

RHYNCHONELLIDA

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Order RHYNCHONELLIDA Kuhn, 1949

[*nom. correct.* MOORE in MOORE, LALICKER, & FISCHER, 1952, p. 221, *pro* order Rhynchonellacea KUHN, 1949, p. 104]

[Diagnosis and Introduction prepared by NORMAN M. SAVAGE, MIGUEL O. MANCENIDO, & ELLIS F. OWEN]

Rostrate articulated brachiopods with biconvex shell that usually has dorsal fold and ventral sulcus; interareas typically low and limited to ventral valve. Shell commonly with coarse costae, sometimes fine; mostly impunctate. Ventral interior typically with dental plates; spondylium normally absent. Dorsal interior commonly with medium septum supporting septalium or hinge plates; outer parts of hinge plates form bases for crura that in recent genera are attached to spirolophous lophophore. *Lower Ordovician (Llanvirn)–Holocene.*

INTRODUCTION

The Rhynchonellida comprise a group distinctive in external morphology, with genera typically rostrate, markedly biconvex, astrophic, strongly ribbed, and with a zigzag anterior commissure. The teeth and sockets are almost always interlocked so that the valves are preserved conjoined and difficult to separate. The ventral valve's internal structures preserved in fossilized material include teeth, often supported by dental plates, and the dorsal valve's internal structures include cardinalia, sometimes supported by a median septum, with anteriorly directed crura. Other important features include muscle attachment scars in both valves.

Many kinds of external and internal structures appear to have evolved several times. Some are variably developed within single species. Muscle scars may be of more taxonomic importance than some of the other

internal features but are commonly poorly known because of the limitations of clarity of serial sections. Classification has been hindered by the various approaches to description and illustration related to differences in preservation. Comparing silicified interiors with internal molds or serial sections impedes accurate differentiation, and workers have sometimes assigned taxonomic significance to features seen in one type of preservation that are rarely visible in other material. Some of these same problems were discussed in the introduction to the rhynchonellide section in the 1965 *Treatise* (MOORE, 1965).

Since the publication of the introductory discussions of SCHMIDT and MCLAREN (1965) on the Paleozoic Rhynchonellida and of AGER (1965) on the Mesozoic and Cenozoic Rhynchonellida in the 1965 *Treatise*, the number of genera has almost tripled, but the approaches and taxonomic procedures adopted by workers describing rhynchonellide genera have changed little, principally because of the limitations imposed by the material. Additional faunas have been collected, and effort has been expended in preparing and illustrating what appear in most instances to be distinctive new taxa. Relatively few comparative taxonomic studies of rhynchonellides on a global scale have been attempted, perhaps because the pace of influx of new taxa has made such studies seem premature. The uneven morphological information made available, particularly with regard to the form of the crura and details of the shell microstructure, may explain why quantitative or cladistic approaches have been rare.

We have attempted to reduce the artificial separation of Paleozoic from Mesozoic and Cenozoic rhynchonellides in our taxonomic treatment, but it remains the case that few

workers truly bridge the Paleozoic-Mesozoic boundary and the associated mass extinction and that there have been resultant terminological and other differences of approach.

GENERIC CHARACTERS OF RHYNCHONELLIDA

As noted above, the number of proposed genera within the Rhynchonellida has expanded rapidly during the past 35 years. Many of the new genera are from newly explored regions. Others reflect the precise discrimination of specialists who become expert in a few families from a relatively small part of the column. In discussing brachiopods in general, COOPER (1970) expressed his view that family characters are found mainly in the interior of the dorsal valve and generic characters on the exterior and in minor details of the interior of both valves but more particularly in the ventral valve. He commented that recent rhynchonellides illustrate the point clearly but that the cardinalia of older rhynchonellides were not sufficiently well known to support the principle. We shall attempt to assess these observations and to examine the relative significance of features used to characterize rhynchonellide genera. Other noteworthy surveys of rhynchonellide features are those of WESTBROEK (1968), whose study is largely confined to the Uncinulidae but with valuable observations on rhynchonellides in general; GRANT (1965a) on Devonian-Permian families; LAURIN (1984) on mid-Jurassic families; JIN (1989) on several Late Ordovician to early Silurian families; and SHI and GRANT (1993) on most Jurassic families.

EXTERNAL FEATURES

Size is significant in a general way. Such genera as *Dorytreta* and *Cryptopora* are always small; others, such as *Ladogia* and *Grandirhynchia*, are consistently large; and most others, such as *Pugnax* and *Tetarrhynchia*, are variable in size. A few extinct giants, like *Septirhynchia* and *Peregrinella*, rivaled in size the largest brachiopods in other orders. Thus size should not be dismissed from generic diagnoses although care should be taken to

allow for the effect of environment, especially temperature and factors causing faunal stunting.

Shape is an important generic feature, notwithstanding the frequency of homeomorphs. The genera *Pleurocornu*, *Hypothyridina*, *Lessinirhynchia*, and many others have a sufficiently distinctive shape that initial diagnosis is unlikely to be reversed by investigation of interior features, although such investigation is always necessary. Outline is rarely diagnostic in itself, but elongation as in *Sphenotreta*, triangularity as in *Oligorhynchia* and *Sphenorhynchia*, circularity as in *Peregrinelloidea*, and transversity as in *Calvinaria* are meaningful diagnostic characters at the genus level. Outline does not, however, appear to be of much familial significance. Other common outline types include subpentagonal, subrhomboidal, securiform, and cordiform. Profile is not as variable or generically diagnostic in the rhynchonellides as in some other brachiopod orders. No genera are resupinate or geniculate in lateral profile, although the terms are often appropriate for describing parts of individual valves, as with the broadly sulcate ventral valve of *Paurorhynchia* and the opposed anterior geniculations of both valves of *Uncinulus*. Although lenticular equibiconvex profiles are common in juveniles, the characteristic lateral profile of rhynchonellides is dorsibiconvex, with varying amounts of dorsal valve inflation. The inflation can become extreme and distinctive, as in *Parapugnax* and *Gibbirhynchia*, but in its less extreme condition is too general to be diagnostically valuable at the genus level. Degree of curvature of the beaks is a profile feature and has been recorded for most genera, yet it usually increases with age and should be used with caution as a generic character. Strength of fold and sulcus in rhynchonellides is often sufficient to be part of the general shape, as with *Pugnax*, *Rhynchonella*, and *Ladogia*. Sometimes the strength, height, and depth of the fold and sulcus are maintained throughout the range of a genus, as exemplified in *Goniorhynchia* and *Rhactorhynchia*.

Further external features that have significance in generic diagnosis include commissure, ornament, presence of marginal spines, development of interareas (rare in Paleozoic rhynchonellides), nature of deltidial plates, and the condition of the foramen. The anterior commissure is of importance as it is variously folded to allow the flow of water into and from the shell. Most rhynchonellides have a strongly uniplicate anterior commissure, although a few genera, such as *Paranorella*, *Camarophorina*, and *Neorhynchia*, have unisulcate commissures. The latter condition, though rare, appears to be more likely to occur in smooth genera. Rhynchonellides usually have costae or stronger plicae superimposed on the fold and sulcus, resulting in a zigzag margin. The extent of the commissural deflection is often great enough to be termed a tongue or linguiform extension. This may be rectangular, as in *Uncinulus* and *Cirpa*, or more rounded, as in *Leiorhynchus* and *Aetheia*. These conditions of the anterior commissure may have generic diagnostic value when they depart from the norm but are otherwise almost routinely present in one of the states described above in any particular family. Although the shape and extent of the anterior commissure is largely determined by the type of fold and sulcus, this is by no means always so. The sulcus of a high-folded species may be shallow with extensive linguiform extension, which might be subquadrate to trapezoidal in general outline. The commissure itself might vary from straight to asymmetrical, as in *Cyclothyris*, or maintain the asymmetry, as in *Torquirhynchia*. In analyzing the posterior part of the lateral commissure one must designate specific features. Beyond the suppression point (Fig. 698.1) of the zigzag deflection (*sensu* RUDWICK, 1970), the commissure is commonly undeflected. A short but pronounced arc, however, sometimes occurs resulting from a semicircular extension of one valve over an underlapping embayment of the other. Paleozoic workers have called such structures squama and glotta (WESTBROEK, 1968). In the Paleozoic genera *Uncinulus* and its allies the arc is ventrally convex (Fig.

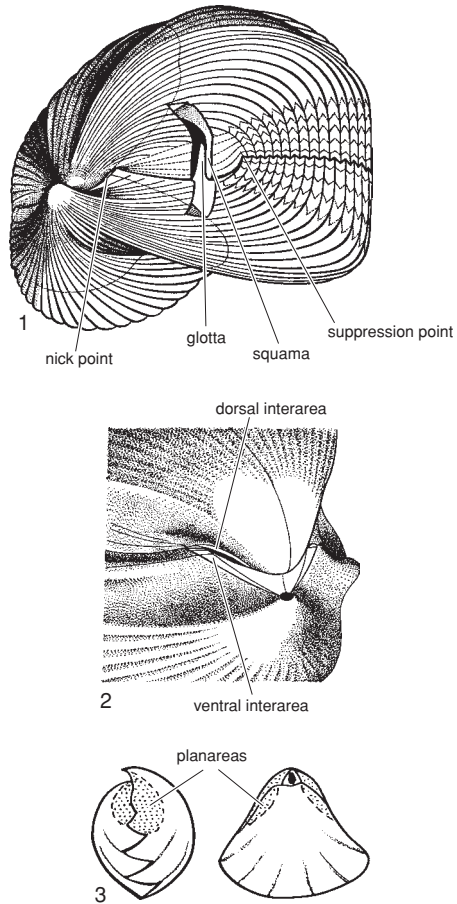


FIG. 698.1, Posterolateral view of *Uncinulus orbignyana* showing lateral commissure; 2, hinge of *Glossinotoechia* showing interareas (adapted from Westbroek, 1968); 3, posterior morphology of rhynchonellid with well-developed planareas, based on *Lokutella* (new).

698.1), whereas in *Plectorhyncha* and *Trigonirhynchia* it is ventrally concave. In post-Paleozoic genera only the ventrally concave condition has been observed (MANCENIDO & OWEN, 1996). The stolidium is a thin, marginal extension of one or both valves that forms a frill protruding at an angle to the main commissural plane of the shell. It is common in genera of the Stenoscismatoidea and exemplified by *Stenoscisma*.

Radial ornament is present in the earliest known rhynchonellides. Smooth forms do not occur until later, becoming increasingly frequent but never prevalent. The details of

ornament are usually of generic value, and the point at which changes occur during the growth of an individual can be diagnostic, such as the change from smooth initially to costate at midlength and then the development of a fold and flanking plicae more anteriorly. Such changes clearly relate to the aspect of the gape at the commissure during successive growth stages. The ratio of body size and water inflow requirement to commissure length increases disproportionately as growth proceeds. The possible need to restrict access to harmful predators or extraneous particles may have influenced the development of the zigzag margin and other flexures. Costae and plicae also increase shell strength. The various combinations of costae, fold and sulcus, and flanking plicae, occasionally with superimposed fine striae, are all of importance in diagnoses. The attention paid by many workers to angularity of costae may be misplaced except for genera where angularity or roundness is especially marked. Usually the angularity is variable within a genus and often within a species. Such genera as *Rhynchotrema* and *Flabellirhynchia* have simple costae continuous from beak to anterior and lateral margins; others such as *Fenestrirostra* and *Sedenticellula* have costae that increase by bifurcation and intercalation, with a tendency toward infrageneric and infraspecific variation. A few genera have distinctive radial striae superimposed on coarser costae, as in *Yunnanella*, *Porostictia*, and *Paraphorhynchus*. Others have fine costae that merge anteriorly to form coarse costae or plicae (antidichotomous ribbing), as in *Schnurella* and *Nayunnella*. Although superimposed striae are distinctive at the genus level, it may be debated whether they have arisen only once and justify the inclusion of these disparate genera in a single family. *Porostictia* is particularly unusual among rhynchonellides in having the fine radial striae separated by rows of fine pits or exopunctae. Some genera develop short spines that tend to follow the radial ornament, although they are truly extensions of the lamellae.

Concentric ornament in rhynchonellides consists of fine growth lines and lamellae and has limited diagnostic value. In a few genera, such as *Lepidocyclus*, the concentric growth features are strongly lamellose and may have taxonomic significance, although whether at the subfamily level, as has been used for the Lepidocyclinae, may be questioned. *Protegorhynchia* and *Tegulorhynchia* have spinelike extensions of the lamellae. Some specimens of *Acanthothiris* have radial spines of this kind that are several centimeters long.

Marginal spines have been discussed in detail by WESTBROEK (1968) and RUDWICK (1970). These spines grew as an enrollment of shelly extensions from the margin and commonly display a suture along their commissural side. They are elongate in representatives of the Uncinulidae, where genera frequently have geniculate dorsal and ventral anterior and lateral valve margins, so that the spines are vertically disposed and fit into notches or grooves in the opposing valve. In *Kransia* the valve margins are straight, but the spines are long and fit into appropriate grooves on the inside of the opposite valve to form a grille that probably restricted access to intruders or extraneous particles, although WESTBROEK (1968) contended that they should be viewed more as a sensory warning system rather than a physical barrier to access. One might reason that they served both functions, initially resulting in the closing of the valves, but eventually permitting sufficient gape for some feeding and respiration. In *Uncinulus* the valve margins are moderately serrated and the spines less elongate but in combination form an effective grille that presumably performed the same service as in *Kransia*. Shorter spines that occur in the genera *Glossinulus* and *Eoglossinulus* arise at the tips of more strongly serrated valve margins, and even shorter spines in *Sphaerirhynchia* arise from the tips of zigzag valve margins and fit into grooves on the inside of the opposite valve.

The rostrate and astrophic nature of most rhynchonellides means that interareas are often absent. The narrow hinge and incurved

nature of the dorsal beak into the ventral delthyrium obscures the interareas even in those genera where they are developed (Fig. 698.2). Interareas have been described in a few thin forms where the umbones are not pronounced, generally from such early Paleozoic genera as *Drepanorhyncha* and *Oligorhynchia*. Mesozoic and Cenozoic genera more commonly have marked interareas that are of diagnostic value. These include *Cardinirhynchia* and *Flabellirhynchia* from the Jurassic and *Cyclothyris* from the Cretaceous. A number of Paleozoic and Mesozoic genera, including all Rhynchotetradoidea and Septirhynchiidae, have flat to concave planareas on either side of the posterior part of one or both valves (Fig. 698.3).

The delthyrium and deltidial plates are of uncertain taxonomic value. Many early rhynchonellides, such as *Ancistrorhyncha*, *Drepanorhyncha*, and *Orthorhynchula*, have an open delthyrium or very narrow marginal thickening that leaves the delthyrium of the ventral valve essentially open. Others, such as *Fenestrirostra*, have narrow elongate deltidial plates that do not meet. Most rhynchonellides, however, have well-developed deltidial plates. Although these are used commonly in generic diagnoses, some variation may occur even within a population of a single species. Conditions include disjunct, as in *Cupularostrum* and *Hemithiris*, conjunct, as in *Hypsiptycha* and *Basiliola*, and duplex, as in *Rhynchotrema* and *Cirpa* (see COOPER, 1970, pl. 2, fig. 12, 15, 17–19). A rounded foramen to accommodate the pedicle is usually present posteriorly near the apex of the valve so that even when the deltidial plates are conjunct they often lack their apical tips, as in *Hypsiptycha*. Occasionally the deltidial plates are alate, as in *Grammetaria* and *Ptilotorhynchus*, but this condition may not be a generic character, sometimes varying within a genus from extreme, as in *Cryptopora rectimarginata* COOPER, to barely evident, as in *Cryptopora gnomon* (JEFFREYS). The position of the foramen relative to the apex of the delthyrium has often been used as a generic character when

it departs significantly from the usual submesothyrid condition, as in *Neorhynchia*, which has a hypothryid foramen. Other types of foramen position, such as epithryid and permesothyrid, and other types of delthyrial covers, such as a notodeltidium or a pseudodeltidium, do not seem to occur in rhynchonellides.

INTERNAL FEATURES

Internal features in the ventral valve variously used in generic diagnosis of rhynchonellides include details of the dental plates and associated lateral umbonal chambers, teeth, and platforms (Fig. 699.1b). Those in the dorsal valve include the details of the hinge plates, cardinal process, median septum, and crura (Fig. 699.1a).

Immediately inside the foramen a pedicle collar may be present, but this is of doubtful value as a taxonomic feature, despite the weight accorded it for younger genera by some workers. Muscle scars are inadequately known for most genera and often have not been included in our diagnoses. This is because they are indistinct in serial sections except in such families as the Leiorhynchiidae, where the muscle attachment areas are deeply impressed. When internal features are readily visible, as in molds, calcined, or silicified shells, the muscle scars may have considerable generic and familial value. In the ventral valve the adductor scars are commonly small and enclosed by the diductor scars, which are long and lacrimiform. In the dorsal valve the adductor scars usually form a quadrate pattern mostly confined to the posterior half of the valve, with the posterior adductors slightly smaller than the anterior adductors. The details of the arrangement are of generic importance, but the variable information about most genera hinders comparison.

Dental plates are present in most rhynchonellides and vary enough to have been used widely in generic diagnosis. They are reasonably constant within a genus and are easily observed except where they are very close to the shell wall or where the associated

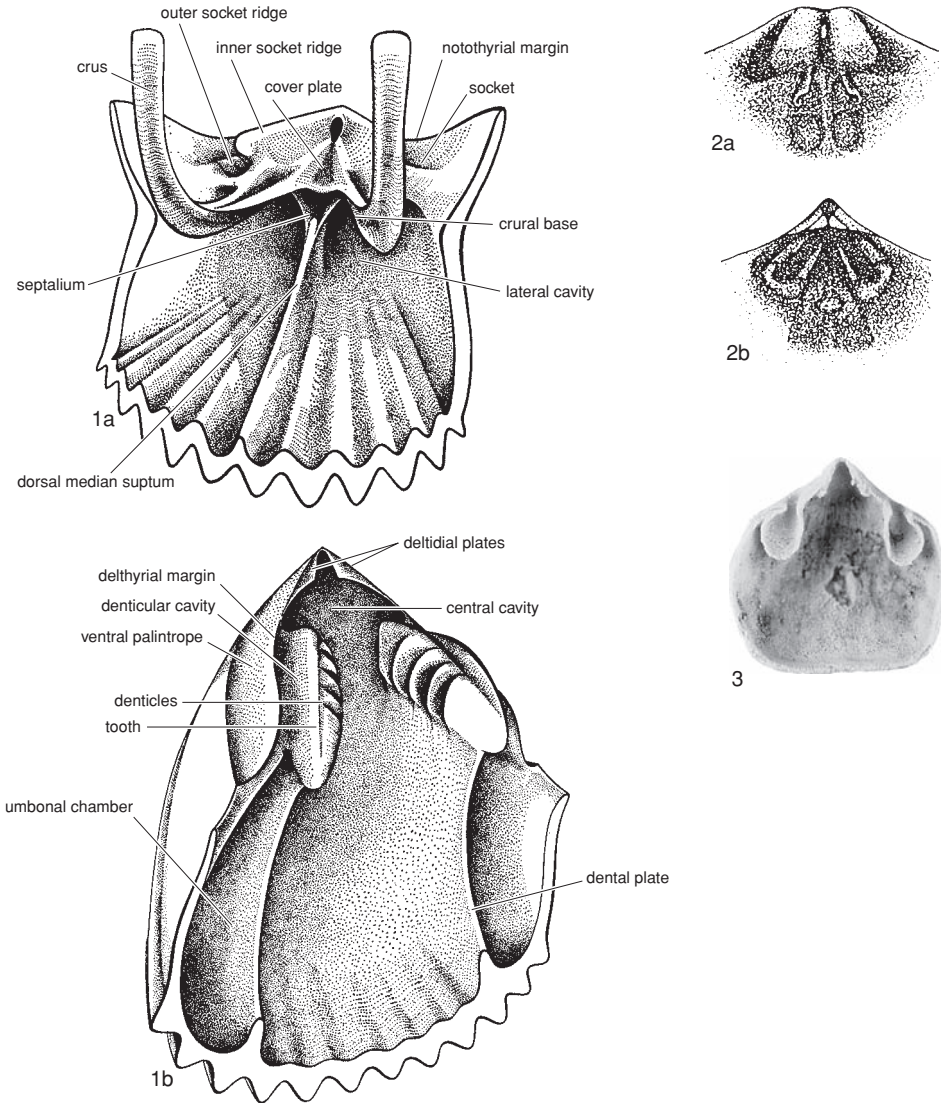


FIG. 699. 1, Internal morphology of posterior of *Trigonirhynchia paretii*, a, dorsal valve, b, ventral valve (adapted from Westbroek, 1968); 2, internal morphology of posterior of *Australirhynchia*, showing a, inflated inner socket ridges in dorsal valve, and b, long, deeply grooved teeth in ventral valve (adapted from Savage, 1968); 3, internal morphology of ventral valve of *Amphipella*, showing pouchlike apricatria (Cooper & Grant, 1976).

lateral umbonal cavities are filled with callus, as in *Uncinulus*, or where the plates are short and only clearly present in younger individuals, as in *Ellesmerhynchia*. The dental plates may be vertical, as in *Petasmaria*; medially convex, as in *Ladogia*; medially concave, as in *Stegorhynchella*; divergent toward the valve floor, as in *Trigonirhynchia*; convergent to-

ward the floor, as in *Prionorhynchia*; convergent to form a spondylium, as in *Rhynchotetra*; or may otherwise display a consistently distinctive form that may be useful in generic and even familial diagnosis. Associated with the dental plates are the lateral umbonal cavities between the plates and the valve wall. The shape and size of the cavities are depen-

dent on the configuration of the plates relative to the contours of the shell wall. The various shapes of the cavities have not been used much in generic diagnosis, and the feature is probably too dependent on infraspecific variation, age of individuals, and degree of callus infilling to be of much value.

Teeth of rhynchonellides are sometimes elongate and transversely corrugated in heavy, thick-shelled genera with sturdy dental plates, as in *Trigonirhynchia* (Fig. 699.1b), or may be small and smooth in genera with short dental plates or more delicate shells, as in *Orthorhynchula*. Crenulated teeth are sometimes present in thin-shelled genera, such as *Basiliola* and *Neorhynchia*. A fossette may be developed on the inner side of the tooth where it presses against the inner socket ridge (Fig. 699.2b). This may add to the rigidity of the articulation, and in extreme cases the fit of the inner socket ridges into the fossettes may become as important in holding the valves together as the fit of the teeth into the sockets. The shape of teeth can vary from a simple deltidiodont condition to a more hooked condition that may help lock the valves together. In general the shape and surface of the teeth have not been given much taxonomic significance by workers, perhaps because they are difficult to describe from sections or because they vary with shell thickness and other age factors.

Muscle platforms are unusual yet of considerable value in generic and familial diagnoses. They help characterize the Stenoscismatoidea, which have a camarophorium in the dorsal valve and usually a spondylium in the ventral valve, and a few other Paleozoic groups, such as the Camerophorinidae, which have a spondylium, and the Tetracameridae and Rhynchotetradidae, which have a low or sometimes sessile spondylium.

The hinge plates form an important part of the rhynchonellide dorsal valve and include all the cardinalia except for the cardinal process, thus comprising the sockets and socket ridges, the outer and inner hinge plates, the crural bases and, if present, the crural plates and septalium (Fig. 699.1a).

The hinge plates as a whole perform two important unrelated functions in rhynchonellides: they provide support for the sockets and provide attachments for the crura. The outermost parts of the hinge plates are connected to the valve walls and are often coincident with the outer socket ridges. Medially from the outer socket ridges lie the sockets and the inner socket ridges. The outer hinge plates then extend medially from the inner socket ridges to the crural bases, and the inner hinge plates or sometimes the crural plates extend medially from the crural bases. The term inner hinge plates is used for plates that are horizontal or subhorizontal, as in *Glossinotoechia* and *Frieleia*. If the plates medial of the crural bases are inclined to meet the valve floor or form a V-shaped septalium supported by a median septum that joins the valve floor, they are generally termed crural plates. Often the crural bases can be seen as discrete structures, distinct from the outer hinge plates laterally and the inner hinge plates or crural plates medially. Occasionally, as in *Trigonirhynchia*, a cover plate caps the septalium for part or all its length. This terminology differs from that of WESTBROEK (1968) and JOHNSON and WESTBROEK (1971), who considered the cover plate over a septalium to be formed by the inner hinge plates. WILLIAMS and ROWELL (1965a) considered that in some rhynchonellides the inner hinge plates and the septalial (crural) plates are two distinct sets of plates that lie successively medial of the crural bases. JIN (1989) defined a septalium as a trough-shaped chamber encompassed by a pair of hinge plates, crural bases, and septalial plates and did not limit the composition of the septalium to any specific pair of these plates. If these features occurred only in rhynchonellides, had a distinctive microstructure, or developed at very different growth periods in individuals, the terminological discrepancies described above would be easier to settle. Hinge plates, however, are present in several different orders, and the component features are variously developed in these orders. The component features are

also variously developed within the rhynchonellides so that more terms are needed to describe the relatively complex hinge plate of *Trigonirhynchia*, with its outer hinge plates, crural bases, septalium, and cover plate (Fig. 699.1a), than that of *Australirhynchia* SAVAGE (1968), where the swollen inner socket ridges almost meet and the crura appear to arise directly from these ridges (Fig. 699.2a). These various structures and their numerous combinations have been assigned great importance by most workers in their generic diagnoses of rhynchonellides.

Outer socket ridges may have considerable taxonomic utility. Those genera that have a relatively wide ventral valve at the hinge line, such as *Glossinulus* and *Eucharitina*, usually have the teeth directed inwardly so that the outer socket ridge may be low. In those with a comparatively narrow ventral valve at the hinge line, such as *Stegerhynchus* and *Lepidocyclus*, outer socket ridges tend to be much larger. The socket floor may be smooth, as in *Glossinulus*, or crenulate, as in *Trigonirhynchia*, and this is used as a generic characteristic where it has been recognized. The length and orientation of the sockets is often dependent on whether the shell is strophic, in which case the sockets are usually short, relatively transverse, and parallel to the hinge line, as in *Sphaerirhynchia*, or astrophic, which is normal in rhynchonellides and causes the teeth and sockets to be more anteriorly directed and relatively locked in position. As these structures really do not articulate to any significant extent, they can become quite elongate, as in *Australirhynchia*, where the sockets are smooth, and in *Trigonirhynchia*, where the sockets are crenulate. Inner socket ridges vary greatly in size and may be small in more strophic shells, such as *Porostictia*, or very large in astrophic shells such as *Australirhynchia*, particularly when these are mature or gerontic specimens (Fig. 699.2a). Medially from the inner socket ridges there is not much outer hinge plate present in many of the earlier rhynchonellides, such as *Rhynchotrema*, but by about Middle Devonian time hinge plates were often broader and more complex so that in

Uncinulus, *Parapugnax*, and *Porostictia* there are distinct horizontal outer hinge plates between the inner socket ridges and the crural bases. The width, inclination, and outline of these have been afforded considerable generic importance by rhynchonellide workers.

Crural bases are usually distinct in the shell interior and in serial sections so that they form a valuable reference point in describing the hinge plates. Individually they form a rodlike or bladelike dense structure along the medial edge of the outer hinge plate. Their distal extensions are generically distinctive and will be discussed below under the section on crura. Inward from the crural bases the hinge plates are often divided, as in *Orthorhynchula* and *Callipleura*, and the outer hinge plates and crural bases may then be supported by crural plates that can extend down to the valve floor, as in *Callipleura* and *Septocrurella*. Alternatively, the crural plates may unite to form a septalium supported by a median septum, with a cover plate, as in *Trigonirhynchia*, or without a cover plate, as in *Hebetoecchia* and *Piarorhynchia*. In addition, the subhorizontal inner hinge plates may be divided, as in *Hispanirhynchia*, or variably united, as in *Frieleia* and *Aetheia*.

Repeatedly referred to above, the septalium is a feature deserving special attention because, since its proposal by LEIDHOLD (1921), it has been sometimes misused or variously given other names. Essentially the same structure is also named in Mesozoic specimens a muscle trough by PEARSON (1977) and in Paleozoic specimens a crural cavity by WELLER (1910) and a cruralium by COOPER (1970). Even the noncommittally named apical V-shaped chamber of COOPER (1959), used for some Cenozoic forms, was subsequently regarded as a septalium by DAGYS (1968). When it occurs, it is a V-shaped or U-shaped structure, restricted in length to the vicinity of the hinge line, and apparently functioning to spread the support from the median septum to the outer hinge plates and thus buttress the sockets (Fig. 699.1a). As employed herein the usage of the term is consistent with CHILDS (1969),

JOHNSON and WESTBROEK (1971), DELANCE and LAURIN (1973), JIN (1989), and BRUNTON, ALVAREZ, and MACKINNON (1996). Genera without such a structure usually have alternative support for the sockets, as with the crural plates of *Callipleura* and *Machaeraria* or the separate oblique septal buttresses directly attached to the valve floor, as in *Crurirhynchia*. The sockets may rest directly on the valve floor or wall, as in *Lepidorhynchia* and *Sulcatina*, or be supported by thick shell material below the hinge plate, as in *Pegmarhynchia*. Thus in one way or another the pressure that the teeth exert on the sockets is spread, and the whole rigid articulation structure that characterizes the rhynchonellides is strengthened. Usually a genus is characterized by a single one of these structures, but JIN (1989) has shown that in *Fenestrirostra* several different structures evolved in successive early Llandoveryan species on Anticosti Island, commencing with thick shell material below the hinge plate in *Fenestrirostra primaeva*, followed by a fairly typical septalium supported on a median septum in *Fenestrirostra glacialis* and then by hinge plates supported by oblique buttresses from the valve walls in *Fenestrirostra pyrrrha*. In each of the species there is some development of a septalium posteriorly, but its importance as a support at the point of articulation differs considerably. If this lineage is a guide, giving too much generic significance to the size of the septalium seems unwise. SHI and GRANT (1993) suggested that in both the ontogeny and phylogeny of some evolutionary lineages the septalium may be a structure that became gradually obsolete.

The dorsal median septum is part of the buttressing structure for the articulation, and, as with the plates of the septalium that it commonly supports, it is variably developed and not always a reliable family character. Some median septa appear not to be supportive of any cardinal structure but seem merely to divide the lophophore or muscles. In many families, such as the Ancistrohynchidae, Allorhynchidae, Petasmatheridae, Amphipellidae, Pontisiidae, and

Basiliolidae, a dorsal median septum is rare or absent, usually because the sockets are small and supported by the valve walls. In other families, such as the Uncinulidae, the presence of a median septum is variable, but usually the hinge plates are close to the valve floor and often supported by crural plates or callus. In families where the median septum is present, as in the Rhynchonellidae, Rhynchotetradidae, and Tetrarhynchiidae, the details of its size and other features are useful generic characters. Much rarer is the development of a ventral median septum, usually supporting a spondylium, as in *Camerophorina*, *Nantanella*, and all Stenoscismatoidea, or exceptionally free, as in *Septirhynchia*.

A cardinal process increased the area of diductor muscle attachment or otherwise made the attachment more secure, varying with the plan of the particular taxon and its stage of growth. It also allowed the diductor attachment surface to protrude into the ventral valve to permit specific valve articulation relationships and muscle arrangements as discussed by RUDWICK (1970) and CARLSON (1989). A cardinal process is more frequent in Paleozoic genera than in post-Paleozoic genera, although absent from such earlier rhynchonellide families as the Ancistrohynchidae, Oligorhynchiidae, Trigoni-rhynchiidae, and Leiorhynchidae. In families where it occurs it is variable but usually regarded as having generic significance. In the Rhynchotrematidae the cardinal process is normally septiform, as in *Rhynchotrema*. This seems to be a primitive condition. In the Orthorhynchulidae a cardinal process is generally present, but in this family the shape varies from septiform, as in *Zlichorhynchus*, to branched, as in *Orthorhynchyllion*. In the Uncinulidae several genera have a tongue-like cardinal process that protrudes well into the ventral valve, as in *Glossinulus* and *Markitoechia*; but others have a broader multilobed process, as in *Glossinotoechia*, or a bulbous process, as in *Uncinulus*. In the Eatoniidae the cardinal process is bilobate, trilobate, or quadrilobate; and in *Eatonia* and *Eucharitina* it is massive, bilobed, and deeply excavated,

forming a structure that occupies much of the hinge plate. Thus, although the cardinal process is not developed at all in several families, it can be complex and have considerable familial and generic diagnostic value when it is present.

The crura of living rhynchonellide genera are paired processes extending from the hinge plates and associated with the proximal ends of the soft lophophore spires. The crural bases enclose an angle within which the food particles are directed from the food grooves of the lophophore and into the mouth. The crura of fossil rhynchonellides are varied, and although several crural types have been recognized, those of most genera are poorly known. This is partly because of difficulty finding delicately preserved specimens that can be sectioned to the distal tips of the crura (SAVAGE, 1996). The lack of knowledge is unfortunate since details of the crura appear to be of considerable taxonomic value. AGER (1965) considered the three most common types of rhynchonellide crura to be those described by ROTHPLETZ (1886) as raduliform, falciform, and septiform. A further 14 types that have been listed or proposed by later workers are discussed and illustrated herein. 1. Arcuiform crura (Fig. 700.1) were first described by WISNIEWSKA (1932, p. 6) based on the genus *Monticlarella*. Later discussion and illustrations of AGER (1965, p. 599, fig. 478,4), SMIRNOVA (1965), and DAGYS (1968, 1974) show that these crura are widely divergent. Each is short and laterally compressed with its distal end flared dorsoventrally. 2. Spinuliform crura (Fig. 700.2) were described by COOPER (1959, p. 9) and also discussed and illustrated by AGER (1965, p. 600, fig. 478,7) and DAGYS (1968, 1974). These crura are also widely divergent. Each is short, narrow, and relatively straight although inclined slightly toward the ventral valve. AGER stated that these could be viewed as laterally compressed variants of the radulifer type with ancestors back in early rhynchonellide stock. 3. Flared arcuiform crura (Fig. 700.3) as in *Tethyrhynchia*. These were called lunifer in LOGAN and ZIBROWIUS, 1994. Each has its

distal end extremely flared dorsoventrally. 4. Falciform crura (Fig. 700.4) were first described by ROTHPLETZ (1886, p. 86). The type has been further discussed and illustrated by COOPER (1959), AGER (1965, p. 598, fig. 478,2), and DAGYS (1968, p. 34, fig. 27b, 28b). These crura arise on the dorsal side of the hinge plates and project more into the dorsal than the ventral valve. The broad subvertical blades are sickle shaped or sigmoidal in section. Falciform crura are associated with divided hinge plates and a reduced median septum. They have been recorded mostly in Mesozoic and Cenozoic genera. 5. Subfalciform crura (Fig. 700.5) resemble falciform crura but have a crescentic (instead of falcoid) cross section and may be serrated distally, as in *Acanthobasiliola*. 6. Hamiform (=prefalciform) crura (Fig. 700.6) of PEARSON (1977), replacing the term prefalcifer of AGER (1962). Each is short, straight, and slightly compressed, as in *Pseudogibbirhynchia*. 7. Septiform crura (Fig. 701.1) were first described by ROTHPLETZ (1886, p. 86) and further discussed and illustrated by AGER (1965, p. 598, fig. 478,3). There is some discrepancy of interpretation, which was emphasized by DAGYS (1968, p. 37). Septiform crura are subparallel. Each is wide proximally with its inner edge descending to meet the valve floor, as in *Septocrurella*. 8. Lyrate septiform crura (Fig. 701.2) are septiform crura that are more divergent and have a lyrate cross section distally, as in *Pygmaella*. 9. Raduliform crura (Fig. 701.3) were first described by ROTHPLETZ (1886, p. 86) and further discussed by COOPER (1959), AGER (1965), and DAGYS (1968). These crura are common and simple. They are relatively long, rodlike projections that curve uniformly forward into the ventral valve and may show considerable variation in cross section (subtriangular, compressed, squarish, elliptical) and in distal ends (barbed, hooked). They are generally accompanied by a more or less well-developed dorsal median septum. They are interpreted here to include the hamuliform type of JIN (1989) that has small, incurved distal hooks on the crura. Raduliform crura are commonly

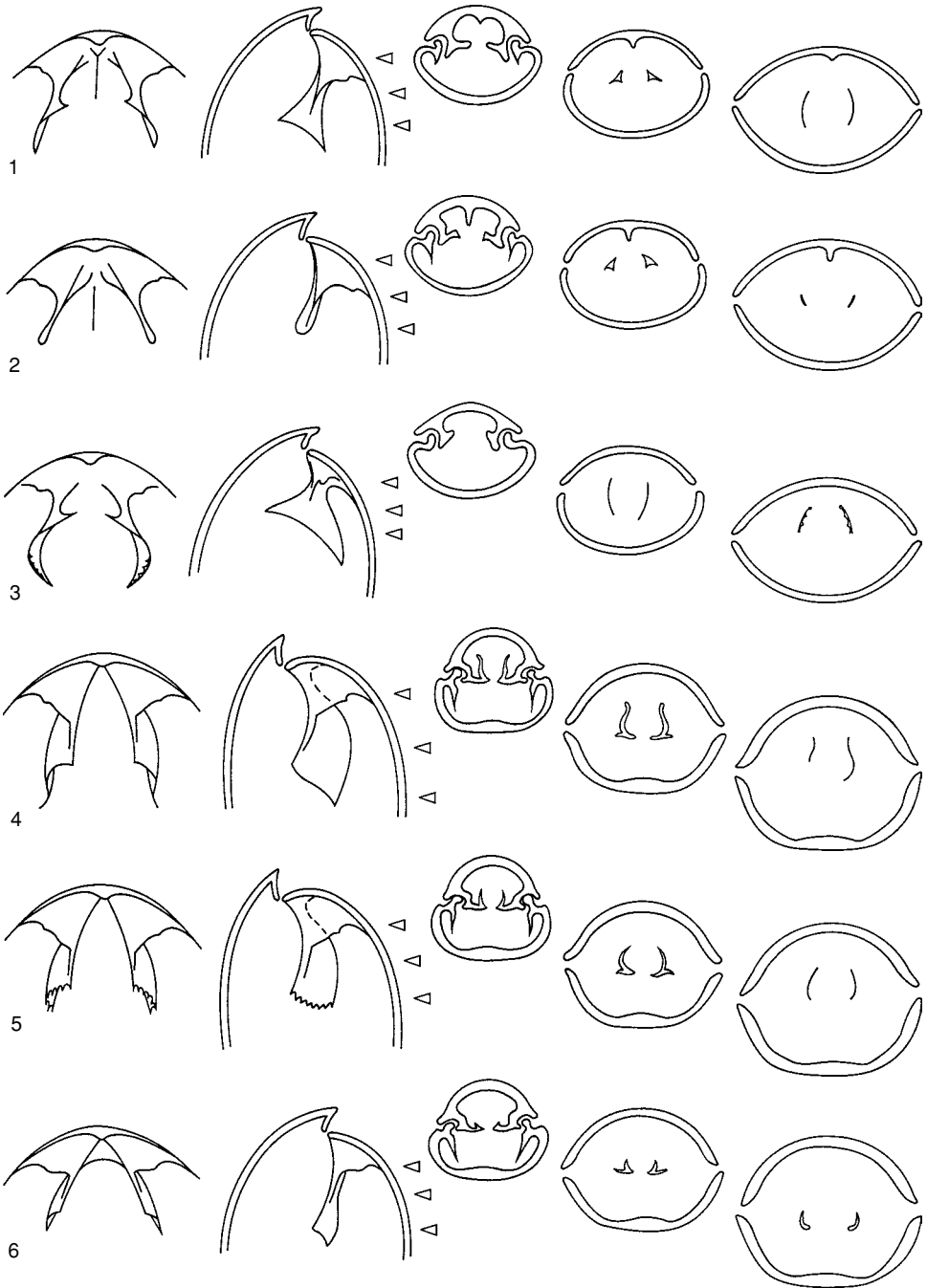


FIG. 700. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; 1, arcuiform crura, based on *Monticlarella*; 2, spinuliform crura, based on *Frieleia*; 3, flared arcuiform crura, based on *Tethyrhynchia*; 4, falciform crura, based on *Lacunosella*; 5, subfalciform crura, based on *Acanthobasiliola*; 6, hamiform (=prefalciform) crura, based on *Pseudogibbirhynchia* (new).

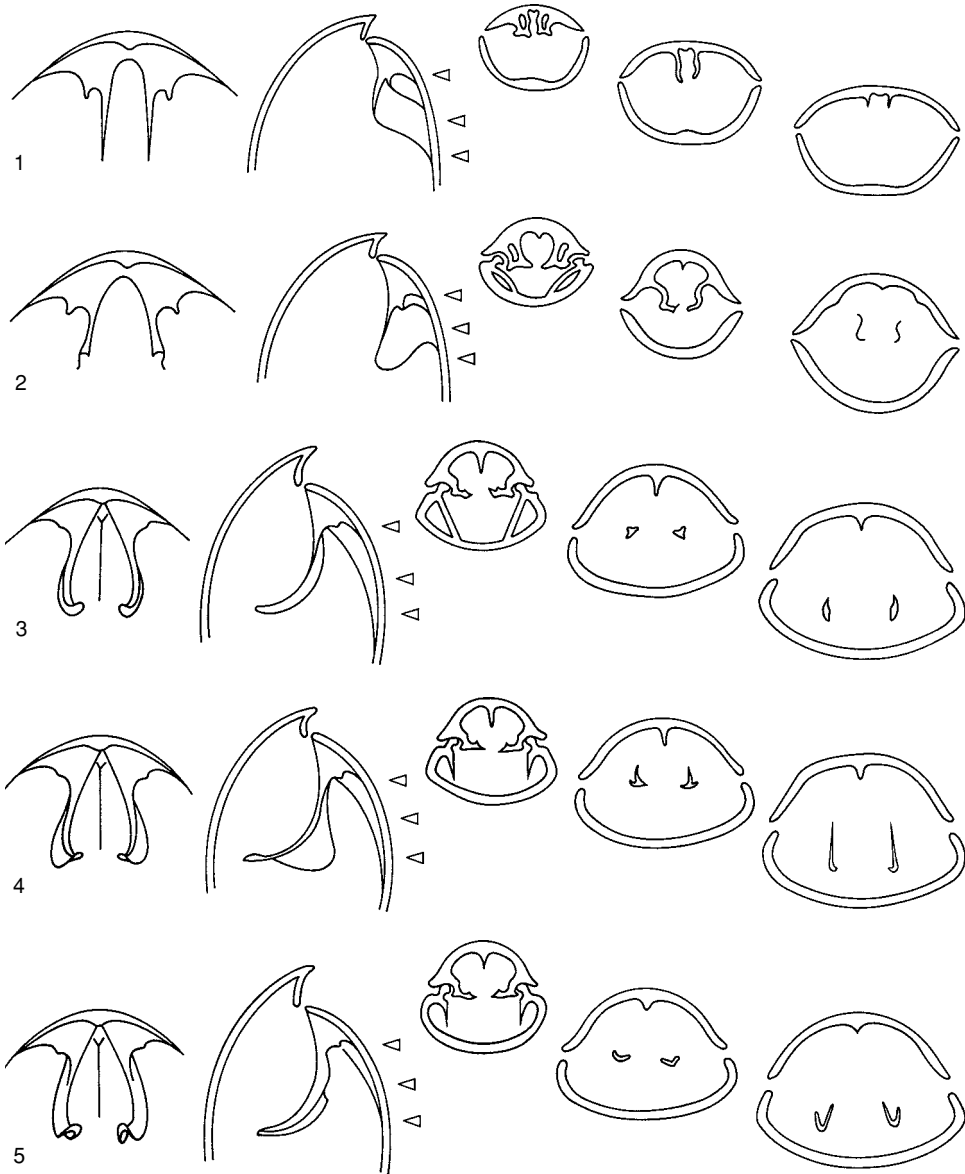


FIG. 701. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; 1, septiform crura, based on *Septoerurella*; 2, lyrate septiform crura, based on *Pygmaella*; 3, raduliform crura, based on *Rhynchonella*; 4, calcariform crura, based on *Rhynchonelloidella*; 5, canaliform crura, based on *Cyclothyris* (new).

FIG. 702. Types of crura in Rhynchonellida, illustrated by reconstructions looking into posterior of dorsal valves, lateral views, and serial sections; *arrows* indicate position of serial sections; 1, mergiform crura, based on *Peregrinella*; 2, submergiform (=terebratuliform) crura, based on *Peregrinelloidea*; 3, ensiform crura, based on *Rhynchonellina*; 4, maniculiform crura, based on *Cryptopora*; 5, ciliform crura, based on *Halorella*; 6, clivuliform crura, based on *Ochotorhynchia* (new).

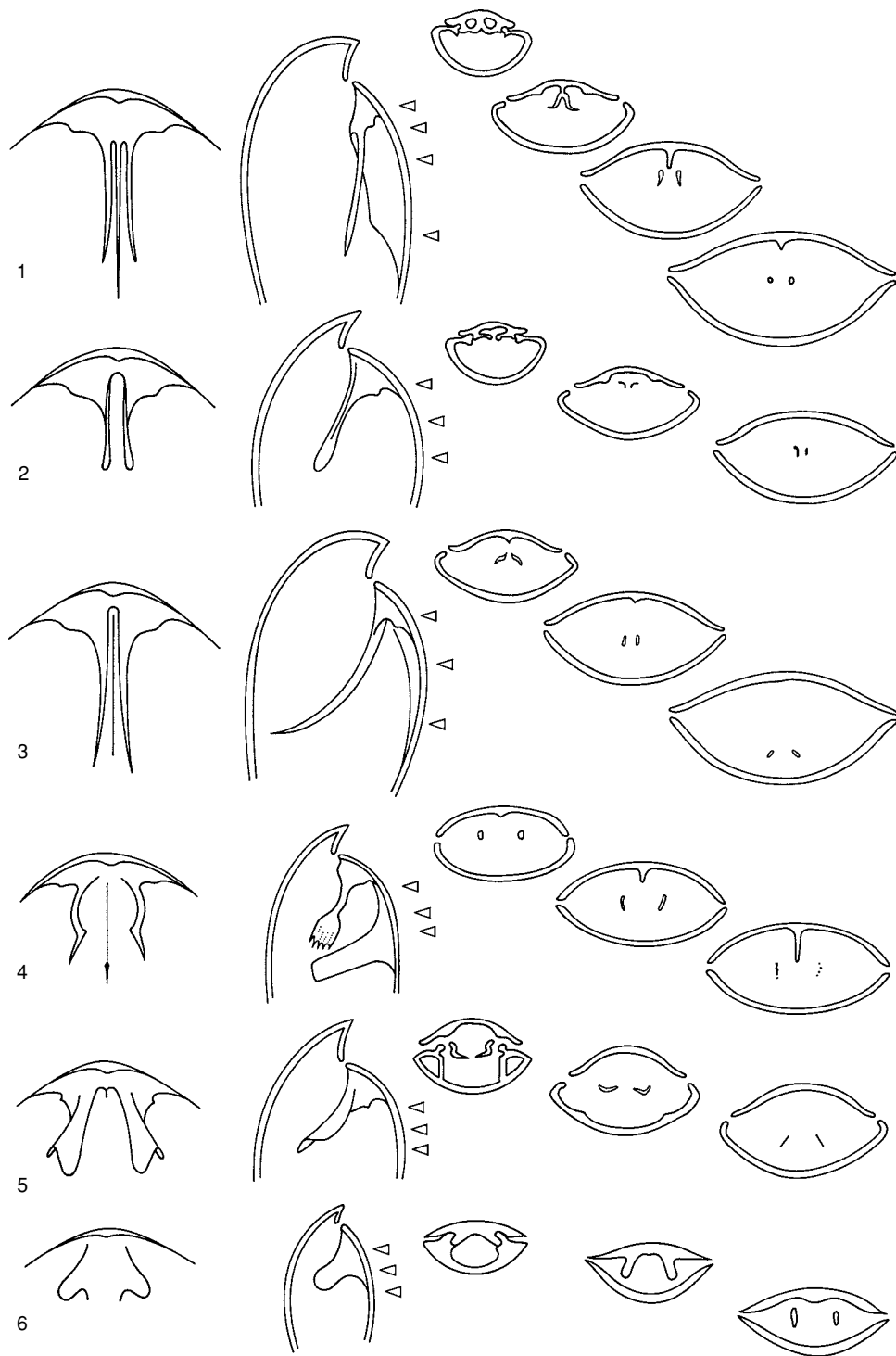


FIG. 702. For explanation, see facing page.

considered the basic type from which others evolved. 10. Calcariform crura (Fig. 701.4) were named by MUIR-WOOD (1934, p. 525) based on crura in the genus *Kallirhynchia*. Later she believed the same type of crura were exemplified in the genus *Rhynchonelloidella*. Modern authors have agreed that these crura are well exemplified in species of *Rhynchonelloidella* and *Thurmannella* (CHILDS, 1969, p. 18; LAURIN, 1984, p. 76). Calcariform crura are initially horizontal but twist to the vertical plane and become directed ventrally. The distal tips are variable. 11. Canaliform crura (Fig. 701.5) were described by AGER (1965, p. 600) but were not illustrated by him or by DAGYS, who discussed the type briefly (1968, p. 34). These are a variation of raduliform crura that are strongly concave dorsally and are characteristic of the Cyclothyridinae. 12. Mergiform crura (Fig. 702.1) were described by AGER (1965, p. 600), based on *Peregrinella*. They are long, very close together, parallel, and arise from the thickened upper edge of a high median septum. DAGYS (1968, p. 39, fig. 31b, 32a) commented that they differ significantly from the raduliform type in being relatively straight and not curved ventrally. 13. Submergiform (=terebratuliform) crura (Fig. 702.2) were described and illustrated by DAGYS (1968, p. 39, fig. 31a, 32b) based on the crura in *Peregrinelloidea*. These subparallel crura are short, narrow, and laterally compressed. They arise from the ventral surface of the hinge plates. Unlike the mergiform crura, they are not associated with a median septum. 14. Ensiform crura (Fig. 702.3) are subparallel, laterally compressed, long, ventrally curved, saberlike blades. 15. Maniculiform crura (Fig. 702.4) were described by COOPER (1959, p. 9) and further discussed and illustrated by AGER (1965, p. 600, fig. 478,6) and DAGYS (1968, p. 39). In these crura the distal extremities are flattened vertically and bear grooves that suggest small fingers on a hand, as in *Cryptopora*. 16. Ciliform crura (Fig. 702.5) were described by AGER (1965, p. 600, fig. 480), based on genera of the Halorellinae and fur-

ther discussed and illustrated by DAGYS (1968, p. 35, fig. 28b, 30i) based on the genus *Halorella*. These crura are proximally flattened in the horizontal plane but distally have their outer edges geniculated vertically. 17. Clivuliform crura (Fig. 702.6) were described and illustrated by DAGYS (1968, p. 40, fig. 31b) based on *Ochotorhynchia*. These crura are massive, fused with the inner socket ridges, strongly divergent, and extend almost to the floor of the ventral valve.

This list of crural types is strongly slanted toward post-Paleozoic crura, mostly because of lack of work on Paleozoic genera, as discussed above. This was also true when the 1965 *Treatise* (MOORE, 1965) was published. Many of the Paleozoic genera have crura that have been classified by their describers as raduliform. This term is probably appropriate in its general sense, but several modifications of raduliform crura probably evolved during Silurian and Devonian times. Further work should lead to the recognition of additional types of Paleozoic crura that may have taxonomic value.

Pouchlike structures were developed in the posterior region of some groups. These are symmetrical cavities close to the hinge line with participation of both valves or entirely within the ventral valve. Paleozoic examples include the conspicuous apricarium of Permian Amphipellidae (Fig. 699.3) and the parathyridium of Carboniferous Lambdarinidae. In the Mesozoic, striking bubblelike ventral pouches occur in the Bilaminellinae, and elongate, pouchlike gutters occur along the cardinal margins in Cardini-rhynchiinae.

Endopunctuation in rhynchonellides is extremely rare, and the few Paleozoic genera that have this feature do not appear to be closely related, though they are provisionally maintained here in the superfamily Rhynchoporoidea. The nature and significance of endopunctae in such rhynchonellides as *Rhynchopora* and *Tretorhynchia* require additional investigation. The poorly known genus *Rariella* is regarded as a *nomen dubium* awaiting further material and information.

ANCISTRORHYNCHOIDEA

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Superfamily ANCISTRORHYNCHOIDEA Cooper, 1956

[*nom. transl.* SAVAGE, 1996, p. 251, *ex* Ancistrorhynchinae COOPER, 1956a, p. 618]

Rhynchonellida with subcircular, transverse or elongate outline; dorsal fold usual but occasionally dorsal sulcus present; ventral interarea low; delthyrium open or with small deltidial plates anteriorly; costae fine to coarse, extending from beaks. Dental plates usually well developed but occasionally absent. Hinge plates divided; dorsal median septum and cardinal process usually absent; crura long, raduliform. *Lower Ordovician (Llanvirn)–Lower Devonian (Pragian)*.

Family ANCISTRORHYNCHIDAE Cooper, 1956

[*nom. transl.* SCHMIDT, 1965b, p. 553, *ex* Ancistrorhynchinae COOPER, 1956a, p. 618]

Ancistrorhynchoidea with subcircular outline; dorsal fold and ventral sulcus; costae fine to medium; delthyrium open. Dental plates usually short. Hinge plates divided; dorsal median septum and cardinal process absent. *Lower Ordovician (Llanvirn)–Lower Devonian (Pragian)*.

Ancistrorhyncha ULRICH & COOPER, 1942, p. 624 [**A. costata*; OD]. Shell small with subcircular outline and subequibiconvex, lenticular profile. Small ventral interarea; ventral beak erect; delthyrium open. Fold and sulcus weak; anterior commissure uniplicate, rounded. Costae fine and numerous, simple, arising at beaks. Dental plates short, strong; ventral muscle impressions weak. Hinge plates divided; sockets deep, partly overhung by inner socket ridges; crura long, curved anteroventrally. *Lower Ordovician (Llanvirn)–Upper Ordovician (Caradoc)*: North America, Baltic, Kazakhstan, central Asia, eastern Siberia, China.—FIG. 703, 1a–j. **A. costata*, lower Caradoc, Bromide Formation, Oklahoma, USA; a–e, hypotype, dorsal, ventral, lateral, anterior, and posterior views, ×2 (Cooper, 1956a); f–j, serial sections, ×6 (Schmidt, 1965b).

Drepanorhyncha COOPER, 1956a, p. 627 [**Porambonites ottawaensis* BILLINGS, 1862, p. 140; OD]. Shell

small with elongate subtriangular outline and subequibiconvex profile; anterior and lateral margins not steep; interareas narrow; delthyrium open; ventral beak erect. Fold and sulcus weak, narrow, arising at midlength; anterior commissure weakly uniplicate, serrate. Costae few but strong, rounded, arising at umbones. Dental plates long and closely set, slightly convergent ventrally; teeth large; ventral musculature indistinct. Hinge plates concave, divided; crural bases arising from underside of notothyrial cavity; crura very long and slender. *Lower Ordovician (middle Llanvirn)–Upper Ordovician (upper Caradoc)*: North America, Europe, Kirghizia, central Asia.—FIG. 703, 2a–g. **D. ottawaensis* (BILLINGS), Caradoc, Rocklandian, Rockland Formation, Paquette Rapids, Ontario, Canada; a–c, lectotype, dorsal, ventral, anterior views; d, hypotype, lateral view, ×1; e, dorsal valve interior, ×3; f, ventral valve interior; g, longitudinal section showing crura, ×2 (Cooper, 1956a).

Kholbotchonia BARANOV, 1988, p. 40 [**Machaeraria pygmaea* ALEKSEEVA, 1967, p. 34; OD]. Small with subcircular outline and subequibiconvex profile; anterior and lateral margins not steep; ventral beak suberect; delthyrium open. Fold and sulcus moderately well developed, arising at umbones; anterior commissure uniplicate, serrate. Costae medium strength, simple, rounded in section. Dental plates short, thin, divergent ventrally. Hinge plates divided; crura bases subtriangular; crura strongly curved ventrally. *Lower Devonian (Lochkovian)*: eastern Siberia.—FIG. 703, 3a–i. **K. pygmaea* (ALEKSEEVA), Sette-Daban subformation, Sette-Daban Range; a–c, hypotype, dorsal, anterior, and lateral views, ×5; d–i, serial sections 1.5, 1.7, 1.9, 2.1, 2.4, 2.8 mm from posterior margin, ×6 (Baranov, 1988).

Nikolaevirhynchus BARANOV, 1988, p. 38 [**N. boldymbensis*; OD]. Small with transversely subcircular outline and subequibiconvex profile; anterior and lateral margins acute. Ventral beak short, suberect; delthyrium open. Fold and sulcus weak; anterior commissure broad, rounded, uniplicate. Costae medium strength, simple, rounded, arising at beaks. Dental plates thick, vertical. Hinge plates divided, thick, subhorizontal; crura stout, ventrally curved. *middle Silurian (Wenlock)*: eastern Siberia.—FIG. 704, 1a–j. **N. boldymbensis*, Ryabina Formation, Tas-Khayaktakh Range; a–d, holotype, dorsal, ventral, anterior, lateral views, ×5; e–j, serial sections, ×6 (Baranov, 1988).

Obscurella BARANOV, 1991, p. 36 [**O. costata*; OD]. Small with subcircular outline and dorsibiconvex profile; lateral and anterior margins steep; ventral beak straight to suberect. Fold and sulcus distinct, arising at umbones; anterior commissure uniplicate, serrate; tongue high, trapezoid. Costae medium

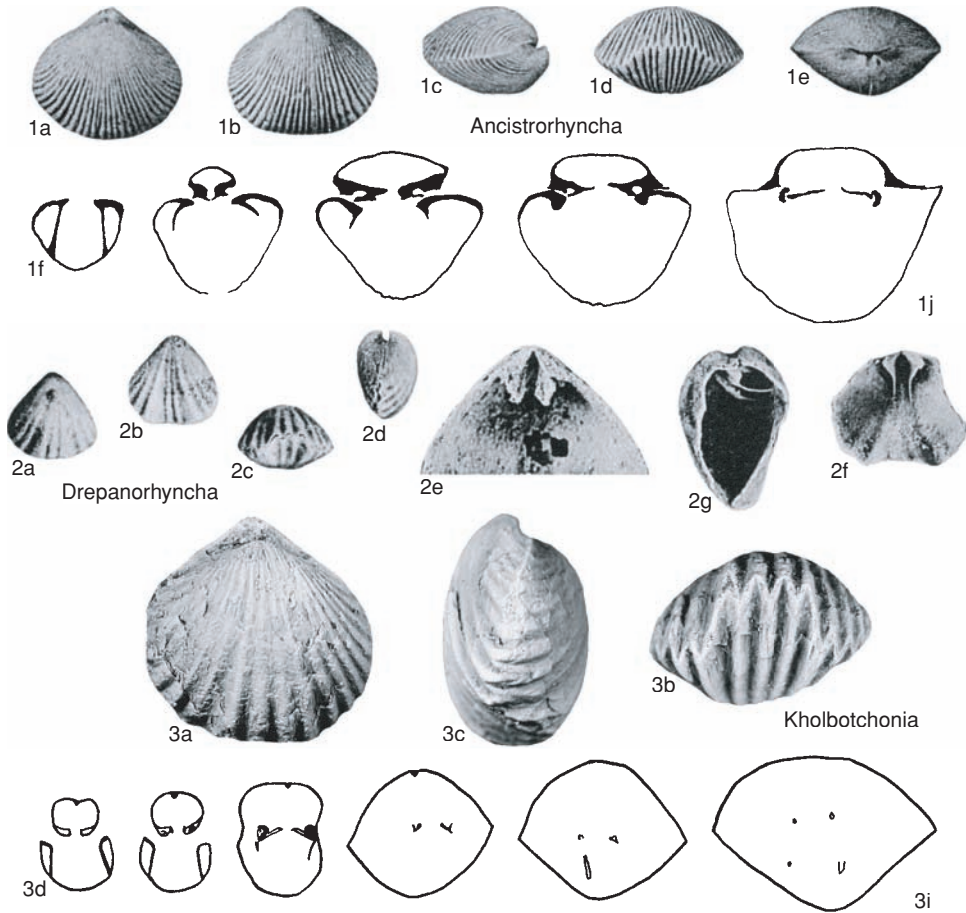


FIG. 703. Ancistrorhynchidae (p. 1041).

strength, subangular, simple, arising at beaks. Dental plates short, thin, vertical. Hinge plates horizontal, may be united; crural bases triangular in section. *Lower Devonian (Pragian)*: eastern Siberia.—FIG. 704,2a–i. **O. costata*, lower Pragian, lower Sagyrskaya Formation, Selennyakhskiy Kryazh, Talyndzhi River, Gon Creek; a–d, holotype, dorsal, ventral, anterior, lateral views, with posterior part removed by sectioning, $\times 2$; e–i, holotype, serial sections, $\times 6$ (Baranov, 1991).

