

PECTINOID BIVALVES OF THE
PERMIAN-TRIASSIC CRISIS

NORMAN D. NEWELL AND DONALD W. BOYD

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PECTINOID BIVALVES OF THE PERMIAN-TRIASSIC CRISIS

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ABSTRACT

This contribution concludes a general revision of genera of pectiniiform bivalves (pectinoids) of the world's marine rocks near the Permo-Triassic boundary. The study includes the morphology, taxonomy, and distribution of some 20 families and 30 genera, several of them new (for new taxa see Contents). It is based on the best material available anywhere, mainly from the western United States.

The known diversity of these early pectinoids declined gradually from about 23 genera in the

Guadalupian (M. Permian) to a minimum of 5 in the Griesbachian (L. Triassic). After the biological decline, they did not recover substantial diversity until Late Triassic (Norian) time. So they shared the great mass extinction with most other groups of marine invertebrates. The crisis extended over some tens of millions of years and was slow, rather than catastrophic. This diversity pattern agrees well with carbon isotope ratios that seem to reflect a depressed oceanic productivity in Early Triassic time.

INTRODUCTION

GENERAL

This is our tenth and final contribution to a revision of those pectinoid bivalves that lived during the 25 million years or so of the Permo-Triassic crisis (Newell and Boyd, 1970, 1985a, 1985b, 1987, 1989, 1990; Boyd and Newell, 1976, 1979, 1984), when an estimated 96% of all animal marine species became extinct in a slow trend. Pectinoids are *Pecten*-like bivalves classified herein in superfamilies Pterinopectinacea, Pseudomonotacea, Aviculopectinacea, Pectinacea, and Monotacea.

Our aim in these studies has been to update and obtain a better understanding of these important groups—their varied morphology, evolution, taxonomy, and distribution spanning the sweeping physical changes of those times (Newell, 1967a; Logan and Hills, 1973).

Studies like this provide a glimpse of long-extinct life, but perception of this paleohistory is, of course, constrained by vagaries of preservation and sampling. We have found it rewarding to explore new localities and repeatedly sample old localities to the point of diminishing returns. However, the undiscovered fossil record seems to be without limit. It continues to yield significant new information.

Our ideas about this record have changed with increased exploration. The benefits are apparent in the wealth of material displaying rarely seen morphology. Our new information requires some revision of the treatment adopted in the *Treatise on Invertebrate Paleontology* (Newell, 1965, and Newell, 1969).

This applies to both stratigraphical and geographical ranges, as well as morphology. We are increasingly impressed by the concept of “Lazarus” taxa (Jablonski, 1986), those fossil taxa that reappear with little change after a long disappearance when they might logically be regarded as extinct. In the Upper Paleozoic, for example, several Mississippian pectinoid genera reappear in the Permian without known Pennsylvanian representatives. A notable example of a Lazarus taxon is the bivalve genus *Megalodon*, which appears abruptly in the Rhineland Devonian, again in the Upper Carboniferous of the Canadian Rockies (McGugan, 1960), and finally, in the Upper Triassic of the Alps. Evidently, the missing bivalves were living “somewhere else” during the missing intervals. Hence, as with other fossil groups, reported ranges must be tentative because of gaps in information.

Poorly documented taxa, subjective synonyms, and the assessment of uneven usage, have all presented us with vexing problems. It is a fact of biology that taxonomic names live forever, and nomenclature must be re-examined by every reviser. Unfortunately, priority of publication, not merit, frequently (but not inevitably) determines the selection of alternative names for a given taxon (Savage, 1990).

COLLECTIONS

The collections on which this work is based were assembled at the AMNH from many sources. They represent our own fieldwork

over several decades, as well as that of several generations of other paleontologists.

Because of preservational bias and inadequate collecting, there has always been a relative scarcity of good pectinoid specimens older than the Middle Triassic (Wang, 1993). Our experience demonstrates the value of patient and repeated field searches. The potential for significant new discoveries in the Permian and Lower Triassic rocks is still great despite the real poverty in the Griesbachian. Nevertheless, we are now able to provide a better glimpse of the pectinoids of those times.

The discovery of diverse tropical invertebrate faunas, many of them silicified, in the Permian rocks of West Texas (see collecting areas in fig. 64), and subsequent development of techniques of mass collecting and extraction of fossils from matrix by commercial hydrochloric (muriatic) acid forged the pathway to undreamed insights into the paleobiology of that and other regions.

Unfortunately, comparable conditions of preservation and accessibility seem to be scarce elsewhere. Although it was suspected in the 19th century, the fabulous potential of silicified invertebrates was not recognized until the 1930s. This outcome resulted from the prodigious work and remarkable discoveries begun in 1939 by many people, especially G. Arthur Cooper, and his colleagues, of the Smithsonian Institution (Cooper and Knight, 1946; Newell et al., 1953; Cooper and Grant, 1972, 1977).

Boyd joined Newell in the 1960s and the two expanded the work to include American Early Triassic bivalves, a previously neglected subject.

In the Permian the bivalve molluscs formed a small component of the faunas, apparently having been inhibited since the Devonian by the more abundant and diverse brachiopods. The almost complete disappearance of brachiopods and many other elements of this fauna, for a time in the latest Permian, left the bivalves dominant in the Triassic, albeit still of limited diversity (Gould and Callo-way, 1980).

The Permo-Triassic pectinoids of our studies have been collected from many scattered localities ranging from West Texas and Nevada to Montana, through an area of ap-

proximately 200,000 sq. mi (see collecting localities in figs. 62, 63, 64).

Except for a few calcareous specimens, our fossils are silicified and were extracted by the leaching of approximately 80 metric tons of selected limestone blocks. Most, but not all, of the Permian work had been done at the U.S. National Museum of Natural History by G. A. Cooper and his colleagues. The Triassic fossils were collected and culled by us from about 5 tons of limestone.

Collecting fossils is a process of chance sampling. Our work illustrates some of the biases inherent in exploring for fossils with the aim of learning about biological traits, abundance, distribution, and diversity of once living populations.

Experience helps in the search for the best material, but usually an outcrop could not be closely evaluated in the field because most of the fossils were completely concealed in limestone matrix. When laboratory preparation indicated a particularly promising locality, we returned for additional material until favorable results seemed to be diminishing.

The pectinoids are surface dwellers. They favor stable bottoms of slow deposition where, after death, their valves are separated, broken, and scattered before burial by other organisms and currents.

The flattened valves of the pectinoids are fragile and frequently disintegrate as they are freed from matrix in the acid. Consequently, their fragments often become part of the insoluble trash in acid and they are therefore much more difficult to prepare than associated brachiopods and snails.

The meager recovery of useful material rarely provided statistically significant population samples. On the other hand, the samples frequently revealed unparalleled evidence of morphological characters heretofore unknown.

PECTINOIDS

For thousands of years the attractive shells of scallops (pectinoids) have been used as ornaments and utensils, and the flesh as food. The ancient Greeks thought that the goddess Aphrodite was born in a scallop shell, and a

stylized *Pecten* has long been a symbol of St. James.

Probably monophyletic, they have been extraordinarily successful. They have a superficial resemblance to brachiopods, thus differing from most other bivalve molluscs in having an upper and a lower valve and in being subcircular. Some are vagrant, others are cemented, or attached by a byssus of organic threads through a byssal notch in the right (lower) valve.

The pectinoids appear with many other invertebrate taxa in the Silurian, possibly earlier. Multiplication of pectinoid clades continued to the present time when the most specialized forms, the Pectinacea, are represented in diverse marine habitats by hundreds of species.

THE GREATEST MASS EXTINCTION

The most remarkable aspect of the fossil record is that it is divided into discrete chapters in the history of life. It provides a stair-like journey through geological time, punctuated at fairly regular intervals (under orbital control?) by episodes of massive extinction of taxa, each event followed by gradual recovery as the evolutionary clock is repeatedly reset (fig. 1).

In 1840, John Phillips chose the base of a German Triassic sequence as a major partition between his Paleozoic and Mesozoic Eras. A year later, Murchison (1841) named the Permian System for a thick succession of rocks above the Carboniferous, thereby limiting the era boundary. Early in the 19th century, many of the major units of the geological sequence were already in use, and field geologists were becoming acquainted with sharp contrasts in successive faunas of the stratigraphical units.

Today, after repeated inventories of the fossil record, it is clear that the boundary between the Permian and Triassic periods marks great physical and biological disturbances of the Earth.

This was a time of broad geographic changes caused by eustatic variations of sea level and crustal warping. There were extensive changes in climates and extraordinary deposition of salt, gypsum, and redbeds. Many ancient animal lineages dropped out in the Permian Pe-

riod (see Newell, 1963, 1967a; Logan and Hills, 1973; Buffetaut et al., 1989; Erwin, 1994).

The pectinoids and other marine Bivalvia were decimated in the Permo-Triassic transition (fig. 2). According to Nakazawa and Runnegar (1973), the estimated number of all kinds of bivalve genera dropped from a peak of 70 in the mid-Permian, diminished to 19 in the Early Triassic, and then climbed to 140 in the Late Triassic.

We find that the pectinoid genera dropped from about 23 in the Permian to 5 in the Early Triassic, a percentage loss of diversity similar to that of other bivalves. This is only a crude assessment because of difficulties in tracing taxa from the Permian into the Triassic. The boundary rock formations are not very fossiliferous and they are geographically greatly restricted.

Fossiliferous Permian sediments over the world are usually followed abruptly by more or less barren drab to red rocks. Normally, there is no compelling evidence of emergence and protracted erosion, such as karst sinks or filled joint fissures. The boundary, as identified by fossils, is ordinarily a parallel bedding plane, a paraconformity (Newell, 1967b).

We favor the view that this curious situation is a result of bypassing sediments over large submarine areas; that is, condensed sequences, usually overlain by lithologically and paleontologically distinct Griesbachian shales and limy siltstones. Although local erosional channels at the contact occur (see Ciriacks, 1963; Paull and Paull, 1982), it is not certain that they are subaerial features, except possibly on the flanks of old uplifts, such as the Ancestral Rockies. The contrasting fossils below and above the boundary suggest a major environmental change other than emergence. Thick dolomite and salt deposits fill Permian basins above the youngest normal marine rocks in West Texas and the North Sea (Newell et al., 1953; Tucker, 1991). These are followed by redbeds of presumed Triassic age.

IS THERE A PRECISE PERMIAN-TRIASSIC BOUNDARY?

In the Rocky Mountains of western America (Newell and Kummel, 1942; Wignall and

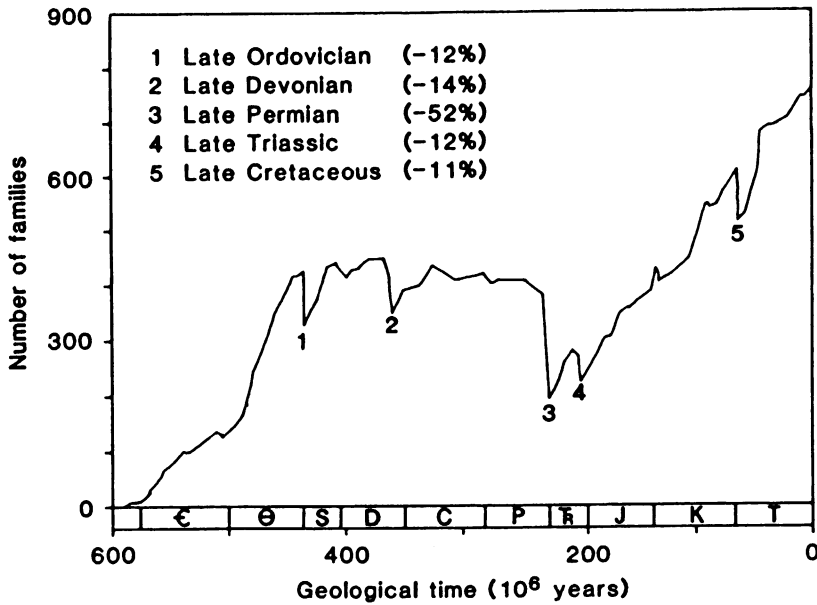


Fig. 1.1. The five major extinctions of the Phanerozoic in marine invertebrates (Raup and Sepkoski, 1982).

Hallam, 1992) and Western Tethys (see Broglio Loriga et al., 1986; Posenato, 1988), the lower Griesbachian contains a sparse and peculiar fauna, with *Lingula* and *Claraia* below and, with some mixing, *Eumorphotis* above.

We regard the so-called mixed fauna below the *Lingula* zone (Alpine Tesero) as Paleozoic (see also Xu and Grant, 1994, for China). A normal Triassic fauna starts to recover with the Nammalian (high Lower Triassic) Stage.

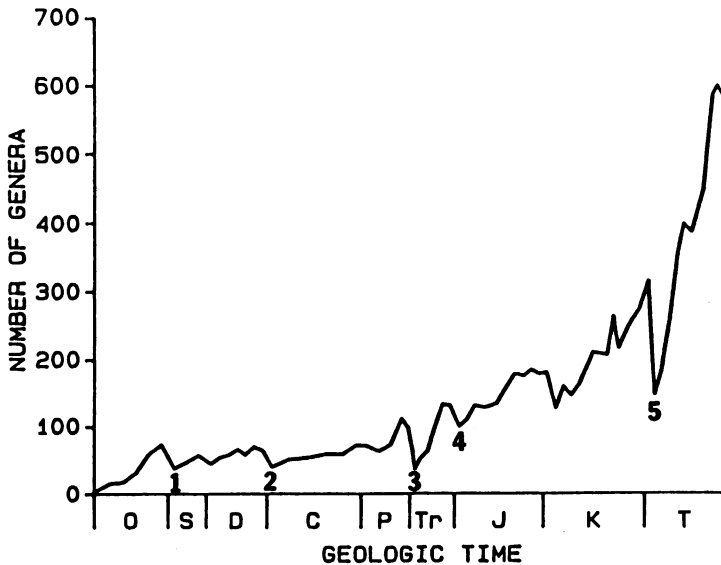
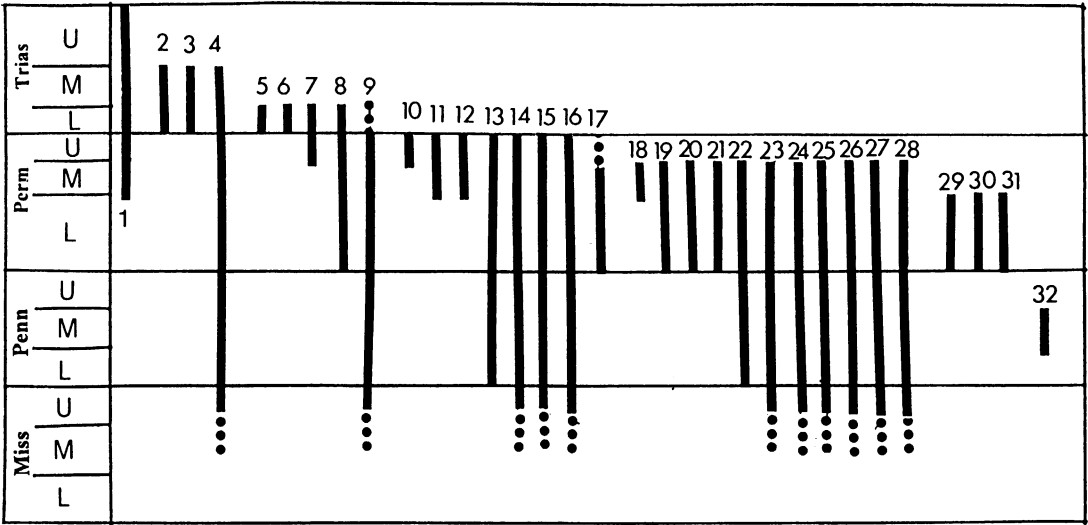


Fig. 1.2. The major extinctions reflected in the bivalve record (Miller and Sepkoski, 1988).



1	<i>Leptochondria</i>	M. Perm. - U.Trias.	18	<i>Denguiria</i>	M. Perm.
2	<i>Pleuronectites</i>	L. - M. Trias.	19	<i>Cassianoides</i>	L. - M. Perm.
3	<i>Entolioides</i>	L. - M. Trias.	20	<i>Fransonia</i>	L. - M. Perm.
4	<i>Streblopteria</i>	Miss. - M. Trias.	21	<i>Cyrtorostra</i>	L. - M. Perm.
5	<i>Eumorphotis</i>	L. Trias.	22	<i>Annuliconcha</i>	Penn. - M. Perm.
6	<i>Crittendenia</i>	L. Trias.	23	<i>Eocamptonectes</i>	Miss. - M. Perm.
7	<i>Claraia</i>	U. Perm. - L. Trias.	24	<i>Euchondria</i>	Miss. - M. Perm.
8	<i>Pegmavalvula</i>	L. Perm. - L. Trias.	25	<i>Aviculopecten</i>	Miss. - M. Perm.
9	<i>Heteropecten</i>	Miss. - L? Trias.	26	<i>Obliquipecten</i>	Miss. - M. Perm.
10	<i>Hunanopecten</i>	U. Perm.	27	<i>Pernopecten</i>	Miss. - M. Perm.
11	<i>Guizhoupecten</i>	M. - U. Perm.	28	<i>Pterinopectinella</i>	Miss. - M. Perm.
12	<i>Vnigripecten</i>	M. - U. Perm.	29	<i>Undopecten</i>	L. Perm.
13	<i>Pseudomonotis</i>	Penn. - U. Perm.	30	<i>Eurydesma</i>	L. Perm.
14	<i>Acanthopecten</i>	Miss. - U. Perm.	31	<i>Deltiopecten</i>	L. Perm.
15	<i>Streblochondria</i>	Miss. - U. Perm.	32	<i>Chaenocardia</i>	M. Penn.
16	<i>Spyridopecten</i>	Miss. - U. Perm.			
17	<i>Girtypecten</i>	L. Perm. - U? Perm.			

Fig. 2. Range diagram showing extinction trend during late Paleozoic, as exemplified in taxa described herein. Ranges extended to nearest series boundary.

This includes echinoderms, ammonoids, and brachiopods, as the *Lingula-Claraia* association drops out.

Geochemical studies of stable carbon isotope ratios seem to record variations in the composition of the marine waters in which the boundary sediments were deposited. In addition to minor variations in percentage of

^{13}C in the carbonate fraction of the boundary rocks, there is a dramatic drop in the ratio $^{13}\text{C}/^{12}\text{C}$ at the culmination of the P/Tr extinction level (Holser et al., 1991).

We may ask, what bearing do the stable isotopes of carbon have on the mass extinctions? The argument is simply that during photosynthesis plants favor ^{12}C over ^{13}C in

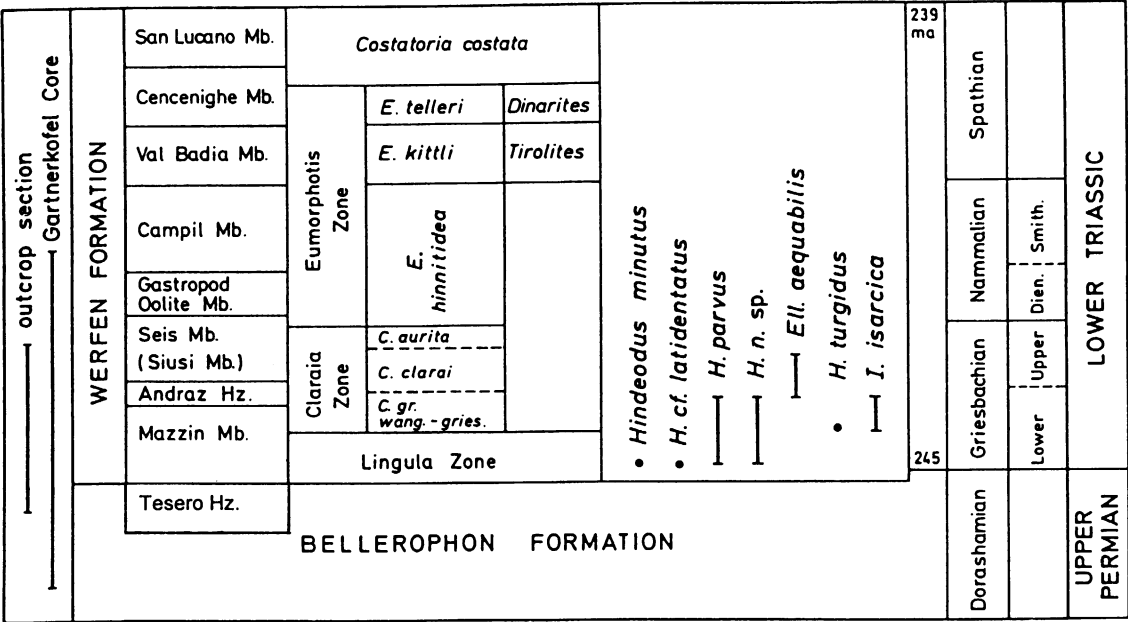


Fig. 3. Stratigraphic subdivisions of the Triassic in the southern Alps. Adapted from Neri and Posenato (1985), Broglio Loriga et al. (1986), Holser et al. (1991), and Schonlaub (1991).

the production of “protoplasm”; whereas the calcareous skeletons of plants and animals are not so enriched (Magaritz, 1989).

Thus, the ratio of ^{13}C to ^{12}C in a particular sedimentary layer is thought to record the relative levels of the two isotopes in the aquatic environment in which the sediment was deposited, and to serve as an index of fluctuations of organic productivity in the sea. A high ^{13}C value reflects massive withdrawal of ^{12}C into the biomass (high productivity); a low value indicates low productivity. This association of chemical and biological events seems well established. The negative excursion of ^{13}C correlates with the marine regression of the Permian, and the following positive excursion closely agrees with the Griesbachian transgression.

In the Permo-Triassic extinction event, the ^{13}C isotope ratio reaches a high level in the mid-Permian with its rich and diverse faunas, followed by a dwindling of taxa and finally by a nearly total extinction of the Permian fauna at the top of the Changxingian (Dorashamian) (Holser et al., 1991).

Recently, Baud et al. (1989) sampled 20

Late Permian–Early Triassic Tethyan sections in Yugoslavia, Turkey, Greece, Armenia, Iran, Pakistan, India, and Nepal. In these places and in SE South China (Gruszczynski et al., 1990), the ^{13}C ratio dips to a minimum at the top of the Dorashamian (Changxingian). Holser et al. (1991) have added detailed analyses in the Italian Alps (figs. 3, 4), Greenland, northwestern Europe, and the USA, with similar results. The same situation seems to have occurred also in British Columbia (Wang et al., 1994).

Hallam (1992, 1994) suggested that the mass extinction at the end of the Paleozoic was caused by a transgression of anoxic waters from oceanic depths. Our evidence suggests that the extinction event was slow and essentially completed before the influx of anoxic waters. Certainly the *Lingula-Claraia* association in the Griesbachian supports the idea of abnormal waters in the earliest Triassic. The extinction might be interpreted as a consequence of a major regression that terminated with an anoxic event.

Decrease in productivity can result from the failure of any or all life-supporting re-

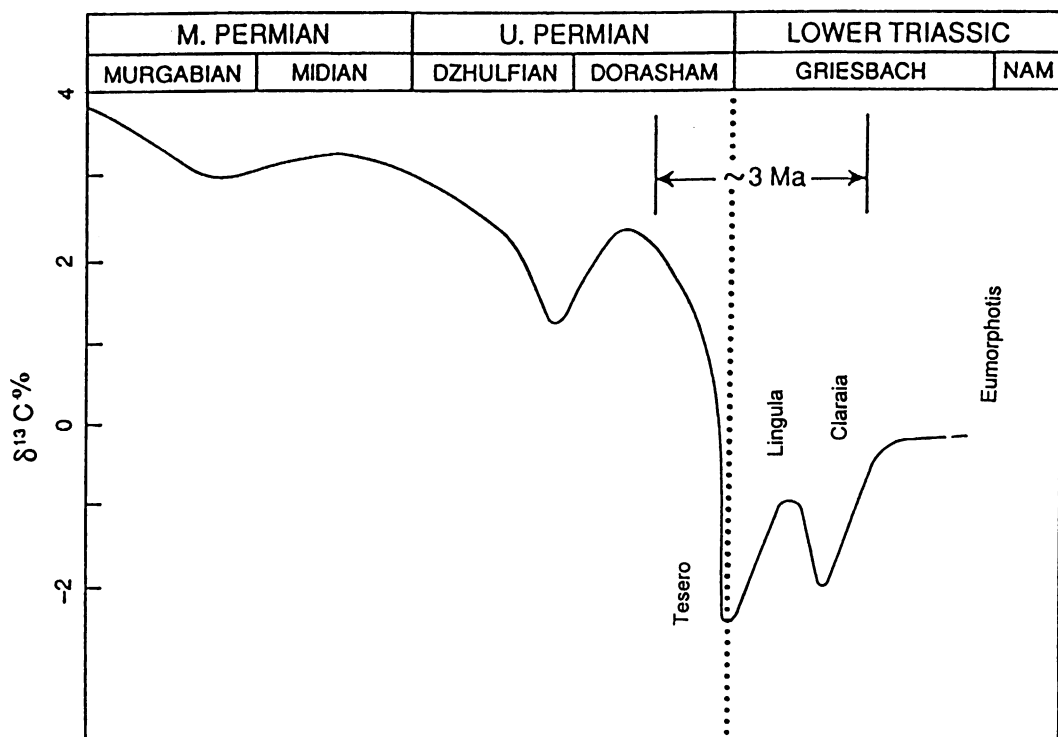


Fig. 4. Regional trend in stable carbon isotopes near the Permo/Triassic boundary throughout Tethys. Adapted from Baud et al. (1989) and Holser et al. (1991). Decline in diversity and biomass coincided with persistent marine regression down to the top of the Tesero Memb. This was followed sharply by unfavorable *Lingula* transgression, then slow recovery.

sources, such as interruption of photosynthesis at the base of the food chain (Tappan and Loeblich, 1973).

The search for some general explanation of the Permo-Triassic mass extinction is still in full swing, with many, by no means mutually exclusive, viable hypotheses—eustatic lowering of the sea level and consequent shrinking of the epicontinental seas; conversely, flooding of the continents by deep-sea anoxic water; freshening of the sea by exceptional deposition of salt; extremely strong volcanic eruptions; climatic oscillations; gamma-ray bursts from super novae, and bolide impacts. All of these explanations have devoted proponents, and multiple factors undoubtedly were involved. In passing, we note the prevalence of evidence indicating that the Permo-Triassic crisis was a dramatic loss of diversity extending over some millions of years, with a negative spike at the

top of the Upper Permian (figs. 1, 4). Summaries are given by Holser and Magaritz (1987), Hallam (1989), Raup (1991), Eldredge (1991), Xu et al. (1993), and Erwin (1993, 1994). We conclude that there is, indeed, a natural boundary between the Permian and Triassic erathems in which there is a coincidence of facies boundaries, and a minimum of biological diversity, and probably of biomass. There is disagreement on how precisely this boundary is expressed in the rock record.

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GENERAL ABBREVIATIONS

In the interest of brevity the following abbreviations are used:

AGSO	Australian Geological Survey Organization (formerly BMR, Bureau of Mineral Resources)
AMNH	American Museum of Natural History
Carb.	Carboniferous
cat.	catalog
Fm.	formation
Gp.	group
KU	Kansas University, Lawrence
L.	lower
Ls.	limestone
LV	left valve
M.	middle
Memb.	member
Miss.	Mississippian
Mt.	mountain
n. sp.	new species
OD	original designation of a type
Penn.	Pennsylvanian
Perm.	Permian
RV	right valve
SD	subsequent designation of a type
Sil.	Silurian
Trias.	Triassic
U.	upper
USNM	U.S. National Museum of Natural History
UW	University of Wyoming
UWA	University of Western Australia

ABBREVIATIONS IN TABLES

(All measurements in millimeters)

AAC	number of costae on anterior auricle
Aur Len	anterior auricle length
BN	byssal notch
Conv	convexity
H	height
Hin Len	hinge length
Hin Sp	number of hinge spines
Len	length
PAC	number of costae on posterior auricle

Resil	resilifer
Sh C	number of shell costae
Um An	umbonal angle

DESCRIPTIVE TERMS

Acuminate. Pointed.
 Alivincular. Having single resilifer pit below each beak.
 Amphidetic. Having ligament both ahead and behind beaks.
 Antimarginal. At right angles to the margin.
 Auricle (ear or "wing"). Lateral extension of shell at the hinge.
 Auricular crus (pl. crura). Nonarticulating internal ridge below each auricular sulcus and bordering visceral area.
 Auricular denticle. Knob at ventral end of auricular crus.
 Auricular sinus. Marginal embayment below auricles.
 Auricular sulcus. External valley between auricle and disc.
 Beak. More or less pointed initial part of shell growth.
 Boss. Massive protuberance on the hinge.
 Bourrelet (Stenzel, 1971). Flat external ligament area on both sides of the resilifer.
 Byssal notch or slit. Opening for foot and byssus below anterior auricle of right valve.
 Cardinal area. Relatively flat exterior surface of hinge plate between dorsal margin and hinge axis. Cardinal area includes resilifer, whereas the bourrelet does not.
 Comarginal. Parallel with the shell margin.
 Commissure. Contact of the valve margins.
 Composite mold. Internal mold with external ornamentation superimposed by compaction.
 Concordant valves. Congruent fit of valve margins.
 Costa (pl. costae). External radial rib.
 Crus (pl. crura). Nonarticulate internal ridge.
 Dextral. Pertaining to right valve.
 Discrepant. Having ornamentation different on opposing valves.
 Disc. Body of shell between auricles.
 Dorsal crura. Nonarticulating ridges just below, and nearly parallel to, hinge axis (as in Entolidae).
 Duplivincular. Having multiple, usually chevron-shaped, ligament bands above hinge axis.
 Equiconvex. Having equally convex valves.
 External ligament. Ligament entirely above hinge axis.
 Fasciole scroll. Thickened marginal ridge above hinge.

Filum (pl. fila). Comarginal ridge, coarser and more regular than growth lines.
 Hinge. Ligament and dentition.
 Hinge axis. Axis of rotation of the valves.
 Hyote. Pertaining to spines (or scales) with U-shaped transverse section, open on underside.
 Inequiconvex. Pertaining to shells having one valve less convex than the other.
 Infracrescent (acline). Pertaining to dominantly ventral marginal growth.
 Internal ligament. Ligament entirely concealed below hinge axis.
 Lamellar dentition. Elongate teeth and sockets on both ends of hinge.
 Marginal ridge. Internal low ridge bordering the disc.
 Multicostate. Having ranks of new costae added during growth.
 Myostracum. Fibrous prismatic aragonite of muscle pads.
 Opisthodetic. Having ligament almost entirely behind beaks.
 Paradiscordant. Commissure of RV apparently smaller than that of LV because of loss of flexible fringe in dead shells.
 Pleurothetic. Reclining on one side (right side in pectinoids).
 Plica (pl. plicae). Radial rib forming interlocking fold on shell margin (plication).
 Prorescent (opisthocline). Having accentuated anterior growth.
 Resilial ridges. Raised lateral margins of resilifer.
 Resilifer. Ligament pit, usually triangular.
 Retrorescent (prosocline). Accentuated posterior growth.
 Scroll (Fasciole). Thickened hinge margin.
 Shell layer 1 (ectostracum). Outermost shell layer in most aviculopectinaceans; absent in most adult pectinaceans.
 Shell layer 2 (endostracum). Second layer in most aviculopectinaceans. Main shell in most pectinoids.
 Transitional ligament. Broad and elongate cardinal area covered with fibrous ligament and bearing a single elastic band along dorsal margin and supplementary band below beaks (Newell and Boyd, 1987: 5).
 Umbo (pl. umbones). Inflated part of shell around beak.
 Umbonal cavity. Internal space within the umbones.
 Unicostate. Number of costae constant after early growth.
 Uniplicate. Number of plicae constant during growth.

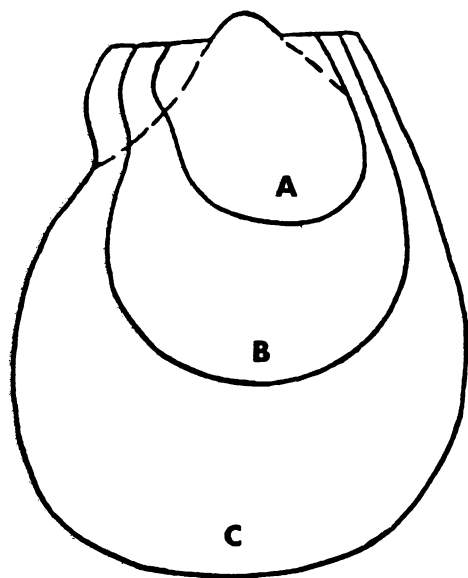


Fig. 5. Growth stages and adult profiles in Aviculopectinacea. **A**, retrorescent; **B**, infracrescent; **C**, prorescent.

MORPHOLOGY

The most evident traits of fossil pectinoids on which taxa are based are external form and sculpture. The two valves usually differ slightly in convexity. The right, or lower, valve commonly is the less convex of the two, which correlate with the animal's pleurothetic habit of lying at rest on that valve. Pectinoids are all lenticular, and more or less circular in profile.

In several living genera of Pectinidae the RV is very convex, and the LV flat or even concave. This specialized form corresponds with a living habit that involves excavation and partial burial in a depression. The scallop then has the upper flat valve flush with the sediment surface.

Asymmetrical growth gradients caused differences in form . . . accelerated growth ventrally (away from the hinge), infracrescent; forward, prorescent; or backward, retrorescent (fig. 5). Our reasons for preferring these terms over the traditional prosocline, acline, and opisthocline are on record (Newell and Boyd, 1970).

We follow Waller's (1991) terminology for sculptural features of pectinoid shells. They

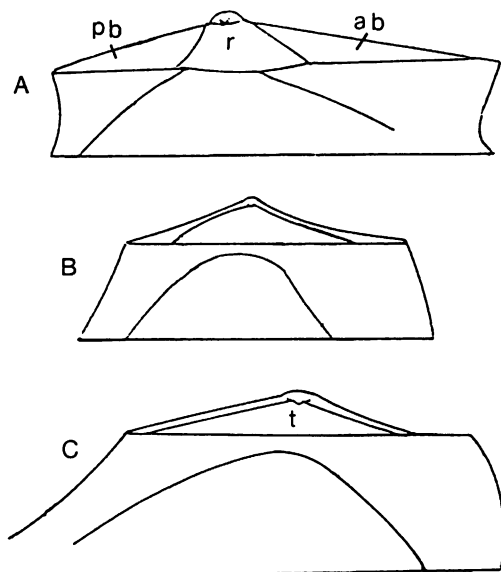


Fig. 6. Comparison of ligament areas in LVs of Aviculopectinacea. Anterior bourrelet (**ab**), posterior bourrelet (**pb**), resilifer (**r**), transitional ligament (**t**). **A**, *Streblochondria*, with broad bourrelets and forward extended resilifer; **B**, *Eocamptonectes*, with elongate resilifer and narrow bourrelets; **C**, *Streblopteria*, with elongate transitional ligament without bourrelets. Resilia and transitional ligaments are fibrous, but lamellar ligaments attached to bourrelets in **A** and **B** are elastic.

may radiate from the beaks, or be comarginal, i.e., parallel to the valve margins. The fine growth increments are fila or lirae, or simply growth lines. In a few taxa, fine rays are nearly perpendicular to the valve margin. These form "antimarginal" ("*Camptonectes*") sculpture.

Less accessible for study are internal characters which, because of poor preservation and difficulty of preparation, are frequently unknown even in commonly cited species and genera—e.g., the hinge assembly, crura, carinae, muscle scars, and shell microstructure.

The hinge consists of a ligament system and, in some, linear teeth and sockets near the dorsal margin. The ligament comprises separate parts of different functions. A thin, elongate elastic ligament lies along the axis of rotation of the two valves and ties them together. A ligamental pad, the resilium, rests in opposing pits (resilifers), or is attached over flattened cardinal areas (bourrelets) mainly

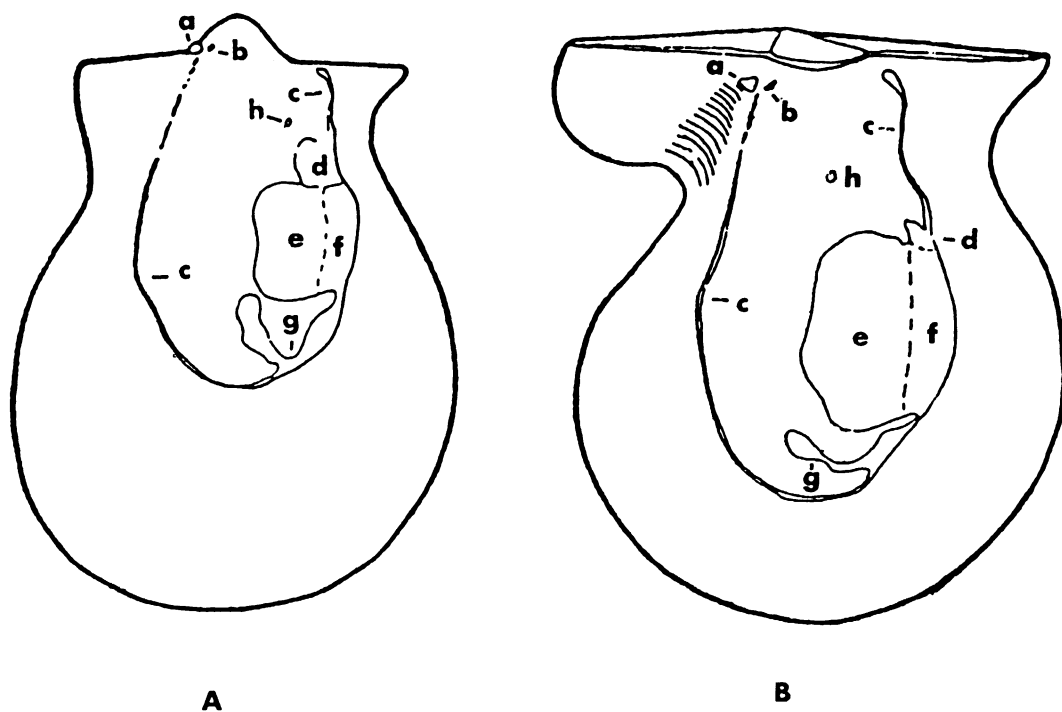


Fig. 7. Musculature of an aviculopectinid, *Heteropecten exemplarius*. After Newell (1937). LV (A) is an internal mold. RV (B) is considerably smaller than LV (not to scale). Pedal levators (a, b), pallial line (c), pedal retractor (d), "quick" muscle (e), "catch" muscle (f), gill suspensors (g, h).

above the hinge axis (fig. 6). This structure opens the valves when the closing muscles are relaxed.

In the most primitive forms the hinge axis migrates ventrally during growth, leaving much of the compressional ligament abandoned as relict sheets over the cardinal area. In the more specialized forms (Pectinacea), the resilium is below the hinge axis, internal, and concealed within the hinge area.

The system in the Pterinopectinacea consists of chevrons of alternating elastic and compressional bands across the ligament areas of the two valves. A transitional grade of ligament is a modification of this (Newell and Boyd, 1987). It may be either opisthodetic (entirely behind the beaks) or amphidetic, consisting of a single exposed band of elastic ligament along the dorsal part of the shell, as for example, in the Deltopectinidae and Eurydesmidae (Newell and Boyd, 1987).

Most Paleozoic and Triassic pectinoids lack hinge teeth, but representatives of the earliest

Pectinacea have linear tooth ridges on both sides of the resilifer that slope gently away from the beaks.

In many specialized pectinoids, there are two pairs of more or less equal lamellar teeth in the RV, a resilial tooth on each side of the resilium, and a dorsal tooth on each side beneath the linear outer ligament. The space between the resilial and dorsal teeth on each side of the RV is occupied by the socket for the infradorsal tooth of the LV (Waller, 1991: 8).

Most Paleozoic pectinoids lack internal carinae—possibly excepting *Leiopecten* (Johnston, 1991: fig. 7.I). The Entoliidae have auricular crura each with a terminal denticle. These are not interlocking teeth, but are opposed buttresses along the internal dorsal edges of the disc (fig. 53).

Muscle scars are not accessible in most Paleozoic bivalves. They have been described in Pennsylvanian forms by Newell (1937) and are reproduced here (figs. 7, 8). The known

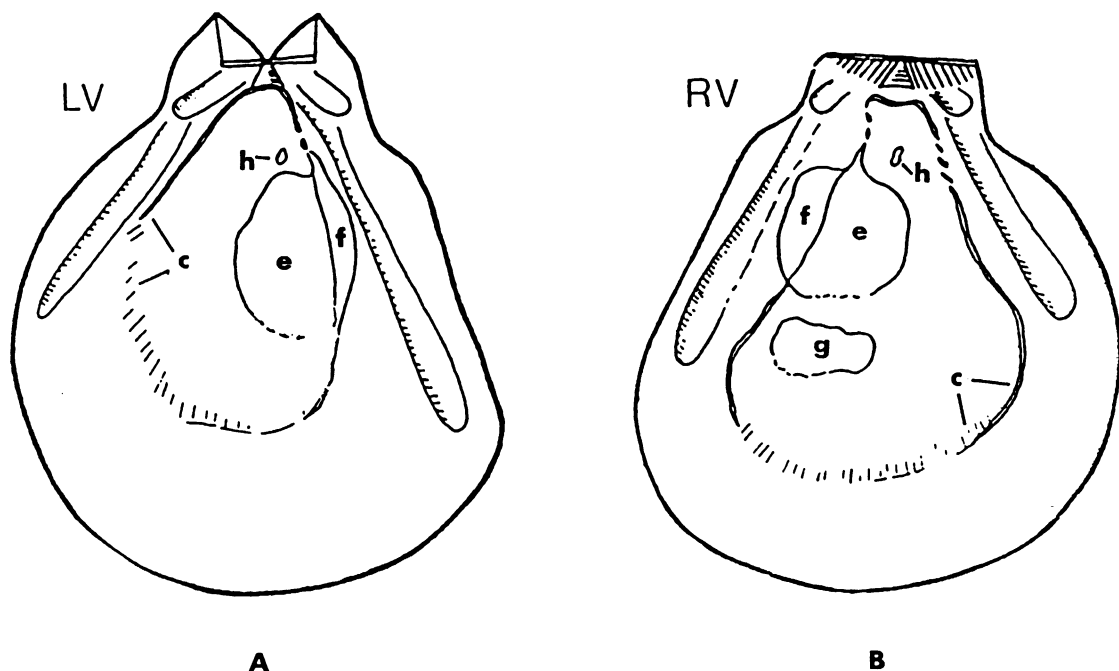


Fig. 8. Musculature of a Paleozoic entoliid, *Pernopecten clypeatus*, based on internal molds, enlarged. After Newell (1937). Pallial line (c), "quick" muscle (e), "catch" muscle (f), gill suspensors (g, h).

examples are readily homologized with living pectinoids. The general features have not changed much since well back in the Paleozoic.

Adult pectinoids possess only one, more or less centrally situated, adductor muscle (monomyarian grade) and this departure from the primitive pair of adductor muscles displayed by most bivalves is one of the most distinctive pectinoid traits.

Contraction of the adductor closes the valves against the resistance of the compressional ligament. This ligament, aided in some forms by the foot, opens the valves for feeding and respiration (Trueman, 1964).

The pectinoid adductor consists of two parts with quite different properties. These are a posterior part, the smooth "catch" muscle, and a larger anterior part, the striated "quick" muscle. The catch muscle contracts slowly and can withstand tension for long periods. The quick muscle reacts rapidly for cleaning the gills, but soon fatigues and relaxes.

