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KANSAS

NEWELL

VOL. X

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STATE GEOLOGICAL SURVEY OF KANSAS

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LATE PALEOZOIC PELECYPODS: MYTILACEA

By NORMAN D. NEWELL

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PREFACE

By Raymond C. Moore

Recently issued publications of the State Geological Survey of Kansas describing the mineral resources of the state and discussing their utilization by war industries are widely recognized by citizens as valuable and timely contributions that embody accumulated results of field studies and laboratory research. Just as every one knows that petroleum, natural gas, coal, zinc, lead, salt, clay deposits, and many other similar materials occurring in the earth are essentials of modern industry and their presence in large quantities in Kansas is an all-important source of the state's prosperity, so does every one—or almost every one—realize the importance of applied geologic science and of engineering work that is needed for the exploration and development of these resources. A considerable sum is expended annually by Kansas in geological investigations and correlated chemical, physical, and engineering work of various sorts that promote the discovery and utilization of rocks and minerals useful to industry. These sums are investments of the state in itself. They have helped Kansas to advance to a position in the first ten mineral-producing states of the nation and to maintain that high rank. Actually, only seven other states now exceed Kansas in the annual total of new wealth produced from beneath the soil. The State Geological Survey is called on daily in one way or another to aid in developing and in properly conserving, also, the natural resources of Kansas. All of this is a matter of more or less common knowledge.

An essential function of the Geological Survey that is not widely known or appreciated is the investigation of somewhat general and basic problems that bear on understanding of geologic conditions in Kansas. Such studies may include very detailed examination of a clay, applying spectroscopic, X-ray, petrographic, chemical, and several other special techniques, with the object of determining all its properties, factors responsible for these properties, and means of utilizing or modifying them for requirements of industry. Research on the conditions of deposition of the clay may be very important. Many scientific investigations that may seem at first to have only academic interest, actually are fundamental, and accordingly they have high practical value. The application of some studies on rock and mineral deposits may not be known at the time of making the examination, as in the case of the first finding of helium in natural gas, which was a result of work by Dr. H. P. Cady, of the University of Kansas, on the chemical nature of Kansas natural gases. Helium is now extracted commercially from natural gas. The economic usefulness of some very specialized studies, on the other hand, is thoroughly understood by geologists even before these researches are undertaken. Paleontologic investigations belong in the last mentioned category, because the structural sequence and chronologic order of stratified rocks are indicated by the nature of their contained fossilized organic remains. Correlation of sedimentary formations in different regions and interpretation of conditions of deposition of the rocks depend either wholly or largely on paleontologic data. It is worthy of notice that the relation of studies on the nature and distribution of fossils in the rock strata of Kansas to practical work in developing mineral resources is like the X-ray photograph of a human interior to the needs of a surgeon or physician who is called to diagnose and treat some part of the body. In both cases, the specially trained technician is indispensible.

The following paper constitutes the second of a projected series of reports on an important but neglected group of fossils that is represented by innumerable specimens in many of the Late Paleozoic rocks of Kansas. The group indicated is that of the pelecypods or clams, which are common invertebrates of modern seas and fresh-water bodies, as well as of ancient marine and nonmarine waters. The author of these papers is a native of Kansas, trained as geologist and paleontologist at the University of Kansas and Yale University, experienced in field and laboratory research as a member of the State Geological Survey of Kansas, and teacher in the Department of Geology at the University of Kansas, and now Associate Professor of Geology at the University of Wisconsin. He has gained national and international recognition as an investigator of the older fossil pelecypods and is widely known also as Editor of the Journal of Paleontology, the largest scientific periodical devoted to research on fossils. The first of Doctor Newell's Kansas Geological Survey reports on Pennsylvanian and Permian pelecypods (vol. 10, 1937) dealt with the Pectinacea, or scallops. It incorporated descriptions and illustrations of numerous specimens in the collections of the University of Kansas, but the research work itself was not financed by the State Geological Survey. Similarly, this second report, which treats the stratigraphically important group Mytilacea, called mytilids and myalinids, is largely based on Kansas fossil collections; but it is a contribution of Doctor Newell's time and labor, aided by a research grant from the University of Wisconsin. The State Geological Survey of Kansas is indebted to Doctor Newell and to the University of Wisconsin for the opportunity to incorporate this report in its publications on the geology and paleontology of Kansas. Few parts of the world offer as fine a record of alternating marine and nonmarine sedimentary deposits of Late Paleozoic age, containing abundant well preserved fossils, as Kansas. This imposes both an opportunity and a responsibility on investigators of Kansas geology to obtain and to disseminate information that serves general advancement of geologic science. Papers of the type represented by this report on fossil clams have much more than local and temporary value. They have bearing on geologic studies in distant corners of the world and possess lasting value in scientific literature.

LATE PALEOZOIC PELECYPODS: MYTILACEA

NORMAN D. NEWELL

INTRODUCTION

Representatives of the pelecypod superfamily Mytilacea are among the most diverse, most abundant, and best preserved of Paleozoic pelecypods. Among these the myalinids are of particular interest because of the remarkable shell beds formed by their remains. At many horizons, particularly in the Pennsylvanian and Early Permian rocks of the Mid-Continent region, there are thin beds of limestone or shale, up to a foot or so in thickness, filled with the massive valves of these pelecypods. Scores of beds of this kind are traceable for tens of miles, and constitute excellent datum horizons for field mapping. Certain "*Myalina* beds," such as occur in the Meadow limestone (Lansing), Vinland shale (Douglas), Stull shale (Shawnee), Caneyville formation (Wabaunsee), and Moran formation, to mention only a few, are incredibly persistent, and represent old shell "banks" comparable with the extensive *Mytilus* and *Ostrea* beds of the present day seas. Unlike modern Mytilidae the Late Paleozoic Mytilidae were not markedly gregarious and, in general, appear to be much more sporadic than the myalinas. Little is known about early Paleozoic ancestors of the Mytilacea, *sensu stricto,* nor are the Devonian and Mississippian Myalinidae and Mytilidae adequately known. It is certain that the splendid material from the Pennsylvanian and Permian rocks herein described will shed much light on the morphology of the more poorly preserved older faunas. The Early Permian (Wolfcampian) Mytilacea are well represented, at least in American faunas, but the later Permian appears to be poor in representatives of the superfamily.

In view of the abundance of good material available, it is surprising that so little attention has been paid by systematists to the Late Paleozoic Mytilacea. Although Hall (1884-1885), DeKoninck (1885), Frech (1891), and Hind (1895, 1897) dealt with these shells in their pioneer studies of Paleozoic pelecypods, their observations did not lead to a satisfactory understanding of this important group of fossils. Indeed, because of a marked tendency for the mytiloids to develop along a few well defined trends, homeomorphy within the group is very common, and we find the earlier students of Paleozoic pelecypods classing some of the myalinids as pteriids ("aviculids") because of a striking similarity in form between various species of the two different stocks.

Greatest interest in Late Paleozoic Mytilacea comes from their hitherto unsuspected stratigraphic value as excellent guide fossils. Several separate phylogenetic groups are recognized, some of which display marked modifications in form as they are traced through the Late Paleozoic sequence. The relative abundance of myalinid shells, together with their limited stratigraphic range, makes these fossils second to no other group of fossil pelecypods known to me as good indices of geologic age. In this respect they are superior to many of the genera of associated brachiopods, in which evolutionary trends are generally not so evident.

As the need for greater refinement in stratigraphic paleontology increases, many paleontologists are turning to statistical methods as a partly objective approach to the evaluation of fossil species. Paleontologists will do well to heed Simpson's (Simpson, 1937, pp. 303-314; also Simpson and Rowe, 1939) plea for more satisfactory documentation of fossil evidence. It is axiomatic that no two animals are exactly alike, even though they may be spawned from the same parents. This inherent variability should be taken into account in describing a species. Many paleontologists select one, or at most a few, of their best specimens for the description and the duplicates are set aside. With Simpson, I believe that the characters of a species cannot be adequately known in absence of frequency graphs or some other form of statistical data. Without some knowledge of the extent of variability of a given species, its limits cannot be defined. Of course it would be absurd to argue that inadequate material should never be described, or even in some instances named, because wholly satisfactory collections are not common. The naming of a distinctive fossil may well be justified even though only one specimen is available. However, the usefulness of such a species in evolutionary paleontology is very limited, and the limitations of such a species should clearly be recognized. Naturally a thorough statistical analysis is impossible with rare or bulky material. There is no justification, however, for failure to employ quantitative data in the descriptions of new species of small gregarious animals, such as Foraminifera or ostracodes. In the present study I have tried to learn the limits of variations within the collections at my disposal.

Since paleontologists seldom can evaluate the ecologic factor in modifications of structure and form of fossil animals it seems important that the statistics of a "species" be based on a collection from a single horizon and locality, wherever practicable. The holotype and "topoparatypes"[1] then, with a high degree of probability, are conspecific and were subject to the same impacts of environment. Other supplementary paratypes obviously are not so valuable in a detailed analysis.

Summary of Results

Paleontologists are gradually coming to admit that different taxonomic groups among fossils do not have equal time value for purposes of dating and correlating rocks. The logical inference to be drawn from this conclusion is that correlations based on objective analysis of percentages of species common to two formations are not so reliable as are the correlations founded on genetic series of certain rapidly evolving groups. However, even among the more celebrated groups of guide fossils, such as the trilobites, graptolites, ammonites, and fusulinids, there are comparatively long ranging genera and species that have only a limited usefulness in correlations.

The pelecypods are no exception to the rule. Some families appear to have been relatively conservative and relatively unchanging through great spans of geologic time; whereas, others underwent conspicuous changes as traced through the rocks. In this latter category belong the myalinas and related mytiloids, herein considered, from the Pennsylvanian and Permian rocks.

It is probable that representatives of the Mytilacea are more abundant in the American Late Paleozoic than any other single group of pelecypods. In the Mid-Continent Pennsylvanian and Lower Permian they are locally so abundant as to make shell beds. A dozen or more of these shell beds are individually traceable for more than one hundred miles.

Down through the years it has been customary to refer almost all Carboniferous and Permian species of the Mytilacea to the genus *Myalina*. The results of the present investigation reveal that there are around a dozen separate phyletic lines represented in these shells. Eight genera and subgenera in two families are recognized among the shells commonly called *Myalina* by American paleontologists.

The two families are readily distinguished by peculiarities of the ligament area and by the shell microstructure. One family, the Mytilidae, seems to be the more primitive and the longest lived, ranging perhaps from Ordovician to Recent. The other, the Myalinidae, seemingly originated in the Devonian but did not survive the close of the Jurassic period.

Eleven genera and three subgenera from the Late Paleozoic are considered in detail. Of these, four genera and two subgenera are here defined for the first time. Early in the progress of this work it became evident that some of the Early and Medial Paleozoic genera of pelecypods may belong to the Mytilacea. Genera of the Ambonychiidae Miller (emend. Ulrich), the Modiolopsidae Fischer, and the Modiomorphidae Miller closely resemble some of the Late Paleozoic forms herein classed as Mytilacea. A thorough revision of the early genera, beyond the scope of this study, is needed before the ancestral Mytilacea can be defined satisfactorily.

Genera in the Late Paleozoic forms are differentiated partly by external form and internal structures, including details in the placement of the muscles. The musculature was essentially like that of modern *Mytilus* and *Volsella*.

Seven species and varieties, four of them new, are recognized among the Mytilidae. It happens that the species within this family are closely similar in form all the way from the Late Paleozoic to the Recent, so that discrimination of individual species requires detailed analysis. The application of some of the elementary principles of statistics has shown that there are useful guide species within this family. Two genera within the family are recognized as new.

Thirty-three species and varieties, 15 of them new, are recognized in the Myalinidae. They are distributed among six genera and subgenera, of which four are new.

Taxonomic innovations are as follows:

New genera, species, and varieties described in this paper.

Mytilidae
  P. romytilus, n. gen.
    P. annosus anosus, n. sp., n. var.
    P. annosus senex, n. sp., n. var.
    P. priscus, n. sp.
    P. vetulus, n. sp.
  Volsellina, n. gen.

Myalinidae
  Myalina DeKoninck, emend.
    M. wyomingensis var. *thomasi*, n. var.
    M. petina, n. sp.
    M. miopetina, n. sp.
    M. pliopetina, n. sp.
    M. glossoidea, n. sp.
    M. arbala, n. sp.
    M. lepta, n. sp.
    M. copha, n. sp.
  Myalinella, n. subgen.
  Orthomyalina, n. subgen.
    O. slocomi var. *parvula*, n. var.
  Selenimyalina, n. gen.
    S. quadrata, n. sp.
    S. dotti, n. sp.
  Septimyalina, n. gen.
    S. burmai, n. sp.
    S. orbiculata, n. sp.
    S. scitula, n. sp.
    S. quadrangularis, n. sp.

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[1] Although I deplore the ridiculously large number of proposed categories for type specimens, the term topoparatype has particular usefulness. A paratype which is also a topotype is obviously more reliable than a paratype which comes from a locality and horizon different from the holotype.

The Myalinidae are much more highly specialized than the Mytilidae, and their ontogenies suggest that they were derived from the latter family. The myalinas constitute some of the best guide fossils among the pelecypods, and there are no other Paleozoic pelecypods that better illustrate consistent trends in evolution than do the members of this family. The progressive modifications in shape through the rock sequence are especially striking and are faithfully recapitulated in the ontogeny of the more specialized species in each phyletic line. The more conspicuous trends in form include changes in shell obliquity and the development of a rear wing. These trends are not peculiar to the Myalinidae but are noted also in the Mytilidae, Ambonychiidae, Pteriidae, and half a dozen more or less unrelated pelecypod families. The parallelism in development recalls homeomorphic trends in the ammonite suture, in the shell form of certain brachiopod stocks, graptolites, corals, and other groups of invertebrates. In the majority of species of Myalinidae, the shells become less oblique at the higher horizons; and the angle at the posterior end of the hinge becomes progressively smaller, until in the extreme cases a posterior wing, reminiscent of some of the Pteriidae, is formed.

At the outset of this work it was found that 32 specific and varietal names had been introduced for American Pennsylvanian and Permian mytiloids. They are indicated in the following list.

Pennsylvanian and Permian mytiloids reported from North America

Naiadites carbonarius Dawson
N. ohioensis Morningstar
Lithophaga subelliptica Sayre
Modiola subelliptica Meek
M. wyomingensis Lea
M. minor Lea
Myalina swallovi McChesney
M. aviculoides Meek and Hayden
M. copei Whitfield
M. recurvirostris Meek and Worthen
M. acutirostris Newell and Burma
M. cuneiformis Gurley
M. meeki Dunbar
M. perattenuata Meek and Worthen
M. orthonota Mather
M. recurvirostris var. *sinuosa* Morningstar
M. ampla Meek and Hayden
M. slocomi Sayre
M. meliniformis Meek and Worthen
M. exasperata Beede
M. sinuata Branson
M. subquadrata Shumard
M. deltoidea Gabb
M. kansasensis Shumard
M. apachesi Marcou
M. pernaformis Cox
M. shannoni Beede
M. bialata Beede
M. recta Shumard
M. girtyi Beede
Mytilus permianus Swallow
M. concavus Swallow

Of these I was able to secure type specimens for the first 20 species. Two of the species, *Modiola minor* and *Myalina exasperata,* are represented by such imperfect types that they can be identified in only a general way. Furthermore, the exact horizon and locality from which the type specimens came is unknown for either species. *M. recurvirostris* is placed in the syonomymy of *M. wyomingensis.* Two additional species, for which the types are not available, *M. subquadrata* Shumard and *M. sinuata* Branson, are more or less securely established on topotype specimens. *M. deltoidea* Gabb is placed in the syonoymy of *M. subquadrata.* The last nine names in the list should be suppressed because the type specimens are either lost or destroyed, the original horizon and locality are not precisely known, and the species were so inadequately described as to be unrecognizable.

The field relations suggest that the Late Paleozoic Mytilacea had habits and habitats similar to those of modern Mytilacea.

It can be demonstrated that the ligament system of such pelecypods as *Perna* and *Arca* are fundamentally different. It seems improper to use Dall's term *multivincular* to describe both types of ligament. Therefore, a new term, *duplivincular,* is herein proposed for the peculiar ligament of *Arca,* Myalinidae, Ambonychiidae, Pseudaviculopectinidae, and many of the Paleozoic genera of so-called Pteriidae.

COLLECTIONS

Practically all of the great American collections of Late Paleozoic pelecypods have been made available for this investigation. The vast collections of the Kansas and Nebraska Geological Surveys, Yale Peabody Museum, and the Texas Bureau of Economic Geology, numbering some thousands of specimens, represent a large proportion of the fossiliferous horizons in the Mid-Continent region. Choice specimens were generously loaned by the Illinois Geological Survey, the U.S. National Museum, Walker Museum at the University of Chicago, and the University of Iowa. Small collections were donated or loaned to me by many individuals. In addition, some hundreds of the Pennsylvanian specimens were collected by me. In the aggregate, the material covered in this study is unquestionably the most extensive collection of Late Paleozoic Mytilacea ever assembled for study. My own field experience, however, leads me to believe that these collections do not faithfully indicate the actual distribution of Mytilacea in the Pennsylvanian and Permian rocks. The collections are very sparse and otherwise unsatisfactory from the early Pennsylvanian and from the later Permian rocks. The Mytilacea are so ubiquitous that I am convinced that every marine fauna in the American Pennsylvanian and Permian contains, at least locally, some of these shells. Therefore, the chief gaps in the record are attributed to incomplete collections, and, if one had the opportunity to examine all of the fossiliferous horizons not now represented in our collections, I am sure that the record of evolution in Late Paleozoic Mytilacea could be made singularly complete.

DISTRIBUTION

Lithologic associations.—Only too seldom have paleontologists recorded the type of rock matrix from which their fossils were derived. The matrix is, in a limited way, indicative of the bottom ecology at the burial site. It is more or less obvious to anyone who has examined shell heaps along the sea shore that the shells may become buried under conditions quite unlike the life habitat of the animals in question. However, fossil bivalve shells may reveal transportation after death through the separation of the valves. The valves of dead Mytilacea become separated almost immediately because there are no interlocking devices capable of holding the valves in position after decomposition of the ligament. In this work I have tried to record the field occurrences of each species. Where the valves are found in apposition it is reasonably certain that the site of burial was the same as the life environment. Under this condition an examination of the rock matrix and associated fossils may furnish clues regarding the life environment of the Mytilacea. Those valves which are fragmentary and separated may have been transported by waves and currents for a considerable distance before burial. Careful consideration of the available evidence indicates that the Late Paleozoic Mytilacea favored the shallow-water, nearshore habitats like those preferred by the majority of modern Mytilacea.

Stratigraphic distribution.—A single chart showing the stratigraphic range of different species of Mytilacea in each of the various provinces is not feasible. Therefore, in order to indicate the general sequence of stratigraphic divisions in the main geologic provinces, the following correlation tables and synthetic range chart have been compiled from various sources, representing the best-established correlations now available.

TABLE 1.—*Principal Divisions of the American Marine Permian Rocks*

West Texas		North Texas	Northern Mid-Continent	Colorado Plateau	Middle Rockies	Russia
Ochoan		Absent	Absent	Absent	Absent	Tartarian Kazanian Kungurian
Guadalupian	Capitan	Quartermaster Whitehorse	Quartermaster Day Creek Whitehorse			
	Word	Absent?	Absent?		Phosphoria	
Leonardian		El Reno Clear Fork Lueders Clyde Belle Plains	El Reno Enid Sumner	Kaibab Toroweap Coconino Supai	Absent?	Artinskian
Wolfcampian		Admiral Putnam Moran Pueblo	Chase Council Grove Admire	Bird Springs	Upper Wells?	Sakmarian

TABLE 2.—*Principal Divisions of the American Pennsylvanian Rocks*

North Texas		Oklahoma	Northern Mid-Continent		Illinois	Allegheny Plateau
Ciscoan	Thrifty Graham	Wabaunsee Shawnee Nelagoney	Virgilian	Wabaunsee Shawnee Douglas	Absent	Monongahela
Canyonian	Caddo Creek Brad Graford Whitt	Ochelata	Missourian	Pedee Lansing Kansas City Bronson Bourbon	Merom	Conemaugh
		Skiatook			Embarass LaSalle Macoupin Shoal Creek Trivoli	
Strawnian	Lone Camp	Holdenville Wewoka Wetumka	Desmoinesian	Marmaton	Gimlet Sparland Brereton St. David Summum	
	Millsap Lake	Calvin Senora Stuart Thurman Boggy Savanna McAlester Hartshorne		Cherokee	Liverpool Greenbush Wiley Seahorne Delong Seville	Allegheny
Lampasan	Smithwick Big Saline	Atoka Barnett Hill	Absent	Absent	Pope Creek Tarter	Pottsville
Morrowan	Marble Falls	Morrow			Babylon	
Absent		Pushmataha			Wayside	

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Especial thanks are due Dr. Raymond C. Moore, University of Kansas; Dr. G. E. Condra, Nebraska Geological Survey; Dr. Carl O. Dunbar, Yale University; Dr. Fred B. Plummer, University of Texas; Dr. J. Marvin Weller, Illinois Geological Survey; Dr. Carey Croneis, University of Chicago; Dr. A. K. Miller, University of Iowa; and Dr. G. Arthur Cooper, U.S. National Museum. These men have placed the great collections under their care at my disposal for purposes of this study. Nearly one hundred other individuals have been of great service in contributing select specimens for study, in granting access to type specimens, and otherwise materially aiding in the furtherance of the study. I have tried to credit these men, many of them for-

TABLE 3.—*Known Stratigraphic Range of Late Paleozoic Mytilacea*[1]

STRATIGRAPHIC RANGE	Guadalupian	Leonardian	Wolfcampian	Virgilian	Missourian	Desmoinesian	Lampasan	Morrowan
Myalina (Myalinella) acutirostris Newell and Burma	* *							
Myalina (Myalina) wyomingensis thomasi, n. var.	* *							
Myalina (Myalina) sinuata Branson	* *							
Myalina (Myalina) aviculoides Meek and Hayden			* *					
Promytilus vetulus, n. sp.			* * * *					
Myalina (Myalina) copei Whitfield			* * * *					
Myalina (Myalina) pliopetina, n. sp.			* * * *					
Septimyalina burmai, n. sp.			* * * *					
Myalina (Orthomyalina) subquadrata Shumard			* *	* *				
Myalina (Myalina) petina, n. sp.				* *				
Myalina (Myalina) miopetina, n. sp.				* *				
Myalina (Orthomyalina) slocomi parvula, n. var.				* *				
Promytilus priscus, n. sp.				* * * *				
Myalina (Myalina) glossoidea, n. sp.				*	*			
Promytilus annosus annosus, n. var.					* *			
Selenimyalina quadrata, n. sp.					* *			
Promytilus annosus senex, n. var.					* *			
Lithophaga subelliptica Sayre					* *			
Promytilus swallovi McChesney					* *			
Myalina (Myalina) arbala, n. sp.					* *			
Septimyalina orbiculata, n. sp.					* *			
Selinimyalina meliniformis Meek and Worthen					? * * *	* ?		
Myalina (Orthomyalina) slocomi Sayre				* *	* * * *	* *		
Myalina (Orthomyalina) ampla Meek and Hayden					* * * *	* ?		
Myalina (Myalinella) meeki Dunbar		* *	* * * *	* * * *	* * * *	* ?		
Septimyalina scitula, n. sp.			* * * *	* * * *	* * * *	*		
Selenimyalina dotti, n. sp.						*		
Myalina (Myalina) wyomingensis Lea			* * * *	* * * *	* * * *	* *		
Myalina (Myalina) lepta, n. sp.						*		
Septimyalina quadrangularis, n. sp.						*		
Myalina (Myalinella) cuneiformis, Gabb						*		
Septimyalina sinuosa (Morningstar)						* * * *		
Myalina (Myalina) copha, n. sp.							*	
Volsellina subelliptica (Meek)				* * * *	* * * *	* * * *	* * * *	
Septimyalina perattenuata (Meek)				* * * *	* * * *	* * * *	* * * *	
Septimyalina orthonota (Mather)								* * * *
Naiadites ohioensis Morningstar								* * * *
Naiadites carbonarius Dawson							* * * *	* * * *

[1] Extreme known range without regard to gaps in record or geographic distribution.

eign colleagues, at appropriate places in the text. If I have neglected to acknowledge specific aid, the oversight is unintentional.

HABITS AND HABITATS

Mytilidae.—Considerable is known about the bionomics of living Mytilidae. Species of *Mytilus*, particularly, have been intensively studied and a large amount of information has been summarized in an excellent monograph by White (1937), from which much of the following generalizations are taken.

Mytilus edulis Linnaeus, the genotype of *Mytilus*, is a cosmopolitan contemporary species of the littoral and shallow neritic zones. Specimens have been found in deeper waters but are smaller and less abundant than normal. The preferred habitat is from the high water mark to depths of only a few fathoms. Although there is a slight ventral gape of the valves for extrusion of the byssus between the closed margins, an extension of the periostracum around the edge, together with manipulation of the mantle margins within the shell, make it possible for the animal to seal itself hermetically within the valves. These "mussels" can live out of water for a long time if the shell is tightly closed, because a quantity of sea water is retained in the pallial cavity. In fact, the animal can live longer if the exterior of the shell remains dry, because periodic wetting of the shell causes the animal to open the valves and the contained sea water then will escape. *Mytilus* under observation has lived normally for over a month in sterile water, and individuals have been found alive after twenty-four days in the hot sun. The adductor muscles still show movements after forty days of anaerobic conditions. It is seen, then, that *Mytilus edulis* is well suited for life under the difficult conditions of the littoral zone.

This species is tolerant of great variations in salinity and occurs in salt, brackish, and in nearly fresh water. The animal can respire normally in water varying from the average salinity up to an admixture of 30 per cent fresh water or with an increase of salinity resulting from the addition of from 5 to 10 per cent of water that has been concentrated to a salinity of 7 per cent. However, addition of fresh water to 60 per cent, or an increase in salinity to 35 per cent of added water, which has been concentrated to 7 per cent salinity, kills the animal quickly.

Variations in salinity, particularly freshening of the water, produce changes in the animal that are shown in shell characters. Decrease below normal salinity of the water produces a corresponding stunting of growth. Studies in the Kaiser Wilhelm canal and in the Baltic, where salinity decreases from west to east, show that there is a progressive decrease in the size of the mussels. The shells seem also to become thinner and more fragile in brackish water.

Adults are always attached by the byssus, and the living animals are consequently not found on sandy shores unless there is some adequate supporting structure present, such as the shells of other mollusks. Empty shells of *Mytilus* very commonly are concentrated on sandy beaches by storm waves, so that the environment of burial is not necessarily the same as the life environment. The mussel is markedly gregarious, so that, where present at all, it usually is abundant; and the surface of the ground at low tide commonly is completely covered with them, no free space being left for other sessile benthos. It has been computed that the density of individuals in a community may be as great as 16,000 to the square foot, but of course this number is exceptional.

Although normally attached by the byssus, the animal is capable of locomotion, sometimes propelling itself by the foot in a way similar to that of the snail. Young individuals crawl with the anterior end foremost, but adults reverse the direction of movement. Mussels have been observed to climb up a perpendicular glass by means of the suctorial tip of the foot, lifting themselves on the foot and then making a byssal thread fast. A second thread is attached above the first, after which the latter may be broken off by a sudden jerk of the foot. When the animal desires more or less permanent anchorage several threads are attached to the substratum, radiating out in various directions. A considerable amount of limited movement is accomplished by means of the byssal muscles, which can, by their contraction and relaxation, vary the tension on various byssal threads. In this way jerky movements can be produced within the limits of the byssus. This is the way in which mussels remain covered for a longer period by receding water, being able to lower themselves somewhat into the water by the byssus.

Experiments indicate that *Mytilus edulis* thrives best in the presence of medium sunlight and a temperature range between 10° and 20° C., but they can retain ordinary activity at temperatures between 0° and 26° C.

The animal is microphagous, filtering detrital material from the sea water. It has been estimated that ten gallons of water pass through the gills in twenty-four hours. Investigations indicate that live phytoplankton does not represent nearly as important food for pelecypods as detritus.

The annelid worm, *Polydora ciliata*, commonly infests oysters and mussels, living in burrows drilled into the shell substance of the pelecypod. The worm enters through a hole the size of a pin and makes a U-shaped burrow in the shell. It does not attack the soft tissues of the animal, but sometimes it does damage to the pelecypod by boring completely through the shell, causing the growth of pearly excrescences on the interior of the shell next to the mantle. Paleozoic Mytilacea were infested by similar boring annelids (pl. 8, figs. 4, 5).

The meroplanktonic larvae of pelecypods permit relatively wide distribution of many species. The larvae of the majority of forms, however, are so sensitive to the physical and biological environment and enjoy such a short free-swimming period that there are innumerable barriers to migration during the larval stage.

Recently it has been shown by Nelson (1928) that *Mytilus edulis* is exceptional, perhaps unique, among pelecypods in adopting the pelagic habit during the early dissoconch stage. Shells up to 941 microns in length have been found floating. According to Nelson (1928, pp. 183-185)

> the presence of well developed dissoconchs floating freely in the water at once raises the question of the means by which this is effected in the absence of the swimming organ or velum of the prodissoconch. When brought to the laboratory for examination . . . a large bubble was found to occupy the posterior part of the pallial cavity, its buoyancy

causing the young bivalve to hang suspended in the water umbones downward, with the posteroventral margin of the valves turned upward.

Some young mussels maintain themselves at the surface through means other than the gas secretion employed by larvae at a depth. It was observed that once in contact with a solid object, such as the wall of the chamber, a rock, or a fragment of sea weed, the mussels exhibited a marked negative geotropism and climbed straight upward until the surface was reached. Here the distal one-third to one-tenth of the foot was extended to the surface film, and with a quick contraction of the foot, aided apparently by contraction also of the pedal retractor muscles, the ventral margins of the mantle were brought into contact with the surface film. While lying with the entire ventral margin of the body in contact with the surface film the byssus gland in a few seconds secreted onto the surface film a small holdfast similar to that which is laid down on rock or piling for the attachment of each byssus thread. A thread 1 to 2 mm long serves to support the young mussel from this float and with foot withdrawn it may hang suspended indefinitely . . . . The 'float' is not a buoyant structure, since when pushed beneath the surface it rapidly sinks. It maintains its position in the surface film, supporting mussels up to 4 mm in length, solely through surface tension.

Other individuals were observed in which the young mussel supports itself solely by the end of the foot in the surface film, recalling the familiar habit of pond snails of hanging from the entire foot spread out in the surface film. Another, but less common, mode of suspension from the surface consists in extending the tops of the tentacles of the incurrent siphon into the surface film and hanging from there.

Of the known genera of marine pelecypods, *Mytilus edulis* and *Teredo navalis* alone are circumpolar in their distribution over the shores of the northern hemisphere. General adaptability to changing conditions and the power to resist adverse surroundings, together with relatively low spawning temperatures, have aided these two forms in attaining their present wide distribution. Transportation through attachment to vessels or to other floating wood has likewise aided in their dispersal, being for *Teredo* the only means by which any great distance could be covered. In the case of *Mytilus edulis,* however, the ability to bridge the period of metamorphosis while remaining pelagic must have been an important factor in securing the wide dispersal which this mollusk now enjoys; as well as a great aid in bringing to a suitable place of attachment a fair proportion of the larvae produced each season. The largest of the pelagic dissoconchs found in Frenchman Bay was fully a month old, during which time it must have been transported over long distances by the tide.

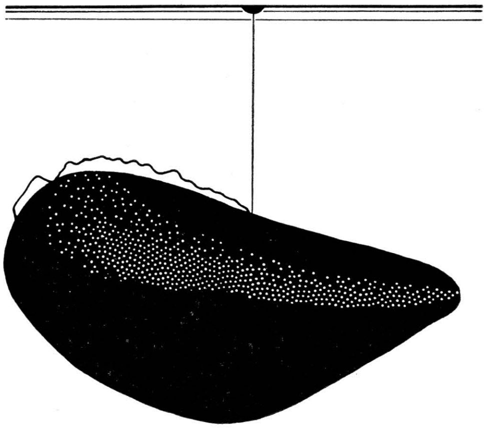


FIGURE 1.—*Mytilus edulis,* early dissoconch (X60), showing one method of suspension from surface film of water by byssal thread.

The genus *Lithophaga* Bolten (*Lithodomus* Cuvier) employs the byssal mode of fixation during the early ontogeny; but at maturity the animal, which is found only in regions of calcareous rocks, bores holes in the rocks by the aid of the acid secretion of glands situated in the anterodorsal and posterodorsal regions of the mantle (Pelseneer, 1906, p. 252). There are a number of citations in literature to Late Paleozoic species of *Lithophaga.* However, I know of no examples of borings in limestone produced by Late Paleozoic pelecypods. A modioloid rock-borer, *Coralidomus concentricus,* from the Cincinnatian rocks of Ohio, was described by Whitfield; but it is not certain that this form belongs to the Mytilacea.

Myalinidae.—Like the Mytilidae, the myalinas were gregarious; and, judging from the musculature, they were byssate for at least a part of their life span. The more specialized myalinas, however, unlike Mytilidae, are very thick-shelled and during life may have had very little need for a byssus. Only relatively strong waves and currents would be able to move some of these shells, and it is doubtful that these animals were sufficiently powerful to drag their shells about after maturity was reached.

The shells of myalinas are found in various sediments ranging from bituminous or argillaceous shales to sandstones. In all of these rocks, shells with both valves in apposition are common, indicating little or no transportation after death. A few species are restricted to, or are more common in, certain kinds of rock. *Naiadites* seems to have preferred the brackish or fresh-water habitat, whereas *Myalinella meeki* is found associated with various biota that suggest quite a range in salinity.

It is doubtful that the larger myalinas were very active, because their heavy shells commonly are encrusted with lamellar deposits of calcium carbonate, suggestive of algal deposits, and the shells commonly are perforated by the U-shaped burrows of annelid worms. Furthermore, the living animal was in some instances very small compared with the size of its shell.

Judging from the commonness of bivalve specimens of Myalinidae having the two valves in apposition, it seems probable that the myalinas preferred relatively quiet water. Separated valves are found, but these seldom show evidences of markedly turbulent water. Since deposits of the littoral zone rarely are preserved in the fossil record, except perhaps in the paralic swamps, there is little to indicate whether or not many of the myalinas favored areas that frequently were exposed to the atmosphere. The Naiadites, however, so characteristic of the carbonaceous shales of the early Pennsylvanian in eastern North America and Europe, probably led an existence much like some *Mytilus edulis,* advancing far inland at the estuaries, attaching themselves to salt marsh vegetation. The faunal associates of *Naiadites* suggest that species of this genus did not normally favor the more typically marine environment.

The more strikingly gregarious myalinas, such as *Orthomyalina, Myalina,* and *Septimyalina,* in some instances occur crowded in a stratum to the near exclusion of other fossils. Perhaps the crowding among the myalinas made some localities practically uninhabitable for other shelled benthos.

The relatively pure limestones in the Pennsylvanian and Permian do not commonly contain representatives of the Myalinidae or Mytilidae, and these seldom are found in direct association with fusulinids. The supposition is that the pure limestones and the majority of other fusulinid-bearing rocks were deposited at depths too great, or distances from the shore too great, to be favored by the Mytilacea. Students of the Pennsylvanian apparently are agreed that the bulk of the deposits in the Mid-Continent region were deposited in water less than 50 fathoms in depth; therefore, it is highly probable that the myalinas and mytiloids preferred even shallower water of the near-shore environment.

There is much to indicate that some of the myalinas were among the first immigrants into the Mid-Continent region, during the frequent incursions of the sea, and among the last marine invertebrates to be destroyed by withdrawal of the sea. It has been shown (Moore, 1936, pp. 20-38) that the Pennsylvanian rocks are characterized by a great number of cyclic repetitions of marine and nonmarine rocks, indicative of numerous minor oscillations of the sea. Very commonly, the myalinas are most numerous shortly below and just above plant-bearing shales and coal beds, in deposits which presumably were laid down closer to the shore than some of the fusulinid-bearing, dominantly calcareous beds further removed, stratigraphically, from the nonmarine beds. Experience shows that members of the Mytilacea are common only in beds 0.2, 0.7, and 0.8 of the "ideal" cyclothem (Moore, 1936, pp. 24-25).

Considering all available evidence, it seems probable that many of the Paleozoic Mytilacea lived under conditions similar to those favored by modern *Mytilus* and *Volsella,* viz., the shallow, turbid waters of the shore zone, tolerating an unusually great amount of variation in the salinity of the water.

EVOLUTIONARY TRENDS

Hardly any group of fossil organisms illustrates parallel trends in evolution any more strikingly than some of the pelecypods. Progressive characters, i.e., characters in which the direction of evolution is in some degree inevitable and, therefore, likely to be repeated in parallel lines along a number of separate lines of descent, are well known in graptolites, corals, cephalopods, brachiopods, foraminifers, and mammals, and can be demonstrated in many other animal groups. Homeomorphy is so common in certain tribes as to suggest that there is a marked "preference" for certain kinds of variation. Certainly the fossil record is replete with illustrations of evolution that *seem* to be unidirectional as regards specific structures. Some progressive characters, such as increase in maximum size of individuals, and increase in specialization, whether or not obviously adaptive, have affected all sorts of animals during their history. There are a few kinds of progressive modifications that have affected so many tribes of pelecypods as to be reasonably regarded as standard evolutionary trends. Some of these trends are to be anticipated in many of the pelecypod stocks. The classification of pelecypods most generally employed by modern zoologists is Pelseneer's, which was based fundamentally on gill structure. The majority of students of fossil pelecypods, and a few of the zoologists now regard gill characters as belonging to the category of progressive characters. Thus Pelseneer's groups are merely grades of gill development, not groups of common ancestry. Douvillé has developed a classification based on the idea of adaptive radiation, a concept which has proved so successful in the taxonomy of the vertebrates. Parallel development due to similar adaptation is too well understood to require further attention here. It should be noted, however, that there are very many examples of parallelism, among the invertebrates, that can as readily be ascribed to a tendency for directed variation as to similarity in adaptation.

In addition to gill modifications and changes in the construction of the ligament described later, there are trends in form and shell structure that have affected many unrelated stocks of pelecypods. Those trends that are thus far recognized in the various tribes of Mytilacea are discussed below.

Size.—Progressive increase in size of adults is a common trend in all kinds of animals, although it is by no means certain that this trend applies to all genera or families of animals. In the Late Paleozoic

Mytilacea, increase in size is admirably exemplified by species of *Myalina* s. s. The oldest representatives of the genus, that I have seen, occur near the middle of the Mississippian rocks (St. Louis limestone, Viséan limestone). The largest of these specimens measure less than 70 mm in length. Specimens of *Myalina* from the Pennsylvanian are commonly somewhat larger, and Permian individuals having a length of 120 mm are common. Throughout this range, normally small adults of separate species are also found. Of course, progressive increase in size in any race of fossil animals is not easy to demonstrate without fairly complete collections. Ecologic variation in size should also be taken fully into account. The progressive increase in size of individuals in the collections under consideration is so marked that it can reasonably be attributed to evolution.

Obliquity.—Compared with the hinge axis, the body of the shell in all primative Pectinacea, Pteriacea, and Mytilacea, as well as certain other pelecypods, is markedly oblique. That is, a line of symmetry drawn through the umbo forms an acute angle with the hinge. This condition I have called prosocline. During the evolution of several of the families, as shown by the fossil sequence, as well as ontogenies, there is a tendency for the shell to assume a more upright form so that the axis of the shell body is more or less normal to the hinge (acline). The more specialized species show a continuation of this trend to a condition in which the ventral part of the shell is carried forward and the mature part of the shell assumes a backward obliquity (opisthocline). This trend is well shown in the Myalinidae and in some of the aviculopectens (Newell, 1938, p. 17). The obliquity is best expressed in angular degrees (angle α) as measured between the umbonal ridge at a *mature* stage and the dorsal margin. In the more specialized species the umbonal ridge is markedly arcuate, with a forward concavity, and the ontogenetic increase in the angle is very striking.

Posterodorsal extremity.—The tendency to develop a rear projection of the shell at the hinge margin is very marked in Pteriacea and Pectinacea and is known to be a mark of specialization. Primative species, as shown by both the ontogenies and the fossil record, invariably lack the posterior auricle. Two genera of the Myalinidae (*Myalina, Septimyalina*) independently developed rear auricles to a marked degree, giving them a pterioid aspect. In primitive species, the rear margin of the shell intersects the dorsal margin at an obtuse and somewhat indefinite angle (angle β). Progressive reduction in this angle is accompanied by increasing prominence of a posterodorsal salient. When the angle becomes acute a well defined auricle is formed. Although posterior auricles are not known in all of the genera of Paleozoic Mytilacea, the majority of them show a distinct tendency for progressive reduction in the value of angle β.

Anterior lobe.—Primitive Mytilacea have distinctly a "modioloid" expression. That is, in addition to possessing the general proportions of *"Modiolus" (Volsella),* they are characterized by an anterodorsal salient, called the anterior lobe, in front of and below the beaks. Reduction of this lobe, with a tendency thereby for the beaks to become progressively more terminal, is distinctly a mark of specialization. *Mytilus* passes through a *Volsella* stage in its ontogeny and was, presumably, derived from the latter through reduction in the anterior lobe. Among the Myalinidae, the genus *Myalina* shows this trend quite strikingly. Primitive myalinas, such as *M. wyomingensis,* are quite lobate, almost modioloid, whereas specialized forms, such as *M. copei* and the species of *Orthomyalina,* have a very inconspicuous anterior lobe.

Loss of symmetry.—The least specialized among living pelecypods show a high order of bilateral symmetry (equivalve). Adaptation to a pleurothetic existence has, apparently, been responsible for loss of the primitive symmetry in a number of tribes of pelecypods, such as the Ostracea, Pteriacea, Pectinacea, etc. The majority of Mytilacea are essentially bilaterally symmetrical and show no preference for one side over the other when they assume an orientation other than the vertical one. Under crowded conditions, living *Mytilus* seems to tolerate any orientation, even commonly suspending themselves by the byssus, in an inverted position, beneath overhanging ledges of rock. Primitive Myalinidae look very much like *Mytilus*, being distinguished chiefly by differences in shell composition and microstructure, which are readily observed in all but poorly preserved material. However, even the most primitive known Myalinas are slightly asymmetrical, having a slightly less convex right valve than left valve. In the more specialized and geologically younger forms the difference in convexity between the two valves is quite marked; and, in some instances, the valves become markedly discordant, that is, the right valve fits slightly within the margin of the left valve. Accompanying this trend, the anterior lobe of the right valve becomes obsolescent more rapidly than that of the left valve; so that there are several species of Myalinidae in which there is little or no distinguishable lobation of the right valve, while a small lobe is still apparent in the left valve. In all of these shells that show marked asymmetry of the two valves, there is a tendency for the beak of the left valve to be especially prominent, so that it overhangs the beak of the opposite valve.

There are no living analogues of the Myalinidae; so it cannot be proved, conclusively, that these animals normally lie on the right valve when at rest. However, a clue may be found in the primitive Pectinacea, which certainly lie with the right valve undermost (Newell, 1938, pp. 18-20). In the pectens, as in the myalinas, there is a very marked tendency for the prismatic structure to be obscure or lost in the left valve, while the primitive prismatic condition remains unmodified in the right valve. I have supposed that the relative conservatism of right valves of Pectinacea (idem, pp. 20-21) is due to the greater stability of the environmental influence, lying, as they often do, with the right valve partly buried in the mud. Also, it may be stressed that right valves of species of Myalinidae are less varied than left valves, so that there are many instances in which the right valves of two distinct species can scarcely be distinguished from each other. By analogy with the pectens, we may suppose that the peculiarities of the right valve in the myalinas were brought about by the assumption of a life position in which the right valve was undermost.

Orientation of muscles.—Cursory examination of figure 6 will reveal that the posterior muscle system in several genera of the Mytilacea is differently placed in respect to the rear extremity of the hinge axis. In all of these shells there is a tendency for the anterior and posterior adductors to assume a position in line with the greatest linear dimension of the shell. For instance, the greatest dimension of the shell in a primitive *Myalina,* such as *M. goldfussiana* (fig. 6E), is measured between the beaks and the posterior margin of the shell. In any mytiloid shell having this general form the posterior muscle system is placed high in the shell not far below the terminus of the hinge. On the other hand, in markedly acline shells, such as those shown in figure 6B, C, G, the greatest dimension of the shell is measured from the ventral margin to the dorsal margin of the shell; and the adductors lie in a line that is nearly dorsoventral in orientation. It is obvious that there is a migration of the posterior muscles toward the ventral part of the shell as the shell itself gradually changes from the prosocline to the acline or opisthocline grade of

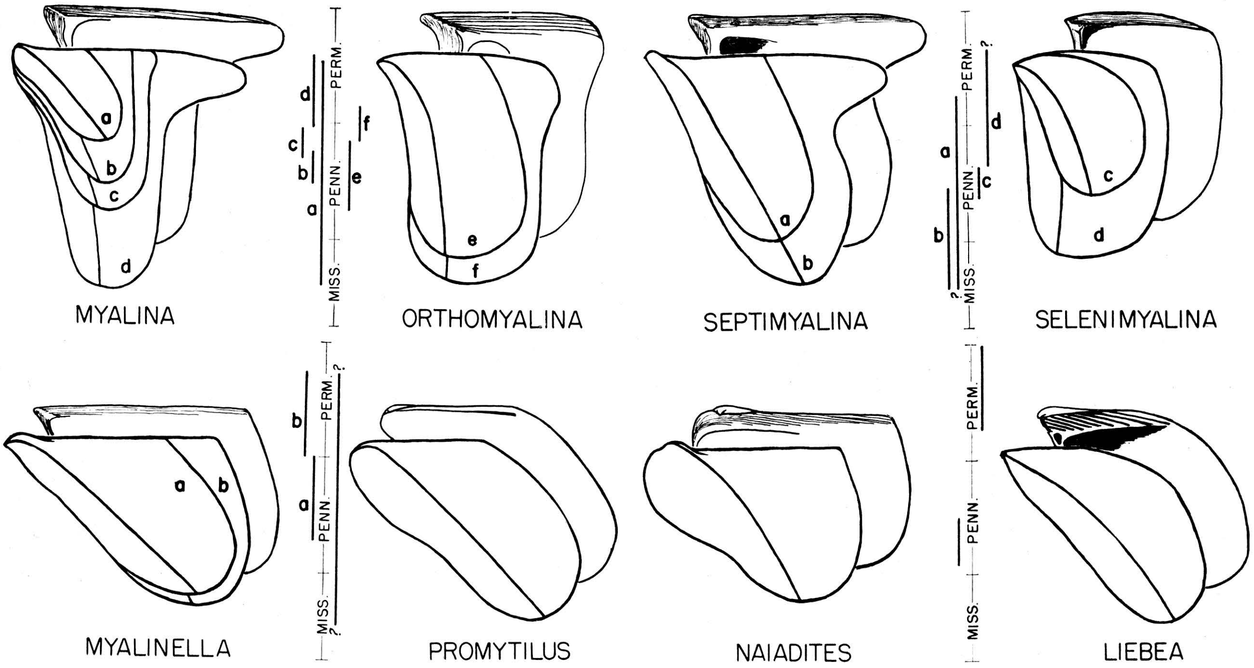


FIGURE 2.—Time value of form trends in some Paleozoic genera and subgenera of Mytilacea. The more striking form stages in the phylogeny are superposed in composite diagrams. The known stratigraphic range of each stage is indicated in the bar scale below each diagram. The three spaces for the Mississippian are: Kinderhookian, Osage-Meramecian, Chesterian; four spaces for the Pennsylvanian are: pre-Desmoinesian, Desmoinesian, Missourian, and Virgilian; four spaces for the Permian represent: Wolfcampian, Leonardian, Guadalupian, and Ochoan. In a few instances a given form stage is represented by more than one species.

obliquity. Concurrently with the migration of the posterior muscles there is indicated also a tendency for the anterior byssal retractor insertions to migrate in a posteroventral direction. These changes in the placement of the muscles apparently are adaptive in the sense that they tend to maintain mechanical efficiency during marked changes in shell form.

SHELL MORPHOLOGY

GLOSSARY OF SHELL TERMS

It is desirable to define briefly some of the terms employed in the text. The following list is arranged in alphabetical order:

Adductor impressions.—In the majority of Mytilacea there are two adductor muscles, an anterior and a posterior adductor, both of which cause distinctive marks at their insertions in the shell. The anterior adductor, always very small, or even absent, is situated beneath the beaks. Under the opposite end of the hinge occurs a large bifid muscle impression produced by the large posterior adductor, the posterior byssal, and pedal retractors. The ventral part of the bifid impression is produced by the posterior adductor.

Angle α.—The angle between the umbonal ridge and the cardinal margin is designated by the conventional Greek letter *α*. During the ontogeny of an individual, and during the phylogeny of some of the mytiloids, as well as other kinds of pelecypods, there is a notable increase in the value of the angle *α*. In view of the fact that the umbonal ridge flattens out somewhat at maturity, a precise measurement of this angle seldom can be obtained; nor is a high order of accuracy needed for useful results.

Angle β.—The angle between the posterior margin and the cardinal margin, neglecting of course any irregularities that obviously have no phylogentic significance, is designated by the Greek letter *β*. In juveniles and primitive species this angle is relatively obtuse and often ill defined. During ontogenetic growth or phylogenetic change the angle decreases progressively until it measures in some forms considerably less than 90°.

Anisomyarian.—The anterior adductor is highly atrophied in the majority of Mytilacea. In some species of living *Mytilus,* as well as species in certain other genera, the anterior adductor completely disappears at maturity. The progressive reduction of the anterior adductor has well recognized taxonomic significance, but no great weight is attached to the final disappearance of the adductor in species that otherwise are similar to forms retaining a small anterior adductor at maturity.

Auricle.—Primitive mytiloids are not auriculate, but some specialized species, through posterior extension of the hinge, develop a salient that is called a posterior auricle, or sometimes a "wing." Such species have a pronounced homeomorphic resemblance to certain pterioids. Anterior projections are not sufficiently conspicuous to be called auricles, although the term "anterior lobe" is commonly used for an anteroventral emargination of the border in some forms like *Volsella.*

Byssal sinus.—The anteroventral margin of practically all mytiloids is more or less concave at an intermediate point, as viewed laterally. In life, the conchiolinous strands of the byssus extend between the slightly gaping margins of the valves near the middle of the sinus. It is convenient to refer to this indentation as the byssal sinus.

Byssal retractors.—Several muscles are attached to the byssal gland at the proximal end of the byssus. They serve to control the orientation and shell movements while anchored by the byssus. A series of insertions occur on the shell just dorsal to the posterior adductor impression and, together with the still more dorsally placed pedal retractor scar, form the posterodorsal prong of the bifid muscle impression, commonly called the "posterior adductor". An anterior byssal retractor muscle is inserted slightly above and behind the anterior adductor. In many Paleozoic forms, two scars occur at the position of the anterior byssal retractor; so, presumably, the muscle was divided in some instances into two parts where it joined the shell.

