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The Paleontology of Rostroconch Mollusks and the Early History of the Phylum Mollusca

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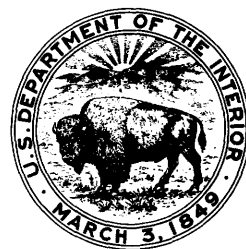


The Paleontology of Rostroconch Mollusks and the Early History of the Phylum Mollusca

By JOHN POJETA, JR., and BRUCE RUNNEGAR

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*An analysis of the functional morphology, taphonomy,
stratigraphic ranges, phylogenetic relationships, and
taxonomic variability of rostroconch mollusks, and the
evolutionary history of other early mollusks*



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THE PALEONTOLOGY OF ROSTROCONCH MOLLUSKS AND THE EARLY HISTORY OF THE PHYLUM MOLLUSCA

By JOHN POJETA, JR., and BRUCE RUNNEGAR¹

ABSTRACT

The class Rostroconchia is known in the fossil record from the Early Cambrian to the Late Permian; the taxa herein included within it have not previously been recognized as a biological entity and are grouped together for the first time. We functionally analyze the morphology of rostroconchs as to orientation, modes of growth, method of opening the valves, musculature, feeding structures, and so forth, and conclude that the group has a common biological pattern which indicates a commonality of descent. Thus, the Rostroconchia are treated here as a separate and extinct class of the phylum Mollusca.

Phylogenetically, it is possible to show that mollusks began to diversify and radiate in the Early Cambrian and that at this time the Monoplacophora gave rise to the Gastropoda and the Rostroconchia. We present evidence that the helcionellans, formerly regarded as gastropods, are monoplacophorans and that they gave rise to the Rostroconchia. The Rostroconchia in turn gave rise to the Pelecypoda in the late Early Cambrian and possibly to the Scaphopoda in the Ordovician. The rostroconchs underwent a major radiation in the Early Ordovician, at which time they were as diverse as the Pelecypoda. Only one order of rostroconchs survived the Ordovician, a fact that we attribute to the competition between rostroconchs and pelecypods for living space and food.

All the known Cambrian and Ordovician species of rostroconchs are described, discussed, and documented stratigraphically. We did not have adequate collections of post-Ordovician material to analyze all species, and we limit our systematic and stratigraphic considerations to those forms that show the generic diversity of the Conocardioida, the single known post-Ordovician order. For the practicing stratigrapher, we present a new tool, a group of organisms heretofore neglected stratigraphically because they were not recognized as a biological entity.

The following new taxa are proposed: families—Bransonidae and Hippocardiidae; genera—*Anisotechnophorus*, *Arceodomus*, *Bigalea*, *Bransonia*, *Heraultipegma*, and *Mulceodens*; species—*Ribeiria australiensis*, *R. taylori*, *Pinnocaris americana*, *Technophorus marija*, *T. milleri*, *Tolmachovia? jelli*, *Eopteria conocardiformis*, *Euchasma jonesi*, *E. mytiliforme*, *Conocardium pseudobellum*, *Bransonia wilsoni*, *B. alabamensis*, *B. cressmani*, *Mulceodens jaanussoni*, *Hippocardia cooperi*, *Bigalea yangi*, *B. ohioensis*, and *B. visbyensis*.

INTRODUCTION

Rostroconchs are a small but widespread and persistent Paleozoic faunal element. To date, they have been little studied because of the lack of adequate material and because they were not recognized as a separate molluscan lineage. It has been general practice to treat the older members of the class as arthropods and the younger members as unusual pelecypods.

The oldest known rostroconchs are assigned to the genus *Heraultipegma* (= *Heraultia* Cobbold) and are from Lower Cambrian rocks in France (Cobbold, 1935). According to Waterhouse (1967), the rostroconch "*Conocardium*" occurs in the Makarewan Stage of New Zealand, which is placed at the top of the Permian System. Thus, rostroconchs range throughout the Paleozoic. We agree with Morris (1967) that the Triassic species placed in *Conocardium* by Healy (1908) probably belong to the pelecypod groups Poromyacea or Burmesiidae.

Herein, we review the paleontology of the rostroconchs throughout their stratigraphic range and indicate the importance of early rostroconchs in the phylogeny of the Mollusca. In order to study any group throughout its stratigraphic range, it is necessary to have sizable collections. It was obviously not possible to collect the entire Paleozoic throughout the world, so we turned to the museums of four continents and borrowed specimens from more than 30 institutions. We examined more than 3,600 specimens ranging in age from Early Cambrian to Late Permian.

The study of what are now called rostroconchs began when Martin (1809) described one species and Sowerby (1815) described two species. Martin's work was subsequently declared invalid for nomenclatural purposes (Hemming, 1954, ICZN Opinion 231). Bronn (1835) named the genus *Conocardium*, citing a single species name, *Cardium elongatum*

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Sowerby, which is the type species of the genus by monotypy. The name *Conocardium* was subsequently used for almost all Silurian-Permian species and some Ordovician species. At least 275 species were assigned to the genus. Herein we subdivide the genus *Conocardium* into seven generic-level taxa.

To date, the study of rostroconchs has largely consisted of the description of species, little attempt having been made at interpretation above this level. Major monographs, summaries of species, or bibliographies of rostroconchs include: Babin (1966), Barrande (1881), Beushausen (1895), Branson (1942a, b; 1948; 1966), Fletcher (1943), Hall (1885), Hind (1900), Kobayashi (1933), LaRocque (1950), Paul (1941), Pohl (1929), Schubert and Waagen (1904), Ulrich (1894), Weller (1898), and Whidborne (1892).

It was not recognized until recently that conocardiaceans are allied to eopteriids (Pojeta, 1971) and ribeirioids (Morris, 1967; Pojeta and others, 1972) and that all three groups are neither pelecypods nor arthropods. Previously, the conocardiaceans had consistently been treated as pelecypods and usually allied to the cardiids. In the *Treatise on Invertebrate Paleontology*, Branson, LaRocque, and Newell (1969) regarded them as pelecypods, but placed them in their own order and regarded the subclass assignment as uncertain. Pojeta (1971) placed *Conocardium*, *Eopteria*, and *Euchasma* in a separate subclass of pelecypods and noted that the rostroconchs formed an enigmatic group whose pelecypod affinities were not well established. In 1972, Pojeta, Runnegar, Morris, and Newell made the rostroconchs a separate class of mollusks, which then included four genera; they also noted that rostroconchs were allied to the ribeirioids.

Although most ribeirioids and their allies have at one time or another been regarded as mollusks, usually pelecypods, in the 20th century they have been consistently placed with the arthropods. Schubert and Waagen (1904) argued against a pelecypod placement of *Ribeiria* and came to the conclusion that it was an apodid arthropod that has been much compressed laterally. Kobayashi (1933) accepted the arthropod placement of *Ribeiria* and its allies and treated them as notostracans. The molluscan nature of ribeirioids is indicated by the presence of a protoconch (pl. 41; pl. 47, figs. 13-15), by the calcareous shells which have growth lines (pl. 5, figs. 13, 14), and by the prominent muscle scars which also show the growth increments (pl. 6, figs. 1, 4, 14).

Because of the need to accumulate large numbers of specimens from many museums, the names of the museums are subsequently abbreviated as follows: AMS, Australian Museum, Sydney; AM, American Museum of Natural History, New York; BM, British Museum (Natural History), London; BMR, Australian Bureau of Mineral Resources, Canberra; FM, Field Museum of Natural History, Chicago, Ill.; GB, Institute of Geological Sciences, London, England; GSC, Geological Survey of Canada, Ottawa, Ont.; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Mass.; MU, Miami University, Oxford, Ohio; NYSM, New York State Museum, Albany; PRI, Paleontological Research Institution, Ithaca, N.Y.; ROM, Royal Ontario Museum, Toronto; SM, Sedgwick Museum, University of Cambridge, England; SMNH, Swedish Museum of Natural History, Stockholm; UCB, University of California, Berkeley; UCM, University of Cincinnati Museum, Cincinnati, Ohio; UI, University of Illinois, Urbana; UM, University of Michigan, Ann Arbor; UMN, University of Minnesota, Minneapolis, Minn.; UNE, University of New England, Armidale, New South Wales, Australia; UO, University of Oslo, Norway; UOK, University of Oklahoma, Norman; UQ, University of Queensland, Brisbane, Australia; USNM, United States National Museum, Washington, D.C.; YU, Yale University, New Haven, Conn.

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FUNCTIONAL MORPHOLOGY

ORIENTATION

In any group of extinct metazoans, the problem of morphological orientation exists. Because rostroconchs are extinct mollusks, the correct orientation of their skeleton is not immediately obvious. Their orientation can be established by comparing rostroconchs with other groups of mollusks and by considering their probable phylogenetic relationships. Previous discussions of this topic have assumed that rostroconchs were either pelecypod mollusks or arthropods, whereas we treat rostroconchs as a separate class of mollusks. Various recent workers (Branson, 1965, 1966; LaRocque, 1950; Nicol, 1970; Wilson, 1970) have oriented the Conocardiacea as we do.

Rostroconchs are bilaterally symmetrical about the commissural plane which separates the valves into mirror images (pl. 40, figs. 4-7). By analogy with other bivalved mollusks, we regard the hinged part of the shell as dorsal (pl. 40, fig. 5). Our phylogenetic conclusions, which indicate an evolutionary relationship of the rostroconchs to the Monoplacophora on the one hand and the Pelecypoda on the other, reinforce this interpretation.

Many older workers (for example, Dall, 1913) regarded the rostrate end of the conocardiacean shell as anterior. This was by analogy with pelecypods, at least in part. In most pelecypods, the direction of coiling of the umbos is toward the anterior, and in conocardiaceans, the umbos coil toward the rostrate end. However, most recent workers regard the rostrate end of rostroconchs as posterior and the gaping end as anterior (LaRocque, 1950; Wilson, 1970).

Conocardiaceans have a relatively large gape at one end of the shell (pl. 40, figs. 6, 11), and a narrow

tubular rostrum at the other (pl. 43, figs. 5, 6). The most logical explanation of the large gape is that it allowed for the protrusion of the foot from the shell. The large gape is therefore anatomically anteroventral and functionally anterior. This interpretation is supported by the existence of analogs among the pelecypods, many of which have large anterior pedal gapes. In addition, most primitive rostroconchs possess a large anterior plate or pegma that connects the valves dorsally (pl. 4, figs. 20–22).

By analogy with scaphopods, pelecypods, and some gastropods, the rostrum of rostroconchs allowed water and excretory products to enter and leave the mantle cavity; it was most likely posterior. The morphology of advanced conocardiaceans, when traced back through morphologically gradational rostroconchs to the most primitive members of the class, reinforces the interpretation of the orientation of the anterior-posterior axis on the basis of the postulated phylogenetic connection of the Rostroconchia with the Monoplacophora and the Pelecypoda.

As in pelecypods (Cox and others, 1969), ventral is more difficult to define. If it be taken to coincide with the sole of the protracted foot, then the large (anterior) shell or pedal gape of many rostroconchs should be anatomically ventral. We adopt a more geometric view and term the margin of the shell opposite the hinge as ventral. We thus treat the four coordinates, anterior, posterior, dorsal, and ventral, as mutually orthogonal directions in the commissural plane. All are related to the hinge, which is fixed as dorsal.

Like pelecypods, rostroconchs may have umbos that coil anteriorly (prosogyral, pl. 28, fig. 13) or posteriorly (opisthogyral, pl. 40, fig. 5). The direction of coiling is related to the geometry of shell growth (as in the Pelecypoda) and has nothing to do with the orientation of the shell.

As a general rule, conocardiaceans are anteriorly expanded, have an anterior gape, and a posterior rostrum (pl. 40, figs. 5–14); most other rostroconchs are posteriorly expanded and have an anterior pegma (pl. 11, fig. 22).

LARVAL SHELL

The valves of rostroconchs have only a single beak because growth originates from a single cap-shaped larval shell situated between the umbos of the juvenile shell (pl. 41; pl. 47, figs. 13–15). This structure, termed the protoconch (Pojeta and others, 1972), is normally destroyed in conocardiaceans by crushing caused by inrolling of the umbos. In ribeirioids, it is

usually visible at the apex of well-preserved specimens (pl. 10, fig. 16; pl. 12, fig. 17). The boundaries of the protoconch are not easily identified, but in most forms the protoconch appears to have been about 300–600 microns in diameter. Its size compares favorably with the larval shell of other mollusks; the prodissoconch II (veliconch) of pelecypods is 200–600 microns in diameter (Cox and others, 1969, p. N95), and the protoconch of bivalved gastropods is about 250 microns in diameter (Kawaguti, 1959).

In the conocardiaceans, the protoconch is a limpet-shaped structure, which is separated from the adjacent valves by shallow concave areas formed as a necessary consequence of the change from a univalved to a bivalved shell (pl. 41, figs. 1–5). Radial ribs first appear after this change has taken place (pl. 41, fig. 5), and the protoconch seems to have been relatively smooth. In the Ribeiriidae and Technophoridae, the valves are less inflated than in conocardiaceans, so that the distinction between the protoconch and the juvenile shell is less clear (pl. 4, figs. 20, 21, 23). Well-preserved internal molds of all genera often have a small cone-shaped elevation in the center of the hinge area; we interpret this to be a natural cast of the interior of the protoconch and early juvenile shell (pl. 22, fig. 11; pl. 23, fig. 1).

The protoconch or its natural mold has been observed in the following genera: *Anisotechnophorus* (pl. 18, figs. 7–9); *Bransonia* (pl. 52, figs. 3–5); *Eopteria* (pl. 22, fig. 11); *Pseudoconocardium* (pl. 41, figs. 1–5); *Pseudotechnophorus* (pl. 20, figs. 13–15); *Ribeiria* (pl. 4, figs. 20, 21, 23); *Technophorus* (pl. 12, fig. 17); and *Hippocardia?* (pl. 47, figs. 13–15).

METAMORPHOSIS

We suggest that the bivalved postlarval shell be known as the dissoconch to conform with the terminology applied to pelecypods. There is no clearly defined junction between the protoconch and the dissoconch except posteriorly in some conocardiaceans, where an obvious transverse cleft separates the protoconch from the rostral area of the shell (pl. 40, fig. 5).

Metamorphosis apparently occurs by accelerated growth of the left and right flanks of the protoconch, producing the two valves of the dissoconch. Because rostroconchs characteristically have no adductor muscles, the two newly formed valves must grow rapidly to encompass the body. One specimen of the conocardiacean *Bransonia wilsoni* shows steplike growth increments on the posterior and lateral flanks

of the immediately postlarval shell (pl. 52, fig. 4), indicating that the juvenile shell remained pyramidal in shape to a size of at least 1.5 mm. Other specimens show that the anterior edge of the postlarval shell developed a shallow sulcus generated by a sinus in the anterior commissure (pl. 47, figs. 14, 15). As growth continued, the lobes on either side of the sulcus enlarged to form the snout region of the valves.

Lateral growth occurred at the same time to produce the flanks of the valves, but because the juvenile flanks are rotated dorsally by subsequent growth at the ventral commissure, even small shells (pl. 47, fig. 15) are deformed where the larval shell becomes obviously bivalved. In the Conocardiacea, this deformation is extreme, and it frequently obliterates the protoconch.

The protoconch survives in forms like *Bransonia wilsoni* because the outermost longitudinal clefts separate the protoconch from the carinal areas of the shell (pl. 51, fig. 17). In contrast to conocardiaceans, the valves of technophorids, ribeiriids, and *Eopteria* are less inflated, so the protoconch is more easily preserved (pl. 22, fig. 11).

The larval and juvenile growth of advanced rostroconchs like *Bransonia* and *Pseudoconocardium* reflects the broad outlines of the phylogeny of the class. The protoconch resembles the monoplacophoran shell; it is succeeded by a simple bilobed shell like that of some ribeirioids, which in turn grows into the inflated radially ribbed shell characteristic of conocardiaceans.

SUBSEQUENT SHELL GROWTH

Adult rostroconchs range in size from 2 mm to 150 mm in length. The postlarval growth of many rostroconch shells produces complex skeletal structures which have no counterparts in other previously described mollusks. Because some of these structures are restricted to one or two genera and because homologies between structures are uncertain, it is convenient to describe the growth of several different forms separately. In this section, we describe the growth of the skeletal elements of *Ribeiria*, *Euchasma*, *Pseudoconocardium*, *Hippocardia*, and *Arceodomus*.

1. Growth of the ribeiriid shell (fig. 1). Our knowledge of the growth of the ribeiriid shell is based mainly on thin-section studies of the shell of *Ribeiria apusoides* Schubert and Waagen from the Ordovician of Bohemia and on silicified exteriors of *Ribeiria calcifera* Billings from the Ordovician of Ontario.

The ribeiriid shell grew from a protoconch situated nearer the anterior end of the dorsal margin (pl. 6, figs. 7, 11, 13). Growth lines on the shell of *Ribeiria apusoides* show that the valves separated a little during growth and that the longer posterior dorsal margin functioned as a hinge. A strong plate, termed the pegma, extends posteroventrally from the apex of the shell (pl. 5, fig. 4). The pegma is attached to both valves (pl. 4, figs. 22, 23; pl. 5, figs. 2-4); it divides the apical area of the shell into anterior and posterior cavities.

In front of the beak, the dorsal margin of the shell drops abruptly, and a second short hinge region occurs between the beak and the dorsal edge of the anterior gape (pl. 5, figs. 9, 12). This is best seen in the silicified replicas of *Ribeiria calcifera*. Because the two hinge axes of *Ribeiria* are approximately parallel, but not colinear, a curved tensional fracture developed below the beak (pl. 4, fig. 9). The ventral edges of each fracture enlarged as growth continued so that the two hinge axes remained the same proportional distance apart, irrespective of the size of the shell. We use the term "anterior clefts" for the right and left ends of this tensional fracture.

In some individuals of *Ribeiria calcifera*, the anterior gape extends posteriorly along the anterior dorsal margin for some distance (pl. 4, fig. 8). If this embayment continued as far as the beak, the need for the anterior clefts would disappear as it does in pelecypods and the bivalved gastropods. In these shells, the valves rotate about the ligament and separate at other parts of the dorsal margin.

Serial thin sections cut perpendicular to the anterior-posterior axis of *Ribeiria apusoides* show that the shell consists of three main layers—a thin outer layer of relatively uniform thickness (pl. 30, fig. 5) formed at the commissure by the outer surface of the outer mantle fold, and thicker middle and inner shell layers separated by a discontinuity formed by the myostracum of the linear lateral muscle bands. The middle and inner shell layers were secreted by the outer surface of the mantle, and they lapped against the inner surface of the outer shell layer (pl. 30, fig. 5). All layers are continuous across the hinge of the shell.

When first formed, the outer shell layer and the immediately underlying middle shell layer were bent in acute angle at the anterior and

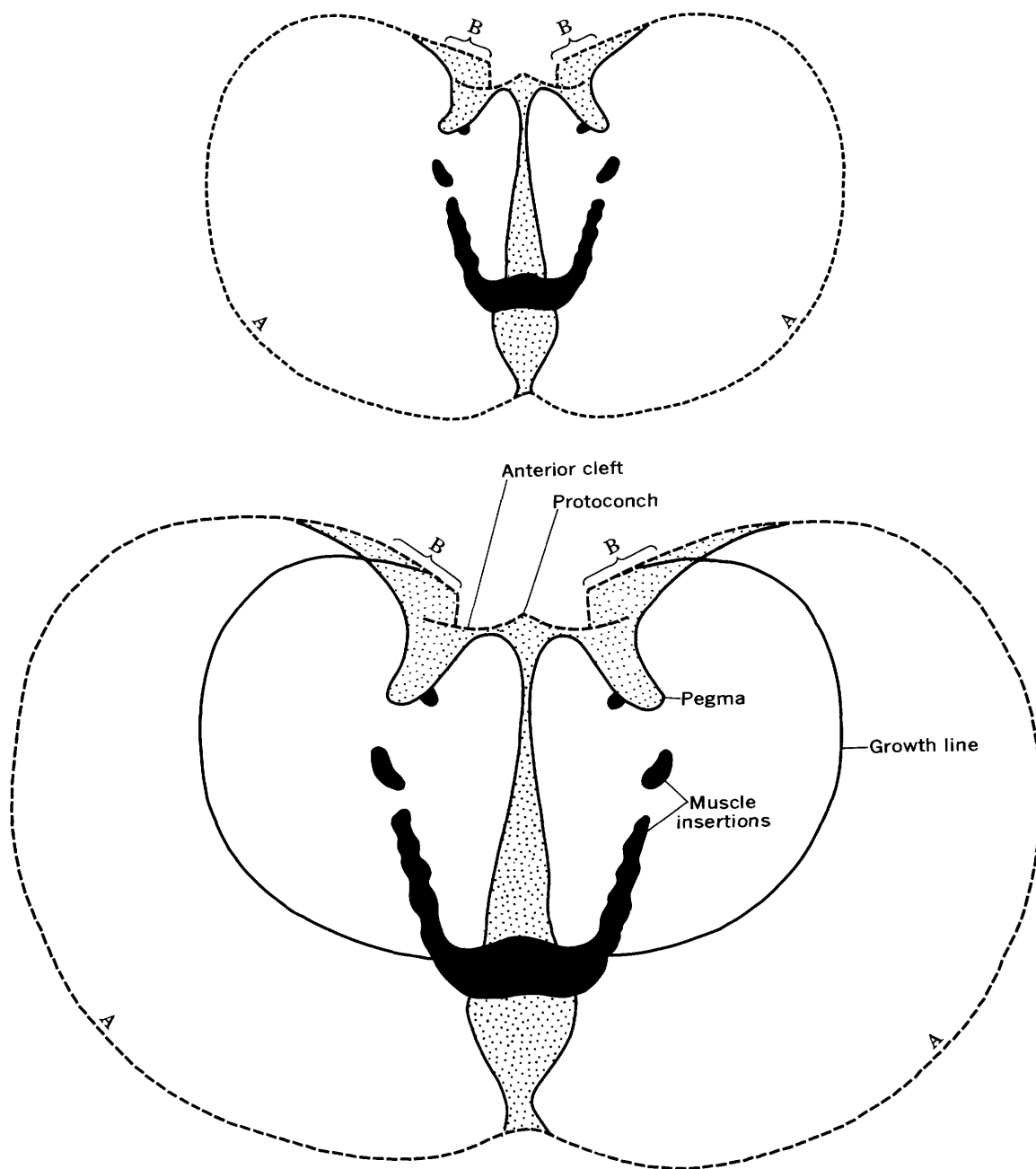


FIGURE 1.—Paper cutout models to illustrate the growth of the ribeirioid shell. Drawings are based on *Ribeiria lucan* (Walcott). Black areas represent muscle insertions; stippled areas show thickness of shell along dorsal margin of completed models. Compare models to see how anterior clefts enlarge mechanically during growth because the shell at the ventral edges of these clefts cannot be resorbed. Growth line on lower model is same size as entire upper model.

Instructions: 1, photocopy page; 2, cut each model from photocopy, cut along *all* dashed lines; 3, use transparent adhesive tape to fix edges marked "B" together; 4, staple points marked "A" together; flatten area below protoconch by gently pushing taped area inwards.

posterior ends of the dorsal margin (pl. 31, figs. 2, 5). Subsequent deposition of thick inner and middle shell layers cemented the hinge into an inverted U-shape (pl. 30, fig. 4), and

the early formed layers were forced apart. This allowed for growth of the shell.

The growing edge of the pegma is concave posteriorly so it appears as two lobes project-

ing from the inner surfaces of the valves in more posterior sections (pl. 31, fig. 3). These lobes coalesce in more anterior sections (pl. 31, fig. 1). Because the posterior face of the pegma is the site of a large muscle insertion (pl. 5, fig. 4; pl. 6, fig. 8), it is marked with growth lines showing successive positions of the ventral edge of the muscle. These growth lines mark the boundaries between successive increments of the middle shell layers forming the pegma. Consequently, sections through the pegma show that the growth increments of the middle shell layers intersect its upper face (pl. 31, fig. 3).

The inner shell layer was deposited behind the linear lateral muscle bands as they migrated ventrally during growth. This layer buried the old muscle insertion areas above the dorsal edges of the muscles. It appears in transverse section as a series of overlapping layers which extend laterally from the dorsal margin (pl. 31, fig. 3). Near the apex of the posterior cavity, the whole posterior face of the pegma is covered with inner shell layer (pl. 30, fig. 2).

Obviously, if the early formed parts of the valves were separated during growth, the pegma would be subjected to tensional stress. Tensional fractures parallel to the commissural (symmetry) plane are visible in thin sections of the early formed parts of the pegma in the two specimens of *Ribeiria apusoides* that were fully examined (pl. 30, figs. 2, 3; pl. 31, fig. 1). Because these fractures do not penetrate subsequently formed shell layers, it is clear that they were not produced after the death of the organism.

2. Growth of *Euchasma*. This interpretation of the growth of *Euchasma* is based mainly on information obtained from silicified replicas of the shells of *E. jonesi* n. sp. and *E. mytiliforme* n. sp. from the Ordovician of Malaysia.

Unlike *Ribeiria*, *Euchasma* has a strongly inflated shell, which is more or less flattened anteroventrally (pl. 29, figs. 6–13). Because of the inflation, the valves must separate more during growth, and prominent umbos appear on either side of the protoconch region. As in *Ribeiria*, the valves are connected by an anterior plate (pl. 29, figs. 3, 11, 14, 15), which also effectively blocks a reduced, almost circular anterodorsal aperture (pl. 28, figs. 15, 16). Also as in *Ribeiria*, there are two hinge axes,

so anterior clefts are well developed (pl. 27, fig. 13; pl. 28, fig. 17). The posterior dorsal margin is the main hinge axis. Posterior clefts may also form (pl. 29, fig. 10); see discussion under 3 for an explanation of posterior clefts.

Because both small and large specimens of *Euchasma* are similar in form and because all have apertural plates (modified pegmas), it is difficult to understand how they grew when the valves were held rigidly together by the apertural plate. Unlike the pegma of *Ribeiria*, the apertural plate of *Euchasma* is attached to the valves at only four points, two dorsal and two lateral (pl. 29, figs. 3, 15). The dorsal attachments could remain more or less static during life without affecting shell growth, but the right and left lateral attachments appear to have moved ventrally as the shell grew. Apparently shell was added to the ventral edge of each lateral attachment and at the same time resorbed from its dorsal edge. In this way, the valves could separate relatively widely during growth, while remaining rigidly joined by the modified pegma or apertural plate.

3. Growth of *Pseudoconocardium* (fig. 2). *Pseudoconocardium lanterna* (Branson) has an inflated shell with a huge anterior gape (pl. 40, figs. 6, 11) but no complex internal skeletal elements. It is known from more than 100 undistorted specimens from the Pennsylvanian of north-central Texas.

Growth started from a well-defined protoconch (pl. 41, figs. 1–5), which merged into the juvenile shell. Growth lines on the shell show that subsequent growth moved the juvenile shells farther and farther apart, as in other invertebrates having paired calcareous valves. By the time the shell was sufficiently large, umbos formed on either side of the protoconch (pl. 41, fig. 2).

The shape of the growth lines on *Pseudoconocardium lanterna* (pl. 40, fig. 3) shows that the valves rotated about the anterior dorsal margin as the shell became larger. We term this the hinge axis. Because the valves are joined along this axis, the hinge must either bend or break as the valves grow. An anterior view of the shell (pl. 40, fig. 6) shows that the dorsal margin forms a smooth U-shaped curve at the commissure. Equivalent earlier formed parts of the shell were progressively deformed as growth proceeded, and were cemented into their deformed shape by subsequently depos-

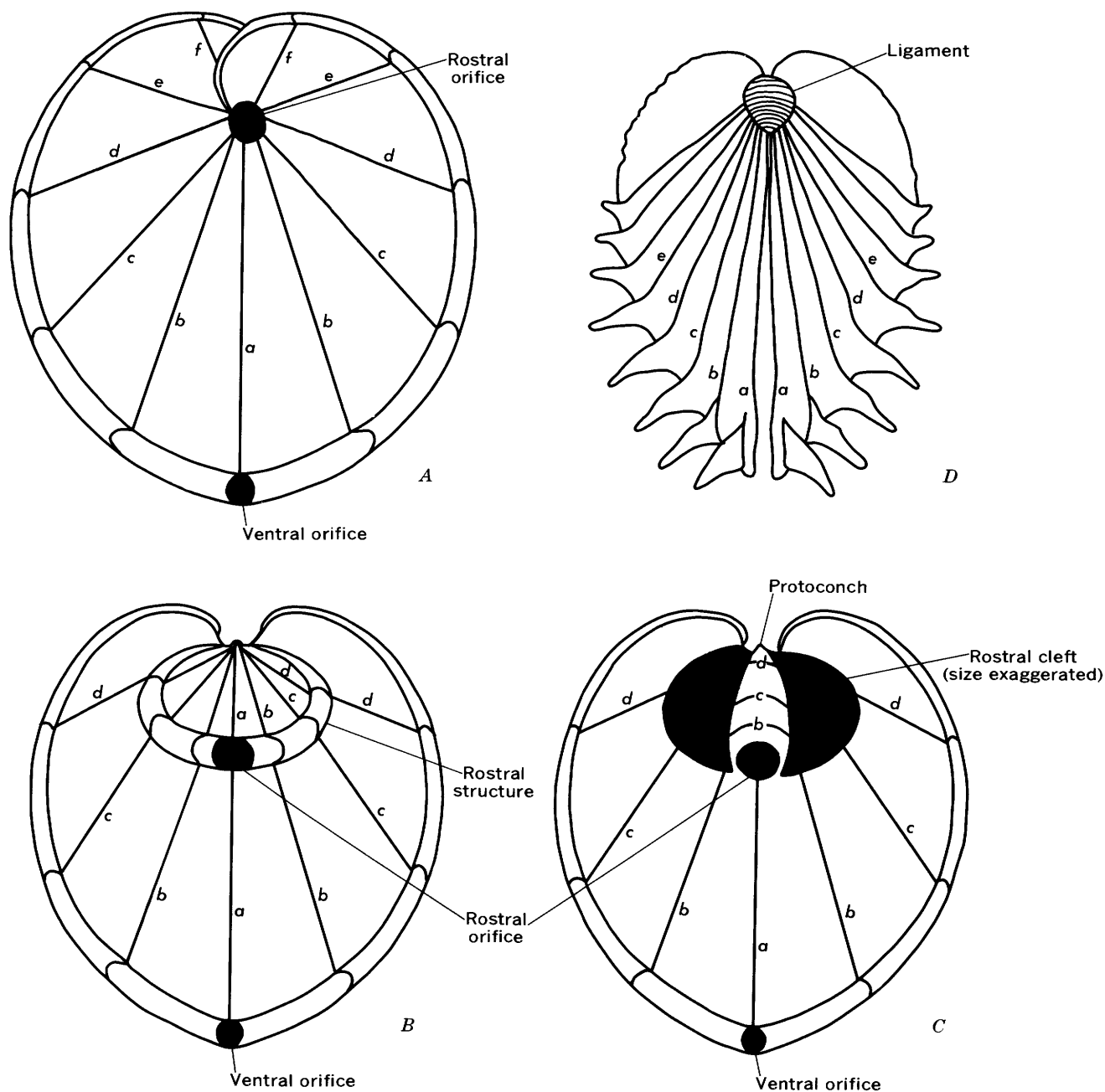


FIGURE 2.—Schematic diagrams illustrating the posterior growth of conocardiid rostroconch and pelecypod shells. A. *Hippocardia hibernica* (Sowerby). Rostral orifice is almost colinear with the hinge axis of the shell, and growth lines (a-f) rotate about rostral orifice as shell grows. Only minor deformation of the upper surface of the rostrum occurs during growth. Note how the dorsal edges of the hood overlap to hide the hinge axis and protoconch. B. *Hippocardia cuneata* (Conrad). Rostral orifice is below hinge axis, and orifice generates hoodlike rostral structure through growth. Growth lines (a-d) continue radially to protoconch. C. *Pseudoconocardium lanterna* (Branson) or *Bransonia wilsoni* n. sp., rostral orifice is below hinge axis, but no rostral structure

is produced. Instead, tension fractures (rostral clefts, exaggerated in this diagram for comparison with B) form between the loci of the ventral edge of the rostral orifice and the sides of the tubular rostrum. These clefts do not penetrate through the shell because new shell layers are continually added internally. Growth lines on such shells are interrupted where they cross the rostral clefts. D. The pelecypod *Hecuba scortum* (Linnaeus) (modified from Carter, 1967, pl. 7, fig. 17), which has spinose carinae. The spines are formed at the posteroventral part of the commissure and are moved outwards during growth in the same way that the rostroconch hood is formed.

ited prograding layers of inner shell material. These layers in turn were deformed by additional growth at the anterior end of the shell, and this growth also reformed the previously formed layers. Each inner shell layer was thus slightly less strained than the next older one.

The effects of this deformation can be seen in thin sections of the hinge of *Pseudoconocardium lanterna* (pl. 32, fig. 2). In the specimen figured, tensional stresses caused by the bending of the shell have fractured the earlier formed shell layers, and the damage has been repaired by the youngest layers. Occasionally the whole anterior hinge may rupture during life (Pojeta and others, 1972, fig. 1).

In *Pseudoconocardium lanterna* and other conocardiceans that we have sectioned, the outer shell layer is not continuous across the hinge (pl. 32, figs. 1, 2), and thus was not normally deformed during growth. However, because the outer shell layer is relatively thin, the hinge of *P. lanterna* is almost as thick as the flanks of the valves (pl. 32, fig. 2).

Because the anterior dorsal margin of conocardiceans is the hinge axis, the posterior dorsal margin must have compensated for valve rotation in some other way. All well-preserved specimens of *P. lanterna* have a series of symmetrical fissures, termed clefts, behind the umbos (pl. 40, figs. 5, 7), which result from the periodic failure of the shell across and on each side of the tubular rostrum. In the past, these clefts were thought to be ligament grooves (Hind, 1900), but they do not penetrate the shell, were not connected to the secretory mantle, and thus could not have contained ligamental material. In transverse section, they appear as V-shaped fissures which penetrate at right angles to the growth lamellae. On some well-preserved exteriors of *P. lanterna*, the outer clefts cut previously formed growth lines. Because the clefts do not extend as far on small shells that are similar in size to the growth lines cut by the clefts on larger shells, we conclude that the clefts are fractures which enlarged as the shell grew. They are comparable to the anterior clefts of *Ribeiria* and *Euchasma*, and formed for much the same reason.

The clefts are best developed in inflated shells such as *P. lanterna* where the rostrum occurs below and at an angle to the hinge axis (pl. 40, fig. 8). In these shells, the posterior

commissure is again defined by the growing edge of the inner shell layers. It extends dorsally from the ventral orifice and continues around the tip of the rostrum. It does not extend along the dorsal surface of the rostrum (pl. 40, fig. 5) as it does in *Hippocardia cuneata* (Conrad) (Case 4). This difference between these shells accounts for the presence of the rostral clefts in *Pseudoconocardium lanterna* but not in *Hippocardia cuneata*. The need for the clefts is easier to understand if *Bransonia wilsoni* n. sp. (pl. 52, figs. 1-5) is considered as an intermediate form.

In lateral view, the ventral surfaces of the rostra of *Hippocardia cuneata* (pl. 48, fig. 8) and *Bransonia wilsoni* (pl. 51, fig. 1) are similar in general form. However, their upper surfaces are quite different because *B. wilsoni* has a pair of deep clefts on either side of the rostrum (pl. 51, fig. 17) and in addition has smaller clefts near the protoconch. Between the large clefts, the rostrum is relatively uniform in width when viewed dorsally (pl. 51, fig. 17).

The outer edges of the large rostral clefts of *Bransonia wilsoni* are topologically equivalent to the angular edges of the rostral structure of *Hippocardia cuneata* (pl. 48, figs. 10, 11), and growth lines on each type of shell intersect these edges in an acute angle which opens anteriorly. In *Hippocardia cuneata*, the growth lines are immediately reflected toward the protoconch, and the upper surface of the rostral structure is covered with growth lines that radiate from the beak. Thus, the dorsal rostral surface of *Hippocardia cuneata* grows like the lunule of a venerid pelecypod.

In contrast, the dorsal surface of the rostrum of shells with a rostrum like *Bransonia wilsoni* and *Pseudoconocardium lanterna* is marked with growth lines that cross the dorsal margin at right angles to the commissural plane. In these shells, the rostrum can only grow distally, ventrally, and internally. In shells where the upper surface of the rostrum is in line with the hinge axis, there is no problem, and the rostrum grows like the posterior wing of various pteriacean pelecypods (pl. 43, figs. 1, 5). But in those forms where the rostrum is below and at an angle to the hinge axis, the rostrum would split dorsally as the valves grew. This is avoided in forms like *Pseudoconocardium lanterna* and *Bransonia wilsoni* by the formation of tensional

fractures, clefts, on either side of the rostrum. These occupy the space filled by additional shell secreted along the dorsal margin of the rostrum in *Hippocardia cuneata*.

There are two kinds of rostral clefts in *Pseudoconocardium lanterna* and most other conocardiids: symmetrical longitudinal clefts resulting from tensional stresses more or less parallel to the rostrum, and one or more transverse clefts which apparently compensate for the required rotation of the rostrum within the commissural plane (pl. 40, figs. 5, 7). If allometric changes in the angle the rostrum makes with the shell are to be avoided, the rostrum must be gradually raised during growth. Apparently the transverse clefts closed slowly during growth and allowed for this rotation. The first-formed transverse cleft separates the protoconch from the rostral area of the dissoconch in this and many other conocardiids (pl. 40, fig. 5).

In thin section, the shells of *Pseudoconocardium lanterna* and *Bransonella wilsoni* are formed of two obviously different layers. The outer shell layer is relatively transparent and coarsely prismatic (pl. 32, fig. 4). The inner shell layers are darker and well laminated, though they show no obvious microstructure (pl. 32, fig. 1, 2, 4). They may have been nacreous, cross-lamellar, or homogeneous.

Because the exterior of the shell is covered with narrow closely spaced radial and comarginal walls (pl. 40, fig. 12), thin sections sometimes give the impression that the outer shell layer contains a series of roofed pits or vacuoles. Similar structures have been reported from other conocardiids (Panella and MacClintock, 1968, pl. 8, fig. 5). These views can result from oblique sections through intersecting radial and comarginal walls, and there is no evidence that the intervening pits were roofed over in *P. lanterna*. In at least some specimens of *P. lanterna*, small secondary ribs run between the vertical lamellae of the comarginal markings in the interspaces between primary ribs (pl. 42, fig. 6). The intersection of the vertical lamellae and the secondary ribs produces a grid pattern that significantly reduces the space open to the exterior between adjacent lamellae.

The inside of the anterior aperture of *Pseudoconocardium lanterna* and many other rostroconchs is lined with a series of blunt pro-

jections (pl. 40, figs. 6, 11) that we have termed commissural (or marginal) denticles. These are formed of the prismatic outer shell layer secreted at the edge of the mantle. Similar smaller denticles line the inside of the rest of the commissure as far as the base of the rostrum. As the shell grew, these commissural denticles were buried by prograding inner shell layers secreted by the external surface of the mantle. As growth continued, the commissural denticles generated internal ribs which were totally submerged by the inner shell layers. Sometimes solution of the inner shell layers before lithification may expose the ribbed internal surface of the outer shell layer, thus giving the impression that the interior of the shell was ornamented with radial ribs (pl. 45, fig. 4). The inner shell layers that bury the submerged ribs are relatively uniform in thickness, and so they form concentric folds over the ribs of the outer shell layer. When the inner shell layers became thick enough, they became relatively flat (pl. 42, figs. 13, 14).

The growth of the anterior dorsal margin of *P. lanterna* also illustrates features found in many conocardiids. Well-preserved specimens normally have two subcircular depressions, one on either side of the middorsal line, just inside the anterior commissure (pl. 40, fig. 11; pl. 42, fig. 5). These depressions are separated by a wall of shell, best shown by views of the growth layers in transverse section (pl. 32, fig. 1). The function of the depressions is uncertain, but they may have been muscle insertions because they are filled by subsequent deposits of inner shell material. The abrupt contact between these latter deposits and the base of the depression may represent the myostracal layer of the muscle insertion.

4. Growth of *Hippocardia* (fig. 2). *Hippocardia cuneata* (Conrad), the most common rostroconch in the northeastern United States Devonian, has a spectacular hood attached to the carinal area of the shell (pl. 48, fig. 2). The species is well known from external molds in New York State, silicified replicas of the outer shell layer from the Falls of the Ohio River along the Kentucky-Indiana border, and original shells from Ohio (pls. 48, 49).

The hood of *Hippocardia* was secreted by a tubular extension of the mantle at the ventral orifice, which is located midventrally on the posterior face of the shell (pl. 49, figs. 5, 6).

The ventral surface of the hood forms a continuous curved surface with the posterior flanks of the valves, but it lacks radial ribs (pl. 49, figs. 4, 10). Both upper and lower surfaces of the hood are ornamented with fine closely spaced growth lines that are continuous with growth lines on the rest of the shell. The growth lines indicate that new shell material was periodically added to the hood along the entire length of the tubular extension of the ventral orifice as the valves gradually separated. Thus, the hood represents a surface generated by a tube at the posterior ventral commissure and was inevitably produced if the tube was maintained throughout the life of the animal. It follows that the hood may have had no function; it may only represent the loci of the edges of the tube. Alternatively, the only function of the tubular extension of the third aperture may have been to generate the hood, and the hood may be the functionally important structure.

There is no evidence for allometric changes in the size of the hood during growth. Consequently, in shells that have inflated valves, the edges of the hood on left and right valves may have interfered with one another as the umbos enrolled. This problem appears to have been solved, as it is in living heart cockles, by having the hood of one valve slightly ahead of that of the other.

Serial transverse sections of the hood of *Hippocardia cunea* show that it is formed of concave lamellae which are separated by open spaces in the distal part of the body (pl. 32, figs. 5, 6). Proximally, these spaces are filled with prismatic outer shell material (pl. 32, fig. 5). Thus, the whole of the hood is constructed of the outer shell layer. Because the outer shell layer of mollusks is normally only secreted at the mantle edge by the outer surface of the outer fold of the mantle, we believe that a hypertrophied part of the outer mantle fold formed the hood of *Hippocardia*.

The rostral structure of *Hippocardia cunea* simulates a second hood (pl. 48, figs. 10, 11). Like the hood, it is a curved surface generated through growth by a tube at the commissure. There are, however, two important differences. First, it is clear by comparison with other conocardiceans that it is the tube, not the structure generated by the tube, that is functionally important. And second, again by com-

parison with other conocardiceans, it is certain that the tube (rostrum) is formed of all shell layers (see 3).

5. Growth of *Arceodomus*. *Arceodomus* is best known from recrystallized original shells of *A. glabrata* (Easton) from the Mississippian and Pennsylvanian of Montana, Nevada, and Texas (pl. 42, figs. 8–10; pl. 43, figs. 1–4; 7–12) and from silicified replicas of *A. langenheimi* (Wilson) from the Permian of California (pl. 43, figs. 13–15). *Arceodomus* resembles *Conocardium* (pl. 38) but lacks radial ornament on the body of the shell. Externally, the growth of *Arceodomus* is similar to that of *Pseudoconocardium*, and small rostral clefts are visible in *A. glabrata* (pl. 43, fig. 10). We use these two species to illustrate the formation and growth of the anterior longitudinal shelves (pl. 43, figs. 12, 13).

Anterior longitudinal shelves are curved plates composed of the outer (prismatic) shell layer (pl. 43, fig. 13) that project more or less horizontally across the snout region of *Arceodomus* and *Conocardium*. As growth continued, the older parts of the shelves were buried in thick deposits of inner shell layer (Wilson, 1970, figs. 10–18). Wilson (1970) recognized the microstructural difference between the shelves and the inner shell layers, but tentatively interpreted the shelves as myostracal layers.

The shelves are unusually enlarged commissural denticles, and clear transitions can be seen in several morphological series, for example, *Pseudoconocardium lanterna* (pl. 40, figs. 6, 11), *Mulceodens jaanussoni* n. sp. (pl. 34, figs. 3–5), *Hippocardia zeileri* (Beushausen) (pl. 47, figs. 8, 9), and *Arceodomus glabrata* (pl. 43, fig. 12). Significance of the shelves lies in the fact that they were formed of the outer shell layer, implying that they were formed by the mantle edge. We conclude that the anterior part of the mantle of *Arceodomus* (and *Conocardium*) was enlarged, that it was complexly folded when withdrawn into the shell, and that the edges of the mantle must have been located at the growing edges of the anterior shelves when the mantle was at rest in the shell.

SUMMARY OF SHELL GROWTH

All rostroconchs grew a bilobed shell (dissoconch) from a univalved protoconch or juvenile shell. Primitive rostroconchs (Ribeirioida) have all shell layers

continuous across the dorsal margin, but in advanced rostroconchs (Conocardiacea), the outer shell layer is dorsally discontinuous, except in the region of the protoconch. Primitive rostroconchs have the valves connected by a stout anterior pegma (Ribeirioida, some Eopteriidae) or anterior and posterior pegmas (Ischyriinioida) which is deformed (*Ribeiria*) or partially resorbed (*Euchasma*) to allow for valve separation during growth.

Parts of the dorsal shell margin of all rostroconchs function as a poorly elastic hinge during growth, but during day-to-day living, the valves were held rigidly together. If the shells are anteriorly elongated (*Pseudotechnophorus*, Conocardiacea), the anterior dorsal margin functions as the hinge. In posteriorly elongated shells (Ribeiriidae, Technophoridae), the reverse is true. Because the dorsal shell margin is rarely straight, transverse and longitudinal tensional fractures called clefts form between the main hinge and the less elevated parts of the dorsal margin. In subequidimensional shells (*Eopteria*, *Euchasma*), clefts are present on both sides of the protoconch; anteriorly or posteriorly elongated shells normally have clefts only at the shorter end of the shell. The distribution of the clefts can be explained by the geometry of shell growth.

All rostroconchs that have visible shell structure have an outer (often prismatic) shell layer formed by the outer edge of the mantle. One or more inner shell layers are lapped against the internal surface of the outer shell layer by the outer surface of the mantle. The hood of *Hippocardia* is formed of outer shell material only; the commissural denticles and anterior shelves of conocardiaceans are also part of the outer shell layer, implying that the edge of the mantle could be withdrawn into the anterior part of the shell in some forms.

OPENING OF THE VALVES

The valves of pelecypods and bivalved gastropods are joined dorsally by an elastic structure called a ligament. Owen, Trueman, and Yonge (1953) showed that the simplest pelecypod ligament consists of three layers (periostracum, lamellar, and fibrous layers), which are continuous with comparable shell layers in the right and left valves. The probable structure of the ligament of the Early Cambrian pelecypod *Fordilla* (Pojeta and others, 1973) and the nature of the ligament of the bivalved gastropod *Berthelinia* (Kawaguti and Yamasu, 1961) support this observation. Thus, the valves and ligament are part of a single structure (the shell) and differ only in the degree of calcification of the pro-

tein matrix. This explanation is supported by the ontogeny of living pelecypods, whereby a single larval shell gland secretes "a saddle-shaped cuticular pellicle, which becomes calcified at two symmetrical points, right and left of the middle line" (Pelseneer, 1906, p. 245).

In engineering terms, the ligament can be described as a spring, because it stores energy supplied by contractions of the adductor muscles attached to each valve. This energy is released when the adductors relax, and experimental studies show that the elastic efficiency of the ligament can be estimated from the size of the hysteresis loop obtained by loading and unloading a freshly killed individual (Trueman, 1953; Hunter and Grant, 1962). Pelecypods having a mechanically inefficient ligament use muscular energy transmitted hydrostatically through the foot or mantle cavity to open the valves (Hunter and Grant, 1962).

The pelecypod ligament is strained when the valves are closed. Above the hinge axis, the strain is tensile; below it, the strain is compressional. Normally the ligament is constructed so that the junction between the functional parts of the lamellar and fibrous layers more or less coincides with the hinge axis, because each layer is resistant to only one kind of stress.

Only some of the energy stored in the pelecypod ligament comes from the adductor muscles. Galtsoff (1964) noted that if the adductor muscle of an oyster is cut, the valves open farther than they do when the oyster is narcotized and the adductor fully relaxed. The origin of this extra energy remains unclear.

Trueman (1949) found that the functional part of the ligament of *Tellina tenuis* is not, as would be expected, the most recently formed part; he suggested that additional secretion of fibrous layer in the middle part of the ligament stretches the lamellar layer so that early formed parts of the ligament remain functional for long periods of time. If this did not happen, only the last formed part of the ligament could function, because the strain on the older parts would be gradually released as the valves opened slowly during growth. In fact, in many pelecypods, the anterior part of the ligament is torn apart as each valve grows in a separate helical spiral (Perkins, 1969, p. N756). Thus, Trueman (1950) found that in *Mytilus edulis*, the whole of the original ligament of a shell 16 mm long is destroyed when the mussel has grown to a length of 70 mm. Thus, only the posterior part of the ligament of *M. edulis* functions at any one time. Trueman concluded that the

ligament of *M. edulis* becomes functional when the lamellar layer is subjected to tensile strain by the growth of the fibrous layer beneath it. This strain is increased when the valves are closed, but a significant part of the opening force is generated biochemically by the mantle during the formation of the ligament. This extra energy may assist in opening the valves for locomotion, burrowing, and feeding, but equally importantly, it enables the valves to open slowly during growth.

Bevelander and Nakahara (1969) reported that the fibrous layer of the ligament of *M. edulis* is formed of long euhedral pseudo-hexagonal needles of aragonite dispersed in a homogeneous organic matrix. The diameter of each needle increases away from the calcification front, and it may be this expansion in volume that stretches the outer layer and activates the ligament. Alternatively, quinone tanning of the protein forming the lamellar layer may cause it to shrink and thus compress the underlying fibrous layer.

A closer analog to the rostroconchs is found in the extraordinary living pelecypod *Pinna*. In *Pinna*, the valves are joined rigidly by a long simple ligament, which has both lamellar and fibrous layers impregnated with calcium carbonate. Yonge (1953b) reported that the ligament of *Pinna* is not elastic and has no opening thrust on the valves. When the adductor muscles contract, the valves are flexible enough to be pulled together, but the ligament does not bend appreciably (Yonge, 1953b, p. 338).

Growth lines on the shell of *Pinna* show that earlier growth increments gape more widely than later formed ones, so that the valves must have opened slowly during the growth of the shell. The force that causes the valves to gape during growth has not been documented, but the ligament may generate this opening moment. If *Pinna* has a self-opening shell, rostroconchs may have functioned in a similar manner.

In contrast to most pelecypods and the bivalved gastropods, all rostroconchs had valves that were rigidly joined dorsally. In some genera like *Conocardium* (pl. 38, figs. 1, 3, 6, 11, 14) and *Arceodomus* (pl. 43, figs. 9, 11, 14), the ventral and posterior shell margins are tightly apposed, but in others like *Ribeiria* (pl. 6, figs. 3, 5, 6) *Eopteria* (pl. 24, figs. 14, 15, 20) and *Pseudoconocardium* (pl. 40, figs. 4, 6, 11), there are prominent shell gapes. Growth lines on both kinds of shells show that the valves opened slowly during life, so that the ventral edges of early increments may eventually gape at angles of 180° or more.

Because the valves of rostroconchs are joined dorsally, energy was needed to separate the valves so that new increments could be added at the commissure. This energy could have been supplied in several, not necessarily mutually exclusive, ways. Although applied in small amounts for long periods of time, the energy was sufficient to rupture parts of the dorsal shell margin in almost all rostroconchs.

The most obvious primary source of mechanical energy in any animal is its musculature. Energy generated by the contraction of muscles could be transmitted hydrostatically to the shell either through fluids in the body cavity, particularly blood in the pedal haemocoel, or by the fluid (sea water) in the mantle cavity. If the volume of blood in the foot of a rostroconch could be kept constant by means of a Keber's valve or some comparable structure, the foot could be protracted between the ventral valve edges by contraction of its intrinsic transverse muscles and then inflated by means of the pedal retractors inserted on the shell. This would force the valves apart. Alternatively, the foot and (or) hypertrophied mantle tissue could be withdrawn into the shell by appropriate muscles, and if no sea water were allowed to escape, hydrostatic pressure would tend to open the valves.

We prefer the former explanation for forms like *Ribeiria*, *Eopteria*, and possibly *Bransonina* and *Pseudoconocardium*, as it is difficult to see how they could have effectively sealed all shell gapes to conserve water in the mantle cavity. However, it is equally difficult to envisage that *Arceodomus* and *Conocardium* had a foot large enough to open the valves, as the anterior gape is almost completely blocked by the anterior longitudinal shelves (pl. 43, fig. 13). In these latter forms, it seems more likely that the withdrawal of mantle tissue increased the hydrostatic pressure in the mantle cavity if muscular energy were used to open the valves.

Muscular energy may not have been the prime or only force that opened the valves of rostroconchs. Other possibilities include growth pressure resulting from the addition of new cells to the body mass, osmotic pressure in the body mass, or the unexplained opening moment of the pelecypod ligament which may be generated by crystallization pressure in the fibrous layer of the ligament.

MUSCULATURE

The principal muscles of shelled mollusks serve the foot and the mantle edges; other smaller muscles may be used to move the head, jaw apparatus, gills, and visceral mass. Most of the muscles are attached

to the shell at surfaces known as insertion areas (muscle scars) where minute microvilli reinforced by cytoplasmic fibrils fill tiny pits in the surface of the shell (Hubendick, 1957). Each muscle insertion moves toward the commissure and increases in size during growth; it also generates a thin shell layer with characteristic ultrastructure and mineralogy known as the myostracum (Oberling, 1964; Taylor and others, 1969; Batten, 1972). If the muscle insertion is linear, the corresponding myostracal layer will be planar, but if the insertion area is circular or oval, it generates a linear piece of myostracum (Waller, 1972).

Growth lines reflecting the shape of the commissural side of the muscle are normally produced on the surface of the insertion area by fluctuations in the rate of deposition of the underlying shell layers or the myostracum. As the trailing edge of the muscle moves toward the commissure during growth, new shell layers wholly or partly obliterate the areas where the muscle was previously inserted. If these shell layers are thinner across the old muscle-insertion areas than they are in other parts of the shell, a smooth concave muscle track is visible on the inside of the shell.

Sometimes a muscle inserted on the shell may run parallel to it for some distance, for example, the siphonal retractor muscles of siphonate pelecypods. In such a case, some individuals in a population may mold shell around the muscle bundles so that a series of linear concave depressions is formed on the inside of the shell (Runnegar, 1972). We refer to these structures as muscle impressions; they give evidence for the direction of action of the muscle.

Muscle insertions in fossil mollusks are best observed on natural or artificial internal molds of the shell. Growth lines on the insertion areas or well-defined muscle tracks unequivocally identify muscle-insertion areas; the shape of the leading and trailing edge of the insertion is also important. Characteristically, the leading edge will be a smooth, poorly defined curve; the trailing edge is usually well defined and is often scalloped. If the insertion is too poorly preserved to show any of these features, a thin section of a shelled specimen may reveal a myostracal layer or a discontinuity representing a thin myostracum.

It must be pointed out that only some of the original muscle insertions may be preserved. Many specimens of Paleozoic pelecypods have well-preserved adductor and pedal muscle-insertion areas but show no trace of a pallial line. Only one specimen in many may show this structure, and one should be

extremely cautious in using such negative evidence. Thus, although many ribeirioids have well-preserved pedal muscle insertions, only a few specimens show traces of the pallial line. We feel that these differences are due to preservation and that a pallial line was probably present in many rostroconchs.

Because there are no living rostroconchs, no modern analogs can be used to predict what rostroconch musculature looked like. Muscle-insertion areas must be recognized in one or more of the ways indicated above, and it is necessary to be most rigorous in assessing the significance of depressions on the interiors of shells.

Yonge (1953a) observed that pelecypods probably differ from primitive ancestral mollusks in having the peripheral part of the mantle attached to the shell by a series of radial muscles, the insertions of which coalesce to form the pallial line. He suggested that pallial attachment probably became necessary as lateral compression enlarged the mantle and shell relative to the foot and visceral mass. When the bivalved condition finally developed, the adductor muscles were formed by cross-fusion of the distal ends of the anterior and posterior radial muscles of the mantle. Yonge therefore made an important distinction between an inner series of shell or pedal muscles that control the foot and support the visceral mass, and an outer set of pallial muscles that control the edges of the mantle and serve to close the valves.

It is the enlarged mantle cavity of rostroconchs and pelecypods that creates the need for strong pallial retractor muscles and hence a well-defined pallial line. Small scattered pallial retractor muscles are present in *Neopilina*, and it also has a broad roughly circular zone where cells in the mantle epithelium are attached to the shell (Lemche and Wingstrand, 1959). Batten (1972) described myostracal shell layers in several Pennsylvanian gastropods which he attributes to muscles attaching the mantle to the shell. Thus, although *Neopilina* and the fossil gastropods lack what is conventionally called a pallial line, they have small muscles or appropriate mantle epithelial cells in comparable positions. Presumably these could be hypertrophied to form a well-defined pallial line if the proper conditions arose.

Yonge's twofold classification of the shell-attached muscles of the pelecypods can be conveniently applied to the Rostroconchia. We distinguish pedal and pallial muscles in many forms. Normally, the pedal muscles are more deeply inserted into the shell and are therefore more commonly preserved than the pallial muscles.

PEDAL MUSCULATURE

The oldest known rostroconchs that have well-preserved muscle-insertion areas are Early Ordovician ribeirioids (fig. 3) and eopteriids (fig. 4). A simple muscle array is shown by *Tolmachovia? jelli* n. sp. (fig. 3C, D; pl. 14, figs. 9–19). This species has subequal oval insertion areas on the anterior and posterior sides of the umbonal cavity (pl. 14, figs. 9–16, 18, 19) which are connected ventrally by linear insertion areas on the left and right umbonal flanks (pl. 14, figs. 11, 12). Because this ribeirioid is approximately equilateral, we feel that the foot projected ventrally and was formed mainly of subequal anterior and posterior retractor muscles inserted on the shell at the two oval depressions. The foot probably also contained circular and transverse intrinsic muscle fibers that were not attached to the shell. These muscles could oppose the longitudinal retractor muscles through the hydrostatic skeleton of the pedal haemocoel to lengthen or broaden the foot for probing and pedal anchorage. The linear insertion areas connecting the two pedal retractor insertions may have contained the ends of longitudinal muscles forming the sides of the foot, or they may have been the areas of attachment of muscles supporting the gills.

The anterior and posterior pedal retractor insertions lie across the midline of the shell. We term these the anterior and posterior median insertions of the anterior and posterior median pedal retractor muscles, and distinguish them from right and left pedal retractor muscle insertions arranged symmetrically in both valves in advanced rostroconchs (pl. 22, figs. 5, 6) and most pelecypods. As we are uncertain of the function of the linear muscles connecting the median muscles, we name them descriptively as the right and left linear insertion areas of the corresponding side muscles.

Anterior and posterior median and left and right linear muscle insertions are present in several ribeirioid genera (fig. 3). In those forms having a well-developed pegma, the anterior median retractor is inserted on the posterior face of the pegma (pl. 5, fig. 4), and all muscle insertions are confined to the posterior umbonal cavity. In *Ribeiria lucan* (Walcott), a series of discrete circular- to kidney-shaped insertions replace the linear insertions of the left and right side muscles (fig. 3E; pl. 8, fig. 14).

Complex right and left linear muscle insertions also are present in the ischyrioid *Ischyria norvegica* Soot-Ryen (fig. 3A; pl. 19, figs. 10–14). It is not known whether *Ischyria* has large anterior and posterior median insertions, but because of the pres-

ence of side muscles, we assume that the anterior and posterior retractors of the foot originated on the inner sides of the two pegmas found in *Ischyria* (pl. 18, figs. 22, 25).

The protoconch of another ischyrioid, *Pseudotechnophorus typicalis* Kobayashi, has a tiny anterior median muscle insertion and an equally small linear insertion area preserved only on the left side of the specimen (fig. 3F; pl. 20, figs. 13–15). We view these structures as the insertions of muscles that were larger in the ancestors of *Pseudotechnophorus* but that became limited to the shell apex when new right and left lateral pedal muscles evolved; the relict structures also indicate a phylogenetic relationship of *Pseudotechnophorus* to the ribeirioids. The lateral pedal muscles of *Pseudotechnophorus* were attached at one large insertion and several smaller insertions on the right and left flanks of the valves (fig. 3G; pl. 20, fig. 8). We term the large lateral pedal muscle, the primary pedal retractor, and the small lateral pedal muscles the "secondary retractors," to differentiate them from the median retractors of ribeirioids and the anterior, umbonal, and posterior pedal retractors of pelecypods.

Eopteria, like *Pseudotechnophorus*, has a large lateral pedal muscle insertion (pl. 22, figs. 5, 6) and three smaller secondary insertions on each valve (pl. 22, figs. 5, 6). A reconstruction of the musculature of *Eopteria* is shown in figure 4. The entire musculature of this genus is not known from any one specimen, and the reconstruction is based on several specimens from the same locality, each of which shows some of the muscle insertions. The interpretation of the musculature of *Eopteria* given here differs from that of Pojeta, Runnegar, Morris, and Newell (1972), in that three small dorsally located insertions shown on the earlier diagram are now thought to be discontinuous muscle insertions forming the dorsal part of the anterior end of the pallial sinus (pl. 22, figs. 3, 4, 7, 8). Figures 3 and 4 on plate 22, show that in this specimen the pallial sinus is discontinuous dorsally but not ventrally, and figures 7 and 8, on plate 22, show three discontinuous small dorsal muscles in the same approximate position as the dorsal part of the pallial line of the other specimen. The similarity of the adult musculature of *Eopteria* and *Pseudotechnophorus* suggests a phylogenetic link between the ischyrioids and the conocardioids.

Some of the few known specimens of conocardiacans that have muscle-insertion areas preserved (fig. 5) have a large primary pedal-retractor inser-

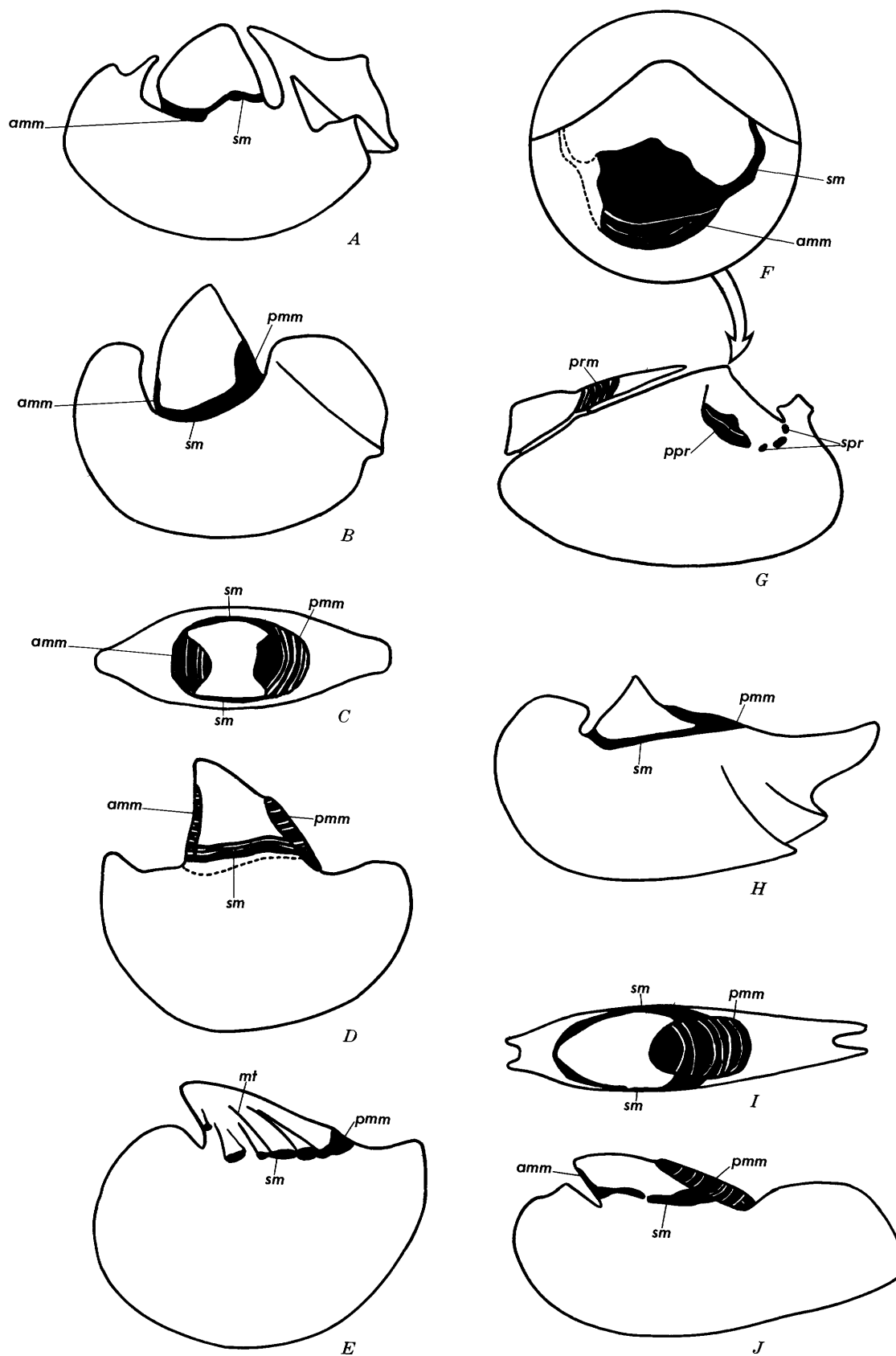


FIGURE 3.—(See explanation on facing page.)

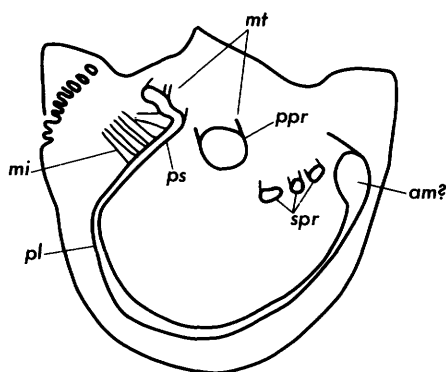


FIGURE 4.—Composite diagram of the muscle insertions of the left valve of *Eopteria ventricosa* (Whitfield); *am*, adductor muscle insertion(?); *mi*, muscle impression; *mt*, muscle track; *ppr*, primary pedal-retractor muscle insertion; *ps*, pallial sinus; *pl*, pallial line; *spr*, secondary pedal-retractor muscle insertions.

tion in the umbonal cavity of each valve (pl. 38, figs. 21, 22, 24). Smaller insertions in this area are regarded as secondary pedal retractors (pl. 53, figs. 21–23). Some conocardiceans show no obvious pedal-retractor-insertion areas (pl. 53, figs. 1–4).

Some pelecypods have muscles inserted on the shell that serve to protract the foot. In some forms, the distal ends of these muscles run transversely around the foot, forming a sphincter which is used to confine blood to the pedal haemocoel. Contraction of the intrinsic transverse muscles of the foot then protracts the foot if the shell-inserted pedal retractors are simultaneously relaxed. The living solenid *Ensis* operates its foot in this way (Trueman, 1967).

Other pelecypods (unionids, arcaceans, trigoniids) have a pedal muscle inserted on the shell below the insertion of the anterior adductor. In these animals, the muscles act in directions that enable them to move the foot anteriorly and ventrally. Such muscles are termed “pedal-protractor muscles.”

FIGURE 3.—Musculature of various genera of the Ischyrinioida and Ribeirioida; *amm*, anterior median muscle insertion; *mt*, muscle track; *pmm*, posterior median muscle insertion; *ppr*, primary pedal-retractor muscle insertion; *prm*, pallial retractor muscle insertion; *sm*, side muscle insertion; *spr*, secondary pedal-retractor muscle insertions. A, Composite diagram of left valve of *Ischyrinia winchelli* Billings and *I. norvegica* Soot-Ryen. B, Left valve of *Tolmachovia concentrica* Howell and Kobayashi. C, D, Dorsal and left-valve views of *Tolmachovia? jelli* n. sp. E, Left valve of *Ribeiria lucan* (Walcott). F, G, Enlargement of larval musculature and a diagram of adult musculature of *Pseudotechnophorus typicalis* Kobayashi. H, Composite diagram of left valve of *Technophorus* sp. I, J, dorsal- and left-valve views of *Ribeiria pholadiformis* Sharpe.

None of the primary and secondary pedal-muscle insertions of rostroconchs are low enough on the shell to have functioned as direct pedal protractors, and we cannot determine whether any of them served as sphincters. Thus, in rostroconchs, pedal protraction seems to have been accomplished only by hydrostatic means.

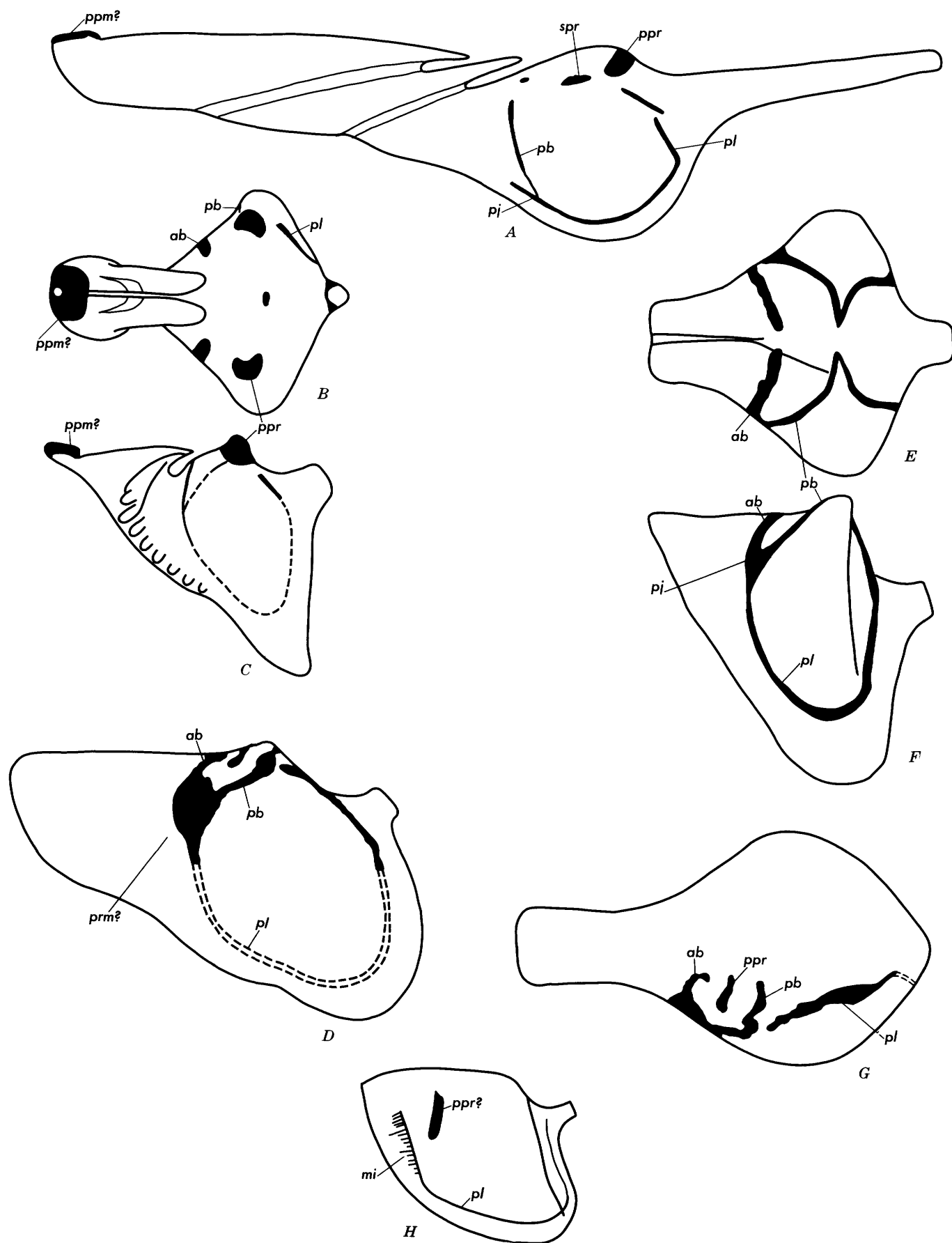
PALLIAL MUSCULATURE

The Ordovician ribeirioid *Wanwania* shows traces of a pallial line (pl. 3, fig. 7). We believe that most ribeirioids, with the possible exceptions of *Heraulti-pegma* and *Watsonella*, had pallial lines where the peripheral parts of the mantle were attached to the shell by radial mantle muscles. As noted, many specimens of many species of Paleozoic pelecypods preserve impressions of the adductor and pedal muscles, but only a very few specimens preserve the pallial line. The internal molds of ribeirioids that we have studied are generally not well enough preserved to show the shallow insertions of the small radial muscles of the mantle.

Several specimens of *Eopteria* preserve parts of the pallial line (fig. 4; pl. 22, figs. 1, 2, 3, 4; pl. 23, figs. 2, 3). There is an obvious anterior pallial sinus, and one specimen shows shallow impressions of the radial muscles of the mantle within the pallial sinus (pl. 22, figs. 5, 6). The absence of visible impressions on other parts of the shell indicates that the radial mantle muscles were both larger and longer in the area of the sinus. If so, the anterior part of the mantle was also enlarged in this area, and, by analogy with pelecypods, could be extended beyond the limits of the shell. We term these enlarged radial muscles of the mantle pallial retractor muscles.