The musculature of aviculopectinaceans embodies features of both the ancestral pteriaceans and the descendant pectinoids. The

differences are in the pedal and pallial muscles. The aviculopectinaceans have pedal muscles like those of the ancestral pterioids. That is, there is a single pedal retractor (d) and two pedal levators (a, b) in each valve (fig. 7). The pectinaceans (e.g., *Pernopecten*), on the other hand, lack a pedal retractor and pedal levators (fig. 8). As with other pectinaceans, the pallial line in the aviculopectinaceans is mainly continuous, not discontinuous, as in most Pteriacea.

SHELL PRESERVATION AND MICROSTRUCTURE

The Danish scientist O. M. Bøggild (1930) demonstrated the taxonomic importance of molluscan shell microstructure and Joseph G. Carter has substantially advanced knowledge of the subject in a great and penetrating work (Carter, 1990) that brings together all available information.

But the shell structure of the older forms is frequently poorly known or completely unknown because of imperfect preservation and lack of study. Application to taxonomic work is further impeded by variability within in-

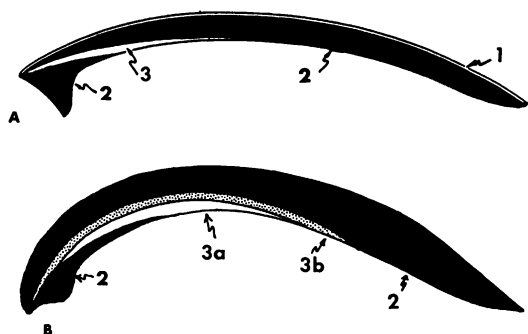


Fig. 9. Pectinoid shell layers. Median radial sections. **A**, aviculopectinid; **B**, pectinid. Showing outer calcite layer (ectostracum) (1) absent in most Pectinidae; inner layer (endostracum) (2) mainly calcite in Pectinidae, usually aragonite in Aviculopectinidae; undifferentiated aragonite (3); fibrous aragonite myostracum (3a); crossed lamellar aragonite (3b).

dividual taxa. Our own observations are incorporated in the diagnoses presented herein, where we make a few generalizations.

The microstructure of the thin outer layer is usually, but not always, different in the two valves; however, the inner parts frequently are alike in the two valves.

The molluscan shell is composed of calcium carbonate particles encased in a matrix of proteinaceous material—conchiolin. Since these constituents are chemically less stable than the calcium phosphate of vertebrate bones and teeth, the fossil mollusc shells more commonly suffer destruction that increases with geologic age. The conchiolin matrix and the more soluble carbonate fraction, aragonite, disappear or recrystallize as calcite, or the whole shell may be replaced by secondary minerals (Boyd and Newell, 1984). The original microstructure is rare in older faunas but occasional examples have been found in rocks as old as Devonian (Carter and Tevesz, 1978).

The deep water pectinoid, *Propeamusium*, is a "living fossil" that closely resembles many long extinct taxa, which aids in their interpretation (Waller, 1972). In this and many Paleozoic genera, the RV possesses a thin outer layer (the ectostracum, fig. 9A: 1) of short, more or less inclined, simple prisms of calcite. The left outer layer is also calcite, either as a chaotic mosaic of irregular tiny crystals ("homogeneous") or as antimarginal fibers.

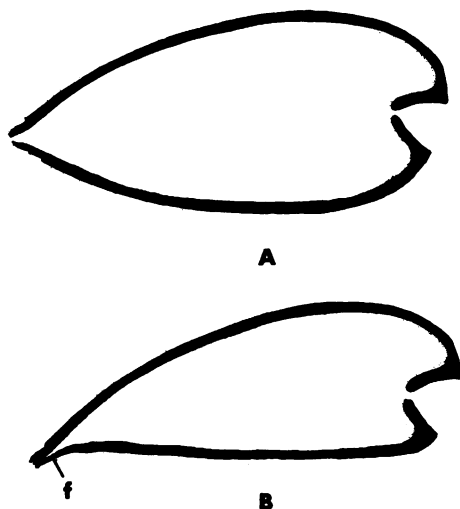


Fig. 10. Diagrammatic median profiles of two types of pectinoids. **A**, concordant valves with near equiconvexity; **B**, paradiscordant valves in which the RV has a flexible prismatic brim (f), rarely preserved in fossils.

The prismatic layer of the RV extends beyond the inner layers as a flexible apron; it is absent on the LV in many forms, a condition that we are calling paradiscordant (fig. 10). The few Paleozoic pectinoids that are concordant tend to be nearly equivalve and largely calcitic with the outer layer of both valves antimarginally fibrous. The main inner layer (endostracum, fig. 9A: 2) of both valves in most Paleozoic taxa consists of crossed lamellae of aragonite in comarginal increments, similar crossed folia of calcite, or, exceptionally, interlayers of nacre and crossed lamellar aragonite.

Waller (1985) was impressed by the fact that most living pectinoids and all oysters have shells composed mainly of foliated calcite, whereas the pteriods are mainly nacreous aragonite; consequently, the differences in shell microstructure and mineralogy might provide criteria for separating morphologically convergent taxa.

Paleozoic pectinoids, however, are mainly composed of crossed lamellar aragonite, as described on the following pages. Furthermore, the shells often are so altered by diagenesis that the original details must be inferred, and therefore are controversial.

In foliated calcite, folia usually are ar-

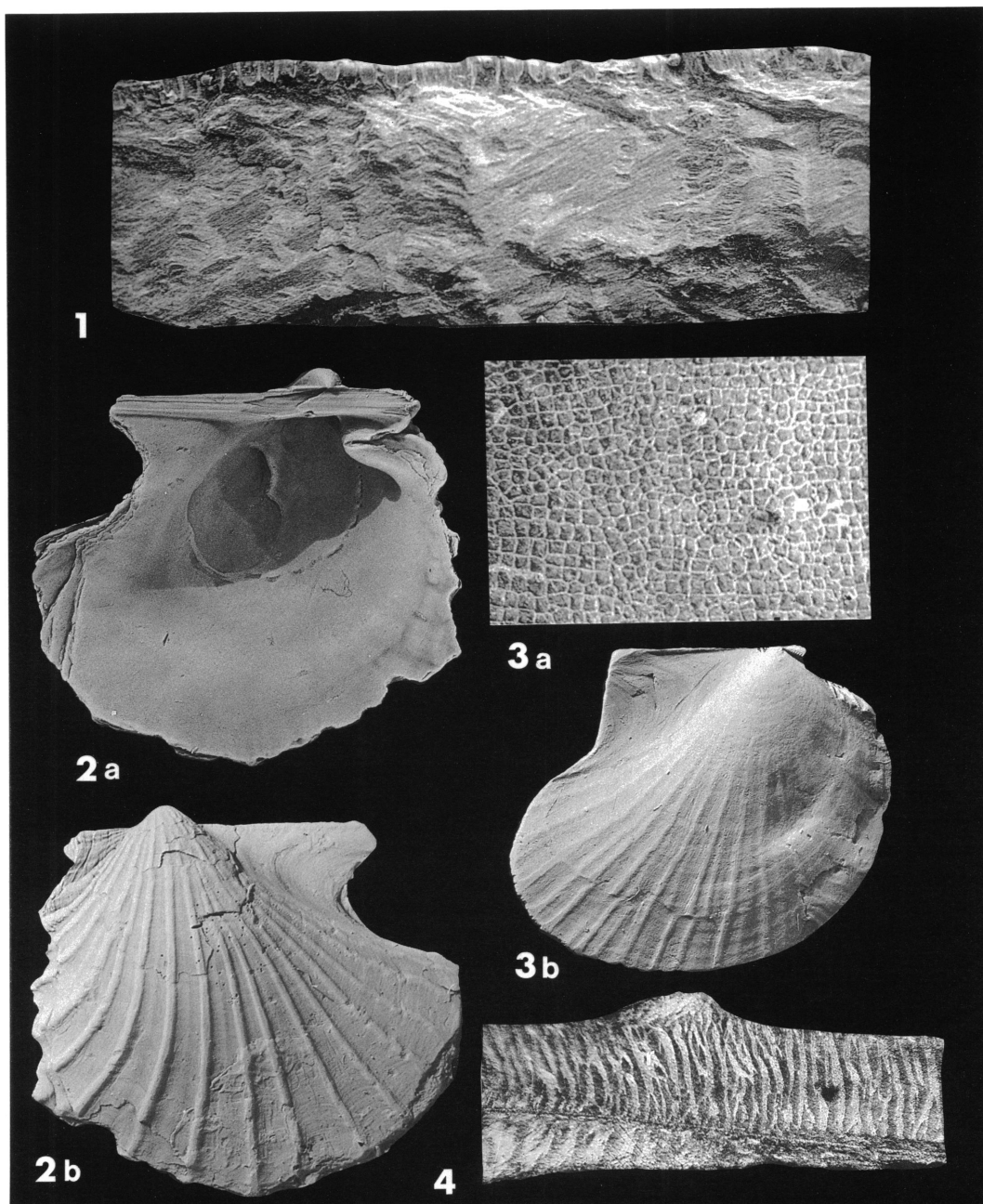


Fig. 11. *Oxytoma expansa* Phillips, 1829. Jurassic (Oxfordian Fm.), Aylesbury, Buckinghamshire, England. 1, RV $\times 50$, radial fracture surface illustrating characteristic low angle of calcite crossed folia below and calcite prismatic layer above, SEM stub 10, AMNH cat. 44065; 2a, b, LV $\times 3$, details of interior, hinge, and multicostate ornamentation, AMNH cat. 44074; 3a, RV $\times 50$, prismatic layer, exterior, SEM stub 21, 3b, same RV $\times 3$, multicostate exterior, AMNH cat. 44067; 4, LV $\times 35$, crossed foliate layers separated by a thin myostracal layer of aragonite, SEM cellulose peel of transverse section (stub 23), AMNH cat. 44068.

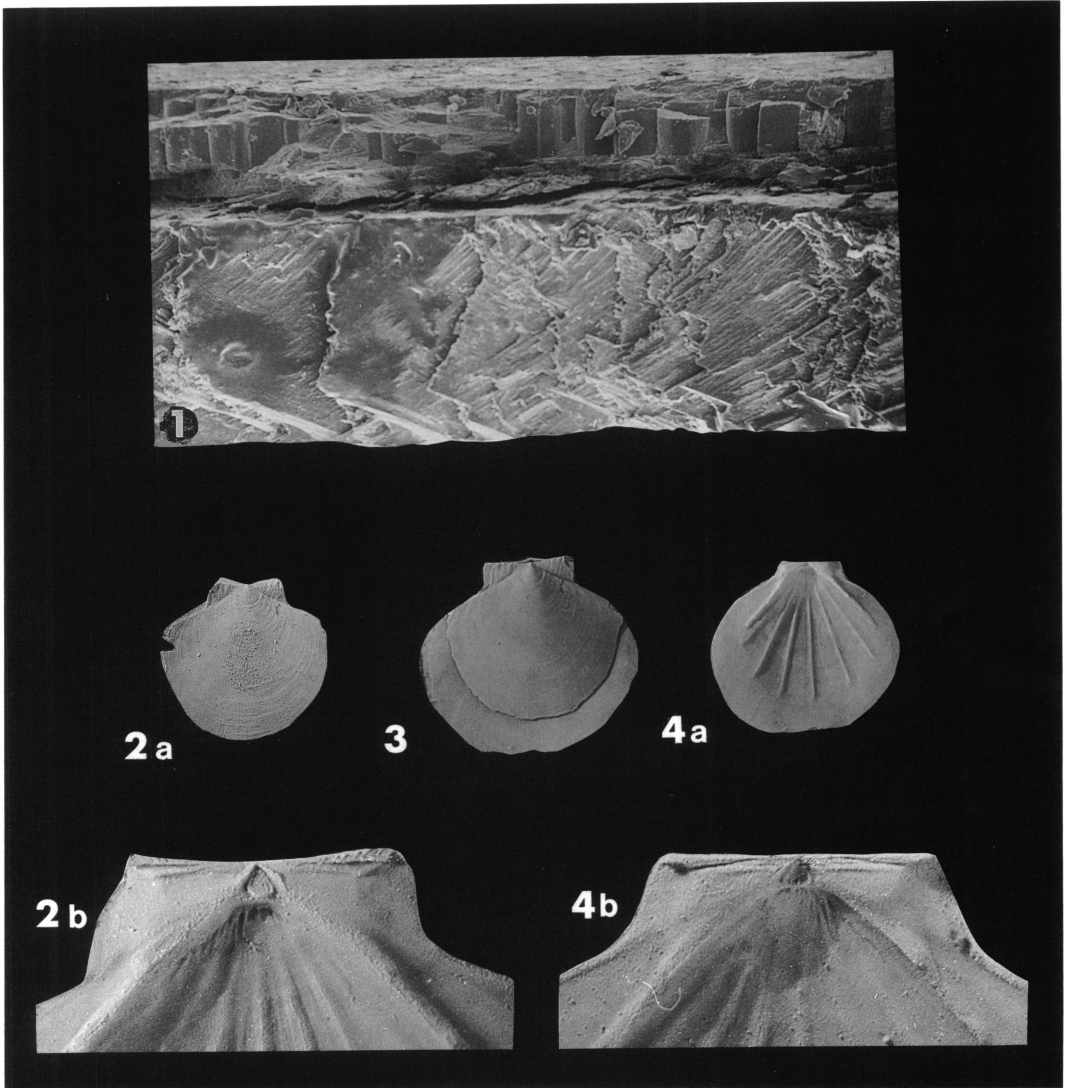


Fig. 12. *Propeamussium sibogai* Dautzenberg and Bavay. Recent. For comparison with *Pernopecten* and *Entolioides*. 1, RV $\times 130$, shows crossed lamellar aragonite layer below and prismatic calcite layer above, SEM stub 200, AMNH cat. 44056; 2a, b, RV, respectively $\times 1$ and $\times 4$, flexible fringe missing, AMNH cat. 44057; 3, joined valves, $\times 1$, LV behind, flexible fringe of RV missing, AMNH cat. 44058; 4a, b, LV, respectively $\times 1$ and $\times 4$, shows internal ribs and rigid margin of crossed lamellar aragonite, AMNH cat. 44059.

ranged at a low angle (fig. 11: 1) to the shell surfaces, and, as Bøggild observed, aragonite lamellae lie at somewhat steeper angles (fig. 12: 1). Features of the outer layer (fig. 9: 1) that we have observed suggest the generalizations in table 1 (however, it should be noted that it is difficult to recognize minor layers in silicified material).

PECTINOID ADAPTATIONS

The evolutionary loss of the anterior muscle and concomitant reduction of the front of the animal can be inferred from the anisomyarian relatives. C. M. Yonge (1953) showed that the reduction of the anterior end of some bivalves involves modification and special-

TABLE 1
Microstructure of Outer Layer

	Left valve	Right valve
<i>Heteropecten</i>	Homogeneous or absent	Prismatic or absent
<i>Limipecten</i>	Homogeneous	Prismatic
<i>Acanthopecten</i>	Homogeneous	Prismatic
<i>Deltopecten</i>	Absent	Absent
<i>Euchondria</i>	Homogeneous	Prismatic
<i>Obliquipecten</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Streblopteria</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Cyrtorostra</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Pleuronectites</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Streblochondria</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Guizhoupecten</i>	Antimarginal fibrous	Antimarginal fibrous
<i>Propeamusium</i>	Antimarginal fibrous	Prismatic
<i>Pernopecten</i>	Antimarginal fibrous	Prismatic
<i>Entolioides</i>	Antimarginal fibrous	Prismatic
<i>Dunbarella</i>	Prismatic	Prismatic
<i>Claraia</i>	Prismatic	Prismatic

ization of the foot for secreting and spinning a byssus through a notch in the lower (anatomically right) valve. The byssus provides anchorage to the substrate.

Beyond this grade, further specialization results in cementation by the RV, or acquisition of a free swimming habit. In both cases the byssal notch and sinus become closed, but it does not necessarily follow that the foot is lost.

The quick muscle is especially strong in scallops. It facilitates cleaning the gills by

flapping the valves. In an extreme specialization, it enables a few species to swim and glide for considerable distances (Gould, 1971; Morton, 1980; Joll, 1989). Such exceptional activity requires an efficient internal resilium.

C. M. Yonge (1936) showed how this adaptation might be an extension of a simple escape mechanism. Using a flow tank, Hayami (1991) made ingenious experiments on the hydrofoil lift-and-drag properties of a variety of streamlined pectinoids. All swim with the ventral margin opposite the beaks as the leading edge, rapidly flapping the valves as though biting the water with the sagittal plane horizontal (fig. 13).

Smooth and flattened, thin-shelled forms are the best swimmers. The record seems to be held by *Amusium* with a measured distance of 23 m. Some bearers of plicate shells can swim a few meters (Waller, 1976). Hayami speculated that living deep-water *Propeamusium* and Entoliidae, such as *Entolium* and *Pernopecten*, were also swimmers since they are shaped like *Amusium* and possess the same efficient internal resilium. The byssus is obsolete in the adults of the best swimmers.

FORM AND ORNAMENTATION

Pectinoids are inequivalved and inequilateral. As with many other Pteriomorpha, the

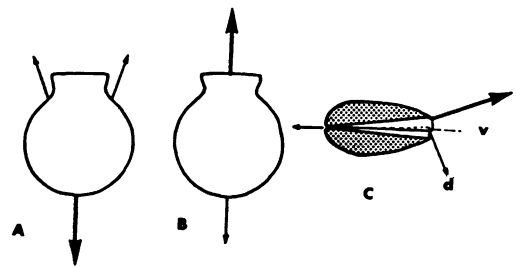


Fig. 13. Jet propulsion in modern scallops (Buddenbrock, 1911). A, Normal swimming is away from the hinge, in direction of large arrow; B, escape movement (in direction of the large arrow), powered by a ventral jet (small arrow); C, water directed downward (d) by the mantle velum (v) causes lift.



Fig. 14. Original color patterns preserved in silicified Perm. pectinoids. 1, 2, *Euchondria cooperi* Newell and Boyd, n. sp., RV, $\times 3$, pattern is present on both inner and outer surfaces, USNM loc. 703, cat. 431321; 3, *Streblopteria* sp. $\times 3.5$, U. Perm., Hydra Island, Greece, USNM cat. 9599-8.

right valve usually possesses a byssal notch at the front of the hinge, at least in juveniles, a characteristic shared by their pteriacean ancestors. Furthermore, surface details of ornamentation are usually different (discrepant) in the two valves. Radial ribs may be introduced both by branching and intercalation even on the same valve; therefore, as a taxonomic character, the details may be quite variable.

Ornamentation of the right valve generally is subdued, or even lacking. Since the two valves are almost invariably separated after death, there is frequently a problem of matching the two. In much of the older literature the two valves were frequently mistaken for separate species.

The RV may even appear to be smaller at the disc margin than the LV, as in many other Pteriomorpha. This anomaly is understandable by reference to living examples of the Pteriidae and Propeamussiidae (fig. 12: 3). Growth of the inner, harder layers of the RV lag behind the outer, prismatic layer, which forms a flexible fringe.

Thin-shelled taxa with paradiscordant valves show a marked preservation bias. In these, RVs usually are less numerous in a collection than LVs. In fact, RVs are even unknown in some taxa. Probably they were less calcified than the LVs.

Concordant shells lack the flexible fringe, and tend to be more convex and more nearly equiconvex; in addition, paradiscordant shells usually do not have interlocking plicae at the

shell margin. In these, the margins are either smooth or have costae, which may increase in number during growth as successive ranks of ribs are inserted. The older costae may split longitudinally. In either case, the shells are multicostate.

The major ribs of plicate shells interlock snugly at the margin and usually remain constant in number after passing through an early multicostate stage. As far as we know, the prismatic layer is lacking in the adults of all plicate shells; the valves are concordant at the margin and subequal in convexity. Plicate shells are common among the family Pectinidae but are exceptional in the Paleozoic pectinoids and the sister group, the pterioids. We agree with Waller (1991) that plication is a secondary, or derived, state.

Radial costae and comarginal threads ("fila") generally originate in the outer layer of the shell, which is secreted by the mantle margin. The inner layers, on the other hand, are secreted by the general surface of the mantle, so they progressively cover the inner surface of the shell and any inner expression there of surface ornamentation.

Where the inner layers were composed of aragonite, hinge structures and muscle impressions may be selectively leached away, or the entire shell may be removed, leaving an open cavity. Subsequent compaction of the resulting space may cause either the outer layer or the impression of the shell surface to be pressed against the inner matrix, forming a "composite" mold with a subdued repli-

cation of the shell ornamentation. The resulting shell patterns preserved on the matrix of the internal mold resemble, and may be mistaken for, external ornamentation.

Occasionally, original color bands are preserved in Paleozoic calcareous bivalves (Mapes and Benstock, 1988). More remarkable are relict color patterns preserved in some of our silicified pectinoids (fig. 14).

CLASSIFICATION AND PHYLOGENY

Much of the formal nomenclature of fossil invertebrates was developed by biostratigraphers engaged in reconnaissance exploration and documentation of strata and their faunas. This has resulted in a typological nomenclature of limited phylogenetic significance. It has, however, yielded an invaluable chronology—the geological time scale. With all its biological shortcomings, the literature tells us much about extinct taxa that compose most of the record. This incomplete and faulted inventory guides the paleobiologist to search for new discoveries.

The taxonomy of Paleozoic pectinoids started, and continues, with the naming of a few, usually fragmentary, specimens. These provide only minimal data on morphology, variability, or even stratigraphic and geographic ranges, but the information is invaluable and has been cumulative.

This biostratigraphic typology is not, of course, an unmixed blessing. Paleobiologists must spend much time trying to evaluate inadequate characterizations from a literature much of which they would like to ignore.

With the recognition that most species are polytypic, and that many populations are strikingly variable (fig. 15), it is evident that a fossil taxon cannot be adequately characterized by a holotype, or even by a handful of imperfect specimens.

Thus, much of the systematic classification of extinct pectinoids has produced an eclectic, nonphylogenetic, nonpopulation hierarchy based on subjective assessments of stratigraphic position, morphology, and provincialism.

The search for genealogical lineages among pectinoids is further complicated by uncer-

If the original pigment was emplaced in the intercrystalline organic matrix of the shell, either the pigment or its inorganic derivative could be transferred as an impurity to the silica as it replaced the original carbonate material.

tainty about cladistic polarity (fig. 16). As with many other fossil bivalve groups, the recognition of primitive versus derived traits tends to be subjective and debatable. Evolutionary relationships are obscure even among living forms. A leading student of these pectinoids, L. G. Hertlein (1969: 308), concluded that many supraspecific taxa resemble others in random iteration of form and structure. He found it expedient to use many informal “groups” instead of family taxa.

According to Waller (1991: 2) there have been approximately 7000 species of Pectinacea described. Most of these were placed in only five genera, based on characters that have appeared repeatedly in different combinations throughout the evolutionary history of the superfamily. Consequently, Waller, like Hertlein, clustered many of the named genera in informal groups.

Our cladistic analysis of late Paleozoic–early Mesozoic pectinoid families is shown in figure 16. Like all cladograms, it is a hypothesis that illustrates our conclusions. For us, the value of the exercise has been to focus our attention on derived characters, both in terms of identifying them and employing them in diagnosing families.

We consider the 17 characters listed in figure 16 to be apomorphic relative to the mainly middle Paleozoic Pterineidae. Although several of its representatives are probably “form genera,” this family seems to be the best choice for an outgroup because of its similar morphology. Various workers have suggested a pterineid ancestor for pectinaceans (e.g., Stanley, 1972; Carter and Tevesz, 1978), although Johnston (1991) argued that these groups had independent origins.

The brevity of the character list reflects the simple morphology of the shells under study, and the relatively few attributes that distinguish them from the chosen outgroup. The 17 features are the apomorphies we found useful in defining and clustering families of late Paleozoic and early Mesozoic pectinoids.

The list includes both characters and character states, in that some of the features are grades of a more general condition. Since we treated the 17 attributes as equals in practice, all are termed "characters," and we do not recognize two hierarchical levels in the list.

The designation of presence vs. absence in the data matrix was not without problems. Some of the characters exhibit intraspecific and/or interspecific variability. In such cases, the choice between presence and absence represents our impression as to the dominant condition in the family.

Incomplete information concerning the occurrence of a given character among the genera under study has also constrained the size of the matrix. Some potentially valuable characters are demonstrable in some genera but are not determinable in others thought to belong to the same family. In such cases we have resisted the temptation to credit the family with that character. For example, microstructure is not represented in the character list because evidence is missing or equivocal for many taxa. Silicification, the mode of preservation of most of our specimens, commonly destroyed the original wall structure. Although we have unequivocal evidence concerning microstructure of the outer layer for some species, we lack it for many others. Our silicified material has yielded no direct evidence of original structure of the inner layer of either valve.

CLASSIFICATION ADOPTED

We are using the suffixes -oida and -acea, respectively, for orders and superfamilies. This follows standard historical and current usage among malacologists.

The classification adopted herein is as follows:

Class Bivalvia

Subclass Pteriomorpha Beurlen, 1944

Order Pterioidea Newell, 1965

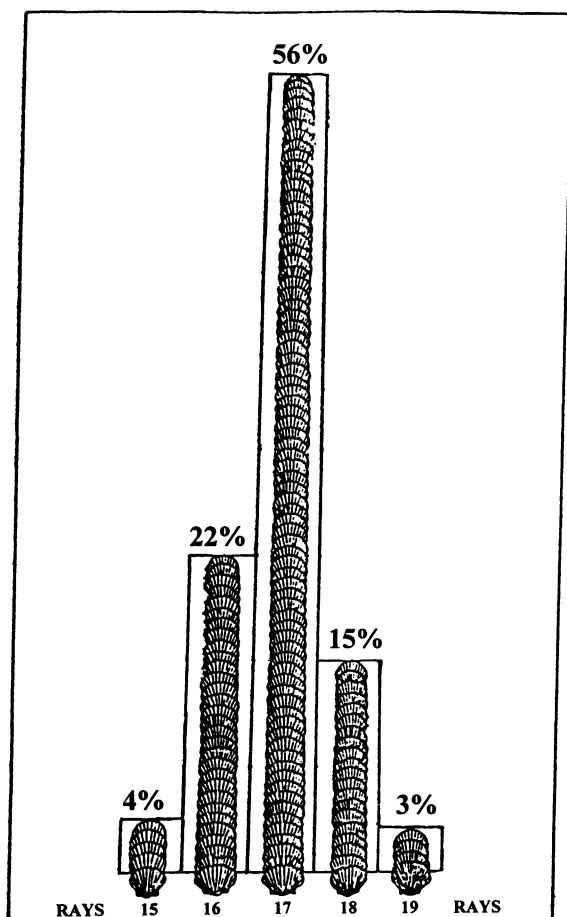


Fig. 15. Bell curve of rib count in a large sample of a population of living scallops, *Argopecten irradians*, from Long Island Sound, New York. From an exhibit at the AMNH by malacologist H. E. Crampton.

Superfamily Ambonychiacea Miller, 1877

Superfamily Pteriacea Gray, 1847

Order Pectinoidea Newell and Boyd, new herein

Superfamily Pterinopectinacea Newell, 1938

Superfamily Aviculopectinacea Meek and Hayden, 1864

Superfamily Pseudomonotacea Newell, 1938

Superfamily Pectinacea Wilkes, 1810

Superfamily Monotacea Fischer, 1887

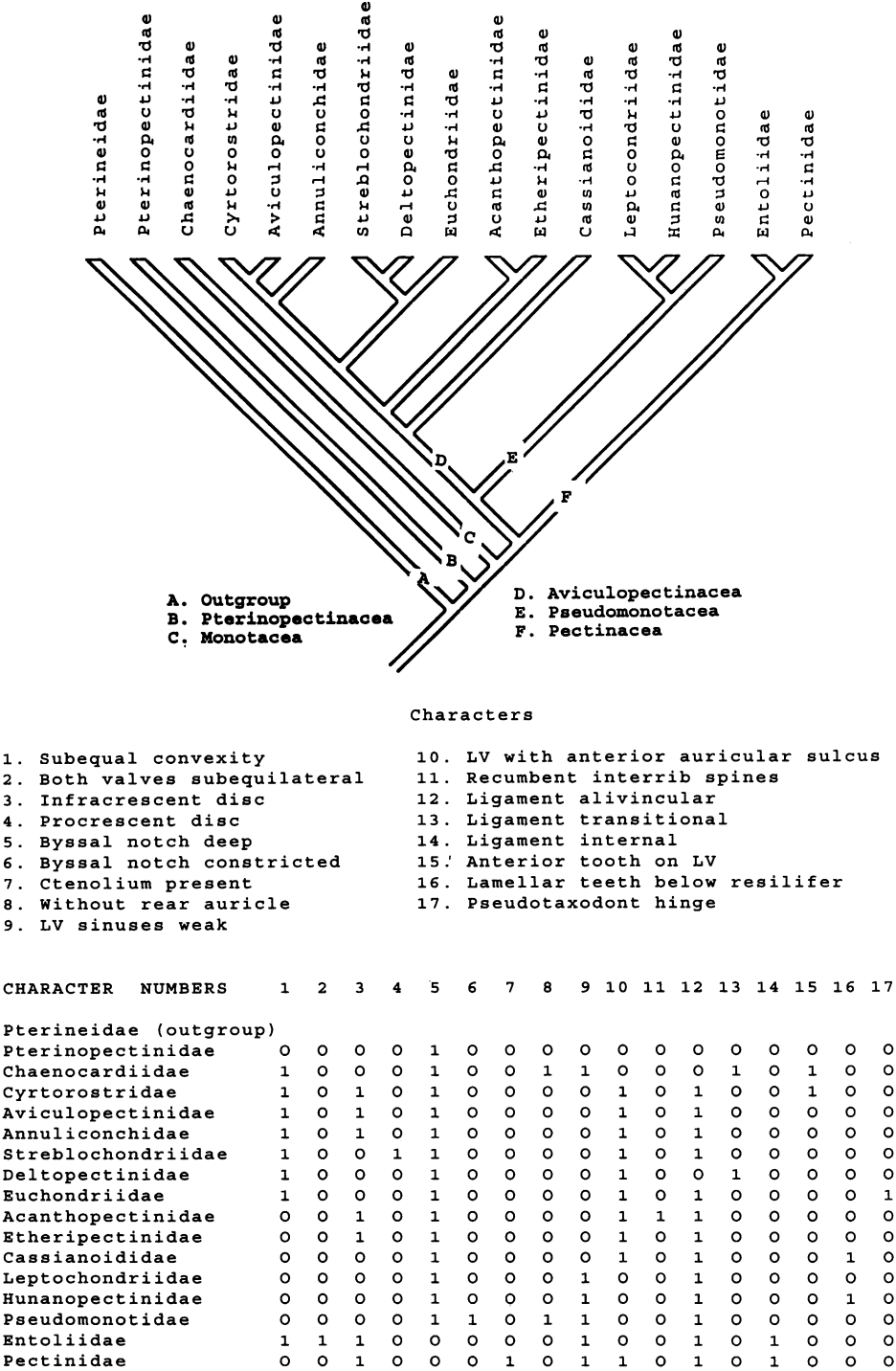


Fig. 16. Hypothesized relationships of the families discussed in this report. This cladogram of 29 steps is one of 72 most parsimonious results obtained by processing the data matrix by PAUP 3.0 (branch and bound search). Graphic representation produced with MacClade 2.1 software.

SYSTEMATICS

PECTINOIDA, NEW ORDER

(from Pectinina Waller, 1978)

Monomyarian rounded pteriomorphs, usually with auricles; RV pleurothetic and commonly with byssal notch, at least in early stages; ligament duplivincular or alivincular; amphidetic, or less commonly opisthodetic; thin outer, simple, prismatic calcite layer in both or only RV, or absent; foliated calcite dominant in many taxa, crossed-lamellar or nacreous aragonite in others.

SUPERFAMILY PTERINOPECTINACEA NEWELL, 1938

(from Pterinopectinidae Newell, 1938)

DIAGNOSIS: Ligament duplivincular; shell concordant, slightly retrocrescent with deep byssal notch; beaks ahead of midpoint of hinge; posterior auricle not sharply differentiated from disc; outer ostracum of both valves typically simple prismatic.

DISCUSSION: Most Paleozoic pectinoid shells possess one or the other of two ligament systems, both of which are external and amphidetic. One, characterizing the Aviculopectinacea, is an external, alivincular ligament; the other, typifying the Pterinopectinacea, is a duplivincular ligament. The latter ligament is especially characteristic of the Devonian, preceding in time the Carb. Aviculopectinacea.

FAMILY PTERINOPECTINIDAE NEWELL, 1938

DIAGNOSIS: As the superfamily Pterinopectinacea.

DISTRIBUTION: Sil.-L. Trias.

Genus *Claraia* Bittner, 1901

Pseudoclaraiia Zhang, 1980.

Pseudoclaraiia aurantiformis Zhang, 1980 (type species) = *Claraia wangi* Patte, 1935 (fide Yin, 1985b).

Claraioides Fang, 1993 (type species).

Claraioides guizhouensis Fang, 1993 (type locality, U. Perm., S. China).

TYPE SPECIES: *Posidonomya clarae* von Hauer, 1851. Lower Triassic, southern Alps; SD Diener, 1923. (The trivial name is usually mistakenly translated to *clarai*.)

DIAGNOSIS: Adults of moderate size (20–50 mm), retrocrescent, orbicular; both valves multicostate, usually with a few irregular, co-marginal folds; LV weakly convex; RV nearly flat, with umbonal attachment scar; hinge slightly more than half shell length; beaks less than one-third behind front of hinge; posterior border broadly rounded; anterior auricle short, narrow; byssal notch deep, originating in a keyhole-shaped foramen with internal collar; both valves with a thin, prismatic calcite outer layer; inner layer thin, probably originally aragonite.

DISTRIBUTION: Widespread in U. Perm. and L. Trias. of Laurasia.

DISCUSSION: Bittner (1901) introduced *Claraia* as a subgenus of *Pseudomonotis*, which it resembles only superficially. We erroneously followed him in this (Newell and Boyd, 1970) until Z. M. Zhang (1980) showed that *Claraia* has a duplivincular ligament and other traits of the Pterinopectinidae and is more comparable with *Dunbarella* (Newell, 1937) and *Denguiria* (Boyd and Newell, 1979) (fig. 17).

In Tunisia, questionable *Claraia* is associated with *Denguiria* in shaly and locally bituminous Permian strata suggestive of an anoxic environment. The shells characteristically are compacted and otherwise distorted and poorly preserved.

Ichikawa (1958: 136) was the first to direct attention to an attachment scar on the right umbo of *Claraia clarae*. Our examples of *C. stachei* also have this feature. However, a substrate of attachment has not been identified.

Claraia is similar to its probable Carb. ancestor, *Dunbarella* (fig. 17: 4–6). That genus has a shallower, more open byssal notch and lacks the byssal foramen, and the anterior auricle is larger than that of *Claraia*. RVs of *Dunbarella* frequently bear split ribs. Both valves in the two genera are thin with a prominent outer prismatic layer.

Claraia has long been considered a reliable indicator of early Triassic age but this is no longer tenable. Ichikawa (1958), Nakazawa (1977), and Yin (1982, 1985a, 1990) cited 33 named Griesbachian species and six from the Dorashamian. None of these is based on pop-

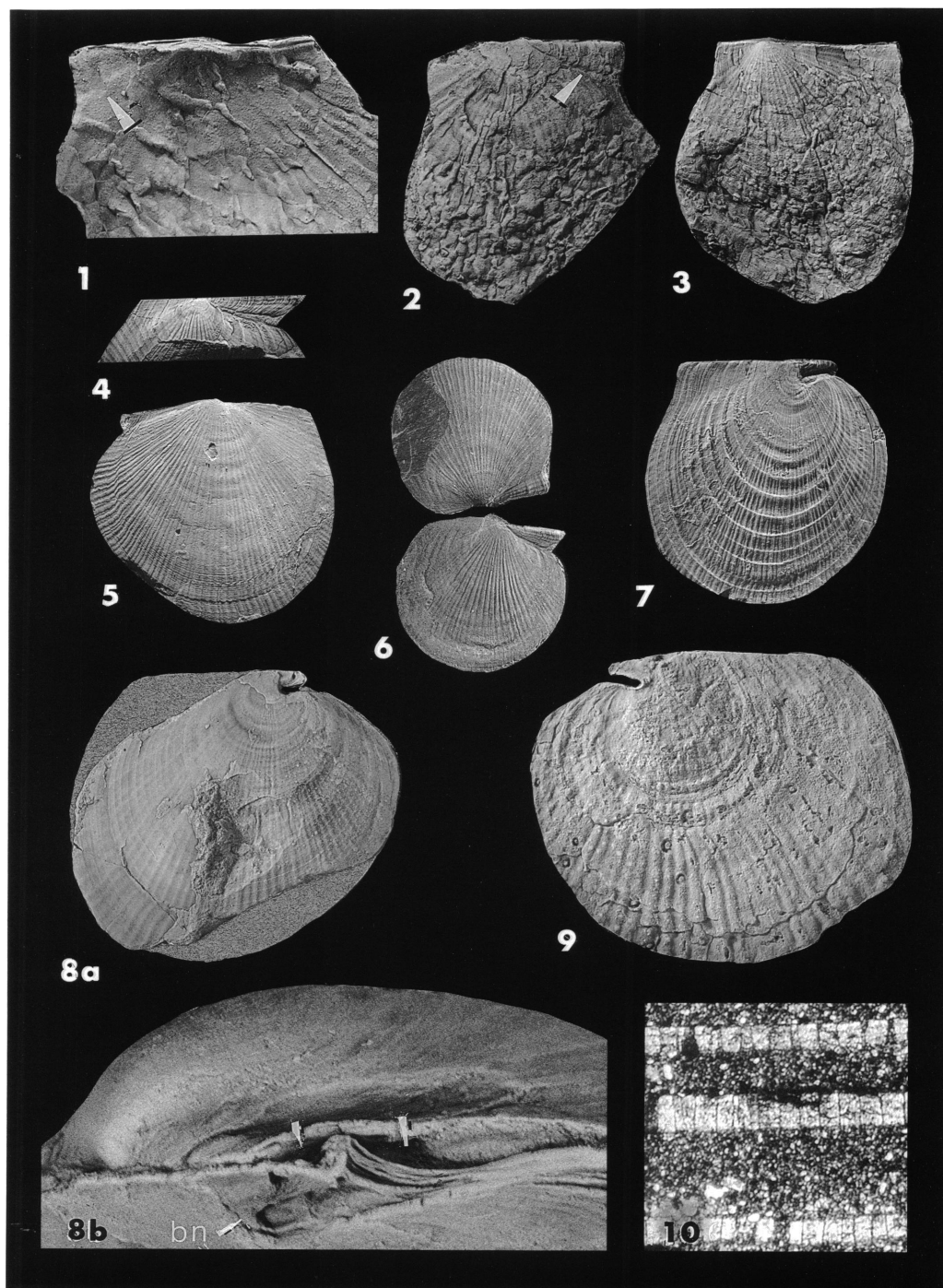


Fig. 17. Pterinopectinidae compared; all calcareous specimens.

1-3, *Denguiria azzouorum* Boyd & Newell, showing track of closed byssal slit (arrows). Late Guadalupian (E27), Djebel Tebaga, Tunisia (Boyd & Newell, 1979). 1, RV × 3, interior, USNM cat. 264363; 2, RV × 3, exterior, USNM cat. 264364; 3, LV, × 2, USNM cat. 264365.

ulation analysis. Very likely there are many specific synonyms.

The nomenclatural problem is compounded by the generally poor preservation and imprecise documentation of place and age.

The experts cited above, daunted by inadequate samples and excessive taxonomic splitting of *Claraia*, have found it useful to gather the many named categories into informal groups. One of these (*C. decidens*) is the basis for our new genus, *Crittendenia*, which is dissimilar to the others.

Nakazawa (1977) distinguished the following groups:

Claraia clarae (von Hauer): umbones smooth, mature part of shell with strong comarginal folds and weak to strong radial ribs.

C. stachei Bittner: entire shell ornamented with ribs; comarginal folds weak or lacking.

C. aurita von Hauer: shell covered with fine fila; comarginal folds weak and irregular, or lacking.

C. decidens Bittner: ornamentation weak, or lacking; LV strongly inflated.

Leonardi (1943) and Nakazawa (1977) noted that some regional forms and intra-population variants intergrade, but these scholars did not hesitate to add new ones to the list of names. Z. M. Zhang (1980) introduced *Pseudoclaraia* for Upper Permian shells supposedly morphologically intermediate between *Dunbarella* and *Claraia*, and Fang (1993) named *Claraioides* for forms with a deep byssal embayment. We class them with *Claraia*. Quantitative and comparative studies of the many local populations are needed.

For convenience we recognize two grades of *Claraia*: those in which comarginal wrinkles, or folds, are dominant (e.g., *C. clarae*:

fig. 17: 7) and those in which multicostation is conspicuous and comarginal ornament inconspicuous (*C. stachei*, fig. 17: 8, 9).

Claraia clarae (von Hauer), 1851

Figure 17: 7

Posidonomya clarae (von Hauer), 1851.

Pseudomonotis clarae Bittner, 1901.

Claraia clarai Leonardi, 1943.

Claraia clarae Ichikawa, 1958.

Claraia clarai Tozer, 1961.

Claraia clarai Ciriacks, 1963.

Claraia clarai Nakazawa, 1977.

Claraia ciriacksi Nakazawa, 1977.

DIAGNOSIS: Having few, usually weak, concentric folds, many slender intercalating costae, and small posterior auricles on both valves.

DISTRIBUTION: L. Griesbachian of west. N. Am., Eurasia.

DISCUSSION: The considerable range of variation, both regional and local, of shells similar to *Claraia clarae* indicates many local populations. However, nothing is gained by naming them before they have been established quantitatively as populations.

Claraia stachei Bittner, 1901

Figure 17: 8–10

Claraia stachei Bittner, 1901.

Claraia stachei Spath, 1930.

Claraia stachei Newell and Kummel, 1942.

Claraia stachei Tozer, 1961.

Claraia stachei Ciriacks, 1963.

DIAGNOSIS: Radial ornament dominant over comarginal; posterior auricle indistinct (table 2).

DISTRIBUTION: L. Trias. and U. Perm.; east.

4–6, *Dunbarella knighti* Newell, for comparison with *Denguiria*. Distinctive right auricle and subquadrate notch. M. Penn., central U.S. (after Newell, 1937). 4, RV × 2, KU cat. 237.1; 5, LV × 1, KU cat. 237.2; 6, a pair × 1, KU cat. 237.3.

7, *Claraia clarae* (von Hauer), RV × 1, L. Trias., Alberta, Canadian Geol. Surv. cat. 14196 (Tozer, 1961).

8–10, *Claraia stachei* Bittner. 8a, × 1, Griesbachian, Wordie Creek, East Greenland, Canadian Geol. Surv. cat. 22737 (Tozer, 1961); 8b, same as 8a, × 5, byssal notch (arrow at left), exhalant opening (arrow at right); 9, *Claraia stachei*, characteristic RV, × 2, inner surface of outer layer showing apparent reversal, L. Trias. (Dinwoody Fm.), east. Nevada, UW loc. B7078, cat. A2357; 10, *Claraia stachei*, SEM × 150, prismatic outer layer fragments in bituminous limestone, same locality as 17.9, AMNH cat. 43305.

TABLE 2
Claraia stachei
 Calcareous Valves, Dinwoody Fm., AMNH loc. B8246

Len	H	Len/H	Hin Len	Len	H	Len/H	Hin Len	BN Len	BN H
Left valves				Right valves					
38.9	38.6	1.0	18.0	37.9	32.2	1.2	20.3	3.2	0.6
33.9	33.7	1.0	15.6	34.1	32.0	1.1	20.2	2.3	0.5
37.9	33.2	1.1	16.2	31.9	30.1	1.1	17.2	2.3	0.6
29.7	29.2	1.0	14.5	29.6	27.6	1.1	16.9	2.2	0.6
27.1	24.4	1.1	13.0	26.6	26.6	1.0	15.6	2.1	0.5
25.0	24.2	1.0	12.6	24.6	22.9	1.1	14.4	2.8	0.6
22.2	22.3	1.0	11.1	22.0	20.3	1.1	11.9	2.2	0.6
22.6	21.5	1.1	10.3	18.5	18.6	1.0	10.4	2.1	0.6
19.8	19.5	1.0	9.6	19.8	17.6	1.1	12.7	2.8	0.4
19.0	19.3	1.0	9.1	10.0	10.0	1.0	6.1	2.0	0.5

Greenland, Novaya Zemlya, south. Alps, and west. U.S.

