ATHYRIDIDA

FERNANDO ALVAREZ and RONG JIA-YU

[University of Oviedo, Spain; and Nanjing Institute of Geology and Palaeontology]

ORDER ATHYRIDIDA

As here defined the order Athyridida includes the suborders Athyrididina, Retziidina, and Koninckinidina. All three suborders are characterized by a shell with a subcircular ventral foramen, in meso- to permesothyridid position and open or closed delthyrium, commonly obscured by the dorsal beak. Internally, cyrtomatodont hinge teeth articulate with dental sockets of variable shape depending on the degree of development of the cardinalia.

The athyridides, as the spiriferides, spiriferinides, and atrypides, developed a calcareous support for the lophophore in the form of spires disposed in cones. The apices of the cones were directed laterally in the athyrididines and retziidines and ventrally in the koninckinidines. Typically, the umbonal blades of the spiralium are sharply bent posterodorsally (posteroventrally in the koninckinidines) from the distal ends of the crura. A more or less elaborate jugum joined the dorsal half of the primary lamellae of each cone. In different stocks within the athyridides, accessory jugal lamellae intercoiled with primary volutions of the main spiralia to the apex of each cone.

More detailed accounts of the morphological variation displayed by the Athyridida are given below in the introductions to the systematic descriptions of each suborder.

SUBORDER ATHYRIDIDINA

The shells of athyrididines display great external morphological variability. Commonly moderately to strongly rostrate and unequally biconvex, the shell may also be planoconvex (e.g., *Lochengia*) or concavoconvex (e.g., *Galeatathyris*). Shapes vary from more or less globose, almost equidimensional, with varied outline (subcircular, e.g., *Nucleospira;* elongate oval to rounded pentagonal, e.g., *Athyris;* subtriangular in *Janiceps;* rhomboidal in *Triathyris*), to very transverse, winged shapes (e.g., *Anathyris*) with also less transverse forms having strongly carinate folds on their opposed valves (e.g., *Plicathyris*).

Athyrididines have a variety of folding patterns. Alternate folding may be uniplicate, parasulcate, or rarely sulcate. Alternate folding in which a variably developed median plica in the dorsal valve is opposed to a sulcus in the ventral valve (uniplicate) may develop two small sulci lateral to the median fold of the dorsal valve (parasulcate), or forms with folding practically opposed, with a median sulcus in both valves bounded laterally by two folds (bilobate) that may be strongly carinate (metacarinate). The great diversity of the anterior commissures of these brachiopods, resulting from different hydrodynamic models, includes a type of folding (mixed folding) in addition to those previously described by BUCKMAN (1907, 1918), THOMSON (1927), and WILLIAMS and ROWELL (1965b). Mixed folding (see ALVAREZ, 1990) is characterized by the presence of unequal folds that tend to be opposed in the middle and most lateral parts of the shell and to alternate in the intervening sectors. Shells with this type of folding tend to have median ventral and lateral dorsal folds that bifurcate. The bifurcated elements have variable development (Fig. 1001). Less common is the radial, ribbed ornamentation of the retzielloids and some athyridoids (athyrisinins, misoliins, and some athyridins); the fine, delayed costation progressively developed medially in *Cardiothyris* and *Triathyris,* and in the pradoiins; or the peculiar ornament of fine lines folded in a zig-zag, chevronlike pattern as in *Septathyris.*

One of the more obvious and, in some, even spectacular characteristics of athyridide shells is the development of varied growth

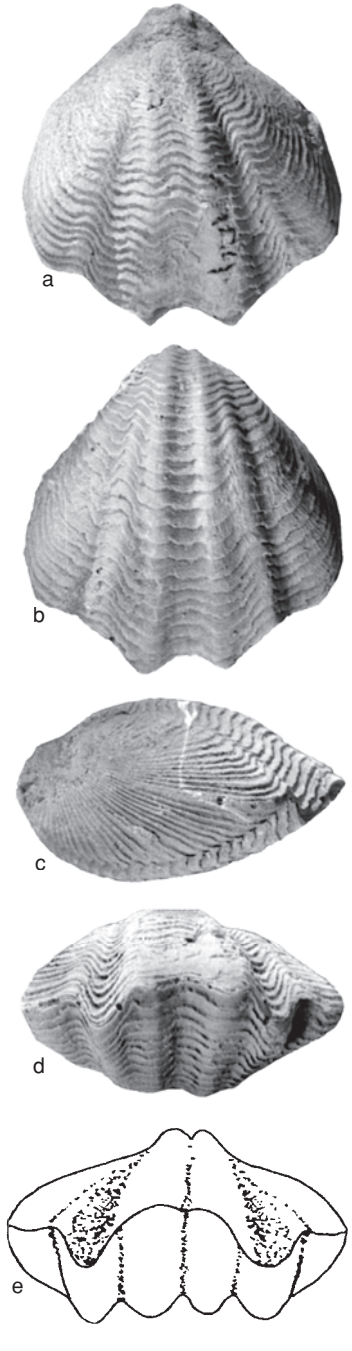


FIG. 1001. Mixed folding pattern in *Hexarhytis bonarensis* ALVAREZ; *a–e,* dorsal, ventral, lateral, anterior, and stylized anterior view, DPO 23921, ×2.5 (Alvarez, 1990).

lamellae (Fig. 1002–1003). The nature of these lamellae is a more significant character than, for example, folding and sulcation, which changed during ontogeny. The ornamentation present on the exteriors of most athyridide shells seems to have formed simply by regularly spaced concentric steps that are more or less strongly developed (e.g., Fig. 1002.6). In radial or longitudinal sections this ornamentation occurs as shelly extensions protruding from the surfaces of the valves at regular intervals and at different angles depending on the species (see ALVAREZ & BRUNTON, 1991). Commonly there are also differences in size, shape, and orientation between the lamellae in the dorsal and ventral valves (ALVAREZ, BRIME, & CURRY, 1987; ALVAREZ, 1990). In most Devonian genera (e.g., the plicathyridins) the lamellae are strongly recurved toward the surface of the valve (Fig. 1003.1, 1003.3) instead of being more or less flat tangents to the outer surface of the shell as happens in most meristelloids. In *Pachyplax,* the lamella are thick and overlap strongly so that the combination of lamellae and the entrapped sediment between them gives a rough, rugose external appearance to the shells. In any of the widely spaced growth lamellae of *Brimethyris* there are up to eight fine growth lines and a papillose microornamentation affecting both the primary layer and apparently most superficial secondary fibers (ALVAREZ, 1990, pl. 1,*2–5*). Some Late Devonian and Carboniferous genera developed long, delicate lamellae that are rarely preserved, with or without fine radiating striations (e.g., *Actinoconchus, Lamellosathyris*) or, as in *Cleiothyridina* and allied genera, the concentric shell lamellae project anteriorly and anterolaterally as flat, spinelike outgrowths, rectangular in section, that appear to be solid (Fig. 1004.1). In the long-ranging *Nucleospira,* both valves are ornamented with irregularly but commonly anteriorly concentrated growth lines and concentrically arranged fine spines of irregular diameter that project radially at high angles from the valve

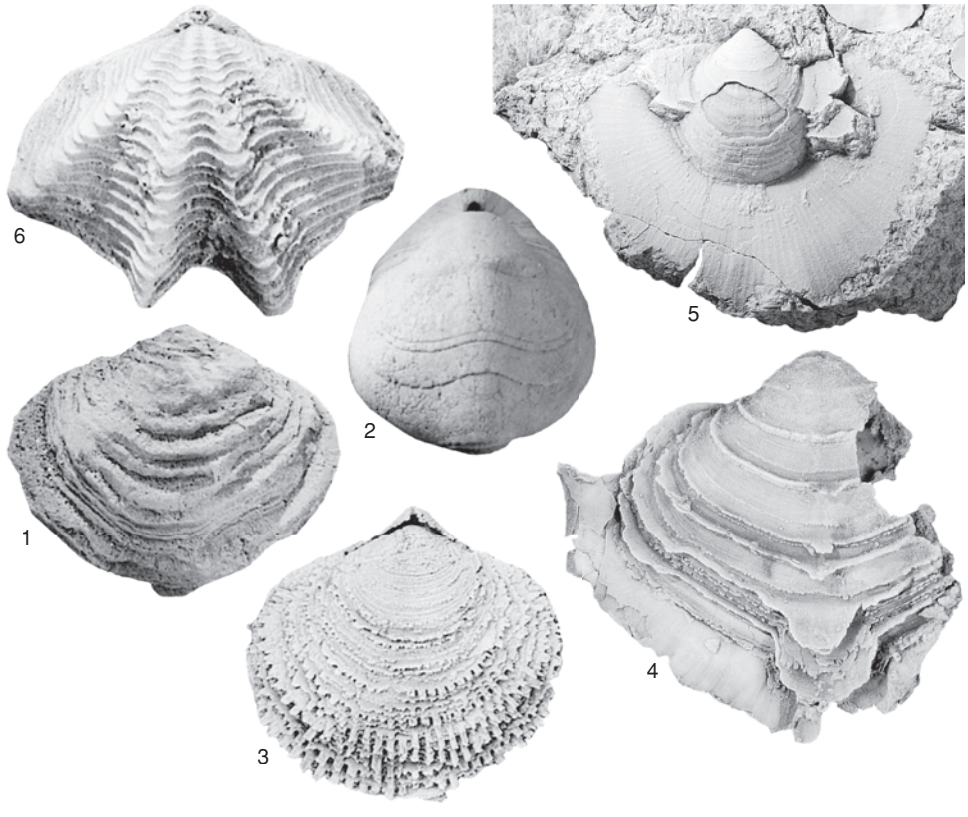


FIG. 1002. Athyridide growth lamellae; *1,* thick lamellae of *Pachyplax transversa* ALVAREZ & BRUNTON, DPO 18642, ×2.5 (Alvarez & Brunton, 1990a); *2,* flat lamellae on silicified specimen of *Spirigerella derbyi* WAAGEN, USNM 212887, ×2 (Grant, 1976; photograph courtesy of the late R. E. Grant); *3, Cleiothyridina fimbriata* (PHILLIPS); silicified specimen showing numerous, concentric, imbricated growth lamellae that project anteriorly as flat, spine-like outgrowths of rectangular section (these appear to be solid), BMNH BB 63452, ×3 (Brunton, 1984; photograph courtesy of C. H. C. Brunton); *4,* preserved marginal shelly flanges on silicified specimen of *Lamellosathyris lamellosa* (LÉVEILLÉ), BMNH BB 63398, ×2 (Brunton, 1984; photograph courtesy of C. H. C. Brunton); *5, Actinoconchus paradoxus* M'COY showing extensive lamellae near the commissure, BMNH BB B5392, ×1.5 (Brunton, 1980; photograph courtesy of C. H. C. Brunton); *6,* regularly spaced concentric lamellae of *Plicathyris ezquerrai* (DE VERNEUIL & D'ARCHIAC), EM 20232, ×3 (Alvarez, 1990).

surfaces (Fig. 1004.2). In some genera, as *Hexarhytis,* it is possible to recognize patches of radially disposed crenulations superimposed on the growth lamellae (see ALVAREZ, 1990, pl. 1,*1;* pl. 24,*19,21*). These are insufficiently developed to be spines but may be openings from which sensitive setae extended along the anterior margin of the mantle, similar to those present in specimens of recent species of *Terebratulina.* All these lamellae seem to have grown by successive outward transgression and regression of the mantle epithelium responsible for secretion of shell at the shell margin (see ALVAREZ, CURRY, & BRIME, 1985; ALVAREZ, BRIME, & CURRY, 1987; BRUNTON & ALVAREZ, 1989; ALVAREZ & BRUNTON, 1990b, 1991; BRUNTON, 1991). Such shells as the Carboniferous *Actinoconchus* or Devonian *Pachyplax* rapidly grew a pair of long lamellae at their valve margins. The lamellae at the edge of each valve grew parallel or subparallel to each other and temporarily formed the functional edges of the shell. Then mantle regression