Tyrrhynchus BARANOV, 1988, p. 39 [**T. tyryensis*; OD]. Small with subcircular to subpentagonal outline and biconvex, lenticular profile; lateral and anterior margins acute; ventral beak straight. Fold and sulcus low; anterior commissure weakly uniplicate. Costae fine, arising at beaks, rounded in section. Dental plates short; teeth stout. Hinge plates rest on valve floor; inner socket ridges high; crura narrow, curved ventrally. *lower Silurian*

(*Llandovery*): eastern Siberia.—FIG. 704,3a–b. **T. tyryensis*, Tayakh Formation, Sette-Daban Range; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 3$; e–h, topotype, serial sections, $\times 2.5$ (Baranov, 1988).

Family SPHENOTRETIDAE Savage, 1996

[Sphenotretidae SAVAGE, 1996, p. 251]

Small and elongate Ancistrorhynchoidea; weak dorsal sulcus and ventral fold; low ventral interarea; costae fine; foramen with small deltidial plates. Dental plates short. Hinge plates small and divided; cardinal process absent. *Lower Ordovician (Llanvirn)*–*Upper Ordovician (Caradoc)*.

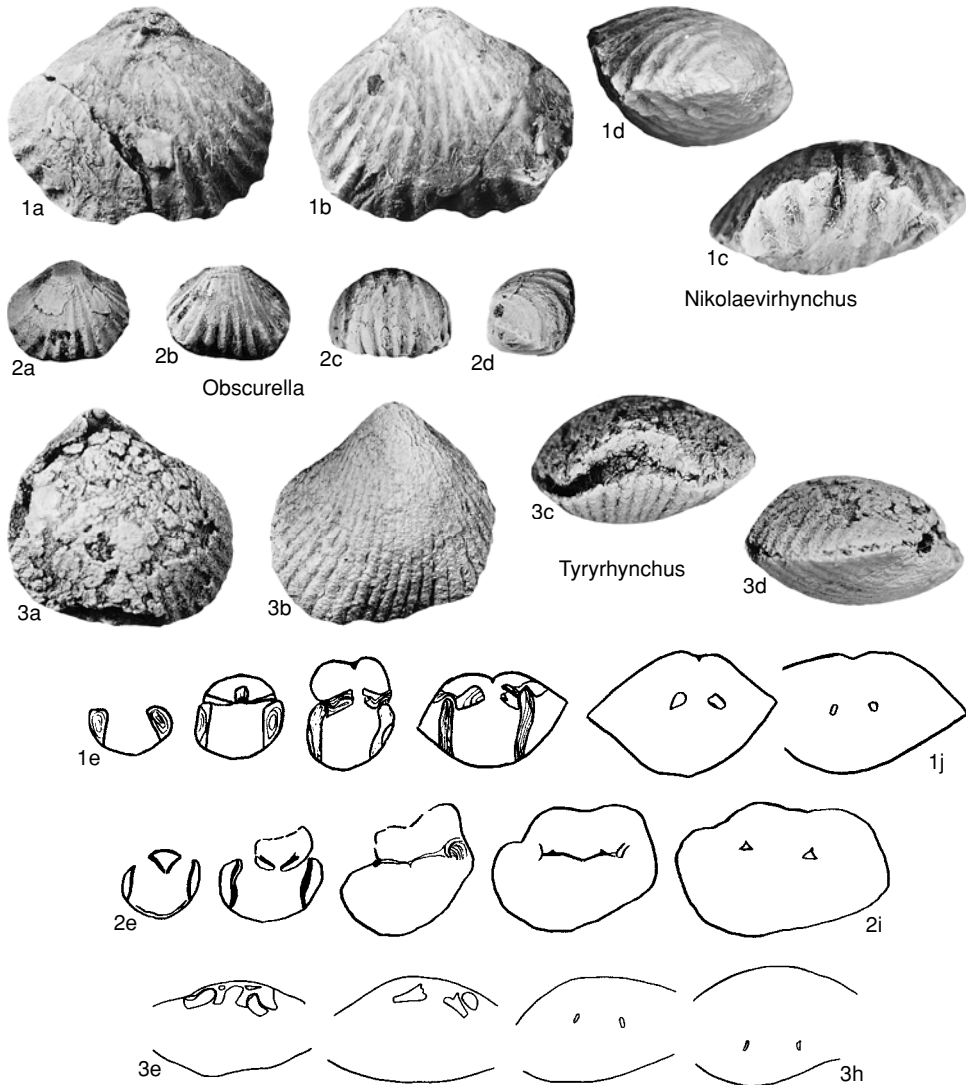


FIG. 704. Ancistrorhynchidae (p. 1041–1042).

Sphenotreta COOPER, 1956a, p. 663 [*S. cuneata*; OD]. Small with elongate subelliptical outline and weakly biconvex profile; beak straight; foramen elongate oval; deltidial plates small, triangular, disjunct. Distinct ventral fold and dorsal sulcus; anterior commissure unisulcate. Costae fine, simple, arising at beaks, narrowly rounded in section. Dental plates short, ventrally divergent. Hinge plate divided; crural bases triangular; crura long, slender, curved ventrally. *Lower Ordovician (Llanvirn)—Upper Ordovician (Caradoc)*: North America, eastern and central Siberia, China.—FIG. 705, 3a–d. **S. cuneata*,

lower Caradoc, Sevier Formation, Athens, Tennessee, USA; holotype, dorsal, ventral, lateral, and anterior views, $\times 4$ (Cooper, 1956a).

Dorytreta COOPER, 1956a, p. 666 [*D. bella*; OD]. Small with elongate subelliptical outline but less elongate than *Sphenotreta*; biconvex profile; lateral and anterior margins rounded; beak straight; foramen elongate; deltidial plates small, triangular, disjunct. Weak dorsal sulcus and ventral fold; anterior commissure almost rectimarginate. Costae numerous but less fine than in *Sphenotreta*, simple, arising at beaks. Dental plates short, divergent ventrally.

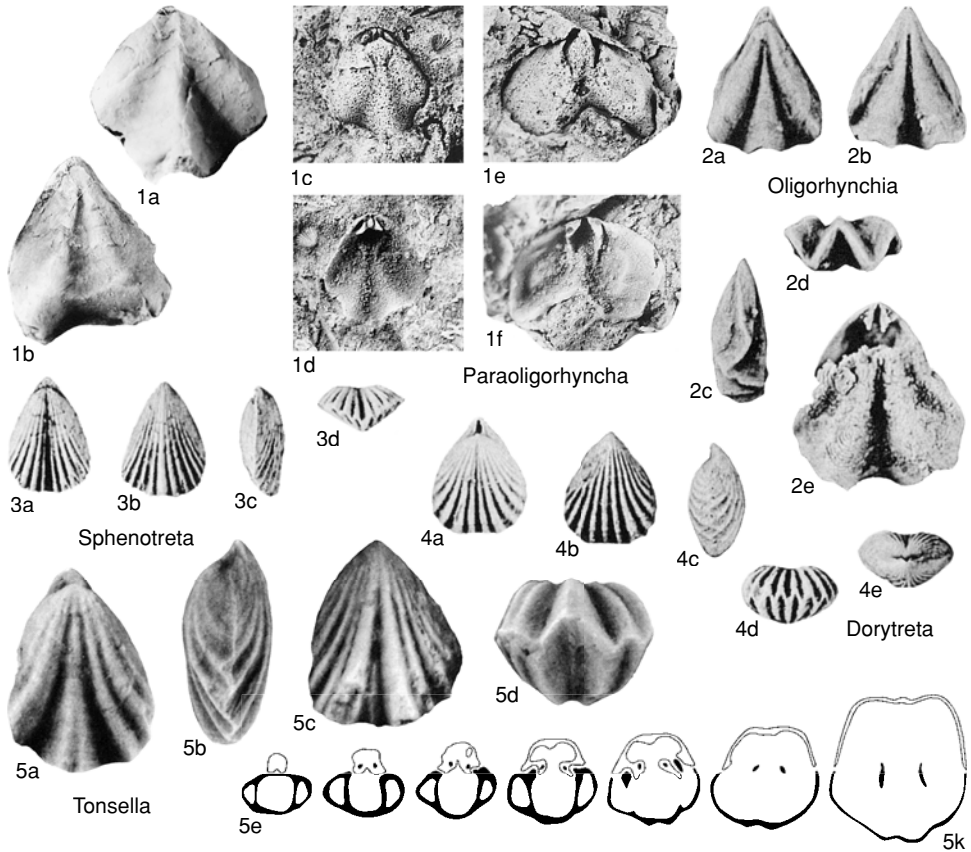


FIG. 705. Sphenotretidae and Oligorhynchiidae (p. 1043–1046).

Hinge plates divided, supported by swelling of median sulcus; crura short, bent abruptly ventrally. *Lower Ordovician (Llanvirn)*: North America, eastern Siberia, Kazakhstan.—FIG. 705, 4a–e. **D. bella*, upper McLish Formation, Pontotoc County, Oklahoma, USA; holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 4$ (Cooper, 1956a).

Family OLIGORHYNCHIIDAE Cooper, 1956

[Oligorhynchiidae COOPER, 1956a, p. 658]

Ancistrorhynchoidea with elongate subtriangular outline; beak suberect; plicae coarse and few; weak dorsal fold masked by coarse plicae; delthyrium with small deltidial plates anteriorly. Dental plates distinct and vertical. Hinge plates divided; dorsal median septum absent, cardinal process usually absent. *Upper Ordovician (Caradoc–Ashgill)*.

Oligorhynchia COOPER, 1935, p. 49 [*O. subplana*; OD]. Small with elongate subtriangular outline and low biconvex profile; ventral beak suberect to straight; foramen elongate-oval; deltidial plates small, triangular. Fold and sulcus weak and masked by 3 angular dorsal plicae and 2 to 4 ventral plicae. Dental plates strong, vertical; teeth long. Divided hinge plates supported by swelling of median anterior sulcus; cardinal process absent; crura long and straight or curved slightly ventrally. *Upper Ordovician (Caradoc–Ashgill)*: North America, Europe, Novaya Zemlya, northern Urals, Kazakhstan.—FIG. 705, 2a–e. **O. subplana*, lower Caradoc, Lincolnshire Formation, Hogskin Member, Tennessee, USA; a–d, hypotype, dorsal, ventral, lateral, anterior views, $\times 4$; e, hypotype, view into dorsal interior showing hinge plates, $\times 6$ (Cooper, 1956a).

Paraoligorhynchia POPOV, 1981, p. 65 [*P. reducta*; OD]. Small with elongate subtriangular outline and dorsibiconvex profile; lateral margins acute. Ventral beak suberect; delthyrium open. Dorsal fold and ventral sulcus masked by very coarse rounded plicae, with 3 dorsal plicae and 2 to 4 ventral plicae;

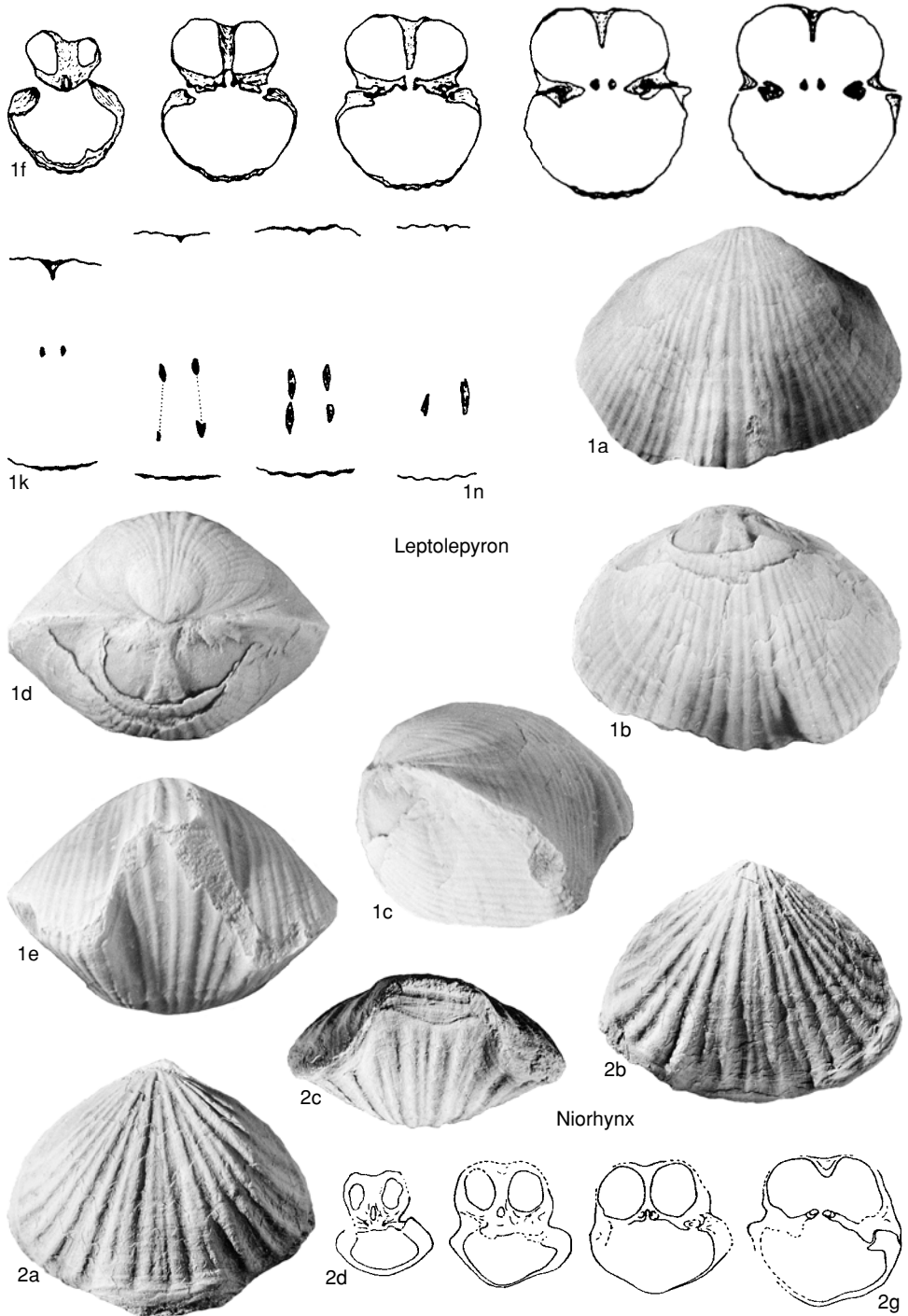


FIG. 706. Niorhyncoidea (p. 1046).

anterior commissure parasulcate. Dental plates long, parallel anteriorly, and diverging ventrally; teeth stout. Hinge plate divided; bulbous cardinal process; crural bases triangular in section. *Upper Ordovician (Ashgill)*: central Asia, Kazakhstan.—

FIG. 705, 1a–f. **P. reducta*, Dulankara horizon, Chullii Range, Dulankara, Kazakhstan; *a*, topotype, dorsal view; *b*, ventral view of another topotype; *c–d*, holotype, dorsal internal mold and impression; *e–f*, ventral internal mold and impression, $\times 5$ (Niki-forova & Popov, 1981).

Tonsella AMSDEN, 1988, p. 21 [**T. parva*; OD]. Small with elongate triangular outline and equibiconvex profile; lateral and anterior margins acute; ventral beak suberect. Plicae coarse, with median dorsal plication emulating fold and median ventral interplical space emulating sulcus; narrow dorsal sinus on median dorsal plication and corresponding narrow ridge in ventral sulcus; anterior commissure parasulcate. Dental plates distinct, vertical. Hinge plates divided; cardinal process absent; crura straight and rodlike but laterally flattened distally. *Upper Ordovician (Ashgill)*: North America.—FIG. 705, 5a–k. **T. parva*, upper Cincinnati, Hirnantian, Cason Oolite, St. Clair Springs, Arkansas, USA; *a–b*, holotype, dorsal and lateral views; *c–d*, topotype, ventral view, anterior view, $\times 5$; *e–k*, topotype, serial sections, $\times 4.5$ (Amsden, 1988).

Family NIORHYNICIDAE Savage, 1996

[Niorhynicidae SAVAGE, 1996, p. 251]

Ancistrorhynchoidea with subcircular outline; low dorsal fold and ventral sulcus; costae coarse; delthyrium with small deltidial plates. Dental plates absent. Dorsal median septum short; septalium short and with or

without cover plate; cardinal process absent. *lower Silurian (Llandovery)—middle Silurian (Wenlock)*.

Niorhynx HAVLÍČEK, 1982b, p. 368 [**Terebratula niobe* BARRANDE, 1847, p. 78; OD]. Subcircular outline and biconvex, lenticular profile with acute lateral margins; beak suberect; delthyrium open except for small disjunct deltidial plates. Low fold and sulcus; anterior commissure uniplicate; tongue low, trapezoid, occasionally with incipient trail. Costae low, rounded, with some intercalation, arising at beaks. Dental plates absent; teeth stout, arising from valve margins. Hinge plates united; narrow septalium supported on short septum and covered by convex plate; septalium flanked by rodlike crural bases. *middle Silurian (Wenlock)*: Bohemia.—FIG. 706, 2a–g. **N. niobe* (BARRANDE), Motol Formation; *a–c*, hypotype, dorsal, ventral, and anterior views, $\times 4$; *d–g*, serial sections, $\times 12$ (Havlíček, 1982b).

Leptolepyron JIN, 1989, p. 113 [**Rhynchonella? argenteum* BILLINGS, 1866, p. 43; OD]. Small to medium with transversely ovate outline and equibiconvex profile; nonprecipitous lateral slopes; beak incurved; delthyrium open, deltidial plates rudimentary. Fold and sulcus shallow to medium; costae fine to medium, arising at beaks, some intercalation and bifurcation. Dental plates absent; teeth stout, arising from valve margins; ventral muscle field well impressed. Hinge plates divided; septalium short, narrow, open; dorsal median septum long, high; crura long, slender, strongly curved ventrally. *lower Silurian (Llandovery)*: Canada.—FIG. 706, 1a–n. **L. argenteum* (BILLINGS), Jupiter Formation, Anticosti Island; *a–e*, lectotype, dorsal, ventral, lateral, posterior, and anterior views, $\times 3$; *f–n*, hypotype, serial sections 1.0, 1.3, 1.4, 1.6, 1.7, 2.0, 3.1, 3.2, 3.3 mm from posterior, $\times 3$ (Jin, 1989).

RHYNCHOTREMATOIDEA

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Superfamily RHYNCHOTREMATOIDEA Schuchert, 1913

[*nom. transl.* SAVAGE, 1996, p. 252, ex Rhynchotrematinae SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *nom. correct. pro* Rhynchotrematinae SCHUCHERT, 1913, p. 396]

Rhynchonellida with subpentagonal outline; dorsal fold and ventral sulcus; costae medium to coarse, usually extending from beaks; delthyrium open or with deltidial plates variously developed. Dental plates present or fused to valve walls. Dorsal median septum usually long, occasionally short or absent; hinge plates thick; septalium variably developed; cardinal process septiform to unilobed, rarely absent; crura long, commonly raduliform. *Lower Ordovician (Llanvirn)–Lower Carboniferous (Viséan)*.

Family RHYNCHOTREMATIDAE Schuchert, 1913

[*nom. transl.* COOPER, 1956a, p. 628, ex Rhynchotrematinae SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *nom. correct. pro* Rhynchotrematinae SCHUCHERT, 1913, p. 396]

Early Rhynchotrematoidea with strong dorsal median septum; hinge plates short, thick; cardinal process septiform. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow)*.

Subfamily RHYNCHOTREMATINAE Schuchert, 1913

[*nom. correct.* SCHUCHERT in SCHUCHERT & LEVENE, 1929a, p. 18, *pro* Rhynchotrematinae SCHUCHERT, 1913, p. 396]

Rhynchotrematidae with strong, simple costae. Delthyrium usually open or with disjunct deltidial plates. Dental plates short. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow)*.

Rhynchotrema HALL, 1860a, p. 68 [**Atrypa increbescens* HALL, 1860a, p. 68; OD]. Shell small to large with subtriangular to subpentagonal outline and equibiconvex profile; lateral and anterior margins generally steep. Beak suberect to incurved; delthyrium partly closed by marginal deltidial plates. Dorsal fold and ventral sulcus arising at umbones; anterior commissure uniplicate; tongue

trapezoid, dentate. Costae subangular, simple, arising at beaks. Dental plates short, almost vertical; teeth stout, with large fossettes; ventral muscle field flabellate. Septalium with distinct septalial plates; dorsal median septum low, thick, extending to midlength; crural bases arising from septal plates; crura long, ventrally curved; cardinal process septiform. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock)*: North America, Europe, northern Africa, Urals, Siberia, Kazakhstan, Kirgizia, China, Australia.—FIG. 707, 1a–l. **R. increbescens* (HALL), Caradoc, upper Trentonian, Sherman Falls Formation, Lakefield, Ontario, Canada; a–d, hypotype, dorsal, lateral, posterior, and anterior views, $\times 2$; e–l, serial sections 1.6, 1.75, 1.95, 2.15, 2.3, 2.75, 3.45, 3.75 mm from posterior, $\times 4$ (new).

Hiscobeccus AMSDEN, 1983a, p. 37 [**Atrypa capax* CONRAD, 1842, p. 264; OD]. Subcircular outline and dorsibiconvex profile; lateral and anterior margins generally steep. Beak erect to incurved; delthyrium wide, deltidial plates absent or incipient. Fold and sulcus strong; anterior commissure uniplicate; tongue distinct, trapezoid, dentate. Costae strong, simple, angular, arising at beaks. Dental plates rudimentary or fused to valve walls; ventral muscle field deeply impressed. Hinge plates thick; dorsal median septum long; cardinal process septiform. *Upper Ordovician (Ashgill)*: North America.—FIG. 707, 2a–h. **H. capax* (CONRAD), Richmondian, USA; a–b, hypotype, dorsal and ventral views, Dismukes, Tennessee, $\times 1.5$; c–e, posterior, anterior, and lateral views; f, hypotype, dorsal valve interior, Fernvale Formation, Tennessee, $\times 2$ (Howe, 1969); g, hypotype, dorsal view showing open delthyrium, Welling Formation, Cherokee County, Illinois; h, neotype, ventral interior, Richmond, Indiana, $\times 2$ (Amsden, 1983a).

Otarorhyncha NIKIFOROVA & POPOV, 1981, p. 62 [**Rhynchotrema otarica* RUKAVISCHNIKOVA, 1956, p. 156; OD]. Transversely subpentagonal outline and dorsibiconvex profile; low, apsacline ventral interarea; delthyrium open. Fold and sulcus strong, arising at umbones; anterior commissure uniplicate; tongue pronounced, trapezoid, serrate. Costae arising at beaks, moderately strong, rounded, some bifurcation. Dental plates very short, hardly distinct from shell wall; ventral muscle field well impressed. Septalium and dorsal median septum very short; small septate cardinal process. *Lower Ordovician (Llanvirn)–Upper Ordovician (Ashgill)*: Anderken-Dulankara horizons, Kazakhstan, central Asia.—FIG. 707, 3a–i. **O. otarica* (RUKAVISCHNIKOVA), Upper Ordovician, Dulankara Formation, Dulankara Mountain, Chu-Ili Range, Kazakhstan; a–d, hypotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–i, serial sections at 1, 2, 2.5, 3, 3.5 mm from posterior (Rukavishnikova, 1956).

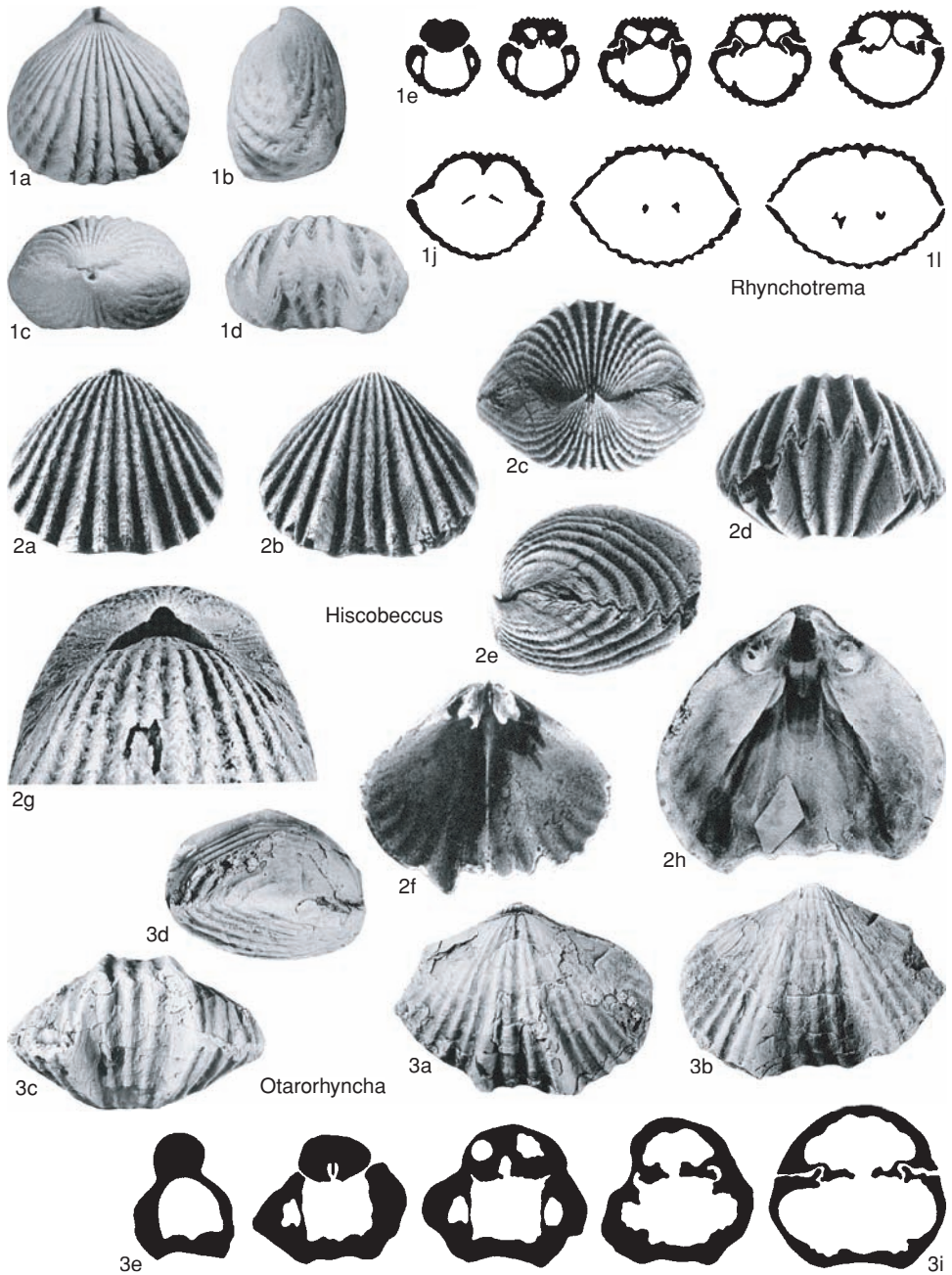


FIG. 707. Rhynchotrematidae (p. 1047).

Pleurocornu HAVLIČEK, 1961, p. 46 [*Rhynchonella amissa* BARRANDE, 1879b, pl. 38, fig. 4; OD]. Small to medium size; distinctive securiform outline with emarginate posterolateral edges; dorsibiconvex profile. Ventral beak narrow, protracted. Dorsal fold

and ventral sulcus evident but masked by strong plicae, with 3 plicae on fold and 2 strong plicae bordering the splayed sulcus; anterior commissure strongly uniplicate, denticulate. Dental plates short, scarcely distinct from thick valve walls; teeth stout;

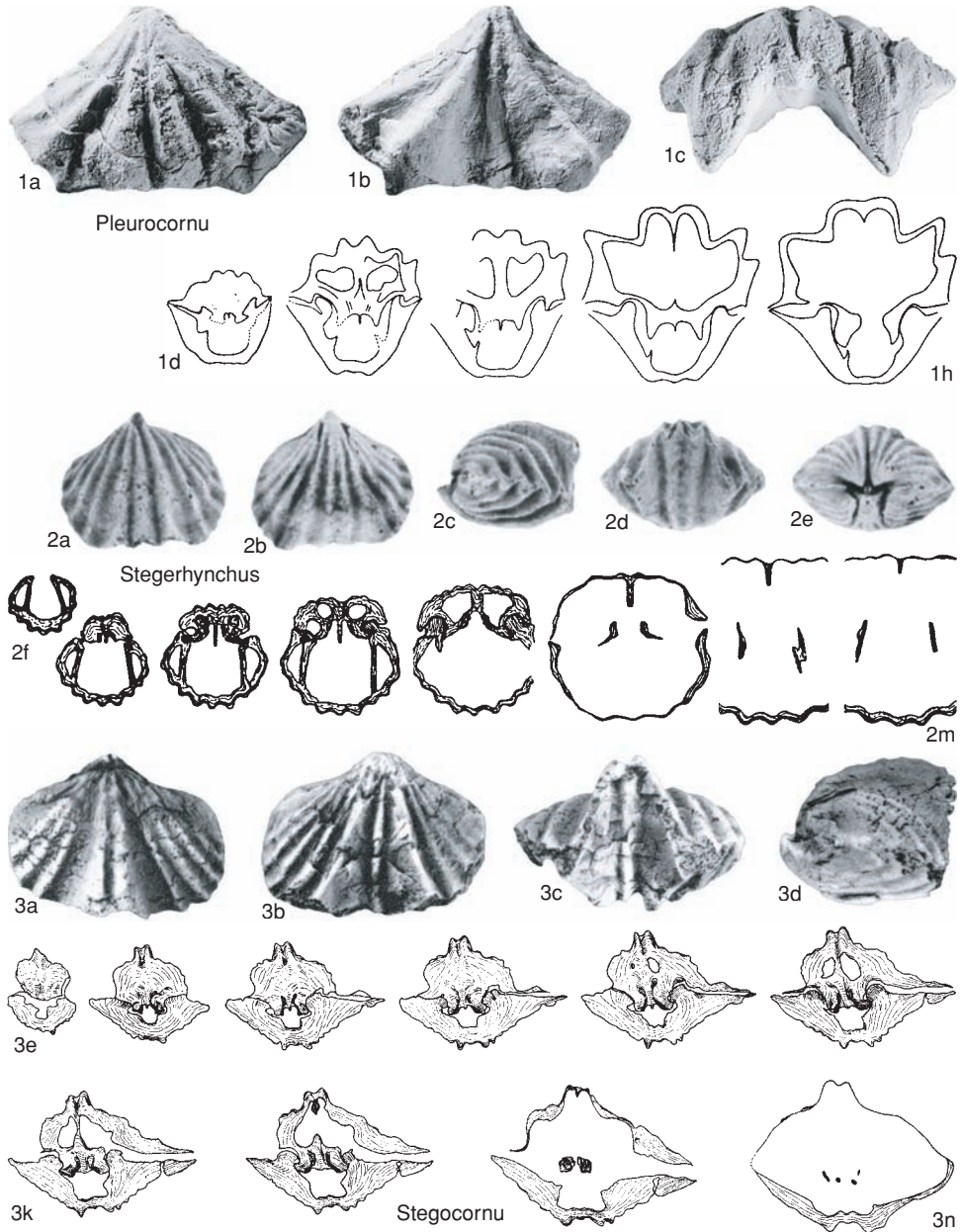


FIG. 708. Rhynchotrematidae (p. 1047–1050).

ventral muscle field well impressed. Hinge plate undivided; notothyrial cavity with septiform cardinal process; dorsal median septum short, thick. *middle Silurian* (Wenlock): Bohemia.—FIG. 708, 1a–h. **P. amissum* (BARRANDE), Lodenice; a–c, lectotype, dorsal, ventral, and anterior views, $\times 2.7$ (new); d–h, serial sections of hypotype at 8.5, 7.8, 7.3, 6.3, 6.0 from anterior, $\times 3$ (Havlíček, 1961).

Stegerhynchus FOERSTE, 1909a, p. 96 [**Rhynchonella* (*Stegerhynchus*) *whittii-praecursor* FOERSTE, 1909a, p. 96; OD; =*Stegerhynchus praecursor* FOERSTE, 1909a, p. 96] [=*Stegerhynchella* RZHONSNITSKAIA, 1959, p. 27 (type, *Stegerhynchus decimPLICATA angaciensis* CHERNYSHEV, 1937, p. 29); *Tungussotoechia* LOPUSHINSKAYA, 1976, p. 60 (type, *Stegerhynchella tungussensis* LOPUSHINSKAYA, 1972, p. 186);

Stegerhynchops AMSDEN, 1978, p. 27 (type, *S. marblensis*). Subtriangular to subpentagonal outline and dorsibiconvex profile. Beak erect to suberect; delthyrium open or with rudimentary deltidial plates. Fold and sulcus narrow, strong, from umbones; anterior commissure uniplicate, trapezoid, serrate. Costae simple, subangular, from beaks. Dental plates short, subvertical, sometimes obscured by callus. Hinge plates thick, short; septalium small, with short septalial plates; dorsal median septum thick, long; cardinal process septiform; crural bases arising from septalial plates; crura laterally flattened, ventrally curved. *lower Silurian (Llandovery)*—*upper Silurian (Ludlow)*: North America, Europe, Siberia, Altai, Mongolia, Australia.—FIG. 708,2a–m. **S. praecursor* (FOERSTE); a–e, topotype, dorsal, ventral, lateral, anterior, and posterior views, lower Silurian, Clinton Beds, Clifton, Tennessee, USA, collected by FOERSTE, $\times 2.4$ (Jones, 1981); f–m, hypotype, serial sections 0.3, 0.6, 0.7, 0.9, 1.0, 1.3, 1.9, 2.0 mm from posterior, lower Silurian, Bescie Formation, Anticosti Island, Canada, $\times 7$ (Jin, 1989).

Stegocornu DÜRKOOP, 1970, p. 185 [**S. procerum*; OD] [= *Xerxespirifer* COCKS, 1979, p. 40 (type, *X. iranicus*, OD)]. Transversely ovate outline and dorsibiconvex profile; anterior margin particularly high. Beak erect to incurved; delthyrium with narrow opening. Fold and sulcus narrow, strong, arising near beaks; anterior commissure high, tapering dorsally, sulciphate. Costae coarse, subangular, arising at beaks, typically 2 on fold and 1 in sulcus. Dental plates lacking or fused to valve walls; ventral muscle field deeply impressed. Hinge plates massive, united; cardinal process septiform; dorsal median septum very short, thick; inner socket ridges massive; crural bases stout, arising from inner socket ridges; crura radulifer. *lower Silurian (Llandovery)*: Afghanistan, Iran.—FIG. 708,3a–n. **S. procerum*, upper Llandovery, Dascht-e-Nawar/East, eastern Afghanistan; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–n, serial sections 1.3, 1.7, 1.9, 2.0, 2.1, 2.3, 2.5, 2.6, 3.2, 4.6 mm from posterior, $\times 1.75$ (Dürkoop, 1970).

Subfamily LEPIDOCYCLINAE

Cooper, 1956

[*nom. transl.* AMSDEN, 1978, p. 26, ex Lepidocyclusidae COOPER, 1956a, p. 657]

Rhynchotrematidae with subcircular to elongate oval outline; strongly biconvex. Costae coarse, crossed by imbricating growth lamellae. Delthyrium usually with conjunct deltidial plates. Dental plates fused to thick shell walls or obscured by callus. *Upper Ordovician (Ashgill)*—*upper Silurian (lower Ludlow)*.

Lepidocyclus WANG, 1949, p. 12 [**L. laddi*; OD]. Medium to large with elongate subcircular to

subcircular outline and strongly biconvex profile. Beak erect to incurved; deltidial plates conjunct to disjunct. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue trapezoid, tapering dorsally, dentate. Costae strong, angular to subangular, simple, from beaks, with lamellose growth lines. Dental plates reduced or fused to valve walls; ventral muscle field deeply impressed. Dorsal median septum extending to valve mid-length; septalium small; cardinal process thin, septiform; hinge plates thick; crural bases horizontal; crura rodlike proximally, becoming laterally flattened distally, ventrolaterally curved. *Upper Ordovician (Ashgill)*: North America, Kazakhstan.—FIG. 709,2a–f. **L. laddi*, upper Cincinnatian, Maquoketa Formation, Elgin Member, Winneshiek County, Orleans township, Iowa, USA; a–d, holotype, dorsal, ventral, lateral, and anterior view; e–f, paratype, dorsal valve interior, ventral valve interior, $\times 1$ (Wang, 1949).—FIG. 709,2g–m. *L. gigas* WANG, upper Cincinnatian, Vaureal Formation, Anticosti Island, Canada; serial sections 1.6, 1.8, 2.0, 2.8, 3.6, 4.3, 5.0 mm from posterior, $\times 2$ (Jin, 1989).

Hypsitycha WANG, 1949, p. 17 [**H. hybrida*; OD]. Elongate-subtriangular outline and strongly dorsibiconvex profile; lateral and anterior margins steep. Beak erect to suberect; delthyrium with conjunct deltidial plates. Fold and sulcus strong, narrow; anterior commissure uniplicate; tongue generally high, trapezoid, dentate. Costae strong, subangular, simple, from beaks, with strongly lamellose growth lines. Dental plates partly fused to shell walls; teeth large, arising from valve margins; ventral muscle field well impressed. Septalium short; cardinal process septiform; dorsal septum short; crura long, strongly curved ventrally. *Upper Ordovician (Ashgill)*: North America.—FIG. 709,3a–f. **H. hybrida*, upper Cincinnatian, Maquoketa Formation, Brainard Member, Jackson County, Fairfield, Iowa, USA; a–d, holotype, dorsal, ventral, anterior, and lateral views; e, ventral valve interior, $\times 2$; f, dorsal valve beak interior, $\times 4$ (Wang, 1949).—FIG. 709,3g–n. *H. anticostiensis* (BILLINGS), upper Cincinnatian, Ellis Bay Formation, Anticosti Island, Canada; serial sections 1.3, 1.6, 1.7, 1.9, 2.3, 3.6, 4.4, and 4.5 mm from posterior, $\times 3$ (Jin, 1989).

Rhytidorhachis JIN & CALDWELL, 1990, p. 32 [**R. hudsonensis*; OD]. Subpentagonal to subtriangular outline and moderately biconvex profile. Beak erect to suberect; delthyrium with conjunct deltidial plates and submesothryd foramen. Fold and sulcus extending from umbones. Costae strong, from beaks, some bifurcation and intercalation anteriorly. Dental plates short and mostly fused to shell walls; teeth short and thick; ventral muscle field well impressed. Dorsal median septum short to absent; hinge plates short, thick, divided anteriorly; cardinal process septiform; crural bases triangular; crura laterally flattened. *lower Silurian (upper Llandovery)*—*upper Silurian (lower Ludlow)*: North America, Europe.—FIG. 709,1a–k. **R.*

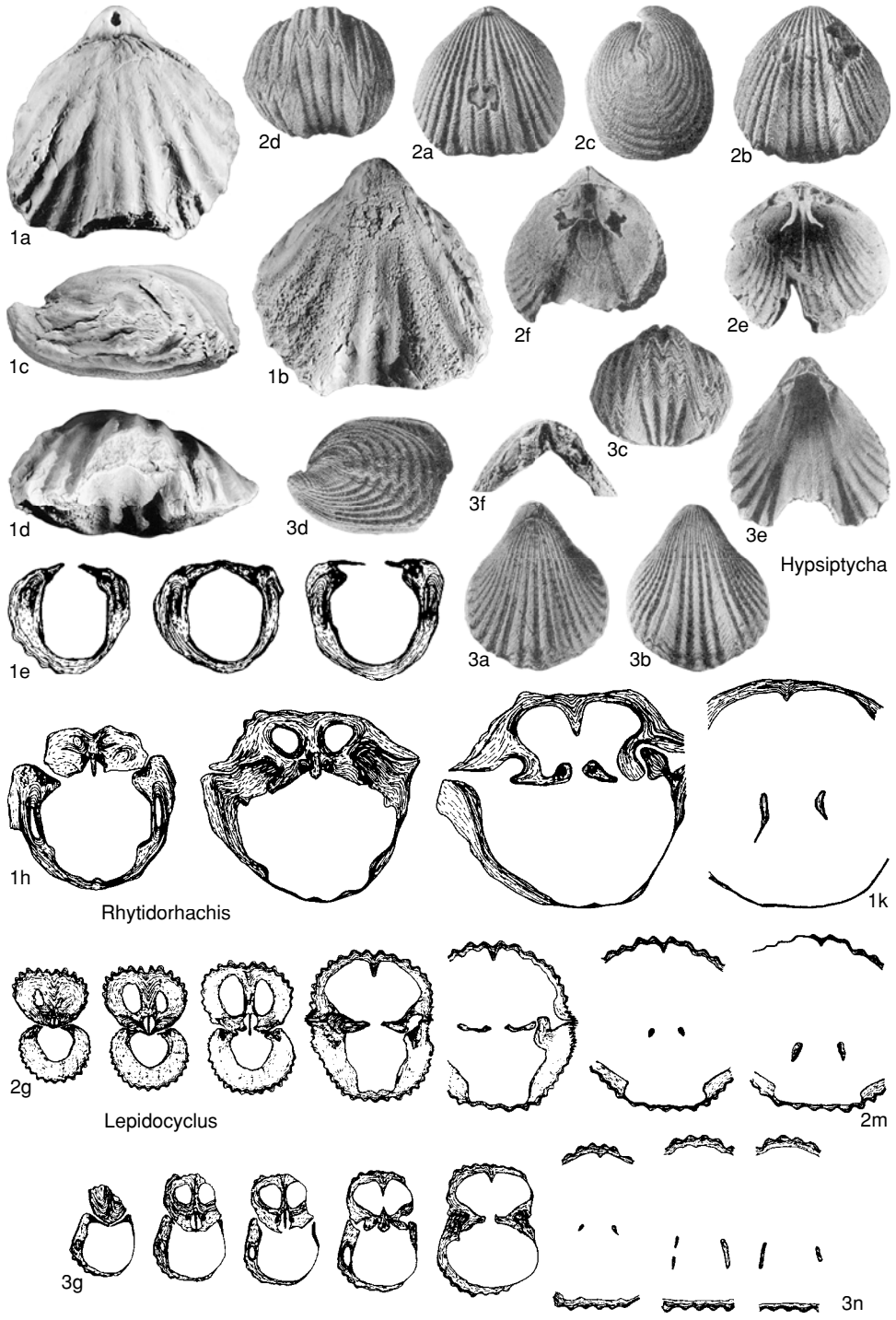


FIG. 709. Rhynchotrematidae (p. 1050–1052).

hudsonensis, upper Llandovery, Ekwon River Formation, Little Current River, Hudson Bay Lowlands, Canada; *a-d*, holotype, dorsal, ventral, lateral, and anterior views, $\times 3$; *e-k*, serial sections 0.8, 0.9, 1.3, 1.6, 2.2, 2.6, 3.2 mm from posterior, $\times 8$ (Jin & Caldwell, 1990).

Family TRIGONIRHYNCHIIDAE

Schmidt, 1965

[Trigonirhynchiidae SCHMIDT, 1965a, p. 2]

Rhynchotrematoidea with subtriangular outline; dorsal fold and ventral sulcus variable; costae often extending from beaks but umbones commonly smooth; delthyrium open or with disjunct to conjunct deltidial plates; anterior commissure often dentate, sometimes spinose. Dental plates and dorsal medium septum present. Septalium with or without cover plate; cardinal process absent. *Lower Ordovician (Llanvirn)–Lower Carboniferous (Viséan)*.

Subfamily TRIGONIRHYNCHIIDAE Schmidt, 1965

[*nom. transl.* SAVAGE, 1996, p. 252, ex Trigonirhynchiidae SCHMIDT, 1965a, p. 2]

Trigonirhynchiidae with covered septalium. *lower Silurian (Llandovery)–Lower Carboniferous (Viséan)*.

Trigonirhynchia COOPER, 1942, p. 228, *non Trigonirhynchia* DAGYS, 1961, p. 94 [**Uncinulina fallaciosus* BAYLE, 1878, pl. 13, fig. 13–16; OD] [= *Uncinulina* BAYLE, 1878, pl. 13, fig. 13–16, *non* TERQUEM, 1862, *Holothuroidea*]. Shell small to medium; subtriangular to subpentagonal outline; strongly biconvex. Beak erect to suberect; delthyrium open, bordered by disjunct deltidial plates. Dorsal fold and ventral sulcus distinct but low, with gentle margins; anterior commissure uniplicate; tongue high, trapezoid, serrate. Costae strong, simple, rounded, from beaks. Dental plates distinct but short; teeth elongate, crenulate. Dorsal septum low, thin, long; septalium well developed, with cover plate; cardinal process absent; crural bases horizontal; crura curved ventrally, ventromedian surfaces concave in section. *middle Silurian (lower Wenlock)–Middle Devonian (lower Eifelian)*: Europe, North America, Siberia, China, Mongolia.—FIG. 710, 1*a–n*. **T. fallaciosus* (BAYLE), Lower Devonian, Néhou, France; *a–d*, hypotype, dorsal, ventral, lateral, and anterior views, $\times 1.2$; *e–n*, hypotype, serial sections 21.3, 21.2, 21.1, 21.0, 20.8, 20.7, 20.4, 20.0, 19.7, 19.3 mm from anterior, $\times 1.6$ (Schmidt, 1965a).

Agarhyncha HAVLÍČEK, 1982b, p. 369 [**Terebratula famula* BARRANDE, 1847, p. 87; OD]. Subpentagonal to subcircular outline; biconvex to globose

profile. Beak suberect to erect; foramen with minute deltidial plates. Fold and sulcus well defined, broad, anterior commissure uniplicate; tongue rectangular, serrate. Costae coarse, rounded, simple, but umbones smooth. Dental plates very short. Dorsal median septum thin; septalium with cover plate anteriorly; crura close to septum posteriorly. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*: Bohemia, Germany, Carnic Alps.—FIG. 710, 2*a–l*. **A. famula* (BARRANDE), lower Ludlow, Kopanina Formation, Bohemia; *a–e*, hypotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 4.6$; *f–l*, serial sections 7.15, 7.05, 7.03, 6.85, 6.65, 6.60, 6.45 from anterior, $\times 12$ (Havlíček, 1982b).

Ancillotoechia HAVLÍČEK, 1959, p. 78 [**Rhynchonella ancillans* BARRANDE, 1879b, pl. 36; OD] [= *Trigonirhynchioides* FU, 1982, p. 144, subj. (type, *T. qinlingensis*, OD)]. Small with subcircular to elongate outline; dorsibiconvex profile. Beak suberect; delthyrium open or with disjunct deltidial plates. Fold and sulcus narrow; anterior commissure uniplicate; tongue high, serrate. Costae strong, simple, from beaks. Dental plates short, thin, vertical. Septalium with cover; dorsal median septum low; cardinal process absent. *middle Silurian (Wenlock)–Lower Devonian (Lochkovian)*: cosmopolitan.—FIG. 711, 1*a–b*. **A. ancillans* (BARRANDE), upper Silurian, Kopanina Limestone, Bohemia; *a–d*, lectotype, dorsal, ventral, anterior, and lateral views, Kopanina Limestone, basal Budnany, V Kozle, near Beroun, $\times 3.5$ (new); *e–h*, serial sections 7.55, 7.50, 7.45, 7.40 mm from anterior, $\times 10$ (Havlíček, 1961).

Aratoechia HAVLÍČEK, 1982b, p. 368 [**Terebratula minerva* BARRANDE, 1847, p. 69; OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak suberect; foramen with conjunct deltidial plates. Fold and sulcus wide; anterior commissure with wide, rounded tongue, sharply dentate. Costae numerous, angular; some bifurcation. Dental plates distinct, slightly convergent ventrally. Septalium with cover; dorsal median septum high, long; cardinal process absent; crural bases horizontal. *middle Silurian (Wenlock)*: Bohemia.—FIG. 711, 2*a–b*. **A. minerva* (BARRANDE), Motol Formation; *a–c*, hypotype, dorsal, ventral, and anterior views, $\times 1.9$ (new); *d–h*, serial sections 13.7, 13.4, 13.3, 12.9, 12.8 mm from anterior, $\times 3.6$ (Havlíček, 1961).

Astua HAVLÍČEK, 1992, p. 85 [**Rhynchonella astuta* BARRANDE, 1879b, pl. 18, case 5, fig. 2*a–e*; OD]. Shell medium to large with subpentagonal outline and emarginate anterior; strongly biconvex, inflated anteriorly. Beak erect to incurved. Dorsal fold and ventral sulcus strong with distinct margins; tongue high; rectangular, serrate. Costae strong, simple, subangular, weak on umbones, numerous on flanks. Dental plates distinct; vertical, divergent anteriorly. Well-developed septalium without cover; dorsal median septum present; cardinal process absent; crura unknown. *Lower Devonian (Lochkovian)*: Bohemia, central Asia.—FIG. 712, 1*a–h*. **A.*

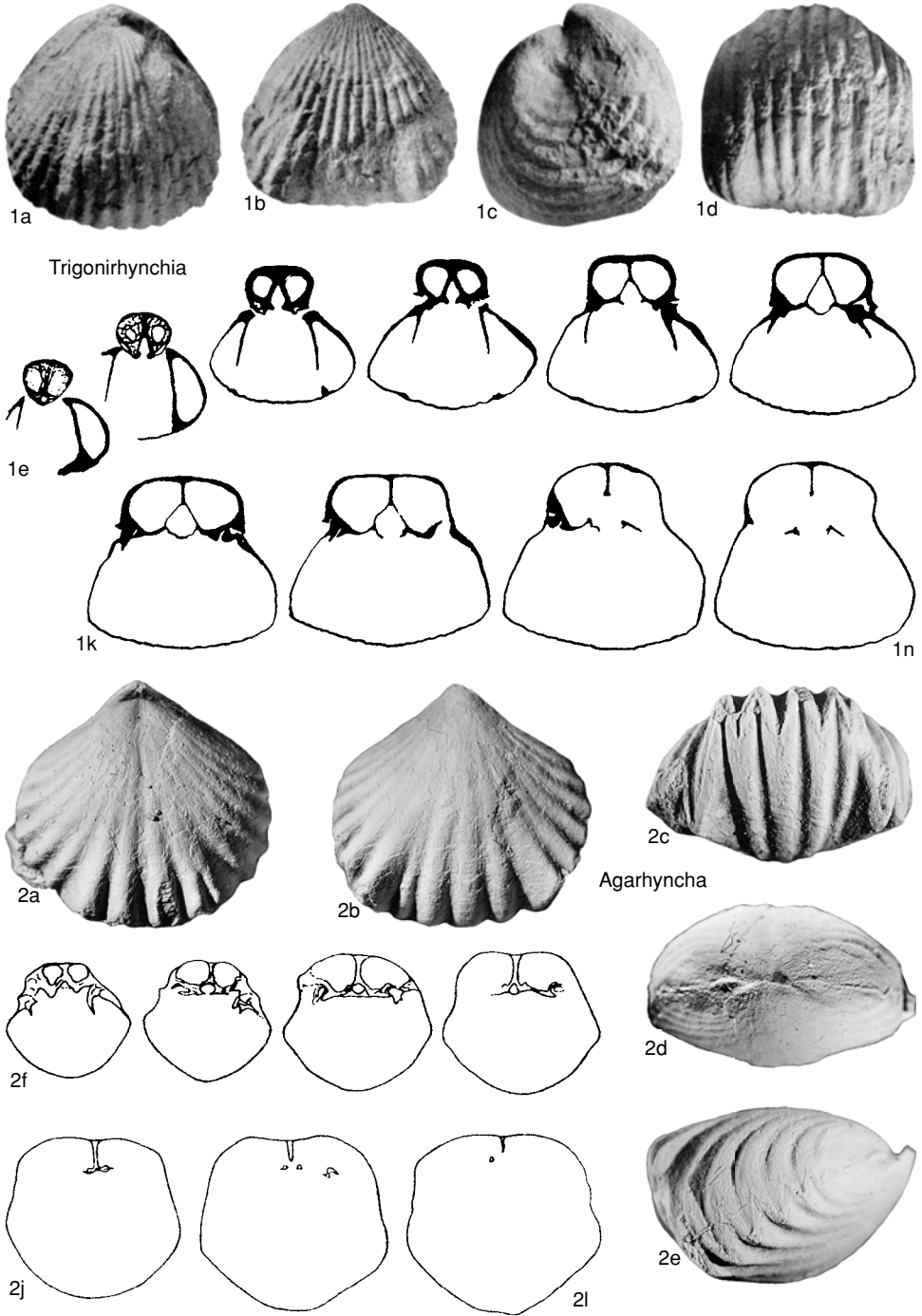


FIG. 710. Trigonirhynchiidae (p. 1052).

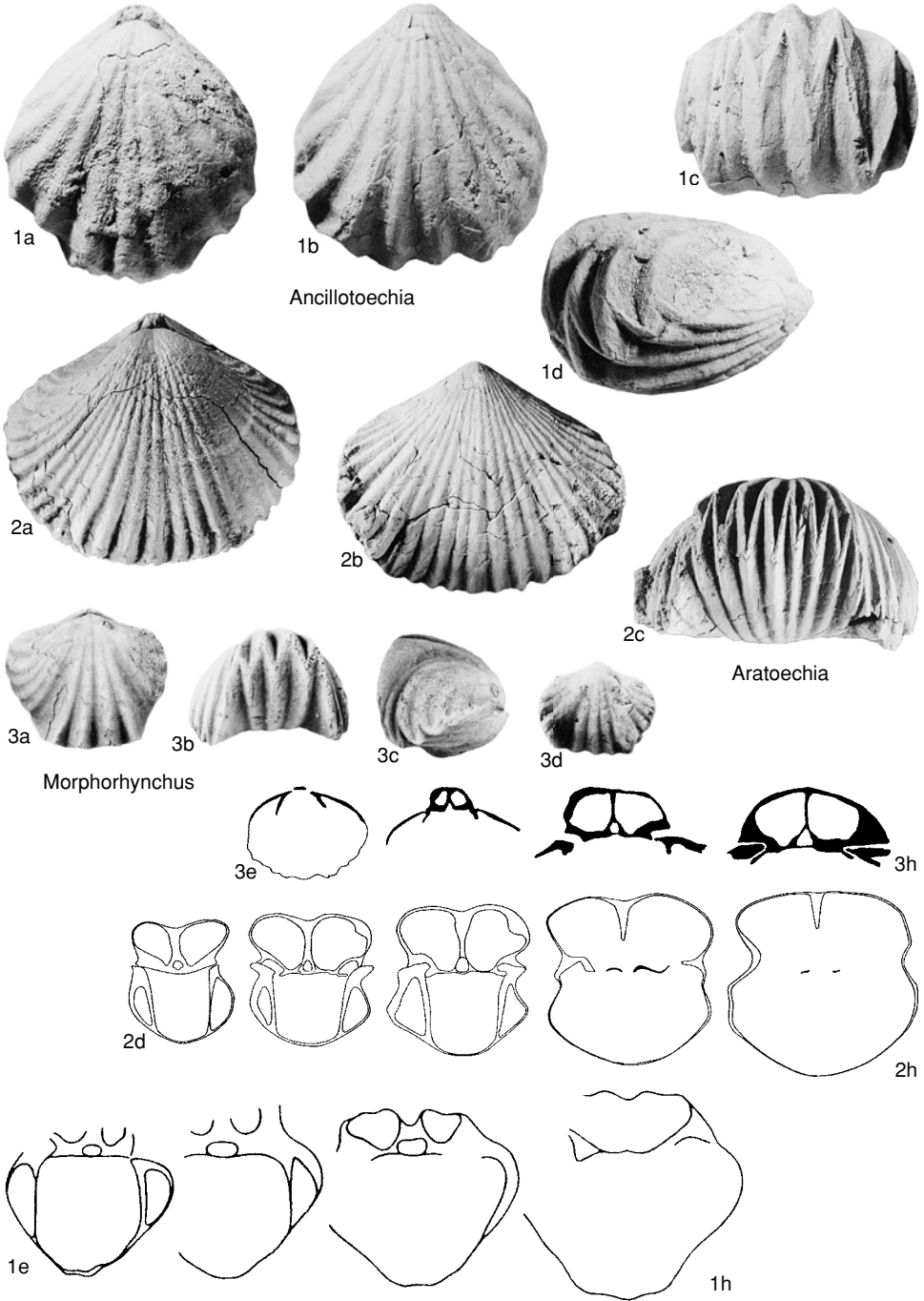


FIG. 711. Trigonirhynchiidae (p. 1052–1059).

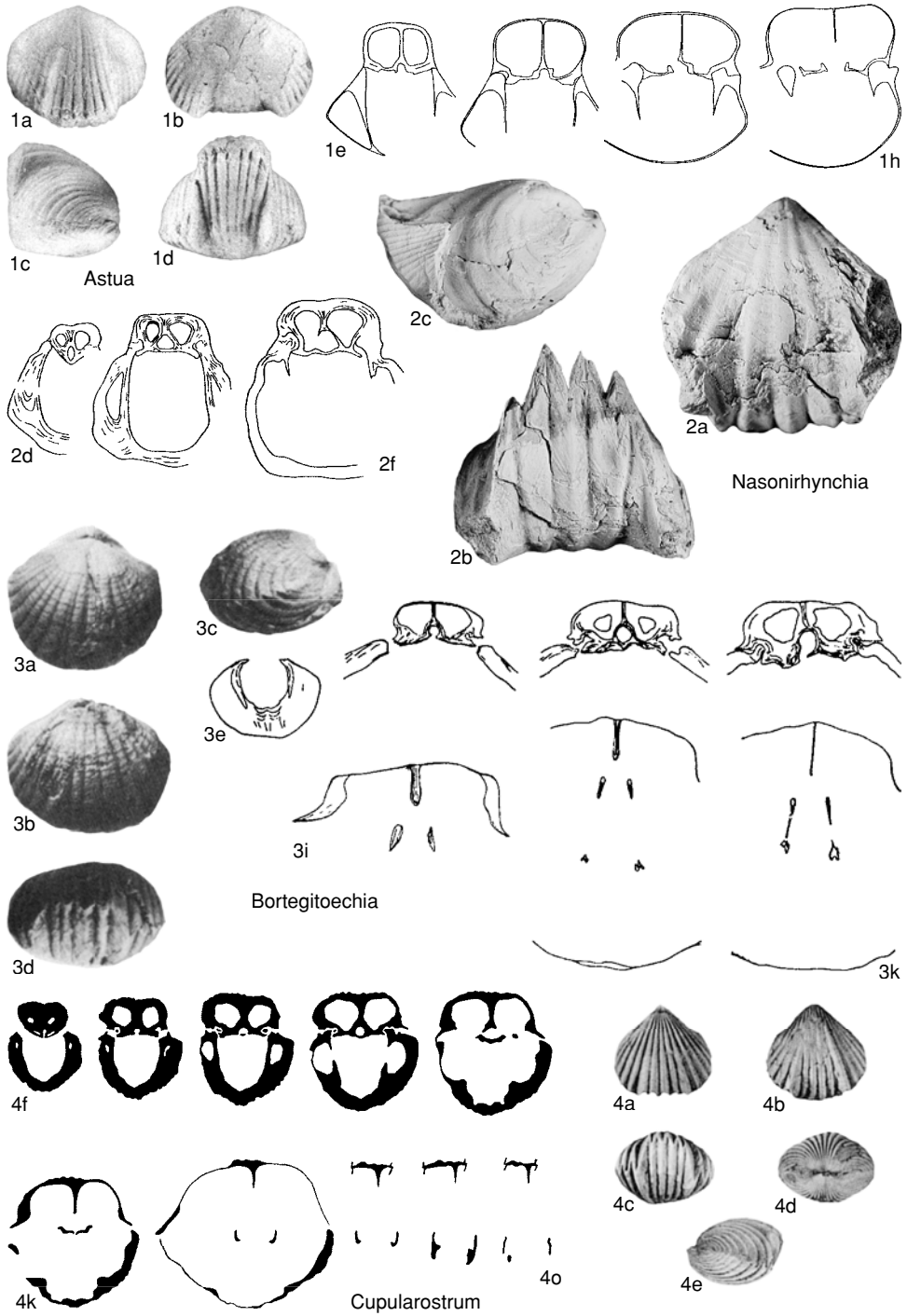


FIG. 712. Trigonirynchiidae (p. 1052–1059).