DISCUSSION: If the naming of *C. clarae* was involved, that of *C. stachei* is even less secure. When Spath (1930) used this name for Greenland specimens, he noted that Bittner's (1901) *C. stachei* was introduced without illustrations, adequate diagnosis, or precise provenance data.

Type specimens are unknown, so *C. stachei* could be regarded as a nomen nudum. It could be legitimized by designation of neotypes by experts who have access to the fossiliferous Griesbachian outcrops in the Tyrol. Meanwhile, because *C. stachei* is so widely used, we follow Spath's 1930 interpretation, based on Greenland material.

Spath's Greenland *C. stachei* was collected in exotic white limestone blocks (olistoliths) of the Cape Stosch Fm. Other associated and lithologically indistinguishable blocks of this coarse breccia contained a characteristic U. Perm. (Zechstein) assemblage (Newell, 1955). According to Stemmerik (Greenland Geol. Surv., Copenhagen, letter of September 19, 1994), "With respect to the white blocks at Kap Stosch, they almost certainly are erosional products derived from what we now call the Wegener Halvø Formation. This unit contains elsewhere common bivalves in the transgressive deposits."

More recently, Muromtseva (1984) found *Claraia stachei* in a Zechstein fauna in Novaya Zemlya. This supports the conclusion

that the Greenland *C. stachei* is also of U. Perm. age, and not the reliable L. Trias. zonal guide previously supposed.

Our hypodigm is a collection from bituminous shale in the L. Dinwoody Fm. (L. Trias.) west of Montello, Nevada (AMNH loc. B7078). The valves have all been flattened by compaction. Furthermore, dissolution of the inner ostracum accompanied by precipitation of a uniform crust on the exterior of the thin prismatic outer surface has resulted in a decal-like image reversal (fig. 17: 9). The apparent exterior of the shell is, in fact, the inner surface of the outer ostracum (Boyd and Newell, 1976). Anterior and posterior features are reversed, and costae are represented by grooves.

Both valves are multicostate, except posteriorly, where ribs are obscure; costae are added by intercalation on both valves, not by splitting. The LV does not have a recognizable anterior auricle. Anterior auricle of the RV is very small, overhanging the narrow, parallel-sided byssal slit. Below the straight dorsal edge, the posterior margin is smooth, with a nearly circular curve.

Genus *Denguiria* Boyd and Newell, 1979

TYPE SPECIES: *Denguiria azzouzororum* Boyd and Newell, 1979, OD.

DIAGNOSIS: Byssal notch secondarily closed, rear auricle subquadrate, otherwise like *Claraia*.

DISTRIBUTION: M. Perm.; Tunisia.

Denguiria azzouzorom

Boyd and Newell, 1979

Figure 17: 1-3

Claraia posidoniformis Termier and Termier, 1977;
U. Perm., Tunisia.

DIAGNOSIS: Auricles flattened, poorly differentiated; beaks approximately at mid-length of hinge; multicostate.

DISTRIBUTION: M. shaly beds of the Perm. (Capitanian, according to Skinner and Wilde, 1967) sequence at Djebel Tebaga, Tunisia (Newell et al., 1976).

DISCUSSION: Possibly cemented or free living, as indicated by lack of an adult byssus, but a cicatrix has not been recognized.

Genus *Pterinopectinella* Newell, 1938

TYPE SPECIES: *Pterinopectinella welleri* Newell, 1938. Pennsylvanian, U.S.

DIAGNOSIS: Pterinopectinids with small tubular spines on radial ribs of both valves. Except for spines, this genus resembles some species of Devonian *Pterinopecten* and *Pseudaviculopecten*.

DISTRIBUTION: Miss., Great Britain; Penn., Midcontinent U.S.; L.-M. Perm. (Leonardian and Guadalupian), West Texas.

Pterinopectinella spinifera

Newell and Boyd, new species

Figures 18, 19

DIAGNOSIS: Shell irregularly plicate with some erratic minor ribs between primaries; shell slightly higher than long, nearly infracrescent; ligament area broad at maturity with 10-15 fine ligament chevrons; auricles short, posterior one poorly differentiated; beak about one-third behind front of hinge; spines numerous, up to 10 mm long, slender, cylindrical, arched downward toward shell margin, with ends approaching or even embedded in shell surface; byssal notch (fig. 19: 2) bordered internally by strong collar (table 3).

DISTRIBUTION: Leonardian and early Guadalupian ls. in silicified reef and near reef facies, Glass Mts., and Guadalupe Mts., West Texas, locs. AMNH 500, 504, 505, 507, 512, 628, 629, USNM 702b, 703c, 714m, 726o, 728.

DISCUSSION: We have many silicified fragments referred to this species because of the

ornament, but only two relatively complete left valves.

This species differs from Carboniferous members of the genus (Newell, 1937) in a few salient characters. Specimens of *P. spinifera* are more infracrescent, with a slight forward obliquity of about 76° on the holotype (fig. 18: 1) as measured from a median costa. The beaks are situated about one-third behind the front of the hinge. The byssal notch is bordered internally by a strong collar. The stratigraphically nearest species, the Penn. *P. welleri* Newell, 1938, has stubby spines, and only about a dozen uniform split ribs on RVs and an equal number of primaries on LVs.

SUPERFAMILY AVICULOPECTINACEA

MEEK AND HAYDEN, 1864

DIAGNOSIS: Auriculate shells with external, typically alivincular, ligament; byssal notch typically deep; well-developed anterior auricular sulcus on LV.

DISCUSSION: Many U. Paleozoic pectinoids were formerly referred to the genus *Aviculopecten* M'Coy, 1851, and even today there is some confusion about the nature of this genus. When the Irish paleontologist Frederick M'Coy (1851) introduced *Aviculopecten*, he distinguished Lower Carboniferous scallops from younger ones by the supposed lack of a resiliifer. We shall show that this generalization probably was in error. Unfortunately, his fossils were not well preserved and the originals appear to be lost (Newell, 1937).

In the next few decades the Paleozoic and Lower Triassic pectinoids were grouped on external traits, first into a subfamily, Aviculopectininae, and more recently a superfamily, Aviculopectinacea (Waller, 1978). As they became subdivided, classifications of some of the extinct genera and species were based on inadequate evidence. Consequently, we have undertaken a general rearrangement established, in part, on new evidence.

The numerous shared characters testify to close relationships among genera of this superfamily. Although we have generally adopted traditional criteria for distinguishing between them, there are difficulties in the mosaic distributions of characters and the probabilities of sporadic convergence.

Two such characters are the shape of growth

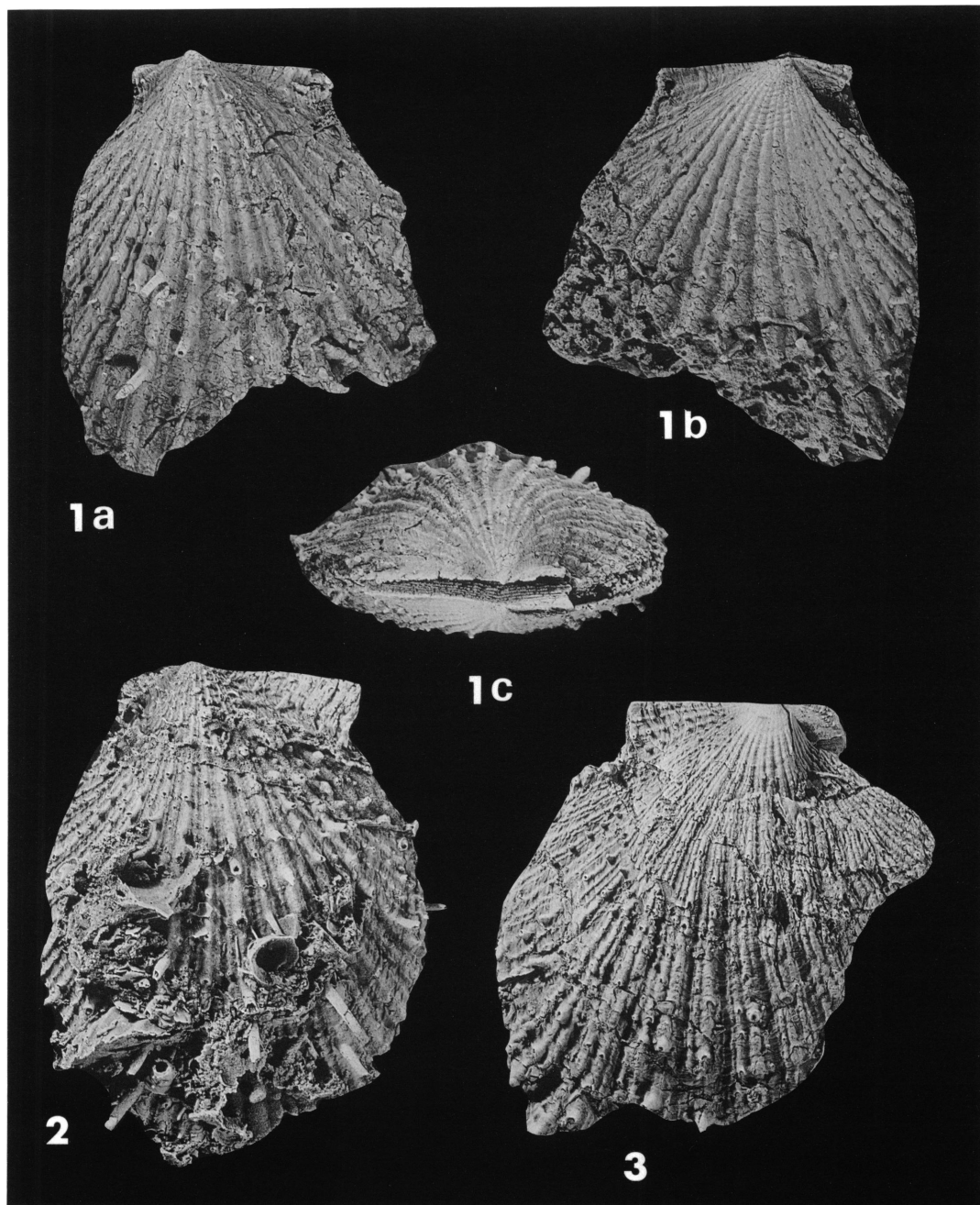


Fig. 18. *Pterinopectinella spinifera* Newell and Boyd, n. sp., silicified, all views $\times 1$, Leonardian (Cathedral Mt. Fm.), Glass Mts., West Texas. 1a-c, Holotype with conjoined valves showing fasciculation and spines of both valves. Lower valve (RV) is the less convex, USNM loc. 702b, cat. 388876; 2, LV with epizoans, USNM loc. 726-o, ct 388877; 3, RV, USNM loc. 702-b, cat. 431318.

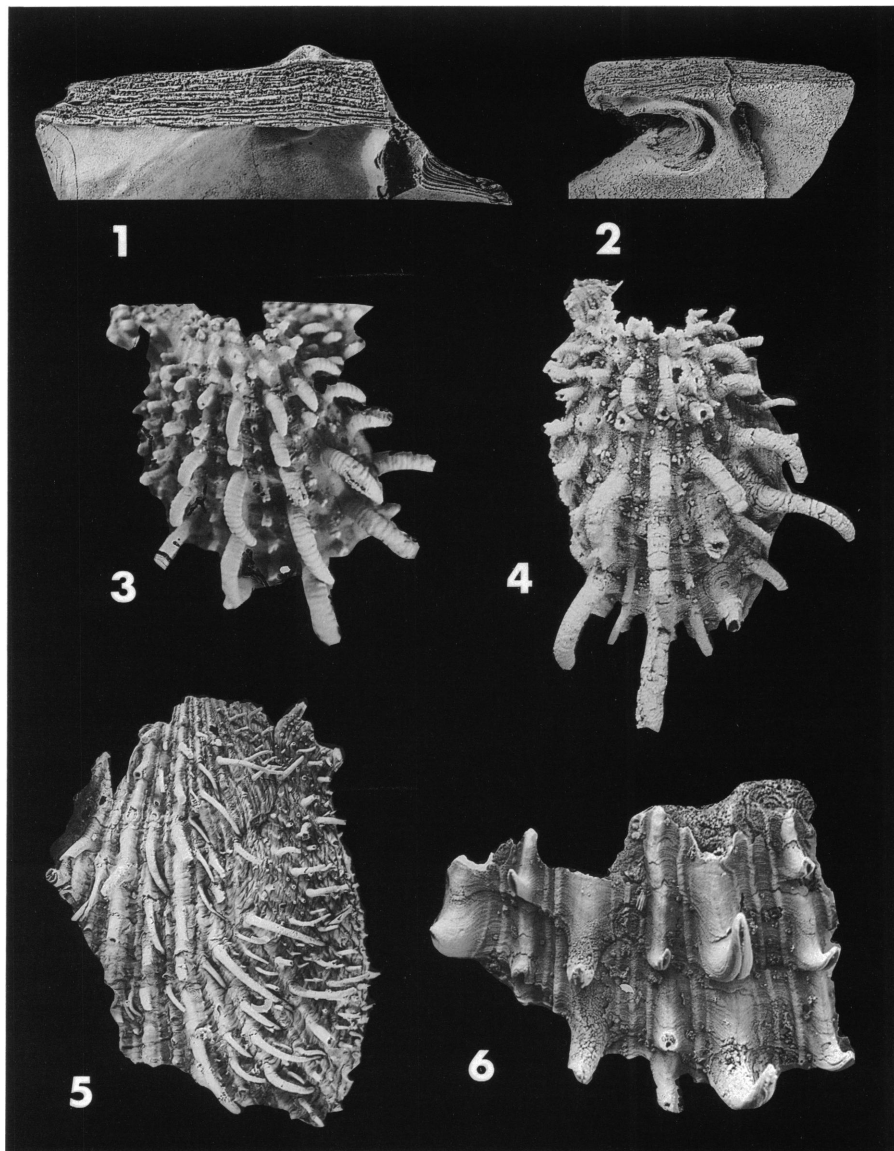


Fig. 19. *Pterinopectinella spinifera*, Newell and Boyd, n. sp. (except 19.6), silicified. Leonardian and Guadalupian, Glass Mts. (except 19.4, Guadalupe Mts.), Texas. 1, LV hinge, $\times 1.3$, characteristic flat duplivincular area with many chevron grooves, Guadalupian (Road Canyon Fm.), USNM loc. 703-c, cat. 388871; 2, RV $\times 1$, byssal notch bounded by circular collar, same loc., cat. 431317; 3, juvenile LV $\times 6$, Leonardian (Cathedral Mt. Fm.), AMNH loc. 500, cat. 43306; 4, Juvenile, LV $\times 4$, shows tubular spines, Guadalupian (L. Getaway Ls.), USNM loc. 728, cat. 388880; 5, LV approx. $\times 1$, showing marginal decrease in spine size and tendency for some to become embedded in the shell, Leonardian (Cathedral Mt. Fm.), AMNH loc. 500, cat. 43308; 6, hyote spines of *Heteropecten vanvleeti* (Beede), $\times 4$, for comparison, Leonardian (Cathedral Mt. Fm.), AMNH loc. 500, cat. 43309.

lines as they swing away from, or toward, the beaks in the intercostal troughs, and the way in which new ranks of costae are added as

the total number increases with growth. Waterhouse (1969), an enthusiastic student of these fossils, has emphasized both traits to

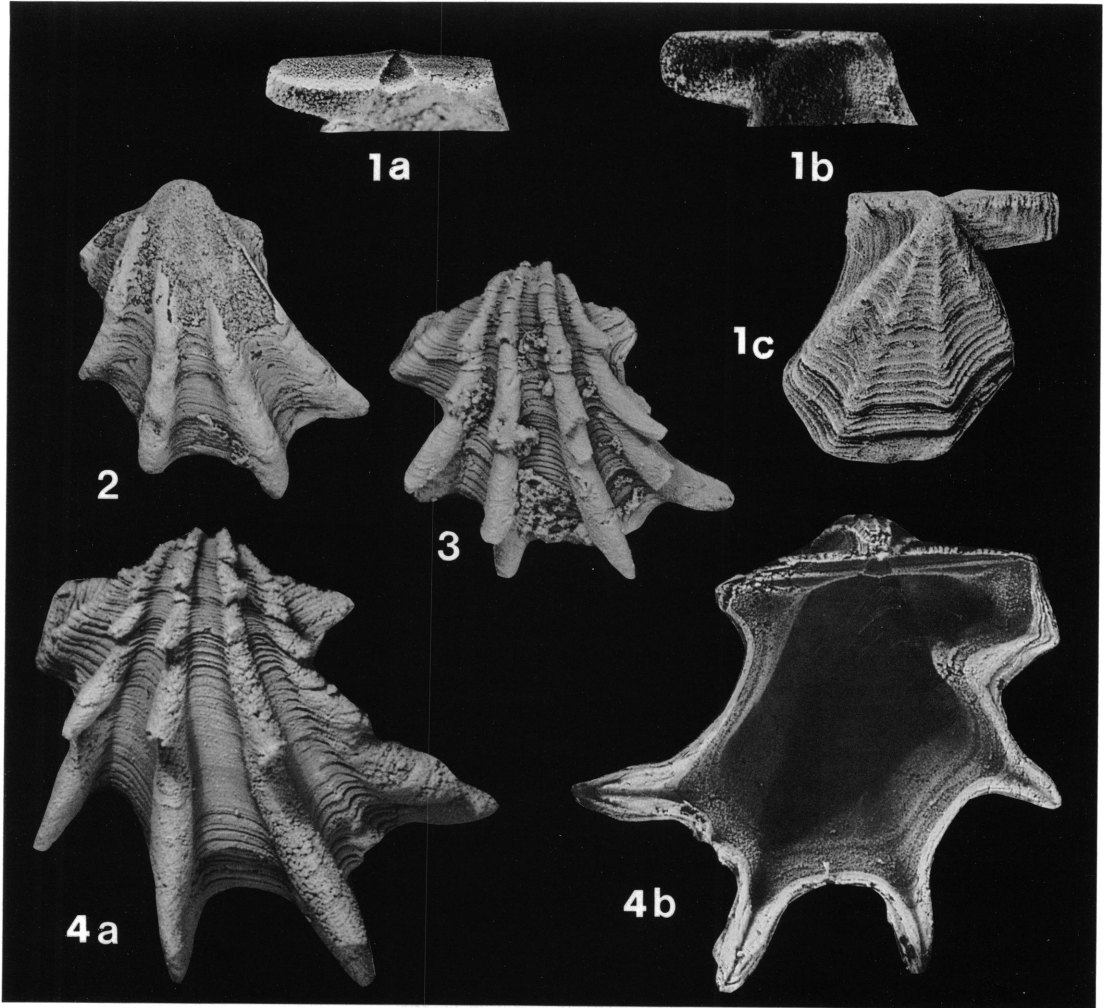


Fig. 20. *Cassianoides kingorum*, n. genus and n. sp., silicified. All except 4a, b $\times 5$, Guadalupian (L. Getaway Ls.) of West Texas, AMNH loc. 512. 1a-c, RV, cat. 43404, specimen 1a tilted to show byssal notch and external alivincular ligament; 2, 3, LVs, showing retrocrescent form and massive hyote spines, respectively cat. 43401, 43402; 4a, b, LV $\times 5.5$, holotype, showing lamellar hinge teeth, cat. 43405.

distinguish aviculopectinacean genera. These features are usually ill-defined and too variable to be relied upon, with the exception of a few plicate genera, such as *Acanthopecten*, or *Limiopecten*, which have intercostal spines. In addition, the latter has conspicuous nacreous elements in the shell (Newell and Boyd, 1990).

CASSIANOIDIDAE

NEWELL AND BOYD, NEW FAMILY

DIAGNOSIS: Small shells, retrocrescent, higher than long, RV nearly flat, LV strongly

convex, with a few widely spaced primary costae and a few comarginal ranks of stout, tubular hyote spines; RV spineless, with subdued radial ornament, anterior auricle large and truncate with wide byssal notch; posterior auricle small or lacking; ligament external, amphidetic; resilifer central, small, symmetrical; hinge of LV with pair of lamellar teeth on each side of resilifer.

DISTRIBUTION: L.-M. Perm., West Texas.

Cassianoides Newell and Boyd, new genus

TYPE SPECIES: *Cassianoides kingorum* Newell and Boyd, new species.

TABLE 3
Pterinopectinella spinifera Newell and Boyd, n. sp.
Cathedral Mt. Fm., USNM locs. 702-b and
726-o, Respectively

Len	H	Len/H	Conv	Hi Len	Aur Len	Um An
Left valves						
45.2	62.2	0.73	15.0	29+	13+	82
55.8	70.0	0.80	13.6	36.5	12.3	78

DIAGNOSIS AND DISTRIBUTION: Same as family Cassianoididae.

DISCUSSION: Somewhat remindful of the Alpine Triassic *Cassianella* Beyrich, 1862, *Cassianoides* is distinguished by many differences, including lack of an internal septum, the possession of large, spinose ribs, and a prominent byssal notch. *Cassianoides* is morphologically isolated, without evident ancestors or descendants.

Cassianoides kingorum Newell and Boyd,
new species
Figure 20

DIAGNOSIS: Both valves ornamented with closely spaced fila, interrupted on LV by four or five comarginal ranks of ventrally directed stout hyote spines borne by four prominent radial ridges; RV ornamented by four widely spaced costae; cardinal area of RV perpendicular to plane of commissure (table 4).

DISTRIBUTION: L.-M. Perm., West Texas; Leonardian, AMNH loc. 600; Leonardian, USNM loc. 728f, 428h; Wordian, USNM loc. 720e, 702d, 702e, 706c, 706, 706e, 723t, 703, 703c, 703j, 728, 732; AMNH loc. 512.

DISCUSSION: The new name honors Philip and Robert King, outstanding students of West Texas Permian rocks and fossils. The species characterization is based on about 300 well-preserved, silicified specimens from the L. Getaway Ls. (Cherry Canyon, Wordian) from AMNH loc. 512; almost all are LVs, only three are RVs. The inner ostracum probably was aragonite, because it is missing or poorly preserved.

FAMILY ETHERIPECTINIDAE
WATERHOUSE, 1982

Aviculopectinidae of authors.

DIAGNOSIS: Valves inequiconvex and paradiacordant; resilifers prosocline, ornamen-

TABLE 4
Cassianoides kingorum
Measurements minus spines, L. Getaway Ls.,
AMNH loc. 512

Len	H	Len/H	Conv	Hin Len
Left valves				
7.5	8.5	0.88	3.2	7.3 (h) ^a
6.2	8.0	0.77	3.2	6.5
5.9	7.7	0.77	3.6	6.6
5.6	7.2	0.78	3.1	5.7
5.4	7.2	0.75	2.9	4.5
5.2	6.9	0.75	2.9	5.7
4.9	6.2	0.79	3.0	4.6
4.1	5.9	0.69	2.8	4.9
3.4	4.8	0.71	2.3	4.2
2.6	3.7	0.70	1.8	3.6
Right valves				
6.5	7.4	0.88	1.6	5.6
5.3	5.7	0.93	1.4	5.1
3.9	3.9	1.00	0.8	4.1

^a Holotype.

tation multicostate, discrepant, subdued on RVs; RV outer layer prismatic; inner layer crossed lamellar or foliate; LV outer layer homogeneous, foliate, or even absent; inner layer crossed lamellar, crossed foliate, or nacreous (only in Limipectininae).

DISTRIBUTION: Cosmopolitan, L. Carb.-L. Trias.

DISCUSSION: A majority of Upper Paleozoic multicostate pectinoids belong to this family. It is a difficult group for which adequate characterization is needed but hard to supply.

The nomenclatural type of *Etheripecten* is *E. striatura* Waterhouse, 1963, a small Permian retrocrescent shell (fig. 21: 2) that resembles juveniles of most Carb. and Perm. multicostate pectinoids.

The name of the New Zealand genus is 12 years younger than *Heteropecten*, a taxon that is well characterized by the work of Kegel and da Costa (1951) and Rocha-Campos (1970).

SUBFAMILY ETHERIPECTININAE
WATERHOUSE, 1982

DIAGNOSIS: Inner shell layer crossed lamellar, or crossed foliate.

DISCUSSION: By contrast, the closely similar Limipectininae is characterized by nacre-

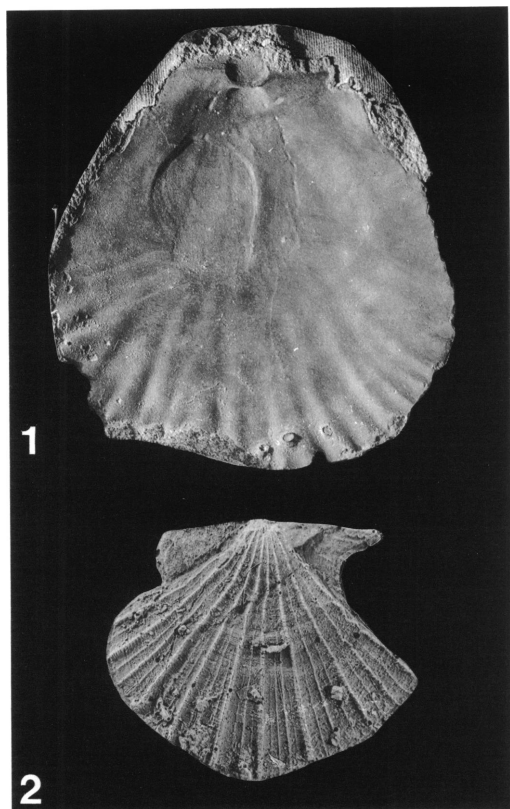


Fig. 21. 1, Large *Heteropecten*? cf. *Aviculopecten mitchelli* Etheridge and Dun, rubber cast of calcareous mold, LV $\times \frac{1}{2}$, L. Perm. periglacial deposits (Marlborough Group) near Bronte, Tasmania. Univ. Tasmania Geol. Dept. cat. 21537; 2, *Etheripecten striatura* Waterhouse, LV $\times 2$, rubber cast of holotype, a juvenile (type species of *Etheripecten*), L. Perm. (Arthurton Gp.), New Zealand Geol. Surv. loc. 533, cat. TM 3630.

ous layers (Newell and Boyd, 1990). That subfamily was covered at length in that publication.

Genus *Heteropecten* Kegel and Costa, 1951

Figure 22

Aviculopecten and *Deltopecten* of authors.
Etheripecten Waterhouse, 1963.
Paradoxipecten Y. X. Zhang, 1981.
Corrugopecten Waterhouse, 1982.
Fletcheripecten Waterhouse, 1982.
Squamuliferipecten Waterhouse, 1986.

TYPE SPECIES: *Aviculopecten catherinae* Reed, 1930; OD, Lower Permian, Brazil.

DIAGNOSIS: Adults generally infracrescent, prominent auricular sinuses; elongate hinge margin; with few costae introduced in successive ranks by intercalation and splitting; with or without hyote spines.

DISTRIBUTION: Cosmopolitan, Miss.-L. Trias.?

DISCUSSION: Most citations of *Aviculopecten*, *Deltopecten*, and *Etheripecten* belong here. Bittner (1899) described several shells as *Eumorphotis* from the L. Trias. of eastern Siberia. Some of these resemble *Heteropecten*, and need reinvestigation.

The published examples of *Heteropecten* generally are small to intermediate specimens less than 30 mm in height, but Branson (1930) cited a Permian shell from Wyoming (as *Aviculopecten vanvleeti*), with a height of 70 mm. We have seen another specimen 156 mm high in the Geological Survey of India referred to *Pseudomonotis gigantea* Waagen, from the *Productus* Ls. of the Salt Range. Some of Etheridge and Dun's (1906) Gondwana "paleopectens" from New South Wales exceed 165 mm in height. Although they are too imperfect for certainty, we tentatively include them in *Heteropecten* (see fig. 21: 1).

We have fragmentary, but extraordinarily well-preserved crossed foliate shells of *Heteropecten* (cf. *H. laticostatus*) from the Permian of western Australia (U.W.A. accession no. 9667). The specimens that we illustrate (figs. 23-26) were collected by R. A. Hobson from the south bank of the Wooramel River, Wooramel District (Madeline Formation, fide Dickins). They are conspecific with material illustrated by Hosking (1931) under the name *Deltopecten subquiquelineatus* M'Coy, var. *comptus* Dana, 1847. We provisionally identify the Hobson collection as *Heteropecten* cf. *laticostatus* (Waterhouse, 1982: 26).

The microstructure of the Australian examples consists of foliated calcite, as determined by independent x-ray diffraction analyses at the American Museum and the University of Wyoming. This is interesting because the inner layer (no. 2) of the American examples of *Heteropecten* was almost certainly secreted as aragonite (cited as *Aviculopecten* by Newell, 1937: 44).

Generally, the diagenetic conversion in fossils of primary aragonite to calcite results in some recrystallization and destruction of

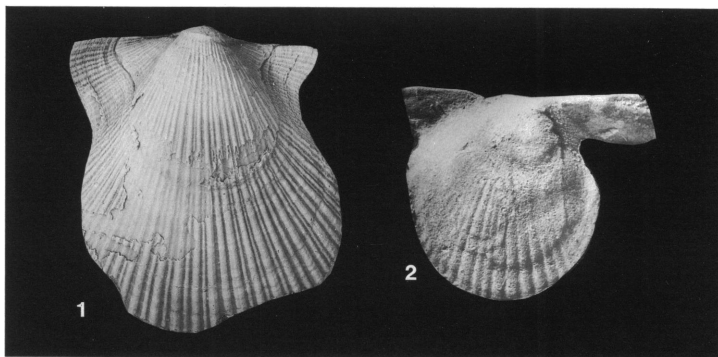


Fig. 22. *Heteropecten catherinae* (Reed), calcareous specimens, $\times 1$, type species of *Heteropecten*, showing characteristic compact ornamentation and irregular division of ribs, L. Perm. (Rio Bonito Fm.), southern Brazil, Univ. Sao Paulo, Inst. Geosci. loc. 416, cat. 7-1112 [photos courtesy A. Rocha-Campos]. 1, LV; 2, RV.

biogenic structural details. Because of the excellent preservation of the crossed foliate fabric and low angle of the folia, we infer that these Australian shells were secreted as primary calcite, a suggestion also made by Waterhouse in another connection (1982: 10).

Many of the Australian pectinoids lived in periglacial seas adjacent to the Gondwana icecap. It is improbable, however, that low temperatures alone were the direct cause of the development of calcite from dominantly

aragonitic shells. There is no simple correlation of mineralogy and temperature among scallops living today. On the contrary, calcite and aragonite bivalves now live together in a wide range of temperatures. Because of uncertainty of the significance of the regional differences in microstructure and mineralogy of the Australian and North American shells, we consider the original shell composition and microstructure as taxonomically less significant than the details of morphology.

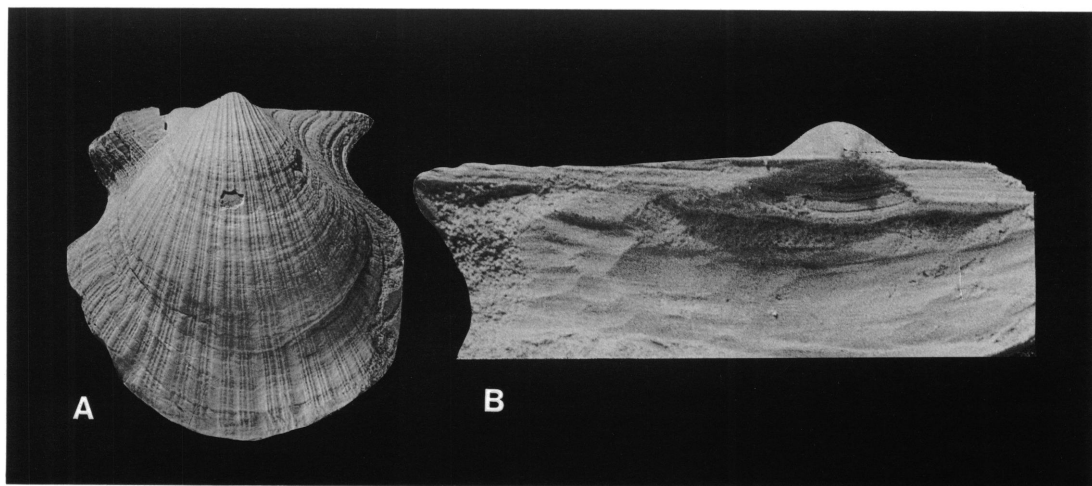


Fig. 23. *Heteropecten* cf. *laticostatus* (Waterhouse), calcareous LV, outer and hinge views, L. Perm. (Lyon Gp., probably Madeline Fm.), West. Australia, s. bank Wooramel River, UWA cat. 121 049. A, $\times 2$, showing several ranks of inserted minor costae and broad major costae that tend to split; B, hinge of same, $\times 5$, horizontal increments suggest seasonal growth.

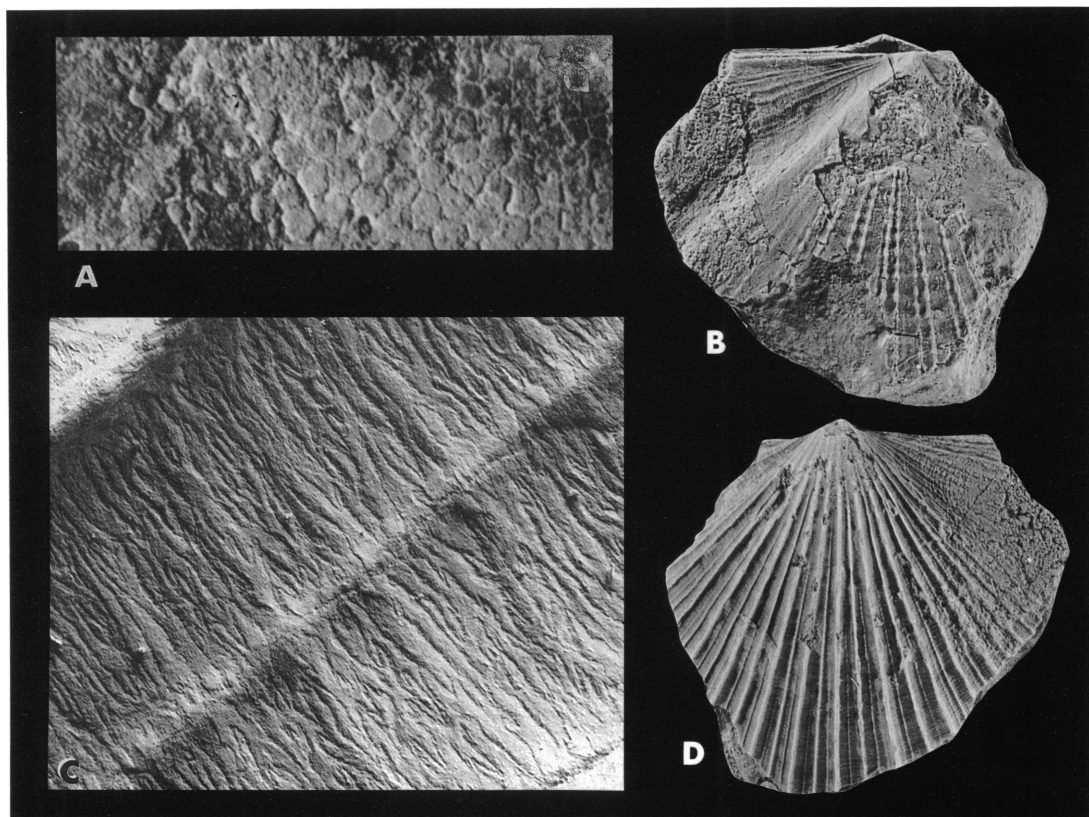


Fig. 24. *Heteropecten* cf. *laticostatus* (Waterhouse), SEM photographs of single calcareous juvenile, same loc. as figure 23, UWA cat. 121 050. A, B, RV, respectively $\times 75$ and $\times 4$, showing surface prisms and multicostate ornamentation; C, D, LV, respectively $\times 75$ and $\times 4$, showing surficial edges of first-order calcite folia.

Heteropecten vanvleeti (Beede), 1902

Figure 27

Aviculopecten vanvleeti Beede, 1902.

Aviculopecten vanvleeti Newell, 1940.

DIAGNOSIS: Form and ornamentation variable, usually slightly higher than long, LV with three or more ranks of costae the largest bearing sparse hyote spines. Hinge margin sloping gently away from the beaks; left anterior auricle commonly slightly larger than posterior one (table 5).

DISTRIBUTION: Leonardian–L. Guadalupian, West Texas. USNM loc. 702c, 703b, 706e, 706b, 706z, 721u, 728; AMNH loc. 503, 512. Whitehorse Sandstone–Dozier Dolomite, L. Guadalupian, Oklahoma and Texas, KU loc. 1, 4–9.

DISCUSSION: Our largest sample, from a

single locality (AMNH 512), consists of about 100 silicified specimens, mostly fragmentary LVs.

Accurate measurements can be determined for only a few. RVs are very scarce, represented by broken hinges and umbones. The right anterior auricle is more prominent than that of the LV, a discrepancy caused by a deep byssal notch and asymmetrical growth of the juvenile part of the disc.

The angle formed by the anterior margin of the disc and the hinge margin of RVs is nearly 70° whereas the comparable angle for the posterior margin is about 40° . The prominent resilifer in these shells varies in length/height ratio from 1.5 to 2.9 in 21 LVs.

Major ribs of mature LVs bear erratically distributed hyote spines. In a sample of 22 specimens, spines first appear during growth

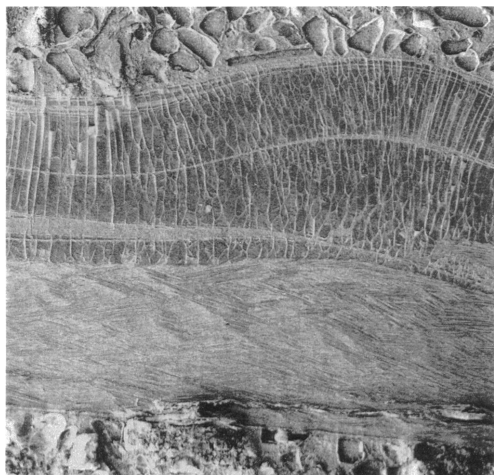


Fig. 25. *Heteropecten* cf. *laticostatus* (Waterhouse), SEM micrograph of unaltered calcite shell, transverse section, cellulose peel, RV $\times 37.5$, replica of inner crossed foliate and outer prismatic layers, L. Perm. (U. Lyon Fm.), west. Australia, AMNH loc. 3120, cat. 44064 (stub 253).

at an average shell height of 14 mm, with an observed range of 11–22 mm. Spine-bearing ribs vary in number from 4 to 11 and they pinch and swell along their courses, with relief less than, or equal to, their width. They develop into weak plications at the ventral margin of the largest shells. Growth lines vary in regularity and configuration from convex apically to nearly straight between costae.

VARIABILITY: Individuals of our sample from AMNH loc. 512 (L. Getaway Ls.) display the entire range of characters cited by Newell (1937) as distinguishing several of his species (then referred to *Aviculopecten*). These variable traits include length/height ratio, relative size, and presence or absence of weak posterior lobation of the disc.

This extreme variability illustrates the instability of names based on isolated variants.

Genus *Eumorphotis* Bittner, 1901

TYPE SPECIES: *Pseudomonotis telleri* Bittner, 1899, L. Trias., Ussuri region, east. Siberia. SD Cossmann, 1902.

DIAGNOSIS: Strongly inequivalved, both valves multicostate with intercalated costellae, with left umbo protruding prominently beyond a moderately high ligament area; RV

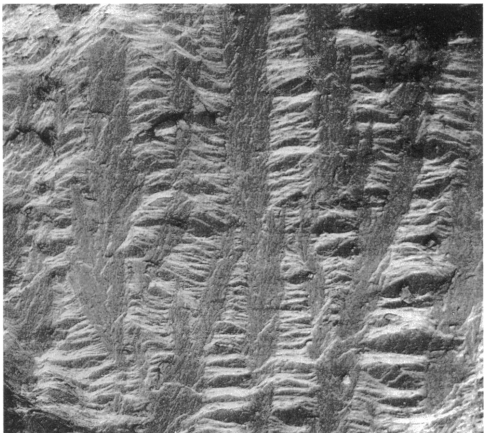


Fig. 26. *Heteropecten* cf. *laticostatus* (Waterhouse), LV, SEM $\times 75$, rough chip, shows concentric calcite folia of no. 2 layer of endostracum, same locality as preceding, cat. 44063 (stub 147).

nearly flat; posterior auricle not well differentiated from umbonal flank; posterior auricular sinus shallow, or absent.

DISTRIBUTION: L. Trias., Pangea.

DISCUSSION: This taxon embraces varied L. Trias. pectinoids named by Bittner (1901) to distinguish them from similar Upper Paleozoic forms. Apparently he was influenced more by geologic age than by morphology. *Eumorphotis* is very close to *Heteropecten* and it is not always practical to distinguish Triassic forms from similar Permian species.

The LV of the type species, *E. telleri*, and some of our examples of *E. multififormis* are slightly more tumid than similar *Heteropec-*

TABLE 5
Heteropecten vanyleeti
L. Getaway Ls., AMNH loc. 512

Len	H	Len/H	Conv
Left valves			
75+	78+	—	23.0
42.5	51.6	0.82	14.7
30.1	33.6	0.90	9.2
26.1	33.6	0.78	7.8
23.3	29.0	0.80	7.3
20.4	22.9	0.89	7.0
18.4	20.4	0.90	6.1
17.5	20.3	0.86	5.5
15.3	16.9	0.91	4.6
12.9	14.9	0.87	3.9

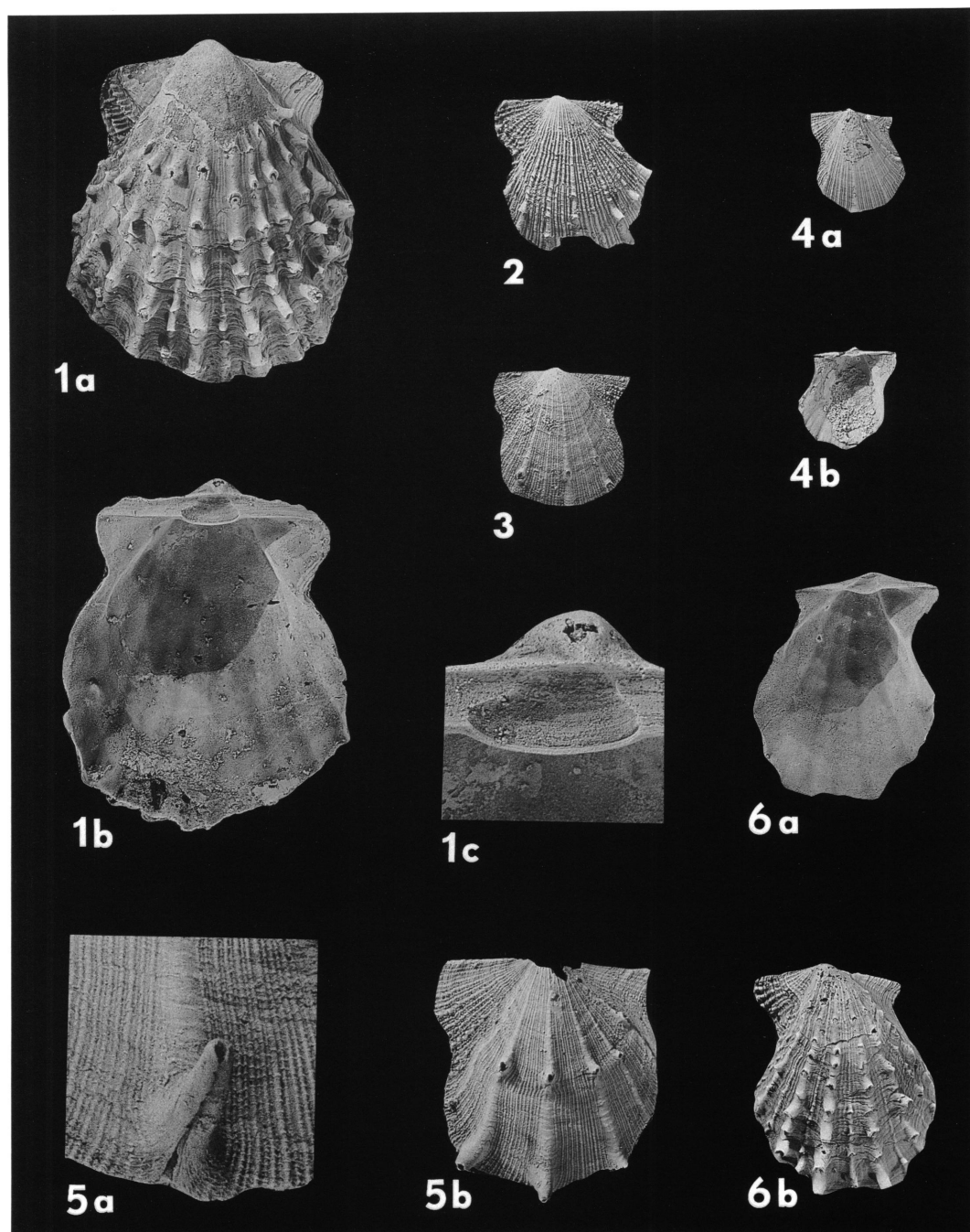


Fig. 27. *Heteropecten vanvleeti* (Beede), silicified LVs, all $\times 1$, except 1c and 5a, which are $\times 3$, showing marked variation in a single population sample, Guadalupian (L. Getaway Ls.), West Texas, AMNH loc. 512. 1a-c, Radial furrows on inner surface of 1b, cat. 42893; 2, cat. 43317; 3, cat. 43316; 4a, b, cat. 43318; 5a, hyote spine, b, cat. 43319; 6a, b, cat. 43315.

ten shells, and the tetragonal resilifer of our *E. multiformis* (apparently previously overlooked) is distinctive. In another context these might be regarded as specific, rather than generic, differences.