Cardinal area.—In the myalinas, as in the arcas, pterias, and some other pelecypods, two flat areas diverge upward from the hinge axis of the two valves. The flattened area of each valve is commonly called a cardinal area. In the above-named groups the cardinal area essentially coincides with the surface occupied by the ligament, in which case the term ligament area is synonymous with cardinal area. The majority of mytiloids, however, do not have cardinal areas.

Cardinal margin.—Dorsal edge of the valves. Since the dorsal margin lies above the hinge axis and does not coincide with it in some pelecypods, such as the myalinas, the two terms are not synonymous. In such instances the term hinge margin is ambiguous.

Convexity.—Because single valves are more common than bivalved specimens, it is convenient to use this term for the maximum convexity of a single valve, measured from the plane of commissure to the outer surface of the shell. In many instances, two valves of a single individual may have quite different convexities (inequivalve), or one valve may fit inside the margin of the other (discordancy); so that where measurements of both valves in apposition are made, such measurements may not be directly comparable to measurements of individual valves.

Discordancy.—Many mytiloids are nearly equivalve, but in some of the more specialized myalinas the right valve is somewhat smaller at the margin than the left. Such a discrepency in the shell margins is called discordancy.

Gill suspensories.—Thick-shelled myalinas commonly possess a linear series of fifteen or twenty muscle impressions extending in a flattened arc from the rear anterior byssal retractor to the front margin of the posterior adductor. Although such muscle pits are not visible in *Volsella* or *Mytilus,* inspection of anatomical structures in these genera reveals that the gills are suspended from the mantle at exactly this position. Presumably the pits alluded to in the myalinas represent the insertion points of small muscle strands that supported the gills.

Greatest dimension.—Although elongated, the majority of mytiloids are markedly oblique in form, so that the greatest linear dimension is neither the length nor height. Measured from the umbones to the most distant point on the shell margin, this dimension is one of the most useful in describing mytiloids. For want of a better term it will be called the greatest dimension.

Growth lines.—It is desirable to distinguish between regular concentric ornamentation and the irregular, less significant lines, on the shell, produced by increments of growth. Ornamentation in the ordinary sense does not occur in Late Paleozoic mytiloids, so there is not much occasion to stress concentric markings on the shell.

Growth lamellae.—It is common in pelecypods, particularly mature individuals, for the mantle to withdraw from the shell margin at successive intervals before secreting new shell deposits. The result is likely to be the formation of imbricating shell lamellae that produce a relatively roughened surface where they are exposed. An important generalization for the myalinas is that right valves are almost invariably smoother than left valves. This difference probably has its origin in the seeming fact that the majority of myalinas, perhaps all of them, lie on the right valve when at rest.

Height.—Normally the length of a pelecypod is measured along a line drawn through the two adductor muscles, and the height is measured along another line at right angles to it. The animal of the mytiloids has undergone considerable torsion, however, from the primitive condition. In order to use shell terminology that is reasonably consistent, it is preferable to measure the length parallel with the hinge axis and the height at right angles to it.

Hinge axis.—The axis of rotation of the two valves is called the hinge axis. Naturally, the hinge axis is invariably a straight line. However, since the axis occurs within the substance of the ligament, and since the ligament is relatively short in some pelecypods, the exact position of the hinge axis is not always easy to locate in fossil specimens.

Hinge teeth and sockets.—Teeth and sockets are present in many kinds of Mytilacea. Generally, the dentition occurs at the front of the hinge below the beaks. On the assumption that the dentition was derived from primitive surface ornamentation of the valves, such teeth have been classed as dysodont. Ontogeny of *Mytilus edulis* and other species, which are normally unornamented, does not indicate the postulated origin of these teeth. Some species of *Mytilus* and *Volsella* become edentulous at maturity, but presumably all possess teeth at some stage in the ontogeny. The majority of Myalinidae possess one tooth beneath the beak of the right valve, and a corresponding socket in the left valve. The trace of the tooth and socket during growth produces a more or less conspicuous ridge and furrow at the front edge of the cardinal area of mature individuals. The ridge and furrow do not interlock, however, except at their postero-ventral extremities.

Hypostracum.—Muscle tissues secrete calcareous material at their insertion in the shell. Generally, this deposit, the hypostracum, is fibrous, the fibers being elongated normal to the shell surface, Commonly they are composed of the mineral aragonite. So far as is now known, the hypostracum of the myalinas consists of calcite.

Length.—The maximum linear distance between the margins of a valve measured parallel with the hinge axis is termed the length.

Ligament.—The ligament commonly consists of two unlike kinds of elastic conchiolin. One kind is impregnated with spicules of aragonite, the fibrous ligament, and is elastic only to compressional stresses. This part of the ligament is located mainly below (ventral to) the hinge axis. The other type of material, the lamellar ligament, contains no calcareous material. It is highly elastic to both compressional and tensional stresses, but chiefly functions as a tensional organ because it lies above the hinge axis. The type of C-spring ligament found in *Mytilus* is called parivincular; the complex ligament of some arcas and myalinas may be called duplivincular.

Ligament area.—This is the cardinal surface to which the ligament is attached. The character of the ligament insertions in the shell gives a clue to the nature of the ligament itself in fossil shells.

Ligament grooves.—The chevron grooves of *Arca* and the linear grooves of *Myalina* represent the locus of attachment of the edges of successive bands of lamellar ligament. This type of ligament may be referred to as duplivincular.

Lobe.—Shells having a "modioloid" contour exhibit a rounded emargination of the anteroventral part of the shell just in front of the beaks. This salient is commonly called the anterior lobe.

Midumbonal line.—The bisectrix of the umbonal ridge is called the midumbonal line. Since the umbonal ridge is not straight, but swings forward during growth, the midumbonal line is arcuate. In some gerontic individuals the midumbonal line swings backward near the ventral margin so that it follows roughly a sigmoidal path across the shell. The angle between the midumbonal line and the cardinal margin is called angle a.

Musculature.—The muscle pits that can be observed in well preserved specimens are as follows: one to three pits in or near the umbonal cavity, one or two anterior byssal retractors, one anterior adductor, which may, however, be absent; the pallial line, broken into disconnected pits toward the anterior adductor; the posterior muscle impression, more or less bifid and made up of impressions of the posterior adductor, posterior byssal muscles, and the posterior pedal retractor; a series of disconnected pits, the gill suspensories, extends from the posterior adductor toward the anterior byssal retractors.

Obliquity. — Primitive Mytilacea are highly oblique, that is, the angle between the umbonal ridge and the dorsal margin (angle a) is relatively small. During ontogeny and phylogeny this angle steadily increases so that the ventral part of the shell swings forward. Where the angle a is less than 90° the obliquity may be called prosocline, where it is approximately 90° acline, and opisthocline where the angle is obtuse.

Ostracum.—The term ostracum is applied to the calcareous shell. In Recent species four component parts of the test are recognized. The outer horny covering is the periostracum; the outer calcareous layer, usually quite thin, is the outer ostracum; the inner ostracum commonly is relatively thick and forms inner features, including the hinge; the hypostracum includes all of the more or less disconnected deposits at the insertions of the muscles.

Pallial line.—Radial muscle strands of the mantle are inserted in a narrow band parallel with the shell margin. In the Mytilidae the pallial line is a continuous obscure furrow, but in the Myalinidae the anterior part of the pallial line is broken into a series of distinct pits.

Pedal retractor.—In Mytilacea there is a long dorsal prolongation of the rear part of the large posterior muscle impression. Most of this salient is produced by the insertions of several byssal retractors. A single large pedal retractor joins the shell on each side at the distal end of the series, not far from the posterior extremity of the hinge in *Mytilus*, but more remote from the hinge in some other forms.

Periostracum.—The outer corneous covering of the shell of many kinds of pelecypods is termed the periostracum. By analogy with living Mytilacea, it may be supposed that all fossil representatives of the superfamily also possessed a periostracum. Fossil periostracum is extremely rare. Unquestioned examples of it from the Paleozoic are not known to me, although there have been several citations to fossil periostracum, particularly in the so-called fresh-water forms from the Pennsylvanian.

Plane of commissure.—The plane which approximately coincides with the valve margins is designated as the plane of commissure.

Pleurothetic.—The majority of inequivalve pelecypods owe their lack of symmetry to the habit of lying at rest on one side. Such shells are called pleurothetic. It has been demonstrated in the pterioids, pectinoids, and oysters that any particular group is remarkably consistent as regards the side that normally is undermost. Practically all of the Ostracea rest on the left valve, whereas Pteriacea and Pectinacea rest almost invariably on the right valve. There seems to be far less variation from the normal condition, in this respect, than there is variation from righthandedness in human beings or from sinistral coiling in normally dextral snails. The pleurothetic habit may cause a secondarily induced torsion of the body within the shell, with consequent atrophy of certain muscles, as in the Pectinacea. Generally, the principal distortion is found in decreasing convexity and reduction of the area of one of the valves. In Ostracea the upper valve commonly is reduced, in Pectinacea and Pteriacea, the lower one. The smaller valve in Myalinidae is the right one, and presumably this valve was undermost.

Prismatic layer.—The outer ostracum of the pelecypod shell in many instances is composed of polygonal prisms of calcite or aragonite, which may be disposed normal to the shell surface (Myalinidae) or nearly parallel with the surface, in which case they are radially disposed in respect to the umbones (Mytilidae). In rare instances the prisms locally give way to homogeneous calcareous material within a single shell. Rarely, the inner ostracum is prismatic. The hypostracum is commonly fibrous, but the fibers are rarely polygonal in section. In pleurothetic pelecypods the outer ostracum of the right valve may be prismatic, while that of the left valve is not (some Pectinacea, some Myalinidae), or both valves may be alike. Examples are unknown to me where the outer ostracum of the right valve is homogeneous while that of the left valve is prismatic.

Resilifer.—Triangular pit along the hinge and under the beak for reception of the compressional part of the ligament (resilium) is called the resilifer. Mytilacea possess resilifers only in the prodissoconch and early dissoconch stages.

Shell thickness.—Shell material of a pelecypod is thickest near the hinge and thinnest near the ends and ventral margin, with more or less gradation in thickness in the intermediate areas. The thickness is, however, for practical purposes nearly uniform over the central area of both valves, and measurements of shell thickness may be given for the central parts of shells having a stated length and height.

Sinus.—Any indentation of the shell margin which may be shown in growth lines is called a sinus.

Umbones.—The protuberant area around the beak of a pelecypod valve, in which the early ontogeny of a shell is shown by growth lines, is defined as the umbo. The distinctness of the umbones varies in different genera.

Umbonal cavity. — The internal space beneath the umbones is known as the umbonal cavity.

Umbonal ridge.—In mytiloids a more or less prominent ridge occurs near the anteroventral margin, extending diagonally across the shell from the beaks to the ventral margin of the shell, being best defined near the beaks. The angular relation between this ridge and the dorsal (cardinal) margin (angle *a*) is a very critical character in phylogenetic studies.

Umbonal septum.—In the majority of mytiloid shells the anterior extremity is extended, or even somewhat acuminate, so that the umbonal cavity is extended far forward under the beaks. In a few of these shells the inner part of the umbonal cavity is partially floored over in the plane of the commissure to produce a small umbonal deck or septum. In some instances the septum supports the anterior adductor muscle. More commonly, the septum seems to represent simply a brace to strengthen a weak part of the shell and to anchor more securely the extension of the animal into the umbonal cavity. It cannot be doubted that an umbonal septum has been independently acquired in relatively unrelated stocks; yet, in conjunction with other characteristics, the presence or absence of an umbonal septum is a useful generic character.

LIGAMENT

Seldom are ligament structures preserved in Paleozoic pelecypods. The surfaces of ligament attachment, or *ligament areas*, of the shell, however, are diverse and in some instances highly distinctive. By analogy with living pelecypod species it is possible to obtain some idea regarding the more or less complicated ligaments of fossil forms. To any

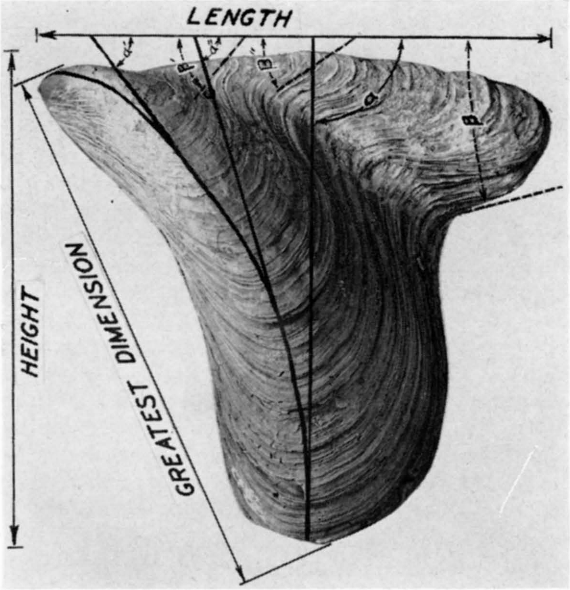


FIGURE 3.—Measurements in mytiloid shells. The length of the shell is the greatest linear dimension measured parallel with the hinge axis, a line which is invariably straight, generally lying somewhat below (ventral) to the dorsal margin. Height is the greatest linear dimension measured at right angles to the hinge axis. The "greatest dimension" is generally measured along a straight line extending from the beak to the posteroventral margin of the shell. During shell growth the angle between the hinge axis and the crest of the umbonal ridge (angle α) increases in size. This ontogenetic change in form has phylogenetic significance; and the value of the angle α, measured at a mature ontogenetic stage, is a useful specific character. In many instances the angle formed by the intersection of the hinge axis with the posterior margin of the shell (angle β) can only be approximated. However, the form of this posterodorsal angle is a very useful specific character. In many Paleozoic mytiloids, as well as pectinoids and pterioids, the angle β decreases in size during both ontogeny and phylogeny. Some tribes tend to develop a posterior auricle.

student of the pelecypods it is evident that tribes of pelecypods are characterized by distinctive kinds of ligaments. Thus, the pterias, pectens, arcas, and unios have markedly different ligaments, as well as other distinctive characters. Neumayr, Bernard, Dall, and others among the pioneer students of pelecypods recognized some of the more striking kinds of ligament and made some use of ligament types in their taxonomic treatment of the bivalve mollusks. Few students of Paleozoic shells, however, have given even cursory attention to ligament characters, thereby more or less ignoring one important clue to obscure phylogenies.

While investigating the Late Paleozoic pectinoids (Newell, 1938, pp. 26-35) I was struck by the diverse appearance of the ligament areas in shells that otherwise are superficially alike. The ontogenetic changes in shell form, as revealed by lines of growth, strongly suggest that these Paleozoic shells of pectinoid habit truly form a phyletic group. Consequently, they were classed in families of the Pectinacea. Perusal of any of the great monographs on Paleozoic pelecypods reveals that there also are several kinds of ligament areas in shells that have distinctly a pterioid aspect or a mytiloid aspect. The problem becomes especially complex when it is noted that mytiloid shells, through rapid evolution, develop pterioid contours, or pterioid shells become modified through minor changes in proportion to the pectinoid form. Perhaps it is not so surprising that the early representatives of the three great superfamilies—Pectinacea, Mytilacea, and Pteriacea—present taxonomic difficulties, because they were just unfolding from a common ancestory, during the Paleozoic era, and had not as yet attained the degree of standardization that characterizes their post-Paleozoic descendants.

Mature consideration of the various types of ligaments possessed by Paleozoic pelecypods leads inevitably to the conclusion that each type thus far recognized represents but a stage in a series of changes undergone by the ligaments in different tribes of pelecypods. Some of these distinctive types of ligament were certainly developed more or less independently in separate families, and therefore do not imply close relationship in shells that otherwise are quite different. A useful analogy might be found in the Ammonoidea, in which the ceratite suture is now known to represent a transition stage between the goniatite and ammonite suture and was acquired independently in several different stocks. The tentative phylogeny of ligament types suggested by me (Newell, 1938, p. 33) incorporates this view. Consideration of Bernard's (1895-1897) studies of the ontogenies of several Cenozoic pelecypods strengthens the belief that any particular type of ligament represents only one of several stages through which the ligament passed in its phyletic development. Further examination of Bernard's evidence, however, forces me to abandon part of the hypothetical sequence alluded to above.

The Paleozoic Mytilidae that I have studied had a ligament like that of modern representatives of the family. The Myalinidae, although clearly members of the Mytilacea, possessed a ligament quite unlike any post-Jurassic representatives of that superfamily. The flat and divergent faces of the ligament area are lined by deep, closely-spaced grooves, or furrows, reminiscent of similar furrows of *Arca, Pectunculus,* and, among Paleozoic genera, by *Pseudaviculopecten, Leiopteria, Ptychodesma,* and others. Many authors, unfamiliar with the ligaments of contemporary pelecypods, have failed to appreciate the significance of these ligament furrows, in some instances referring to them as "growth-lines." The ligament grooves in Myalinidae are peculiar in that they are nearly or entirely opisthodetic, in harmony with the fact that the beaks in these, as in the majority of Mytilacea, are terminal. Otherwise, the ligament grooves seem to be entirely homologous with the chevron grooves of some Arcacea. In order to obtain an understanding of the ligaments of Paleozoic Mytilacea I have examined the ligaments of some modern Mytilidae and Arcidae.

Ligament of Mytilidae.—Like the ligament of other pelecypods, that of *Mytilus* and *Volsella* consists of two parts which are structurally and functionally unlike. A dorsal layer (fig. 4A-C, 2) consists of highly elastic, conspicuously lamellar, conchiolin. Because this lamellar structure lies almost entirely above the axis of rotation of the valves, it is subjected to tensile stresses when the valves are closed. The ventral part of the ligament system consists of a layer of conchiolin (fig. 4A-C, 3) in which are suspended closely packed calcareous needles arranged more or less normal to the ventral or growing surface of the ligament. Petrographic analysis by Dr. R. C. Emmons, University of Wisconsin, reveals that these calcareous fibers have a thickness of approximately one micron and are composed of aragonite. There is a marked tendency for the fibrous ligament to split parallel to the fibers, so that it is very weak to tensile stresses. However, since it lies almost wholly below the hinge axis, it is subjected, normally, only to compression. The fibrous ligament separates the lamellar ligament from the ligament gland of the mantle over the front part of the ligament; but, since the fibrous ligament does not extend to the posterior part of the hinge, the lamellar ligament is

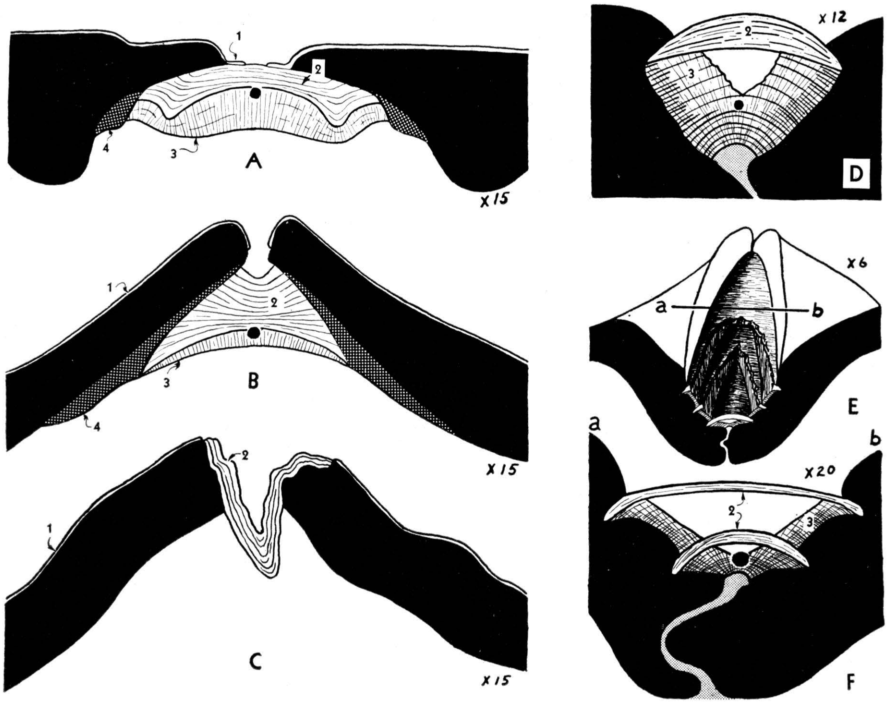


FIGURE 4.—Ligament structures in *Volsella* (*"Modiolus"*) and *Arca* (*D-F*). *A-C*, Series of transverse sections through the ligament of *Volsella modiola* (Linnaeus), valves closed, near the beaks (*A*), at the middle of the hinge (*B*), and at the posterior end of the hinge (*C*), respectively. *D*, transverse section cut midway through the ligament of *Arca pexata* (Say). *E-F*, transverse sections cut through the ligament of *Arca transversa* (Say), near the middle of the hinge (*E*), and near the posterior end along the line a-b, (*F*). Solid black, shell material; black dot near center, position of axis of rotation; 1, periostracum; 2, laminar ligament; 3, fibrous ligament; 4, secondary calcareous ligament buttress.

in contact with the ligament gland near the rear extremity of the hinge.

The ligament of Mytilidae is of the type commonly called "internal," viz., most of the ligament is concealed beneath the overhanging margins of the dorsal edge of the shell. In order to give the ligament better foothold on the surface of attachment on the shell a ridge of spongy calcareous material is added below the ligament on each side. The resulting depression, or furrow, in which the ligament is lodged is called the ligament groove and, of course, is quite invisible exteriorly, even where the ligament has been stripped from the shell.

Ligament of some Arcidae.—In connection with the study of Paleozoic pectinoids I made certain observations, on some pelecypod ligaments (Newell, 1938, pp. 26-35), which now require further comment and correction.

The fibrous ligament of *Arca* consists of a rather thin sheet covering the two flat and divergent surfaces of the broad ligament area. Both Dall (1895, p. 500) and Bernard (1896, pp. 67, 71) refer to this covering as an epidermal (lamellar) ligament. For the species (*A. transversa* Say, *A. pexata* Say) that I have studied, there can be no doubt that this part of the ligament is fibrous and compressional where it joins the two valves at their contact below the axis (fig. 4*D*,*F*, 3). My earlier observations on fibrous ligaments must be revised, as follows: In cross sections of the ligament of *Arca transversa* (fig. 4*E*,*F*), the fibrous ligament exhibits distinct growth lamellae, which I originally mistook for calcareous fibers. The fibrous ligament is iridescent or "pearly" through the outer one-third to one-half of its thickness. When the hinge axis migrates downward, during shell growth, to a position below a given part of the fibrous ligament, that part is subjected to tensile stress and soon parts, or splits, along a vertical plane just above the axis. The reaction of the lamellae after breaking is greater near the surface where there is more space in which to expand than next to the shell surface, and the resulting strain of the lamellae produces the marked iridescence.

The fibers of calcareous material are imbedded in the conchiolin *normal* to the ventral or growing surface of the ligament, not parallel with it as I formerly thought. Being interested in the characteristics of the calcareous spicules, I referred them to Dr. R. C. Emmons, who has reported that they are composed of acicular fibers of aragonite somewhat less than one micron in diameter. The spicules are relatively long, seemingly extending at least through several growth lamellae.

These observations apply equally well to the fibrous ligament of *Arca pexata, Pinctada, Yoldia, Volsella,* and *Mytilus,* and probably characterize pelecypods in general. The errors into which I fell were due to my inability to separate satisfactorily the organic conchiolin from the aragonite fibers; and, consequently, I did not realize how exceedingly fine they are. Specimens of fibrous ligament treated for a day or so in a slightly alkaline solution of H_2O_2 of 30 per cent concentration are freed of organic material and take on the appearance, at 500 diameters, of a fine camels-hair brush. It seems as though the calcareous spicules in the observed specimens make up more than one-half of the entire volume of the fibrous ligament.

Ontogenetic development of the ligament.—Bernard made the extremely important observation that the ligament is invariably internal when it appears first in the young pelecypod, and that it is lodged in a small oblique resilifer just below the beaks. In some genera, such as *Pecten, Nucula, Pteria, Lima,* and *Ostrea,* this condition apparently continues to maturity; although, in the last three genera, growth expansion of the two valves at their margins causes the resilifers to become exposed exteriorly, resulting in an "external" ligament. For this type of ligament, Dall (1895, p. 500) suggested the term *alivincular.* Seemingly, the part of the ligament that is lodged in the resilifers of adults of the above mentioned genera is largely, if not wholly, of fibrous type, although I formerly thought otherwise (1938, pp. 31-35). Whether or not the central ligament of the early dissoconch stage is homologous with the fibrous ligament is not certainly known, but it is invariably compressional in shells having the functional part of the ligament below the hinge axis.

Since the alivincular ligament appears early in the ontogeny of so many genera *(Nucula, Pectunculus, Arca, Mytilus, Volsella, Modiolarca, Lasaea, Lucina, Crassatella, Cytherea, Venus, Mactra, Donax),* it is reasonable to suspect, with Bernard, that this was the primitive ligament from which other types were derived.

Jackson (1890, pp. 327-333) has shown that the multiple ligament of the Pernidae passes through an alivincular stage in the early ontogeny, where the ligament is like that of *Pteria.* In this type new resilia are added successively at the rear of the hinge margin. Dall (1895, p. 500) proposed the term *multivincular* to describe this type of ligament. In both the alivincular and multivincular types the compressional "resilium," composed of fibrous ligament, does most of the work in opening the valves, whereas the lamellar ligament serves chiefly to tie the two margins of the shell together (Newell, 1938, pp. 26-35).

The term *parivincular* was introduced by Dall (1895, p. 500) to describe the C-spring type of ligament found in *Cardium, Tellina, Unio, Mytilus,* and *Volsella* (fig. 4*A-C*). Some of the arcas (fig. 4*D*) also have a parivincular ligament in the adult stage; probably all of the arcas pass through a parivincular stage somewhere in the ontogeny. Bernard (1895-1897) has shown that the prodissoconch and early dissoconch stages are alike in many pelecypods in possessing an "internal" triangular resilium bounded behind and ahead by two series of small interlocking denticulations along the hinge margins of the valves. These denticulations correspond to a sort of taxodont dentition, which in most cases is lost and replaced by other teeth in the later ontogeny. In *Mytilus edulis,* Bernard (1896, p. 415) found that the posterior row of denticles early becomes divided into two parts separated by a shallow depression, in which is lodged a new part of the ligament destined to become the true ligament of the adult *Mytilus.* He was not able to determine the relationship between the embryonic ligament and the secondary one. In many of the arcas

> the primitive ligamentary fossette, occupied by the cartilage, does not remain simple; it is subdivided into two parts, which diverge, forming thus the first two chevron furrows, which are continued to the top of the cardinal edge where they abut against the thin grooves at the cardinal margin. Other grooves for the cartilage appear a little later near the center and are divided in the same manner, and so on. (Bernard, 1896, p. 71).

Bernard's allusion to "cartilage" grooves is unfortunate, for in the arcas with which I am familiar the chevron grooves contain the insertions of the lamellar bands of ligament; and the fibrous ligament ("cartilage") covers the general surface of the ligament area (fig. 4*D-F*).

It is certain that all arcas possessing multiple bands of tensional lamellar ligament pass through an ontogenetic stage in which there is only one of these bands; because the ligament bands are added in succession, one at a time, each making its first appearance near the center of the hinge axis, and there is migration during growth towards the hinge extremities in order to make space for new ligament bands. As pointed out by Bernard (1896, pp.

71-72), several species show a delay in differentiation of the parivincular ligament until rather late in the ontogeny. In other species the ligament does not progress beyond the parivincular condition.

It is clear, then, that the multiple ligament of some arcas represents a sort of reduplication of the parivincular ligament and has somewhat the same relation to that ligament as the multivincular ligament (as typified by the Pernidae) has to the more primitive alivincular ligament. It seems quite improper to class the multiple ligament of *Arca* with the multivincular type illustrated by *Perna*, because the ligaments of the two genera are structurally different and have different ontogenies. The term "arcid ligament" previously used by me seems inappropriate. Therefore, I propose to employ the term *duplivincular* for ligaments of the type possessed by *Arca transversa* (fig. 4*E,F*). All Myalinidae known to me had a duplivincular ligament in the adult stage, differing from modern types principally in being opisthodetic instead of amphidetic. A restoration of a typical myalinid ligament is shown in text figure 5.

MUSCULATURE

Mytilacea are anisomyarian. That is, through progressive atrophy of the anterior adductor the posterior adductor has assumed most of the function that seems to have been divided originally almost equally between the two adductor muscles. Whether or not the progressive decrease in size of the anterior adductor represents an evolutionary trend that many times independently affected more or less distantly related tribes, or whether this condition had a common origin in a single ancestral stock, cannot yet be positively determined. Of course, it is known that the Tridacnidae have lost the anterior adductor independently of other types of pelecypods. The remaining anisomyaria and monomyaria, such as the oysters, scallops, pterias, mytiloids, and others, commonly are classed together in an order called Dysodonta, on the supposition that they have had a common origin. All of the living members of this order are byssate during part of the life of the animal, and it has been supposed that the adoption of the byssal mode of fixation led to a compression and crowding-out of the organs of the anterior part of the body. In the monomyarian stage the complete disappearance of the anterior adductor was accompanied by a ventral migration of the posterior adductor to a centrally located position to restore a symmetrical relation of the closing muscle to the hinge. There are other factors, however, not yet understood, that affect the placement of the posterior muscles, because there are species of *Mytilus* in which the anterior muscle is entirely lacking in the adult, yet the posterior adductor remains in its normal place near the rear of the shell, as in anisomyarian forms of the genus. Seemingly, the anterior adductor is not indispensible in Mytilidae, because damage to or complete removal of the anterior adductor in living specimens does not seriously affect the ability of the animal to close its valves tightly.

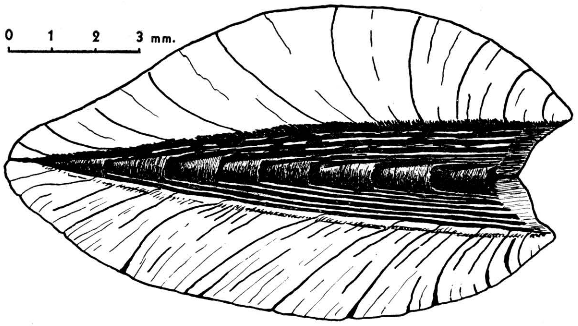


FIGURE 5.—Ligament construction in *Myalinidae, Liebea squamosa,* Permian of Germany, dorsal view, with valves tightly closed. Drawn from the specimen illustrated on plate 15, figure 3. Several conical bands of lamellar ligament, partly invaginated, occur along the hinge line, being inserted in diverging grooves (shown in white) in the ligament area. A thin fibrous ligament occurs (judging from analogy with *Arca*) in the area between ligament grooves. This type of ligament corresponds to the posterior part of the chevrons of Arcidae.

The musculature of the myalinas, judging from the muscle impressions in fossil shells, was practically identical with that of modern Mytilidae, and rather unlike that of other dysodonts, such as the Pteriidae. It is the similarity of the muscle systems, as well as close likeness of form between primitive myalinas and the Mytilidae, that convinced me that the myalinas are Mytilacea instead of Pteriacea, as supposed by many previous workers.

Anterior muscles.—Two conspicuous muscle impressions occur near the front end of the shell of living Mytilidae, such as *Mytilus* and *Volsella.* One of these, the anterior adductor, occurs at the front terminus of the pallial line, near the anterior extremity of the shell. The other pit lies somewhat behind and dorsal to the adductor, situated very close to the hinge axis. This muscle impression is produced by the anterior byssal retractor, a strong muscle that extends posteroventrally about one-half the length of the shell to the byssal gland at the proximal end of the foot. In some genera (e.g., *Septifer*) the anterior adductor is attached to the shell on a calcareous shelf, or umbonal septum. In Paleozoic Myalinidae the anterior adductor impression may be located approximately as in *Mytilus,* in a small pit near the anteroventral margin of the shell (*Myalina, Naiadites, Orthomyalina*), or on a septum, as in *Septifer* and *Liebea*, or underneath a septum with which it has no obvious relationship (*Septimyalina*). Perhaps the anterior adductor is missing in some species. In all of the better known Myalinidae there are two muscle pits that seem to correspond to the single byssal retractor of the Mytilidae. Presumably, the byssal retractor of the Myalinidae had a bifid insertion at the anterior end.

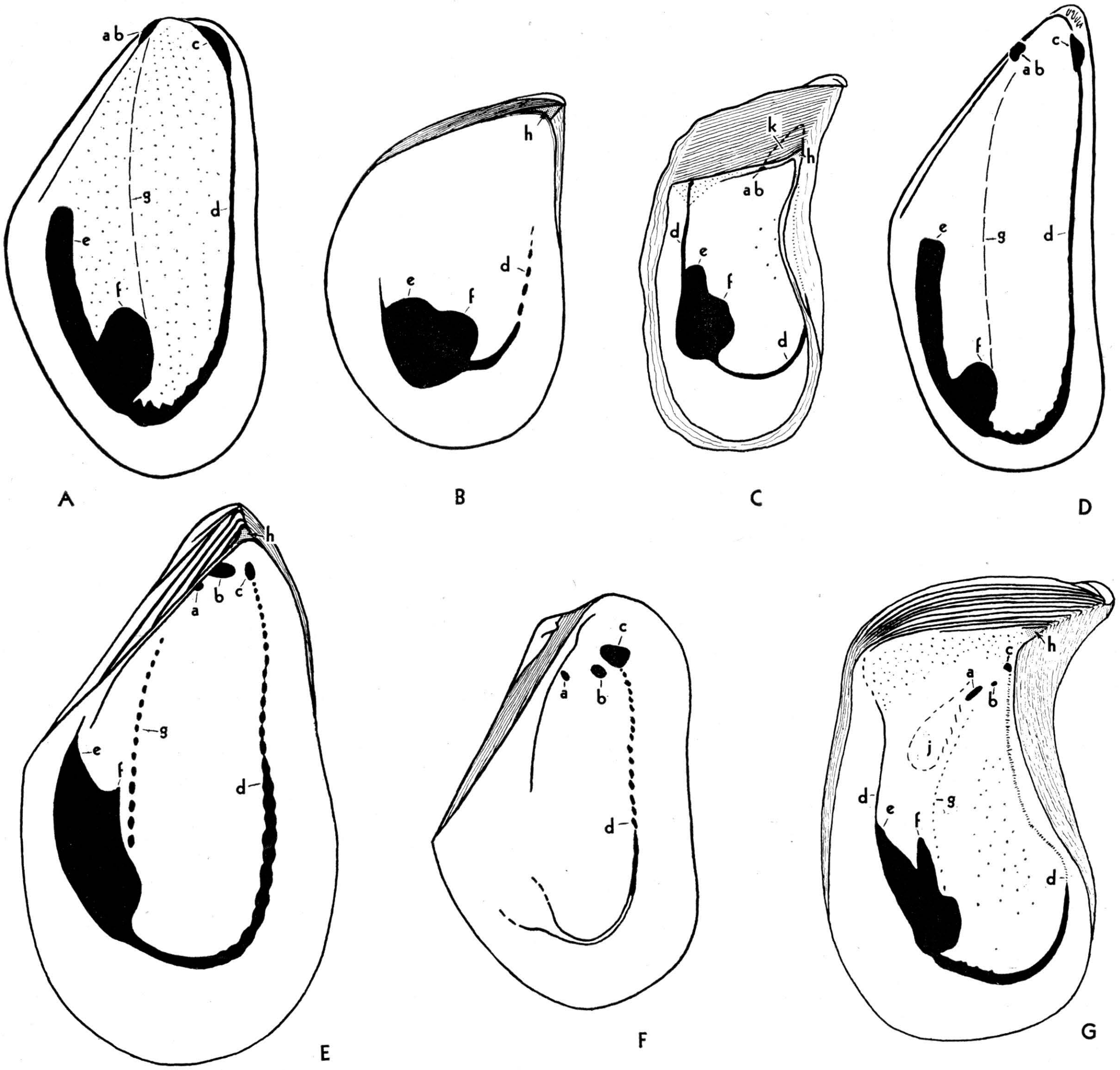


FIGURE 6.—Musculature in genotypes of Paleozoic and Recent Mytilacea. *A Volsella modiola*, Recent; internal mold of right valve, X1; *B, Selenimyalina meliniformis*, Pennsylvanian, left valve, X2; *C, Septimyalina perattenuata*, Pennsylvanian, left valve, X1; *D, Mytilus edulis*, Recent, internal mold, right valve, X1; *E, Myalina goldfussiana*, Viséan, left valve, X1; *F, Naiadites carbonarius*, Pennsylvanian, left valve, X2; *Orthomyalina slocomi*, Pennsylvania, left valve, X1.

Musculature essentially the same in both valves. *ab*, Anterior byssal retractor; *a, b*, insertions of bifid anterior byssal retractor; *c*, anterior adductor, seemingly absent in figure *C; d*, pallial line; *e*, posterior byssal and pedal retractor; *f*, posterior adductor; *g*, gill suspensories, not visible on shell in figures *A* and *D; h*, dental socket, or fulcral point, absent in *A, D*, and *F; j*, muscle pits of uncertain function; *k*, umbonal cavity, especially characteristic of *Septimyalina*, figure C. Small pits over the general interior in figures *A, C*, and *G* represent points of attachment of the mantle. They are not visible in all specimens, and their arrangement does not seem to be significant.

Posterior muscles.—In the Mytilacea several muscles are inserted in a small area in the rear part of the shell. Unfortunately, these separate muscles seldom produce discrete spots in the shell so that the general area of insertion cannot readily be differentiated into all of the component parts. The form of the large posterior impression, however, is quite distinctive, and is uniform within a species or genus. The muscle area in the shell is strongly bilobed, divided into two distinct prongs by a well defined dorsal or anterodorsal cleft. The larger ventral lobe, to which the rear end of the pallial line is attached, is the impression of the posterior adductor. The posterior or dorsal lobe is produced by a series of byssal and foot retractors. The pedal retractor muscle, extending from the distal end of the foot, is inserted in the shell at the dorsal extremity of this lobe. Between the pedal retractor and the posterior adductor is a series of six or seven posterior byssal retractors, attached to the byssal gland at the proximal end of the foot, near the middle of the shell. The insertions of the byssal retractors cannot be differentiated in the shell, but they form the main body of the dorsal lobe of the great posterior impression. In the Myalinidae the dorsal lobe seems to be considerably shorter than in the Mytilidae.

Pallial line.—The pallial line in Mytilidae is a continuous, rather distinct furrow extending around the margin of the interior of the shell between the two adductor impressions. Examination of the pallial system in the animal of *Mytilus* or *Volsella* reveals that the free margin of the mantle is provided with a large number of radial muscles whose function is the withdrawal of the mantle from between the valve margins, preparatory to closing the valves. The insertions of these radial muscles produce the pallial line in the shell.

In the Myalinidae the anterior one-half or two-thirds of the pallial line is composed of discrete pits, which evidently mark the insertions of radial muscles of the mantle. These are spaced more widely than in *Mytilus*. The rear part of the pallial line, where it joins the posterior adductor impression, is as in the Mytilidae. In a few of the Myalinidae the posterior muscles are withdrawn so far from the hinge line that there is space for a dorsal extension of the pallial line above the muscle impression. In this instance the line is relatively thin and obscure but continuous.

Other muscles of the mantle.—Some of the Myalinidae show irregularly disposed fine pits or punctations of the inner surface of the shell inside the limits of the pallial line. Similar pits are common in some of the early Paleozoic Ambonychiidae. Living Mytilidae are relatively thin-shelled, so that distinct muscle marks are commonly lacking in the shells. However, an occasional *Mytilus* or *Volsella* exhibits similar punctations. In some instances they are more or less regularly disposed in radial rows (fig. 6*A*). Microscopic examination of the mantle of such animals indicates that these punctations represent the insertions of tiny bits of outer surface of the mantle where it is attached to the shell. Mantle attachments of this type are unknown to me outside of the examples mentioned.

Gill attachments.—In some of the better known Myalinidae an arcuate row of muscle pits extends from the anterior margin of the posterior adductor impression to a point near the rear impression of the anterior byssal retractor (figs. 6*E, g;* 6*G, g*). This line corresponds exactly in position with the location of the attachment of the gills to the mantle in Mytilidae (figs. 6*A, g;* 6*D, g*), although the gills seemingly are not directly attached to the shell, and therefore do not produce muscle pits in *Mytilus* and *Volsella*. Presumably the gills in Myalinidae were attached at muscle insertions directly to the shell.

SHELL STRUCTURE

Shells belonging to the Myalinidae are among the best preserved pelecypods found in Late Paleozoic rocks. Associated Mytilidae are commonly less well preserved. Reasons for these differences are found in the construction of the shells. Myalinid shells typically are very thick and massive, considering the relatively small volume occupied by the living animal. Some gerontic shells of *Myalina copei* Whitfield, from Lower Permian rocks, have an interior cavity amounting to less than an estimated one-eighth of the volume of the calcareous matter of the shell. In some instances the maximum thickness of each valve is around one-half inch, which is of the same order of thickness as the visceral cavity between the valves. Some species have comparatively thin shells, as species of *Myalinella;* but, on the whole, the shells are heavy and therefore relatively strong to mechanical stresses applied before and after burial. Late Paleozoic *Promytilus* and *Volsellina* possessed very thin and fragile shells, comparable in every respect with modern representatives of Mytilidae. In part, the rarity of good specimens belonging to these genera may be due to the fragility of their shells.

In pelecypods, as a rule, both calcite and aragonite occur in the same shell, and these two minerals have a separate distribution within the shell. Where both minerals are present, the calcite occurs in an outer layer and the aragonite occurs underneath, in an inner, commonly nacreous, layer. According to Bøggild (1930, p. 239), an exception is in the Pectinidae, where an aragonite layer occurs between two layers of calcite. There are many kinds of shells, however, which are composed (except for a small amount of conchiolin) exclusively of either calcite or aragonite.

According to Bøggild (idem), temperature is not a controlling factor that determines the formation of aragonite or calcite in mollusks. On the other hand

> between the salinity of the water and the composition of the shells there seems to be a more pronounced connection. . . . It is very obvious, however, that almost all the forms which consist of both elements (aragonite and calcite) are confined to salt water. Especially among the Mytilidae we find that most members of that family, which are built up of calcite and aragonite, are found in salt water, whereas the comparatively few living in brackish or fresh water, as the *Congeria* and the *Dreissensia,* are purely aragonitic. I have only found one example of calcite-bearing shells among all the mollusks living in fresh water, viz. the genus *Neritina,* all members of which examined by me possess a very thin, upper calcite layer.
>
> Any more direct influence of the salinity of the water upon the composition of the shells is not to be found. If we compare specimens of the same species of *Neritina* from fresh water with others from brackish water, we shall find that both possess a thin calcite layer which is not more developed in the latter specimens than in the former. And the same is found in *Mytilus edulis.* Specimens of that animal from water of the least possible salinity (0.5%) are very small and thin as compared with those from salt water, but the relative amounts of calcite and aragonite are almost the same in both forms. (Bøggild, 1930, p. 242).

Owing to the relative instability of aragonite, this mineral tends to be dissolved or to be altered to the more stable calcite, with the common result that fossil pelecypod shells that originally contained some aragonite exhibit unequal preservation of the aragonite structures as compared with the calcite structures. Quite commonly the inner aragonite part of the shell, bearing muscle impressions, hinge, and ligament characters, is lacking in fossil shells; whereas, the outer film of calcite remains, with external ornamentation, perfectly preserved. Circulating ground water undoubtedly will dissolve aragonite from shells under conditions in which the calcite is not affected. Immediate reprecipitation of the carbonate in the form of calcite will cement calcite shells together to form a coquinoid limestone. Probably many organic limestones are formed in just this manner.

The amount of time necessary for the complete alteration of aragonite to calcite varies widely under different conditions. Contrary to popular belief among geologists, aragonite shells are not unknown in Paleozoic rocks, although they certainly are restricted largely to the post-Mississippian part of the Paleozoic sequence. On the other hand, aragonite shells are dissolved, leaving molds in very young rocks ranging up to the Recent. My own observations agree with those of Bøggild, that aragonite has the best chances for survival in calcareous-argillaceous rocks, particularly those in which water permeability is comparatively low. Dense "clay-ironstone" concretions and carbonaceous limestone concretions ranging upward from the Upper Mississippian commonly contain aragonite shells. A less common medium of preservation is found in asphaltic limestones and sandstones in which the bituminous material evidently was introduced early in the history of the rock. Relatively nonargillaceous calcitic limestones and dolomitic limestones, as well as permeable sandstones, practically never contain aragonite shells. Rocks containing very little calcium carbonate, such as siliceous or ferruginous rocks, commonly lose rather quickly both aragonite and calcite shells. Observers seem to be agreed that transformation of aragonite to calcite generally is accompanied by loss in detailed structure. Shells that have undergone this change commonly reveal only coarsely crystalline texture and are true pseudomorphs. As pointed out below, however, many specimens of *Myalina* show perfectly the nacreous structure of the inner layer, composed now of calcite. There are good reasons to believe that in this instance details of shell structure are retained after the alteration of the original aragonite to calcite.

Structure in Mytilidae.—In fossil, as well as Recent representatives of the Mytilidae, the shell consists of an outer thin layer of calcite, ranging between 0.05 mm and 1.0 mm in thickness, and an inner one of aragonite, ranging from 0.5 mm to more than 5 mm in thickness. The structure of the calcite is

> typically homogeneous or indistinctly prismatic with the axes horizontal in the radial direction, or nearly so; the aragonitic layer is nacreous and only in a few instances partially prismatic.
>
> The common *Mytilus edulis* (Recent) possesses a thick calcitic layer of blue colour; the axes are strongly reclined and in the upper part nearly horizontal. The structure is markedly irregular, being sometimes perfectly homogeneous and sometimes finely prismatic; and the prisms may, in some instances, be very indistinct, in others more marked, and there may be sharp boundaries between the different parts. The directions of the prisms are nearly parallel to those of the optic axes, though generally a little more horizontal so that each prism gets a somewhat oblique extinction. The aragonitic, white layer is normally nacreous. (Bøggild, 1930, p. 272).

Bøggild might have indicated also that the prisms in *M. edulis* are so oriented that their outer termini are closer to the beak of the shell than the inner ends. In *Volsella modiola,* according to my observations, the reverse is true, i.e., the inner ends of the calcite fibers are closer to the beak than the outer ends. In the older Mytili studied by Bøggild, the outer calcite layer varies from finely prismatic, with radial, nearly tangential prisms, to a homogeneous calcite, with no trace of prisms. The aragonite layer consists in some instances of prisms arranged normal to the shell surface. *Congeria* and *Dreissena,* both of which are composed of aragonite throughout the shell, are known to have had a somewhat different history from other mytiloids, and they are classed by some in a separate family, the Dreissenidae.

Pennsylvanian representatives of the Mytilidae studied by me seem to have had an original shell structure like that of *Mytilus edulis. Promytilus swallowi,* together with its near relatives, displays an outer prismatic shell layer that, in fundamental respects, is like that of modern *Mytilus.* The fibers are very fine, less than 2 microns in diameter, and are arranged almost tangent to the outer surface of the shell, extending in a radial direction so that somewhat corroded specimens exhibit radial striations that have been mistaken for ornamentation. Below the surface of the outer ostracum the prisms are rather abruptly declined ventrally at an angle of 45° to 50° with the inner surface of the shell. It now seems possible that it was this kind of shell structure which, in part, I have called radial crossed-lamellar structure (Newell, 1938, pl. 1, figs. 3, 15). The hypostracum, secreted at the surface of attachment of the muscles, is rather obscure in thin-shelled forms such as *Mytilus.* Imbedded within the nacreous layer, it consists also of aragonite, but the mineral occurs as fine, irregular fibers arranged normal to the growing surface. The nacreous layer does not show the original structure in any of the Paleozoic specimens of Mytilidae that I have seen. However, the coarsely crystalline structure of the inner ostracum indicates the former existence of aragonite.

Structure in Myalinidae.—Myalinas showing fine details of original shell structure are not rare. My evidence suggests that the majority of the shells, however, have lost their original aragonite. X-ray analyses were made for me by Bernard Steierman, University of Wisconsin, on the hypostracum, inner, and outer ostracum of excellently preserved specimens of *Myalina (Orthomyalina) subquadrata* and *Septimyalina perattenuata* from the Pennsylvanian of Kansas. These specimens show no obvious recrystallization; and, although I had supposed that the shells contain a large amount of aragonite, the X-ray study revealed no trace of that mineral. Good specimens of several of the genera of Myalinidae have not been available for this kind of study. It may be that aragonite will be found in some forms.

A few specimens of *Orthomyalina subquadrata* at my disposal retain only the outer ostracum, the massive inner part of the shell having been completely dissolved during fossilization. Certainly the inner ostracum in these shells was composed of a less stable mineral—aragonite—than the outer calcite film. Several specimens of *Orthomyalina* and *Septimyalina* reveal excellently preserved hypostracum, with long, irregular fibers having a diameter of 2 or 3 microns. These fibers are now composed of calcite. Whether or not they were originally aragonite I am not sure. It is not easy to explain why the microscopic fibers of the hypostracum and the lamellae of the inner ostracum are so well shown if there has been complete transformation from aragonite to calcite. Perhaps such alteration can be accomplished without loss of detailed structures. Microscopic structures of the shell in fossil cephalopods commonly are preserved. As far as we know, the conch of the cephalopod invariably is composed of aragonite.

As in some other pleurothetic pelecypods (Newell, 1938, p. 25), many of the myalinas show marked differences in the outer ostracum of the two valves. Presumably these differences are correlated with the invariable habit of resting on one side in preference to the other. In Pectinacea and seemingly also in the Myalinidae the right valve normally was undermost, with consequent differences in form and structure in the two valves.

The right outer ostracum, 0.1 mm to 0.3 mm in thickness, consists of rather short, robust polygonal prisms of calcite, having irregular form. The prisms range in size up to about 40 microns in diameter but are much smaller when they first are recognizable in the juvenile parts of the shell on the umbones. There seems to be a progressive ontogenetic increase in size of the prisms during shell growth. Neither size nor shape of the prisms characterizes generic types within the family.

The left outer ostracum of different myalinas exhibits one of two types of structure. Shells that are most nearly equivalve, such as *Naiadites, Myalinella,* and *Selenimyalina,* seem to have an identical shell microstructure in the two valves. The markedly inequivalve forms, however, such as the species of *Myalina, s. s., Orthomyalina,* and *Septimyalina,* are characterized by a left outer ostracum composed of very fine, perpendicular prisms or fibers having a diameter of the order of 1 micron. Only execptionally well preserved specimens reveal this structure. Other specimens show what seems to be a homogeneous outer ostracum.

The inner ostracum consists of very thin lamellae, probably originally aragonite, built up successively to form a structure that is very massive in the majority of species. This structure seems to be nacreous. The layer ranges in thickness from about 1 mm to 10 mm in thickness in different shells. As far as can be determined, the inner ostracum is identical in both valves.

The hypostracum consists of fibrous calcite, perhaps originally aragonite, oriented normal to the inner surface of the shell. As in other pelecypods, the shell growth causes migration of the muscle "scars" from the beaks in radial directions. Earlier deposits of hypostracum in the muscle areas are covered by later deposits of the inner ostracum, so that the full course of migration of the hypostracum can be studied only in thin sections of the shell, cut in a radial direction through a muscle impression. As in other pelecypods the hypostracum is identical in structure in the two valves.

