

PARALLEL EVOLUTION IN
EARLY TRIGONIACEAN BIVALVES

NORMAN D. NEWELL AND DONALD W. BOYD

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ABSTRACT

The present work is a morphologic-taxonomic revision and inquiry into the evolution of geologically ancient (late Paleozoic and Triassic) marine bivalves of a formerly cosmopolitan superfamily Trigoniacea that are represented today by a single Australian genus *Neotrigonia*. Trigoniaceans, after a very long period of extreme conservatism, underwent a notable radiation in the Jurassic and Cretaceous periods, then nearly became extinct immediately afterward.

Particular attention is devoted here to stratigraphic-morphologic analysis from which it is concluded that the complex hinge of the younger genera probably is of diverse origin as apparently it was attained after divergence of separate lines. Each line is characterized by chronological proximity of relatively stable surface markings and external form.

The modified taxonomic arrangement adopted here recognizes the polyphyletic attainment of the derived hinge characters shared in common by the most advanced genera of trigo-

niaceans. It results in improved resolution of phylogenetic and biostratigraphic problems as contrasted with the more generalized conventional "horizontal" scheme of classification.

Much of the memoir reports our original observations on morphologic details and anatomy of living and fossil trigoniaceans from Australia, Europe, and America and attempts a taxonomic revision of 27 North American Upper Carboniferous and Permian species.

New families introduced here are the: Eoschizodidae, Eoastartidae, and Costatoriidae. The following genera are given more than perfunctory attention: Devonian only: *Eoschizodus*, *Rhenania*, *Hefteria*; Devonian to Permian: *Schizodus*; Permian only: *Heteroschizodus*, new genus, *Lyro-schizodus*, new genus, *Procostatoria*, new genus, *Paraschizodus*, new genus, *Scaphellina*, *Eoastarte*, and *Kaibabella*; both Permian and Triassic: *Neoschizodus* and *Costatoria*; Triassic only: *Heminajas*, *Pachycardia*, *Trigonodus*, *Gruenewaldia*, *Lyrionomyophoria*, and *Costatoria*.

INTRODUCTION

"few comparative anatomists . . . would have been induced . . . to study the minutiae of osteology were it not that in such minutiae lie the only keys to the most interesting riddles offered by the extinct animal world."—T.H. HUXLEY

TRIGONIACEAN HISTORY

The first two centuries of invertebrate paleontology as a scientific discipline were mainly concerned with exploration of the stratigraphic record and the recording of distributional data for the special needs of biostratigraphy. Because of the immensity of the task and the narrow interests of most of the contributing taxonomists our existing inventory of the fossil record is woefully lacking in coverage and quality. Broad works of revision and biological synthesis based on new and original studies are needed before the vast, largely untapped, resources of the fossil record can be fully available for ecological and community analysis.

The present¹ study is an attempt to organize and evaluate knowledge of the early history of an important fossil taxon, the Trigoniacea. This extraordinary group of marine clams constitutes a solitary superfamily of the order Trigonioidea (Newell, in Cox, et al., 1969c, p. N471) which has been morphologically and phyletically isolated at least since the Late Silurian.

A long interval of marked conservatism and stability of the trigoniaceans in the Devonian and Carboniferous was followed by a modest radia-

¹ This is our third monograph on Late Paleozoic and Early Mesozoic marine bivalves. We have dealt previously with crassatellaceans (Boyd and Newell, 1968) and oyster-like forms (Newell and Boyd, 1970).

tion in Leonardian-Artinskian (late Early Permian) times, as expressed in increased diversity (fig. 1), the sporadic appearance of well-defined sculpture, and limited parallel elaborations of a basically simple and characteristic hinge in several lines. The parallel trend in hinge evolution is one of the most interesting and widely applicable conclusions of this study.

Interrupted only briefly by notable extinctions in the Late Permian, the radiation increased momentum through the Mesozoic Era terminating abruptly at the end of the latest Cretaceous (Maastrichtian) coincidental with mass extinc-

tions that mark the world biotic crisis of that time. The ultimate causes of these Late Cretaceous mass extinctions which cut indiscriminately across major adaptive zones probably lie in sweeping geographic, climatic, and other short-term environmental changes (Newell, 1971).

During the Cenozoic, a few trigoniaceans survived in temperate waters of the continental shelf of Australia where they were represented by *Eotrigonia*, now extinct, and a surviving genus, *Neotrigonia* (fig. 2). The long evolutionary stagnation of the latter and its geographic isolation

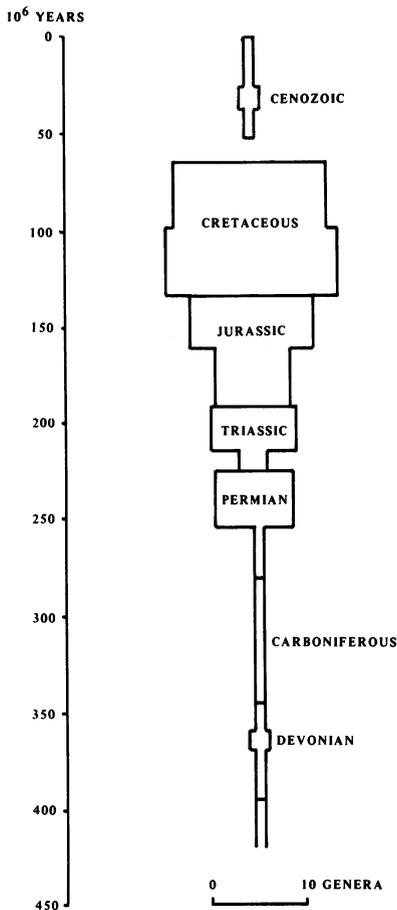


FIG. 1. Generic diversity of Trigoniacea through their known history. Note decline at the close of the Cretaceous when only two stocks survived the mass extinction.

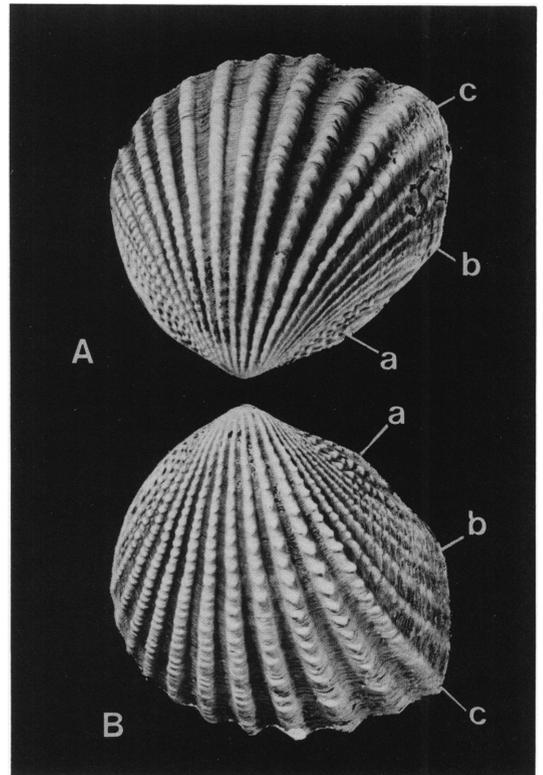


FIG. 2. *Neotrigonia margaritacea* (Lamarck). Recent, Western Port, Victoria, Australia. A. Right valve, AMNH 29145. B. Left valve, AMNH 29144. Obscure angulations of posterior border of shell, a-c, commonly are recognizable throughout superfamily Trigoniacea. Posterior margin of escutcheon, poorly differentiated in *Neotrigonia*, is embraced by letters a and b. The respiratory border is indicated by b-c.

constitute an interesting problem reminiscent of such geographic relicts as *Limulus*, *Nautilus*, and others. However, in the dimensions of geologic time, most of the major groups of bivalve molluscs have displayed similar resistance to change. This homeostatic conservatism probably is not attributable to a lack of adaptive potential but rather to generally available and frequently sheltered modes of life.

Given access to new and sufficiently stable adaptive zones, particularly under conditions of effective isolation, some pelecypods have demonstrated a capacity to undergo explosive radiation within a short geologic interval, say, a million years or so (Runnegar and Newell, 1971). This capacity to evolve rapidly under certain conditions in small isolated and perhaps now inaccessible populations may be responsible for the general difficulty in tracing the origins of most of the higher categories of bivalves, including the Trigoniacea.

Generic longevity in the Trigoniacea is about average for the normally conservative class Bivalvia, with mean survivorship in the superfamily of about 45 to 50 million years per genus. The known record of *Neotrigonia*, the only living member of the group, is only about one-fourth this, because the genus apparently originated in the Miocene (Fleming, 1964).

Early trigoniaceans have not previously been subjected to a comprehensive survey, and most of the scattered literature on the superfamily has been a by-product of biostratigraphic work on the later history of the superfamily, in the Jurassic and Cretaceous. Even these studies are now outdated. Fossils of the early trigoniaceans are not ubiquitous, but they are represented in many marine faunas from the Silurian through the Triassic. Well-preserved specimens, however, generally are quite rare.

Brief reviews of the Myophoriidae (*sensu lato*) are given by Rübénstrunk (1909), Cox (1952) Fleming (1964), Kobayashi and Tamura (1968), and Cox et al. (1969). These works provide time perspective and they have been very helpful in the present study. At the same time, they point up a pressing need for more numerous and better observational data and for comparisons of the fossils with living *Neotrigonia*.

The older trigoniaceans are relatively poor in

characters diagnostic of particular populations and species. Consequently, isolated specimens and fragmentary assemblages commonly cannot confidently be identified with a given species. In a survey of the literature of North American Mississippian, Pennsylvanian, and Permian species we found 57 species names, all but five of which were described under *Schizodus* (or its junior synonyms). Some of these names are based on single usually very imperfect valves and may be regarded as presently unrecognizable.

ADAPTIVE STRATEGY IN THE TRIGONIACEA

Living *Neotrigonia* is said to inhabit terrigenous muddy sands where the adults are free but, as with many other groups of bivalves, they possess a larval byssus (Gould, 1969). It seems clear that they are moderately active, asiphonate shallow burrowers in soft substrates and filibranch suspension feeders, possibly supplementing their diet of living plankton and bacteria with organic detritus (Purchon, 1957). The living animals of *Neotrigonia margaritacea* (Lamarck) submerge themselves more or less completely in sediment with the respiratory margin approximately level with the sediment surface (McAlester, 1966).

Examination of the fossil record in a lithologic-stratigraphic context leads us to infer that many aspects of this general mode of life were characteristic of past trigoniaceans. However, it clearly would be erroneous to conclude that all extinct trigoniaceans were similar to the living forms in being limited to shallow, cool waters of normal salinity.

The use of *Neotrigonia* as a morphological, behavioral, and ecological model for the entire superfamily must, of course, be flexible. In fact, in the perspective of geologic time the composite adaptive zone of the superfamily Trigoniacea must be broader than that of most of its representatives.

Judged by rock matrix and stratigraphic setting, the trigoniaceans have exploited a broad range of chemical, and probably also climatic, factors of environment not directly reflected by anatomical and morphological characteristics.

However, at least one family, the Scaphellinidae of the Permian (fig. 65), departed from the

common mold in developing siphons that enabled them to exploit deeper sediment levels than other mostly asiphonate trigoniaceans. The siphonate forms simulate and may have led phylogenetically to some of the Mesozoic desmodonts.

Paleozoic and Mesozoic trigoniaceans inhabited diverse environments within the epeiric seas. Evidently, these animals were physiologically adaptable to, or tolerant of, a wide range of salinities (poikilohaline), as indicated by the frequent occurrence of their shells with stenohaline forms, such as ammonoids and in dolomites in association with evaporites and redbeds. Within various lithologic facies, many species were quite gregarious and tended to dominate their bottom communities, as inferred from many occurrences in Permian dolomites and shales (Blaine, Dog Creek) of Texas and Oklahoma, and dolomites of the Lower Cretaceous (Walnut Formation) of Texas. But individual genera of trigoniaceans commonly range through a variety of sedimentary materials, bituminous shales, fine- to medium-grained muddy quartz sandstones, and many kinds of calcarenite rocks.

PHYLOGENY

In general, the stratigraphic succession of fossils provides abundant and incontrovertible evidence of changes through time. Each successive community, or even the fortuitous mechanical mixtures of quite unrelated communities (e.g., planktonic and benthonic organisms) tend taxonomically to be intermediate between comparable older and younger assemblages. This record of successive replacement of old by new communities provides the biostratigrapher with his tools, the paleontologic zones, for determining stratigraphic position and relative geologic age.

However, when we extract a single taxon such as the Trigoniacea from the geological column and examine its changes through space and time we are confronted generally by a strongly uneven and fragmented record that requires interpolation and extrapolation. This is not peculiar to paleontology. Comparative studies of living organisms also involve great lacunae to be bridged.

In spite of these limitations, the fossil record provides very many sequences of directional morphological changes. These are the trends ("programme evolution") or lineages of paleontologists that have strongly influenced and imparted evolutionary tone to many taxonomic arrangements. The Trigoniacea ideally illustrate such morphological chronoclines.

The principles and objectives of phylogenetic systematics are susceptible to diverse interpretations (e.g., Simpson, 1961; Hennig, 1968; Brun-
din, 1968; Darlington, 1972; Schaeffer, Hecht, and Eldredge, 1972) attributable in part to nuances of the term phylogeny.

For our present purpose we understand phylogeny as a kind of gross chronology, that is, a history of ascent (or descent) of organisms in which taxonomic ancestry, parentage and offshoots, are arranged morphologically in the inferred chronological order of appearance, that is, in chronoclines. In the following pages (figs. 3, 4) we attempt to present a classification of early Trigoniaceans that reflects our phylogenetic conclusions. These as are all phylogenies, are not more than hypothetical genealogies based on a highly subjective estimate of probabilities.

The parentage of a taxon may be a mating pair or an interbreeding population of organisms but generally these are unknowable in both fossil and living taxa. Hence, we follow the general practice of regarding higher taxa, which may, in fact, be genetically heterogeneous, as the sources of derived branches even though their inherent polytypic complexity virtually insures that the collective offspring stem from diverse ancestral populations of genetically somewhat disparate lineages. Thus, common ancestry refers not in any real sense to a mating pair of organisms but to a chronologically older morphology, a taxon that in most cases probably is heterogeneous, hence in a narrow sense genetically polyphyletic.

Under these circumstances most morphological grades, orders, superfamilies, families, and even genera of both living and fossil organisms probably should be only provisionally regarded as monophyletic in the Hennigian sense.

Detection of strict monophyly is a useful ideal in phylogenetic classification. The evidence available for constructing a phylogenetic hypothesis

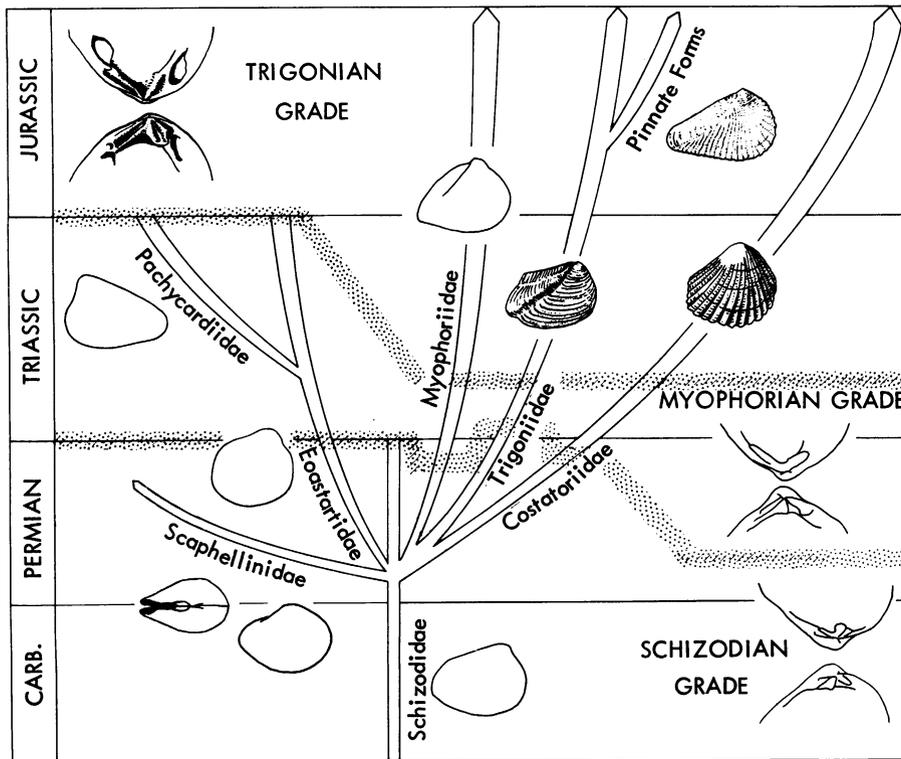


FIG. 3. Morphological diagram of early Trigoniacea based on conclusion that shell ornamentation is more diagnostic of main lines of phyletic divergence than are details of hinge morphology. In Early Permian (late Leonardian, Road Canyon) time, the most primitive stock (Schizodiidae) gave off five branches, four of which soon evolved a more elaborate hinge (myophorian grade). Three surviving branches continued through Mesozoic all independently acquiring most evolved (trigonian) hinge in the Middle Triassic. Interpretation is based on stratigraphic continuity of stable external form and surface details as contrasted with chronologically changing hinge modifications. Derivation of the Pachycardiidae from the Eoastartidae is conjectural. Alternative hypothesis is given in figure 4 where the Pachycardiidae are derived from Myophoriidae.

in paleontology is phenotypic propinquity (“distance”) and chronologic sequence of the times of origin of component groups.

The present work illustrates a limitation of, but does not invalidate, the Hennigian emphasis on shared derived characters of sister lineages (Schaeffer, Hecht, and Eldredge, 1972). In the primitive trigoniaceans some of the derived characters are independently acquired by separate but related stocks. Our examples are not unique in this respect. They are comparable to well-documented parallel chronoclines in other groups, for example among graptolites (Bulman,

1933), bivalves (Newell, 1942), brachiopods (Williams, 1953), and mammals (Simpson, 1959, p. 267). Examples of parallel evolution of foraminifera, ammonites, and other groups also are very numerous, and on theoretical grounds we must conclude that parallel trends constitute general, not unusual, phenomena inherent in the evolutionary process. Sister groups necessarily are genetically similar and are likely to display similar adaptive responses to similar environmental pressures. Hence, although similar morphological trends may suggest genetic alliance, “identical” structures within these trends may

originate long after the fission of sister groups.

From these considerations, it seems highly probable that most taxa above the level of the biological species, as presently defined, represent morphological-anatomical segments, or grades, in evolutionary trends. Probabilities are indeed minimal that such morphological grades (commonly expressed as taxonomic units) are monophyletic in the strict sense and this must be true of both living and extinct organisms.

It is inevitable that paleontological work deals most frequently with supraspecific categories, rather than with single populations, and that the higher categories are employed as evolutionary

units in the formulation of phylogenetic conclusions.

In this survey of early trigoniaceans we have tested a suggestion by Schaeffer, Hecht, and Eldredge (1972) of undertaking morphological analysis before assessing the chronological and geographic evidence. This approach involved a review of some 30 characters among 19 genera of pre-Jurassic trigoniaceans.

Our attempts to devise comprehensive cladograms based solely on morphology proved to be of limited usefulness in directing our attention to some associations overlooked in our first impressions. The effort was frustrated at a more refined

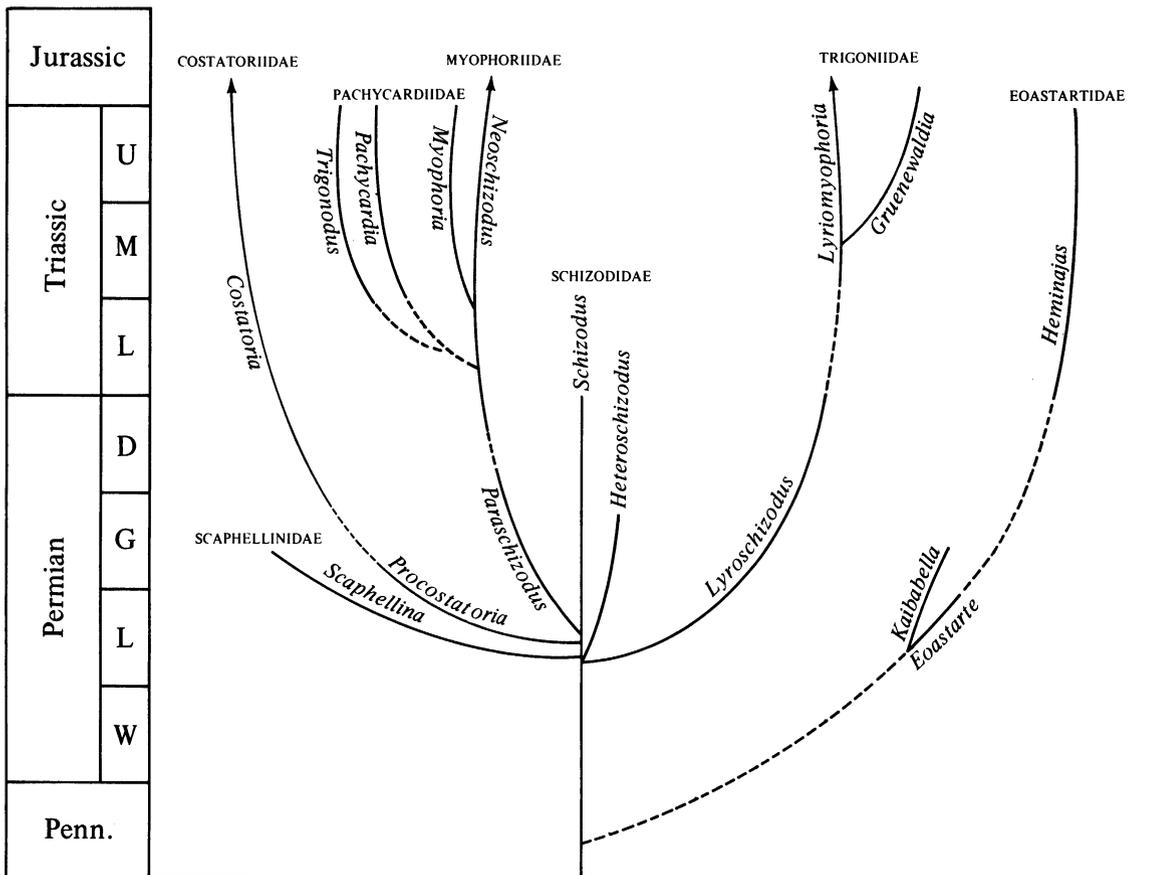


FIG. 4. Cladogram indicating inferred times of divergence and estimated morphological propinquity of early Trigoniacea. This portrays one alternative phylogenetic hypothesis. The Pachycardiidae (leading possibly to the Unionacea) may have stemmed from the Eoastartidae as indicated in fig. 3.

Abbreviations: D, Djulfian; G, Guadalupian; L, Leonardian; W, Wolfcampian.

level, however, by lack of detailed criteria for evaluating evolutionary polarity and degrees of primitiveness and by lack of knowledge about the functional significance, if any, of many of the shell characters. The deliberate suppression of available stratigraphic evidence of inferred relative times of appearance in the construction of phylogenetic cladograms was singularly unrewarding for the material that we have studied. Very commonly, the only clue for the direction of polarity in the Trigoniacea is the stratigraphic sequence. This is rationalized on the grounds that gene flow necessarily is unidirectional, from ancestors toward descendants.

On a trial basis, we also adopted an assumption that shared derived characters are more limited than shared ancestral characters in any taxonomic unit. Thus, a primitive morphological detail will generally be shared by a majority of the members. Such assumptions clearly are misleading in the Trigoniacea where parallelism is rampant and taxonomic work has been uneven, concentrated mainly in the younger and more specialized forms.

In summary phylogeny, as used here, is an interpretation of the historical and genetic relationships as inferred from both morphological similarities and stratigraphic position. Our conclusions about the trigoniaceans have been based on interplay of evidence from both sources.

PARALLEL TIME SERIES

Most Paleozoic and Triassic trigoniaceans have been conventionally incorporated in a single family the Myophoriidae (our schizodian and myophorian grades, fig. 3) and apparently no member of this group survived the biologic revolution at the close of the Triassic (Newell, 1967). Several Middle and Upper Triassic, and all post-Triassic, species, on the other hand, generally are classed in a single more highly evolved family (our trigonian grade, fig. 3), Trigiidae (Cox et al., 1969, pp. 471-489).

Shells in the latter category tend to be relatively robust, with a maximum length up to 6 or 8 cm. or more, whereas the geologically older examples rarely exceed a length of more than 3 or 4 cm.

The pectinate hinge of some Triassic and all post-Triassic forms is complex and stable, and

shell surfaces in most species bear well-defined ornamentation (fig. 3) as contrasted with the generally unstriated teeth and less ornate shells of the older forms. There are, of course, intermediate morphological states and these are displayed by a few species in the Permian and Triassic rocks.

Although this conventional arrangement accurately reflects the chronologic appearance of morphological grades in the trigoniaceans and therefore represents one phylogenetic hypothesis, we believe that it is deficient with respect to resolution of the many discernible evolutionary lineages within the group. Consequently, we are employing family names here for more restricted groups based on propinquity of species of comparable form and sculpture. Each of these displays chronological hinge changes apparently reached quite independently along separate evolutionary routes. Thus the families, as here employed, show a high order of parallelism in hinge characters (fig. 3).

The explanation of evolutionary parallelism that we favor is that this phenomenon is a response of similar gene complexes to similar selection pressures. In theory, parallelism is inherent in phyletic splitting and should be displayed by all branches stemming from a common ancestral stock.

THE NATURE OF THE EVIDENCE

Collections

Our collections were assembled from all accessible sources known to us. For the most part, they belong to the National Museum of Natural History, Smithsonian Institution, and the American Museum of Natural History, and they represent the accomplishments of generations of dedicated field paleontologists. These have been considerably augmented by loans of collections and specimens of other institutions throughout the world. We have examined many of the principal known field localities of primitive trigoniaceans in the United States and have collected many of the specimens. Wherever possible, we have favored "homogeneous" hypodigms as morphological standards for populations, that is, contemporaneous samples derived from a single locality (Newell, 1942).

American Pennsylvanian and Permian genera and species are best represented in our collections and these are emphasized and revised here, but many older and younger genera were also studied for comparison and have been illustrated with instructive specimens. The general objective has been to determine and to interpret morphological and chronological series and to develop a classification based on phylogenetic considerations. An outcome of our investigations has been confirmation that available collections provide only a meager sample of the potentially available riches of the fossil record. Large series of well-preserved and competently prepared specimens of the early trigoniaceans simply do not exist among pre-World War II collections, which characteristically were obtained as by-products of regional stratigraphic studies. Many of the taxa were established long ago on specimens that are unsatisfactory in light of present-day standards and requirements.

Preservation

Foremost in our study material are extraordinarily well-preserved silicified specimens obtained by G. A. Cooper of the National Museum of Natural History, Smithsonian Institution, from the Permian of west Texas. They are siliceous pseudomorphs, or casts, removed from calcareous matrix by Cooper, with hydrochloric acid. Because well-preserved and complete shells of early trigoniaceans are comparatively rare in our collections, this material provides much new information about morphological details. Our views about the mode of preservation in these and other silicified bivalves have already been set forth in preceding publications (Newell and Boyd, 1970; Boyd and Newell, 1972).

Calcareous shells of the older trigoniaceans generally are recrystallized and only rarely do they display details of the original microstructure of the inner layers. However, many calcareous specimens show at least the microscopic surface pattern of the external shell layer. Microstructural details of inner layers are occasionally well preserved in argillaceous matrix.

Many of our specimens are preserved as natural molds in which the shell material has been selectively dissolved. Our experience convinces us

that these molds must be converted to artificial casts before they can be accurately analyzed. We have employed synthetic liquid latex for this purpose. Published photographs of internal molds usually are difficult to interpret.

Photographic Illustrations

We are impressed with the difficulty of accurately illustrating all significant shell characteristics of *Bivalvia* by conventional means. Variations in incidence of illumination or in orientation of specimens during photography may distort, conceal, or exaggerate such features as ornamentation and hinge teeth. The use of black dye before whitening our specimens with ammonium chloride significantly aids in bringing into plain view details that are otherwise almost invisible, and we have tried to achieve the best result by repeatedly photographing difficult subjects until acceptable compromise has been obtained. The photographic illustrations shown herein are natural size unless otherwise indicated. Stereoscopic views of hinge details may be essential in some cases (fig. 12).

ACKNOWLEDGMENTS

We have been aided in our present project over a period of years by many colleagues and institutions to whom we extend our gratitude. If we have failed to acknowledge specific aid we apologize.

We have been substantially aided by grants from the National Science Foundation (GB-69005X, GB-30795 and GB-2194), and are indebted to Dr. G. Arthur Cooper, National Museum of Natural History, Smithsonian Institution, who collected, prepared, and made available to us many of the specimens herein described.

Our photographic illustrations were made and processed by Mr. G. Robert Adlington, and most of the figure arrangements were prepared by Mr. Sidney Horenstein; both of these men are colleagues in the Department of Fossil and Living Invertebrates, the American Museum of Natural History. Mr. Frank Lombardi, also of that department, prepared most of the calcareous specimens and latex casts for study.

Dr. Roger L. Batten, our associate at the

American Museum of Natural History provided us with SEM photographs and helped us with interpretations of the fine structure of shells. Mrs. Donald W. Boyd made many of the biometrical computations. Dr. Niles Eldredge of the American Museum of Natural History read sections of the manuscript and spent hours discussing evolutionary problems of the trigoniaceans. Dr. Stephen J. Gould, Harvard University, and Dr. A. Lee McAlester, Yale University, made available to us their original observations on morphology, anatomy, and behavior of the living *Neotrigonia margaritacea*, the closest living analog to the fossils under study. Dr. Copeland MacClintock, also of Yale, helped us interpret SEM photographs of microstructure of our fossils. Dr. J. Hope MacPherson, National Museum of Victoria, Melbourne, Australia, supplied us with preserved specimens of *Neotrigonia margaritacea* and Prof. E. R. Trueman, The University of Manchester, England, provided us with decalcified microtome sections from some of these specimens. Dr. Keiji Nakazawa shared with us his broad familiarity with Permian and Triassic trigoniaceans. Mr. William Rohrer and Dr. Roy Breckenridge discovered the blocks that yielded our best specimens of the new species *Paraschizodus elongatus*.

The following persons and institutions lent us especially significant collections or other data for our studies. The abbreviations are used in the text in certain cases for names of contributing institutions.

AMNH, the American Museum of Natural History, New York
 BS, Bayerische Staatssammlung für Paläontologie und historische Geologie, Munich; Dr. Dietrich Herm
 CU, Sedgwick Museum, Cambridge University; Drs. C. L. Forbes, H. B. Whittington
 FM, Field Museum of Natural History, Chicago
 G, University of Glasgow; Prof. T. Neville George
 HU, Museum für Naturkunde, Humboldt-Universität, Berlin; Dr. J. Helms
 IGS, Illinois State Geological Survey, Urbana; Mrs. Lois S. Kent

INGB, Institute of Geological Sciences of Great Britain; Dr. Adrian Rushton
 ISU, Iowa State University, Iowa City; Dr. Harrell L. Strimple
 IU, The University of Illinois, Urbana; Dr. J. L. Carter
 KK, VEB Kombinat Kali, Sondershausen 54; Dr. H. Ullrich
 KU, The University of Kansas, Lawrence; Dr. Roger L. Kaesler, Mr. Alan K. Kamb
 KUJ, Kyoto University, Kyoto; Dr. Keiji Nakazawa
 M, Istituto di Paleontologia, University of Modena; Dr. E. Montanaro Gallitelli
 MCZ, Museum of Comparative Zoology, Harvard University, Cambridge; Dr. Bernhard Kummel
 MNA, The Museum of Northern Arizona, Flagstaff
 MU, The University of Missouri, Columbia
 NMI, National Museum of Ireland, Dublin; Dr. C. E. O'Riordan
 OU, The University of Oklahoma, Norman
 PI, Paläontologisches Institut, Universität, Vienna; Prof. Helmuth Zapfe
 QU, Queen's University, Belfast; Prof. Alwyn Williams
 SM, Natur-Museum und Forschungs-Institut "Senckenberg," Frankfurt-am-Main; Dr. L. Werner
 SU, Stanford University, Stanford; Dr. Norman J. Silberling
 TB, Division of Economic Geology, University of Texas, Austin; Dr. Peter T. Flawn
 UMMP, University of Michigan Museum of Paleontology, Ann Arbor; Dr. Robert V. Kesling
 USNM, National Museum of Natural History, Smithsonian Institution, Washington, D.C.; Dr. John Pojeta
 UT, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; Prof. Adolf Seilacher
 USGS, United States Geological Survey, Washington, D.C.; Dr. Ellis Yochelson
 VM, Naturhistorisches Museum, Vienna; Dr. Heinz Kollman
 WU, University of Wyoming, Laramie
 YPM, Peabody Museum, Yale University, New Haven; Mrs. May D. Dasch

TRIGONIACEAN MORPHOLOGY AND ANATOMY

Any systematic study of organisms—their classification, paleontology, ecology, evolution—must in large measure be based on a fair understanding of their morphology. Consequently, we have given highest priority to this aspect of our study. General reviews of morphology of the more advanced trigoniaceans were given by Lebküchner (1933) and Savaliev (1958). From these, from our own observations, and from original data supplied to us by Stephen Jay Gould of Harvard University we have selected material that may promote better understanding of the early trigoniaceans. Although they are widely referred to in the literature, general knowledge of these fossils has been quite diffuse and unsatisfactory.

GENERAL CHARACTERISTICS

Most trigoniacean taxa are generalized (hence “primitive”) as compared with many other superfamilies of Bivalvia. The following generalized trigoniacean features are characteristic of the superfamily: (1) they are free, mainly vagrant; (2) they are essentially bilaterally symmetrical and isomyarian; (3) they tend to be somewhat trigonal or ovoid with relatively narrow posterior and semicircular anterior extremity; (4) for the most part, except in certain Upper Paleozoic forms, they are asiphonate with mantle margins completely free below the dorsal isthmus; (5) living representatives are filter-feeding filibranchs; (6) the ligament is external, parivincular, and opisthodetic; (7) hinge teeth are strong, stable, consisting of two or three radiating elements in each valve; (8) the original calcareous constitution of the shell as far as known is wholly aragonite and commonly prismato-nacreous.

SHELL TOPOGRAPHY

One of the most characteristic traits of shells of this superfamily is the external form that inspired the name of the typical genus, *Trigonia*. However, few species are literally triangular. They are more properly described as subovoid with semicircular anterior margin, slightly elon-

gate body and tapering, commonly obliquely truncate, posterior margin. A majority of species are moderately inflated. Characteristically, an arcuate shoulder called the posterior ridge extends diagonally from the umbones toward the posteroventral angle but in many, including *Neotrigonia* (fig. 2), this feature is hardly differentiated. In others, the ridge is a well-defined keel, termed here, the carina (fig. 87).

In every case it seems to mark the ventral limit of the respiratory part of the shell, separating the posterodorsal corselet area from the flanks below, which commonly are covered with their own distinctive patterns of surface sculpture (Cox, 1969, p. N40). Only rarely, among the early trigoniaceans, does the corselet contain a differentiated escutcheon between the umbo and the upper angle of the respiratory margin.

Most of the early trigoniaceans are lacking in features of distinctive surface ornamentation. The surface tends to be rather smooth as compared with other pelecypods (fig. 56). Growth lines are subdued and unevenly spaced. However, regular growth annulae are displayed over the anterior surfaces in some Permian shells (fig. 90) and this feature increases in frequency and prominence in some lineages with time and becomes a useful taxonomic character.

We do not believe that annual ornamentation is solely a function of environmentally induced oscillations in growth. But we do not ignore the probability that external rhythms have played some part in the genetic fixation of concentric patterns of ornamentation. Our collections are not adequate for us to identify and demonstrate diurnal, monthly, or annual growth rhythms.

Radial ornamentation, apart from the posterior ridge that bounds the corselet below, consists of costae or plicae. The former are narrow radial ribs that are not reflected on the inner surface of the shell (fig. 69). They are mainly confined to the outer layer of the shell (ectostracum). Plicae, or plications, are radial folds that extend through the entire thickness at the shell margin (fig. 98). They are progressively filled and smoothed over by growth increments of the inner shell layer (en-

dostracum). Plicated shells of Trigoniacea first appear well above the base of the Permian (in *Procostatoria*) and they become increasingly significant in the Triassic and later rocks.

Jurassic and Cretaceous trigoniaceans, not considered here, all display the trigonian grade of hinge development and external ornamentation commonly is heavy. A few (e.g., *Nipponitrigonia* and *Liotrigonia*) are nearly smooth. We do not know whether this lack of ornamentation is primary, as in the Schizodidae, or secondary.

Some examples of simple annulate forms with trigonian hinges, which we would class in the Trigoniidae are *Australotrigonia*, *Eotrigonia*, *Eselaevitrigonia*, *Freguelliella*, *Kumatrigonia*, *Laevitrigonia*, *Opisthotrigonia*, *Praegonia*, *Prosogyrotigonia*, and *Trigonia*.

Examples of Mesozoic and Cenozoic trigoniaceans with simple radial ribs and trigonian hinges, which we would class in the Costatoriidae, are *Neotrigonia* and *Myophorigonia*.

Many of the Jurassic-Miocene genera combine concentric and radial ornamentation (*Eotrigonia*) or concentric ornamentation in juveniles changing to tangential or obliquely radial ribs in mature individuals (*Pterotrigonia*, *Scabrotigonia*, and *Iotrigonia*). Likewise, pinnate (V-ornamented) genera (such as *Heterotrigonia*, *Iotrigonia*, and *Vaugonia*) are annulate in the early ontogeny.

In the Jurassic and later trigoniids that we have examined plications have a tendency to alternate in the two valves, providing interlocking marginal folds. In some of the early forms, *Costatoria* and *Procostatoria* (figs. 94, 96), however, the plications of matching valves commonly do not alternate. Generally, they are in direct apposition.

Stanley (1969) and Seilacher (1972) have suggested that there are selective advantages of surface sculpture in solving diverse problems of burrowing by pelecypods. It may be that divaricate and other heavy ornamentation (fig. 3) of many of the Jurassic and Cretaceous trigoniaceans (e.g., Pinnatae), not covered here, was an adaptation for rocking motions during burrowing.

MICROFABRIC OF THE SHELL

Probably, the shells of trigoniaceans (fig. 5)

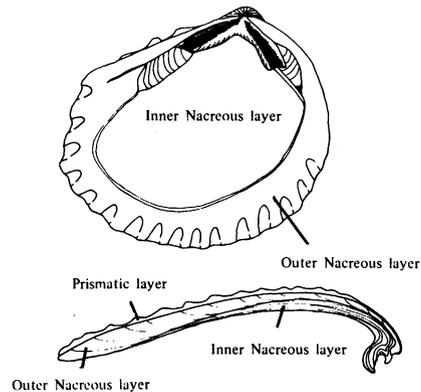


FIG. 5. *Neotrigonia margaritacea* (Lamarck). Recent, Australia. Diagrams illustrating distribution of calcareous shell components of aragonite. Periostracum not shown. (Modified from Taylor, Kennedy, and Hall, 1969.)

have always been entirely aragonitic and mainly prismato-nacreous as they are in living examples (Bøggild, 1930; Oberling, 1964; Taylor, Kennedy, and Hall, 1969). There is a consensus among malacologists that these are primitive traits but their adaptive significance is unknown. Living monoplacophorans, nuculoids, and gastropods possessing prismato-nacreous shells also generally have unspecialized organ systems. However, other supposedly primitive groups such as the Paleozoic bellerophonts (MacClintock, 1967) display crossed-lamellar layers in their shells. Certain other prismato-nacreous shells, on the other hand, may display features of marked specialization (e.g., living pteroid clams and freshwater mussels). This corresponds to a well-established principle that all organisms incorporate both primitive and derived characters and the possession of one does not per se exclude the other.

A few calcareous shells of trigoniaceans ranging at least as far back as Early Pennsylvanian (Morrowan) time display original features of shell fabric readily visible with an optical microscope. Basically, the structure in these ancient forms is prismato-nacreous as with modern *Neotrigonia* (figs. 5, 6). However, at least one species of *Schizodus* (*Schizodus alpinus*) and perhaps one of *Costatoria* possessed a crossed-lamellar layer in addition to prismatic and nacreous layers (figs. 8, 9). This association of nacre and crossed-lamellar

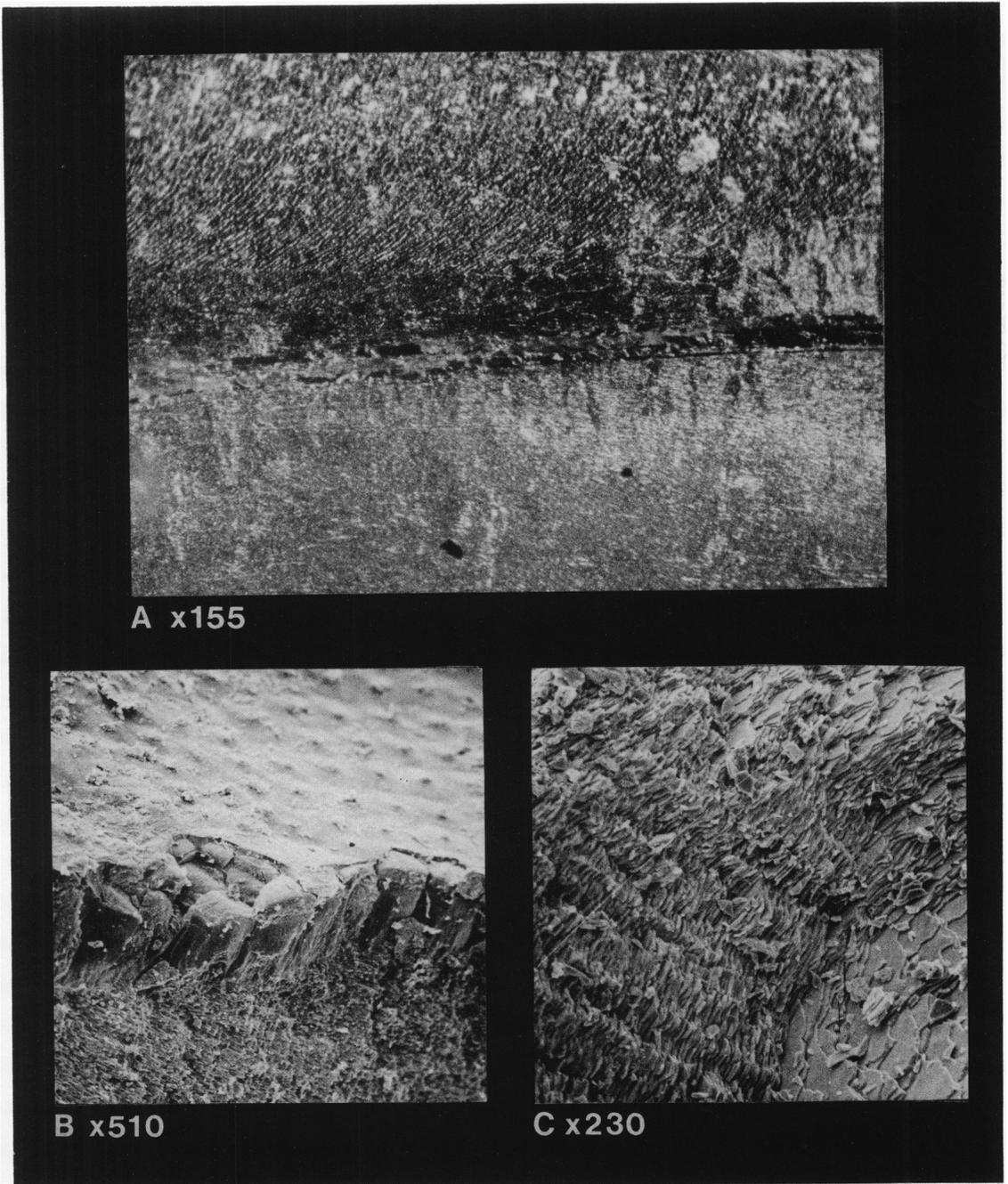


FIG. 6. *Neotrignonia margaritacea* (Lamarck). Recent, Western Port, Victoria, Australia. Ultrastructure of the three aragonite layers. A. Outer nacreous layer (inclined growth lamellae) above, and inner nacreous layer (horizontal lamellae) below. Cellulose peel, transmitted light, partial extinction. AMNH 29191. B. Prismatic layer above, nacre below. AMNH 29192. C. Stacked nacre of outer nacreous layer. AMNH 29192. B and C are SEM micrographs, courtesy Roger L. Batten.

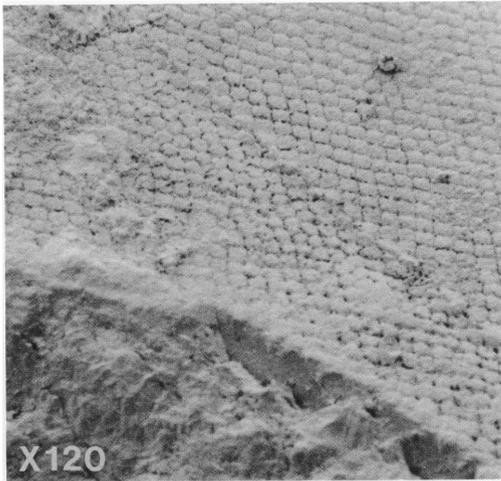


FIG. 7. Prismatic outer shell layer of the Pennsylvaniaian *Schizodus alpinus* (Hall). One growth line crosses surface from upper left to lower right. Upper Cherokee Shale (Pottsville), Henry County, Missouri, sect. 23, Township 42, Range 26. Electron micrograph X120. AMNH 29256.

layers is rare in pelecypods, occurring elsewhere, as far as we know, only in Pholadomyidae, Pernidae, Dreissenidae, Mactridae, and Myidae. Possible phylogenetic significance of these similarities is unknown.

Prisms of the outer shell layer in *Neotrigonia* are simple (MacClintock, 1967, p. 13), more or less regular, polygonal columns embedded in a conchiolin matrix that forms a thin wall around each prism (Taylor, Kennedy, and Hall, 1969). The prisms are relatively short and may be strongly reclined toward the shell margin. They are laterally marked by characteristically conspicuous, downward-divergent striations. The outer terminus of each prism bears a concentrically striated boss, the initial center of calcification. In ridges and tubercles of surface ornamentation the prisms lose their regularity and the prismatic structure may become obscure. Prisms of *Schizodus*, *Costatoria*, and *Gruenewaldia* are similar to those of *Neotrigonia* (figs. 6-10). We cannot detect any evolutionary trend in the shell fabric.

Lying within the prismatic layer and situated outside (marginally to) the pallial line, there is an outer nacreous layer that is separated from an

inner nacreous layer by a hiatus marking the trace of the pallial myostracum. The latter is usually not distinguishable as a separate layer (figs. 5, 6A).

THE HINGE

As with most bivalve molluscs the hinge of trigoniaceans consists of an opening mechanism, the ligament, and interlocking teeth and sockets along the dorsal margin of the shell, the dentition. It is interesting that the ligament displays virtually no evolution throughout the long history of the superfamily, whereas the dentition shows marked chronological modifications repeated within several morphological and stratigraphic contexts (fig. 3). This repetition is regarded here as constituting branching phylogenetic lines. There is a marked tendency for the evolution of dental characters to pass through a characteristic time sequence of stages or grades. These will be described separately in the following discussion.

Ligament

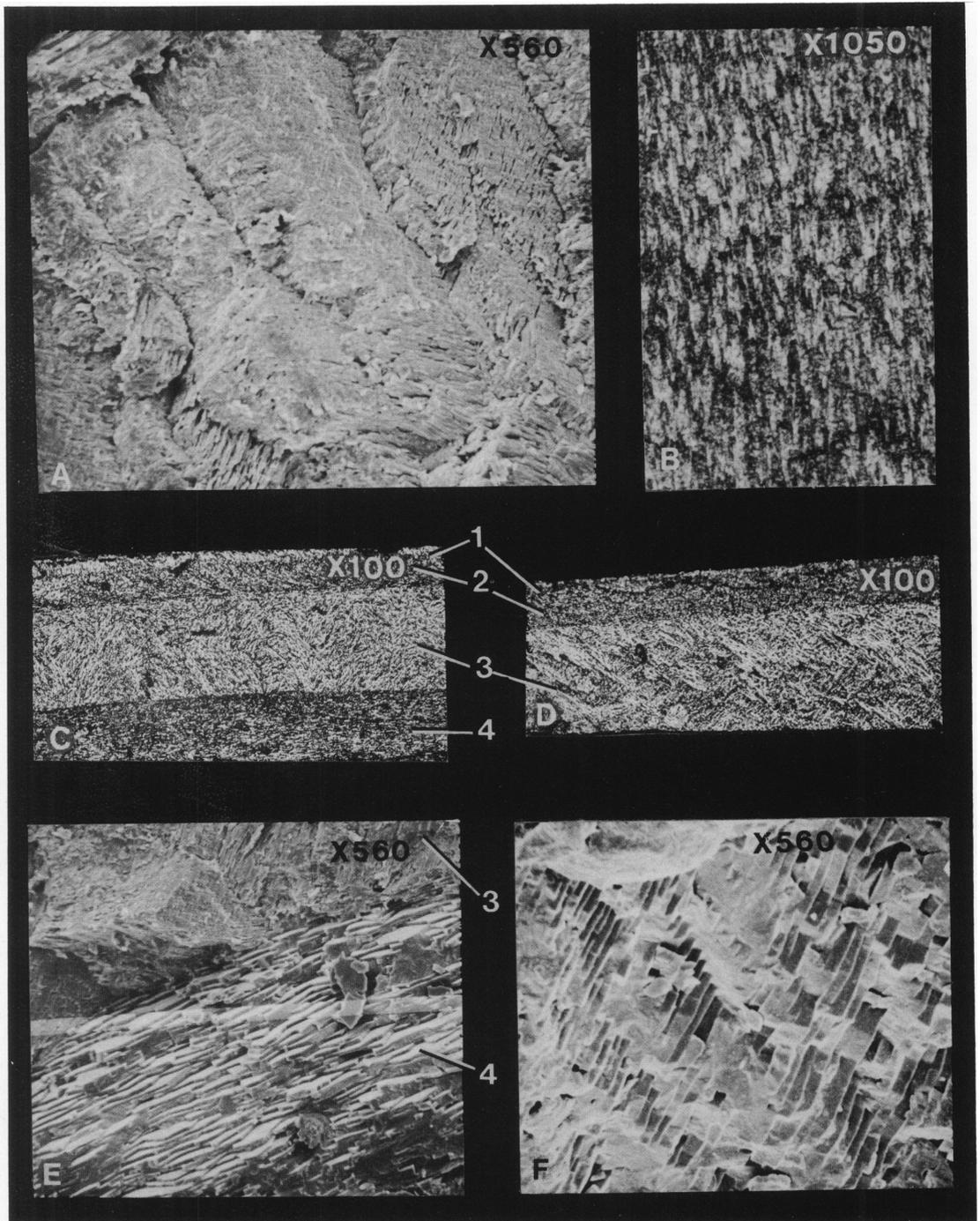
The ligament of all trigoniaceans (fig. 11) is situated on nymphs behind the beaks (opisthodontic) and it approximates a C-spring in form (parivincular). The fusion layer of the periostracum, ordinarily intact in the posterior part of the ligament, tends to break away in the forward part. Below this is a laminated middle layer and an inner fibrous layer. Normally, the fibrous layer is under compression when the valves are closed; the outer two layers mainly are subject to tensional stresses.

