

OYSTER-LIKE PERMIAN BIVALVIA

NORMAN D. NEWELL AND DONALD W. BOYD

BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
VOLUME 143 : ARTICLE 4 NEW YORK : 1970

OYSTER-LIKE PERMIAN BIVALVIA

NORMAN D. NEWELL

Chairman and Curator, Department of Invertebrate Paleontology

The American Museum of Natural History

Professor of Geology, Columbia University

DONALD W. BOYD

Professor of Geology

University of Wyoming, Laramie

BULLETIN

OF THE

AMERICAN MUSEUM OF NATURAL HISTORY

VOLUME 143 : ARTICLE 4

NEW YORK : 1970

BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Volume 143, article 4, pages 217–282

figures 1–34, tables 1–6

Issued December 28, 1970

Price \$2.75 a copy

Printed in Great Britain by Lund Humphries

CONTENTS

INTRODUCTION	221
Acknowledgments	221
Epifaunal Bivalves	222
ADAPTATIONS OF THE PTERIOIDA TO PLEUROTHETIC LIFE	224
Convexity and Orientation	224
Asymmetry of Shell Fabric	224
Resupinate Condition of Living Oysters	227
Anchorage in Pleurothetic Bivalves	228
Byssal Attachment	228
Cementation	228
Form and Ornamentation	229
Taxonomic Implications of Attachment Mode in the	
Pseudomonotidae and Aviculopectinidae	230
Pallial Attachment and Fusion in the Pseudomonotidae	231
ORIGIN OF THE OSTREINA	233
Stratigraphic Evidence	233
Comparison of the Pseudomonotidae and the Gryphaeidae	233
Similarities	233
Differences	234
MORPHOLOGY OF THE PSEUDOMONOTIDAE	235
Musculature	235
The Ligament	235
FOSSILIZATION OF THE STUDY SPECIMENS	239
SYSTEMATIC DESCRIPTIONS	242
REFERENCES	278

INTRODUCTION

THE HISTORY OF EXPLOITATION of ecological niches by organisms in the geological past is recorded occasionally by chronological sequences of fossils. It is with examples of these and related phenomena that the present essay is concerned. We shall endeavor to document Permian fossil sequences (table 1) from which may be deduced evolutionary, probably iterative, trends by which bivalve mollusks of several families (the Pseudomonotidae, Terquemiidae, Anomiidae) achieved an oyster-like mode of life in late Paleozoic time. Moreover, we submit evidence in support of a hypothesis that some of these very probably led to the oysters, spondylids, and anomiiids of the Mesozoic. Shells of all the Paleozoic animals considered in the present paper possess a byssal notch in the right valve; hence these animals are not true oysters (*Ostreina*) which they otherwise closely resemble.

The present review of late Paleozoic oyster-like fossils is the first to be undertaken in the 30 years or more that have elapsed since one of us (Newell, "1937" [1938]) reported on mainly Pennsylvanian pseudomonotids from the mid-continental region of the United States. It is the first of a series of monographs on the Bivalvia based principally on celebrated collections of silicified Permian fossils of the Glass Mountains, Texas, and the Wind River Mountains, Wyoming. Other Permian and Pennsylvanian collections, from many sources, are also included.

ACKNOWLEDGMENTS

Most of the fossils described herein are siliceous pseudomorphs collected over several decades by Dr. G. Arthur Cooper in reef and near-reef facies of Permian rocks of the Glass Mountains in western Texas; these specimens belong to the United States National Museum of the Smithsonian Institution, Washington, D.C., where they are now preserved. Without access to the United States National Museum collections and without Dr. Cooper's continuous encouragement, this work could not have been undertaken. Consequently, it is a pleasure to dedicate the results of our labors to him.

Other collections of silicified Permian bivalves covered here were obtained independently by Newell and his students in southwestern United States, and by Boyd in Wyoming. The Wyoming collections stem from an important discovery of a Permian bivalve assemblage in the Wind River Mountains by Mr. Benjamin Weichman while he was a student at the University of Wyoming (Boyd and Newell, 1968). The fossils were obtained on the ranch of Mr. John Auer, whose property subsequently was purchased by Mr. Clair Milton. Both the Auers and the Miltons have encouraged us in our studies.

Most of the Wyoming specimens described herein are in the American Museum of Natural History in New York. Other specimens from

TABLE 1
STRATIGRAPHIC SOURCES OF WESTERN AMERICAN PERMIAN PSEUDOMONOTIDS

Age	Western Texas	New Mexico	Arizona	Wyoming
Guadalupian	Apple Ranch ("Word Limestone 4") Willis Ranch ("Word Limestone 3") – Lower Getaway Limestone China Tank ("Word Limestone 2")	--- ? ---		Park City
Leonardian	Road Canyon ("Word Limestone 1") Cathedral Mountain Skinner Ranch – Hess	San Andres	Kaibab	
Wolfcampian	Neal Ranch – Hueco			

many places were borrowed from various institutions cited in the following text.

Although the silicified fossils enhance our understanding of early oyster-like bivalves, the extreme scarcity of really instructive specimens is indicated by the fact that they constitute a very minor element among the five million or so associated silicified brachiopods and other fossils extracted at great labor and expense from approximately 100 tons of limestone. They were freed from the rock matrix by leaching carefully selected blocks of limestone with dilute commercial-grade hydrochloric acid. The laboratory work was done by Cooper at the United States National Museum (Cooper, 1946), by Newell at the American Museum of Natural History, and by Boyd at the University of Wyoming.

Substantial assistance, in the form of supplemental specimens and information needed in our work, was received from the following persons: Dr. Roger L. Batten, the American Museum of Natural History; Dr. Arthur L. Bowsher, Sinclair Oil and Gas Company, Tulsa, Oklahoma; Dr. John L. Carter, University of Illinois, Urbana; Dr. P. J. Coleman, the University of Western Australia, Nedlands; Dr. J. M. Dickins, Australian Bureau of Mineral Resources, Canberra; Dr. J. Helms, Institut für Paläontologie und Museum der Humboldt-Universität zu Berlin, and the custodians of collections of the Museum für Naturkunde in Gera, Germany; Mrs. Lois S. Kent, Illinois State Geological Survey, Urbana; Dr. Bernhard Kummel, Harvard University, Cambridge, Massachusetts; Dr. Marius LeCompte, Musée Royal d'Histoire Naturelle de Belgique, Brussels; Dr. Piero Leonardi, Istituto dell'Università di Ferrara, Italy; Dr. Copeland MacClintock, Yale University, New Haven, Connecticut; Dr. S. Ritzkowski, Geologisch-Palaeontologisches Institut der Georg-August Universität, Göttingen, West Germany; Dr. A. J. Rowell, University of Kansas, Lawrence; Dr. E. R. Trueman, University of Manchester, England; Dr. Ellis Yochelson, United States Geological Survey, Washington, D.C. To these, and to any others to whom we may have unintentionally failed to make acknowledgments, we give our thanks.

The excellent photographs published herein were made by our colleague Mr. G. Robert Adlington, of the American Museum of Natural History.

This research was supported by National

Science Foundation Grant GB-6905X to the University of Wyoming.

The following abbreviations of the names of institutions are used:

A.M.N.H., the American Museum of Natural History
G.S.C., Geological Survey of Canada, Ottawa
I.S.G.S., Illinois State Geological Survey, Urbana
I.S.M., Illinois State Museum, University of Illinois, Urbana

M.C.Z., Museum of Comparative Zoology, Harvard University

M.M.C.U., Mineralogical Museum of Copenhagen University

M.N.G., Museum für Naturkunde, Gera, East Germany

U.K., the University of Kansas, Lawrence

U.S.N.M., United States National Museum, Smithsonian Institution

U.W.A., University of Western Australia, Nedlands.

The above initials used with a number alone refer to localities. The initials used with the abbreviation "No." refer to catalogued specimens.

EPIFAUNAL BIVALVES

A characteristic shared by a majority of bivalves is their preference for soft substrates which provide concealment for the filter-feeding burrowers and nestlers and nutrition for the few sediment feeders of the class.

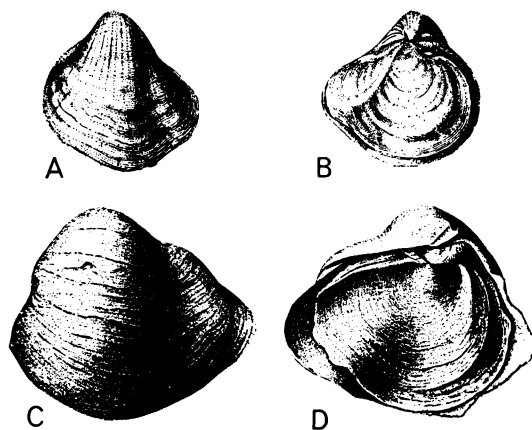


FIG. 1. A, B. *Pseudomonotis speluncaria* (Schlotheim), Permian (after King, 1850). C, D. *Gryphaea convexa* (Say), Cretaceous (after Weller, 1907). Inequivalved shells, such as these, are characteristic of most of the pleurothetic Pteriomorphia. *Pseudomonotis*, a byssate pectinacean, was attached by the flat right valve; *Gryphaea*, an ostreacean, was cemented at the beak of the convex left valve.

Members of the subclass Pteriomorpha (fig. 1), which includes the shells discussed herein, have, however, demonstrated a preference for epifaunal habitats from the early Ordovician to the present. These animals, including the marine mussels, arks, pearl clams, scallops, anomians, oysters, and a few other heteromyarians and monomyarians, have occupied a relatively exposed adaptive zone upon the sea floor with the aid of special anchoring facilities. During the late Paleozoic, they competed for space among rich epifaunas dominated by brachiopods, bryozoans, echinoderms, and coelenterates, mostly characteristic of stable and firm substrates.

Some of the members of the Pteriomorpha referred to in this paper are as follows:

- Subclass Pteriomorpha
 - Order Pterioida
 - Suborder Pteriina
 - Superfamily Ambonychiacea
 - Superfamily Pteriacea
 - Superfamily Pectinacea
 - Family Pectinidae
 - Family Aviculopectinidae
 - Family Oxytomidae
 - Family Plicatulidae
 - Family Pseudomonotidae
 - Family Terquemiidae
 - Family Spondylidae
 - Superfamily Anomiacea
 - Superfamily Limacea
 - Suborder Ostreina
 - Superfamily Ostreacea
 - Family Ostreidae
 - Family Gryphaeidae

Physiological adaptation to abnormal salinities has enabled many present-day bivalves to colonize brackish and hypersaline waters of

estuaries, where competition is small and attack by oceanic predators minimal. Collectors of Paleozoic marine invertebrates of the shallow interior seas are familiar with a tendency for species of pelecypods, including some Pteriomorpha, to avoid habitats dominated by brachiopod-bryozoan-crinoid-coral communities under situations that suggest abnormal, or variable, salinity requirements. For example *Pseudomonotis hawni* (Meek and Hayden) forms a few persistent shell beds in hypersaline calcarenites of the Big Blue Series (Wolfcampian) of Kansas and Nebraska to the near exclusion of other species. Such monospecific communities of marine bivalves frequently are correlated with abnormal salinities of bays and estuaries, situations widely exploited by the post-Paleozoic oysters.

The pseudomonotids and aviculopectinids of the upper Paleozoic were sparsely represented in a wide range of habitats of shelf seas, from euryhaline salinities to organic reefs of normal salinities. Attached representatives of these families and the Anomiidae are most characteristic of reef and near-reef environments. Probably they found rocky substrates most congenial. There was a marked tendency of the hermatypic pseudomonotids and aviculopectinids to develop spines, a phenomenon shared with many Permian reef brachiopods.

Although circumstantial evidence of shell morphology strongly indicates intimate adherence of the lower valve of these forms to the substrate throughout life, the character of that substrate, or host, rarely is manifest in xenomorphic (superimposed) growth patterns in the species studied. The byssate forms were attached snugly to the substrate, commonly a fragment of shell of the same or of another species.

ADAPTATIONS OF THE PTERIOIDA TO PLEUROTHETIC LIFE

CONVEXITY AND ORIENTATION

EPIFAUNAL BIVALVES are readily divisible, on a basis of shell symmetry, into two groups—approximately equivalved and strongly inequivalved. Among the groups represented by still-living forms, the inequivalved animals generally are pleurothetic; that is, they rest laterally on the substrate, at least during early ontogeny, with the sagittal plane more or less parallel with, rather than perpendicular to, the bottom surface. Among these, old or even mature heavy-shelled forms commonly are free on the sea floor. Thin-shelled bivalves frequently suspend themselves by a byssus to overhanging ledges of rock or to the branches of seaweeds, corals, and gorgonians, and even driftwood, or they are cemented by one valve.

The order Pterioida, to which the Pseudomonotidae, Aviculopectinidae, Terquemiidae, and Anomiidae belong, are the “flatfish” of the bivalves. The order also includes such important extant groups as the pearl clams, scallops, and oysters. In the early Paleozoic, the ancestors of these animals abandoned the upright in favor of the reclining, or pleurothetic, condition. One valve became morphologically ventral; the other valve, dorsal. Selective advantages of the pleurothetic mode of life might include minimal resistance to current and wave action and reduced exposure to predators. Groups other than Pterioida independently also produced cemented pleurothetic forms (e.g., the rudists, Chamacea, Aetheriidae) at various times, and it is not surprising that some of these show superficial convergence with oysters.

In harmony with the pleurothetic attitude, the Pterioida basically are inequivalved (fig. 1). The juvenile left valve in many living forms and the left valve of adults of most of the families are more convex than the right, commonly with a comparatively conspicuous left umbo (Jackson, 1890; Erdmann, 1934; Jørgensen, 1946). Larval shells of others are approximately equivalved. But the reverse situation, in which the juvenile right valve is the more convex of the two, is unknown. This curious asymmetry pertains whether or not the lower valve is anatomically right or left. Probably it is fundamental and of ancient

origin, because the adults of a majority of Paleozoic Pterioida display these characteristics (e.g., Newell, “1937” [1938]). Evidently, the right-left asymmetry is under rigorous genetic control.

In most cases, the lower valve is anatomically the right valve. The only conspicuous exceptions are the suborder Ostreina (*Gryphaea*, *Exogyra*, *Lopha* and others) and the anomiacean family Placunidae, all of which are sinistral (left side undermost). This difference has proved to be quite reliable for distinguishing between the suborders Pteriina (dextral) and Ostreina (sinistral).

Discordant valves, in which the margin of the left valve overlaps that of the right, are common among oysters, pteriaceans, and pectinaceans (Newell and Merchant, 1939). The difference in valve size in these, however, is more apparent than real. The inner ostracum of the right valve may not spread peripherally as rapidly as that of the left, even though the thin outer ostracum and periostracum do keep pace with the margin of the left valve. Thus, the weaker marginal part of the right valve is subject to marginal attrition, except in the hinge area where the two valves usually are equal in size.

The early Paleozoic Ambonychiidae probably are exceptions to the rule of sagittal asymmetry among the Pteriina, as shells of that family characteristically are equivalved. Judged from their form and weight, the shells of Ambonychiidae must have been pleurothetic, but they may have been ambidextrous, because the byssus was shared about equally by the two valves, and we know of no evidence of preferential orientation, such as a persistent concentration of epizoans on right or left valves.

ASYMMETRY OF SHELL FABRIC

In addition to the disparate convexity of the two valves, the outer ostracum of several living pleurothetic groups, such as the anomians, scallops, and oysters, displays inequalities, as was shown by Jackson in his great monograph on these shells (Jackson, 1890). This asymmetry of shell fabric is also found in some Paleozoic representatives of the Pseudomonotidae, Avicu-

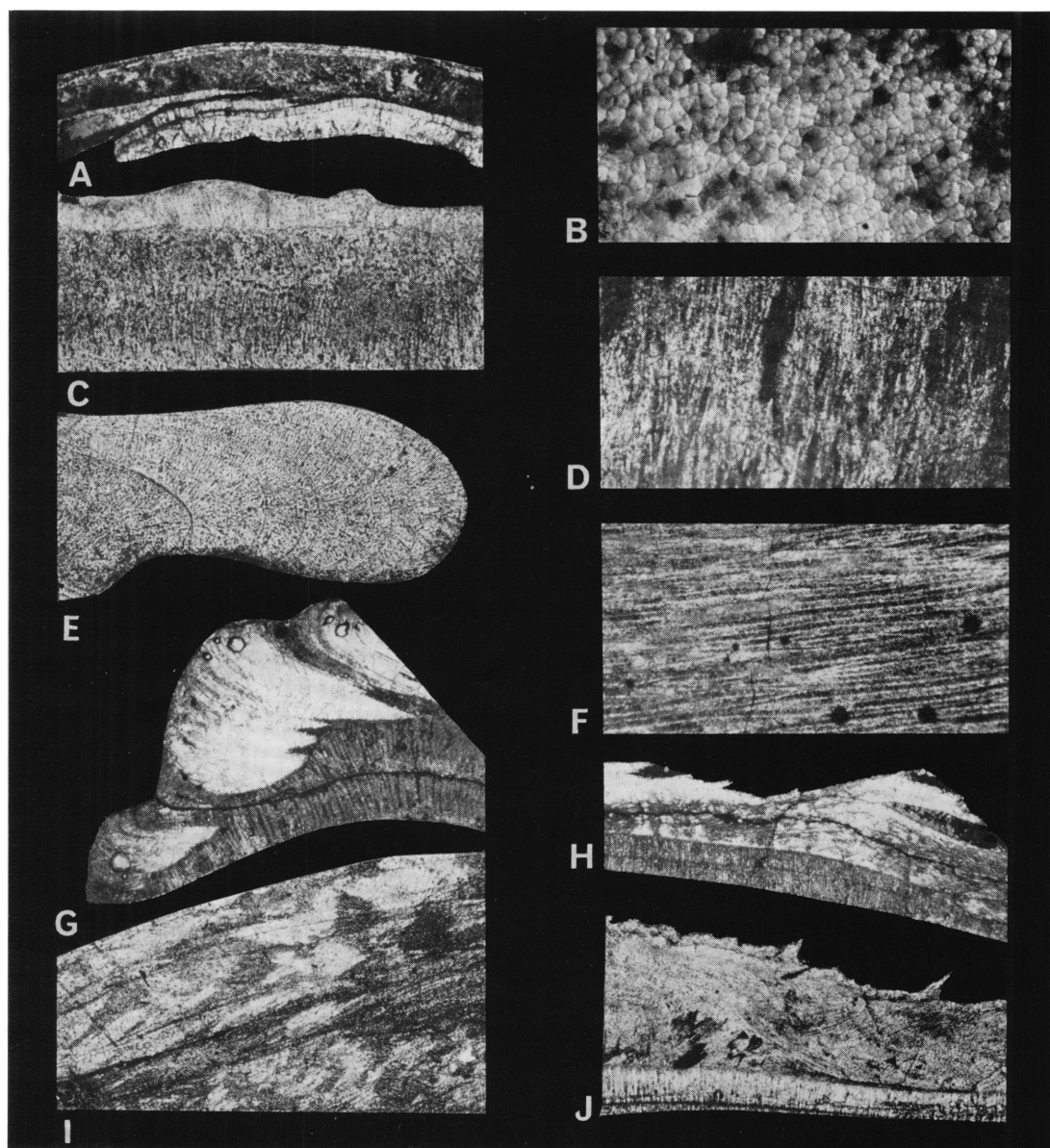


FIG. 2. A-E. *Pseudomonotis equistriata* Beede, Pennsylvanian. A. Right valve, radial section, imbricating prismatic layer (below), crossed-lamellar and hypostracum (above) layers, U.S.N.M. No. 154963. B. Prismatic layer, U.S.N.M. No. 154964. C. Radial section, outer ostracum (above) and crossed-lamellar layer (below), U.S.N.M. No. 154965. D. Tangential section, right valve, crossed lamellar, U.S.N.M. No. 154966. E. Resilifer section, right valve, concentric crossed lamellar, U.S.N.M. No. 154967. F-H. *Pseudomonotis (Trematiconcha) wandageensis* Newell and Boyd, new species, Permian, Western Australia. F. Concentric crossed lamellar, U.W.A. No. 27453. G, H. Radial sections, hinge and ventral margins, respectively, right valve, concentric crossed lamellar (below) and intercalations of foliate outer ostracum, U.W.A. No. 27409. I. *Gryphaea incurva* (Sowerby), Jurassic, radial section, right valve, foliate, A.M.N.H. No. 28913. J. *Spondylus americanus* Hermann, Recent, Florida, radial section, right valve, concentric crossed-lamellar (below) and foliate layers, A.M.N.H. No. 28914. A, C, $\times 66$; B, D-F, $\times 39$; G, H, J, $\times 66$; I $\times 11.5$.

lopectinidae, and Myalinidae (Newell "1937" [1938], 1942).

In the cited groups, the outer ostracum of right valves generally is plainly prismatic, whereas that of left valves is "homogeneous" or very finely fibrous (fig. 2A–C). The inner ostracum of both valves is non-prismatic and similar in the two valves. This persistent fabric asymmetry of the two valves is, however, not universal among pleurothetic Pterioidea. Deep-sea *Amussium*, shallow-water *Pinctada*, *Eurydesma*, and plicated oysters of the genus *Hyotissa* display prismatic or cellular structure about equally in the outer ostracum of the two valves. The significance of these differences and similarities of the two valves is unknown to us, but suffice it to say that shells in which are combined a left outer prismatic layer and a right homogeneous layer are unknown.

We had assumed earlier that diagenetic conversion of aragonite of molluscan shells to calcite invariably resulted in extensive destruction of the characteristic microfabric. It is now evident that such is not the case. Bathurst (1964) has shown that organic lamination of the original aragonite may be well preserved as relict fabric. Dr. D. Vincent Manson, of the American Museum of Natural History, has ascertained for us, by X-ray analysis, that the crossed-lamellar inner ostracum (fig. 2G, H) of *Pseudomonotis* (*Trematiconcha*) *wandageensis*, new species, from Australia, does not contain aragonite. Furthermore, the application of Feigl's solution as a stain test for aragonite fails to show any trace of aragonite.

It has been known for some time that extinct primitive Pterioidea, such as *Aviculopecten* and *Oxytoma*, unlike nacreous modern *Pteria*, or the foliate Ostreidae, possessed a concentric crossed-lamellar inner ostracum (Newell, "1937" [1938]; Ichikawa, 1958). In fossils, this inner layer commonly has been converted to calcite, or has been leached away selectively, leaving a well-preserved outer ostracum. In *Aviculopecten* the inner ostracum originally was composed of the mineral aragonite; the outer, of calcite, as with many living bivalves. The crossed-lamellar structure in living pelecypods generally is formed of aragonite (Taylor, Kennedy, and Hall, 1969). However, Bøggild (1930), described crossed-lamellar structure in calcite layers of several fossil molluscs, and Hudson and Palframan (1969) have demonstrated satisfactorily

that the crossed-lamellar inner ostracum of *Oxytoma*, a Jurassic genus, was instead composed of calcite.

Representatives of some of our genera (*Prospondylus*, *Paleowaagia*, *Pegmavalvula*) are preserved only as siliceous pseudomorphs or empty molds. Many of the shells of *Prospondylus*, however, have suffered extensive selective leaching of the inner ostracum before silicification, whereas the outer ostracum displays relative freedom from selective corrosion (fig. 9C, D).

As far as we can learn, crossed-lamellar structure is unknown in the living Ostreidae, and is confined to the inner layers in the Pectinacea and Limacea. Bøggild (1930) and Oberling (1964) recognized this structure in the living Spondylidae and many pectinids as far back as the Liassic *Pecten equivalvis*, and in several Jurassic species of *Gryphaea* (Majewski, 1969, p. 50, pl. 11). Bøggild's suggestion (*ibid.*) that the foliate calcite shell of modern oysters and scallops was in some way derived from ancestors with crossed-lamellar shells was reaffirmed by Newell ("1937" [1938]) who may have been the first to recognize crossed-lamellar fabric in Paleozoic pectinaceans.

Bøggild (1930), Oberling (1964), and Taylor, Kennedy, and Hall (1969) have found significant variation in shell fabric and mineralogy within genera and families of bivalves. Consequently, the taxonomic and phylogenetic significance of these characters must be worked out independently for each taxon. There is evidence that modifications in character and distribution of the fine elements of the shell may be ecologically induced, but living pectinids and oysters are relatively stable with respect to shell structure and mineralogy.

In the course of the present study we have been handicapped by the extreme rarity of specimens retaining original shell fabric and minerals. Nevertheless, specimens of *Pseudomonotis equistriata* from the Upper Pennsylvanian Jacksboro Limestone near Jacksboro, Texas, show that this species possessed a shell of asymmetrical fabric similar to that of *Aviculopecten* (Newell, "1937" [1938]). The outer ostracum of the two valves is asymmetrical, the right being prismatic calcite, with prisms about 20 μ in diameter, whereas the left apparently is homogeneous (fig. 2A–E). The inner ostracum is concentric crossed-lamellar in both valves. This layer, which also composes the hinge, frequently

is selectively leached away in *Pseudomonotis* and *Aviculopecten*, so it is judged to have been secreted as aragonite.

Well-preserved shells of *Pseudomonotis* (*Trematiconcha*) *wandageensis*, from Western Australia, display significantly different shell microstructure, very like that of the living Spondylidae (fig. 2F–H). The inner ostracum is composed of concentrically crossed-lamellar calcite. This layer is selectively leached away in one specimen, suggesting that it was originally aragonite.

The outer layer in *P. (Trematiconcha) wandageensis* in both valves consists of irregularly foliate calcite (fig. 2G, H) similar to the main shell in *Gryphaea* (fig. 2I), living oysters, or the outer ostracum of living individuals of *Spondylus* (fig. 2J).

From analogies provided by this admittedly meager evidence, we suppose that the crossed-lamellar aragonitic inner layer of the Paleozoic shells became obsolete in the oysters. The outer ostracum of *P. (Trematiconcha)*, then, may be compared more readily with the outer ostracum of *Spondylus* (fig. 2J), or the main shell layer (excepting the myostracum) of most of the *Ostreina* (fig. 2I), that is, they are probably homologous. Possible selective advantages of the different kinds of shell microstructure, or their demonstrable evolutionary trends, are unknown.

RESUPINATE CONDITION OF LIVING OYSTERS

In the true oysters (suborder *Ostreina*), attachment is by the left valve; in other pleurothetic (reclining) Pteriomorphia, by the right valve (fig. 1). We are not aware of any reason why living scallops and oysters should not occasionally display morphological inversion, as do the flounders, among fishes, or certain gastropod species, but such inversion among living and fossil Pterioda is not known to us.

A comparison of pteriod bivalves with flounders may be useful here. Each of the four families of flatfishes normally is only dextral or sinistral, and both eyes have migrated to the upper side. Specimens with the eyes on the side that is normally blind are said to be reversed. This condition is regarded as abnormal, or resupinate. There is some evidence that sinistral individuals of normally dextral flounders are less viable than right-sided ones. Ambilaterality,

a primitive condition, is common only in one family.

Mirror imaging is incomplete in reversed flounders, as it is in the inferred evolutionary jump from the Pteriina to the *Ostreina*. Certain flounder structures, such as the optic nerves, are not affected by the reversal. Also the viscera are constantly bilateral in both normal and reversed forms. These elements of symmetry are fixed before metamorphosis. One specimen studied by Hubbs and Hubbs (1945) was a notable exception. Only in this individual was there a complete reversal of asymmetry of the optic nerves and viscera, fundamentally comparable with that in sinistrally coiled snails. Reversal in the gastropods has been traced to a 180-degree change in the direction of cell cleavage, according to Ludwig (1932). Evidently, the determination of laterality among the Pterioda is genetically more complex than is that of snails or flounders, because reversal of symmetry is unknown in these groups.

We may suppose that, although partial inversion took place in oysters when they abandoned the basic dextrality of their ancestors in favor of sinistral attachment, some conspicuous traits of the pectinacean asymmetry are incorporated in oysters and are not directly affected by the inversion.

The evidence of similar anatomy, incomplete inversion, and stratigraphic sequence suggests that the gryphaeid oysters were derived from Paleozoic pseudomonotids. Resupination and loss of the foot and byssal apparatus in the larval oyster immediately after cementation may have stemmed from one or more genetic mutations. But this inversion did not affect shell microstructure or the primitive asymmetrical convexity, both of which are similar in the young and adults of many living oysters and scallops and may be taken as evidence of kinship. Shell characters developed by pseudomonotid ancestors in the late Paleozoic, when the right valve was undermost, are still preserved in the upper valve of living oysters (fig. 1).

It is probable that the transition from dextrality, the condition of the suborder Pteriina to sinistrality, the condition of the *Ostreina*, was accomplished in a single mutation, perhaps involving dependent morphological changes and a loss of the byssal notch. The ratio of sinistral to dextral individuals in the earliest populations may have been small, increasing gradually

through Triassic time, but there is no well-documented evidence of such an increase, and the historical facts remain obscure.

Such a single mutation might be termed a macromutation by some investigators, in the sense of Goldschmidt (1940). Many other characters, however, distinguish the living Pteriina and Ostreina, and their character complexes surely must have resulted from the accumulation of many mutations over a considerable span of time.

ANCHORAGE IN PLEUROTHETIC BIVALVES

BYSSAL ATTACHMENT

Living Pteriomorpha, as do many other epifaunal invertebrates, occupy an adaptive zone in which anchorage is a requisite. Anchorage enables them to live in more or less exposed situations, accomplished in larvae and many adults by attachment with a flexible byssus. Other adults lose the byssus and become cemented by the lower valve to a shell fragment or a rock surface. In these actions the bivalve departs from the primitive upright position to one in which the animal reclines on one side—the pleurothetic condition.

Although the resulting immobilization severely restricts physical adjustments of individuals to oscillations of environment, there are compensating benefits, e.g., the free circulation of oxygen- and nutrient-bearing waters and comparatively low rates of sedimentation that characterize stable substrates. Living scallops and oysters possess especially efficient facilities for pumping water and for freeing the mantle cavity of sediment and pseudofeces (Yonge, 1953); correlated metabolic efficiency enables some species to pack a maximum number of individuals into favorable areas. Because of the wasteful reproductive methods of bivalve molluscs, closely spaced individuals are likely to be reproductively more efficient than are dispersed individuals. These attributes have enabled many species of bivalves, including the oysters, to take advantage of the richest feeding grounds that exist in the inshore euryhaline waters of bays and estuaries, and the great epeiric seas of the past.

Temporary fixation by a byssus is widely employed among larval Bivalvia of many orders. Byssate adults, however, are most characteristic

of the subclass Pteriomorpha. Because the byssate condition at present is most prevalent among larvae, byssiferous adult bivalves might be regarded as neotinous, or paedomorphic, with respect to this character (Yonge, 1962). All orders of the subclass, however, have very long geologic histories, and an alternative hypothesis is suggested here—that byssal fixation is an ancient and highly successful adaptation characteristic of many epifaunal bivalves, whether larval or adult. Thus, the larval byssus may be a generalized ancestral character that has been lost by infaunal and cemented epifaunal species which do not require anchorage.

CEMENTATION

Attachment by cementation is a culminating stage in the ontogeny and evolution of some Pterioida, probably attained several times in families of the Pectinacea. It is interesting that many cemented pectinaceans show a tendency during growth for reversal of the juvenile shell convexity. The cemented valve of the adults may become relatively deep and the free valve more or less operculiform (as with *Paleowaagia*, new genus)—trends common also in cemented brachiopods. The prodissoconch shell, however, is rather uniform throughout the Pteriomorpha. It may be more or less equivalved, or the right valve may be less convex than the left. As far as we know, in no case is the prodissoconch right valve the larger of the two.