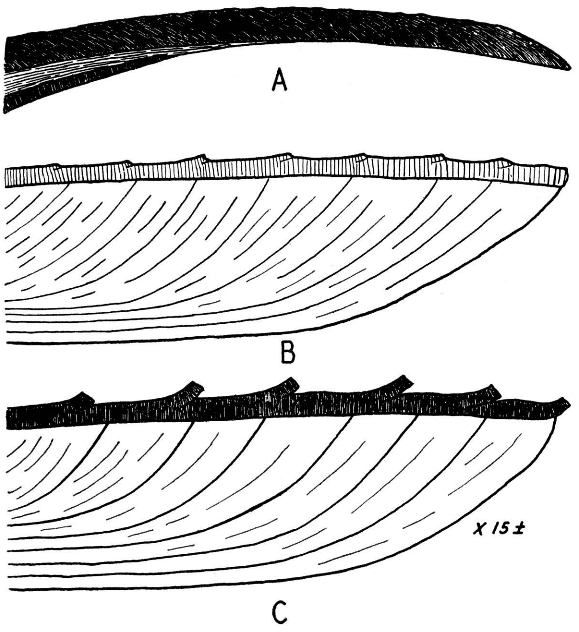


FIGURE 7.—Shell structure of some *Mytilacea.* Ventral margin at right, beak toward the left; approximately X15.

A, Mytilus edulis, showing very fine fibrous outer ostracum composed of calcite; the nacreous layer and fibrous hypostracum, both of aragonite are shown below. The Paleozoic *Promytilus* has a similar shell except that the outer ostracum is relatively thinner.

B, right valve, and *C,* left valve, of *Myalina* (*Orthomyalina*) *slocomi.* The outer ostracum is calcite; the inner one was probably originally aragonite. In the right valve the prisms are relatively coarse (25 to 40 microns in diameter), but in the left valve the structure is fibrous, individual fibers being in the order of 1 micron in diameter. All of the studied species of *Orthomyalina, Myalina,* and *Septimyalina* have the structure described for *Orthomyalina slocomi.* The two valves in *Selenimyalina* and *Myalinella* seem to be identical in shell structure, being comparable to the right valves (*B*) of other myalinas.

SYSTEMATIC PALEONTOLOGY

THE EARLIEST MYTILACEA

Biologists are pretty well agreed that only the later ontogeny is a reasonably reliable index to the phylogenetic history of animals. Also, form may be profoundly affected through adaptation so that animals having similar shapes may not be closely related. Nevertheless, ontogenetic changes in form in the various classes of mollusks have proved to be of great supplemental value in establishing near relationships. Convergences in shell form due to adaptation, or other causes, can be commonly recognized and interpreted by reference to shell ontogeny as revealed by growth lines. Unrelated shells that may look identical at maturity are likely to appear quite different in the early growth stages. Even the discovery that some mollusks underwent most of the evolutionary change in the larval stages (proterogenesis) does not alter the established usefulness of the principles of palingenesis.

Even though Jackson (1890) long ago showed the importance of ontogenetic studies in working out phylogenies of pelecypods, only a few paleontologists have subsequently given attention to this contributory line of evidence. In existing classifications of the pelecypods are found many instances in which shells differing markedly in shape are classed together. Critical ontogenetic studies of these forms may reveal that they are polyphyletic. Extensive consideration of the problem indicates the following generalizations: (1) Some of the major tribes of pelecypods diverged early and have undergone very little differentiation in form since the Medial or Early Paleozoic; such persistence and conservatism of form is recognized to some extent in existing classifications, viz., Pectinacea, some of the Pteriacea, Trigoniacea, and others. (2) Where there has been marked differentiation in form within a single tribe, the changes have been wrought in response to adoption of a radically new type of life, such as cementation of one valve in *Chama* and *Myochama,* or adoption of the boring habit, as in *Lithophaga* and *Teredo.* (3) In the majority of superfamilies, or even families, the characters of the hinge (ligament and dentition), shell microstructure, ornamentation, and musculature show greater potentialities for variation than do certain broad features of external configuration of the shell.

To be wholly consistent with the above conclusions I should class the great host of Paleozoic shells having the mytiloid (or "modioloid") shape with the Mytilacea. To do so, however, would be very decidedly premature in view of the fact that some of the Paleozoic genera of the Ambonychiidae, Pleurophoridae, and others, while having the general appearance of Mytilacea, exhibit certain features of dentition that have caused the exclusion of these shells thus far from that superfamily in the majority of classifications. Also, some of these shells are obviously closely related to others having a pterioid aspect. There is a very marked resemblance between certain Ambonychiidae and Myalinidae, as for instance *Anomalodonta* Miller and *Orthomyalina,* n. gen., or *Plethomytilus* Hall and *Selenimyalina,* n. gen. In absence of information on the ontogenies of any ambonychiids, it is not at present possible to determine whether the resemblance is homeomorphic or is really indicative of close relationship.

In form and hinge characters the genus *Modiolopsis* Hall as represented in the Ordovician must be very like the ancestor of all of the Mytilacea. *Modiolopsis* is so closely similar to living *Volsella* (*"Modiolus"*) that nobody has yet satisfactorily shown any difference. Dall (1895, pp. 527-528) was hardly justified in following Fischer in recognition of a separate family, the Modiolopsidae, in view of the absence of any known characters by which the Mytilidae and Modiolopsidae can be separated consistently. It is true that the Modiolopsidae are supposed to be invariably isomyarian, but there are living species of *Volsella,* for instance, which are also isomyarian. If, however, the shell microstructure in *Modiolopsis* differs from that of *Mytilus* and *Volsella,* I think that it might advantageously be placed in a separate family.

Any adequate understanding of the Early and Medial Paleozoic mytiloids must await further original investigations, made with particular attention to ontogenies and shell microstructure. At the present time it seems to me likely that the majority of Paleozoic genera referred to the Ambonychiidae, Mytilidae, Modiolopsidae, Myalinidae, and Modiomorphidae, as well as many unresolved genera, should be referred to the Mytilacea.

SUPERFAMILY MYTILACEA FERUSSAC

FAMILY MYTILIDAE FLEMING

Shell relatively thin, equivalve, obliquely elongated, with beaks at or near the relatively small anterior end; posterior margin broadly rounded, ventral margin with a slight byssal gape, at least in the young; ligament marginal or submarginal, parivincular, opisthodetic; hinge edentulous, or with cardinal teeth $\frac{1}{2a, 2b}$, or taxodont both before and behind the ligament in direct correlation with any radial sculpture that is present; inner shell layer composed of aragonite, either homogeneous or finely prismatic, outer layer consisting of calcite, either homogeneous or finely prismatic, the prisms and optic axes more or less tangent with the shell surface and directed radially with respect to the beaks (Bøggild); musculature characteristically anisomyarian, but with a few monomyarian (some *Mytilus*) and isomyarian (some *Musculus*) species.

Remarks.—A good many Paleozoic shells that should be classified in other families have in the past been placed in the Mytilidae. Some of the Ambonychiidae and all of the Myalinidae have at one time or another been classed as mytilids by several authors. Indeed, homeomorphy is so prevalent in these three families that it is not surprising that the genera *Mytilus,* or *"Modiolus" (Volsella),* have frequently been cited from rocks as old as the Silurian and Devonian. Several of the myalinas are so nearly identical with *Mytilus* and *Volsella* in form that they cannot be differentiated without some knowledge of the hinge characters (ligament) and shell microstructure. It is significant that the critical differences in shell structure between Myalinidae and Mytilidae commonly can be distinguished directly with a hand lens or low-power microscope, without recourse to thin-sections or polished surfaces. The peculiar radial-tangential prisms of the outer calcite shell layer in many genera of the Mytilidae produce a very finely striate appearance, sufficiently coarse in some instances to be mistaken for radial ornamentation. In a few instances this surface texture is reflected in good external molds. All of the Paleozoic species herein described under the Mytilidae clearly show this characteristic feature.

In the Myalinidae the outer layer of calcite is composed of short, polygonal prisms or fibers which, in the right valve, invariably are coarse enough to be seen at 10 diameters magnification. Unlike the prisms in the Mytilidae those of the myalinas are perpendicular to the shell surface instead of tangential to it. Because the prisms in both families are composed of calcite, they generally are well preserved in specimens which are not too badly recrystallized.

Genus MYTILUS Linnaeus, 1758, emend.

Mytilus LINNAEUS, 1758, Syst. Nat., Ed. 10, p. 704.

Genotype (by subsequent designation), *Mytilus edulis* Linnaeus, Gray, Zool. Soc. London, Proc. for 1847, p. 198, 1847. Geologic range of genotype, Pliocene to Recent; cosmopolitan.

Shell elongate, thin, with terminal, pointed beaks, anterior lobe and anteroventral sinus very obscure or lacking; surface generally smooth, or with radial ribs, which may be broad and indefinite, or fine and uniform; hinge edentulous, or with cardinal teeth $\frac{1}{2a, 2b}$, or with variable number of taxodont teeth retained from the embryonic provinculum.

Range, Mesozoic to Recent.

Genus VOLSELLA Scopoli, 1777, emend.

Volsella SCOPOLI, *1777*, Introd. Hist. Nat., p. 397.

Modiolus LAMARCK, *1799*, Mem. Soc. Hist. Nat. Paris, p. 87.

Genotype (by subsequent designation), *Mytilus modiolus* Linnaeus, Gray, Proc. Zool. Soc. London, for 1847, p. 198, 1847. Geologic range, Pliocene to Recent; cosmopolitan.

Shell highly convex, elongate, thin, with subterminal, rounded beaks, which commonly rise slightly above the hinge line; more or less prominent anterior lobe bounded by broad anteroventral sulcus extending ventrally to broad byssal sinus at middle of anteroventral margin; surface generally somewhat rugose from projecting growth lamellae, or with fine radial ribs; hinge edentulous in adults.

Range, Mesozoic to Recent.

Remarks.—Grant and Gale (1931, p. 248) have shown that legally the name *Volsella* has unquestioned priority over the more familiar term *Modiolus.* Both genera are based on the same genotype and therefore are absolute synonyms. It is unfortunate that such an authority as Thiele (1935, p. 798) refuses to recognize the prior claim of *Volsella* on the grounds that Scopoli misunderstood the characters of the shell which later became the genotype. An author's ideas about his genus have no legal standing whatsoever where they are at variance with the characters of the type species.

In these days paleontologists have a distaste for long-ranging genera and species, and many follow the practice of evaluating observed characters of shells in terms of their stratigraphic position, and in many instances very similar fossils have been given different names to better emphasize unlike stratigraphic occurrences. Where the stratigraphic measure is employed, however, in differentiating fossil units, the classification should by all means be based on proven shell characters and not simply on suspected distinction.

Painstaking research on the material available to me reveals certain obscure but consistent characters by which the Paleozoic forms herein described under the Mytilidae can be distinguished from the majority of similar Mesozoic and Cenozoic forms whose generic affinities with *Volsella* (or *Modiolus*) have not seriously been questioned. One would suppose, *a priori,* that a comprehensive genus like *Volsella,* under which there are so many hundreds of described species, both fossil and Recent, is poorly defined, possibly polyphyletic, incorporating as it does shells that vary considerably in external details. It must be noted, however, that variation in form within the genus is limited, so that modern species can nearly be matched in the fossil faunas from all of the geologic systems back at least to the Jurassic. It seems that *Volsella* is another example of those remarkably virile, conservative tribes of animals which, like *Lingula* and *Limulus,* has undergone little differentiation for vast ages in earth history.

DIFFERENTIATION IN PALEOZOIC MYTILIDAE

Disregarding the pre-Carboniferous species for the moment, two distinct groups of *Volsella*-like mytilids are recognizable in Late Paleozoic rocks. One of these, characterized by Lower Carboniferous forms like *"Modiolus" patulus* M'Coy, *Lithodomus lingualis* Phillips, *Lithodomus lithodomoides* R. Etheridge, Jr., from the British Isles, and Upper Carboniferous and Permian species, such as the American *Myalina swallovi* McChesney, *Promytilus annosus,* n. gen., n. sp., *P. priscus,* n. sp., and *P. vetulus,* n. sp., is characterized by shells of rather marked convexity, having a prominent, though broadly rounded umbonal ridge, and distinctly indented ventral margin. The beaks are nearly, but not quite, terminal, being in this respect somewhat intermediate between the type species of *Volsella* and of *Mytilus.* The anterior lobe, although poorly defined in some of the Paleozoic species, is more strongly developed than in typical *Mytilus.* This group of species seems to constitute a true gens and deserves a separate generic name. The new generic name *Promytilus* is proposed for this group. In the Carboniferous some of the younger species of *Promytilus* tend to have a relatively greater angle *a* and, correspondingly, a greater relative height than the older species, seemingly paralleling the marked change in form in the evolution of the Myalinidae. For instance, the Irish species *"Modiolus" patulus,* of Viséan age, which is here assigned to *Promytilus,* has a much longer shell (length/height, 2.15), and smaller angle *a* (30°) than any known similar Pennsylvanian or Permian species.

The second group of species, typified by *"Modiolus" subellipticus* (Meek) from the American Pennsylvanian, and *"Modiolus" transparens* (Waagen), from the uppermost Permian of the Salt Range, is certainly distinct in having flatter valves, beaks distinctly posterior to the anterior margin, and only a very obscure indentation of the ventral margin. The angle *a* is consistently small in these forms (40°); and, judging from the trends in other related groups, these species probably are more primitive, more like the ancestral stock of *Volsella,* than the *Promytilus* alluded to above. Furthermore, the crest of the umbonal ridge is narrow, in some instances quite angular, a circumstance not noted in *Volsella, Mytilus,* or *Promytilus.* Although specimens of the *"Modiolus" subellipticus* group are rare, a comparatively large proportion of the specimens known to me possess both valves intact, which suggests that these forms preferred an environment lacking current or wave action competent to dissociate the valves of dead individuals. This situation is in marked contrast to specimens of the *Promytilus patulus* gens in which bivalved specimens are extremely rare. For *"M." subellipticus* and related species the generic name *Volsellina* is proposed.

Judging from the general appearance of shells of the *Promytilus patulus* group, it is not at all unlikely that this stock contains the ancestry of the typical *Mytilus* of Mesozoic and later time. It is highly probable that some of the citations to *Mytilus* in the Paleozoic are to species that should be referred to the Myalinidae. The Mesozoic and Cenozoic volsellas, with their beaks placed well back of the front margin of the shell, are more like the *Volsellina subelliptica* group.

In the Devonian, the genus *Mytilops* Hall seems to be a near relative of *Volsellina,* being characterized by a very elongate form and a relatively small angle *a. Mytilops* is inadequately known, so that critical comparison with Late Paleozoic species is not possible.

Unfortunately, my collections are relatively extensive for only the Missourian, Virgilian, and Wolfcampian divisions of the Late Paleozoic. Nowhere abundant, specimens of *Volsellina* and *Promytilus* are especially rare in the Lower Pennsylvanian and later Permian rocks of North America, and I have had no opportunity to study material from these parts of the geologic column.

Genus PROMYTILUS Newell, n. gen.

Genotype, *Promytilus annosus* Newell, n. sp. Geologic range of genotype, Missourian series, Pennsylvanian.

Shell elongate, thin, with terminal beaks, and a slender anterior termination of the shell, corresponding to the beaks and anterior lobe; lobe well defined but not extended anteriorly beyond the beaks, set off from main part of shell by a broad but well defined sulcus, which extends from the beaks backward to the ventral margin where it coincides with a broad, clearly marked sinus in the shell margin; umbonal ridge well defined, rounded; shell microstructure and hinge as in *Mytilus.*

Range, Mississippian to Permian, Mesozoic?

Remarks.—For a time I debated using *Mytilus* or *Volsella* for the Late Paleozoic shells commonly referred to *Myalina swallovi.* However, the well developed lobe readily separates these species from forms like *Mytilus edulis,* and the terminal character of the beaks distinguishes the Paleozoic forms from typical volsellas of the *modiola* type. Details of form, such as the prominent umbonal ridge and ventral sinus, also differentiate the species in question from Recent *Volsella* and *Mytilus.* In many respects *Promytilus* is structurally and morphologically intermediate between *Volsella* and *Mytilus.* Inasmuch as the Paleozoic genus is somewhat more specialized than *Volsella,* it probably does not lie in the ancestry of that genus. More probably the reduction of the anterior lobe led to development of *Mytilus,* because *Mytilus* passes through an ontogenetic stage similar in form to *Promytilus.* Some of the Triassic and Jurassic shells commonly referred to *Modiolus* may belong to *Promytilus.*

PROMYTILUS SWALLOVI *(McChesney)*

Plate 1, figures 8a, b, 13

Myalina swallovi MCCHESNEY, *1860,* Descriptions of new species of fossils from the Palaeozoic rocks of the Western States, p. 57; ——, *1865,* Plates illustrating in part the new species of fossils from the Palaeozoic rocks of the Western States, and two new species noticed March 1860, published 1865, pl. 2, figs. 6a, b.

Valves "modioloid," with a well developed anterior lobe, and a pronounced anteroventral byssal sinus, which is symmetrical in respect to the anterior and ventral extremities; characterized especially by a relatively upright form, and large angle *a,* around 55°.

Dimensions of the plastotype are as follows: length, 24 mm, height, 18 mm; hinge length, 20 mm ±; convexity, 4 mm ±; greatest dimension, 26 mm; angle *a,* 60° ±.

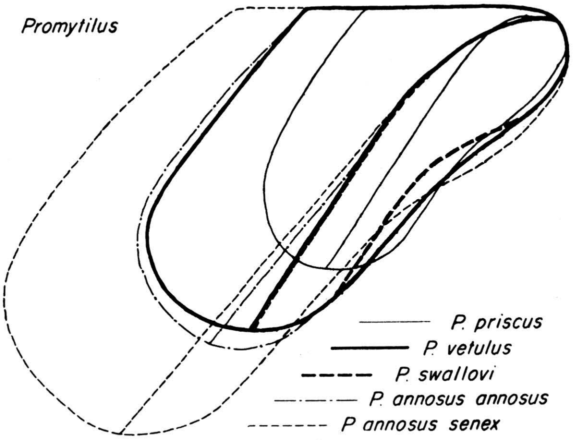


FIGURE 8.—Comparison of form in species of *Promytilus.*

TABLE 4.—*Species of Promytilus, Showing Age and Minimum, Average, and Maximum Dimensions*[1]*, in Millimeters*

Species	Age	Length	Height	Greatest Dimension	Form Ratio	Angle a
		27	20	31	1.35	63.5°
P. vetulus	Wolfcampian	21(6)	16(6)	23(6)	1.34(6)	55.0°(6)
		16	12	17	1.33	49.5°
		32	27	37	1.44	72.0°
P. priscus	Virgilian	15(40)	13(40)	18(40)	1.21(39)	55.5°(41)
		6	5	7	1.04	35.0°
		29	26	32	1.67	62.5°
P. annosus annosus	Upper Missourian	21(42)	17(42)	24(42)	1.31(42)	50.5°(49)
		14	9	15	1.06	34.5°
		36	29	42	1.63	61.5°
P. annosus senex	Middle Missourian	28(124)	21(121)	31(124)	1.33(122)	48.0°(128)
		19	14	20	1.07	36.0°
		24	18	26	1.33	64.5°
P. swallovi	Lower Missourian	21(4)	16(4)	22(3)	1.32(4)	55.0°(4)
		13	10	15	1.30	47.5°

[1] Figures in parentheses indicate number of specimens used. Dimensions given in millimeters.

Comparison.—Table 4 shows that *Promytilus swallovi* differs from *P. annosus* and its varieties in having a greater value for the angle a, and in the smaller average size of the shell. The present species characteristically is somewhat more robust in shell size than is the case in *P. priscus*. Although the angle a is approximately the same in the two species, specimens of *P. swallovi* are relatively longer (1.32) on the average than those of *P. priscus* (1.21). Inspection of average dimensions of specimens of the various species tabulated in table 4 indicates no significant difference between *P. swallovi* and *P. vetulus*. The two are readily distinguished by differences in form, however, especially the greater identation of the byssal sinus in *P. swallovi*.

Material.—This is not a common species, and seemingly all but the original references are to other species of *Promytilus*. Only four of the specimens before me are referable to *P. swallovi*, and these include a sulphur cast of the original. The holotype was long ago destroyed, but artificial casts of it are preserved in the U.S. National Museum and Walker Museum, at Chicago. Only the exterior is visible in the shells at hand, but the form and peculiar shell structure of the Mytilidae is well shown. Commonly, the corrosion of a *Promytilus* shell produces the illusion of faint radial costellae by the unequal solution of the fine radially directed calcite prisms. The artificial cast of the holotype of *P. swallovi* shows faint radial markings, suggestive of radial prisms in the original.

Occurrence.—As known at present, the species seems to be characteristic of the lower part of the Missourian series, but future collecting probably will reveal a somewhat longer stratigraphic range.

There is some uncertainty regarding the horizon from which the holotype was collected, the only information available being that it came from "12 miles northwest" of Richmond, Mo. The stratigraphic section at this locality ranges from uppermost Des Moines beds through the lower part of the Missourian series. Other hypotypes came from lower Missourian beds near Pleasant Hill, Mo. and the middle Missourian Winterset limestone, Dennis formation, Kansas City, Mo.

The shells occur in argillaceous and carbonaceous limestone, associated with brachiopods and mollusks, indicative of a marine environment. One specimen (pl. 1, figs. 8a, b) from Pleasant Hill, Mo. has the two valves in apposition, indicating relatively quite deposition and burial *in situ*.

PROMYTILUS ANNOSUS ANNOSUS Newell, n. sp., n. var.

Plate 1, figures 9, 10

Shell obliquely elongate, with a well developed anterior lobe and sulcus, of which the latter joins the anteroventral margin near the middle to produce a marked sinus; distinguished by an intermediate average value for the angle a, 50.5°, and an intermediate form ratio (length/height), 1.31.

Dimensions of the holotypes are: length, 17 mm;

height, 16 mm; greatest dimension, 21 mm; angle *a*, 62.5°.

Comparison.—The typical variety of the species *Promytilus annosus* is most similar to *P. annosus senex,* from which it differs in having slightly less robust shells, in being relatively shorter, and in having a larger angle between the umbonal ridge and the dorsal margin. Although the differences are well marked where a large suite of specimens of the two varieties are compared, it is probable that they could not be distinguished from each other if adequate collections were lacking. Comparison of the measurements of *P. annosus annosus* with other Late Paleozoic forms is indicated in table 4.

Material.—The variety is based on 42 specimens, all of which were measured and studied. The shell material is relatively well preserved; and, although the inner ostracum seems to be recrystallized, the outer ostracum of both valves shows the peculiar radial prismatic structure of the Mytilidae in the majority of specimens. Hinge characters and musculature were not observed. The holotype (no. 7559) and paratypes are at the University of Kansas.

Occurrence.—As represented in the collection before me, the variety Promytilus annosus annosus occurs in molluscan limestone facies of the upper Kansas City and Lansing groups (upper Missourian), especially Farley limestone, various localities in northeastern Kansas; Bonner Springs shale, shell coquina in the vicinity of Kansas river; Springhill limestone (Plattsburg), Bonner Springs, Ottawa, and Garnett. Kan.; undifferentiated Stanton limestone at the "Mound," Bartlesville, Okla., same, sec. 32, T. 28 S., R. 15 E., Kansas; sandstone of the Rock Lake member, Stanton limestone, sec. 27, T. 11 S., R. 22 E., Kansas; South Bend limestone member, Stanton limestone, 2 miles south of Lansing, Kan., at Nine-Mile school (holotype).

The shells occur in shaly and sandy beds and in shell breccias, suggesting that the living animal preferred a littoral or sublittoral habitat, or at least lived in an environment where the shells could periodically be attached and broken up by waves and currents. All known specimens are separated valves, indicating disturbance of the shells after death.

PROMYTILUS ANNOSUS SENEX Newell, n. sp., n. var.

Plate 1, figures 11, 12; plate 2, figures 4a, b, 6

Myalina? swallovi SAYRE, *1931,* Kansas Geol. Survey, Bull. 17, p. 117, pl. 11, figs. 1, 1a. (Date of imprint, 1930).

Shells similar to the typical variety, but on the average more robust with greatest dimensions 31 mm, as compared with 24 mm for *Promytilus annosus annosus,* with a somewhat longer shell, and a smaller value for the angle *a* (48° as compared with 50.5°).

Dimensions of the holotype are: length, 29 mm; height, 23 mm; greatest dimension, 34; angle *a*, 53°.

Comparison.—Comparative measurements are given in Table 4. The variety *Promytilus annosus senex* has a relatively slender form, due to the small average angle *a*. In respect to the size of the angle this variety has a smaller angle, 48° on the average, than any of the other Pennsylvanian and Permian species thus far discovered. Also, specimens of *P. annosus senex* are larger than other comparable material examined during the present study. Since absolute size of individuals in *Volsella* and *Mytilus* is commonly dependent on ecological conditions, this character in the present form may be without phylogenetic significance.

Material.—The variety *Promytilus annosus senex* is based on more extensive collections than commonly are available for Paleozoic Mytilidae, 128 specimens having been used in framing the above description. The shell material, although somewhat recrystallized, is fairly well preserved, and the characters of form and of the hinge are well shown. In general, the outer surface of the shell is perfectly preserved and shows no appreciable wear. The radial prismatic structure of the outer octracum is evident in both valves in the majority of specimens.

The holotype (no. 7563) and many of the paratypes are at the University of Kansas. Other paratypes are deposited in the Walker Museum, University of Chicago; Peabody Museum, Yale University; and the paleontological collection, University of Wisconsin.

Occurrence.—This variety characterizes the molluscan facies of the cross-laminated oolitic limestones of the Westerville and Drum formations (Kansas City group) of Kansas and Missouri and is represented by numerous specimens in every large collection of fossils from these rocks throughout Kansas and Missouri. Thus far, the variety is not well represented in nonoolitic facies in the Kansas City group. The holotype was collected from the Westerville oolite, at Kansas City, Mo. Other specimens of this variety are from the Graford and Brownwood formations (Missourian), Texas.

The valves are invariably dissociated, and their occurrence in strongly cross-laminated beds indicates burial in the zone of strong wave or current action. Few of the specimens are worn or were broken before burial, but many are coated with a calcareous deposit reminiscent of the algal de-

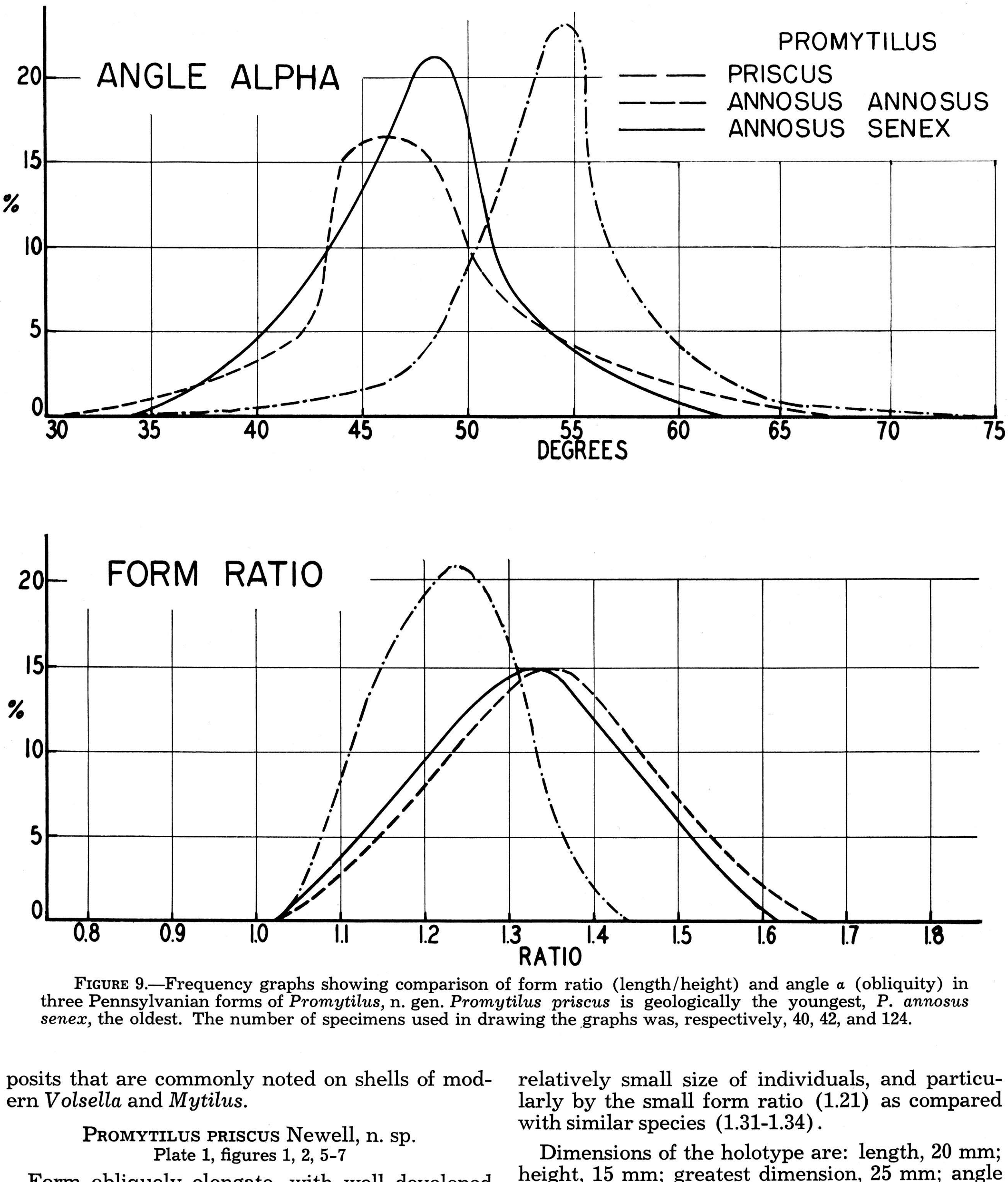


FIGURE 9.—Frequency graphs showing comparison of form ratio (length/height) and angle α (obliquity) in three Pennsylvanian forms of *Promytilus*, n. gen. *Promytilus priscus* is geologically the youngest, *P. annosus senex*, the oldest. The number of specimens used in drawing the graphs was, respectively, 40, 42, and 124.

posits that are commonly noted on shells of modern *Volsella* and *Mytilus*.

PROMYTILUS PRISCUS Newell, n. sp.

Plate 1, figures 1, 2, 5-7

Form obliquely elongate, with well developed anterior lobe and sulcus, and otherwise similar to other Late Paleozoic forms; distinguished by the relatively small size of individuals, and particularly by the small form ratio (1.21) as compared with similar species (1.31-1.34).

Dimensions of the holotype are: length, 20 mm; height, 15 mm; greatest dimension, 25 mm; angle *a*, 46.0°.

Comparison. — Comparative measurements of

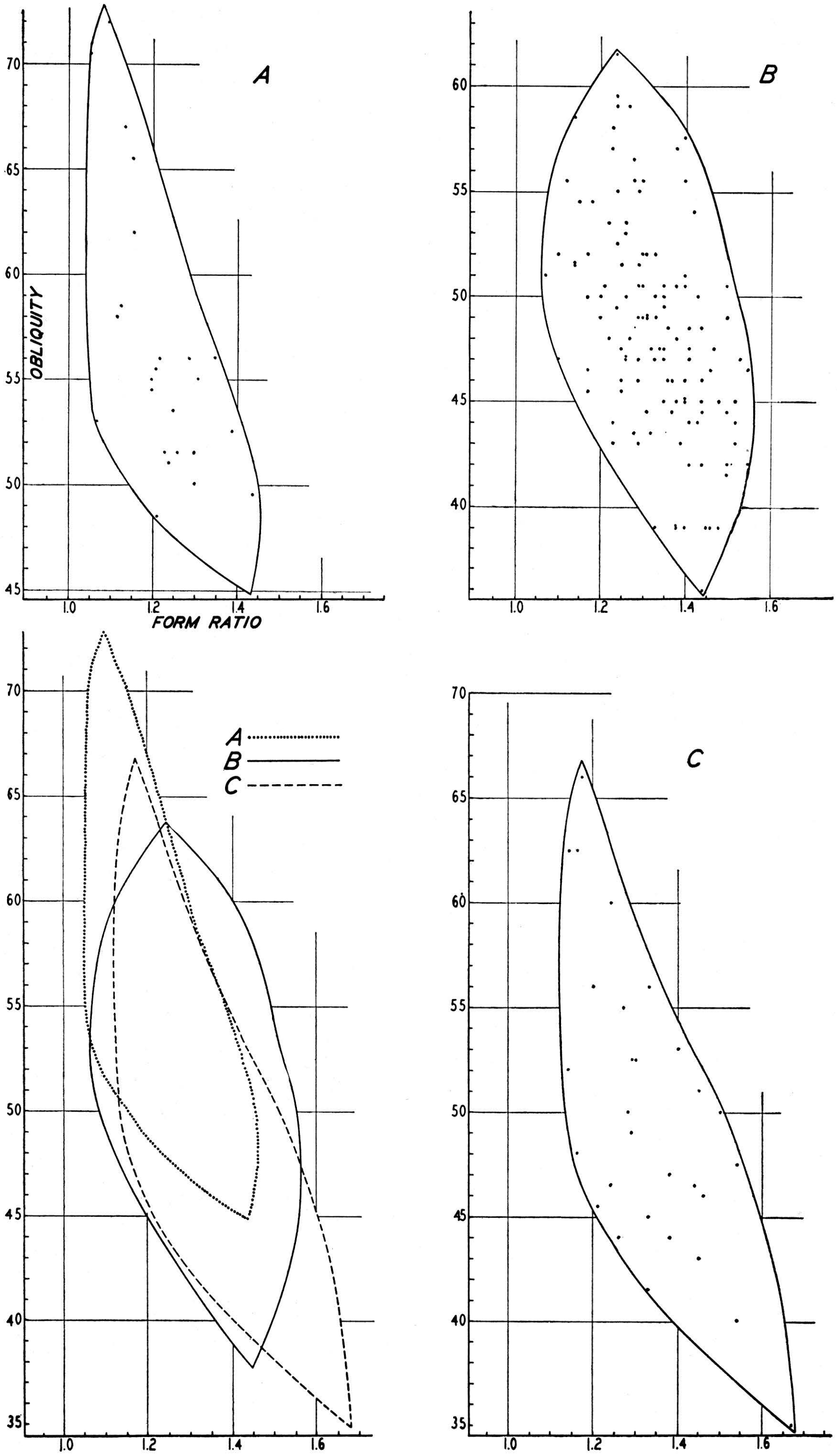


FIGURE 10.—Scattergrams comparing shape in three forms of *Promytilus.* Obliquity is expressed in size of the angle *α*. *A, P. annosus annosus; B, P. annosus senex; C, P. priscus.*

Promytilus priscus and other similar forms are given in table 4. The relatively great height (form ratio 1.21) as compared with similar species distinguishes the present form.

Material.—Forty-one specimens, all dissociated valves, were used in framing the above description. The majority of the specimens are well preserved, but a few, including the holotype, show signs of some surficial corrosion, suffered probably before fossilization. The characteristic structure of the outer ostracum of the Mytilidae is well shown by the radial striations of etched specimens. Hinge characters and interior not observed. The holotype (no. 7751) and several topoparatypes are at the University of Kansas. A few paratypes are in the paleontological collections at the University of Wisconsin.

Occurrence.—The new species *Promytilus priscus* seems to be rather widely distributed in Virgilian rocks of the northern Mid-Continent area. In the collections before me specimens of the species are recognized from the Tarkio limestone (Wabaunsee), sec. 32, T. 10 S., R. 10 E., Kansas; Auburn shale (Wabaunsee), near Foraker, Okla.; Wakarusa limestone (Wabaunsee), near Thurman, Iowa and Osage county, Okla.; limestone above Brownville horizon (Wabaunsee?), near Thurman, Iowa; Lawrence shale (Douglas), Ft. Leavenworth, Kan.; Doniphan shale (Shawnee), Snyderville, Neb. and Greenwood county, Kan.; and the Dover limestone (Wabaunsee), NW cor. sec. 14, T. 13 S., R. 13 E., Kansas (includes holotype and several topoparatypes).

The specimens occur in association with other pelecypods and gastropods in arenaceous and argillaceous limestones. The fact that the valves are separated suggests burial within the zone of wave and current action. However, none of the material at hand is badly macerated, and few valves show any signs of wear prior to burial.

PROMYTILUS VETULUS Newell, n. sp.

Plate 1, figures 3, 4

This species is closely similar to *Promytilus swallovi* as regards size, proportions, and the value of the angle *a*. There is, however, a slightly more pronounced indentation of the anteroventral margin in *P. swallovi,* and in the present species the anterior part of the shell is somewhat more slender. Comparative measurements of *P. vetulus* are given in table 4.

Dimensions of the holotype are as follows: Length 27 mm; height, 20 mm; greatest dimension, 31 mm; angle *a*, 55°.

Material.—This species is based on seven specimens from various horizons in the Big Blue (Wolfcampian) rocks of Kansas. The material is not adequate to permit generalizations regarding the normal environment under which the shells were buried. The matrix adherent to the specimens, however, is an argillaceous limestone and argillaceous dolomite, and in each case the valves are separate, suggesting some current action at the site of deposition. Some of the specimens are sufficiently well preserved to exhibit the shell structure of the Mytilidae, but internal characters are not shown.

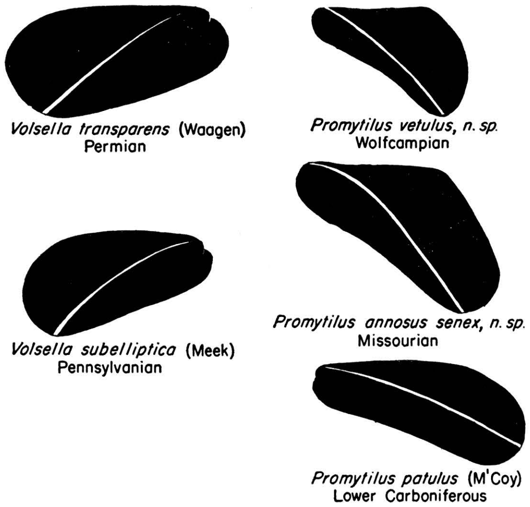
The holotype (no. 7552) and paratypes are deposited at the University of Kansas.

Occurrence.—Thus far the species has been recognized only in rocks of Wolfcampian age. The holotype was collected from the Admire group, 1.7 miles south of Americus, Kan. Paratypes came from the Admire group, just west of Neosho river, Kansas; Fort Riley limestone (Chase group), at the railroad quarry, NE¼ sec. 36, T. 16 S., R. 7 E., Kansas; Florence limestone (Chase group), Grand Summit, Kan.

Genus VOLSELLINA Newell, n. gen.

Genotype, *Pleurophorus subellipticus* Meek. Geologic range of genotype, Pennsylvanian.

Shell elongate, thin, with subterminal beaks, and a small, but distinct anterior lobe, which extends slightly ahead of the beaks; dorsal and ventral margins relatively straight, diverging posteriorly in the order of 20°, more or less; anterior sulcus and ventral sinus very obscure or lacking; umbonal ridge narrow, subangular, only slightly arcuate, with



Volsella transparens (Waagen)
Permian

Promytilus vetulus, n. sp.
Wolfcampian

Volsella subelliptica (Meek)
Pennsylvanian

Promytilus annosus senex, n. sp.
Missourian

Promytilus patulus (M'Coy)
Lower Carboniferous

FIGURE 11.—Form series in *Volsellina* and *Promytilus*. There is a tendency for younger *Promytilus* to become more upright in form.

backward convexity, extending to the posterior end of ventral margin where the shell is slightly angular; convexity of valves rather low, posterior end rounded, laterally flattened, nearly spatulate; ligament, shell microstructure, as in other Mytilidae; endentulous.

Range, Pennsylvanian to Permian.

Remarks.—Superficially, this group of shells recalls the heterodont genus *Pleurophorus,* but it is nearly certain that they are not closely related, differing markedly in hinge structures. From *Volsella ("Modiolus")* and similar Mytilidae it differs in the flattened valves, narrow costa-like umbonal ridge, and in the nearly straight ventral margin. Almost all of the shells examined by me are in the bivalved condition, denoting quiet water deposition, as contrasted with the *Promytilus,* and were found in argillaceous shales. One specimen of *V. subelliptica* from the Atoka formation is preserved as an internal mold in a fine, calcareous sandstone. Only one valve is represented.

In addition to the Pennsylvanian *Volsellina subelliptica,* this new genus is represented by *V. transparens* (Waagen), from the Upper Productus limestone (*Cyclolobus* zone of the Permian).

VOLSELLINA SUBELLIPTICA (Meek)

Plate 1, figures 14-16

Pleurophorus subellipticus MEEK *1867,* Am. Jour. Sci., vol. 44, p. 181.

Modiola? subelliptica MEEK, *1872,* U.S. Geol. Survey of Nebraska, p. 211, pl. 10, fig. 5.

Shell elongate, laterally flattened, lenticular, equivalve, with relatively straight dorsal and ventral margins which diverge posteriorly at about 20°; beaks low, broadly rounded, not extended generally above the hinge line; hinge margin about two thirds of the shell length, the shell being broadly spatulate and wedge-shaped in the posterior one-third; posteroventral margin angular where the straight ventral margin meets the rounded posterior margin; umbonal ridge narrow, subangular, extending nearly straight across the shell, or in a shallow arc, from the beaks to the posteroventral angle of the shell margin; the angle *a* is relatively small, 35° to 44°, increasing only slightly during growth, because of the small curvature of the umbonal ridge; form ratio about 2.0, and the length equal to the greatest dimension.

Measurements of Volsellina subelliptica

	Length (mm)	*Height (mm)*	*Thickness (mm)*	*Angle a*
Holotype	24.0	13.0	......	38°
Hypotype 1	22.0	11.0	3.5	44°
Hypotype 2	34.0	17.0	6.0	44°

Comparison.—The only species with which I am acquainted that is closely comparable to this one is *Volsellina transparens* (Waagen), from the uppermost Permian of the Salt Range in India. From Waagen's figures it seems that the Permian species differs from *V. subelliptica* in having a relatively short hinge, extending only about one half the shell length. Also the Indian specimen is larger than the largest known American specimen. As in *V. subelliptica,* the Permian species has a narrow and well defined umbonal ridge, but there is a pronounced tendency in the latter for the ridge to become subdued and ill-defined toward the posterior extremity.

Material.—This species has been cited from many horizons and localities; but in the absence of adequate illustrations, I am relatively certain of the identification in only two collections that have been available to me. Meek's type material came from the Willard shale (Wabaunsee), at Nebraska City, Neb. A poorly preserved internal mold was collected from the lower Atoka beds near Muskogee, Okla. Two hypotypes included in this study are from a shale in the Jacksboro limestone (lower Virgil), 4½ miles east of Jacksboro, Tex. The holotype is at the U.S. National Museum and two hypotypes are at the University of Wisconsin.

Occurrence.—Stratigraphic occurrences are indicated above. Undoubtedly this species has a relatively long range and will ultimately be recorded from many horizons in the Pennsylvanian. Probably bases for specific or varietal differentiation within these shells will be discovered when adequate material is available. Both the Texas and Nebraska occurrences are in fine argillaceous shale, and specimens with the valves in position indicate burial in relatively quiet waters as contrasted with the usual occurrence of *Promytilus,* in which the valves generally are separated and commonly broken, being imbedded in cross-bedded coquinoid limestones.

Genus LITHOPHAGA Bolten, 1798

Lithophaga J. F. BOLTEN, *1798,* Mus. Boltenianum, p. 156.

Lithodomus CUVIER, *1817,* Le Régne, vol. 2, p. 471.

Genotype, by monotypy, *L. mytiloides* Bolten=*Mytilus lithophagus* Gmelin. Geologic range of genotype, Recent.

Shell relatively small, smooth, elongate, subcylindrical, with terminal or subterminal beaks and a laterally compressed wedge-shaped posterior.

Geologic range, Carboniferous to Recent.

Remarks.—The shell of *Lithophaga* is distinguished from *Volsella* and similar Mytilidae chiefly by its cylindrical form, being similar to other mytilids in other respects. *Lithophaga* is, however, highly specialized as to habit and habitat, modern species being confined to the shallow water littoral and sublittoral zones of limestone coasts in warm waters, where the living animal bores cylindrical holes in the limestone within which the animal spends its life. According to Pelseneer (1906, p. 252), *Lithophaga*

> bores its hole by the aid of the acid secretion of glands situated in the anterodorsal and posterodorsal regions of the mantle.

Specimens of *Lithophaga* are quite rare in Paleozoic rocks, but several species have been described from the Lower and Upper Carboniferous and Permian in many parts of the world. There is nothing to indicate whether or not the Paleozoic lithophagas had acquired the rock boring habit. It is even possible that the close resemblance between these early forms and the Recent species is homeomorphic. However, no good reason has thus far been advanced for placing the Paleozoic species in a separate genus or subgenus.

LITHOPHAGA SUBELLIPTICA Sayre

Plate 4, figures 3-5

Lithophaga subelliptica SAYRE, *1931*, Kansas Geol. Survey, Bull. 17, p. 123, pl. 12, figs. 9, 9a. (Date of imprint, 1930).

This species is extremely rare, being represented in our collections by only three specimens that are at all instructive, and of these only the holotype, an immature individual, is complete. The holotype is clearly congeneric with many of the other Carboniferous species from Europe and Asia that have been referred to *Lithophaga*. It should be obvious, however, that the specified characters cannot be known from the scanty material at hand. Two topotypes before me are many times larger than the holotype, but they both are incomplete so that the details of form are not well shown.

All of the specimens are subcylindrical, relatively smooth, with subparallel ventral and dorsal margins; slight anterior lobe extends just perceptibly beyond the low, rounded and non-protuberant beaks; approximately two thirds of the shell length behind the front margin, the posterior edge slopes downward obliquely at a low angle to form a somewhat narrow and extended posterior extremity. The dimensions of the holotype are as follows: Length, 11.5 mm; height, 4.5 mm.

Occurrence. — Westerville limestone (Kansas City group), Kansas City, Mo. (topotypes, nos. 7566 and 7567, Univ. Kansas) and Muncie, Kan. (holotype, no. 59, Univ. Kansas). The shells were found in cross-bedded oolite, indicative of deposition under conditions of strong current action.

Genus LITHODOMINA Waagen, 1881

Lithodomina WAAGEN, *1881*, India Geol. Survey, Mem., Palaeontologia Indica, ser. 13, pp. 264-266.

Genotype, *Lithodomina typa* Waagen, 1881; range of genotype, uppermost Permian, India.

According to Waagen, the shells of *Lithodomina*

> are more or less elongate, equivalve, very excentric, with subanterior beaks, little developed anterior part of the shell and very elongated posterior part, and with nearly parallel dorsal and ventral margins. The beaks are singularly flattened as in *Lithodomus (Lithophaga)*. The hinge is edentulous. Along the hinge line extends a long, not very deep, furrow for the insertion of an internal ligament. There seem to be two muscular impressions, between which an entire pallial line seems to extend, but no distinct observation on this point is possible. The structure of the shell is very thin, devoid of every kind of sculpture and, if well preserved, shining smooth. Only with a strong magnifying lens, very fine distant striae of growth are observable.
>
> From all these characters it appears that the shells belonging to *Lithodomina* are most nearly related to *Lithodomus*, the chief difference consisting in a more strongly developed anterior part of the shell, which is very likely coincident with a stronger development of the anterior adductor.

Geologic range of the genus, zone of *Cyclolobus*, Salt Range, India.

Remarks.—There is sufficient ground for separating this group of shells from *Lithophaga* on form differences alone. Unfortunately, the characters of *Lithodomina* are not adequately known and Waagen admitted the possibility that these shells may not even belong to the Mytilacea. At the present time the genus is unknown outside the original occurrence in the uppermost beds of the Upper Productus limestone, in the Salt Range.

FAMILY MYALINIDAE FRECH, EMEND. NEWELL.

Shell inequivalve, the right valve slightly less convex and slightly smaller at the margin than the left; beaks at or near the small and projecting anterior end; posterior margin subovate, quadrate, or extended in a posterodorsal auricle; ligament external, duplivincular, mainly opisthodetic, but with amphidetic remnant before the beaks in some genera; hinge edentulous, or with weak cardinal teeth $\frac{1}{2a, 2b}$ at the front end of hinge; inner shell layer lamellar, probably aragonite; outer layer composed of calcite, either homogeneous or finely prismatic, the prisms and optic axes nearly normal to the shell surface; musculature characteristically anisomyarian, but monomyarian in a few species. The genera that unquestionably belong here do not possess well defined radial ornamentation, and all pass through a form stage in the early ontogeny similar to adult *Modiolopsis*.

Remarks.—The phylogeny of this family cannot as yet be determined with any degree of completeness, because the shell structure, ontogeny, and internal characters are unknown for the majority of Mississippian and older species that may belong here. Several of the Ambonychiidae resemble some of the myalinas so closely as to suggest that the similarities are more than superficial. Furthermore, some of the genera tentatively included under the Myalinidae have not yielded adequate data on the early growth stages as yet, and it may be that further information will indicate that some of these genera do not belong in this family.

The origin of the family is not known, but presumably both the Mytilidae and Myalinidae were derived from an Ordovician or Silurian pelecypod having a configuration like *Modiolopsis* and a parivincular ligament. The oldest genera known to me that I would tentatively include in the Myalinidae are *Myalinoptera* and *Hoplomytilus* from the Devonian. Neither of these is well known.

The family is well represented in the Mississippian and, particularly, is an important element in the Pennsylvanian faunas, undergoing a marked decline in the Permian. Triassic and Jurassic species in many parts of the world have been referred to *Myalina*, and almost certainly the few forms known to have had a duplivincular ligament should be referred to the family. So far as I am aware, members of the Myalinidae are not known in Cretaceous or younger rocks.

Genus MYALINA De Koninck, 1842

Myalina DE KONINCK, *1842*, Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique, p. 125[1]. HIND, *1897*, Palaeontographical Soc., vol. 51, p. 103; NEWELL, *1940*, Am. Jour. Sci., vol. 238, pp. 286-295, pl. 1, text figs. 1, 2.

Genolectotype, *Myalina goldfussiana* De Koninck, 1842, designated by Stoliczka, 1871, Palaeontologia Indica, vol. 3, p. 366. Geologic range of genotype, Viséan.

Mytiliform shells with terminal beaks and a pronounced forward obliquity, generally unornamented, but the left valve in some species roughened by relatively prominent growth lamellae; right valve slightly smaller (discordant) and less convex than the left valve; ligament area opisthodetic, relatively broad, traversed by several coarse parallel ligament grooves, which descend posteriorly from a place under the beak toward the hinge axis; area bounded anteriorly on the right valve by a large ridge, which extends posteroventrally from the beak across the end of the ligament area to form a kind of tooth whose ventral extremity articulates with the ventral end of a corresponding furrow of the left valve; anisomyarian; umbonal musculature consisting of three pits in a closely spaced posterodorsal-anteroventral series, of which the middle impression is the largest; pallial line consisting of closely spaced, discrete pits, which tend to coalesce and form a continuous line in the posterior half of the shell; posterior impressions elongated parallel to the rear margin, extended dorsally into two processes, of which the rear one is the longer; a series of closely spaced muscle pits extending from the inner margin of the posterior muscle impression forward into the umbonal cavity.

