), two pelecypod lineages appear: babinkids and conocardiids (fig. 6). These are infaunal forms, and their almost simultaneous appearance near the base of the Ordovician suggests that this mode of life is the primitive one for pelecypods. This reenforces Yonge's (1962) conclusion that the presence of a byssus in the adult represents the persistence of a postlarval organ and that pelecypods having an adult byssus are neotonous (paedomorphic) in this respect. By the end of Early Ordovician time (Arenig), seven pelecypod groups are represented in the known record: babinkids, conocardiids, cycloconchids, lyrodesmatids, modioliform modiomorphids, nuculoids, and redoniids (figs. 6, 7). Of these only the modioliform modiomorphids and perhaps some of the conocardiids are likely to include representatives which were infaunal. Perhaps at this stage of the development of the class, epifaunal pelecypods would have had to compete for living space with the epifaunal articulate brachiopods. It may be that pelecypods met less competition as part of the infauna, although knowledge of the soft-bodied Ordovician infauna is poor at best.

As far as pelecypods are concerned, the early Middle Ordovician (Whiterock-Porterfield) is especially noteworthy because of the introduction of undoubted epifaunal groups. It was at this time that the first ambonychiids, cyrtodontids, and pterineids appeared; these three groups initiate the known fossil record of the subclass Pteriomorphia which has been predominantly epifaunal throughout its history. Ambonychiids were a highly successful early Paleozoic group (Pojeta, 1966), many members of which are mytiliform in shape and probably had a life habit similar to that displayed by *Mytilus*. The remaining early Middle Ordovician pelecypod fauna is made up of the same groups as are found in the late Early Ordovician (fig. 6).

The late Middle Ordovician (Wilderness-Barneveld) was a time of diversification for the pelecypod groups which had originated previously, especially for the cyrtodontids, modioliform modiomorphids, and nuculoids. It was also at this time that undoubted infaunal anomalodesmatans appear in the fossil record. Of groups which originated earlier the redoniids and babinkids are not known from these or younger rocks (fig. 8).

With the exception of the vlastids and possibly the lunulacardiids, no new family-level taxa appear in the Late Ordovician (Cincinnatian). There is some expan-

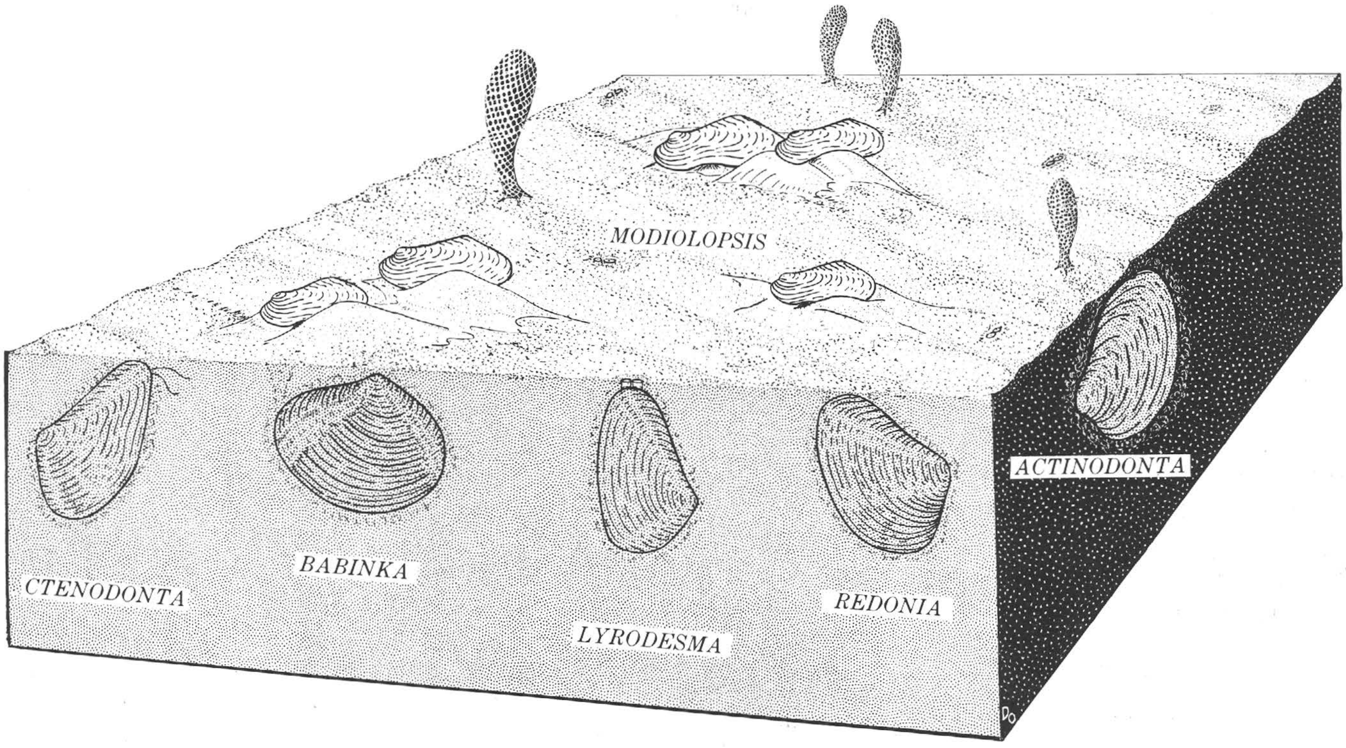

FIGURE 7.—Life-habit reconstructions of late Early Ordovician pelecypod fauna. This composite diagram shows representative genera of pelecypods in their probable life positions. Specimens are not drawn to relative or actual scale. Note the lack of diversification of the epifauna. Idealized algae are included in the diagram. *Actinodonta* drawn from Phillips and Salter (1848), *Babinka* drawn from McAlester (1965), *Lyrodesma* drawn from Barrois (1891) and Babin (1966), *Modiolopsis* drawn from Barrois (1891) and Babin (1966), *Redonia* drawn from Born (1918) and Babin (1966).

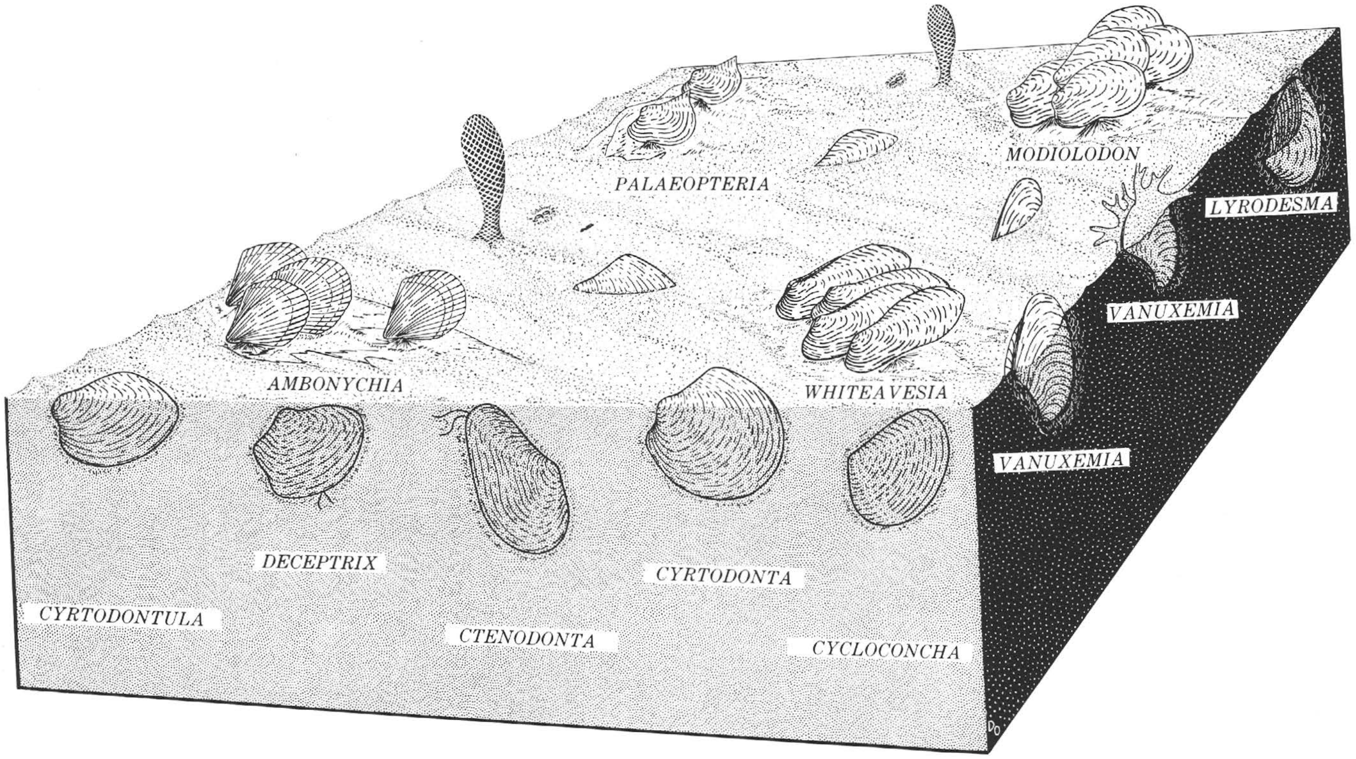

FIGURE 8.—Life-habit reconstructions of late Middle Ordovician pelecypod fauna. This composite diagram shows representative genera of pelecypods in their probable life positions. Specimens not drawn to relative or actual scale. Drawings are based on specimens figured on the plates. Note the diversification of the epifauna. Idealized algae are included in the diagram.

sion of a few groups and contraction of others in the number of known species, and there are some changes at the generic level, but overall the Late Ordovician is similar to the late Middle Ordovician in having about the same number of known species and the same composition at the higher taxonomic levels. However, ecologically the oldest well-documented nestling modioliform modiomorphids (fig. 9) are found in Richmond Age rocks (late Late Ordovician; pl. 16, figs. 4, 5) ; some of the Richmond ambonychiids also seem to have been nestlers, although for these the evidence is not as direct as for the modioliform modiomorphids. The probable boring clam *Corallidomus* is known only from Richmond Age rocks.

Both suspension feeders (*Lyrodesma*) and deposit feeders (*Ctenodonta*) are known from the late Early Ordovician onward.

ORDOVICIAN EPIFAUNA

Ordovician byssate epifaunal groups are: ahtioconchids, most ambonychiids, probably some cyrtodontids of the *Vanuxemia* type, some modioliform modiomorphids, and pterineids. Cyrtodontids underwent a complex radiation of their own which seems to have resulted in epifaunal, semi-infaunal, and infaunal forms, and this group is discussed separately after the section on the Ordovician infauna.

Modioliform modiomorphids probably were similar in mode of life to those living mytilaceans which have an anterior lobe and nonterminal beaks (for example, *Arcuatula*, *Modiolus*, and *Mytella*). These animals can live on or in a variety of substrates including hard bottoms where they are raised above the substrate, although often nestled in nooks and crannies (Kauffman, 1969, p. N144) ; soft bottoms where they are partly buried in the substrate up to about the depth of the posterior part of the umbonal ridge (I have seen some individuals of *Arcuatula demissus* (Dillwyn) living in this fashion, both in aquaria and in nature) ; and in many populations of *A. demissus* embedded in peat mats where they are often completely buried and almost vertical in position with the posterior end uppermost (personal observation and S. M. Stanley, oral commun., 1968). Thus, pelecypods with a *Modiolus* shape can be epifaunal, semi-infaunal, or infaunal. As I could not distinguish these different modes of life in the Ordovician on the basis of data currently available to me, I have drawn all the Ordovician forms on hard bottoms raised above the substrate (figs. 7–9) which seems to be a reasonably common life position in Holocene species. In one Ordovician species of *Modiolopsis* it was possible to document

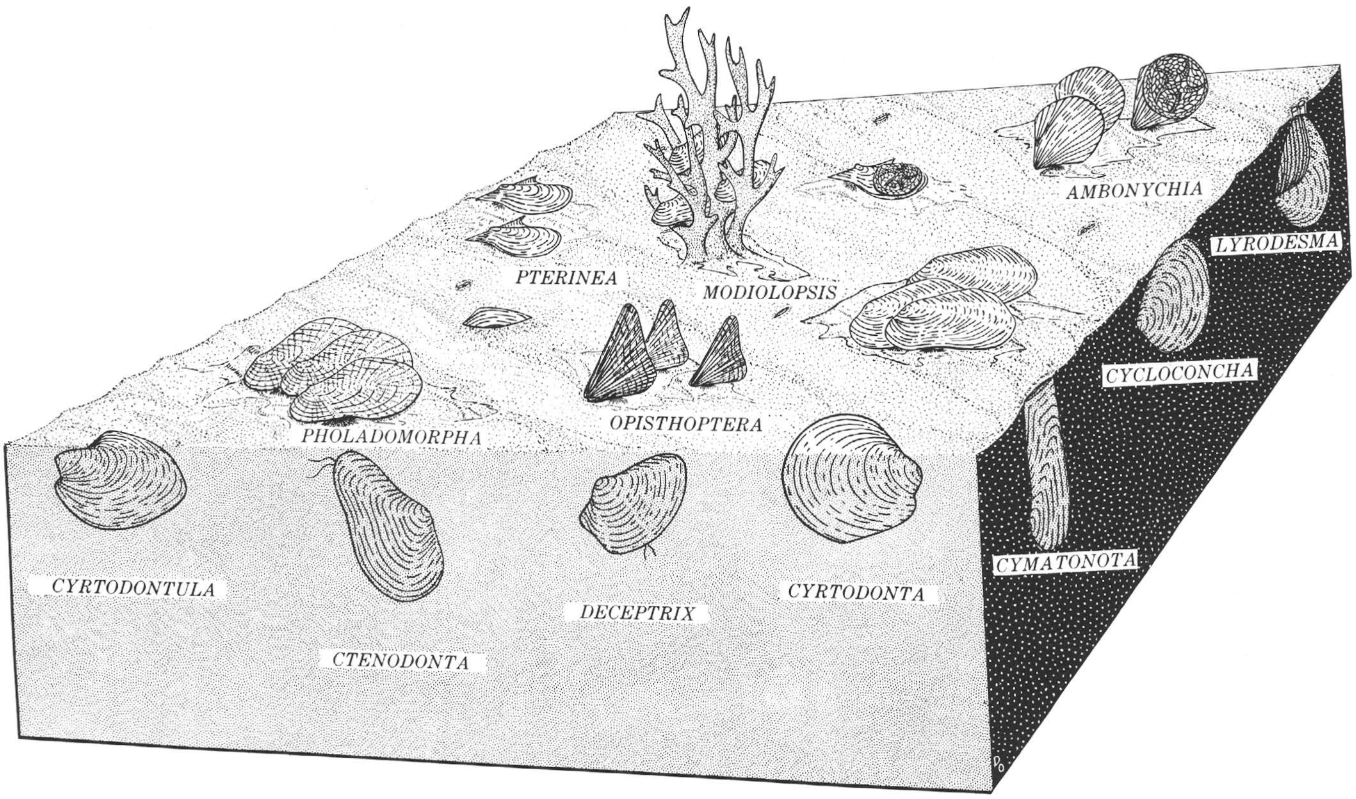

FIGURE 9.—Life-habit reconstructions of Late Ordovician pelecypod fauna. This composite diagram shows representative genera of pelecypods in their probable life positions. Note the further diversification of the epifauna. Specimens not drawn to relative or actual scale. Drawings are based on specimens figured on the plates.

that it was a nestler on trepostome bryozoan colonies (pl. 16, figs. 4, 5). The trepostome was identified as probably a species of *Hallopora* by O. L. Karklins, U.S. Geological Survey.

In some places, Ordovician modioliform modiomorphids are found crowded on single bedding planes or forming single thin beds with many of the shells being articulated and varying in size. These facts suggest that at least some species were gregarious like some living mytilaceans. *Corallidomus*, the one probable Ordovician borer, looks much like a modioliform modiomorphid. (See Whitfield, 1893 [1895], p. 493, pl. 13.)

The first ambonychiids to appear in the fossil record already show a marked reduction of the anterior end of the shell. This reduction indicates that the group was already specialized and had already undergone a more or less long period of evolution. From nearly the beginning of their known history, ambonychiids can be divided into two groups: those which possess an anterior lobe (pl. 10, fig. 5) and those which lack such a lobe (pl. 10, figs. 1, 12). Ambonychiids are both ecological and morphological homeomorphs of the recent mytilids. Those ambonychiids which have lost the anterior lobe (such as *Ambonychia*, figs. 8, 9) are much like living species of *Mytilus* in shape and body construction and probably lived in an epifaunal fashion like members of *Mytilus*. This genus projected above the bottom and was attached to hard substrates. Ambonychiids which have an anterior lobe are often deeper bodied than mytilids with a similar lobe; however, it seems likely that these ambonychiids showed the same variations in life habits as *Modiolus*-like mytilaceans.

Some late Late Ordovician (Richmond) Ambonychias are occasionally found in beds which contain large numbers of branching trepostome bryozoans that seem to surround "crack-out" specimens of the clams. This occurrence suggests that these Ambonychias were nestling on the bryozoans. Although the evidence for nestling among ambonychiids is not as direct as the evidence for nestling of modioliform modiomorphids, it seems likely that the ambonychiids also would have exploited this mode of life.

The peculiar ambonychiid genus *Opisthoptera* (pl. 10, figs. 1, 2) is also found in Richmond Age rocks. *Opisthoptera* is an equivalved, markedly alate form which may have lived much like modern species of *Pteria* attached to various erect substrates and using the wing as a rudder to orient itself to the currents

(Kauffman, 1969, p. N132, N144). No specimens of *Opisthoptera* have been found in this position, and they may have been attached to hard horizontal substrates as shown in figure 9.

Some Ambonychiids, like modioliform modiomorphids, are found in large numbers on single bedding planes or forming a single thin bed with many of the shells still articulated and varying in size. These features suggest that some species were gregarious like some living mytilids. Some Ordovician ambonychiids are found with edrioasteroids attached to them (fig. 9).

Ordovician pteriaceans are placed in two families. The Ahtioconchidae is poorly known and is represented by the single species *Ahtioconcha auris* Öpik. It is markedly inequivalved and left convex and was presumably attached by a byssus.

Ordovician pteriaceans placed in the genus *Pterinea* have both a well-developed anterior lobe and a posterior wing. In shell shape they are pteriaform; however, their pronounced valve inequality is more like *Pinctada*. Like their living counterparts, Ordovician forms were probably entirely epifaunal. The known specimens of *Pterinea* to which edrioasteroids are attached always have the latter on the left valve. This placement suggests that this valve was uppermost and that the commissure of the shell was never at right angles to the substrate the way it is in some living species of *Pteria* which are pendant on alcyonarians. All Ordovician pterineids may not have had the right valve flat against the substrate as shown in figure 9; they may have also been attached with the commissure at some acute angle to the substrate as shown for *Palaeopteria* in figure 8. *Palaeopteria* is far less inequivalved than *Pterinea* and may have been attached to trepostome bryozoans the way *Pteria* attaches to alcyonarians, although there is no direct evidence for this.

ORDOVICIAN INFAUNA

The Ordovician infauna is highly varied and, as mentioned previously, includes babinkids, most conocardiids, cycloconchids, cyrtodontids of the *Cyrtodonta* type (p. 37), anomalodesmatans, lyrodesmatids, nuculoids, redoniids, probably some modioliform modiomorphids, and possibly some ambonychiids. The possible infaunal and semi-infaunal representatives of the last two groups are discussed in the preceding section on Ordovician epifauna.

Lyrodesma and *Babinka* were infaunal siphonate suspension feeders. *Lyrodesma* is sinupalliate and elongate and therefore was probably a "normal" siphonate pelecypod (figs. 7–9). *Babinka* lacks a pallial sinus and was probably a mucous tube feeder like the later lucinoids (fig. 7). Among the anomalodesmatans with elongate gaping shells a pallial sinus is unknown; however, at least some of them probably were sinupalliate. As far as known the remaining Ordovician infaunal forms were integropalliate, and the shell was probably in contact (or nearly in contact) with the sediment-water interface at the point of origin of the inhalant current.

Lyrodesma is the oldest known siphonate pelecypod which has a pallial sinus; this feature combined with the anteriorly-posteriorly elongated shell strongly suggests that the genus was infaunal with only the siphons reaching the sediment-water interface (figs. 7–9). The rostrate nature of the posterior end of the shell is similar to such living forms as *Anomalocardia* and suggests a vertical life position. The oldest known specimens of *Lyrodesma* which show a pallial sinus are early Late Ordovician in age (Eden and Maysville); however, Middle and Early Ordovician shells with the same shape and dentition as the Late Ordovician species of *Lyrodesma* probably had the same mode of life.

Paleozoic pelecypods in which an undoubted pallial sinus is present are not known to be numerous; however, the structure is known to occur in three subclasses and has an early origin. In addition to *Lyrodesma*, sinupalliate pelecypods include the palaeotaxodont genera *Palaeoneilo* and *Antraconeilo* (McAlester, 1963b, 1968); the trigonicean *Scaphellina* (Newell and Ciriacks, 1962); and the anomalodesmatan genera *Wilkingia* (Wilson, 1959), *Pyramus* (Newell, 1956), *Crassiconcha* (Netschajew, 1894), *Casterella* (Mendes, 1952), *Vacunella*, *Chaenomya*, and perhaps *Oblicarina* (Waterhouse, 1967). The structure is probably more widespread than the above list indicates, although it has not been documented because the pallial line is unknown in many Paleozoic genera. The fact that the pallial sinus occurs in Ordovician pelecypods indicates that siphonate suspension feeding was an early adaptation of the group, although the possibilities opened up by this mode of life were not fully exploited until the post-Paleozoic (Stanley, 1968).

McAlester's reconstruction of the mode of life of *Babinka* as a shallow infaunal element is highly probable, and his figure of that genus is copied here in figure 7.

Ordovician nuculoids like their living counterparts were probably deposit-feeding infauna. In general, they can be divided into two groups: nuculiform shells such as *Deceptrix* and nuculaniform shells such as *Ctenodonta* s.s. Reconstructions of Ordovician nuculoids in figures 7–9 are largely based on the studies of the habits of living species by Yonge (1939), Drew (1899), and Stanley (1968, 1970). No Ordovician solemyids are known, although the name *Solemya* (as *Solenemya*) has occasionally been used for Ordovician clams (Ruedemann, 1912).

Yonge's studies of *Nucula* indicate that the animal positions itself in the sediment with the anterior end uppermost, whereas *Yoldia* positions itself with the posterior end uppermost. Although Drew and Yonge figured *Yoldia* in an almost vertical position with the posterior end above the sediment-water interface, Stanley (1968) has shown that it burrows diagonally and does not expose the posterior end of the shell. However, an equally important point is that the life position of nuculaniform shells such as *Yoldia* is the reverse of nuculiform shells such as *Nucula.*

Yonge noted that in its life position in the substrate, *Nucula nucleus* has an anterior inhalent current and is shallowly buried with the anterior end approximately parallel to the sediment-water interface, and this end is covered with a thin veneer of sediment. It is assumed herein that Ordovician *Nucula*-like shells such as *Deceptrix* and *Similodonta* lived in a similar fashion (figs. 8, 9).

The burrowing habits of such nuculaniform shells as *Malletia*, *Nuculana*, and *Yoldia* are varied; in addition, these animals have posterior incurrent and excurrent siphons which may insert into a prominent pallial sinus. Because of these characteristics it is difficult to compare these living forms to such integropalliate nuculaniform shells as *Ctenodonta* s.s. Still it seems likely, based on shell shape, that *Ctenodonta* s.s. lived in a manner similar to one or another of the living nuculaniform species.

Malletia, a deeper water form having a thin transparent shell, burrows parellel to the sediment-water interface and not at some angle to it. According to Yonge (1939), this species is unlike other nuculaniform shells he examined in that it tends to move about more or less continuously; probably this mode of life has little significance for interpreting the life habit of such thick-shelled forms as *Ctenodonta.*

The species of *Lemubulus* and *Yoldia* studied by Yonge and Stanley burrow diagonally, completely burying the shell. It seems likely that *Ctenodonta* lived in a manner similar to one of these genera (figs. 7–9).

Ordovician soleniform anomalodesmatans such as *Cymatonota* are interpreted as burrowing forms based on their elongate shell shape, subparallel dorsal and ventral margins, reduced umbos, and anterior and posterior shell gapes. These features reoccur in various distantly related pelecypod groups which have become relatively deep burrowers, such as myids, solemyids, and solenids. Nothing is known of the hinge line or pallial line of Ordovician soleniform shells and little is known of their musculature; however, their general shell shape points up their infaunal habits. The depth to which these forms could burrow is uncertain; it would depend upon the extensibility of the siphons, but nothing is known of the pallial line.

The general morphology and shell shape of the equivalved, elongated telliniform genus *Cycloconcha* suggests that it was a shallow infaunal form. There is nothing to suggest that *Cycloconcha* is closely related to Tellinacea, rather it seems to be related to the late Paleozoic crassatellaceans (Newell, 1958; Boyd and Newell, 1968). Redoniids also were probably infaunal elements; based on Babin's figures (1966, p. 246) of this group, they probably lived in a manner similar to *Cycloconcha* (figs. 7–9).

Most conocardiids were probably infaunal elements, although such forms as *Euchasma* from the Early Ordovician (pl. 20, figs. 18–21) may have been epifaunal. Conocardiids are not included in any of the reconstructions shown here as there is still much debate about such basic morphological interpretations as which end is anterior in this group.

CYRTODONTIDAE

Cyrtodontids present a perplexing melange of forms which are difficult to evaluate as there is nothing quite like them in modern seas. They are abundant in the upper Middle and Upper Ordovician rocks of North America (fig. 6) and are known to range upward into the Devonian rocks of Europe (Frech, 1891; Maillieux, 1937). In Ordovician time the group underwent an obvious adaptive radiation which produced *Glycymeris*-like shells (pl. 6, figs. 21–23), *Noetia*-like shells (pl. 7, fig. 6), *Crenella*-like shells (pl. 8, fig. 11), and *Septifer*-like shells (pl. 8, fig. 1). Some of the cyrtodontids show a pronounced reduction of the anterior end, all of them have the umbos displaced anteriorly, and all are robust shells. The range of variation of Ordovician cyrtodontid shell form suggests that they were adapted to a variety of niches and probably habitats.