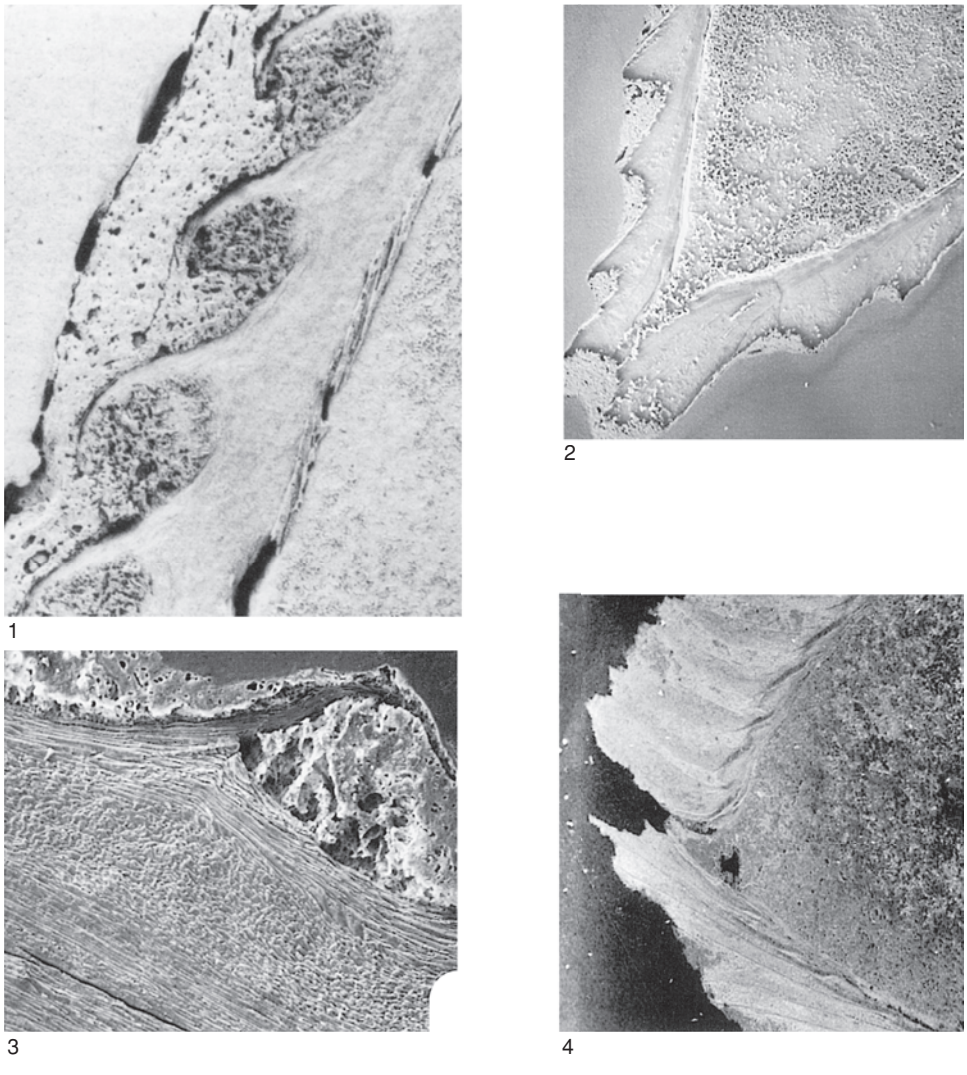
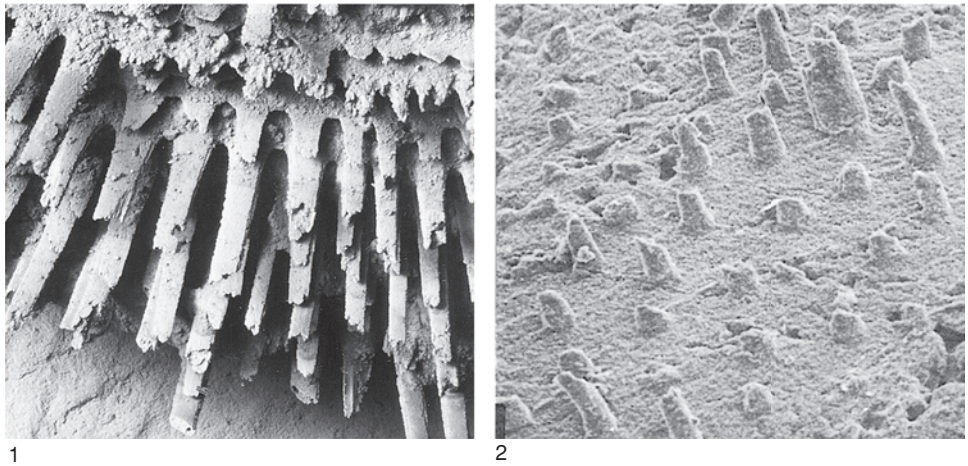


FIG. 1003. SEM photographs of longitudinal sections of athyridide shells showing size, shape, and disposition of growth lamellae; *1, Hexarhytis campomanesi* (DE VERNEUIL & D'ARCHIAC), DPO 16972, ×70 (Alvarez, Brime, & Curry, 1987); *2, Pachyplax elongata* ALVAREZ & BRUNTON, DPO 18740, ×15 (Alvarez & Brunton, 1990a); *3, Anathyris phalaena* (PHILLIPS), DPO 24484, ×166 (Alvarez, 1990); *4, Pachyplax transversa* ALVAREZ & BRUNTON, DPO 21160, ×19 (Alvarez & Brunton, 1990a).

took place, back to the true valve margin, which by this stage was left behind internally, well posterior to the margins of the lamellae (Fig. 1005.2). As forward growth was resumed between the pair of lamellae, the true valve edges grew obliquely toward each other for a short distance. This growth both increased the size of the valve and increased the depth of the mantle cavity, but at the same time it separated the inner surfaces of the lamellae so that space was left for the development of the next pair of lamellae. This development took place as a result of a change in direction of the growth of the mantle at a low angle away from the surfaces of the valves.



1 2

FIG. 1004. External spinose ornamentation present in *1, Cleiothyridina fimbriata* (PHILLIPS), detail of the anterior region of silicified dorsal valve showing concentric, imbricated, growth lamellae that project anteriorly as flat, spine-like outgrowths of rectangular section (these appear to be solid), BMNH BB 63452, SEM, ×12 (Alvarez, 1999b); *2, Nucleospira carlukensis* (DAVIDSON), detail of the anteromedial region of silicified ventral valve showing microspinous ornamentation, BMNH BB 61625, SEM, ×150 (Brunton, 1984; photograph courtesy of C. H. C. Brunton).

Posteriorly, the ventral valve has an area or palintrope, poorly delimited laterally by the umbonal ridges or not differentiated, usually containing a round pedicle foramen and triangular delthyrium. The opening is commonly obscured by the dorsal beak and usually laterally restricted by narrow deltidial plates that widen toward the base of the delthyrium and that may meet and interlock medially as in *Septathyris.* In *Anisactinella* the delthyrium is partially covered by a unique and irregularly triangular, flat or slightly curved, symphytium (the atypical pseudodeltidium of BENIGNI & FERLIGA, 1992), which bears no relationship to the foramen that, in this genus, occupies a supra-apical position (see BENIGNI & FERLIGA, 1992).

The ventral umbo of most athyrididines and retziidines has been partly destroyed by the expanding foramen, which commonly occupies a transapical, meso- to permesothyridid or more rarely epithyridid, position. Exceptionally the pedicle emerged between the apex of the ventral umbo and the hinge; subapical foramina with deltidial plates are present in the Silurian *Didymothyris* and young *Nucleospira,* while in mature *Nucleospira* a triangular, externally concave plate (deltidium) covers the delthyrium.

In most athyrididines, the beak of the ventral valve is divided internally into three unequal cavities by the dental plates, more or less parallel to the plane of symmetry. The wider central cavity is called the delthyrial cavity or pedicle chamber. The two lateral, narrower subtriangular cavities are the lateral apical cavities (Fig. 1005.1a). Between the dental plates, some didymothyridins have a peculiar structure, the pedicle support or pedicle fulcrum of RUBEL and MODZALEVSKAYA (1967) and MODZALEVSKAYA (1985), which consists of two curved plates formed of secondary-layer shell material deposited parallel to the dental plates. These curved plates divide the posterior portion of the delthyrial cavity into three parts, two laterally and a quite small one ventrally. They probably did not act as a real fulcrum for lifting but as a support for the pedicle. *Collarothyris,* an externally similar didymothyridin, instead has a dorsally convex delthyrial plate.

Pedicle collars, delthyrial plates, and other structures related to the pedicle are not easy to use as diagnostic characters because of

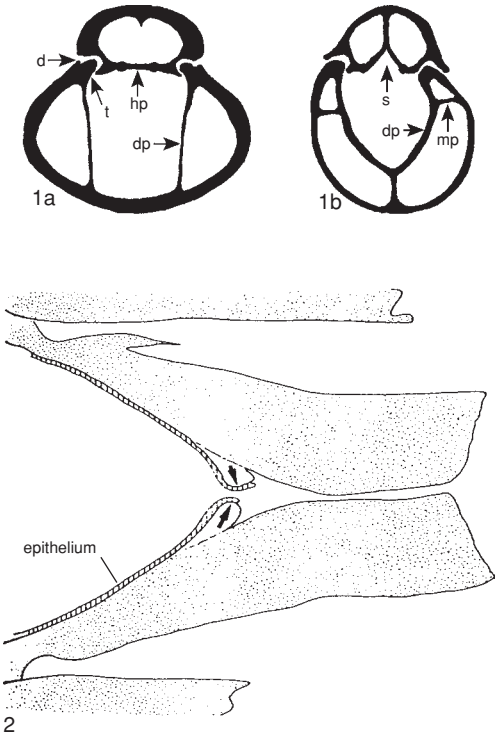


FIG. 1005. *1,* Enlarged drawings of transverse sections of *1a,* an athyridoid, ×3, and *1b,* a meristelloid, ×8, showing articulation and disposition of posteriorly placed structures: *d,* denticulum; *dp,* dental plates; *hp,* hinge plate; *mp,* mystrochial plates; *s,* septalium; *t,* tooth (new); *2,* stylized longitudinal section of anterior shell edge of *Pachyplax* showing bases of 2 pairs of most recently formed lamellae and true valve margins (*arrowed*) (adapted from Alvarez & Brunton, 1991, and Brunton, 1991).

their irregular and only sporadic calcification and preservation. Complete rings or pipelike structures similar to the ones developed in the retziidines do not occur in the athyrididines, but it seems clear that there was a trend toward greater complexity of ventral umbonal structures during Permian and Triassic times. Many specimens of Permian genera (*Spirigerella*) have a relatively small pedicle foramen bridged internally by a pair of plates that are analogous to the delthyrial plates of spiriferides. These plates slid past the dorsal beak as it entered the ventral valve during opening of the shell. They are conjunct in large adult specimens, disjunct in young adults, and incipient in juveniles. When conjunct, they cut off the foramen from the visceral chamber of the shell to leave the foramen as a mere recess, suggesting that the pedicle atrophied in adults. Triassic genera (*Tetractinella, Dioristella*) also possess more or less thick delthyrial plates that may be supported by a short septum as in *Clavigera.* Toward the apex of the beak, this plate contributes to the thickening of the cavity and may serve as a sessile pedicle collar, as in *Oxicolpella,* or it may be very complex, filling the delthyrial cavity almost completely, as in *Majkopella.* Such structures are not free in the manner of pedicle collars but fused laterally to the valve wall.

