Phil. Trans. R. Soc. Lond. B. **284**, 225–246 (1978) [225]
Printed in Great Britain

The origin and early taxonomic diversification of pelecypods

By J. Pojeta, Jr
U.S. Geological Survey, E-501 U.S. National Museum, Washington, D.C. 20560, U.S.A.

[Plates 1–15]

A series of Cambrian morphologically intermediate forms show that the bivalved shell of pelecypods is probably derived from the pseudobivalved shell of rostroconchs, which in turn is probably derived from the univalved shell of helcionellacean monoplacophorans.

In Ordovician time, pelecypods underwent their first major radiation, which produced seven major groups herein called subclasses. The subclasses Orthonotia and Lucinata are newly named herein; the subclass Actinodontia is elevated to this rank from the rank of order. The group Heterodonta may be polyphyletic, as the taxa included within it seem to be derived from various Ordovician groups, herein regarded as subclasses. It seems likely that the solemyids are descendants of Ordovician palaeotaxodonts. The duplivincular ligament may have had a polyphyletic origin, having evolved independently in the Arcacea, Myalinidae, and Pteriacea.

Introduction

This paper attempts to show how a bivalved shell can evolve from a univalved shell and describes what is currently known about the first major radiation of the Pelecypoda in Ordovician time. The documentation for the evolution of the bivalved shell consists of a series of small Early and Middle Cambrian shells that are morphologically transitional between helcionellacean monoplacophorans and the earliest known pelecypod *Fordilla troyensis*. The documentation for the first major radiation consists of more than 40000 Ordovician pelecypods that I have examined; this documentation is presented primarily in visual form in figure 1 and in the plates. Two of the conclusions derived from the first major radiation are (1) that at least seven subclasses of pelecypods are represented in the Ordovician and (2) that the Heterodonta as presently constituted may be polyphyletic.

At present, about 123 generic names are used for Ordovician pelecypods, although as many as 227 generic names have been used for these animals at one time or another. I have reduced many names to synonymy, whereas other genera such as *Arca*, *Nucula* and *Pteria* do not occur in the Ordovician. Some homeomorphs of *Nucula* (plate 2, figures 7 and 8) and *Pteria* (plate 11, figure 5) are present in Ordovician rocks which misled early investigators. Figure 1*a* shows the diversification of pelecypods throughout the Ordovician based upon the number of genera known per time interval used. At present, about 1450 species names are available for Ordovician pelecypods.

In attempting to understand the diversity of Ordovician pelecypods, a thorough search of the literature was made. I have also examined the type specimens of more than 400 species, as well as the type specimens of the type species of 94 genera, and have visited many museums in North America, Australia, Czechoslovakia, England, France, and Sweden, borrowing all the better preserved specimens of Ordovician pelecypods. I have collected extensively from the Middle and Upper Ordovician rocks of the tri-State area of Ohio, Indiana, and Kentucky.

The Royal Society is collaborating with JSTOR to digitize, preserve, and extend access to *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences.* www.jstor.org

The rocks of this area are probably the best in North America for collecting Ordovician pelecypods, as these fossils are abundant, diverse, and often silicified. Some 16.3 t of rock was collected and etched. In addition, I have etched collections from the Ordovician rocks of various American and Australian States as well as two Canadian Provinces. Because various stratigraphic terms must be used for the subdivision of Ordovician time, these terms are shown in figure 1.

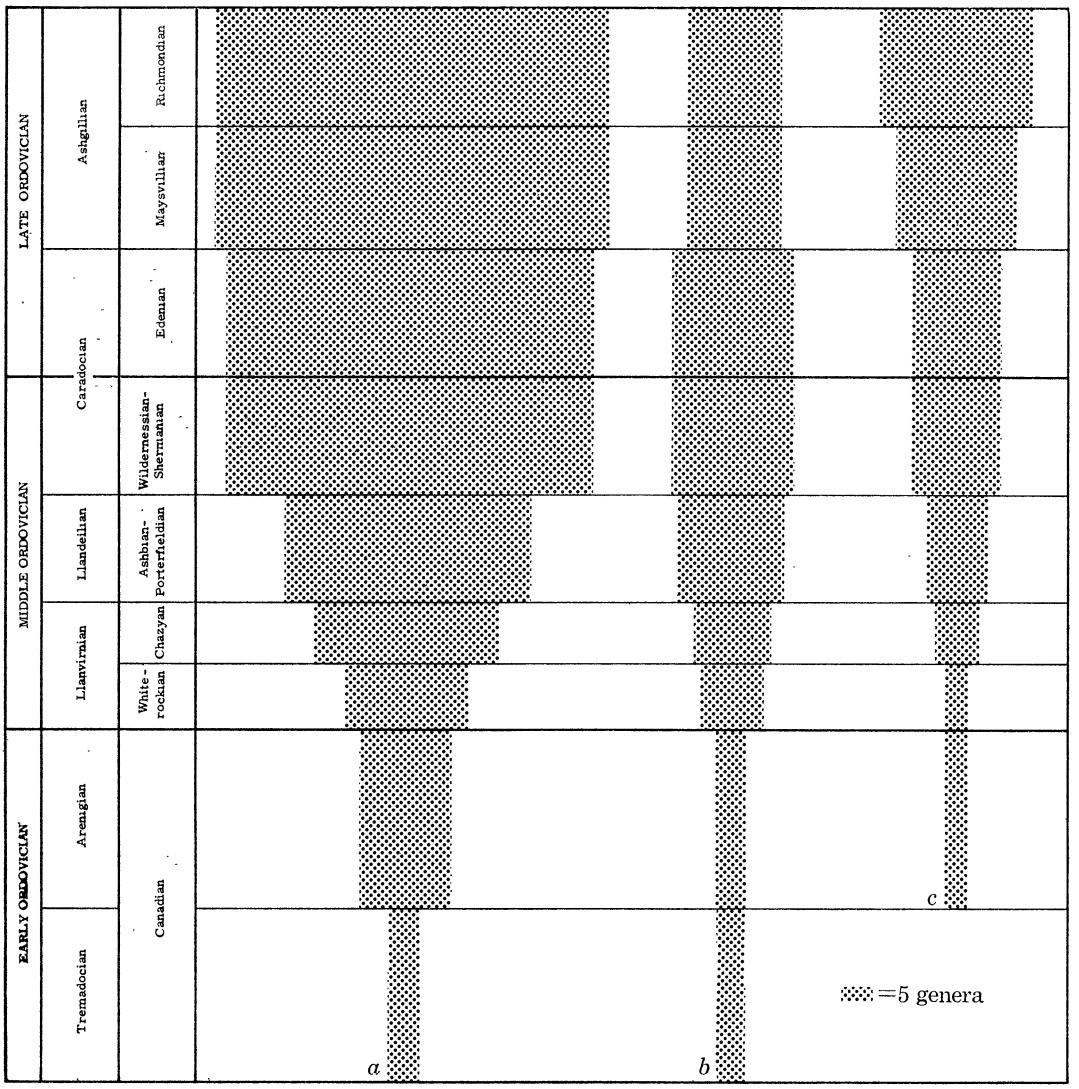


FIGURE 1. Chart showing the stratigraphic subdivisions of the Ordovician Period and the relative abundances of pelecypods (column *a*), and of the subclasses Palaeotaxodonta (column *b*) and Pteriomorphia (column *c*). Abundance figures based on the number of genera known per stratigraphic interval.

The bulk of our knowledge of Ordovician pelecypods is based upon shallow-water forms from eastern North America, western Europe, and northern Australia (Pojeta & Gilbert-Tomlinson 1977). This material is sufficient to determine the broad outlines of the Ordovician history of the Pelecypoda and to make reasonable speculations about the ancestors of many post-Ordovician higher Palaeozoic taxa.

The ecological diversification of Ordovician pelecypods was discussed by Pojeta (1971).

The most significant addition to our knowledge since that time is the occurrence of facultative boring forms in Upper Ordovician rocks (Pojeta & Palmer 1976).

All new genera and species figured are shown elsewhere (Pojeta & Gilbert-Tomlinson 1977) or under investigation and are not named here; they are simply listed as new genus 1, new genus 2, etc.

Origin of the Pelecypoda

The oldest known pelecypod is *Fordilla troyensis*, which is best preserved in upper Lower Cambrian rocks of New York, where it is part of the *Elliptocephala asaphoides* fauna. The New York specimens show a fully bivalved shell with adductor and pedal retractor muscle scars and a pallial line (Pojeta & Runnegar 1974; Pojeta 1975; plate 1, figure 7 herein). A fully bivalved shell of similar size and shape to *Fordilla troyensis* occurs in upper Lower Cambrian rocks (Lenian) of Siberia (plate 1, figures 3–6) and shows the presence of a single cardinal tooth and socket in each valve. Figure 2 is a composite drawing of *Fordilla* based on the American and Siberian material.

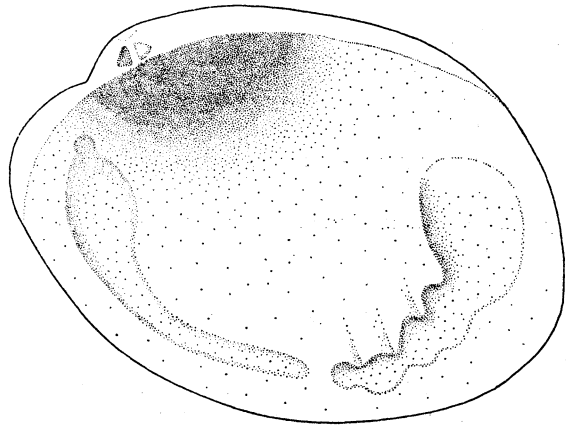


FIGURE 2. Composite reconstruction of *Fordilla troyensis* Barrande, the oldest known pelecypod.

It now seems likely that no pelecypods significantly older than *Fordilla* will be found because the probable ancestors of *Fordilla* are known. A series of taxa which are morphologically transitional from helcionellacean monoplacophorans to *Fordilla* are found in Lower Cambrian to middle Middle Cambrian rocks.

Heraultipegma occurs in the lowermost Cambrian rocks (Tommotian) of Siberia (Missarzhevsky 1974; Matthews & Missarzhevsky 1975, as *Heraultia*) and in slightly younger Lower Cambrian rocks (Georgien) of France (Pojeta & Runnegar 1976). *Heraultipegma* is the oldest known rostroconch mollusc; it is of about the same size and has a lateral profile similar to that of *Fordilla*, although *Heraultipegma* is pseudo-bivalved in that it lacks a dorsal commissure and it gapes along the anterior, posterior, and ventral margins. *Heraultipegma* is, in effect, a laterally compressed univalve. Decalcification of the posterodorsal margin in such organisms in successive generations could have produced the opisthodetic ligament of pelecypods. An organism that suggests that this is indeed what happened is *Myona? queenslandica* from the middle Middle Cambrian (post-Templetonian) of Australia. *M.? queenslandica* has a univalved protoconch and is thus classified as a rostroconch, but the dorsal margin may have been flexible, as a few specimens have the valves separated from one another along what was probably the hinge axis (Runnegar & Jell 1976, fig. 8D–7).

Heraultipegma can in turn be related to the univalves through such laterally compressed helcionellacean monoplacophorans as *Anabarella* (Tommotian; Pojeta & Runnegar 1976, pl. 17, fig. 8) and *Mellopegma* (Runnegar & Jell 1976, Ordian–post-Templetonian). These helcionellaceans show a curved rather than straight apertural margin, which indicates that the shell gape was extended up the anterior and posterior ends of the shell and was not limited to the ventral margin. Such extensive shell gapes are characteristic of early rostroconchs (Pojeta & Runnegar 1976). *Mellopegma* and *Anabarella* can in turn be related to more typical helcionellaceans such as *Helcionella* and *Latouchella* (Runnegar & Jell 1976, fig. 9C–D), which are not laterally compressed and in which the shell aperture is limited to the ventral side.

DESCRIPTION OF PLATE 1

FIGURES 1 AND 2. *Deceptrix* (*Deceptrix*) n. sp. 1. Nuculiform palaeotaxodont from the Grier Limestone Member of the Lexington Limestone, central Kentucky (upper Middle Ordovician). Figure 1. Right valve, showing dentition (magn. ×4), U.S.N.M. 162705. Figure 2. Right valve, showing muscle scars (magn. ×4), U.S.N.M. 162704.

FIGURES 3–6. *Fordilla* cf. *F. troyensis* Barrande.

FIGURES 3–5. Internal mould, left-lateral view, showing shape (magn. ×36); anterior view of dorsum, showing dentition (magn. ×60); entire dorsum, showing dentition (magn. ×36). Lower part of the Lenian Stage (Lower Cambrian) Khara-Ulach, Chekurovea, Lena River, Siberia. U.S.N.M. 247821.

FIGURE 6. Dorsal view, showing dentition (magn. ×36). Horizon and locality the same as in figures 3–5. U.S.N.M. 247822.

FIGURE 7. *Fordilla troyensis* Barrande. Internal mould of right valve, showing muscle scars (magn. ×30). Lower Cambrian, Troy, New York, U.S.N.M. 15372.

DESCRIPTION OF PLATE 2

FIGURES 1 AND 2. *Deceptrix filistriata* (Ulrich). Figure 1. Left valve (magn. ×4), Kope Formation (lower Upper Ordovician), southwestern Ohio, U.S.N.M. 40487. Figure 2. Right valve (magn. ×4), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 70465.

FIGURE 3. New genus 1, new species 1, Pojeta & Gilbert-Tomlinson (1977). Right valve internal mould (magn. ×2), Stairway Sandstone (lower Middle Ordovician), southern Northern Territory, Australia, Bureau of Mineral Resources (B.M.R.) 15523.

FIGURES 4–6. New genus 1, new species 2, Pojeta & Gilbert-Tomlinson (1977). Internal mould, dorsal, right lateral, and anterior views (magn. ×3), Stairway Sandstone (lower Middle Ordovician), southern Northern Territory, Australia, B.M.R. 15514.

FIGURES 7 AND 8. *Similodonta similis* (Ulrich). Left and right valves (magn. ×5), Maquoketa Shale (upper Upper Ordovician), Bristol, Minnesota, U.S.N.M. 47037 *a*, *b*.

FIGURES 9 AND 10. New genus 2 *pectunculoides* (Hall), under investigation. Right (magn. ×3) and left (magn. ×7) valves, Kope Formation (lower Upper Ordovician), northern Kentucky, U.S.N.M. 47056*a*, *b*.

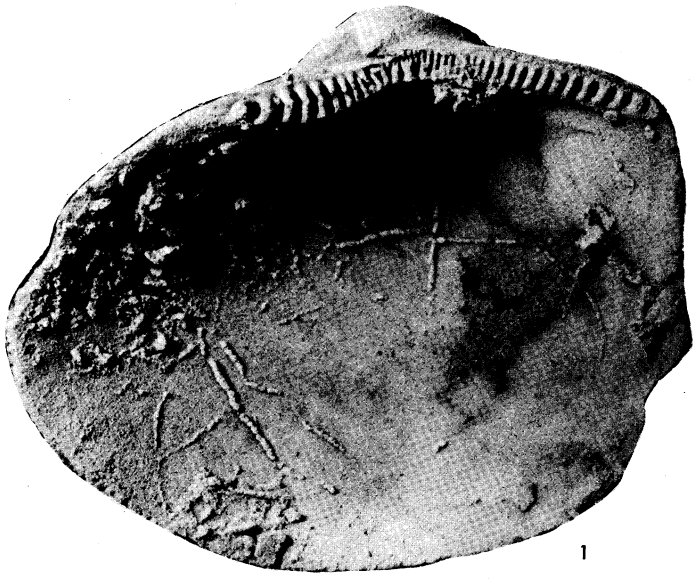
FIGURES 11 AND 12. New genus 2 *cingulata* (Ulrich), under investigation. Left and right valves (magn. ×3), probably from the Ashlock Formation (middle Upper Ordovician), central Kentucky, Yale Peabody Museum (Y.P.M.) 27823.

FIGURES 13 AND 14. New genus 3, new species 1, Pojeta & Gilbert-Tomlinson (1977). Right valve exterior and left valve interior (magn. ×5) Gordon Limestone (upper Middle or lower Upper Ordovician), near Queenstown, Tasmania, Australia, University of Tasmania (U.T.) 82743*a*, *b*.

FIGURE 15. *Cardiolaria beirensis* (Sharpe). Internal mould of left valve (magn. ×9), lower Middle Ordovician rocks (Llandeilian), Finistère, France, University of Western Brittany (U.W.B.) 505.

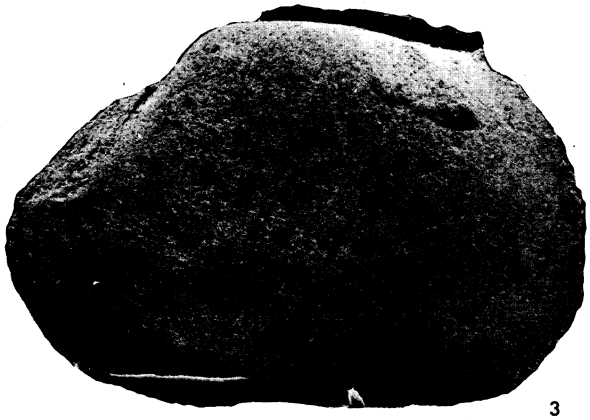
FIGURE 16. New genus 4, new species 1, under investigation. Internal mould right valve (magn. ×3), lower Middle Ordovician rocks (Llanvirnian), Central Wales. University of Cambridge (U.C.).

FIGURES 17 AND 18. New genus 4, species 2, Pojeta & Gilbert-Tomlinson (1977). Right and left valves (magn. ×3), Stairway Sandstone (lower Middle Ordovician), southern Northern Territory, Australia. B.M.R. 15480, 15483.



1

2

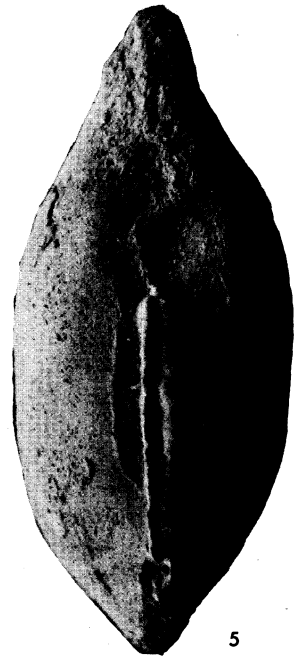


3

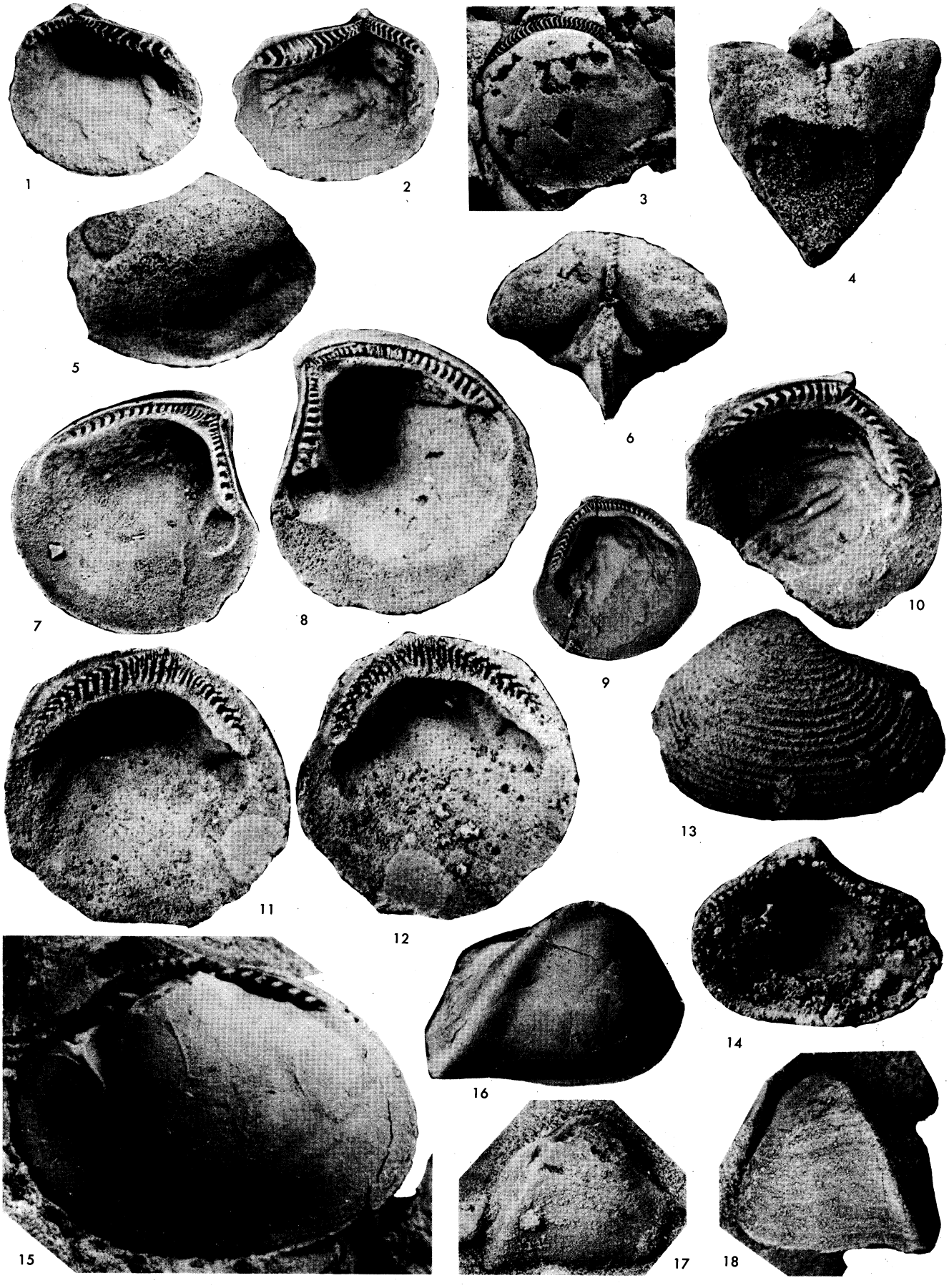
6

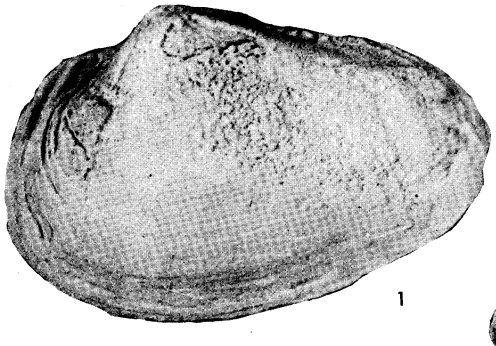
4

7

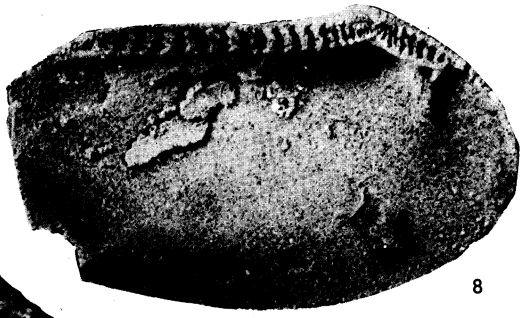


5

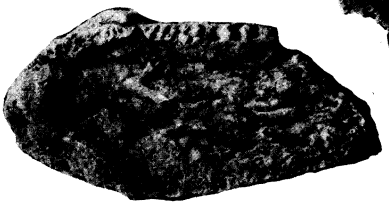

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18



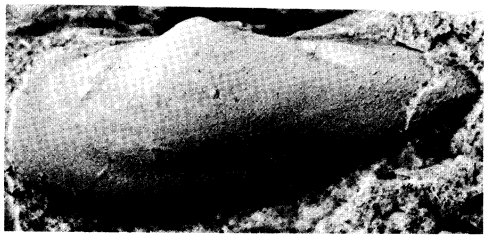
1



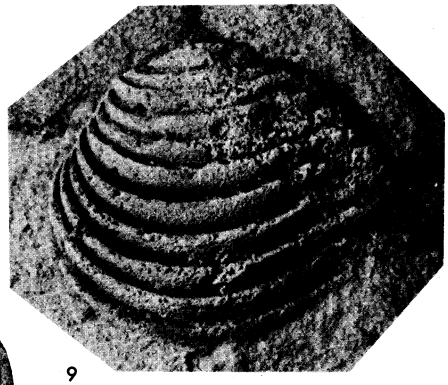
8



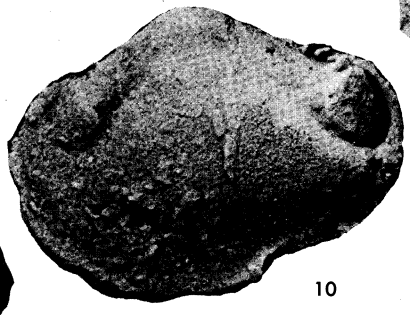
6



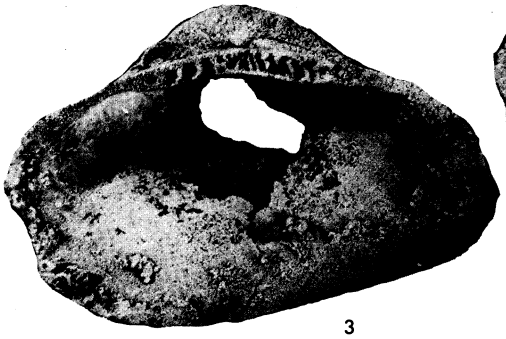
2



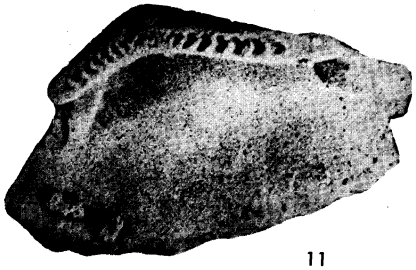
9



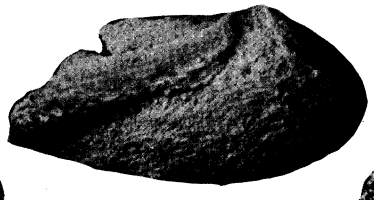
10



3

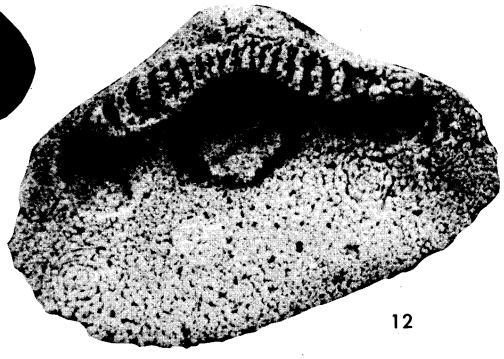


11



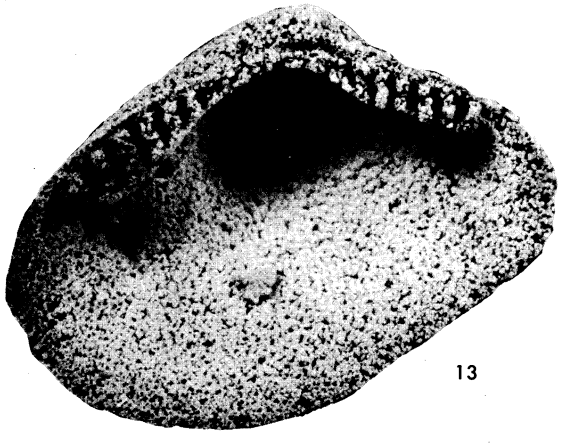
7

4



12

5

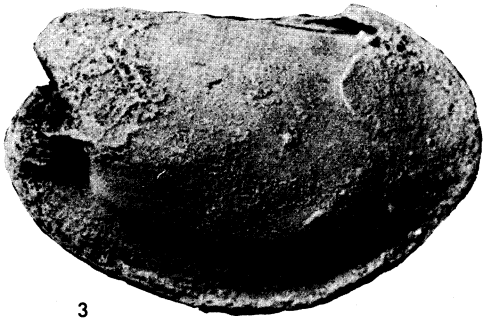


13

1

2

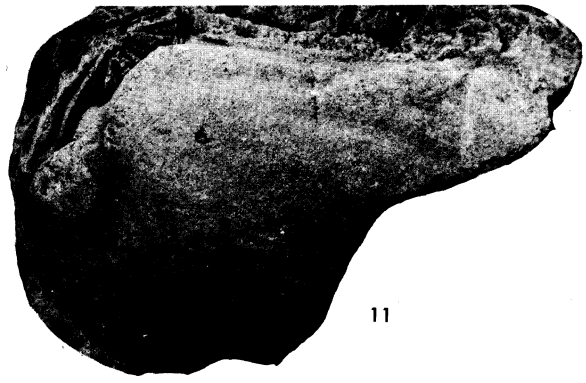
6


3

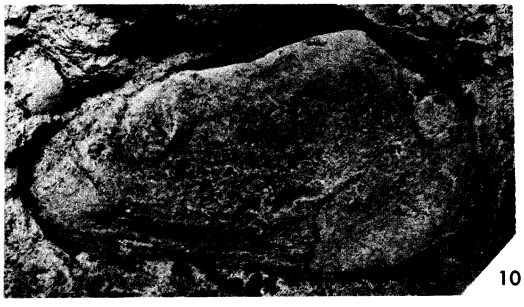
5

4

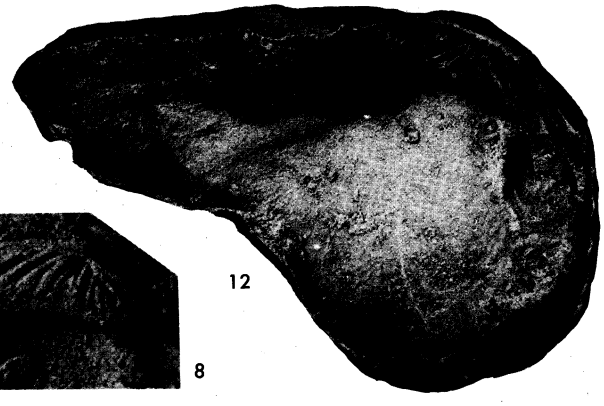
7


11

9


10

8


12

Latouchella is known from rocks as old as the Tommotian (Rozanov *et al.* 1969; Matthews & Missarzhevsky 1975).

It has been postulated (Pojeta & Runnegar 1976; Runnegar & Jell 1976) and is here reiterated that the sequence leading from forms such as *Latouchella* to *Anabarella* and *Mellopegma* to *Heraultipegma* to *Myona*? *queenslandica* and finally to *Fordilla* adequately depicts how bivalves arose from univalves.

The lateral compression of the shell in some helcionellaceans provided a mechanism by which epifaunal grazers could become burrowers in the sediment. Such a shell was maintained by *Heraultipegma* and *Fordilla* and reinforces the argument based on general morphology that these animals were infaunal suspension feeders.

Description of plate 3

Figure 1. *Myoplusia carpenderi* (Schuchert). Internal mould left valve (magn. × 4), lower Upper Ordovician rocks, Putnam Highland, Baffin Island, Canada, U.S.N.M. 124640.

Figure 2. *Ctenodonta yoldiaformis* (Ulrich). Internal mould left valve (magn. × 6), Kope Formation (lower Upper Ordovician), northern Kentucky, U.S.N.M. 46315.

Figure 3. *Ctenodonta logani* Salter. Right valve (magn. × 2), upper Middle Ordovician rocks (Lerayan–Rocklandian) Allumette Island, Quebec, Canada, Geological Survey of Canada (G.S.C.) 1181*a*.

Figures 4 and 5. *Ctenodonta nasuta* (Hall). Figure 4. Right valve (natural size), upper Middle Ordovician (Blackriveran) rocks, Ottawa, Ontario, Canada, U.S.N.M. 14718. Figure 5. Left valve showing posterior lateral teeth (magn. × 3), Cannon Limestone (upper Middle Ordovician), Hartsville, Tennessee, U.S.N.M. 247942.

Figures 6 and 7. New genus 5, species 1, Pojeta & Gilbert-Tomlinson (1977). Interior and exterior right valve (magn. × 3), Gordon Limestone (upper Middle or Lower Upper Ordovician) Zeehan, Tasmania, Australia, B.M.R. 15495.

Figure 8. New genus 6, new species 1, under investigation. Interior left valve, (magn. × 4), Clays Ferry Formation (Middle and lower Upper Ordovician), central Kentucky, U.S.N.M. 247823.

Figures 9 and 10. New genus 7, species 1, Pojeta & Gilbert-Tomlinson (1977). Exterior (magn. × 2) and interior (magn. × 3) left valves, Stairway Sandstone (lower Middle Ordovician), southern Northern Territory, Australia, B.M.R. 15487, and South Australia Museum (S.A.M.) T 1223*b*.

Figure 11. *Tancrediopsis* new species 1, under investigation. Right valve (magn. × 3), Setul Formation (upper Lower Ordovician), Langkawi Islands, Malaysia, U.S.N.M. 162693.

Figure 12. *Tancrediopsis cuneata* (Hall). Right valve (magn. × 5), lower Middle Ordovician rocks, Tablehead, Newfoundland, Canada, G.S.C. 570*b*.

Figure 13. *Tancrediopsis abrupta* (Billings). Right valve (magn. × 5), upper Middle Ordovician rocks, Lake St John, Quebec, Canada, Y.P.M. 27824.

Description of plate 4

Figures 1–4. *Redonia bohemica* Barrande. Figure 1. Latex replica left valve (magn. × 6), Field Museum Natural History (F.M.) 8561*a*. Figure 2. Latex replica right valve (magn. × 6), F.M. 8561*b*. Figures 3 and 4. Left and right valves of internal mould (magn. × 4), Museum of Comparative Zoology (M.C.Z.) 18077. All from rocks of early Middle Ordovician age (probably Šárka Formation), Bohemia, Czechoslovakia.

Figure 5. *Redonia deshayesiana* Rouault. Latex replica left valve (magn. × 4), Middle Ordovician, Almaden, Spain, Y.P.M. 3598/B.

Figures 6–8. New genus 8, species 1, Pojeta & Gilbert-Tomlinson (1977). Left valve, right valve, and hinge of left valve (magn. × 4), Nora Formation (upper Lower Ordovician or lower Middle Ordovician), Toko Range, western Queensland, Australia, University of Queensland (U.Q.) F 67219, U.S.N.M. 247824, B.M.R. 15594.

Figures 9–12. *Actinodonta cuneata* Phillips. Latex replica and original of right valve (magn. × 1.5) and original and latex replica of left valve (magn. × 2.5), upper Llandoverian (Lower Silurian), Marloes Bay, Great Britain, Institute of Geological Sciences, London (G.B.) 59825, 59829.

ORDOVICIAN PELECYPODS

No unequivocal fossils of pelecypods are presently known from Middle and Upper Cambrian rocks, although Suneja (1975) has described some shells from the Middle Cambrian of northern India that he regarded as pelecypods. From the Tremadocian (early Early Ordovician) onward, pelecypods have a continuous fossil record; they radiated rapidly, invading new habitats, which means that they occur in a greater variety of rock types. Pelecypods also increased in size from a known maximum length of 5 mm in the Early Cambrian to double that length in the Tremadocian making them easier to find. Now that Cambrian pelecypods are known, it is probably only a matter of time until Middle and Late Cambrian representatives of the class are found.

Ordovician pelecypods can be grouped into seven major categories on the basis of dentition, ligament type, shape, and ornament: (1) Palaeotaxodonta – forms with taxodont teeth, and their relatives (nuculoids and solemyoids); (2) Actinodontia – shells with numerous teeth, all of which reach or nearly reach the beaks; teeth not separated into anterior and posterior elements by an edentulous space (redoniids, lyrodesmatids, and cycloconchids); (3) Pteriomorphia – byssally attached forms; teeth, when present, separated into anterior and posterior elements by an edentulous space, some with chevron-shaped ligamental insertions (cyrtodontids, ambonychiids, and pterineids); (4) Isofilibranchia–modioliform byssally attached shells lacking ligamental chevrons; teeth, when present, limited to anterior elements below the beaks (modiomorphids); (5) Orthonotia – soleniform gaping shells (orthonotids); (6) Anomalodesmata – elongate shells with comarginal rugae and sometimes with radiating tubercles (grammysiids); (7) Lucinata – anteriorly elongated luciniform shells (babinkids).

These seven groups represent what is known of the primary radiation of the class Pelecypoda; most groups that originated in the post-Ordovician Palaeozoic can readily be related to one or another of the seven Ordovician groups. I therefore propose that the class be subdivided into seven subclasses on the basis of its primary radiation in Ordovician time. Of the names of the seven subclasses, Orthonotia and Lucinata are new and Actinodontia is elevated from ordinal status.

Palaeotaxodonta

The oldest known Ordovician pelecypods are Tremadocian in age; they are all palaeotaxodonts that have been reported from Argentina (Harrington 1938), Afghanistan (Termier & Termier 1971), and perhaps southern France (Thoral 1935). The reported occurrences of isofilibranchs and lucinatans from Tremadocian rocks cannot now be supported. Harrington (1938) reported the isofilibranch genus *Cosmogoniophorina* from the Tremadocian of Argentina; however, as pointed out by Pojeta (1975), Harrington's specimens are probably palaeotaxodonts allied to the genus *Deceptrix*. Thoral (1935) reported the lucinatan genus *Babinka* from rocks that he dated as Tremadocian in France; however, Soot-Ryen (1969) noted that *Babinka* is probably not known from rocks older than Arenigian (upper Lower Ordovician).