After initial cementation of the pelecypod shell by conchiolin secreted by the byssal gland and applied by the foot, the lower valve is directly attached by successive growth increments along the mantle margin. The attachment surface varies in dimensions in different species from a millimeter or so to several centimeters around the uncemented juvenile part of the shell (fig. 3). During mature growth, the shell margin tends to rise above the substrate.

More than one evolutionary route to cementation has been followed by monomyarian bivalves. This is apparent in hinge structures and, in some cases, is indicated by the shell fabrics and mineralogic composition that characterize various taxa. For example, the oldest gryphaeid oysters, the Pectinidae, and the Spondylidae, not certainly known below the Upper Triassic, had already diverged considerably in morphological and anatomical characters. The fossil record of the most likely Paleozoic ancestors of

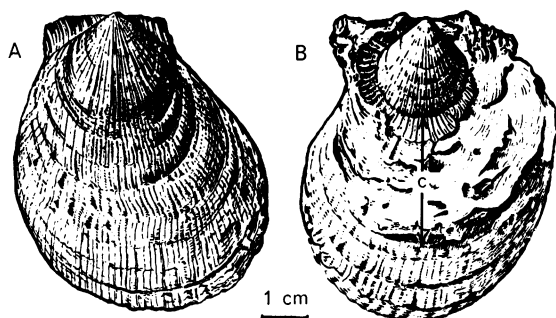


FIG. 3. *Hinnites cortesi*, Tertiary of Europe (after Jackson, 1890). A. Left valve. B. Right valve, showing scar of cemented attachment (c) outside juvenile free-living stage. Note that byssal notch is lost after free-living stage.

these families, the Aviculopectinidae, the Pseudomonotidae, and the Terquemiidae, suggests that the phyletic splitting leading to Mesozoic oysters, scallops, and spondylids was initiated well back in the Paleozoic, perhaps as early as the Devonian. The inner ostracum of the shell in both the Aviculopectinidae and the Pseudomonotidae was crossed-lamellar aragonite, but this layer was lost, or modified, and most of the shell came to be composed of foliated calcite in Mesozoic time. Probably the modifications in shell fabric took place independently in the two stocks.

Another evolutionary tendency was the recurrent loss of the adult pedal aperture (byssal notch) in the Paleozoic Pseudomonotidae and later in the Plicatulidae, Spondylidae, and certain of the Pectinidae (*Hinnites*).

In *Plicatula* and the true oysters, cementation immediately follows the planktonic veliger, and a byssal notch does not develop at any stage. Thus, the Plicatulidae, although commonly classed as Pectinacea because they are dextral and possess filibranch gills, are very oyster-like in many characters. It is interesting to speculate on the possible close relationship of *Plicatula* and the similar *Lopha*, neither of which is byssate in the nepionic stage. *Spondylus* and *Hinnites*, however, show a byssal notch in the early post-prodissoconch.

In cemented pectinaceans (excepting *Plicatula*) the foot, much reduced, and changed in function from byssus spinning to mantle cleansing, is retained throughout life, as is shown by the retention of the foot and pedal muscles in

living forms, and pedal muscle scars in the fossils. In the suborder Ostreina, this trend is carried a step farther. The larval foot and byssal gland, shared equally by both valves, atrophy and are lost immediately after attachment of the spat, as in *Plicatula* (Erdmann, 1934).

FORM AND ORNAMENTATION

Individual growth of the shell in cemented bivalves is influenced, of course, by the character of the substrate. In the Permian forms, shells of the same species most commonly provided a suitable surface of attachment, much as in oysters. Living crinoid columns also were frequently selected for attachment (fig. 28A). There is much experimental evidence from living bivalves that spatfall is not fortuitous, which may have been true also of the Permian species. The veliger probably possessed considerable ability to choose or reject an anchorage site.

In spite of individual modifications of form imposed by variations in substrate, persistent growth tendencies are apparent in the ontogenetic sequence of growth lines of the Pseudomonotidae. For example, the nepionic valves may display approximately a rounded rhombic outline with a forward obliquity, or the principal growth gradient may be downward, resulting in a more or less equilateral symmetry. For these, the terms prosocline and acline, respectively, have been used (Newell, "1937" [1938]). During growth, some scallop shells display a change from posteroventral to anteroventral growth, resulting in a crescentic deflection forward of the principal growth axis. If accentuated, this forward acceleration of the anteroventral growth gradient produces a more or less backward obliquity of the mature portion of the shell, an advanced condition of many pectinaceans that has been termed opisthocline (Newell, "1937" [1938]). Unfortunately, these terms were poorly chosen, because they do not adequately describe growth vectors. Consequently, in the present study, we employ terms that specify the directions of principal growth gradients: retrocrescent, procrescent, and infracrescent, respectively, for shells in which ventral accretion shows a marked backward, forward, or mainly downward component. Procrescent shells generally display an early retrocrescent growth stage, followed by an infracrescent one.

The Paleozoic Anomiidae, as are their modern relatives, are characterized by unornamented,

irregular, nondescript shells subcircular or oval in outline.

Ornamentation in the Pseudomonotidae is variable within circumscribed limits. Most right valves and many left valves display irregular concentric folds. The shells of some species essentially lack radial or other regular sculpture, especially in the umbonal areas, but somewhat irregular growth varices, perhaps related to seasonal interruptions, are prevalent. Radial ornamentation, consisting of one or more intercalating ranks of costellae or costae, are found on most species, and those of the right valve commonly are finer and more numerous than those of the left.

In some shells, especially those associated with reefs, projecting frills and radially divided spatulate, arched, or tubular (hyote) spines split along the lower face and rise tangentially over the general surface of the shell where the imbricating growth lamellae intersect the coarser radial ribs.

Commonly, the scales and spines are rather irregular and variable in form, size, and distribution. In general, they resemble similar features of some species of *Spondylus*, whereas the smooth and plicate pseudomonotids more resemble living oysters.

It is an interesting fact that spinosity is far more marked and prevalent among the Permian pseudomonotids than among the Carboniferous or Triassic examples, but these general differences may be related to the fact that most of the Permian species are from reef and near-reef habitats.

TAXONOMIC IMPLICATIONS OF ATTACHMENT MODE IN THE PSEUDOMONOTIDAE AND AVICULOPECTINIDAE

Unlike Mesozoic oysters, well-preserved pseudomonotid shells are rare fossils, and the stratigraphic record of the Pseudomonotidae is too erratic and discontinuous to permit the development of a detailed chronology of the course of evolution within this family. Consequently, morphologic trends must be deduced mainly from ontogenetic criteria, and there is no direct evidence that variations in attachment mode were or were not the products of long and persistent evolutionary changes. A similar problem exists with respect to recent species of *Hinnites* (fig. 3), cemented versions of the scallop *Chlamys*,

which is alternatively interpreted as a distinct pectinid genus or an ecological variant within populations of free scallops.

The stratigraphic distribution of the several morphological groups of pseudomonotids is not illuminating. For example, *Pachypteria*, from the Lower Carboniferous, although the oldest known representative of the family, is one of the most specialized, in that the cemented attachment was achieved early in ontogeny and the adult deviates very far from the presumed aviculopectinid-like juvenile (fig. 7F). Conversely, the geologically younger *Pseudomonotis* (fig. 12), contrary to an earlier view (Newell, "1937" [1938]), does not display any tendency for cementation in our material. Free and cemented mature pseudomonotids are not found in direct association, and there is no evidence of local intergradation between the two extreme conditions.

Apparently the habit of cementation was developed several times in the Pseudomonotidae at successive epochs in the history of the group and at least once in the Aviculopectinidae. The erratic known stratigraphic distribution of the several morphologic groups suggests iterative acquisition of the cemented habit.

Cemented plicated forms similar to *Lopha* and *Plicatula* appear in the late Permian of Japan (Nakazawa and Newell, 1968), and the early Triassic of East Greenland (Spath, 1930, 1935), becoming common in the Middle Triassic. Their ancestry is unknown, and probably they are only distantly related to the gryphaeas that are known in the Upper Triassic of many regions (Diener, 1923; Kutassy, 1931). It is this latter group that closely resembles and may have been derived from the Paleozoic Pseudomonotidae. The postulated transition from the pectinacean pseudomonotids to the Mesozoic gryphaeas, then, may have taken place either rapidly or slowly within the Triassic during a time interval of some 20 million years from which fossils pertinent to this problem are not yet known. Another branch probably led from the Pseudomonotidae possibly via the Terquemiidae to the Spondyliidae.

Through the courtesy of Dr. Piero Leonardi, of the University of Ferrara, we reproduce here (fig. 4) photographs of an Upper Triassic terquemiid, *Newaagia*, from the San Cassian beds of Cortina d'Ampezzo. These shells display rudimentary isodont dentition that may be con-

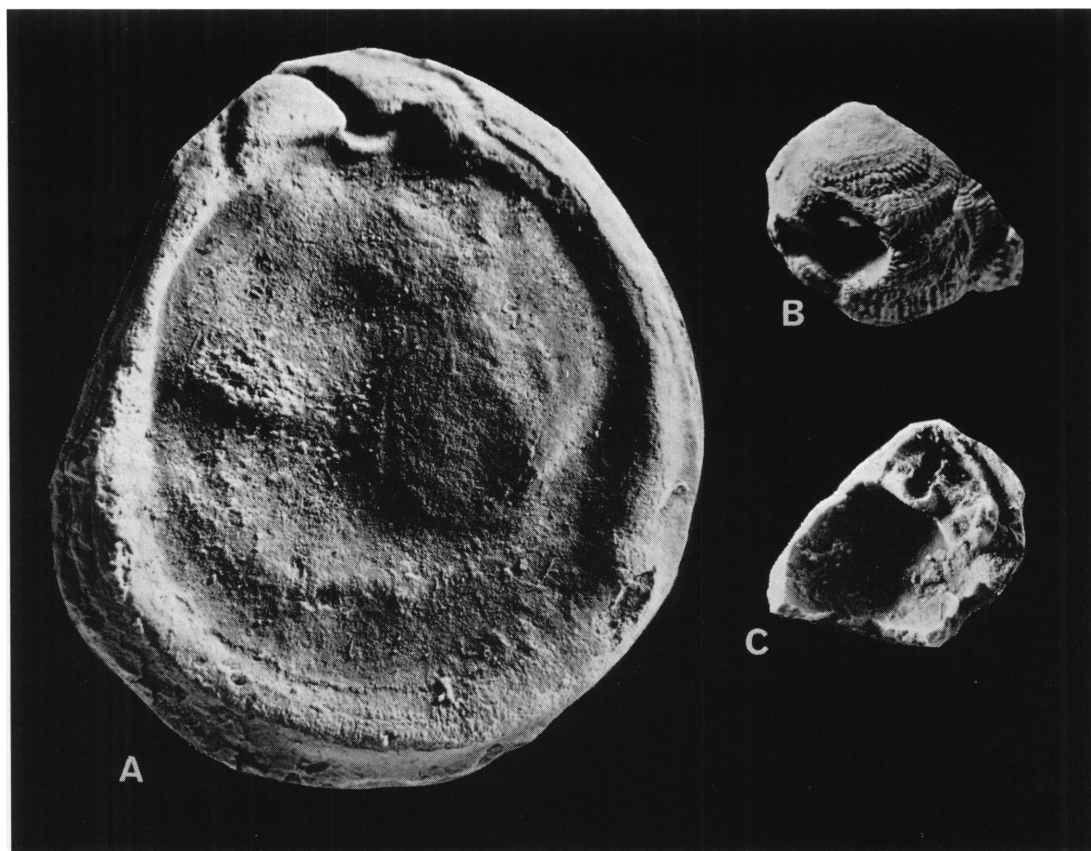


FIG. 4. Triassic terquemiids, Cassian near Cortina d'Ampezzo (courtesy of Dr. Piero Leonardi, University of Ferrara; figured by Leonardi, 1943, pl. 5, figs. 11a, b, pl. 6, fig. 10). A. *Terquemia* sp.?, interior of right valve. B, C. *Newaagia denticostata* (Laube), left valve. Ligamental area and other hinge features are reminiscent of the Spondylidae. Approximately $\times 5$.

sidered the initiation of a development leading to the strong interlocking teeth of *Spondylus*. Such a possibility remains to be investigated.

Reef and near-reef limestones of the Glass Mountains of western Texas contain a spiny bivalve that we are interpreting as a primitive terquemiid, *Paleowaagia*, new genus, the first reported from the Paleozoic. This is morphologically transitional from *Prospondylus* to *Newaagia*. The Permian shells resemble those of the Terquemiidae in possessing a deep right valve and an opercular left valve. They are exceptional in being spiny and possessing a nepionic byssal notch. The morphological series *Pseudomonotis*-*Prospondylus*-*Paleowaagia*-*Newaagia*-*Spondylus* approximates a time series and roughly approximates a phylogeny.

By Jurassic time, oysters and gryphaeas are

well represented by densely gregarious populations in most of the better-known fossil marine faunas. The circumstances suggest that this gregariousness, with all the implications for efficiency of reproduction and utilization of the environment, has played an important role in the success and later ecological deployment of the oysters. But the cemented pectinaceans have never been so successful. Generally, they occur as scattered individuals or clusters in both fossil and living species.

PALLIAL ATTACHMENT AND FUSION IN THE PSEUDOMONOTIDAE

Among the order Pterioida, the living *Pinctada* are generalized and may be compared with Paleozoic aviculopectinids and pseudomonotids (Newell, "1937" [1938], fig. 1). Unlike that of

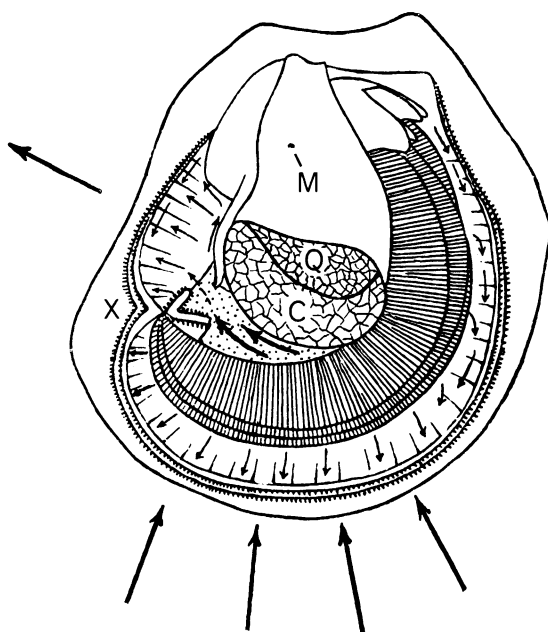


FIG. 5. General anatomy and water circulation in *Ostrea edulis* Linné (modified from Yonge, 1936), viewed from right side with shell removed. Inhalant and exhalant respiratory currents indicated by heavy arrows; cleansing currents by small arrows.

Abbreviations: C, catch muscle; M, Quenstedt muscle; Q, quick muscle; X, palliobranchial fusion point (branchitellum) of mantle and ctenidia, a feature reflected in some shells of the Ostreacea and the Pseudomonotidae.

most bivalves, the mantle in these and other pteriaceans is not attached directly to the shell but, instead, is supported by radial pallial retractor muscles inserted at discrete points along a discontinuous pseudopallial line.

The mantle of many of the Pectinacea differs in having a more or less continuous attachment of the mantle along a pseudopallial line. In oysters, on the other hand, the pallial line may be indistinct or lacking. It is Yonge's (1953, p. 462) view that pallial attachment in these forms is secondary and not homologous with the pallial line of the dimyrians.

Animals of the subclass Pteriomorpha are not provided with circulatory siphons, and, in most families, the mantle margins are separated around the margin. Characteristically, inhalant water enters along some two-thirds of the antero-ventral periphery as far as the posterior extremities of the gills, and the exhalant current (except for sporadic cleansing jets) is concentrated in a small sector of the margin between the posterior tips of the gills and the posterior adductor above (fig. 5). But, in certain oysters, a part of this current also passes above the adductor muscles (Yonge, 1953).

A notable innovation among the Ostreina is a fusion point joining the two mantle margins at the posterior extremity of the gills. This fusion provides a barrier between inhalant and exhalant currents, doubtless increasing the efficiency of respiration, and it aids in cleansing the gill chamber of pseudofeces. The palliobranchial fusion point frequently is reflected in some gryphaeid oysters and pseudomonotids in a marginal shell sinus and external sulcus behind the adductor scar (fig. 1). The existence of this characteristic in both the Ostreina and the Pseudomonotidae may indicate common origin or convergence. We favor the former possibility. There is little evidence in shell form of palliobranchial fusion in the Aviculopectinidae.

ORIGIN OF THE OSTREINA

STRATIGRAPHIC EVIDENCE

THE ORIGIN OF THE TRUE OYSTERS has always been uncertain because of inadequacies in the fossil record of early Triassic oysters. A prevailing view has been that the earliest known plicated oysters appeared, fully formed, in the Middle Triassic, as in Jordan (Cox, 1932) and Germany (Seilacher, 1954), becoming widely established by the close of the period. But Nakazawa and Newell (1968) have reported examples from the Japanese late Permian. These oyster-like forms commonly are referred to *Lopha* or *Enantiostreon*. They differ in many ways from *Ostrea* and *Gryphaea*. Concerning the Jordanian species, Cox thought that "the plicated oyster thus appears to be merely the Muschelkalk *Ostracites cristadiformis* Schlotheim, which should be referred to *Lopha* and not to *Enantiostreon*." *Enantiostreon* has a costate, not a plicate, shell.

Henri and Geneviève Termier, pondering the numerous reports of right-valve attachment, had already suggested that some of the Triassic oysters may have been ambidextrous, attached indifferently by either valve (Termier and Termier, 1949, p. 294). Our examination of the literature on this subject, however, fails to reveal any well-documented case of right-valve attachment in Middle or Lower Triassic oyster-like bivalves.

Dextrally cemented plicated shells superficially similar to those of *Lopha* are reported as *Plicatula* from the Upper Triassic of many regions (Diener, 1923; Kutassy, 1931), and the mutual relationships of early *Lopha* and *Plicatula* are not known. As the hinge structures and muscle scars are not known in most of the described species, they should be further investigated.

Commonly, it has been assumed that shells of *Lopha* are invariably opisthogyre, but some of the Permian (Nakazawa and Newell, 1968) and Triassic plicated oysters are orthogyre. In cases in which the adductor scar is not visible, which seems to be the usual situation, right and left valves have been identified solely by the curvature of the beaks. Consequently, although we recognize a possibility that some of the early plicated oysters may have been ambidextrous,

we note that ambidexterity really has not been established.

The oyster genus *Lopha* does not resemble bivalves older than latest Permian. Consequently, its ancestry is very uncertain. These plicated oysters are different from other oysters in many respects, and possibly they represent a line distinct from the gryphaeas.

Gryphaea has been reported from the Upper Triassic of widely scattered areas in the Northern Hemisphere (Diener, 1923; Kutassy, 1931), and it is anticipated stratigraphically by the similar *Pseudomonotis* of the Permian (fig. 1).

The early Mesozoic genera *Terquemia* Tate, 1867; *Enantiostreon* Bittner, 1901; and *Newaagia* Hertlein, 1952 (fig. 4B, C) are similar costate, but not plicate, forms cemented at the umbo of the strongly convex right valve. Cox (1964) has placed them in a separate family, the Terquemiidae, leading probably to the Spondylidae. Dextral attachment led Cox to regard the Terquemiidae as pectinaceans. Certainly both families lack the byssal notch in adults. In the Spondylidae, this feature commonly is visible in early growth lines.

As far as we can determine from the literature, and from the few Triassic specimens of the Terquemiidae that we have seen, the presence or absence of a larval byssal notch or slit within the attachment cicatrix cannot be demonstrated in ordinary specimens. Consequently, we are left with uncertainty in regard to this significant character. If the notch were really lacking at all ontogenetic stages, we would regard them as possibly transitional to the Plicatulidae which differ from pseudomonotids and oysters in possessing an internal ligament and isodont dentition.

COMPARISON OF THE PSEUDOMONOTIDAE AND THE GRYPHAEIDAE SIMILARITIES

In spite of their sinistrality and lack of byssal apparatus, some gryphaeas are remarkably similar to the Paleozoic Pseudomonotidae. The similarities are so numerous that we regard them as evidence of relationship rather than the results of adaptive convergence.

Some anatomical differences conveniently distinguish gryphaeas and oysters from the Pseudomonotidae, e.g., loss of the foot and lack of a byssal notch in the former. Modern oysters possess a higher grade of gill structure than the Pectinacea. The former more closely resemble eulamellibranch ctenidia than the filibranch ctenidia of the pectinaceans. Unfortunately, gill characters cannot be assessed in fossils. We know that the Pseudomonotidae had shells similar to those of the Aviculopectinidae in general form, ligament, and shell microfabric. The inner ostracum in both probably was composed of aragonite (Newell "1937" [1938]), and we can now demonstrate that it was crossed-lamellar in *Pseudomonotis*, *sensu stricto*, as in *Aviculopecten*. Consequently, we conclude that these two families are closely related and probably had a common origin in the early Mississippian or Devonian.

Late in the Paleozoic, and in the Triassic, a number of groups of the Pterioidea developed foliated calcite shells with, or without, crossed-lamellar inner layers. This innovation may have occurred independently in different groups, which include *Pseudomonotis* (*Trematiconcha*) *wandageensis*, new species, the Ostreina, the Pectinidae, and the Anomiidae.

The Pseudomonotidae are classed here as pectinaceans very close to the Aviculopectinidae. We also entertain the view expressed long ago by Termier and Termier (1949) that the Pseudomonotidae may lie in the ancestry of the Gryphaeidae (see also Newell, 1960). As indicated above, the Pseudomonotidae may also have given rise to the family Spondylidae. The Plicatulidae, on the other hand, apparently represent a separate, possibly independent branch.

We may now summarize the fundamental characteristics possessed in common by the Paleozoic Pseudomonotidae and the post-Paleozoic Gryphaeidae:

1. The left valve commonly is more convex than the right.
2. The left valve in some cases overlaps the right, that is, the two valves may be discordant. The reverse asymmetry is unknown.
3. The outer ostracum of the left valve, in

most cases, is homogeneous (or foliate), not prismatic, whereas the outer ostracum of the right valve commonly shows patches of prismatic structure, at least in juvenile stages.

4. The outer ostracum of both valves in *Pseudomonotis* (*Trematiconcha*) *wandageensis*, new species, displays foliate structure similar to that of *Ostrea* and *Gryphaea* (fig. 2).

5. Many species of both groups are cemented to the substrate at some ontogenetic stage.

6. Some species of the Paleozoic Pseudomonotidae bear ornamentation very like the sculpture of *Crassostrea*, *Exogyra*, or *Gryphaea*.

7. Many species in both groups display a posteroventral marginal embayment and corresponding radial fold and sulcus corresponding to a palliobranchial fusion point and retraction of the mantle margin just below an exhalant orifice (fig. 1). This feature is lacking in other members of the Pterioidea.

DIFFERENCES

Cementation of bivalves to the substrate results, in most cases, in marked variability of shape and ornamentation. Much of this variability does not directly reflect the impressed details of the substrate but rather is caused by interference with growth at the mantle margin. Nevertheless, cemented bivalves of unrelated groups may display general convergence of form. "The ostrean form is due to the conditions of a direct cemented fixation acting upon a pelecypod shell. Given such conditions, and a closely similar form is the result in widely separated genera of the class" (Jackson, 1890, p. 322). Several superfamilies of bivalves (Ostreacea, Pectinacea, Chamacea, Unionacea) have at one time or another produced cemented, oyster-like shells, but we are concerned here with the oysters of the suborder Ostreina—such genera as *Ostrea*, *Lopha*, *Gryphaea*, and *Exogyra*.

The characters of the Ostreina that distinguish this suborder from cemented pectinaceans (except the filibranch Plicatulidae, which also lose the foot and byssus at metamorphosis) are: (1) byssal notch lacking at all growth stages; (2) foot and most pedal muscles lacking in post-veliger stages; and (3) cemented valve anatomic-ally the left valve.

MORPHOLOGY OF THE PSEUDOMONOTIDAE

MUSCULATURE

THE PRODISSOCOCH of the Pteriomorpha possesses two approximately equal adductor muscles, but the anterior adductor in all the pleuroconchs of this subclass atrophies early in growth and is missing in most adults of the Pteriina and Ostreina, which characteristically are monomyarians. Anthony (1905) and Yonge (1936, 1953) have summarized evolutionary consequences of the loss of an anterior adductor, which they attribute to byssal fixation.

The single posterior adductor muscle in the Pteriomorpha is inserted slightly behind the center of each valve. It is differentiated into an anterior or anterodorsal striated "quick" muscle and a posterior or posteroventral unstriated "catch" muscle (fig. 5). The former is employed in quick closure of the shell as a means of freeing the interior of sediment. In the Pectinidae and Limidae this part of the adductor is employed in swimming and escape movements. The catch muscle, on the other hand, contracts slowly but has the remarkable ability to remain contracted for days or weeks at a time.

Yonge (1936) has shown that the form and relative dimensions of the insertion areas of these two portions of the adductor vary taxonomically and probably are related to function. In general, the most active animals of the group, the swimmers, display a relatively large quick muscle which has two or three times the area, in cross section, of the catch muscle. In cemented forms such as *Spondylus* or *Plicatula* and the oysters, the catch muscle may be as large as or larger than the quick muscle (fig. 5). Galtsoff (1964, p. 42) has documented marked variability in the shape of adductor scars in *Crassostrea virginica*. Rounded shells tend to have broad muscle scars, whereas high, slender shells of the same species display correspondingly narrow scars.

Among the Paleozoic shells described in the present study, the details of the adductor muscle commonly are not visible, but there is at least a suggestion that the quick muscle was relatively large in right valves of some forms (*Pachypteria*) and relatively small in others (*Pseudomonotis*), with ratios, respectively, of about 3.5/1 and 0.5/1, but our material is not adequate for a firm conclusion to be drawn. The muscle scars gener-

ally are not clearly defined, and precise delineation and measurement are not possible. Consequently, we are not prepared to attribute any fundamental significance to these apparent differences.

Small, somewhat variable, anterodorsal muscle impressions occur in Paleozoic pseudomonotids. By analogy with modern species of *Pinctada* these are interpreted as pedal levators (Newell, "1937" [1938], fig. 1). They are shallow and only rarely visible in our specimens; consequently, our interpretations must be regarded as tentative.

Unusual and anomalous features of some pseudomonotids, as compared with living oysters, are the apparent differences in form and symmetry of the adductor muscle scar in each of the two valves (figs. 6 and 7).

The adductor scar of the left valve is longer and somewhat different in shape from that of the right (fig. 6). The posterodorsal extremity of this scar (r) extends farther toward the hinge than does that of the right valve. This difference recalls the situation in the Pectinidae in which a single pedal retractor occupies a position above the quick muscle of the left valve (Newell, "1937" [1938], fig. 1b). Much more work is needed, however, on pseudomonotid musculature as instructive specimens become available.

THE LIGAMENT

Shell features associated with the ligament in the Aviculopectinidae and Pseudomonotidae (Newell, "1937" [1938]) are closely similar to those of the living pearl clam *Pinctada* and to those of *Lima*. Presumably, the ligament of the extinct families was similar to that of the living forms. An obliquely triangular resilifer below the beak in each valve lies near the middle of a broad, flat cardinal area. In these forms, the symmetrically paired resilifers are shallow depressions.

The ligament area in oysters is similar, but differs somewhat in that the mid-portion of the resilifer of the right valve is elevated in a boss (fig. 8), instead of being concave. In adult living pteriids and oysters, e.g., *Pinctada* and *Crassostrea*, respectively, the axis of rotation in the closing motion of the valves varies in position

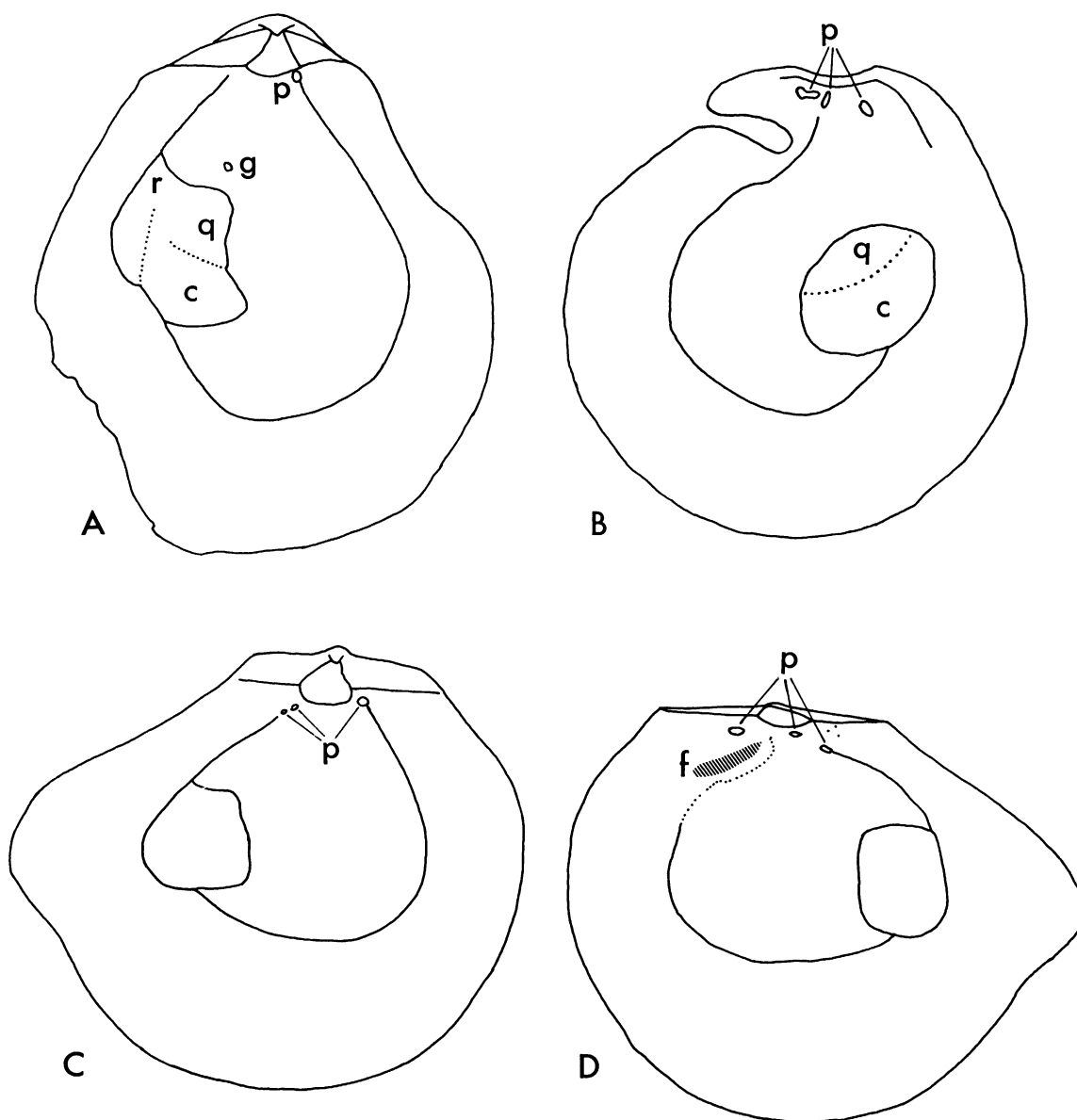


FIG. 6. Interpretative diagrams of musculature in *Pseudomonotis*. A, B. *Pseudomonotis sinuata* (Meek and Worthen), Pennsylvanian, Illinois, composite of several specimens. A. Left valve. B. Right valve. C, D. *Pseudomonotis (Trematiconcha) likharevi* Newell and Boyd, new species, Permian, western United States, composite of several specimens in the American Museum of Natural History. A, B, approximately $\times 2.5$; C, D, slightly less than $\times 1$. Abbreviations: c, catch muscle; f, byssal foramen; g, Quenstedt muscle; p, pedal levator muscles (incomplete in A); q, quick muscle; r, pedal retractor.