The shell microstructure in the type species is unknown. In various species that are clearly congeneric with *Myalina goldfussiana*, the shell consists of a relatively thick inner lamellar ostracum, probably originally composed of aragonite, and a thin outer ostracum made up of very fine, irregularly polygonal prisms of calcite arranged normal to the shell surface. The prisms of the right valve are much coarser than those of the left valve in the typical subgenus.

For the sake of documentation, the measurements of three specimens of the genotype are given. Numbers 1 and 2 are right and left valves, respectively, of the holotype; number 3 is a left valve in the Burrow collection at Cambridge (no. 463).

Measurements of Myalina goldfussiana, in millimeters

	no. 1	*no. 2*	*no. 3*
Convexity	11	14	....
Length	58	60	45
Height	48	50	37
Hinge length	42	43	33
Greatest dimension	....	....	49

Remarks.—Accompanying the original diagnosis of *Myalina* were the descriptions of three new species,—*M. goldfussiana*, *M. lamellosa*, and *M. virgula*. In the absence of designation of a genotype, these species automatically were genosyntypes. All of them were originally found in the Viséan rocks of Belgium. The earliest legal designation of a genolectotype that comes to my attention was made by Stoliczka in 1871. He selected *M. goldfussiana* as the type of *Myalina*, thereby specifically establishing the characteristics of the genus.

Without exception, writers subsequent to De Koninck have turned to the published diagnoses of that author to learn the fundamental characters of *Myalina*. Modern writers are learning that this procedure, though convenient, leads all too often to perpetuation of erroneous concepts. Hardly any descriptions of fossils are wholly objective, nor is it necessarily desirable that they should be. Each writer is obligated to evaluate his specimens to the best of his ability, and to avoid cluttering up the literature with extraneous details that seem not to be significant. It is fairly well understood today that an author's conclusions regarding his own genera or species have no validity where they are at variance with the characters exhibited by the type specimens.

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[1] This work bears the date of imprint 1842-1844. I am assuming that the first part of the book containing descriptions of pellecypod species, was published in 1842, because that is the date given for these fossils in De Koninck's later writings.

De Koninck's diagnosis of *Myalina* is at variance with the characters of the subsequently designated genotype. How he arrived at the characters of the genus as reported by him has no legal bearing on the case. The original diagnosis of *Myalina* is as follows (free translation):

> Shell equivalve, not equilateral, elongated or oblique, straight or slightly arched at the cardinal edge. Hinge without teeth. Ligament internal, covering completely a large facet, traversed longitudinally by a number of narrow furrows incised parallel to the cardinal border. Beaks terminal, acute, ordinarily small and slightly recurved. Internally, and immediately adjoining these, occurs a small septiform lamina similar to that observed in certain species of *Mytilus*.
>
> The external form of the genus *Myalina* resembles that of *Mytilus*. In the form of its ligamentary facet it resembles *Pterinea*. Generally it seems to be intermediate between the two and seems to form a natural transition from one to the other. The valves of the species that we report on here are hermetically closed on all sides. It is then not probable that the animal possessed a byssus by which it could attach itself to submarine objects. Their shell is rather thick. Although we have not been able to inspect the muscle impression of this genus we suppose that it must be placed among the dimyarian mollusks since it is rather probable that the small lamina situated next to the beaks served as a surface of attachment of the anterior muscle. (De Koninck, 1842, p. 125)

At a later date De Koninck corrected some of the errors in the original diagnosis:

> Valves subequal, mytiliform, ordinarily higher than long; beaks generally pointed, terminal, provided with an anterior septum; cardinal margin broad, flat, with several longitudinal cartilage furrows; two muscle impressions, pallial line simple . . .
>
> When I created this genus I had at my disposition only a small number of fragmentary Carboniferous examples, which all appeared to be equivalved. However, W. King and F. McCoy, having had occasion to study entire well preserved Permian species related to the genus, have made the observation that the right valve is nearly always smaller than the left. Since then I have had occasion to note the same on some Carboniferous species, and I am in accord with these paleontologists in concluding that the shell must not necessarily be equivalved to belong to the genus, providing that it possesses other characters indicated in the diagnosis. (De Koninck, 1885, p. 167).

Through the good auspices of Dr. Pierre Bonnet I have had the privilege of studying the holotype of *Myalina goldfussiana,* property of the École des Mines, in Paris. The holotype consists of incomplete portions of two massive complementary valves lacking the posteroventral one third of the shell. The substance of the shell is recrystallized, so that the original microstructure cannot be determined. The shell is mytiliform, and the right valve is both smaller and slightly less convex than the left valve. Preparation of the interior of the valves has revealed that this species does not possess an umbonal septum. The ligament area is relatively broad, and is traversed by four, coarse ligament grooves which converge with the hinge axis posteriorly at an acute angle. On the right valve the anterior terminus of the ligament area is marked by a large, vertical ridge or tooth, which corresponds in position to a shallow furrow, or socket, in the left valve. When the valves are in tight apposition, only the ventral portion of the tooth is in contact with the socket; and the two diverge upward at an angle corresponding with the divergence of the ligament areas of the two valves above the hinge axis.

The shell form is not well shown by the imperfect holotype, so observations were made on a supplementary specimen of the same species from the Carboniferous limestone of Settle, England. It was lent to me by Dr. O. M. B. Bulman, of Cambridge University. This specimen, a left valve, was erroneously identified by Hind as *Myalina peralata* De Koninck (Hind, 1895, p. 119, pl. 7, fig. 3). The muscle pattern within the umbonal cavity of both valves of the holotype is well shown (pl. 9, figs. 5a-6b) but much of the general musculature had to be interpreted from another Viséan specimen of *M. goldfussiana* described by De Koninck (1885, pl. 29, fig. 7). Photographs of this specimen were sent me by Dr. F. Demanet, of the Musée Royal d'Histoire Naturelle, in Brussels.

As herein defined, the genus *Myalina* seems to be restricted to Carboniferous and Permian rocks. Similar Devonian and post-Paleozoic forms commonly referred to the genus probably should be differently classified.

Three subgenera of *Myalina* are recognized, *Myalina* s.s., *Orthomyalina,* and *Myalinella.* Critical examination of the evidence reveals that these groups, for all their superficial resemblance, followed different paths of evolution during the Late Paleozoic. They are not form groups, but represent true genetic series.

Subgenus MYALINA s.s.

Thick-shelled species like the genotype, which have a well developed anterior lobe, at least in the left valve; primitive species have a marked prosocline obliquity and a marked homeomorphic resemblance to *Promytilus,* advanced species become acline, or opisthocline, and develop a posterior auricle, reminiscent of some Pteriidae and some Ambonychiidae; in primitive forms the valves are nearly equal; in advanced forms the valves are markedly unequal, left valves commonly more rugose than right valves, being particularly roughened on the anterior lobe.

Geologic range, Carboniferous and Permian.

Remarks.—Species of the subgenus *Myalina* present one of the most complete records of subgeneric evolution known to me among Paleozoic pele-

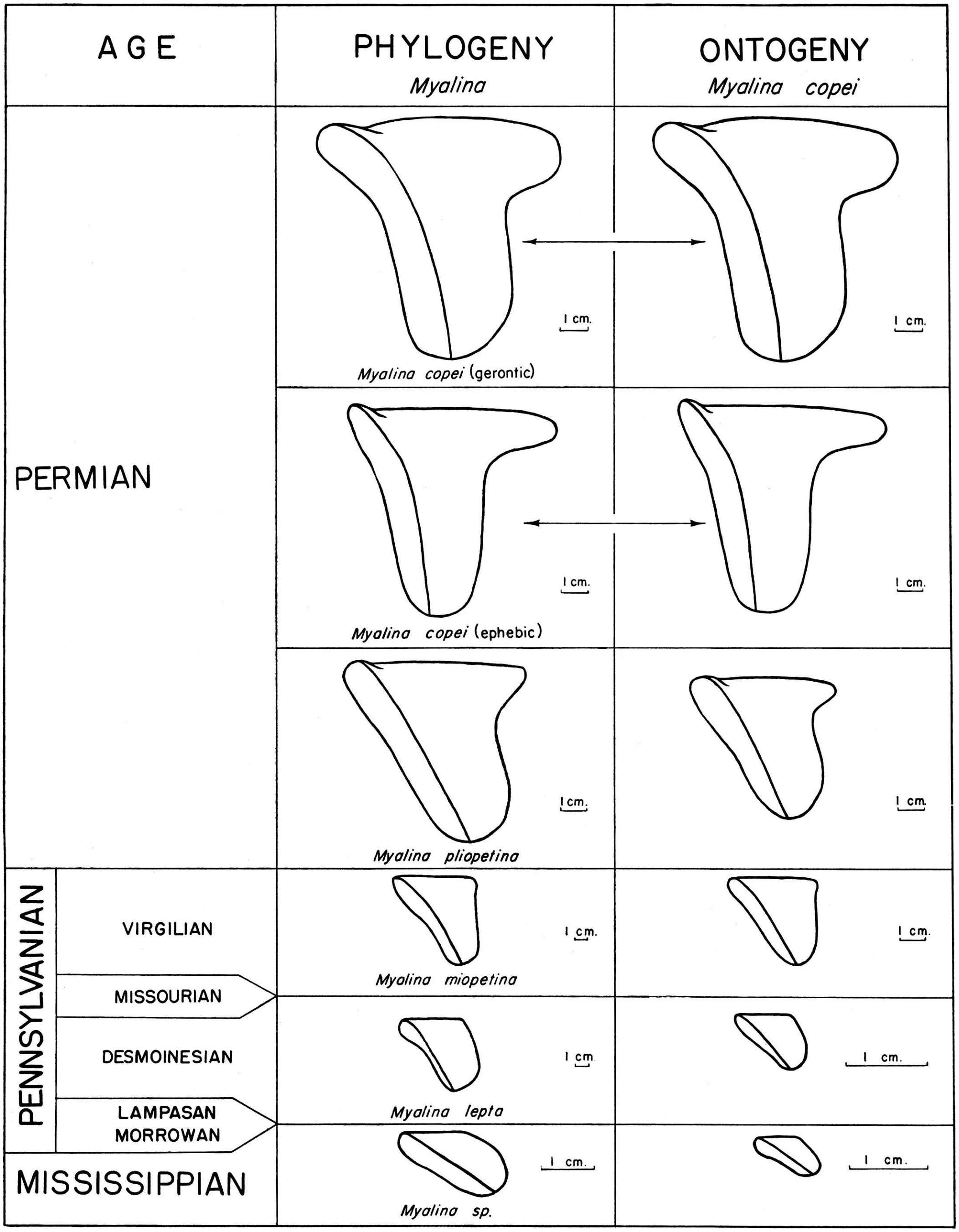

FIGURE 12.—Palingenesis of some species of *Myalina* (*Myalina*). The outlines of a succession of species are shown in stratigraphic succession. These outlines are correlated with ontogenetic stages of one of the most highly specialized species, *M. copei*. Only a critical examination will reveal form differences in the two series. The gerontic stage of *M. copei* illustrates the interesting fact that gerontism is not reached simultaneously in all bio-characters. The cessation of expansion of the rear auricle, and general slackening of peripheral increase are interpreted as gerontic characters. However, the forward curvature of the umbonal ridge, responsible for decreasing obliquity, seems to be unchecked.

TABLE 5.—*Species of Myalina (Myalina), Showing Age and Minimum, Average, and Maximum Dimensions*[1]*, in Millimeters*

Species	Age	Length	Height	Greatest Dimension	Form Ratio	Angle *a*	Angle β
M. (M.) sinuata[2]	Lower Guadalupian	85.0 (1)	75.0 (1)		1.10 (1)	60° 67°(4) 75°	Very acute
M. (M.) wyomingensis var. *thomasi*	Lower Guadalupian	32.0 47.0 (10) 59	28.0 43.0 (11) 57.0	39.0 56.0 (10) 70.0	1.00 1.11 (10) 1.27	47° 55°(16) 73.0°	Obtuse, broadly rounded
M. (M.) copei	Wolfcampian	68.0 78.0 (17) 92.0	71.0 83.7 (17) 94.0	74.0 80.9 (17) 101.0	0.83 0.94 (17) 1.01	76.0° 84.0°(17) 104.0°	14.0° 32.0°(17) 48.0°
M. (M.) pliopetina	Wolfcampian	56 76 (2) 97	59.0 10.4 (5) 95.0	70.0 81.2 (5) 114.0	0.95 0.98 (2) 1.02	59.0° 62.3°(5) 70.0°	40° 47° (2) 55°
M. (M.) aviculoides	Wolfcampian	37 (1)	41 (1)	44 (1)	0.90 (1)	78° (1)	95° (1)
M. (M.) petina	Virgilian	46.0 47.0 (2) 48.0	54.0 55.0 (2) 56.0	63.0 64.0 (2) 65.0	0.82 0.85 (2) 0.88	64.0° 68.0°(2) 72.0°	75° 76° (2) 76.5°
M. (M.) miopetina	Virgilian	52.0 56.6 (3) 60.0	48.0 41.2 (3) 61.0	63.0 70.6 (3) 75.0	0.98 1.03 (3) 1.08	59.0° 61.0°(3) 63.0°	82.0° 89.0°(3) 96.0°
M. (M.) glossoidea	Virgilian and upper Missourian	26.0 48.3 (8) 65.0	30.0 55.7 (8) 74.0	33.0 61.5 (8) 82.0	0.83 0.87 (8) 0.90	73.0° 76.3°(8) 83.0°	93.0° 109.0°(8) 118.0°
M. (M.) arbala	Missourian	26 52 (4) 69	27 60 (14) 77	33 69 (14) 92	0.71 0.88 (14) 1.10	58.0° 71.3°(14) 87.0°	80.0° 94.0°(13) 117.0°
M. (M.) wyomingensis	Desmoinesian to Wolfcampian	13.0 32.5 (11) 51.0	12.0 32.6 (11) 48.0	16.0 39.4 (11) 58.0	0.87 1.05 (11) 1.12	65.0° 70.5°(12) 81.0°	95.0° 116.0°(11) 139.0°
M. (M.) lepta	Desmoinesian	26.0 28.2 (4) 33.0	23.0 24.7 (4) 28.0	30.0 33.5 (4) 40.0	1.1 1.1 (4) 1.2	55.0° 55.5°(4) 59.0°	108.0° 119.0°(4) 124.0°
M. (M.) copha	Lampasan	5.0 10.4 (16) 25.0	4.5 8.1 (16) 20.0	6.0 11.5 (16) 27.0	0.9 1.2 (16) 1.5	43.0° 55.5°(16) 75.0°	Obtuse, broadly rounded

[1] Figures in parentheses indicate number of specimens used. Dimensions given in millimeters.

[2] Known only from internal molds; therefore, measurements are not reliable.

cypods. There is a graded series of forms from species like *Myalina wyomingensis* to highly specialized species like *Myalina copei*. The progression of form displayed in the ontogeny of some of the Permian species corresponds with the stratigraphic sequence of the fossils, so that the record seems to be unusually complete (text figs. 12, 14, and 15). Inasmuch as some species have the anterior lobe much more pronounced in the left valve than in the right, isolated right valves may be mistaken for representatives of the subgenus *Myalinella* or *Orthomyalina*, in which the anterior lobe is lacking, or nearly so. Species of *Myalina*, s. s., are among the most useful guide fossils among Late Paleozoic pelecypods, and rank favorably with many of the brachiopod families. It is unfortunate that the record of the myalinas seems to be extremely scant outside of the United States.

It is difficult to make any generalizations about the ecology of *Myalina*. The shells are found in all sorts of limestones and limy calcareous shales, less commonly in sandstones. Bivalved shells are common, as are shells that obviously were torn apart by current or wave action. It is possible that species of this subgenus lived under a variety of ecological conditions.

MYALINA (MYALINA) COPHA Newell, n. sp.

Plate 7, figure 3

Valves almost, but not quite equally convex, relatively small for a *Myalina,* shaped like *Promytilus,* with an elongate form, marked prosocline obliquity, pronounced anterior lobe and deep, well-defined sulcus; left valves quite rugose with projecting shell lamellae, right valves relatively smooth. Comparative measurements are given in Table 5. Measurements of the holotype are as follows: Length, 13.5 mm; height, 10.0 mm; greatest dimension, 14.0 mm; angle *a*, 49°.

Comparison.—This species is closely similar in form with the juveniles of geologically younger myalinas, so presumably it is more like the ancestral stock than are the majority of myalinas. Comparison of *Myalina (Myalina) copha* with the undescribed Mississippian form shown on plate 7, figure 4, suggests that the latter is even more primitive than *M. (M.) copha* in the smaller value of the angle *a*. The close resemblance between *M. (M.) copha* and other primitive myalinas with *Promytilus* is probably homeomorphic. The two can be distinguished, of course, by differences in ligament areas and shell microstructure, distinctions by which the Myalinidae and Mytilidae are differentiated. Species of *Promytilus* known to me have very smooth shells and are equivalve. The possibility must be recognized that the material on which *M. (M.) copha* is based is not fully mature, in which case the small size of the individuals, and their primitive characters are juvenile features and do not have the significance that I have ascribed to them. However, the species is founded on quite a number of specimens, the largest of which shows the characters believed to be distinctive of the new species.

Material.—The species is based on 16 specimens, holotype and topoparatypes, from thin, impure limestones. The material is not very well preserved, but the critical characters of the Myalinidae can be observed. The holotype (no. 7568) and some topoparatypes are at the University of Kansas. Other topoparatypes are at Yale University.

Occurrence.—Associated with other pelecypods and brachiopods in thin impure limestones at the top of the Webber's Falls sandstone member of the Atoka formation (Lampasan), in the bed of Verdigris river at Okay, northeast of Muskogee, Okla.

MYALINA (MYALINA) LEPTA Newell, n. sp.

Plate 3, figures 6a, b, 9a, b

Shell slender, markedly prosocline, with nearly parallel anteroventral and posterodorsal margins; anterior lobe well developed in left valve, but wholly lacking in the right valve; hinge line about two thirds as long as the shell length; the two valves only slightly and about equally rugose, except for the anterior lobe of the left valve, which is roughened by imbricating growth lamellae; distinguished especially by the relatively great length (average form ratio, 1.1), the small angle *a* (average 55.5°), and a large value for the angle *b* (average, 119°); the outer ostracum in both valves is prismatic. Comparative measurements are given in table 5. Measurements of the holotype are as follows: length, 33 mm; height, 28 mm; greatest dimension, 40 mm; angle *a*, 59°; angle *b*, 120°.

Comparison.—*Myalina (Myalina) lepta* is quite similar to the young of the majority of myalinas, and individuals are relatively small, characteristics which indicate that the species is a primitive representative of the genus. In many respects *M. (M.) lepta* is intermediate in characters, as well as geologic age, between *M. (M.) copha* and *M. (M.) wyomingensis.* From *M. (M.) copha* the present form is distinguished by having a less prominent anterior lobe on the left valve and no perceptible lobe on the right valve. The shell is somewhat shorter than in *M. (M.) copha* (form ratio 1.1 compared with 1.2), but the principal difference lies in the relative prominence of the umbones in the latter species. In *M. (M.) lepta* the right valve is relatively much smaller and flatter than the right valve in *M. (M.) copha.*

Myalina (Myalina) wyomingensis is distinctly more advanced than *M. (M.) lepta* in being shorter (form ratio 1.05 as against 1.1), in having a larger angle *a* (70.5° as compared with 55.5°), and a smaller value for the angle *b* (116° as compared with 119°).

Material.—This species is based on four well preserved specimens that exhibit details of form and structure. The holotype (no. 21205) and three topoparatypes are in the collections of the University of Wisconsin.

Occurrence.—Associated with brachiopods and other mollusks in fine, argillaceous shales of the middle Boggy formation (Desmoinesian) at the center of sec. 17, T. 2 N., R. 7 E., Oklahoma.

MYALINA (MYALINA) WYOMINGENSIS (Lea)

Plate 3, figures 1-4, 7, 10; plate 7, figure 6

Modiola wyomingensis LEA, *1853,* Philadelphia Acad. Nat. Sci., Jour., vol. 2, p. 205, pl. 20, fig. 1a.

Myalina recurvirostris MEEK AND WORTHEN, *1860,* Philadelphia Acad. Nat. Sci., Proc., p. 456; ——, *1866,* Illinois Geol. Survey, vol. 2, p. 344, pl. 26, figs. 9a-c.

Myalina wyomingensis GIRTY, *1903,* U. S. Geol. Survey, Prof. Paper 16, p. 422, pl. 8, figs. 8-13; ——, *1908,* U.S. Nat. Museum, Proc., vol. 34, p. 290, pl. 19, figs. 2, 3.

Shell volselloid, with a well developed anterior lobe on the left valve and a distinct, though relatively small, lobe on the right valve; left valve quite rugose, right valve relatively smooth and somewhat smaller (discordant) and flatter than the left valve; beak of left valve prominent, rising well above the hinge line, and markedly prosogyre, right beak relatively blunt and not especially prominent; outer ostracum of both valves prismatic, composed of short polygonal prisms of calcite arranged normal to the shell surface; especially characterized by a relatively large angle *a* (average 70.5°) as compared with other volselloid myalinas. Dimensions of the holotype are as follows: length, 44 mm; height, 42 mm; greatest dimension, 52 mm; angle *a*, 67°; angle *b*, 125°; comparative measurements are given in table 5.

Comparison.—Because of the well developed anterior lobe this species has frequently been compared with species of *Naiadites* (Hind, 1895, p. 132), with which it has very little in common. There has been a tendency to refer species of *Myalina* having a prominent recurved left beak to *M. recurvirostris,* on the assumption that these characters of the beak are of specific value. Actually, nearly all of the myalinas have a relatively prominent left beak, which tends to overhang that of the right valve.

In any critical study *Myalina (Myalina) wyomingensis* is likely to be confused only with *M. (M.) lepta,* which has a markedly smaller angle *a* (55.5° as compared with 70.5°), or with the variety of *M. (M.) wyomingensis thomasi,* which has a more massive and distinctly larger shell.

Material.—The material used in this study includes the holotype of *Myalina (Myalina) wyomingensis* (U.S. Nat. Museum, no. 33900), and the holotype and a topoparatype of *M. recurvirostris* (Univ. Illinois, no. x-214), as well as several hypotypes from several localities and horizons. The material is sufficiently well preserved for the study of all significant characters. In the original illustration of *M. recurvirostris* by Meek and Worthen, the holotype of that species was shown as a bivalved individual. The right valve is now lost but may be in the collections of the University of Illinois.

Occurrence.—The species seems to have a fairly long range for a *Myalina,* being identified with some confidence from various horizons ranging from early Desmoinesian (*Myalina* bed, McCoy formation, near Bond, Colo.) through the Missourian, well into the Virgilian (Rico formation, 125 feet above base, Scotch Creek, Rico Quadrangle, Colorado; the associated *Myalina (Orthomyalina) subquadrata* is not known elsewhere above upper Virgilian). The horizon that yielded the holotype is unknown, the specimen having come from a coal mine near Wilkesbarre, Pa. The types of *M. recurvirostris* seemingly are Missourian in age ("about the horizon of coal number 11, of the Upper Coal Measures, La Salle, Illinois"). The species is common in the Rock Lake shale (sandstone facies) of the upper Missourian, in northeastern Kansas, and is known in the Graham formation (lower Virgilian) of Young county, Texas.

The majority of material available to me was collected from argillaceous shales, and some of the specimens retain both valves in apposition, denoting burial under quiet-water conditions. Other material occurs in a matrix of fine quartz sandstone, with the valves separated. The holotype is imbedded in a hard carbonaceous shale. Probably the conditions of burial were markedly different in the various occurrences. In those instances where the valves remain in apposition the burial apparently was *in situ.*

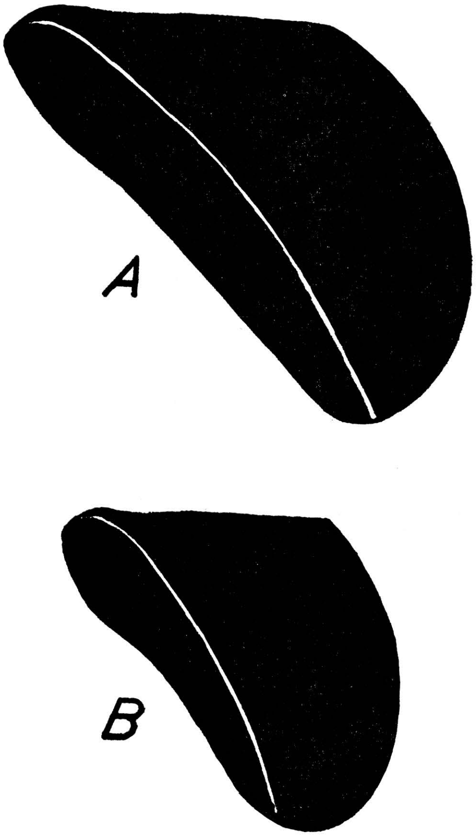

FIGURE 13.—Comparison of form in (*A*) *Myalina (Myalina) wyomingensis thomasi,* n. var., from the Permian, with (*B*) *Myalina (Myalina) wyomingensis,* from the Pennsylvanian.

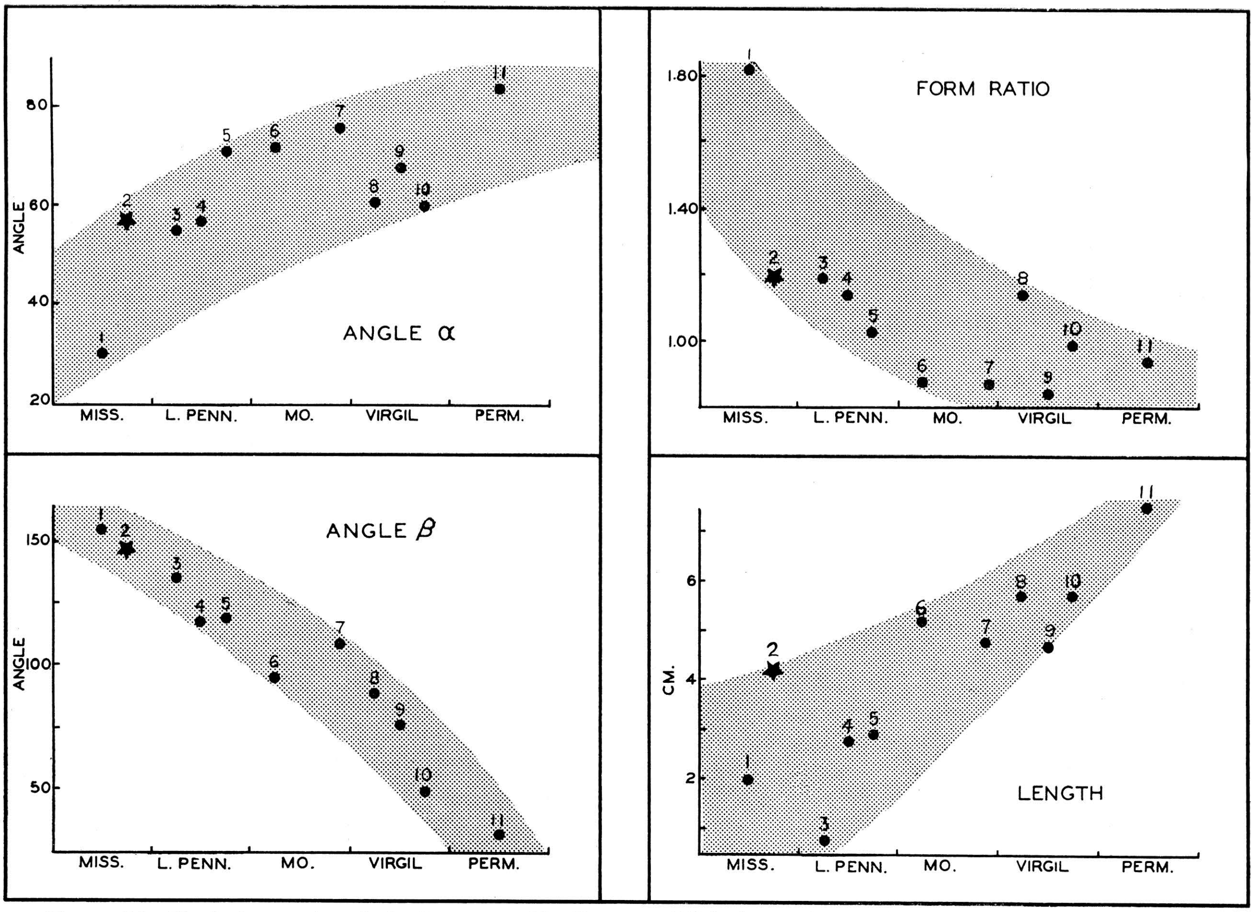

Figure 14.—Evolutionary trends in the genus *Myalina*, *s. s.* With decreasing geologic age the size of the angle α increases, the shells become relatively shorter and higher, the posterodorsal angle β decreases, and the shells increase in absolute size. 1, *Myalina* sp., St. Louis limestone; 2, *M.* (*M.*) *goldfussiana*, the genotype, Viséan; 3, *M.* (*M.*) *copha*, Atoka; 4, *M.* (*M.*) *lepta*, Boggy; 5, *M.* (*M.*) *wyomingensis*, Desmoinesian to Wolfcampian; 6, *M.* (*M.*) *arbala*, Missourian; 7, *M.* (*M.*) *glossoidea*, Lansing to Douglas; 8, *M.* (*M.*) *miopetina*, Shawnee; 9, *M.* (*M.*) *petina*, Wabaunsee; 10, *M.* (*M.*) *pliopetina*, Wolfcampian; 11, *M.* (*M.*) *copei*, *Wolfcampian.* The points plotted represent the earliest occurrence in the stratigraphic record.

Myalina (Myalina) wyomingensis var. thomasi Newell, n. var.

Plate 14, figures 15, 16

This variety is very like *Myalina (Myalina) wyomingensis*, *s. s.*, differing from the typical form principally in being considerably more robust. The larger size of mature individuals, taken alone, would probably be insufficient grounds for the erection of a new variety. However, the new variety has a considerably smaller angle α, 55° on the average, as compared with about 70° in the typical form. *M. (M.) wyomingensis thomasi* is considerably younger than the youngest known specimens of *M. (M.) wyomingensis*, a fact that does not harmonize well with the general tendency for geologically younger myalinas to exhibit a more upright form than their older relatives. Comparative measurements are given in table 5. Dimensions of the holotype are as follows: length, 59 mm; height, 57 mm; greatest dimension, 70 mm; angle α, 70°. The posterodorsal extremity in the material at hand is broadly obtuse, and the angle of intersection between the hinge axis and the posterior margin is even greater than in *M. (M.) wyomingensis*. In general, the configuration is more primitive than that of *M. (M.) wyomingensis*, except perhaps for the fact that the anterior lobe in both valves of *M. (M.) wyomingensis thomasi* is less pronounced than in the typical variety. The ventral part of the shell seems to be slightly more slender in var. *thomasi* than in *M. (M.) wyomingensis*, *s. s.*

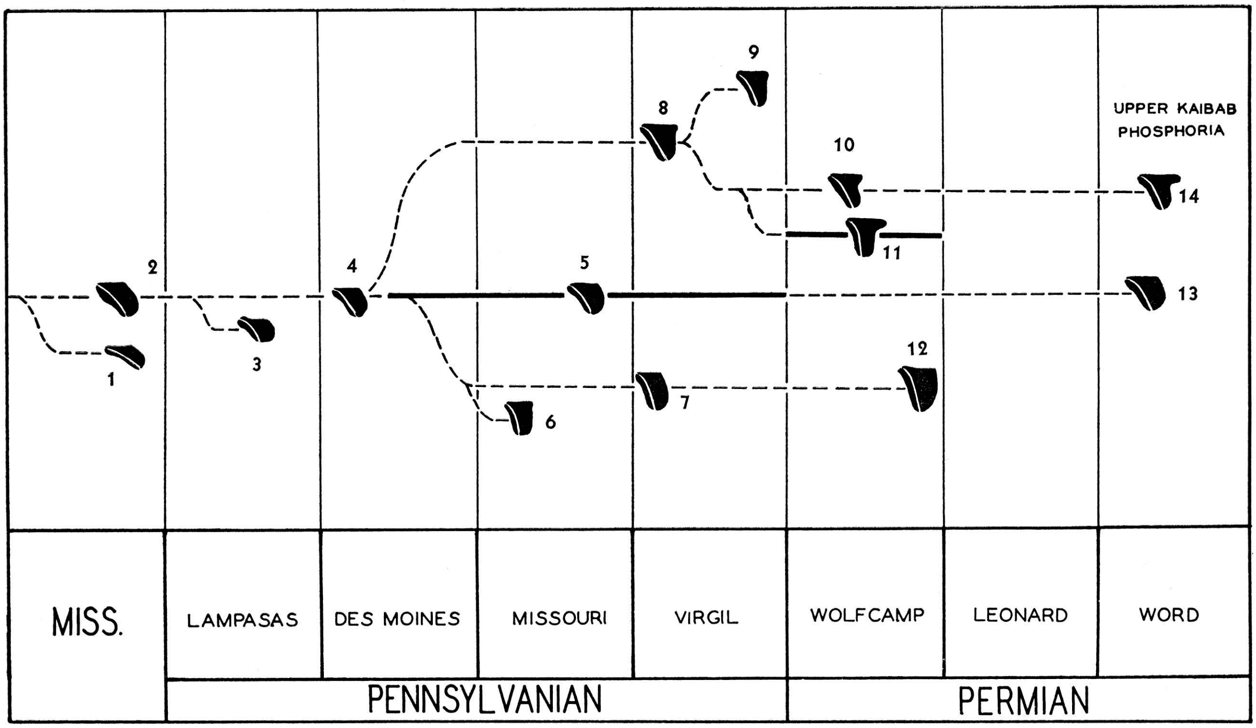

FIGURE 15.—Inferred phylogeny of *Myalina*, s. s., determined by ontogeny and stratigraphic position. 1, *Myalina* sp., St. Louis limestone; 2, M. *(M.) goldfussiana*, Viséan; 3, *M. (M.) copha*, Atoka; 4, *M. (M.) lepta*, Boggy; 5, *M. (M.) wyomingensis*, Desmoinesian to Wolfcampian; 6, *M. (M.) arbala*, Missourian; 7, *M. (M.) glossoidea*, Lansing to Dougas; 8, *M. (M.) miopetina*, Shawnee; 9, *M. (M.) petina*, Wabaunsee; 10, *M. (M.) pliopetina*, Wolfcampian; 11, *M. (M.) copei*, Wolfcampian; 12, *M. (M.) aviculoides*, Wolfcampian; 13, *M. (M.) wyomingensis thomasi*, Satanka shale (Word?); 14, *M. (M.) sinuata*, Phosphoria (Word).

Material.—The new variety is based on a large collection of poorly preserved specimens from a single locality. Only 16 specimens were sufficiently instructive to be used in this study. All of the material occurs in the form of molds, and none of the original shell remains. The holotype, no. 21193, and most of the topoparatypes are at the University of Wisconsin. Some topoparatypes are at the University of Wyoming.

Occurrence.—Local dolomitic limestone at the base of the Satanka shale (Word?), Red Mountain, sec. 9, T. 12 N., R. 76 W., Wyoming. The majority of specimens retain both valves in apposition.

MYALINA (MYALINA) ARBALA Newell, n. sp.

Plate 7, figures 9, 10

Obliquity slightly prosocline to acline; both valves provided with a prominent anterior lobe, that of the right valve being somewhat more pointed than the left; left valve only slightly rugose, covered with nonprismatic outer ostracum of seemingly homogeneous calcite, beak prominent, extending well above hinge line; right valve nearly smooth, slightly flatter than the left, with prismatic outer ostracum, beak pointed and not projected above hinge line; a broad, slight sinus just below the posterodorsal angle produces a fairly well defined auricle. Comparative measurements are given in table 5. Dimensions of the holotype are as follows: length, 63 mm; height, 77 mm; greatest dimension, 83 mm; angle *a*, 82°; angle *b*, 84°.

Comparison.—The upright form of this species and the small posterior auricle are reminiscent of *Myalina (Orthomyalina) subquadrata.* The resemblance is entirely superficial, however, because in the present form anterior lobes are well developed in both valves; whereas, in *Orthomyalina,* the anterior lobe is entirely lacking in right valves, and is missing or very obscure in left valves. In the majority of acline species of *Myalina, s. s.,* as in *M. (M.) arbala,* the ventral margin is narrowly rounded, instead of broadly rounded as in species of *Orthomyalina,* tending to give the shell a somewhat triangular outline, the ventral margin being the apex of the triangle. *M. (M.) arbala* is closely akin to *M. (M.) glossoidea,* n. sp., and in absence of reasonably complete collections it might be difficult to distinguish them. There is a tendency for *M. (M.) glossoidea,* the younger of the two, to have slightly larger angle *a,* and especially a larger angle *b.* The situation is somewhat anomalous in that the older species, *M. (M.) arbala,* invariably exhibits a small rear auricle in adults, whereas such an auricle is more commonly missing in *M. (M.) glossoidea.* Judging from other myalinas, the development of the rear auricle is a mark of specialization, becoming most marked in the youngest species. Probably *M. (M.) glossoidea* is not derived from *M. (M.) arbala,* since the former species, although geologically the youngest, is in some respects more primitive than the latter. The two species are distinguished also by the fact that the length of that part of the shell halfway between the hinge and the ventral margin is longer in *M. (M.) arbala* than in *M. (M.) glossoidea,* giving to the former a relatively massive appearance.

Material.—This species is based on fourteen specimens, all from the Winterset limestone (early Missourian). The material is well preserved, although part of the shell substance is recrystalized. The holotype is no. 7569, University of Kansas. Topoparatypes are at the University of Kansas, Yale University, and the U.S. National Museum.

Occurrence.—Carbonaceous phase of the Winterset limestone (Bronson group, Missourian series) in the Kansas City area, associated with a fauna of brachiopods, pelecypods, nautiloids, and gastropods. The shells most commonly occur as separate valves, suggesting fairly strong current action in the depositional environment.

MYALINA (MYALINA) GLOSSOIDEA Newell, n. sp.

Plate 7, figures 1a, b, 5, 7, 8a, b

Most of the comments on *Myalina (Myalina) arbala* apply to this species. Like the species just mentioned, *M. (M.) glossoidea* superficially resembles *Orthomyalina,* but can be distinguished from species of that subgenus by the prominent anterior lobe on each valve. The majority of specimens of *M. (M.) glossoidea* lack the posterior auricle that characterizes adults of *M. (M.) arbala,* and the lower part of the shell in *M. (M.) glossoidea* is shorter, therefore more slender than in the older species. Another species that is closely comparable with both *M. (M.) glossoidea* and *M. (M.) arbala* is the lower Permian *M. (M.) aviculoides* Meek and Hayden. Judging from the holotype, *M. (M.) aviculoides* is almost truly acline, having no conspicuous forward or backward obliquity, being more distinctly upright than either of the other two species in question. Seemingly, *M. (M.) aviculoides* is like *M. (M.) glossoidea* in lacking a posterior auricle.

Comparative measurements are given in table 5. Dimensions of the holotype of *M. (M.) glossoidea* are as follows: Length, 65 mm; height, 74 mm; greatest dimension, 82 mm; angle *a,* 75°; angle b, 100°.

Material.—This species is based on eight specimens, all of which are relatively well preserved. The holotype is no. 7573, University of Kansas. Topoparatypes and paratypes are also at the University of Kansas.

Occurrence.—The holotype and associated topoparatypes were found as isolated valves in calcareous shale in the upper Vinland shale, Stranger formation (early Virgilian), 1½ miles south and ¼ mile east of Homewood, Franklin county, Kansas. Paratypes from the Rock Lake shale (Stanton formation), upper Missourian, were collected near the center of the south side of sec. 27, T. 11 S., R. 22 E., Kansas. These specimens also occur as separated valves in calcareous shale.

MYALINA (MYALINA) AVICULOIDES Meek and Hayden

Plate 7, figure 2

Shell nearly acline, subquadrate, with a narrow, sharply rounded ventral margin, and prominent extended beaks; anterior lobe well defined; left valve relatively smooth, right valve and shell microstructure unknown. Comparative measurements are given in table 5. Dimensions of the lectotype are as follows: length, 37 mm; height, 41 mm; greatest dimension, 44 mm; angle *a,* 78°; angle *b,* 95°.

Comparison.—This species clearly belongs to the group of *Myalina (Myalina) arbala* and *M. (M.) glossoidea,* and is more closely akin to the latter. The three species are relatively advanced in having lost much of the primitive obliquity, but are somewhat anomalous in the weak development, or lack of a posterior auricle. In general form these species are similar to *Orthomyalina,* but the possession of a well developed anterior lobe, which is absent or obsolescent in *Orthomyalina,* indicates that these species are better classed with *Myalina, s. s.* From *M. (M.) glossoidea* the present species is different in having a truly quadrate posterodorsal extremity.

Material.—This species is not well founded. The only very instructive specimen that I have seen is designated here as the lectotype, no. 2526 at the U.S. National Museum. The most critical part of the shell, the posterodorsal extremity, is not entirely complete. However, extrapolation of the growth lines indicates that it originally had a quadrate angle *b.* The shell is not especially well preserved.

Occurrence.—The lectotype came from "South Cottonwood Creek," in central Chase county, Kansas. The most extensive outcrops in this area are in the Big Blue (Wolfcampian). Study of the rock matrix suggests that the type collection was taken from the Herington limestone, a formation that is known to have yielded other material described by Meek and Hayden. The rock in which the types occur is a light buff, somewhat cavernous dolomitic limestone, in which the majority of fossils are preserved as molds. A single specimen was collected from the upper nautiloid beds of the Casper sandstone, 1 mile south of Forelle, Wyo.

MYALINA (MYALINA) MIOPETINA Newell, n. sp.

Plate 3, figures 5a, b, 8a, b

Form roughly that of an isosceles triangle, the apex at the posterodorsal extremity; anteroventral margin only slightly sinuate, lobe well developed on both valves; left valve somewhat rugose, with homogeneous outer ostracum, right valve nearly smooth, with prismatic outer ostracum; posterior margin provided with an obscure sinus about one fourth of the height below the hinge margin, delimiting a rounded and obscure posterior auricle; ventral margin narrow, subangular; characterized by subquadrate posterodorsal angle (average value of angle *b*, 89°). Comparative measurements are given in table 5. Measurements of the holotype are as follows: length, 60 mm; height, 61 mm; greatest dimension, 75 mm; angle *a*, 63°; angle *b*, 82°.

Comparison.—*Myalina (Myalina) miopetina* is a distinctive shell and need not be confused with other species. *M. (M.) petina* is similar in a general way, but has a more pronounced auricle and a broadly rounded ventral margin. The latter species has a shorter shell (form ratio. 0.85, as against 1.03 for *M. (M.) miopetina*), and a more acute angle *b* (76° as compared with 89° in *M.* (*M.*) miopetina). *M.* (*M.*) *pliopetina* is a considerably more advanced shell in having a very acute posterior auricle (47°).

Material.—This species is based on three relatively complete, separate left valves and one fragmentary right valve, all from one locality. The holotype, no. 7565, and topoparatypes are at the University of Kansas.

Occurrence.—From a shale somewhere near the horizon of the Lecompton limestone (lower Virgilian), probably the Stull shale, in sec. 7, T. 30 S., R. 12 E., Kansas, associated with abundant *Myalina (Orthomyalina) subquadrata* and *Septimyalina perattenuata.*

MYALINA (MYALINA) PETINA Newell, n. sp.

Plate 6, figures 2a-3b

Shell relatively upright for a *Myalina,* with a short posterior auricle, and a subcircular ventral margin; anteroventral margin only slightly sinuate, lobe well developed in both valves; left valve somewhat rugose, with homogeneous outer ostracum, right valve smooth, with prismatic outer ostracum; characterized by a relatively small form ratio (length/height), about 0.85, and a subquadrate posterodorsal extremity (angle *b* about 76°). Comparative measurements are given in table 5. Measurements of the holotype are as follows: length, 46 mm; height, 56 mm; greatest dimension, 65 mm; angle *a*, 64°; angle *b*, 75°.

Comparison.—The poorly developed posterior auricle of this species causes a superficial resemblance to *Myalina (Myalina) miopetina.* The subangular ventral margin, greater form ratio (1.03 as compared with 0.85), and larger angle *b* (89° as compared with 76°) in the latter species distinguishes the two. *M.(M.) petina* is conspicuously more upright in form than the relatively oblique *M. (M.) miopetina.*

Material.—The species is based on two well preserved specimens, the holotype, no. 1526, and a paratype, no. 12003, Texas Bureau of Economic Geology.

Occurrence.—Beds formerly classified as Harpersville, now thought to be upper Thrifty (Virgilian), 6 miles west of Cisco, Tex. The shells occur as isolated valves in calcareous shale.

MYALINA (MYALINA) PLIOPETINA Newell, n. sp.

Plate 6, figures 1a, b, 6

Form trigonal, with relatively straight anteroventral margin; anterior lobe well developed in both valves; left valve rugose, with homogeneous outer ostracum, right valve smooth to only slightly rugose, with prismatic outer ostracum; posterior margin marked by a relatively deep sinus, which varies in position from about a fourth of the height down from the hinge margin to an intermediate position between the ventral extremity and the hinge; rear auricle slender, extended; ventral margin narrow, nearly semicircular; characterized by the nearly straight anteroventral margin and correspondingly straight, oblique umbonal ridge. Comparative measurements are given in table 5. Measurements of the holotype are as follows: length, 56 mm; height, 59 mm; greatest dimension, 70 mm; angle *a*, 59°; angle *b*, 40° ±.

Comparison.—In a general way *Myalina (Myalina) pliopetina* is similar to *M. (M.) copei,* with which it is associated locally, and it is like the much younger species *M. (M.) sinuata.* From *M. (M.)*

copei it differs principally in the relatively acute angle with the dorsal margin (angle *a* about 62.3°), as compared with *M. (M.) copei* (average, about 84°). Unfortunately, *M. (M.) sinuata* is not well known, so that in some respects a detailed comparison with *M. (M.) pliopetina* is impossible. However, topotypes of *M. (M.) sinuata* are characterized by a relatively high convexity, correlated with an unusually thick visceral cavity. The living animal of *M. (M.) sinuata* must have been twice as thick as the animal of *M. (M.) pliopetina.* In other respects the two species were apparently quite similar, although some of the fragmentary specimens of *M. (M.) sinuata* that are available seem to have had a somewhat longer posterior auricle than in *M. (M.) pliopetina.*

Material.—The species is based on five well preserved specimens from Texas. The holotype, no. 8364/4, and a topoparatype, no. 8364/1A, are at the American Museum. Other paratypes are at the University of Texas.

Occurrence.—The holotype came from McKenzie's Trail, near Ft. Griffin, Shackelford county, Texas, and is one of the paratypes of Whitfield's *Myalina copei.* It is probable, but not certain, that Whitfield's collection came from a single horizon and locality. It seems significant that in none of the various other collections available to me do the two species *M. (M.) copei* and *M. (M.) pliopetina* occur in direct association. According to F. B. Plummer (personal communication) it is probable that the Whitfield material from near Ft. Griffin came from the Moran or the Pueblo formation (Wolfcampian). The preservation of the shells is similar to that found in other material known to have been collected from the Moran formation. The species also is represented in collections from the Pueblo of Texas (Wolfcampian) and the Fort Riley (Wolfcampian) of Kansas.

The species is represented in argillaceous shales and in dolomitic limestone. A few of the specimens retain both valves in position indicating burial under fairly quiet conditions.

MYALINA (MYALINA) COPEI Whitfield

Plate 4, figures 1a-2c; plate 5, figures 1-3.

Myalina copei WHITFIELD, *1902,* Am. Mus. Nat. History Bull., vol. 16, pp. 63-66, text fig. 2, not text fig. 1.

Shell of adults acline or nearly so, with narrow, rounded ventral margin and extended anterior and posterior terminations of the dorsal part of the shell, giving the shell roughly the form of a "T"; anterior lobe distinct, but relatively small on both valves; posterodorsal extremity in an elongate and slender auricle having a rounded termination, delimited below by deeply incised sinus, the apex of which is from a fourth to a third of the shell height below the dorsal margin; anterior and posterior margins of the shell nearly perpendicular in the lower third of the shell; anterior margin concave and broadly arcuate, paralleling the regularly arcuate umbonal ridge; left valve rugose, outer ostracum homogeneous, right valve nearly smooth, with a prismatic outer ostracum; right valve flatter and slightly smaller than the left valve (discordant), particularly along the anterior border, where the margin of the right valve fits within the edge of the left valve; mature shells show a tendency for the socket of the left valve to develop an obscure median ridge, or tooth, the tooth of the right valve being correspondingly divided by a narrow and shallow furrow which may or may not occur at the middle of the tooth; mature shells relatively large, compared with other myalinas, ranging up to a maximum of around 100 mm for the greatest dimension. Comparative measurements are given in table 5. Dimensions of the lectotype are: length (restored), 82 mm; height, 82 mm; angle *a,* 77°.

Comparison.—The greatly extended posterior auricle of this species distinguishes it from all known myalinas, excepting *Myalina (Myalina) pliopetina* and *M. (M.) sinuata.* Both of the last two forms are characterized by oblique shape and a nearly straight anterior margin, differing rather markedly from the arcuate anterior margin and upright form of *M. (M.) copei.*

Material.—The type collection consists of several separated specimens and one bivalved individual (lectotype, no. 8364/1) at the American Museum. Although more or less fragmentary, the material is well preserved. Together with various supplementary hypotypes, the collection of instructive examples available for this study numbered 17 specimens. Several scores of specimens, too incomplete for critical measurements, were examined.

Occurrence.—This species is highly characteristic of the Wolfcampian series and equivalents. It has been recognized in many of the fossiliferous Wolfcampian limestones in Nebraska and Kansas, is abundant at several horizons in the Pueblo, Moran, and Putnam formations of north-central Texas, and occurs sparingly in the Hueco formation of the Hueco Mountains, West Texas. The types were collected on McKenzie's Trail, near Fort Griffin, Shackelford county, Texas, possibly from the Pueblo formation, but more probably from the Moran formation. *Myalina (Myalina) pliopetina* occurs in the type collection of *M. (M.) copei.* Presumably all of the material came from the same horizon. However, the two species are not associated together in any of the other collections that I have seen. In the northern Mid-Continent region of Kansas and Nebraska the species has been recognized in the Neva, Funston, Florence, Fort Riley, Gage, Cresswell, Krider, and Herington limestones. In all of these occurrences the shells are found in argillaceous limestones or dolomitic limestones. In Texas the shells occur in argillaceous shales and impure limestones. Bivalved specimens are not uncommon.

MYALINA (MYALINA) SINUATA Branson

Plate 6, figures 4 and 5

Myalina sinuata BRANSON, *1930,* Missouri University Studies, vol. 5, p. 45, pl. 12, fig. 1.