A maximum of four genera of palaeotaxodont pelecypods is known from Tremadocian rocks: *Ctenodonta*, *Palaeoneilo*, *Afghanodesma*, and an unnamed genus allied to *Deceptrix*. None of the Tremadocian palaeotaxodonts are morphologically well known. Dentition is known only in *Afghanodesma desparmeti* and '*Deceptrix*' *lenuicostata*, and muscle scars are known only in *Afghanodesma desparmeti*; the other generic assignments are based on shell shape. Figure 1*b* shows the relative abundance of palaeotaxodonts during the Ordovician on the basis of the number of genera known from each time interval indicated.

As early as the Tremadocian, nuculiform and nuculaniform Palaeotaxodonts are present. The nuculiform type of shell is represented by *Afghanodesma*, and the nuculaniform type, by *Ctenodonta iruyensis*, which Harrington (1938) placed in the genus *Palaeoneilo*. Plates 1–3 show some of the diversity in shell form of Ordovician nuculiform and nuculaniform palaeotaxodonts. There is no sign of a resilifer in any of the known Ordovician palaeotaxodonts.

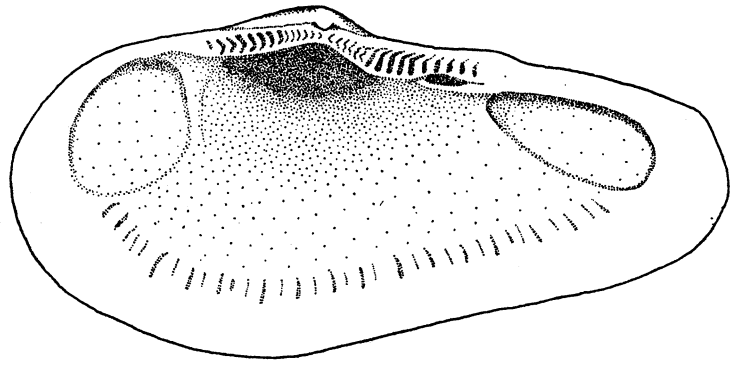


FIGURE 3. Composite reconstruction of *Ctenodonta nasuta* (Hall), showing the development of some solemyid features.

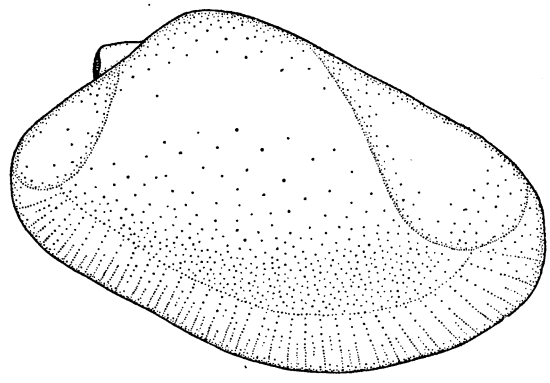


FIGURE 4. Composite reconstruction of '*Nucula*' *aedilis* Eichwald, showing various solemyid features.

The Ordovician period was about 60 Ma long, and from the rocks of this period about 30 genera of palaeotaxodonts are known. Of these genera, 14 are new. The bulk of our knowledge of Ordovician palaeotaxodonts is based on specimens collected from shallow-water platform sediments; as yet we have no way to compare deeper water forms with modern deep-water protobranchs such as those described by Sanders & Allen (1973) and Allen & Sanders (1973).

By Middle Ordovician time (Wildernessian) some palaeotaxodonts, such as *Ctenodonta nasuta* (figure 3), showed an expansion of the anterior part of the shell and a concomitant increase in the size of the anterior adductor muscle so that the general appearance of the shell is solemyiform. Shells that are even more solemyiform are known from the Middle Ordovician (Kuckers) of Estonia. These shells have a greatly enlarged anterior adductor muscle, a greatly expanded anterior part of the shell, and the ligament is on the short end of the shell (figure 4). The dentition of the Estonian forms is not known, and the shells are more gibbous than are those of younger solemyids. The Estonian solemyiform shells are placed in a new genus which is under investigation; they were described by Eichwald (1860) as *Nucula aedilis*. The ctenodontids and the Estonian shells suggest that solemyids were derived from palaeotaxodonts.

Morris & Fortey (1976) indicated that palaeotaxodonts are descended from actinodontians. They regarded the posterior taxodont teeth of palaeotaxodonts as having arisen from striations on the elongate teeth of some actinodontians. The anterior teeth of palaeotaxodonts are believed to have evolved from a direct but gradual increase in the number of anterior cardinal teeth of actinodontians. Morris & Fortey based their conclusions on the early Middle Ordovician (Llanvirnian) palaeotaxodont *Tironucula*, which has anterior chevron-shaped palaeotaxodont teeth and some elongate posterior teeth more or less parallel to the ligament, and on the Early Ordovician actinodontian '*Actinodonta*' *naranjoana*. One specimen of *Ctenodonta nasuta* (plate 3, figure 5) shows the presence of a posterior lateral tooth, but this feature is unknown in all other specimens of the species seen by me. Some specimens of *Cardiolaria beirensis* show the presence of enlarged cardinal teeth below the beak separated by a space from posterior taxodont teeth (Bradshaw 1970; plate 2, figure 15 herein). Thus there is considerable variation in the dentition of Middle Ordovician palaeotaxodonts, suggesting that other dental patterns could have arisen from this group.

Allen & Sanders (1969) suggested that the Nuculidae, Nucinellidae, and Solemyidae originated from early Palaeozoic actinodontians. Central to their argument is the thought that the dentition of the Holocene species *Nucinella serrei* is similar to the dentition of the Ordovician and Silurian genus *Actinodonta*. At the same time, they noted that *Nucinella* resembles *Nucula* externally, whereas anatomically *Nucinella* is closest to *Solemya*. The teeth of *Actinodonta cuneata*, the type species of *Actinodonta*, radiate outward and downward from under the beaks (plate 4, figures 9–12), and the species has long and prominent anterior and posterior 'lateral' teeth. The teeth of *Nucinella* do not radiate outward from under the beak; rather, the posterior teeth are vertical and there is only a single anterior lateral tooth.

Because the taxodont dentition of arcaceans and unionaceans seems to have arisen from ancestors with cardinal and lateral teeth, Pojeta & Runnegar (1974) and Pojeta (1975) suggested that the taxodont dentition of palaeotaxodonts could have arisen in the same way from the cardinal and lateral teeth of actinodontians.

Allen & Sanders (1973) figured a number of remarkable deep-sea protobranchs of the families Siliculidae and Lametilidae that lack or nearly lack taxodont dentition. The dentition of the protobranchs is closely similar to that of the actinodontians, consisting of elongate lamellar teeth radiating outward from the beaks. In *Prelametila clarkei*, the teeth closest to the beaks are chevron-shaped, whereas the teeth farthest from the beaks are elongate and lamellar; the teeth in between these two points are chevron-shaped, but with a short dorsal arm to the chevron and a long ventral arm. These facts suggest that lamellar teeth could have arisen from taxodont teeth, the opposite of the picture suggested by *Tironucula*.

The presently available evidence suggests a phylogenetic relation between actinodontians and palaeotaxodonts. Which group gave rise to the other is not clear, although palaeotaxodonts appear in the fossil record before actinodontians. Also, it seems likely that solemyids are descended from palaeotaxodonts and do not need to be placed in a separate subclass as was done by Newell (1969).

Actinodontia

The subclass Actinodontia is characterized by the presence of elongate lamellar teeth, all of which reach or nearly reach the beaks; there are no edentulous spaces between the cardinal and anterior and posterior teeth, and the posterior teeth extend under the elongate external ligament. Some of the younger Ordovician representatives of the subclass lose the elongate

lamellar teeth. Three Ordovician families are presently assigned to the subclass: Redoniidae, Cycloconchidae, and Lyrodesmatidae. At present only about eight genera of Ordovician actinodontians are known.

Redoniidae

The Redoniidae contains small gibbous shells (plate 4, figures 1–5) with two or three elongate lamellar teeth in each valve. Sometimes there is a single conical cardinal tooth in one valve and a corresponding socket in the other valve. None of the teeth are anterior to the beaks, and sometimes the teeth have denticles. Only the genus *Redonia* is presently assigned to the family, which has a stratigraphic range of late Early Ordovician (Arenigian) through early Middle Ordovician (Llandeilian). *Redonia* is best known from Bohemia and Iberia, although it also occurs in France, Great Britain, and northern Africa.

The phylogenetic relations of redoniids to younger forms are not clear. Babin (1966) regarded redoniids as ancestral heterodonts related to such genera as *Cypricardinia*, and thus they are possible crassatellaceans. However, in *Cypricardinia*, the anterior and posterior teeth are separated by an edentulous space, and there is a byssal sulcus; neither of these features is known in redoniids, and there is no evidence of byssal attachment in any of the actinodontians. Chavan (1954, 1966*a*, *b*, 1967) regarded *Redonia* as ancestral to the Permophoridae, which he placed in the Carditacea; however, Chavan (1969) placed *Redonia* with question in the Permophoridae. Permophorids too have an edentulous space between the anterior and posterior teeth and are thought to have possessed a byssus. Although some pre-Carboniferous species have been placed in the Permophoridae, undoubted members of the family are not known before the Early Carboniferous.

Cycloconchidae

Three Ordovician genera are presently placed in the Cycloconchidae (plate 4, figures 6–8; plate 5, figures 1–10), and the family is known to range into the Early Silurian (plate 4, figures 9–12). Cycloconchids are characterized by numerous elongate teeth that lack denticles; teeth are present both anterior and posterior to the beaks as well as below the beaks. Because the teeth are elongate and many of them reach or nearly reach the beaks, they cannot be readily subdivided into laterals and cardinals.

Cycloconchids are widespread geographically, occurring in western Europe, North America, northern Africa, and Australia. The Ordovician stratigraphic range of cycloconchids is upper Lower Ordovician (Arenigian) through upper Upper Ordovician (Richmondian).

The general shell form and the dentition of such cycloconchids as *Cycloconcha* (plate 5, figures 2–10) are remarkably similar to late Palaeozoic crassatellaceans figured by Newell (1958) and Boyd & Newell (1968); Pojeta (1971) has suggested that cycloconchids are ancestral to crassatellaceans. The hinge of late Palaeozoic crassatellaceans also lacks denticles, and teeth are present both anterior and posterior to the beaks as well as below the beaks. Because the teeth all reach or nearly reach the beaks, it is difficult to separate cardinals from laterals.

Lyrodesmatidae

Lyrodesmatids (plate 6; plate 7, figure 6) have most or all of the teeth short and flaring ventrally from immediately below the beak (plate 6, figures 7–14). Primitive members of the group have one or two elongate posterior teeth that reach the beak (plate 6, figure 6; plate 7,

figure 6); geologically younger members of the family are not known to have the elongate teeth. Some or all of the teeth have denticles; the cardinal teeth are mounted on a stout hinge plate.

Three genera are presently assigned to the Lyrodesmatidae, two of these are new and are described elsewhere (Pojeta & Gilbert-Tomlinson 1977). The oldest known lyrodesmatids are in upper Lower Ordovician rocks (Arenigian), and they range upward to latest Ordovician time (Richmondian). Harrison & Harrison (1975) figured representatives of the family from Lower Silurian rocks. Lyrodesmatids are known from Europe, North America, and Australia.

Lyrodesma is unique in being the earliest known siphonate pelecypod to possess a pallial sinus (plate 6, figures 2–5) and thus shows that infaunal siphonate pelecypods are known from early in the history of the class.

The phylogenetic relations of *Lyrodesma* seem to be with the trigonioids. In *Lyrodesma*, as in younger trigonioids, there are ventrally flaring teeth with denticles, the entire musculature is high in the shell, and the pedal retractors are at the anterior and posterior ends of the hinge

---

DESCRIPTION OF PLATE 5

FIGURE 1. New genus 8, species 1, Pojeta & Gilbert-Tomlinson (1977). Right valve (magn. × 4), Nora Formation (upper Lower or lower Middle Ordovician), Toko Range, western Queensland, Australia, B.M.R. 15595.

FIGURES 2–6 AND 8. *Cycloconcha ovata* Ulrich. Figure 2. Dentition right valve (magn. × 6), Kope Formation (lower Upper Ordovician), northern Kentucky, U.S.N.M. 46163. Figure 3. Exterior right valve (magn. × 3), Clays Ferry Formation (Middle and lower Upper Ordovician), central Kentucky, U.S.N.M. 247825. Figure 4. Interior left valve (magn. × 4), locality the same as in figure 2, Miami University (M.U.) 129T. Figure 5. Interior left valve (magn. × 3), locality the same as in figure 3, U.S.N.M. 247826. Figure 6. Internal mould right valve, showing muscle scars (magn. × 4), locality the same as in figure 2, U.S.N.M. 49972. Figure 8. Dentition left valve (magn. × 6), locality unknown, U.S.N.M. 162681.

FIGURES 7 AND 9. *Cycloconcha milleri* (Meek). Figure 7. Left valve, showing dentition (magn. × 4), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 47344*a*. Figure 9. Left valve, showing muscle scars (magn. × 3), locality the same as in figure 7, M.C.Z. 18078.

FIGURE 10. *Cycloconcha mediocardinalis* Miller. Right valve (magn. × 4), Kope Formation (lower Upper Ordovician), southwestern Ohio, F.M. 8893.

DESCRIPTION OF PLATE 6

FIGURES 1 AND 7–13. *Lyrodesma subplanum* Ulrich. Figures 1 and 10. Teeth, showing denticles (magn. × 7) and interior right valve (magn. × 4), Clays Ferry Formation (Middle and lower Upper Ordovician), central Kentucky, U.S.N.M. 247827. Figure 7. Left valve (magn. × 4), locality the same as in figure 1, U.S.N.M. 247828. Figure 8. Oblique view right valve, showing muscle scars (magn. × 5), locality the same as in figure 1, U.S.N.M. 247829. Figure 9. Oblique view right valve, showing muscle scars (magn. × 5), locality the same as in figure 1, U.S.N.M. 247830. Figure 11. Left valve exterior (magn. × 4), locality the same as in figure 1, U.S.N.M. 247831. Figure 12. Left valve (magn. × 4), Point Pleasant Tongue of the Clays Ferry Formation (Middle and lower Upper Ordovician), northern Kentucky, U.S.N.M. 247832. Figure 13. Right valve (magn. × 4), locality the same as in figure 1, U.S.N.M. 247833.

FIGURE 2. *Lyrodesma conradi* Ulrich. Left valve internal mould, showing sinuate pallial line (magn. × 4), Kope Formation (lower Upper Ordovician), northern Kentucky, U.S.N.M. 46220.

FIGURES 3–5. *Lyrodesma poststriatum* (Emmons). Right valve internal mould (magn. × 3), right valve internal mould (magn. × 3), left valve internal mould (magn. × 4), Pulaski Shale (middle Upper Ordovician), central New York, U.S.N.M. 10197, 162686, M.C.Z. 18079.

FIGURE 6. New genus 9, species 1, Pojeta & Gilbert-Tomlinson (1977). Latex replica left valve (magn. × 4), Nora Formation (upper Lower or lower Middle Ordovician), Toko Range, western Queensland, Australia, U.Q.F 67218.

FIGURE 14. *Lyrodesma major* (Ulrich). Oblique view right valve (magn. × 3), locality the same as in figure 1, U.S.N.M. 247834.

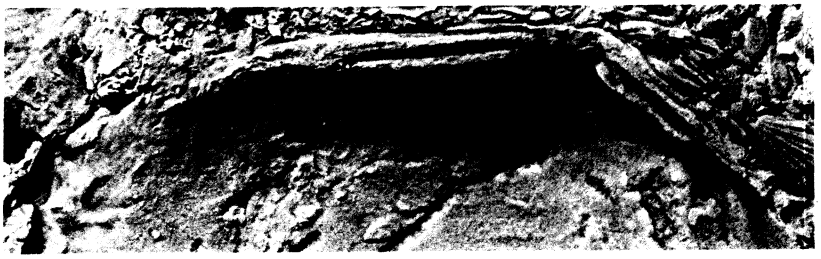
1

2

3

4

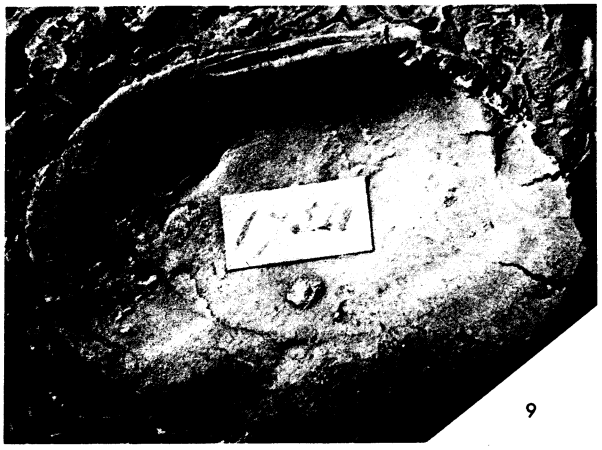
5



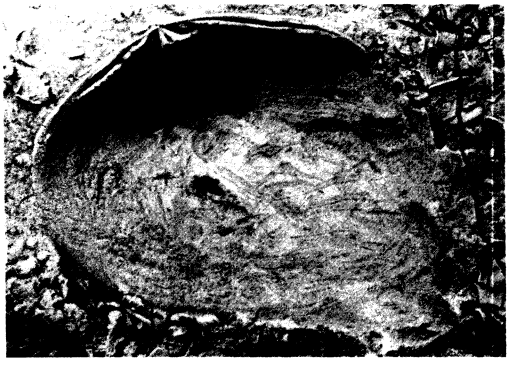
7

6

8



9



10

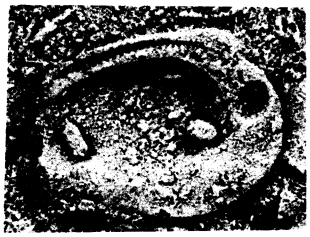
1

2

3

4

5

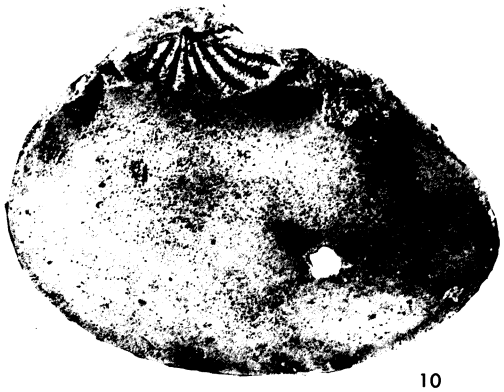


6

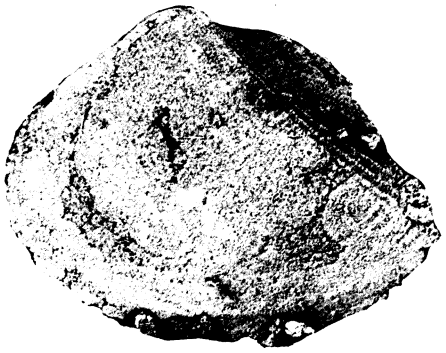
7

8

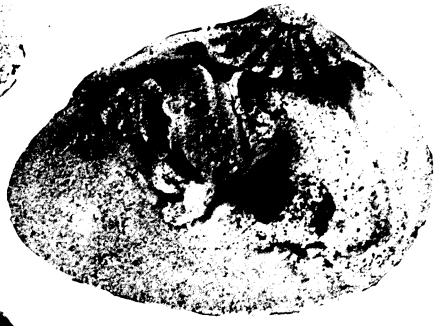
9



10



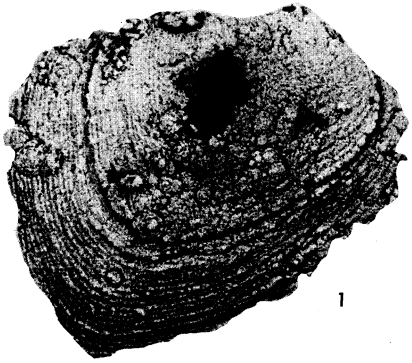
11



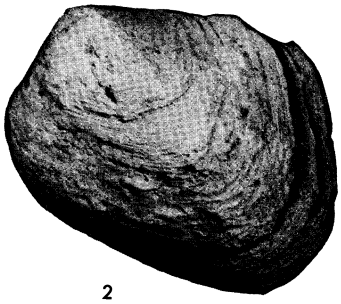
12

13

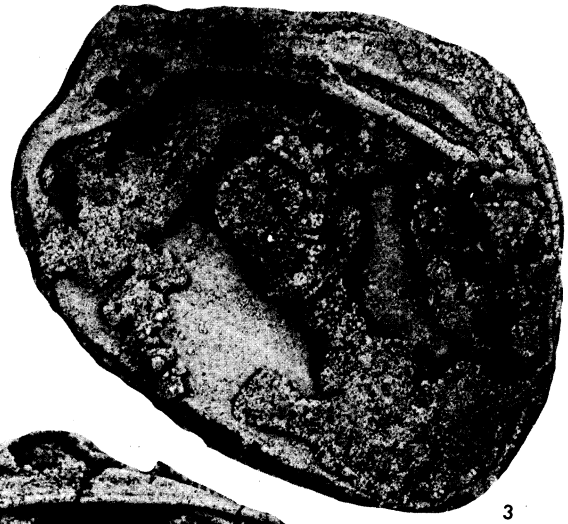
14



1



2



3

4

7

5

9

6

8

1
2
3
4
5
6
7
8
9
10
11

plate. The trigonioid features of *Lyrodesma* are closer to Mesozoic trigonioids than to late Palaeozoic ones (Newell & Boyd 1975). The late Palaeozoic trigonioids have fewer teeth than *Lyrodesma* and often the teeth lack denticles, although, as in other trigonioids, the musculature of the late Palaeozoic forms is placed high in the shell, and the pedal retractors are placed close to the ends of the hinge plate.

Pteriomorphia

Ordovician pteriomorphs, a byssate group of pelecypods, have a ligament area that is either crossed by parallel longitudinal and nearly horizontal grooves (Cyrtodontidae and Ambonychiidae) or that has multiple ligament insertions arranged as chevrons (Pterineidae). When teeth are present, they are separated into anterior and posterior elements with an edentulous space between. Three Ordovician families are currently assigned to the Pteriomorphia: Cyrtodontidae, Ambonychiidae, and Pterineidae. Figure 1*c* shows the relative abundance of pteriomorphs in the Ordovician on the basis of the number of genera known from each time interval indicated.

Cyrtodontidae

Cyrtodontids (plate 7, figures 1–5, 7–9; plate 8; plate 9) are equivalved, nonalate, possess a well developed anterior end to the shell, which is sometimes reduced to an anterior lobe,

---

DESCRIPTION OF PLATE 7

FIGURES 1–5. *Ortonella hainesi* (Miller). Figure 1. Right valve exterior (magn. ×3), Dillsboro Formation (upper Upper Ordovician), southeastern Indiana, U.S.N.M. 24835. Figure 2. Exterior left valve (magn. ×2), Richmondian (upper Upper Ordovician), southeastern Indiana, F.M. 8787. Figure 3. Interior right valve (magn. ×3), locality the same as in figure 1, U.S.N.M. 247836. Figure 4. Interior right valve (magn. ×2), locality the same as in figure 1, U.S.N.M. 247837. Figure 5. Internal mould left valve (magn. ×2), Whitewater Formation (upper Upper Ordovician), Richmond, Indiana, U.S.N.M. 46277.

FIGURE 6. New genus 9, species 1, Pojeta & Gilbert-Tomlinson (1977). Latex replica of right valve (magn. ×10), Nora Formation (upper Lower or lower Middle Ordovician), Toko Range, western Queensland, Australia, U.Q.F 67217.

FIGURES 7–9. *Sphenolium* new species 1, under investigation. Figure 7. Hinge and ligament area right valve (magn. ×4), Logana Member, Lexington Limestone (upper Middle Ordovician), central Kentucky, U.S.N.M. 247838. Figures 8 and 9. Incomplete right valve (magn. ×1.2) and enlargement of dorsal part of same (magn. ×2.2), locality the same as in figure 7, U.S.N.M. 247839.

DESCRIPTION OF PLATE 8

FIGURES 1–5. *Cyrtodonta huronensis* Billings. Figure 1. Dorsal view, showing ligament (magn. ×2), Carters Limestone (upper Middle Ordovician), Shelbyville, Tennessee, U.S.N.M. 247840. Figure 2. Right valve (magn. ×2), upper Middle Ordovician (Wildernessian), Braeside, Ontario, Canada, U.S.N.M. 162715. Figure 3. Right valve (magn. ×1.5), locality the same as in figure 2, U.S.N.M. 247841. Figure 4. Left valve (magn. ×1.5), Perryville Limestone Member, Lexington Limestone (upper Middle Ordovician), central Kentucky, U.S.N.M. 247842. Figure 5. Left valve (magn. ×2), locality the same as in figure 2, U.S.N.M. 162715.

FIGURE 6. *Sphenolium* new species 1, under investigation. Right valve exterior (magn. ×2), Logana Member, Lexington Limestone (upper Middle Ordovician), central Kentucky, U.S.N.M. 247843.

FIGURE 7. *Cyrtodonta grandis* (Ulrich). Internal mould of anterior dentition (magn. ×3), locality the same as in figure 4, U.S.N.M. 247844.

FIGURES 8–11. *Cyrtodonta saffordi* (Hall). Figures 8 and 9. Oblique dorsal view of ligament area (magn. ×3) and view of hinge line and ligament area (magn. ×4), locality the same as in figure 4 above, American Museum Natural History (A.M.N.H.) 36762. Figure 10. Exterior left valve (magn. ×2), Grier Limestone Member, Lexington Limestone (Middle Ordovician), central Kentucky, U.S.N.M. 247845. Figure 11. Interior right valve (magn. ×2), Catheys Limestone (upper Middle Ordovician), Nashville, Tennessee, U.S.N.M. 46191*a*.

and are anisomyarian. They possess strong well developed teeth with the anterior teeth near or above the anterior adductor scar, but not necessarily below the beaks, and with the posterior teeth above the posterior adductor scar. Usually the anterior teeth are mounted on a hinge plate and the posterior teeth on a shell thickening. The ligament area is crossed by numerous fine, nearly horizontal grooves.

There are 19 known Ordovician genera of cyrtodontids, which range in age from the late Early Ordovician (Arenigian) to the end of the period (Richmondian). They show considerable variation in ornament, the presence of a rounded anterior margin or an anterior lobe, dentition, shape, and the presence or absence of an umbonal septum. The pallial line is integripalliate and continuously inserted. A number of genera with anterior lobes formerly included in the Ambonychiidae (Pojeta 1966) are herein placed in the Cyrtodontidae. The family is known to occur in North America, Europe, Australia, and Kazakhstan, U.S.S.R.

The ligamental areas of cyrtodontids are traversed by a series of parallel longitudinal grooves and ridges, which are shortest in the oldest part of the shell and longest in the youngest part of the shell (plate 8, figures 8 and 9). Because of this and because the grooves and ridges are parallel to the dorsal margin and not inclined to it they cannot be insertion areas of a duplivincular ligament as thought by Pojeta (1971). Chevrons of a duplivincular ligament, as occur in arcaceans, or half chevrons, as occur in myalinids, are inclined to the dorsal commissure and are shortest in the youngest part of the shell. The grooves and ridges of cyrtodontids could be interpreted as growth lines, but this seems unlikely, as the growth lines both anterior and

---

DESCRIPTION OF PLATE 9

FIGURES 1–5. *Vanuxemia hayniana* (Safford). Figure 1. Left valve (magn. ×2), the museum label gives the locality as 'Trenton, Haynies, Tennessee,' U.S.N.M. 162730. Figure 2. Left valve, locality the same as in figure 1, U.S.N.M. 162726. Figure 3. Left valve (magn. ×3), Cannon Limestone (upper Middle Ordovician), Carthage, Tennessee, U.S.N.M. 247846. Figure 4. Right valve (magn. ×3), Perryville Limestone Member, Lexington Limestone (upper Middle Ordovician), A.M.N.H. 36763. Figure 5. Right valve (magn. ×3), Curdsville Limestone Member, Lexington Limestone (upper Middle Ordovician), U.S.N.M. 46941.

FIGURE 6. *Vanuxemia* sp. Right valve (magn. ×3), so-called 'Wykoff beds' (upper Upper Ordovician), Bristol, Minnesota, U.S.N.M. 25033.

FIGURES 7–10. *Vanuxemia inconstans* Billings. Figure 7. Left valve (magn. ×2), upper Middle Ordovician (Wildernessian), Braeside, Ontario, Canada, U.S.N.M. 162728. Figure 8. Right valve (magn. ×3), locality the same as in figure 7, U.S.N.M. 162720. Figure 9. Left valve (magn. ×3), locality the same as in figure 7, U.S.N.M. 162721. Figure 10. Right valve (magn. ×3), locality the same as in figure 7, U.S.N.M. 162725.

DESCRIPTION OF PLATE 10

FIGURES 1–3. *Anomalodonta gigantea* Miller. Figures 1 and 3. Left valve exterior (natural size) and hinge (magn. ×1.5), Upper Ordovician, Versailles, Indiana, Y.P.M. 23325. Figure 2. Internal mould showing muscle scars (natural size), locality unknown, M.U. 71T.

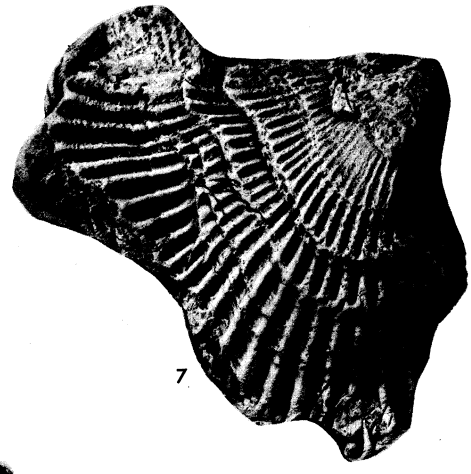
FIGURES 4–10. *Ambonychia alata* Meek. Figures 4 and 5. Internal mould left valve (natural size) and latex replica of same (magn. ×1.5), locality unknown, University of Cincinnati Museum (U.C.M.) 35923. Figure 6. Left valve hinge (magn. ×1.5), Bull Fork Formation (upper Upper Ordovician), Cincinnati, Ohio, U.C.M. 35913. Figure 7. Latex replica of exterior (natural size), Upper Ordovician, southwestern Ohio, U.S.N.M. 67520. Figure 8. Left valve hinge (magn. ×2), locality the same as in figure 6, U.C.M. 35909. Figure 9. Latex replica of left valve (magn. ×2), locality unknown, U.C.M. 35912. Figure 10. Left valve hinge (natural size), locality the same as in figure 6, U.C.M. 35911.

FIGURES 11–13. *Opisthoptera casei* (Meek and Worthen). Figure 11. Left valve exterior (magn. ×1.5), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.C.M. 35890. Figure 12. Right valve exterior (natural size), locality the same as in figure 11, U.S.N.M. 46267. Figure 13. Internal mould left valve (natural size), Whitewater Formation (upper Upper Ordovician), Richmond, Indiana, U.C.M. 35881.