This type of ligament is shared by many diverse pelecypods including, as far as we know, all of the trigoniaceans. Preserved fossil examples are occasionally encountered at various horizons (fig. 57C, D).

The length of the nymph in fossil shells provides an index of ligament dimensions and may be indicative of the strength of the opening movement. In some species the nymphs are extraordinarily short (fig. 97). In others, they are relatively long (figs. 12E, 41A, C, F).

Dentition and Hinge Plate

Trigoniaceans contain two or three principal



teeth in each valve, most commonly two in the right and three in the left valve (figs. 12-14). Homologies generally are self-evident among the various subordinate taxa. Their arrangement with respect to the beaks and their respective shapes provide a convenient basis for defining distinctive grades of organization.

It is an entrenched view that the pseudolateral teeth of trigoniaceans and unionaceans probably are not homologous with heterodont laterals and we are not prepared to dispute or confirm this.

Douvillé (1912, 1913), although stressing dental differences between these (schizodonts) and "lucinoids," nevertheless applied the Bernard notation to all of them in the conviction that vaguely similar structures among these forms are homologous. In this, he has been followed by many students. A single, relatively large tooth in the left valve commonly lies behind the largest submedian tooth of the right in many trigoniaceans and lucinoids, and a few unionaceans.

A modified Steinmann notation for the denti-

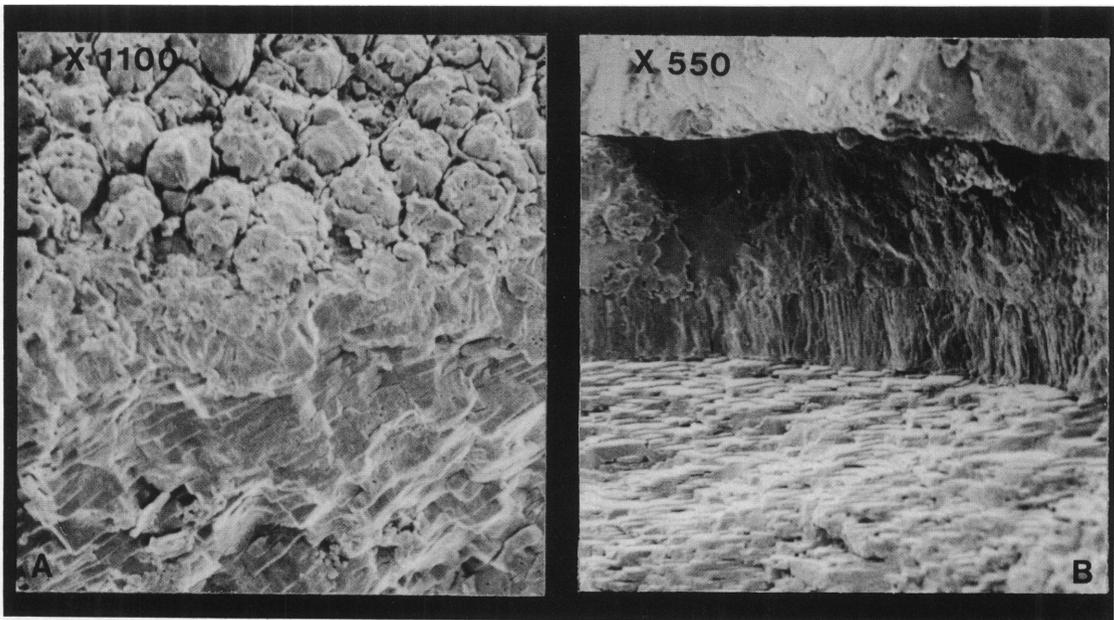


FIG. 9. Shell ultrastructure in *Costatoria harpa* (Münster). Middle Triassic (Cassian), Cortina d'Ampezzo, Italy. A. Oblique view of nacre, below, and prismatic outer layer, above. Electron micrograph X1100. B. Nacre below, overlain by myostracum layer. Layer at top is unidentified. It may be crossed lamellar. Electron micrograph X550. AMNH 29151.

FIG. 8. Shell fabric in a Lower Pennsylvanian schizodid, *Schizodus alpinus* Hall, Kendrick Shale (Atokan), Kentucky. YPM 27822; loc. 3449/1. A. Crossed-lamellar layer and outer nacreous layer, upper left. Surface obliquely cuts four first-order units in crossed-lamellar layer; note opposing dips of adjacent sets of second-order units. B. Optical photograph of cellulose peel, tangential to valve surface, showing first-order units of crossed-lamellar layer. C, D. Optical photographs of cellulose peels parallel to growth direction and perpendicular to valve surface (top) in umbonal and peripheral regions, respectively. E. SEM view of crossed-lamellar and inner nacreous layer, below. F. Outer nacreous layer exhibiting stepped pattern (treppen) of units.

Symbols: 1, prismatic outer layer of valve; 2, outer nacreous layer; 3, crossed-lamellar layer; 4, inner nacreous layer (visceral area). Umbonal direction in C and D to right. Electron micrographs courtesy Roger L. Batten.



FIG. 10. Outer surface of *Gruenewaldia decussata* (Münster) showing pyramidal bosses at prism ends. Electron micrograph X495. Middle Triassic (Stuores Mergel, San Cassiano, Italy). AMNH 29257.

tion is used here. It avoids objectionable a priori implications of homologies (Boyd and Newell, 1969, pp. N908-N913). However, because of the simplicity of the arrangement and number of teeth, the basic formula does not communicate very well any hinge differences that exist among the many genera of the superfamily.

Lateral teeth ("pseudolaterals" of many authors) are more or less well differentiated in some trigoniaceans and may resemble those of unionaceans (figs. 24, 25). In most cases they are clearly, and in others probably, modified cardinal teeth. In a few unionaceans the posterior laterals of adults originate at a distance from the beaks and these closely resemble heterodont lateral teeth. Even in these, however, the laterals tend to extend proximally well under the ligament, as in the trigoniaceans, whereas in most heterodonts,

posterior laterals tend to lie well behind the ligament. The laterals of Trigoniacea and many Unionacea generally continue to the beaks or they join a median cardinal as a posterior limb. These and other similarities probably justify the term "schizodont" for the hinges of these two groups (for a contrary view, see Cox, 1969, p. N52).

The large median tooth of the left valve in virtually all post-Triassic trigoniaceans (fig. 12A-B) is greatly expanded and divided below into two divergent elements. On the other hand, in many Triassic and all Paleozoic trigoniaceans, there is an outstanding pivotal tooth in each valve, that of the left lying behind that of the right valve.

Where the marginal teeth are relatively elongate and nearly parallel with the shell margin, they per se become laterals, as this term is used here only in a descriptive sense.

Generally the teeth and sockets are supported by a hinge plate. In some species, however, a hiatus occurs in the hinge plate at the median socket of the right valve (fig. 12E). We find this character quite variable at the level of genera and families and we cannot distinguish family groups by the presence or absence of the hiatus (see Fleming, 1964, p. 197 for a different conclusion).

The dentition in trigoniaceans displays several long-term evolutionary tendencies. The teeth are proportionally more elongate in later than in earlier forms (fig. 12) and they acquire interlocking secondary striations at various times during the Triassic. In Jurassic hinges the gliding surfaces of the major teeth are covered by interlocking striations.

Dental ("pectinate") striations clearly constitute a derived character in Trigoniacea as in certain heterodonts (e.g., Astartidae, see Boyd and Newell, 1968); and Devonian actinodonts, Carydiidae (see Newell, 1969a, p. 400). We conclude that pectinate teeth represent a hinge grade acquired independently and at somewhat different times by many lines of trigoniaceans. Their function may be inferred. They result in a tight hinge with minimal eccentricity of axial motions, as may be demonstrated by examination of articulated specimens of living *Neotrigonia*, and this tightness and inherent strength prevent slipping

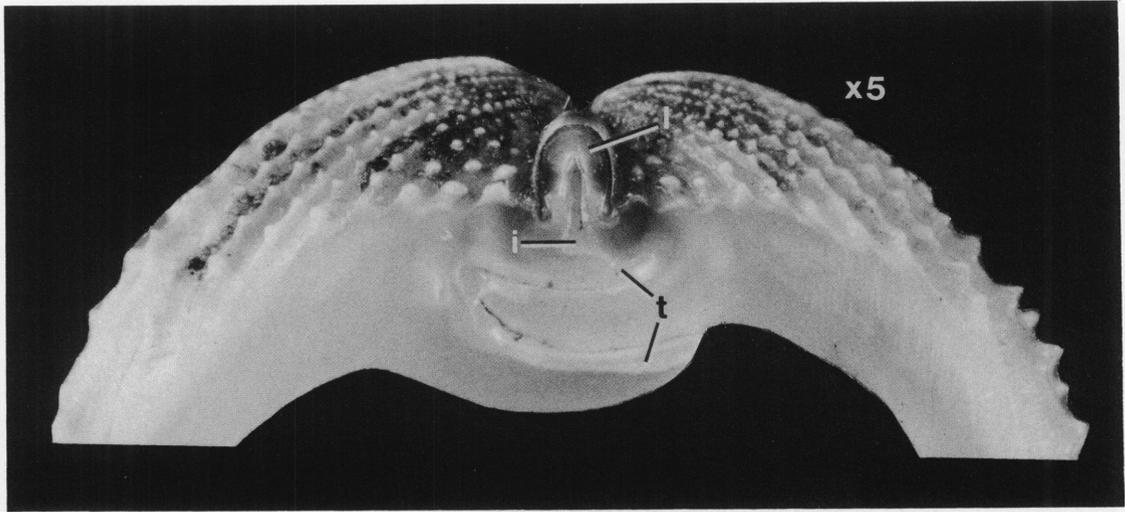


FIG. 11. *Neotrigonia margaritacea* (Lamarck). Recent, Western Port, Victoria, Australia. Vertical section behind beaks showing relationship of ligament (l) to mantle isthmus (i) and teeth (t).

of one valve against the other when gaping or closed.

The hinge plate is reinforced by an anterior myophorous buttress in a few Paleozoic and virtually all Mesozoic trigoniaceans. In every case it appeared chronologically before the dental striations, and the correlation of these two characters is imperfect.

Three major hinge states are readily distinguishable in the superfamily: trigonian, myophorian, and schizodian (fig. 12). These are named from family groups in which they are well illustrated but are not in themselves unique to particular families.

The Trigonian Hinge Grade

The most advanced hinge, the trigonian grade, characterizes all post-Triassic and a few Middle and Upper Triassic genera in which it is associated with diverse shell form and ornamentation (fig. 3). There are three principal teeth in the left valve and two in the right. The largest tooth of the left is broad and conspicuous, and it has the form of a gabled roof, or chevron, with two limbs separated by a lower channel. Its occluding surfaces bear vertical striae that tightly engage alternating striae and ridges of the corresponding socket of the right valve. In harmony with the

form and size of this tooth, the embracing socket of the opposite valve is strongly and symmetrically divergent from the beak at a wide angle (75° , more or less) and its gliding surfaces also are striated. The interlocking details of the two valves have a tight and precise fit so that paired valves in modern examples may be separated only with difficulty and at a high risk of breakage. A consequence of this tight articulation is to strengthen the hinge and there is hardly any possibility of erratic movements of the axis of rotation. Indubitably, this is a strong hinge and the strength that it imparts doubtless also confers a selective advantage to the animals that possess it.

In most species and genera, the median socket of the right valve and adjacent teeth are incompletely braced by a low platform of the hinge plate at the umbo, or the platform may be absent (hiatus) and the teeth are attached directly to the floor of the valve. In any case, an anterior myophorous buttress is present.

For trigoniaceans in general, we suggest capital letters in the hinge notation to indicate major dental elements and small letters to indicate minor but persistent elements. Parentheses may be used for items that are weakly developed, ephemeral, or uncertain. The right valve is indicated by RV, left by LV, the nymph by n. In most

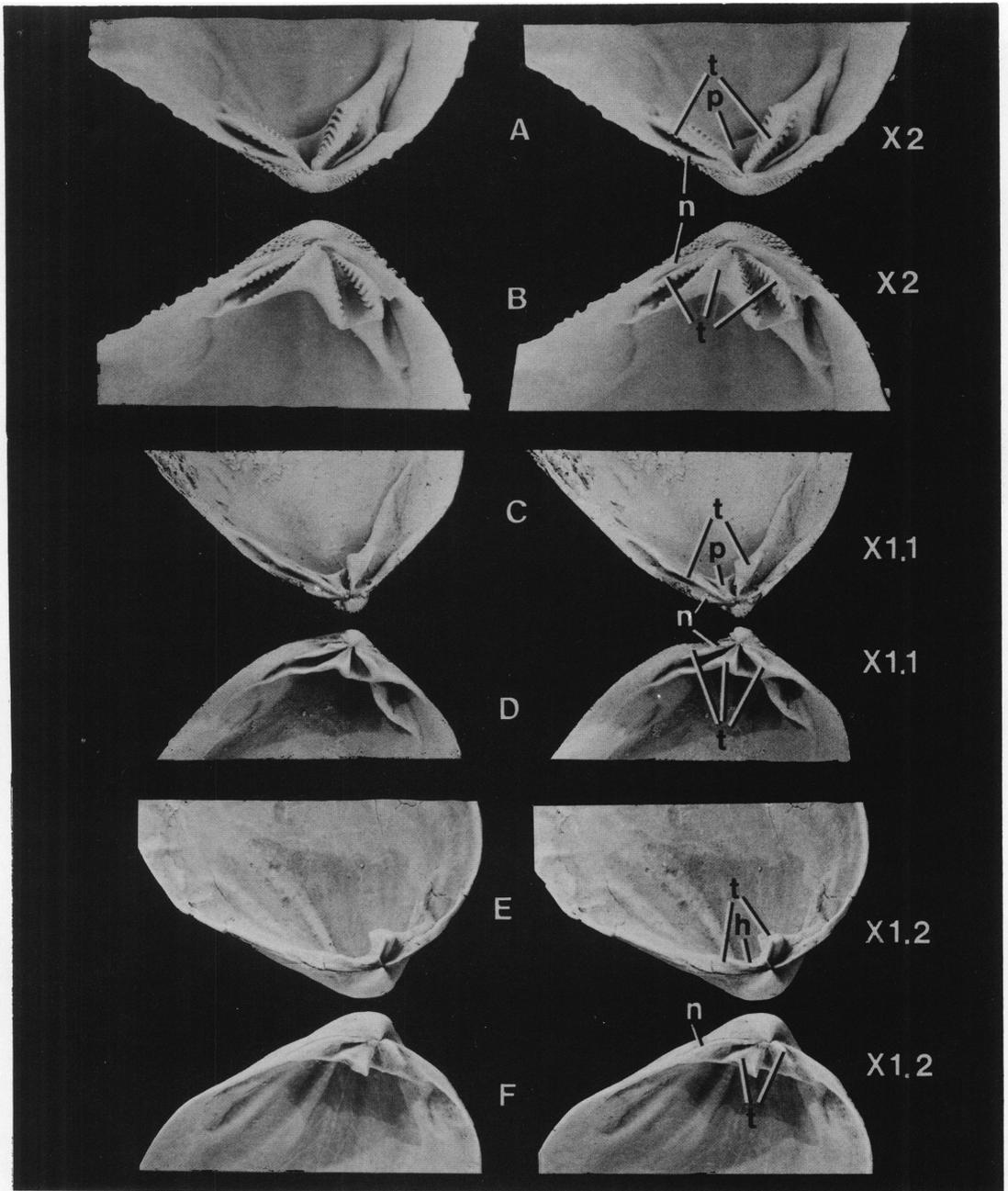


FIG. 12. Comparative morphology of three hinge grades in the trigoniaceans. A, B. Trigonian grade. *Neotrignonia margaritacea* (Lamarck). Striated (pectinate) teeth. Recent, Western Port, Victoria, Australia. AMNH, 29144-29145. C, D. Myophorian grade. *Neoschizodus laevigatus* (Goldfuss). Teeth commonly not striate. Middle Triassic (Ober Muschelkalk), Crailsheim, Ober Franken. C = HU M. B.-M. 7. 1. D = Zimmern bei Rottweil, Württemberg, TU 1415/5. E, F. Schizodian grade. *Schizodus ulrichi* Worthen. Hiatus in hinge plate found occasionally in the other hinge grades. Upper Pennsylvanian (Lane Shale, Missourian), Kansas City, Missouri, USNM 27674.

Abbreviations: h, hiatus in hinge plate; n, nymph; p, umbonal platform; t, teeth.

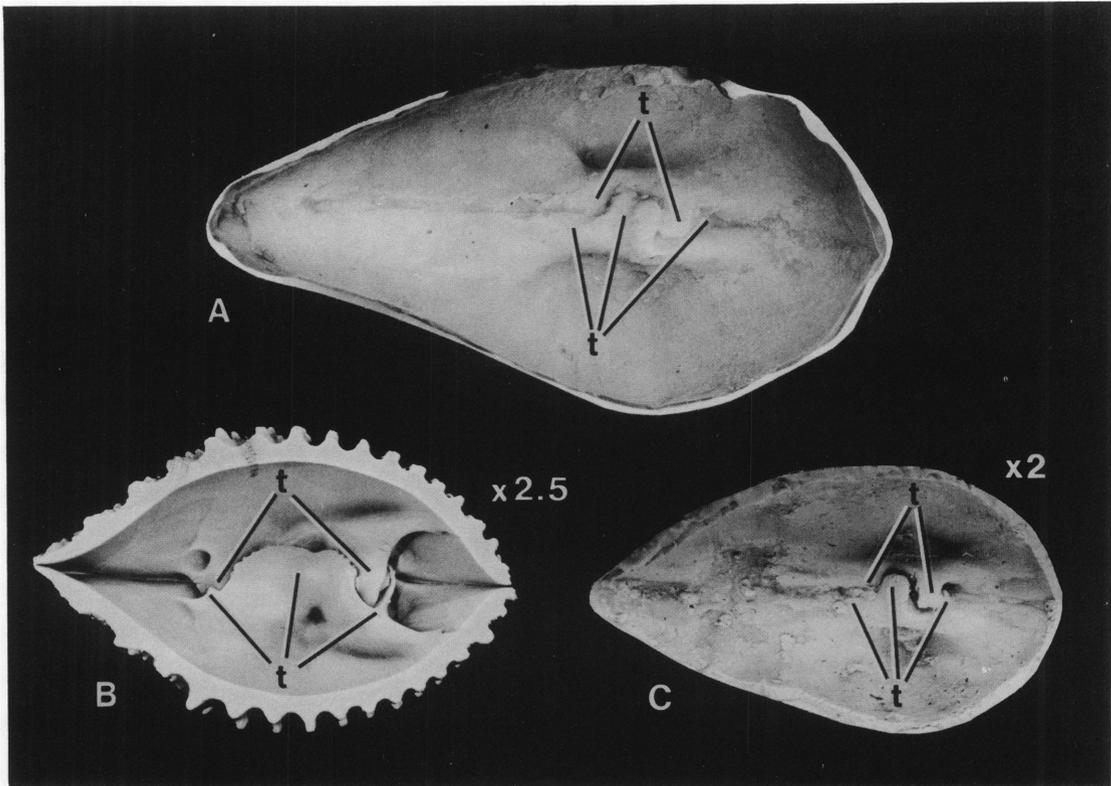


FIG. 13. Dentition in trigoniaceans. Horizontal sections, right valves above. A, C. *Schizodus texanus* Clifton, latex casts. A. Extra large individual (natural size), Kaibab Limestone, Gamma Member, Jones Crossing, southwest of Flagstaff, Arizona. MNA G2-2080. C. Holotype of *Schizodus texanus* Clifton. Blaine Formation, Acme Member, northwest of Quanah, Hardeman County, Texas. ISU 1453. B. *Neotrigonia margaritacea* (Lamarck), Recent, West Port, Victoria, Australia. AMNH 29148.

trigoniaceans, the left median tooth bears a deep valley, or channel on its umbonal surface (fig. 12). Hence, where this is pronounced, it may be diagrammatically represented by a chevron, or inverted V.

The bifurcation of the left median tooth prompted the term schizodont for advanced members of the Trigoniacea and this term also later came to be applied in a taxonomic sense to the more primitive trigoniaceans, in which the tooth is not divided, and to all the unionaceans, which display highly diverse dental patterns.

The notation for the trigonian hinge may be represented as follows:

	RV	no I O I O	
Posterior	LV	ni 0 Λ O I	Anterior

The trigonian hinge occurs in advanced genera of three families, as recognized herein: Myophoriidae, Costatoriidae, and Trigoniidae (fig. 3).

The Myophorian Hinge Grade

Certain Permian and Triassic genera display hinge features that are intermediate to, but significantly different from, the trigonian and schizodontian hinge (fig. 12C, D). These constitute the myophorian hinge. In most species there is no trace of dental striations. Others display incipient incomplete striations. The teeth and sockets of these are relatively smaller than those of the trigonian hinge and they show more marked differentiation of cardinals and laterals. The pivotal tooth of the left valve is biramous, with the an-

terior portion forming the main mass of the tooth. The posterior limb of this tooth is elongate and functions as a second, inner lateral tooth. The two limbs of this tooth and the walls of the corresponding socket of the right valve diverge from the beak downward at an angle as small as 50 degrees. The narrow posterior tooth of the right valve is conspicuously elongate. In some species and genera, there is a total hiatus in the hinge plate below the median socket of the right valve. All the post-Permian, and some Permian, species display a strong myophorous buttress behind the anterior adductor, but some schizodians also display a similar buttress in each valve (fig. 12) and even a second, posterior buttress just ahead of the posterior adductor. This is a variable trait.

Because dental striations are variable in the myophorian hinge, it is pertinent to inquire into the mode by which they were acquired in the course of trigoniacean evolution. The oldest examples with dental striae are representatives of *Neoschizodus thaynesianus* (fig. 72D) from the

upper Thaynes (Lower Triassic, Smithian) of Utah. Three species from the Middle Triassic of Europe that we have examined also show variable striation of some of the hinge surfaces. These are *Gruenewaldia decussata*, *Lyriomyophoria elegans*, and *L. intermedia*. Cox et al. (1969, p. 473) also cited variability in dental striations in the genera *Myophoria* and *Costatoria*.

In any case, the introduction of limited and sporadic dental striations in late Early Triassic time initiated a trend that was completed by Liassic time throughout the superfamily.

There is no preferred site of first appearance of the striations. Small lots of *Gruenewaldia decussata*, *Lyriomyophoria intermedia*, and *Neoschizodus thaynesianus* that we have examined display considerable variation ranging from completely smooth articular facets to those in which all but the most posterior gliding surfaces are striated.

In general, the myophorian hinge is more variable than the trigonian hinge and forms a character state intermediate between the latter and the schizodian hinge to be described below. It characterizes primitive and intermediate species of Myophoriidae, intermediate species of Trigonidae and Costatoriidae (fig. 3) and is found in all of the Pachycardiidae. It also occurs in advanced forms of Eoastartidae (e.g., *Heminajas*).

The myophorian notation may be written as follows:

	RV n o l O l o	
Posterior		Anterior
	LV n i 0 A 0 i	

The most characteristic association of hinge characters that forms the complex which we term myophorian is: (1) elongate posterior limb of the biramous pivotal tooth of the left valve forming an additional inner lateral tooth; (2) elongate marginal (lateral) teeth in both valves; (3) small posterior tooth in left valve; (4) anterior myophorous buttress.

These are cited above in the general order of their first appearance in the fossil record and they are cumulative—once acquired, they are not lost. The four invariably are associated above the Permian in all trigoniaceans and are first found together in full expression in the mid-Permian species *Neoschizodus kitakamiensis* Nakazawa and Newell, from Japan.

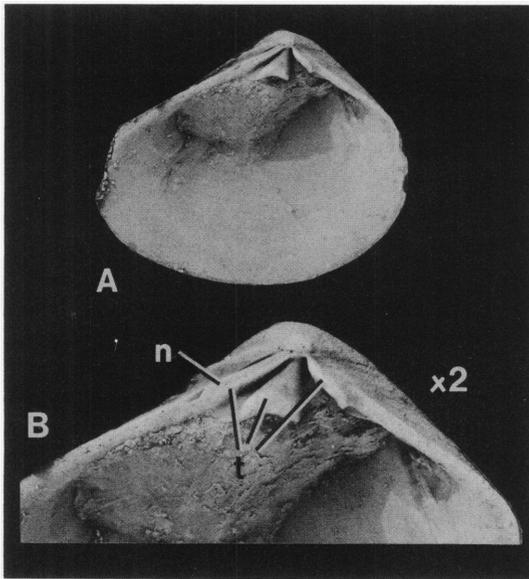


FIG. 14. *Schizodus* sp. A, B. Latex cast of a left valve from San Andres Formation, near Cloudcroft, New Mexico. Posterior tooth is obscure ridge poorly differentiated from nymph. It articulates with a shallow, but distinct furrow on right valve. AMNH 29170.

Abbreviations: n, nymph; t, teeth.

The first character cited above appears as early as Pennsylvanian time in *Schizodus ulrichi* and *S. compressus*. In all other respects the hinges of these forms are schizodian and are therefore so classified here. We somewhat arbitrarily consider the combination of characters 1 and 2 above as minimal requirements for assigning a particular hinge to the myophorian grade of organization.

The Schizodian Hinge Grade

The Carboniferous and most of the Permian species of trigoniaceans display a fairly uniform and stable hinge pattern that we designate schizodian, from the genus *Schizodus* (figs. 3, 12E, F). The schizodian hinge disappeared with the extinction of *Schizodus* in the highest Permian (Djulfian).

Hinge teeth are short, and the pivotal tooth of the left valve in all but a few advanced species (e.g., *S. compressus*) is not extended posteriorly. In some species the head of this tooth is a more or less equilateral triangle (fig. 63B). In others, it is chisel, or wedge-shaped (fig. 40B) with a faint median sulcus on the lower (umbonal) side, the precursor of the channel or cleft in this position in all higher trigoniaceans. The main tooth of the right valve is the anterior of the principal teeth of the two valves and it is reinforced by an arcuate ridge reaching from the distal end of the tooth backward along the rim of the hiatus, terminating in a short bladelike posterior tooth.

The left valve in most species possesses only two teeth (fig. 12F) but rarely an obscure ridge along the lower margin of the nymph functions as a tooth (fig. 14) perhaps anticipating the weak posterior tooth of left valves in the myophorian hinge. The schizodian hinge characterizes all Schizodiidae and Scaphellinidae, most Eoastartidae, and primitive species of Trigoniidae and Costatoriidae.

The schizodian formula is:

	RV	n(o)	i	o	I	o	
Posterior							Anterior
	LV	n(i)	o	I	o	i	

Hinge Transposition

From time to time individual pelecypod shells

in a living or fossil population sample display partial or complete mirror image exchange of hinge elements between the two valves (Boyd and Newell, 1968, p. 18-21). The proportions of these aberrant shells are invariably small and they presumably result from accidents of chromosomal inversion. It is tempting to compare them with sinistrality among snails and humans, but the genetic basis for hinge transposition in clams apparently has not been investigated. It is prudent to watch for examples of transposition that demonstrably have created new higher taxa in a single generation, so to speak. But we have no evidence that such examples exist.

Our collection of *Schizodus wyomingensis*, new species, from a single horizon and locality at Beaver Creek, Wyoming (AMNH loc. 2010) contains 115 individual hinges among which one left valve displays transposed dentition (fig. 61H). Its teeth and sockets are arranged in the order that would appear in a mirror reflection of a normal hinge. This is the first instance that has come to our attention of transposition in the Trigoniacea.

RESPIRATORY REGION

The mantle edges in living trigoniaceans are free below the hinge line. *Neotrigonia* does not possess tubular siphons or a pallial sinus, a condition that probably reflects broader adaptation and greater lability than does the siphonate condition. Only a very few fossil trigoniaceans, and these are all of Late Paleozoic age (figs. 15-17), possess at least a rudimentary pallial sinus, and by inference, fused mantle margin, at least in the rear and respiratory siphons. Wherever the sinus can be demonstrated we conclude that at least limited fusion of the mantle margins has taken place in the siphonal region but lack of the pallial sinus in the shell does not necessarily indicate lack of fused siphons since several living siphonate heterodonts lack the pallial sinus. Presumably these are mainly shallow burrowers. We do not consider the possession of a weakly developed pallial sinus in the Trigoniacea to be of great classificatory significance except where correlated morphological modifications indicate considerable specialization of the anatomy and significant influence on modes of life, as in the Scaphellinidae. The genus *Scaphellina*, along with

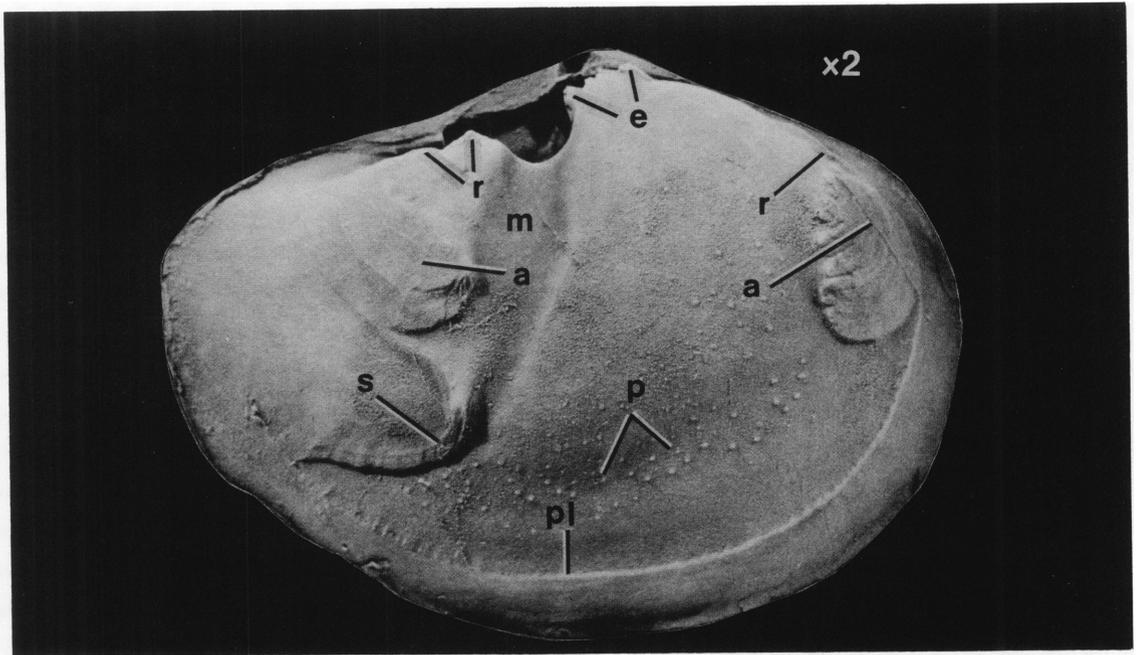


FIG. 15. *Scaphellina concinna* (Branson), 1930. Latex mold displaying muscle attachments of silicified right valve. Grandeur Member (Leonardian), Park City Formation, Wyoming. AMNH 29196; loc. 2010.

Abbreviations.: a, separation of quick and catch (peripheral) muscles of adductors; e, quadriceps elevator; m, posterior myophorous buttress; p, pallial punctations; pl, pallial line; r, pedal retractors; s, pallial sinus.

a few pholadomyids (Runnegar, 1967), is unusual in acquiring the adaptation for "deep" burrowing in Permian times. Apparently, the extreme radiation into the deeper levels of the substrate so characteristic of modern heterodonts did not begin until considerably later, possibly in Jurassic times (Stanley, 1968).

Separation of incurrent and excurrent streams in *Neotrigonia* is accomplished by a pair of opposed radial ridges of the mantle lobes, the pallial ridge (Gould, In press), behind and just above the gills. The two pallial ridges, when pressed together, effectively divide the mantle chamber into branchial and effluent compartments (figs. 18, 19). Tactile papillae along the posterior edges of the mantle are differentiated into two kinds. Those bordering and defending the incurrent aperture below are large and complex; those adjacent to the excurrent aperture above are small and simple (Duvernoy, 1854).

Although the respiratory apertures are not directly reflected in shell features in living *Neotrigonia*, many Jurassic and Cretaceous Trigoniidae possess an internal radial ridge which occupies about the same position as the pallial ridge of *Neotrigonia*. These may have possessed fused siphons for shallow burrowing. Usually, this internal shell ridge is reflected in the external topography of the shell (fig. 20).

The margin of the shell is almost straight at the respiratory apertures in some trigoniaceans, producing an obliquely truncate aspect. In the usual life position, the truncate posterior of the shell probably tends to be flush with the sediment surface. An *in situ* animal, therefore, would not be expected to be quite vertical in the substrate but would be tilted slightly forward. This part of the marginal profile forms an angle of about 110 degrees with an axis drawn through the centers of the adductor muscles (fig. 18A).

Whereas the truncate respiratory margin of the shell is characteristic of many trioniaceans, others are more rounded posteriorly and some are narrowly produced (fig. 44) as in many Corbulidae.

Internally, the upper and lower respiratory borders in *Neotrigonia* are delimited by shallow furrows. Externally in this and a few other genera and internally in some the position of these borders is marked approximately by radial ridges of which the lower, the marginal ridge, or carina is the more prominent (fig. 18A). The escutcheon carina, where present, passes above the dorsal border of the posterior adductors and the escutcheon lies entirely above the respiratory area (figs. 56, 57, 61).

CTENIDIA

The triangular gill leaves in *Neotrigonia* are filibranch, hence simple in structure, and they consist of two demibranchs (fig. 18B). Descending lamellae are united dorsally by an axis, whereas the ascending lamellae are free above. The gills occupy a position between the adductors just below the siphonal hemiseptum.

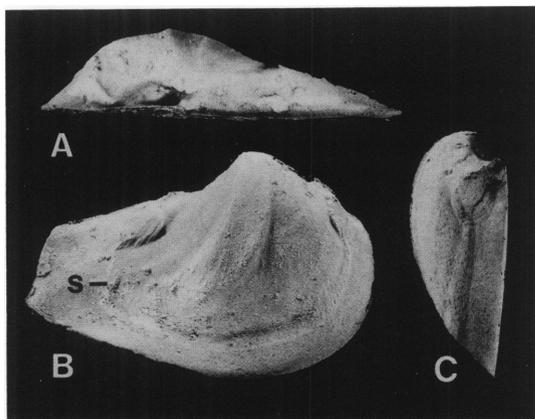


FIG. 16. *Schizodus wyomingensis* Newell and Boyd, new species. Latex mold of right valve of holotype (also see fig. 61E). Pallial line shows posterior truncation, suggestive of incipient sinus (s). Radial ridges across middle of B reflect morphological features of uncertain significance. They are situated approximately in the position of the inner (anterior) and outer gill plates. AMNH 29180; loc. 2010.

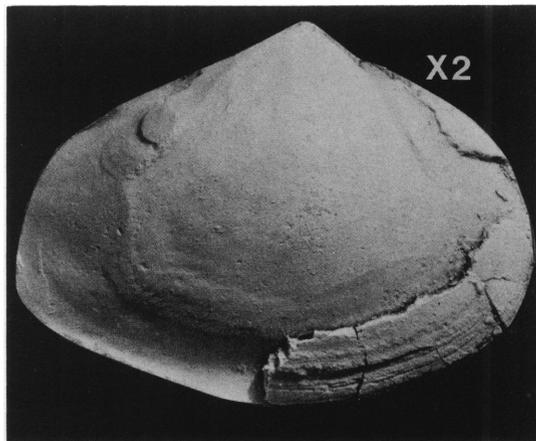


FIG. 17. *Schizodus ehlersi* Driscoll (? = *S. sectoralis* Winchell). Marshall Sandstone (Osageian) Mississippian, Battle Creek, Michigan. Holotype, showing incipient pallial sinus below posterior adductor. UMMP 44299.

FOOT

Neotrigonia has an L-shaped muscular foot (figs. 18, 21) somewhat similar in form and function to that of the Cardiidae. The upright cylindrical trunk of the foot contains the alimentary tract and other visceral organs. The ordinary function of the foot is to draw the animal below the sediment surface whenever accidentally uncovered, but it is also used for "jumping," a reaction employed by many families of bivalves when the animals are uncovered, molested or unable to penetrate the substrate (Ansell, 1969). A vestigial byssal gland occurs in the foot but a byssus is lacking in adults (Gould, 1969).

Four pairs of foot muscles are inserted in pits within the dorsal part of the shell (figs. 21, 22). Two are anterior in position, one is median and one is posterior. The protractor muscles, used to extend the foot, are inserted just below the anterior adductor.

The anterior pedal retractor muscles are relatively large and flat and they are inserted just above the anterior adductor. The two attachment areas are unequal in many advanced trioniaceans because of asymmetry of the adjacent hinge teeth. In *Neotrigonia*, that of the right valve is a narrow furrow just within and parallel with the anteriormost tooth. The insertion in the left

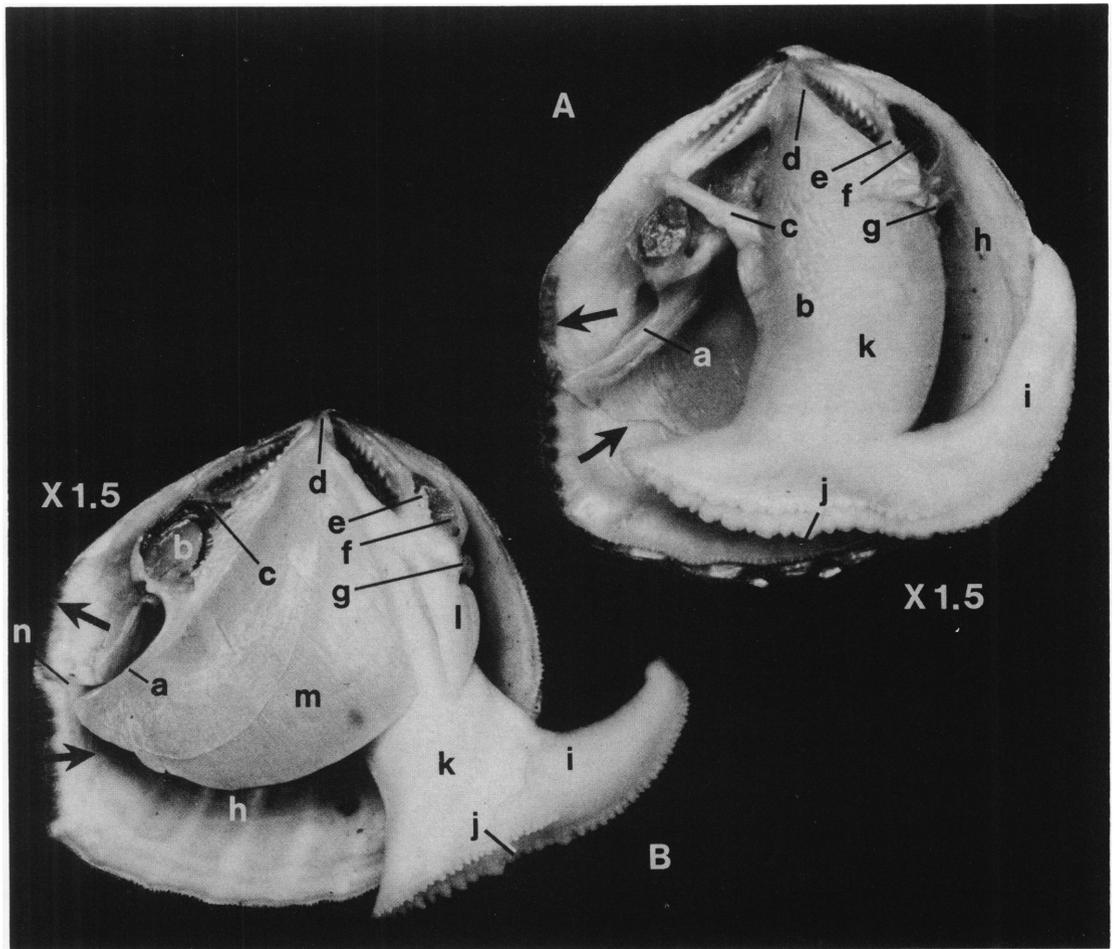


FIG. 18. *Neotrigonia margaritacea* (Lamarck). Two individuals with right valve removed, from shallow water at Western Port, Victoria, Australia. A. Gill leaves and palp removed. B. With gills and palps intact. Arrows indicate respiratory circulation. Specimen prepared by Stephen J. Gould.

Abbreviations: a, axis of gill plates; b, posterior adductor immediately above rectum; c, posterior retractor; d, elevator; e, anterior retractor; f, anterior adductor; g, protractor; h, mantle; i, anterior portion of foot; j, sole of foot; k, trunk of foot containing visceral organs; l, labial palp; m, gill plates; n, pallial ridge of mantle separating incurrent and excurrent water.

valve is a triangular pit in the distal end of the anteriormost tooth (fig. 22). In primitive trigoniaceans, they are subequal, and more or less detached, and subcircular (figs. 78, 82), or slit-like furrows continuous with the adductors (figs. 39C, 74C).

The elevator pedis muscles also may be asymmetrical in advanced trigoniaceans. The insertion

pits are situated in the apex of the umbonal cavity, that of the left valve sometimes being more conspicuous than that of the right (fig. 22). This has given rise to speculation that the elevator pedis muscle may have been absent in right valves of certain trigoniaceans (Fleming, 1964) but we believe that it was present and approximately equal in the two valves in all the Paleozoic and

Triassic forms that we have studied (figs. 74, 77G). These foot muscles are standard equipment in pelecypods, and we are inclined to regard asymmetry, wherever demonstrable, as a derived rather than a primitive condition.

The posterior retractors in *Neotrigonia* are a pair of thin, flattened, equal muscles that unite as they emerge from the posterior side of the foot, thence separating and diverging toward the insertion areas. They are attached in small but deep, detached circular impressions just above the posterior adductors (fig. 22), and a similar arrangement occurs in some of the more primitive forms (fig. 77). In others (figs. 39C, 74D), the posterior retractors were inserted in narrow furrows attached to the posterior adductors.

ADDUCTOR AND PALLIAL MUSCLES

The muscle scars of the two adductors are

high in the shell, about one-third to one-fourth of the shell height below the beaks, higher in the Trigoniidae, lower in more primitive forms. They are approximately equal in area but that of the anterior adductor is vertically elliptical, whereas the posterior scar is subcircular (fig. 22). The adductors in some of the older forms are kidney-shaped. In *Neotrigonia*, each is bounded along the inner margin by a rectilinear shell-ridge, the myophorous buttress (figs. 12, 23). The buttress of the anterior adductor is narrow and high, that of the posterior adductor low and rounded. Evidently, they strengthen the hinge plate and the shell areas around the adductor insertions but the possible range of functions of the ridges is uncertain. They are lacking in many of the older forms. Possibly they are related to greater activity or susceptibility to predation of the geologically younger species, all of which possess a strong anterior myophorous buttress. In the Pale-

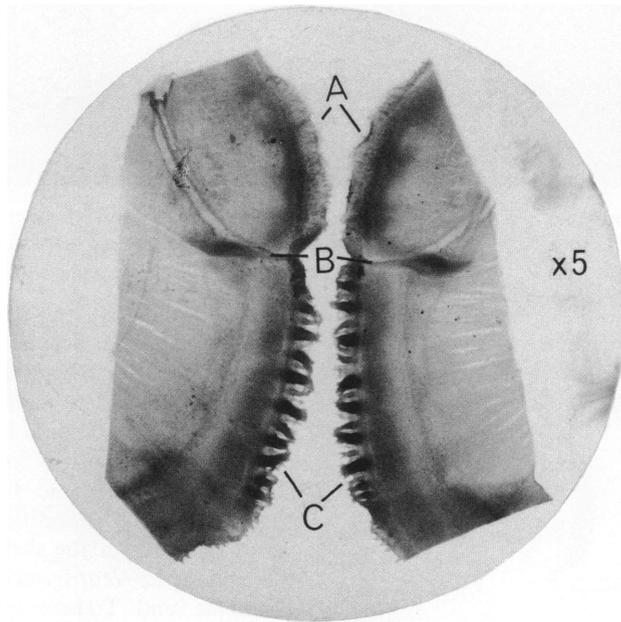


FIG. 19. *Neotrigonia margaritacea* (Lamarck). Recent, Western Port, Victoria, Australia. Inner surface of respiratory margin of mantle. Relatively large tactile tentacles (C) form sensory fringe at inhalant border. Presumably, these discriminate among potential food particles. Exhalant border tentacles (A) are much finer and more numerous. Inhalant and exhalant sectors are separated by tubular ridge, or hemiseptum (B) within each mantle lobe. These divide opposing water streams. In some Trigoniidae (e.g., *Pterotrigonia*) position of each of pallial ridges is roughly reflected by inner shell ridge near posterior border. Preparation by Stephen J. Gould.

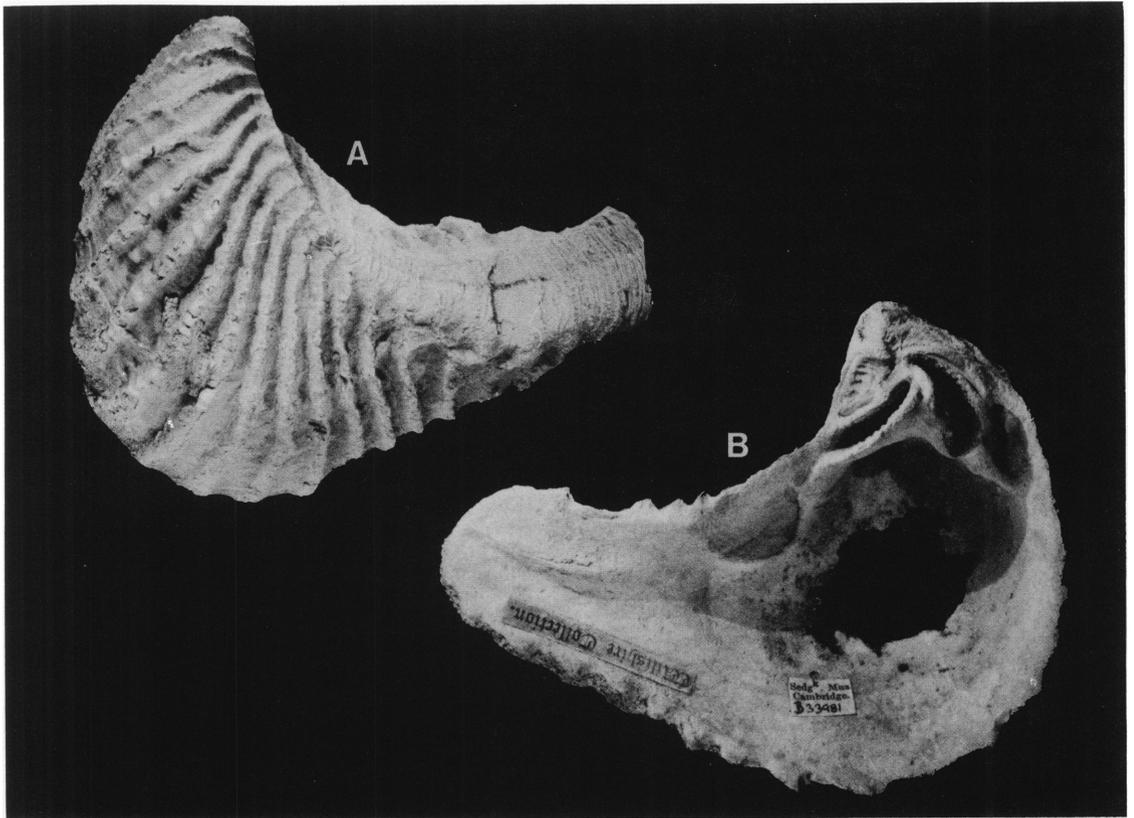


FIG. 20. *Pterotrigonia scabricola* (Lycett). Blackdown Greensand, Lower Cretaceous (Albian), Blackdown, England. A. Exterior left valve, showing furrow marking separation of excurrent and incurrent respiratory channels, CU B33982. B. Interior, left valve showing shell ridge between excurrent and incurrent respiratory channels. CU B33981.

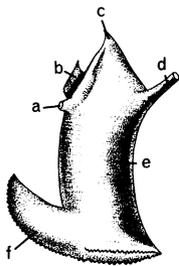


FIG. 21. *Neotrigonia margaritacea* (Lamarck). Left side of foot showing general form and sites of pedal muscles. Recent, Western Port, Victoria, Australia.

Abbreviations: a, anterior retractor; b, protractor; c, elevator; d, posterior retractor; e, visceral trunk of foot enclosing stomach and other digestive organs; f, anterior limb of foot. Dissection by Stephen J. Gould.

ozoic family the Scaphellinidae, the posterior buttress is quite strong, the anterior one hardly visible (fig. 65). The pallial line connecting the adductors in *Neotrigonia* is continuous and without a sinus, a primitive condition. But, as noted above, some Paleozoic forms display a sinus, clearly a derived condition. The pallial line is about one-fifth of the shell height from the ventral margin in *Neotrigonia*, usually much less in Paleozoic and Triassic trigoniaceans, probably correlated with systematic differences in placement of the adductors.

COMMENTS ON UNIONACEANS

It has long been conventional to associate Trigoniacea and Unionacea (the freshwater mussels) in classifications of the Bivalvia (Cox, 1960, pp.