- astuta* (BARRANDE), Kotys Limestone, Svaty Jan pod Skalou, Bohemia; *a-d*, lectotype, dorsal, ventral, lateral, and anterior views, $\times 1$; *e-b*, serial sections 13.6, 13.3, 12.7, 12.6 mm from anterior, $\times 2.5$ (Havlíček, 1961).
- Bortegioechia** ERLANGER, 1994, p. 94 [**B. tsogtella*; OD]. Transversely subcircular outline and dorsibiconvex profile. Beak incurved; foramen unrecorded. Fold and sulcus weak, arising anteriorly; anterior commissure uniplicate; tongue low, trapezoid, serrate. Costae rounded, arising at beaks; some bifurcation; concentric growth lines distinct. Dental plates very short, obscured by callus. Dorsal median septum low, long; septalium short, open posteriorly and anteriorly but with cover plate at midlength; hinge plates divided anterior of septalium; crural bases and crura closely set, laterally flattened. *Lower Devonian (Lochkovian)*: Mongolia.—FIG. 712, 3*a-k*. **B. tsogtella*, Bortegsk Series, eastern Gobi, Bortegst Massif, Tsogt-Obo; *a-d*, holotype, dorsal, ventral, lateral, and anterior views, $\times 1.5$; *e-k*, serial sections 2.65, 3.15, 3.35, 3.65, 4.15, 4.35, 5.05 mm from posterior, $\times 2.5$ (Erlanger, 1994).
- Cupularostrum** SARTENAER, 1961d, p. 2 [**C. recticostatum*; OD]. Subcircular outline; strongly biconvex. Beak suberect; delthyrium with small foramen, deltidial plates disjunct. Fold and sulcus arising from umbones; anterior commissure uniplicate with trapezoid tongue; serrate. Costae strong, straight, simple, subangular, from beaks. Dental plates distinct, umbonal cavities may be set in thick shell walls; ventral muscle area deeply impressed. Dorsal median septum low, long; well-developed septalium with arched cover plate anteriorly; crura laterally flattened, concave medially. *Lower Devonian (Emsian)–Upper Devonian (Frasnian)*: cosmopolitan.—FIG. 712, 4*a-o*. **C. recticostatum*, Givetian, Skaneateles Formation, Hamilton, New York, USA; *a-e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 1$; *f-o*, serial sections 1.3, 1.7, 2.0, 2.2, 2.4, 2.55, 3.2, 3.3, 3.5, 3.7 mm from posterior, $\times 3$ (Sartenaer, 1961d).
- Hercotrema** JIN, 1989, p. 87 [**H. bulbicostatum*; OD]. Small to medium with transversely subcircular outline and biconvex profile. Beak small, incurved; delthyrium open to partly covered by rudimentary deltidial plates. Fold and sulcus with few large costae; anterior commissure sulciphate. Costae very coarse, rounded, extending from beaks. Dental plates high, thin; teeth small, arising from valve margins. Septalium small, lacking cover plate but with opening restricted by lateral extensions of hinge plates; cardinal process absent; crural bases horizontal; crura laterally flattened, digitose distally. *lower Silurian (Llandovery)–Lower Devonian (Lochkovian)*: North America, Bohemia.—FIG. 713, 1*a-o*. **H. bulbicostatum*, Llandovery, Jupiter Formation, Bai du Naufrage, Anticosti Island, Canada; *a-e*, holotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 3$; *f-o*, paratype, serial sections 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 1.9, 2.2, 2.3 mm from posterior, $\times 4$ (Jin, 1989).
- Iberirhynchia** DROT & WESTBROEK, 1966, p. 165 [**I. santaluciensis*; OD]. Shell small with trigonal to subpentagonal outline and dorsibiconvex profile, anteriorly inflated; apical angle acute to right angular. Beak erect; large delthyrium with incipient disjunct deltidial plates. Fold and sulcus weak; anterior commissure uniplicate with low, rectangular tongue, dentate. Costae simple, subangular; extending from beaks. Dental plates distinct, long, vertical; teeth large. Dorsal median septum long; septalium with cover plate; cardinal process absent; crura laterally flattened. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Spain, Bohemia.—FIG. 713, 2*a-n*. **I. santaluciensis*, Emsian-Eifelian boundary, upper Santa Lucia Formation, Pic Aguasalio, Leon Province, Spain; *a-d*, dorsal, ventral, lateral, and anterior views, $\times 2$; *e-l*, topotype, serial sections; *m-n*, topotype, anterior and anterolateral views of plastic model based on serial sections (Drot & Westbroek, 1966).
- Lissopleura** WHITFIELD, 1896, p. 232 [**Rhynchonella aequivalvis* HALL, 1857a, p. 66; OD]. Small with subtriangular outline and biconvex profile. Beak small, suberect. Foramen not recorded. Fold and sulcus weak; anterior commissure uniplicate; tongue low on holotype but moderately high and rectangular on most specimens. Umbones smooth. Costae fine, rounded to somewhat flattened. Dental plates short, ventrally convergent; ventral muscle field well impressed. Dorsal median septum strong, long; septalium deep, short, with cover plate anteriorly; hinge plates united, extend slightly anterior of septalium; crural bases triangular; crura with V-shaped cross section, open dorsally. *Lower Devonian (Lochkovian)*: North America.—FIG. 714, 1*a-p*. **L. aequivalvis* (HALL), lower Helderberg, Albany County, New York, USA; *a-d*, holotype, dorsal, ventral, lateral, and anterior views of cast; *e-h*, hypotype, dorsal, ventral, anterior, and lateral views, $\times 1.5$; *i-p*, serial sections 1.0, 1.45, 1.75, 2.35, 2.55, 3.35, 4.2, 4.65 mm from posterior, $\times 2.2$ (new).
- Macropotamorhynchus** SARTENAER, 1970a, p. 24 [**Camarotoechia mitcheldeanensis* VAUGHAN, 1905, p. 302; OD]. Small with subtrigonal to subpentagonal outline and dorsibiconvex profile. Beak suberect to erect; foramen small, ovate; delthyrium with conjunct deltidial plates. Fold and sulcus weak, arising at umbones; anterior commissure uniplicate; tongue moderately high, dentate. Costae angular, strong, simple, arising at beaks. Dental plates short, vertical. Dorsal median septum low, long, extending to about half valve length; septalium short, generally with cover plate; hinge plates divided immediately anterior of septalium; crural bases triangular; crura laterally flattened. *Lower*

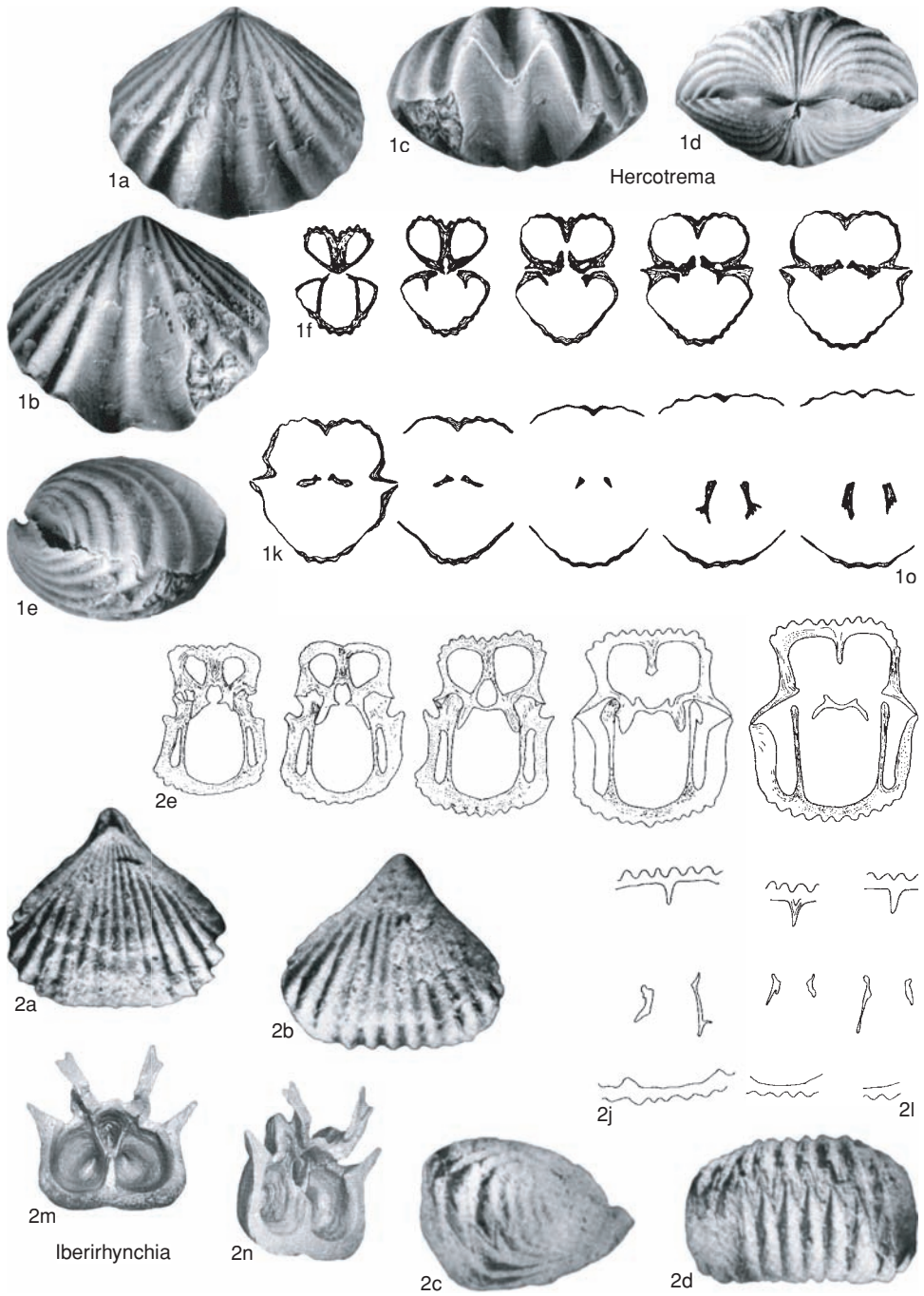


FIG. 713. Trigonirhynchiidae (p. 1056).

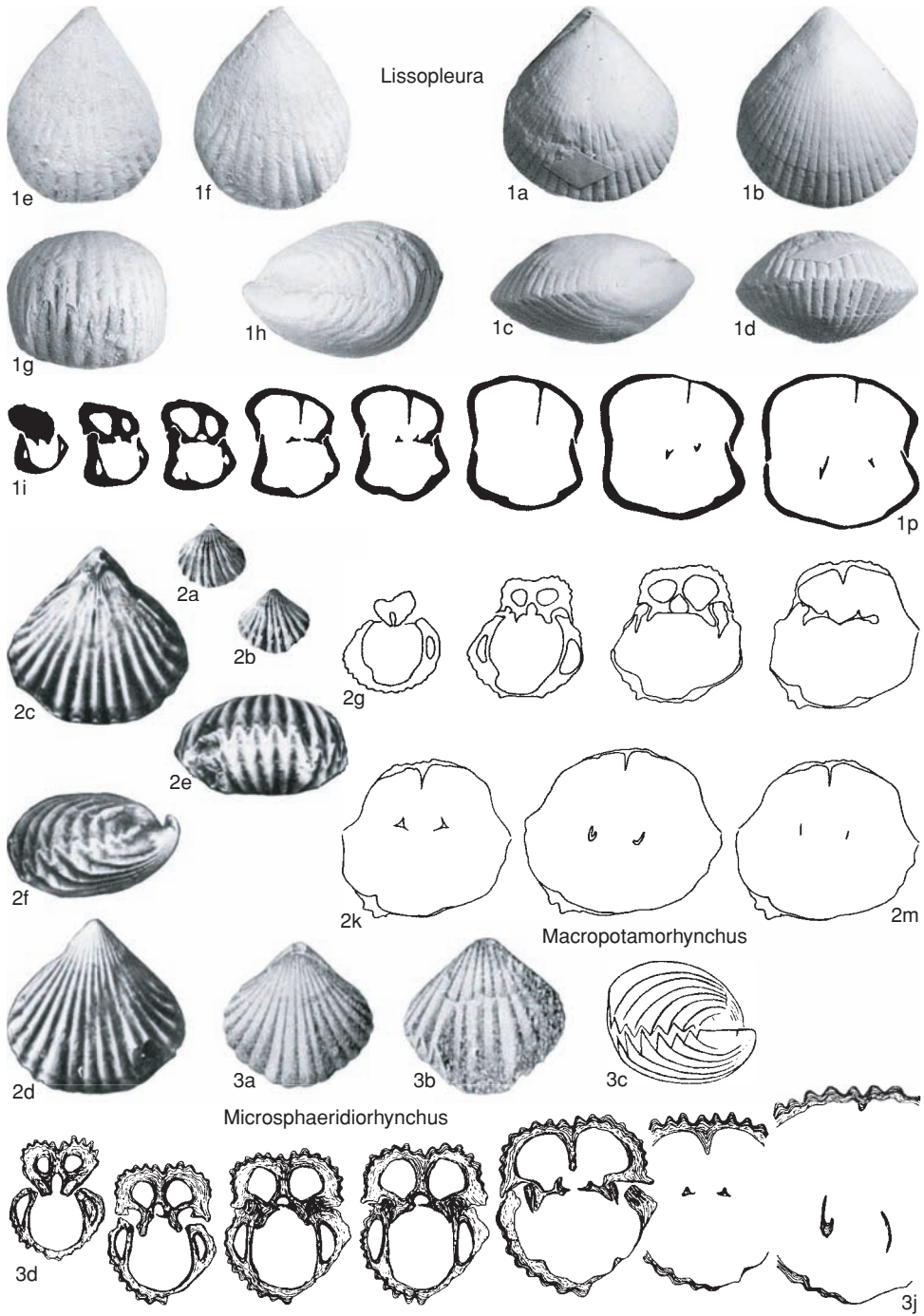


FIG. 714. Trigonirynchiidae (p. 1056–1059).

- Carboniferous (lower Tournaisian)*: western and eastern Europe, Asia, North America, Australia.—FIG. 714,2a–b. **M. mitcheldeanensis* (VAUGHAN), Carboniferous Limestone, Gloucestershire, Mitcheldean, England; holotype, dorsal and ventral views, $\times 1$ (Vaughan, 1905).—FIG. 714,2c–m. *M. curiosus*, Banff Formation, Alberta, Forbidden Creek, Canada; c–f, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; g–m, serial sections 1.4, 1.7, 2.0, 2.3, 2.6, 3.0, 3.8 mm from posterior, $\times 4.5$ (Carter, 1987).
- Microsphaeridiorhynchus** SARTENAER, 1970a, p. 27 [**Rhyntonella* (?) *litchfieldensis* SCHUCHERT, 1903, p. 167; OD]. Rounded trigonal outline and strongly biconvex profile. Ventral beak incurved; delthyrium bordered by narrow disjunct deltidial plates. Fold and sulcus strong, from umbones; anterior commissure uniplicate, dentate. Costae strong, simple, angular, from beaks. Dental plates distinct but short; vertical. Dorsal median septum thick, long; well-developed septalium with cover plate; cardinal process absent; crura laterally flattened, concave dorsomedially. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian)*: North America, Europe, China.—FIG. 714,3a–c. **M. litchfieldensis* (SCHUCHERT), Přídolí, Coblestone Limestone, Litchfield, New York, USA; lectotype, dorsal, ventral, and lateral views, $\times 1$ (Schuchert, 1903).—FIG. 714,3d–j. *M. nucula* (SOWERBY), hypotype, serial sections 0.7, 0.9, 1.0, 1.1, 1.4, 1.5, 2.3 mm from posterior from Eke Beds, Ludlow, Lau Backar, Gotland, $\times 5$ (Jin, Caldwell, & Norford, 1993).
- Moorefieldella** GIRTY, 1911, p. 62 [**Rhyntonella eurekensis* WALCOTT, 1884, p. 223; OD]. Subtrigonal to ovate outline and biconvex profile. Beak erect to suberect; foramen partly closed by narrow disjunct deltidial plates. Fold and sulcus low, flat, developed anteriorly; tongue low, trapezoid. Costae fine, arising at about one-third shell length; concentric growth lines commonly visible anteriorly. Dental plates short, ventrally divergent; subtriangular ventral muscle field weakly impressed. Dorsal median septum high in type species but may be low in others; septalium very short, partly covered in type species by fused inner hinge plates; crura short, closely set and dorsally concave in type species. *Lower Carboniferous (Tournaisian–Viséan)*: North America.—FIG. 715,2a–e. **M. eurekensis* (WALCOTT), Meramecian, Spring Creek Limestone, Moorefield, White River Junction, Arkansas, USA; dorsal, ventral, lateral, anterior, and posterior views of specimen illustrated by COOPER, 1942, $\times 1.5$ (new).—FIG. 715,2f–n. *M. prisca* CARTER, Kinderhookian, Banff Formation, Jasper Park region, Alberta, Canada; serial sections at 1.4, 1.5, 1.7, 2.0, 2.2, 2.4, 2.6, 2.9, 3.1 mm from posterior, $\times 1.5$ (Carter, 1987).
- Morphorhynchus** COOPER & DUTRO, 1982, p. 71 [**M. varicostatum*; OD]. Subrectangular outline and strongly dorsibiconvex profile; inflated anteriorly. Beak incurved; foramen small, deltidial plates disjunct. Fold and sulcus strong; anterior commissure uniplicate; tongue high, with subrounded margins. Costae strong and subangular, arising from umbones. Dental plates diverging ventrally toward valve floor. Dorsal median septum long; septalium with cover plate anteriorly; inner socket ridges high, thin; crura long, flattened distally. *Middle Devonian (upper Givetian)*: western North America.—FIG. 711,3a–h. **M. varicostatum*, Orfiate Formation; a–c, holotype, dorsal, anterior, lateral views, $\times 2$; d, ventral view, $\times 1.5$; e–h, paratype, serial sections 0.9, 1.2, 1.3, 1.6 mm from posterior, $\times 3$ (Cooper & Dutro, 1982).
- Myrmirhynch** HAVLÍČEK, 1982b, p. 366 [**Rhyntonella myrmex* BARRANDE, 1879b, pl. 28, case 3, fig. 1–15; OD]. Shell small; subtriangular outline; moderately biconvex with shape dominated by strong plicae. Ventral beak erect to incurved; foramen with disjunct deltidial plates. Dorsal fold and ventral sulcus low but with distinct margins. Plicae increasing by bifurcation and intercalation; anterior commissure sulcinate. Dental plates short, converging ventrally toward valve floor. Short septalium with cover; cardinal process absent. *middle Silurian (Wenlock)–upper Silurian (Ludlow)*: Bohemia.—FIG. 715,1a–h. **M. myrmex* (BARRANDE), Ludlow, *Cromus beaumonti* layer, Kopanina Formation, Zadni Kopanina; a–c, hypotype, dorsal, ventral, and anterior views, $\times 5$; d–h, hypotype, serial sections 7.95, 7.80, 7.65, 7.60, 7.50 mm from anterior, $\times 12$ (Havlíček, 1982b).
- Nasonirhynchia** HAVLÍČEK, 1992, p. 83 [**N. naso*; OD]. Subpentagonal outline with emarginate anterior; strongly biconvex, inflated anteriorly. Beak erect to incurved, deltidial plates unknown. Dorsal fold and ventral sulcus strong with steep margins, arising at umbones; tongue high, dentate. Plicae strong, simple, angular, weak on umbones and flanks. Dental plates distinct but short; subvertical. Well-developed septalium with cover plate; dorsal median septum low; cardinal process absent; crura unknown. *Lower Devonian (Pragian)*: Bohemia.—FIG. 712,2a–f. **N. naso*, Koneprusy Limestone, Zlatý kun Hill; a–c, holotype, ventral, anterior, and lateral views, $\times 2$; d–f, topotype, serial sections 14.25, 13.25, 13.0 mm from anterior, $\times 3.8$ (Havlíček, 1992).
- Nekhoroshevia** BUBLICHENKO, 1956, p. 101 [**N. altaica*; OD]. Subpentagonal outline; strongly dorsibiconvex to inflated. Beak incurved. Fold and sulcus very wide with rounded margins, arising at umbones. Costae rounded to flattened, from beaks. Dental plates vertical; dorsal median septum high, slender; septalium deep, with convex cover; crura unknown. *Upper Devonian (lower Famennian)–Lower Carboniferous (upper Tournaisian)*: Altai, Kazakhstan, Verkhoian.—FIG. 716,2a–e. **N. altaica*; a–d, holotype, dorsal, ventral, anterior, and

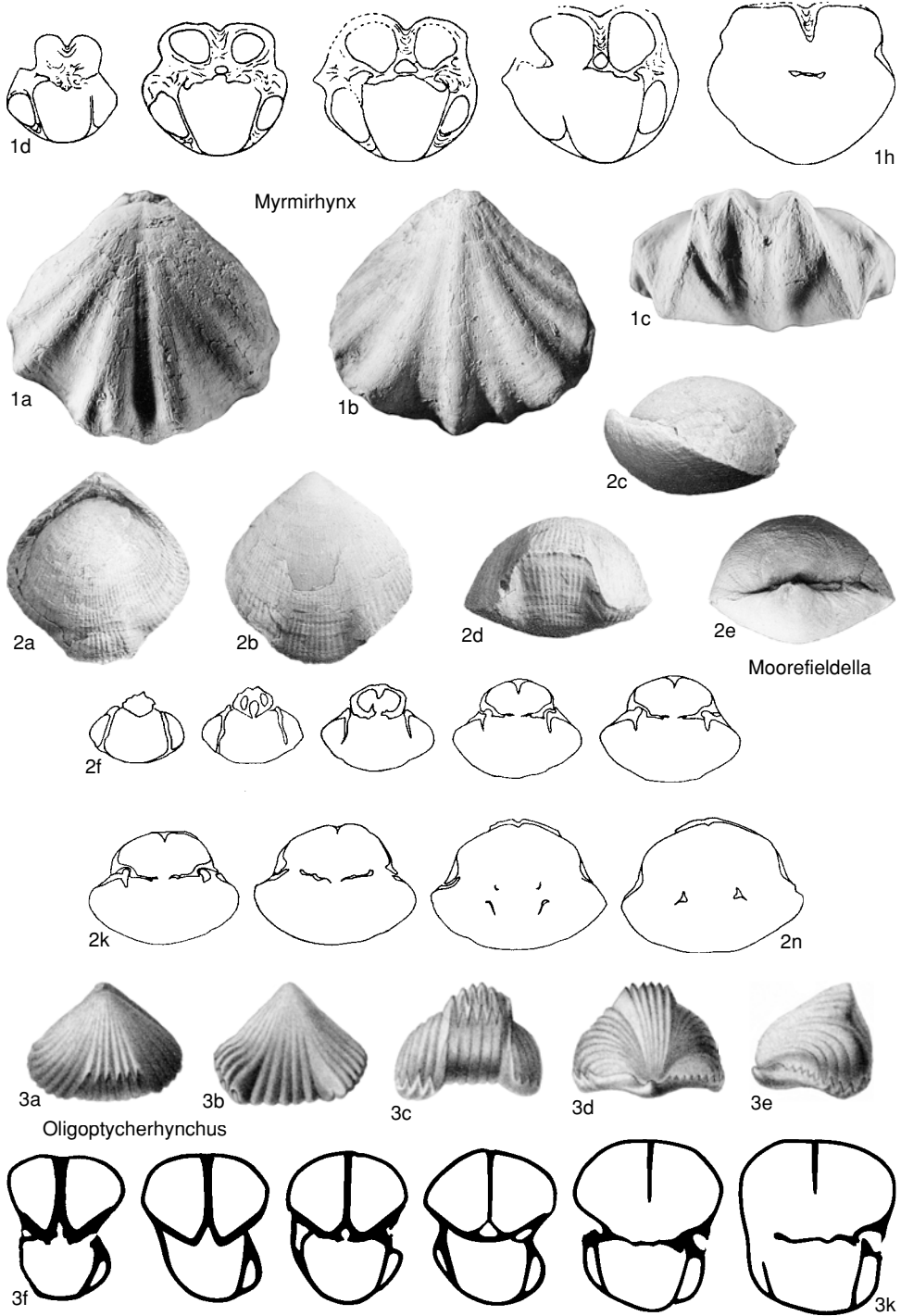


FIG. 715. Trigonirynchiidae (p. 1059–1062).

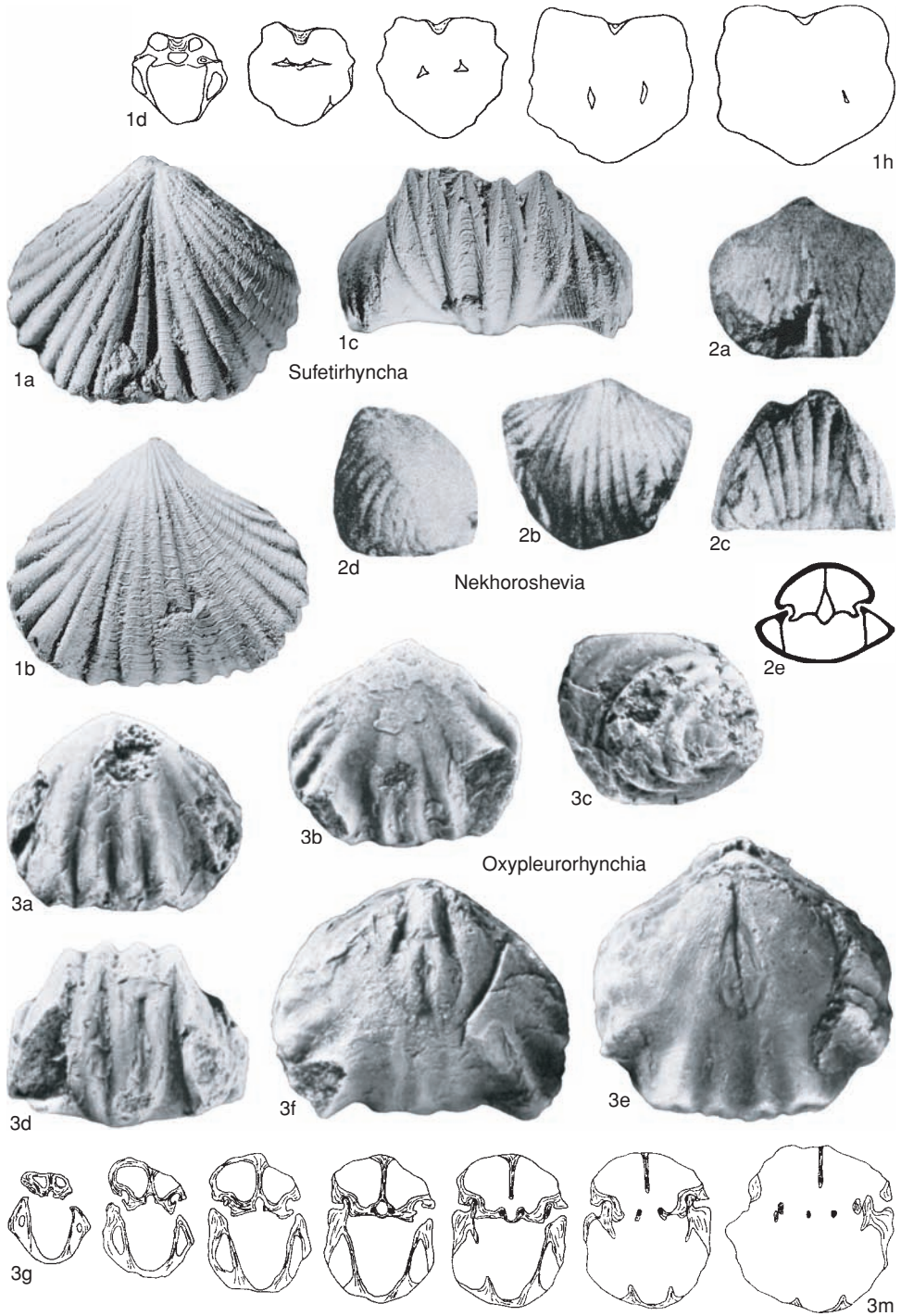


FIG. 716. Trigonirynchiidae (p. 1059–1062).

- lateral views, $\times 1$; *e*, serial section near posterior, $\times 2$ (Bublichenko, 1974).
- Oligoptycherhynchus** SARTENAER, 1970a, p. 20 [**Terebratula hexatoma* SCHNUR, 1851, p. 3; OD]. Subtrigonal to subpentagonal outline; strongly dorsibiconvex; beak suberect to erect. Fold and sulcus strong; arising at umbones; anterior commissure uniplicate; tongue high, rectangular, dentate. Costae strong, simple, angular, from beaks. Dental plates distinct, ventrally convergent. Dorsal median septum long, high; septalium with cover anteriorly; crura unknown. *Lower Devonian (lower Emsian)–Middle Devonian (upper Eifelian)*: Europe, Morocco, Canada.—FIG. 715,3a–k. **O. hexatomus* (SCHNUR), lower Eifelian, Gondelsheimer Formation, Geeser bed, Uxheim, Eifel, Germany; *a–e*, dorsal, ventral, anterior, posterior, and lateral views of original figured specimen, $\times 2.6$ (Schnur, 1853); *f–k*, serial sections of specimen from same formation, $\times 4$ (Schmidt, 1941a).
- Oxypleurorhynchia** PŁODOWSKI, 1973, p. 85 [**O. acutiplicata*; OD]. Subtrigonal to subpentagonal outline and dorsibiconvex profile. Beak erect to incurved; foramen small. Fold and sulcus pronounced, from umbones; tongue high in mature specimens. Costae coarse, rounded, simple, arising at umbones. Dental plates well developed, ventrally convergent; ventral muscle field narrow, bilobed, with marginal rim. Dorsal median septum prominent, extending to valve midlength; septalium long, with cover for part of length; crura closely set, rod-like proximally. *upper Silurian (Přídolí)*: Austria (Carnic Alps).—FIG. 716,3a–m. **O. acutiplicata*, lower Přídolí, upper “eosteinhornensis” Zone, Lawinenrinne am E-Hand des Cellon, Carnic Alps; *a–d*, paratype, dorsal, ventral, lateral, and anterior views, $\times 2$; *e*, holotype, dorsal surface of internal mold; *f*, holotype, ventral surface of internal mold, $\times 3$; *g–m*, serial sections 0.7, 0.8, 1.3, 1.4, 1.6, 1.8, 2.2 mm from posterior, $\times 3.5$ (Płodowski, 1973).
- Sinotectirostrum** SARTENAER, 1961c, p. 3 [**S. medicinale*; OD]. Equidimensional to elongate subpentagonal outline; dorsibiconvex. Beak erect to incurved; foramen small, epithyrid. Fold and sulcus low; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, from beaks. Dental plates short, slender, vertical; teeth arising from valve margins; ventral muscle field moderately impressed. Hinge plates united; septalium with cover plate anteriorly; crural bases horizontal; crura with gutterlike surface directed dorsomedially. *Upper Devonian (Famennian)*: Canada, ?Belorussia.—FIG. 717,2a–o. **S. medicinale*, Alexo Formation, Medicine Lake, Alberta, Canada; *a–e*, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 1$; *f–o*, paratype, serial sections 1.60, 1.95, 2.3, 2.6, 2.8, 3.0, 3.35, 3.8, 4.4, 4.75 mm from posterior, $\times 3$ (Sartenaer, 1969).
- Stenorhynchia** BRICE, 1981b, p. 195 [**Terebratula nymphea* BARRANDE, 1847, p. 66; OD] [= *Stenorhynchites* HAVLÍČEK in HAVLÍČEK & ŠTORCH, 1990, p. 145 (type, *Rhynchonella infelix* BARRANDE, 1879b, pl. 28, case 1, fig. 3–4)]. Subpentagonal outline and strongly dorsibiconvex, inflated, profile; lateral and anterior shell margins precipitous. Fold and sulcus strong, wide, from umbones, with high anterior tongue. Beak erect to incurved. Costae strong, simple, from beaks; interspaces extended into spines at anterior commissure. Dental plates distinct, well separated from valve walls. Dorsal median septum long; septalium perforate posteriorly but covered anteriorly; cardinal process absent; crural bases arising from septalium cover plates; crura ventrally curved, convex ventrolaterally in cross section. *upper Silurian (Ludlow)–Lower Devonian (Emsian)*: Europe, northern Africa, Urals, Tadzhikistan, Mongolia.—FIG. 717,1a–p. **S. nymphea* (BARRANDE), Lower Devonian; *a–d*, neotype, dorsal, ventral, anterior, and lateral views, Koneprusy Limestone, Koneprusy, Bohemia, $\times 1$; *e–h*, hypotype, serial sections 10.5, 10.3, 10.2, 10.1 mm from anterior, Koneprusy Limestone, Koneprusy, Bohemia, $\times 2.5$ (Havlíček, 1961); *i–p*, hypotype, serial sections 1.0, 1.1, 1.2, 1.7, 2.0, 2.6, 2.9, 3.2 mm from posterior, upper Emsian, Margettes Formation, Brittany, France, $\times 3$ (Brice, 1981b).
- Sufetirhyncha** HAVLÍČEK, 1982b, p. 367 [**Ancillotoechia radvani* HAVLÍČEK, 1961, p. 62; OD]. Small to medium with subpentagonal outline and dorsibiconvex profile. Beak straight to suberect. Dorsal fold and ventral sulcus low but distinct, wide anteriorly; fold with median depression, sulcus with corresponding low rise; anterior commissure sulciphate; tongue low, broad, dentate. Costae strong, increasing by bifurcation and intercalation, from beaks; crossed by concentric rugae. Dental plates very short, converging toward valve floor. Dorsal median septum short; septalium low, with cover plate; crural bases triangular; crura laterally compressed. *upper Silurian (Ludlow)*: Bohemia.—FIG. 716,1a–h. **S. radvani* (HAVLÍČEK), Kopanina Formation, Velka Morina; *a–c*, hypotype, dorsal, ventral, and anterior views, $\times 3.8$; *d–h*, hypotype, serial sections 5.3, 5.15, 4.85, 4.55, 4.4 mm from anterior, $\times 9$ (Havlíček, 1982b).
- Tetratomia** SCHMIDT, 1941a, p. 13 [**Terebratula tetratomia* SCHNUR, 1851, p. 4; OD]. Small with elongate subtriangular to subpentagonal outline and biconvex profile. Beak erect to incurved. Fold and sulcus strong, narrow, from umbones; anterior commissure uniplicate, strongly serrate. Costae strong, simple, from beaks. Dental plates short, vertical, may be obscured by callus. Dorsal median septum short; hinge plates united by convex plate; septalium absent; cardinal process absent; crura laterally compressed. *Lower Devonian (Pragian)–Middle Devonian (Eifelian)*: Europe, Morocco.—FIG. 718,1a–j. **T. tetratomia* (SCHNUR), lower Eifelian, Eifel, Germany; *a–c*, ventral, lateral, and anterior views, $\times 2$ (Schmidt, 1941a); *d–j*, serial sections, $\times 5.3$ (McLaren, 1965).
- Wilsoniella** KHALFIN, 1939, p. 83, *non Wilsonella* NIKIFOROVA, 1937a [**W. prima*; OD] [= *Usovia* KHALFIN, 1955, p. 239, obj.]. Large with elongate-

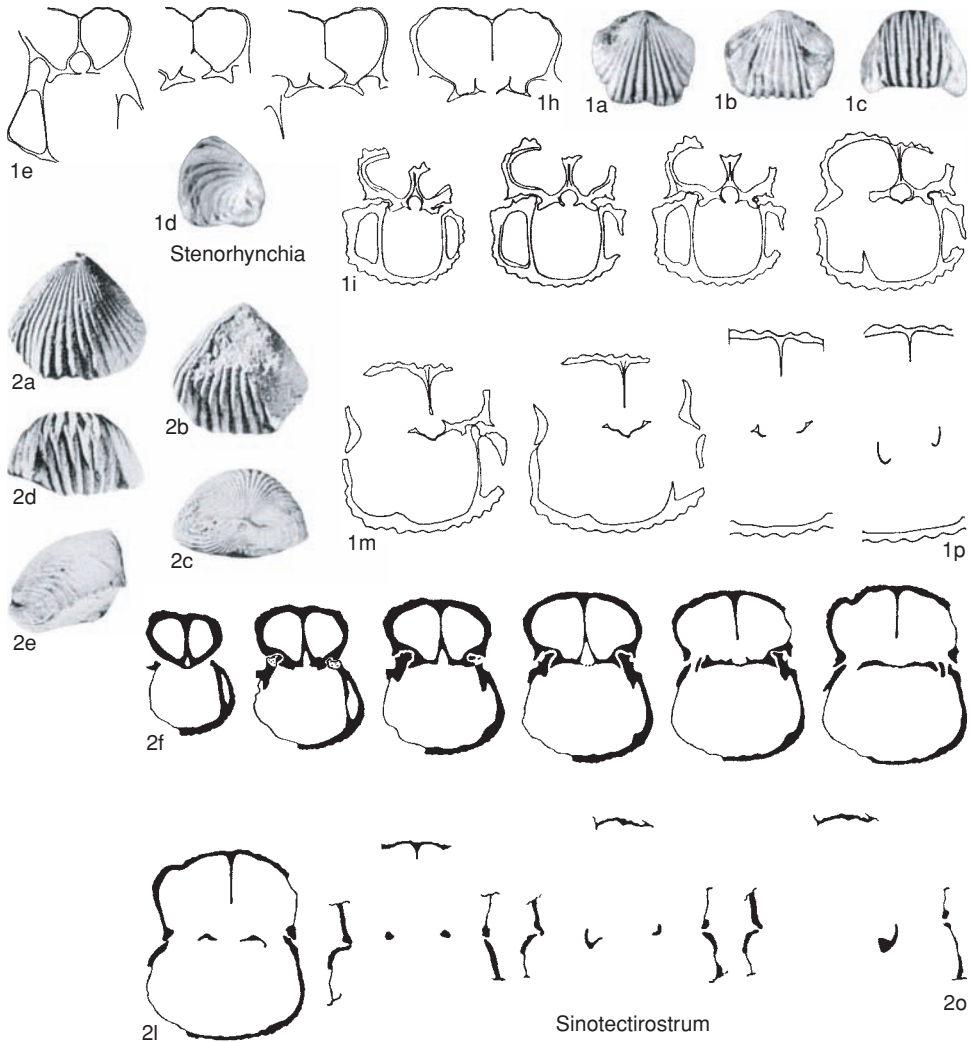


FIG. 717. Trigonirhynchiidae (p. 1062).

oval to subtrigonal outline and inflated dorsibiconvex profile. Beak incurved; foramen small. Fold and sulcus developed anteriorly; anterior commissure uniplicate; tongue high, trapezoid. Costae numerous, simple, arising at beaks, rounded in profile with narrow interspaces, flattened anteriorly. Dental plates convex medially. Hinge plates united posteriorly; dorsal median septum low, long; septalium covered posteriorly but open, large, and wide anteriorly where supported on median septum; crural bases arising from vertical walls of septalium, crura laterally flattened. *Lower Devonian (Pragian–Emsian)*: Altay, Mongolia.—FIG. 718, 2a–d. **W. prima*, Pragian, northwestern Mongolia; dorsal and lateral, ventral and lateral

views, $\times 1$ (Erlanger, 1994).—FIG. 718, 2e–m. *W. prisca* ERLANGER, Pragian, northwestern Mongolia; serial sections 3.3, 3.85, 4.2, 4.7, 5.3, 5.7, 5.85, 7.1, 8.25 mm from posterior, $\times 1.75$ (Erlanger, 1994).

Subfamily ROSTRICELLULINAE Rozman, 1969

[Rostricellulinae ROZMAN, 1969, p. 94]

Early Trigonirhynchiidae with uncovered septalium and costae crossed by distinct concentric lamellae; delthyrium open or with

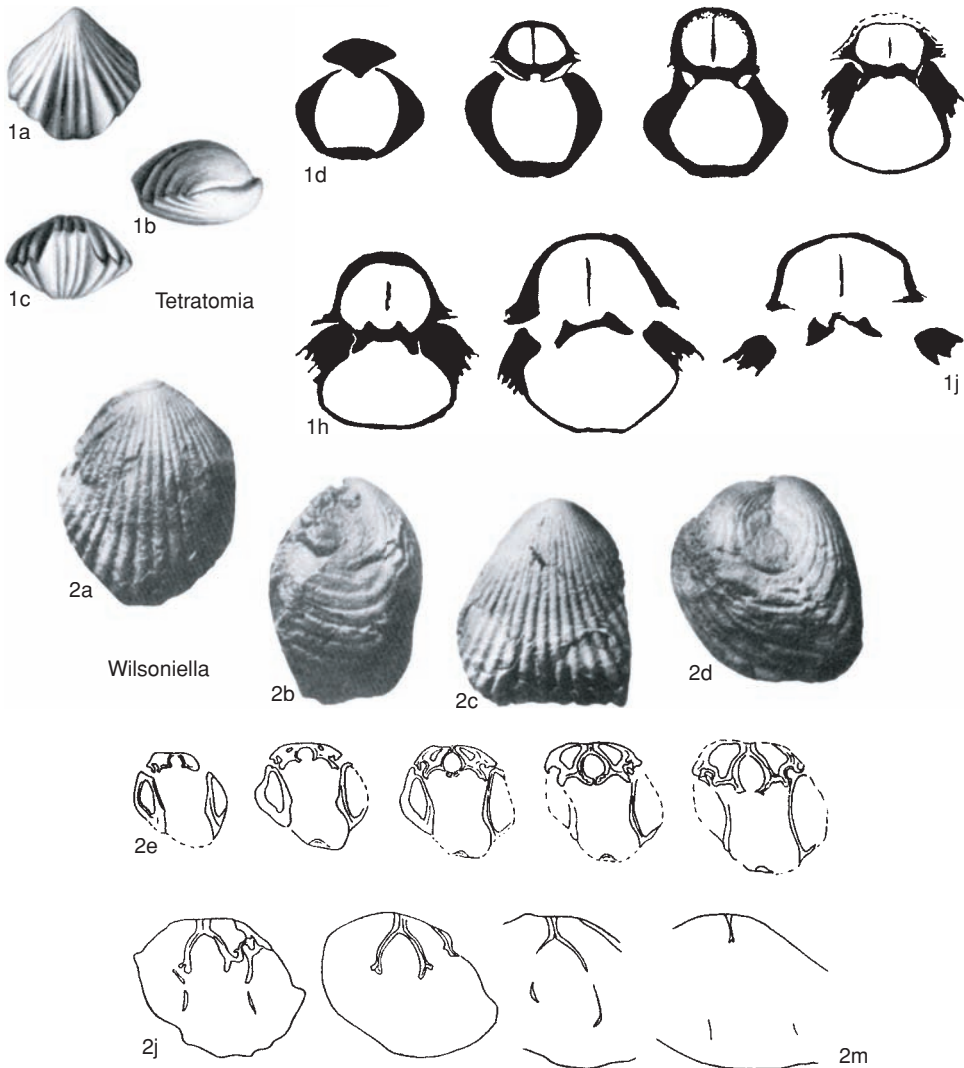


FIG. 718. Trigonirynchiidae (p. 1062–1063).

incipient deltidial plates; dorsal median septum short. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery)*.

Rostricellula ULRICH & COOPER, 1942, p. 625 [**R. rostrata*; OD] [= *Longxianirynchia* FU, 1982, p. 143 (type, *L. transversa*, OD)]. Subtrigonal to subpentagonal outline; moderately biconvex. Beak erect to incurved; delthyrium open to partly closed by incipient deltidial plates. Fold and sulcus distinct with rounded margins; anterior commissure uniplicate; tongue low, serrate. Costae fine to medium, simple, extending from umbones; crossed by

concentric growth lamellae. Dental plates distinct but short. Dorsal median septum to midlength; septalium short, without cover; hinge plates divided anterior of septalium; crural bases subhorizontal; crura distally slender, ventrally curved. *Lower Ordovician (Llanvirn)–lower Silurian (Llandovery)*: North America, Europe, Asia.—FIG. 719, 1a–h. **R. rostrata*, Lebanon Formation, Middle Ordovician, Clinton, Tennessee, USA; a–e, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 1$; f, paratype, ventral valve interior, $\times 2$; g–h, paratypes, dorsal valve interiors showing cardinalia and crura, $\times 4$ (Ulrich & Cooper, 1942).

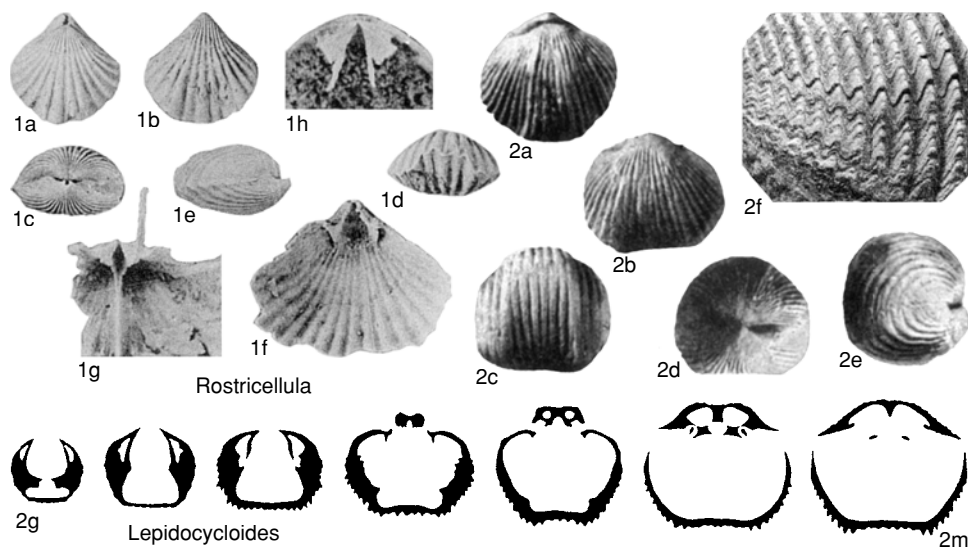


FIG. 719. Trigonirhynchiidae (p. 1064–1065).

Azamella LAURIE, 1991, p. 93 [*A. rotunda*; OD]. Transversely ovate outline; strongly biconvex. Beak erect to incurved; delthyrium open. Fold and ventral sulcus with rounded margins; anterior commissure weakly uniplicate; costae strong, simple, extending from umbones, crossed by lamellose concentric growth lines. Dental plates distinct but short; ventral muscle field well impressed. Hinge plates divided anterior of short septalium, without cover; dorsal median septum long, to midlength; crura ventrally curved. *Lower Ordovician (upper Llanvirn)*: southeastern Australia (Tasmania).—FIG. 720, 2a–b. *A. rotunda*, Benjamin Limestone, lower Limestone Member, Florentine Valley; a–d, holotype, dorsal, ventral, anterior, and lateral views; e–f, paratype, interior views of ventral valve; g, paratype, interior of dorsal valve; b, paratype, interior of dorsal valve showing crura, $\times 3.25$ (Laurie, 1991).

Evenkorhynchia ROZMAN, 1969, p. 102 [*Rostricellula dichotomians* ROZMAN, 1968, p. 71; OD]. Subcircular to subpentagonal outline and biconvex to dorsibiconvex profile. Beak suberect to erect; delthyrium open with narrow rudimentary deltidial plates. Fold and sulcus flattened, distinct anteriorly; anterior commissure uniplicate; tongue prominent, trapezoid. Costae strong, rounded, from beaks, some intercalation and bifurcation, crossed by fine tuberculate growth lamellae. Dental plates short, vertical. Dorsal median septum short, thick; septalium short, open; crural bases horizontal; crura distally slender, ventrally curved. *Upper Ordovician (upper Caradoc–Ashgill)*: northeastern Siberia.—FIG. 720, 3a–i. *E. dichotomians* (ROZMAN), Ashgill, Nirundinian, Selennyakh Range; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–i,

serial sections 0.8, 1.0, 1.2, 1.4, 2.3 mm from posterior, $\times 6$ (Rozman, 1970).

Lepidocycloides NIKIFOROVA, 1961, p. 212 [*L. baikiticus*; OD]. Medium to large size; globular. Beak incurved; foramen mesothyrid, delthyrium open, deltidial plates absent. Fold and sulcus distinct, arising at umbones; tongue high, rectangular to subrounded. Costae fine, simple, or with rare bifurcations, arising at beaks; crossed by distinct concentric lamellae. Dental plates short, vertical to ventrally divergent; ventral muscle area deeply impressed. Septalium short, open, wide; dorsal median septum low, short. *Upper Ordovician (Caradoc–Ashgill)*: central Siberia, Altai, China.—FIG. 719, 2a–m. *L. baikiticus*, Dolborsky Stage, lower Chunku River, Baikit; a–e, holotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 1$; f, enlargement of costae showing lamellae, $\times 4$; g–m, serial sections 14.1, 13.8, 13.5, 12.8, 12.1, 11.6, 11.3 mm from anterior, $\times 1.5$ (Nikiforova, 1961).

Plectothyrella TEMPLE, 1965, p. 412 [*P. platystrophoides*; OD; =*P. crassicosta* (DALMAN), 1828, p. 131]. Subcircular to subtrigonal; strongly biconvex. Beak suberect; delthyrium open. Dorsal fold and ventral sulcus from umbones but faint ventral fold and dorsal sulcus posteriorly. Costae strong, subangular, from beaks; some intercalation. Growth lamellae closely spaced; strongest anteriorly. Dental plates convergent ventrally; teeth small, cyrtomatodont; ventral muscle field deeply impressed. Dorsal median septum low, thick; septalium short, without cover; hinge plates divided; inner socket ridges massive; sockets thin; crural bases thick; crura long, thick. *Upper Ordovician (Ashgill)*: Europe, eastern North America, northern Africa, South Africa, South America, Siberia, China.—FIG. 720, 1a–e.

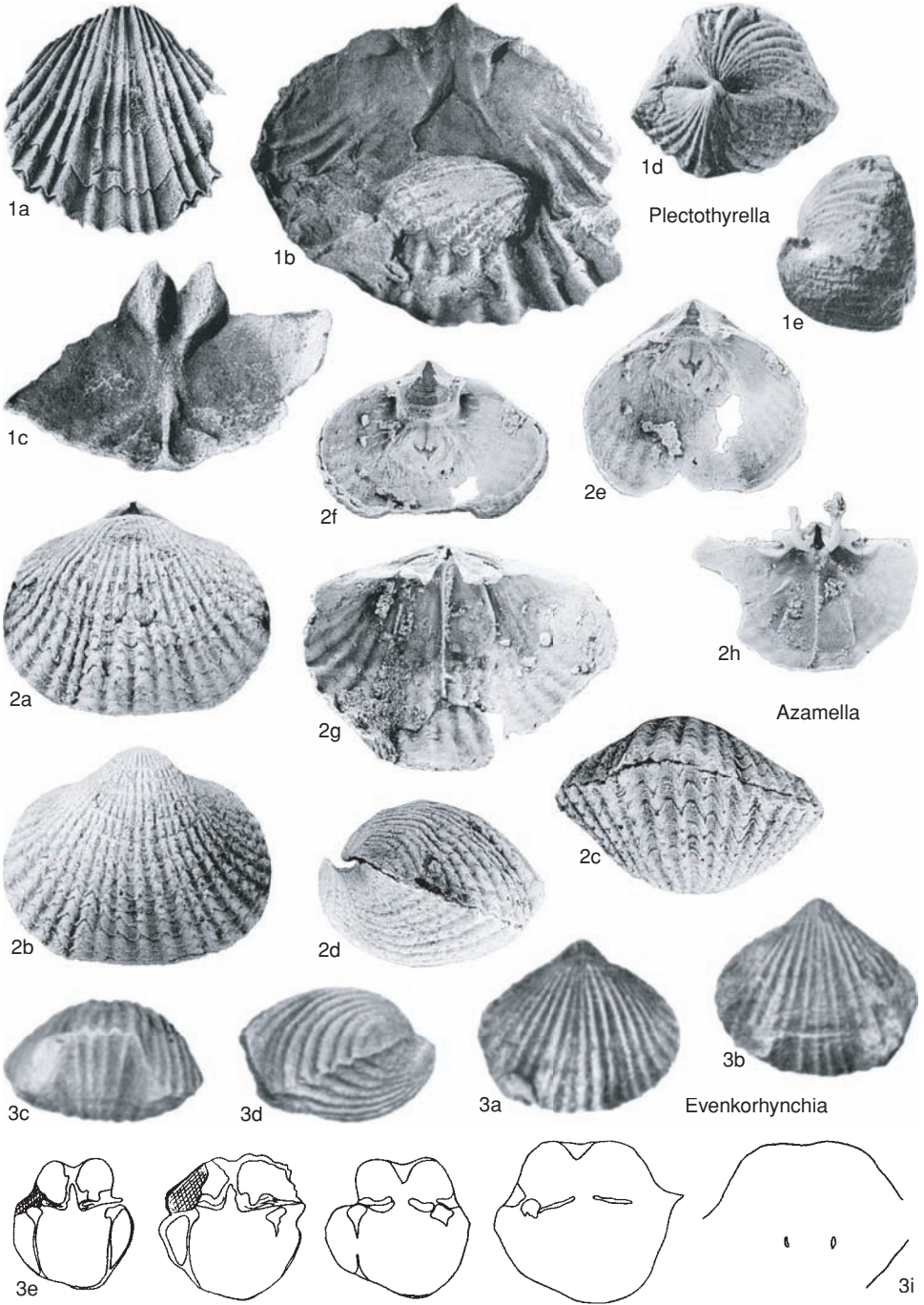


FIG. 720. Trigonirynchiidae (p. 1065–1067).

**P. crassicosta* (DALMAN), upper Ashgill, Hirnantian; *a*, ventral valve exterior, Bestorp, Sweden, $\times 1.2$; *b*, interior of same, Bestorp, Sweden, $\times 2$; *c*, interior of dorsal valve posterior, Bestorp, Sweden, $\times 2.6$ (Bergström, 1968); *d-e*, posterior and lateral of broken conjoined shell, Quebec, Percé, Canada, $\times 1.5$ (Lespérance & Sheehan, 1976).

Subfamily HEMITOECHIIINAE Savage, 1996

[Hemitoechiinae SAVAGE, 1996, p. 252]

Trigonirhynchiidae with uncovered septalium. Lower Ordovician (Llanvirn)—Lower Carboniferous (Tournaisian).

Hemitoechia NIKIFOROVA, 1970, p. 103 [**H. distincta*; OD] [= *Linterella* AMSDEN, 1988, p. 20 (type, *Camarotoechia perryvillensis* AMSDEN, 1949a, p. 56, OD); *Undulorhyncha* AMSDEN, 1988, p. 21 (type, "*Camarotoechia*" *hollandi*, OD); *Pseudocamarotoechia* KULKOV, 1974, p. 53 (type, *P. nuculaeformis*, OD); *Tichirhynchus* BARANOV, 1989, p. 42 (type, *T. settedabanicus*, OD)]. Subcircular to subpentagonal outline; biconvex. Beak suberect; small foramen, deltidial plates not recorded. Fold and sulcus moderately strong, with gentle margins; anterior commissure uniplicate; tongue trapezoid, serrate. Costae medium, simple, rounded, from umbones. Dental plates distinct, slightly concave medially. Dorsal median septum long but low; septalium without cover; cardinal process absent; crural bases subtriangular; crura strongly curved ventrally. upper Silurian (*Ludlow*)—Lower Devonian (*Lochkovian*): cosmopolitan.—FIG. 721, 1a–m. **H. distincta*, upper Silurian, Chatanzeisky horizon, Vaigatch Island, Belushja Bay, Arctic Russia; *a–b*, holotype, dorsal and ventral views; *c–f*, paratype, dorsal, ventral, lateral, and anterior views, $\times 1$; *g–m*, serial sections of posterior of another paratype (Nikiforova, 1970).

Alorostrum SAVITSKII, 1992, p. 107 [**A. elegans*; OD]. Transversely subpentagonal in outline and subequibiconvex profile. Beak suberect to erect. Fold and sulcus moderately strong, arising near umbones; anterior commissure uniplicate; tongue wide, trapezoid, dentate. Costae numerous, angular, arising at beaks and covering entire surface. Dental plates distinct, vertical to slightly convergent ventrally, extending past hinge line, well separated from valve walls. Dorsal median septum absent but with wide median ridge; hinge plates divided, horizontal; crural bases triangular in section; crura with crescentic section, concave medially. Lower Devonian (upper Emsian): Tian Shan.—FIG. 721, 2a–j. **A. elegans*, Liaglian Horizon, Alaisk Range, Liaglian River, southern Tian Shan; *a–b*, holotype, dorsal and anterior views; *c*, hypotype, lateral view, $\times 1$; *d–j*, serial sections 1.1, 1.3, 1.8, 2.2, 2.6, 2.9, 3.8 mm from posterior, $\times 4$ (Savitskii, 1992).

Bathyrhyncha FUCHS, 1923, p. 854 [**B. sinuosa*; OD]. Medium to large size with dorsibiconvex, inflated profile. Fold and sulcus distinct, arising at umbones; anterior commissure uniplicate; tongue pronounced, trapezoid. Costae arising at or near beaks. Dental plates long; ventral muscle field well impressed, elongate. Dorsal median septum long; septalium seemingly without cover. Other external and internal features poorly known. Lower Devonian (*Lochkovian*): Belgium, Germany.—FIG. 722, 2a–c. **B. sinuosa*, upper Gedinnian, Schistes de Weismes, Malmedy, Gdoudmont, Belgium; *a*, holotype, ventral internal mold, $\times 1$ (Dahmer, 1942); *b–c*, anterior and posterior views of internal mold, $\times 2$ (Boucot, 1960).

Browneella CHATTERTON, 1973, p. 117 [**B. browneae*; OD]. Small to medium size with subpentagonal outline and dorsibiconvex profile. Beak erect to suberect; delthyrium open; deltidial plates narrow, disjunct. Fold and sulcus developed anteriorly; anterior commissure uniplicate; tongue trapezoid. Costae strong, arising at beaks, some multiplication. Dental plates short. Dorsal median septum weak; septalium small, without cover; hinge plates divided anterior of septalium; crura radulifer; cardinal process unknown. Lower Devonian (*Emsian*): southeastern Australia.—FIG. 721, 3a–g. **B. browneae*, upper Emsian, "Receptaculites" Limestone, Yass, New South Wales; *a*, holotype, dorsal view, $\times 3.7$; *b*, holotype, ventral view, $\times 2.75$; *c*, holotype, lateral view, $\times 3.7$; *d*, paratype, anterior view, $\times 2.5$; *e*, ventral valve interior; *f*, interior of dorsal valve posterior, $\times 5$; *g*, reconstruction of posterior of dorsal valve interior (Chatterton, 1973).

Centrorhynchus SARTENAER, 1970a, p. 11 [**Camarotoechia baitalensis* REED, 1922, p. 94; OD]. Medium to large with subpentagonal outline and dorsibiconvex profile. Beak suberect; foramen circular, mesothyrud; deltidial plates disjunct to conjoined. Fold and sulcus arising at umbones, prominent anteriorly; anterior commissure uniplicate; tongue high, trapezoid, triplicate to quadruplicate. Costae strong, simple, subangular, from beaks. Shell thick. Dental plates short, convergent ventrally; teeth short, strong, crenulated; ventral muscle field flabellate, deeply impressed. Dorsal median septum thick, long, fairly high; septalium moderately wide and long, usually with posterior cover plate; hinge plates divided immediately anterior of septalium, horizontal; sockets large and crenulated; dorsal muscle field distinct; crura closely set, ventrally curved, distal part with gutterlike section open dorsally. Upper Devonian (*Famennian*): Iran, Afghanistan, Turkey, Pamir, China, western Europe, Russia, North America, Australia.—FIG. 721, 4a–c. **C. baitalensis* (REED), Ak Baital, Pamir; *a–b*, lectotype, dorsal and ventral views; *c*, anterior view of different specimen, $\times 1.5$ (Reed, 1922).—FIG. 721, 4d–l. *C. charakensis* (BRICE), Afghanistan, Ghok; serial sections 0.7, 1.0, 1.6, 1.9, 2.0, 2.5, 3.3, 3.7, 4.1 mm from posterior, $\times 2$ (Brice, 1970).