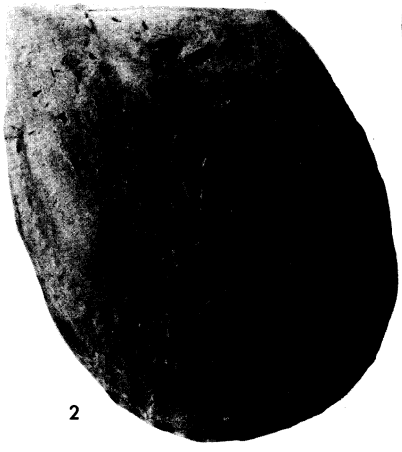
1
2
3
4
5
6
7
8
9
10

1

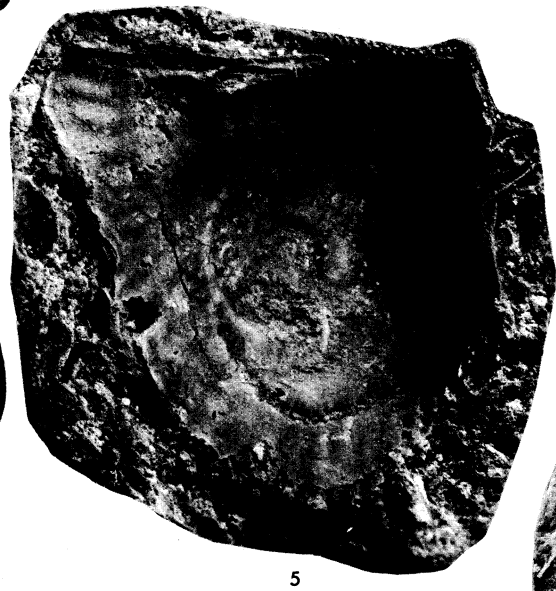
4



7



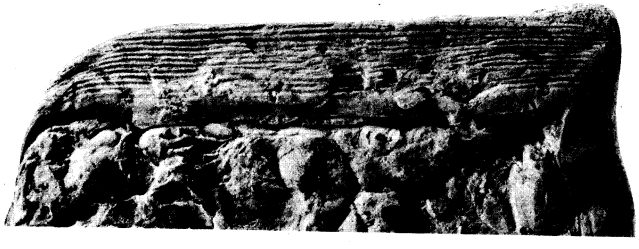
2



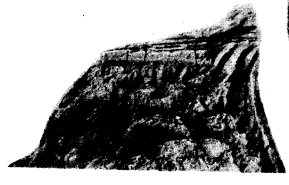
5

8

9

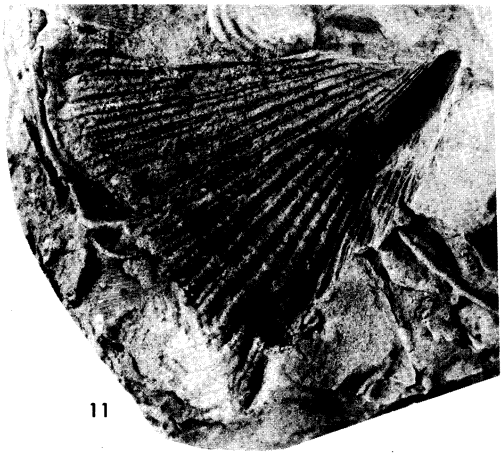


3

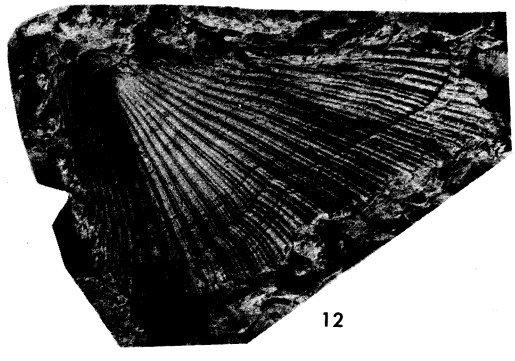


6

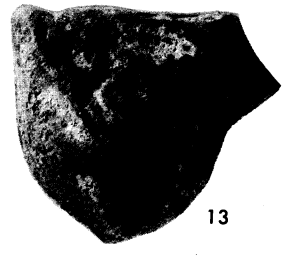
10



11



12

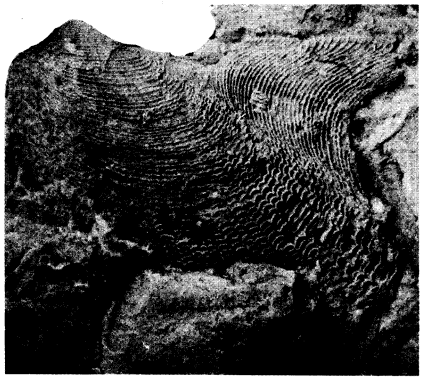


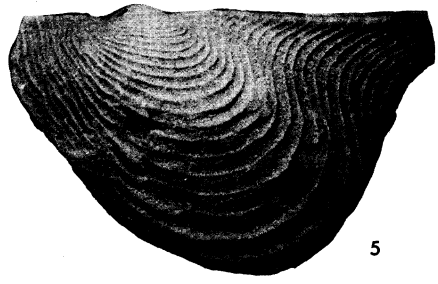
13

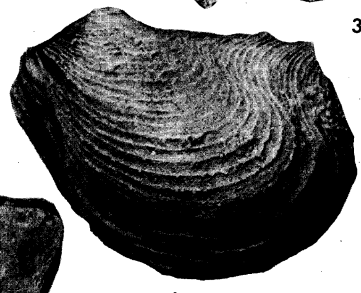
1

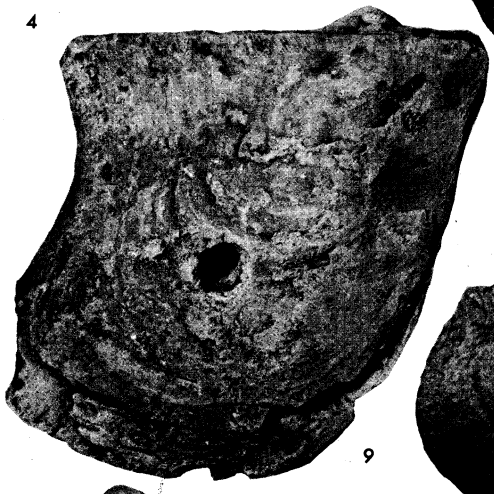
2

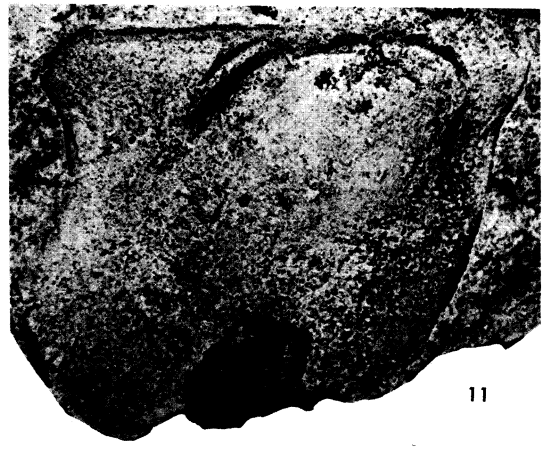
3


4

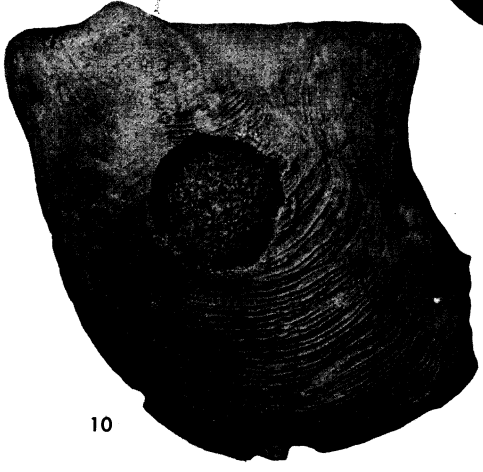

5


6


9


11

7

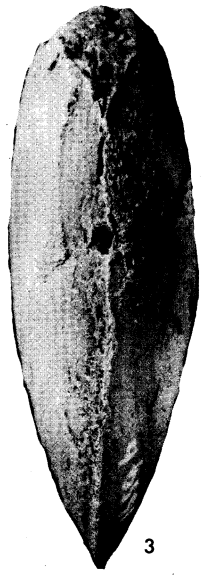

10

8

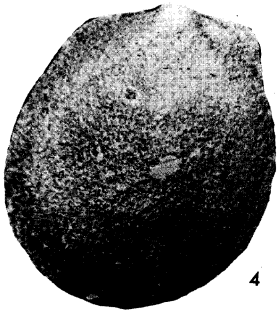
12

1

2

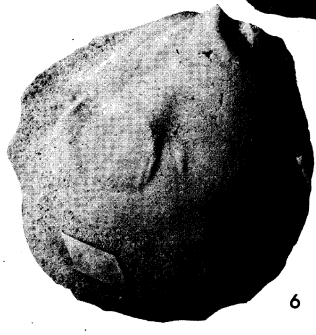


3



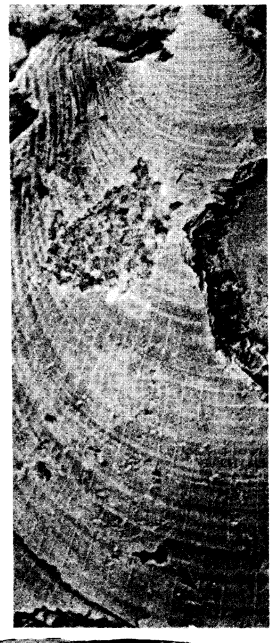
4

5



6

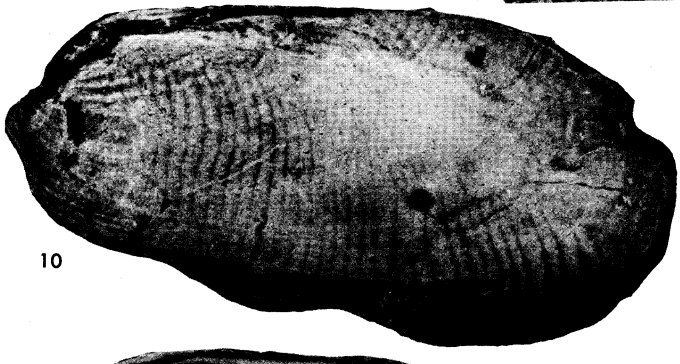
7



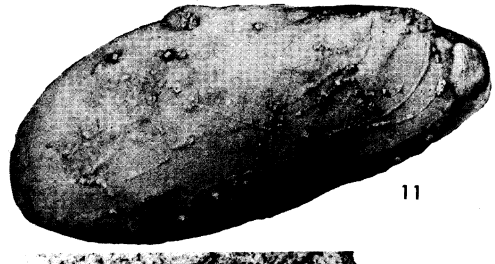
8

9

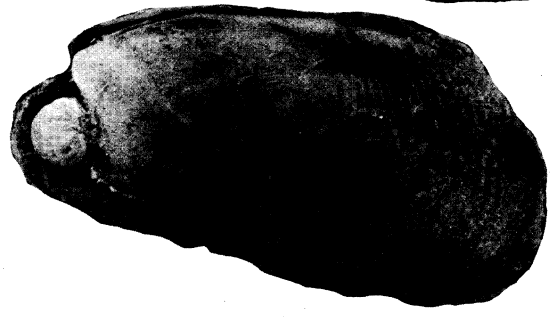
12



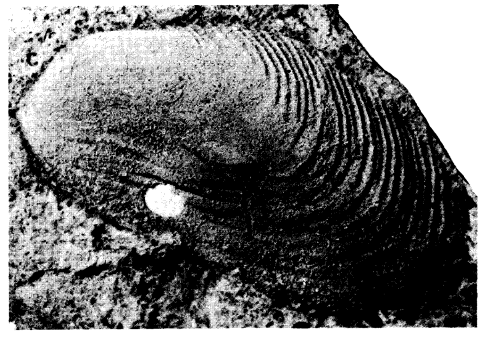
10



11



13



14

posterior to the ligament area (plate 8, figure 8) are much coarser and fewer in number than the grooves and ridges of the ligament area. Possibly the grooves on the ligament areas of cyrtodontids represent successive insertions of a ventrally migrating opisthodetic ligament, a thought that was first suggested to me by R. D. K. Thomas (oral communication, 1976). This suggestion is supported by a specimen of *Cyrtodonta huronensis* in which a silicified replica of the ligament is preserved (plate 8, figure 1), which is inserted in the lowest groove on the ligament areas. The oldest known occurrence of a duplivincular ligament is in early Late Ordovician pteriaceans (plate 11, figure 2), which have ligamental chevrons inclined at a low angle to the dorsal margin.

Cyrtodontids are probably the ancestral pteriomorphs because they have the least modified shell of any Ordovician members of the subclass. Because cytodontids have such well developed dentition, it seems reasonable to regard the actinodontians as ancestral to them. The major difference in the dentition of the two groups is the edentulous space between the anterior and posterior teeth in cyrtodontids. Cyrtodontids could be derived paedomorphically from the actinodontians by the neotenous retention of the larval byssus into the adult stage.

It is generally agreed that cyrtodontids are the most probable ancestors of the arcaceans (Newell 1954, 1965; Cox 1960). This hypothesis requires the development of the duplivincular

---

Description of plate 11

Figures 1–3. *Palaeopteria* new species 1, under investigation. Figure 1. Left valve (magn. × 6), Perryville Limestone Member, Lexington Limestone, (upper Middle Ordovician), central Kentucky, U.S.N.M. 162737. Figure 2. Left valve showing ligament chevrons (magn. × 3), Millersburg Member, Lexington Limestone (Middle and lower Upper Ordovician), central Kentucky, U.S.N.M. 247847. Figure 3. Right valve (magn. × 6), locality the same as in figure 1, U.S.N.M. 247848.

Figure 4. *Caritodens corrugata* (James). Left valve showing ornament (magn. × 3), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 46489.

Figures 5–12. *Caritodens demissa* (Conrad). Figure 5. Left valve (magn. × 4), Fairview Formation (middle Upper Ordovician), Cincinnati, Ohio, F.M. 8879. Figures 6–8. Left valve, right valve, dorsal view (magn. × 3), Maysvillian (middle Upper Ordovician), Cincinnati, Ohio, U.S.N.M. 162736. Figures 9 and 10. Right and left valves (magn. × 2), Maysvillian (middle Upper Ordovician), Cincinnati, Ohio, Y.P.M. 2361. Figure 11. Right valve internal mould (magn. × 2.5), Pulaski Shale (middle Upper Ordovician), Thorold, Ontario, Canada, U.S.N.M. 34598*a*. Figure 12. Left valve internal mould (magn. × 2), locality the same as in figure 11, U.S.N.M. 34598*b*.

Description of plate 12

Figures 1–8. New genus 10 *hermione* Billings, under investigation. Figure 1. Right valve internal mould (magn. × 1.5), 'Shermanian' (upper Middle Ordovician), Osnabruck Township, Ontario, Canada, G.S.C. 1659. Figure 2. Left valve internal mould (magn. × 2), Trenton Group (upper Middle Ordovician), Trenton Falls, New York, M.C.Z. 18080. Figure 3. Anterior view internal mould (magn. × 2.5), locality the same as in figure 1, G.S.C. 1659*b*. Figures 4 and 5. Right valve and anterior view (magn. × 2), locality the same as in figure 2, M.C.Z. 18081. Figures 6 and 7. Right valve (magn. × 1.5) and anterior view (magn. × 3) of internal mould, lower Upper Ordovician rocks, Frobisher Bay, Baffin Island, Canada, U.S.N.M. 28166. Figure 8. Exterior, showing ornament (magn. × 4), Middle Ordovician, Montreal, Canada, G.S.C. 1658.

Figures 9–11. *Pholadomorpha pholadiformis* (Hall). Figure 9. Composite mould left valve (natural size), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 46655. Figure 10. Composite mould showing ornament (magn. × 1.5), Maysvillian (middle Upper Ordovician), southwestern Ohio, F.M. 8813. Figure 11. Internal mould right valve, locality the samas in figure 10, U.S.N.M. 40578.

Figures 12–14. *Corallidomus concentrica* (Hall and Whitfield). Figure 12. Right valve (magn. × 1.5), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 40554. Figure 13. Composite mould, left valve (magn. × 1.5), Upper Ordovician, Cincinnati, Ohio, U.S.N.M. 247849. Figure 14. Latex replica right valve (magn. × 1.5), locality the same as in figure 12, U.S.N.M. 46245.

ligament and a rearrangement of the dentition, with the parallelodontids being intermediate between the cyrtodontids and the younger arcaceans.

In Silurian time, the megalodontids first appear in the fossil record; they are usually classified as heterodonts. The only Ordovician pelecypods that have a dentition even beginning to approach that of the megalodontids are the cyrtodontids; perhaps the ancestors of the former family should be sought in the latter family. The megalodontids may also be an entirely new development from some Silurian stock.

Ambonychiidae

The Ambonychiidae (plate 10) has received the most recent monographic treatment of any Ordovician pelecypods (Pojeta 1962, 1966, 1968). The ambonychiids are equivalved, strongly inequilateral, lack an anterior lobe, and are monomyarian. Many ambonychiids possess teeth, although these are not as robust as those in cyrtodontids; when present, the anterior teeth are below the beak and the posterior teeth are near the end of the posterodorsal margin and above the posterior adductor. The ligament areas are crossed by relatively coarse parallel longitudinal grooves and ridges.

There are about 12 known genera of Ordovician ambonychiids, which range in age from early Middle Ordovician (Chazyan) to late Late Ordovician (Richmondian). The family is known from Europe, North America, Australia, and possibly Podolia, U.S.S.R. Ambonychiids show considerable variation in ornament, shape, and dentition, and some are alate posteriorly. The pallial line is integripalliate and often discontinuous in attachment.

The ligament areas of ambonychiids are traversed by a series of parallel longitudinal grooves and ridges which differ from those of cyrtodontids only in being stouter (plate 10, figures 3, 6, 8 and 10). The ambonychiid ligament probably functioned and grew in the same manner as the ligament of cyrtodontids discussed above.

Ambonychiids probably evolved from cyrtodontids by reduction of the anterior end and the consequent development of the monomyarian condition. Whether the ambonychiid condition arose once from the cyrtodontids or whether it is polyphyletic cannot now be determined. The similarity of the ligament insertion areas of ambonychiids and cyrtodontids suggests a close phylogenetic relationship.

Ambonychiids have been regarded as ancestral to the late Palaeozoic myalinids (Pojeta 1966), and the two families were placed in the same superfamily by Newell (1965, 1969). Kauffman & Runnegar (1975) indicated a relation of ambonychiaceans to the inoceramids through such intermediate genera as *Atomodesma.*

If, as seems likely, cyrtodontids and ambonychiids had a preduplivincular ligament, but their presumed descendants the arcaceans and myalinids both have the duplivincular ligament, then the duplivincular ligament probably had a polyphyletic origin. The pteriaceans seem to have developed a duplivincular ligament before any other pteriomorphs in the early Late Ordovician (plate 11, figure 2). Thus, at present, it seems likely that the duplivincular ligament was evolved at least three times.

Pterineidae

Ordovician pteriaceans (plate 11) form a small group of eight known genera which range in age from early Middle Ordovician (Llanvirnian) through late Late Ordovician (Richmondian). They are known from Australia, Europe, and North America. Pterineids differ from

other Ordovician pteriomorphs in their shape, in the presence of a duplivincular ligament, and in being inequivalved, the left valve more convex than the right valve. Teeth are present and divided into anterior and posterior elements with an edentulous space separating them; the anterior teeth may or may not be located below the beak.

Pteriaceans seem the likely ancestors of pinnaceans through such intermediate genera as *Pteronitella* and *Palaeopinna* from the Silurian and Devonian respectively.

Pteriomorphs incertae sedis

Pectiniform or limiform pteriomorphs are known from rocks as old as the Trenton Group (Middle–Upper Ordovician) of New York (plate 12, figures 1–8). These are equivalved shells that form a new genus which is under investigation. The ornament of these shells consists of comarginal growth lines and fine radial ribs (plate 12, figure 8).

The shape and valve equality is strongly reminiscent of limaceans that have not been reported previously from rocks older than Early Carboniferous. Unfortunately, nothing is known of the ligament or dentition of the Ordovician forms, and the musculature is poorly known.

Isofilibranchia

Ordovician isofilibranchs, a byssate group of pelecypods, are modioliform in shape, equivalved, anisomyarian, and lack a resilial ridge and multiple insertion grooves on the ligament area. Teeth, when present, are limited to anterior elements that are placed below the beaks. The Modiomorphidae (Modiolopsidae) is the only Ordovician family currently placed in the subclass. About 19 Ordovician genera are placed in the Modiomorphidae, but many of these are poorly conceptualized. However, there is a core group of genera such as *Modiolopsis* (plate 14, figures 1–6), *Modiolodon* (plate 13, figures 10–15), *Corallidomus* (plate 12, figures 12–14), *Pholadomorpha* (plate 12, figures 9–11), and perhaps *Eurymya* (plate 13, figures 1–6) and *Colpomya* (plate 13, figures 7–9) all of which have a similar shell form but differ in ornament and dentition and which appear to be closely related. This group of genera is used here for the concept of Ordovician modiomorphids.

Ordovician modiomorphids range in age from the late Early Ordovician (Arenigian) through the late Late Ordovician (Richmondian); their greatest generic level diversification is in the Late Ordovician (Edenian–Richmondian). Geographically modiomorphids are found in the Ordovician rocks of North America, Europe, U.S.S.R., Australia, and Korea.

The modiomorphids are the likely ancestors of the Mytilidae, which first appear in Carboniferous rocks. Ordovician modioliform modiomorphids are like late Palaeozoic and younger mytilaceans in shell shape, musculature, byssal attachment, and, in a more general way, ligament type and dentition. They differ by specifics of dentition and in the lack of a resilial ridge. The late Palaeozoic modioliform myalinids are convergent to the Mytilacea, as neither the modiomorphids nor the mytilids are known to have had a duplivincular ligament.

Ordovician modiomorphids do not have well developed dentition (Pojeta 1971) and were probably not derived from the actinodontians. They may have originated from *Fordilla*-like ancestors by the paedomorphic retention of the byssus in the adult (Pojeta 1975). Waller (1978, this volume), regarded isofilibranchs as being related to the pteriomorphs, although he felt that the two groups diverged early in the evolution of pelecypods.

Orthonotia

A group of gaping soleniform shells with subparallel dorsal and ventral margins, that is here placed in the new subclass Orthonotia, begins in early Middle Ordovician time (Llanvirnian) and ranges throughout the Palaeozoic. Five Ordovician genera are placed in the Orthonotia: *Cymatonota* (plate 15, figures 9–13); *Orthodesma* (plate 15, figure 14); *Palaeosolen*; *Psiloconcha* (plate 14, figures 7–9); and a new genus. In the later Palaeozoic, such genera as *Orthonota*, *Solenomorpha*, and *Prothyris* are included in the Orthonotia. All orthonotians are currently placed in the family Orthonotidae. In the Ordovician, orthonotids occur in North America, Europe, and Australia.

Because little is known of the details of the morphology of Ordovician orthonotians (Pojeta 1971, pl. 18), it is difficult to compare them with other Ordovician groups and to consider their phylogenetic relations. Some Ordovician orthonotians are slightly higher posteriorly than anteriorly (plate 15, figure 10) and somewhat similar in shape to Ordovician isofilibranchs. On this basis there might be a relationship between the two groups.

DESCRIPTION OF PLATE 13

FIGURES 1–6. *Eurymya plana* (Hall). Figures 1 and 2. Right valve internal mould (magn. ×3) and dorsal view (magn. ×5), stratigraphic position uncertain, Argyle, Wisconsin, University of Minnesota (U.M.). Figures 3–5. Left valve internal mould (magn. ×3), dorsal view (magn. ×4), latex replica of dorsum (magn. ×4), Platteville Limestone (upper Middle Ordovician), Beloit, Wisconsin, U.S.N.M. 25345. Figure 6. Exterior of left valve (magn. ×2.5), Platteville Limestone (upper Middle Ordovician), Minneapolis, Minnesota, U.S.N.M. 46202.

FIGURES 7–9. *Colpomya constricta* Ulrich. Figure 7. Left valve (magn. ×3), Devils Hollow Member, Lexington Limestone (upper Middle Ordovician), central Kentucky, U.S.N.M. 247850. Figure 8. Right valve exterior (magn. ×3), locality the same as in figure 7, U.S.N.M. 247851. Figure 9. Left valve (magn. ×3), locality the same as in figure 7, U.S.N.M. 247852.

FIGURES 10–15. *Modiolodon oviformis* (Ulrich). Figure 10. Interior of dorsal part of shell (magn. ×2), U.S.N.M. 247853. Figures 11 and 12. Left valve (magn. ×2), interior umbonal view (magn. ×3), showing small byssal–pedal retractor scars (arrow points to the most posterior of three scars), U.S.N.M. 162754. Figure 13. Exterior of right valve (magn. ×2), U.S.N.M. 247854. Figure 14. Right valve (magn. ×2), U.S.N.M. 247855. Figure 15. Right valve (magn. ×2), U.S.N.M. 247856. All specimens from the Logana Member, Lexington Limestone (Middle Ordovician), central Kentucky.

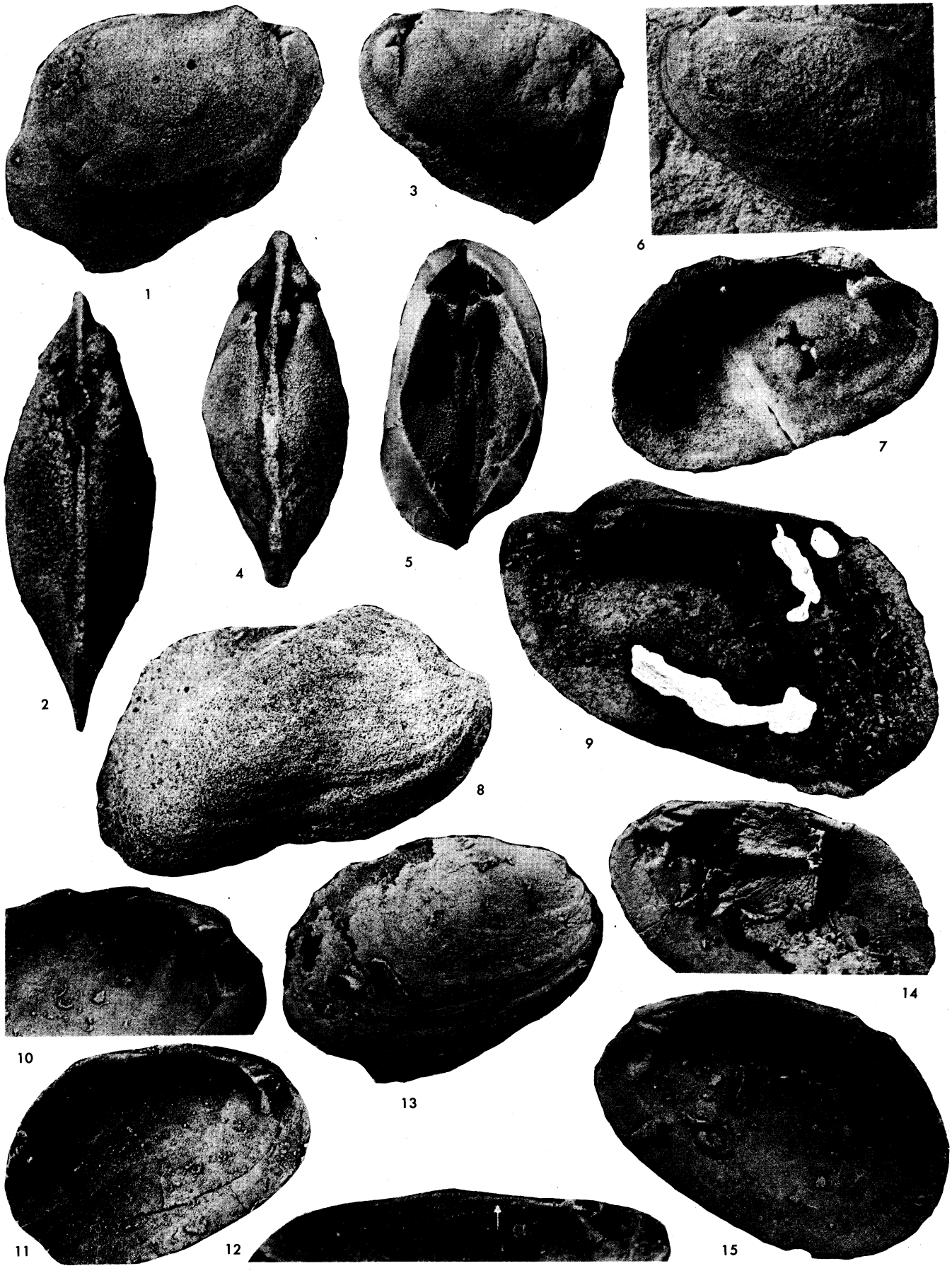
DESCRIPTION OF PLATE 14

FIGURES 1–4. *Modiolopsis modiolaris* (Conrad). Figure 1. Composite mould of right valve (natural size), Pulaski Shale (middle Upper Ordovician), Rome, New York, New York State Museum (N.Y.S.M.) 2758. Figure 2. Composite mould left valve (natural size), Pulaski Shale (middle Upper Ordovician), Worthville, New York, U.S.N.M. 87097. Figure 3. Left valve internal mould (natural size), Upper Ordovician, Oneida County, New York, M.C.Z. 18082. Figure 4. Latex replica of internal mould, showing edentulous hinge (magn. ×1.5), Upper Ordovician, Utica, New York, M.C.Z. 18083.

FIGURES 5 AND 6. *Modiolopsis* spp. Figure 5. Right valve showing hinge line (magn. ×1.5), Millersburg Member, Lexington Limestone (Middle and lower Upper Ordovician), central Kentucky, U.S.N.M. 247857. Figure 6. Internal mould showing musculature (magn. ×1.5), Kope Formation (lower Upper Ordovician), northern Kentucky, U.S.N.M. 101449.

FIGURES 7–9. *Psiloconcha grandis* Ulrich. Ventral view showing shell gapes (arrows), right valve and left valve views, all magn. ×1.5, Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 46283.

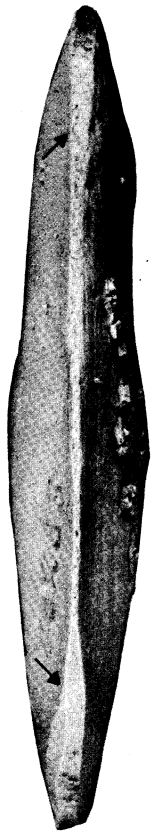
FIGURES 10 AND 11. *Babinka prima* Barrande. Two views of a right valve, showing the muscle scars and dentition; figure 10 magn. ×3; figure 11 magn. ×5; lower Middle Ordovician (Llanvirnian), Bohemia, Czechoslovakia. Figures from McAlester (1965), copied with the permission of the Palaeontological Association from the original figures in *Palaeontology*.


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15

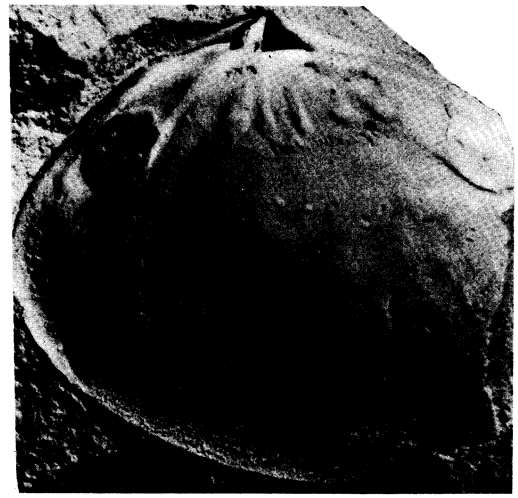
1

2

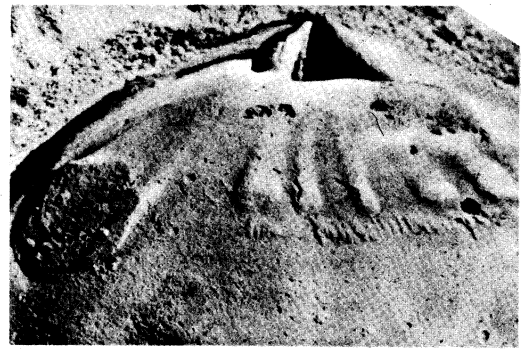
3



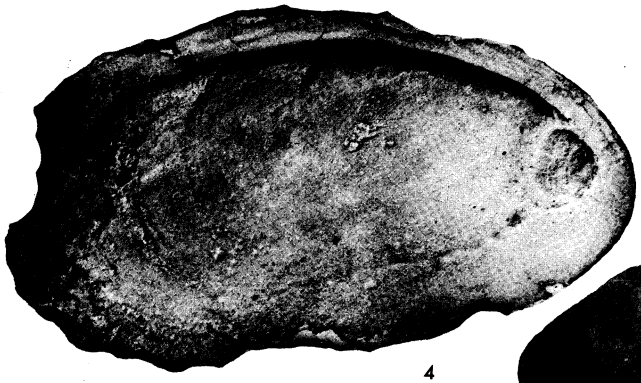
7



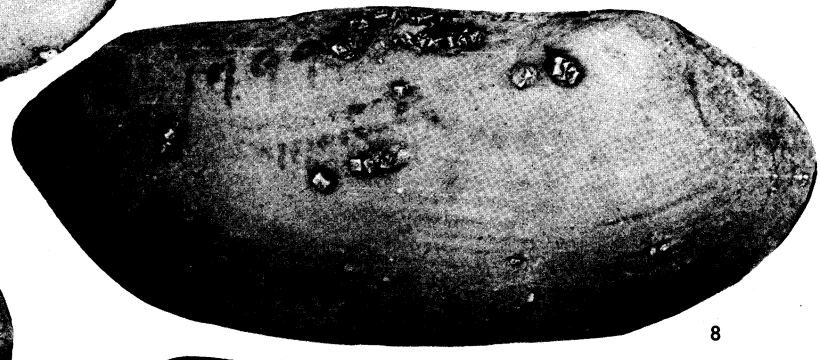
10



11

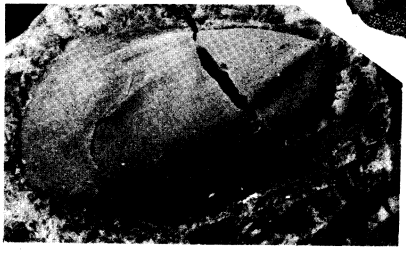


4

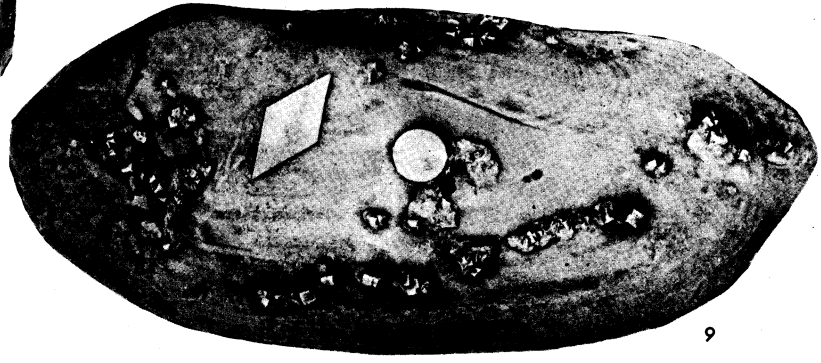


8

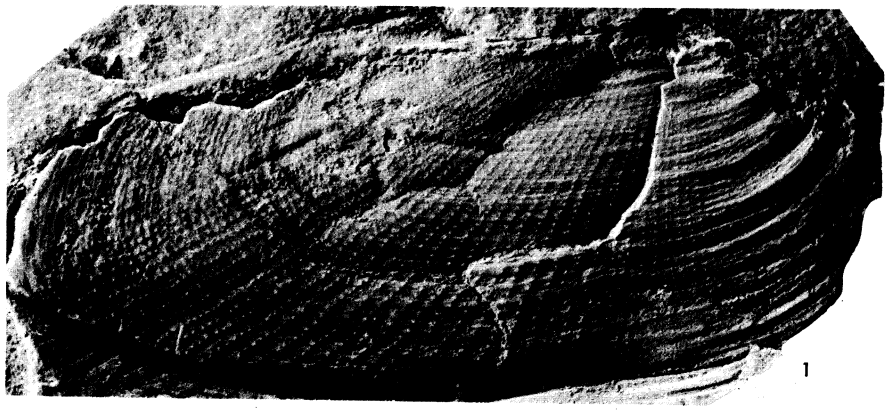
5

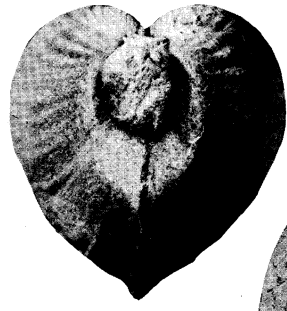


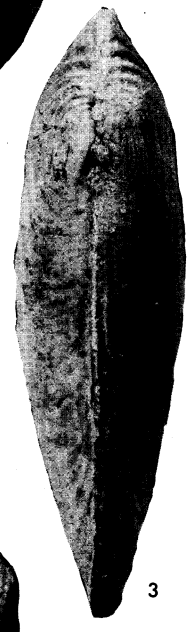
6

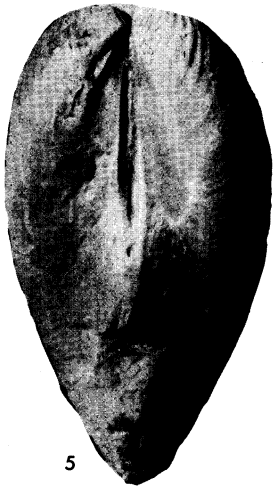


9

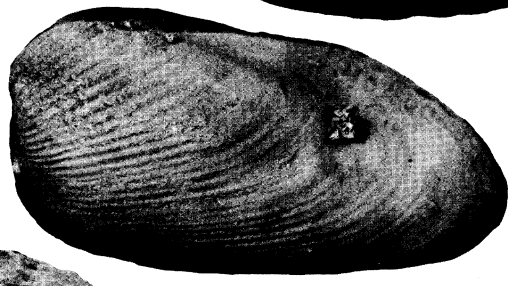

1

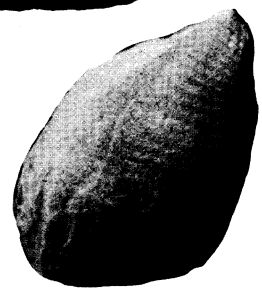

4


3

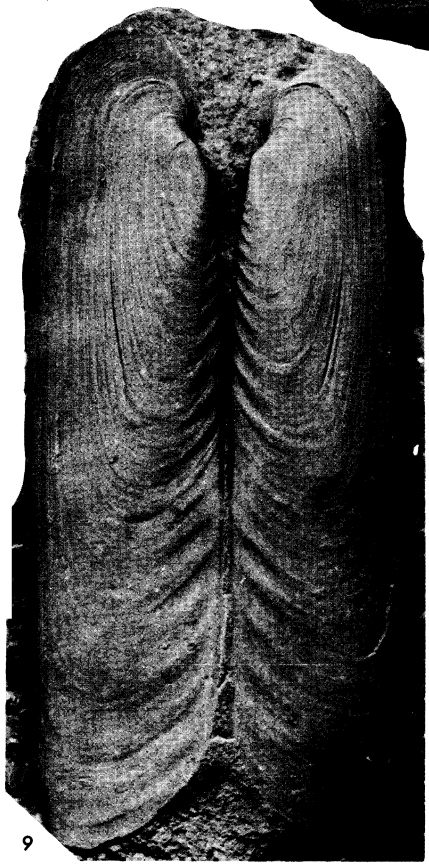

5

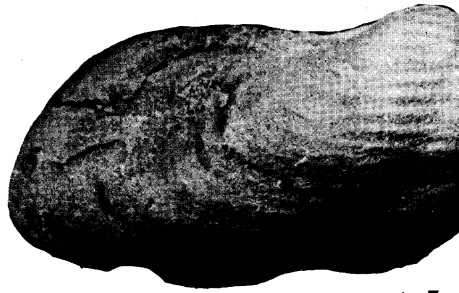
2


6


8

13


9


7

11

12

14

10

Runnegar (1974) noted some similarity between the musculature and teeth of Permian specimens of *Palaeosolen* and the Solenacea and suggested a relationship between orthonotians and solenaceans. This relationship would indicate that another group of heterodonts had an Ordovician origin and that the solenaceans are not necessarily related to the actinodontians.

Anomalodesmata

Runnegar (1974) dealt with the subclass Anomalodesmata and agreed with Pojeta (1971) that the Ordovician genera *Cuneamya* (plate 15, figures 4–7) and *Rhytimya* (plate 15, figures 1–3) are early anomalodesmatans. A third Ordovician genus, *Ceromyopsis* (plate 15, figure 8), is probably an anomalodesmatan, but it is known from only one poorly preserved specimen.

These genera are placed in this subclass largely because of their ornament of comarginal rugae and sometimes radiating rows of tubercles (plate 15, figure 1). Virtually nothing is known of the details of the internal morphology of the shell of Ordovician anomalodesmatans. The Ordovician forms appear to be closely related to such younger Palaeozoic genera as *Grammysia* and *Wilkingia*; some of the Ordovician species even have a radiating umbonal sulcus similar to that of younger grammysiids (plate 15, figure 7). All the Ordovician genera are placed in the Grammysiidae. Ordovician grammysiids first appear in the fossil record in middle Middle Ordovician time (Wildernessian) and are known from North America and Europe.

Because so little is known about Ordovician anomalodesmatans, their possible evolutionary relations to other Ordovician pelecypods are difficult to determine, although some orthonotians show rugose ornament along the dorsal margin (plate 15, figure 9). Runnegar (1974) suggested that the pholads may have arisen from the anomalodesmatans.

Description of plate 15

Figure 1. *Rhytimya radiata* Ulrich. Right valve exterior, showing ornament (magn. ×4), lower or middle Upper Ordovician, Rome, New York, U.S.N.M. 102037.

Figure 2. *Rhytimya michelboroughi* (Whitfield). Left valve (magn. ×2.5), Fairview Formation (middle Upper Ordovician), Cincinnati, Ohio, U.S.N.M. 15861.

Figure 3. *Rhytimya byrnesi* (Miller). Dorsal view (magn. ×2), Richmondian (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 247858.

Figure 4. *Cuneamya* sp. Anterior view (magn. ×2), Trenton Group (Middle Ordovician), Watertown, New York, U.S.N.M. 92331*a*.

Figures 5 and 6. *Cuneamya miamiensis* Hall and Whitfield. Figure 5. Dorsal view (magn. ×2), locality unknown, U.S.N.M. 162768. Figure 6. Left valve (magn. ×2), Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 40600.

Figure 7. *Cuneamya* sp. Right valve (magn. ×1.5), locality the same as in figure 4, U.S.N.M. 92331*b*.

Figure 8. *Ceromyopsis obliquata* Meek. Right valve (magn. ×3), Upper Ordovician, Cincinnati, Ohio, M.C 18084.

Figure 9. *Cymatonota recta* Ulrich. Dorsal view, showing ornament (magn. ×3), Pulaski Shale (middle Upper Ordovician), Rome, New York, U.S.N.M. 92281.