Although this species is almost certainly distinct from the other myalinas herein described, it is not adequately known. All of the specimens of *Myalina (Myalina) sinuata* known to me are so fragmentary that a satisfactory description cannot yet be made. The available collection of fragmentary topotypes indicates a very large and massive shell, larger in adults than any other myalinas known to me. Some of the specimens seemingly were originally over 100 mm in height and had an even greater length. The most distinctive feature of the internal molds is their very great convexity, indicating a visceral cavity of much greater depth than that of *M. (M.) pliopetina* and *M. (M.) copei.* Judging from the fragments, the complete shell probably was very like that of *M. (M.) pliopetina* in form, with a rather marked prosocline obliquity. Adults, however, were seemingly nearly half again as convex as in *M. (M.) pliopetina* and probably had a slightly more extended posterior auricle. The measurements given in table 5 are for internal molds and therefore cannot be relied on to give an accurate impression of external shell characters. Nevertheless, the characters which seemingly distinguish the species are easily recognized.

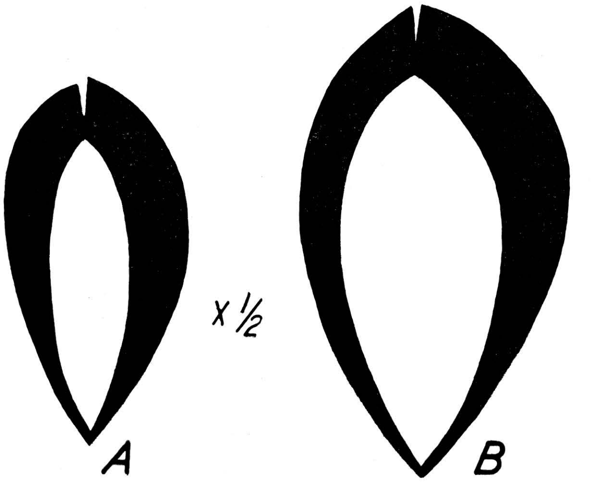

FIGURE 16.—Anterodorsal-posteroventral sections of (*A*) *Myalina (Myalina) pliopetina,* n. sp., and (*B*) *Myalina (Myalina) sinuata* Branson, drawn parallel to the greatest dimension of the shell, to show the relative shell convexities of the two species. The diagram of *M. (M.) sinuata* is a reconstruction, based on internal molds.

Material.—The holotype, which is supposed to be in the collections of Colorado College, at Colorado Springs, cannot be located. A dozen or so fragmentary topotypes, chiefly internal molds, have been made available for this study by Alfred Fischer. These specimens are at the University of Wisconsin. Two inadequate internal molds, from the upper part of the Kaibab limestone of northern Arizona, were lent by the curators of the Museum of Northern Arizona.

Occurrence.—Upper limestone of the Phosphoria (Word?) of the Wind River Mts., Wyoming; and the upper part of the Kaibab limestone (upper *Bellerophon* beds, Word?), northern Arizona. The type specimen was collected by Branson at Bull Lake, in the Wind River Mts., near Du Bois, Wyo. The Phosphoria specimens occur in cherty light gray to bluish-gray limestone; those from the Kaibab occur in a matrix of cavernous dolomitic limestone.

Subgenus ORTHOMYALINA Newell, n. subgen.

Subgenotype, *Myalina slocomi* Sayre. Geologic range of subgenotype, Desmoinesian—Virgilian, Pennsylvanian.

Subquadrate, nearly acline, massive-shelled myalinas, in which the anterior lobe is obsolete in both valves, and the posterior adductor system is placed far down toward the posteroventral margin of the valves (text fig. 6*G*).

Geologic range, Desmoinesian—Wolfcampian.

Remarks.—The early ontogeny of shells of *Orthomyalina,* as revealed in growth-lines on the umbones, shows clearly that this phyletic group of shells sprang from a prosocline, lobate *Myalina* like *Myalina (Myalina) lepta,* possibly in the early Desmoinesian epoch, because representatives of *Orthomyalina* are as yet unknown in rocks older than mid-Desmoinesian. As in other Myalinidae, there is a marked tendency for the geologically younger species to develop a posterior auricle, and an auriculate form, *O. subquadrata,* replaces the quadrate varieties in the Wabaunsee and Wolfcamp horizons.

Species of *Orthomyalina* are by far the most abundant representatives of the Myalinidae in the Missourian and Virgilian series of the Pennsylvanian in the Mid-Continent region. Commonly the shells are crowded by the thousands in a matrix of limestone or calcareous shale, to the near exclusion of other fossils. Less commonly they occur in a sandstone matrix. Juvenile shells are practically unknown in these *Orthomyalina* beds. Inspection of mature shells reveals that they reached a large size before the shell became thickened (pl. 8, figs. 1, 3). New ligament grooves were added as the shell was thickened. Consequently, the number of ligament grooves is an index of the relative maturity of a shell. Probably the very small juveniles were so fragile and, like *Mytilus,* so heavily charged with organic material that they were destroyed during the fossilization process.

Bivalved shells of *Orthomyalina* are so common that it is certain that the living animals favored relatively quiet waters. The construction of hinge and ligament was such that even moderate current action after death would have quickly separated the valves. It does not follow that the water inhabited by these animals was relatively deep, because the very flat bottom that seemingly characterized so many of the Pennsylvanian seas in the Mid-Continent area would tend to preclude extensive and vigorous surf action.

MYALINA (ORTHOMYALINA) SLOCOMI *Sayre*

Plate 8, figures 1-6; plate 10, figure 6

Myalina (?) slocomi SAYRE, *1931,* Kansas Geol. Survey, Bull. 17, p. 117, pl. 11, figs. 1-1a. (Date of imprint, 1930)

Myalina subquadrata of authors, in part.

Shell massive, approximately acline, sublinguate, and commonly slightly expanded ventrally, higher than long in about the ratio of 3/2; beaks slender, projected forward beyond the front margin of the body of the shell below, anterior lobe absent on both valves except in the very early juvenile stages; posterodorsal extremity broadly obtuse to rounded (compare pl. 8, figs. 1 and 4), rarely subquadrate (fig. 6). In 25 well-preserved specimens from the Stull shale, Shawnee group, Virgilian, near Waverly, Kans., the dimensions are as follows: length, maximum 63 mm, average, 55 mm, minimum, 44 mm; height, maximum, 90 mm, average, 78 mm, minimum, 64 mm; greatest dimension, maximum, 93 mm, average, 81 mm, minimum, 67 mm; angle *a,* maximum, 91°, average, 87°, minimum, 76°.

Comparison.—The typical variety of *Myalina (Orthomyalina) slocomi* is readily distinguished from the variety *M. (O.) slocomi parvula* and the species *M. (O.) ampla* by notable differences in size. *M. (O.) slocomi parvula* seems to be a dwarf, reaching full maturity (as shown by the thickened shell and large number of ligament grooves) at about half the size of typical *M. (O.) slocomi.* Shells of *M. (O.) ampla* are not only somewhat larger than *M. (O.) slocomi,* but are relatively longer, with shorter beaks, and they show no tendency for the ventral expansion of the shell typical of *M. (O.) slocomi.* There are rare specimens in the lower Wabaunsee (Virgilian) rocks that are nearly intermediate in form between *M. (O.) subquadrata* and *M. (O.) slocomi.* Such specimens form less than one per cent of the collections, however, and the possession of an obscure posterior auricle distinguishes *M. (O.) subquadrata* from the older form.

The holotype of *Myalina (Orthomyalina) slocomi* Sayre (pl. 8, fig. 6) is a young, therefore thin-shelled representative of the species from the Westerville oolite (Missourian) of the Kansas City region.

Material.—The collections at my disposal are more voluminous than for any other species. There are more than a thousand valves in the assembled collection, representing almost every fossiliferous horizon in the mid-continent region from Wewoka (late Desmoinesian) to early Wabaunsee (Virgilian). Naturally there is considerable variation exhibited in this material. Intensive studies indicate the impracticability of attempt to recognize stratigraphically useful subdivisions of the typical variety of *Myalina (Orthomyalina) slocomi* as herein defined.

The holotype, a poorly preserved immature left valve, is in the University of Kansas collections, no. 50.1.

Occurrence.—*Myalina (Orthomyalina) slocomi* is probably the most abundant of all the myalinas known to me. Numerous beds in the Missourian and Virgilian series are crowded with the shells of this species. *Septimyalina perattenuata* is a common companion of *M. (O.) slocomi* in these myalina beds. Horizons in the northern Mid-Continent area, at which these species are, at least locally, extremely abundant are: Farley limestone (Wyandotte formation), Rock Lake shale (Stanton formation), Vinland shale (Stranger formation, Heumader shale (Oread formation), Stull shale (Kanwaka formation), Ost limestone (Tecumseh formation). These horizons are in the Missourian and lower Virgilian series.

In the northern Mid-Continent area the species is at least sparsely represented in almost every mollusk-bearing formation from the Marmaton group (upper Desmoinesian) to the Howard limestone (lower Wabaunsee). In Texas the species is well represented in the Mineral Wells, Graford, Brad, and Graham formations, of Missourian and early Virgilian age. In Illinois the species has been recognized in the Shoal Creek, Centralia, and Macoupin formations of Missourian age.

The shells occur in various kinds of sediments, but most commonly are found in calcareous shales. In this instance the valves commonly are in direct apposition, except where they have been separated by weathering.

MYALINA (ORTHOMYALINA) SLOCOMI var. PARVULA Newell, n. var.

Plate 10, figures 2 and 3

Shell small, commonly less than 60 mm high and 40 mm long, otherwise like the typical variety of *Myalina (Orthomyalina) slocomi.* The following measurements are taken from 10 valves of the type collection, collected from the Rakes Creek shale (Tecumseh formation), Shawnee group, 2½ miles northwest of Michigan Valley, Kan. Height, maximum, 63 mm, average, 49 mm, minimum, 40 mm; length, maximum, 41 mm, average, 36 mm, minimum, 30 mm; angle *a,* maximum, 93°, average, 84°, minimum 76°.

The holotype has a height of 50 mm, length, 35 mm, angle *a,* 80°.

It is probable that this variety is simply an ecological variant of *M. (O.) slocomi.* The large number of ligament grooves (up to 15) shown by some of the specimens demonstrates their advanced maturity, so they are not to be regarded simply as the young of the typical variety.

Material.—The new variety is based on more than a score of specimens from a single locality. They are not associated with larger myalinas of the *M. (O.) slocomi* type. The holotype is numbered 7582 at the University of Kansas, where the entire collection of types is stored.

Occurrence.—Calcareous shale of the Rakes Creek member, Tecumseh formation, early Virgilian, where the variety is rather widely distributed through central eastern Kansas. It was found also at a slightly lower (?) horizon, in the fossiliferous shales of the Jacksboro limestone, Caddo Creek group, 4½ miles east of Jacksboro, Tex. In all of the known occurrences the shells seem to have been buried in relatively quiet water.

MYALINA (ORTHOMYALINA) AMPLA Meek and Hayden

Plate 10, figure 5

Myalina ampla MEEK AND HAYDEN, *1864,* Paleontology Upper Missouri, Smiths. Contr. Knowledge, 172, p. 32.

Shell robust, with relatively short beaks and only slightly incurved anterior margin; compared with other orthomyalinas the shell is relatively longer, therefore not so slender as commonly is the case in species of the subgenus. The holotype has a height of 98 mm and a length of 65 mm. The angle *a* is approximately 90°.

Comparison.—This species is quite similar to *Myalina (Orthomyalina) slocomi,* and it is possible that the shells referred here to *M. (O.) ampla* may be ecological variants of *M. (O.) slocomi.* The differences between the two are sufficiently distinctive, however, to warrant retention of both names. *M. (O.) ampla* is characterized by a larger, more massive shell, which is appreciably less slender than in *M. (O.) slocomi.* The beaks are less produced and somewhat more blunt in the latter species. Also, there is a less pronounced tendency in *M. (O.) ampla* for the ventral edge of the shell to be expanded than in *M. (O.) slocomi* or *M. (O.) subquadrata.*

Material.—The only moderately complete valve of this species at my disposal is the holotype, no. 998, at the U.S. National Museum. However, the same species is abundantly represented in my collections from the Lansing group (Merriam limestone, Plattsburg formation) by fragmentary internal molds. It is almost certain that the holotype came from the same horizon.

Occurrence.—Judging from the field occurrence this species preferred clear and quiet waters. All of the material even tentatively referred to *M. (O.) ampla* occurs in a limestone matrix; consequently, it is very difficult to collect good specimens. The majority of material is bivalved.

The holotype was collected along the Missouri River, below Ft. Leavenworth, Kan., from an undesignated horizon. The entire Lansing group is exposed in the river bluffs in this place, but there is only one horizon of *Myalina (Orthomyalina) ampla*—the Merriam limestone, basal member of the Plattsburg formation. Southwestward, about as far as Miami county, Kansas, large specimens of *M. (O.) ampla* are common in the Merriam limestone but are rare or absent farther to the southwest. In northwestern Missouri the species is common at this horizon. Questionable representatives of the species have been found in the Winterset limestone around Kansas City and in the lower limestone of the Fort Scott formation, Fort Scott, Kan.

MYALINA (ORTHOMYALINA) SUBQUADRATA

Plate 9, figures 1-4

Myalina subquadrata SHUMARD, *1855,* Missouri Geol. Survey, Ann. Repts. 1 and 2, p. 207, pl. C, fig. 17.

Myalina deltoidea GABB, *1859,* Philadelphia Acad. Nat. Sci., Proc., p. 297; ——, *1860,* idem., p. 55, pl. 1, figs. 1a-c.

Quadrate orthomyalinas characterized by a relatively long hinge, a shallow, broad sinus at the posterior margin, and a more or less distinct, but short posterior auricle; anteroventral margin somewhat produced, giving some shells a slightly opisthocline obliquity, which is not indicated in measurements of the angle *a* because the umbonal ridge becomes flattened and indistinguishable before the margin is reached in adults. Dimensions of 10 specimens from the Caneyville formation (Kansas and Oklahoma), upper Virgilian, are as follows: length, maximum, 78 mm, average 64 mm, minimum, 53 mm; height, maximum, 97 mm, average, 84 mm, minimum, 63 mm; angle *a*, maximum, 97°, average, 85°, minimum, 75°.

Comparison.—The rear sinus and auricle in *Myalina (Orthomyalina) subquadrata* distinguish this species from the similar *M. (O.) slocomi.* Both species show some variations in form, and it is not surprising that a very few upper Shawnee and lower Wabaunsee forms are so nearly intermediate between the two species that they might with equal propriety be referred to either species. Experience shows that a small proportion, less than one per cent, of the specimens of *M. (O.) slocomi* from lower Shawnee beds possess a quadrate posterodorsal extremity, as shown in plate 10, figure 4. Even these specimens show littte or no posterior sinus. Upper Wabaunsee collections of *M. (O.) subquadrata* contain a very few specimens, like that of plate 9, figure 4, which closely resemble *M. (O.) slocomi* in form. All of these specimens are relatively quadrate and show at least a slight posterior sinus. Our collections of orthomyalinas are not so complete for intervening horizons, i.e., upper Shawnee and lower Wabaunsee. Probably separation of the two species must be based on statistical studies in these transition beds. Ontogenies of *M. (O.) subquadrata* reveal without question that this species developed directly out of *M. (O.) slocomi.* Judging from the phylogenies of other myalinas we are justified in anticipating the discovery of a long-winged descendant of *M. (O.) subquadrata* in upper Wolfcampian or Leonardian strata. However, thus far *M. (O.) subquadrata* is the youngest *Orthomyalina* known.

Material.—As nearly as I can determine the holotypes of *Myalina (Orthomyalina) subquadrata* and *M. deltoidea* are lost to science. Because of that fact, I would not hesitate to urge abandonment of both species were it not for the fact that the horizon and locality for the type of each species can be fairly well determined. Furthermore, illustrations of the type specimens were published so that their significant features are readily evident. *M. (O.) subquadrata* was collected "on Missouri River, two miles below the mouth of the Little Nemaha" at Aspinwall, Nemaha county, Neb. According to Condra (1927, p. 112) the horizon of abundant *Myalina* in this area is zone 4 of the Table Creek shale, upper Wabaunsee.

Myalina deltoidea seems to be synonymous with *M. (O.) subquadrata* on subjective grounds, and came originally from about the same horizon. According to Gabb, his holotype came from just above a coal bed at Ft. Belknap, Tex. This horizon clearly is the lower part of the Harpersville formation of the older literature or the upper Thrifty of recent usage (Cheney, 1940, p. 66). The horizon of abundant myalinas at Ft. Belknap occurs just above the coal in the upper Thrifty formation. The age of these beds in terms of the northern Mid-Continent section is uppermost Wabaunsee.

Occurrence. — *Myalina (Orthomyalina) subquadrata* has been reported in the literature from various formations throughout the Pennsylvanian and Permian. Needless to say, the great majority of these citations are in error. Carelessness in the identification of myalinas has become the rule, so that traditionally almost every large *Myalina* in the Late Paleozoic has been called *Myalina subquadrata* without regard to form or other significant characters. This species is abundant only in a

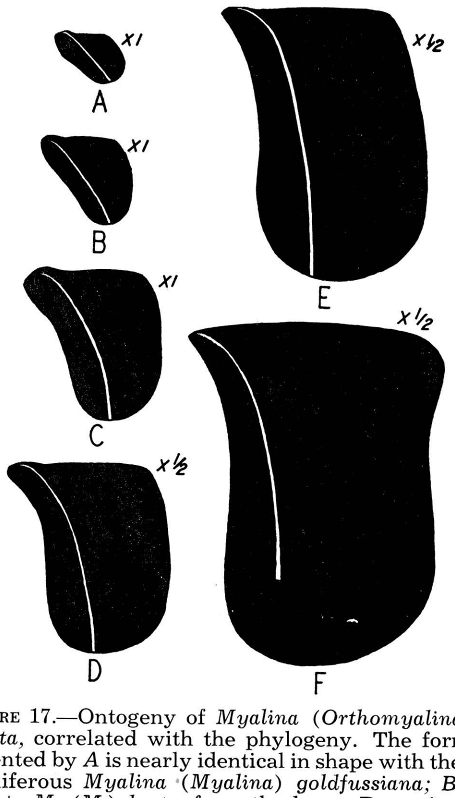

FIGURE 17.—Ontogeny of *Myalina (Orthomyalina) subquadrata*, correlated with the phylogeny. The form stage represented by *A* is nearly identical in shape with the Lower Carboniferous *Myalina (Myalina) goldfussiana; B* corresponds to *M. (M.) lepta*, from the lower Desmoinesian; *C* corresponds to *M. (M.) wyomingensis*, which appears first in the lower Desmoinesian; *D* and *E* correspond to *M. (Orthomyalina) slocomi*, which appears first in the upper Desmoinesian; *F* represents the adult form of *M. (O.) subquadrata*, appearing first in the Wabaunsee equivalents, upper Virgilian.

limited part of the upper Wabaunsee. Early in the progress of this study I was under the impression that the species is confined to the Caneyville formation. Acquisition of further collections, totaling some hundreds of specimens, from Nebraska, Kansas, Oklahoma, Texas, and New Mexico, reveals that the species appears at least as low as the Auburn shale (mid-Wabaunsee) and ranges at least as high as the Foraker limestone (lower Wolfcampian). So far as I am aware, the species occurs in persistent "*Myalina* beds" only in the Friedrich, French Creek, and Caneyville formations of the upper Wabaunsee and in the equivalent upper Thrifty formation of Texas. Other occurrences are for the main part sporadic. Dr. M. L. Thompson contributed typical representatives of the species from the upper Magdalena limestone of central New Mexico, where it is associated with species of *Schwagerina*.

Subgenus MYALINELLA Newell, n. subgen.

Subgenotype, *Myalina meeki* Dunbar. Geologic range of the subgenotype, Desmoinesian (?) to lower Leonardian.

Shell strongly prosocline, triangular, with nearly straight anteroventral posterior and dorsal margins; beaks slender, not lobed; left valve only slightly more rugose than the right valve, outer ostracum of both valves composed of irregular polygonal prisms about 10 to 15 microns in diameter; shell very thin, seldom exceeding 1 mm. even in the largest shells; shells commonly less than 20 mm in the greatest dimension; musculature unknown.

Geologic range, Desmoinesian-upper Guadalupian? (Quartermaster).

Remarks.—The marked prosocline obliquity and triangular form of shells of *Myalinella* are "primitive" features when considering the family as a whole. Yet, the near or complete lack of an anterior lobe below the beaks is clearly a mark of specialization. Juveniles and the geologically older forms generally display an anterior lobe. *Myalinella* certainly is not as closely related to *Myalina, s.s.*, as is *Orthomyalina*. Even in the very early ontogeny, the form of the shell does not closely duplicate any of the typical myalinas. The lack of differentiation in shell structure between the two valves also sets this group apart from *Orthomyalina* and *Myalina, s.s.* For these reasons, it might logically be argued that *Myalinella* is deserving of separate generic rank. Because of the fragile character of the shells, good material is very rare and my information on this group is far from complete. Consequently, a more conservative course has been adopted; that is, *Myalinella* is classed under *Myalina*, as a subgenus.

The best evidence that *Myalinella* constitutes a genetic series lies in the discovery that one of the characteristic evolutionary trends of the Mytilacea is displayed by the myalinellas as they are traced through the Late Paleozoic. In all significant respects but one, the shells of this subgenus are constant in various horizons. The only conspicuous change is seen in progressive reduction of the posterodorsal angle (angle *b*). The oldest species has a remarkably obtuse angle, larger than any other myalinid known to me. At the higher horizons this angle is progressively reduced, though none of the species thus far recognized reaches the place where the angle β is quadrate.

The subgenotype was first recognized with associations that suggest a freshwater or brackish-water habitat (Dunbar 1924, p. 201), and it has been noted at other horizons in association with a well preserved terrestrial fauna and flora. *Myalina (Myalinella) meeki* and some other species of the subgenus commonly occur in association with marine invertebrates, however. I am impelled to the conclusion that species of *Myalinella* were tolerant of rather great variations in salinity of the water. That these animals lived at least partly in quiet waters is indicated by the fact that many of the specimens from various horizons and localities retain the two valves in close association.

MYALINA (MYALINELLA) MEEKI Dunbar

Plate 14. figures 7-14

Myalina meeki DUNBAR, *1924*, Am. Jour. Sci., vol. 7, p. 201, fig. 3.

?*Myalina pernaformis* Cox, *1857*, Geol. Rep. Kentucky, vol. 3, p. 569, pl. 8, fig. 8.

?*Myalina? exasperata* BEEDE, *1899*, Kansas Univ. Quart., vol. 8, p. 128, pl. 32.

Shell small, fragile; form slender, subtriangular, posteroventral margin, however, being rather broadly rounded; anteroventral lobe almost imperceptible in both valves, except where shells have been distorted by mashing; beaks extended, slender; umbonal ridge nearly straight except in the umbonal region, where it is slightly arched; inequivalve, the right valve being slightly less convex and smaller around the margin than the left valve; surface of both valves relatively smooth;

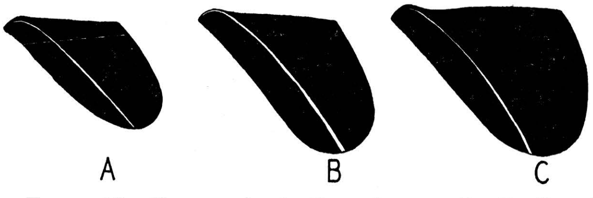

FIGURE 18.—Form series in the subgenus *Myalinella*. A, *Myalina (Myalinella) cuneiformis* Gurley, Desmoinesian; B, *M. (M.) meeki* Dunbar, Desmoinesian?-Leonardian; C, *M. (M.) acutirostris* Newell and Burma, Guadalupian. All figures X1.

outer ostracum of both valves composed of short irregular polygonal prisms of calcite 25 to 40 microns in diameter; internal characters unknown. Measurements based on six type specimens are as follows:

Measurements of Myalina (Myalinella) meeki

	Length (mm)	*Height (mm)*	*Angle a*	*Angle β*	*Greatest dimen. (mm)*
Maximum	52	43	47°	125°	65
Average	26	22	43°	127°	33
Minimum	17	16	40°	131°	21
Holotype	52	43	45°	129°	65

Comparison.—This form is distinguished from other myalinellas by the distinctive size of the angle *a*. From primitive myalinas like *Myalina (Myalina) wyomingensis,* which it superficially resembles, this species differs in the relatively smooth left valve and absence of an anterior lobe. The form of the beaks is quite similar to that of many species of *Septimyalina.* The resemblance is heightened by the fact that left valves of some species of *Septimyalina,* such as *S. scitula,* are nonrugose. The posterior margin of the shell in *S. scitula* is generally rounded, instead of straight, and the posteriodorsal corner of the shell is not as angular as ordinarily is the case with *Myalina (Myalinella) meeki. S. scitula,* like other species of *Septimyalina,* is a relatively thick-shelled form and possesses an umbonal deck, or septum, a feature which is lacking in all myalinellas.

Two poorly known species are similar to *Myalina (Myalinella) meeki* and possibly are identical with it. *Myalina pernaformis* Cox was described from the Providence limestone above Coal No. 11 at Providence, Ky. The horizon is in the Allegheny formation, approximately equivalent to the Pawnee limestone (Marmaton) of Kansas. The original description and figure are not adequate for recognition of this species in any critical work, but discovery of topotype specimens will some day solve the status of this species.

Myalina? exasperata Beede (pl. 10, figs. 1a, b) was based on very poor specimens from an unknown horizon associated with a coal bed (Nodaway coal?, Wabaunsee) west of Topeka, Kans. In the absence of good authentic specimens, this form is unrecognizable.

Material.—The specimens on which this description is based include some dozen or so shells, most of which show the original form quite well. A few of the specimens retain the original shell, and are undeformed. All of the type specimens occur in soft, calcareous shale, and are somewhat flattened by compaction. In all of these latter specimens, the inner ostracum of the shell has been removed by solution.

The types are the property of Yale University, no. 3496.

Occurrence.—The species seems to be long-ranging. A specimen from the lower Fort Scott limestone (Marmaton group), (pl. 14, fig. 11) is the oldest shell of the *Myalina (Myalinella) meeki* type in my collections. This shell is roughly like the form described by Cox as *M. pernaformis,* from about the same horizon (limestone above Coal No. 11) at Providence, Hopkins county, Ky. In the absence of topotype specimens, however, it is by no means certain what kind of a shell Cox described. Other specimens have been collected from the *Walchia* beds in the Rock Lake shale near Garnett, Kans., where they are associated with a peculiar mixture of plant remains, reptiles, fishes, scorpions, and macerated remains of marine invertebrates. Many of the fossil myalinellas are bivalved and therefore occur near the spot where they lived. The best specimens occur associated with a normal marine fauna, in a thin, sandy limestone in the Calhoun shale (Shawnee), at the NW cor. sec. 1, T. 21 S., R. 13 E., Coffey county, Kansas. The type specimens came from the famous fossil insect beds in the Carlton limestone, 3½ miles southeast of Elmo, Kan. The Carlton limestone occurs in the Wellington shale (upper Sumner) above the great salt beds of the Wellington, lower Permian. These shells probably were deposited in quiet waters, because many of them are bivalved. The ordinary marine species are absent. The salinity of the water may have been higher than normal sea water, or on the other hand it may have been relatively low, or even fresh (Dunbar 1924, p. 201).

MYALINA (MYALINELLA) CUNEIFORMIS Gurley

Plate 14, figures 1-4

Myalina cuneiformis GURLEY, *1883,* New Carboniferous fossils, Bull. 1, p. 4—GIRTY, *1903,* U.S. Geol. Survey, Prof. Paper 16, p. 420, pl. 8, figs. 14-17.

Shell small for a *Myalina,* mature specimens measuring less than one inch in length, fragile; form slender, subtriangular, the cardinal and posterior margins forming two nearly equal sides and the fairly straight anteroventral margin the base of an obtuse isosceles triangle; anteroventral lobe absent in right valve, barely perceptible in the left; beaks extended, very slender, depressed slightly at their extremities; angle *a* relatively small, around 35°; angle β broadly obtuse, about 130°; umbonal ridge slightly arched in the region of the umbones, but tending to become straight in the mature part of the shell; inequivalve, the right valve being distinctly the smaller of the two; surface of both valves relatively smooth, that of the left being only slightly more rugose than the right valve;

ligament area narrow, seemingly with only two or three relatively fine ligament grooves, in harmony with the thinness of the shell; right valve provided with a single prominent but thin hinge tooth, which occurs just behind the beak; the axis of elongation of this tooth is about 125° or more to the hinge axis, being directed downward and forward; left valve provided with a deep and narrow socket hardly more than a notch in the shell margin, corresponding to the tooth of the complementary valve, and occuring immediately below and behind the beak; musculature and shell microstructure unknown.

Measurements of two specimens are as follows: (1) lectotype, a juvenile right valve, length, ±13 mm; height, 8 mm; convexity, ±3 mm hinge length, ±9 mm; greatest dimension (measured parallel to the umbonal ridge), ±14 mm; angle *a*, 40°; angle *b*, 130°; (2) hypotype, mature bivalved specimen, length, 20 mm; height, 13..5 mm hinge length, 14 mm; convexity left valve, ±3.5 mm; convexity right valve, ±3 mm; greatest dimension, 23 mm; angle *a*, 45°; angle *β*, 125°.

Comparison.—This species is readily distinguished from other myalinellas by the remarkably small angle *a*.

Material.—Gurley's types before me are two in number, a juvenile, which, being the better speciman, is designated here as the lectotype (Univ. Chicago, no. 6318), and a larger badly crushed bivalved paratype, about 25 mm long. Both specimens occur in dark gray to black micaceous, sandy limestone. Without good supplementary material, I would have been uncertain about the recognition of this species. Such material, fortunately, is available in several silicified specimens from the lower part of the Tensleep sandstone of western Wyoming (Yale University, nos. 16342 to 16344). Most of the above description was based on the Tensleep material. These specimens occur in a siliceous dolomitic limestone matrix and were collected by Dr. J. D. Love on Black Mountain, eastern end of the Washakie Range, Wyoming (Love, J. D., 1939, p. 30). Only one of the specimens at hand is not fragmentary.

Occurrence.—Girty (1903, p. 421), who studied the Carboniferous faunas from Ouray, Colo., whence the types of *Myalina (Myalinella) cuneiformis* came, concluded that Gurley obtained the original specimens from the lowest exposed Carboniferous beds at Ouray, probably from the cliffs on either side of a little cascade just east of town. He classed these beds as Hermosa? formation. He also recognized the species in the "Weber" limestone in the Crested Butte district, Colorado. In the collection at hand, the species is represented by a few silicified specimens, mainly fragments, collected by J. D. Love, 30 feet above the base of the Tensleep sandstone in section 1 or 2, T. 6 N., R. 4 W., Wyoming. The Hermosa and Tensleep formations are probably about the same age and are generally correlated with some part of the *Wedekindellina* zone of the Cherokee of the Mid-Continent region.

MYALINA (MYALINELLA) ACUTIROSTRIS Newell and Burma

Plate 14, figures 17-19

Myalina sp. NEWELL, *1940*, Geol. Soc. America, Bull., vol. 51, p. 256, pl. 2, fig. 1.

Myalina acutirostris NEWELL AND BURMA in Roth, *1941*, Jour. Paleontology, vol. 15, p. 315, pl. 45, figs. 11-15.

Shell subtriangular to subrhombic, relatively small, fragile, slightly more upright in form than other myalinellas; beaks slender, extended anteriorly; surface of both valves relatively smooth; hinge relatively long, about 0.6 to 0.7 as long as the shell length and about equal to the shell height; angle *a* increasing during ontogeny to around 60° in mature specimens angle *β* decreasing during ontogeny to about 110° in mature specimens; ventral margin of shell tending to be narrowly rounded and placed well back of a midpoint on the shell. Measurements, based on five specimens, are as follows:

Measurements of Myalina (Myalinella) acutirostris

	Length (mm)	*Height (mm)*	*Angle a*	*Angle β*
Maximum	25	19	60°	128°
Average	16	12	53°	118°
Minimum	7.5	6.5	45°	110°
Holotype	25.0	19.0	45°	110°

Comparison.—The angle *a* is larger in adults of *Myalina (Myalinella) acutirostris* than in other myalinellas and the angle *β* is smaller. Otherwise, the species closely resembles *M. (M.) meeki* and *M. (M.) cuneiformis*. The general appearance of *M. (M.) acutirostris* recalls *Septimyalina scitula (Myalina perattenuata* of authors), particularly the shape of the slender, projecting beaks. The latter form, however, in addition to possession of an umbonal deck, is a more massive, thick-shelled form, and tends to be distinctly more upright.

Material.—The species was based on four left valves and one right valve. In general, the specimens are fairly well preserved, although features of hinge and musculature are not well shown. The holotype, no. 20846 and three topoparatypes, nos. 20843-20845, are at the University of Wisconsin. One paratype, no. 16326, is at Yale University.

Occurrence.—Restricted, so far as is known, to sandy and oolitic dolomite in the red beds of northern Texas. Dozier lens, Whitehorse group (Guadalupian), south side sec. 78, block 19, H. G. and N.

Survey, Texas; basal Doxey shale, Quartermaster group (Guadalupian?), center sec. 63, block E-2, D. and S. F. R.R. Survey, Texas. The shells are separated, and somewhat macerated. Cross-lamination of the enclosing sediments is common, suggesting that the waters at the site of burial were strongly agitated.

Genus SELENIMYALINA Newell, n. gen.

Genotype, *Myalina meliniformis* Meek and Worthen. Geological range of the genotype, upper Desmoinesian to Missourian or Virgilian?

Shell strongly prosocline to acline, nearly equivalve, the right valve being almost imperceptibly less convex than the left, apparently not discordant; both valves smooth, lacking any trace of an anterior lobe in adults, and the beaks are neither extended nor acuminate but form a well defined acute angle at the anterior extremity of the hinge, and the umbones are flattened and ill-defined; posterodorsal margin broadly rounded, never angular; dorsal broadly rounded, never straight; ventral margin semicircular; ligament area traversed by exceedingly fine and numerous opisthodetic ligament furrows; dentition similar to *Myalina*, except that the single cardinal tooth of the right valve and the single triangular socket of the left valve are situated on a sort of hinge plate which partly covers a very shallow umbonal recess; musculature similar to *Myalina* (text fig. 6*B*), but differs in having a cordate posterior adductor impression; outer ostracum alike in the two valves, consisting of irregular polygonal prisms of calcite 15 to 20 microns in diameter and more than 100 microns in length; inner ostracum relatively thick and apparently like that of *Myalina*.

Geological range, Desmoinesian—Virgilian.

Remarks.—The group of shells placed under *Selenimyalina* is so different from other Myalinidae that its probable relationships are not at all clear. *Selenimyalina* is closely comparable with the Devonian *Mytilarca* Hall. Although similar forms are not known from the Mississippian rocks, it seem probable that the Late Paleozoic genus was derived from the Devonian form. The shell microstructure and musculature is not known in *Mytilarca*, but there seems to be very close agreement between the two genera in form and characters of the ligament area.

The only obvious difference lies in characters of the dentition. As illustrated by Hall (1884, pls. 31-33), *Mytilarca* is characterized by several cardinal teeth and sockets, as well as an equivalent number of posterior lateral teeth and sockets. *Selenimyalina* possesses only one cardinal tooth and socket, and seemingly has no posterior laterals. *Mytilarca* is commonly classed with the Ambonychiidae, and its subgenus *Plethomytilus* certainly looks more like the ambonychiids than any of the Myalinidae. Unfortunately, none of my specimens of *Selenimyalina* is sufficiently well preserved to show the form at early ontogenetic stages. In the material at hand there is no trace of an anterior lobe, which is so characteristic of at least the young of Myalinidae. Considering the scanty evidence now available, it is quite possible that *Selenimyalina* was derived from a stock different from the Myalinidae and that its resemblance to that family is superficial.

Species of this genus are not yet known in the Pennsylvanian below upper Desmoinesian beds, nor above the lower Virgilian. Permian representatives are unknown. A great host of Lower Triassic myalinas closely resemble *Selenimyalina*, and close scrutiny may reveal that they should be so classed. I refer here to such species as *Myalina schamarae* Bittner, *M. vetusta* Bittner, and *M. platynotus* White.

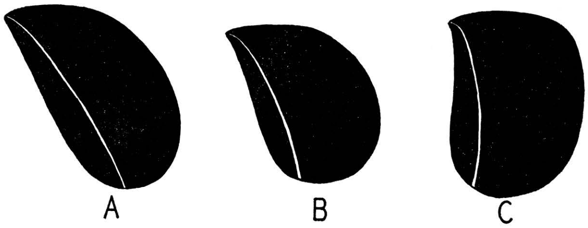

FIGURE 19.—Form series in the genus *Selenimyalina* n. gen. *A*, *S. dotti*, n. sp., Desmoinesian; *B*. *S. meliniformis* (Meek and Worthen), Desmoinesian-Virgilian?; *C*, *S. quadrata*, n. sp., Missourian. All figures X 1.

Nearly all of the specimens of *Selenimyalina* that I have seen retain both valves in apposition, and all were collected from argillaceous shales. These circumstances suggest that members of the genus favored a muddy bottom in quiet waters.

SELENIMYALINA MELINIFORMIS (Meek and Worthen)

Plate 2, figures 1, 2

Myalina meliniformis MEEK AND WORTHEN, *1866*, Illinois Geol. Survey, vol. 2, p. 343, pl. 27, fig. 3.

Shell relatively small, greatest linear dimension less than 30 mm, moderately prosocline, with a slightly concave anterior margin; dorsal, posterior, and ventral margins almost uniformly convex, without angulations; umbonal ridge poorly defined, beaks small and short; hinge characters unknown; outer ostracum in both valves consists of slender, polygonal prisms of calcite 15 to 20 microns in diameter, or possibly larger in some individuals; inner ostracum composed of laminated calcite, probably originally aragonite; musculature as in text figure 6*B*. Measurements[1] for three specimens are as follows:

Measurements of Selenimyalina meliniforis

	Length (mm)	*Height (mm)*	*Greatest dimension*	*Angle a*
Holotype	20	21	26	62°
Topoparatype	23	23	28	65°
Hypotype	20	22	26	82°

Comparison.—This species differs from the similar *Selenimyalina dotti,* n. sp., in having a shorter shell and less oblique form.

Material.—Seemingly, this species is quite rare. Only three specimens were available for this study, all of them bivalved. Two primary types, University of Illinois X-210, are internal molds composed of limonite; the hypotype, U.S. National Museum no. 51146, is a relatively well preserved, testiferous specimen.

Occurrence.—The types were collected from a ferruginous shale on Saline Creek, Gallatin county, Illinois, from a horizon correlated roughly with no. 11 coal of western Kentucky (Marmaton equivalent). The single hypotype was found at an unknown horizon in Gentry county, Missouri. According to the geological map of Missouri, the Pennsylvanian rocks exposed in that county range from the Missourian series into lower Virgilian. The preservation of this specimen indicates that it was collected from a shale bed. The retention of both valves in all of the specimens at hand suggests a quiet water environment at the site of burial.

SELENIMYALINA DOTTI Newell, n. sp.

Plate 2, figures 7, 8

Shell of moderate size, greatest linear dimension being less than 40 mm, markedly prosocline, with an angle *a* around 65° to 70°; anterior margin markedly concave in mature individuals, nearly straight in young ones; dorsal, posterior, and ventral margins smoothly convex, with only a trace of an angulation at the posterodorsal extremity; umbonal ridge broad and poorly defined, beaks rather slender in mature specimens, and extended well forward; general shell form relatively slender and elongated along the anterodorsal-posteroventral axis as compared with other species of the genus; characters of musculature, shell microstructure, and hinge unknown. Measurements for two type specimens are as follows:

Measurements of Selenimyalina dotti

	Length (mm)	*Height (mm)*	*Greatest dimension*	*Angle a*
Holotype	31	30	37	68°
Topoparatype	24	21	29	65°

Comparison.—This form seems to be more primitive than *Selenimyalina meliniformis* and *S. quadrata* in the marked obliquity and resembles somewhat the early growth stages in the last two species. *S. dotti* is distinctly more slender than the other two selenimyalinas.

Material.—The new species is based on two well preserved bivalved specimens from a single horizon. They are nos. 7560 (holotype) and 7561 at the University of Kansas.

Occurrence.—Middle part of the Holdenville formation (upper Marmaton equivalent), above a heavy sandstone, center south line sec. 14, T. 7 N., R. 8 E., Oklahoma. The specimens were found in a soft argillaceous shale, associated with a well preserved fauna of pelecypods and brachiopods.

SELENIMYALINA QUADRATA Newell, n. sp.

Plate 2, figures 3a, b

Shell acline, subquadrate, seemingly a little higher than long, with a broadly concave anterior margin, and convex dorsal, posterior, and ventral margins; intersection of anterior and dorsal margins forms nearly a right angle; musculature unknown, features of shell structure and hinge as in other species of *Selenimyalina.* The only known specimen is incomplete. Estimates of the original dimensions are as follows: Length, 19 mm; height, 25 mm; greatest dimension, 25 mm; angle *a,* 90° (more or less).

Comparison.—In general form this species recalls *Myalina (Orthomyalina) slocomi,* particularly the dwarf variety *M. (O.) slocomi parvula.* However, the resemblances are only superficial. Left valves of *Orthomyalina* are rugose, whereas those of *Selenimyalina* are smooth; the character of the ligament area and dentition are different in the two groups, a hinge plate being absent in *Orthomyalina.*

Material.—Based on a single, fragmentary left valve, which, however, is particularly well preserved, showing the hinge characters and sufficiently distinct growth-lines to permit reconstruction of the probable adult form. The holotype is no. 7562, at the University of Kansas.

Occurrence.—Argillaceous shale, Vilas formation (Lansing), brick plant of Kansas State Prison, Lansing, Kan.

Genus SEPTIMYALINA Newell, n. gen.

Genotype, *Myalina perattenuata* Meek. Geologic range of genotype, Lampasan—Virgilian, Pennsylvanian.

Prosocline to acline, thick-shelled Myalinidae, with slender, extended prosogyre beaks, and an obsolescent anterior lobe just under each beak; both valves smooth, or rugose, in the latter in-

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[1] The holotype and topoparatyps are internal molds; therefore, the measurements are not so reliable as for the hypotype, which is testiferous.

stance the surface of the left valve being markedly more rugose than that of the right; inequivalve, the right valve being slightly flatter and smaller around the ventral periphery than the left; umbonal cavity extending far into the umbones, and partly floored over by large or small umbonal deck or septum, which joins the anterior part of the hinge axis with the anterior margin of the shell; septum in majority of species having no obvious function other than the mechanical strength that it imparts to the shell[1]; dentition similar to that of *Myalina,* consisting of a functional tooth at the anterior end of the hinge of the right valve, which fits into a pivotal depression at a similar position in the left valve, the trace of both tooth and socket in the growth lamellae being marked by narrow ridge extending from the apex of the umbonal deck to the beak; ligament and shell microstructure as in *Myalina;* musculature similar to *Myalina* (text fig. 6*C*) except that the anterior adductor has been completely lost, at least in the species of Pennsylvanian and Permian age.

Geologic range, Viséan to Wolfcampian.

Remarks.—The mention of an umbonal septum in the original diagnosis of the genus *Myalina* by De Koninck shows that this structure was known to him. Unfortunately, the genotype of *Myalina* does not possess the umbonal septum, and De Koninck evidently drew his diagnosis from several Myalinidae having diverse structures.

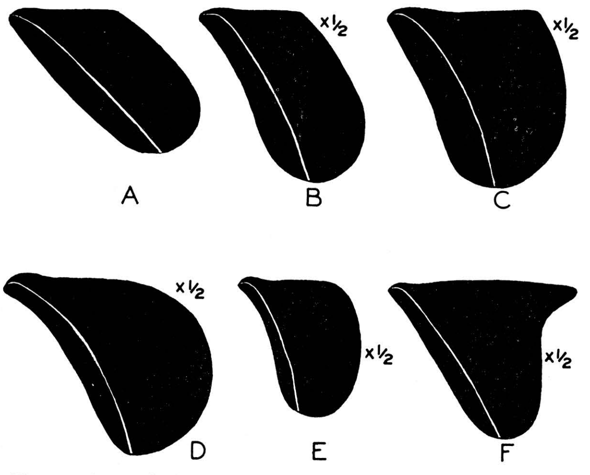

FIGURE 20.—Shell form in species of *Septimyalina. A, S. orthonota* (Mather), X1, from the Morrowan series; B. S. *perattenuata* (Meek and Hayden) (*Myalina kansasensis* of authors), X1/2, Atoka to Wabaunsee; *C, S. burmai,* n. sp., X1/2, from beds of Wolfcampian age; *D, S. orbiculata,* n. sp., X1/2, from Marmaton beds; *E, S. scitula,* n. sp. (*Myalina perattenuata* of some authors) X1/2, from the Wabaunsee group; *F, S. sinuosa* (Morningstar), X1/2, an auriculate species characteristic of beds of Desmoinesian age.

The ontogeny of species of *Septimyalina* indicates that the genus was derived from typical *Myalina,* and the evolutionary trends, arrived at independently, parallel those of *Myalina, s. s.,* to a surprising degree. The majority of species of *Septimyalina,* even the more specialized ones, retain the primitive obliquity, but the tendency to develop a posterior auricle has produced several species that bear a marked homeomorphic resemblance to species of *Myalina.* For instance, the Chester *Septimyalina angulata* (Meek and Worthen), the British Lower Carboniferous *S. redesdalensis* (Hind), and the Desmoinesian *S. sinuosa* (Morningstar) are strongly reminiscent of the Wolfcampian species *Myalina (Myalina) copei.* Although the more completely known species of *Septimyalina* herein described are unquestionably monomyarian, a typical *Septimyalina* from the British Lower Carboniferous, *S. redesdalensis* (Hind) (1897, p. 109), shows a small but distinct anterior adductor pit near the center of the umbonal deck. Much of my material from the Pennsylvanian rocks is so perfectly preserved that the faintest muscle impressions are perfectly shown; and, furthermore, the muscle marks, including the pallial line, are pigmented so that there is no reasonable possibility that I have overlooked the anterior adductor pit. The trace of the pivotal pit, or socket of the left valve in *Myalina,* is a well defined furrow extending to the beak. Except at its distal end this furrow is not functional, because it does not come in contact with the corresponding ridge of the opposite valve. The left valve of *Septimyalina* differs in that a well defined ridge occupies the position of the dental furrow of other Myalinidae. The trace of the pivotal pit in the growth lamellae produces a ridge instead of a furrow.

It is interesting to note that the auriculate septimyalinas seem to be confined to Upper Mississippian equivalents and to the Lower Pennsylvanian, being unknown above Desmoinesian beds. The representatives of the genus ranging into the Upper Pennsylvanian and Lower Permian are decidedly more primitive in general aspect. There is nothing extraordinary about this situation, however, because the more primitive animal stocks in the geologic record commonly are comparatively long ranging.

Much of the confusion over recognition of species in this group of shells in the past is seemingly due to the fact that internal molds commonly give

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[1] The umbonal deck shows a small but distinct anterior adductor impression in *S. redesdalensis* (Hind), from the British Lower Carboniferous.

a very erroneous impression of the original shell form. The shells are relatively thick as compared with the visceral space. Noteworthy is the tendency for the space occupied by the living animal to decrease in volume in the gerontic stage (pl. 13), as in oysters. Unlike most myalinas, the mantle withdrew from the ventral margin in old age.

It is not easy to obtain a general idea of the range of habitats of members of the genus. Species of *Septimyalina* are found in a wide range of rock types—sandstone, various types of limestone, and shales. Some of the shells are bivalved, indicating burial in quiet waters, whereas specimens of some species, particularly *S. perattenuata,* are common in shell breccias, which indicate burial in the zone of active wave action. Of course, it is possible that the broken and fragmentary shells were concentrated and removed by waves and currents from the life environment. In any event, it seems that the environmental range of species of *Septimyalina* was somewhat greater than for the majority of other myalinids. Although shells of *Septimyalina* are generally found associated with other myalinas, they also occur in places where other representatives of the family are absent.

SEPTIMYALINA PERATTENUATA Meek and Hayden

Plate 12, figures 3-12

Myalina perattenuata MEEK AND HAYDEN, *1858,* Albany Inst., Trans., vol. 4, p. 77; —— *1859,* Philadelphia Acad. Nat. Sci., Proc., p. 28; ——, *1864,* Paleontology Upper Missouri, p. 32, pl. 1, figs. 12 a-b.

?*Myalina kansasensis* SHUMARD (in Shumard and Swallow), *1858,* St. Louis Acad. Sci., Trans., vol. 1, p. 213.

Prosocline slender thick-shelled forms with extended beaks and prominent umbones; hinge margin straight, forming a broadly obtuse angle with the straight or slightly curved posterior margin; ventral margin rather narrowly rounded and linguiform, anterior margin strongly concave above and generally slightly convex below; left valve covered by rugose, more or less regular projecting lamellae, which in well preserved adults develop hemicylindrical prone spines that project from the shell margin; right valve marked only by non-projecting, somewhat irregular growth lamellae; right outer ostracum composed of polygonal calcite prisms ranging in diameter between about 7 and 15 microns, left outer ostracum composed of "fibrous' calcite in which individual fibers are of the order of 1 micron in diameter, alignment in both instances being normal to the shell surface; inner ostracum finely lamellar, probably originally aragonite; ligament area as in other Myalinidae, except that the furrows are very fine, 15 to 20 occupying a space of 5 mm; internal characters as indicated in the generic diagnosis. Measurements are indicated in the following tables:

Measurements of Septimyalina perattenuata

Thirty specimens from the Stull shale, Shawnee group, Virgilian

	Length (mm)	*Height (mm)*	*Angle α*	*Angle β*
Maximum	53	60	74°	139°
Average	44	49	63°	125°
Minimum	35	41	51°	114°

Thirty-two specimens from the Vinland shale, Douglas group, Virgilian

	Length (mm)	*Height (mm)*	*Angle α*	*Angle β*
Maximum	60	71	75°	140°
Average	49	51	62°	122°
Minimum	39	40	53°	110°

Thirty-one specimens from the Missourian series[1]

	Length (mm)	*Height (mm)*	*Angle α*	*Angle β*
Maximum	54	58	78°	133°
Average	41 (16)	42 (17)	59° (31)	121° (12)
Minimum	28	30	47°	105°

Comparison.—From the two most similar species, *Septimyalina orthonota* and *S. burmai,* this form differs in its obliquity, being almost intermediate between the very oblique *S. orthonota* and the upright *S. burmai.* It is probable that the three species form a genetic series, inasmuch as *S. orthonota* is geologically the oldest as well as the most primitive, and *S. burmai* is the youngest and most specialized. *S. scitula* and *S. orbiculata* are relatively less rugose and shaped differently. *S. orthonota* is rather poorly known, however, and may represent the young of *S. perattenuata.*

Material.—The above description was based on more than one hundred instructive specimens, many of them perfectly preserved, from many horizons and localities in the Mid-Continent Pennsylvanian. The majority of these specimens are at the University of Kansas.