81-82; Cox et al., 1969, pp. 393-484). Both appear abruptly in the stratigraphic record and their ultimate ancestry has not yet been identified. Mutual similarities in modern representa-

tives (prismato-nacreous shells, generally free mantle margins, radial dentition, etc.) probably are primitive rather than derived characters. In general, morphological and anatomical differ-

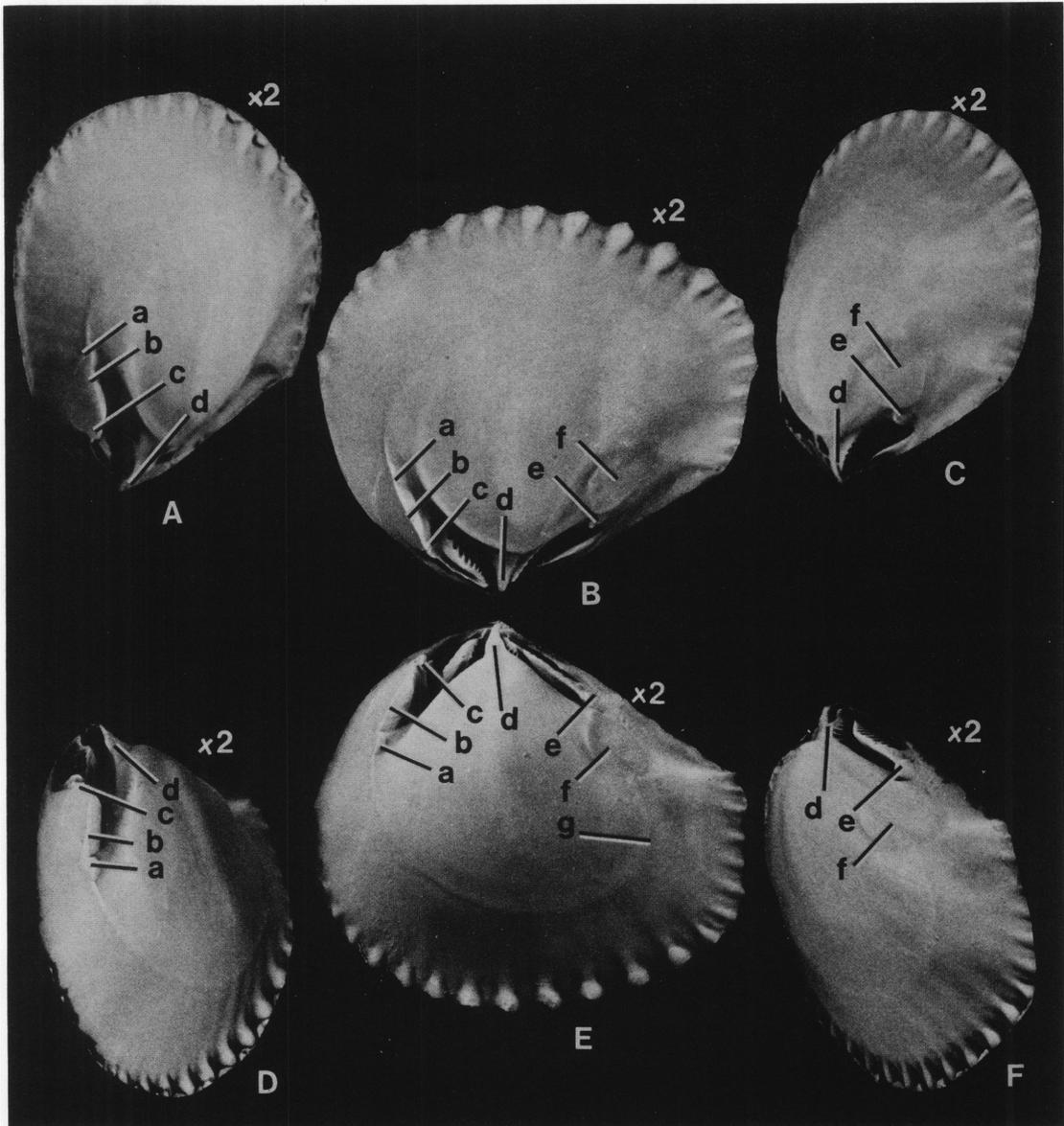


FIG. 22. *Neotrigonia margaritacea* (Lamarck). Latex casts of Recent shells illustrating musculature. Western Port, Victoria, Australia. AMNH 29146. A-C. Right valve. D-F. Left valve.

Abbreviations: a, protractor mark; b, border between quick and catch portions of anterior adductor; c, anterior retractor; d, elevator; e, posterior retractor; f, border between quick and catch portions of posterior adductor; g, pallial line.

ences between living examples of the two groups are rather great. The glochidial larva peculiar to Unionacea is an adaptation to freshwater dispersal and does not guarantee phylogenetic homogeneity of the superfamily.

Students of the unionaceans long have been frustrated by the high level of dental variability correlated, probably, with marked population fragmentation characteristic of fluvial and lacustrine animals, and possibly with polyphyletic origins. Nevertheless, as Modell (1942) has shown, several groups of freshwater mussels are characterized by distinctive hinge states and some of these are similar to the myophorian hinge. The oldest unionid in our collections, an upper Triassic species from Arizona, has dentition like that of the Eocene unionid illustrated in figure 24. The myophorian notation is applicable to both, although their marginal teeth are longer and have stronger development distally than is usual in the myophorian grade. Hinge similarity between the Arizona unionid and many Triassic trigoniaceans suggests phylogenetic relationship, but study of additional early unionids is needed to demonstrate whether the Arizona hinge is typical or unusual among primitive Unionidae. Considering both hinge details and overall form, Triassic representatives of the Pachycardiidae

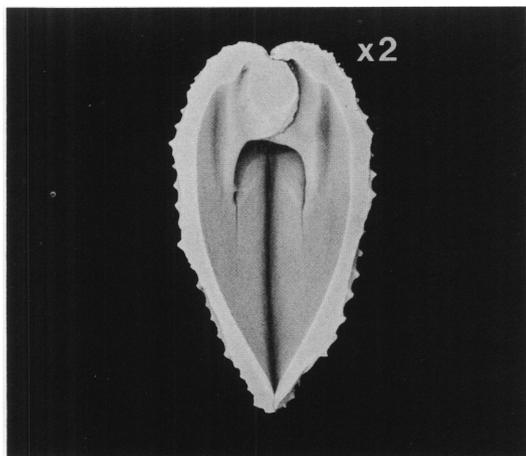


FIG. 23. *Neotrigonia margaritacea* (Lamarck). Vertical section, view toward front of shell showing massive myophorous buttress and anterior adductor insertion in each valve. Recent, Western Port, Victoria, Australia. AMNH 29150.

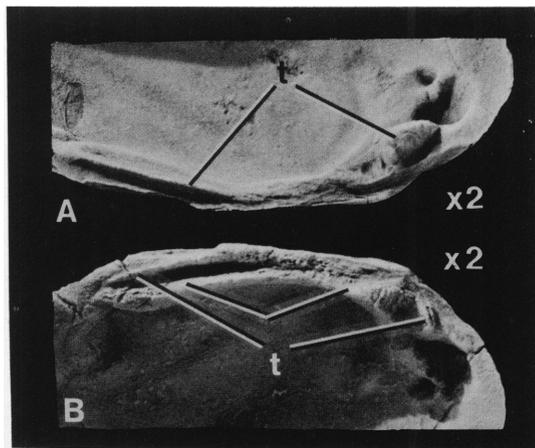


FIG. 24. Hinge of matching valves of fossil *Unio* sp., showing similarities to myophorian hinge. Eocene (Wasatchian), south of Otto, Big-horn Basin, Wyoming. A. Right valve, AMNH 29217. B. Left valve, AMNH 29218.

Abbreviation: t, hinge teeth.

most resemble the unionids. Similarities and differences are discussed in our diagnosis of the Pachycardiidae.

A characteristic feature of many unionaceans is the irregular fine imbrication or subdividing of the distal ends of the subumbonal teeth in which separation tends to be radial with respect to the beaks (fig. 24A, B). Details of the secondary dental subdivision are quite variable within contiguous members of single populations. Deep clefts may simulate primary sockets and result in somewhat inconstant and confusing patterns. For example, the hinge of *Alasmidonta* (fig. 25C, D) resembles the myophorian grade in that marginal teeth persist into the umbonal area. However, the lower marginal tooth of the left valve is separated from the pivotal tooth by an irregular depression. The dental notation is:

	RV n0I0i0I0	
Posterior		Anterior
	LV nI0I0I0I	

This hinge can be derived from the myophorian pattern by splitting the pivotal tooth of the myophorian left valve. The isolation of an inner marginal tooth thereby achieved and the formation of a minor tooth on the right valve corresponding

to the new socket are innovations that differ from the myophorian grade.

Only slightly more credulity is required to homologize the dentition of unionids such as *Pleurobema* with the myophorian hinge. This hinge (fig. 25A, B) differs from that of *Alasmidonta* in restriction of lateral teeth to the posterodorsal margin. A major step toward this condition, resembling the sharp differentiation between cardinal and lateral teeth of heterodont hinges, could have been accomplished by separation of proximal and distal parts of the inner marginal tooth of a myophorian left valve.

There are numerous anatomical differences between living Trigoniacea and even the most primitive unionaceans (Unionidae). The former have filibranch, the latter eulamellibranch ctenidea. As with many traits of bivalves, the structure of the gills appears to be phylogenetically "progressive," that is, subject to linear trends of evolutionary grades. The eulamellibranch grade is more evolved and probably more efficient than the filibranch, but these characters are not help-

ful in pointing to a particular parent or sister group for either superfamily (Newell, 1969b, p. N212).

In unionids the protractor muscle is inserted adjacent to the posteroventral margin of the anterior adductor instead of at the ventral extremity of the anterior border of that muscle, as in trigoniaceans. In the former, the anterior retractor is at the crest of an incipient myophorous buttress at a midpoint along the posterior margin of the anterior adductor or at its posterodorsal corner, instead of above it. More succinctly, the three muscles of trigoniaceans lie in a line along the trend of the pallial line. In general, the ligament is relatively long in unionaceans and the major teeth are irregularly rough where the edges of imbricating lamellae form the distal surfaces.

In short, the Unionacea and Trigoniacea possess a few primitive characters in common, but they are separated by very many specialized characters. We propose, however, to class them together here in a single order, the Trigonioida Dall, 1889.

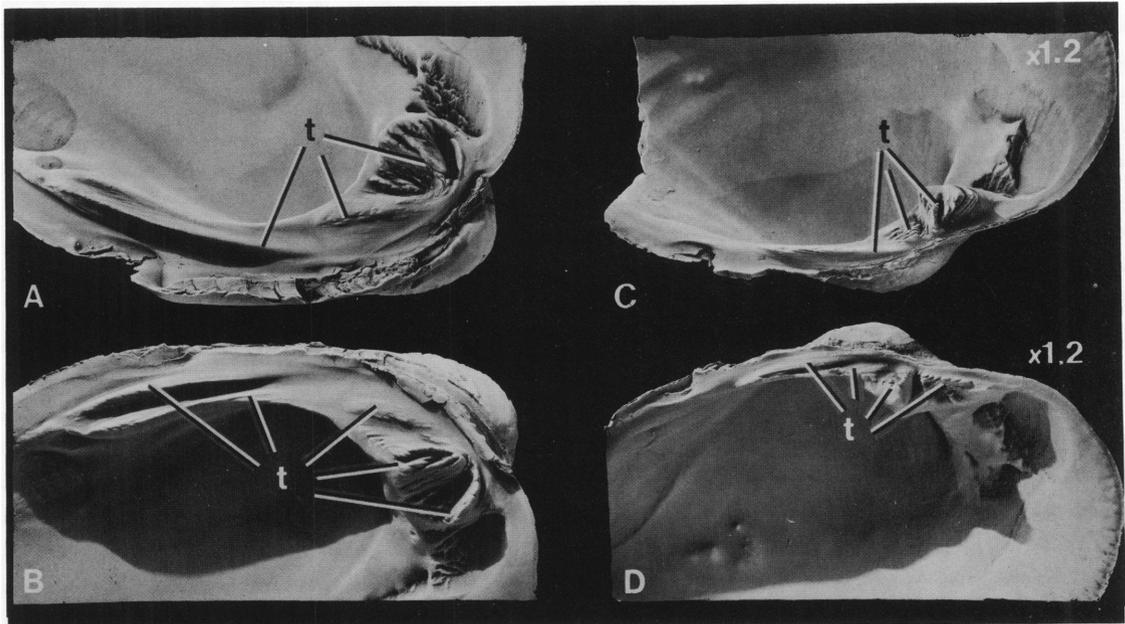


FIG. 25. Hinge teeth (t) of matched valves in recent unionids illustrated for comparison with the myophorian hinge. A, B. *Pleurobema cicatricosa* (Say), United States, AMNH 30643. C, D. *Alasmidonta undulata* (Say) United States, AMNH 31148. Unlike typical myophorian hinge anterior teeth and sockets show irregular secondary radial splitting in plane of commissure. Dental striations of trigoniaceans are quite different—more regular and more or less normal to plane of commissure.

PRE-CARBONIFEROUS TRIGONIACEANS

Adrian Rushton of the Institute of Geological Sciences, in London, called our attention to some small Silurian pelecypods he discovered in the Upper Elwy Group (Lower Ludlovian, *Cucullograptus scanicus* zone) of Wales (fig. 33). The specimens include 10 natural molds, imperfect to varying degrees, representing both external and internal surfaces of a trigonal shell slightly longer than high with rounded posterior ridge. No single mold exhibits a complete hinge but the composite impression gained from the sample is that of schizodian dentition. As is common in upper Paleozoic trigoniaceans, the triangular pivotal tooth of the left valve is flanked by floored sockets, whereas the bulbous major tooth of the right valve is in front of a hiatus in the hinge plate. Minor teeth appear to conform to the schizodian pattern, although neither the anterior tooth in the left valve nor the posterior one in the right valve is sharply defined on the rubber replicas. These Upper Silurian specimens are the oldest representatives of the Trigoniacea known to us. Although transversely striated teeth of *Lyrodesma* (Middle and Upper Ordovician) are reminiscent of those in post-Paleozoic trigoniaceans, the intervening stratigraphic interval with its record of transition from schizodian to myophorian grades indicates that the Ordovician hinge was an independent development in bivalve evolution.

Trigoniaceans occur sparingly in many Devonian marine faunas but their morphological details are poorly known. We have been unable to locate many well-preserved specimens after a most extensive search in American and European collections. Our admittedly inadequate evidence suggests the following generalizations: The Devonian shells are unornamented and are short and high

in proportion. Posterior shoulders are weakly differentiated, and the respiratory margin is more than one-half the shell height.

The most informative specimens are referred respectively to *Toechomya* Clark (fig. 31) and *Eoschizodus* Cox (fig. 28). From the right hinge, we judge that the former is a schizodid but we cannot be sure since left valves are not presently available to us.

The hinge of *Eoschizodus* somewhat resembles myophorian dentition. Indeed, a number of Rhineland species of *Eoschizodus* were long ago referred to *Myophoria* (e.g., Beushausen, 1895). Nevertheless, *Eoschizodus* possesses a hinge that differs significantly from the myophorian or other grades of trigonian dentition.

Unlike myophorian dentition, there is only one posterior lateral in the left valve of *Eoschizodus* (fig. 28) and the median cardinal of that valve is not extended in a posterior limb. The posterior lateral in the left valve is completely separate from the pivotal cardinal, a situation that also exists in some unionids (fig. 25). The type species, *E. truncatus* (Beushausen), and an American Upper Devonian species *Eoschizodus? rhombeus* (Hall) both possess three teeth in the left valve.

Right valves of *Eoschizodus* (fig. 28) are myophorian in aspect. However, there is not any inner lateral in the opposite valve. The formula is:

	R \check{V} n 0 I 0 I o				
Posterior					Anterior
	L \check{V} n I 0 I 0 i				

The hinge is basically quite primitive, reminiscent of actinodont ancestors and sufficiently distinctive to form the basis of a monogeneric family, the Eoschizodidae to be discussed later in the systematic section of this memoir.

SYSTEMATICS OF THE PRIMITIVE TRIGONIACEANS

MORPHOLOGICAL AND STRATIGRAPHICAL BASIS OF CLASSIFICATION

The conventional "horizontal" taxonomic treatment of the Trigoniacea (e.g., Cox et al., 1969) is based on hinge morphology and geologic

age, and implies a single derivation of each of the two families. We have adopted a different course which stresses inferred relative times of divergence and inherent stability of a few basic kinds of sculpture each of which we believe characterizes a separate evolutionary line. Ornamentation is

weighted here because the basic types appear to show little significant deviation during their long history, and field occurrences show no tendency for the discrete types of ornamentation to intergrade as might be expected if this were a result of trivial genetic diversity.

The general morphology and chronologic succession among the early members of the smooth, radiate, and annulate trigoniaceans give us confidence that these kinds represent separate divergent stocks in which the hinge, the anterior myophorous buttress, and the pedal muscles underwent parallel evolutionary modifications through time (fig. 3). Approximately equivalent late Mesozoic analogues of these groups (Glabrae, Costatae, Undulatae) were recognized as early as 1841 by Louis Agassiz.

Without substantial stratigraphic and morphologic controls for the whole sweep of trigoniacean history, the direction (polarity) of evolutionary changes would be debatable. Consequently, we regard stratigraphic position as a taxonomic trait essential for evaluation of the morphologic grades. Although the total history of a particular taxon among the Trigonacea is unknown, indeed, unknowable, the estimated times of divergence are offered by us as valuable taxonomic characters.

Sporadic dental striations are known to occur with the myophorian hinge and anterior myophorous buttress in unornamented shells as far back as the Early Triassic (late Scythian). The fully developed trigonian grade was reached during the Middle Triassic (Ladinian) in some unornamented species (Fleming, 1964). The myophorian and trigonian grades were attained in the annulate stock by Middle Triassic (*Lyriomyophoria* spp. and *Trigonia* spp.). The radiate line reached the myophorian hinge grade in the Late Permian of Japan (Gujo Formation) and the trigonian grade in Late Triassic (Fleming, 1964).

Unornamented trigoniaceans are especially characteristic of, but not confined to, the Paleozoic and it appears that all pre-Permian forms (Eoschizodidae, Schizodidae) are smooth (fig. 3). Early in the Permian these split into four unornamented groups, Schizodidae, Scaphellinidae, Eostartidae, Myophoriidae, one radiate group, Costatoriidae, and one annulate group, Trigonii-

dae. The smooth stock divided again in the Triassic to produce an additional branch, Pachycardiidae, bearing some resemblance to certain Unioniidae. The annulate group probably gave rise to the Pinnatae, characterized by oblique ribs, in the Jurassic. The latter group reached its acme (fig. 26) during the Cretaceous, but did not survive that period.

The episode of mass extinction that nearly eliminated the ammonities and many reptiles at the close of the Triassic also coincided with the disappearance of all forms with the myophorian hinge grade so characteristic of the Triassic. The diversity of Jurassic and Cretaceous trigoniaceans suggests increasing tempo of radiation until the general disruption of world ecosystems in the latest Cretaceous (Maastrichtian).

PREVIOUS WORK ON UPPER PALEOZOIC SPECIES OF TRIGONIACEANS

Published work on Devonian trigoniaceans is sparse and very much in need of revision. We have encountered 54 published species names for trigoniacean fossils from American Mississippian, Pennsylvanian, and Permian strata. All but three of these names were introduced as species of *Schizodus*, four from rocks of uncertain age. Twenty-four were proposed for Mississippian, 17 for Pennsylvanian, and nine for Permian specimens. Most of this species-naming took place during the last half of the nineteenth century when all but four of the 41 Carboniferous species names were introduced.

We conclude that most of the names are presently incomprehensible. Some (e.g., *S. randolphensis* Worthen, 1890) are based on unrecognizable fragments, and others (e.g., *S. pandatus* Girty, 1899) were founded on imperfect single valves. Small differences in shell outline, no doubt resulting from intrapopulation variability, or from sediment compaction, were grist for the mills of several nineteenth-century taxonomists. For example, eight of the Mississippian species are based on stratigraphically associated specimens from Waverly strata of central Ohio. Published species descriptions typically offer little more than a loose, albeit sometimes wordy, characterization of valve configuration. One can seldom be sure whether a particular author was

limited more by inadequacy of material or by lack of interest and insight. Illustrations are mostly inadequate drawings based on specimens that have long since disappeared.

Population diversity in upper Paleozoic trigoniaceans is less impressive than might be inferred from the number of described species and most of the published illustrations depict relatively minor variations on two basic shapes, loosely designated Form A and Form B for purposes of the ensuing discussion. Form A has roughly an equilateral outline in which centrally placed beaks and approximately equal length and height are conditions approximated if not literally realized (fig. 38). Such valves are distinguished by a steeply inclined respiratory margin extending more than half the height of the valve. Variations on this form involve differences in prominence and position of umbones, prominence of the posterior ridge, length of dorsal margin, extent and steepness of slope of respira-

tory margin, position of maximum valve length relative to valve height, and degree of curvature of the different sectors of the valve margin.

With posterior elongation, Form A gives way to an elongate outline with markedly anterior beaks termed Form B. The respiratory margin is commonly inclined at a more acute angle to the muscle-scar axis that is the case in Form A, and its extent is not more than half of valve height. Variations in this form involve several features in addition to those noted above in connection with Form A. One is the extent of inflation of the posterodorsal part of the valve. Valves notably flat in this area have a distinctive appearance accentuated by the accompanying tendency for a narrow umbone and a sharply defined posterior ridge. We have observed gradation between the inflated and deflated extremes of Form B in *Schizodus ulrichi* from Pennsylvanian strata in the vicinity of Jacksboro, Texas (fig. 56). Another variation on the Form B theme involves the spiral angle of

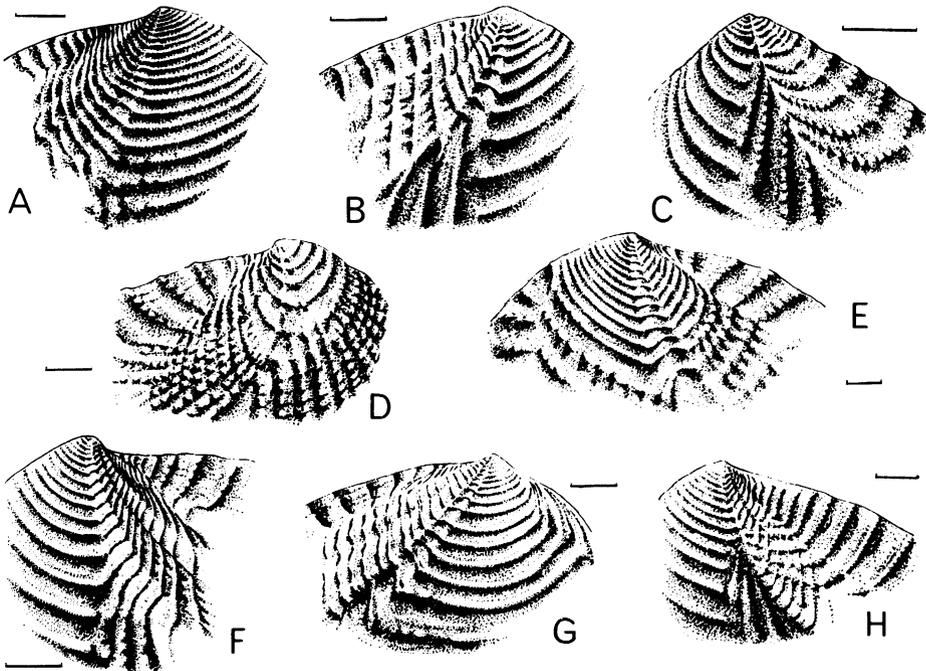


FIG. 26. Ornamentation in pinnate trigoniaceans from Japanese Cretaceous. A-C, F-H. Species of *Apiotrigonia*. D. *Heterotrigonia*. E. *Microtrigonia*. Bar scale = one mm. (After Tashiro, 1972.) Note ontogenetic growth changes which together with stratigraphic position support hypothesis of derivation from *Undulatae*.

the valve. Forms with relatively high spiral angle have low convexity, and the valve summit is close to the hinge margin. A third variant of Form B is distinctive in having a uniformly convex anterior outline from beak to ventral margin, whereas a fourth is characterized by orthogyrous or slightly opisthogyrous umbone (fig. 48).

Even a casual review of the literature demonstrates the presence of these two basic shell shapes in many upper Paleozoic formations. Very possibly these are recurring adaptive forms. Considering examples encompassed by Form A, there is a striking similarity in shape between de Koninck's (1885, pl. 22, fig. 4) *Protoschizodus wortheni* from the Lower Carboniferous of Belgium and our illustration (fig. 50A) of *Schizodus supaiensis* from the Permian of Arizona. Likewise, the shape of Girty's (1927, pl. 25, figs. 46-49) *Schizodus semistriatus* from the Idaho Mississippian closely approximates that of *S. altus* (see fig. 40) from the Wyoming Permian.

Turning to Form B, examples of Permian *S. texanus* (e.g., Clifton, 1942, pl. 101, figs. 20-28; present paper, fig. 53) are reminiscent of Hind's (1900 [1896-1900] pl. 16, fig. 10) *S. axiniformis* from the Upper Carboniferous of England and the Meek and Worthen (1866, pl. 23, figs. 6a, b) *S. chesterensis* from the Mississippian of Illinois. As another example, the unusually elongate form of the Permian *Paraschizodus elongatus* (see fig. 73) is represented in the Pennsylvanian by Girty's (1899, pl. 72, figs. 7b, c) *S. meekanus*.

Whenever a particular valve shape is recognized at successive levels in the late Paleozoic, one might speculate that a direct line of descent is represented. For example, elongate valves with orthogyrous umbones have been recorded from the Mississippian (e.g., *S. rostratus* as figured by Driscoll, 1965, pl. 16, figs. 6-21), the Pennsylvanian (e.g., *S. meekanus* of Girty, 1899, pl. 72, fig. 7), and the Permian (*S. texanus*, our fig. 53). To determine whether these forms are components of a single evolutionary lineage would require much more stratigraphic control than is now available. Furthermore, other morphological features such as hinge characteristics and muscle scars should be evaluated, but such information commonly is not obtainable.

Our survey of the literature suggests that the apparently sporadic recurrence of such forms

does not signify a complete lack of trends in upper Paleozoic trigoniacean history. Considering the stratigraphic distribution of previously described species in the United States, Form A seems to be dominant in Mississippian strata, whereas Form B becomes increasingly common through Pennsylvanian and Permian strata. Half the described Mississippian species can be referred to Form A, but it is represented by only slightly more than a third of the Pennsylvanian species and by less than a third of the Permian ones. A similar impression for the Mississippian is obtained from consideration of faunas from England and Belgium. Hind (1900 [1896-1900]) recognized 17 Lower Carboniferous trigoniacean species. Three of these probably belong to other groups. Of the rest, seven represent Form A, four represent Form B, and three are intermediate. In de Koninck's (1885) monograph on the Lower Carboniferous faunas of Belgium, 12 trigoniacean species are identified. Half of these are intermediate between Forms A and B, five exemplify Form A, and one Form B.

Because many names eventually must be abandoned as subjective synonyms, a simple tabulation of described species is not compelling evidence for an evolutionary trend. Further study will be required to confirm or deny our impression that Mississippian trigoniacean assemblages are dominated by high, roughly equilateral forms with extensive respiratory margins. However, it appears to us that such forms are progressively less common in Pennsylvanian and Permian rocks, whereas posterior elongation and reduction of the respiratory margin, correlated possibly with deeper penetration of the substrate, characterize an increasing percentage of uppermost Paleozoic and Triassic trigoniacean species. An accompanying tendency is suggested toward a more acute angle between respiratory margin and a line drawn through the muscle scars.

TREATMENT OF SPECIES IN THE PRESENT WORK

Our main purpose has been to study and interpret existing collections of Pennsylvanian and Permian trigoniaceans, and we have not attempted a general revision of all nominate taxa of upper Paleozoic and lower Mesozoic species.

In only two cases have we assembled collec-

tions that could justify an amplified characterization for a previously named Carboniferous species. *Schizodus alpinus* (Hall, 1858), the first upper Paleozoic trigoniacean species described in America, typifies one of the two basic trigoniacean shapes found in upper Paleozoic strata. *Schizodus ulrichi* Worthen, 1890, exemplifying the second, is the only other Carboniferous species for which we have an adequate study collection on which to base a new diagnosis.

Many more collections are needed for evaluating the population structure and diversity of Carboniferous trigoniaceans. In view of the typological approach of past authors, existing species nomenclature clearly is highly artificial. We assume that extensive intrapopulation variability demonstrated by our Permian collections is also characteristic of the less well-represented populations.

Morphologic terms employed in the taxonomic descriptions that follow are defined either in previous pages of the present memoir or in the glossary of the Bivalvia section in Cox et al. (1969, p. 102). In regard to shell dimensions, length is the greatest linear dimension measured parallel to a line drawn through the centers of the adductor scars, roughly parallel to the hinge axis. Height is the greatest dimension at right angles to this axis. Partial length is the linear extension of the shell ahead of the beaks. It will be

understood that the standard form ratio, length/height, is abbreviated L/H; H/C is the ratio of height/convexity of single valves. L/PL is the ratio of length/partial length, and n = number of specimens. Form analyses follow Imbrie (1956) for calculation of the bivariate statistics of the regression line or "reduced major axis":

N = number of pairs of measurements

s = standard deviation

OR = observed range

σ = standard error

\bar{x} = mean of x

\bar{y} = mean of y

x = abscissa

y = ordinate

r = correlation coefficient

a = growth ratio

b = initial growth index

Dd = coefficient of relative dispersion

In the following section, arrangement of genera within a family and of species within a genus is alphabetical with the exception that either a type genus or a type species is placed first in its group. Recorded stratigraphic ranges of species and genera are shown in figure 27. Stratigraphic relationships of American Upper Paleozoic formations cited in species descriptions are expressed in tables 1 and 2.

SYSTEMATICS

CLASS BIVALVIA LINNÉ, 1758

ORDER TRIGONIOIDA DALL, 1889

SUPERFAMILY TRIGONIACEA LAMARCK, 1819

The taxonomic arrangement adopted here agrees with most works (e.g., Nevekkaya et al., 1971) in combining the trigoniaceans and uni-onaceans in a single order, rather than in two orders, as in Cox et al. (1969).

Diagnosis. Trigoniacean shell equivalve, isomyarian, mainly prismatonacreous, trigonal, ovoid or rhomboid; anterior edge semicircular; umbones typically prominent; posterior margin produced, obliquely truncate or subtruncate; ligament external, opisthodontic, parivincular; hinge teeth two or three in each valve, radiating from beak, laterals lacking or poorly differentiated;

mainly with unfused mantle margin; gills filibranchiate in living representatives.

Distribution. Cosmopolitan, marine. Upper Silurian to Recent, inclusive. We do not presently accept the Ordovician *Lyrodesma* as a trigoniacean.

EOSCHIZODIDAE NEWELL AND BOYD,
NEW FAMILY

This family is monogeneric, hence the characters are those of the genus. Superficially, it resembles certain Myophoriidae, such as *Neoschizodus* but the dentition is fundamentally different.

GENUS *EOSCHIZODUS* COX, 1951

Figure 28

Homonymy. Replaces preoccupied *Kefer-*

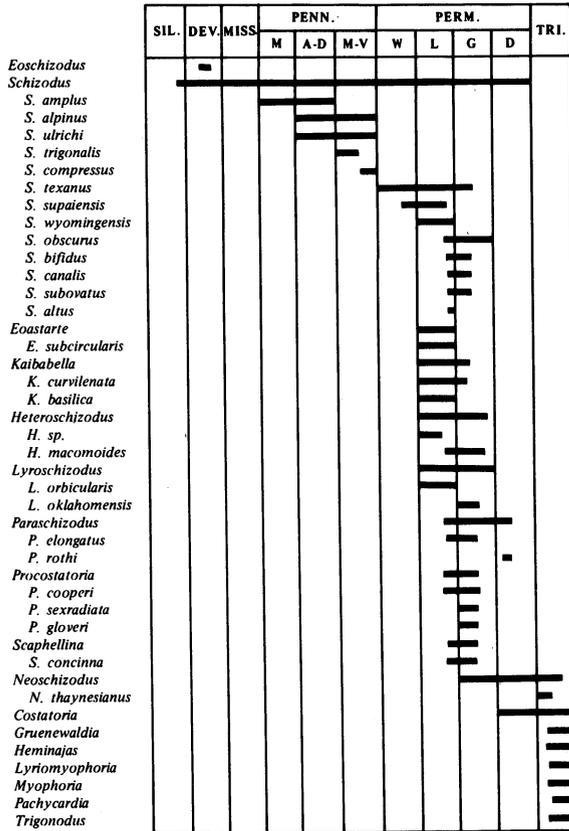


FIG. 27. Generalized chronologic distribution of taxa discussed in the text. Explanation: M, Morrowan; A-D, Atokan and Desmoinesian; M-V, Missourian and Virgilian; W, Wolfcampian; L, Leonardian (including Road Canyon); G, Guadalupian; D, Djulfian.

steinia Neumayr, 1891 (*non* Quatrefages, 1865).

Type Species. The Devonian *Megalodus truncatus* Goldfuss, 1837, by original designation.

Diagnosis. Unornamented, subtrigonal slightly prosogyrous shells with approximately median, protruding umbones and well-defined posterior ridge; lunule, escutcheon and myophorous buttresses not developed; principal tooth and socket of right valve rounded and keeled, as with *Schizodus*, and posterior tooth of both valves elongate as in the myophorian condition; left valve superficially myophorian, except that the median triangular tooth lacks the long posterior branch and there is only one rather than two posterior laterals.

Distribution. Very rare, limited to the type species. Upper Middle Devonian (*Stringocephalus* Zone), Rhineland, Germany.

The hinge formula may be written as follows:

$$\begin{array}{c}
 \text{Posterior} \qquad \qquad \qquad \text{Anterior} \\
 \text{RV } n \ 0 \ 1 \ 0 \ 1 \ 0 \\
 \text{LV } n \ 1 \ 0 \ 1 \ 0 \ i
 \end{array}$$

This is like that of Schizodidae but in the latter the posterior teeth are short.

Discussion. The hinge is structurally closer to the schizodian than to the myophorian condition although it superficially resembles the latter. The outermost of the two posterior laterals of the myophorian left valve corresponds to the single posterior tooth of the left valve in *Eoschizodus*. The innermost posterior lateral in myophorians is an extension of the pivotal tooth and is without a homologue in *Eoschizodus* or *Schizodus*.

The phyletic placement of *Eoschizodus* is presently uncertain. Possibly it is an early offshoot

TABLE 1

SOME AMERICAN PENNSYLVANIAN STRATIGRAPHIC UNITS CITED IN THE TEXT

	TEXAS	OKLAHOMA	NORTH MID- CONTINENT	ILLINOIS	OHIO, KENTUCKY
VIRGILIAN	Wayland Sh. Finis Sh.		Shawnee Gr. Haskell Ls.	Mattoon Fm.	
MISSOURIAN			Lane Sh. Westerville Ls.		
DESMOINESIAN	Millsap Lake Fm.	Holdenville Fm. Wetumka Sh. Wewoka Fm. Hartshorne Ss.	Cherokee Gr.		
ATOKAN		Atoka Fm. Lester Fm.		Seville Ls.	Boggs Mem. Lower Mercer Ls. Kendrick Sh.
MORROWAN		Wapanucka Ls.			

TABLE 2
SOME AMERICAN PERMIAN STRATIGRAPHIC UNITS CITED IN THE TEXT

	TEXAS	COLORADO PLATEAU	WYOMING
LOWER TRIASSIC	ABSENT	Thaynes Woodside Moenkopi-	
DJULFIAN (?)	Doxey	ABSENT	ABSENT
GUADALUPIAN	Capitan Appel Ranch Willis Ranch- Lower Getaway China Tank Dozier Dog Creek	GENERALLY ABSENT	Ervay Shedhorn Franson
LEONARDIAN	Road Canyon-Blaine Cathedral Mt. Hess Bone Spring	San Andres-Kaibab Fort Apache	Park City Grandeur Goose Egg GENERALLY ABSENT
WOLFCAMPIAN	Skinner Ranch Hueco Neal Ranch Talpa	GENERALLY ABSENT	GENERALLY ABSENT

from an ancestor in common with *Schizodus*. It seems to us improbable from available evidence that *Eoschizodus* was directly ancestral to either Schizodidae or Myophoriidae. Beuhausen (1895) illustrated several eoschizodids from the Rhineland Stringocephalenkalk under species of *Myophoria*. Many of these are quite small shells with hinges similar to that of *Eoschizodus truncatus*. They may represent juveniles of that species.

FAMILY UNCERTAIN

GENUS *RHENANIA* WAAGEN, 1907

Type Species. The Devonian *Myophoria schwelmensis* Beuhausen, 1895, by subsequent designation, Cox, in Cox et al., 1969, p. 475.

Diagnosis. Differs from *Eoschizodus* mainly in possession of arcuate, radial costellae over the corselet.

Distribution. Upper Middle Devonian (*Stringocephalus* Zone), Rhineland, Germany.

Discussion. We have not examined specimens of *Rhenania*, but judging from Beuhausen's 1895 work, the shells are quite small and may represent juveniles of the associated *Eoschizodus truncatus*, but this is by no means certain.

GENUS *HEFTERIA* DAHMER, 1948

Figure 29

Type Species. The Lower Devonian *Cardinia carinata* Roemer, 1885, by original designation.

This poorly understood genus has been referred erroneously, we think, to the Myophoriidae (Cox, in Cox et al., 1969, p. 473). We have two natural molds of valves from the Harz Mountains of Germany. The shell is quite elongate, and the cardinal teeth resemble those of the Permophoridae in the Carditacea. However, we are unable to identify the posterior lateral tooth characteristic of that family and *Hefteria* may belong elsewhere. It probably is not a trigoniacean.

SCHIZODIDAE NEWELL AND BOYD, NEW FAMILY

Diagnosis. Mainly unornamented shells with rounded umbonal ridge and poorly differentiated corselet; hinge teeth short, not striated; pivotal teeth subequal; principal socket of left valve partly floored by hinge plate; myophorous buttresses lacking or very weak; pallial sinus lacking, or very weak; dental pattern as follows:

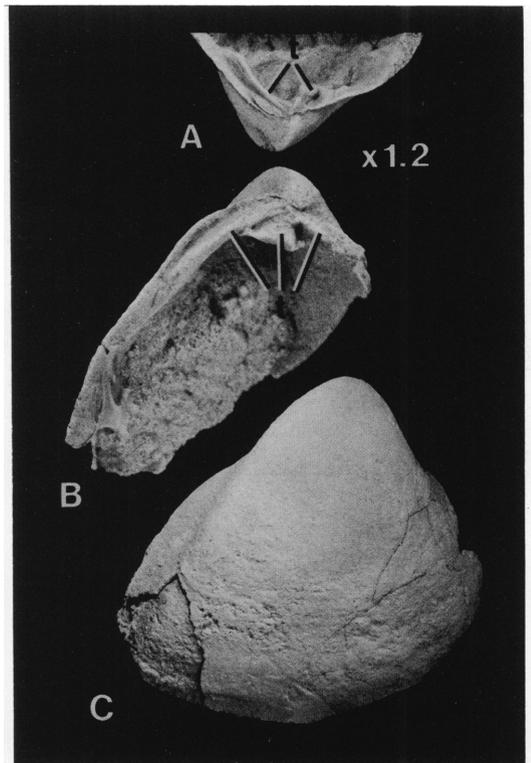


FIG. 28. *Eoschizodus truncatus* (Goldfuss). Calcareous specimen from the Middle Devonian of Germany, type species of *Eoschizodus*. A, C. Right valve, a much figured hypotype (Gruenewaldt, 1851; Frech, 1889; Beuhausen, 1895) from the *Stringocephalus* beds at Paffrath, Rheinland. HU M.B.-M. 1.1. B. Left valve, a hypotype (Beuhausen, 1895), same horizon and locality as A and C. An apparent elongate socket above posterior tooth (t) is caused by shadow on flat shelf in plane of commissure. HU M.B.-M.I.3.

	RV	n(o)	i	O	I	o	
Posterior							Anterior
	LV	n(i)	o	I	O	i	

Rarely, the nymph of the left valve carries an ill-defined linear tooth.

Distribution. Upper Silurian to Upper Permian, cosmopolitan.

Discussion. All members of this family have essentially unornamented shells and display the schizodian hinge grade. This is the only family of trigoniaceans from the Lower Carboniferous known to us and significant evolutionary modifi-

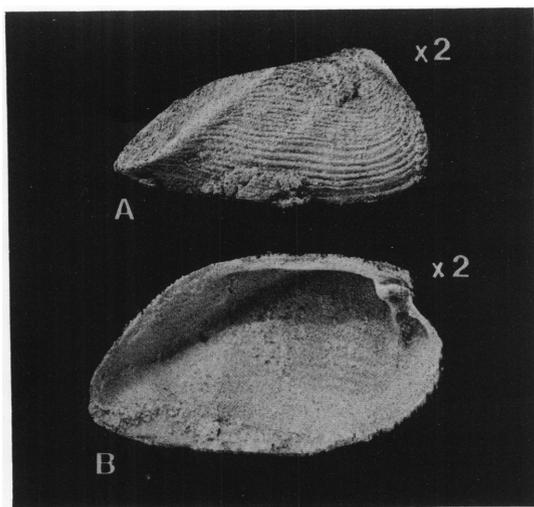


FIG. 29. *Hefteria carinata* (Roemer). Examples of the type species of *Hefteria*, described as a myophoriid, but probably a permophorid. Lower Devonian (Emsian), Rhineland, Germany. A. Latex cast, right valve. Koblenz Quartzit, Kühkopf, Koblenz. SM XV(1640d). B. Latex cast, left valve. Upper Koblenz beds, Alkenbachtal east of Münnichsberges. SM XV(1640b).

cations do not appear until the Upper Carboniferous. Consequently, we interpret the Schizodiidae as relatively primitive and ancestral to most of the trigoniacean families (fig. 3).

GENUS *SCHIZODUS* DE VERNEUIL
AND MURCHISON, 1844

Figures 12E, F, 14, 16, 17, 30-62

Priscaonia Conrad, 1867.

Protoschizodus de Koninck, 1885.

Type Species. *Axinus obscurus* J. Sowerby, 1821. Subsequent designation by de Verneuil, 1845.

Diagnosis. Length to height ratio commonly 1.1/1 to 1.5/1 and beaks generally well ahead of midpoint of length. Height/convexity of single valves about 3/1 with the maximum convexity slightly posterior of the beak. Umbones typically prominent, submedian, and slightly prosogyrous. Beaks strongly incurved approaching hinge line. Anterior and ventral outline without conspicuous interruptions in curvature. Posterior outline usually somewhat obliquely truncate. Posterior ridge broadly rounded in most species; corselet poorly differentiated and plane to slightly concave. Lunule and escutcheon generally absent. Ornamenta-

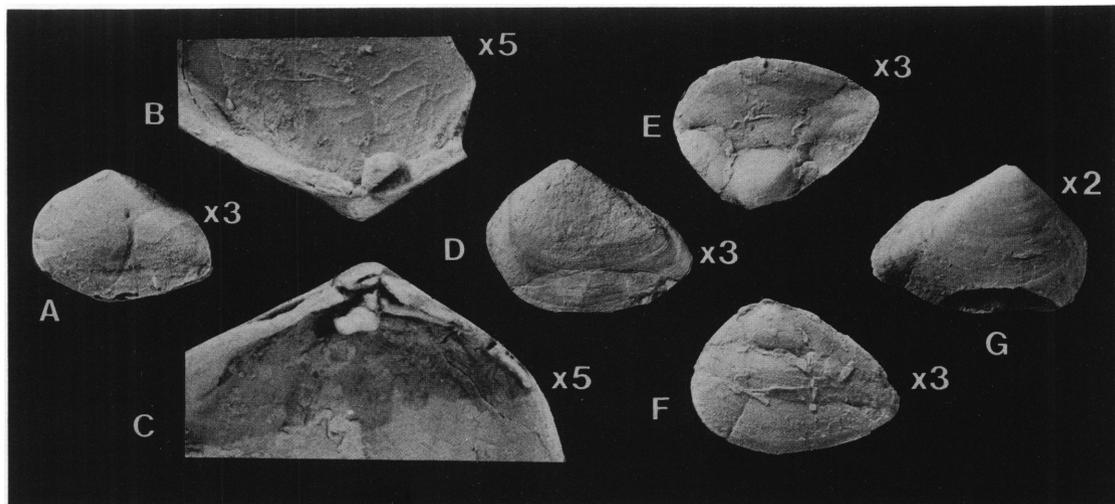


FIG. 30. *Schizodus nuculoides* (McCoy), 1844. McCoy's original specimens from Northern Ireland. Type species of *Protoschizodus* De Koninck, 1885. Lower Carboniferous (Visean) black shale, Drumard, Draperstown, County Londonderry, Ireland. A. Holotype, left valve, X3. NMI G7/1.1971. B. Hinge of right valve, X5. CU E.917.2. C. Hinge of left valve, X5. CU E.918.1. D. Left valve, exterior of figure C, X3. E, F. Crushed bivalved specimen, X3. CU E.917.3. G. Larger right valve, X2. CU E.917.4.

tion lacking or limited to weak, closely spaced concentric annulae mainly on the anterior slope. Ligament groove length commonly between one and two times distance from beak to distal end of pivotal tooth. For dental formula, see family diagnosis.

Distribution. Upper Silurian-Permian, cosmopolitan.

Discussion. Representatives of this genus are conservative, and discrimination among many of the named species consequently is quite difficult or impossible without extraordinary samples.

There are two consistently identifiable teeth in each valve with the anterior member of the series on the left valve; rarely, a weak third tooth occurs posteriorly along the margin of the nymph of left valves corresponding to a weak groove along the nymph base of right valves, but this character is variable. The undersurface of the large tooth of left valves bears a median furrow which frequently gives it a somewhat bifid aspect; the ventral edge of this tooth is slightly oblique along an anteroventral-posterodorsal axis, and the anterior side is curved. The large tooth of the right valve is somewhat irregular in form, knob-shaped to subconical, lying approximately in the plane of commissure, and the exposed surface of this tooth under the beak bears a narrow ridge that curves around the adjacent major socket and continues along the crest of the posterior tooth (fig. 12E). This character is found also in *Eoschizodus*.

The large socket of each valve is unfloored for half or more the length of the adjacent major tooth. Myophorous buttresses are absent or very poorly developed. One or two internal radial ridges and furrows, most conspicuous in old shells, trend posteroventrally from the umbonal cavity in a few species. The pallial line commonly is unrecognizable. Subequal anterior and posterior adductor scars are above the mid-height of the shell; the anterior pedal retractor scar forms a short dorsal extension at the top of the anterior adductor; an elongate posterior pedal retractor scar is parallel to the valve margin and continuous with, or narrowly isolated from, the upper extremity of the posterior adductor scar; a pedal elevator scar lies at the apex of the umbonal cavity in both valves.

The Lower Devonian Kahleberg quartzite of

the Harz Mountains in West Germany has yielded natural molds of small schizodids described under several specific names of *Schizodus* and *Myophoria* by Beushausen (1884, 1895). Clarke in 1899 assigned the name *Toechomya* to some of these and Cox (1951, p. 368) designated *Schiz-*

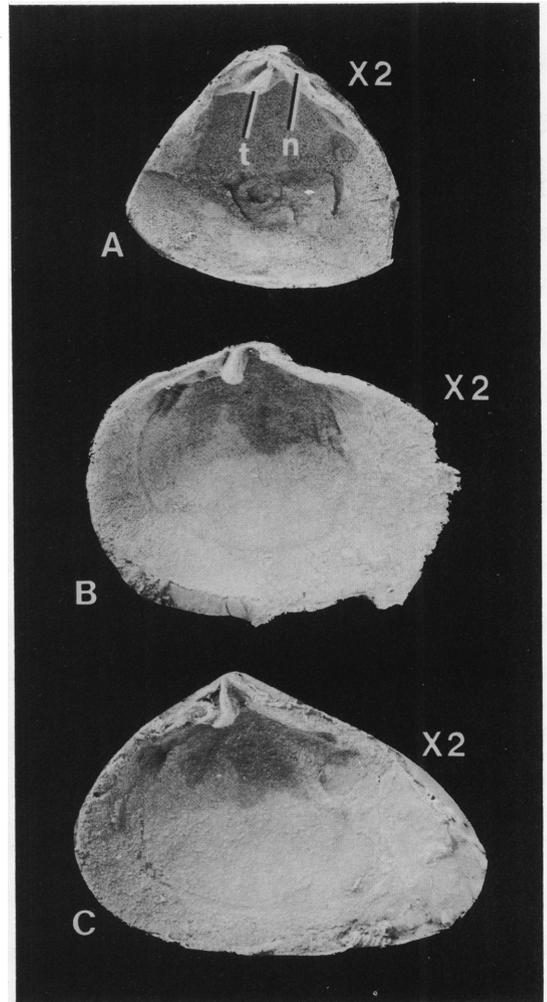


FIG. 31. Latex casts of right valves of *Toechomya transversa* (= *kahlebergensis*) (Beushausen). Coblenzian, Lower Devonian, of Germany. Poorly understood genus apparently similar to, and possibly synonymous with, *Schizodus*. A. From Schalke. YPM 2918A. B. From Kahleberg Sandstein, Ober Kellerhalsteich. SM XV 2084. C. From Baybachtal. SM XV 2083.

Abbreviations: n, nymph; t, pivotal tooth.

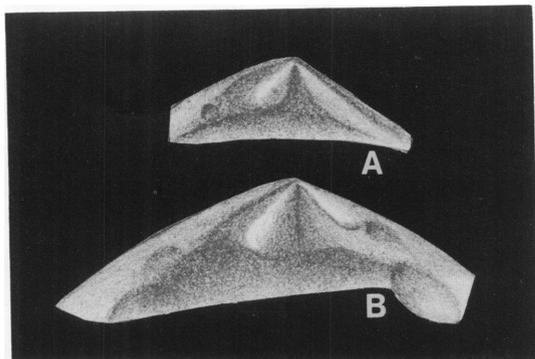


FIG. 32. *Schizodus ? circularis* (Beushausen). Replicas of natural molds. Coblenzian, Oberlahnstein, Harz Mountains, Germany (after Beushausen, 1895, pl. 10, figs. 12A, 14A). A. Right valve. B. Left valve. This form is similar to, and possibly identical with, the type species of *Toechomya*.

odus transversus Beushausen, 1884 as the type species. Unfortunately, we have been unable to obtain good specimens of this or stratigraphically associated forms (fig. 30). The hinge of *Myopho-*

ria circularis Beushausen, 1895 (fig. 32), apparently a similar form as illustrated by Beushausen (1895, pl. 10, figs. 12-14), closely resembles that of *Schizodus, sensu stricto*. If this species may be regarded as a junior synonym of *Toechomya transversa* (Beushausen), 1884, then *Toechomya* may be morphologically indistinguishable from *Schizodus*. However, our data are incomplete and we are not now prepared to adopt this conclusion.