Figure 10. *Cymatonota* sp. Right valve (magn. ×3). Pulaski Shale (middle Upper Ordovician), Trenton Falls, New York, U.S.N.M. 23617.

Figures 11–13. *Cymatonota typicalis* Ulrich. Anterior, posterior, and dorsal views showing shell gapes, all magn. ×2, Waynesville shale (upper Upper Ordovician), southwestern Ohio, U.S.N.M. 46170*a*.

Figure 14. *Orthodesma* sp. Right valve internal mould (magn. ×1.5), Upper Ordovician, Cincinnati, Ohio, F.M. 324.

Lucinata

In Ordovician time the subclass Lucinata is known only from the genus *Babinka* (plate 14, figures 10 and 11) which is placed in the family Babinkidae. Although lucinoids were represented throughout the Palaeozoic their real diversification was post-Palaeozoic. McAlester's (1964, 1965, 1966) arguments for regarding *Babinka* as the oldest known lucinoid pelecypod were based on its shape, some elongation of the anterior adductor muscle scar, and dentition. He suggested (1966) that the lucinoids be assigned to a separate pelecypod taxon at the highest rank, although he did not propose a name for that taxon. I agree that the lucinoids represent an ancient pelecypod lineage, which originated in the first large-scale radiation of the class, and suggest that they be placed in the new subclass Lucinata.

Starobogatov (1971) is the most recent critic of the lucinoid affinities of *Babinka*; he maintained that McAlester misorientated *Babinka* and that what he regarded as anterior is actually posterior. The first consideration in orientating a pelecypod is the direction in which the beaks point; in *Babinka* they point toward the longer part of the shell, which McAlester regarded as anterior. Further, McAlester was able to find a ligament space behind the beaks and a lunule in front of them. Starobogatov maintained that both the ligament space and lunule, as defined by McAlester, were occupied by ligament; thus he regarded the ligament of *Babinka* as being amphidetic, and he compared it with the ligament of the unionids. In the unionids, there is no fibrous ligament layer anterior to the beaks, and in this sense the ligament is not amphidetic. Starobogatov also believed that he saw an extra muscle scar on the inside of the adductor muscle scar that McAlester regarded as posterior (plate 14, figure 11) and he compared the arrangement of the muscle scars at this end of *Babinka* with the arrangement of the muscle scars at the anterior end of unionids. In my opinion, such an extra muscle scar is not obvious in McAlester's figures. It seems to me that one sees the trace of this adductor, its scar and the pedal retractor scar above the adductor and I agree with Bretsky (1976) who accepted McAlester's orientation of *Babinka* and regarded the genus as the probable ancestor of the lucinaceans.

The oldest specimens of *Babinka* are from rocks of Arenigian Age (late Early Ordovician) from France and Sweden. The youngest known specimens are from rocks of Llanvirnian Age (early Middle Ordovician) of Czechoslovakia.

McAlester suggested that *Babinka* and the lucinoids were direct descendents of monoplacophorans independent of the rest of the Pelecypoda. Starobogatov (1971), Pojeta (1971), and Soot-Ryen (1969) were critical of this point of view for various reasons. Just how *Babinka* is related to the rest of the pelecypods is difficult to determine. It has one large triangular cardinal tooth in the right valve and two small wedge-shaped cardinal teeth in the left valve; the lateral surfaces of the teeth are covered with widely spaced parallel ridges. The dentition of *Babinka* is little advanced over that of *Fordilla*, which has a single cardinal tooth in each valve, and it may be that *Babinka* is a direct descendent of a *Fordilla*-like pelecypod.

I should like to thank Marija Balanc (U.S. Geological Survey) for printing the photographs and Janine M. Higgins (U.S. Geological Survey), who made the composite drawings used for figures 2–4. A. Yu. Roszanov (Palaeontological Institute, Akademia Nauk SSSR) provided the specimens of *Fordilla* from Siberia.

References (Pojeta)

Allen, J. A. & Sanders, H. L. 1969 *Malacologia* **7**, 381–396.

Allen, J. A. & Sanders, H. L. 1973 *Mus. comp. Zool., Harvard Coll. Bull.* **145**, 263–309.

Babin, C. 1966 *Mollusques bivalves et céphalopodes du Paléozoïque Armoricain.* Brest: Imprimerie Commerciale et Administrative.

Boyd, D. W. & Newell, N. D. 1968 *Am. Mus. Novit.* 2328, 52 pages.

Bradshaw, M. A. 1970 *Palaeontology* **13**, 623–645.

Bretsky, S. 1976 *Palaeont. am.* **7**, 219–337.

Chavan, A. 1954 *Cah. geol. Thoiry* **22**, 200.

Chavan, A. 1966*a* *Soc. géol. Fr. C. r.* **4**, 163–164.

Chavan, A. 1966*b* *Soc. géol. Fr. C. r.* **10**, 408–409.

Chavan, A. 1967 *Soc. géol. Fr. C. r.* **2**, 44–46.

Chavan, A. 1969 In *Treatise on invertebrate paleontology* (ed. R. C. Moore), part N (Mollusca 6), **2**. New York and Lawrence, Kans.: Geol. Soc. America and Univ. Kansas Press.

Cox, L. R. 1960 *Malacol. Soc. Lond. Proc.* **33**, 60–88.

Eichwald, E. 1860 *Lethaea rossica ou paléontologie de la Russie.* Stuttgart: E. Schweizerbart.

Harrington, H. J. 1938 *La Plata Univ. Nac. Inst. Mus. Rev.* **1**, 290.

Harrison, W. B. & Harrison, L. K. 1975 *Bull. Am. Paleont.* **67**, 193–234.

Kauffman, E. G. & Runnegar, B. 1975 *J. Paleont.* **49**, 23–41.

Matthews, S. C. & Missarzhevsky, V. V. 1975 *J. geol. Soc. Lond.* **131**, 289–304.

McAlester, A. L. 1964 *Science, N.Y.* **146**, 1293–1294.

McAlester, A. L. 1965 *Palaeontology* **8**, 231–246.

McAlester, A. L. 1966 *Malacologia* **3**, 433–439.

Missarzhevsky, V. V. 1974 In *Biostratigraphy and paleontology of the Lower Cambrian of Europe and northern Asia*, pp. 179–189. Akedemiya Nauk SSSR, Geologicheskii Institut, Sibirskoe otdelenie, Institut geologii i geofiziki. [In Russian.]

Morris, N. J. & Fortey, R. A. 1976 *J. Paleont.* **50**, 701–709.

Newell, N. D. 1954 *Harvard Coll. Mus. comp. Zool. Bull.* **112**, 161–172.

Newell, N. D. 1958 *Am. Mus. Novit.* 1857, 6 pages.

Newell, N. D. 1965 *Am. Mus. Novit.*, 1878, 25.

Newell, N. D. 1969 In *Treatise on invertebrate paleontology* (ed. R. C. Moore), Part N (Mollusca 6), **1**. New York and Lawrence, Kans.: Geol. Soc. Amer. and Univ. Kansas Press.

Newell, N. D. & Boyd, D. W. 1975 *Am. Mus. nat. Hist. Bull.* **154**, 53–162.

Pojeta, J., Jr 1962 *Palaeont. am.* **4**, 169–216.

Pojeta, J., Jr 1966 *Palaeont. am.* **5**, 129–241.

Pojeta, J., Jr 1968 *J. Paleont.* **42**, 1255–1257.

Pojeta, J., Jr 1971 *U.S. geol. Surv. prof. Pap.* 695, 46 pages.

Pojeta, J., Jr 1975 *Bull. Am. Paleont.* **67**, 363–384.

Pojeta, J., Jr & Gilbert-Tomlinson, J. 1977 *Aust. Bur. Min. Resc. Bull.* **174**, 64 pages.

Pojeta, J., Jr & Palmer, T. J. 1976 *Alcheringa* **1**, 167–179.

Pojeta, J., Jr & Runnegar, B. 1974 *Am. Scientist* **62**, 706–711.

Pojeta, J., Jr & Runnegar, B. 1976 *U.S. geol. Surv. prof. Pap.* 968, 88 pages.

Rozanov, A. Y. *et al.* 1969 *Dokl. Akad. Nauk. SSSR* **206**, 380. [In Russian.]

Runnegar, B. 1974 *J. Paleont.* **48**, 904–936.

Runnegar, B. & Jell, P. A. 1976 *Alcheringa* **1**, 109–138.

Sanders, H. L. & Allen, J. A. 1973 *Harvard Coll. Mus. comp. Zool. Bull.* **145**, 237–261.

Soot-Ryen, H. 1969 *Palaeontology* **12**, 173–177.

Starobogatov, Y. I. 1971 *Paleont. Zhur.* **5**, 384–386. (Translation published by the American Geological Institute, March 1972.)

Suneja, I. J. 1975 *Curr. Sci.* **44**, 787.

Termier, G. & Termier, H. 1971 In *Geobios* **4**, 143–150.

Thoral, M. 1935 *Contribution à l'etude paléontologique de l'Ordovicien Inférieur de la Montagne Noire et révision sommaire de la faune Cambrienne de la Montagne Noire.* Montpellier: Imprimerie de la Charité.

Waller, T. R. 1978 *Phil. Trans. R. Soc. Lond.* B **284**, 345–365 (this volume).

The plates in this paper have been printed at the University Press, Oxford.

Discussion

E. L. YOCHELSON (*U.S. Geological Survey, E-501 Museum of Natural History, Washington, D.C. 20560, U.S.A.*). I am impressed with the bulk of Dr Pojeta's work, summarized in the second paragraph of his abstract. Because of concepts expressed in his first paragraph and because the symposium was titled 'Evolutionary systematics of bivalve molluscs' rather than 'Bivalvia', it is appropriate to write a minority report on both the title of the symposium and on several of Dr Pojeta's concepts.

It should be obvious that there is a difference between Bivalvia and bivalved molluscs. We should not forget *Berthelinia* and other bivalved opisthobranchs; there is more than one way to develop two valves and hold them together! Information on Recent taxa of this design has been admirably summarized by Kay (1968).

A more serious problem is concerned with the Early and Middle Cambrian *Stenothecoides* and its allies. In 1968 I proposed the extinct molluscan class Stenothecoida; Akserina proposed Probivalvia for essentially the same concept. Runnegar & Pojeta (1974, p. 316) wrote 'Yochelson interpreted *Senothecoides* as a brachiopod-like mollusc. We offer the alternative suggestion that it may have been a bivalved monoplacophoran, with the lower (smaller?) valve formed by the sole of the foot.' They then gave a reference to *Hipponyx*. Subsequently, Pojeta & Runnegar (1976, p. 40) wrote of *Hipponyx* and *Stenothecoides* as having 'two subequal valves, but they are anatomically and functionally dorsal and ventral'. It is not clear whether this extinct class was rejected or accepted, for Runnegar & Pojeta continue to refer to Rostroconchia as the only extinct class of molluscs. Possibly Stenothecoida is included in the Mollusca as Runnegar & Pojeta (1974, fig. 1) and Pojeta & Runnegar (1976, fig. 14) do show it as part of their subphylum Diasoma, even though the class is not derived from any ancestral form, in contrast to other members of the assemblage.

Additional specimens from Kazakistan showing internal markings were illustrated (Koneva 1976), and an unfigured specimen is known from western Utah. They reinforce my observation that markings on the steinkern (internal shell filling) are unlike muscle scars of Silurian Monoplacophora such as *Tryblidium* and *Pilina*. Restudy of slightly asymmetrical specimens from the early Middle Cambrian, first noted by Robison in 1964, confirms the presence of a peg-like tooth in one valve and a plate-like socket in the other.

Association of *Stenothecoides* to *Hipponyx* seems a poorly chosen analogy. The hard part morphologic data on the class Stenothecoida indicated a group of asymmetrical inequivalved molluscs with curious markings on the interior of at least one valve. I am not firmly committed to the reconstruction of soft parts I proposed in 1969, but this still seems the simplest which accords with the data. The molluscan class Stenothecoida has not been refuted; a general treatment of bivalved molluscs ought to consider it.

It is also appropriate to examine the claim that *Fordilla* is the earliest member of the class Pelecypoda (= Bivalvia). According to Pojeta *et al.* (1973), internal markings show anterior and posterior adductor scars connected by a pallial line, along with pedal retractor scars and one or two small umbonal scars. The same thought with some changes in wording and some additional photographs are provided by Pojeta & Runnegar (1974), Pojeta (1975) and Pojeta & Runnegar (1976). This last work gives four alternative reconstructions of presumed musculature and associated anatomy.

I have re-examined the primary types plus all additional illustrated specimens, as well as

several others I have collected. Muscle impressions may be present, but at best the evidence requires the Scottish verdict of 'not proven'. I see no posterior scar and doubt the presence of a pallial line; alternative reconstructions of anatomy may be proposed. Specimens are quite small and subtle changes in elevation on the steinkern can be variously interpreted. 'The eye beholds what the mind perceives', and if one perceives *Fordilla* with the notion that extinct genera go into extant molluscan classes, obscure markings inside the shell are likely to be interpreted as homologous to those in a pelecypod.

Pojeta (1971) has documented in the Ordovician a dramatic radiation of bivalves, with nuculoid forms appearing first. It is curious that *Fordilla* shows no nuculoid features of gross shell shape or dentition. The nuculoids are shallow burrowers, and from them the lines of descent appear moderately clear to later major groups of burrowing and surface-dwelling clams. Tevesz & Aller (1975) suggest *Fordilla* may have lived on the surface, an interpretation with which I concur.

One might suggest that the Early Ordovician occurrence of pelecypods and their subsequent radiation from a shallow burrowing life habit is a neat evolutionary story, but if *Fordilla* is added, this story has a long vague confusing preamble.

To deal in *paleoecometaphysics*, the essence of evolution in Cephalopoda was development of buoyancy. In a like vein for Bivalvia, it was able to burrow; this requires certain modification of two valves. To burrow shallowly, valves should be interlocked with teeth and sockets, and muscle fibres should be so firmly affixed to the shell as to interfere with shell growth and form scars. Trueman and Stanley have shown that burrowing requires a great deal of movement of shell and foot. *Fordilla* developed two valves and could presumably close them once they were opened, but I do not see the other features required to cast this genus in the rôle of an ancestral bivalve. I judge *Fordilla* to be yet another novel experiment in functional morphology.

References

Kay, E. A. 1968 *Zool. Soc. Lond. Symp.* **22**, 109–134.
Koneva, S. P. 1976 *Paleont. Zhuhr.* **2**, 125–128 [In Russian].
Pojeta, J., Jr *et al.* 1973 *Science, N.Y.* **180**, 66–68.
Runnegar, B. & Pojeta, J. Jr 1974 *Science, N.Y.* **186**, 311–317.
Tevesz, M. J. S. & McCall, P. L. 1976 *Paleobiology* **2**, 183–190.

J. POJETA. *Fordilla* has a bivalved shell which is symmetrical about the commissural plane. The new Siberian specimens show cardinal teeth. On American specimens, muscle markings are found along the peripheral parts of the anterior, ventral, and posterior margins of the shell. Anteriorly and posteriorly, these muscle markings are enlarged, and above the anterior enlargement is a smaller muscle scar. In my opinion, these data are best interpreted by considering *Fordilla* to be a pelecypod.

By Early Ordovician time, pelecypods had developed at least three distinct dental patterns in the palaeotaxodonts, actinodonts, and babinkids. Babinkids are like *Fordilla* in having only cardinal teeth, and some Ordovician actinodonts have shell shapes much like those of *Fordilla*.

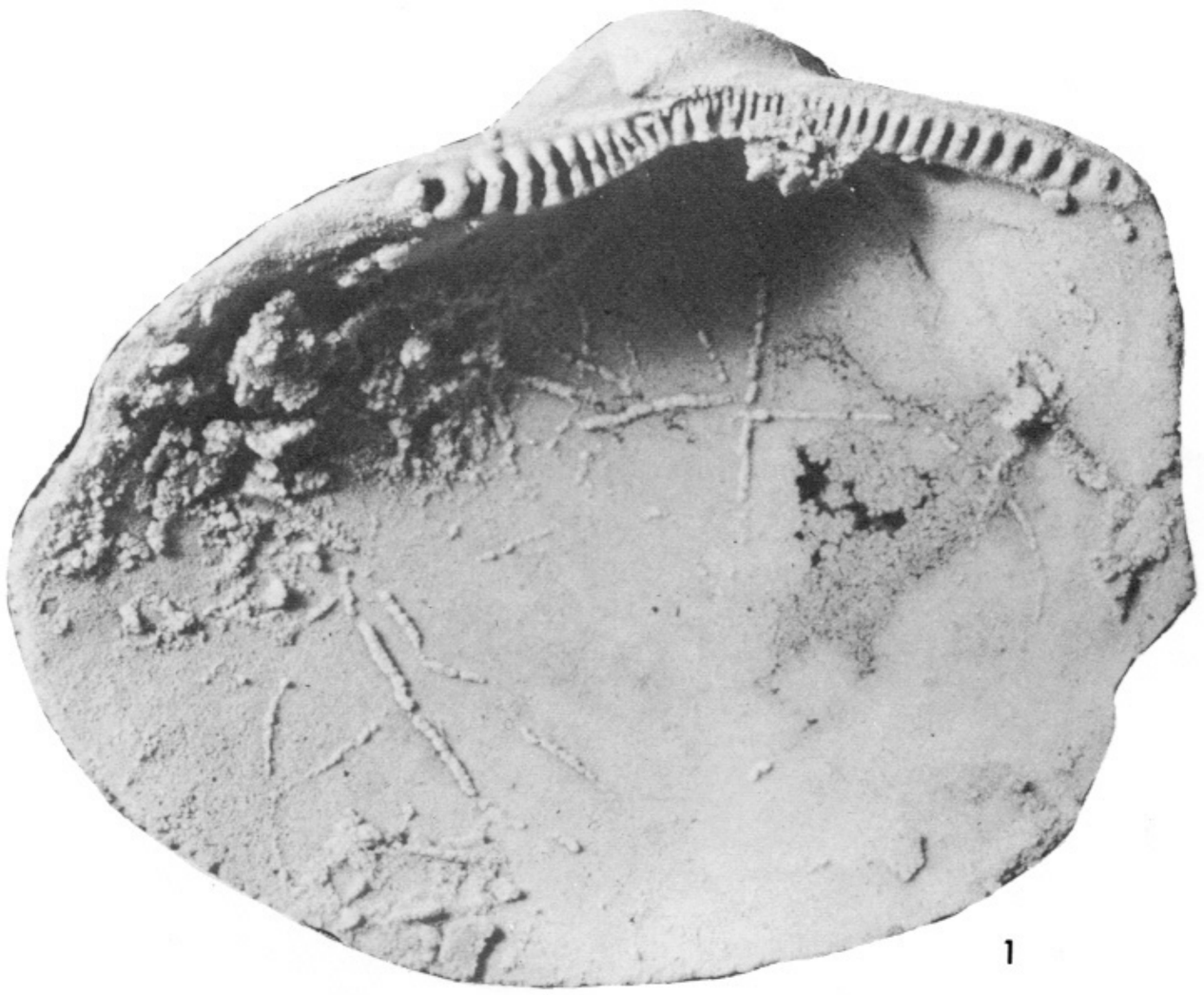
Of the various taxa used to demonstrate a transition from a univalved to a bivalved condition, *Latouchella*, *Anabarella*, *Heraultipegma*, and *Fordilla* occur in Lower Cambrian rocks; the first three genera are known from rocks as old as the Tommotian, and *Fordilla* occurs in younger Lower Cambrian rocks. *Mellopegma* is found in rocks as old as the Ordian, which is variously placed in the latest Early Cambrian or the earliest Middle Cambrian. *Myona* is not yet known

from rocks older than the middle Middle Cambrian. All these taxa show that organisms morphologically transitional between univalves and bivalves actually existed.

M. D. Brasier (*Geology Department, Hull University, Cottingham Road, Hull UH6 7RX, U.K.*). Neither *Fordilla* nor *Heraultipegma* fit as neatly into the evolutionary lineage as one might wish. *Fordilla* was reported by Cobbold from the Hyolithes limestone of Nuneaton, now known to be of Tommotian age. Further collection has produced only helcionellid molluscs, but these do at least show indications of a formerly prismatic shell structure. Müller's research on *Heraultipegma* indicated crustacean features such as the cellular shell microstructure and a dimorphic adult stage. One might also interpret the 'pegma' as a slender antennal notch. Can Dr Pojeta demonstrate that it was not a crustacean?

J. Pojeta. Cobbold assigned one specimen from Nuneaton with question to *Fordilla troyensis*. Whether the specimen is properly assigned or not cannot be determined on the basis of his figure.

Müller's point of view on *Heraultipegma* is discussed in this symposium by B. Runnegar; I refer you to his paper for an analysis of the reasons why *Heraultipegma* is probably not an arthropod.