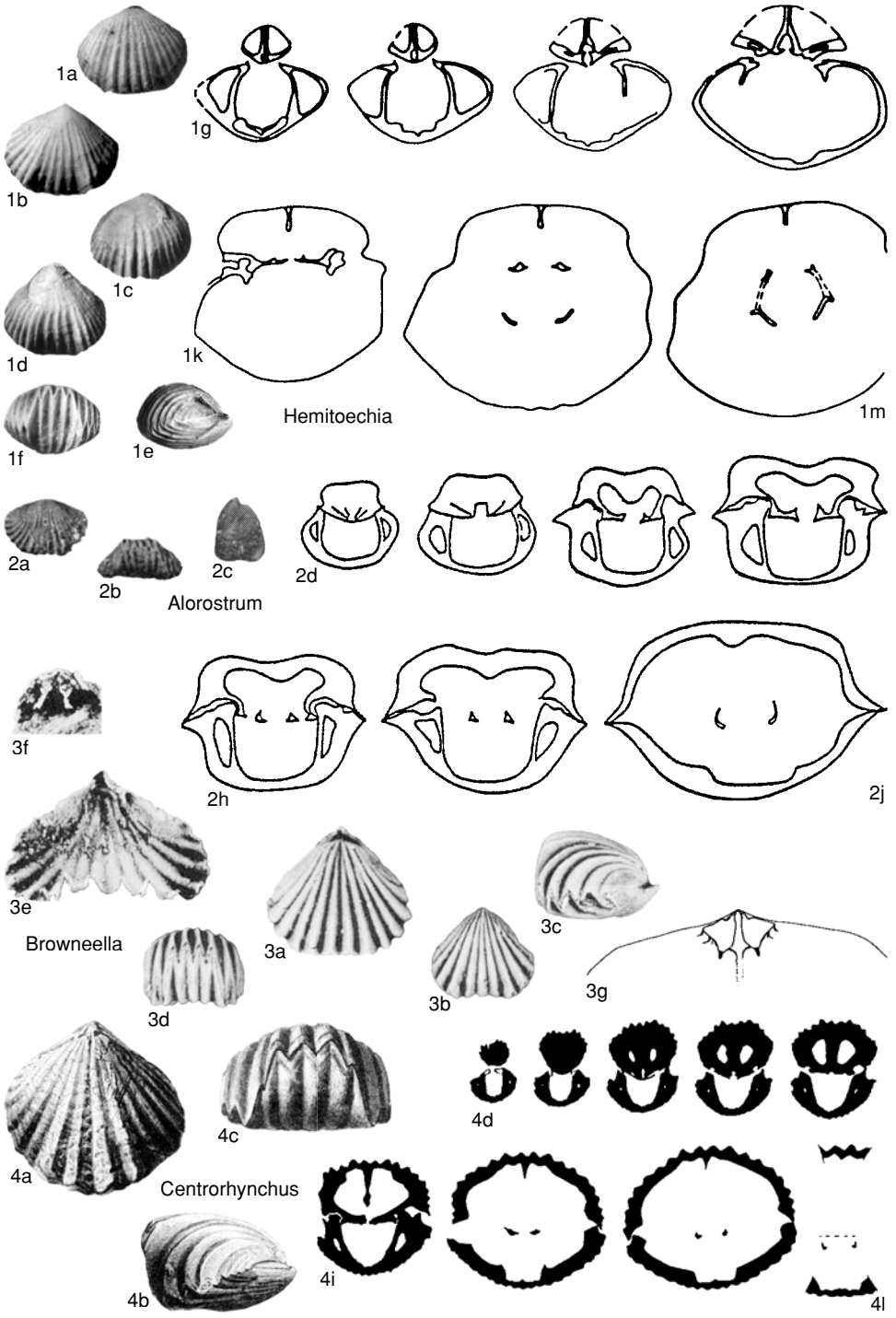


FIG. 721. Trigonirynchiidae (p. 1067).

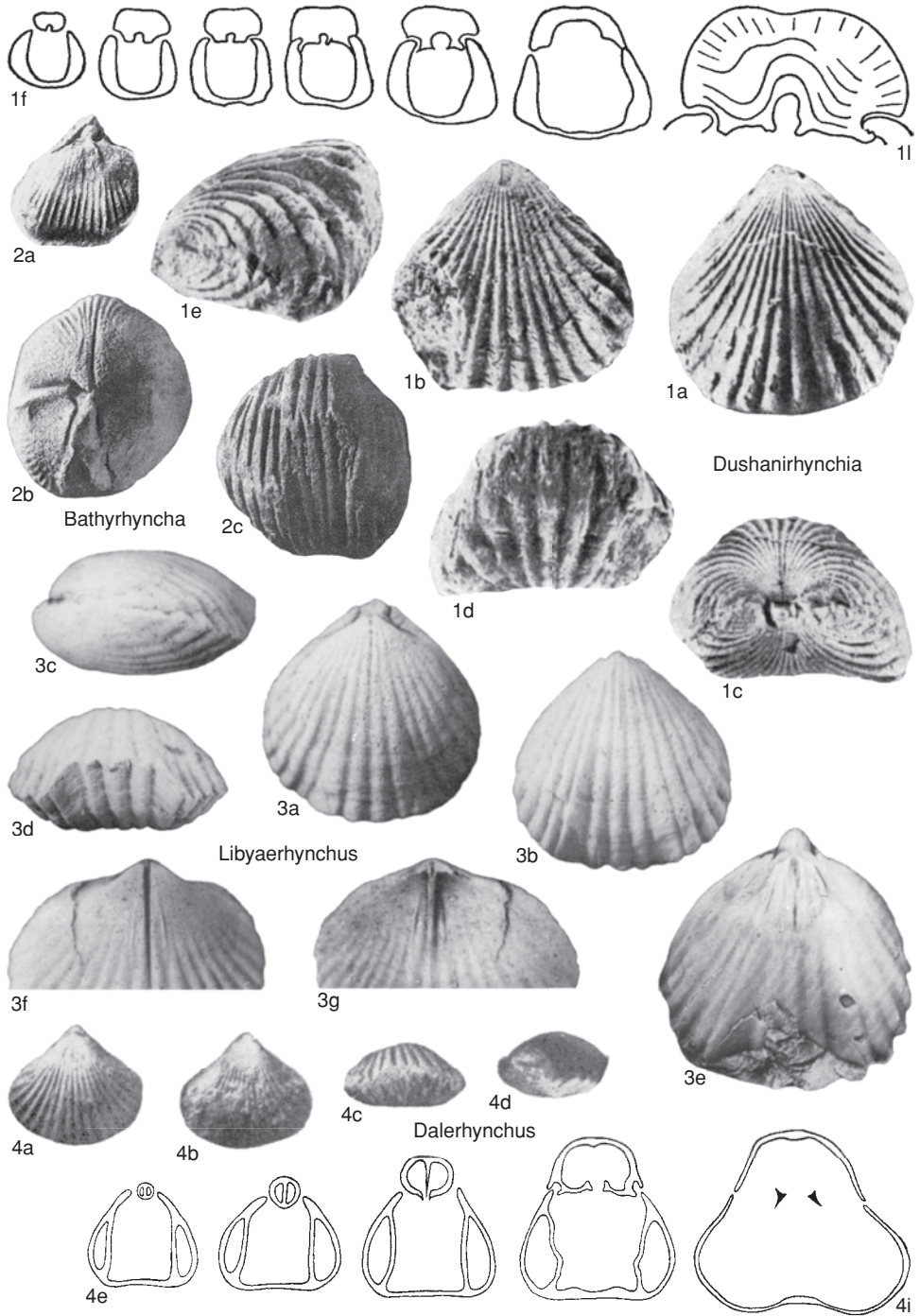


FIG. 722. Trigonirhynchiidae (p. 1067–1070).

- Dalerhynchus** BAI, 1978, p. 51 [**D. dingshanlingensis*; OD]. Transversely subpentagonal outline and moderately biconvex profile. Beak erect to suberect; large foramen at apex. Fold and sulcus very weak; anterior commissure weakly uniplicate. Costae numerous, simple, subangular, arising at beaks. Dental plates convex medially. Dorsal median septum short, low; septalium and cardinal process absent; crural bases triangular in section; crura strongly curved ventrally. *Lower Devonian (Emsian)*: China.—FIG. 722,4a–i. **D. dingshanlingensis*, Dale Formation, Xiangzhou County, Dale, Guangxi; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–i, serial sections, interval and scale not given (Bai, 1978).
- Dushanirhynchia** WANG & ZHU, 1979, p. 42 [**D. inflata*; OD]. Subpentagonal in outline and strongly biconvex profile. Beak erect to incurved; foramen not observed. Fold and sulcus strong, from umbones; tongue high. Numerous strong, angular, simple costae extending from beak. Shell wall thick. Dental plates weak or obscured in thick callus of shell wall. Divided hinge plates resting on thick callus. Dorsal median septum and septalium absent. *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian)*: southern China.—FIG. 722,1a–l. **D. inflata*, Eifelian, Longdongshui Formation, Guizhou, Houshan; a–e, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 2$; f–k, serial sections at 0.95, 1.50, 1.55, 1.9, 2.1, 2.4 mm from posterior, $\times 2.5$; l, serial section of dorsal valve at 1.75 mm from posterior, $\times 5$ (Wang & Zhu, 1979).
- Lenatoechia** NIKIFOROVA, 1970, p. 106 [**Camarotoechia elegans* NIKIFOROVA, 1961, p. 205; OD]. Small to medium; subcircular to transversely ovate in outline; biconvex with gentle lateral and anterior slopes. Beak erect to suberect; delthyrium open apically, deltidial plates poorly known but may be disjunct. Fold and sulcus moderate, from midlength; anterior commissure uniplicate with low rounded tongue. Costae fine, numerous, simple, evenly covering fold, sulcus, and flanks. Dental plates long, concave medially. Dorsal median septum low, long, thick; septalium wide, long, without cover; cardinal process absent; crura poorly known. *Lower Ordovician (Llanvirn)–upper Silurian (Ludlow)*: northern Siberian platform, Novaya Zemlya, northern Urals.—FIG. 723,3a–h. **L. elegans* (NIKIFOROVA), Llandoverly, northern Siberian platform, Morkoka River, Lena River Basin; a–d, holotype, dorsal, ventral, lateral, and anterior views, $\times 2$; e–h, paratype, serial sections 13.8, 13.7, 13.3, 12.7 mm from anterior, $\times 6$ (Nikiforova, 1961).
- Libyaerhynchus** MERGL & MASSA, 1992, p. 65 [**L. fragosus*; OD]. Subcircular to elongate oval in outline and subequibiconvex profile. Beak suberect to erect. Fold and sulcus low, arising at umbones, fold with flat crest; anterior commissure uniplicate; tongue low, trapezoid. Costae strong, simple, subangular, from umbones. Dental plates short, convergent ventrally; teeth large; ventral muscle field gently impressed, subovate. Dorsal median septum thick, long, fairly high; septalium small,
- narrow, open; hinge plates small, horizontal; sockets narrow, widely divergent; dorsal muscle field weakly impressed, elongate; no cardinal process; crural bases short, widely divergent. *Upper Devonian (lower Frasnian–upper Famennian)*: Libya.—FIG. 722,3a–g. **L. fragosus*, lower Frasnian, Aouinat Ouenine II Formation, Ghadamis Basin, Awaynat Wanin type section; a–d, dorsal, ventral, lateral, and anterior views of steinkern, $\times 2$; e, holotype, ventral valve internal mold, $\times 1.4$; f–g, dorsal valve, internal mold and latex cast, $\times 2$ (Mergl & Massa, 1992).
- Losvia** BREIVEL & BREIVEL, 1976, p. 116 [**Pugnoides(?) operosa* KHODALEVICH, 1951, p. 53; OD]. Medium to large with subtriangular to flabellate outline; dorsibiconvex profile with precipitous lateral and anterior margins and concave posterolateral margins. Beak erect; foramen and deltidial plates not recorded. Fold and sulcus weak, extending from midlength; anterior commissure weakly uniplicate, dentate; tongue low to absent. Costae strong, angular, simple, almost straight, extending from beaks. Dental plates thin, vertical, very close to walls. Dorsal median septum long, high; septalium very short, without cover plate; cardinal process absent; crural bases triangular; crura closely set. *Lower Devonian (Emsian)*: Urals.—FIG. 723,1a–i. **L. operosa* (KHODALEVICH), Emsian, Vizhaik layer, Vizhai River; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1.3$ (Khodalevich, 1951); e–i, serial sections of posterior, distances not given, $\times 4$ (Breivel & Breivel, 1977).
- Luterella** AMSDEN, 1988, p. 20 [**Camarotoechia altisulcata* AMSDEN, 1951, p. 86; OD]. Transversely subpentagonal in outline and with dorsibiconvex profile. Beak suberect; foramen mesothyrid. Fold and sulcus strong, wide, from umbones; tongue high, trapezoid. Costae prominent, angular, simple, arising at beaks; anterior commissure strongly dentate. Dental plates vertical; ventral muscle field weakly impressed. Dorsal median septum short, low, supporting short, wide, uncovered septalium. *Silurian (Ludlow–Pridoli)*: USA.—FIG. 723,4a–d. **L. altisulcata* (AMSDEN), Henryhouse Formation, Arbuckle Mountains, Oklahoma; a–c, holotype, dorsal, ventral, and anterior views, $\times 1$; d, interior of posterior of dorsal valve, $\times 3$ (Amsden, 1951).—FIG. 723,4e–j. *L. carmelensis* (AMSDEN), Brownsport Formation, Cedar Grove Church, western Tennessee; e–g, holotype, dorsal, lateral, and anterior views, $\times 1$; h, interior of posterior of dorsal valve, $\times 5$; i–j, transverse sections 1.5, 2.5 mm from posterior of different specimens, $\times 4$ (Amsden, 1949a).
- Nymphorhynchia** RZHONSITSKAIA, 1956c, p. 53 [**N. bischofooides*; OD] [= *Wenxianirhynchus* ZHANG Yan, 1983a, p. 316 (type, *W. platiformis*, OD)]. Subtrigonal to subpentagonal outline; delthyrium open. Fold and sulcus wide, low; anterior commissure uniplicate; tongue high, dentate. Costae strong, angular, simple, from beaks. Dental plates very close to vertical valve walls; dorsal median septum high; septalium without cover; crura unrecorded. *upper Silurian (Pridoli)–Middle Devonian (Givetian)*: Kuznetsk, Urals, Altai, Mongolia,

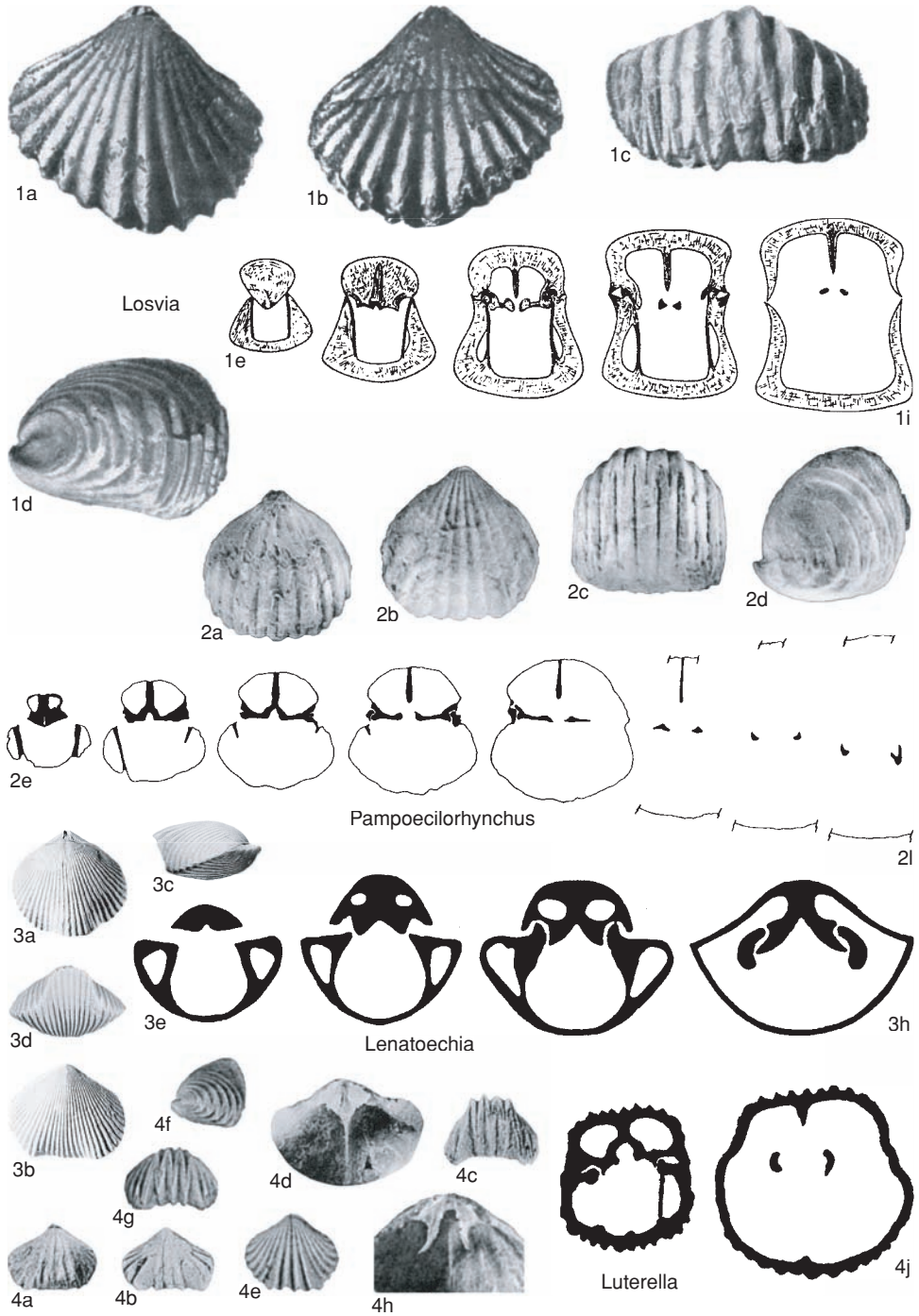


FIG. 723. Trigonirynchiidae (p. 1070–1073).

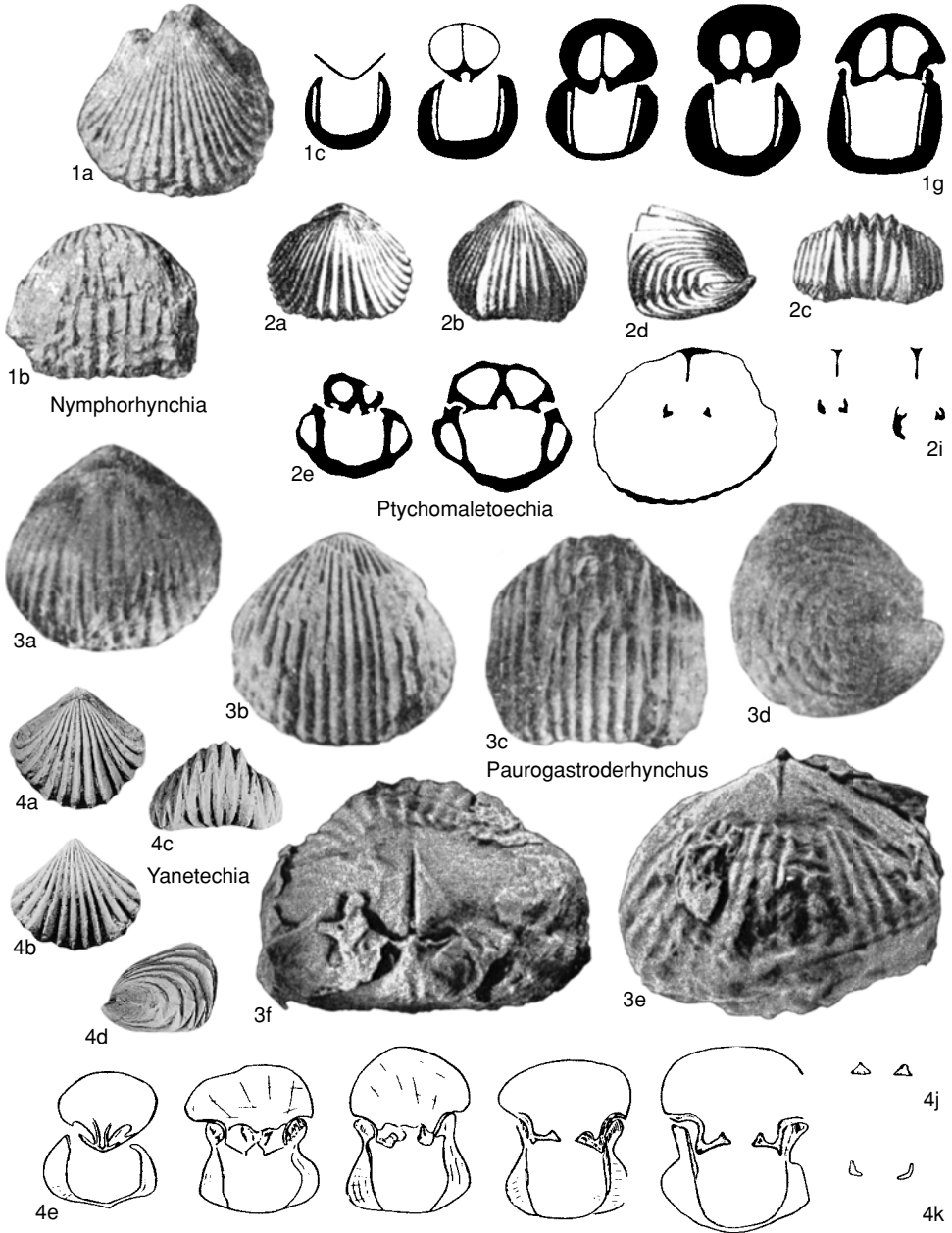


FIG. 724. Trigonirhynchiidae (p. 1070–1074).

China, Bohemia, Canada.—FIG. 724, 1a–g. **N. bischofoides*, Kuznetsk, Eifelian; a–b, holotype, dorsal and anterior views, $\times 1.5$; c–g, serial sections of posterior, $\times 3$ (Rzhonsnitskaia, 1956c). *Pampoecilorhynchus* SARTENAER, 1968d, p. 3 [**Rhynchonella nux* GOSSELET, 1887, p. 210; OD]. Medium to large with subpentagonal outline and

dorsibiconvex globular profile. Beak erect; foramen small with disjunct deltidial plates. Fold and sulcus obscured by shell inflation; anterior commissure uniplicate; tongue high, often rounded, denticulate. Costae strong, simple, from beaks. Dental plates short, slightly convergent ventrally; ventral muscle field flabellate, not strongly impressed. Dorsal

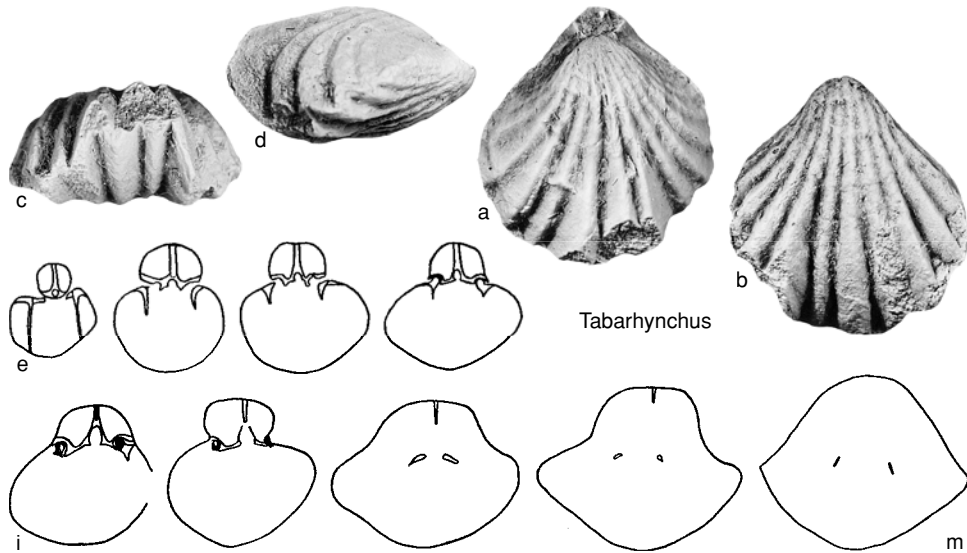


FIG. 725. Trigonirhynchiidae (p. 1073).

median septum thin, moderately high; septalium wide, long, V-shaped; hinge plates divided immediately anterior of septalium, horizontal; dorsal muscle field weak; crura short, only slightly ventrally curved, tips with phrygian cap section open dorsally. *Upper Devonian (lower Famennian)*: Europe, Morocco, Iran, Afghanistan.—FIG. 723,2a–l. **P. nux* (GOSSELET), Belgium; a–d, dorsal, ventral, anterior, and lateral views, $\times 1$ (Sartenaer, 1958); e–l, serial sections 0.95, 1.65, 1.85, 2.05, 2.65, 3.45, 4.8, 5.15 mm from posterior, $\times 2$ (Sartenaer, 1968d).

Paurogastroderhynchus SARTENAER, 1970a, p. 25 [**Camarotoechia*(?) *naliukini* ABRAMIAN, 1957, p. 48; OD]. Medium to large with subcircular outline and globular, biconvex profile. Beak erect to incurved. Fold and sulcus weak; anterior commissure uniplicate, tongue high. Costae strong, simple, straight, evenly developed over fold, sulcus, and flanks. Dental plates long. Dorsal median septum short, thick; septalium short; hinge plates divided anterior of septalium; crura with crescentic distal cross section. *Upper Devonian (upper Famennian)*: Armenia, Iran, Afghanistan, Algeria.—FIG. 724,3a–d. **P. naliukini* (ABRAMIAN), Armenia; dorsal, ventral, anterior, and lateral views, $\times 1$ (Abramian, 1957).—FIG. 724,3e–f. *P. sp.*, Algeria; dorsal and posterior views of internal mold, $\times 1$ (Sartenaer, 1975a).

Ptychomaletoechia SARTENAER, 1961c, p. 7 [**Rhynchonella Omaliusi* GOSSELET, 1877b, p. 314; OD]. Transversely subpentagonal outline; strongly dorsibiconvex with steep lateral margins. Beak erect to suberect; foramen circular, with deltidial plates disjunct to conjunct. Fold and sulcus distinct, from umbones; tongue high, rectangular, dentate. Costae strong, angular, simple, arising at beaks. Dental

plates slightly convergent ventrally. Dorsal median septum low, long; septalium deep, without cover; crural bases triangular; crura closely placed, concave dorsomedially in section. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian)*: Europe, Afghanistan, Altai, China, North America.—FIG. 724,2a–i. **P. omaliusi* (GOSSELET), Famennian, Senzeilles beds, Senzeilles, Belgium; a–d, lectotype, dorsal, ventral, anterior, and lateral views, $\times 1$ (Gosselet, 1877b); e–f, topotype, serial sections 0.85, 1.15 mm from posterior, $\times 3.4$; g–i, serial sections 2.93, 3.08, 3.18 mm from posterior of another topotype, $\times 2.7$ (Sartenaer, 1961c).

Tabarhynchus BARANOV, 1989, p. 45 [**T. mirandus*; OD]. Subtriangular to subpentagonal in outline; moderately biconvex. Beak suberect; fold and sulcus weak to moderate, from umbones; anterior commissure uniplicate; tongue low, serrate. Costae coarse, rounded, simple, arising at beaks. Dental plates very short. Dorsal median septum long, thin; septalium without cover; crural bases subhorizontal; crura thin, laterally flattened. *Upper Devonian (Frasnian)*: eastern Siberia.—FIG. 725a–m. **T. mirandus*, Mauchanskaya Formation, Sette-Daban Range; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2.5$; e–m, topotype, serial sections 7.7, 7.8, 7.85, 7.95, 8.05, 8.45, 8.65, 9.15, 9.45 mm from posterior, $\times 3.5$ (Baranov, 1989).

Yanetechia BARANOV, 1980, p. 85 [**Y. excelsa*; OD]. Subtriangular to subpentagonal outline and dorsibiconvex profile, inflated anteriorly. Beak erect to incurved; delthyrium open, narrow deltidial plates disjunct. Fold and sulcus moderately strong, extending from umbones; anterior commissure uniplicate; tongue high, arcuate, dentate. Costae strong, angular, simple, extending from beaks. Dental plates vertical, mostly fused to valve walls.

Dorsal median septum absent; septalium very short, open; hinge plates divided; crural bases triangular; crura ventrally curved, concave dorsomedially in section. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: eastern Siberia, Salair.—FIG. 724, 4a–k. **Y. excelsa*, Seymchan Formation, Yakutskaya, Ulakhan-Sis Range, eastern Siberia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; *e–k*, serial sections, $\times 4.5$ (Baranov, 1980).

Subfamily VIRGINIATINAE Amsden, 1974

[*nom. correct.* SAVAGE, 1996, p. 252, *pro* Virginiatinae AMSDEN, 1974, p. 68]

Trigonirhynchiidae with elongate subtriangular outline; apical angle acute; equibiconvex lateral profile; fold and sulcus weak to absent; anterior commissure rectimarginate to moderately unisulcate or uniplicate; costae coarse, straight, simple, arising at beaks or on umbones; ventral beak straight to erect; delthyrium with disjunct or conjunct deltidial plates. Dental plates well developed, close to valve walls, vertical. Dorsal median septum short, low, thick; septalium open or with partial cover plate. *Upper Ordovician (Ashgill)–upper Silurian (Ludlow)*.

Virginiata AMSDEN, 1968, p. 56 [**Camarotoechia arkansana* THOMAS, 1926, p. 388; OD]. Small size; elongate subtriangular outline; subequally weakly biconvex. Beak erect to incurved; delthyrium open to partly closed by rudimentary deltidial plates. Fold and sulcus lacking; anterior commissure rectimarginate, serrate. Costae low, from umbones; mostly simple but some umbonal bifurcation. Dental plates distinct but short; vertical. Small septalium covered posteriorly; dorsal median septum short. *Silurian (Llandovery–Ludlow)*: North America, Siberia, China.—FIG. 726, 1a–i. **V. arkansana* (THOMAS), Wenlock, Arkansas, Batesville district, USA; *a–d*, hypotype, dorsal, ventral, lateral, and anterior views, St. Clair Limestone, $\times 3$; *e*, lectotype, dorsal view, St. Clair Limestone, $\times 2$; *f–i*, serial sections 0.4, 0.6, 0.8, 1.0 mm from posterior, $\times 7.5$ (Amsden, 1968).

Hostimex HAVLIČEK, 1982b, p. 370 [**H. hostimensis*; OD]. Shell small; elongate subtriangular in outline; weakly biconvex profile. Beak suberect. Fold and sulcus weak; anterior commissure uniplicate; tongue low, wide. Costae arising at umbones, numerous, simple, or with minor bifurcation. Dental plates long, umbonal cavities distinct; ventral muscle area weakly impressed. Dorsal median septum low, extending to one-third valve length; septalium small, with cover plate; cardinal process absent. *Silurian (upper Wenlock–Ludlow)*: Bohemia.—FIG. 726, 3a–f. **H. hostimensis*, upper

Wenlock, Motol Formation, V Kozle Rock, between Beroun and Hostim; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 4.6$; *e*, internal mold of ventral valve, $\times 6.2$; *f*, internal mold, posterior view, $\times 7.8$ (Havlíček, 1982b).

Rhynchotreta HALL, 1879, p. 166 [**Terebratula cuneata* DALMAN, 1828, p. 141; OD] [= *Bailongjiangella* FU, 1982, p. 139 (type, *B. astuta*, OD)]. Small; elongate triangular outline; apical angle acute; biconvex. Beak straight to suberect; ventral interarea long, delthyrium long with circular foramen bounded anteriorly by conjunct to disjunct deltidial plates. Fold and sulcus weak; anterior commissure uniplicate, serrate. Costae strong, rounded, simple, usually from beaks. Dental plates well developed, close to valve walls, vertical; teeth stout. Dorsal median septum short, low, thick; septalium without cover; cardinal process absent; crural bases subtriangular; crura long, laterally compressed, concave medially in section. *lower Silurian (Llandovery)–upper Silurian (Ludlow)*: Europe, Urals, Altai, China, North America.—FIG. 727 a–o. **R. cuneata* (DALMAN), upper Wenlock–lower Ludlow; *a–c*, lectotype, dorsal, ventral, and anterior views, Klinteberg Beds, Klinteberg, Gotland, $\times 3$ (Bassett & Cocks, 1974); *d–h*, hypotype, dorsal, ventral, posterior, anterior, and lateral views, Klinteberg Beds, Bryten, near Klinte, Gotland, $\times 2.5$; *i*, enlargement of delthyrial area showing deltidial plates, $\times 8.3$; *j–o*, hypotype, serial sections 1.6, 1.8, 2.2, 2.9, 3.4, 3.5 mm from posterior, Klinteberg Beds, Bryten, near Klinte, Gotland, $\times 8.3$ (Jin & Caldwell, 1990).

Thebesia AMSDEN, 1974, p. 69 [**Rhynchotreta thebesensis* FOERSTE, 1909a, p. 94; OD]. Small with elongate subtriangular outline; apical angle acute and posterolateral margins slightly concave; profile biconvex. Beak straight to suberect; delthyrium open to partly closed by rudimentary deltidial plates. Fold and sulcus absent; anterior commissure rectimarginate, serrate. Costae strong, simple, subangular, slightly curved outward. Dental plates distinct. Small open septalium; dorsal median septum short; crura not recorded. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery)*: North America, Europe, Asia.—FIG. 726, 2a–h. **T. thebesensis* (FOERSTE), Ashgill, Edgewood Group, USA; *a–e*, lectotype, dorsal, ventral, anterior, posterior, and lateral views from the Leeman Formation, near Thebes, Illinois, $\times 2$; *f–h*, hypotype, serial sections at 0.5, 0.8, 0.9 mm from posterior, $\times 12$ (Amsden, 1974).

Subfamily RIPIDIORHYNCHINAE Savage, 1996

[Ripidiorhynchinae SAVAGE, 1996, p. 252]

Late Trigonirhynchiidae with strong fold and sulcus; anterior tongue conspicuous; delthyrium with deltidial plates usually conjunct; costae numerous, straight, arising

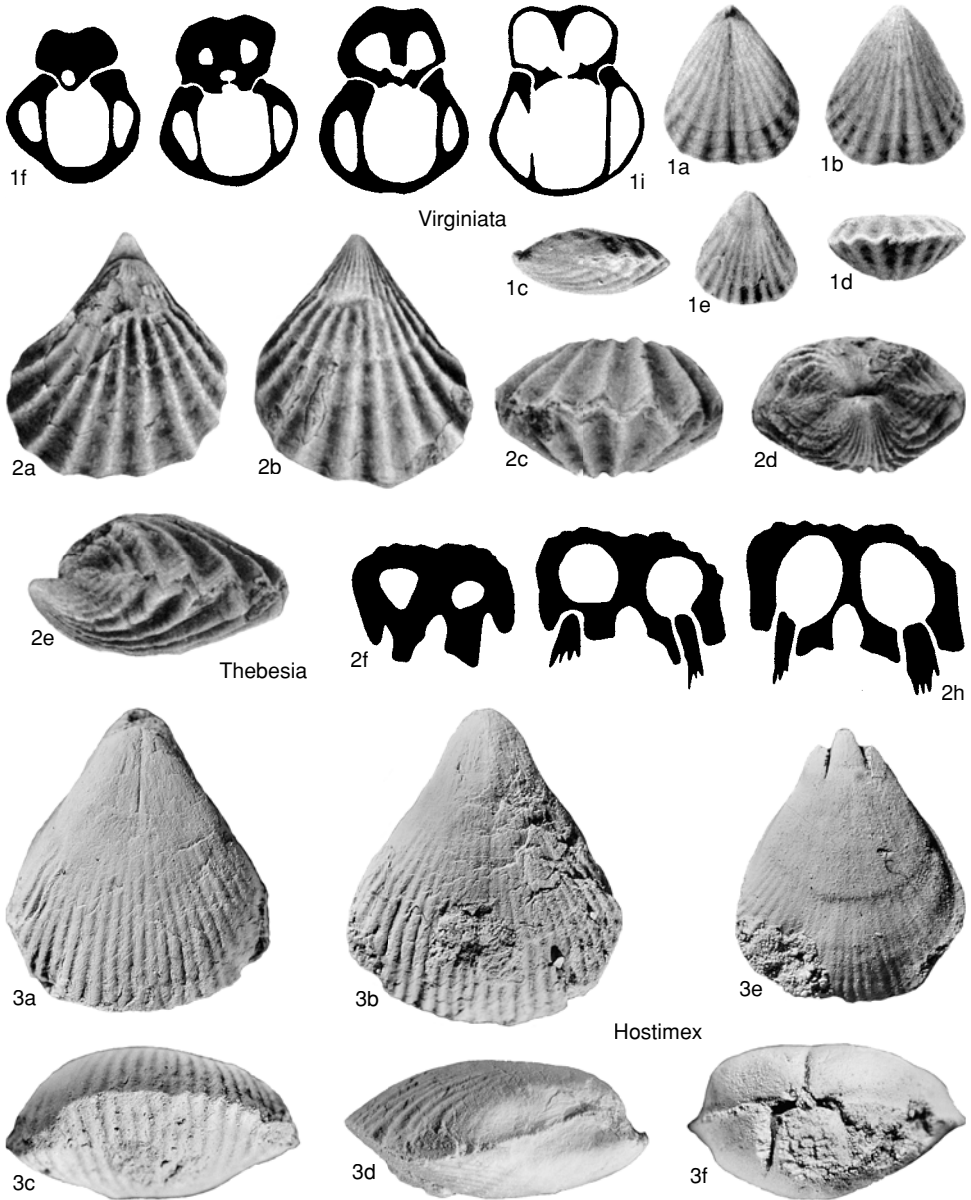


FIG. 726. Trigonirhynchiidae (p. 1074).

from beaks. Dental plates long. Dorsal median septum short; septalium may have cover plate anteriorly. *Middle Devonian (upper Givetian)–Lower Carboniferous (Tournaisian)*.

Ripidiorhynchus SARTENAER, 1966b, p. 2 [**Terebratulula livonica* VON BUCH, 1834, p. 57; OD]. Subpen-

tagonal to transversely ovate in outline, often emarginate anteriorly; strongly biconvex to inflated. Beak erect to incurved; delthyrium with wide base, circular foramen, deltidial plates almost meeting. Fold and sulcus strong, narrow, extending from umbones; anterior commissure uniplicate; tongue high, rounded to acuminate. Costae medium, rounded, simple, from beaks. Dental plates long, almost straight, strongly convergent ventrally.

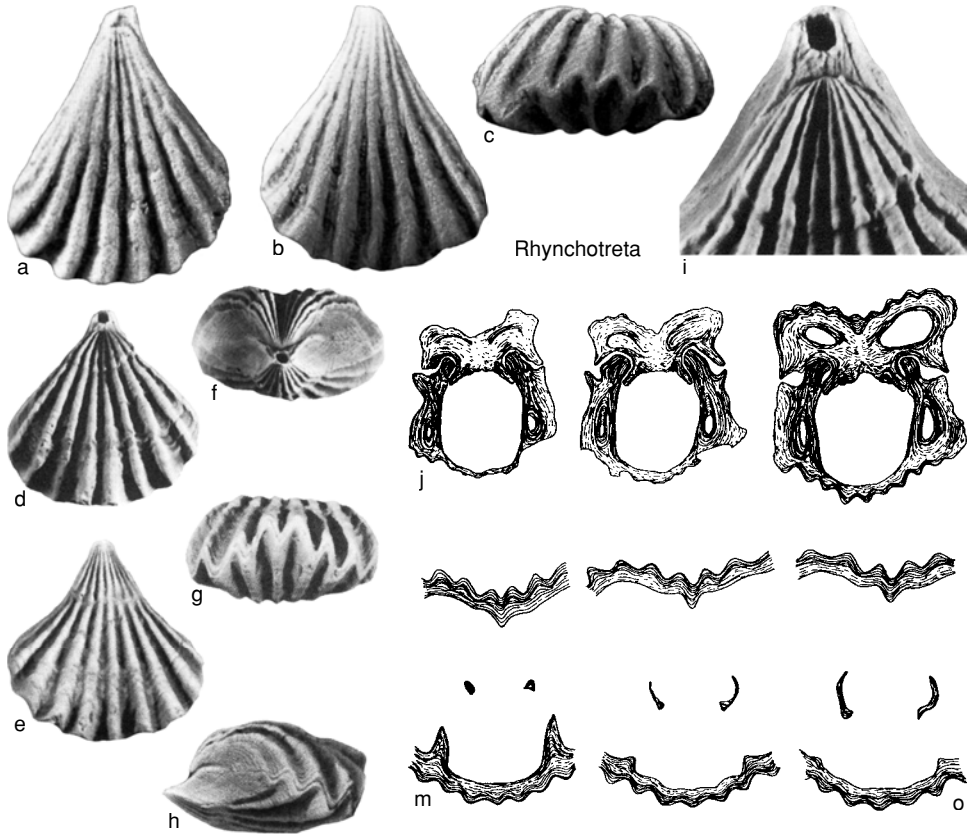


FIG. 727. Trigonirhynchiidae (p. 1074).

Dorsal median septum short; septalium with cover plate anteriorly; crura with cross section concave dorsomedially. *Middle Devonian (upper Givetian)–Upper Devonian (lower Famennian)*: Europe, Asia, northern Africa, North America.—FIG. 728, 3a–n. **R. livonicus* (VON BUCH), Frasnian, lectotype and paralectotypes earlier thought to come from Adsel, Latvia but because of preservation now considered by SARTENAER (1985a, p. 324) to come from Izborsk, near Pskov; a–e, lectotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 1$; f–n, paralectotype, serial sections 0.7, 0.79, 0.94, 1.12, 1.35, 1.5, 1.75, 2.45, 2.85 mm from posterior, $\times 4.5$ (Sartenaer, 1966b).

Cyphoterorhynchus SARTENAER, 1965c, p. 51 [**Ucinulus (Ucinulina) koraghensis* REED, 1922, p. 40; OD]. Subcircular in outline and strongly biconvex profile. Beak suberect to erect; foramen minute. Fold and sulcus weak, developed only anteriorly; anterior commissure uniplicate; tongue high, rounded. Costae fine, numerous, simple, rounded, covering all of shell. Dental plates close to shell walls, not convergent ventrally; ventral muscle field

moderately impressed. Dorsal median septum short, thin, moderately high; septalium V-shaped, with cover plate anteriorly; hinge plates united anterior of septalium; crura short, with V-shaped tips open dorsally. *Upper Devonian (middle Frasnian–upper Frasnian)*: Pakistan, Iran, Afghanistan, Armenia, Spain, Libya.—FIG. 728, 1a–n. **C. koraghensis* (REED), middle or upper Frasnian, Chitral, Koragh Ridge, northwestern Pakistan; a–d, hypotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–n, serial sections 1.1, 1.65, 2.0, 2.2, 2.4, 2.6, 2.85, 3.3, 4.0, 4.25 mm from posterior, $\times 1.6$ (Sartenaer, 1965c).

Hemiplethorhynchus VON PEETZ, 1898, p. 178 [**H. fallax*; OD] [= *Greenockia* BROWN, 1952, p. 91 (type, *G. snaringensis*, OD)]. Subcircular to subpentagonal in outline; moderately biconvex. Beak small, erect to incurved; delthyrium with deltidial plates. Fold and sulcus rather weak, but distinct anterior tongue present. Costae fine to medium, simple, angular, from beaks. Dental plates concave medially and slightly convergent ventrally. Dorsal median septum long, low; septalium with-

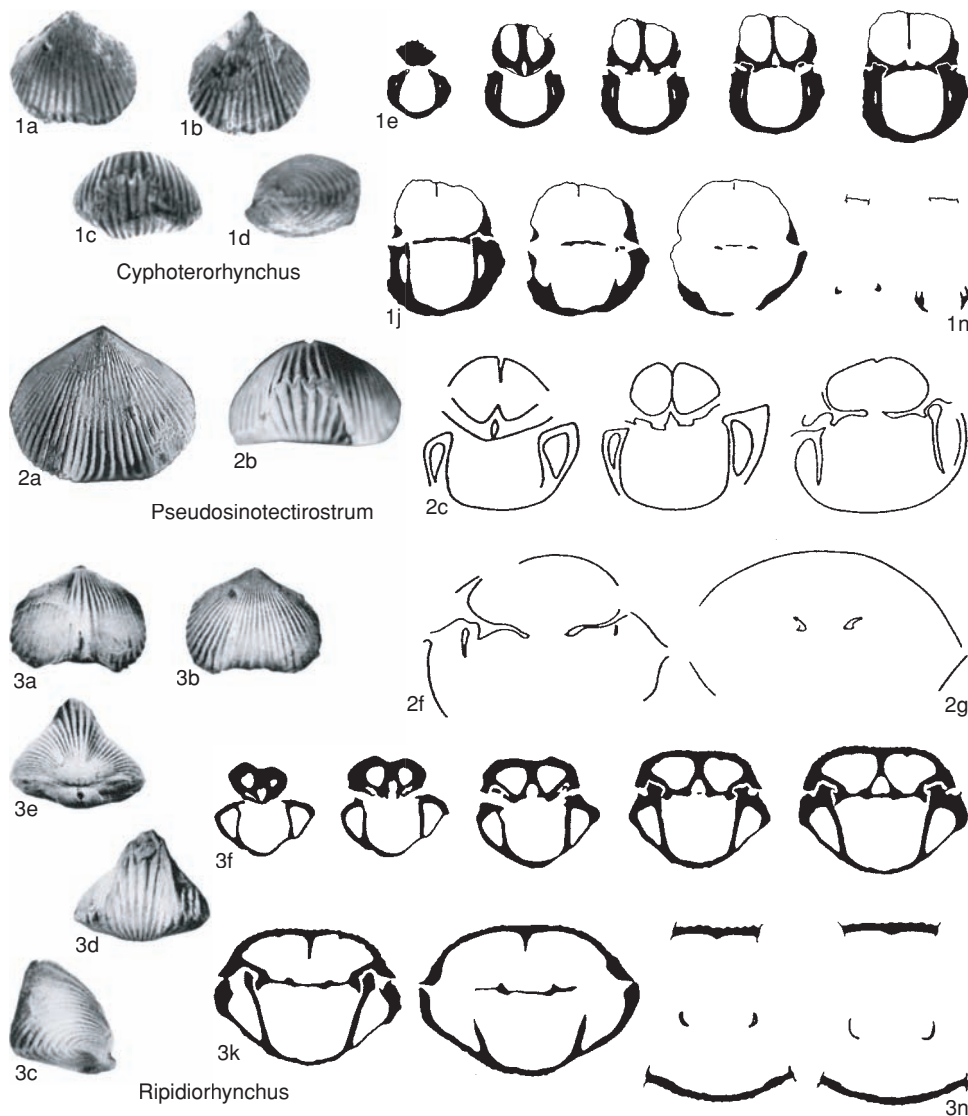


FIG. 728. Trigonirynchiidae (p. 1075–1077).

out cover but anteriorly from septalium, crural bases meet medially; distal parts of crura with V-shaped cross section, open dorsally. *Lower Carboniferous (Tournaisian)*: Altai, Europe, China, North America.—FIG. 729a–l. **H. fallax*, upper Tournaisian; a–d, dorsal, ventral, anterior, and lateral views, Altai, $\times 1$ (Sarytcheva & others, 1963); e–l, hypotype, serial sections 1.6, 2.5, 2.85, 3.35, 3.5, 3.7, 4.35, 4.9 mm from posterior, Kuznetzk basin, $\times 3$ (Sartenaer, 1965a).

Pseudosinotectirostrum YUDINA, 1991, p. 45 [*P. arcticum*; OD]. Subcircular to subpentagonal in

outline; moderately biconvex; foramen with deltidial plates. Dorsal fold and ventral sulcus distinct but with rounded margins. Costae fine, numerous, simple, extending from beaks. Dental plates short, vertical. Dorsal median septum low, short; septalium short, without cover plate. *Upper Devonian (Famennian)*: Russia (Timan, Pechora).—FIG. 728, 2a–g. **P. arcticum*, middle Famennian, Ust'-Pechora Horizon, northern Timan, Pechora Province; a–b, holotype, ventral and anterior views, $\times 1.3$; c–g, topotype, serial sections 0.8, 1.1, 1.4, 2.0, 2.2 mm from posterior, $\times 4$ (Yudina, 1991).

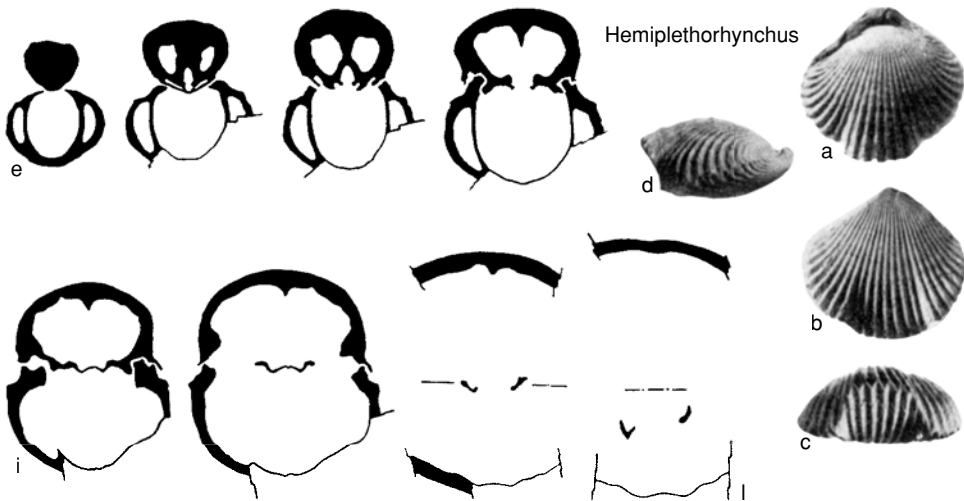


FIG. 729. Trigonirhynchiidae (p. 1076–1077).

Family ORTHORHYNCHULIDAE Cooper, 1956

[Orthorhynchulidae COOPER, 1956a, p. 669]

Rhynchotremaoidea with delthyrium open or with incipient deltidial plates; ventral interarea commonly present; dental plates reduced; hinge plates slope medially to join septalium that is sessile or supported on low median septum; cardinal process septiform, lobed, or branching. *Upper Ordovician (Caradoc)–middle Silurian (Wenlock)*.

Orthorhynchula HALL & CLARKE, 1893, p. 181 [*Orthis? linneyi* JAMES, 1881, p. 41; OD]. Transversely ovate to subcircular outline and dorsibiconvex profile. Beak suberect; ventral interarea prominent; delthyrium open. Fold and sulcus moderate, from umbones; anterior commissure unipli- cated; tongue low, serrate. Costae rounded, simple, from beaks. Dental plates fused to valve walls; ventral muscle field quadrate. Very short septalium supported on median ridge; hinge plates divided, prolonged anteriorly, concave ventrally; cardinal process septiform to lobate; crural bases subhorizontal. *Upper Ordovician (Ashgill)–lower Silurian (Llandovery)*: North America, ?western Europe.—FIG. 730, 1a–m. **O. linneyi* (JAMES), Ashgill, Maysvillian, Kentucky, USA; a–e, hypotype, dorsal, ventral, anterior, lateral, and posterior views, $\times 1.5$; f–g, hypotypes, dorsal valve interior and ventral valve interior, Brannon Formation, Devils Hollow, Coletown, $\times 1.5$ (new); h–m, serial sections 13.2, 13.0, 12.8, 12.5, 12.3, 12.0

mm from anterior margin, $\times 3.75$ (Schmidt, 1965b).

Orthorhynchuloides WILLIAMS, 1962, p. 240 [*Hemithyris nasuta* MCCOY, 1852, p. 203; OD]. Elongate-oval outline and dorsibiconvex profile. Ventral beak incurved; delthyrium open with only traces of deltidial plates. Fold and sulcus pronounced anteriorly; tongue pronounced. Costae numerous, weak posteriorly. Dental plates long, ventrally convergent; ventral muscle field well impressed. Sessile septalium merges anteriorly into median septum extending to midlength; cardinal process absent; crura unknown. *Upper Ordovician (Caradoc)*: Scotland.—FIG. 730, 2a–e. **O. nasuta* (MCCOY), lower Caradoc, Craighead Limestones, Girvan; a–c, lectotype, dorsal, ventral, and anterior views, $\times 1.3$; d, dorsal internal mold, $\times 2$; e, ventral internal mold, $\times 1.5$ (Williams, 1962).

Orthorhynchyllion JIN, 1989, p. 72 [*Rhynchotrema prinstanum* TWENHOFEL, 1928, p. 208; OD]. Subpentagonal to subtriangular outline with dorsibiconvex profile. Ventral beak small, incurved; triangular interareas on both valves; delthyrium open. Fold and sulcus broad, low, developed anteriorly. Costae numerous, from beaks, simple, rounded. Dental plates short, subvertical. Dorsal median septum thin, long; hinge plates wide, inclined dorsally; septalium large with strong septalial plates; cardinal process septiform with branched crest; crura laterally flattened. *Upper Ordovician (Ashgill)*: Canada.—FIG. 731, 2a–m. **O. prinstanum* (TWENHOFEL), upper Ashgill, Hirnantian, Ellis Bay Formation, Anticosti Island; a–e, holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 3$ (new); f–m, hypotype, serial section 0.7, 0.8, 1.0, 1.3, 1.4, 1.9, 2.8, 3.1 mm from posterior, $\times 4$ (Jin, 1989).

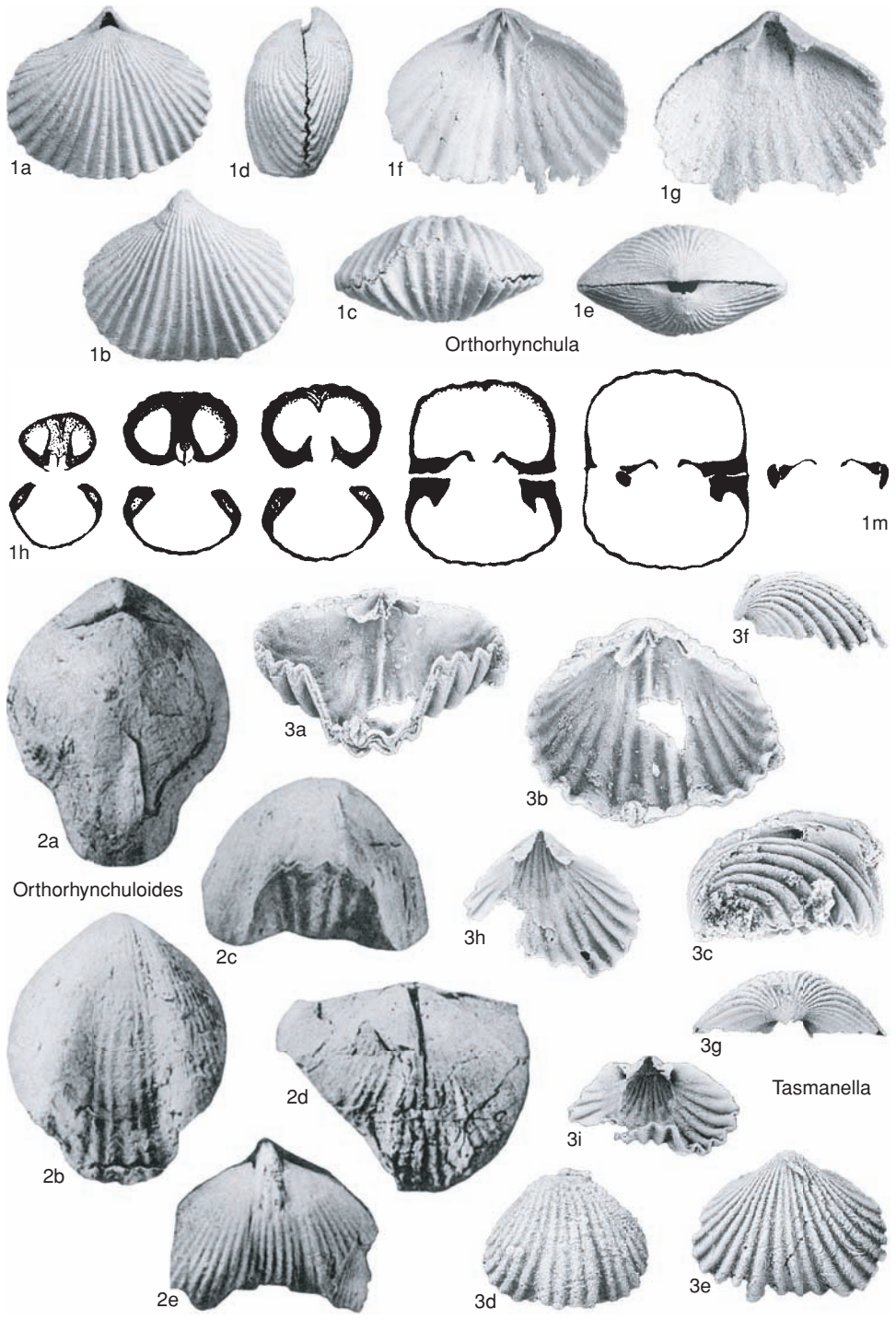


FIG. 730. Orthorhynchulidae (p. 1078–1081).

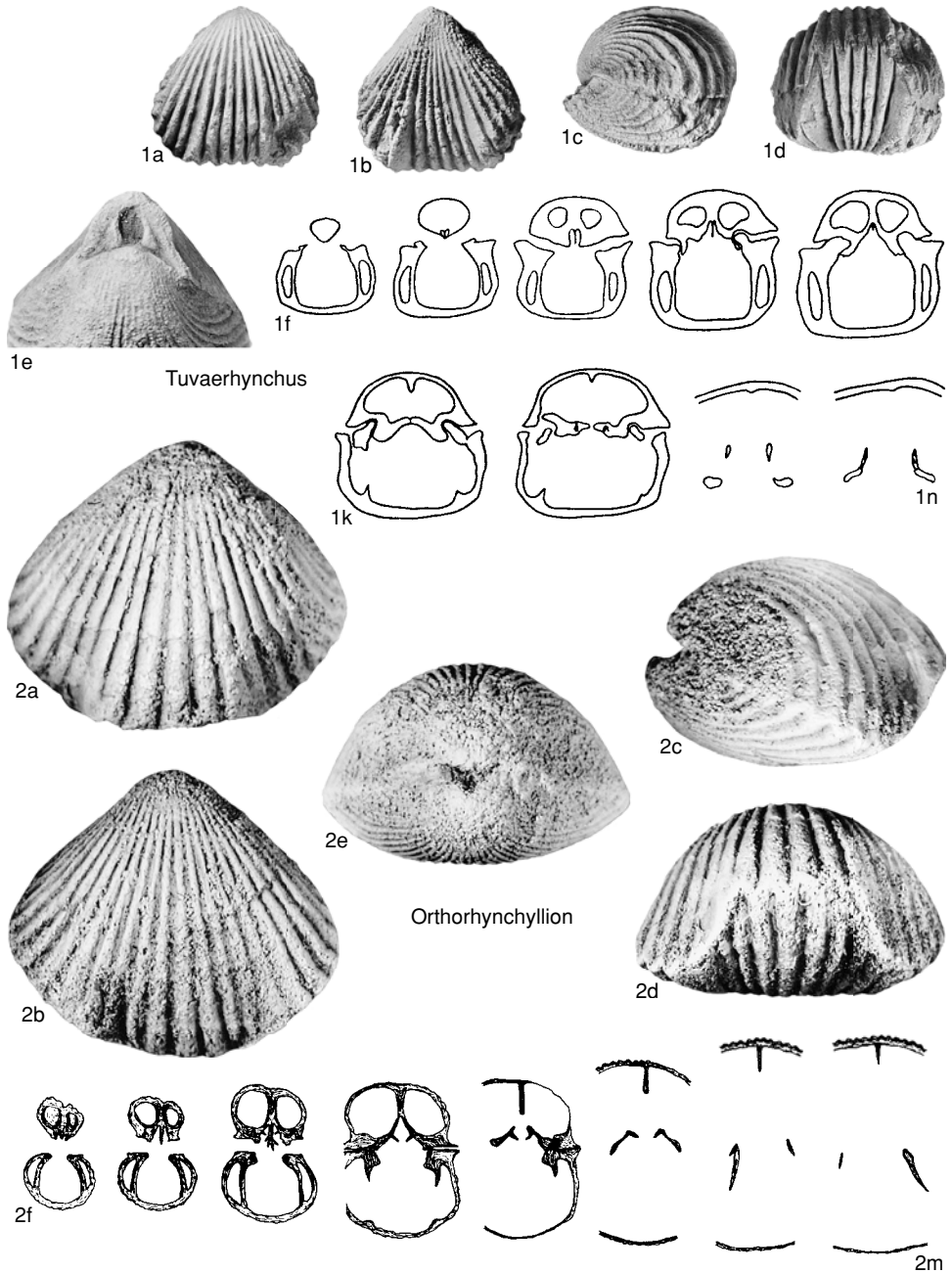


FIG. 731. Orthorhynchulidae (p. 1078–1081).