The pallial line and associated radial muscle tracks are best preserved in one specimen of *Euchasma* from the Lower Ordovician of Newfoundland (pl. 27, fig. 9). The bending of the pallial line laterally in the anterodorsal region of the shell shows that an anterior pallial sinus was also present in *Euchasma*, but this part of the specimen is not well preserved, and no radial mantle muscle impressions are visible.

Pseudotechnophorus has a large muscle insertion in the isolated cavity of the shell above the anterior pegma (fig. 3G; pl. 20, figs. 10, 11). A muscle originating in this position is unlikely to have been connected to the foot, because the pegma effectively separates this cavity from the main mantle cavity. We assume that *Pseudotechnophorus* had radial mantle muscles, even though a pallial line is not preserved on any of the specimens seen by us; and we interpret the muscle in the anterior umbonal cavity



as an enlarged radial mantle muscle which functioned as a pallial retractor.

We do not have many conocardiaceans that have preserved pallial muscle insertions. In the few specimens we do have, the pallial line is smooth (fig. 5; pl. 53, figs. 1-4, 21-23). In *Bransonia?* sp. (fig. 5E, F; pl. 53, figs. 1-4), and *B. robustum* (Fletcher) (fig. 5D, G; pl. 53, figs. 21-23), the anterodorsal part of the pallial line is Y-shaped and has anterior, posterior, and ventral branches; in these two species, the junction of these three branches (the pallial junction) is the site of a larger muscle insertion (pl. 53, figs. 1, 21, 23). In *B. cressmani* n. sp. (pl. 54) and *Conocardium elongatum* (Sowerby) (pl. 38, fig. 22), the anterior part of the pallial line is not Y-shaped. In *Conocardium aliforme?* (Sowerby) the posterior branch is not connected with the anterior and ventral branches (fig. 5H; pl. 51, fig. 11). This species has well-defined radial mantle impressions emanating from the anterior and possibly the posterior branch of the pallial line (fig. 5H; pl. 51, fig. 11), indicating that as in *Eopteria*, these parts of the pallial line had pallial retractor muscles which could withdraw mantle tissue extended from the aperture of the shell. The larger muscle insertion at the junction of the branches of the pallial line in *Bransonia?* sp. and *B. robustum* probably housed a muscle that performed the same function.

Several conocardiacean species have circular to elongate depressions on both sides of the hinge just inside the anterior aperture of the shell (fig. 5B, C; pl. 40, fig. 11; pl. 47, fig. 12). These depressions were filled by subsequently deposited inner shell layers as the shell grew. We interpret them to be muscle insertions and suggest that they housed muscles used to protract mantle tissue from the anterior aperture of the shell (pallial protractor muscles). This interpretation helps to explain their unusual position on the shell and suggests the method used by conocardiaceans to protract the mantle. No similar insertions are known in either *Eopteria* or *Pseudotechnophorus*, and we assume that mantle protraction

in these forms was accomplished entirely by hydrostatic means.

Pojeta, Runnegar, Morris, and Newell (1972) argued that no rostroconchs had cross-fused radial mantle muscles and therefore no adductor muscles. This statement was based on the premise that cross-fusion could not have occurred because the mantle lobes were not embayed dorsally. We now feel that the large insertion at the posterior terminus of the pallial line in *Eopteria* (fig. 4; pl. 22, figs. 1, 2) may have housed an adductor muscle that served to flex the shell and to create water currents in the mantle cavity. No other rostroconch is known to have had a comparable structure.

ALIMENTARY CANAL

Rostroconchs are regarded as having an anterior mouth and a posterior anus. This conclusion is supported by the lack of any evidence of torsion in rostroconchs and by the likelihood that they are descended from monoplacophorans and were ancestral to pelecypods. In primitive rostroconchs like *Heraultipectegma* and *Ribeiria*, the mouth was probably close to the anterior gape, but in such highly specialized genera as *Conocardium* and *Arceodomus*, the mouth was probably situated at the anterior end of the mantle cavity, near the junction of the body and snout. We assume that the mouth moved posteriorly (in a relative sense) as the feeding structures of the snout became increasingly more complex.

Before the development of a prominent posterior rostrum, the anus probably was near the dorsal side of the posterior shell gape. Because of the small diameter of the rostrum in many forms, the anus was probably not at its distal end. We conclude that in rostrate forms, the anus was near the proximal end of the rostrum and that water currents generated by cilia removed feces from the mantle cavity.

FEEDING STRUCTURES

Various rostroconchs have features indicating that structures could be protruded from the anterior shell gape. These features are: (1) the anterior pallial sinuses of *Eopteria* (pl. 22, figs. 1-4; pl. 23, figs. 2-3), *Euchasma* (pl. 27, fig. 9), and perhaps *Wanwanian* (pl. 3, fig. 7); (2) the impressions of enlarged radial muscles of the mantle at the anterior end of the pallial line of *Eopteria* (pl. 22, figs. 5, 6) and *Conocardium* (pl. 51, fig. 11); (3) the apertural denticles of all conocardioids, probably formed by folds in the enlarged mantle as it was withdrawn into the shell (pl. 34; figs. 9-10); and (4) the muscle insertions interpreted as pallial protractor muscles

FIGURE 5.—Musculature of various genera of the Conocardacea; *ab*, anterior branch of the pallial line; *mi*, muscle impression; *pb*, posterior branch of the pallial line; *pj*, pallial junction; *pl*, pallial line; *ppm*, pallial-protractor muscle insertion (?); *ppr*, primary pedal-retractor muscle insertion; *prm*, pallial retractor muscle insertion; *spr*, secondary pedal retractor muscle insertion. A, Reconstruction of *Conocardium elongatum* (Sowerby). B, C, Dorsal and left-lateral views of *Hippocardia zeileri* (Beuhausen). D, G, Left and dorsal views of *Bransonia robustum* (Fletcher). E, F, Dorsal and left-lateral views of *Bransonia?* sp. H, Left-lateral view of *Conocardium aliforme?* (Sowerby).

that occur inside the edge of the anterior aperture in conocardiaceans (pl. 47, fig. 12). We believe that rostroconchs used this enlarged and extendible mantle tissue for deposit feeding.

Scaphopods and palaeotaxodont pelecypods use cephalic tentacles (captaculae and palp proboscides) in deposit feeding to collect food particles; similar structures are used for the same purpose by various prosobranch gastropods. It seems likely that many primitive rostroconchs used cephalic outgrowths to gather food. However, in the Conocardiidae, at least, these structures seem to have been superseded by outgrowths of pallial (mantle) tissue. In *Conocardium* and *Arceodomus*, the snout was effectively blocked by several pairs of enlarged marginal denticles, called longitudinal shelves (pl. 43, figs. 12, 13; pl. 44, figs. 2, 4). These shelves contained complex folds of the mantle, because the growing edges of the shelves, which oppose one another at the midline, are formed of outer shell layer. This composition implies that the mantle edge rested along the edges of the longitudinal shelves when the mantle was withdrawn. Because the mantle epithelium of mollusks is characteristically ciliated, we feel that the mantle resting on these anterior longitudinal shelves formed a complex sorting structure which collected and sorted food for eventual transmission to the mouth. The mouth was at the end of an elongate passage that penetrated between the various pairs of shelves (pl. 43, fig. 13). Because another characteristic of the molluscan mantle is the widespread occurrence of tentacles fringing the mantle edge, it is reasonable to believe that similar pallial tentacles may have assisted in the food-gathering process of rostroconchs. We thus view the feeding structure of conocardiids as a set of forward-opening ciliated cones that acquired food by means of an inhalent water current and the manipulative abilities of fringing pallial tentacles. The food particles were moved posteriorly by cilia lining the cones, sorted, and transferred to the mouth through a small aperture on the posteroventral side of the cones. Inhaled sediment was transferred anteriorly and exited along a rejection tract at the ventral edge of the feeding aperture.

The shape of conocardiids suggests that they both lived and fed infaunally. The scaphopods are good functional analogs for such genera as *Conocardium* (pl. 38, figs. 2, 8) and *Arceodomus* (pl. 43, figs. 5, 15), except that they use cephalic captaculae rather than mantle tissue to collect food.

Conocardium and *Arceodomus* are highly specialized rostroconchs. More primitive rostroconchs have

less complex anterior skeletal structures, and we speculate that they had a primitive version of the conocardiid feeding apparatus. Probably they used enlarged flaps of the mantle to collect and funnel food to the mouth. Some forms may have had a structure analogous to a pelecypod siphon which projected from the anterior gape. We envisage such a structure as being present in the ischyriiniid *Pseudotechnophorus* because the anterodorsal gape is oval or kidney shaped, and because an insertion of a large muscle, which probably retracted the mantle (fig. 3G), is dorsal to the anterior pegma. Living tellinacean pelecypods use their posterior siphons for deposit feeding in this way (Pohlo, 1969).

Most technophorid rostroconchs as well as the genus *Ischyria* have no anterior gape. These forms are laterally compressed, have a posterior rostrum, and probably lived infaunally. It seems likely that they were filter feeders which used cilia on the gills or mantle to pump water and suspended food in the posterior shell apertures.

The mode of life of the eopteriid *Euchasma* is more difficult to interpret. All species of this genus have the anterior end of the shell reduced. The shells of *E. blumenbachii* (pl. 27, figs. 1-16) and *E. mytiliforme* (pl. 29, figs. 6-8) resemble those of living epifaunal mytilid and dreissenid pelecypods. *E. jonesi* has a small anterior lobe, and the shell is more or less similar to that of living modioliform pelecypods (pl. 28, figs. 12-15).

By analogy with living pelecypods (Stanley, 1972), the mytiliform *Euchasmas* probably lived epifaunally, and the modioliform *Euchasmas* may have lived semi-infaunally. The narrowness of the anteroventral shell gape (pl. 29, figs. 8, 9, 12) of *Euchasma* and the shell shape suggest that this genus was sessile. This conclusion is supported by the narrowness of the ventral shell gape, which would make it difficult for a foot to project ventrally. If, however, *Euchasma* is compared with the epifaunal cowrie gastropods, which it also approximates in form, a different interpretation results. This comparison shows that a large and effective foot can project through a narrow shell aperture, so *Euchasma* may have been a motile epifaunal or semi-infaunal animal. The presence of marginal denticles lining the ventral gape indicates that mantle tissue at least was probably extended through this aperture.

Euchasma has a sizable circular shell aperture above the anteroventral gape. This circular hole is formed by the edges of both valves (pl. 28, figs. 15, 16). It is effectively blocked by the pegma (pl. 29, figs. 3, 11, 14, 15), although there are small holes

on either side between the pegma and the valves (pl. 29, fig. 15). *Euchasma* has an anterior pallial sinus (pl. 27, fig. 9), so mantle tissue could probably have been extended from and withdrawn into this area of the shell. This mantle tissue may have been used for deposit feeding, as it was in other rostroconchs, and the pegma may have blocked sediment from entering the shell. The circular aperture is anatomically anterior but functionally ventral, as during life, it would have been apposed to the substrate. Thus, *Euchasma* may have been an epifaunal to semi-infaunal deposit feeder which "vacuumed" organic matter from the sediment-water interface. This unusual mode of life may explain why it could not compete successfully with epifaunal suspension-feeding pelecypods, which first became abundant in the Middle Ordovician.

An alternative explanation of the mode of life of *Euchasma* is that the circular anterior aperture contained a structure for attaching the animal to the substrate. The attachment structures may have been similar to the byssus of pelecypods or the pedicle of brachiopods, and the animal may have suspension-fed from the posterior shell gape. Because rostroconchs probably had hypertrophied anterior pallial structures, *Euchasma* may have been attached by one or more hypertrophied pallial tentacles. These tentacles could have been manipulated by contained fluid and pallial retractor muscles attached at the anterior pallial sinus. On the whole, we prefer the explanation that *Euchasma* was a mobile epifaunal or near epifaunal deposit feeder.

CLEANING THE MANTLE CAVITY

Suspension-feeding organisms that have an enclosed mantle cavity have the problem of eliminating unwanted particulate matter (pseudofeces) swept into the mantle cavity along with the food. Pseudofeces continually accumulate in enclosed shells and must be continually removed. In most pelecypods, pseudofeces fall from the gills and mantle to the floor of the mantle cavity and are then ejected by sudden contractions of the adductor muscles (Cox and others, 1969, p. N19). In brachiopods, reversal of the frontal cilia of the lophophore transports the pseudofeces to the mantle, and then mantle cilia move them to the mantle edge. They are expelled when the valves are adducted (Rudwick, 1970, p. 121).

Some pelecypods have the ventral edges of the mantle extensively fused together, leaving only the two posterior siphonal orifices and a relatively small aperture for the foot. Many such animals also have

a small fourth aperture between the pedal and siphonal orifices (Yonge, 1948; Runnegar, 1972). In active burrowers like *Ensis*, this aperture acts as a safety valve to lower the fluid pressure in the mantle cavity which peaks with adduction in the digging cycle (Trueman, 1968). In more passive burrowers, the fourth aperture functions as an outlet for pseudofeces carried to it by ciliated tracts on the mantle and visceral mass (Yonge, 1948).

Nearly all rostroconchs that have reduced posterior and ventral shell apertures retain a small circular ventral orifice between the posterior end of the anterior gape and the rostrum (pl. 40, fig. 7). This orifice probably functioned in the same way as the fourth aperture of less actively burrowing pelecypods—as an outlet for pseudofeces. Such a ventral orifice does not occur in the Conocardiidae, but, as mentioned previously, these rostroconchs may have had effective sediment screens in their anterior gapes and thus may not have been troubled by the accumulation of pseudofeces in the mantle cavity.

WATER CURRENTS AND GILLS

The helcionellacean univalves, like *Neopilina* (Lemche and Wingstrand, 1959), probably drew water in under the anterolateral eaves of the shell and passed it out posterolaterally (figs. 6, 9). We assume that the gills were laterally disposed in these animals and that cilia on the gills and epithelium of the mantle cavity generated the water currents. In the univalve genera *Yochelcionella* (pl. 1, figs. 1–7) and *Anabarella* (pl. 17, fig. 8), the water current probably entered anteriorly (figs. 6, 9). When the shell became modified into the ribeiriid shape, water was drawn in through the anterior gape and left the shell posteriorly (fig. 6). This water current was used for feeding as well as respiration. *Ribeiria* may have had a single pair of gills, the blood vessel being connected with the heart through the discontinuity in the side muscles seen in some species (fig. 3J).

A similar water flow may have taken place in the eopteriids and conocardiceans. However, it is equally likely that the Conocardiacea drew water for respiration in through the posterior rostrum. Scaphopods use the posterior shell aperture to obtain water for respiration, although they deposit feed anteriorly. In the conocardiceans, the exhalent current may also have flowed out the rostral orifice, or it may have left through the ventral orifice. Perhaps both apertures were used for this purpose. We suggest that all rostroconchs had gills because they all have an expanded mantle cavity.

The technophorids and *Ischyria* have no anteri-

or shell apertures. We conclude that water entered and left the mantle cavity via the two posterior shell apertures.

FUNCTION OF THE HOOD

Some Ordovician through Mississippian conocardiacans have a hood attached to the carinal areas of the valves (pl. 45, figs. 10–13; pl. 48, fig. 2). There are two obvious possible explanations for the existence of the hood, and either or both may have functional significance. First, the significant structure may be the hood, which could have been used to support the shell in a soft substrate, or it could have deflected water currents to or away from the rostral orifice. Some hooded rostroconchs resemble some living tropical cardiid pelecypods that are flattened in an anterior-posterior direction because the body tissue contains symbiotic algae which receive sunlight through the thin shell (Kawaguti, 1950). These clams lie exposed and are metabolically connected with the algae in their tissue. However, the resemblance of these cardiids to hooded rostroconchs is only superficial. The hood is a totally external structure, composed of the outer shell layer, which contained living tissue only along its central axis, the elongated ventral orifice. Thus, the hood probably had some other function.

The second possibility is that the final structure, the hood, is not of primary functional significance; rather the structure that forms it, the elongated ventral orifice, is the functionally significant structure. If rostroconchs evolved a long thin tube at the posteroventral commissure, they could maintain such a structure during growth only by generating a planar structure on each valve. We speculate that the prolongation of the ventral orifice, for whatever functional reason, may have had more functional significance than the finished hood. Once the hood formed, it may have provided support, enabling the animal to live in soft substrates, but the hood may have just been the necessary consequence of the elongation of the ventral orifice.

TAPHONOMY

Post-Ordovician rostroconchs (Conocardioida) are most common in marine shales and silts and reef limestones. Older rostroconchs are presently known most commonly from the carbonate sequences of epicontinental seas. Jameison (1971, p. 1334) noted that "*Conocardium*" has only been found in marginal reef deposits in the Devonian of western Canada, "and is therefore considered indicative of shallow, turbulent, open marine conditions." Similarly, conocardiids are common in Viséan (Mississippian)

shoreline cliff talus of the Wagon Creek Breccia (Veivers and Roberts, 1966) in northwestern Australia (John Roberts, oral commun., May 1972).

In contrast, *Pseudoconocardium* and *Arceodomus* are most common in low-energy marine shales of the Pennsylvanian of north-central Texas. *Bransonia* occurs in a similar environment in coastal outcrops of the middle Permian Wandrawandian Siltstone in New South Wales, Australia. At one important locality, a recent shore platform at the town of Ulladulla, many specimens of *Bransonia robustum* (Fletcher) occur in silty beds. They are associated with many other fossils, most specimens of which have been preserved in situ. These include life-oriented productoid and spiriferoid brachiopods; shallow-burrowing, free-swimming, and endobyssate pelecypods; collapsed but articulated crinoids; large unbroken colonies of lacy fenestrate bryozoans; and discoidal poriferans.

The section of the Wandrawandian Siltstone exposed at Ulladulla contains several thin sands that vary in thickness from a few centimetres to tens of centimetres. These sands are also fossiliferous, but most of the fossils they contain are transported. The sands appear to have formed during rare high-energy events and therefore contain disoriented skeletons of organisms that (1) inhabited the surface of the silt and were light enough or were sufficiently loosely attached to be transported with the sand; and (2) that were unable to disinter themselves after burial in the sand. The sand beds also contain life-oriented burrowing pelecypods that rapidly recolonized the substrate after each high-energy event.

Extensive collecting has shown that there are few if any specimens of *Bransonia* in the sand beds. Nor are there any byssate pelecypods or attached echinoderms. At least three alternative explanations are possible: (1) *Bransonia* burrowed so deeply that it was never disinterred by the high-energy currents that deposited the sands; this is unlikely, as there is no evidence of an elongate rostrum or large posterior siphons in *Bransonia*. (2) *Bransonia* was attached to the substrate by some structure comparable with the pelecypod byssus; this too is unlikely, as *Bransonia* shows no anterior reduction, a feature seen in the epifaunal species of *Euchasma*. (3) *Bransonia* was sufficiently mobile to tunnel out of the sand after transportation and burial; this seems to be the most reasonable alternative and is the one we prefer.

We have searched for specimens of rostroconchs encrusted with other organisms that might provide some clue to the life habits of the rostroconchs. Such

specimens are difficult to find in museum collections, and it is always difficult to prove conclusively that the encrusting organisms lived during the life of the rostroconch rather than encrusting it after death. The most useful specimen we have found is an individual of *Hippocardia* encrusted by an aulopodid tabulate coral (pl. 33, figs. 1–2). The coral colony on this specimen seems to have been broken at least three times by the growth of the hood of the *Hippocardia*, suggesting that both organisms were growing simultaneously. The coral growth in this specimen also suggests that in life this species of *Hippocardia* had the whole of the dorsal surface of the hood exposed and was at most semi-infaunal.

A more equivocal example is a bryozoan holdfast attached to the rostral area of the right valve of a specimen of *Bransonia wilsoni* (pl. 52, fig. 9). On this specimen, a matching mark on the corresponding part of the left valve suggests, but does not prove, that the holdfast was attached to the rostroconch while the rostroconch was alive. Similar holdfasts on the interiors of productid brachiopod valves at the same locality show that bryozoans were growing on some of the dead organisms.

In summary, we have very limited paleoecological evidence. Most of the specimens for this study were gathered from museums, and paleoecological information must usually be gathered in the field. What information we do have tends to confirm the conclusions reached on comparative and functional morphology, that is, that most rostroconchs were mobile members of the shelf benthos and lived wholly or partially buried in the sediment. We have been unable to devote much time for research in this area and suggest it as a profitable and challenging direction for further enquiry.

PHYLOGENY

Living and fossil mollusks constitute the second largest and most variable invertebrate phylum (Barrington, 1967; Stasek, 1972). Most mollusks can be described as free-living metazoans that utilize a dorsal calcareous exoskeleton to provide structural support for a muscular foot (or its specialized derivative) and to provide an enclosed space outside the body (mantle cavity) that is used for feeding, respiration, and sometimes, locomotion. Because mollusks are so variable, no single unique character is present in all members of the phylum; they are unified by morphological gradations between different forms, by embryonic similarities, and by fossil evidence of their evolutionary history.

We recognize eight classes of mollusks and refer these to four subphyla:

Phylum MOLLUSCA Cuvier, 1797

Subphylum ACULIFERA Hatschek, 1891

Class APLACOPHORA von Ihering, 1876

Subphylum PLACOPHORA von Ihering, 1876

Class POLYPLACOPHORA de Blainville, 1816

Subphylum CYRTOSOMA Runnegar and Pojeta, 1974

Class MONOPLACOPHORA Wenz, 1940

Class GASTROPODA Cuvier, 1797

Class CEPHALOPODA Cuvier, 1797

Subphylum DIASOMA Runnegar and Pojeta, 1974

Class ROSTROCONCHIA Pojeta,

Runnegar, Morris, and Newell, 1972

Class PELECYPODA Goldfuss, 1820

Class SCAPHOPODA Bronn, 1862

We do not doubt that the forms Yochelson (1966, 1969) placed in the classes Mattheva and Stenothecoida (=Probivalvia Aksarina, 1968) are mollusks, but we prefer to assign them to other molluscan classes. They are discussed in subsequent parts of this section. Tentaculites, lapworthellids, cornulitids, hyoliths, and hyolithellids probably belong to other phyla (Fisher, 1962; Matthews, 1973; Runnegar and others, 1975).

ORIGIN OF THE MOLLUSCA

Stasek (1972) produced a thoughtful review of the data pertinent to this problem. We agree with his conclusion that the mollusks evolved from a pre-annelid stock of small ciliated acoelomate, vermiform organisms that had a diverticulated gut, longitudinal nerve cords, and a series of dorsoventral body muscles. None of the known Ediacaran fossils of soft-bodied organisms of late Precambrian age (Glaessner, 1971) resemble this hypothetical ancestor, but it is obviously similar to known living turbellarian flatworms.

THE ANCESTRAL MOLLUSK

Nineteenth century biologists visualized the common ancestor of mollusks as a bilaterally symmetrical untorted snail-like animal that had a limpet-shaped shell and a posterior anus opening into a small mantle cavity containing a pair of simple ctenidia (Pelseneer, 1906). This concept of an archetypical mollusk was derived mainly from studies of

the comparative anatomy of living forms, but it was also widely accepted by paleontologists.

When the living monoplacophoran *Neopilina* Lemche was discovered (Lemche, 1957), it was hailed as a living archetype. The only significant difference between *Neopilina* and the theoretical ancestral mollusk lies in the structure of the gills, which are arranged in a series lateral to the foot in *Neopilina*.

Because of the close similarity of *Neopilina* and early Paleozoic Monoplacophora, *Neopilina* is often considered to resemble the ancestor of all other molluscan classes. This archetypal concept has been criticized by Yochelson (1963), Horný (1965), Harry (1969), and Stasek (1972). An alternative view advocated by some authors is to derive the Monoplacophora and the other molluscan classes from nonshelled organisms that may have existed before and with early monoplacophorans. In this scheme, the differences between the various classes are produced in the nonshelled organisms, and calcification occurs after the characters of each class have been attained.

Stasek (1972) argued that the Aplacophora, Polyplacophora, and Monoplacophora were derived sequentially from an evolving ancestral stock. At present little evidence from fossils supports, or contradicts this suggestion. However, the Polyplacophora may have been derived from monoplacophorans that evolved multiple centers of calcification (Runnegar and Pojeta, 1974). Our study is largely concerned with the Monoplacophora and the five molluscan classes that we suggest were derived from it. This radiation began in the earliest Cambrian and is adequately shown in the fossil record (Runnegar and Pojeta, 1974).

THE OLDEST KNOWN FOSSIL MOLLUSKS

Russian stratigraphers divide the Early Cambrian of the Siberian Platform into four stages: from oldest to youngest Tommotian, Atdabanian, Botomian, and Lenian (Zhuravleva, 1970). The Tommotian deposits predate the first trilobites in the Siberian succession, and they contain a characteristic biota of archaeocyaths, mollusks, hyoliths, algae, and Problematica (Rozanov and others, 1969). In the fossil record, the base of the Tommotian appears to reflect the first appearance, in abundance, of animals that had calcareous skeletons, which is one definition of the beginning of the Cambrian (Zhuravleva, 1970; Webby, 1973).

Tommotian mollusks are small or minute limpet-shaped planispiral or helically coiled univalves (Rozanov and others, 1969). They include forms re-

sembling the widely known Cambrian genera *Scenella* Billings, *Helcionella* Grabau and Shimer, and *Pelagiella* Matthews, which are variously regarded as monoplacophorans, gastropods, or representatives of other primitive classes of mollusks (Knight, 1952; Rasetti, 1957; Horný, 1965; Yochelson, 1963, 1967). Rozanov and others (1969) referred all these univalves to the superfamilies Helcionellacea Wenz, 1938, and Pelagiellacea Knight, 1956, and considered them to be gastropods.

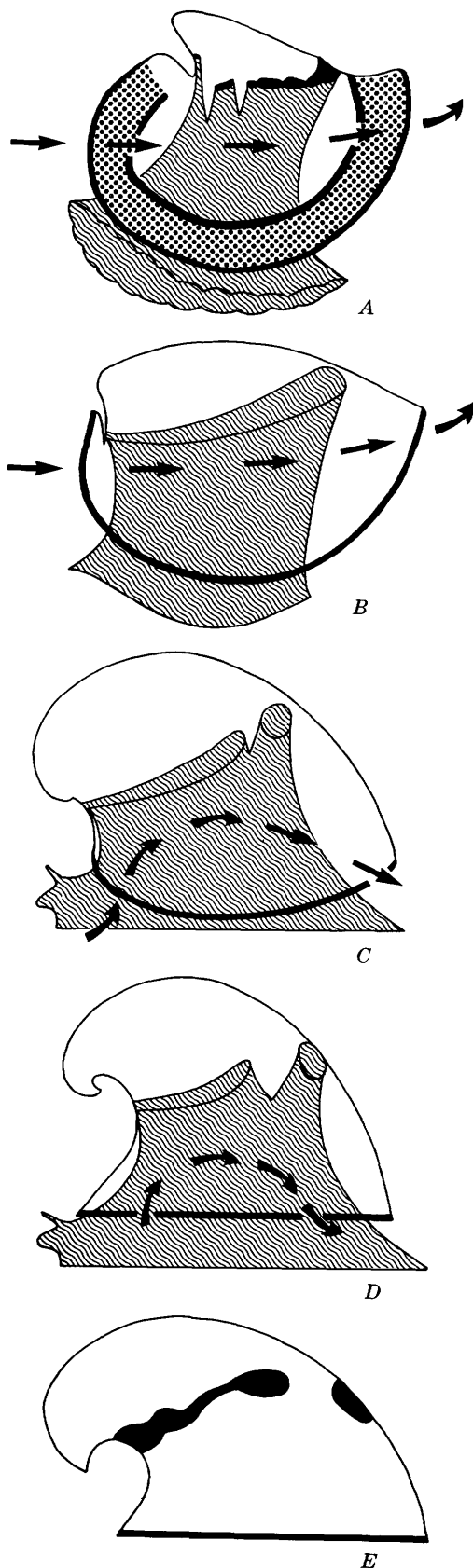
One of the Tommotian mollusks, the genus *Anabarella* Vostokova, is a laterally compressed planispiral univalve having a ventral margin that is obviously curved when the shell is viewed laterally (figs. 6, 7; pl. 17, fig. 8). *Anabarella* is intermediate in shell form between more typical Cambrian univalves like *Helcionella*, *Latouchella* Cobbold, and *Igorella* Missarzhevsky, and the first ribeiriid rostroconch, *Heraultipegma* n. gen. (= *Heraultia* Cobbold), from the Lower Cambrian of France (fig. 6; pl. 2). If *Heraultipegma* is derived from *Anabarella*, it is unlikely that *Anabarella* was a gastropod, as the Late Cambrian and Ordovician descendents of *Heraultipegma* show no evidence of torsion. It is therefore pertinent to examine the biological placement of *Anabarella* and other Early Cambrian univalves.

EARLY CAMBRIAN UNIVALVES

The class Gastropoda comprises animals that have a distinct head, a solelike foot adapted for creeping, a radula, and a visceral mass that is apparently rotated 180° about a vertical axis so that the anus and organs of the mantle cavity are above the head. This twisting of the visceral mass is known as torsion; in living gastropods, it occurs in early ontogeny by rapid contraction of the asymmetrical right larval retractor muscle and by differential growth (Fretter, 1969). The torsion seen in all primitive and most advanced gastropods isolates them from their presumed ancestors, the Monoplacophora (Knight and others, 1960).

Most gastropods have the body contained in a calcareous univalved shell which coils posteriorly away from the head and is therefore termed "endogastric." With the exception of the specialized limpets and a few aberrant forms, living gastropods have the shell coiled in a helical spiral. Normally this coiling is orthostrophic and dextral, but rare individuals or species have hyperstrophic (ultradextral) or sinistral shells.

Planispiral (isostrophic) shells resembling gastropods in external ornament and other features occur as fossils from the earliest Cambrian to the



Early Triassic (Knight and others, 1960). These are now normally referred to the gastropod suborder Bellerophontida, though there has been a long debate as to whether they were torted (gastropods) or untorted (monoplacophorans) (Yochelson, 1967). Recent studies have suggested that externally similar planispiral shells housed both monoplacophorans and gastropods (Rollins and Batten, 1968). If the shells have several bilaterally symmetrical muscle insertions, they are believed to be untorted and hence monoplacophorans; all others have been considered to be gastropods until proved otherwise. This argument is supported by the obvious asymmetry of the shell musculature in the otherwise symmetrical bivalved snails (Kawaguti and Yamasu, 1960), and by the presence of only one pair of pedal muscles in some bellerophontids (Knight, 1947; Peel, 1972).

If no muscle insertions are preserved, other criteria have been used. Knight (1952) and others suggested that the presence of (1) an anal slit or sinus, (2) secondary inner shell layers (parietal deposits) covering the exterior of earlier formed parts of the coil, and (3) an elongate trail, could be used to distinguish torted bellerophontids from untorted monoplacophorans (Rollins and Batten, 1968). The most compelling argument related to the anal slit or sinus, as it was believed that these structures only became necessary when torsion juxtaposed the anus and gills. Subsequently, Rollins and Batten (1968) showed that the Devonian planispiral univalve *Sinuitopsis* Perner has a series of bilaterally symmetrical muscle insertions (fig. 8) as well as a deep sinus, and they concluded that it was a sinus-bearing monoplacophoran. They speculated that a posterior anal sinus was probably advantageous in achieving maximum separation of respiratory currents and excretory products. They discouraged the use of a sinus as a tool for recognizing gastropods and emphasized the criteria of parietal deposits and posterior trails.

No Early Cambrian univalves have parietal deposits, but some have the concave side of the shell

FIGURE 6.—Speculative view of the origin of the ribeiriid rostroconchs (A–B) from Early Cambrian helcionellacean monoplacophorans. Arrows indicate probable path of water currents through the mantle cavity. The extent of the shell aperture is shown by the thick black line. Dotted shading in A represents the radial mantle muscles attached to the shell at the pallial line. Pedal muscle insertions in D are modeled from the Devonian cyclomyan monoplacophoran shown in E. A, *Ribeiria*, Late Cambrian-Ordovician; B, *Heraultipegma*, Early Cambrian; C, *Anabarella*, Early Cambrian; D, *Latouchella*, Early-Late Cambrian; E, *Cyrtionella*, Middle Devonian.

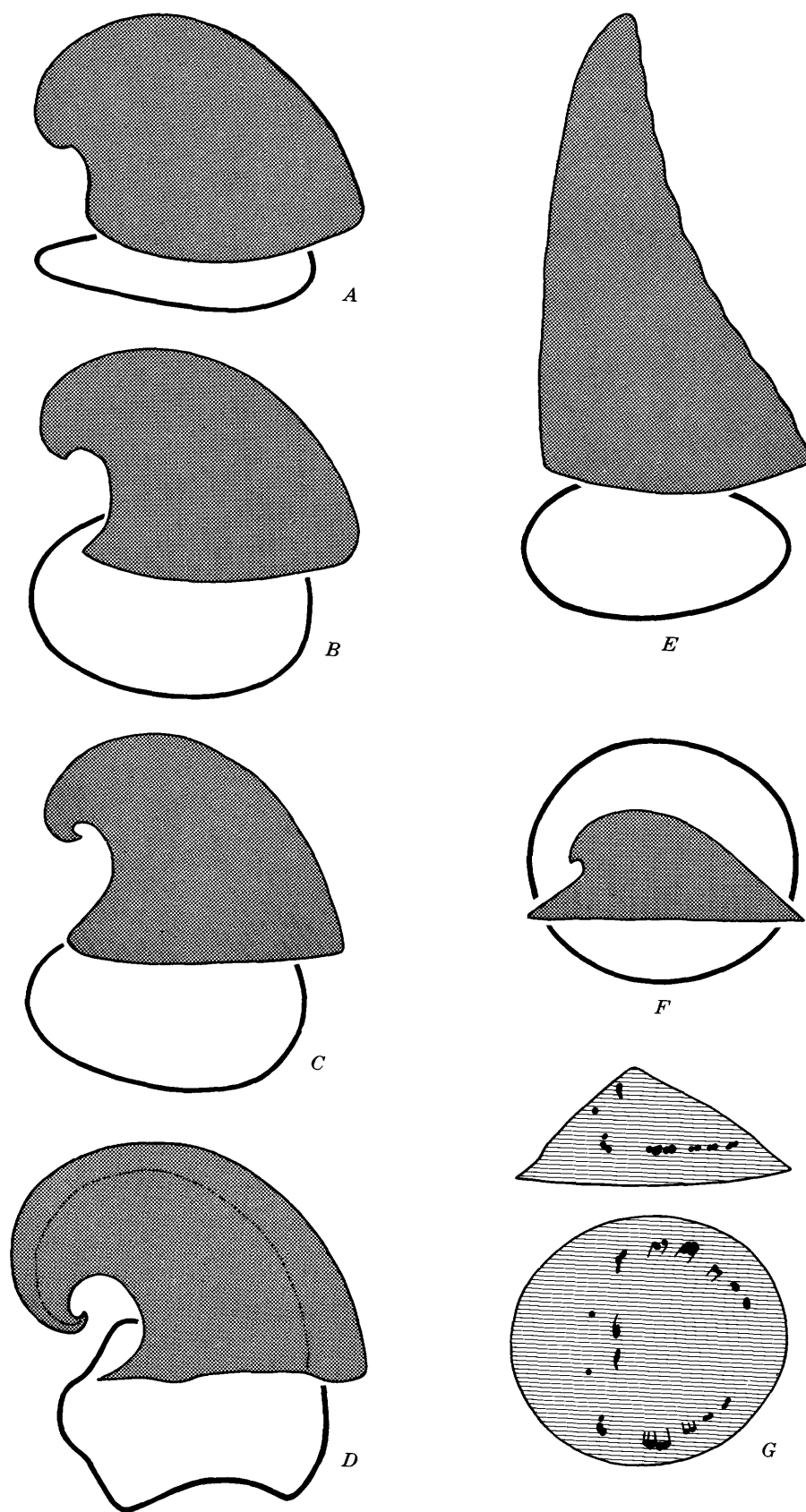


FIGURE 7.—(See explanation on facing page.)

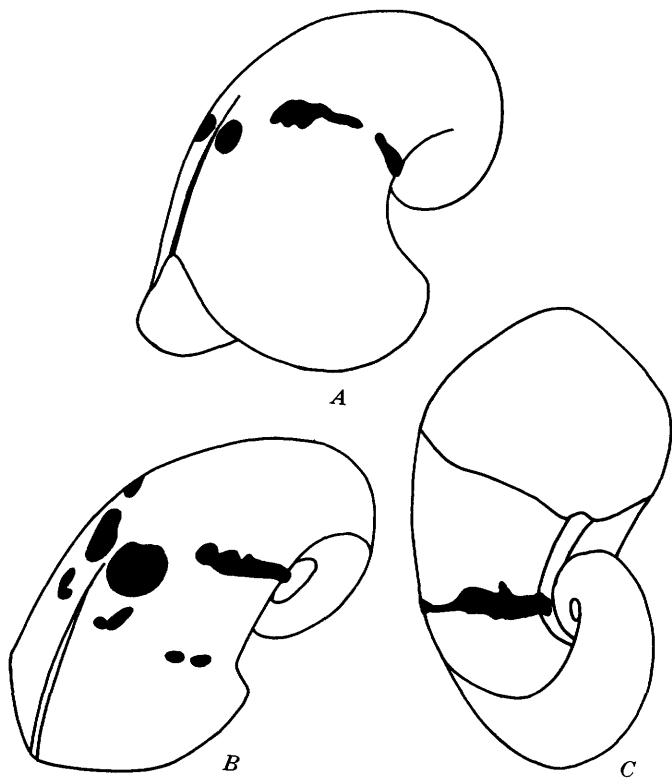


FIGURE 8.—Shell muscle insertions of cyclomyan monoplacophorans. A, *Sinuitopsis*, data from Rollins and Batten (1968); B and C, *Cyrtolites*, modified from Horný (1965).

expanded to form a trail (fig. 9). Knight (1952) argued that a trail would impede the maneuverability of the protracted head of the animal and concluded that such shells must have been coiled endogastrically away from the head (fig. 9A, modified from Knight (1952)). For this reason, Knight referred *Helcionella* and related Early Cambrian univalves to the Gastropoda. No muscle insertions have been seen in these forms.

In 1954, Rasetti illustrated internal molds of a small limpet-shaped shell from the Middle Cambrian Mt. Whyte Formation of British Columbia. These specimens have a number of small muscle insertions that are effectively bilaterally symmetrical. Rasetti referred the specimens to *Scenella* and concluded that they were monoplacophorans. A reconstruction of the body, modeled from *Neopilina* (fig. 10), vindicates this decision.

Knight and others (1960) referred *Scenella* and the enigmatic genus *Palaeacmaea* Hall and Whitfield to a separate family of the Monoplacophora. Rozanov and others (1969), however, referred the externally similar genus *Tannuella* Missarzhevsky to the Helcionellacea, and there is a gradation in external shell form from *Helcionella* through *Bemella* Missarzhevsky, *Ginella* Missarzhevsky, and *Tannuella* to *Scenella* (Rozanov and others, 1969). We therefore believe that the Helcionellacea are monoplacophorans, not gastropods.

Additional support for the monoplacophoran placement of the Helcionellacea comes from the Australian Cambrian helcionellid, *Yochelcionella* Runnegar and Pojeta, 1974 (pl. 1), which differs from other helcionellids by having a tube attached to the concave side of the shell. Figure 9 shows normal and tube-bearing helcionellids reconstructed as gastropods and monoplacophorans. The first reconstruction (fig. 9A) is modified from Knight (1952), who described it as a "harmonious and plausible picture." We agree. However, if the tube-bearing helcionellid is reconstructed in the same way (fig. 9C), the tube has no apparent function. By analogy with other mollusks, the tube probably carried water in or out of the mantle cavity. It could do this if the animal were an exogastric monoplacophoran (fig. 9D), an endogastric monoplacophoran (fig. 9F), or an exogastric gastropod (fig. 9E).

Because of torsion, and hence by definition, all gastropods are endogastric (Knight and others, 1960). The gradations in shell form between *Helcionella* and *Scenella*, and *Helcionella* and *Heraultipagma* indicate that the helcionellids were exogastric (shell coiled forward over the head). We conclude that the Helcionellacea were exogastric monoplacophorans, not endogastric gastropods.

RADIATION OF THE MONOPLACOPHORA

Horný (1965) divided the Monoplacophora into two groups designated by the terms Tergomya and Cyclomya. As the names imply, tergomyan monoplacophorans normally have a series of discrete muscle insertions on each side of the shell (as in *Scenella* and *Neopilina*), whereas the cyclomyans have the muscle insertions more or less fused into a ring. The

FIGURE 7.—Variation in shell form of Cambrian univalves. The shells are shown in left-lateral profile. Heavy lines show approximate shape of generating curves (apertural shape). A, *Anabarella plana* Vostokova, from pl. 17, fig. 8. B, *Igorella unguolata* Missarzhevsky, modified from Rozanov and others, 1969, pl. 4, fig. 21. C, *Latouchella insulcata* (Rasetti), modified from Rasetti, 1957, pl. 122, fig. 11. D,

Helcionella carinata Rasetti, modified from Rasetti, 1957, pl. 122, fig. 5. E, *Hypseloconus bessemerense* (Ulrich, Foerste, and Miller), modified from Stinchcombe and Echols, 1966, pl. 79, fig. 13. F, *Helcionella? rugosa* var. *comleyensis* Cobbold modified from Cobbold, 1921. G, *Scenella* sp., showing muscle-insertion areas, modified from Rasetti, 1954, pl. 12, figs. 5–8.

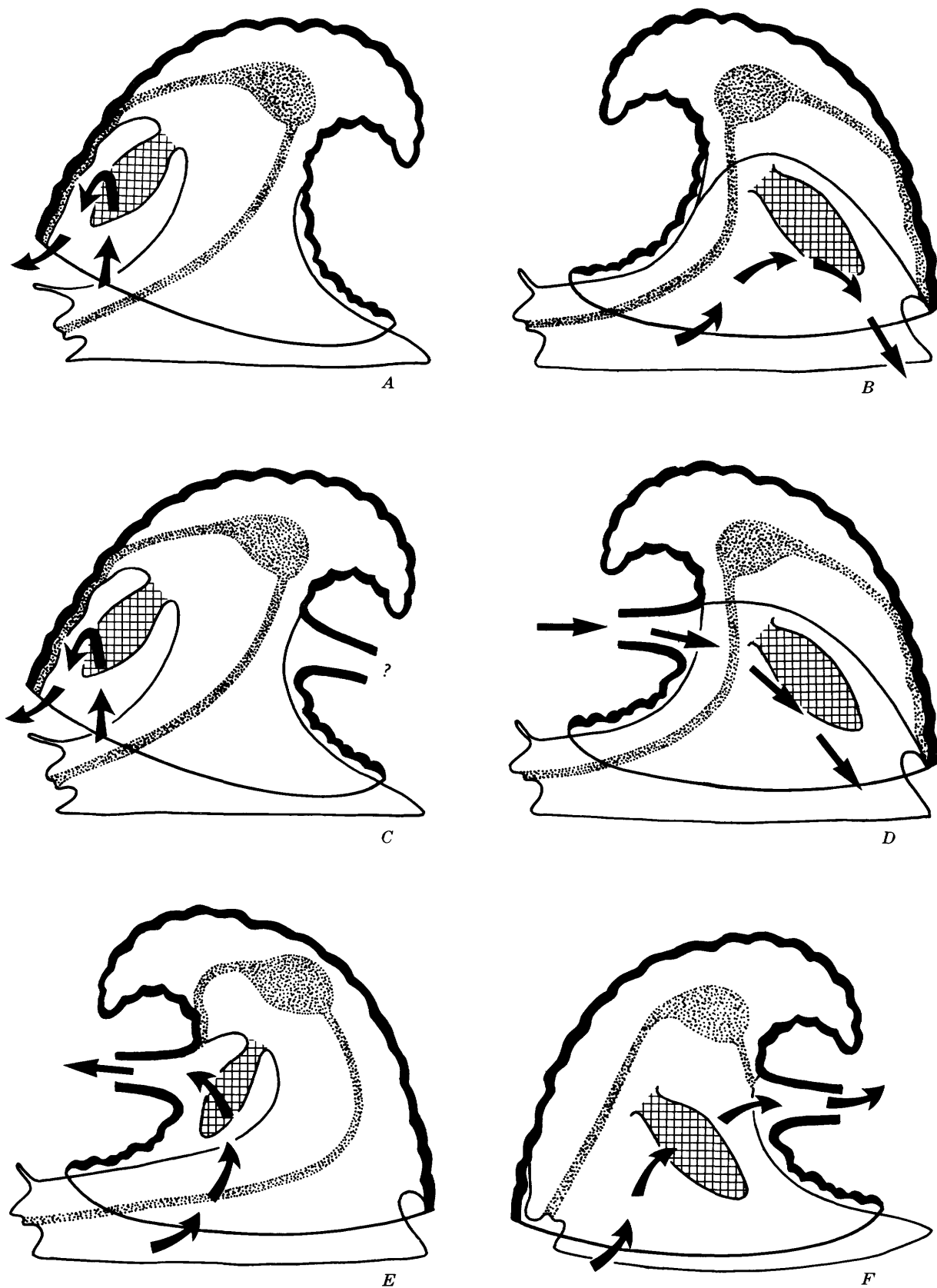


FIGURE 9.—(See explanation on facing page).

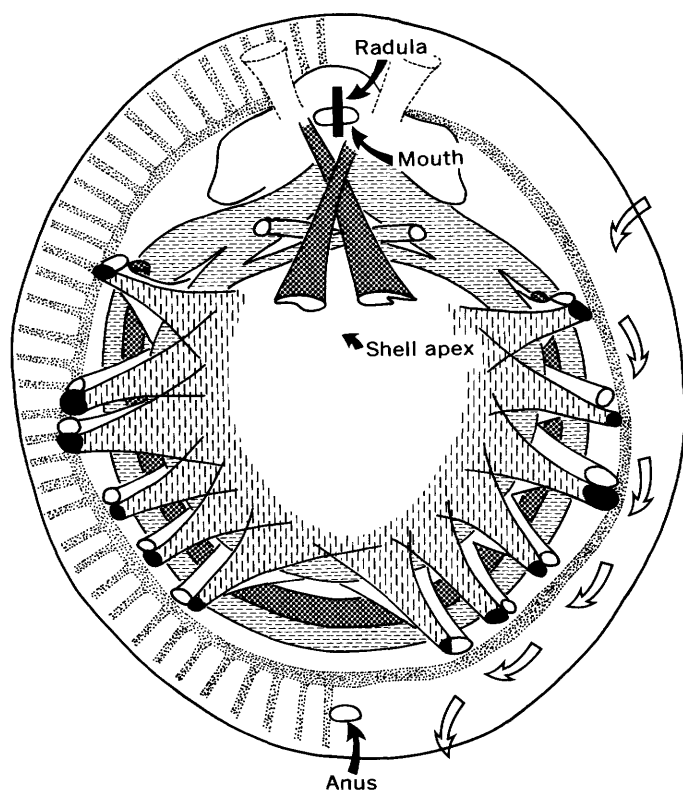


FIGURE 10.—Rasetti's Middle Cambrian specimens of *Scenella* reconstructed as a monoplacophoran, using *Neopilina* for a model. Stippled ring represents incipient pallial line indicated by change in slope of shell. Radial fluting of shell outside pallial line probably reflects weak radial mantle muscles shown here on left side only by short stippled lines. Other features shown are radial and circular muscles of the foot and muscles controlling head (anterior pair hypothetical). Arrows indicate probable direction of water flow through the right mantle cavity. Data from Rasetti (1954); from Runnegar and Pojeta (1974, fig. 2). Copyright 1974 by the American Association for the Advancement of Science, published with permission.

tergomyans are normally limpet shaped, and the cyclomyans are taller coiled shells.

Little distinguishes Ordovician, Silurian, and Devonian cyclomyan monoplacophorans like *Cyrtolites* Conrad (Horný, 1965), *Yochelsonellis* Horný (Horný, 1965), and *Cyrtonella* Hall (Rollins, 1969) from helcionellids like *Latouchella* (Cobbold, 1921) and *Igorella* (Rozanov and others, 1969), except for the anterior trail in some forms. The external orna-

ment of *Scenella* and of some species of *Helcionella*, *Anabarella*, and *Cyrtonella* is quite similar (Knight, 1941; Rozanov and others, 1969), consisting of fine radial threads between comarginal ribs, rugae, or other elements. We suggest that the post-Cambrian cyclomyan monoplacophorans are derived directly from the Helcionellacea.

Most students of molluscan phylogeny derive the cyclomyan monoplacophorans from apparently more primitive limpet-shaped shells. The Tommotian fossil record suggests that the reverse may have been true. The oldest zone of the Tommotian Stage yields the relatively tall shells *Bemella*, *Igorella*, *Anabarella*, and *Latouchella* (Rozanov and others, 1969, table 9). The intermediate form *Ginella* appears in the two succeeding zones, and the limpet-shaped shells *Tannuella* and *Helcionella* [sic] are absent until the base of the overlying Atdabanian stage. As the taller, coiled helcionellaceans are closer to the earliest gastropods, rostroconchs, and cephalopods than the limpet-shaped shells are, we suggest that the tergomyan monoplacophorans are not the ancestral stock but were secondarily adapted for benthic grazing.

ORIGIN OF THE GASTROPODA

Most malacologists consider the Bellerophontacea to be intermediate between the planispiral monoplacophorans and helically coiled primitive gastropods (Knight, 1952; Knight and others, 1960; Morton and Yonge, 1964; Batten and others, 1967; Stasek, 1972). In this scheme, planispiral coiling precedes torsion and helical coiling follows it. The model implies that the shell and visceral mass rotate 180° with respect to the head and foot so that the gut becomes twisted, the left and right gills come to lie on right and left sides of the body, and the nervous system forms a figure of eight. It has always been difficult to imagine how this process could occur phylogenetically and to explain its adaptive significance (Knight and others, 1960; Ghiselin, 1966; Stasek, 1972). Stasek (1972) summarized two long-held theories: (1) that torsion had adaptive significance for the swimming veliger larva by bringing the mantle cavity into a position where the tender vellum could be more easily retracted into the shell; and (2) that torsion would be beneficial to the adult, as it would move the sensory osphradia and gills away from water dirtied by the locomotion of the animal. Stasek rejected both explanations and suggested that torsion resulted from the temporary need of juvenile and adult monoplacophorans to be able to twist the body to provide space for a protractible head. This, he suggested,

FIGURE 9.—*Helcionella* and related tube-bearing helcionellid *Yochelsonella* Runnegar and Pojeta reconstructed as an endogastric gastropod (A, C), an exogastric monoplacophoran (B, D), an exogastric gastropod (E), and an endogastric monoplacophoran (F). B and D are considered correct. See text for further explanation. A, Modified from Knight (1952).

resulted in muscular asymmetry that was transferred to the larval stage in gastropods.

Ghiselin (1966) had a different explanation of the adaptive significance of torsion, which is more consistent with the early Tommotian fossil record. He argued that planktonic larvae with a helically coiled exogastric shell would have problems settling because the spire would interfere with their locomotion. Unfortunately, Ghiselin relied mainly on deductions from the morphology of the protoconch and shell of *Neopilina galathea* for his functional interpretation. This species was reported to have a helically coiled protoconch by Lemche (1957) and Lemche and Wingstrand (1959). Other species of *Neopilina* taken subsequently have a bilaterally symmetrical bulbous protoconch (N. W. Riser, written commun., 1974), similar to that found on comparably shaped early Paleozoic forms (pl. 15). Consequently, we believe that all known living and extinct monoplacophorans are bilaterally symmetrical at all stages of growth. In a rejoinder to Ghiselin's paper, Batten, Rollins, and Gould (1967) attempted to relate Ghiselin's model to the fossil record. They suggested that Ordovician-Devonian planispiral cyclomyans were the ancestors of the gastropods.

Pelagiella Matthew is a small helically coiled shell that is widely distributed in Lower Cambrian rocks (Knight and others, 1960). Although it resembles younger gastropods in shape, most authors have preferred to regard it as an end-product of early molluscan experimentation rather than a primitive member of the class Gastropoda (Wenz, 1938; Knight, 1952; Knight and others, 1960; Yochelson, 1963).

The oldest zone of the Tommotian Stage yields ribbed and smooth helically coiled pelagiellids referred to species of *Aldanella* Vostokova (Runnegar and Pojeta, 1974; Rozanov and others, 1969). Coarsely plicated helcionellids called *Latouchella memorabilis* and *Latouchella korobkovi* occur in the same beds. Both genera are preserved as minute phosphatic internal molds; we conclude that they were closely related. Specimens of *Pelagiella* from the English Lower Cambrian (Runnegar and Pojeta, 1974) are intermediate in form between *Aldanella* and *Latouchella*.

If *Latouchella* were a monoplacophoran, it had an anterior mouth, posterior anus, and probably one or more pairs of gills attached to the lateral or posterolateral flanks of the body (fig. 6D). All body structures were bilaterally symmetrical; *Latouchella* was untorted.

Latouchella has a bilaterally symmetrical shell; in life, its plane of symmetry was probably vertical (fig. 6D). *Aldanella* has an asymmetric shell coiled in a low dextral spiral (Runnegar and Pojeta, 1974; fig. 13). Although the shells of *Aldanella* are very small (maximum diameter about 2 mm), they are significantly larger than the larval shells of living prosobranch gastropods that remain for an unusually long time in the plankton (Fretter and Graham, 1962, p. 462-463). Unless *Aldanella* was adapted for postlarval planktonic life, therefore, it would probably have settled out of the plankton when the shell reached a size of 300-400 microns (J. Taylor, oral commun., 1973) and had one or two whorls of coiling. Some species of *Pelagiella* are much larger (Knight, 1941), suggesting that the whole group lived benthonically as adults.

During its planktonic larval life, the shell of *Aldanella* could have been coiled exogastrically over the head. During settling, this orientation would be awkward, because in living prosobranchs the foot is poorly formed at this stage (Fretter and Graham, 1962; Ghiselin, 1966), and the larva would have difficulty balancing the shell vertically. Furthermore, to creep along the substrate, it would have to carry the spire and visceral mass instead of dragging them behind (Ghiselin, 1966). Between periods of activity, the shell probably rested on one side; the newly settled larva of the living archaeogastropod *Haliotis* rests on its posttorsional left side during this period of its development (Fretter and Graham, 1962, p. 435). The dextrally coiled shells of *Aldanella* would probably have fallen onto their umbilical side. Other dextrally coiled species referred to *Pelagiella* are significantly flattened on the side away from the umbilicus (Robison, 1964, pl. 92, figs. 7-10; Hill and others, 1971, pl. 2, figs. 25-28), suggesting that the opposite side of the coil may have been the resting surface. Knight and others (1960, p. 323) reported that some species of *Pelagiella* contain both dextral and sinistral individuals, indicating that the side on which the larval shell rested may not have been rigidly fixed.

Aldanella is consistently dextrally coiled and probably rested with its umbilicus downward during and after settlement. If the body of *Aldanella* was organized in the same way as the body of *Latouchella*, the head and foot of *Aldanella* would need to rotate about 90° in the shell aperture to compensate for the change in orientation with respect to the substrate. This would allow the animal to protract its foot over the functionally ventral edge of the shell aperture and to move the coil from an anterior to a posterior

position (fig. 13). The unlikely alternative is that the animal protracted its foot by contracting the intrinsic circular muscles, anchored the end of the foot in the substrate, and then contracted the shell-inserted pedal retractor muscles to lift the shell into a vertical position above the head. We prefer the former explanation because: (1) it would have adaptive significance for the settling larva and juvenile animal; (2) it shows how torsion could have originated as a result of a small change in life orientation; (3) it implies that pelagiellids are primitive gastropods, as their shape suggests; and (4) it allows us to derive the Gastropoda directly from the Helcionellacea in the Early Cambrian.

Because of the asymmetry of the spire of *Aldanella*, the side of the aperture that is homologous with the left side of the shell of *Latouchella* is relatively enlarged, and the aperture is now asymmetric. This differential growth may have shifted the anus in the opposite direction to the mouth in the shell aperture. *Aldanella crassa* (Rozanov and others, 1969, pl. 3, fig. 16) has a small apertural sinus above the peripheral part of the whorl, suggesting that the anus had moved in this way. We conclude that various parts of the body of *Aldanella* were probably rotated between 30° and 90° in two directions with respect to their positions in *Latouchella*. We note that the peripheral part of the shell of *Aldanella* is homologous with the convex edge of the shell of *Latouchella*; in a geometric sense, both shells are exogastric.¹

If *Aldanella* is oriented like a primitive gastropod (fig. 13), however, the shell would be described as endogastric (coiling away from the head), and the body is partly or completely torted. The anus lies above and slightly left of the head, the left gill on its right side. The nervous system forms a figure of eight, and the gut is bent into a simple U. We conclude that *Aldanella* and *Pelagiella* were primitive gastropods. Only a small readjustment is needed to produce the organization found in living pleurotomariid gastropods (Knight, 1952; Knight and others, 1960).

We conclude that earliest Cambrian planispiral exogastric monoplacophorans evolved directly into helically coiled, torted, primitive gastropods (Pelagiellids) when the orientation of the shell with respect to the substrate changed. During the initial period of experimentation, both sinistral and dextral forms developed, depending on whether the left or

right side of the ancestral monoplacophoran came to lie on the substrate. When this occurred, torsion became necessary because the head-foot had to operate in a direction away from the coil instead of beneath it. This relatively small change converted the animals from untorted exogastric monoplacophorans to torted endogastric gastropods.

In living primitive gastropods, torsion is caused by a separation in the time of development of left and right larval retractor muscles (Fretter and Graham, 1962; Fretter, 1969). The pretorsional veliger develops only the right retractor muscle; when torsion begins, this muscle contracts rapidly (within 3–6 hours) and rotates the dorsal side of the velum to the pretorsional right side of the shell (Fretter and Graham, 1962, fig. 227). This muscle becomes the posttorsional left pedal retractor when the velum is lost. The right pedal retractor muscle develops later, during the period when differential growth completes the torsional process.

It is not only the delayed development of the posttorsional right pedal retractor muscle which allows the initial 90° rotation of the velum to occur; most of the torque exerted by the pretorsional right larval retractor results from the way the distal ends of the fibers of this muscle run around the velum and are inserted on its pretorsional left side (Fretter and Graham, 1962, fig. 227; Morton and Yonge, 1964, fig. 3). If this did not happen, it would be difficult or impossible for a shell-inserted retractor muscle to rotate the velum in the plane of the shell aperture.

Ordovician, Silurian, and Devonian planispiral monoplacophorans have simpler shell musculature than *Neopilina*, *Scenella*, and most other limpet-shaped tergomyans (Horný, 1965; Rollins and Batten, 1968; Lemche and Wingstrand, 1959). Presumably this difference is related to shell form; as the shells became taller, the insertions of the longitudinal (retractor) muscles of the foot would coalesce or be reduced in number, and the circular muscles of the foot that are inserted on the shell in *Neopilina*, *Tryblidium* Lindström, and *Scenella* (Lemche and Wingstrand, 1959) would no longer be attached to the shell. It would be difficult for any of these muscles to rotate the head-foot in the shell aperture. Stasek (1972) has suggested that the delayed development of the left muscles of one or more pairs of pedal retractors would have allowed the cyclomyan monoplacophorans to twist the shell and visceral mass on the head-foot and so become preadapted for torsion. We disagree; even if these muscles were asymmetrically developed (spatially or temporally), they could only retract the head-foot into the shell.

¹ The distinction between endogastric and exogastric gastropods is not the same as the distinction between endogastric and exogastric cephalopods. In gastropods, both shells coil the same way, but the orientation on the head-foot differs; in cephalopods, the two types of shells are believed to have coiled in opposite directions.

In the tall, helically coiled shells, where the muscle insertions are about 90° of coiling from the shell aperture, it would be impossible for differential contraction of the longitudinal muscles of the foot to rotate the head-foot in the shell aperture.

An alternative explanation is that the pelagiellids were virtually untorted when the foot was withdrawn. It was only when the foot was protracted by contraction of its circular muscles that the shell assumed a posterior position. Individuals that could twist the head-foot efficiently would be selected for, particularly if the torsion was visible before the larva settled. Thus, torsion may have had adaptive significance for both the larva (as suggested by Garstang, 1928) and the adult. The limited information does not allow us to suggest whether the pelagiellids were functionally (temporarily) or morphogenetically (permanently) torted; they may have been both.

A corollary of this explanation for the origin of torsion and the Gastropoda is that the planispiral Bellerophonacea are no longer required as intermediates and may not have been torted (Runnegar and Pojeta, 1974). Our explanation only allows them to be torted if they are secondarily symmetrical, having descended from primitive helically coiled forms.

As mentioned previously, Rollins and Batten (1968) used three criteria to identify bellerophonaceans as gastropods: (1) a long trail on the concave side of the shell, said to impede the maneuverability of a protracted head (Knight, 1952); (2) secondary inner shell layers (parietal deposits) covering the exterior of earlier formed parts of the coil; and (3) paired muscle insertions limited to the left and right sides of the columella (Knight, 1947).

By treating the Helcionellacea as monoplacophorans, we dispute criterion 1; possibly the trail provided structural support for a sessile head and radular apparatus as in *Neopilina* (Lemche and Wingstrand, 1959). Cowries and other gastropods secrete secondary shell layers on all parts of the shell; the argument that the parietal deposits of bellerophonaceans could not be secreted by epithelium near the head is questionable (N. J. Morris, oral commun., May 1973). The difference in shell musculature in externally similar planispiral univalves is more problematical. Starobogatov (1970) suggested that the main muscles of a planispiral gastropod would be inserted on the columella of the spire to counterbalance its weight over the posterior part of the foot. Planispiral monoplacophorans would need their main muscles on the opposite side of the shell be-

cause the spire was suspended over the head. We agree that it is unlikely that planispiral gastropods could have muscles on the outer side of the shell, but there is no reason why similarly shaped monoplacophorans could not have had their main pedal muscles attached to the columella. Morris (oral commun. May, 1973) has suggested that planispiral monoplacophorans that had lateral gills could have had their main pedal muscles attached posteriorly; those that had more posterior gills may have emphasized the anterior musculature.

We conclude that the small dextrally coiled Early Cambrian shells *Aldanella* and *Pelagiella* are the first gastropods; they gave rise to the sinuopeids, raphistomenids, and eotomariids of the Late Cambrian (Knight and others, 1960).

ORIGIN OF THE CEPHALOPODA

Cephalopods have the mouth and anus juxtaposed, but the body is not torted; it is still bilaterally symmetrical. Most living cephalopods lack a calcareous exoskeleton and are thought to be derived from more primitive shelled forms (Teichert, 1967). Apart from the enigmatic fossil *Vologdinella* Balashov (Ruzhentsev and others, 1962), no septate shells that could be cephalopods have been found in rocks older than the Late Cambrian (Teichert, 1967; Yochelson and others, 1973). These primitive cephalopods, referred to the family *Electronoceratidae* Kobayashi, have elongate, straight, or endogastrically curved shells, many closely spaced septa, and large ventral siphuncles (Flower, 1964; Teichert and others, 1964). The apparently oldest and most primitive genus is *Electronoceras* Ulrich and Foerste, in which the shell expands rapidly towards the aperture.

As noted previously, most monoplacophorans have exogastrically coiled shells. However the Late Cambrian and Early Ordovician genera *Hypseloconus* Berkey and *Yochelsoniella* Flower, are tall, laterally compressed shells, which appear to have been endogastrically coiled (Knight and others, 1960; Stinchcombe and Echols, 1966; Yochelson and others, 1973). Such shells first appear in the early Late Cambrian (Lochman and Duncan, 1944, pl. 12, figs 37-38). Some forms have apical septa, and Yochelson, Flower, and Webers (1973), suggested that they became primitive cephalopods when they developed a siphuncle. We believe that the hypseloconids were derived from Early Cambrian orthocones like *Tannuella* (Rozanov and others, 1969); as Yochelson, Flower, and Webers (1973) suggested, the class Cephalopoda probably did not appear before the Late Cambrian.

Flower (1964, 1968), Teichert (1967), and Teichert and others (1964) have discussed the subsequent radiation of the Cephalopoda.

ORIGIN OF THE ROSTROCONCHIA

The Early Cambrian genus *Heraultipegma* n. gen. (= *Heraultia* Cobbold) is a simple laterally compressed shell that has gaping anterior, ventral, and posterior margins (pl. 2, figs. 1–13). It is the oldest known rostroconch. We envisage a laterally compressed monoplacophoran such as *Anabarella* (fig. 6; pl. 17, fig. 8) giving rise to *Heraultipegma* by the middle Early Cambrian. Internally, *Heraultipegma* is poorly known, but it clearly has a small pegma (pl. 2, figs. 7, 8) produced by a fold in the shell between the dorsal edge of the anterior gape and the anterior slope. We assume that *Heraultipegma* gave rise to a *Ribeiria*-like animal when the fold of shell beneath the beak thickened internally to form a transverse plate or pegma.

Heraultipegma is known only from ferruginous internal molds which abound at the type locality (Thoral, 1935, pl. 1, fig. 3). It had only one center of calcification because the growth rugae cross the dorsal margin at right angles to the midsagittal plane (pl. 2, fig. 12). *Watsonella* Grabau is another laterally compressed shell from the Lower Cambrian of Massachusetts, which is probably allied to *Heraultipegma*; however, it is known only from the type specimens which are not well preserved (pl. 3, figs. 1–4) and yield little additional information about this type of animal.

The change in shell form from a univalved monoplacophoran to a pseudobivalved ribeiriid like *Heraultipegma* was probably accompanied by a change in life habits. Both Harry (1969) and Stasek (1972) described hypothetical animals which they felt must have existed as intermediates between monoplacophorans and pelecypods; both authors accurately describe the morphology of *Anabarella*, *Heraultipegma*, and other ribeiriid rostroconchs.

Stasek's fuller explanation (1972, p. 31–32 is particularly pertinent:

By and large, the monoplacophorans and primitive gastropods (Helcionellacea) of the early Cambrian seem to have been sluggish grazers of surface films or larger benthic algae. It was earlier inferred that within the herbivorous adaptive zone, and while the phylogenetically fertile Monoplacophora were still less than 1 cm long, some side groups were experiencing anatomical trends toward increased efficiency of individual pairs of their pseudometamerous organ systems. In relation to the heightened form of the body and mantle cavity, some of these monoplacophorans had already successfully reduced the number of ctenidia to one pair. Ciliation upon the surfaces

of the gill filaments continued to function in creating a respiratory water current and in removing particulate matter from it and the gills. This unwanted material undoubtedly included detritus and living plankton; that is, it comprised a quantity of material drawn from the same bank of organic energy that, from their earliest history, entire other phyla, especially the sponges and brachiopods, had tapped as a source of food. It is not surprising that one or more of the archaic monoplacophoran populations should have gradually come to exploit the same bank for its food supply, since a collecting mechanism already existed in the ciliary cleaning device of its gills. The source, but not the kind of food would have changed, for the original filter-feeding types probably retained the essentially herbivorous habits of their ancestors.

Some gastropods, such as *Crepidula*, utilize similar mechanisms for collecting food, but having arisen late, found their potential for radiation somewhat stifled by preexisting and highly diversified filter-feeding mollusks. The Cambrian filter-feeding types, on the other hand, had entered an adaptive zone that had been untried by previous members of the phylum.

The filter-feeding Monoplacophora [*Anabarella*, *Heraultipegma*, *Ribeiria*] are envisaged to have undergone trends toward increasing the length of the gill axes and of the filaments upon them in correlation with ventral expansion of the eaves of the mantle and shell, which housed the body cavity. Passage of mucus-bound material anteriorly may originally have been by way of ciliary tracts on the surface of the body, but channeling devices and flaps of the body wall soon funneled potential food into the mouth. These flaps, the labial palps, later expanded and acquired a sorting mechanism based on the relative sizes of the particles gathered by the ctenidia.

Retrospectively, the Bivalvia (Pelecypoda) are descendents of these hypothetical monoplacophorans.

Eventually the ribeiriids became adapted for infaunal life, becoming deposit feeders or filter feeders rather than browsers or grazers. This allowed them to diversify and to exploit the soft-sediment environment. We speculate that decephalization may have accompanied this change.

RADIATION OF THE ROSTROCONCHIA

In so far as possible, we rely on the stratigraphic succession in placing the gradations in morphology between various rostroconch taxa in their proper phylogenetic sequence. Thus, primitive characters are those known to have arisen first and are found in the oldest members of the class; advanced characters occur in younger forms thought to have evolved from primitive members. Admittedly, this approach presents some difficulties. New discoveries may change present thoughts on correlations, they may extend the ranges of critical taxa, or they may provide specimens that show morphological features not previously known. Sometimes a late-surviving primitive form may provide more insight into phylogenetic relationships than stratigraphically older forms. Nevertheless, the stratigraphic succession of organisms is basic to our notions of primitive and

advanced features and ancestors and descendents; each instance where it is not used is individually justified.

Rostroconchs are not common fossils. Yet, in spite of this, we can demonstrate close morphological gradations between all major taxa, and in most cases, we can relate these changes to the stratigraphic succession. It is the kind of paleontological situation which is theoretically called for, but which all too often cannot be observed in the fossil record. This situation makes systematic subdivision of the class difficult, because the taxa (both major and minor) that we recognize are parts of a continuum and are therefore difficult to define in the Linnean hierarchical system.

The only Early Cambrian rostroconchs known are *Heraultipegma varensalense* (Cobbold) from southern France (pl. 2, figs. 1–13), and *Watsonella crosbyi* Grabau from Massachusetts (pl. 3, figs. 1–4). Both occur with trilobites and are therefore Atdabanian or younger in age. They are small laterally compressed pseudobivalves, which gape anteriorly, ventrally, and posteriorly.

In the Late Cambrian, *Ribeiria taylori* n. sp. is known from Trempealeauan rocks of New York State (pl. 8, figs 12, 13); *R. australiensis* (pl. 4, figs 26–29) is present in the Mindyallan rocks of Queensland, Australia; *Wanwania cambrica* Kobayashi (pl. 3, figs 5, 11–14) occurs in the Cambrian *Tsinania* Zone of Manchuria; and *Oepikila cambrica* (pl. 10, figs 14, 15) is found in the Idamean rocks of Queensland. These Late Cambrian ribeiriids retain the prominent comarginal ornament of *Heraultipegma* and *Watsonella*, the gaping margins, and the dominant posterior growth component. They are larger than *Heraultipegma* and *Watsonella* and have a larger and more prominent pegma.

What we know of Cambrian rostroconchs shows that a minimum radiation of the group took place at that time: two families, five genera, and six species. In the Early Ordovician, rostroconchs underwent their greatest radiation, diversifying into four known families, 14 genera, and about 43 species. In comparison, only one family, genus, and species of Cambrian pelecypods are known. By the Early Ordovician there are six families, 16 genera, and about 45 species of pelecypods. All mollusks, and indeed many invertebrates, radiated rapidly in the Early Ordovician (Tremadocian-Arenigian; Canadian), although they are known from few forms in the Cambrian.

In the Middle and Late Ordovician, rostroconchs remained at about the same level of diversity as in

the Early Ordovician: five families, 10 genera, and about 40 species. In contrast, pelecypods continued to radiate explosively and are represented by about 16 families, 140 genera, and 1,400 species in the same period of time.

In the remainder of the Paleozoic, rostroconchs are represented by two families, seven genera, and about 275 known species. Pelecypods of the same age are referred to approximately 75 families, many hundreds of genera, and thousands of species. Thus rostroconchs form one of the smaller classes of mollusks, comparable in the number of named taxa to the Aplacophora, Monoplacophora, and Scaphopoda.

The dominant rostroconchs of the Ordovician were ribeiriids, technophorids, and eopteriids; ischyriiniids and bransoniids were present in smaller numbers. Technophorids, eopteriids, and ischyriiniids show a melange of primitive and advanced features, indicating that the Ordovician was a time of adaptive radiation for the class; various marine habitats were invaded, and several modes of life were evolved. Of the various combinations of morphology known in Ordovician rostroconchs, only the combination seen in the bransoniids (Conocardiacea) survives the end of the period. Perhaps only the conocardiaceans evolved a morphology that enabled them to exist with the far more efficient pelecypods during the latter part of the Paleozoic. The last rostroconchs occur in some of the youngest Permian deposits known (Newell, 1940; Waterhouse, 1967, p. 178); their fossil record terminates at the close of the Paleozoic.

We now review the history of the class in greater detail. The most primitive family is the Ribeiriidae; it is the first to appear, its oldest members grade morphologically into primitive monoplacophorans, and all species referred to it have a simply constructed shell, little different from the earliest member of the family. Most ribeiriids are posteriorly elongated (fig. 11), have a well-developed pegma, and have a shell that gapes anteriorly, ventrally, and posteriorly (primitive forms: *Heraultipegma*, *Ribeiria*, *Ribeirina*), or only anteriorly and posteriorly (advanced forms: *Ribeiria*, *Wanwania*, *Pinno-caris*). Assuming that all ribeiriids had similar shell musculature, the foot was attached to the shell by anterior and posterior median pedal retractors and possibly by left and right side muscles; the mantle was attached to the shell along a pallial line that had a shallow sinus near its anterior end. Ribeiriids probably had one pair of laterally disposed gills which created anterior to posterior water currents in the mantle cavity. The animals were motile, lived infaunally, and obtained food by a combination of

deposit and filter-feeding methods. Although the pegma may have provided needed structural support for the anterior retractor muscle of the foot, its presence created problems during growth, and as a result the shell and mantle cavity remained narrow. Primitive ribeiriids are therefore laterally compressed; only in the advanced species *Wanwania cambrica* Kobayashi (fig. 11j) does the shell become inflated, thus showing a trend toward the eopteriid *Euchasma*.

Like ribeiriids, technophorids also have a large and prominent anterior pegma (pl. 11, figs 21, 22), anterior and posterior median muscle insertions, and left and right linear muscle insertions (fig. 3H, 11n). The occurrence of these primitive features and the general similarity in shell form indicates a close phylogenetic relationship between technophorids and ribeiriids; this relationship is reflected in the systematics of the class by placing both families in the same order (Ribeirioida).