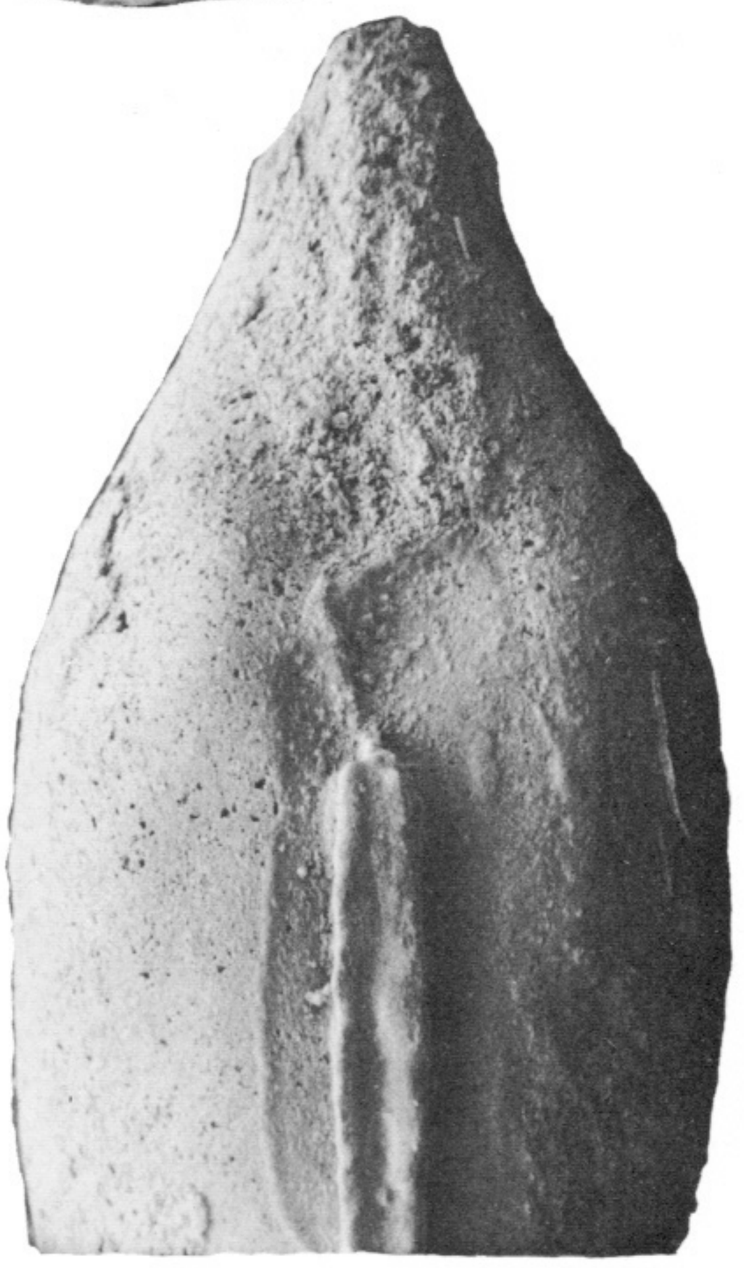


1

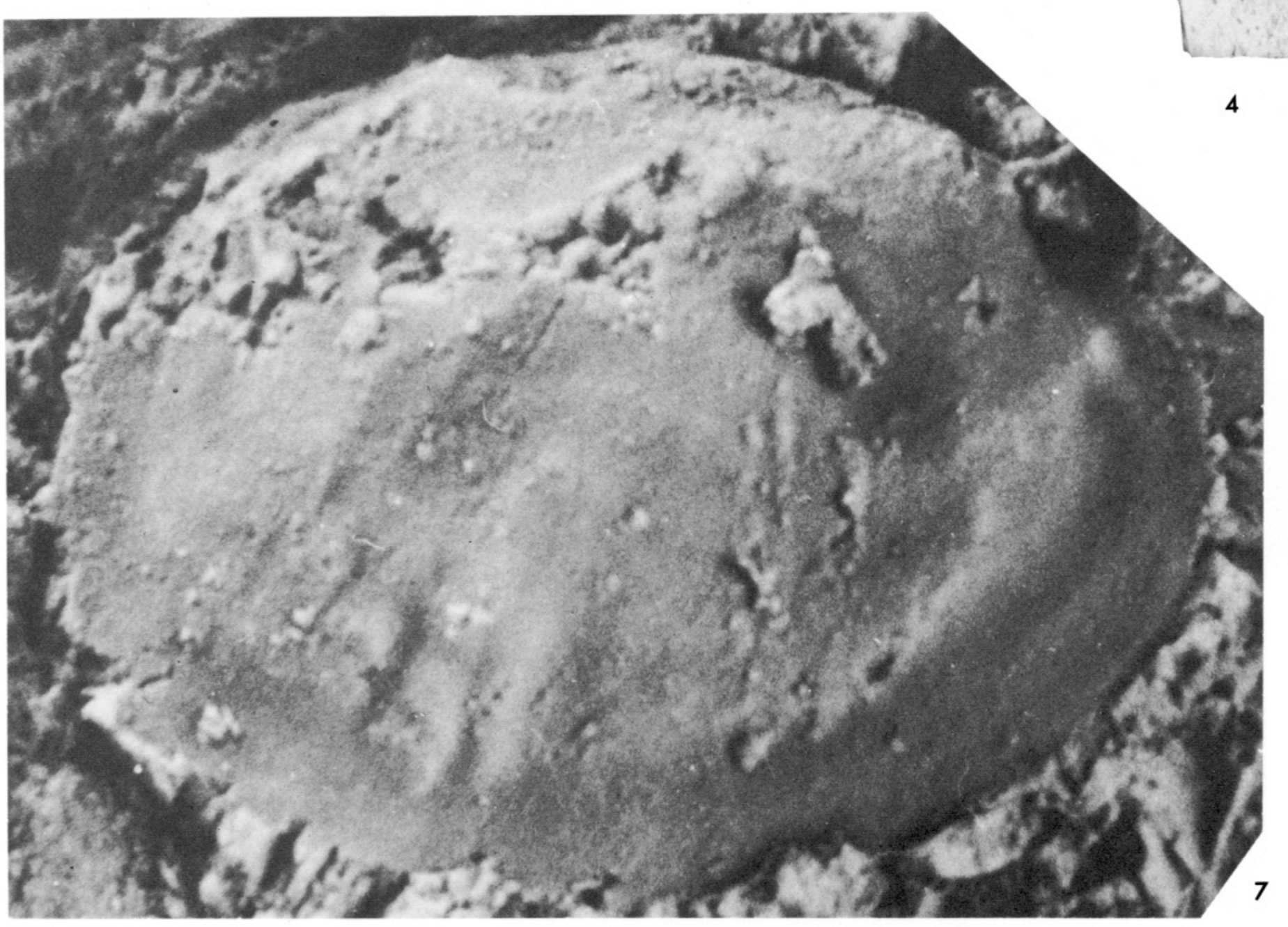
2

3

6



4

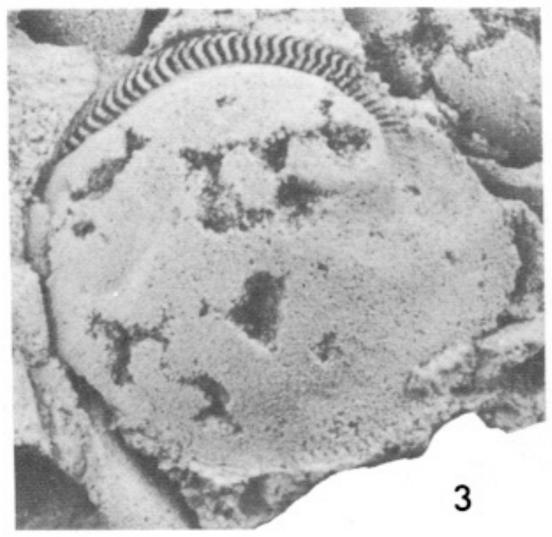


7

5

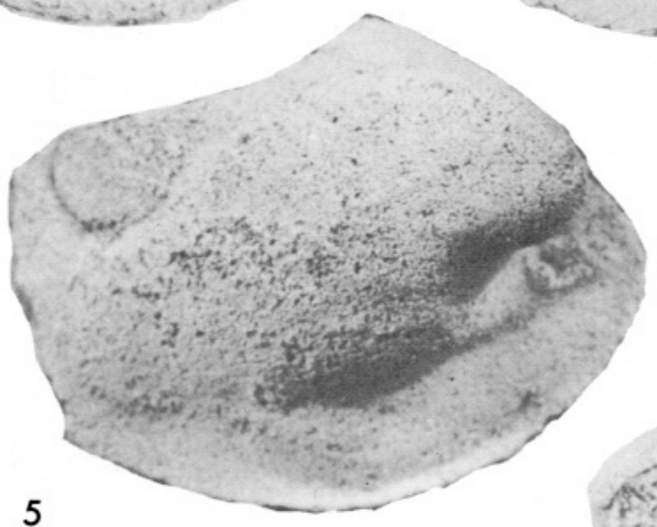
1

2

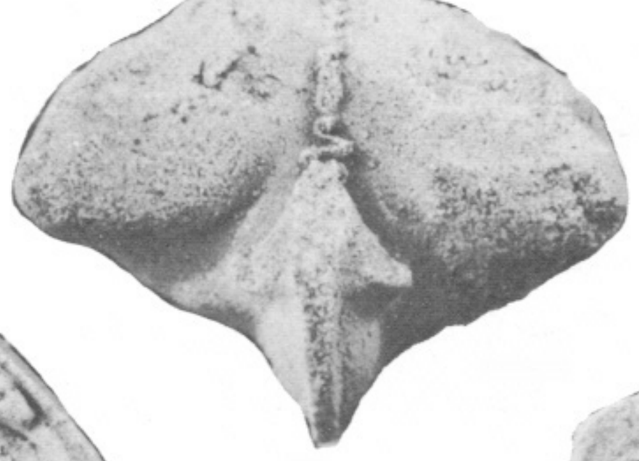


3

4



5



6

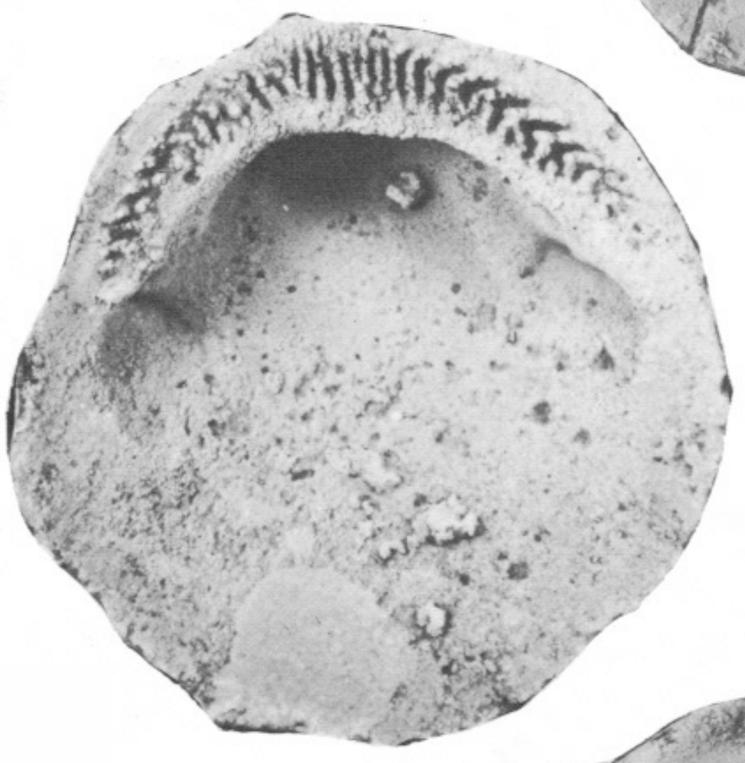
7

8

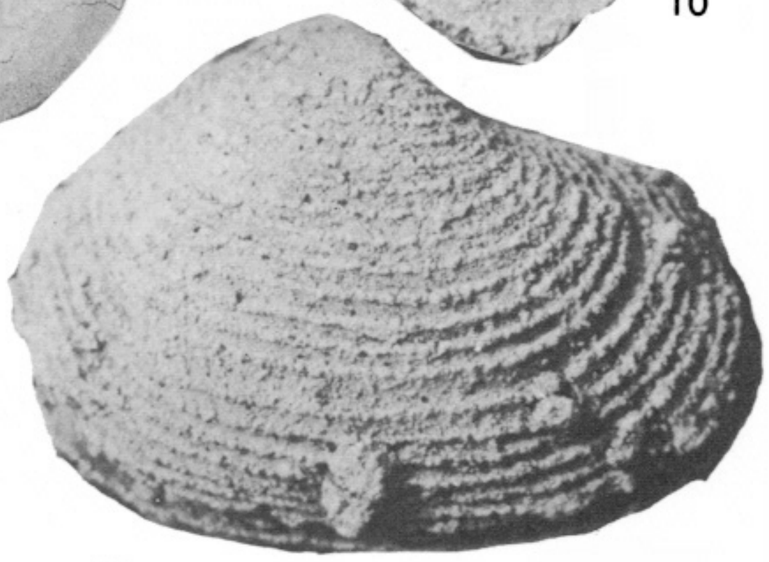
9

10

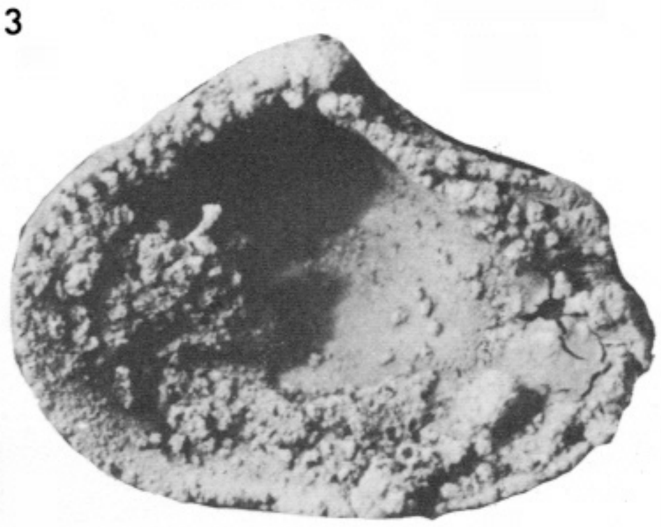
11



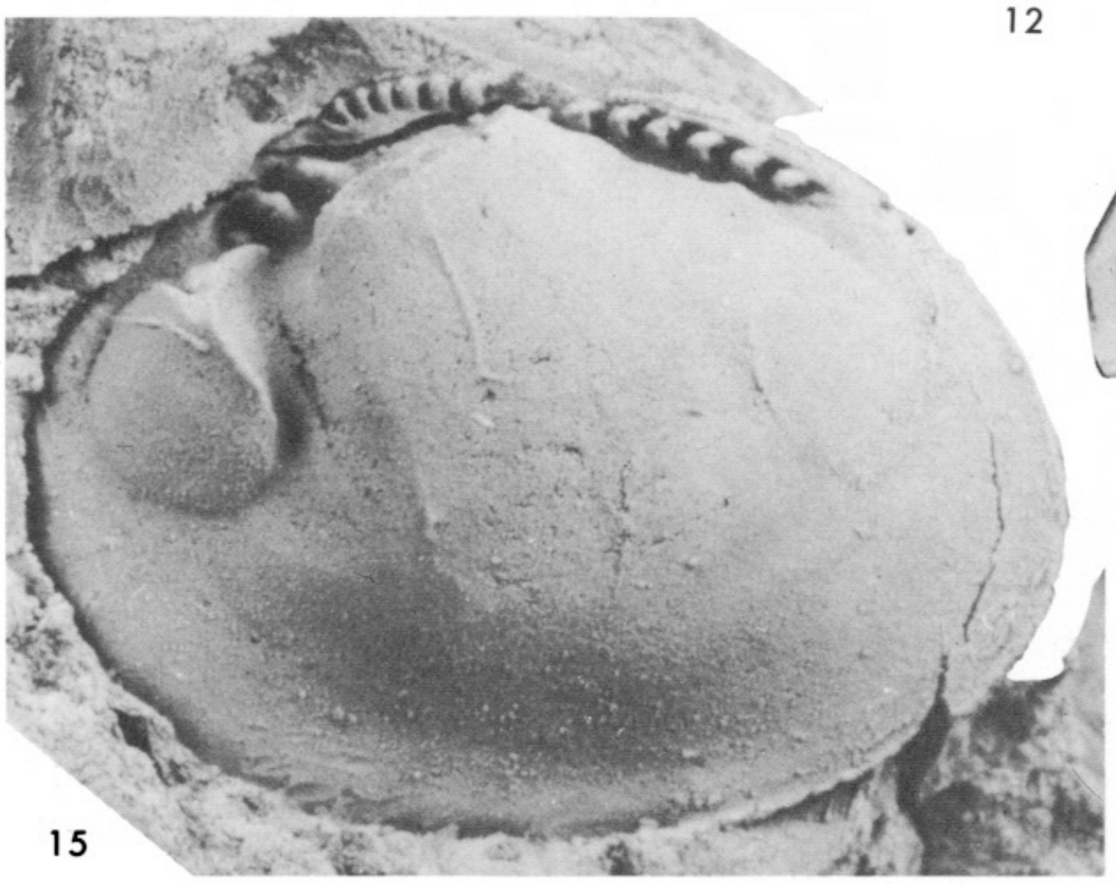
12



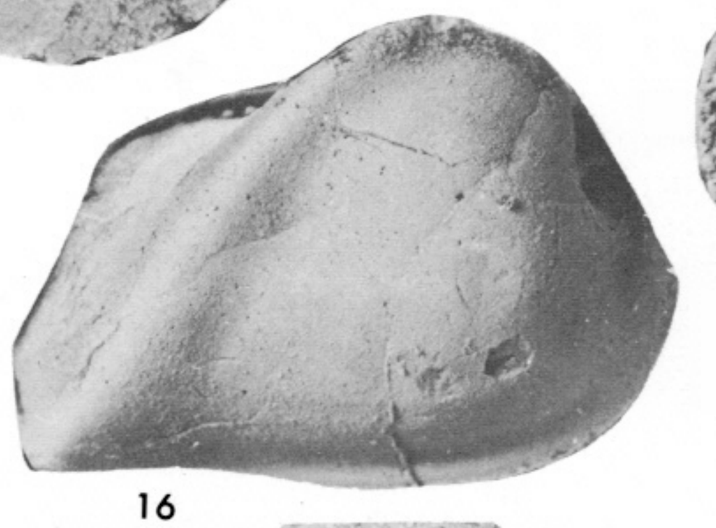
13



14

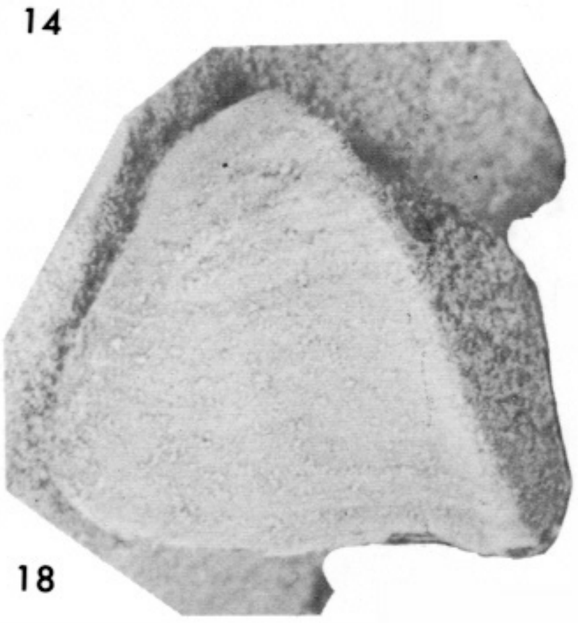


15

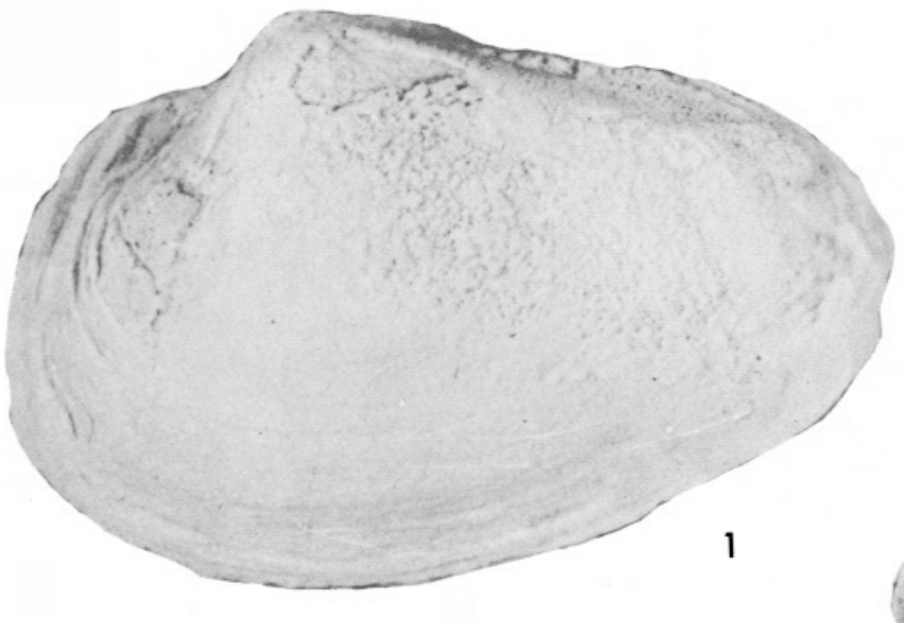


16

17

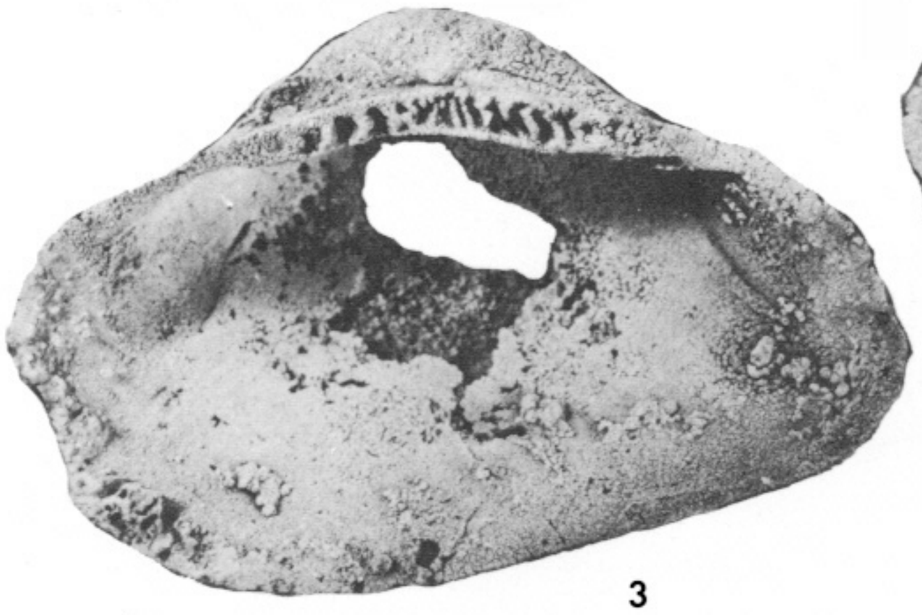


18



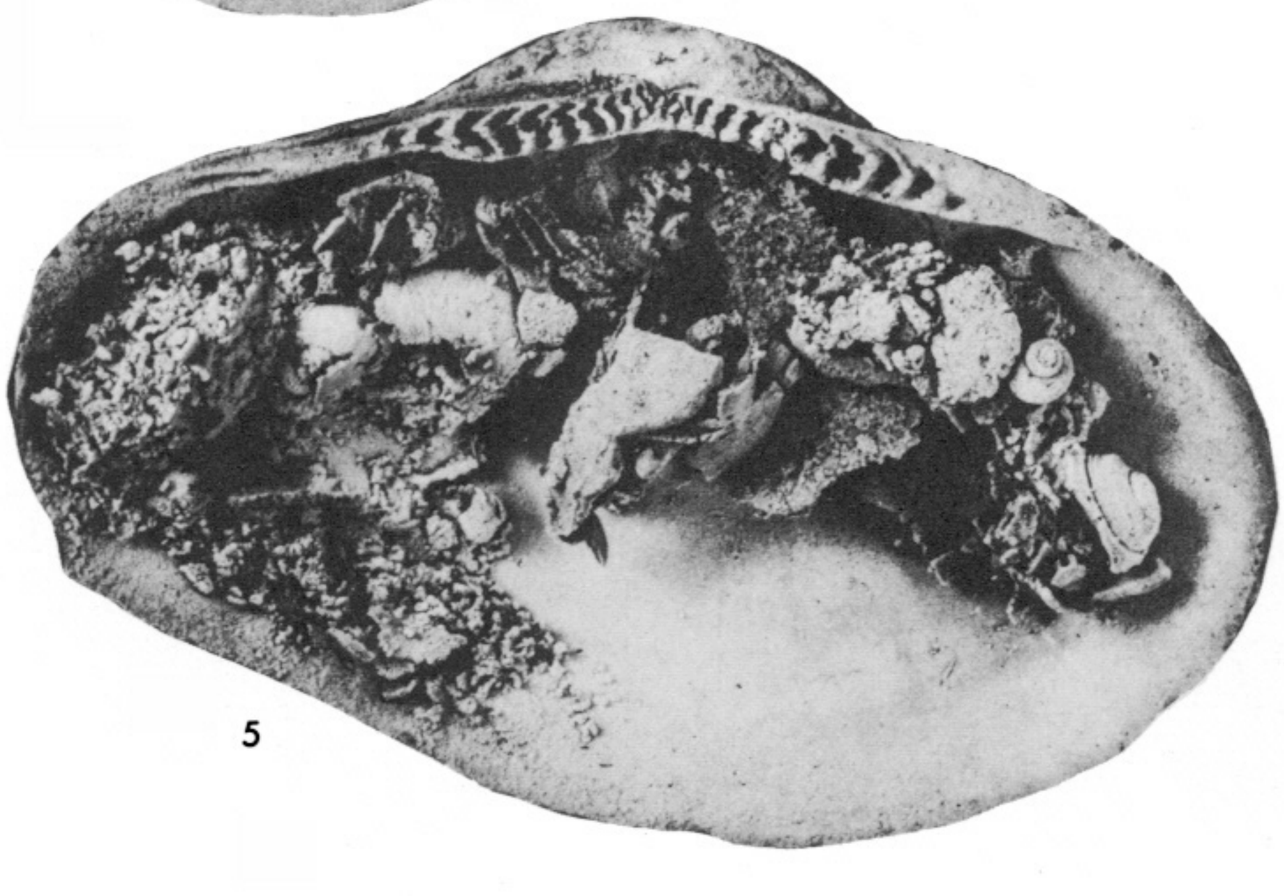
1

2



3

4

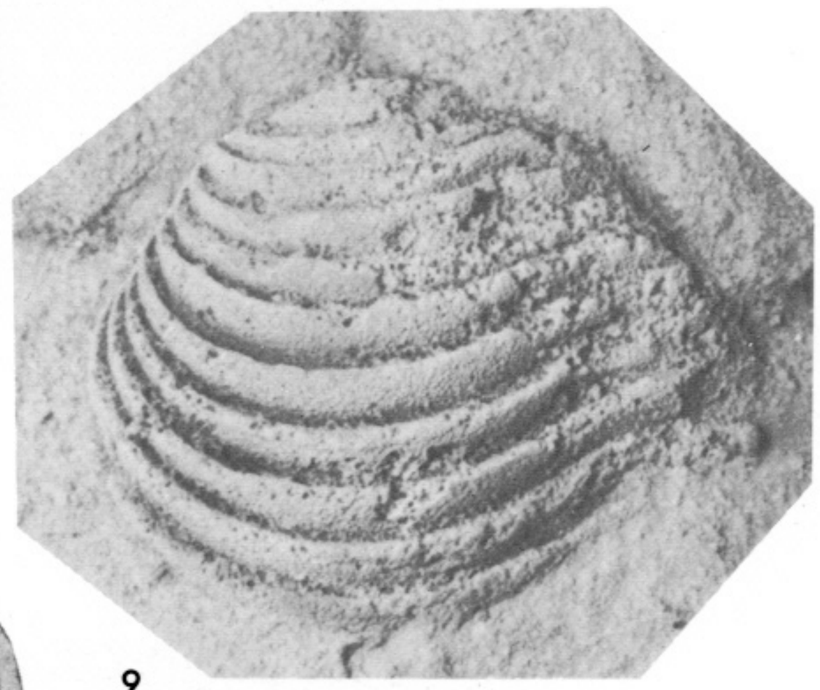


5

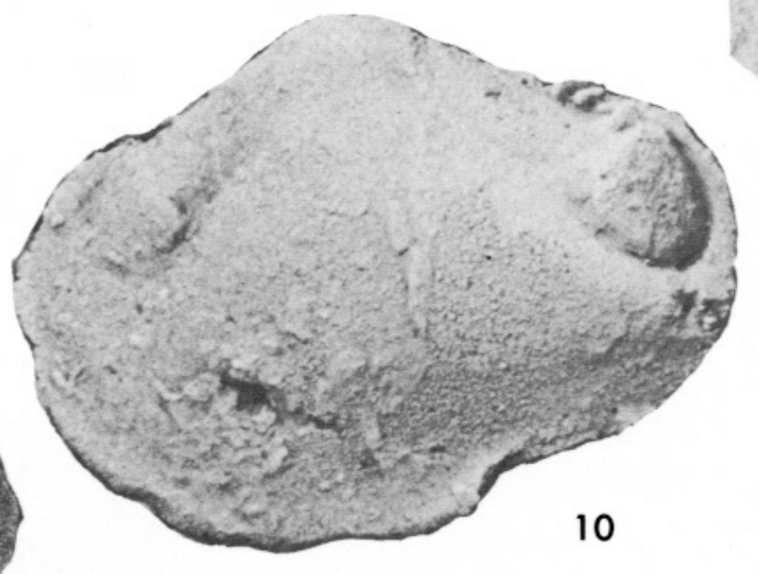
6

7

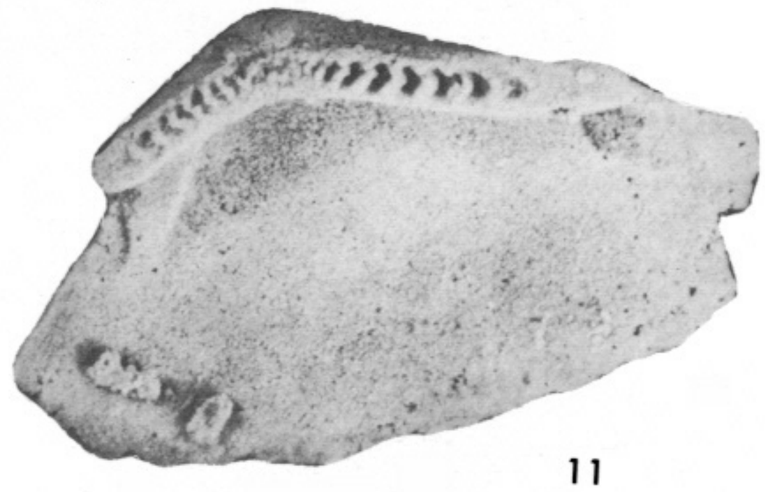
8



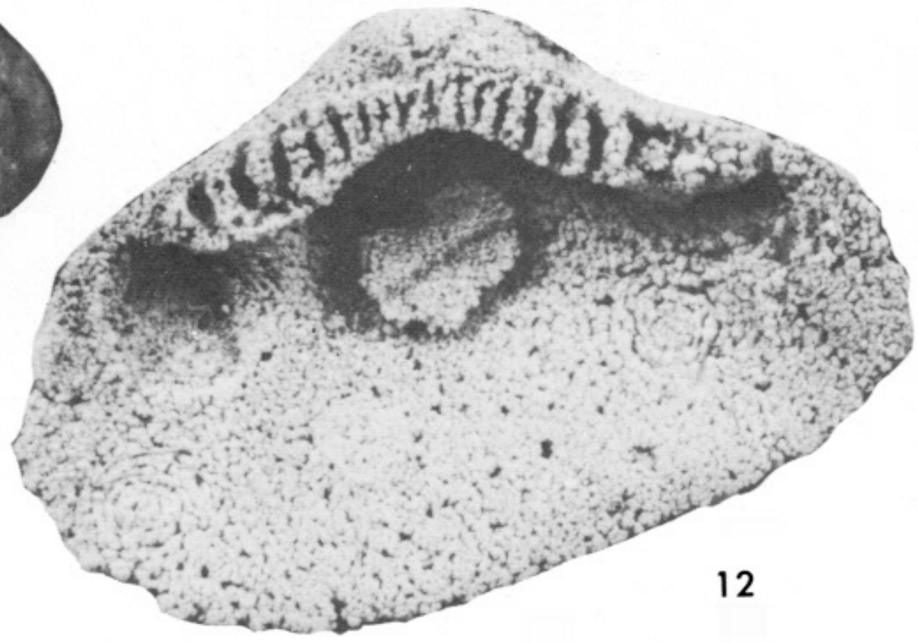
9



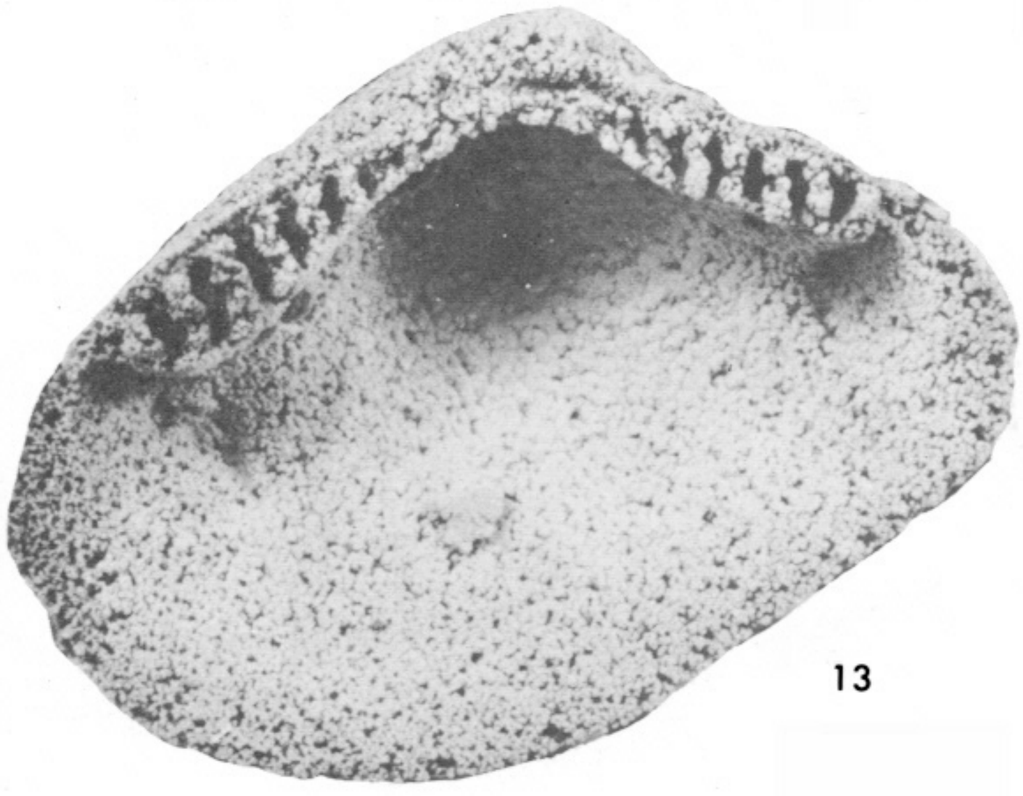
10



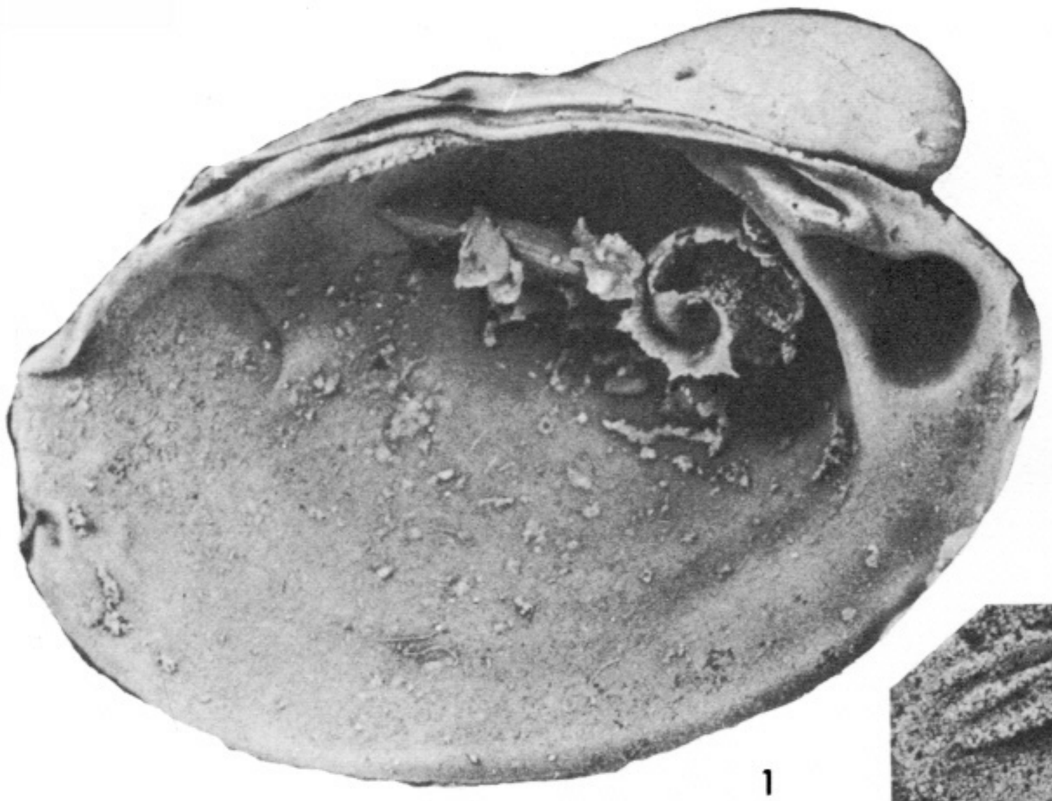
11



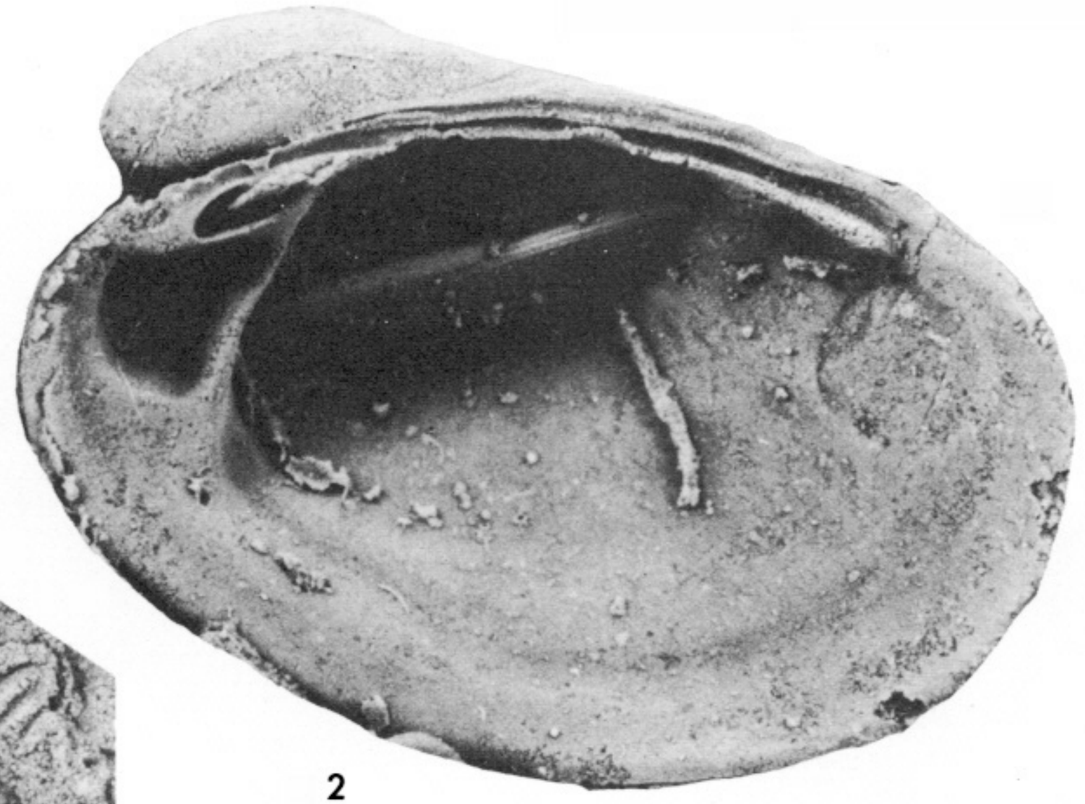
12