By Devonian time, cyrtodontids were no longer as varied or as large as in Ordovician time, and as noted by Douvillé (1913) some of them had begun to approach Carboniferous and Mesozoic parallelodontids and arcids in shell shape and dentition.

Cyrtodontids of the *Vanuxemia* type (pl. 8) show some features, which are usually found in byssally attached pelecypods, including some reduction of the anterior end of the shell (pl. 9, fig. 7), some reduction in the size of the anterior adductor muscle (pl. 8, fig. 8), anterior displacement of the beaks (pl. 8, fig. 5), and the elevation of the anterior adductor muscle on either a shell thickening (pl. 8, fig. 6) or an umbonal septum (pl. 8, fig. 1). They show no byssal gape (pl. 8, fig. 3); however, some specimens show a slight deflection of the anterodorsal margin forming a byssal sinus (pl. 9, fig. 7).

Cyrtodontids of the *Vanuxemia* type are characterized by having the anterior teeth immediately below the beaks (pl. 8, figs. 1, 5, 6, 8, 13) and by having the anterior adductor muscle displaced medially and originating on a raised shell thickening (pl. 8, fig. 5) or on an umbonal shelf or septum (pl. 8, fig. 1) which floors the anterodorsal part of the shell. The anterior end of the pallial line terminates at the umbonal shelf (pl. 9, fig. 7) or thickening (pl. 8, fig. 9), and in forms in which the shelf is well developed there is usually some development of a myophoric notch on its posteroventral surface (pl. 8, figs. 1, 2; pl. 9, figs. 5–7). The myophoric notch probably served as the seat and passageway of an accessory muscle. In forms which lack an umbonal septum, but have a shell thickening, an accessory muscle scar is present on the lateral-posterior face of the anterior adductor scar (pl. 8, figs. 6–9); this scar is in a position homologous with the myophoric notch.

A notched umbonal septum, similar to the septum of *Vanuxemia*, is found in living species of the byssally attached mytilid genus *Septifer* (pl. 9, figs. 14–17). In *Septifer*, as in *Vanuxemia*, the umbonal septum serves as the seat of the anterior adductor muscle, and in both genera the depth of the myophoric notch shows individual variation (pl. 9, figs. 4–7, 11–14) and species variation (pl. 8, fig. 1; pl. 9, figs. 5–17). The notch is always deep in some species and always shallow in others, but it is not developed to the same depth in all individuals of a species.

In *Septifer bilocularis* the myophoric notch is either undeveloped or only shallowly developed (pl. 9, figs. 8–13), whereas, in *S. excisus* it is always deep (pl. 9, figs. 14–17). In attempting to determine what structure forms the notch, I only had specimens of *S. bilocularis* for dissection, and as noted above in this species, the notch is at best only shallowly developed. When present, the notch is equally developed in the umbonal septa of each valve of an individual, and it extends along the lateral face of each septum as a groove, thus the notches must be formed by paired structures (pl. 9, figs. 16, 17). The most likely paired structures to have formed the myophoric notches in *Septifer* are the anterior byssal retractor muscles. In *S. bilocularis*, these muscles insert into the byssal apparatus immediately posterior to the umbonal septum and probably would be in contact with the septum only when contracted. Although I did not have preserved specimens of *S. excisus* to dissect, the large size of the myophoric notches and the grooves on the lateral faces of the shelves suggest that in this species the anterior byssal retractors are in more or less continuous linear contact with the septum.

To the best of my knowledge, it is only in byssate pelecypods that an umbonal shelf is present. Among living forms it is found in the mytilid genus *Septifer* and in the dreissenid genera *Dreissenia* and *Congeria*. In fossil forms it is known in some myalinids such as *Septimyalina* (Newell, 1942) and *Atomodesma* (Dickens, 1963), and perhaps in the ambonychiid genera *Ambonychiopsis* and *Congeriomorpha* (Pojeta, 1966).

Because the umbonal septum is known only in byssally attached pelecypods, its presence suggests that cyrtodontids of the *Vanuxemia* type were byssate. Also these cyrtodontids show the additional features of byssally attached pelecypods cited above, as well as some flattening of the anterior face of the shell (pl. 8, fig. 3), and an articulated specimen will often balance on this face. However, the anterior edge of the shell remains rounded (pl. 8, fig. 8), and a specimen balanced on it is definitely unstable. A byssus would help stabilize the shell, but it seems unlikely that cyrtodontids of the *Vanuxemia* type were epifaunal after the fashion of *Mytilus* or *Ambonychia*. They may have been semi-infaunal in the sense of being partly buried in the sediment as are some pinnids, burrowing arcs (Lim, 1966), and modioliform mytilids, or they may have dwelt in depressions and concavities as do many of the byssally attached arcs. Supporting the view that cyrtodontids with an umbonal shelf or thickening were not entirely epifaunal are rare specimens in which the posterior end is encrusted with epibionts (pl. 8, fig. 14), whereas, the anterior end is free of epibionts; to date all specimens of this type seen by me have been single valves. The byssus, as in some of the burrowing arcs, may have been used to maintain the position of the partly buried shell in the sediment (fig. 8).

Sardeson (1939) thought that shells of the *Vanuxemia* type did not crawl about or burrow in the sea bottom, but rather that they were anchored to solid objects either permanently or temporarily or that they rolled about with the storms and currents. He regarded them as anchored by the foot.

Cyrtodontids with an umbonal septum were evolving in a manner of their own, and although they may have nestled in concavities on the sea bottom like the younger byssally attached arcs, they do not seem to be on the direct line of descent leading to the arcaceans. Shells of the *Vanuxemia* type were showing a stabilization in position of the dental elements, whereas, shells of the *Cyrtodonta* type are highly variable in this regard especially in the number and placement of the anterior teeth. Also cyrtodontids with an umbonal septum show more or less typical features of byssally attached anisomyarian duplivincular pelecypods, whereas, byssally attached arcaceans do not; the latter retain the anterior end of the shell, the beaks are displaced far back from the anterior margin, and they possess a midventral byssus.

Cyrtodontids of the *Cyrtodonta* type lack an umbonal shelf or shell thickening (pl. 7, fig. 2), and some or all of the anterior teeth are not placed immediately below the beaks (pl. 7, figs. 1–4, 7, 8). In this group, an accessory muscle scar is present on the lateral surface of the hinge plate opposite the anterior teeth (pl. 6, figs. 18–20); one specimen I have seen may have an accessory scar in a position homologous to that of the accessory scar of cyrtodontids of the *Vanuxemia* type (pl. 7, fig. 2).

Some of the cyrtodontids which lack an umbonal shelf may have been byssally attached because of the presence of such features as reduction of the anterior part of the shell and significant anterior displacement of the beaks (pl. 7, figs. 2–4). However, others seem to have been infaunal including the *Glycymeris*-like and *Noetia*-like shells (pl. 6, figs. 21–23; pl. 7, figs. 5, 6).

The *Noetia*-like shells are primarily a Late Ordovician development and are placed in the genus *Cyrtodontula* [Whitella] (pl. 7, figs. 5, 6; fig. 9). Living *Noetia* (S. M. Stanley, oral commun., 1968) burrow in sandy bottoms often to the depth of the posterior margin of the shell, but some only to the depth of the umbonal ridge with the posterior end of the shell remaining exposed. Lim (1966) has shown that some species of living *Anadara* live in a similar position and substrate. Some of the Anadaras burrow 6–10 cm below the surface with the posterior end of the shell totally out of contact with the sediment surface. It cannot yet be determined whether or not some of the Ordovician *Noetia*-like shells lived in the latter fashion; however, it seems likely that they were burrowing forms having a mode of life similar to burrowing arcs like *Noetia* and *Anadara*.

The *Glycymeris*-like cyrtodontids are placed in the genus *Cyrtodonta* and were probably shallow burrowers based on their general shell form. They may have burrowed like *Cyrtodontula*, leaving the posterior end of the shell sticking up out of the sediment (fig. 8); *Glycymeris* is known to adopt such a life position at times (Vlès, 1906).

Sardeson (1924) suggested that *Cyrtodonta megambona* was probably epifaunal or semi-infaunal; he thought it could have lived on any shell edge except the posterior and that it probably anchored itself to the substrate by its foot.

The most variation in shell shape and anterior dentition is among cyrtodontids of the *Cyrtodonta* type, and it is probably from this group that arcaceans arose in Devonian time. The fact that cyrtodontids were so varied and actively radiating in Ordovician time suggests that they are ancestral to the other duplivincular ligament forms.

REFERENCES CITED

Allen, J. A., 1958, On the basic form and adaptations to habitat in the Lucinacea (Eulamellibranchia): Royal Soc. London Philos. Trans., ser. B, v. 241, no. 684, p. 421–484, pl. 18.

Allen, J. A., and Sanders, H. L., 1969, *Nucinella serrei* Lamy (Bivalvia: Protobranchia), a monomyarian solemyid and possible living actinodont: Malacologia, v. 7, p. 381–396.

Babin, Claude, 1966, Mollusques bivalves et céphalopodes du Paléozoïque Armoricain: Brest, Imprimerie Commerciale et Administrative, 471 p., 18 pls.

Barrande, Joachim, 1881, Système Silurien du centre de la Bohême, v. 6, Acéphalés: Paris and Prague, 342 p., 361 pls. (Bound in four volumes.)

Barrois, Charles, 1891, Memoire sur la faune du grès armoricain: Soc. Géol. Nord Annales, v. 19, p. 134–237, pls. 1–5.

Bassler, R. S., 1915, Bibliographic index of American Ordovician and Silurian fossils: U.S. Natl. Mus. Bull. 92, 1521 p., 4 pls. (Bound in two volumes.)

Bayer, T. N., 1967, Repetitive benthonic community in the Maquoketa Formation (Ordovician) of Minnesota: Jour. Paleontology, v. 41, no. 2, p. 417–422, pl. 51.

Bekker, Hendrik, 1921, The Kuckers Stage of the Ordovician rocks of NE Estonia: Eesti Vabariigi Tartu Ülikoole (Tartu University), Toimetused (Acta et Commentationes, Universitatis Dorpatensis), ser. A, no. 2, p. 1–92, pls. 1–12.

Bergström, S. M., and Sweet, W. C., 1966, Conodonts from the Lexington Limestone (Middle Ordovician) of Kentucky and its lateral equivalents in Ohio and Indiana: Bulls. Am. Paleontology, v. 50, no. 229, p. 271–441, pls. 28–35.

Beurlen, Karl, 1944, Beiträge zur Stammesgeschicte der Muschelen: Bayerische Akad. Wiss. Math.-Naturw. Abt. Sitzungsber. 1944, no. 1–2, p. 133–145.

Bigsby, J. J., 1868, Thesaurus Siluricus: London, John van Voorst, 1ii, 214 p.

Billings, Elkanah, 1865, Palaeozoic fossils, v. 1: Canada Geol. Survey, 426 p.

Born, Axel, 1918, Die Calymene Tristani=Stufe (mittleres Untersilur) bei Almaden, ihre Fauna, Gliederung und Verbreitung: Senckenbergische Naturf. Gesell. Abh., v. 36, no. 3, p. 309–358, pls. 24–27.

Boyd, D. W., and Newell, N. D., 1968, Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera: Am. Mus. Novitates, no. 2328, 52 p.

——— 1969, Limitations of Bernard and Munier-Chalmas system for bivalve hinge notation, *in* Moore, R. C., ed., Treatise on invertebrate paleontology, pt. N, v. 2, Mollusca 6, Bivalvia: Boulder, Colo., and Lawrence, Kans., Geol. Soc. America and Univ. Kansas Press, p. N908–N913.

Branson, C. C., 1948, Bibliographic index of Permian invertebrates: Geol. Soc. America Mem. 26, 1049 p.

Butts, Charles, 1941, Geology of the Appalachian Valley in Virginia; Virginia Geol. Survey Bull. 52, pt. 2, 271 p., pls. 64–135 [1942].

Chavan, André, 1954, Les *Pleurophorus* et genres voisins: Cahiers Geol. Thoiry, no. 22, p. 200.

———1966a, Remarques sur l'origine des Lucinacea (Mollusques Pélécypodes) : Soc. Géol. France Compte Rendu, 1966, pt. 4, p. 163–164.

———1966b, Sur l'évolution de la charnière des Hétérodontes (Mollusques Pélécypodes) : Soc. Géol. France Compte Rendu, 1966, pt. 10, p. 408–409.

———1967, Sur les Hétérodontes du Dévonien Rhénan (Mollusques Pélécypodes) : Soc. Géol. France Compte Rendu, 1967, pt. 2, p. 44–46.

Clarke, J. M., 1904, Naples fauna in western New York, pt. 2: New York State Mus. Mem. 6, p. 199–454, pls. 1–20.

Clarke, A. H., and Menzies, R. J., 1959, *Neopilina* (*Vema*) *ewingi*, a second living species of the Paleozoic class Monoplacophora : Science, v. 129, no. 3355, p. 1026–1027.

Cloud, P. E., Jr., and Barnes, V. E., 1948, The Ellenburger group of central Texas: Texas Univ. Pub. 4621, 473 p., 44 pls.

Conrad, T. A., 1838, Report on the palaeontological department of the survey [of New York] : New York Geol. Survey Ann. Rept. 2, p. 107–119.

———1841, Fifth annual report on the palaeontology of the State of New York: New York Geol. Survey Ann. Rept. 5, p. 25–57.

Cooper, G. A., 1956, Chazyan and related brachiopods: Smithsonian Misc. Colln., v. 127, 1245 p., 269 pls. (In two volumes.)

Cox, L. R., 1937, Notes on Jurassic Lamellibranchia : Malacological Soc. London Proc., v. 22, pt. 4, p. 190–204, pls. 15, 16.

———1959, The geological history of the Protobranchia and the dual origin of taxodont Lamellibranchia : Malacological Soc. London Proc., v. 33, p. 200–209.

———1960, Thoughts on the classification of the Bivalvia : Malacological Soc. London Proc., v. 34, p. 60–88.

Cuvier, Georges, 1797, Tableau élémentaire de l'histoire naturelle des animaux : Paris, 710 p., 14 pls.

Dall, W. H., 1889, On the hinge of pelecypods and its development, with an attempt toward a better subdivision of the group: Am. Jour. Sci., ser. 3, v. 38, p. 445–462.

———1900, Pelecypoda, *in* Zittel-Eastman textbook of paleontology, 1st ed. : London, Macmillan and Co., v. 1, p. 364–429.

Dean, W. T., 1966, The Lower Ordovician stratigraphy and trilobites of the Landeyran Valley and the neighboring district of the Montagne Noire, south-western France : British Mus. (Nat. History) Bull., Geology, v. 12, no. 6, p. 247–353, pls. 1–21.

Dechaseaux, Colette, 1952, Classe des Lamellibranches, *in* Piveteau, Jean, ed., Traité de paléontologie: Paris, Masson et Cie, v. 2, p. 220–246 and 261–364.

Dickens, J. M., 1963, Permian pelecypods and gastropods from Western Australia: Australia Bur. Mineral Resources, Geology and Geophysics Bull. 63, 203 p. 26 pls.

Douvillé, Henri, 1907, Les lamellibranches cavicoles on desmodontes: Soc. Géol. France Bull., ser. 4, v. 7, p. 96–114.

———1912, Un essai de classification phylogénique des lamellibranches: Acad. Sci. Comptes Rendus 1912, p. 1677–1682.

———1913, Classification des lamellibranches: Soc. Géol. France Bull., ser. 4, v. 12, p. 419–467.

Drew, G. A., 1899, The anatomy, habits and embryology of *Yoldia limatula*, Say: Johns Hopkins Univ. Biol. Lab. Mem., v. 4, no. 3, 37 p., 5 pls.

Driscoll, E. G., 1964, Accessory muscle scars, an aid to protobranch orientation: Jour. Paleontology, v. 38, no. 1, p. 61–66, pl. 16.

———1965, Dimyarian pelecypods of the Mississippian Marshall Sandstone of Michigan: Palaeontographica Americana, v. 5, no. 35, p. 64–128, pls. 7–18.

Eberzin, A. G., ed. 1960, Osnovy paleontologii, spravochnik diya paleontologov i geologov SSSR; [v. 3], Mollyuski; pantsirnye, dvustvorchatye, lopatonogie: Moscow, Akad. Nauk SSSR, 300 p., 44 pls.

Eichwald, Edouard, 1860, Lethaea Rossica ou Paléontologie de la Russie: Stuttgart, E. Schweizerbart, 1657 p. (bound in two volumes), 59 pls. (Bound separate from text and published in 1859.)

Endo, Riuji, 1935, Additional fossils from the Canadian and Ordovician rocks of the southern part of Manchoukuo: Tōhoku Imp. Univ. Sci. Repts., ser. 2 (Geology), v. 16, no. 4, p. 191–223, pls. 10–15.

Fischer, Paul, 1880–87, Manuel de conchyliologie et de paléontologie conchyliologique ou histoire naturelle des mollusques vivants et fossiles: Paris, F. Savy, p. 1–112, 1880; p. 113–304, 1881; p. 305–416, 1882; p. 417–608, 1883; p. 609–688, 1884; p. 689–896, 1885; p. 897–1008, 1886; p. 1009–1369, 1887.

Flower, R. H., 1964, The nautiloid order Ellesmeroceratida (Cephalopoda) : New Mexico Bur. Mines and Mineral Resources Mem. 12, 234 p.

Frech, Fritz, 1891, Die devonischen aviculiden Deutschlands: Abh. Geol. Specialkarte Preussen und Thüringischen Staaten, v. 9, no. 3, 261 p., 18 pls. (Bound in two volumes.)

Fritz, M. A., 1951, The pelecypod genus *Vlasta* in the Ordovician of North America: Jour. Paleontology, v. 25, no. 5, p. 696–698.

Fuchs, A., 1919, Beitrag zur kenntnis der devonfauna der Verse- und Hobräcker Schichten des sauerlandischen faciesgebietes: Preuss. Geol. Landesanstalt, Jahrbuch 1918, v. 29, pt. 1, no. 1, p. 58–95, pls. 5–9.

Gigout, Marcel, 1951, Études géologiques sur la Meseta Marocaine occidentale (arrière-pays de Casablanca, Mazagan et Safi) : Morocco Service Géol., Notes et Mém., no. 86, 507 p.; Inst. Sci. Chérifien, Travaux no. 3, t. 1, 507 p.

Goldfuss, G. A., 1820, Handbuch der zoologie, *in* Schubert, G. H., ed., Handbuch der naturgeschichte: Nürnberg, J. L. Schrag, Theil 3, abtheilung 1, 696 p., 2 pls.

———1836, Petrefacta Germaniae: Düsseldorf, Arnz & Comp., Theil 2, lief 5, p. 66–140, pls. 47–121.

Grabau, A. W., 1922, Ordovician fossils of north China : Palaeontologia Sinica, v. 1, pt. 1, p. 1–127, pls. 1–9.

Haffer, Jürgen, 1959, Der Schlossbau früh-heterodonter Lamellibranchiaten aus dem rheinischen Devon: Palaeontographica, v. 112, abt. A, p. 133–192, pls. 11–14.

Hall, James, 1847, Description of the organic remains in the lower division of the New York system: Palaeontology of New York, v. 1, 338 p., 88 pls.

Harper, J. C., 1947, The Caradoc fauna of Ynys Galed, Caernarvonshire: Annals and Mag. Nat. History, ser. 11, v. 14, p. 153–175, pls. 6, 7.

Harrington, H. J., 1938, Las faunas del Ordoviciano inferior del norte Argentino: La Plata Univ. Nac. Inst. Mus. Rev., new ser., v. 1, Sec. Paleontologia, no. 4, 290 p., 14 pls.

Hertwig, R., 1895, Lehrbuch der zoologie, 3te auflage: Jena, xii, 599 p.

Hicks, Henry, 1873, On the Tremadoc rocks in the neighborhood of St. David's, south Wales, and their fossil contents: Geol. Soc. London Quart. Jour., v. 29, p. 39–52, pls. 3, 4.

Hill, Dorothy, Playford, G., and Woods, J. T., 1969, Ordovician and Silurian fossils of Queensland: Brisbane, Queensland Palaeontographical Soc., 15 p., 7 pls. (Ordovician), 18 p., 8 pls. (Silurian).

Hind, Wheelton, 1910, The lamellibranchs of the Silurian rocks of Girvan: Royal Soc. Edinburgh Trans., v. 47, pt. 3, p. 479–548, pls. 1–5.

Horný, Radvan, 1957, Problematicheski mollyuski (?Amphineura) iz nizhnego kembriya yuzhnoi i vostochnoi Sibiri (SSSR): Czechoslovakia, Ústřed. Ústav. Geol. Sbornik, sv. 23 (1956), Paleontológie, p. 397–432, pls. 1–4. (with Czech and English summaries).

——— 1960, On the phylogeny of the earliest pelecypods, Mollusca): Czechoslovakia, Ústřed. Ústav. Geol. Vestnik, v. 35, p. 479–482, pl. 1.

Iredale, Tom, 1939, Great Barrier Reef expedition 1928–29, Scientific Reports, v. 5, no. 6, Mollusca pt. 1: London, British Museum (Nat. History), p. 209–425, pls. 1–7.

Isberg, Orvar, 1934, Studien über lamellibranchiaten des Leptaenakalkes in Dalarna: Lund, Håkan Ohlssons Buchdruckerei, 493 p., 32 pls.

Jackson, R. T., 1890, Phylogeny of the Pelecypoda; the Aviculidae and their allies: Boston Soc. Nat. History Mem., v. 4, no. 8, p. 277–400, pls. 23–30.

Johnston, R. M., 1888, Systematic account of the Geology of Tasmania: Hobart, J. Walch & Sons, 408 p., 57 pls.

Kauffman, E. G., 1969, Form, function and evolution, *in* Moore, R. C., ed., Treatise on invertebrate paleontology, pt. N, v. 1, Mollusca 6, Bivalvia: Boulder, Colo., and Lawrence, Kans., Geol. Soc. America and Univ. Kansas Press, p. N129–N205.

Khalfin, L. L., 1958, Plastinchatozhabernye mollyuski ordovika Chu-Iliyskikh gor: Akad. Nauk SSSR, Geol. Inst. Trudy, v. 9, p. 139–196, pls. 1–7.

Knight, J. B., and Yochelson, E. L., 1960, Monoplacophora, *in* Moore, R. C., ed., Treatise on invertebrate paleontology, pt. I, Mollusca 1: New York and Lawrence, Kans., Geol. Soc. America and Univ. Kansas Press, p. 177–184.

Kobayashi, Teiichi, 1933, Faunal study of the Wanwanian (basal Ordovician) series with special notes on the Ribeiridae and the ellesmereoceroids: Tokyo Imp. Univ. Fac. Sci. Jour., sec. 2, v. 3, pt. 7, p. 249–328, pls. 1–10.

——— 1934, The Cambro-Ordovician formations and faunas of south Chosen, pt. 2, Lower Ordovician faunas: Tokyo Imp. Univ. Fac. Sci. Jour., sec. 2, v. 3, pt. 9, p. 521–585, pls. 1–8.

——— 1937, The Cambro-Ordovician shelly faunas of South America: Tokyo Imp. Univ. Fac. Sci. Jour., sec. 2, v. 4, pt. 4, p. 369–522, pls. 1–8.

——— 1954, Fossil estherians and allied fossils: Tokyo Univ. Fac. Sci. Jour., sec. 2, v. 9, pt. 1, p. 1–192.

Lamont, Archie, 1946, Lamellibranchs from the lower Drummuck Group (Ashgillian), Girvan, Scotland: Cement, Lime and Gravel, v. 20, no. 10, p. 364–366, pl. 1.

Lemche, Henning, and Wingstrand, K. G., 1959, The anatomy of *Neopilina galatheae* Lemche, 1957: Galathea Report, v. 3, p. 9–71, pls. 1–56.

Lim, C. F., 1966, A comparative study on the ciliary feeding mechanisms of *Anadara* species from different habitats: Biol. Bull., v. 130, no. 1, p. 106–117.

Lockman, Christina, 1956, Stratigraphy, paleontology, and paleogeography of the *Elliptocephala asaphoides* strata in Cambridge and Hoosick quadrangles, New York: Geol. Soc. America Bull., v. 67, no. 10, p. 1331–1396, pls. 1–10.

Maillieux, Eugène, 1937, Les lamellibranchs du Dévonien Inférieur de l'Ardenne: Mus. Royale Histoire Nat. Belgique, Mém. 81, 273 p., 14 pls.

——— 1939, L'ordovicien de Sart-Bernard: Mus. Royale Histoire Nat. Belgique Mém. 86, 59 p., 3 pls.

McAlester, A. L., 1963a, Revision of the type species of the Ordovician nuculoid pelecypod genus *Tancrediopsis:* Postilla, no. 74, 19 p.

——— 1963b, Pelecypods of the Snyder Creek Shale (Upper Devonian) of Missouri: Jour. Paleontology, v. 37, no. 5, p. 981–1000, pls. 121–127.

——— 1964, Transitional Ordovician bivalve with both monoplacophoran and lucinacean affinities: Science, v. 146, no. 3649, p. 1293–1294.

——— 1965, Systematics, affinities, and life habits of *Babinka*, a transitional Ordovician lucinoid bivalve: Paleontology, v. 8, pt. 2, p. 231–246, pls. 26–28.

——— 1966, Evolutionary and systematic implications of a transitional Ordovician lucinoid bivalve: Malacologia, v. 3, no. 3, p. 433–439.

——— 1968, Type species of Paleozoic nuculoid bivalve genera: Geol. Soc. America Mem. 105, 143 p., 36 pls.