Commonly the dental plates support the hinge teeth, reinforce the umbonal region of the valve, and possibly act as places of attachment for the muscles. Their variability is closely related to that of the external morphology of the beak. In the athyrididines there is neither an angular difference nor a

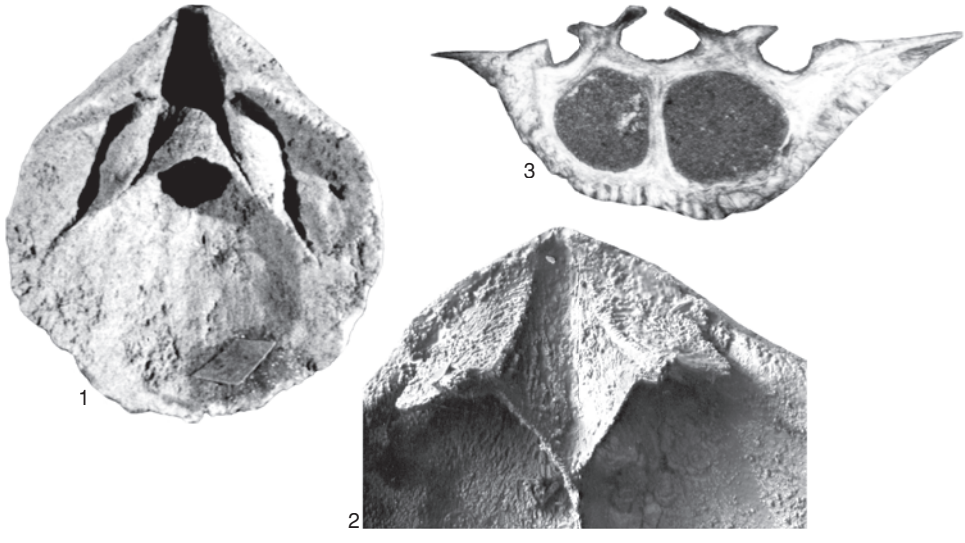


FIG. 1006. *1,* Ventral shoe-lifter in *Camarium typum* HALL, I1540, Hall collection, ×3 (Alvarez & Brime, 2000); *2,* septalium in *Meristella lata* (HALL), USNM 497416, SEM, ×10 (new); *3,* transverse section of *Retziella minor* (HAYASAKA), cardinalia, DPO F24241, ×10 (new).

clear groove separating the dental plate into components of a ventral adminiculum and dental flange, as commonly happens in the narrowly hinged spiriferides (BRUNTON, ALVAREZ, & MACKINNON, 1996, fig. 8), but these terms are helpful when describing, for example, the dental plates of some Triassic athyridoids (*Ochotathyris, Dioristella*) that are weakly developed anteroventrally (short adminicula) but strongly developed below the teeth (long dental flanges). The lateral apical cavities can be partly or completely filled by secondary shell material in adult specimens of some genera (*Meristella, Majkopella*). The posterior thickening observed in some specimens seems to have had a functional significance in relation to the acquisition of a more suitable orientation so that the center of gravity of the shell moved posteriorly to a position close to the point of attachment. As in other groups of articulated brachiopods, athyrididine dental plates can converge and fuse above the floor of the ventral valve in a spondylium, usually elevated above the floor by the septum duplex formed by coalescence of the dental plates. The spondylium resembles a deep, boat-shaped trough in the posterior part of the valve and becomes shallow and scoop shaped anteriorly where the dental plates terminate and only the base persists. In *Camarophorella* and some other genera, the spondylium may be supported not only by the median septum but also by more or less well-developed plates (mystrochial plates) that are confined to the umbonal region and extend anteriorly and laterally to the valve wall, nearly parallel to the plane of the lateral commissure (Fig. 1005.1b). Some genera, as *Camarium,* developed an arched platform (shoe-lifter) of secondary shell (with a chamber or cella beneath) that bore part of ventral muscle field (Fig. 1006.1).

A variably developed median septum is present in the ventral valve of some genera. In *Nucleospira* the medium septum is long, projecting from the umbonal cavity toward the anterior commissure. In some diplospirellins such as *Anisactinella quadriplecta,* the median septum is not elevated. At about one-third the total length of the valve, it thickens and stops (in some instances making a pronounced protrusion), branching into two elevated lateral septa and a small median septum. In others, as *Diplospirella wissmanni,* it appears initially as a thin ridge

growing from a low, broad platform, subsequently becoming more massive and triangular in section (Benigni & Ferliga, 1990, 1992).

ARTICULATION

Athyridides normally have strong teeth and sockets. The hinge teeth are cyrtomatodont, commonly subrectangular to ovate in section. This type of dentition allows great flexibility in growth, remaining functional during ontogeny even in those athyridides that commonly have dorsal and ventral umbos very close together in their adult stages. In some genera, as in *Anisactinella,* teeth are massive, directed posteromedially, and supported by thick, poorly differentiated plates that seem to have grown from the anterior side of the symphytium in a posterolateral direction instead of posteroanteriorly, the common situation. The cyrtomatodont hinge teeth fit dental sockets of variable shape, narrow near the umbones and widening anterolaterally. They are bordered internally by normally prominent inner socket ridges and externally by less well-developed outer socket ridges. The shape of the dental sockets depends on the degree of development of the inner socket ridges, which usually rise ventrally and then curve laterally overhanging the socket. In some specimens the ventral end of the inner socket ridge fits against a groove or small cavity (crural fossette) in the inner part of the tooth, thus aiding articulation. In addition, the posterior edge of the cardinal area of the ventral valve (denticulum) is articulated with a socket present in the outer socket ridges of the dorsal valve (accessory socket). A small ridge on the outer socket ridge also inserts into the socket (denticular cavity) between the tooth and the posterior edge of the valve (Fig. 1005.1). The articulation described above is reinforced by the cardinalia and, in the more transverse forms, by the posterior edges of both valves that remained in contact during opening and closing movements. In most transverse forms (e.g., *Anathyris*) the palintrope is a morphological artifact allowing opening of the shell. The combined action of all these structures prevents lateral movement of one valve against the other.

CARDINALIA

In athyridides, as in other articulated groups, a wedge of shell, the outer hinge plate, is laid down between the inner socket ridge and the growth traces of the paired crura. Inner hinge plates, extending medially from the crural bases, commonly form a trough supported by the dorsal median septum that is Y-shaped in cross section. This is the usual form of a septalium (Fig. 1006.2). Less commonly the inner hinge plates fuse directly to the valve floor, forming a V-shape in cross section (sessile septalium; e.g., *Charionella*). The meristelloids characteristically have septalia of different types and shapes. A functional relationship between adjustor muscles and the inclined plates forming the sides of the septalium (inner hinge plates) is not clear in fossil groups; therefore the term crural plate is commonly used for these inclined plates (Brunton, Alvarez, & MacKinnon, 1996). A cruralium is present in some meristelloids (e.g., *Rowleyella*). The cruralium extends anteriorly much farther than a septalium, commonly well anterior of the distal ends of the sockets or to the origins of the crura. In some retziellids, as *Retziella,* paired plates extend ventromedially over shallow septalia from the outer hinge plates (Rong & others, 1994). These covering plates resemble posteriorly an incomplete connectivum (Havlíček, 1961), but evidence from serial sections (Fig. 1006.3) shows them to differ from the situation that occurs in most rhynchonellides (see discussion by Brunton, Alvarez, & MacKinnon, 1996).

In athyridoids the inner hinge plates extend medially from the crural bases, commonly parallel to the commissure (Fig. 1007). In hyattidinins they do not meet

medially, but in all other athyridoids the inner hinge plates are well developed (although they may not be differentiated medianly), forming a hinge plate (Fig. 1007). When the crural bases do not form ridges on the surface of the hinge plates, it is difficult to differentiate outer and inner hinge plates, and a single plate (cardinal plate) extends between the inner socket ridges. In some diplospirellins (*Diplospirella*), the hinge plate is not parallel to the commissure but is steeply inclined posterodorsally, delimiting a triangular depression at the apex of the cardinalia (cardinal pit of BENIGNI & FERLIGA, 1990, p. 45 and fig. 4).

In many earlier athyridides, either the hinge plate or cardinal plate is perforated posteromedially by a hole connecting the beak chamber to its ventral surface. This dorsal foramen (Fig. 1007.1–1007.2), first described and figured by KING (1850), has been termed a visceral foramen by several authors (e.g., BEECHER, 1892, p. 147; HALL & CLARKE, 1894, p. 819; SCHUCHERT, 1897, p. 113) in the belief that it served as an anal opening. Other authors, however, considered that this foramen accommodated the dorsal ends of the diductor muscles (COOPER & GRANT, 1976a; ALVAREZ & BRUNTON, 1990b; BRUNTON, ALVAREZ, & MACKINNON, 1996). During the evolution of athyridides the diductor muscles probably migrated from the dorsal beak via the dorsal foramen to the hinge plates, as can be observed during the ontogeny of *Eohemithiris* (ALVAREZ & BRUNTON, 1990b; BRUNTON, ALVAREZ, & MACKINNON, 1996). In geologically younger taxa, the adult diductor muscles attached to the posterior region of the hinge plate where exaggerated shelly flanges (cardinal flanges) grew at the posterior ends of the inner socket ridges (Fig. 1007.3). The dorsal foramen shows signs of having been overgrown or filled by shell late in ontogeny. This suggests that the foramen may commonly have been a functional feature in adult athyridides in the geologically earliest stocks but was reduced to a nonfunctional canal that was subsequently infilled in most Late Paleozoic and Mesozoic species.

The detailed development and appearance of cardinal flanges among adults varies considerably within the athyridides, although in most they seem also to have aided articulation by overhanging the posterior ends of the sockets and in sealing the posterior valve margin by curving ventroposteriorly into the ventral beak cavity (Fig. 1007.3b). In some taxa, as *Anathyris, Composita,* and *Anisactinella* (DAGYS, 1974; ALVAREZ, 1990; BENIGNI & FERLIGA, 1992; BRUNTON, ALVAREZ, & MACKINNON, 1996), there are grooves on the lateral surfaces of the cardinal flanges fitting against different denticulum-like structures protruding from the ventral valve below the teeth. In some Triassic species of *Anisactinella,* a well-developed, subrectangular cardinal flange abuts the symphytium and seems to prevent excessive anterior opening of the shell (BENIGNI & FERLIGA, 1992). The main function of the cardinal flanges in many genera, however, was as the site of attachment for the diductor muscles. In Devonian genera (e.g., *Pachyplax*) and some species of *Composita*, these elevated flanges are confined posteriorly on the hinge plate and became serrated myophores. In others, diductor myophores spread over most of the ventral surface of a reduced but heavily thickened cardinal plate, as in some examples of *Lamellosathyris* (Fig. 1008.1) or Permian *Composita* (Fig. 1007.3c).

In general the athyridides display a phylogenetic trend from Devonian genera, with no cardinal flanges or only small ones and an open dorsal foramen, to late Paleozoic genera that lost the dorsal foramen and developed strong cardinal flanges that became united into a single structure (some with paired diductor pits, as in *Spirigerella;* Fig. 1008.2). Such a structure resembles the cardinal process (DAVIDSON, 1853b) of most orthides and strophomenides *s.l.,* but its