A welcome summary of the named species of *Eumorphotis* has been published by Broglio Loriga and Mirabella (1986). Their work emphasizes how little is known about these frequently cited bivalves. The authors recorded a literature of some 38 species ranging from Perm. to M. Trias., a taxonomy generally based on small samples of poorly preserved material.

Judging from published illustrations, the shells range from multicostate to nearly smooth, and apparently, many are composite and worn internal molds. Important details of musculature, hinge characters, and shell microstructure generally are unknown. We are optimistic, however, that patient exploration will eventually improve this situation.

Eumorphotis multiformis (Bittner), 1899

Figure 28

Pseudomonotis multiformis Bittner, 1899. L. Trias., S. Ussuri, Siberia.

Pseudomonotis (Eumorphotis) multiformis Bittner, 1900

Eumorphotis multiformis Newell and Kummel, 1942. Dinwoody Fm., L. Trias., Montana.

Eumorphotis multiformis Ciriacks, 1963. Dinwoody Fm., Idaho, Montana; Thaynes Fm., Utah.

DIAGNOSIS: RVs vary from slightly convex to flat; right auricular sulcus narrow and deep, expressed internally as anteroventral buttress extending from anterior margin of resilifer, and terminating in subcircular collar around inner margin of byssal notch; costae of LV intercalate in three or more ranks, narrow, subequal, crowded and commonly warped or offset at growth lines; exterior of RV rugose, occasionally with fine, intercalate costellae. The largest left valve from Thaynes Fm. at Fall Creek, Idaho, is 60 mm long, 66 mm high, and 20 mm in convexity.

Cardinal area broad, with subparallel dorsal and ventral margins, and a deep subtrapezoidal posteriorly extended resilifer; LV ligament area approximately in commissural plane, while that of RV forms 55° angle with commissural plane.

DISTRIBUTION: This species has been reported from the L. Trias. of Siberia, Spitzbergen, and several Asian localities (Yin, 1985a: 584). Ciriacks (1963) recorded it from the Dinwoody Formation of Idaho and Montana, and the Thaynes Fm. of Utah. Our own specimens are from the Thaynes of Utah and Idaho and the Virgin Memb. of the Moenkopi Fm. of Nevada (AMNH 315, B7854, B7858, B7861, B8517, B8830, B8840).

DISCUSSION: Our best material consists of a dozen valves, six left and six right, from the U. Thaynes at Fort Douglas, Utah. These are preserved in an unusual mode as quartz silt casts in limestone matrix (table 6).

Genus *Spyridopecten*

Campbell and McKelvey, 1972

TYPE SPECIES: *S. monstrosus* Campbell and McKelvey, 1972, OD. Miss., N.S.W., Australia.

DIAGNOSIS: Circular, with moderately short hinge and shallow byssal notch; both valves with numerous crowded costellae in two or three ranks increasing in number with growth, typically by bifurcation.

DISTRIBUTION: Miss., Australia; U. Penn., Texas.

DISCUSSION: This genus is distinguished from other Etheripectinidae by the large number of very slender, split ribs on both valves.

Spyridopecten sp.

Figure 29: 1a-c

DESCRIPTION: In addition to general family characters, RV about 142 mm high and long; LV 152 mm high and 144 mm long; both valves with about 100 costellae intercalated in three ranks; biconvexity about 16 mm; the resilifer somewhat extended backward; 8 mm long by 2.5 mm high.

DISCUSSION: This solitary specimen (USNM cat. no. 388890) is introduced here because of its similarity to the Permian *Undopecten keyserlingianus*, described on the following pages. It was collected by Mrs. J. H. Renfro, of Jacksboro, Texas, in the Graham (Jacksboro) Shale, U. Penn., 3½ mi e of Jacksboro, Texas (USNM loc. Renfro 43).

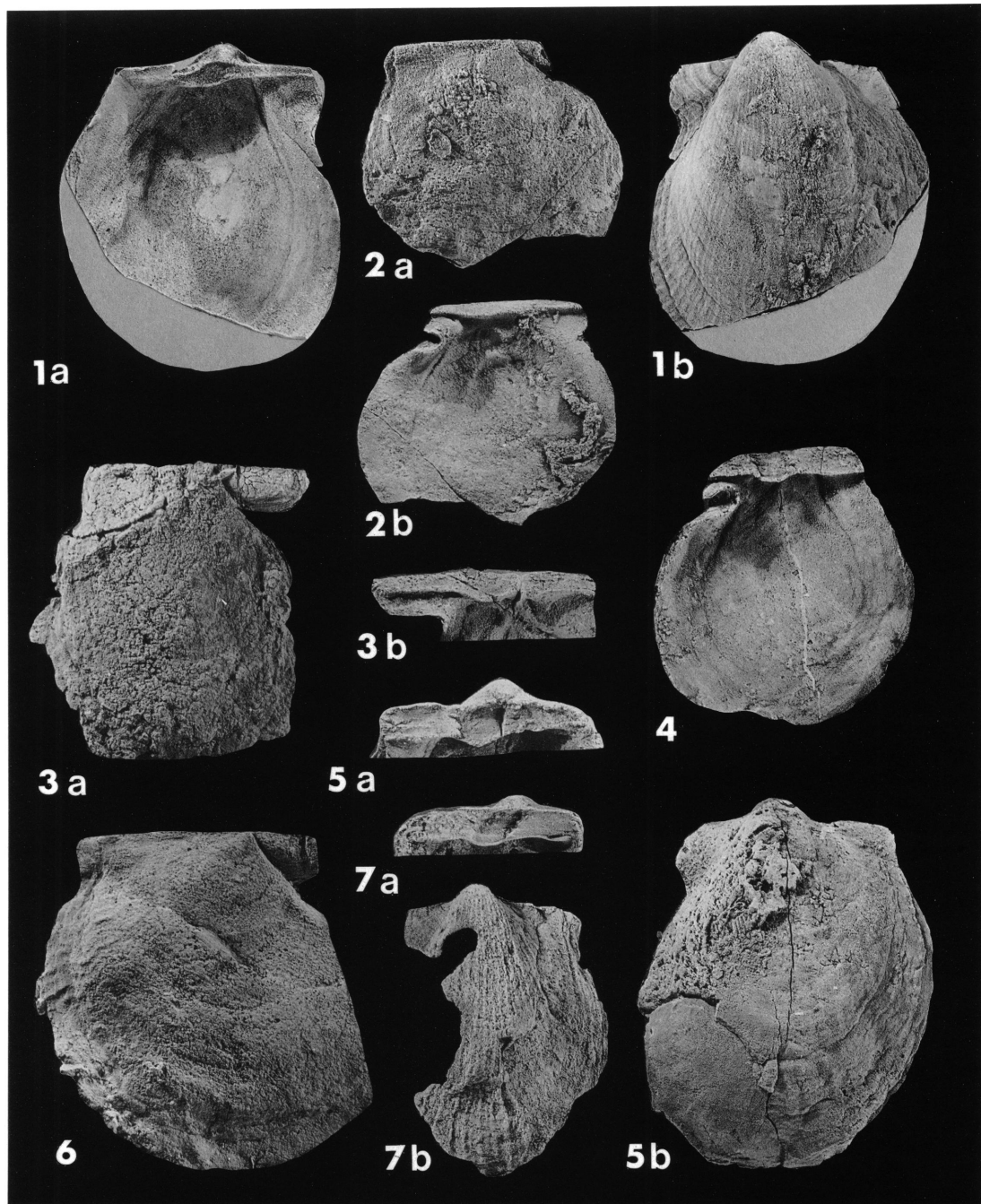


Fig. 28. *Eumorphotis multiformis* (Bittner), $\times 1$, natural casts of quartz silt (U. Thaynes Fm.), Ft. Douglas, Utah, AMNH loc. 315. 1a, b, LV, cat. 42892; 2a, b, RV, subcircular form characteristic of RVs, cat. 42894; 3a, b, RV, characteristic form of byssal notch and anterior auricle, cat. 42896; 4, RV, pallial line and byssal collar, cat. 42895; 5a, b, LV, characteristic hinge and tongue-shape of this valve, cat. 42897; 6, RV, with traces of radial ornamentation, cat. 43275; 7a, b, LV, trapezoidal resiliifer, and characteristic shell form, cat. 42898.

Genus *Undopecten* Waterhouse, 1982

Morrisipecten Muromtseva and Guskov: 1984, L. Perm., west. Siberia.

Altaipecten Yang and Chen, 1985, Perm., China.

TYPE SPECIES: *Pecten fittoni* Morris, 1845, OD, L. Perm., Tasmania; *Deltopecten fittoni* (Morris), Fletcher and Dun, 1929, New South Wales, Australia.

DIAGNOSIS: Shell subcircular, 15–25 plicae; both valves with crowded, slender costellae that increase early in growth, by both intercalation and bifurcation; almost equiconvex with a moderately short hinge and deep byssal notch.

DISTRIBUTION: L. Perm.; Tasmania, New South Wales, and west. Siberia.

DISCUSSION: A frequently cited species of *Undopecten* from the Sakmarian of the Russian Timan region (Irgina River), is *Pecten keyserlingianus* Stuckenbergl (1875) (fig. 29: 2), better known from Licharew (1927) by the name *Aequipecten keyserlingi*. Excepting the plicae, *Undopecten* resembles the Carboniferous *Spyridopecten*. Most known examples of *Undopecten* are right valves. The valves seem to be concordant. Shell microstructure unknown.

Genus *Girtypecten* Newell, 1938

TYPE SPECIES: *Aviculopecten sublaqueatus* Girty, 1908, OD, Newell, 1938, Guadalupian. Texas.

DIAGNOSIS: Subcircular, multicostate, with symmetrical grid of widely spaced radial and comarginal ridges; auricles elongate, sometimes acuminate; LV with recurved hemicylindrical hyote spines at ridge intersections; RV nearly flat, spineless, with subdued grid; resilifer posteriorly elongate.

DISTRIBUTION: L.-M. Perm., west. U.S.; U? Perm., Pakistan, and China.

DISCUSSION: Chen (1962) described *Girtypecten spinosus* from southwest. China (U. Perm.?). Another is *Acanthopecten chitralensis* from India and Pakistan, described by Reed (1925). This material extends the geographic range of *Girtypecten* but is inadequate to characterize populations.

TABLE 6
Eumorphotis multiformis

Len	H	Len/H	Conv	Hin	Len	AMNH Locs.
Left valves						
59	66	0.89	24	?		B7858
?	64	—	25	48		B8830
55	57+	—	17	33		B8830
52	61	0.85	?	38		B7854
43	54	0.80	19	30		315
41	56	0.73	19	?		315
40+	44+	—	19	29		315
?	43+	—	15	24		315
40	38+	—	13	27		315
39	44	0.89	14	37		315
Right valves						
52	52+	—	?	39+		B7858
50+	50	—	8	35+		315
46	50+	—	6	46		B8840
39+	44+	—	7	33		315
39	43	0.91	8	28+		315
39	41	0.95	7	17+		315
38	?	—	5	23		315
38	42	0.91	5	30		B8517
24	24	1.00	1	23		B8517
12	14	0.86	1	14		B8517

Girtypecten sublaqueatus (Girty), 1908

Figure 30

Aviculopecten sublaqueatus Girty, 1908.

Girtypecten sublaqueatus Newell, 1938.

DIAGNOSIS: Disc subcircular, auricles elongate, set off by broad, almost semicircular marginal sinuses; distal end of posterior auricle acuminate, commonly extending to, or beyond, posterior edge of disc; ornament variable. Five to twelve widely spaced primary costae separated by costellate or nearly smooth areas; costellae fine, increasing in number with shell growth to as many as 20 between pairs of costae; posterior and anterior costae located at disc boundaries, but 10 or 12 comarginal ridges continue across auricles and fade near border in largest specimens (table 7).

DISTRIBUTION: Common to abundant in M. Perm. of West Texas (U. Wolfcampian–U. Guadalupian), and rare in the Franson Memb. Park City Fm. (Guadalupian, Wyoming). USNM loc. 702, 702a–e, 702ent., 702un.,

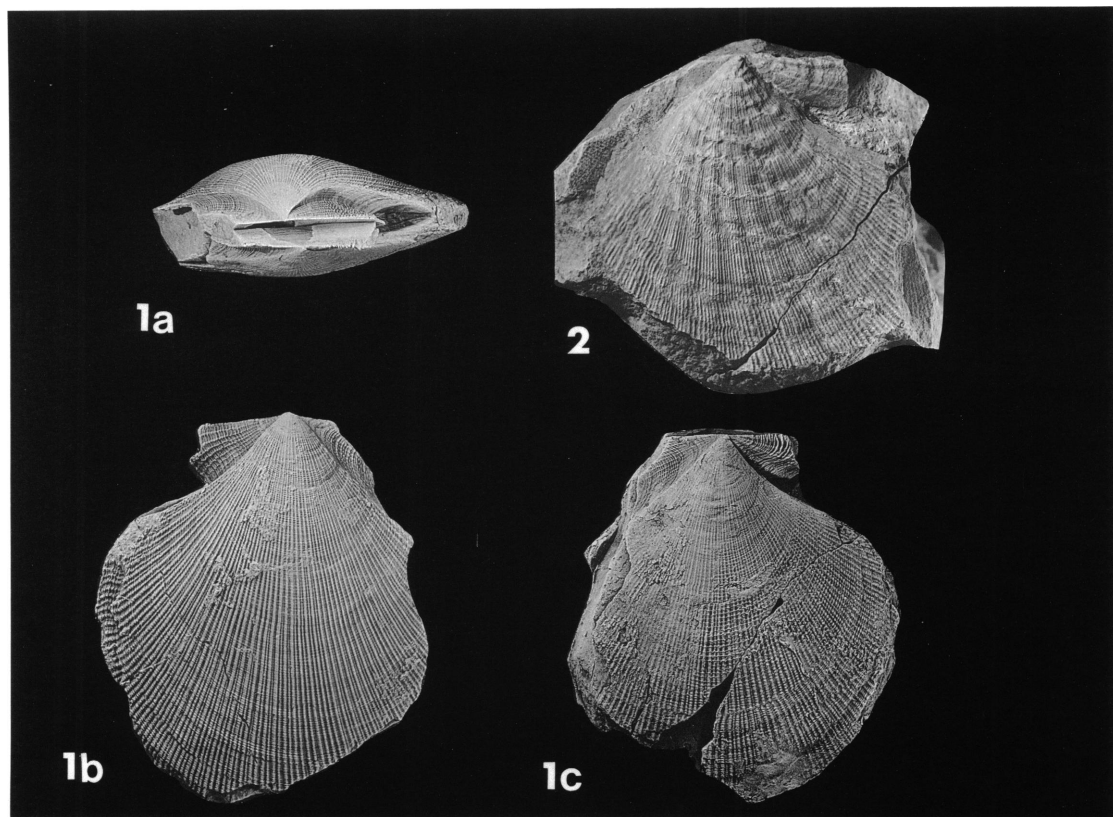


Fig. 29. **1a-c**, *Spyridopecten* sp., $\times 1$, calcareous, showing fine, uniform ornamentation of genus, U. Penn. (Jacksboro Fm.), Texas, USNM loc. Renfro 43, cat. 388890; **2**, *Undopecten keyserlingianus* (Stuckenberg), $\times 1$, calcareous, L. Perm. (Sakmarian Fm.), Irgina River, Timan, Russia. [Photo courtesy VSEGEI, St. Petersburg]

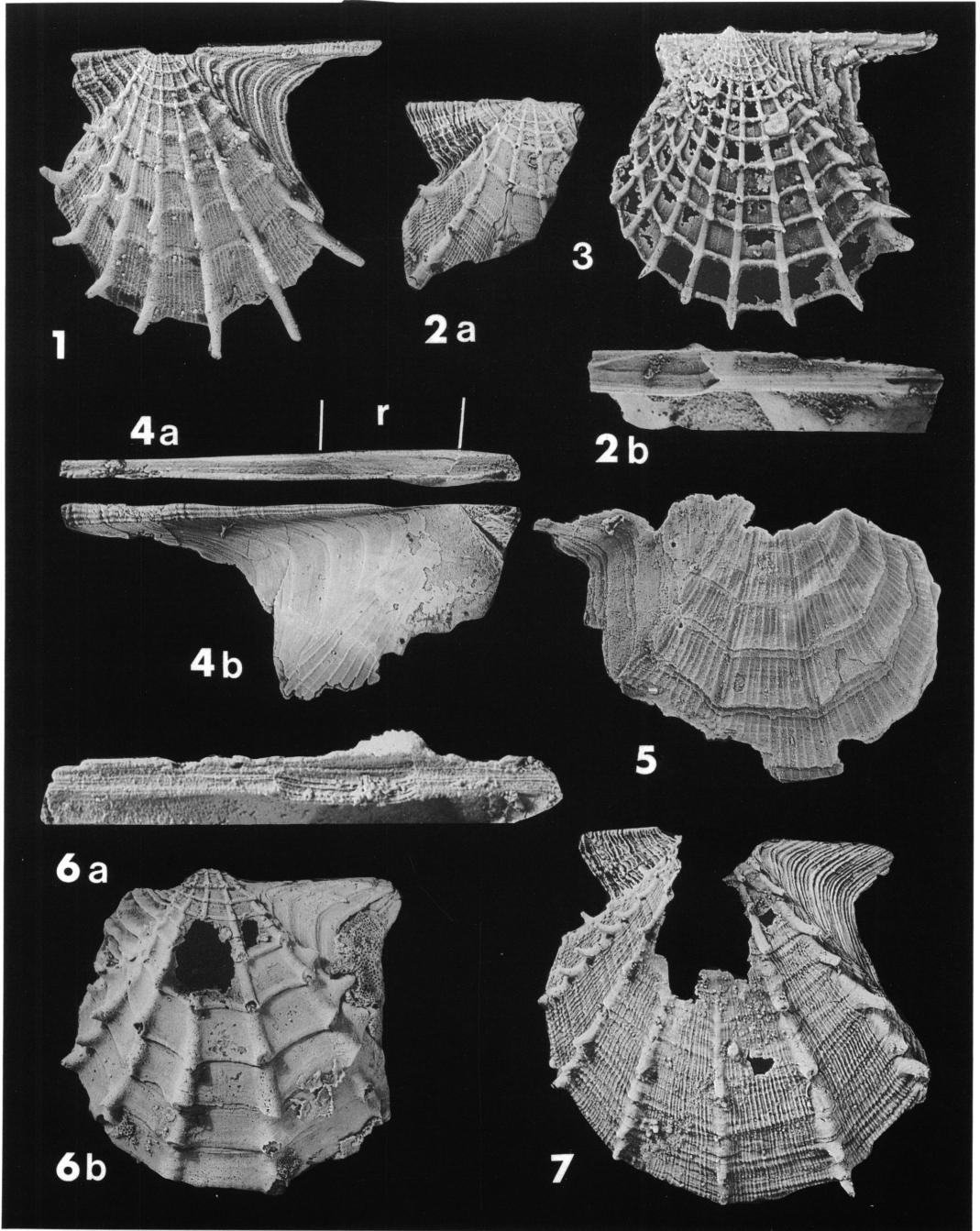
703, 703a-c, 706, 706b, c, 706e, 708, 710d, 719x, 719z, 720d, 721s, 721u, 722L, 723t, u, 724b, 726d, 726o, 726z, 727j, 727u, 728, 728e, 731, 732, 732j, 733q, 760. AMNH loc. 29, 369a, 500, 505, 512.

DISCUSSION: Only two identifiable fragments of RVs are in our collection that contains some 350 fragmentary LVs. We take this to indicate that the species (and the genus) probably had paradiscordant valves. The

inner ostracum, originally aragonite, is missing or poorly preserved.

The primary costae first appear more or less simultaneously within the first two or three mm of shell growth and they are preceded by comarginal ridges. The grid of the RV is strikingly different from the left (fig. 30: 5). The comarginal ridges are low and the primary radial ornament consists of shallow grooves, each with a median costella; the in-

Fig. 30. *Girtypecten sublaqueatus* (Girty), silicified, Perm. (Guadalupian and Leonardian), West Texas. **1**, LV, $\times 2$, showing symmetrical distribution of spines and latticed ornamentation; comarginal ridges become obsolescent with growth, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 382768; **2a, b**, LV, $\times 1$, showing alivincular external ligament, Guadalupian (L. Getaway Ls.), AMNH loc. 512, at. 43284; **3**, decorticated LV, $\times 2$, in which strong comarginal ridges are maintained throughout growth, Leonardian (Cathedral Mt. Fm.), USNM loc. 703-b, cat. 431312; **4a, b**, fragment of RV, $\times 2$, with



spineless ribs, and asymmetrical resiliifer (between markers), Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43283; 5, RV, $\times 2$, showing subdued ornamentation as compared with LV, Guadalupian (lens between Willis Ranch and Appel Ranch Fms.), USNM loc. 706b, cat. 388874; 6a, b, LV, respectively $\times 2$ and $\times 1$, unusual in lack of costellae between major ribs, striae on resiliifer suggest seasonal growth, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 382777; 7, LV, $\times 1$, showing marked obsolescence of comarginal ornamentation with growth simulating the ornamentation of *Heteropecten*, Guadalupian (Willis Ranch Fm.), USNM loc. 706, cat. 388873.

TABLE 7
Girtypecten sublaqueatus
Willis Ranch Fm., USNM loc. 706e

Len	H	Len/H	Conv	Um An
Left valves				
37.1	40.6	0.91	11.4	80
35.0	32.7	1.07	8.1	83
33.9	32.8	1.03	—	—
30.5	30.1	1.01	6.9	77
23.5	23.6	0.99	5.6	78
20.4	20.9	0.98	4.5	81
13.5	13.6	0.99	3.1	87
12.2	12.0	1.02	2.8	78
9.6	9.7	0.99	2.7	73
5.8	5.7	1.02	1.6	70
3.6	3.7	0.97	1.2	68

tervening costellae are similar to those of the LV. The umbonal angle in most specimens is between 70 and 80°; the ratio of hinge margin over disc length, 0.72–1.55, without any central tendency.

Intrapopulation variability is illustrated by LVs from locality 512 (Guadalupian, L. Get-away). In these the L/H ratio of the resilifer ranges from 2.7 to 5.4. Ontogenetic discontinuation of the comarginal ornament occurs late, at valve height ranging from 13 to 27 mm, where a few specimens also lose costellae.

Genus *Vnigripecten* Muromtseva, 1984

TYPE SPECIES: OD, *Aviculopecten phosphaticus* Girty, 1910. Permian (Phosphoria), U.S.

DIAGNOSIS: LV as in other Etheripectini-dae; RV nearly flat, with several long spines along hinge margin; suborbicular, paradiscordant, and discrepant, with numerous poorly developed costae, generally of a single order, a few being added by splitting; auricles elongate, byssal margin broad and open.

DISTRIBUTION: M. Perm., Wyoming; and U. Perm., Siberia.

DISCUSSION: The dorsal spines are unique among Paleozoic pectinoids, possibly also younger forms. Consequently, their function is conjectural. Ciriacks (1963) suggested that the spines stabilized the shell on the sea floor. We doubt that there was a functional byssus since there is no byssal notch.

Vnigripecten phosphaticus (Girty), 1910
Figure 31

Aviculopecten phosphaticus Girty, 1910.
Aviculopecten phosphaticus Ciriacks, 1963.
Vnigripecten phosphaticus Muromtseva, 1984.

DIAGNOSIS: Shell somewhat variable in form from retrorescent to prorescent; LV strongly convex, multicostate with second-order costae added by intercalation; RV less convex, suborbicular, ornamented with long

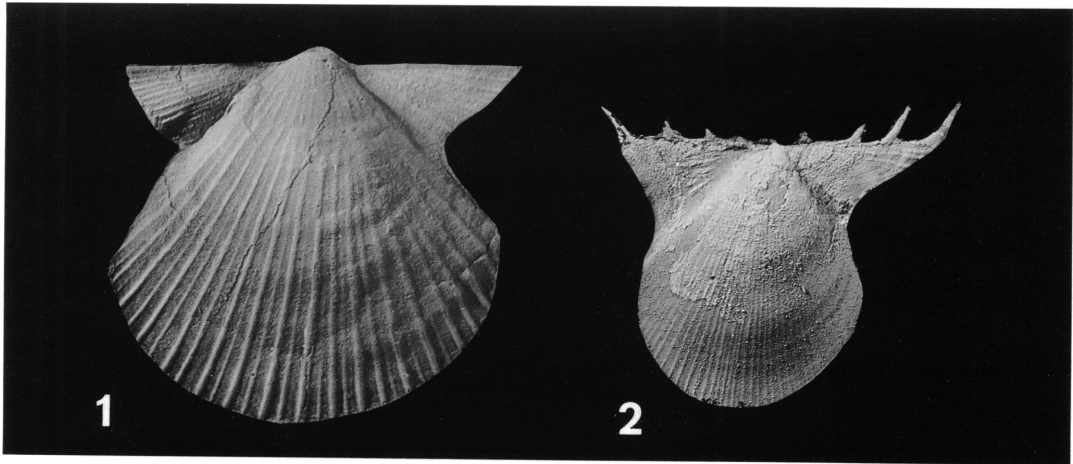


Fig. 31. *Vnigripecten phosphaticus* (Girty), calcareous, M. Perm. (Phosphoria Fm., Meade Peak Memb.), near Cokeville, Wyoming, 1, LV, ×3, with convergent characters of *Heteropecten*, USNM cat. 140473; 2, RV, ×2.6, showing fine costellae and remarkable cardinal spines of *Vnigripecten*, USNM cat. 140475.

TABLE 8
Vnigripecten phosphaticus
From Ciriacks, 1963, p. 47

Len	H	Hin Len	Hin Sp	Sh C	PAC	AAC
Left valves						
32.0	31.5	—	—	54	—	—
23.5	24.0	—	—	44	—	—
19.0	19.0	15+	—	33	?8	—
17.5	17.0	14+	—	35	7	8+
18.0	16.5	18.0	—	35	9	12
15.5	16.0	13+	—	33	7	?6
16.0	15.0	18.0	—	29	13	15
8.5	8.0	8.5	—	27	7	9
9.0	7.5	9.0	—	23	7	9
8.5	7.5	9.0	—	21	6	?7
Right valves						
15.5	14.5	21.5	?10	—	—	—
12+	14.0	16.0	8	35+	9	6+
15.5	13.0	21.0	9+	—	—	—
10.5	12.5	15.0	8	36	—	?3
9.5	11.5	14.5	8	30+	6+	5+
12.5	10.5	16.5	6+	—	—	3+
8.0	7.5	11.0	9+	—	—	—
8.0	7+	12.5	?8	—	—	—
8.0	7.0	11.0	9	—	?5	3+
5.5	6.0	9.0	4	—	—	—

dorsal spines varying in number up to 10 (table 8).

DISTRIBUTION: According to Ciriacks (1963), this species is abundant in the Phosphoria Fm. (Meade Peak Memb.), Cokeville, Wyoming, and common to abundant at the same horizon at Hot Springs, Idaho. It is rare in the Meade Peak at Coal Canyon, Wyoming. The calcareous and cherty mudstones at these and other nearby localities are phosphatic. Muromtseva (1984) reported this species from the Ufimian and Kazanian (U. Perm.) over a broad area in the Siberian Arctic (Novaya Zemlya, Gizhigi River Basin, Kanin Peninsula, and the Pechora Basin).

ACANTHOPECTINIDAE
NEWELL AND BOYD, NEW FAMILY

DIAGNOSIS: Uniplicate, orbicular, or slightly retrocrescent with elongate auricles, posterior acuminate and longer than anterior one; LV, and rarely RV, crossed by regularly spaced comarginal ridges bearing distally pointed spines between plicae; ornament of RV subdued; outer layer RV prismatic, prob-

ably paradiscordant; outer layer LV uncertain, probably homogeneous.

DISTRIBUTION: Widely distributed in north. continents, rare in Gondwanaland (Dickins, 1963); Miss.-U. Perm.

DISCUSSION: The spines are located between ribs and externally concave unlike the tubular spines of most Etheripectinidae, or the solid spines of some Annuliconchidae.

Genus *Acanthopecten* Girty, 1903

TYPE SPECIES: *Pecten carboniferus* Stevens, 1858, OD. Penn., Illinois.

DIAGNOSIS: As for family.

Acanthopecten coloradoensis
(Newberry), 1861
Figures 32, 33

Pecten (*Monotis*?) *coloradoensis* Newberry, 1861.
Acanthopecten coloradoensis Newell, 1938.
Acanthopecten coloradoensis Ciriacks, 1963.

DIAGNOSIS: Subcircular, slightly elongate, dorsal margin straight; LV anterior auricle defined by narrow sulcus and overhanging

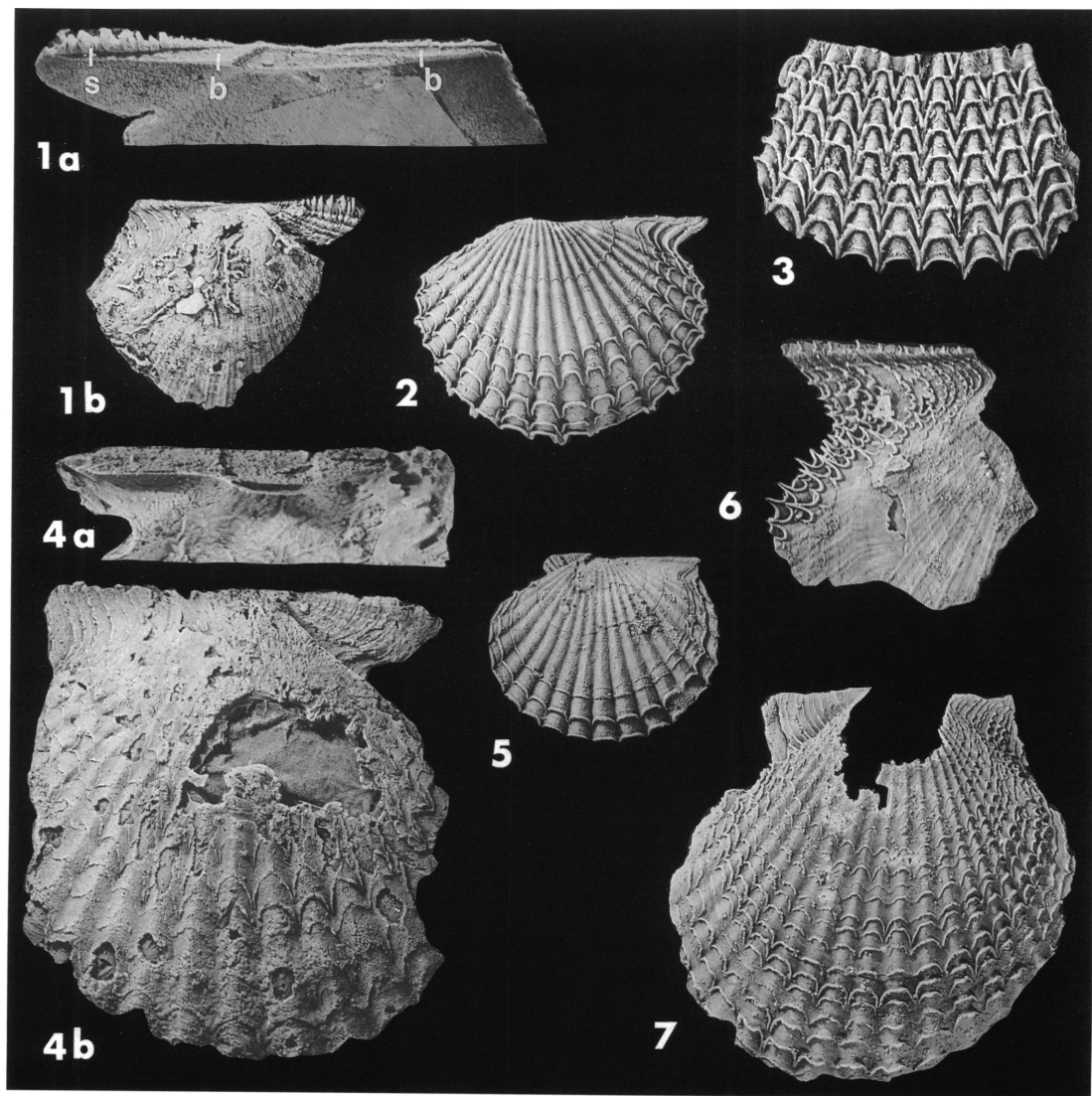


Fig. 32. *Acanthopecten coloradoensis* (Newberry), silicified, Leonardian and Guadalupian, West Texas. **1a, b**, RV, respectively $\times 2$ and $\times 1$, showing robust anterior scroll (s) and asymmetrical elongate resilifer bordered by well-defined bourrelets (b), Leonardian (Bone Spring Fm.), AMNH loc. 46, cat. 43399; **2**, LV, $\times 1$, Guadalupian (Willis Ranch Fm.), USNM loc. 706, cat. 258968; **3**, LV, $\times 1$, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 258969; **4a, b**, RV, $\times 1$, unusually large specimen, USNM loc. 706e, cat. 258971; **5**, Juvenile LV, $\times 1$, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 258970; **6**, RV, $\times 1$, Leonardian (Road Canyon Fm.), USNM loc. 702c, cat. 258966; **7**, LV, $\times 1$, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 388896.

disc margin; posterior sulcus weak; RV ornament similar to LV, but very subdued (table 9).

DISTRIBUTION: Leonardian and Guadalupian of West Texas: USNM loc. 702, 702c,

702e, 703a, 703b, 706, 706c, 707e, 715i, 719x, 719z, 721r, 721s, 721u, 721x, 723t, 724u, 726o, 727j, 728h; AMNH loc. 46, 369, 500, 512; also Phosphoria (Guadalupian?) of Montana, Wyoming, Utah, Ciriacks, 1963.

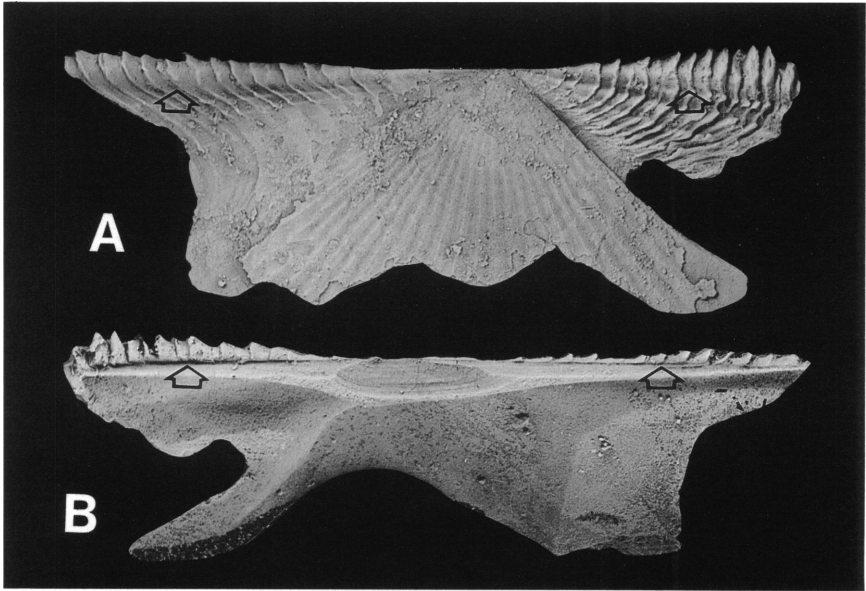


Fig. 33. *Acanthopecten coloradoensis* (Newberry), silicified RV, $\times 2$, unusually large specimen, Early Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43371. A, exterior showing cardinal scrolls (arrows), nearly flat disc, and low plicae, each with single axial costella; B, interior, showing scrolls (arrows) above flat bourrelets.

DISCUSSION: There are hundreds of fragments of this species in our collection of silicified LVs from 24 localities in West Texas but only one locality (USNM 706e, Willis Ranch Mem.) supplied a few useful specimens, including some fragments of RVs. The collection is inadequate for significant quantitative analysis.

The ligament area is preserved on one large RV (fig. 33), forming a 55° angle with the commissural plane; the posteriorly elongated resilifer has a L/H ratio of 1.44 and its ventral margin is convex. The first comarginal ridge appears at a shell height of about 20 mm or less and subsequent ridges gradually increase in prominence toward the margin.

As shown in table 9, small valves are appreciably longer than high, becoming more nearly circular with growth. The umbonal angle averages about 115°, with an observed range of 90–120°. The number of plicae, including Ciriacks' observations on Phosphoria specimens, ranges from 16 to 25.

Girty's (1908) *Aviculopecten laqueatus*, which Newell (1937) assigned to *Acanthopecten*, we now tentatively refer to *Girtypecten sublaqueatus* (Girty), 1908.

FAMILY EUCHONDRIIDAE
NEWELL, 1938

DIAGNOSIS: Adult hinge pseudotoxodont; ligament alivincular external, with small, symmetrical resilifer; shell nearly equiconvex, higher than long; retrocriscent; LV multicostate, with concentric crossed lamellar inner ostracum, and homogeneous outer os-

TABLE 9
Acanthopecten coloradoensis
Word Fm. (Willis Ranch Memb.)
USNM loc. 706e

Len	H	Len/H	Conv
Left valves			
62.5	58.4	1.07	17.5
54.2	53.9	1.00	14.0
43.6	32.3	1.35	9.1
31.1	25.2	1.23	6.9
28.8	23.0	1.25	7.1
24.1	19.3	1.25	6.2
18.6	14.1	1.32	4.2?
Right valve			
60+	66.7	—	13.2

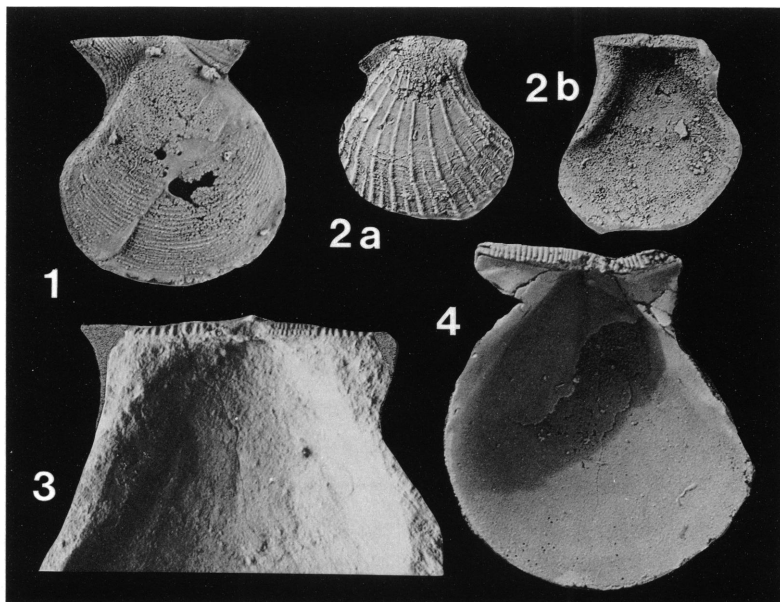


Fig. 34. *Euchondria*, Penn. and Perm., U.S. 1, *Euchondria cooperi*, Newell and Boyd, n. sp., silicified RV, $\times 3.7$, L. Perm., Leonardian (Road Canyon Fm.), Glass Mts. West Texas, USNM loc. 707e, cat. 431320; 2a, b, *Euchondria cooperi*, Newell and Boyd, n. sp., silicified LV, holotype, $\times 2.7$, Guadalupian (Willis Ranch Fm.), Glass Mts., USNM loc. 706e, cat. 431319; 3, *Euchondria subcancellata* Newell, calcareous LV, $\times 4$, U. Carb., Des Moinesian (Labette Shale), St. Louis, Mo., Univ. Kansas loc. (J. B. Knight collection) 43-2, cat. 40193; 4, *Euchondria cooperi* Newell and Boyd, n. sp., silicified RV with damaged hinge, $\times 4$, Guadalupian (Road Canyon Fm.), Glass Mts., Texas, USNM loc. 703, cat. 431321.

tracum; RV with inconspicuous fila, outer ostracum prismatic.

DISTRIBUTION: Cosmopolitan in Laurasia. Devonian?, Miss.-M. Perm.

DISCUSSION: The Devonian genus *Crenipecten* may be a synonym of *Euchondria*. In any case we class both in the Euchondriidae, for many reasons noted in the diagnosis, although in at least one Penn. species, the prisms of the RV are quadrate in section (Newell, 1937). This peculiarity was not confirmed in other material.

Genus *Euchondria* Meek, 1874

TYPE SPECIES: *Pecten neglectus* Geinitz, 1866. Pennsylvanian, Nebraska. OD, Meek.

DIAGNOSIS AND DISTRIBUTION: As for Euchondriidae.

DISCUSSION: The general aspect of *Euchondria* is similar to that of small juveniles of some modern pectinids. However, the latter differ in having an internal ligament, elaborate teeth, and a foliate calcite shell.

Euchondria cooperi Newell and Boyd, new species

Figures 14: 1, 2; 34

DIAGNOSIS: Valves almost equiconvex. LV with slender widely spaced costae; growth lines crowded (16–20 per mm), and arching upward toward beak between costae; right disc ornamented by closely spaced fila (6–8 per mm) which continue, undiminished, across posterior auricle; right anterior auricle with radial costae (table 10).

DISTRIBUTION: U. Leonardian (Road Canyon Fm.)–L. Guadalupian (Willis Ranch Fm.). USNM loc. 703, 703c, 706, 706e, 707e, 735a; AMNH loc. 503.