Occurrence.—This species is one of the most ubiquitous of the myalinas. It occurs, associated with various other myalinas, throughout the Pennsylvanian, and in some places, is the only representative of the family. The species is sparingly represented in a number of collections from the Atoka and Desmoinesian equivalents, and it becomes particularly abundant in the later Pennsylvanian, being found in greater or less abundance in every molluscan facies of the Missourian and Virgilian series.

Shells of this species are found in a wide range of lithologic types, indicating life under variety of ecologic conditions. Specimens are rarely found,

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[1] Various horizons. Numbers in parentheses indicate the number of specimens on which the significant measurements could be taken.

however, in carbonaceous rocks. Bivalved specimens are less common than separated valves, and the common occurrence of the species in brecciated limestones and relatively coarse sandstones suggests that the animal thrived in agitated waters near the zone of effective wave action.

SEPTIMYALINA ORTHONOTA (Mather)

Plate 13, figures 1, 2

Myalina orthonota MATHER, *1915,* Denison Univ. Bull., Jour. Sci. Labs., vol. 18, p. 221, pl. 15, fig. 4.

All of the shells in the type collection are relatively small, the largest being only slightly more than one inch in the greatest dimension; thin-shelled; form slender, subtriangular, hinge line relatively short, anterior and posterior margins relatively long and subparallel; anteroventral lobe inconspicuous or absent; beaks slender but not markedly extended; angle *a* relatively small, about 45°; angle β broadly obtuse, about 145°; umbonal ridge almost straight except in the beaks, broadly rounded, becoming rather obscure below the middle of the shell; surface of left valve coarsely lamellose, right valve unknown; hinge, musculature, and shell microstructure unknown.

Measurements of two specimens are as follows: (1) holotype, a juvenile left valve; length, 13 mm; height, 13 mm; hinge length, ±9 mm; convexity, ±3.6 mm; greatest dimension, ±17 mm; angle *a*, ±45° angle β, ±130°; (2) paratype, a larger left valve, collected with the holotype; length, 23 mm; height, 18 mm; hinge length, 14 mm; convexity, 6 mm; greatest dimension, 27 mm; angle *a*, ±45°; angle β, ±145°.

Comparison.—The specimens available to me do not permit a wholly satisfactory evaluation of this species. It is not certain that the specimens are fully mature, nor does the preservation allow detailed comparison with juveniles of similar but larger species in my collections. The general aspect recalls the form described above as *Septimyalina perattenuata,* and the similarity is heightened by the rugosity of the surface of left valves. This species may simply have been founded on the young of *S. perattenuata.* Additional topotype material is needed for a final judgment.

Material.—Four of Mather's types from the University of Chicago are before me. They are preserved in dark gray, crystalline limestone. Only the two specimens mentioned above are sufficiently complete to exhibit pertinent characters. The holotype is no. 16045 at Walker Museum, University of Chicago. The three paratypes bear the catalogue number 16583.

Occurrence.—The types were collected from the Hale formation (Morrow), East Mountain, Fayetteville, Ark. Other occurrences are unknown.

SEPTIMYALINA BURMAI Newell, n. sp.

Plate 12, figures 1-6

?*Myalina apachesi* MARCOU, *1858,* Geol. North America, p. 44, pl. 7, figs. 6, 6a.

Myalina apachesi GIRTY, *1909,* U.S. Geol. Survey, Bull. 389, p. 81, pl. 9, figs. 6, 7.

Shell rather robust, about as long as high in adults, somewhat prosocline, but less markedly so than several species of the genus; both valves marked by prominent, regular lamellae of growth, which tend to become projected in short, hemicylindrical spines; anterior margin only slightly concave, nearly parallel with the broadly convex posterior margin; ventral margin broadly convex, dorsal margin straight; particularly characterized by a relatively large angle *a*, and a relatively great shell length. Dimensions of the holotype are as follows: length, 48 mm; height (restored slightly), 46 mm; greatest dimension (restored slightly), 57 mm; angle *a*, 70°; angle β, 122°.

Comparison.—This species is similar to *Septimyalina perattenuata,* but adults differ from the latter in being less slender in form and in having a distinctly larger angle *a*. At a given shell size the hinge margin is considerably longer in *S. burmai* than in *S. perattenuata.* Juveniles of the two species are almost indistinguishable. In fact, ontogenetic stages in *S. burmai* simulate closely the adults of *S. orthonota* (pl. 12 figs. 2 and 5) and *S. perattenuata* (pl. 12, fig. 4). Specimens of *S. burmai* less than 35 mm in height are likely to be confused with *S. perattenuata.* It is probable that the three species just named form a natural gens, for they appear successively in the geologic column in the same order in which their form equivalents are introduced in the ontogeny of the youngest species, *S. burmai.* The remaining species of *Septimyalina* are sufficiently distinct that they probably belong in separate tribes of the genus.

It seems that Girty was not justified in reviving Marcou's *Myalina apachesi* for this species. The species is not recognizable from Marcou's description and illustrations. The types are lost, and the exact horizon and locality are not known.

Material.—This species is abundantly represented in my collections from rocks of Wolfcampian age. The overwhelming majority of specimens are so poorly preserved, however, as to supply no basis for a statistical analysis. Most of the material is in the form of internal molds, which are grossly misleading. The size and shape of the visceral cavity of the shell is much more variable than the shell itself. Inasmuch as this is a thick-shelled species, the shell form can be determined only from shells or external molds. The specimen selected for the holotype (U.S. Geol. Survey, no. 2497) is characteristic of the species and is exceptional only in its unusually good preservation.

Occurrence. — Characteristic of almost every molluscan facies in the Council Grove, Chase, and Sumner groups, Lower Permian, in the northern Mid-Continent region. The species has been recognized in the Burr limestone, Cottonwood limestone, Florena shale, and Eiss limestone, of the Council Grove group; the Oketo shale, Chase group; the Krider and Herington limestones, Sumner group. Girty found the species in the Abo sandstone of New Mexico (Wolfcampian), about 50 feet above the base of the red beds at Abo canyon.

SEPTIMYALINA ORBICULATA Newell, n. sp.

Plate 11, figures 1-3

Shell robust, massive; rear margin of shell broadly rounded, so that in some instances there is no distinct angulation at the posterodorsal margin; anterior margin broadly and distinctly concave; beaks very slender, extended far forward; ligament furrows relatively coarse, as compared with other septimyalinas, eight furrows lying in a space of about 5 mm; right valve smooth, left valve slightly rugose. Measurements of the holotype are as follows: length, 57 mm; height (somewhat restored), 46 mm; greatest dimension (somewhat restored), 64 mm; angle *a*, 65°; posterodorsal extremity rounded. The angle *a* in three other topoparatypes measures 60°, 58°, and 64°, respectively.

Comparison.—This species needs comparison only with *Septimyalina scitula*. Undoubtedly the two are closely related, and it may be that the former lies directly in the lineage of *S. scitula*. The latter species, at equivalent size, is distinctly less oblique and less massive. Furthermore, the surface of both valves in *S. scitula* is about equally smooth.

Material.—The species is based on well preserved but very fragmentary material, a half dozen specimens, from a single locality. The holotype (no. 7584) and topoparatypes are at the University of Kansas.

Occurrence.—Shaly limestones at about the horizon of the Lenapah limestone ("Eleventh Street limestone"), upper Marmaton group, near Beggs, NW¼ sec. 19, T. 15 N., R. 12 E., Oklahoma. The specimens occur both in the limestone and in calcareous shale.

SEPTIMYALINA SCITULA Newell, n. sp.

Plate 11, figures 4-14

Myalina perattenuata of authors, in part.

Shell relatively small, upright, almost acline, surface of both valves nearly smooth; beaks slender, extended forward; anterior margin markedly concave in adults, subparallel to convex rear margin, ventral margin relatively narrow, rounded, dorsal margin straight, intersecting rear margin at a well defined obtuse angle of about 100° in most specimens; umbonal deck relatively broad, ligament grooves relatively fine, comparable with those of *S. perattenuata*. Measurements, based on six specimens, are as follows:

Measurements of Septimyalina scitula

	Length (mm)	*Height (mm)*	*Angle a*
Maximum	35	37	77°
Average	20	20	60°
Minimum	14	13	54°
Holotype	23	21	55°

Comparison.—Juveniles of *Septimyalina scitula* are very similar to *S. orbiculata* in general form; although they tend to have a straighter anterior margin; and, of course, they are smaller and less massive than adults of the latter species. More confusing is the similarity between some specimens of *S. scitula* and *Myalina (Myalinella) meeki*. In some instances poorly preserved material can not be differentiated. In addition to the presence of an umbonal deck in the former and its absence in the latter, there are minor differences in form between the two species. The majority of mature specimens of *S. scitula* exhibit a concave front profile. The anterior margin in *M. (M.) meeki* generally is nearly straight. There is a tendency for the beaks in *S. scitula* to be very slightly more acuminate than in *M. (M.) meeki*. Large (fully mature) specimens of *S. scitula* are distinctly more upright in form than mature individuals of *M. (M.) meeki*.

Material.—The holotype and several topoparatypes are located at the University of Kansas, nos. 7587-7592; other paratypes are at the National Museum, no. 7035.

The material on which the species is based is well preserved, but unfortunately the majority of specimens are not fully mature.

Occurrence.—Undoubted representatives of this species are recognized only in Virgilian horizons. The types were collected from the Iowa Point shale (Shawnee) at the NW¼ sec. 1, T. 21 S. R. 13 E., Coffey county, Kansas. Other specimens are from unspecified Wabaunsee beds in northeastern Kansas. Fragmentary and otherwise unsatisfactory material, about which the identification is not positive, comes from Wolfcampian strata in northern Texas and in Kansas. Specimens have been found in separated condition in sandy limestone, and bivalved pyritized specimens have been collected from carbonaceous shales, associated with coal.

Too little is known about field occurrences, in general, to warrant drawing conclusions about the environments in which *S. scitula* lived.

SEPTIMYALINA QUADRANGULARIS Newell, n. sp.
Plate 12, figures 7-9

Shell relatively upright, almost acline in adults, subtriangular, with the narrow ventral margin forming the apex of an inverted triangle; anterior margin only slightly concave; posterior margin slightly convex, hinge margin straight; septum relatively small, ligament furrows fine, as in *Septimyalina perattenuata,* surface of both valves relatively smooth. Measurements of two type specimens are as follows.

Measurements of Septimyalina quadrangularis

	Length (mm)	*Height (mm)*	*Angle α*	*Angle β*
Holotype	38	49	72°	75°
Topoparatype	21	25	72°	87°

Comparison.—In a general way, this species recalls *Septimyalina burmai* and *S. scitula* in the erectness of the shell. From both it differs in the narrowness of the ventral margin and the relatively small value of the angle β. The relative smoothness of both valves removes any likelihood of confusion with *S. burmai. S. quadrangularis* is relatively specialized, as shown by its upright form. The ontogeny, as revealed by growth lines, suggests derivation from a shell shaped like *S. perattenuata,* which, however, is quite rugose, unlike the present form, and may not lie directly in the lineage of *S. quadrangularis.*

Material. — This is a very rare species. Only three specimens occur in my collection, all of them from a single locality. They are preserved as molds in very fine, calcareous sandstone. The holotype, no. 21194, and two topoparatypes, nos. 21195, 21196, are at the University of Wisconsin.

Occurrence.—Savanna sandstone (middle Desmoinesian), near Pittsburg, Okla. The valves are separated, indicating deposition in agitated waters.

SEPTIMYALINA SINUOSA (Morningstar)
Plate 12, figures 10-13

Myalina recurvirostris var. *sinuosa* MORNINGSTAR, *1922,* Ohio Geol. Survey, Bull. 25, p. 219, pl. 11, figs. 10-12.

Shell of moderate size for the genus, and relatively massive; mature form subrhombic except for the posterodorsal extremity which is extended in a prominent but slender auricle; beaks very slender and extended anterodorsally above the hinge, virtually without lobation; beaks markedly prosogyre, the left one being somewhat more conspicuous and rising dorsally above the right beak; umbonal ridge relatively straight below the region of the umbones, so that the anterior margin of the shell also is nearly straight; angle α ranges from about 53° to 58°; angle β acute, ranging from about 40° to 50°; valves apparently somewhat discordant, the right valve being slightly smaller and less convex than the left; both valves marked by relatively uniformly spaced edges of growth lamellae, which are somewhat rugose in the left valve, less so in the right, and distributed about four in the space of 10 mm along the umbonal ridge, at a shell height of 50 mm or more; ligament area relatively broad, measuring up to 7 mm in one mature individual in which there are at least 20 very fine ligament grooves. These grooves descend to the hinge axis at a low angle so that at least six intersect the axis in one incomplete specimen within a horizontal distance of about 36 mm; dentition in right valve unknown, that in the left valve consisting of a shallow pivotal socket occurring at the posterior end of a narrow ridge, which extends downward and backward from the beak at an angle to the hinge axis of about 16°; umbonal deck or septum rather massive in left valve lying nearly in a plane with the ligament area, that of right valve not observed; outer ostracum in right valve composed of short irregularly polygonal prisms of calcite about 15 to 20 microns in diameter, that of the left valve consisting of fibrous calcite with fibers about 1 micron in diameter normal to the shell surface; inner ostracum of both valves lamellar, probably originally, aragonite; musculature unknown.

Measurements of specimens of Septimyalina sinuosa, in millimeters

	Lectotype (no. 15273)	*Topoparatype* (no. 15272)	*Topoparatype* (no. 9819)
Length	51	....	....
Height	45	....	60±
Convexity	14	16	20
Hinge length	51	....	....
Greatest dimension	54	....	78±
Angle α	53°	55°	58°
Angle β	30°-40°	35°	....

Comparison.—The parallelism between this species and *Myalina (Myalina) copei* is very striking. Critical inspection, however, reveals that the resemblance is superficial and largely produced by the possession of a rear auricle in both species. *M. (M.) copei* possesses a conspicuous anterior lobe, and the septum of *Septimyalina* is lacking. *S. angulata* (Meek and Worthen) (1866, p. 300, pl. 23, figs. 7a, b) from the Chesterian series, near Chester, Illinois, is a closely related form but has a smaller angle α and less prominent auricle, as might be expected of an older and more primitive species. The British species *S. redesdalensis* (Hind, 1897, p. 109, pl. 3, figs. 1-5, 7-13; pl. 5, fig. 1; pl. 7, figs. 1, 1a) from the Lower Carboniferous, is another auriculate *Septimyalina,* which also has a smaller angle α and less extended rear auricle than the present form. Judging from the relatively great value of the angle *a* and the extended auricle, *S. sinuosa* is the most highly specialized species within the genus. It very likely is one of the terminal members of a series of septimyalinas, which, during the Late Mississippian and Early Pennsylvanian, progressively increased the length of the hinge by development of the rear auricle.

Material.—The most instructive representatives of this species at my disposal are part of the original suite on which the species was based. There are five specimens from the University of Ohio, three good left valves and two crushed specimens retaining both valves in opposition. They bear the catalogue numbers 15273 (designated here the lectotype), 15272, 9819, 4621. The shell material is well preserved and occurs in a calcareous gray shale or argillaceous limestone. Other fragmentary specimens occur in argillaceous shale.

Occurrence.—Lower Mercer limestone (upper Pottsville), northern part of Madison Township, Muskingum county, Ohio, one fourth mile south of the county line near Adams Mills (the types); questionably from the upper Pottsville or lower Allegheny equivalents on Otter Creek, near Brazil, Ind.; Labette shale (Marmaton), St. Louis, Mo.; from an unknown horizon in the McCoy formation (Desmoinesian), near Bond, Colo.

Genus NAIADITES Dawson, 1860

Naiadites DAWSON, *1860,* Acadian Geology, Supplement, 1st edition, p. 43; DAWSON, *1894,* Quart. Jour. Geol. Soc. London, vol. 50, pp. 435-437; HIND, *ibid.,* pp. 437-442; HIND, *1895,* Palaeontographical Soc., vol. 49, pp. 126-131; DAVIES AND TRUEMAN, *1927,* Quart. Jour. Geol. Soc. London, vol. 83, pp. 236-237; DIX AND TRUEMAN, *1930,* The Naturalist, pp. 15-18; NEWELL, *1940,* Am. Jour. Sci., vol. 238, pp. 292-295.

Genolectotype, *Naiadites carbonarius* Dawson, 1860, designated by Hind, 1894, Quart. Jour. Geol. Soc. London, vol. 50, p. 439.

Modioliform shells having the beaks situated distinctly behind the anterior terminus of the hinge; surface devoid of radial ornamentation; hinge without well defined teeth, ligament areas external, as in other Myalinidae, but slightly amphidetic, with relatively fine ligament furrows; anisomyarian, with two relatively small pedal scars located in the umbonal recess just behind and above the larger anterior adductor; pallial line differentiated into a series of separate pits, at least in the anterior part; posterior adductor probably as in other Myalinidae (text figure 6F); shell microstructure alike in the two valves, consisting of a relatively thick inner lamellar ostracum and thin outer ostracum of fine (about 30 microns in diameter), short, irregularly polygonal prisms of calcite arranged normal to the shell surface.

The left valve of *Naiadites carbonarius,* on which most of the above observations were made (McGill College, no. 2.1172), has the following measurements: length, 18 mm; height, 13 mm; hinge length, 15 mm; greatest dimension, 20 mm; angle of hinge with umbonal ridge, about 60°; posterodorsal angle, 125°.

The zone of *Naiadites,* which seems to include the entire known range of the genus, embraces the Lanarkian and Westphalian stages (Pottsville) of European Upper Carboniferous. Davies (1930) has called attention to the fact that *Naiadites,* together with its customary associates *Anthracomya* and *Carbonicola,* although not common, are rather widely distributed in the Pottsville and Allegheny beds of the Appalachian region. In view of the great stratigraphic interest of these forms, it is unfortunate that exhaustive collections have not been made and studied in the United States. Since I do not now have access to satisfactory collections, an extended treatment of the species of *Naiadites* must be deferred. At present, it seems that the genus is represented in North America only in the eastern areas, in deposits of Early Pennsylvanian age. Future studies may reveal that *Naiadites* is represented also in the coal-bearing deposits of the Mid-Continent region.

Remarks.—Much has been written about Coal Measures pelecypods that are referred to the genera *Naiadites, Anthracomya,* and *Carbonicola.* Their remains are common in the roof shales of coal beds in various Upper Carboniferous basins of western Europe. The high order of stratigraphic usefulness of these shells has led to the publication of several outstanding monographic studies (Amalizky, 1892; Hind, 1894-1896; Davies and Trueman, 1927; Tchernyshev, 1931; and other important works) with the result that a succession of zones based on these "fresh-water" pelecypods of the late Paleozoic is recognized in all of the important coal basins of the Upper Carboniferous of Europe.

The majority of students of these shells generally are agreed that the species of *Naiadites, Anthracomya, and Carbonicola* were of estuarine or freshwater habit, although Tchernyshev (1931, pp. 105-111) finds reason to regard them as near-shore marine. His observations in the Donetz basin reveal an occasional association of these pelecypods with forms usually regarded as typically marine *(Lingula, Aviculopecten, Myalina, Bucania, Murchisonia,* and goniatites.) The association of freshwater and marine shells in the deltaic and estuarine environments of modern coasts is too common to merit discussion here. It is pertinent, however, to remark that the exceptional occurrences of shells of the three pelecypod genera with undoubted marine shells does not necessarily imply that *Naiadites, Anthracomya,* and *Carbonicola* invaded the normal marine habitat during their life.

Since the publication of Hind's monograph (1894-1896), *Anthracomya* and *Carbonicola* have been referred to the Unionidae by many authors and to the Cardiniidae by others. Since these two genera are not related to the myalinas, they will not be discussed further here.

The genus *Naiadites* erroneously has been classed with *Carbonicola* and *Anthracomya* by many authors. Hind and his followers, however, recognized the affinities of *Naiadites* with the Mytilacea and classified the genus along with *Myalina* in the Mytilidae. Although I prefer to place these genera in the family Myalinidae, it would be ungenerous not to point out that Hind's assignment was perfectly proper in consideration of the broad limits given the family Mytilidae in his day.

While making his pioneer geological studies in Nova Scotia, Sir William Dawson found large numbers of small, distinctive pelecypods in the roof shales of coal beds of the Upper Carboniferous. Association of the mollusks with plant remains and fossil amphibians suggested to him that the pelecypods had lived in a brackish or fresh-water habitat. To these shells he gave the name *Naiadites,* although he later admitted that they represented more than one genus. A genotype was not designated in the original publication of *Naiadites.* Three years later, in 1863, Salter (Quart. Jour. Geol. Soc., vol. 19, p. 80) introduced the generic name *Anthracoptera* for Dawson's *Naiadites carbonarius,* ignoring the priority of *Naiadites.* Salter's genus has no valid claim for recognition, as has been pointed out by subsequent investigators, and therefore need receive no further attention here. Hind apparently was the first to designate a genotype for *Naiadites,* and his selection of *N. carbonarius* in 1894 is legally correct. In the last analysis, our concept of the genus must be determined largely by the character of *N. carbonarius.*

Through the kindness of Dr. T. H. Clark of McGill University, I have been able to make some pertinent observations on specimens that may be syntypes of the species. Doctor Clark supplies the following information:

> We have nearly all of Dawson's material here; but, inasmuch as Dawson's illustrations were, for the most part, sketches and inasmuch as he did not mark his type specimens, it is almost impossible today to be absolutely sure which specimen he used as a type. Occasionally an imperfection reproduced in the drawing or the shape of the rock helps. From time to time various people have tried to determine Dawson's type specimens among our collections, not altogether with success, however. I am sending you four such specimens determined by various museum workers here, but I am not satisfied that Dawson must have used these specimens.

Although some doubt exists regarding the identity of Dawson's type specimens, the specimens that have been made available to me were identified by Dawson, and were collected by him from the same locality as the types, South Joggins, Nova Scotia, from beds generally correlated with some part of the Pottsville series.

Students of Pennsylvanian faunas often have remarked on the close resemblance of *Naiadites* to *Myalina.* For instance, Hind says,

> The question . . arose as to whether de Koninck's *Myalina* might not even supersede *Naiadites,* . . . but there still remained the fact that de Koninck affirmed a rostral plate or myophore in his description, which was, however, conspicuously absent in his figures, and more markedly so in the illustrations in pl. 29 of his later work, "Faune du Calcaire Carbonifère de la Belgique," 1885 . . . . I have therefore adopted the name *Naiadites* Dawson for the Mytiliform shells of the Coal-measures for a twofold reason. First, because they do not possess myophorial septa; and second, because they do not occur with a typically marine fauna as a rule . . . (Hind, 1895, pp. 129-130.)

Had Hind understood that the type species of *Myalina* actually does not possess the septum postulated by De Koninck, it is highly probable that he would have relegated *Naiadites* to the synonymy of *Myalina.* As it is, I have been confronted by the problem of searching for significant features in the respective genotypes of the two genera to determine whether or not *Naiadites* can in practice be distinguished objectively from *Myalina.* With this end in view many species of *Naiadites* from the Lower Coal Measures of England were borrowed from the U.S. National Museum and from Yale University, and comparisons were made directly with several species of *Myalina* that can be regarded as being closely like the genotype. These observations indicate that *Naiadites* and *Myalina* are persistently different.

Species of *Myalina,* including the genotype, are characterized by the possession of an anteroventral lobe or emargination of the shell, producing a somewhat superficial resemblance to *Volsella.* In spite of the similarity, there is no *Myalina,* to my knowledge, that can truly be called volselloid, because the beaks of *Myalina* are located at the extreme anterior end of the cardinal margin, whereas in *Volsella* the beaks are situated distinctly back of the front extremity of the shell. In respect to the beaks and the anteroventral lobe, *Naiadites* is like *Volsella,* though differing from that genus, of course, in characters of musculature, ligament, and shell microstructure.

Species of *Naiadites,* such as *N. carbonarius, N. modiolaris,* and *N. carinatus* are alike in certain distinctive characters of the anterior muscles, Three muscle impressions occur in the umbonal cavity. The largest of these is at the terminus of the pallial line and occurs just back of the most anterior projection of the shell. It is evidently the anterior adductor impression. A pit about half as broad occurs just behind and above the anterior adductor, and, judging from its position, this represents the point of attachment of one of the pedal muscles. Behind this scar, and almost in line with the other two, occurs a still smaller pit, the superior pedal attachment.

Like *Naiadites*, typical species of *Myalina* have three anterior muscle pits, and the impressions are arranged approximately the same. However, there is a marked tendency for the three pits to be more closely spaced in *Myalina*, and the anterior adductor impression is relatively small, becoming obsolescent in certain species.

The exact character of the posterior adductor impression has not been determined in the type species of *Naiadites*, but the pallial line is like that of *Myalina* in being broken anteriorly into a series of small muscle pits.

The shell microstructure in *Naiadites carbonarius* seems to be the same in both valves, consisting of a relatively thick, lamellar inner ostracum and a thin outer ostracum composed of very small, irregularly polygonal calcite prisms arranged normal to the shell surface.

The shell form in *Naiadites* is similar to very primitive or very young *Myalina*. The assumption that *Naiadites* is the most primitive member of the Myalinidae seems a fair one. The conclusion is further borne out by the fact that this is the only genus that had not yet acquired a completely opisthodetic ligament; therefore, *Naiadites* presumably is very similar to the ancestral radicle of the family Myalinidae. Unfortunately for this theory, undoubted *Naiadites* is unknown below the Upper Carboniferous. It is possible that *Naiadites* was derived from a more distinctly amphidetic form like the Devonian *Ptychodesma* Hall.

Henderson (1935, pp. 60, 61) cites nine species of *Naiadites* in American paleontological literature. They are *N. carbonarius* Dawson, 1860; *N. fragilis* (Meek and Worthen), 1866; *N. longus* Dawson, 1894; *N. mytiloides* Dawson, 1894; *N. ohioensis* Morningstar, 1922; *N. politus* White, 1878; *N. triassicus* Pilsbry, 1926; *N. wanneri* Pilsbry, 1926. In my opinion *N. fragilis*, from Mississippian rocks, and the Upper Triassic species, *N. wanneri*, and *N. triassicus*, should be referred to other genera. The following specific descriptions are limited to the two species—*N. carbonarius* and *N. ohioensis*—of which I have seen typical material.

NAIADITES CARBONARIUS Dawson

Plate 15, figures 2a-b

Naiadites carbonarius DAWSON, *1860*, Acadian Geology, Supplement, 1st edition, p. 204. ——, NEWELL, *1940*, Am. Jour. Sci., vol. 238, pp. 292-295, text fig. 1b, pl. 2, figs. 4a-c.

Shell volselloid, the beaks located about one-sixth of the shell length behind the anterior extremity of the shell; relatively small, having in a typical specimen a length of 18 mm, height, 13 mm; hinge length, 15 mm; greatest dimension, 20 mm; umbonal angle, about 60°; posterodorsal angle, about 125°; a well defined sulcus marks off a prominent anterior lobe of the shell, but the posterodorsal margin of the umbonal ridge is only obscurely delimited by a very broad sulcus, which corresponds in position with nearly all of the posterodorsal part of the shell; ligament area relatively narrow, about 0.5 mm in breadth at the widest place under the beaks, and traversed by seven or eight very fine ligament grooves in the specimen at hand; dentition seemingly lacking, nor is there any trace of an umbonal septum such as is found in some genera of Myalinidae; the musculature is not wholly determinable from material at hand, but so far as shown is quite distinctive as compared with species of other known genera, the anterior adductor impression being relatively large and deep, situated directly below the beak in the anterior lobe of the shell; anterior byssal retractor impressions relatively small, being located slightly behind and above the adductor; pallial line and posterior musculature unknown; shell microstructure identical in both valves, consisting of a relatively thick, lamellar ostracum of aragonite, and a thin outer ostracum of small (about 30 microns in diameter), irregularly polygonal calcite prisms arranged normal to the shell surface.

Comparison.—Typical representatives of this species have been directly compared with *Naiadites ohioensis* Morningstar and found to be very similar. The two can be distinguished, however, by differences in the posterior profile and by the fact that the umbonal ridge in the Ohio species is more sharply delimined by rather narrow, well-defined sulci; probably also the Ohio form is relatively more ventricose. This species is very like the European *N. modiolaris* (Sowerby), and I am by no means certain that they are specifically different. Statistical studies on adequate collections of both species will be necessary to solve this problem.

Material.—The above observations were made on several fragmentary specimens and one nearly complete left valve reposing in the McGill College collection, no. 2.1172. This collection is thought to be part of Dawson's original suite of specimens and was collected in the "Lower Coal Measures," probably upper Pottsville, of South Joggins, Nova Scotia, where the species is said to be very abundant.

NAIADITES OHIOENSIS Morningstar

Plate 14, figures 5a-6b

Naiadites ohioense MORNINGSTAR, *1922*, Ohio Geol. Survey, Bull. 25, p. 221, pl. 12, figs. 10-13.

Shell rather fragile, relatively small for the genus, volselloid, the beaks located about one-sixth of the shell length behind the front end of the shell; umbonal ridge delimited on both sides by a rather narrow and well defined sulcus, the intersection of the posterodorsal sulcus with the rear margin of the shell being marked by a shallow notch or sinus in the profile; shell very ventricose, the two valves in apposition being only slightly less thick than the shell height; posterior end somewhat truncated in appearance so as to produce a roughly subquadrate posterodorsal angle; right valve very slightly less convex than the left but apparently not discordant; musculature unknown, except for the anterior adductor which is relatively large for the genus, covering of the inner surface of the anterior lobe of the shell.

Measurements of specimens of Naiadites ohioensis, in millimeters

	Lectotype (no. 15281)	*Topoparatype* (no. 15279)	*Topoparatype* (no. 15280)
Length	11.5	13.0	12.5
Height	8.0	8.0	9.0
Thickness	6.0	7.0	6.5
Hinge length	10.0	10 ±	10 ±
Greatest dimension	12.0	12.5	12.0
Angle α	48° ±	45°	45° ±
Angle β	65-75°	70-87°	....

Comparison. — Although similar to *Naiadites carbonarius* in lateral profile, this species is significantly smaller, has smaller angle α and β, and it is especially distinguished by a slight indentation of the posterior margin corresponding to the location of a narrow sulcus that borders the umbonal ridge posterodorsally. The marked obesity of the shell seems to be distinctive.

Morningstar (1922, p. 221) has stated that the shell gapes in this species along the ventral and posterior margins, but examination of the types leads me to the conclusion that there is no appreciable gape. The two valves are very slightly and about equally rugose, but this characteristic does not seem to distinguish the species from other *Naiadites*.

Material.—The above observations were made on the type collection, lectotype 15281, and topoparatypes 15279 and 15280, University of Ohio. The specimens are rather well preserved and excepting no. 15279, which is an internal mold, retain the original shell. The material was collected in nodules of "iron ore" and seems to have a matrix of clay ironstone.

Occurrence.—Morningstar states that the shells were found associated with *Anthracomya elongata* (Dawson) but no other fossils were present. The fossils were found in concretions that lie in the shale above the Sharon coal in the roof of the John Alexander mine near the head of Higgins Run, northern part of sec. 15, Madison Township, Scioto county, Ohio. This horizon occurs low in the Ohio Pottsville and is correlated by Wanless (1939, p. 64) with some part of the Morrowan series of Oklahoma and Arkansas.

Genus LIEBEA Waagen, 1881

Liebea WAAGEN, *1881*, Palaeontologia Indica, ser. 13, pp. 292-295; NEWELL, *1939*, Jour. Paleontology, vol. 13, pp. 589-593, pl. 68.

Genolectotype, *Liebea squamosa* (J. de C. Sowerby), 1829, designated by Cox, 1936, Geol. Soc. London, Quart. Jour., vol. 92, pp. 38-39.

Shell small, rarely attaining a length greater than 25 mm, mytiloid, subrhombic, with arched dorsal margin; anterior margin lacking anterior lobation, except in the earliest juvenile stages; relatively biconvex, subequivalve, with right valve almost imperceptibly less convex than the left valve; surface of right valve relatively smooth, left valve more or less conspicuously lamellose; anterior margin of both valves crenulated below beaks and in front of angular ridge, which bounds front margin of ligament area, crenulations consisting of one crest and one sinus each, the crest of the left valve being above the sinus and that of the right valve being placed below a sinus, crests and

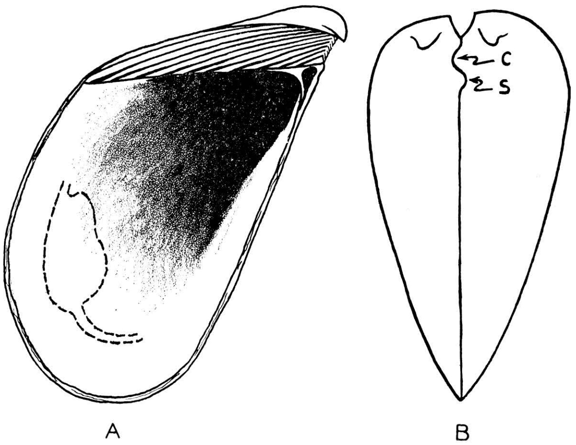

FIGURE 21.—Hinge characters and dentition in *Liebea*. *A*, Interior of left valve of *L. squamosa* showing myalinid ligament area, umbonal septum, and anterior adductor pit on septum; *B* front view of bivalved specimen showing interlocking denticulations of front margin; *C*, crest; *S*, sinus. Approximately X3.

sinuses interlocking to produce a sort of "dysodont" dentition seen in some species of *Mytilus;* hinge like that of *Septimyalina* otherwise; anisomyarian, with anterior adductor lodged in a deep pit along the anteroventral edge of a small umbonal septum, or deck, which walls off a rather deep umbonal cavity; posterior adductor indistinct, seemingly located rather low under posterior extremity of hinge; position of other muscles uncertain, but probably similar to *Septimyalina.*

From *Septimyalina* this genus is distinguished by the interlocking crenulations of the anterior margin below the beaks, by the deep adductor pit on the septum, and by the mytiloid contour. It is probable that *Liebea* arose from a primitive *Septimyalina* in which the anterior adductor was not completely lost.

Geologic range, Permian of Greenland and the eastern hemisphere. Unknown in the United States.

Dimensions of Liebea squamosa from Zechstein near Gera, Germany[1]*, in millimeters*

Specimen	1	2	3	4	5	6
Length	....	18	16	17	22	15
Height	....	15	14	14	15	12
Thickness	10	10	12	11	....	9
No. lig. grooves	8	7	7	8	....	8

Remarks.—A small mytiliform pelecypod commonly referred to *Liebea squamosa* (J. de C. Sowerby), or its more widely employed synonym *L. hausmanni* (Goldfuss) (1837), is widely distributed and locally abundant in the late Permian Zechstein-Kazan provinces of northern and northwestern Europe, and is associated with a Zechstein fauna in the east Greenland geosyncline (Frebold, 1931). The species has been reported also from the Italian Alps (Merla, 1931) and, doubtfully, from the Karoo beds of Tanganyika (Cox, 1936), and the Bone Springs and Capitan horizons of West Texas (Girty, 1908). I think that the last mentioned citation is in error, and the material on which Girty based his identification is too poorly preserved to warrant generic identification.

Similar species described under *Liebea* have been recorded from the "*Bellerophon* beds" of the Carnic alps (*Liebea dieneri* Gortani, 1906) and the uppermost Permian of Madagascar (*Liebea dieneri* Treat, 1933, not Gortani, 1906). Other species referred to *Liebea* have been described from the Lower Productus limestone (*Parafusulina* beds) of India (Waagen, 1881) and the Maping limestone of China, "early" Permian (Grabau, 1936).

Unfortunately, most of the references to *Liebea* have been based on external form without information on the ligament and internal characters that distinguish *Liebea* from other Late Paleozoic mytiloid shells. The fact that the Permian rocks of many regions contain these diminutive shells, which agree closely in form, is of great stratigraphic interest and suggests that they may indeed all be closely related. It is urgent, however, that an attempt be made to determine whether or not all of the above-mentioned forms possess the critical characters of *Liebea.*

Characteristics of Liebea.—Waagen (1881, pp. 292-295) established *Liebea* on small mytiloid shells from the German Zechstein, characterized, as he thought, by the following features: (a) Byssal notch lacking, (b) ligament internal, lodged in a number of resilifer pits observable only in old specimens, and (c) by certain peculiarities of the anterior "auricles." His interpretation of the ligament was erroneous. The original diagnosis is quoted:

> Shell inequivalve, the right valve smaller than the left one: inequilateral, mytiliform, with a small, not very distinct, posterior wing in both valves, and with a very small anterior wing in the left valve only. The position of this latter wing is not as in other Aviculidae, but is placed about vertically to the plane of the valve, turning round the smaller right valve and embracing it partially. This wing is compressed from both sides, bearing on its top a sharp ridge which projects at about right angles from below and in front of the beak of the left valve, treminating the area of that valve anteriorly and giving it a squarish shape.
>
> In the right valve the existence of an anterior wing is barely indicated. In its place there is an incision of the shell, into which fits the bent-over anterior wing of the left valve.
>
> Both valves are provided with a more or less distinct sharply defined area, which is linear in young specimens and very broad in old ones. It is smooth and only covered by distinct striae of growth, parallel to the hinge margin.
>
> The area in the left valve is broader than that in the right one.
>
> The entire hinge line serves for the attachment of a quite internal ligament. This ligament seems to be linear in young specimens, but in old ones it is distinctly divided in several parts, which are attached to a number of pits, between which the hinge margins of both valves seem to have nearly touched each other. The number of pits is generally four or five. The first is situated just below the beaks, the others are distributed over the posterior part of the hinge line.
>
> The hinge seems to have been quite edentulous, as no trace of teeth has been detected up to the present.
>
> Internally, below and in front of the beaks, there is in each valve a small septum, which separates the anterior wing from the remainder of the shell.
>
> The muscular and pallial impressions cannot be observed in any of the specimens at my disposal. They have been described accurately by King, only the position of the anterior adductor, as indicated by him, seems to be somewhat doubtful. If the anterior adductor had been attached to the anterior wing of the shell, it must have been much larger in the left than in the right valve, as in the latter this wing is so rudimentary that there was not much place for the attachment of a large muscle. (Waagen, 1881, pp. 293-294).

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[1] All the specimens are bivalved internal molds except No. 1, which is a cast.

Kings observations on the same species are pertinent:

> As J. de C. Sowerby and Goldfuss have overlooked two or three important characters of this interesting species, it is necessary for me to add, that it is inequivalved; has recurved umbones, a horizontal septum within the umbonal cavity of each valve, and a wide longitudinally-grooved cartilage-furrow or fulcrum. Its muscular system has already been noticed; but it may be added, that the anterior visceral or pedal muscles, judging from the position of their impressions, must have been situated much further back than is usual in *Mytilus* (King, 1850, p. 160.)

It should be noted that King described the ligament area ("cartilage furrow") as being longitudinally grooved in *Liebea squamosa;* whereas, Waagen described it as being smooth, marked only by growth lines. There can scarcely be any question as to King's meaning in reference to the ligament grooves, because he described and illustrated the same feature in another species generally referred to the same genus, *L. septifer* (King) (1850, p. 161, pl. 14, fig. 13). *L. septifer,* as described by King, certainly had a ligament system similar to that of *Myalina* de Koninck, and judging from King's description of *L. squamosa,* this species also had a similar ligament.

Maslennikov, while studying Kazanian specimens from the Timan Mountains of northern Russia, was puzzled at being unable to confirm Waagen's observations on *Lieba* (Maslennikov, 1935, pp. 63-66). After cleaning some of the Russian specimens, he concluded that the hinge does not possess multiple resilifers such as those described by Waagen. Instead, he found the hinge area marked only by parallel striations, which he interpreted as growth lines. Maslennikov's plate 2, figure 11, indicates ligament grooves rather than growth lines on the hinge area of one imperfect specimen. He expressed somewhat hesitantly the possibility that the Russian species may differ from the Zechstein *L. hausmanni* (= *L. squamosa*), pointing out that the Russian form lacks the peculiar anterior auricle on the left valve and that the musculature varies slightly from descriptions of the western European specimens. He might have added also that the specimens illustrated by him differ considerably in form from the Zechstein representatives, and have a much narrower ligament area. Although the Russian form was described under the name *Liebea hausmanni,* Maslennikov intimated that perhaps his material should be classed with *Myalina* instead of *Liebea.*

When Waagen framed the original diagnosis of *Liebea,* he had under consideration two species, *L. hausmanni* (Goldfuss), from the German Zechstein, and *L. indica* Waagen, from the basal beds of the lower Productus limestone of India (horizon of primitive *Parafusulina*). Although most of Waagen's observations were made on the German species, he failed to designate it as the genotype; therefore the two species were genosyntypes. The first formal designation of a genotype for *Liebea,* to my knowledge, was made by Cox (1936, pp. 38-39) when he indicated *L. squamosa* as the type of *Liebea.* This designation is valid, in the absence of earlier designations, inasmuch as Cox placed *L. hausmanni* in the synonymy of the earlier described *L. squamosa.* It is my opinion that the two names, as Cox also believed, are subjective synonyms. Although the species *L. squamosa* would not be recognizable from Sowerby's description of 1829, King (1850) redescribed the species with Sowerby's specimens before him. Seemingly no one has questioned the identity of the form described by King as *L. squamosa* with the German *L. hausmanni* of Goldfuss.

Through the generosity of Mr. Kenneth Oakley of the British Museum of Natural History, I have examined four specimens of *Liebea squamosa.* Two of them are from the Magnesian limestone of England and are essentially topotypes of Sowerby's species. The other two are from the Zechstein of Gera, Germany, the locality that yielded Waagen's specimens. All of the specimens are internal molds, as were most of Waagen's. One of the English specimens is extraordinary in retaining a portion of the external mold of the ligament area of the left valve. This specimen, although imperfect, clearly had a ligament like that of other Myalinidae.

Another collection of specimens was made available for this study from the collections of the Geologisches Landesmuseum at Berlin, through the kindness of Dr. O. H. Schindewolf. These specimens are all from the Zechstein dolomites of the Gera district. Some, perhaps all of them, are from

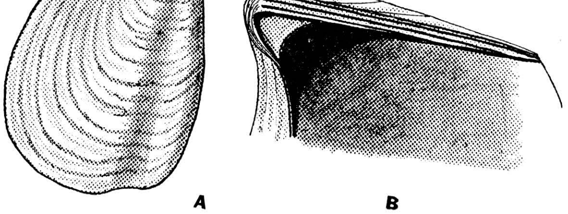


FIGURE 22.—Myalinid genera *Atomodesma* Beyrich and *Maitaia* Marwick. *A,* Diagram of Atomodesma exarata Beyrich, X2/3, genotype of *Atomodesma,* from the Lower Triassic of Timor (redrawn from Wanner, 1922); *B,* diagram of *Maitaia trechmanni* Marwick, X1/3, from the Maitai beds (Permian?) of New Zealand (redrawn from Marwick, 1935).

the middle Zechstein horizon. The more instructive specimens consist of six internal molds, some of which exhibit features of musculature, and one incomplete but superb external mold, which shows perfectly the ligament characters and form of the shell (pl. 15, figs. 3a-d; text fig. 5). This specimen is unique among all described Myalinidae in showing perfectly the imprint of the original conchiolin structures of the ligament, and verifies my prediction (Newell, 1938, pp. 34-35, pp. 26-30, fig. 6) that the ligament of *Myalina* and similar Paleozoic shells was comparable structurally to that of modern *Arca*.

Genus ATOMODESMA Beyrich, 1864

Atomodesma BEYRICH, *1864*, Konigl. Akad. Wiss. Berlin, Abhand., p. 68; ——, C. WANNER, *1922*, Pal. von Timor, Lief. XI. no. XVIII, pp. 60-70.

Genolectotype, *Atomodesma exarata* Beyrich, *1864*, designated by C. Wanner, idem., p. 63; range of genotype, Lower Triassic, Timor.

Wanner's diagnosis: Shell equivalve, transversely oval, more or less elongated diagonally, flat to strongly convex. Beak terminal, bluntly pointed, bent forward and inward, either free or fused with the cardinal margin. Cardinal margin straight, toothless, on the average up to half as long as the shell, with an equally long ligament groove, which is not divided by vertical septa into individual ligament pits, but occasionally carries fine longitudinal ridges. Prismatic layer of the shell very strongly developed, as in *Inoceramus*. Surface ornamented with irregular concentric wrinkles, and radial furrows of variable strength and number.

Geologic range, Permian and Lower Triassic of Timor; uppermost Permian (zone of *Cyclolobus*), Salt Range, India.

Remarks. — Unfortunately Wanner's observations on the hinge characters do not conclusively establish the type of ligament possessed by *Atomodesma*. The general expression of the shells suggests that they are indeed myalinids, and presumably the ligament was of the *Myalina* type. I am more impressed by the similarity of *Atomodesma* with *Aphanaia* than was Wanner (1922, p. 62), the principal difference being that the typical species of *Aphanaia* is said to be strongly inequivalve, the right valve being more convex and having a longer beak than the left valve. Externally, Marwick's *Maitaia* is very like *Atomodesma*, and has a similar shell microstructure. *Maitaia* possesses a true myalinid hinge and, in addition, possesses an umbonal deck. Unfortunately, the presence or absence of an umbonal deck in *Aphanaia* or *Atomodesma* has not been disclosed.

Genus MAITAIA Marwick, 1934

Maitaia MARWICK, *1934*, Fifth Pacific Science Congress, Proc., p. 948; ——, *1935*, New Zealand Roy. Soc., Trans. and Proc., vol. 64, p. 295.

Genotype, by monotypy, *Maitaia trechmanni* Marwick, *1934;* range of genotype, Maitai beds (Late Paleozoic, Permian?), New Zealand.

Marwick's diagnosis: Shell of moderate size, mytiliform, winged posteriorly, equivalve; beaks terminal, slightly raised above the long, straight dorsal margin. Hinge edentulous, margin thickened and flat, and having about three well-defined longitudinal, ligamental grooves. The shell margins, towards the beaks, thickened and bevelled, and below the beaks, internally, a septal plate was well developed in large shells. Shell substance consisting chiefly of the prismatic layer. Surface with low, rather irregular, concentric waves. Muscle-impressions weak, posterior adductor scar semicircular, of moderate size, placed far back and somewhat nearer the dorsal than the ventral margin.

Geologic range, Late Paleozoic (Permian?), New Zealand.

Remarks.—Like the typical species of *Atomodesma, Maitaia trechmanni* is a relatively upright, nearly acline form. The external resemblance between the two genera, including peculiarities of the shell microstructure, suggests that they are closely related, or even congeneric. Unfortunately, the hinge and other internal characters of *Atomodesma* are not yet adequately known for a detailed comparison with similar genera. *Aphanaia,* so far as can be determined at the present time, seemingly did not possess an umbonal septum.

Genus APHANAIA De Koninck, 1877

Aphanaia DE KONINCK, *1877,* Soc. royale Sci. Liége, Mém., 2nd ser., vol. 2.; ——, *1898,* Geol. Survey, N. S. Wales, Mem. 6, p. 238.

Genolectotype, *Inoceramus mitchelii* M'Coy, 1847, herein designated; Geologic range of genotype, Permian, Australia.

De Koninck's diagnosis: This shell is inequivalved, inequilateral, gibbous, with a posterior obtuse wing, and an apparently edentulous, straight hinge. Its beaks are anterior and separated by a hollow area, and having also a ligament. The surface is marked with large concentric rings, usually very unequal, and like those of some species of *Inoceramus*, to which some authors have assigned examples of *Aphanaia*. Their chief characteristic lies in the number and shape of their muscular impressions; the impression of the adductors is double, very large, placed posteriorly, and very much nearer the ventral margin than the hinge line; the diameter of one is nearly double that of the other; the larger, which is usually closest to the ventral margin, is generally reniform, while the smaller is suborbicular. A very much smaller impression than the preceding, probably that of the foot, is seen just behind the beaks, very close to the hinge line. (De Koninck, 1898, pp. 238-239.)

Range of the genus, Permian of Australia, Siberia, ?South Africa.

Remarks.—De Koninck described two species of *Aphanaia* with the original diagnosis of the genus. They are *A. mitchellii* (M'Coy), and *A. gigantea* De Koninck. These two species were genosyntypes. I am not aware of any formal designation of a genolectotype; therefore, I am designating *A. mitchellii*, the holotype of which is said to be in the Clarke Collection in the Sedgwick Museum, Cambridge.

It is unfortunate that the genus *Aphanaia* still is hardly any better understood than it was in De Koninck's day. Characters of the hinge are not adequately known and the shell microstructure is unknown in *A. mitchellii.* Externally the species might be confused with *Posidonia, Inoceramus, Atomodesma, Mataia,* and probably some other similar genera. In discussing a supposed *Aphanaia* (*A. haibensis* Reed,) from the Upper Dwyka beds of South Africa, Reed (1936, p. 162, 163) remarks that

> It was at once recognized that this shell bore a great resemblance to De Koninck's genus *Aphanaia* from the Permo-Carboniferous beds of New South Wales, and a comparison with the type specimen of *Aphanaia mitchellii* (M'Coy) in the Clarke Collection in the Sedgwick Museum, Cambridge, strongly supported this view, though our African specimen does not show the striated ligamental area and we cannot be certain that the shell is inequivalve.

By implication, I would judge that Reed has recognized a "striated ligamental area" in the type specimen of *A. mitchellii,* even though such a feature was not mentioned either by M'Coy or De Koninck. The bilobed adductor scar as described and illustrated by M'Coy and De Koninck is very like that of *Septimyalina* Newell, n. gen. (text fig. 6, C). Circumstantial evidence suggests that *Aphanaia mitchellii* is indeed one of the Myalinidae, but there seems to be one striking feature unknown in other myalinids. That is, according to De Koninck (idem, p. 239), the right valve in *A. mitchellii,* as well as *A. gigantea,* is conspicuously larger than the left valve. In all other myalinids known to me the reverse is the rule. Any conclusions regarding the shell microstructure in *Aphanaia* are, at the present time, assumptions. Without more complete knowledge of *Aphanaia,* based on authentic specimens of *A. mitchellii,* I do not see how the genus can be recognized with any certainty. The genus *Atomodesma* Beyrich is very similar, at least superficially, to *Aphanaia,* and was established first and is better known. However, if *Aphanaia* is really strongly inequivalve, as indicated, this character will distinguish the two genera.

Licharew (1934 and 1939, p. 142, pl. 34, fig. 14) has reported *Aphanaia* from the Kolyma region in Siberia. I have had the privilege of examining this material in Professor Licharew's laboratory in Leningrad. The specimens are noteworthy for having a very massive shell consisting principally of very long calcite prisms, recalling the shell of *Inoceramus.* However, the beaks are not terminal, and the ligament area does not exhibit the furrows characteristic of the Myalinidae.

GENERIC STATUS OF SOME FOREIGN SPECIES OF MYTILACEA

The proper generic assignment of various species of the Mytilacea from the literature alone is made especially difficult because many critical characters of the hinge and shell microstructure are unknown for the majority of described species. Consequently, the following classification of the species described in a few of the classical monographs is probably accurate only in part. Some of the genera of Mytilacea are sufficiently distinctive as to be recognizable from external form alone. No pretense of completeness in the following list is made. It has been compiled chiefly to aid paleontologists to an understanding of my classification.