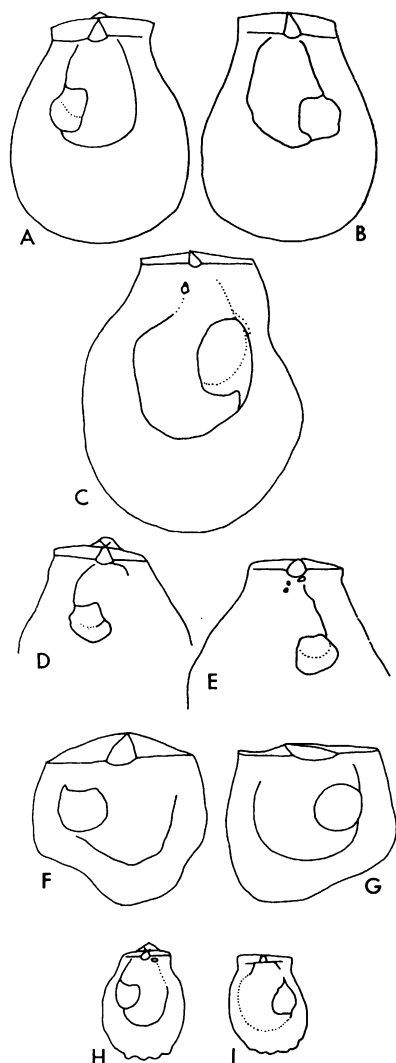


FIG. 7. Musculature, incomplete owing to poor preservation, in *Pegmaivalvula*, *Pachypteria*, *Prospondylus*, and *Paleowaagia*. A, B. *Pegmaivalvula gloveri* Newell and Boyd, new species, Permian, Texas. C. *Pachypteria nobilissima* (Koninck), Lower Carboniferous, Belgium, right valve. D, E. *Prospondylus liebeanus* Zimmermann, Permian, Germany. F, G. *Paleowaagia cooperi* Newell and Boyd, new species, Permian, Texas. H, I. *Pegmaivalvula delicata* Newell and Boyd, new species, Permian, Texas. A-G, approximately $\times 0.5$; H, I, approximately $\times 0.75$.

from about one-half to three-fourths of the height of the resilium below its apex.

During ontogeny, the shell material of the hinge becomes greatly thickened by internal

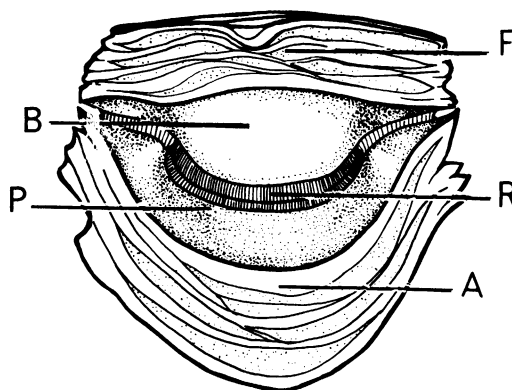


FIG. 8. Asymmetry of the oyster resiliifer, as illustrated by present-day *Crassostrea virginica* (Gmelin), horizontal section, view below beaks, enlarged (after Galtsoff, 1964), left valve below. In all other members of the Pterioida, the resiliifers of both valves are concave, as in the left valves of oysters.

Abbreviations: A, attached, or left, valve; B, resiliifer boss, right valve; F, free, or right, valve; P, resiliifer pit of left valve; R, compressional, fibrous ligament, or resilium.

accretion, the axis of rotation at the shell inner margin migrates ventrally as the hinge margin is extended, and external, divergent, flat ligament areas (interareas, or cardinal areas) are produced by the growth trace of the hinge margin. The broken and worn ligament adheres to the outward-diverging surfaces of this ligament area. Some pectinaceans, e.g., the Aviculopectinidae, Pseudomonotidae, Spondylidae, and *Hinnites*, also show this growth phenomenon in which the hinge axis is separated from the dorsal margin of the shell by divergent, flat ligament areas.

Both Trueman (1951) and Galtsoff (1964) have regarded this kind of ligament as "internal," but we prefer to limit that designation to resilia that lie entirely below the hinge axis, as in the Pectinidae, Nuculidae, and Crassatellidae. Such forms do not display flattened external ligament areas in normal adult shells. In these, ordinarily, there is little or no tendency for the hinge axis to migrate downward from the dorsal margin of the shell during growth.

The right, or lower, interarea commonly intersects the plane of the valves at a high angle, more or less 90 degrees, a condition termed "catacline" in brachiopods.

The cardinal area of left (dorsal) valves is

most frequently about parallel to the plane of commissure. This is the "orthocline" condition of dorsal valves of brachiopods (e.g., see Williams and Rowell, 1965, p. H60).

These differences of inclination in ligament

area of the two valves in pseudomonotids clearly are determined by unequal convexity of the corresponding valves, and the interareas show something of the marked variability of the shell form.

FOSSILIZATION OF THE STUDY SPECIMENS

AN UNDERSTANDING of the significance of various modes of preservation of fossil bivalves is essential for the correct interpretation of their morphology. Consequently, we have given some attention to details of fossilization of our specimens (fig. 9).

A few of our specimens from New Mexico are preserved as natural molds in dolomitic limestone, and the selectivity of leaching of fossil shells from carbonate matrix constitutes a major problem which we are not prepared to discuss here. Most of the specimens on which this study is based are siliceous pseudomorphs from western Texas and Wyoming obtained by the dissolving of selected blocks of limestone in hydrochloric acid. Complete specimens obtained in this way are very rare. Because of the extraordinary fragility of the silicified pseudomonotids, a majority of specimens disintegrate during laboratory leaching. Breakage before burial probably was also a contributory factor in this damage.

The diagenetic processes by which fossil invertebrates are preserved as molds or replaced by silica are not well understood. Possibly the original organic content of the calcareous skeletons provided conditions essential for changes leading to substitution of quartz for calcareous shells. Many of our silicified shells may be considered as casts formed by silica infilling of natural molds. In other cases, the modifications evidently were complex, involving multiple stages of leaching. The genetic significance of these variations is not presently understood. In all examples, the original microscopic fabric of the molluscan shells has been completely destroyed. Only the topography has been more or less well preserved.

The silicified shells display several modes of preservation, some of which are rather characteristic of different localities, which suggests local variations in conditions of fossilization and diagenesis.

In one kind of fossilization of pseudomonotids found in the Glass Mountains Permian, a thin outer-shell layer is preserved in fine detail as silica, whereas the inner layer, bearing muscle attachment sites and hinge structures, has been selectively leached away. Comparison of these

shells with better-known related bivalve groups (the Aviculopectinidae and Pteriidae) indicates that the two layers, before silicification, were the outer ostracum, of calcite, and the inner ostracum, of metastable aragonite. Calcareous shells of fossil bivalves in which the inner aragonitic ostracum has been removed by differential leaching are well known (Newell, "1937" [1938], 1942). Our silicified examples have evidently been subjected to an additional diagenetic stage in which fine-grained quartz was in some manner substituted for the calcite outer ostracum.

Commonly, the outer ostracum in these shells is preserved so faithfully as to reproduce original details of surface sculpture and topography marred only by scattered beekite rosettes. The inner surface of the outer ostracum, originally covered by the inner shell deposits, also displays growth lines and subdued reflection of outer ornamentation. But why is a siliceous equivalent of the inner ostracum lacking in these specimens? We can only suppose that the aragonitic inner ostracum was dissolved, and that the space originally occupied by it was closed by compaction before the onset of silicification.

Although the loss of the internal layer is an obstacle to studies of several shell features, it presents at least one advantage. Many cemented right valves of *Prospondylus* are still attached to the original substrate—a brachiopod, another bivalve, or a bryozoan colony. The attachment object normally would conceal the earliest growth stages of the cemented valve. Where the inner layer of this valve has been selectively removed by dissolution, the configuration of the nepionic shell is shown in the early growth lines of the inner surface of the outer ostracum (fig. 9F).

Silicified, small, encrusting epizoans—bryozoans, spirorbids, spiny brachiopods—frequently are in contact with the inner surface of the outer ostracum, an anomalous relationship that requires close attention (fig. 9I, J). The more common relationship, however, shows that missing shell material once intervened between epizoan and outer ostracum (fig. 9E). Intermediate cases are represented by several valves in which juvenile brachiopods are attached by

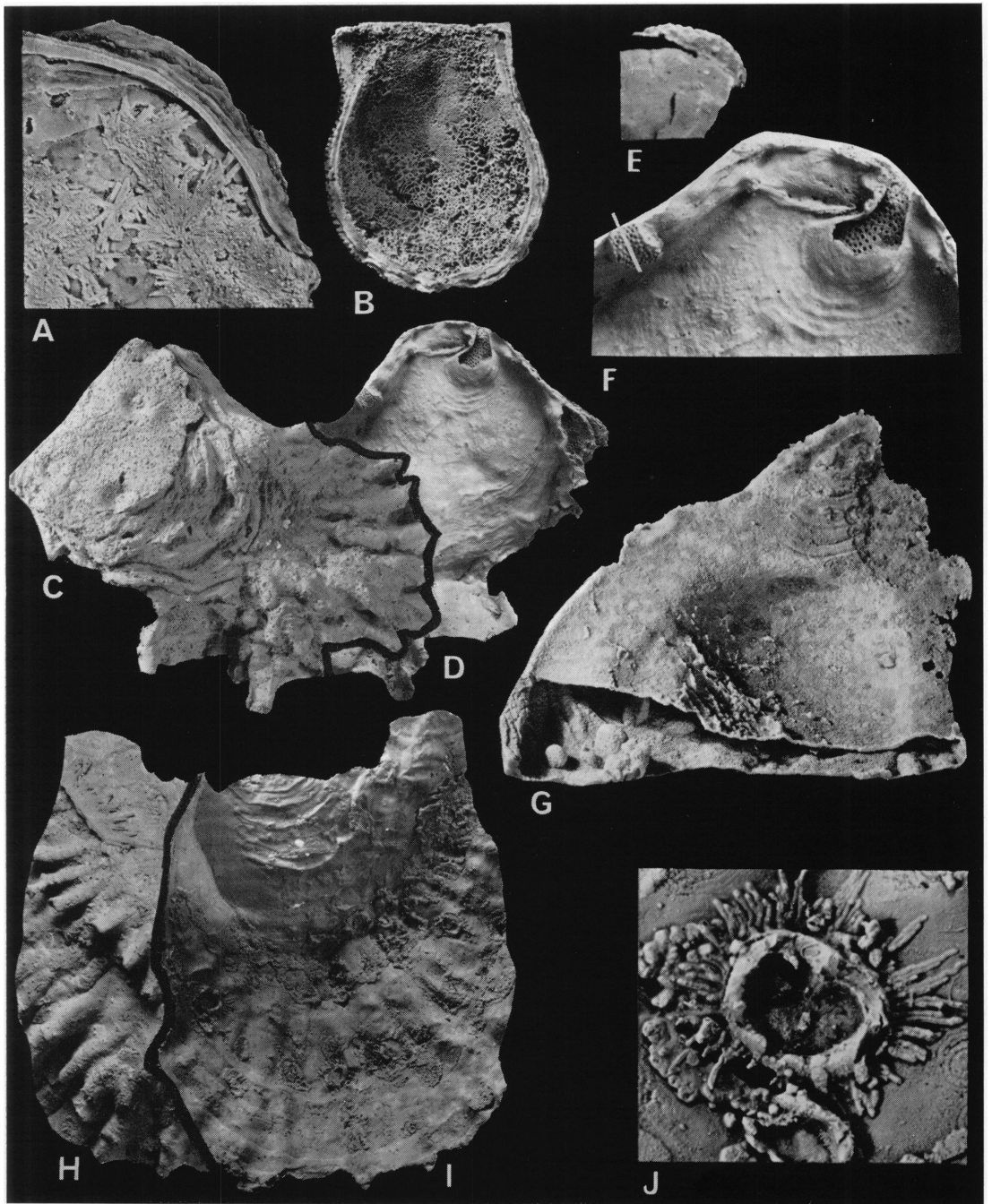


FIG. 9. A, C-F, H-J. *Prospondylus acinetus* Newell and Boyd, new species. A. Inner ostracum imperfectly replaced by quartz blades, A.M.N.H. No. 28915. C, D. Outer and inner surfaces of siliceous replica of outer ostracum, inner ostracum lacking, U.S.N.M. No. 154981. E, F. Siliceous pseudomorph of bryozoan colony at upper left of F encrusting outer ostracum at valve's edge, overhanging gap left by missing inner ostracum, U.S.N.M. No. 154981. H, I. Outer and inner surfaces of siliceous replica of outer ostracum, right valve; minute brachiopods pressed against inner surface of outer ostracum after inner ostracum was dissolved in early diagenesis. J. Brachiopod, enlargement of I. B. *Pegmavalvula delicata* Newell and Boyd, new species. Inner ostracum represented by alveolar quartz, right valve, A.M.N.H. No. 28916. G. *Paleowaagia cooperi* Newell and Boyd, new species. Thin-walled, siliceous capsule cast; interior prominences are replicas of polychaete borings, U.S.N.M. No. 154979. A, G, $\times 1.5$; B, $\times 3$; C, D, H, I, $\times 1$; E, $\times 4$; F, $\times 2$; J, $\times 4$.

spines to a partly leached inner layer. In these cases, the attachment sites of spines of individual brachiopods overlap more than one shell lamina.

Some of the cases described above might encourage the view that the aragonitic inner ostracum was either partially or completely removed by selective dissolution before the shells were colonized by epizoans. We know of no modern example of leaching of aragonitic shells on a carbonate sea floor, although Reymont (1958, p. 134) recorded etching in modern *Nautilus* shells after several days in aerated salt water. Investigators of the Cretaceous Chalk of southern England have cited circumstantial evidence that aragonitic shells were dissolved on the sea floor while calcitic ones were unaffected (Jefferies, 1962, p. 614; Hudson, 1967, p. 477). Gill and Cobban (1966, p. 42) also found evidence of pre-burial etching of ammonite shells in the Cretaceous Pierre Shale of Wyoming, but this was a non-carbonate depositional environment.

An encrusting calcitic organism originally cemented to the surface of the inner layer could be pressed against the outer ostracum by compaction after selective removal of the inner ostracum by dissolution. Wherever the inner ostracum is unusually thin, as beneath an external furrow, the inferred compaction would be minimal. Seilacher (1963, p. 611) has interpreted calcitic epizoans on ammonite steinkerns as reflecting dissolution of the aragonitic ammonite shell during diagenesis.

In summary, we have much evidence of post-burial corrosion of the inner ostracum and compaction of inner matrix against the outer shell layer of Permian pseudomonotids, and it appears to us probable that compaction usually has prevented the development of open spaces during dissolution of the aragonitic layer. Yet the thin outer ostracum of these silicified shells commonly does not display deformation clearly attributable to compaction, and a gap between epizoan and inner surface of the outer ostracum is present in many cases. This indication that compaction has been negligible directed our attention to the few

specimens that might be cited in support of a hypothesis for pre-burial selective leaching of aragonitic shells on the sea floor. In such specimens epizoans apparently are cemented directly to the inner surface of the outer ostracum. Are appearances here deceiving?

Although the pseudomonotid shells at some localities in the Glass Mountains characteristically lack a replica or mold of an inner ostracum, such a replica or mold is morphologically intact in shells from other localities. The inner surface of the valves is well represented in siliceous pseudomorphs of whole valves (fig. 20). In the latter case, it is convenient and accurate to regard each silicified valve as a natural cast of the calcareous original. Microcrystalline or cryptocrystalline quartz underlies all shell surfaces, with minute crystal pyramids directed inward into space formerly occupied by calcium carbonate. Some valves are preserved, thus, as thin-walled, hollow, siliceous capsules. In others, the molds tend to be filled with inwardly directed, drusy quartz crystals that become coarser toward the dividing plane that separates the inner and outer halves of the geode. In this latter kind of preservation the valve cannot be differentiated into an inner and outer ostracum.

In still other types of preservation, the inner and outer ostracum are clearly distinguishable by unlike secondary fabrics. The topography of the outer ostracum is commonly well preserved in fine-grained quartz, but original shell fabrics are not recognizable. In one type of preservation, the inner ostracum is represented by extensive patches of alveolar quartz (fig. 9B). In another type, the original topography of the valve interior is preserved by a continuous layer of blades, each with its two longest dimensions in the original surface (fig. 9A). Beneath this surface layer, the blades are commonly edgewise to the outer surface and loosely packed, resulting in a spongy interior. In cases in which the inner surface is not preserved over the entire valve, its present margin is characterized by fans of radiating blades.

SYSTEMATIC DESCRIPTIONS

SUPERFAMILY PECTINACEA RAFINESQUE, 1815

FAMILY PSEUDOMONOTIDAE NEWELL, "1937" [1938]

From Pseudomonotinae NEWELL, "1937" [1938].

DIAGNOSIS: Weakly to strongly intercalate-costate, left valve characteristically appreciably more convex than the right; byssate in juveniles, suborbicular to irregular; monomyorian, edentulous, with short hinge line, bluntly rounded or obtuse auricles, divergent flat cardinal areas, and triangular median resilifers; byssal notch of right valve distally constricted, with an internally thickened rim, sealed from within by secondary deposits in adults of cemented species; juvenile shell pectinoid, varying in form from retrocrescent to procrescent¹ generally set off from the mature shell by growth changes in convexity and ornamentation; shell microstructure in *Pseudomonotis*, *sensu stricto*, as in Aviculopectinidae, inner ostracum crossed-lamellar; right outer ostracum coarsely prismatic; left outer ostracum finely prismatic or homogeneous. In subgenus *P.* (*Trematiconcha*), outer ostracum foliate and inner ostracum concentric crossed-lamellar, in both valves.

DISTRIBUTION: Lower Carboniferous (Viséan), Belgium, ?Mauritania; Upper Carboniferous, Soviet Union, United States; Permian, Lower Triassic, cosmopolitan.

DISCUSSION: There is considerable variation in the nature of the pallial line in shells referred to this family. In many, no trace of a pallial line is observable, a situation commonly modified by faint cross striations reflecting radial strands of the pallial muscles. In many shells, the line becomes discontinuous at the two dorsal terminations, being represented there by a few pits of the pallial muscles somewhat smaller than the impressions of the pedal muscles.

Several mainly Mesozoic bivalve genera not reviewed herein are similar in shell form and

microstructure to the Paleozoic Pseudomonotidae and the Aviculopectinidae. They include *Meleagrinella* Whitfield, 1885; *Leptochondria* Bittner, 1891; *Mccoyella* Etheridge, 1892; *Eopecten* Douvillé, 1897; *Claraia* Bittner, 1891; and *Arctotis* Boydlevsky, 1960. These have been variously referred to the Aviculopectinidae, the Pseudomonotidae, the Pectinidae, the Terquemidae, and the Oxytomidae. As far as we can ascertain, none of these genera is markedly spiny and none displays any tendency for obsolescence of the byssus or cementation to the substrate.

The fossil *Claraia* of the Lower Triassic and *Leptochondria*, however, do share a number of morphological characters in common with the type species of *Pseudomonotis*. In *Claraia*, these characters include a tendency for the right valve to display concentric corrugations, the byssal notch to be distally constricted, and the proximal part of the notch internally to bear a thickened, spoutlike rim (fig. 10). The species of *Claraia* characteristically are less convex, more circular in profile, and lack the distinctive posterior lobe of *Pseudomonotis speluncaria*. Unfortunately, internal features and the shell microfabric of *Claraia* are unknown.

Leptochondria is even less well understood. In form and ornamentation, it resembles juveniles of *Pseudomonotis speluncaria*, the type species of *Pseudomonotis*, but hinge details, internal features, and shell microstructure are unknown. It may represent a paedomorphic development stemming from Permian *Pseudomonotis*. Unlike *Pseudomonotis*, however, *Leptochondria* and *Claraia* possess comparatively thin, delicate shells.

GENUS PSEUDOMONOTIS BEYRICH, 1862

TYPE SPECIES: *Gryphites speluncaria* Schlotheim, 1816, Zechstein, Permian, Germany, subsequently designated by Stoliczka, 1871.

SUBJECTIVE SYNONYMY: ?*Aviculomonotis* Grabau, 1931, Permian, Mongolia (unrecognizable). = *Eumicrotus* Meek, 1864. Type species: *Monotis hawni* Meek and Hayden, 1858, Lower Permian (Big Blue Series), Kansas.

DIAGNOSIS: Pectinoid shells with vertical growth axis, deeply inflated, almost hemispherical left valve, and concave or flat right valve; ornamentation obsolescent or composed

¹ In the former condition the most rapid growth-rate vectors are posteroventral in direction, the primitive condition in the Pterioidea. In some advanced forms, the principal growth axis changes direction during ontogeny, first becoming infracrescent, more or less equilateral, then anteroventral in direction, or procrescent.

of simple, scaly costae or costellae, usually somewhat finer on right valve, increasing in both valves by intercalation; cardinal areas subequal; byssal slit externally narrow, or limited to a foramen near the beak; left valves of adults commonly with broad, shallow, posterior sulcus and corresponding marginal sinus forming lower border of exhalant quadrant; posterior auricle commonly obtuse.

DISTRIBUTION: Pennsylvanian-Permian, United States, Soviet Union; Lower Permian, Western Australia; Upper Permian (Zechstein), western Europe, England, Greenland.

DISCUSSION: Two Scythian species, *Halobia occidentalis* Whiteaves, and *Monotis boreas* Oeberg, referred by Tozer (1961), to *Pseudomonotis* superficially recall *Leptochondria* Bittner, or juvenile *P. speluncaria*.

Logan (1967) has shown that the left valve of *P. speluncaria* passes through a nearly equilateral juvenile stage. At this growth stage, shells of *P. speluncaria* are very similar in form and ornamentation to adult *Leptochondria*. The right valve of *Leptochondria* is not adequately known; consequently, we are uncertain about the family affiliations of this genus.

The genus *Eumicrotus* Meek, 1864, as illustrated by the holotype of the type species, *hawni* Meek and Hayden, 1858, possessed an open byssal slit throughout life (Newell, "1937" [1938], pl. 17, figs. 11a, b). In this respect, and in other critical characters, it is not significantly different from *Pseudomonotis*, *sensu stricto*. Specimens thought by Newell to be cemented, and referred by him to *P. hawni*, are equivocal and

should be reinvestigated (Newell, "1937" [1938], e.g., pl. 18, figs. 11a, b).

**PSEUDOMONOTIS SUBGENUS
(PSEUDOMONOTIS)
BEYRICH, 1862**

Figures 1A, B, 2A-E, 6A, B, 11-13

DIAGNOSIS: Byssal notch entire throughout ontogeny, proximally enlarged; two or three pedal muscle insertions on both valves near proximal extremity of byssal slit in front of umbonal cavity.

DISTRIBUTION: Pennsylvanian, Lower Permian (Wolfcampian), United States; Upper Carboniferous-Permian, Soviet Union; Upper Permian (Zechstein), Germany, England, Greenland. Characteristic shells of this subgenus have not yet been recognized above the Wolfcampian in North America.

DISCUSSION: The species of *Pseudomonotis*, *sensu stricto*, are characterized by rather subdued ornamentation, and they are relatively free from spines (figs. 11, 12). The subgenus *Pseudomonotis* is represented in argillaceous and calcareous shales and dolomitic calcarenites. It is also well represented in the so-called Zechstein reefs.

***Pseudomonotis speluncaria* (Schlotheim), 1816**

Figures 1A, B, 12, 13

DIAGNOSIS: Left valve strongly inflated, with posterior sulcus and lobe well developed in specimens more than about 20 mm. high; height and length of left valve about equal; right valve flat; umbo of left valve beaked, opisthogyrate; shell prosocline in earliest ontogeny, passing through infracrescent stage in juveniles to slightly retrocrescent, secondarily, at maturity; hinge margin short, with bluntly rounded posterior ear; sculpture variable (fig. 13), weakly to strongly costate, with ribs of one to three intercalating ranks, becoming nearly smooth in a majority of large adults; concentric lamellae commonly with vaulted frills at intersection with costae; right valve subcircular, with concentric rugae and more or less obsolescent costae; byssal slit narrow, internally teardrop-shaped, constricted distally, open throughout ontogeny; resilifer inclined obliquely backward, correlated with opisthogyre beaks.

DISTRIBUTION: This species is widely distributed in Upper Permian (Zechstein, Kazanian) calcareous rocks of northwestern Europe, Eng-

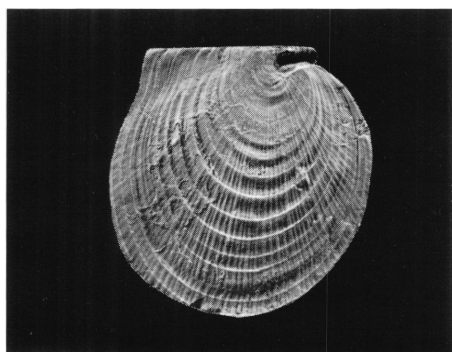


FIG. 10. *Claraia clarai* (Emmrich), G.S.C. No. 14196, right valve, Lower Triassic, Spray River Group, Brazeau River, Alberta.

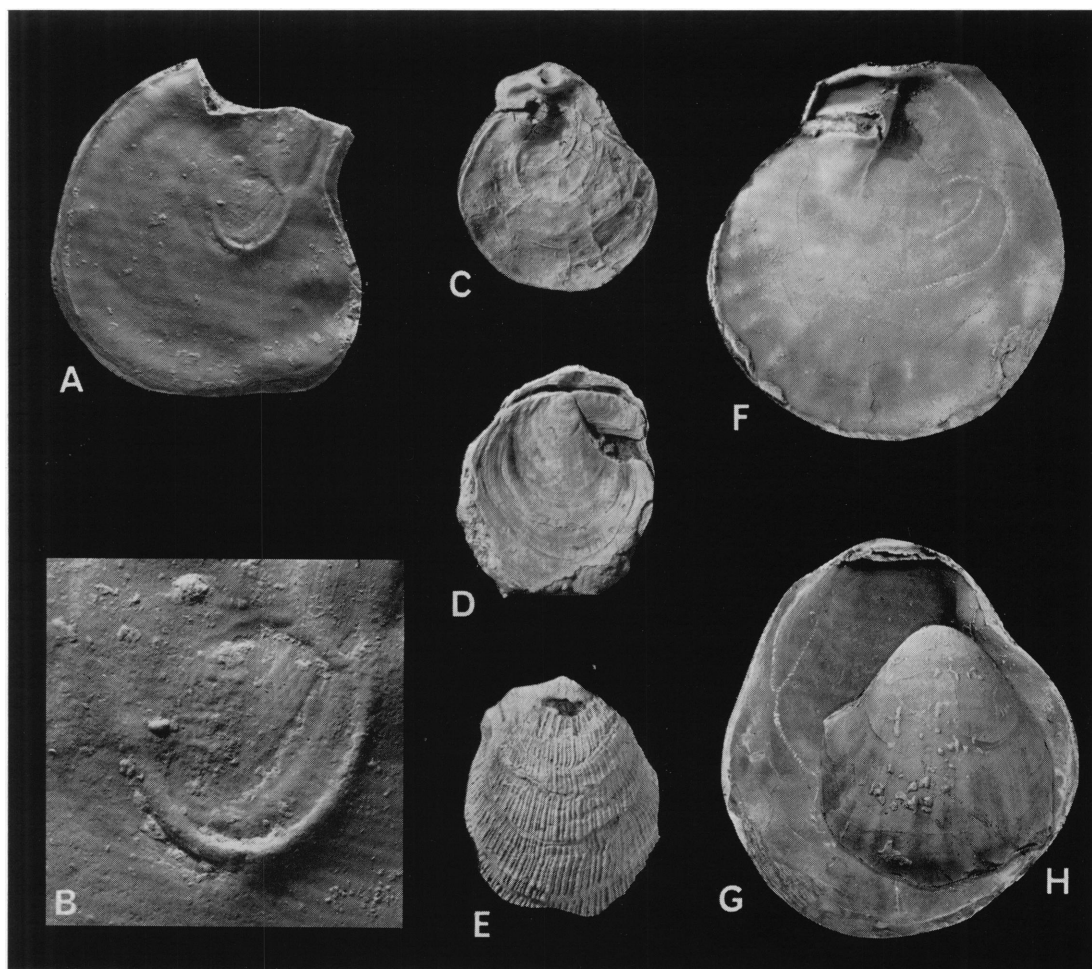


FIG. 11. Pennsylvanian *Pseudomonotis*. A-D. *Pseudomonotis equestriata* Beede. A, B. Westerville oölite, U.K. No. 40165. B. Details of adductor mark. C. Interior of right valve, U.S.N.M. No. 154987, Lower Graham shale, Texas; U.S.N.M. 515g. D, E. Right and left valves, A.M.N.H. No. 28917, Finis shale, Texas; A.M.N.H. 13. F-H. *Pseudomonotis sinuata* (Meek and Worthen) (= *P. beedei* Newell, "1937" [1938]). F, G. Latex casts of holotype, I.S.M. No. 10914, right and left valves, respectively; I.S.M. $\times 722$. H. Paratype, I.G.S. No. 2971. A, C, H, $\times 1$; B, D-G, $\times 2$.

land, and Greenland. It has been reported dubiously from the Tethyan regions.

DISCUSSION: An extensive and competent review of this species was made by Logan (1967) who has substantially advanced our knowledge of *P. speluncaria*. He showed (fig. 13) that variation within this species is mainly in details of ornamentation of the left valve. The right valve commonly displays only traces of costae, together with low rugae and growth lines. The largest specimen cited by Logan was 38 mm. high.