DISCUSSION: Named for G. Arthur Cooper, who collected most of our specimens. This species is rare in our collections. From seven localities we have only 17 RVs and 12 LVs with no more than four valves from any single locality. The preponderance of RVs is unusual in pectinoids that have prismatic right valves.

The number of primary costae of the left disc is 10 to 12 with 6 to 10 or more secondaries added by intercalation. An auricular crus occurs in some individuals at the disc margin just below the anterior auricle. A more prominent posterior marginal ridge is found just below the midheight of the shell. Several RVs show vestiges of radial color bands (fig. 14). The presence of sharply defined costae over the left disc distinguishes this species from the similar Penn. *E. subcancellata* Newell, 1938.

FAMILY DELTOPECTINIDAE

DICKINS, 1957

DIAGNOSIS: Valves orbicular, concordant, nearly equiconvex; ligament transitional, external, amphidetic; shell smooth, costate, or plicate; beaks slightly behind midpoint of hinge, and hinge margin about half of shell length; rear auricles relatively small or lacking; byssal notch open and broad; microstructure in type genus foliate calcite.

DISTRIBUTION: Carb.–L. Trias., cosmopolitan.

DISCUSSION: A young geologist, James Dwight Dana, with the first American round-the-world Wilkes scientific expedition (1838–1842) was intrigued by giant Permian pectinoids in eastern Australia (Dana, 1847). These were monographed by Etheridge and Dun (1906) under the informal name “Palaeopectens.” They, and many subsequent authors, failed to note that the type genus and its near relatives lacked a median resilifer.

It remained for Kegel (1953) and Dickins (1957) to show that *Deltopecten* is defined by the transitional ligament type, and not by the deltoid resilifer displayed by some associated “Palaeopectens” that remain to be sorted into other genera. To date, at least 15 species names have been assigned to the large Gondwana shells, none of which have been subjected to morphological and population analysis.

For the present purpose we include four rather dissimilar genera in the Deltopectinidae: *Deltopecten* (essentially a giant Gondwana form), *Streblopteria*, *Crittendenia*, and *Eocamptonectes*. The ornamentation in these forms is very diverse, so the family assignment must be considered provisional.

TABLE 10

Euchondria Cooperi Newell and Boyd, n. sp.
Road Canyon Fm., USNM locs. 703a, 703c, 707E,
735a; Word Fm. (Willis Ranch Memb.), USNM
locs. 706c, 706E

Len	H	Len/H	Conv	Hin Len
Left valves				
8.5	8.6+	—	1.6	—
8.0	8.5	0.95	1.6	5.6
7.5	8.1	0.92	1.3	5.6
6.3	7.1	0.88	1.2	—
5.4	6.0	0.90	1.0	4.0
Right valves				
9.4	10.3	0.91	1.6	—
8.2	9.9	0.83	2.0	5.3+
8.4	8.8	0.95	1.6	6.2
5.1	6.3	0.81	1.0	4.5
5.1	6.0	0.85	0.9	3.9+

Genus *Deltopecten* Etheridge, Jr., 1892

TYPE SPECIES: *Pecten illawarensis* Morris, 1845, OD.

DIAGNOSIS: Large, plicate deltopectinids.

DISTRIBUTION: L. Perm. Periglacial, eastern Australia, Tasmania, Argentina, and India.

DISCUSSION: Among the Australian “palaeopectens” only *D. illawarensis* is known to lack the median resilifer. The others belong to alivincular genera, yet to be sorted out. One of our *D. illawarensis* from New South Wales exhibits major growth interruptions of the ligament area (fig. 35: 1). These probably represent seasonal bands.

Deltopecten illawarensis (Morris), 1845

Figures 35, 36

Pecten illawarensis Morris, 1845.

Deltopecten illawarensis Newell, 1938.

Deltopecten waterfordi Dickins, 1963.

DIAGNOSIS: Large (14 cm or more in height); coarsely ribbed shells with 20–30 similar, rounded disc plicae.

DISTRIBUTION: L. Perm., Gondwana.

DISCUSSION: This is one of the large Gondwana pectinoids described by Etheridge and Dun (1906), Fletcher and Dun (1929), and others.

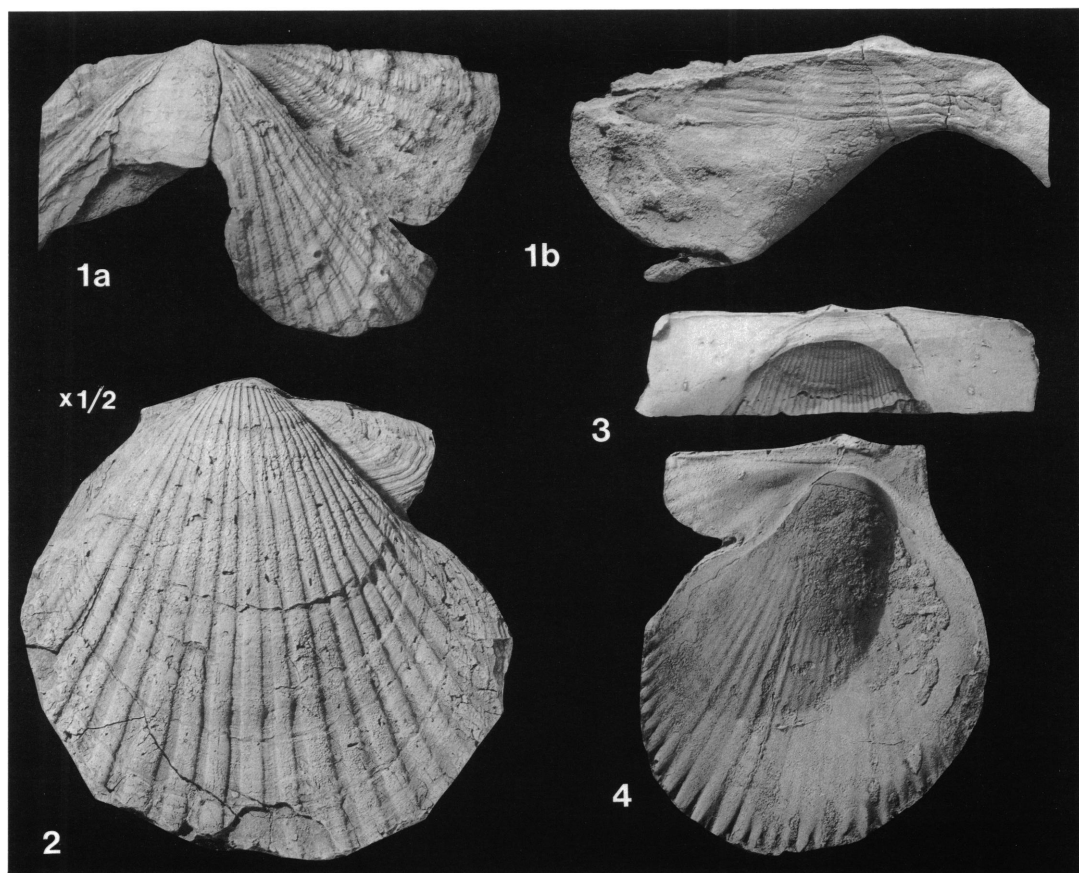


Fig. 35. Variable *Deltopecten*, all referred provisionally to *D. illawarensis* (Morris), L. Perm. periglacial occurrences of Australia. 1a, b, paratype of *Deltopecten waterfordi* Dickins, calcareous RV, $\times 0.80$, Callytharra Fm., unusual grooves on ligament area indicate rhythmic, possibly seasonal, growth, AGSO cat. CPC 3921; 2, calcareous RV, $\times 0.40$, Dickins' holotype of *D. waterfordi*, Callytharra Fm., AGSO cat. F2353; 3, *Deltopecten* cf. *illawarensis* (Morris), calcareous LV, $\times 0.80$, transitional ligament area almost smooth and mainly in front of umbo, Lymington Fm., Tasmania, Tasmania Bur. Mines cat. TMF 449104; 4, *Deltopecten* cf. *illawarensis* (Morris), RV, $\times 0.80$, rubber cast of specimen from Pelican Creek, S. Kennedy, Queensland, Australia. AMNH cat. 14424.

Genus *Streblopteria* M'Coy, 1851

Eumicrotis Meek and Hayden, 1864, not Hind, 1903.

Glabripecten Waterhouse, 1982.

Orbiculopecten Gonzalez, 1978.

Imoella Hoare et al., 1989.

TYPE SPECIES: *Meleagrina laevigata* M'Coy, 1844. SD Meek and Worthen, 1866.

DIAGNOSIS: Circular to slightly procrecent, smooth valves; ligament located near middle of dorsal margin; bourrelets lacking; dentition consisting of one small tooth in front of ligament in RV.

DISTRIBUTION: Cosmopolitan, Miss.-Perm.; M. Trias. of Arctic Siberia (fide Kurushin, 1982: 60).

DISCUSSION: The taxa listed above as synonyms are distinguished by trivial characters that we regard as varietal or specific, rather than generic, differences.

Streblopteria montpelierensis (Girty), 1908

Figure 37

Aviculopecten? *montpelierensis* Girty, 1910.

Streblochondria? *montpelierensis* Newell, 1938.

Streblochondria? *montpelierensis* Ciriacks, 1963.

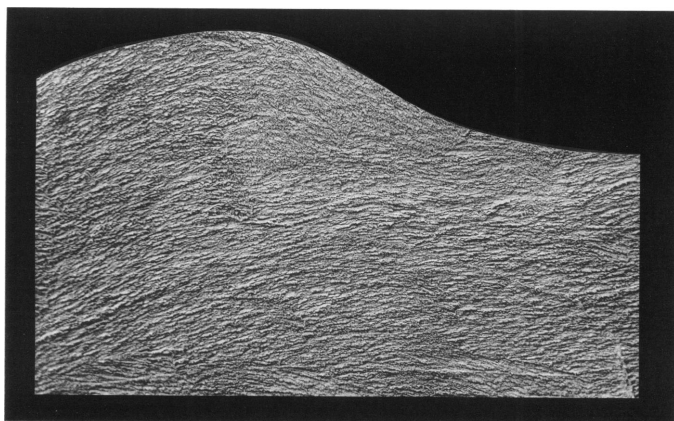


Fig. 36. *Deltopecten* cf. *illawarensis* (Morris), LV, $\times 50$, SEM photo, cellulose peel. Transverse section through rib, exterior above, crossed foliate calcite fabric, L. Perm. (Callytharra Fm.), Western Australia, AMNH loc. 3118, cat. 44034.

DIAGNOSIS: Smooth, strongly biconvex shells subequal in height and length; beak barely projecting above dorsal margin; posterior auricle inconspicuous; anterior auricle of LV lacking byssal sinus; dorsal margin ter-

minating at each end in obtuse angle; transitional ligament area about six times as long as high; short lamellar tooth occurring in RV at anterior end of ligament and engaging with opposing socket of LV; small internal knob,

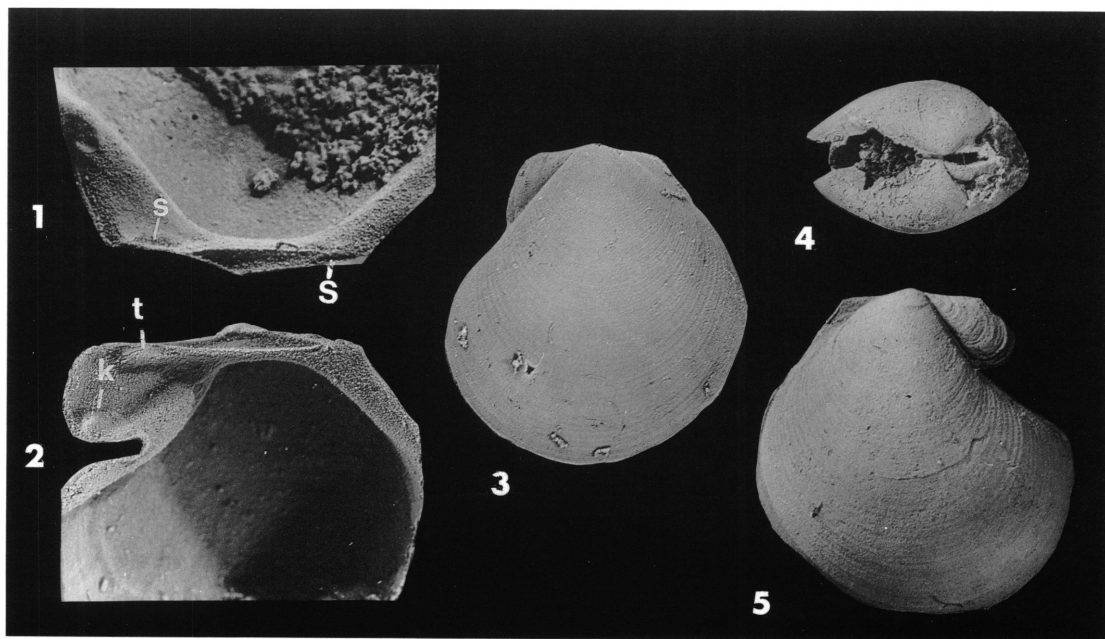


Fig. 37. *Streblopteria montpelierensis* (Girty), silicified, Guadalupian (L. Getaway Ls.), Guadalupe Mts., AMNH loc. 512. 1, LV, $\times 6.3$, showing socket (s), and transitional ligament without bourrelets, cat. 44028; 2, RV, $\times 6$, showing lamellar tooth (t), and knob (k), at lower extremity of anterior auricle, and thickened byssal notch, cat. 42891; 3, LV, $\times 2$, cat. 44029; 4, joined valves, RV below, $\times 2$, showing nearly equivalve convexity, cat. 43302; 5, RV, $\times 3$, cat. 43303.

TABLE 11
Streblopteria montpelierensis
L. Getaway Ls., AMNH loc. 512

				Aur	Hin	Aur
Len	H	Len/H	Conv	Len	Len	Len/ Hin Len
Left valves						
18.9	19.9	0.95	5.0	4.3	8.1	0.53
17.3	18.2	0.95	6.2	3.7	6.7	0.55
15.3	16.5	0.93	4.7	3.6	6.8	0.53
14.3	15.7	0.91	4.0	3.6	6.5	0.55
14.5	15.5	0.94	3.6	3.7	6.0	0.62
13.8	14.9	0.93	4.5	3.2	6.2	0.52
13.1	14.0	0.94	4.6	2.6	5.5	0.49
10.5	11.5	0.91	2.7	2.5	4.6	0.54
8.6	9.3	0.92	2.6	2.0	3.8	0.53
6.9	7.3	0.95	1.9	1.8	3.3	0.55
Right valves						
18.6	20.0	0.93	5.4	4.9	8+	0.61
17.5	18.6	0.94	5.1	4.3	8.0	0.54
15.6	16.2	0.94	4.5	3.7	6.5	0.57
15.1	15.7	0.96	5.1	3.3	6.5	0.51
11.6	12.6	0.92	3.8	3.1	5.5	0.56
12.1	12.5	0.97	3.5	3.0	5.5	0.55
10.8	11.5	0.94	2.7	2.7	4.7	0.57
9.3	10.2	0.91	2.7	2.1	4.0	0.52
8.5	8.9	0.96	1.9	2.1	3.7	0.57
8.1	8.7	0.93	2.3	2.0	3.6	0.55

or boss, occurring at upper extremity of byssal notch (table 11).

DISTRIBUTION: This is one of the most abundant and wide-ranging bivalves in the west. American Perm. ranging through most of the West Texas section into the L. Capitanian (Hegler). In the platform Perm. of the Middle Rockies it is common to abundant in the Meade Peak Memb. (Phosphoria Fm.) in Montana, Idaho, and Wyoming (Ciriacks, 1963).

West Texas: Wolfcampian-Capitanian. AMNH loc. 46, 369, 433, 505, 512, 592. USGS loc. 6983. USNM loc. 702, 702c, 702d, 702f, 703, 703a-d, 706, 706b,e, 707e, 707ha, 707la, 708u, 710d, 713, 715i, 719z, 720b, 721u, 721z, 722, 722l, 723t, 726z, 727j, 728e, 728f, 729, 731, 733q, 735a, 741a.

DISCUSSION: We have a large number of silicified fragments, both L and RVs, from 40 W. Texas localities. Most lack the hinge and interior details. One articulated speci-

men (fig. 37: 4) shows that the two valves are almost equally convex and concordant.

The Pennsylvanian *S. oklahomensis* Newell is similar but more upright. *S. laevigata*, the type species, from the British L. Carb., has a more prominent byssal sinus on the left valve. Its beak is somewhat forward of the midpoint of the dorsal margin.

Ours is the only material known to us in which the hinge is shown. Much remains to be learned about the genus *Streblopteria*, however we interpret the hinge teeth as specializations.

Crittendenia Newell and Boyd, new genus

TYPE SPECIES: *Crittendenia kummeli* Newell and Boyd, n. sp., *Meekoceras* zone, Thaynes Fm., northeastern Nevada.

DIAGNOSIS: Shell ovoid, smooth; LV strongly convex with prominent umbo and projecting beak; RV less convex, with deep byssal notch, umbo with small attachment imprint which is occasionally a coiled negative impression of an ammonoid umbilicus.

DISTRIBUTION: L. Trias., Laurasia.

DISCUSSION: Named for Crittenden Spring, near Long Canyon, N. E. Nevada. Bittner (1899), when writing about numerous bivalves associated with ceratites in the lowermost Triassic in the Himalayas, noted that the bivalve shells were not quite like anything from the southern Alps. He classed some of the Indian fossils as new species of *Pseudomonotis*: *griesbachi*, *painkhanda*, and *decidens*.

We have before us two small collections of *P. decidens* (fig. 39), collected by Kummel and Teichert from Pakistan (Salt Range) representing a single population about the same age as Bittner's forms and our Nevada material. The Pakistan fossils exhibit the morphological range of Bittner's forms and suggest that he also was dealing with a single population. Nakazawa (1977), following Ichikawa (1958), doubtfully used the name *Claraia* for Kashmir shells like Bittner's and referred them to the "group" *Claraia decidens* Bittner. Others (e.g., Kurushin, 1982) have referred them to *Streblopteria*.

We conclude that *decidens* is significantly unlike both *Claraia* and *Streblopteria*. Con-

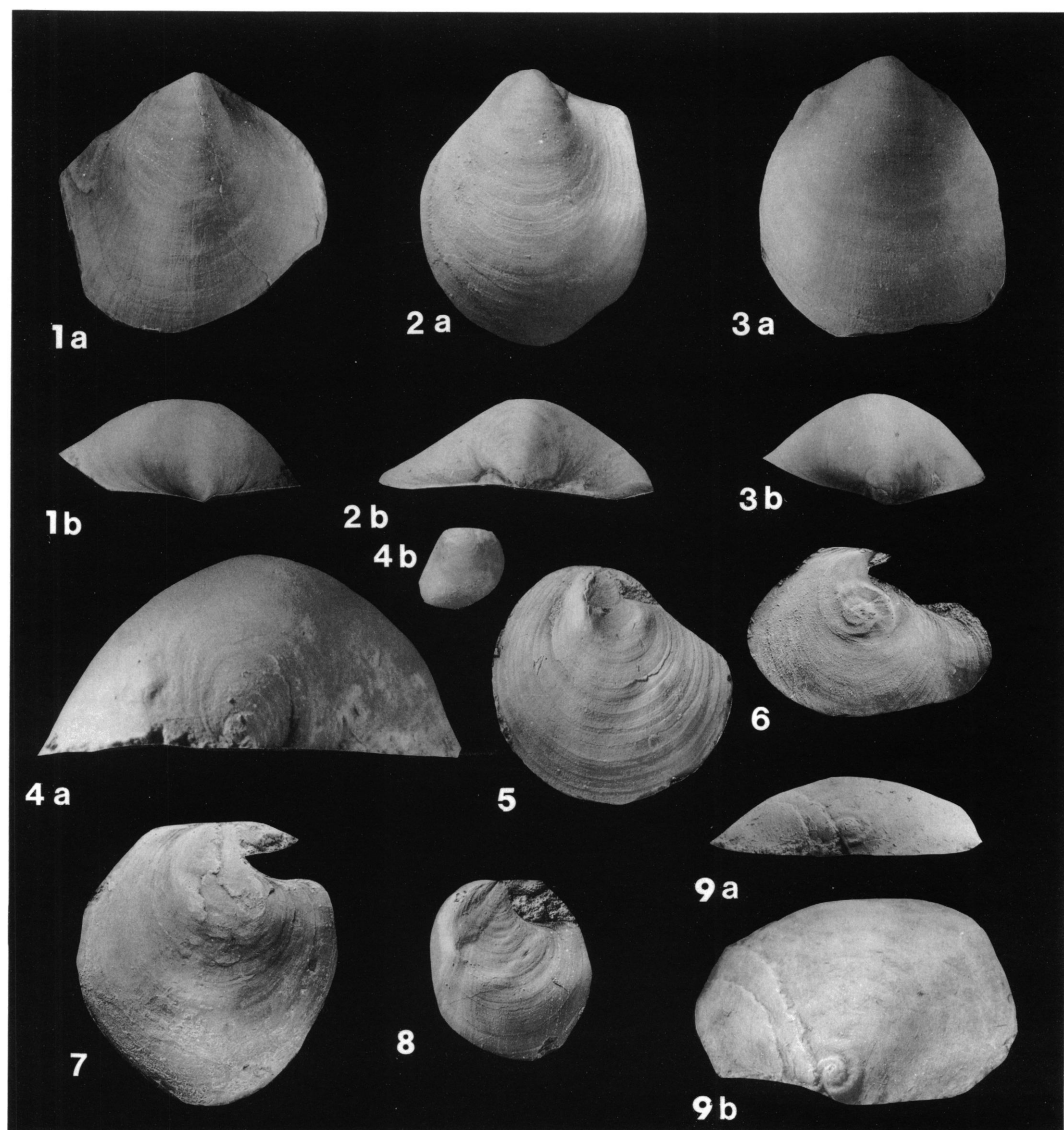


Fig. 38. *Crittendenia kummeli* Newell and Boyd, new genus and n. sp., calcareous specimens and latex cast (6) from L. Thaynes Fm. (*Meekoceras* zone), northeast. Nevada, AMNH loc. B9075. 1, 2, 3, LVs, $\times 2$, cat. 44040, 43299, 44039 (holotype), respectively; 4a, b, LV, $\times 4$, and $\times 1$, respectively, juvenile showing early growth lines, cat. 44041; 5–9; RVs; 5, $\times 3$, showing cicatrix of attachment and obscure byssal notch, cat. 44043; 6, $\times 2$, showing imprint of ammonoid umbilicus below byssal notch, cat. 44044; 7, $\times 2$, with flattened cicatrix, cat. 44045; 8, $\times 2$, with irregular attachment cicatrix, cat. 44046; 9a, b, $\times 2$, two views of umbonal area showing imprint of ammonoid umbilicus, cat. 44042.

sequently, we are introducing a new genus, *Crittendenia*, for the *decidens* group. External similarities caused us to put *Crittendenia* in the same family with *Streblopteria*, despite the lack of information on ligament and shell structure.

Crittendenia kummeli Newell and Boyd,
new species
Figures 38, 39

DIAGNOSIS: Shells with length and height subequal; hinge length about half valve height;

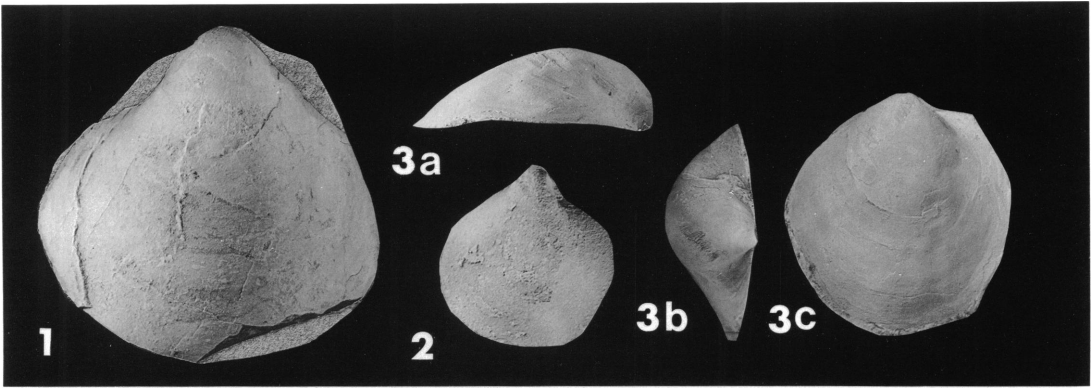


Fig. 39. *Crittendenia kummeli*, L. Trias., (Mitwali Fm.), Salt Range, Pakistan, (Kummel and Teichert, 1970), Kummel and Teichert loc. K6-27A. 1, 2, LVs $\times 1$, 3, LV $\times 0.88$, calcareous. These differ from Nevada specimens in having slightly more slender beaks and steeper umbonal slopes, RVs unknown, AMNH cat. 44048, 44049, 44050, respectively.

hinge extremities obtuse; umbonal angle variable, generally about 90° ; LV strongly convex with beak projecting well over hinge; umbo of RV variably flattened or concave, reflecting substrate imprint (table 12).

DISTRIBUTION: L. Trias., east. Nevada, associated with *Meekoceras* fauna, L. Thaynes Ls., AMNH loc. B9075, and Pakistan.

TABLE 12
Crittendenia kummeli Newell and Boyd, n. sp.
Thaynes Fm., L. Trias., AMNH loc. B9075

Len	H	Len/H	Conv	Conv/H
Left valves				
23.0	24.5	0.84	7.4	0.30
22.7	25.3	0.90	6.9	0.27
18.6	21.5	0.86	7.0	0.32
18.5	21.6	0.86	6.4	0.30
17.3	19.5	0.89	4.5	0.23
16.4	18.7	0.87	6.3	0.34
14.8	15.3	0.97	5.5	0.36
11.8	13.9	0.85	4.0	0.29
10.9	11.7	0.93	3.9	0.33
8.9	9.9	0.90	3.5	0.35
Right valves				
19.1	19.4	0.98	3.5	0.18
17.7	18.5	0.96	4.0	0.21
16.3	15.6	1.04	3.5	0.22
14.2	14.5	0.98	3.0	0.21
12.4	12.4	1.00	1.8	0.15
12.4	11.9	1.04	3.0	0.25
12.1	14.4	0.84	2.7	0.19
11.2	12.6	0.89	1.5	0.12
9.8	10.7	0.92	2.5	0.23
7.5	8.6	0.87	1.0	0.12

DISCUSSION: Named after Bernhard Kummel, master student of L. Trias. ammonoids (Kummel and Teichert, 1970). An area around the beak of some RVs is smoothly concave, reflecting growth on an extraneous, possibly soft, object. In others, this area bears a spiral imprint of the inner whorls of an ammonoid. The bivalves were byssate and apparently were not cemented to the ammonoids. Presumably some individuals of this species were pseudoplanktonic, anchored tightly by the byssus to floating objects, while others were pseudopelagic on the ammonoids.

Machalski (1989) has shown why both valves of pleurothetic bivalves may not share imprints of the substrate. Where lateral growth of the upper valve lags behind that of the lower valve, the upper one may mold the accreted inner surface of the lower valve rather than the substrate.

Our species differs very little from Bittner's Himalayan group of *C. decidens* and Kurushin's *Strebloteria*. A revision based on representative population samples is needed.

Genus *Eocamptonectes* Newell, 1969

Camptonectes? *asperatus* Girty, 1908.

TYPE SPECIES: *Camptonectes?* *papillatus* Girty, 1908. OD.

DIAGNOSIS: Procrascentic, slightly higher than long; dorsal margin slopes away from beak, terminating in obtuse angle at each end; anterior auricle larger than posterior one; re-

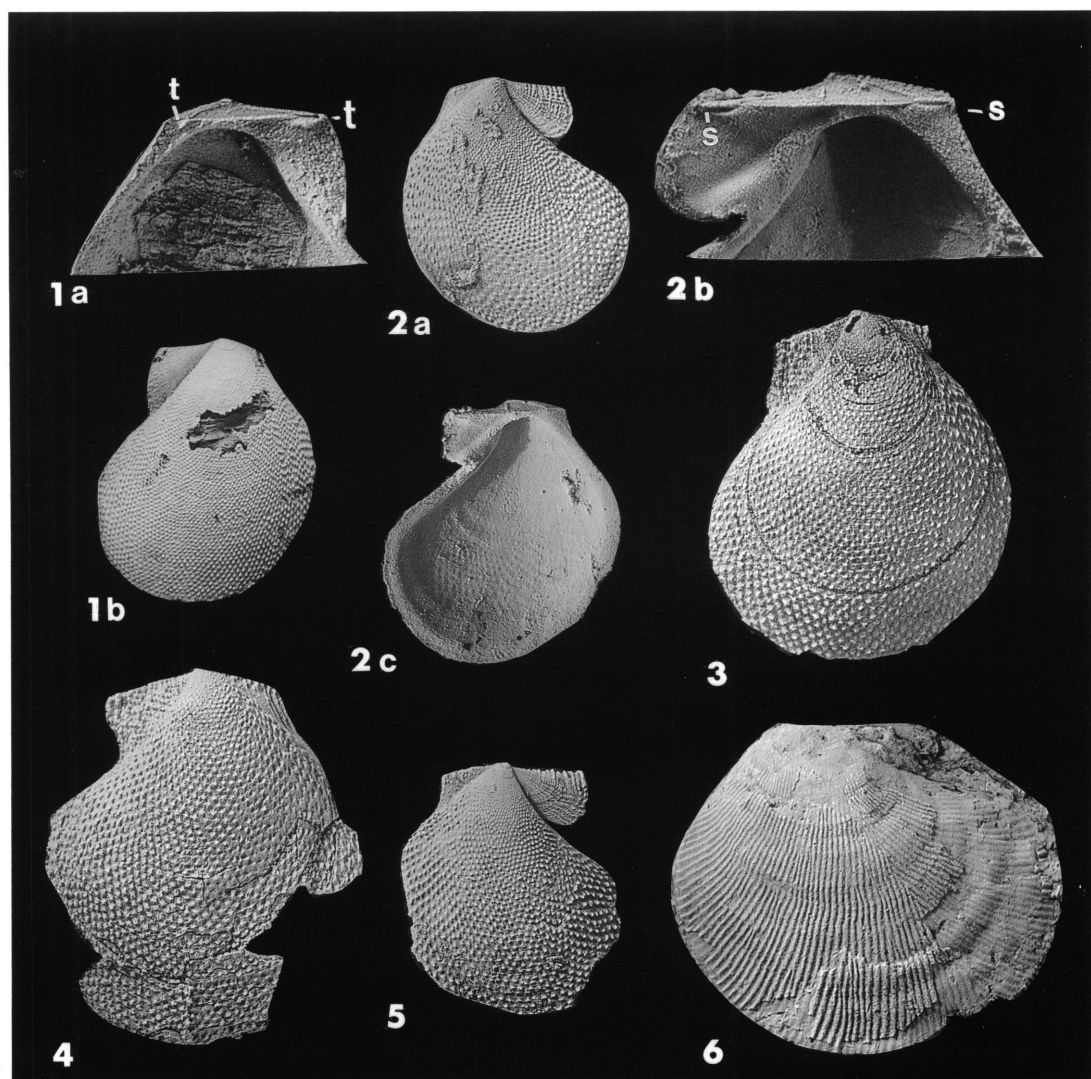


Fig. 40. *Eocamptonectes*. 1-5, *Eocamptonectes papillatus* (Girty), silicified, Perm., West Texas. 1a, LV, $\times 3$, teeth (t), Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43286; 1b, exterior of same, $\times 2$; 2a, b, c, RV, $\times 2$, $\times 4$, $\times 2$, respectively, 2b showing slender sockets (s) that received two teeth of LV, Guadalupian (Willis Ranch Fm.), USNM loc. 706, cat. 388879; 3, 4, LVs, $\times 2$, Leonardian (Road Canyon Fm.), USNM loc. 703c, cat. respectively, 431316 and 431315; 5, RV, $\times 2$, China Tank Memb. (Word Fm.), USNM loc. 703-c, cat. 388886; 6, *Eocamptonectes sculptilis* (Girty), calcareous RV, $\times 2$ (Ciriacks, 1963), Guadalupian (Park City Fm., Franson Memb.), AMNH cat. 28325.

silifer elongate, more than half length of dorsal margin; LV with anterior buttress below hinge plate; short lamellar tooth occurring at each end of hinge, with corresponding sockets in RV.

DISTRIBUTION: M. Perm., West Texas and Wyoming; L. Carb., China (R. Zhang and Yan, 1993).

Eocamptonectes papillatus (Girty), 1908
Figure 40: 1-5

DIAGNOSIS: Surface with cancellate pattern produced by small scales arranged in two sets of diagonal rows (table 13).

DISTRIBUTION: Perm.: L. Wolfcampian-U. Guadalupian. AMNH loc. 500x, 501, 503,

TABLE 13
Eocamptonectes papillatus
Road Canyon Fm., USNM loc. 703c

Len	H	Len/ H	Conv/ H	Aur Len	Hin Len	Aur Len/ Hin Len
Left valves						
21.8	24.5	0.89	4.7	0.19	5.5	10.5
15.0	16.9	0.89	3.7	0.22	4.0	8.0
14.2	16.7	0.85	3.7	0.22	4.4	7.2+
13.7	15.5	0.88	3.2	0.21	4.3	8.0
13.3	15.4	0.86	3.1	0.20	3.6	6.6
9.6	11.4	0.84	2.4	0.21	3.1	5.2
9.7	11.1	0.87	2.2	0.20	3.0	5.4
5.6	6.9	0.81	1.7	0.25	1.6	3.5
Right valves						
21.9	23.1	0.95	5.6	0.24	7.0	12.5
20.7	22.9	0.95	3.6	0.16	5.3	10.2
19+	22.6		4.9	0.22	5+	9+
19.8	21.6	0.92	4.1	0.19	5.6	10.9
10.5	11.4	0.92	2.0	0.17	3.1	5.8
9.3	10.9	0.85	2.0	0.18	3.3	5.6
7+	8.9		1.6	0.18	2.7	5.1
5.2	6.1	0.85	1.2	0.20	1.9	3.3

504, 512; USNM loc. 702, 702a, 702c, 702u, 703, 703a, 703b, 703c, 703d, 706, 706e, 707e, 719x, 720d, 721j, 721s, 721u, 721y, 724b, 726d, 726o, 726z, 728, 731, 732c, 741a, 741i, 741j.

DISCUSSION: This is one of the most widely distributed bivalves in the West Texas Permian, represented in our collection usually by fragmented material from 34 localities. However, it is abundant at only one site, USNM 720d, where the specimens are of poor quality. Our best material is from the Road Canyon Fm. at USNM 703c. The ornament varies in detail within populations.

Eocamptonectes sculptilis (Girty), 1908
Figure 40: 6

Camptonectes? sculptilis Newell, 1938.
Camptonectes? sculptilis Ciriacks, 1963.

DIAGNOSIS: Characterized by smooth rather than scaly rays. Divergence of rays from anteroventrally directed axis forming divaricate pattern of inverted Vs.

DISTRIBUTION: Perm. (Middle Capitanian), West Texas, USGS loc. 352; Phosphoria (Franson Memb.), S. Fork Canyon, Wyoming (Ciriacks, 1963).

DISCUSSION: Very rare, known from only a few fragments, all RVs.

FAMILY STREBLOCHONDRIIDAE NEWELL, 1938

Ex *Streblochondriinae* Newell, 1938;
Newell and Boyd, 1985b, 1987

DIAGNOSIS: Valves upright to slightly pro-crescent, ovate, nearly equiconvex, costate or plicate, with short hinge and small, subquadrate or obtuse posterior ear; with or without small lamellar hinge teeth; hinge plate supported by buttress on each side of resilifer; resilifer short, extended slightly forward; outer shell layer antimarginal fibrous in both valves.

DISTRIBUTION: Miss.-U. Perm., Laurasia.

Genus *Streblochondria* Newell, 1938

TYPE SPECIES: OD, *Aviculopecten sculptilis* Miller, 1891; Penn., USA.

DIAGNOSIS: Valves of low convexity, costellate and/or cancellate; without hinge teeth.

DISTRIBUTION: Miss.-U. Perm., Laurasia.

DISCUSSION: Included here for comparison; described fully by Newell, 1937, and Newell and Boyd, 1985b.

Streblochondria sculptilis (Miller),
1891
Figure 41

Aviculopecten sculptilis Miller, 1891.
Streblochondria sculptilis Newell and Boyd, 1985b.

DIAGNOSIS: Shell slightly higher than long in a ratio of 1.1/1 to 1.2/1 with 60–70 costellae on both valves in two ranks of alternating size, smaller ones inserted in early growth at height usually less than 10 mm; regular fila cross ribs in cancellated pattern with tiny hyote scales at the intersections; hinge margin about half to three-quarters disc length; anterior ear about half to three-fifths hinge length.

DISTRIBUTION: U. Penn.-M. Perm. (Capitanian), especially Bone Spring Fm. (Leon-

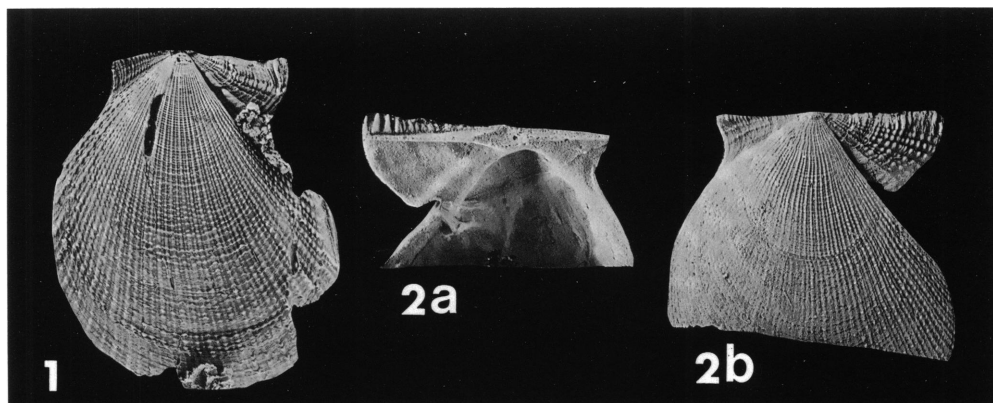


Fig. 41. *Streblochondria sculptilis* (Miller), silicified RVs. 1, $\times 1$, Leonardian (Cathedral Mt. Fm.), USNM loc. 702, cat. 388868; 2a, b, approximately $\times 2$, Leonardian (Road Canyon Fm.), USNM loc. 722g, cat. 388869.

ardian), AMNH loc. 629 and USNM loc. 728f, West Texas.

DISCUSSION: This species was described more fully by Newell, 1937, and Newell and Boyd, 1985b.

Genus *Guizhoupecten* Chen, 1962

TYPE SPECIES: OD, *Guizhoupecten wangi* Chen, 1962; U. Perm., China.

DIAGNOSIS: Plicae with both intercalating and branching costellae; ridge crests with graded small hyote scales, especially on umbones; discs ovoid, nearly equilateral to slightly prorescent; beaks situated about two-thirds behind front of relatively short hinge; posterior ear small, subquadrate; resilifer almost symmetrical in juveniles, bounded on each side by pair of lamellar teeth, those of RV underlying corresponding teeth of LV; large adults edentulous, wall structure as for family Streblochondriidae.

DISTRIBUTION: M. and U. Perm., Laurasia.

DISCUSSION: As we noted in 1985, this genus has a startling external resemblance to much younger "*Chlamys*" from which it differs in the superfamily characters of the hinge (Waller, 1993).

Guizhoupecten cheni Newell and Boyd, 1985

Figure 42

DIAGNOSIS: Shell height-length ratio about 1.2/1, ranging upward in size to maximum

height about 70 mm and length of 66 mm; hinge margin short, about 60–70 percent of disc length; plicae highly variable in form, ranging from 12 to 23 and averaging 17 or 18 in number.

DISTRIBUTION: M. Perm. (Willis Ranch Ls.) USNM loc. 707e; (L. Getaway Ls.) AMNH, loc. 512; (Bell Canyon Ls.) USNM loc. 728p., West Texas.

DISCUSSION: In our paper on Streblochondriidae (Newell and Boyd, 1985b) we discriminated two contemporaneous populations as distinguishable subspecies of *Guizhoupecten cheni*. It is indeed rare in our experience that adequate population samples of silicified pectinoids are available for quantitative comparisons. The statistics are given in that paper.

ANNULICONCHIDAE

NEWELL AND BOYD, NEW FAMILY

DIAGNOSIS AND DISTRIBUTION: Same as for the genus *Annuliconcha*.

Genus *Annuliconcha* Newell, 1938

TYPE SPECIES: *Aviculopecten interlineatus* Meek and Worthen, 1860, OD. U. Penn., Illinois.

DIAGNOSIS: Subequivalved, orbicular, umbones inconspicuous; auricles elongate, posterior slightly longer of the two; LV ornament progressively spaced coarse comarginal ridges and intervening fine fila; few radial cos-

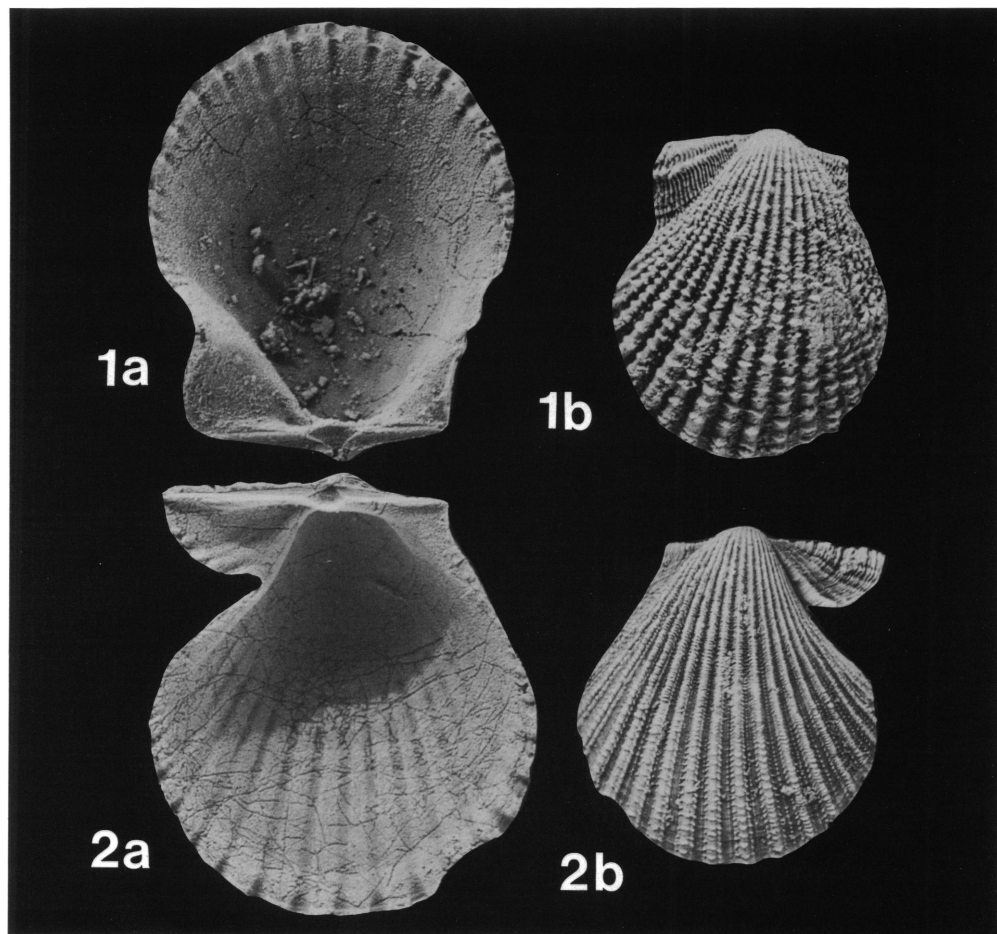


Fig. 42. *Guizhoupecten cheni* Newell and Boyd, silicified, illustrating complex hinge and plicae, L. Getaway Ls., AMNH loc. 512. **1a, b**, LV, respectively $\times 5$ and $\times 3$, cat. 42884; **2a, b**, RV, respectively $\times 5$ and $\times 3$, AMNH 42885.

tellae appear at maturity in some forms; RV similar but nearly smooth.