The dental pattern of the Lower Devonian forms is:

	RV niOIo	
Posterior	LV noIOi	Anterior

An undescribed Upper Silurian species from the Elwy Group (Lower Ludlovian, *Cucullograptus scanicus* zone) of Wales (fig. 33) was supplied by Adrian Rushton of the Institute of Geological Sciences, in London. It somewhat resembles the type species of *Toechomya*, cited above, but like our examples of that form the specimens are too imperfect for critical comparisons. They are roughly 1 cm. high. The hinge probably was schiz-

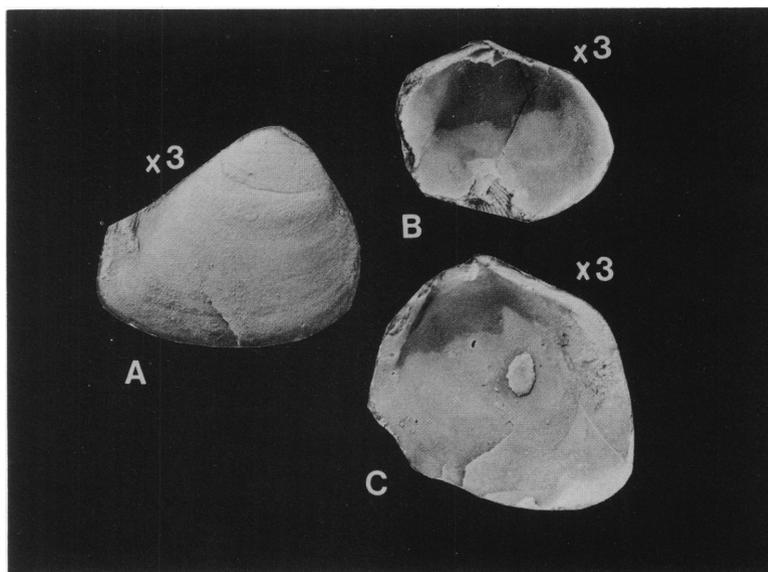


FIG. 33. *Schizodus ?* sp. Latex replicas of natural molds from the Silurian Lower Ludlovian, Elwy Group (*Cucullograptus scanicus* Zone) 9.6 km. southeast of Conway, Wales. A. Right valve. INGB RK 1981. B. Left valve. INGB RK 1999. C. Right valve. INGB RK 1992. These are the oldest undoubted trigoniaceans known to us.

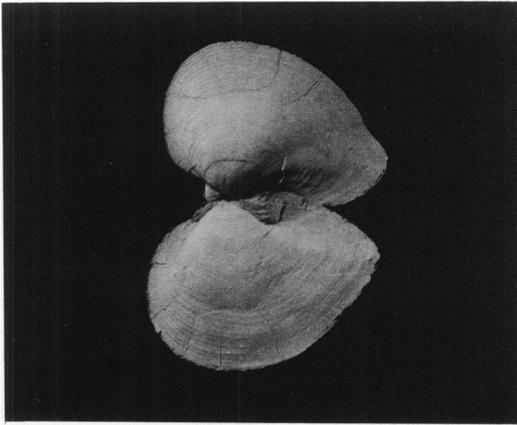


FIG. 34. Type species of *Schizodus* de Verneuil and Murchison. Associated valves of a single individual of *Schizodus obscurus* (J. Sowerby). Manchester Marl (Zechstein), Lowton, Lancashire, England. DM 4285, Institute of Geological Sciences, Leeds, England.

odian in structure and pattern. It is quite unlike that of the Devonian *Eoschizodus*. The dental arrangement apparently is as follows:

RV niOI(o)
 Posterior Anterior
 LV noIO(i)

Schizodus obscurus (J. Sowerby, 1821)

Figures 34-37

Axinus obscurus J. Sowerby, 1821, p. 12, pl. 314.
Cucullaea schlotheimi Geinitz, 1841, p. 638, pl. 11, fig. 6.
Axinus (Schizodus) truncatus King, 1844, vol. 1, p. 505.
Axinus ovatus Meek and Hayden, 1858, p. 262; 1864 (1865), p. 59, pl. 2, figs. 11a, 11b.
Schizodus subobscurus Licharew, 1933, p. 39. Maslennikov, 1935, p. 93, pl. 5, fig. 2. Lyutkevitch and Lobanova, 1960, p. 59, pl. 4, figs. 2-5.
Schizodus obscurus; Newell, 1955, p. 31, pl. 1, figs. 6-8, 10; Lyutkevitch and Lobanova, 1960, p. 58, pl. 4, fig. 1. Ullrich, 1964, p. 71, pl. 8, figs. 5-8, pl. 9, figs. 1-4. Logan, 1967, p. 47, pl. 8, figs. 2-4. Pattison, 1970, p. 149, pl. 21, fig. 12, pl. 22, figs. 1-3.¹

¹See Ullrich, 1964, and Logan, 1967, for expanded synonymies.

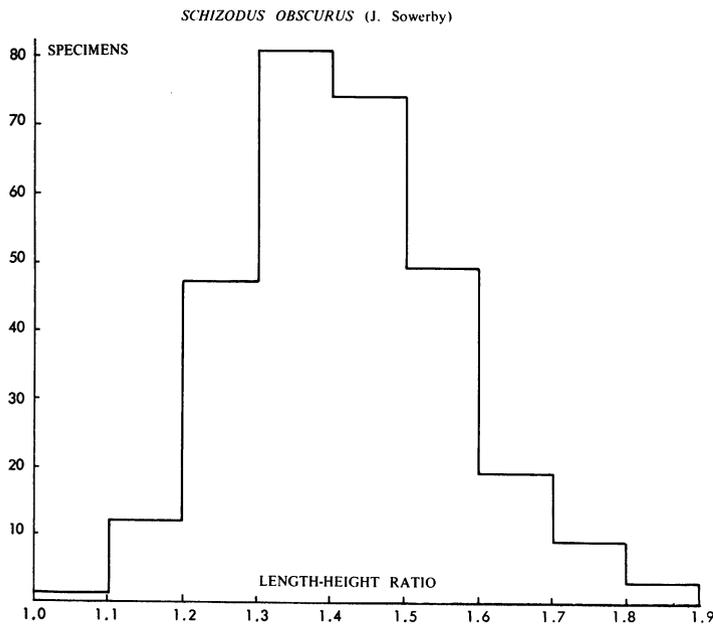


FIG. 35. Form ratios in a sample of shells of *Schizodus obscurus* (J. Sowerby). Data from Pattison, 1970. Manchester Marl (Zechstein), northwestern England.

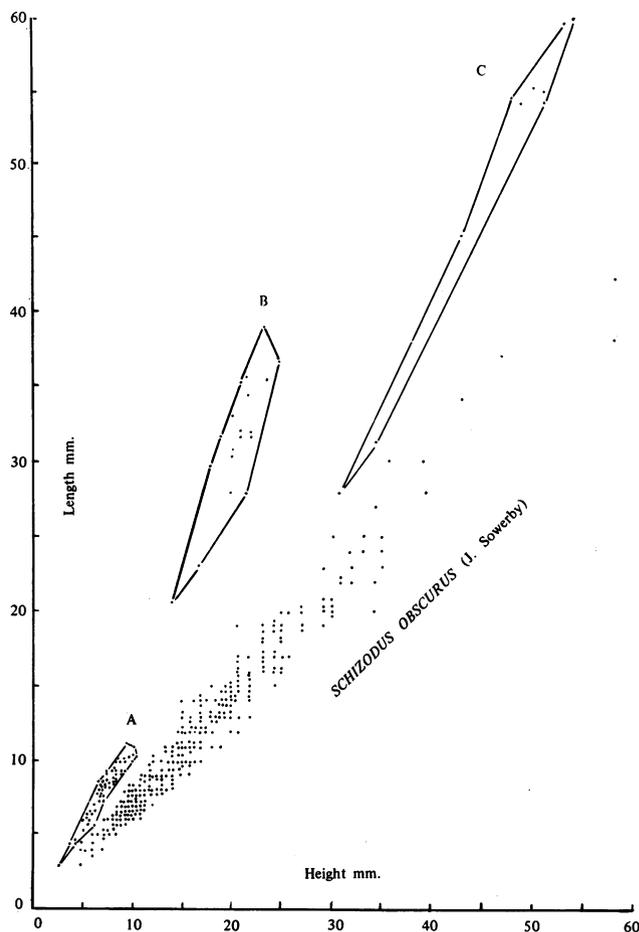


FIG. 36. Form ratios of three species of *Schizodus* of Late Leonardian age (Grandeur Member, Park City Formation, AMNH loc. 2010) compared with the type species, *Schizodus obscurus*. A. *Schizodus altus* Newell and Boyd, new species. B. *Schizodus bifidus* Ciriacks, 1963. C. *Schizodus wyomingensis* Newell and Boyd, new species. Data on *Schizodus obscurus* from Pattison, 1970. Manchester Marl (Zechstein), northwestern England.

Diagnosis. Shell somewhat inflated, ovoid, with broadly rounded ventral margin and extended, narrower, posterior; prominent umbones and beaks placed forward about 60 to 70 percent of shell length; typical length/height ratio 1.38/1; surface unornamented save for a few regular concentric annulae over anterior slope in unworn individuals; extreme length commonly less than 40 mm.

Distribution. Widely distributed in the Per-

mian boreal realm, especially in dolomitic facies, Zechsteinian of Greenland, United Kingdom, Germany (Upper Leonardian-Guadalupian); Kazanian and equivalents of the Soviet Union.

Discussion. Museum collections of this and other species of *Schizodus* frequently are based on internal molds that are significantly more elongate than the complete shells (fig. 37, compare nos. 2, 13). The median tooth of the left

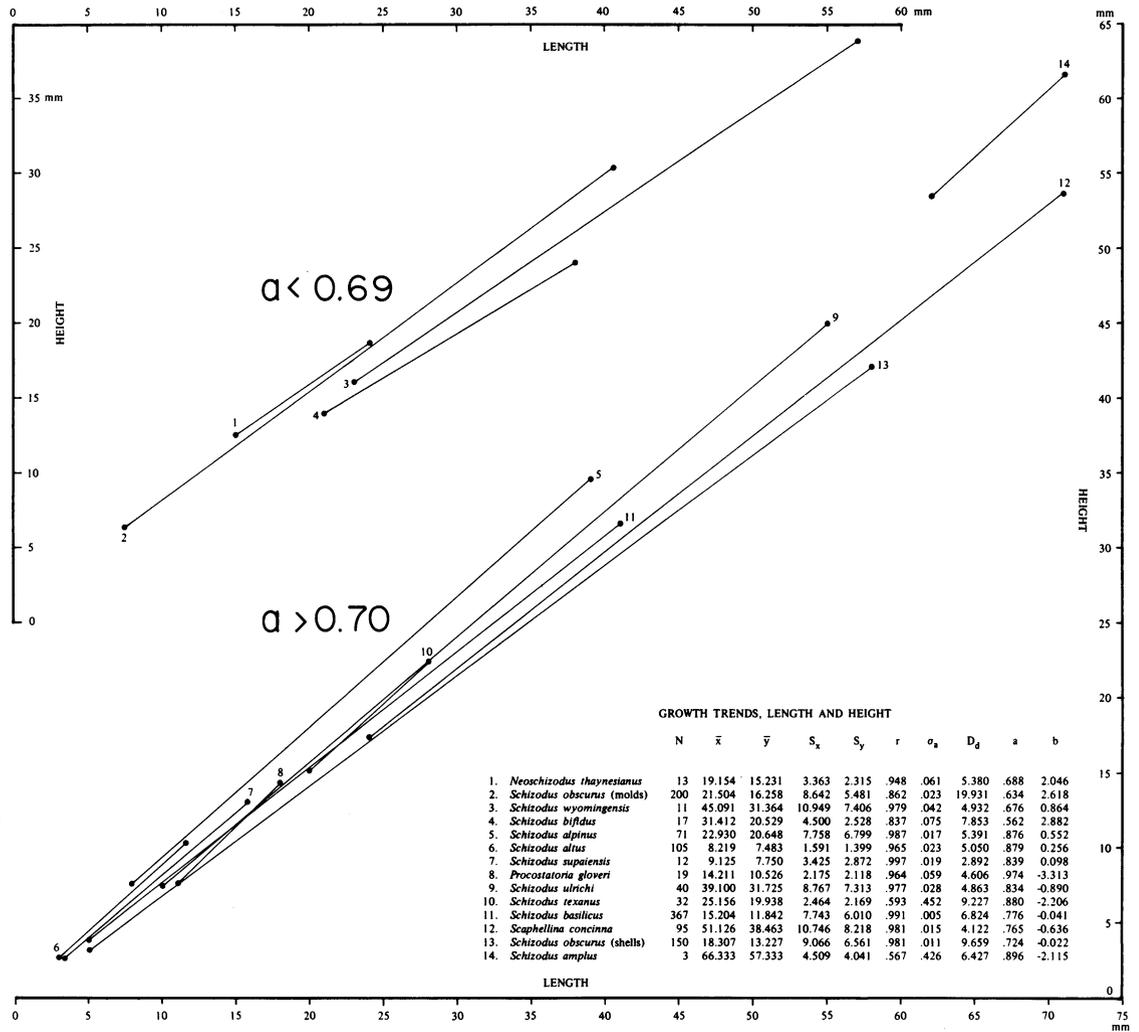


FIG. 37. Shell proportions in certain primitive Trigoniacea. The ontogenetic changes in form are essentially isometric and the growth trend intercepts and slopes do not vary greatly between diverse taxonomic groups. See page 90 for definitions of statistics used here.

Provenance of samples:

1. Triassic, Utah, Thaynes Formation, AMNH loc. 319A.
2. Permian, Zechstein Formation, Germany, data from Ullrich, 1964.
3. Permian, Grandeur Member, Wyoming, AMNH loc. 2010.
4. Permian, Grandeur Member, Wyoming, AMNH loc. 2010.
5. Pennsylvanian, USA, several localities.
6. Permian, Grandeur Member, Wyoming, AMNH loc. 2010.
7. Permian, Ft. Apache Limestone, Arizona, AMNH 28028.
8. Permian, Lower Getaway Limestone, Texas, AMNH loc. 512.
9. Pennsylvanian, USA, several localities.
10. Permian, San Andres Formation, Arizona, AMNH loc. 1067.
11. Permian, San Andres Formation, Arizona, AMNH loc. 1067.
12. Permian, Grandeur Member, Wyoming, AMNH loc. 2010.
13. Permian, Manchester Marl, data from Pattison, 1970.
14. Pennsylvanian, Holdenville Formation, Oklahoma U. loc. 4337.

valve is flanked by two slender radial teeth. The posterior of these is an obscure, low ridge along the base of the nymph and it engages a definite furrow along the face of the opposite nymph. The sockets are fully floored by the hinge plate except the principal socket of the right valve in which the floor recedes in a re-entrant leaving the distal one-half of the gap without a floor.

Schizodus texanus from western United States is a very closely similar form with a slightly shorter shell, length/height ratio about 1.26/1 (fig. 37, no. 10).

Schizodus alpinus (Hall, 1858)

Figures 7, 8, 37 no. 5, 38, 39

Dolabra? alpina Hall, 1858, p. 716, pl. 29, fig. 2.
Schizodus alpinus (Hall): Meek and Hayden, 1864 (1865), p. 58.

Schizodus symmetricus Calvin, 1890, p. 176, pl. 2, figs. 3a, 3b.

Diagnosis. Length slightly greater than height, almost equilateral. Anterior umbonal flank not sharply differentiated. Respiratory margin commonly more than half the shell height, producing truncate posterior outline. Posterior ridge rounded, bounding gently concave corselet, which in some valves bears narrow, faint radial

ridge. Posterior retractor extends dorsally as long, narrow groove, deepest toward anterior end. L/H=1.11 (n=72); H/C=3.01 (n=57); L/PL=2.34 (n=72).

Distribution. Long-ranging in the Pennsylvanian System in the United States; Atokan through the Virgilian of Kentucky, Ohio, Illinois, Nebraska, Kansas, Oklahoma, and Texas.

Discussion. Hall's description is a general characterization of external form accompanied by one figure. Our study collection consists of calcareous specimens from many horizons, including 63 shells from Texas and Oklahoma, 18 from Iowa, Missouri, and Illinois, and six from the Kendrick Shale of Kentucky. But these specimens yielded little information concerning internal features. The southwestern specimens are articulated shells and most of the midwestern ones, including the type specimen, exhibit only external surfaces.

The Kendrick Shale is a good source of molluscan shells retaining original aragonite, and it is a Kendrick specimen of *Schizodus alpinus* which possesses the crossed-lamellar shell structure illustrated in figure 8. The valve microstructure, from exterior inward, consists of a thin prismatic layer, a nacreous layer, a crossed-lamellar layer, and an inner nacreous layer. The prismatic layer

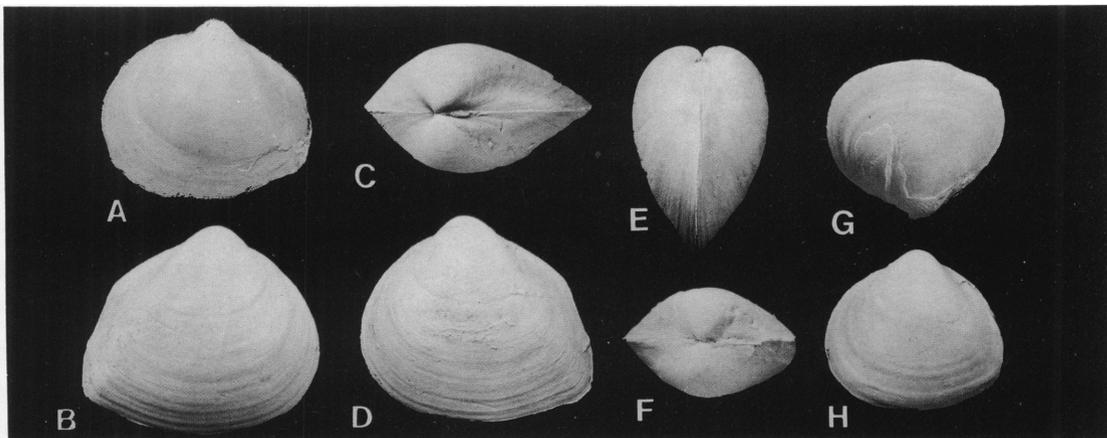


FIG. 38. *Schizodus alpinus* (Hall). Calcareous specimens from Middle and Upper Pennsylvanian rocks, Midcontinent, United States. A. Left valve, holotype, Cherokee Shale (probably Desmoinesian), Alpine, Wapella County, Iowa, AMNH 8388. B-E. Bivalved individual retaining the ligament. Wayland Shale (Virgilian), 1.2 miles south of Gunsight, Texas. USNM 76950. F-H. Bivalved specimen from the Kendrick Shale (Atokan) Cows Creek, Floyd County, Kentucky. YPM 27821; loc. 3449/1.

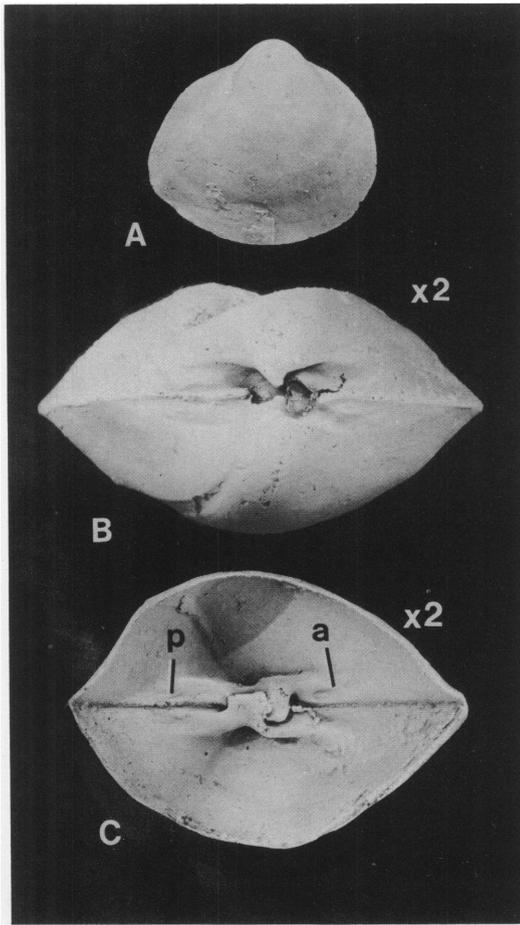


FIG. 39. *Schizodus alpinus* (Hall). Holotype of *S. symmetricus* Calvin, 1890, regarded here as junior subjective synonym of *S. alpinus*. "Upper Coal Measures" Pennsylvanian, at Braddyville, Page County, Iowa. ISU 7-090. A. Right side view. B. Umbonal view. C. Interior of hinge of latex cast oriented with right valve above.

Abbreviations: a, anterior retractor; p, posterior retractor.

is preserved to varying degrees in many calcareous shells of this species from various localities in the United States. Surface expression of the prisms can be easily observed at 30X magnification or less. By contrast, the nacreous and crossed-lamellar structures in this species have been recognized only in the Kendrick material at

TABLE 3
BIVARIATE STATISTICAL CHARACTERIZATION OF *SCHIZODUS ALPINUS* FROM A SINGLE LOCALITY, AMNH LOC. 8, WETUMKA FORMATION, DESMOINESIAN, NEAR ADA, OKLAHOMA^a

	Height Length	Partial Length Length	Convexity Height
N	21	21	16
\bar{x}	19.48	19.48	18.44
\bar{y}	17.57	8.48	6.06
s_x	7.44	7.44	6.83
s_y	6.23	3.20	1.95
r	0.99	0.95	0.95
OR _x	33-11	33-11	29-10
a	0.84	0.43	0.29
σ_a	0.03	0.03	0.02
b	1.25	0.09	0.81

^aSee page 90 for explanation of statistical parameters.

TABLE 4
BIVARIATE STATISTICAL CHARACTERIZATION OF *SCHIZODUS ALPINUS* FROM MANY LOCALITIES^a
(The sample is composite.)

	Height Length	Partial Length Length	Convexity Height
N	72	72	57
\bar{x}	22.86	22.86	21.28
\bar{y}	20.60	9.79	7.04
s_x	7.73	7.73	6.69
s_y	6.77	3.31	1.96
r	0.99	0.96	0.95
OR _x	39-8	39-8	31-8
a	0.88	0.43	0.29
σ_a	0.02	0.01	0.01
b	0.58	-0.00	0.79

^aSee page 90 for explanation of statistical parameters.

higher magnification of 100X or so. Preparations of other valves proved to be recrystallized.

Small shells of *Schizodus alpinus* probably are not distinguishable from those of *S. ulrichi*. With increased size, the shells of *S. alpinus* differ from those of *S. ulrichi* by virtue of more centrally placed beaks, lower L/H value, longer respiratory

margin relative to valve height, and a more concave corselet.

A bivariate statistical evaluation of differences between *S. alpinus* and *S. ulrichi* with regard to reduced major axes for L/H, H/C, and L/PL indicates significant differences (table 5).

Subsequent to Hall's description of *S. alpinus*, many names were introduced for Carboniferous shells of similar form. These will be credible as distinct species only if future work demonstrates that they represent populations significantly different from *S. alpinus*. Meanwhile, the published characterizations of the following species seem to us to be inadequate to distinguish them from *S. alpinus*: (Mississippian) *S. aequalis* Hall, 1885; *S. cuneus* Hall, 1883; *S. curtiforme* Walcott, 1884; *S. harlamensis* Herrick, 1888; *S. medinaensis* Meek, 1871; *S. newarkensis* Herrick, 1888; *S. prolongatus* Herrick, 1888; *S. quadrangularis* Hall, 1870; *S. semistriatus* Girty, 1927; (Pennsylvanian) *S. affinis* Herrick, 1887; *S. curtus* Meek and Worthen, 1866.

***Schizodus altus* Newell and Boyd, new species**

Figures 37 no. 6, 40

Etymology. *altus*, Latin, high, deep.

Diagnosis. Small, convex shells almost as high as long. Beak orthogyrous. Respiratory margin very high and rectilinear, meeting dorsal margin at obtuse angle. Posterior ridge bounds flat to slightly concave, steeply sloping corselet; area immediately in front of posterior ridge either flat or site of very shallow sulcus terminating at slight re-entrant in ventral margin, producing a somewhat projecting posteroventral corner. Ligament groove short, commonly not longer than distance

TABLE 5
STATISTICAL COMPARISON OF REDUCED
MAJOR AXES FOR *SCHIZODUS ALPINUS*
AND *SCHIZODUS ULRICHI*

Variates	Z ₁	Z ₂	Significant Difference
L/H	1.30	-5.34	Z ₂ (at 1% level)
H/C	-3.50	-	Z ₁ (at 1% level)
L/PL	2.46	-	Z ₁ (at 5% level)

Symbols: Z₁, a test of the hypothesis of equal slopes of the lines; Z₂, a test of the hypothesis of equal positions of the lines (Imbrie, 1956).

from beak to distal end of major tooth; nymph in both valves a narrow ridge easily mistaken for tooth. Major tooth in each valve variably bilobed, and with unusually broad, obliquely inclined, distal end; small posterior tooth on right valve expressed as prominence on anterior end of blade-like ridge. Weak myophorous buttresses on each side of hinge separating retractor grooves from deep umbonal cavity. Adductor scars commonly indistinct; retractor scars distinct elongate furrows near margin at each end of hinge area, anterior retractor clearly connected to adductor scar but posterior retractor more or less isolated from adjacent adductor. L/H=1.09 (n=159); H/C=2.75 (n=156).

Distribution. Grandeur Member (Upper Leonardian), Park City Formation, Wind River Mountains, Wyoming, AMNH 2010. The species may also be represented in younger members (Fran-

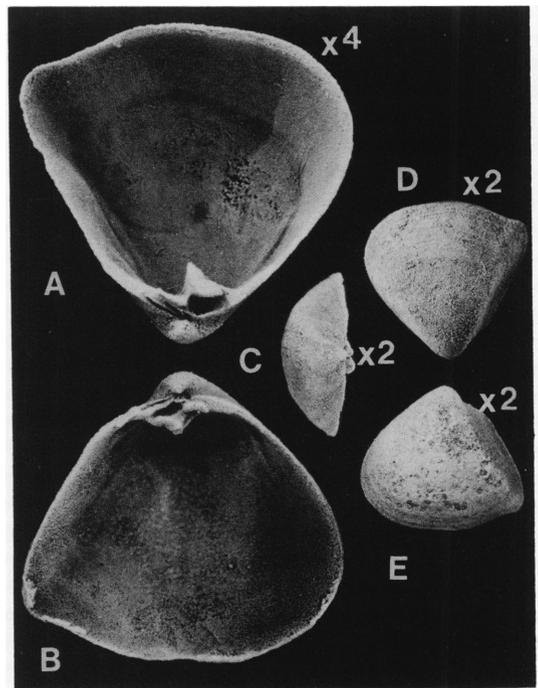


FIG. 40. *Schizodus altus* Newell and Boyd, new species. Silicified specimens from Grandeur Member (Leonardian), Park City Formation, Wyoming. AMNH loc. 2010. A, C, D. Right valve, holotype. AMNH 29177. Note suggestion of incipient pallial sinus in A, B, E. Left valve, AMNH 29178.

TABLE 6
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS ALTUS
FROM GRANDEUR MEMBER OF PARK CITY
FORMATION AT BEAVER CREEK,
WYOMING, AMNH LOC. 2010^a

	Height Length	Convexity Height
N	105	106
\bar{x}	8.22	7.40
\bar{y}	7.48	2.73
s_x	1.59	1.49
s_y	1.40	0.67
r	0.97	0.94
OR _x	11.7-3.0	10.7-2.8
a	0.88	0.45
σ_a	0.02	0.02
b	0.26	-0.61

^aSee page 90 for explanation of statistical parameters.

son and Ervay members) of the Park City Formation as the material assigned to *Schizodus* sp. B by Ciriacks (1963, p. 62) may belong to *altus*.

Discussion. More than 400 silicified specimens, many of them nearly complete, were examined from a 5-inch layer at Beaver Creek, Wyoming (AMNH loc. 2010).

This species resembles *Schizodus supaiensis* Winters. The two species overlap broadly in scatter diagrams for convexity versus length, and there is significant overlap of length versus height. The length-height ratio for *S. supaiensis* is slightly greater than that for *S. altus*. The type specimens of *supaiensis* have a convex posterior margin, in contrast to the straight to slightly con-

cave margin in *S. altus*. The posterior and dorsal margins are gradational through a curve in *S. supaiensis*, whereas they form an angular (115°-125°) extension in *S. altus*. Compared with *S. supaiensis*, *S. altus* commonly has a more sharply defined posterior ridge, with the corselet very steeply sloping and flat to slightly concave, rather than distinctly concave. The fine regular concentric ornamentation of juveniles of *S. supaiensis* has not been observed on *S. altus* and articulated specimens of the two species differ in proximity of beaks. They are 0.15 mm. apart on the holotype of *S. supaiensis*, whereas an *S. altus* specimen of the same height has beaks 0.7 mm. apart.

The two species differ in hinge details. Left valves of *S. altus* possess a less complete floor below the major socket, and the posterior socket is not so elongate in *altus*. The distal end of the major tooth of the right valve of *S. altus* is notably broad and tilted in comparison with the equivalent tooth of *S. supaiensis*. The ligament groove in the latter species is longer than the distance from the beak to the distal end of the major tooth, whereas the ligament groove of *S. altus* is not longer than that dimension.

One of Girty's (1915, pl. 9, fig. 12a) illustrations of *S. depressus* var. *abruptus* from the Mississippian Batesville Sandstone of Arkansas is very similar in form to *S. altus*, as are his figures (1927, pl. 25, figs. 46-49) of *S. semistriatus* from the Mississippian Brazer Limestone of Idaho. No information on hinge features or internal characteristics is available for the Mississippian species, but *S. altus* is more triangular than both, and it lacks the concentric ornament of *S. semistriatus*. It is distinguishable from the Permian *Lyroschizodus orbicularis* by the same considerations.

TABLE 7
MEASUREMENTS (IN MILLIMETERS) OF NEARLY
COMPLETE VALVES OF *SCHIZODUS AMPLUS*

No.	Left Valves			Partial Length	No.	Right Valves			Partial Length
	Length	Height	Convexity			Length	Height	Convexity	
1 ^a	71	58	21	18	2 ^a	62	53	18	17
2	—	—	—	—	3 ^b	66	61	21	17

^aWapanucka Formation, Oklahoma.

^bHolotype from the Seville Limestone, Illinois.

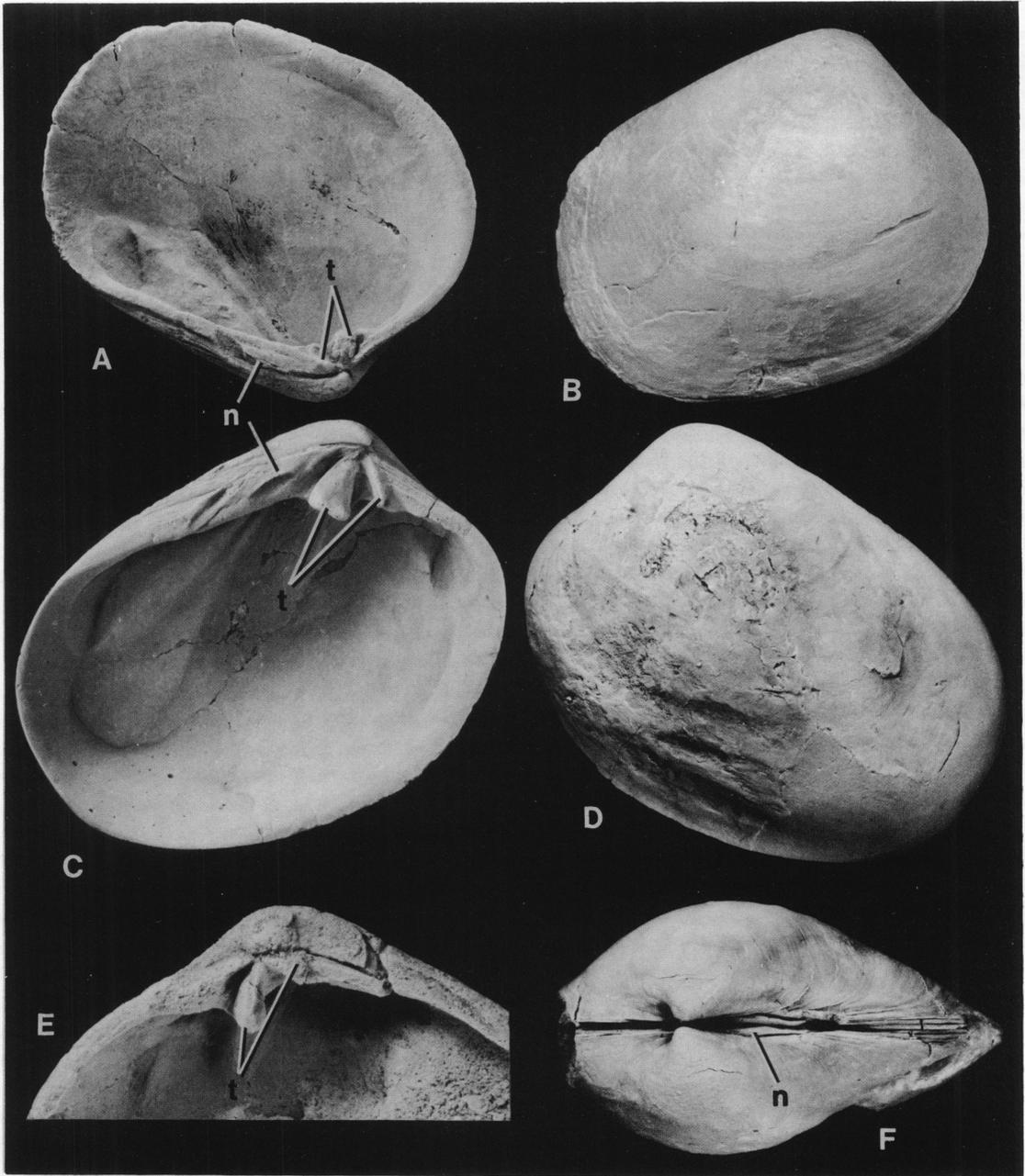


FIG. 41. *Schizodus amplus* Meek and Worthen. Calcareous examples from the Lower and Middle Pennsylvanian of the Midcontinent region, United States. A, B. Right valve, Wapanucka Limestone (Morrowan), NW 1/4 SE 1/4 sect. 8, T. 1N., R. 7e, near Fittstown, Oklahoma. AMNH 29186. C, D. Left valve, same horizon and locality as A and B. AMNH 29187. E. Right valve, top of Holdenville Formation (Desmoinesian), near Beggs, Okmulgee County, Oklahoma. OU 4337. F. Hinge view of bivalved individual from Millsap Lake Formation (Desmoinesian), Potato Knob, Gold Tap Road, Palo Pinto County, Texas, TB 13093.

Abbreviations: n, nymph; t, teeth.

Schizodus amplus Meek and Worthen, 1870

Figures 37 no. 14, 41-43

Schizodus amplus Meek and Worthen, 1870, pp. 41-42; 1873, p. 579, pl. 27, figs. 6a, 6b.

Schizodus mooresi Miller, 1889, p. 511, figs. 918, 919.

Diagnosis. Large, quadrate valves with strongly prosogyrous and anteriorly situated beaks; umbo not well differentiated; broad posterior margin; posterior ridge not differentiated or represented only by faint carina on uniformly convex surface. Ligament groove nearly twice length of major tooth, continuing behind broad nymph as oblique furrow across dorsal margin. Major socket of left valve floored for about two-thirds length of adjacent large tooth. Hinge plate of right valve reinforced by partial floor beneath major socket. Major tooth of right valve not distally expanded. Broad internal posterodorsal ridge terminated posteriorly at adductor scar and bounded by radial grooves. Both retractor pedal scars are elongate slits above adductor scars and largely isolated from them. $L/H=1.16$ ($n=3$); $H/C=2.87$ ($n=3$); $L/PL=3.82$ ($n=3$).

Distribution. Morrowan-Desmoinesian (Pennsylvanian), United States. Boggs and Lower Mercer of Ohio; Seville of Illinois; Wapanucka, Lester, and Holdenville of Oklahoma; Millsap Lake of Texas.

Discussion. The holotype (fig. 41) is a steinkern from the Seville Limestone (Atokan) of Illinois which we have compared directly with several calcareous shells of the same age from the Wapanucka Limestone of Oklahoma. Only two of these, one left valve and one right, are complete. Fragments of six left valves and four right valves show hinge features in varying degrees of preservation. Remnants of prismatic structure similar to that of *Schizodus alpinus* are preserved in the external layer of some specimens.

This species differs from most species of *Schizodus* in its subquadrate form and broad posterior margin. The dorsal and ventral margins are subparallel and inclined with respect to the muscle scar axis.

The major sockets of both valves are partly floored by the hinge plate. The two major teeth of the left valve diverge at an acute angle embracing an unusually narrow major tooth of the right valve. Unlike the situation in many *Schizo-*

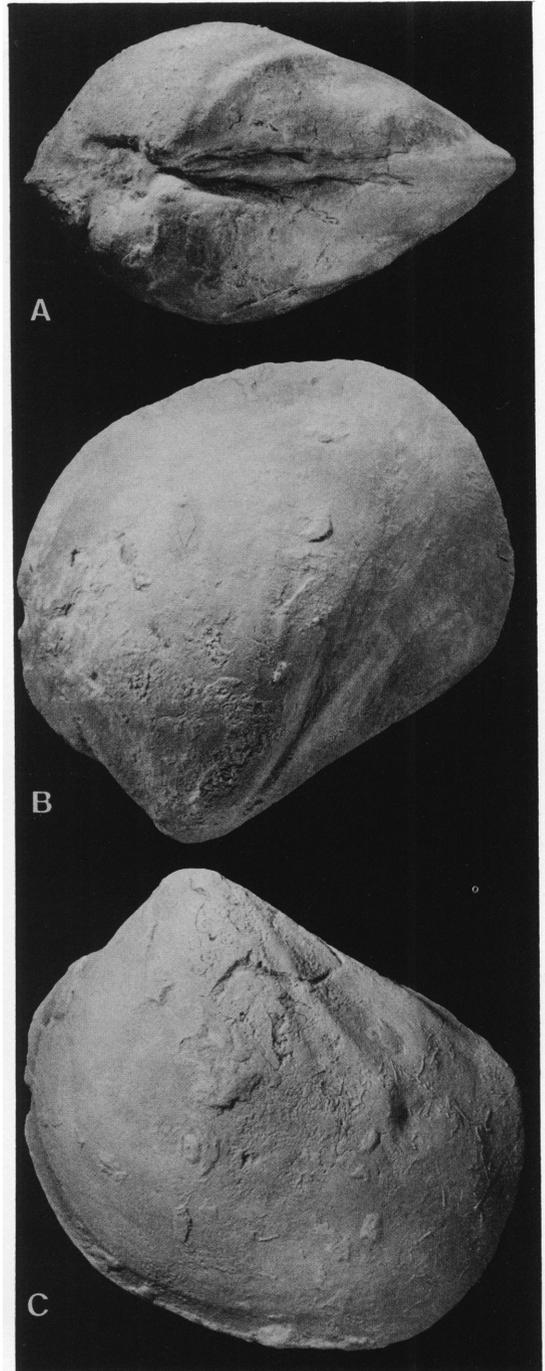


FIG. 42. *Schizodus amplus* Meek and Worthen. Holotype, calcareous internal mold. Seville Limestone (Atokan), Seville, Fulton County, Illinois. IU X-199. A. Dorsal aspect. B. Right side. C. Left side.

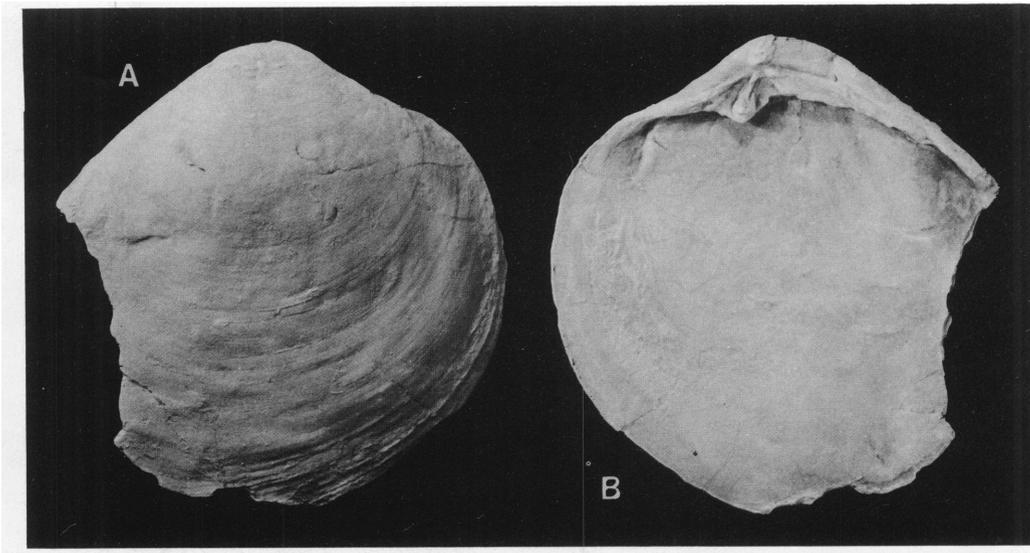


FIG. 43. *Schizodus amplus* Meek and Worthen. Calcareous right valve, holotype of *Schizodus mooresi* Miller, placed here in synonymy of *amplus*. From Middle Pennsylvanian (Atokan, probably Lower Mercer Limestone), Carbon Hill, Hocking County, Ohio. Fm 8857. A. Exterior. B. Interior.

us species, both pedal retractor scars are isolated, or nearly so, from the associated adductor scars.

Certain features of *S. amplus* suggest that it may be in the lineage from which *Eoastarte* evolved. These include general form, the strongly prosogyrous beak, virtual lack of the posterior shell ridge so prevalent in trioniaceans, form and orientation of teeth of the left valve, and the partially floored socket of the left valve. The species differs from *Eoastarte* as exemplified by *E. subcircularis* in greater length-height ratio, less pronounced umbo, and the less complete floor of the main socket in the left valve. The hinge plate in *Eoastarte* is entire.

Miller (1889) based his description of *S. mooresi* on a broken right valve from Atokan rocks of Ohio. His characterization and figures do not distinguish it from *S. amplus* and we consider *S. mooresi* to be a junior synonym.

Schizodus bifidus Ciriacks, 1963

Figure 44

Schizodus bifidus Ciriacks, 1963, pp. 59-60, pl. 10, figs. 13-15.

Diagnosis. Posteriorly slender shells with

beaks varying from distinctly opisthogyrous to nearly orthogyrous; beaks about one-third valve length behind anterior extremity. Maximum valve convexity anterior of beak. Ventral margin variably concave where it borders broad shallow sulcus behind mid-length. Corselet steeply sloping and slightly concave. Major tooth of left valve strongly sulcate, commonly bifid. Oval posterior retractor scar isolated from adjacent adductor scar. $L/H=1.53$ ($N=17$); $H/C=2.57$ ($N=45$).

Distribution. Park City Formation, Permian (Grandeur through Ervay members), Wyoming and Montana.

Discussion. In his characterization of this species, Ciriacks (1963, p. 60) commented on the rarity of well-preserved specimens. We have subsequently collected numerous silicified shells from Beaver Creek, Wyoming; they are the source of the observations that follow. It should be noted that our material is from the lower Park City Formation (Grandeur Member), whereas Ciriacks's characterization was based on material generally from a younger member (Shedhorn) of that formation.

The original description of the species provides an L/H value of 1.33, whereas our best-

preserved specimens are relatively longer (1.51-1.63). Beaks are typically a little less than one-third valve length behind the anterior extremity in our collection rather than between one-third and one-half as noted by Ciriacks. The different conclusions probably reflect difference in preservation of valve extremities between the two samples. In our material, the dorsal margin is straight rather than concave for most of its extent behind the beak. The concavity of the ventral margin and the associated sulcus are more prominent than suggested by the illustrations of holotype and paratype. Our complete valves have a much more pointed and elongated posterior than do the type specimens. This distinctive posterior area is vulnerable to damage and is found intact on relatively few specimens. Such individuals show no evidence of siphonal gape. The rostrate area has notable convexity, even relatively close to the posterior extremity. The original description refers to concentric ornamenta-

tion, about one ridge per mm., on the anterior umbonal slope. Few of our specimens show concentric features other than growth lines. Those with traces of concentric ridges vary in ridge spacing from 2 to 5 per mm.

Ciriacks described the minor posterior tooth of the left valve ("tooth 4b") as indistinct or possibly absent. The best valves in the Beaver Creek collection do not alter this interpretation; at best, the tooth is a minor ridge along the inner (anterior) edge of the nymph. The large tooth of the left valve has a deep groove on its posteroventral face, resulting in two lobes, one above and posterior to the other. Rarely, the groove doesn't persist to the distal end of the tooth. The large tooth of the right valve is typically less bifid than that of the left valve, and shows no subdivision in some specimens.

This species differs from *Schizodus obscurus* and *S. texanus* in possessing a well-defined posterior ridge, rostrate posterior, opisthogyrous

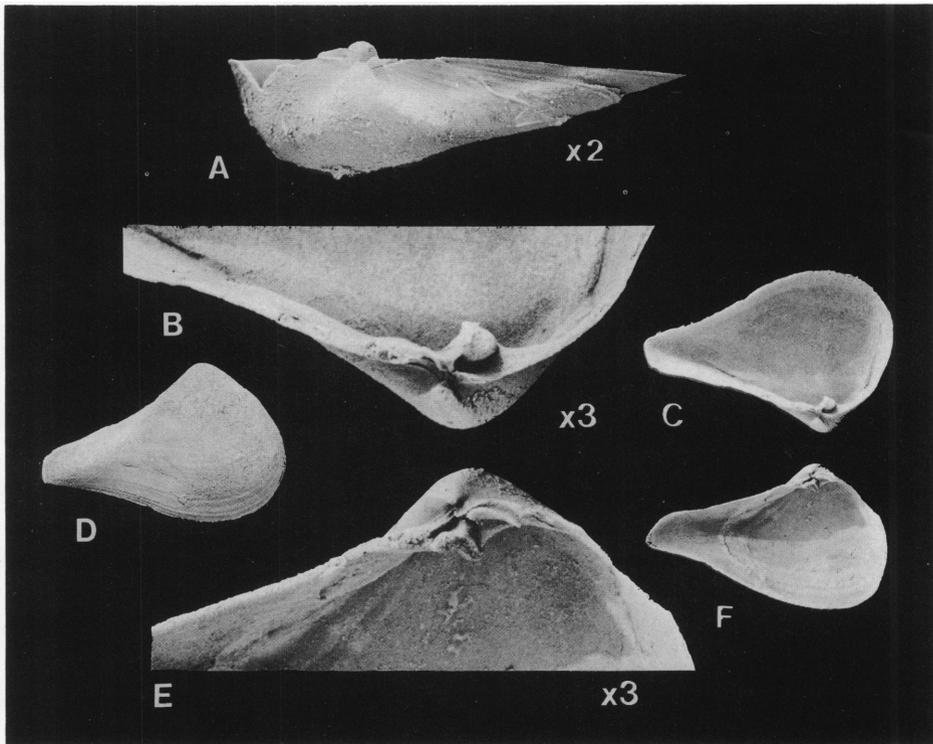


FIG. 44. *Schizodus bifidus* Ciriacks. Silicified specimens. Grandeur Member (Upper Leonardian), Park City Formation, Wyoming, AMNH loc. 2010. A, E, F. Left valve. AMNH 29171. B-D. Right valve. AMNH 29172. This species is convergent in general external form with the Cuspidariidae.

beaks, maximum convexity in front of the beaks, and bifid tooth on the left valve. However, those species include a wide range of variation and broken valves of the three species lacking the distinctive posterior region are not easily distinguished.

The species is associated with larger valves of *Schizodus wyomingensis* at Beaver Creek, and at first we considered the possibility that the two forms represent different ontogenetic stages of one species. However, there is some overlap in valve size among distinguishable representatives of the two groups. Furthermore, features such as beak orientation and posterior ridge which typify the smaller form do not characterize the first-formed part of the large valves.

Schizodus canalis Branson, 1930

Figures 45, 46

Schizodus canalis Branson, 1930, pp. 46-47, pl. 13, fig. 1.

Diagnosis. Trigonal; small valves nearly equilateral, larger ones posteroventrally elongated. Beak orthogyrous. Respiratory margin forming very obtuse angle with posterodorsal margin; posteroventral margin concave. Posterior ridge angular, carinate, bordered anteriorly by shallow sulcus. Corselet steep, concave. Fine, close-

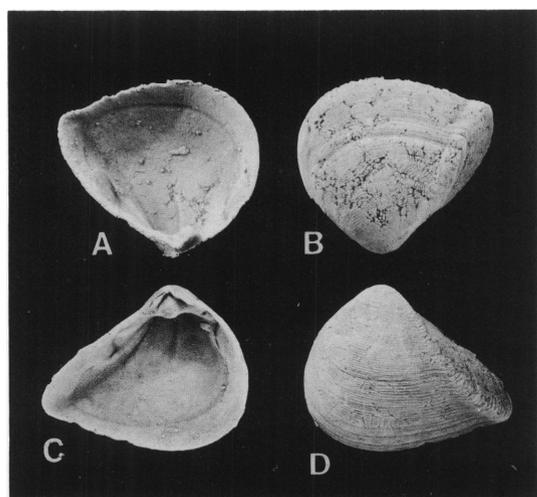


FIG. 45. *Schizodus canalis* Branson. Silicified specimens. Franson Member of the Park City Formation (Lower Guadalupian), near Lander, Wyoming. AMNH loc. 3107. A, B. Right valve, AMNH 29283. C, D. Left valve, AMNH 29284.

TABLE 8
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS BIFIDUS
FROM GRANDEUR MEMBER, PARK CITY
FORMATION, AT BEAVER CREEK,
WYOMING, AMNH LOC. 2010^a

	Height Length	Convexity Height
N	17	44
\bar{x}	31.41	20.55
\bar{y}	20.53	8.09
s_x	4.50	2.59
s_y	2.53	1.29
r	0.84	0.71
OR _x	38-21	29-14
a	0.56	0.50
σ_a	0.07	0.05
b	2.88	-2.14

^aSee page 90 for explanation of statistical parameters.

spaced concentric ridges, rarely conspicuous. Posterior retractor scar more elongate than anterior one, both partially isolated from subjacent adductor scars. L/H=1.17 (n=37); H/C=2.83 (n=37).