BRITISH CARBONIFEROUS MYTILACEA

The species described by Hind (1896-1905), chiefly from the Lower Carboniferous are classified by me as follows:

MYALINA
  Myalina verneuilii
  Myalina peralata
SEPTIMYALINA
  Myalina redesdalensis
  Myalina pernoides
  Myalina flemingi
  Myalina lamellosa
  Myalina sublamellosa
?SELENIMYALINA
  Posidoniella elongata
  Posidoniella pyriformis
  Posidoniella variabilis
PROMYTILUS
  Modiola patula
  Lithodomus lingualis
  Lithodomus lithodomoides
?PROMYTILUS
  Modiola megaloba
  Modiola transversa
  Modiola emaciata
  Modiola macadamii
  Modiola lata
LITHOPHAGA
  Lithodomus carbonarius
  Modiola jenkinsi
?NAIADITES
  Modiola ligonula

CARBONIFEROUS MYTILACEA FROM THE DONETZ BASIN, U. S. S. R.

Fedotov's monograph (1932) on the Donetz Basin pelecypods includes a number of species of Mytilacea. Fedotov unfortunately has employed the names of American species for a large proportion of his pelecypods. His identifications suggest a precise understanding of the characters of American species. Until restudied in the light of modern concepts and techniques a great host of forms described in the early days cannot be understood from the literature alone.

ORTHOMYALINA
  Myalina ampla
?SELENIMYALINA
  Myalina monroensis
SEPTIMYALINA
  Myalina aff. *aviculoides*
  Myalina perattenuata
  Myalina verneuilii
  Myalina sp.
MYALINELLA
  Myalina cf. *elongata*
PROMYTILUS
  Myalina swallovi
?VOLSELLINA
  Modiola cf. *illinoiensis*
LITHOPHAGA
  Lithophagus cf. *batesvillensis*

UPPER CARBONIFEROUS AND LOWER PERMIAN, NORTH CHINA

Chao's report (1927) on the Taiyuan formation includes two species. I would classify them as follows:

PROMYTILUS
  Myalina swallowi (pl. 1, figs. 29, 30)
?SEPTIMYALINA
  Myalina swallowi (pl. 1, fig. 31)

UPPER CARBONIFEROUS, U. S. S. R.

Stuckenberg (1898, 1905) has described the following Mytilacea:

PROMYTILUS
  Modiola gigantea
?VOLSELLINA
  Sanguinolites sp.

PERMIAN, SALT RANGE, INDIA

Waagen's (1881) report on the Permian pelecypods of the Salt Range includes the following:

LITHODOMINA
  Lithodomina typica
  Lithodomina abbreviata
ATOMODESMA
  Atomodesma indicum
LIEBEA
  Liebea hausmanni
  Liebea indica
LITHOPHAGA
  Lithodomus atavus
VOLSELLINA
  Modiola transparens
?MYALINELLA
  Mytilus patriarchalis
?SELENIMYALINA
  Septifer squama

REFERENCES

Amalizky, W., *1892, Palaeontographica,* vol. 39, pp. 125 et seq.

Beede, J. W., *1899,* New fossils from the Kansas Coal Measures: *Kansas Univ. Quart.,* vol. 8, pp. 123-130, pls. 32, 33.

Bernard, F., *1895-1897,* Notes sur le dévelopement et la morphologie de la coquille chez Lamellibranches: *Soc. géol. France, Bull.;* Première note, vol. 23, pp. 104-154, 1895; Deuxième note (Taxodontes) vol. 24, pp. 54-82, 1896; Troisième note (Anisomyaires, vol. 24, pp. 412-449, 1896; Quatrième et dernière note, vol. 25, pp. 559-566, 1897.

Bøggild, O. B., *1930,* The shell structure of the mollusks: *Danske Vidensk. Selsk. Skrifter, Naturvidensk. og Mathem. Afd.,* 9 Raekke, vol. 2, pp. 233-325, 15 pls.

Branson, C. C., *1930,* Paleontology and stratigraphy of the Phosphoria formation: *Missouri University Studies,* vol. 5, 99 pp., 16 pls.

Chao, Y. T., *1927,* Fauna of the Taiyuan formation of north China; Pelecypoda: *Palaeontologia Sinica,* ser. B, vol. 9, fasc. 3, 64 pp., 4 pls.

Cheney, M. G., *1940,* Geology of north-central Texas: *Am. Assoc. Petr. Geol., Bull.,* vol. 24, pp. 65-118.

Cox, E. T., *1857,* Paleontological report of Coal Measure Mollusca: *Kentucky Geol. Survey,* vol. 3, pp. 557-576 (plates issued in brochure, titled maps and illustrations referred to in vols. 2 and 3, *Kentucky Geol. Survey* repts., 1857.)

Cox, L. R., *1936,* Karroo Lamellibranchia: *Geol. Soc. London, Quart. Jour.,* vol. 92, pp. 32-57.

Dall, W. H., *1895,* Tertiary fauna of Florida, part 3, A new classification of the Pelecypoda: *Wagner Free Inst. Sci., Trans.,* vol. 3, part 3, pp. 483-570.

Davies, J. H., and A. E. Trueman, *1927,* A revision of the non-marine lamellibranchs of the Coal Measures: *Geol. Soc. London, Quart. Jour.,* vol. 83, pp. 210-259, pls. 16-17.

Davies, J. H., *1930,* Non-marine shells of Upper Carboniferous rocks of North America: *Proc. and Coll. Wyoming* (Pennsylvania) *Hist. and Geol. Soc.,* vol. 21, pp. 98-106, 11 figs.

Dawson, J. W., *1860, Acadian Geology,* Supplement, 1st edition, p. 43.

———, *1894,* Note on the genus *Naiadites,* as occurring in the Coal Formation of Nova Scotia: *Geol. Soc. London, Quart. Jour.,* vol. 50, pp. 435-437.

DeKoninck, L. G., *1842-1844, Description des animaux fossiles qui se trouvent dans le terrain carbonifère de Belgique,* 649 pp.

———, *1876-1877,* Recherches sur les fossiles paléozoiques de la Nouvelle Galles du Sud: *Soc. royale Sci. Liége, Mém.,* 2d ser., vol. 2.

———, *1898,* Descriptions of the Palaeozoic fossils of New South Wales: *Geol. Survey N. S. Wales, Mem.* 6, 298 pp., 24 pls.

———, *1885,* Faune du calcaire carbonifère, Lamellibranches: *Mus. royale histoire* nat. Belgique, Annales, vol. 11, text 277 pp., atlas, 41 pls.

Dix, E., and A. E. Trueman, *1930,* Shell structure of some Carboniferous lamellibranchs: *The Naturalist,* pp. 15-18.

Dunbar, Carl O., *1924,* Kansas Permian insects, part 1. The geologic occurrence and the environment of the insects: *Am. Jour. Sci.,* vol. 7, pp. 171-208.

Fedotov, D. M., *1932,* The Carboniferous pelecypods of the Donetz Basin: *United Geol. Prospecting Service, U.S.S.R., Trans.,* fasc. 103, 241 pp., 18 pls.

Frebold, H., *1931,* Fauna, stratigraphische and palaeogeographische Verhaltnisse des ostgrönlandischen Zechsteins: *Meddelelser om Grönland,* Bd. 84, 55 S.

Frech, F., *1891,* Die devonischen Aviculiden Deutschlands: *Abhandl. z. geol. Specialkarte v. Preussen und den Thuringischen Staaten,* vol. 9, no. 3, 253 pp., text and atlas.

Gabb, W. M., *1859,* Description of two new species of Carboniferous fossils, brought from Fort Belknap, Texas, by Dr. Moore: *Philadelphia Acad. Nat. Sci., Proc.,* p. 297; Idem, *1860,* p. 55, pl. 1, figs 1a-c.

Girty, G. H., *1903,* Carboniferous formations and faunas of Colorado: *U. S. Geol. Survey, Prof. Paper* 16, 544 pp., 10 pls.

———, *1908,* On some new and old species of Carboniferous fossils: *U.S. Nat. Museum, Proc.,* vol. 34, pp. 281-303, pls. 14-21.

———, *1908,* The Guadalupian fauna: *U. S. Geol. Survey, Prof. Paper* 58, 651 pp.

———, *1909,* Paleontology of the Manzano group of the Rio Grande valley, New Mexico: *U. S. Geol. Survey, Bull.* 389, 41-136, pls.

Goldfuss, *1837, Petrefacta Germaniae,* Bd. 2, p. 168.

Gortani, M., *1906,* Paleontographia Italica, vol. 12, p. 113.

Grabau, A. W., *1936,* Early Permian fossils of China, Pt. 2: *Palaeontologia Sinica,* vol. 8, 320 pp.

Gurley, W. F. E., *1883, New Carboniferous fossils,* Bull. no. 1, pp. 1-9.

Hall, James, *1884,* Lamellibranchiata I; descriptions and figures of the Monomyaria of the upper Helderberg, Hamilton, and Chemung groups: *New York Geol. Survey, Paleontology,* vol. 5, pt. 1, 268 pp., plates.

Henderson, Junius, *1935,* Fossil non-marine Mollusca of North America: *Geol. Soc. America, Spec. Paper* 3, 313 pp.

Hind, Wheelton, *1894,* in Dawson, Note on the genus *Naiadites,* as occurring in the Coal Formation of Nova Scotia: *Geol. Soc. London, Quart Jour.,* vol. 50, pp. 437-442.

———, *1895,* A monograph on *Carbonicola, Anthracomya* and *Naiadites: Palaeontographical Soc.,* vol. 49, pp. 81-170, pls. 12-20.

———, *1896-1905,* Monograph of the British Carboniferous Lamellibranchiata, vol. 1, 1896-1900; vol. 2, 1901-1905: *Palaeontographical Soc., Mon.,* 708 pp., plates.

Jackson, Robert Tracy, *1890,* Phylogeny of the Pelecypoda, the Aviculidae and their allies: *Boston Soc. Nat. History, Mem.,* vol. 4, pp. 277-400.

King, William, *1850,* Permian fossils of England: *Palaeontographical Soc.,* vol. 1, 258 pp.

Lea, I., *1853,* On some new fossil molluscs in the anthracite seams of the Wilkesbarre coal formation: *Philadelphia Acad. Nat. Sci., Jour.,* vol. 2, pp. 203-206, pl. 20.

Licharew, B. K., *1934,* Die Fauna der permischen Ablagerungen des Kolymagebietes: *Akad. Sci. U.S.S.R., Lief.* 14, 139 S., 11 Taf.

Licharew, Boris, et al, Atlas of the leading forms of the fossil fauna U.S.S.R., vol. 6, Permian: *Central Geol. and Prospecting Institute,* 1939. 268 pp., 56 pls.

Love, J. D., *1939,* Geology along the southern margin of the Absaroka Range, Wyoming, *Geol. Soc. America, Spec. Paper* 20, 134 pp.

Marcou, J., *1858,* Paleontology, in *Geology of North America;* with two reports on the prairies of Arkansas and Texas, the Rocky Mountains of New Mexico, and the Sierra Nevada of California, pp. 32-53, pls. 1-7.

MARWICK, J., *1934, Fifth Pacific Congress,* Proc., p. 948.

———, *1935,* Some new genera of the Myalinidae and Pteriidae of New Zealand: *Royal Society of New Zealand, Trans. and Proc.,* vol. 64, pp. 295-303, pls. 34-36.

MASLENNIKOV, D., *1935,* The upper Permian pelecypods of the northern region: *Central Geol. and Prospecting Inst., Trans.,* fasc. 29, 123 pp.

MATHER, KIRTLEY F., *1915,* Fauna of the Morrow group of Arkansas and Oklahoma: *Denison Univ. Bull., Jour. Sci. Labs.,* vol. 18, pp. 59-284, pls. 1-16.

M'COY, F., *1847, Ann. Mag. Nat. Hist.,* vol. 20, 1st., p. 299, pl. 14, fig. 1.

MCCHESNEY, J. H., *1860, Descriptions of new species of fossils from the Palaeozoic rocks of the Western States,* p. 57.

———, *1865, Plates illustrating in part the new species of fossils from the Palaeozoic rocks of the Western United States, and two species noticed March 1860, published 1865,* pls. 1-11.

MEEK, F. B., *1867, Am. Jour. Sci.,* vol. 44, p. 181.

———, *1872,* Report on the paleontology of eastern Nebraska, with some remarks on the Carboniferous rocks of that district; *Final Rep. U. S. Geol. Survey, Nebraska,* pp. 83-264, 11 pls.

MEEK, F. B., and F. V. HAYDEN, *1858,* Description of new organic remains from northeastern Kansas, indicating the existence of Permian rocks in that territory; *Albany Inst., Trans.,* vol. 4, pp. 73-88.

———, *1859,* Geological explorations in Kansas Territory; *Philadelphia Acad. Nat. Sci., Proc.,* pp. 8-30.

———, *1860,* Descriptions of new organic remains from the Tertiary, Cretaceous, and Jurassic rocks of Nebraska: *Philadelphia Acad. Nat. Sci., Proc.,* pp. 175-185.

———, *1864,* Palaeontology of the Upper Missouri: *Smithsonian contributions to knowledge,* vol. 172, 135 pp., 5 pls.

———, *1860,* Descriptions of new Carboniferous fossils from Illinois and other western states: *Philadelphia Acad. Nat. Sci., Proc.,* pp. 447-472.

———, *1866,* Descriptions of invertebrates from the Carboniferous system: *Illinois Geol. Survey,* vol. 2, pp. 145-411, pls. 14-20, and 23-32.

MERLA, G., *1931, Padova Univ., Inst. Geol., Mem.,* vol. 9, p. 115.

MOORE, R. C., *1936,* (date of imprint, 1935), Stratigraphic classification of the Pennsylvanian rocks of Kansas: *Kansas Geol. Survey,* Bull. 22, 256 pp.

MORNINGSTAR, HELEN, *1922,* The Pottsville fauna: *Ohio Geol. Survey,* Bull. 25, 311 pp., 16 pls.

NELSON, T. C., *1928,* Pelagic dissoconchs of the common mussel, *Mytilus edulis,* with observations on the behavior of the larvae of allied genera: *Woods Hole Marine Biol. Lab., Biol., Bull.,* vol. 55, pp. 180-192.

NEWELL, NORMAN D., *1938,* Late Paleozoic pelecypods: Pectinacea: *Kansas Geol. Survey,* vol. 10, 123 pp., 20 pls.

———, *1939,* Permian pelecypod genus *Liebea: Jour. Paleontology,* vol. 13, pp. 589-593, pl. 68.

———, *1940,* Paleozoic pelecypods *Myalina* and *Naiadites: Am. Jour. Sci.,* vol. 238, pp. 286-295, pls. 1-2.

NEWELL, NORMAN D., and FRANK E. MERCHANT, *1939,* Discordant valves in pleurothetic pelecypods: *Am. Jour. Sci.,* vol. 237, pp. 175-177, pl. 1.

NEWELL, NORMAN D., ET AL, *1940,* Invertebrate fauna of the late Permian Whitehorse sandstone: *Geol. Soc. America, Bull.,* vol. 51, pp. 261-336, 10 pls.

REED, F. R. COWPER, *1936,* A new lamellibranch from the Upper Dwyka beds of South-West Africa: *Roy. Soc. South Africa, Trans.,* pp. 161-163, pl. 5.

ROTH, ROBERT, NORMAN D. NEWELL, and B. BURMA, *1941,* Permian pelecypods in the lower Quartermaster formation, Texas: *Jour. Paleontology,* vol. 15, pp. 312-317, pl. 45.

SAYRE, A. N., *1930,* The fauna of the Drum limestone of Kansas and western Missouri: *Kansas Univ. Sci. Bull.,* vol. 19, pp. 75-202, 21 pls. (Reprint *Kansas Geol. Survey, Bull.* 17), not released until 1931.

SHUMARD, B. F., *1855,* Description of new species of organic remains: *Missouri Geol. Survey. Ann. Repts.* 1 and 2, pp. 185-208, pls. A-C.

SHUMARD, B. F., and G. C. SWALLOW, *1858,* Descriptions of new fossils from the Coal Measures of Missouri and Kansas: *St. Louis Acad. Sci., Trans.,* vol. 1, pp. 198-227.

SIMPSON, G. G., *1937.* Pattern of phyletic evolution: *Geol. Soc. America, Bull.,* vol. 48, pp. 303-314.

SIMPSON, G. G., and ANNE ROWE, *1939, Quantitative Zoology,* 414 pp. 52 figs., McGraw-Hill, New York.

SOWBERBY, J. DE C., *1829, Geol. Soc. London, Trans.,* vol. 3, p. 120.

STOLICZKA, F., *1871,* Cretaceous fauna of southern India; the Pelecypods: *India Geol. Survey, Mem., Palaeontologia Indica,* ser. 6, vol. 3.

STUCKENBERG, A., *1898,* Allgemeine geologische Karte von Russland, Blatt 127, Palaeontologischer Theil: *Comité Géologique,'Mém.,* vol. 16, no. 1, pp. 331-362, 5 pls.

———, *1905,* Die fauna der Obercarbonischen Suite des Wolgadurchbruches bei Samara: *Comité Géologique, Mém.,* n. s., Liv. 23, 144 pp., 13 pls.

TCHERNYSHEV, B., *1931, Carbonicola, Anthracomya,* and *Naiadites* of the Donetz Basin: *United Geol. Prosp. Service U.S.S.R., Trans.,* vol. 72, 125 pp., 4 pls.

TREAT, V. C., *1933,* Paleontologie de Madagascar: *Annales de Paléontologie,* vol. 22, pp. 39-96.

WAAGEN, WILLIAM, *1881, Productus* limestone fossils, III. Pelecypods: *India Geol. Survey, Mem., Paleontologia Indica,* ser. 13, pp. 185-238, pls. 17-25.

WANNER, C., *1922,* Die Gastropoden und Lamellibranchiaten der Dyas von Timor: *Paläontologie von Timor,* XI Lieferung, Teil XVIII, pp. 1-82, pls. CLI-CLIV.

WHITE, KATHLEEN M., *1937, Mytilus: Liverpool marine biology committee, Mem.,* vol. 21, 117 pp., 10 pls.

WHITFIELD, R. P., *1902,* Description of a new form of *Myalina* from Coal Measures of Texas: *Am. Mus. Bull.,* vol. 16, pp. 63-66, text figs. 1-2.

Plates 1 to 15

PLATE 1.—Pennsylvanian and Lower Permian Promytilus, and Pennsylvanian Volsellina

Figure

1, 2, 5-7—Promytilus priscus Newell, n. sp., from Virgilian beds in Kansas and Nebraska ....p. 40

1, 2—Two paratypes, X2, right and left valves, respectively; Doniphan shale (Lecompton formation, Shawnee group), Snyderville quarry, Nebraska; Nebraska Geol. Survey, nos. 302 and 301.

5—Right valve, the holotype, X2, slightly etched by weathering to show radiating lines indicative of the peculiar shell microstructure of the Mytilidae; near horizon of Dover limestone (Wabaunsee group), NW cor. sec. 14, T. 13 S., R. 13 E., Kansas; Univ. Kansas, no. 7551.

6—Left valve, a topoparatype, X2; same locality and horizon as preceding; Univ. Kansas, no. 7550.

7—Right valve, paratype, X2; Auburn shale (Wabaunsee group), 7 miles northeast of Foraker, Okla.; Univ. Kansas, no. 7556.

3, 4—Promytilus vetulus Newell, n. sp., from the Early Permian (Wolfcampian) of Kansas..............................p. 42

3—Left valve, the holotype, X2; Admire group, 1¾ miles south of Americus, Kan., at bridge; Univ. Kansas, no. 7552.

4—An internal mold of a right valve, a paratype, X2; Fort Riley limestone (Chase group), railroad quarry, NE¼ sec. 36, T. 16 S., R. 7 E., Kansas; Univ. Kansas, no. 7553.

8a, b, 13—Promytilus swallovi (McChesney), from the Missourian series in Missouri..p. 37

8a, b—Views of a hypotype, X2; limestone (Bronson group?), one-half mile west of Pleasant Hill, Cass county, Mo.; Univ. Kansas, no. 7555.

Figure

13—Sulphur cast of the holotype, X2, of which the original has been destroyed; exact horizon unknown, probably Bronson group (lower Missourian), 12 miles northwest of Richmond, Mo.; Univ. Chicago.

9, 10—Promytilus annosus annosus Newell, n. sp., n. var., from upper Missourian rocks of Kansas......................p. 38

9—Left valve, the holotype, X2; South Bend limestone (Stanton formation, Lansing group), 2 miles south of Lansing, Kan., at Nine-Mile School; Univ. Kansas, no. 7559.

10—Right valve, a paratype, X2; upper Vilas shale (Lansing group), SW cor. sec. 13, T. 28 S., R. 15 E., Kansas; Univ. Kansas, no. 7554.

11, 12—Promytilus annosus senex Newell, n. sp., n. var., from beds of Missourian age in Kansas and Missouri ....p. 39

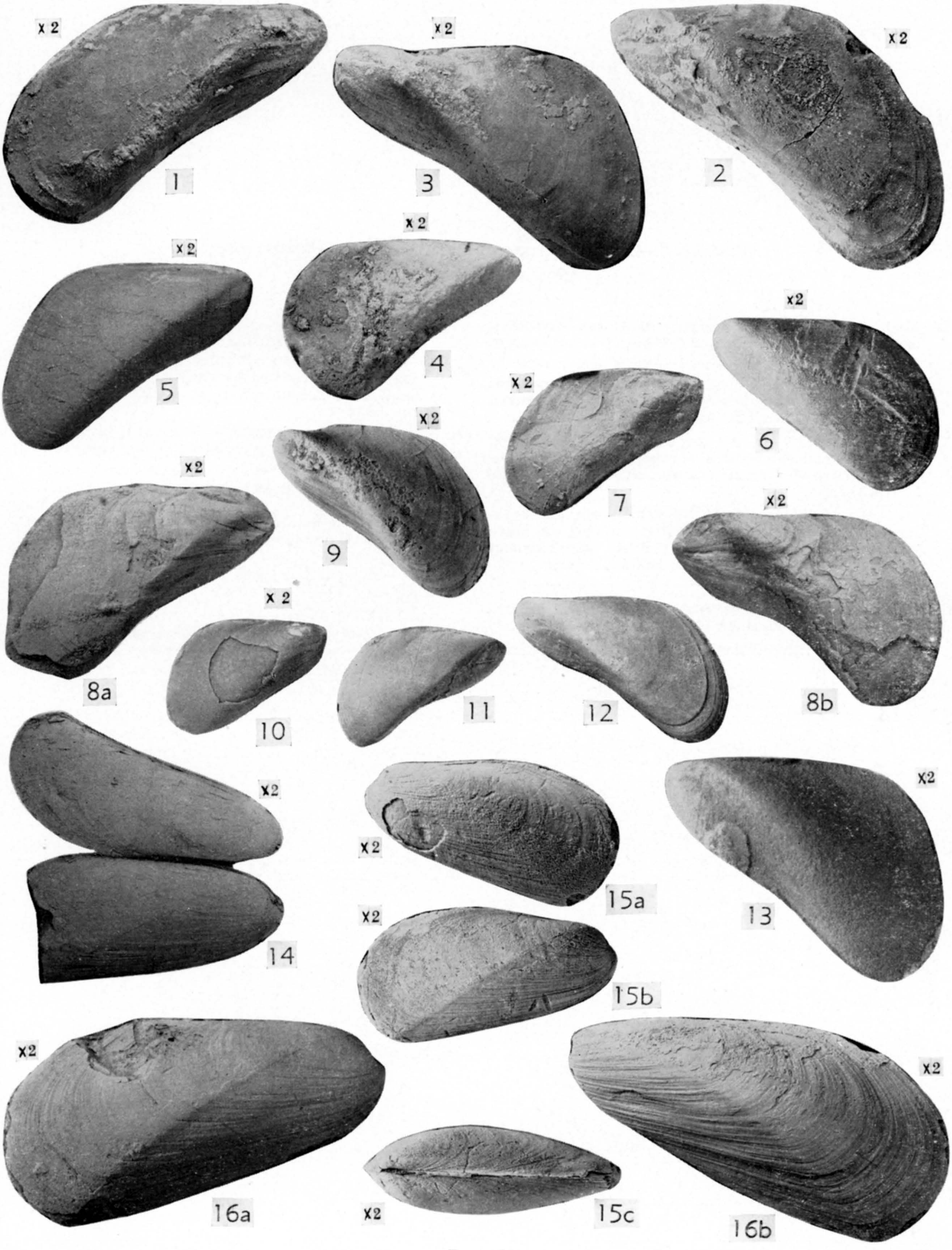
11—Right valve, topoparatype, X1; Westerville oolite (Kanas City group), Muncie, Kan.; Univ. Kansas, no. 7557.

12—Robust left valve, topoparatype, X1; same locality and horizon as preceding; Univ. Kansas, no. 7558.

14-16b—Volsellina subelliptica (Meek), from rocks of Missourian and Virgilian age, Texas and Nebraska......p. 43

14—An imperfect individual retaining parts of both valves, the holotype, X2; Willard shale (Wabaunsee group), Nebraska City, Neb., U.S. National Museum, no. 6490.

15a-16b—Two fine bivalved hypotypes, X2, showing well the features of form and ornamentation; from shale in Jacksboro limestone (Graham formation, 4½ miles east of Jacksboro, Tex.; Univ. Wisconsin, nos. 21206, 21207.



x 2
1
x 2
3
x 2
2
x 2
5
x 2
4
x 2
6
x 2
7
x 2
9
x 2
8a
x 2
8b
x 2
10
11
12
x 2
14
x 2
15a
x 2
13
x 2
15b
x 2
16a
x 2
15c
x 2
16b

PLATE 1

PLATE 2.—PENNSYLVANIAN SELENIMYALINA, PROMYTILUS, AND RECENT VOLSELLA

Figure

1a-2b—*Selenimyalina meliniformis* (MEEK AND WORTHEN), genotype of *Selinimyalina*, mid-Pennsylvanian rocks of Illinois and Missouri ....p. 63

1a, b—Characteristic bivalved specimen, a hypotype, *X*2; exact horizon unknown, Gentry county, Missouri; U.S. National Museum, no. 51146.

2a, b—The holotype, *X*2, an internal mold, showing rather well some features of musculature; exact horizon unknown, Gallatin county, Illinois; Univ. Illinois, no. X-210.

3a, b—*Selenimyalina quadrata* NEWELL, n. sp., the holotype, X2, a fragmentary left valve, showing the hinge characters, including the exceedingly fine ligament grooves; Vilas shale (Lansing group), Leavenworth, Kan.; Univ. Kansas, no. 7562..p. 64

4a, b, 6—*Promytilus annosus senex* NEWELL, n. sp., n. var., from mid-Pennsylvanian rocks ....p. 39

4a, b—A left valve, *X*2, the holotype, showing the form and hinge characters; Westerville oolite (Kansas City group), Kansas City, Mo.; Univ. Kansas, no. 7563.

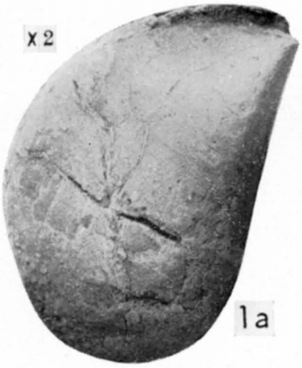
6—Internal mold of a left valve, a hypotype, *X*3, showing the imprint of ligament furrow; exact horizon unknown, Saline county, Illinois; U.S. National Museum, no. 27693.

5—*Volsella modiola* (LINNAEUS), internal mold (rubber), *X*1, Recent, illustrating similarity of hinge between this and the preceding species.

7a-8b—*Selenimyalina dotti* NEWELL, n. sp., type specimens, *X*2, from the middle part of the Holdenville formation (uppermost Desmoinesian), above a heavy sandstone, center south line sec. 14, T. 7 N., R. 8 E., Oklahoma ....p. 64

7a, b—Topoparatype, a nearly complete bivalved shell showing well the mytiloid form of the species; Univ. Kansas, no. 7561.

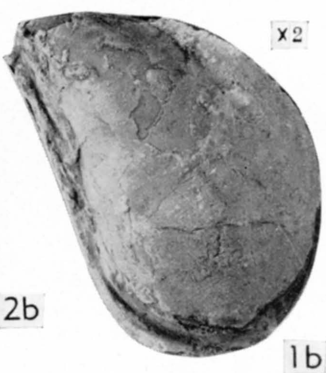
8a, b—Holotype, a robust specimen, somewhat incomplete at ventral margin; Univ. Kansas, no. 7560.



1a

2a

2b



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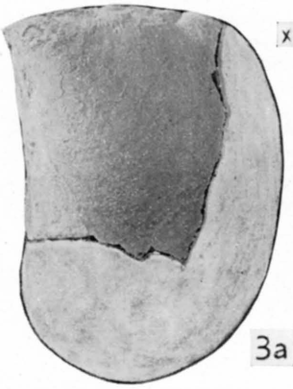
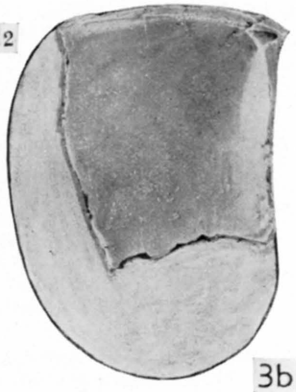


3a

4a



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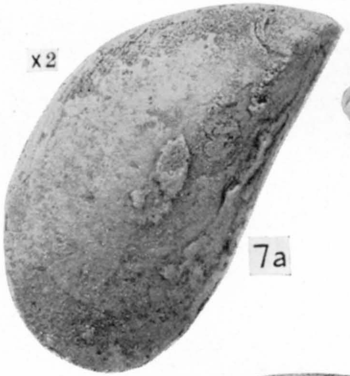
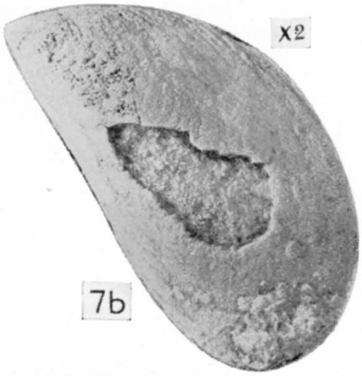


7a

4b



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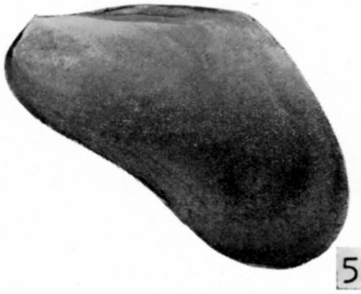

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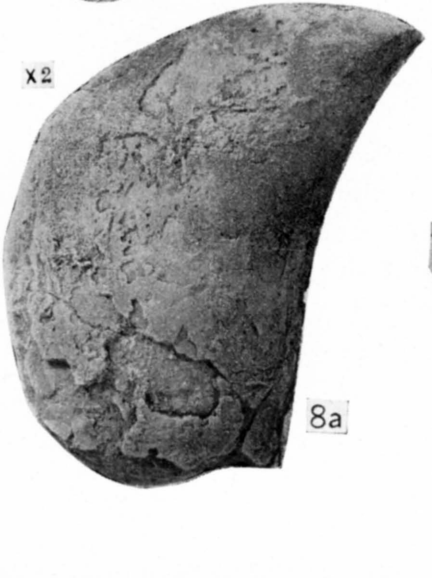

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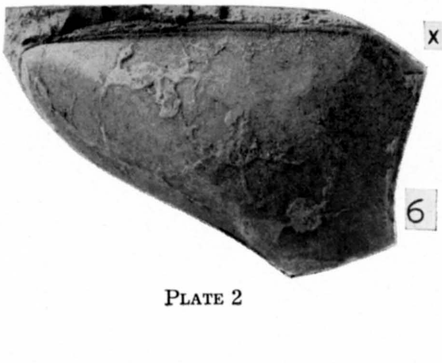

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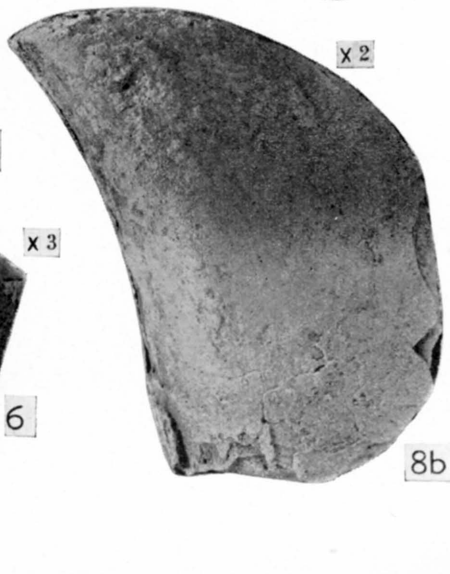


8b

PLATE 2

PLATE 3.—PENNSYLVANIAN MYALINA

Figure

1-4, 7, 10—Myalina (Myalina) wyomingensis (LEA), rocks of Desmoinesian and Missourian age, Illinois, Colorado, and Pennsylvania ....p. 49

1a, b—One of the paratypes of *Myalina recurvirostris* Meek and Worthen, placed here in the synonymy of *M. (M.) wyomingensis;* a flattened and somewhat distorted bivalved specimen. From "about the horizon of coal no. 11, of Upper Coal Measures" (Missourian), La Salle, Ill.; Univ. Illinois, no. x-214.

2a, b—Right and left views of a hypotype. From a bed (Roth and Skinner's no. 183) near the middle of the McCoy formation, of early Desmoinesian age, one-fourth mile southeast of Tunnel 43, Denver and Salt Lake R. R., near Bond, Colo., Univ. Wisconsin, no. 21201.

3a, b, 4a, b—Two hypotypes from the same locality and horizon as the preceding; Univ. Wisconsin, nos. 21202, 21203.

7a-c—The holotype of *Myalina recurvirostris* Meek and Worthen, a nearly perfect left valve from "about the horizon of coal no. 11, of Upper Coal Measures, La Salle, Illinois" (Missourian); Univ. Illinois, no. x-214. Fig. *7c,* showing modioloid juvenile stage on the beak, X5.

Figure

10—The holotype of *Myalina wyomingensis* (Lea) from an unknown horizon in a coal mine near Wilkesbarre, Pa., presumably of Desmoinesian age; U.S. National Museum, no. 33900.

5a, b, 8a,b—Myalina (Myalina) miopetina NEWELL, n. sp., early Virgilian of Kansas ....p. 54

5a, b—External and internal views of a right valve from a horizon near the Lecompton limestone, probably the Stull shale (Shawnee), in sec. 7, T. 30 S., R. 12 E., Kansas; Univ. Kansas, no. 7564.

8a, b—The holotype, a left valve, showing well the incipient rear auricle, one of the characteristics of the species; same locality and horizon as the preceding; Univ. Kansas, no. 7565.

6a, b, 9a, b—Myalina (Myalina) lepta NEWELL, n. sp., Desmoinesian of Oklahoma ....p. 49

6a, b—The holotype, a bivalved specimen from the middle Boggy shale, center sec. 17, T. 2 N., R. 7 E., Oklahoma; Univ. Wisconsin, no. 21205.

9a, b—A less perfect paratype, same locality and horizon as the preceding; Univ. Wisconsin, no. 21204.

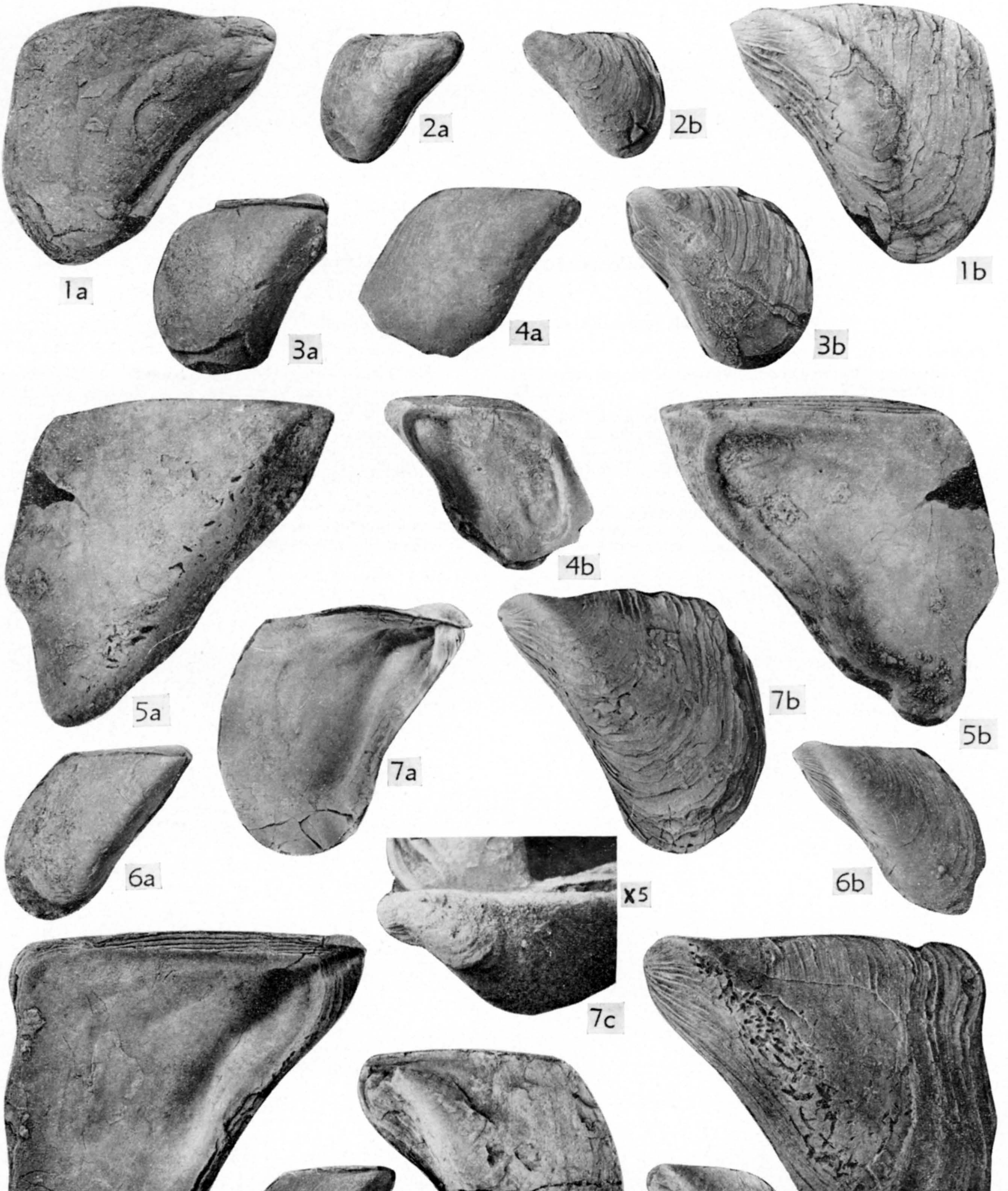


Plate 3

PLATE 4.—WOLFCAMPIAN MYALINA AND MISSOURIAN LITHOPHAGA

(All figures X1, except where otherwise indicated)

Figure

1, 2—Myalina (Myalina) copei WHITFIELD, Moran formation (Wolfcampian), Texas .... p. 55

1a-e—A fine bivalved hypotype, showing well the form of the species; front, right, posterior, dorsal, and left views; Moran formation, 2 miles north of Moran, Shackelford county, Tex.; Texas Bur. Econ. Geology, locality 208-T-3, 4251.

2a-c—An immature left valve, hypotype, showing well the early ontogenetic stages: *2a,* enlargement of the beak, X5; Moran formation, 1 mile south of Brazos cliff, 3 miles west of the eastern boundary of Shackelford county, Tex.; Texas Bur. Econ. Geology, locality 208-T-13, P-10362.

3-5—Lithophaga subelliptica SAYRE, Westerville oolite (Kansas City group), Kansas and Missouri.......... p. 44

3-4—Relatively large left and right valves, respectively, hypotypes; Westerville oolite, Kansas City, Mo.; Univ. Kansas, nos. 7566, 7567.

5—The holotype, an immature left valve, X2; Westerville oolite, Muncie, Kan.; Univ. Kansas, no. 59.

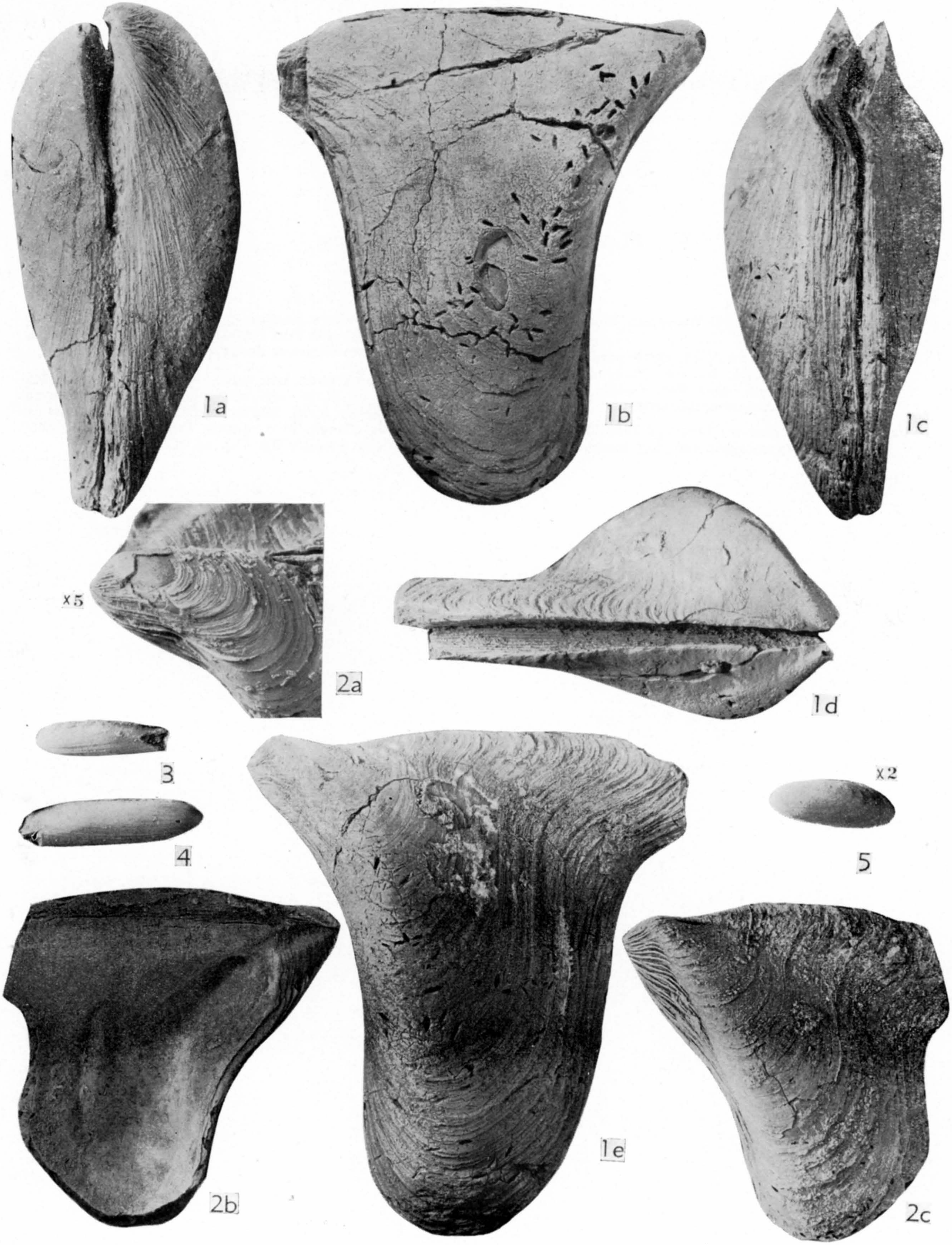


PLATE 4

PLATE 5.—Wolfcampian Myalina

(All figures X1)

Figure

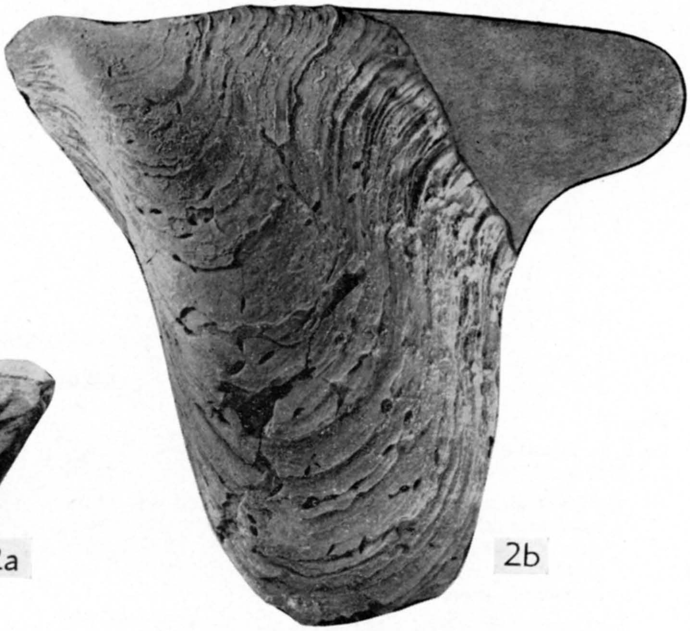
1-3—*Myalina (Myalina) copei* **Whitfield**, Moran formation (Wolfcampian), Texas ....p. 55

1—Interior view of a small left valve, paratype, showing part of musculature; horizon uncertain (Moran?), McKenszie's Trail, near Fort Griffin, Shackelford county, Texas; American Museum, no. 8364/2.

2a-d—A well preserved bivalved individual, selected here as lectotype; right, left, left interior, and right interior views; horizon uncertain (Moran), McKenszie's Trail near Fort Griffin, Shackelford county, Tex.; American Museum, no. 8364/1.

3a, b—A gerontic left valve, hypotype, showing features of hinge and musculature and ontogenetic changes in form; Moran formation, 2 miles north of Moran, Shackelford county, Tex.; Texas Bur. Econ. Geology, locality 208-T-3, no. 4250.


1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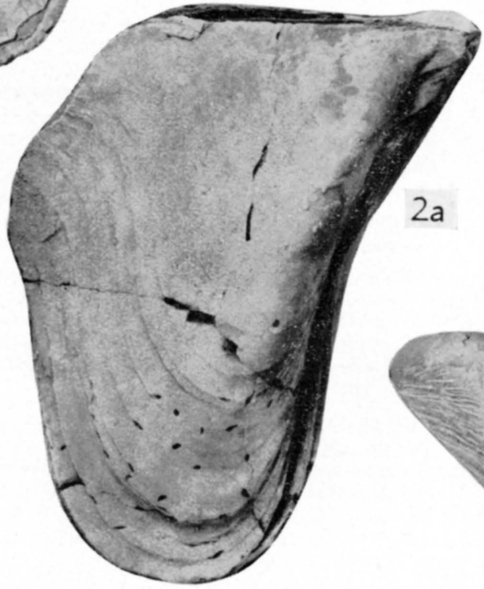
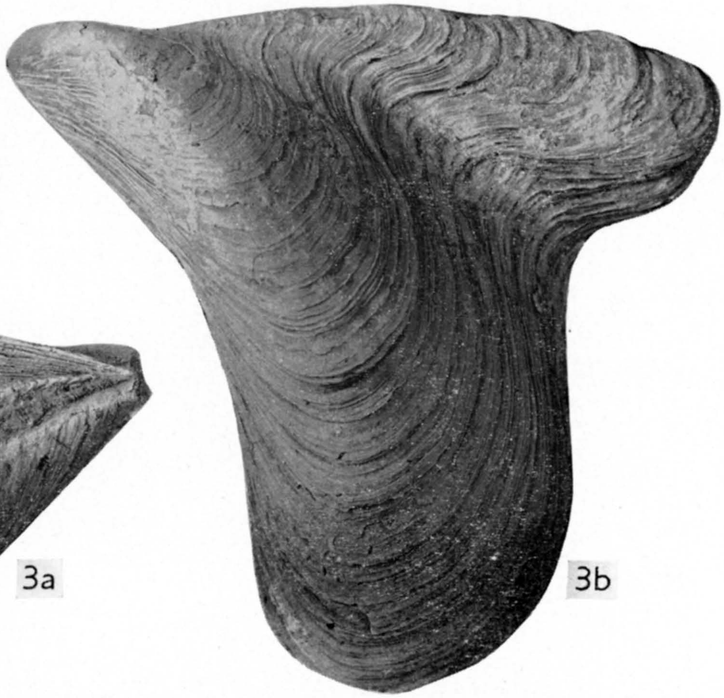
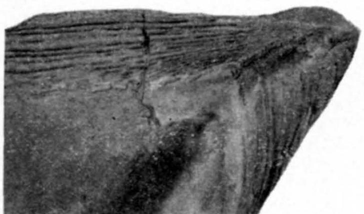

2a


3b


3a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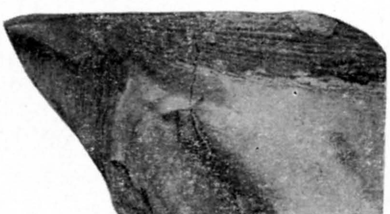

2d

Plate 5

PLATE 6.—PERMIAN MYALINA

(All figures X1)

Figure

1a, b, 6—*Myalina (Myalina) pliopetina* NEWELL, n. sp., Moran (?) (Wolfcampian) formation, Texas............p. 54

1a, b—A small but characteristic specimen, the holotype, one of Whitfield's types of *Myalina copei;* horizon uncertain, but probably Moran, McKenszie's Trail, near Fort Griffin, Shackelford county, Tex.; American Museum, n. 8364/4.

6—Large right valve, a paratype, also one of Whitfield's types of *Myalina copei;* same horizon and locality as preceding; American Museum, no. 8364/1A.

2a-3b—*Myalina (Myalina) petina* NEWELL, n. sp., lower Pueblo (Wolfcampian) formation, Texas..................p. 54

2a, b—A left valve, the holotype, showing relatively shallow posterior sinus characteristic of the species; "Harpersville" (lower Pueblo) formation, 6 miles northwest of Cisco, Earland county, Tex.; Texas Bur. Econ. Geology, locality 67-T-13, no. 1526.

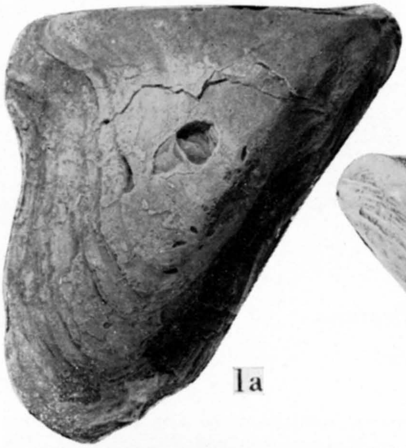
Figure

3a, b—Right valve, a paratype; "Harpersville" formation (lower Pueblo), 3 miles southwest of Newcastle, Young county, Tex.; Texas Bur. Econ. Geology, locality 251-T28, no. 12003.