Tasmanella LAURIE, 1991, p. 96 [**T. nova*; OD]. Transversely subcircular outline and dorsibiconvex profile. Ventral beak erect; ventral interarea prominent; delthyrium open. Fold and sulcus well developed, from umbones; anterior commissure uniplicate;

tongue trapezoid. Costae strong and angular, simple, from beaks. Dental plates fused to shell walls; ventral muscle field well impressed. Hinge plates anteriorly extended, concave; dorsal median septum short, high; septalium narrow, short,

elevated; cardinal process septiform; crura unknown. *Upper Ordovician (Caradoc)*: southeastern Australia (Tasmania).—FIG. 730,3a–i. **T. nova*, lower Caradoc, Benjamin Limestone, Florentine Valley; a–c, holotype, interior and lateral views of dorsal valve; d, dorsal view of dorsal valve; e–g, paratype, ventral, lateral, and posterior views of ventral valve; h–i, interior and inclined interior views of ventral valve, $\times 2$ (Laurie, 1991).

Tuvaerhynchus KULKOV, 1985, p. 123 [**T. khalifni*; OD]. Small with subpentagonal to subtriangular outline and dorsibiconvex profile. Beak suberect; delthyrium with disjunct deltidial plates. Fold and sulcus strong, narrow, well defined, from umbones; anterior commissure uniplicate; tongue high, trap-ezoid, dentate. Costae numerous, simple, angular. Dental plates short, vertical, close to valve wall. Septalium short, wide; hinge plates concave, slope medially; cardinal process septiform, thin; crura short, curved sharply ventrally. *lower Silurian (Llandovery)*—*middle Silurian (Wenlock)*: Tuva.—FIG. 731,1a–n. **T. khalifni*, Wenlock, Dashtygoisk Beds; a–d, holotype, dorsal, ventral, lateral, and anterior views, $\times 1$; e, topotype, delthyrium, $\times 3$; f–n, topotype, serial sections 0.6, 0.8, 1.0, 1.3, 1.7, 2.0, 2.1, 2.7, 3.0 mm from posterior (Kulkov, 1985).

Family LEPTOCOELIIDAE Boucot & Gill, 1956

[Leptocoeliidae BOUCOT & GILL, 1956, p. 1174]

Rhynchotrematoidea with subcircular to subpentagonal outline; lateral profile planoconvex to biconvex; valves meet at acute angle laterally; fold and sulcus weak; costae simple, strong, extending from beaks; delthyrium open or with disjunct deltidial plates. Dental plates usually absent. Dorsal median septum weak or absent; hinge plates sessile; cardinal process large to absent. *lower Silurian (Llandovery)*—*Middle Devonian (upper Eifelian)*.

Leptocoelia HALL, 1857a, p. 107 [**L. propria*; SD OEHLERT, 1887a, p. 1324; =*Atrypa flabellites* CONRAD, 1841, p. 55; *Leptocoelia propria* HALL, 1857a, p. 108]. Small to medium with subcircular to subpentagonal outline and subequally biconvex to planoconvex profile. Beak erect to incurved; deltidial plates disjunct; foramen small, circular. Weak, narrow dorsal fold and ventral sulcus developed anteriorly in larger specimens; anterior commissure weakly uniplicate to rectimarginate. Costae simple, strong, rounded, extending from beaks. Dental plates absent; stout crenulate teeth fused directly to valve walls; ventral diductor field flabellate, enclosing small, oval adductor impressions. Cardinal process large, bulbous, base attached to large inner socket plates and thick median ridge that extends to about valve midlength; sockets

crenulate; anterior adductor impressions larger than posterior adductors. *Lower Devonian (upper Lochkovian)*—*Middle Devonian (middle Eifelian)*: North America, South America, Asia.—FIG. 732,1a–d. **L. flabellites* (CONRAD), Oriskanian, Glenerie Limestone, Glenerie, New York, USA; a, exterior of dorsal valve, $\times 1$; b, interior of dorsal valve, $\times 2$; c–d, exterior and interior of ventral valve, $\times 1$ (Boucot & Gill, 1956).

Anabaia CLARKE, 1893, p. 141, fig. 124–127 [**A. Paraia*; OD] [=*Harringtonina* BOUCOT, 1972, p. 10 (type, *H. australis*, OD; =*Leptocoelia acutiplicata* KAYSER, 1897, p. 295, non CONRAD, 1841, p. 54, sensu DE MELO & BOUCOT, 1990, p. 365)]. Subcircular outline and biconvex profile. Dorsal fold with median groove; anterior commissure sulcinate. Costae coarse, simple, straight, rounded, extending from beaks. Short dental plates; stubby teeth; flabellate diductor impressions surrounding small oval adductors. Dorsal interior with stout myophragm to midlength; small crural plates; cardinal process not evident. *lower Silurian (lower Llandovery)*—*upper Silurian (Prídolí)*: South America.—FIG. 732,2a–b. **A. paraia*, Llandovery, Trombetas Formation, Pitinga Member, Pará, Trombetas River, Viramundo Rapids, Brazil; paralectotypes, dorsal and ventral internal molds, $\times 2.5$ (de Melo & Boucot, 1990).

Australocoelia BOUCOT & GILL, 1956, p. 1174 [**Atrypa palmata* MORRIS & SHARPE, 1846, p. 276; OD; =*Australocoelia tourteloti* BOUCOT & GILL, 1956, p. 1175]. Small to medium with subcircular outline and ventribiconvex profile. Beak suberect. Dorsal sulcus and ventral fold low; anterior commissure weakly sulcate. Costae strong, simple, rounded, arising at beaks. Dental plates absent; teeth stout, attached to posterior valve walls; deeply impressed pedicle scar; elongate diductor and smaller adductor impressions well impressed. Pronounced notothyrial platform with stout median ridge supporting large cardinal process; adductor field ovate, well impressed. *Lower Devonian (Lochkovian)*—*Middle Devonian (Eifelian)*: South America, South Africa, Falkland Islands, Australia.—FIG. 732,3a–g. **A. palmata* (MORRIS & SHARPE), Emsian, Argentina, Bolivia, Falkland Islands; a–b, dorsal and ventral external views, San Juan, Lomas de los Piojos, Argentina, $\times 1$ (Boucot & Gill, 1956); c, posterior of a dorsal valve showing cardinal process, San Juan, Lomas de los Piojos, Argentina, $\times 4$ (Amos & Boucot, 1963); d, dorsal internal mold, San Juan, Quebrada de Talacasto, Argentina, $\times 2$; e, ventral internal mold, Santa Cruz, Comorapa-Tunal region, Bolivia, $\times 2$; f–g, latex casts of dorsal and ventral valve interiors of figured material of MORRIS & SHARPE, 1846, Falkland Islands, $\times 1$ (Boucot & Gill, 1956).

Eocoelia NIKIFOROVA, 1961, p. 252 [**Atrypa hemisphaerica* J. DE C. SOWERBY, 1839, p. 637; OD]. Subcircular to transversely elliptical outline with subbiconvex to planoconvex profile. Delthyrium open. Weak ventral fold and dorsal sulcus often evident, or merely weak narrow trough on dorsal valve; anterior commissure rectimarginate. Costae

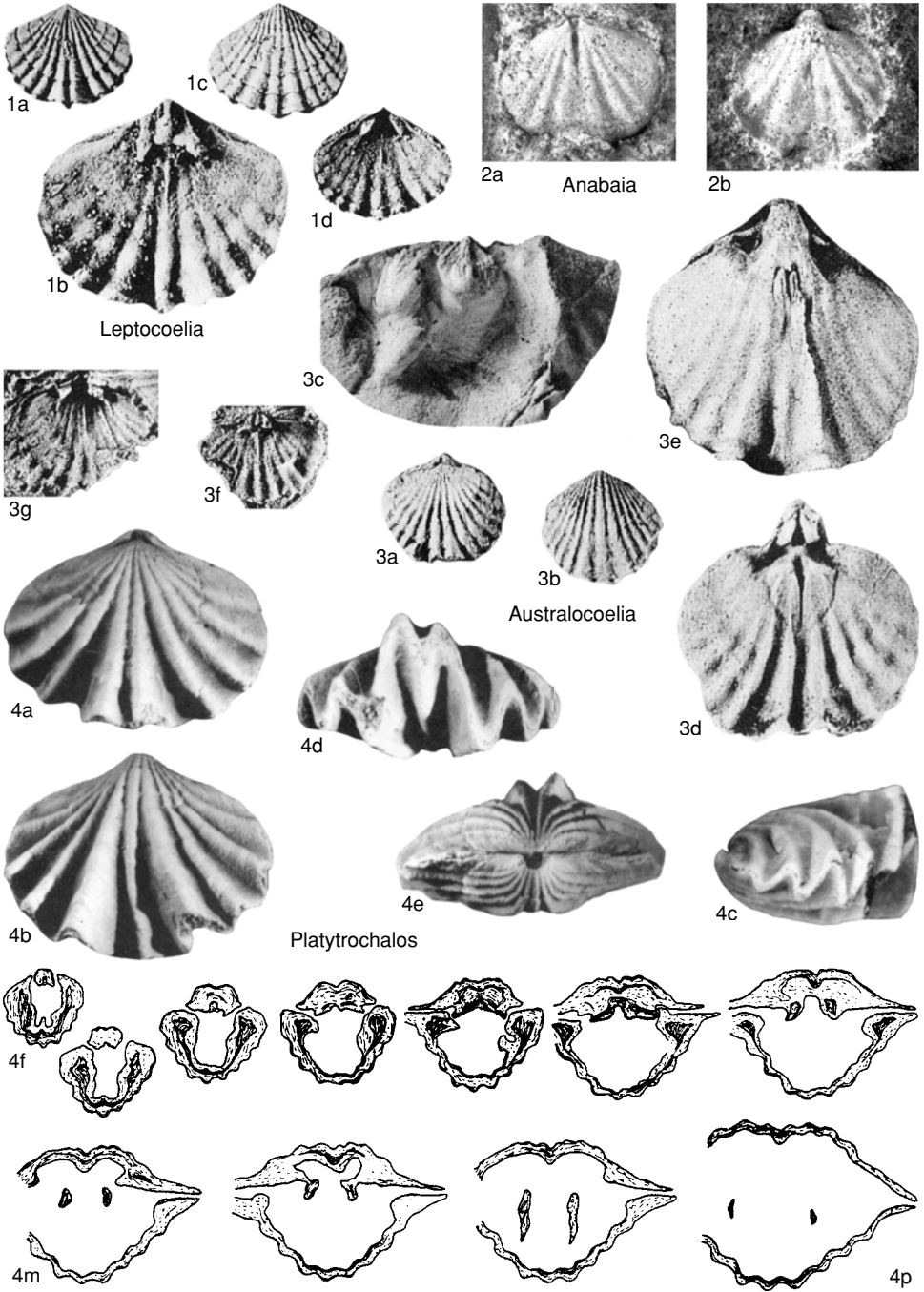


FIG. 732. Leptocoeliidae (p. 1081–1083).

simple, strong, rounded, extending from beaks. Dental plates short to absent; teeth arising from posterior valve walls and bear fossettes on median face; muscle scars not impressed. Dorsal valve with short, robust socket plates bounding deep, divergent sockets; broad, low median ridge reflecting exterior trough; muscle field not impressed; costae strongly reflected internally; cardinal process rare to absent. *lower Silurian (lower Llandovery)–middle Silurian (upper Wenlock)*: Europe, Asia, North America, South America, Australia.—FIG. 733,3a–g. **E. hemisphaerica* (SOWERBY), upper Llandovery, Cowleigh Park Beds, Worcestershire, Ankerdine Hill, England; *a*, original illustration of SOWERBY (1839), $\times 1$; *b*, lectotype, ventral external mold of *a*, $\times 2$ (Murchison, 1839); *c*, dorsal external mold; *d–e*, ventral internal mold and latex cast; *f–g*, dorsal internal mold and latex cast, $\times 4$ (Ziegler, 1966b).

Leptocoelina JOHNSON, 1970b, p. 170 [**L. squamosa*; OD]. Subpentagonal outline and biconvex profile. Beak suberect with apical foramen. Pronounced dorsal fold and ventral sulcus; anterior commissure sulciphate. Costae few, coarse, low, rounded, arising at beaks; numerous imbricate growth lamellae. Dental plates absent; teeth attached to posterior valve margin, with fossettes present medially; diductor field elongate, triangular, well impressed; adductor field distinct within diductor field. Dorsal interior with knoblike cardinal process and prominent inner socket plates; short, wide, median ridge present posteriorly; adductor field elongate oval. *Lower Devonian (lower Pragian–upper Emsian)*: USA (Nevada).—FIG. 733,1a–g. **L. squamosa*, lower Pragian, Coal Canyon; *a–e*, holotype, dorsal, ventral, lateral, posterior, and anterior views, $\times 2$; *f*, interior of dorsal valve, $\times 3$; *g*, interior of ventral valve, $\times 2$ (Johnson, 1970b).

Pacificocoelia BOUCOT, 1975a, p. 361 [**Leptocoelia murphyi* JOHNSON, 1970b, p. 165; OD]. Medium to large with subovate to subpentagonal outline and biconvex profile. Beak erect to incurved with small apical foramen; delthyrium absent. Anteriorly flaring low dorsal fold and ventral sulcus; anterior commissure sulciphate. Costae extending from beaks, strong, rounded, simple, flaring anteriorly; growth lamellae few, pronounced. Dental plates short to absent; teeth stout, elongate; diductor field bilobed, strongly impressed but often with bounding ridges; adductor field small and situated within diductor field. Dorsal interior with prominent, bilobed cardinal process on thick notothyrial platform; short, thick median ridge present; sockets deep, short; dorsal adductor field ovate, tapering anteriorly; crura thin, ventrally curved. *Lower Devonian (middle Lochkovian)–Middle Devonian (upper Eifelian)*: North America, South America.—FIG. 733,2a–g. **P. murphyi* (JOHNSON), middle Pragian, Sulphur Spring Range, Nevada, USA; *a–e*, holotype, dorsal, ventral, lateral, posterior, and anterior

views, $\times 1.5$; *f*, paratype, posterior of ventral valve interior, $\times 3$; *g*, interior of dorsal valve, $\times 2$ (Johnson, 1970b).

Platytrichalos JIN, 1989, p. 106 [**P. crudicostatus*; OD]. Small to medium with subcircular outline and weakly biconvex profile, but with high anterior fold. Beak erect to incurved; delthyrium open; foramen small, mesothyrid. Dorsal fold and ventral sulcus narrow, strong anteriorly; anterior commissure sulciphate. Costae strong, simple, rounded, arising at beaks. Dental plates fused to shell walls; teeth small; short, low ventral median ridge developed posteriorly; ventral muscle field weakly impressed. Hinge plates sessile; cardinal process and dorsal median septum absent; crural bases stout, arising from sessile hinge plates at hinge line; crural bases triangular in section; crura thick and laterally flattened, tapering distally. *lower Silurian (Llandovery)*: eastern Canada.—FIG. 732,4a–p. **P. crudicostatus*, Jupiter Formation, Richardson Member, Anticosti Island; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 3.75$; *f–p*, serial sections 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 1.2, 1.3, 1.5, 1.6, 2.0 mm from posterior, $\times 6$ (Jin, 1989).

Family MACHAERARIIDAE

Savage, 1996

[Machaerariidae SAVAGE, 1996, p. 252]

Rhynchotrematoidea with subpentagonal to triangular outline; dorsal fold and ventral sulcus strong; costae medium to coarse, extending from beaks; delthyrium with deltidial plates disjunct to conjunct. Dental plates short or fused with valve walls; teeth elongate and swollen. Dorsal median septum and septalium incipient to absent; hinge plates undivided and sessile; inner socket ridges prominent to massive; cardinal process septiform or unilobed. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian)*.

Machaeraria COOPER, 1955, p. 55 [**Rhynchonella formosa* HALL, 1857a, p. 76; OD] [= *Qinlingotoechia* FU, 1983a, p. 331 (type, *Q. simplex*, OD)]. Subpentagonal to subcircular outline and dorsibiconvex profile; lateral margins usually acute. Beak suberect; delthyrium partly closed by disjunct deltidial plates. Fold and sulcus sharply defined; anterior commissure uniphate; tongue trapezoid, narrowing dorsally. Dental plates short and thin; teeth with small fossettes. Dorsal median septum absent; crural plates meeting valve floor; cardinal process with thin shaft and crinkled myophore; crura with pronounced ventral curvature, crescentic in section. *Lower Devonian (Lochkovian)*: cosmopolitan.—FIG. 734,1a–h. **M. formosa* (HALL),

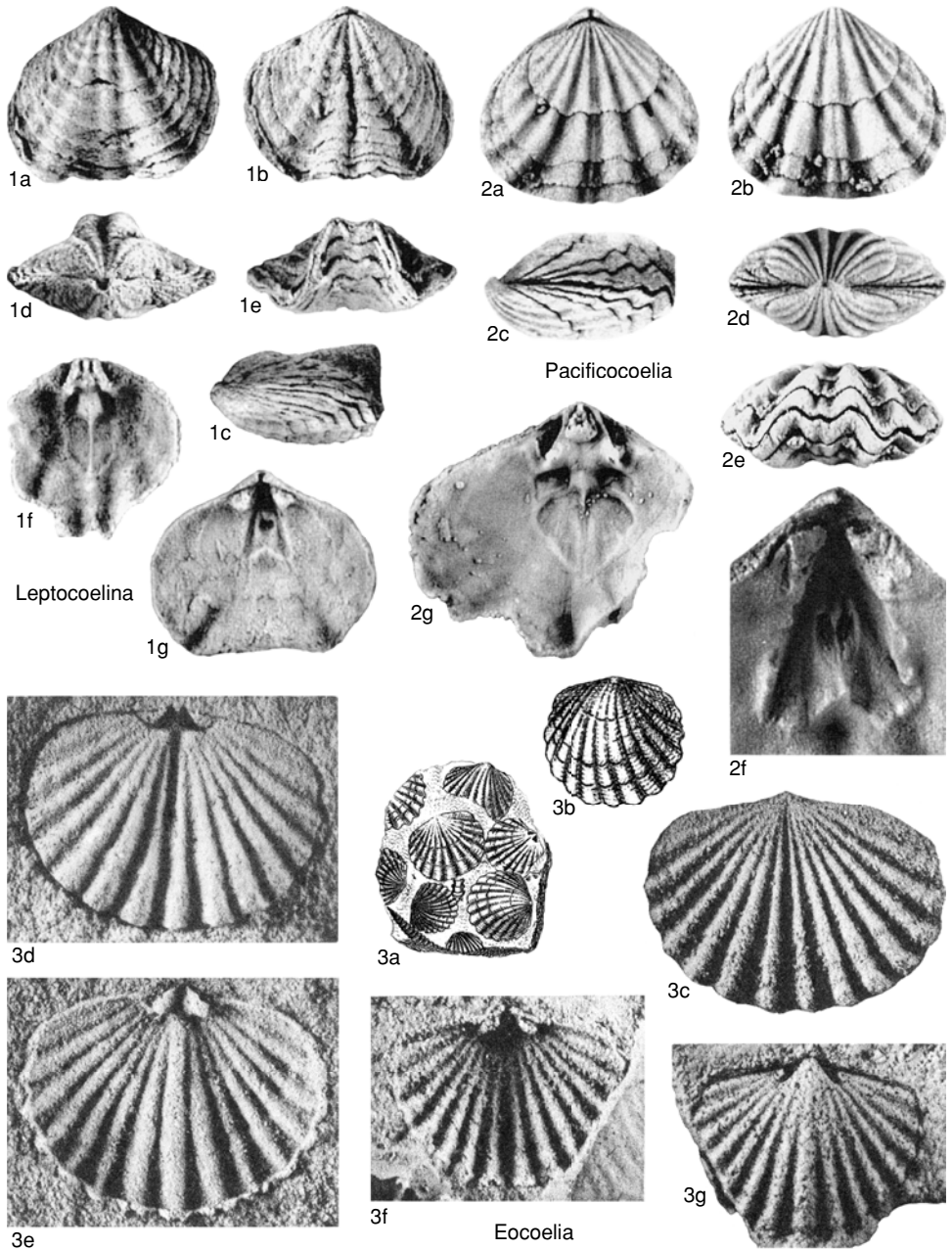


FIG. 733. Leptocoeliidae (p. 1081–1083).

New York, USA; *a–e*, hypotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 1$; *f*, hypotype, posterior showing dental plates and cardinalia, $\times 4$; *g*, hypotype, part of dorsal interior showing cardinalia, $\times 4$; *h*, hypotype, ventral interior, $\times 3$ (Cooper, 1955).

Australirhynchia SAVAGE, 1968, p. 731 [*A. cudalensis*; OD]. Small to medium with transversely subpentagonal outline and dorsibiconvex profile; lateral margins steep. Beak straight to suberect; delthyrium small, with circular foramen, deltidial plates almost meeting. Fold and sulcus pronounced, from

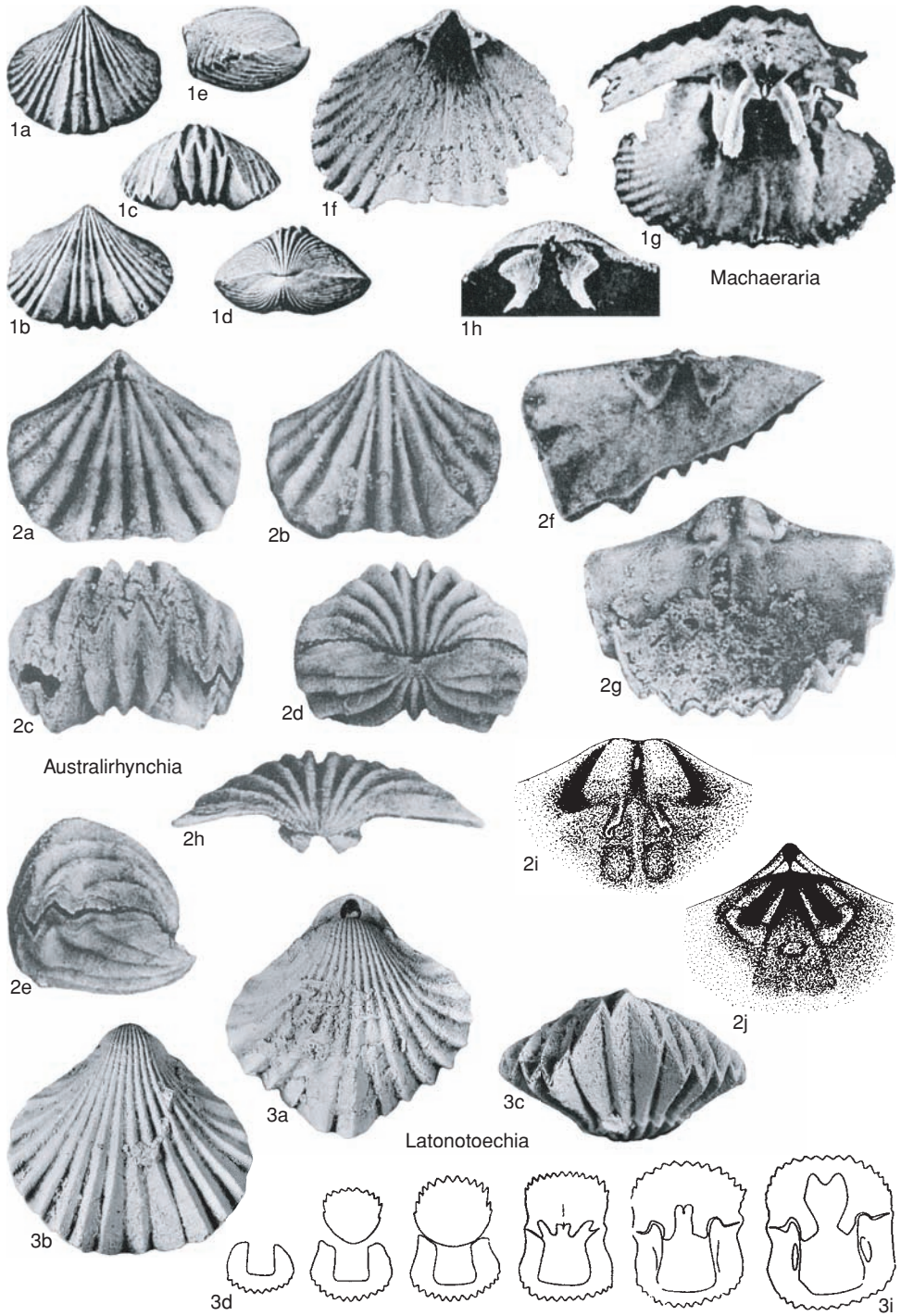


FIG. 734. Machaerariidae (p. 1083–1086).

- umbones; anterior commissure uniplicate; tongue trapezoid, dentate. Costae strong, angular, from beaks, bifurcating on fold, intercalating in sulcus. Dental plates absent or fused to valve walls; teeth long, thick, grooved to fit inner socket ridges; adductor muscle field small, rounded, set within elongate diductor field. Dorsal median septum absent; hinge plates fused to valve floor; inner socket ridges large, inflated; cardinal process small, bosslike; crura crescentic in section. *Lower Devonian (Lochkovian)*: eastern Australia, Altai.—FIG. 734,2a–j. **A. cuddalensis*, Mandagery Park Formation, Manildra, New South Wales, eastern Australia; a–e, holotype, dorsal, ventral, anterior, posterior, and lateral views; f, topotype, interior view of ventral valve; g–h, topotype, interior and posterior views of dorsal valve, $\times 6$; i–j, drawings of interiors of dorsal and ventral valves, $\times 8$ (Savage, 1968).
- Callipleura** COOPER, 1942, p. 228 [**Rhynchospira nobilis* HALL, 1860b, p. 83; OD] [= *Cyclorhina* HALL & CLARKE, 1893, p. 206, non PETERS, 1871]. Medium to large with transversely subpentagonal outline and lenticular dorsibiconvex profile; lateral margins acute. Beak with large, circular foramen; deltidial plates disjunct to barely conjunct. Fold and sulcus from umbones, well defined anteriorly; anterior commissure uniplicate; tongue low, dentate. Costae strong, angular, numerous, simple, arising at beaks. Dental plates distinct but partly fused to valve wall, anteriorly divergent; ventral muscle field raised, extending almost to valve midlength. Crural plates resting on valve floor; cardinal process septiform and very delicate; crura sharply curved ventrally. *Middle Devonian (Givetian)*: North America.—FIG. 735,2a–g. **C. nobilis* (HALL); a–e, hypotype, dorsal, ventral, posterior, anterior, and lateral views, New York, USA, $\times 1.3$ (new); f–g, interiors of dorsal and ventral valves, upper Givetian, Traverse Group, Thunder Bay Formation, Thunder Bay Quarry, Ann Arbor, Michigan, USA, $\times 1.3$ (new).
- Cherubicornea** HAVLIČEK, 1992, p. 70 [**Terebratula amalthea* BARRANDE, 1847, pl. 19, fig. 6; OD]. Subtriangular outline and alate cardinal margins; convexoplane profile with acute lateral margins. Beak straight to suberect; delthyrium with circular, permesothyrid foramen, deltidial plates conjunct. Fold and sulcus well developed, from umbones; anterior commissure uniplicate; tongue narrow, low, distinct, dentate. Costae strong, angular, from beak, with some bifurcation; growth lamellae crowded. Dental plates thin, close to shell walls. Hinge plate steeply sloping to valve floor, underlain by callus; septalium not developed; bladlike cardinal process deeply recessed in notothyrial cavity; crura unknown. *Lower Devonian (Pragian–upper Emsian)*: Bohemia, France.—FIG. 735,3a–c. **C. amalthea* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; hypotype, dorsal, ventral, and anterior views, $\times 1.8$ (Havlíček, 1992).
- Ferganella** NIKIFOROVA, 1937a, p. 39 [**F. turkestanica*; OD]. Subpentagonal to rounded outline and biconvex profile. Beak suberect; delthyrium open but small deltidial plates may be present. Fold and sulcus low; anterior commissure uniplicate; tongue broad, low, dentate. Costae strong, angular, from beaks, rare bifurcation. Dental plates short, vertical. Septalium with cover, septalial plates long; hinge plates conjunct posteriorly; cardinal process septiform, within septalium, merges with dorsal median septum that extends to midvalve. *Lower Devonian (Lochkovian)*: Fergana.—FIG. 736,3a–f. **F. turkestanica*, lower Lochkovian, Manak Beds; a–d, dorsal, ventral, lateral, and anterior views, $\times 1$ (Nikiforova, 1937a); e, serial section, $\times 2.5$; f, serial section, $\times 3.5$ (Jones, 1981).
- Latonotoechia** HAVLIČEK, 1960, p. 244 [**Terebratula latona* BARRANDE, 1847, p. 89; OD]. Medium to large with elongate to subpentagonal outline and biconvex profile; lateral margins acute. Beak suberect; foramen hypothryid, bounded anteriorly by large, disjunct deltidial plates. Fold and sulcus narrow, often asymmetrical; anterior commissure uniplicate; tongue tapering dorsally, dentate. Costae strong, simple, sharply angular, from beaks. Dental plates close to valve wall or cavities filled with callus; teeth stout. Hinge plates underlain by callus; inner socket ridges thick, sessile; dorsal septum absent; cardinal process septiform; crura unknown. *Lower Devonian (Pragian)*: Europe, North America, Urals, Altai, Salair, Tadzhikistan, China.—FIG. 734,3a–i. **L. latona* (BARRANDE), Koneprusy Limestone, Zlatý kun Hill, Bohemia; a–c, hypotype, dorsal, ventral, and anterior views, $\times 1.5$ (Havlíček, 1992); d–i, serial sections 17.7, 17.0, 16.3, 16.0, 15.3, 14.8 mm from anterior, $\times 2$ (Havlíček, 1961).
- Machaeratoechia** HAVLIČEK, 1992, p. 63 [**M. marsyas*; OD]. Elongate to subtriangular outline; moderately biconvex; lateral margins acute. Beak suberect; foramen hypothryid to submesothyrid, bounded anteriorly by conjunct deltidial plates. Fold and sulcus distinct but low; anterior commissure weakly uniplicate; tongue low, broad, serrate. Costae strong, simple, rounded, from beaks. Dental plates absent; teeth stout, arising from valve margins; ventral muscle field deeply impressed. Hinge plates triangular, sloping medially to valve floor, attached to valve floor by curved crural plates; dorsal median septum absent; cardinal process weak, septiform; crura unknown. *Lower Devonian (Pragian–upper Emsian)*: Bohemia.—FIG. 735,1a–f. **M. marsyas*, Emsian, Zlichov Limestone, Hlubocepy quarry; a–c, hypotype, dorsal, ventral, and anterior views, $\times 2.4$; d, hypotype, dorsal view showing deltidial plates, $\times 1.5$; e, hypotype, ventral valve interior, $\times 2.8$; f, holotype, dorsal valve interior, $\times 3.7$ (Havlíček, 1992).
- Sicorhyncha** HAVLIČEK, 1961, p. 28 [**Stegerhynchus trinacrius* HAVLIČEK, 1956, p. 571; OD]. Small to medium with elongate trigonal outline; posterolateral margins emarginate; weakly biconvex profile with lateral margins low, rounded. Beak short, straight; delthyrium small with deltidial plates conjunct, foramen permesothyrid to epithyrid. Fold and sulcus weak; anterior commissure weakly uniplicate; tongue low, dentate. Costae fine,

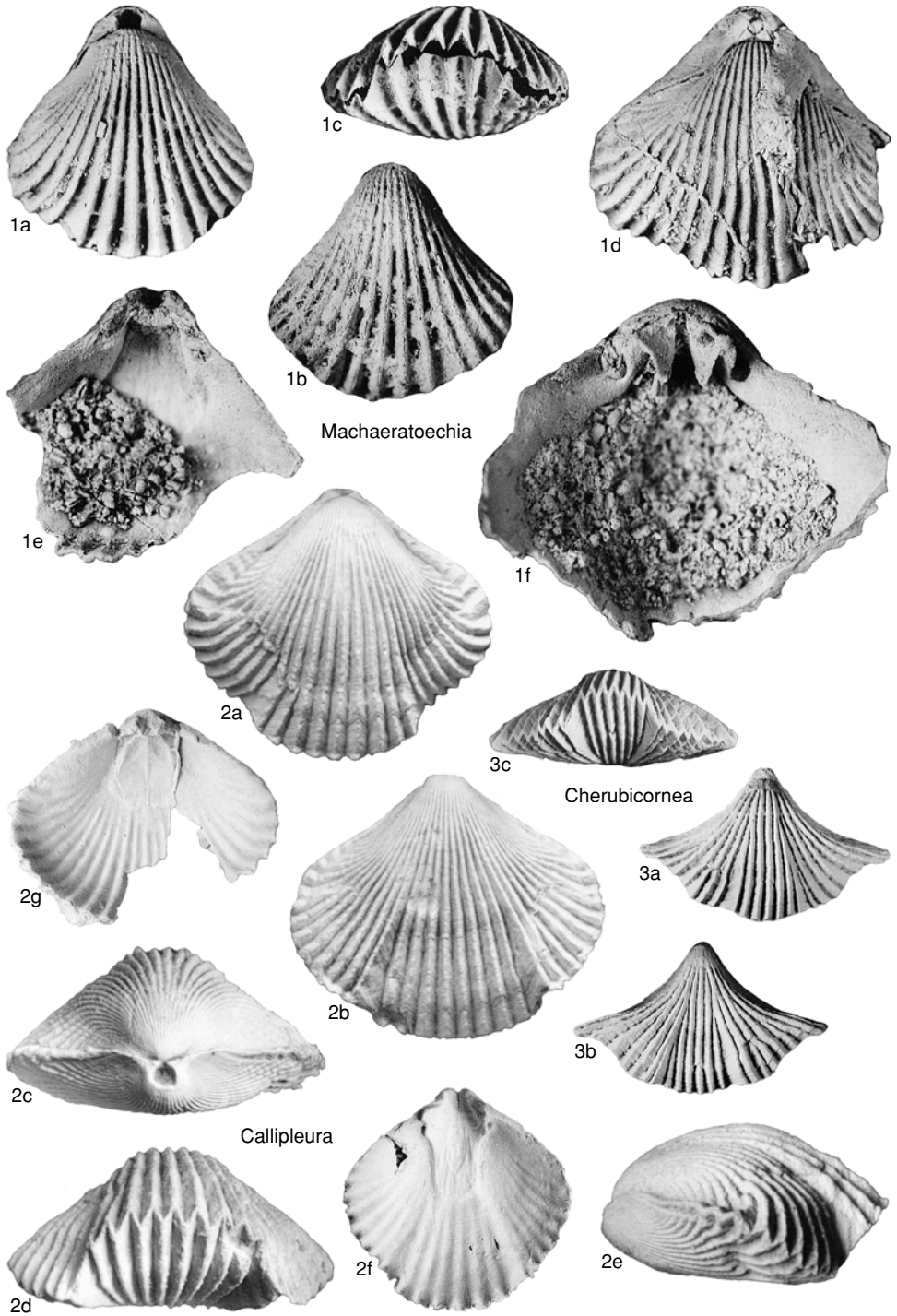


FIG. 735. Machaerariidae (p. 1086).

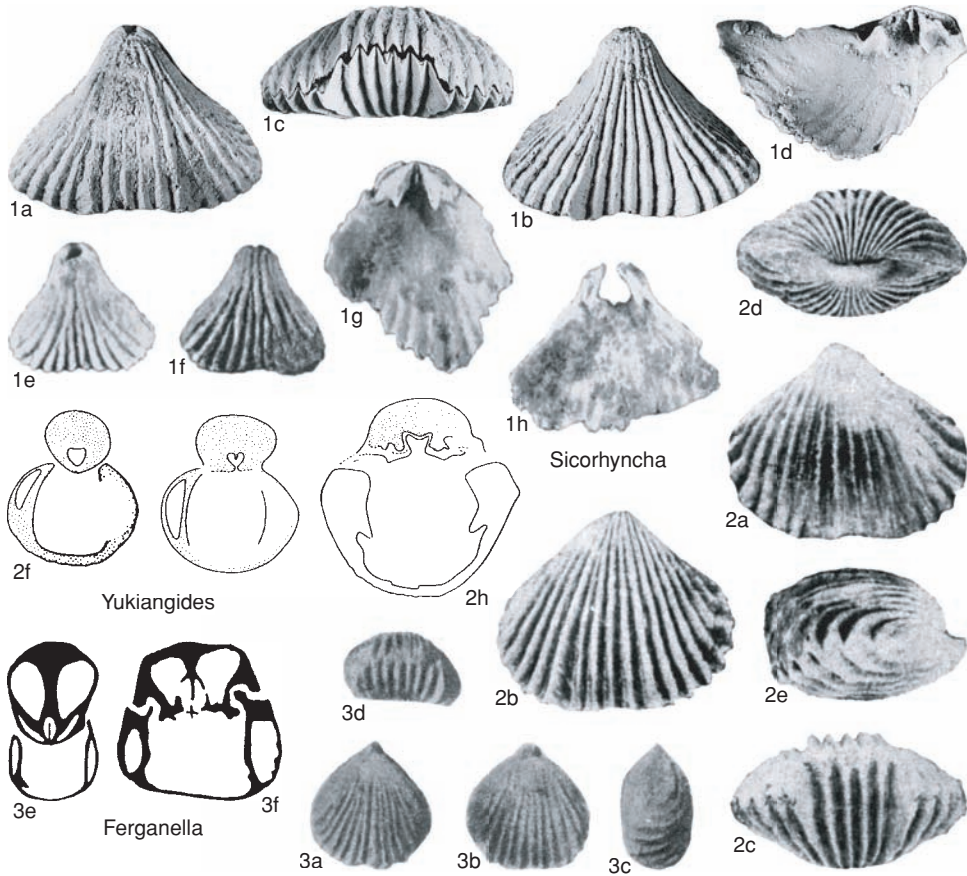


FIG. 736. Machaerariidae (p. 1086–1089).

angular, from beaks; some bifurcation and intercalation. Dental plates largely fused to valve walls. Hinge plates small, triangular, posteriorly sessile; dorsal median septum absent; cardinal process septiform; crura strongly curved, laterally flattened. *Lower Devonian (Pragian–Emsian)*: Europe, Morocco, Urals, Salair, Tadzhikistan.—FIG. 736, 1a–b. **S. trinacria* (HAVLIČEK), Emsian, Zlichov Limestone, Hlubocepy, Bohemia; a–c, hypotype, dorsal, ventral, and anterior views, $\times 2.3$; d, hypotype, dorsal valve interior, $\times 3.9$ (Havlíček, 1992); e–f, holotype, dorsal and ventral views, $\times 2.5$; g, dorsal valve interior; h, ventral valve interior, $\times 2.8$ (Havlíček, 1956).

Thliborhynchia LENZ, 1967, p. 1188 [**T. julli*; OD] [= *Franklinella* LENZ, 1973, p. 1405 (type, *F. pedderi* LENZ, 1973, p. 1407), non STEWART & HENDRIX, 1945, Ostracoda]. Subtriangular outline; postero-lateral margins emarginate; profile convexoplane. Beak erect to suberect; delthyrium with oval foramen, deltidial plates disjunct. Fold and sulcus low, from midlength; anterior commissure weakly uniplicate, dentate. Costae strong, simple, from beaks,

angular. Dental plates thin, close to shell walls. Hinge plates concave, sessile; septalium not developed; dorsal median septum absent but low myophragm present posteriorly; inner socket ridges massive; cardinal process septiform; crura strongly curved ventrally, laterally compressed proximally, then twisted to horizontal distally. *Lower Devonian (Lochkovian–Pragian)*: North America.—FIG. 737, 1a–g. **T. julli*, Royal Creek, Yukon, Canada; a–c, holotype, dorsal, lateral, and posterior views; d–e, hypotype, ventral and anterior views, $\times 1$; f, hypotype, ventral valve interior, $\times 2$; g, hypotype, dorsal valve interior, $\times 3$ (Lenz, 1967).

Yukiangides HAVLIČEK, 1992, p. 61 [**Camarotoechia parasappho* WANG, 1956, p. 141; OD]. Transversely subpentagonal outline and dorsibiconvex profile. Beak straight to suberect; foramen hypothyriform with conjunct deltidial plates. Fold and sulcus low but distinct anteriorly; anterior commissure uniplicate. Costae mostly simple, from beaks, subangular. Dental plates short with umbonal cavities mostly filled with callus; teeth stout, arising from valve margins. Hinge plates massive, sessile; cardinal

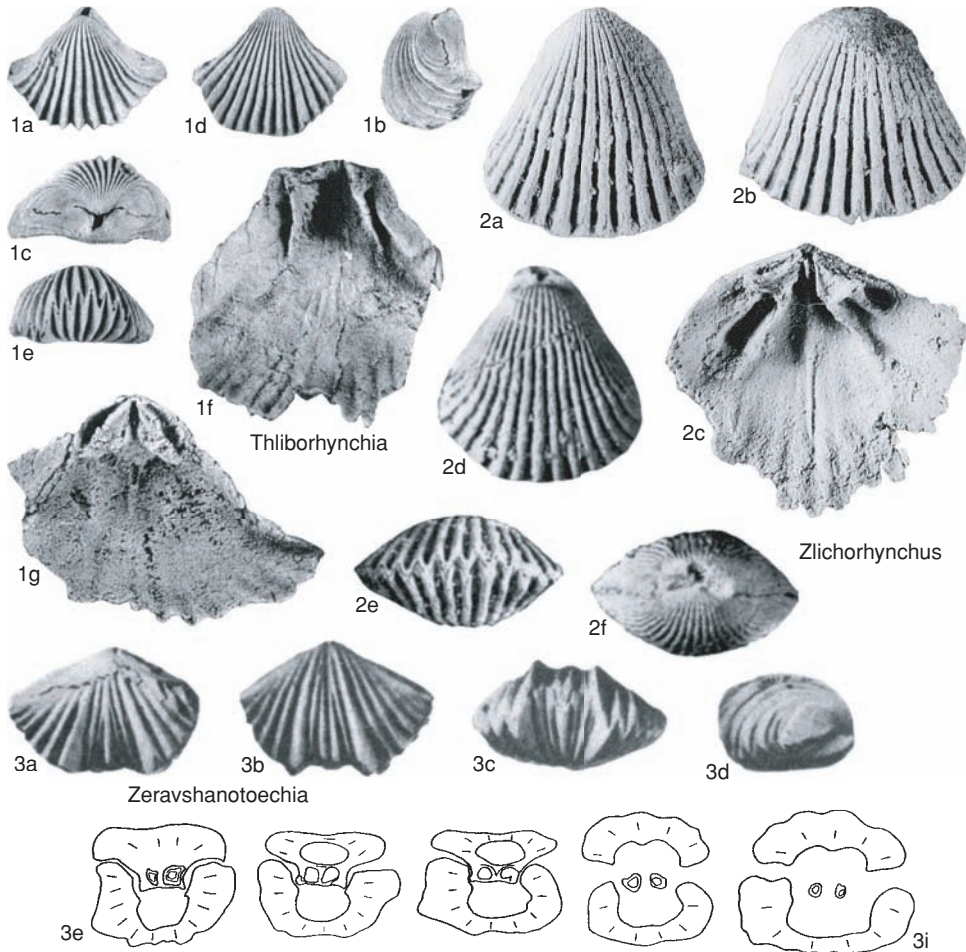


FIG. 737. Machaerariidae (p. 1088–1091).

process septiform; crura short, curved ventrally. *Lower Devonian (Lochkovian–Emsian)*: China, Altai, Urals, Bohemia.—FIG. 736,2a–e. **Y. parasappho* (WANG), Pragian–Emsian, Yukiang Formation, central Guangxi, southern China; holotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 1.5$ (Wang, 1956).—FIG. 736,2f–b. *Y. vesta* (BARRANDE), Lochkovian, Lochkov Formation, Bohemia; f–g, hypotype, serial sections 10.2, 10.0 mm from anterior, $\times 3.8$; h, serial section of another specimen, $\times 2.6$ (Havlíček, 1961).

Zeravshanotoechia RZHONSNIITSKAIA, 1977, p. 127 [**Z. zeraushanica*; OD]. Small to medium with angular subpentagonal outline, tending toward alate; dorsibiconvex profile. Dorsal fold bearing sulcuslike depression, and sulcus with marked medial rib; anterior commissure sulcificate, denticulate. Costae of varying size, fasciculate, most pronounced bordering fold and sulcus. Shell wall very thick. Den-

tal plates absent; teeth massive, arising from valve margin. Hinge plates undivided, sessile posteriorly; septalium not developed; dorsal median septum absent; cardinal process septiform, with notothyrial cavity roofed by cover plate; crura long, rather straight. *Lower Devonian (Pragian)–Middle Devonian (Eifelian)*: Tadjhikistan, Urals.—FIG. 737,3a–i. **Z. zeraushanica*; a–d, holotype, dorsal, ventral, anterior, and lateral views, Zlichovian, Zeravshansk Range, Tadjhikistan, $\times 2$; e–i, serial sections 1.0, 1.7, 2.1, 2.4, 2.7 mm from posterior, $\times 2.5$ (Rzhonsniitskaia, 1977).

Zlichorhynchus HAVLÍČEK, 1963, p. 403 [**Z. hiatus*; OD]. Small with rounded subtriangular elongate outline, widest at about three-quarter length; biconvex profile. Beak straight; foramen large mesothyrid, flanked by thin disjunct deltidial plates. Fold and sulcus absent; anterior commissure rectimarginate. Costae straight, narrow, rounded,

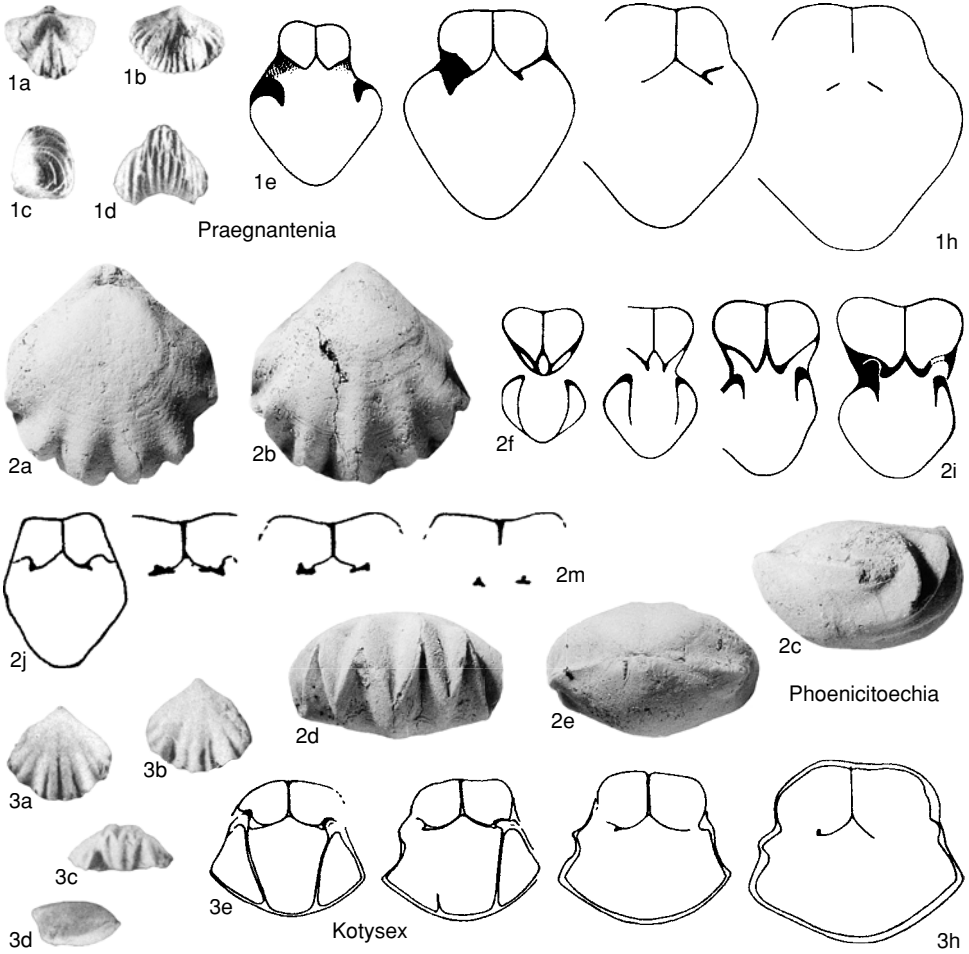


FIG. 738. Phoenicitoechiidae (p. 1091).

never bifurcating. Dental plates short, commonly fused with valve walls. Hinge plates triangular, concave, inner edges extending anteriorly as long crural plates that bound muscle field; dorsal median septum absent; cardinal process septiform, within deep notothyrial cavity; crura unknown. *Lower Devonian (Pragian–Emsian)*: Bohemia, China, Australia.—FIG. 737, 2a–f. **Z. hiatus*, Emsian, Zlichov Limestone, Hlubocepy, Bohemia; a–b, holotype, dorsal and ventral views; c, hypotype, dorsal valve interior, $\times 3.1$; d–f, hypotype, dorsal, anterior, and posterior views, $\times 2.8$ (Havlíček, 1992).

Family PHOENICITOECHIIDAE Havlíček, 1990

[Phoenicitoechiidae HAVLÍČEK, 1990b, p. 216]

Rhynchotrematoidea with subcircular to subtrigonal outline; fold and ventral sulcus moderate to strong; costae strong, simple or sometimes arising by bifurcation and intercalation; umbones generally smooth; delthyrium with disjunct to conjunct deltidial plates. Dental plates short, thin. Hinge plates form wide, open, ventrally convex septalium; cardinal process absent. *Lower Devonian (Lochkovian–Emsian)*.

Phoenicitoechia HAVLÍČEK, 1960, p. 242 [**Terebratula phoenix* BARRANDE, 1847, p. 75; OD]. Subtriangular to transversely ovate outline; equibiconvex, lateral and anterior margins precipitous. Beak erect; foramen open; deltidial plates disjunct to conjunct. Fold and sulcus weak, from midlength; anterior commissure weakly uniplicate, denticulate. Costae few, strong, subangular, restricted to lateral and anterior margins. Dental plates short, slender. Dorsal median septum high, long; septalium long, wide, without cover plate; crural bases subtriangular. *Lower Devonian (lower Pragian–lower Emsian)*: Europe, Urals, China.—FIG. 738, 2a–m.

**P. phoenix* (BARRANDE), Pragian, Koneprusy Limestone, Bohemia; a–e, holotype, dorsal, ventral, lateral, anterior, and posterior views, Koneprusy, $\times 3.5$ (new); f–i, hypotype, serial sections 8.6, 8.55, 8.5, 8.4 mm from anterior, $\times 3$ (Havlíček, 1961); j–m, hypotype, serial sections showing crural bases, $\times 7.5$ (Schmidt, 1965b).

Kotysex HAVLÍČEK, 1990b, p. 218 [**Rhynchonella simulans* BARRANDE, 1879b, pl. 147, case 7, fig. 1a–d; OD]. Subcircular to subpentagonal in outline; equibiconvex, lenticular, not inflated anteriorly, never truncated at lateral and anterior margins. Beak suberect to erect; foramen open; deltidial plates disjunct to conjunct. Fold and sulcus weak, from umbones; anterior commissure uniplicate; tongue broad, low, serrate. Costae few, subangular, arising anterior of smooth umbones, with some bifurcation. Dental plates thin, short, slightly convergent ventrally. Septalium large, wide, long; median septum thin, high; crura unknown. *Lower Devonian (Lochkovian–Pragian)*: Bohemia, Carnic Alps.—FIG. 738, 3a–b. **K. simulans* (BARRANDE); a–d, lectotype, dorsal, ventral, anterior, and lateral views, Vinarice Limestone, Menany, Bohemia, $\times 1$ (Havlíček, 1961); e–h, hypotype, serial sections, $\times 5.25$ (Havlíček, 1990b).

Praegnantenia HAVLÍČEK, 1961, p. 99 [**Terebratula praegnans* BARRANDE, 1847, p. 72; OD]. Subpentagonal outline; dorsibiconvex, strongly inflated anteriorly. Beak small, incurved; delthyrium open posteriorly to leave small foramen; deltidial plates disjunct to conjunct. Fold and sulcus strong, from umbones; anterior commissure uniplicate; tongue high, rounded, dentate. Costae low, angular, present on fold, sulcus, and flanks, some bifurcation; umbones smooth. Dental plates thin, short. Septalium large, wide, supported by high, long dorsal median septum. *Lower Devonian (lower Pragian–lower Emsian)*: Bohemia, southern Urals.—FIG. 738, 1a–b. **P. praegnans* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; a–d, lectotype, dorsal, ventral, lateral, and anterior views, $\times 1$; e–h, hypotype, serial sections 7.2, 7.0, 6.85, 6.75 mm from anterior, $\times 5$ (Havlíček, 1961).

UNCINULOIDEA

NORMAN M. SAVAGE

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Superfamily UNCINULOIDEA Rzhonsnitskaia, 1956

[*nom. transl.* SAVAGE, 1996, p. 252, ex Uncinulidae RZHONSNITSKAIA, 1956a, p. 125]

Rhynchonellida with globular, cuboid, or lenticular shape; dorsal fold and ventral sulcus weak; tongue high; costae numerous, flattened anteriorly on *paries geniculatus*; anterior and lateral margin spines usually present; foramen small, commonly with conjunct to disjunct deltidial plates anteriorly; squamae and glottae often developed. Dental plates weak or infilled with callus. Dorsal median septum, septalium, and cardinal process generally present; crura commonly raduliform. *lower Silurian (Llandovery)–Upper Devonian (upper Famennian)*.

Family UNCINULIDAE Rzhonsnitskaia, 1956

[Uncinulidae RZHONSNITSKAIA, 1956a, p. 125]

Uncinuloidea with thick shell; anterior marginal spines long. Dental plates short or obscured by umbonal callus. Dorsal median septum present; septalium usually infilled by callus; cardinal process wide, multilobed. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian)*.

Uncinulus BAYLE, 1878, pl. 11, fig. 11, 12, 15, 16 expl. [**Hemithyris subwilsoni* d'ORBIGNY, 1850 in 1849–1852, p. 92; SD OEHLERT, 1884, p. 423] [= *Tridensilis* SU, 1976, p. 193 (type, *T. gibbosa*, OD); *Uncina* KAPLUN, 1991, p. 125 (type, *U. bublitschenkoi*, OD)]. Medium to large size; subcircular to subpentagonal outline; hinge line strophic; articulation with squamae and glottae; strongly biconvex to globular profile; anterior margin and flanks vertical. Beak erect to incurved; foramen absent or minute. Dorsal fold and ventral sulcus weak but rectangular to subrectangular anterior tongue distinct. Costae fine, from beaks, some bifurcation and intercalation, grooved at commissure to accommodate marginal spines. Dental plates well developed, convex medially, umbonal cavities commonly filled with callus; ventral muscle area

deeply impressed, divided by thin septum. Septalium small, usually filled with callus; dorsal median septum buried in callus; cardinal process wide, multilobed, filling posterior of septalial cavity. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: cosmopolitan.—FIG. 739, 2a–p. **U. subwilsoni* (D'ORBIGNY), Lower Devonian, northwestern France; a–d, dorsal, ventral, anterior, and lateral views; e, interior of ventral valve, $\times 95$; f, interior of dorsal valve, enlarged (Bayle, 1878); g–p, serial sections 13.0, 12.8, 12.6, 12.3, 11.8, 11.7, 11.6, 11.5, 11.2, 10.2 mm from anterior, $\times 2$ (Schmidt, 1965b).—FIG. 739, 2q–s. *Uncinulus*, marginal spines (schematic); q, both valves connected, slightly opened; r, dorsal valve; s, ventral valve, approximately $\times 1.5$ (Schmidt, 1937).

Bulgania ERLANGER, 1994, p. 109 [**B. mongolica*; OD]. Subovate to subcircular outline; lateral profile strongly biconvex and anteriorly inflated but ventral valve slightly resupinate; anterior and lateral margins vertical. Beak erect; foramen submesothyrid; tongue high, rectangular. Fold and sulcus weak. Costae fine, arising at umbones, flattened and bearing grooves anteriorly on *paries geniculatus*; intercostal furrows extending as marginal spines. Dental plates very short to absent, obscured by thick callus; ventral muscle field deeply impressed, divided by low ridge. Dorsal interior with massive, linguiform, trilobed cardinal process filling short, low septalium; dorsal median septum high, long; crura long, closely set. *Upper Devonian (Frasnian)*: Mongolia.—FIG. 739, 1a–l. **B. mongolica*, Bulgan area, 2 km northeast of Mt. Zagin-Khar-Ula, southwestern Mongolia; a–e, holotype, dorsal, ventral, posterior, lateral, and anterior views, $\times 1$; f–l, serial sections 1.1, 1.95, 2.8, 3.1, 3.2, 3.9, 3.95 mm from posterior, $\times 2.5$ (Erlanger, 1994).

Eucharitina SCHMIDT, 1955, p. 121 [**Terebratula eucharis* BARRANDE, 1847, p. 68; OD]. Medium to large size; subcircular outline; dorsibiconvex to convexoconcave lateral profile; lateral and anterior margins steep to vertical. Beak erect to incurved; foramen absent. Fold and sulcus low, from mid-length; anterior commissure uniplicate; tongue low, wide. Costae flattened, with longitudinal grooves on lateral and anterior shell margins; commissure denticulate with marginal spines that taper uniformly to point, extending under costae of opposite valve. Dental plates very short; ventral muscle field deeply impressed, divided by small septum. Septalium small, filled by large cardinal process that is multilobed posteriorly but massively bilobed anteriorly; crura long, slender, closely set. *Lower Devonian (Pragian)*: Europe, northern Africa.—FIG.

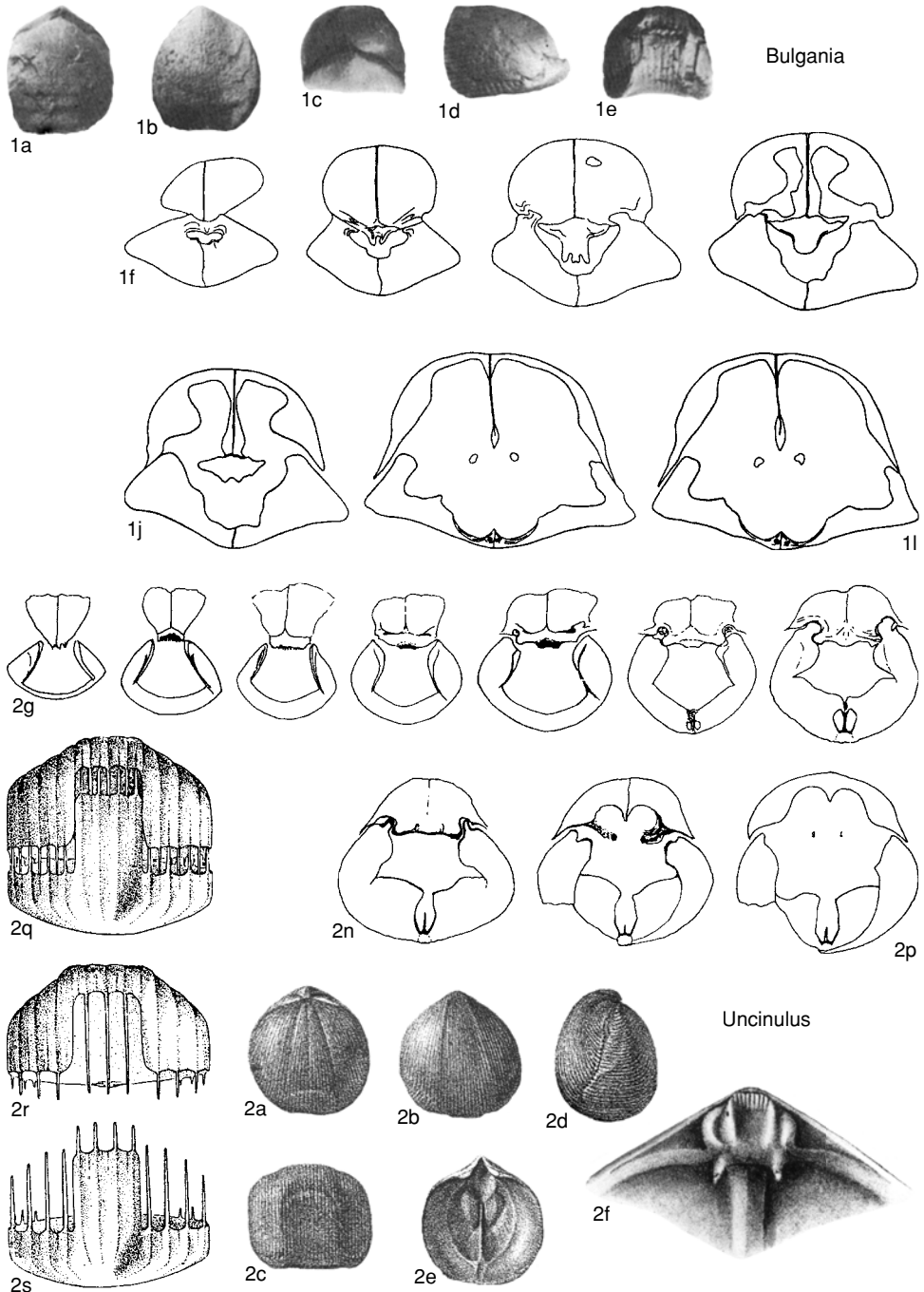


FIG. 739. Uncinulidae (p. 1092).