Distribution. Upper Leonardian-Lower Guadalupian (Permian) Park City Formation (Grandeur, Meade Peak, Franson and Ervay? Members), Wyoming; Road Canyon Formation and Appel Ranch Member of Word Formation, western Texas; Kaibab Limestone (Alpha Member), Arizona; San Andres Formation, New Mexico and Arizona. AMNH locs. 56, 1067, 3107; USNM locs. 703, 703c, 721r, 726za.

Discussion. Branson's holotype is from the Grandeur Member of the Park City Formation in the Wind River Mountains of Wyoming. We have a good collection of silicified valves from the basal Franson Member of the Park City in the same region. *Schizodus canalis* is associated here with *S. subovatus*. The former species has a smaller height-convexity ratio, more prominent umbones, straighter and more steeply sloping dorsal margins on both sides of the beak, and shorter ligament groove. These aspects of *S. canalis* augment its carinate posterior ridge, bordering sulcus, and reentrant in the posteroventral margin as criteria for distinguishing the two forms.

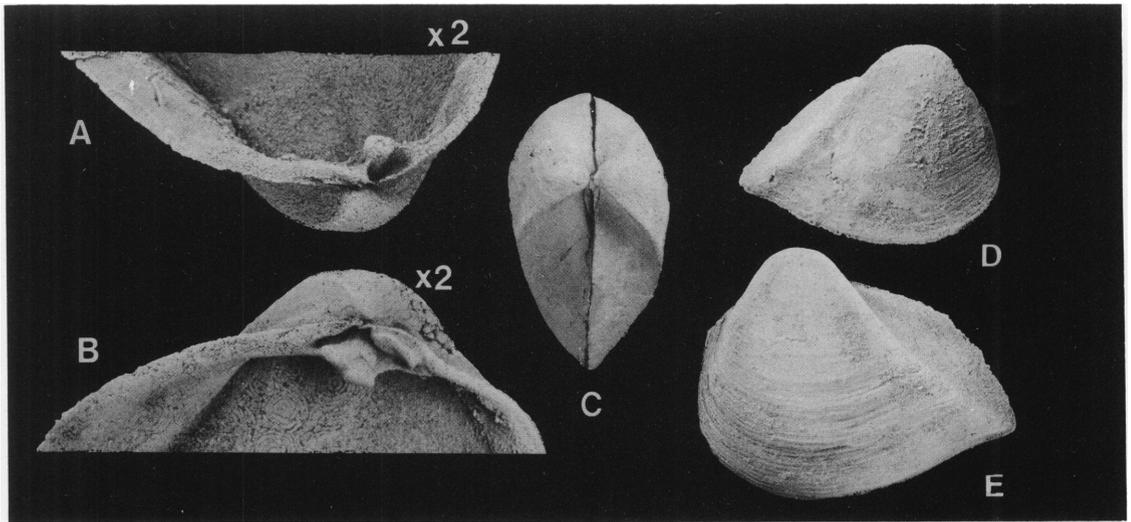


FIG. 46. *Schizodus canalis* Branson. Silicified specimens. San Andres Formation (Leonardian), St. Johns, Arizona. AMNH loc. 1067. A, D. Right valve. AMNH 29209. B. Left valve, AMNH 29210. C. Slightly disparate valves of two individuals. AMNH 29213 and 29209. E. An almost perfect left valve. AMNH 29211.

An Arizona collection from the San Andres Formation near St. Johns (AMNH loc. 1067) includes 13 complete silicified valves and 20 in-

complete ones. We have assigned these to *Schizodus canalis* although the specimens differ in some respects from the Wyoming material (fig. 45).

TABLE 9
MEASUREMENTS (IN MILLIMETERS) OF VALVES OF *SCHIZODUS CANALIS* FROM FRANSON MEMBER, PARK CITY FORMATION, NEAR LANDER, WYOMING, AMNH LOC. 3107
(Measurements provided by Stephanie Wald.)

Length	Left Valves		Length	Right Valves	
	Height	Convexity		Height	Convexity
27.5	24.2	9.6	26.0	23.4	8.7
26.3	23.9	8.9	24.0	19.7	6.9
23.9	20.3	7.0	22.0	18.8	6.7
24.4	20.5	7.4	21.2	19.8	6.7
25.4	20.5	7.8	20.5	17.7	6.3
22.3	19.8	6.6	20.4	17.0	5.7
18.5	16.1	5.7	19.5	16.1	4.2
14.8	13.1	4.5	17.1	14.4	4.6
12.2	10.9	3.4	12.1	10.2	3.4
25.6	23.2	8.0	24.0	19.8	7.2
20.9	18.3	6.8	21.6	19.0	6.4
21.8	18.0	6.1	24.1	20.8	7.5
25.4	23.0	8.2	21.9	18.0	6.7
27.3	22.4	9.2	24.0	20.1	7.4
27.1	23.2	7.5	23.7	19.0	7.1
24.8	21.8	7.7	23.3	21.0	6.6
16.6	13.4	4.9	16.4	14.1	5.0
28.0	24.0	8.5	19.8	16.3	6.0
			20.3	17.5	6.0

TABLE 10
MEASUREMENTS (IN MILLIMETERS) OF VALVES IN A COLLECTION OF *SCHIZODUS CANALIS*
FROM SAN ANDRES FORMATION, ST. JOHNS, ARIZONA, AMNH LOC. 1067

Length	Left Valves			Length	Right Valves		
	Height	Convexity	Partial length		Height	Convexity	Partial length
41	32	12	15	37	29	11	12
41	32	11	14	35	27	10	11
38	32	10	14	—	—	—	—
38	31	11	12	—	—	—	—
35	26	9	13	—	—	—	—
34	27	10	12	—	—	—	—

The Arizona form (fig. 46) has more prominent umbones, more strongly incurved beaks, broader respiratory margin, longer ligament groove, and is slightly more elongate ($L/H = 1.27$).

The Arizona specimens are associated with *S. texanus* (fig. 52), from which they are distinguished by their angular posterior ridge, concave corselet, straighter anterior margin, and more sharply defined respiratory margin.

Schizodus canalis is very similar morphologically to *Procostatoria cooperi*, the most primitive member of *Procostatoria* and suggests a plausible derivation of that genus.

Schizodus compressus Rogers, 1900

Figure 47

Schizodus compressus Rogers, 1900, pp. 157-158, pl. 22, figs. 6, 6d.

Diagnosis. Low-convexity valves with opisthogyrous umbones; beaks about one-third of valve length behind anterior extremity. Anterior profile semicircular from beak to venter; respiratory margin less than half valve height forming obtuse angle with dorsal margin. Posterior ridge in juveniles sharply defined, with angular transverse profile, becoming rounded in adult stage. Corselet narrow, sloping steeply near umbones and more gently distally, commonly marked by broad, indistinct radial costa. Major tooth of left valve biramose with a broad furrow on the inner face and a greatly extended posterior limb and adjacent posterior socket; major socket of left valve completely floored. Hinge of right valve has narrow major tooth and unfloored major socket; posterior tooth of right valve appreciably shorter than its corresponding socket, narrow. Anterior and posterior pedal re-

tractor scars circular and isolated from subjacent adductor scars. $L/H=1.42$ ($n=1$); $H/C=3.83$ ($n=4$); $L/PL=3.38$ ($n=1$).

Distribution. Haskell Limestone, Virgilian (Pennsylvanian), Kansas.

Discussion. Few specimens in our collection of 22 calcareous valves have adequately preserved hinges and only one has a relatively complete posterior margin. Traces of a prismatic outer layer of the shell are recognizable on several specimens. *Schizodus compressus* could have been derived from *Schizodus ulrichi* by changes in umbonal symmetry from prosogyrous to slightly opisthogyrous, by completion of the floor of the major socket of the left valve, and by elongation of the posteroventral corner of the major tooth of the left valve. The posterior socket of the left valve of *S. compressus* is unusually long for *Schizodus*, and extends ventrally well beyond the adjacent major tooth. Some specimens of *S. ulrichi* from the Hartshorne Sandstone of Oklahoma exhibit an intermediate stage in this respect between the more common condition in *S. ulrichi* and *S. compressus*. The umbo of the Hartshorne specimens is not so strongly prosogyrous as is usual in *S. ulrichi*, and the major socket of the left valve is more extensively floored. Furthermore, the variable major tooth of the left valve shows significant posteroventral elongation in some specimens. However, this tooth in the Hartshorne specimens is distally broad with curved sides as ordinarily is the case in *Schizodus*, whereas the equivalent tooth in *S. compressus* is much narrower and its anterior face is a vertical plane.

Aside from the distinctive opisthogyrous umbo, the left valve of *S. compressus* resembles that

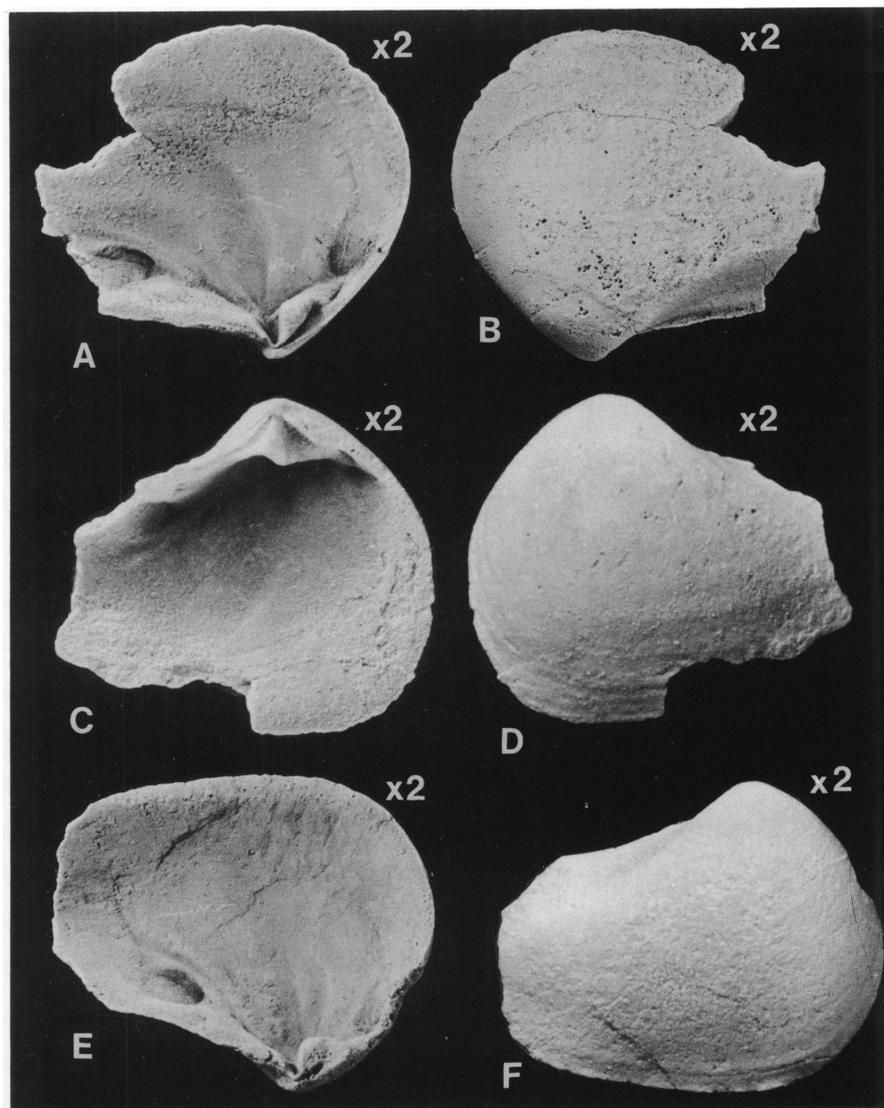


FIG. 47. *Schizodus compressus* Rogers. Calcareous specimens of type series of species from Haskell Limestone (lower Virgilian), Lawrence, Kansas. A, B. Right valve, KU 76576. C, D. Left valve, KU 76577. E, F. Right valve, selected here as lectotype. KU 76578.

of *Kaibabella basilica* in convexity, summit location of beak, hinge, and muscle scars. The right valve hinge of *S. compressus*, however, is that of *Schizodus*.

The posteroventral elongation of the posterior socket in the left valve of *S. compressus* is reminiscent of the more pronounced condition which is typical of *Paraschizodus*. However, the posterior tooth of the right valve is short and

unimpressive in comparison with *Paraschizodus*.

Slightly opisthogyrous umbones and uninterrupted anterior profile are found in a few schizodids. *Schizodus cuneatus* from Atokan (Pennsylvanian) strata of Ohio (Meek, 1875, pl. 20, fig. 7; Morningstar, 1922, pl. 13, figs. 1, 2) is similar in anterior outline, but has narrower, more prominent umbones and a broader corselet. Its hinge is unknown to us.

TABLE 11
MEASUREMENTS (IN MILLIMETERS) OF
VALVES IN A COLLECTION OF *SCHIZODUS COMPRESSUS*
FROM HASKELL LIMESTONE, LAWRENCE, KANSAS
(The large left valve was measured on Roger's [1900] figure 6d.)

Length	Height	Left Valves		Partial Length	Right Valves	
		Convexity			Height	Convexity
27	19	—		8	22	6
—	22	6		—	20	5
—	—	—		—	20	5

Schizodus cf. meekanus Girty, 1899
Figure 48

Schizodus meekanus Girty, 1899, pp. 583-584,
pl. 72, figs. 7a-7c.

Discussion. Girty based his description of *S. meekanus* on specimens from the "upper Coal Measures" of Oklahoma. His characterization is more confusing than enlightening and we lack the additional specimens needed for an evaluation of the species. Two of the three specimens he figured are very elongate small valves and the third is a large specimen very similar to that shown in figure 48 of the present paper. Girty expressed doubt that the large specimen should be referred to *S. meekanus*, yet his diagnosis seems to be influenced by it. The main features the three figured valves share are elongation and orthogyrous umbo, although the latter feature is not mentioned in the characterization. In fact, an elongate prosogyrous specimen figured by Meek (1872, pl. 10, figs. 1e, 1f) as *S. wheeleri* is cited by Girty as probably conspecific with his material.

The resemblance of the smaller cotypes to *Paraschizodus elongatus* in overall form is notable but, as indicated in the discussion of that species, additional information on the hinge of the Pennsylvanian form is necessary for more meaningful comparison. Girty's large specimen, together with the mold illustrated in our figure 48, may belong with *S. ulrichi*. The orthogyrous umbo is unlike characteristic specimens of *S. ulrichi*, but this condition probably is inherent in an internal mold of an old individual.

Schizodus meekanus Girty, 1899, is presently an unrecognizable taxonomic unit.

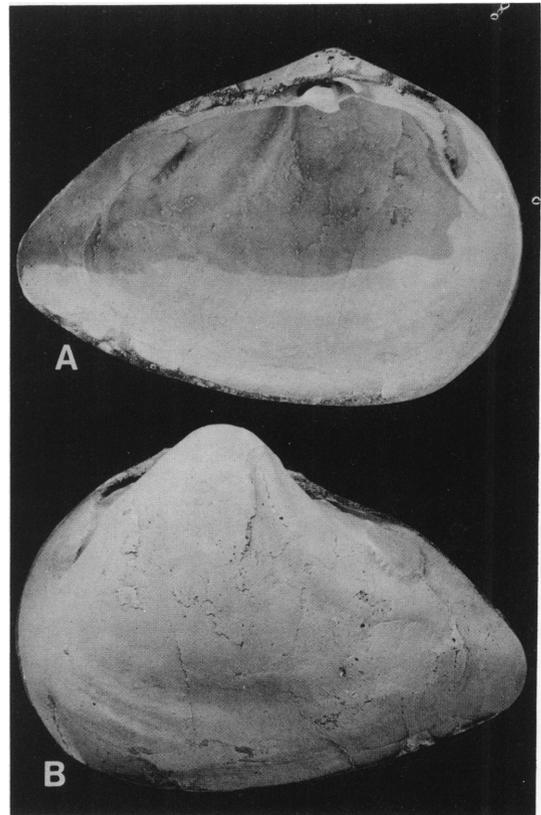


FIG. 48. *Schizodus cf. meekanus* Girty. Latex cast and internal mold of single left valve from Atoka (Middle Pennsylvanian), quartz sandstone bed, Clarita, Oklahoma. AMNH 29179.

Schizodus subovatus Ciriacks, 1963
Figure 49

Schizodus subovatus Ciriacks, 1963, pp. 60-61,
pl. 10, figs. 1-6.

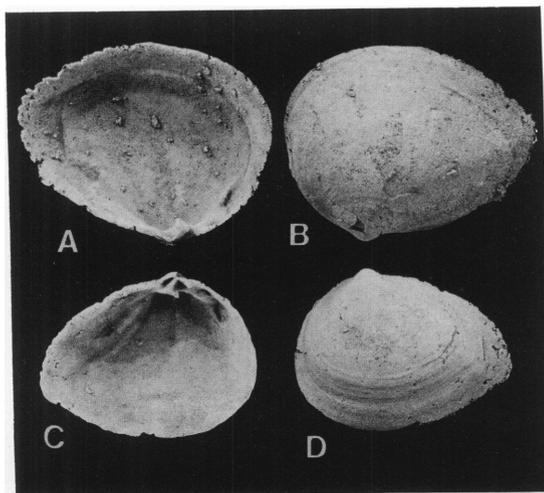


FIG. 49. *Schizodus subovatus* Ciriacks. Silicified valves. Franson Member (Lower Guadalupian), Park City Formation, Wind River Mountains near Lander, Wyoming. AMNH loc. 3107. A, B. Right valve. AMNH 29286. C, D. Left valve. AMNH 29285.

Diagnosis. Ovate shells with orthogyrous beaks near shell summit. Ventral margin evenly convex; respiratory margin commonly half or more of valve height, meeting dorsal margin at curved junction. Posterior ridge broad and evenly rounded. Corselet poorly defined, gently sloping. Ligament groove length between one and two times the distance from beak to distal end of major tooth. Anterior retractor scar circular; iso-

lated from subjacent adductor scar; posterior retractor scar a long furrow parallel to valve margin, anterodorsal to faint posterior adductor scar. $L/H=1.24$ ($n=10$); $H/C=3.25$ ($n=10$).

Distribution. Upper Leonardian-Lower Guadalupian (Permian). Park City Formation (Grandeur Member, Utah; Franson Member, Wyoming).

Discussion. In his description of this species, Ciriacks (1963, p. 61) noted that his collection from the Grandeur Member in Utah was inadequate for a complete characterization. Our description is based on a large collection of silicified valves recently obtained from the basal Franson Member (AMNH loc. 3107) near Lander, Wyoming. At this locality, *S. subovatus* occurs with *S. canalis*. The two forms are contrasted in the discussion of *S. canalis*.

In contrast with *S. texanus*, *S. subovatus* is less convex, has less prominent umbones, and has a longer ligament groove relative to length of major tooth.

Schizodus supaiensis Winters, 1963
Figures 37 no. 7, 50, 51

Schizodus supaiensis Winters, 1963, pp. 58-59, pl. 9, figs. 1-3.

Diagnosis. Orthogyrous to slightly prosogyrous beaks. Uniformly curved ventral margin; gently sloping respiratory margin equal in extent to almost half valve height. Corselet slightly concave. Weak, close-spaced concentric ridges on anterior slope. Left valve hinge exhibiting postero-

TABLE 12
MEASUREMENTS (IN MILLIMETERS) OF VALVES OF
SCHIZODUS SUBOVATUS FROM FRANSON MEMBER,
PARK CITY FORMATION, NEAR LANDER, WYOMING, AMNH LOC. 3107
(Measurements provided by Stephanie Wald.)

Length	Left Valves		Length	Right Valves	
	Height	Convexity		Height	Convexity
36.5	30.1	8.9	32.9	26.0	8.2
35.6	28.5	8.5	22.9	17.5	5.0
31.3	24.7	7.1	26.1	22.0	6.9
29.5	25.1	8.4	—	—	—
28.1	21.8	7.1	—	—	—
31.1	24.6	8.1	—	—	—
20.3	16.1	4.5	—	—	—

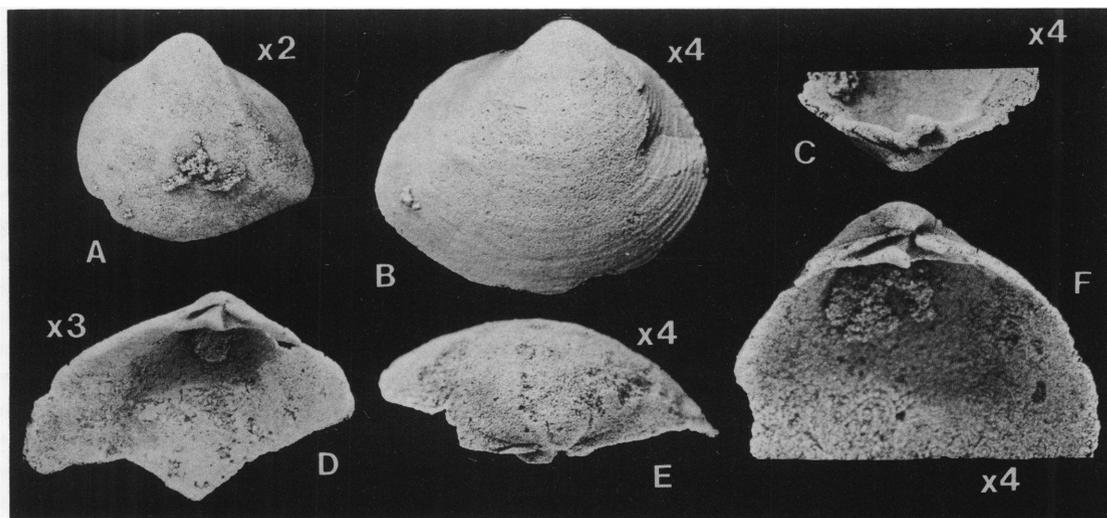


FIG. 50. *Schizodus supaiensis* Winters. Silicified specimens. Fort Apache Limestone (Leonardian), near Fort Apache, Arizona. A. Left valve. AMNH 28028/1:2. B. Right valve, the holotype. AMNH 28028/1:1. C. Right valve. AMNH 28028/1:3. D. Left valve. AMNH 28028/1:4. E, F. Left valve. AMNH 28028/1:5.

ventral elongation of major tooth and partial floor in major socket. $L/H=1.18$ ($n=12$); $H/C=2.86$ ($n=12$).

Distribution. Upper Wolfcampian-Lower Leonardian (Permian). Fort Apache Limestone, Arizona; Cathedral Mountain Formation, Texas; Hess Formation, Texas; Hueco Limestone?, Texas.

Discussion. This species is represented in our collection primarily by the small hypodigm of Winters. The Fort Apache Limestone specimens are small juveniles. However, two large (50 mm.), articulated shells in our collection from other localities may belong to this species.

Winters (1963, p. 59) noted the close resemblance between his species and *Lyroschizodus oklahomensis*. *Schizodus supaiensis* also resembles in some respects the new species *L. orbicularis*, *Paraschizodus rothi*, and *Schizodus altus*. However, the shape is not exactly repeated in any of those species. *Schizodus supaiensis* is characterized by its length-height ratio (1.18), curved junction of dorsal and respiratory margins, near-contact of opposing beaks of articulated valves, and broadly rounded rather than sharply defined posterior ridge. Weak concentric ornamentation

displayed by some of the juveniles is less prominent and less extensive over the valve surface than in *Lyroschizodus*, and is completely lacking in the adults.

Schizodus supaiensis is distinguished from the Pennsylvanian *S. alpinus* by greater convexity, more gently sloping respiratory margin, and more prominently curved ventral margin.

We find no third (posterior) tooth on left valves, and conclude that the feature so described by Winters is the narrow ligament nymph. However, other hinge features are distinctive. The large tooth of the left valve exhibits some posterior elongation. Associated lengthening of the socket just behind that tooth is more extensive than is usual in *Schizodus* but is not so developed as in *Paraschizodus*. The floor in the major socket of the left valve of *Schizodus supaiensis* is absent in *S. altus*, *Lyroschizodus oklahomensis*, *L. orbicularis*, and *Paraschizodus rothi* which are otherwise somewhat similar. We note that a left valve of *S. supaiensis* is mislabeled as a right valve in the caption for plate 9, figure 1 (Winters, 1963) and right valves are mislabeled as left valves in captions for figures 2 and 3a on the same plate.

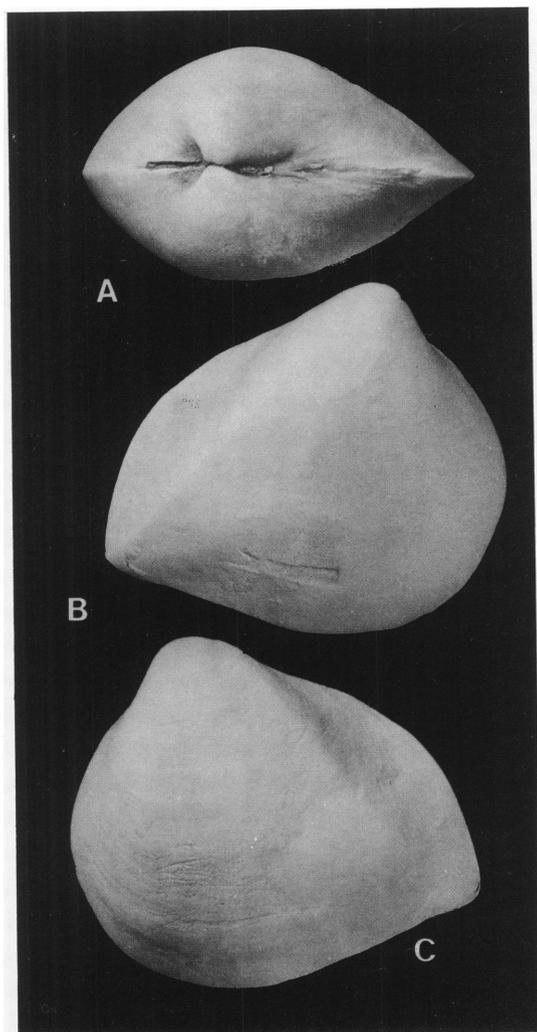


FIG. 51. *Schizodus supaiensis* Winters. Silicified bivalve. Cathedral Mountain Formation (Leonardian). A. Dorsal view. B. Right side. C. Left side. Glass Mountains, Texas, USNM loc. 702 un. USNM 177169.

Schizodus texanus Clifton, 1942
Figures 13A, C, 37 no. 10, 52, 53

Schizodus texanus Clifton, 1942, pp. 691-693,
pl. 101, figs. 20-28, pl. 102, figs. 10-13.

Diagnosis. Orthogyrous umbones: anterior margin an uninterrupted curve from beak through ventral extremity. Dorsal and ventral terminations of respiratory margin rounded rather than angular. Posterior ridge broadly

TABLE 13
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS SUPAIENSIS
FROM FORT APACHE LIMESTONE,
ARIZONA^a
(Measurements from Winters, 1963.)

	Height Length	Convexity Height
N	12	12
\bar{x}	9.13	7.75
\bar{y}	7.75	2.73
s_x	3.43	2.87
s_y	2.87	1.01
r	0.99	0.98
OR _x	15.7-3.4	13-2.9
a	0.84	0.35
σ_a	0.019	0.02
b	-0.58	-0.03

^aSee page 90 for explanation of statistical parameters.

rounded, lacking linear expression. Weak concentric annulae on anterior slopes of some valves. Ligament groove length commonly equal to, or slightly greater than, distance from beak to distal end of major tooth. Posterior retractor muscle scar extends from anterodorsal corner of posterior adductor scar as a long furrow equal in extent to height of adductor scar. L/H=1.28 (n=32); H/C=2.70 (n=31); L/PL=2.92 (n=32).

Distribution. Widely distributed in many Permian dolomitic limestones of Wolfcampian to Early Guadalupian age inclusive in red beds-evaporite sequence of Texas, New Mexico, and Arizona, with most abundant representation in San Andres, Blaine, and Kaibab formations. AMNH locs. 512, 1066, 1067, 2020, 2021, 2022, 2079; USNM locs. 600, 702, 703, 704, 706b, 706e.

Discussion. Specimens assignable to this species are represented in our collections from numerous southwestern localities, commonly as internal molds. Only one collection, from the San Andres Formation near St. Johns, Arizona, contains abundant and well-preserved specimens. This silicified material includes some thirty complete valves and dozens of broken ones; it is the basis for the diagnosis and bivariate statistical characterization of figure 37.

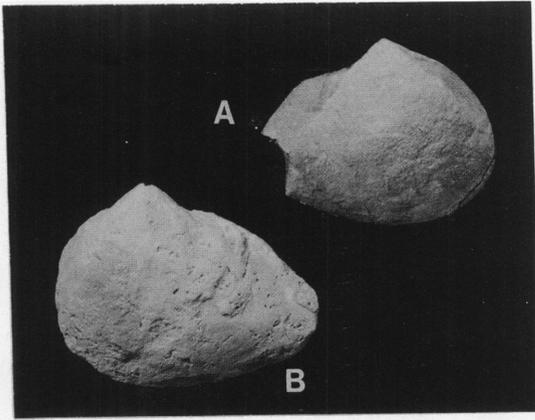


FIG. 52. *Schizodus texanus* Clifton. A. Poorly preserved internal mold of dolomite, holotype of *Axinus* (*Schizodus*) *ovatus* Meek and Hayden, 1858. "South Cottonwood Creek, Kansas," of Wolfcampian or early Leonardian age (Chase Group). USNM 3960. Illustrated here for comparison. *Schizodus ovatus* Meek and Hayden is unrecognizable and we regard it as a *nomen oblitum*. B. Holotype of *Schizodus texanus* Clifton, poorly preserved dolomite internal mold. Acme Member, Blaine Formation (Leonardian), Harde- man County, Texas. ISU 1453. See also figure 13C of *S. Texanus*.

Clifton (1942, p. 692) reported the length of his specimens as ranging from 35 to 47 mm. The average L/H value for the six complete specimens he figured is 1.39/1, but most of his specimens are internal molds. Both Clifton (1942) and Chronic (1952) refer to concentric ornamentation on their specimens. In our material, concentric ornamentation is at best indistinct, and it does not extend over the entire surface, being limited to the anterior slope. Clifton mentions a third (posterior) tooth on immature left valves. Our collections lack consistent representation of this tooth and its unequivocal presence is very rare.

Our specimens are similar to those from the Permian of England assigned to *Schizodus obscurus* and *S. schlotheimi* by Logan (1967, pl. 8, figs. 2-7) considered by us to be about the same age. Pattison (1970), after studying a collection of 300 specimens from the Manchester Marl, concluded that he could not distinguish between those two species. A statistical evaluation of dif-

ferences between Pattison's collection of *S. obscurus* and our Arizona collection of *S. texanus* in regard to reduced major axis for L/H indicates a significant difference (table 15).

Five similar species with orthogyrous umbones have been described from Carboniferous strata. Judged by illustrations of the types of the Mississippian *Schizodus batesvillensis*, *S. chesterensis*, and *S. rostratus*, and of the Pennsylvanian *S. meekanus*, all have a greater length-height ratio (more than 1.4) than in *S. texanus*. The Mississippian *S. sectoralis* is similar to *S. texanus* in lateral view but has a greater height-convexity ratio. Furthermore, the left side of the hinge illustrated by Driscoll (1965) differs from *S. texanus* in possessing a floored major socket and an anteriorly elongated major tooth.

Schizodus trigonalis Sayre
Figure 54

Schizodus trigonalis Sayre, 1931 (1930), p. 118, pl. 11, figs. 2, 2a.

Diagnosis. Small trigonal shell with quadrate dorsal profile as viewed from side, with produced posterior extremity, flattened lateral surfaces, rounded anterior extremity, rounded posterior ridge, and narrow corselet.

TABLE 14
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS TEXANUS FROM
SAN ANDRES FORMATION
NEAR ST. JOHNS,
ARIZONA, AMNH LOC. 1067^a

	Height Length	Partial Length Length	Convexity Height
N	32	32	31
\bar{x}	25.156	25.156	19.516
\bar{y}	19.938	8.688	7.258
s_x	2.464	2.464	1.913
s_y	2.169	1.148	0.729
r	0.593	0.679	0.786
OR _x	30-19	30-19	23-16
a	0.880	0.466	0.381
σ_a	0.125	0.060	0.042
b	-2.206	-3.032	-0.179

^aSee page 90 for explanation of statistical parameters.

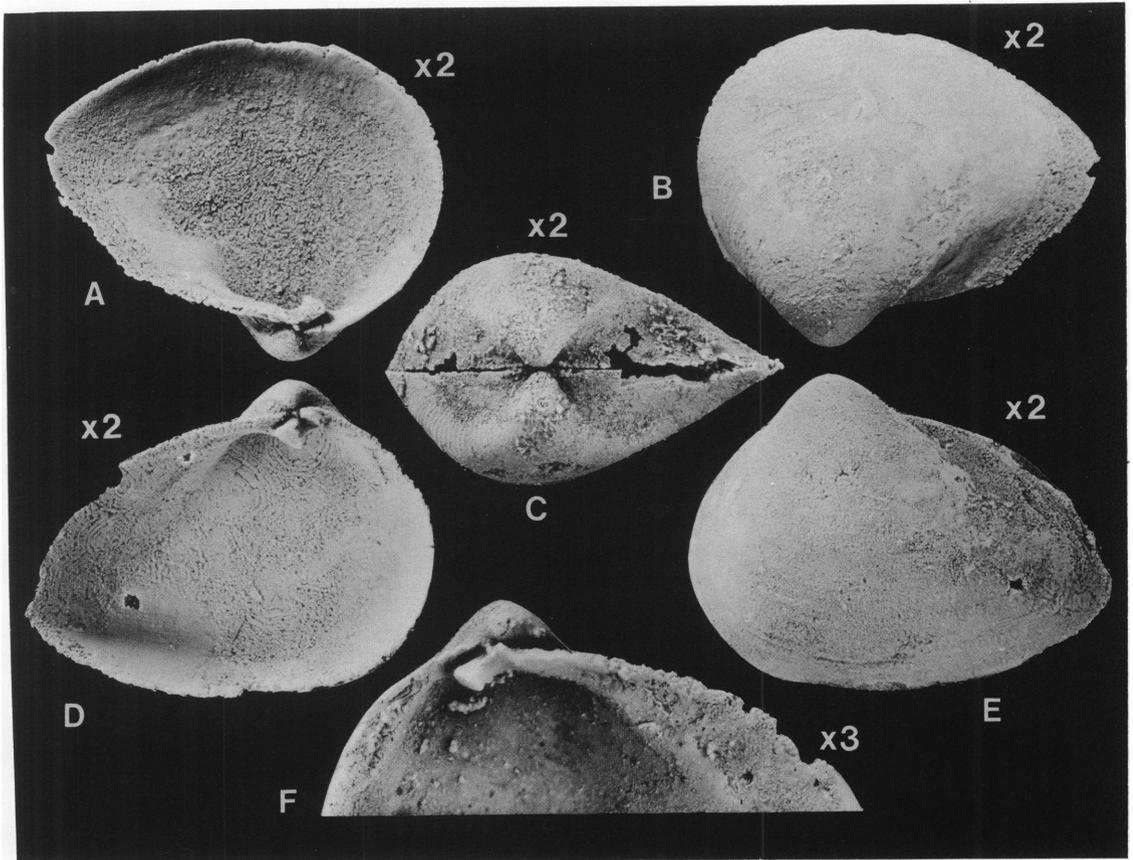


FIG. 53. *Schizodus texanus* Clifton. Silicified specimens. San Andres Formation (Leonardian), near St. Johns, Arizona. AMNH loc. 1067. A, B. Right valve. AMNH 29165. C. Bivalved individual. AMNH 29166. D, E. Left valve. AMNH 29167. F. Hinge view of right valve. AMNH 29168.

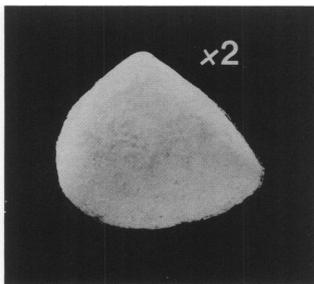


FIG. 54. *Schizodus trigonalis* Sayre. Calcareous shell, lectotype. Westerville oolite, Upper Pennsylvanian (Missourian), Muncie, Wyandotte County, Kansas. KU 57798.

The lectotype, figure 53, herein designated, is 13.8 mm. long, 12 mm. high. With both valves in place the biconvexity is 3.8 mm.

Distribution. Westerville ("Drum") Forma-

tion (Missourian), Pennsylvanian, Muncie, Kansas.

Discussion. This shell is quite distinctive in shape. Although information about the hinge and other internal characters is lacking, there is a possibility that the species should be classed elsewhere. In spite of its small size, the lectotype probably is mature, as is inferred from its low convexity. The species is very rare and restricted, apparently, to cross-bedded oolite at the type locality.

Schizodus ulrichi Worthen, 1890

Figures 12E, F, 37 no. 9, 55-60

Schizodus ulrichi Worthen, 1890, p. 110, pl. 20, fig. 9, pl. 21, figs. 1, 1a, 1b.

Schizodus harii Miller, 1892, p. 701, pl. 20, figs. 1-3.

Diagnosis. Beak slightly anterior of mid-

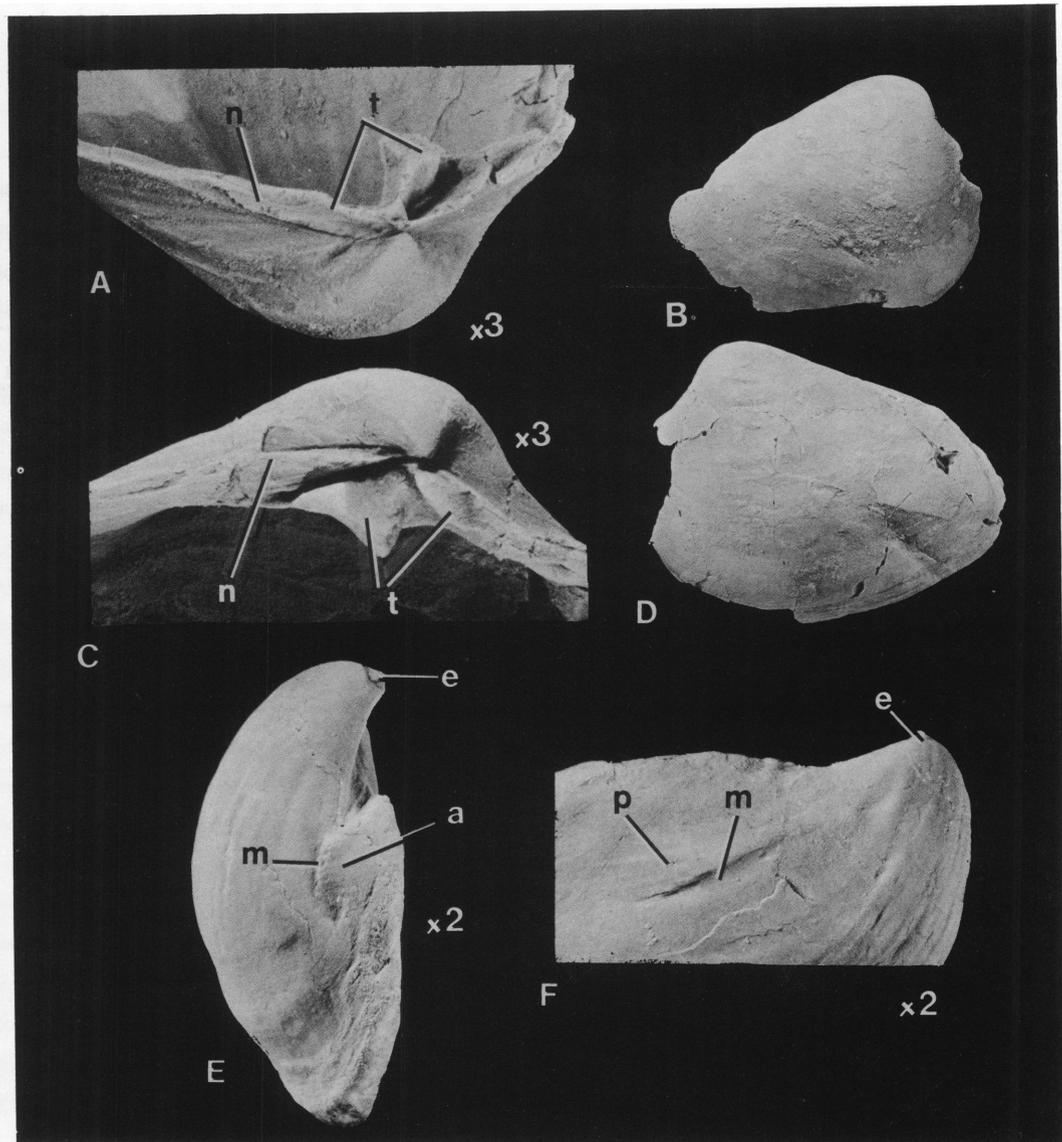


FIG. 55. *Schizodus ulrichi* Worthen, 1890. Calcareous specimens of original type suite from Upper Pennsylvanian, probably Matoon Formation (Virgilian), near Fairfield, Wayne County, Illinois. A, B. Right valve. IGS 2584 D. C, D. Left valve selected here as lectotype. IGS 2584 A. E, F. Internal mold, right valve showing details of musculature. IGS 2584 B.

Abbreviations.: a, anterior adductor; e, elevator; m, incipient myophorous buttress; n, nymph; p, posterior adductor; t, teeth.

length in small specimens, but markedly anterior in large shells. Umbonal flanks not sharply differentiated. Respiratory margin, approximately half valve height, merging with ventral margin through sharp curve and meeting dorsal margin at

obtuse rounded angle. Posterior ridge commonly broad and poorly defined. In some valves, corselet bears low, indistinct ridge between beak and dorsal limit of respiratory margin. Ligament groove approximately twice length from beak to

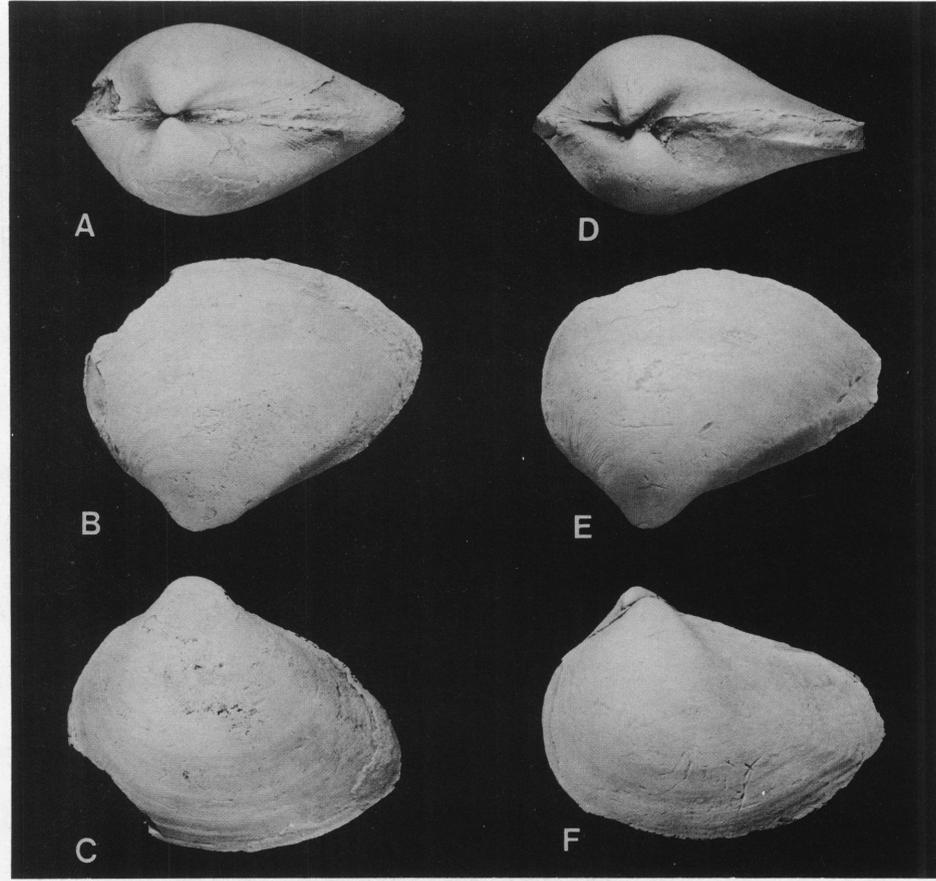


FIG. 56. *Schizodus ulrichi* Worthen, 1890. Calcareous examples. Upper Pennsylvanian Finis Shale, Graham Formation (Virgilian), Texas. A-C. Bivalved individual with symmetrical valves, 3/8 mile east of Prospect River and 3 1/2 miles north of Jacksboro. USNM 177156. D-F. Slightly crushed bivalved individual, 2 miles south of highway 24, just north of Stradeley School, Jack County. USNM 177157.

distal end of major tooth. Major socket of left valve floored for half to two-thirds length of adjacent major tooth. Anterior myophorous buttress weakly developed, limited to large valves. Posterior retractor scar extends dorsally as a long

(twice adductor height) narrow slit, deepest toward dorsal end. $L/H=1.24$ ($n=40$); $H/C=2.92$ ($N=35$); $L/PL=3.20$ ($n=40$).

Distribution. Pennsylvanian, Atokan through Virgilian; Midcontinent region, Illinois, many localities.

Discussion. In addition to four of Worthen's syntypes from Illinois, we have studied 81 calcareous specimens including 20 from Missouri and Kansas, and 61 from Oklahoma and Texas. Twenty-three of these are disarticulated valves exhibiting hinge features. Remnants of prismatic structure similar to that of *S. alpinus* are preserved on the outer surfaces of some specimens.

One collection from the Hartshorne Sand-

TABLE 15
STATISTICAL COMPARISON OF REDUCED MAJOR AXES FOR *SCHIZODUS OBSCURUS* AND *SCHIZODUS TEXANUS*

Variates	Z ₁	Z ₂	Significant Difference
L/H	1.165	12.116	Z ₂ (at 1% level)

Symbols as for table 5.

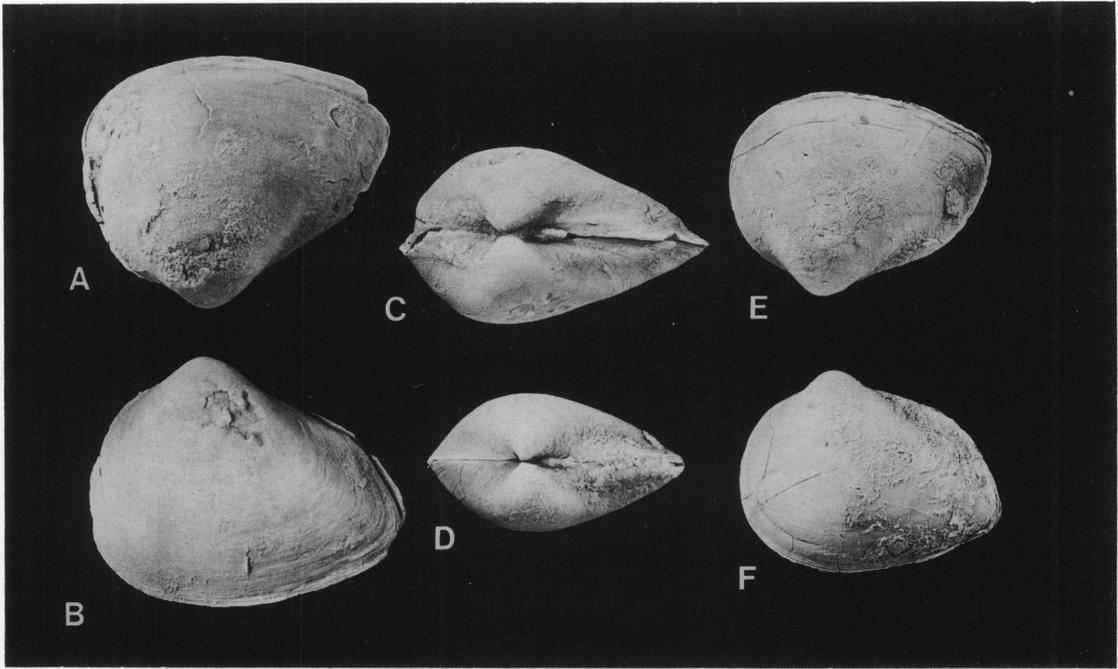


FIG. 57. *Schizodus ulrichi* Worthen, 1890. Calcareous bivalved specimens with preserved ligament. Holdenville Formation (Desmoinesian, Oklahoma). A-C. AMNH 29184. D-F. AMNH 29185.

stone of Oklahoma includes valves intermediate in some respects between *S. ulrichi* and *S. compressus*. The range of variation in the left valve hinge, for example, includes some specimens with posteroventral elongation of the major tooth. This produces an elongate posterior socket similar to that of *Schizodus compressus*.

Another collection consists of 34 specimens from the Finis shale in the vicinity of Jacksboro, Texas. Many of these valves are easily distinguished from midwestern specimens of *S. ulrichi* by several features. In the Finis specimens (fig. 56D-F), the beak and older part of the umbo form a narrow, strongly prosogyrous prominence with deeply concave posterior side. The general posterodorsal region of the valve is deflated, and the posterior ridge is a faint carina interrupting this broadly concave area. The ventral margin is strongly curved. The respiratory margin is low (less than half valve height) and forms a very obtuse angle with the hinge margin. A lunule is vaguely differentiated on some valves by a poorly defined ridge, concave toward commissure, from beak to anterodorsal margin. These distinctive

features give way to those more characteristic of *S. ulrichi* (fig. 56A-C) as convexity increases in the posterodorsal region, and a wide range of form is exhibited by the Jacksboro collection. Statistical comparisons of midwestern and southwestern collections in regard to length-height, height-convexity, and length-partial length indicate in each case no significant difference in slopes of the growth trend lines, but significant difference in positions of the lines. However, our samples are suspect because each is a composite representing numerous localities. For this reason, and because of the spectrum of forms shown by the Jacksboro collection, we have refrained from setting the Jacksboro material apart as a separate species.

Specimens from the "Coal Measures" at Kansas City, Missouri, served as the basis for Miller's (1892, pl. 20, figs. 1-3) *Schizodus harii*. We have studied several good specimens from the same provenance (fig. 58). Because we find essentially no difference between them and Worthen's types of *S. ulrichi*, we consider *S. harii* to be a junior synonym of Worthen's species.

As with the type specimen of *S. harii*, the specimen on which Swallow (1863) based *S. wheeleri* was collected from Pennsylvanian strata of Missouri. The only illustration (Hayden, 1872, pl. 10, fig. 1b) of the type specimen is a tracing by Meek of a drawing he obtained from Swallow. It differs from the figured types of *S. ulrichi* and *S. harii* in size, details of anterior outline, slightly greater length-height ratio, and prominence of posterior ridge. Whether these differences are within the range of intrapopulation variability we cannot say. For any practical consideration *swallowi* is unrecognizable.