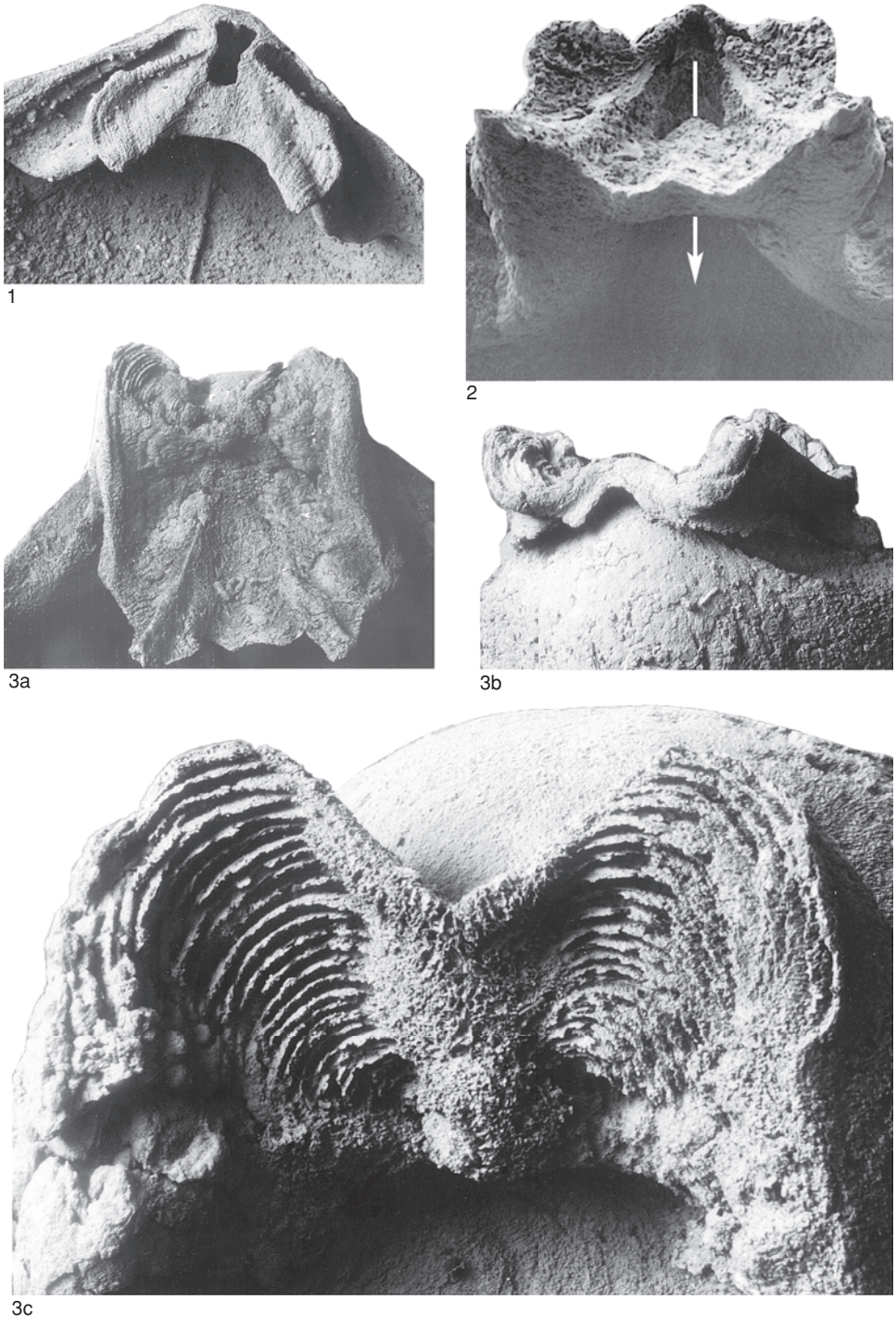


FIG. 1007. *For explanation, see facing page.*

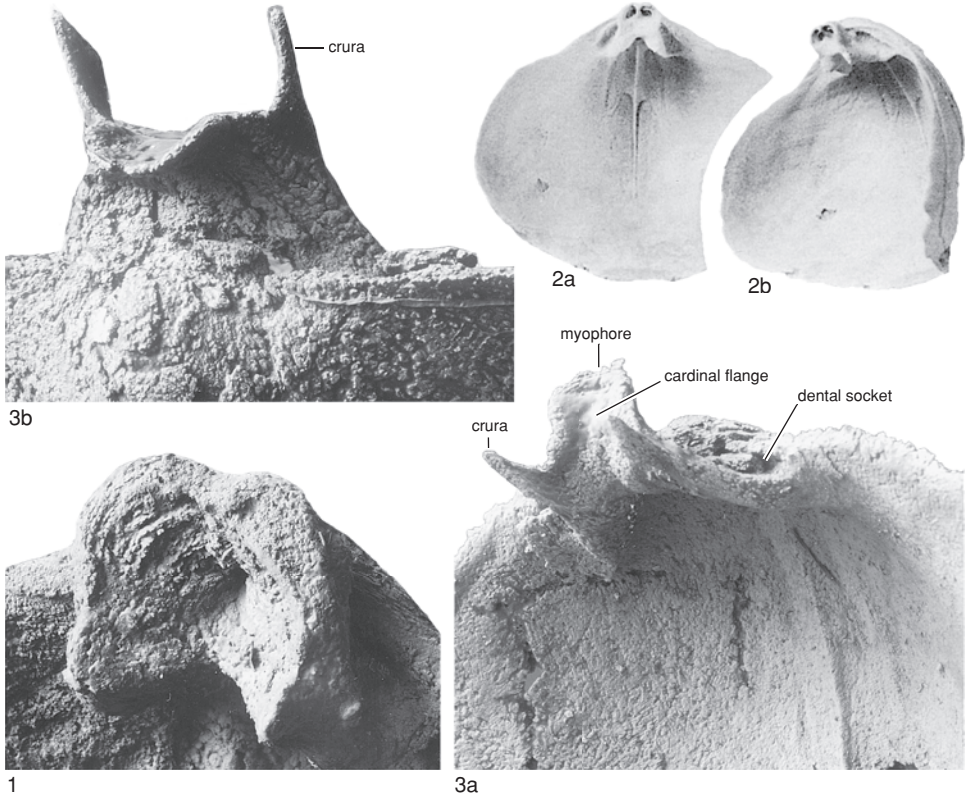


FIG. 1008. *1, Lamellosathyris lamellosa* (LÉVEILLÉ), cardinalia in which diductor myophores spread over most of ventral surface of reduced, but heavily thickened, cardinal plate, BMNH BB 63399, SEM, ×10 (Brunton, Alvarez, & MacKinnon, 1996); *2a–b, Spirigerella derbyi* WAAGEN, dorsal interior straight on and tilted showing pair of diductor myophore pits surrounded by strong and unified cardinal flange, USNM 212890, ×2 (Grant, 1976; photographs courtesy of the late R. E. Grant); *3a–b, Nucleospira carlukensis* (DAVIDSON); *3a,* anterolateral view of cardinalia showing dental sockets, crura, and myophore on distal, ventral face of united cardinal flanges, BMNH BB63459, SEM ×22; *3b,* oblique posterior view of same specimen showing crura and posteriorly recurved cardinal flange with no trace of myophores externally, BMNH BB63459, SEM, ×28 (Brunton, Alvarez, & MacKinnon, 1996).

FIG. 1007. SEM photographs showing different athyridoid cardinalia: *1, Cleiothyridina seriata* GRANT, cardinalia with posteriorly enlarged dorsal foramen, USNM 486331, ×5.7 (Brunton, Alvarez, & MacKinnon, 1996); *2, Pachyplax gyralea* ALVAREZ & BRUNTON, cardinalia showing ventral opening to dorsal foramen (*arrowed*), general dorsal convexity of inner hinge plates with their slight ventral surface median ridge, and prominent shelly flanges posteriorly on inner socket ridges, DPO 25013, ×35 (Alvarez & Brunton, 1990a); *3a–c, Composita crassa* COOPER & GRANT; *3a,* ventral view of cardinalia showing broken crura, crural bases, and cardinal flanges, united and elevated posteriorly on hinge plate, USNM 153009h, ×8 (Brunton, Alvarez, & MacKinnon, 1996); *3b,* posterior, slightly posterolateral view of dorsal umbo showing prominent cardinal flanges that, curving ventroposteriorly into ventral beak cavity, restrict delthyrial space and help with sealing of posterior shell margin, USNM 485991, ×8 (Brunton, Alvarez, & MacKinnon, 1996); *3c,* enlarged view of well-preserved serrated myophores on cardinal flange, USNM 485990, ×30 (Brunton, Alvarez, & MacKinnon, 1996).

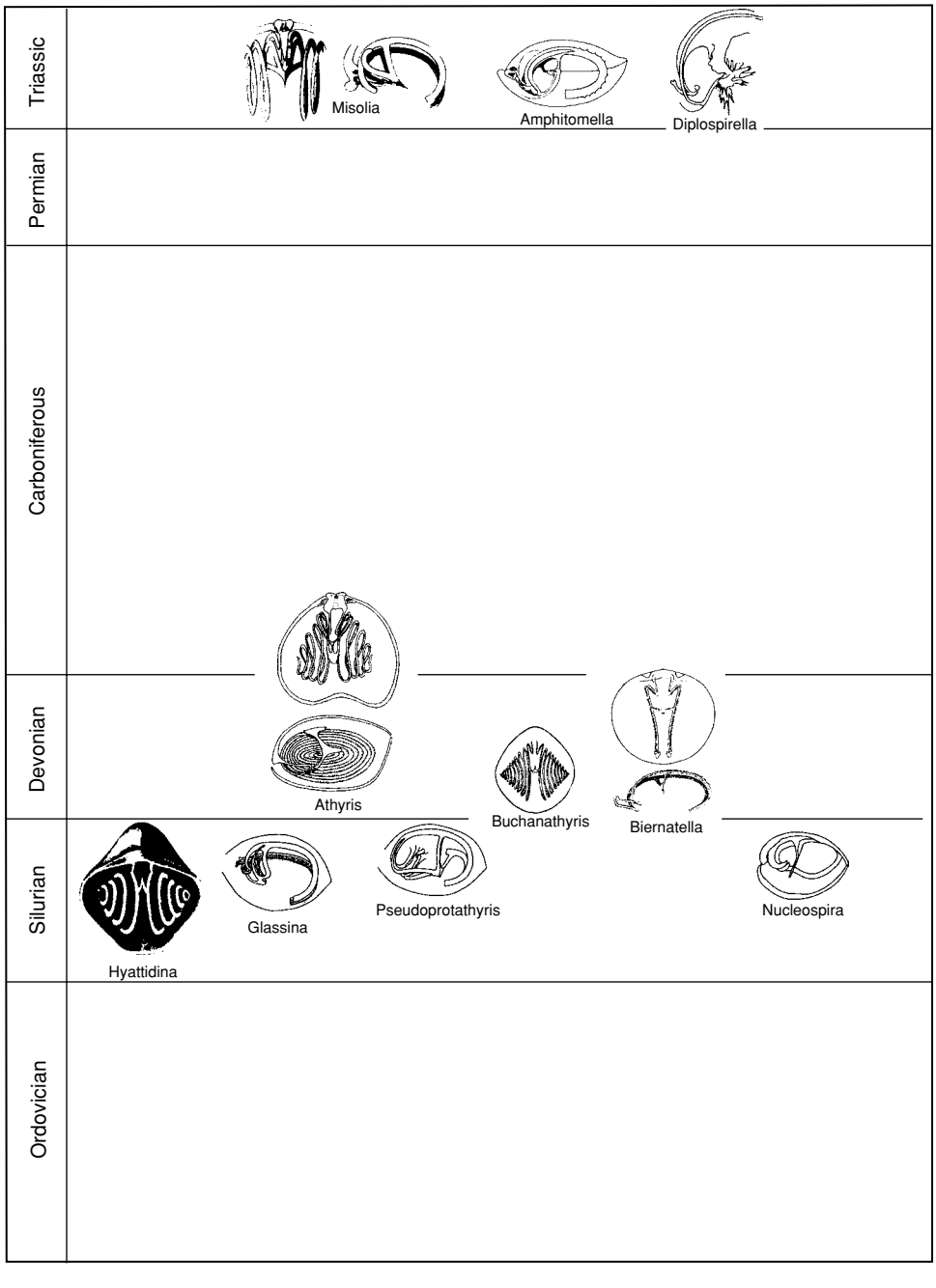


FIG. 1009. Main types of athyridoid and nucleospiroid brachidium (new).