DISTRIBUTION: Widespread in U. Carb. and M. Perm. of Laurasia.

Annuliconcha interlineata
(Meek and Worthen), 1860

Figure 43: 2-5

Aviculopecten interlineatus Meek and Worthen, 1860.

Annuliconcha interlineata Newell, 1938.

DIAGNOSIS: Disc subcircular with 10 or 11 coarse comarginal ridges separated by 10 to 16 fila; coarse ridges first appear ontogenet-

ically at shell height of about 0.5 mm; at 8 to 10 mm about 24 fine, low, rounded ribs appear in some variants and continue to shell margin; valves gape at both ends.

DISTRIBUTION: We have a dozen incomplete Permian specimens from Wolfcampian, Leonardian, and Guadalupian rocks in West Texas, USNM loc. 701a-3, 701h, 701k, 707w, 710d, 720e, 721d, 721u, and 728e; also present in Pennsylvanian strata of the Midcontinent region (Newell, 1937), and the Carb. Russian Platform (Muromtseva, 1974).

DISCUSSION: Distinguished from *Annuliconcha dentata* by a lack of spines on the coarse comarginal ridges.

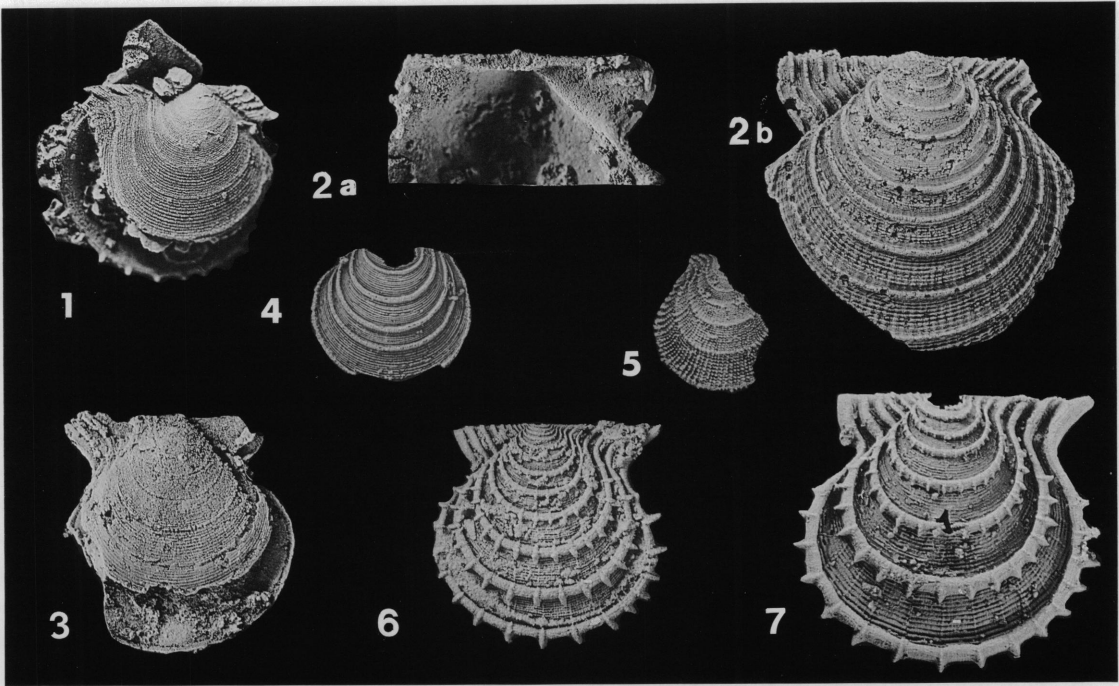


Fig. 43. *Annuliconcha* spp. Newell, silicified, Perm., West Texas. 1, 6, 7, *Annuliconcha dentata*, n. sp. 1, Juvenile RV and associated LV, $\times 4.5$, of same individual, Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43390; 6, holotype, LV, $\times 1.8$, Leonardian (Skinner Ranch Fm.), USNM loc. 707w, cat. 258958; 7, LV, $\times 2.7$, Guadalupian (Willis Ranch Fm.), USNM loc. 706e, cat. 431314; 2 to 5, inclusive, *Annuliconcha interlineata* (Meek and Worthen), Perm. shells referred to the Penn. species; 2a, b, LV, $\times 2.7$, showing elongate external alivincular resilifer and spineless exterior, USNM loc. 701k, cat. 258952; 3, RV, $\times 1.8$, with conjoined LV, showing discordance of margins, Leonardian (Road Canyon Fm.), USNM loc. 721-o, cat. 431313; 4, fragment LV, $\times 1.8$, Wolfcampian (Neal Ranch Fm.), USNM loc. 701a, cat. 258959; 5, fragment RV, $\times 1.8$, Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43389.

Annuliconcha dentata Newell and Boyd,
new species

Figure 43: 1, 43: 6, 43: 7

DIAGNOSIS: Valves orbicular with dorsal margin approximately equal to height; posterior auricle acuminate, anterior less so; ligament bourrelets low, resilifer elongated posteriorly, with straight ventral margin; comarginal ridges of left valve with outwardly directed solid, blunt spines of uniform size and spacing (table 14).

DISTRIBUTION: West Texas, Perm.: Wolfcampian-L. Guadalupian, USNM loc. 700v, 701a-3, 701k, 701L, 702, 702a, 702b, 702c, 702un, 703, 703a, 703b, 703bs, 703c, 706, 706c, 706e, 707e, 710d, 714w, 719x, 721j, 721o, 721s, 721u, 721z, 722L, 723t, 724b, 724u, 726d, 726o; AMNH loc. 501, 505.

TABLE 14
Annuliconcha dentata Newell and Boyd, n. sp.
Word Fm. (Willis Ranch Memb),
USNM loc. 706e

Len	H	Len/H	Conv	Hi Len
Left valves				
20.5	18.5	1.11	5.2	?
15.8	15.6	1.01	4.5	13.2
14.8	13.7	1.08	3.5	12.5
14.2	13.3	1.07	3.5	13.0
12.8	11.9	1.08	2.6	12.1
12.1	11.6	1.04	2.9	11.5
10.7	10.3	1.04	2.4	10.1
10.2	10.3	0.99	2.4	10.3
9.0	8.7	1.03	1.9	9.2
6.5	6.6	0.98	1.4	7.5

DISCUSSION: Comarginal spines distinguish this species from *A. interlineatus*. We have some 200 small, silicified LVs the largest of which is 21 mm long. Nearly a quarter of these are from a single locality (USNM 706e). There is a single small RV (USNM 721o).

The beaks and inner valve layer are missing from almost all of the specimens, and only two show the resilifer which has a length/height ratio of 5.

Some specimens scattered throughout the sequence have a few costellae between the comarginal ridges. A few oldest (Wolfcampian) valves differ from the others in the form of the spines, which are thicker and more elevated and the shells lack radial ornament. There is not enough material to segregate them under a different name.

FAMILY AVICULOPECTINIDAE

MEEK AND HAYDEN, 1864

(Transl. S. A. Miller, 1889

ex Aviculopectininae Meek and Hayden)

DIAGNOSIS: Adults plicate, with or without costellae; concordant; equiconvex.

DISTRIBUTION: L. Carb.–L. Trias., cosmopolitan.

Genus *Aviculopecten* M'Coy, 1851

Hayasakapecten Nakazawa and Newell, 1968. L. Perm., Japan.

TYPE SPECIES: *Aviculopecten planoradiatus* M'Coy, 1851: 171, SD Hind, 1903: 66.

DIAGNOSIS: Aviculopectinids with simple plicae, commonly with few widely scattered hyote spines.

DISTRIBUTION: L. Carb.–M. Perm., Laurasia.

DISCUSSION: A L. Carb. plicate LV in the Sedgwick Museum, Cambridge University, England (cat. no. 5988) is generally considered to be M'Coy's original of *A. planoradiatus*. Hind (1903), Newell (1937), and Waterhouse (1960) independently studied and refigured this specimen. Actually, it does not closely resemble M'Coy's original illustration (1851), which may or may not represent an artist's attempt to restore specimen imperfections. In any case, if M'Coy's original is lost, as seems probable, the Cambridge spec-

imen can serve as a neotype for *planoradiatus*.

Hind (1903) was confused about this specimen when he referred to it as the type of M'Coy's *Pecten tabulatus*, 1844, which it clearly is not, if we accept M'Coy's own figure of *A. tabulatus* (his pl. 16, fig. 12). So we cannot agree with Hind that *A. planoradiatus* is a junior synonym of *A. tabulatus*.

M'Coy frequently regarded right and left valves as separate species. We think that an unidentified right valve of *planoradiatus* must have been very like M'Coy's plicate *Pecten flexuosus* (M'Coy, 1844: 93, pl. 18, fig. 1). Girty (1904) seems to have arrived at the same conclusion.

In any case, *A. flexuosus* resembles right valves of our *Aviculopecten americanus*, n. sp., in having more or less uniform plicae and, for a Paleozoic pectinoid, unusually high convexity. From this circumstantial evidence, we conclude that *A. planoradiatus* was probably almost equiconvex and therefore concordant. Unfortunately, the microstructure is unknown in any of these shells.

The beak ornament of *A. planoradiatus* is multicostate (see Newell, 1937: pl. 5, fig. 13b). This, rather than plicae, seems to be a juvenile character in Paleozoic pectinoids. We interpret this as an indication that the plicate ornament of adult *Aviculopecten* is a derived, rather than primitive, state.

It is interesting that M'Coy (1851) subsequently realized that the name *A. flexuosus* was preoccupied by a Portlock (1843) species, so he replaced the name *flexuosus* with *docens* (Latin for teacher).

Hayasakapecten Nakazawa and Newell, 1968, has the essential qualities of *Aviculopecten* s. s., as defined here: subequal valves, simple plicae, and strong biconvexity. Consequently, we treat it as a junior synonym of *Aviculopecten*.

Species of *Heteropecten*, long classed with *Aviculopecten*, are inequivalved, and not plicate.

Aviculopecten americanus Newell and Boyd,
new species
Figure 44

DIAGNOSIS: Adult plicae of opposing valves similar, closely spaced, about 24–28 in num-

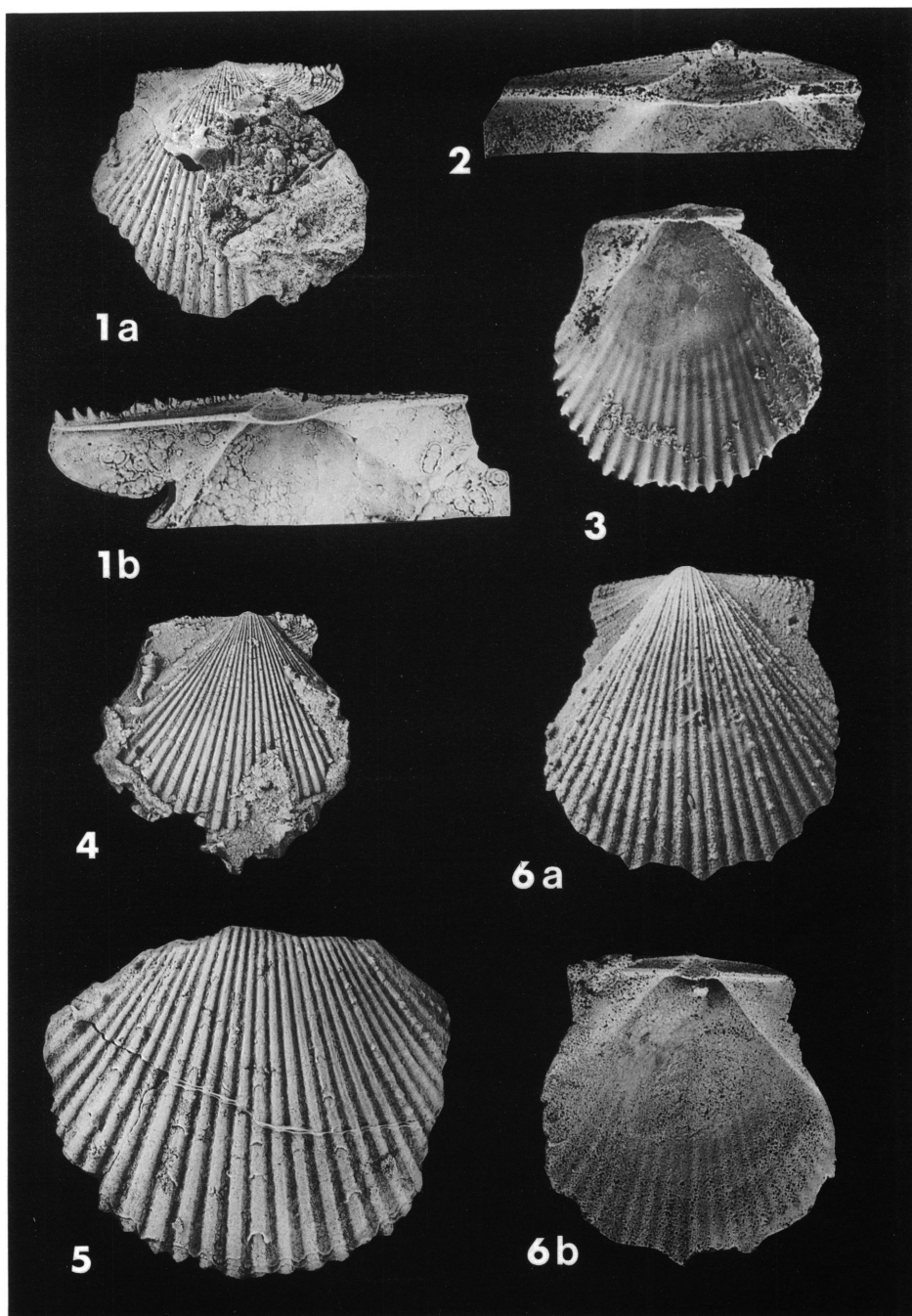


Fig. 44. *Aviculopecten americanus*, n. sp., silicified, Perm., Leonardian (Cathedral Mt. and Road Canyon Fms.), Glass Mts. **1a**, RV, $\times 2$, Leonardian, USNM loc. 702, cat. 388893; **1b**, hinge of same, $\times 3$; **2**, LV, $\times 3$, Guadalupian, USNM loc. 703a, cat. 388894; **3**, LV, $\times 4$, Leonardian, USNM loc. 703b, cat. 388895; **4**, RV, $\times 1$, Leonardian, USNM loc. 702, cat. 388891; **5**, LV, $\times 1$, Leonardian, USNM loc. 702, cat. 388892; **6a, b**, LV, $\times 3$ holotype, Leonardian, USNM loc. 702, cat. 388881.

TABLE 15

Aviculopecten americanus Newell and Boyd, n. sp.

Len	H	Len/H	Conv	Um An	Rib No.
Left valves					
32+	34+	—	9.5+	93°	26
16.1	17+	—	4.5	77°	25
13.7	14.9	0.92	4.4	83°	25
10.7	11.7	0.91	3.2	84°	24
Right valves					
38.6	—	—	8.5	93°	26
30+	32+	—	9.0	91°	26

ber; secondary ribs inserting within first 2 or 3 mm below beaks, abruptly becoming indistinguishable from primaries; both valves with few small, scattered hyote spines on mature ridges; right anterior auricle bearing prominent costae and growth rugae; right posterior auricle weakly ornamented as are both auricles of LV; dorsal margin essentially straight in large valves, sloping gently from beak in small ones; angle between cardinal area and extended plane of commissure about 25° in LVs and 50° in RVs (fig. 44: 1b, 2); resilifer symmetrical in small valves becoming slightly elongated posteroventrally in large ones (table 15).

DISTRIBUTION: L. and M. Perm. USNM Cathedral Mt. Fm., loc. 702, 703a, 703b; Bone Spring Fm., loc. 723e; Road Canyon Fm., loc. 702c, 721u, 728e, 735a. AMNH loc. 504.

DISCUSSION: We have 15 specimens (12 LVs, 3 RVs), mostly fragmentary, but the hinge area is preserved in several.

CYRTOROSTRIDAE

NEWELL AND BOYD, NEW FAMILY

DIAGNOSIS AND DISTRIBUTION: As for genus *Cyrtorostra*.

DISCUSSION: Many investigators have placed Permian species of *Cyrtorostra* (India, Russia, Timor, and Sicily) in the Jurassic genus *Oxytoma* (see fig. 11). The two genera have very little in common. Without consideration of *Cyrtorostra*, Ichikawa (1958) erected the subfamily Oxytominae, which was elevated to family rank by Cox (1961). Oxytomidae apparently does not occur below the Jurassic.

Genus *Cyrtorostra* Branson, 1930

Oxytoma Meek, 1864, in part.
Blandfordina Reed, 1944.

TYPE SPECIES: *Cyrtorostra varicostata* Branson OD.

DIAGNOSIS: Shell suborbicular to circular, concordant, moderately convex, multicostate, infracrescentic, with RV slightly flatter than LV; beaks narrow, prosogyrate, extending above short hinge line; auricles offset by deep sulci on both valves with deep byssal notch in RV; posterior auricle small, acuminate, left anterior auricle subquadrate, right anterior auricle tongue-shaped and notched above, bearing one or more costae; disc ornamented with bundles of costae, which terminate in long, stout, marginal spines; bundles are each marked internally by deep and narrow furrow; they are externally separated by broad spaces, being occupied by a single primary costa.

Ligament areas troughlike, subexternal, amphidetic with finely grooved resilifers; microstructure of inner shell unknown; outer ostracum antimarginal fibrous.

DISTRIBUTION: L.-M. Perm.; cosmopolitan in Northern Hemisphere.

Cyrtorostra varicostata Branson, 1930

Figures 45, 46

DIAGNOSIS: Disc circular, or slightly higher than long; knoblike tooth on both valves at anterior end of ligament area, left protuberance accommodated by prominent furrow, or socket, in front of right one; usually 12 marginal spines on each valve (table 16).

DISTRIBUTION: USNM loc.: West Texas, Wolfcampian (Neal Ranch Fm.), 701k; Leonardian (Cathedral Mt. Fm.), 702, 702b, 703b, 707q, 721u, 726o, 726u; Wordian (Road Canyon Fm.), 702c, 703, 703a, 703c, 707e, 710z, 719x, 721j, 721s, 721z, 722e, 724b, 724c, 726d, 726z; Willis Ranch Fm. 706, 706e, 723b, Ls. between Willis Ranch Fm. and Appel Ranch Fm., 706b; Appel Ranch Fm., 706d, 719z, 727j; below Appel Ranch Fm., 732c; Capitanian (Bell Canyon Fm.), 731, 740j; Wyoming, Park City Fm. (Franson Memb.), 760. AMNH loc.: West Texas, Leonardian (Road Canyon Fm.), 507; Willis Ranch Fm., 506; L. Getaway Ls., 512.

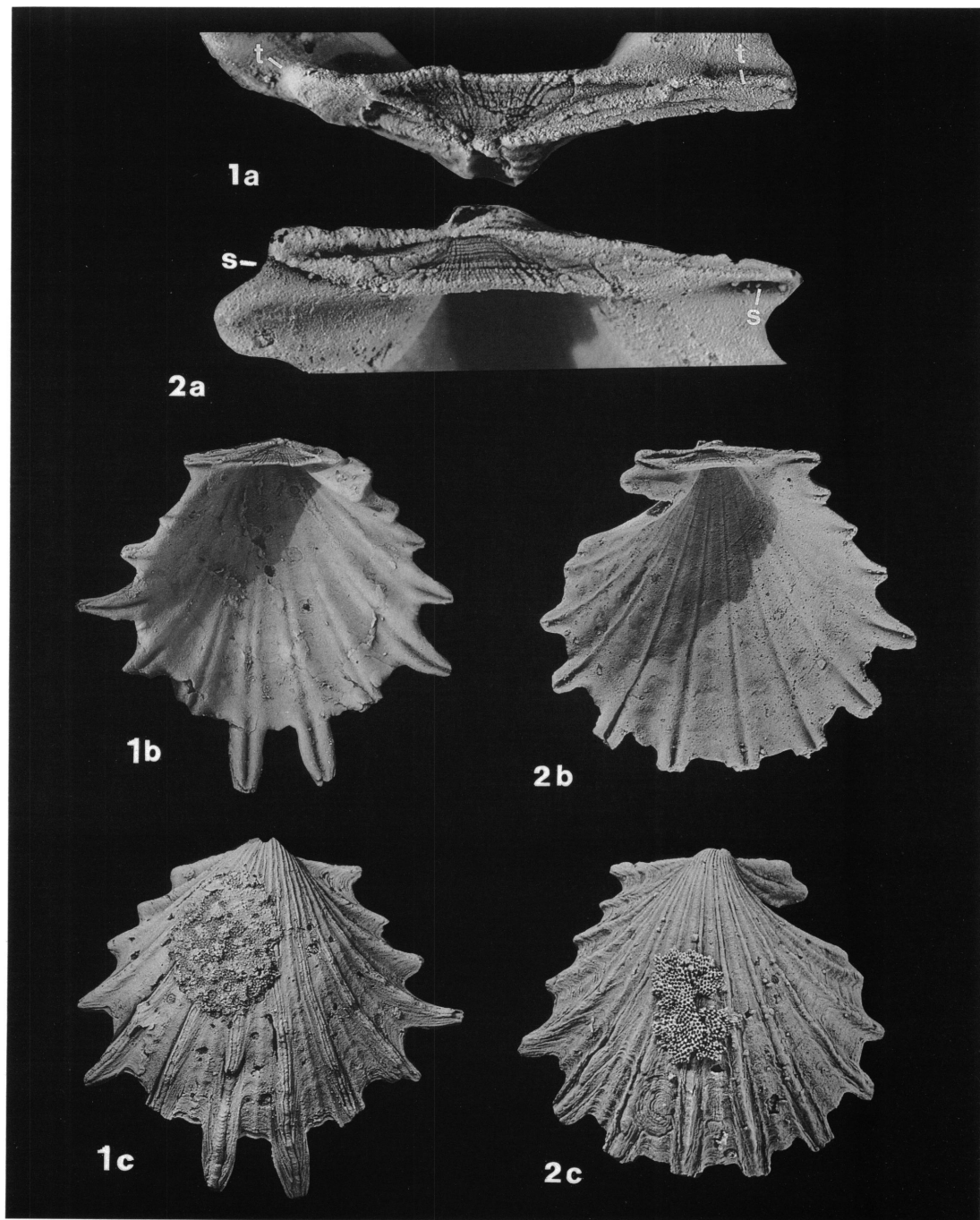


Fig. 45. *Cyrtorostra varicostata* Branson, silicified, Guadalupian (Willis Ranch Fm.), Glass Mts., Texas, USNM loc. 706. 1a-c, USNM 388882; 2a-c, USNM 388883. 1a, Left hinge, $\times 6$, tooth (t); 1b, 1c, LV $\times 2$; 2a, right hinge, $\times 6$, socket (s); 2b, 2c, RV, $\times 2$; striated resiliifer may combine features of both alivincular and duplivincular ligaments.

TABLE 16
Cyrtorostra varicostata
from Ciriacks, 1963, p. 58. Park City Fm.
(Franson Memb.)

Len	H	Len/H	Hin Len
Left valves			
19.5	20.5	0.95	11.5
13.6	17.0	0.80	—
12.0	14.6	0.82	—
12.4	14.4	0.86	—
6.4	7.4	0.86	—
5.4	6.2	0.87	—
4.6	5.4	0.85	3.8+
4.2	5.2	0.81	3.4+
4.2	5.2	0.81	—
4.0	4.8	0.83	2.8
Right valves			
28.2	33.6	0.84	
25.0	26.4	0.95	13.2
18.0	21.0	0.86	11.0
20.0	20.0	1.00	13.0
12.8	14.8	0.86	6.4+
10.8	13.6	0.79	6.4
8.8	11.0	0.80	—
8.5	11.0	0.77	— (Holotype)
9.0	10.4	0.87	4.4+
5.6	6.4	0.87	—

Ciriacks (1963) reported this species in the Ervay, Tosi, Shedhorn, and Rex Chert members of the Park City–Phosphoria complex in Wyoming.

DISCUSSION: *C. varicostata* is one of the most abundant bivalves in both the basin and platform facies of the Permian of western U.S. However, we offer the caveat that the superior preservation of the calcite shells makes the numbers somewhat misleading. Other species preserved only, or mainly, as fragments may have been equally abundant.

The characterization that we give above is based on 150 silicified valves from a single locality and population, USNM loc. 706 (Willis Ranch Fm.). The separated valves in our collection are reasonably complete and well preserved, numbering 86 LVs and 64 RVs. The original thickness is preserved on all specimens, suggesting that they were originally composed of foliated calcite. Ciriacks (1963: 58) noted that the Wyoming examples of *Cyrtorostra* are indistinguishable from the

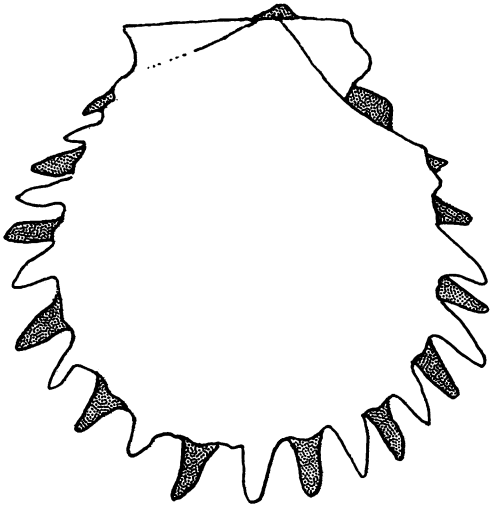


Fig. 46. *Cyrtorostra varicostata* Branson, restoration of conjoined valves showing alternation of marginal spines, RV (unshaded) covers all of LV except spines and beak (shaded).

shells from the Wordian of the Glass Mountains and we agree.

Some of the stratigraphically lower West Texas material exhibits minor differences from the Wordian material. The older specimens frequently have 10 or 11 spines, whereas the younger ones usually have 12 spines. The postumbonal interspine areas commonly are more sharp-crested and scale-bearing in contrast to the flatter, smooth areas of the Willis Ranch and Appel Ranch valves. These are not consistent differences and we do not have enough information to separate two subspecies.

The Canadian Arctic *Cyrtorostra arctica* Logan, 1970, lacks the hinge protuberances and seems to be more circular in outline. Its posterior auricles are truncate rather than acuminate, the dorsal margin of the right anterior auricle is straight rather than concave, and the byssal notch is less prominent than in *C. varicostata*.

SUPERFAMILY PSEUDOMONOTACEA
NEWELL, 1938

DIAGNOSIS: Upright pectiniform shells with external, alivincular ligament; auricular sinuses on LV absent or inconspicuous.

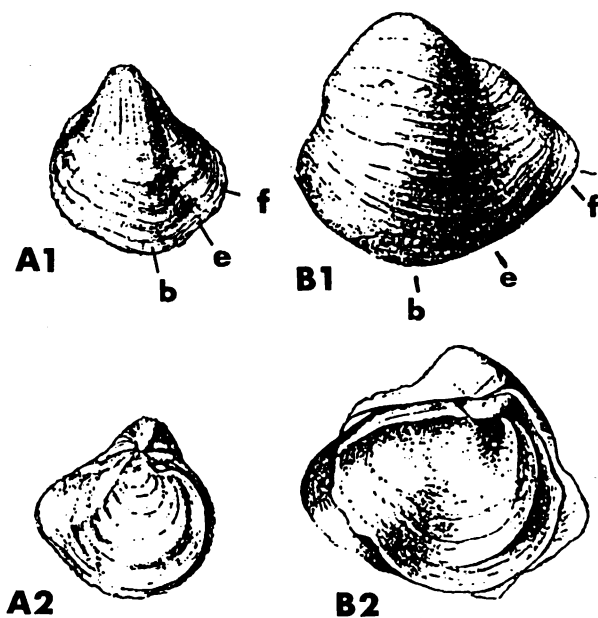


Fig. 47. *Pseudomonotis* and *Gryphaea*, showing close resemblance of shell features. A1, A2, *Pseudomonotis speluncaria* (von Schlotheim), LV and RV respectively, U. Perm., England, exhalant flange (f), posterior sulcus (e) marking location of palliobranchial fusion point, "branchitellum" (b); B1, B2, *Gryphaea convexa* Say, LV and RV, respectively, U. Cretaceous, New Jersey.

FAMILY PSEUDOMONOTIDAE
NEWELL, 1938

DIAGNOSIS: As for genus *Pseudomonotis*.

DISTRIBUTION: Miss.-L. Trias., cosmopolitan.

DISCUSSION: We have noted in detail (Newell and Boyd, 1970, 1989) a close resemblance between the pseudomonotids and Gryphaeidae (fig. 47). Notable differences are microstructure and the fact that the latter are cemented by the LV rather than the RV.

Genus *Pseudomonotis* Beyrich, 1862
Figure 47A

TYPE SPECIES: *Gryphites speluncaria* von Schlotheim, 1816. SD Stoliczka, 1871. (See Pseudomonotidae and *Pseudomonotis* in Newell and Boyd, 1970, 1989.)

DIAGNOSIS: Usually attached, oysterlike, irregular upright shells, with short hinge, narrow to grypheate left umbo; generally without posterior auricles; smooth to multicostate with or without numerous hyote scales; LV frequently with posterior radial sulcus; nearly smooth to multicostate; byssal notch distally

constricted, becoming filled and obsolete in adults as shell becomes cemented at right umbo; adults usually with posteroventral extension (branchitellum), and posterodorsal exhalant flange.

DISTRIBUTION: Penn.-U. Perm., Laurasia, West. Australia.

Genus *Pegmavalvula* Newell and
Boyd, 1970

TYPE SPECIES: *Pegmavalvula gloveri* Newell and Boyd, 1970, OD. Perm., West Texas.

DIAGNOSIS: Small cemented pectiniform pseudomonotids with relatively small, similar, auricles and obsolescent byssal notch.

DISTRIBUTION: West Texas, L. and M. Perm.; Nevada and Utah, L. Trias.

Pegmavalvula triassica Newell and Boyd,
new species
Figure 48

DIAGNOSIS: Irregular shells (approximately 1 cm high); auricles poorly defined; byssal slit narrows distally, becoming closed in adults; both valves multicostellate with crowded,

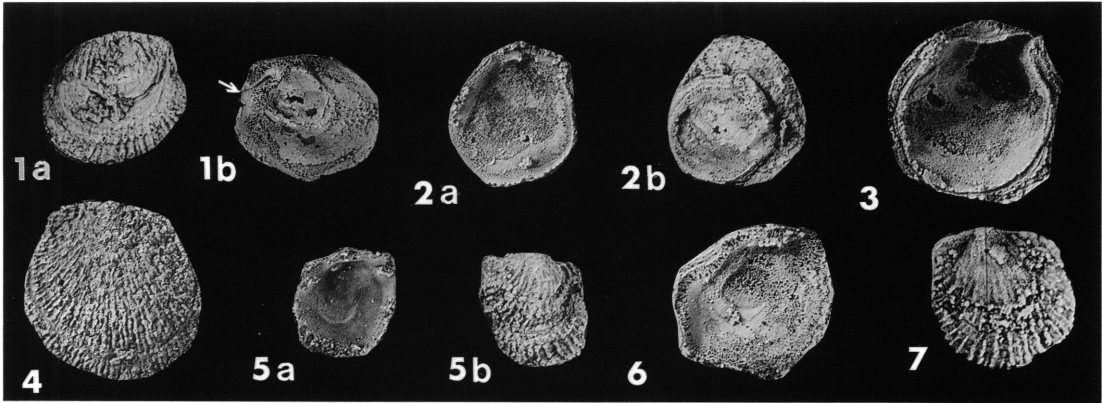


Fig. 48. *Pegmavalvula triassica* Newell and Boyd, n. sp., silicified, $\times 2.5$, Trias., Smithian (Virgin Ls.), s. Nevada. 1a, b, holotype, RV, exterior and interior with costae, cicatrix, and overgrown byssal notch (arrow), AMNH loc. B7977, cat. 43336; 2a, b, LV, with marginal brim and attached RV of another individual, AMNH loc. B7977, cat. 43339; 3, LV, with marginal brim and broad resilifer, AMNH loc. B7977, cat. 43345; 4, LV, with unusually fine costae, AMNH loc. B7977, cat. 43346; 5-7, additional LVs illustrating variation; 5, AMNH loc. B8517, cat. 43327; 6, AMNH loc. B7977, cat. 43343; 7, AMNH loc. B8517, cat. 43328.

slender costellae irregularly marked with tiny hyote scales; cardinal area narrow with centrally located, symmetrical resilifer (table 17).

DISTRIBUTION: L. Trias., south. Nevada, south. Utah. AMNH Loc. B7977, B8111, B8517.

DISCUSSION: We have 39 silicified specimens 30 of which are LVs. All but one are from the Virgin Ls. They resemble juveniles of *Pegmavalvula delicata* (fig. 49), from the Permian. They differ from *delicata* in being

smaller and misshapen, attached over almost the whole surface of the RV. In contrast to *P. delicata*, the Triassic species lacks plicae and RV spines.

FAMILY HUNANOPECTINIDAE
YIN, 1985

DIAGNOSIS: Small, less than 14 mm high; disc orbicular to slightly retrocriscent, inequiconvex, concordant; RV smooth, LV smooth or multicostellate; posterior auricles subquadrate and small; ligament external alivincular, one lamellar tooth at each end of short, triangular resilifer; byssal notch well developed.

DISTRIBUTION: Perm., Wyoming; U. Perm., S. China.

DISCUSSION: Yin (1985a) emphasized cardinal crura as a criterion for referring *Hunanopecten* to the Pectinidae. The ridges in his figure 12 lie above the main part of the resilifer, and the dorsal ridge is near the dorsal margin of the shell. He thought the resilium was internal, as in modern pectinids. By contrast, Fang (1989) regarded the lamellar teeth of *Hunanopecten* as radiating from the base of the resilifer, which would have housed an external ligament. This is clearly the situation in *Fransonia*, described below.

TABLE 17
Pegmavalvula triassica Newell and Boyd, n. sp.
Virgin Ls., AMNH loc. B7977

Len	H	Len/H	Conv	Hin Len
Left valves				
9.5	10.9	0.87	2.3	5.1
9.8	10.1	0.97	3.0	6.1
8.8	9.1	0.97	1.5	5.5
7.2	8.0	0.90	1.6	3.7
7.8	7.9	0.99	1.9	4.6
7.6	7.3	1.04	2.8	4.5
6.3	6.0	1.05	1.7	3.0
Right valves				
8.6	8.7	0.99	negligible	4.6
8.6	7.9	1.09	negligible	5.5
8.2	7.3	1.12	negligible	4.8
5.8	5.9	0.98	negligible	4.2

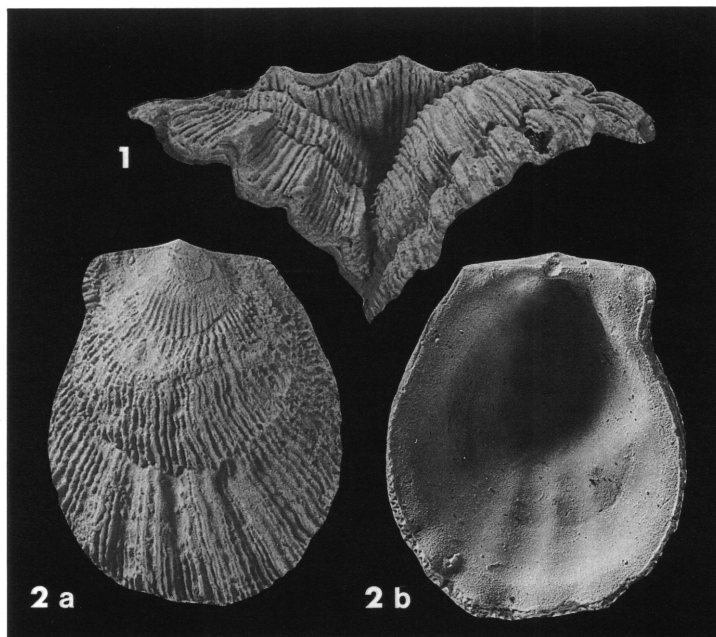


Fig. 49. *Pegmavalvula delicata* Newell and Boyd, silicified, $\times 4$. Showing fine costae and plicae (introduced for comparison with fig. 48), Guadalupian (L. Getaway Ls.), AMNH loc. 512. 1, Three cemented RVs, cat. 28916; 2a, b, LV, cat. 28928.

Genus *Hunanopecten* Zhang, 1977

TYPE SPECIES: *Hunanopecten exilis* Zhang, 1977, OD.

DIAGNOSIS: With deep byssal notch and both valves unornamented.

DISTRIBUTION: U. Perm., S. China.

DISCUSSION: Yin (1985a) inferred a pseudoplanktonic habit for this genus as indicated by the low-energy lithofacies and associated ammonoids. But Fang (1989) thought that *Hunanopecten* was epibenthic, byssate, and from shallow-water. The Chinese examples frequently retain both valves and display very little breakage.

Fransonia Newell and Boyd, new genus

TYPE SPECIES: OD, *Fransonia wyomingensis* Newell and Boyd, new species. L.-M. Perm., U.S.

DIAGNOSIS: LV finely multicostellate, RV without radial ornament; opposing bourrelets diverge dorsally above hinge teeth, microstructure unknown.

DISTRIBUTION: L.-M. Perm., Texas, Wyoming.

DISCUSSION: Named from Franson Memb. of the Park City Fm. The type species of *Hunanopecten* and *Fransonia* are very similar, except for ornament in the latter and deeper byssal notch in the former.

Fransonia wyomingensis Newell and Boyd, new species Figure 50

DIAGNOSIS: Small, orbicular to infracrescent shells; height and length subequal; anterior auricle larger than posterior; beak of LV barely projecting above straight dorsal margin; dorsal margin nearly three-fourths disc length; LV with shallow auricular sinuses and weak auricular sulci; interior surface of anterior auricle bisected by ridge just below midheight of auricle (table 18).

DISTRIBUTION: Perm., Leonardian and L. Guadalupian, West Texas; Park City Fm. (Franson Memb.), Wyoming. Loc. AMNH 512, 702, 703c, B72212.

DISCUSSION: We have about 60 separated valves, mostly from the Franson Memb. at loc. 3107. RVs are twice as abundant as LVs. Two specimens are articulated shells.

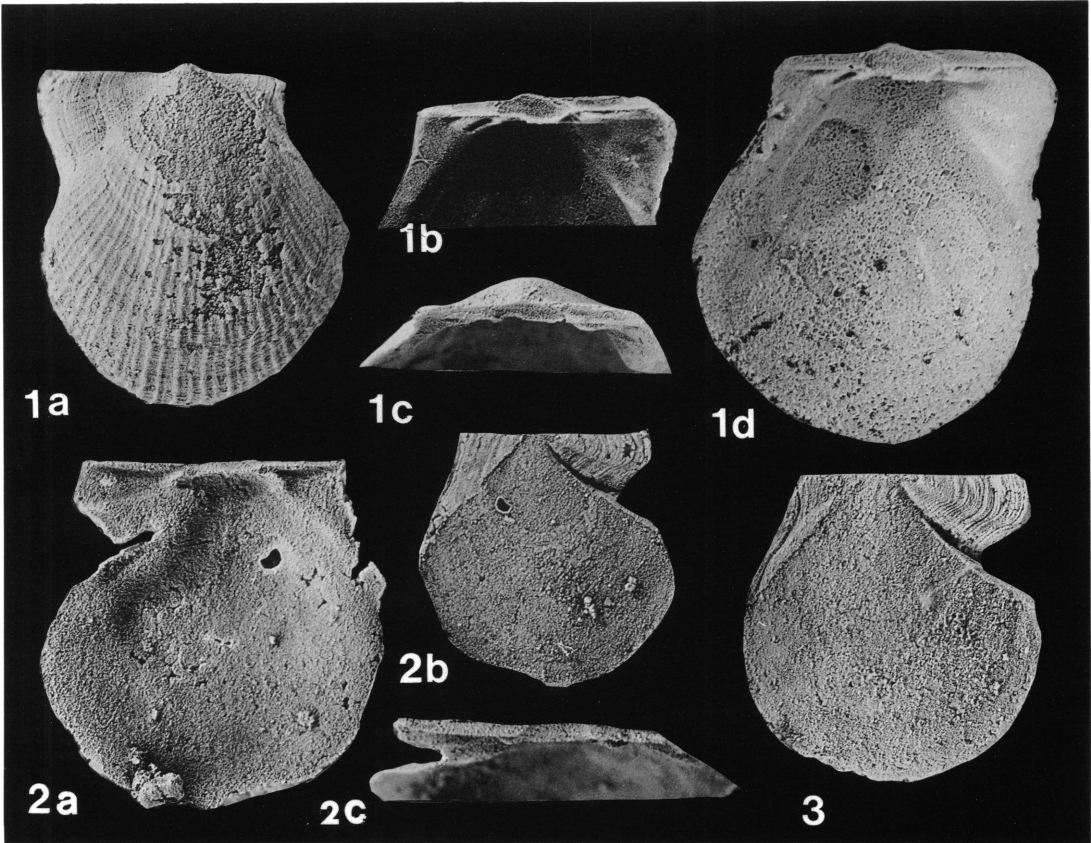


Fig. 50. *Fransonia wyomingensis* Newell and Boyd, n. gen. and n. sp., silicified, Guadalupian (Park City Fm., Franson Mem.), Wyoming, and L. Getaway Ls., West Texas. 1a-d, holotype, LV $\times 4$, AMNH loc. 512, cat. 44036, b and c showing tooth and socket at each end; 2a, b, c, RV, $\times 3$, $\times 2$, $\times 3$, respectively, AMNH loc. B72212-a, cat. 44037, 2a and 2c showing where two teeth of RV (1b and 1c) articulate inside those of LV; 3, RV, $\times 3.5$, AMNH loc. 3107, cat. 44038.

TABLE 18
Fransonia wyomingensis Newell and Boyd, n. sp.
Park City Fm. (Franson Memb.),
AMNH loc. 3107=B72212-a

Len	H	Len/H	Conv	Conv/L	Hin Len
Left valves					
12.5	12.9	0.97	3.0	0.24	9.1
10.9	11.2	0.97	2.6	0.24	8.0
9.4	10.2	0.92	2.1	0.22	?
9.0	9.7	0.93	2.0	0.22	6.0
8.4	9.5	0.88	2.1	0.25	?
Right valves					
12.3	11.7	1.05	1.4	0.11	9.0
11.3	11.2	1.00	1.2	0.11	8.5
9.8	10.5	0.93	1.3	0.13	7.4
9.7	9.8	0.99	0.9	0.09	7.2
8.6	9.1	0.95	1.0	0.12	5.7+

The distinctive dentition is most easily described from RV hinge. Here, an elongate tooth is located at each side of the resilifer and below the cardinal area. Each tooth slopes outward and downward from the resilifer corner, isolating a socket above its distal end accommodating a LV tooth.

LV teeth are not as symmetrical as their right counterparts. The posterior tooth is prominent because it slopes posteroventrally, whereas the anterior one is closer to the ventral margin of the ligament area. Furthermore, the posterior tooth in some individuals is bordered below by a minor tooth. Where present, it defines the lower border of a socket that received the posterior tooth of the RV.

The interior of one LV shows a sharply defined subcircular adductor scar high on the

posterior slope (fig. 50: 1d). Its ventral margin is at the valve midheight. The symmetrical resilifer is longer than high. Its outline is triangular on LVs, whereas on RVs it lacks the apex.