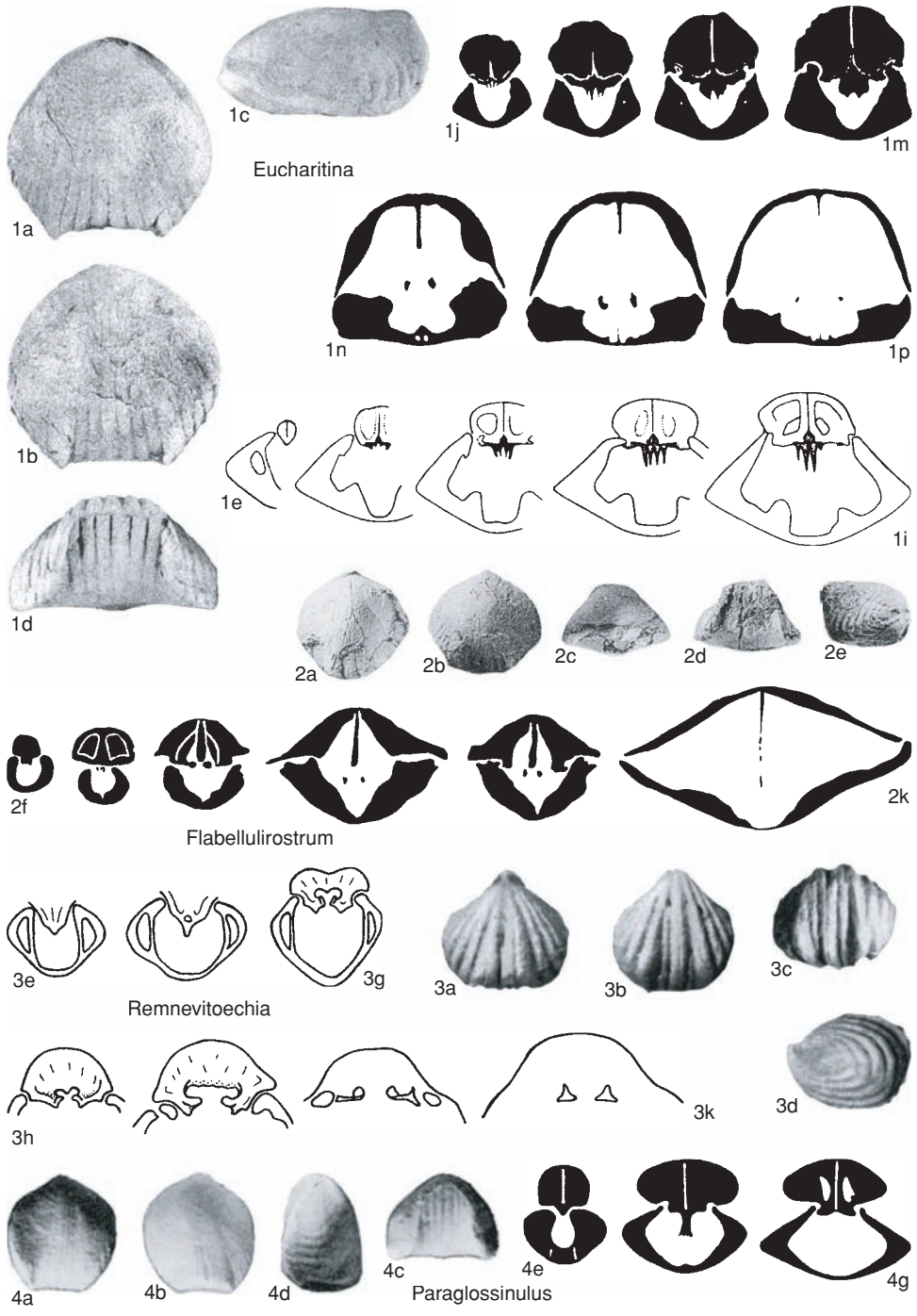


FIG. 740. Uncinulidae (p. 1092–1097).

- 740, 1a–i. **E. eucharis* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; a–d, holotype, dorsal, ventral, lateral, and anterior views, $\times 1$; e–i, hypotype, serial sections 29.1, 29.0, 28.9, 28.7, 28.6 mm from anterior (Havlíček, 1961).—FIG. 740, 1j–p. *E. oehlerti* (BAYLE), Pragian, Saint-Cenéré section, northwestern France; j–m, hypotype, serial sections 1.1, 2.0, 2.6, 2.9 mm from posterior, $\times 1.8$; n–p, serial sections 6.4, 7.2, 8.7 mm from posterior of another hypotype, $\times 1.3$ (Brice, 1991).
- Fitzroyella** VEEVERS, 1959a, p. 104 [**F. primula*; OD]. Medium to small with subpentagonal outline and biconvex profile. Beak suberect; foramen small, circular, bounded by conjunct deltidial plates. Costae coarse, uneven, multiplying by intercalation and bifurcation; costae flattened and grooved anteriorly and anterolaterally; short marginal spines present. Dental plates well developed, ventrally divergent; ventral muscle field bilobed; socket holes for spines prominent around anterior internal margin. Dorsal median septum short, low; septalium very short; hinge plates anterior of septalium divided, horizontal; cardinal process small, low. *Middle Devonian (middle Givetian)–Upper Devonian (middle Frasnian)*: Western Australia, Germany, England, Poland.—FIG. 741, 1a–m. **F. primula*, lower Frasnian, Sadler Formation, Fitzroy basin, Sadler Ridge, Western Australia; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 4$; e, interior of ventral valve showing marginal spine socket holes, $\times 6$; f–m, serial sections 0.65, 0.80, 0.85, 0.90, 0.95, 1.10, 1.15, 1.70 mm from posterior, $\times 4$ (Veevers, 1959a).—FIG. 741, 1n–p. *F. alata* BIERNAT, lower Frasnian, Holy Cross Mountains, Kielce, Poland; dorsal, lateral, and anterior views, $\times 3.6$ (Biernat, 1969).—FIG. 741, 1q. *F. juxi*, lower Frasnian, Refrath Formation, Bergisches Land, Germany; transverse section showing cardinal process, $\times 10$ (Struve, 1978).
- Flabellulirostrum** SARTENAER, 1971a, p. 5 [**Uncinulus wolmericus* VEEVERS, 1959a, p. 96; OD]. Medium size with subcircular to transversely ovate outline and dorsibiconvex profile. Beak erect to incurved; foramen mesothyrid. Fold and sulcus arising near umbones; anterior commissure uniplicate; tongue medium to high, trapezoid, projecting. Costae simple, strong on fold and in sulcus, weaker on flanks, separated by narrow grooves; short marginal spines present. Dental plates short to absent; ventral muscle field narrow, in thick callus. Hinge plates short, breaking up early; cardinal process large with longitudinal lobes; dorsal median septum long, high; dorsal muscle field narrow, in thick callus; crura closely set, ventrally curved. *Middle Devonian (upper Givetian)–Upper Devonian (middle Frasnian)*: Western Australia, Europe, northern Africa.—FIG. 740, 2a–k. **F. wolmericus* (VEEVERS), lower Frasnian, Sadler Formation, Fitzroy basin, Sadler Ridge, Western Australia; a–b, holotype, dorsal and ventral views; c–e, hypotype, posterior, anterior, and lateral views, $\times 1$; f–k, serial sections 0.4, 0.6, 1.0, 1.35, 1.8, 3.5 mm from posterior, $\times 3.2$ (Veevers, 1959a).
- Markitoechia** HAVLÍČEK, 1959, p. 81 [**Uncinulus (U.) marki* HAVLÍČEK, 1956, p. 568; OD]. Shell small; subcircular to subpentagonal outline; biconvex with truncated anterior and lateral margins. Beak suberect; foramen mesothyrid, bounded by conjunct deltidial plates. Fold and sulcus weak; tongue high, rounded to rectangular. Most of valves smooth; costae arising close to anterior and lateral margins, flattened and grooved on *paries geniculatus*; spines at commissure. Dental plates thin, close to valve walls; ventral muscle field well impressed. Dorsal median septum low, long; septalium small, with arched cover plate anteriorly and filled posteriorly with very high, rodlike cardinal process. *Lower Devonian (Emsian)*: Europe, northern Africa.—FIG. 741, 2a–i. **M. marki* (HAVLÍČEK), Zlichov Limestone, Hlubocepy, Bohemia; a–b, holotype, dorsal and ventral views; c, anterior view, $\times 2.4$ (Havlíček, 1956); d–e, serial sections, $\times 7$ (Havlíček, 1961); f–i, hypotype, dorsal, ventral, lateral, and anterior views, $\times 4.5$ (Havlíček, 1992).
- Paraglossinulus** MARTYNOVA, 1988, p. 41 [**P. parvus*; OD]. Shell small; subtriangular to subcircular; anteriorly inflated but ventral valve slightly resupinate; anterior and lateral margins vertical. Fold and sulcus strong, arising from umbones; anterior commissure uniplicate; tongue high, rounded. Costae arising at umbones, flattened and bearing grooves anteriorly. Dental plates and septalium very short; dorsal median septum reaching valve midlength; cardinal process high, linguiform. *Upper Devonian (Frasnian)*: Kazakhstan.—FIG. 740, 4a–g. **P. parvus*, Maya bed, Cischingiz, Koryk River, central Kazakhstan; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–g, serial sections, $\times 3.6$ (Martynova, 1988).
- Plethorhyncha** HALL & CLARKE, 1893, p. 191 [**Rhynchonella speciosa* HALL, 1857a, p. 81; SD SCHUCHERT & LEVENE, 1929a, p. 99]. Medium to large with elongate oval outline; inflated, lateral and anterior margins vertical. Beak incurved; foramen absent; squamae and glottae prominent. Fold and sulcus weak, tongue low; anterior commissure weakly uniplicate, zigzag denticulation. Costae arising at beaks, simple, flattened anteriorly where they bear grooves that accommodate marginal spines. Dental plates absent or obscured by callus; teeth attached to valve walls; ventral muscle field elongate, deeply impressed. Dorsal median septum extending to valve midlength; septalium small, open; large bilobed cardinal process; crura short, straight. *Lower Devonian (Emsian)*: North America, ?Europe.—FIG. 742, 1a–b. **P. speciosa* (HALL), Oriskanian, Cumberland, Maryland, USA; a–c, posterior, anterior, and lateral views, $\times 0.8$; d, interior of ventral valve; e, interior of young dorsal valve, $\times 1$; f, interior of mature dorsal valve, $\times 0.8$ (Hall & Clarke, 1895); g, interior of silicified dorsal

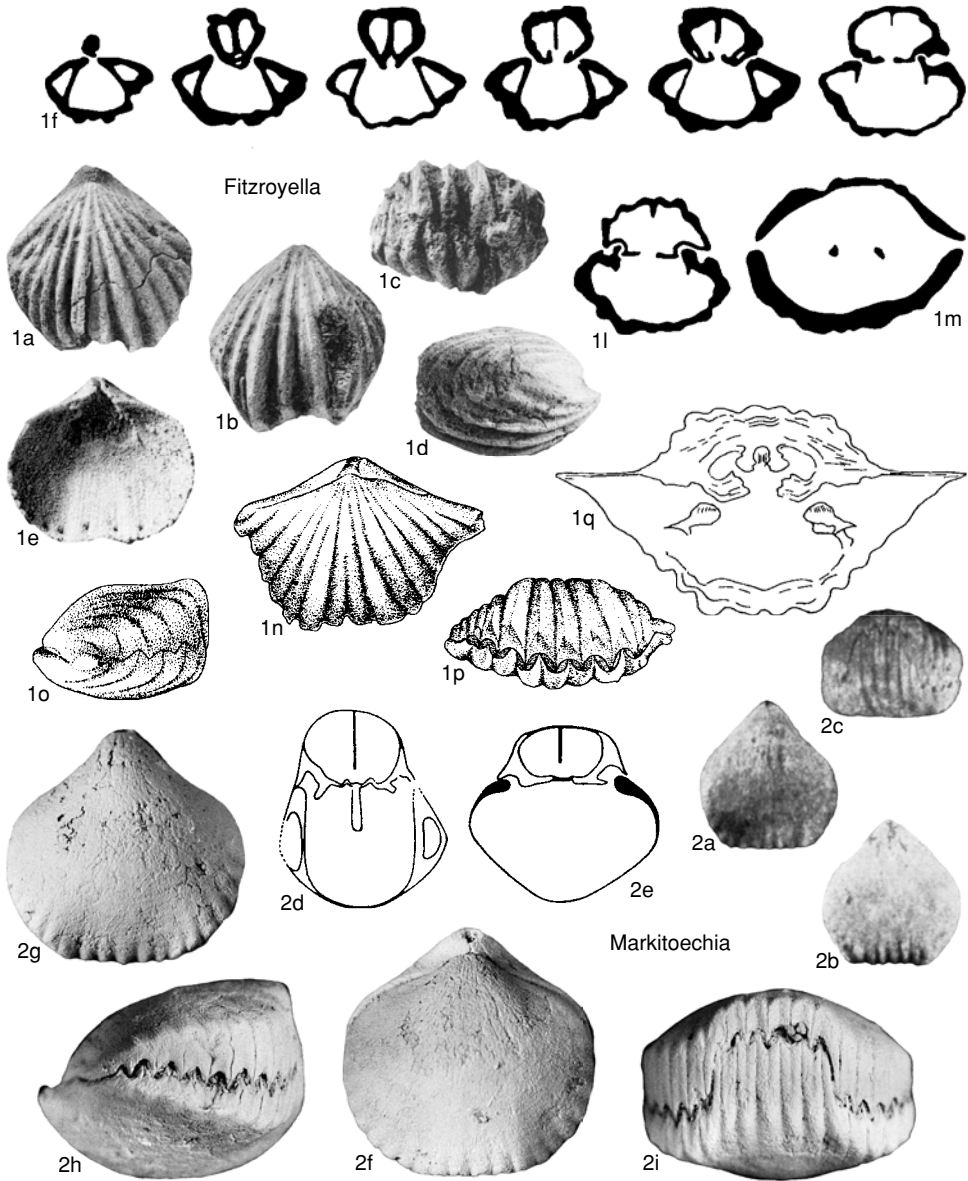


FIG. 741. Uncinulidae (p. 1095).

fragment showing cardinalia, $\times 1.6$; *b*, interior of silicified ventral fragment showing teeth and muscle field, $\times 1.3$ (new).

Remnevitoechia GRATSANOVA, 1970, p. 97 [**R. pseudogurjevskensis*; OD]. Small size with subpentagonal outline and strongly biconvex profile. Beak erect to incurved; foramen small, mesothyrid. Fold and sulcus well defined, from umbones; tongue high, rectangular. Costae coarse, uneven, from beaks, some splitting and intercalation, flattened

and bearing grooves at *paries geniculatus*, marginal spines developed. Dental plates distinct, vertical. Cardinal process massive, single lobed. Dorsal median septum and septalium absent. Hinge plates supported on thick callus, divided. Crura long, sharply curved ventrally, triangular in cross section. *Lower Devonian (Lochkovian)*: Salair, Altai.—FIG. 740, 3*a–k*. **R. pseudogurjevskensis*, Tom'chumyshskie Beds, northeastern Salair Gurevsk; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; *e–g*,

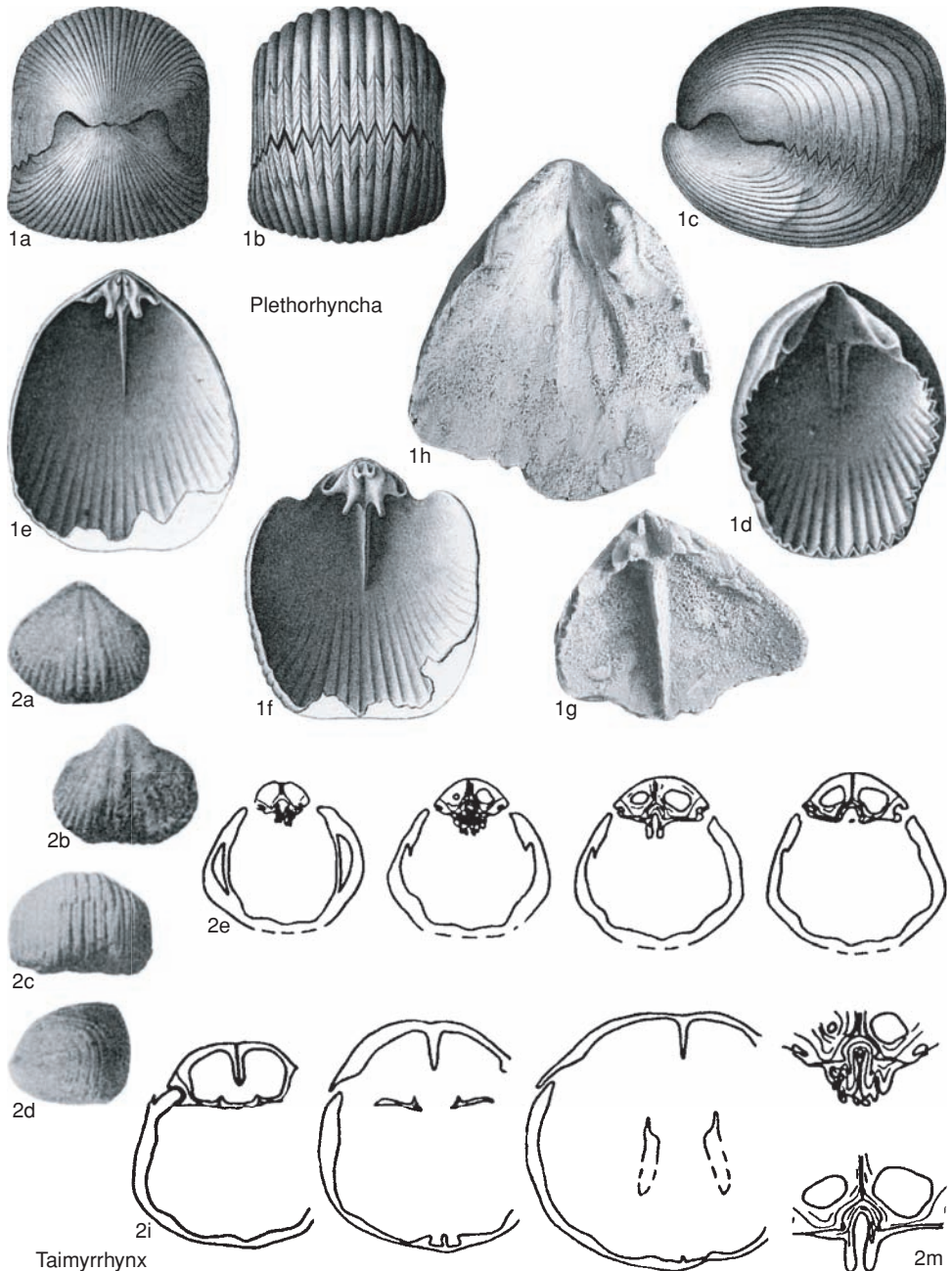


FIG. 742. Uncinulidae (p. 1095–1098).

serial sections 0.3, 0.5, 0.7 mm from posterior; *h–k*, serial sections 0.6, 0.8, 1.0, 1.2 mm from posterior of different specimen, approximately $\times 6$ (Gratsianova, 1970).

Taimyrrhynx HAVLIČEK, 1983, p. 154 [**Uncinulus irbitensis taimyricus* NIKIFOROVA, 1960b, p. 365;

OD]. Subpentagonal outline; strongly biconvex to globular profile. Beak erect to incurved; foramen small, with minute conjunct deltidial plates. Fold and sulcus weak; tongue rectangular. Costae from beaks, some bifurcation and intercalation, flattened and grooved on *paries geniculatus*; marginal spines

present. Dental plates short, close to valve walls; ventral muscle field divided by thin septum. Septalium small, filled posteriorly with large cardinal process that is multilobed posteriorly but high and bilobed anteriorly; septalium with cover anteriorly; dorsal median septum low, long. *Lower Devonian (upper Emsian)—Middle Devonian (lower Eifelian)*: Urals, Bohemia.—FIG. 742,2a–m. **T. taimyricus taimyricus* (NIKIFOROVA), upper Emsian, central Taimyr; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–k, serial sections, $\times 5$; l–m, enlargements of cardinal process sections in *f* and *g*, $\times 10$ (Tcherkesova, 1968).

Family EATONIIDAE Schmidt, 1965

[Eatoniiidae SCHMIDT, 1965b, p. 570]

Ucinuloidea with subcircular to elongate outline; costae usually extending from beaks, often with superimposed striae; dorsal fold and ventral sulcus strong but narrow; lateral margins of valves generally meet at acute angle, never truncated; foramen with conjunct deltidial plates anteriorly; anterior and lateral valve margins commonly with stubby spines that project into notches in opposite valve. Dental plates absent or infilled with callus; ventral muscle field large with strong border and distinct myophragm; large diductor scars enclose small adductor scars, also with strong border and myophragm. Dorsal median septum usually weak or absent; cardinal process very large, linguiform, bilobed to quadrilobed; hinge plates usually united by cardinal process; crural bases stout; crura short, laterally compressed. *lower Silurian (Llandovery)—Lower Devonian (upper Pragian)*.

Eatonia HALL, 1857a, p. 90 [**Atrypa medialis* VANUXEM, 1842, p. 120; SD HALL & CLARKE, 1893, p. 205] [= *Pareatonia* MCLERNAN, 1918, p. 137, obj.]. Large with subcircular to transversely ovate outline and dorsibiconvex profile; lateral margins not steep. Beak erect to incurved; foramen small, deltidial plates large, conjunct. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, serrate. Costae strong, simple, extending from beak; fine radial striae superimposed on costae; at anterior and lateral valve margins stubby spines project into notches in opposite valves. Dental plates cemented to valve walls; ventral muscle field deeply impressed, bounded by marked border; diductor muscle field bilobed, large, ovate, divided by

myophragm; adductor field small, enclosed by diductors, also divided by distinct myophragm, covered posteriorly. Cardinal process large, very high, trilobed, merging with and dominating hinge plates; sockets deep, short; low median septum extending two-thirds valve length; adductor muscle field large, ovate, divided by myophragm; crural bases stout, rounded, arising from beneath cardinal process; crura fairly straight with tips laterally compressed. *Lower Devonian (Lochkovian)*: North America, Australia, China.—FIG. 743,1a–g. **E. medialis* (VANUXEM), upper Helderbergian, upper Helderberg Group, Maryland, USA; a–e, hypotype, dorsal, ventral, posterior, anterior, and lateral views, Iron Mountain, Cumberland, $\times 1$; *f*, interior of ventral valve, Licking Creek, Indian Springs, $\times 1.5$; *g*, latex impression of dorsal valve, Licking Creek, Indian Springs, $\times 1.2$ (new).

Aratanea SCHMIDT, 1967, p. 92 [**A. monodi*; OD]. Elongate oval outline and equibiconvex profile. Beak erect to incurved. Fold and sulcus distinct but low; anterior commissure uniplicate; tongue low, wide, serrate. Costae medium to coarse, variable, some bifurcation, rounded, arising at beaks. Dental plates short, thick, ventrally divergent, usually cemented to valve walls or obscured by callus; ventral muscle field weakly impressed. Cardinal process small to lacking; median myophragm extending to about midlength; adductor field large, elongate, quadripartite; hinge plates united, comprising stout crural bases directed anteriorly and thick inner socket ridges directed anterolaterally. *middle Silurian (Wenlock)—upper Silurian (Ludlow)*: Mauritania.—FIG. 743,2a–b. **A. monodi*, Grès à Brachiopodes, Majābat al-Koubrā; a–e, holotype, dorsal, ventral, anterior, lateral, and posterior views of internal mold, $\times 1.3$; *f*, paratype, interior of latex cast showing dental plates and cardinalia; *g*, paratype, interior of latex cast of dorsal valve mold showing cardinalia; *h*, paratype, interior of latex cast of dorsal valve mold showing cardinalia and muscle field, $\times 2$ (Schmidt, 1967).

Boucotella BOWEN, 1966, p. 186 [**Camarotoechia gigantea* MAYNARD, 1913, p. 354; OD]. Large with subcircular to subtriangular outline and dorsibiconvex profile. Beak erect to incurved; small permesothryid to mesothryid foramen; deltidial plates conjunct. Fold and sulcus strong anteriorly, narrow; tongue high, tapering dorsally. Costae medium size, rounded. Dental plates short, close to valve walls or obscured by callus; ventral muscle field deeply impressed, cardiform with medial myophragm. Cardinal process very large, bilobed, high, tongue-like, excavated ventrally and anteriorly, extending almost to ventral valve floor and filling space between dental plates. *upper Silurian (Přídolí)*: eastern USA.—FIG. 744,2a–j. **B. gigantea* (MAYNARD), upper Přídolí, middle Keyser Limestone, Virginia; a–e, hypotype, dorsal (beak broken, not perforate), ventral, posterior, anterior,

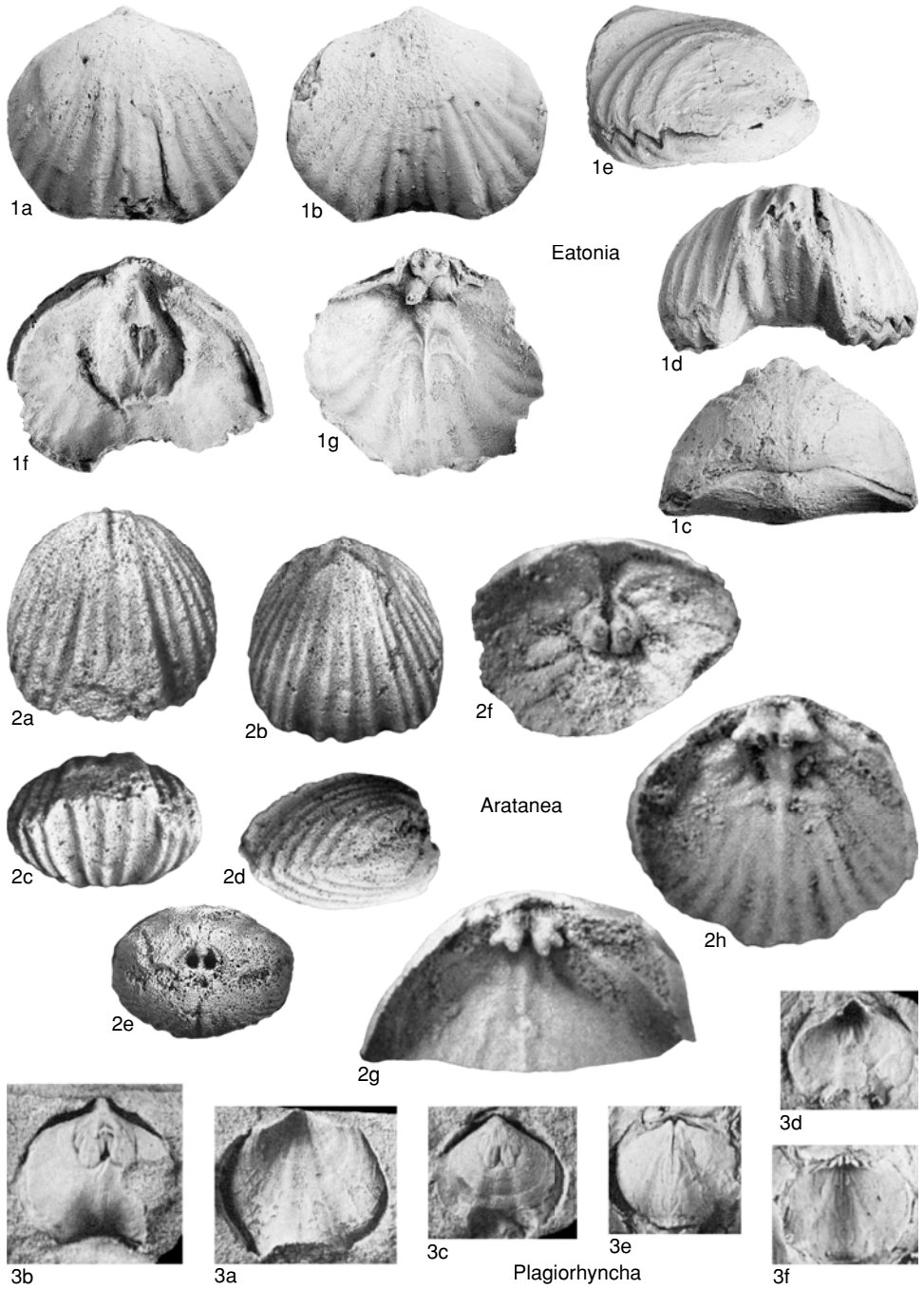


FIG. 743. Eatoniidae (p. 1098–1104).

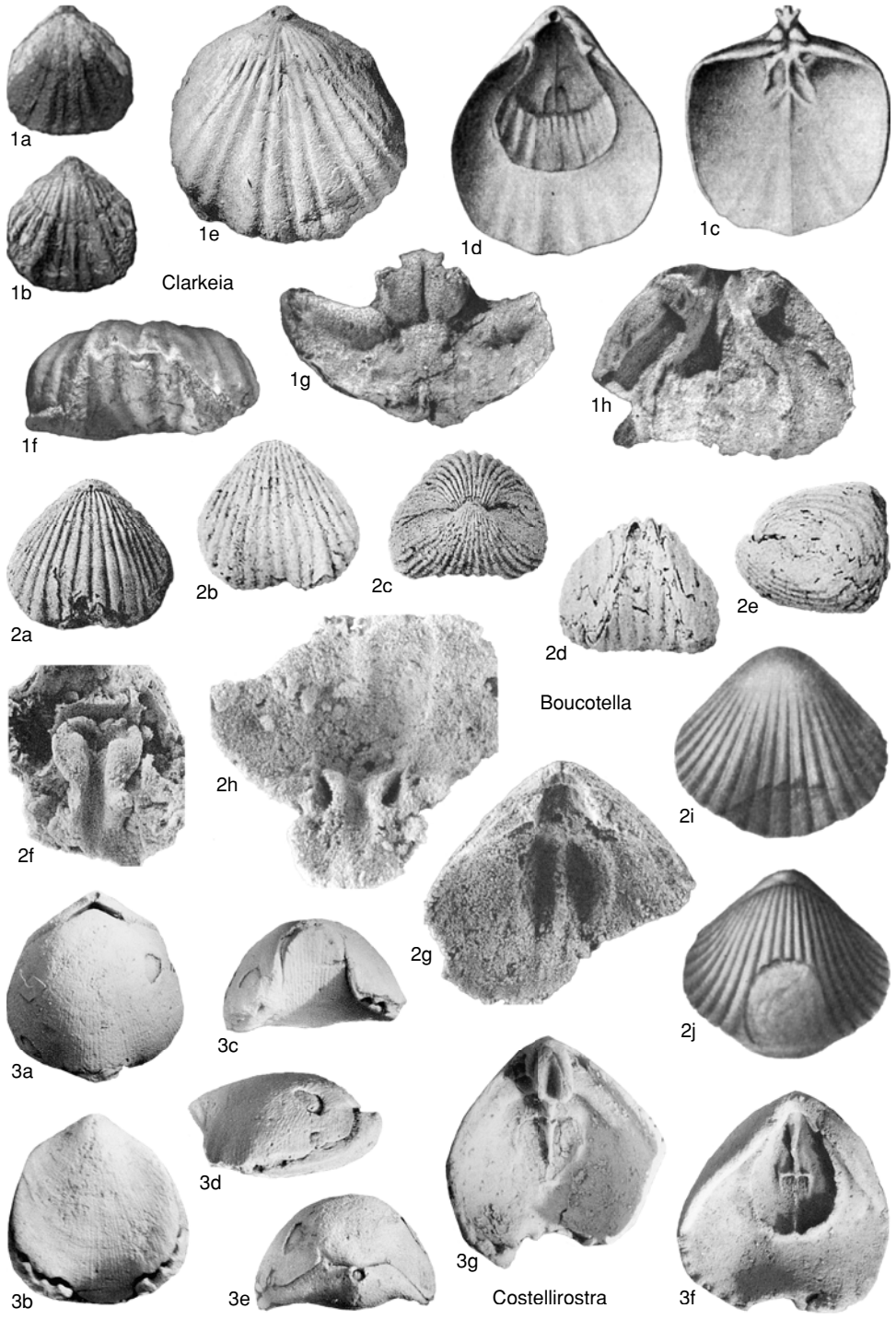


FIG. 744. Eatoniidae (p. 1098–1101).

- and lateral views, Warm Springs, $\times 1$; *f*, cardinal process of dorsal valve articulated with broken ventral valve showing dental plates, Lantz Mountain; *g*, hypotype, interior of broken ventral valve, Lantz Mountain; *h*, interior of broken conjoined valves, Lantz Mountain, $\times 2$ (Bowen, 1966); *i-j*, holotype, dorsal and ventral views, Devil's Backbone, $\times 1$ (Maynard, 1913).
- Clarkeia** KOZŁOWSKI, 1923, p. 86 [**Terebratula antisienensis* D'ORBIGNY, 1847 in 1847–1849, p. 36; OD]. Subcircular outline and moderately biconvex profile. Beak erect to incurved; foramen small, dorsal beak filling remainder of delthyrium. Fold and sulcus distinct, low, arising at umbones; anterior commissure uniplicate, wide, trapezoid to rounded, serrate. Costae coarse, variable in width, rounded, arising at beaks. Dental plates short, thick, ventrally divergent, usually evident but may be obscured by callus; ventral muscle area well impressed, bisected by low myophragm; diductor scars ovate to flabellate, large; adductor scars surrounded by diductor scars. Cardinal process large, tongue-like, bilobed, trilobed, or tetralobed; median myophragm extending to about midlength; adductor field large, elongate, quadripartite with oblique ridges between posterior and anterior adductors; crural bases stout, merging with cardinal process dorsolaterally, crura short, tapering, ventrally curved. *lower Silurian (Llandovery)–upper Silurian (Pridoli)*: South America, western Africa, Europe.—FIG. 744, 1a–h. **C. antisienensis* (D'ORBIGNY), Wenlock, South America; *a–b*, hypotype, dorsal and ventral views, Bolivia, $\times 1$; *c–d*, dorsal and ventral valve interior, Bolivia, $\times 2$ (Kozłowski, 1923); *e–f*, dorsal and anterior views, San Juan Province, Argentina, $\times 2$; *g*, latex cast of dorsal valve internal mold showing cardinal process and crural bases, San Juan Province, Argentina, $\times 3$; *h*, latex cast of ventral valve internal mold showing dental plates and muscle field, San Juan Province, Argentina, $\times 3$ (Cocks, 1972).
- Costellirostra** COOPER, 1942, p. 231 [**Atrypa peculiaris* CONRAD, 1841, p. 56; OD]. Elongate oval to subtriangular outline and dorsibiconvex profile; lateral margins sloping. Beak erect to incurved, rounded foramen at apex, deltidial plates conjunct. Fold and sulcus weak, evident only anteriorly; anterior commissure uniplicate; tongue high, rounded. Costellae fine, numerous, bifurcating. Narrow, gutterlike groove extending around anterior and lateral valve margins from which stubby spines project into notches in opposite valve. Dental plates cemented to valve walls; ventral muscle field ovate, deeply impressed, with high border; diductor field bilobed, divided by myophragm; adductor field small, surrounded by diductors, divided by myophragm, partly covered posteriorly. Cardinal process very large and high with 2 large outer lobes and 2 small inner lobes; crura short, stout. *Lower Devonian (Pragian)*: North America, USA, Canada, Mexico.—FIG. 744, 3a–g. **C. peculiaris* (CONRAD), Oriskanian, Glenerie Limestone, Glenerie, New York, USA; *a–e*, paralectotype, dorsal, ventral, anterior, lateral, and posterior views; *f–g*, paralectotype, interior of ventral valve, interior of dorsal valve, $\times 1.5$ (new).
- Diabolirhynchia** DROT, 1964a, p. 111 [**D. hollardi*; OD]. Small to medium with elongate oval outline and biconvex profile. Beak suberect to erect; delthyrium with short rectangular deltidial plates. Sulcate fold and plicate sulcus; 2 large costae on fold, 1 large costa in sulcus, costae on flanks smaller and more numerous, arising near beaks. Dental plates long, vertical or slightly convergent ventrally. Hinge plates undivided; cardinal process very large, high, trilobed; septalium absent; dorsal median septum long, thick, low; crural bases triangular in section; crura long, ventrally curved, concave dorsomedially. *upper Silurian (Ludlow)*: Morocco, Mauritania.—FIG. 745, 1a–k. **D. hollardi*, Ludlow Series, Morocco; *a–c*, holotype, dorsal, lateral, and anterior views, $\times 1$; *d–k*, serial sections 0.2, 1.0, 1.2, 1.4, 1.7, 2.2, 2.5, 3.5 mm from posterior (Drot, 1964a).
- Eatonioides** MCLERN, 1918, p. 137 [**E. lamellornatus*; OD]. Large with subcircular to transversely ovate outline and dorsibiconvex profile; lateral margins not steep. Beak erect to incurved. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, serrate. Costae strong, simple, extending from beak, separated by angular interspaces; crossed by widely spaced, imbricated growth lamellae. Dental plates cemented to valve walls; teeth stout, rounded; ventral muscle field deeply impressed, circular to oval, bounded by marked border; diductor muscle field divided by myophragm; adductor field small, elongate, enclosed by diductors, also divided by myophragm. Cardinalia consist of hinge plates supported medially by septalium; cardinal process may be merged with hinge plates posteriorly; sockets deep, short; low median septum extending to one-third valve length; crural bases originating from anteromedian edge of hinge plates; adductor muscle field not impressed. *upper Silurian (Ludlow)*: eastern North America.—FIG. 746, 1a–i. **E. lamellornatus*, lower Ludlow, Arisaig Group, Moydart Formation, Lower Member, Nova Scotia, Arisaig, Canada; *a–b*, internal mold and latex impression of ventral valve; *c–d*, internal mold and latex impression of dorsal valve; *e–h*, holotype, dorsal, ventral, anterior, and lateral views; *i*, ventral valve external mold, $\times 1.2$ (Harper, 1973).
- Pegmarhynchia** COOPER, 1955, p. 58 [**P. zimmi*; OD]. Medium size with subcircular outline and dorsibiconvex profile. Beak erect to incurved; foramen triangular, deltidial plates absent. Fold and sulcus weak posteriorly, strong and narrow anteriorly; anterior commissure uniplicate; tongue high, narrow, rounded, typically biserrate. Costae simple, rounded, arising at beaks, covering entire shell. Dental plates absent, ventral muscle area large, flabellate, well impressed, commonly divided by low myophragm. Hinge plates united to form prominent bilobed cardinal plate that probably incorporated

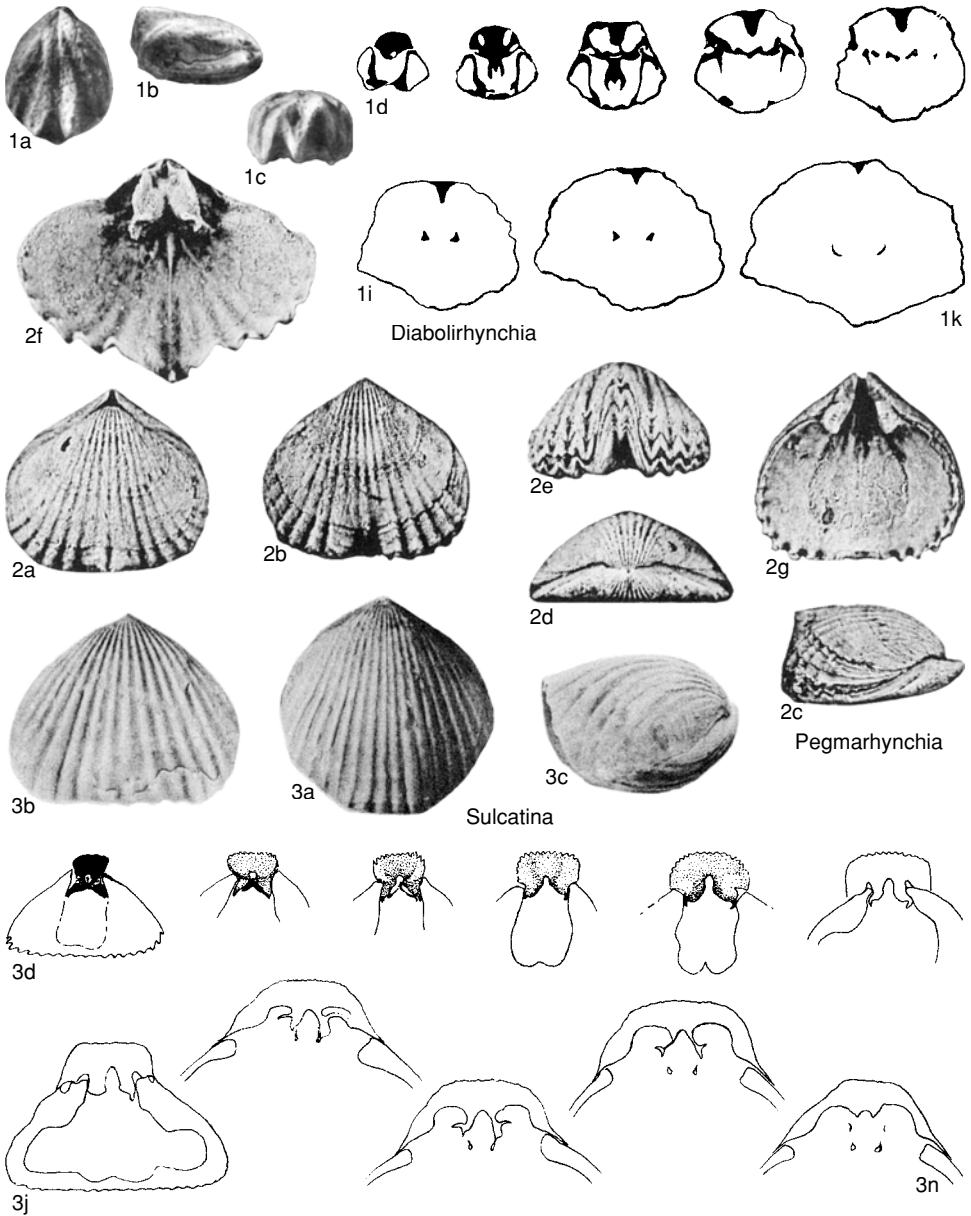


FIG. 745. Eatoniidae (p. 1101–1104).

cardinal process posteriorly; crescentic crural bases arising from cardinal plate anteriorly. *Lower Devonian (upper Pragian)*: USA (New York, Maryland).—FIG. 745, 2a–g. **P. zimmi*, Oriskanian, Glenerie Limestone, Glenerie, New York; a–d, holotype, dorsal, ventral, lateral, and posterior views;

e, paratype, anterior view; f, dorsal valve interior; g, paratype, ventral valve interior, $\times 2$ (Cooper, 1955). *Plagiorhynchia* MCLEARN, 1918, p. 138 [**Rhynchonella glassii* DAVIDSON, 1883, p. 155; OD; =*Atrypa depressa* J. DE C. SOWERBY, 1839, p. 629, subj.]. Small to medium with subcircular outline; lateral

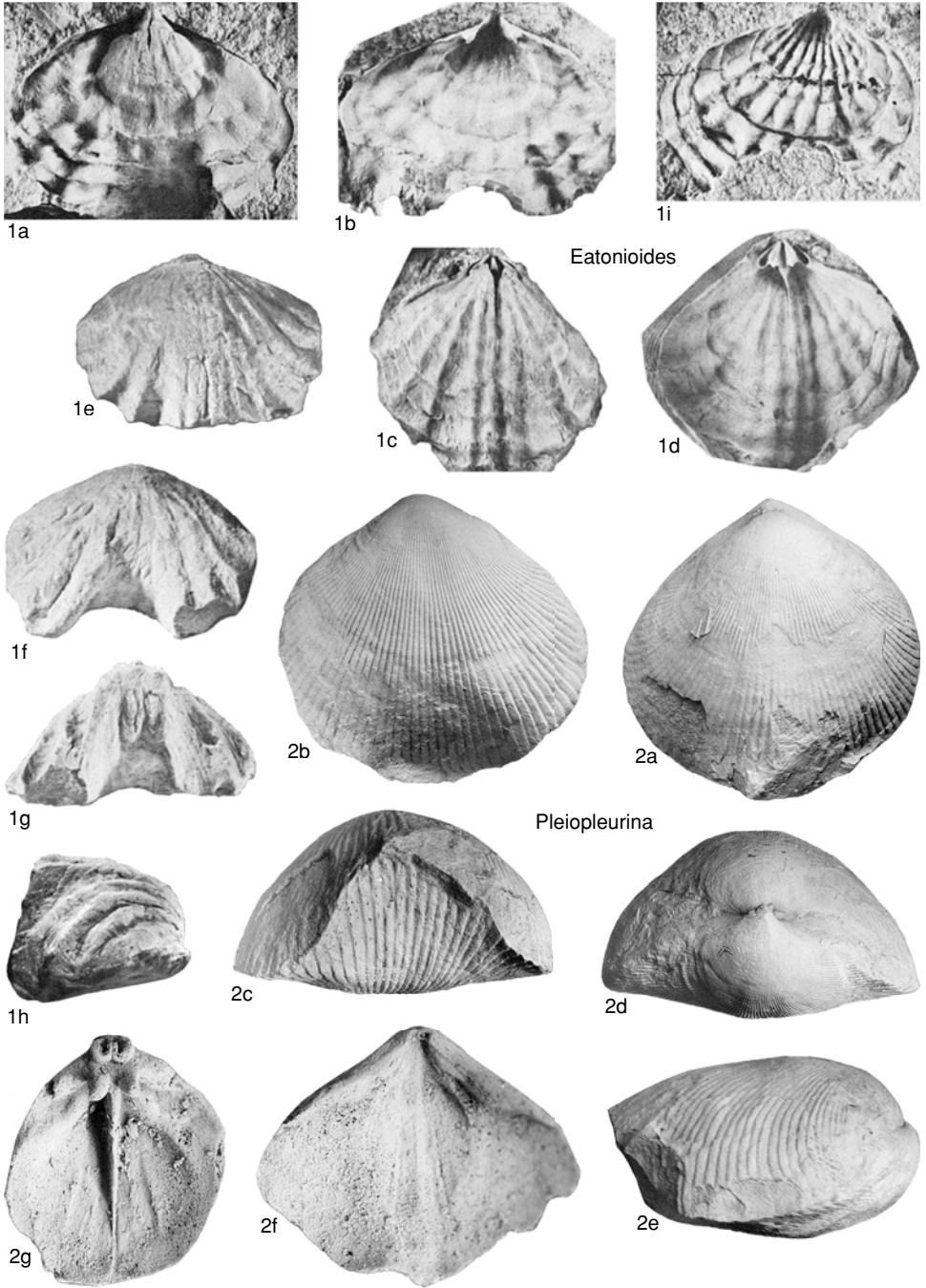


FIG. 746. Eatoniiidae (p. 1101–1104).

margins flat or recurved ventrally; posterior margin of some dorsal valves recurved to be concave dorsally. Delthyrium triangular; open. Fold and sulcus distinct, arising near umbones; anterior commissure uniplicate, undulate. Costae weak, broad, extending from umbones; fine costellae usually present. Dental plates cemented to valve walls; teeth small, rounded; ventral muscle field large, deeply impressed, scalloped outline, bounded by marked border; diductor muscle field divided by myophragm; adductor field small, elongate oval, enclosed by diductors. Hinge plates merge posteriorly with bilobed cardinal process; sockets distinct, bounded by socket ridges laterally; low median septum extending one-half valve length; adductor muscle field with small oval posterior adductors and larger elongate anterior adductors. *lower Silurian (Llandovery)*—*upper Silurian (Ludlow)*: Europe, eastern North America.—FIG. 743,3a–f. **P. glassii* (DAVIDSON), upper Llandovery, Ross Brook Formation, Middle Member, Nova Scotia, Pictou County, Arisaig, Canada; a–b, external and internal mold of ventral valve, $\times 2$; c–d, internal mold and latex impression of ventral valve; e–f, internal mold and latex impression of dorsal valve, $\times 1.5$ (Harper, 1973).

Pleiolepturina SCHMIDT, 1964, p. 506 [**Atrypa pleioleptura* CONRAD, 1841, p. 55; OD]. Very large with subcircular outline and dorsibiconvex profile; lateral margins not steep; ventral valve shallow. Beak small, incurved. Dorsal fold and ventral sulcus prominent anteriorly, arising at about midlength; anterior commissure uniplicate; tongue rounded to acuminate, dentate. Costae strong, angular, simple, straight, arising at beaks. Dental plates obscured by callus; ventral muscle field deeply impressed, ovate, divided by low ridge. Cardinal process very large, high, bilobed, with each lobe excavated; dorsal median septum long, thick, low; hinge plates thick, sessile; crural bases stout; dorsal adductor field large, well impressed, flabellate. *Lower Devonian (upper Pragian)*: USA, Canada.—FIG. 746,2a–g. **P. pleioleptura* (CONRAD); a–e, dorsal, ventral, anterior, posterior, and lateral views, Oriskanian, Gaspé Limestone, Cape Gaspé, Shiphead, Quebec, $\times 0.9$ (new); f, ventral valve interior, Oriskanian, Glenerie Limestone, Glenerie, New York, $\times 1.5$; g, dorsal valve interior, Oriskanian, Glenerie Limestone, Glenerie, New York, $\times 2$ (new).

Sulcatina SCHMIDT, 1964, p. 506 [**Trigonirhynchia sulcata* COOPER, 1942, p. 234; OD]. Large with subtriangular outline and dorsibiconvex profile; lateral margins not steep; ventral valve shallow. Beak small, incurved. Dorsal fold and ventral sulcus low, wide, arising at about midlength; anterior commissure uniplicate, rounded. Costae strong, simple, straight, arising at beaks. Dental plates obscured by callus; ventral muscle field deeply impressed, bilobed. Cardinal process very large, high, bilobed, ventrally and anteriorly excavated, extending anteriorly to merge with hinge plate and crural bases. *middle Silurian (Wenlock)*: North America.—FIG. 745,3a–n. **S. sulcata* (COOPER), upper Wenlock,

Waldron Shale, Waldron, Indiana, USA; a–c, holotype, dorsal, ventral, and lateral views, $\times 1$ (Cooper, 1944); d–n, serial sections 26.2, 26.1, 26.0, 25.7, 25.2, 24.8, 24.6, 23.6, 23.2, 22.9, 22.8 mm from posterior, $\times 1.7$ (Schmidt, 1965a).

Family HEBETOECIIIDAE Havlíček, 1960

[Hebetoeciidae HAVLÍČEK, 1960, p. 243]

Uncinuloidea that are strongly biconvex to globular with fold and sulcus weak; lateral and anterior margins vertical in mature specimens; tongue high; costae numerous, flattened and grooved on *paries geniculatus*; marginal spines developed; small foramen with disjunct to conjunct deltidial plates usually present; squamae and glottae frequently developed. Dental plates vertical to ventrally convergent. Dorsal median septum distinct; septalium deep, without cover plate, often infilled with callus; cardinal process usually absent or incipient in early genera, larger and commonly multilobed or longitudinally striated in later genera. *middle Silurian (Wenlock)*—*Middle Devonian (Givetian)*.

Subfamily HEBETOECIIINAE Havlíček, 1960

[*nom. transl.* SCHMIDT, 1965b, p. 566, *ex* Hebetoeciidae HAVLÍČEK, 1960, p. 243]

Hebetoeciidae with few, relatively coarse costae; umbones smooth; marginal spines short. Dental plates short; dorsal median septum distinct. Septalium present; low, calluslike cardinal process usually developed. *upper Silurian (Prídolí)*—*Lower Devonian (Emsian)*.

Hebetoecia HAVLÍČEK, 1959, p. 79 [**Terebratula hebe* BARRANDE, 1847, p. 86; OD]. Subcircular to subpentagonal outline; dorsibiconvex to subglobular. Beak erect to incurved; squamae and glottae absent; foramen small, deltidial plates conjunct. Fold and sulcus low, from umbones; high rectangular tongue, dentate. Costae arising on umbones, rounded, simple, flattened and grooved on *paries geniculatus*; marginal spines short. Dental plates converging slightly ventrally. Dorsal median septum short, low; calluslike cardinal process sometimes present in posterior part of septalium, may be bilobed anteriorly, but cardinal process absent in some species; crural bases subhorizontal. *upper*

- Silurian (Přídolí)—Lower Devonian (Lochkovian)*: Europe, northern Africa, Asia, North America, Australia.—FIG. 747, 1a–m. **H. hebe* (BARRANDE), upper Silurian, Přídolí Limestone, Dlouha Hora, Bohemia; *a–e*, holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 2.7$ (new); *f–i*, hypotype, serial sections 9.9, 9.7, 9.5, 9.4 mm from anterior, $\times 3$ (Havlíček, 1961); *j–m*, serial sections 10.35, 10.1, 9.95, 9.5 mm from anterior of different hypotype (Havlíček, 1983).
- Gerrhynx** BARANOV, 1991, p. 40 [**G. vesicus*; OD]. Small to medium size; subpentagonal outline; strongly biconvex. Fold and sulcus low, from umbones; tongue distinct, subrectangular. Costae medium to coarse, rounded, arising at midlength, leaving umbones smooth, bifurcating on fold to form 2 clusters; costae at anterior margin flat and grooved. Dental plates thin, ventrally convergent. Dorsal septum long; septalium short, filled with bilobed to quadrilobed cardinal process; hinge plates united anterior of septalium. *Lower Devonian (Pragian)*: eastern Siberia.—FIG. 748, 3a–m. **G. vesicus*, Pragian, Khobochalinskaya Formation, Tas-Khayakhtakh Range; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 3$; *e–m*, topotype, serial sections 0.3, 0.5, 0.7, 0.9, 1.2, 1.3, 1.4, 1.5, 1.6 mm from posterior, $\times 7$ (Baranov, 1991).
- Lanceomyonia** HAVLÍČEK, 1960, p. 243 [**Terebratula tarda* BARRANDE, 1847, p. 85; OD] [= *Cratorhynchonella* TONG, 1982, p. 333 (type, *C. biconvexa*, OD)]. Medium to large size; subcircular to subpentagonal outline. Beak incurved; foramen absent. Fold and sulcus developed anteriorly; umbones smooth; tongue strong, rectangular. Costae broad, low, longitudinally grooved at *paries geniculatus*; marginal spines present. Dental plates short, ventrally convergent; ventral muscle field well impressed. Dorsal median septum high, long; septalium open. *upper Silurian (Přídolí)—Lower Devonian (Lochkovian)*: Europe, northern Africa, Asia, North America, Australia.—FIG. 748, 1a–g. **L. tarda* (BARRANDE), Přídolí, Přídolí Limestone, Dvorce, Bohemia; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; *e–g*, hypotype, serial sections 20.7, 20.0, 19.8 mm from anterior, $\times 3$ (Havlíček, 1961).
- Lapradella** BARANOV, 1989, p. 49 [**L. definita*; OD]. Trigonal to subpentagonal outline; dorsibiconvex profile. Beak suberect to erect; foramen permesothyrid, deltidial plates conjunct. Fold and sulcus developed anteriorly; tongue high, rectangular; umbones smooth. Costae coarse, rounded, simple, flattened and grooved on *paries geniculatus*; short marginal spines present. Dental plates short, close to shell walls; ventral muscle field well impressed. Dorsal median septum thick, short; hinge plates united; septalium wide; cardinal process small; crural bases horizontal; crura closely set. *Lower Devonian (Lochkovian)*: eastern Siberia.—FIG. 748, 2a–o. **L. definita*, upper Lochkovian, base of Sagyrshaya Formation, Selennyakhskiy Kryazh, Serp Creek on right bank Sakyndzha River, eastern Siberia; *a–d*, holotype, dorsal, ventral, lateral, and anterior views, $\times 1$; *e–o*, serial sections of shell posterior and crura 0.5, 1.4, 1.8, 2.1, 2.3, 2.6, 2.8, 3.2, 3.3, 3.6, 5.2 mm from posterior, $\times 4$ (Baranov, 1989).
- Mongolorhynx** ERLANGER, 1992, p. 54 [**M. drosdovae*; OD]. Small to medium size; subpentagonal outline; strongly biconvex. Fold and sulcus low, developed anteriorly; tongue distinct, subrectangular to trap-ezoid. Costae medium, rounded, arising at mid-length leaving umbones smooth; costae at anterior margin grooved. Dental plates thin, ventrally convergent; dorsal septum low, short; septalium short, filled with multilobed cardinal process; hinge plates united anterior of septalium. *Lower Devonian (Emsian)*: western Mongolia.—FIG. 747, 2a–b. **M. drosdovae*, upper Emsian, Tsagankhalsginsk layer, northern shore of Lake Khara-Us-Nur; *a–e*, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 2$; *f–h*, paratypes, serial sections, $\times 15$ (Erlanger, 1994).
- Voskoptoechia** HAVLÍČEK, 1992, p. 105 [**V. orbona*; OD]. Small size; subpentagonal outline; biconvex. Fold and sulcus short, arising at midlength; tongue high; umbones smooth. Costae restricted to margins, flattened and grooved on *paries geniculatus*; marginal spines present. Dental plates short; ventral muscle field well impressed. Dorsal median septum thin; septalium short, wide, filled with large, calluslike, bilobed cardinal process; hinge plates undivided, horizontal; crural bases vertical, becoming horizontal anteriorly. *Lower Devonian (Pragian–Emsian)*: Bohemia.—FIG. 747, 3a–f. **V. orbona*, Pragian, Koneprusy Limestone, Na Voskope Hill; *a–b*, holotype, ventral, and anterior views, $\times 5$; *c–f*, serial sections 5.7, 5.55, 5.4, 5.25 mm from anterior, $\times 9.5$ (Havlíček, 1992).

Subfamily SPHAERIRHYNCHIIINAE Savage, 1996

[Sphaerirhynchiiinae SAVAGE, 1996, p. 253]

Globular Hebetoechiidae with weak fold, high tongue, and fine, distally grooved costae. Dental plates convergent ventrally. Dorsal median septum well developed; cardinal process absent or calluslike. *middle Silurian (Wenlock)—Lower Devonian (Lochkovian)*.