4, 5—*Myalina (Myalina) sinuata* BRANSON, upper Phosphoria (Word), and upper Kaibab (Word?) of Wyoming and Arizona ....p. 56

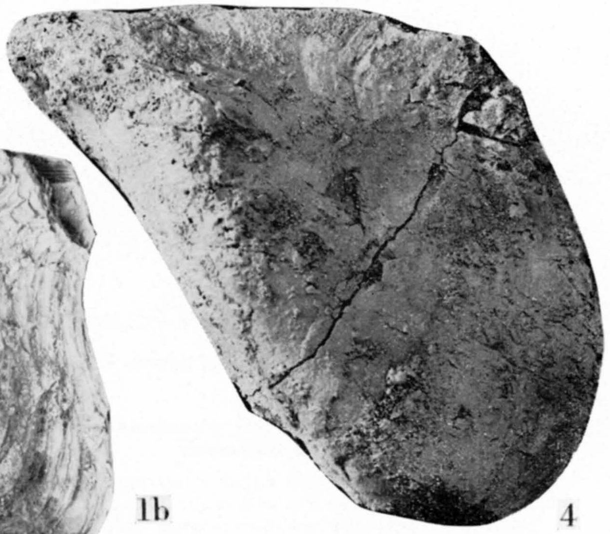
4—Left side of a poorly preserved topotype, an internal mold showing faint growth lines indicative of configuration very like that of *M. (M.)pliopetina* (fig. *1b*); upper limestone of the Phosphoria formation, Bull Lake, Wind River Mts., near Lander, Wyo.; Univ. Wisconsin, no. 21200.

5—Left side of a hypotype, an internal mold which does not give a satisfactory indication of the form of the original shell; upper Kaibab (*Bellerophon* beds); Museum Northern Arizona, no. 492/2429.



1a

1b



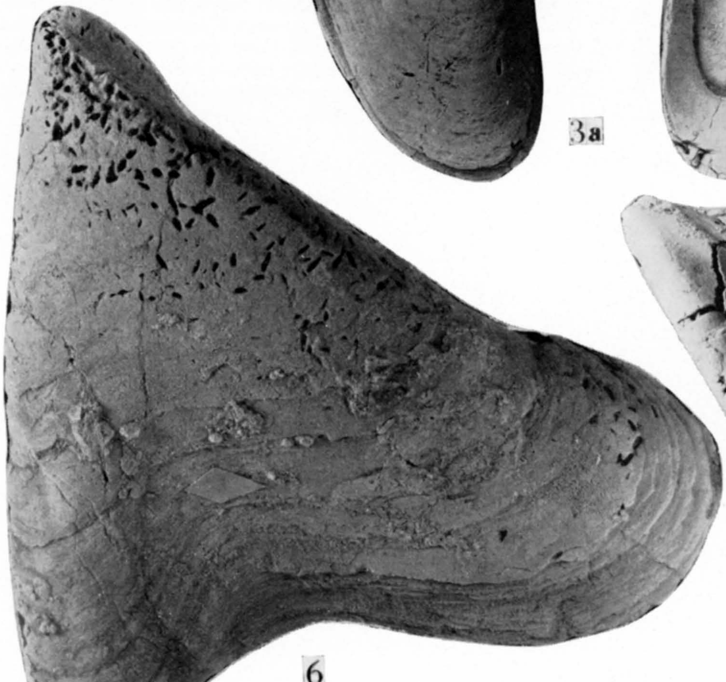
4

2a

3a

3b

2b



6

5

PLATE 6

PLATE 7.—CARBONIFEROUS AND PERMIAN MYALINA

(All figures X1, except where otherwise indicated)

Figure

1a, b, 5, 7, 8a, b—*Myalina (Myalina) glossodoidea* NEWELL, n. sp., early Virgilian rocks of Kansas ....p. 53

1a, b—A medium-sized left valve, a topoparatype, from the upper part of the Vinland shale (Douglas group), 1½ miles south and one-fourth mile east of Homewood, Franklin county, Kan.; Univ. Kansas, no. 7570.

5—A large left valve, the holotype, same locality and horizon as preceding; projecting growth lamellae are somewhat covered by algal (?) deposits. Compare with the specimen of *M. (M.) arbala* shown as figure *10,* Univ. Kansas, no. 7573.

7—An unusually orbicular left valve, a topoparatype, same locality and horizon as preceding; Univ. Kansas, no. 7572.

8a, b—A small right valve, a topoparatype; Univ. Kansas, no. 7571.

2—*Myalina (Myalina) aviculoides* MEEK AND HAYDEN, early Permian (Wolfcampian) of Kansas. This specimen, a left valve, is selected here for the lectotype; it came from "South Cottonwood Creek" in central Chase county, Kansas, and careful examination of the matrix suggests that it was collected from the Herington limestone; U.S. National Museum, no. 2526........................p. 53

3—*Myalina (Myalina) copha* NEWELL, n. sp., Atoka formation of Oklahoma; a medium-sized left valve, X3, the holotype; Univ. of Kansas, no. 7568 ....p. 49

4—*Myalina* sp., St. Louis limestone, Mississippian, near Ames, Iowa; 24 feet above base of St. Louis limestone, S½ NW¼ SW¼ sec. 23, T. 84 N., R. 24 W., Story county, Iowa; introduced here as an example of an exceedingly primitive *Myalina;* Univ. Wisconsin, no. 21199.

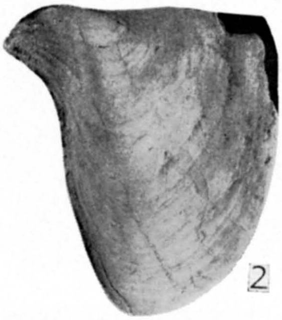
6—*Myalina (Myalina) wyomingensis* (LEA), Rico formation (Virgilian?), Scotch Creek, Rico Quadrangle, left valve; U.S. Geological Survey, no. 216 (U.S. National Museum, no. 35308) ....p. 49

9, 10—*Myalina (Myalina) arbala* NEWELL, n. sp., early Missourian of Kansas and Missouri ....p. 52

9—Artificial (rubber) cast of a small left valve, X2, showing details of musculature and hinge; note complete lack of posterior auricle at this stage; from the Winterset limestone near Kansas City, Mo.; U.S. National Museum.

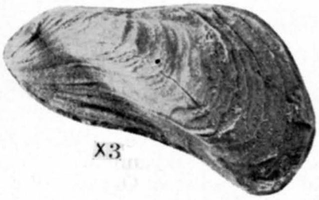
10—Partially decorticated left valve, the holotype; from the Winterset limestone, near Kansas City, Mo. This species differs from the very similar *M. (M.) glossoidea* in having a better defined sinus below a posterior auricle, and in having a less oblique form; Univ. Kansas, no. 7569.

1a



2

1b



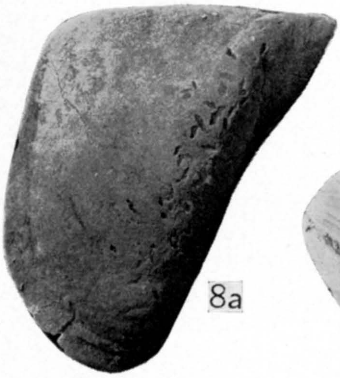
x3 3

x2 4

5

6

7



8a

10

9 x2

8b

PLATE 7

PLATE 8.—PENNSYLVANIAN ORTHOMYALINA

(All figures X1)

Figure

1-6—*Myalina (Orthomyalina) slocomi* SAYRE, from Missourian and Virgilian rocks of Kansas ....p. 57

1a, b—A fine right valve, showing characteristic features of form, ornamentation, and interior; upper Stull shale (Shawnee group), center of the west line of sec. 17, T. 20 S., R. 15 E., Kansas; Univ. Kansas, no. 7577.

2a, b—Another right valve, with a somewhat shorter hinge than ordinary, and showing several muscle pits where the mantle evidently was attached; upper Stull shale, 1 mile west of the intersection of highways 50-S and 75 near Waverly, Kan.; Univ. Wisconsin, no. 21198.

3—Interior of a left valve, rather less mature than the specimens shown as figs. *1, 2,* and *5,* judging from the small number of ligament grooves; upper Stull shale, center of the west line of sec. 17, T. 20 S., R. 15 E., Kansas; Univ. Kansas, no. 7576.

4—Left valve, with characteristic rugose ornamentation, and annelid borings of types that are common in myalinas; Ozawkie limestone (Deer Creek, Shawnee group), 1 mile south of Lyndon, Kan.; Univ. Kansas, no. 7574.

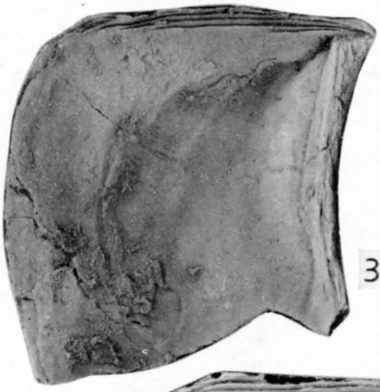
5a, b—A characteristic left valve, with borings of commensal worms; upper Stull shale, center of the west line of sec. 17, T. 20 S., R. 15 E., Kansas; Univ. Kansas, no. 7575.

6—A small, imperfect left valve, the holotype of this species, supposed to be characterized by a very thin shell and narrow hinge area; like fig. *3* this specimen is a young individual; from the Westerville oolite (Kansas City group), near Kansas City; Univ. Kansas, no. 50.1.


1a


2a


1b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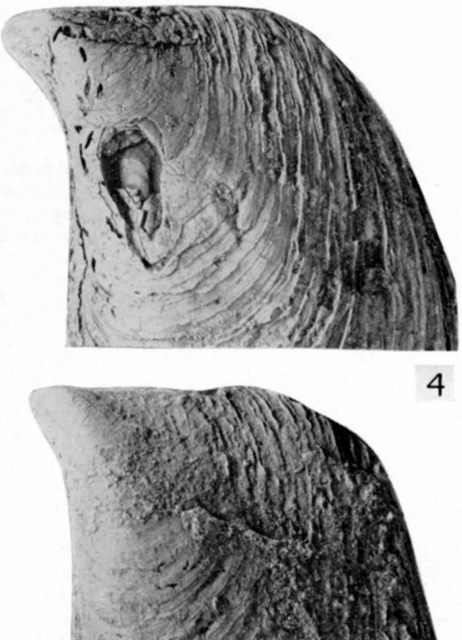
2b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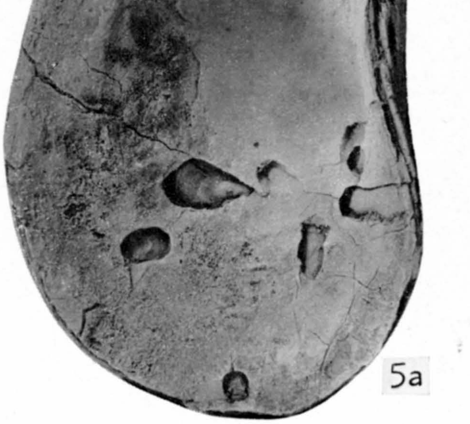
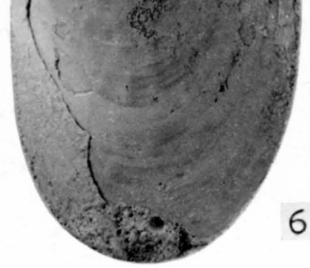

5a


6


5b

PLATE 8

PLATE 9.—VIRGILIAN ORTHOMYALINA AND VISEAN MYALINA

(All figures X1)

Figure

1-4—*Myalina (Orthomyalina) subquadrata* **SHUMARD**, from the Wabaunsee (Virgilian) of Oklahoma and Kansas .... p. 58

1a, b—Views of a normal right valve, a topotype, showing characteristic form, ornamentation, and hinge; lower (?) Caneyville limestone (Wabaunsee group), ½ mile east of Admire, Kan.; Nebraska Geol. Survey, no. 303.

2—A small, but mature left valve showing marked opisthocline obliquity, a hypotype; Severy shale (Wabaunsee group), near Howard, Kan.; Univ. Kansas, no. 7578.

3—Large left valve showing form and ornamentation typical of left valves of the species, a topotype; Pony Creek shale (Wabaunsee group), center north side sec. 15, T. 23 N., R. 6 W., Oklahoma; Univ. Kansas, no. 7579.

Figure

4—Left valve showing less than normally prominent auricle, paratype; Pony Creek shale, same locality as preceding; Univ. Kansas, no. 7580.

5a-6b—*Myalina goldfussiana* **DE KONINCK**, genotype of *Myalina*, from the Viséan of Belgium. Left and right valves of the holotype, deposited in the Paris École des Mines .... p. 45

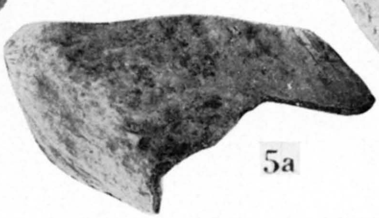
5a, b—Exterior and interior of the fragmentary left valve.

5c—Interior of same, tilted to show better the muscle pits in the umbonal cavity.

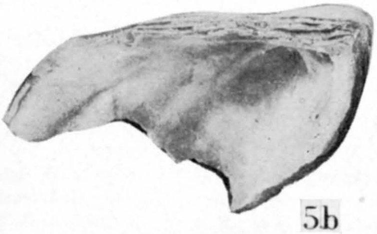
5d—Rubber mold of same showing better the distribution of the three points of muscle attachment.

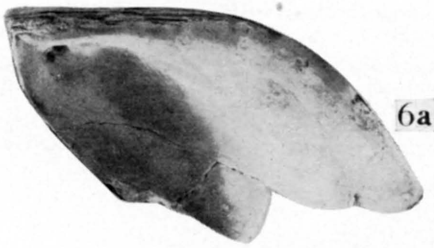
6a, b—Interior and exterior of fragmentary right valve, showing relatively weak development of anterior lobe.


1a

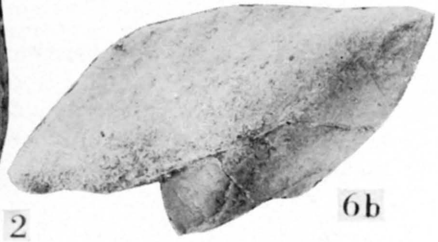

5a


1b


5b

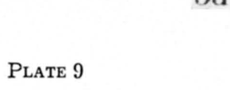

6a


2


6b


3


5c


5d


4

PLATE 9

PLATE 10.—PENNSYLVANIAN MYALINELLA AND ORTHOMYALINA

(All figures X1)

Figure

1a, b—Myalina (Myalinella) exasperata **BEEDE**, right and left side views of an internal mold, the holotype, so imperfect as to be practically unrecognizable; roof of a coal bed (possibly Nodaway coal, lower Wabaunsee), west of Topeka, Kan.; Univ. Kansas, no. 3570............p. 61

2a, b, 3—Myalina (Orthomyalina) slocomi parvula **NEWELL**, n. var., from the Shawnee (middle Virgilian) beds of Kansas ....p. 58

2a, b—Two views of a normal right valve, a topoparatype; inspection of the ligament area (compare with fig. *4b*) shows that this is not simply a juvenile of *M. (O.) slocomi;* 2½ miles northwest of Michigan Valley, Kan., roadcut on the Overbrook road; Univ. Kansas, no. 7581.

3—A fully mature left valve, the holotype; same horizon and locality as the preceding; Univ. Kansas, no. 7582.

Figure

4a, b—Myalina (Orthomyalina) slocomi **SAYRE**, views of a left valve showing a more pronounced rear auricle than is ordinary for the species, so that this specimen resembles the more quadrate individuals of *M. (O.) subquadrata;* upper Stull shale (Shawnee); center of the west side of sec. 17, T. 20 S., R. 15 E., Kansas; Univ. Kansas, no. 7583.

5—Myalina (Orthomyalina) ampla **MEEK AND HAYDEN**, the holotype, from the Lansing group, Missourian series (probably Merriam member of the Plattsburg limestone), near Leavenworth, Kan.; U.S. National Museum, no. 998.

6a, b—Myalina (Orthomyalina) slocomi **SAYRE**, views of a hypotype, showing discrepancy in size and form between the two valves of an undeformed specimen; Wewoka formation (upper Desmoinesian), near Allen, Okla.; Yale Univ., no. 3478/5..............................p. 57

6a—Front view. *6b*—Right side.

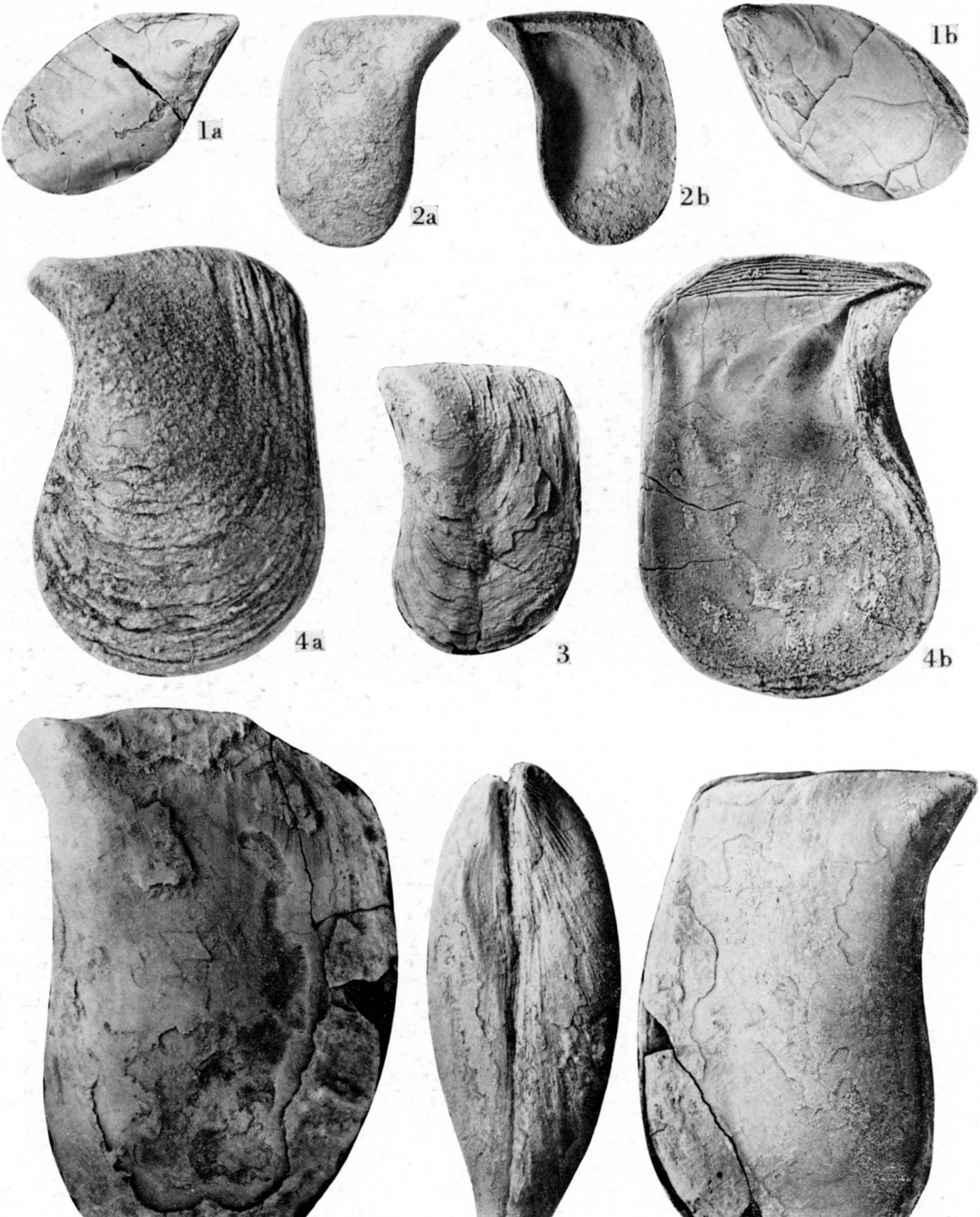


PLATE 10

PLATE 11.—PENNSYLVANIAN AND PERMIAN SEPTIMYALINA

(All figures X1 except where otherwise indicated)

Figure

1-3—*Septimyalina orbiculata* NEWELL, n. sp., types from shaly limestone equivalent to the Lenapah limestone (Marmaton), 2½ miles northwest of Beggs, Okla., NW ¼ sec. 19, T. 15 N., R. 12 E. ....p. 68

1—Badly perforated right valve, a topoparatype; Univ. Kansas, no. 7586.

2a, b—Fragmentary left valve, a topoparatype, showing septum, below which pallial line extends into umbonal cavity; Univ. Kansas, no. 7585. Since the anterior adductor, if present, is invariably located at the front terminus of the pallial line, it is evident that the umbonal septum did not serve as a muscle platform.

3—Left valve, the holotype, showing distinctive form; Univ. Kansas, no. 7584.

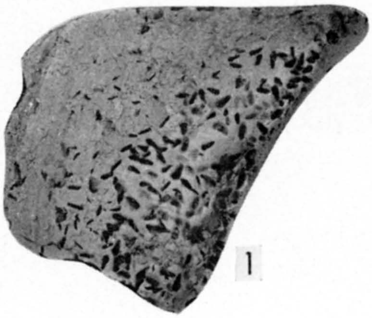
4-9, 11-14—*Septimyalina scitula* NEWELL, n. sp., from Virgilian rocks of Kansas; this is one of the species which erroneously has been classed with *Myalina perattenuata* ....p. 68

Figure

4-9—Collection of types from Shawnee (Iowa Point shale) rocks, NW¼ sec. 1, T. 21 S., R. 13 E., Coffey county, Kansas; *4*, the holotype, Univ. Kansas, no. 7589; *5-9*, a series of paratypes, Univ. Kansas, nos. 7592, 7591, 7587, 7590, and 7588; all X2.

11-14—A series of pyritized paratypes collected by the Hayden Survey of Nebraska, and identified by Meek as *Myalina perattenuata;* these specimens show the umbonal septum which characterizes the genus, and figs *12a, b* show the adult form of the species; from "Iowa Indian Reserve," in what is now northeastern Nemaha, Brown, and Doniphan counties, Kansas found "near coal," unquestionably some part of the Wabaunsee group; U.S. National Museum, no. 7035.

10—*Septimyalina scitula?* NEWELL, n. sp., from the Hollenberg limestone (upper? Wolfcampian equivalent), NW ¼ sec. 4, 4 miles northwest of Aulne, Kan.; Univ. Kansas, no. 7593.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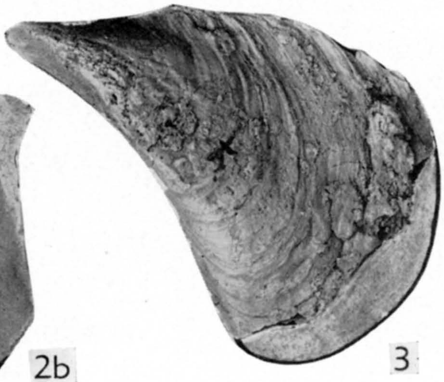
2a


2b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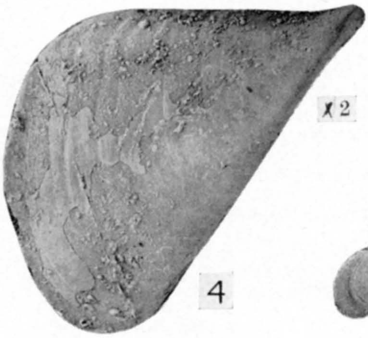
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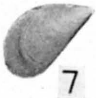
4


X 2

5


X 2

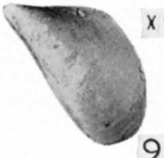
6


X2

7


X 2

8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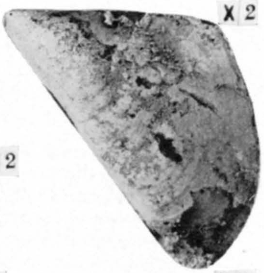
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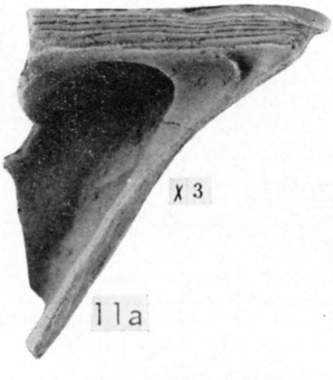
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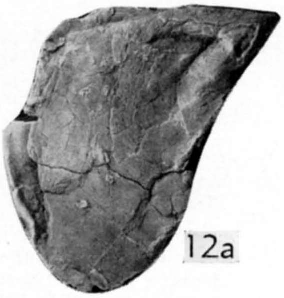
11a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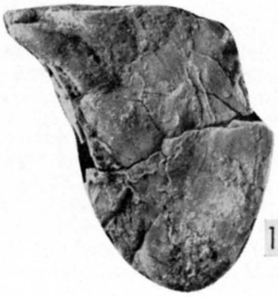
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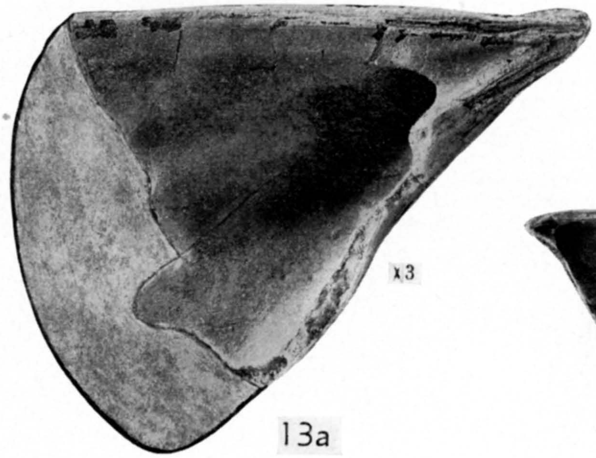
X 3

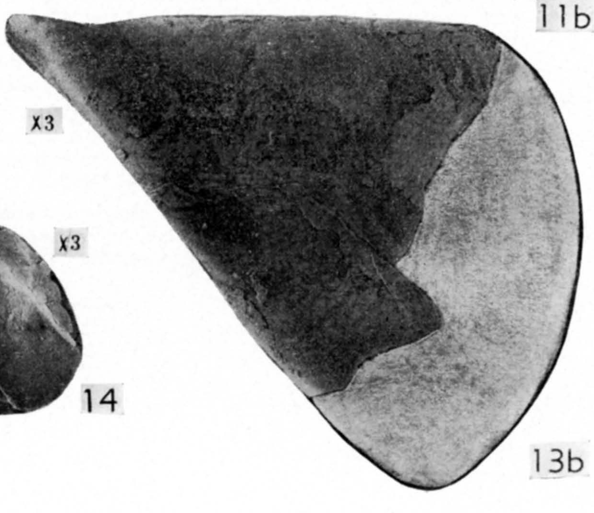
11b


X3

13a


X3

14


X3

13b

PLATE 11

PLATE 12.—PENNSYLVANIAN AND LOWER PERMIAN SEPTIMYALINA

(All figures X1 except where otherwise indicated)

Figure

1a-6—*Septimyalina burmai* NEWELL, n. sp., this early Permian (Wolfcampian) form has generally been referred to *Myalina kansasensis* Shumard or to *M. apachesi* Marcou, neither of which is recognizable ....p. 67

1a, b—Right and left side views, respectively, of the holotype, showing the relatively greater hinge length that distinguishes this species from the similar *S. perattenuata* from the Pennsylvanian; early Permian (probably Florena shale, Council Grove group), Beaumont, Kan.; U.S. Geol. Survey, no. 2497 .

2a, b—Right and left side views, respectively, of a juvenile paratype, X3, showing a form very like that of adults of the early Pennsylvanian *S. orthonota* (Mather); early Permian (Florena shale, Council Grove group), Grand Summit, Kan.;) Univ. Kansas, no. 7595.

3—Internal mold of a moderate sized left valve, illustrated here to stress the marked difference in appearance between shells and internal molds; although this specimen recalls *S. perattenuata,* a comparison with a similarly preserved specimen of the latter (pl. 13, fig. 4) shows the greater hinge length in the present species; this is one of the hypotypes used by Meek and Hayden (1864, pl. 2, fig. 7) to illustrate *Myalina permiana* (Swallow), a species which is unrecognizable; early Permian, probably from the Herington limestone, Sumner group, near the mouth of the Smoky Hill River, Kansas; U.S. National Museum, no. 1153.

4a-c—Right, hinge, and left views, respectively, of a well preserved paratype, X1, showing the subrhombic form and relatively longer hinge which distinguishes mature specimens of this species from *S. perattenuata;* Florena shale (Council Grove group), Grand Summit, Kan.; Univ. Kansas, no. 7596.

5a, b—Right and left views, respectively, of a juvenile paratype, X3; Florena shale (Council Grove group), Grand Summit, Kan.; Univ. Kansas, no. 7594.

6—Immature left valve of a paratype; this is one of the specimens used by Girty (1909, pl. 9, fig. 6) to illustrate *Myalina apachesi* Marcou, a species which is unrecognizable; Abo sandstone, about 50 feet above base of red beds (Wolfcampian), Abo Canyon, New Mexico; U.S. Geol. Survey, no. 1423.

Figure

7-9—*Septimyalina quadrangularis* NEWELL, n. sp., types from early Pennsylvanian rocks (Savanna sandstone, middle Desmoinesian) near Pittsburg, Okla. ....p. 69

7—The holotype, internal mold of a left valve, showing well the subquadrate posterodorsal extremity of the hinge line; Univ. Wisconsin, no. 21194.

8—A deformed right valve, rubber cast of a topoparatype, which has an unusually obtuse posterodorsal angle because of injury and repair during life; Univ. Wisconsin, no. 21195.

9—A rubber cast of right valve, a topoparatype; Univ. Wisconsin, no. 21196.

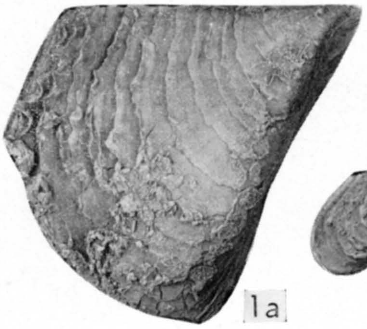
10-13—*Septimyalina sinuosa* (MORNINGSTAR), from early Pennsylvanian (Pottsville) rocks of Ohio and Indiana ....p. 69

10—A small left valve, selected here as the lectotype; lower Mercer limestone (upper Pottsville), northern part of Madison township, Muskingum county, Ohio, one-fourth mile south of the county line, near Adams Mills; Univ. Ohio, no. 15273.

11—A large imperfect left valve, a topoparatype, showing the tendency for the anterior and posterior margins to become parallel at an advanced stage in growth; same horizon and locality as the preceding; Univ. Ohio, no. 9819.

12a, b—Two views of a fragmentary left valve, a topoparatype, showing the form and hinge characters of the species; same horizon and locality as the lectotype; Univ. Ohio, no. 15272.

13—A large left valve somewhat tentatively referred to this species; the preservation is not good and it may be that the stubby appearance of the rear auricle is deceptive; from an unknown horizon (upper Pottsville or lower Allegheny) in the early Pennsylvanian on Otter Creek, near Brazil, Ind.; U.S. National Museum.


1a

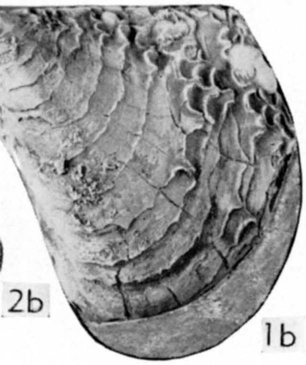
x 3


2a


3

x 3


2b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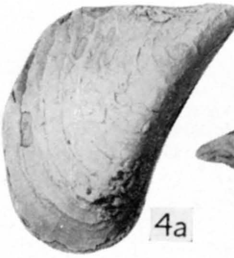
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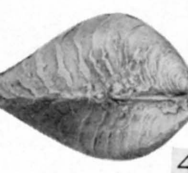
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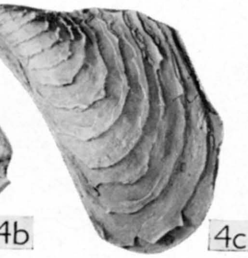
4c


5a


5b


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7


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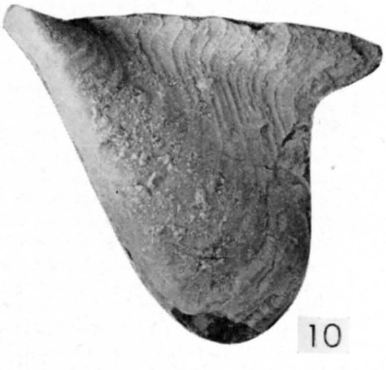

10


12a


11


12b


13

PLATE 12

PLATE 13.—Pennsylvanian Septimalina

(All figures X1, except where otherwise indicated)

Figure

1, 2—*Septimyalina orthonota* (Mather), two of the original types, X2, showing the marked obliquity that characterizes adults of this early Pennsylvanian species (Hale formation, Morrowan series), East Mountain, Fayetteville, Ark., as compared with adults of *S. perattenuata* and *S. burmai,* which are otherwise very similar .... p. 67

1—Relatively large and presumably fully mature left valve, a topoparatype; Univ. Chicago, no. 16583.

2—The holotype, a small left valve, showing well the shape and ornamentation of the species; Univ. Chicago, no. 16045.

3-12—*Septimyalina perattenuata* (Meek and Hayden), a species which seems to characterize the Desmoinesian, Missourian, and Virgilian series of the Pennsylvanian, commonly referred to *Myalina kansasensis,* an unrecognizable species .... p. 66

3-5—Syntypes of *S. perattenuata,* from the late Pennsylvanian (unknown Virgilian horizon) "opposite the northern boundary of Missouri" in Nebraska; unfortunately this material is so poorly preserved as to make satisfactory comparisons difficult; however, comparison with other material from equivalent horizons permits recognition of the species. *3,* Internal mold of a juvenile left valve; U.S. National Museum, no. 1022. *4,* An internal mold of an immature right valve; internal molds of these thick-shelled forms are nearly useless for identification; U.S. National Museum, no. 1022. *5,* The best specimen, an immature right valve retaining some of the outer ostracum of the shell, selected here as the lectotype in spite of the fact that the poor preservation and immaturity of the shell give it a superficial resemblance to the ancestral *S. orthonota;* U.S. National Museum, no. 1022.

6—An internal mold of a left valve, erroneously used by Morningstar (1922, pl. 11, fig. 9) to illustrate *Myalina pernaformis;* early Pennsylvanian (Boggs member, Pottsville), near Hopewell, Muskingum county, Ohio; Univ. Ohio, no. 15271.

Figure

7—Interior of a fine left valve, showing ligament area, small septum, and musculature; late Pennsylvanian (upper Stull shale, Kanwaka formation, Shawnee group), 1 mile west of the intersection of highways 50-S and 75, west of Waverly, Kan.; Univ. Wisconsin, no. 21208.

8—A mature right valve, showing relatively great height and obscure sinus below the posterodorsal extremity, sometimes seen in this species; late Pennsylvanian (upper Stull shale, Kanwaka formation, Virgilian series), near the center of the west side of sec. 20, T. 19 S., R. 16 E., Kansas; Univ. Kansas, no. 7598.

9a, b—Two views of a gerontic left valve, showing tendency to develop a very broad hinge area and for the space occupied by the living animal to become progressively reduced during later stages of growth; late Pennsylvanian (Vinland shale, Stranger formation, Douglas group), Palmyra township, Douglas county, Kansas; Univ. Kansas, no. 7602.

10a, b—Two views of a somewhat smaller specimen than the preceding, but likewise gerontic; late Pennsylvanian (Heumader shale, Oread formation Shawnee group), NE cor. sec. 7, T. 19 S., R. 17 E., Kansas; Univ. Wisconsin, no. 21209.

11a, b—Two views of a gerontic right valve, showing a tendency for the ventral part of the shell to migrate backward with growth; late Pennsylvanian (upper Stull shale, Kanwaka formation, Shawnee group), near the center of the west side of sec. 20, T. 19 S., R 16 E., Kansas; Univ. Kansas, no. 7599.

12a, b—Views of a gerontic left valve, showing the scaly character of the surface in an unworn specimen; generally these surface spines were worn off during life, or by recent weathering; late Pennsylvanian (Heumader shale, Oread formation, Shawnee group), NE cor. sec. 7, T. 19 S., R. 17 E., Kansas; Univ. Kansas, no. 7597.

X 2

1

X 2

2

3

4

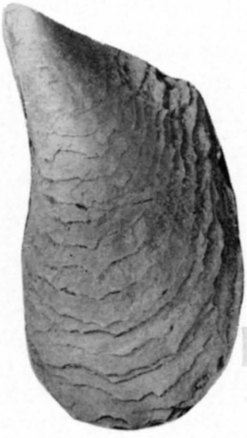
8

6

7

5

9a



10a

10b

11a

9b

12a

12b

11b

PLATE 13

PLATE 14.—PERMIAN MYALINA, PENNSYLVANIAN AND PERMIAN MYALINELLA, AND EARLY PENNSYLVANIAN NAIADITES

Figure

1-4—*Myalina (Myalinella) cuneiformis* GURLEY, from rocks of Desmoinesian age in Colorado and Wyoming......p. 61

1a, b—A fine bivalved individual, hypotype, X2, showing well the discordancy of the valves, and the form of the shell; Tensleep sandstone (Desmoinesian), 30 feet above the base, sec. 1 or 2, T. 6 N., R. 4 W., Wyoming; Yale Univ., no. 16342.

2, 3—Fragments of left and right valves, hypotypes, X5, showing features of the hinge; same horizon and locality as the preceding; Yale Univ., nos. 16343, 16344.

4—Right valve, one of Gurley's types, selected here as lectotype, X2; Hermoosa formation, Ouray, Colorado; University of Chicago, Walker Museum.

5a-6b—*Naiadites ohioensis* MORNINGSTAR, from the Sharon ore (Pottsville, probably Morrowan), Higgins Run, Scioto county, Ohio ....p. 73

5a-c—Views of a good internal mold, topoparatype, X3; Univ. Ohio, no. 15279.

6a, b—Views of a testiferous specimen selected here for the lectotype, X2; Univ. Ohio, no. 15281.

7-10, 12-14—*Myalina (Myalinella) meeki* DUNBAR, from Virgilian and Leonardian horizons in Kansas .... p. 60

7-10—Several topoparatypes of the species, X1; Carlton limestone (Wellington shale), upper Sumner group, 3½ miles southeast of Elmo, Kan.; Yale Univ., no. 3496.

12, 13—Right and left valves, respectively, showing typical form of uncrushed specimens, hypotypes, X2, Iowa point shale (Shawnee group), NW ¼ sec. 1, T. 21 S., R. 13 E., Kansas; Univ. Kansas, nos. 7600, 7601.

14—Large left valve, somewhat flattened by compaction, holotype, X1; Carlton limestone (Wellington shale), Sumner group, 3½ miles southeast of Elmo, Kan.; Yale Univ., no. 3496.

Figure

11—*Myalina (Myalinella) meeki* DUNBAR?, a somewhat imperfect left valve, somewhat reminiscent of the original figure of Cox's *M. pernaformis* from about the same horizon; however, the types of *M. pernaformis* are lost, and the species cannot be recognized from the published illustration; shale above the Mulky coal (uppermost Cherokee), Desmoinesian series, 12 miles west of Nevada, Mo.; Univ. Wisconsin, no. 21191..........................p. 60

15, 16—*Myalina (Myalina) wyomingensis thomasi* NEWELL, n. var., from Satanka shale in southeastern Wyoming, age equivalent of the Phosphoria formation..............p. 51

15—A medium-sized right valve, internal mold, X1, a topoparatype; basal Satanka shale, Red Mountain, sec. 9, T. 12 N., R. 76 W., Wyoming; Univ. Wisconsin, no. 21192.

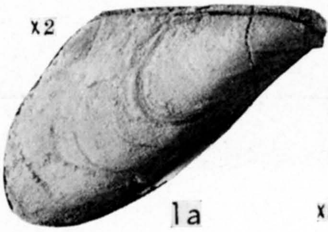
16—Robust left valve, internal mold, X1, the holotype; same locality and horizon as the preceding; Univ. Wisconsin, no. 21193.

17-19—*Myalina (Myalinella) acutirostris* NEWELL AND BURMA, from Whitehorse and Quartermaster (Guadalupian) red-beds of northern Texas ....p. 62

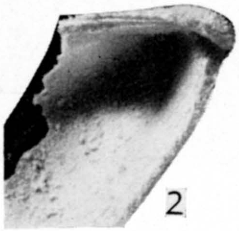
17—Right valve, artificial cast, X2; Dozier lens, Whitehorse group, south side of sec. 78, block 19, H. G. and N. Survey, Texas; Yale Univ., no. 16326.

18—Left valve, X2, topoparatype; dolomitic limestone at base of the Doxey shale, Quartermaster group, center sec. 63, block E-2, D. and S.F.R.R. Survey, Texas; Univ. Wisconsin, no. 20845.

19—Left valve, X2, holotype; same locality and horizon as the preceding; Univ. Wisconsin, no. 20846.


x2

1a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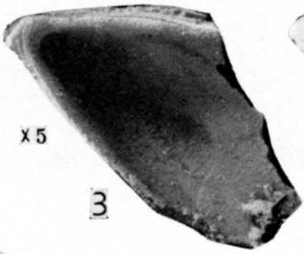
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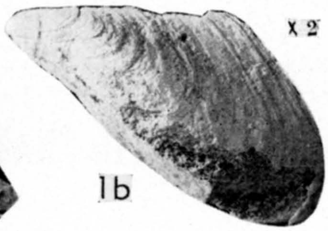
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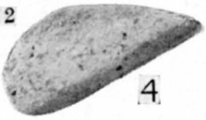
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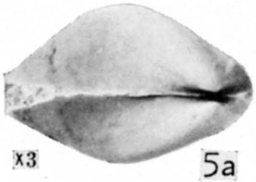
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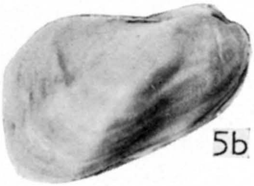
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x 3

5c


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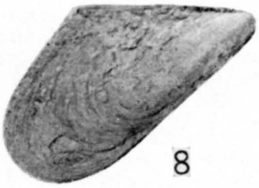
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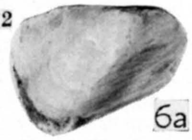

x2

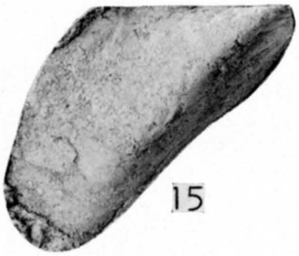
6a


x2

6b


x 2

17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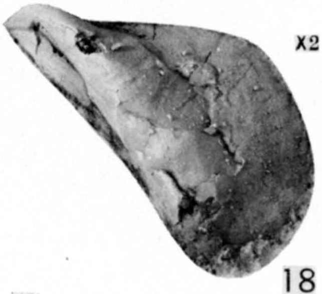
x2

12


x 2

13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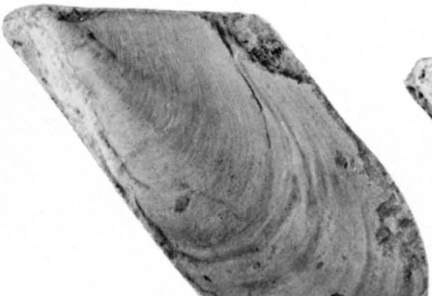
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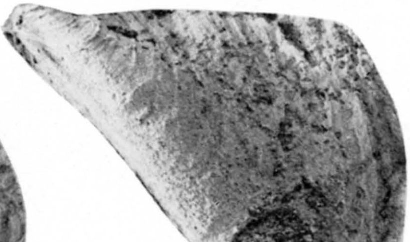

x2

19

PLATE 14

PLATE 15.—PENNSYLVANIAN NAIADITES AND PERMIAN LIEBEA

Figure

1a, b—*Naiadites quadrata* (SOWERBY), right and left views of an internal mold, X2, hypotype, showing musculature characteristic of the genus; from early Upper Carboniferous rocks (roof of Hard Mine coal) Adderly Green at Longton, Staffordshire, England; U. S. National Museum, no. 70654.

2a, b—*Naiadites carbonarius* DAWSON, genotype of *Naiadites.* Two views of a left valve, possibly one of Dawson's types, from lower Pennsylvanian rocks (Pottsville) of the Joggins formation at Joggins, Nova Scotia; McGill College, no. 21172..p. 72

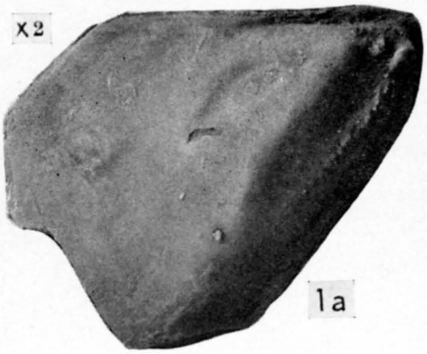
2a—View of hinge, X5, showing amphidetic ligament area and relatively fine ligament grooves. *2b*—External view, X3, showing modioloid form typical of the genus; internal molds, are commonly misleading in that the anterior lobe does not appear to be so prominent as in shells.

3a-5—*Liebea squamosa* (SOWERBY), genotype of *Liebea* Waagen, from upper Permian horizons of western Europe ....p. 74

3a-d—Rubber cast, X6, prepared from external mold of the most remarkable specimen (a hypotype) of *Liebea* ever described, showing well the *Myalina*-like cardinal areas, and the form and distribution of the original organic structures of the ligament; from the oolitic beds of the middle Zechstein dolomitic limestone, near Gera, Germany; Geologisches Landesmuseum, Berlin. *3a,* front view, sighted parallel to the hinge axis, showing prosogyre beaks, and interlocking margins of the two valves indicative of dentition similar to that of *Myalina, 3b,* dorsal view showing eight ligament cones. *3c-d,* right and left sides showing mytiloid contour.

4a, b—Dorsal left side views of another individual, an internal mold (hypotype), X3, showing general form and dorsal pustules along hinge line; these pustules are the molds of the ventral termination of relatively course ligament grooves of the *Myalina* type; from (middle?) Zechstein, near Gera, Germany; British Museum of Natural History, no. PL 243.

5—Rubber cast, X6, of a left valve (hypotype) showing anterior pit, presumably an adductor pit, and umbonal septum; the general form of the species is not accurately shown due to the imperfections of the original specimen, but the umbonal region seems to be perfectly represented; middle Zechstein, Gera. Germany; Geologisches Landesmuseum, Berlin.



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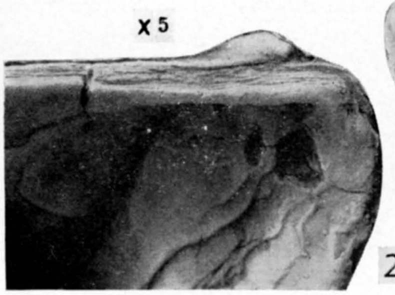

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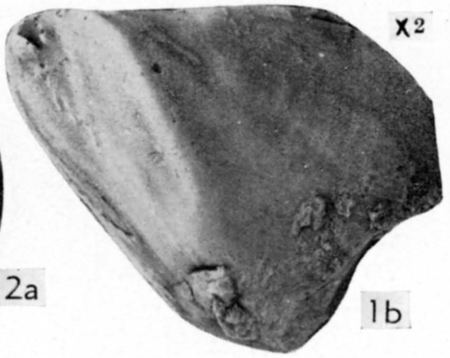
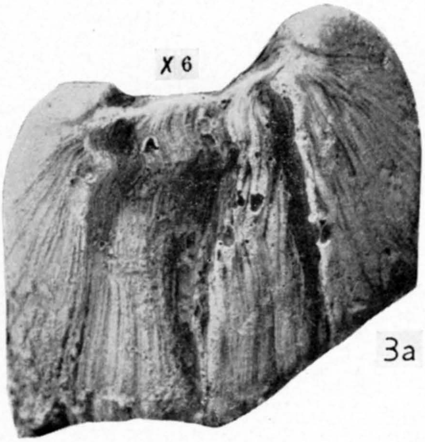


1b



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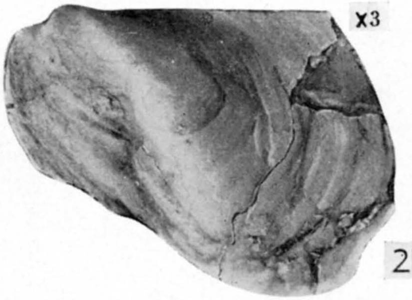

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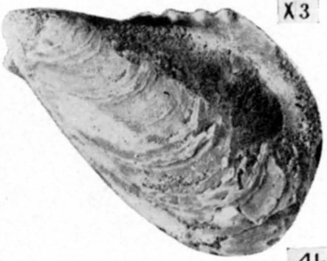

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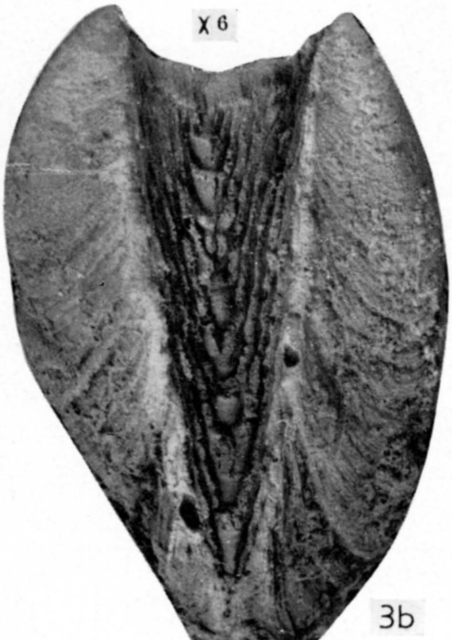
4a

5



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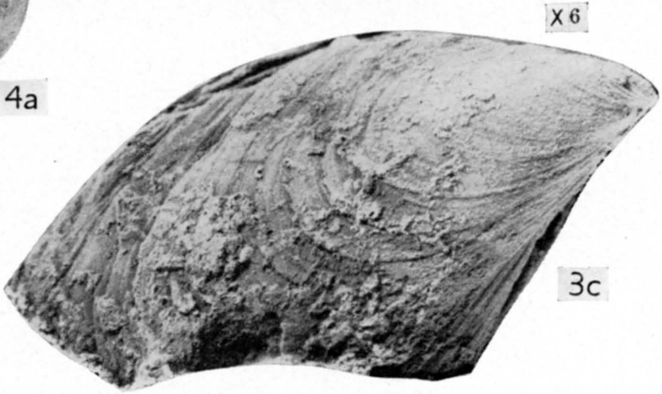

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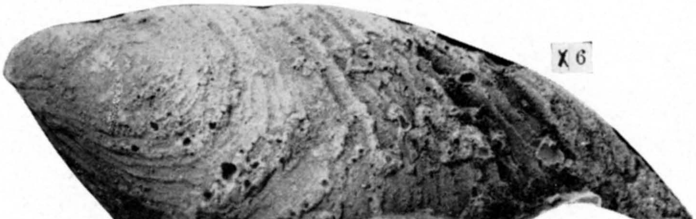

3d

PLATE 15

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