LEPTOCHONDRIIDAE
NEWELL AND BOYD, NEW FAMILY

DIAGNOSIS: Hinge external alivincular, with elongate resilifer; bourrelets narrow or absent; shell usually less than 20 mm high, with relatively short dorsal margin; LV multicostate and convex, RV almost smooth and less convex; valves discordant; posterior auricles small, subquadrate to obtuse, anterior auricle of LV rounded to obtuse, that of RV large and rounded with wide byssal notch.

DISTRIBUTION: Perm.–Trias.

Genus *Leptochondria* Bittner, 1891

Antijanira Bittner, 1901.

Amphijanira Bittner, 1901; Trias, discussed by Al-lasinaz, 1972.

TYPE SPECIES: *Pecten aeolicus* Bittner, 1891, monotypic as recognized here; U. Trias. (No-rian), Anatolia.

DIAGNOSIS: As for family Leptochondri-idae.

DISTRIBUTION: Widespread, long ranging. Perm. (Guadalupian), U.S.; Perm. (Chang-xingian), China and Japan; Trias. (Virgin Ls., Thaynes Fm.), U.S.; Trias. (Nammalian–No-rian), Alps, Asia.

DISCUSSION: Several generic and specific names have been proposed, probably includ- ing synonyms falling in two variable groups— those with numerous fine costellae, and those with moderately coarse costae, as exemplified by the American species described below. The genus has a superficial resemblance to *Fran-sonia* and *Euchondria*, but the hinges are quite different in the three.

Leptochondria curtocardinalis
(Hall and Whitfield), 1877
Figure 51: 1, 2

Aviculopecten curtocardinalis Hall and Whitfield, 1877.

Monotis bregeri Girty, 1927.

Monotis thaynesiana Girty, 1927.

Monotis? landerensis Branson, 1930.

Monotis? landerensis Ciriacks, 1963.

Monotis? thaynesiana Ciriacks, 1963.

TABLE 19
Leptochondria curtocardinalis
Virgin Ls., AMNH locs. B7977 and B7978

Len	H	Len/H	Conv	Aur Len	Hin Len
Left valves					
13.2	14.6	0.90	3.1	2.6	6.2
12.4	13.1	0.95	2.7	3.0	6.3
11.9	13.1	0.91	2.6	3.0	7.7
12.0	12.6	0.95	2.0	3.3	8.2
10.7	11.9	0.90	1.9	3.0	8.0
10.2	11.2	0.91	1.9	2.8	7.2
10.5	10.9	0.96	2.0	2.6	5.3
9.7	10.8	0.90	2.0	2.7	5.4
8.6	9.1	0.95	2.0	2.5	5.7
6.7	7.5	0.89	1.2	2.3	5.2
Right valves					
9.5	9.2	1.03	negligible	3.1	7.4
8.7	9.2	0.95	negligible	2.7	6.2
8.1	8.6	0.94	negligible	2.6	6.3
8.3	8.4	0.99	negligible	2.6	7.1
7.6	8.0	0.95	negligible	2.8	6.2
7.2	7.9	0.91	negligible	2.6	6.7
8.0	7.7	1.04	negligible	2.5	6.4
7.1	7.3	0.97	negligible	2.3	6.2
6.5	7.3	0.89	negligible	2.2	5.9
6.3	6.5	0.97	negligible	2.2	5.4

DIAGNOSIS: Weakly costellate shells with posterior auricle larger than anterior auricle (table 19).

DISTRIBUTION: Widespread and long-rang- ing. Perm., (Guadalupian), Texas; Park City Fm., Wyoming; L. Trias. (Virgin Ls., Thaynes Fm.), Nevada; Salt Range, Pakistan, East Asia, cosmopolitan.

DISCUSSION: Fine ornament in LVs and slightly forward position of the beaks distin- guish this species from *L. occidaneus*.

RVs are uncommon, perhaps because they were weakly calcified. This circumstance led Girty (1927) to conclude that these pecti- noids were equivalved, similar to the Triassic genus *Monotis*. However, the forward loca- tion of the beaks shows that he dealt only with LVs.

Yin (1982: 356) cited the widespread dis- tribution of forms closely similar to *L. cur- tocardinalis* in the U. Perm. (Changxingian) and L. Trias. of Asia. For the present we are referring all the local populations to a single species.

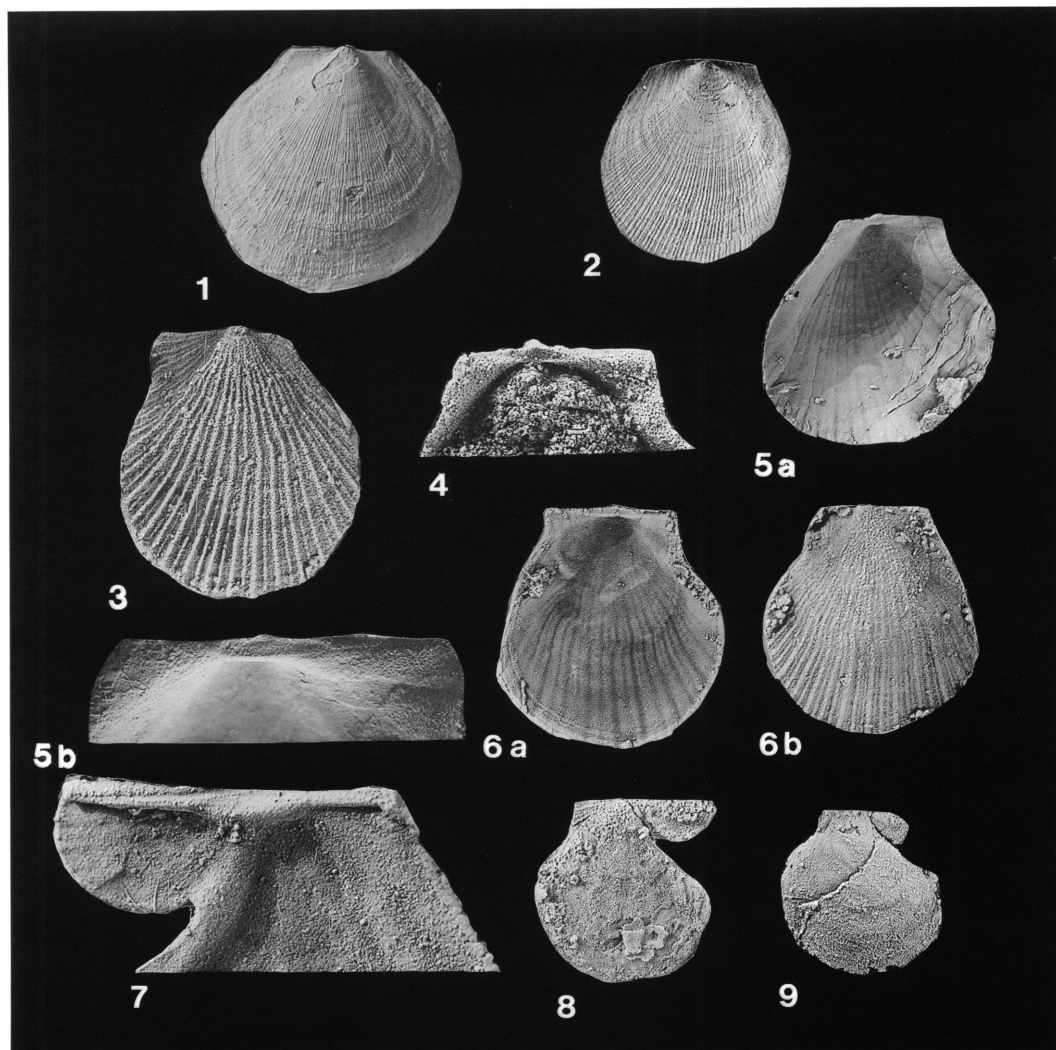


Fig. 51. *Leptochondria* Bittner from L. Trias. 1, *Leptochondria curtocardinalis* (Hall and Whitfield), calcareous LV, $\times 2$, Mittwali Fm., Salt Range, Pakistan, loc. K6-27A (Kummel and Teichert, 1970), AMNH cat. 44032; 2, *Leptochondria curtocardinalis* (Hall and Whitfield), calcareous LV, $\times 2$, after Girty (1927) as *Monotis thaynesiana*, Nammalian, Meekoceras zone (Thaynes Fm.), Idaho, USGS loc. 7878, cat. 120775; 3-9, *Leptochondria occidaneus* (Meek), silicified, Nammalian, Virgin Ls., s. Nevada; 3, LV, $\times 2$, AMNH loc. B8517, cat. 44033; 4, LV $\times 3$, with elongate external ligament area, AMNH loc. B7979, cat. 44035; 5a, LV, $\times 1.5$, AMNH loc. B8517, cat. 43366; 5b, same, $\times 4.5$; 6a, b, LV, $\times 2$, AMNH loc. B8517, cat. 44073; 7, RV, $\times 5$, hinge view with strong scroll and amphidetic external ligament area, AMNH loc. B7979, cat. 62628; 8, RV $\times 2$, AMNH loc. B8517, cat. 43311; 9, slightly more convex RV, $\times 2$, Thaynes Fm., n. east Nevada, AMNH loc. B72219, cat. 44047.

Leptochondria occidaneus (Meek), 1877

Figure 51: 3-9

Aviculopecten occidaneus Meek, 1877.

Aviculopecten weberensis Hall and Whitfield, 1877.

Aviculopecten parvulus Hall and Whitfield, 1877.

Aviculopecten? superstrictus White, 1879.

Monotis superstricta var. *parksii* Girty, 1927.

DIAGNOSIS: Infracrescent, slightly higher than long, LV costellae numerous, slender, sharply defined, evenly intercalated; RV

smooth except for radial costellae on both auricles; narrow groove curving from beak to apex of broad byssal notch; beaks slightly behind midpoint of hinge; posterodorsal angle of LV quadrate to obtuse, that of RV acute to obtuse.

LV lacking well-defined bourrelet; hinge axis ill-defined, and resilifer sunken into narrow shelf beneath beak; dorsal edge of RV bearing small scroll bordered by very narrow bourrelet; resilifer reinforced anteriorly by weak auricular buttress (table 20).

DISTRIBUTION: L. Trias. (Nammalian): Moenkopi Fm. (Virgin Ls.) of south. Nevada and Thaynes Fm. of north. Nevada and Utah; loc. AMNH 3112; B7979; B8517.

DISCUSSION: Our characterization is based on a silicified sample of mainly LVs from locality B7979. Many others, mainly fragmentary LVs from elsewhere, were also evaluated. The interior surfaces and hinges are poorly preserved.

An exploration by the King party along the 40th parallel in the west. U.S. brought back fossils described separately by Meek, and by Hall and Whitfield, in King's 1877 report. Unknown to each other, they named several small, costate pectinoids from rocks in Utah now classed as Thaynes Fm. (Boutwell, 1912). The differences among these fossils appear to be no greater than the variation in our population samples from south. Nevada, so we have applied Meek's species name on the basis of page priority.

SUPERFAMILY PECTINACEA
WILKES, 1810

DIAGNOSIS: Auriculate pteriomorphians with internal alivincular ligament.

DISCUSSION: The earliest Pectinacea, represented by *Pernopecten*, were remarkably conservative, first appearing in the L. Carb. of west. Europe, and changing markedly as they gave rise to Mesozoic *Entolium*. Attribution of the family group was called to our attention by Waller (1993: 198).

FAMILY PECTINIDAE
WILKES, 1810

DIAGNOSIS: Scallops with ctenolium, and concordant dominantly calcitic, irregularly crossed, foliated shells.

TABLE 20
Leptochondria occidaneus
Virgin Ls., AMNH loc. B7979 and B8517

Len	H	Len/H	Conv	Aur Len	Hin Len
Left valves					
21.3	22.3	0.96	5.1	5.6	10.0
19.4	20.5	0.95	3.9	6.3	10.2
16.3	17.8	0.92	4.6	5.2	8.6
15.5	15.6	0.99	3.4	5.5	9.5
13.8	15.8	0.87	3.9	5.2	9.1
13.7	14.0	0.98	3.1	5.2	8.9
10.0	10.6	0.94	2.7	4.1	6.9
7.5	8.7	0.86	2.3	3.1	5.6
5.7	6.9	0.83	2.0	2.8	5.2
5.1	6.1	0.84	1.8	2.3	4.3
Right valves					
14.8	16.5	0.91	negligible	6.2	9.8
14.2	14.1	1.00	negligible	6.9	11.9
12.2	12.9	0.96	negligible	5.6	9.6
10.2	11.1	0.92	negligible	4.6	7.3
9.4	10.1	0.93	negligible	4.8	7.7
8.8	9.5	0.93	negligible	3.7	7.0
8.0	9.0	0.89	negligible	4.2	7.0
7.2	8.2	0.88	negligible	4.5	6.2
7.5	8.0	0.84	negligible	3.8	6.5
7.0	7.1	0.99	negligible	2.8	6.3

DISTRIBUTION: Trias.—Recent; cosmopolitan.

Genus *Pleuronectites* von Schlotheim,
1820

TYPE SPECIES: *Pleuronectites laevigatus* von Schlotheim, 1820, SD Fischer, 1886. M. Trias., Germany.

DIAGNOSIS: Surface smooth; orbicular with prosogyrate beaks; LV moderately convex, RV less convex.

DISCUSSION: Cox, 1969: 339 classed *Pleuronectites* with the Aviculopectinidae, even though his *Pleuronectites* has a ctenolium, a characteristic of the Pectinidae (Waller, 1984).

Through the courtesy of Dr. Hans Hagdorn, of the Muschelkalkmuseum in Ingelfingen, Germany, we have examined a few specimens like those of Cox, which were thought by Hagdorn to belong to the type species of *Pleuronectites*. These clearly possess a ctenolium. They are robust shells, five times the size of the American examples described below. The American material is too

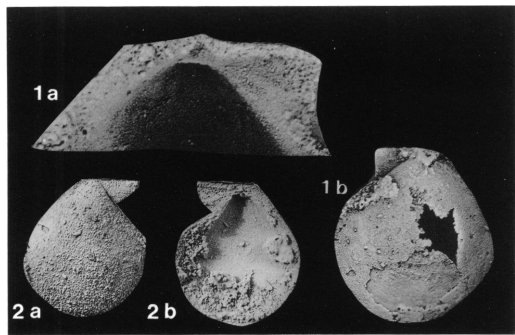


Fig. 52. *Pleuronectites meeki*, Newell and Boyd, n. sp., L. Trias., Virgin Ls. (Moenkopi Fm.), s. Nevada. 1a, b, Holotype, LV, $\times 5$ and $\times 3$, respectively, AMNH loc. B8517, cat. 44069; 1a, with internal alivincular hinge, and resilial ridges; 1b, smooth surface, subquadrate anterior auricle and very small posterior auricle; 2a, b, RV, $\times 2$, showing characteristic obtuse posterior auricle, internal hinge, and location of beak just behind midpoint of hinge, AMNH loc. B8517, cat. 44051.

poorly preserved to determine the presence or absence of a ctenolium.

Allasinaz (1972: fig. 43.6) reported a RV of *P. balatonicus* from the Alpine M. Trias. that seems to display bourrelets, which he interpreted as an external ligament area. Some of his other specimens, however, are clearly pectinacean rather than aviculopectinacean. *Pleuronectites* is included in the pectinid subfamily Camptonectinae by Waller and Marinovich (1992).

DISTRIBUTION: L. Trias., Nevada; M. Trias., Europe.

Pleuronectites meeki Newell and Boyd,
new species
Figure 52

DIAGNOSIS: Valves higher than long; posterodorsal angle of auricles varying from about 125 to 145°; anterior margin of LVs with obscure auricular sinus; ill-defined internal knob at anteroventral corner of anterior auricle; RV with prominent byssal notch and sharply defined anterior auricular sulcus; anterodorsal end of this auricle inwardly concave, slightly higher than the beak, and curling inward to form small scroll; outer shell layer in both valves fibrous; ligament internal, amphidetic (table 21). Named for F. B.

TABLE 21
Pleuronectites meeki Newell and Boyd, n. sp.
Virgin Ls., AMNH loc. B8517

Len	H	Len/H	Conv	Aur Len	Hin Len
Left valves					
16.6	18.4	0.90	4.1	4.5	7.7
14.5	16.2	0.89	4.0	4.3	6.5
11.3+	13.4	—	2.9	3.0	4.9
11.4	13.1	0.87	2.8	3.1	4.5
10.9	12.5	0.87	3.1	3.0	4.7
	12.4	—	3.1	3.4	
9.5	11.1	0.86	2.3	2.7	4.5
Right valves					
15.7	17.2	0.91	3.7	5.0	7.5
12.7	14.3	0.89	3.0	4.0	6.3
12.4	13.8	0.90			
11.7	13+	—	2.6	3.9	6.0
11.1	12.9	0.86	3.0		
11.4	12.7	0.90	2.3	3.2	5.0
5.3	6.5	0.82	1.0	1.9	3.0

Meek, pioneer paleontologist of the western U.S.

DISTRIBUTION: L. Trias. Virgin Ls., south. Nevada (AMNH loc. B-7978, B-7979, B-8517).

DISCUSSION: This species is represented in our collection by 55 poorly preserved silicified valves, 33 of them RVs, from three localities.

Most are lacking inner ostracum, and surfaces are marred by imprints of ooids and other matrix grains. Discs are less convex than, but otherwise similar to, those of *Streblopteria*. However, the ligament in the present species is internal, whereas the ligament in *Streblopteria*, an aviculopectinacean, is external; and the anterodorsal corner of both valves in the new species is subquadrate, but obtuse in *Streblopteria*.

FAMILY ENTOLIIDAE
VON TEPPNER, 1922

DIAGNOSIS: Suborbicular, valves concordant, nearly equilateral, low convexity and nearly equiconvex; smooth or with fine radial or comarginal ornament, byssal notch lacking in most adults; LV auricles in some genera projecting above hinge margin, RV hinge margin straight; auricular crura well developed.

DISCUSSION: The prevalent aragonite inner shell in the Paleozoic representatives of *Pernopecten* is replaced in the Jurassic *Entolium* with calcite. The nature of the transformation is conjectural (see Waller, 1984).

Waller (1991) postulated that the Pectinidae may have been derived from this family.

DISTRIBUTION: Miss.-U. Cretaceous, Laurasia.

Genus *Pernopecten* Winchell, 1865

Protoentolium Yanishevskiy, 1960.

TYPE SPECIES: *Aviculopecten limaformis* White and Whitfield, 1862, OD.

DIAGNOSIS: Orbicular to slightly retrocrescent, smooth or with fine radial ornament; auricles small, triangular, those of LV pointed above and extending high over hinge; auricles depressed abruptly below general surface; front and rear parts of disc with broad sulci bounding flattened marginal brim extended slightly at posteroventral margin of shell; brim bounded internally on each side of shell by low marginal ridge; anterior and posterior auricular crura each terminating in low boss; byssal notch visible in early growth lines but absent in adults; shell with slight anterior and posterior gape; inner microstructure concentric crossed lamellar; outer layer RV prismatic.

DISTRIBUTION: Miss.-M. Perm., cosmopolitan in Laurasia.

DISCUSSION: The thin shell, internal ligament, and obsolete byssal notch suggest that *Pernopecten* was active and the circular shell is remindful of modern *Amusium*, the most active living scallop. It even more closely resembles deep sea *Propeamusium* (fig. 12), however it should be noted that the two genera differ as to which valve has the dorsally protruding auricles.

Although *Pernopecten* is not a rare taxon in the Texas Permian, its shells are fragile and difficult to collect and prepare, especially in the silicified condition, because they tend to break up as they are separated from matrix in acid. Crossed foliate (calcite) shells seem to be more durable when silicified.

Newell (1937) and K. A. Astafieva-Urbaitis (1977) have discussed *Pernopecten* at length and described a number of Penn. species which they referred to the family Amus-

TABLE 22
Pernopecten yini Newell and Boyd, n. sp.
L. Getaway Ls., AMNH loc. 512

Len	H	Len/H	Conv	Hin Len	Um An
Left valves					
35+	41	—	5.0	11+	111°
	28	—	4.1	11	108°
19	21	0.90	2.1	7	102°
16+	18	—	2.1+	5+	104°
12.5	13.5	0.93	2.0	5.4	100°
12.0	13.5	0.89	2.0	5.5	96°
11+	13.0	—	2.1	5.0	99°
9+	10.5	—	1.5	—	93°
8.7	10.0	0.87	1.2	3.2	94°
Right valves					
42	41	1.03	6.8	18+	122°
34	35	0.97	4.2	14+	114°
27+	29	—	4.4	—	111°
22	22	1.00	3.1	10+	107°
17+	18	—	2.7	—	105°
13.8	14.5	0.95	2.1	6.0	102°
13.7	14	0.98	2.0	4.6+	95°
12.5+	14	—	1.5	5.5+	97°
8.1+	8.8	—	1.0	3.6+	94°
7.5	8.6	0.87	1.1	3.4+	96°

siidae, following Hind (1903), who referred his Lower Carboniferous pernopectens to the modern genus *Amusium*.

Pernopecten yini Newell and Boyd,
new species
Figure 53

DIAGNOSIS: Equilateral shells with length almost equal to height; small, symmetrical resilifer with resilial ridges; posterior auricular crus and marginal ridge longer than their anterior counterparts (table 22).

DISTRIBUTION: Leonardian-Wordian; AMNH loc. 369, 503, 509, 512; USNM loc. 702, 703, 703a, 703c, 706, 706b, 706c, 706e, 707e, 710d, 712a, 720d, 721j, 721s, 721u, 728, 738L.

DISCUSSION: The species is named after Yin Hongfu, the eminent student of Chinese Permian pectinoids. Our collection consists of 90 separated silicified valves—most of them fragments—from 19 West Texas localities.

Our species is slightly more symmetrical than the Carboniferous members of the ge-

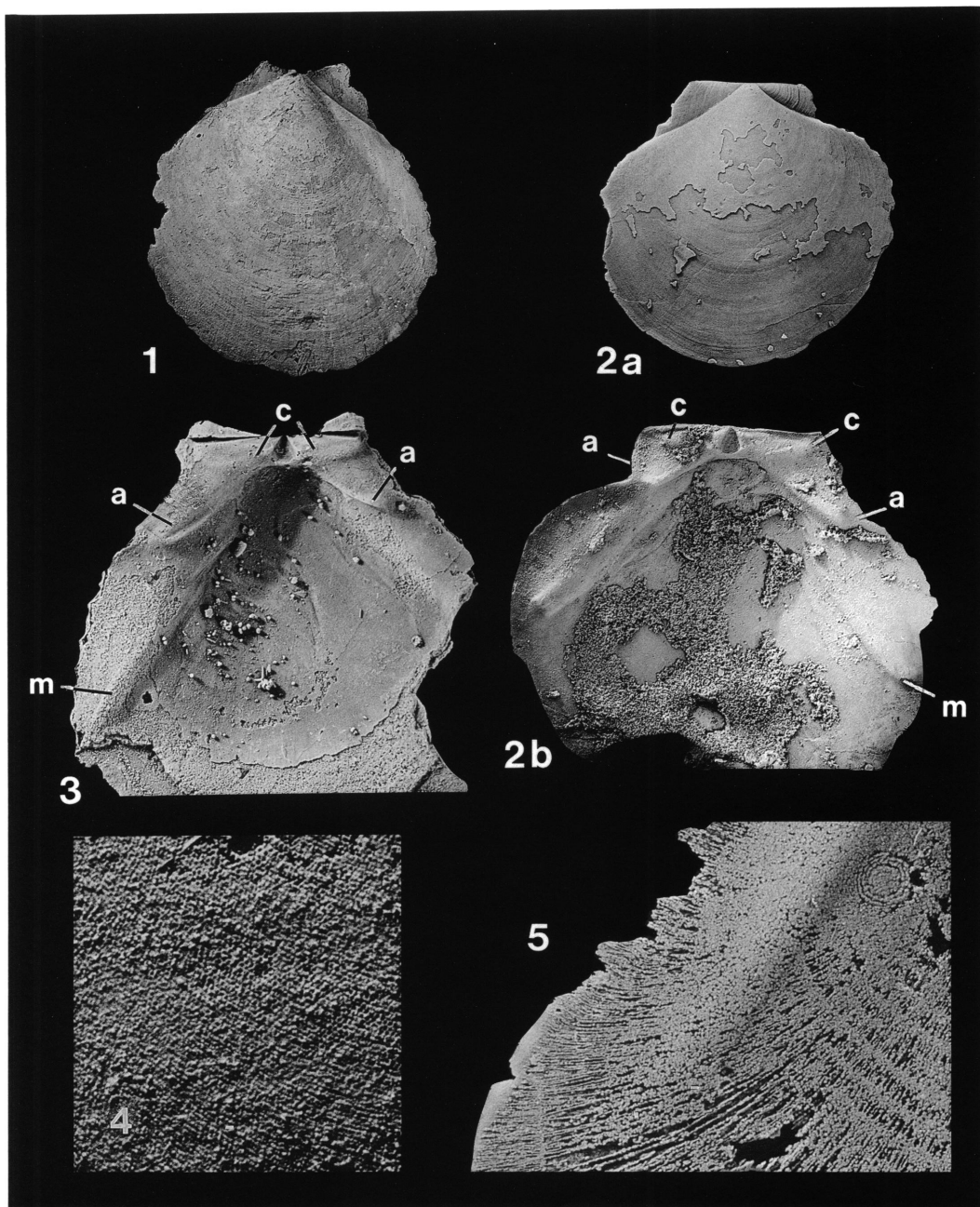


Fig. 53. *Pernopecten yini*, n. sp., silicified, Perm., West Texas. 1, Holotype, LV, $\times 2$, Guadalupian (L. Getaway Ls.), AMNH loc. 505, cat. 44030; 2a, RV exterior, $\times 1$, with slight asymmetry of auricles, juvenile byssal notch indicated in growth lines, Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 44031; 2b, same, interior, $\times 1.5$, with alivincular internal resiliifer and nonarticulating ridges and crura (c); 3, LV, $\times 2$, with auricles elevated above ligament groove, cardinal crura (c), auricular crura (a), and marginal ridge (m), separating visceral area from flattened posterior, USNM loc. 724, cat. 388870; 4, RV, $\times 10$, detail of fig. 2a, showing comarginal rows of prisms; 5, LV, $\times 10$, inner view of fibrous external layer, Leonardian (Cathedral Mt. Fm.), USNM loc. 702, cat. 382758.

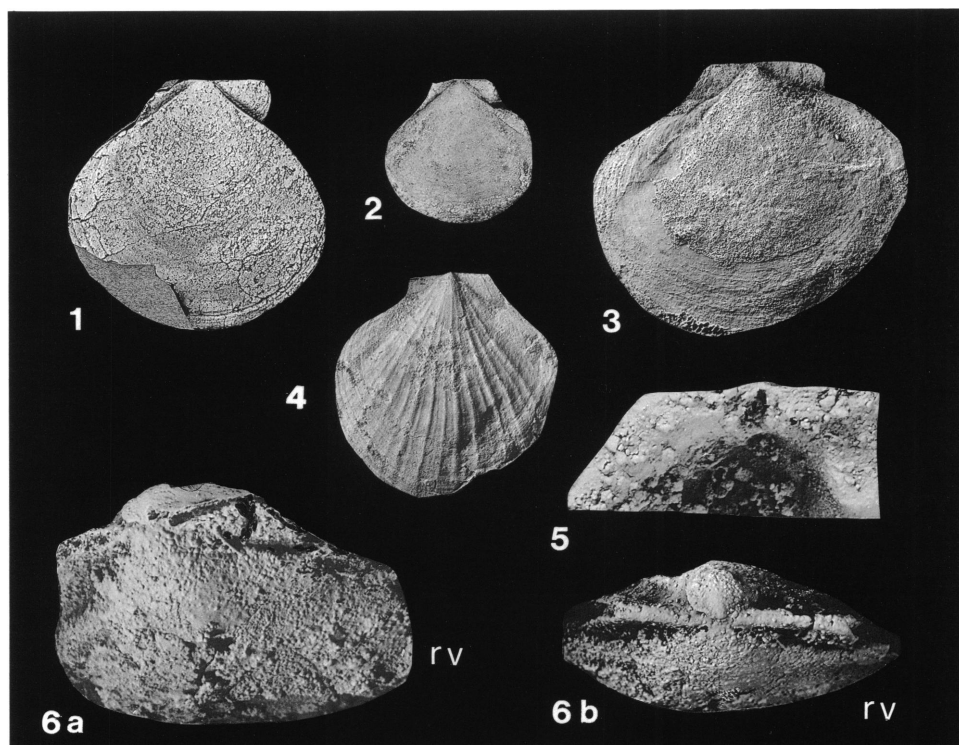


Fig. 54. *Entolioides utahensis* (Meek), L. Trias. (Thaynes Fm.), west. U.S. 1, Silicified RV, $\times 1$, showing equilateral, orbicular unornamented disc, obtuse auricles, and obsolescent byssal notch, s. west Montana, AMNH loc. B8834, cat. 44070; 2, RV, $\times 1$, rubber cast of calcareous mold, east. Nevada, AMNH loc. B8836, cat. 44062; 3, RV, $\times 1$, rubber cast of composite calcareous mold showing reflection of internal marginal ridges similar to those of *Pernopecten*, east. Nevada, AMNH loc. B8836, cat. 44071; 4, LV, $\times 1$, Rubber cast of multicostate calcareous mold, east Nevada, AMNH loc. B8836, cat. 44060; 5, silicified LV, $\times 4$, showing internal resiliifer, s. east. Idaho, AMNH loc. B-7858, cat. 43356; 6a, b, silicified bivalved individual (RV below), $\times 2$, showing nearly equiconvex valves and hinge axis at dorsal margin, s. west. Montana, AMNH loc. B8537, cat. 44072.

nus. Neither of its subequal auricles has a marginal sinus, although growth lines indicate that one was present beneath the anterior auricle of juvenile right valves.

The West Texas form lacks several features that characterize the Carboniferous species as described by Newell (1937). These characters are: retrocrescentic outline and comb-like ridges on each side of RV resiliifer. Girty's *P. obliquus*, 1908, from the Capitan Ls., poorly characterized, is more slender (see Newell, 1937: 113).

Genus *Entolioides* Allasinaz, 1972

TYPE SPECIES: *Pecten zitteli* Woehrmann and Koken, 1892, M. Trias., Alps.

DIAGNOSIS: Shell usually slightly longer than high, almost equiconvex, discordant; LV multicostate, RV smooth; hinge margin short, straight, with beaks at or near midpoint; auricles subequal, obtuse posteriorly and rounded at front; front and rear borders of disc flattened; byssal notch shallow; interior of anterior RV auricle with low boss at ventral juncture with disc; outer microstructure entire LV and auricles and adjacent area of RV all antimarginal fibrous; outer layer of most of RV disc prismatic.

DISTRIBUTION: L. Trias. (Thaynes Fm.), M. Rocky Mts., U.S.; M. Trias. (Carnian), Alps.

DISCUSSION: This taxon is closely similar to the much younger *Propeamussium* de Gregorio, 1884, especially in form and micro-

TABLE 23
Entolioides utahensis
 Thaynes Fm., AMNH loc. B8836

Len	H	Len/H	Conv	Hin Len
Left valves				
55	49	1.12	5.5	25
44+	45		3.8	17+
34	34	1.00	3.8	12
Right valves				
43	36+		4.1	16
29	25	1.16	2.4	12
23	51	1.10	2.2	8

structure, but differs in that the interior of both valves of *Propeamussium* has ribs, and the exterior is unornamented (fig. 12). The LV of *Entolioides* is multicostate while the RV is smooth; and the RV of *Entolioides* has a straight hinge margin whereas that of *Propeamussium* is concave dorsally.

Entolioides utahensis (Meek), 1877
 Figure 54

Aviculopecten utahensis Meek, 1877.

DIAGNOSIS: Has marginal ridges remindful of *Pernopecten*.

DISTRIBUTION: L. Trias. (Thaynes Fm.): AMNH loc. Nevada, B8836; Idaho, B8251, B8828; Montana, B8537. Meek's originals were from the "Carboniferous Limestone" at the southwest end of the Butte Mts., Nevada.

DISCUSSION: Our collection consists of about 60 valves among which RVs and LVs are equally common. At loc. B8836, the shells are calcareous and the preservation is poor. Outer shell layer seldom breaks free from hard matrix and inner shell layer is not preserved. Nonselective silicification at other localities resulted in shells welded to matrix.

SUPERFAMILY MONOTACEA
 FISCHER, 1887

Buchiacea Waller, 1978.

DIAGNOSIS: Shell ovoid, with gibbous umbones, almost lacking sculpture; posterior auricle in both valves lacking; RV auricle well developed, commonly curving downward toward umbonal cavity, bordered by arcuate, deep byssal slit; ligament generally transitional, mainly opisthodontic; Mesozoic rep-

resentatives have crossed foliate calcite microstructure with thin prismatic outer ostracum.

DISTRIBUTION: L. Carb.-Cretaceous.

DISCUSSION: The monotaceans, as did the Buchiidae, underwent a major radiation in the Mesozoic before dying out in the Cretaceous Period. Cox (1969), Waller (1978), and Begg and Campbell (1985) have given summaries of the group. We are adding to the Monotacea a new family of three Paleozoic genera: *Eurydesma*, *Chaenocardia*, and *Obliquipecten*. The oldest known monotacean is *Obliquipecten*, which first appeared at about the same time (L. Carb.) as the oldest *Aviculopecten*. We have not found likely ancestors for either one. However, we place the Chaenocardiidae in the Monotacea since they share some traits with the Buchiidae that set them apart from the Aviculopectinacea, with which they have been confused. These features are: shell form usually obliquely oval, lacking posterior auricles, unornamented, commonly crossed foliate; ligament transitional and usually opisthodontic. The Oxytomidae (Ichikawa, 1958) differ conspicuously, and belong elsewhere. Since they are not known before the Jurassic, they are not covered here (see fig. 11).

FAMILY CHAENOCARDIIDAE
 MILLER, 1889

DIAGNOSIS: Exterior nearly smooth except for microscopic antimarginal fibers; shell higher than long; hinge margin short, straight, with obtuse extremities; auricles small and poorly differentiated, except for RV anterior auricle which is semicircular; byssal notch wide; valves concordant, nearly equiconvex; ligament opisthodontic, transitional; dentition weak, consisting of LV socket behind anterior tooth; RV with corresponding obscure tooth and socket.

DISTRIBUTION: Penn., N. America; L. Perm., Gondwana.

GENUS *CHAENOCARDIA*
 MECK AND WORTHEN, 1869

TYPE SPECIES: *Chaenocardia ovata* Meek and Worthen, 1869, OD. M. Penn., U.S.

DIAGNOSIS: Ovoid, retrocrescent to procrescent; higher than long; RV anterior au-

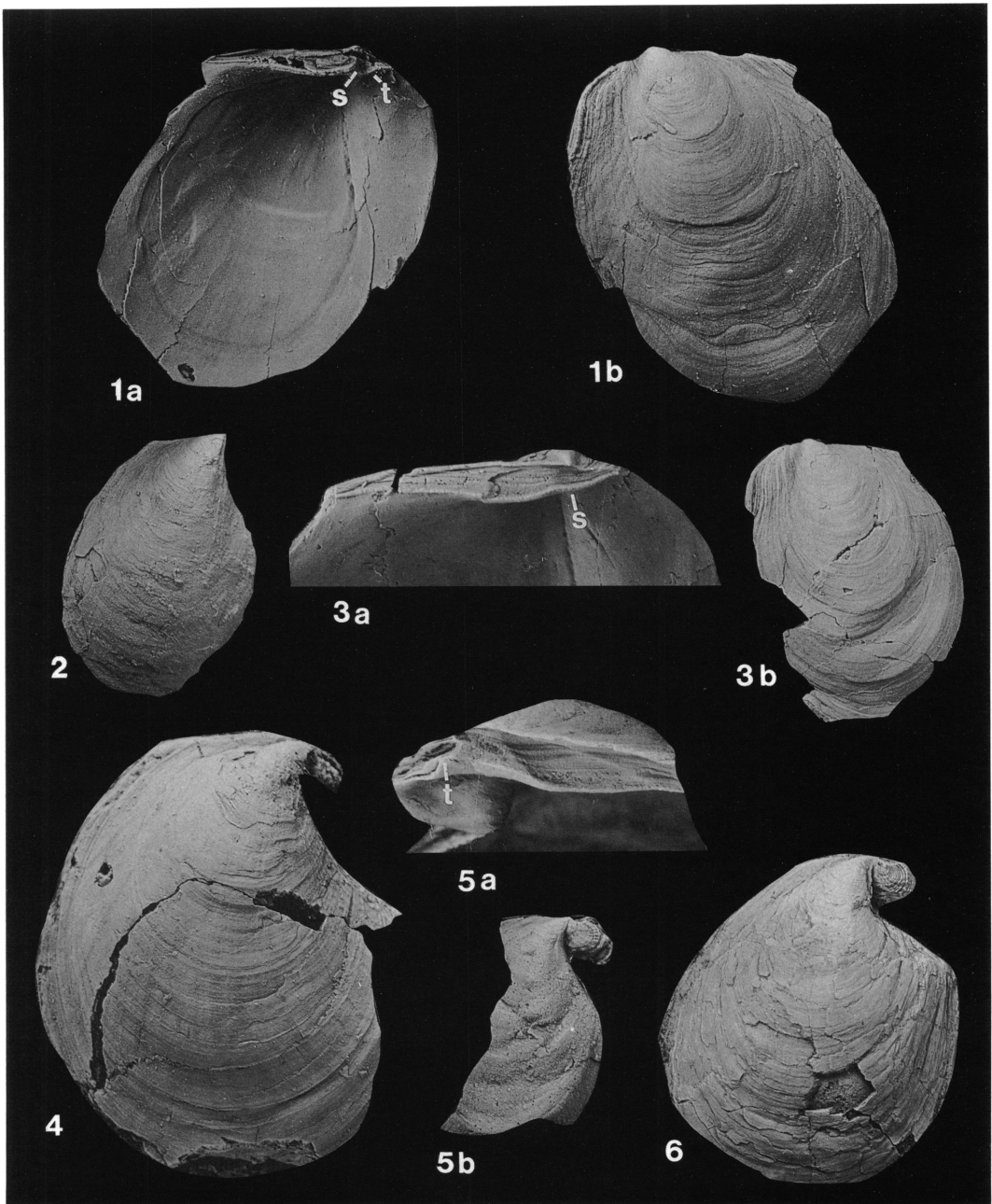


Fig. 55. *Chaenocardia ovata* Meek and Worthen, type species of *Chaenocardia*, Penn., Desmoinesian Series, shown for comparison with *Obliquipecten* and *Eurydesma*. 1, 2, 3, 5, uncataloged calcareous shells from Crory Road, Vanport Ls., Ellesport Township, Mahoning Co., Ohio, Collection of James Murphy, Columbus, Ohio. 1a, b, LV, $\times 2$, showing external mainly opisthodetic ligament with elongate rear bourrelet and retrorescent profile, socket (s), obscure tooth (t); 2, RV, $\times 2$, anterior auricle missing; 3a, LV, $\times 5$, with oblique resilifer, elongate posterior bourrelet and obscure socket (s); 3b, same $\times 2$; 5a, RV, $\times 3$, showing oblique resilifer and anterior tooth (t); 5b, same, $\times 1$; 4, 6, RVs, $\times 1$, calcareous, Buckhorn Asphalt Memb. (Atoka Fm.), near Sulfur, Oklahoma; 4, Chicago Field Mus. (Walker collection) cat. 51880. 6, AMNH cat. 44054.

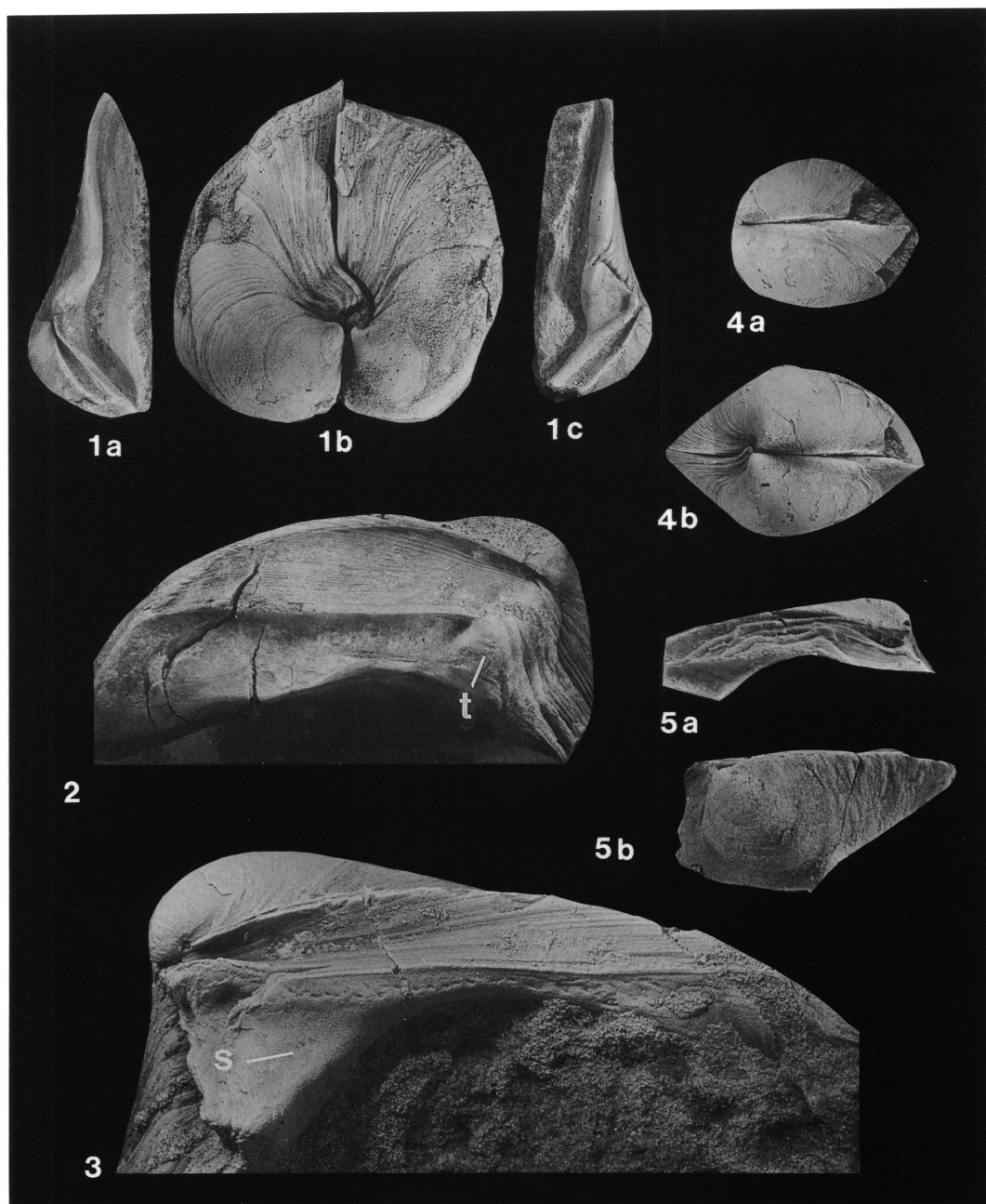


Fig. 56. 1-4, *Eurydesma*, L. Perm., Australia, all calcareous. 1a-c, *Eurydesma playfordi* Dickens, $\times 1$, matched valves of an individual (hinge below); 1a, LV; 1b, anterior view of both; 1c, RV; U. Lyons Group, 1 mi west of Callytharra Spring, Carnarvon Basin, AGSO loc. WB 62, cat. 33203; 2, *Eurydesma konincki* Johnston, LV, $\times 0.5$, tooth (t), Cattle Creek Fm., AGSO loc. Sp. 720, cat. CPC 8117; 3, 4, *Eurydesma playfordi*, AGSO loc. WB 62; 3, RV, $\times 2$, AGSO cat. 2232; 4, bivalved specimen, $\times 1$, AGSO cat. 33204; 5, silicified LV of unknown affinity, $\times 3$, superficially similar to *Eurydesma*, but apparently possessing duplivincular ligament, Road Canyon Fm., West Texas, AMNH loc. 501, cat. 44055.