Worthen (1884) introduced three names for as many internal molds of Mississippian fossils, not

illustrated until several years later (Worthen, 1890, pl. 18, fig. 2, pl. 19, fig. 7, pl. 20, fig. 3). His characterizations and illustrations of *S. varsoviensis* and *S. nauvoensis* are too generalized to permit evaluation of these fossils. The large, incomplete specimen he named *S. magnus* is probably not a schizodid.

Walcott's (1897, pl. 22, fig. 5) *S. deparcus* from the Mississippian of Nevada and Herrick's *S. spellmani* from the Pennsylvanian of Ohio differ from *S. ulrichi* in posterior outline. Weller's (1888, pl. 20, figs. 8, 9) *S. batesvillensis* from the Mississippian of Arkansas is more elongate. Furthermore, two internal molds that he illustrated lack the prosogyrous umbo of *S. ulrichi*.

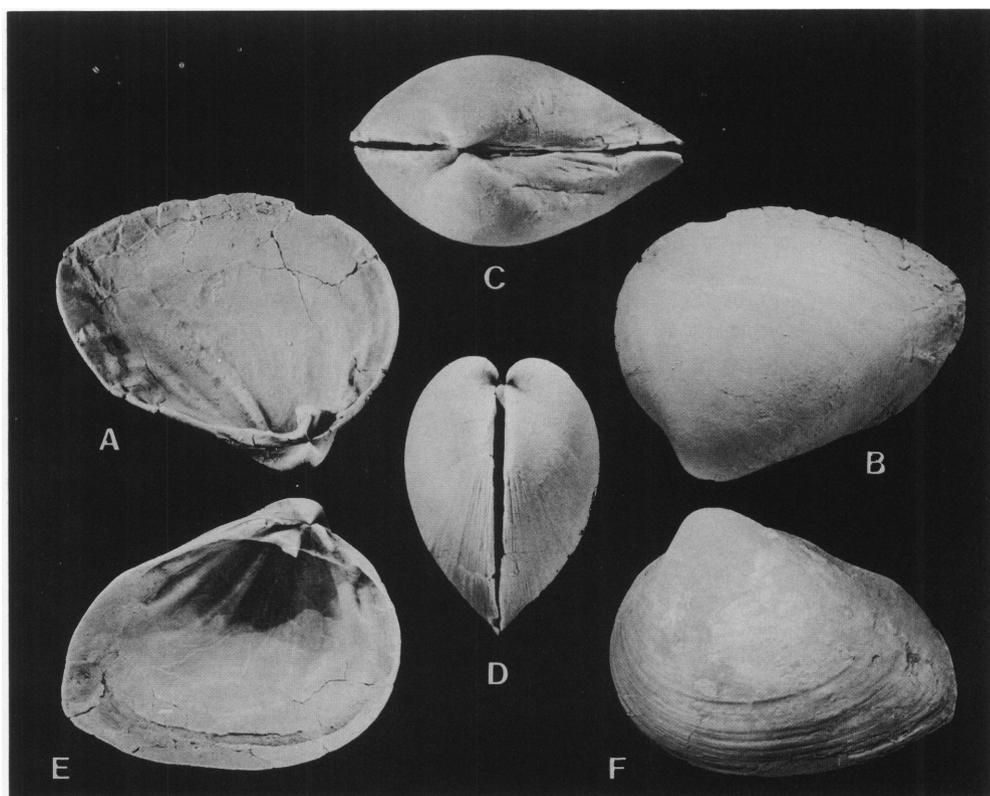


FIG. 58. *Schizodus ulrichi* Worthen. Matched calcareous valves of a single individual. Upper Pennsylvanian of Missouri. USNM 27674 (same as fig. 12E, F). A, B. Right valve. C, D. Dorsal and anterior views of articulated valves. E, F. Left valve. Note low myophorous buttresses and ridge in umbonal cavity which apparently lies just ahead of dorsal margin of gills.

Schizodus wyomingensis Newell and Boyd,
new species

Figures 16, 37 no. 3, 61, 62

Etymology. *wyomingensis*, from the State of Wyoming.

Diagnosis. Beak orthogyrous to slightly progyrous and situated about one-third of valve length behind anterior extremity. Maximum convexity commonly slightly anterior of line through beak parallel to height. Dorsal margin behind beak forms straight to slightly concave line extending to subangular intersection with short (one-third of valve height) steeply inclined respiratory margin; posteroventral margin straight or slightly concave. Posterior ridge inconspicuous. Indistinct concentric ridges, about 2 per mm., on anterior slope of some valves, and rarely on ventral flank. Long ligament groove, up to twice the distance from beak to distal edge of major tooth, bounds narrow but relatively high nymph. Pallial line posteriorly truncate, but rarely distinct. Elongate posterior pedal retractor muscle scar not quite continuous with adjacent adductor scar. $L/H=1.44$ ($n=11$); $H/C=2.57$ ($n=42$).

Distribution. Leonardian (Permian). Park City Formation (Grandeur Member), Wyoming, AMNH loc. 2010; Bone Spring Limestone, Sierra Diablo, Texas, AMNH loc. 46.

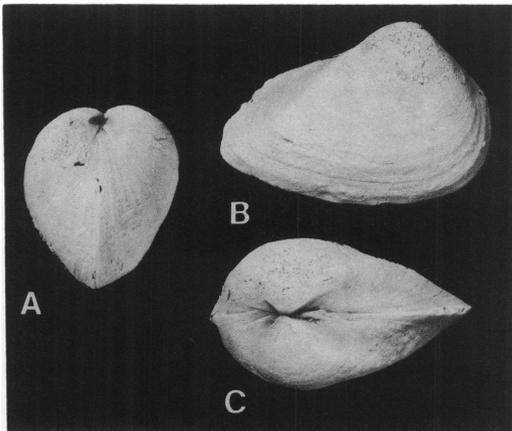


FIG. 59. *Schizodus* cf. *ulrichi* Worthen. Calcareous shell. Lower Permian Talpa Formation (Wolfcampian), at Herrings Bluff on Colorado River, Runnels County, Texas. BEG 8509; loc. 199-T-7-P-19. A. Front aspect. B. Right side. C. Hinge view.



FIG. 60. ?*Schizodus ulrichi* Worthen, 1890. Holotype of *S. insignis* Drake, 1897, fragmentary internal mold of left valve in fine quartz sandstone. This specimen not adequate for recognition of the species, and topotypes are not presently available. Middle Pennsylvanian (Desmoinesian), Wewoka Formation, 5 miles east of McDermott, Oklahoma. SU 814.

Discussion. Our silicified specimens from Beaver Creek, Wyoming, include 11 complete and more than 100 fragmentary valves. As dis-

TABLE 16
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS ULRICHI

(The sample is a composite representing many localities.^a)

	Height Length	Partial Length Length	Convexity Height
N	40	40	35
\bar{x}	39.10	39.10	30.66
\bar{y}	31.73	12.40	10.69
s_x	8.77	8.77	6.92
s_y	7.31	3.07	2.68
r	0.97	0.86	0.93
OR _x	55-10	55-10	44-13
a	0.83	0.35	0.39
σ_a	0.03	0.03	0.02
b	-0.89	-1.29	-1.17

^aSee page 90 for explanation of statistical parameters.

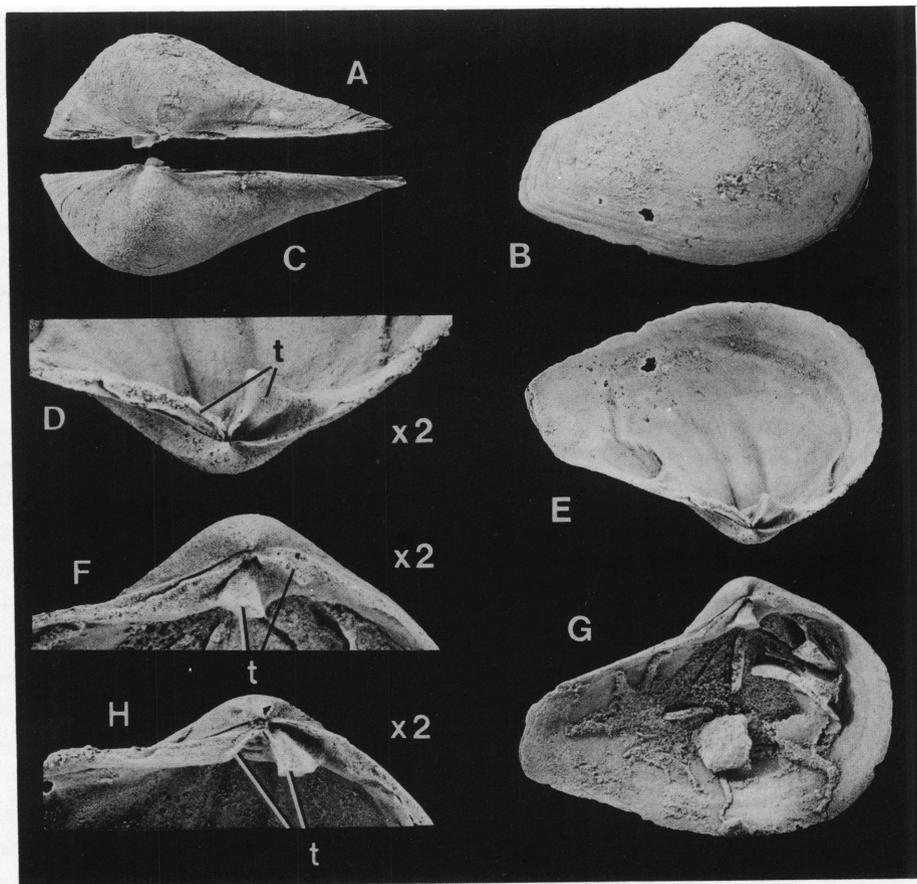


FIG. 61. *Schizodus wyomingensis* Newell and Boyd, new species. Silicified examples. Grandeur Member (late Leonardian), Park City Formation, Beaver Creek, Wind River Mountains, AMNH loc. 2010. A, B, D, E. Right valve, holotype, AMNH 29180. Note posterior truncation of pallial line. C, F, G. Left valve, AMNH 29181. H. Another left valve, with transposed hinge teeth similar to a normal right valve, AMNH 29182. Compare figure D. Teeth are indicated by t.

cussed on a preceding page, one left valve bears transposed dentition (fig. 61H).

This species differs from *S. texanus* in extended posterior region, straight or slightly concave posteroventral margin, small and steeply inclined respiratory margin, long ligament furrow, and short posterior retractor muscle scar partially isolated from the adjacent adductor scar. A statistical analysis of form differences between these two species and between *S. wyomingensis* and *S. bifidus* is presented in tables 18 and 19.

Schizodus wyomingensis differs from *S. bifidus* in having sharply outlined, commonly slightly prosogyrous beaks, inconspicuous poste-

rior ridge, and less extended posterior region. In *S. bifidus*, the ligament groove is only a little longer than the distance from beak to the distal end of the major tooth, whereas in *S. wyomingensis* it is commonly twice that distance. The large tooth of the left valve in *S. bifidus* is divided and the principal tooth of the right valve commonly is slightly bilobed. The corresponding teeth of *S. wyomingensis* lack these features.

However, the pivotal tooth of the left valve in *S. wyomingensis* does have a concave distal margin in small specimens. The distal margin of this tooth is roughly parallel to the long axis (through the two adductors) in *S. wyomingensis*, whereas

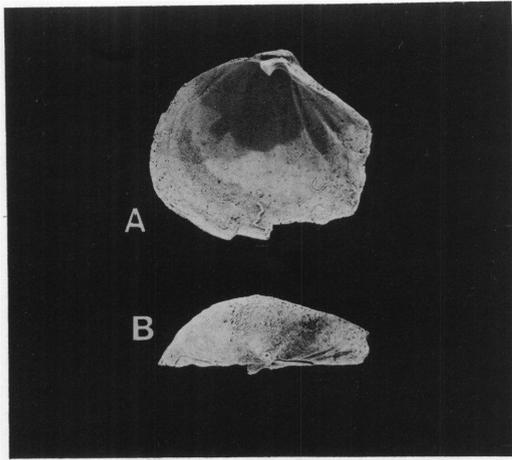


FIG. 62. *Schizodus wyomingensis* Newell and Boyd, new species. Two views of a fragmentary, silicified right valve. Bone Spring Limestone (Leonardian), of western Texas. AMNH 29183; loc. 46. Radial ridges, of uncertain significance, are approximately in the position of the inner (anterior) and outer gill plates.

it is distinctly oblique in *S. bifidus*. As with the preceding character, the *S. wyomingensis* collection is not without variation, especially among the smaller specimens.

As most of our *S. wyomingensis* valves are larger than those of *S. bifidus*, one may speculate that the two forms represent different ontogenetic stages of the same species. Evidence against this is that there is considerable overlap in valve size in the two collections without the expected morphological gradation and the beak outline and angular posterior ridge that characterize the smaller form are not observable in the first-formed part of the large valves of *S. wyomingensis*.

**HETEROSCHIZODUS NEWELL AND BOYD,
NEW GENUS
Figures 63, 64**

Type species. Heteroschizodus macomoides Newell and Boyd, new species.

Etymology. Heteroschizodus, from the Greek *heteros*, other, different; *schizein*, split; and *odon*, tooth.

Diagnosis. Shells with small hinge and large height-convexity ratio; beak near summit; umbo

inconspicuous. Anterior margin smoothly curved and convex-outward from beak through merger with ventral margin. Posterior ridge indistinct. Ligament groove long. Dental formula is given under the family diagnosis.

Distribution. Leonardian and Lower Guadalupian (Permian), western Texas.

Discussion. *Heteroschizodus* differs from *Schizodus* in its small hinge, large height-convexity ratio, and lack of concavity in the antero-dorsal profile. The modest dimensions of the hinge plate are such that the distance from the beak to ventral corner of the major tooth is less than one-eighth valve height. The position of the beak near the valve summit and the inconspicuous umbo are other characters not found in typical species of *Schizodus*.

Heteroschizodus macomoides Newell and Boyd,
new species
Figure 63

Etymology. macomoides, from the pelecypod *Macoma*, and the Greek *-oides*, like.

Diagnosis. Oval shells with beak orthogyrous, positioned from 40 to 50 percent of valve length behind anterior extremity. Anterior margin

**TABLE 17
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCHIZODUS WYOMINGENSIS
FROM GRANDEUR MEMBER OF PARK CITY
FORMATION AT BEAVER CREEK,
WYOMING, AMNH LOC. 2010^a**

	Height Length	Convexity Height
N	11	42
\bar{x}	45.09	30.98
\bar{y}	28.64	12.21
s_x	10.95	6.50
s_y	10.43	2.96
r	0.57	0.95
OR _x	57-40	43-16
a	0.95	0.46
σ_a	0.24	0.02
b	-14.33	-1.89

^aSee page 90 for explanation of statistical parameters.

TABLE 18
STATISTICAL COMPARISON OF REDUCED
MAJOR AXES FOR *SCHIZODUS*
WYOMINGENSIS AND *SCHIZODUS TEXANUS*

Variates	Z ₁	Z ₂	Significant Difference
L/H	0.27	-3.54	Z ₂ (at 1% level)
H/C	1.58	1.20	None

Symbols as for table 5.

smoothly curved from beak to merger with ventral margin, with anterior extremity near mid-height; respiratory margin half valve height in

TABLE 19
STATISTICAL COMPARISON OF REDUCED
MAJOR AXES FOR *SCHIZODUS*
WYOMINGENSIS AND *SCHIZODUS BIFIDUS*

Variates	Z ₁	Z ₂	Significant Difference
L/H	-1.57	-1.52	None
H/C	0.74	-2.89	Z ₂ (at 1% level)

Symbols as for table 5.

large valves. Corselet slightly concave. Ligament groove length in large valves two or more times the distance from beak to distal end of major

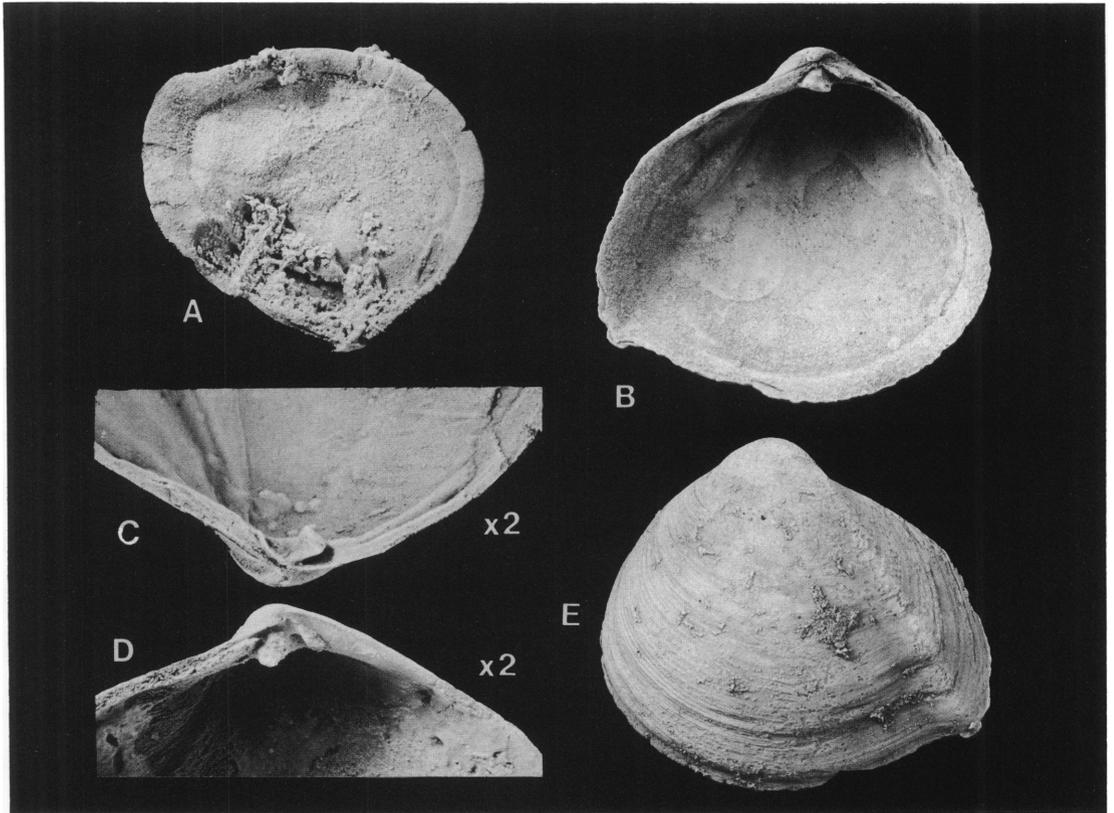


FIG. 63. *Heteroschizodus macomoides* Newell and Boyd, new species. Silicified examples. Lower Guadalupian, western Texas. A. Right valve interior, showing pallial line. Appel Ranch Member, Word Formation, Glass Mountains. USNM 117165; loc. 714-o. C. Right valve. China Tank Member, Word Formation, 3.7 miles N 36° E of Hess Ranch House, Glass Mountains. AMNH 29214; loc. 508 (same as USNM loc. 706c). B, E. Left valve, holotype. Lower Getaway Limestone Member, Cherry Canyon Formation, Guadalupe Mountains. AMNH 29212; loc. 512. D. Left valve. Willis Ranch Member, Word Formation, Glass Mountains. USNM 177166; loc. 706e.

TABLE 20
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES IN THE STUDY COLLECTION
OF *HETEROSCHIZODUS MACOMOIDES* NEWELL AND BOYD, NEW SPECIES

Length	Left Valves			Length	Right Valves		
	Height	Convexity	Partial length		Height	Convexity	Partial length
51 ^a	46	14	21	52+	41	9	25
50	42	9	22	48+	40	7	21
49	40	8	20	46	40	—	19
48	38	8	18	—	—	—	—

^aHolotype.

tooth. Anterior and posterior retractor scars long, narrow furrows near valve margins, and equal in extent in large valves to height of adjacent adductor scars. Pallial line simple. L/H=1.20 (n=7); H/C=4.66 (n=6); L/PL=2.37 (n=7).

Distribution. Upper Leonardian to Lower Guadalupian in western Texas. Road Canyon Formation, Word Formation (China Tank, Willis Ranch, and Appel Ranch members), and Cherry Canyon Formation (Lower Getaway Limestone Member); AMNH loc. 512; USNM locs. 702c, 706b-706e, 714o, 726d, 728.

Discussion. Our study collection consists of 44 silicified valves, mostly fragments; the largest sample from one locality (lower Getaway Limestone; AMNH loc. 512) includes 25 valves of which four are complete.

The major tooth of the left valve varies in shape from narrow (fig. 63D) to expanded (fig. 63B). Discrimination between ontogenetic and stratigraphic variation within our collection is handicapped by unequal distribution of small and large specimens between older and younger samples. Small valves lack floors in the major socket of each valve, whereas equivalent sockets are partially floored in large valves. The ligament groove length in small specimens is only slightly more than the distance from beak to distal end of the major tooth but it is twice or more that dimension in large individuals.

Heteroschizodus sp.

Figure 64

We have only two specimens of the unusual schizodid illustrated in figure 64. Both are small, incomplete right valves from the lower Bone Spring Limestone, Leonardian (Permian); AMNH

loc. 46. Distinctive aspects include elongate form, lack of concavity in the anterodorsal profile, inconspicuous umbo, long ligament groove, small hinge plate, and prominent, subcircular anterior retractor scar isolated from the adjacent adductor scar. Unlike the condition in most schizodid right valves, the major tooth is angular, with planar rather than curved sides. The adjacent major socket is largely floored.

Several of the distinctive aspects listed above also characterize *Heteroschizodus macomoides*, but in regard to length-height ratio and character of the anterior retractor scar, the two forms are quite different.

FAMILY SCAPHELLINIDAE
NEWELL AND CIRIACKS, 1962

Diagnosis. Similar to the Schizodidae except for strong siphonal gape, heavy ligament nymphs, well-developed posterior myophorous buttress, and deep pallial sinus. Monogeneric.

Distribution. Upper Leonardian and Guadalupian (Permian), Arizona, Montana, and Wyoming.

Discussion. The deep pallial sinus indicates mantle fusion and possession of well-developed siphons, a specialization for deep burrowing and an evolutionary advance over Schizodidae.

GENUS SCAPHELLINA
NEWELL AND CIRIACKS, 1962
Figures 15, 37 no. 12, 65-67

Type Species. *Schizodus bradyi* Newell and Ciriacks, 1962 (= *Schizodus concinnus* Branson, 1930; ?*S. phosphoriensis* Branson, 1930), by original designation.

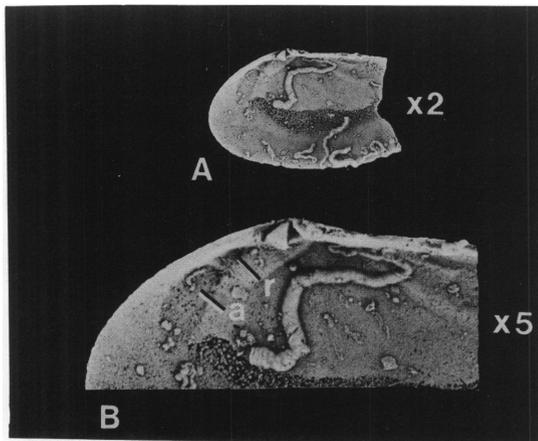


FIG. 64. *Heteroschizodus* sp. Fragment of silicified right valve. Bone Spring Limestone (Leonardian), Sierra Diablo, western Texas. AMNH 29200; loc. 46.

Abbreviations: a, anterior adductor; r, anterior retractor.

Characters and range as with the family Scaphellinidae.

Scaphellina concinna (Branson, 1930)
 Figures 15, 37 no. 12, 65-67

Schizodus concinnus C. C. Branson, 1930, p. 46, pl. 13, figs. 12, 13.

?*Schizodus phosphoriensis* C. C. Branson, 1930, p. 47, pl. 13, figs. 2-7.

Diagnosis. Posteriorly gaping shells with centrally placed, opisthogyrous beaks; maximum convexity below beaks. Anterior and ventral margins forming uninterrupted curve from beak to posteroventral corner at mid-height; respiratory margin curved, about one-fourth valve height in extent. Posterior ridge inconspicuous. Ligament groove long, intersecting dorsal margin one-fourth to one-third the distance from beak to posterior end of valve; massive nymph with flat to concave dorsal surface, undergirded by posterior part of myophorous buttress. Dentition schizodian, with addition of an ephemeral posterior tooth in the right valve:

	RV	n (i) (o) i O I o	
Posterior			Anterior
	LV	n (o) (i) o I O i	

Anterior adductor scar higher than long; posterior adductor scar longer than high; retractor muscle scars typically prominent, above each adductor scar; multiple insertion pits for elevator muscle in apex of umbonal cavity. L/H=1.33 (n=95); H/C=2.79 (n=95).

Distribution. Leonardian and Guadalupian. Kaibab Limestone (Gamma Member), Arizona; Park City Formation (Grandeur and Ervay members), Wyoming; Shedhorn Sandstone and Park City Formation (Franson Member), Montana; AMNH locs. 1068, 2010.

Discussion. Our study collection consists mainly of some 1100 silicified specimens, about evenly divided between left and right valves, from one layer of the Park City Formation at Beaver Creek, Wyoming. Most were extensively broken before burial (Boyd and Newell, 1972), and only 70 are essentially complete. The variation exhibited by this sample from a single population deserves comment.

Considering the lateral profile, beak position varies from mid-length to distinctly anterior of that point, and the dorsal margin behind the beak varies in orientation from approximately parallel with shell length to inclined relative to length. The ventral extremity ranges from directly beneath the beak to slightly anterior or, rarely, slightly posterior of that point.

Newell and Ciriacks (1962, p. 3) described the prominent tooth on the left valve as broad, distally notched, and gable shaped. However, our collection demonstrates that this tooth is highly variable in form (fig. 66). In some valves it is narrow and elongate, trending anteroventrally from the beak. More commonly (fig. 67), a posteroventral projection gives the tooth the outline of an asymmetric triangle. Rarely, the tooth is symmetrically triangular with a concave base. The posterior tooth of the left valve is sharply defined on some valves, inconspicuous on many, and absent on still others, including all the very small specimens. On right valves, the anterior tooth is nearly parallel to the adjacent valve margin in small valves but diverges from the margin with increasing valve size. As a result, this tooth on large valves is typically convex dorsally. The right valve major socket coincides with a hiatus in the hinge plate in very small valves, but a partial floor is present beneath this socket in larger

specimens. The minor tooth bordering the posterior side of this socket has a strong posterior in-

clination in very small right valves. Ventral lengthening of this tooth characterized later

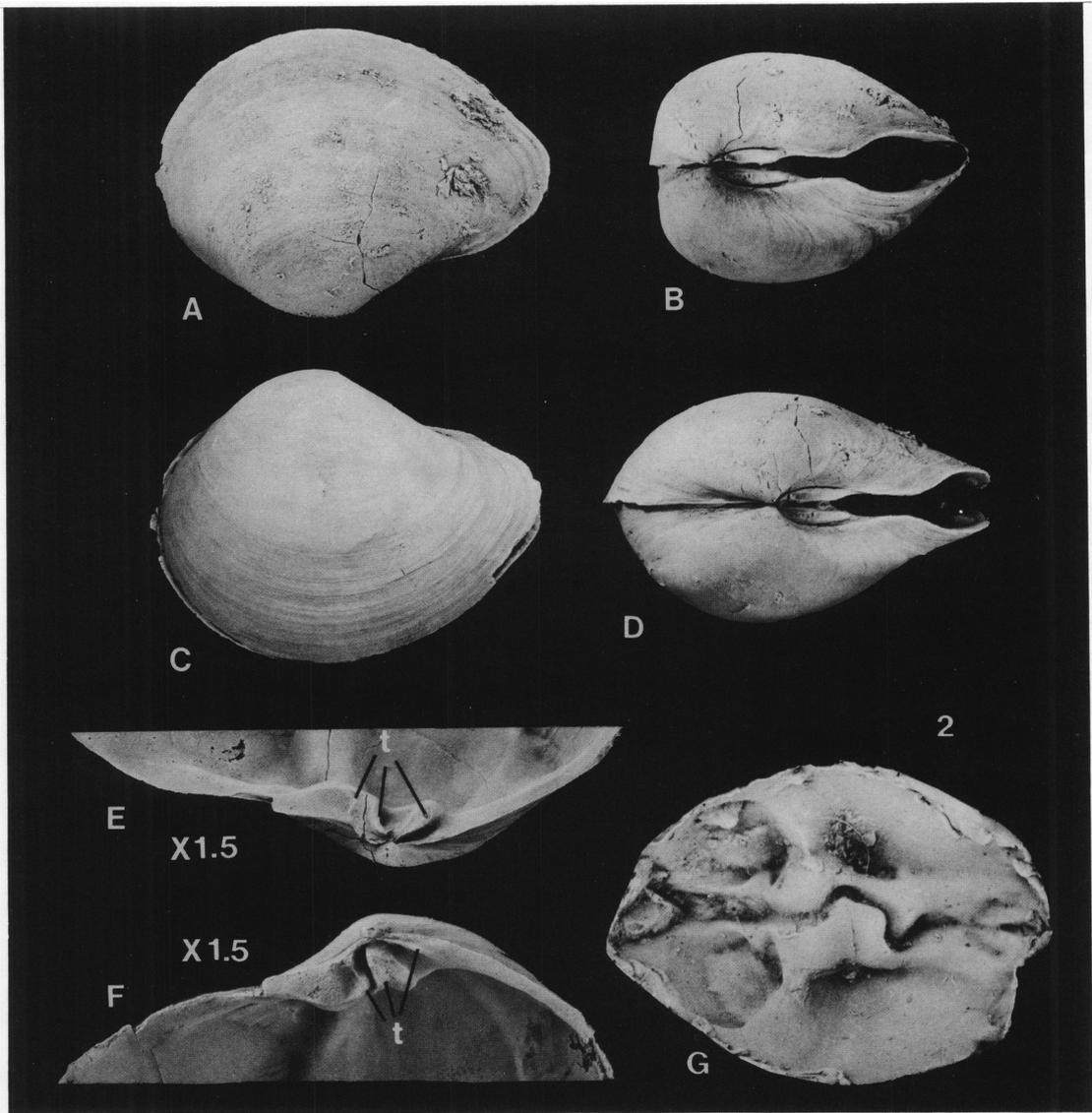


FIG. 65. *Scaphellina concinna* (Branson), 1930. Dolomites of Leonardian age, Wyoming and Arizona. A-D. Unmatched pair of silicified valves artificially joined and closed. Grandeur Member, Park City Formation, Wyoming. AMNH 29205 (right) and 29206 (left); loc. 2010. E. Right valve, same as A. AMNH 29205. F. Left valve. Same locality and horizon, AMNH, 29207. G. *In situ* latex cast of hinge from a natural mold (not collected). Gamma Member, Kaibab Limestone. Jones Crossing of East Clear Creek, Arizona.

Abbreviation: t, tooth.

TABLE 21
BIVARIATE STATISTICAL
CHARACTERIZATION OF
SCAPHELLINA CONCINNA
FROM GRANDEUR MEMBER OF PARK CITY
FORMATION AT BEAVER CREEK,
WYOMING. AMNH LOC. 2010.^a

	Height Length	Convexity Height
N	95	95
\bar{x}	51.13	38.46
\bar{y}	38.46	14.19
s_x	10.75	8.22
s_y	8.22	3.84
r	0.98	0.96
OR _x	71-24	53-18
a	0.76	0.47
σ_a	0.02	0.01
b	-0.64	-3.76

^aSee page 90 for explanation of statistical parameters.

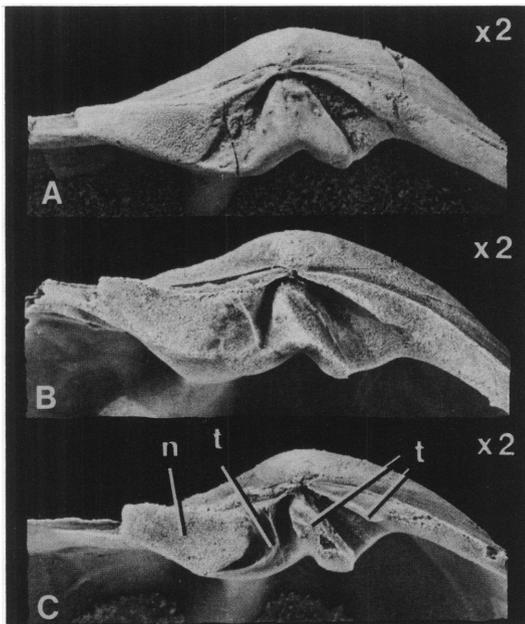


FIG. 66. *Scaphellina concinna* (Branson), 1930, showing range of variation in dentition of left valve in a single population sample. Silicified specimens. Lower Permian (Upper Leonardian), Grandeur Member, Park City Formation. AMNH 29221, 29220, and 29219, respectively; loc. 2010. Wind River Mountains, Wyoming.

Abbreviations: n, nymph; t, tooth.

growth stages, with the result that this tooth in large valves is convex posteriorly. On some right valves, a third tooth is recognizable between nymph and small posterior socket. Where present, it varies from a broad mound to a sharply defined low ridge trending roughly perpendicular to the hinge axis.

The anterior retractor muscle scar, elongate and seldom subdivided, is isolated from the sub-adjacent anterior adductor scars. The posterior retractor scar is typically subdivided into two or more irregular pits along the anterodorsal margin of the posterior adductor scar.

We have compared the Wyoming shells with the latex casts of Arizona specimens studied by Newell and Ciriacks (1962) and conclude that morphologic differences between the two quite unequal collections reflect geographic variation in a single species. The Arizona specimens have longer and thicker teeth, and a narrower anterior adductor scar. The myophorous buttress is narrower bordering the posterior adductor scar and the slope is steeper from the buttress crest to the scar than in typical Wyoming specimens. Ventral continuation of the buttress is less extensive in large Arizona specimens than in their Wyoming counterparts.

EOASTARTIDAE NEWELL AND BOYD,
NEW FAMILY

Diagnosis. Typically unornamented shells with posterior ridge inconspicuous or absent. Ligament groove length between one and two times distance from beak to distal end of major tooth. Schizodian or myophorian dentition; left valve hinge having floor beneath all sockets; relatively narrow major tooth of left valve having steep anterior face and strong posterior inclination; teeth not striated. Posterior retractor scar isolated above adjacent adductor scar.

Distribution. Permian (North America) and Triassic (Europe).

Discussion. Permian representatives superficially resemble astartids, but lack lateral teeth. They have unusually well-developed hinge plates for the schizodian grade, especially on the left valve where the major socket is completely floored. An anterior myophorous buttress is absent or rudimentary in Permian forms, but accompanies the myophorian hinge of Triassic representatives.

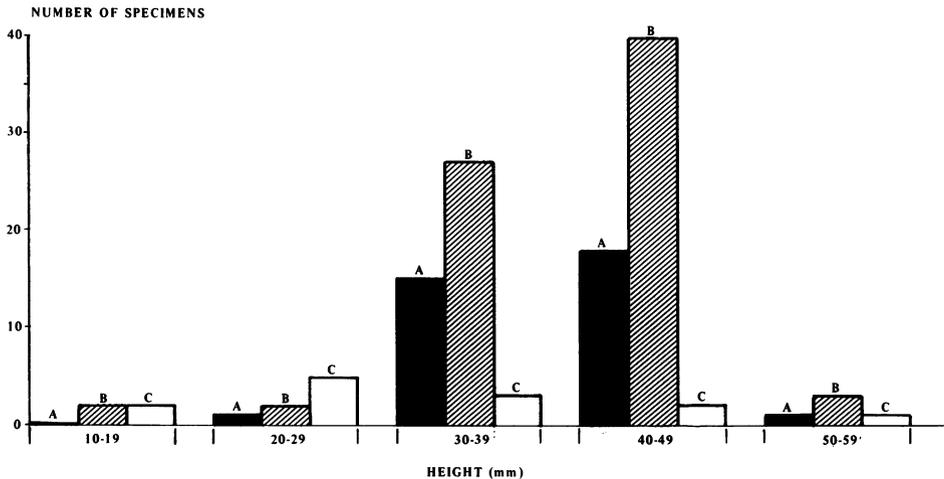


FIG. 67. A single population sample of 122 silicified valves of *Scaphellina concinna* from Beaver Creek, Wyoming (AMNH loc. 2010), divided into five size classes on the basis of valve height measured in mm. Histograms show occurrence in these size classes of the three tooth forms (A, B, C) of figure 66.

Kaibabella curvilenata is exceptional in possessing concentric ridges.

which he homologized with astartid teeth by using the notation of Bernard and Munier-Chalmas,

GENUS *EOASTARTE* CIRIACKS, 1963

Figures 68-70

Type Species. *Eoastarte subcircularis* Ciriacks, 1963, by original designation.

Diagnosis. Subcircular to oval, with height approximately equal to length; umbones prominent and prosogyrous. Posterodorsal margin slightly steeper and flatter than anterodorsal margin. Hinge schizodian; left valve hinge plate well developed, with ventral edge inclined forward relative to muscle-scar axis. Anterior pedal retractor scar subcircular, posterior retractor scar elongate, both more or less isolated from adjacent adductor scars; pedal elevator scar at apex of umbonal cavity. Pallial line simple and distinct.

Distribution. Leonardian-Wyoming, Texas, and Arizona.

Discussion. Some aspects of *Eoastarte* are reminiscent of the astartids. These include external form (most notable in small individuals), the narrow, plane-sided major tooth of the left valve, and the fully developed hinge plate of that valve. Impressed by these similarities, Ciriacks (1963) assigned the genus to the Astartidae. He suggested that the simple dentition of *Eoastarte*,

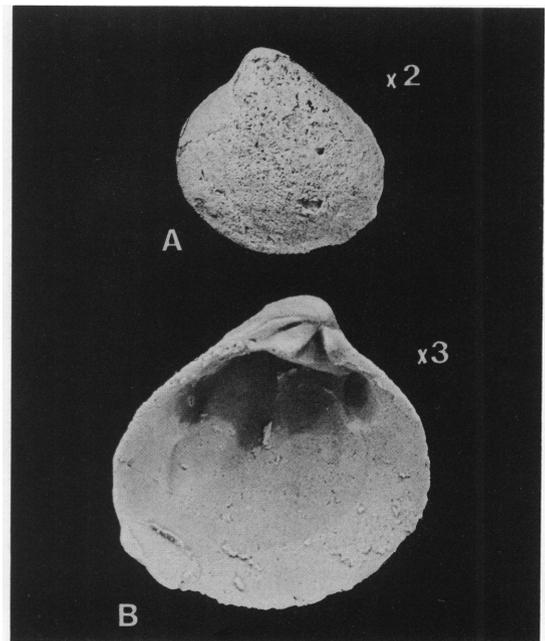


FIG. 68. *Eoastarte subcircularis* Ciriacks, 1963. Silicified left valve, holotype, juvenile. Grandeur Member (upper Leonardian), Park City Formation, Willow Creek, southern Wind River Mountains, Wyoming. AMNH 28337.

might be ancestral to the heterodont astartid hinge. However, the hinge in *Eoastarte* is, in our opinion, schizodian with respect to numbers, relative positions, and sizes of teeth. We believe the resemblance between shells of this genus and the astartids reflects superficial convergence rather than near kinship. Fully developed astartids such as *Astartella* are well documented in the

upper Paleozoic where the origin of that family is clearly pre-Pennsylvanian (Boyd and Newell, 1968).

The well-developed hinge plate of the left valve of *Eoastarte* and the flat-sided major tooth of that valve are also typical of *Kaibabella*. However, the latter has these same features on both valves. It differs further from *Eoastarte* in having

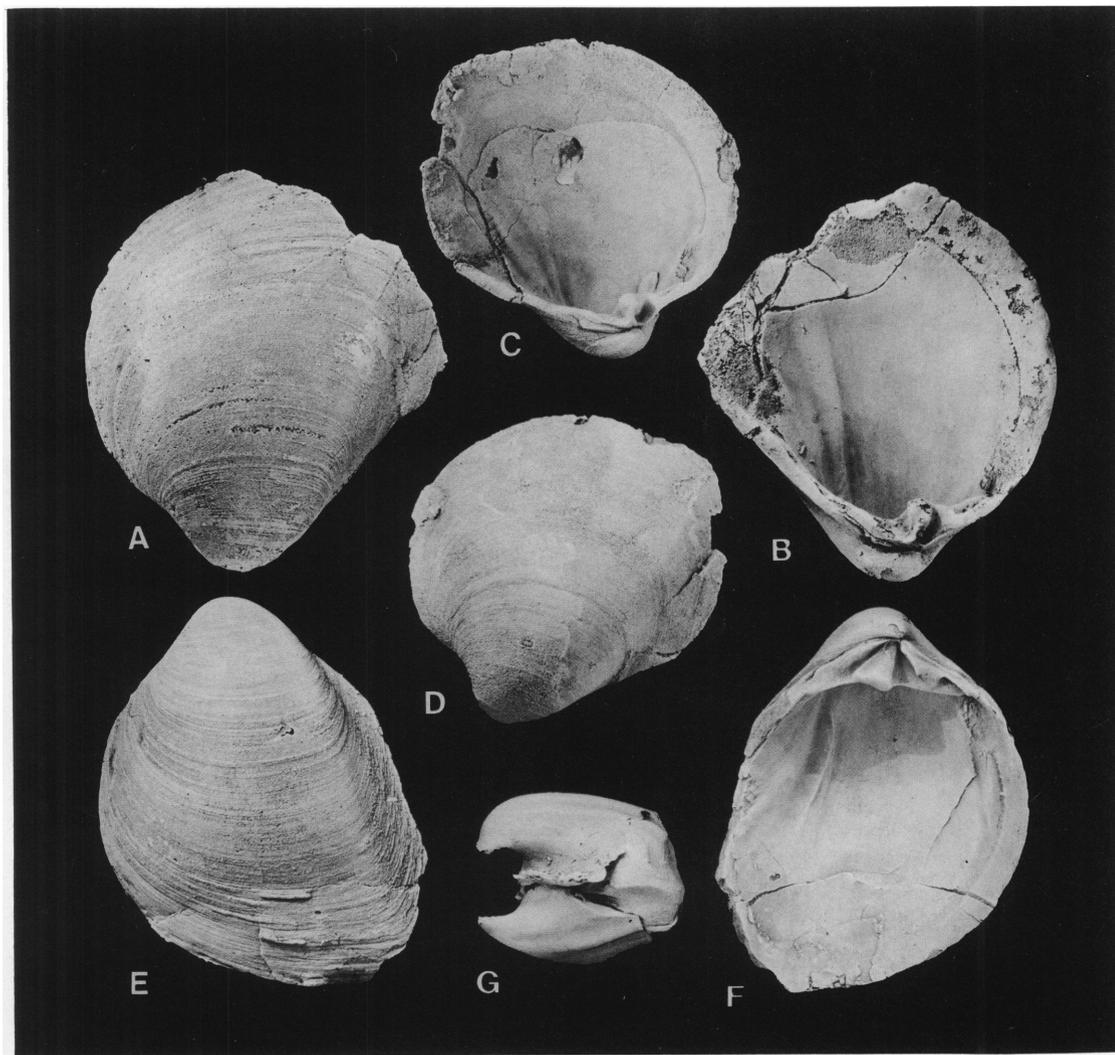


FIG. 69. *Eoastarte subcircularis* Ciriacks, 1963. Silicified specimens. Road Canyon Formation (Upper Leonardian), Glass Mountains, western Texas (USNM loc. 703). A, B. Right valve. USNM 174470. C, D. Right valve. USNM 174471. E, F. Left valve. USNM 174472. G. Composite latex mold of B and F, viewed posteriorly, showing apical pedal elevator scars. Posterior radial furrows (ridges on latex molds) are interpreted here as possible attachment areas of two pairs of gill plates.

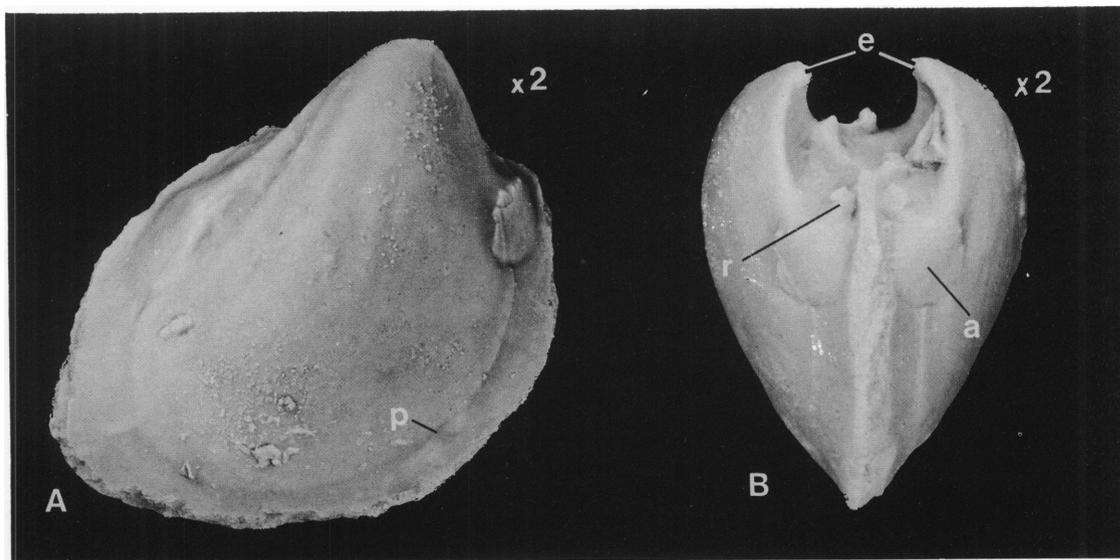


FIG. 70. *Eoastarte subcircularis* Ciriacks, 1963. Dolomite internal mold. Gamma Member of Kaibab Limestone (Leonardian), Jones Crossing, south of Flagstaff, Arizona. MNA G2.6185.

Abbreviations: a, anterior adductor; e, pedal elevators; p, pallial line; r, anterior pedal retractor.

a weak myophorous buttress, and in having a beak very near the summit instead of being incurved.

The middle Pennsylvanian *Schizodus amplus* anticipates a number of *Eoastarte* traits and suggests possible origin of the latter.

Eoastarte subcircularis Ciriacks, 1963
Figures 68-70

Eoastarte subcircularis Ciriacks, 1963, pp. 66-67, pl. 12, figs. 11-15.

Diagnosis. Strongly prosogyrous beak situated well below summit. Circular outline of ventral two-thirds of lateral profile in small shells gives way to posteroventral elongation in large specimens. Ligament groove in large valves nearly twice as long as distance from beak to distal end of major tooth. Thickened anterior end of hinge plate merges with valve interior at dorsal margin of anterior adductor muscle scar. $L/H=1.03$ ($n=4$); $H/C=2.98$ ($n=4$); $L/PL=2.72$ ($n=4$).

Distribution. Permian, Leonardian, Park City Formation (Grandeur Member), Wyoming; Cathedral Mountain Formation and Road Canyon Formation, western Texas; ?Kaibab Formation (Gamma Member), Arizona; AMNH loc. 2010; USNM locs. 703, 703c, 703d, 723p.

Discussion. Our study collection of silicified specimens includes only a few complete valves. Our largest sample from one formation consists of 20 specimens, mainly imperfect, from the Road Canyon Formation of Texas. The small hypodigm of Ciriacks includes only juveniles, whereas the Texas valves are very much larger. However, only one specimen from the latter suite is sufficiently complete to be represented in the table of measurements (table 22).

A collection of some 30 small silicified valves, mostly fragments, from the San Andres Formation of New Mexico exhibits certain characteristics of *Eoastarte subcircularis*. A few small specimens from the Yeso Formation of New Mexico probably represent the same form. Our only large specimen is an internal mold (fig. 14) from the San Andres Formation. The small valves resemble *E. subcircularis* in circular outline, convexity, indistinct posterior ridge, well-developed floor in major socket of left valve, and form and arrangement of adductor and retractor muscle scars. However, the New Mexico specimens have a much less prosogyrous beak closer to the valve summit, and the sloping sides and ventral furrow of the major tooth of the left valve are typically schizodian. Furthermore, with increasing size valve shape becomes more like that of many

TABLE 22
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES IN THE STUDY COLLECTIONS
OF *EOASTARTE SUBCIRCULARIS*

(Left valves are from Park City Formation, Willow Creek, Wyoming;
right valve is from Road Canyon Formation, Texas.)

Length	Left Valves			Length	Right Valve		
	Height	Convexity	Partial length		Height	Convexity	Partial length
13.7 ^a	13.6	4.3	5.1	41	42	14	14
11.1	10.7	3.6	4.4	—	—	—	—
10.7	9.8	3.5	3.9	—	—	—	—

^aHolotype.

Schizodus species. The length-height ratio is 1.0 at 9 mm. length, 1.21 at 17 mm. length, and 1.28 for the large (41 mm.) mold. Valve margins on each side of the beak become straighter in company with the increase in length-height ratio (fig. 14). A few small valves have close-spaced concentric ridges on anterior and ventral surfaces. On balance, the New Mexico material appears more like *Schizodus* than *Eoastarte*. Considering the unusual combination of characteristics and notable ontogenetic variation, the available sample is inadequate for specific characterization.

GENUS *KAIBABELLA* CHRONIC, 1952
Figures 71-74

Type Species. *Kaibabella curvilenata* Chronic, 1952, by original designation.

Diagnosis. Subcircular to ovate shells with inconspicuous umbones. Beak orthogyrous to slightly prosogyrous, essentially coincident with valve summit, centrally situated (small valves) to anteriorly (large valves). Unornamented, or partially covered with concentric, rounded ridges. Schizodian hinge with all sockets floored; major tooth in each valve triangular, with steep, planar anterior and posterior faces. Myophorous buttress rudimentary. Adductor scars subequal, elongate parallel to adjacent valve margins; anterior and posterior retractor scars circular, isolated above adjacent adductor scars; elevator scar at apex of umbonal cavity; pallial line simple, indistinct.

Distribution. Permian, Leonardian, and Lower Guadalupian; Arizona, New Mexico, western Texas, and Wyoming.

Discussion. Several aspects of the hinge are unique within the schizodian grade. First, the hinge plates of both valves are complete; floors extend beneath all sockets. Second, the major tooth of each valve is triangular with steep, planar anterior and posterior faces, and without a ventral furrow. Third, the two teeth of the right valve are not connected beneath the beak by a narrow ridge. As is common in species with schizodian dentition, a rudimentary third (posterior) tooth is recognizable in a small percentage of left valves.