Ontogenetic changes in form and ornamentation of the shell do not indicate early metamorphosis, as in some species of the family, and there is no cicatrix around the umbo of the right valve. These facts, in context with the open slit, suggest that *P. speluncaria* retained a functional byssus throughout life, a conclusion also reached by Nicol (1944). On the other hand, the uneven contours of the exterior of the right valve suggest adherence to the substrate by means of a heavy byssus. Several species of *Pseudomonotis* display an

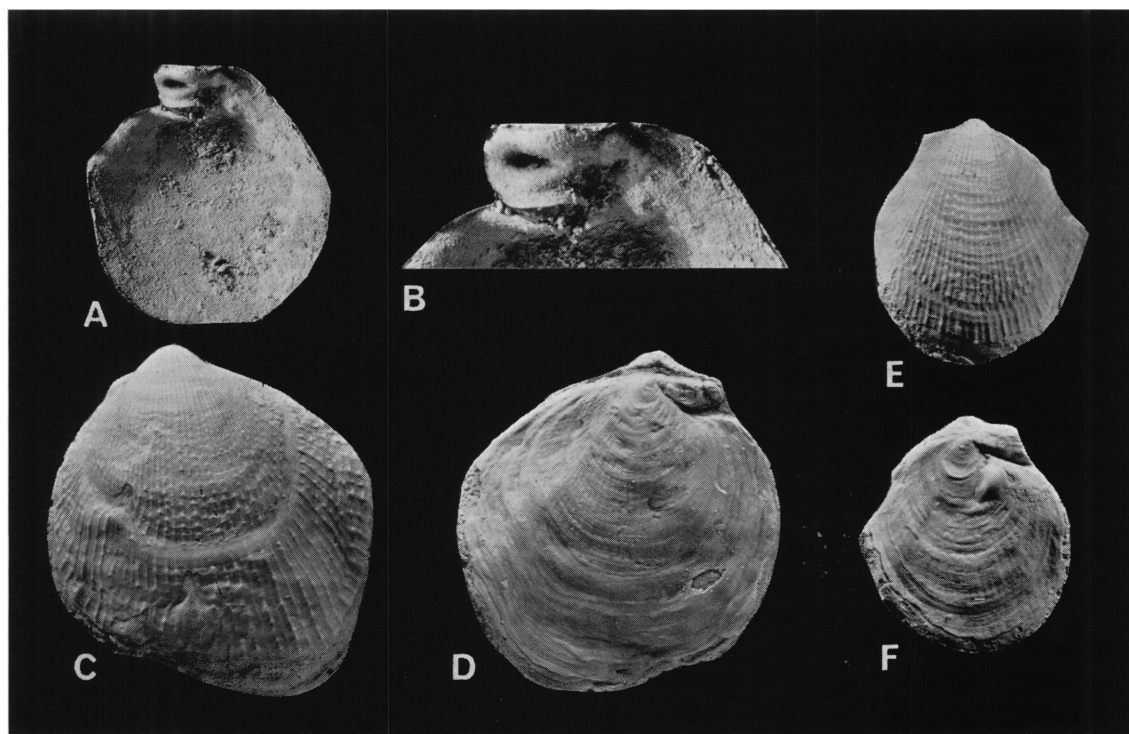


FIG. 12. *Pseudomonotis speluncaria* (Schlotheim), type species of *Pseudomonotis*, Middle Zechstein reef, Permian Pösneck, East Germany, in the Geologisch-Palaeontologisches Institut der Georg-August Universität, Göttingen A, B. Latex cast, interior of right valve. C, D. Left and right side views of a bivalved specimen. E, F. Left and right side views of smaller bivalved specimen. A, $\times 1$; B-D, $\times 2$; E, F, $\times 3$.

incipient circular foramen at the proximal extremity of the byssal slit (fig. 11C), a feature doubtless homologous with the byssal aperture in the subgenus *Trematiconcha*. Such an incipient foramen is not, however, displayed by *Pseudomonotis speluncaria*.

As pointed out on a previous page, left valves of juveniles of this species (fig. 13G) are similar to adults of *Leptochondria* Bittner, 1891, and it is possible that the latter is a neotenous descendant of *Pseudomonotis*. We are unable, however, to ascertain the nature of the byssal slit in *Leptochondria*, a genus that has been referred to the Aviculopectinidae and the Pectinidae. The phylogenetic placement of *Leptochondria* is, for the present, uncertain.

Pseudomonotis speluncaria resembles the American Pennsylvanian *P. equistriata* Beede rather closely in form and ornamentation (Newell, "1937" [1938]). The latter (fig. 11A-E), however, has slightly finer and more numerous ribs, and the anterior auricle of the left valve is better

developed than in *P. speluncaria*. Generally, the posterior sulcus and lobe, so characteristic of adults of *P. speluncaria*, are lacking in *P. equistriata*.

PSEUDOMONOTIS (TREMATICONCHA) NEWELL AND BOYD, NEW SUBGENUS

Figures 2F-H, 6C, D, 14, 15, 16

TYPE SPECIES: *Pseudomonotis* (*Trematiconcha*) *wandageensis* Newell and Boyd, new species.

DIAGNOSIS: Shells robust at maturity, commonly higher than 10 cm., thick-shelled; cardinal areas subequal; ribs obsolescent, or weak to strong, fewer in left than in right valve, scaly or spinose; byssal opening closed at anterior margin of right valve at intermediate growth stage, modified thus as a circular or elongate foramen near right beak; foramen slitlike and externally rugose, rounded and smooth internally and rimmed by a prominent collar.

DISTRIBUTION: Permian, widespread. Represented in America by a single variable species

which is characteristic of highest Leonardian equivalents in Texas (Road Canyon), New Mexico (San Andres), Arizona, (Kaibab, Gamma Member), and Wyoming (Park City, Grandeur Member). Fragmentary specimens referable with some confidence to this subgenus, but specifically uncertain, were recognized at lower and higher Permian levels in southwestern United States (Hueco, Colina, Concha, Cathedral Mountain, Cherry Canyon, and beds between limestones 3 and 4 of the Word Formation). In Greenland, the subgenus is represented by *Pseudomonotis sparsicostata* Frebold, in white blocks of the Cape Stosch Formation with a Zechstein fauna (Newell, 1955). It also occurs in Kazanian rocks of the Lena Delta, Soviet Union, as "*Prospondylus*" *noinskiyi* Likharev. It was in this species that Boris Likharev (1931) first described the byssal foramen on which we are now basing the new subgenus. *Trematiconcha* occurs in Western Australia, in the Byro Group,

of late Artinskian age, where it is represented by the type species of the subgenus *P.* (*Trematiconcha*) described below.

Large shells of *Trematiconcha* commonly contain polychaete burrows similar to those of present-day *Polydora* (fig. 15).

Pseudomonotis (Trematiconcha) wandageensis

Newell and Boyd, new species

Figures 2F-H, 14A-C

DIAGNOSIS: Large, thick-shelled, more or less equilateral, with protruding left umbo, conspicuous exhalant lobe, and small, rounded-quadrate posterior auricle; left valve externally deeply convex, with relatively smooth umbo and 20 to 30 coarse, squamose costae over mature three-quarters of shell; right valve more rugose, irregularly concave, marked over juvenile shell by three or more ranks of fine costellae; markedly prosogyre in early growth, with prorescent

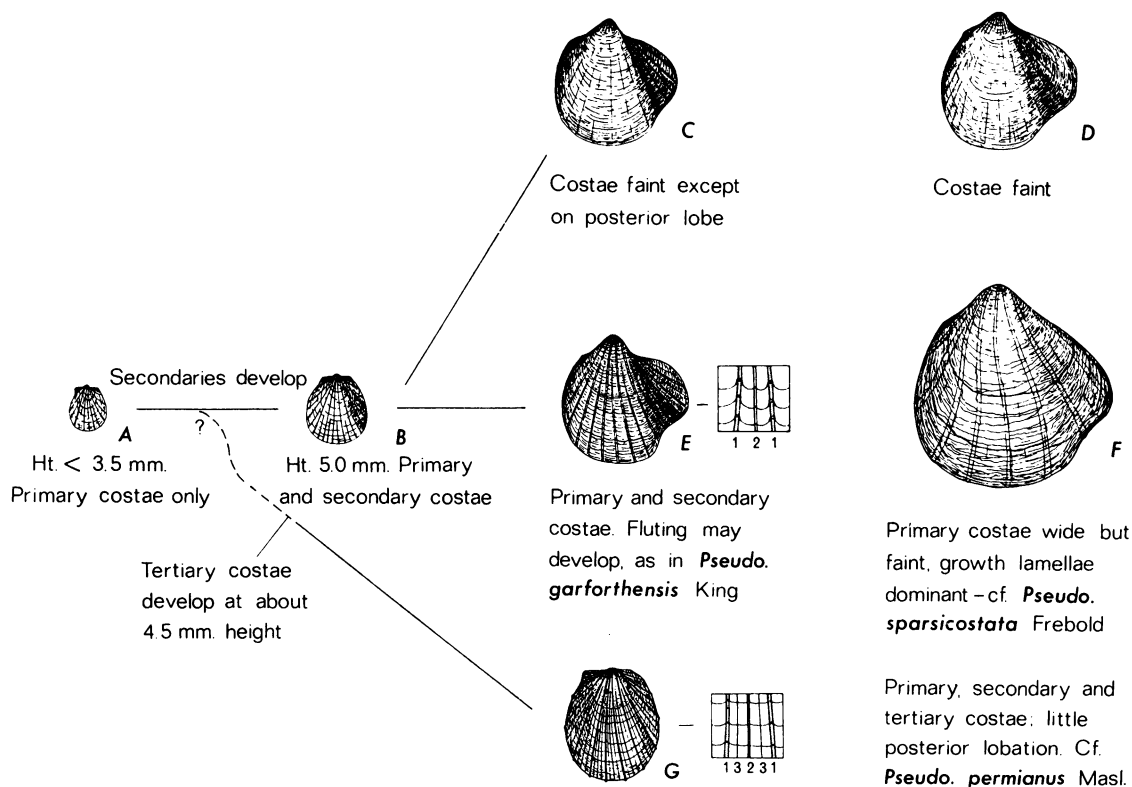


FIG. 13. Characteristic phenotypes in an English population of the Permian *Pseudomonotis speluncaria* (Schlotheim). (From Logan, 1967).



FIG. 14. A-C. *Pseudomonotis* (*Trematiconcha*) *wandageensis* Newell and Boyd, new species. U.W.A. No. 27123, type species of *Trematiconcha*, new subgenus, Lower Permian, Wandagee Formation, Minilya River, Carnarvon Basin, Western Australia. D. *Pseudomonotis* (*Trematiconcha*) *sparsicostata* (Frebold), M.M.C.U. No. 9680, Stosch Formation ("white blocks"), Permian, east Greenland. A, C, $\times 1$; B, $\times 2$; D, $\times 1.5$.

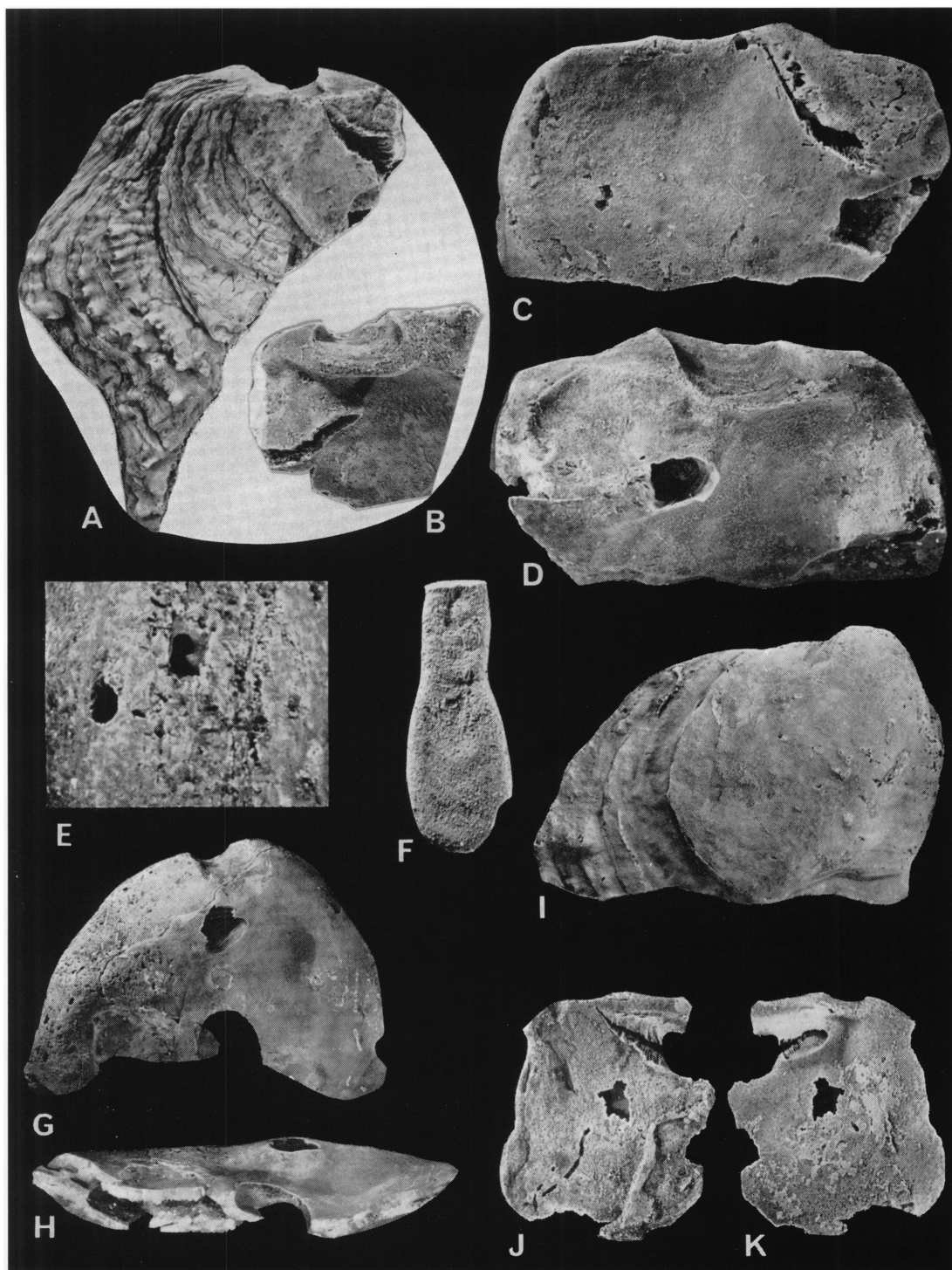


FIG. 15. *Pseudomonotis* (*Trematiconcha*) *likharevi* Newell and Boyd, new species, silicified examples, Park City (Grandeur) Formation, Lower Permian, Wind River Mountains, Wyoming; A.M.N.H. 2010. A, B. Young right valve, A.M.N.H. No. 28920, with distal part of auricle barely in contact with body of shell. C, D. Worn fragment of right valve, A.M.N.H. No. 28921, showing external slit (C) communicating with internal byssal foramen (D). E. Polychaete borings, enlargement of lower left-hand area of G. F. Latex cast of boring. G, H. Worn fragment of thick shell, A.M.N.H. No. 28922, showing internal byssal foramen (above) and large polychaete boring (below). I. Fragment of large left valve, A.M.N.H. No. 28924. J, K. Juvenile, A.M.N.H. No. 28925. A–D, J, K, $\times 1$; E, $\times 3$; F, $\times 6$; G–I, $\times 0.5$.

acceleration of anterior margin followed at maturity by more ventral, infracrescent, or slightly backward, retrocrescent, growth; resiliifers approximately bilaterally symmetrical. Measurements of left valve of the holotype: height, 10.3 cm.; length, 8.3 cm.; dorsal margin, 4.2 cm.

DISTRIBUTION: Wandagee Formation, Byro Group (late Artinskian), Western Australia.

DISCUSSION: From the American *P. (Trematiconcha) likharevi*, new species, the Australian species differs in its relatively short hinge margin, subquadrate auricles, and more upright, less orbicular form. It is more similar to *P. Trematiconcha sparsicostata* (Frebold) from Greenland (fig. 14D). From that species, *wandageensis*

differs in its larger size, subquadrate auricles, and delicate costellae of the right valve.

Pseudomonotis (Trematiconcha) likharevi

Newell and Boyd, new species

Figures 6C, D, 15, 16

SYNONYMY: ?*Pseudomonotis laevis* Girty, 1909 (unrecognizable), Leonardian, New Mexico (Newell, "1937" [1938]).

DIAGNOSIS: Shell large, orbicular to bluntly acuminate, left umbo subdued or prominent, surfaces marked by irregular growth rugae and, over mature areas, a few coarse primary costae bearing scales or subcylindrical spines; posterior extremity extended in well-developed posterior lobe.

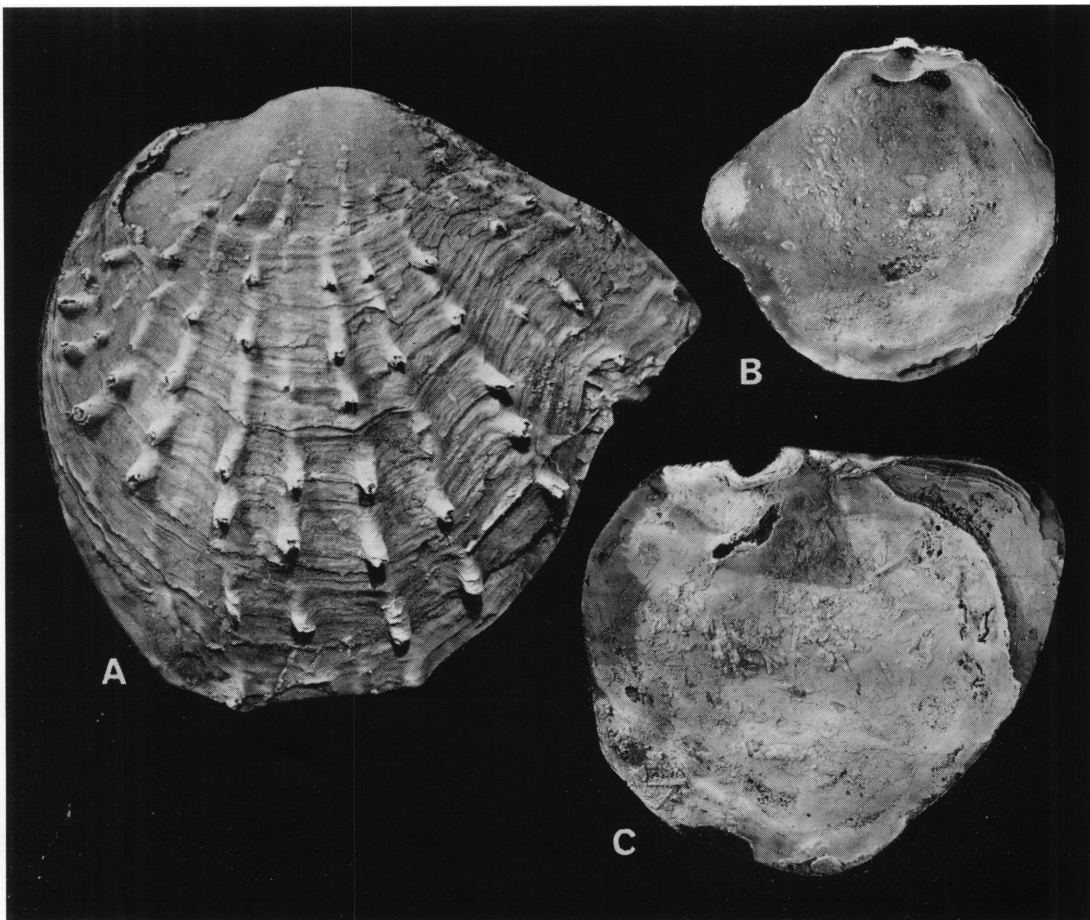


FIG. 16. *Pseudomonotis (Trematiconcha) likharevi* Newell and Boyd, new species, San Andres Limestone, near Artesia, New Mexico; A.M.N.H. 2079. A. Latex cast of holotype, A.M.N.H. No. 28938, exterior of left valve. B. Latex cast of a paratype, A.M.N.H. No. 28939, interior of left valve. C. Latex cast of a paratype, A.M.N.H. No. 28940, interior of right valve, showing byssal foramen. A, $\times 1$; B, C, $\times 0.6$.

DISTRIBUTION: Rare in the San Andres Formation (A.M.N.H. 2079), New Mexico; Park City (Grandeur) Formation (A.M.N.H. 2010), Wyoming. It is also tentatively identified in fragmentary material from the high Word Formation (between limestones 3 and 4, U.S.N.M. 706b), Texas; Cherry Canyon (Lower Getaway) Formation (A.M.N.H. 512), Texas; Road Canyon Formation (U.S.N.M. 703d), Texas; Kaibab (Gamma) Limestone (A.M.N.H. 1068), Arizona; Cathedral Mountain Formation (U.S.N.M. 702), Texas; Bone Spring Formation (A.M.N.H. 46), Texas; Hueco Limestone (U.S.N.M. 728d), Texas; Colina Limestone (A.M.N.H. 1064), Arizona; Concha Formation (A.M.N.H. 1065), Arizona. These occurrences suggest a cumulative range of Wolfcampian-Middle Guadalupian, inclusive.

DISCUSSION: Shells of this species attain the largest dimensions of any pseudomonotids known to us and must be included among the largest Paleozoic bivalves. We have observed individuals, which are thought to represent this species, nearly 15 cm. high, from the Kaibab Limestone of the Grand Canyon region. A nearly complete right valve from the San Andres Formation measures 10.7 cm. long and 1.7 cm. thick below the foramen.

The right umbonal region is commonly irregular and flat to slightly concave. Although this shape suggests conformity to the substrate, we have not encountered recognizable xenomorphic impressions of attachment hosts, and none of the right valves is now adherent to foreign objects. It is concluded, therefore, that the shells were not fixed in a single position.

Small and medium-sized right valves display a prominent anterior auricle, very like that of *Pseudomonotis*, *sensu stricto*, and the posterior margin of the shell meets the hinge line at a slightly obtuse angle. Large right valves do not display subauricular marginal re-entrants, so that the angle between the anterior margin and the hinge line is, in some cases, more strongly obtuse than the comparable posterior angle, which is also the case with some large left valves. Left valves lack distinct auricles, although lateral slopes flatten somewhat away from the umbo, and they possess a posteroventral sulcus.

A growth series of right valves from Wyoming shows conspicuous ontogenetic changes in the anterodorsal margin. The smallest instructive right valve has an anterior auricle 14 mm. long

and 5.5 mm. high at the distal end.

Except for the proximal part, both upper and lower surfaces of the byssal opening are characterized by a kind of ctenolium of very closely spaced laminae projecting straight into, and nearly meeting along, the axis of the notch.

Successively larger right valves show that increase in thickness of the shell was accompanied by ventral displacement of the byssal aperture. Thus, the top and bottom surfaces of the notch slope both inward and ventrally, and during growth the height of the free end of the anterior auricle increases. As a result, the external trace of the byssal slit is distinctly curved, convex ventrally. By contrast, the slit, as viewed from within, is aligned roughly parallel to the hinge line. With increasing valve thickness, a smooth but pronounced internal ridge, or collar, develops around the byssal slit. In valves more than 4 or 5 cm. in height, the slit becomes closed distally, leaving a very small, elongate, or sub-circular foramen which opens externally near the beak, and the thickened collar may persist as a smooth rim around the much larger internal opening.

TABLE 2
RESTRICTION OF BYSSAL OPENING IN RELATION TO VALVE GROWTH IN *Pseudomonotis* (*Trematiconcha*) *likharevi*, NEW SPECIES, FROM THE GRANDEUR MEMBER, PARK CITY FORMATION, WIND RIVER MOUNTAINS, WYOMING

Resilifer Height ^a (in Cm.)	Distal End of Byssal Slit
0.75	Open
0.97	Open
1.42	Open
2.2	Barely closed
2.0+	Closed
2.0+	Closed

^aResilifer height is the only feature measurable on all the specimens.

Ornamentation is obsolescent on most valves. In fact, the largest left and right valves from Wyoming show no surface sculpture other than gross irregularities and discontinuities in growth. The lack of ribs in these large specimens may in part reflect imperfect preservation, but their rounded edges suggest pre-burial wear. Some surfaces have been significantly modified by boring organisms. Very weak ribbing also

characterizes *Pseudomonotis laevis* Girty, a virtually unrecognizable form from New Mexico (Newell, "1937" [1938]), and it may be that the new species *likharevi* will eventually be placed in synonymy with *P. laevis*, but their relationships cannot now be determined.

Other specimens in the collection exhibit concentric rows of spiny excrescences. Some of these are simply arched scales of the marginal lamina. Others are more sharply defined subcylindrical spines formed by an incurving of the lower edges of the arched lamellae; the spines are characteristically irregular in size and spacing from valve to valve. Exceptional specimens, however, possess spines that are consistent in size and orientation over limited parts of a valve, and they may be closed below, distally forming cylindrical tubes (fig. 16A).

Right valves exhibit irregular, roughly concentric growth discontinuities in the dorsal area, and one specimen is delicately costate in this region. Spines characterize the ventral part of several valves beyond a height of 4 cm.

The cardinal area is dominated by a prominent triangular resilifer in each valve. The area decreases in height rather abruptly away from the resilifer. The cardinal area of the right valve forms a right angle, or slightly less, with the plane of commissure, whereas the area on left valves ranges from being parallel to the plane of commissure or deviating only slightly from this condition. In right valves, the resilifer is postero-ventrally oblique.

A shallow umbonal cavity is created by the ventral expansion of the central part of the hinge plate. In general, the cavity is relatively shallow in small specimens and increasingly prominent in larger ones. Valve thickening in late growth stages produced, however, a counter effect, and the largest right valve shows little concavity below the hinge plate. The collection includes few specimens with good preservation of the posteroventral area, and the adductor muscle scar is not sharply defined on these valves. A small, but sharply defined pedal muscle scar is situated on both valves just below the antero-ventral corner of the resilifer.

GENUS *PACHYPTERIA* KONINCK, 1885

Figures 7C, 17

TYPE SPECIES: *Ostrea nobilissima* Koninck, 1851 (1842–1851), monotypic, Lower Carboniferous (Viséan), Belgium.

DIAGNOSIS: Ostreiform, dextrally cemented, irregularly ovoid. Shells with juvenile byssal slit becoming obsolete at early growth stage; left valve only moderately convex, with inconspicuous umbo; right valve flattened, with submerged byssiferous nepionic shell; auricles poorly defined, subquadrate; shell surfaces irregularly wrinkled and marked by uneven, imbricating lamellae, radial ornament lacking at all stages; cardinal areas subequal.

DISTRIBUTION: Lower Carboniferous (Viséan), Belgium, ?England, ?United States (Kinderhook, Burlington, Iowa).

DISCUSSION: This genus is very like the Permian *Prospondylus*, from which it differs in the non-protuberant left umbo and absence of radial ornamentation.

The great disparity in geological age of the two genera poses a problem. *Pachypteria* cannot readily be derived from any known ancestor, and it is not connected with *Prospondylus* by intergrading forms. Therefore the relationship between the two is highly conjectural. Possibly each evolved independently from separate genera of the Aviculopectinidae, comparable to the multiple origins of *Gryphaea* from *Ostrea* (Sylvester-Bradley, 1958).

Koninck's descriptions and illustrations of *Pachypteria* were based on rather poor and incompletely prepared specimens. Through the courtesy of Prof. Bernhard Kummel, of Harvard University, we have examined two topotypes of *P. nobilissima* in the Museum of Comparative Zoology (fig. 17A, C–F). One of these clarifies details of the ligament area and the ontogeny not heretofore known. We conclude that citations of *Pachypteria* from Britain (Hind, 1904 [1896–1905, vol. 2]), Iowa (Paul, 1941), and Mauritania (Termier and Termier, 1949) are not well substantiated. In these, the critical characters of form, ornamentation, and ligament of *Pachypteria* were not demonstrated. Even more dubious are reports of *Pachypteria* in the Devonian of Belgium (Maillieux, 1935) and Germany (Frech, 1891). The affinities of the former are uncertain because of poor preservation. Possibly the fossils in question are brachiopods. *Pachypteria* (?*Ostrea*) *vetusta* Beyrich was described by Frech (1891) from the *Stringocephalus* limestone of Nassau. After examining the holotype (by courtesy of Dr. J. Helms of the Institut für Paläontologie und Museum der Humboldt-Universität zur

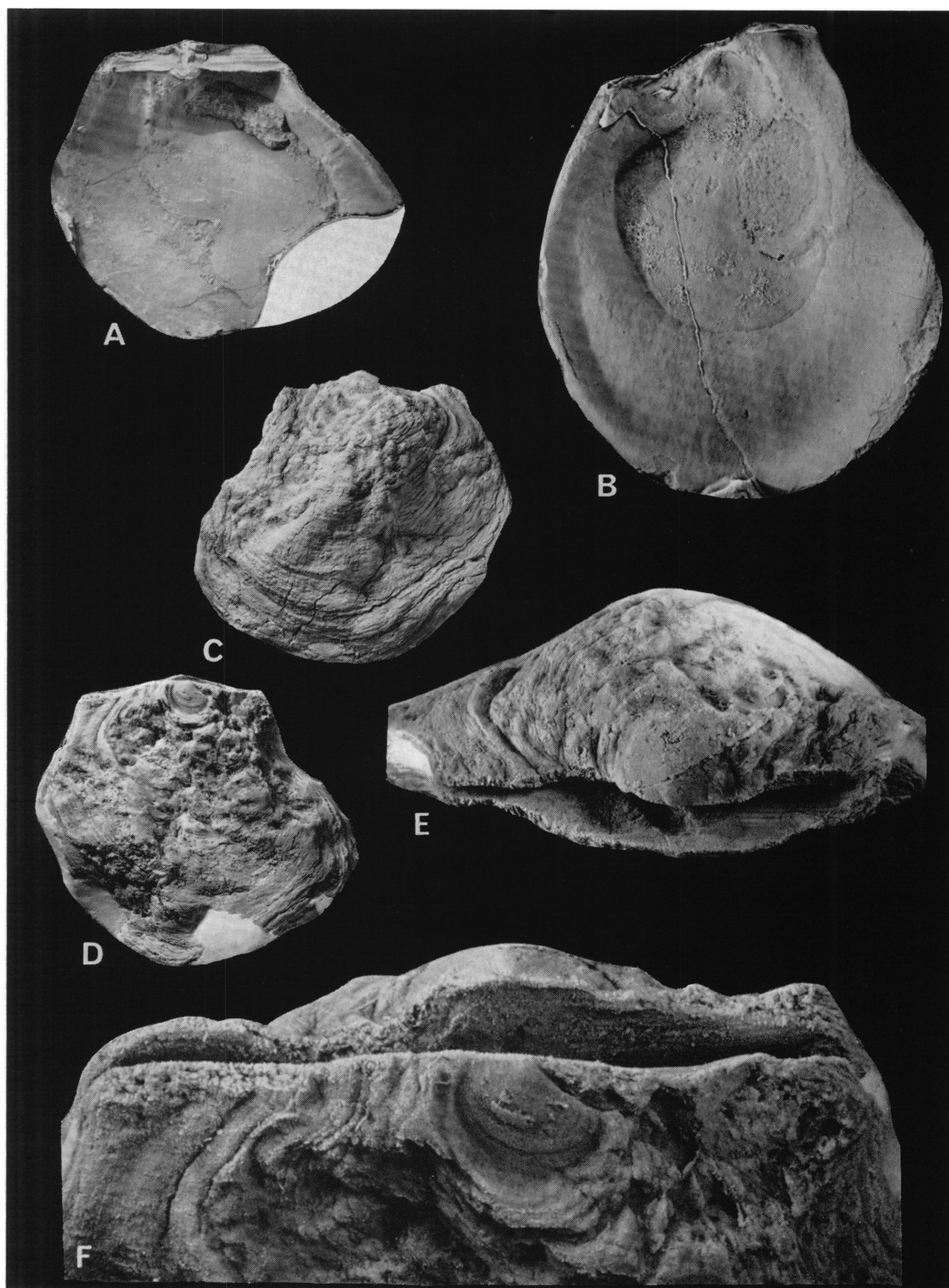


FIG. 17. *Pachypteria nobilissima* (Koninck), topotypes of type species of *Pachypteria*, Viséan, Visé, Belgium. A. Latex cast, M.C.Z. No. 87, interior of left valve. B. Koninck hypotype (Koninck, 1885, pl. 40, fig. 5). latex cast, interior of right valve. C–F, M.C.Z. No. 348. C. Left valve. D. Right valve. E, F. Hinge views, A–D, $\times 1$; E, $\times 2$; F, $\times 3$.

Berlin), we believe that it is a fragmentary brachiopod similar to *Davidsonia*.

The musculature in *Pachypteria* is essentially like that of other members of the Pseudomonotidae (fig. 7C).

***Pachypteria nobilissima* (Koninck), 1851**
Figures 7C, 17

Ostrea nobilissima KONINCK, 1851 (1842–1851).

Pachypteria nobilissima (KONINCK), 1885.

DIAGNOSIS: Same as the generic diagnosis.

DISTRIBUTION: Visé limestone, at Visé, Belgium.