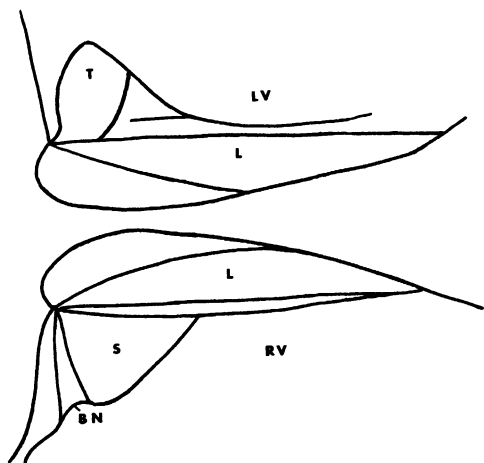


Fig. 57. Dentition of *Eurydesma playfordi* (diagrammatic), one external tooth occurs in the LV (T) and broad, saddle shaped socket (S) in RV, tooth slides over socket as far as byssal notch (BN) to cover hinge from exterior, position of opisthodontic transitional ligament indicated by (L).

ricles small and rounded; ligament variable, essentially opisthodontic, with long posterior bourrelet and vestigial anterior one.

DISCUSSION: This genus is rare and exam-

ples are usually poorly preserved. Further work is needed.

DISTRIBUTION: Penn. (Desmoinesian, Buckhorn Asphalt, near Sulfur, Oklahoma; Vanport Ls., Ohio).

Chaenocardia ovata Meek and Worthen, 1869

Figure 55

DIAGNOSIS: This is the only known species of *Chaenocardia* so the diagnosis coincides with that of the genus.

DISTRIBUTION: Same as for genus.

Genus *Eurydesma* Morris, 1845

Figures 56–60

Leiomyalina Frech, 1891.

Glendella Runnegar, 1970.

TYPE SPECIES: *Eurydesma cordatum* Morris 1845.

DIAGNOSIS: Smooth, nonauricular, concordant, massive, and inflated, usually equiconvex shells (except *Glendella*) with short hinge; margin nearly circular, truncated anteriorly and dorsally; umbones prominent, prosogyrate; ligament opisthodontic, transitional, sub-

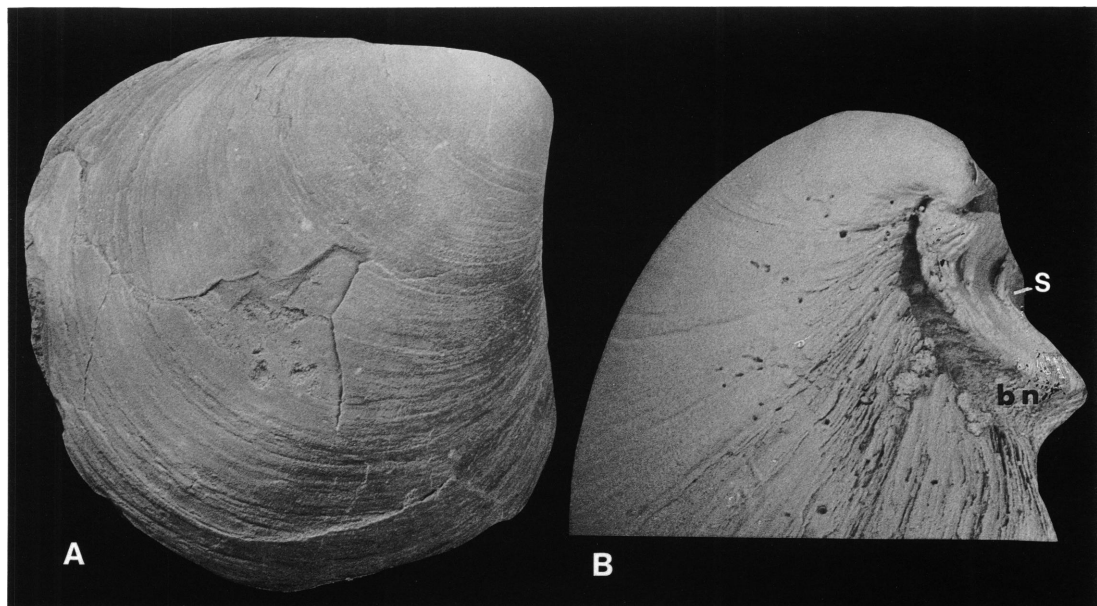


Fig. 58. *Eurydesma playfordi* Dickens, paratype D, L. Perm., east. Australia, RV, AGSO loc. WB62, cat. 2232 (same as fig. 56.3). A, Side view, $\times 1$; B, front view, $\times 2$, showing byssal notch (bn), and broad socket (s).

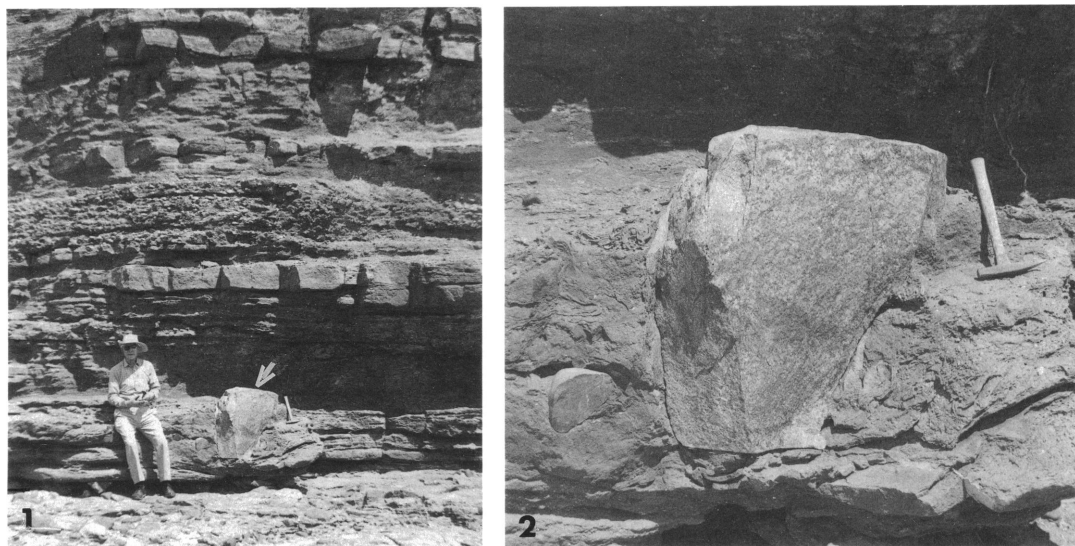


Fig. 59. Periglacial *Eurydesma* beds, Fossil Cliffs, Maria Island, Tasmania. 1, Interbedded siltstones and *Eurydesma* coquina, granite dropstones below center of view; 2, close-up of granite dropstones. [Photographs by Gillian Newell]

internal with broad, hemicylindrical ligament areas; RV with deep byssal slit bordered posteriorly by saddle-shaped socket; LV with corresponding external tooth; microstructure: apparently crossed foliate calcite.

DISTRIBUTION: Locally abundant in periglacial L. Perm. rocks of Australia, India, South Africa, and Argentina (fig. 60).

DISCUSSION: This Gondwana bivalve has been studied by many investigators. Carter (1990), Dickins (1957, 1983), Runnegar (1970, 1979), Waterhouse and Gupta (1982), and others have described many local pop-

ulations as species and have expressed uncertainty about their affiliations.

Eurydesma has been variously classed with Pteriacea, Aviculopectinacea, Ambonychiacea, and the Mesozoic Buchiidae. For the present we place it in a structurally unique family, the Chaenocardiidae, near the Mesozoic buchias. Runnegar (1970: 86) observed that the musculature in *Eurydesma* is similar to that of Upper Paleozoic pectinoids.

The baroque hinge topography in front of the ligament area is difficult to describe in terms of conventional teeth and sockets. On the RV, a narrow groove generated by the byssal notch is bordered by a concave platform (fig. 56: 3). Its anterior margin (fig. 58: b) fits against the posterior edge of a prominent callosity below the LV beak (fig. 56: 2). In an articulated shell (fig. 56: 1b), this thickened margin of the LV overlaps and conceals the underlying concave platform of the RV. The LV callosity and the anterior part of the RV platform are in the position of the anterior auricles of the pectinoids, and are possibly homologous. The socket-like area on the LV is reminiscent of the "Gelenkgrube" of the Jurassic buchiid *Malayomaorca* Jeletsky (1963).

Both Runnegar (1970) and Dickins (1983) have suggested that *Eurydesma* possessed an

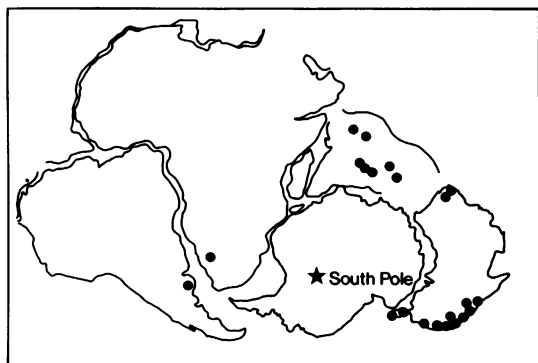


Fig. 60. Distribution of *Eurydesma* in Gondwanaland (Runnegar, 1979).

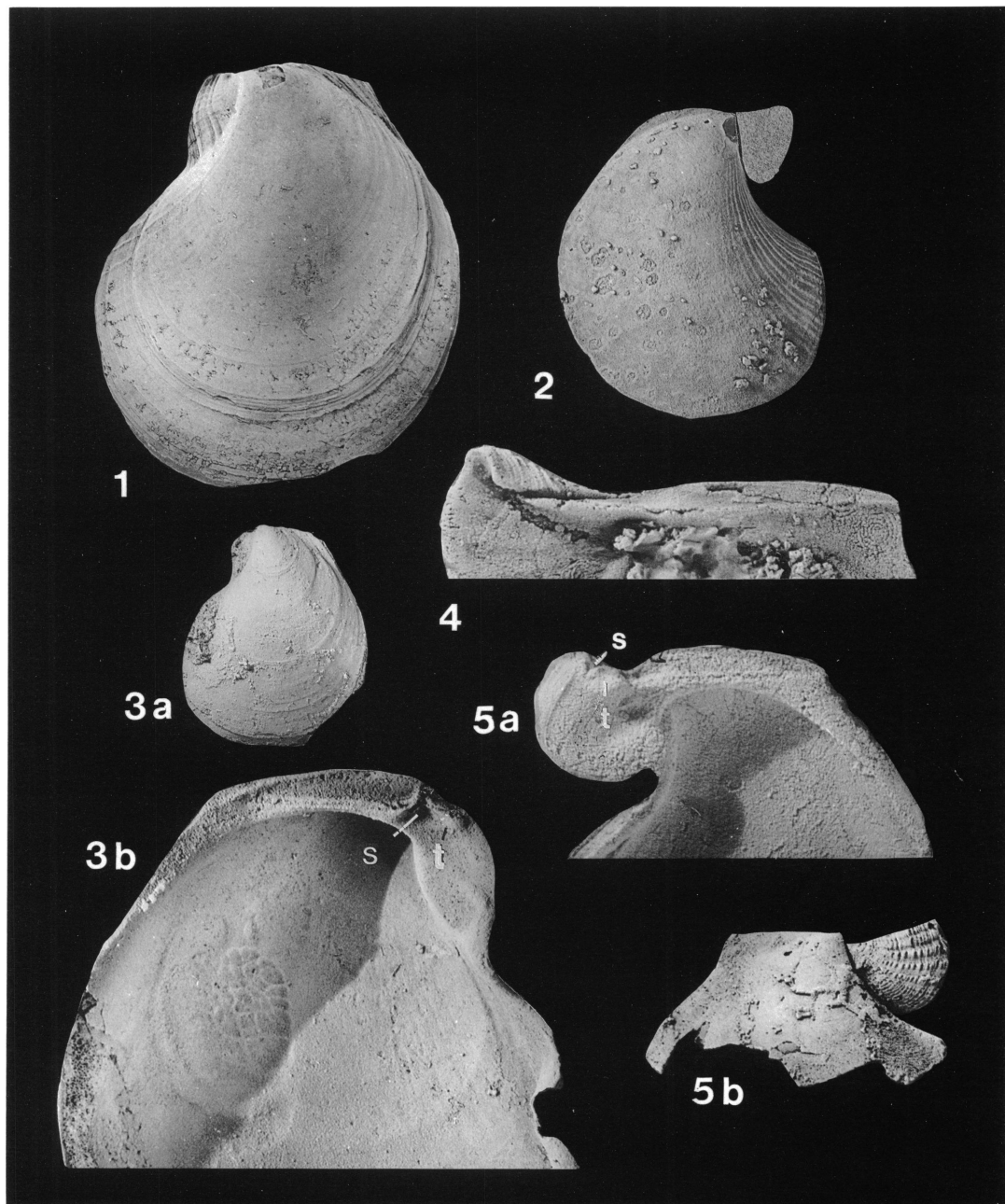


Fig. 61. *Obliquipecten granti*, n. sp., silicified, Perm., Glass and Guadalupe Mts., West Texas. 1, LV, holotype, $\times 1.5$, Leonardian (Road Canyon Fm.), USNM loc. 703a, cat. 388884; 2, RV, $\times 2$, front auricle restored, Guadalupian (Willis Ranch Fm.), USNM loc. 706, cat. 388885; 3a, b, LV, $\times 1$ and $\times 3$, respectively, Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43293; 4, RV $\times 3$, Guadalupian (L. Getaway Ls.), AMNH loc. 512, cat. 43291; 5a, b, RV, $\times 4$ and $\times 3$, respectively, showing details of ligament area and dorsal exterior, tooth (t), socket (s), AMNH loc. 512, cat. 43296.

TABLE 24
Obliquipecten granti Newell and Boyd, n. sp.
 L. Getaway Ls., AMNH loc. 512

Len	H	Len/H	Conv	Aur Len	Hin Len	Aur Len/ Hin Len	Resil Len
Left valves							
27.0	31.5	0.86	6.7	4.5	13.0	0.35	8.5
26.8	29.8	0.90	6.0	3.9	12.5	0.31	—
26.4	29.9	0.88	6.9	4.5	12.7	0.35	—
24.0	27.5	0.87	5.7	4.2	10.2	0.41	6.4
21.9	25.3	0.87	5.1	4.1	10.6	0.39	6.2
17.8	20.5	0.87	3.9	3.8	8.7	0.44	4.7
15.1	17.2	0.88	3.4	2.7	7.6	0.36	3.8
6.8	8.5	0.80	1.8	1.6	3.5	0.46	—
Right valves							
29.6+	34.3	0.86	7.5	6.3	14.8	0.43	
22.3	24.2+	0.89	4.9	5.1	11.8	0.43	6.5?
20.9	23.2	0.90	5.1	5.2	12.0	0.43	6.4
20.6	23.0	0.90	5.3	6.2	12.9	0.48	?
13.3	14.7	0.90	2.8	3.3	7.5	0.44	3.5
9.5	12.4	0.77	2.6	2.4	5.1	0.47	?
8.9	11.5	0.77	2.4	2.2	4.6	0.48	2.0?

endostracum of nacre. This seems unlikely because the shells generally do not exhibit differential leaching and our material shows traces of crossed microstructure in layers 1 and 2, suggestive of original calcite.

The many named species are said by their authors to be variable, but the overall impression is that the variability is slight and that the illustrated specimens are representatives of local populations distinguishable mainly by geographical location. Available material is not suited for biometrical analysis.

Our understanding of *Eurydesma* is mainly based on a few instructive specimens of *E. playfordi* and *E. hobartense* loaned to us by Dickins. Runnegar (1979) noted an upward trend in size in *E. hobartense*, with thickened umbones and loss of the byssus. We have observed individuals 10 cm or so across on Maria Island, Tasmania (fig. 59). As noted by Runnegar (1979), some apparently are in situ with umbones down and the commissural plane nearly vertical, as with modern *Tridacna*. They are among the heaviest of Paleozoic bivalves.

Runnegar (1979), who has given more attention to *Eurydesma* than anyone else, ob-

served that "the byssal notch in the RV is well developed in juveniles up to 3–5 cm in size."

It seems that adults of the stratigraphically higher and more common forms abandoned byssal fixation early in life and relied on the heavy umbones to maintain their life orientation.

Genus *Obliquipecten* Hind, 1901

TYPE SPECIES: *Obliquipecten laevis* Hind, 1901.

DIAGNOSIS: Procrascent, flattened valves, nearly smooth except for a few costellae on the anterior flank and auricle of each valve; hinge margin short; ligament transitional, opisthodetic; posterior dorsal margin obtuse; RV anterior auricle large, semicircular, with concave dorsal outline leading to anterior scroll higher than beak; tooth and socket at front of ligament in each valve.

DISTRIBUTION: Miss., Europe; Perm. (Wolfcampian–Guadalupian), West Texas. Unknown in the U. Carb.

DISCUSSION: Presumably the genus occupied a haven somewhere during the interval between the Miss. and the Perm., since Penn. examples have not yet been discovered.

Obliquipecten granti Newell and Boyd,
new species
Figure 61

DIAGNOSIS: Ovoid in profile, a little higher than long; dorsal margin behind beak slightly convex; RV anterior auricle with coarse co-marginal ridges and three or four costae (table 24).

DISTRIBUTION: Perm. (U. Wolfcampian–L. Guadalupian), West Texas. Hess Fm. (Taylor Ranch Memb.), Cathedral Mtn. Fm., Road Canyon Fm., L. Getaway Ls., Willis Ranch and Appel Ranch Ls. AMNH Loc. 505, 509, 512, 585; USNM Loc. 702, 702a, 702c, 702e, 703a, 703c, 706, 706b, 706e, 719z, 722t, 726d, 726o, 728, 732.

DISCUSSION: Named in honor of the late Dr. Richard E. Grant, Permian expert at the U.S. National Museum, who collected some of our specimens. This species differs only slightly from Hind's type species in smaller size, longer resiliifer, dorsal profile, and the topography of the anterior auricle.

Unrecognizable Genera

The following names are not used here because they are, in most cases, based on poorly

illustrated, very small samples of worn or fragmented specimens that show nothing of population variation. Hinge characters and shell microstructure are not demonstrated. There is a possibility that ample collections of topotypes may eventually be discovered and described to validate the names as generic taxa.

Xingiangopecten Yang zhi-rong and Chen Jin-hua, 1985

Junggarochondria Yang Zhi-rong and Chen Jin-hua, 1985

Binipecten Feng Qing-lai and Liu Ben-pei, 1990

Tianshanopecten Feng Qing-lai, 1988

Endocostapecten Feng Qing-lai, 1988

Turbopecten Astafieva, M. M., 1991

Crenipectinella Astafieva, M. M., 1991

Adornatipecten Astafieva, M. M., 1991

Saturnella Astafieva, M. M., 1994

Ivanovipecten Astafieva, M. M. and K., 1994

Striochondria Waterhouse, 1983

COLLECTING LOCALITIES

Permian Collecting Localities for Figure 62

B631, Minnekahta Ls. equivalent in Meade Peak Mem., Phosphoria Fm. NE $\frac{1}{4}$, sec. 15, T30N, R97W, Schlichting Mt. 7 $\frac{1}{2}$ ' Quad., WY.

B65112-b, Franson Mem., Park City Fm., Center, E $\frac{1}{2}$, sec. 28, T42N, R94W, Wedding of the Waters 7 $\frac{1}{2}$ ' Quad., WY.

B65116, Ervay Mem., Park City Fm., Center, S $\frac{1}{2}$, sec. 5, T6N, R6E, Wedding of the Waters 7 $\frac{1}{2}$ ' Quad., WY.

B65129, Ervay Mem., Park City Fm., Center, E $\frac{1}{2}$, sec. 28, T42N, R94W, Wedding of the Waters 7 $\frac{1}{2}$ ' Quad., WY.

B65133, Ervay Mem., Park City Fm., n. wall canyon in E $\frac{1}{2}$, sec. 26, T43N, R100W, Anchor Reservoir 7 $\frac{1}{2}$ ' Quad., WY.

B672, Park City Fm., SW $\frac{1}{4}$, sec. 1, T6N, R4W, Johnson Draw 7 $\frac{1}{2}$ ' Quad., WY.

B672-a, Ervay? Mem., high Park City Fm., SW $\frac{1}{4}$, sec. 26, T29N, R97W, on s. side Sweetwater River, Lewiston Lakes 7 $\frac{1}{2}$ ' Quad., WY.

B673, Franson? Mem., Park City Fm., SE $\frac{1}{4}$, sec. 36, T37N, R115W, Clause Peak 7 $\frac{1}{2}$ ' Quad., WY.

B674, Shedhorn Sandstone, NW $\frac{1}{4}$, sec. 11, T38N, R110W, Klondike Hill, 7 $\frac{1}{2}$ ' Quad., WY.

B6711, Park City Fm., NW $\frac{1}{4}$, SE $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 4, T52N, R102W, Shoshone Canyon 7 $\frac{1}{2}$ ' Quad., WY.

B6819, Park City Fm., sec. 19 and 30, T2N, R3W, Bull Lake W. 7 $\frac{1}{2}$ ' Quad., WY.

B6820, Ervay Mem., Park City Fm., SW $\frac{1}{4}$, sec. 22, T1N, R3W, at top of Phosphoria dip slope, Wise Flat 7 $\frac{1}{2}$ ' Quad., WY.

B6821, basal Franson Mem., Park City Fm., SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 1, T2N, R4W, Bull Lake W. 7 $\frac{1}{2}$ ' Quad., WY.

B6822, Franson Mem., Park City Fm., SE $\frac{1}{4}$, sec. 2, T2N, R4W, Bull Lake 7 $\frac{1}{2}$ ' Quad., WY.

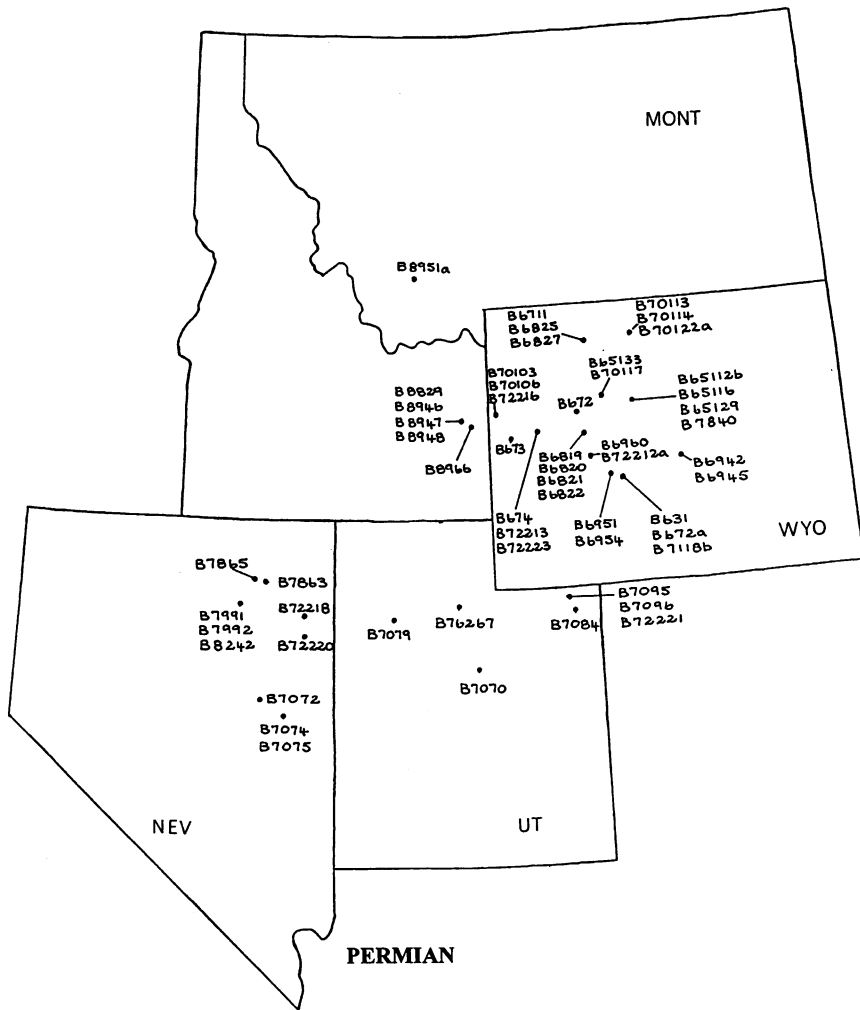


Fig. 62. Permian collecting localities in Rocky Mountains and Great Basin, AMNH. Not all localities yielded identifiable pectinoids. For West Texas AMNH and USNM localities see figure 64.

B6825, Ervay? Mem., high Park City Fm., Center, S $\frac{1}{2}$, sec. 34, T53N, R102W, Shoshone Canyon 7 $\frac{1}{2}$ ' Quad., WY.

B6827, Tosi Chert? Mem., Park City Fm., SW $\frac{1}{4}$, sec. 20, T53N, R102W, Shoshone Canyon, 7 $\frac{1}{2}$ ' Quad., WY.

B6942, Ervay Mem., Goose Egg Fm., SE $\frac{1}{4}$, sec. 4, T32N, R87W, Garfield Peak 7 $\frac{1}{2}$ ' Quad., WY.

B6945, Forelle? Mem., Goose Egg Fm., NE $\frac{1}{4}$, sec. 10, T33N, R88W, Garfield Peak 7 $\frac{1}{2}$ ' Quad., WY.

B6951, Grandeur Mem., Park City Fm., Center, sec. 11, T30N, R99W, Miner's Delight 7 $\frac{1}{2}$ ' Quad., WY.

B6954, Grandeur Mem., Park City Fm., Center N $\frac{1}{2}$, sec. 20, T31N, R99W, Wolf Point 7 $\frac{1}{2}$ ' Quad., WY.

B6960, Grandeur Mem., Park City Fm., NW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 26, T33N, R101W, Mt. Arter 7 $\frac{1}{2}$ ' Quad., WY.

B7070, Franson Mem., Park City Fm., SW $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 19, T7S, R5E, Granger Mt. 7 $\frac{1}{2}$ ' Quad., UT.

B7072, Pequop Fm., sec. 7, T17N, R59E, and sec. 12, T17N, R58E, Hamilton 7 $\frac{1}{2}$ ' Quad., NV.

B7074, Loray Fm., NW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 3, T15N, R62E, Ely 7 $\frac{1}{2}$ ' Quad., NV.

B7075, Loray Fm., SE $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 34, T16N, R62E, Ely 7 $\frac{1}{2}$ ' Quad., NV.

- B7079**, probably Gerster Fm., on w. flank Cedar Mts., probably SE $\frac{1}{4}$, sec. 21, T2S, R10W, Quincy Spring 7 $\frac{1}{2}$ ' Quad., UT.
- B7084**, Franson Mem., Park City Fm., 40°37'10"N, 109°29'40"W (unsurveyed), Donkey Flat 7 $\frac{1}{2}$ ' Quad., UT.
- B7095**, **B72221**, top beds Park City Fm., Center, N $\frac{1}{2}$, SE $\frac{1}{4}$, sec. 9, T2N, R20E, Manila 7 $\frac{1}{2}$ ' Quad., UT.
- B7096**, top beds Park City Fm., short distance down gully from B7095.
- B70103**, **B72216**, basal Franson Mem., Park City Fm., at top of USGS Meade Peak trench, E $\frac{1}{2}$, sec. 12, T41N, R118W, Rendezvous Peak 7 $\frac{1}{2}$ ' Quad., WY.
- B70106**, Blacktail Mem., Park City Fm., at top of USGS Retort trench, E $\frac{1}{2}$, sec. 12, T41N, R118W, Rendezvous Peak 7 $\frac{1}{2}$ ' Quad., WY.
- B70113**, Ervay Mem., Park City Fm., NW $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 21, T53N, R93W, Greybull N. 7 $\frac{1}{2}$ ' Quad., WY.
- B70114**, Ervay Mem., Park City Fm., SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 22, T53N, R93W, Greybull N. 7 $\frac{1}{2}$ ' Quad., WY.
- B70117**, Ervay Mem., Park City Fm., W $\frac{1}{2}$, sec. 25, T43N, R100W, on n. rim canyon, Anchor Reservoir 7 $\frac{1}{2}$ ' Quad., WY.
- B70122-a**, Ervay Mem., Park City Fm., SW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 2, T53N, R94W, Sheep Canyon 7 $\frac{1}{2}$ ' Quad., WY.
- B7118-b**, Grandeur Mem., Park City Fm., Center, NW $\frac{1}{4}$, sec. 31, T30N, R97W, Schlichting Mt. 7 $\frac{1}{2}$ ' Quad., WY.
- B72212-a**, Franson Mem., Park City Fm., SW $\frac{1}{4}$, sec. 25, T33N, R1W, Mt. Arter 7 $\frac{1}{2}$ ' Quad., WY.
- B72213**, **B72223**, Ervay Mem., Park City Fm., SW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 7, T38N, R110W, Klondike Hill 7 $\frac{1}{2}$ ' Quad., WY.
- B72216**, same as B70103.
- B72218**, Gerster Fm., sec. 3, T31N, R65E, Spruce Mt. 7 $\frac{1}{2}$ ' Quad., NV.
- B72220**, Gerster Fm., probably SW $\frac{1}{4}$, sec. 27, T28N, R65E, Currie 7 $\frac{1}{2}$ ' Quad., NV. Bissell stop no. 4 in 1971 Permian-Triassic Conf. Guidebook.
- B72221**, same as B7095.
- B72223**, same as B72213.
- B76267**, Grandeur Mem., Park City Fm., Center, NE $\frac{1}{4}$, sec. 31, T1S, R2E, Sugarhouse 7 $\frac{1}{2}$ ' Quad., UT.
- B7840**, Ervay Mem., Park City Fm., NW $\frac{1}{4}$, sec. 28, T42N, R94W, Wedding of the Waters 7 $\frac{1}{2}$ ' Quad., WY.
- B7863**, Gerster Fm., SE $\frac{1}{4}$, sec. 16, T37N, R58E, Morgan Hill 7 $\frac{1}{2}$ ' Quad., NV.
- B7865**, undifferentiated Permian of Ketner, SE $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 28, T38N, R56E, Coal Mine Basin 7 $\frac{1}{2}$ ' Quad., NV., USGS loc. 5151.
- B7991**, **B7992**, **B8242**, Gerster Fm., SE $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 32, T34N, R54E, Hunter 7 $\frac{1}{2}$ ' Quad., NV.
- B7992**, same as B7991.
- B8242**, same as B7991.
- B8829**, **B8946**, **B8947**, **B8948**, Franson tongue in Rex Chert, NE $\frac{1}{4}$, NW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 36, T2N, R42E, Conant Valley 7 $\frac{1}{2}$ ' Quad., ID.
- B8946**, same as B8829.
- B8947**, same as B8829.
- B8948**, same as B8829.
- B8951-a**, Blacktail Mem., Park City Fm., NW $\frac{1}{4}$, sec. 27, T4S, R8W, Block Mt. 7 $\frac{1}{2}$ ' Quad., MT.
- B8966**, Franson tongue in Rex Chert, NW $\frac{1}{4}$, SE $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 17, T1N, R43E, Conant Valley 7 $\frac{1}{2}$ ' Quad., ID.

Triassic Collecting Localities for Figure 63

- B6956**, Thaynes Fm., Aspen Grove 7 $\frac{1}{2}$ ' Quad., Utah. B6956-a, SE $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 7, T4S, R4E, B6956-b, NE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 8, T4S, R4E, B6956-c, NW $\frac{1}{4}$, NW $\frac{1}{4}$, sec. 9, T4S, R4E.
- B7078**, **B76268**, **B8246**, Dinwoody Fm., S $\frac{1}{2}$, SE $\frac{1}{4}$, sec. 13, T39N, R67E, Montello Canyon 7 $\frac{1}{2}$ ' Quad., NV.
- B70100**, **B7850**, **B8825**, Thaynes Fm., crest Commissary Ridge where crossed by Smiths Fork Road in NW quarter (unsurveyed) of Poison Meadow 7 $\frac{1}{2}$ ' Quad., WY.
- B72217**, Thaynes Fm., SW $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 29, T3N, R44E, Stouts Mt. 7 $\frac{1}{2}$ ' Quad., ID.
- B72219**, Thaynes Fm., where 6720 contour crosses w. boundary of sec. 31, T31N, R65E, Boone Spring, 7 $\frac{1}{2}$ ' Quad., NV.
- B76268**, same as B7078.
- B76277**, **B7858**, **B8251**, **B8830**, Thaynes Fm., SE $\frac{1}{4}$, NE $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 18, T1N, R43E, Conant Valley 7 $\frac{1}{2}$ ' Quad., ID.
- B7850**, same as B70100.
- B7851**, **B8826**, **B8827**, Thaynes Fm., SW $\frac{1}{2}$ sec. 29, T6S, R44E, Lanes Creek 15' Quad., ID.
- B7852**, **B7853**, Thaynes Fm., NW $\frac{1}{4}$ sec. 30, T6S, R44E, Lanes Creek 15' Quad., ID.
- B7854**, Thaynes Fm., float blocks from NW $\frac{1}{4}$, SW $\frac{1}{4}$, NE $\frac{1}{4}$ sec. 9, T31N, R118W, outcrop (source of float) at SW $\frac{1}{4}$, NW $\frac{1}{4}$, NE $\frac{1}{4}$ sec. 4, T31N, R118W, Afton 7 $\frac{1}{2}$ ' Quad., WY.
- B7858**, same as B76277.
- B7861**, Thaynes Fm., SW $\frac{1}{4}$ SE $\frac{1}{4}$, SW $\frac{1}{4}$, sec. 34, T1N, R1E, Fort Douglas 7 $\frac{1}{2}$ ' Quad., UT.
- B7977**, Virgin Ls. Mem. Moenkopi Fm., 36°11'40"N, 114°57'27"W, Frenchman Mt. 7 $\frac{1}{2}$ ' Quad., NV.
- B7978**, Virgin Ls. Mem. Moenkopi Fm., 36°11'08"N, 114°56'40"W, Frenchman Mt. 7 $\frac{1}{2}$ ' Quad., NV.
- B7979**, Virgin Ls. Mem. Moenkopi Fm., NW $\frac{1}{4}$,

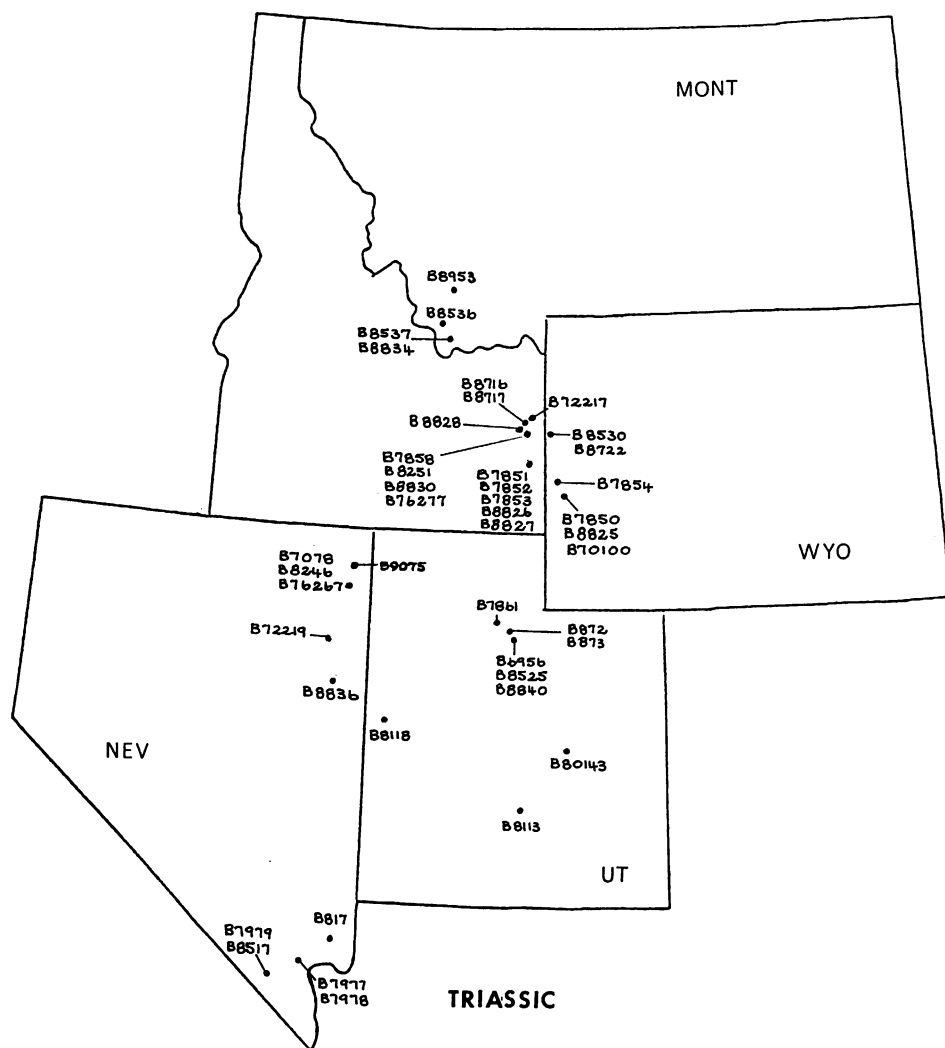


Fig. 63. L. Trias. collecting localities in Rocky Mountains and Great Basin, AMNH. Not all localities yielded identifiable pectinoids.

SE $\frac{1}{4}$ sec. 11, T23S, R58E, Goodsprings 7 $\frac{1}{2}$ ' Quad., NV.

B80143, Sinbad Ls. Mem. Moenkopi Fm., SW $\frac{1}{4}$, SW $\frac{1}{4}$ sec. 10, T21S, R11E, The Wickiup 7 $\frac{1}{2}$ ' Quad., UT.

B817, Virgin Ls. Mem. Moenkopi Fm., NW $\frac{1}{4}$, NW $\frac{1}{4}$ sec. 16, T16S, R66E, Moapa 7 $\frac{1}{2}$ ' Quad., NV.

B8113, Sinbad Ls. Mem. Moenkopi Fm., NE $\frac{1}{4}$ sec. 20, T29S, R5E, Torrey 15' Quad., UT.

B8118, Thaynes Fm. of Hose and Repenning, USGS Misc. Geol. Inv. Map I-378, T16S, R16W, Confusion Range, UT.

B8246, same as B7078.

B8251, same as B76277.

B8517, Virgin Ls. Mem. Moenkopi Fm., Center sec. 2, T23S, R58E, Goodsprings 7 $\frac{1}{2}$ ' Quad., NV.

B8525, same as B6956c.

B8530, **B8722**, Thaynes Fm., at 9000' elevation on ridge extending SE from Smoky Hollow Peak in SW $\frac{1}{4}$ of Teton Pass 7 $\frac{1}{2}$ ' Quad., WY.

B8536, Dinwoody Fm., NE $\frac{1}{4}$ sec. 28, T10S, R11W, Garfield Canyon 7 $\frac{1}{2}$ ' Quad., MT.

B8537, **B8834**, Thaynes Fm., NE $\frac{1}{4}$ sec. 27, T13S, R10W, Dixon Mt. 7 $\frac{1}{2}$ ' Quad., MT.

B872, Thaynes Fm., SW $\frac{1}{4}$, NW $\frac{1}{4}$, SE $\frac{1}{4}$, sec. 9, T2S, R3E, Park City West 7 $\frac{1}{2}$ ' Quad., UT.

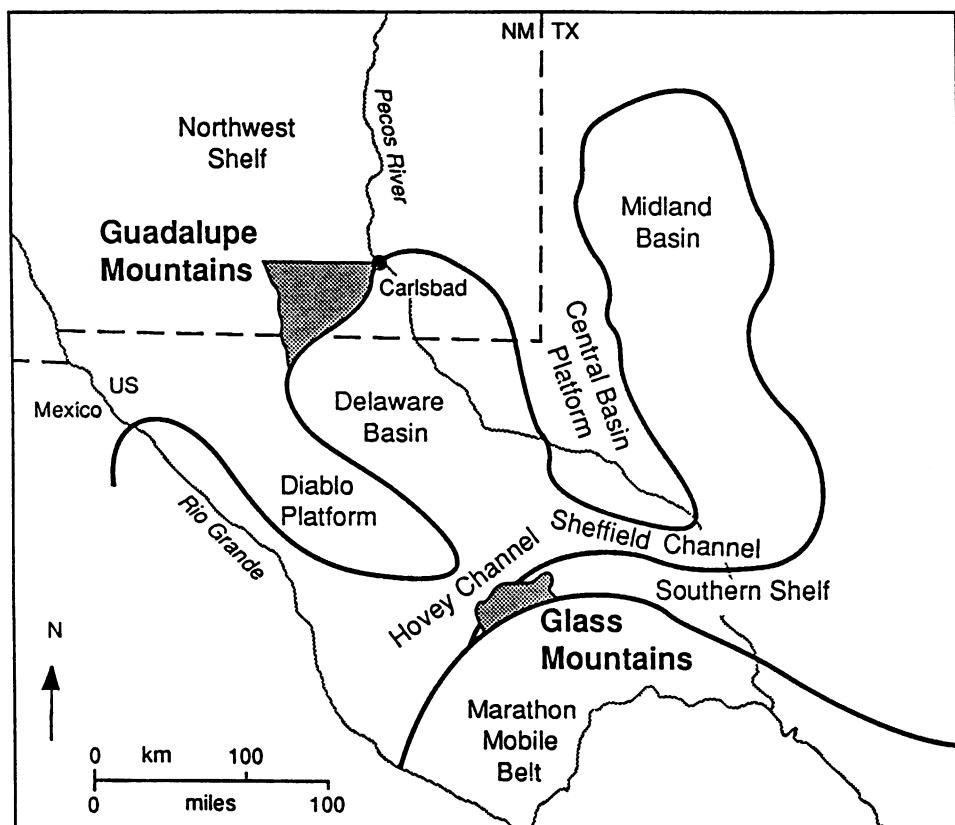


Fig. 64. Chief Permian collecting areas (shaded) in West Texas and New Mexico (map courtesy of Glenister et al., 1992). For specific localities see also Cooper and Grant, 1972, 1977.

B873, Thaynes Fm., SE $\frac{1}{4}$, NE $\frac{1}{4}$, SE $\frac{1}{4}$ sec. 9, T2S, R3E, Park City West 7 $\frac{1}{2}$ ' Quad., UT.

B8716, **B8717**, Thaynes Fm., NE $\frac{1}{4}$, NE $\frac{1}{4}$ sec. 8, T3N, R43E, Wheaton Mt. 7 $\frac{1}{2}$ ' Quad., ID.

B8722, same as B8530.

B8825, same as B70100.

B8826, **B8827**, same as B7851.

B8828, Thaynes Fm., SW $\frac{1}{4}$, NE $\frac{1}{4}$, NE $\frac{1}{4}$, sec. 35, T2N, R42E, Conant Valley 7 $\frac{1}{2}$ ' Quad., ID.

B8830, same as B76277.

B8834, same as B8537.

B8836, Dinwoody Fm. (?), NE $\frac{1}{4}$, NE $\frac{1}{4}$ sec. 31, T25N, R66E, Becky Peak 7 $\frac{1}{2}$ ' Quad., NV.

B8840, same as B6956-c.

B8953, Dinwoody Fm., sec. 24, T5S, R10W, Twin Adams Mt. 7 $\frac{1}{2}$ ' Quad., MT.

B9075, Thaynes Fm. (*Meekoceras* beds), Long Canyon (where 5400' contour crosses stream) south-central Dairy Valley 15' Quad., NV.

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