Technophorids have advanced beyond the ribeiriid stage in that, except for *Myocaris* Salter, they no longer have an anterior or ventral shell gape (pl. 11, figs 10, 11). In most forms, the posterior gape of the ribeiriids has been reduced to two small orifices formed by opposing folds (plicae) of the posterior part of the shell. Some technophorids (*Technophorus*) developed a primitive rostrum, formed by an extension of the posterior dorsal margin of the shell (pl. 14, figs 6, 7); this rostrum terminated in a relatively larger dorsal posterior orifice (pl. 11, fig. 9). We homologize the smaller lower orifice, with the more distinct ventral orifice of younger conocardiacans; this structure appears for the first time in the Technophoridae.

The organization of the body of ribeiriids and technophorids appears to have been similar, but the shell of the technophorids is effectively closed anteriorly and ventrally, except perhaps when the foot forced the valves apart. We conclude that technophorids could not have moved around easily and that water entered and left the mantle cavity through the two posterior orifices. By analogy with younger conocardiacans, the dorsal rostral orifice was the inhalant (and possibly exhalant aperture); the ventral orifice may have served as an exit for pseudofeces. We regard technophorids as infaunal suspension feeders, functionally analogous to coeval and younger pelecypods. As in the Ribeiriidae, the pegma inhibited the inflation of the mantle cavity. This and the other restrictions of an inflexible hinge reduced their chances of competing successfully with the Pelecypoda.

Two technophorids, *Tolmachovia? jelli* n. sp. and *Tolmachovia concentrica* Howell and Kobayashi, are almost equally expanded anteriorly and posteriorly (figs. 3B–D, 11k). In *Tolmachovia*, the cavity of the shell that contained the visceral mass is bounded anteriorly and posteriorly by transverse shelly partitions—anterior and posterior pegmas. These subequilateral species connect the technophorids to the genus *Ischyrinia* Billings of the late Middle and Late Ordovician (fig. 3A). Significantly, there is a close resemblance between the Middle Ordovician *Tolmachovia concentrica* and the oldest species of *Ischyrinia*, *I. norvegica* Soot-Ryen, from the upper Middle Ordovician of Norway.

The ischyriniids are the first rostroconchs to have a dominant anterior growth component, so that the umbos came to lie at the center of the hinge, or posterior to the center (fig. 11o–q). They retained the anterior pegma, and in *Pseudotechnophorus* Kobayashi this pegma has evolved into a greatly elongated structure (pl. 20, figs. 10, 11). In addition to the anterior pegma, all ischyriniids have a posterior pegma. Like technophorids, *Ischyrinia* lacks anterior and ventral shell gapes, and the posterior gape is restricted to two discrete orifices. *Pseudotechnophorus* has an oval or kidney-shaped anterior dorsal aperture and a small posterior rostrum.

In *Ischyrinia*, the more dorsal of the two posterior orifices forms the aperture of the projecting rostrum, well differentiated in *Ischyrinia winchelli* Billings (pl. 18, figs. 22–25). In two species of *Ischyrinia*, the ventral orifice coincides with a posterior carina and is a widely flaring transverse aperture that appears to form late in ontogeny (fig. 3A; pl. 18, fig. 23).

The musculature of *Ischyrinia* is apparently ribeiriidlike. It consists of a linear muscle insertion connecting the ends of the two pegmas (fig. 3A), and presumably of anterior and posterior median pedal retractor insertions. *Pseudotechnophorus* has more advanced lateral pedal insertions, like those of the conocardiacan *Eopteria*, and another large muscle insertion which forms a ring or a horseshoe in the cavity in front of the anterior pegma. For reasons explained elsewhere, we interpret this latter insertion as the attachment point of hypertrophied radial muscles of the mantle, termed pallial retractor muscles. Significantly, the protoconch of *Pseudotechnophorus* has a tiny anterior median muscle insertion and an equally small linear insertion that passes from the anterior median muscle posteriorly behind the beak. We view these structures as the insertions of atrophied ribeiriid pedal muscles and conclude

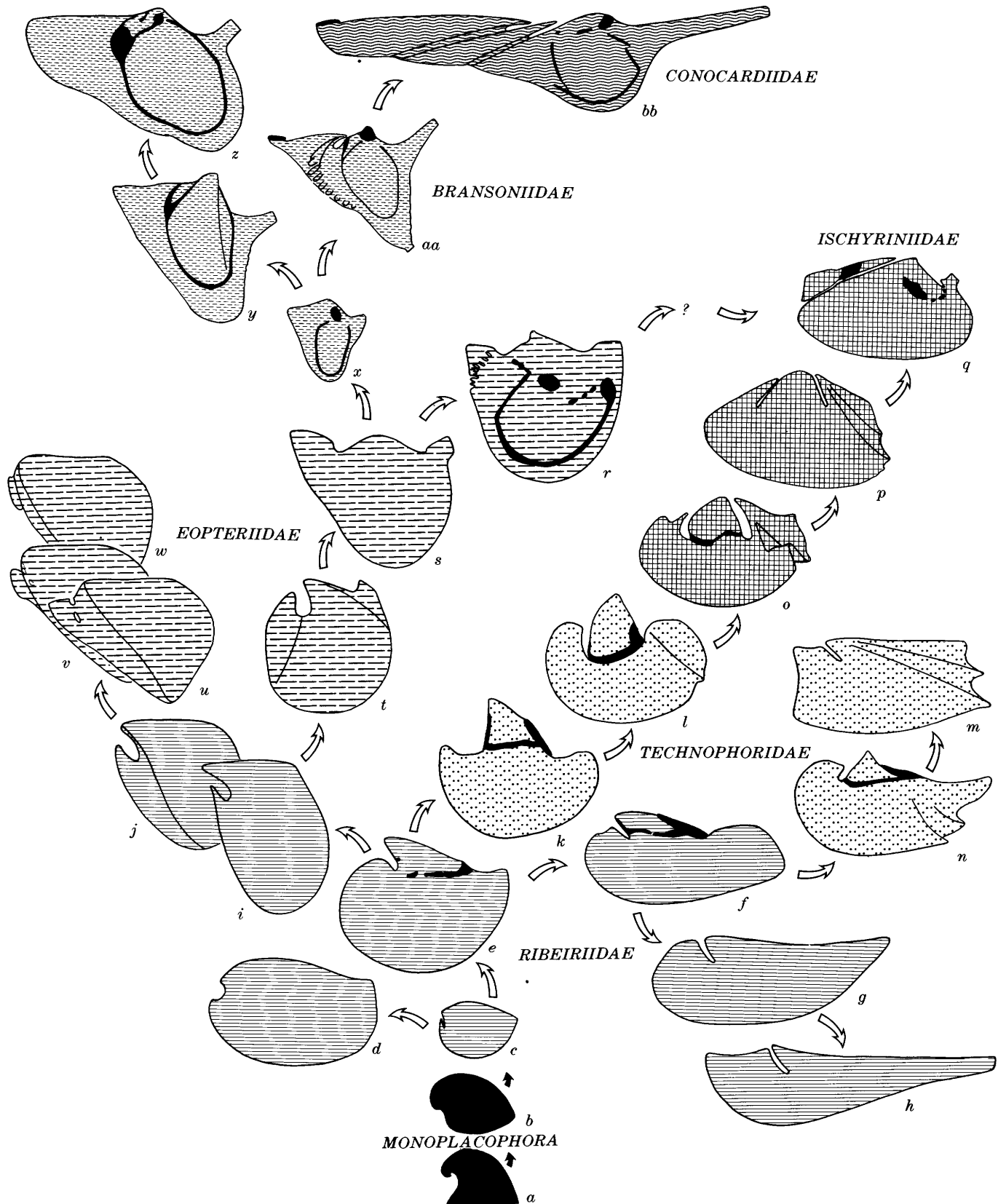


FIGURE 11.—(See explanation on facing page.)

that the functional pedal muscles of *Pseudotechnophorus* were a new development.

Ischyria and *Pseudotechnophorus* are referred to the same family (Ischyriiniidae) and order (Ischyriinioida) because of their similarities in shell form. However, *Pseudotechnophorus* is more advanced than *Ischyria* in its shell musculature. It cannot have been derived from *Ischyria* if *Ischyria* is descended from *Tolmachovia*, because *Pseudotechnophorus* is Early Ordovician in age. *Pseudotechnophorus* may have evolved from *Eopteria*, which is also found in the Early Ordovician and which resembles *Pseudotechnophorus* in shell musculature and to some extent in shell form (fig. 11). We realize the Ischyriiniidae may be a nonphylogenetic grouping, but find it convenient at this stage of knowledge. It is difficult to place too much emphasis on stratigraphic occurrences at this time because the ischyriiniids are known from only a handful of specimens from a few localities.

Both *Ischyria* and *Pseudotechnophorus* have relatively few primitive characteristics and have departed farther from the ribeiriid stem stock than have the technophorids. Primitive features are the presence of an anterior pegma and the ribeiriidlike musculature of *Ischyria* and the protoconch of *Pseudotechnophorus*; advanced features include the closing of the anterior and ventral parts of the shell, the development of a rostrum and specialized ventral orifice, the addition of a second pegma, and the dominant anterior growth component. Despite these relatively complex features, which to some extent mimic features found in younger conocardiaceans, we believe that the ischyriinioids, like the technophorids, are a side branch of the rostroconch evolutionary tree. Throughout their history, conocardiaceans retained an anterior gape and lacked a pegma. We regard the less elaborate Eopteriidae as the ancestors of the Conocardiaceae. In the Early Ordovician radiation of rostroconchs, several lineages developed comparable structures by parallel evolution; such parallel features include the closing of the ventral shell gape, the development of a rostrum,

and restriction of the posterior shell gape to one or two apertures.

The inhomogeneity of the Ischyriinioida is also reflected in our interpretation of the life habits and soft-part morphology of *Ischyria* and *Technophorus*. *Ischyria* probably developed the suspension feeding habit of its technophorid ancestors. It was probably buried to the depth of the carina, remained stationary, and fed and obtained oxygen through its posterior orifices.

In contrast, we believe that *Pseudotechnophorus* was motile, had an anterior to posterior water current, and used protractible mantle tissue to deposit feed from the sediment-water interface. This presumed life habit also places *Pseudotechnophorus* closer to *Eopteria* than to *Ischyria*, but the similarities may be due to convergence.

All other rostroconchs are referred to the order Conocardioida. The Early and Middle Ordovician Eopteriidae are the oldest members of this order, and they are connected through *Wanwanella* Kobayashi (Eopteriidae) and *Wanwania* (Ribeiriidae) to the Ribeiriidae (fig. 11).

The Eopteriidae includes the genera *Eopteria* Billings (pls. 22–26) and *Euchasma* Billings (pls. 27–29), which are the first known rostroconchs to have marginal denticles (pl. 23, figs. 4, 5; pl. 24, fig. 14; pl. 29, fig. 4) and external radial ribs (pl. 24, figs. 12, 18; pl. 28, figs. 12–15), features seen on all subsequent conocardiaceans. The ribeiriid affinities of the Eopteriidae are shown by the presence of an anterior pegma in *Euchasma* (pl. 29, figs. 3, 11, 15) and *Wanwanella* (pl. 21, figs. 18–20), and by the fact that the eopteriids still have gaping anterior, ventral, and posterior valve margins (pl. 24, figs. 14, 15, 20).

The shell musculature of *Eopteria* is well known from *E. ventricosa* (Whitfield) (fig. 4; pl. 22, figs. 1–6; pl. 23, figs. 2, 3). Like *Pseudotechnophorus*, *Eopteria* has the pedal muscles inserted laterally on each valve, but there is no trace of the relict ribeiriid musculature seen in *Pseudotechnophorus*. The pallial line is well preserved; there is an anterior sinus which housed pallial retractor muscles, and there is possibly a posterior adductor muscle. This latter muscle may have been used to flex the valves and so create water currents in and out of the mantle cavity.

Some Middle Ordovician species of *Eopteria* show a dominant anterior growth component (pl. 26, figs. 12–18) at about the time that conocardiaceans first appear in the fossil record. Both *Euchasma* and *Eopteria* developed an incipient rostrum at the posteri-

FIGURE 11.—Diversity of form in the Class Rostroconchia. Arrows indicate probable paths of evolution. Genera belonging to the same family are shaded in the same way. a, *Latouchella*; b, *Anabarella*; c, *Heraultipegma*; d–f, *Ribeiria*; g–h, *Pinnocaris*; i–j, *Wanwania*; k–l, *Tolmachovia*; m, *Myocaris*; n, *Technophorus*; o–p, *Ischyria*; q, *Pseudotechnophorus*; r–s, *Eopteria*; t, *Wanwanella*; u–w, *Euchasma*; x–z, *Bransonia*; aa, *Hippocardia*; bb, *Conocardium*.

or end of the shell (pl. 24, figs. 11, 12; pl. 28, figs. 12, 13), and all eopteriids had a more inflated shell and mantle cavity than the ribeiriids and technophorids. Thus, the presence in the eopteriids of a combination of ribeiriid and conocardiacean features suggests that they are descended from the former and are ancestral to the latter.

The loss of the pegma in *Eopteria* and the modification of its edges in *Euchasma* allowed the valves to grow in tighter spiral, thus enlarging the mantle cavity. This lateral expansion of the shell produced umbones on either side of the beak of *Euchasma*, as it did in all members of the Conocardiacea. At this evolutionary level, the shells of rostroconchs, although still starting growth from a univalved protoconch, became clearly bivalved and thus superficially resemble the shells of pelecypods.

The inflation of the mantle cavity also affected the topography of the hinge. It became increasingly difficult for rostroconchs to maintain an approximately rectilinear hinge; tensional fractures called clefts developed between topographically high and low parts of the hinge. These are visible in front of the beak of some ribeiriids (pl. 4, fig. 9), but they are much more obviously developed in the eopteriids (pl. 27, fig. 13) and conocardiaceans (pl. 40, figs. 5, 7). In general, those forms having a dominant posterior growth component like *Euchasma* have well-developed anterior clefts (pl. 27, fig. 13); those having a dominant anterior growth component (Conocardiacea) have posterior clefts (pl. 34, figs. 6–8); and those having subequilateral shells (*Eopteria*) may have clefts on both sides of the beak. The need for the clefts is explained by figure 1.

As well as being strongly inflated, most species of *Euchasma* are flattened anteroventrally, and one species, *Euchasma mytiliforme* n. sp. has the external shell forms of epibyssate mytilid and dreissenid pelecypods (pl. 29, figs. 6–15). This suggests that *Euchasma* lived epifaunally. Although the shell of *Euchasma* has a narrow ventral to posterior gape (pl. 29, figs. 8, 9), the only sizable shell aperture is a circular hole formed by the edges of both valves at the dorsal anterior margin, just in front of the pegma (pl. 28, figs. 15, 16). If *Euchasma* were orientated as an epifaunal animal, this hole would face the substrate. We speculate that it contained a structure formed by hypertrophy of one or more pallial tentacles and that was manipulated by pallial retractor muscles attached in an anterior sinus in the pallial line (pl. 27, fig. 9). *Euchasma* may have lived attached to the substrate by this structure and may have suspension fed from water entering and leaving

the mantle cavity through the posterior gape. *Euchasma* may have been a sessile epifaunal suspension feeder.

By contrast, *Eopteria* seems to have been a motile semi-infaunal deposit feeder which collected food from the sediment-water interface, using hypertrophied mantle tissue and possibly pallial tentacles for the collecting structure. This tissue was extruded from the anterior gape and withdrawn by pallial retractor muscles located in the anterior pallial sinus. A narrow pelecypodlike foot was used for locomotion, and a posterior adductor muscle may have been used to clean the mantle cavity.

Eopteria is a suitable ancestor for the Conocardiacea, and in fact, only the presence of a well-developed posterior rostrum distinguishes the Ordovician conocardiacean *Bransonina cressmani* n. sp. (pl. 52, figs. 10–14; pl. 53, figs. 6–21) from *Eopteria* (pl. 26, figs. 12–18). *Eopteria* is similar to the conocardiaceans in retaining an anterior gape, in lacking a pegma, in its musculature, and in having well-developed external ribs and commissural denticles. It differs from conocardiaceans in having a continuous posteroventral gape instead of a rostrum and a discrete ventral orifice. *Eopteria* is also more variable in shape. Only some species are anteriorly expanded (pl. 26, figs. 12–18) like the Conocardiacea; others are subequilateral (pl. 26, figs. 1, 2) or posteriorly expanded (pl. 25, fig. 15).

The technophorids and *Ischyrimia* differ from eopteriids, ribeiriids, and conocardiaceans in that they have a closed anterior end; they disappear by the end of the Ordovician. Only the anteriorly gaping Conocardiacea are found in the post-Ordovician Paleozoic.

There is evidence that most of the advanced rostroconch genera having anteriorly gaping shells had hypertrophied mantle tissue which could be protracted through the anterior gape. The three important indications of the existence of this tissue are: (1) commissural denticles, formed by folds in the enlarged mantle as it was withdrawn into the shell (functionally analogous to the denticles lining the apertures of living cowrie shells); (2) the anterior pallial sinuses of *Wanwanina*, *Eopteria*, and *Euchasma*; and (3) the impressions of the radial muscles of the mantle seen in species of *Eopteria* and *Bransonina* n. gen. In more primitive rostroconchs like *Eopteria* and *Pseudotechnophorus*, the mantle tissue seems to have been protracted hydrostatically. In the Conocardiacea, pallial protractor muscles inserted just inside the anterior end of the hinge probably pulled the mantle tissue out of the shell.

In the highly complex rostroconchs *Conocardium* Bronn and *Arceodomus* n. gen., the anterior gape is largely obstructed by internal calcareous shelves (pl. 43, fig. 13). These are formed of outer shell layer, implying that the outer edge of the mantle formed them. We conclude that the mantle was complexly folded in these areas in these forms. We homologize the shelves with the marginal denticles found in all other conocardiaceans, because these are also formed initially of the outer shell layer.

In all conocardiaceans, the posterior shell gape is reduced to the small aperture at the end of the rostrum, and in most an even smaller ventral orifice. The Conocardiidae have only the rostral orifice. We therefore doubt that any of these animals could have been posterior suspension feeders and conclude that they were all anterior deposit feeders using hypertrophied mantle tissue and perhaps pallial tentacles to accumulate food. The more primitive forms probably operated like *Eopteria*; the most advanced forms (Conocardiidae) may have had complex sorting structures formed by ciliated mantle surfaces resting on the anterior shelves.

The inflated mantle cavity of all conocardiacean rostroconchs suggests that all genera had gills. This may account for the most striking difference in form between species like *Conocardium elongatum* and its functional analog, the tusk-shaped scaphopods. We assume that these gills pumped water in and out of the rostrum to supply oxygen to the organism and to remove body wastes. The ventral orifice may have been used to remove pseudofeces from the mantle cavity; its absence in the Conocardiidae may reflect the sophisticated sorting devices at the anterior end of the shell which prevented anything but food from entering the mantle cavity. We conclude that all conocardiaceans were deposit feeders. The filter-feeding rostroconchs (technophorids, *Ischyrinia*, and *Euchasma*) became extinct by the end of the Ordovician. The Ordovician was a time of major expansions in the suspension-feeding pelecypods and brachiopods, and competition for this mode of life may have led to the extinction of suspension-feeding rostroconchs.

As mentioned above, the unspecialized eopteriid *Eopteria* gave rise to the most primitive conocardiaceans, the Bransoniidae, in the Middle Ordovician. The bransoniids rapidly diverged into two long-ranging types, the hooded and nonhooded forms. *Bransonia* n. gen. (pl. 51, figs. 1-10, 12-16) is a simple conocardiacean having a large anterior gape, small commissural denticles, a small rostrum sharply delimited by posterior clefts, coarse full body rib-

bing, and a well-defined ventral orifice. *Hippocardia* Brown has all of the conocardiacean features of *Bransonia*, but has in addition a hood (pl. 48, fig. 2) attached to the umbonal areas of the valves, an extended ventral orifice where the left and right sides of the hood meet, and enlarged anterior marginal denticles or small anterior shelves.

The hooded lineage begins with *Hippocardia*, which gives rise to the Silurian-Devonian genus *Bigalea* n. gen. This form possesses two small hoods, one anterior to the other (pl. 37, fig. 4). Each hood has an aperture along the ventral margin, so that *Bigalea* has four commissural orifices, rather than the three usually found in conocardiaceans. In *Bigalea*, the hoods are always small and never reach the enormous size of some species of *Hippocardia* (pl. 48, fig. 2).

The most complex rostroconchs belong to the family Conocardiidae. These have elaborate longitudinal shelves in the anterior aperture and an elongate shell clearly separable into three regions—rostrum, body, and snout (pl. 43, figs. 7, 5, 13, 15). Two genera are placed in this family, *Conocardium* Bronn (pl. 38) and *Arceodomus* n. gen. (pl. 43). They differ principally in the ornament on the body of the shell and are clearly closely related; *Conocardium* is the older of the two and presumably ancestral to *Arceodomus*.

As noted above, the longitudinal shelves are probably enlarged commissural denticles. In the bransoniid genus *Mulceodens* n. gen., the denticles in the ventral part of the aperture are enlarged so that those from opposite sides are in contact (pl. 34, figs. 9-14). The denticles project into the aperture and are elongated anteroposteriorly (pl. 34, figs. 3-5). Further enlargement of such denticles could easily lead to longitudinal shelves, and the bransoniids probably gave rise to the conocardiids.

Pseudoconocardium Zawodovsky is a bransoniid having an anterior gape that occupies almost the entire anterior face. The gape is not restricted to an anterodorsal position as it is in other conocardiaceans. It seems likely that *Pseudoconocardium* was derived from *Bransonia* by an enlargement of the anterior aperture in a ventral direction.

In summary, ribeiriids are looked upon as the rostroconch stem stock, which in the Ordovician gave rise to the technophorids, ischyriniids, and eopteriids. The ribeiriids continued until the end of the Ordovician. In the Middle Ordovician, *Eopteria* produced the first conocardiacean, which rapidly diversified into the hooded and nonhooded lineages of the Hippocardiidae and Bransoniidae. The most spe-

cialized rostroconchs, the Conocardiidae, were derived from the bransoniids in the middle Paleozoic. The class became extinct at the end of the Permian. The Ordovician was the period of greatest radiation and diversification of the Rostroconchia; during this time, rostroconchs became adapted for infaunal and epifaunal suspension feeding as well as infaunal deposit feeding. Only the deposit feeders survived the end of the Ordovician.

ORIGIN OF THE PELECYPODA

BIVALVED CONDITION IN THE MOLLUSCA

Several kinds of mollusks have a bivalved shell, and the bivalved condition is the distinctive feature of the classes Rostroconchia, Pelecypoda, and the enigmatic group Stenothecoida. A few gastropods have a bivalved shell, and at least one species of octopus habitually inhabits discarded pelecypod shells.

Other mollusks have shells composed of two or more parts (chitons, gastropods having opercula, pholad pelecypods having accessory plates, cephalopods having aptychi), which are normally separate, but which in rare cases may be joined by a flexible structure resembling the pelecypod ligament. Such structures occur in some of the plates of the living chiton *Schizoplax* Dall (Dall, 1878; Knight and others, 1960; Harry, 1969) and in the junction between the operculum and shell of the Virgin Islands land snail *Thyrophorella* (Girard, 1895; Boettger, 1962; Harry, 1969). None of these shells are bivalved, but they demonstrate that two or more centers of calcification have arisen independently in many different kinds of mollusks.

Some mollusks may be secondarily univalved, having descended from bivalved ancestors. Some clavagellid pelecypods clearly fit this category, and there is some embryological evidence that the ancestors of the Scaphopoda had a bivalved shell (Lacaze-Duthiers, 1856-57; Yonge, 1957). By contrast, the oldest rostroconchs are morphologically intermediate between univalved monoplacophorans and younger bivalved forms. In this case, there is no clear distinction between bivalved and univalved shells.

The phylogenetic and behavioral changes accompanying the attainment of a bivalved shell may or may not be reflected by major changes in the organization of the body. Thus, the body and habits of the living bivalved opisthobranch snails (Juliidae) differ very little from those of related univalved opisthobranchs (Kay, 1968); the oldest pelecypod, *Fordilla* Barrande (Pojeta and others, 1973), however, had its body organized quite differently from

its univalved monoplacophoran ancestor. Despite these differences, the shells of the simplest juliid *Berthelinia* Beets and *Fordilla* are remarkably similar in external form.

The orientation of the valves on the body also varies. Rostroconchs, pelecypods, and bivalved opisthobranch gastropods have the valves disposed on right and left sides of the body, the junction between the valves being in the anatomically dorsal position. The gastropods and rostroconchs retain this primitive orientation of the organism with respect to the substrate, but many pelecypods lie on left or right valves or even on the hinge (Cox and others, 1969). Oysters, for example, developed valves that are functionally dorsal and ventral as in some productid brachiopods (Grant, 1966). Tridacnid clams have the plane of symmetry vertical but lie on the hinge (Yonge, 1953a).

The stenothecoids (Yochelson, 1969) and the bivalved limpets *Hipponix antiquatus* (Linnaeus) (Yonge, 1953b) and *Cheilea equestris* (Linnaeus) have two subequal valves, but these are anatomically and functionally dorsal and ventral. The soft-part morphology of *Stenothecoides* Resser and related genera is not easily reconstructed, but the ventral valve of *Hipponix* is formed by the sole of the foot, and thus is in no way analogous to the right and left valves of other mollusks.

LIMITS OF CONVERGENCE IN SHELL FORM

All pelecypods have a shell that is bivalved from the time that calcification begins (Raven, 1958). Before this stage, there is a single dorsal uncalcified cuticle (shell gland) on the larva. When calcification begins, it starts at two points on left and right sides of the saddle-shaped cuticle; these points eventually become the beaks of the valves. The intervening uncalcified zone becomes the ligament, or the ligament may suddenly appear in this region in later ontogeny (Chanley and Chanley, 1970, pl. 3).

Initially the hinge is long and straight so that the early larval shells of most pelecypods are characteristically D-shaped. As inflation of the valves proceeds, umbos form on either side of the hinge, and the ligament becomes proportionally shorter. In most adult pelecypods, the ligament is relatively short, so that the valves are circular or oval. The growth lines reflecting the edge of the mantle curve towards the beaks and cross the hinge at the posterior and functionally anterior ends of the ligament.

In the Rostroconchia, the larval shell is univalved, there is only one center of calcification, and the bivalved condition arises through postlarval accentu-

ated growth of the lateral lobes of the shell. Because the valves are always effectively closed, there is no need for deep anterior and posterior embayments, so the growth lines are not recurved towards the beak.

In the bivalved opisthobranch gastropods, the larva has a helically coiled shell and an operculum that is eventually shed. When the bivalved shell begins to form, it is not symmetrical because the ligament forms on the right side of the helical protoconch (Kawaguti, 1959). This is a third situation in which there is originally a single center of calcification (the protoconch) and a second center of calcification (the right valve), develops subsequently. The adult shell is superficially bilaterally symmetrical but has the asymmetrically placed protoconch and a different arrangement of muscles attached to each valve (Kawaguti and Yamasu, 1960).

For the pelecypod or gastropod ligament to function efficiently, it must be relatively straight. Because the generating curve of primitive pelecypod and bivalved snail shells is approximately circular or elliptical, it would be mechanically inefficient to have the hinge on both sides of the beaks. In primitive pelecypods, the ligament is always behind the beaks (opisthodontic) and grows from its posterior end; in the bivalved opisthobranch snails, the reverse is true, and the ligament is entirely prosodontic. The resulting shells are quite similar in external form except that the left valve of a primitive pelecypod like *Fordilla* resembles the right valve of the bivalved gastropod *Berthelinia*.

The origin of the bivalved condition in the Stenothecoida is not well understood, but the growth lines on each valve run completely round the beak, producing a good deal of interumbonal growth (Yochelson, 1969, fig. 3). Analogous growth increments are found in many brachiopods, where the valves are totally separate structures growing at all edges; growth lines also occur in the shells of the bivalved limpets. This growth pattern reinforces the view that stenothecoids are only remotely related to rostroconchs and pelecypods.

ROSTROCONCHS AS ANCESTORS OF THE PELECYPODA

Fordilla troyensis Barrande from the Early Cambrian is the oldest known pelecypod (Pojeta and others, 1973; Pojeta and Runnegar, 1974; Pojeta, 1975). It has a laterally compressed shell, and prominent, but not rugose, comarginal ornament. *Fordilla* is about the same size and age as the ribeiriid *Heraultipegma* (pl. 2, figs. 1-13), and the two genera have similar lateral profiles. *Fordilla* has a bivalved

larval shell, a simple ligament-insertion area, adductor muscles, pelecypodlike pedal muscles, and a well-developed pallial musculature. There are no shell gapes; when the adductors contracted, the valve margins were tightly closed. In contrast, *Heraultipegma* has a univalved larval shell, a pseudobivalved adult shell, and an anterior through posterior shell gape; by analogy with younger ribeiriids, *Heraultipegma* probably lacked adductor muscles.

Several Cambrian-Ordovician ribeiriids resemble coeval pelecypods in external form, and decalcification of the posterior dorsal margin in successive generations could have produced the primitive opisthodontic parivincular ligament found in early pelecypods. Such a ligament could only function if the anterior embayment of the shell extended as far as the beak, and both evolutionary changes may have progressed simultaneously. Increasing flexibility of the posterior hinge would have enabled the valves to open wider anteriorly, and less shell may have been secreted along the anterior dorsal margin. Obviously the pegma would have inhibited valve movement, so forms like *Heraultipegma* that have a small pegma are more likely to have developed a flexible hinge.

The main difference, however, between pelecypods and rostroconchs is that in pelecypods, the shell is bivalved from the very beginning of its growth. Rostroconchs have a univalved larval shell and only one primary center of calcification. This is a fundamental difference; there can be no intermediates. Once a flexible ligament was established in the larval shell, the adult would inevitably resemble a pelecypod. The hinge would remain relatively short to retain flexibility, and each center of calcification would have a generating curve that terminated at the ends of the hinge. By contrast, the ribeiriids could never produce a pelecypodlike shell because the univalved protoconch remains attached to both valves.

The conchological differences between rostroconchs and early pelecypods like *Fordilla*, *Redonia* Rouault, *Babinka* Barrande, and *Lyrodesma* Conrad are considerable (Pojeta, 1971), but most of the differences relate to the geometric effects of growth from two centers of calcification. The shape of the valves and the presence of the ligament on the longer side of the shell are a direct consequence of two growth centers, as precisely the same structures are found in primitive pelecypods and bivalved opisthobranch gastropods. We believe that a single mutation producing a flexible hinge in the larval shell would be sufficient to convert a ribeiriid into a pelecypod, if the difference were judged on shell form

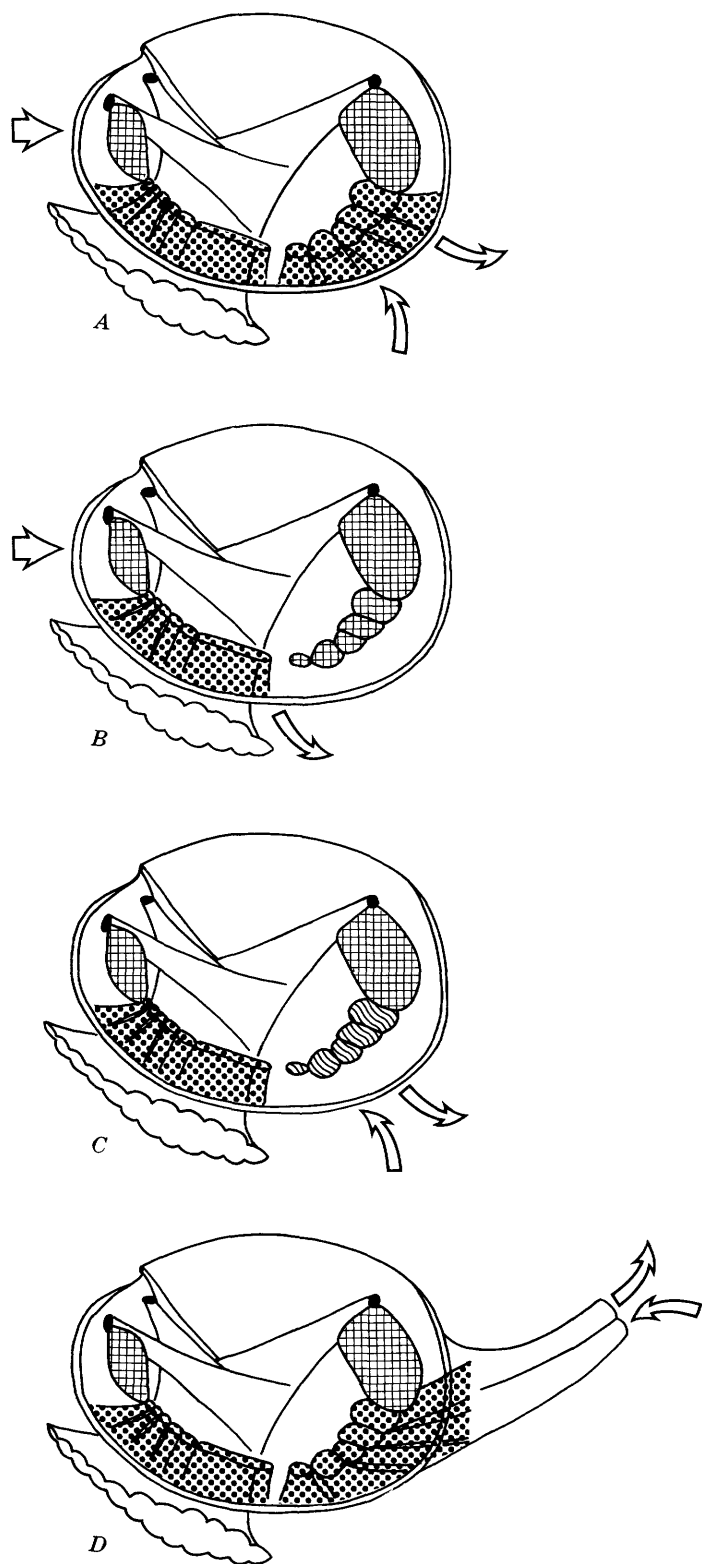


FIGURE 12.—Four possible explanations of the shell muscle insertions of the Early Cambrian pelecypod *Fordilla*. Adductor muscles are cross hatched; radial pallial muscles are stippled; muscles extending from the shell to the inner surface of the mantle are diagonally shaded; pedal muscle

alone. This change probably occurred in the Atdebanian Stage of the Early Cambrian, when *Fordilla* evolved from *Heraultipegma* or some closely related form.

ACCOMPANYING MODIFICATION OF BODY FORM

Judging from *Neopilina* and the muscle insertions visible on fossil monoplacophoran shells, Cambrian-Ordovician monoplacophorans were untorted snail-like animals with a head, a visceral mass, laterally disposed gills, and a ventrally flattened creeping foot attached to the shell by muscles inserted in a continuous or discontinuous ring. Tiny muscles controlling the edges of the mantle occur in *Neopilina*, but none of the ancient or modern shells shows a well-differentiated pallial line.

In marked contrast, ancient pelecypods resemble their modern counterparts in having a reduced head and a laterally flattened probing foot attached to the shell mainly above the anterior and posterior adductor muscles. The radial muscles in the mantle are greatly enlarged to form a continuous pallial line, and the adductor muscles which close the valves are believed to be hypertrophied radial muscles which have been cross-fused in the anterior and posterior embayments (Yonge, 1953a). The pedal musculature of *Fordilla* is particularly significant, as the main pedal retractors are inserted anteriorly and posteriorly, implying that the extrinsic muscle fibers of the foot were arranged in a geodetic net as in modern pelecypods (Trueman, 1967). Thus, the foot of *Fordilla* must have been used for burrowing rather than creeping.

Fordilla also has an unusually large set of muscle insertions forming the posterior part of the pallial line (fig. 12). None of the explanations of the function of these muscles offered by Pojeta, Runnegar, and Křiz (1973) (siphonal retractors, accessory adductors, muscles retracting the inner surface of the mantle) would be logical if *Fordilla* were a monoplacophoran having a bivalved shell. We conclude that *Fordilla* and similar Ordovician genera were already well adapted for life as bivalved organisms. They were pelecypods and not bivalved monoplacophorans.

We have already noted that the ribeiriids are transitional between the Monoplacophora and Pelecypoda in shell form. The ribeiriid shape would allow the animal to become adapted for life in a bivalved

insertions are black. Arrows indicate possible water flow in and out of the mantle cavity. Note that if *B* were correct, the whole of the posterior end of the shell would be effectively sealed. *A* and *B* are less likely, *C* and *D* more likely.

shell before the truly bivalved condition developed. Presumably, *Heraultipegma* and *Watsonella* were infaunal animals capable of deposit or filter feeding. They may have lacked a well-formed head, and their foot was probably already adapted for probing rather than creeping. Thus, they may have had the soft-part morphology of early pelecypods in an effectively univalved shell. A single mutation producing two centers of calcification in the larval shell would then produce a pelecypod, preadapted for exploiting the new shell form.

We have no information on the musculature of *Heraultipegma* or *Watsonella*, and ribeiriids in which the muscle insertions are known postdate *Fordilla* by some 50–70 million years. Ribeiriids are almost as rare as pelecypods throughout the Cambrian, so our interpretation of the evolution of the pelecypods from the monoplacophorans via the ribeiriids is based as much on comparative morphology as on stratigraphic sequence. However, we believe that the Ordovician representatives of all three groups retain the fundamental features of their Cambrian ancestors, just as living fish, reptiles, and mammals reflect their Mesozoic and early Cenozoic counterparts.

If this be so, some Cambrian ribeiriids, like their Ordovician descendents, had probably developed a pallial line. The pedal musculature still formed a ring on the shell, as in the Cambrian-Ordovician monoplacophorans. Eventually the muscles on the midline were enlarged to operate a pelecypodlike foot. When the truly bivalved condition was attained, the anterior and posterior radial muscles of the mantle cross-fused to form adductors, and the anterior and posterior median muscles split to form the paired pedal retractors attached above the adductor insertions on each valve. The remaining parts of the pedal musculature, already fragmented in some ribeiriids, formed the small visceral/pedal muscles found in *Fordilla* and many Ordovician pelecypods.

It is the adductor muscles and well-developed hinge teeth of Cambrian-Ordovician pelecypods that so clearly separate them from coeval rostroconchs, but both of these structures would normally be unnecessary until a flexible ligament evolved. Both are present in bivalved snails, suggesting they can form rapidly when the need arises. As some univalved snails have an adductor muscle that is used to pump water in and out of the mantle cavity (Marcus and Marcus, 1956), some rostroconchs may have developed adductors for the same purpose. *Eopteria*, for example, seems to have a posterior adductor muscle. If some primitive ribeiriids had adductor muscles,

they would obviously have been more successful when the ligament evolved.

RADIATION OF THE PELECYPODA

Apart from the curiously enlarged pallial muscles, *Fordilla troyensis* is a suitable ancestor for all the known subclasses of the Pelecypoda (Pojeta and others, 1973; Pojeta and Runnegar, 1974). Recent discoveries summarized by Pojeta (1975) show that the pelecypod subclasses visible in the Ordovician (Pojeta, 1971) could easily have stemmed from a single Cambrian stock. We conclude that the class appeared from the ribeiriid rostroconchs in the Adabanian Stage of the Early Cambrian, remained an almost insignificant component of the biosphere until the Tremadocian, and then radiated rapidly into all the existing subclasses by the late Middle Ordovician (Pojeta, 1971).

ORIGIN OF THE SCAPHOPODA

Scaphopods have a tubular shell which is often gently curved and is invariably open at both ends. Growth proceeds by the deposition of new shell at the larger end of the tube and simultaneous resorption at the opposite end.

Coarsely silicified replicas of tusk-shaped shells resembling later undoubted scaphopods are known from the Ordovician of the United States. We believe the class was probably well differentiated by this time. However, Yochelson (oral commun., 1973) maintains a more conservative view of the range of the class, preferring to accept only Devonian and younger tusk-shaped shells as scaphopod mollusks. The presence of a slit in the smaller shell aperture is probably the best evidence for distinguishing scaphopods from similarly shaped worm tubes or other organisms. Unfortunately, the Ordovician specimens are too poorly preserved to show this feature.

The ontogeny of the living scaphopod *Dentalium* shows that the larval mantle and shell first appear dorsally and then grow left and right lobes which eventually coalesce ventrally to produce the tubular juvenile and adult shell (Lacaze-Duthiers, 1856–57). This embryological observation has led to the belief that scaphopods are more closely related to the Pelecypoda than they are to any other group of extant mollusks.

We also rely on the embryological evidence to postulate that the Scaphopoda may have evolved from the ribeiriid rostroconchs. If the inner edges of the mantle lobes of a ribeiriid fused ventrally, the shell could still grow normally, as it does in pelecypods that have ventrally fused mantle margins. Subse-

quent fusion of the outer edges of the mantle could have produced a ventrally fused shell. As soon as this happened, the postlarval shell would become tubular, and all subsequent growth would proceed as in living scaphopods. The result would be the immediate production of a scaphopodlike shell; there could be no morphological intermediates between the two growth forms. If our reasoning be correct, we are unlikely to discover fossils that prove the phylogenetic connection between the two classes.

Intermediate forms could occur if ventral fusion of the shell first occurred in late ontogeny and was subsequently transferred to the larval shell. For example, the juvenile bivalved shell is preserved on the dorsal side of the tubular "adventitious" shell of the clavagellid pelecypod *Brechites* (Purchon, 1960). So far, no fossil ribeiriids showing similar features have been discovered.

If we can demonstrate a connection between the monoplacophorans and ribeiriids, it would allow us to argue that the ancestral group would have shared primitive anatomical features found in living scaphopods. In particular, living scaphopods have a radula. If the scaphopods developed from the ribeiriids, we can conclude that some or all ribeiriids also had a radula. The ribeiriid *Pinnocaris* (pl. 9, figs. 11–24) has a shell form approaching that of scaphopods but still has a prominent pegma.

MATTHEVA AND STENOTHECOIDA (PROBIVALVIA)

Yochelson (1966, 1968, 1969) and Aksarina (1968) placed two small groups of enigmatic Early Cambrian fossils in separate molluscan classes called *Mattheva* Yochelson 1966 and *Stenothecoida* Yochelson 1968 or *Probivalvia* Aksarina 1968. The names *Stenothecoida* and *Probivalvia* Aksarina are objective synonyms; Yochelson's name was published in an abstract in August 1968, and Aksarina's at an unspecified time in 1968. As Harry (1969) also used *Probivalvia* in a different sense, and the name has some phylogenetic connotations, we suggest that Yochelson's name be used for this group of organisms.

The class *Mattheva* is based on a single genus, *Matthevia*. It is known from two, co-occurring, subequal, massive conical plates that are flattened on one side and that have two tapering cavities on the side that was attached to the animal. The plates show growth lines and probably formed part or all of the exoskeleton of a primitive mollusk (Yochelson, 1966). Runnegar and Pojeta (1974) suggested that *Matthevia* is a primitive chiton.

The class *Stenothecoida* is more diverse; it probably includes the following genera: *Stenothecoides* Resser, *Bagenovia* Radugin, *Cambridium* Horný, *Bagenoviella* Aksarina, *Sulcocarina* Aksarina, *Kaschkadokia* Aksarina, and *Makarakia* Aksarina (Aksarina, 1968; Yochelson, 1969). *Stenothecoids* are demonstrably or inferentially bivalved shells that are normally found disarticulated. The valves resemble coeval limpet-shaped tergomyan monoplacophorans in shape, except that they are slightly asymmetrical, and valves that look like the right and left valves of some pelecypods can usually be distinguished (Poulsen, 1932; Yochelson, 1969). The few articulated specimens known (Aksarina, 1968; Yochelson, 1969) are slightly inequivalved.

The shell morphology is best known from *Stenothecoides* (Rasetti, 1954; Horný, 1957; Robison, 1964; Yochelson, 1969). The valves are unornamented except for obvious comarginal growth lines and a subangular carina that runs from the beak to near the midpoint of the opposite part of the commissure. Apparently well preserved internal molds have a relatively smooth median zone that appears to coincide with this external carina, and a series of branching elevations that reflect grooves in the shell that run away from the central zone on both sides of the valve. These grooves may reflect bilaterally arranged canals or tubes in the mantle; if so, these grooves branch towards the margin of the shell, and they all appear to join the central zone.

Externally, *stenothecoids* vary from relatively smooth shells to elongate oysterlike forms ornamented by divergent angular folds in the shell (Aksarina, 1968). These folds interlock at the valve margins and may be homologous with radial markings on the interiors of the smoother shells. Yochelson interpreted *Stenothecoides* as a brachiopodlike mollusk. Runnegar and Pojeta (1974) offered the alternative suggestion that it may have been a bivalved monoplacophoran, the lower (smaller?) valve being formed by the sole of the foot. A few living limpets form a second valve in this way, although in the limpets, the lower valve is cemented to rocks.

MOLLUSCAN SUBPHYLA

Stasek (1972) theorized that the extant mollusks are the progeny of three lineages that separated before the phylum was well established. He noted that no known intermediate forms, fossil or living, bridge the "enormous gaps between any two of the three lineages." He therefore treated each as a separate subphylum. They are: (1) the subphylum *Aculifera*,

containing only the class Aplacophora, derived from the most primitive of the ancestors of the Mollusca; (2) the subphylum Placophora, containing only the class Polyplacophora and emphasizing the pseudometamerism of its more advanced premollusk ancestor; and (3) the subphylum Conchifera, containing the class Monoplacophora and the other classes derived from it.

We have no expert knowledge of the aplacophoran and polyplacophoran mollusks, but we agree with Stasek that major differences exist between these organisms and other mollusks. We adopt his basic subdivisions of the phylum but suggest that the Conchifera can itself be separated into two major lineages worthy of the rank of subphylum (fig. 13). The fossil record indicates that the Monoplacophora gave rise to the Gastropoda, Cephalopoda, and Rostroconchia, and that the Pelecypoda and Scaphopoda are derived from the Rostroconchia. These last three classes thus form a lineage that diverged from the Monoplacophora in the Early Cambrian. They emphasized a shell that in all groups is primitively open at both ends, allowing the gut to remain relatively straight, and having an anterior mouth and posterior anus. We coined the term Diasoma (through-body) for the subphylum containing the three classes Rostroconchia, Pelecypoda, and Scaphopoda (Runnegar and Pojeta, 1974). The remaining three classes (Monoplacophora, Gastropoda, and Cephalopoda) emphasize a conical univalved shell,

usually twisted into a spiral. The relatively small single shell aperture forces the anus to lie close to the mouth, and the gut is bent into a U. We use the name Cyrtosoma (hunchback-body) for the subphylum containing these three classes (Runnegar and Pojeta, 1974). Strictly speaking, the cyrtosomes are the ancestors of the diasomes, but in fact both subphyla appeared and began to diversify within a few millions of years in the Early Cambrian. The Cambrian-Ordovician record of molluscan higher taxa is shown in figure 14.

GLOSSARY OF MORPHOLOGICAL TERMS

acline. Perpendicular to hinge or almost so.

adductor muscle. Muscle used to draw the two halves of a bivalved shell together; believed to have developed by cross-fusion of distal ends of opposing pallial retractor muscles (pl. 22, figs. 1, 2).

anterior. Edge of shell having gape and commissural denticles (Eopteriidae, Conocardiidae) (pl. 24, fig. 14; pl. 40, fig. 6); or end of shell having pegma (Ribeiriidae, Technophoridae) (pl. 6, fig. 7; pl. 11, fig. 22).

anterior branch. Part of pallial line extending dorsally from the pallial junction toward the midline (pl. 53, fig. 1).

anterior clefts. Tension fractures formed during growth on either side of shell in front of beak (pl. 4, fig. 9; pl. 28, fig. 17).

anterior gape. Opening at anterior end of shell (pl. 2, fig. 12; pl. 6, fig. 5; pl. 24, fig. 14; pl. 28, fig. 15; pl. 40, fig. 6; pl. 43, fig. 13).

anterior umbonal cavity. Part of umbonal cavity of ribeirioids in front of pegma (pl. 5, fig. 9).

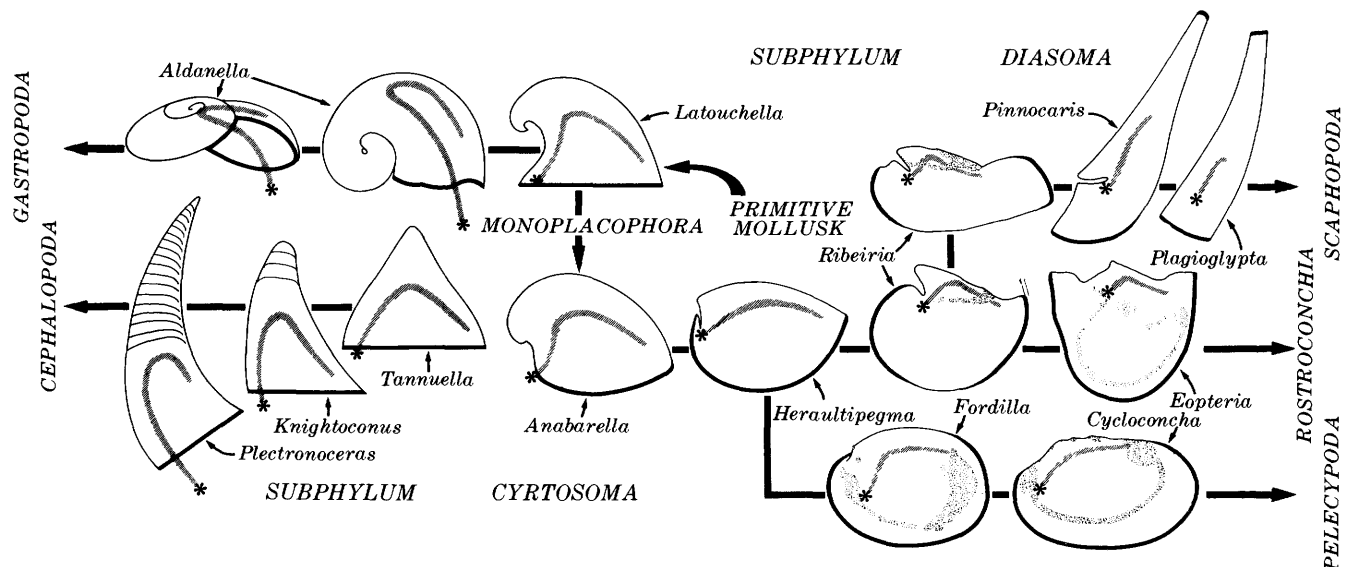


FIGURE 13.—Schematic view of the origin of the univalved and bivalved molluscan classes. Most drawings are based on internal molds of the shells. Thick lines show extent of shell apertures; stippled areas represent muscle insertions; shaded areas show probable position of gut, and mouth is indicated by asterisk. From Runnegar and Pojeta, 1974, figure 4; Copyright 1974 by the American Association for the Advancement of Science, published with permission.

apertural plate. Internal subcircular disk attached to both valves behind the anterior gape of some eopteriids; a modified pegma (pl. 29, figs. 14, 15).

apertural (longitudinal) shelves. Curved plates of outer shell layer projecting horizontally across the snout region of some conocardioids (pl. 43, figs. 12, 13).

beak. Projecting juvenile part of shell (pl. 6, fig. 7).

bivalved shell. Shell having two obviously expanded lateral lobes (valves), not necessarily distinguished in early ontogeny.

body of shell. Inflated part of shell between snout and rostrum (pl. 43, fig. 5).

carina. Angulation of umbo (pl. 29, figs. 6, 7; pl. 50, fig. 38).

comarginal. Feature on exterior surface of shell parallel to growing margin.

commissure. Growing edge of shell.

commissural (marginal) denticle. Visible part of submerged rib immediately inside commissure (pl. 34, figs. 9, 13).

dissoconch. Postlarval shell.

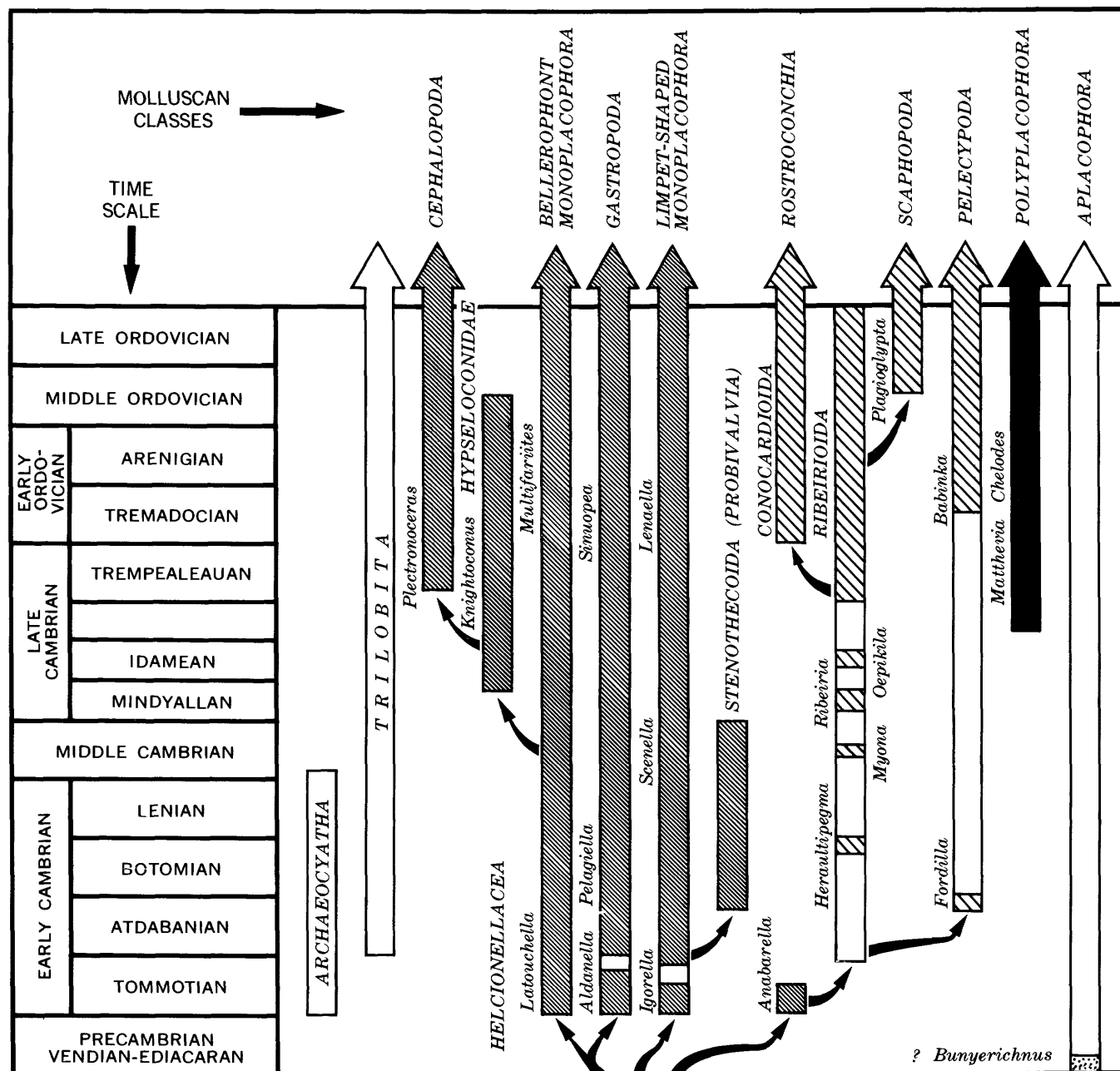


FIGURE 14.—Historical record of the initial radiation of the Mollusca, scaled against time divisions based primarily on the succession of fossil archaeocyaths and trilobites. The two largest molluscan subphyla (Cyrtosoma, fine-shaded columns, and Diasoma, coarse-shaded columns) separated in the Early Cambrian. Modified from Runnegar and Pojeta, 1974, figure 1.

- divaricate.** Exterior ornament which is neither simply radial nor simply comarginal (pl. 11, fig. 16; pl. 14, fig. 2).
- dorsal.** Fused junction of midsagittal plane passing between valves.
- height.** Distance between two planes parallel to hinge axis and perpendicular to plane of symmetry, which just touch most dorsal and ventral parts of shell.
- hinge.** Dorsal margin of shell which rotates during growth.
- hinge axis.** Imaginary line about which the valves rotate during growth.
- hood.** Curved lamellose plates connected to carinae in Conocardidae; growing edges form tubular extension of ventral orifice (=collar, schleppe, eventail, fringe, Kragen) (pl. 45, fig. 14; pl. 47, fig. 1; pl. 48, fig. 2).
- inflation.** Distance between two planes parallel to midsagittal plane, which just touch the lateral edges of the shell.
- insertion, insertion area.** Place where a muscle is attached to the shell (=muscle scar).
- length.** Distance between two planes perpendicular to hinge axis and just touching anterior and posterior extremities of shell.
- longitudinal clefts.** Rostral clefts that are subparallel to the rostrum (pl. 40, fig. 5; pl. 43, fig. 10).
- median muscles.** Single anterior and posterior pedal retractor muscles inserted across the dorsal midline of the shells of ribeirioids (pl. 6, figs. 4, 14).
- muscle impression.** Mold of muscle bundle on interior of shell.
- muscle track.** Depression of inner surface of shell caused by thinning of shell layers over underlying myostracum; shows direction of movement of muscle insertion during growth.
- myostracum.** Shell layer formed at muscle-insertion area.
- opisthodontic.** Wholly behind the protoconch.
- pallial junction.** Junction of anterior and posterior branches of pallial line (pl. 53, fig. 1).
- pallial line.** Linear, continuous or discontinuous insertion area of radial muscles of mantle (pl. 22, figs. 1, 2, 3, 4, 13).
- pallial muscles.** Radial muscles of the mantle attached to the shell.
- pallial protractor muscles.** Radial muscles of the mantle that serve to protract the mantle edge (pl. 47, fig. 12).
- pallial retractor muscles.** Radial muscles of the mantle that serve to retract the mantle edge (pl. 20, figs. 10, 11).
- pallial sinus.** Embayment of pallial line due to retreat of pallial muscle insertions away from commissure (pl. 22, figs. 1, 2, 3, 4, 13).
- pedal muscles.** Muscles of the foot (pl. 5, fig. 4; pl. 6, fig. 14; pl. 22, figs. 5, 6).
- pegma.** Plate connecting right and left valves in umbonal part of shell (pl. 4, figs. 21, 22; pl. 5, figs. 2, 4); supports large muscle in ribeirioids.
- posterior.** End of shell opposite that having anterior gape and (or) pegma.
- posterior branch.** Posterior part of pallial line extending dorsally from the pallial junction along the anterior slope (pl. 53, fig. 1).
- posterior clefts.** Tension fractures formed during growth on either side of the shell behind the beak (pl. 40, fig. 5).
- posterior gape.** Relatively large opening at posterior end of shell (pl. 6, fig. 6).
- posterior umbonal cavity.** Part of umbonal cavity of ribeirioids behind pegma (pl. 6, fig. 15).
- primary pedal retractor muscles.** Relatively large bilaterally paired pedal muscles inserted on the body of the shell of advanced rostroconchs (pl. 22, figs. 1, 2, 5, 6).
- prosocline.** Shells having demarcation line inclined posteriorly.
- prosodontic.** Anterior to protoconch.
- protoconch.** Larval shell (pl. 41; pl. 47, figs. 13-15).
- rostral area.** Area surrounding rostrum, bordered by hood, carina, or prominent rib.
- rostral clefts.** Elongate tension fractures bordering or crossing the dorsal part of the rostrum (pl. 40, fig. 5).
- rostral orifice.** Hole in commissure at end of rostrum (pl. 43, fig. 11).
- rostral structure.** Curved, hoodlike structure generated at rostral orifice of some conocardoids (*see* hood).
- rostrum.** Tubular extension of posterodorsal part of shell (pl. 39, fig. 3; pl. 43, fig. 5).
- secondary pedal retractor muscles.** Relatively small bilaterally paired pedal muscles inserted on the body of the shell of advanced rostroconchs (pl. 22, figs. 5, 6).
- shell muscles.** Muscles inserted on the shell that are used to control the foot and support the visceral mass.
- side muscles.** Lateral pedal and (or) visceral muscles of ribeirioids; insertions form left and right linear connections between anterior and posterior median muscle insertions (pl. 6, fig. 8; pl. 7, fig. 1; pl. 8, fig. 14; pl. 12, figs. 13, 17).
- snout.** Enlarged anterior part of shell, separated from body by sulcus and differences in sculpture (pl. 38, fig. 2; pl. 43, fig. 7).
- submerged ribs.** Ribs generated by commissural denticles and covered by growth of inner shell layers (pl. 43, fig. 1; pl. 45, fig. 4; pl. 50, fig. 2).
- transverse clefts.** Clefts that cross the rostrum (pl. 40, fig. 5).
- umbo.** Dorsal projection of valve above protoconch (pl. 42, fig. 1).
- ventral.** Part of shell opposite fused dorsal margin.
- ventral orifice(s).** Small aperture(s) in commissure between rostrum and anterior gape (pl. 24, fig. 15).

SYSTEMATIC PALEONTOLOGY

SYNOPTIC CLASSIFICATION OF KNOWN

ROSTROCONCH MOLLUSKS

Phylum MOLLUSCA

Subphylum DIASOMA

Class ROSTROCONCHIA

Order RIBEIRIOIDA

Family RIBEIRIIDAE

*Ribeiria**Heraultipegma**Pinnocaris**Ribeirina**Wanwania**Watsonella*

Family TECHNOPHORIDAE

*Technophorus**Anisotechnophorus**Myocaris**Oepikila**Tolmachovia*

Order ISCHYRINIOIDA

Family ISCHYRINIIDAE

*Ischyrinia**Eoischyrina**Pseudotechnophorus*

Order CONOCARDIOIDA

Superfamily EOPTERIACEA

Family EOPTERIIDAE

*Eopteria**Euchasma**Wanwanella**Wanwanoidea*

Superfamily CONOCARDIACEA

Family CONOCARDIIDAE

*Conocardium**Arceodomus*

Family BRANSONIIDAE

*Bransonia**Mulceodens**Pseudoconocardium*

Family HIPPOCARDIIDAE

*Hippocardia**Bigalea*Rostroconchia *incertae sedis**Euchasmella**Myona**Pseudoeuchasma*

Phylum MOLLUSCA Cuvier, 1797

Subphylum DIASOMA Runnegar and Pojeta, 1974

Class ROSTROCONCHIA Pojeta, Runnegar, Morris, and Newell, 1972

Diagnosis.—Mollusks with an uncoiled and untorted univalved larval shell which straddles the dorsal midline, and a bivalved adult shell with one or more shell layers continuous across the dorsal margin so that a dorsal commissure is lacking.

Stratigraphic distribution.—Lower Cambrian (Georgien)—Upper Permian (Makarewan). We agree with Morris (1967) that the Triassic species placed in *Conocardium* by Healy (1908) are pelecypods probably belonging to the Poromyacea or the Burmesiidae.

Order RIBEIRIOIDA Kobayashi, 1933

Diagnosis.—Rostroconchs with all shell layers continuous across the dorsal margin, an anterior pegma, and a dominant posterior growth component; musculature consists of anterior and posterior median pedal retractor muscles connected by right and left side muscles.

Stratigraphic distribution.—Lower Cambrian (Georgien)—Upper Ordovician (Ashgillian).

Discussion.—This order contains two families and 11 genera and includes the stratigraphically oldest,

morphologically simplest, and phylogenetically most primitive rostroconchs. All the forms included here have previously been classified as bivalved (conchostracan) arthropods (Ulrich and Bassler, 1931; Kobayashi, 1933; Salter, 1864; Etheridge, 1878). Molluscan nature of these forms is indicated by the presence of a protoconch, comarginal growth increments growth increments on the muscle scars, and a pallial line in some forms.

Family RIBEIRIIDAE Kobayashi, 1933

Diagnosis.—Ribeirioids with anterior and posterior shell gapes and lacking radial ornament.

Stratigraphic distribution.—Lower Cambrian (Georgien)—Upper Ordovician (Ashgillian). The stratigraphic range of each species is shown in table 1.

Discussion.—Our concept of this family differs significantly from that of Kobayashi (1933) in that he included all nonconocardiacean rostroconchs in the Ribeiriidae. In 1936, he maintained the same concept of the family but used the name Eopteriidae Miller (1889). As used herein, this family contains six known genera and approximately 23 known species. It is presently known from all continents except Antarctica, and is known from a greater number of geographic localities in North America than on the other continents.

Genus RIBEIRIA Sharpe, 1853

Plates 4–9, 30, 31

1853. *Ribeiria* Sharpe, in Ribeiro, Geol. Soc. London Quart. Jour., v. 9, p. 157.
1865. *Ribeiria* Sharpe [partim], Billings, Palaeozoic Fossils, v. 1, p. 339.
1877. *Ribeiria* Sharpe, Tromelin, Soc. Linnean Normandie Bull, ser. 3, v. 1, p. 35.
1886. *Ribeiria* Sharpe [partim], Whitfield, Am. Mus. Nat. History Bull., v. 1, p. 343.
1889. *Ribeiria* Sharpe [partim], Miller, North American Geology and Paleontology, p. 566.
1890. *Ribeiria* Sharpe [partim], Etheridge, Woodward, and Jones. British Assoc. Adv. Sci., Rept. 59th Mtg. 1889, p. 66.
1900. *Ribeiria* Sharpe [partim], Cleland, Bulls. Am. Paleontology, v. 3, no. 13, p. 20.
1904. *Ribeiria* Sharpe [partim], Schubert and Waagen, K. K. Geol. Reichsanstalt Jahrb., v. 53, p. 41.
1904. [Non] *Ribeiria* Clarke, New York State Mus. Mem. 6, pt. 2, p. 406.
1924. *Ozomia* Walcott, Smithsonian Misc. Colln., v. 67, no. 9, p. 531.
1933. *Ribeiria* Sharpe [partim], Kobayashi, Tokyo Imp. Univ., Fac. Sci. Jour., sec. 2, v. 3, pt. 7 p. 289.
1935. *Ribeiria* Sharpe, Thoral, Contr. étude paléont. Ordovician inférieur *** Montagne Noire, p. 200.
1957. *Ribeiria* Sharpe, Yang, Acad. Sinica, Inst. Paleontology, p. 320.

TIME SCALE		SPECIES																							
				<i>Heraulitopegma varenisense</i>	<i>Watsonella crosbyi</i>	<i>Wanwanian cambrica</i>	<i>W. compressa</i>	<i>W. ambonychiiformis</i>	<i>Ribeiria australiensis</i>	<i>R. taylori</i>	<i>R. turgida</i>	<i>R. lucan</i>	<i>R. bassleri</i>	<i>R. manchurica</i>	<i>R. compressa</i>	<i>R. calcifera</i>	<i>R. parva</i>	<i>R. pholadiformis</i>	<i>R. complanata</i>	<i>R. apusoides</i>	<i>R. magnifica</i>	<i>R. conformis</i>	<i>R. spp.</i>	<i>Ribeiria longiuscula</i>	<i>Pinnocaris lapworthi</i>
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)																								
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)																								
	Marmorian-Porterfieldian (Llanvirnian-Caradocian)																								
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)																								
LATE CAMBRIAN	Mindyallan-Trempealeuan																								
MIDDLE CAMBRIAN																									
EARLY CAMBRIAN																									

TABLE 1.—Range chart showing the known stratigraphic distribution of all species of *Ribeiriidae* recognized herein
[Species roughly arranged according to stratigraphic order, from oldest to youngest, for each genus]

1965. [?] *Technophorus* Branisa, Bolivia Serv. Geol. Bol. 6, p. 76.

Type species.—*Ribeiria pholadiformis* Sharpe, 1853 (p. 158) by monotypy.

Diagnosis.—Posteriorly elongated ribeiriids in which the dorsal and ventral margins are not subparallel and which lack rugose comarginal ornament.

Stratigraphic distribution.—Upper Cambrian (Mindyallan)—Upper Ordovician (Ashgillian).

Discussion.—It is not our intention to describe each of the species that we regard as belonging to *Ribeiria*. We have not been able to obtain specimens of certain species, and for knowledge of these species we are totally dependent upon an aging literature. The known material of some species is not well preserved, and detailed description would provide little more information than the figures provided on our plates. In the following section, we list all the species known to us, figure and diagnose those for which we have been able to obtain adequate material, make various comments, and provide descriptions only for those species that are newly named herein.

***Ribeiria pholadiformis* Sharpe, 1853**

Plate 7, figures 3–16

Diagnosis.—*Ribeiria* with shell thickening above posterior median pedal retractor muscle, producing a prominent notch in the posterior dorsal margin of internal molds. Also in internal molds, apical part of shell usually projecting well above rest of dorsum.

Types and materials.—This is the type species of the genus. It is based upon a syntypic suite of which we choose as the lectotype the specimen figured by Sharpe, 1853, on his plate 9, figures 17 b-c (GB 7798), which is figured herein on plate 7, figures 3–7. The paralectotypes are figured herein on plate 7, figures 8–10 (BM PL 4176a, b; BM PL 4177). We had three other specimens of this species (pl. 7, figs. 11–16) in addition to the type material.

Stratigraphic distribution.—On the basis of the geographic information given by Sharpe (1853, p. 158) and the associated mollusks, many of which were redescribed by Babin (1966), the type material of *R. pholadiformis* is probably Llandeilian (Middle Ordovician) in age from Portugal. Two specimens of the species from Normandy, France (pl. 7, figs. 11, 12), are at the Sedgwick Museum, University of Cambridge, England, and are listed as middle Arenigian (Early Ordovician) in age.

***Ribeiria apusoides* Schubert and Waagen in Perner, 1903**

Plate 5, figures 1–14; plate 6, figures 1–12, 14, 15; plate 7, figures 1, 2; plate 30, figures 1–5; plate 31, figures 1–5

Diagnosis.—Large *Ribeiria* with gently concave dorsal margin lacking a prominent posterior dorsal notch.

Types and materials.—*R. apusoides* is based upon a syntypic suite, of which we choose as the lectotype the specimen figured by Schubert and Waagen, in Perner, 1903, plate 49, figures 18–20 (Schubert and Waagen, 1904, pl. 1, fig. 9). A plastotype (USNM 209402) of this specimen is shown herein on plate 6, figures 1–4. Plastotypes of paralectotypes of the species are shown herein on plate 5, figures 9–11, 13, 14. In addition to the plastotypes, we had 16 other specimens of *R. apusoides* to examine.

Stratigraphic distribution.—According to Kříz (oral commun., July 1973), the type material of this species is from the Caradocian (Middle-Late Ordovician) of Bohemia, Czechoslovakia. Also according to Kříz, the specimen shown herein on plate 6, figure 5, may be Llanvirnian (Middle Ordovician) in age; however, this is uncertain. So far as known, the species is limited to the Middle and Upper Ordovician rocks of Bohemia. The specimen assigned to *R. apusoides* by Termier and Termier (1950, pl. 184, fig. 45) from the Llanvirnian of Morocco does not belong to this species as it has a gently convex dorsal margin.

***Ribeiria australiensis* n. sp.**

Plate 4, figures 26–29

Description.—Small *Ribeiria* with straight to gently concave dorsal margin, posteriorly attenuated; shell gaping posteriorly, ventrally, and anteriorly, with anterior gape extending dorsally to protoconch; protoconch terminal. The only internal feature presently known is a small pegma.

Types.—The holotype (BMR CPC 14670) is shown on plate 4, figures 27, 29; it is 9.4 mm long and 5.9 mm high. One paratype (BMR CPC 14671) is shown on plate 4, figures 26, 28; it is 9.6 mm long and 5.7 mm high.

Type locality.—All specimens of this species are presently known only from one locality, Australian Bureau of Mineral Resources locality G 128 (Öpik, 1967); western Queensland, Australia, lat. 22°, 17' S., long 139°, 01' E., Glenormiston 1:250,000 Geological Series Sheet SF 54–9 (Casey and others, 1965). The locality is indicated on the Glenormiston sheet. The specimens are from the Mungerebar Limestone.

Stratigraphic distribution.—According to Öpik (1967) the age of G-128 is Mindyallan (early Late Cambrian). *R. australiensis* n. sp. is only one of six known species of Cambrian rostroconchs and is the oldest known species of the genus *Ribeiria*.

Etymology.—The species name is derived from Australia.

***Ribeiria bassleri* Kobayashi, 1933**

Discussion.—This species is known from only one specimen which was figured by Kobayashi (1933, pl. 4, figs. 4a, b). Although we have seen a replica of this specimen, it is not well executed, and we can do little more than to list the species here.

Stratigraphic distribution.—Kobayashi (1933, p. 292) listed the species as coming from the "Wanwankou dolomite; Wan-wan-kou in the Niuhsintai Basin, South Manchuria." On p. 259, he indicated that the Wanwankou Dolomite is assigned to the Wanwanian Stage (Early Ordovician).

***Ribeiria bussacensis* Tromelin, 1877**

Discussion.—This species name is listed by Tromelin (1877, p. 35) and Etheridge, Woodward, and Jones (1890, p. 67) as a synonym of *R. pholadiformis* Sharpe and is credited to Sharpe. The Sharpe reference given by both papers that cite *R. bussacensis* is exactly the same as that for *R. pholadiformis* down to plate and figure number. Apparently *R. bussacensis* was intended as a substitute name for *R. pholadiformis*. To our knowledge, Sharpe never used *R. bussacensis* in print, and the reason for the possible substitute name is not given by either Tromelin or Etheridge, Woodward, and Jones.

***Ribeiria calcifera* Billings, 1865**

Plate 4, figures 1-24

Diagnosis.—*Ribeiria* with convex dorsal margin and anterior clefts.