Mendes, J. C., 1952, A formação Corumbatai na região do rio Corumbataí (estratigrafia e descriçao dos lamelibrânquios): San Paulo Univ. Fac. Filosofia, Ciências e Letras, Bol. 145, Geologia, no. 8, 119 p., 4 pls.

Miller, S. A., 1874, Monograph of the Lamellibranchiata of the Cincinnati group: Cincinnati Quart. Jour. Sci., v. 1, no. 3, p. 211–231.

——— 1877, The American Palaeozoic fossils, a catalogue of the genera and species: Cincinnati, 253 p.

——— 1889, North American geology and palaeontology: Cincinnati, 664 p.; First appendix, 1892, p. 665–718; Second appendix, 1897, p. 719–793.

Morris, N. J., 1967, Mollusca: Scaphopoda and Bivalvia, *in* Harland, W. B., and others, The fossil record: London, Geol. Soc. London, p. 469–477.

Netschajew (Nechaeva), A., 1894, Fauna Permskikh' otlozheniy vostochnoy polosy Evropeysroy Rossii: Kazan Univ. Obshch. Estestvoispytateley Trudy, v. 27, no. 4, p. 1–503, 12 pls.

Neumayr, M., 1884, Zur Morphologie des Bivalvenschlosses: K. Akad. Wiss. Wien Sitzungsber., v. 88, no. 2, Jahrgang 1883, p. 385–419, pls. 1–2.

——— 1891, Beiträge zu einer morphologischen Eintheilung der Bivalven: K. Akad. Wiss. Wien Denkschr., v. 58, p. 701–801. (Forward by E. Suess, p. 701–705).

Newell, N. D., 1937, Late Paleozoic pelecypods: Pectinacea: Kansas Geol. Survey [Rept.], v. 10, pt. 1, 123 p., 20 pls. [1938].

——— 1942, Late Paleozoic pelecypods: Mytilacea: Kansas Geol. Survey [Rept.], v. 10, pt. 2, 110 p., 15 pls.

——— 1954, Status of invertebrate paleontology, 1953, V, Mollusca: Pelecypoda: Harvard Coll. Mus. Comp. Zoology Bull., v. 112, no. 3, p. 161–172.

——— 1956, Primitive desmodont pelecypods of the Australian Permian: Am. Mus. Novitates, no. 1799, 13 p.

——— 1957, Notes on certain primitive heterodont pelecypods: Am. Mus. Novitates, no. 1857, 14 p.

——— 1958, A note on Permian crassatellid pelecypods: Am. Mus. Novitates, no. 1878, 6 p.

——— 1965, Classification of the Bivalvia: Am. Mus. Novitates, no. 2206, 25 p.

Newell, N. D., and Ciriacks, K. W., 1962, A new bivalve from the Permian of the western United States: Am. Mus. Novitates, no. 2121, 4 p.

Nicol, David, 1958, A survey of inequivalve pelecypods: Washington Acad. Sci. Jour., v. 48, no. 2, p. 56–62.

Öpik, A., 1930, Beiträge zur kenntnis der Kukruse-(C_2–C_3–) Stufe in Eesti: Acta et Commentationes Universitatis Tartuensis (Dorpatensis), ser. A, v. 19, 34 p., 6 pls.

Pfab, Leo, 1934, Revision der Taxodonta des böhmischen Silurs: Palaeontographica, v. 80, abt. A, p. 195–253, pls. 2–4.

Phillips, John, and Salter, J. W., 1848, Palaeontological appendix to Professor John Phillips' memoir on the Malvern Hills, compared with the Palaeozoic districts of Abberley, etc.: Great Britain Geol. Survey, Mem., v. 2, pt. 1, p. 331–386, pls. 4–30.

Pojeta, John, Jr., 1962, The pelecypod genus *Byssonychia* as it occurs in the Cincinnatian at Cincinnati, Ohio: Palaeontographica Americana, v. 4, no. 30, p. 169–216, pls. 22–31.

——— 1966, North American Ambonychiidae (Pelecypoda): Palaeontographica Americana, v. 5, no. 36, p. 129–241, pls. 19–47.

——— 1968, Additional data on the Paleozoic pelecypod family Ambonychiidae: Jour. Paleontology, v. 42, no. 5, p. 1255–1257, pls .163–164.

Poulsen, Chr., 1932, The Lower Cambrian faunas of east Greenland: Medd. Grönland, v. 87, no. 6, 66 p., 14 pls.

——— 1967, Fossils from the Lower Cambrian of Bornholm: Copenhague Univ. Mus. Minéralogie et Géologie Commun. Paléont., no. 140, 48 p., 9 pls.

Purcheon, R. D., 1959, Phylogenetic classification of the Lamellibranchia, with special reference to the Protobranchia: Malacological Soc. London Proc., v. 33, p. 224–230.

——— 1960, Phylogeny in the Lamellibranchia: Centenary and Bicentenary Congress of Biology, Singapore, December 2–9, 1958, Proc., p. 69–82.

——— 1963, Phylogenetic classification of the Bivalvia with special reference to the Septibranchia: Malacological Soc. London Proc., v. 35, p. 71–80.

Rasetti, Franco, 1954, Internal shell structures in the Middle Cambrian gastropod *Scenella* and the problematic genus *Stenothecoides:* Jour. Paleontology, v. 28, no. 1, p. 59–66, pls. 11, 12.

Raymond, P. E., 1916, The Pelecypoda of the Chazy Formation: Carnegie Mus. Annals, v. 10, p. 325–343, pls. 29, 30.

——— 1946, The genera of fossil Conchostraca—An order of bivalved Crustacea: Harvard Coll. Mus. Comp. Zoology Bull., v. 96, no. 3, p. 218–307, pls. 1–6.

Reed, F. R. C., 1912, Ordovician and Silurian fossils from the central Himalayas: India Geol. Survey Mem., Palaeontologia Indica, ser. 15, v. 7, no. 2, 168 p., 20 pls.

——— 1915, Supplementary memoir on new Ordovician and Silurian fossils from the northern Shan States: India Geol. Survey Mem., Palaeontologia Indicia, new ser., v. 6, no. 1, 122 p., 12 pls.

——— 1917, Ordovician and Silurian fossils from Yun-Nan: India Geol. Survey Mem., Palaeontologia Indica, new ser., v. 6, no. 3, 84 p., 8 pls.

——— 1944, Some New Ordovician lamellibranchs from Girvan: Annals and Mag. Nat. History, v. 11, ser. 11, p. 209–215, pls. 2, 3.

——— 1946, Notes on some lamellibranchs from Quarrel Hill, Girvan: Geol. Mag., v. 83, no. 5, p. 201–205, pl. 14.

——— 1952, Revision of certain Ordovician fossils from county Tyrone: Royal Irish Acad. Proc., v. 55, sec. B, no. 3, p. 29–136, pls. 1–5.

Robison, R. A., 1964, Late Middle Cambrian faunas from western Utah: Jour. Paleontology, v. 38, no. 3, p. 510–566, pls. 79–92.

Ruedemann, Rudolf, 1912, The Lower Siluric shales of the Mohawk Valley: New York State Mus. Bull. 162, 151 p., 10 pls.

Runnegar, Bruce, 1966, Systematics and biology of some desmodont bivalves from the Australian Permian: Geol. Soc. Australia Jour., v. 13, pt. 2, p. 373–386.

Rusconi, Carlos, 1954, Acerca de los fósiles Ordovicicos de la quebrada Empozada, sud del cerro aspero: Mus. Historia Nat. Mendoza Rev., v. 7, p. 61–79, pl. 1.

——— 1955, Fósiles Cámbricos y Ordovicicos al oeste de San Isidro, Mendoza: Mus. Historia Nat. Mendoza Rev., v. 8, p. 3–65, pls. 1–5.

Sardeson, F. W., 1896, The Saint Peter Sandstone: Minnesota Acad. Nat. Sci. Bull., v. 4, no. 1, p. 64–88, pls. 2–4.

——— 1924, Habit of an Ordovicic pelecypod: Pan-Am. Geologist, v. 42, p. 345–356, pl. 22.

——— 1939, Early pelecypod *Vanuxemia* in Minnesota: Pan-Am. Geologist, v. 71, p. 283–293, pl. 19.

Schuchert, Charles, 1900, On the Lower Silurian (Trenton) fauna of Baffin Land: U.S. Natl. Mus. Proc., v. 22, p. 143–177, pls. 12–14.

Schuchert, Charles, and Dunbar, C. O., 1934, Stratigraphy of western Newfoundland: Geol. Soc. America Mem. 1, 121 p., 11 pls.

Sharpe, Daniel, 1853, Description of the new species of Zoophyta and Mollusca (appendix B to Ribeiro, Carlos, Carboniferous and Silurian formations of the neighborhood of Bussaco in Portugal): Geol. Soc. London Quart. Jour., v. 9, p. 146–158, pls. 7–9.

Soot-Ryen, Helen, 1969, A new species of *Babinka* (Bivalvia) from the Lower Ordovician of Öland, Sweden: Palaeontology, v. 12, pt. 2, p. 173–177, pl. 34.

Soot-Ryen, Helen, and Soot-Ryen, Tron, 1960, The middle Ordovician of the Oslo region, Norway, 11, Pelecypoda: Norsk Geol. Tidsskr., v. 40, pt. 2, p. 81–122, pls. 1–4.

Soot-Ryen, Tron, 1955, A report on the family Mytilidae (Pelecypoda): Allan Hancock Pacific Expeditions, v. 20, no. 1, 175 p., 10 pls.

Stanley, S. M., 1968, Post Paleozoic adaptive radiation of infaunal bivalve molluscs—a consequence of mantle fusion and siphon formation: Jour. Paleontology, v. 42, no. 1, p. 214–229.

——— 1970, Relation of shell form to life habits in the Bivalvia (Mollusca): Geol. Soc. America Mem. 125, 296 p., 40 pls.

Stasek, C. R., 1963, Synopsis and discussion of the association of ctenidia and labial palps in the bivalved molluscs: Veliger, v. 6, no. 2, p. 91–97.

Stewart, B. H., 1920, The stratigraphy and paleontology of Toronto and vicinity; part 1, The Pelecypoda: Ontario Dept. Mines Ann. Rept., v. 29, pt. 6, 59 p., 5 pls.

Stout, W. E., Ver Steeg, Karl, and Lamb, G. F., 1943, Geology of water in Ohio (a basic report): Ohio Div. Geol. Survey, Bull. 44, 4th ser., 694 p.

Sytchev (Sychev), I. A., 1960, Tip Molluska, Class Lamellibranchiata, *in* Biostratigrafiya Paleozoya Sayano-Altayskoy Gornoy Oblasti, t. 1, Nizhniy Paleozoy: Sibir. Nauchno-issled. Inst. Geologii, Geofiziki, i Mineral'nogo Syr'ya (SNIGGIMS) Trudy, vyp. 19, p. 253–256.

Tate, Ralph, 1896, Paleontology Larapintine Series (Ordovician): Horn Scientific Expedition to Central Australia, Rept., pt. 3, Geology and Botany, p. 97–116, pls. 1–3.

Termier, Geneviève, and Termier, Henri, 1950, Paléontologie Marocaine; II, Invertébrés de l'ere primaire, pt. III, Mollusques: Morocco, Service Géol., Notes et Mém. no. 78, 246 p., pls. 123–183.

Thoral, Marcel, 1935, Contribution à l'etude paléontologique de l'Ordovicien Inférieur de la Montagne Noire et révision sommaire de la faune Cambrienne de la Montagne Noire: Montpellier, 326 p., 35 pls.

Trueman, E. R., 1950, Observations on the ligament of *Mytilus edulis:* Quart. Jour. Microscopical Science, v. 91, pt. 3, p. 225–235.

Ulrich, E. O., 1890a, New Lamellibranchiata, No. 1, containing descriptions of new species of *Modiolopsis:* Am. Geologist, v. 5, no. 5, p. 270–284.

——— 1890b, New Lamellibranchiata, No. 2, on two new genera and six new species: Am. Geologist, v. 6, no. 3, p. 173–181.

——— 1890c, New Lamellibranchiata, No. 3, descriptions of new species, with remarks on others: Am. Geologist, v. 6, no. 3, p. 382–389.

——— 1892a, New Lower Silurian Lamellibranchiata, chiefly from Minnesota rocks: Minnesota Geol. and Nat. History Survey, Ann. Rept. 19 (for 1890), p. 211–248.

——— 1892b, New Lamellibranchiata, No. 4, descriptions of one new genus and eight new species: Am. Geologist, v. 10, no. 2, p. 96–104, pl. 7.

——— 1893, New and little known Lamellibranchiata from the Lower Silurian rocks of Ohio and adjacent states: Ohio Div. Geol. Survey Rept. Inv., v. 7, pt. 2, p. 627–693, pls. 45–56 [1895].

——— 1894, The Lower Silurian Lamellibranchiata of Minnesota: From vol. 3 of the Final Rept., Minnesota Geol. and Nat, History Survey, p. 475–628, pls. 35–42. (Published under separate cover prior to the entire v. 3.)

——— 1897, The Lower Silurian Lamellibranchiata of Minnesota: Minnesota Geol. and Nat. History Survey, final rept., v. 3, pt. 2, Paleontology, p. 475–628, pls. 35–42. (This is a reprinting of the 1894 paper above.)

——— 1924, *Modiodesma* n. gen. Ulrich, and the genotype of *Modiolopsis* Hall, *in* Foerste, A. F., Upper Ordovician faunas of Ontario and Quebec: Canada Geol. Survey Mem. 138, p. 183–190, pls. 32–33.

Ulrich, E. O., and Bassler, R. S., 1931, Cambrian bivalved Crustacea of the order Conchostraca: U.S. Natl. Mus. Proc., v. 78, art. 4, 130 p., 10 pls.

Verneuil, E., and Barrande, J., 1855, Description des fossiles trouvés dans les terrains Siluriens et Dévoniens d'Almaden, d'une partie de la Sierra Morena et des montagnes de Tolède: Soc. Géol. France Bull., ser. 2, v. 12, p. 964–1025, pls. 23–29.

Vinassa de Regny, P., 1927, Fossili Ordoviciani Sardi: Della R. Accad. Naz. Lincei Atti, Cl. Sci. Fis., Mat. e Nat. Mem., ser. 6, v. 2, pt. 16, p. 437–496, pls. 1–4.

Vlès, Fred, 1906, Notes sur la locomotion du *Pectunculus Glycymeris* Lk.: Soc. Zool. France Bull., v. 31, no. 5, p. 114–117.

Vogel, Klaus, 1962, Muscheln mit Schlosszähnen aus dem spanischen Kambrium und ihre bedeutung für die Evolution der Lamellibranchiaten: Akad. Wiss. u. Literatur Mainz, Math.-Naturw. Kl., Abh. no. 4, p. 197–244, pls. 1–5.

Vokes, H. E., 1954, Some primitive fossil pelecypods and their possible significance: Washington Acad. Sci. Jour., v. 44, no. 8, p. 233–236.

——— 1967, Genera of the Bivalvia: A systematic and bibliographic catalogue: Bulls. Am. Paleontology, v. 51, no. 232, 394 p.

Walcott, C. D., 1884, Paleontology of the Eureka district: U.S. Geol. Survey Mon. 8, 298 p., 24 pls.

Waterhouse, J. B., 1967, *Oblicarina*, a new Permian bivalve genus: Queensland Mus. Mem., v. 15, pt. 1, p. 53–57, pl. 7.

Whiteaves, J. F., 1897, The fossils of the Galena-Trenton and Black River formations of Lake Winnipeg and its vicinity: Canada Geol. Survey, Palaeozoic Fossils, v. 3, pt. 3, p. 129–242, pls. 16–22.

Whitfield, R. P., 1893, Contributions to the paleontology of Ohio: Ohio Div. Geol. Survey, v. 7, pt. 2, p. 407–494, pl. 13 [1895].

Wilson, A. E., 1956, Pelecypoda of the Ottawa Formation of the Ottawa-St. Lawrence lowland: Canada Geol. Survey Bull. 28, 102 p., 9 pls.

Wilson, R. B., 1959, *Wilkingia* gen. nov. to replace *Allorisma* for a genus of Upper Palaeozoic lamellibranchs: Palaeontology, v. 1, pt. 4, p. 401–404, pl. 71.

——— 1960, A revision of the types of the Carboniferous lamellibranch species erected by J. Fleming: Great Britain Geol. Survey Bull. 16, p. 110–126, pls. 8–10.

Yochelson, E. L., 1969, Stenothecoida, a proposed new class of Cambrian Mollusca: Lethaia, v. 2, no. 1, p. 49–62.

Yochelson, E. L., and Jones, C. R., 1968, *Teiichispira*, a new Early Ordovician gastropod genus: U.S. Geol. Survey, Prof. Paper 613–B, 15 p., 2 pls.

Yonge, C. M., 1939, The protobranchiate Mollusca; a functional interpretation of their structure and evolution: Royal Soc. London Philos, Trans., serv. B, v. 230, no. 566, p. 79–147, pl. 15.

——— 1962, On the primitive significance of the byssus in the Bivalvia and its effects in evolution: Marine Biol. Assoc. United Kingdom Jour., v. 42, no. 1, p. 113–125.

Ziegler, A. M., Cocks, L. R. M., and Bambach, R. K., 1968, The composition and structure of Lower Silurian marine communities: Lethaia, v. 1, no. 1, p. 1–27.

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[Italic numbers indicate major references]

PLATES 1–20

Contact photographs of the plates in this report are available, at cost, from U.S. Geological Survey Library, Federal Center, Denver, Colorado 80225.

PLATE 1

Figures 1, 2. *Astarte cuneiformis* Conrad; oblique interior views of right and left valves showing multiple small accessory muscle scars in apex of umbonal cavity, × 3. Collected by C. Buddenhagen from zone 10 of the Calvert Formation (Miocene), 3 feet above beach level, 1.25 miles south of wharf at Plum Point, Md. USNM 162676 and 162677.

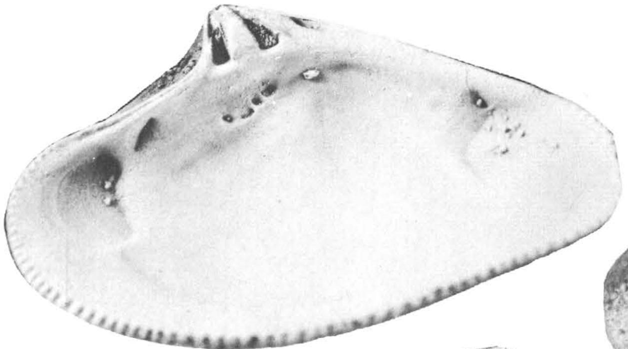
3–5. *Actinodonta cuneata* Phillips; 3, right valve exterior; 4, left valve internal mold; 5, right valve, internal mold showing musculature and dentition, × 1. All figures from Phillips and Salter (1848, pl. 21).

6. *Ischyrodonta decipiens* Ulrich; syntype; left valve showing cardinal teeth and possible remnants of duplivinicular ligament, × 2. The museum label lists the horizon and locality as: "Richmond (Whitewater), Oxford, Ohio." USNM 46205.

7. *Redonia deshayesiana duvaliana* Rouault; right valve internal mold showing posterior teeth and adductor muscle scar, × 1. Figure from Born, 1918, pl. 25.

8–11. *Palaeoneilo fecunda* (Hall); Ulrich hypotype; 8, left valve, × 3.5; 9, right valve, × 3.5; 10, right valve, × 1; 11, dorsal view, × 3.5. The museum label lists the horizon and locality as: "Maquoketa (Richmond), near Dubuque, Iowa." USNM 46130.

12–14. *Babinka prima* Barrande; three views of a right valve internal mold showing the musculature and dentition of the species; 12, × 5; 13, × 5; 14, × 3. Šárka Beds (approximately Llanvirn), Prague, Czechoslovakia. All figures from McAlester (1965). Copied with the permission of the Palaeontological Association from the original figures in "Palaeontology."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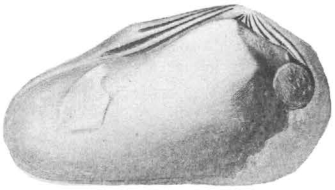
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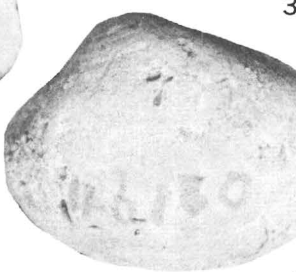
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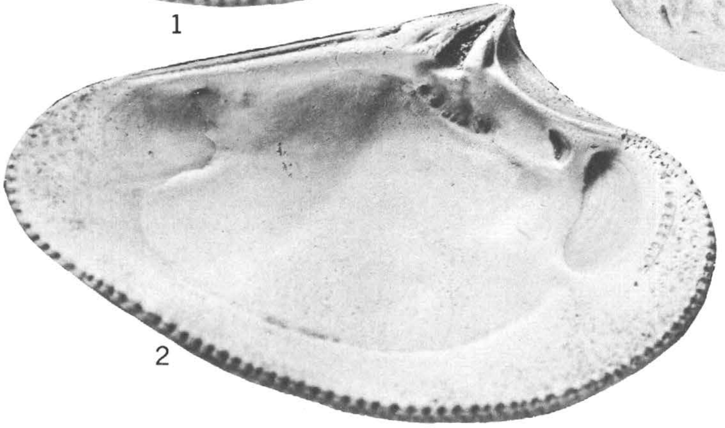
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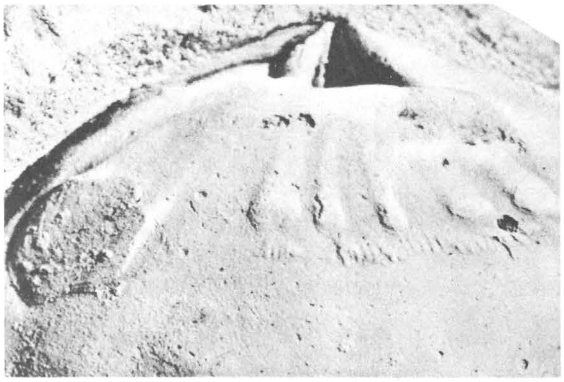
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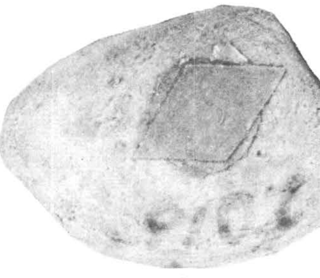
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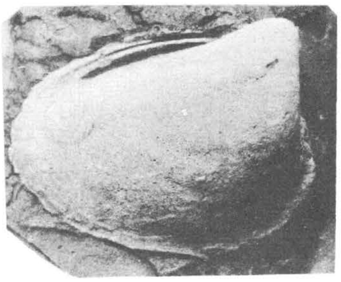
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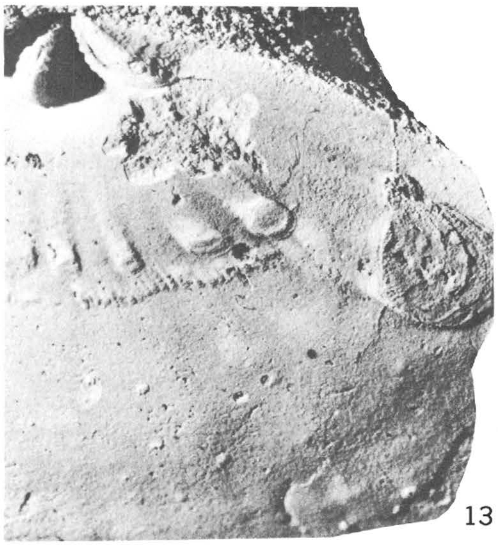
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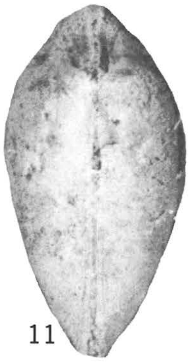
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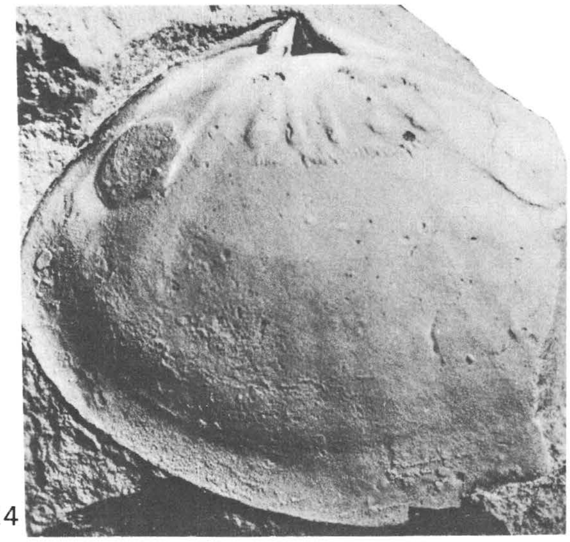
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ASTARTE, ACTINODONTA, ISCHYRODONTA, REDONIA, PALAEONEILO, AND *BABINKA*

PLATE 2

FIGURES 1–3. *Allodesma subellipticum* Ulrich; syntype; 1, left valve, × 1; 2, left valve internal mold, × 4; 3, dorsal view showing imprints of cardinal teeth, × 10. The museum label lists the horizon and locality as: "Trenton, near Cannon Falls, Minnesota." See fig. 1*F*, *G*, page for Ulrich's reconstruction of the hinge line of this species. USNM 162678.

4, 5. *Allodesma subellipticum* Ulrich; syntype; 4, right valve, × 4; 5, dorsal view showing imprints of cardinal teeth, × 10. Horizon and locality the same as in fig. 1 above. USNM 46078.

6. *Cycloconcha milleri* (Meek); Ulrich hypotype; left valve, × 1. The museum label lists the horizon and locality as: "Richmond (Waynesville), Versailles, Indiana." USNM 70464.

7. *Cycloconcha milleri* (Meek); Ulrich hypotype; right valve, × 1. Horizon and locality the same as in fig. 6 above. USNM 46162.

8, 9. *Cycloconcha* sp.; right and left valves showing dentition and multiple accessory muscle scars, × 3. Horizon and locality unknown. USNM 162680–162681.