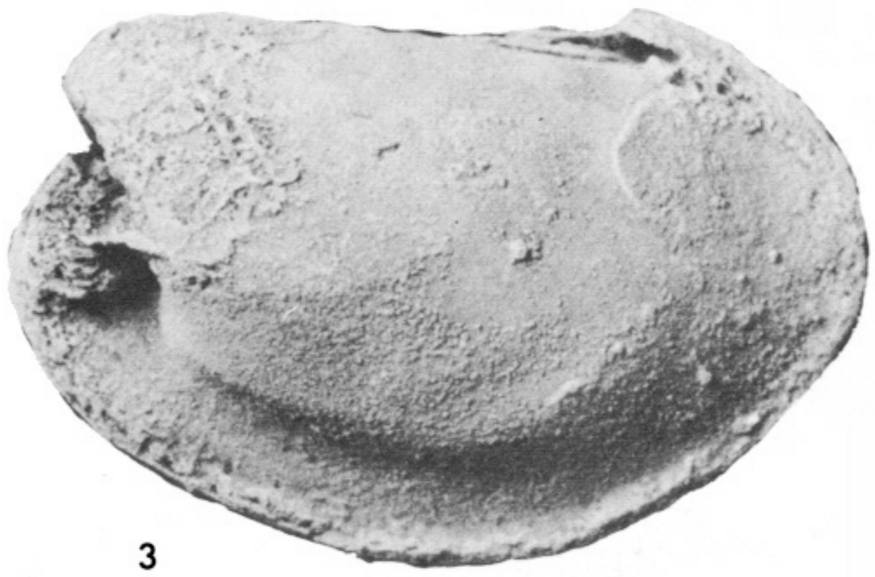
13



1

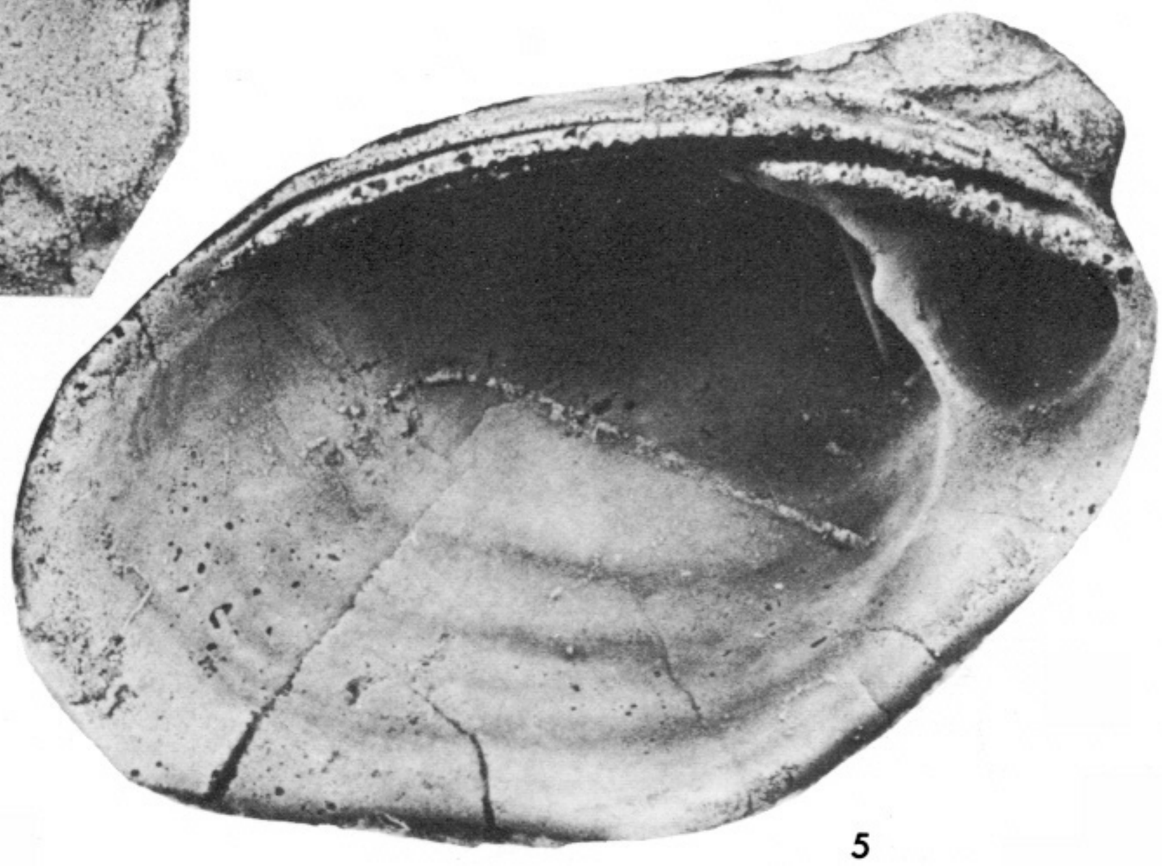


2



3

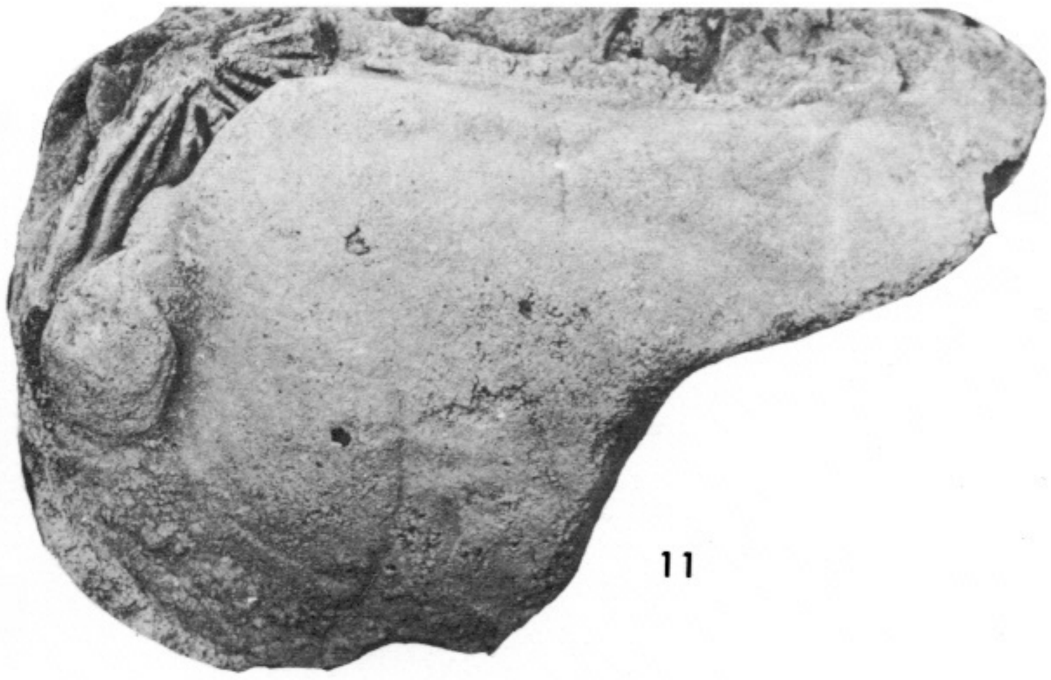
6



5

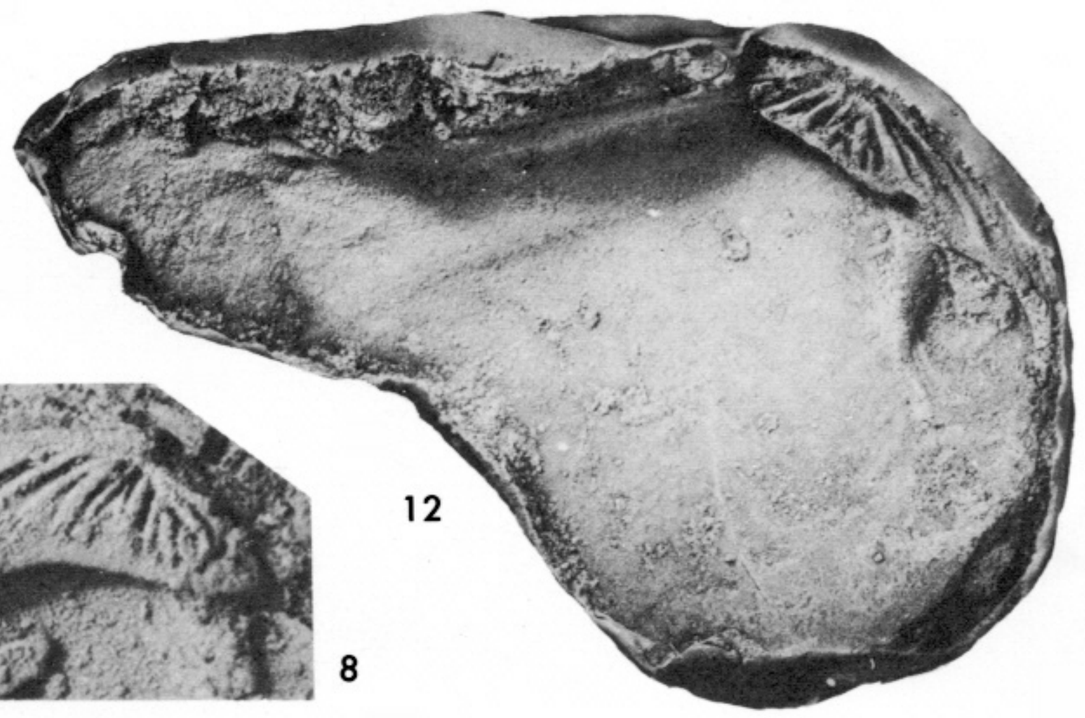
4

7

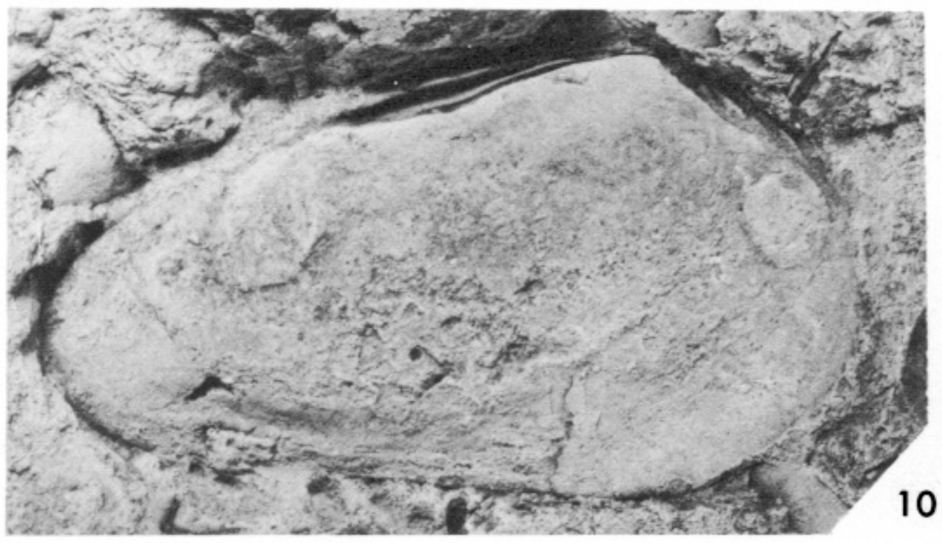


11

9



12



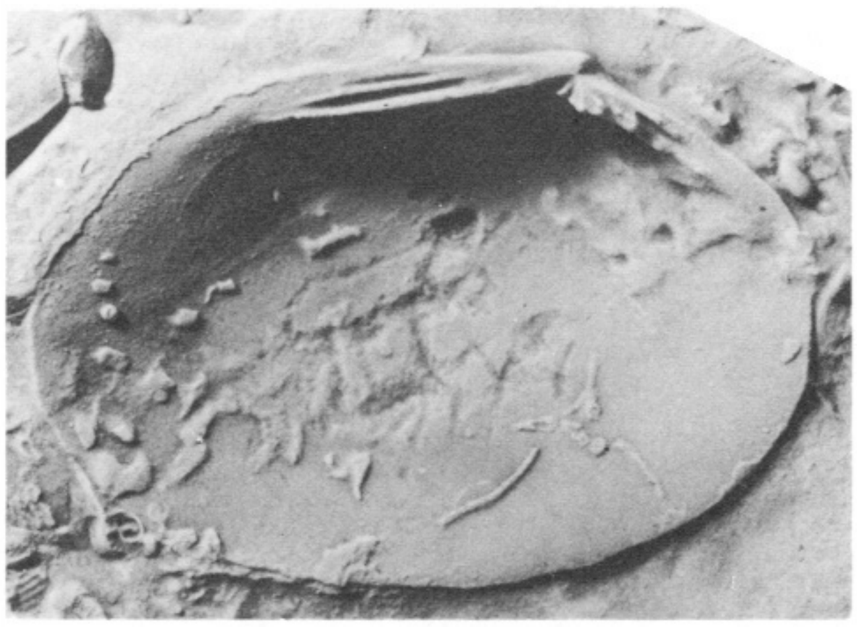
10

8

1

2

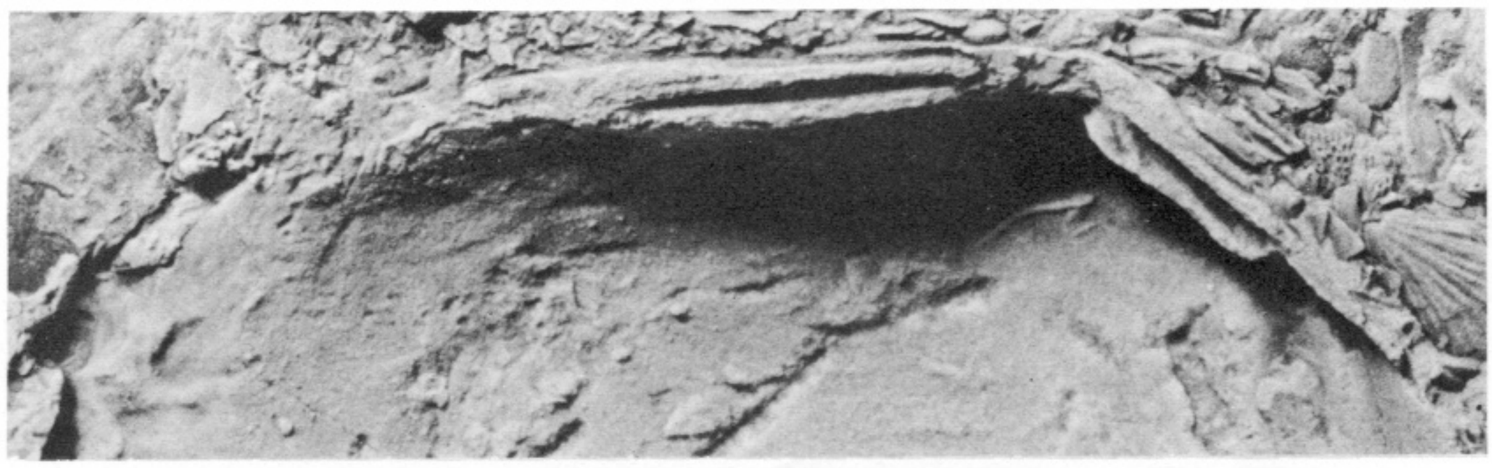
3



4

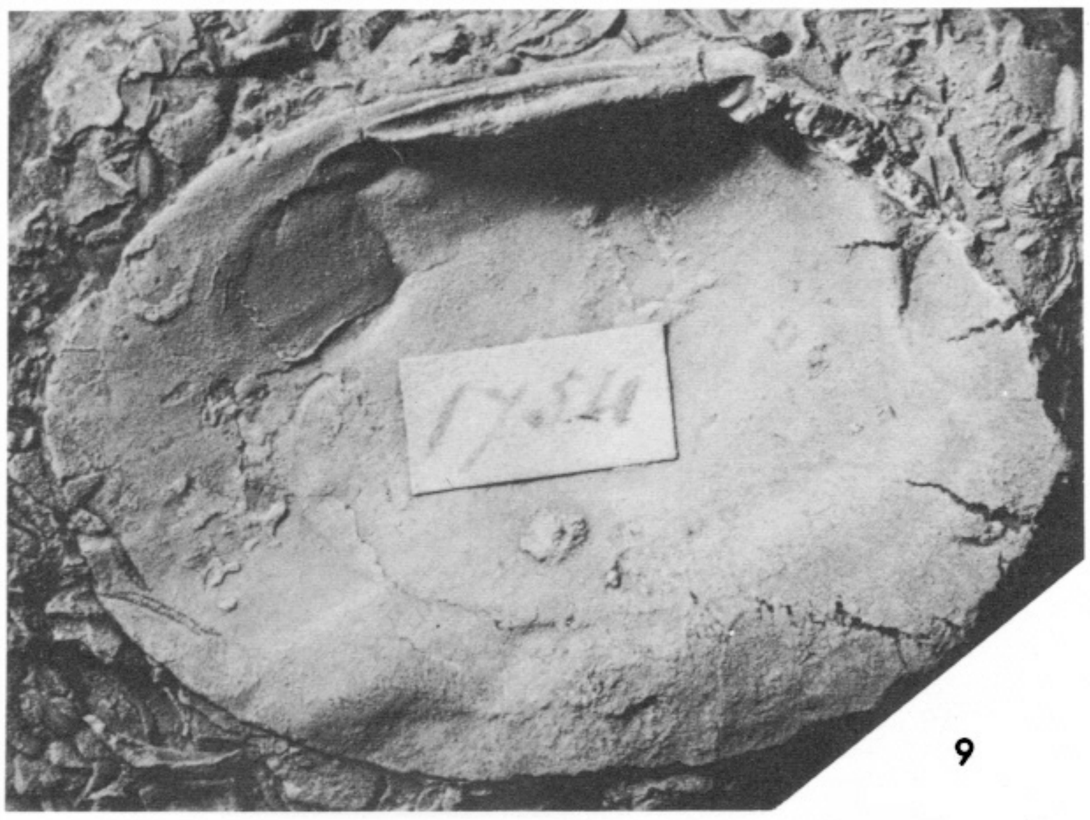
5

6



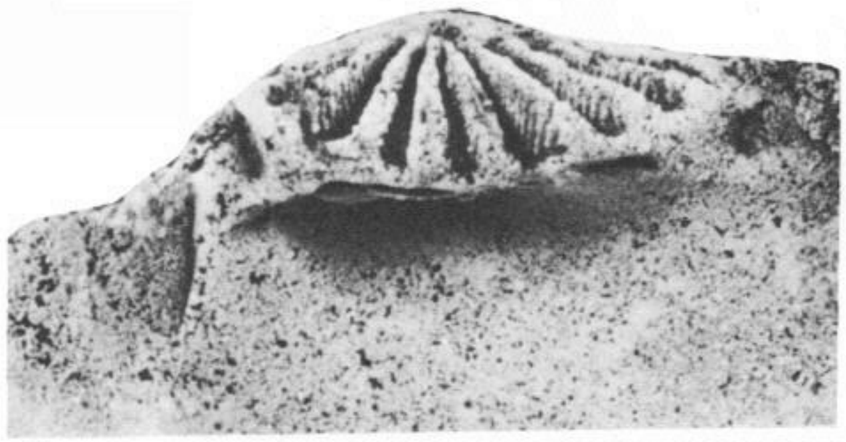
7

8

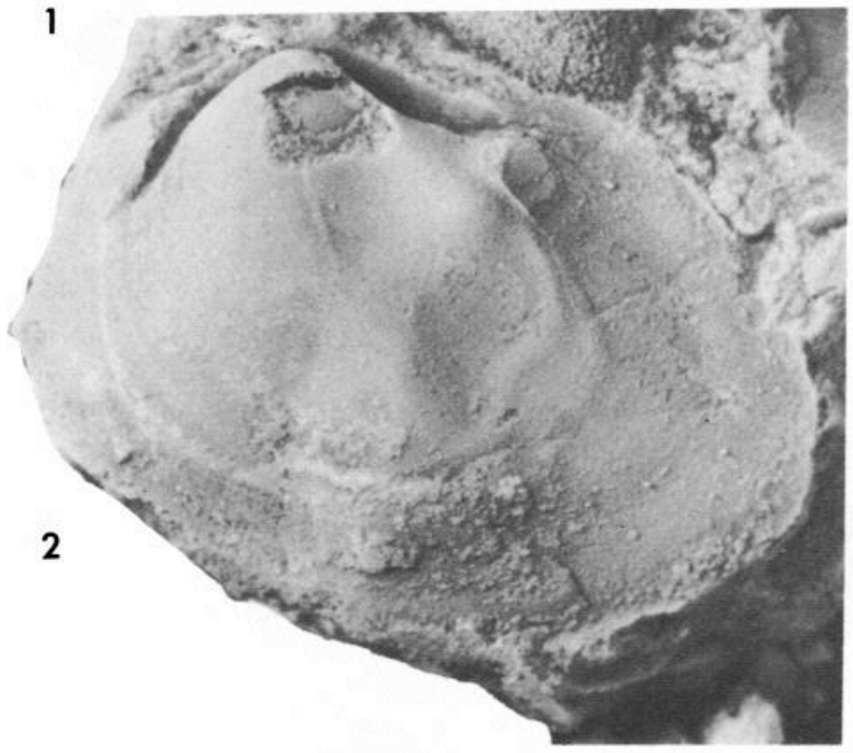


9

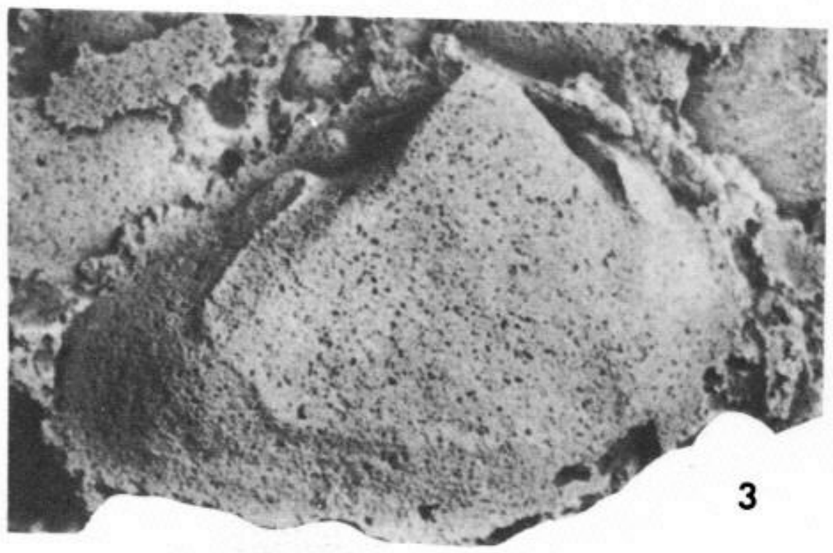
10



1

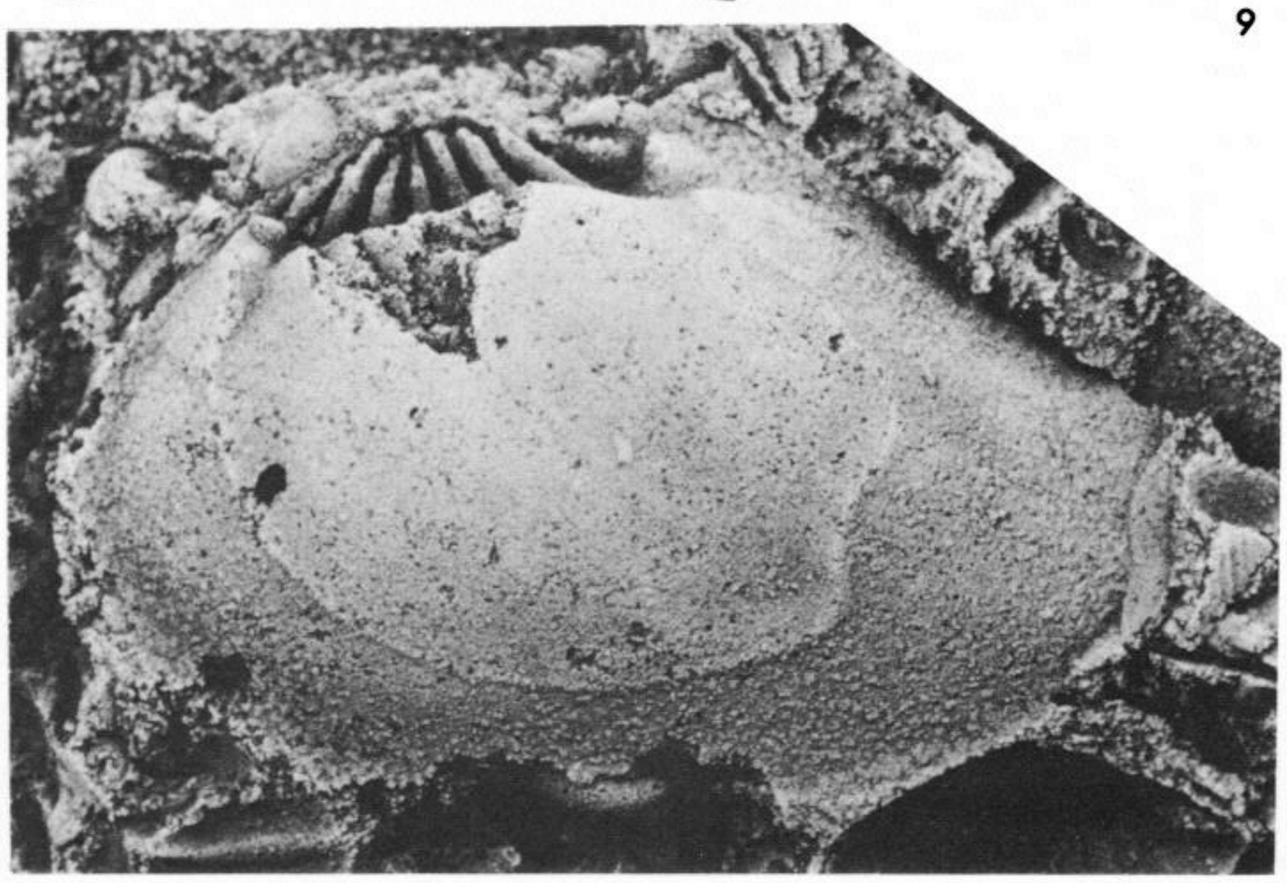


2



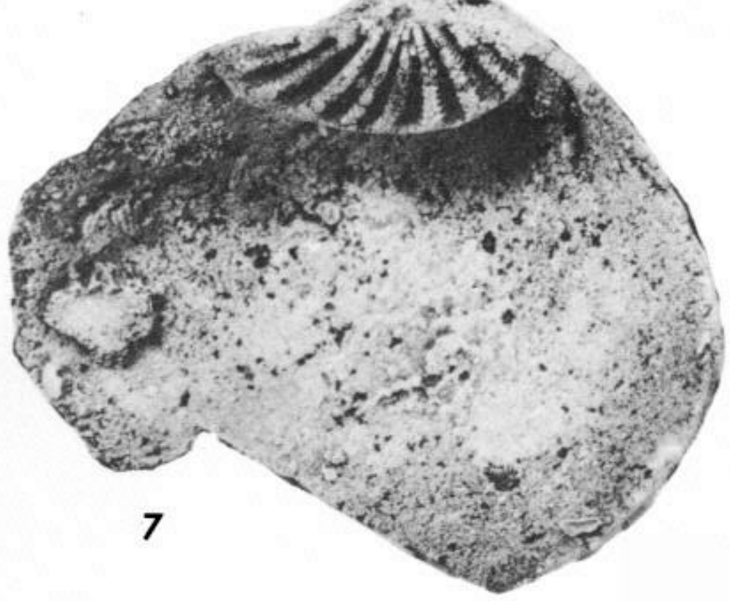
3

4



5

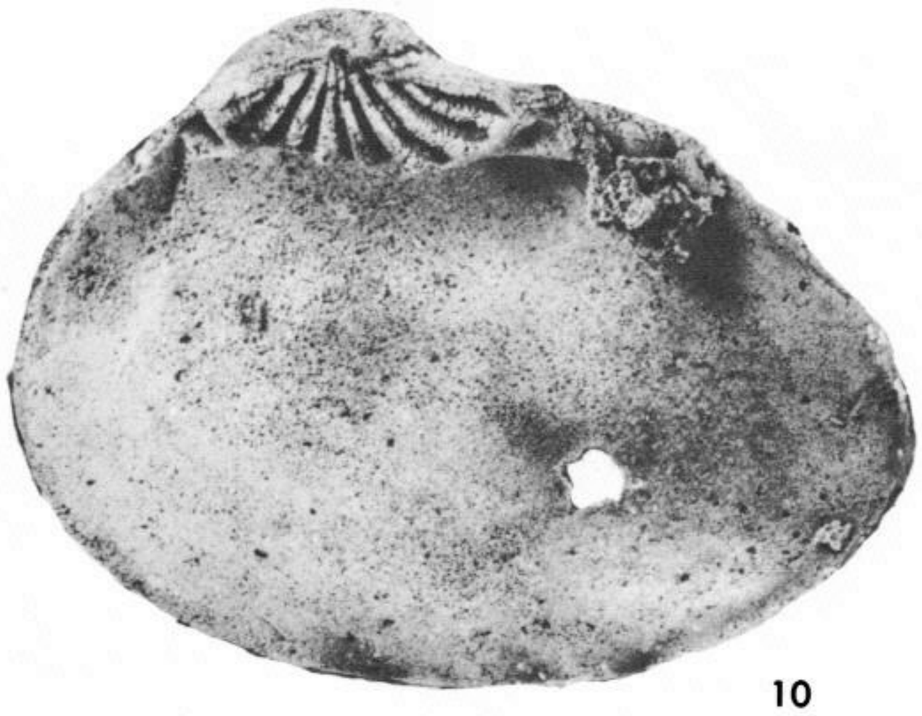
6



7

8

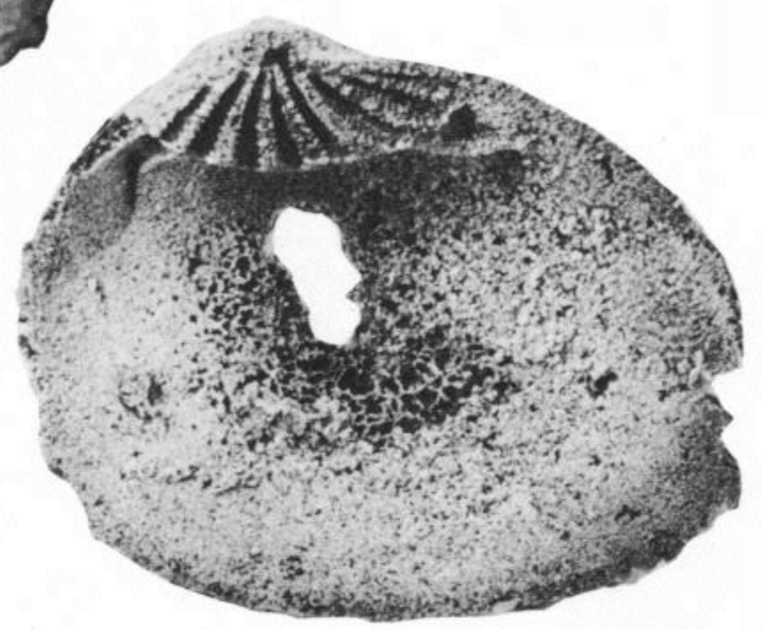
9



10

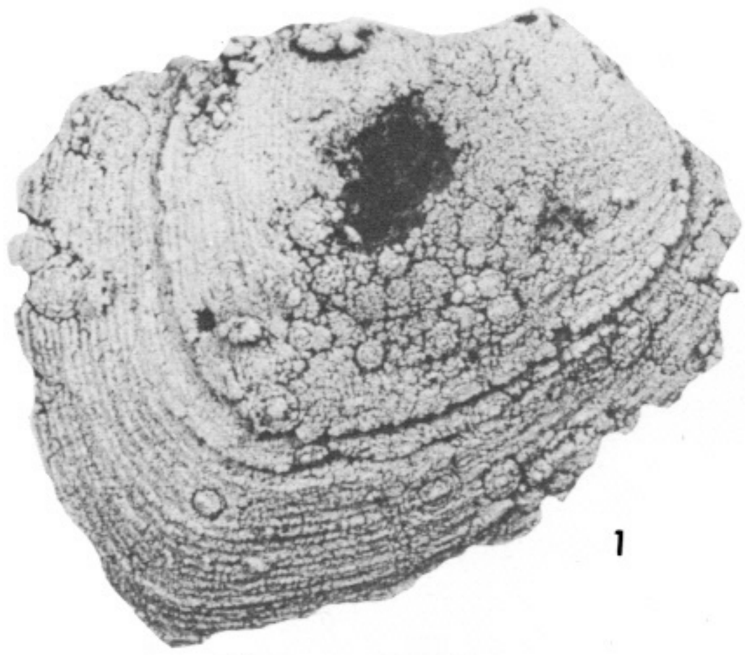
11

12

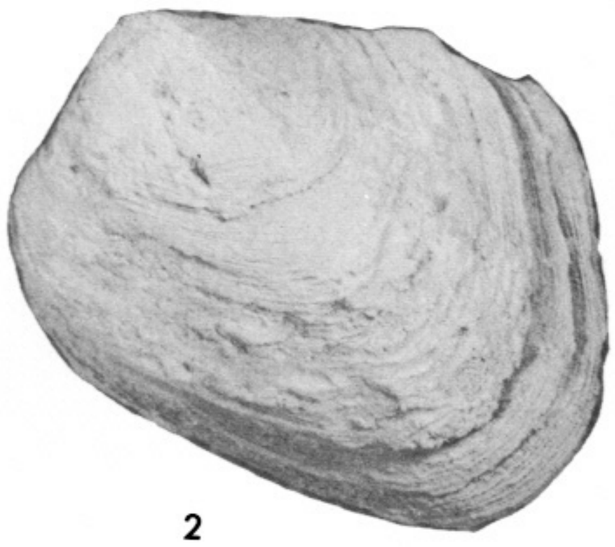


13

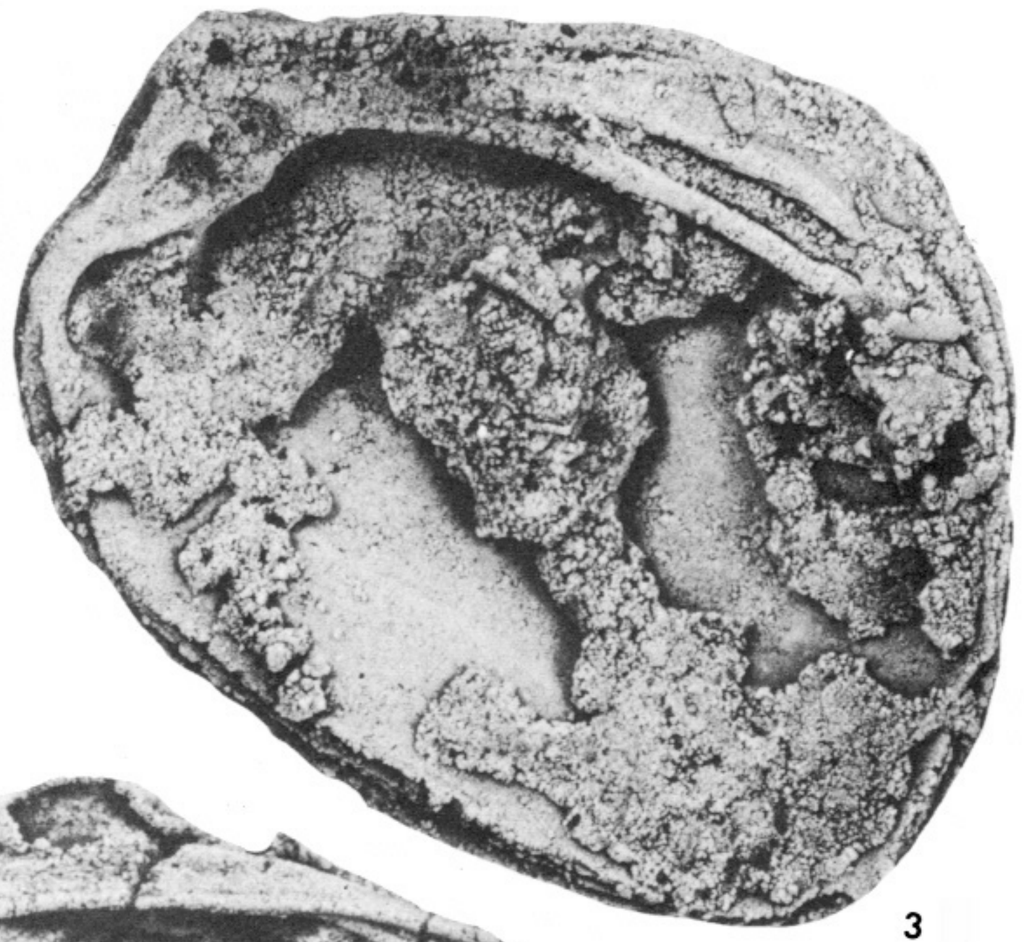
14



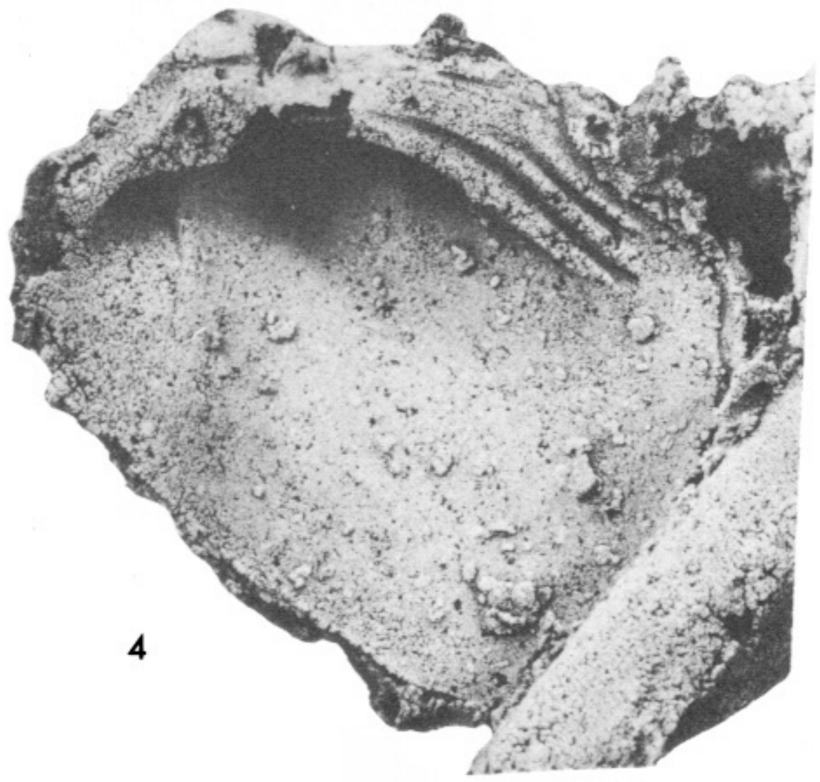
1



2



3



4

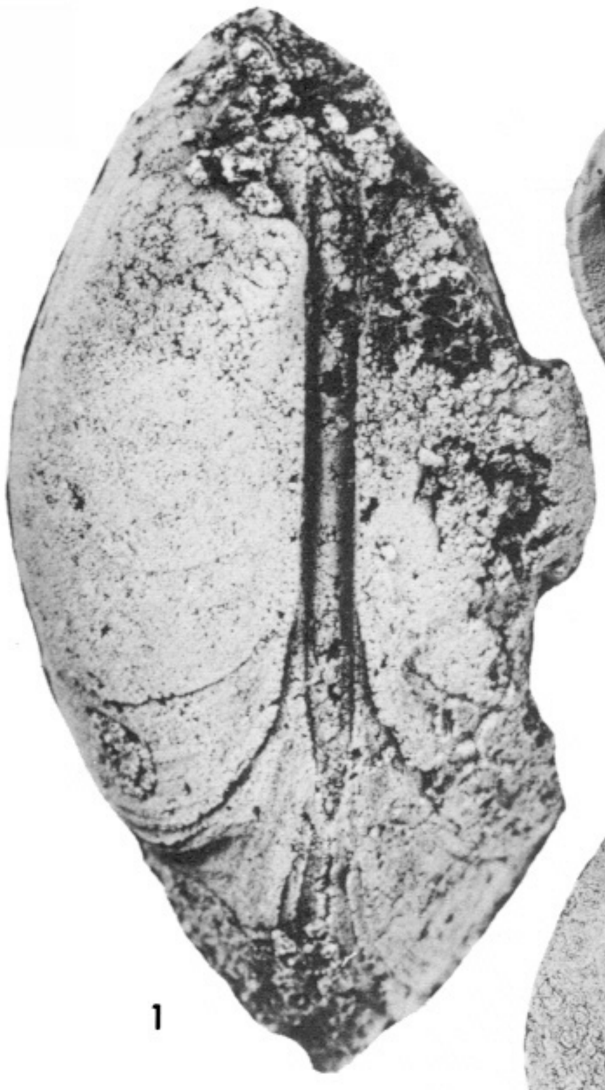
5

6

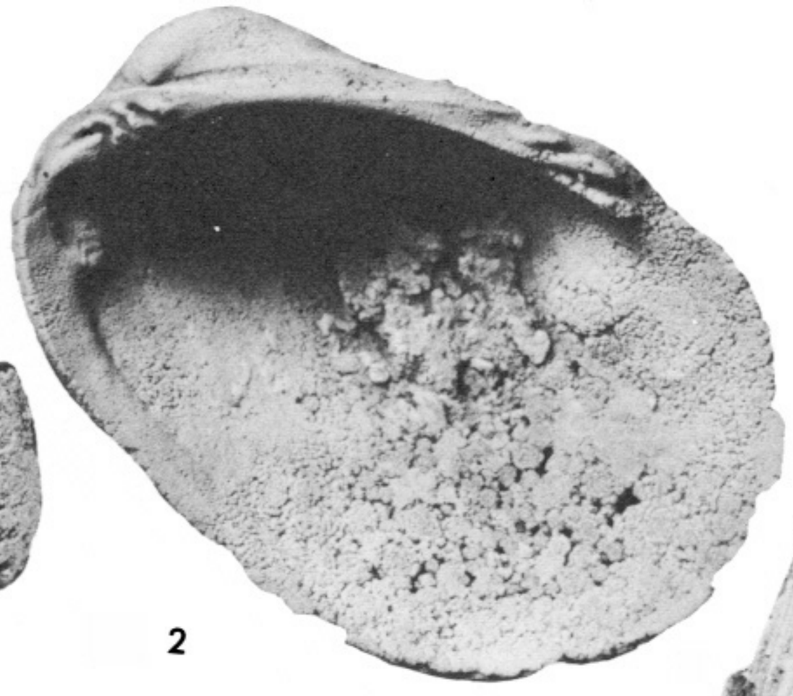