Types and materials.—This species is also based on a syntypic series, of which we choose the specimen shown here on plate 4, figures 4-6 as the lectotype (GSC 469). Paralectotypes are shown on plate 4, figures 1-3, 7-12 (GSC 469a, b, d). In addition to the type suite, we figure four other specimens of the species (pl. 4, figs. 13-24).

Stratigraphic distribution.—*R. calcifera* is known from several localities in the Beekmantown Group (Lower Ordovician) of Ontario, Canada. Recent work by Yochelson and Copeland (1974) indicates that the beds containing this species are latest Canadian (late Early Ordovician) in age in Ontario. Two specimens from the Tanyard Formation of Texas (lower Lower Ordovician) are herein also

assigned to *R. calcifera* (USNM 127908, 127909); these specimens were previously figured by Cloud and Barnes (1948). The Texas specimens show that the pegma of *R. calcifera* is almost horizontal.

***Ribeiria complanata* Salter, 1866**

Plate 9, figure 10

Discussion.—This species is known only from the holotype (GB 12434), which is not markedly attenuated posteriorly and which has a nearly straight dorsal margin. This specimen is from the lower Llandeilian (Middle Ordovician) of North Wales.

***Ribeiria compressa* Whitfield, 1886**

Plate 8, figures 1-5

Diagnosis.—Narrowly convex *Ribeiria* with markedly straight dorsal margin.

Types and materials.—The type material of *R. compressa* consists only of the holotype (pl. 8, figures 1, 2; AM 491). We place in synonymy with *R. compressa*, the name *R. nuculitiformis equilatera* Cleland. We choose as the lectotype of *R. nuculitiformis equilatera* the specimen figured by Cleland (1900, pl. 16, fig. 15), which is figured herein on plate 8, figures 3-5 (PRI 5081).

Stratigraphic distribution.—The museum label lists the holotype of *R. compressa* as coming from the "Ft. Cassin bed, Fort Cassin, Vermont" (upper Canadian, upper Lower Ordovician). Cleland (1900, p. 22) listed *R. nuculitiformis equilatera* as coming from the "Calciferous [Beekmantown] at Fort Hunter, N.Y." (Lower Ordovician). We have found *R. compressa* to be abundant in the "Fonda Limestone Member" of the Tribes Hill Formation (lower Canadian; lower Lower Ordovician) of New York State.

***Ribeiria conformis* Tromelin, 1877**

Discussion.—This name was first proposed as a nomen nudum by Salter, in Bigsby (1868, p. 141). The species has never been figured, and Tromelin (1877, p. 35) is the only author to have commented upon the form. He felt that it was probably synonymous with *R. pholadiformis* Sharpe (*R. bussacensis*). *R. conformis* is from the Budleigh-Salterton Pebble Bed, a Triassic unit which contains Caradocian (Middle-Upper Ordovician) fossils in the pebbles.

***Ribeiria crassa* (Thoral), 1935**

Discussion.—We have seen no specimens of this species, and to our knowledge it is known only from the material figured by Thoral (1935, pl. 10, figs. 9a, b). Thoral placed the species in the genus *Ribeir-*

ella Schubert and Waagen, which we regard as synonymous with *Technophorus* Miller. We do not regard *Ribeiria crassa* as belonging to *Technophorus* because it lacks radial ornament. On his plate 10, Thoral listed the species as occurring in the "Tremadoc supérieur-Arenig inférieur" (Lower Ordovician), St. Chinian, France. On his p. 209, figure 14, he gave the stratigraphic occurrence as "Tremadoc supérieur (?)"; also on p. 209, under Horizon and Locality he listed *R. crassa* as occurring in the "Arenig inférieur."

***Ribeiria inflata* Schubert and Waagen, 1904**

Discussion.—This species is much like *R. apusoides*; we have seen no specimens of *R. inflata*. Schubert and Waagen (1904) felt that there might be intermediates between the two forms. It is probably best to consider *R. inflata* as a synonym of *R. apusoides*; both forms are known only from the Caradocian (Middle-Upper Ordovician) of Bohemia, Czechoslovakia.

***Ribeiria lucan* (Walcott), 1924**
Plate 8, figures 14–24

Diagnosis.—*Ribeiria* with pegma at high angle to dorsal margin and with side muscles bundled into discontinuous attachment areas.

Types and materials.—This species is known only from the type suite, of which we choose the specimen herein figured on plate 8, figure 14, as the lectotype (USNM 209397). Paralectotypes are shown on plate 8, figures 15–24.

Stratigraphic distribution.—*R. lucan* is known only from the Mons Formation (Lower Ordovician) of Alberta, Canada.

Discussion.—Walcott (1924) made this form the type species of his genus *Ozomia*, a name which may prove useful in the future. At present, however, *Ribeiria lucan* is well within the range of variation shown by species that we place in the genus *Ribeiria*.

***Ribeiria magnifica* Tromelin, 1877**

Discussion.—This name was first proposed as a nomen nudum by Salter, in Bigsby (1868, p. 141). The species has never been figured, and Tromelin (1877, p. 36) is the only author to have commented on the form. *R. magnifica* is from the Budleigh-Salterton Pebble Bed, a Triassic unit which contains Caradocian (Middle-Upper Ordovician) fossils in the pebbles.

***Ribeiria manchnrica* Kobayashi, 1933**
Plate 8, figures 6–11

Diagnosis.—Tumid *Ribeiria* with small rounded pegma.

Types and materials.—This species is known only from the material described by Kobayashi (1933, p. 291). We were able to obtain replicas of the holotype (pl. 8, figs. 6, 7; USNM 209394) and of a previously unfigured paratype (pl. 8, figs. 8–11; USNM 209395). In addition, we saw two poorly preserved specimens of the species which are not figured herein.

Stratigraphic distribution.—Kobayashi (1933, p. 291) listed the species as coming from the "Wanwankou dolomite; Wan-wan-kou in the Niuhsintai Basin, South Manchuria." He (1933, p. 259) indicated that the Wanwankou Dolomite is assigned to the Wanwanian Stage (Lower Ordovician).

***Ribeiria manchurica pennata* Kobayashi, 1933**

Discussion.—We have seen no specimens of this form, and the only known figures are those of Kobayashi (1933, pl. 9, figs. 4a, b). Kobayashi (1933, p. 292) noted that: "If complete specimens [of *R. manchurica pennata*] be procured, it may not be possible to separate this specifically from the typical form [*R. manchurica*]." Probably this form should be regarded as a synonym of *R. manchurica*. The stratigraphic occurrence and locality are the same as for *R. manchurica*.

***Ribeiria parva* Collie, 1903**
Plate 9, figures 7–9

Diagnosis.—*Ribeiria* with subcircular lateral outline.

Types and materials.—*R. parva* is known only from the holotype (YU 7933), which is figured herein on plate 9, figures 7–9.

Stratigraphic distribution.—This species is known only from the Beekmantown Formation (Lower Ordovician), Bellefonte, Pennsylvania.

***Ribeiria personata* Thoral, 1935**

Discussion.—We have seen no specimens of this species. Thoral (1935, p. 201) gave the name of the species as *R. personata*; on the explanation for his plate 10, figures 6a, b, he gave the name as "*R. personata forme typica*." Thoral (p. 202) gave the occurrence of the form as "Tremadoc supérieur ou de la base de l'Arenig des environs de Saint Chinian," France.

***Ribeiria personata lata* Thoral, 1935**

Discussion.—We have seen no specimens of this form. Thoral (1935, pl. 10, fig. 7) gave the occurrence as: "Arenig inférieur, St. Chinian" (Lower Ordovician), France.

***Ribeiria personata obsoleta* Thoral, 1935**

Discussion.—We have seen no specimens of this form. Thoral (1935, p. 205, fig. 12) gave the stratigraphic occurrence as: "Trémadoc supérieur-Arenig inférieur" (Lower Ordovician), France.

***Ribeiria soleaeformis* Thoral, 1935**

Discussion.—We have seen no specimens of this form. Thoral (1935, pl. 10, fig. 8) gave the occurrence as: "Tremadoc supérieur-Arenig inférieur, St. Chinian" (Lower Ordovician), France.

Comments about the species of Ribeiria proposed by Thoral (1935).—*R. soleaeformis* is much like *R. pholadiformis* Sharpe (1953) in shell shape, in having a projecting apical area in internal molds, and in having a prominent notch in the posterior dorsal margin of internal molds. *R. soleaeformis* is probably a synonym of *R. pholadiformis*. The other species proposed by Thoral appear to be based on incomplete specimens which preserve only the anterior two-thirds of the valves. They are much like *R. pholadiformis* in shape and have a projecting apical area; it seems likely that they are synonyms of *R. pholadiformis*. Because we have not seen Thoral's original material, it is difficult to synonymize his names with *R. pholadiformis*, however, on the basis of his figures, this synonymization seems likely. Forms similar to those figured by Thoral and to *R. pholadiformis* were figured by Gigout (1951, pl. 2, figs. 15–16) and Termier and Termier (1950, pl. 184, figs. 32–35) from the Llanvirnian and Llandeilian (Middle Ordovician) of Morocco.

***Ribeiria taylori* n. sp.**

Plate 8, figures 12, 13

Description.—Small *Ribeiria* with colinear parts of the hinge anterior and posterior to the beak. Beak projecting but little above the dorsal margin, not recumbent.

Type.—The holotype (USNM 209396) is shown on plate 8, figures 12, 13. It is an incomplete specimen with the posterior end missing. We have polished the posterior face in an effort to examine shell microstructure. The microstructure was not visible although shell layers were recognizable.

Type locality.—The holotype is from USGS loc. 470B (old series), Hall Farm, 1 mile northeast of Whitehall, N.Y. (Taylor and Halley, 1974, p. 32).

Stratigraphic distribution.—The species is from the Whitehall Formation, *Saukia* Zone, probably *Saukiella serotina* (Trempealeuan, Upper Cambrian), of New York. According to Taylor and Halley (1974), the Cambrian-Ordovician boundary occurs in the Whitehall Formation.

Etymology.—The species name is proposed for M. E. Taylor, U.S. Geological Survey, who brought the holotype to our attention.

***Ribeiria turgida* Cleland, 1903**

Plate 9, figure 1

Discussion.—This form is known only from a specimen in the collections of the U.S. National Museum (USNM 84630; pl. 9, fig. 1), which is labeled holotype. The specimen does not resemble either of the figures given by Cleland (1903, pl. 3 figs. 6, 7). We assume that the specimen is correctly labeled; however, it is incomplete, and it is thus difficult to determine the concept indicated by this name. The museum label gives the occurrence of the holotype as: "Tribes Hill ls., Canajoharie?, New York" (Lower Ordovician).

***Ribeiria* spp.**

Plate 4, figure 25; plate 6, figure 13;
plate 7, figures 17, 18; plate 9, figures 2–6

Discussion.—The forms figured and discussed under this heading are based upon incomplete or poorly preserved specimens of *Ribeiria*. They do add data to the stratigraphic and geographic distribution of the genus. The specimen shown on plate 4, figure 25, is from the Lower Ordovician part (Warendian) of the Ninmaroo Formation at northern peak of Digby Peaks, 60 miles north of Boulia, Queensland, Australia. The specimen shown on plate 6, figure 13, is a paralectotype of *R. apusoides* Schubert and Waagen from the Ashgillian (Upper Ordovician) rocks of Bohemia, Czechoslovakia; it differs from other specimens assigned to *R. apusoides* in its straight dorsal margin and in its length-height ratio. It is also the youngest known specimen of the genus *Ribeiria*.

The specimens shown on plate 7, figures 17, 18, are from the Lower Ordovician of Utah; they are both incomplete posteriorly. The specimens shown on plate 9, figures 2–6, are from the Stonehenge Formation (Lower Ordovician) of Maryland.

Genus HERAULTIPEGMA new genus

Plate 2

- 1920. [Non]*Heraultia* Villeneuve, Soc. Entomol. Belgique, Annales v. 60, p. 119.
- 1935. *Heraultia* Cobbold, Annales and Mag. Nat. History, ser. 10, v. 16, p. 37.
- 1974. *Heraultia* Cobbold, Runnegar and Pojeta, Science, v. 186, p. 315.
- 1974. *Heraultia* Cobbold, Pojeta and Runnegar, Am. Scientist, v. 62, p. 711.
- 1975. *Heraultia* Cobbold, Pojeta, Bulls. Am. Paleontology, v. 67, p. 375.

Type species.—*Heraultia varensalensis* Cobbold, 1935 (p. 38), is designated the type species of the genus *Heraultipegma*.

Diagnosis.—Posteriorly elongate ribeiriids with a small pegma, wide anterior, posterior, and ventral shell gapes, and prominent rugose comarginal ornament.

Stratigraphic distribution.—Upper Lower Cambrian (Georgien).

Geographic distribution.—The genus is unequivocally known only from the St. Geniès de Varensal area in the Hérault district of France. One specimen, which was placed in *Fordilla troyensis* by Shaler and Foerste (1888), from the Lower Cambrian of Massachusetts has the shape of *Heraultipegma*; it may belong to that genus or to *Watsonella*, but nothing is known of its ornament or shell gapes.

Discussion.—The new generic name *Heraultipegma* is proposed for those rostroconchs placed in *Heraultia* by Cobbold (1935). The name *Heraultia* Cobbold is a junior homonym of *Heraultia* Villeneuve (1920) which was used for a dipteran insect.

Etymology.—*Hérault*, a region of France; *pegma*, Greek, meaning fastened or fixed; also a structure in rostroconchs. Gender neuter.

***Heraultipegma varensalense* (Cobbold), 1935**

Plate 2, figures 1–13

Diagnosis.—Small *Heraultipegma* with about equally developed anterior, ventral, and posterior shell gapes.

Types and materials.—We have not seen Cobbold's (1935) types of this species. However, S. C. Matthews of the University of Bristol, England, has generously given us topotypes of the species; these topotypes are figured herein (USNM 209414–209417).

Stratigraphic distribution.—All specimens of *H. varensalense* are presently known only from the Georgien (Lower Cambrian) rocks near St. Geniès de Varensal, France.

Genus PINNOCARIS Etheridge, 1878

Plates 9, 10

- 1878. *Pinnocaris* Etheridge, Royal Soc. Edinburgh Proc., v. 4, p. 167.
- 1880. *Pinnocaris* Etheridge, Nicholson and Etheridge, Mon. Silurian Fossils Girvan District in Ayrshire, v. 1, p. 207.
- 1892. *Pinnocaris* Etheridge, Jones, and Woodward, Mon. British Paleozoic Phyllopora, pt. 2, p. 117.
- 1895. *Pinnocaris* Etheridge, Jones, and Woodward, Geol. Mag., Decade 4, v. 2, p. 542.
- 1907. *Pinnocaris* Etheridge, Reed, Geol. Mag., Decade 5, v. 4, p. 110.

Type species.—*Pinnocaris lapworthi* Etheridge, 1878 (p. 169), by monotypy.

Diagnosis.—Posteriorly elongated compressed ribeiriids with anterior clefts and with posterior end drawn out into a rostrum.

Stratigraphic distribution.—Lower Caradocian (Middle Ordovician)–Ashgillian (Upper Ordovician).

***Pinnocaris lapworthi* Etheridge, 1878**

Plate 9, figures 13–23

Diagnosis.—*Pinnocaris* with a nearly straight dorsal margin, a long straight rostrum, and rugose comarginal ornament.

Types and materials.—This is the type species of the genus. It is based upon a syntypic series, of which we choose as the lectotype the specimen figured by Etheridge, 1878, on his plate 2, figure 5 (BM In 20367); this specimen is figured herein on plate 9, figure 21. The paralectotypes are figured herein on plate 9, figures 20, 22 (BM In 20366, In 20368). In addition, we figure four other specimens of the species.

Stratigraphic distribution.—This species is presently known only from Scotland. It is from the Balclatchie Group which Whittington (1972) placed in the lower Caradocian (Middle Ordovician).

***Pinnocaris americana* n. sp.**

Plate 9, figures 11, 12

Description.—*Pinnocaris* lacking rugose ornament, with a gently concave dorsal margin and a short posterior rostrum. The only known internal feature is the pegma.

Types.—*P. americana* is presently known only from two specimens. The holotype is shown on plate 9, figure 12 (USNM 209393); it is about 20 mm long and 7.5 mm high. The paralectotype (USNM 209392) is shown on plate 9, figure 11; it is about 20 mm long and 8 mm high. Both specimens show the anterior clefts.

Type locality.—The museum label gives the locality as: "Elkader, Iowa."

Stratigraphic distribution.—The museum label gives the horizon as: "Prosser limestone", (Middle Ordovician).

Etymology.—The species name is derived from America.

***Pinnocaris curvata* Reed, 1907**

Plate 9, figures 24, 25; plate 10, figures 1–10

Diagnosis.—*Pinnocaris* with a markedly concave dorsal margin.

Materials.—We have not seen Reed's type material; we figure seven other specimens of the species.

Stratigraphic distribution.—*P. curvata* is presently known only from the Drummuck Group (Upper Ordovician) of Scotland.

Genus RIBEIRINA Billings, 1865

Plate 3

1865. *Ribeirina* Billings [partim], Palaeozoic fossils, v. 1, Geol. Survey Canada, p. 340.

1934. [Non] *Ribeirina* Parker, Monog. frogs Microhylidae, p. 115.

Type species.—*Ribeiria?* *longiuscula* Billings, 1865 (p. 341), designated herein.

Diagnosis.—Posteriorly elongated ribeiriids with nearly parallel dorsal and ventral margins.

Stratigraphic distribution.—Upper Canadian (upper Lower Ordovician).

***Ribeirina longiuscula* (Billings), 1865**

Plate 3, figures 15–23

Diagnosis.—*Ribeirina* with small beak and with flaring shell margins to either side of the anterior gape.

Types and materials.—The holotype of the species (GSC 470) is shown on plate 3, figures 21–23; it is about 32 mm long and 15 mm high. The species is known from only two specimens besides the holotype; these are shown on plate 3, figures 15–20.

Stratigraphic distribution.—Two of the known specimens (GSC 470; ROM 26 cal.) of the species are labeled "Beekmantown" (Lower Ordovician), Ontario, Canada. The third specimen (USNM 209413) is from the Oxford Formation (GSC loc. 89453), Ontario, Canada; recent work by Yochelson and Copeland (1974) suggests that this specimen is latest Canadian (late Early Ordovician) in age.

Genus WANWANIA Kobayashi, 1933

Plate 3

1933. *Wanwania* Kobayashi Tokyo, Imp. Univ. Fac. Sci. Jour., v. 3, pt. 7, p. 282.

1957. *Wanwania* Kobayashi, Yang, Chung-kuo piao chun hua shih, p. 320.

Type species.—*Wanwania cambrica* Kobayashi, 1933 (p. 292), by original designation.

Diagnosis.—Dorsoventrally elongated ribeiriids in which the shell is higher than long or is subquadrate.

Stratigraphic distribution.—Upper Cambrian (*Tsinania* Zone, Yingtzu Series)—Lower Ordovician (Wanwanian) of Manchuria.

***Wanwania cambrica* Kobayashi, 1933**

Plate 3, figures 5, 11–14

Diagnosis.—Subquadrate *Wanwania* in which the length and height are subequal.

Materials.—We had three plastotypes of this species to examine. The plastoholotype is figured on plate 3, figures 11–14 (USNM 209412), and a plastoparatype is shown on plate 3, figure 5 (USNM 209409).

Stratigraphic distribution.—According to Kobayashi (1933, p. 283), this species is known only from the: "Upper Cambrian, *Tsinania* zone, Paichia-shan, in the northern part of the Wuhutsui Basin and at Hsishan in the southern part of the same basin, at the neck of the Liaotung Peninsula, Manchuria." On p. 259, he showed the *Tsinania* zone as occurring in the lower Yingtzu Series. Jones, Shergold, and Druce (1971) show the Yingtzu Series as being late Late Cambrian in age.

***Wanwania compressa* Kobayashi, 1933**

Plate 3, figures 6–9

Diagnosis.—Small *Wanwania* in which the height is greater than the length, and with an anteriorly sinuate pallial line.

Materials.—This species is known only from the holotype, of which we had a replica (USNM 209410). The holotype is incomplete posteriorly, and the plastoholotype clearly shows the anterior gape (pl. 3, fig. 9), the pegma (pl. 3, fig. 7), and the pallial line (pl. 3, fig. 7).

Stratigraphic distribution.—Wanwanian (Lower Ordovician). According to Kobayashi (1933, p. 284), *W. compressa* is from the Wanwankou Dolomite, Wan-wan-kou in the Niuhsintai Basin, south Manchuria.

Discussion.—*W. compressa* is much like *W. ambonychiformis* and may be a synonym of that species. Kobayashi (1933) separated them on slight differences in shape. As we had only one plaster replica of each species to examine, we cannot be positive about the synonymy; however, it seems likely that the two names belong to the same form.

***Wanwania ambonychiformis* Kobayashi, 1933**

Plate 3, figure 10

Diagnosis.—Large *Wanwania* in which the height is greater than the length.

Material.—Although Kobayashi (1933, p. 284) noted that this was a common form, we had only a replica of the holotype to examine (USNM 209411).

Stratigraphic distribution.—Wanwanian (Lower Ordovician). Wanwankou Dolomite, Wan-wan-kou in the Niuhsintai Basin, south Manchuria.

Discussion.—As noted above under *W. compressa*, this species is probably synonymous with that species.

Genus *WATSONELLA* Grabau, 1900

Plate 3

1900. *Watsonella* Grabau, Boston Soc. Nat. History Occas. Papers, v. 4, pt. 2, p. 631.
 1912. [Non] *Watsonella* Thiele, Deutsch. Südpolar Exped. 1901-03, v. 13, Zool. 5, p. 237.
 1935. *Watsonella* Grabau, Cobbold, Ann. and Mag. Nat. History, ser. 10, v. 16, p. 38.
 1938. *Stenotheca* Salter [partim], Resser, Smithsonian Misc. Colln., v. 97, no. 10, p. 24.

Type species.—*Watsonella crosbyi* Grabau, 1900 (p. 631), by original designation and monotypy.

Diagnosis.—Small concentrically marked forms, probably with small anterior and posterior shell gapes.

Stratigraphic distribution.—Lower Cambrian of eastern Massachusetts.

Discussion.—Cobbold (1935) noted the similarity of *Watsonella* to *Heraultipegma*. His analysis was based on Grabau's (1900) figures of *Watsonella*, which are stylized; the known specimens of *Watsonella* are not as well preserved as indicated by Grabau's figures. It may be that *Watsonella* and *Heraultipegma* are synonymous, but the known material of *Watsonella* suggests that it had small anterior and posterior gapes, unlike the large gapes of *Heraultipegma*. On the basis of the known material of *Watsonella*, the genus is similar to such helcionellacean monoplacophorans as *Anabarella*.

Watsonella crosbyi Grabau, 1900

Plate 3, figures 1-4

Discussion.—The known material of this species is not well preserved. It does show that *W. crosbyi* is a laterally compressed form with comarginal ornament. We choose as the lectotype the specimen figured by Grabau (1900) on his plate 31, figure 9b. This specimen is herein figured on plate 3, figure 1.

Stratigraphic distribution.—Grabau's specimens of *W. crosbyi* are all from Lower Cambrian boulders at Sandy Cove and Pleasant Beach, Cohasset, Mass.

Family *TECHNOPHORIDAE* Miller, 1889

Diagnosis.—Ribeirioids with radial ornament, some with both divaricate and radial ornament.

Stratigraphic distribution.—Upper Cambrian (Idamean)—Upper Ordovician (Richmondian). The stratigraphic range of each species is shown in table 2.

Discussion.—This family contains five known genera and approximately 21 known species. It is known from all continents except Africa and Antarctica; more than half the known species occur in North America.

Genus *TECHNOPHORUS* Miller, 1889

Plates 10-14

1889. *Technophorus* Miller, North American Geology and Palaeontology, p. 514.
 1894. *Technophorus* Miller, Ulrich, Lower Silurian Lamelli-branchiata of Minnesota, from Minnesota Geol. and Nat. History Survey Final Rept. v. 3, p. 612 [Published under separate cover prior to entire v. 3.]
 1897. *Technophorus* Miller, Ulrich, Minnesota Geol. and Nat. History Survey Final Rept., v. 3, pt. 2, p. 612 [Reprinting of 1894 paper.]
 1904. *Ribeirella* Schubert and Waagen, K.K. Geol. Reichsanst. Jahrb., v. 53, p. 45.
 1933. *Ribeirella* Schubert and Waagen, Kobayashi, Tokyo Imp. Univ. Fac. Sci. Jour., Sec. 2, 3, pt. 7, p. 292, 316.
 1933. *Technophorus* Miller, Kobayashi, Tokyo Imp. Univ. Fac. Sci., Sec. 2, v. 7, pt. 2, p. 299, 316.
 1935. [Non] *Ribeirella* Thorol, Contr. étude Paléont. Ordovicien inférieur *** Montagne Noire, p. 208.
 1936. *Technophorus* Miller, Kobayashi, Geol. Soc. Japan, Jour. v. 43, p. 350, [?] 352.
 1936. *Ribeirella* Schubert and Waagen, Kobayashi, Geol. Soc. Japan, Jour. v. 43, p. 350.
 1960. *Technophorus* Miller, Soot-Ryen, Norsk Geol. Tidsskr., v. 40, p. 125.
 1965. [Non?] *Technophorus* Branisa, Bolivia Serv. Geol. Bol. 6, p. 76.

Type species.—*Technophorus faberi* Miller, 1889 (p. 514), by original designation and monotypy.

Diagnosis.—Small, equivalved, posteriorly elongate technophorids, with a single pegma which is at or nearly at a right angle to the dorsal margin, and with well-developed posterior radial ribs.

Stratigraphic distribution.—Lower Ordovician (Wolungian)—Upper Ordovician (Richmondian).

Discussion.—As with *Ribeiria*, and for the same reasons, it is not our intention to describe each of the species we regard as belonging to *Technophorus*. In the following section, we list all the species known to us, figure and diagnose those for which we have been able to obtain material, make various comments, and provide descriptions only for those species that are newly named herein. We have not been able to locate the holotypes of *T. divaricatus* Ulrich and *T. extenuatus* Ulrich and regard them as lost, nor have we been able to locate the type material of *T. otoviensis* Kobayashi. Of *T. coreanica* (Kobayashi), we have seen only a replica of the holotype. We have significant new material of *Technophorus* from Australia, Bohemia, Indiana, Kentucky, Minnesota, Ohio, and Siberia.

Technophorus faberi Miller, 1889Plate 10, figures 16-21;
plate 11, figures 1-6

Diagnosis.—*Technophorus* with two posterior

TIME SCALE		SPECIES															
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)	<i>Oepikila cambrica</i>	<i>Anisotechnophorus nuculitiformis</i>	<i>Tolmachovia? jelli</i>	<i>T. concentrica</i>	<i>Myocaris lutraria</i>	<i>Technophorus coreanica</i>	<i>T. stoermeri</i>	<i>T. bellistriatus</i>	<i>T. divaricatus</i>	<i>T. extenuatus</i>	<i>T. fillistriatus</i>	<i>T. subacutus</i>	<i>T. cancellatus</i>	<i>T. marija</i>	<i>T. cincinnatiensis</i>	<i>T. faberi</i>
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)																
	Marmorian-Porterfieldian (Llanvirnian-Caradocian)																
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)																
LATE CAMBRIAN	Mindyallan-Trempealeuan																

TABLE 2.—Range chart showing the known stratigraphic distribution of all species of *Technophoridae* recognized herein
[Species roughly arranged according to stratigraphic order, from oldest to youngest, for each genus]

radial ribs and markedly concave dorsal margin in adults.

Types and materials.—The species is based upon two syntypes, of which we choose the specimen herein figured on plate 11, figures 5, 6, as the lectotype (FM 8831). The paralectotype is shown on plate 10, figures 16, 17 (FM 8831). In addition to the type suite, we had about 30 other specimens of this species to examine; most of these were poorly preserved. We figure the four best preserved specimens on plate 10, figures 18–21 and plate 11, figures 1–4.

Stratigraphic distribution.—All the known material of the species is from Edenian and Maysvillian (Upper Ordovician) rocks in Ohio and Kentucky.

***Technophorus bellistriatus* Branson, 1909**

Plate 11, figures 7–13

Diagnosis.—*Technophorus* with reticulate ornament over the body of the shell and with divaricate ornament between the posterior ribs; the more anterior of the two posterior ribs weakly expressed.

Types and materials.—The species is known from only two specimens; the holotype (FM 11551) is shown on plate 11, figures 10–13. The other specimen is shown on plate 11, figures 7–9 (FM 23942).

Stratigraphic distribution.—*T. bellistriatus* is known from the "Auburn Chert" and Decorah Shale (Middle Ordovician) of Missouri.

***Technophorus cancellatus* Ruedemann, 1901**

Plate 11, figures 15–20, 23

Diagnosis.—*Technophorus* with reticulate ornament over the body of the shell and with divaricate ornament between the posterior ribs; the more anterior of the two posterior ribs well developed.

Types and materials.—The type suite of *T. cancellatus* contains six syntypes, of which the specimen shown herein on plate 11, figure 16, is chosen as the lectotype (NYSM 3190). In addition to these specimens, Ruedemann (1912) figured two hypotypes (NYSM 9890, 9891), which are shown herein on plate 11, figures 15, 19. We place in synonymy with *T. cancellatus*, *T. punctostriatus quincuncialis* Foerste, 1914; we choose as the lectotype (GSC 8415) of the latter species the specimen figured herein on plate 11, figure 23.

Stratigraphic distribution.—Ruedemann's specimens of *T. cancellatus* are from the Snake Hill Formation (Middle Ordovician) of New York. The type material of *T. punctostriatus quincuncialis* is labeled as coming from the Upper Ordovician, Chambly, Quebec, Canada.

***Technophorus cincinnatiensis* Miller and Faber, 1894**

Plate 12, figures 4–11

Diagnosis.—*Technophorus* with two posterior radial ribs which do not reach the protoconch and with a prominent rostrum.

Types and materials.—The holotype of the species is shown herein on plate 12, figures 4–6 (UCM 3886). We had four other specimens of this species, two of which form the type suite of *Technophorus punctostriatus* Ulrich, 1895 (USNM 46313, 209383), which species we regard as synonymous with *T. cincinnatiensis*. We choose as the lectotype of *T. punctostriatus* the specimen figured herein on plate 12, figure 7 (USNM 46313).

Stratigraphic distribution.—*T. cincinnatiensis* is known from Edenian and Maysvillian (Upper Ordovician) rocks of Ohio and Kentucky.

***Technophorus coreanica* (Kobayashi), 1934**

Plate 11, figure 14

Discussion.—This species is known only from the holotype, of which we had a replica (USNM 209389) to examine. It is a small internal mold which shows a nearly vertical pegma and either the side muscle or the ridge that parallels this muscle. Kobayashi (1934) questionably placed the form in *Ribeiria*; however, its shape and erect pegma indicate it should be placed in *Technophorus*.

Stratigraphic distribution.—*T. coreanica* is from the *Clarkella* Zone (Lower Ordovician; Wolungian, Tateiwa, 1958, p. 16) of Saisho-ri, South Korea.

***Technophorus divaricatus* Ulrich, 1892a**

Plate 14, figures 2–5

Discussion.—The holotype of this species could not be located, and we assume it to be lost. As figured by Ulrich (1892a, pl. 7, figs. 15, 16), it has one posterior rib and divaricate ornament impinging on this rib. According to Bassler (1915, p. 1258), *T. divaricatus* is from the Decorah Shale (Middle Ordovician) of Minnesota.

We have a specimen of *Technophorus* from the Decorah Shale of Minnesota (pl. 14, fig. 2) which shows divaricate ornament. It has two posterior radial ribs; however, the more anterior of these ribs is weakly expressed. This specimen is herein tentatively placed in *T. divaricatus*. In addition, we have two specimens from the Elkhorn Formation (Upper Ordovician) of Indiana, which have divaricate ornament (pl. 14, figs. 3–5). They have comarginal ornament similar to the specimen from Minnesota in that it is not simple growth lines; rather, the comarginal

markings bifurcate (pl. 14, fig. 3). These two specimens are also tentatively placed in *T. divaricatus*.

***Technophorus extenuatus* Ulrich, 1892b**

Discussion.—The holotype and only known specimen of this species could not be located, and we assume it to be lost. As figured by Ulrich (1892b, fig. 8), it has only one posterior rib and a concave dorsal margin. Bassler (1915, p. 1258) noted that the species is from the Decorah Shale (Middle Ordovician) of Minnesota.

***Technophorus filistriatus* Ulrich, 1892a**

Plate 13, figures 15, 16;
plate 14, figure 1

Diagnosis.—*Technophorus* with a single posterior rib, not markedly attenuated posteriorly, and with termination of rib at or below midpoint of posterior margin.

Types and materials.—The holotype of the species is shown on plate 13, figure 16 (USNM 46312). In addition, we had two other specimens of the species (USNM 47204; UMN 12236).

Stratigraphic distribution.—The holotype of the species is from Blackriveran rocks (Middle Ordovician) of Minnesota. Of the other two specimens, one is listed as coming from the Trentonian (Middle Ordovician?) of Minnesota, and the other is listed as coming from the Decorah Shale (Middle Ordovician) of Minnesota.

***Technophorus marija* n. sp.**

Plate 12, figures 12–15

Description.—Robust and tumid *Technophorus* with two subdued posterior radial ribs, convexity of both valves about equal to height of shell. Internally there is a prominent thick pegma, well-developed side muscles, and a relatively small posterior median muscle.

Types.—At present this species is known only from the holotype (Geological Museum, Academy of Sciences, U.S.S.R., 1849/2027) which measures about 14 mm long, 8 mm high, and 7 mm in convexity (both valves).

Type locality.—The museum label reads: "Boulder on right bank of Moyero River, 6 miles above mouth of Ukdama River, Khatango-Anabar Region, northern Siberia."

Stratigraphic distribution.—The museum label gives the stratigraphic occurrence as Middle Ordovician.

Etymology.—The species is named for Marija Balanc, U.S. Geological Survey, in appreciation of

her helpfulness in translating literature from several languages.

***Technophorus milleri* n. sp.**

Plate 14, figures 6, 7

Description.—Markedly elongate *Technophorus* with two prominent posterior radial ribs, divaricate ornament between the radial ribs, and with the dorso-posterior margin strongly drawn out into a prominent tubular posterior rostrum. The only internal feature presently known is the pegma.

Types.—At present, the species is known only from the holotype (MU 6848), which consists of part and counterpart and measures about 14 mm long and 5.5 mm high.

Type locality.—The holotype is from Dodge's Creek, 0.5 miles north of Oxford, Ohio.

Stratigraphic distribution.—The holotype is from the lower Whitewater Formation (Richmondian, upper Upper Ordovician).

Etymology.—The species is named for S. A. Miller who named the genus *Technophorus* and pioneered in the study of these animals.

***Technophorus? otaviensis* Kobayashi, 1936**

Discussion.—As figured by Kobayashi (1936, figures 5–7), this form does not show posterior ribs or a pegma. We have seen no specimens or replicas. According to Kobayashi (1936, p. 352), the form is from "a late Middle(?) Ordovician sandstone of Otavi, Bolivia * * *." Branisa (1965) tentatively assigned a specimen from the Llanvirnian (Middle Ordovician) of Bolivia to this species, his specimen appears to belong to *Ribeiria*.

***Technophorus plicatus* (Billings), 1866**

Plate 12, figures 1–3

Discussion.—The holotype of this species (GSC 2291) is a weathered specimen from which most of the shell has been removed (pl. 12, figs. 1, 2). It has two posterior ribs, relict divaricate ornament, and reticulate ornament on the still adhering parts of the shell. Another specimen from the same locality as the holotype also shows relict divaricate ornament between the posterior ribs (pl. 12, fig. 3; YU 3063/40); this specimen is tentatively assigned to *T. plicatus*. Billings placed this species in the genus *Ischyrinia*; however, as noted by Ulrich (1894, 1897) and Twenhofel (1928), the species should be placed in *Technophorus* because it has only a single pegma.

Stratigraphic distribution.—The holotype is from the Ellis Bay Formation (Upper Ordovician), Junction Cliff, Anticosti Island, Quebec, Canada.

Technophorus sharpei (Barrande) in Perner, 1903
Plate 12, figures 18, 19; plate 13, figures 1-14

Diagnosis.—Markedly posteriorly attenuated *Technophorus* with a single posterior rib and a bilobed posterior gape.

Types and materials.—*T. sharpei* is based upon a syntypic series of which we had replicas to examine (USNM 209381, 209382, 209387, 209388). We do not choose a lectotype of this species because all the syntypes figured in Perner (1903) are right valves, whereas all the replicas we have are left valves; possibly the original figures were reversed, but this is still uncertain. In addition, we figure six other specimens of the species.

Stratigraphic distribution.—The species ranges in age from Llanvirnian (Middle Ordovician) to Ashgillian (Late Ordovician) of Bohemia, Czechoslovakia.

Technophorus stoermeri Soot-Ryen, 1960

Plate 14, figure 8

Discussion.—This species is known only from the holotype (UO 5849), which is a small specimen with a single posterior rib. Soot-Ryen (1960) noted that *T. stoermeri* is similar to *T. sharpei*, and the two names may be synonymous.

Stratigraphic distribution.—This species is known from the middle Caradocian (4b β , Middle Ordovician), Ostoya, Baerum, Norway.

Technophorus subacutus Ulrich, 1892a

Plate 11, figure 22

Discussion.—This species is known only from the holotype (UMN 8338), which is a small specimen with two posterior ribs and a prominent posterodorsal notch.

Stratigraphic distribution.—Ulrich (1892a, p. 101) gave the horizon and locality of *T. subacutus* as "Upper part of the limestone of the Trenton Formation at Minneapolis, Minnesota." Bassler (1915, p. 1259) gave the horizon as "Black River (Platteville)." Presumably the species is from the Middle Ordovician.

"*Technophorus*" *yoldiaformis* (Ulrich), 1879

Plate 10, figures 11, 12

Discussion.—This species was originally placed in the pelecypod genus *Nuculites* Conrad by Ulrich (1879). In 1892, Ulrich (1892b) placed it in the genus *Technophorus*. As noted by Kobayashi (1936), "*T. yoldiaformis* is a pelecypod; this placement is indicated by the anterior and posterior adductor

muscle scars and the dorsal commissure. The species is under study by Pojeta.

Technophorus spp.

Plate 11, figure 21; plate 12, figures 16, 17

Discussion.—The specimens discussed under this heading are not well enough preserved to be placed in one of the named species; they are included here because they provide new stratigraphic, geographic, or morphological information about the genus.

The form shown on plate 11, figure 21, is known from only one small silicified internal mold. It is the first known representative of the genus *Technophorus* from Australia occurring in the upper Ninmaroo Formation (Lower Ordovician; Warendian) at northern peak of Digby Peaks, 60 miles north of Boulia, Queensland.

The specimens shown on plate 12, figures 16, 17, are from the Edenian (Upper Ordovician) of Kentucky. They show the side muscles and an unusual almost square protoconch.

Genus *ANISOTECHNOPHORUS* new genus

Plate 18

1900. *Ribeiria* Sharpe [partim], Cleland, *Bulls. Am. Paleontology*, v. 3, no. 13, p. 20.

Type species.—*Ribeiria? nuculitiformis* Cleland, 1900 (p. 21), is herein designated the type species of the new genus *Anisotechnophorus*.

Description.—Small, inequivalved, posteriorly elongate technophorids with a single pegma which is oblique to the dorsal margin, and with well-developed posterior radial ribs. The posterior terminations of the ribs alternate with one another on the two halves of the shell, producing a zigzag posterior commissure.

Stratigraphic distribution.—Canadian (Lower Ordovician) of New York State.

Etymology.—*Anisos*, Greek, meaning unequal; *Technophorus*, a genus of ribeirioids. Gender masculine.

Anisotechnophorus nuculitiformis (Cleland), 1900

Plate 18, figures 1-21

Diagnosis.—*Anisotechnophorus* in which the length of the shell is about twice the height of the shell.

Types and materials.—The species is based upon a syntypic series, of which we choose the specimen shown on plate 18, figures 1-6, as the lectotype (PRI 5080). The paralectotypes are shown on plate 18, figures 13, 15, 16, and 19 (PRI 5079). We had literally thousands of specimens of this species to exam-

ine, as it is extremely abundant at some localities in the "Fonda Limestone Member" of the Tribes Hill Limestone of New York State. None of the many known specimens of this species are preserved well enough to show internal details other than the pegma.

Stratigraphic distribution.—The type suite is simply labeled "Calciferous [Beekmantown, Lower Ordovician], Fort Hunter Section, New York." As noted above, we have found the species to be extremely abundant at some outcrops of the "Fonda Limestone Member" of the Tribes Hill Limestone (lower Lower Ordovician) of central New York State. M. E. Taylor gave us one specimen (pl. 18, fig. 18) from the *Missisquoia* Zone (basal Lower Ordovician) of the upper Whitehall Formation of eastern New York State. In addition, we have two specimens (pl. 18, figs. 7–10, 20), the museum labels of which suggest that the species may occur in the latest Cambrian of New York State. One label reads: "Ozarkic (Little Falls), Fort Hunter, New York," and the other label reads: "Little Falls, Fort Hunter, N.Y." If the "Little Falls" in the two labels refers to the Little Falls Dolomite, this unit is regarded as Late Cambrian in age. Thus, *A. nuculitiformis* may occur in the uppermost Cambrian; it is well documented to occur in the lower Lower Ordovician.

Genus MYOCARIS Salter, 1864

Plate 10

1864. *Myocaris* Salter, Geol. Mag., v. 1, p. 11.

Type species.—*Myocaris lutraria* Salter, 1864 (p. 11) by monotypy.

Diagnosis.—Large technophorids with radial ribs projecting posteriorly beyond body of shell.

Stratigraphic distribution.—Middle Ordovician (from the Budleigh-Salterton Pebble Bed), Devon, England.

Myocaris lutraria Salter, 1864

Plate 10, figure 13

Discussion.—This species is known from one complete specimen, the holotype (pl. 10, fig. 13; BM I 7204), and several fragmentary specimens. It is unusual because of its large size (about 60 mm long); in fact, it is the largest known Ordovician rostroconch. The concave anterior margin is also unusual, for it suggests the presence of an anterior gape, a feature unknown in other technophorids. Only the finding of additional material will determine whether or not an anterior gape is present.

Stratigraphic distribution.—The museum label accompanying the holotype reads: "Ordovician, Llan-

deilo, from Trias Pebble Bed, Budleigh-Salterton, Devon," England.

Genus OEPIKILA Runnegar and Pojeta, 1974

Plate 10

1940. [Non] *Öpikella* Thorsland, Sveriges Geol. Undersökning ser. c, no. 436, p. 181.

1974. *Opikella* Runnegar and Pojeta, Science, v. 186, p. 315.

1974. *Oepikila* Runnegar and Pojeta, Science, v. 186, p. 316.

Type species.—*Opikella cambrica* Runnegar and Pojeta, 1974 (p. 317) by original designation and monotypy.

Diagnosis.—Small technophorids with protoconch projecting prominently above the dorsal margin, and with radial ornament consisting of a single umbonal carina.

Stratigraphic distribution.—Idamean (Upper Cambrian), Queensland, Australia.

Etymology.—The genus was named for A. A. Öpik, Australian Bureau of Mineral Resources, who collected the known material.

Oepikila cambrica (Runnegar and Pojeta), 1974

Plate 10, figures 14, 15

Diagnosis.—Subquadrate *Oepikila* in which the umbonal carina divides the shell into nearly equal anterior and posterior halves.

Types.—The species is presently known only from the holotype (BMR CPC 13953; pl. 10, figs. 14, 15), which preserves both the part and counterpart.

Stratigraphic distribution.—Presently known only from BMR locality W9, western Queensland, Australia, north-central part of Mount Whelan 1:250,000 Geological Series Sheet SF 54–13 (1966, Reynolds). The locality is indicated on the Mount Whelan Sheet, and the specimen is from the Georgina Limestone. According to Öpik (oral commun., 1973) the fossils from locality W9 are Idamean (early Late Cambrian) in age.

Genus TOLMACHOVIA Howell and Kobayashi, 1936

Plates 14, 16, 17

1936. *Tolmachovia* Howell and Kobayashi, Carnegie Mus. Annals, v. 25, p. 60.

Type species.—*Tolmachovia concentrica* Howell and Kobayashi, 1936 (p. 60), by original designation and monotypy.

Diagnosis.—Equivalved technophorids with anterior and posterior pegmas and weakly developed posterior ribs.

Stratigraphic distribution.—Warendian (Lower Ordovician)—Middle Ordovician of Australia and Siberia; Ordovician of Portugal.

***Tolmachovia concentrica* Howell and Kobayashi, 1936**

Plate 16, figures 1-10; plate 17, figures 1-7, 9-11

Diagnosis.—*Tolmachovia* with narrow pegmas and rugose concentric ornament over the anterior half of the shell.

Types.—This species is known only from its type series; these specimens are presently at Princeton University, but they bear the numbers of the Geological Museum of the Academy of Science, U.S.S.R., and are herein listed under those numbers. The holotype (Academy of Science, U.S.S.R. 1849/2027a) is figured on plate 16, figures 8-10. Nine paratypes are figured.

Stratigraphic distribution.—The museum label reads: "Middle Ordovician, boulder on right bank of Moyero River, 6 miles above mouth of Ukdama River, Khatanga-Anabar region, northern Siberia."

***Tolmachovia? jelli* n. sp.**

Plate 14, figures 9-19

1969. *Ribeiria?* Hill, Playford, and Woods, Ordovician and Silurian Fossils Queensland, p. O 10.

Description.—*Tolmachovia* with wide pegmas; as in *T. concentrica*, the anterior pegma is bounded by a dorsal projection of the shell in front of the pegma; posteriorly no dorsal projection bounds the pegma; lacking anterior concentric rugose ornament.

Types.—The holotype of the species is shown on plate 14, figures 9-12 (UQ F 60117); it is about 13.8 mm long and 10 mm high. The holotype shows the anterior and posterior median muscles and the side muscles. In addition, we figure three paratypes (pl. 14, figs. 13-19).

Type locality.—Northern peak of Digby Peaks, about 60 miles north of Boulia, Queensland, Australia.

Stratigraphic distribution.—In the top beds of the Ninmaroo Formation, just below the Swift Formation contact (Warendian, Lower Ordovician); presently only known from the type locality.

Etymology.—The species is named for John S. Jell, University of Queensland, who collected the known material.

Discussion.—The species is tentatively assigned to the genus *Tolmachovia*, as at present it is only known from internal molds.

***Tolmachovia* sp.**

Plate 16, figures 11-14

Discussion.—This subcircular form is known from only one specimen (BM PL 4434) which is labeled as coming from the "Ordovician of Portugal."

Order ISCHYRINIOIDA new order

Diagnosis.—Donaciform rostroconchs with a dominant anterior growth component so that the protoconch is at or posterior to the center of the shell, and with two pegmas and overall radial ornament.

Stratigraphic distribution.—Lower Ordovician (Wanwanian)—Upper Ordovician (Richmondian). The stratigraphic range of each species is shown in table 3.

Family ISCHYRINIIDAE Kobayashi, 1933

(nom. transl. Ischyriiniinae Kobayashi, 1954)

Discussion.—This is the only family placed in the order at present; it has the same definition and stratigraphic range as the order. The family contains three known genera and six named species. It is known only from North America and Eurasia, where it has a northern-latitude distribution.

Genus ISCHYRINIA Billings, 1866

Plates 18, 19

- 1866. *Ischyria* Billings [partim], Catalogues Silurian Fossils, Island of Anticosti, p. 16.
- 1889. *Ischyria* Billings [partim], Miller, North American geol. and paleontology, p. 483.
- 1894. *Ischyria* Billings, Ulrich, Lower Silurian Lamellibranchiata Minnesota, Minnesota Geol. and Nat. History Survey Final Rept. v. 3, p. 612. [Published under separate cover prior to entire v. 3.]
- 1897. *Ischyria* Billings, Ulrich Minnesota Geol. and Nat. History Survey Final Rept., v. 3, pt. 2, p. 613. [Reprinting of 1894 paper.]
- 1930. *Ischyria* Billings, Teichert, Palaeont. Zeitschr. v. 12, p. 130.
- 1933. *Ischyria* Billings, Kobayashi, Tokyo Imp. Univ. Fac. Sci. Jour., sec. 2, v. 3, pt. 7, p. 299, 316.
- 1943. *Ischyria* Billings, Müldner, Z. Geschiebeforschung, v. 18, p. 93.
- 1960. *Ischyria* Billings, Soot-Ryen, Norsk Geol. Tidsskr., v. 40, p. 127.

Type species.—*Ischyria winchelli* Billings, subsequent designation of Miller, 1889 (p. 483).

Diagnosis.—Ischyriiniids with anterior and posterior pegmas of about equal length, and with adult musculature consisting of side muscles and probably anterior and posterior median muscles.

Stratigraphic distribution.—Middle Ordovician (*Cyclocrinus* Shale, 4b, Middle Caradocian)—Upper Ordovician (Richmondian).

***Ischyria winchelli* Billings, 1866**

Plate 18, figures 22-25; plate 19, figures 1-8

Diagnosis.—Subquadrate *Ischyria* with fine radial ribs, carinate posterior umbonal slope, and flaring posteroventral gape.

TIME SCALE		SPECIES	
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)	<i>Pseudotechnophorus typicalis</i>	
		<i>Eoischyrina billingsi</i>	
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)	<i>Ischyrina norvegica</i>	
		<i>I. winchelli</i>	
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)	<i>I. schmidtii</i>	
		<i>Eopteria flora</i>	
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)	<i>E. obsolata</i>	
		<i>E. crassa</i>	
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)	<i>E. typica</i>	
		<i>E. ventricosa</i>	
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)	<i>E. richardsoni</i>	
		<i>E. conocardiformis</i>	
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)	<i>Euchasma wanwanense</i>	
		<i>E. blumenbachii</i>	
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)	<i>E. jonesi</i>	
		<i>E. mytiliforme</i>	
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)	<i>E. shorinense</i>	
		<i>Wanwanella? alta</i>	
LATE ORDOVICIAN	Cincinnatian (Caradocian-Ashgillian)	<i>W.? asiatica</i>	
		<i>W. striata</i>	
MIDDLE ORDOVICIAN	Wildernessian-Shermanian (Caradocian)	<i>W. tumida</i>	
		<i>Wanwanoides trigonalis</i>	
EARLY ORDOVICIAN	Canadian-Whiterockian (Tremadocian-Arenigian)	<i>W. trigonalis delicata</i>	

TABLE 3.—Range chart showing the known stratigraphic distribution of all species of *Ischyriniidae* and *Eopteridae* recognized herein

[Species roughly arranged according to stratigraphic order from oldest to youngest, for each genus]

Types and materials.—The type suite consists of two remaining specimens, of which we choose as the lectotype the specimen herein figured on plate 18, figures 23–24 (GSC 2114a). The paralectotype (GSC 2114) is shown on plate 18, figure 25. A second paralectotype is presumed to be lost, as Billings (1866, p. 16) figured three specimens; we could not locate the specimen shown in his figure 4c. In addition to the type suite, we had 25 other specimens of the species to examine from the collection of the Peabody Museum, Yale University; of these we figure the four best preserved specimens.

Stratigraphic distribution.—The species is known only from the Upper Ordovician, English Head and Ellis Bay Formations (Richmondian) of Anticosti Island, Quebec, Canada.

Ischyrinia elongata Müldner, 1943

Discussion.—We have seen no specimens of this species. As indicated by its name, it is an elongate form, and it has a prominent rostrum.

Stratigraphic distribution.—According to Neben and Krueger (1973), *I. elongata* is from the Backsteinkalk near Oderberg, Germany; they place the Backsteinkalk in the lower Caradocian (Middle Ordovician).

Ischyrinia norvegica Soot-Ryen, 1960

Plate 19, figures 10–14

Diagnosis.—Elongate *Ischyrinia* lacking a posterior carina.

Types.—This species is only known from the type suite. The holotype (UO 38267) is shown on plate 19, figures 10–11; three previously unfigured paratypes (UO 38267, 37861) are shown on plate 19, figures 12–14.

Stratigraphic distribution.—*I. norvegica* is known from the Middle Ordovician *Cyclocrinus* Shale, 4b (middle Caradocian) of Norway.

Ischyrinia schmidtii Teichert, 1930

Diagnosis.—Coarsely ribbed elongate *Ischyrinia* with a weakly developed posterior carina.

Types.—We have not seen the types or any other specimens of this species, and our analysis of the form is based upon Teichert (1930).

Stratigraphic distribution.—*I. schmidtii* is known only from the Upper Ordovician (Ashgillian) Lyckholm-Stufe of Estonia.

Ischyrinia spp.

Plate 19, figures 9, 15–17

Discussion.—The specimens listed under this heading provide additional stratigraphic and geographic information about the genus.

The form shown on plate 9, figure 9, is from the Whitehead Formation (Upper Ordovician), Mt. St. Anne, Percé, Quebec, Canada. The specimens illustrated on plate 19, figures 15, 16, are from the Ordovician, Haverfordwest, Wales. The poorly preserved specimen shown on plate 19, figure 17, is from the Middle Ordovician of Siberia, and is herein tentatively assigned to *Ischyrinia*.

Genus *EOISCHYRINA* Kobayashi, 1933

1933. *Eoischyrina* Kobayashi, Tokyo Imp. Univ. Fac. Sci. Jour., v. 3, pt. 7, p. 298, 316.

Type species.—*Eoischyrina billingsi* Kobayashi, 1933 (p. 298), by original designation and monotypy.

Diagnosis.—Slightly anteriorly elongate nearly subquadrate forms with radial ornament.

Stratigraphic distribution.—Lower Ordovician (Wanwanian) of Manchuria.

Discussion.—On the basis of the known figures and the material available to us, this genus is tentatively placed in the Ischyriniidae.

Eoischyrina billingsi Kobayashi, 1933

Discussion.—This species is known from two specimens, of which we had a replica of the holotype to study. The replica was not well executed and is not figured herein. On the basis of the overall shell ribbing, the development of a posterior rostrum, and the lack of anterior and ventral gapes, it seems likely that the species is an ischyriniid.

Stratigraphic distribution.—According to Kobayashi (1933, p. 298) both known specimens of the species are from the "Wanwankou Dolomite [Wanwanian, Lower Ordovician]; Wan-wan-kou in the Niuhsintai Basin, South Manchuria."

Genus *PSEUDOTECHNOPHORUS* Kobayashi, 1933

Plate 20

1933. *Pseudotechnophorus* Kobayashi, Tokyo Imp. Univ., Fac. Sci. Jour., v. 3, pt. 7, p. 300, 317.

Type species.—*Pseudotechnophorus typicalis* Kobayashi, 1933 (p. 300), by original designation and monotypy.

Diagnosis.—Ischyriniids in which the anterior pegma is several times the length of the posterior pegma and in which the median muscles and side muscles are confined to the larval shell; the adult musculature consists of a large primary pedal retractor muscle and several smaller secondary pedal retractor muscles in each valve.

Stratigraphic distribution.—Lower Ordovician (Wanwanian) of Manchuria.

***Pseudotechnophorus typicalis* Kobayashi, 1933**

Plate 20, figures 1-15

Diagnosis.—*Pseudotechnophorus* in which the length is about twice the height.

Types and materials.—We had a replica (USNM 209371; pl. 20, figs. 1, 2) of the specimen figured by Kobayashi (1933, pl. 9, fig. 8) to examine. In addition, we had four specimens to examine (pl. 20, figs. 3-15).

Stratigraphic distribution.—The species is known only from the Wanwankou Dolomite (Wanwanian, Lower Ordovician), Wan-wan-kou in the Niuhsintai Basin, south Manchuria.

Order CONOCARDIOIDA Neumayr, 1891

Diagnosis.—Rostroconchs with external and internal ribs, the latter expressed as marginal denticles on the inside edge of the commissure, and with an anterior gape and dorsal clefts.

Stratigraphic distribution.—Lower Ordovician (Canadian)—Upper Permian (Makarewan).

Superfamily EOPTERACEA Miller, 1889

(nom. transl. herein)

Diagnosis.—Conocardioids with anterior or both anterior and posterior dorsal clefts; anterior, ventral, and posterior shell gapes (which are continuous with one another), rostrum rudimentary or lacking, shell posteriorly elongate in most forms.

Stratigraphic distribution.—Lower Ordovician (Canadian)—Middle Ordovician (Wildernessian). The stratigraphic range of each species is shown on table 3.

Family EOPTERIIDAE Miller, 1889

Discussion.—This is the only family presently assigned to the Eopteracea, and it has the same definition and stratigraphic range as that superfamily.

As herein used, the EopterIIDae contains four known genera and about 19 species; it is presently known only from North America and Eurasia.

Genus EOPTERIA Billings, 1865

Plates 22-26

1865. *Eopteria* Billings Palaeozoic fossils, v. 1, Canada Geol. Survey, p. 221, 306.
1889. *Eopteria* Billings, Miller, North American Geology and Paleontology, p. 480.
1933. *Eopteria* Billings [partim], Kobayashi, Tokyo Imp. Univ., Fac. Sci. Jour., v. 3, pt. 7, p. 295.
1935. *Pterinea* Thoral, Contr. étude paléont. Ordovicien inférieur *** Montagne Noire, p. 175.
1944. *Eopteria* Billings, Shimer and Shrock, Index fossils of North America, p. 659.

1957. *Eopteria* Billings, Yang, Chung-kuo piao chun hua shih, p. 320.

1971. *Eopteria* Billings, Pojeta, U.S. Geol. Survey, Prof. Paper 695, p. 22.

1972. *Eopteria* Billings, Pojeta, Runnegar, Morris, and Newell, Science, v. 177, p. 264.

Type species.—*Eopteria typica* Billings, 1865 (p. 221) by indication.

Diagnosis.—Eopteriids with a prominent anterior snout and lacking a pegma.

Stratigraphic range.—Lower Ordovician (Canadian)—Middle Ordovician (Wildernessian).

Discussion.—Two species, *E. alta* Kobayashi and *E. asiatica* Kobayashi are placed by us in the genus *Wanwanella* Kobayashi.

***Eopteria typica* Billings, 1865**

Discussion.—Unfortunately, the type material of the type species of the genus cannot be located; we assume it to be lost. Also unfortunately, Billings (1865, p. 221) did not figure the species. Cloud and Barnes (1948) figured a form which they assigned to *E. typica*; we figure this specimen on plate 25, figures 2-4, and place it in *E. richardsoni* Billings. According to Bassler (1915, p. 491), Billings' material of *E. typica* was from the Canadian (Quebec-G., Lower Ordovician) of Port aux Choix, Newfoundland.

***Eopteria conocardiiformis* n. sp.**

Plate 26, figures 12-18

Description.—*Eopteria* with markedly elongated anterior snout so that the beak is posterior to the center of the length of the shell.

Types.—The holotype (USNM 209322) is shown on plate 26, figures 12-15; it is about 11 mm long and 8 mm high. Two paratypes are shown on plate 26, figures 16-18 (USNM 209333; 209334).

Type localities.—The holotype is from a quarry about 2 miles north of Pelham, Ala. One paratype is from Highbridge, Ky., and the other is from the intersection of Bailey Gap Road with main road, 1.75 miles northeast of New Hope Church, Ala.

Stratigraphic distribution.—The holotype and the paratype from Alabama are both from the Little Oak Limestone (Porterfieldian; Middle Ordovician). The paratype from Kentucky is from the High Bridge Group (Wildernessian; Middle Ordovician).

Etymology.—The species name is derived from the genus *Conocardium* whose shape *Eopteria conocardiiformis* mimics.

Discussion.—*E. conocardiiformis* shows anterior elongation of the snout to a much more marked degree than does any other species of the genus *Eop-*

teria; it is becoming conocardiac in shape, although the ventral gape still persists.

Eopteria crassa (Thoral), 1935

Discussion.—This species was questionably assigned to the pelecypod genus *Pterinea* Goldfuss by Thoral (1935, p. 175). It is a robust small form whose shape and marginal denticles indicate that it should be placed in *Eopteria*. We have not seen Thoral's material, and our analysis is based upon his description and figures.

Stratigraphic range.—Lower Arenigian (Lower Ordovician) of southern France.

Eopteria flora Kobayashi, 1933

Plate 24, figures 1, 2

Discussion.—We had only a replica of the holotype of this species to examine (USNM 94042); it clearly shows the shape and elongated anterior snout of *Eopteria*. *E. flora* is from the Wanwankou Dolomite (Wanwanian; Lower Ordovician) of south Manchuria.

Eopteria obsolata Kobayashi, 1933

Plate 24, figures 3, 4

Discussion.—We had only a replica of the holotype of this form to examine (USNM 94041); it shows the elongated anterior snout of *Eopteria*. Horizon and locality the same as for *E. flora* above.

Eopteria? ornata Billings, 1865

Discussion.—This species was questionably placed in *Eopteria* by Billings (1865, p. 307). Billings' material can no longer be located and we presume it to be lost. He listed the species as coming from "Point Lévis [Quebec] in the upper part of limestone No. 2, Quebec Group." Bassler (1915, p. 491) noted that *E. ornata* came from a Lévis erratic and gave the age as "Ozarkian?."

Eopteria richardsoni Billings, 1865

Plate 24, figures 5–20; plate 25, figures 2–19; plate 26, figures 1–11

Diagnosis.—*Eopteria* with radial ornament of fine ribs.

Types and materials.—This is the only species of *Eopteria* described by Billings (1865), of which the type material is still extant. The holotype (GSC 756) is figured herein on plate 24, figures 5, 6. The species occurs widely in North America, and we figure specimens from Arkansas, Missouri, Nevada, Quebec, and Texas.

Stratigraphic distribution.—*E. richardsoni* is limited to rocks of Early Ordovician age (Canadian-Whiterockian). In Quebec, it occurs in the Beekman-

town Group (Canadian); in Nevada, it occurs in the Antelope Valley Limestone (Whiterockian); in Arkansas, it occurs in the Smithville Formation (Canadian); in Missouri, it occurs in the Cotter Dolomite and Jefferson City Dolomite (Canadian); and in Texas, it occurs in Honeycut Formation and Scenic Drive Formation of Flower (1964) (Canadian).

Eopteria ventricosa (Whitfield), 1886

Plate 22, figures 1–15; plate 23, figures 1–10

Diagnosis.—*Eopteria* with dominantly comarginal ornament.

Types and materials.—The type suite of *E. ventricosa* consists of two specimens, of which the one figured herein on plate 22, figure 11, is chosen as the lectotype (AM 492); the paralectotype (AM 492) is shown on plate 22, figure 14. In addition to the types, we figure 17 other specimens of the species.

Stratigraphic distribution.—*E. ventricosa* is known only from the "Fort Cassin Limestone" (Canadian, Lower Ordovician), at Fort Cassin, Vt.

Discussion.—This is the morphologically best known species of *Eopteria*, in that some specimens show some of the muscle scars. None of the known material shows all of the muscle scars, and our diagram (fig. 4) of the musculature of this species is a composite.

Eopteria sp.

Plate 25, figure 1

Discussion.—This form is known from three specimens, of which one is figured (USNM 209335). It is by far the largest known *Eopteria*, as much as 50 mm long, and is probably a distinct species. However, the known material is poorly preserved.

Stratigraphic distribution.—Cotter Dolomite (Lower Ordovician) of Arkansas.

Genus *EUCHASMA* Billings, 1865

Plates 27–29

1865. *Euchasma* Billings, Paleozoic fossils, v. 1, Canada Geol. Survey. p. 220, 360.

1889. *Euchasma* Billings, Miller, North American geology and paleontology, p. 480.

1933. [Non] *Euchasma* Billings, Kobayashi, Tokyo, Imp. Univ. Fac. Sci. Jour., v. 3, pt. 7, p. 292.

1955. *Euchasma* Billings, Nicol, Jour. Paleontology, v. 29, p. 552.

1971. *Euchasma* Billings, Pojeta, U.S. Geol. Survey, Prof. Paper 695, p. 22.

1972. *Euchasma* Billings, Pojeta, Runnegar, Morris, and Newell, Science, v. 177, p. 264.

Type species.—*Conocardium blumenbachii* Billings, 1859 (p. 350), by monotypy.

Diagnosis.—Tumid oblique eopteriids with rudimentary rostrum, anterior pegma, a broad anterior face, and snout reduced to an anterior lobe; anterior gape keyhole shaped.

Stratigraphic range.—Lower Ordovician (Canadian-Whiterockian).

Euchasma blumenbachii (Billings), 1859

Plate 27, figures 1-16

Diagnosis.—Large coarsely ribbed *Euchasma* with prominent anterior lobe, dorsal part of keyhole gape elliptical.

Types and materials.—The type suite consists of two syntypes, of which the specimen shown on plate 27, figures 1-4, is herein chosen as the lectotype (GSC 455); the specimen shown on plate 27, figures 7, 8, is the paralectotype (GSC 455a). In addition, we had 19 other specimens of the species to examine, six of which are figured here. All known North American specimens of *Euchasma* are herein placed in *E. blumenbachii*; the species is not presently known to occur outside North America. It occurs widely in North America, and we figure specimens from Newfoundland, Quebec, Texas, and Virginia.

Stratigraphic distribution.—*E. blumenbachii* is limited to rocks of Early Ordovician (Canadian) age. In Newfoundland, it occurs in the St. George Group; in Quebec, it occurs in the Romaine Formation and the Luke Hill Limestone; in Texas, it occurs in the Scenic Drive Formation of Flower (1964); and in Virginia, it occurs in the Beekmantown Group.

"*Euchasma*" eopteriforme Kobayashi, 1933

Discussion.—We had only one poorly preserved specimen of this species to examine, and it is not figured herein. Kobayashi's (1933) figures of the species show a coarsely ribbed form which does not have the shape of other species placed in *Euchasma*. We do not regard the species as belonging to *Euchasma*, but at present we cannot assign it to any of the other known ribbed rostroconch genera. The form is from the Wanwankou Dolomite (Wanwanian, Lower Ordovician) of Manchuria.

Euchasma jonesi n. sp.

Plate 28, figures 12-18; plate 29, figures 1-5

Description.—Small finely ribbed *Euchasma* with dorsal part of keyhole gape subcircular and having a dorsal scooplike projection; rostrum rudimentary, but marked off from rest of shell by depressed areas.

Types.—This species is known from about 150 silicified specimens, most of which are fragmentary. The holotype is shown on plate 28, figures 12-15 (USNM 162790); it is about 17.5 mm long and 11 mm high. Seven paratypes are figured.

Type locality.—The known material is from off south point of Pulau Langgun, Langkawi Islands, Malaysia.

Stratigraphic distribution.—At present, the species is known only from the lower shelly facies of the Setul Formation of Malaysia. Yochelson and Jones (1968) dated this part of the Setul Formation as late Canadian (Early Ordovician) in age.

Etymology.—As pointed out by Yochelson and Jones (1968, p. B1), Clive Jones and Richard Jones were instrumental in collecting the material of this species. The species name is derived from their common last name.

Euchasma mytiliforme n. sp.

Plate 29, figures 6-15

Description.—*Euchasma* with highly reduced anterior lobe which does not project forward of the umbonal peaks; anterior face strongly flattened and broad; ribs weak; poorly developed rostrum.

Types.—This species is known from about 50 specimens, most of which are fragmentary. The holotype (USNM 209312) is shown on plate 29, figures 6-10; it is about 45 mm long and 41 mm high; in addition to the holotype, we figure three paratypes.

Type locality.—The known material of *E. mytiliforme* is from the east side of Pulau Langgun, Langkawi Islands, Malaysia.

Stratigraphic distribution.—At present, the species is known only from the lower shelly facies of the Setul Formation of Malaysia (upper Canadian; Lower Ordovician).

Etymology.—The species name is derived from the pelecypod genus *Mytilus* whose shape *Euchasma mytiliforme* mimics.

Euchasma shorinense (Kobayashi), 1933

Plate 28, figures 8-11

Discussion.—This species is known only from the holotype, of which we had a replica (USNM 209317) to examine. The specimen has the general shape of species of *Euchasma*, including a small anterior lobe. The specimen is not well preserved and cannot be compared in detail with other species assigned to the genus. Kobayashi (1933, p. 286) placed the species in the genus *Wanwanella*, an assignment with which we do not agree.

Stratigraphic distribution.—According to Kobayashi (1933, p. 287), the species is known from the "Shorin Bed of Shorinri, near Kenjiho Koshu-gun, Kokai-do in northern Korea" (Lower Ordovician, Tateiwa, 1958).

Euchasma wanwanense (Kobayashi), 1933

Plate 28, figures 4–7

Discussion.—This species is known from the holotype and a paratype; we had a replica (USNM 209316) of the former to examine. The specimen has the general shape of *Euchasma*, including a small anterior lobe. The known material is not well preserved and cannot be compared in detail with other species of the genus. Kobayashi (1933, p. 286) assigned the species to *Wanwanella*, an assignment with which we do not agree.

Stratigraphic distribution.—The species is known only from the Wanwankou Dolomite (Wanwanian, Lower Ordovician) of Manchuria.

Euchasma? sp.

Plate 28, figures 1–3

Discussion.—This form has a shape similar to *Euchasma*, but it is not well enough known for us to exclude the possibility that it is a pelecypod. It is from the Holonda Limestone (Whiterockian, Lower Ordovician) of Norway.

Genus *WANWANELLA* Kobayashi, 1933

Plate 21

1933. *Wanwanella* Kobayashi, Tokyo Imp. Univ. Fac. Sci., Jour., v. 3, pt. 7, p. 284.

Type species.—*Wanwanella striata* Kobayashi, 1933 (p. 285) by original designation.

Diagnosis.—Erect eopteriids with a pegma.

Stratigraphic range.—Wanwanian (Lower Ordovician) of Manchuria.

Discussion.—We had very little material assignable to this genus to examine; most of what we did have were replicas of Kobayashi's (1933) types. Thus, we do not attempt to diagnose each species; rather we discuss and make comments about each. Two species, *W. shorinensis* and *W. wanwanensis*, have been placed by us in the genus *Euchasma*.

Wanwanella striata Kobayashi, 1933

Plate 21, figures 9–16

Discussion.—We had a replica (USNM 209369) of a Kobayashi syntype (1933, pl. 7, fig. 7) and two specimens (MCZ 4425, YU 28149) of this species to examine. The form is radially ribbed with a prominent pegma; all specimens that we saw were missing the posterodorsal part. The species is prominently

rounded anteriorly, giving it an erect appearance not seen in *Eopteria* or *Euchasma*.

Stratigraphic distribution.—Wanwankou Dolomite (Wanwanian, Lower Ordovician), at Wanwankou in the Niuhsintai Basin, southern Manchuria.

Wanwanella? alta (Kobayashi), 1933

Plate 21, figure 21

Discussion.—We had an old poorly executed replica of the holotype (USNM 94045) and a poorly preserved specimen of this form to examine. Both show overall body ribbing, a pegma, and a rounded anterior end. Kobayashi (1933) placed this form in *Eopteria*; because of the presence of the pegma and the rounded anterior end, we do not accept this assignment. We regard the form as being closest to species placed in *Wanwanella*.

Stratigraphic distribution.—Wanwankou Dolomite (Wanwanian, Lower Ordovician), Wanwankou in the Niuhsintai Basin, south Manchuria.

Wanwanella? asiatica (Kobayashi), 1933

Discussion.—We had only a poorly executed replica of the holotype of this species to examine, which we do not figure. The form has overall body ribbing, a pegma, and a rounded anterior end. Kobayashi (1933) placed the species in *Eopteria*; because of the pegma and the rounded anterior end, we do not accept this assignment. We regard the form as being closest to species placed in *Wanwanella*.

Stratigraphic distribution.—Wanwankou Dolomite (Wanwanian, Lower Ordovician), Wanwankou in the Niuhsintai Basin, southern Manchuria.

Wanwanella striata auriculata Kobayashi, 1933

Plate 21, figures 17–20

Discussion.—We had a replica of the holotype of this form to examine (USNM 209370). It has a prominent posterodorsal auriculate rostrum. The known specimens of *W. striata* are missing this part of the shell, and it seems likely that *W. striata auriculata* is a junior synonym of *W. striata*. According to Kobayashi (1933, p. 286), *W. striata auriculata* is known from "One specimen obtained in the same locality with *Wanwanella striata* s. str."

Wanwanella tumida Kobayashi, 1933

Plate 21, figures 7, 8

Discussion.—We had a replica of the holotype of this form to examine (USNM 209368). The specimen is much like *W.? alta* in shape, and the two names may be synonymous, *W. tumida* having page precedence. The two forms are from the same horizon and locality.

Genus WANWANOIDEA Kobayashi, 1933

Plate 21

1933. *Wanwanoidea* Kobayashi, Tokyo, Imp. Univ. Fac. Sci., Jour., v. 3, pt. 7, p. 287.

Type species.—*Wanwanoidea trigonalis* Kobayashi, 1933 (p. 287), by original designation.

Discussion.—The only specimens assignable to this genus that we have seen are replicas of the holotype of one subspecies and the figured syntype of the other species. When the replicas are compared with Kobayashi's figures (1933, pl. 8, fig. 6; pl. 9, fig. 3), it is obvious that neither specimen is complete. They do show full body ribbing and a pegma, and in this regard are like *Wanwanella*. Kobayashi (1933, p. 315) distinguished them primarily on shape. On the basis of the material of *Wanwanoidea* that we have seen, we are not in a position to diagnose the genus. In addition to the material that he figured, Kobayashi (1933, p. 288) noted that he had three unfigured syntypes of the type species.

Stratigraphic distribution.—Wanwanian (Lower Ordovician) of Manchuria.

Wanwanoidea trigonalis Kobayashi, 1933

Plate 21, figures 4–6

Discussion.—We had only a replica of a syntype of this species to examine (USNM 209367); as noted above, the original is an incomplete specimen. The species is from the Wanwankou Dolomite (Wanwanian, Lower Ordovician) of southern Manchuria.