The thickened anterior end of the hinge plate meets the valve floor along the upper margin of the anterior adductor scar, and a retractor scar is deeply imprinted in this area. In some valves, a ventral prong of the thickened area borders the posterodorsal margin of the adductor, but this rudimentary myophorous buttress extends no more than half the height of the adductor scar.

Kaibabella differs from heterodonts in the absence of lateral teeth. It is unlike *Eoastarte* in lacking prominent prosogyrous umbones, and in the nonschizodian aspects of the right valve hinge described above.

Kaibabella curvilenata Chronic, 1952
Figure 71

Kaibabella curvilenata Chronic, 1952, p. 150, pl. 10, figs. 1-4.

Diagnosis. Subcircular shells incompletely ornamented with rounded, concentric ridges. Beak subcentral, at valve summit. Ventral margin strongly curved; respiratory margin approximately one-third of valve height. L/H=1.19 (n=13); H/C=2.04 (n=13).

Distribution. Leonardian-Lower Guadalupian. Kaibab Limestone (Alpha Member), Arizona; Yeso Formation and San Andres Formation, New Mexico. AMNH locs. 56, 57, 1071.

Discussion. Differences between *Kaibabella curvilenata* and *K. basilica* are discussed under the latter species. The most striking difference between the two is the ornamentation of *K. curvilenata*, and we are uncertain as to its significance. The concentric ridges vary in prominence from valve to valve, and from one growth stage to another on the same valve. Our study collection for this species is small, and we are unable to determine whether the surface relief reflects environmental or genetic control.

The ratios of length-height and height-convexity in the above diagnosis were calculated from measurements published with the original description of the species.

***Kaibabella basilica* Newell and Boyd, new species**
Figures 72-74

Etymology. *basilica*, from the Greek *basilikos*, royal.

Diagnosis. Smooth, ovate shells with beaks forward of mid-length. Posterodorsal margin long and straight, sloping toward narrow and ill-defined respiratory margin. $L/H=1.29$ ($n=62$); $H/C=3.57$ ($n=62$).

Distribution. Leonardian. Park City Formation (Grandeur Member), Wyoming; Bone Spring Limestone and Road Canyon Formation, western Texas. AMNH loc. 2010; USNM loc. 703c; USGS loc. 6983.

Discussion. Our large study collection consists mainly of some 1500 silicified valves from one layer at Beaver Creek, Wyoming (AMNH loc. 2010). Many of these specimens consist of little more than the hinge plate, but right and left valves are represented in approximately equal numbers. Variation in dentition is negligible in this collection. By contrast, the rudimentary myophorous buttress is quite variable in width and ventral extent. A posterior ridge is distinct on a few valves but inconspicuous on most. Other variable traits are posterior elongation and curvature of ventral margin. *Kaibabella basilica* differs from *K. curvilenata* in lacking concentric ridges, and in possessing a more angular dorsal profile and greater posterior elongation. Con-

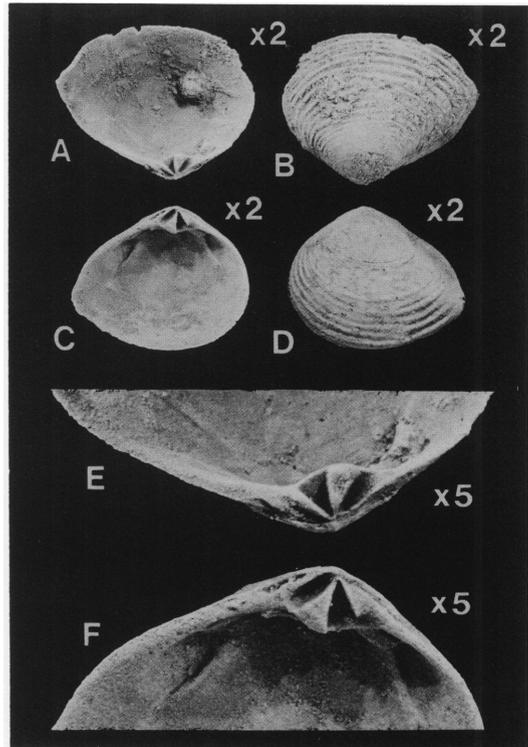


FIG. 71. *Kaibabella curvilenata* Chronic. Silicified topotype specimens of type species of *Kaibabella*. Uppermost Kaibab Limestone of Grand Canyon region, Arizona. AMNH loc. 1071. A, B, E. Right valve. AMNH 29194. C, D, F. Left valve. AMNH 29195.

versely, the broader respiratory margin and more centrally placed beaks of *K. curvilenata* produce a near-equilateral appearance. *Kaibabella basilica* also differs from *K. curvilenata* in having a slightly larger hinge plate and a somewhat longer and narrower major tooth in the left valve. The height-convexity ratio is notably higher for *K. basilica* than for *K. curvilenata*.

GENUS *HEMINAJAS* NEUMAYR, 1891
Figure 75

Type Species. *Myophoria fissidentata* Wöhrmann, 1889, by monotypy.

Diagnosis. Smooth, posteriorly elongate shells with prosogyrous umbones and incurved beaks. Myophorian hinge with third (anterior) tooth on right valve. Myophorous buttress extending full height of anterior adductor scar.

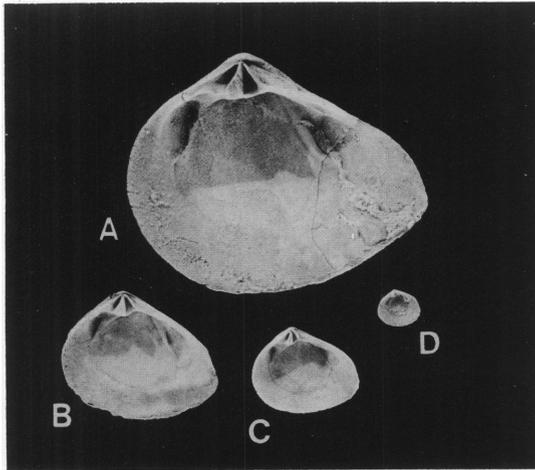


FIG. 72. *Kaibabella basilica* Newell and Boyd, new species. Series of silicified right valves showing progressive elongation during growth characteristic of the genus *Kaibabella*. Grandeur Member (Leonardian), Park City Formation, Wyoming. AMNH loc. 2010. A. Mature individual, holotype, AMNH 29201. B, C, D. Juveniles. AMNH 29202, 29203, and 29204, respectively.

Distribution. Middle-Upper Triassic. Europe.
Discussion. *Heminajas* shares with pachycardiids its general form, myophorian hinge, and myophorous buttress. Its angular central teeth with steep, planar faces link it to the Eoastartidae. The same is true for the strong posterior inclination of the major axis of the pivotal tooth of the left valve. The unexpected anterior tooth of the right valve and its corresponding socket in the left valve result in a hinge with two anterior components not present in the standard myophorian dentition:

	RV n o I O I o l	
Posterior	LV n l 0 A 0 l o	Anterior

FAMILY PACHYCARDIIDAE COX, 1961

Diagnosis. Similar to the Eoastartidae, but with myophorian hinge with central tooth of each valve being relatively large and irregular.

Distribution. Triassic of Eurasia, North America, and New Zealand.

Discussion. Members of this family are reminiscent of certain Unionidae in external form, very long ligament groove, and hinge configuration.

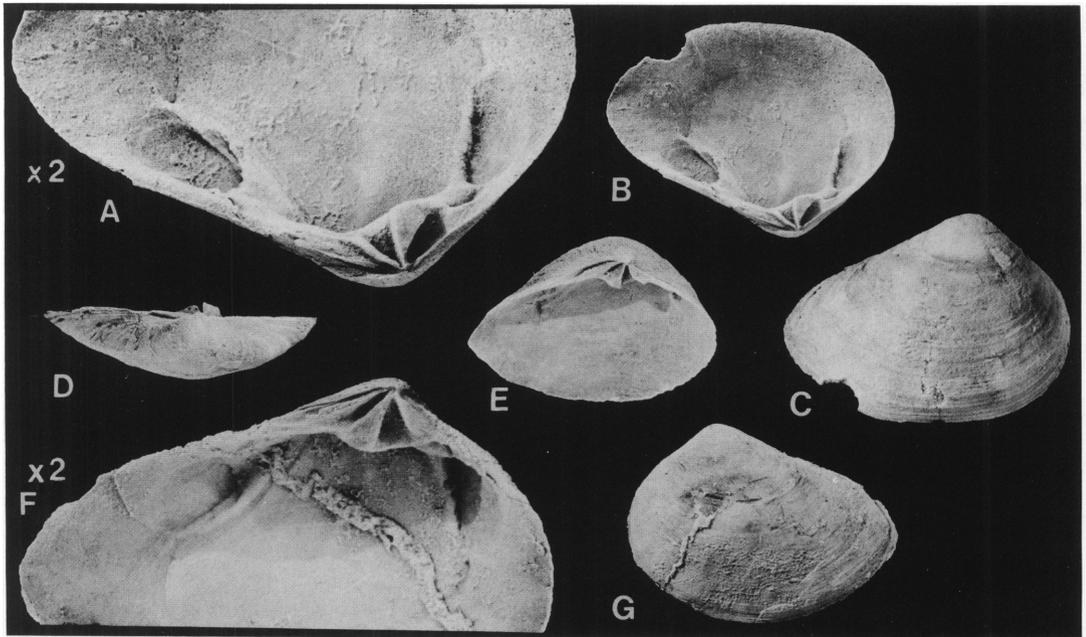


FIG. 73. *Kaibabella basilica* Newell and Boyd, new species. Silicified shells. Grandeur Member (Leonardian); Park City Formation, Wyoming. AMNH loc. 2010. A-D. Right valve. AMNH 29208. E. Left valve. AMNH 29198. F, G. Left valve. AMNH 29199.

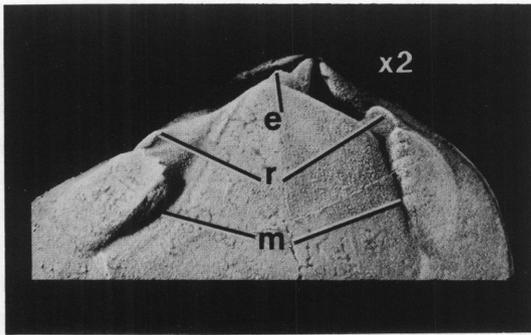


FIG. 74. *Kaibabella basilica* Newell and Boyd, new species. Latex mold of interior of right valve. Grandeur Member (Leonardian), Park City Formation, Wyoming. AMNH 29197; loc. 2010.

Abbreviations: e, pedal elevator; r, pedal retractor; m, myophorous buttresses bordering inner margins of adductors.

Little difference can be seen, for example, between the tooth arrangement of *Trigonodus* (fig. 77A, B) and that of the Triassic unionid shown in figure 24 or the modern one portrayed in figure 25C, D. Furthermore, the hinge of *Trigonodus* includes secondary subdivision of major teeth and sockets, a unionid trait. In our experience, however, two features distinguish all pachycardiids from similar unionids. The latter have a protractor scar adjacent to the posteroventral

corner of the anterior adductor, and their lateral teeth and sockets commonly do not extend to the beak area. Moreover, unionids we have examined have the anterior retractor scar either just behind the anterior adductor or at its posterodorsal corner. In pachycardiids and other trigoniaceans, this small scar typically is dorsal or anterodorsal to the large one.

Both *Trigonodus* and *Pachycardia* are listed by Cox (in Cox et al. 1969, p. 468) as brackish-water or marine forms.

GENUS PACHYCARDIA HAUER, 1857

Figures 76, 77

Type Species. *Pachycardia rugosa* Hauer, 1857, by original designation.

Diagnosis. Shells with prominent, prosogyrous umbones; maximum convexity behind beaks. Posterodorsal margin long and steeply sloping, meeting narrow respiratory margin below mid-height; ventral margin relatively straight.

Distribution. Middle-Upper Triassic. Europe.

Diagnosis. Although lacking ornamentation some valve surfaces display irregular concentric wrinkles. Compared with *Heminajas* and *Trigonodus*, *Pachycardia* exhibits a more abrupt convergence of posterodorsal and ventral margins; it has a myophorian hinge with two teeth in the right valve rather than the three of *Heminajas*. The central teeth and sockets in *Pachycardia* have neither the angular, flat faces of *Heminajas* nor the unionid-like subdivisions of *Trigonodus*.

GENUS TRIGONODUS SANDBERGER

IN ALBERTI, 1864

Figure 78

Type Species. *Trigonodus sandbergeri* Alberti, 1864, subsequently designated by Stoliczka, 1871.

Diagnosis. Smooth, elongate shells with prosogyrous beaks situated far forward. Broad respiratory margin forms very obtuse angle with posterodorsal margin. Subumbonal teeth and sockets slightly subdivided; marginal teeth very long. Retractor muscle scars circular and semi-isolated from adjacent adductor scars. Pallial line distinct, simple.

Distribution. Middle-Upper Triassic. Eurasia, North America, New Zealand.

TABLE 23
BIVARIATE STATISTICAL
CHARACTERIZATION OF
KAIBABELLA BASILICA FROM PARK
CITY FORMATION, BEAVER CREEK,
WYOMING, AMNH LOC. 2010^a

	Height Length	Convexity Height
N	124	123
\bar{x}	15.31	12.02
\bar{y}	11.95	3.55
s_x	7.92	6.18
s_y	6.21	2.10
r	0.99	0.99
OR _x	41.5	32.5
a	0.78	0.34
σ_a	0.01	0.01
b	-0.06	-0.54

^aSee page 90 for explanation of statistical parameters.

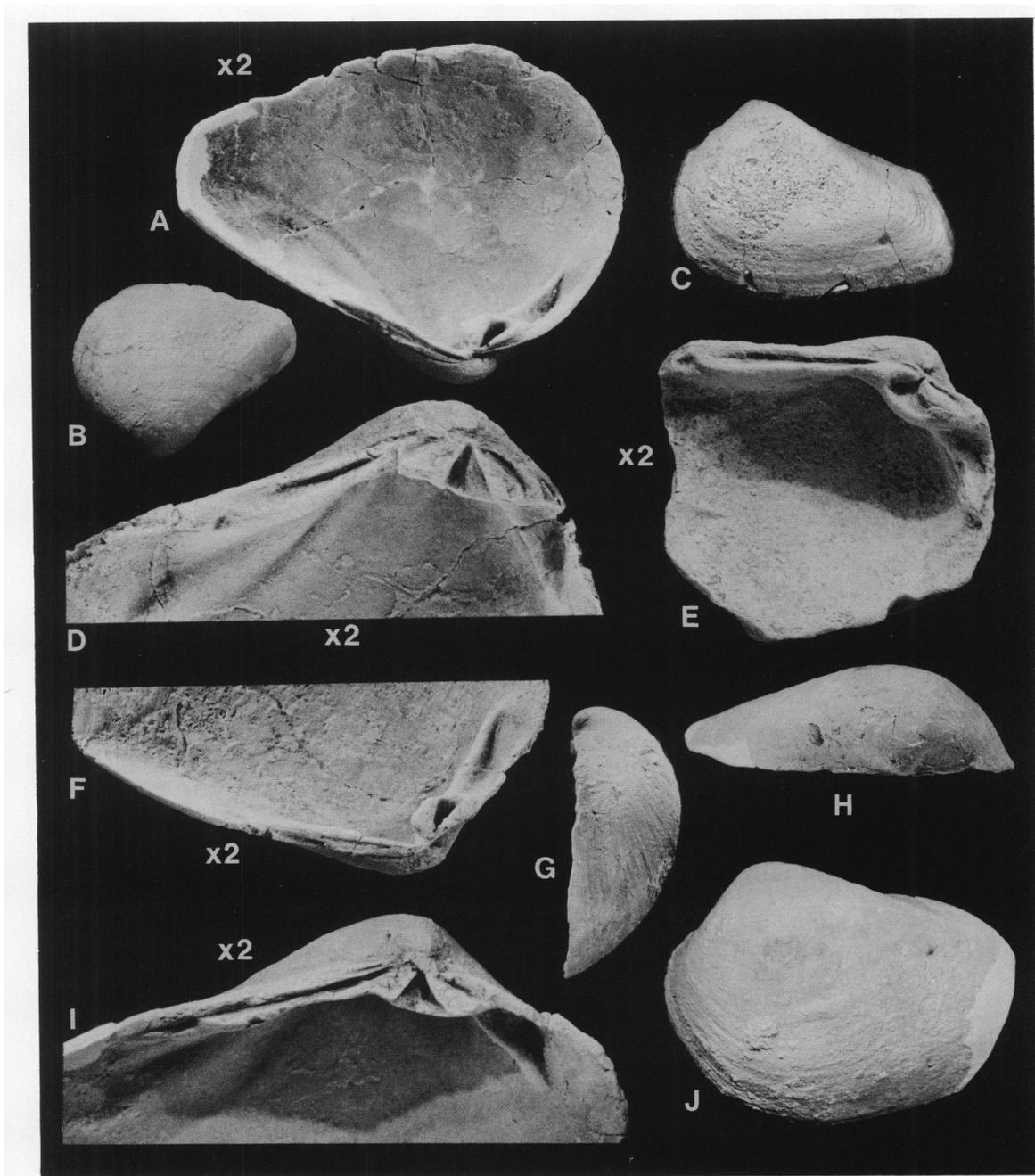


FIG. 75. *Heminajas* spp. Calcareous specimens. Middle and Upper Triassic of Italian Alps. A, B, D-J. *Heminajas fissidentata* (Wöhrmann), type species of *Heminajas*, Pachycardientuff, Seelaus, Seiser Alp, near Frombach. C. *Heminajas wohrmanni* Waagen. Raibler Schichten, Schlern Plateau. A, B. Right valve. BS 1903 IX 1000. C. Left valve. VM D 935. D. Left valve. BS 1903 IX 1002. E. Left valve. BS 1903 IX 1003. F. Right valve. BS 1903 IX 1001. G-J. Left valve. BS 1903 IX 304.

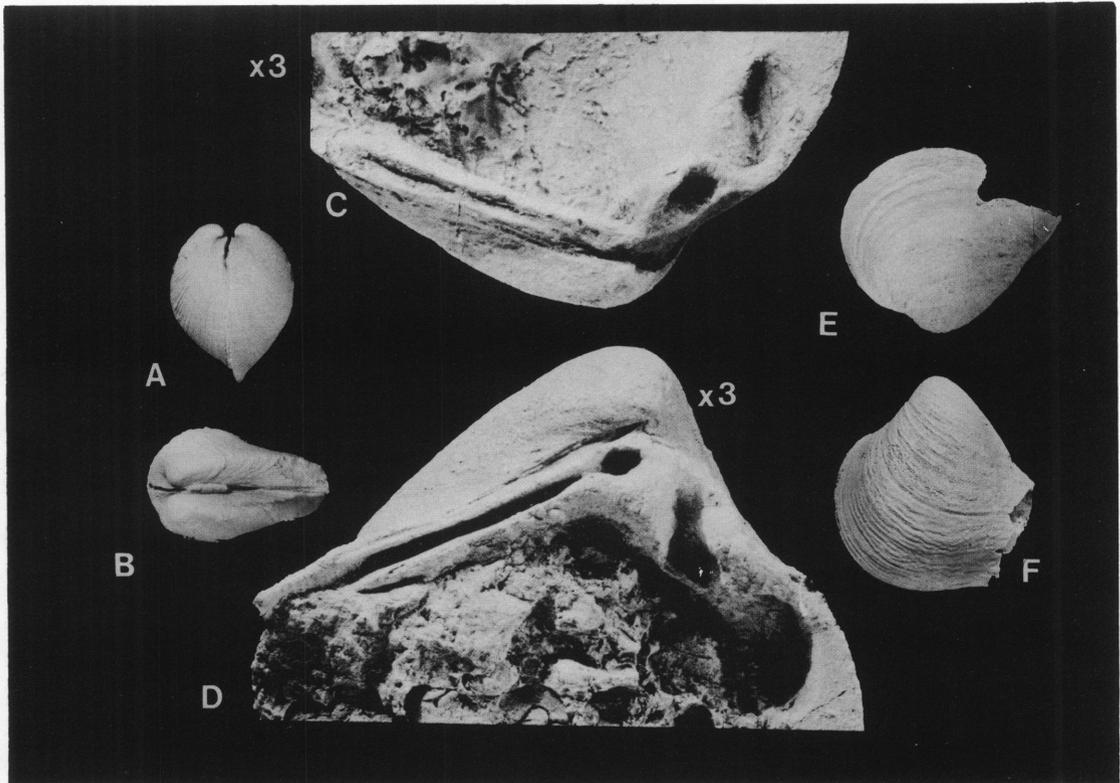


FIG. 76. *Pachycardia*. Calcareous valves. Middle Triassic of Italian Alps. A, B. *Pachycardia zitteli* Bittner. Ladinian, San Cassian, VM 1969 No. 825. C-F. *Pachycardia rugosa* Hauer, type species. C, E. Right valve. D, F. Left valve. Pachycardientuff of Tschapitbach, Seiser Alp. BS 1903.IX., respectively 279, 278.

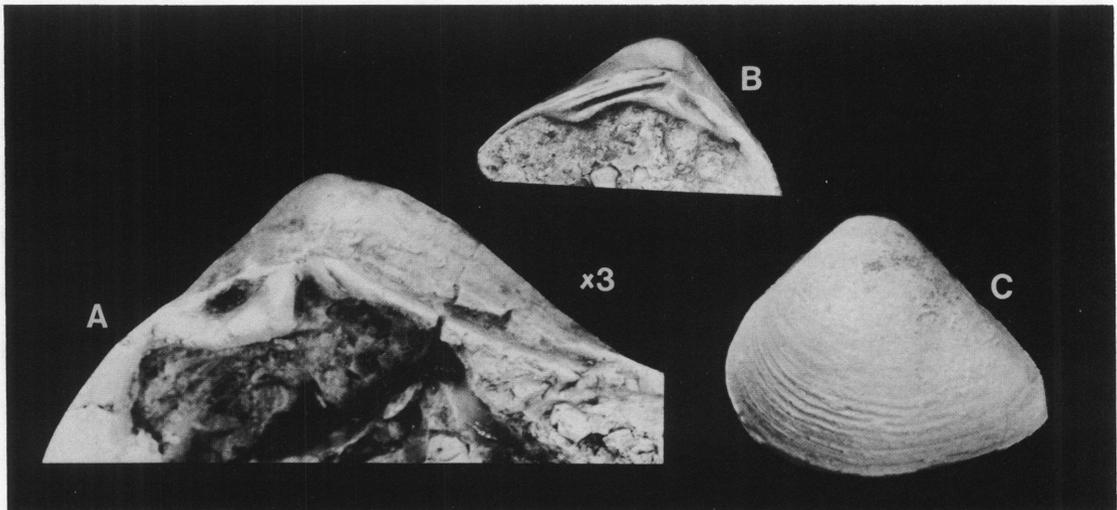


FIG. 77. *Pachycardia rugosa plieningeri* Broili. Calcareous valves. Middle Triassic (Ladinian), Frombach, Italian Alps. A. Hinge of right valve. VM 1969, 826/3. B. Hinge of left valve. VM 1969, 826/1. XI. C. Exterior of B.

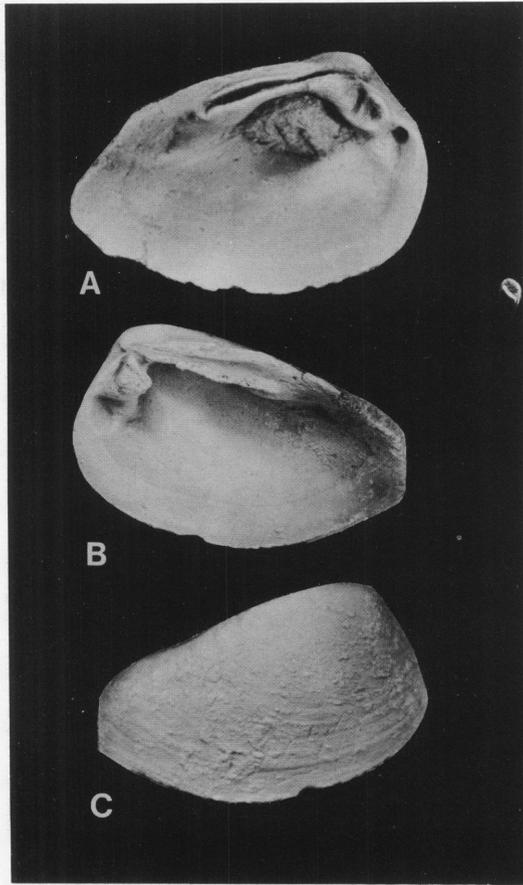


FIG. 78. *Trigonodus problematicus* (Klipstein). Calcareous shells. Upper Triassic, Raibler Schichten, Lesno brdo, Krain, northwestern Yugoslavia. A. Left valve. VM 1971, 1436. B, C. Right valve. VM 1969, 829.

Discussion. The few European valves we borrowed for study exhibit the unionid traits as discussed in our characterization of the Family Pachycardiidae. With the exception of one latex hinge whose significance we cannot assess, the long teeth beneath the posterodorsal margin extend under the beaks in typical myophorian fashion.

FAMILY MYOPHORIIDAE BRONN, 1849

Diagnosis. Mainly unornamented shells with prosogyrous to orthogyrous umbo and myophorian or trigonian hinge. Anterior myophorous buttress typically prominent.

Distribution. Lower Permian (*Paraschizodus*)-Upper Cretaceous (*Nipponitrigonia*).

Discussion. The most primitive genus of this family, *Paraschizodus*, from the Permian of the United States, is exceptional in having only a weakly developed anterior myophorous buttress like that of the Schizodidae. Transverse striations of the hinge teeth appear sporadically in several Triassic genera and apparently are well developed in all Jurassic and Cretaceous forms.

GENUS *MYOPHORIA* BRONN, 1834

Figures 79-81

Type Species. *Trigonellites vulgaris* Schlotheim, 1820, subsequently designated by Herrmannsen, 1847.

Diagnosis. Prosogyrous shells with carinate posterior ridge. Posteroventral margin concave, corselet smooth or with discontinuous costae; escutcheon lacking. Broad, shallow sulcus in front of posterior ridge, followed anteriorly by

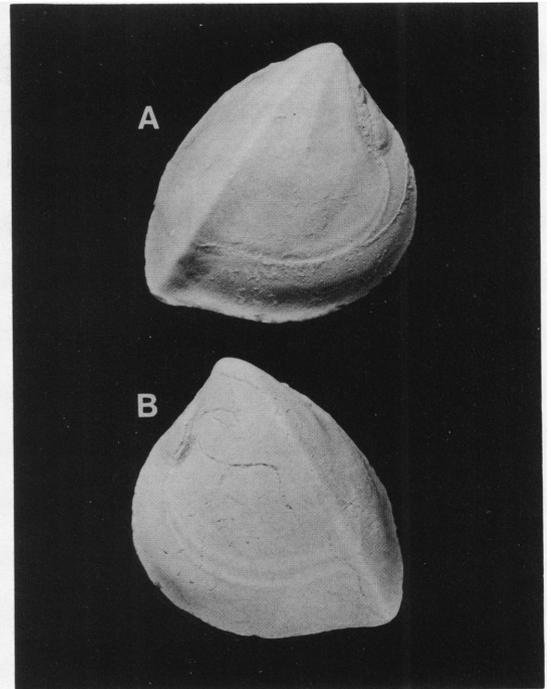


FIG. 79. *Myophoria vulgaris* (Schlotheim). One of Schlotheim's syntypes, a calcareous internal mold, selected here as lectotype. A. Right side. B. Left side. Upper Muschelkalk, Thuringia, Germany. BS, Qu. kat., p. 1102, T.1.1.

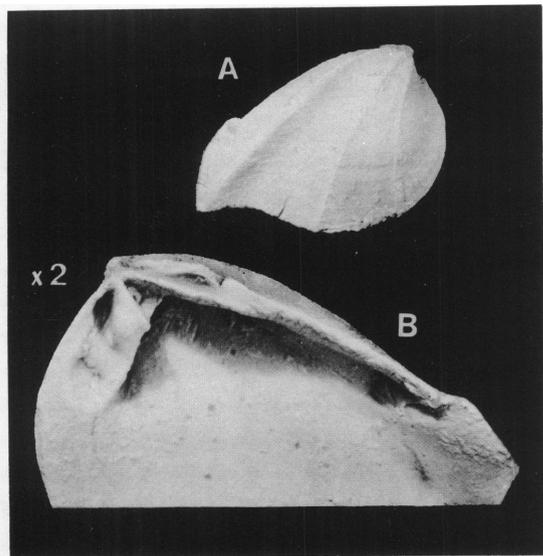


FIG. 80. *Myophoria kefersteini formalis* Waagen, Upper Triassic. Calcareous specimen from the Raibler Schichten, Lesno brdo, north-western Yugoslavia. VM 1969, No. 842.

one or two narrow costae. Myophorian hinge; main teeth smooth or with rudimentary striations.

Distribution. Middle-Upper Triassic of Eurasia and North Africa.

Discussion. We have examined several European calcareous shells and steinkerns representing *Myophoria vulgaris* (figs. 79, 81A-D), *M. kefersteini* (fig. 80), and *M. intermedia* (fig. 81E-G). One of Schlotheim's syntypes (fig. 79) is here designated as lectotype for *M. vulgaris*, the type species of *Myophoria*.

Myophoria intermedia is exceptional in possessing close-spaced concentric ornamentation (fig. 70F, G). The ridges are too fine to be comparable with the concentric ornamentation of *Lyriomyophoria*.

GENUS *NEOSCHIZODUS* GIEBEL, 1855

Figures 12C, D, 37 no. 1, 82, 83

Type Species. *Lyrodon laevigatum* Goldfuss, 1837, subsequently designated by Stoliczka, 1871; Middle Triassic of Germany.

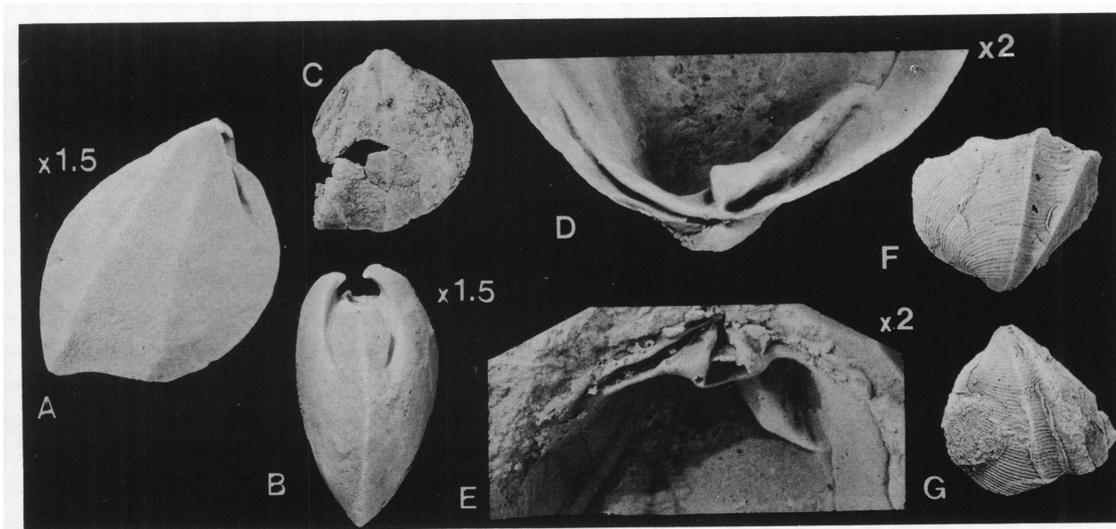


FIG. 81. *Myophoria*. Middle Triassic (upper Muschelkalk). Calcareous specimens from southern Germany. A-D. *Myophoria vulgaris* (Schlotheim), type species of *Myophoria*. A, B. Internal mold of rather oblique and asymmetrical individual. Thuringia. BS. AsVII, 380. C, D. Right valve. Lohberg, near Tonn, Thuringia. Note partial floor under large socket. MCZ 10210.1. E-G. *Myophoria intermedia* (Schauroth), characterized by concentric fine ornamentation. Trigonodus Dolomite, Württemberg. E. Latex cast of left valve from Crailsheim. TU 1415/4. F, G. Right and left valves, respectively, from Schwieberdingen. TU 1415/2, 1415/3.

Diagnosis. Orthogyrous to moderately prosogyrous shells with slightly incurved beaks. Respiratory margin obliquely truncate and pointed. Posterior ridge angular to subangular in transverse profile. Myophorian hinge; teeth and sockets smooth or bearing transverse striations.

Distribution. Middle and Upper Permian, Kitakami and Gujo formations, Japan; Lower Triassic, upper Thaynes Formation, Utah and Nevada; Middle Triassic, Muschelkalk Series, Germany.

Discussion. Several German specimens of *N. laevigatus* were borrowed for study. They are calcareous specimens with well-preserved hinges (figs. 12C, D, 82). *Eoschizodus* and *Schizodus* are similar but possess neither a posterior extension of the pivotal tooth of the left valve nor an elongate marginal tooth on the right valve, hence are not myophorian. Phylogenetic and taxonomic significance of incipient striation of the teeth in this genus are uncertain because this character seems to be quite variable within populations.

Farsan (1972) has contributed to an understanding of *Neoschizodus* and its type species.

***Neoschizodus thaynesianus* Newell and Boyd,
new species**

Figures 37 no. 1, 83

Etymology. *Thaynesianus*, from the Latin, pertaining to the Thaynes Formation.

Diagnosis. Beak near summit, approximately one-third of valve length behind anterior extremity; umbo slightly prosogyrous. Maximum convexity situated on posterior ridge. Front and rear sectors of dorsal margin rectilinear; broad respiratory margin of variable inclination. Posterior ridge subangular to rounded. Corselet very steep and slightly concave, with inconspicuous radial costa. Ligament groove length between one and two times the distance from beak to distal end of major tooth. Myophorian hinge, with anterior tooth of left valve prominent and slightly longer than triangular central tooth; posterior tooth of left valve inconspicuous, forming rim along straight ventral border of nymph; coarse transverse striations on some teeth. Anterior retractor scar forms dorsal extension of adjacent adductor scar; posterior retractor scar isolated above adjacent adductor. Pallial line indistinct, simple, about one-fifth of valve height above ventral mar-

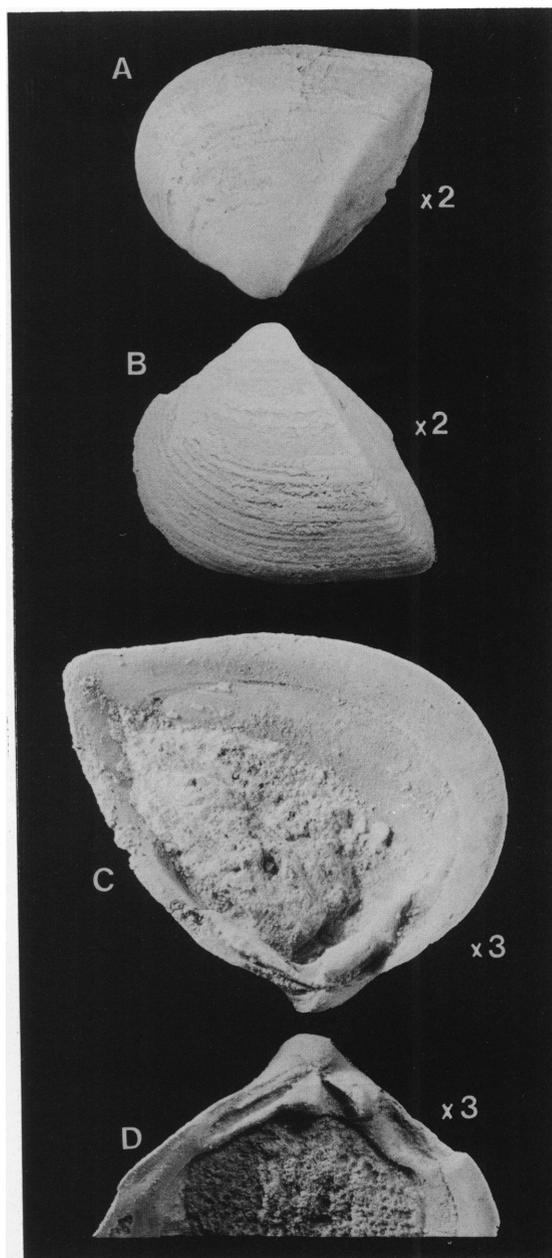


FIG. 82. *Neoschizodus laevigatus* (Goldfuss), type species of *Neoschizodus*, from Middle Triassic Schaumkalk (Lower Muschelkalk), Rüdersdorf bei Berlin, Germany. A, C. Calcareous right valve. HU M. B.-M. 5. B, D. Calcareous left valve. HU M. B.-5.1.

gin of shell. L/H=1.26 (n=13); H/C=2.86 (n=13); L/PL=2.63 (n=13).

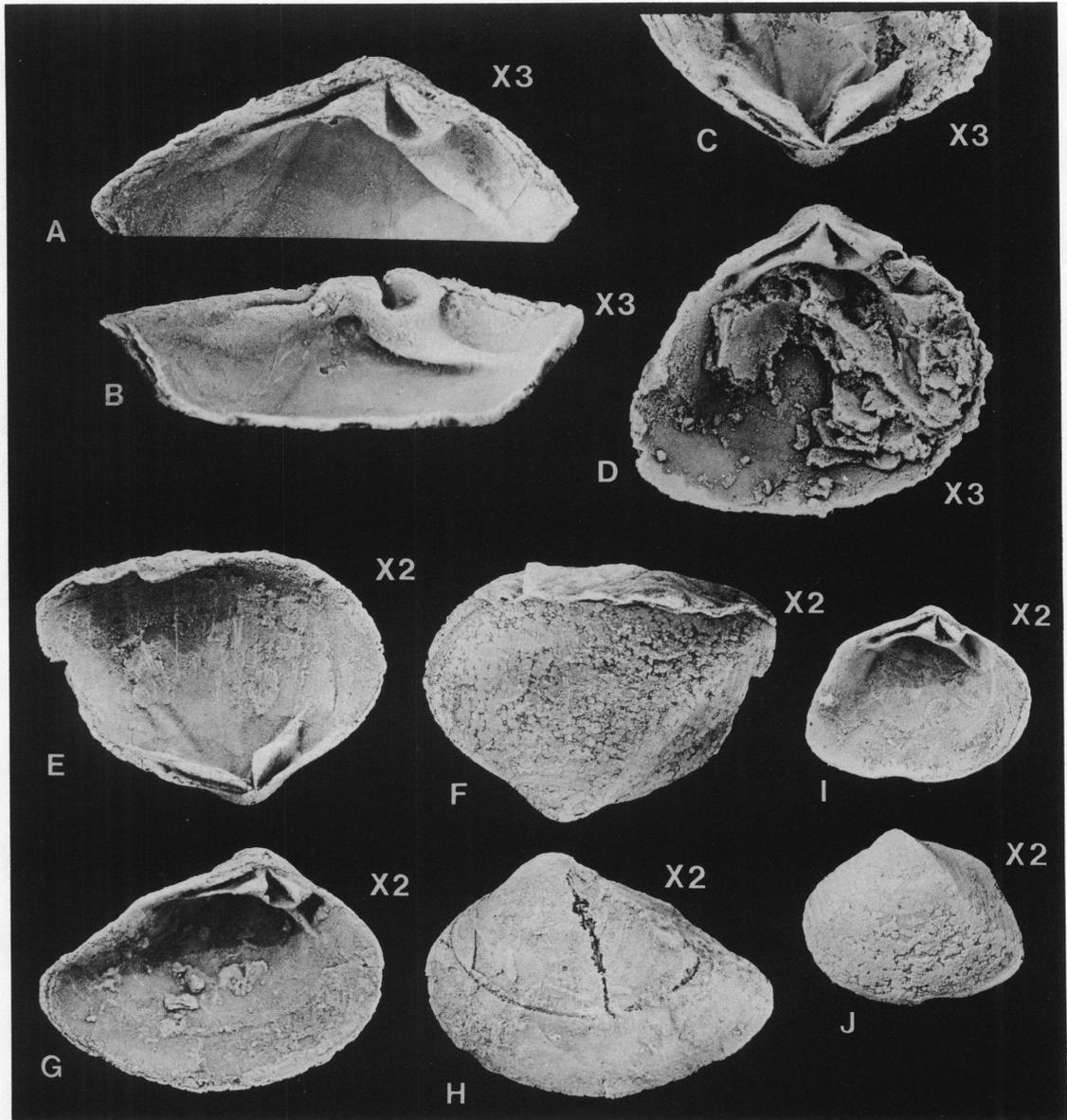


FIG. 83. *Neoschizodus thaynesianus* Newell and Boyd, new species. Silicified shells. Upper Thaynes (Owenitan), Lower Triassic, near Midland, Utah (AMNH loc. 319A). A, B. Hinge of a left valve. AMNH 29155. C. Right valve. AMNH 29156. D. Left valve with grooved median tooth. AMNH 29157. E, F. Right valve. AMNH 29159. G, H. Left valve, holotype. AMNH 29158. I, J. Left valve, with grooved median tooth, AMNH 29160.

Distribution. Lower Triassic of the Wasatch Mountains, Utah (upper Thaynes Formation). AMNH loc. 319A.

Discussion. The study collection consists of

36 silicified valves, about half of them essentially complete. Small valves typically have a smaller length-height ratio than do larger ones. Valves of similar size vary in degree of inclination of the

TABLE 24
BIVARIATE STATISTICAL
CHARACTERIZATION OF
NEOSCHIZODUS THAYNESIANUS
FROM THE UPPER THAYNES
FORMATION NEAR MIDLAND, UTAH,
AMNH LOC. 319A^a

	Height Length	Partial Length Length	Convexity Height
N	13	13	13
\bar{x}	19.15	19.15	15.23
\bar{y}	15.23	7.46	5.38
s_x	3.36	3.36	2.31
s_y	2.31	1.71	1.12
r	0.95	0.75	0.89
OR _x	24-15	24-15	20-12
a	0.69	0.51	0.48
σ_a	0.06	0.09	0.06
b	2.05	-2.29	-199

^aSee page 90 for explanation of statistical parameters.

respiratory margin and in distance at which the beak is situated behind the anterior extremity.

Tooth striations are absent in some hinges. In other cases, coarse striations are present on either the anterior face or both faces of the central tooth of left valves, and on complementary faces of right valves.

The anterior retractor scar in the left valve is subcircular due to dorsal confinement by the anterior end of the hinge plate, which also roofs it. Such restriction is not present in the right valve and the anterior retractor scar forms a finger-like extension of the anterodorsal corner of the adductor scar.

Neoschizodus thaynesianus resembles *N. laevigatus* from Germany and Afghanistan (Farsan, 1972). The American form differs in having the beak closer to the summit, a higher angle between respiratory margin and dorsal margin, and a more rounded posteroventral corner. Internally, *N. thaynesianus* has even less floor beneath the major socket of the right valve than does *N. laevigatus*, and the posteroventral corner of the central tooth in the left valve rises more sharply above the ventral border of the adjacent socket. The indistinct third (posterior) tooth in the left valve of *N. thaynesianus* is more sharply defined in some illustrations of *N. laevigatus*.

PARASCHIZODUS NEWELL AND BOYD,
NEW GENUS
Figures 84-86

Etymology. *Paraschizodus*, from the Greek *para*, near.

Diagnosis. Trigonally ovate to elongate shells with orthogyrous to slightly prosogyrous umbones, beaks near summit; maximum convexity of shell below beaks or slightly in front of beaks; marginal profile without angularity, respiratory margin poorly defined; posterior ridge and corselet indistinct; ligament groove relatively long, as much as twice the distance from beaks to distal end of major tooth; hinge of rudimentary myophorian grade, with anterior myophorous buttress weak or absent; muscles placed high in the shell; pedal retractor scars narrow, distinct, situated above the adductors.

Distribution. Permian, Upper Leonardian-Djulfian. Park City and Goose Egg formations, Wyoming; Quartermaster Formation, Texas.

Discussion. The hinge represents the minimal development of the myophorian grade, lacking consistent expression of both a third (posterior) tooth on the left valve and an anterior myophorous buttress.

A precursor and possibly ancestral combination of hinge characters is displayed by some specimens of the Middle Pennsylvanian *Schizodus ulrichi* and by the rare Upper Pennsylvanian *S. compressus* (fig. 47) in which the pivotal tooth of the left valve displays a rudimentary posterior prong, but the right valve hinge is short, as in the more characteristic schizodians. These examples are transitional between the families Schizodidae and Myophoriidae, and are somewhat arbitrarily classed here as the Schizodidae.

Paraschizodus elongatus Newell and Boyd,
new species
Figures 84, 85

Etymology. *elongatus*, from the Latin, long.

Diagnosis. Elongate ovoid shells with subdued umbones; beak markedly anterior and slightly prosogyrous. Maximum convexity slightly anterior of beak; long posteroventral and posterodorsal margins converging at low angle, bounding narrow posterior margin. Third (posterior) tooth on left valve rarely conspicuous as narrow ridge

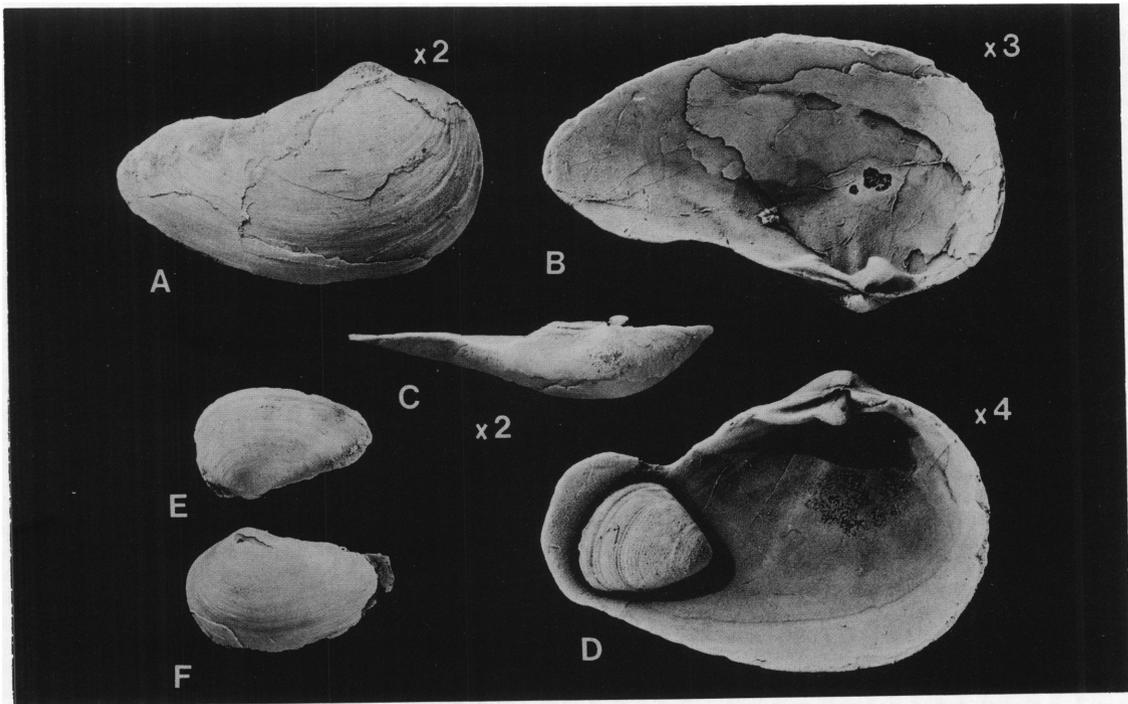


FIG. 84. *Paraschizodus elongatus* Newell and Boyd, new species. Silicified specimens. Grandeur Member, Park City Formation, Wyoming. AMNH loc. 3113. A-C. Right valve, holotype. AMNH 29173. D. Left valve, displaying myophoriid dentition, but lacking strong myophorous buttress. AMNH 29176. E. Another right valve. AMNH 29174. F. Left valve. AMNH 29175.

along ventral edge of nymph; corresponding socket on right valve, where present, forming shallow groove along base of nymph; posterior tooth of right valve long, low ridge parallel to valve margin. Posterior end of hinge exhibiting buttress-like thickening especially prominent on right valve. Anterior and posterior pedal retractor muscle scars each forming narrow groove extending dorsally from associated adductor scar, with posterior retractor equal in length to adductor scar height. $L/H=1.59$ ($n=3$); $H/C=2.61$ ($n=6$); $L/PL=3.22$ ($n=3$).

Distribution. Park City Formation (Grandeur Member) and lower Goose Egg Formation, Wyoming. AMNH loc. 3113; Red Mountain, near Laramie, Wyoming.

Discussion. Our collection from the Park City Formation is from a coquina layer in which silicification has welded adjacent specimens. We have examined about 20 hinges, but very few

complete valves could be freed from the matrix. Many specimens clearly were broken and worn before burial. Specimens from the Goose Egg Formation are steinkerns.

The ratio of shell length/height is comparable with that of *Schizodus texanus* but the hinge and details of external form are quite different. The elongate rounded lateral profile of this species readily distinguishes it from *P. rothi*.

***Paraschizodus rothi* Newell and Boyd,
new species
Figure 86**

Schizodus oklahomensis of Roth, Newell, and Burma, 1941, p. 316-317; pl. 45, figs. 2-9.

Etymology. *rothi*, named for Robert Roth who collected the type specimens.