10, 11. *Cycloconcha milleri* (Meek); Ulrich hypotype; 10, anterior view, × 2; 11, ventral view, × 2. Horizon and locality the same as in fig. 6 above. USNM 162679.

12, 13. *Cycloconcha milleri* (Meek); 12, dorsal view showing ligament, × 2; 13, anterior end of right valve showing growth lines, × 3. Horizon and locality the same as in fig. 6 above. UCM 3507.

14. *Cycloconcha ovata* Ulrich; left valve showing dentition, × 3. The museum label lists the horizon and locality as: "Eden, Covington, Kentucky." MU 129T.

15. *Cycloconcha ovata* Ulrich; left valve showing dentition, × 4. The museum label lists the horizon and locality as: "Cincinnatian (Utica), Covington, Kentucky." USNM 33472.

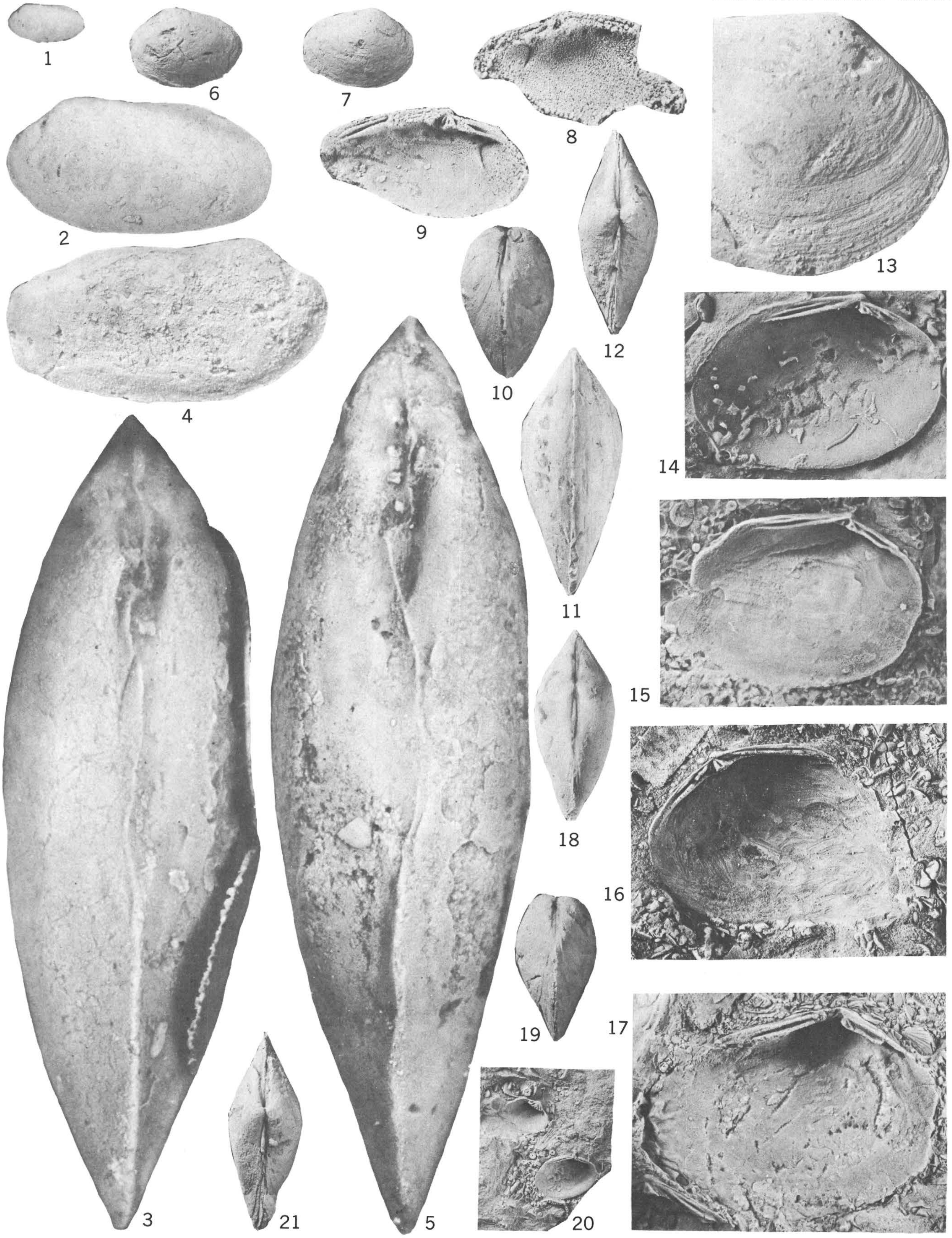
16. *Cycloconcha mediocardinalis* Miller; syntype; right valve showing dentition, × 3. The museum label lists the horizon and locality as: "Cincinnatian, Cincinnati, Ohio." WM 8893.

17. *Cycloconcha milleri* (Meek); Ulrich hypotype; left valve showing lateral teeth, × 2. The museum label lists the horizon and locality as: "Richmond (Waynesville), Hanover, Ohio." USNM 47344.

18, 19. *Cycloconcha milleri* (Meek); previously unfigured syntype; 18, dorsal view showing ligament, × 2; 19, anterior view, × 2. The museum label lists the horizon and locality as: "Cincinnati Group, 40 miles west of Cincinnati, Ohio." USNM 26409.

20. *Cycloconcha ovata* Ulrich; × 1 view of a specimen showing dentition. On the same slab occur *Lyrodesma* (above) and *Deceptrix* (below). The museum label lists the horizon and locality as: "Cincinnatian (Utica), Covington, Kentucky." USNM 162682.

21. *Cycloconcha milleri* (Meek); dorsal view showing ligament, × 2. The museum label lists the horizon and locality as: "Richmond (Waynesville), Aurora, Indiana." USNM 100766.



ALLODESMA AND *CYCLOCONCHA*

PLATE 3

FIGURES 1–3. *Cycloconcha* cf. *C. mediocardinalis* Miller; 1, right valve, internal mold showing musculature and pallial line, × 3; 2, natural cast of fig. 1 preserving shell material, × 3; 3, dorsal view of fig. 1 showing multiple accessory muscle scars × 3. The museum label lists the horizon and locality as: "Eden (Southgate), Covington, Kentucky." USNM 49972.

4. *Cycloconcha* cf. *C. oblonga* Foerste; left valve, × 2. Point Pleasant Limestone, near intersection of U.S. Route 52 and Ohio Route 133 along the Ohio River. USGS locality 6146–CO. USNM 162683.

5–8. *Lyrodesma subplanum* Ulrich; 5, left valve, × 1; 6, right valve, × 1; 7, anterior view, × 3; 8, dorsal view, × 3. The museum label lists the horizon and locality as: "Cynthiana section [probably upper Lexington Limestone], ½ mile south of Cynthiana, Kentucky." USNM 162684.

9. *Lyrodesma subplanum* Ulrich; specimen showing dentition with elongate posterior teeth, × 3. Upper Lexington Limestone, on Kentucky Route 982 0.4 of a mile south of Cynthiana, Ky. USGS locality 6146–CO. USNM 162685.

10. *Lyrodesma acuminatum* Ulrich; syntype showing dentition, × 3. The museum label lists the horizon and locality as: "Black River, six miles south Cannon Falls, Minnesota." USNM 46215.

11. *Lyrodesma armoricana* Tromelin and Lebesconte; mold, left valve showing elongate posterior lateral teeth, × 3. The museum label accompanying the specimen contains the following information: "Malroche, Pont-Réan, 35. Arenie supérieur. Stratut & No. 735." LGB.

12. *Lyrodesma inornatum* Ulrich; syntype; right valve showing seven cardinal teeth, × 3. The museum label lists the horizon and locality as: "Middle Beds [probably Maysville] Cincinnati Group, Covington, Kentucky." USNM 46222.

13–15. *Lyrodesma major* (Ulrich); syntype; 13, right valve, exterior, × 1; 14, dorsal view, × 2; 15, hinge line view, × 3. The museum label lists the horizon and locality as: "Cincinnati Group, Clarksville, Ohio." USNM 46223.

16. *Lyrodesma poststriatum* (Emmons); right valve, internal mold showing the pallial sinus, × 2. The museum label lists the horizon and locality as: "Pulaski drift, near Trenton Falls, New York." USNM 162686.

17. *Lyrodesma conradi* Ulrich; syntype; left valve, internal mold showing the pallial sinus, × 2. The museum label lists the horizon and locality as: "Eden (Southgate), Covington, Kentucky." USNM 46220.

18, 19. *Lyrodesma poststriatum* (Emmons); 18, right valve, internal mold showing pallial line, pallial sinus, and adductor and pedal muscle scars, × 3; 19, oblique dorsal view showing impressions of teeth and pedal and adductor muscle scars, × 2. Horizon and locality the same as in fig. 16 above. USNM 10197.

20. *Lyrodesma conradi* Ulrich; shelled specimen showing teeth with denticles and pedal and adductor muscle scars, × 5. The museum label lists the horizon and locality as: "Cincinnatian (Utica), Covington, Kentucky." USNM 33473.

21, 22. *Lyrodesma major* (Ulrich); syntype; 21, dorsal view, internal mold showing adductor and pedal scars and umbonal apices and impressions of teeth, × 3. 22, left valve internal mold showing adductor and pedal scars and anterior buttress, × 3. The museum label lists the horizon and locality as: "Richmond (Waynesville), Clarksville, Ohio." USNM 46224.

23. *Lyrodesma caelata* Salter; rubber mold of holotype showing the elongated posterior teeth, × 3. USNM 162687. Original from the Budleigh Salterton Pebble Bed (?lower Caradoc), British Museum (Natural History) W. Vicary collection L. 15690.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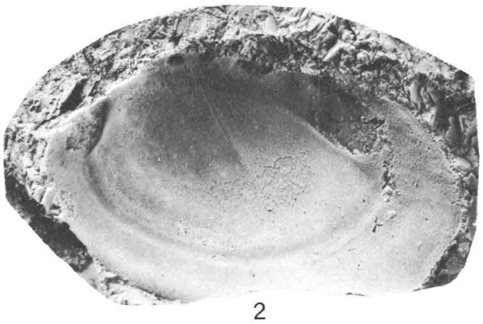
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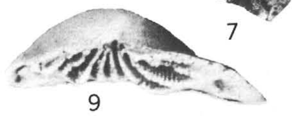
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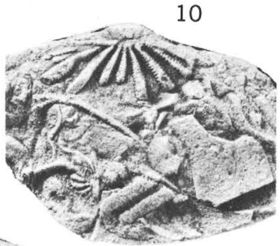
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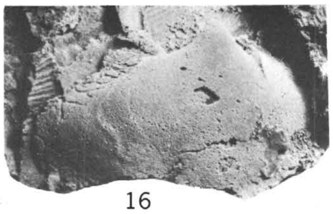
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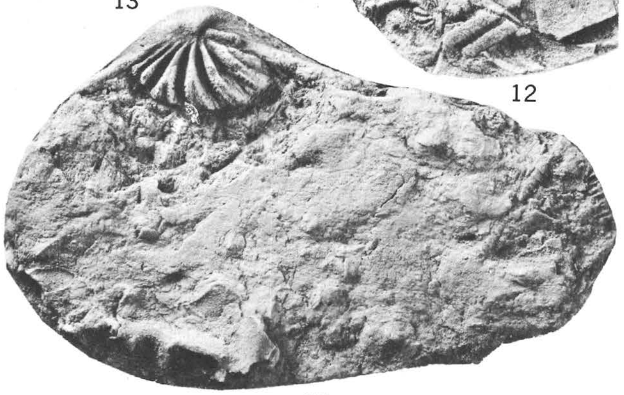
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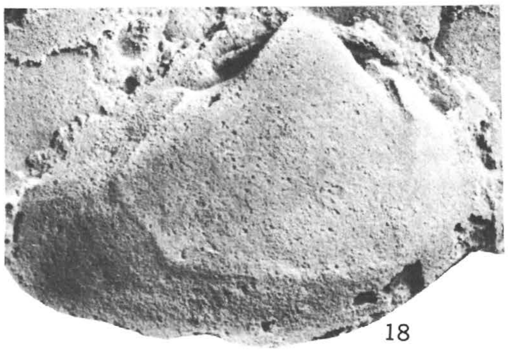
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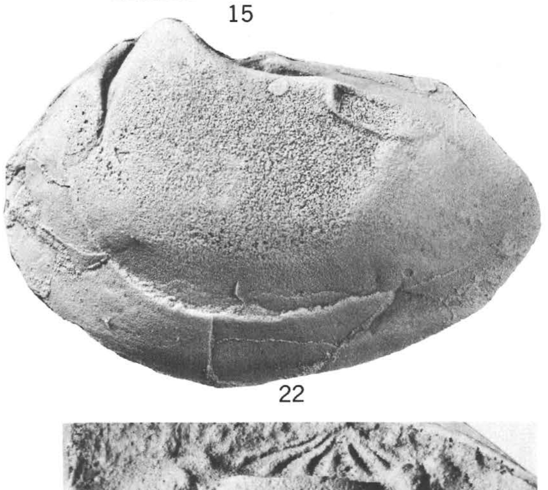
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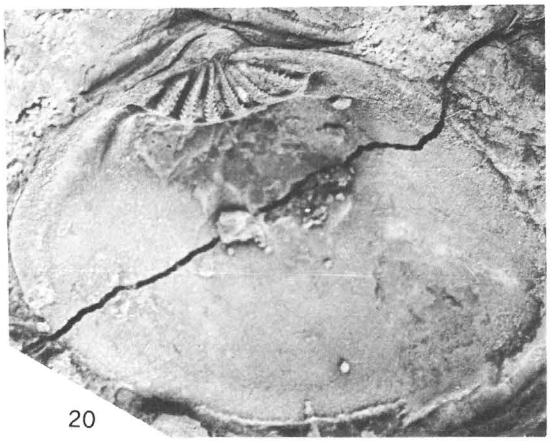
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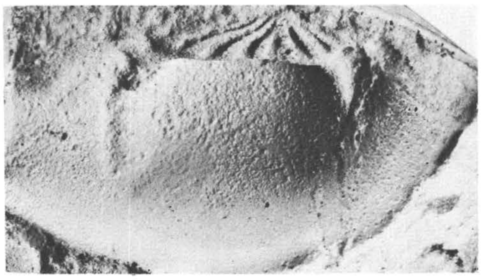
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CYCLOCONCHA AND *LYRODESMA*

PLATE 4

FIGURE 1. *Ctenodonta nasuta* (Hall); lectotype (McAlester, 1968); right valve, × 1. The museum label lists the horizon and locality as: "Trenton Limestone, Middleville, New York." AM 723/la.

2, 3. *Ctenodonta nasuta* (Hall); paratype; 2, right valve, × 1; 3, dorsal view, × 1. Horizon and locality the same as in fig. 1 above. AM 723/lb.

4. *Ctenodonta nasuta* (Hall); dorsal view showing external ligament insertion groove, × 1.5. East bank Ottawa River, half a mile below Pauquette Rapids. USNM locality 9253. USNM 162688.

5–7. *Ctenodonta nasuta* (Hall); 5, dorsal view showing external ligament insertion groove, × 1.1; 6, interior of right valve, × 1.1; 7, exterior of right valve, × 1.1. The museum label lists the horizon and locality as: "Black River, Pauquette Rapids, Ottawa, Canada." USNM 14718.

8, 9. *Ctenodonta* cf. *C. iphigenia* Billings; 8, hinge line view, × 2; 9, exterior view right valve, × 1. The museum label lists the horizon and locality as: "Richmond (Waynesville), Hanover, Ohio." USNM 40501.

10. *Ctenodonta nasuta* (Hall); interior view of right value showing teeth, anterior buttress, adductor muscle scars, and pallial line, × 1.4. The museum label lists the horizon and locality as: "Upper Black River, Pauquette Rapids, Ottawa River, Canada." USNM 162689.

11, 12. *Ctenodonta* sp.; 11, dorsal view showing ligament insertion grooves, × 1; 12, left exterior view, × 1. The museum label lists the horizon and locality as: "Stones River (Murfreesboro), 1.5 miles north Murfreesboro, Tennessee." USNM 47065.

13. *Ctenodonta nasuta* (Hall); hinge line view showing continuous tooth rows and the lack of an internal ligament, × 2. Ottawa Formation, near Braeside, Ontario, Canada. USNM locality 9254. USNM 162690.

14, 15. *Ctenodonta* sp.; 14, dorsal view showing ligament insertion groove, × 3; 15, right interior showing teeth, × 1. Collected by C. L. Sainsbury. Ordovician, Seward Peninsula, Alaska. USGS collection 6027–CO. USNM 162691.

16, 17. *Ctenodonta* sp.; 16, exterior right valve, × 1; 17, interior right valve showing continuous tooth rows, × 2. Antelope Valley Limestone, southeast end Groom Range, Nevada. USGS locality D–1571–CO. USNM 162692.

18, 19. *Ctenodonta nasuta* (Hall); 18, interior view of left valve showing teeth, anterior buttress, and adductor muscle scars, × 1.4; 19, interior umbonal view showing features seen in fig. 18 and pedal retractor muscle scars, × 2.5. The museum label lists the horizon and locality as: "Trenton, Ottawa, Canada." USNM 18034.

20–22. *Ctenodonta* sp.; 20, interior right valve view showing teeth and adductor muscle scars, × 2; 21, exterior right valve view, × 1; 22, dorsal view showing ligament insertion groove, × 2. Lower shelly facies of the Setul Formation, off south point of Pulau Langgun, Langkawi Islands, Malaysia. Gastropods and brachiopods from this collection suggest a late Canadian (Early Ordovician) age, Yochelson and Jones (1968). USNM 162693.

23, 24. *Ctenodonta nasuta* (Hall); 23, exterior view left valve, × 1.1; 24, interior view left valve showing anterior buttress, adductor muscle scars, and integropalliate pallial line, × 1.1. The museum label lists the horizon and locality as: "Upper Black River, Pauquette Rapids, Ottawa River, Canada." USNM 92269.


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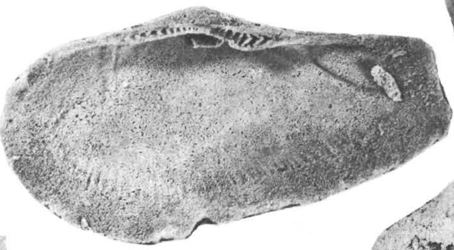
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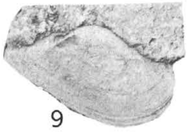
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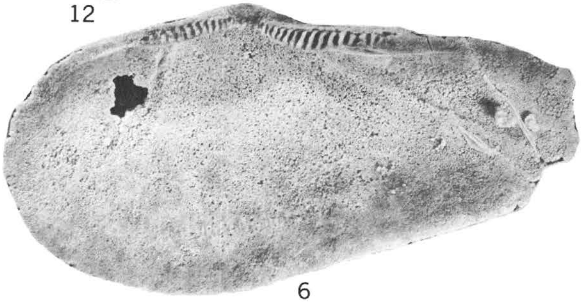
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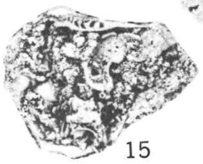
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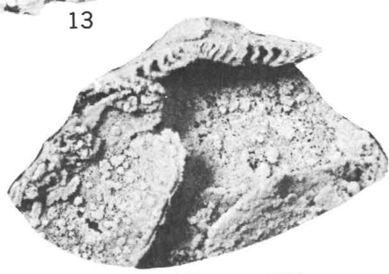
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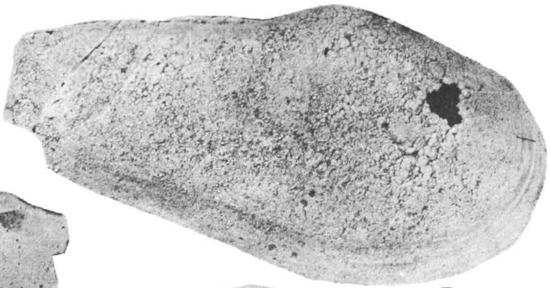
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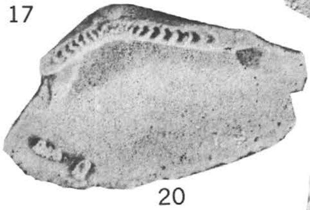
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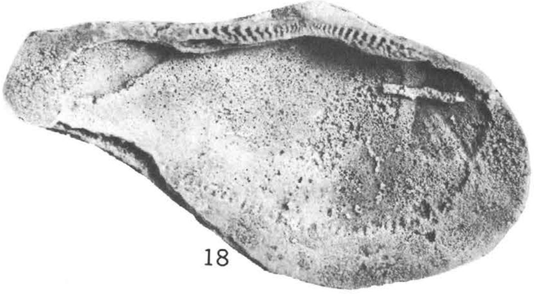
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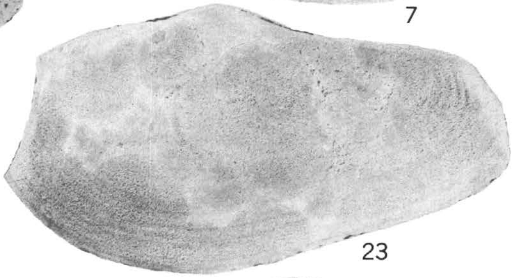
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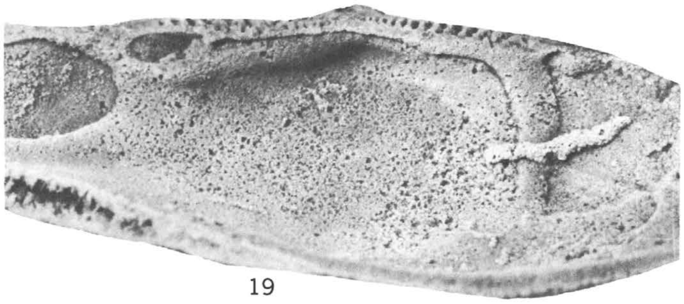
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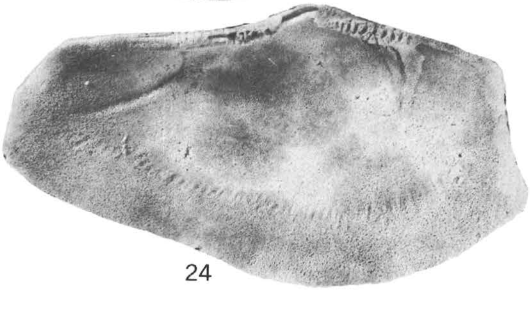
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CTENODONTA

PLATE 5

FIGURE 1. *Similodonta similis* (Ulrich); left valve, × 4. The museum label lists the horizon and locality as: "Richmond (Maquoketa), Bristol, Minnesota." USNM 25021.

2. *Similodonta similis* (Ulrich); paratype; right valve, × 3.5. The museum label lists the horizon and locality as: "Richmond (Maquoketa), Spring Valley, Minnesota." USNM 163508=USNM 145663, McAlester (1968).

3. *Similodonta similis* (Ulrich); interior view right valve showing tooth rows and adductor muscle scars, × 3.5. Horizon and locality the same as in fig. 1 above. USNM 47037.

4, 5. *Similodonta similis* (Ulrich); 4, anterior view showing lunule, × 3; 5, dorsal view showing escutcheon, × 3. Horizon and locality the same as in fig. 1 above. USNM 162694.

6. *Similodonta similis* (Ulrich); interior view right valve, × 1. Horizon and locality the same as in fig. 1 above. USNM 162695.

7. *Deceptrix* aff. *D. hartsvillensis* (Safford); left valve, × 3.5. Grier Limestone Member, Lexington Limestone, YMCA Camp, Jessamine County, Ky. USGS locality 5096–CO. USNM 162696.

8. *Deceptrix* aff. *D. hartsvillensis* (Safford); right valve, × 3.5. Horizon and locality the same as in fig. 7 above. USNM 162697.

9, 10. *Deceptrix* aff. *D. hartsvillensis* (Safford); 9, dorsal view showing ligament space posterior to the beaks, × 3.5; 10, anterior view, × 3.5. Grier Limestone Member, Lexington Limestone, west side of U.S. Route 227, north of Ford, Ky. USGS locality 5067–CO. USNM 162698.

11. *Deceptrix* sp.; right valve interior, × 3. Antelope Valley Limestone, Ike's Canyon section, Toquima Range, Nev. USGS locality D–1519–CO. USNM 162699.

12. *Deceptrix* sp.; right valve exterior, × 3. Horizon and locality the same as in fig. 11 above. USGS locality D–1520–CO. USNM 162700.

13. *Deceptrix* cf. *D. hartsvillensis* (Safford); left valve, × 1. The museum label gives the horizon and locality as: "Trenton, Hartsville, Tennessee." USNM 47017.

14. *Deceptrix albertina* (Ulrich); syntype; hinge line view, × 3. The museum label lists the horizon and locality as: "Richmond (Waynesville), Clarksville, Ohio." USNM 162701.

15. *Deceptrix filistriata* (Ulrich); syntype; left valve showing dentition, × 3. The museum label lists the horizon and locality as: "Eden (Economy), Covington, Kentucky." USNM 46131.

16. *Deceptrix albertina* (Ulrich); syntype; left valve showing dentition, × 3. Horizon and locality the same as in fig. 14 above. USNM 46122.

17. *Deceptrix* aff. *D. hartsvillensis* (Safford); dorsal view showing ligament space posterior to beaks, × 3. Horizon and locality the same as in fig. 9 above. USNM 162702.

18. *Deceptrix albertina* (Ulrich); syntype; × 1. Horizon and locality the same as in fig. 14 above. USNM 162703.

19. *Deceptrix* aff. *D. hartsvillensis* (Safford); oblique interior view showing adductor and pedal muscle scars, × 3.5. Horizon and locality the same as in fig. 9 above. USNM 162704.

20. *Deceptrix* aff. *D. hartsvillensis* (Safford); right valve showing continuous tooth rows, × 3.5. Grier Limestone Member, Lexington Limestone, Antioch Church Road section, Jessamine County, Ky. USGS locality 4879–CO. USNM 162705.