Wanwanoidea trigonalis delicata Kobayashi, 1933

Plate 21, figure 3

Discussion.—We had only a replica of the holotype of the subspecies to examine (USNM 209366); as noted above, the original is an incomplete specimen. This form is from the Wanwankou Dolomite (Wanwanian, Lower Ordovician) of southern Manchuria.

Superfamily CONOCARDIACEA Miller, 1889

(nom. transl. Conocardiidae Miller, Newell, 1965)

Diagnosis.—Anteriorly elongate conocardioids with well-developed rostrum and posterior dorsal clefts when the hinge and rostrum are not colinear; prominent anterior gape, posterior gape reduced to aperture of rostrum and ventral orifice (when present), ventral gape absent. Inner shell layer continuous across the dorsal margin.

Stratigraphic distribution.—Middle Ordovician (Marmorian)—Upper Permian (Makarewan; Waterhouse, 1967).

Discussion.—We cannot review all species of conocardiaceans herein; at least 275 species have been

placed in this superfamily, and we have not been able to obtain specimens of all of these. We discuss all Ordovician species and those post-Ordovician forms for which we could obtain specimens that illustrate the morphological diversity and stratigraphic and geographic occurrence of the group.

Family CONOCARDIIDAE Miller, 1889

Diagnosis.—Markedly anteriorly elongate conocardiaceans with shell clearly regioned into a posterior rostrum, median body, and anterior snout; internally, snout has elongate apertural (longitudinal) shelves; hood absent.

Stratigraphic distribution.—Lower Devonian (Schoharie Formation)—Lower Permian (McCloud Limestone).

Genus CONOCARDIUM Bronn, 1835

Plates 37–40

Type species.—*Cardium elongatum* Sowerby, 1815 (p. 188) by monotypy. *Arcites rostratus* Martin, 1809, is often cited as the type species of *Conocardium* (Hind 1900) because the specimens figured by Martin (1809) and Sowerby (1815) are regarded as conspecific; in fact, Hind (1900) felt that the figures of both authors might be based on the same specimen. Whether or not this is the case was made moot by the International Commission on Zoological Nomenclature, which has declared Martin's *Petrifactor derbiensis* invalid for nomenclatural purposes (Hemming, 1954, ICZN Opinion 231). Bronn (1835), when he proposed *Conocardium*, mentioned only *Cardium elongatum* Sowerby, which becomes the type species by monotypy. Sowerby (1815, p. 188), following the name *Cardium elongatum*, indicated that the species was illustrated on his plate 82, figure 3; his description clearly indicates that *C. elongatum* is illustrated on his plate 82, figure 2.

Diagnosis.—Conocardiids in which the body of the shell is externally fully radially ribbed.

Stratigraphic distribution.—Lower Devonian (Schoharie Formation)—Pennsylvanian. The youngest specimen (USNM 100704) we have seen of *Conocardium* is labeled "Pennsylvanian, St. Joseph, Missouri."

Conocardium elongatum (Sowerby), 1815

Plate 37, figures 16, 17; plate 38, figures 1–24

Types and materials.—The holotype (BM PL 794) of *C. elongatum* is figured herein on plate 38, figures 9–14; the photographs of this specimen are courtesy of the Department of Palaeontology, British Museum (Natural History). The specimen was also figured by Hind (1900, pl. 51, figures 6, 6a, b). The

holotype is a radially ornamented subcylindrical shell broken at both ends. In addition to the holotype, we had four specimens of this species from England (pl. 38, figs 8, 15–24). One of these, a topotype (BM L 13496), shows the presence of longitudinal shelves in the species. Another (SM E.549, pl. 38, fig. 8) shows that there is little radial ribbing on the snout. The remaining two (BM PL 4431, 4432) show the muscle-insertion areas. Because the hinge and dorsal margin of the rostrum are approximately colinear, the valves were able to rotate during growth, and there are no well-defined rostral clefts; ventral aperture lacking.

In addition to the English material, we have two specimens from North America (pl. 37, figs. 16, 17; pl. 38, figs. 1–7) which are similar to the English material in shape and general body form but differ in having a radially ribbed snout. Just what weight should be given to this characteristic is as yet uncertain, because it has not been possible to gather together the material of the known species of *Conocardium*. Probably the American specimens represent a different species, and they are herein treated as *Conocardium* aff. *C. elongatum*.

Stratigraphic distribution.—The English specimens of this species are all from Carboniferous (Mississippian) limestone. The American specimens are from the Carterville Formation (Upper Mississippian) of Missouri (pl. 38, figs. 4–7), and the Pennsylvanian of Missouri (pl. 37, figs. 16, 17; pl. 38, figs. 1–3).

***Conocardium aliforme* (Sowerby), 1815**

Plate 39, figures 8–10; plate 51, figure 11

Material.—We figure two specimens of this species, one of which is a Hind (1900, pl. 54, fig. 8; SM E.561) hypotype. The body of the shell of this species is more erect and less rounded than in *C. elongatum*.

Stratigraphic distribution.—Carboniferous (Mississippian) limestone of England.

***Conocardium attenuatum* (Conrad), 1842**

Plate 39, figures 11–13; plate 40, figures 1, 2

Material.—We figure three specimens of this form, none of which are complete and two of which are Hall (1885) hypotypes. They clearly show the presence of longitudinal shelves (pl. 39, fig. 11; pl. 40, fig. 1) and radial ribs on the body of the shell (pl. 39, figs. 12, 13; pl. 40, fig. 2).

Stratigraphic distribution.—The species is known only from the Schoharie Formation (Lower Devonian) of New York State.

***Conocardium normale* Hall, 1883**

Plate 39, figures 4–7

Type.—We figure the lectotype (AM 5349/1) of the species (herein chosen) which shows the ribbing on the body of the shell and unusually thick longitudinal shelves. The body of the shell is more oblique than in *C. aliforme* but not rounded as in *C. elongatum*.

Stratigraphic distribution.—The species is known from the Hamilton Group (Middle Devonian) of Maryland.

***Conocardium pseudobellum* n. sp.**

Plate 38, figures 25, 26; plate 39, figures 1–3

Description.—Posterior carina at junction of rostral area with body of shell, small ventral aperture at posterior commissural junction of the carinae; rostrum long; body of shell oblique as in *C. attenuatum*, but apertural shelves not as robust as in that species.

Types.—The holotype (USNM 209299) is shown on plate 38, figure 25 and plate 39, figures 1, 2. It is about 28 mm long and 16 mm high. The rostrum of the specimen was reconstructed in plaster by Yang (1939). In addition to the holotype, we figure two paratypes of the species (USNM 209300; UM 47287), which show the longitudinal shelves and the elongate rostrum. Yang (1939) made serial and oblique sections of this species, showing a pair of longitudinal shelves which terminate posteriorly as enclosed tubes in the umbonal region of the shell.

Type locality.—The types are from Four Mile dam, Thunder Bay River, 2 miles upstream from Alpena, Mich.

Stratigraphic distribution.—The species is presently known from the upper Alpena Limestone and Four Mile Dam Formation (Middle Devonian) of Michigan.

Discussion.—*C. pseudobellum* resembles *Hippocardia bella* (Cooper and Cloud) (pl. 44, figs. 5–14) in general external form and was identified with that species by Yang (1939). However, *H. bella* differs in having a small but obvious hood (pl. 44, figs. 5, 6, 11) and in lacking longitudinal shelves.

Etymology.—*Pseudo*, Greek, meaning false, lie; *Bella*, a species of *Hippocardia* externally similar to *Conocardium pseudobellum*.

Genus ARCEODOMUS new genus

Plates 42–44

Type species.—*Conocardium glabratum* Easton, 1962 (p. 95) is herein designated the type species of the new genus *Arceodomus*.

Description.—Conocardiidae with one or more pairs of longitudinal shelves within the anterior gape; shell strongly regioned into posterior rostrum, medial body, and anterior snout. Junction of body and snout marked by pronounced change in shell ornament; body of shell ornamented only with comarginal markings, snout strongly radially ribbed.

Stratigraphic distribution.—Upper Mississippian (Heath Formation, Diamond Peak Formation)—Lower Permian (McCloud Limestone).

Geographic distribution.—In the United States, the genus is presently known from California, Montana, Nevada, and Texas. Outside the United States it occurs in the U.S.S.R.

Etymology.—*Arcea*, Latin, meaning to shut up or enclose; *Domus*, Latin meaning home. Gender feminine.

Discussion.—Two named species are assigned to this genus, *A. glabrata* (Easton), 1962, and *A. langenheimi* (Wilson), 1970. Other forms that belong to the genus are herein listed as showing affinities to one of the named species, or as *Arceodorus* sp.

Arceodorus glabrata (Easton), 1962

Plate 42, figures 8–11; plate 43, figures 1–3, 7–12;
plate 44, figures 1–4

Types and materials.—The holotype (USNM 118858) is shown on plate 43, figures 1–3; it clearly shows the comarginal ornament on the body of the shell and the impressions of the longitudinal shelves. Dorsally, the specimen has been weathered, and the internal ribs show where the comarginal ornament has been removed. Anteriorly, the specimen is incomplete, and most of the snout is not present.

In addition to the holotype, we assign two other Mississippian specimens to this species (pl. 42, figs. 8–10; pl. 43, figs. 7–12); these specimens clearly show the radial ribs of the snout. The two specimens were brought to our attention by Mackenzie Gordon, Jr. A form similar to *A. glabrata* occurs in the Pennsylvanian of Texas and is figured on plate 42, figure 11, and plate 44, figures 1–4.

Stratigraphic distribution.—The holotype and the two specimens assigned unequivocally to this species are from the Upper Mississippian of Montana (Heath Formation) and Nevada (Diamond Peak Formation). The specimens from Texas, which are regarded as showing affinities to *A. glabrata*, are from rocks of Late Pennsylvanian age ("Dickerson Shale").

Arceodorus langenheimi (Wilson), 1970

Plate 43, figures 13–15

Types.—This species is known only from the type suite which was figured by Wilson (1970). Herein we figure the holotype (UCB 10589), which is a large, exceptionally well-preserved silicified specimen. It shows that the anterior gape is largely occluded by the longitudinal shelves.

Stratigraphic distribution.—At present, this species is known only from the McCloud Limestone (Lower Permian), Bollibokka Mountain, Shasta County, Calif.

Arceodorus sp.

Plate 43, figures 4–6

Discussion.—This form clearly belongs to the genus *Arceodorus*; it is presently known from only one specimen at the British Museum (BM L 15570) which is labeled as coming from the "Carboniferous" of the U.S.S.R. R. J. Cleavelly, of the British Museum (written commun., 1975) noted that Norman Newell had annotated the specimen label: "Probably from *Schwagerina lutugini* Beds, one of the "Shikhan reefs, Bashkiria (Sakmorian)," after sectioning the limestone to which it was attached."

Family BRANSONIIDAE new family

Description.—Conocardiaceans lacking anterior longitudinal shelves in snout of shell; snout and body of shell ribbed, not always clearly separated from one another; hood absent.

Stratigraphic distribution.—Middle Ordovician (Marmorian)—Upper Permian (Capitanian).

Genus BRANSONIA new genus

Plates 32, 50–54

Type species.—*Bransonia wilsoni* n. sp. is herein designated the type species of the new genus *Bransonia*.

Description.—Bransoniids with a reduced anterior gape which is largely limited to the dorsal part of the anterior face, although it may extend ventrally as a narrow slit.

Stratigraphic distribution.—Middle Ordovician (Marmorian)—Middle Permian (Tiverton Formation).

Etymology.—The genus is named for C. C. Branson, University of Oklahoma, who has long worked with conocardiaceans. Gender feminine.

Discussion.—This long-ranging genus is proposed for conocardiaceans of generalized body form; probably when the group becomes better known it will be divided into several generic-level taxa.

Bransonia wilsoni n. sp.

Plate 32, figure 4; plate 51, figures 1-10, 17; plate 52, figures 1-5, 9

Description.—Large *Bransonia* with prominent snout and rostrum, rostrum shorter than snout, body of shell carinate posteriorly, rostrum and hinge not colinear and rostral clefts prominent, ventral aperture present.

Types.—The holotype (UNE F14789) is shown on plate 51, figures 1-6; it is about 28 mm long and 22 mm high. In addition to the holotype, we figure five paratypes.

Type locality.—The types are from the ridge southeast of Homevale Homestead, Nebo District, Queensland, Australia.

Stratigraphic distribution.—Middle part of "Homevale Beds," lower Tiverton Formation (Middle Permian).

Etymology.—The species is named for E. C. Wilson, Los Angeles County Museum, in recognition of the work he has done with Permian conocardiaceans.

Bransonia alabamensis n. sp.

Plate 50, figures 28-37

Description.—Small *Bransonia* with body of shell carinate posteriorly, rostrum prominent and about equal in length to snout.

Types.—The holotype (USNM 209271) is shown on plate 50, figures 32-34; it is about 4.5 mm long and 3.6 mm high. We had 12 other specimens besides the holotype, of which three paratypes are figured.

Type locality.—The types are from the Crossroads, 1.75 miles northeast of New Hope Church, Alabama.

Stratigraphic distribution.—The species is known only from the Little Oak Limestone (Porterfieldian, Middle Ordovician) of Alabama.

Etymology.—The species name is derived from the state of Alabama.

Bransonia beecheri (Raymond), 1905

Plate 50, figures 20-24

Diagnosis.—Small elongate *Bransonia* with body of shell rounded posteriorly rather than carinate, shape eopteriiform.

Types and materials.—*B. beecheri* is based upon a syntypic series of which we choose the specimen figured herein on plate 50, figure 20, as the lectotype (YU 15322C). In addition to the type suite, we had three other specimens of this species, which are figured on plate 50, figures 22-24.

Stratigraphic distribution.—The type suite is from rocks of Chazy (Marmorian, Middle Ordovician)

Age, on Sloop Island, near Valcour Island, Lake Champlain, N.Y. We have been to this locality to try and collect topotype material but found no additional specimens. The species also occurs in Chazy (Marmorian) Age rocks, Isle LaMotte, Vt. (pl. 50, fig. 24), the Mosheim Member of Lenoir Limestone (Marmorian) of Tennessee (pl. 50, fig. 23), and the Row Park Limestone (Marmorian-Ashbyian) of Pennsylvania (pl. 50, fig. 22).

Discussion.—This species has a subcentral beak and a general eopteriiform shape. The presence of a well-developed rostrum, a high anterior gape, and the lack of a ventral gape indicate that the species is not *Eopteria*. There is a good morphological progression from an eopteriid like *Eopteria conocardiformis* to a bransoniid like *Bransonia beecheri*. Stratigraphically, the two species are not in sequence, as *B. beecheri* is older. We interpret *Eopteria conocardiformis* to be a late-surviving primitive type, which provides insight into the origin of conocardiaceans.

Bransonia cressmani n. sp.

Plate 52, figures 6, 7, 10-14; plate 53, figures 6-20; plate 54

Description.—Small subquadrate *Bransonia* with body of shell rounded, not carinate posteriorly; rostrum small but rostral clefts well developed, rostral area oblique to dorsal margin in lateral view; snout considerably longer than rostrum; musculature consisting of pallial line and primary pedal retractor muscle.

Types.—The holotype is shown on plate 52, figures 10-14 (USNM 209266). It is about 3.6 mm long and 3.2 mm high. We had more than 150 specimens of this species, of which most are silicified replicas; some are phosphatic internal molds which show the musculature. In addition to the holotype, we figure seven paratypes.

Type locality.—The holotype is from USGS loc. 5015-CO, a small quarry on east side of Mitchellsburg Road, 0.4 miles south of Perryville, Ky. Some of the paratypes are from the same locality as the holotype; others are from two additional localities: USGS loc. 6916-CO, large quarry on west side of U.S. Route 68, 1 mile north of junction with U.S. Route 150 in Perryville, Kentucky; and USGS loc. D-1200-CO, Frankfort East Section on eastbound lanes of Interstate Highway 64, east side of Kentucky River, Franklin County, Ky.

Stratigraphic distribution.—The specimens from USGS loc. 5015-CO and 6916-CO are from the Perryville Limestone Member of the Lexington Limestone (Middle Ordovician). The specimens from locality D-1200-CO are from the Tanglewood Lime-

stone Member of the Lexington Limestone (Middle and Upper Ordovician).

Etymology.—The species is named for Earle Cressman, U.S. Geological Survey, who has been a long-continuing help in collecting the fauna of the Lexington Limestone.

***Bransonia? immatura* (Billings), 1863**

Discussion.—The lectotype (GSC 1180a, Wilson, 1956) of this species is an incomplete silica replica with an unusually elongate rostrum. It is not figured herein, and because of the state of its preservation, we are unsure of its generic assignment.

Stratigraphic distribution.—The lectotype is from Leray-Rockland Beds of Wildernessian Age (Middle Ordovician), Paquette Rapids, Ottawa, Ontario, Canada.

***Bransonia isbergi* (Branson), 1942b**

Discussion.—This species is known only from one specimen which was not seen by us. As figured by Isberg (1934, pl. 29, fig. 7), it is a small form with the rostrum about equal in length to the snout and body of the shell. It is from the Upper Ordovician (Upper *Leptaena* Limestone) of Sweden.

***Bransonia lindstromi* (Isberg), 1934**

Discussion.—We have not seen any specimens of this species. The specimen figured by Isberg (1934, pl. 29, fig. 6) is articulated but incomplete at each end; it has a highly prominent ridge on the body of the shell. The species is known from the Upper Ordovician (Upper *Leptaena* Limestone) of Sweden.

***Bransonia paquettensis* (Wilson), 1956**

Plate 50, figures 25–27, 38

Discussion.—The holotype (GSC 11585; pl. 50, fig. 38) of this species is the largest known Ordovician conocardiacan. The body of the shell has a prominent posterior carina. The holotype is from rocks of Wildernessian Age (Leray-Rockland Beds) (Middle Ordovician), Paquette Rapids, Ottawa River, Ottawa, Ontario, Canada.

A much smaller specimen, more or less similar in shape to the holotype of *B. paquettensis*, occurs in the Holston Formation (Middle Ordovician), Porterfield quarry, 5 miles east of Saltville, Va. (pl. 50, figs. 25–27; USNM 144969) and is herein classified as *Bransonia* aff. *B. paquettensis*.

Genus MULCEODENS new genus

Plates 34, 35

Type species.—*Mulceodens jaanussoni* n. sp. is herein designated the type species of the new genus *Mulceodens*.

Description.—Bransoniids with short rostrum, dorsal part of snout rounded in frontal view and separated by a constriction from ventral part of snout; anterior marginal denticles strongly developed and enlarged so that they extend to the midline and touch or almost touch those on the opposite side of the shell.

Stratigraphic distribution.—Silurian (Wenlockian)—Middle Devonian (Hamiltonian).

Geographic distribution.—The genus is presently known from the Silurian of Sweden and the Devonian of Michigan and New York.

Etymology.—*Mulceo*, Latin, meaning touch lightly; *Dens*, Latin, meaning tooth. Gender masculine.

***Mulceodens jaanussoni* n. sp.**

Plate 34, figures 1–16; plate 35, figures 1–3, 11, 12

Description.—Small *Mulceodens* with prominent rostral clefts, marginal denticles of two valves alternate with one another, and with strong constriction below dorsal part of snout.

Types.—The holotype (SMNH Mo. 151245) is shown on plate 35, figures 1–3, 11, 12; it is about 6.7 mm long and 4.7 mm high. In addition to the holotype, we figure 13 paratypes.

Type locality.—All known specimens are from the Island of Gotland, Sweden.

Stratigraphic distribution.—At present, the species is known only from the Silurian (Wenlockian-Ludlovian) rocks of Gotland.

Etymology.—The species is named for Valdar Jaanusson, Swedish National Museum, for his kindness in sending us a great many conocardiacans from Sweden.

***Mulceodens bifarius* (Winchell), 1866**

Plate 35, figures 8–10

Discussion.—We figure one specimen of this species (USNM 209306) from the upper Alpena Limestone (Middle Devonian) of Michigan, which shows the enlarged anterior denticles which almost touch. The holotype was figured by Branson (1942a).

***Mulceodens denticulatus* (Hall), 1883**

Discussion.—According to Branson (1942a), the original material of this species cannot be located. Hall's (1883, pl. 68, figs. 24, 25) figures show enlarged marginal denticles which alternate with one another, each set extending well beyond the midline of the shell. The species is from the Middle Devonian (Hamiltonian) of New York.

Mulceodens eboraceus (Hall), 1860

Plate 35, figures 4-7

Discussion.—The species is known from two syntypes, of which the lectotype (AM 5347/1, herein chosen) is figured on plate 35, figures 4-7. Neither of the original specimens is complete; however, the lectotype shows the enlarged touching marginal denticles (pl. 35, fig. 7). The types are from the Middle Devonian (Hamiltonian) rocks of New York State.

Genus PSEUDOCONOCARDIUM Zavodowsky, 1960

Plates 32, 40-42

Type species.—*Pseudoconocardium licharewi* Zavodowsky, 1960 (p. 31), by monotypy and original designation.

Diagnosis.—Bransoniids with snout and body of shell not obviously demarked from one another; has large anterior gape which extends the full height of the anterior margin, lacks longitudinal shelves, and has the marginal denticles limited to the edges of the gape.

Stratigraphic distribution.—Upper Pennsylvanian—Upper Permian.

***Pseudoconocardium licharewi* Zavodowsky, 1960**

Discussion.—We have seen no specimens of this species. Zavodowsky's (1960, pl. 6, figs. 1, 2) figures show that it is elongate, strongly ribbed, and has a posterior carina.

Stratigraphic distribution.—Limestones of the Khivachsk Beds (Upper Permian) of the Gizhigi and Omolona River areas of the U.S.S.R.

***Pseudoconocardium lanterna* (Branson), 1965**

Plate 32, figures 1, 2; plate 40, figures 3-14; plate 41; plate 42, figures 1-7, 12-14

Discussion.—This is the only species of the genus presently known from North America. It is more quadrate than the type species. In cross section, the inner shell layer of *P. lanterna* is continuous across the dorsal margin (pl. 32, figs. 1, 2); the outer shell layer is not continuous. Zavodowsky (1960, p. 32, fig. 2) showed a drawing of a cross section of *P. licharewi*; in this cross section, neither shell layer is continuous across the dorsal margin and there is thus a dorsal commissure. On the basis of what we have seen of rostroconchs we consider this to be unlikely. In none of the forms examined by us was the shell bivalved in the sense of a pelecypod. All rostroconchs have at least one shell layer continuous across the dorsal margin and, thus, there is no dorsal commissure.

Stratigraphic distribution.—*P. lanterna* occurs abundantly in rocks of Late Pennsylvanian age

(Cisco Group, Gaptank Formation (in part), Graford Formation and its Brownwood Shale Member, Graham Formation, "Hog Creek Shale Member" of Caddo Creek Formation, and Palo Pinto Limestone of Texas; and Union Valley Formation of Oklahoma).

Family HIPPOCARDIIDAE new family

Description.—Conocardiaceans with one or more hoods around the rostral area of the shell, each hood consisting of right and left halves; longitudinal shelves present or absent in anterior gape.

Stratigraphic distribution.—Middle Ordovician (Llandeilian)—Mississippian (Tournaisian).

Discussion.—This is a large family which at present we have divided into two genera: *Hippocardia* and *Bigalea* are distinguished by the number of posterior hoods present in each genus. In the future, additional generic subdivision of the family may be based upon such criteria as the presence or absence of longitudinal shelves in the anterior gape, type of ornamentation, etc., but at present we do not have sufficient material of hippocardiids to attempt such subdivision.

Genus HIPPOCARDIA Brown, 1843

Plates 32, 44-50

Type species.—*Cardium hibernicum* Sowerby, 1815 (p. 187) by original designation and monotypy. Sowerby (1815, p. 187), following the name of *Cardium hibernicum*, indicated that the species was illustrated on his plate 82, figures 1, 2; his description clearly indicates that *C. hibernicum* is illustrated on his plate 82, figures 1, 3. *Pleurorhynchus* Phillips (1836, p. 210), is an invalid senior objective synonym of *Hippocardia*, as both are based upon the same type species. The name *Pleurorhynchus* was previously used by Rudolphi (1801) as an invalid emendation of *Pleurorinchus* Nau (1787).

Diagnosis.—Hippocardiids with one hood around the rostral area of the shell.

Stratigraphic distribution.—Middle Ordovician (Llandeilian)—Mississippian (Tournaisian).

Discussion.—This long-ranging genus contains all conocardiaceans with a single hood; it seems likely that when the group becomes better known it will be divided into several generic-level taxa.

***Hippocardia hibernica* (Sowerby), 1815**

Plate 46, figures 1-12

Diagnosis.—Large *Hippocardia* with large arcuate hood, markedly constricted snout, and longitudinal shelves in the anterior gape.

Types and materials.—The lectotype of this species was chosen by Hind (1900, explanation for his figure 11, plate 53). We figure five specimens of the species.

Stratigraphic distribution.—The species is known from Lower Carboniferous (Mississippian) rocks of England, Ireland, and Belgium.

***Hippocardia antiqua* (Owen), 1852**

Plate 50, figure 14

Discussion.—The holotype (USNM 17897) of the species is figured herein; it has a carina at the junction of the body of the shell with the rostral area, but nothing of the hood is preserved. Branson (1942b, pl. 59, fig. 8) figured a specimen of this species showing the hood. The species is from Ordovician rocks, Lower Fort Garry, Red River of the North, Manitoba, Canada.

***Hippocardia bella* (Cooper and Cloud), 1938**

Plate 44, figures 5–14

Discussion.—This species is from the Devonian rocks of Illinois. It has a small but obvious hood. The snout is larger, in proportion to the whole shell, than that of *H. hibernica*. The anterior gape is largely restricted to the dorsal part of the snout. We figure the holotype of the species (USNM 95192a) and three paratypes.

***Hippocardia bohémica* (Barrande), 1881**

Plate 32, figure 3; plate 47, figures 1–7

Discussion.—*H. bohémica* is known from the Devonian of Konieprus, Bohemia, Czechoslovakia. It has a prominent hood and a rostrum with an unusually tall base. We figure two specimens.

***Hippocardia calcis* (Baily), 1860**

Discussion.—We have seen no specimens of this species, but Baily's figures (1860, p. 11) clearly show the presence of a hood. Baily gave the stratigraphic occurrence as "Llandeilo?" (Middle Ordovician); it is from the townland of Reafadda, County Tipperary, Northern Ireland.

***Hippocardia cooperi* n. sp.**

Plate 45, figures 10–14

Description.—Small *Hippocardia* with hood forming prominent flanges on either side of the shell, sculpture of snout reticulate, ventral part of anterior gape slitlike.

Types.—The holotype (USNM 162786) is figured on plate 45, figures 10–14; it is about 5.5 mm long and 6 mm high. In addition to the holotype, we had 11 fragmentary specimens, none of which are figured. All specimens are silicified replicas, and only

the outer shell layer is preserved. Pojeta (1971) figured this species as *Conocardium* sp.

Type locality.—All known material of *H. cooperi* is from USNM loc. 600 near Strasburg, Va.

Stratigraphic distribution.—Lower Chambersburg Limestone (Middle Ordovician).

Etymology.—The species is named for G. A. Cooper, U.S. National Museum, who collected the specimens and gave them to us to examine.

***Hippocardia cunea* (Conrad), 1840**

Plate 32, figures 5, 6; plate 33, figures 1, 2; plate 48, figures 1–15; plate 49, figures 1–15; plate 50, figures 1, 2

Discussion.—*Hippocardia cunea* is a widely distributed species in the Devonian rocks of the northeastern United States. It is a large species with a hood that can exceed the length of the rest of the shell. The rostrum is a scooplike structure different from other conocardiaceans and is described in the section on growth (p. 10–11). According to Branson (1942a), Conrad's types are mixed with Hall's (1885) hypotypes and can no longer be identified. Three of Hall's hypotypes are herein figured on plate 48, figures 1, 5, 8–11 (NYSM 2313, AM 2853a/3, FM 12500).

Stratigraphic distribution.—Lower-Middle Devonian of the northeastern United States.

***Hippocardia?* diptera (Salter), 1851**

Discussion.—We have not seen the specimens of this species figured by Salter (1851) or Hind (1910). One of the specimens figured by Hind (1910, pl. 5, fig. 30) appears to have a remnant of the hood, and on this basis, we tentatively place the species in *Hippocardia*. The species is from the Llandeilian (Middle Ordovician) of Scotland.

***Hippocardia fusiformis* (McCoy), 1844**

Plate 45, figures 5–9

Discussion.—This is the largest known conocardiacean, reaching a maximum length of at least 100 mm and having longitudinal shelves. We figure two specimens of the species from the Mississippian (Tournaisian) of Belgium. Hind (1900) figured McCoy's holotype and noted that the species occurs in the Mississippian of Ireland.

***Hippocardia limatula* (Bradley), 1930**

Plate 50, figures 15–19

Discussion.—This small species has a prominent hood and occurs in the Kimmswick Limestone (Middle Ordovician) of Illinois and Missouri.

***Hippocardia monroica* (Grabau), 1910**

Plate 44, figures 15, 16; plate 45, figures 1-4

Discussion.—The specimens of this species figured by us do not show the hood; however, this structure is well figured by Branson (1942a) and LaRocque (1950). The species occurs in the Middle Devonian (Amherstburg Formation, Lucas Formation) of Michigan and Ontario.

***Hippocardia praepristis* (Reed), 1952**

Discussion.—We have seen no specimens of this species. Reed's (1952) figures show the presence of a hood. *H. praepristis* is from the Ordovician of County Tyrone, Northern Ireland.

***Hippocardia pygmaea* (Hisinger), 1837**

Plate 50, figure 3

Discussion.—We figure Branson's (1942b) hypotype (USNM 98871) of this species which clearly shows the hood. The museum label lists the specimen as coming from the "Borkholm Beds, Silurian, Borkholm, Estonia." Valdar Jaanusson (written commun., 1975) noted that the specimen is probably from Upper Ordovician rocks, Porkuni Stage, Porkuni ("Borkholm"), Estonia.

***Hippocardia richmondensis* (Foerste), 1910**

Plate 50, figures 6-10

Discussion.—We figure the holotype (USNM 87041) and a second specimen of this species (MU 209T); both clearly show the presence of a small hood. The species is known from Upper Ordovician (Richmondian) rocks of Indiana and Ohio.

***Hippocardia?* *zeileri* (Beushausen), 1895**

Plate 47, figures 8-12

Discussion.—This species has the general form and appearance of species placed in *Hippocardia*, although none of the material seen by us shows a hood. The hood is readily detached from the umbos and does not leave a recognizable scar. We tentatively place this species in *Hippocardia*. *H.?* *zeileri* is from the Devonian of Germany.

***Hippocardia* spp.**

Plate 50, figures 4, 5, 11-13

Discussion.—The forms discussed under this heading add data about the stratigraphic and geographic distribution of *Hippocardia* but cannot now be placed in a species. The specimen shown on plate 50, figures 4, 5 is from the Silurian (Wenlockian) rocks of the Island of Gotland, Sweden. It shows a well-developed hood and in general body form is similar to *H. cooperi* n. sp.

The specimen shown on plate 50, figure 11 is incomplete, but shows the occurrence of the genus in the Middle Ordovician (Platteville Limestone) of Illinois. The form shown on plate 50, figure 12, shows the occurrence of *Hippocardia* in the Ordovician of England. The specimen shown on plate 50, figure 13, is crushed and incomplete, but it shows the occurrence of the genus in the Middle Ordovician (Porterfieldian) of Virginia.

Genus BIGALEA new genus

Plates 35-37

Type species.—*Bigalea yangi* n. sp. is herein designated the type species of the new genus *Bigalea*.

Description.—Hippocardiids with two small posterior rostral hoods, each with a separate ventral aperture; ventral part of anterior gape slitlike.

Stratigraphic distribution.—Silurian (Wenlockian)—Middle Devonian ("Petoskey Limestone" in Traverse Group).

Geographic distribution.—The genus is presently known from the Silurian of Sweden and the Devonian of the Falls of the Ohio River, Michigan, and Germany.

Etymology.—*Bi*, Latin, meaning two; *Galea*, Latin, meaning helmet. Gender feminine.

***Bigalea yangi* n. sp.**

Plate 36, figures 13-16; plate 37, figures 1-4

Description.—*Bigalea* with posterior hoods close together and near posterior end of umbo; rostral area flat not produced ventrally, rostrum short; marginal denticles of two valves touching medially in ventral part of anterior gape; length about equal to height.

Types.—The holotype (USNM 209301) is shown on plate 37, figures 1-3; it is about 18.6 mm long and 13 mm high. In addition, we figure two paratypes (FM 18331, 18332).

Type locality.—The holotype is from a quarry at Mud Lake, about 1.5 miles northeast of Bay View, Emmet County, Michigan. The paratypes are from Kegomic, Little Traverse Bay, Mich.

Stratigraphic distribution.—The species is presently known only from the "Petoskey Limestone" in the Traverse Group (Middle Devonian) of Michigan.

Etymology.—The species is named for S. Y. Yang who studied the Devonian mollusks of Michigan at Yale University in the late 1930's.

***Bigalea clathra* (d'Orbigny), 1850**

Plate 37, figures 5-15

Diagnosis.—*Bigalea* with hoods at anterior and posterior ends of umbo, hoods of about equal length;

marginal denticles of two valves not touching in ventral part of anterior gape.

Materials.—We have not seen the type material of this species. We figure four specimens from the collections of the Museum of Comparative Zoology, Harvard University, and the University of Michigan.

Stratigraphic distribution.—*B. clathra* is presently known only from the Devonian of Germany.

Bigalea ohioensis n. sp.

Plate 36, figures 5–12

Description.—*Bigalea* with hoods close together, but both not at posterior end of umbo; the anterior of the two hoods extends down the umbo with a significant gap between it and the posterior hood; anterior hood longer than posterior; rostral area produced ventrally; significantly longer than high.

Types.—The holotype (USNM 209302) is shown on plate 36, figures 5–7; it is about 8.7 mm long and 5.5 mm high. In addition, we figure three paratypes (USNM 209303–209305).

Type locality.—The locality of the known material of this species is uncertain; it probably came from the Falls of the Ohio River.

Stratigraphic distribution.—The stratigraphic occurrence of the species is uncertain; it is probably from Devonian rocks at the Falls of the Ohio River.

Etymology.—The species name is derived from the Ohio River.

Bigalea visbyensis n. sp.

Plate 35, figures 13–17; plate 36, figures 1–4

Description.—*Bigalea* with significant space between two hoods as in *B. ohioensis*; posterior hood longer than anterior and extended ventrally beyond the shell proper; rostrum long and colinear with hinge; marginal denticles of two valves touching at midline in ventral part of anterior gape.

Types.—The holotype (SMNH Mo. 18552) is shown on plate 35, figures 16, 17, plate 36, figures 1, 2; it is about 9.3 mm long and 6.7 mm high. In addition, we figure two paratypes (SMNH Mo. 18553, 18554).

Type locality.—Visby on the Island of Gotland, Sweden.

Stratigraphic distribution.—The species is presently known only from the Silurian (Wenlockian) rocks of the Island of Gotland.

Etymology.—The species name is derived from Visby, Sweden.

ROSTROCONCHIA INCERTAE SEDIS

Discussion.—Three monotypic genera of rostroconchs, or probable rostroconchs, remain, which at

present cannot be placed in a family or order. Some of the uncertainty about these forms is due to the fact that we have not seen specimens or adequate replicas of the species concerned. We briefly discuss these forms under this heading.

Euchasmella multistriata Kobayashi, 1933

Discussion.—This species is known from two specimens, of which one was figured by Kobayashi (1933). We had a plaster replica of the holotype to examine; this plastotype was much deteriorated with age and is not figured herein. As figured by Kobayashi (1933, pl. 8, fig. 5), the species is a large finely ribbed form with a pegma. It may be allied to the EopterIIDae.

According to Kobayashi (1933, p. 295), *E. multistriata* is from the "Wanwankou dolomite [Lower Ordovician]; Wan-wan-kou in the Niuhsintai Basin, South Manchuria."

Myona flabelliformis Kobayashi, 1935

Discussion.—This species is known only from the material described by Kobayashi (1935). It resembles some rostroconchs in shell shape and what appears to be the presence of side muscles. *M. flabelliformis* is presently known only from internal molds preserved on bedding planes. No articulated specimens are known. Extending distally from the supposed side muscle scars and from the posterior dorsal margin are a series of ridges which Kobayashi (1935, p. 325) compared with the vascular sinuses of brachiopods.

We have seen no specimens, or replicas of specimens, of this species; we suggest that it is a rostroconch on the basis of its shape and the presence of apparent side muscle scars. At present, *M. flabelliformis* is known only from the "Drepanura zone, Seison Slate, upper Middle Cambrian, of Saisho-ri, South Korea" (Kobayashi, 1935, p. 58, 326).

Pseudoeuchasma typica Kobayashi, 1933

Plate 21, figures 1, 2

Discussion.—This species is known from two specimens, of which one was figured by Kobayashi (1933). We had a plaster replica of the holotype (USNM 94011) to examine. It shows a markedly flattened surface of the shell at one end and a carinate umbo; the species bears resemblances to the Hippocardiidae. According to Kobayashi (1933, p. 302), *P. typica* is from the "Wanwankou dolomite [Lower Ordovician]; Wan-wan-kou in the Niuhsintai Basin, Manchuria."

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PLATES 1-54

Contact photographs of the plates in this report are available, at
cost, from U.S. Geological Survey Library, Federal Center,
Denver, Colorado 80225

PLATE 1

FIGURES

1-7. *Yochelcionella cyrano* Runnegar and Pojeta, 1974 (p. 27).

Holotype, USNM 204698; USGS 5959-CO. Collected by Brian Daily from the "first discovery limestone", *Redlichia chinensis* Zone, Ordian Stage, lower Middle Cambrian, Mootwingee Range area, New South Wales, Australia. 1-6 ($\times 22$); 7 ($\times 60$). 1, Oblique left anterior view; 2, Posterior view; 3, Anterior view; 4, Dorsal view; 5, Right-lateral view; 6, Left-lateral view; 7, Enlargement of apex (protoconch?) of shell showing ornament.

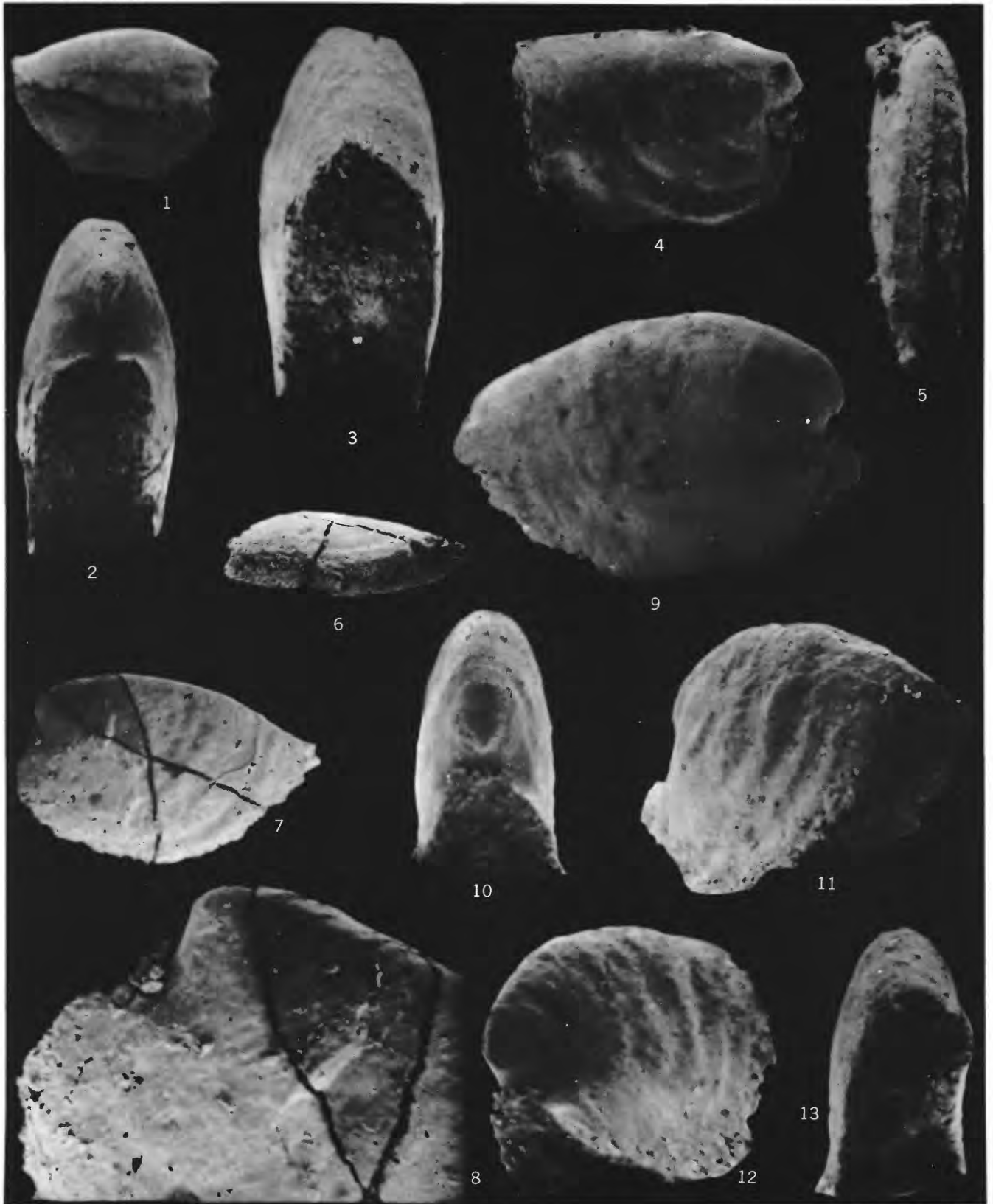


YOHELACIONELLA

PLATE 2

FIGURES

- 1-13. *Heraultipegma varensalense* (Cobbold), 1935 (p. 54).
Topotypes. 1-3, Right, anterior, and posterior views of USNM 209414, 1 ($\times 15$), 2, 3 ($\times 45$). 4, Right-lateral view of USNM 209415 ($\times 33$). 5, Dorsal view of USNM 209416 ($\times 43$). 6-8, Ventral, left-lateral, and enlargement of anterodorsal area with remnant of the pegma (USNM 227467); 6, 7 ($\times 20$); 8 ($\times 65$). 9-13, Left-lateral, anterior, oblique left posterior, oblique right anterior, and posterior views of USNM 209417 ($\times 47$).

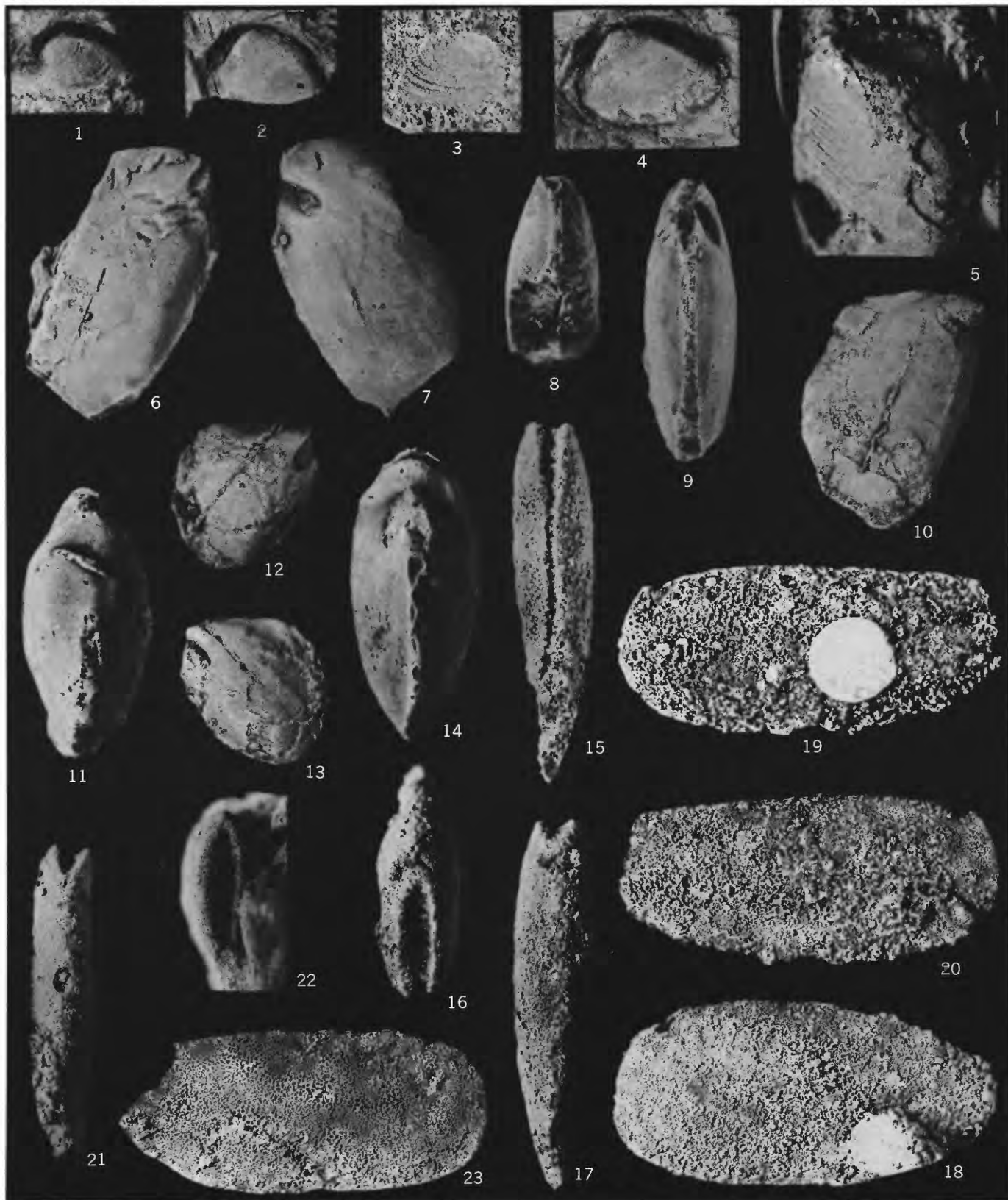


HERAULTIPEGMA

PLATE 3

FIGURES

- 1-4. *Watsonella crosbyi* Grabau, 1900 (p. 56).
The type suite, of which the specimen shown in figure 1 is herein chosen as the lectotype (Grabau, 1900, pl. 31, fig. 9b). From Lower Cambrian boulders, Sandy Cove and Pleasant Beach, Cohasset, Mass. All left-lateral views ($\times 4$). Specimens at the MCZ where they are cataloged under the Boston Society of Natural History Nos. 11951-11954.
- 5, 11-14. *Wanwanania cambrica* Kobayashi, 1933 (p. 55).
 5. Plastoparatype (Kobayashi, 1933, pl. 9, fig. 7), left valve ($\times 5$). Upper Cambrian (*Tsinania* Zone), Paichia-shan, Wuhutsui Basin, Manchuria. USNM 209409.
 - 11-14. Plastoholotype (Kobayashi, 1933, pl. 7, fig. 1), dorsal ($\times 4$), right-lateral ($\times 2$), left-lateral ($\times 2$), and anterior ($\times 4$) views. Formation and locality the same as in figure 5 above. USNM 209412.
- 6-9. *Wanwanania compressa* Kobayashi, 1933 (p. 55).
Plastoholotype (Kobayashi, 1933, pl. 7, fig. 5), right-lateral, left-lateral, dorsal, and anterior views ($\times 3$). Wanwankou Dolomite (Lower Ordovician), Wan-wan-kou in the Niuhsintai Basin, south Manchuria. USNM 209410.
10. *Wanwanania ambonychiformis* Kobayashi, 1933 (p. 55).
Plastoholotype (Kobayashi, 1933, pl. 7, fig. 4), right-lateral view ($\times 2$). Formation and locality the same as in figures 6-9 above. USNM 209411.
- 15-23. *Ribeirina longiuscula* (Billings), 1865 (p. 55).
 - 15-18. Ventral, anterior, dorsal, and left-lateral views ($\times 2$). Oxford Formation (Lower Ordovician), Ottawa-Carleton Highway 3, 2.4 miles northwest of intersection with County Highway 4 (GSC loc. 89453), Ontario, Canada. USNM 209413.
 - 19, 20. Left- and right-lateral views ($\times 2$). Beekmantown Group (Lower Ordovician), Marlborough Township, Ontario, Canada. ROM 26 cal.
 - 21-23. Dorsal, anterior, and right-lateral views of holotype ($\times 2$). Beekmantown Group (Lower Ordovician), Oxford Township, Ontario, Canada. GSC 470.



WATSONELLA, WANWANIA, AND RIBEIRINA

PLATE 4

FIGURES

- 1-24. *Ribeiria calcifera* Billings, 1865 (p. 51).
 - 1-3. Right-lateral, left-lateral, and dorsal views of paralectotype ($\times 2$). Beekmantown Group (Lower Ordovician), Oxford Township, Ontario, Canada. GSC 469a.
 - 4-6. Left-lateral, anterior, and dorsal views of lectotype ($\times 2$). Formation and locality the same as in figures 1-3 above. GSC 469.
 - 7-10. Left-lateral ($\times 2$), dorsal ($\times 2$), anterior ($\times 4$), and posterior ($\times 2$) views of paralectotype. Formation and locality the same as in figures 1-3 above. GSC 469b.
 - 11, 12. Posterior and right-lateral views of paralectotype ($\times 2$). Formation and locality the same as in figures 1-3 above. GSC 469d.
 13. Anterior view ($\times 2$). Beekmantown Group (Lower Ordovician), Marlborough Township, Ontario, Canada. ROM 13 cal.
 - 14-17. Left-lateral, posterior, ventral, and dorsal views ($\times 2$). Formation and locality the same as on plate 3, figures 15-18. USNM 209408.
 - 18, 19. Posterior ($\times 4$) and right-lateral ($\times 2$) views. Staendebach Member, Tanyard Formation (Lower Ordovician), 3.25 miles airline east-southeast of Round Mountain, Blanco County, Tex. This hypotype was previously figured by Cloud and Barnes (1948). USNM 127909.
 - 20-24. Left-lateral ($\times 2$), right-lateral ($\times 2$), latex mold of anterior face showing pegma ($\times 2$), anterior ($\times 3$), and posterior ($\times 4$) views. Staendebach Member, Tanyard Formation (Lower Ordovician), 1.5 miles west from the ranch headquarters of Mack Yates, Sr., southeastern San Saba County, Tex. This hypotype was previously figured by Cloud and Barnes (1948). USNM 127908.
25. *Ribeiria* sp. (p. 53).
 - Left-lateral view of fragmentary specimen ($\times 3$). Lower Ordovician (Warendian) part of the Ninmaroo Formation, at northern peak of Digby Peaks, 60 miles north of Boulia, Queensland, Australia. UQ F 67149.
- 26-29. *Ribeiria australiensis* n. sp. (p. 50).
 - 26, 28. Posterior ($\times 4$) and right-lateral ($\times 4$) views of paratype, Mungerebar Formation (Upper Cambrian), Glenormiston, Queensland, Australia. BMR CPC 14671.
 - 27, 29. Dorsal and anterior views of holotype ($\times 5$). Formation and locality the same as in figures 26, 28 above. BMR CPC 14670.

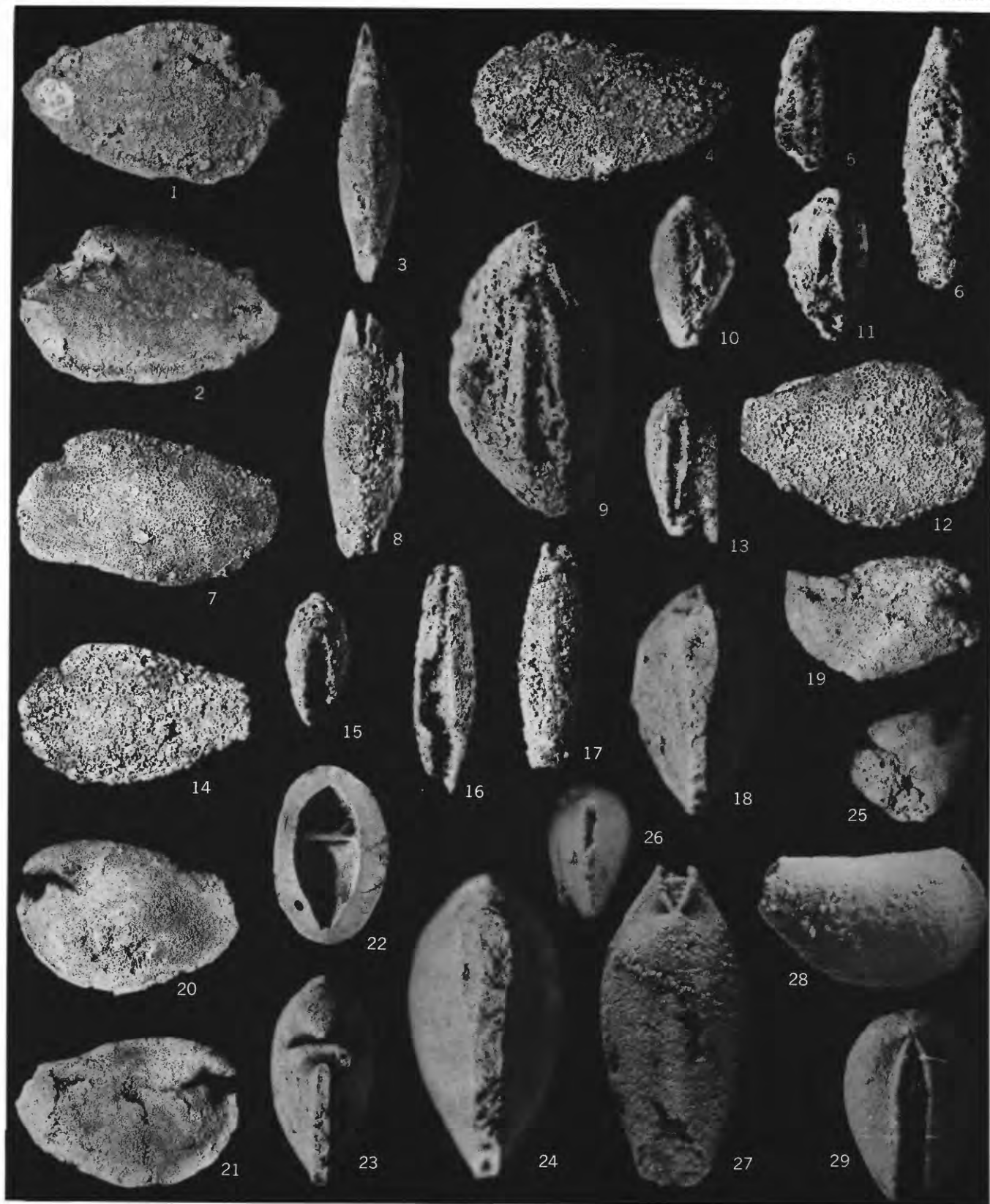
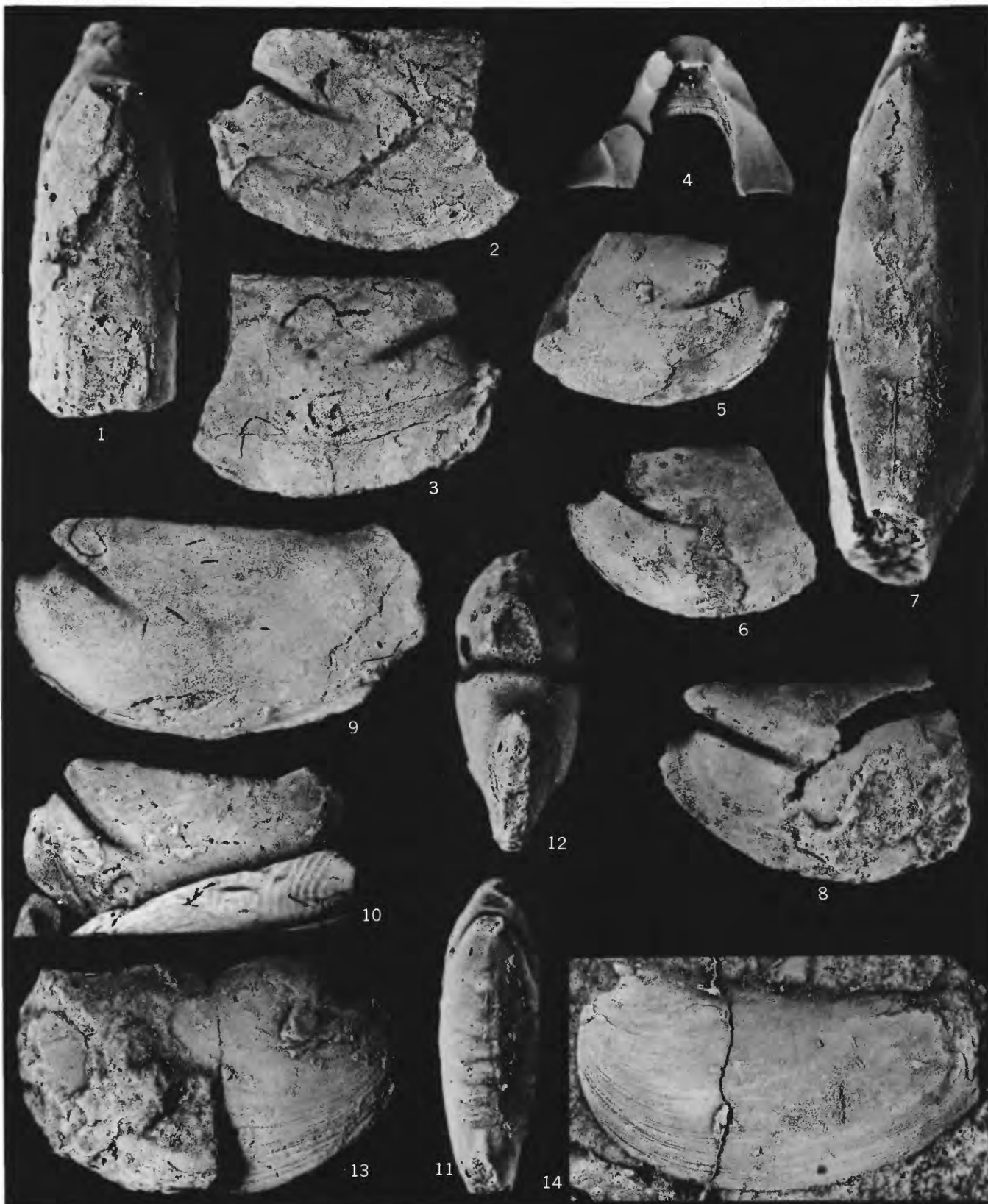
*RIBEIRIA*

PLATE 5

FIGURES

- 1-14. *Ribeiria apusoides* Schubert and Waagen, 1903 (p. 50).
- 1-4. Dorsal ($\times 3$), left-lateral ($\times 2$), right-lateral ($\times 2$), and latex replica of posterodorsal face of pegma, showing muscle insertion area ($\times 2$). Ordovician (D), Bohemia, Czechoslovakia. MCZ 18008.
- 5, 6. Right- and left-lateral views ($\times 2$). Horizon and locality the same as in figures 1-4 above. MCZ 18009.
- 7, 8. Dorsal ($\times 3$) and left-lateral ($\times 2$) views. Horizon and locality the same as in figures 1-4 above. MCZ 18010.
9. Latex replica of paralectotype (Schubert and Waagen, *in* Perner, 1903, pl. 49, fig. 21), left valve ($\times 2$). Zahorany Formation (Caradocian, Ordovician), Loděnice, Bohemia, Czechoslovakia. USNM 209404.
- 10, 11. Left-lateral and dorsal views ($\times 2$) of replica of paralectotype (Schubert and Waagen, *in* Perner, 1903, pl. 49, figs. 5, 6). Horizon and locality the same as in figure 9 above. USNM 209405.
12. Anterior view showing gape ($\times 4$). Horizon and locality the same as in figures 1-4 above. MCZ 18011.
13. Right valve exterior ($\times 2$) of latex replica of paralectotype (Schubert and Waagen, *in* Perner, 1903, pl. 49, figs. 22-23). Caradocian (Ordovician), Liben, Bohemia, Czechoslovakia. USNM 209406.
14. Left valve exterior ($\times 2$) of latex replica of paralectotype (Schubert and Waagen *in* Perner, 1903, pl. 49, figs. 24, 25; Schubert and Waagen, 1904, pl. 1, fig. 8). Horizon and locality the same as in figure 9 above. USNM 209407.



RIBEIRIA

PLATE 6

FIGURES 1–12, 14, 15. *Ribeiria apusoides* Schubert and Waagen, 1903 (p. 50).

- 1–4. Left-lateral ($\times 2$), right-lateral ($\times 2$), anterior ($\times 3$), and dorsal ($\times 3$) views of latex replica of lectotype (Schubert and Waagen *in* Perner, 1903, pl. 49, figs. 18–20; Schubert and Waagen, 1904, pl. 1, fig. 9). Caradocian (Ordovician), Loděnice, Bohemia, Czechoslovakia. USNM 209402.
5. Anterior view showing gape ($\times 4$). Llanvirnian(?) (Middle Ordovician), Rokycany, Bohemia, Czechoslovakia. MCZ 18012.
6. Posterior view showing gape ($\times 4$). Caradocian(?) (Ordovician), Loděnice, Bohemia, Czechoslovakia. MCZ 18013.
7. Right-lateral view ($\times 3$). Horizon and locality the same as in figure 5 above. MCZ 18014.
8. Right-lateral view showing side muscle ($\times 3$). Horizon and locality the same as in figure 5 above. MCZ 18015.
9. Right-lateral view ($\times 3$). Horizon and locality the same as in figure 5 above. MCZ 18016.
10. Left-lateral view ($\times 2$). Horizon and locality the same as in figure 5 above. MCZ 18017.
11. Left-lateral view ($\times 2$). Horizon and locality the same as in figure 5 above. MCZ 18018.
12. Right-lateral view ($\times 3$). Horizon and locality the same as in figure 5 above. MCZ 18019.
14. Right-lateral view showing elongate posterior median muscle scar ($\times 2$). Ordovician (D), Bohemia, Czechoslovakia. MCZ 18020.
15. Left-lateral view ($\times 2$). Ordovician (D), Bohemia, Czechoslovakia. MCZ 18021.
13. *Ribeiria* sp. (p. 53).
Right-lateral view of replica of paralectotype of *R. apusoides* ($\times 2$) (Schubert and Waagen *in* Perner, 1903, pl. 49, figs. 15–17). This is the youngest known *Ribeiria* and is probably not *R. apusoides*. Ashgillian (Upper Ordovician), Lejskov, Bohemia, Czechoslovakia. USNM 209403.

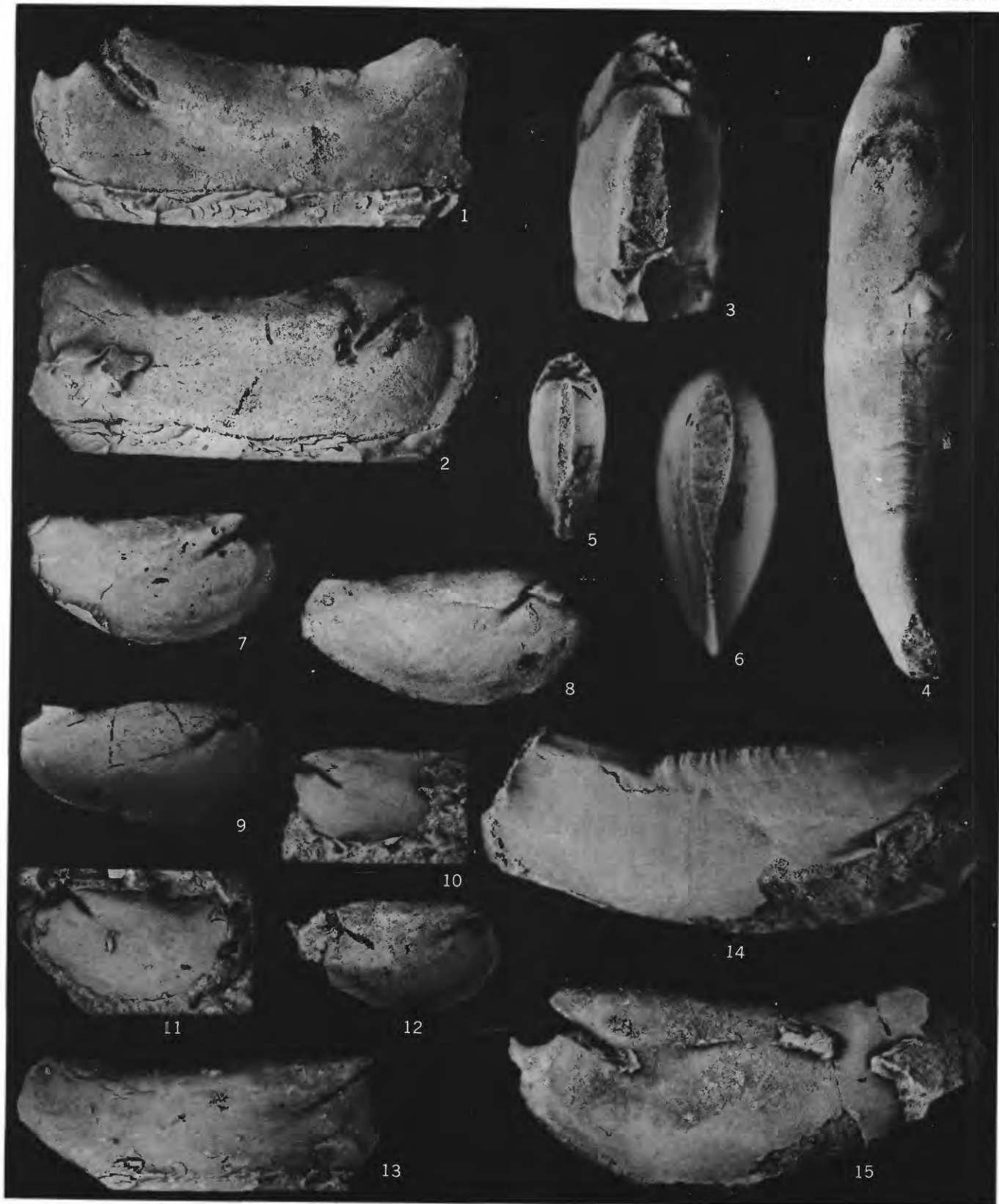
*RIBEIRIA*

PLATE 7

FIGURES

- 1, 2. *Ribeiria apusoides* Schubert and Waagen, 1903 (p. 50).
 1. Left-lateral view showing side muscle scar and posterior median muscle scar ($\times 3$). Ordovician (D), Bohemia, Czechoslovakia. MCZ 18022.
 2. Dorsal view showing posterior median muscle scar ($\times 2$). Ordovician (D), Bohemia, Czechoslovakia. MCZ 18023.
- 3-12. *Ribeiria pholadiformis* Sharpe, 1853 (p. 50).
 - 3-7. Dorsal, ventral, right-lateral, left-lateral, and anterior views ($\times 2$) of lectotype (Sharpe, 1853, pl. 9, figs. 17b, c). Llandeilian(?) (Middle Ordovician) of Portugal. GB 7798.
 8. Right valve external mold, paralectotype ($\times 2$). Horizon and locality the same as in figures 3-7 above. BM PL 4176a.
 9. Left valve external mold, paralectotype ($\times 2$). Horizon and locality the same as in figures 3-7 above. BM PL 4176b.
 10. Left valve external mold, paralectotype ($\times 2$). Horizon and locality the same as in figures 3-7 above. BM PL 4177.
 11. Left-lateral view ($\times 2$). Middle Arenigian (Lower Ordovician), from small abandoned quarry in hillside, about 200 feet above and 0.25 miles east of road from Carteret to Hattainville, Manche, Normandy, France. SM A.60181.
 12. Right-lateral view ($\times 2$). Horizon and locality the same as in figure 11 above. SM A.60182.
- 13-16. *Ribeiria* cf. *R. pholadiformis* Sharpe, 1853 (p. 50).
 - Left-lateral, right-lateral, latex replica of exterior, and dorsal views ($\times 2$). SM A 46270d, e.
- 17, 18. *Ribeiria* sp. (p. 53).
 - Two specimens showing right- and left-lateral views ($\times 2$). From the H Zone of Hintze (1951) at the Ibex section, Ibex, Utah (Lower Ordovician), Sec. 6, T. 23 N., R. 14 E. USNM 209400, 209401.

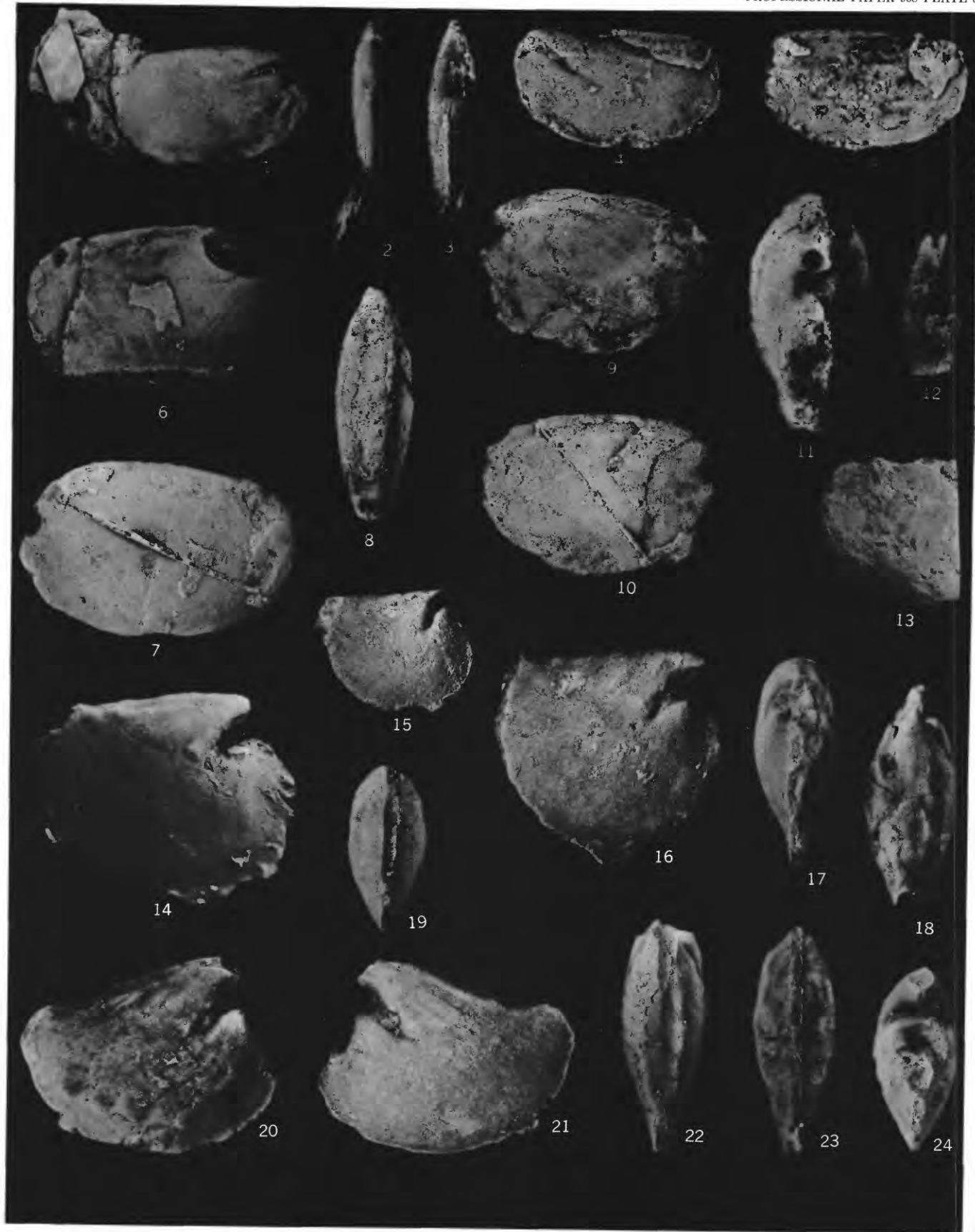


RIBEIRIA

PLATE 8

FIGURES

- 1-5. *Ribeiria compressa* Whitfield, 1886 (p. 51).
 - 1, 2. Right-lateral and dorsal views of holotype ($\times 2$). The museum label gives the horizon and locality as: "Ft. Cassin bed, Fort Cassin, Vermont" (Lower Ordovician). AM 491.
 - 3-5. Dorsal, left-lateral, and right-lateral views ($\times 3$) of lectotype of *Ribeiria equilatera* Cleland (1900, pl. 16, fig. 15). Cleland (1900, p. 22) gave the horizon and locality as "Calciferos at Fort Hunter, New York" (Lower Ordovician). PRI 5081.
- 6-11. *Ribeiria manchurica* Kobayashi, 1933 (p. 52).
 - 6, 7. Right-lateral and left-lateral views of a replica of the holotype ($\times 2$). Wanwankou Dolomite (Lower Ordovician), Wan-wan-kou in the Niuhsintai Basin, southern Manchuria. USNM 209394.
 - 8-11. Dorsal ($\times 2$), left-lateral ($\times 2$), right-lateral ($\times 2$), and anterior ($\times 3$) views of a replica of a previously unfigured paratype. Horizon and locality the same as in figures 6, 7. USNM 209395.
- 12, 13. *Ribeiria taylori* n. sp. (p. 53).
 - Dorsal and left-lateral views of holotype ($\times 4$). Whitehall Formation, *Saukia* Zone, probably *Saukiella serotina* (Upper Cambrian). USGS loc. 470B (old series), Hall Farm, 1 mile northeast of Whitehall, N.Y. (Taylor and Halley, 1974, p. 32). USNM 209396.
- 14-24. *Ribeiria lucan* (Walcott), 1924 (p. 52).
 14. Right-lateral view ($\times 4$) of lectotype of *Ozomia lucan* Walcott, (1924, p. 531), showing multiple insertions of side muscle. Mons Formation (Lower Ordovician), thin-bedded gray limestone 255 feet from summit of Mons, 8.7 miles northeast in airline of Lake Louise Station on the Canadian Pacific Railway at the east foot of Fossil Mountain, Alberta, Canada. USNM 209397.
 15. Right-lateral view ($\times 4$), paralectotype. Horizon and locality the same as in figure 14 above. USNM 209398.
 - 16-18. Right-lateral, anterior, and dorsal views ($\times 4$) of paralectotype. Horizon and locality the same as in figure 14 above. USNM 209399.
 - 19-24. Posterior, right-lateral, left-lateral, dorsal, ventral, and anterior views ($\times 4$) of paralectotype. Horizon and locality the same as in figure 14 above. USNM 69801.