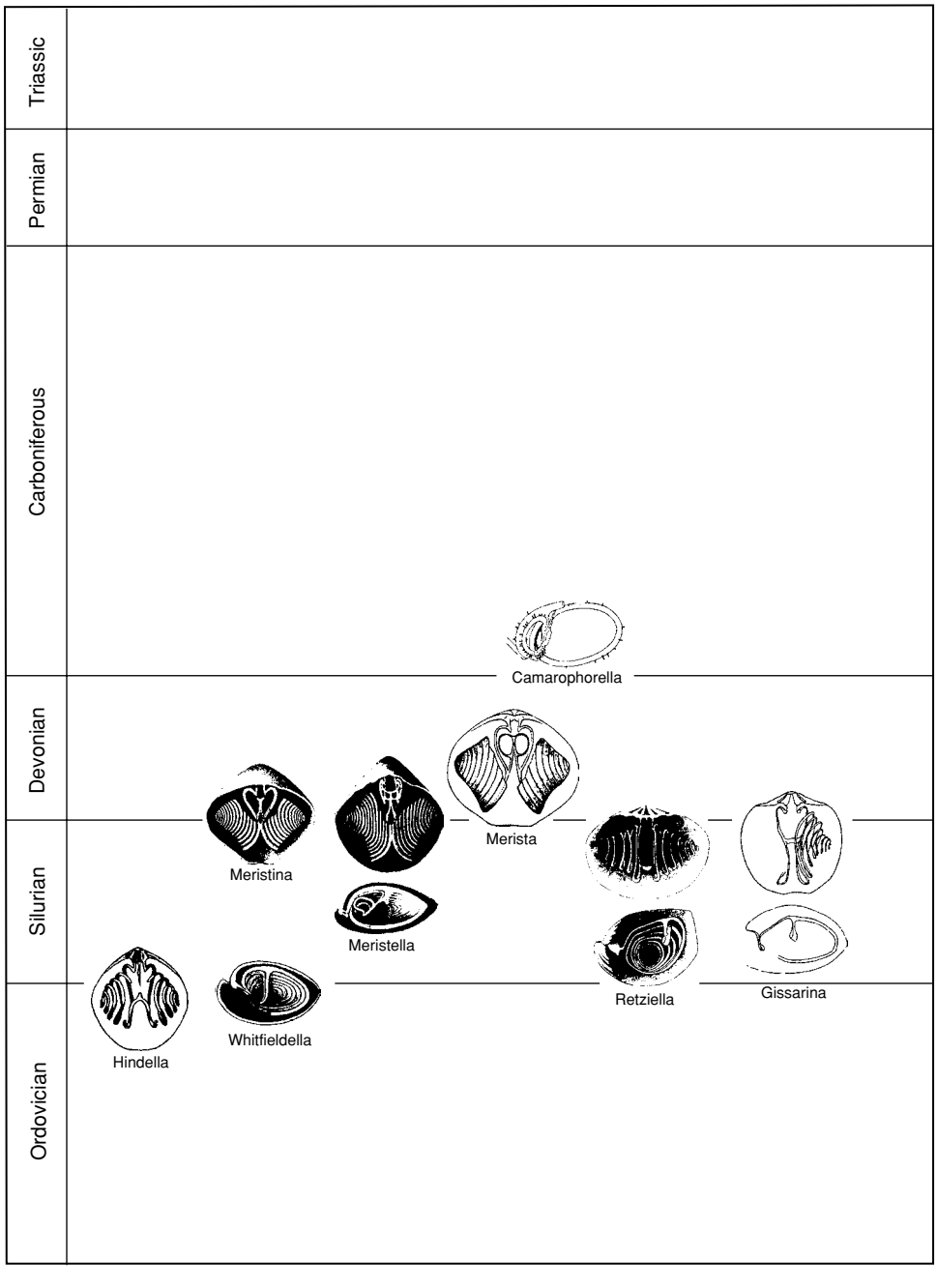


FIG. 1010. Main types of meristelloid and retzielloid brachidium (new).

position on the cardinal plate and its origin show it to be different (Brunton, Alvarez, & MacKinnon, 1996). In *Nucleospira* the juvenile seat of diductor muscle attachment was on small cardinal flanges posteriorly placed between the crural bases. By adulthood a fused and exaggerated cardinal flange had grown posteroventrally, carrying the myophores deeply into the ventral umbo (Fig. 1008.3). The posterior face of this structure is entirely smooth, indicating that it was covered by outer epithelium responsible for its secretion; it bears no trace of the myophore growth (Brunton, Alvarez, & MacKinnon, 1996, fig. 20a–b). In most athyrididés, a relatively low ridge or myophragm of secondary shell developed medianly between paired muscle scars, typically separating adductor muscle scars. This structure contrasts with the meristelloid septum, a high, bladelike structure that may be seen in cross section as a strong inward flexure in the secondary layer fibers, normally originating close to the primary to secondary layer boundary.

Analyses, description, and comparison of such internal structures as dental plates, pedicle collars, cardinalia, brachidia, dorsal median septa, and the myophragm are especially difficult when reconstructing them from serial sections made from one (or at best a few) specimens. The myophragm and septum are easily misunderstood if compared from serial sections of specimens of different ages or convexity or if the sections were made at different angles in the different specimens.

BRACHIDIUM

The brachidium is a highly fragile structure feebly connected to the cardinalia and thus subject to postmortem mechanical damage from infilling with coarse sediment. It is easily obliterated during diagenesis. Silicified material presenting preserved brachidia is scarce. Consequently the brachidium and particularly the jugal structure have been clearly observed in only a few genera, and there is almost no information about growth or intraspecific variation. The configuration of this important structure is known for fewer than 50 percent of the genera commonly considered as athyrididés. Until their jugal structure is determined, a confident decision concerning the relationship between genera and suprageneric taxa cannot be made, and remains speculative.

A pair of small calcareous supports, the crura, commonly extend ventrally or anteroventrally from the anterior edge of the cardinal plate, parallel to or converging slightly toward the plane of symmetry. After some distance, the crura give rise to the primary lamellae of the brachidium. In athyrididines and retziidines, the umbonal blades of the spiralia curve posteriorly, passing close to the sockets or inner socket ridges, and then curve toward the front, parallel with the plane of symmetry. They thus differ from spiriferides and spiriferinides in which the primary lamellae of the spiralia are direct prolongations of crura. The primary lamellae of atrypides typically curve laterally from the crura parallel with the commissural plane. It is reasonable to assume that the umbonal blades spring from the crura (see discussion by Alvarez, 1999a), but forms in which the brachidium is discontinuous with the crura have been recorded among Paleozoic Athyrididae (Copper, 1986a, 1986b; Copper in Copper & Gourvennec, 1996) and Triassic species (Benigni & Ferliga, 1990).

Two different interpretations of the growth of spiralia have been proposed by Samtleben (1972) and MacKinnon (1971, 1974). In the athyrididés, secondary fibers seem to have been secreted only on the basal side of the spire. The opposite side (the one facing the apex of the spiral cone or apical side) does not bear secondary layer mosaic. This single-sided growth pattern is quite distinct from the double-sided growth pattern of atrypides and spiriferides (MacKinnon, 1974, 1991). The primary lamellae continue in a helical fashion as a set of spires, whose number varies depending on the size and

TABLE 18. States of 37 characters used in cladistic analyses (Fig. 1011) of the order Athyridida (new).

1. size: small (0); moderate (1); large (2); very large (3).
2. lateral profile: biconvex (0); plano or concavoconvex (1).
3. radial ornament: smooth (0); plica (1); ribs (2); fine lines (3); delayed costation (4).
4. spines: absent (0); rounded (1); tabular (2); hollow (3); fimbriae (4).
5. growth lines: absent (0); weak (1); strong (2).
6. frills: absent (0); short (1); long (2).
7. fold and sulcus: absent (0); weak (1); strong (2); fold both valves (3); sulcus both valves (4).
8. adult folding: alternate (0); opposite (1); mixed (2).
9. palintrope: reduced (0); moderate (1); extensive (2).
10. palintrope orientation: catacline-apsacline (0); apsacline (1); apsacline-orthocline (2); orthocline (3).
11. hinge line: strophic (0); almost strophic (1); astrophic (2).
12. hinge line width: short (0); medium (1); long (= greatest shell width) (2).
13. pedicle opening: hypothyridid (0); meso-permesothyridid (1); permeso-epithyridid (2); epithyridid (3).
14. delthyrium: open (0); partially covered (1); completely covered (2).
15. pedicle supports: absent (0); pedicle collar (1); delthyrial plate (2).
16. dental plates: absent (0); short (1); medium (2); long, not extending as ridges anteriorly along muscle scars (3); long extending (4); indistinct (5).
17. mystrochial plates: absent (0); present (1).
18. ventral shoe-lifter: absent (0); present (1).
19. spondylial structure: absent (0); present (1).
20. ventral median septum: absent (0); short (1); long, supporting spondylium (2); long, not related to spondylium (3).
21. ventral muscle field: deeply impressed (0); moderately (1); weakly (2).
22. cardinal plate: absent (0); without inner hinge plate (1); disjunct (2); apically perforate (3); not perforate and thick (4); not perforate, inner hinge plates short, supported by high septum (5); not perforate, inner hinge plates very short or absent, low dorsal median septum or myophragm present (6).
23. cardinal process: absent (0); moderate (1); strong (2).
24. myophragm: absent (0); present (1).
25. dorsal median septum: absent (0); short, moderately high (1); short, very high (2); long, moderately high (3); long, very high (4).
26. septalium: absent (0); deep, narrow, and partially covered (1); shallow and partially covered (2); deep, narrow, and uncovered (3); shallow and uncovered (4); wide and uncovered (5).
27. cruralium: absent (0); present (1).
28. dorsal shoe-lifter: absent (0); present (1).
29. brachidium: absent (0); present, tips directed laterally (1); ventrally (2).
30. primary lamellae: absent (0); curving posterodorsally from crura (1); curving laterally from crura (2).
31. jugum: absent (0); present between spiral cones (1).
32. lateral branches of jugum: absent (0); vertical (1); inclined anteriorly (2); posteriorly (3); strong posteriorly (4); almost parallel to commissural plane (5).
33. jugal saddle: absent (0); directed anteriorly (1); directed posteriorly (2).
34. jugal stem: absent (0); short (1); long (2).
35. arms of the jugum: absent (0); present (1).
36. accessory jugal lamellae: absent (0); free and short (1); reunite with stem (2); reunite with lateral branches of jugum (3); free, ending near lateral branches of jugum (4); free, intercalated with spiralia to apex (5); secondarily connected with spiralia (6).
37. shell structure: impunctate (0); punctate (1).

morphology of the specimens, to produce spiral cones with the apex directed laterally, anterolaterally, or ventrally (in koninckinidines). The anterior half of the more basal whorls is much longer than the posterior half; apical whorls are more nearly circular or oval. Variation of shell convexity does not appear to have altered significantly the direction of the axes of the cone. The number of whorls in a spiral cone may vary with each genus and, depending on the size of the individuals, also with different species of one