21. *Deceptrix baffinense* (Ulrich); left valve, × 2. The museum label lists the horizon and locality as: "Shale Member, Putnam Highland Formation, northwest segment Silliman's Fossil Mount, Baffin Island." USNM 124612.

22. *Deceptrix levata* (Hall); right valve, × 1. The museum label lists the horizon and locality as: "Trenton, Sacketts Harbor, New York." USNM 4707.


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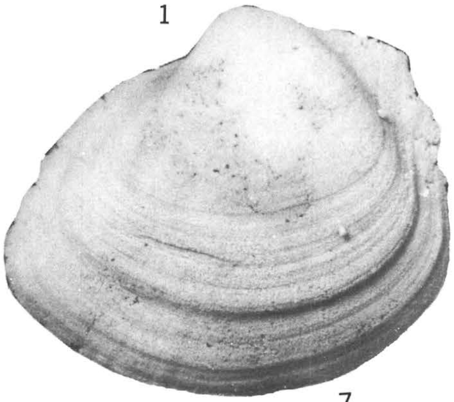
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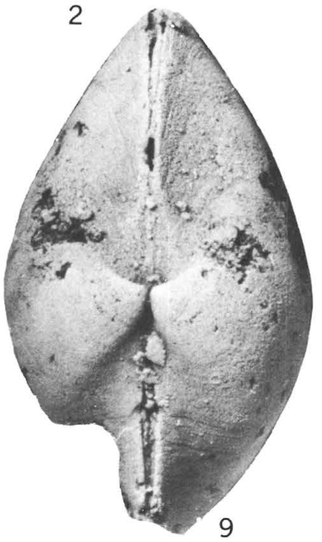
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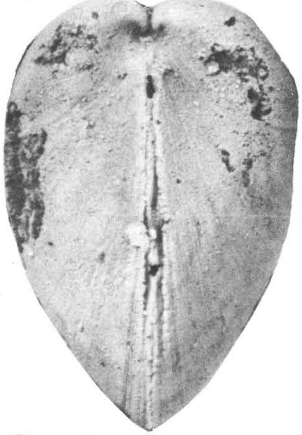
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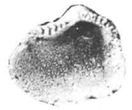
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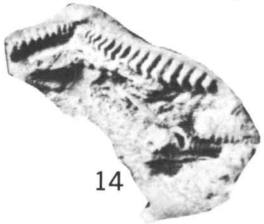
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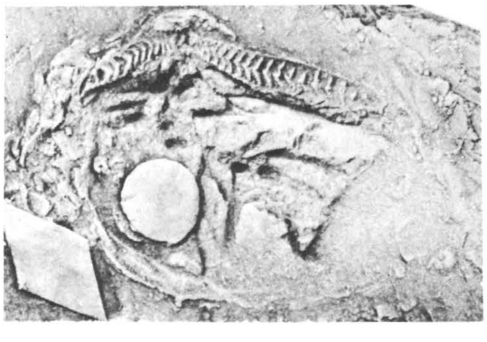
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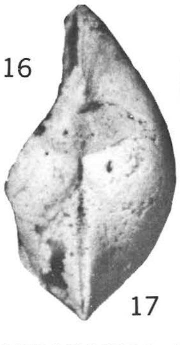
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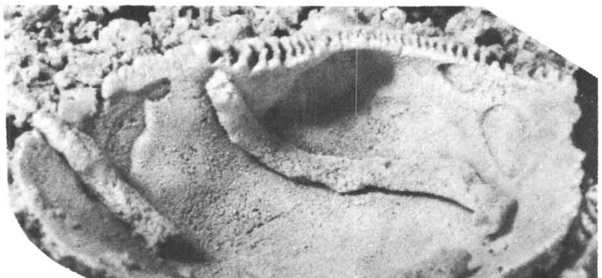
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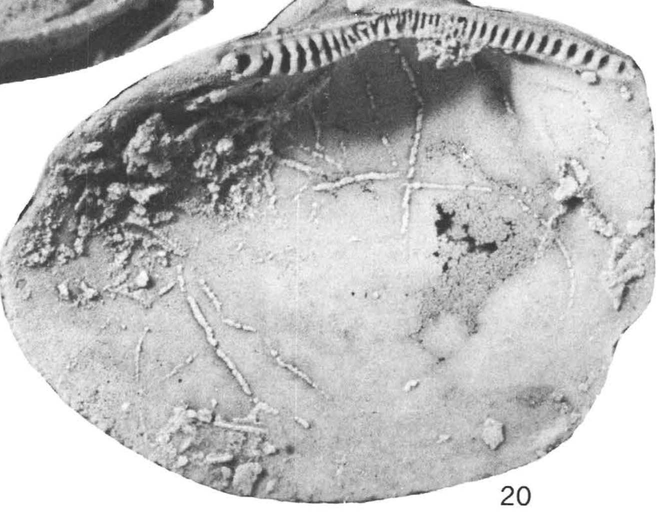
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SIMILODONTA AND *DECEPTRIX*

PLATE 6

FIGURE 1. *Nuculites* [*Cleidophorus*] *planulata* Conrad; mold right valve showing slitlike impression of buttress, × 3. The museum label lists the horizon and locality as: "Pulaski drift, near Trenton Falls, New York." USNM 162706.

2. *Nuculites* [*Cleidophorus*] *planulata* Conrad; mold right valve showing slitlike impression of buttress, × 3. Horizon and locality the same as in fig. 1 above. USNM 162707.

3–5. *Myoplusia carpenderi* (Schuchert); 3, dorsal view, × 1; 4, right valve, × 1; 5, left valve, × 1. The museum label lists the horizon and locality as: "Trenton, head of Frobisher Bay, Baffin Land." USNM 28164.

6–8. *Palaeoconcha faberi* Miller; syntype; 6, anterior view, × 5; 7, dorsal view, × 5; 8, right valve, × 5. The museum label lists the horizon and locality as: "Cincinnatian, Versailles, Indiana." WM 8870.

9. *Tancrediopsis cuneata* (Hall); interior left valve showing tooth rows and adductor muscle scars, × 4. Ottawa Formation, about half a mile below Pauquette Rapids, Ontario, Canada. USNM locality 9253. USNM 162708.

10. *Tancrediopsis cuneata* (Hall); exterior left valve, × 4. The museum label lists the horizon and locality as: "Upper Black River, Pauquette Rapids, Ottawa River, Canada." USNM 72265.

11. *Tancrediopsis gibberula* (Salter); left valve internal mold, × 1. The museum label lists the horizon and locality as: "Black River (Platteville), Beloit, Wisconsin." USNM 15881.

12. *Tancrediopsis gibberula* (Salter); dorsal view, internal mold showing adductor and pedal muscle scar impressions, × 1. Horizon and locality the same as in fig. 11 above. USNM 162709.

13. *Tancrediopsis gibberula* (Salter); right valve, internal mold showing impressions of adductor muscle scars and pallial line, × 4. Horizon and locality the same as in fig. 11 above. USNM 15662.

14. *Tancrediopsis* aff. *T. cuneata* (Hall); right valve, × 1. Antelope Valley Limestone, Central Pahranagat Range, Nev. USGS locality D–1374–CO. USNM 162710.

15. *Tancrediopsis cuneata* (Hall); oblique interior view showing adductor and pedal muscle scars, × 4. Horizon and locality the same as in fig. 9 above. USNM 162711.

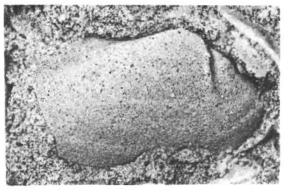
16, 17. *Cyrtodonta grandis luculentus* (Sardeson); 16, anterior view, × 1; 17, posterior view, × 1. The museum label lists the horizon and locality as: "Richmond, Bristol, Minnesota." USNM 25060.

18. *Cyrtodonta* sp.; dorsal interior of articulated valves showing accessory muscle scars (horizontal arrows) and anterior adductor muscle scar (oblique arrow), × 3.5. Ottawa Formation, near Braeside Ontario, Canada. USNM locality 9254. USNM 162712.

19. *Cyrtodonta* sp.; dorsal interior view of right valve showing accessory muscle scar (vertical arrow) on lateral face of hinge plate, anterior adductor muscle scar to left (horizontal arrow), × 10. Horizon and locality the same as in fig. 18 above. USNM 162713.

20. *Cyrtodonta* sp.; dorsal interior view of left valve showing accessory muscle scar on lateral face of hinge plate (short arrow) and anterior adductor muscle scar (long arrow), × 4. Horizon and locality the same as in fig. 18 above. USNM 162714.

21–23. *Cyrtodonta grandis* (Ulrich); syntype; 21, right valve, × 1; 22, dorsal view, × 1; 23, left valve, × 1. The museum label gives the horizon and locality as: "Trenton, 1½ miles south Burgin, Kentucky." USNM 46182.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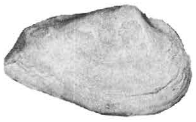
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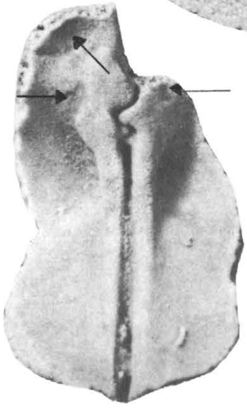
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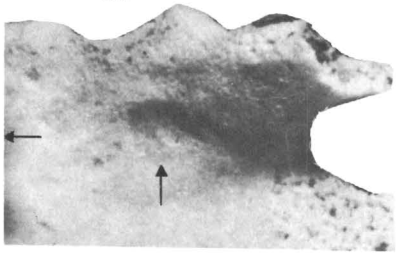
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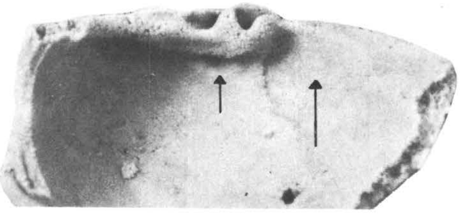
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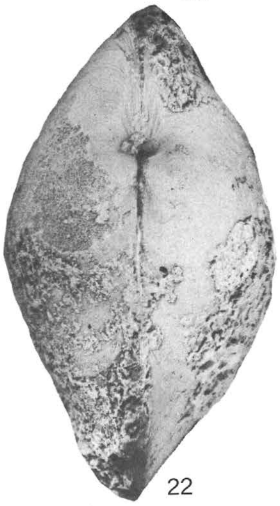
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NUCULITES, MYOPLUSIA, PALAEOCONCHA, TANCREDIOPSIS, AND *CYRTODONTA*

PLATE 7

FIGURE 1. *Cyrtodonta saffordi* (Hall); Safford hypotype, × 2. Note the peculiar anterior dentition. The museum label lists the horizon and locality as: "Trenton (Catheys), Nashville, Tennessee." USNM 46191.

2. *Cyrtodonta* cf. *C. huronensis* Billings; right valve showing dentition, anterior adductor muscle scar, and what may be an accessory muscle scar (arrow), × 3.5. Ottawa Formation, near Braeside, Ontario, Canada. USNM locality 9254. USNM 162715.

3. *Cyrtodonta* cf. *C. huronensis* Billings; right interior, × 2. Horizon and locality the same as in fig. 2 above. USNM 162716.

4. *Cyrtodonta* cf. *C. huronensis* Billings; left valve, × 2. Horizon and locality the same as in fig. 2 above. USNM 162717.

5. *Cyrtodontula rugatina* (Ulrich); left valve, × 1. The museum label lists the horizon and locality as: "Black River (Decorah), Minneapolis, Minnesota." USNM 46357.

6. *Cyrtodontula scofieldi* (Ulrich); left valve, Ulrich hypotype, × 1. Note the bryozoan incrustation on the posterior umbonal slope which suggests that this part of the shell projected above the sediment-water interface. The museum label lists the horizon and locality as: "Black River (Decorah), St. Paul, Minnesota." USNM 46358.

7. *Cyrtodonta beckneri* Conkin; right value interior, × 1. Liberty Formation (upper Dillsboro Formation), upstream from Oldenburg-Enochsburg Road crossing of Salt Creek, Ind. USGS locality 6139–CO. USNM 162718.

8. *Cyrtodonta* sp.; left valve interior, note the ligamental grooves and ridges, × 2. The museum label lists the horizon and locality as: "Richmond, Gore Bay, Manitoulin Island." USNM 100850.

9, 10. *Vanuxemia gibbosa* Ulrich; 9, oblique interior view showing the myophoric notch (arrow), × 3; 10, left valve showing dentition, anterior adductor muscle scar, myophoric notch, and ligamental grooves and ridges, × 5. The museum label lists the horizon and locality as: "Trenton, Haynies, Tennessee." Also see pl. 9, fig. 7. USNM 46942.


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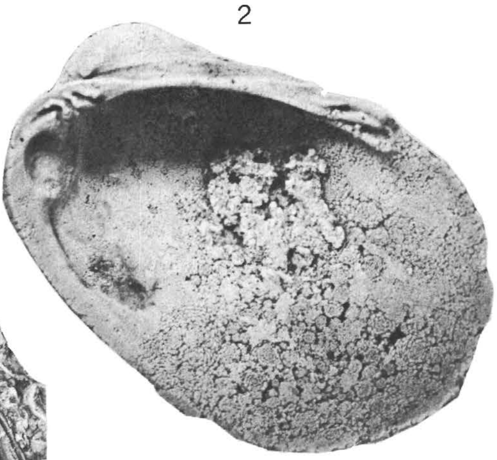
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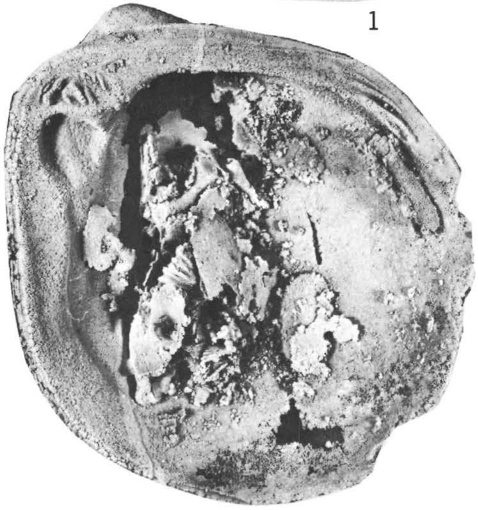
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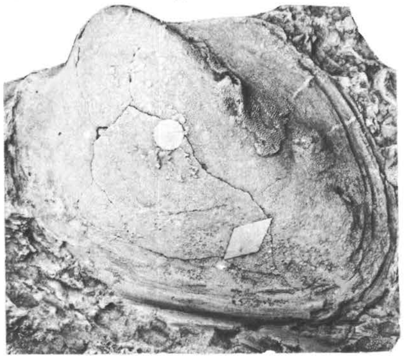
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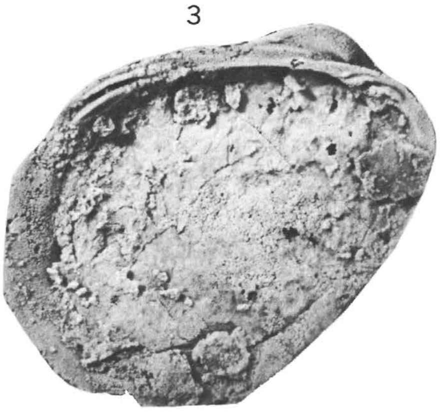
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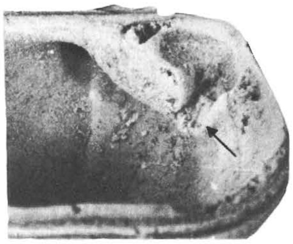
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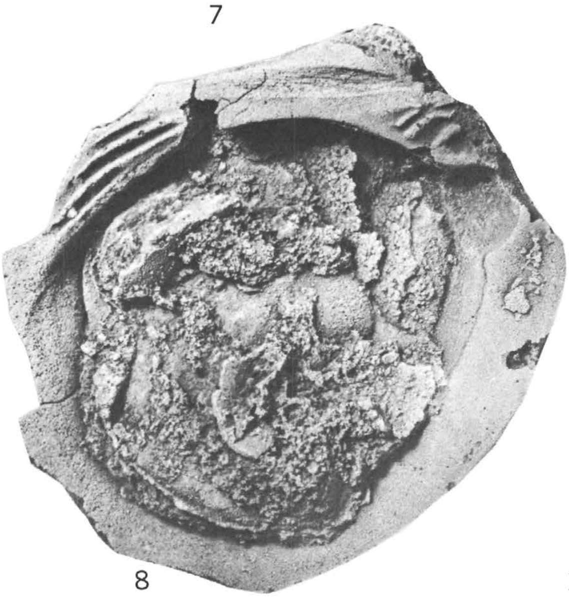
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CYRTODONTA, *CYRTODONTULA*, AND *VANUXEMIA*

PLATE 8

FIGURES 1, 2. *Vanuxemia* sp.; 1, right valve showing umbonal septum and denticles on anterior teeth, × 3.5; 2, oblique interior view showing myophoric notch (white arrow), umbonal septum (left, black arrow), and hinge plate (right, black arrow), × 3.5. The museum label lists the horizon and locality as: "Lorraine (Upper), Bristol, Minnesota." USNM 25033.

3. *Vanuxemia gibbosa* Ulrich; anterior view, × 1. Basal part of the Curdsville Limestone Member, Lexington Limestone, behind Old Crow Distillery, Woodford County, Ky. USGS locality 5072–CO. USNM 162719.

4, 5. *Vanuxemia* cf. *V. inconstans* Billings; 4, right exterior, × 1.2; 5, right interior, × 4. Ottawa Formation, near Braeside, Ontario, Canada. USNM locality 9254. USNM 162720.

6, 7. *Vanuxemia* cf. *V. inconstans* Billings; 6, left valve, × 3; 7, oblique interior view showing accessory scar (arrow), × 3. Horizon and locality the same as in fig. 4 above. USNM 162721.

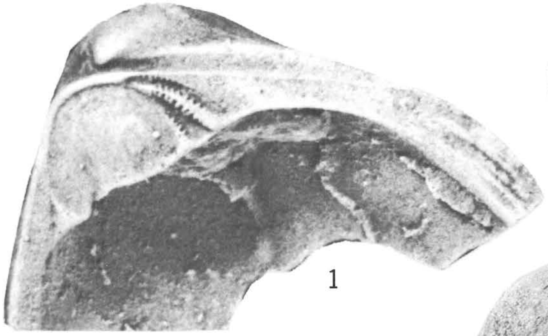
8–10. *Vanuxemia* cf. *V. inconstans* Billings; 8, left interior, × 2; 9, oblique interior view showing accessory scar (arrow), × 2.5; 10, exterior view, × 3. Horizon and locality the same as in fig. 4 above. USNM 162722.

11. *Vanuxemia* cf. *V. inconstans* Billings; left exterior, × 2.2. Horizon and locality the same as in fig. 4 above. USNM 162723.

12. *Vanuxemia gibbosa* Ulrich; dorsal view of articulated specimen, × 2. The museum label lists the horizon and locality as: "Trenton, Haynies, Tennessee." USNM 162724.

13. *Vanuxemia* cf. *V. inconstans* Billings; right valve showing ligament grooves and ridges and denticles on posterior teeth, × 4. Horizon and locality the same as in fig. 4 above. USNM 162725.

14. *Vanuxemia gibbosa* Ulrich; left exterior showing incrustation of trepostome bryozoans on the posterior half of the shell, × 3. Horizon and locality the same as in fig. 12 above. Also see pl. 9, fig. 6. USNM 162726.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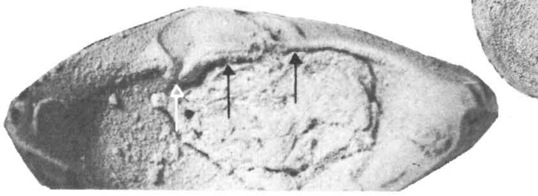
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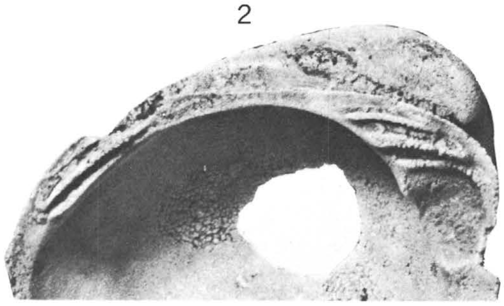
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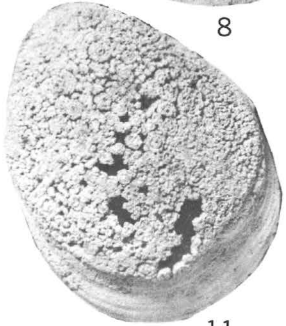
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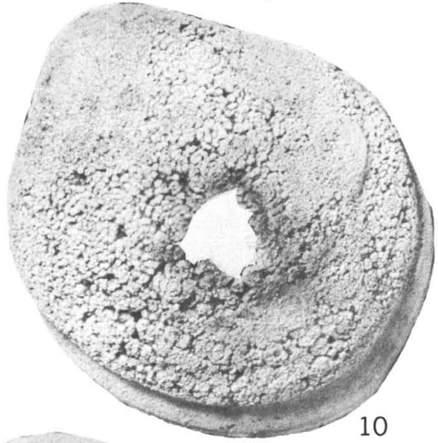
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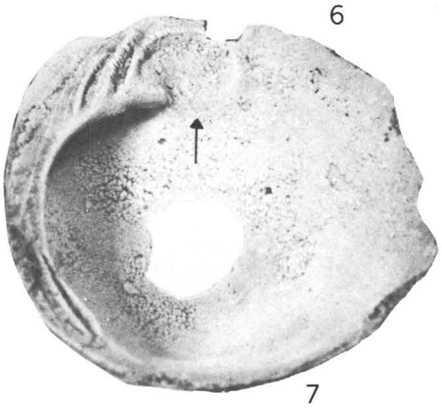
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VANUXEMIA

PLATE 9

FIGURE 1. *Vanuxemia gibbosa* Ulrich; hinge line view showing the dentition and ligament grooves and ridges, × 4. The museum label lists the horizon and locality as: "Trenton, Haynies, Tennessee." USNM 162727.

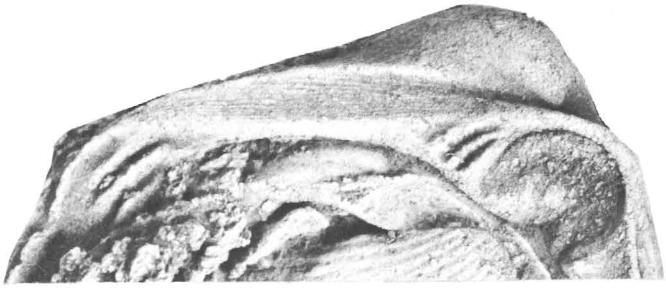
2. *Vanuxemia* cf. *V. inconstans* Billings; left valve showing denticles on anterior teeth, × 3. Ottawa Formation, near Braeside, Ontario, Canada. USNM locality 9254. USNM 162728.

3. *Vanuxemia* cf. *V. inconstans* Billings; left valve showing denticles on anterior teeth, × 3. Horizon and locality the same as in fig. 2 above. USNM 162729.

4–7. *Vanuxemia gibbosa* Ulrich; four specimens of the same species showing how the myophoric notch is developed to differing degrees in different individuals, × 2. Horizon and locality the same as in fig. 1 above. USNM 46942, 162726, 162730, 162731.

8–13. *Septifer bilocularis* (Linné); paired valves of three individuals of the species showing varying degrees of myophoric notch development, × 2. 8, 9, little or no notch; 10, 11, slight development of notch; 12, 13, notch well developed. Semporna Reef, North Borneo. USNMDM. 658045a–c.