RIBEIRIA

PLATE 9

FIGURES

1. *Ribeiria turgida* Cleland, 1903 (p. 53).
Right-lateral view of holotype ($\times 3$). The museum label gives the horizon and locality as: "Tribes Hill ls., Canajoharie?, New York" (Lower Ordovician). USNM 84630.
- 2-6. *Ribeiria* sp. (p. 53).
2. Right-lateral view ($\times 3$) of a specimen figured by Sando (1957, pl. 10, fig. 3). Stonehenge Formation (Lower Ordovician), pasture northeast of Barn on Forsythe Farm, 1.0 miles S. 5° E. of St. Pauls Church, Washington County, Md. USNM 123847.
3, 4. Right-lateral and dorsal views ($\times 3$). Stonehenge Formation (Lower Ordovician), 1.35 miles S. 20° W. of Charlton in pasture 300 feet southeast of barn, Washington County, Md. USNM 146208.
5, 6. Dorsal and right-lateral views ($\times 3$). Horizon and locality the same as in figures 3, 4 above. USNM 209391.
- 7-9. *Ribeiria parva* Collie, 1903 (p. 52).
Right-lateral, dorsal, and left-lateral views of holotype ($\times 4$). Collie (1903, p. 419) gave the horizon and locality as: "Bellefonte, Pennsylvania, in the middle Beekmantown horizon" (Lower Ordovician). YU 7933.
10. *Ribeiria complanata* Salter, 1866 (p. 51).
Left-lateral view of holotype ($\times 3$). Lower Llandeilian (Middle Ordovician), Lord's Hill, Shelve, North Wales. GB 12434.
- 11, 12. *Pinnocaris americana* n. sp. (p. 54).
11. Right-lateral view of paratype ($\times 2$). The museum label gives the horizon and locality as: "Prosser limestone, Elkader, Iowa" (Middle Ordovician). USNM 209392.
12. Right-lateral view of holotype ($\times 2$). Horizon and locality the same as in figure 11. USNM 209393.
- 13-23. *Pinnocaris lapworthi* Etheridge, 1878 (p. 54).
13, 14. Left valve mold of exterior and latex replica of mold ($\times 2$). Hypotype figured by Jones and Woodward (1895, pl. 15, figs. 8, 9). The museum label gives the horizon and locality as: "Upper Ordovician, Lower Ardmillan series, Balclatchie Group; Balclatchie, Girvan, Ayrshire," Scotland. BM In 20372.
15-17. Anterior view showing gape ($\times 4$), left-lateral ($\times 2$) right-lateral ($\times 2$) views. The museum label reads: "Balclatchie." SM A 33722b.
18, 19. Part and counterpart of right valve ($\times 2$). Horizon and locality the same as in figures 13, 14 above. BM In 20422.
20. Broken and distorted left valve ($\times 2$), paralectotype (Etheridge, 1878, pl. 2, fig. 3). Etheridge (1878, p. 169) gave the horizon and locality as: "Balclatchie [sic], south-east of Girvan, in rocks of Silurian [Ordovician] age; exact horizon not yet determined." BM In 20366.
21. Crushed right valve ($\times 2$), lectotype (Etheridge, 1878, pl. 2, fig. 5). Horizon and locality the same as in figure 20 above. BM In 20367.
22. Left valve ($\times 2$), paralectotype (Etheridge, 1878, pl. 2, fig. 4). Horizon and locality the same as in figure 20 above. BM In 20368.
23. Left-lateral view ($\times 2$). Horizon and locality the same as in figures 15-17 above. SM A 33722b.
- 24, 25. *Pinnocaris curvata* Reed, 1907 (p. 54).
Latex replica and original of a mold of a right valve ($\times 2$). The museum label gives the horizon and locality as: "Upper Ordovician, Ardmillan series, Drummuck Group, Starfish Bed; Thraive Glen, Girvan, Ayrshire," Scotland. BM In 20290.

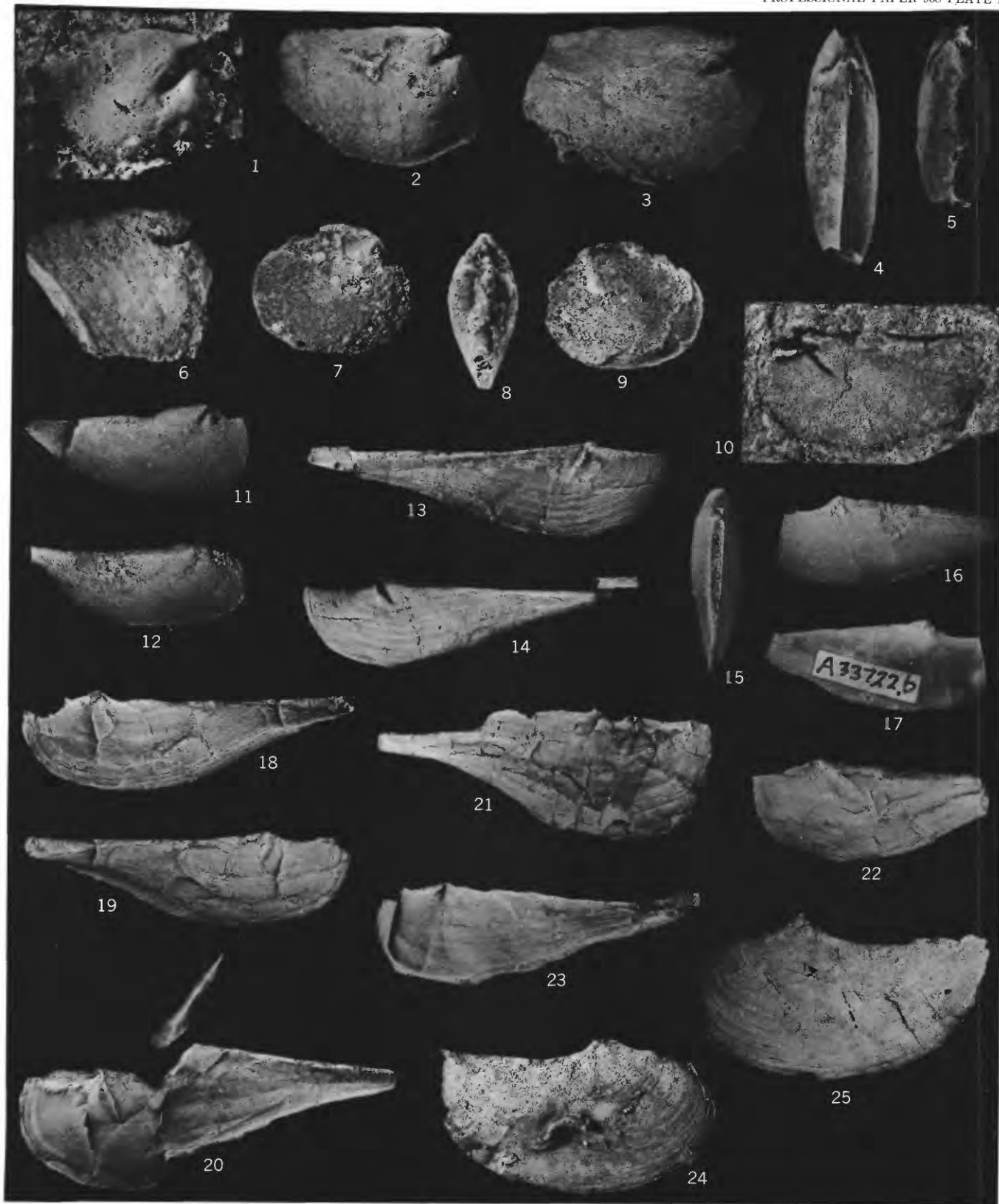
*RIBEIRIA AND PINNOCARIS*

PLATE 10

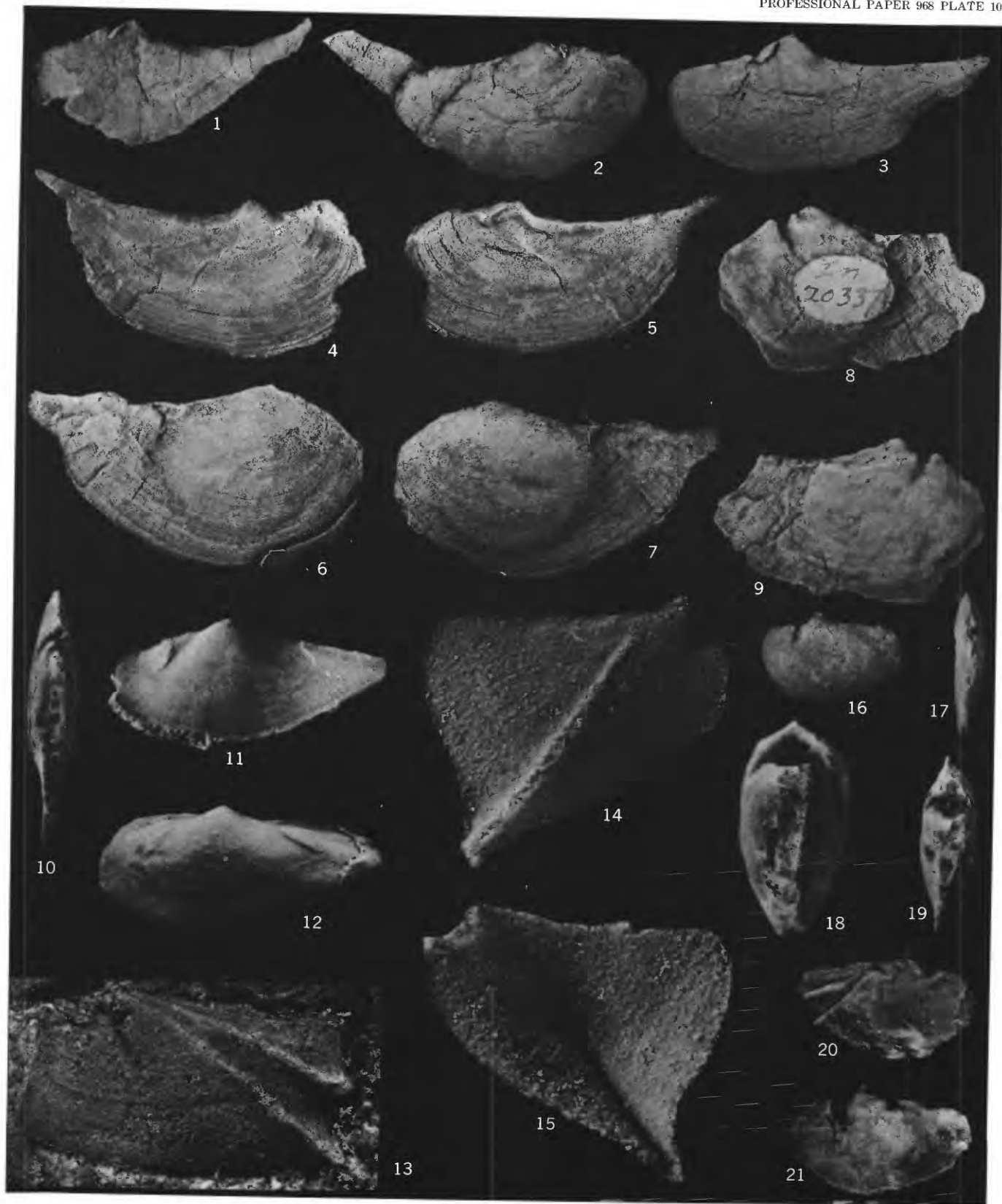
FIGURES

- 1-10. *Pinnocaris curvata* Reed, 1907 (p. 54).
 1. Internal mold left valve ($\times 2$). Horizon and locality the same as in figures 24, 25, plate 9. BM In 20283.
 2. Right-lateral view ($\times 2$). The museum label gives the horizon and locality as: "Starfish Bed, Upper Drummuck Group: Thraive Glen, Girvan, Ayrshire," Scotland (Upper Ordovician). SM A 525594.
 3. Left-lateral view ($\times 2$). Horizon and locality the same as in figures 24, 25, plate 9. BM In 20309.
 - 4, 5. Original and latex replica of an external mold of left valve ($\times 2$). This is the other valve of the specimen shown on plate 9, figures 24, 25. Horizon, locality, and museum number the same as on plate 9, figures 24, 25.
 - 6, 7. Original and latex replica of external mold of left valve ($\times 2$). Horizon and locality the same as on plate 9, figures 24, 25. BM In 20337.
 - 8-10. Left-lateral, right-lateral, and dorsal views ($\times 2$). Horizon and locality the same as on plate 9, figures 24, 25. BM 20337.
- 11, 12. "*Technophorus*" *yoldiaformis* (Ulrich), 1879 (p. 60).

Left-lateral views of two syntypes showing pelecypod adductor muscle impressions ($\times 5$). Cincinnati (Upper Ordovician), Covington, Ky. USNM 209390, 46315.
13. *Myocaris lutraria* Salter, 1864 (p. 61).

Left-lateral view ($\times 1$) of holotype (Salter, 1864, fig. 4). The museum label gives the horizon and locality as: "Ordovician, Llandeilo, from Trias Pebble Bed, Budleigh-Salterton, Devon," England. BM I 7204.
- 14, 15. *Oepikila cambrica* (Runnegar and Pojeta), 1974 (p. 61).

Part and counterpart of right valve ($\times 15$), holotype. Georgina Limestone, *Erixanium sentum* Zone, Idamean Stage (Upper Cambrian), western Queensland, Australia. BMR CPC 13953.
- 16-21. *Technophorus faberi* Miller, 1889 (p. 56).
 - 16, 17. Left-lateral and dorsal views ($\times 2$) of paralectotype (Miller, 1889, p. 513, left-hand figure in fig. 930). The museum label gives the horizon and locality as: "Cincinnatian, near Sharonville, Ohio" (Upper Ordovician). FM 8831 (Walker Mus. coll).
 - 18-21. Anterior ($\times 4$), dorsal ($\times 2$), right-lateral ($\times 2$), and left-lateral ($\times 2$) views. The museum label gives the horizon and locality as: "Utica, Cincinnati, Ohio" (Upper Ordovician). USNM 40611.



PINNOCARIS, "*TECHNOPHORUS*," *MYOCARIS*, *OEPIKILA*, AND *TECHNOPHORUS*

PLATE 11

FIGURES

- 1-6. *Technophorus faberi* Miller, 1889 (p. 56).
 - 1, 2. Dorsal and left-lateral views ($\times 2$) of a hypotype (Miller and Faber, 1894, pl. 1, fig. 20). Maysvillian (Upper Ordovician), Sharonville, Ohio. FM 8832 (Walker Mus. coll.).
 3. Left-lateral view ($\times 3$). The museum label gives the horizon and locality as: "Eden Shale, Covington, Kentucky" (Upper Ordovician). USNM 72019.
 4. Right-lateral view ($\times 3$). The museum label gives the horizon and locality as: "Maysville Grp. (Fairmount beds), Cincinnati, Ohio" (Upper Ordovician). USNM 40612.
 - 5, 6. Right-lateral and left-lateral views of lectotype ($\times 3$). Horizon, locality, and museum number the same as on plate 10, figures 16, 17.
- 7-13. *Technophorus bellistriatus* Branson, 1909 (p. 58).
 - 7-9. Left-lateral, dorsal, and posterior views ($\times 4$); the last shows the gape of the posterior rostrum. Decorah Shale (Middle Ordovician), 2.5 miles west of St. Genevieve, Mo. FM 23942 (Walker Mus. coll.).
 - 10-13. Anterior, ventral, right-lateral, and left-lateral views of holotype ($\times 4$). The museum label gives the horizon and locality as: "Stones River, Auburn, Lincoln Co., Mo." (Middle Ordovician). FM 11551 (Walker Mus. coll.).
14. *Technophorus coreanica* (Kobayashi), 1934 (p. 58).

Right-lateral view ($\times 7$) of replica of holotype (Kobayashi, 1934, pl. 4, fig. 18). Kobayashi (1934, p. 576) gave the horizon and locality as: "Clarkella zone of Saisho-ri," South Korea (Lower Ordovician). USNM 209389.
- 15-20. *Technophorus cancellatus* Ruedemann, 1901 (p. 58).
 15. Right-lateral view ($\times 6$) of hypotype (Ruedemann, 1912, pl. 9, fig. 17). The museum label gives the horizon and locality as: "Snake Hill beds, Snake Hill, Saratoga Co., N.Y." (Middle Ordovician). NYSM 9890.
 16. Right-lateral view ($\times 4$) of lectotype (Ruedemann, 1901, pl. 1, figs. 19, 20). The museum label gives the horizon and locality as: "Snake Hill shale, Green Island, Albany Co., N.Y." (Middle Ordovician). NYSM 3190.
 17. Right-lateral view ($\times 4$) of paralectotype (Ruedemann, 1901, pl. 1, fig. 21). Horizon and locality the same as in figure 16 above. NYSM 3191.
 18. Left-lateral view ($\times 4$) of paralectotype (Ruedemann, 1901, pl. 1, fig. 22). Horizon and locality the same as in figure 16 above. NYSM 3192.
 19. Right-lateral view ($\times 3$) of hypotype (Ruedemann, 1912, pl. 9, fig. 18). Horizon and locality the same as in figure 15 above. NYSM 9891.
 20. Left-lateral view ($\times 4$) of paralectotype (Ruedemann, 1901, pl. 1, fig. 23). Horizon and locality the same as in figure 16 above. NYSM 3193.
21. *Technophorus* sp. (p. 60).

Right-lateral view ($\times 4$). Lower Ordovician (Warendian) part of the Ninmaroo Formation, at northern peak of Digby Peaks, 60 miles north of Boulia, Queensland, Australia. UQ F67150.
22. *Technophorus subacutus* Ulrich, 1892a (p. 60).

Left-lateral view of holotype ($\times 3$). Ulrich (1892a, p. 101) gave the horizon and locality as: "Upper part of the limestone of the Trenton formation at Minneapolis, Minnesota." Bassler (1915, p. 1259) gave the horizon as: "Black River (Platteville)" (Middle Ordovician). UMN 8338.
23. *Technophorus* cf. *T. cancellatus* Ruedemann, 1901 (p. 58).

Right-lateral view ($\times 4$) of lectotype of *T. punctostriatus quincuncialis* Foerste (1914, pl. 2, fig. 13b). The museum label gives the horizon and locality as: "Upper Ordovician, Chambly, Quebec," Canada. GSC 8415.

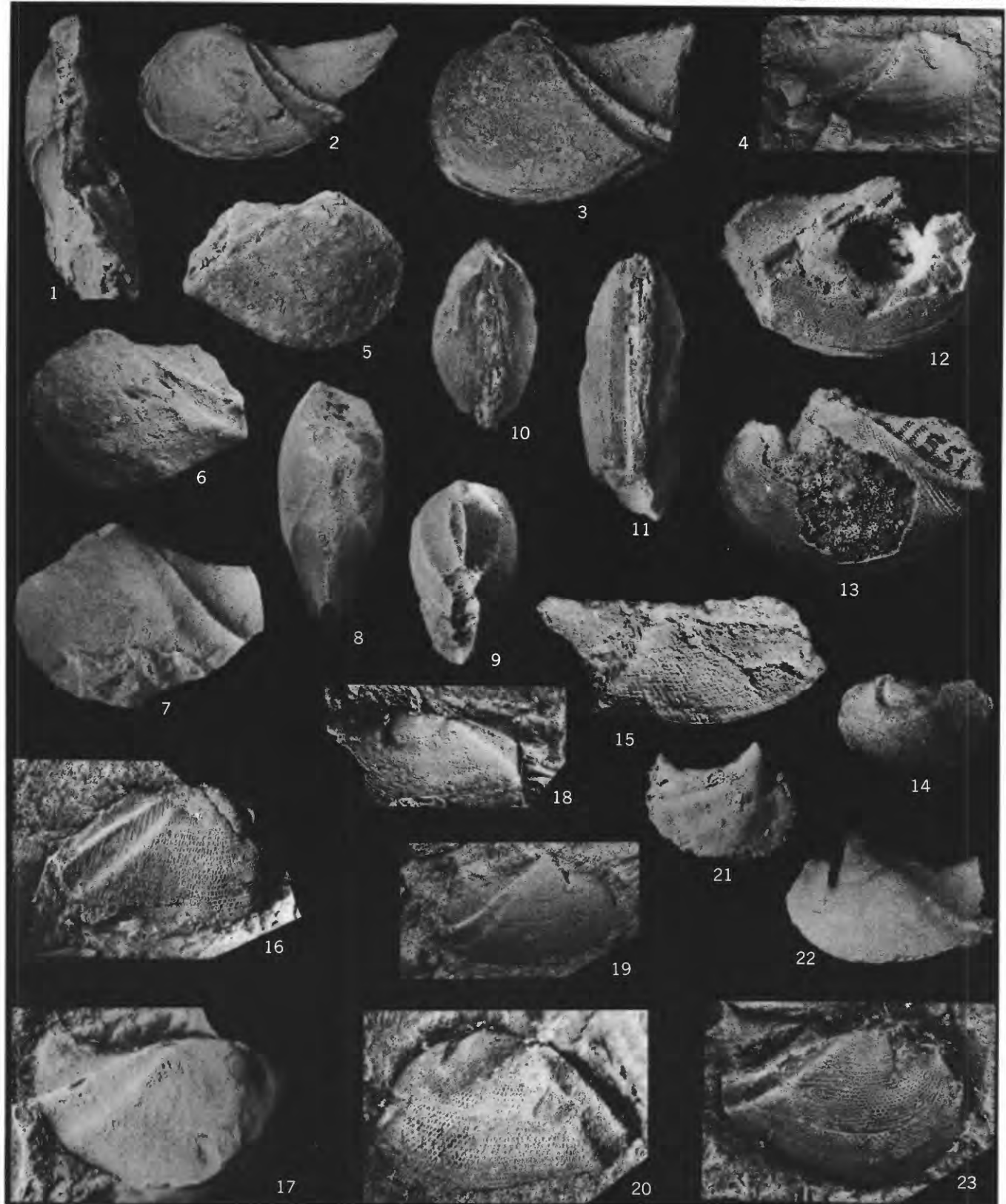
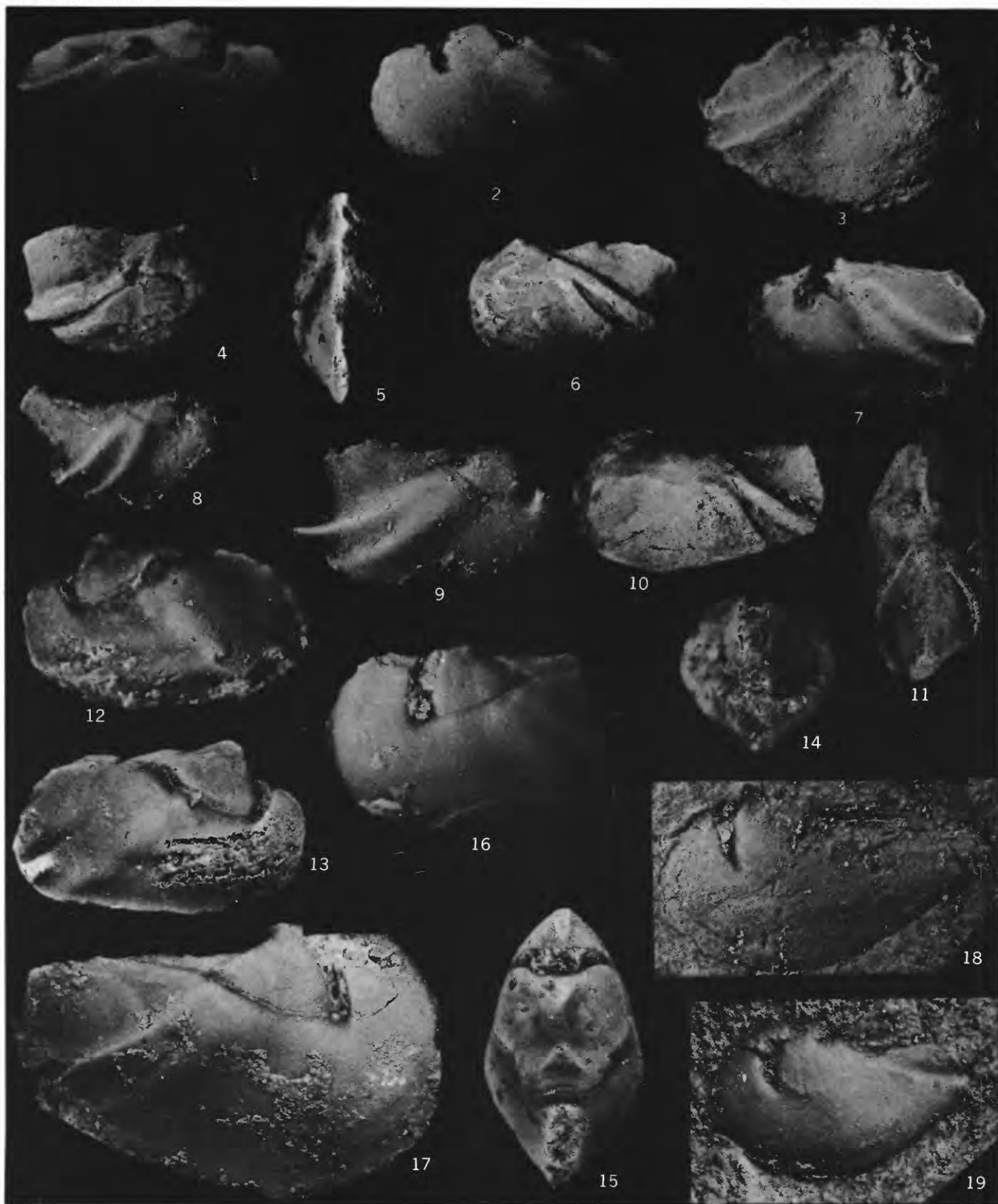
*TECHNOPHORUS*

PLATE 12

FIGURES

- 1, 2. *Technophorus plicatus* (Billings), 1866 (p. 59).
Right-lateral and left-lateral views of holotype ($\times 3$). The museum label gives the horizon and locality as: "Ellis Bay, Upper Ordovician, Junction Cliff, Anticosti Island," Quebec, Canada. GSC 2291.
3. *Technophorus* cf. *T. plicatus* (Billings), 1866 (p. 59).
Right-lateral view ($\times 3$). Ordovician of Anticosti Island, Quebec, Canada. YU 3063/40.
- 4-11. *Technophorus cincinnatiensis* Miller and Faber, 1894 (p. 58).
4-6. Right-lateral, dorsal, and left-lateral views of holotype ($\times 5$). The museum label gives the horizon and locality as: "Eden-Economy, Cincinnati (?), O." (Upper Ordovician). UCM 3886.
7. Left-lateral view ($\times 5$) of lectotype of *T. punctostriatus* Ulrich ([1895], pl. 47, fig. 11). The museum label gives the horizon and locality as: "Lorraine, Covington, Kentucky" (Upper Ordovician). USNM 46313.
8. Right-lateral view ($\times 5$) of paralectotype of *T. punctostriatus* Ulrich ([1895], pl. 47, figs. 10, 12). Horizon and locality the same as in figure 7 above. USNM 209383.
9. Right-lateral view ($\times 5$). The museum label gives the horizon and locality as: "Eden Shale, Covington, Kentucky" (Upper Ordovician). USNM 72018.
10, 11. Left-lateral and dorsal views ($\times 5$). The museum label read: "Lexington Pike, near Covington, Kentucky" (Upper Ordovician). USNM 209384.
- 12-15. *Technophorus marija* n. sp. (p. 59).
Left-lateral, right-lateral, posterior, and dorsal views of holotype ($\times 4$). The museum label reads: "Middle Ord., Boulder on right bank of Moyero River, 6 miles above mouth of Ukdama River, Khatango-Anabar Region, northern Siberia." Geological Museum, Academy of Science, U.S.S.R., 1849/2027.
- 16, 17. *Technophorus* sp. (p. 60).
Two specimens, left and right valves, respectively, showing the side muscles ($\times 5$). Kope Formation (Upper Ordovician), 68.3 m above base of section at 497,600 ft N.; 930,000 ft E., Demossville 7.5-minute quadrangle, Kenton County, Ky. Collected by D. M. Lorenz. USNM 209385, 209386.
- 18, 19. *Technophorus sharpei* (Barrande) in Perner, 1903 (p. 60).
18. Left-lateral view of latex replica of syntype ($\times 4$). The museum label accompanying this specimen cites it as a replica of Barrande in Perner (1903, pl. 49, fig. 9), which is shown as a right valve. Caradocian (Ordovician), Vinice, Bohemia, Czechoslovakia. USNM 209387.
19. Left-lateral view of latex replica of syntype ($\times 4$). The museum label accompanying this specimen cites it as a replica of Barrande in Perner (1903, pl. 49, fig. 7), which is shown as a right valve. Caradocian (Ordovician), Liben, Bohemia, Czechoslovakia. USNM 209388.



TECHNOPHORUS

PLATE 13

FIGURES

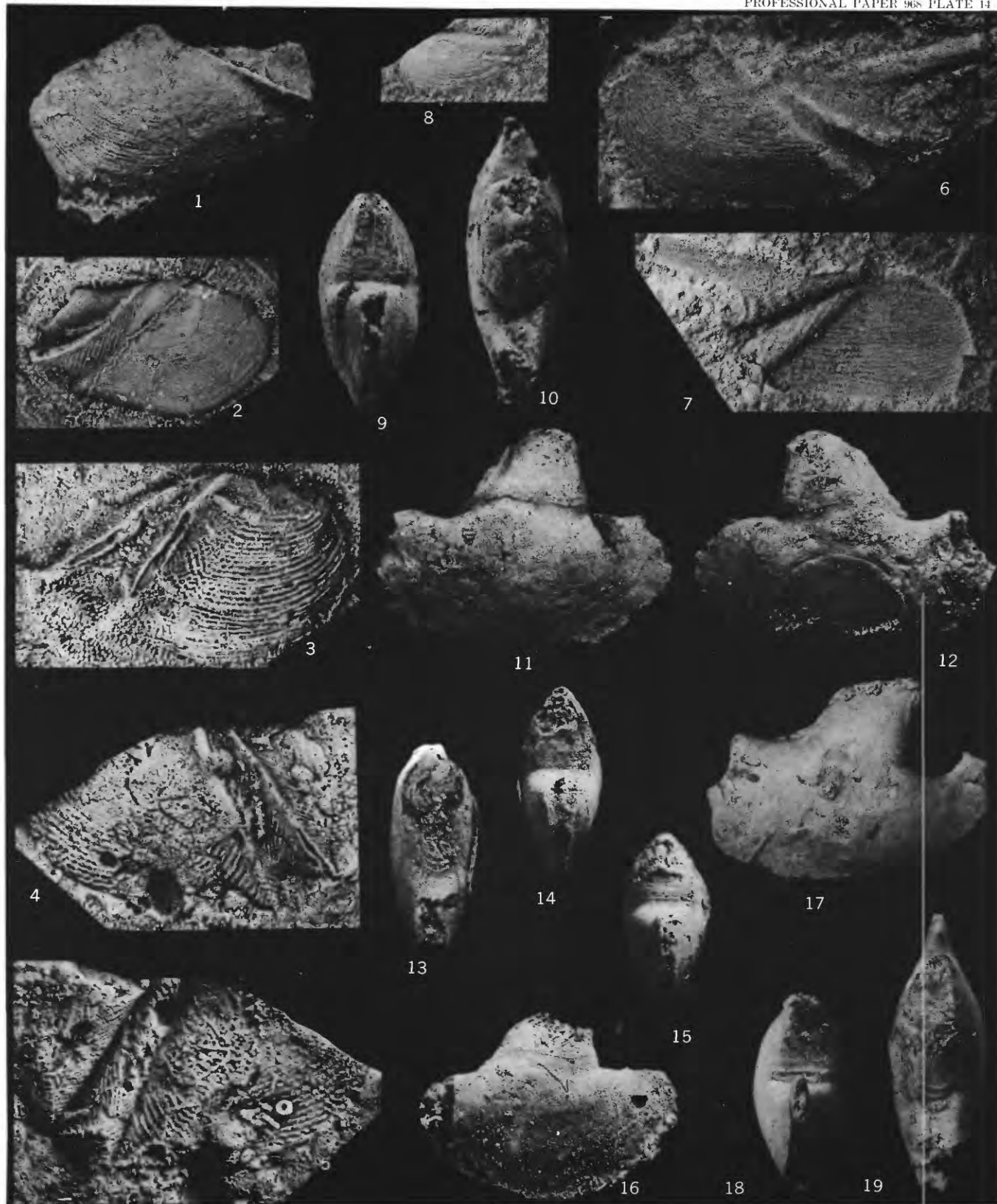
- 1-14. *Technophorus sharpei* (Barrande) in Perner, 1903 (p. 60).
 1. Left-lateral view of latex replica of syntype ($\times 4$). The museum label accompanying this specimen cites it as a replica of Barrande in Perner (1903, pl. 49, fig. 8), which is shown as a right valve. Caradocian or Ashgillian (Ordovician), Bohemia, Czechoslovakia. USNM 209381.
 2. Left-lateral view of latex replica of syntype ($\times 4$). The museum label accompanying this specimen cites it as a replica of Barrande in Perner (1903, pl. 49, figs. 10, 11), which is shown as a right valve. Bohdalec Formation (Caradocian, Ordovician), Velka Chuchle, Bohemia, Czechoslovakia. USNM 209382.
 3. Left-lateral view of internal mold ($\times 5$). Ordovician (Caradocian?), Velka Chuchle, Bohemia, Czechoslovakia. MCZ 18024.
 4. Right-lateral view of composite mold ($\times 5$). Horizon and locality the same as in figure 3 above. MCZ 18025.
 5. Left-lateral view of internal mold ($\times 5$). Horizon and locality the same as in figure 3 above. MCZ 18026.
 - 6-8, 13. Right-lateral, left-lateral, dorsal, and anterior views ($\times 5$). Horizon and locality the same as in figure 3 above. MCZ 6908/3.
 - 9-12. Right-lateral ($\times 5$), left-lateral ($\times 5$), anterior ($\times 8$), and dorsal ($\times 5$) views. Ordovician of Bohemia, Czechoslovakia. MCZ 18027.
 14. Posterior view showing the bilobed posterior shell gape ($\times 8$). Horizon and locality the same as in figures 9-12 above. MCZ 18028.
- 15, 16. *Technophorus filistriatus* Ulrich, 1892a (p. 59).
 15. Right-lateral view of internal mold ($\times 5$). The museum label gives the horizon and locality as: "Trenton, Kenyon, Minnesota" (Middle Ordovician). USNM 47204.
 16. Left-lateral view of holotype ($\times 3$). The museum label gives the horizon and locality as: "Black River, 6 miles south of Cannon Falls, Minnesota" (Middle Ordovician). USNM 46312.

*TECHNOPHORUS*

PLATE 14

FIGURES

1. *Technophorus filistriatus* Ulrich, 1892a (p. 59).
Left-lateral view of exterior ($\times 3$). The museum label gives the horizon and locality as: "Decorah sh., b. 5, Cannon Falls," Minnesota (Middle Ordovician). UMN 12236.
- 2-5. *Technophorus* cf. *T. divaricatus* Ulrich, 1892a (p. 58).
 2. Latex replica of the exterior of a right valve ($\times 5$). The museum label gives the horizon and locality as: "Decorah sh., b. 4, St. Paul," Minnesota (Middle Ordovician). UMN 12237. Replica USNM 209379.
 3. Latex replica of exterior of a right valve ($\times 4$). Elkhorn Formation (Upper Ordovician), along road west of Hamburg, Ind. MU 6849. Replica USNM 209380.
 - 4, 5. Latex replica and specimen of ventral part of left valve ($\times 4$). Horizon, locality, and museum number the same as in figure 3 above.
- 6, 7. *Technophorus milleri* n. sp. (p. 59).
Part and counterpart of holotype showing ornament and elongated posterior rostrum ($\times 5$). Lower Whitewater Formation (Upper Ordovician), Dodge's Creek, 0.5 miles north of Oxford, Ohio. MU 6848.
8. *Technophorus stoermeri* Soot-Ryen, 1960 (p. 60).
Left-lateral view of holotype ($\times 4$). Middle Caradocian (Middle Ordovician), Ostøya, Baerum, Norway. UO 5849.
- 9-19. *Tolmachovia? jelli* n. sp. (p. 62).
 - 9-12. Anterior, dorsal, right-lateral, and left-lateral views of holotype ($\times 4$). Lower Ordovician part (Warendian) of the Ninmaroo Formation, northern peak of Digby Peaks, about 60 miles north of Boulia, Queensland, Australia. UQ F 60117.
 - 13, 14. Dorsal and anterior views of paratype ($\times 4$). Horizon and locality the same as in figures 9-12 above. UQ F 60119.
 - 15, 16. Anterior and right-lateral views of paratype ($\times 4$). Horizon and locality the same as in figures 9-12 above. UQ F 60118.
 - 17-19. Right-lateral, anterior, and dorsal views of paratype ($\times 4$). Horizon and locality the same as in figures 9-12 above. UQ F 67152.



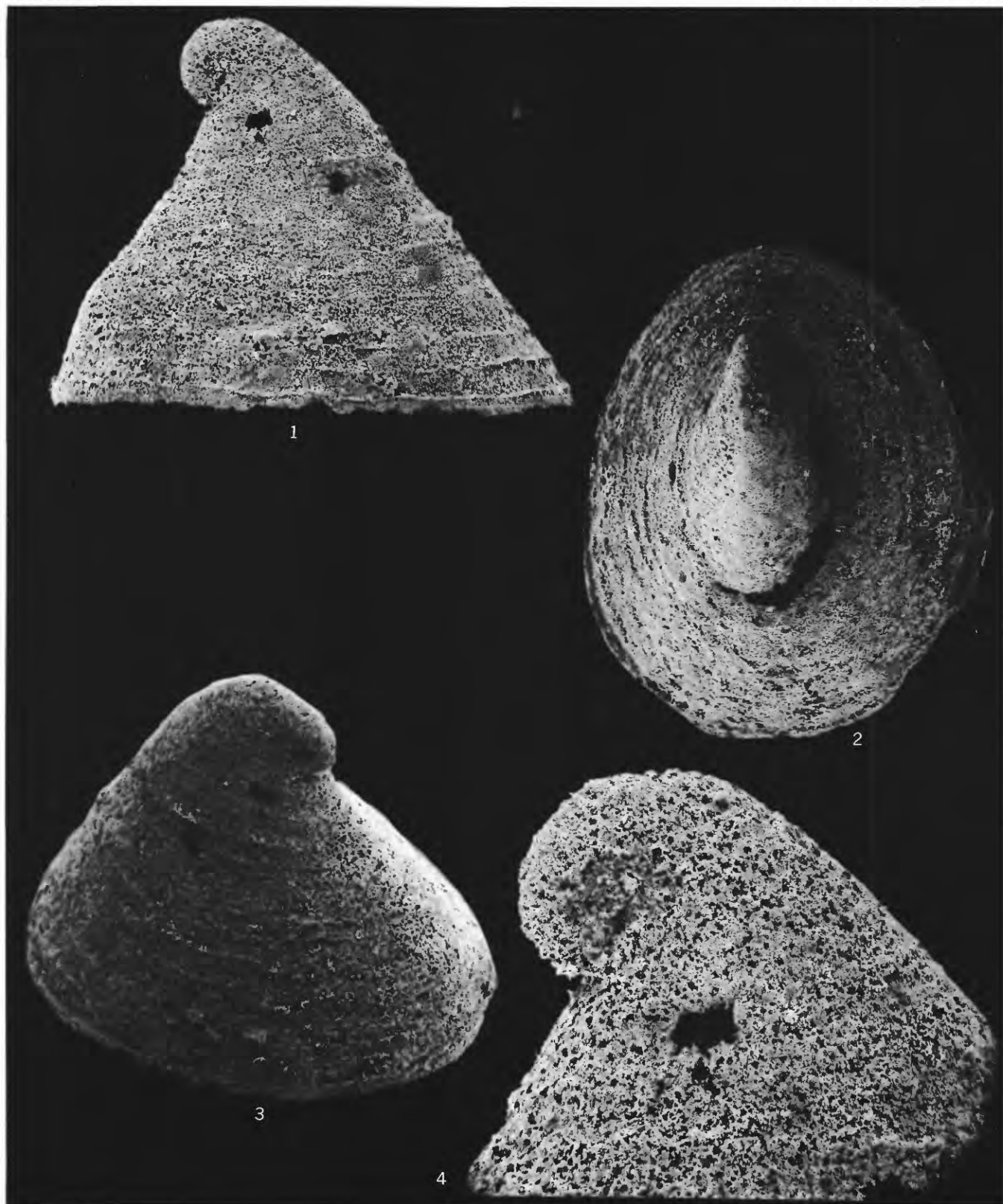
TECHNOPHORUS AND TOLMACHOVIA

PLATE 15

FIGURES

1-4. ?*Macroscenella* cf. *M. montrealensis* (Billings), 1865 (p. 30).

Left, dorsal, oblique right ($\times 27$) views, and enlargement of protoconch ($\times 68$) of a monoplacophoran showing a planispirally coiled protoconch. Lower Chambersburg Limestone (Middle Ordovician), near Strasburg, Va., USNM locality 600. Specimen identified by E. L. Yochelson, USNM 209378.



?MACROSCENELLA

PLATE 16

FIGURES

- 1-10. *Tolmachovia concentrica* Howell and Kobayashi, 1936 (p. 62).
1-4. Right-lateral, anterior, posterior, and left-lateral views of a previously unfigured paratype ($\times 5$). The museum label gives the horizon and locality as: "Middle Ordovician, boulder on right bank of Moyero River, 6 miles above mouth of Ukdama River, Khatanga-Anabar region, northern Siberia." Geological Museum of the Academy of Science, U.S.S.R. 1849/2027.
5, 6. Right-lateral and left-lateral views of paratype ($\times 5$). Horizon and locality the same as in figures 1-4 above. Geological Museum of the Academy of Science, U.S.S.R. 1849/2027c.
7. Right-lateral view of a previously unfigured paratype ($\times 5$). Horizon and locality the same as in figures 1-4 above. Geological Museum of the Academy of Science, U.S.S.R., 1849/2027d.
8-10. Left-lateral, right-lateral, and dorsal views of holotype ($\times 5$). Horizon and locality the same as in figures 1-4 above. Geological Museum of the Academy of Science, U.S.S.R., 1849/2027a.
- 11-14. *Tolmachovia* sp. (p. 62).
Ventral, anterior, posterior, and left-lateral views ($\times 3$). Ordovician of Portugal. BM PL 4434.

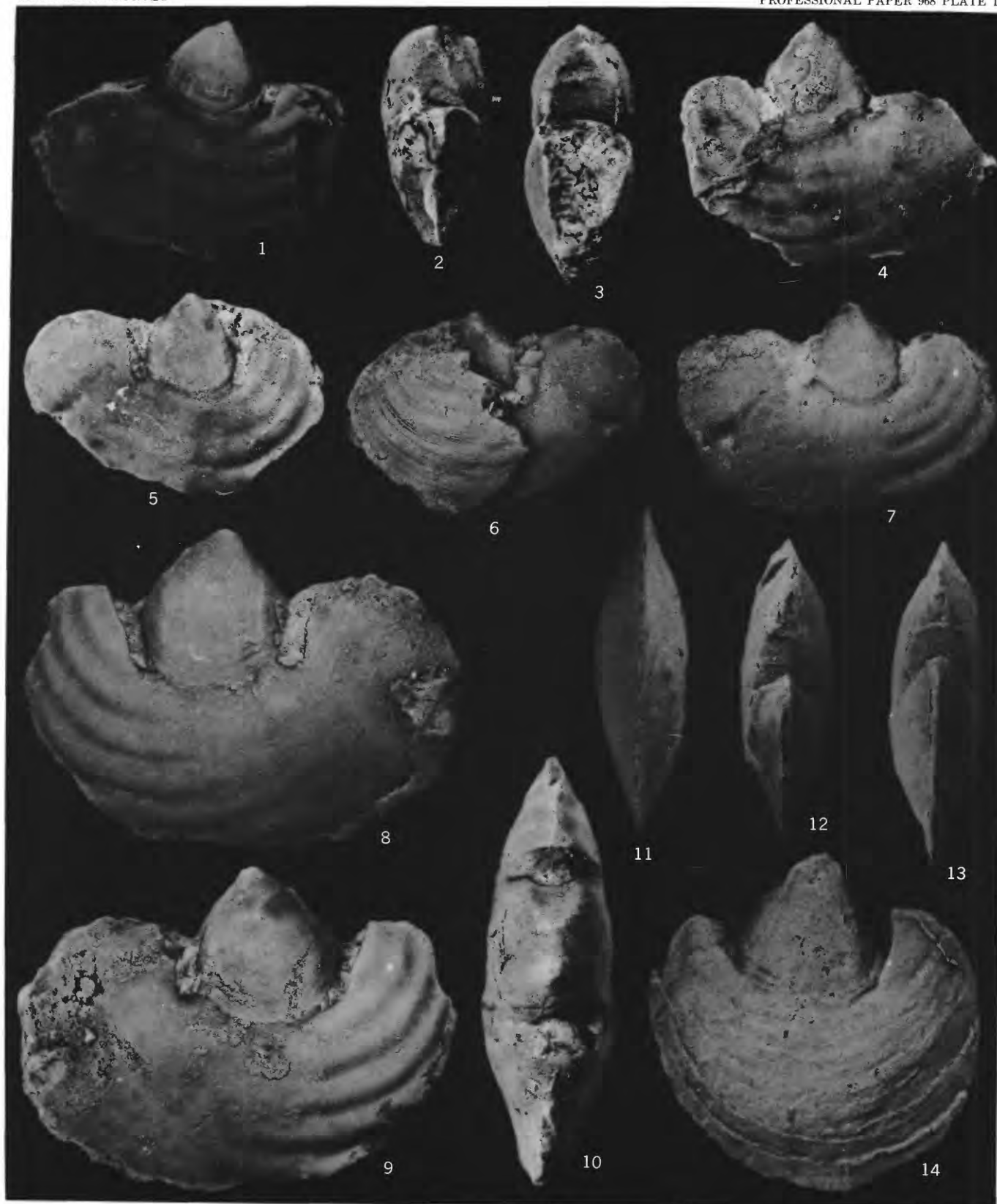
*TOLMACHOVIA*

PLATE 17

- FIGURES 1-7, 9-11. *Tolmachovia concentrica* Howell and Kobayashi, 1936 (p. 62).
- 1, 2, 11. Right-lateral, dorsal, and left-lateral views of paratype ($\times 5$). Horizon and locality the same as in plate 16, figures 1-4. Geological Museum of the Academy of Science, U.S.S.R., 1849/2027b.
 - 3, 4. Right-lateral and anterior views of a previously unfigured paratype ($\times 5$). Horizon, locality, and museum number the same as in plate 16, figures 1-4.
 - 5, 6. Right-lateral and anterior views of a previously unfigured paratype ($\times 5$). Horizon, locality, and museum number the same as in plate 16, figures 1-4.
 - 7. Posterior view of a previously unfigured paratype ($\times 5$). Horizon, locality, and museum number the same as in plate 16, figures 1-4.
 - 9. Anterior view of previously unfigured paratype ($\times 5$). Horizon, locality, and museum number the same as in plate 16, figures 1-4.
 - 10. Posterior view of a previously unfigured paratype ($\times 5$). Horizon, locality and museum number the same as plate 16, in figures 1-4.
 - 8. *Anabarella plana* Vostokova (p. 33).
Left-lateral view of a specimen from the Tommotian (Lower Cambrian) rocks of Siberia ($\times 12$). Photograph kindly provided by S. C. Matthews and Robin Goodwin, University of Bristol, Bristol, England.



TOLMACHOVIA AND ANABARELLA

PLATE 18

FIGURES

- 1-21. *Anisotechnophorus nuculitiformis* (Cleland), 1900 (p. 60).
 - 1-6. Left-lateral ($\times 3$), right-lateral ($\times 3$), posterior, anterior, ventral, and dorsal ($\times 5$) views of lectotype. Cleland (1900, p. 21) gave the horizon and locality as: "Calciferous, Fort Hunter Section, New York" (Lower Ordovician). PRI 5080.
 - 7-10. Left-lateral, right-lateral, dorsal, and posterior views ($\times 5$). The museum label gives the horizon and locality as: "Ozarkic (Little Falls), Fort Hunter, New York" (Upper Cambrian?). YU 2580.
 - 11, 12. Dorsal and anterior views ($\times 5$). Horizon, locality, and museum number the same as in figures 7-10 above.
 13. Right-lateral view of paralectotype ($\times 5$). Horizon and locality the same as in figures 1-6 above. PRI 5079.
 14. Posterior view ($\times 5$). Horizon, locality, and museum number the same as in figures 7-10 above.
 15. Left-lateral view of paralectotype ($\times 5$). Horizon, locality, and museum number the same as in figure 13 above.
 16. Dorsal view of paralectotype ($\times 5$). Horizon, locality, and museum number the same as in figure 13 above.
 17. Dorsal view ($\times 5$). Horizon, locality, and museum number the same as in figures 7-10 above.
 18. Right-lateral view ($\times 5$). USGS loc. 7098-CO. *Missisquoia* Zone (Lower Ordovician) upper Whitehall Formation, Skene Mountain, N.Y. (Taylor and Halley, 1974, p. 33). USNM 209375.
 19. Dorsal view of paralectotype ($\times 5$). Horizon, locality, and museum number the same as in figure 13 above.
 20. Dorsal view ($\times 5$). The museum label gives the horizon and locality as: "Little Falls, Fort Hunter, N.Y." (Upper Cambrian?). USNM 209376.
 21. Posterior view ($\times 5$). Horizon and locality the same as in figure 20 above. USNM 209377.
- 22-25. *Ischyrinia winchelli* Billings, 1866 (p. 62).
 22. Right-lateral view ($\times 2$). English Head Formation (Upper Ordovician), 1 mile west of White Cliff, Anticosti Island, Quebec, Canada. YU 3063/13.
 - 23, 24. Right-lateral and posterior views of lectotype ($\times 2$). The museum label reads: "'English Head'=Vaureal, Upper Ordovician, Macasty Bay, Anticosti Island," Quebec, Canada. GSC 2114a.
 25. Right-lateral view of paralectotype ($\times 2$). Horizon and locality the same as in figures 23, 24 above. GSC 2114.

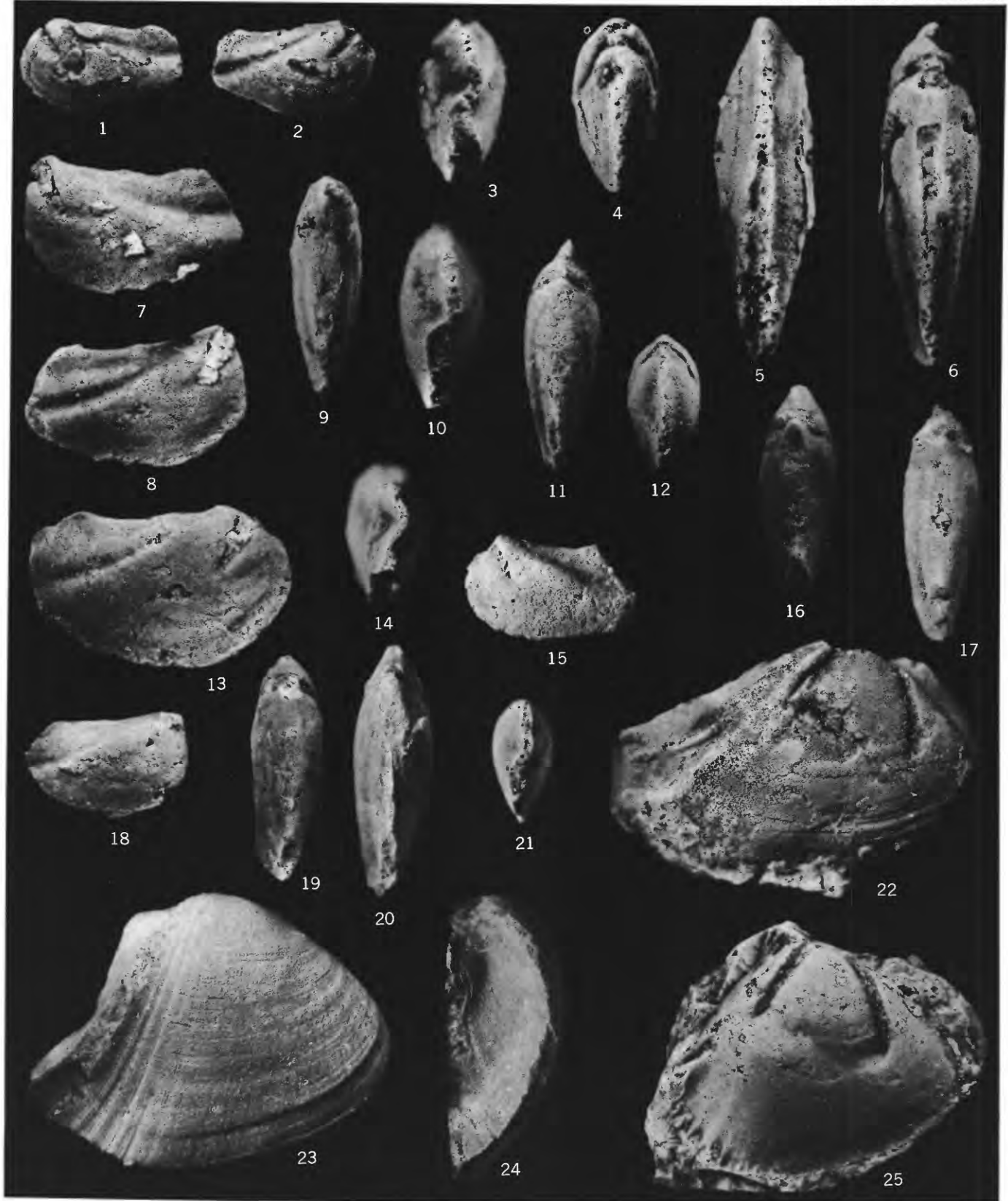
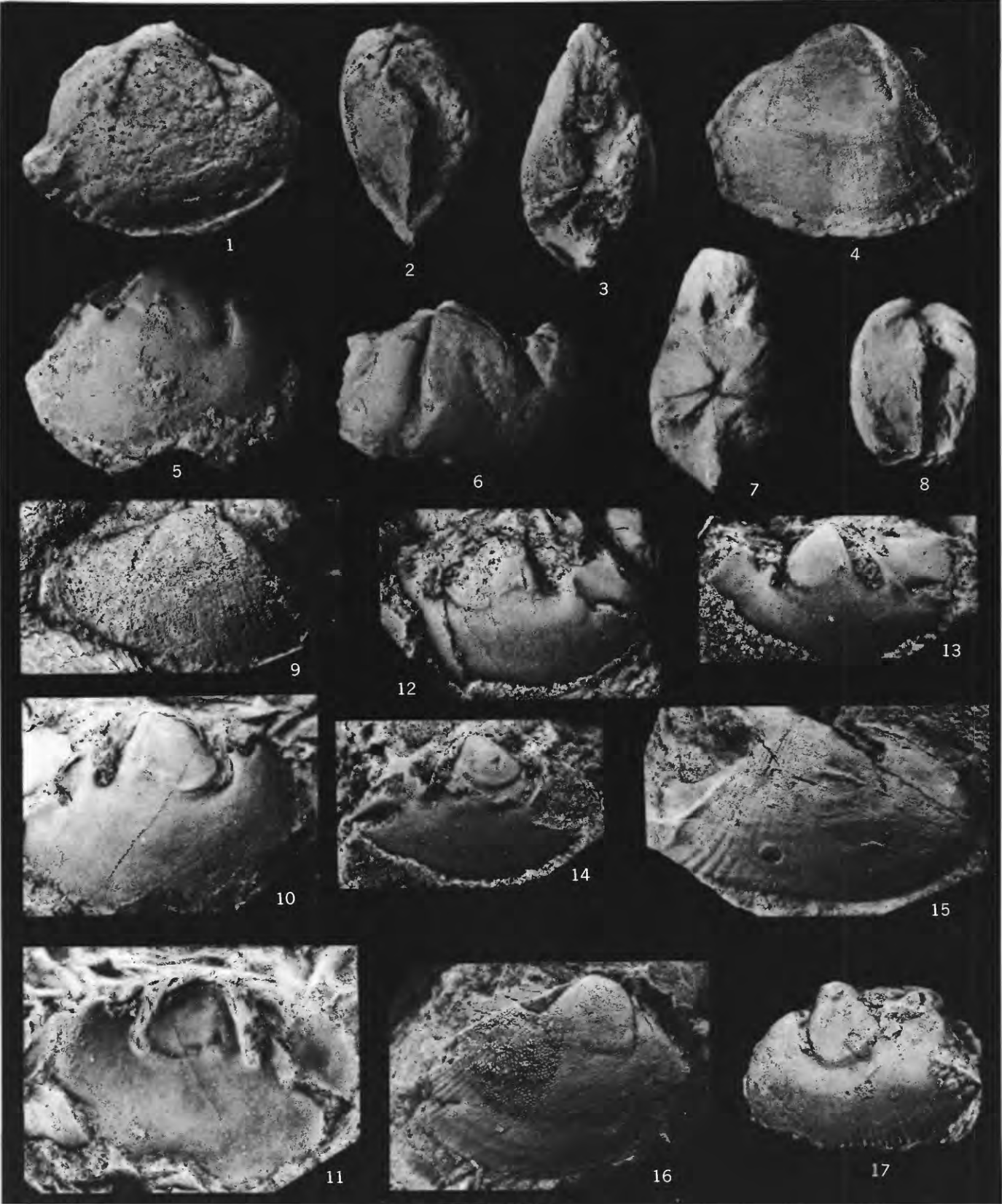
*ANISOTECHNOPHORUS AND ISCHYRINIA*

PLATE 19

FIGURES

- 1-8. *Ischyrinia winchelli* Billings, 1866 (p. 62).
 - 1-4. Right-lateral, posterior, dorsal, and left-lateral views ($\times 2$). English Head Formation (Upper Ordovician), east side Little Macasty Bay, Anticosti Island, Quebec, Canada. YU 3063/10.
 5. Right-lateral view ($\times 2$). English Head Formation (Upper Ordovician), cliff 1 mile west of White Cliff, north shore, Anticosti Island, Quebec, Canada. YU 748.
 - 6-8. Left-lateral, dorsal, and posterior views ($\times 2$). The museum label lists no formation; presumably the specimen is Late Ordovician in age. North side Anticosti Island, Quebec, Canada. YU 3063/30.
- 9, 15, 16. *Ischyrinia* sp. (p. 64).
 9. Left-lateral view ($\times 3$). Whitehead Formation (Upper Ordovician), road at Amphitheater, west side Mt. St. Anne, Percé, Quebec, Canada. USNM 209372.
 - 15, 16. Two specimens, both right valves ($\times 2$). The museum label reads: "Quarry at Evan's Saw Mills, North Gate, Haverfordwest" Wales (Ordovician). SM A. 30893-30894.
- 10-14. *Ischyrinia norvegica* Soot-Ryen, 1960 (p. 64).
 - 10, 11. Right-lateral view of holotype and latex replica of same ($\times 3$). Middle Caradocian (Middle Ordovician), Furuberget, Hamar, Norway, UO 38267. Replica, USNM 209373.
 12. Left-lateral view of previously unfigured paratype ($\times 3$), on same slab as holotype. Horizon, locality, and museum number the same as in figures 10, 11 above.
 13. Latex replica of left valve of paratype ($\times 3$). Horizon and locality the same as in figures 10, 11 above. UO 37861. Replica USNM 209374.
 14. Right-lateral view of previously unfigured paratype ($\times 3$). Horizon, locality, and museum number the same as in figure 13 above.
17. *Ischyrinia?* (p. 64).
 - Left-lateral view ($\times 5$). The museum label gives the horizon and locality as: "Middle Ordovician, boulder on right bank of Moyero River, 6 miles above mouth of Ukdama River, Khatanga-Anabar region, northern Siberia." Geological Museum Academy of Science, U.S.S.R. 1849/2027.

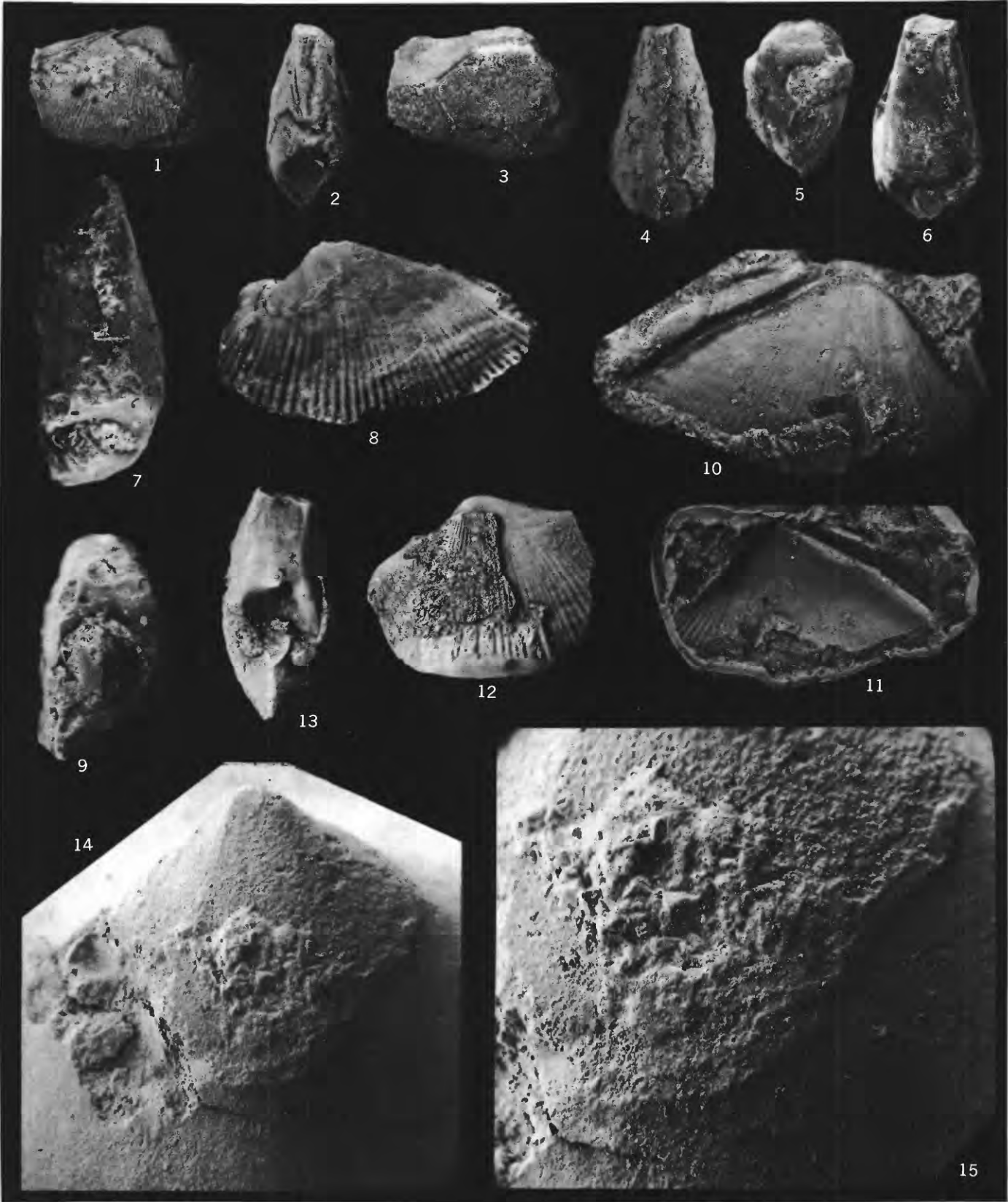


ISCHYRIA

PLATE 20

FIGURES

- 1-15. *Pseudotechnophorus typicalis* Kobayashi, 1933 (p. 65).
- 1, 2. Left-lateral and dorsal views ($\times 3$) of a replica of the specimen figured by Kobayashi (1933, pl. 9, fig. 8). Wanwankou Dolomite (Lower Ordovician), Wan-wan-kou in the Niuhsintai Basin, south Manchuria. USNM 209371.
- 3-6. Left-lateral, ventral, posterior, and dorsal views ($\times 3$). Horizon and locality the same as in figure 1, 2 above. YU 28148.
- 7-9. Dorsal, right-lateral, and posterior views ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 94039.
- 10, 11. Left-lateral view ($\times 4$) and latex replica of same ($\times 3$). Horizon and locality the same as in figures 1, 2 above. MCZ 4426.
- 12-15. Right-lateral view ($\times 3$), dorsal view showing protoconch ($\times 3$), enlargement of anterior face of protoconch showing larval musculature ($\times 60$), further enlargement of larval musculature ($\times 100$). Horizon and locality the same as in figure 1, 2 above. MCZ 6907.

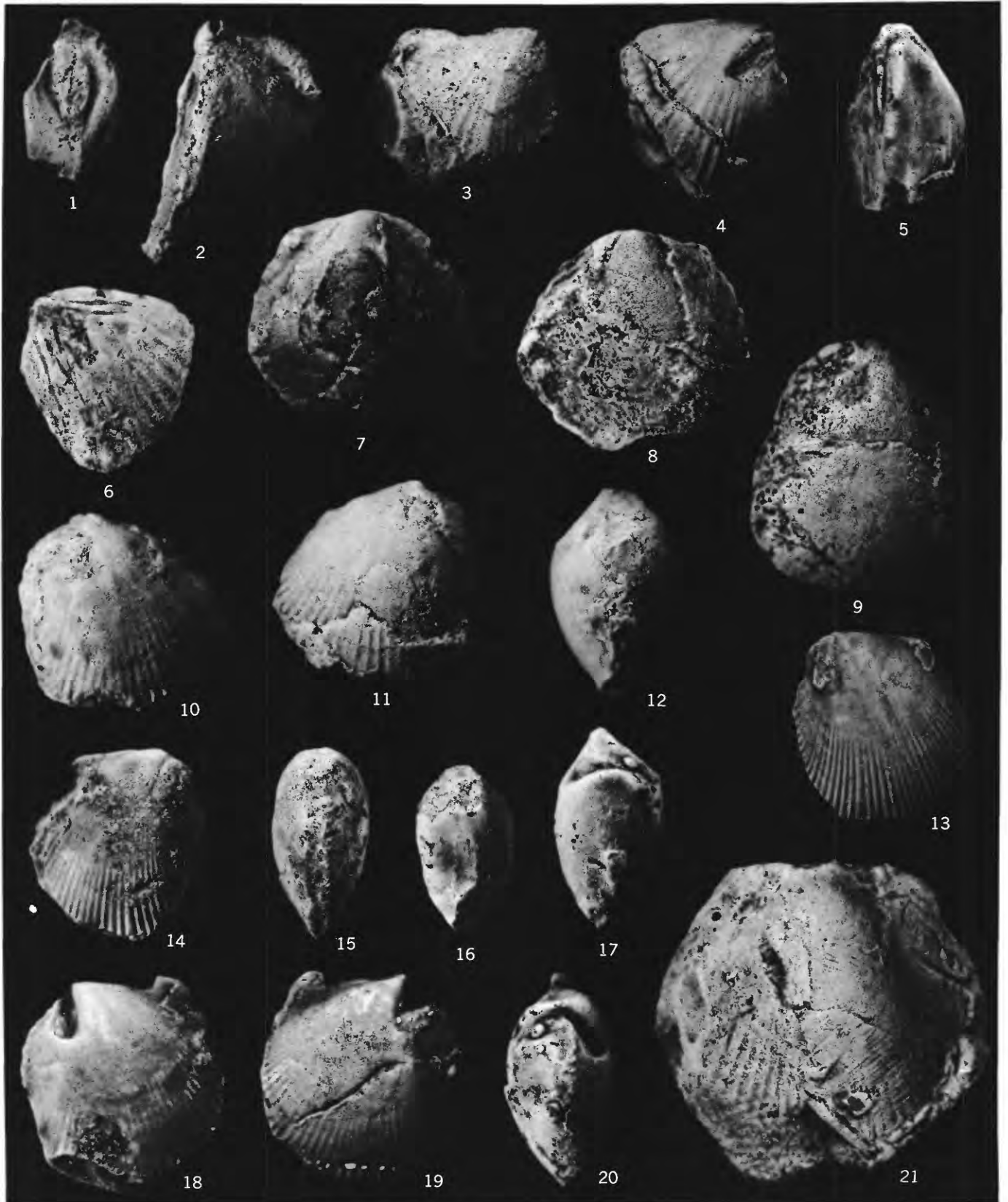


PSEUDOTECHNOPHORUS

PLATE 21

FIGURES

- 1, 2. *Pseudoeuchasma typica* Kobayashi, 1933 (p. 77).
Posterior and right-lateral views ($\times 4$) of replicas of holotype (Kobayashi, 1933, pl. 9, figs. 10a, b). Wanwankou Dolomite, Wan-wan-kou in the Niuhsintai Basin, south Manchuria (Lower Ordovician). USNM 94011.
3. *Wanwanoidea trigonalis delicata* Kobayashi, 1933 (p. 69).
Right-lateral view ($\times 4$) of replica of holotype (Kobayashi, 1933, pl. 8, fig. 6). Horizon and locality the same as in figures 1, 2 above. USNM 209366.
- 4-6. *Wanwanoidea trigonalis* Kobayashi, 1933 (p. 69).
Right-lateral, dorsal, and left-lateral views ($\times 4$) of replica of syntype (Kobayashi, 1933, pl. 9, fig. 3). Horizon and locality the same as in figure 1, 2 above. USNM 209367.
- 7, 8. *Wanwanella tumida* Kobayashi, 1933 (p. 68).
Right-lateral and left-lateral views ($\times 8$) of replica of holotype (Kobayashi, 1933, pl. 7, fig. 10). Horizon and locality the same as in figures 1, 2 above. USNM 209368.
- 9-16. *Wanwanella striata* Kobayashi, 1933 (p. 68).
9. Replica of syntype (Kobayashi, 1933, pl. 7, fig. 7) ($\times 5$). Horizon and locality the same as in figures 1, 2 above. USNM 209369.
10-12. Left-lateral, right-lateral, and dorsal view ($\times 5$). Horizon and locality the same as in figures 1, 2 above. MCZ 4425.
13-16. Left-lateral, right-lateral, anterior, and dorsal views ($\times 5$). Horizon and locality the same as in figures 1, 2 above. YU 28149.
- 17-20. *Wanwanella striata auriculata* Kobayashi, 1933 (p. 68).
Dorsal, left-lateral, right-lateral, and anterior views ($\times 5$) of replica of holotype (Kobayashi, 1933, pl. 7, fig. 6) Horizon and locality the same as in figures 1, 2 above. USNM 209370.
21. *Wanwanella? alta* (Kobayashi), 1933 (p. 68).
Replica of holotype ($\times 4$). Horizon and locality the same as in figures 1, 2 above. USNM 94045.