7

8

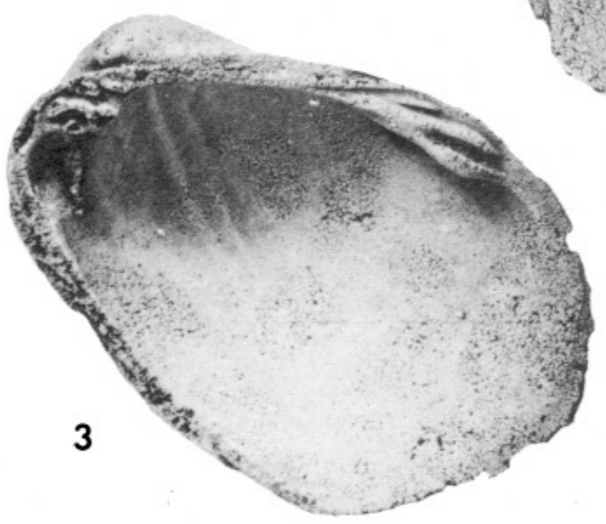
9



1



2

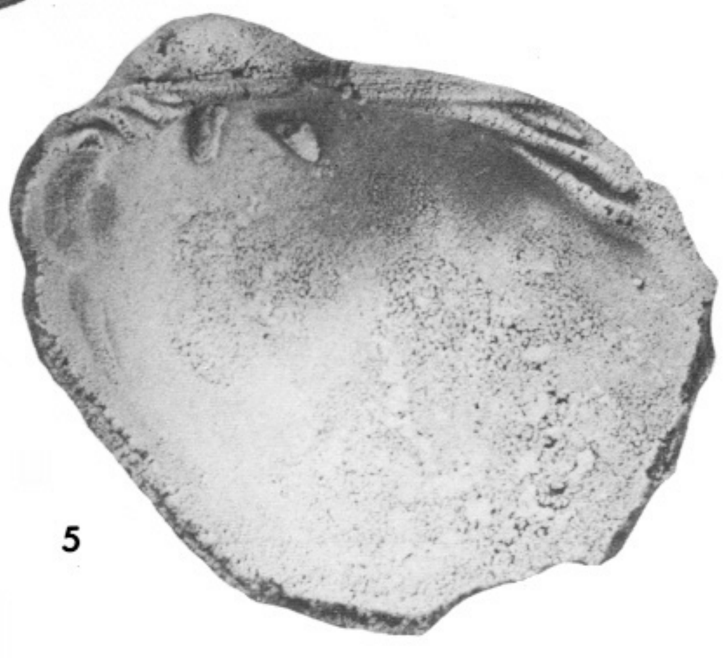


3

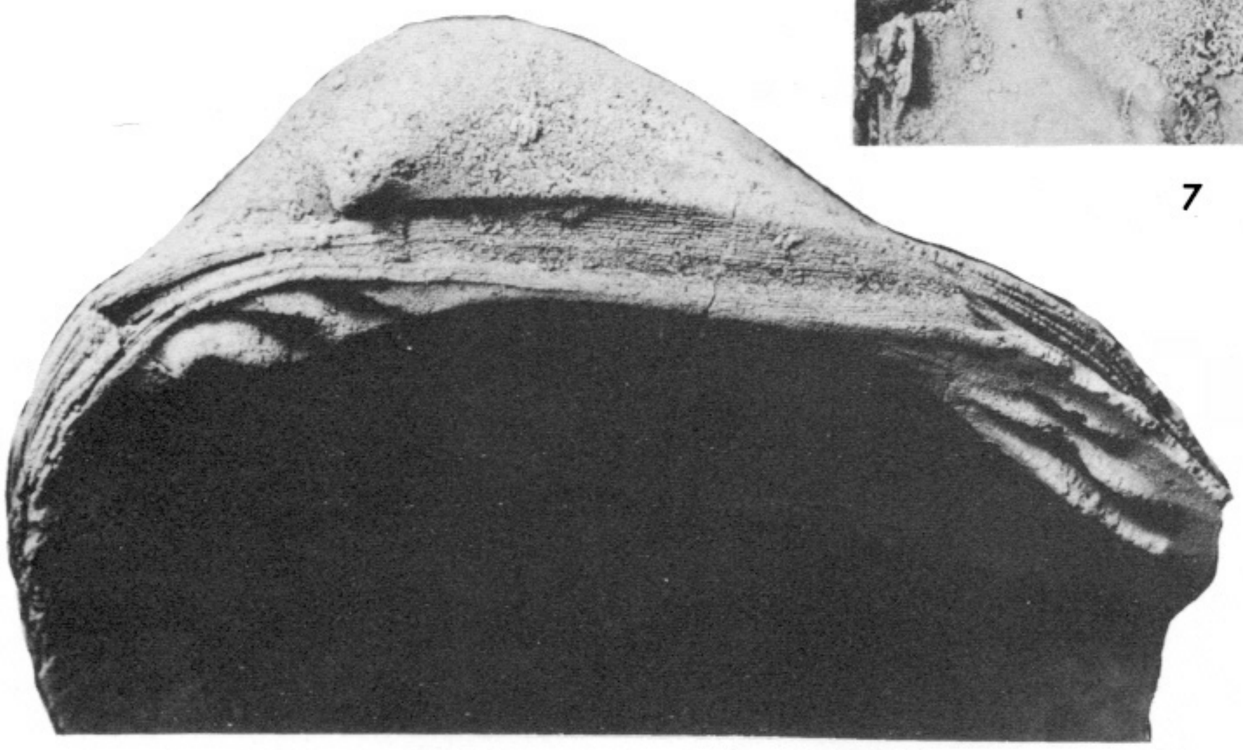
4

7

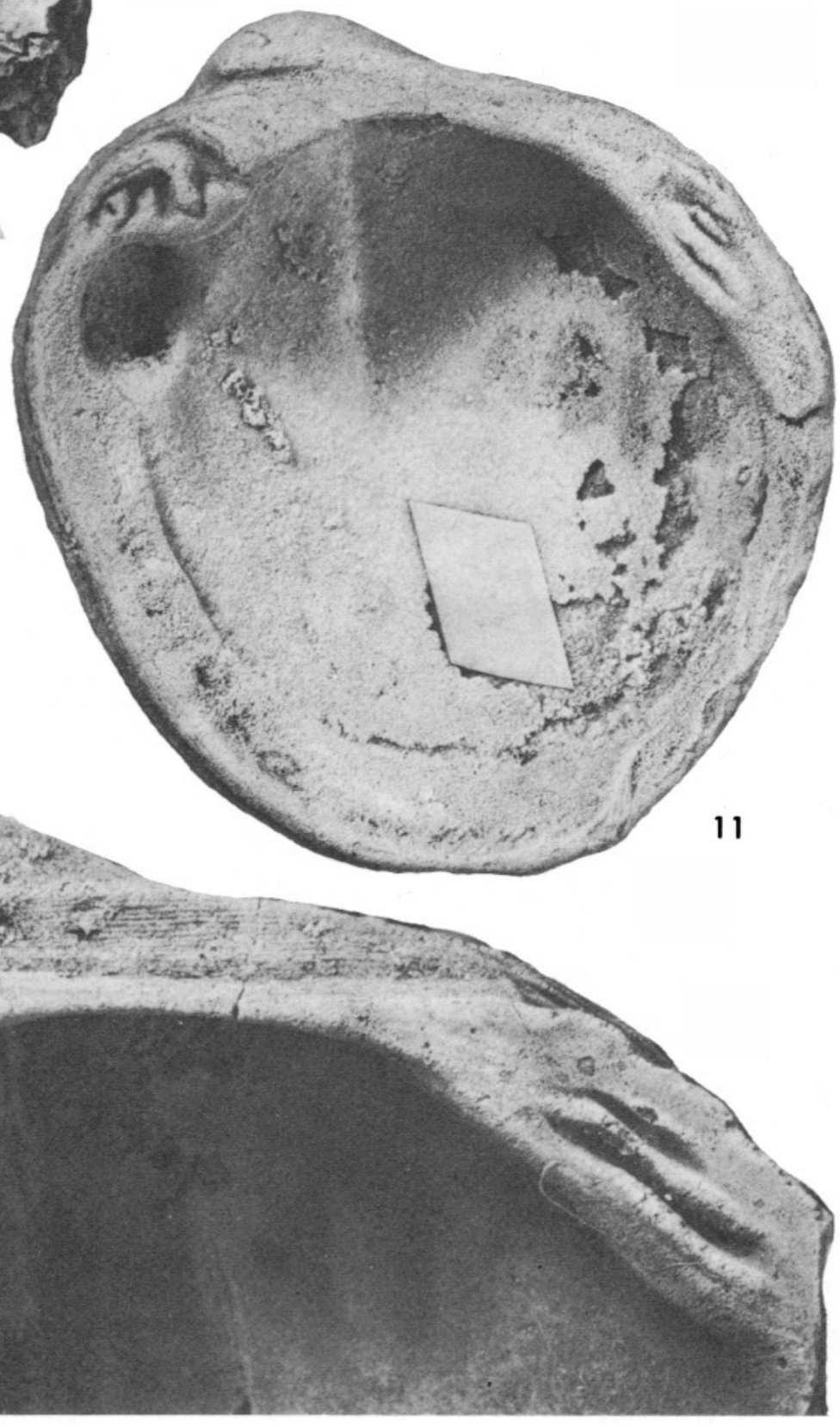
6



5

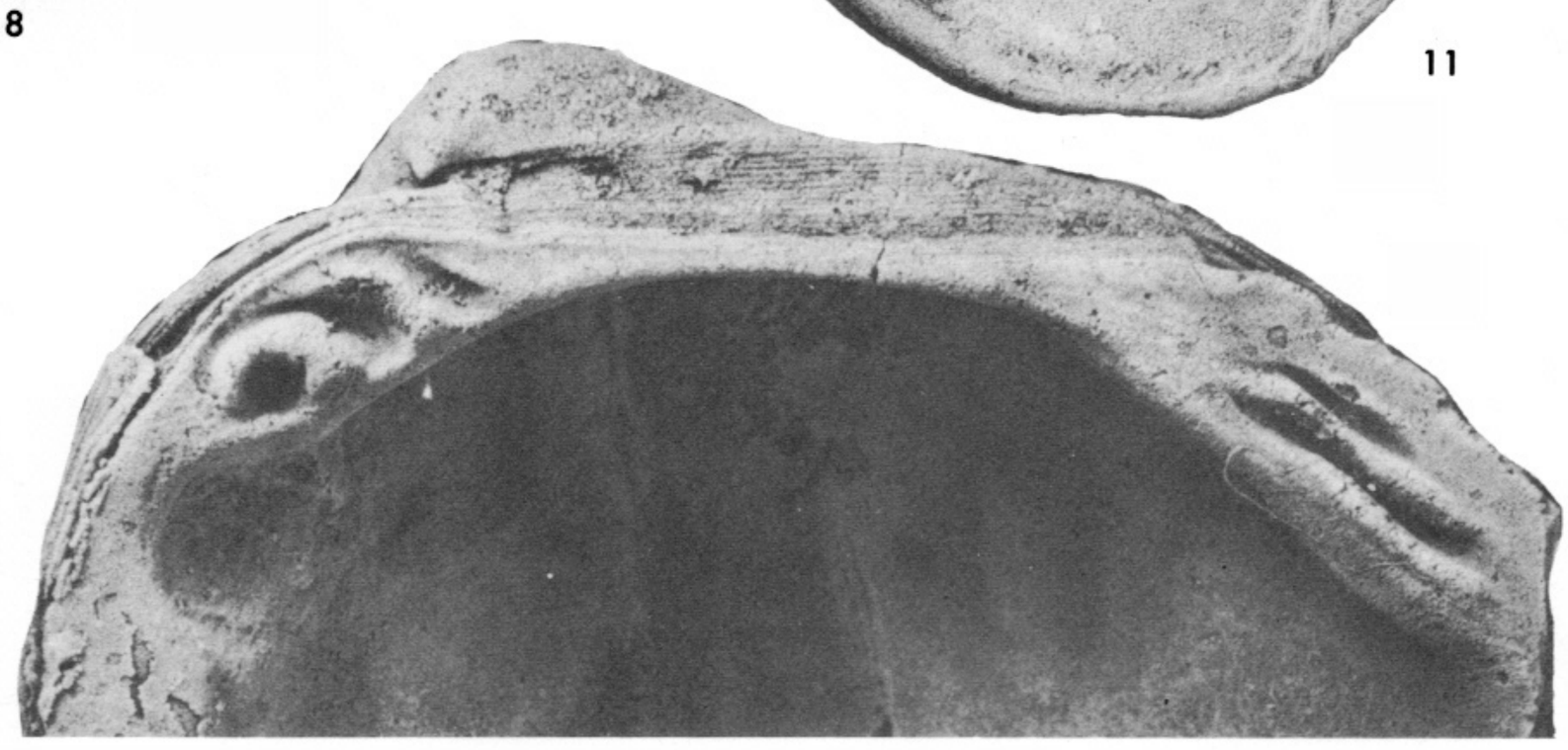


8

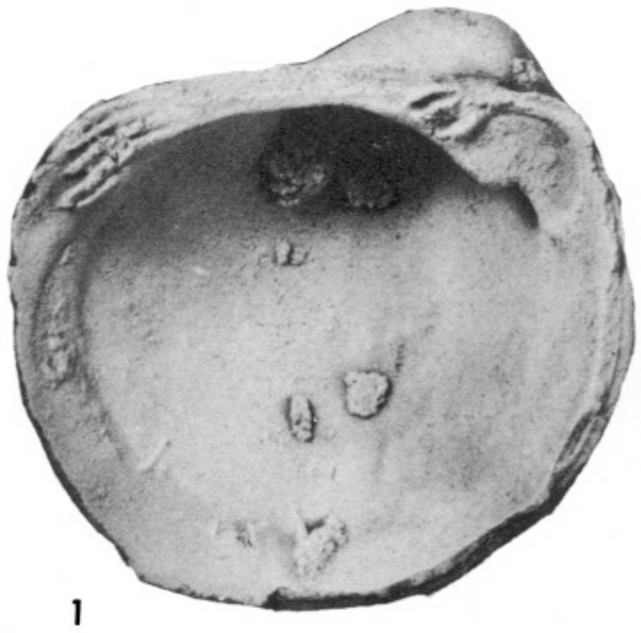


11

10

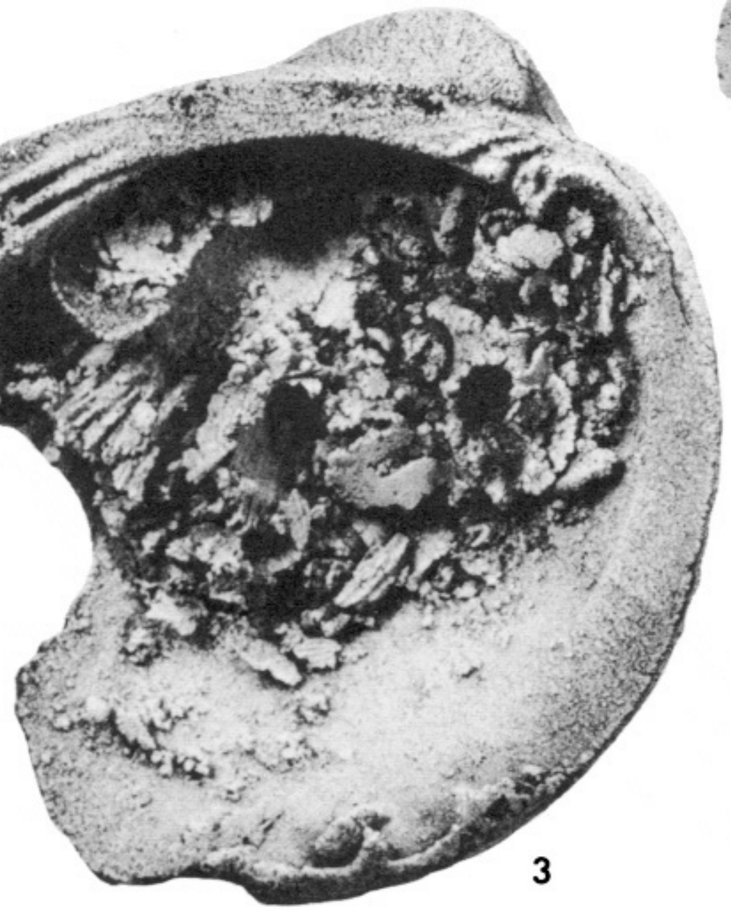


9



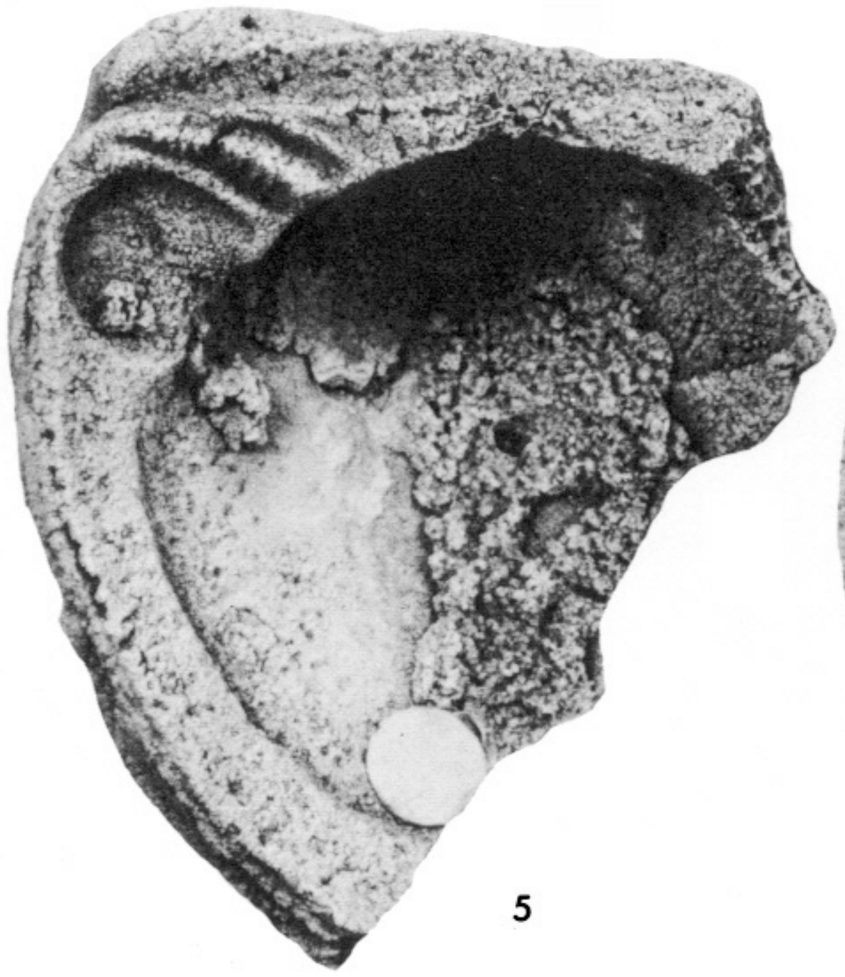
1

2



3

4



5

6

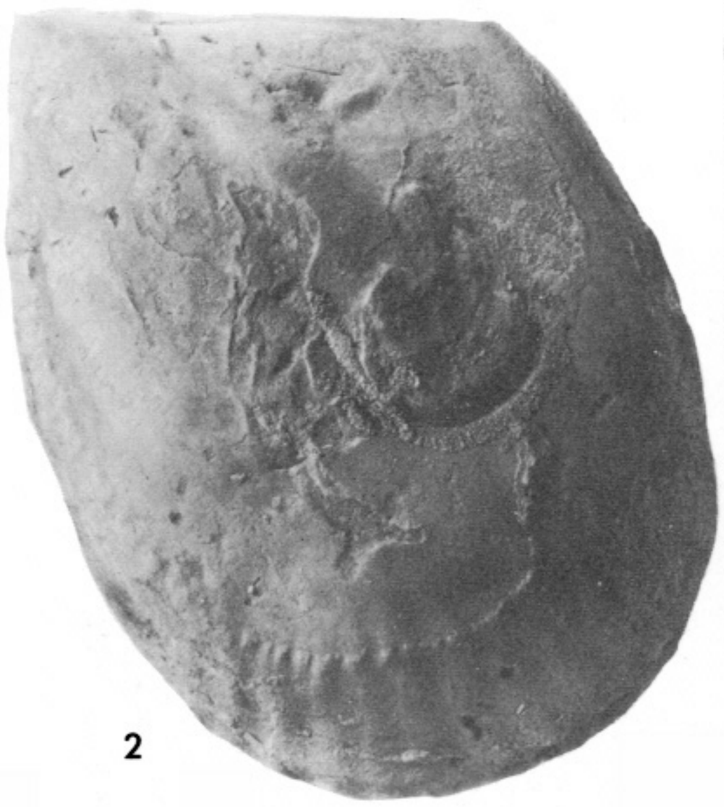
7

8

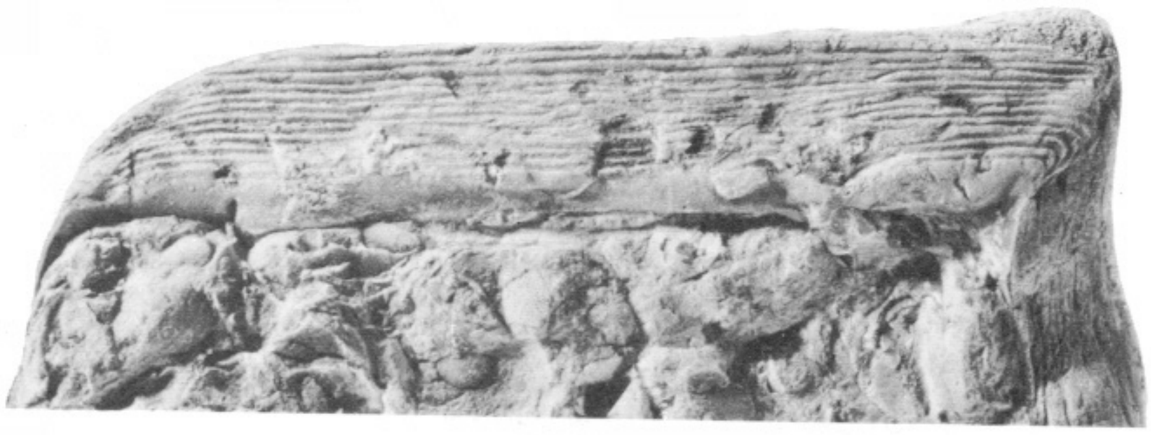
9

10

1

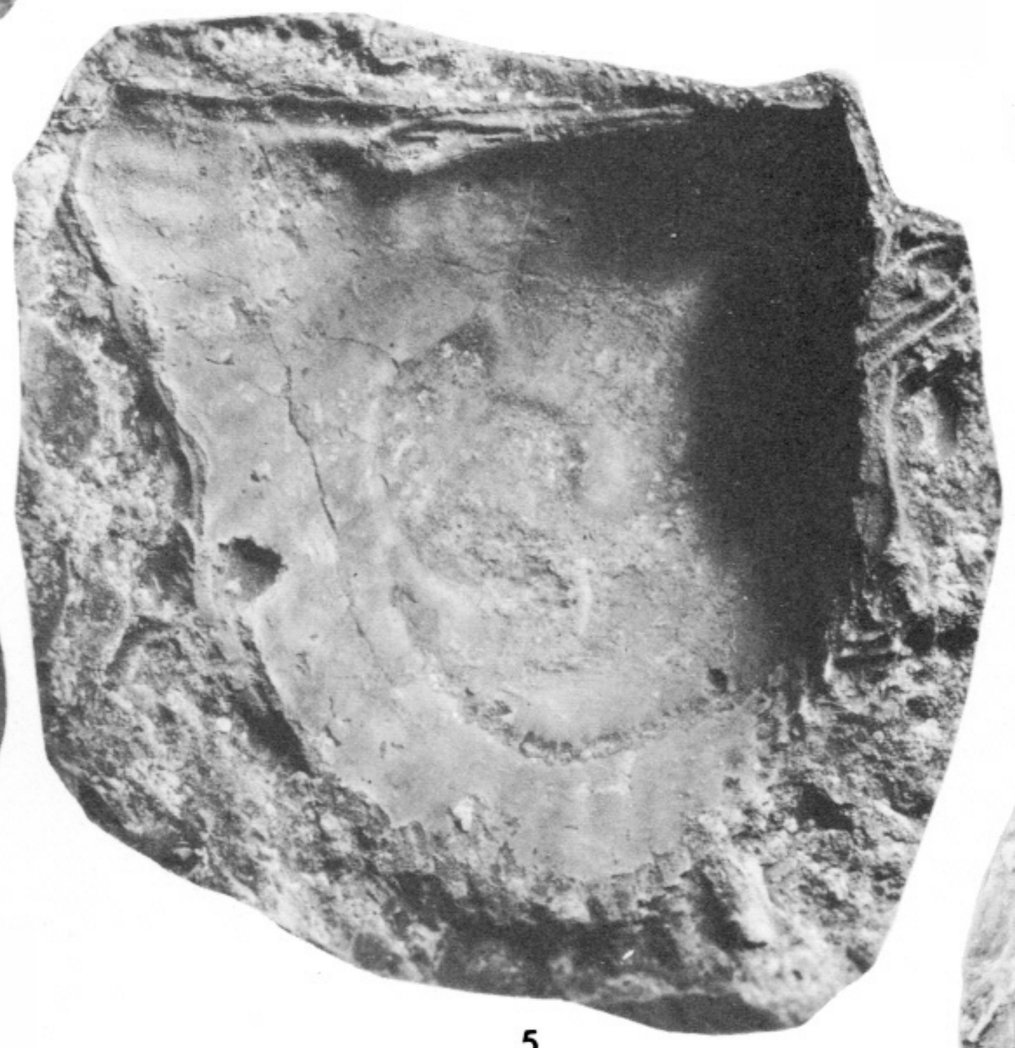


2

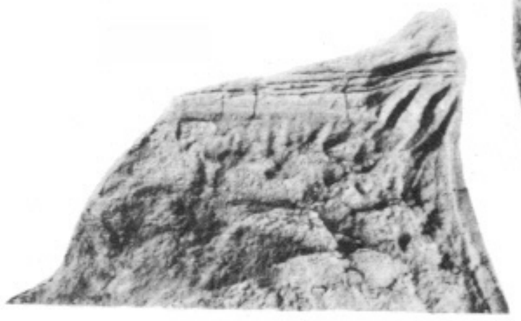


3

4



5

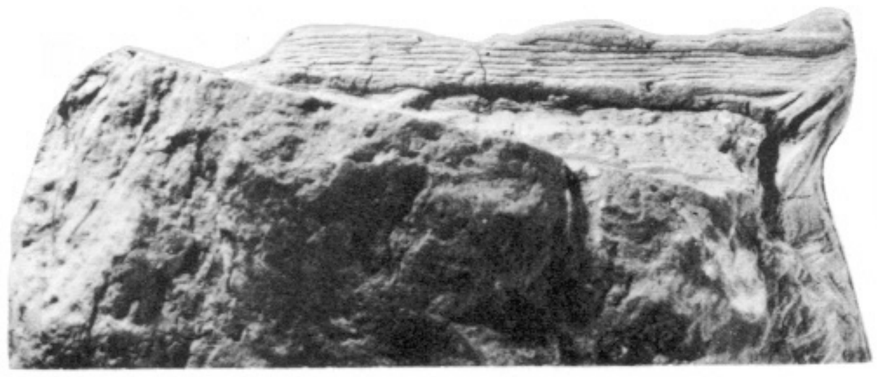


6

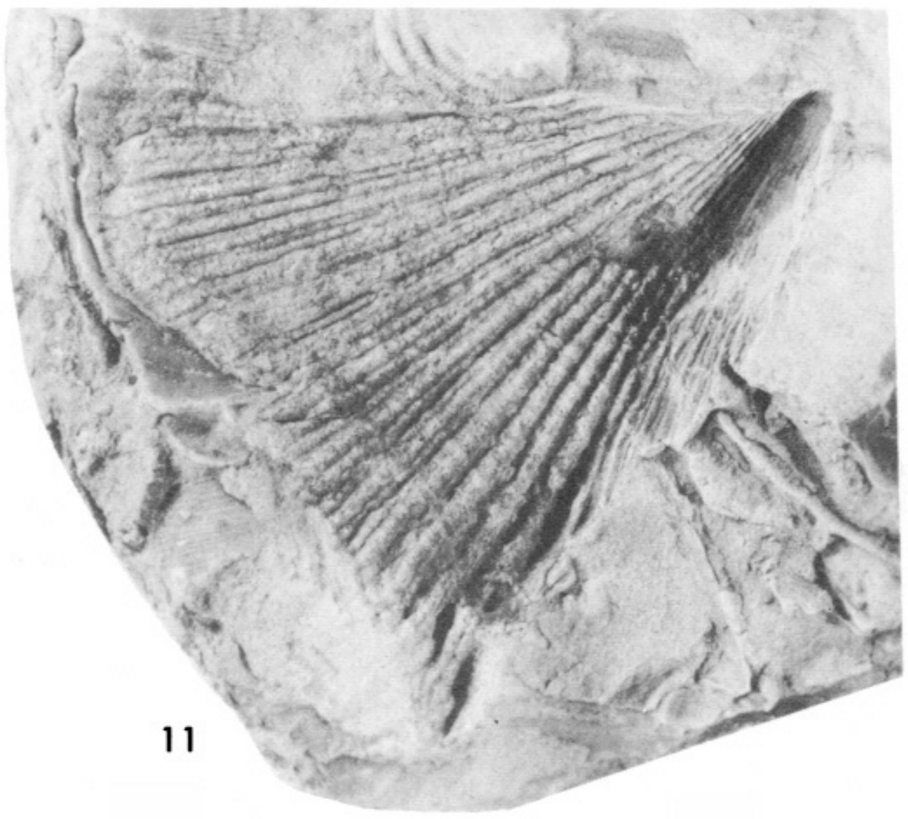
7

8

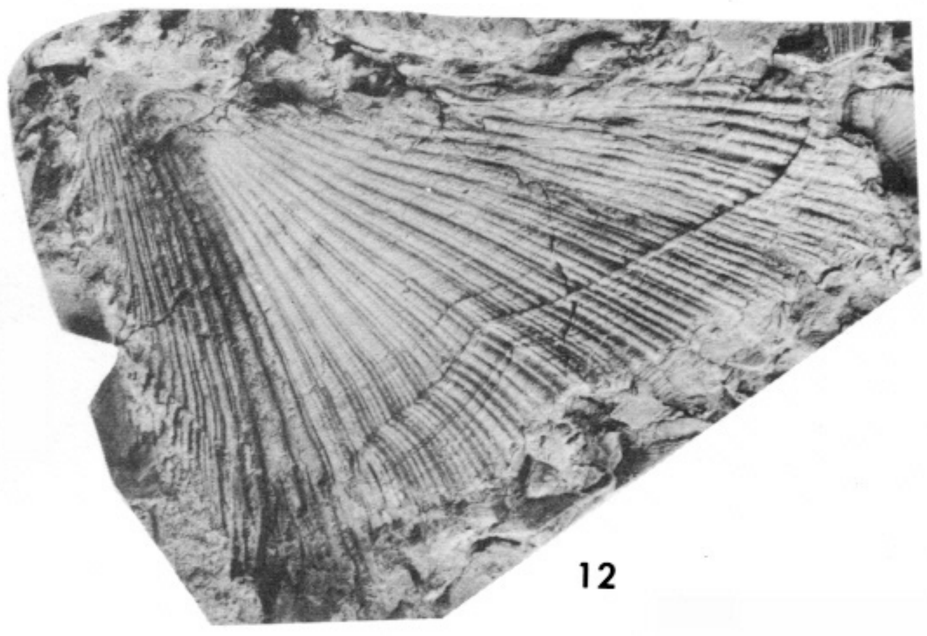
9



10



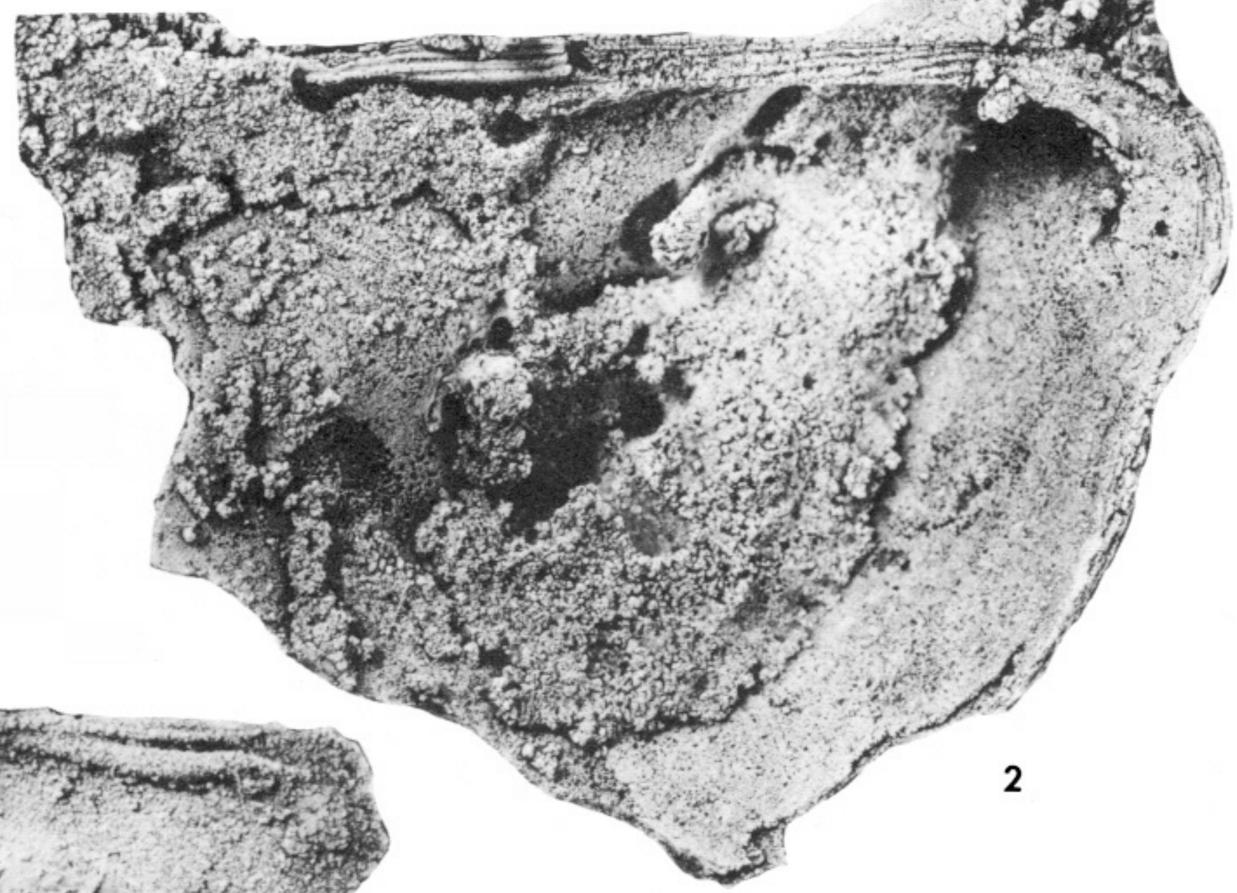
11



12

13

1



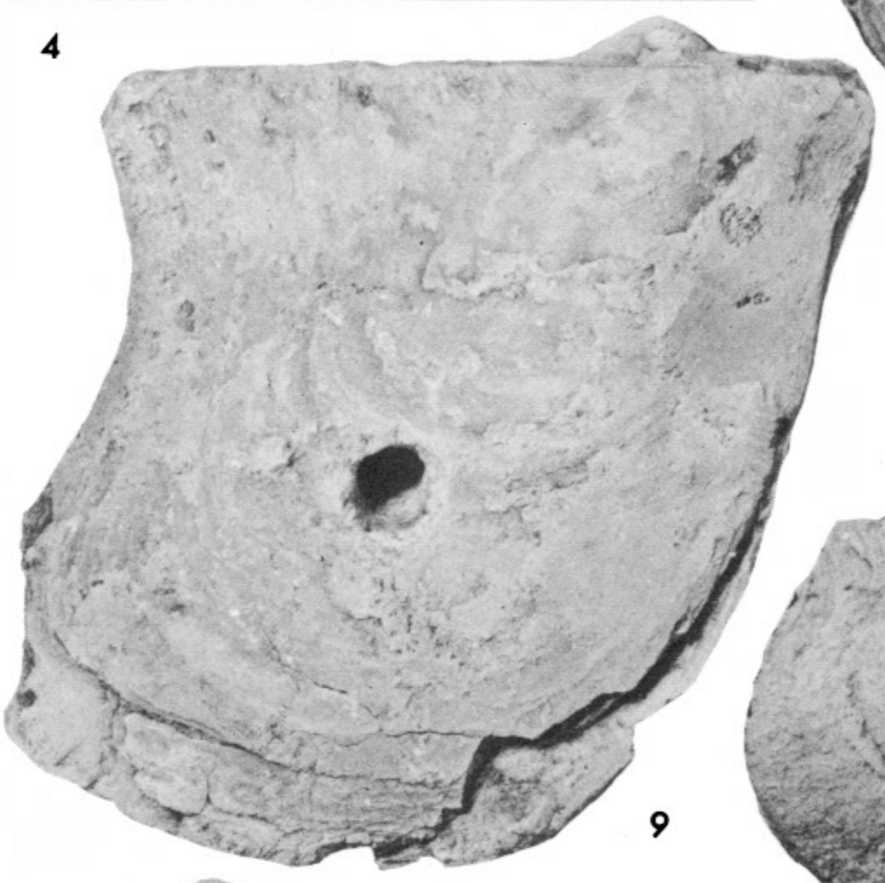
2

3

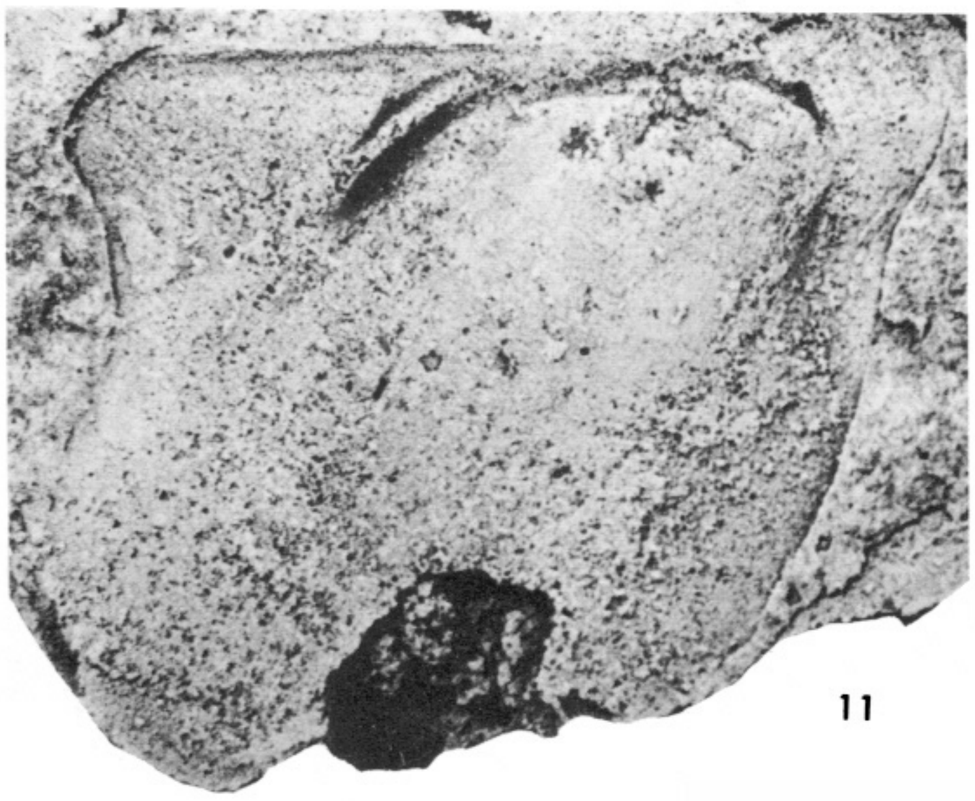
4

5

6



9



11

7

10

8

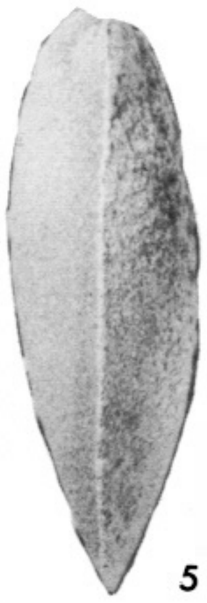
12

1

2

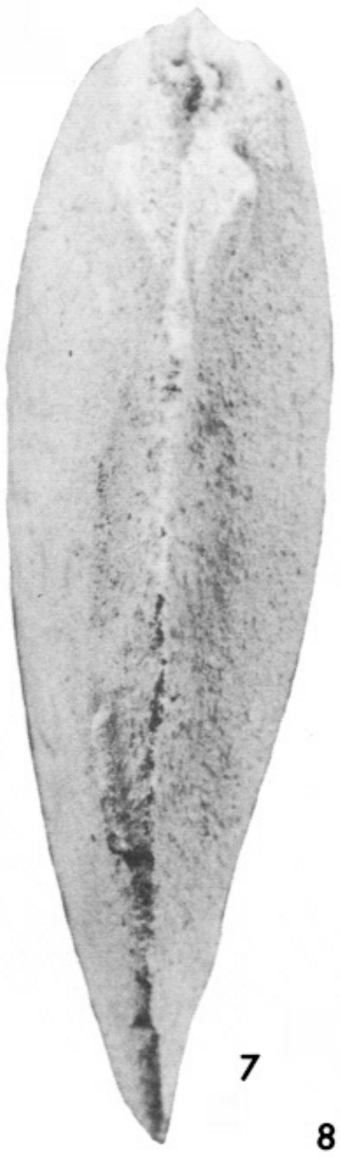
3

4