DISCUSSION: Shells of this species are extremely rare. To our knowledge there are five specimens collected by Koninck. Two of these (fig. 17A, C–F) are topotypes now in the Museum of Comparative Zoology, Harvard University. The location of the lectotype, the sole specimen figured in 1851 by Koninck, is unknown to us. Two additional topotypes published by Koninck in 1885 are now in the Musée Royal d'Histoire Naturelle de Belgique, in Brussels. These were made available to us by Prof. Marius LeCompte. One of them is illustrated here (fig. 17B).

The approximate linear dimensions (in millimeters) of the five specimens are: lectotype, height 50, length 50; topotype, 1 height 70, length 60; topotype 2, height 57, length 51; topotype 3, height 45, length 49; topotype 4, height 55, length 55.

GENUS PROSPONDYLUS ZIMMERMANN, 1886

Figures 18–24

TYPE SPECIES: By monotypy; *Prospondylus liebeanus* Zimmermann, 1886.

DIAGNOSIS: Ovoid, pyriform and linguiform shells with smooth, obsolescent ribs or strong, spiny, coarse, and irregular costae; left beak much more prominent than right; cardinal areas of two valves subequal and diverging at 45 degrees or less; cardinal area of left valve incurved or approximately in plane of commissure; byssal notch of right valve completely closed in adults, but open and probably functional throughout nepionic stage (e.g., to shell height of about 20 mm.), beyond which byssal aperture covered by accretions of inner ostracum, and adult margin without byssal notch or sinus; outside nepionic shell an area of right umbo some 20–40 mm. across cemented to substrate.

DISTRIBUTION: Cathedral Mountain Forma-

tion (Leonardian) to Word Formation (Apple Ranch Member, Guadalupian), United States; Lower Zechstein, Germany.

DISCUSSION: This genus differs from *Pseudomonotis*, *sensu stricto*, and *P. (Trematiconcha)* in the complete closure of the byssal notch during early ontogeny, and in the cemented habit of adults. It differs also from *Pachypteria* Koninck in its greater regularity of form and in the possession of scaly costae, whereas the latter lacks radial ornamentation; from *Newaagia* Hertlein and *Paleowaagia*, new genus, *Prospondylus* differs in its subequal convexity of the two valves and subequal cardinal areas. From some of the Ostreidae, which it closely resembles, *Prospondylus* differs in possessing a nepionic byssal notch in the right valve, and in being cemented by the right umbo of the post-nepionic stage. Ostreids, on the other hand, lack the byssal notch at all ontogenetic stages, and become cemented after the prodissoconch stage by the left valve. Both *Hinnites* and *Spondylus* possess submerged (internal) resilia. *Spondylus* possesses isodont dentition wholly lacking in *Prospondylus*.

Zimmermann (1886) demonstrated that mature shells of the type species, *Prospondylus liebeanus*, lack the byssal slit. But Frech (1912), who evidently had not seen good examples of the species, argued that the apparent lack of the byssal notch was a result of faulty preservation. He employed *Prospondylus* for a wide range of shells which, besides the type species, included early Triassic species of *Eumorphotis*. Likharev (1931) affirmed the accuracy of Zimmermann's observations, but he expanded the concept of *Prospondylus* to include forms possessing a byssal foramen. Later, Newell ("1937" [1938]), influenced by Frech, classed *Prospondylus* as a junior synonym of *Pseudomonotis*.

We now believe that *Prospondylus* is a member of a morphological series, *Pseudomonotis* (*Pseudomonotis*) – *Pseudomonotis* (*Trematiconcha*) – *Prospondylus* – *Paleowaagia* – *Newaagia* – *Spondylus*, which may also represent a phyletic series.

The genus *Prospondylus* must be interpreted in light of the characteristics of the type species. With the assistance of Dr. Jochen Helms, Institut für Paläontologie der Humboldt-Universität zu Berlin, we have been able to examine artificial casts and some natural molds of the collection on which the type species, *Prospondylus liebeanus*, was based. The types, now in the Museum für Naturkunde in Gera, were collected from

Lower Zechstein rocks near Pössneck, between Ranis and Crölpa, in East Germany.

Although the type specimens are preserved as molds in dolomitic limestone (fig. 18), they satisfactorily show the following characters: a pear-shaped silhouette, a circular adductor, a relatively short, non-auriculate hinge, and the lack of a byssal opening. The median, triangular, external resilifer is vertical or slightly declined backward. A small pedal muscle pit is visible at the anterior extremity of the pallial line. Another

muscle pit lies just above the adductor. By analogy with the living Pectinacea, this should represent a gill retractor muscle.

The original microstructure of the shell is unknown. The inner ostracum of some of the American shells, however, was selectively leached away, leaving perfectly preserved details of both surfaces of the outer ostracum, after which the latter was replaced by silica (fig. 9). This mode of preservation indicates that the inner ostracum, unlike that of members of the

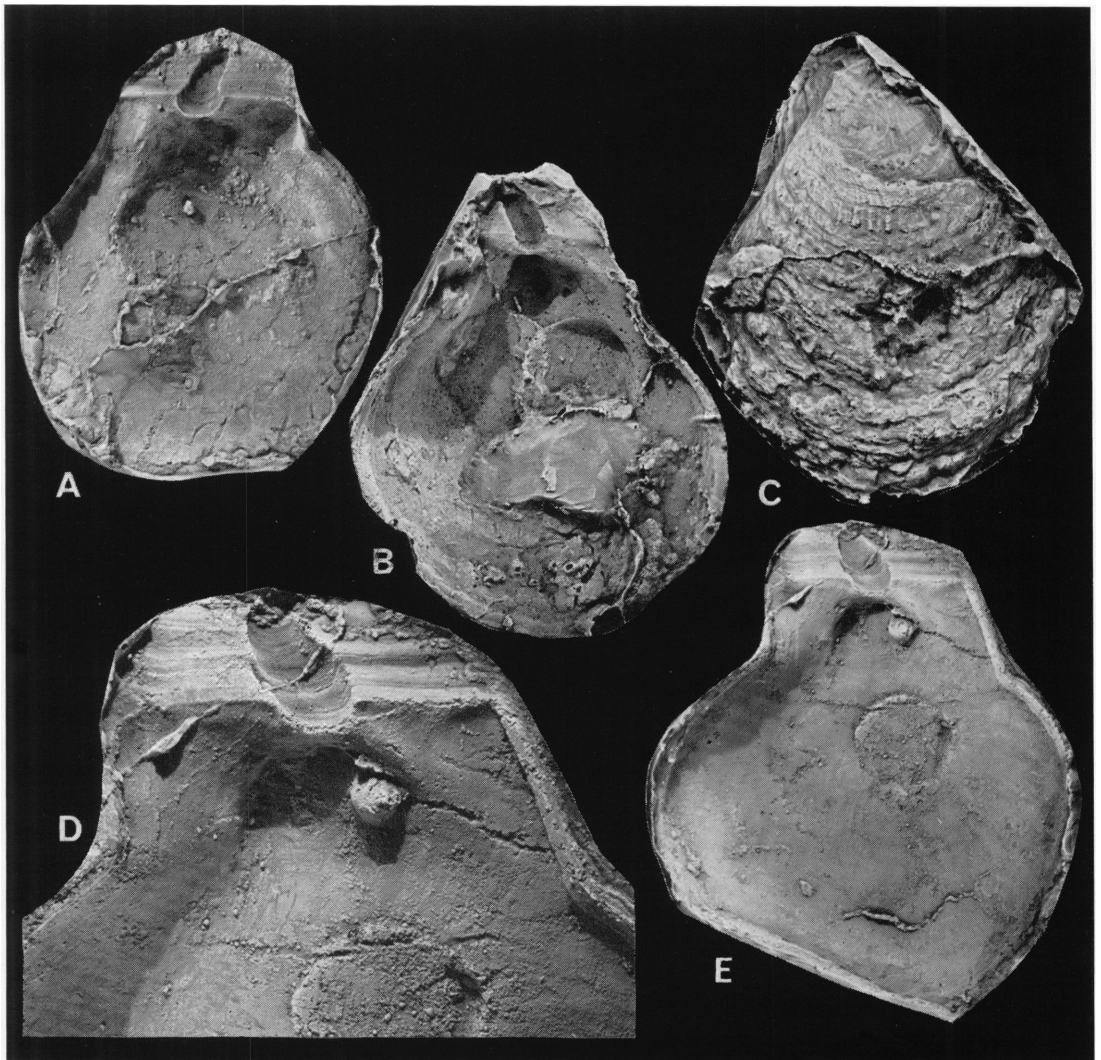


FIG. 18. *Prospodylus liebeanus* Zimmermann, type species of *Prospodylus*, Zechstein, Permian, East Germany. A. A paratype, M.N.F. No. 852, latex cast of left valve. B, C. A paratype, M.N.F. No. 851, latex casts of exterior and interior of right valve. D, E. Holotype, latex cast of right valve. A-C, E, $\times 1$; D, $\times 2$.

Ostreacea, was composed of the less stable aragonite, whereas the outer ostracum presumably was calcite. Elimination of the inner shell layer has exposed the nepionic shell with its byssal notch, a detail ordinarily not visible from the interior.

Prospendylus acinetus Newell and Boyd,
new species

Figures 19-24

DIAGNOSIS: Large, for Permian bivalves, ranging upward to estimated height well in excess of 10 cm., nearly smooth, or ornamented only over mature part of shell with irregular, broad, low radial ribs and equally broad and shallow, radial furrows crossed by irregular and unevenly spaced concentric growth frills that project tangentially, or at high angle from costae as flaring, inverted half-cones or half-cylinders; nepionic area of left valves nearly bald, or ornamented only by very fine costellae that disappear on mature shell; strong internal buttress curving around posterior margin of visceral cavity from posterior adductor to rear margin of resilifer, in both valves.

DISTRIBUTION: Wolfcamp (bed 12); U.S.N.M. 701b) to Upper Word Formation (Apple Ranch), western Texas. Leonardian (Cathedral Mountain): A.M.N.H. 507; U.S.N.M., 702, 702b, 703b, 721u, 726o, 726u. Leonardian (Road Canyon): U.S.N.M. 702c, 703, 703a, 703c, 707e, 719x, 721s, 721t, 721y, 724b, 724j, 726d, 726z-a. Cherry Canyon (Lower Getaway): A.M.N.H. 496, 512, 600; U.S.N.M. 728, 730. Word (Willis Ranch): A.M.N.H. 505; U.S.N.M. 706. Word (China Tank): U.S.N.M. 706c. Word (between Willis Ranch and Apple Ranch): U.S.N.M. 706b. Word (Apple Ranch): U.S.N.M. 719z and 722t.

DISCUSSION: From *Prospendylus liebeanus* Zimmerman, of the Zechstein of Germany, adult shells of *P. acinetus* can be distinguished by its having a much stronger internal buttress. American shells range from nearly smooth to coarsely costate forms, but in every case they lack costellae in the intercostal furrows.

Some of the shells of *Prospendylus acinetus* show resemblance in the surface features to the modern oyster *Crassostrea* (Galtsoff, 1964) and Cretaceous *Exogyra* (Lerman, 1965), with variations in form and ornamentation that are very oyster-like. As in oysters, much of the variability can be attributed to the effect on the mantle

margin of the cemented habit. Environmental influences on form and ornamentation are well established with *Crassostrea virginica*, but Lerman (1965) was unable to find such relationship in *Exogyra*. In any case, although there are local concentrations of rather distinctive shells (treated herein as Forms A-C), we cannot impute either ecological or temporal significance to the variation pattern.

The largest more or less complete valve measured 10 cm. in height and 7.5 cm. in length. Almost all specimens are fragmentary, but only a few would be larger, possibly 13 cm. high, if restored. Both valves undergo striking changes in form and ornamentation during ontogeny, but the changes are not closely correlated between right and left valves, and they are not very abrupt.

Up to a height of 1 to 1.5 cm., right valves are pectiniform, with a functional byssal notch, and they are slightly concave externally. This early stage apparently was not cemented, and the animal probably was free to move about, snail-like, as do the young of the modern Pectinidae. The uncemented status is indicated not only by the shell symmetry, but also by the circumstance that this portion of the shell frequently is broken away from the surrounding cemented part of the umbo of the right valve. The pectiniform (nepionic) stage exhibits anteroventral expansion, a prominent anterior auricle, and a sharply defined byssal notch. The trace of the notch, as reflected by growth lines, is commonly about 5 mm. long. Beyond this dimension, the antero-dorsal margin lacks the growth trace of a notch, and the slit is covered from within by deposits of the inner ostracum.

The attached area around the umbo of the right valve ranges in height from about 2 to 6 cm., and most right valves diverge sharply outward from the substrate at a height of 3 or 4 cm. The shape of the attached area was, of course, controlled by the configuration of the underlying surface; therefore the profile at right angles to a hinge at this stage may be concave, flat, or convex, with about equal frequency.

Only the thin, external layer is preserved in most specimens, so the relationship of the right valve to the underlying object in the area of attachment is commonly readily apparent. Where the underlying object presented a smooth, continuous surface, the encrusting surface of the right valve followed it in direct contact over the

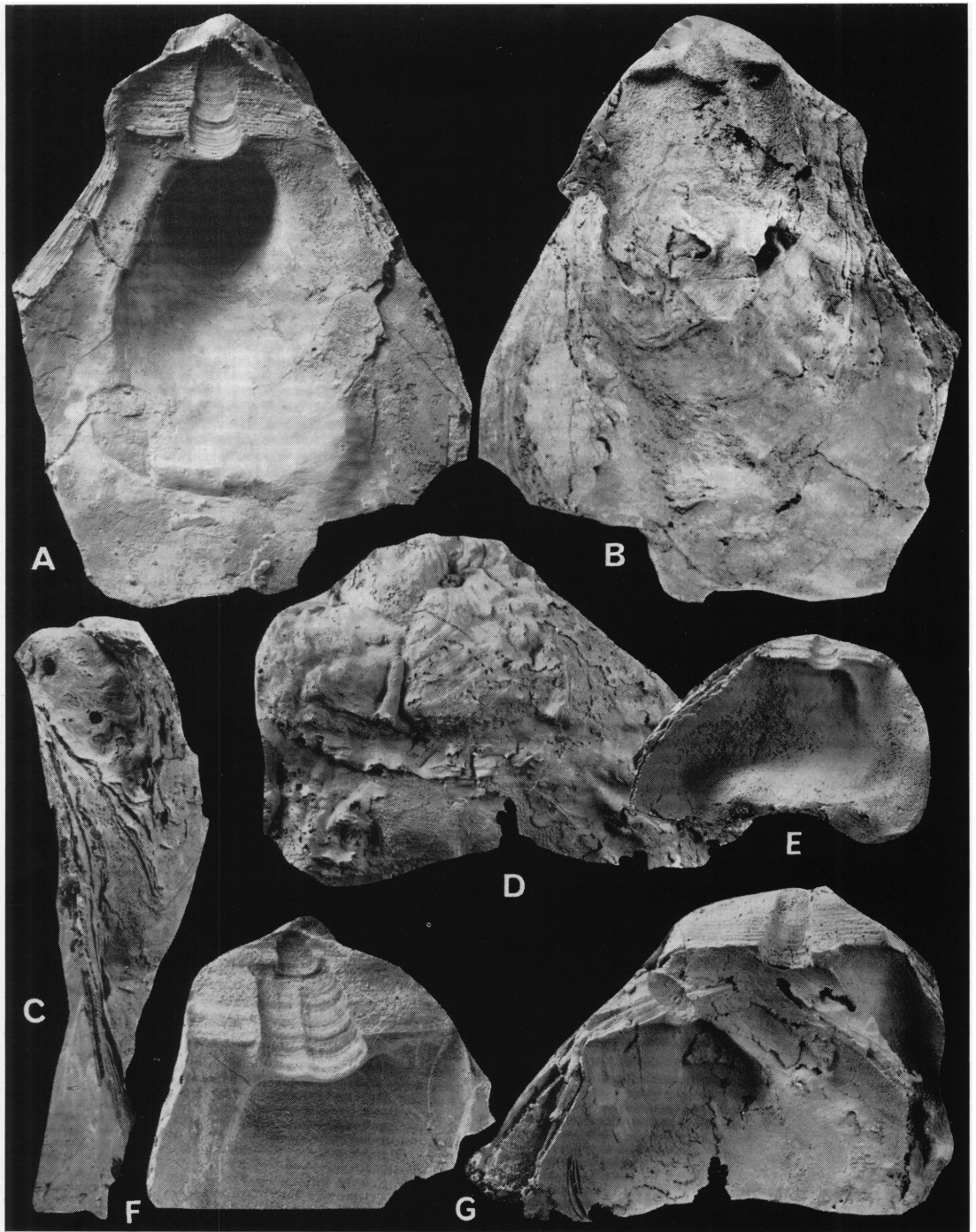


FIG. 19. *Prospodylus acinetus* Newell and Boyd, new species, smooth form, silicified specimens, Glass Mountains, western Texas, Road Canyon Formation unless specified otherwise. A–C. External and internal views of left valve, U.S.N.M. No. 154985; another specimen, a right valve, cemented to exterior of umbo; two cylindrical borings, origin unknown, near top of C; U.S.N.M. 703. D, G. Internal and external views of right valve, U.S.N.M. No. 154982; ramose bryozoan embedded in exterior, and smaller right valve of *acinetus* cemented to interior of shell; U.S.N.M. 703c. E. Interior of right valve, U.S.N.M. No. 154984; Neal Ranch Member, Word Formation, U.S.N.M. 701. F. Hinge area, left valve, U.S.N.M. No. 154983, with damaged or pathological resilifer; U.S.N.M. 703. All $\times 1$.

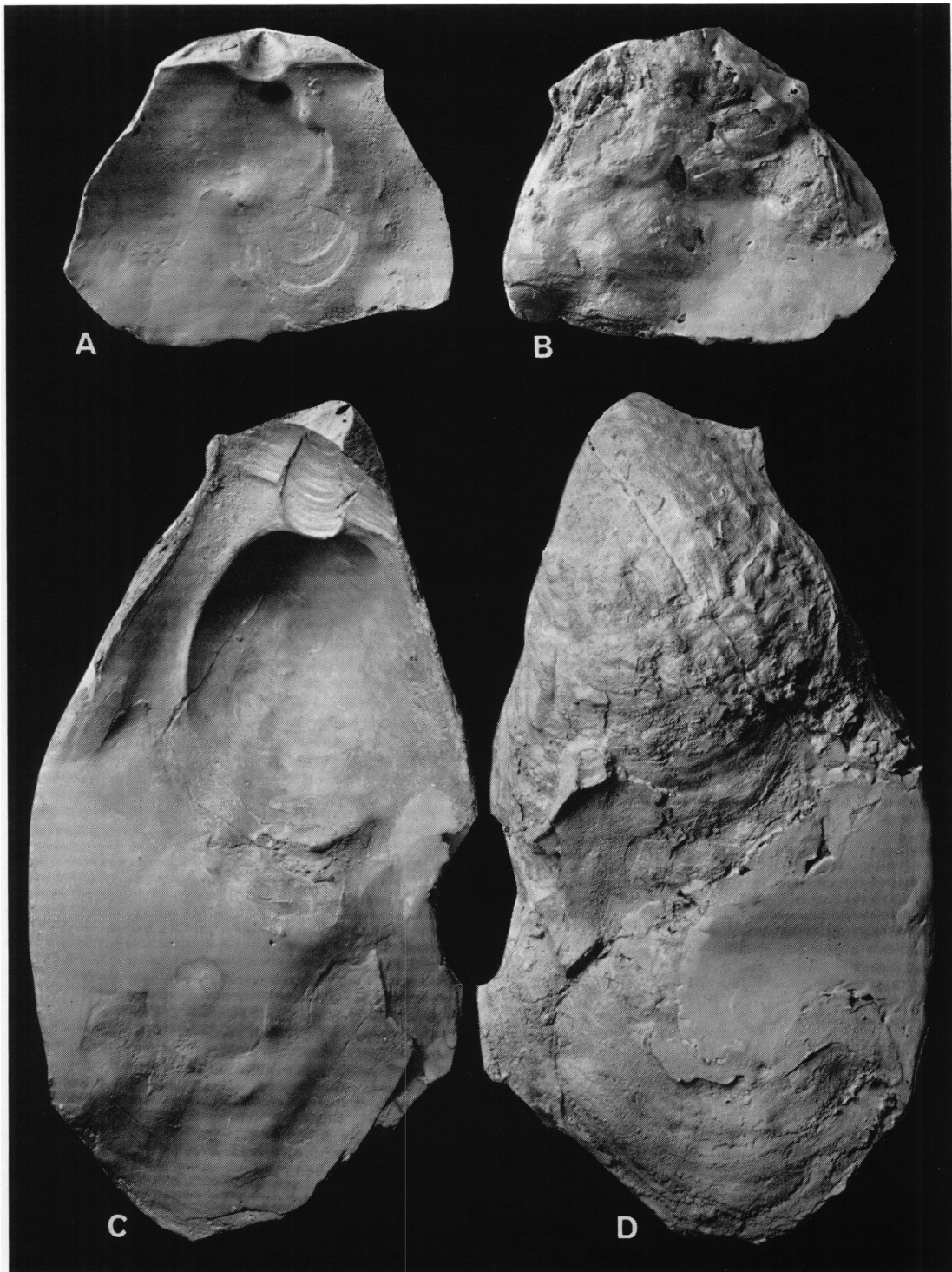


FIG. 20. *Prospodylus acinetus* Newell and Boyd, new species, smooth variety, silicified specimens, Permian, Glass Mountains, western Texas. A, B. Right valve, U.S.N.M. No. 154978; U.S.N.M. 703c, China Tank Member. A. Interior. B. Exterior. C, D. Partly restored left valve, U.S.N.M. No. 154977; U.S.N.M. 703, Road Canyon Formation. C. Interior. D. Exterior. All $\times 1$.

entire attachment area. In such cases, the thin exterior layer of the shell reflects delicate features such as brachiopod growth lines. In many instances, however, the right valves are attached to spiny objects, including the left valves of others of their kind. In these cases, the attachment area is discontinuously cemented to the spines of the host shell. The configuration of the thin exterior layer rises over spines and sags

between them without reaching the base of the spines. As many as four small right valves may be attached to a single adult left valve.

Beyond the area of direct attachment, right valves are shaped like irregular saucers or very shallow bowls; external profiles at right angles to the hinge vary from flat to gently convex. Median longitudinal profiles are irregularly convex, with the lateral slopes of about equal

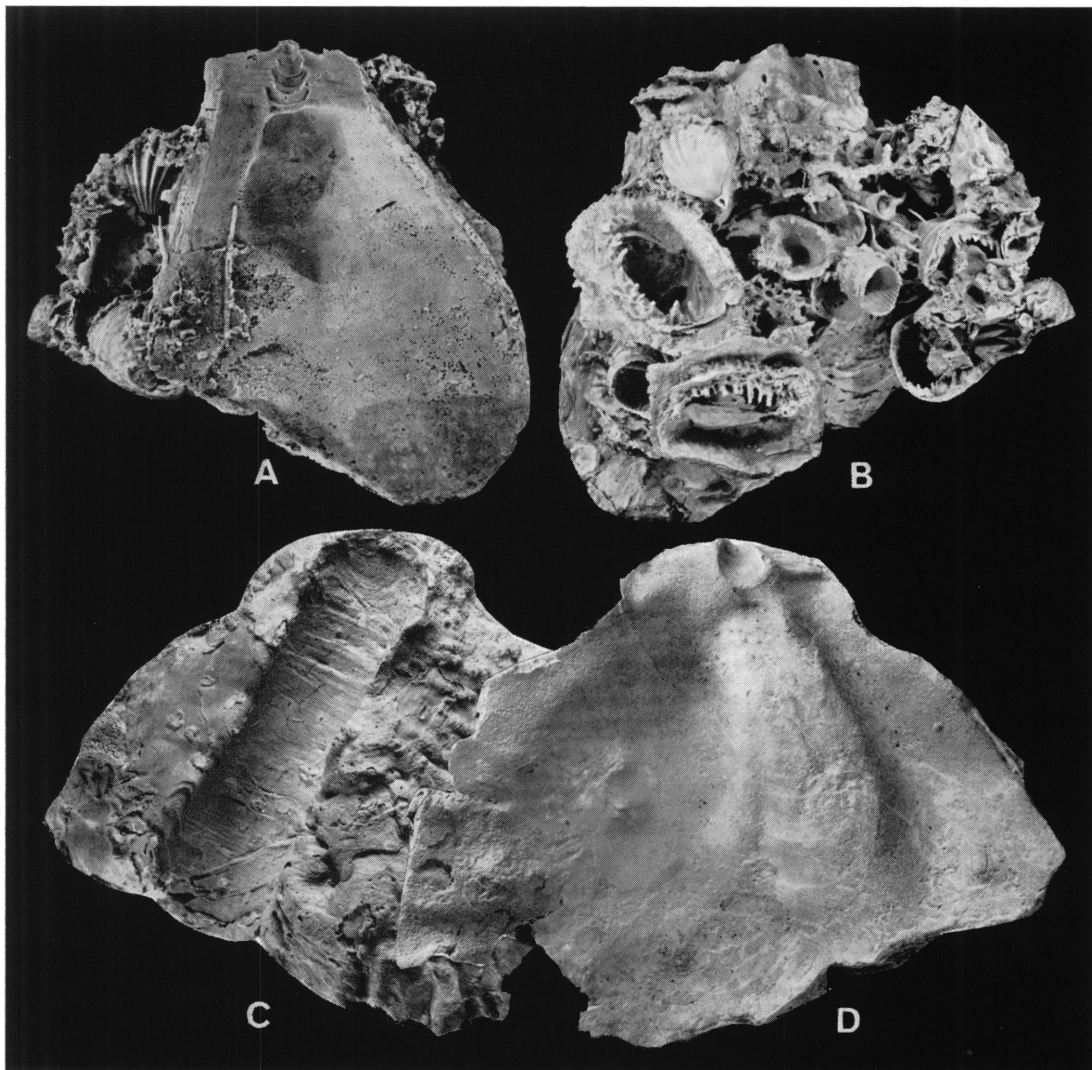


FIG. 21. *Prospodylus acinetus* Newell and Boyd, new species, spiny variety, silicified specimens, Permian, western Texas. A, B. Left valve, U.S.N.M. No. 154986, encrusted externally by heavy growth of spiny brachiopods, bryozoans, and corals; U.S.N.M. 7260, Cathedral Mountain. C, D. Right valve, outer and inner views, A.M.N.H. No. 28932, with impression of unidentified host organism that served as substrate; A.M.N.H. 512, Lower Getaway. All $\times 1$.

inclination, or with the anterior slope somewhat steeper. Linear growth of the hinge of the right valve is about equal on each side of the beak in some valves, but in others there is a greater posterior increment. In shells in which growth extended the hinge area beyond the surface of attachment, small subquadrate auricles are present. These are characterized by a flattening of the surface and by a modification or reversal of the inward slope of the valve outline approaching the hinge.

The shape of the left valve also changed notably during growth. Early growth resulted in a short, high, strongly convex form, smooth or ornamented by very fine costellae. Beyond a height of from 2 cm. to 4 cm., this pattern gives way to greater lateral expansion and an over-all flattening of the valve. As a result, profiles along the vertical dimension are strongly convex in the dorsal region, becoming gently convex or flat toward the venter. Growth extension of the hinge line commonly is greater posteriorly than

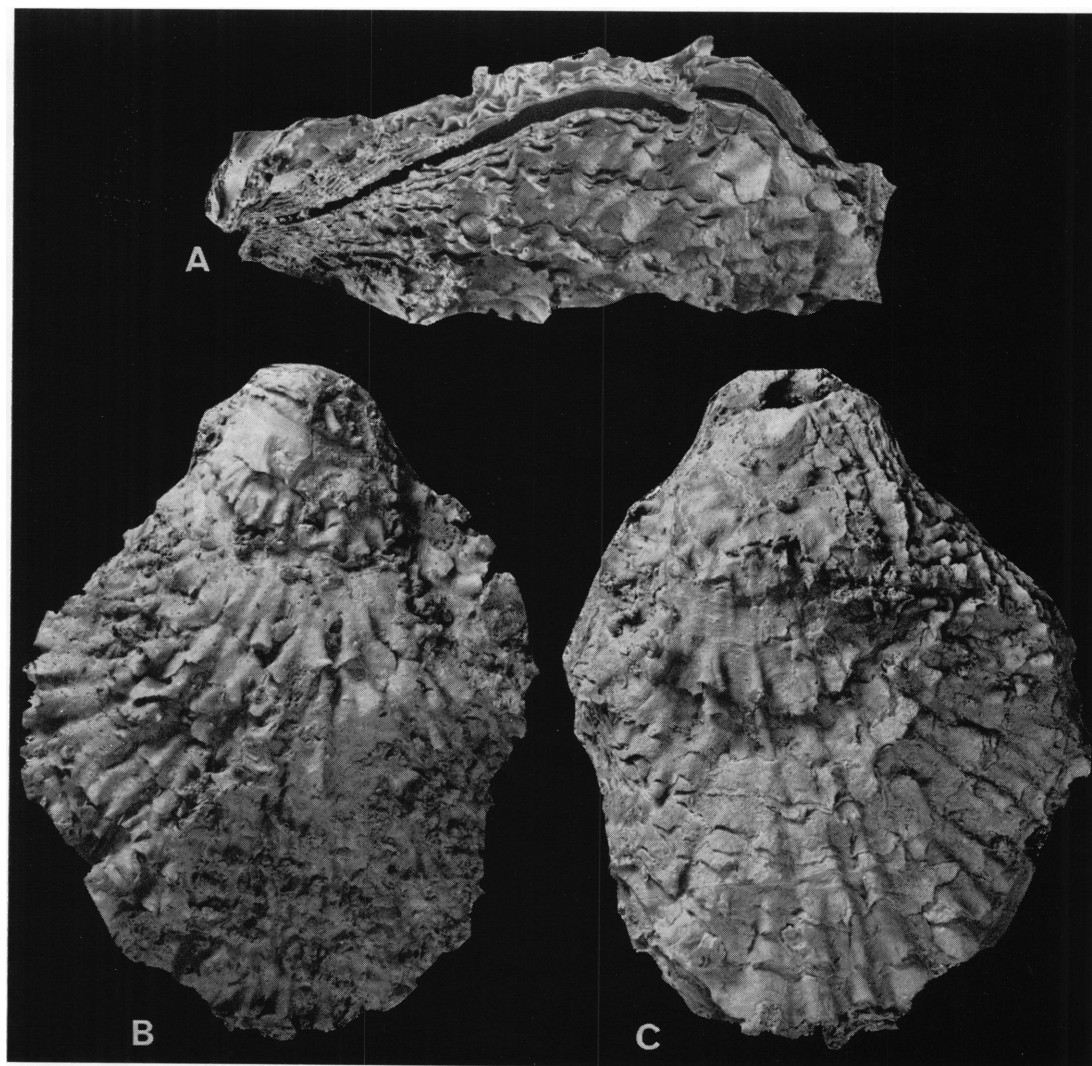


FIG. 22. *Prospodylus acinetus* Newell and Boyd, new species, holotype, U.S.N.M. No. 154968, bivalved specimen, Permian, Road Canyon Formation, Glass Mountains, western Texas; U.S.N.M. 702c. A. Anterior view, right valve below. B. Left valve, exterior. C. Right valve, exterior. All $\times 1$.