TABLE 19. Character-state matrix used in PAUP analysis (Fig. 1011) of characters as listed in Table 18. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ancistrorhynchidae	1	0	2	0	0	0	1	0	0	2	2	0	0	0	0	2	0	0	0
Athyridinae	2	0	0	0	2	1	1	0	0	1	2	0	1	0	0	2	0	0	0
Athyrisininae	2	0	2	0	2	2	2	0	0	2	2	1	1	0	0	2	0	0	0
Camarophorellinae	1	0	0	0	1	0	0	1	0	3	2	0	1	0	0	3	1	0	1
Clavigerinae	3	0	1	0	1	1	4	1	2	3	0	2	2	0	0	2	0	0	0
Cleiothyridininae	2	0	0	2	2	2	1	0	0	2	2	0	1	0	0	1	0	0	0
Comelicaniinae	3	0	1	0	1	1	1	0	1	2	1	2	0	0	0	1	0	0	0
Didymothyridinae	1	0	0	0	1	0	1	0	0	2	2	0	9	9	9	1	0	0	0
Diplospirellinae	0	0	0	0	1	0	0	1	0	3	2	0	2	0	0	1	0	0	0
Helenathyridinae	0	0	0	4	1	1	0	1	0	2	2	0	9	9	0	1	0	0	0
Hungarispirinae	0	0	1	0	1	0	4	1	2	3	1	2	2	2	0	0	0	0	0
Hustediinae	1	0	1	0	1	0	1	0	1	3	1	1	1	2	1	0	0	0	0
Hyattidinidae	1	0	0	0	1	9	2	0	0	2	2	0	9	0	0	1	0	0	0
Koninckinoidea	1	1	0	0	0	0	1	0	0	2	0	2	9	9	0	2	0	0	0
Lochengiinae	3	0	0	0	2	1	0	1	0	3	2	1	1	0	0	0	0	0	0
Meristellinae	2	0	0	0	1	0	1	0	0	2	2	0	1	1	0	5	0	0	0
Meristinae	2	0	0	0	1	0	1	0	0	2	2	0	1	0	0	4	1	1	0
Misoliinae	2	0	2	0	1	0	0	1	0	3	2	0	2	9	0	1	0	0	0
Mongolospiroidea	1	0	0	0	0	0	0	1	0	3	2	0	1	2	0	1	0	0	0
Neoretziinae	2	0	1	0	1	0	9	9	1	3	1	1	2	2	1	0	0	0	0
Nucleospiroidea	1	0	0	1	1	0	1	0	0	1	1	1	0	2	2	0	0	0	0
Ochotathyridinae	3	0	0	0	1	0	1	0	0	2	2	0	2	0	2	5	0	0	0
Parazygidae	1	0	2	3	2	1	1	0	0	1	2	1	1	2	1	2	0	0	0
Plectospirinae	0	0	1	0	1	0	1	0	1	2	1	1	1	2	0	0	0	0	0
Plicathyridinae	2	0	1	0	2	2	2	2	1	3	1	1	1	0	0	2	0	0	0
Pradoiinae	2	0	4	1	1	9	4	1	1	3	2	0	1	0	0	2	0	0	0
Retzielloidea	1	0	2	0	1	0	1	0	1	2	2	0	1	0	0	1	0	0	0
Retziidae	2	0	2	0	1	0	1	0	1	2	2	0	2	2	1	0	0	0	0
Rhynchospirinidae	1	0	2	0	2	0	1	0	0	1	2	1	1	2	9	9	0	0	0
Rowleyellinae	0	0	0	0	1	0	0	1	0	3	2	0	1	0	0	3	1	0	1
Septathyridinae	2	0	3	0	1	0	2	0	0	2	2	1	1	2	0	3	0	0	0
Spirigerellinae	2	0	0	0	1	1	1	0	0	2	2	0	1	0	0	2	0	0	0
Tetractinellinae	1	0	1	0	2	1	1	1	1	3	1	1	2	0	2	2	0	0	0
Triathyridinae	2	0	3	0	1	0	3	1	0	2	2	0	3	1	0	1	0	0	0
Trigonirhynchiidae	1	0	2	0	0	0	1	0	0	2	2	0	0	1	0	2	0	0	0
Whitfieldellinae	2	0	0	0	1	0	0	1	0	2	2	0	1	0	0	1	0	0	0
Xenosariinae	1	0	0	0	1	0	4	1	0	2	1	0	0	0	0	0	0	0	0

genus. This variation is small, however, and not useful taxonomically.

There is no apparent evolutionary trend toward an increase or decrease of spiral lamellae in the cones. A relationship between size, shape, and disposition of brachidium whorls, folds, and anterior projections of the shell was noted for several genera, as well as a relationship between shape, size, and jugal arch; the location of the median folds of the shell; and the disposition of the anterior commissure (ALVAREZ, 1990, fig. 154–156, 159; BENIGNI & FERLIGA, 1992).

Near the middle or in the posterior third of the primary lamella on the ventral edge is a jugal process (the lateral branch of the jugum), that projects anteriorly, anteroventrally, ventrally, or more rarely posteriorly until it joins the lateral branch of the jugum from the opposed spiral cone to form the jugal arch. This arch can be acute, as in most meristelloids, or rounded (commonly in athyridoids). The lateral branches may arise near the middle of the dorsal part of the primary lamellae (which is the approximate midpoint of the dorsal valve) or posterior or

TABLE 19. *(Continued).*

Character no.	20	21	22	23	24	25	26	27	28	29	30	31	22	33	34	35	36	37
Ancistrorhynchidae	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Athyridinae	0	2	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Athyrisininae	0	2	3	9	9	0	0	0	0	1	1	1	2	1	2	1	1	0
Camarophorellinae	2	9	0	0	0	4	4	0	1	1	1	1	2	9	2	1	3	0
Clavigerinae	1	0	4	2	1	0	0	0	0	1	1	1	2	9	2	1	1	0
Cleiothyridininae	0	1	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Comelicaniinae	0	2	3	2	0	0	0	0	0	1	1	1	9	9	9	9	4	0
Didymothyridinae	0	2	3	0	1	0	0	0	0	1	1	1	9	1	2	1	4	0
Diplospirellinae	0	2	4	2	1	0	0	0	0	1	1	1	2	0	2	1	5	0
Helenathyridinae	0	2	3	0	0	0	0	0	0	1	1	1	2	9	2	1	5	0
Hungarispirinae	0	2	6	2	0	4	0	0	0	1	1	1	0	0	2	1	5	1
Hustediinae	0	2	6	2	0	1	0	0	0	1	1	1	2	0	2	0	0	1
Hyattidinidae	0	2	2	9	0	0	0	0	0	1	1	1	9	0	0	0	0	0
Koninckinoidea	0	2	0	9	0	0	0	0	0	2	2	1	5	0	9	1	5	0
Lochengiinae	0	2	3	1	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Meristellinae	0	0	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Meristinae	0	9	0	0	0	4	4	0	0	1	1	1	3	0	2	1	3	0
Misoliinae	0	2	4	2	1	0	0	0	0	1	1	1	2	0	9	9	4	0
Mongolospiroidea	0	9	9	9	0	4	0	0	0	1	1	1	2	0	0	0	0	1
Neoretziinae	0	2	6	2	0	4	0	0	0	1	1	1	2	0	2	1	6	1
Nucleospiroidea	3	2	0	2	1	0	0	0	0	1	1	1	1	0	2	0	0	0
Ochotathyridinae	0	2	4	2	1	0	0	0	0	1	1	1	2	1	2	1	4	0
Parazygidae	0	2	5	1	1	0	0	0	0	1	1	1	2	2	0	0	0	1
Plectospirinae	0	2	6	9	0	3	0	0	0	1	1	1	1	0	2	0	0	1
Plicathyridinae	0	2	3	1	1	0	0	0	0	1	1	1	2	1	2	1	4	0
Pradoiinae	0	2	3	1	1	0	0	0	0	1	1	1	2	1	2	1	1	0
Retzielloidea	0	2	0	0	0	3	2	0	0	1	1	1	1	9	0	0	0	0
Retziidae	0	2	6	2	0	0	0	0	0	1	1	1	2	0	2	1	0	1
Rhynchospirinidae	0	2	5	1	0	1	0	0	0	1	1	1	1	2	0	0	0	1
Rowleyellinae	2	9	0	0	0	4	5	1	1	9	9	9	9	9	9	9	9	0
Septathyridinae	0	2	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Spirigerellinae	0	2	3	2	0	0	0	0	0	1	1	1	1	1	2	1	4	0
Tetractinellinae	0	2	4	2	1	0	0	0	0	1	1	1	1	1	2	1	4	0
Triathyridinae	0	2	0	0	0	3	4	0	0	1	1	1	3	0	2	1	2	0
Trigonirhynchiidae	0	2	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0
Whitfieldellinae	0	2	0	0	0	2	1	0	0	1	1	1	1	0	1	0	0	0
Xenosariinae	0	2	3	0	0	0	0	0	0	1	1	1	9	9	9	9	9	0

anterior to it but are always parallel to the plane of symmetry. Lateral branches may be a straight rod or ribbon that is smooth or spiny laterally, more or less twisted, or even folded back and forked dorsally. In the plicathyridins, the lateral branches of the jugum arise almost perpendicular to the primary lamellae and project ventrally for a short distance, up to a point at which they curve abruptly laterally or anterolaterally; they then project anteroventrally at a low angle until they join as a jugal arch (ALVAREZ, 1976, 1990). In some diplospirellins (*Anisactinella*), the lateral branches of the jugum are very short or absent, fusing with the thickened primary lamellae ventrally, which curl up toward the plane of symmetry until they coalesce in a massive jugum (BENIGNI & FERLIGA, 1992). Although the spiralium and jugum are continuous structures that are difficult to delineate as separate entities or with possible different functions of their own, we use such terms as primary lamella, umbonal blade, lateral branch, saddle, arch, and stem since we consider them useful in defining some morphological areas.

TABLE 20. Synapomorphy scheme for internal nodes of cladogram shown in Figure 1011 (new).

Node	Character states		
1	31:1		
2	29:1	30:1	
3	25:2		
4	26:1		
5	26:2		
6	26:4		
7	17:1	36:3	
8	19:1	20:2	28:1
10	3:3		
11	22:2		
12	22:3		
23	22:4		
28	37:1		
29	22:5		
31	22:6		

In the athyridides and retziidines the jugum is placed between the spiral cones, not below them (near the dorsal interior), and consists of a single complete structure that connects both spiralial cones instead of acting as a lever for movement of the spiralium as suggested by COPPER (1967b) for the jugal processes of atrypid genera. The jugal arch may project anteriorly as a more or less well-developed saddle of variable shape and size, sometimes with a spinous anterior edge. In some genera (diplospirellins) it is thickened by variously developed apophyses directed ventrally, laterally, anteriorly, or dorsally, which commonly have long, thin spines. Less frequently, the jugal arch has a miniature saddle directed posteriorly from the posterior extremity of which a little spiniform process extends straight backward (BEECHER & CLARKE, 1889). This occurs in early meristelloids (*Hindella, Whitfieldella*) and some athyridoids (*Buchanathyris, Johnsonathyris*). Rarely, the jugum takes the form of a backwardly inclined cross with its upper tips curved outward without a spiniform process or saddle (*Glassina*), or the jugum rests on a high dorsal median septum (*Camarophorella*). The posterior end of the jugal arch usually extends as a calcareous appendix (jugal stem) that may be spinose, protruding straight, or elbow shaped and directed posteriorly, posteroventrally, or ventrally finally reaching a position close to the crural ends (some *Hindella, Nucleospira*). A median septum may be present on the saddle, extending backward as far as the jugal stem in *Spirigerella.* The jugal stem may bifurcate distally, giving rise to two short stubs, jugal arms (*Meristina*) that may extend as accessory jugal lamellae that may rejoin the stem (*Meristella*) or the lateral branches of the jugum (*Merista*). In most athyridids, accessory jugal lamellae diverge and curve into a more or less complete loop or half circle that is parallel to that of the primary lamellae and lies between them and the secondary lamellae (although always closer to the former) and ending posteriorly or near the origin of the lateral branches of the jugum. In a few genera (*Pseudoprotathyris, Missolia*) the accessory jugal lamellae extend posterodorsally directly from the jugum or anteriorly pointed jugal saddle. The accessory lamellae may extend, intercoiling with primary lamellae (diplospirellins, helenathyridins). When composed of two lamellae, the primary (principal) lamella is commonly larger, and the accessory lamellae are smaller and more slender. Both primary and accessory lamellae may have long, thin fimbriae distributed along their external edges (Fig. 1009–1010).