14–17. *Septifer excisus* Wiegm; paired valves of two individuals showing varying degrees of myophoric notch development, in this species the notch is always well developed, × 2. 14, 15, notch of moderate depth; 16, 17, notch exceptionally deep. Kashiwajima, Tosa, Japan. USNMDM 304298a, b.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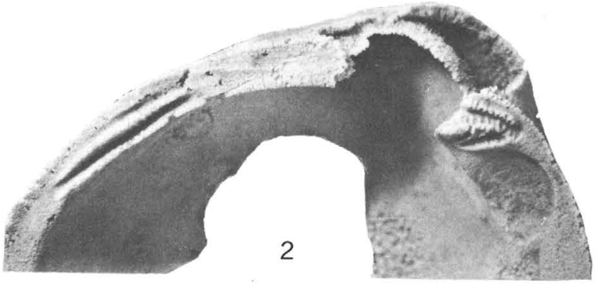
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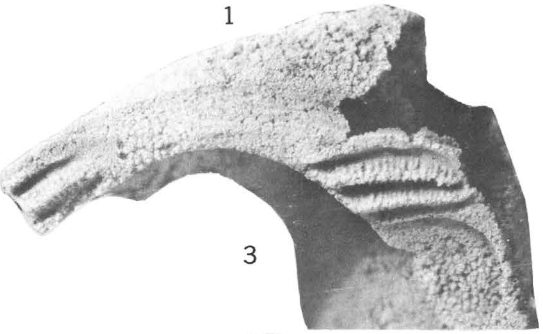
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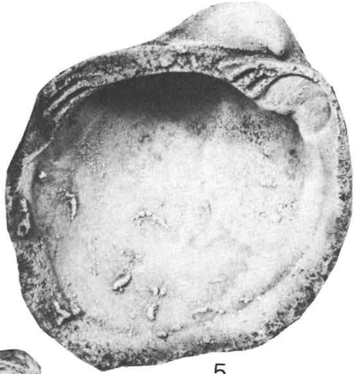
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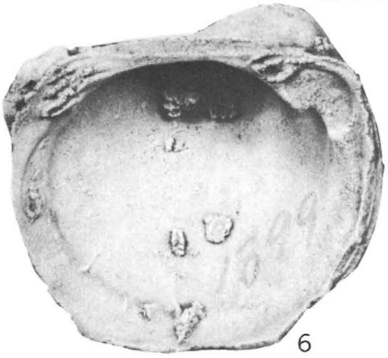
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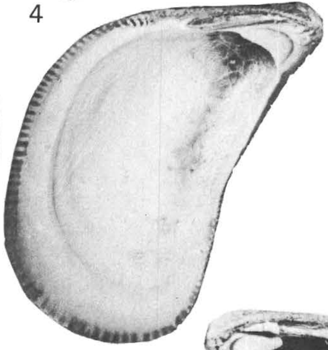
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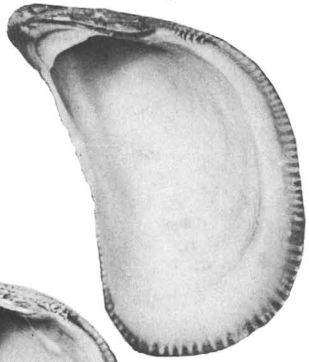
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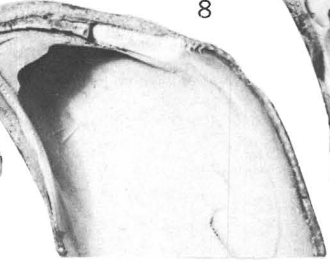
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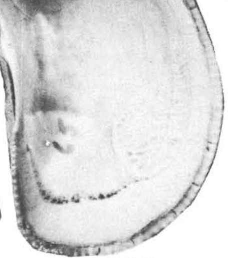
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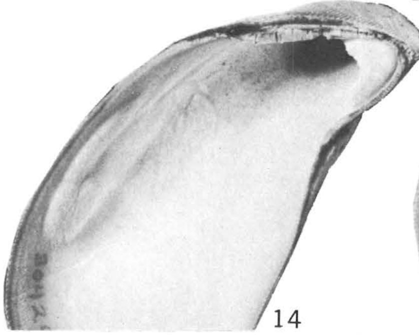
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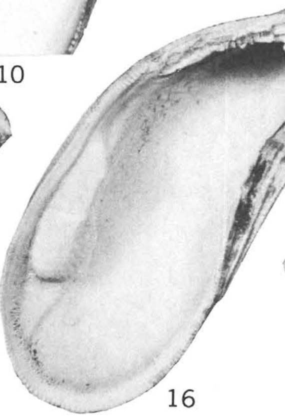
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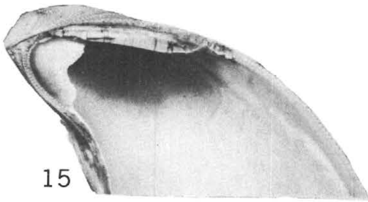
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VANUXEMIA AND *SEPTIFER*

PLATE 10

FIGURE 1. *Opisthoptera casei* (Meek and Worthen); left valve internal mold, × 2. Whitewater Formation, Richmond, Ind. USNM 46265.

2. *Opisthoptera casei* (Meek and Worthen); rubber mold of right valve showing sculpture, × 1. Waynesville Shale, Claksville, Ohio. USNM 46267.

3. *Ambonychia* cf. *A. ulrichi* (Pojeta); right valve, × 1. Perryville Limestone Member, Lexington Limestone, near Perryville, Ky. USGS collection 5015–CO. USNM 162733.

4. *Ambonychia ulrichi* (Pojeta); anterior view showing byssal gape, × 1. "Hudson River Group," Lindleys' Hirl, Tenn. AM 1124/4.

5. *Allonychia flanaganensis* Foerste; anterior view showing anterior lobe, × 1. Millersburg Member, Lexington Limestone, near Winchester, Ky. USGS locality 5066–CO. UCM 35906.

6. *Anomalodonta gigantea* Miller; hinge line view showing ligament grooves and ridges, × 1. "Hudson River Group," Versailles, Ind. YPM 23324.

7. *Ambonychia alata* Meek; rubber mold of left valve showing posterior muscle scars, pallial line, and remnants of posterior teeth, × 1. Locality and horizon unknown. UCM 35923.

8. *Ambonychia alata* Meek; hinge line showing ligament grooves and ridges and anterior teeth, × 5. Oregonia Member, Arnheim Formation of Stout and others (1943), excavation at intersection of Westwood-Northern Boulevard and Boudinot Avenue, Cincinnati, Ohio. UCM 35913.

9. *Ambonychia alata* Meek; rubber mold of left valve showing posterior teeth, × 1. Arnheim Formation, near Morrow, Ohio. USNM 46087.

10. *Ambonychia radiata* Hall; internal mold, right valve showing posterior dentition, posterior muscle scars, and pallial line, × 1.5. "Hudson River Group," Pulaski, N.Y. AM 928/2.

11. *Ambonychia radiata* Hall; right valve showing posterior teeth, × 1.5. Eden Formation of former usage, Covington, Ky. MU 2.

12. *Ambonychia casteri* (Pojeta); anterior view of composite mold showing pallial line and byssal gape, × 1. Fort Ancient Member, Waynesville Formation of Stout and others (1943), Bull Run Creek, south of Oxford, Ohio. MU 1.

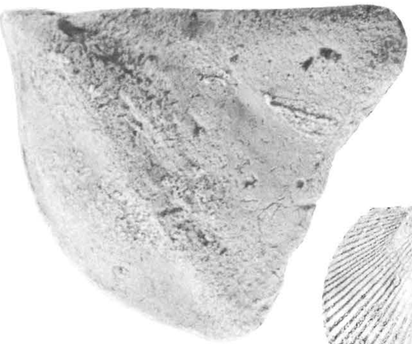
13. *Ambonychia* sp.; a specimen showing an entire attached edrioasteroid, × 1. The museum label gives the horizon and locality as: "Maysville, Cincinnati, Ohio." USNM 53900.

14. *Pterinea* sp.; left valve with attached edrioasteroids and bryozoans, × 1. The museum label gives the horizon and locality as: "Maysville Group (Corryville beds), Cincinnati, Ohio." USNM 40741.

15. *Pterinea* sp.; left valve with attached edrioasteroid and bryozoans, × 2. Corryville Shale Member, McMillan Formation, Stonelick Creek, downstream from crossing of Ohio Route 131, near Modest, Ohio. USNM 162734.

16. *Ambonychia* sp. undet.; left valve showing remains of an edrioasteroid, × 1. Bellevue Limestone Member, McMillan Formation, excavation for Liberal supermarket across from Frisch's drive-in, Hamilton Avenue, North College Hill, Ohio. USNM 162735.

17. *Ambonychia obesa* (Ulrich); dorsal view showing multiple anterior byssal retractor scars, × 1.5. Whitewater Formation, 2 miles south Richmond, Ind. on Route 27. UCM 35921.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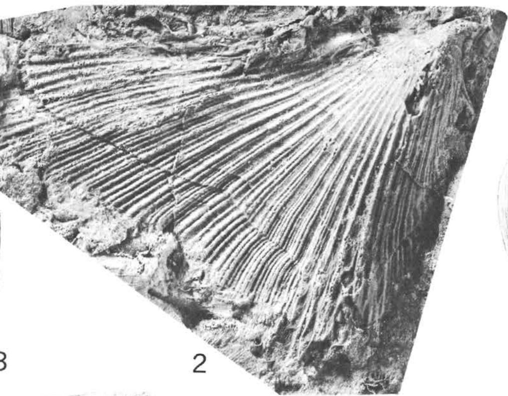
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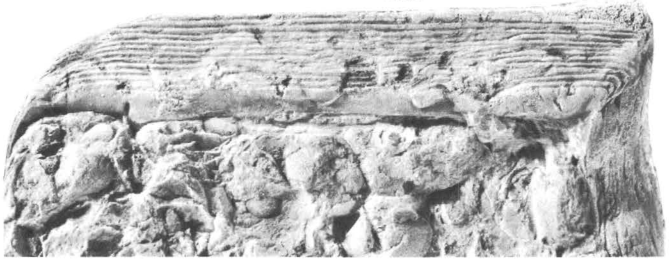
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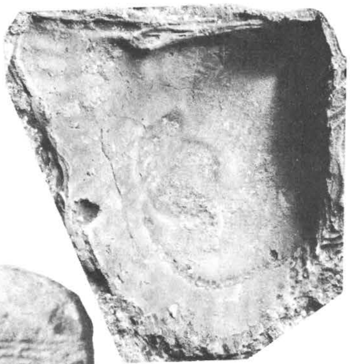
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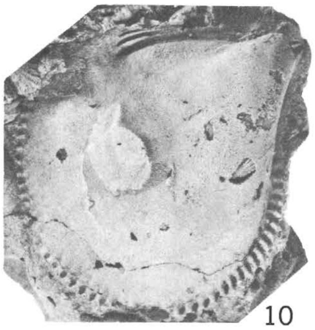
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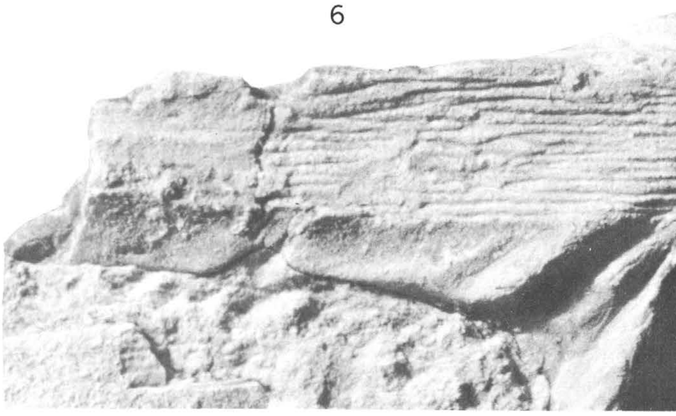
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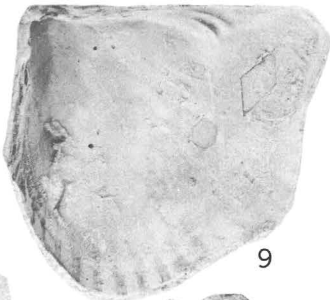
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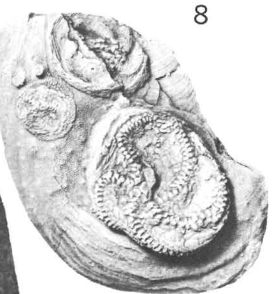
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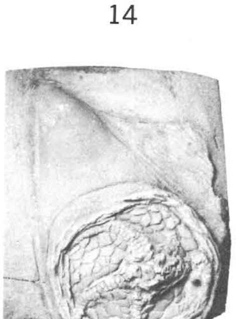
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OPISTHOPTERA, *AMBONYCHIA*, *ALLONYCHIA*, *ANOMALODONTA*, AND *PTERINEA*

PLATE 11

FIGURES 1–4. *Pterinea demissa* (Conrad); 1, left valve, × 1.1; 2, right valve, × 1.1; 3, dorsal view, × 2; 4, anterior view, × 2. The museum label lists the horizon and locality as: "Arnheim Formation, Waynesville, Ohio." USNM 40525.

5–8. *Pterinea cincinnatiensis* Miller and Faber; 5, dorsal view, × 4; 6, anterior view, × 4; 7, left valve, × 1.5; 8, right valve, × 1.5. The museum label lists the horizon and locality as: "Maysville, Cincinnati, Ohio." USNM 162736.

9. *Palaeopteria* sp.; interior left valve showing the teeth, × 4. Perryville Limestone Member, Lexington Limestone, near Perryville, Ky. USGS locality 5015–CO. USNM 162737.

10, 11. *Pterinea demissa* (Conrad); 10, left valve internal mold, × 1; 11, enlargement of dorsal part of fig. 10 showing anterior and posterior teeth, anterior muscle scars, and ligamental grooves and ridges, × 3. The museum label lists the horizon and locality as: "Pulaski drift, Thorold, Ontario." USNM 34598.

12. *Pterinea* sp.; left valve showing the inner surface of the outer shell layer, × 1.5. The museum label lists the horizon and locality as: "Richmond (Waynesville), Versailles, Indiana." USNM 46487.

13. *Pterinea welchi* (James); left valve showing prominent wing and growth lines, × 2. The museum label lists the horizon and locality as: "Richmond (upper Liberty), near Springfield Church, Todd's Fork, Ohio." USNM 70089.

14. *Pterinea demissa* (Conrad); left valve showing anterior adductor scar, × 1. The museum label lists the horizon and locality as: "Pulaski, near Trenton Falls, New York." USNM 23606.

15, 16. *Aristerella nitidula* Ulrich; syntype; 15, dorsal view showing that the specimen is nearly equivalved, × 5; 16, right valve, × 5. The museum label lists the horizon and locality as: "Black River, Chatfield, Minnesota." USNM 46092.

17. *Aristerella nitidula* Ulrich; syntype; right valve, × 5. Horizon and locality the same as in fig. 15 above. USNM 162738.

18. *Aristerella nitidula* Ulrich; syntype; left valve, × 5. Horizon and locality the same as in fig. 15 above. USNM 162739.

19, 20. *Aristerella nitidula* Ulrich; 19, left valve, × 5; 20, dorsal view, × 5. The museum label lists the horizon and locality as: "Black River, St. Paul, Minnesota." USNM 46647.

21. *Aristerella nitidula* Ulrich; syntype; right valve, × 5. Horizon and locality the same as in fig. 15 above. USNM 162740.

22. *Aristerella nitidula* Ulrich; syntype; left valve, × 5. Horizon and locality the same as in fig. 19 above. USNM 46093.

23. *Aristerella nitidula* Ulrich; syntype; dorsal view, × 5. Horizon and locality the same as in fig. 15 above. USNM 162741.

24. *Aristerella nitidula* Ulrich; syntype; right valve, × 5. Horizon and locality the same as in fig. 15 above. USNM 162742.

25, 26. "*Aristerella*"; 25, left valve showing adductor muscle scars, × 1; 26, right valve, × 1. The museum label lists the horizon and locality as: "Ord. (Jerve, D_1), Baron Toll's Estate, near Jerve, Esthonia." USNM 162743.

27–30. "*Aristerella*"; 27, right valve, × 1; 28, left valve showing adductor muscle scars, × 1; 29, dorsal view, × 1; 30, anterior view, × 1. Horizon and locality the same as in fig. 25 above. USNM 99198.

31. *Modiolus americanus* Leach; Holocene mytilid showing shell shape, × 1. Open surf beach, south shore Sanibel Island, Florida, near the "rocks." USNM 16744.

32. *Arcuatula demissa* (Dillwyn); Holocene mytilid showing shell shape, × 1. Woodmere golf course, Nassau County, Long Island, N.Y. USNM 162745.


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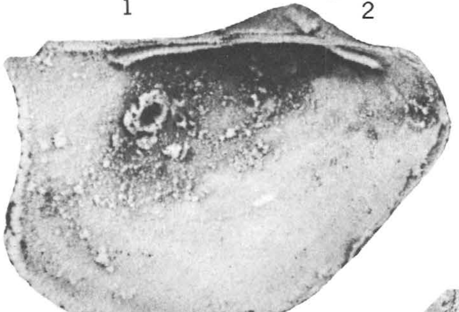
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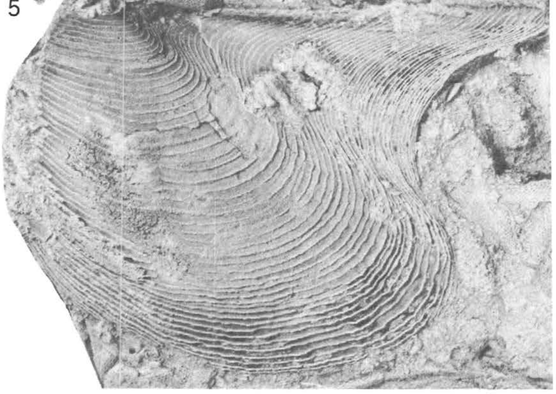
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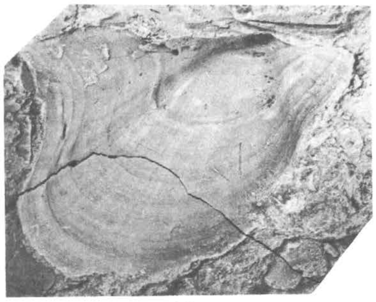
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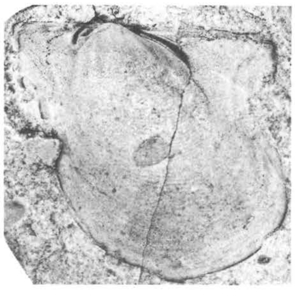
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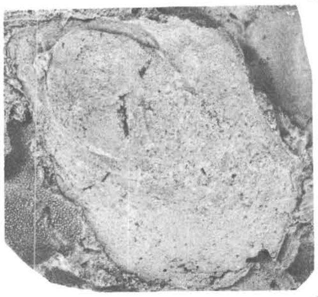
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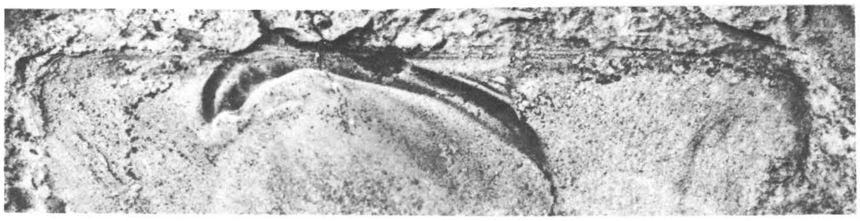
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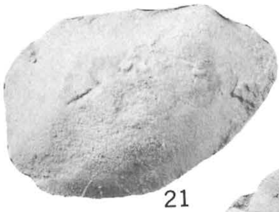
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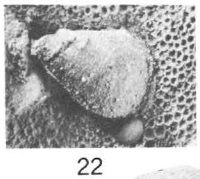
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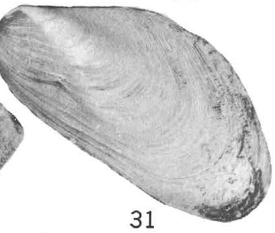
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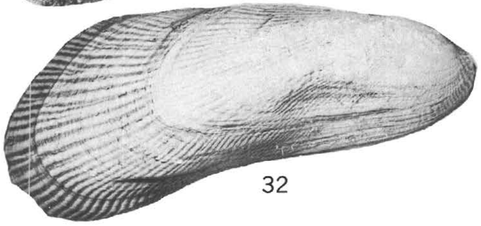
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PTERINEA, *PALAEOPTERIA*, *ARISTERELLA*, *MODIOLUS*, AND *ARCUATULA*

PLATE 12

FIGURES 1,2. *Colpomya constricta* Ulrich; 1, exterior left valve, × 3.5; 2, interior left valve showing anterior dentition, × 3.5. Devils Hollow Member, Lexington Limestone, Franklin County, Ky. USGS locality 5087-CO. USNM 162746.

3. *Colpomya constricta* Ulrich; syntype; right valve showing anterior dentition, × 4. The museum label lists the horizon and locality as: "Trenton (Perryville), Frankfort, Kentucky." USNM 46120.

4. *Modiolopsis modiolaris* (Conrad); Ulrich hypotype showing dorsal longitudinal groove, × 2. The museum label lists the horizon and locality as: "Upper Pulaski, 1 mile above Pulaski, New York." USNM 101314.

5. *Pholadomorpha pholadiformis* (Hall); articulated specimen showing divaricating sculpture, × 1. The museum label lists the horizon and locality as: "Richmond (Waynesville), Clarksville, Ohio." USNM 70414.

6,7. *Pholadomorpha pholadiformis* (Hall); Ulrich hypotypes showing some aspects of the hinge line; 6, right valve, × 3; 7, left valve, × 3. The museum label lists the horizon and locality as: "Richmond (Waynesville), Clarksville, Ohio." USNM 46342 and 162747.

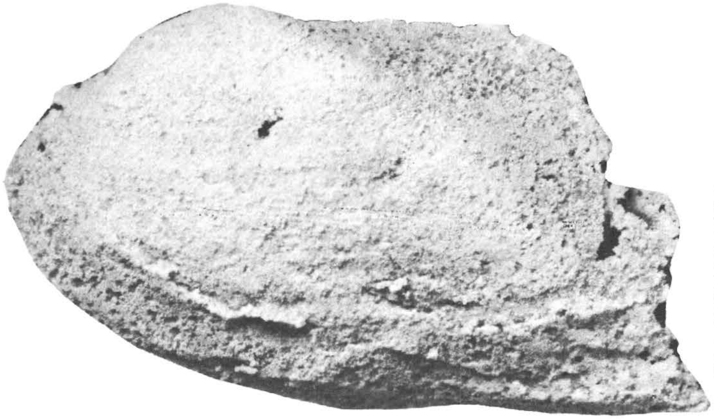
8. *Pholadomorpha pholadiformis* (Hall); left valve showing sculpture, × 1. The museum label lists the horizon and locality as: "Richmond Group (Waynesville Formation), Waynesville, Ohio." USNM 40578.

9. *Pholadomorpha pholadiformis* (Hall); left valve, × 1. Horizon and locality the same as in fig. 8 above. USNM 162748.

10–12. *Saffordia ventralis* Ulrich; syntype; 10, dorsal view showing tooth and escutcheon, × 1; 11, view of hinge line showing cardinal tooth, × 2; 12, left valve exterior, × 1. The museum label lists the horizon and locality as: "Richmond (Maquoketa), Spring Valley, Minnesota." USNM 46309.

13. *Modiolopsis* aff. *M. rogersensis* Foerste; left valve, × 1. The museum label lists the horizon and locality as: "Eden Group, Southgate Member, Warner St., central Covington, Kentucky." USNM 101443.

14. *Sphenolium striatum* Ulrich; holotype; right valve, × 1. The museum label lists the horizon and locality as: "Trenton (Prosser), 13 miles south Cannon Falls, Minnesota." USNM 46311.



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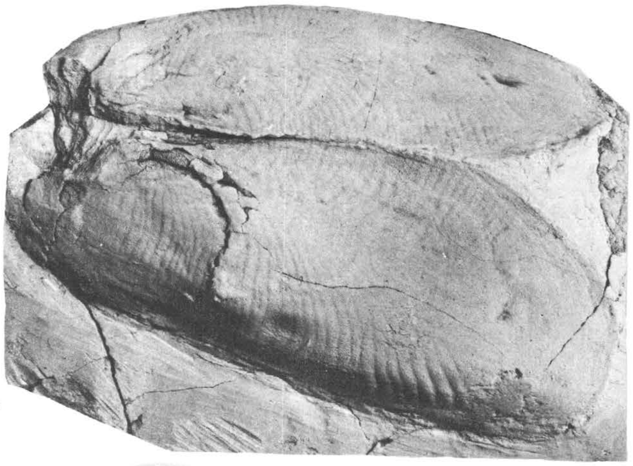

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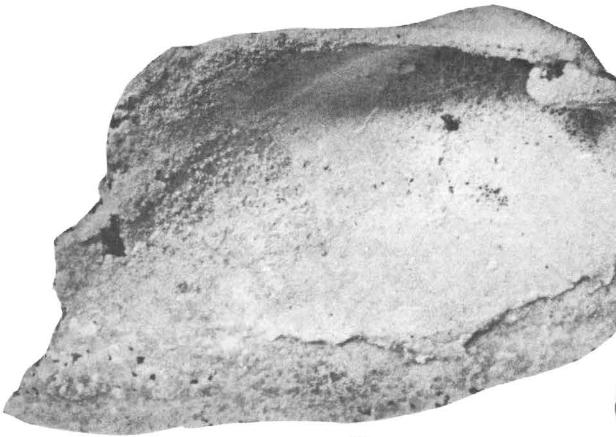

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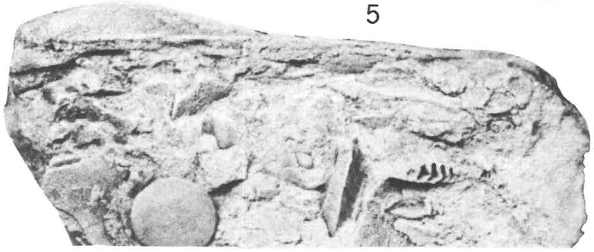

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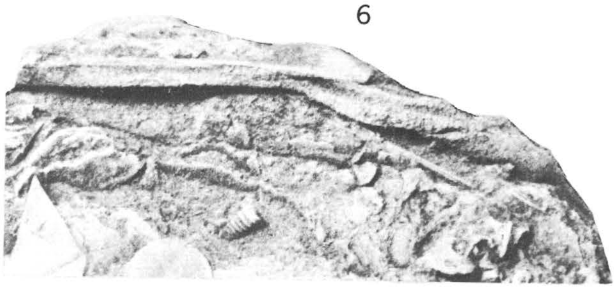

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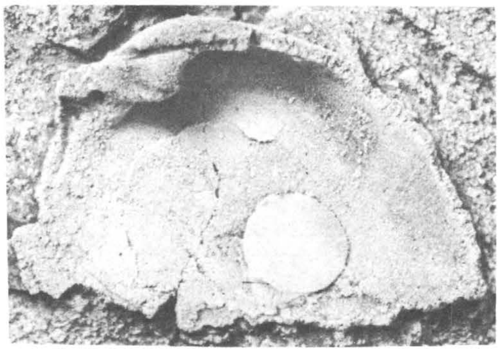

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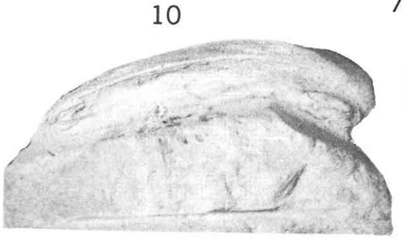

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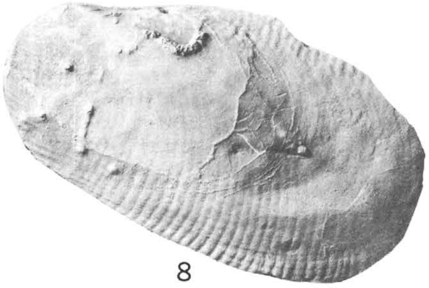

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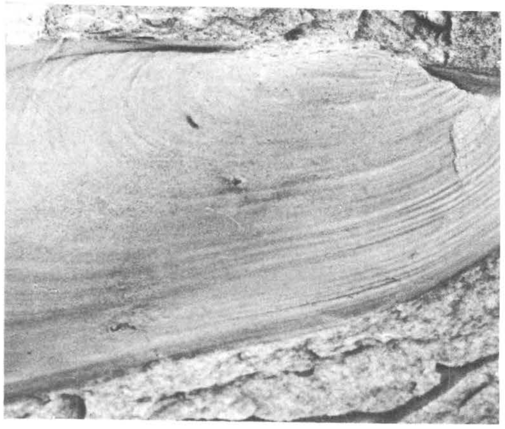

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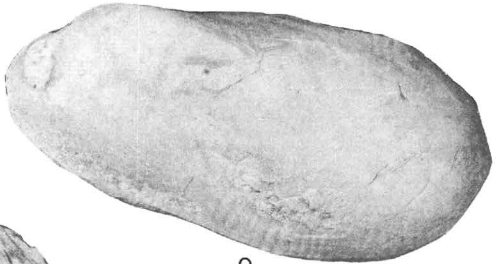

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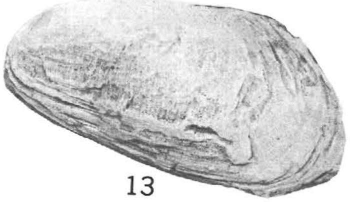

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COLPOMYA, *MODIOLOPSIS*, *PHOLADOMORPHA*, *SAFFORDIA*, AND *SPHENOLIUM*

PLATE 13

FIGURES 1–14. *Modiolodon oviformis* (Ulrich); 1, right valve, × 1, USNM 162749; 2, left valve, × 1, USNM 162750; 3, left valve, × 1, USNM 162751; 4, left valve, × 1, USNM 162752; 5, left valve, × 1, USNM 162753; 6, 7—6, interior left valve showing adductor muscle scars, teeth, and pallial line, × 2, 7—dorsal interior view showing multiple byssal retractor muscle scars, arrow points to most posterior scar, × 3, USNM 162754; 8, right valve showing teeth, × 3, USNM 162755; 9, right valve showing teeth, × 2, USNM 162756; 10, view of posterior end of broken shell showing two shell layers, × 3, USNM 162757; 11, dorsal interior view showing multiple byssal retractor muscle scars, arrow points to the most posterior scar, × 3, USNM 162758; 12, dorsal view, × 2, USNM 162759; 13, 14—13, anterior view, × 3, 14—ventral view, × 3, USNM 162760. Logana Member, Lexington Limestone, U.S. Highway 62 crossing of Kentucky River. USGS locality 5092–CO.