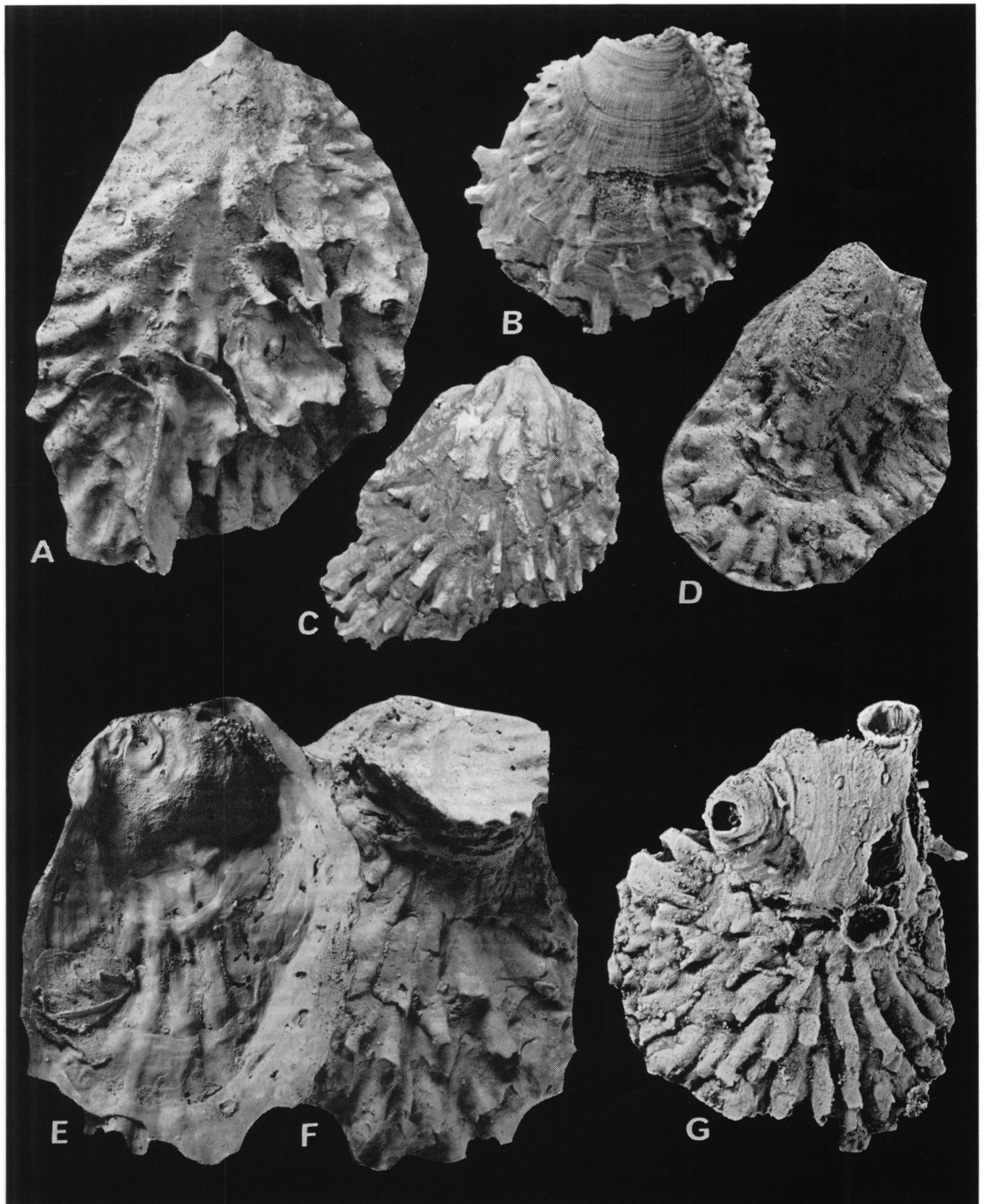


FIG. 23. *Prospodylus acinetus* Newell and Boyd, new species, spiny variety, silicified examples, Permian, western Texas. A. Left valve, U.S.N.M. No. 154969, with adherent juveniles of same species; U.S.N.M. 706e, Willis Ranch. B. Left valve, U.S.N.M. No. 154970, with juvenile costellation over umbo; U.S.N.M. 721s, Road Canyon. C. Left valve, A.M.N.H. No. 28933; A.M.N.H. 600, Lower Getaway. D. Left valve, U.S.N.M. No. 154971; U.S.N.M. 706c, China Tank. E. Right valve, U.S.N.M. No. 154972, inner view of outer ostracum, showing juvenile pectiniform stage and cementing brachiopods (leptodid, strophalosiid) pressed against bivalve shell after leaching of inner ostracum; U.S.N.M. 706, Willis Ranch. F. Outer view of same. This shell was cemented to a bryozoan colony which had grown over a brachiopod. G. Right valve, U.S.N.M. No. 154973, attached to a richthofenid brachiopod; U.S.N.M. 719z. A, C-G, $\times 1$; B, $\times 2$.

anteriorly. Small auricles are present in some valves in which slight flattening develops laterally to the umbo. On left valves characterized by this development, the posterior auricle is the more prominent.

General growth expansion of both valves proceeded more or less equally anteroventrally and posteroventrally, until the shell attained a height of about 4 cm. From this point, most valves exhibit accelerated anteroventral expansion.

In mature individuals, the resilifer, which commonly extends slightly below the rest of the ventral margin of the cardinal area, is slightly higher than wide, upright rather than oblique, and similar in the two valves. Some individuals display a median fold in the resilifer, interpreted as a result of pathologic splitting or division of the resilium (fig. 19F).

Left valves commonly have a large, broadly rounded umbonal cavity, whereas most right valves have only a small low recess under the ventral part of the resilifer. In exceptional right and left valves the cavity is lacking.

The interiors of both valves possess distinctive curved buttress ridges, around the visceral cavity, trending from the posteroventral corner of the resilifer across the floor of the valve to the posterodorsal corner of the adductor muscle scar. In the left valve, this ridge is commonly less conspicuous, as it coincides with an angular change in slope from the convex umbonal region to the flatter marginal zone.

The detailed characteristics of musculature are not visible. The adductor scar is rather weakly imprinted on the posterior side of the valve between one-third and one-half of the height of a valve below the beak.

The cardinal area is relatively short in both right and left valves, is two to four times its height, and is very much shorter than the maximum shell length. The cardinal area of the right valve slopes ventrally inward some 110 to 120 degrees with respect to the plane of commissure (apsaline condition in brachiopod terminology: Williams and Rowell, 1965, p. H60), and the highest part of the cardinal area coincides with the apex of the valve. The cardinal area of the left valve is approximately parallel to the plane of commissure or slightly incurved (apsaline). The umbo rises well above the cardinal area.

The ornamentation over the mature parts of the shell is similar on the two valves. It is highly variable, and there is a tendency for certain

combinations of form and ornamentation to characterize samples from individual localities, tempting us to conclude that we might be dealing with geographic races or ecophenotypes. The tantalizing suggestion of segregation, however, cannot be quantified or documented with the small and generally fragmentary samples available. Three arbitrary classes of ornamentation in what appears to be a continuum distinguish Forms A–C.

Some or all of the individuals at all localities exhibit costae, and these commonly are discontinuous. This rough and irregular ornamentation first appears on left valves at a height of 1 to 4 cm., and the fine costellae of the umbonal area do not continue onto the adjacent mature surface.

No individual ridge of the mature surface persists very far before bending downward into the general surface, terminating as a tangential hollow spine overhanging the subsequent valve increment, or terminating as an erect spine by an upturn of the lamina. Some of the last mentioned even recurve outward and upward toward the hinge. New costae appear both by branching and by implantation. Spines commonly vary in size, shape, and orientation on a single valve. In fact, individual spines commonly vary in these respects throughout their length. The spines are arched projections of a thin outer-shell lamina and thus are hollow and open on the under side. They vary in frequency from individual to individual, and in lateral and longitudinal spacing.

The most common expression, Form A (figs. 22, 23), is characterized by irregular, coarse costae surmounted by scattered, tangential, hollow spines. Frequently, these originate as low ridges and are distinct projections only at their distal ends. Other ridges, instead of terminating in low spines, plunge and disappear before reaching the shell margin. These may give the effect of crude, discontinuous plications. This ornamentation is relatively uncommon in the stratigraphically older specimens of *P. acinetus*, but predominates near the top of its known range, in the Word Formation (Willis Ranch Member).

A second expression in ornamentation is found in Form B (fig. 24). These shells have a frilled appearance due to projecting scales. The scales are curved upward, and their free lateral margins expand outward and upward instead of

curving downward as in subcylindrical spines. Thus, the terminal part of each scale is not a point but a tongue-shaped, concave-upward projection. Where adjacent spines coalesce, the effect becomes one of individual shell lamellae overlapping younger ones like irregular shingles,

with the free edge of a lamina rising outward from the underlying surface. This type of ornamentation characterizes nearly all specimens of the species from one locality in the Cathedral Mountain Formation of the Glass Mountains, western Texas (U.S.N.M. 702c). It is also found

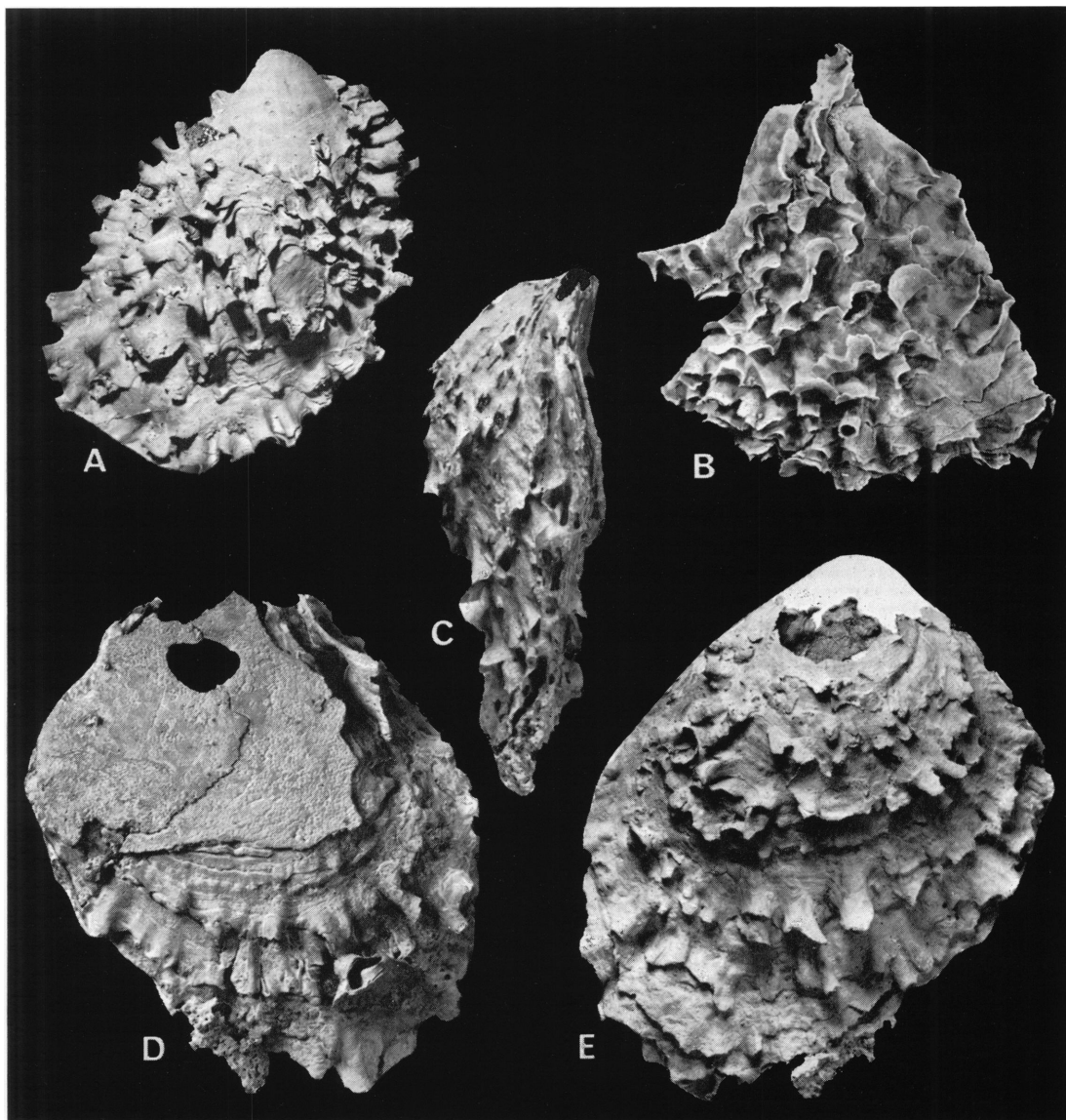


FIG. 24. *Prospodylus acinetus* Newell and Boyd, new species, frilled variety, silicified examples, Permian, Glass Mountains, western Texas. A. Left valve, U.S.N.M. No. 154974; U.S.N.M. 702c, Road Canyon. B. Fragment of left valve, U.S.N.M. No. 154975; U.S.N.M. 702c, Road Canyon. C-E, Bivalved specimen, U.S.N.M. No. 154976, showing inequivalved profile and character of ornamentation; U.S.N.M. 706, Willis Ranch. D. Cephalopod fragment which served the bivalve as a substrate for attachment by right valve. All $\times 1$.

in other Leonardian collections but is rare in younger material.

A third grade of surface is recognized in Form C (figs. 19, 20). These shells are nearly devoid of ornamentation over the mature shell except that localized areas of some valves show a tendency for the development of obscure, coarse radial ribs, and fine costellae over juvenile area of umbones. This type of ornamentation predominates in a small area in the Road Canyon Formation of the Glass Mountains, western Texas (U.S.N.M. 703, 703c), but it also occurs sparsely at other horizons.

The new species is based on a fair number of silicified specimens, all from the Glass Mountains, western Texas. Form A is represented by 19 specimens that adequately display surface ornamentation and marginal profiles, plus 54 in which inner surface features are shown.

Form B is represented by five specimens with intact margin, and 32 more fragmentary valves. Internal characteristics are preserved in material from five localities.

Form C is represented by one nearly complete valve and 20 instructive fragmentary specimens. Four localities yielded specimens showing internal details.

In addition, there are hundreds of shell fragments that provide useful information about ornamentation, but little else.

PEGMAVALVULA NEWELL AND BOYD,
NEW GENUS

Figures 7A, B, H, I, 25-27

TYPE SPECIES: *Pegmavalvula gloveri* Newell and Boyd, new species.

DIAGNOSIS: Small pectiniform, cemented, nearly equivalved pseudomonotids with relatively uniform radial ribs and small auricles; byssal notch lost early in growth.

DISTRIBUTION: Leonardian and early Guadalupian, western Texas.

DISCUSSION: Some individuals among these shells are characterized by moderate procrescentic growth (figs. 25A, B, 27A), which, in context with a fairly well-developed posterior auricle and valves of nearly equal convexity, present a general expression quite similar to that of the aviculopectinid genus *Streblochondria* (Newell, "1937" [1938]). Consequently, we considered the possibility that *Pegmavalvula* is a cemented version of one of the *Streblochondriinae*, such as *Guizhoupecten* Chen. This hypo-

thesis envisioned an evolutionary parallelism with the ancestral-descendent relationship seen in the free scallop *Chlamys* and its cemented derivative, *Hinnites* (fig. 3). The relationship of *Pegmavalvula* however, more probably is with *Prospondylus*, which it resembles more closely than any member of the *Streblochondriinae*. *Pegmavalvula* is distinguishable from other genera of the Pseudomonotidae by being nearly, but not quite, equivalved and equilateral; from the *Streblochondriinae* it is distinguishable by its cementation and spinosity.

Pegmavalvula gloveri¹ Newell and Boyd, new species

Figures 7A, B, 25, 26

DIAGNOSIS: Nearly equilateral, short-hinged and pear-shaped, with subquadrate auricles and broad subauricular sinuses; ornamentation consisting of weak plications corresponding to coarse costae bearing tangential cylindrical spines; these separated by radial sulci bearing several fine costellae; origination of successive ranks of costae on left valves generally by intercalation, on right valves by indistinct bifurcation; surface elements commonly appreciably coarser and more sharply defined on left than on right valves.

DISTRIBUTION: Leonardian-early Guadalupian, western Texas. Bone Spring Limestone (Leonardian): U.S.N.M. 728f. Road Canyon: U.S.N.M. 721j, 721s, 721z, 726d. Willis Ranch: U.S.N.M. 706, 706e. Lens between Willis Ranch and Apple Ranch: U.S.N.M. 706b. Lower Getaway: A.M.N.H. 512, 600; U.S.N.M. 728, 730.

DISCUSSION: Two slightly different forms are recognized. A long-ranging and widely distributed form, Form A (fig. 25), is characterized by recurved spines (fig. 25G), incipient plication, or heavy ribs separated by broad radial furrows bearing from four to nine fine costellae (fig. 25A). Form B (fig. 26), restricted in our collections to the Road Canyon Formation, has somewhat different ornamentation. The ornamentation consists mainly of irregular radial rows of imbricating tangential spines reflected internally as plicae. The external furrows be-

¹ Named in honor of Mr. and Mrs. Walter H. Glover, landlords of the Pine Spring Ranch near Guadalupe Pass, at the foot of the Guadalupe Mountains, western Texas. These fine people have been benefactors and hosts to several generations of students of the Permian rocks of that region.

tween the spines bear only a single thin costella. Form A is represented in the collections by several dozen valves; Form B, by 24 valves.

In both forms, the valves commonly approach equilaterality, possess auricles, and have their greatest length below mid-height.

Both left and right valves are only slightly

convex, and right valves are difficult to distinguish from left valves in which the attachment area is small or missing because of breakage.

The attachment area of the right valves varies in vertical dimensions from 1 to 3.5 cm. The valve profile along this part of the height was

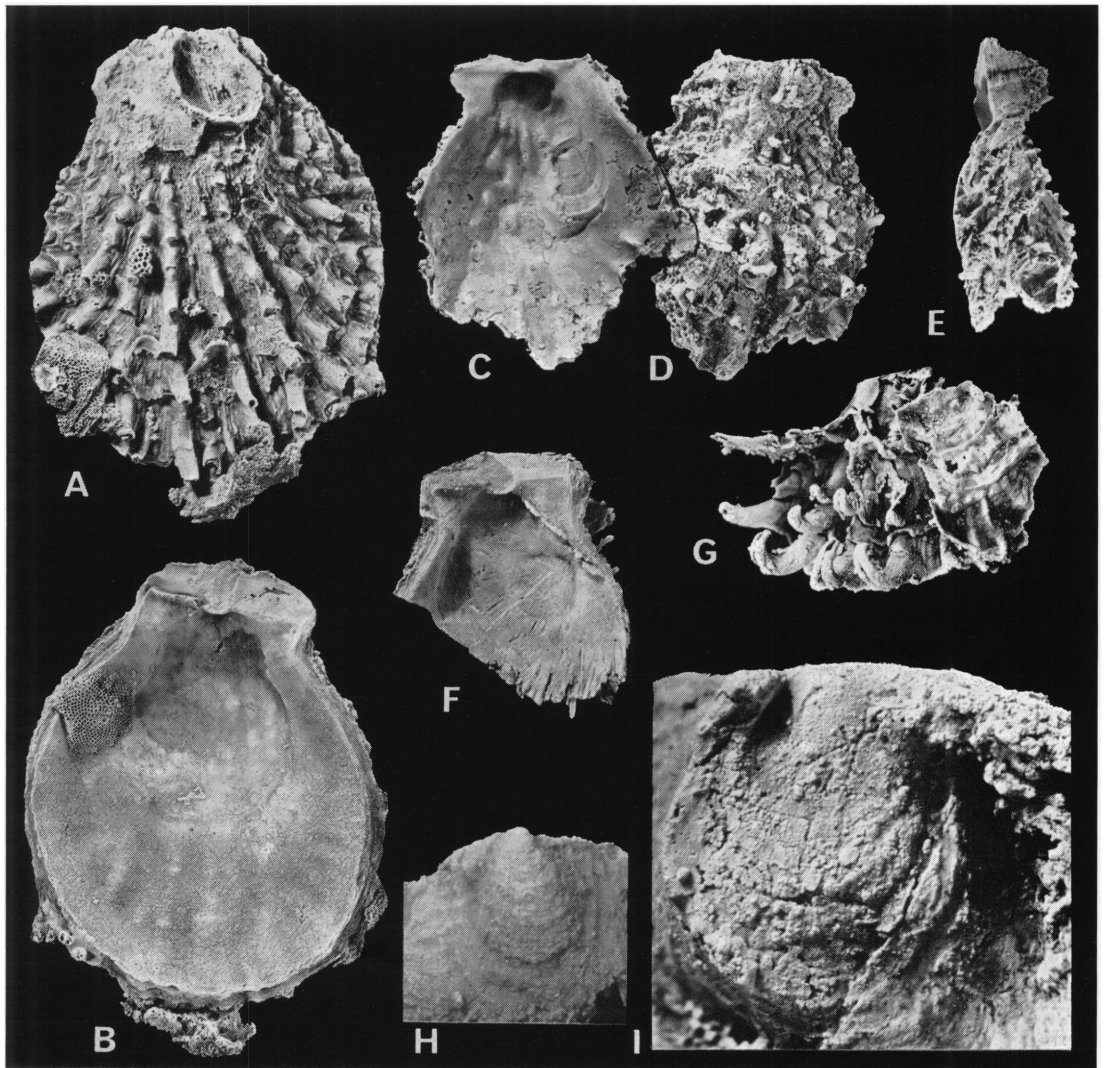


FIG. 25. *Pegmavalvula gloveri* Newell and Boyd, new species, silicified specimens, Permian, western Texas. A, B. Holotype, A.M.N.H. No. 28918, left valve with cemented epizoans, including *gloveri* spat; A.M.N.H. 512, Lower Getaway. C-E. Right valve, A.M.N.H. No. 28927; A.M.N.H. 512, Lower Getaway. F. Right valve, U.S.N.M. No. 155004; U.S.N.M. 706e, Willis Ranch. G. Fragment of margin of right valve, U.S.N.M. No. 155005, showing recurvature of spines; U.S.N.M. 706e, Willis Ranch. H. Beak of left valve, U.S.N.M. No. 154966, showing form of juvenile, free-living stage; U.S.N.M. 706e, Willis Ranch. I. Beak of right valve, A.M.N.H. No. 28923, showing byssal notch and pectiniform juvenile stage; A.M.N.H. 512, Lower Getaway. A-F, $\times 1$; G, $\times 2$; H, $\times 8$; I, $\times 10$.

controlled by the nature of the underlying object, and about equal numbers of specimens represent concave, flat, and convex external profiles. The umbonal region of the left valve varies from slightly convex to moderately convex, and the beak area rises only slightly above the cardinal area in a hinge view. The principal growth gradient of the left valve umbonal area is commonly downward (infracrescent), rarely forward (prorescent). Commonly, the beak is situated medially along the hinge, and in numerous specimens it is slightly anterior of the mid-point.

The subequal auricles are set apart from the main body of the valve by flattening and by subauricular sinuses of the valve margin; these indentations are essentially equal in a single valve. The vertical profile beyond the attachment area tends to be slightly convex to flat in both left and right valves. The curvature of the

surface as viewed along the plane of commissure is constant, but some individuals exhibit a steeper posterior or anterior slope. Although the main body of the valve is approximately equilateral, some specimens are slightly extended forward or backward.

Early growth of the right valve produced an infracrescent, unattached pectiniform stage (fig. 25H, I). This stage persisted to a height of 2 to 4.5 mm., beyond which the valve became cemented to the substrate (fig. 26C). The few specimens with a well-preserved umbonal area show a byssal notch in the pectiniform stage. The trace of the notch, delineated by growth lines, varies from 1 to 2 mm. long. In most specimens the pectiniform stage is not sharply differentiated from the adjacent part of the valve. In one specimen the hinge line of the pectiniform stage is along the edge of the triangular cardinal area and anterior to the apex.

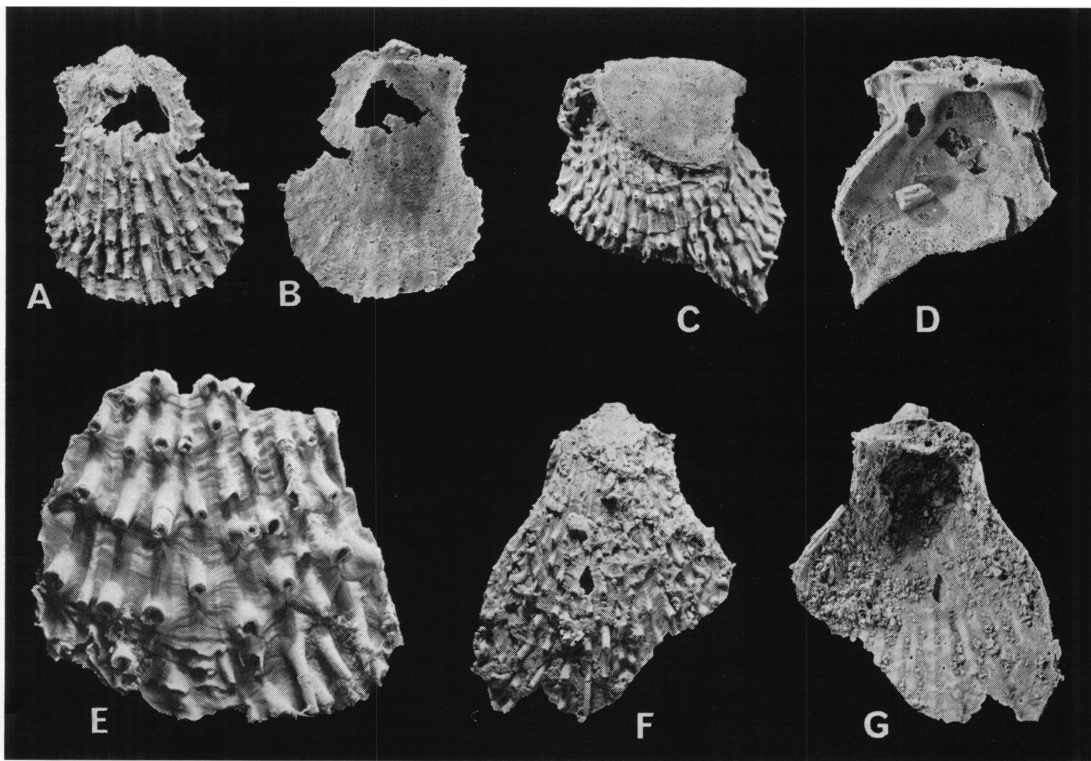


FIG. 26. *Pegmavalvula gloveri* Newell and Boyd, new species, Permian, Road Canyon Formation, Glass Mountains, western Texas. A, B. Left valve, U.S.N.M. No. 155006; U.S.N.M. 721j. C, D. Right valve, U.S.N.M. No. 154987, cemented to umbo to shell fragment; U.S.N.M. 721s. E. Shell fragment, U.S.N.M. No. 154988, showing cylindrical spines; U.S.N.M. 721j. F, G. Holotype, U.S.N.M. No. 154989, left valve; U.S.N.M. 726d. A-D, F, G, $\times 1$; E, $\times 2$.

TABLE 3
DIMENSIONS (IN CENTIMETERS) OF A SAMPLE OF *Pegmaulvalva gloveri* NEWELL AND BOYD, NEW SPECIES

Length	Height	Hinge Length	Cardinal Area Height	Resilifer Length	Resilifer Height
4.7	5.7	2.3	0.70	0.42	0.67
3.7	—	1.9	0.75	0.37	0.73
3.0+	—	1.9	0.45	0.37	0.55
2.9	3.3	1.3	0.25	—	—
2.9	—	1.5	—	0.25	—
2.7	3.0+	1.6	—	—	—
2.7	3.5	1.6	—	—	—
2.6	3.2	1.5	0.34	0.30	0.34
2.6	3.3	1.6	—	—	—
2.6	—	1.6	0.45	0.25	0.35
2.4	—	1.1	0.25	0.20	0.28
2.2	3.1	1.3	0.40	0.30	0.40
1.7	2.1	1.3	—	—	—

On left valves, the pectiniform stage is more convex than the adjacent surfaces, and it exhibits a prominent anterior subauricular sinus (fig. 25H). In the two best-preserved examples, this juvenile stage terminated at a height of 2.4 and 2.7 mm., respectively. Well-developed, subequal auricles characterize subsequent growth.

Early growth stages are non-plicate, although costae are present on umbonal areas of some valves. Plication is introduced at valve heights ranging from 0.65 to 2 cm. Spinosity, prominence of costae, and plication continuity, relief, and cross section all vary from valve to valve. The plications are relatively straight and continuous, and they are more sharply defined on left valves than on right. In the former case they commonly originate by implantation. Points of origin are not sharply defined on right valves, but new ridges seem to originate by rather indistinct bifurcation. The relief of individual plications above adjacent troughs varies from less than trough width to equal to trough width. In transverse section, their profiles vary from an inverted V to flat-topped to rounded. The costae vary from valve to valve in radial persistence, and they become less conspicuous in the ventral areas of some valves.

The primary ridges give rise to cylindrical spines. Some recurve sufficiently so that their tips are directed dorsally, whereas the distal parts of others bend forward or backward. The

spine orientation tends to vary along the height of a single valve, and the density of spines varies from specimen to specimen. The proximal part of a spine exhibits on its upper surface very fine, closely spaced growth lines convex ventrally. Spine-forming growth laminae first develop an external arch. With further growth, the lower margins of the arch approach each other and meet on the under side of the spine to form a cylinder with a longitudinal suture along the under side. Thus, the larger spines are closed, hollow, and thick-walled.

Cardinal areas vary in outline from triangular to nearly rectangular. Their variation in dimensions is shown in table 3. The right cardinal area commonly forms a 90-degree angle with the plane of commissure. In the smallest specimens the cardinal area ranges from the plane of commissure to an attitude nearly at right angles to that plane. On the other hand, the cardinal area of the left valve characteristically is parallel with the plane of commissure. Less commonly, it curves slightly inward (apsacline) or outward (anacline).

The resilifers of both valves are triangular, and the height of the resilifer is invariably greater than its length along the hinge (table 3).