In groups such as the athyridids with few external characters with many variants and with quite complex and at the same time poorly known interiors, it is not easy to envisage phyletic lineages. Phylogenetic relationships among athyridides *s.l.* were analyzed using outgroup methods of polarity determination. Information was compiled on 37 morphological characters of skeletal anatomy well displayed in the athyridides *s.l.,* including valve form and ornament, hinge region, and dorsal and ventral valve interior, especially the cardinalia and spiralium and shell structure (see Tables 18 and 19). Except for those related to the

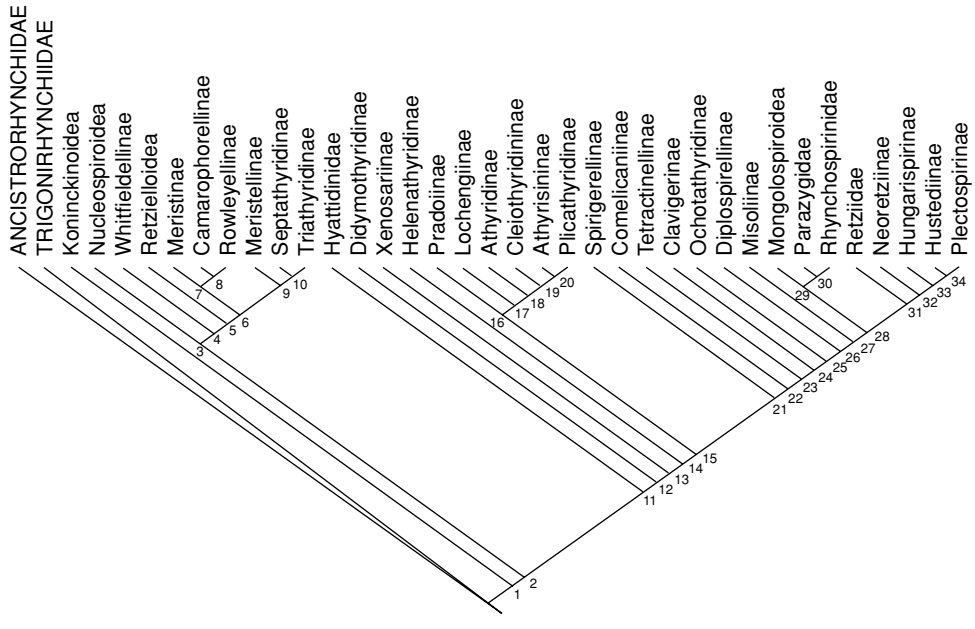


FIG. 1011. Second of the three equally most parsimonious cladograms; numbered nodes supported by character states listed in Table 20; see also Table 18–19 (new).

external ornamentation (the cardinalia and the character of the shell substance, punctate or not), all other characters were equally weighted. Four characters (numbers 3, 5, 6, and 25) were weighted three times greater than the others; three characters (numbers 22, 23, and 26) five times greater; and the character (punctate or impunctate) of the shell structure (number 37) 13 times. The character numbers 6 (frills), 22 (cardinal plate), 23 (cardinal process), and 26 (septalium) in Table 18 were ordered. None was constrained to be irreversible. Ordovician rhynchonellides, commonly considered as ancestral to athyridides (e.g., IVANOVA, 1967; RUDWICK, 1970; GRUNT, 1989; ALVAREZ & CARLSON, 1998; ALVAREZ, RONG, & BOUCOT, 1998), were specified as the outgroup. The analysis yielded three equally most-parsimonious cladograms, each of length 367 and consistency index of 0.488 (0.484 excluding uninformative characters). The cladogram was rooted at an internal node with a basal polychotomy. Agreement between the stratigraphical first appearance of athyridid subfamilies and their cladistic rank was quite good except for the koninckinoids, suggesting that both outgroup and traditional paleontological methods indicate a similar direction of character polarity in the evolution of the group (Fig. 1011–1012). In the fifty percent majority-rule consensus cladogram, all nodes are supported by one hundred percent of the cladograms. Synapomorphies for internal nodes of the cladogram (Fig. 1011) are shown in Table 20. The topology of the consensus diagram is almost identical to cladogram two (Fig. 1011). The koninckinoids appear at the base of the cladogram. Typically they have a plano- or concavoconvex lateral profile, the tips of the spiralia are directed dorsomedially, and the primary lamella of the spiralium (umbonal blades) curves laterally from the crura. The nucleospiroids are smooth but have fine solid spines that cover the entire shell (Fig. 1004.2). The nucleospiroids appear at the base of two sister groups: the Meristelloidea,

Athyrididina	Meristelloidea	Meristellidae, Triathyrididae, Meristidae
	Athyridoidea	Hyattidinidae, Athyrididae, Diplospirellidae
	Nucleospiroidea	Nucleospiridae
	Retzielloidea	Retziellidae
Retziidina	Retzioidea	Retziidae, Neoretziidae
	Rhynchospirinoidea	Rhynchospirinidae, Parazygidae
	Mongolospiroidea	Mongolospiridae
Koninckinidina	Koninckinoidea	Koninckinidae

FIG. 1012. Chronostratigraphic range of athyridid suprageneric taxa (new).

characterized by inner hinge plates forming a septalium, and the Athyridoidea, characterized by horizontal inner hinge plates, forming a hinge plate (Fig. 1005.1; Fig. 1006.2; Fig. 1007; Fig. 1008.1–1008.2). The retzielloids, plicate or costate rhynchonelliform athyrididines *s.l.,* cluster with the meristelloids, partially due to their short and slightly covered septalium (Fig. 1006.3). The Whitfieldellinae are at the base of the meristelloids and the meristids appear as their most derived group. *Hyattidina* appears ancestral to the athyridoids, and the Spirigerellinae and the Comelicaniinae occur at the base of the diplospirellids, athyridids with derived characters as the possession of an imperforate cardinal plate and well- to strongly developed cardinal flanges (Fig. 1007.3; Fig. 1008.1–1008.2). The athyrisinids cluster within the athyridids. Finally, the retziidines appear at the end of the cladogram as the most derived group.

The classification here proposed is based on a mix of external and internal characters that persisted during unbroken lineages. It is hierarchical, so characters are mentioned at their first appearance and may not be repeated at lower taxon levels. Thus, several taxon levels have to be read to gain the most complete description of a subfamily or genus. More detailed analyses of the phylogenetic relationships among higher taxa of the athyridides and spire-bearing brachiopods in general was done by ALVAREZ and CARLSON (1998) and ALVAREZ, RONG, and BOUCOT (1998).

ACKNOWLEDGMENTS

We thank numerous colleagues who have responded to and commented upon our enquiries about type specimen repositories, species distribution, or offered helpful comments and discussions over recent years. In particular we thank R. E. Alekseeva, V. V. Baranov, C. Benigni, R. K. Biswas, R. B. Blodgett, A. J. Boucot, D. Brice, C. H. C. Brunton, D. E. Butler, J. L. Carter, the late Chen Yuan-ren, L. R. M. Cocks, the late A. S. Dagys, R. Doescher, Fu Li-pu, J. Godefroid, the late R. E. Grant, R. T. Gratsianova, D. Holloway, P. W. Jackson, the late H. Jaeger, Jin Yu-gan, E. Landing, N. H. Landman, Liao Zhuo-ting, S. Long, F. N. Mitra, T. L. Modzalevskaya, N. Monoghan, I. Percival, N. Podevigne, R. Posenato, A. Prieur, M. Rubel, D. L. Strusz, the late W. Struve, J. A. Talent, Xu Gui-rong, and Zhang yan for providing access to collections in their care, specimen data, photographs, material on loan, and space and other facilities for conducting research. P. K. Tubbs and J. D. D. Smith kindly offered advice on nomenclatorial doubts; C. Jones helped in examination by SEM of many specimens. We

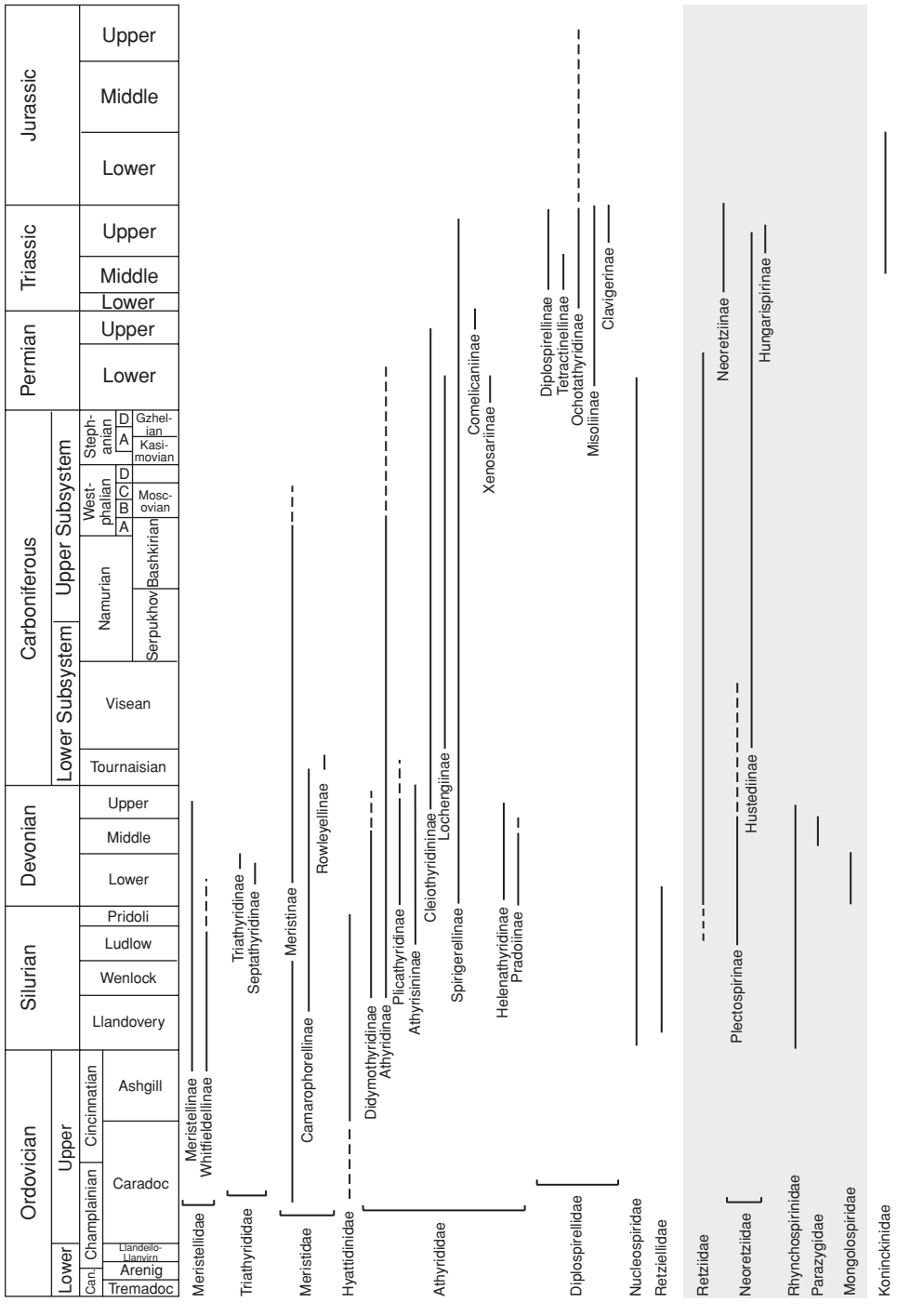


FIG. 1012. *(Continued).*

also thank many authors, journals, and institutions for kindly providing permission to reproduce illustrations: Academia Sinica, *Acta Palaeontologica Polonica, AGSO, Alcheringa, Bulletins of American Paleontology,* Carnegie Museum of Natural History (Pittsburgh), Ceskoslovenské akademie, Estonian Academy Publishers, Geological Society of London, Gordon and Breach Publishers, *Milwaukee Public Museum Contributions in Biology and Geology,* NAUKA Publishers, *Neue Denkschriften des Naturhistorischen Museums in Wien, Rivista Italiana di Paleontologia e Stratigrafia, Senckenbergiana lethaea,* Societa dei Naturalisti in Napoli, Taylor and Francis Ltd., the Minister of Public Works and Government Services Canada, 2000 and the Geological Survey of Canada, The Natural History Museum, London, The Royal Society of Edinburgh, and the Systematics Association.