Sphaerirhynchia COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Wilsonella* NIKIFOROVA, 1937a, p. 35, *non* CARTER, 1885 [**Terebratula wilsoni* SOWERBY, 1816 in 1815–1818, p. 38; OD]. Medium to large size; globular. Beak suberect to incurved; foramen in younger specimens mesothyrid, circular, deltidial plates incipient; in older specimens foramen obscured by curvature of beak; squamae and glottae absent. Fold and sulcus very weak; tongue high, rectangular. Costae arising at beaks, fine, rarely splitting, grooved distally; marginal

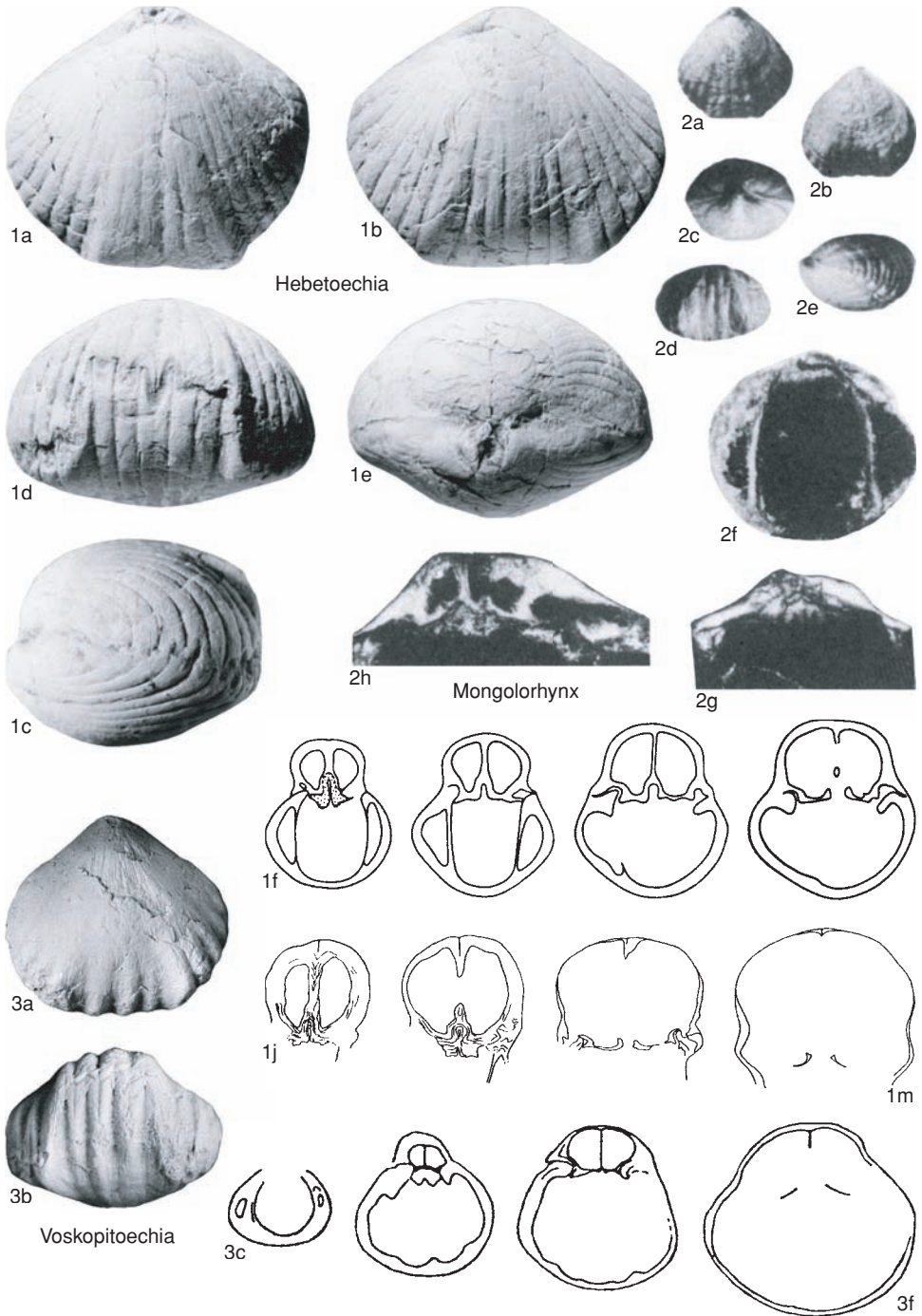


FIG. 747. Hebetoechiidae (p. 1104–1106).

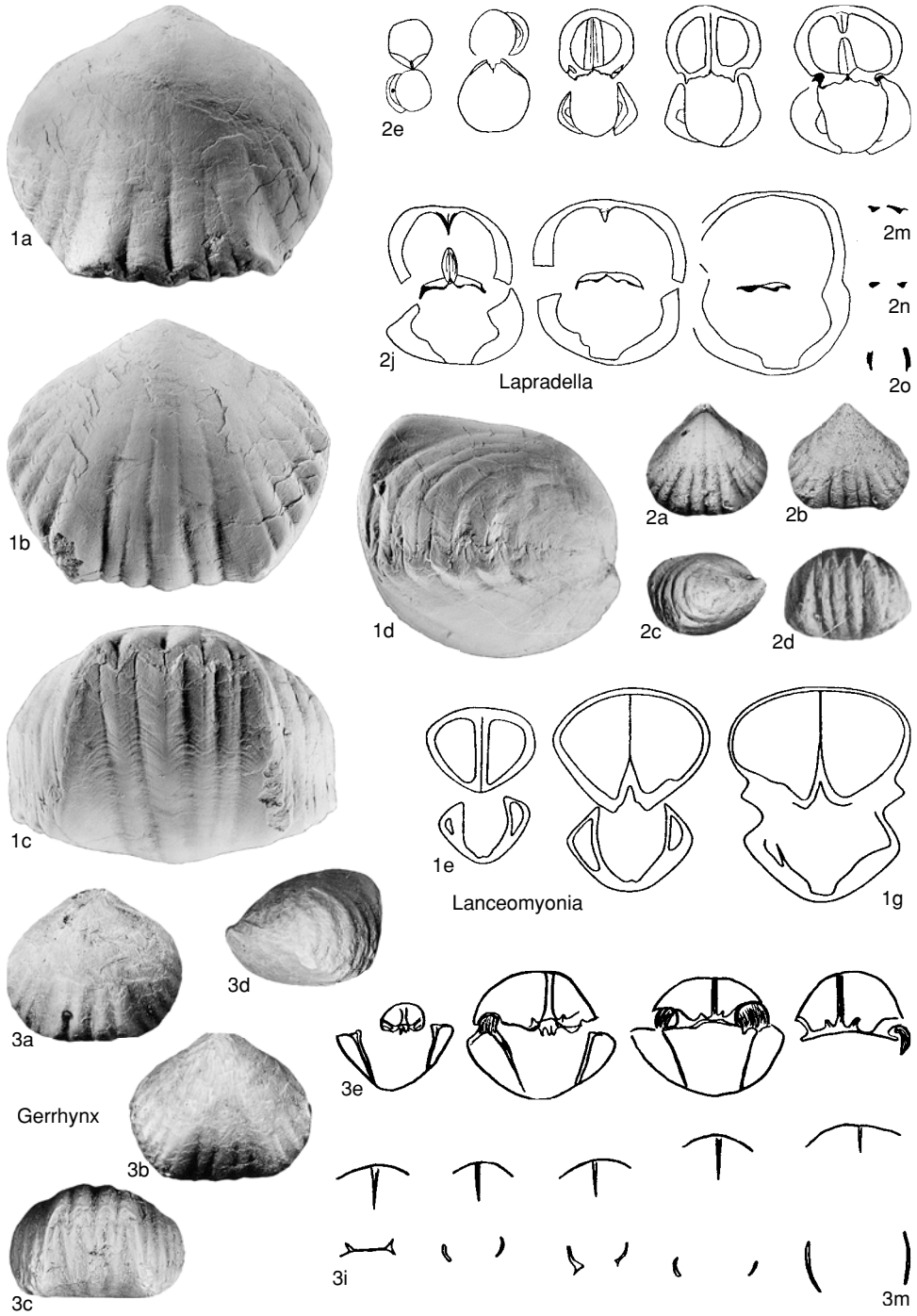


FIG. 748. Hebetoechiidae (p. 1105).

- spines present. Dental plates short, convergent ventrally; ventral muscle field deeply impressed. Dorsal median septum long; septalium short, lacking cover; cardinal process absent; crura long, thin. *middle Silurian* (Wenlock)–*Lower Devonian* (Lochkovian): Europe, Urals, Salair, Altai, China, Australia, North America.—FIG. 749,1a–n. **S. wilsoni* (SOWERBY), Wenlock Series, Shropshire, England; a–c, dorsal, lateral, anterior views, $\times 1$ (Davidson, 1869); d–m, serial sections 1.2, 1.4, 1.6, 1.8, 2.0, 2.4, 2.6, 2.8, 3.0, 3.9 mm from posterior, $\times 2.2$ (new); n, sketch of part of the *paries geniculatus* and marginal spines, based on serial sections, approximately $\times 2.5$ (Westbroek, 1968).
- Estonirhynchia** SCHMIDT, 1954, p. 236 [*Sphaerirhynchia* (E.) *estonica*; OD]. Globular; beak erect to incurved; foramen not observed. Fold and sulcus very weak; tongue high, rectangular. Umbones smooth; costae simple, lacking anterior grooves or spines; anterior commissure zigzag. Dental plates short, convergent ventrally; ventral muscle field weakly impressed. Dorsal median septum thick, long; septalium short, without cover plate; cardinal process absent; crura unknown. *middle Silurian* (Wenlock)–*upper Silurian* (Ludlow): Baltic.—FIG. 749,2a–f. **E. estonica* (SCHMIDT), upper Wenlock, Oesel Group, Oesel, Estonia; a–d, holotype, dorsal, ventral, lateral, and anterior views, $\times 3$; e–f, sections of posterior of different specimens, $\times 4$ (Schmidt, 1954).
- Notoconchidium** GILL, 1951, p. 187 [*N. thomasi* GILL, 1951, p. 188; OD; *N. thomasi* GILL, 1950, p. 243, *nom. nud.*, no description or illustration given] [= *Notoconchidium* GILL, 1950, p. 242, *nom. nud.*, no type species given]. Large size; elongate sub-trigonal outline; strongly inflated to globular. Fold and sulcus weak; tongue high, rectangular to trapezoid. Costae simple or with rare bifurcation, rounded, flattened and grooved on *paries geniculatus*; umbones smooth. Dental plates long, ventrally and anteriorly convergent; ventral muscle field long, narrow, deeply impressed. Dorsal median septum long; septalium distinct; cardinal process absent or poorly developed. *upper Silurian* (Pridoli): Australia, New Zealand.—FIG. 750a–e. **N. thomasi*, Mount Ida Formation, Victoria, Heathcote, Australia; a, holotype, ventral view of ventral valve internal mold, $\times 2$ (Wright & Garratt, 1991); b–c, plaster replica and rubber impression of dorsal internal mold, $\times 1.5$; d–e, plaster replica and rubber impression of ventral internal mold, $\times 1.5$ (Boucot, Johnson, & Staton, 1964).—FIG. 750f–h. *N. tasmaniensis* (ETHERIDGE), Florence Sandstone, Silver Bell, near Zeehan, Tasmania; lateral, anterior, and posterior views of internal mold of conjoined shell, $\times 1.5$ (Wright & Garratt, 1991).
- Tadschikia** NIKIFOROVA, 1937a, p. 35 [*Wilsonella* (T.) *wilsoniaformis*; OD]. Medium to large size; sub-circular outline; globular profile. Beak suberect to erect; foramen small, circular. Fold and sulcus weak; tongue high. Costae medium, simple, flattened and grooved on *paries geniculatus*. Dental plates long, convergent ventrally. Dorsal median septum long; septalium with low, calluslike cardinal process posteriorly and with cover plate anteriorly. *middle Silurian* (Wenlock): Turkestan, China.—FIG. 749,3a–g. **T. wilsoniaformis* (NIKIFOROVA), Turkestan; a–d, dorsal, ventral, lateral, and anterior views, $\times 1$; e, serial section at articulation area, $\times 2$ (Nikiforova, 1937a); f–g, sections through septalium, $\times 2$ (Havlíček, 1961).

Subfamily AMSDENELLINAE new subfamily

[Amsdenellinae SAVAGE, herein]

Hebetoeciidae with rounded lateral margins; numerous fine costae arising at beaks; marginal spines short. Dental plates lacking; ventral muscle field deeply impressed. Hinge plates sessile; cardinal process large, bilobed. *Lower Devonian* (Lochkovian).

Amsdenella TILLMAN, 1967, p. 1251 [*Rhynchonella abrupta* HALL, 1857a, p. 68; OD]. Medium to large with subcircular to subpentagonal outline and dorsibiconvex profile with rounded lateral margins. Beak erect to incurved; foramen mesothyrid. Fold and sulcus prominent but with gentle margins; tongue high, often rounded. Costae numerous, simple, rounded, arising at beaks; costae flattened and grooved on *paries geniculatus* of mature specimens, and taper uniformly into points. Dental plates lacking; ventral muscle field ovate, deeply impressed, with large, flabellate diductor field enclosing small adductor field; adductor field divided by low median septum and partly covered by a thin ridge posteriorly. Cardinal process large, high, bilobed, with each lobe excavated; dorsal median septum long, low; hinge plates sessile; crural bases stout, rounded, arising from beneath cardinal process; dorsal muscle scars weakly defined. *Lower Devonian* (Lochkovian): eastern USA.—FIG. 751a–g. **A. abrupta* (HALL), Helderbergian, New Scotland Formation, West Virginia; a–c, hypotype, dorsal, lateral, and anterior views, near Franklin, $\times 2$; d, ventral view of ventral valve, near Mustoe; e, lateral view of dorsal valve, near Mustoe, $\times 1.8$; f, ventral valve interior, near Mustoe, $\times 2$; g, dorsal view of cardinal process, Bullpasture Mountain, $\times 4$ (Tillman, 1967).

Subfamily GLOSSINULININAE Savage, 1996

[Glossinulininae SAVAGE, 1996, p. 253]

Transversely subpentagonal Hebetoeciidae with sharply delineated fold and sulcus, rectangular tongue, fine costae that are flattened and grooved on *paries geniculatus*, and well-developed marginal spines. Dental

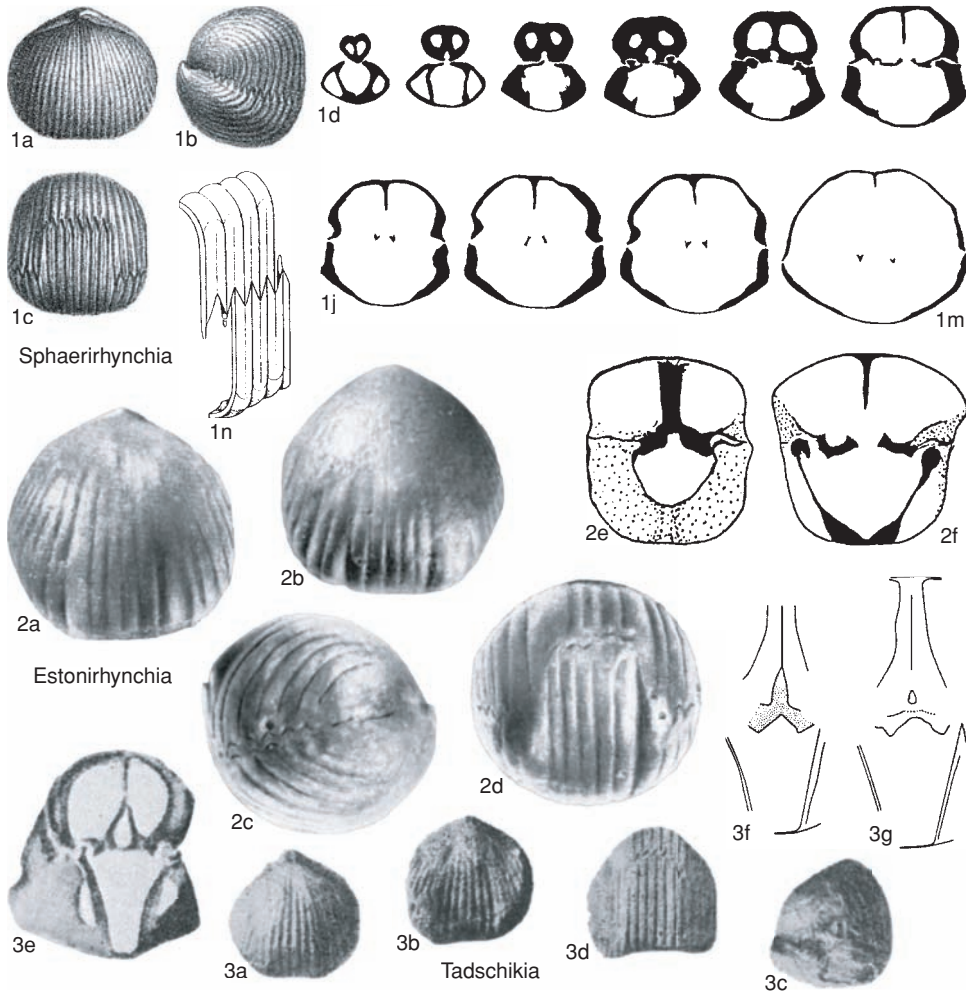


FIG. 749. Hebetoechiidae (p. 1105–1108).

plates short or obscured by callus. Septalium reduced; cardinal process small to absent. *Lower Devonian (Pragian–Emsian).*

Glossinulina JOHNSON, 1975, p. 958 [**G. khodalevichi*; OD]. Transversely subpentagonal outline; dorsal valve strongly convex, ventral weakly convex. Beak erect to incurved; foramen unknown. Fold and sulcus wide, strong, well delineated; median groove on fold, median ridge in sulcus; tongue high, rectangular. Umbones smooth; costae medium, simple, flattened and grooved on *paries geniculatus*; commissure with spines. Dental plates short, ventrally convergent. Dorsal median septum high, thin, long; septalium short, shallow; cardinal process small, with ridges. *Lower Devonian (Emsian)*: Arctic

Canada.—FIG. 752, 1a–n. **G. khodalevichi*, Disappointment Bay Formation, Lowther Island; a–e, holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 2$; f–n, serial sections 8.0, 7.8, 7.7, 7.6, 7.5, 7.4, 7.3, 7.2, 7.1 mm from anterior, $\times 4$ (Johnson, 1975).

Glossulinirhynchia BARANOV, 1991, p. 41 [**G. venusta*; OD]. Small to medium size; thick shell; subpentagonal outline; strongly biconvex; beak suberect. Fold and sulcus wide, strong; tongue high, rectangular. Costae rounded in section but on *paries geniculatus* flattened and grooved; umbones smooth; costae on fold gathered into 2 clusters with gentle sinus between, those in sulcus raised along medial part. Dental plates absent or umbonal cavities infilled; ventral muscle field deeply impressed. Dorsal median septum short, low; septalium

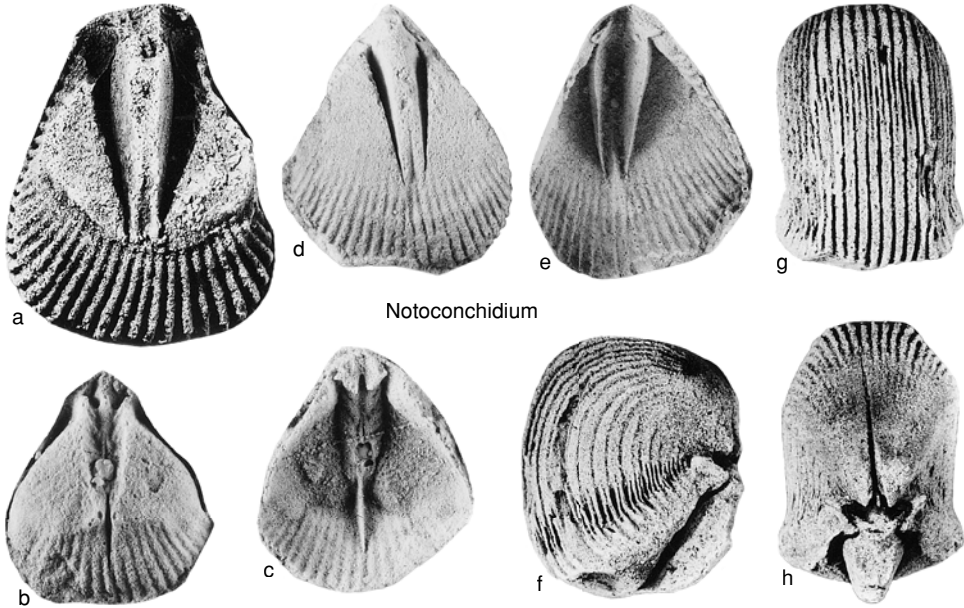


FIG. 750. Hebetoechiidae (p. 1108).

reduced; hinge plates anterior of septalium divided, horizontal; cardinal process short, with ridges; crura long, closely set. *Lower Devonian (Pragian)*: eastern Siberia.—FIG. 752,2a–l. **G. venusta*, Nelichen-skaya Formation, Selennyakhskiy Kryazh; a–d, holotype, dorsal, ventral, lateral, and anterior views, $\times 1$; e–l, successive serial sections through posterior, intervals not given, $\times 3$ (Baranov, 1991).

Nordotoechia TCHERKESOVA, 1965, p. 80 [**N. tumida*; OD]. Large with transversely oval outline; biconvex profile, dorsal valve inflated; lateral and anterior margins vertical; beak incurved. Fold and sulcus distinct; tongue high, rectangular. Costae dichotomizing, flattened and grooved on *paries geniculatus*; arising at beaks; marginal spines present. Dental plates thin, short; ventral muscle area deeply impressed. Septalium and dorsal median septum very short; cardinal process absent; crura arising from edges of septalium, long, closely set. *Lower Devonian (Emsian)*: Novaya Zemlya.—FIG. 753,2a–q. **N. tumida*, Val'nevsk layer, mouth of Sakhanin River; a–d, holotype, ventral, lateral, anterior, and posterior, $\times 1$; e, enlargement of left anterior margin, $\times 5$; f–k, serial sections 1.1, 1.55, 1.85, 2.1, 2.15, 2.35 mm from posterior, $\times 1.4$; l–q, serial sections 2.6, 2.8, 2.96, 3.05, 3.2, 3.35 mm from posterior of different specimen, $\times 1.4$ (Tcherkesova, 1965).

Pseudoglossinotoechia TCHERKESOVA, 1967, p. 9 [**P. atalanta*; OD] [= *Tainotoechia* TCHERKESOVA, 1967, p. 5 (type, *Sphaerirhynchia* (?) *subarmoricana* NIKIFOROVA, 1960a, p. 347, OD)]. Medium to large

size; subpentagonal outline; strongly inflated, almost cuboidal. Beak incurved; delthyrium with small slitlike foramen almost closed by deltidial plates. Fold and sulcus low but distinct, with median groove on fold; tongue prominent, rectangular. Costae fine, bifurcating, arising at beaks, flattened and grooved anteriorly where internal marginal spines developed. Dental plates close to shell walls; ventral muscle field deeply impressed and divided anteriorly by low median ridge. Dorsal median septum long, low; septalium short, open or filled by cardinal-process-like callus in gerontic specimens; crura closely set. *Lower Devonian (Emsian)*: Novaya Zemlya, Urals.—FIG. 753,1a–q. **P. atalanta*, Val'nevsk horizon, South Island, Novaya Zemlya; a–e, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 1$; f, hypotype, enlargement of commissure and spine traces, $\times 2$; g–q, serial sections 1.45, 2.65, 2.8, 2.9, 3.0, 3.2, 3.5, 3.95, 4.05, 4.3, 5.75 mm from posterior, approximately $\times 1.5$ (Tcherkesova, 1967).

Subfamily BETTERBERGIINAE Savage, 1996

[Betterbergiinae SAVAGE, 1996, p. 253]

Thick-shelled, rounded Hebetoechiidae with low fold, fine costae that are flattened and grooved anteriorly, and long marginal spines. Dental plates short or obscured by

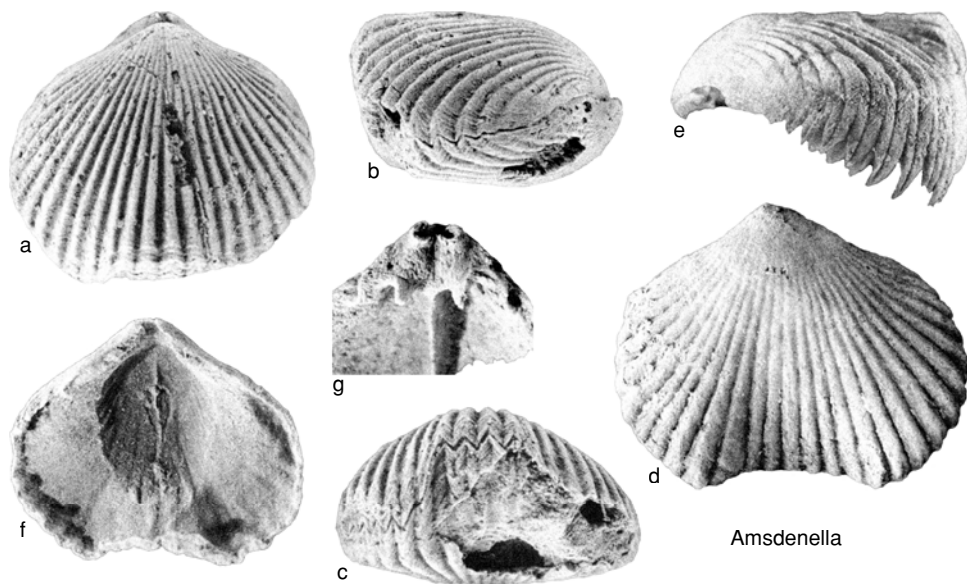


FIG. 751. Hebetoechiidae (p. 1108).

callus. Dorsal median septum and septalium short; cardinal process commonly present. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*.

Betterbergia SCHMIDT, 1981, p. 218 [**Camarotoechia betterbergiana* SCHMIDT, 1950, p. 79; OD]. Medium to large size with subtriangular outline and biconvex profile; lateral and anterior margins steep. Beak incurved; foramen small. Fold and sulcus moderate, extending from midlength; anterior commissure uniplicate; tongue broad, low. Costae fine, simple, numerous, from umbones, flattened and grooved on *paries geniculatus*; marginal spines present. Dental plates short, subvertical, commonly buried in callus; ventral muscle field well impressed. Dorsal median septum and septalium short; hinge plates divided anteriorly; cardinal process absent; crura with V-shaped cross section, open dorsomedially. *Middle Devonian (Eifelian)*: Germany.—FIG. 754, 1a–k. **B. betterbergiana* (SCHMIDT), middle Eifelian, Ahrdorf Formation, Flesten Member, Hillesheimer Mulde, Dollendorf, Eifel; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–k, serial sections, $\times 3$ (Schmidt, 1981).

Kransia WESTBROEK, 1968, p. 81 [**Terebratula parallelepipedata* BRONN, 1837, p. 71; OD]. Subpentagonal outline; strongly biconvex profile. Beak erect; well-developed mesothryd foramen with small, conjunct deltidial plates; squamae and glottae present. Fold and sulcus weak; high, rounded tongue. Costae simple, arising on um-

bones, flattened anteriorly and grooved to accommodate long marginal spines. Dental plates short, subparallel, close to valve walls; ventral muscle scars deeply impressed in thick shell. Dorsal median septum low, long; septalium short; cardinal process bearing several longitudinal ridges; hinge plates united anterior of septalium. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Europe, northern Africa, Urals, Afghanistan, China.—FIG. 754, 2a–m. **K. parallelepipedata* (BRONN), Givetian; a, hypotype, dorsal view, $\times 3$; b, hypotype, anterior view; c, lateral view of another hypotype, $\times 3$; d–k, hypotype, serial sections 0.4, 0.5, 0.6, 0.7, 0.9, 1.2, 1.4, 1.7 mm from posterior, upper Givetian, northwestern France, $\times 4$ (Brice & Morzadec, 1983); l, reconstruction of apical interior, based on serial sections; m, reconstruction of marginal spines, based on serial sections (Westbroek, 1968).

Nalivkinaria RZHONSNIITSKAIA, 1968c, p. 117 [**N. lacunata*; OD]. Subpentagonal outline; hinge line wide; profile strongly dorsibiconvex. Beak small, incurved; mesothryd foramen, disjunct deltidial plates. Fold and sulcus strong, arising near umbones; tongue high, rectangular. Costae numerous, rounded, rarely dividing, arising at beak, flattened anteriorly and grooved. Dental plates very short, close to valve walls or obscured by callus, converging ventrally; teeth small; ventral muscle scars deeply impressed in thick shell. Dorsal median septum high, thick, long; septalium short; cardinal process massive, typically with 2, high lateral lobes; hinge plates divided. *Middle Devonian (Eifelian–Givetian)*: Kuznets, Spain.—FIG. 755, 2a–j. **N.*

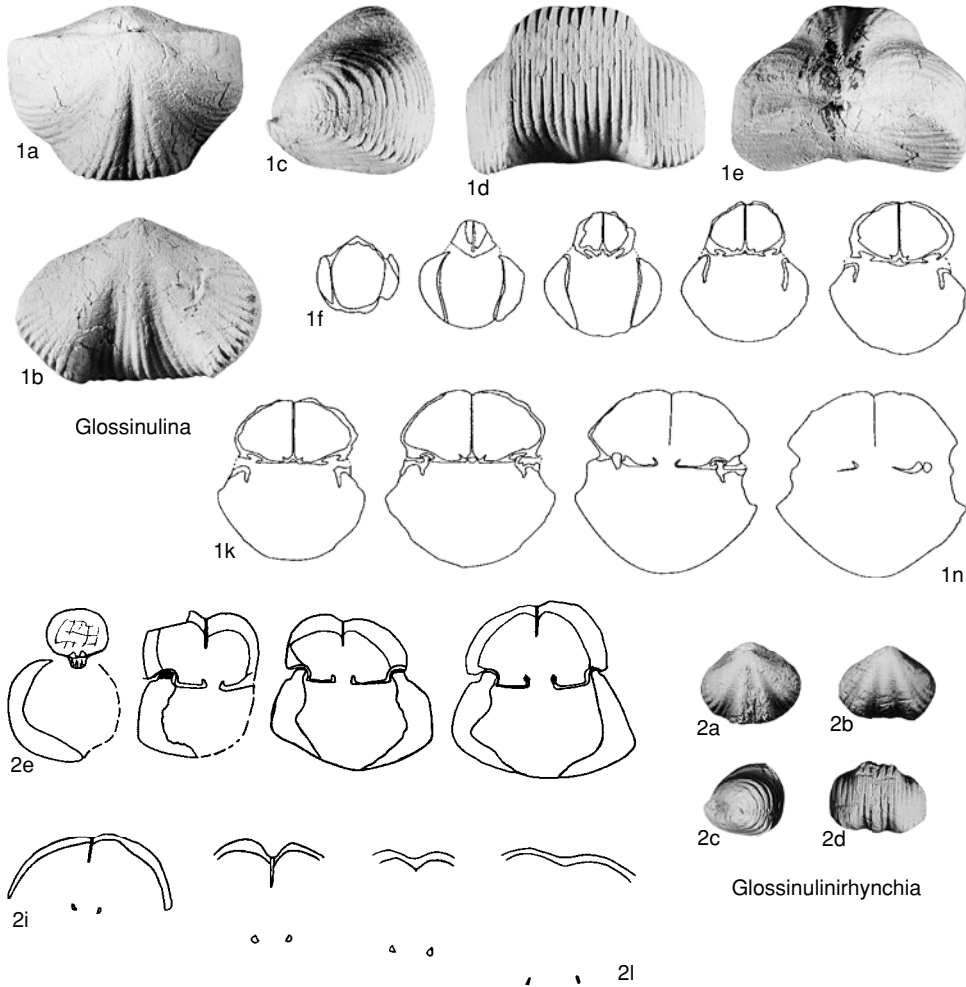


FIG. 752. Hebetoechiidae (p. 1109–1110).

lacunata, Eifelian, Kuznets basin; *a–d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; *e–j*, transverse serial sections across shell posterior, approximately $\times 2.5$ (Rzhonsnitskaia, 1968c).

Primipilaria STRUVE, 1992, p. 549 [**Terebratula primipilaris* VON BUCH, 1834, p. 88; OD]. Medium to large size; subcircular outline; biconvex profile, inflated anteriorly. Beak erect; mesothyrid foramen with conjunct deltidial plates. Fold and sulcus medium size; anterior commissure with high, rounded tongue; articulation with squamae and glottae well developed. Costae fine, arising at beaks, multiplying, flattened anteriorly and grooved; long marginal spines; commissure without zigzag deflections. Dental plates short, subparallel, close to valve walls;

ventral muscle scars deeply impressed in thick shell, separated by median myophragm. Dorsal median septum thick, low, extending to valve midlength; septalium short, filled by cardinal process bearing longitudinal ridges; hinge plates united anterior of septalium. *Middle Devonian (Eifelian–Givetian)*: Europe.—FIG. 755, *1a–g*. **P. primipilaris* (VON BUCH), Givetian, Skaly Beds, Holy Cross Mountains, Poland; *a*, hypotype, dorsal view, $\times 2.7$; *b*, hypotype, lateral view, $\times 2.1$; *c*, anterior view of another hypotype; *d*, ventral view of another hypotype; *e*, dorsal interior; *f*, ventral interior, $\times 2.5$ (Biernat, 1966); *g*, reconstruction of *paries geniculatus* and marginal spines, based on serial sections, approximately $\times 2.5$ (Westbroek, 1968).

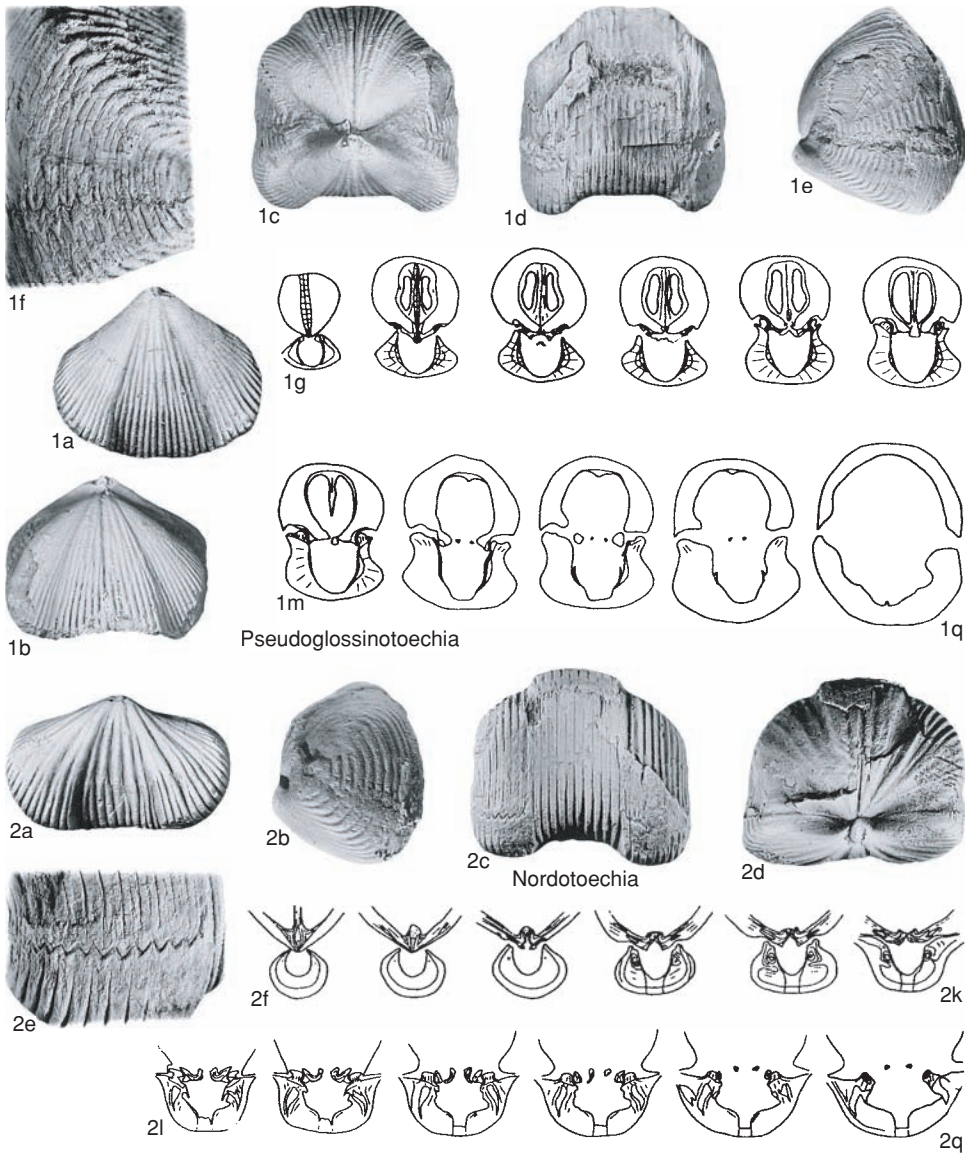


FIG. 753. Hebetoechiidae (p. 1110).

Subfamily BECKMANNIINAE
Savage, 1996

[Beckmanniinae SAVAGE, 1996, p. 253]

Subcircular Hebetoechiidae with broad fold, smooth umbones, rounded exterior features; marginal spines weakly developed. Dental plates short. Dorsal median septum

may be prominent; calluslike cardinal process generally present. *Middle Devonian* (*Givetian*).

Beckmannia MOHANTI, 1972, p. 166 [**Uncinulus minor beckmanni* SCHMIDT, 1951, p. 89; OD]. Shell small; subcircular to subpentagonal outline; lenticular biconvex profile; flanks generally rounded, not truncated. Beak erect to incurved; foramen

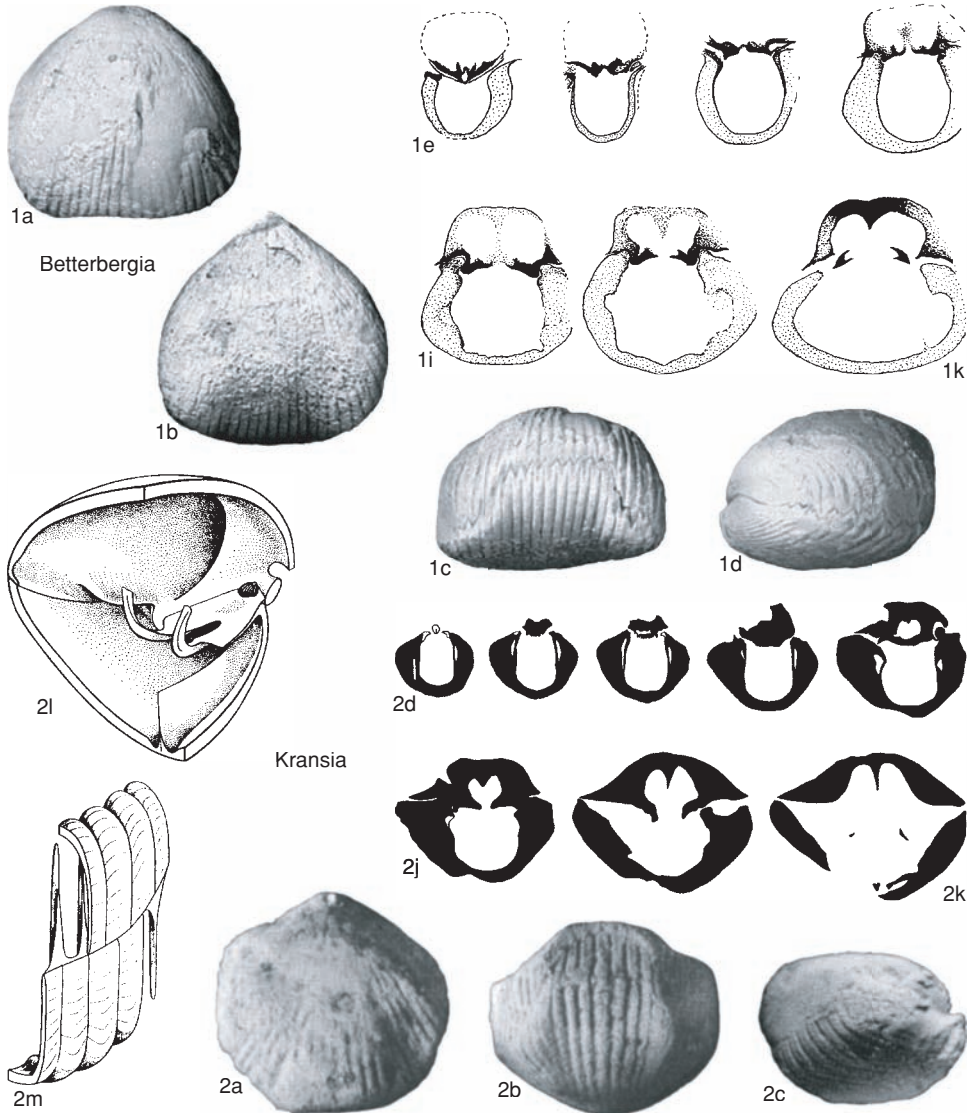


FIG. 754. Hebetoechiidae (p. 1111).

mesothyrid, deltidial plates conjunct. Fold and sulcus weak; anterior commissure weakly uniplicate. Costae coarse, rounded in section; marginal spines short. Dental plates short, ventrally divergent; ventral muscle field well impressed. Dorsal median septum short, thin; septalium absent; calluslike cardinal process may join hinge plates posteriorly; hinge plates divided anteriorly. *Middle Devonian (Givetian)*: Europe, Urals, Tadjikistan.—FIG. 756, 1a–l. **B. minor beckmanni* (SCHMIDT), lowest Givetian; a–b, holotype, dorsal, anterior views, Letmathe, near Dortmund, Germany, $\times 3.3$; c–d,

holotype, ventral and lateral views, Letmathe, near Dortmund, Germany, $\times 3$ (Schmidt, 1951); e–b, topotype, serial sections, intervals not given, Letmathe, near Dortmund, Germany, $\times 7.2$ (Mohanti, 1972); i–l, dorsal, ventral, lateral, and anterior views, basal Member B, Portillo Formation, Los Barrios de Luna near Leon, northwestern Spain, $\times 4.3$ (Mohanti, 1972).

Cassidirostrum MCLAREN, 1961, p. 2 [*C. pedderi*; OD]. Subcircular to subpentagonal in outline, and profile dorsibiconvex. Beak erect to incurved; small foramen at apex of delthyrium bounded by small

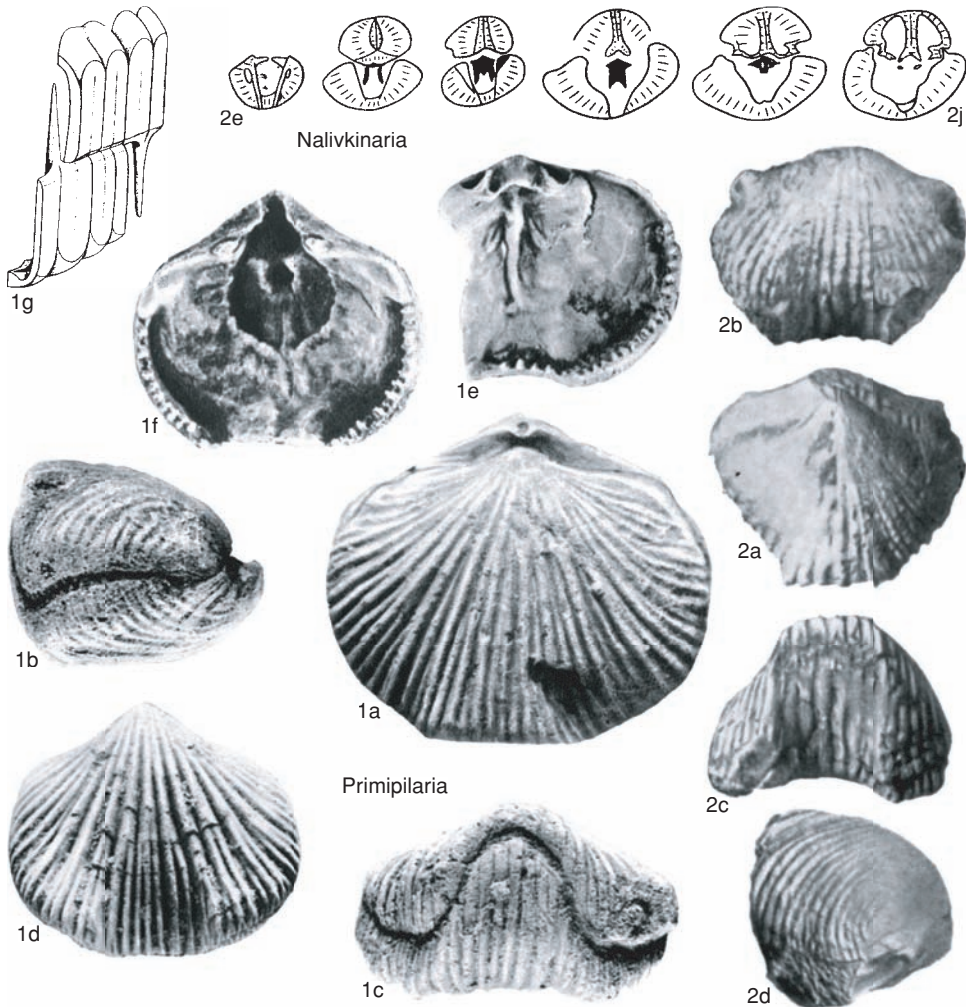


FIG. 755. Hebetoechiidae (p. 1111–1112).

triangular deltidial plates. Fold and sulcus distinct, from midlength; anterior commissure uniplicate; tongue, broad, rounded, dentate. Costae numerous, angular, simple, arising at umbones, covering all surface; some specimens have marginal spines. Dental plates converging ventrally; ventral muscle field well impressed. Dorsal median septum long, high; septalium short, commonly filled with callus, which may be developed into bilobed cardinal process; hinge plates divided anteriorly; dorsal muscle field long, narrow, well impressed; crura ventrally curved, gutterlike anteriorly with open side directed dorsally, tips laterally compressed. *Middle Devonian (lower Givetian)*: western North America, Spain, Libya.—FIG. 756,3a–m. **C. pedderi*, Hare Indian Formation, Anderson River, Northwest Territories;

a–e, holotype, dorsal, ventral, posterior, anterior, and lateral views, $\times 1$; *f–m*, serial sections 2.2, 2.8, 3.0, 3.3, 3.6, 5.9, 6.3, 6.35 mm from posterior, $\times 1.5$ (McLaren, 1962).

Homeocardiorynchus SARTENAER, 1985b, p. 220 [**H. pityinus*; OD]. Transversely oval outline; moderately biconvex, with lateral and anterior margins not steep. Beak suberect to erect; foramen small, circular, mesothyrid, deltidial plates present. Fold and sulcus weak; tongue low. Umbones smooth; costae few, rounded, simple, flattened and grooved at anterior margin. Dental plates converging ventrally. Dorsal median septum thick, extending to one-third valve length; septalium wide, deep, open; small cardinal process present; crura arising from inner edges of septalium, closely set. *Middle*

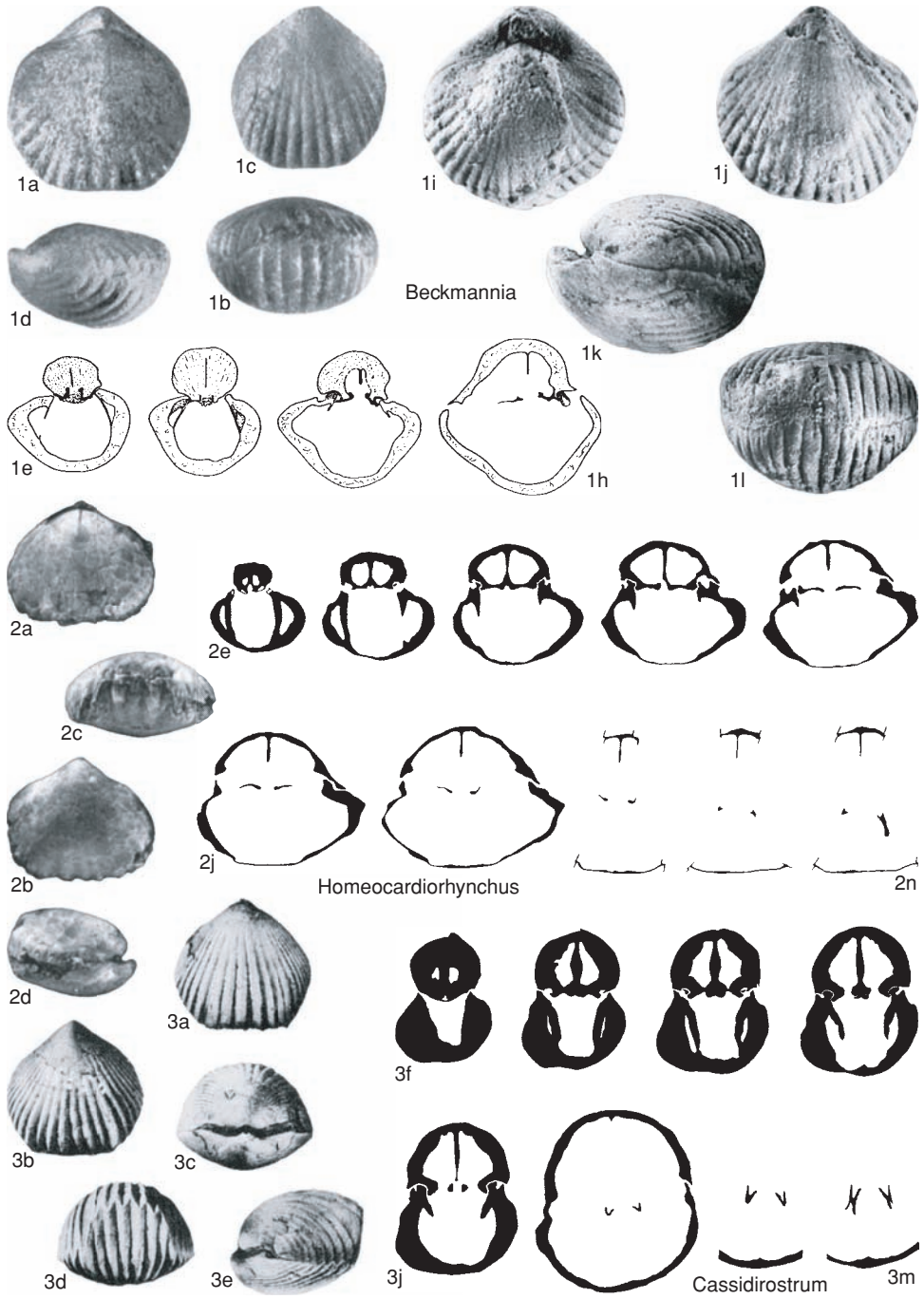


FIG. 756. Hebetoechiidae (p. 1113–1117).

Devonian (Givetian): western Canada.—FIG. 756, 2a–n. **H. pitynus*, middle Givetian, Pine Point Formation, Great Slave Lake; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–n, paratype, serial sections 2.2, 2.6, 3.0, 3.45, 3.8, 4.15, 4.4, 4.6, 5.25, 5.45 mm from posterior, $\times 2.8$ (Sartenaer, 1985b).

Family OBTURAMENTELLIDAE Savage, 1996

[Obturamentellidae SAVAGE, 1996, p. 253]

Uncinuloidea with very thick shell; costae coarse; marginal spines short. Dental plates rudimentary, mostly infilled with callus. Teeth massive, longitudinally grooved, arising from shell walls; ventral muscle field deeply impressed. Dorsal median septum low, thick, long; septalium filled posteriorly with massive, linguiform, bilobed cardinal process. *upper Silurian (lower Ludlow)–Lower Devonian (Pragian)*.

Obturamentella AMSDEN, 1958, p. 99 [**Wilsonia wadei* DUNBAR, 1919, p. 53; OD]. Small to medium; subcircular outline; biconvex profile. Beak suberect; delthyrium with well-developed foramen and deltidial plates. Fold and sulcus from about midlength; tongue high, narrow, rectangular. Costae coarse, rounded in section, arising at umbones; marginal spines short. Dental plates not distinguishable in thick shell material; teeth supported by shell wall; ventral muscle field deeply impressed and divided by long, low ventral median myophragm. Dorsal median septum low, short; septalium rudimentary, filled with callus that forms bilobed or variable cardinal process posteriorly. *Lower Devonian (Lochkovian–Pragian)*: North America, Europe.—FIG. 757, 2a–j. **O. wadei* (DUNBAR), Lochkovian, Oklahoma, Tennessee, USA; a–c, hypotype, dorsal, ventral, and lateral views, Oklahoma, $\times 2$; d–e, lectotype, anterior and ventral views, Ross Limestone, Grandview, Tennessee, $\times 2$; f, hypotype, ventral interior, $\times 3$; g–i, serial sections at 0.5, 1.0, 1.3 mm from posterior, $\times 4$; j, enlarged view of dorsal part of *b*, showing shell structure, $\times 12$ (Amsden, 1958).

Pectorhyncha MCLEARN, 1918, p. 137 [**Atrypa obtusiplicata* HALL, 1852, p. 279; OD]. Small to medium; subtriangular to subovate outline; biconvex to gibbous profile; lateral margins not vertical; beak erect. Fold and sulcus arising at umbones; anterior commissure uniplicate, trapezoid, serrate. Costae coarse, simple, rounded in section, from beaks. Shell thick. Dental plates mostly obscured by infilling of umbonal cavities; ventral muscle field deeply impressed. Dorsal median septum thick, low; septalium long, wide, filled posteriorly with

large, calluslike, bilobed to multilobed cardinal process; crura long, convex laterally. *Silurian (lower Ludlow)*: eastern North America.—FIG. 757, 1a–r. **P. obtusiplicata* (HALL), Niagaran, Lockportian, Lockport, New York, USA; a–e, hypotype, dorsal, ventral, lateral, anterior, and posterior views from type area, $\times 2$; f–r, hypotype, serial sections 0.85, 0.95, 1.05, 1.25, 1.65, 2.15, 2.6, 2.8, 3.0, 3.2, 3.6, 3.8, 4.1 mm from posterior of another hypotype from type area, $\times 2$ (new).

Family INNAECHIIDAE Baranov, 1980

[Innaechiidae BARANOV, 1980, p. 78]

Uncinuloidea lacking septalium and cardinal process. *upper Silurian (Ludlow)–Middle Devonian (Eifelian)*.

Subfamily INNAECHIINAE Baranov, 1980

[*nom. transl.* SAVAGE, 1996, p. 253, ex Innaechiidae BARANOV, 1980, p. 78]

Innaechiidae with median septum; dental plates very short. *Lower Devonian (Lochkovian)*.

Innaechia BARANOV, 1980, p. 78 [**I. retracta*; OD]. Medium to large with transversely subpentagonal outline; dorsibiconvex; anteriorly inflated. Beak erect; delthyrium closed by deltidial plates. Fold and sulcus developed anteriorly; tongue high, rectangular. Costae medium, simple, developed laterally and anteriorly only, flattened and grooved on *paries geniculatus*; marginal spines present. Dental plates short, close to shell walls. Dorsal median septum slender, long; hinge plates divided, horizontal. *Lower Devonian (Lochkovian)*: eastern Siberia.—FIG. 758, 1a–l. **I. retracta*, lower Sagyr Formation, Selennyakh ridge, Talyndzha River; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–j, serial sections of shell 1.0, 1.2, 1.4, 1.6, 2.0, 2.1 mm from posterior; k–l, sections of crura 2.3, 3.7 mm from posterior of shell, $\times 3$ (Baranov, 1980).

Subfamily CORVINOPUGNACINAE Savage, 1996

[Corvinopugnacinae SAVAGE, 1996, p. 253]

Innaechiidae with fold and sulcus low, wide; costae numerous; short dental plates present. *upper Silurian (Ludlow)–Middle Devonian (Eifelian)*.

Corvinopugnax HAVLÍČEK, 1961, p. 36 [**Rhynchonella corvina* BARRANDE, 1847, p. 70; OD]. Transversely subpentagonal outline; subcuboid with steep lateral and anterior margins. Beak incurved. Fold and

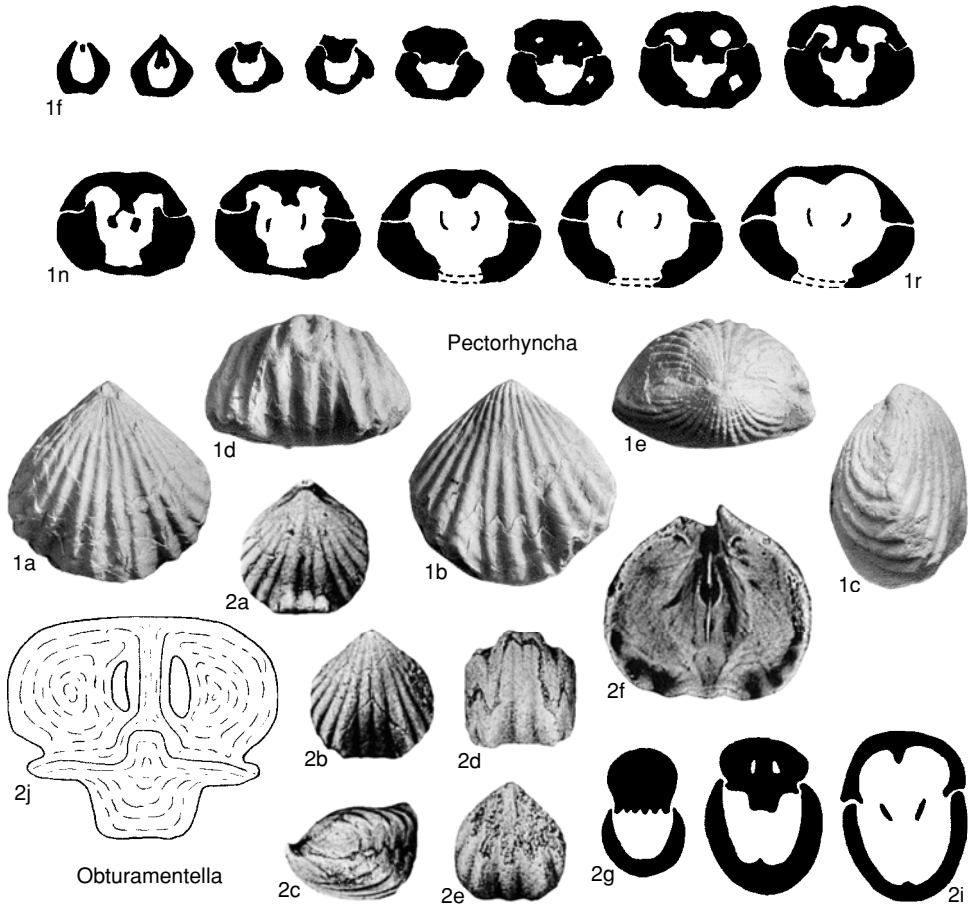


FIG. 757. Obturamentellidae (p. 1117).

sulcus distinct, from midlength; tongue wide, rectangular. Costae strong, simple, restricted to anterior third of shell, rounded in profile except on *paries geniculatus* where flattened and grooved; marginal spines well developed. Dental plates short, convergent ventrally. Dorsal median ridge short and low; hinge plates divided; septalium, median septum, and cardinal process absent. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Europe, northern Africa, Urals, Siberia, China.—FIG. 759a–i. **C. corvinus* (BARRANDE), upper Emsian, Suchomasty Limestone, Koneprusy, Bohemia; a–e, holotype, dorsal, ventral, lateral, anterior, and posterior views, $\times 2$ (new); f–i, serial sections, $\times 3$ (Havlíček, 1961).—FIG. 759j–p. *C. crassus* (LE MAITRE), lower Eifelian, Morocco; serial sections 1.15, 1.55, 1.8, 2.1, 2.5, 2.8, 3.1 mm from posterior, $\times 8$ (Drot, 1980).

Aseptulum HOU & XIAN, 1975, p. 37 [**Uncinulus guangxiense* WANG, 1965, p. 72; OD]. Medium to

large with transversely subpentagonal outline and dorsibiconvex profile. Fold and sulcus well defined; tongue wide, rectangular. Costae numerous, strong, simple, from beaks, flattened and grooved on *paries geniculatus*; marginal spines pronounced. Dental plates short, convergent ventrally; ventral muscle field deeply impressed. Dorsal interior with very short crural plates posteriorly, sometimes meeting on valve floor; outer hinge plates horizontal, divided; median ridge short and low; crura long, rod-like; septalium, dorsal median septum, and cardinal process absent. *Lower Devonian (Pragian–Emsian)*: China.—FIG. 760, 1a–k. **A. guangxiense* (WANG), upper Pragian–lower Emsian, Nagaoling Formation, Guangxi, Henxian County, Lijiang, southern China; a–d, dorsal, ventral, anterior, and lateral views, $\times 2.2$ (Hou & Xian, 1975); e–k, serial sections, $\times 3.3$ (new).