Pegmaulvalva delicata Newell and Boyd,
new species

Figures 7H, I, 27

DIAGNOSIS: Shell small, ovoid, a little higher

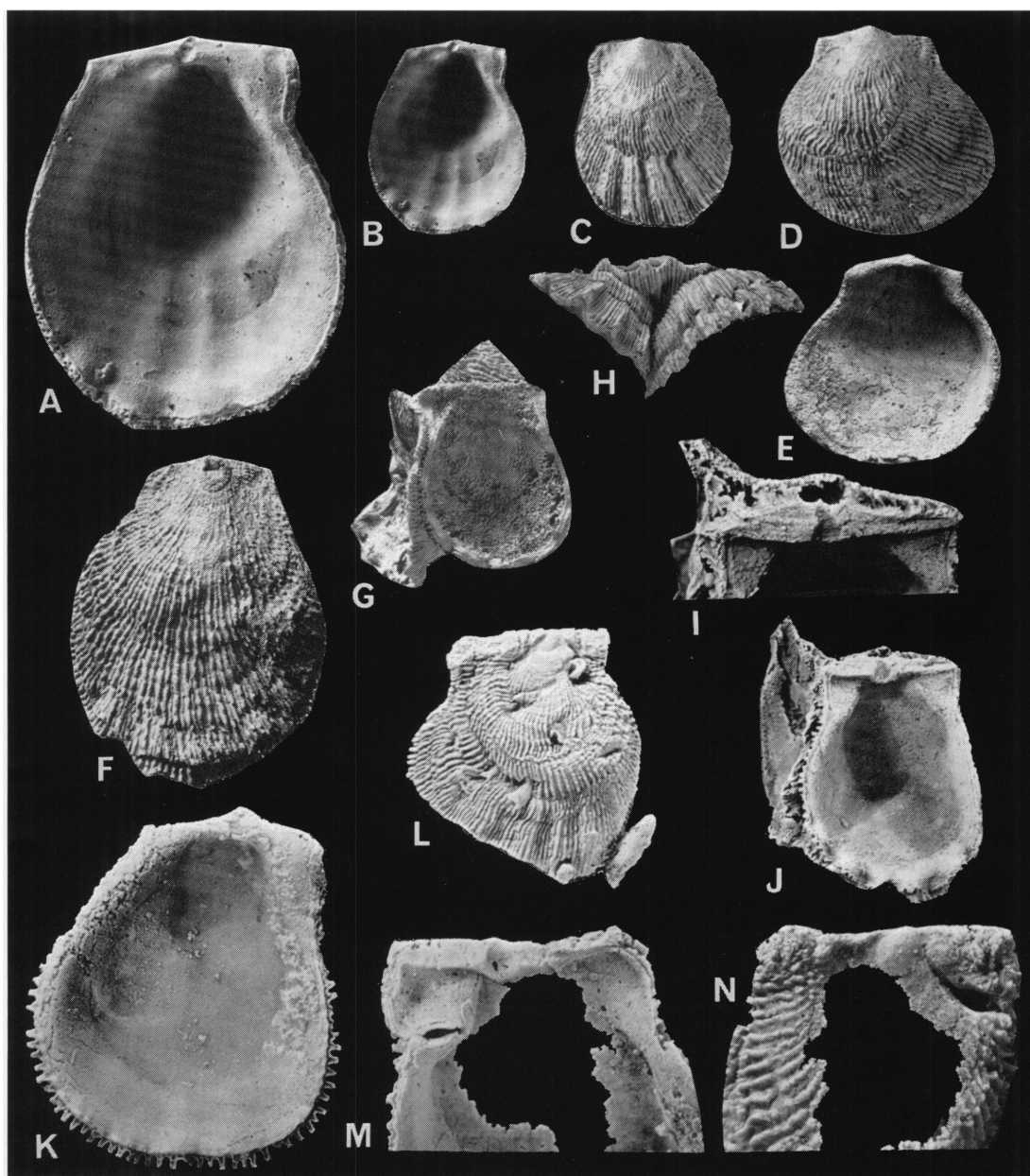


FIG. 27. *Pegmavalvula delicata* Newell and Boyd, new species, Permian, western Texas. A–C. Holotype, A.M.N.H. No. 28928, left valve; A.M.N.H. 512, Lower Getaway. D, E. Left valve, A.M.N.H. No. 28929; A.M.N.H. 512, Lower Getaway. F. Relatively large left valve, U.S.N.M. No. 155008; U.S.N.M. 703c, Road Canyon. G, H. Two right valves, A.M.N.H. No. 28916, cemented to a third; A.M.N.H. 512, Lower Getaway. I, J. Right valve, A.M.N.H. No. 28931, showing spine attachment along cardinal margin, except at nepionic stage, over beak; A.M.N.H. 512, Lower Getaway. K. Left valve, A.M.N.H. No. 28934, showing marginal spines and adductor mark; A.M.N.H. 512, Lower Getaway. L. Right valve, A.M.N.H. No. 28930, with embedded shell fragments; A.M.N.H. 512, Lower Getaway. M, N. Right valve, U.S.N.M. No. 155009, showing obsolescent byssal notch in early growth stage; U.S.N.M. 721u, Cathedral Mountain. A, $\times 4$; B–H, L, $\times 2$; I, K, M, N, $\times 5$; J, $\times 3$.

than long, plicated, sculptured with closely spaced, fine, scaly costellae of uniform width and spacing, approximately 80 to 100 in number along shell margin; attached over upper one-third, or more, of right valve and by small spines along hinge margin on both sides of beak; hinge relatively long, about three-fifths of length of shell, cardinal areas equal and narrow.

DISTRIBUTION: Leonardian-early Guadalupian, western Texas. Cathedral Mountain: U.S.N.M. ?702, 702a, 702b, 721u, 726o. Road Canyon: U.S.N.M. 703c. Willis Ranch: U.S.N.M. 706e. Lower Getaway: A.M.N.H. 496, 512; U.S.N.M. 728, 732.

DISCUSSION: The proportions vary in these small shells. Their convexity, more easily measured in left valves than in the attached right valves, is commonly slightly more than one-third of their length. The maximum length is slightly ventral of mid-height and varies from being nearly equal to the height to being significantly less than the height. The median radial profile of the right valve is controlled in the attachment area by the form of the substrate. In cases in which this resulted in a flat or concave external profile, subsequent growth commonly was outward from the attachment surfaces. The result is relief approaching that of the left valve.

When the profile is viewed normal to the hinge, front and rear slopes are equal in most left valves, and also in some right valves, but many of the latter have either the anterior or the posterior slope relatively steeper.

The straight hinge margin forms the dorsal extremity of the right valve, whereas in the left valves the beak rises slightly above the hinge line and generally, but not invariably, is situated at the midpoint of the hinge.

There is an anterior auricle, and in many valves a smaller posterior auricle is developed. Rarely, the two are equal in size. Valve margins are characterized by a slight to moderately well-developed re-entrant below the anterior auricle. A sinus also is present beneath the posterior auricle in some individuals. In cases in which a re-entrant is absent, the posterior margin meets the hinge line at a right or larger angle. Apart from the asymmetry of the auricles, most valves are approximately equilateral, but some are expanded posteroventrally (retrocrescent) and a few are expanded anteroventrally (procrescent).

An early free stage is recognizable at the beak of the right valve. Several examples consistently achieved a hinge length of 1.4 mm. before cementation took place. Subsequent lengthening of the hinge was characterized by cementation. The byssate stage appears to have persisted to a

TABLE 4
DIMENSIONS (IN CENTIMETERS) OF A SAMPLE OF *Pegmavalvula delicata* NEWELL AND BOYD, NEW SPECIES,
FROM LOWER GETAWAY LIMESTONE (A.M.N.H. 512)

Length	Height	Hinge Length	Cardinal Area Height	Resilifer Length	Resilifer Height
1.7	1.9	1.1	—	—	—
1.5	1.4	0.8	—	—	—
1.5	1.5	1.0	—	—	—
1.4	1.7	0.8	—	—	—
1.3	1.6	0.8	—	—	—
1.3	1.6	1.0	—	—	—
1.1	1.3	0.8	0.09	0.08	0.10
1.1	1.4	0.6	—	—	—
1.1	1.3	0.5	0.07	0.08	0.10
1.1	1.3	0.9	—	—	—
1.1	1.3	0.7	0.07	0.06	0.08
1.0	1.4	0.6	—	—	—
0.9	1.2	—	—	0.07	0.10
0.9	1.2	0.5	0.09	0.07	0.10
0.9	1.0	0.5	—	—	—
0.8	1.1	0.6	0.12	0.09	0.12
0.8	1.1	0.4	—	—	—
0.7	0.9	0.6	—	—	—

valve height of 6 mm. On left valves, an early growth stage at the beak is set apart by absence or near absence of ornamentation and, in some cases, by greater convexity than that of the adjacent surface area. In a sample of 10 left valves, the height of this early stage varies from 1.7 to 4.5 mm.

The costellae are sharply defined and closely spaced. The relief of an individual costella above the valve surface generally is equal to, or greater than, the space between adjacent costae, and they increase in number by implantation. Very fine, closely spaced growth lines form ventrally concave arcs in depressions between costae and form chevrons downward convex on the costae. The longitudinal continuity of the costae is interrupted by growth irregularities, and in places they are sinuous. Some valves show strong plication in late stages of growth; others show only a trace of plication; and some lack it entirely. The plications are folds affecting the entire thickness of the valve near the ventral margin. The exterior surface maintains uniform costellate sculpture both on the ridges and in the troughs.

The cardinal area on both left and right valves is very low and, in most cases, is indistinct. The central part bears a small resilifer, and the distal parts commonly grade imperceptibly into the auricles. The cardinal area is parallel to the plane of commissure in most left valves, but in some left valves the cardinal area slopes inward slightly (apsacine). This attitude of the cardinal area is difficult to categorize in most of our right valves because of inadequacies of preservation and small size. In two specimens, the area slopes slightly inward (apsacine); in another, slightly outward (procline).

No internal ridge of the sort found in *Pro-spondylus acineta* is present between resilifer and muscle scar. The single adductor scar, slightly above mid-height on the posterior side, is rather large in the few valves in which it is recognizable. Its height approaches one-fourth of that of the valve. In most valves the scar is not recognizable.

FAMILY TERQUEMIIDAE COX, 1964

Figures 4, 7F, G, 28–32

DIAGNOSIS: Small, irregularly subovate shells with radial ribs; right valve deeply convex, with high cardinal area; ligament amphidetic, external, with triangular resilifers; shell cemented at right valve umbo, or at intermediate areas of

right valve; auricles absent or poorly developed, byssal notch absent in adults; with or without primitive isodont dentition similar to Spondylidae.

DISTRIBUTION: Lower Permian (Wolfcampian) to Upper Jurassic (Oxfordian).

DISCUSSION: This poorly understood, mainly early Mesozoic, family has been reviewed by Cox (1969). None of the genera is adequately understood. We have been unable to obtain good representative specimens of the family. Evidently, the terquemiids are rare fossils.

Some of the citations in the literature to early and middle Triassic *Enantiostreon* Bittner pertain to oyster-like, plicated shells rather than to costate forms such as the type species of *Terquemina* Tate, 1867; *Newaagia* Hertlein, 1952; and *Enantiostreon* Bittner, 1901. The plicated shells probably are oysters related to *Lopha* Röding, 1798. Cox (1969) doubtfully referred *Placunopsis* Morris and Lycett, 1853, to this family; we believe that it does not belong there.

It appears that our Texas Permian specimens, described below, are by far the best-preserved and most abundantly represented members of this group. They probably are related to the Triassic genera *Terquemina* and *Newaagia*, but some uncertainty will remain until those genera are adequately understood.

PALEOWAAGIA NEWELL AND BOYD. NEW GENUS

Figures 7F, G, 28–32

DIAGNOSIS: Finely costate, spiny, ostreiform shells with deeply convex right valve possessing a high cardinal area and a nearly flat left valve; nepionic shell pectiniform, with byssal notch which is overgrown and disappears during later growth; dentition lacking.

DISTRIBUTION: Wolfcampian–early Guadalupian, western Texas.

*Paleowaagia cooperi*¹ Newell and Boyd, new species

Figures 7F, G, 28–32

DIAGNOSIS: Same as for genus *Paleowaagia*.

DISTRIBUTION: Wolfcampian–early Guadalupian, western Texas. Neal Ranch: U.S.N.M. 701a, 701b, 701c, 701g, 701h, 727e. Skinner

¹ Named in honor of Dr. G. Arthur Cooper, of the United States National Museum, who discovered the shells of this species.

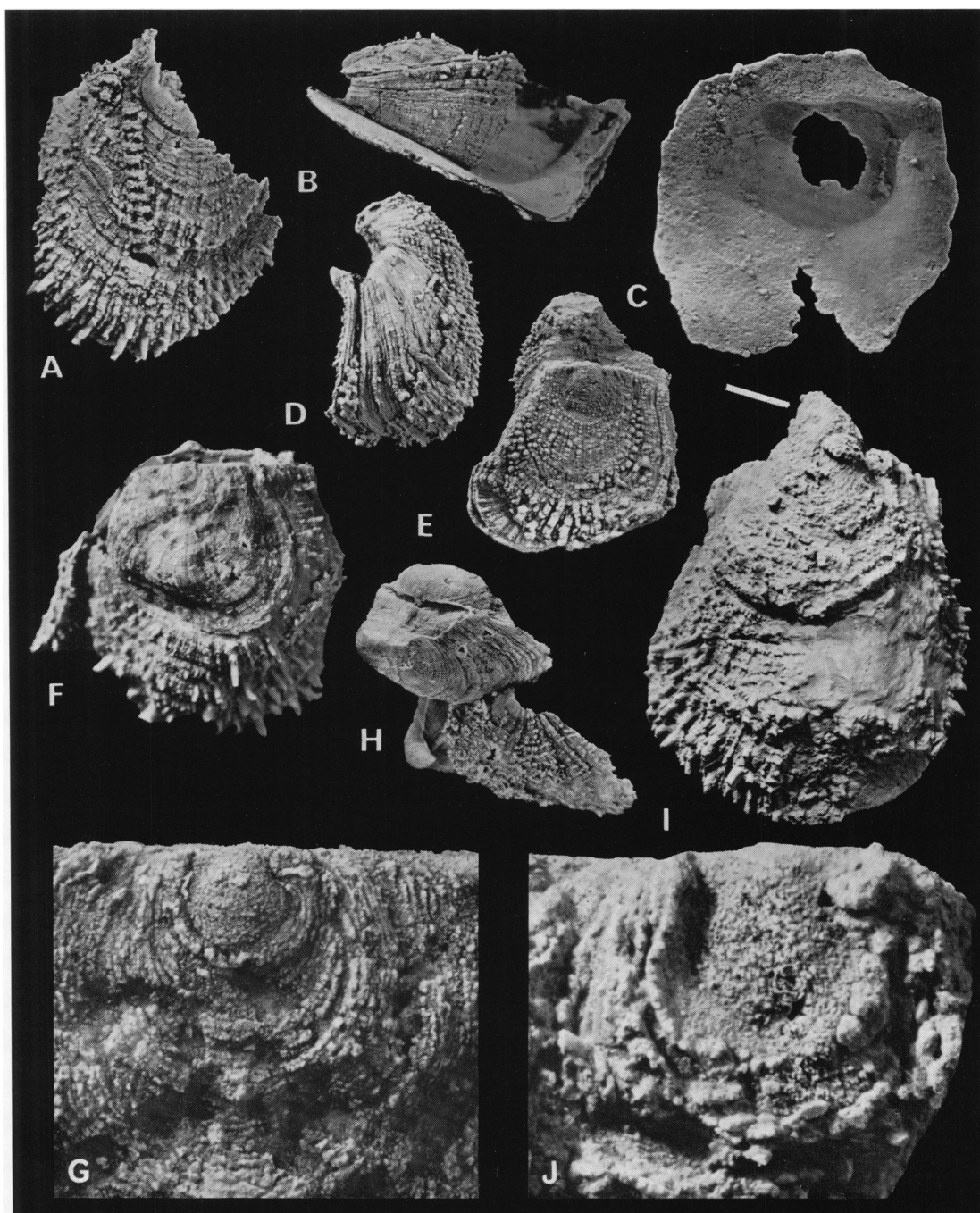


FIG. 28. *Paleowaagia cooperi* Newell and Boyd, new species, silicified specimens, Wolfcampian, Neal Ranch Formation, Glass Mountains, western Texas, from U.S.N.M. 701g, except otherwise indicated. A. Right valve, U.S.N.M. No. 154997, attached to crinoid column. B. Anterior view of bivalved individual, U.S.N.M. No. 155003, cemented to shell fragment. C. Interior opercular left valve, U.S.N.M. No. 154998; U.S.N.M. 707d. D, E. Posterior and left side views, respectively, of U.S.N.M. No. 155000, showing resupinate convexity. F, G. Umbonal area, right valve, U.S.N.M. No. 155001. F. Showing ontogenetic changes in ornamentation. G. Showing early byssal notch. H. Right valve (below), U.S.N.M. No. 155002, cemented to two orthotetid brachiopods. I, J. Right valve, U.S.N.M. No. 154999, showing early pectiniform stage asymmetrically placed on left side of umbo (see pointer). A, H, $\times 1$; B, D-F, I, $\times 2$; C, $\times 1.5$; G, J, $\times 20$.

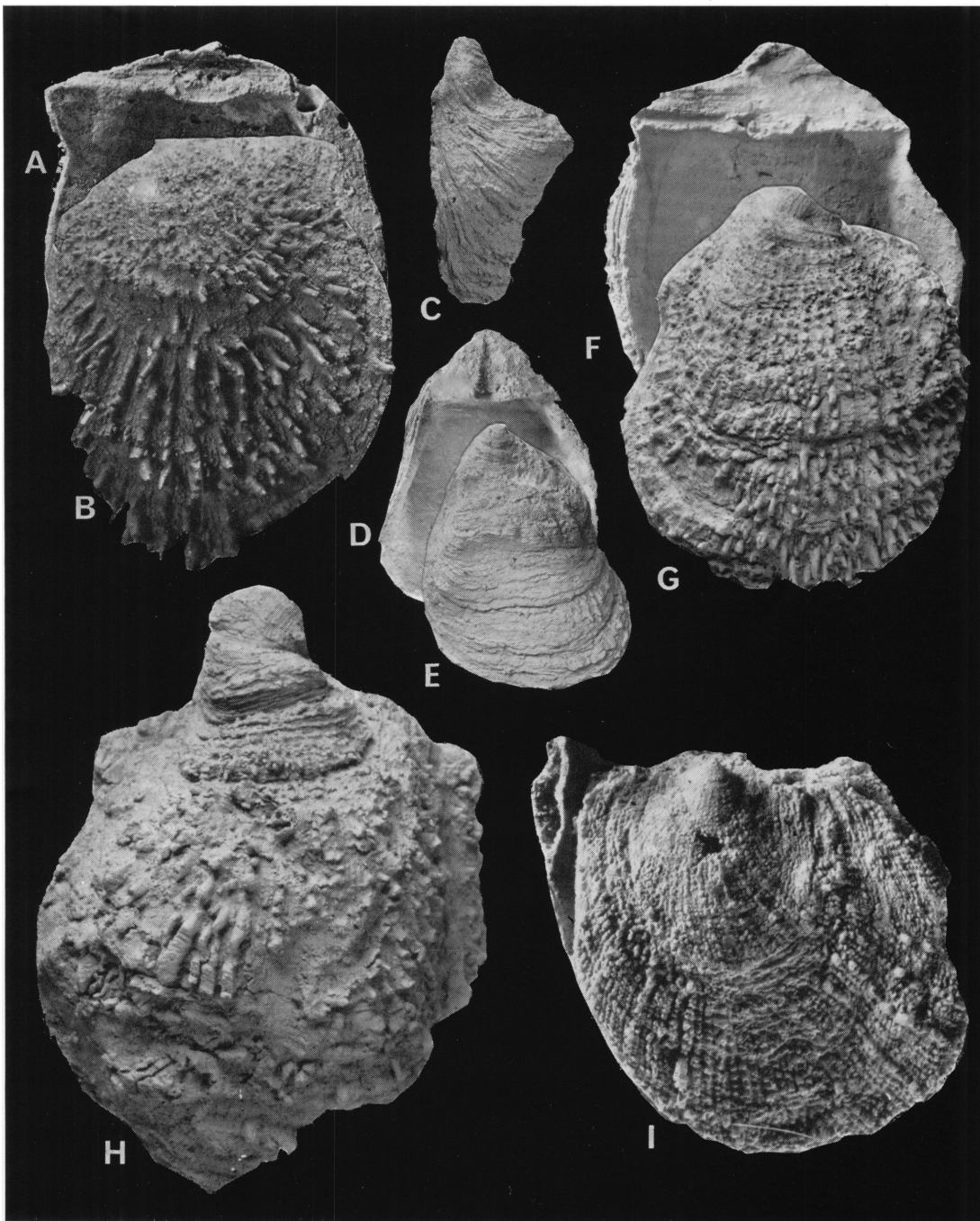


FIG. 29. *Paleowaagia cooperi* Newell and Boyd, new species, silicified specimens, Wolfcampian, Neal Ranch Formation, Glass Mountains, western Texas. A, B. Left valve, U.S.N.M. No. 154990; U.S.N.M. 701g. C-E, Right valve, U.S.N.M. No. 154991; U.S.N.M. 701a. F, G. Right valve, U.S.N.M. No. 154992; U.S.N.M. 701g. H. Right valve, U.S.N.M. No. 154993; U.S.N.M. 701a. I. Left valve, U.S.N.M. No. 154994; U.S.N.M. 701a. A, B, F, G, $\times 2$; C-E, $\times 1$; H, $\times 4$; I, $\times 5$.

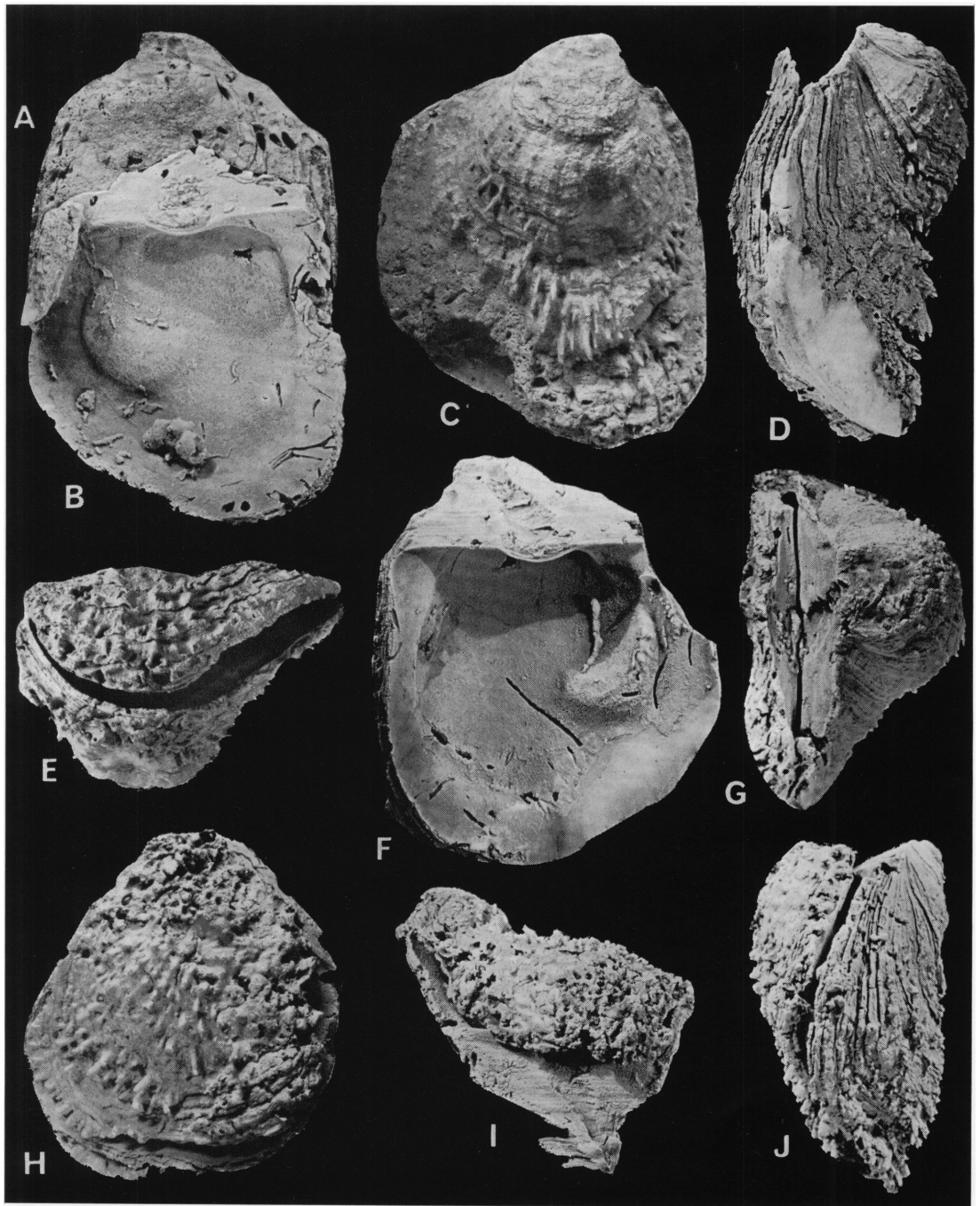


FIG. 30. *Paleowaagia cooperi* Newell and Boyd, new species, silicified specimens, Permian, Cathedral Mountain Formation, Glass Mountains, western Texas; U.S.N.M. 702. Salient features include resupinate convexity, elevated adductor marks, and relatively more concentrated barnacle borings on the relatively flat left (upper) valve. A-G. Holotype, U.S.N.M. No. 154995. A, B. Left valve. C. Right valve. D. Posterior view of articulated valves. E. Ventral view, right valve, below. F. Interior, right valve. G. Hinge view, right valve to right. H-J. Another bivalved individual, U.S.N.M. No. 154996. All $\times 1$.

Ranch: U.S.N.M. 707d, 707w, ?720e. Cathedral Mountain: U.S.N.M. 702, 721u. Road Canyon: U.S.N.M. 710u, 721j, ?722e, ?726d. Willis Ranch: U.S.N.M. ?706, 706e. Lower Getaway: A.M.N.H. 512.

DISCUSSION: The large collection of shells available for study was obtained mainly from two localities. Many more right valves than left valves are represented, and relatively few articulated shells are present. Most valves in the collection range in height from 2 to 4 cm., although the total height range in the collection is from less than 1 to more than 6 cm. The change in height and length with increase in size is shown in figure 31.

There is a striking but superficial resemblance to certain brachiopods, such as aulostegids and strophalosiids, created by development of a high cardinal area of the attached (right) valve and by the roughly equilateral symmetry of the shell.

The bowl-shaped right valves vary greatly in median radial profile (fig. 32). Such profiles typically are convex outward in varying degrees, but geniculate profiles probably reflect induced changes in growth. Some median radial profiles show a tendency for reversal of convexity late in ontogeny.

Right valves are asymmetrically convex, with the anterior slope usually steeper than the posterior. These valves possess a prominent, triangular cardinal area in which the height commonly is about one-half of the length of its base, but these proportions are quite variable. The triangle is essentially symmetrical in a few cases, but ontogenetic increase in hinge length is unequal on the two sides of the beak, and such cardinal areas are anteriorly or posteriorly extended in about equal frequency within our sample.

The average base of the cardinal area is about two-thirds of the length of the shell.

An acutely triangular resilifer occupies the central part of the cardinal area and, in its superficial resemblance to a delthyrium, enhances the resemblance between this bivalve and certain brachiopods. The width of the resilifer along the hinge line varies from one-fourth to three-fourths of its height, although the ratio is commonly between one-third and one-half. The angle formed by the cardinal area and the plane of commissure commonly is greater than 45 degrees (apsacline), and in some valves it is more or less parallel with the commissure.

Auricles are present on some right valves, but they are not prominent. Other valves lack auricles. In right valves possessing auricles the longer of the two may be either anterior or posterior.

The relatively flat left valves are less variable in form than are the right valves. The position of the beak along the hinge line varies from being slightly anterior to being slightly posterior to the midpoint.

The shells of this genus commonly display a rectangular outline. Median radial profiles through the beak in left valves commonly are flat to slightly convex, rarely concave outward. In the latter case, there is an ontogenetic change from convex in the umbonal region to concave peripherally.

The low cardinal area of the left valve lies approximately in the plane of the commissure or forms an obtuse angle to it, a relationship that is fairly characteristic throughout the Aviculopectinidae and Pseudomonotidae. The resilifer

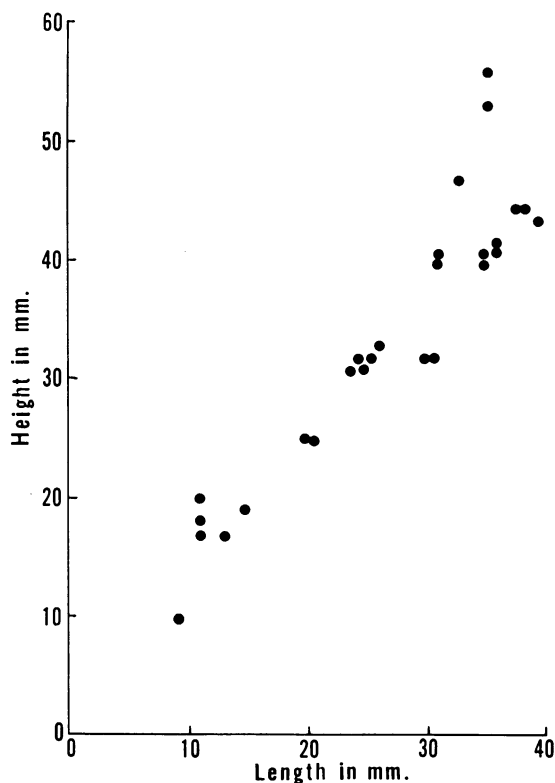


FIG. 31. Scattergram of linear dimensions of *Paleowaagia cooperi* Newell and Boyd, new species, showing an orthometric growth trend for these variates.

is wider along the hinge than the dimension of the height, and it extends slightly below the hinge axis.

Many left and right valves give an over-all impression of bilateral symmetry in their later growth stages, but others show a slight tendency for either retrorescent or prorescent expansion. These conditions are about equally frequent in the collection.

Surface spines vary from valve to valve in area of distribution, spine size, spacing, and orientation. Among the right valves of the collection, very few are spinose over the whole surface, and many more are relatively free of spines. The latter have a rather gnarled aspect reflecting interruptions and irregularity of growth not so apparent in the spiny individuals. In a few valves, the spines are arranged in radial rows, whereas in others the spines are crowded and lack any obvious pattern.

The spines commonly are short and straight, and many are nearly solid. All possess the longitudinal furrow on the under side characteristic of hyote spines. They range from being tangential to the shell surface to being nearly erect. In cases in which they are arranged in orderly rows, their spacing within the rows is variable. In these cases, rows of large spines are commonly separated by rows of minute spines. Rows of tiny granules coalesce to form costae in some cases. The relatively few articulated specimens retaining both valves are mostly small shells. These generally are more spinose on the left than on the right valve.

In early development the right valve is pectiniform, and this growth stage is retained at or near the apex of the umbo. This stage evidently was uncemented and free-living, because it bears the growth traces of a byssal notch 1 mm. or less in length. On one specimen, the beak of the pectiniform stage bears a small knob 0.24 mm. in diameter, with traces of several concentric

growth lines. This may be the prodissoconch. The byssal notch is not traceable to the beak of the pectiniform stage, and the prodissoconch presumably lacked the notch.

Growth of the right valve, subsequent to the nepionic pectiniform state, closed the byssal notch and assumed a quite different pattern. An increase in height of the cardinal area accelerated in rate as compared with the lateral growth. Later growth in some individuals involved abrupt lateral and ventral expansion which characterized mature growth. In such shells, the early formed part of the right valve resembles a proboscis from 0.3 to 1 cm. in length. In other cases, growth changes are gradual, and the early part of the valve is roughly pyramidal in form.

The location of the early pectiniform stage in adult valves varies greatly as a result of unequal growth gradients along the hinge. In one individual the hinge line of the pectiniform stage lies along the posterodorsal edge of the cardinal area, forming an angle of 65 degrees with the adult hinge line. In another case the nepionic hinge lies along the anterior margin of an asymmetric cardinal area and forms an angle of 110 degrees with the adult hinge.

These irregularities of the right valve were probably induced by variations in the substrate. For example, some valves are welded transversely to crinoid stems and brachiopods, (fig. 28A, H). The right valve was molded around these and other objects. There is, however, no xenomorphic reflection on the left valve.

Relatively few valves are attached to other *Paleowaagia* shells. Mostly they are cemented to brachiopods. Only one specimen was observed to bear an imprint of a foreign object in its beak area. In this case, initial growth caused the shell to spread over the flat surface of a crinoid columnar for about 5 mm. It then grew abruptly outward, forming a deflection of 110 degrees in its profile.

The left valves lack a sharply defined nepionic stage. No sharply defined outline analogous to the pectinoid form of the right valve was observed. The shell surface is not ornamented in the beak area. This smooth surface extends for a radius of several millimeters from the beak.