Diagnosis. Small and trigonally ovate; maxi-

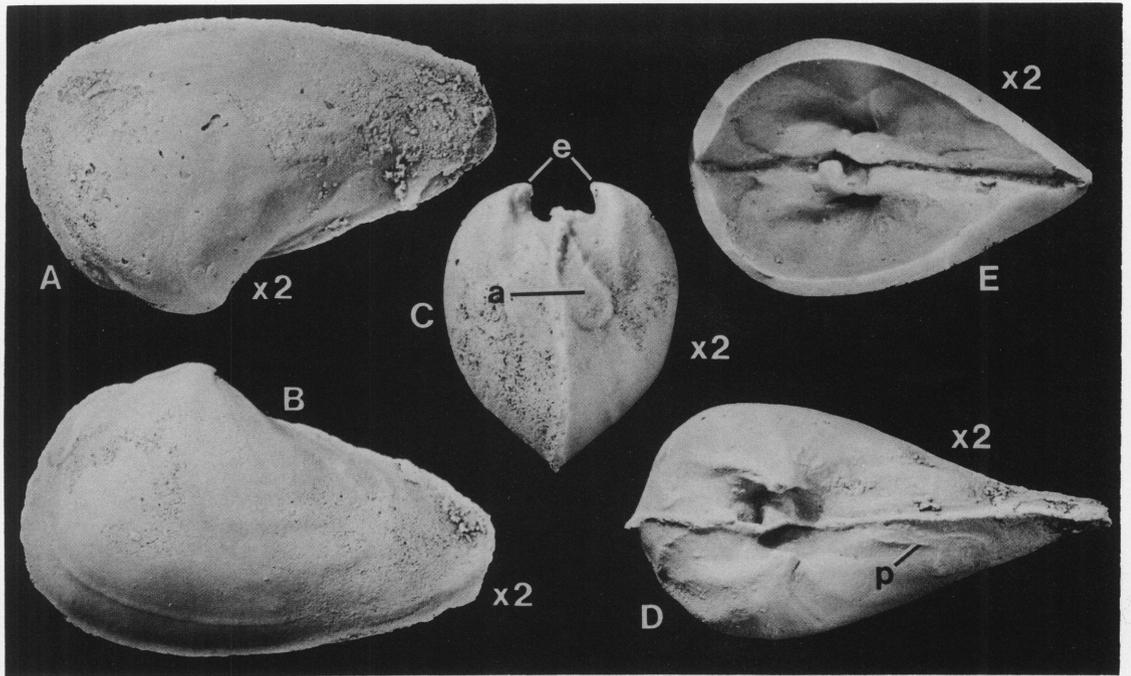


FIG. 85. *Paraschizodus elongatus* Newell and Boyd, new species. Calcareous steinkern from redbeds of lower Goose Egg Formation (Leonardian), Wyoming. Red Mountain, sect. 9, T. 12N, R. 76W, near Laramie. AMNH 29188. A-D. Views of steinkern showing musculature. E. Interior of hinge of latex cast oriented with right valve above. Hinge teeth mutilated.

Abbreviations: a, anterior adductor; e, pedal elevator; p, posterior retractor.

num convexity below beak. Posterior border slightly convex rather than truncate, meeting dorsal margin in curved rather than angular junction. Broadly rounded posterior ridge; slightly concave corselet, bisected rarely by radial costa. Traces of concentric ornamentation common but rarely developed over entire surface. Weakly developed anterior myophorous buttress in some valves. Anterior pedal retractor scar a dorsal continuation of subjacent adductor scar; posterior retractor scar weakly isolated from faint adductor scar below it. $L/H=1.29$ ($n=8$); $H/C=2.90$ ($n=7$).

Distribution. Doxey Shale, lower Quartermaster Formation (Djulifian), center of sect. 63, block E-2, D. & S. F. R. R. Survey, Briscoe Co., Texas.

Discussion. The specimens figured by Roth, Newell, and Burma (1941) were studied, together with associated material. Thirty-one valves were examined of which 12 exhibit internal features. The specimens are not silicified, but display good surface detail.

Roth and his co-authors interpreted these shells as juveniles or stunted specimens of *Lyro-schizodus oklahomensis*. However, the hinge ex-

TABLE 25
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES IN THE STUDY
COLLECTION OF *PARASCHIZODUS ELONGATUS* FROM GRANDEUR MEMBER,
PARK CITY FORMATION, BALDWIN CREEK, WYOMING, AMNH LOC. 3113

Length	Left Valves			Length	Right Valve		
	Height	Convexity	Partial length		Height	Convexity	Partial length
26	17	7	9	24	14	5	7
20	13	5	6	—	—	—	—

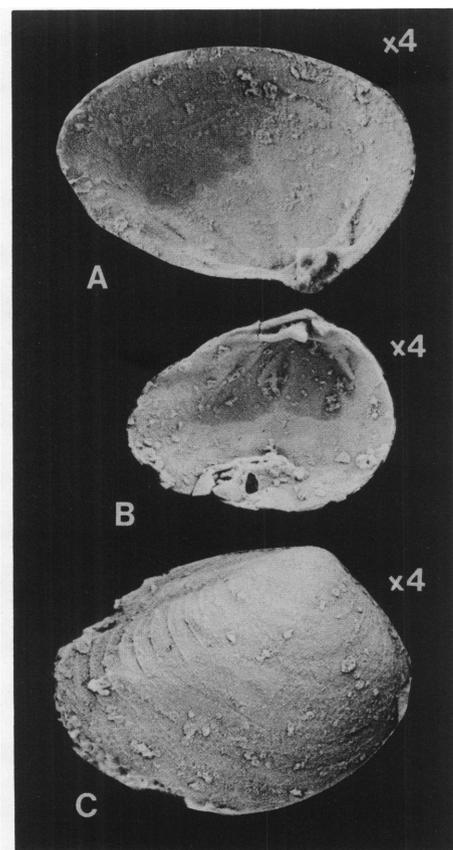


FIG. 86. *Paraschizodus rothi* Newell and Boyd, new species. Doxey Shale (Quartermaster Formation, Ochoan), Briscoe County, Texas. A. Right valve. AMNH 27503/1:1 B. Left valve, holotype. AMNH 27503/1:2. C. Right valve. AMNH 27503/1:3.

hibits the distinctive elongate posterior socket (left valve) and elongate posterior tooth (right

valve) of *Paraschizodus*. Moreover, the small anterior tooth on the left valve of *P. rothi* is less sharply set apart from the valve margin than in *L. oklahomensis*, and the floor of the right valve anterior socket extends farther ventrally (to end of adjacent tooth) in *P. rothi* than in *L. oklahomensis*. In side view, *L. oklahomensis* has more prominent umbones and a more truncate posterior. The form ratio and lateral profile of *P. rothi* readily distinguish it from *P. elongatus*.

FAMILY TRIGONIIDAE LAMARCK, 1819

Diagnosis. Annulate shells with prosogyrous to opisthogyrous beaks. Posterior ridge rounded to prominently carinate. Hinge schizodian, myophorian, or trigonian; anterior myophorous buttress lacking in primitive species. Anterior and posterior retractor muscle scars variable in shape and degree of separation from adjacent adductor scars.

Distribution. Permian through Cretaceous. Cosmopolitan.

Discussion. Permian representatives possess schizodian hinges and lack myophorous buttresses. Myophorian and trigonian hinges are represented among Triassic members of the family, whereas post-Triassic representatives all exhibit the trigonian grade. Teeth are nonstriated in primitive shells, partly striated in intermediate ones, and prominently and uniformly grooved in advanced forms.

GENUS *GRUENEWALDIA* WÖHRMANN, 1899 Figures 10, 87, 88

Type Species. *Cardita decussata* Münster, 1837, by monotypy.

TABLE 26
MEASUREMENTS (IN MILLIMETERS) OF *PARASCHIZODUS ROTHII*
FROM QUARTERMASTER FORMATION, TEXAS
(Data from Roth et al., 1941, p. 316.)

Length	Left Valves Height	Convexity	Length	Right Valves Height	Convexity
11.0	8.0	3±	12.0	9.0	3±
8.5	6.5	2.5±	12.0	9±	3±
7.5	5.5	2±	8.0	6.0	2±
—	—	—	7.0	5.0	—

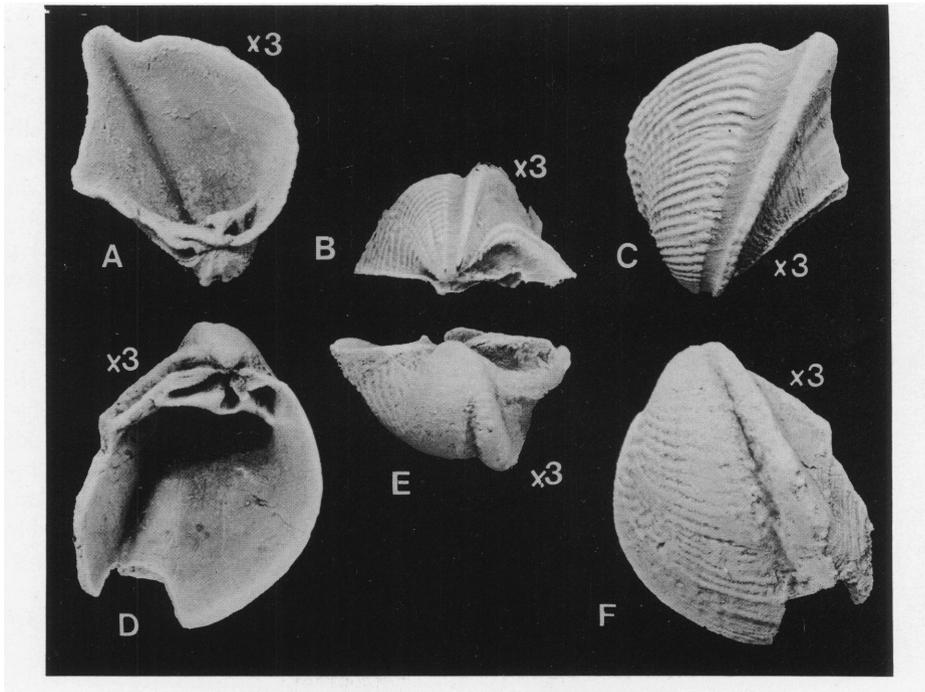


FIG. 87. *Gruenewaldia decussata* (Münster). Type species of *Gruenewaldia*. Calcareous specimens. Middle Triassic, Cassian, (Stuores Mergel). San Cassian, Italian Alps. A-C. Right valve. AMNH 29153. D-F. Left valve. AMNH 29154.

Objective Synonymy. *Elegantinia* Waagen, 1907, p. 393; *Trigomyophoria* Kobayashi, 1954, p. 66.

Diagnosis. Rhomboidal shells with prosogyrous umbones and incurved beaks. Respiratory margin concave, greater than half valve height; posteroventral margin notched, corresponding to narrow trough in front of posterior ridge. Maximum shell convexity along prominent, narrow posterior ridge. Corselet concave, subdivided by radial groove. Radial costae sparse, subordinate to concentric ornamentation. Ligament groove similar in length to distance from beak to distal end of major tooth. Myophorian hinge; major tooth of left valve commonly asymmetric with anterior face overhanging adjacent socket; transverse striations on some teeth. Anterior myophorous buttress.

Distribution. Middle-Upper Triassic. Eurasia.

Discussion. The prominent concentric ornamentation of the anterior part of a valve gives way to inconspicuous, close-spaced ridges over the sulcus, posterior ridge, and corselet. The

hinge is notable for high relief, and for steep to overturned faces of the major teeth. The posterior socket of the left valve is relatively short for the myophorian grade.

GENUS *LYRIOMYOPHORIA* KOBAYASHI, 1954

Figure 89

Type Species. *Lyriodon elegans* Dunker, 1849, by original designation.

Diagnosis. Prosogyrous shells with subdued umbones and truncate posterior. Respiratory margin greater than half valve height. Posterior ridge bounded anteriorly by narrow trough. Corselet interrupted by radial groove; concentric ridges prominent on corselet as well as flank. Ligament groove length between one and two times distance from beak to distal end of major tooth. Myophorous hinge; transverse striations on some teeth. Myophorous buttress. Anterior retractor scar forming short extension of upper corner of anterior adductor scar; posterior retractor scar circular, above adjacent adductor scar.

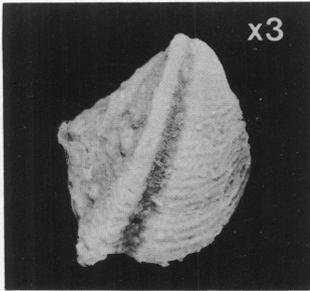


FIG. 88. *Gruenewaldia decussata* (Münster). Holotype. Calcareous specimen. Cassian (Middle Triassic), Seiser Alm, Seelaus Alp, Italian Alps. BS 1877X881.

Distribution. Triassic. Eurasia, North Africa, New Zealand.

Discussion. The posterior ridge, commonly noncarinate, is defined primarily by the break in slope related to the bordering trough.

LYROSCHIZODUS NEWELL AND BOYD,
NEW GENUS
Figures 90-93

Type Species. *Lyroschizodus orbicularis* Newell and Boyd, new species.

Etymology. *Lyroschizodus*, from the Greek *Lyra*, a lyre.

Diagnosis. Concentrically ornamented shells with schizodian dentition. Beak prosogyrous to slightly opisthogyrous. Maximum convexity below beak to slightly behind beak. Anterior profile strongly curved; posterior truncate. Posterior ridge rounded to angular in transverse profile. Corselet concave, varying in slope adjacent to posterior ridge from gentle to very steep. Ligament groove length between one and two times the distance from beak to distal end of major tooth. Anterior retractor scar forming short dorsal extension from anterodorsal corner of anterior adductor; posterior retractor scar variable in form.

Distribution. Permian, Leonardian-Guadalupean, Texas, Oklahoma, Japan.

***Lyroschizodus orbicularis* Newell and Boyd,**
new species
Figures 90, 91

Etymology. *orbicularis*, from the Latin *orbiculus*, a circle.

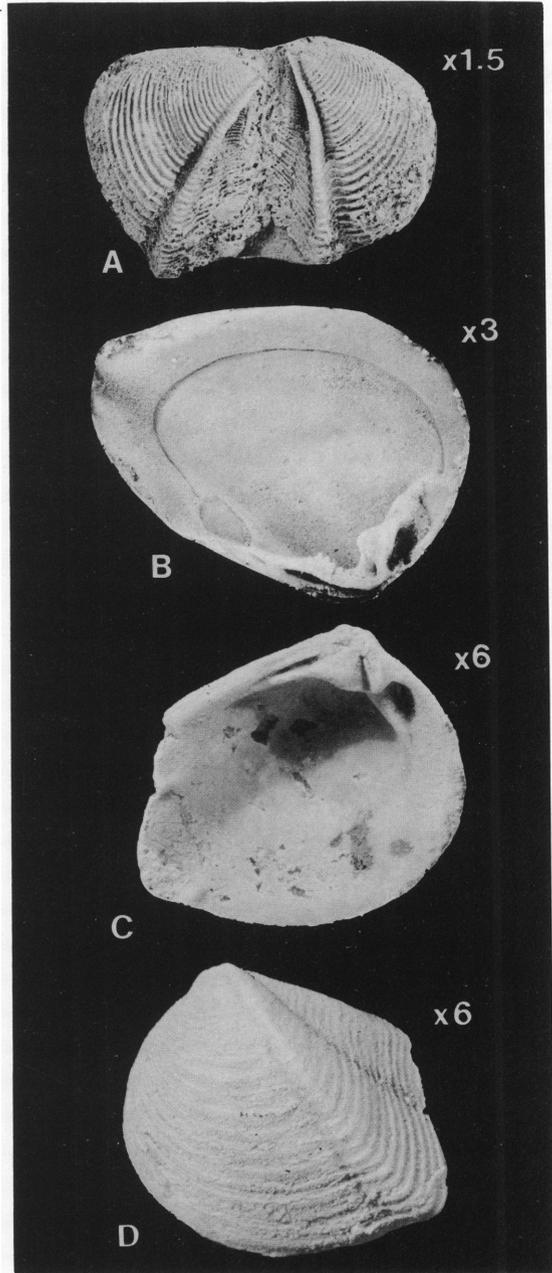


FIG. 89. *Lyriomyophoria elegans* (Dunker). Calcareous specimens of the type species of *Lyriomyophoria*. Middle Triassic of Germany. A. Paired valves of an individual. Lower Muschelkalk, Saalburg bei Bad Kösen. HU M.B.-M.3.1. B. Right valve. Schaumkalk (Lower Muschelkalk), Rüdersdorf bei Berlin. HU M.B.-M.4.4. C, D. Juvenile left valve, same locality. HU M.B.-M.4.1.

Diagnosis. Shells with height nearly equal to length; beak prosogyrous, slightly anterior of mid-length. Maximum convexity slightly posterior of beak. Anterior margin strongly convex

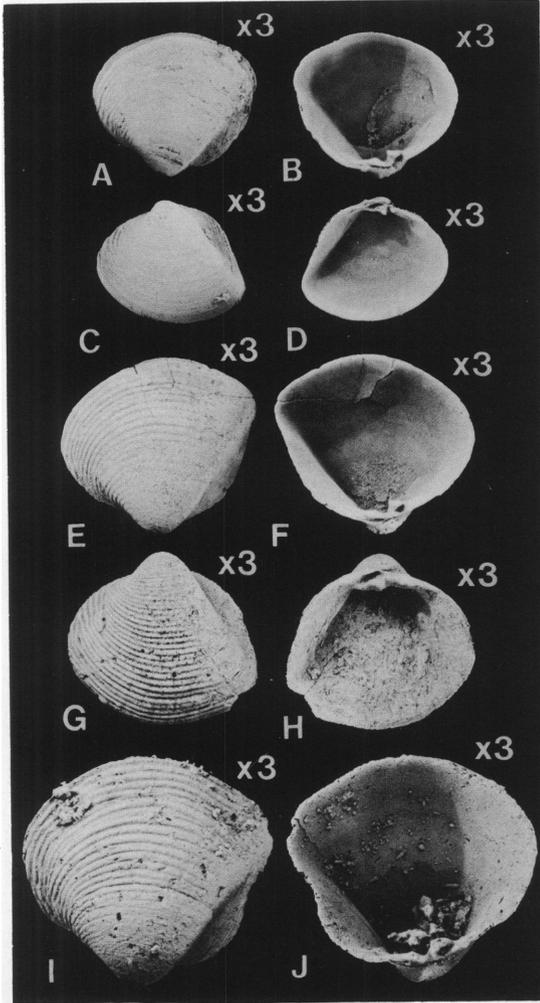


FIG. 90. *Lyroschizodus orbicularis* Newell and Boyd, new species. Silicified specimens of the type species of *Lyroschizodus*. Leonardian and Lower Guadalupian, western Texas. A, B. Right valve. Road Canyon Formation. USNM 177158; loc. 703. C, D. Left valve, displaying hardly any sculpture, same locality and horizon as A and B. USNM 177159. E, F. Right valve, same locality and horizon as A and B. USNM 177160. G, H. Left valve, holotype. China Tank Member, Word Formation. USNM 177161; loc. 726-R. I, J. Right valve, Cathedral Mountain Formation. USNM 177162; loc. 721 U.

with anterior extremity near mid-height; respiratory margin greater than half valve height. Posterior ridge sharply defined, especially angular in juvenile stage. Corselet concave, with gentle slope near valve margin but very steep adjacent to posterior ridge. Concentric ridges narrower and more closely spaced on corselet than on valve flank. Length of ligament groove nearly twice the distance from beak to distal end of major tooth. Major tooth of left valve with ventral furrow and slightly lengthened posteroventral corner; minor (posterior) tooth of right valve relatively thick and prominent for a schizodian hinge. Anterior retractor scar an extension of upper corner of anterior adductor; posterior retractor scar subcircular and isolated from subjacent adductor. $L/H=1.12$ ($n=7$); $H/C=2.99$ ($n=7$); $L/PL=2.33$ ($n=7$).

Distribution. Leonardian. Cathedral Mountain Formation and Road Canyon Formation, western Texas.

Discussion. Our small collection consists of nine silicified specimens, most of them complete, including one articulated shell. Although the concentric pattern of close-spaced, rounded ridges is typically prominent, surface relief varies within the collection and rare valves are nearly smooth.

Lyroschizodus orbicularis resembles *Schizodus supaiensis* in size and general proportions. In addition to the difference in ornamentation, *L. orbicularis* is distinguished by more angular posterior ridge, very steep corselet, and location of maximum convexity behind rather than directly below the beak. Its ligament groove is slightly longer than that of *S. supaiensis*.

The teeth of *L. orbicularis* are more robust than their counterparts in *L. oklahomensis* and *L. tobai*. The posterior ridge is more sharply defined than in *L. oklahomensis* but less angular than in the Japanese species (fig. 92).

Lyroschizodus oklahomensis (Beede, 1907)
Figure 93

Schizodus oklahomensis Beede, 1907, p. 157, pl. 7, fig. 6.

Diagnosis. Beak slightly opisthogyrous, about one-third valve length behind anterior extremity. Maximum convexity below beak. Respiratory margin slightly less than half valve height. Posterior ridge rounded. Corselet sloping gently away

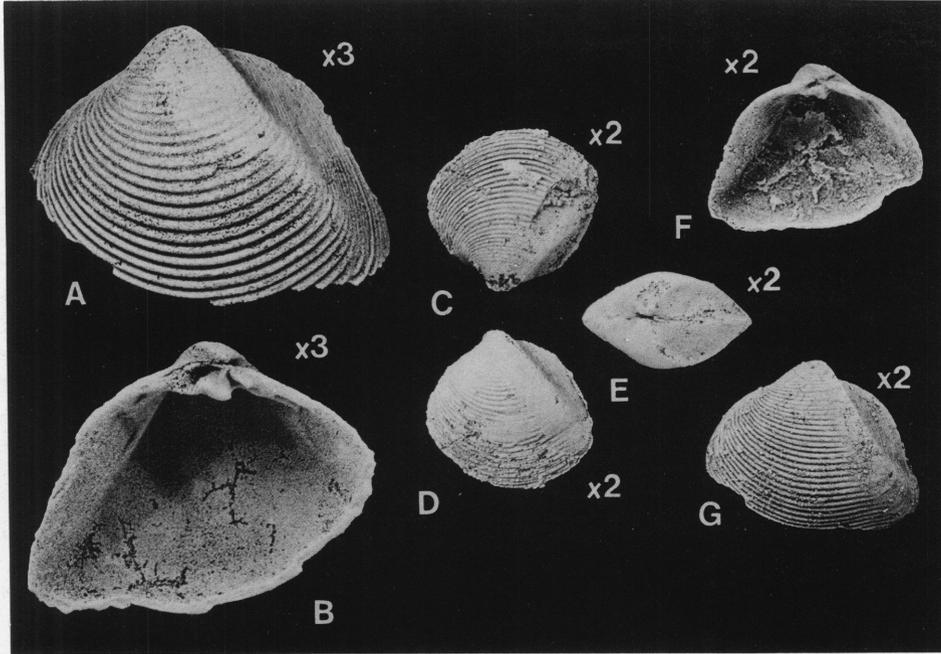


FIG. 91. *Lyroschizodus orbicularis* Newell and Boyd, new species. Silicified specimens. Road Canyon Formation (Upper Leonardian), Glass Mountains, western Texas. A, B. Left valve. USNM 177164; loc. 703. C, D, E. Bivalved specimen. AMNH 29189; loc. 369. F, G. Left valve. AMNH 29190; loc. 592.

from posterior ridge and slightly concave, bisected by obscure, radial costa. Ornamentation consisting of concentric ridges, relatively indistinct on corselet. Major tooth on each valve typically notched by ventral furrow. Muscle scars poorly defined. L/H=1.34 (n=4); H/C=3.69 (n=4).

Distribution. Lower Guadalupian. Whitehorse Formation (Dozier Member), Oklahoma and Texas.

Discussion. Our small collection of *Lyroschizodus oklahomensis* consists of the few molds

and replicas previously studied by Newell (1940). Their concentric ornamentation is weak compared with other species of *Lyroschizodus*, and it is possible the poorly developed annular pattern reflects tidal influence or other environmental control on a *Schizodus* population. However, we think the weakness is likely a result of poor preservation.

Beede's original description provided no information on internal features, but cited posterior ridge, truncate posterior outline, and obtuse angle formed at the junction of posterior and

TABLE 27
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES OF
LYROSCHIZODUS ORBICULARIS NEWELL AND BOYD, NEW SPECIES
FROM WESTERN TEXAS^a

Length	Height	Left Valves		Length	Height	Right Valves	
		Convexity	Partial Length			Convexity	Partial Length
12.8	11.6	4.2	5.6	11.0	10.0	3.7	5.2
11.3	10.8	3.2	4.8	9.4	8.2	2.7	3.9
6.7	5.5	1.7	2.7	8.8	7.8	2.6	3.7
—	—	—	—	7.2	6.5	2.3	3.2

^aLargest left valve is from China Tank Member, Word Formation. Largest right valve is from Cathedral Mountain Formation. Others are from Road Canyon Formation.

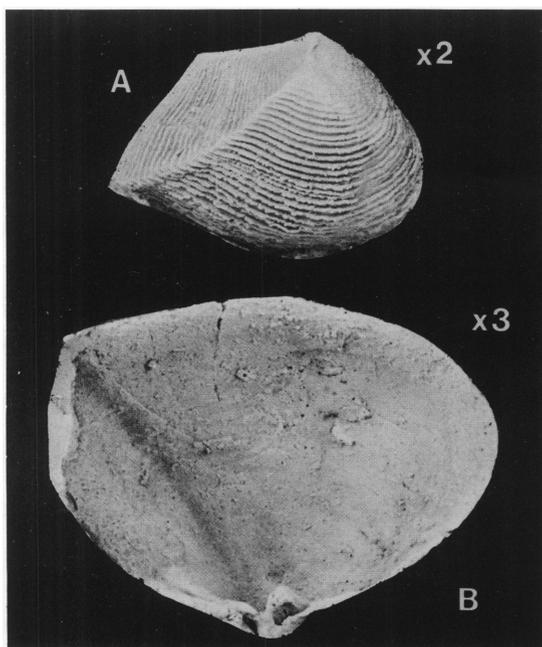


FIG. 92. *Lyroschizodus tobai* (Hayasaka). Latex casts of single right valve. Permian, Lower Kanakura Formation, Shigejizawa Member (Guadalupian), at Kamiyassa, Kessennuma City, northeast Japan. A. Exterior. KIJ JP 10051B B. Interior. JP 10051A.

dorsal margins as features characteristic of the species. Beede also noted prominent beaks and ornamentation in the form of "heavy undulations" on the convex part of the shell.

Newell (1940) supplemented Beede's characterization with a discussion of better material from the Whitehorse Formation. He noted that the holotype is abnormally long relative to height. The weakly developed buttress he reported is an anterior thickening of the hinge plate where it joins the valve interior at the dorsal margin of the anterior adductor scar. It does not extend ventrally along the scar.

Specimens from the Quartermaster Formation of Texas assigned to this species by Roth, Newell, and Burma (1941) are unique in several important features. The Quartermaster material is described in the present study as *Paraschizodus rothi*.

Newell (1940, p. 293) noted similarity in external appearance of *Lyroschizodus oklaho-*

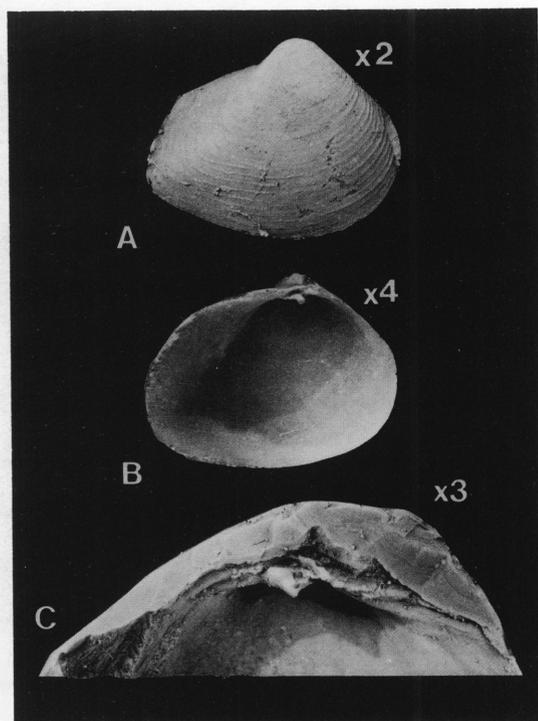


FIG. 93. *Lyroschizodus oklahomensis* (Beede) from Dozier Member, Whitehorse Formation (Guadalupian). A. Latex cast of right valve. Naco Butte (Mt. Nebo), 3 miles west of Estelline, Hall County, Texas. AMNH 27525. B. Wax cast of smaller left valve. Southwestern Collingsworth County, Texas, sect. 43, Block 19, H. G. and N. Survey. AMNH 29288. C. Wax cast of hinge of right valve. Naco Butte (Mt. Nebo), 3 miles west of Estelline, Hall County, Texas. AMNH 29287.

mensis with *Schizodus praecox* (Waagen) from Permian strata of the Salt Range. His illustration of one of Waagen's specimens shows a valve of greater height, more uniform anterior curvature, and more strongly curved ventral margin than is typical of *L. oklahomensis*. He noted that Waagen did not provide adequate information to allow a comparison of hinges in the two species.

COSTATORIIDAE NEWELL AND BOYD, NEW FAMILY

Diagnosis. Shells with radial ribs. Umbo prominent to inconspicuous. Respiratory margin broad. Posterior ridge bearing either prominent

TABLE 28
MEASUREMENTS (IN MILLIMETERS) OF *LYROSCHIZODUS OKLAHOMENSIS*
 (Data from Newell, 1940, p. 291.)

Length	Left Valves Height	Convexity	Length	Right Valve Height	Convexity
23	17	4	18	14	4
16.5	12	3	—	—	—
12	9	3	—	—	—

keel, or plica similar to others in front of it. Hinge schizodian, myophorian, or trigonian; myophorous buttress absent, rudimentary, or well developed.

Distribution. Permian (United States, Japan)-Mesozoic (cosmopolitan); Miocene, Recent (Australia).

Discussion. Primitive forms have schizodian dentition, no myophorous buttresses, and as few as two radial ribs. Advanced forms have myophorian or trigonian hinges, myophorous buttresses, and numerous plicae.

GENUS *COSTATORIA* WAAGEN, 1906
 Figures 9, 94, 95

Type Species. *Donax costata* Zenker, 1833, subsequently designated by Nakazawa, 1960.

Diagnosis. Plicate shells with slightly prosogyrous beak; umbo inconspicuous. Posterior ridge marked by plica comparable in relief to those in front of it. Corselet bearing one or more well-defined radial costae. Ligament groove length between one and two times distance from beak to distal end of major tooth. Hinge myophorian; major teeth with or without transverse striations. Anterior myophorous buttress well developed.

Distribution. Permian, Capitanian, and Djulfian, Japan; Triassic (cosmopolitan).

PROCOSTATORIA NEWELL AND BOYD,
NEW GENUS
 Figures 37 no. 8, 96-98

Type Species. *Deltopecten sexradiata* Branson, 1930.

Etymology. *Procostatoria* from the Latin, *pro-*, before; *costatoria*, condition of being ribbed.

Diagnosis. Beak orthogyrous to prosogyrous;

maximum convexity posterior of beak, typically along posterior ridge. Respiratory margin equal to half or more of valve height. Posterior ridge keeled. Corselet steep, flat to concave. One or more plicae in front of posterior ridge. Ligament groove short, approximately equal to distance

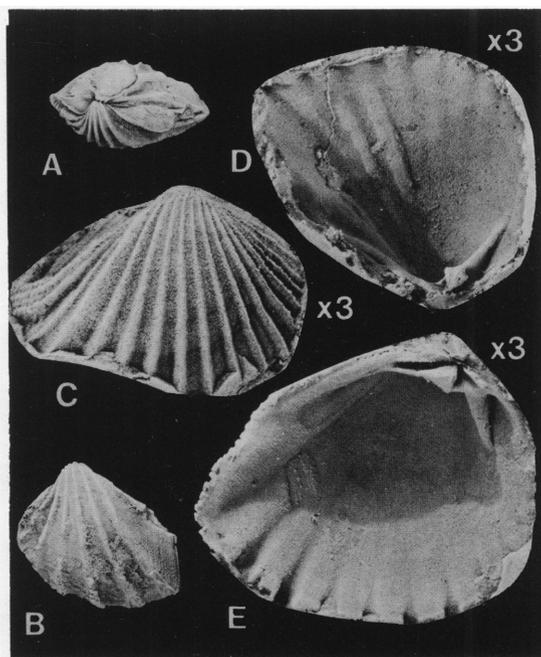


FIG. 94. *Costatoria* spp. Middle Triassic, Europe. A, B. *Costatoria harpa* (Münster). Cassian, Cortina d'Ampezzo, Italian Alps. AMNH 29151. C, D. *Costatoria goldfussi* (Alberti). Latex casts of right valve. Upper Muschelkalk (*Trigonodus Dolomit*), Rothenmünster, Württemberg, Germany. HU, B p. 221, no. 204, coll. Alberti. E. Same species as C and D, latex cast of left valve showing myophorian hinge. Upper Muschelkalk, Zimmern bei Rottweil, Germany. TU 1415/1.

from beak to distal end of major tooth. Dentition schizodian. Anterior myophorous buttress absent or rudimentary. Anterior retractor muscle scar forming narrow extension of upper corner of anterior adductor scar; posterior retractor scar elongate and isolated from subjacent posterior adductor.

Distribution. Permian, Upper Leonardian-Lower Guadalupian; western Texas and Wyoming.

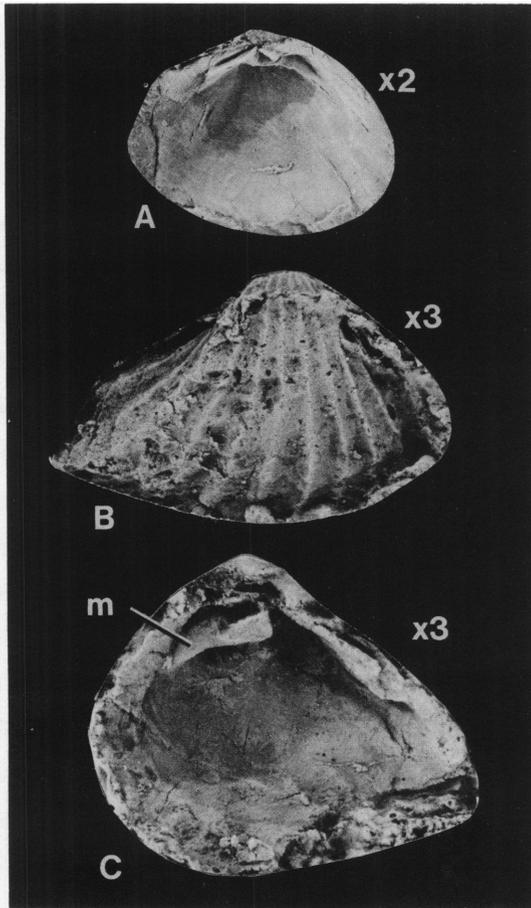


FIG. 95. Upper Permian *Costatoria* from Japan, latex casts from silty shale molds. A. Left valve of *Costatoria kobayashii* Kambe. Gujo Formation, at Gujo, Oe-cho, near Kyoto, Japan. AMNH 29152. B, C. Right valve of *Costatoria katsurensis* Nakazawa. Katsura Formation, Katsura, Sakawa-cho, Kochi Prefecture, Japan. KUP JP 10156.

Abbreviation: m, myophorous buttress.

Discussion. *Procostatoria* is distinguished by the combination of schizodian hinge and plicate ornamentation. The number of plicae per valve varies within the genus from two (including the keeled posterior ridge) to 13. The ligament groove is distinctively short considering its association with robust hinge teeth. Its modest length is particularly noteworthy in the more elongate shells.

Procostatoria sexradiata (Branson, 1930)

Figure 96

Deltopecten sexradiata Branson, 1930, p. 50, pl. 11, figures 1, 2.

Diagnosis. Height equal to length in small valves, but conspicuous posteroventral elongation in large specimens. Beak orthogyrous, well below valve summit; umbo prominent. Anterior margin relatively straight; posteroventral corner projecting beyond adjacent part of ventral margin. Posterior ridge bearing high keel more prominent than other plicae. Corselet very steep, concave. Ornamentation consisting of several plicae in front of keeled posterior ridge; faint concentric ridges on anterior flanks. $L/H=1.19$ ($n=3$); $H/C=2.48$ ($n=3$); $L/PL=3.26$ ($n=3$).

Distribution. Guadalupian. Word Formation (China Tank Member), western Texas; Park City Formation (Franson and Ervay members), Wyoming; ? Shedhorn Sandstone, Montana. USNM loc. 706c.

Discussion. Our study collection from western Texas includes 18 silicified valves of which only three are complete. The few Wyoming specimens previously described by Branson (1930, p. 50) and Ciriacks (1963, p. 63) are internal molds.

In our collection, plicae in front of the keeled posterior ridge vary in number from five to six. Ciriacks reported a total of five to seven plicae on the Wyoming molds, with the exception of one specimen with about 10.

Procostatoria cooperi Newell and Boyd,

new species

Figure 97

Etymology. *cooperi*, named in honor of Dr. G. Arthur Cooper, discoverer and collector of the type specimens.

Diagnosis. Radial ornament consisting of two keels, more prominent one forming crest of angular posterior ridge and second terminating at an-

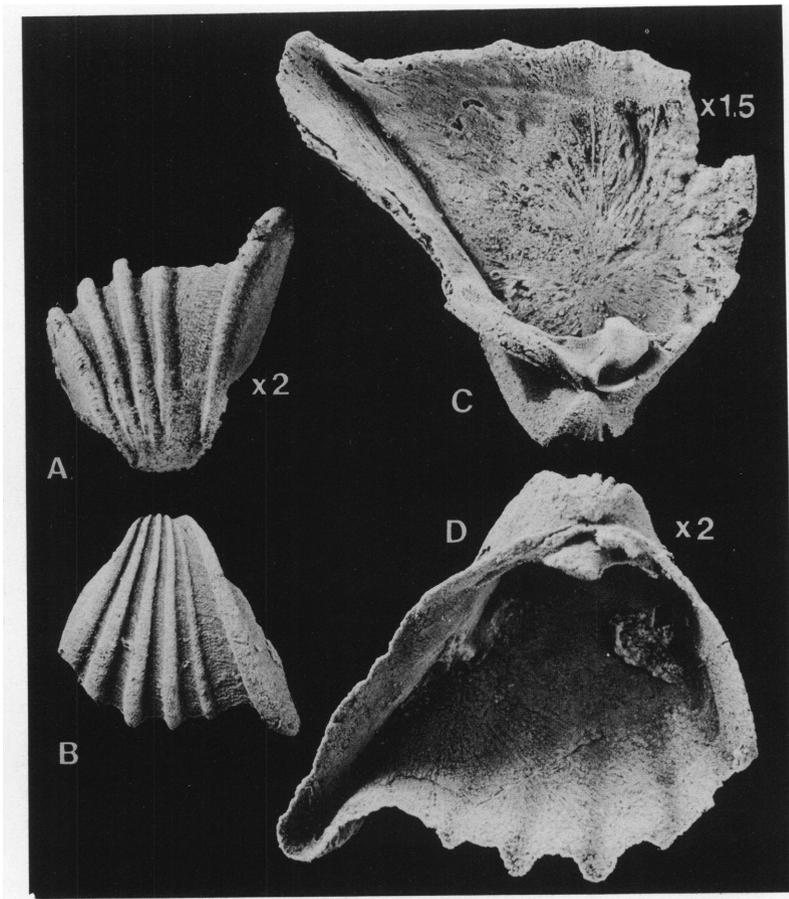


FIG. 96. *Procostatoria sexradiata* (Branson), type species of *Procostatoria* Newell and Boyd, new genus. Silicified specimens. China Tank Member, Word Formation, USNM loc. 706c. A. Right valve. USNM 177172. B, D. Left valve; note schizodian hinge and essential lack of myophorous buttresses. USNM 177167. C. Right valve. USNM 177168.

teroverventral corner. Beak in anterior third of valve, strongly incurved, orthogyrous. Umbo prominent, bounded by steep anterior and posterior flanks. $L/H=1.27$ ($n=3$); $H/C=2.76$ ($n=3$); $L/PL=3.64$ ($n=3$).

Distribution. Upper Leonardian-Lower Gua-

dalupian. Road Canyon Formation, western Texas; Park City Formation (Franson Member), Wyoming. USNM locs. 703, 703c, 726d.

Discussion. Our collection of silicified specimens consists of three essentially complete valves and six incomplete ones. *Procostatoria cooperi* is

TABLE 29
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES IN THE STUDY COLLECTION OF *PROCOSTATORIA SEXRADIATA* FROM CHINA TANK MEMBER, WORD FORMATION, TEXAS, USNM LOC. 706c

Length	Height	Left Valve		Length	Height	Right Valves	
		Convexity	Partial length			Convexity	Partial length
32	28	10	10	43	35	14	12
-	-	-	-	18	15	7	6

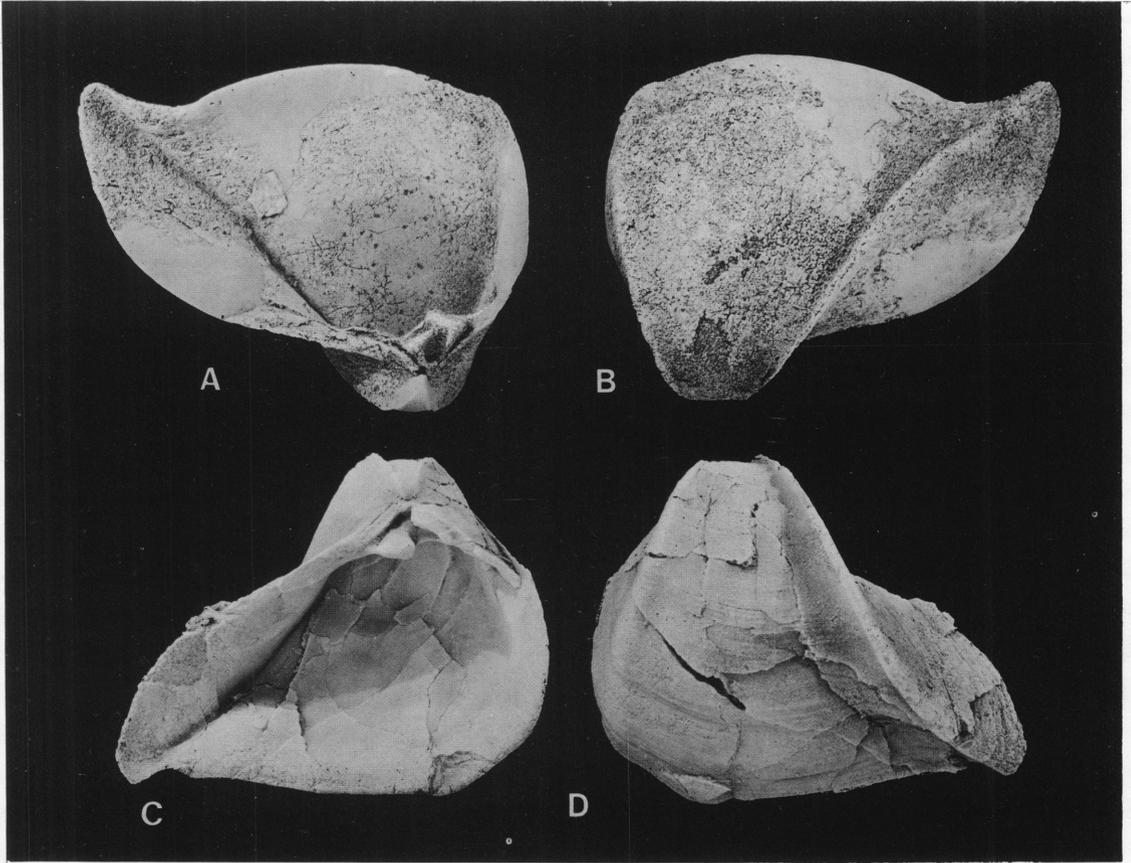


FIG. 97. *Procostatoria cooperi* Newell and Boyd, new species. Silicified right and left valves, respectively. USNM 177170; loc. 703 and 177171; loc. 703c. Road Canyon Formation (Upper Leonardian), Glass Mountains, Texas.

distinguished from *Schizodus canalis* by its anterior radial ridge. Moreover, its posterior keel is more prominent than that of most specimens of *S. canalis*, and its umbonal flanks are higher and steeper, especially the anterior one, than typical of *S. canalis*. The very short ligament groove of *P. cooperi* is a striking feature considering the size and elongation of the shell.

***Procostatoria gloveri* Newell and Boyd,
new species
Figures 37 no. 8, 98**

Etymology. *gloveri*, named in honor of the late Mr. Walter Glover of Pine Springs Camp, Delaware Mountains, West Texas.

Diagnosis. Small, plicate shells. Prosogyrous

**TABLE 30
MEASUREMENTS (IN MILLIMETERS) OF COMPLETE VALVES IN THE STUDY COLLECTION
OF *PROCOSTATORIA COOPERI***

(Specimens are from Road Canyon Formation, Texas, USNM Locs. 703, 703c.)

Length	Left Valve			Right Valves			
	Height	Convexity	Partial length	Length	Height	Convexity	Partial length
50+	40	13	14	59	46	17	15
—	—	—	—	58	45	18	17

beak not far below valve summit; umbo inconspicuous. Anterior margin strongly curved; respiratory margin broad, gently inclined, forming very obtuse angle at junction with short dorsal mar-

gin. Posterior ridge marked by plica little more conspicuous than those in front of it. Corselet bearing prominent radial costa near posterior ridge; second, inconspicuous costa commonly

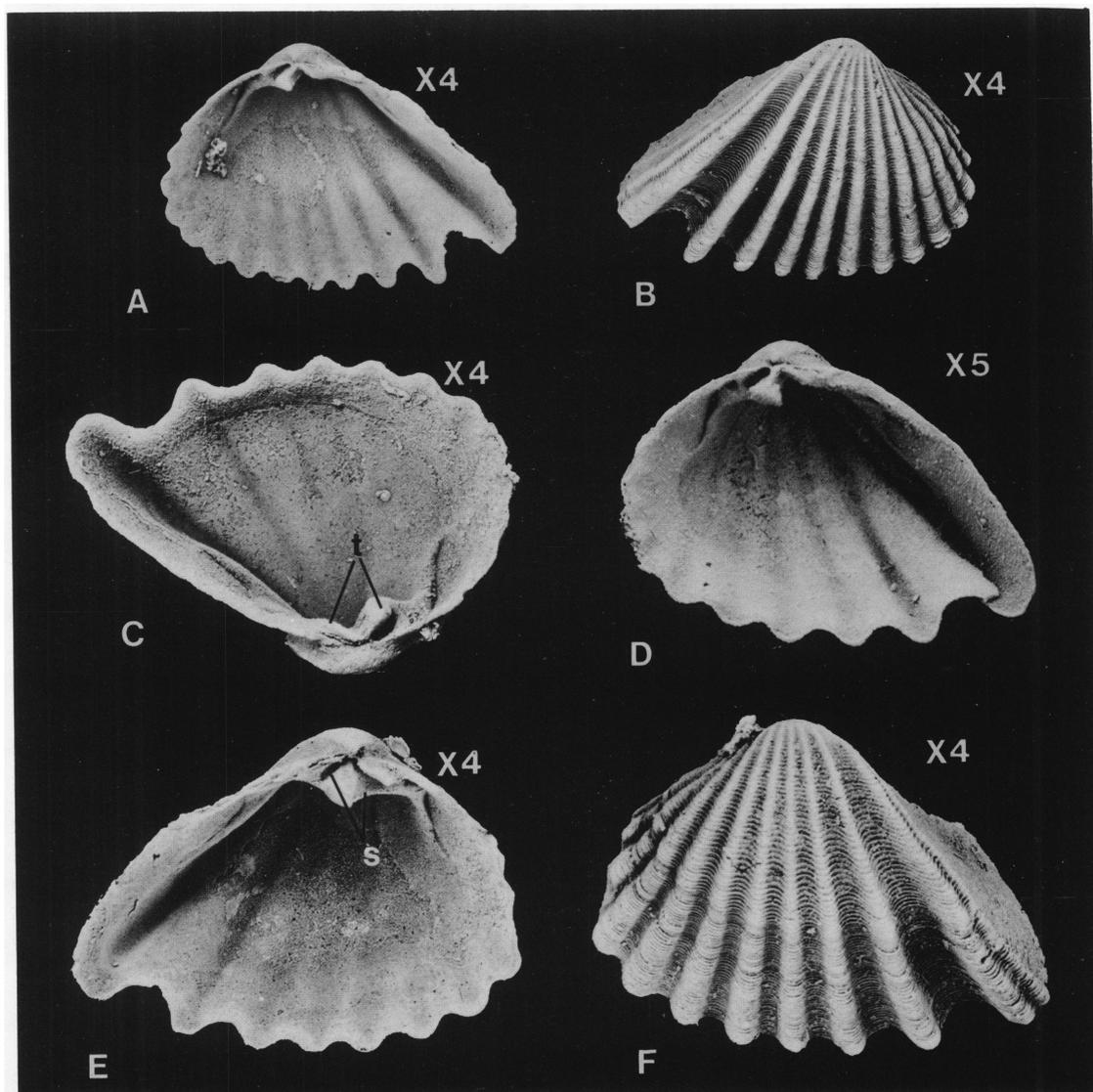


FIG. 98. *Procostatoria gloveri* Newell and Boyd, new species. Silicified specimens. Lower Getaway Limestone, Middle Guadalupian (= Willis Ranch Member, Word Formation), Guadalupe Mountains, Texas, AMNH loc. 512. A, B. Right valve. AMNH 29161. C. Right valve. AMNH 29162. D. Right valve. AMNH 29163. E, F. Left valve, holotype showing weak myophorous buttresses, and schizodian hinge. AMNH 29164.

Abbreviations: s, sockets; t, teeth.

present. Ornamentation consisting of 10 to 13 prominent plicae with superimposed concentric pattern of tiny, close-spaced terraces. Rudimentary anterior myophorous buttress. $L/H=1.36$ ($n=19$); $H/C=2.66$ ($n=19$); $L/PL=2.62$ ($n=19$).

Distribution. Lower Guadalupian. Lower Getaway Limestone, Word Formation, limestone lens between Willis Ranch and Appel Ranch members; Appel Ranch Member, western Texas. AMNH loc. 512; USNM locs. 706b, 706d.

Discussion. Our study collection consists of 38 silicified valves, half of them complete. In general shape and ornamentation, the specimens resemble typical representatives of *Costatoria*. However, the hinge of *P. gloveri* is schizodian. Although it has a floor under the greater part of the major socket of the left valve, it lacks the third (posterior) tooth on that valve, elongation of the posterior tooth on the right valve, and corresponding socket characteristics. The weak anterior myophorous buttress extends ventrally only part way along the posterior margin of the anterior adductor scar.

TABLE 31
BIVARIATE STATISTICAL
CHARACTERIZATION OF
PROCOSTATORIA GLOVERI
FROM LOWER GETAWAY LIMESTONE,
TEXAS, AMNH LOC. 512^a

	Height Length	Partial Length Length	Convexity Height
N	19	19	19
\bar{x}	14.21	14.21	10.53
\bar{y}	10.53	5.47	3.95
s_x	2.18	2.18	2.12
s_y	2.12	1.02	0.71
r	0.96	0.88	0.95
OR _x	18-11	18-11	14-8
a	0.97	0.47	0.33
σ_a	0.06	0.05	0.02
b	-3.31	-1.19	0.44

^aSee page 90 for explanation of statistical parameters.

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