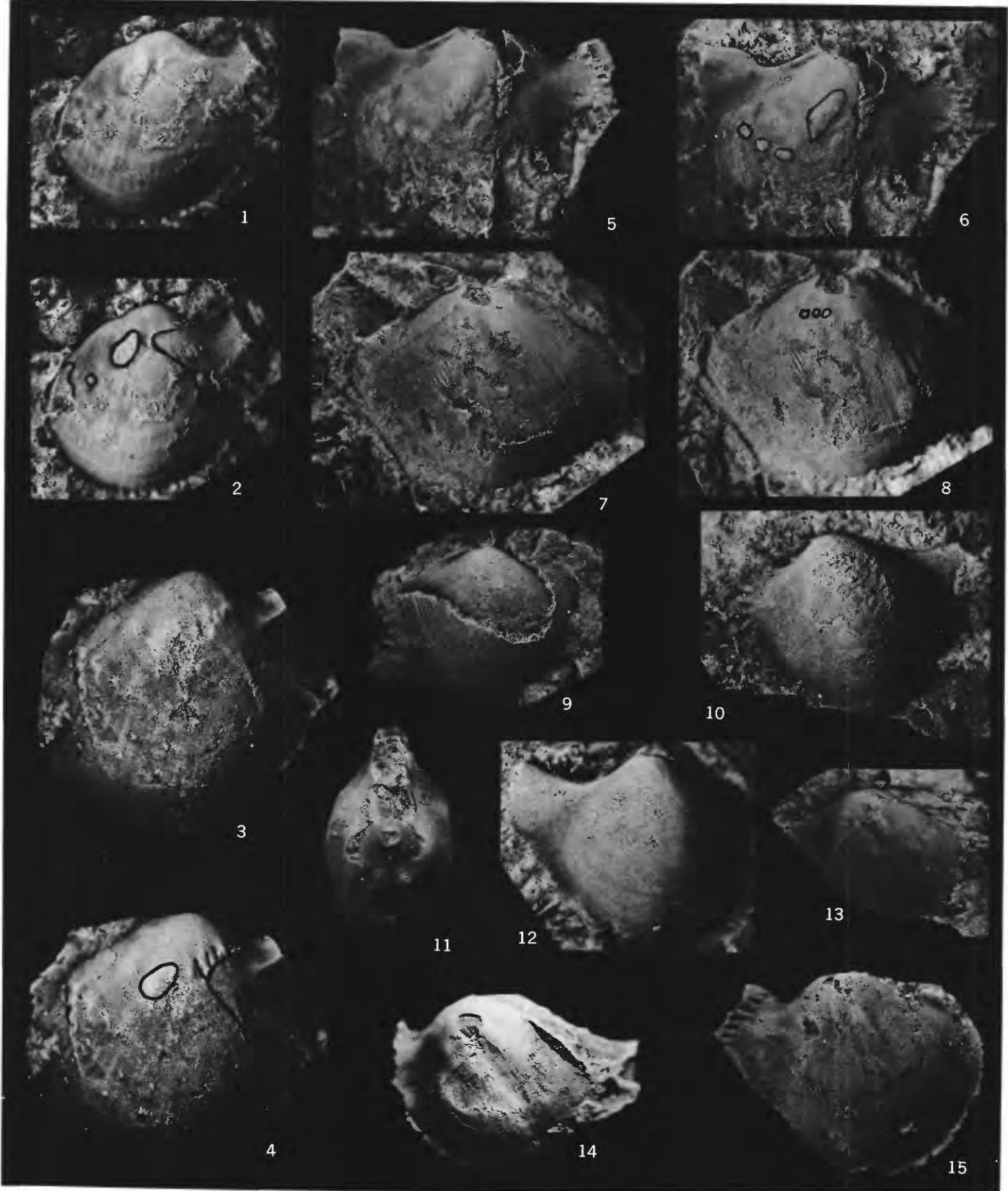


PSEUDOEUCHASMA, WANWANOIDEA, AND WANWANELLA

PLATE 22

FIGURES

- 1-15. *Eopteria ventricosa* (Whitfield), 1886 (p. 66).
1. Right-lateral view of internal mold showing muscle impressions ($\times 3$). 2, Same specimen, same view and magnification, muscle scars outlined in ink. Fort Cassin Limestone (Lower Ordovician), Fort Cassin, Vt. USNM 209357.
3. Right-lateral view of internal mold showing muscle scars ($\times 3$). 4, Same specimen, same view and magnification, muscle scars outlined in ink. Horizon and locality the same as in figures 1, 2 above. USNM 209358.
5. Right-lateral view of internal mold showing muscle scars ($\times 3$). 6, Same specimen, same view and magnification, muscle scars outlined in ink. Horizon and locality the same as in figures 1, 2 above. USNM 209359.
7. Left-lateral view of internal mold showing three small muscle markings ($\times 3$). These may be separate muscles or simply the muscle tracts left by the dorsal part of the pallial sinus, as suggested by the specimen shown in figures 3, 4 above. 8, Same specimen, same view and magnification, the muscle markings outlined in ink. Horizon and locality the same as in figures 1, 2 above. USNM 209360.
9. Left-lateral view of a shelled specimen ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 209361.
10. Left-lateral view showing marginal denticles ($\times 5$). Horizon and locality the same as in figures 1, 2 above. USNM 209362.
11. Dorsal view of lectotype showing internal mold of protoconch ($\times 3$). Horizon and locality the same as in figures 1, 2 above. AM 492.
12. Left-lateral view ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 209363.
13. Left-lateral view showing anterior pallial sinus ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 209364.
14. Left-lateral view of paralectotype ($\times 3$). Horizon and locality the same as in figures 1, 2 above. AM 492.
15. Left valve showing marginal denticles ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 209365.



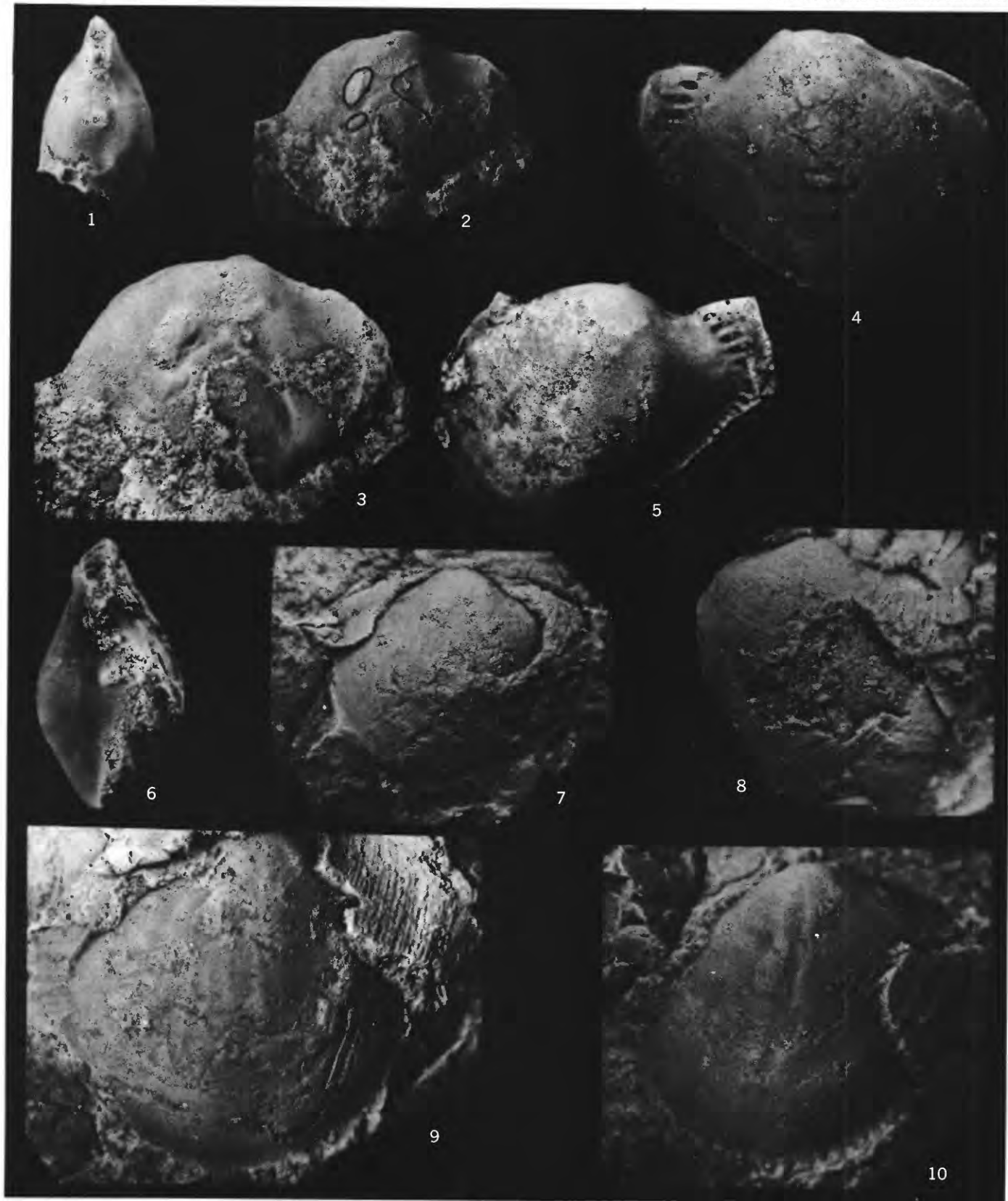
EOPTERIA

PLATE 23

FIGURES

1-10. *Eopteria ventricosa* (Whitfield), 1886 (p. 66).

1. Dorsal view showing internal mold of protoconch ($\times 3$). 2. Right-lateral view of internal mold, with muscle scars outlined in ink ($\times 3$). 3. Same specimen, same view showing muscle scars ($\times 5$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209349.
4. Left valve showing anterior marginal denticles ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209350.
5. Right valve internal mold showing marginal denticles and protoconch ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209351.
6. Dorsal view showing internal mold of protoconch ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209352.
7. Right-lateral view ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209353.
8. Right-lateral view ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209354.
9. Right lateral view ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209355.
10. Right-lateral view ($\times 3$). Horizon and locality the same as on plate 22, figures 1, 2. USNM 209356.

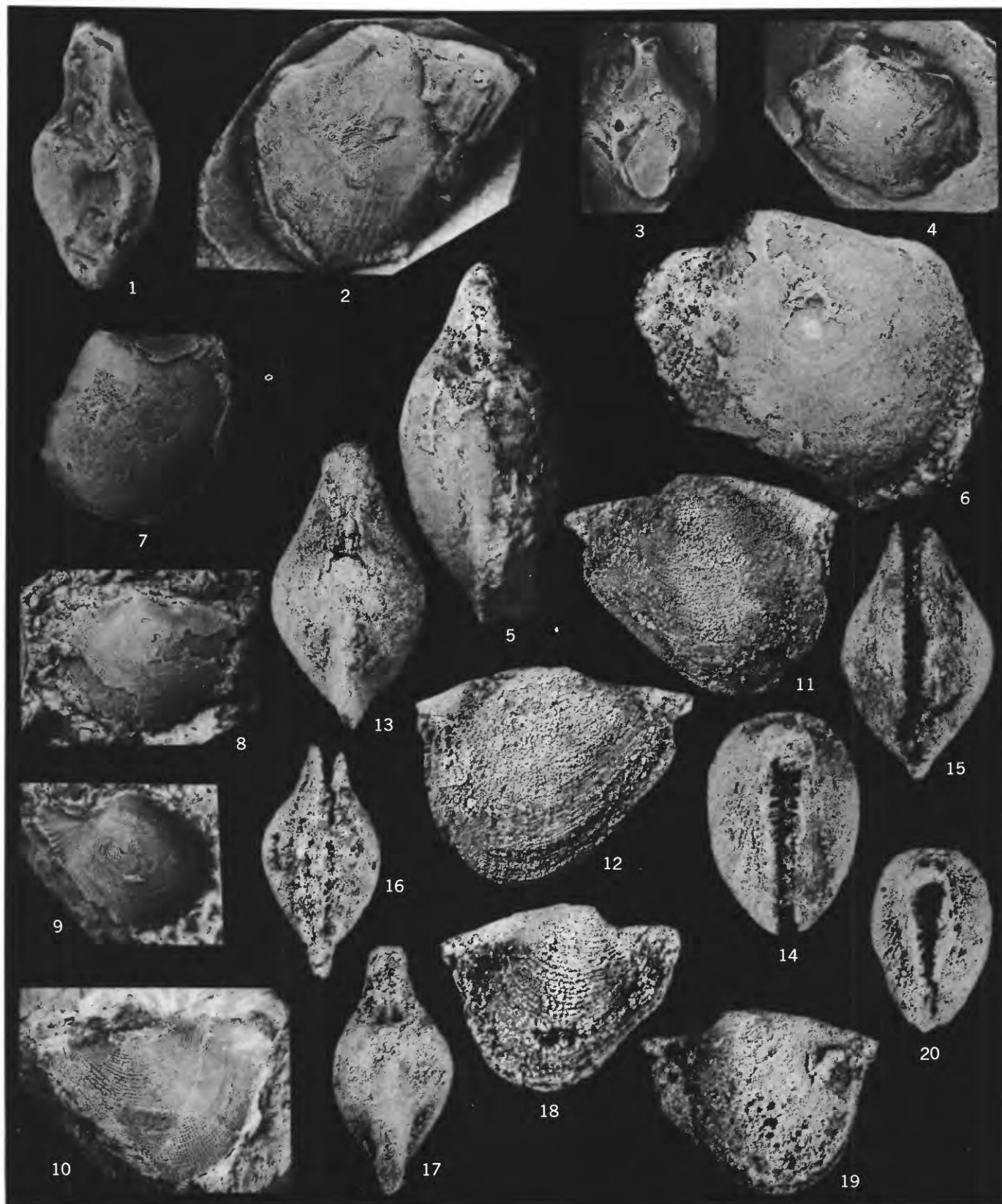


EOPTERIA

PLATE 24

FIGURES

- 1, 2. *Eopteria flora* Kobayashi, 1933 (p. 66).
Dorsal and right-lateral views ($\times 3$) of replicas of the holotype. Wanwankou Dolomite (Lower Ordovician), Wan-wan-kou in the Niuhsintai Basin, south Manchuria. USNM 94042.
- 3, 4. *Eopteria obsolata* Kobayashi, 1933 (p. 66).
Dorsal and right(?) -lateral views of replicas of the holotype ($\times 3$). Horizon and locality the same as in figures 1, 2 above. USNM 94041.
- 5, 6, 11-20. *Eopteria richardsoni* Billings, 1865 (p. 66).
5, 6. Dorsal and left-lateral views of holotype ($\times 3$). The museum label lists the horizon and locality as: "Beekmantown, St. Antoine de Tilly, Quebec," Canada (Lower Ordovician). GSC 756.
11-15. Left-lateral, right-lateral, dorsal, anterior, and ventral views ($\times 5$). Smithville Formation (Lower Ordovician), 1.5 miles north of Smithville, Ark. USNM 162781.
16-20. Ventral, dorsal, right-lateral, left-lateral, and anterior views ($\times 5$). Horizon and locality the same as in figures 11-15 above. USNM 162782.
- 7-10. *Eopteria* cf. *E. richardsoni* Billings, 1865 (p. 66).
7. Left-lateral view ($\times 3$). USGS loc. D-1973-CO, Antelope Valley Limestone, from bioherm 60-65 feet above base of bioherm, Meiklejohn Peak section, Nevada (Whiterockian, Lower Ordovician?). R. J. Ross collector. USNM 209347.
8. Left-lateral view ($\times 3$). U.S.G.S. loc. D-1990-CO, Antelope Valley Limestone, from about 45 feet above base of bioherm, Meiklejohn Peak section, Nevada (Whiterockian, Lower Ordovician?). R. J. Ross collector. USNM 167236.
9. Left-lateral view ($\times 3$). Horizon and locality the same as in figure 7 above. USNM 209348.
10. Left-lateral view ($\times 3$). USGS loc. D-1966-CO, Antelope Valley Limestone, 50 feet above base of bioherm, Meiklejohn Peak section, Nevada (Whiterockian, Lower Ordovician?). R. J. Ross collector. USNM 162780.



EOPTERIA

PLATE 25

FIGURES

1. *Eopteria* sp. (p. 66).
Right-lateral view ($\times 1$). Cotter Dolomite or Powell Formation (Lower Ordovician), Graceland mines, 3–5 miles northwest of Smithville, Ark. USNM 209335.
- 2–19. *Eopteria richardsoni* Billings, 1865 (p. 66).
 - 2–4. Right-lateral, dorsal, and left-lateral views ($\times 3$). Honeycut Formation (Lower Ordovician), *Ceratopea capuliformis* Zone, about 2.5 miles airline, N. 1° W. from headquarters J. F. Barnes ranch, northwest of Ellenburger Hills, southeastern San Saba County, Tex. USNM 127900.
 5. Left-lateral view ($\times 5$). Horizon and locality the same as on plate 24, figures 11–15. USNM 209336.
 6. Right-lateral view showing anterior marginal denticles ($\times 3$). The museum label gives the horizon and locality as: "Jefferson City chert (residual), Lower Ordovic, 50 yds. N of U.S. Highway No. 60, $1\frac{1}{4}$ mi. east of Birch Tree, Mo." AM 29322.
 7. Anterior view showing gape and marginal denticles ($\times 4$). Canadian (Lower Ordovician), 3 miles south of Bolivar, Mo. (Jefferson City Dolomite?). USNM 209337.
 - 8–10. Anterior, right-lateral, and posterior views of an internal mold ($\times 4$). Horizon and locality the same as in figure 7 above. USNM 209338.
 11. Dorsal view showing protoconch ($\times 3$). Smithville Formation (Lower Ordovician), 1.5 miles northeast of Smithville, Ark., on road to Imboden. USNM 209339.
 12. Right-lateral view ($\times 3$). Canadian (Lower Ordovician), at old sinkhole in railroad cut, Lutesville, Mo. USNM 209340.
 13. Left-lateral view ($\times 4$). Scenic Drive Formation of Flower (1964), Franklin Mts., Scenic Drive, El Paso, Tex. R. H. Flower collector. USNM 209341.
 14. Anterior view showing gape ($\times 3$). Horizon and locality the same as in figure 11 above. USNM 209342.
 15. Latex replica of external mold ($\times 4$). Cotter Dolomite (Lower Ordovician), on road between Swan and Elkhorn Creeks, short distance above confluence, near Chadwick, Mo., USNM 209343.
 - 16, 17. Right-lateral and dorsal views ($\times 4$). Canadian (Lower Ordovician), hill just west of Turkey Creek on road from Humansville to Sacville, Mo., 19 miles west of Humansville. USNM 209344.
 18. Right-lateral view ($\times 4$). Horizon, locality, and collector the same as in figure 13 above. USNM 209345.
 19. Anterior view ($\times 4$). Horizon and locality the same as in figures 16, 17 above. USNM 209346.

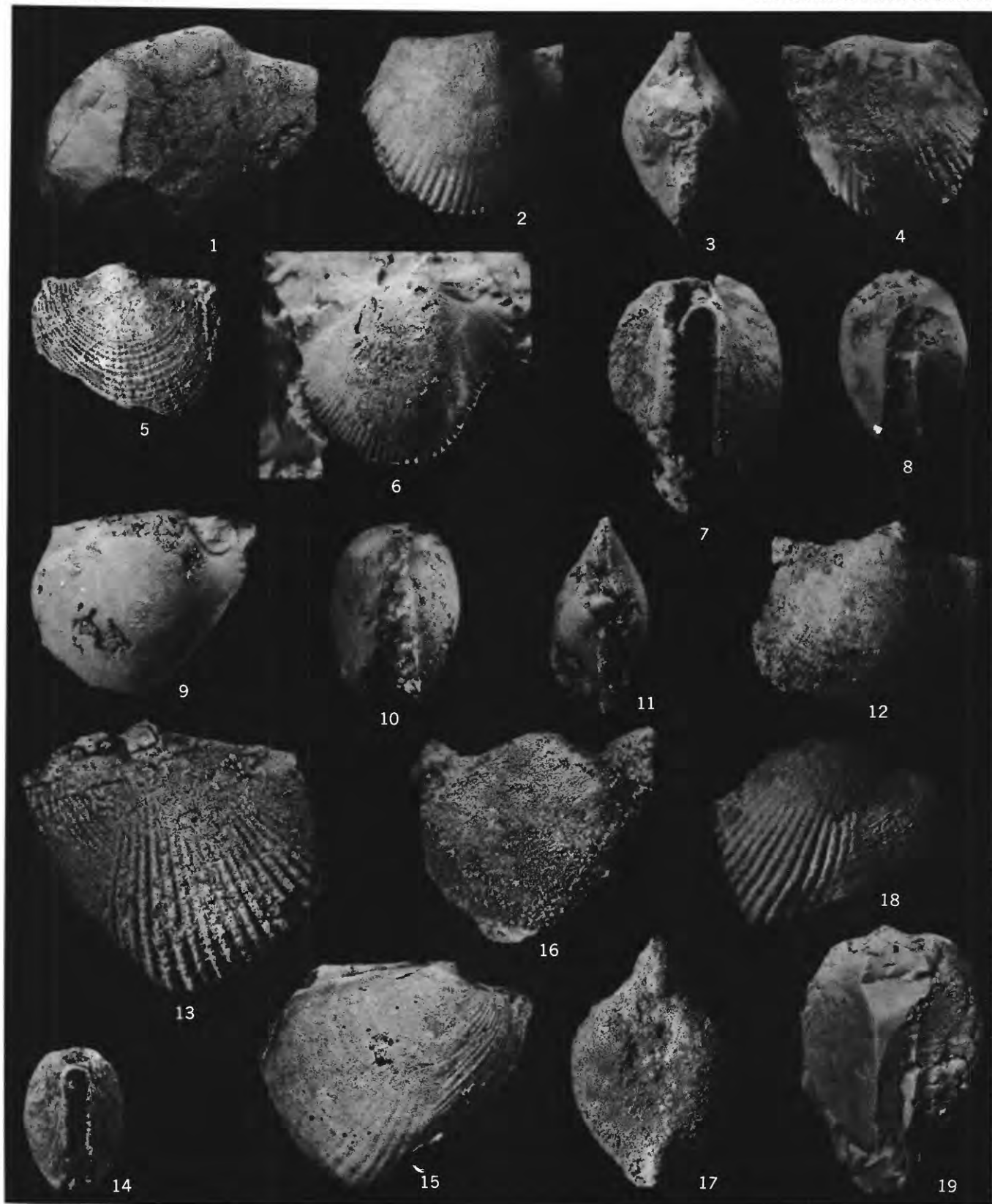
*EOPTERIA*

PLATE 26

FIGURES

- 1-11. *Eopteria richardsoni* Billings, 1865 (p. 66).
 - 1-4. Right-lateral, left-lateral, ventral, and anterior views ($\times 3$). Canadian (Lower Ordovician), west side of Honey Creek, Llano County, Tex. USNM 209325.
 5. Dorsal view ($\times 3$). Canadian (Lower Ordovician), 1.5 miles east Buffalo, Mo. USNM 209326.
 6. Anterior view ($\times 3$). Horizon and locality the same as on plate 25, figure 15. USNM 209327.
 7. Dorsal view ($\times 3$). Horizon and locality the same as on plate 25, figure 15. USNM 209328.
 8. Anterior view ($\times 3$). Horizon and locality the same as on plate 25, figure 15. USNM 209329.
 9. Left-lateral view ($\times 4$). Horizon, locality, and collector the same as in plate 25, figure 13. USNM 209330.
 - 10, 11. Internal and external views showing denticles and ornament ($\times 4$). Smithville Formation (Lower Ordovician), Iowa mine, 2 miles north of Smithville, Ark. USNM 209331.
- 12-18. *Eopteria conocardiformis* n. sp. (p. 66).
 - 12-15. Anterior, dorsal, right-lateral and left-lateral views of holotype ($\times 5$). Little Oak Limestone (Middle Ordovician), quarry about 2 miles north of Pelham, Ala. USNM 209332.
 16. Right-lateral view of paratype ($\times 3$). High Bridge Group (Middle Ordovician), High Bridge, Ky. USNM 209333.
 - 17, 18. Posterior and right-lateral views ($\times 6$). Little Oak Limestone (Middle Ordovician), intersection of Bailey Gap Road with main road, 1.75 miles northeast of New Hope Church, Ala. USNM 209334.

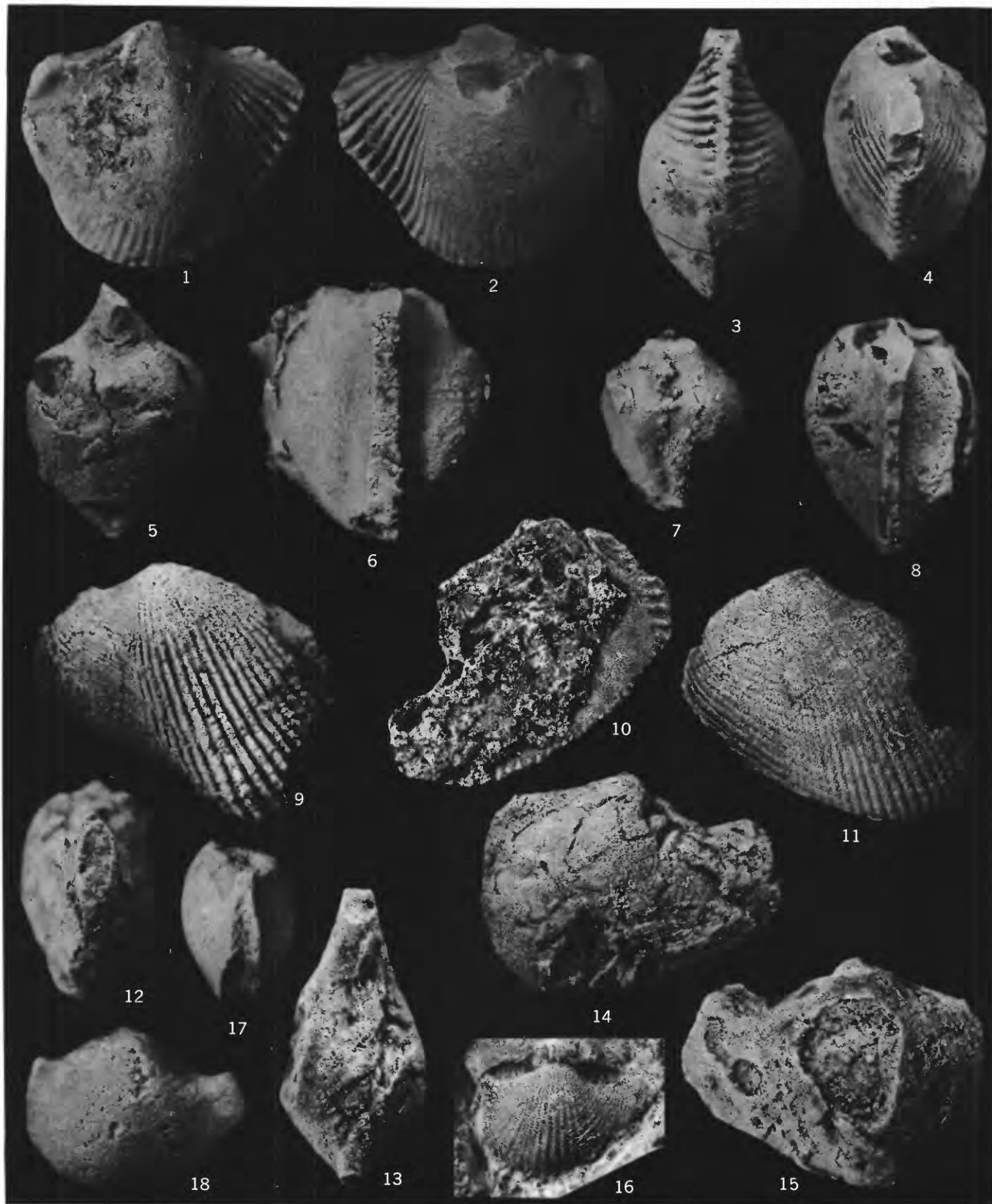
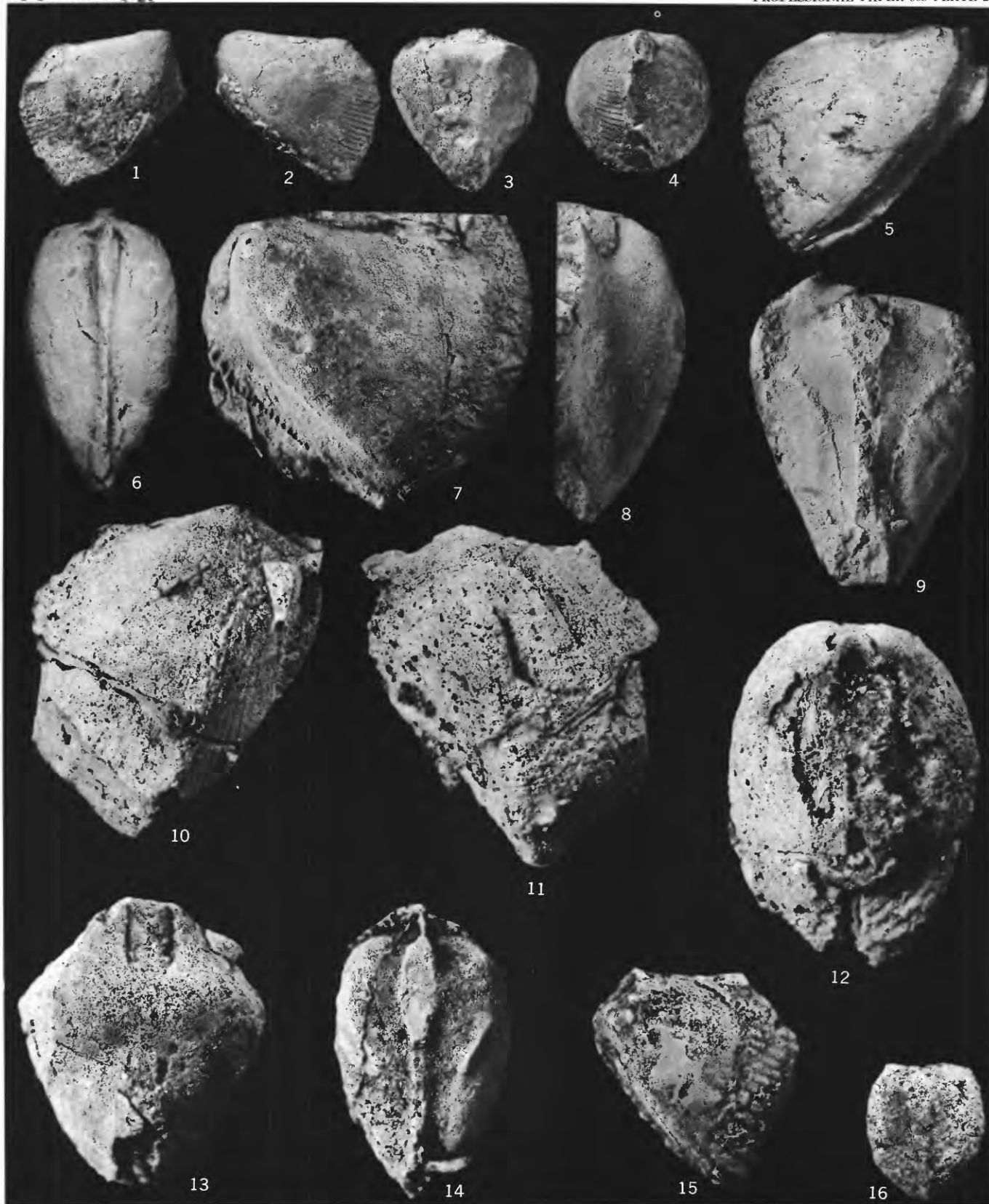
*EOPTERIA*

PLATE 27

FIGURES

- 1-16. *Euchasma blumenbachii* (Billings), 1859 (p. 67).
 - 1-4. Right-lateral, left-lateral, dorsal, and posterior views ($\times 2$) of lectotype. The museum label gives the horizon and locality as: "Beekmantown (Romaine), Mingan Islands, Quebec," Canada (Lower Ordovician). GSC 455.
 - 5, 6. Right-lateral and anterior views of Butts' hypotype (1941). The museum label lists the horizon and locality as: "Beekmantown, Brushy Hills, west of Lexington, Virginia" (Lower Ordovician). USNM 97333.
 - 7, 8. Left-lateral and anterior views of paralectotype ($\times 2$). Horizon and locality the same as in figures 1-4 above. GSC 455a.
 9. Anterior view showing the pallial line with an anterior pallial sinus ($\times 1.5$). Graveyard, hillside immediately northeast of lower cove, south side St. George Peninsula, Newfoundland. St. George Group (Lower Ordovician). R. H. Flower collector. GSC 41173.
 - 10-13. Right-lateral, left-lateral, anterior, and dorsal views ($\times 2$). Middle of Scenic Drive Formation of Flower (1964), nameless canyon west of Ranger Peak, Franklin Mts., northwest edge of El Paso, Tex. (Lower Ordovician). Collected by R. H. Flower. USNM 209321.
 14. Anterior view ($\times 2$). Upper Canadian (Lower Ordovician), Brushy Hills Chert, near Lexington, Va. USNM 209322.
 15. Left-lateral view ($\times 2$). Horizon and locality the same as in figure 14 above. USNM 209323.
 16. Anterior view ($\times 3$). Luke Hill Limestone (Lower Ordovician), ridge east of Phillipsburg, Quebec, Canada. USNM 209324.



EUCHASMA

PLATE 28

FIGURES

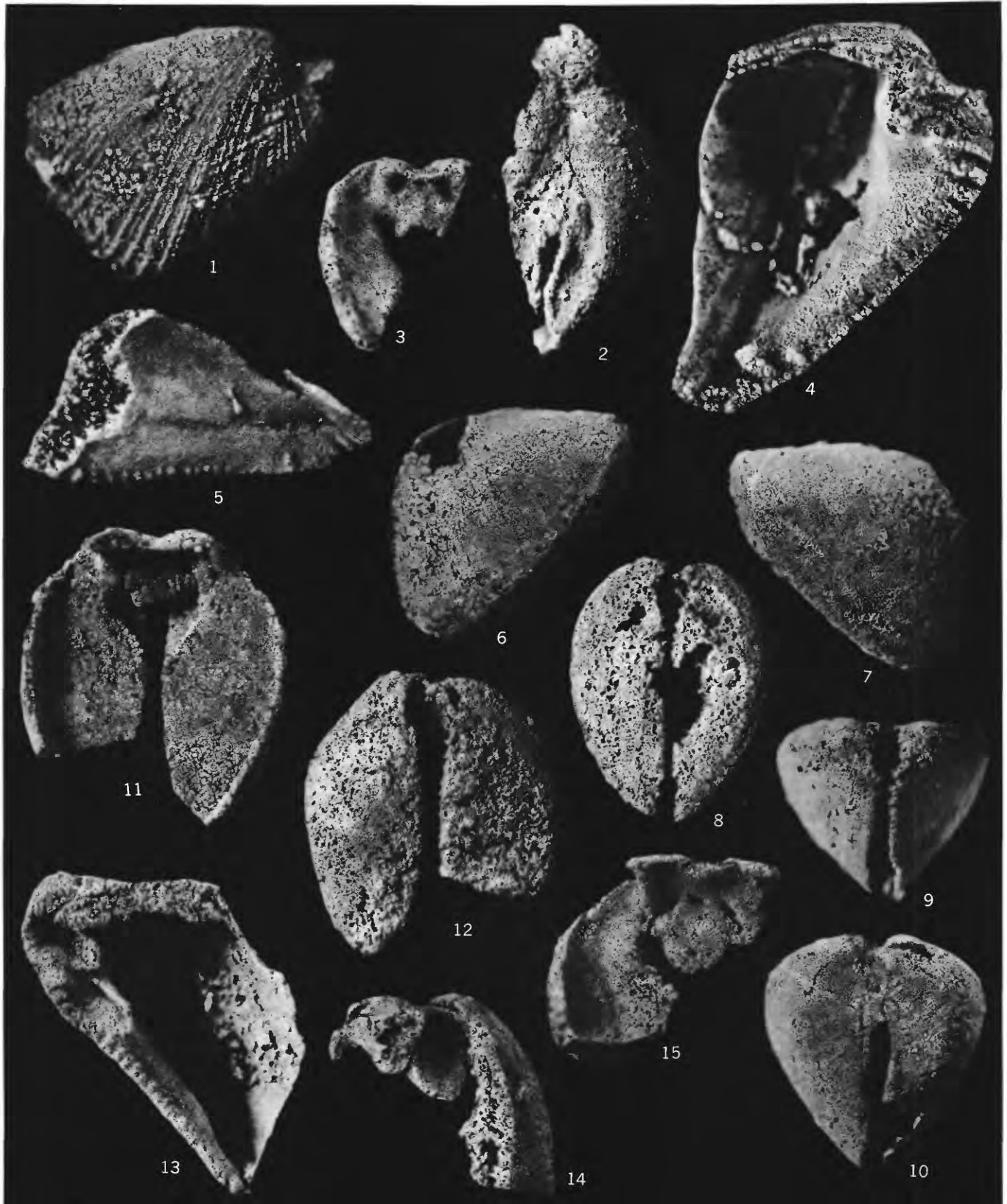
- 1-3. *Euchasma?* sp. (p. 68).
Right-lateral, dorsal, and anterior views of latex replica ($\times 2$). Høllonda Limestone (Whiterockian, Lower Ordovician), Trotland Farm, Trondheim, Norway (Neuman and Bruton, 1974). UO 89105. Replica USNM 209418.
- 4-7. *Euchasma wanwanense* (Kobayashi), 1933 (p. 68).
Right-lateral, left-lateral, anterior, and dorsal views of replica of holotype ($\times 3$). Wanwankou Dolomite, Wan-wan-kou in the Niuhsintai Basin, South Manchuria (Lower Ordovician). USNM 209316.
- 8-11. *Euchasma shorinense* (Kobayashi), 1933 (p. 67).
Dorsal, right-lateral, left-lateral, and anterior views of replica of holotype ($\times 3$). Shorin Bed of Shorinri, near Kenjiho Koshu-gun, Kokai-do in northern Korea (Lower Ordovician). USNM 209317.
- 12-18. *Euchasma jonesi* n. sp (p. 67).
12-15. Posterior, dorsal, right-lateral, and anterior views of holotype ($\times 2$). Lower shelly facies of the Setul Formation, off south point of Pulau Langgun, Langkawi Islands, Malaysia (Lower Ordovician). USNM 162790.
16. Anterodorsal part of a broken shell showing the circular part of the anterior gape (paratype, $\times 2.5$). Horizon and locality the same as in figures 12-15 above. USNM 209318.
17. Anterior part of the dorsal side showing clefts on either side of the projecting circular part of the anterior gape (paratype, $\times 2.5$). Horizon and locality the same as in figures 12-15 above. USNM 209319.
18. Interior view of left valve showing marginal denticles (paratype, $\times 3$). Horizon and locality the same as in figures 12-15 above. USNM 209320.

*EUCHASMA*

PLATE 29

FIGURES

- 1-5. *Euchasma jonesi* n. sp. (p. 67).
 - 1, 2. Right-lateral and dorsal views (paratype, $\times 3$). Lower part of the Setul Formation (Lower Ordovician), from a small inlet, Pulau Anak Tikas, on the south tip of Pulau Langgun, in the Langkawi Islands, western Malaysia. Collected by T. E. Yancey. USNM 209309.
 3. View looking from posterior to anterior (posterior part of shell broken off) showing the umbonal cavities on either side of the pegma (paratype, $\times 3$). Horizon and locality the same as on plate 28, figures 12-15. USNM 209310.
 4. Enlargement of plate 28, figure 18 ($\times 5$).
 5. Posteroventral part of shell showing a color line which probably represents the insertion of the pallial line (paratype, $\times 3$). Horizon and locality the same as on plate 28, figures 12-15. USNM 209311.
- 6-15. *Euchasma mytiliforme* n. sp. (p. 67).
 - 6-10. Right-lateral, left-lateral, anterior, ventral, and dorsal views of holotype ($\times 2$). East side Pulau Langgun, Langkawi Islands, Malaysia (Lower Ordovician). USNM 209312.
 - 11, 12. Paratype. 11, View looking posterior to anterior inside of shell (posterior part of shell broken off) showing the anterior gape and the pegma ($\times 2.5$). 12, Same specimen anterior view showing the gape ($\times 2.5$). Horizon and locality the same as in figures 6-10 above. USNM 209313.
 13. Interior view of right valve of paratype showing marginal denticles ($\times 2$). Lower part of Setul Formation (Lower Ordovician), north shore of main island, Pulau Langkawi, Langkawi Islands, western Malaysia. Collected by T. E. Yancey. USNM 209314.
 - 14, 15. Paratype. 14, Oblique anterior view of broken specimen showing the pegma ($\times 2.5$). 15, Same specimen looking posterior to anterior (posterior part of shell broken off), showing the pegma and its points of attachment to the shell. Horizon and locality the same as in figures 6-10 above. USNM 209315.

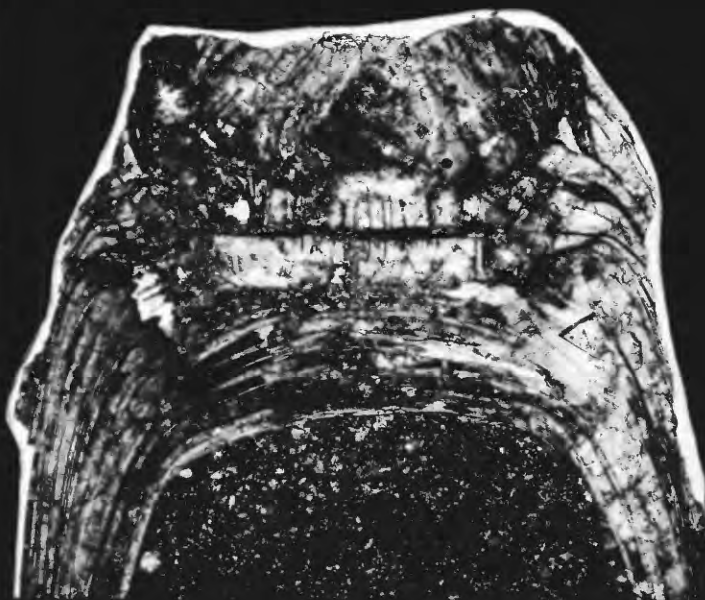
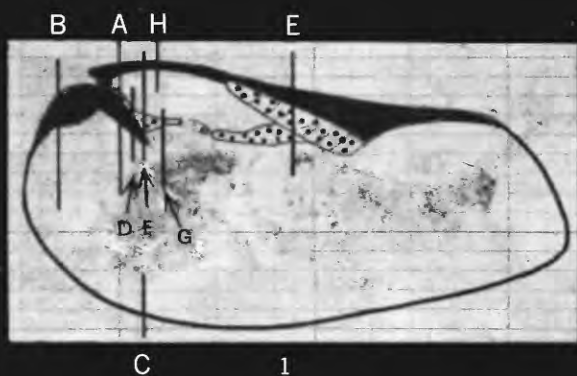


EUCHASMA

PLATE 30

FIGURES

1. Schematic diagram of *Ribeiria apusoides* Schubert and Waagen, (p. 50), to show position of the sections illustrated in this plate, figures 2-5, and plate 31, figures 1-5. Solid black shows thickness of shell in midsagittal plane; stippled areas are muscle insertions of the left valve.
- 2, 3. Section A in figure 1 (USNM 209308). 2, $\times 10$; 3, $\times 30$. Sections of anterior part of pegma showing fractured layers underlain by younger unfractured inner shell layers.
4. Section B of figure 1 (USNM 209308). $\times 10$. Showing growth layers continuous across anterior dorsal margin of shell.
5. Section C of figure 1 (USNM 209308). $\times 30$. Growing edge of shell (inner surface to left); growth lamellae reflected outwards to produce fine comarginal growth lines.



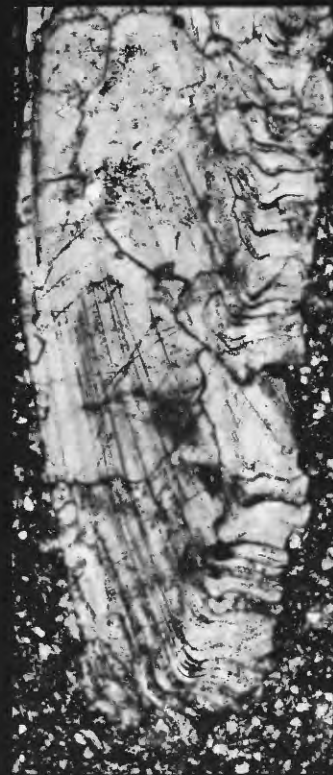
2 (A)



4 (B)



3 (A)



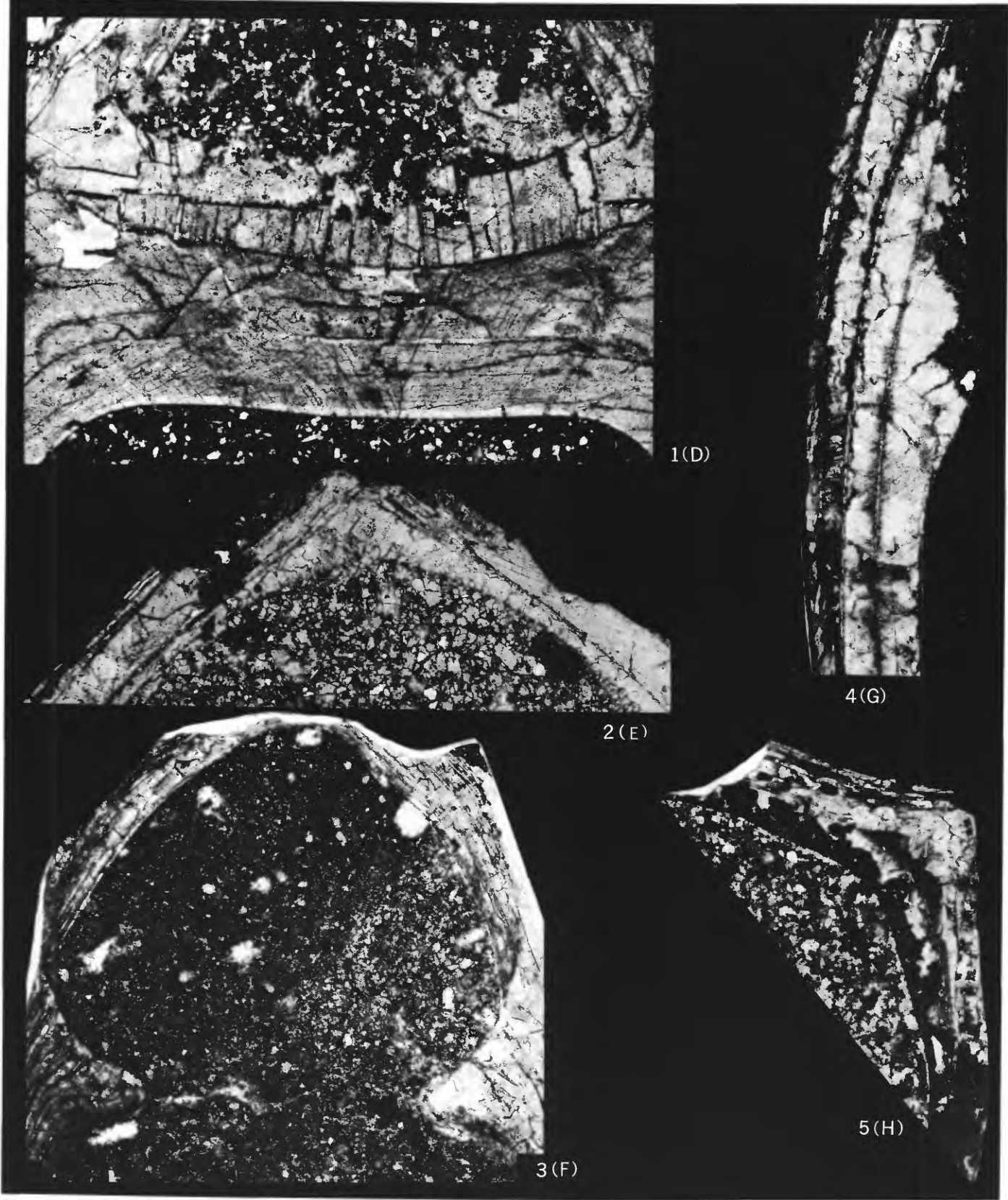
5 (C)

RIBEIRIA

PLATE 31

FIGURES

1. Section D of plate 30, figure 1. (MCZ 7005/4). \times 30. Section of pegma showing upper fractured layer underlain by younger unfractured layers.
2. Section E of plate 30, figure 1 (MCZ 18029). \times 10. Section of posterior dorsal margin of shell.
3. Section F of plate 30, figure 1 (USNM 209308). \times 10. Section across curved growing edge of pegma showing growth lines intersecting upper face of pegma and discontinuity on each side defining position of myostracal layer.
4. Section G of plate 30, figure 1 (MCZ 18030). \times 30. Section of shell across linear muscle insertion on left valve (muscles are attached above the bulge).
5. Section H of plate 30, figure 1 (MCZ 18031). \times 30. Cross section of hinge just behind the beak.



RIBEIRIA

PLATE 32

FIGURES

- 1, 2. *Pseudoconocardium lanterna* (Branson), 1965 (p. 74).
 - 1, Transverse section of anterior part of hinge showing inverted foldlike structure formed of inner shell layers ($\times 30$). 2, Transverse section of anterior part of hinge showing progressive deformation of inner shell layers from youngest to oldest ($\times 10$). USNM 176950.
3. *Hippocardia bohémica* (Barrande), 1881 (p. 75).

Vesicular shell structure near anterior gape ($\times 10$). Oklahoma Geol. Survey A-17.
4. *Bransonia wilsoni* n. sp. (p. 72).

Section of edge of shell showing outer prismatic layer above and recrystallized, probably originally nacreous, inner layer below. Growth lines extend across both layers ($\times 30$). UNE F12636.
- 5, 6. *Hippocardia cunea* (Conrad), 1840 (p. 75).
 - 5, Section of hood showing cross section of tubular extension of ventral aperture and prismatic structure of the hood in this area ($\times 10$). 6, Section of one side of the hood cut perpendicular to the plane of symmetry of the shell; prismatic structure is confined to the inner part (up) of the hood. Outer part (down) consists of curved lamellae originally separated by open spaces ($\times 30$). USNM 86915.



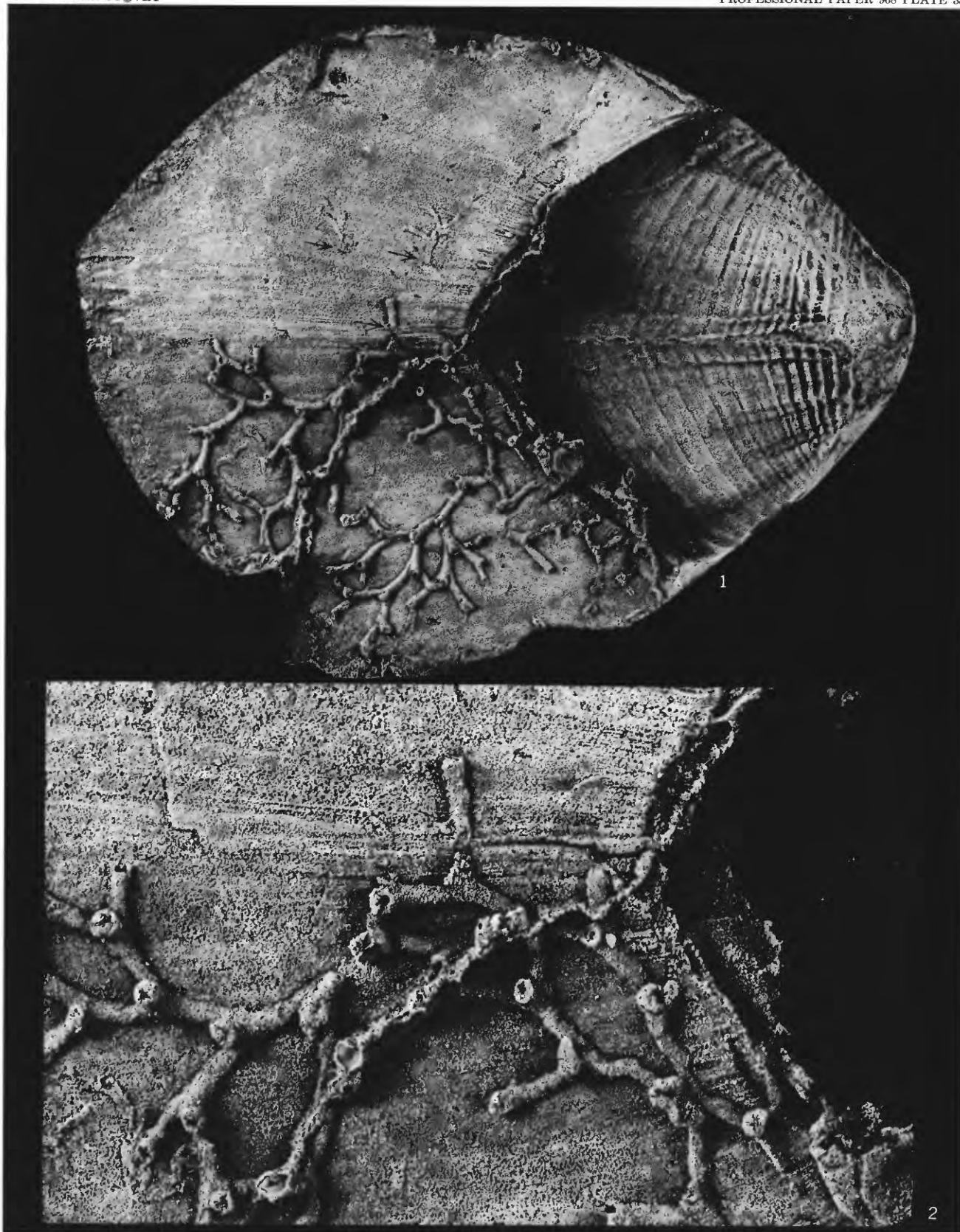
PSEUDOCONOCARDIUM, HIPPOCARDIA, AND BRANSONIA

PLATE 33

FIGURES

1, 2. *Hippocardia cunea* (Conrad), 1840 (p. 75).

Latex replica of original. Arrows point to places where the encrusting auloporoid coral colony has broken by subsequent growth of the rostroconch hood; 1 ($\times 2$), 2 ($\times 6$). FM 12502 (Walker Mus. coll.). Replica USNM 209307.



HIPPOCARDIA

PLATE 34

FIGURES

- 1-16. *Mulceodens jaanussoni* n. sp. (p. 73).
 - 1, 2. Anterior ($\times 7$) and right-lateral ($\times 9$) views of paratype. Silurian (Ludlovian, Eke, Marl), Gotland, Ronehamn, Sweden. SMNH Mo. 18563.
 3. Interior of left valve of paratype showing marginal denticles ($\times 5$). Silurian (Wenlockian, Mulde Marl), Gotland, Parish of Eksta, Djupvik, Sweden. SMNH Mo. 18302.
 4. Interior of left valve of paratype showing marginal denticles ($\times 5$). Horizon and locality the same as in figure 3 above. SMNH Mo. 18303.
 5. Interior of right valve of paratype showing marginal denticles ($\times 5$). Horizon and locality the same as in figure 3 above. SMNH Mo. 18304.
 6. Dorsal view of paratype showing protoconch and rostral clefts ($\times 7$). Silurian (Wenlockian, Slite Beds), Gotland, Parish of Othem, Samsugn, Sweden. SMNH Mo. 18336.
 7. Dorsal view of paratype showing protoconch and rostral clefts ($\times 8$). Horizon and locality the same as in figure 6 above. SMNH Mo. 18337.
 8. Dorsal view of paratype showing protoconch and marginal denticles ($\times 8$). Horizon and locality the same as in figure 6 above. SMNH Mo. 18338.
 9. Anterior view of paratype showing marginal denticles ($\times 7$). Silurian, Gotland, Sweden, SMNH Mo. 18464.
 10. Anterior view of paratype showing marginal denticles ($\times 7$). Horizon and locality the same as in figure 3 above. SMNH Mo. 18560.
 11. Anterior view of paratype showing marginal denticles ($\times 7$). Silurian (Ludlovian, Hamra Beds), Gotland, Parish of Öja, Storviks Kanal, Sweden. SMNH Mo. 18322.
 - 12, 13. Left-lateral and anterior views ($\times 7$). Silurian (Ludlovian, Hamra Beds), Gotland, Parish of Grötlingbo Uddvide, Sweden. SMNH Mo. 18546.
 14. Anterior view of paratype ($\times 7$). Horizon and locality the same as in figures 12-13 above. SMNH Mo. 18547.
 - 15, 16. Dorsal and right-lateral views of paratype ($\times 7$). Horizon and locality the same as in figure 3 above. SMNH Mo. 151244.

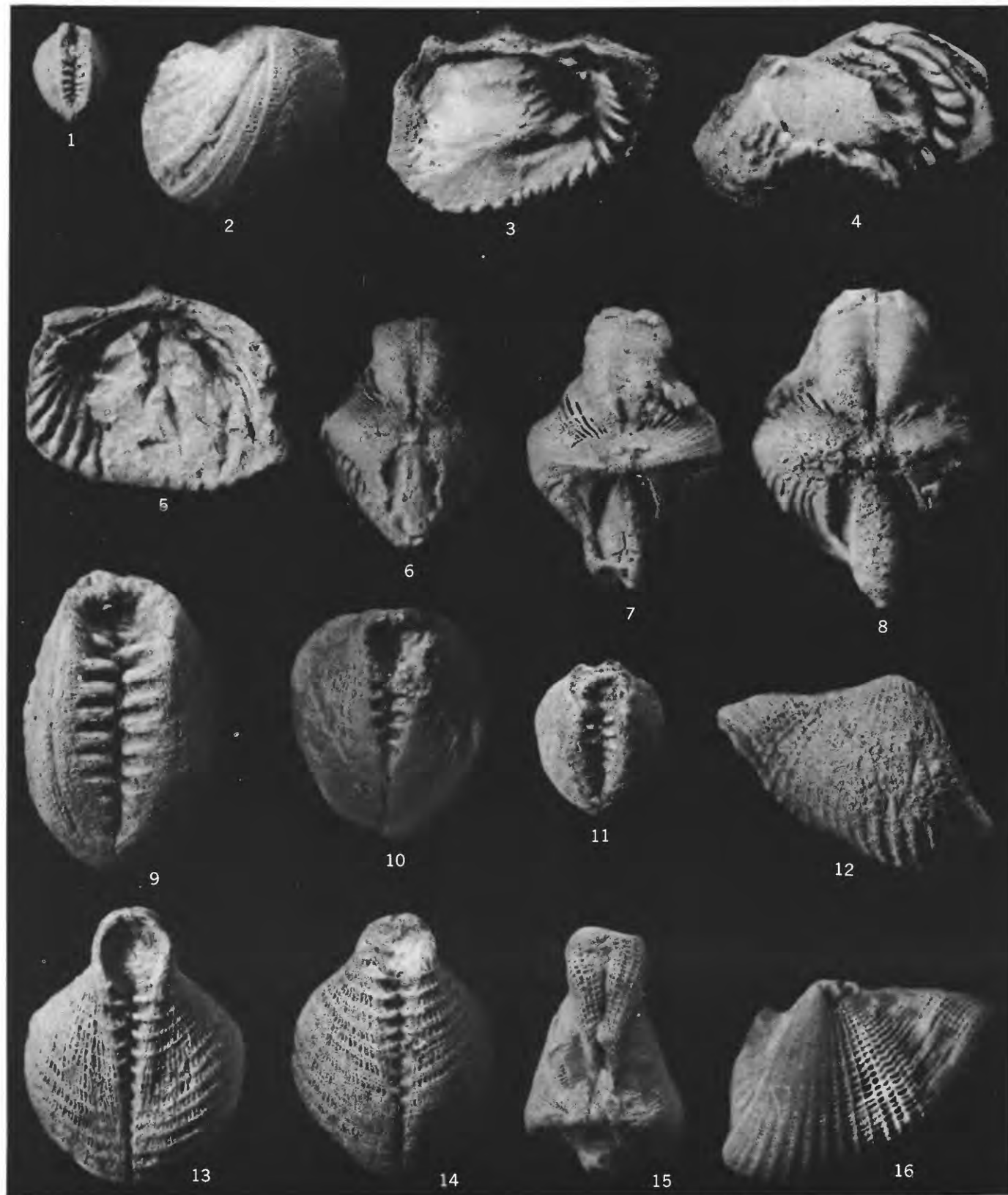
*MULCEODENS*

PLATE 35

- FIGURES 1-3, 11, 12. *Mulceodens jaanussoni* n. sp. (p. 73).
Left-lateral, dorsal, right-lateral, anteroventral, and posterior views of holotype ($\times 7$). Horizon and locality the same as on plate 34, figure 3. SMNH Mo. 151245.
- 4-7. *Mulceodens eboraceus* (Hall), 1860 (p. 74).
Right-lateral, left-lateral, dorsal, and anterior views of lectotype ($\times 3$). Hamilton Group (Middle Devonian), York, Livingston County, N.Y. AM5347/1.
- 8-10. *Mulceodens bifarius* (Winchell), 1866 (p. 73).
Dorsal, anterior, and right-lateral views ($\times 3$). Traverse Group, upper Alpena Limestone, 4 Mile dam, Alpena County, Mich. (Middle Devonian). USNM 209306.
- 13-17. *Bigalea visbyensis* n. sp. (p. 77).
13-15. Left-lateral, ventral, and right lateral views of paratype ($\times 6$). Silurian (Wenlockian, formation unknown), Visby, Gotland, Sweden. SMNH Mo. 18554.
16, 17. Right-lateral and ventral views of holotype ($\times 7$). Horizon and locality the same as in figure 13-15 above. SMNH Mo. 18552.

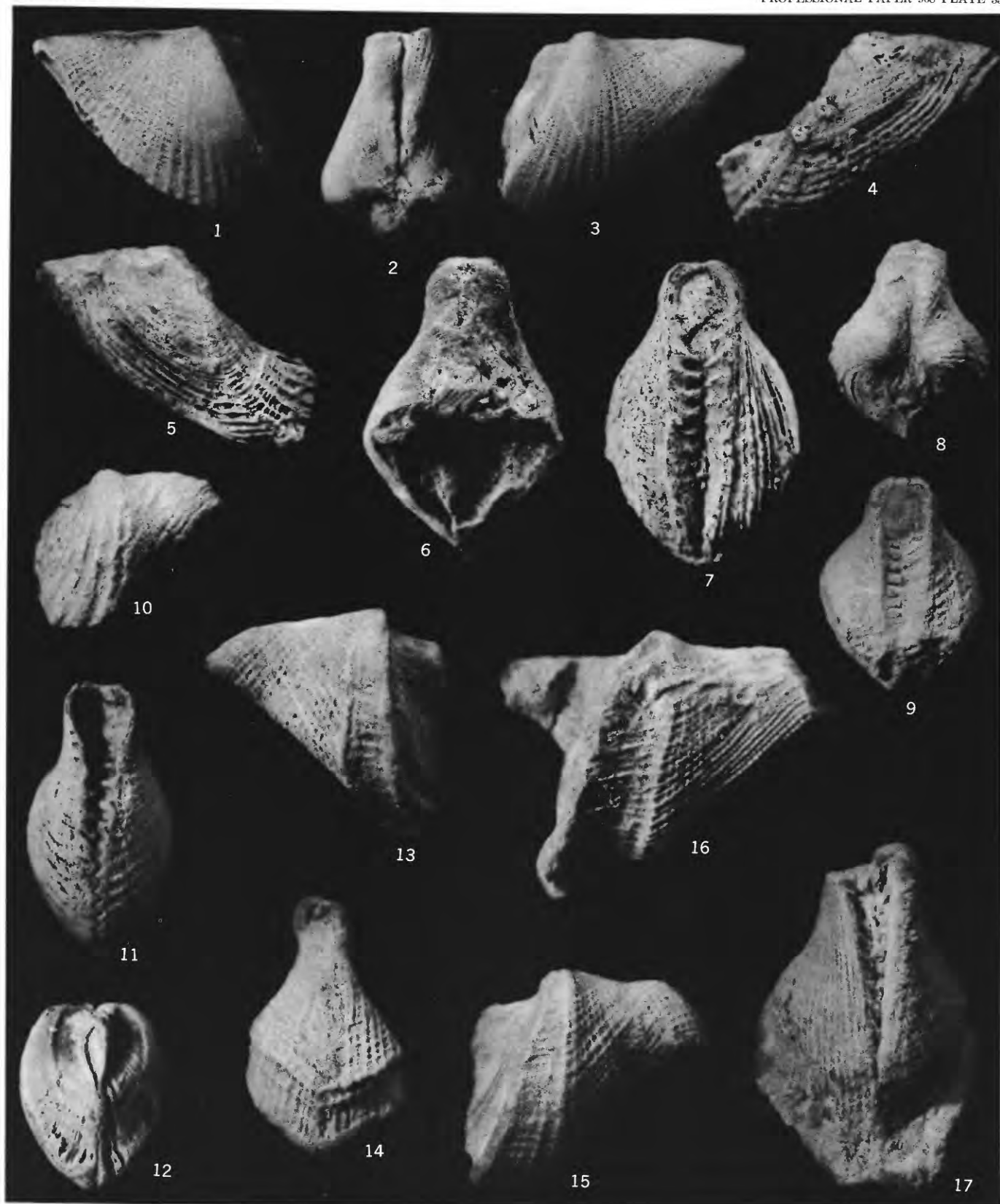
*MULCEODENS AND BIGALEA*

PLATE 36

FIGURES

- 1-4. *Bigalea visbyensis* n. sp. (p. 77).
1, 2. Left-lateral and dorsal views of holotype ($\times 7$). Horizon and locality the same as on plate 35, figures 13-15. SMNH Mo. 18552.
3, 4. Left-lateral and dorsal views of paratype ($\times 7$). Horizon and locality the same as on plate 35, figures 13-15. SMNH Mo. 18553.
- 5-12. *Bigalea ohioensis* n. sp. (p. 77).
5-7. Oblique posterior ($\times 4$), right-lateral, and ventroposterior views ($\times 6$) of holotype. Horizon and locality uncertain, probably from Devonian rocks exposed at the Falls of the Ohio River. USNM 209302.
8, 9. Left-lateral and dorsal views of paratype ($\times 6$). Horizon and locality the same as in figures 5-7 above. USNM 209303.
10, 11. Right-lateral and posterior views of paratype ($\times 6$). Horizon and locality the same as in figures 5-7 above. USNM 209304.
12. Highly oblique posteroventral view of paratype ($\times 6$). Horizon and locality the same as in figures 5-7 above. USNM 209305.
- 13-16. *Bigalea yangi* n. sp. (p. 76).
Oblique posterior view from left side, ventral, left-lateral, and anterior views of paratype ($\times 3.5$). Traverse Group (Middle Devonian), Kegonic, Little Traverse Bay, Mich. FM 18331.

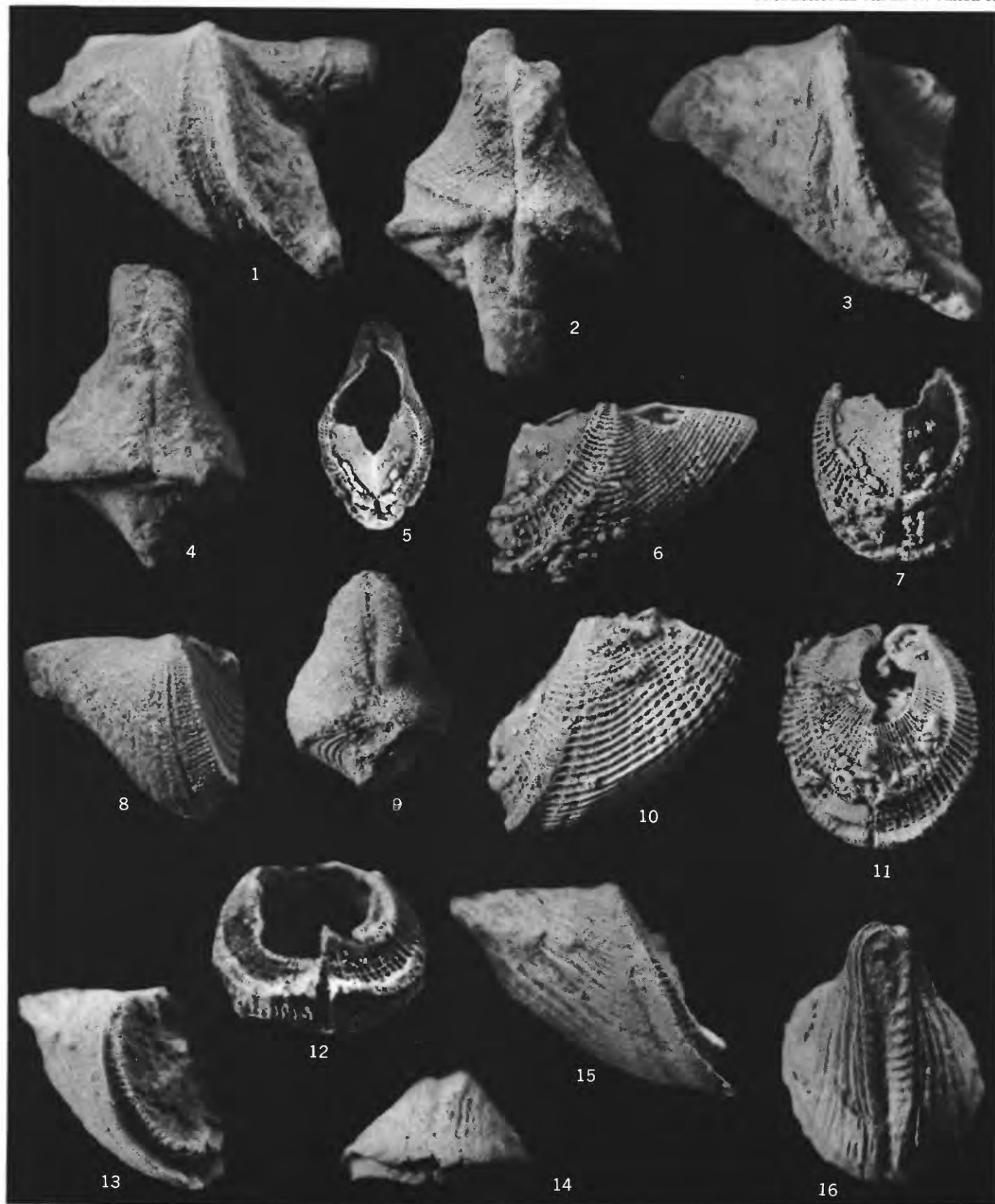
*BIGALEA*

PLATE 37

FIGURES

- 1-4. *Bigalea yangi* n. sp. (p. 76).
 - 1-3. Dorsal, posterior, and left-lateral views of holotype ($\times 3.5$). "Petoskey Limestone" in the Traverse Group (Middle Devonian) quarry at Mud Lake, about 1.5 miles northeast of Bay View, Emmet County, Mich. USNM 209301.
 4. Posterior view of paratype ($\times 6$). Traverse Group (Middle Devonian), Kegonic, Little Traverse Bay, Mich. FM 18332.
- 5-15. *Bigalea clathra* (d'Orbigny), 1850 (p. 76).
 - 5-9. Left-lateral ($\times 3.5$), dorsal ($\times 3$), ventral ($\times 3$), posterior ($\times 3.5$), and anterior ($\times 3.5$) views. Devonian, Pelm, Germany?. MCZ 15395.
 - 10-12. Left-lateral, dorsal, and right-lateral views. ($\times 3.5$). Devonian, Prüm, Germany?. MCZ 15608.
 - 13, 14. Ventral and right-lateral views ($\times 3$). Devonian?, Eifel, Germany. UM 1788.
 15. Right-lateral view ($\times 3.5$). Horizon, locality, and museum number the same as in figures 10-12 above.
- 16, 17. *Conocardium* aff. *C. elongatum* (Sowerby), 1815 (p. 69).
 - Left-lateral and dorsal views ($\times 2.5$). Pennsylvanian, St. Joseph, Mo. USNM 100704.

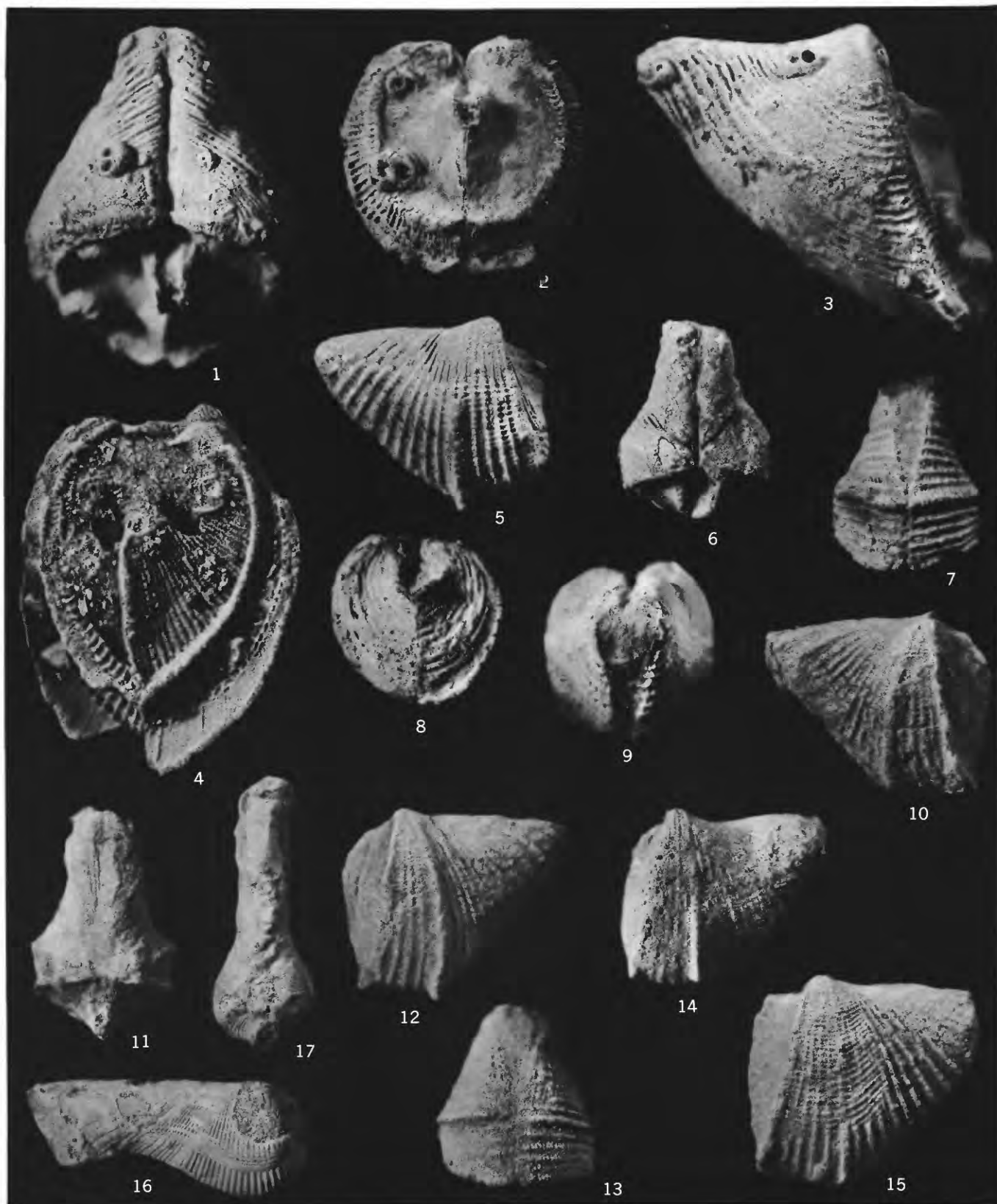
*BIGALEA AND CONOCARDIUM*

PLATE 38

FIGURES

- 1-7. *Conocardium* aff. *C. elongatum* (Sowerby), 1815 (p. 69).
 - 1-3. Ventral, right-lateral, and posterior views ($\times 2.5$). Horizon, locality, and museum number the same as on plate 37, figures 16, 17.
 - 4-7. Anterior, dorsal, ventral, and left-lateral views ($\times 2.5$). Carterville Formation (Upper Mississippian), mine dump near Duenweg, Mo. USNM 209298.
- 8-24. *Conocardium elongatum* (Sowerby), 1815 (p. 69).
 8. Left-lateral view of Hind (1900, pl. 51, fig. 8) hypotype ($\times 2$). Carboniferous (Mississippian) Limestone of Settle, England. SM E.549.
 - 9-14. Right-lateral, left-lateral, ventral, dorsal, anterior, and posterior views of holotype ($\times 2$). Carboniferous (Mississippian), Derbyshire, England. Photographs courtesy British Museum (Natural History). BM PL 794.
 - 15-20. Topotype. 15-18, Ventral, dorsal, left-lateral, and posterior views ($\times 2$). 19, 20, Same figure of polished anterior end showing a longitudinal shelf on the right side (arrow fig. 20) ($\times 5$). Carboniferous Limestone (Mississippian), Derbyshire, England. BM L 13496.
 21. Right-lateral view internal mold showing some muscle scars ($\times 3$). Four Laws Limestone (Vissean, Mississippian), Redesdale, Northumberland, England. BM PL 4431.
 - 22-24. Right-lateral, dorsal, and oblique left-lateral views showing some muscle scars ($\times 4$). Horizon and locality the same as on figure 21 above. BM PL 4432.
- 25, 26. *Conocardium pseudobellum* n. sp. (p. 70).
 25. Posterior view of holotype ($\times 2.5$). Traverse Group, upper Alpena Limestone (Middle Devonian), Four Mile dam, Alpena County, Mich. USNM 209299.
 26. Polished section of dorsal surface of paratype showing longitudinal shelf on right side ($\times 3$). Horizon and locality the same as in figure 25 above. USNM 209300.