15. *Modiolodon oviformis* (Ulrich); syntype; internal mold showing some of the pallial line and the anterior adductor muscle scar, × 1. The museum label lists the horizon and locality as: "Trenton (Hermitage), Curdsville, Mercer County, Kentucky." USNM 46231.

16. *Modiolopsis concentrica* Hall and Whitfield; left valve composite mold, × 1. Clarksville Member, Waynesville Formation of Stout and others (1943), Sewell's Run northeast of Clarksville, Ohio. USNM 162761.

17. *Modiolopsis concentrica* Hall and Whitfield; right valve composite mold, × 1. Horizon and locality the same as in fig. 16 above. USNM 162762.

18. *Mytilus edulis* Linné; Holocene mytilid showing teeth just below the beak and the white resilial ridge, × 1.5. Locality unknown. USNM 162763.

19. *Arcuatula demissa* (Dillwyn); Holocene mytilid showing edentulous hinge and the white resilial ridge with a piece of the ligament still attached, × 1.5. Woodmere golf course, Nassau County, Long Island, N.Y. USNM 162764.

20. *Perna pincta* (Born); Holocene mytilid showing the ligament, white resilial ridge, and hinge plate with a single tooth, × 1. Algiers. USNMDM 199369.


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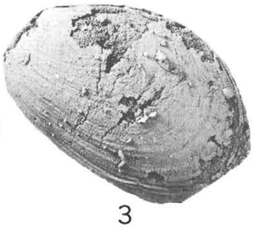
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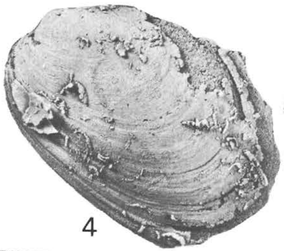
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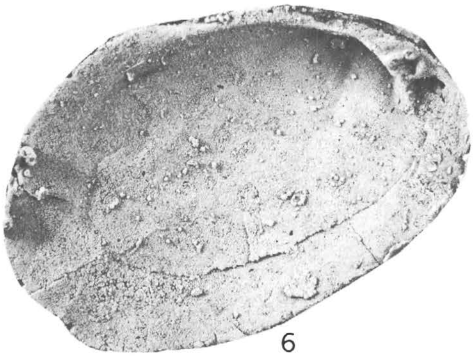
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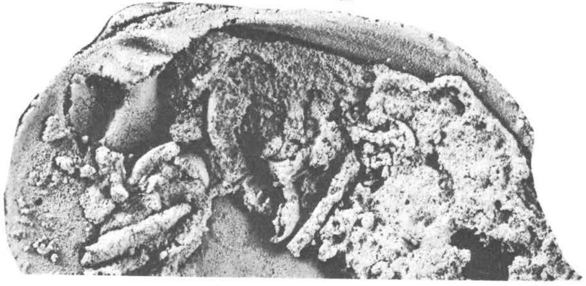
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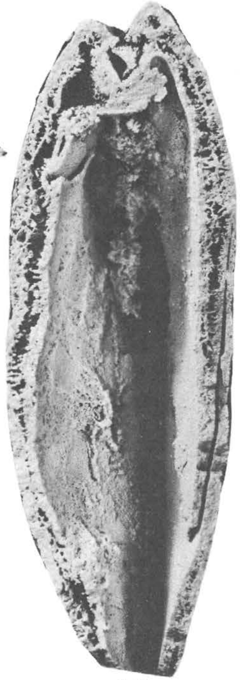
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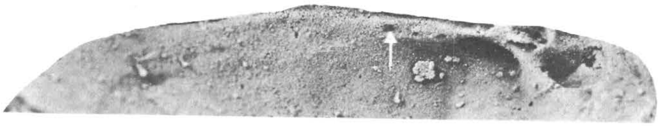
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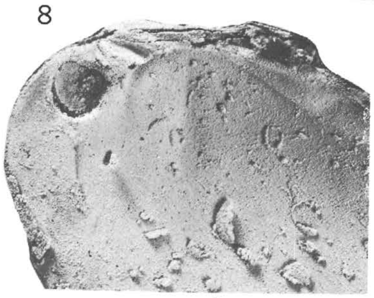
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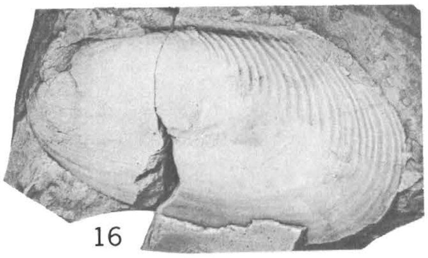
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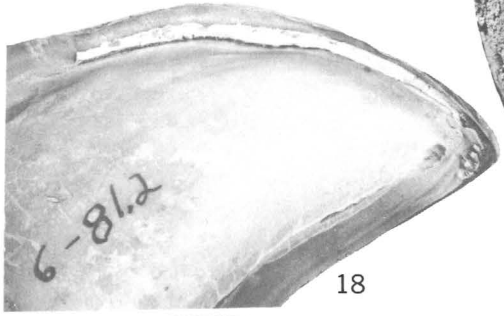

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MODIOLODON, *MODIOLOPSIS*, *MYTILUS*, *ARCUATULA*, AND *PERNA*

PLATE 14

FIGURE 1. *Modiolcpsis valida* Ulrich; syntype; right valve showing absence of cardinal teeth, × 2. The museum label lists the horizon and locality as: "Richmond (Waynesville), Waynesville, Ohio." USNM 46260.

2. *Modiolopsis* aff. *M. simulatrix* Ulrich; left valve showing absence of cardinal teeth, × 4. The museum label lists the horizon and locality as: "Eden Group, Southgate Member, Warner St., central Covington, Kentucky." USNM 101330.

3. *Modiclopsis* aff *M. simulatrix* Ulrich; right valve showing absence of cardinal teeth, × 4. The museum label lists the horizon and locality as: "Eden Group, Southgate Member, Newport, Kentucky." USNM 101440.

4. *Modiolopsis* aff. *M. simulatrix* Ulrich; right valve showing the edentulous hinge area, × 4. Horizon and locality the same as in fig. 2 above. USNM 162765.

5. *Modiolopsis versaillensis* Miller; Ulrich hopotype showing absence of cardinal teeth, × 5. The museum label lists the horizon and locality as: "Richmond (Waynesville), Versailles, Indiana and 2 miles southeast of Weisburg, Indiana." USNM 46261.

6. *Modiolopsis* aff. *M. simulatrix* Ulrich; internal mold showing adductor muscle scars and pallial line, × 2. The museum label lists the horizon and locality as: "Eden Group, Southgate Member, creeks in southwest side of Covington, Kentucky." USNM 101449.

7, 8. *Plethocardia umbonata* Ulrich; previously unfigured syntype; 7, right exterior view, × 1; 8, view of hinge line, × 2. The museum label lists the horizon and locality as: "Black River, Mercer County, Kentucky." USNM 47359.

9–12. *Plethocardia umbonata* Ulrich; syntype; 9, hinge line view (compare to reconstruction in fig. 1 H, p. 11), × 2; 10, dorsal view, × 1; 11, anterior view, × 1; 12, left exterior view, × 1. The museum label lists the horizon and locality as "Black River, 6 miles south Cannon Falls, Minnesota." USNM 46279.


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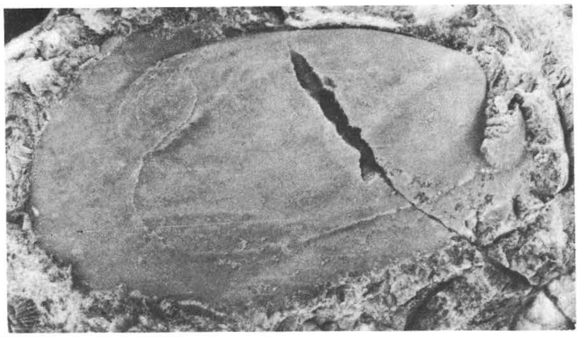
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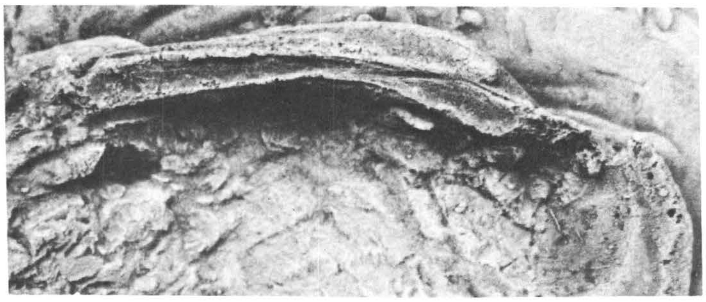
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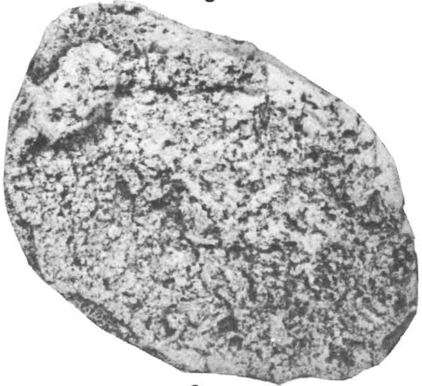
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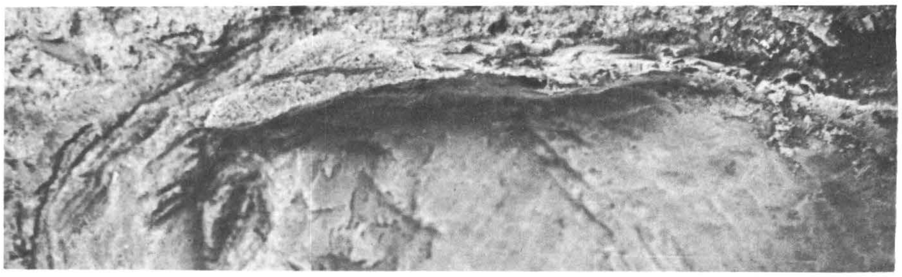
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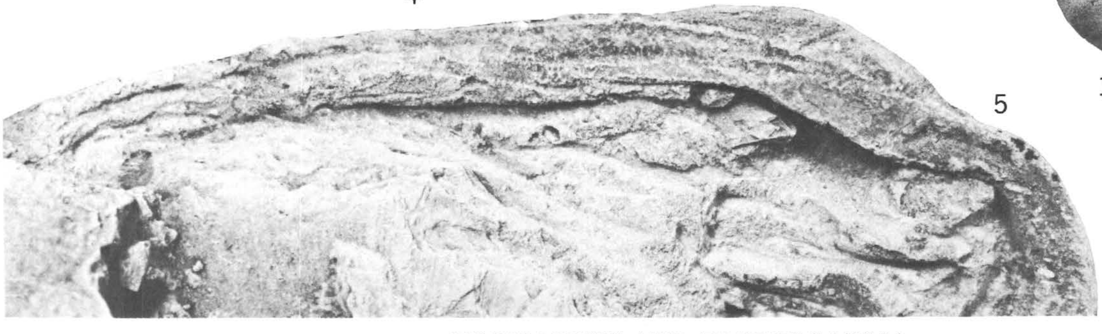
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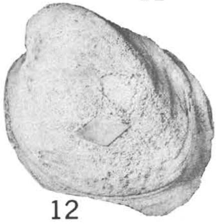
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MODIOLOPSIS AND *PLETHOCARDIA*

PLATE 15

FIGURES 1–3. *Modiolopsis modiolaris* (Conrad); holotype; 1, view of entire specimen showing articulated valves, × 1; 2, left valve, × 1; 3, right valve, × 1. The museum label lists the horizon and locality as: "Pulaski beds, Rome, New York." This specimen was figured by Hall, 1847, pl. 81, fig. 1a and Ulrich, 1924, pl. 32, fig. 1. NYSM 2758.

4, 5. *Modiolopsis modiolaris* (Conrad); holotype *M. angustifrons* (Conrad); 4, right valve composite mold, × 1; 5, dorsal view showing dark stain remnant of the ligament between the two valves, photographed unwhitened, × 3. The museum label lists the horizon and locality as: "Pulaski beds, Rome, New York." This specimen was figured by Hall, 1847, pl. 81, fig. 1b and Ulrich, 1924, pl. 32, figs. 4, 5. NYSM 2759.

6. *Modiolopsis* cf. *M. modiolaris* (Conrad); articulated specimen showing dark organic film covering valves and remains of the ligament, × 1, photographed unwhitened. The museum label lists the horizon and locality as: "Maysville (Fairmount), Covington, Kentucky." USNM 46230.

7. *Modiolopsis* sp.; internal mold left valve showing adductor muscle scars and pallial line, × 1. The museum label lists the horizon and locality as: "Maysville (Fairview), Newport, Kentucky." USNM 46707.

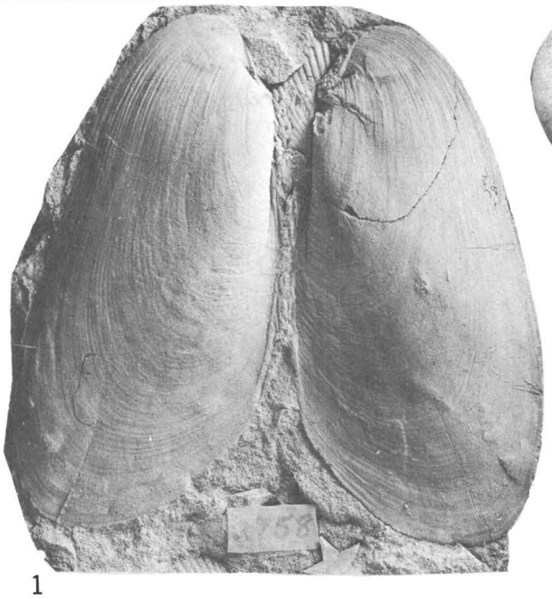
8. *Modiolopsis* cf. *M. pogonipensis* Walcott; internal mold right valve, × 1. Collected by L. Hintze. Lehman Formation, from the K-north section of Hintze, Ibex area, Utah. USNM 162766.

9, 10. *Cuneamya miamiensis* Hall and Whitfield; 9, left valve, × 1; 10, right valve, × 1. Horizon and locality unknown. USNM 162767.

11. *Cuneamya* cf. *C. scapha* Hall and Whitfield; anterior view showing lunule, × 1. The museum label lists the horizon and locality as: "Richmond (Waynesville), Richmond, Indiana and Waynesville, Ohio." USNM 47217.

12. *Cuneamya miamiensis* Hall and Whitfield; dorsal view showing ligament space, × 1. Horizon and locality unknown USNM 162768.

13, 14. *Cuneamya* cf. *C. scapha* Hall and Whitfield; 13, posterior view, × 1; 14, ventral view, × 1. Horizon and locality same as in fig. 11 above. USNM 162769.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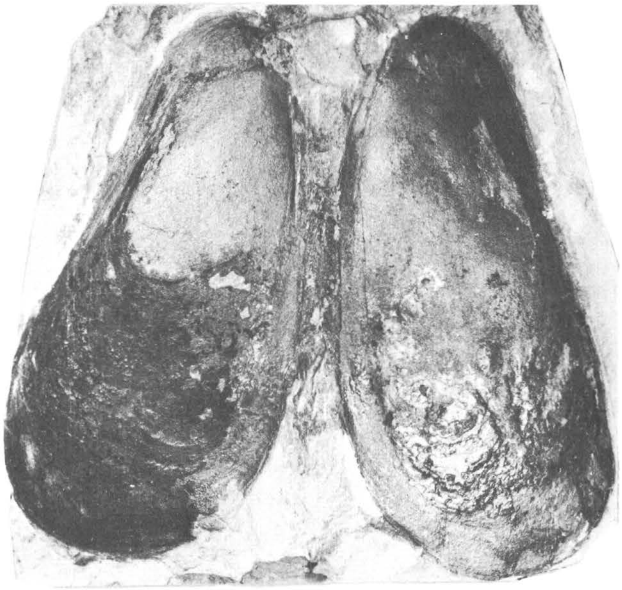
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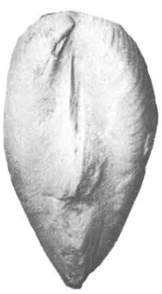
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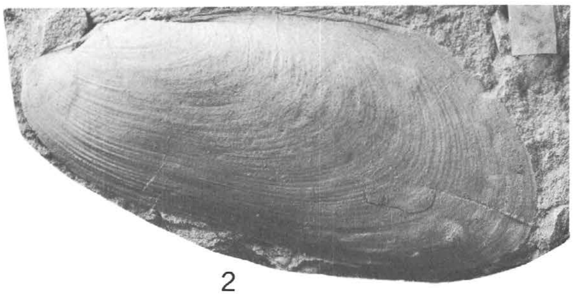
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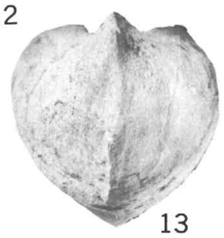
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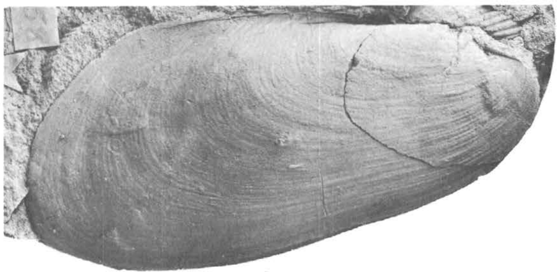
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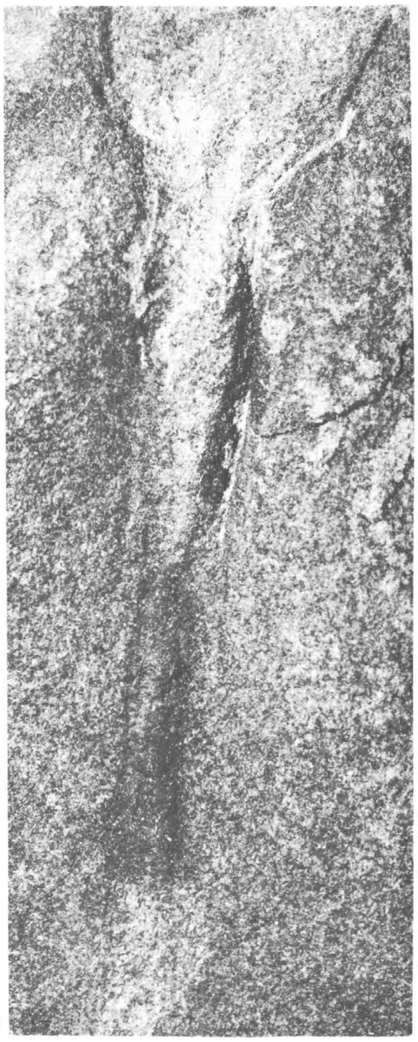
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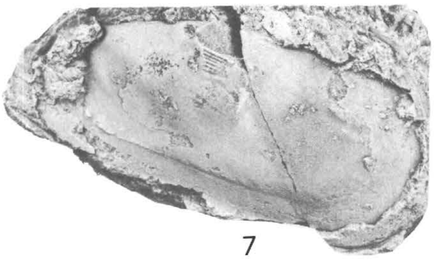
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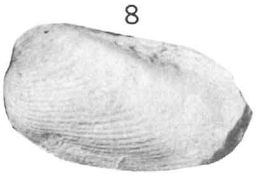
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10

MODIOLOPSIS AND *CUNEAMYA*

PLATE 16

FIGURES 1–3. *Modiolopsis modiolaris* (Conrad); 1, enlargement of anterior end of internal mold showing adductor muscle scar, pallial line, and multiple accessory scars anterior to the beak (arrow), × 3; 2, entire specimen shown in fig. 1, × 1; 3, rubber mold of the specimen shown in fig. 2, × 1. The museum label lists the horizon and locality as: "Pulaski drift, Trenton Falls, New York." USNM 101464.

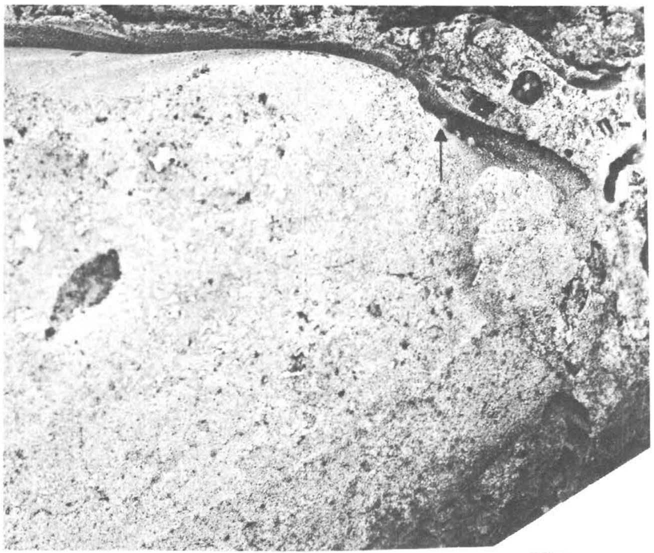
4, 5. *Modiolopsis* sp.; 4, enlargement of upper right hand part of fig. 5 showing nestling modioliform modiomorphid pelecypod and trematid inarticulate brachiopod, × 2; 5, entire trepostome bryozoan colony showing two nestling modioliform modiomorphids (right-hand facing arrow and longer left-hand facing arrow) and trematid brachipod (shorter left-hand facing arrow), × 1. The museum label lists the horizon and locality as: "Richmond (Waynesville), Clarksville, Ohio." USNM 70458.

6. *Matheria rugosa* Ulrich; syntype; right valve showing cardinal teeth and ligament grooves and ridges, × 2. The museum label lists the horizon and locality as: "Trenton (Prosser), 6 miles south Cannon Falls, Minnesota." USNM 46226.

7–9. *Matheria tener* Billings; syntype; 7, exterior left valve, × 2; 8, exterior left valve, × 1; 9, interior left valve showing cardinal teeth and ligament grooves and ridges, × 4. The museum label lists the horizon and locality as: "Trenton, Blue Point, Lake St. John, Quebec." GSC 1670.

10. *Rhytimya mickelboroughi* (Whitfield); Ulrich hypotype; left valve, × 1. The museum label lists the horizon and locality as: "Maysville (Fairmount), Cincinnati, Ohio." USNM 46301.