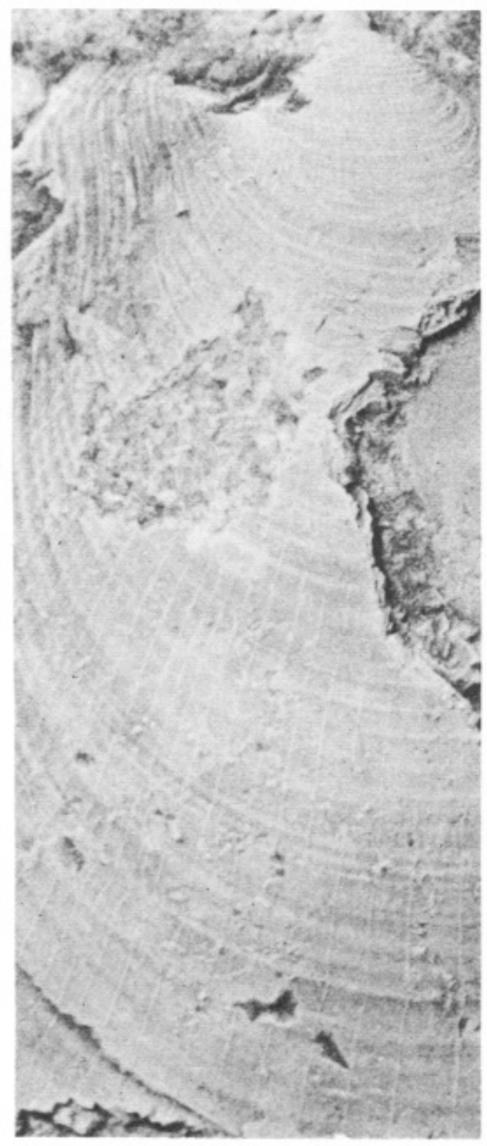


5

6



7



8

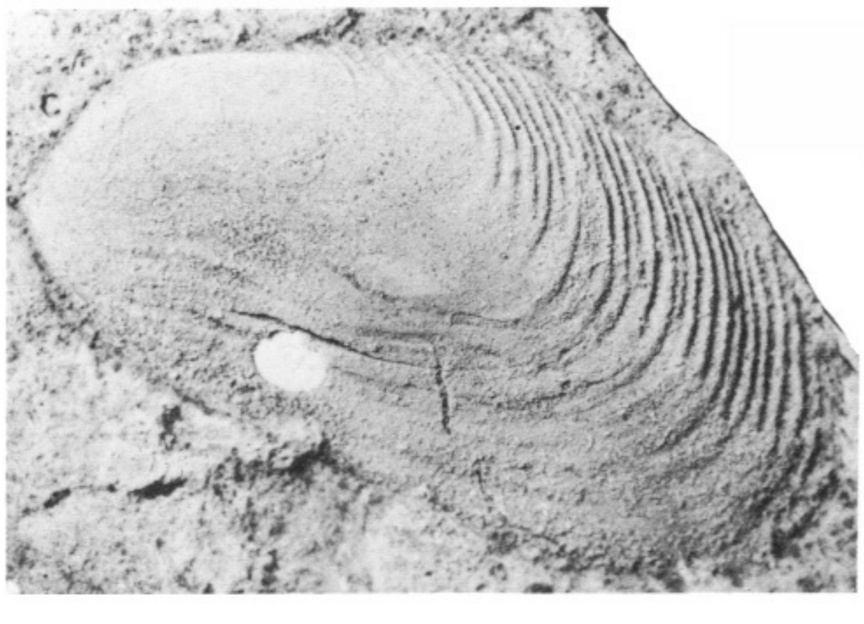
9

10

11

12

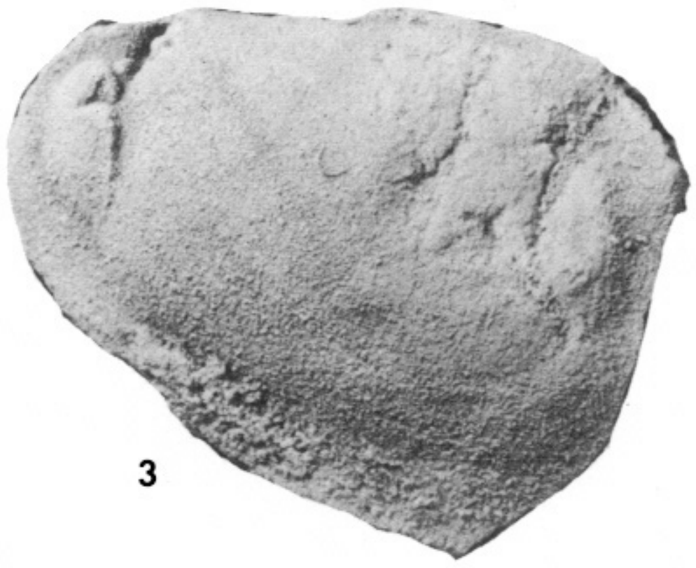
13



14

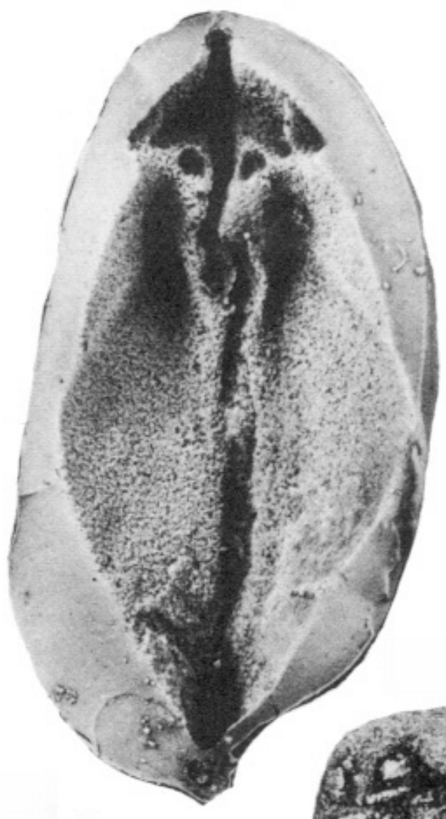
1

2



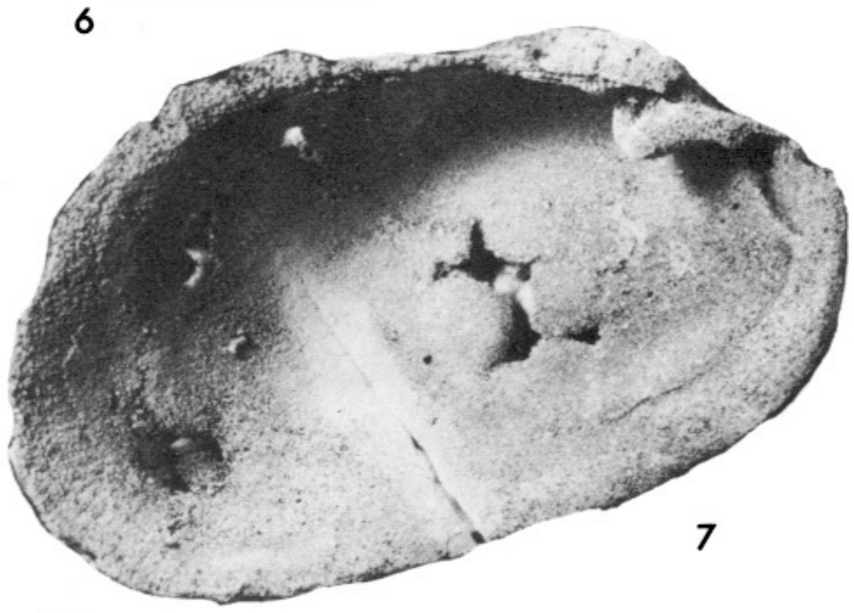
3

4



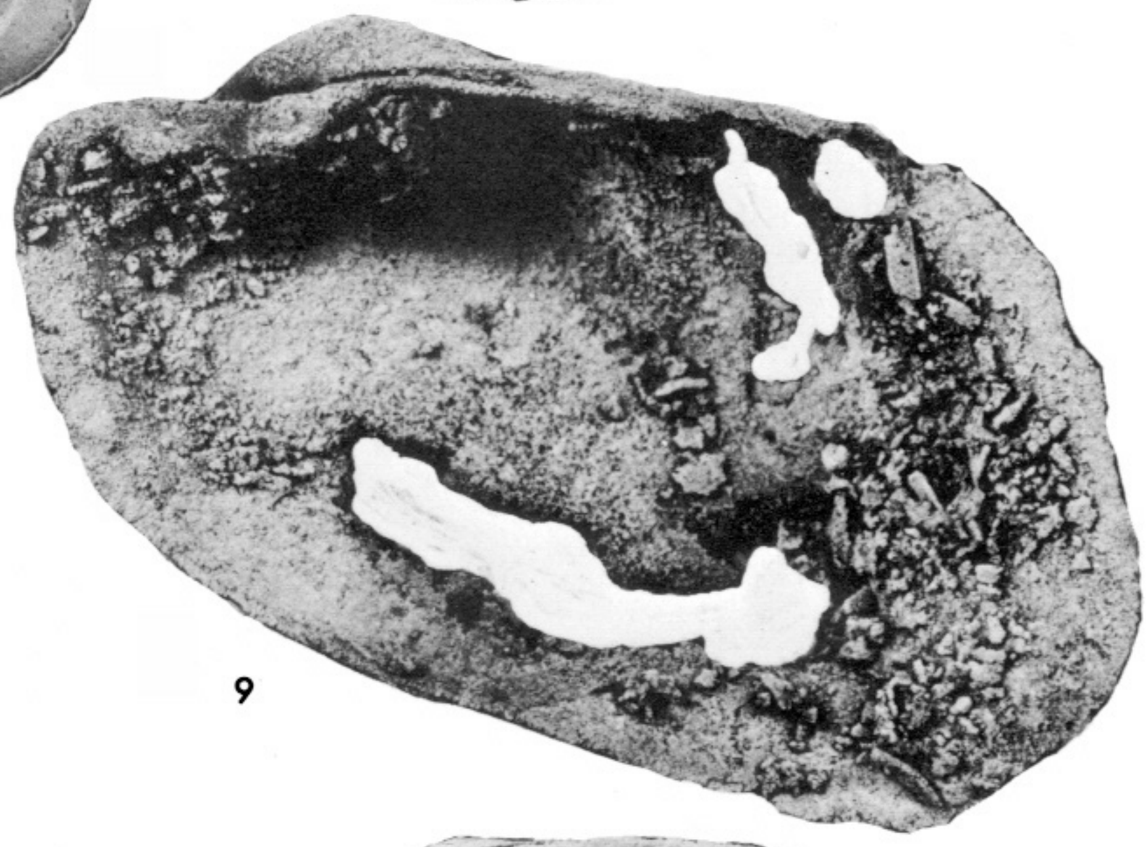
5

6



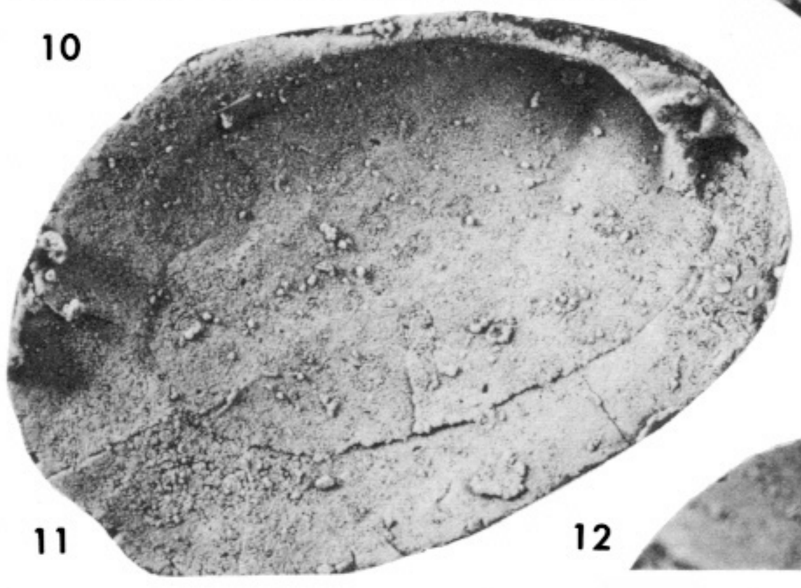
7

8



9

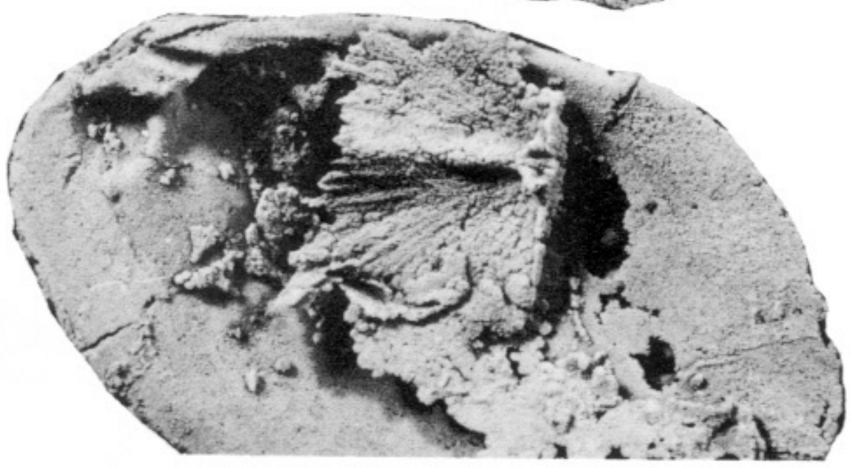
10



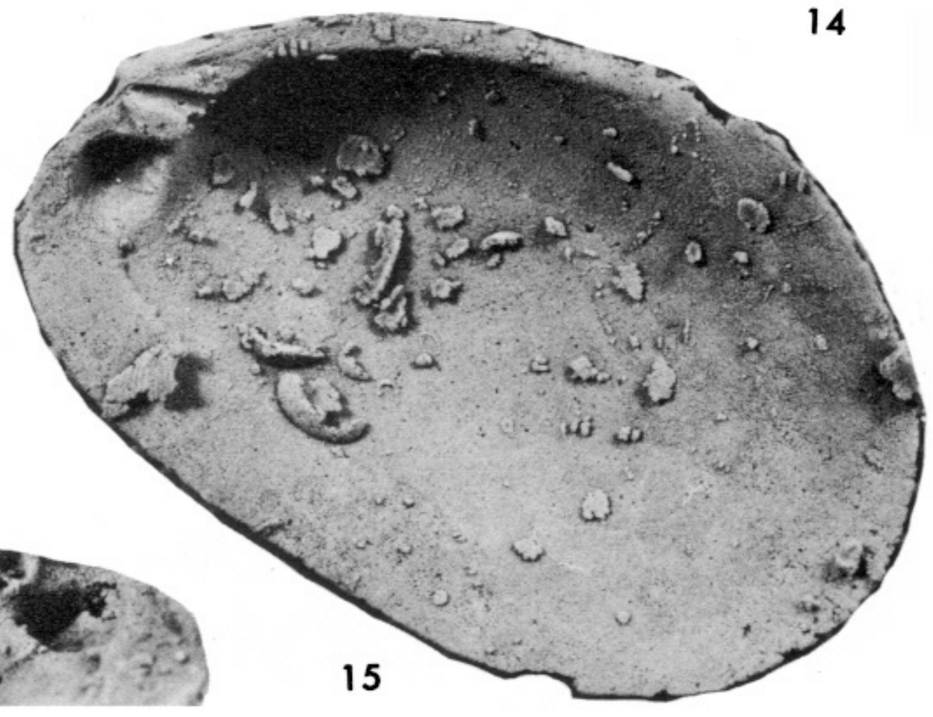
11

12

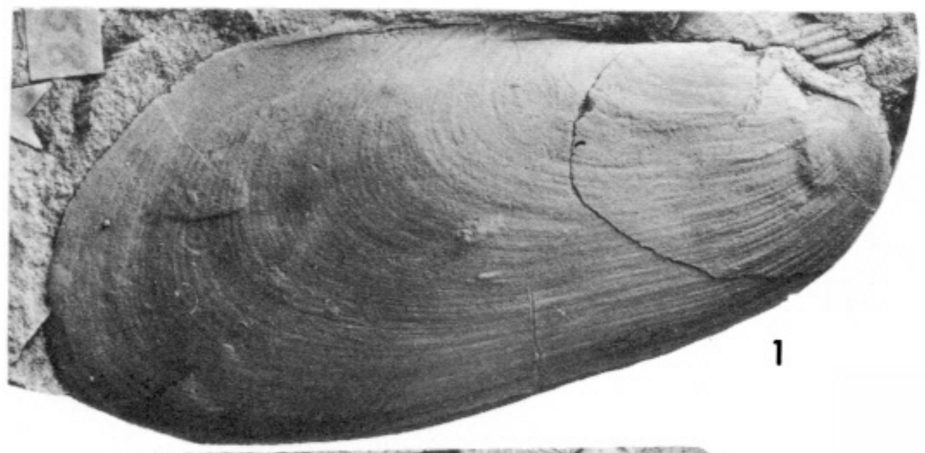
13



14



15

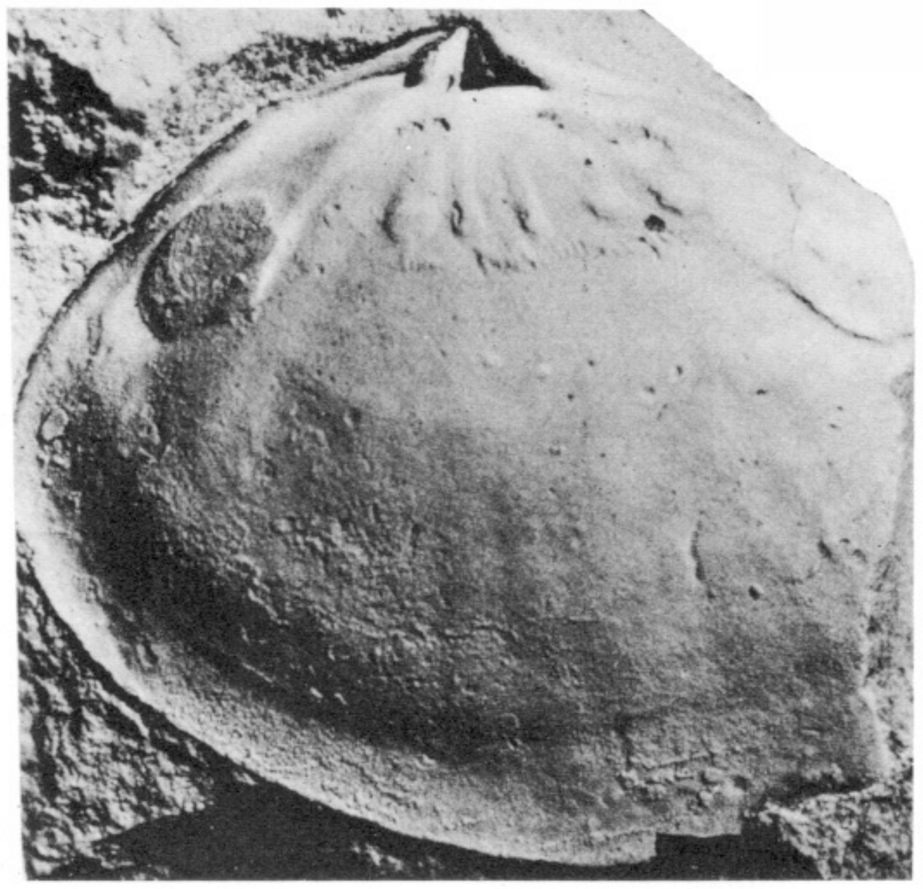


1

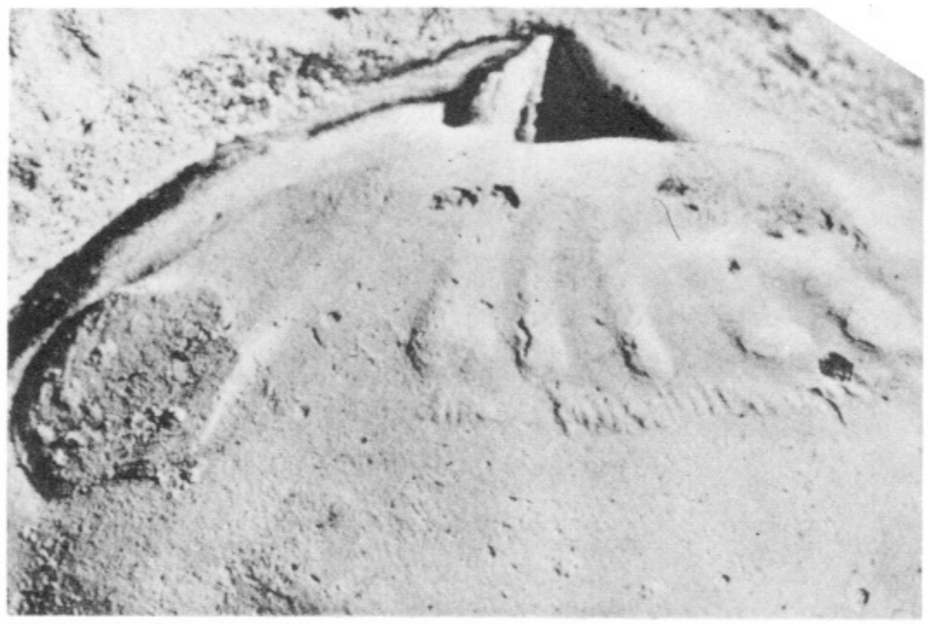
2

3

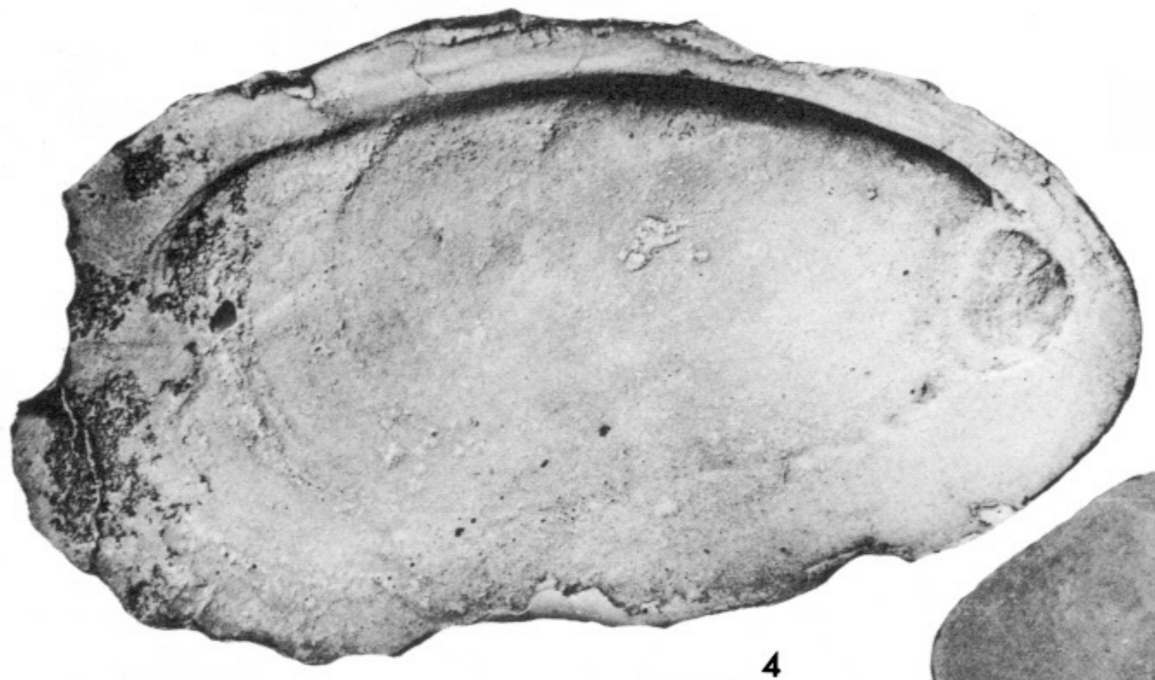
7



10



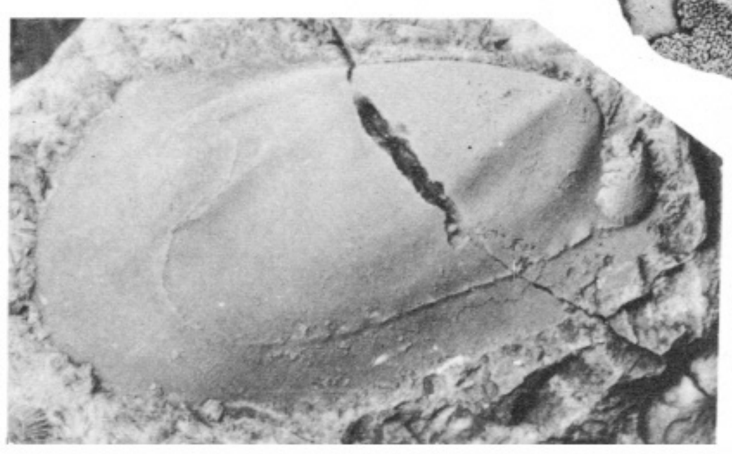
11



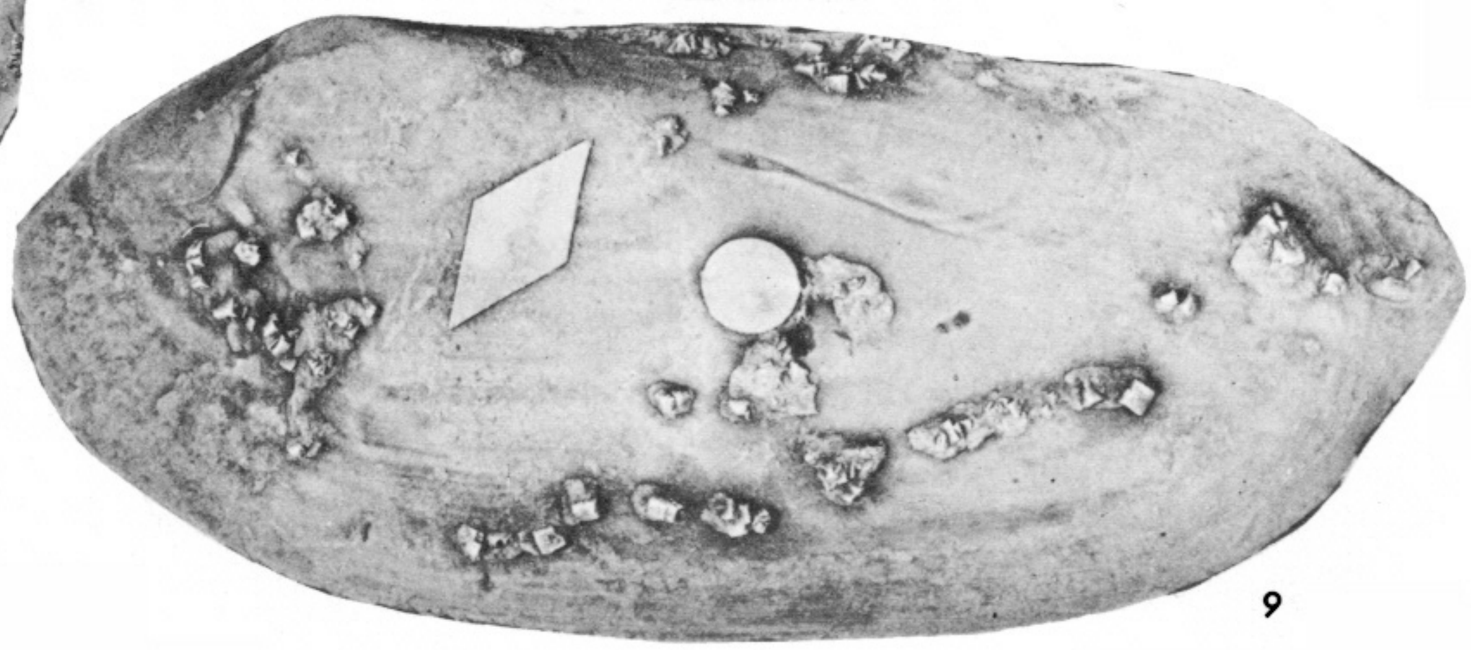
4

8

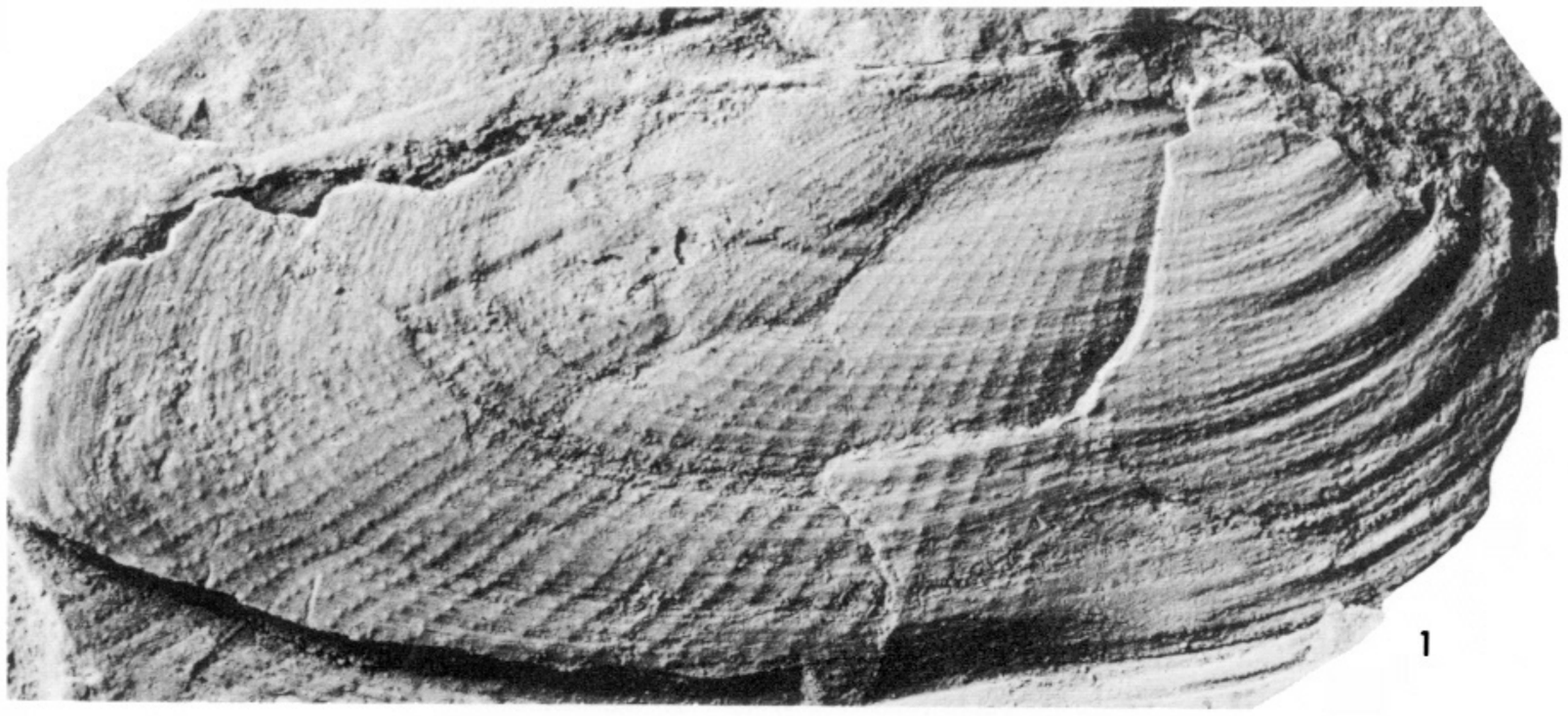
5



6



9



1

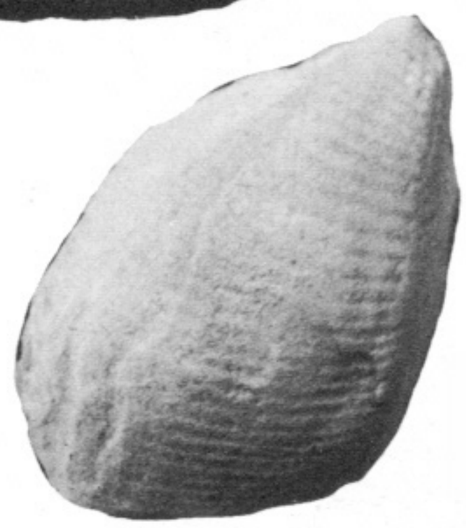
4

3

2

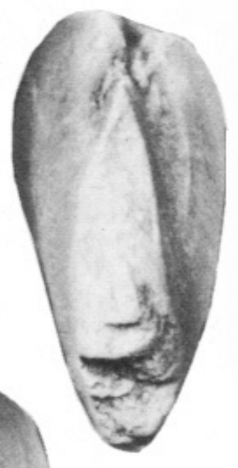
5

6

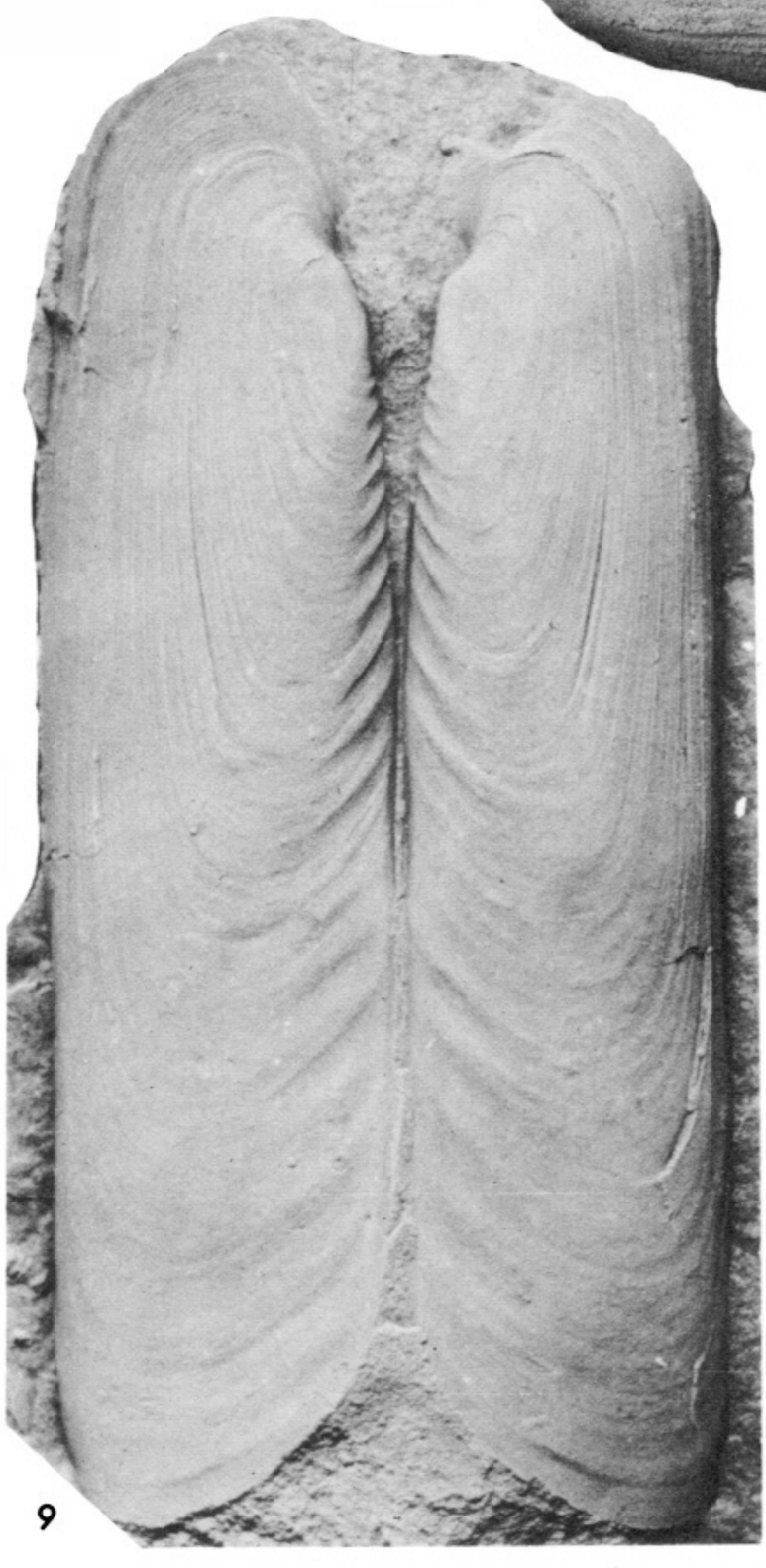


8

7



11

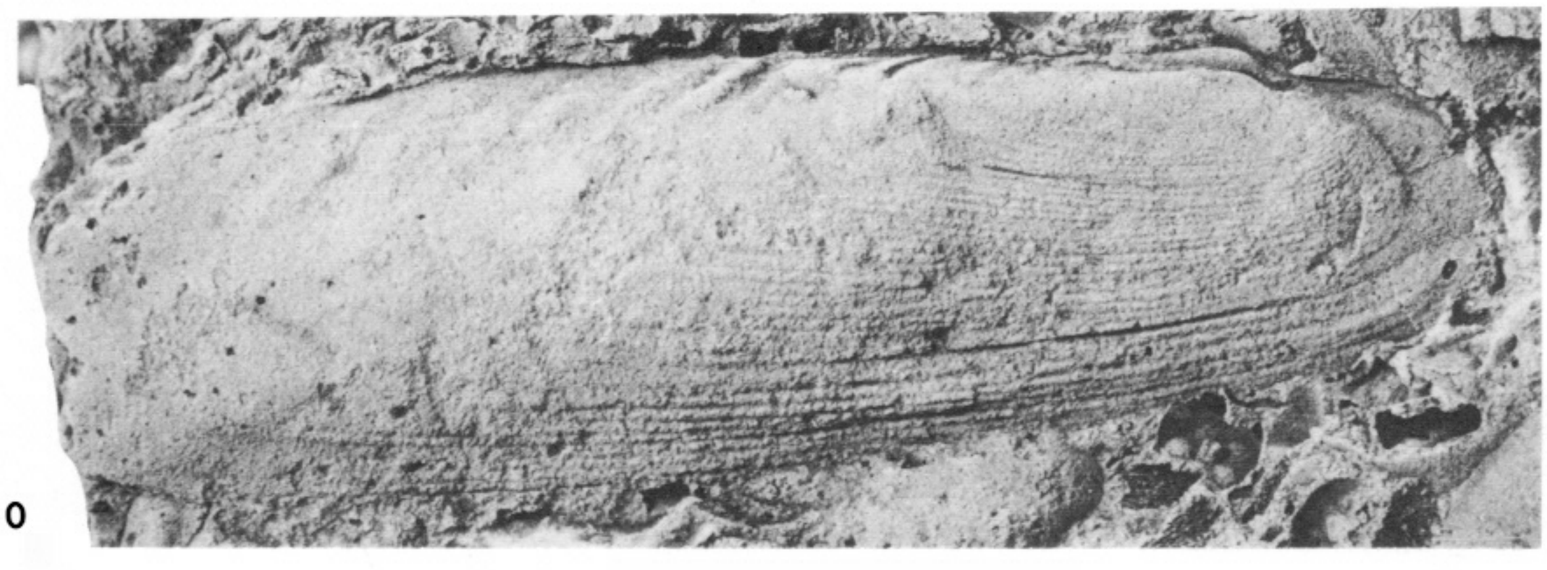


9

14

12

13



10