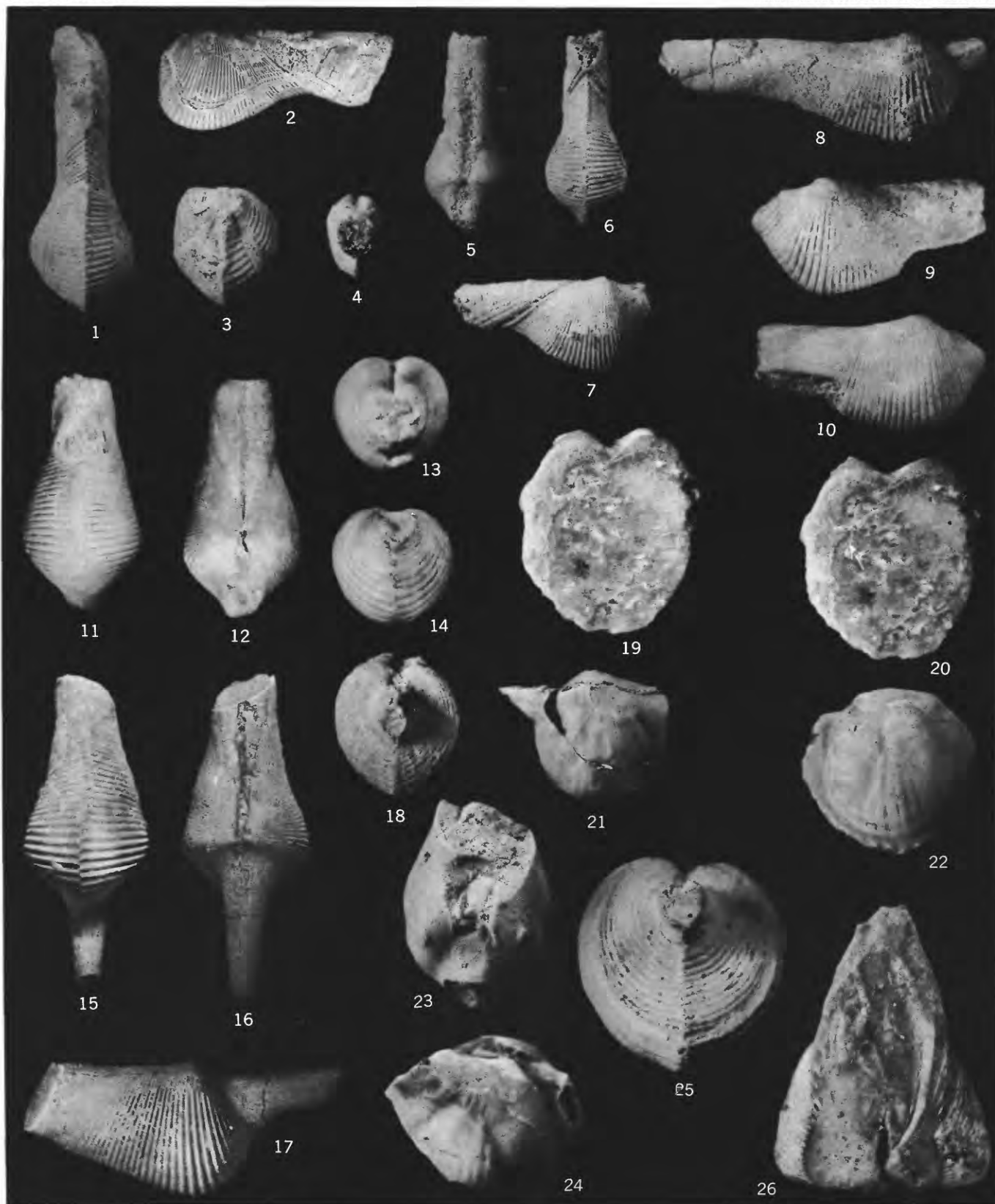
*CONOCARDIUM*

PLATE 39

FIGURES

- 1-3. *Conocardium pseudobellum* n. sp. (p. 70).
 - 1, 2. Dorsal and left-lateral views of holotype ($\times 2.5$). Rostrum rebuilt in plaster. Horizon, locality, and museum number the same as on plate 38, figure 25.
 3. Left-lateral view of paratype showing elongate rostrum ($\times 2.5$). Four Mile Dam Formation (Middle Devonian), Four Mile Dam on Thunder Bay River, 2 miles upstream from Alpena, Mich. UM 47287.
- 4-7. *Conocardium normale* Hall, 1883 (p. 70).

Lectotype. Right-lateral, left-lateral, and dorsal views and latex replica of posterior end showing unusually thick longitudinal shelves ($\times 1.5$). Hamilton Group (Middle Devonian), Cumberland, Md. AM 5349/1.
- 8-10. *Conocardium aliforme* (Sowerby), 1815 (p. 70).

Posterior, left-lateral, and dorsal views ($\times 2$) of Hind (1900, pl. 54, fig. 8) hypotype. Carboniferous Limestone (Mississippian) of Settle, England. SM E 561.
- 11-13. *Conocardium attenuatum* (Conrad), 1842 (p. 70).

Dorsal, right-lateral, and ventral views ($\times 2$) of a Hall hypotype. Schoharie Formation (Lower Devonian), Schoharie, N.Y. NYSM 2321.

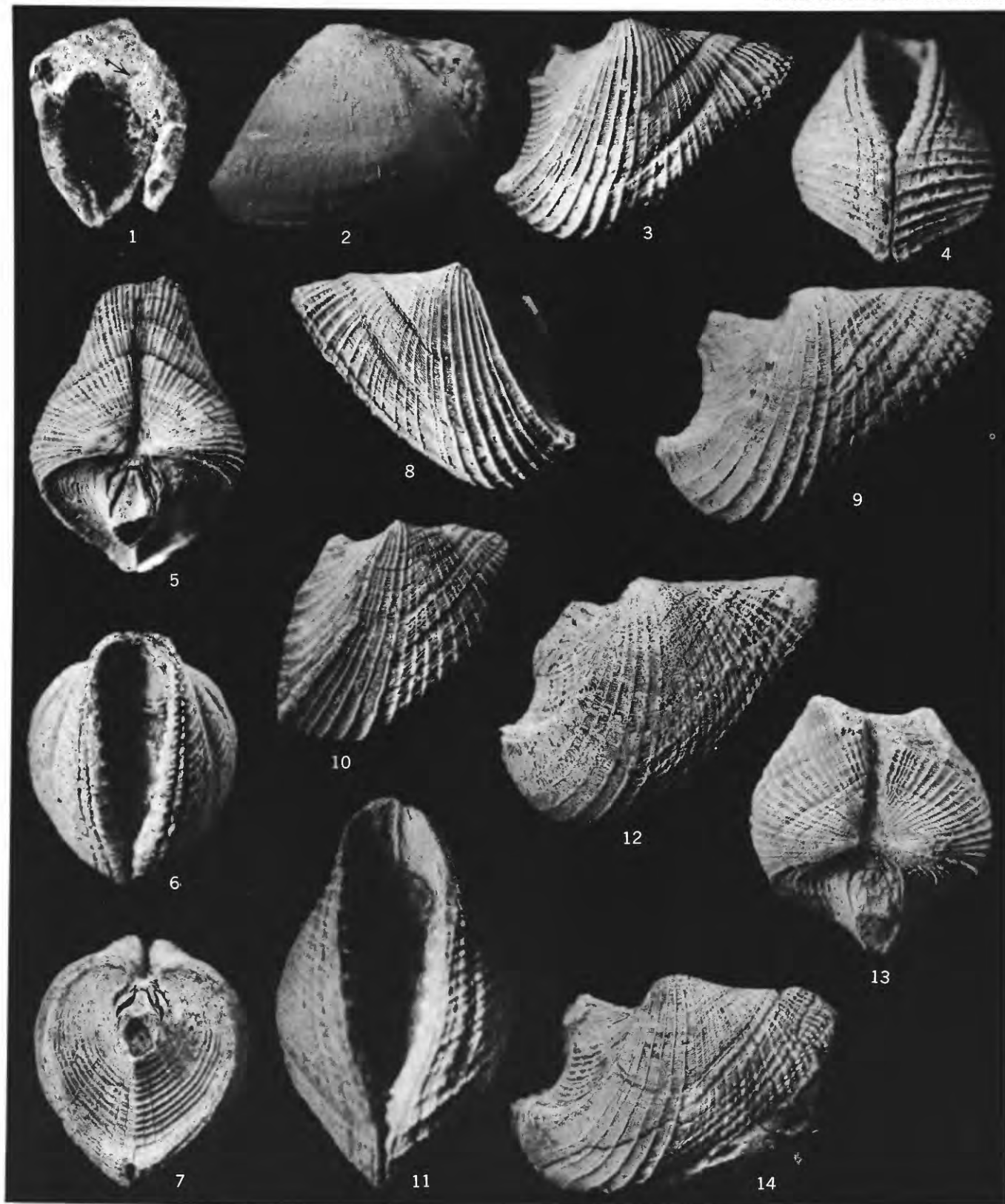


CONOCARDIUM

PLATE 40

FIGURES

- 1, 2. *Conocardium attenuatum* (Conrad), 1842 (p. 70).
 1. Polished section of anterior end showing longitudinal shelves (arrow) ($\times 2.5$). Schoharie Formation (Lower Devonian), 1.75 miles north-northwest of Clarksville, N.Y. USNM 100705.
 2. Right-lateral view ($\times 2$) of Hall hypotype (1885, pl. 67, fig. 9). Schoharie Formation, Schoharie, N.Y. (Lower Devonian). AM 2850/3.
- 3-14. *Pseudoconocardium lanterna* (Branson), 1965 (p. 74).
 - 3-8. Right-lateral, ventral, dorsal, anterior, posterior, and left-lateral views ($\times 2$). Cisco Group (Pennsylvanian), Graham, Young County, Tex. USNM 209293.
 9. Right-lateral view ($\times 2$). Brad Formation, "Hog Creek Shale Member" of Caddo Creek Formation (Pennsylvanian), 6 miles west of Chico, 1.5 miles north of highway, Wire County, Tex. USNM 209294.
 10. Right-lateral view ($\times 4$). Horizon and locality unknown. UOK 800.
 - 11, 12. Anterior and right-lateral views ($\times 2$). Pennsylvanian, Martin's Lake, 3 miles southwest of Bridgeport, Tex. USNM 209295.
 13. Dorsal view ($\times 2.5$). Horizon and locality unknown. USNM 209296.
 14. Right-lateral view ($\times 2$). Brownwood Shale Member of the Graford Formation (Pennsylvanian), Signal Peak, Tex. USNM 209297.



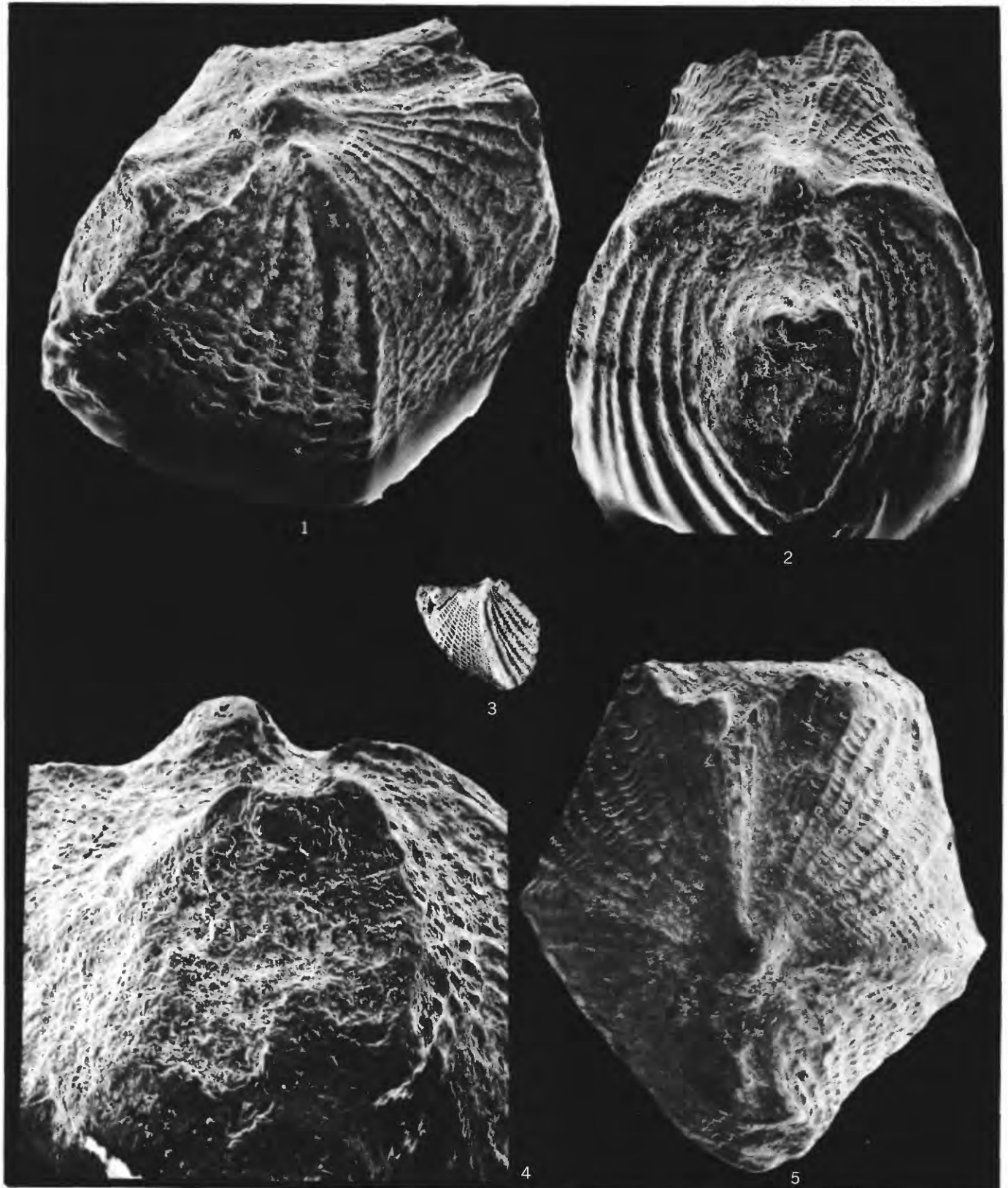
CONOCARDIUM AND PSEUDOCONOCARDIUM

PLATE 41

FIGURES

1-5. *Pseudoconocardium lanterna* (Branson), 1965 (p. 74).

SEM photographs of protoconch. 1, Posteroright-lateral view ($\times 26$); protoconch is the bump at the junction of the linear ridges and the umbonal ridges. 2, Posterodorsal view ($\times 26$); protoconch is the raised area between the umbonal ridges. 3, Left-lateral view of specimen ($\times 4$). 4, Oblique posterior view ($\times 60$); protoconch is the raised area dorsal to the projecting rostrum. 5, Dorsal view ($\times 28$); protoconch is the dark area in the posterocentral part of the shell. Gaptank Formation (Pennsylvanian), 2 miles S. 17° E. of Gaptank, 23.5 miles northeast of Marathon, Tex. USNM 209292.



PSEUDOCONOCARDIUM

PLATE 42

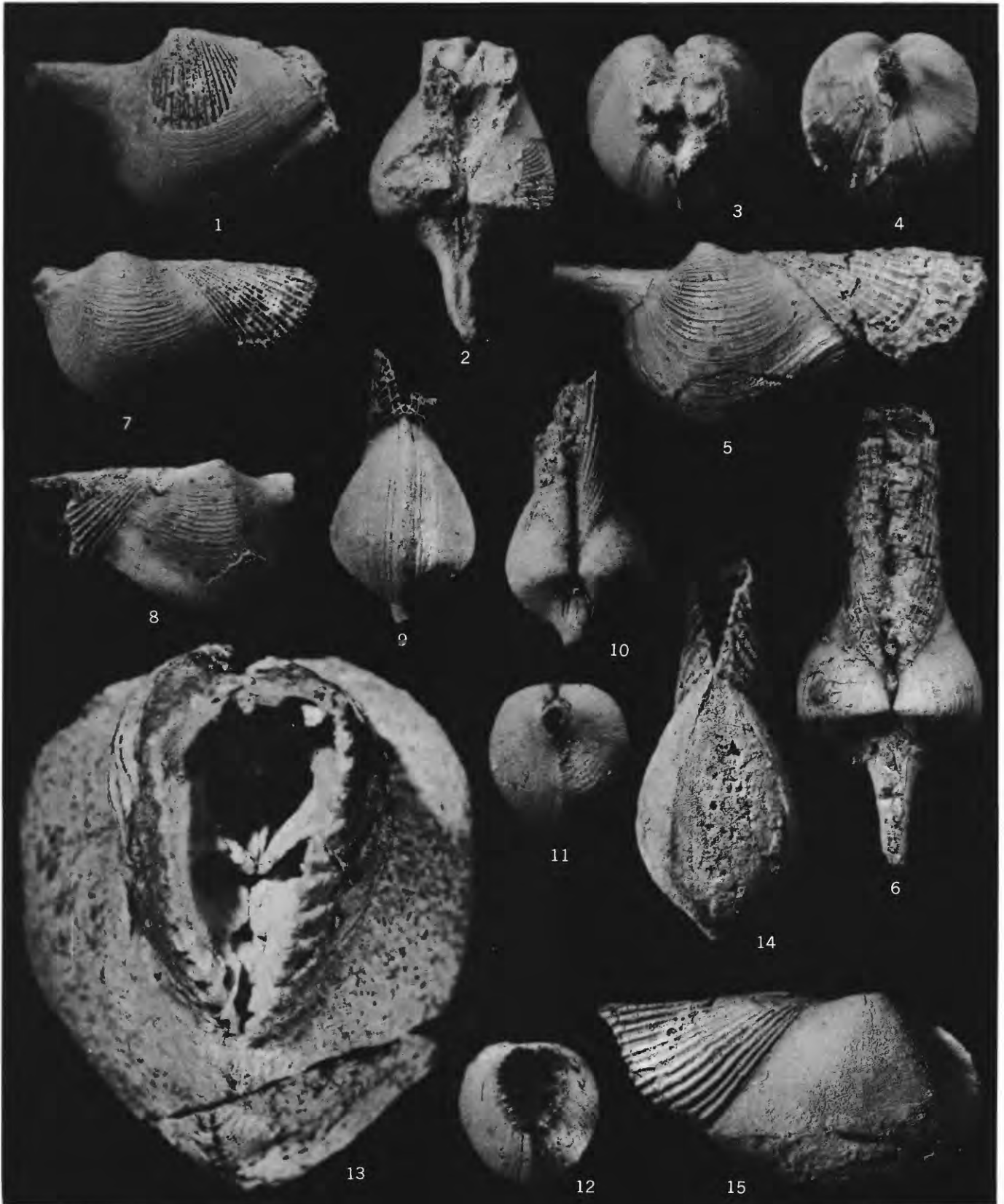
- FIGURES 1-7, 12-14. *Pseudoconocardium lanterna* (Branson), 1965 (p. 74).
- 1, 2. Posterior and ventral views ($\times 2$). Graford Formation (Pennsylvanian), Martin's Lake, 1.35 miles south of Bridgeport, Wise County, Tex. USNM 209287.
 - 3, 4. Right-lateral and dorsal views of an internal mold ($\times 2$). Graham Formation (Pennsylvanian), 0.5 miles west of S. Bend, Young County, Tex. AM 28992.
 5. Posteroventral view ($\times 2$). Palo Pinto Limestone (Pennsylvanian), west side Martin's Lake, 2 miles south of Bridgeport, Wise County, Tex. UOK 798.
 6. Right-lateral view ($\times 4$). Graford Formation (Pennsylvanian), west side of Martin's Lake, 2 miles south of Bridgeport, Wise County, Tex. USNM 209288.
 7. Right-lateral view ($\times 7$). Horizon and locality the same as on plate 41, figures 1-5. USNM 209289.
 - 12-14. Right-lateral, dorsal, and left-lateral views ($\times 2$) of an internal mold that preserves remnants of muscle scars. Union Valley Formation (Pennsylvanian), 3 miles southeast of Ahloso, Okla. NE $\frac{1}{4}$, sec. 29, T. 3 N., R. 7 E. UOK 794.
 - 8-10. *Arceodomus glabrata* (Easton), 1962 (p. 71).
Left-lateral, right-lateral, and dorsal views ($\times 2.5$). Diamond Peak Formation (Mississippian), SW $\frac{1}{4}$, SE $\frac{1}{4}$, NE $\frac{1}{4}$, Sec. 28, T. 19 N., R. 58 E. (USGS loc. 23837-PC), White Pine County, Nev. USNM 209290.
 11. *Arceodomus* aff. *A. glabrata* (Easton), 1962 (p. 71).
Ventral view ($\times 2$). Pennsylvanian. Little Kickapoo Creek, 0.7 miles southeast of Kickapoo Falls, Hood County, Tex. USNM 209291.



PSEUDOCONOCARDIUM AND ARCEODOMUS

PLATE 43

- FIGURES 1-3, 7-12. *Arceodomus glabrata* (Easton), 1962 (p. 71).
1-3. Right-lateral, dorsal, and anterior views of holotype ($\times 3$). The anterior view shows the longitudinal shelves. Heath Formation (Mississippian), Stonehouse Canyon, Golden Valley County, Mont. USNM 118858.
7-12. Right-lateral, left-lateral, ventral, dorsal, posterior, and anterior views ($\times 2.5$). Horizon and locality the same as on plate 42, figures 8-10. USNM 209286.
- 4-6. *Arceodomus* sp. (p. 71).
Posterior, right-lateral, and dorsal views ($\times 2$). Permian (Sakmarian) of the U.S.S.R. BM L 15570.
- 13-15. *Arceodomus langenheimi* (Wilson), 1970 (p. 71).
Anterior ($\times 3$), ventral, and left-lateral views ($\times 1.5$) of holotype. Figure 13 courtesy of E. C. Wilson. McCloud Limestone (Permian), Bollibokka Mountain, Shasta County, Calif. UCB 10589.



ARCEODOMUS

PLATE 44

FIGURES

- 1-4. *Arceodomus* aff. *A. glabrata* (Easton), 1962 (p. 71).
 - 1, 2. External and internal views of right valve showing ornament and longitudinal shelves ($\times 2$). "Dickerson Shale" (Pennsylvanian), just under Kickapoo Falls Limestone, 45 miles east north-east of Lipan, Hood County, Tex. USNM 209284.
 - 3, 4. Right-lateral and anterior views ($\times 2.5$). "Dickerson Shale" (Pennsylvanian), southeast of Kickapoo Falls in creek, Hood County, Tex. USNM 209285.
- 5-14. *Hippocardia bella* (Cooper and Cloud), 1938 (p. 75).
 5. Right-lateral view of paratype ($\times 2$). Devonian, first hollow south of Kritsville, Calhoun County, Ill. USNM 95192b.
 - 6, 7. Right-lateral and posterior views of paratype ($\times 4$). Horizon and locality the same as in figure 5 above. USNM 95192d.
 - 8-10. Right-lateral, posterior, and dorsal views of paratype ($\times 2.5$). Horizon and locality the same as in figure 5 above. USNM 95192c.
 - 11-14. Right-lateral, posterior, ventral, and dorsal views of holotype ($\times 2.5$). Horizon and locality the same as in figure 5 above. USNM 95192a.
- 15, 16. *Hippocardia monroica* (Grabau), 1910 (p. 76).
 15. Left-lateral view of La Rocque (1950) hypotype ($\times 2$). Detroit River Group, Amherstburg Formation (Middle Devonian), Cummins' quarry about 6 miles south and 1.75 miles east of Petersburg, Monroe County, Mich. UM 24524.
 16. Dorsal view ($\times 2$). Amherstburg Formation (Middle Devonian), Amherstburg, Ontario, Canada. USNM 60022.

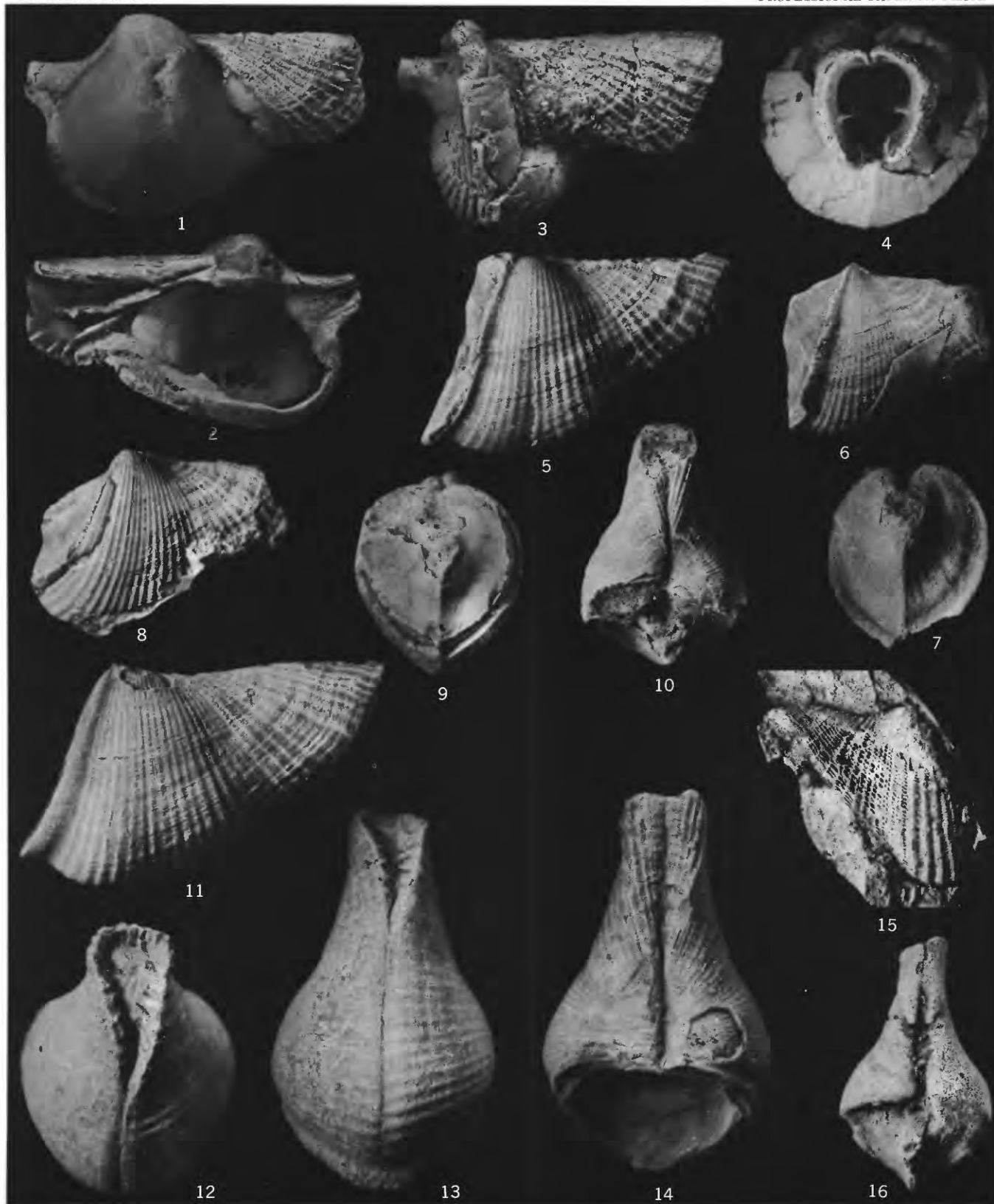
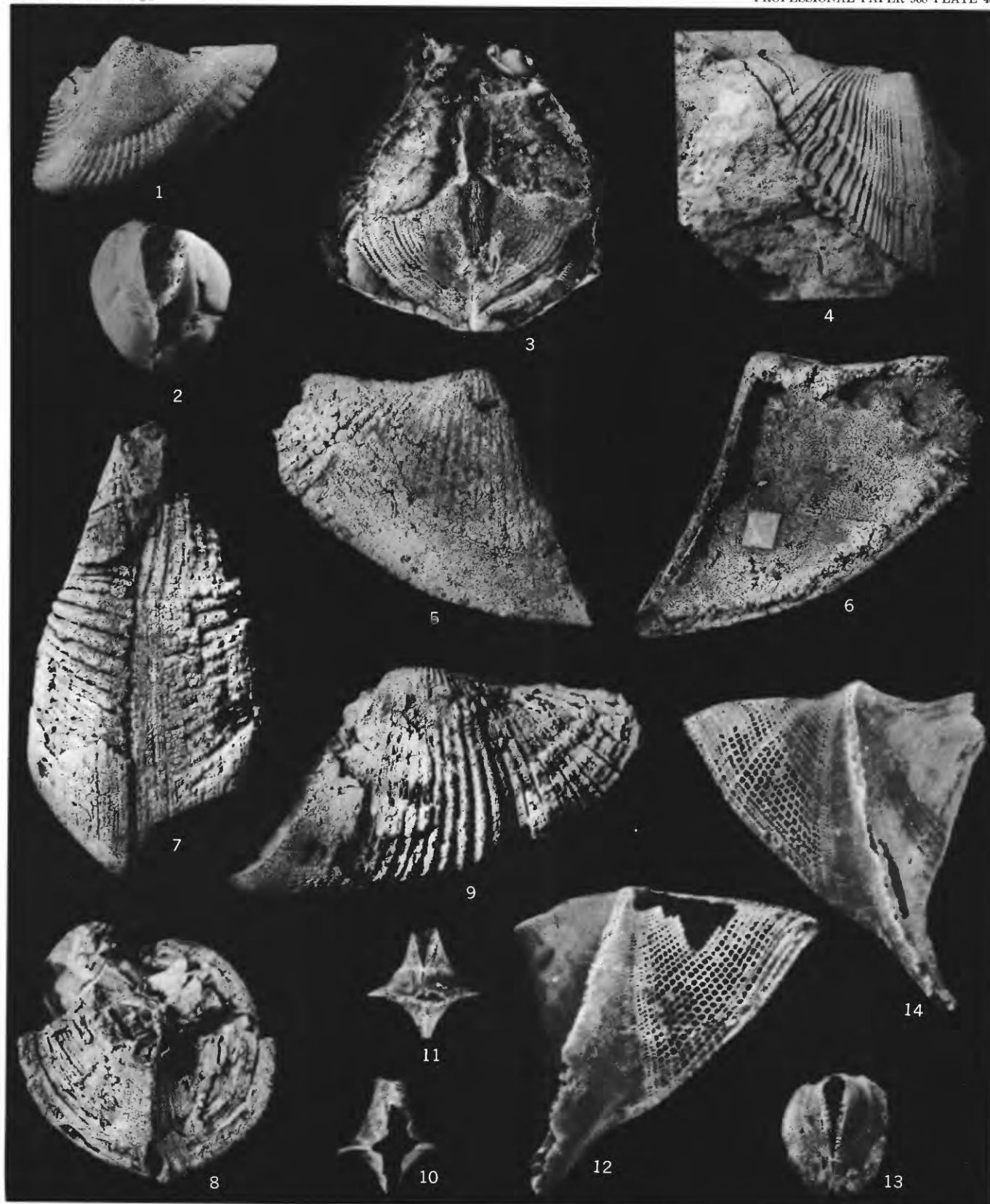
*ARCEODOMUS AND HIPPOCARDIA*

PLATE 45

FIGURES

- 1-4. *Hippocardia monroica* (Grabau), 1910 (p. 76).
 - 1, 2. Right-lateral and anterior views of paratype ($\times 2$). Horizon, locality, and museum number the same as on plate 44, figure 16.
 3. Oblique dorsal view of latex replica of La Rocque (1950) hypotype ($\times 2$). Amherstburg Formation (Middle Devonian). Livingstone Channel, Detroit River, Wayne County, Mich. UM 24529. Replica USNM 209283.
 4. Left-lateral view ($\times 2$). Lucas Formation (Middle Devonian), Patrick quarry, Grosse Isle, Mich. UM 24534.
- 5-9. *Hippocardia* cf. *H. fusiformis* (McCoy), 1844 (p. 75).
 - 5, 6. Interior and exterior views of left valve ($\times 1$). Tournaisian (Mississippian), Tournai, Belgium. YU 28150.
 - 7-9. Ventral, posterior, and right-lateral views ($\times 0.75$). Carboniferous (Mississippian?), Tournai, Belgium. USNM 63372.
- 10-14. *Hippocardia cooperi* n. sp (p. 75).
 - Dorsal ($\times 3$), ventral ($\times 3$), right-lateral ($\times 10$), anterior ($\times 3$), and left-lateral ($\times 10$) views of holotype. Lower Chambersburg Limestone (Middle Ordovician), near Strasburg, Va., USNM loc. 600. USNM 162786.



HIPPOCARDIA

PLATE 46

FIGURES

- 1-12. *Hippocardia hibernica* (Sowerby), 1815 (p. 74).
1-3. Posterior, dorsal, and anterior views of polished surface showing longitudinal shelves (arrow) ($\times 1$). Carboniferous (Mississippian), Tournai, Belgium. MCZ 433.
4. Posterior view ($\times 1$). Carboniferous (Mississippian), Castle Cormell, County Limerick, Ireland. USNM 100712.
5-7. Posterior, right-lateral, and dorsal views ($\times 1$). Carboniferous (Mississippian), St. Doulagh's, County Dublin, Ireland. SM E1169.
8, 9. Left-lateral and posterior views ($\times 1$). Carboniferous (Mississippian), Ireland. SM E1176.
10-12. Ventral, right-lateral, and posterior views showing hood and elongate rostrum ($\times 1$). Carboniferous (Mississippian), St. Doulagh's, County Dublin, Ireland. SM E1185.

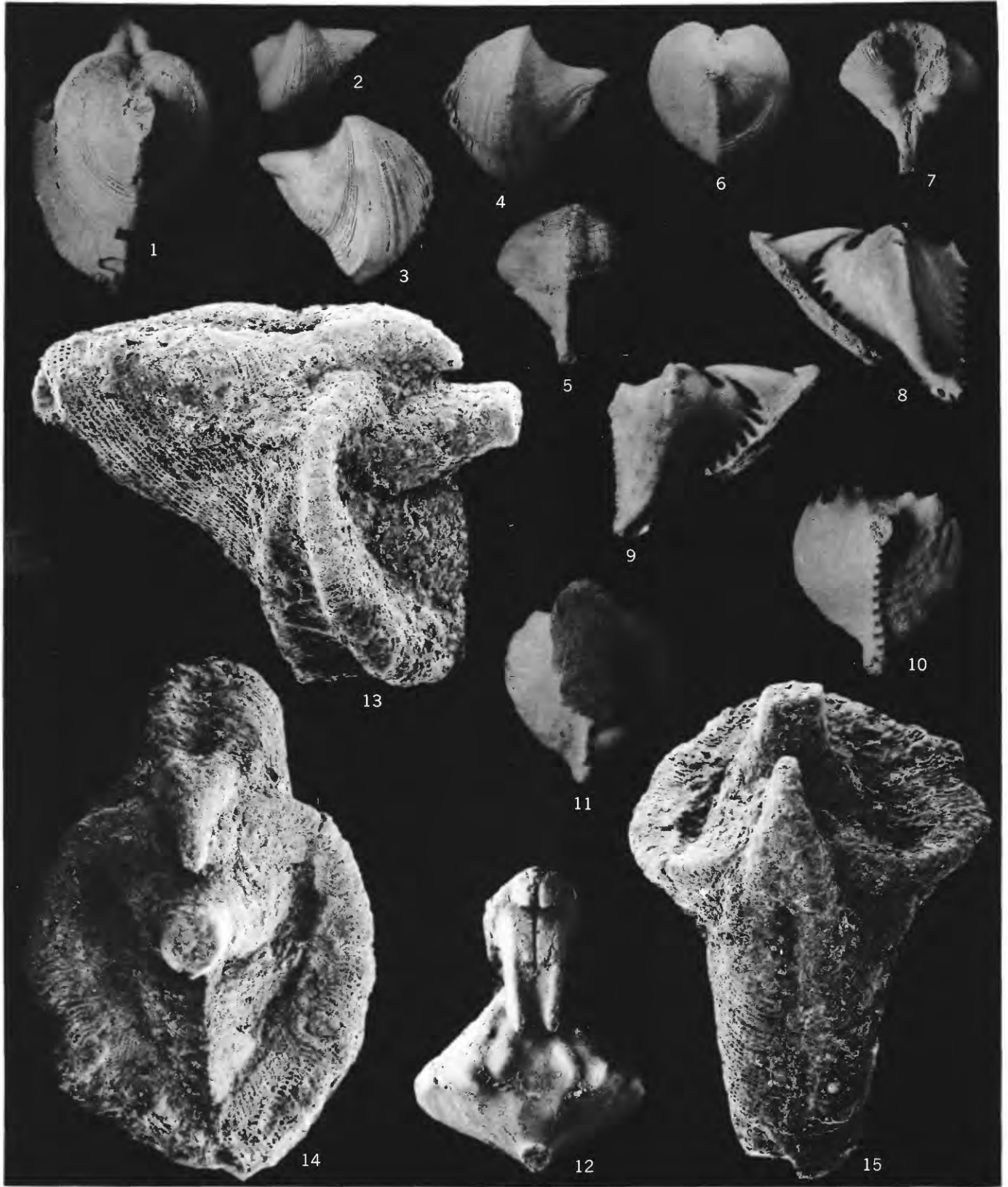


HIPPOCARDIA

PLATE 47

FIGURES

- 1-7. *Hippocardia bohémica* (Barrande), 1881 (p. 75).
1, 2. Posterior view showing hood on left side ($\times 2$) and right-lateral view ($\times 1$). Devonian, Konieprus, Bohemia, Czechoslovakia. USNM 100623.
3-7. Right-lateral, left-lateral, ventral, posterior, and dorsal views ($\times 2$). Lower Devonian, Konieprus, Bohemia, Czechoslovakia. USNM 209282.
- 8-12. *Hippocardia? zeileri* (Beushausen), 1895 (p. 76).
Left-lateral, right-lateral, posterior, anterior ($\times 3$), and dorsal ($\times 3.5$) views showing some muscle scars. Devonian, Germany. MCZ 18032.
- 13-15. *Hippocardia?* (p. 4).
Oblique left-lateral, posterior, and dorsal views ($\times 44$) of a specimen showing a recumbent, snout-shaped protoconch. Shale below Lester Shale (Pennsylvanian), SW SW SW SW sec. 10, T. 6 S., R. 2 E., Love County, Okla. UOK 6083.



HIPPOCARDIA

PLATE 48

FIGURES

- 1-15. *Hippocardia cuneata* (Conrad), 1840 (p. 75).
 1. Ventral view of Hall (1885, pl. 67, fig. 29) hypotype ($\times 1$). Schoharie Grit (Lower Devonian), Schoharie, N.Y. NYSM 2313.
 2. Ventral view of a specimen showing the entire hood ($\times 1$). Schoharie Grit (Lower Devonian), Saugerties, N.Y. NYSM 6667.
 - 3, 4. Left-lateral and dorsal views of an internal mold showing the longitudinal shelves ($\times 2$). Devonian, Columbus, Ohio. FM 59845 (Walker Mus. Coll.).
 5. Dorsal view of Hall (1885, pl. 68, fig. 13) hypotype ($\times 2$). Upper Helderberg Limestone (Lower Devonian), Columbus, Ohio. AM 2853a/3.
 - 6, 7. Posterodorsal and ventral views showing the filling of the elongate ventral aperture developed in forms with a hood ($\times 1$). Devonian (Middle Devonian?, Silver Creek Limestone?), near Louisville, Ky. USNM 33581.
 - 8-11. Right-lateral ($\times 2$), posterior ($\times 1$), oblique posterior ($\times 1$), and dorsal ($\times 2$) views of Hall (1885, pl. 68, figs. 10, 11) hypotype. Onondaga Limestone (Jeffersonville?, Middle Devonian?), near Louisville, Ky. FM 12500 Walker Mus. Colln.).
 - 12-14. Fragment of shell showing outer shell layer with ornament on one side and marginal denticles forming internal ribs on the other side. 12, Outside of shell showing ribs ($\times 2$). 13, Inside of shell showing marginal denticles which form internal ribs as they grow ($\times 2$). 14, Ventral edge of shell showing that marginal denticles and ornament are continuous at the shell margin ($\times 2$). Horizon and locality uncertain, possible Middle Devonian (Beechwood Limestone?), at the Falls of the Ohio River. USNM 209280.
 15. Oblique view looking into shell at ventral commissure; inner shell layer dissolved away and dorsal part of shell broken off. Hole at bottom leads into elongate ventral aperture running the length of the hood ($\times 2$). Horizon and locality the same as in figures 12-14 above. USNM 209281.

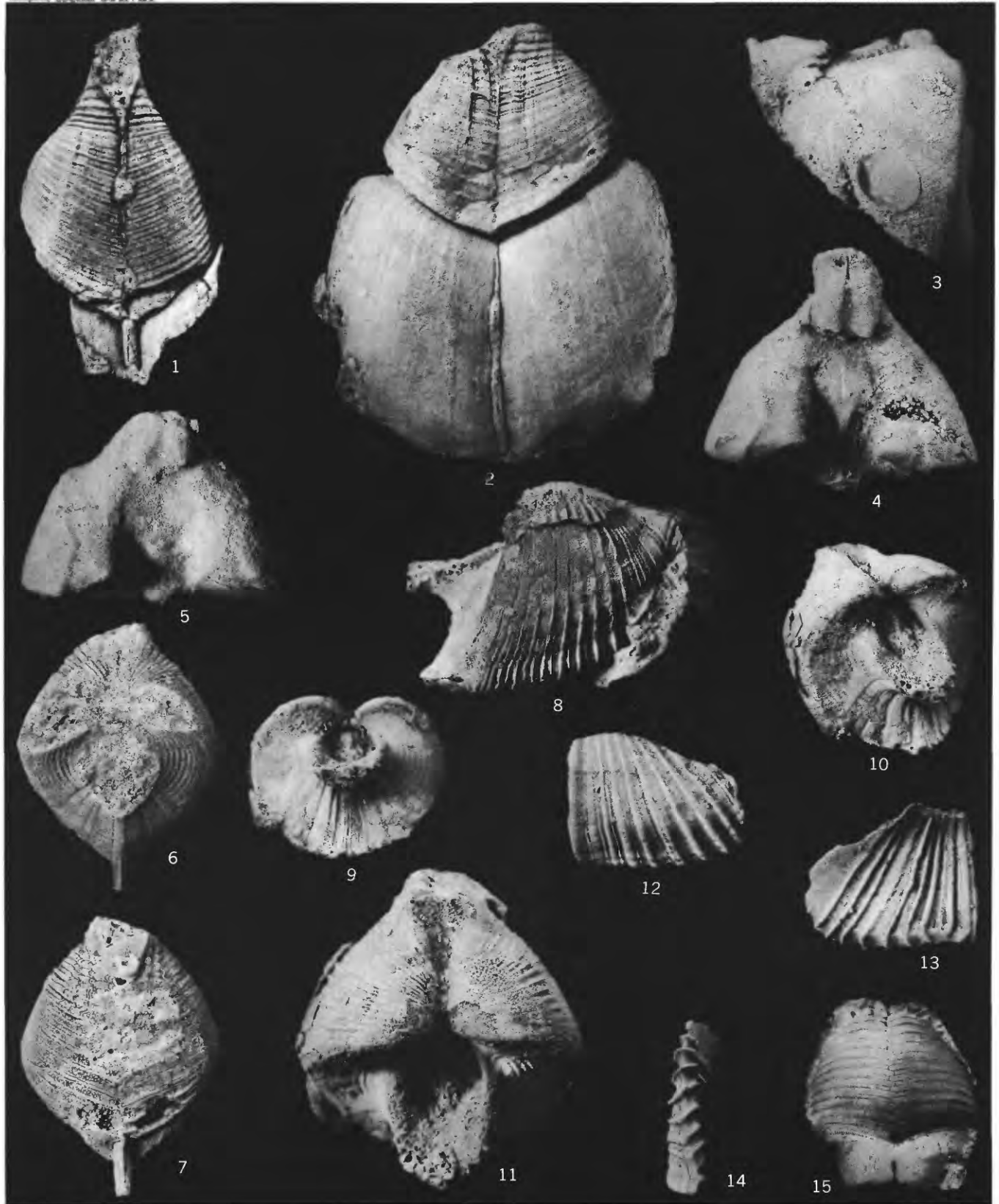
*HIPPOCARDIA*

PLATE 49

FIGURES

1-15. *Hippocardia cunea* (Conrad), 1840 (p. 75).

1-5. Right-lateral ($\times 2$), oblique dorsal ($\times 1.5$), anterior ($\times 1.5$), ventral ($\times 1.5$), and posterior ($\times 2$) views. The last view shows the lamellae that make up the hood in cross section. Horizon and locality the same as on plate 48, figures 12-14. USNM 209276.

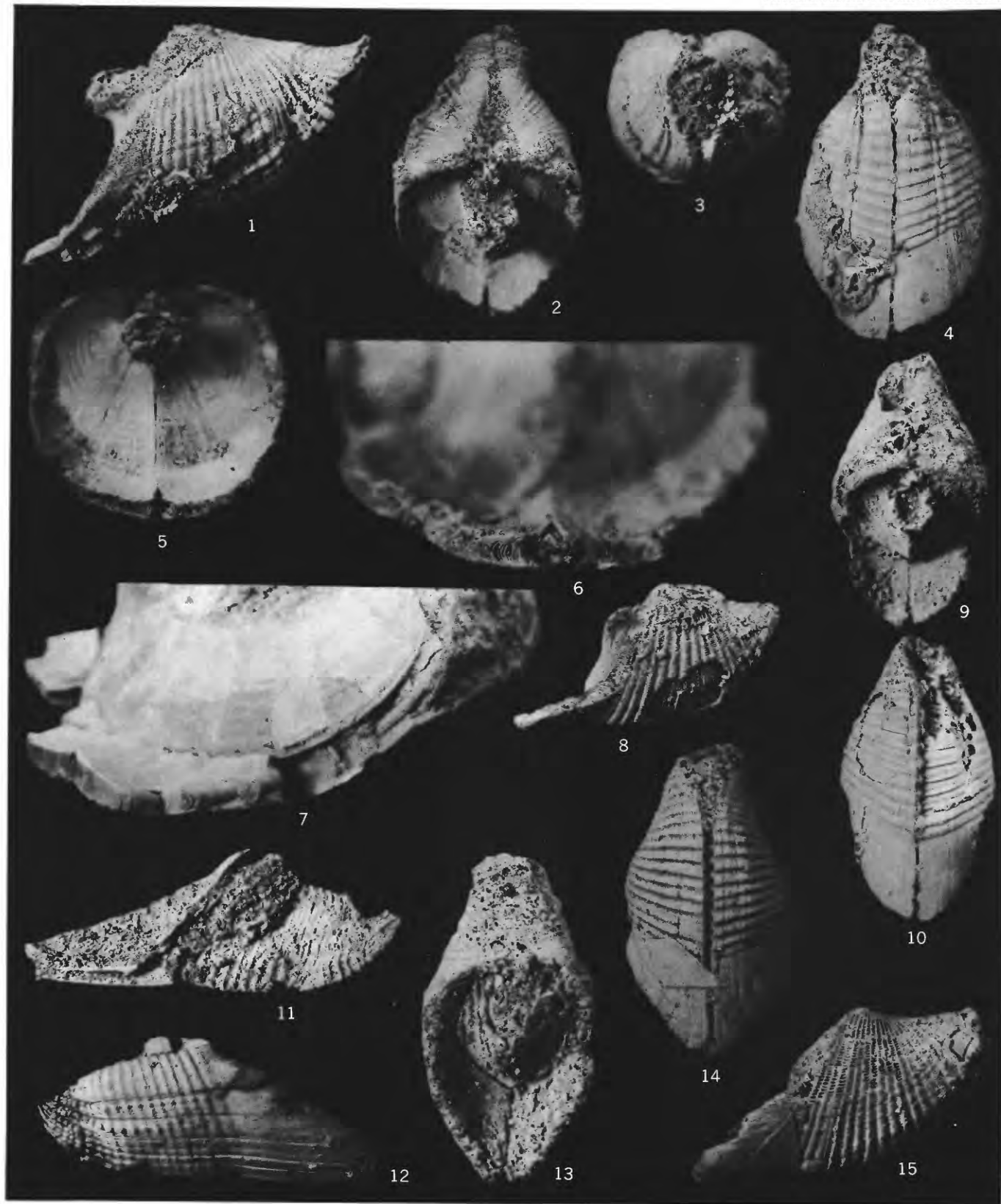
6. Posterior view of edge of hood showing lamellae in cross section ($\times 3.5$). Devonian (Jeffersonville Limestone), Falls of the Ohio River. USNM 51373.

7. Oblique view of broken right edge of hood showing length of lamellae which make up that hood ($\times 3$). Devonian, 2 miles southwest of Sylvania, Lucas County, Ohio. MU 323.

8-10. Right-lateral, oblique dorsal, and ventral views ($\times 1.5$). Horizon and locality the same as on plate 48, figures 12-14. USNM 209277.

11, 12. Interior and exterior views of outer shell layer of posteroventral part of right valve with attached part of hood. Hood begins where radial ribbing stops ($\times 1$). Horizons and locality the same as on plate 48, figures 12-14. USNM 209278.

13-15. Oblique dorsal, ventral, and right-lateral views ($\times 3$) of Nettleroth hypotype (1889, pl. 5, figs. 16-18). Horizon and locality as in figure 6 above. USNM 209279.



HIPPOCARDIA

PLATE 50

FIGURES

- 1, 2. *Hippocardia cunea* (Conrad), 1840 (p. 75).
 1. Right-lateral view ($\times 2$). Horizon and locality the same as on plate 48, figures 12–14. USNM 209267.
 2. Inner surface of outer shell layer of right valve showing the internal ribs built by the marginal denticles and the tubular extension of the ventral aperture into the hood. Horizon and locality the same as on plate 48, figures 12–14. USNM 209268.
3. *Hippocardia pygmaea* (Hisinger), 1837 (p. 76).

Posterior view showing hood ($\times 3$) of Branson hypotype (1942b, pl. 59, fig. 17). According to Valdar Jaanusson (written commun., 1975), the specimen is from Upper Ordovician rocks, Porkuni Stage, Porkuni "Borkholm", Estonia. USNM 98871.
- 4, 5, 11–13. *Hippocardia* sp. (p. 76).
 - 4, 5. Left-lateral and dorsal views ($\times 3$). Silurian (Wenlockian, Slite Beds), Gotland, ditch between Angelbos and Norvarg, Parish of Lärbro, Sweden. SMNH Mo. 18326.
 11. Ventral view showing hood ($\times 3$). Platteville Limestone and Briton Member of Mifflin Formation of Templeton and Willman 1952 (Middle Ordovician), Medusa Portland Cement Co., Lee County, near Dixon, Ill. UI 5261.
 12. Right-lateral view ($\times 2$). Ordovician, quarry north of Church Stake Hall, Criburg district, west Shropshire, England. USNM 100707.
 13. Ventral view showing hood ($\times 2.5$). Middle Ordovician, Rich Valley, Porterfield quarry, 5 miles east of Saltsville, Va. USNM 206509.
- 6–10. *Hippocardia richmondensis* (Foreste), 1910 (p. 76).
 - 6–8. Right-lateral, dorsal, and left-lateral views of holotype ($\times 4$). Elkhorn Formation (Upper Ordovician), 3 miles south of Richmond, Ind. USNM 87041.
 - 9, 10. Right-lateral and left-lateral views ($\times 4$). Richmondian (Upper Ordovician), Ohio. MU 209T.
14. *Hippocardia antiqua* (Owen), 1852 (p. 75).

Left-lateral view of holotype ($\times 3$). Ordovician; the museum label reads: "Lower Fort Garry, Red River of the North, Manitoba," Canada. USNM 17897.
- 15–19. *Hippocardia limatula* (Bradley), 1930 (p. 75).
 15. Left-lateral view of paralectotype ($\times 3$). Kimmswick Limestone (Middle Ordovician), 1 mile north of Batchtown, Ill. FM 29052 (Walker Mus. Colln.).
 16. Right-lateral view of lectotype ($\times 3$). Horizon, locality, and museum number the same as in figure 15 above.
 17. Posterior view showing hood of paralectotype ($\times 3$). Horizon, locality, and museum number the same as in figure 15 above.
 18. Posterior view of paralectotype showing remnant of hood ($\times 3$). Horizon, locality, and museum number the same as in figure 15 above.
 19. Left-lateral view ($\times 3$). Kimmswick Limestone (Middle Ordovician), New Hope, Mo. USNM 209273.
- 20–24. *Bransonia beecheri* (Raymond), 1905 (p. 72).
 20. Left-lateral view of lectotype ($\times 5$). Chazy (Middle Ordovician), Sloop Island, near Valcour Island, N.Y. YU 15322C.
 21. Left-lateral view of paralectotype ($\times 5$). Horizon and locality the same as in figure 20 above. YU 15322B.
 22. Left-lateral view ($\times 3$). Row Park Limestone (Middle Ordovician), 200 feet above base section, 1.3 miles west of Marion, Pa. USNM 209274.
 23. Left-lateral view ($\times 4$). Mosheim Member of Lenoir Limestone (Middle Ordovician), Climer P.O., 7 miles east of Cleveland, Tenn. USNM 209275.
 24. Left-lateral view ($\times 3$). Chazy (Middle Ordovician), Isle LaMotte, Vt. USNM 100709.
- 25–27. *Bransonia* aff. *B. paquettensis* (Wilson), 1956 (p. 73).

Left-lateral, right-lateral, and posterior views ($\times 3$). Holston Formation (Middle Ordovician), Porterfield quarry, 5 miles east of Saltville, Va. USNM 144969.
- 28–37. *Bransonia alabamensis* n. sp. (p. 72).
 28. Right-lateral view of paratype ($\times 5$). Little Oak Limestone (Middle Ordovician), crossroads 1.75 miles northeast of New Hope Church, Ala. USNM 209269.
 - 29–31. Left-lateral, right-lateral, and dorsal views of paratype ($\times 5$). Horizon and locality the same as in figure 28 above. USNM 209270.
 - 32–34. Left-lateral, dorsal, and right-lateral views of holotype ($\times 5$). Horizon and locality the same as in figure 28 above. USNM 209271.
 - 35–37. Right-lateral, dorsal, and left-lateral views of paratype ($\times 5$). Horizon and locality the same as in figure 28 above. USNM 209272.
38. *Bransonia paquettensis* (Wilson), 1956 (p. 73).

Right-lateral view of holotype ($\times 2$). Leray-Rockland Beds (Middle Ordovician), Paquette Rapids, Ottawa River, Ottawa, Ontario, Canada. GSC 11585.

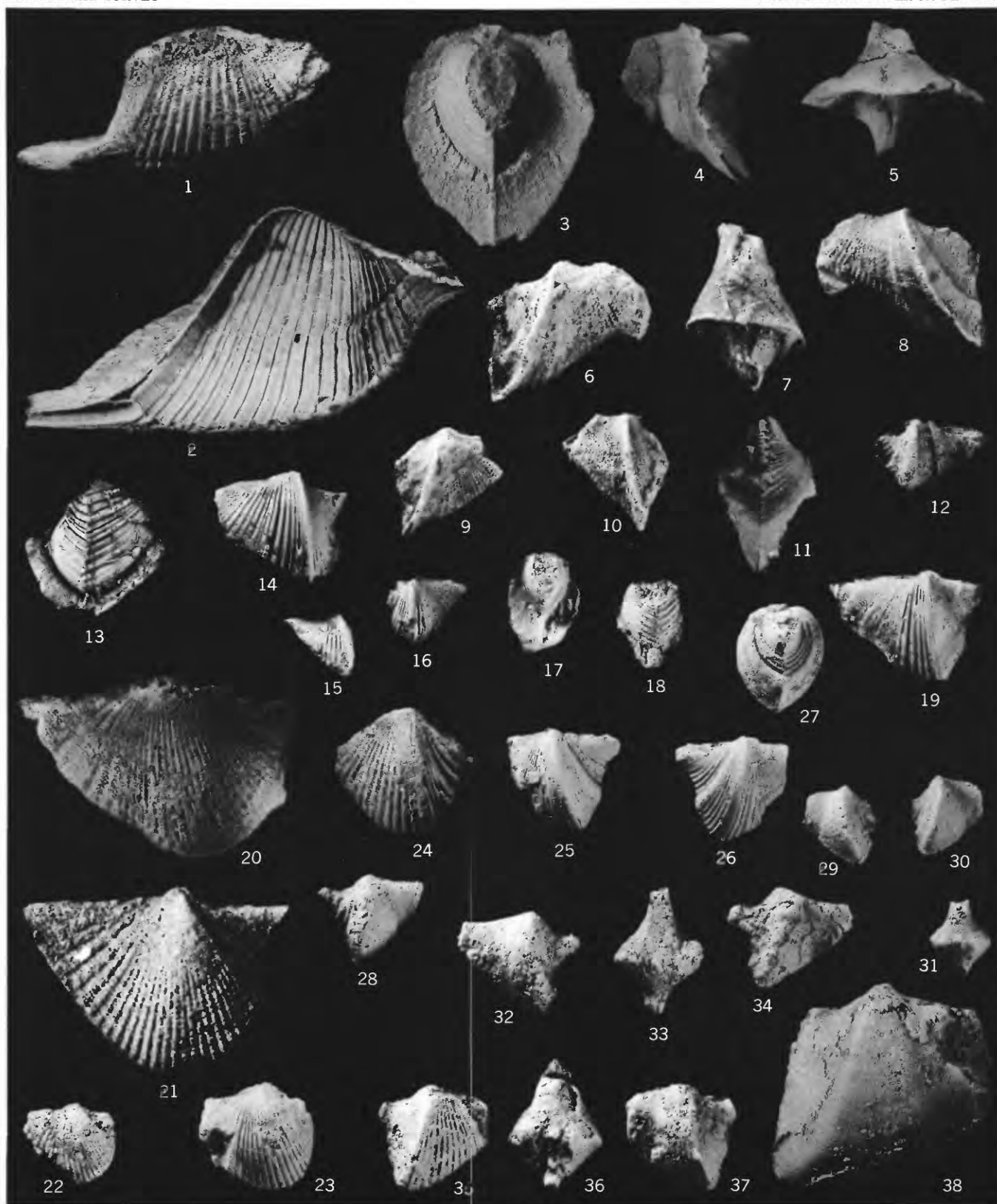
*HIPPOCARDIA AND BRANSONIA*

PLATE 51

- FIGURES 1-10, 17. *Bransonia wilsoni* n. sp. (p. 72).
- 1-6. Left-lateral, right-lateral, dorsal, ventral, anterior, and posterior views of holotype ($\times 1.5$). Middle part of "Homevale beds," lower Tiverton Formation (Permian), ridge southeast of Homevale Homestead, Nebo District, Queensland, Australia. UNE F14789.
 - 7-10. Posterior, anterior, right-lateral, and dorsal views of paratype ($\times 1.5$). Horizon and locality the same as in figures 1-6 above. UNE F14790.
 - 17. Oblique dorsal view of latex replica of paratype ($\times 1.5$). Horizon and locality the same as in figures 1-6 above. UNE F14790.
 - 11. *Conocardium aliforme?* (Sowerby), 1815 (p. 70). Left-lateral view showing muscle impressions ($\times 3$). Carboniferous limestone (Mississippian), Lowick, Northumberland, England. SM E1151.
 - 12-16. *Bransonia robustum* (Fletcher), 1943 (p. 19). Dorsal, ventral, right-lateral, posterior, and anterior views ($\times 1.5$). Permian (Wandrawandian Siltstone), Wyro, near Ulladulla, New South Wales, Australia. AMS F21930.

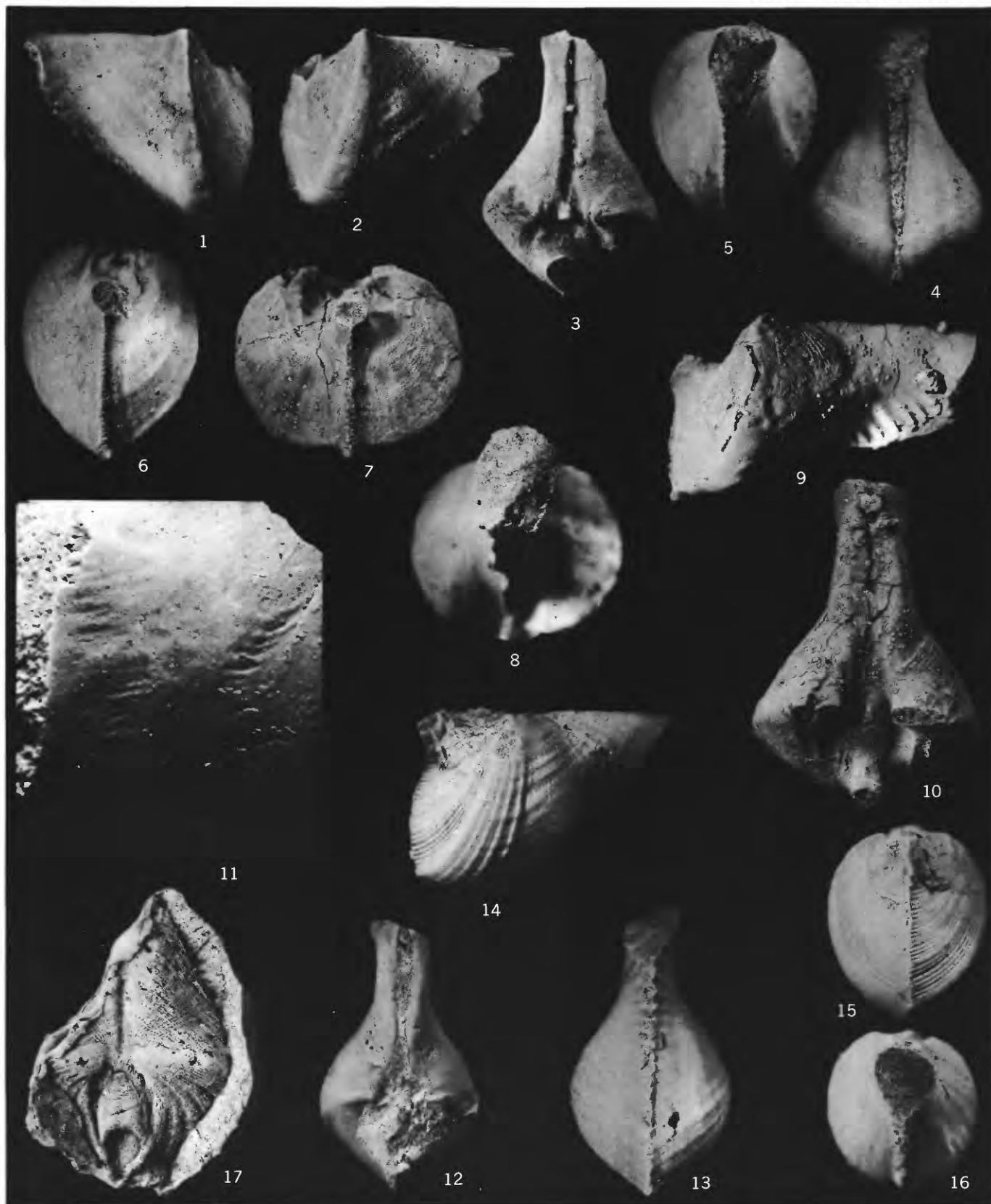
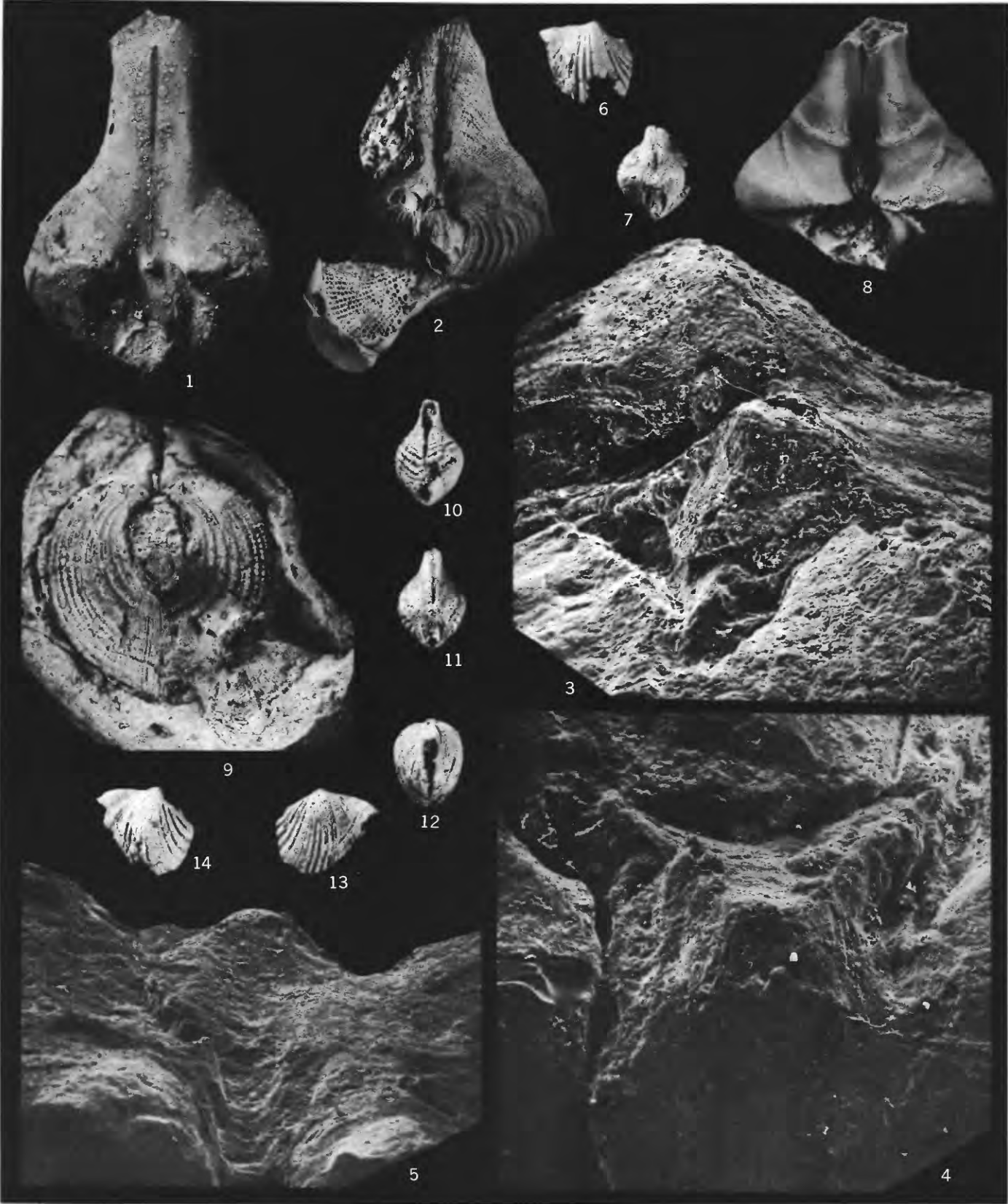
*BRANSONIA AND CONOCARDIUM*

PLATE 52

- FIGURES 1-5, 9. *Bransonia wilsoni* n. sp. (p. 72).
1. Dorsal view of paratype showing internal mold of protoconch ($\times 1.5$). Horizon and locality the same as on plate 51, figures 1-6. UNE F14791.
 - 2-5. Paratype. 2, Latex replica showing ornament and fenestellate bryozoan attached to left posterior face ($\times 1.5$). 3-5, SEM photographs showing protoconch ($\times 25$). Horizon and locality the same as on plate 51, figures 1-6. UNE F14792.
 9. Posterior view of latex replica of paratype showing attached bryozoan ($\times 1.5$). Horizon and locality the same as on plate 51, figures 1-6. UNE F14793.
- 6, 7, 10-14. *Bransonia cressmani* n. sp. (p. 72).
- 6, 7. Left-lateral and dorsal views of paratype ($\times 5$). Salvisa Bed, Perryville Limestone Member of the Lexington Limestone (Middle Ordovician), quarry on Mitchellsburg Road, 0.4 miles south of Perryville, Ky. (USGS loc. 5015-CO). USNM 209265.
 - 10-14. Ventral, dorsal, posterior, right-lateral, and left-lateral views of holotype ($\times 5$). Horizon and locality the same as in figures 6, 7 above. USNM 209266.
8. *Bransonia?* sp. (p. 19).
- Dorsal view of internal mold showing muscle scars ($\times 3$). Windom Formation (*Vitulina* Zone, Hamiltonian, Middle Devonian), Tinkers Falls, Truxton, Cortland County, N.Y. USNM 100703.



BRANSONIA

PLATE 53

FIGURES

- 1-5. *Bransonia?* sp. (p. 19).
Right-lateral, anterior, oblique anterior, left-lateral, and posterior views of an internal mold showing muscle scars ($\times 3$). Horizon, locality, and museum number the same as on plate 52, figure 8.
- 6-20. *Bransonia cressmani* n. sp. (p. 72).
6, 7. Dorsal and right-lateral views of paratype ($\times 5$). Perryville Limestone Member of the Lexington Limestone (Middle Ordovician), quarry on west side of U.S. Route 68, 1 mile north of junction with U.S. Route 150 in Perryville, Ky. (USGS loc. 6916-CO). USNM 209260.
8-10. Left-lateral, right-lateral, and dorsal views of paratype ($\times 5$). Horizon and locality the same as in figures 6, 7 above. USNM 209261.
11-16. Right-lateral, ventral, dorsal, posterior, left-lateral, and anterior views of paratype ($\times 5$). Horizon and locality the same as in figures 6, 7 above. USNM 209262.
17-19. Right-lateral, left-lateral, and dorsal views of paratype ($\times 5$). Horizon and locality the same as on plate 52, figures 6, 7. USNM 209263.
20. Dorsal view of paratype ($\times 5$). Horizon and locality the same as in figures 6, 7 above. USNM 209264.
- 21-23. *Bransonia robustum* (Fletcher), 1943 (p. 19).
Oblique right-lateral, dorsal, and right-lateral views of paratype showing muscle scars ($\times 3$). Horizon and locality the same as in figures 11-16, plate 51. AMS F. 21928.

*BRANSONIA*

PLATE 54

Bransonia cressmani n. sp. (p. 72).

Stero triplet of internal mold showing a large muscle scar in the top center of the right side; anteriorly from this muscle scar passes a part of the pallial line (\times 52). Tanglewood Limestone Member of the Lexington Limestone (Middle and Upper Ordovician), 81 feet above the Macedonia Bed of Grier Limestone Member of Lexington Limestone (Middle Ordovician) in the Frankfort East section on eastbound lanes of Interstate Highway 64, east side of Kentucky River crossing, Franklin County, Ky. USGS loc. D-1200-CO. USNM 209259.



BRANSONIA