Decoropugnax HAVLÍČEK, 1960, p. 244 [**Terebratula berenice* BARRANDE, 1847, p. 77; OD]. Transversely

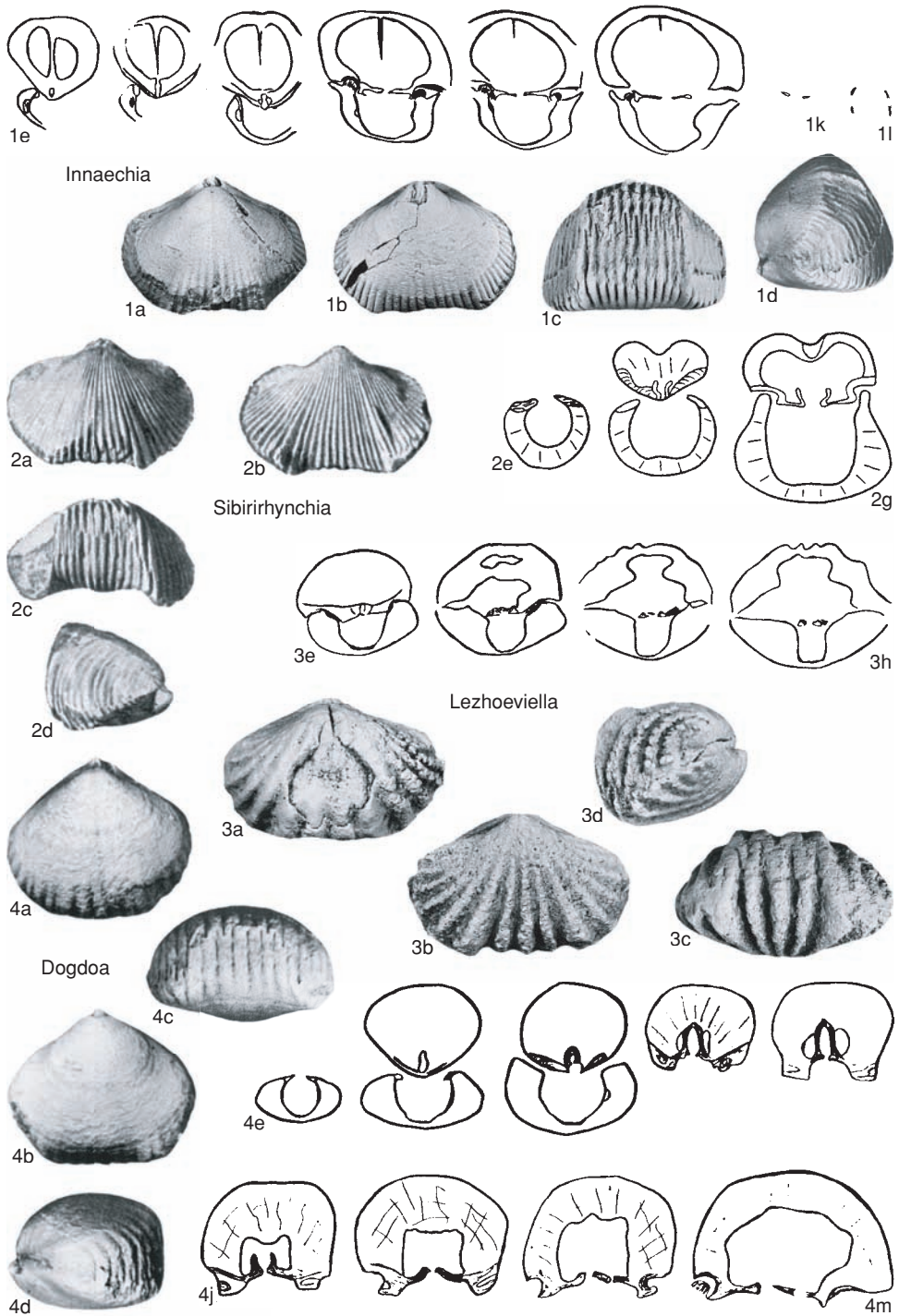


FIG. 758. Innaechiidae (p. 1117–1122).

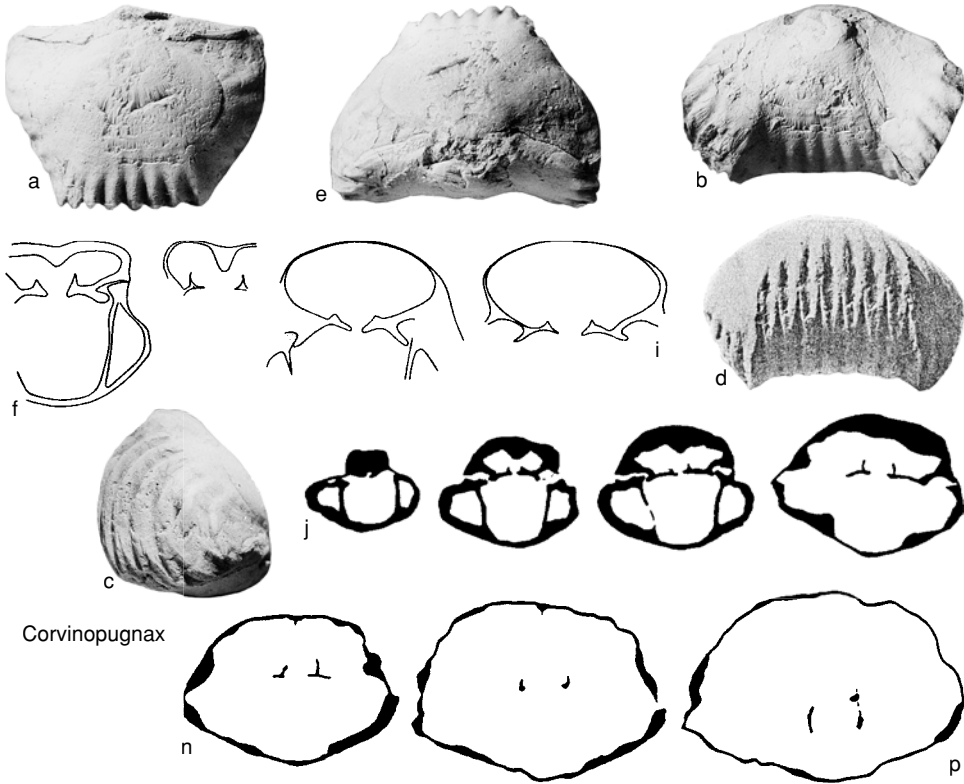


FIG. 759. Innaechiidae (p. 1117–1118).

trigonal outline; moderately biconvex to tabular profile. Beak erect; delthyrium triangular, open, deltidial plates incipient to absent. Fold and sulcus weak, broad; tongue wide, low, rectangular. Costae fine, simple, restricted to anterior third of shell; costae rounded in profile except on *paries geniculatus* where flattened and grooved; marginal spines pronounced. Dental plates short, vertical. Dorsal median septum, septalium, and cardinal process lacking. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian)*: Bohemia, Urals, Altai, Yakutsk, Tadzhikistan, northwestern Canada. —FIG. 760, 2a–e. **D. berenice* (BARRANDE), Ludlow, Dlouha Hora, Bohemia; a–c, dorsal, ventral, and anterior views, $\times 3.7$ (new); d–e, serial sections, $\times 6$ (Havlíček, 1961).

Xeniopugnax HAVLÍČEK, 1982a, p. 111 [**Terebratula modica* BARRANDE, 1847, p. 76; OD]. Subtriangular outline; moderately biconvex profile; beak incurved. Fold and sulcus wide, low, restricted to anterior half of valves; tongue low, very wide, dentate. Costae coarse, rounded, only present anteriorly, flattened and grooved on low *paries geniculatus*. Dental plates thin, short, convergent toward valve

floor. Hinge plates divided, thin, horizontal; dorsal median septum and septalium absent. *upper Silurian (Ludlow)*: Bohemia. —FIG. 760, 3a–f. **X. modicus* (BARRANDE), Kopanina Formation, *Cromus beaumonti* horizon, Dlouha hora; a–d, dorsal, ventral, lateral, and anterior views, $\times 3.2$; e–f, serial sections 8.75, 8.55 mm from anterior, $\times 10$ (Havlíček, 1982a).

Subfamily DOGDOINAE Baranov, 1982

[Dogdoinae BARANOV, 1982, p. 42]

Innaechiidae lacking dental plates and dorsal median septum. *Lower Devonian (Lochkovian–Emsian)*.

Dogdoa BARANOV, 1982, p. 42 [**D. chalimensis*; OD]. Subpentagonal outline; biconvex profile. Beak erect; delthyrium with small foramen and narrow deltidial plates. Fold and sulcus weak; tongue distinct, rectangular. Valves smooth posteriorly but with rounded costae anteriorly; costae becoming flattened and grooved on *paries geniculatus*; marginal spines short. Dental plates absent or buried in

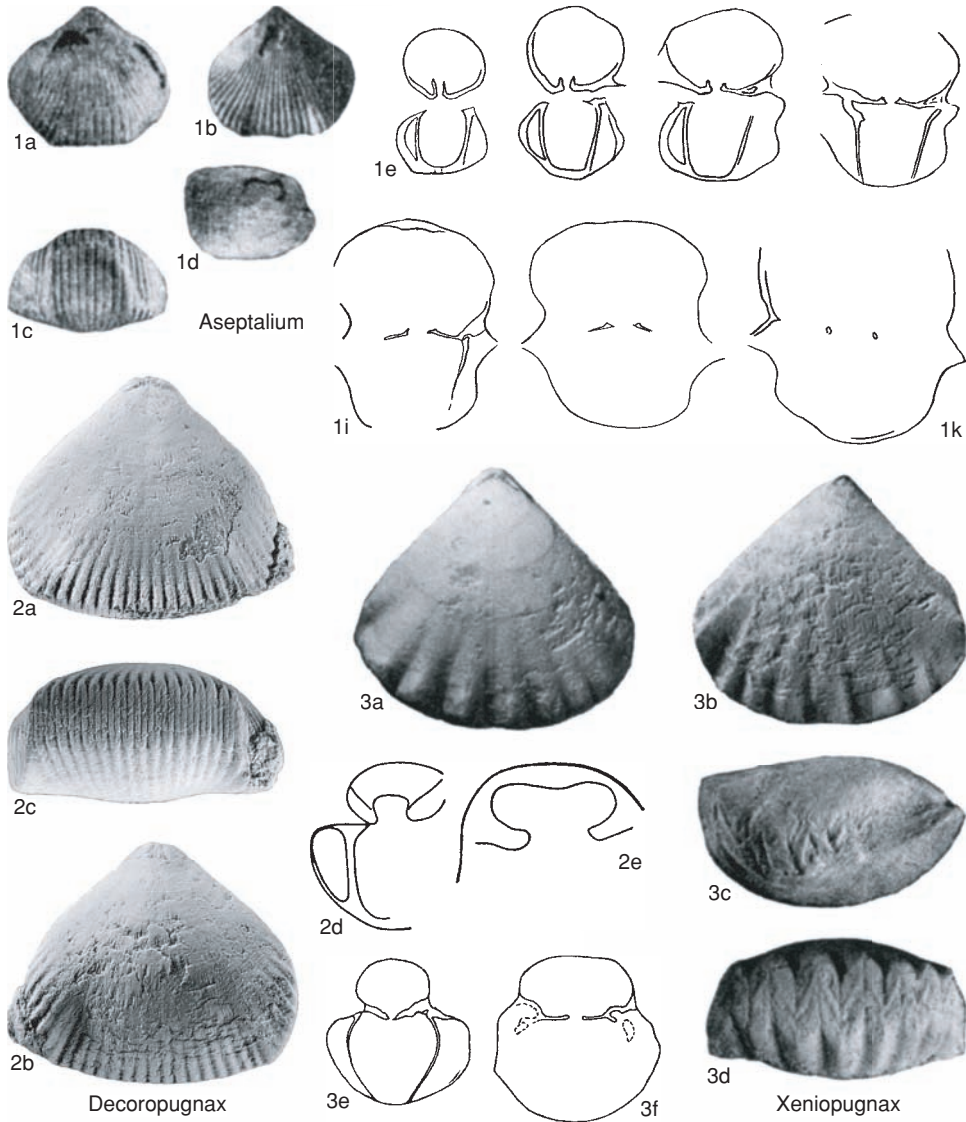


FIG. 760. Innaechiidae (p. 1118–1120).

callus. Hinge plates divided, horizontal; septulum, dorsal septum, and cardinal process absent; crural plates meeting valve floor, forming cruralium. Lower Devonian (Lochkovian): eastern Siberia.—FIG. 758,4a–m. **D. chalimensis*, upper Datninskaya Formation, eastern Yakutia, Tas-Khayakhtakh Range; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–g, serial sections through conjoined valves; b–m, serial sections through dorsal

valve 0.5, 0.6, 0.7, 0.8, 0.9, 1.0 mm from posterior, $\times 7$ (Baranov, 1982).

Lezhoevella BARANOV, 1978, p. 48 [*L. protensa*; OD]. Transversely subpentagonal outline; dorsibiconvex profile. Fold and sulcus arising at umbones, strong anteriorly; tongue distinct, trapezoid. Costae coarse, extending from umbones, rounded in profile except on *paries geniculatus* where flattened and grooved. Dental plates absent; ventral and dorsal muscle

areas deeply impressed. Hinge plates divided; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Emsian)*: eastern Siberia. —FIG. 758, 3a–b. **L. protensa*, lower Emsian, Nelichensk Series, Yakutia, Selenniakhsk Ridge; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–b, serial sections 0.2, 0.7, 0.9, 1.1 mm from posterior, $\times 4.5$ (Baranov, 1978).

Sibirirhynchia RZHONSNITSKAIA, 1978, p. 182 [**Hyporhynchia alata* KHODALEVICH, 1951, p. 50; OD] [= *Sibirirhynchia* RZHONSNITSKAIA, 1968a, p. 41, *nom. nud.*, no description, illustration, or type species given]. Transversely ovate outline; strongly biconvex profile. Beak suberect; foramen with marginal deltidial plates. Fold and sulcus wide with distinct lateral margins; tongue high, rectangular. Costae numerous, fine, simple, from beak, flattened and grooved on *paries geniculatus*. Dental plates absent. Divided hinge plates horizontal; septalium, dorsal septum, and cardinal process absent. *Lower Devonian (upper Emsian)*: Kuznetsk, Urals, eastern Siberia, Tadzhikistan. —FIG. 758, 2a–d. **S. alata* (KHODALEVICH), Sverdlovsk, eastern Urals; holotype, dorsal, ventral, anterior, and lateral views, $\times 1$ (Khodalevich, 1951). —FIG. 758, 2e–g. *S. alata fainecostata* (TORBAKOVA), northeastern slope of Urals; serial sections, $\times 7$ (Sapelnikov, Mizens, & Shatrov, 1987).

Subfamily VLADIMIRIRHYNCHINAE Baranov, 1982

[Vladimirirhynchinae BARANOV, 1982, p. 44]

Innaechiidae with short dental plates; median furrow dividing fold, corresponding ridge dividing sulcus; dorsal median septum commonly absent. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*.

Vladimirirhynchus BARANOV, 1982, p. 44 [**V. lezboevi*; OD]. Small size; subcircular to subpentagonal outline; biconvex profile. Beak erect to incurved; foramen permesothryd. Fold strong with weak median sinus, sulcus with corresponding ridge; tongue high; trapezoid to tapering. Costae coarse, rounded in section, bifurcating on fold and in sulcus; costae on *paries geniculatus* bear grooves. Dental plates short. Hinge plates divided, dorsally inclined; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Lochkovian)*: eastern Siberia. —FIG. 761, 1a–l. **V. lezboevi*, lower Sagyr Formation, Yakutia, Ulakhan-Sis Range; a–c, holotype, dorsal, anterior, and lateral views, $\times 2$; d–l, serial sections 0.4, 0.6, 0.7, 0.8, 0.9, 1.0, 1.1, 1.3, 1.6 mm from posterior, $\times 3.5$ (Baranov, 1982).

Alekseevella BARANOV, 1980, p. 80 [**A. sulcata*; OD]. Small size; elongate subpentagonal outline; dorsal valve inflated. Beak erect to incurved; foramen permesothryd, deltidial plates conjunct. Fold divided by groove, sulcus with corresponding ridge. Costae bundled on fold and sulcus, flattened and

grooved on *paries geniculatus*. Dental plates short. Dorsal median septum thin; septalium lacking; hinge plates divided, horizontal; cardinal process absent; crura ventrally curved, narrow. *Middle Devonian (Eifelian)*: eastern Siberia. —FIG. 761, 2a–n. **A. sulcata*, lower Seymchan Formation, Ulakhan-Sis Range, Pravyy Naanchan River; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–l, serial sections of shell 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 mm from posterior; m–n, sections of crura, intervals not given, $\times 3.5$ (Baranov, 1980).

Selennjachia BARANOV, 1982, p. 45 [**S. abaimovae*; OD]. Small size; subpentagonal outline; moderately biconvex profile. Beak suberect; foramen mesothryd. Fold and sulcus low, fold divided by sinus, sulcus divided by weak ridge; umbones smooth. Costae rounded in profile, flattened and grooved anteriorly. Dental plates very short or obscured by callus. Hinge plates divided, subhorizontal; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: eastern Siberia. —FIG. 761, 4a–k. **S. abaimovae*, Zlichovian–Eifelian, Seymchan Formation, Selennyakh Range, eastern Yakutia; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–k, serial sections 0.2, 0.25, 0.35, 0.45, 0.65, 0.95, 1.05 mm from posterior, $\times 3.5$ (Baranov, 1982).

Sulcicostula BARANOV, 1989, p. 47 [**Corvinopugnax tichiensis* ALEKSEEVA, 1967, p. 65; OD]. Small size; subpentagonal outline; biconvex profile. Beak erect; foramen permesothryd; umbones smooth. Fold divided by weak sinus, sulcus divided by low ridge. Costae rounded in section but flattened and grooved on *paries geniculatus*. Dental plates short; dorsal median septum, septalium, and cardinal process absent. *Lower Devonian (Lochkovian)*: eastern Siberia. —FIG. 761, 3a–k. **S. tichiensis* (ALEKSEEVA); a–d, holotype, dorsal, ventral, anterior, and lateral views, upper Lochkovian, middle Sette-Daban Formation, Sette-Daban Range, $\times 2.5$; e–g, serial sections, upper Lochkovian, middle Sette-Daban Formation, Sette-Daban Range, $\times 6$ (Aleksseeva, 1967); h–k, hypotype, dorsal, ventral, anterior, and lateral views, base of Sagyrskaya Formation, $\times 2$ (Baranov, 1989).

Tatjania BARANOV, 1982, p. 47 [**T. trigona*; OD]. Small size; subpentagonal outline; highly inflated dorsal valve. Beak erect. Fold divided by weak sinus; sulcus divided by low ridge; tongue high. Most of valves smooth, with costae restricted to anterior third; costae flattened and grooved on *paries geniculatus*. Dental plates convergent ventrally; ventral muscle field deeply impressed. Hinge plates divided; dorsal median septum, septalium, and cardinal process absent; crura close set anteriorly. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: eastern Siberia. —FIG. 762, 1a–m. **T. trigona*, lower Eifelian, Seymchan Formation, Ulakhan-Sis Range, eastern Yakutia; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–m, serial sections 0.9, 1.2, 1.4, 1.5, 1.7, 1.9, 2.1, 2.2, 2.3 mm from posterior, $\times 2.5$ (Baranov, 1982).

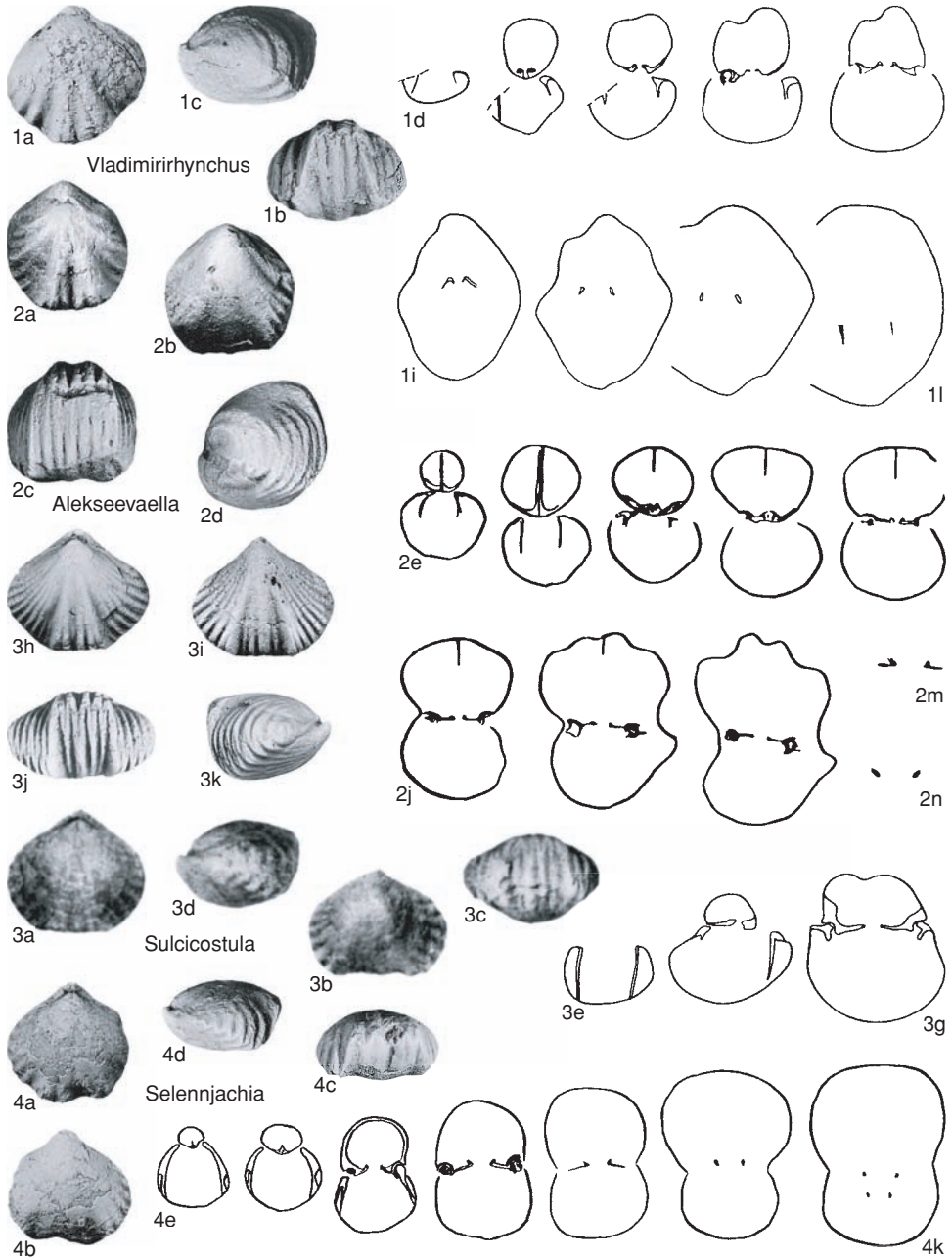


FIG. 761. Innaechiidae (p. 1122).

Yakutijaella BARANOV, 1977, p. 77 [**Y. dubatolovi*; OD]. Subpentagonal to transversely ovate outline and moderately biconvex profile. Beak erect; foramina small, rounded. Fold and sulcus weak, from umbones, with groove on fold, plication in sulcus;

tongue low, denticulate; umbones smooth. Costae weak, subangular, arising near umbones. Dental plates absent. Dorsal median septum and septulum absent; hinge plates united, thick; crural bases large, concave dorsolaterally, developing on dorsal side of

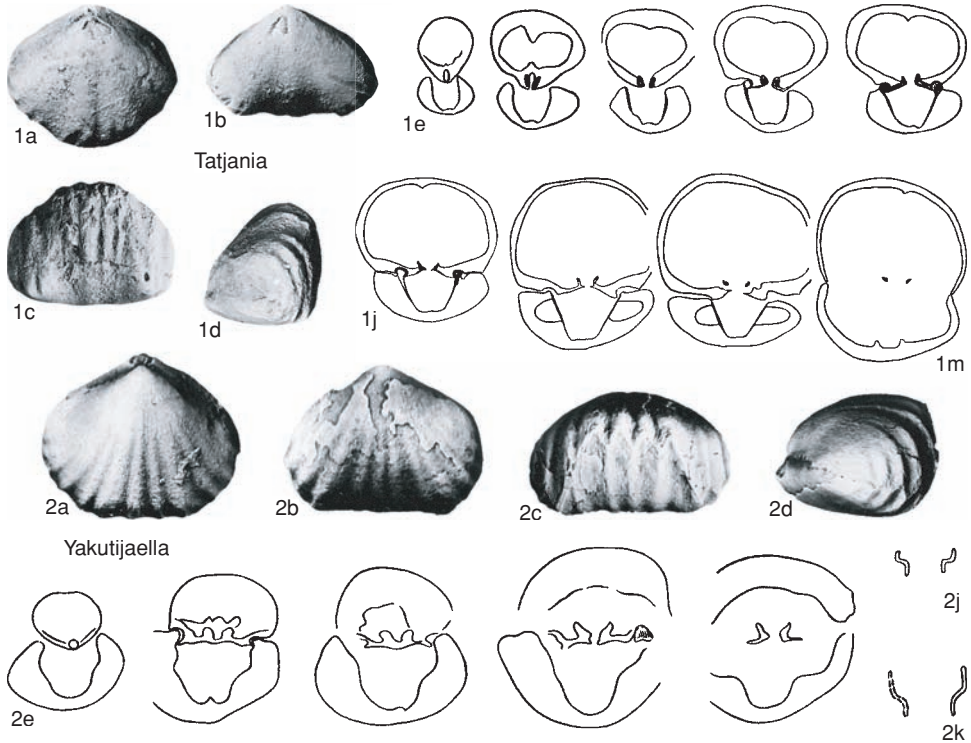


FIG. 762. Innaechiidae (p. 1122–1124).

hinge plates as prominent ridges; crura long, laterally compressed, sigmoidal in section. *Lower Devonian (lower Emsian)*: northeastern Siberia.—FIG. 762, 2a–k. **Y. dubatolovi*, Nelichenian suite, Yakutsk, Selennyakh Ridge; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–k, serial sections at 1.7, 2.2, 2.4, 2.7, 2.8, 4.1, 4.4 mm from posterior, $\times 3.7$ (Baranov, 1977).

Family GLOSSINOTOECHIIDAE

Havlíček, 1992

[Glossinotoechiidae HAVLÍČEK, 1992, p. 92]

Uncinuloidea with cordiform to subtriangular outline, acuminate posteriorly; tongue distinct; costae numerous, flattened anteriorly; marginal spines developed; foramen mesothyrid with conjunct deltidial plates. Dental plates short, close to valve walls. Septalium usually with cover plate; cardinal process high, linguiform, often striated. *upper Silurian (Ludlow)–Middle Devonian (Eifelian)*.

Glossinotoechia HAVLÍČEK, 1959, p. 79 [**Terebratula henrici* BARRANDE, 1847, p. 84; OD]. Subtriangular outline with acuminate posterior angle; ventral valve flat to concave, dorsal valve highly inflated; anterior and lateral margins sharply truncated in adults. Beak straight; mesothyrid foramen with conjunct deltidial plates. Fold and sulcus weak to absent but tongue high and rectangular; squamae and glottae poorly developed. Costae arising at beaks, rounded in profile but flattened and grooved anteriorly. Dental plates distinct but close to shell walls. Dorsal median septum long, low, thick; septalium completely filled with callus; large multi-lobed to linguiform cardinal process. *Lower Devonian (Pragian)–Middle Devonian (lower Eifelian)*: Europe, northern Africa, Urals, Siberia, China.—FIG. 763, 1a–k. **G. henrici* (BARRANDE), Pragian, Koneprusy Limestone, Koneprusy, Bohemia; a–d, lectotype, dorsal, ventral, anterior, and lateral views, $\times 2$; e–k, serial sections 13.4, 13.2, 13.0, 12.8, 12.6, 12.2, 12.0 mm from anterior, $\times 2$ (Havlíček, 1961).

Chlupacitoechia HAVLÍČEK, 1992, p. 100 [**Uncinulus (Glossinotoechia) chlupaci* HAVLÍČEK, 1956, p. 569; OD]. Subtriangular with emarginate posterolateral and anterior margins; dorsibiconvex profile but

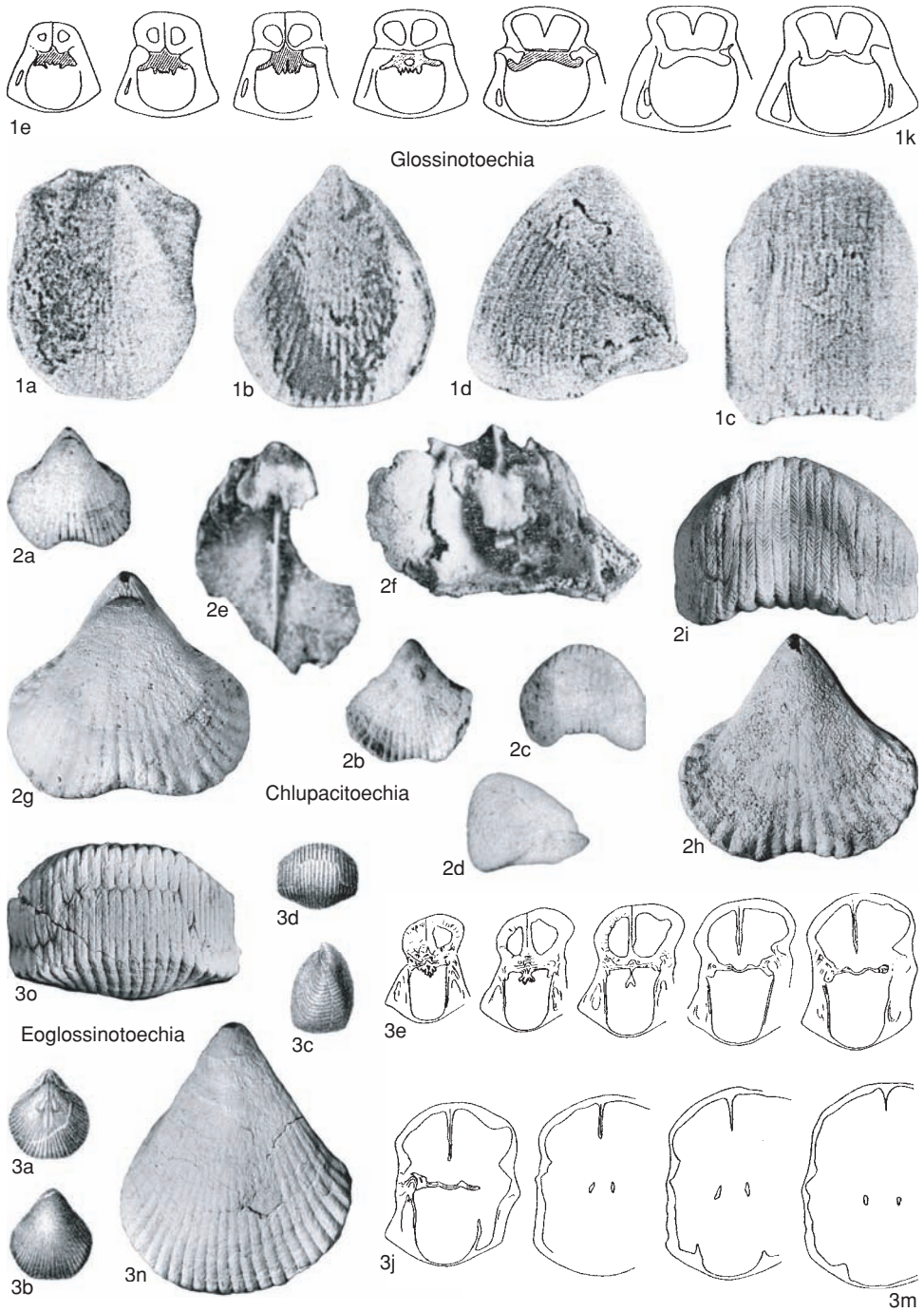


FIG. 763. Glossinotoechiidae (p. 1124–1126).

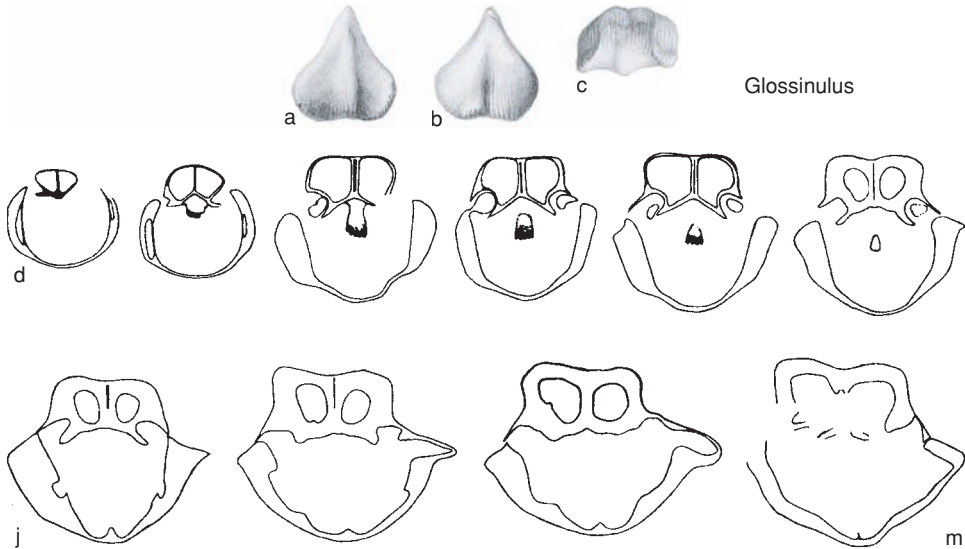


FIG. 764. Glossinotoechiidae (p. 1126).

with concavity on ventral valve; anterior margin and flanks vertical to truncated. Beak straight to suberect; foramen small, circular, mesothyrid, deltidial plates conjunct. Dorsal fold and ventral sulcus weak; anterior tongue distinct, high, rectangular. Costae fine, grooved at commissure to accommodate marginal spines. Dental plates well developed, strongly divergent anteriorly, close to valve margins; septalium large, commonly filled with callosity. Dorsal median septum high, extending to valve midlength; cardinal process wide, high, posteriorly striated. *Lower Devonian (Pragian)*–*Middle Devonian (lower Eifelian)*: Bohemia, Spain, France.—FIG. 763,2*a*–*i*. **C. chlupeci* (HAVLÍČEK), Emsian, Zlichov Limestone, Hlubočepý, Bohemia; *a*–*d*, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$ (Havlíček, 1961); *e*, dorsal interior, $\times 3.8$; *f*, articulated umbonal interior showing dental plates, septalium, and cardinal process, $\times 5$; *g*–*i*, hypotype, dorsal, ventral, and anterior views, $\times 2.4$ (Havlíček, 1992).

Eoglossinotoechia HAVLÍČEK, 1959, p. 81 [**E. cacuminata*; OD]. Small size; subtriangular acuminate outline; biconvex with truncated anterior and lateral margins. Beak suberect; foramen small, deltidial plates large, conjunct. Fold and sulcus weak to absent; tongue distinct, rectangular. Costae fine, rounded in section, arising at beaks, becoming flattened and grooved on *paries geniculatus*; marginal spines short. Dental plates distinct, subparallel; ventral muscle field deeply impressed. Dorsal median septum high, long; septalium small, filled with cardinal process; hinge plates united; cardinal process multilobed posteriorly, linguiform,

and bilobed or trilobed anteriorly. *upper Silurian (Ludlow)*–*Lower Devonian (Emsian)*: cosmopolitan.—FIG. 763,3*a*–*o*. **E. cacuminata*, Pragian, Slivenec Limestone, Dvorce, Bohemia; *a*–*d*, holotype, dorsal, ventral, lateral, and anterior views, $\times 1$ (Barrande, 1879b); *e*–*m*, serial sections 11.35, 11.2, 11.05, 10.9, 10.7, 10.55, 10.2, 10.05, 9.65 mm from anterior, $\times 4$; *n*–*o*, holotype, ventral and anterior views, $\times 3.2$ (Havlíček, 1992).

Glossinulus SCHMIDT, 1942, p. 394 [**Rhynchonella adolfi mimica* BARRANDE, 1879b, p. 178; OD; =*Glossinulus mimicus* (BARRANDE), 1879b, p. 178]. Triangular outline, posteriorly acuminate; tabular profile, flattened to concave ventral valve with low median fold, flattened to slightly convex dorsal valve with gentle median sulcus; truncated anterior and lateral margins; tongue high, rectangular. Beak suberect; foramen small, circular, mesothyrid, deltidial plates conjunct. Costae fine, arising on umbones, flattened and grooved on *paries geniculatus*; spines at anterior and lateral margins. Dental plates very short, close to shell wall; ventral muscle field deeply impressed; low ventral median myophragm. Dorsal median septum low; septalium wide, filled posteriorly with high, linguiform cardinal process bearing fine longitudinal ridges; inner socket ridges prominent. *Lower Devonian (Emsian)*–*Middle Devonian (Eifelian)*: Europe, northern Africa, Siberia, China.—FIG. 764*a*–*m*. **G. mimicus* (BARRANDE), Emsian, Eifel, Germany; *a*–*c*, dorsal, ventral, and anterior views, $\times 1$ (Schmidt, 1965b); *d*–*m*, serial sections 6.9, 6.6, 6.4, 6.3, 6.2, 6.1, 6.0, 5.9, 5.8, 5.7 mm from anterior, $\times 4$ (Havlíček, 1961).

Family HYPOTHYRIDINIDAE
Rzhonsnitskaia, 1956

[Hypothyridinidae RZHONSNITSKAIA, 1956a, p. 125]

Uncinuloidea with dorsal median septum and septalium weak or lacking. Cardinal process usually wide, with myophore consisting of numerous vertical ridges, but cardinal process sometimes poorly developed or absent. *Lower Devonian (Emsian)–Upper Devonian (upper Famennian)*.

Hypothyridina BUCKMAN, 1906, p. 324, *nom. nov. pro Hypothyris* PHILLIPS, 1841, p. 55, *non* HÜBNER, 1821 [**Atrypa cuboides* SOWERBY, 1840a, pl. 56, fig. 24; SD KING, 1846, p. 28]. Medium to large with subcircular to subrectangular outline; strongly biconvex to inflated; lateral and anterior margins very steep. Beak suberect to erect; foramen small, circular, usually obscured by inflated dorsal umbo. Fold and sulcus weak; tongue very high, rectangular to rounded. Costae numerous, evenly developed, simple, flattened on *paries geniculatus*; marginal spines present. Dental plates short, subvertical to vertical. Dorsal median septum and septalium weak to absent; hinge plates short, horizontal, divided, or sometimes united by cardinal process; cardinal process usually short, with several lobes. *Middle Devonian (Eifelian)–Upper Devonian (Famennian)*: cosmopolitan.—FIG. 765, 1a–e. **H. cuboides* (SOWERBY); a–b, dorsal and anterior views, Givetian, Plymouth Limestone, Plymouth, England, $\times 1$ (Sowerby, 1840a); c–e, dorsal, anterior, and lateral views, Frasnian, Philippeville, Belgium, specimen 67298, Smithsonian, $\times 1$ (new).—FIG. 765, 1f–g. *H. sp. cf. H. impleta* (SOWERBY), Upper Devonian, Langennaubach, Germany; transverse sections of different young specimens, $\times 7$ (Schmidt, 1965b).

Glosshypothyridina RZHONSNITSKAIA, 1978, p. 180 [**Rhynchonella procuboides* KAYSER, 1871, p. 513; OD]. Transversely subpentagonal outline and dorsibiconvex profile; dorsal valve very inflated, ventral valve almost flat. Beak erect. Fold and sulcus pronounced, from umbones; tongue rectangular. Costae fine, numerous, flattened and grooved on *paries geniculatus*. Dental plates very short, ventrally convergent. Septalium and dorsal median septum absent; cardinal process low, bilobed; hinge plates horizontal, divided anterior of cardinal process. *Middle Devonian (Eifelian)*: Germany, Belgium, European Russia, Urals.—FIG. 766, 1a–j. **G. procuboides* (KAYSER), Eifel, Germany; a–b, holotype, anterior and lateral views, lower Eifelian, Gondelsheimer Formation, $\times 1$ (Kayser, 1871); c–f, serial sections, lower Eifelian, Gondelsheimer Formation, $\times 2.5$ (Schmidt, 1941a); g–j, serial sections 16.9, 16.7, 16.5, 16.4 mm from anterior, $\times 5$ (Schmidt, 1965b).

Lorangerella CRICKMAY, 1963, p. 10 [**L. phaulomorpha*; OD]. Small size with subcircular outline and lenticular to subglobose profile. Beak erect to incurved; foramen minute. Fold and sulcus weak but subrectangular tongue distinct. Valves mostly smooth, with low, rounded costae developed only at anterior margin; costae grooved at commissure. Dental plates very short, divergent ventrally. Cardinal process small, multilobed, close to posterior apex, supported by short median ridge. Hinge plates short, divided; septalium absent; crura curved sharply ventrally. *Upper Devonian (Frasnian)*: North America, Europe.—FIG. 765, 2a–m. **L. phaulomorpha*, lower Frasnian, Waterways Formation, Alberta, Canada; a–e, holotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 2.3$ (Crickmay, 1963); f–m, serial sections 0.2, 0.6, 0.8, 0.9, 1.0, 1.2, 1.6, 1.9 mm from posterior, $\times 5$ (McLaren, 1965).

Pseudouncinulus RZHONSNITSKAIA, 1968b, p. 111 [**P. mamontovensis*; OD]. Small to medium with sub-trigonal outline. Beak erect. Fold and sulcus weak; tongue rectangular. Costae arising at umbones, rounded in section, rarely bifurcating, flattened and grooved on *paries geniculatus*. Dental plates very short, close to shell walls. Septalium and dorsal median septum absent; cardinal process wide, with several longitudinal ridges; hinge plates anterior of cardinal process horizontal, united by dorsally concave plate. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Salair, Kuznetz, Urals, Yakutskaya.—FIG. 766, 3a–b. **P. mamontovensis*, southwestern Kuznetz basin; a–d, holotype, dorsal, ventral, anterior, and lateral views, $\times 1$; e–h, serial sections, intervals and scale not given (Rzhonsnitskaia, 1968b).—FIG. 766, 3i–u. *P. pusillis* BARANOV, Seymchan Formation, Yakutskaya, Ulakhan-Sis Range, eastern Siberia; i–k, holotype, ventral, anterior, and lateral views, $\times 2$; l–u, serial sections at 0.2, 0.4, 0.6, 0.8, 1.0, 1.1, 1.2, 1.3, 1.4, 1.9 mm from posterior, $\times 8$ (Baranov, 1980).

Uchtella LJASCHENKO, 1973, p. 50 [**Hypothyridina praesemilukiana* LJASCHENKO, 1958, p. 130; OD]. Subcircular to subpentagonal outline and strongly dorsibiconvex to subglobose profile; lateral and anterior margins steep to vertical. Beak small, incurved. Fold and sulcus weak posteriorly but distinct anteriorly; anterior commissure uniplicate; tongue wide, high, subrectangular to rounded. Valves smooth posteriorly but with low, rounded costae developed from about midlength; costae flattened and grooved anteriorly and especially on *paries geniculatus*. Dental plates very short. Hinge plates short, divided. Dorsal median septum absent. Cardinal process not recorded. *Upper Devonian (Frasnian)*: European Russia, Urals.—FIG. 766, 2a–e. **U. praesemilukiana* (LJASCHENKO), upper Timanski bed, southern Timan, Ukhtinsk region, European Russia; a–c, holotype, dorsal, anterior, and lateral views, $\times 1$; d–e, transverse sections near posterior, approximately $\times 6$ (Ljaschenko, 1973).

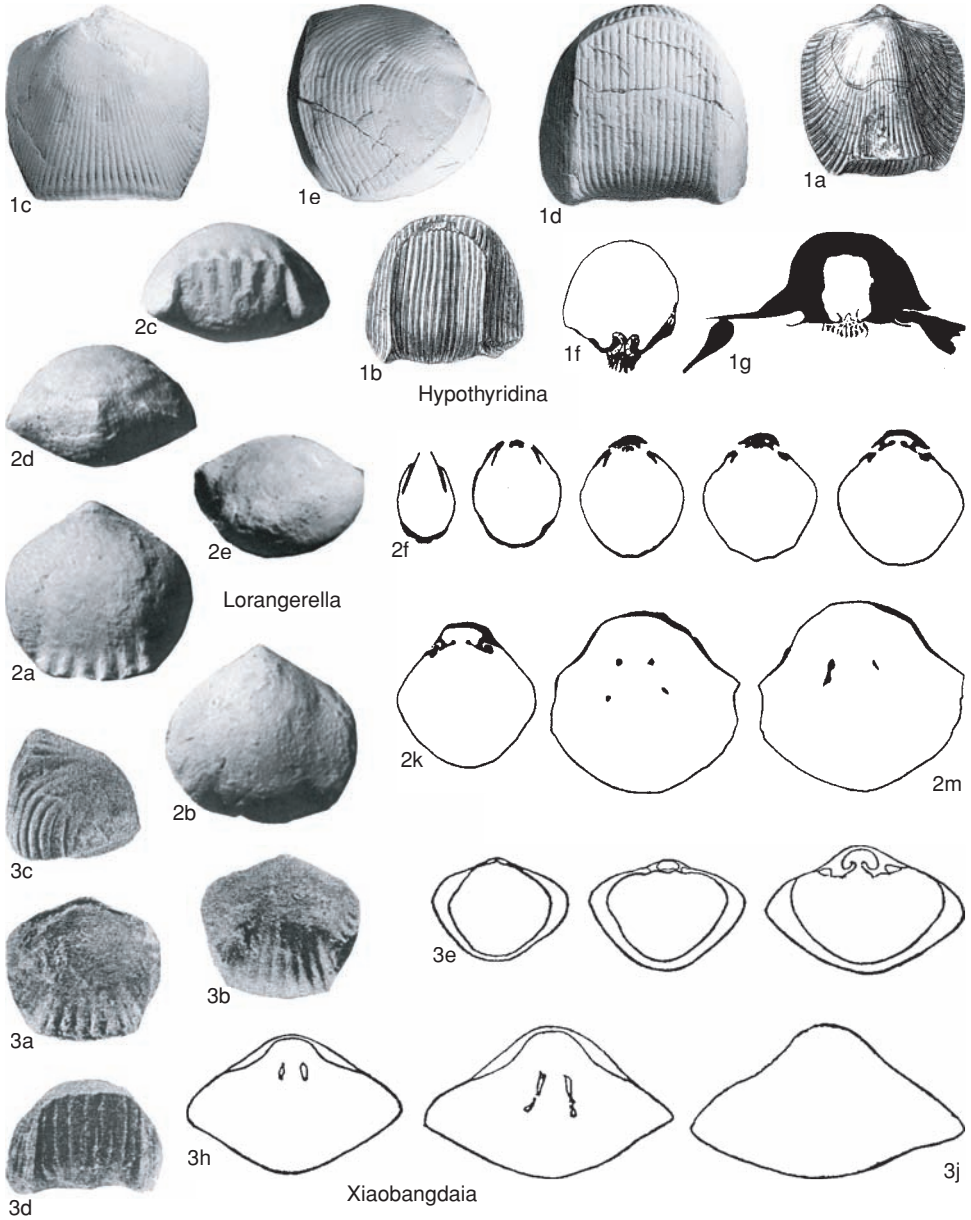


FIG. 765. Hypothyridinidae (p. 1127–1129).

Xiaobangdaia WANG, 1985, p. 200 [**X. zhuogedongensis*; OD]. Subcircular to subpentagonal outline and strongly anteriorly inflated, biconvex profile. Beak erect. Fold and sulcus distinct anteriorly; tongue high, rounded to subquadrate. Costae broad and low, restricted to anterior third of shell; flattened and grooved on *paries geniculatus*; mar-

ginal spines well developed, insert in line of holes just inside interior margin of opposite valve. Dental plates absent. Hinge plates short, united posteriorly but divided anteriorly. Dorsal median septum absent; cardinal process not recorded; crura short, strongly curved ventrally. *Upper Devonian (upper Famennian)*: Tibet.—FIG. 765, 3a–j. **X.*

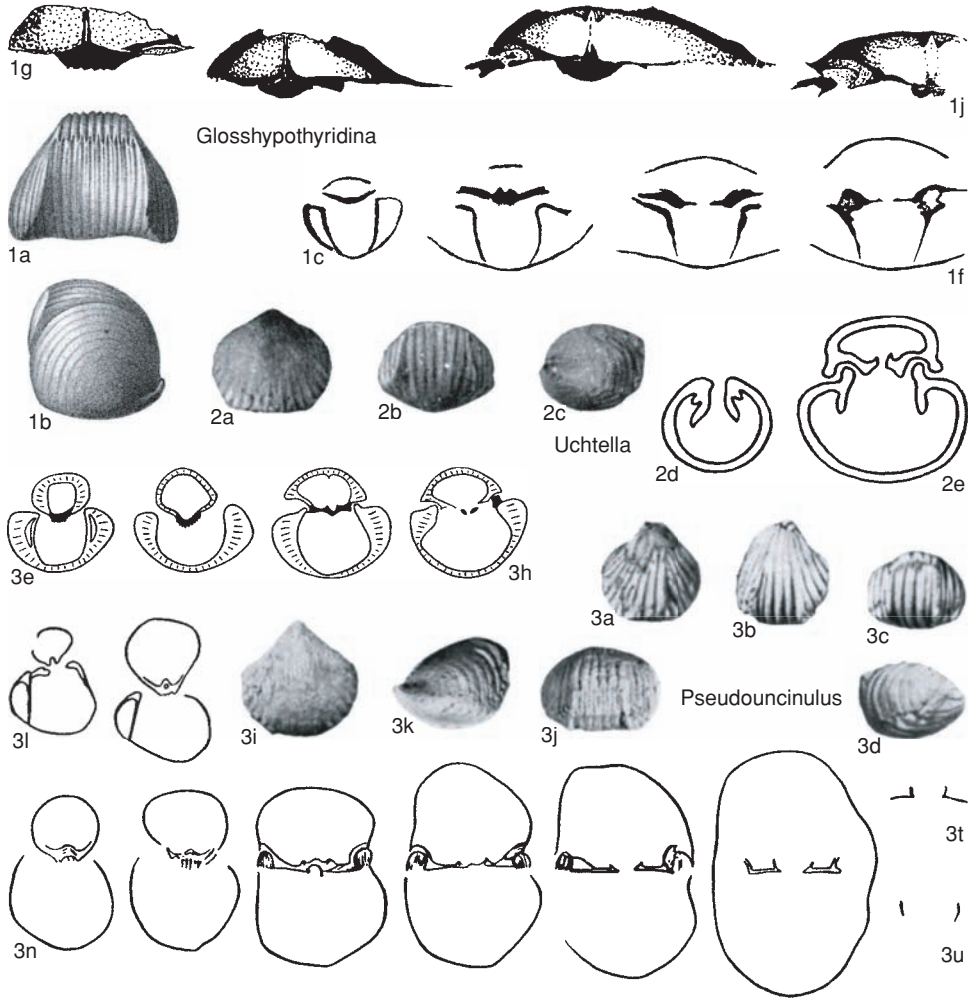


FIG. 766. Hypothyridinidae (p. 1127).

zhuogedongensis, upper Famennian, Zhougedong Formation, Markham County, Xiaobangda; *a-d*, holotype, dorsal, ventral, lateral, and anterior views, $\times 2$; *e-j*, serial sections 1.0, 1.2, 1.4, 1.7, 2.0, 2.3 mm from posterior, $\times 3.2$ (Wang, 1985).

Family HADRORHYNCHIIDAE
McLaren, 1965

[*nom. transl.* SAVAGE, 1996, p. 253, ex Hadrorhynchiinae McLAREN, 1965, p. 569]

Uncinuloidea with coarse costae; commissure acutely denticulate with marginal grooves; fold and sulcus developed anteriorly; tongue high, rectangular to acute. Small

septalium; hinge plates horizontal, divided; bilobed calluslike cardinal process may be present. *Middle Devonian (Eifelian–Givetian)*.

Hadrorhynchia McLAREN, 1961, p. 3 [**Pugnoides sandersoni* WARREN, 1944, p. 115; OD]. Medium to large with subpentagonal outline; dorsibiconvex; lateral and anterior margins steep. Beak erect; foramen elliptical, submesothyrid, with disjunct to conjunct deltidial plates. Fold and sulcus prominent anteriorly; tongue high, rectangular to acute. Much of valves smooth, with coarse, rounded costae developed only near lateral and anterior margins; superimposed fine, radial capillae commonly

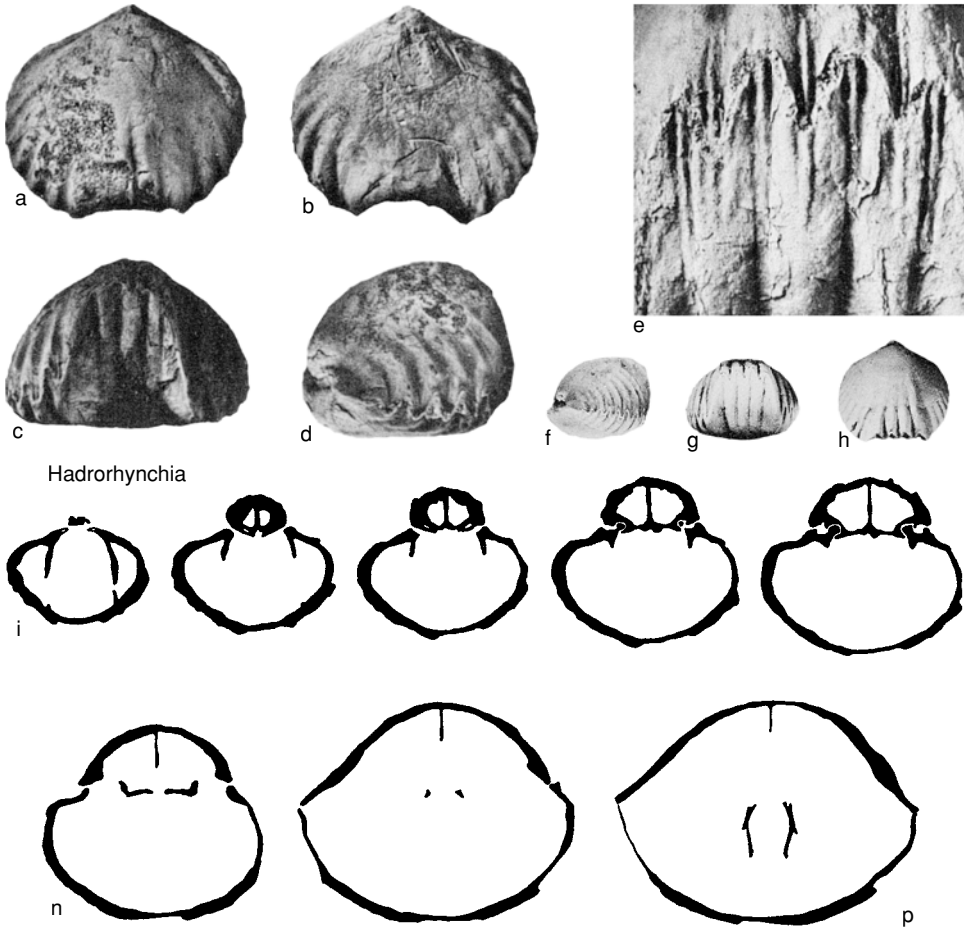


FIG. 767. Hadorrhynchiidae (p. 1129–1130).

developed; commissure denticulate with marginal grooves; marginal spines present. Dental plates short, subvertical. Dorsal median septum long, thin; small septalium; bilobed calluslike cardinal process. *Middle Devonian (Givetian)*: western North America, Siberia, China.—FIG. 767*a–p*. **H. sandersoni* (WARREN), Givetian, Mackenzie District, western Canada; *a–d*, lectotype, dorsal, ventral, anterior, and lateral views, $\times 1$; *e*, hypotype, spines at commissure, $\times 3$; *f–h*, hypotype, lateral, anterior,

and dorsal views, $\times 1$; *i–p*, serial sections 1.2, 1.65, 1.75, 2.15, 2.35, 2.65, 3.35, 3.9 from posterior, $\times 3$ (McLaren, 1962).

Droharhynchia SARTENAER, 1985b, p. 218 [**Hadorrhynchia intermissa* CRICKMAY, 1963, p. 2; OD]. Transversely subpentagonal outline; dorsibiconvex; anteriorly inflated. Beak suberect; foramen large, oval, submesothyrid, small deltidial plates disjunct. Fold and sulcus broad, arising at umbones; tongue strong, trapezoid, dentate. Umbones smooth; costae

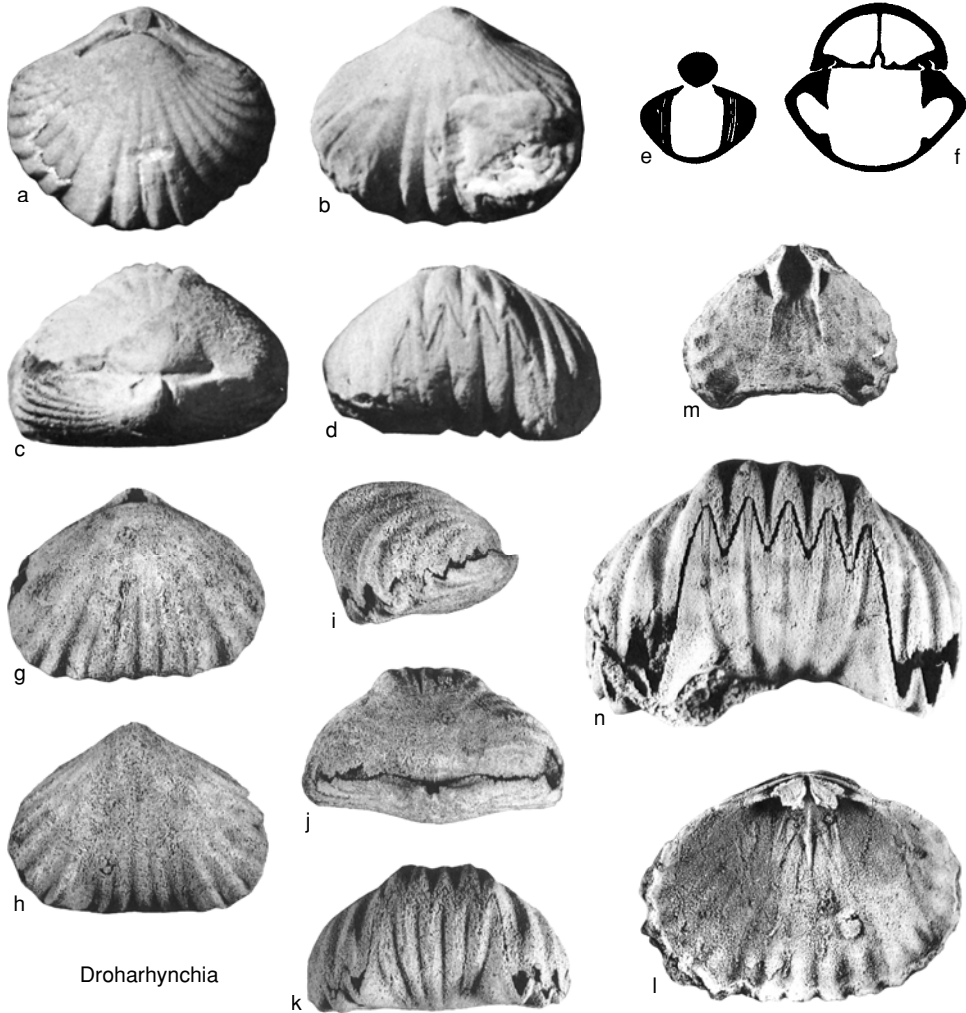


FIG. 768. Hadrorhynchiidae (p. 1130–1131).

coarse, low, rounded, simple, flattened and grooved on *paries geniculatus*. Dental plates distinct, ventrally convergent; ventral muscle field well impressed. Dorsal median septum thin, septalium distinct, open; dorsal median septum high, thin; cardinal process absent. *Middle Devonian (Eifelian-Givetian)*: western Canada, USA (Alaska).—FIG. 768a–f. **D. intermissa* (CRICKMAY), middle Givetian, Pine Point Formation, Great Slave Lake, Dis-

trict of Mackenzie, western Canada; a–d, holotype, dorsal, ventral, posterior, and anterior views, $\times 2$; e–f, serial sections 1.5, 2.5 from posterior, $\times 3$ (Crickmay, 1963).—FIG. 768g–n. *D. rzhonsnitskayae* BAXTER & BLODGETT, lower Eifelian, west-central Alaska; g–k, holotype, dorsal, ventral, lateral, posterior, and anterior views, $\times 2$; l, dorsal interior, $\times 2.6$; m, ventral interior, $\times 2$; n, paratype, anterior, $\times 2.8$ (Baxter & Blodgett, 1994).