The inner layer is not preserved in many valves. In this condition the cardinal area is also missing. On well-preserved valves, the single muscle scar is nearly 1 cm. in diameter, distinctly

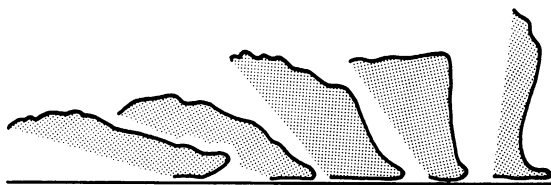


FIG. 32. Variation in profile of right valves of *Paleowaagia cooperi* Newell and Boyd, new species, as viewed from posterior margin.

imprinted to the posterior and well above mid-height. More commonly, the muscle impression is faint, or there is no visible trace at all.

The right valves have a broadly rounded umbonal cavity beneath the hinge plate. Left valves exhibit a small and low umbonal cavity. In some cases, this is simply a small excavation below the resilifer.

SUPERFAMILY ANOMIACEA RAFINESQUE, 1815

FAMILY ANOMIIDAE RAFINESQUE, 1815

DIAGNOSIS: Thin-shelled, ostreiform, sub-circular filibranch bivalves adapted to hard substrates to which they adhere dextrally by means of a subcentral calcified byssus that passes through a deep byssal aperture below dorsal margin of right valve; byssus attached to left valve by greatly enlarged and modified retractor, the byssal "adductor" muscle, which aids valve adductor muscle in opening and closing movements; anterior and posterior pedal retractor scars clustered around byssus in dorsal part of mantle chamber; hinge edentulous, with amphidetic internal ligament supported on right valve by chondrophore process; cardinal areas and hinge line lacking.

DISCUSSION: The general physiognomy of our Permian fossils clearly is anomiacean. The more or less equilateral form, usually somewhat deformed by attachment, the lack of auricles and cardinal areas, the central complex of muscles—all are strongly reminiscent of neotremate brachiopods, and it is probable that the superficial similarities represent evolutionary convergence toward a common mode of life.

In any case, *Permanomia* bears little resemblance to early pectinaceans or any other Paleozoic Pterioida. Unfortunately, our examples are silicified so that we cannot ascertain the original microfabric of the shell. For example, did those forms possess an inner shell layer of crossed-lamellar aragonite? Nothing is known about the ancestry of the Permian species, and anomiiids are not recorded in the Lower Triassic. In fact, little is known of the morphology of early Mesozoic representatives of the family. Right valves of *Permanomia* are not represented in our collection, so many questions about the genus must for the present be unanswered.

To our knowledge, these fossils represent the first acceptable record of Paleozoic anomiaceans. Gemmellaro's *Anomia prisca* from the Sosio

Permian beds of Sicily (Gemmellaro, 1892, pl. 24, figs. 28, 29) may be, but is not certainly, an anomiacean also. The few other references to Paleozoic occurrences of the group are unwarranted.

PERMANOMIA NEWELL AND BOYD, NEW GENUS

Figures 33, 34

TYPE SPECIES: *Permanomia texana* Newell and Boyd, new species.

DIAGNOSIS: Left valve unornamented; musculature consisting of many elements distributed around a large, elevated, horseshoe-shaped, pedal adductor scar which embraces below a small, centrally situated valve adductor; posterior pedal retractor underlying rear prong of pedal adductor, more ventrally situated semi-circular chain of muscle pits, probably gill suspensors; two or three small muscle pits below ligament, probably pedal adjusters; ligament submedian, amphidetic, duplivincular.

DISTRIBUTION: Leonardian, early Guadalupian, western Texas.

DISCUSSION: From other genera of the Anomiidae, *Permanomia* is distinguishable by general features of its musculature, and its duplivincular ligament is unknown in other anomiiids.

These characteristics may warrant the creation of a separate new family for the Permian forms. Such action, however, would be premature until the characteristics of right valves can be made known.

Permanomia texana Newell and Boyd, new species

Figures 33, 34

DIAGNOSIS: Same as for the genus *Permanomia*.

DISTRIBUTION: This species is known thus far only from western Texas in Leonardian and early Guadalupian beds: Bone Spring Limestone: U.S.N.M. ?728e, 728f. Cathedral Mountain Formation: U.S.N.M. 702, 721u, 726o. Road Canyon Formation: U.S.N.M. 703c, 721z, 726z. Willis Ranch Member, Word Formation: U.S.N.M. 706, 706e; A.M.N.H. 505. Limestone lens between Willis Ranch and Apple Ranch members, Word Formation: U.S.N.M. 706b. Word Formation: U.S.N.M. 732c. Lower Getaway Limestone Member, Cherry Canyon Formation: U.S.N.M. 728; A.M.N.H. 512.

DISCUSSION: Some 170 anomiid valves in our Permian collections from western Texas are referred to this species.

Curiously, right valves have not been recognized. Although a few relatively flat valves are present, in all cases they either exhibit left-valve musculature or the umbonal area is broken, and the presence or absence of a byssal opening cannot be determined.

The two largest valves have a maximum dimension of 4.20 cm., but most of the specimens are less than 3.50 cm. across. They are rounded in outline, with the beak at the margin, and many are nearly equilateral. Less symmetrical valves exhibit posterior more commonly than anterior expansion. Proportions vary, from valves with circular outlines to those with the height somewhat greater than the length to others in which the length is the greatest dimension.

Commonly bowl-shaped, the valves differ in convexity from being very shallow to being very deep. The ratio of convexity to maximum dimension varies from 1/6 to 1/2 (table 5). There is a tendency for development of a low umbo in some valves.

Exterior surfaces vary from smooth to gnarled, with irregular growth lines and wrinkles.

TABLE 5

DIMENSIONS (IN CENTIMETERS) OF A SAMPLE OF LEFT VALVES OF *Permanomia texana* NEWELL AND BOYD, NEW SPECIES, LOWER GETAWAY MEMBER, CHERRY CANYON FORMATION (A.M.N.H. 512)

Valve	Maximum Linear Dimension	Convexity
1	1.12	0.21
2	1.46	0.35
3	1.79	0.38
4	1.80	0.30
5	1.99	0.61
6	2.00	0.93
7	2.16	0.89
8	2.50	0.54
9	2.53	0.98
10	3.10	0.95
11	3.18	1.54
12	3.23	0.78
13	3.23	1.01
14	3.65	0.75
15	3.92	0.77

TABLE 6

DIMENSIONS (IN CENTIMETERS) OF A SAMPLE OF LEFT VALVES OF *Permanomia texana* NEWELL AND BOYD, NEW SPECIES, LOWER GETAWAY MEMBER, CHERRY CANYON FORMATION (A.M.N.H. 512)

Valve	Maximum Linear Dimension	Ligament Width	Ligament Height
1	3.20	0.78	0.37
2	3.00	0.64	0.25
3	4.00	0.70	0.23
4	3.20	0.81	0.30
5	4.00	0.91	0.25
6	2.50	0.52	0.15
7	2.86	0.46	0.14

All well-preserved interiors exhibit a prominent, commonly elevated, horseshoe-shaped scar, the pedal adductor. This scar is symmetrical in some examples, whereas in others the posterior lobe is shorter and broader than the anterior. Other muscle attachment sites are less distinct.

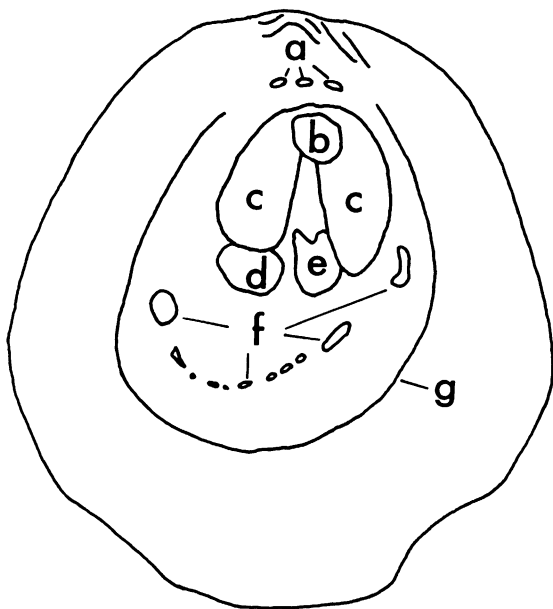


FIG. 33. Composite diagram, interpreting muscle marks in left valve of *Permanomia texana* Newell and Boyd, new species.

Abbreviations: a, probably pedal adjusters; b, proximal end of byssal plug; c, bifid pedal adductor; d, posterior pedal retractor; e, valve adductor; f, possibly gill suspensories; g, pallial line.

A roughly circular indentation, probably the posterior byssal retractor attachment site, typically is found just below the posterior lobe of the horseshoe-shaped scar.

Other topographic depressions possibly related to muscle attachment are found less con-

sistently in the collection both above and to the upper left of the horseshoe-shaped scar.

The umbonal area is missing in many specimens. In those that retain this area, the dorsal margin is thickened, especially in larger valves, and this margin is interrupted by a triangular

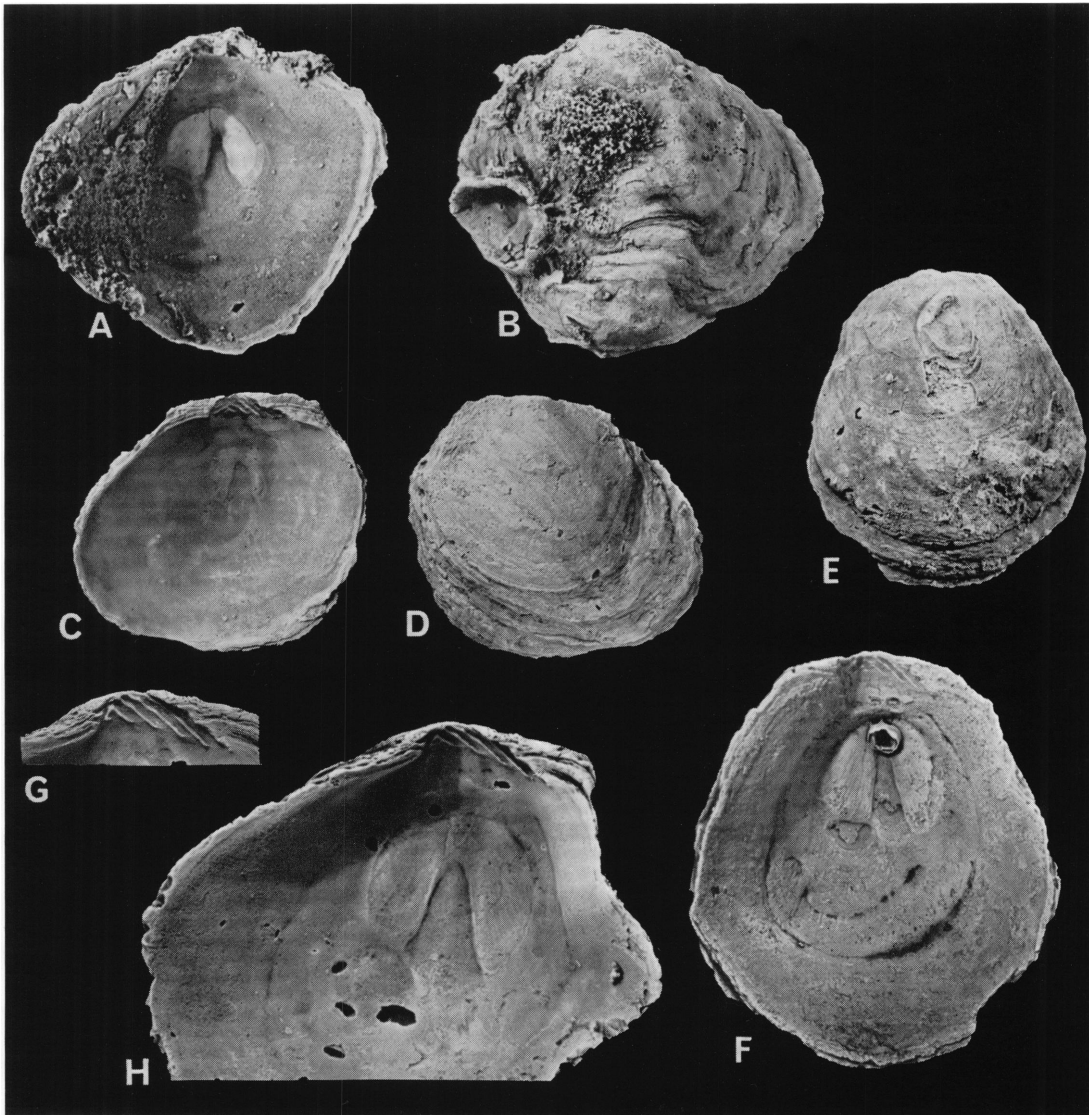


FIG. 34. *Permanomia texana* Newell and Boyd, new species, from a single locality, Permian, Lower Getaway Limestone, Cherry Canyon, Guadalupe Mountains area, western Texas. A, B. U.S.N.M. No. 155010, specimen with numerous external epizoans and well-preserved, hoof-shaped pedal adductor, the most distinguishing feature of the genus; U.S.N.M. 728. C, D. A.M.N.H. No. 28935, specimen showing hinge and musculature; A.M.N.H. 512. E, F. Holotype, A.M.N.H. No. 28936, showing musculature and hinge; A.M.N.H. 512. G, H. Topotype, A.M.N.H. No. 28937, showing unusually well-preserved hinge details; A.M.N.H. 512. A-D, H, $\times 2$; E, $\times 1$; F, $\times 1.5$; G, $\times 3$.

ligament depression beneath the beak. The base of the depression, or resilifer, commonly is two to three times its height (table 6).

The ligament depression contains as many as five sloping ridges between multiple ligament grooves. The first-formed ones are parallel to the anterior margin of the area, whereas commonly

one or two of the last-formed ridges include a smaller, posteriorly inclined leg, thus forming asymmetric chevrons.

This species is represented in collections from Bone Spring Limestone, Getaway Member of the Cherry Canyon Formation, and Word Limestone 3 (see tables 1 and 2).

REFERENCES CITED

- ANTHONY, R.
1905. Influence de la fixation pleurothétique sur la morphologie des mollusques Acéphales Dimyaires. *Ann. Sci. Nat., Zool.*, vol. 1, pp. 165–397.
- BATHURST, R. G. C.
1964. The replacement of aragonite by calcite in the molluscan shell mold. In Imbrie, John, and Norman D. Newell (eds.), *Approaches to Paleocology*. New York, John Wiley and Sons, Inc., pp. 357–376.
- BEYRICH, H. E.
1862. Zwei aus dem deutschen Muschelkalk nach nicht bekannte aviculiartige Muscheln. *Deutsche Geol. Gesell. Zeitschr.*, vol. 14, pp. 9–10.
- BØGGILD, O. B.
1930. The shell structure of the mollusks. *Danske Vidensk. Selsk. Skr., Nat. Math. Afd.*, ser. 9, vol. 2, pp. 233–325, 10 figs., 15 pls.
- BOYD, D. W., AND NORMAN D. NEWELL
1968. Hinge grades in the evolution of crassatellacean bivalves as revealed by Permian genera. *Amer. Mus. Novitates*, no. 2328, 52 pp., 24 figs.
- COOPER, G. A.
1946. Permian studies at the Smithsonian Institution, Washington. *Science*, vol. 104, pp. 15–16.
- COOPER, G. A., AND RICHARD E. GRANT
1966. Permian rock units in the Glass Mountains, west Texas, U.S. Geol. Surv. Bull. 1244–E, 9 pp.
- COX, L. R.
1932. Further notes on the Trans-Jordan Trias. *Ann. Mag. Nat. Hist.*, ser. 10, vol. 10, pp. 93–113.
1964. Notes concerning the taxonomy and nomenclature of fossil Bivalvia (mainly Mesozoic). *Proc. Malac. Soc. London*, vol. 36, pp. 39–48, 1 pl.
1969. Terquemiidae. In Moore, R. C. (ed.), *Treatise on invertebrate paleontology*, part N (Mollusca 6). Lawrence, Geological Society of America and the University of Kansas Press, p. N380.
- DAKIN, W. J.
1928. The anatomy and phylogeny of *Spondylus*, with a particular reference to the lamelli-branch nervous system. *Proc. Roy. Soc.*, London, ser. B, vol. 103, pp. 337–354, 7 figs.
- DALL, W. H.
1886. Report on the Mollusca. Part I. Brachio-poda and Pelecypoda. In Reports on the results of the dredging, under the supervision of Alexander Agassiz, in the Gulf of Mexico (1877–78) and in the Caribbean Sea (1879–80), by the U.S. Coast Survey Steamer “Blake”, Lieut.-Commander C. D. Sigsbee, U.S.N., and Commander J. R. Bartlett, U.S.N., Commanding. *Bull. Mus. Comp. Zool.*, vol. 12, pp. 171–318, pls. 1–9.
- DIENER, C.
1902. Über den Typus der Gattung *Pseudomonotis* Beyr. *Zentralbl. Min.*, pp. 342–344.
1903. Nach ein Wort über den Typus der Gattung *Pseudomonotis*. *Ibid.*, pp. 17–19.
1923. Lamellibranchiata triadica I. In *Fossilium catalogus*, I. Animalia. Berlin, pt. 19, pp. 1–259.
- DREW, GILMAN ARTHUR
1906. The habits, anatomy and embryology of the giant scallop (*Pecten tenuicostatus* Mighels). *Maine Univ. Studies*, no. 6.
- ERDMANN, W.
1934. Untersuchungen über die Lebensgeschichte der Auster. Nr. 5. Über die Entwicklung und die Anatomie der “ansatzreifen” Larve von *Ostrea edulis* mit Bemerkungen über die Lebensgeschichte der Auster. *Wissensch. Meeresuntersuchungen*, new ser., Abt. Helgoland, vol. 19, no. 6.
- FRECH, F.
1891. Die devonischen Aviculiden Deutschlands, ein Beitrag zur Systematik und Stammesgeschichte der Zweischaler. *Geol. Spezialk.*

- Preussen u. Thüringischen Staaten, Abhandl., vol. 9, 253 pp., 23 figs., 5 pls., atlas of 18 pls.
1912. Die Leitfossilien der Werfener Schichten. In *Resultate der Wissenschaftlichen Erforschung des Balatonsees*. Vienna, vol. 1, pt. 1, Paleontologie der Umgebung des Balatonsees, vol. 2, no. 1, pp. 1-96.
- GALTISOFF, P.
1964. The American oyster *Crassostrea virginica* Gmelin. U.S. Dept. Interior Fishery Bull., vol. 64, 480 pp.
- GEMMELLARO, G. G.
1892. I Lamellibranchi della fauna dei calcari con Fusulina della valle del fiume Sosio nella provincia di Palermo. Soc. Sci. Nat. Econ. Palermo, Bull., no. 1, pp. 4-11.
- GILL, J. R., AND W. A. COBBAN
1966. The Red Bird section of the Upper Cretaceous Pierre Shale in Wyoming, with a section on a new echinoid from the Cretaceous Pierre Shale of eastern Wyoming by P. M. Kier. U.S. Geol. Surv. Prof. Paper, no. 393A, pp. 1-73.
- GIRTY, GEORGE H.
1909. Palaeontology of the Manzano group of the Rio Grande valley, New Mexico. U.S. Geol. Surv. Bull. 389, pp. 41-136.
- GOLDSCHMIDT, RICHARD
1940. The material basis of evolution. New Haven, Yale University Press, 436 pp.
- GRABAU, A. W.
1931. The Permian of Mongolia. In *Natural History of Central Asia*, vol. 4. New York, the American Museum of Natural History, 665 pp., 35 pls.
- HERDMAN, W. A.
1903. Observations and experiments on the life-history and habits of the pearl oyster. In *Report to the Governor of Ceylon on the pearl oyster fisheries of the Gulf of Manaar*. London, Royal Society, pt. 1, pp. 125-146, 47 figs.
- HIND, WHEELTON
1896-1905. A monograph of the British Carboniferous Lamellibranchiata. London, Palaeontographical Society, vol. 1 (1896-1900), vol. 2 (1901-1905), 708 pp.
- HORNELL, JAMES
1909. Report upon the anatomy of *Placuna placenta*, with notes upon its distribution and economic uses. In *Report to the government of Baroda on the marine zoology of Okhmandal in Kattiawar*. London, Williams and Norgate, pt. 1, pp. 43-97., figs. 1-2, pls. 1-5.
- HUBBS, CARL L., AND LAURA C. HUBBS
1945. Bilateral asymmetry and bilateral variation in fishes. Michigan Acad. Sci., Arts, Lett., vol. 30, pp. 229-310.
- HUDSON, J. D.
1967. Speculations on the depth relations of calcium carbonate solution in recent and ancient seas. *Marine Geol.*, vol. 5, pp. 473-480.
- HUDSON, J. D., AND D. F. B. PALFRAMAN
1969. The ecology and preservation of the Oxford Clay fauna at Woodham, Buckinghamshire. *Quart. Jour. Geol. Soc. London*, vol. 124, pp. 387-418.
- ICHIKAWA, KOICHIRO
1958. Zur Taxionomia und Phylogenie der triadischen "Pteriidae" (Lamellibranch.). *Paleontographica*, vol. 3, pp. 131-212.
- JACKSON, ROBERT TRACY
1890. Phylogeny of the Pelecypoda, the Aviculidae and their allies. *Boston Soc. Nat. Hist., Mem.*, vol. 4, pp. 277-400.
- JEFFERIES, R. P. S.
1962. The palaeoecology of the *Actinocamax plenus* subzone (lowest Turonian) in the Anglo-Paris basin. *Palaeontology*, vol. 4, pp. 609-647.
- JØRGENSEN, C. B.
1946. Lamellibranchia. In *Thorson, Gunnar, Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund)*. Meddel. Komm. Danmarks Fiskeri- og Havundersøgelser, ser. Plankton, vol. 4, pp. 277-311.
- KING, W.
1850. Monograph of the Permian fossils of England. *Monogr. Palaeontogr. Soc.*, vol. 3, pt. 1, pp. i-xxxviii, 1-258, pls. 1-28.
- KONINCK, L.-G. DE
1842-1851. Description des animaux fossiles qui se trouvent dans le terrain Carbonifère de Belgique. [With supplement.] Liège, Belgium, H. Dessain, 716 pp., 60 pls.
1885. Faune du calcaire Carbonifère de la Belgique. *Lamellibranches. Mus. Roy. d'Hist. Nat. Belgique, Ann.*, vol. 11, 285 pp., 41 pls.
- KUTASSY, A.
1931. Lamellibranchiata triadica II. In *Fossilium catalogus, I. Animalia*. Berlin, pt. 51, pp. 260-477.
- LEONARDI, P.
1943. La fauna cassiana di Cortina d'Ampezzo, parte 1ª: Introduzione geologica e lamellibranchi. *Mem. Inst. Geol. Univ. Padova*, vol. 15, 78 pp., 11 pls.
- LERMAN, ABRAHAM
1965. Evolution of *Exogyra* in the late Cretaceous of the eastern United States. *Jour. Paleont.*, vol. 39, pp. 414-435.

- LIKHAREV, B.
1927. Upper Carboniferous Pelecypoda of Ural and Timan. Comité Geol. Mém., livr. 164, 126 pp., 6 pls.
1931. Materials to the knowledge of the fauna of the upper Permian of the northern provinces. Geol. Prospecting Serv., U.S.S.R., Trans., fasc. 71, 42 pp. 3 pls.
- LOGAN, A.
1967. The Permian Bivalvia of northern England. Monogr. Palaeontogr. Soc., vol. 121, no. 518, pp. 1-72, pls. 1-10.
- LOOSANOFF, VICTOR L., HARRY C. DAVIS, AND PAUL E. CHANLEY
1966. Dimensions and shapes of larvae of some marine bivalve mollusks. Malacologia, vol. 4, pp. 351-435.
- LUDWIG, WILHELM
1932. Das Rechts-Links Problem in Tierreich und beim Menschen. Berlin, Julius Springer, 496 pp.
- MAILLIEUX, EUGÈNE
1935. Contribution à la connaissance de quelques brachiopodes et pélecypodes Devonien. Mus. Roy. d'Hist. Nat., Paris, Mém., no. 70, 42 pp., 4 pls.
- MAJEWSKE, OTTO P.
1969. Recognition of invertebrate fossil fragments in rocks and thin sections. Leiden, E. J. Brill, 101 pp., 106 pls.
- MEEK, F. B.
1864. Remarks on the family Pteriidae (=Aviculidae) with descriptions of some new fossil genera. Amer. Jour. Sci., ser. 2, vol. 37, pp. 212-220.
- MEEK, F. B., AND F. V. HAYDEN
1858. Descriptions of new organic remains collected in Nebraska Territory together with some remarks on the Black Hills and portions of the surrounding country. Acad. Nat. Sci. Philadelphia, Proc., pp. 41-59.
- MOORE, RAYMOND C., CECIL G. LALICKER, AND ALFRED G. FISCHER
1952. Invertebrate fossils. New York, McGraw-Hill, 766 pp.
- NAKAZAWA, KEIJI, AND NORMAN D. NEWELL
1968. Permian bivalves of Japan. Mem. Fac. Sci., Kyoto Univ., Ser. Geol. Min., vol. 35, no. 1, pp. 1-108, pls. 1-11.
- NEWELL, N. D.
"1937" [1938]. Late Paleozoic pelecypods: Pectinacea. Kansas Geol. Surv. Bull., vol. 10, 123 pp., 20 pls.
1942. Late Paleozoic pelecypods: Mytilacea. *Ibid.*, vol. 10, pt. 2, 80 pp., 15 pls.
1955. Permian pelecypods of East Greenland. Meddel. om Grønland, vol. 110, no. 4, 36 pp.
1960. The origin of the oysters. Internatl. Geol. Congr., Rept., 21st Sess., Norden, pt. 2, pp. 81-86.
- NEWELL, NORMAN D., AND FRANK E. MERCHANT
1939. Discordant valves in pleurothetic pelecypods. Amer. Jour. Sci., vol. 237, pp. 175-177.
- NICOL, DAVID
1944. Observations on *Pseudomonotis*, a late Paleozoic pelecypod. Nautilus, vol. 57, pp. 90-93.
1968. Are pelecypods primarily infaunal animals? *Ibid.*, vol. 82, pp. 37-45.
- OBERLING, J. J.
1964. Observations on some structural features of the pelecypod shell. Naturf. Gesell. Bern, Mitt., new ser., vol. 20, 63 pp.
- PAUL, H.
1941. Lamellibranchiata infracarbonica. In Fossilium catalogus. Neubrandenburg, pt. 91, 348 pp.
- RAFINESQUE, C. S.
1815. Analyse de la nature ou tableau de l'univers et des corps organisés, Palermo, 224 pp.
- REYMENT, R. A.
1958. Some factors in the distribution of fossil cephalopods. Stockholm, Contrib. Geol., vol. 1, pp. 97-184.
- SCHLOTHEIM, E. F.
1816. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. Akad. Wiss. München, Denkschr., Math.-Phys., Kl., vol. 6, pp. 13-36. 8 pls.
- SEILACHER, ADOLF
1953. Studien zur Palichnologie I. Über die Methoden der Palichnologie. Neues Jahrb. Geol. Paläont., vol. 96, pp. 421-452, 14 figs., 2 pls.
1953. Studien zur Palichnologie II. Die fossilen Ruhrspuren (Cubichnis). *Ibid.*, vol. 98, pp. 87-124, 5 figs., pls. 7-13.
1954. Ökologie der triassischen Muschel *Lima lineata* (Schloth.) und ihrer Epöken. Neues Jahrb. Geol. Paläont., Monatsh., pp. 163-183.
1963. Umlagerung und Rolltransport von Cephalopoden-Gehäusen. *Ibid.*, pp. 593-615, 9 figs.
- SPATH, L. F.
1930. The Eotriassic invertebrate fauna of East Greenland. Meddel. om Grønland, vol. 83, no. 1, 90 pp., 12 pls.
1935. Additions to the Eotriassic invertebrate fauna of East Greenland. *Ibid.*, vol. 98, no. 2, 115 pp., 23 pls.
- STAFFORD, JOSEPH
1913. The Canadian oyster. Its development, environment and culture. Committee on

- Fisheries, Game and Fur-bearing Animals. Commission of Conservation Canada. Ottawa, the Mortimer Co., 159 pp.
- STANLEY, STEVEN M.
1968. Post-Paleozoic adaptive radiation of in-faunal bivalve molluscs—a consequence of mantle fusion and siphon formation. *Jour. Paleont.*, vol. 42, pp. 214–229.
- STOLICZKA, F.
1871. Cretaceous fauna of southern India: the Pelecypoda. *India Geol. Surv., Mem., Palaeont. Indica*, ser. 6, vol. 3.
- SUMNER, F. B., AND R. H. HUESTIS
1921. Bilateral asymmetry in its relation to certain problems of genetics. *Genetics*, vol. 6, pp. 445–485.
- SYLVESTER-BRADLEY, P. C.
1958. Iterative evolution in fossil oysters. 15th Internatl. Congr. Zool., sect. 2, paper 12, 4 pp., 4 figs.
- TAYLOR, J. W., W. J. KENNEDY, AND A. HALL
1969. The shell structure and mineralogy of the Bivalvia. Introduction. *Nuculacea-Trigonacea*. *Brit. Mus. (Nat. Hist.), Bull., Zool., Suppl.* 3, pp. 1–125, figs. 1–77, pls. 1–29.
- TERMIER, HENRI, AND GENEVIEVE TERMIER
1949. Role des Aviculopectinidae dans la morphogénèse des dysodontes Mésozoïques. *Mus. Natl. d'Hist. Nat., Paris, Bull.*, vol. 21, pp. 292–299.
- TOZER, E. T.
1961. Triassic stratigraphy and faunas, Queen Elizabeth Islands, Arctic Archipelago. *Geol. Surv. Canada, Mem.* 316, pp. 1–116, 30 pls.
- TRUEMAN, E. R.
1951. The structure, development, and operation of the hinge ligament of *Ostrea edulis*. *Quart. Jour. Micros. Sci.*, vol. 92, pp. 129–140.
- VERRILL, A. E.
1897. A study of the family Pectinidae, with a revision of the genera and subgenera. *Connecticut Acad. Sci., Trans.*, vol. 10, pp. 41–96.
- WELLER, STUART
1907. A report on the Cretaceous paleontology of New Jersey. *Geol. Surv. New Jersey, Paleont. Ser.*, vol. 4, 871 pp.
- WILLIAMS, ALWYN, AND A. J. ROWELL
1965. Morphology. In Moore, R. C. (ed.), *Treatise on invertebrate paleontology*, part H, Brachiopoda (1). Lawrence, Geological Society of America and the University of Kansas Press, pp. H57–H155.
- YONGE, C. M.
1936. The evolution of the swimming habit in the Lamellibranchia. *Mus. Roy. d'Hist. Nat. Belgique, Mém.*, ser. 2, fasc. 3, pp. 77–100.
1951. Studies on Pacific Coast mollusks. 3. Observations on *Hinnites multirugosus* Gale. *Univ. California Publ. Zool.*, vol. 55, pp. 409–420, 6 figs.
1953. The monomyarian condition in the Lamellibranchia. *Trans. Roy. Soc. Edinburgh*, vol. 62, pp. 443–478.
1962. On the primitive significance of the byssus in the Bivalvia and its effects in evolution. *Jour. Marine Biol. Assoc. United Kingdom*, vol. 42, pp. 113–125.
- ZIMMERMANN, ERNST H.
1886. Ein neuer Monomyarier aus dem ostthüringischen Zechstein (*Prospendylus liebeanus*). *Jahrb. K. Preussischen Geol. Landesant. Bergakad. Berlin*, for 1885, pp. 105–119, pl. 2.