11. *Rhytimya* sp.; right valve showing shell sculpture of concentric undulations and radiating granules, × 3. The museum label lists the horizon and locality as: "Lorraine or Eden, Rome, New York." USNM 102037.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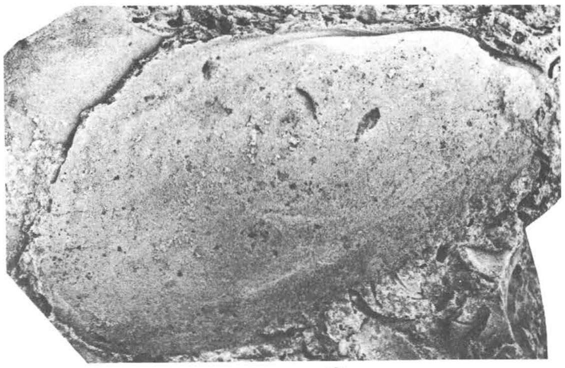
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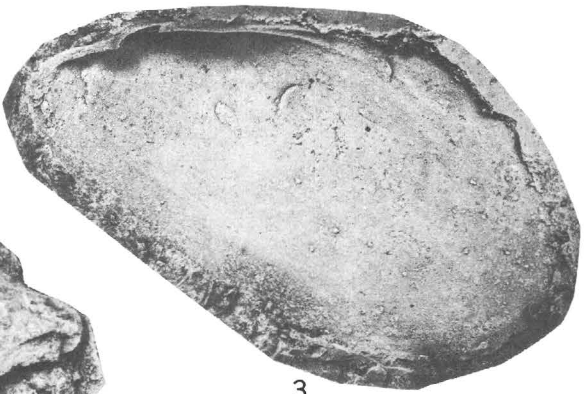
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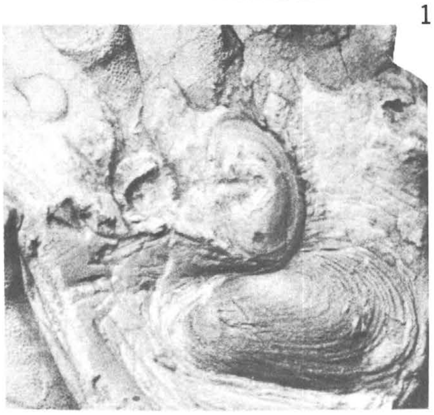
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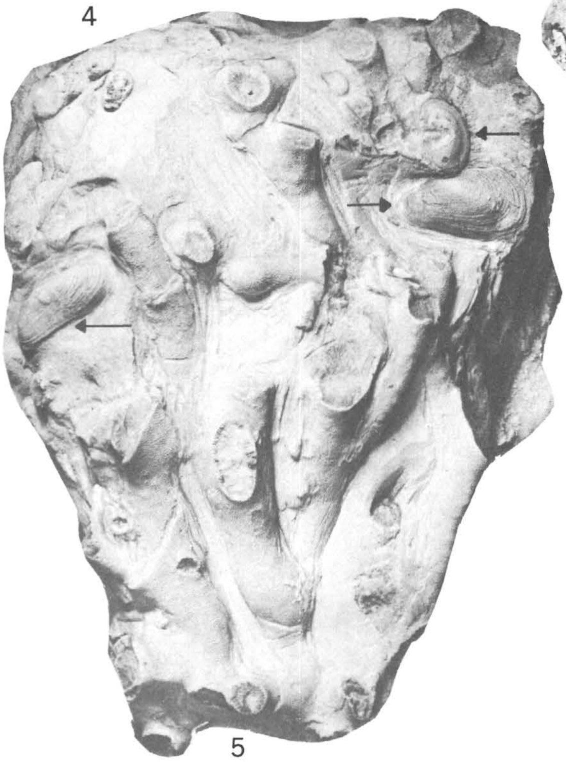
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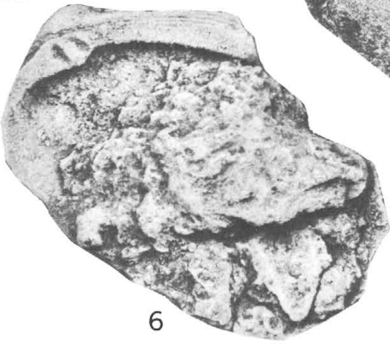
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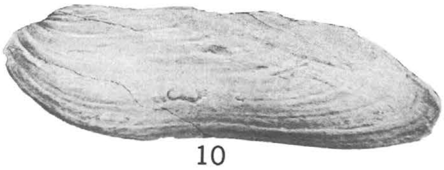
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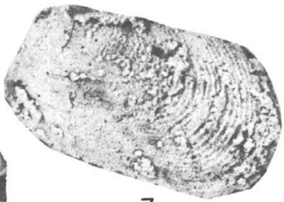
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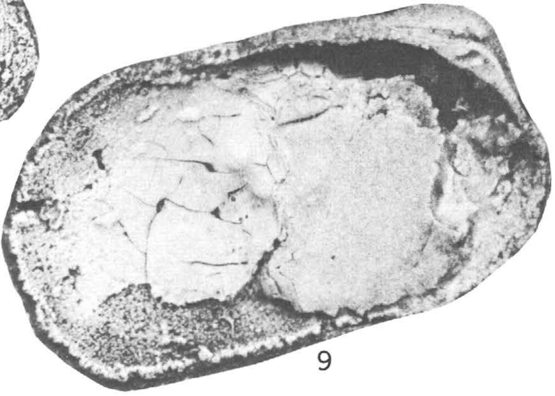
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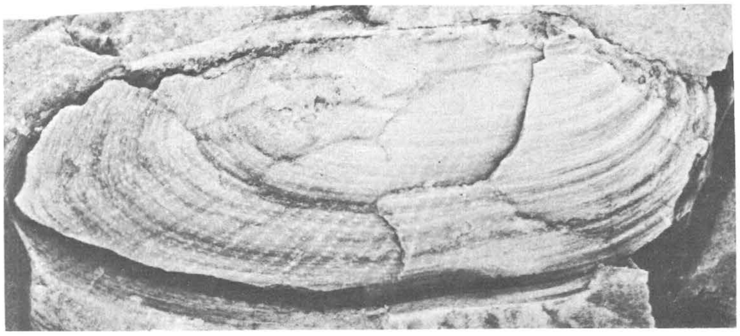
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MODIOLOPSIS, *MATHERIA*, AND *RHYTIMYA*

PLATE 17

FIGURES 1, 2. *Whiteavesia cincinnatiensis* (Hall and Whitfield); 1, left valve showing lack of posterior teeth, × 2; 2, exterior left valve showing numerous fine growth lines, × 1. Logana Member, Lexington Limestone, on hill above Old Crow distillery, Woodford County, Ky. USGS locality 5073–CO. USNM 162770.

3, 4. *Whiteavesia cincinnatiensis* (Hall and Whitfield); 3, right valve interior showing lack of posterior teeth, × 2; 4, right valve exterior, × 1. Logana Member, Lexington Limestone, U.S. Route 62 crossing of Kentucky River. USGS locality 4865–CO. USNM 162771.

5. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); left valve showing lack of cardinal teeth, × 3.5. Perryville Limestone Member, Lexington Limestone, quarry south of Perryville, Ky. USGS locality 5015–CO. USNM 162772.

6. *Whiteavesia cincinnatiensis* (Hall and Whitfield); right valve composite mold, × 1. The museum label lists the horizon and locality as: "Trenton (Cynthiana), West Covington, Kentucky." USNM 162773.

7. *Whiteavesia cincinnatiensis* (Hall and Whitfield); Ulrich hypotype; horizon and locality the same as in fig. 6 above. USNM 46339.

8. *Whiteavesia cincinnatiensis* (Hall and Whitfield); right valve composite mold, × 1. Horizon and locality the same as in fig. 6 above. USNM 92317.

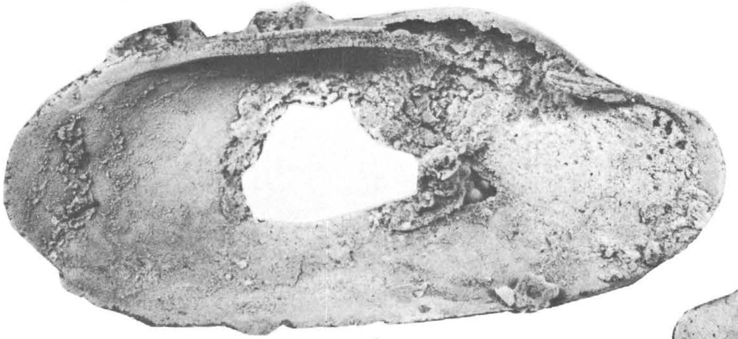
9. *Whiteavesia cincinnatiensis* (Hall and Whitfield); right valve exterior, × 3. Horizon and locality the same as in fig. 3 above. USNM 162776.

10. *Whiteavesia cincinnatiensis* (Hall and Whitfield); Ulrich hypotype; this is the specimen upon which Ulrich based the analysis of the hinge line of the species, × 3. Horizon and locality the same as in fig. 6 above. USNM 162777.

11, 12. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); 11, left valve interior showing lack of cardinal teeth, × 2; 12, left valve exterior, × 1. Horizon and locality the same as in fig. 5 above. USNM 162774.

13, 14. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); 13, right valve interior showing lack of cardinal teeth, × 2; 14, right valve exterior, × 1. Horizon and locality the same as in fig. 5 above. USNM 162775.

15. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); left valve interior, × 2. Horizon and locality the same as in fig. 5 above. USNM 162778.



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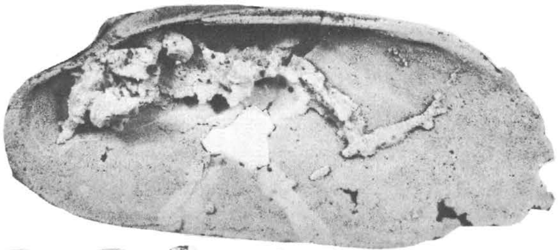

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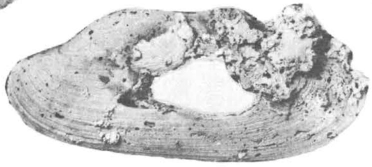

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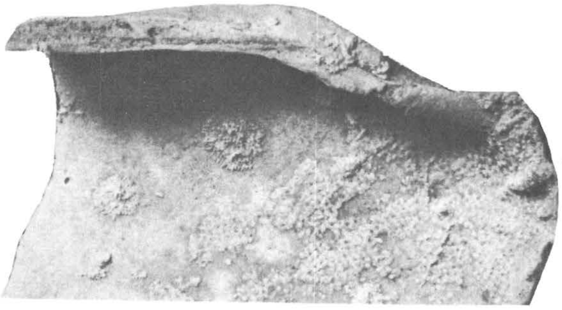

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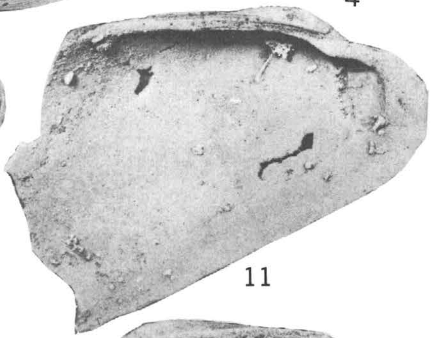

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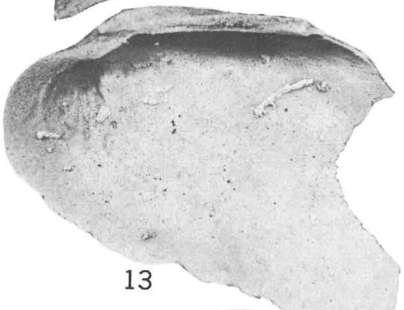

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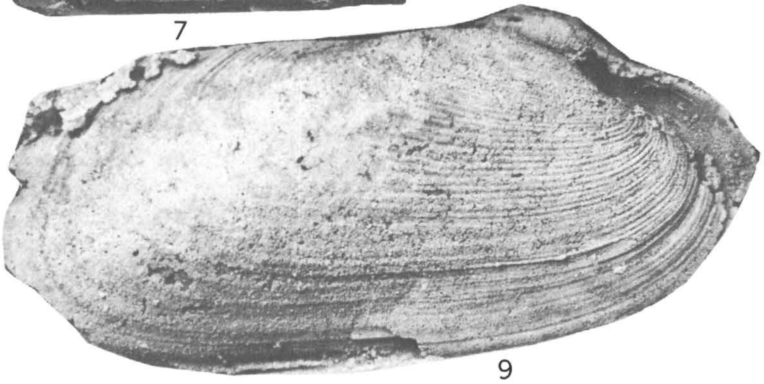

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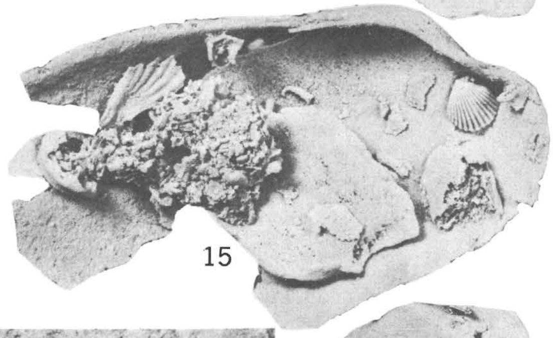

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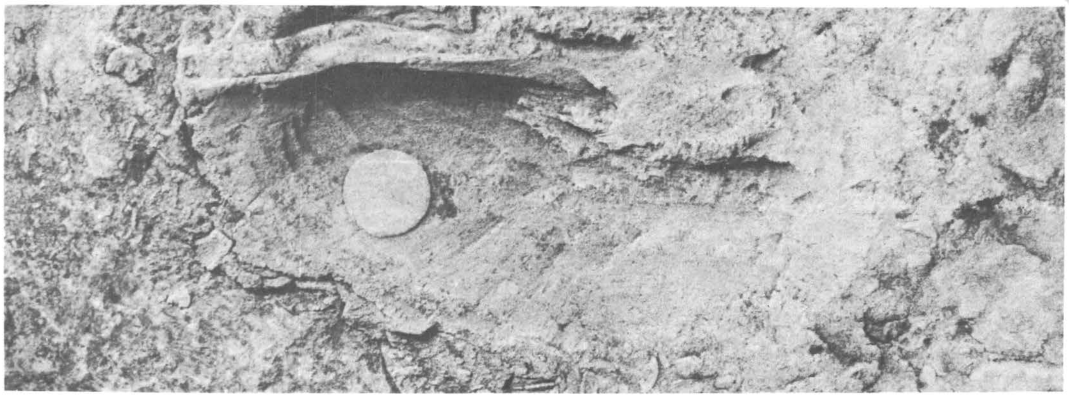

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WHITEAVESIA

PLATE 18

FIGURES 1–6. *Psiloconcha grandis* Ulrich; syntype; 1, left valve showing adductor muscle scars, × 2; 2, right valve, × 2; 3, ventral view showing shell gapes (arrows), × 2; 4, dorsal view showing shell gapes (arrows), × 2; 5, posterior view showing gape, × 3; 6, anterior view showing gape, × 3. The museum label lists the horizon and locality as: "Richmond (Waynesville), Waynesville, Ohio." USNM 46283.

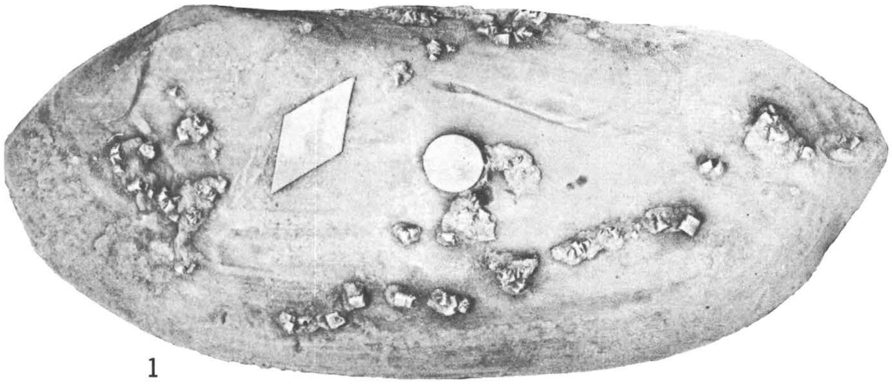
7. *Orthodesma* sp.; right valve, × 1. The museum label lists the horizon and locality as: "Maysville (*Orthorhynchula* Bed), Tuscarora Mt., 1½ miles southeast of McConnellsburg, Pennsylvania." USNM 66172.

8, 9. *Orthodesma* sp.; right valve internal mold showing adductor muscle scars and pitted pallial line, × 2; 9, natural cas, of fig. 8, × 2. The museum label lists the horizon and locality as: "Eden (Southgate) ,north end of Amsterdamt Covington, Kentucky." USNM 101634.

10, 11. *Cymatonota typicalis* Ulrich; syntype; 10, posterior view showing shell gape, × 2; 11, anterior view showing shell gape, × 2. The museum label lists the horizon and locality as: "Richmond (Waynesville), Waynesville, Oh io." USNM 46170.

12. *Cymatonota recta* Ulrich; syntype; left valve, × 1.5. The museum label lists the horizon and locality as: "Maysville (Bellevue), Cincinnati, Ohio." USNM 46168.

13. *Cymatonota recta* Ulrich; syntype; left valve, × 1.5. Horizon and locality the same as in fig. 12 above. USNM 162779.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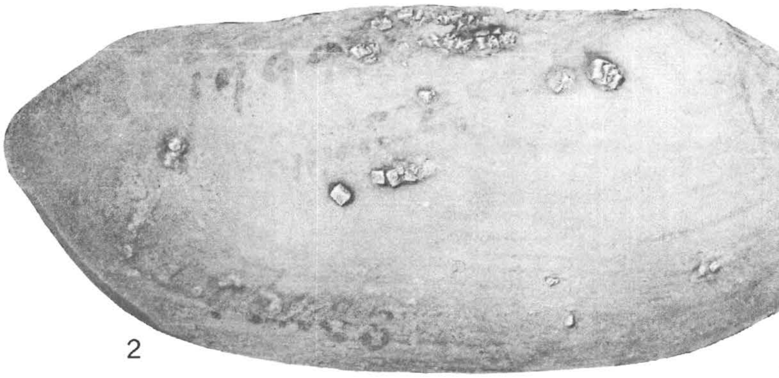
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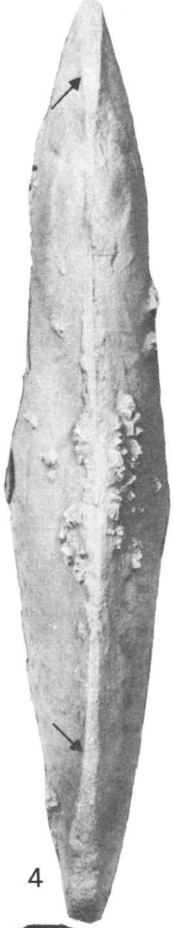
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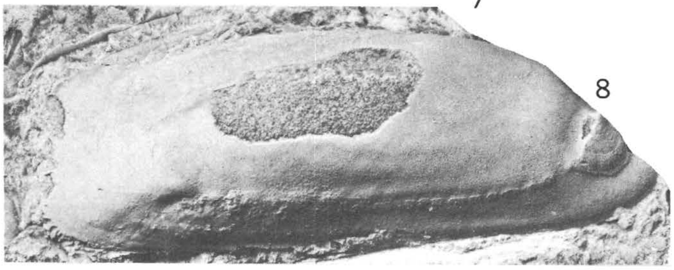
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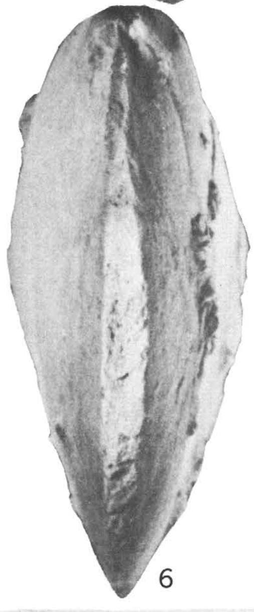
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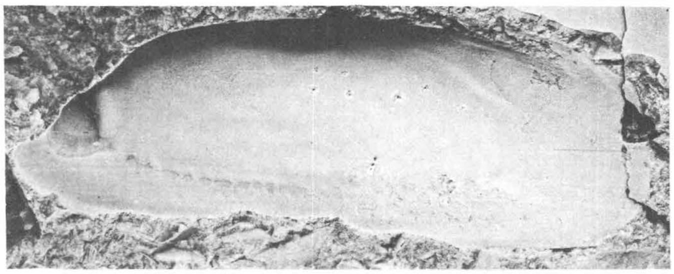
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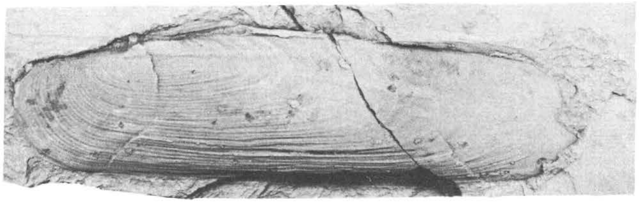
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PSILOCONCHA, *ORTHODESMA*, AND *CYMATONOTA*

PLATE 19

FIGURES 1–3. *Eopteria richardsoni* Billings; holotype; 1, left(?) valve, × 1; 2, left(?) valve, × 3; 3, dorsal view, × 3. The museum label lists the horizon and locality as: "Beekmantown, St. Antoine de Tilly, Quebec." GSC 756.

4. *Eopteria* sp.; left(?) valve, × 2. Specimen from the bioherm at the Meiklejohn Peak section, Nevada (Ross, 1967). USGS locality D–1966–CO. USNM 162780.

5–9. *Eopteria* sp.; 5, right(?) valve, × 5; 6, left(?) valve, × 5; 7, dorsal view, × 5; 8, ventral view, × 5; 9, anterior(?) view, × 5. The museum label lists the horizon and locality as: "Smithville Formation, 1½ miles north Smithville, Arkansas." USNM 162781.

10–14. *Eopteria* sp.; 10, ventral view, × 5; 11, dorsal view, × 5; 12, right(?) valve, × 5; 13, left(?) valve, × 5; 14, anterior (?) view, × 5. Horizon and locality the same as in fig. 5 above. USNM 162782.

15. *Conocardium* cf. *C. immaturum* Billings; left(?) valve, × 5. The museum label lists the horizon and locality as: "Upper Black River, Pauquette Rapids, Ottawa River, Canada." USNM 92270.

16. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); right interior view, × 2. Perryville Limestone Member, Lexington Limestone, quarry south of Perryville, Ky. USGS locality 5015–CO. USNM 162783.

17. *Whiteavesia cincinnatiensis* (Hall and Whitfield); right valve showing lack of cardinal teeth, × 3.5. Logana Member, Lexington Limestone, Interstate Route 64 crossing of Kentucky River. USGS collection D–1196–CO. USNM 162784.

18. *Whiteavesia* cf. *W. cincinnatiensis* (Hall and Whitfield); right valve showing lack of cardinal teeth, × 10. Horizon and locality the same as in fig. 16 above. USNM 162785.


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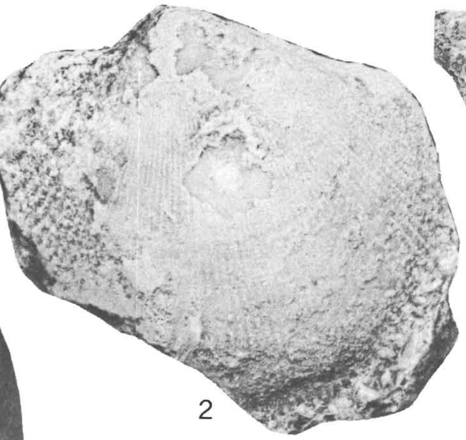
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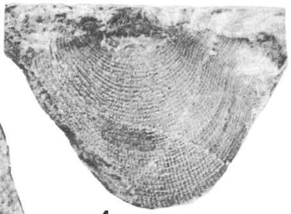
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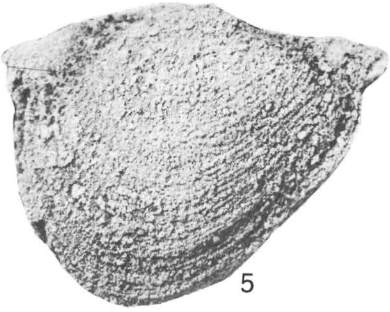
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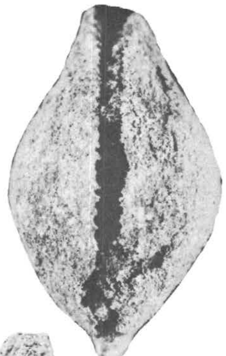
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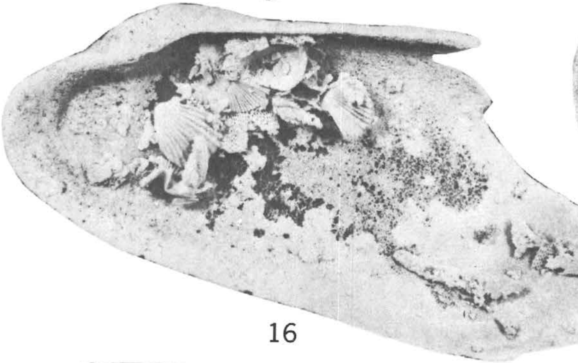
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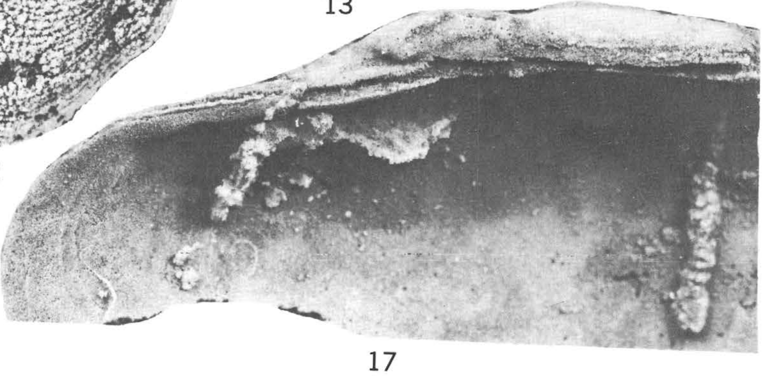
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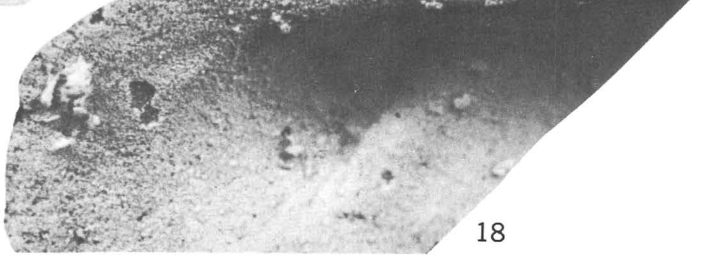
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EOPTERIA, *WHITEAVESIA*, AND *CONOCARDIUM*