Order ATHYRIDIDA Boucot, Johnson, & Staton, 1964

[*nom. transl.* Dagys, 1974, p. 152, *ex* suborder Athyridoidea Boucot, Johnson, & Staton, 1964, p. 815; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 833]

Biconvex, rarely concave or planoconvex, smooth, ribbed or plicate articulated shells; commonly astrophic, rarely strophic; concentric ornamentation more or less developed or absent; occasionally with solid or hollow spines; commonly with alternate folding in adults, less frequently opposite or mixed; ventral cardinal area (palintrope) commonly well developed in later forms; ventral beak commonly with circular foramen, in meso- to permesothyridid (rarely submesothyridid) position, and open or closed delthyrium; different type of pedicle support may be present; dental plates commonly absent in later forms; cardinal plate or septalium commonly present; umbonal blades of spiralia sharply bent from tips of crura commonly in posterodorsal direction, posterolateral in koninckinidines; spiral cones commonly laterally directed, ventrally in koninckinidines; more or less elaborate jugum joins primary lamellae of each conus; accessory lamellae of different disposition and length may be present; shell commonly impunctate, punctate in retziidines; tertiary layer may be present. *Upper Ordovician (Caradoc)–Lower Jurassic, ?Upper Jurassic.*

Suborder ATHYRIDIDINA Boucot, Johnson, & Staton, 1964

[*nom. correct.* Boucot, Johnson, & Staton, 1965, p. 654, *pro* suborder Athyridoidea Boucot, Johnson, & Staton, 1964, p. 815; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 834] [=suborder Rostrospiracea Moore, 1952, p. 221]

Astrophic to strophic, slightly to strongly rostrate athyridides with concentric growth lamellae in various states of expression that occasionally project anteriorly and anterolaterally as flat, spinelike outgrowths, rectangular in section, that appear to be solid; ventral cardinal area (palintrope) reduced to moderately developed, apsacline to orthocline; delthyrium commonly concealed by beak of dorsal valve; dental plates commonly present; outer hinge plates variably developed, inner hinge plates forming septalium or flat hinge plate apically perforated in other than late forms, inner hinge plates rarely absent or not fused medially; jugal saddle variably developed or absent; jugal stem and accessory jugal lamellae commonly present; shell impunctate; tertiary layer may be present. *Upper Ordovician (Caradoc)–Upper Triassic (Norian), ?Upper Jurassic.*

Superfamily ATHYRIDOIDEA Davidson, 1881

[*nom. correct.* Alvarez & Brunton, 1993, p. 310, *pro* Athyridacea Boucot, Johnson, & Staton, 1965, p. 654, *nom. correct. pro* Athyracea Williams, 1956, p. 284, *nom. transl. ex* Athyridae Davidson, 1881a, p. 4; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 840] [=Rostrospiracea Schuchert, 1929, p. 21 (invalid name not based on a family group)]

Athyrididines commonly subequally biconvex, rarely concave or planoconvex; anterior margin may be emarginate; numerous growth lines commonly with short to long frills that may project anteriorly and anterolaterally as flat spinelike outgrowths, rectangular in section, that appear to be solid, except in early and some late forms; dorsal fold and ventral sulcus variably developed or absent; shallow sulcus may develop in both valves; ribs or costae may be present;

foramen small to medium size, in meso- to permesothyridid position; delthyrium concealed by beak of dorsal valve, rarely by symphytium; ventral median septum may be present in late forms; pedicle support may be present, simple in early forms, elaborate in Permian and Triassic genera; cardinal plate flat, thin, subtriangular, inner hinge plates separated by narrow fissure or fused medially and apically perforated by usually large foramen in early forms, subquadrate, commonly thick, not pierced apically in most late Paleozoic forms; cardinal flanges poorly developed or absent in early forms and serrated, moderately to strongly developed, may become united into single structure in most Permian and Triassic forms; jugum commonly projecting anteriorly as jugal saddle and posteroventrally as thin jugal stem that bifurcates into accessory jugal lamellae that terminate posterior of lateral branches of jugum or intercalate with spiralial loops up to apex; rarely, the accessory jugal lamellae extend posterodorsally directly from jugal saddle. *Upper Ordovician (?Caradoc, Ashgill)–Upper Triassic (Norian), ?Upper Jurassic.*

Family ATHYRIDIDAE Davidson, 1881

[*nom. correct.* Boucot, Johnson, & Staton, 1964, p. 817, *pro* Athyridae Davidson, 1881a, p. 4]

Small to very large athyridoids; dental plates commonly of medium length, short or absent in late forms; pedicle supports commonly absent (except *Didymothyris* and *Collarothyris*); ventral muscle field weakly to moderately impressed; cardinal plate subtriangular to subtrapezoidal (absent in some helenathyridins), apically perforate, dorsal foramen may be infilled in gerontic individuals; cardinal flanges poorly developed or absent; late Carboniferous and Permian forms with thicker cardinal plate, dorsal foramen commonly small, may be infilled in latest stocks, and cardinal flanges serrated, moderately to strongly developed. [Athyridae as proposed by Phillips, 1841 or M'Coy, 1844 is not an available group name under Art. 11.7 (ICZN, 1999; see Alvarez, Brime, & Brunton, 1980 for discussion).] *Silurian (Wenlock)–Upper Triassic.*

Subfamily ATHYRIDINAE Davidson, 1881

[*nom. correct.* Boucot, Johnson, & Staton, 1964, p. 819, *pro* Athyrinae Waagen, 1883, p. 450, *nom. transl. ex* Athyridae Davidson, 1881a, p. 4]

Shell small to large, moderately rostrate; commonly with numerous, short to very long growth lamellae, flat or radially striated; dorsal fold commonly low and ventral sulcus shallow; dental plates of medium length (except *Protathyris*), thin subparallel, slightly concave; lateral branches of jugum almost vertical, starting midway along length of dorsal valve; jugal saddle well developed (except *Johnsonathyris*); accessory jugal lamellae terminating slightly posterior of lateral branches of jugum. *Silurian (?Wenlock, Ludlow)–Carboniferous (Bashkirian), ?Lower Permian.*

Athyris M'Coy, 1844, p. 146 [**Terebratula concentrica* von Buch, 1834, p. 103; SD King, 1850, p. 136] [=*Cliothyris* Agassiz, 1846, p. 90, obj.; *Spirigera* d'Orbigny, 1847, p. 268, obj.; *Spirithyris* Quenstedt, 1868 in 1868–1871, p. 30, obj.; *Euthyris* Quenstedt, 1869 in 1868–1871, p. 442, obj.]. Small- to medium-sized, dorsi- to strongly dorsibiconvex, equidimensional to slightly transverse, rounded subpentagonal shells covered by numerous, regular, thin, and slightly lamellose growth lines; uniplicate anterior commissure with ill-defined fold in anterior half of adult shell and relatively narrow sulcus originating at ventral beak, groovelike posteriorly but widening strongly anteriorly to about half width of very flat ventral valve; ventral muscle field moderately impressed; cardinal plate flat or slightly concave ventrally; low myophragm may be present. *Devonian, ?Lower Carboniferous:* cosmopolitan.——Fig. 1013*a–g.* **A. concentrica* (von Buch), Eifelian, Eifel, Germany; *a–e,* neotype, dorsal, ventral, lateral, anterior, and posterior views, SMF 5480, ×2; *f–g,* ventral and lateral views showing reconstructed jugum (Alvarez, Brunton, & Struve, 1996).——Fig. 1014*a–s.* **A. concentrica* (von Buch), Eifelian, Eifel, Germany; tangential serial sections, parallel to commissural plane, 1.8, 2.2, 2.5, 2.9, 3.3, 3.6, 3.8, 4.2, 4.6, 5.0, 5.4, 5.8, 5.9, 6.5, 6.6, 7.0, 7.2, 7.3, 11.0 mm from dorsal valve, SMF 50013 (Alvarez, Brunton, & Struve, 1996).——Fig. 1014*t–ii. A. concentrica murchisoni* Brice, Upper Devonian, Ferques, France; transverse serial sections 0.6, 1.1, 2.0, 2.8, 3.3, 3.9, 4.2, 5.0, 6.2, 6.9, 7.8, 8.3, 8.8, 9.3, 11.3, 11.5 mm from ventral umbo, BMNH BD12052 (Alvarez, Brunton, & Struve, 1996).——Fig. 1013*h. A. spiriferoides* (Eaton), Givetian, Michigan, USA; posterolateral view of open shell showing jugum, ventral up, I1106, Hall collection, ×2.5 (new).——Fig. 1013*i. A. waratahensis* (Talent),

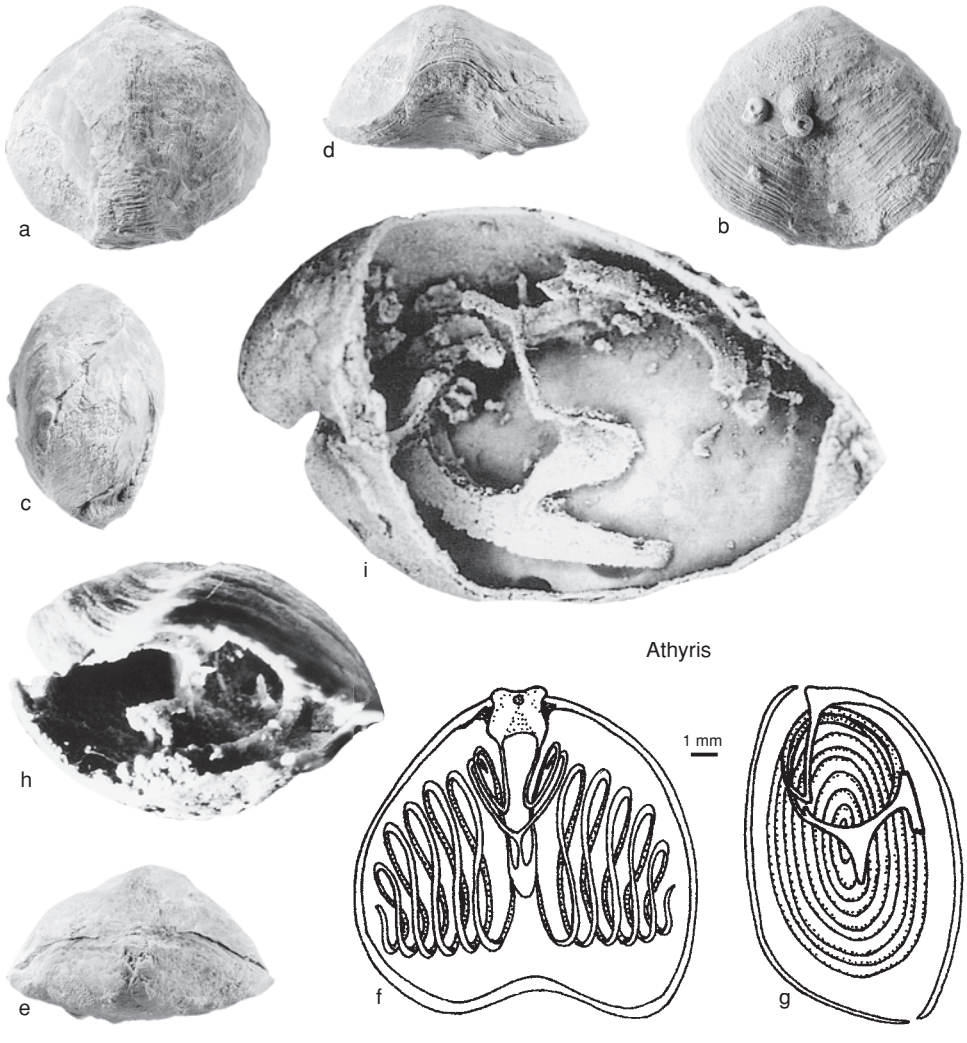


FIG. 1013. Athyrididae (p. 1497–1498).

Lower Devonian, New South Wales, Australia; lateral view of broken specimen showing jugum, ventral up, ANU 18998, approximately ×5(Alvarez, 1999a; photograph courtesy of B. D. E. Chatterton).

Actinoconchus M'COY, 1844, p. 149 [**A. paradoxus;* M] [=*Actinoconchus* M'COY in GRIFFITH, 1842, p. 18, *nom. nud.*]. Medium to large, biconvex, elongate oval, subcircular to transversely oval shells, very long, flat, delicate, radially striated, nonspinose flanges of shell from rugae or strong growth lines on both valves; dorsal fold and ventral sulcus absent or with shallow sulci on both valves forming ligate anterior; internal characters imperfectly known; jugum essentially as in *Athyris.* [*A. paradoxus* was the only species described under *Actinoconchus* so it must be considered the type by monotypy. DAVIDSON (1859) placed *A. paradoxus* into subjective synonymy with *Athyris planosulcata* (PHILLIPS, 1836) and many authors have accepted this. We agree with CARTER (1967) and BRUNTON (1980) in believing the two species to be distinct and so retain the name *A. paradoxus* for the type species of *Actinoconchus.*] *Upper Devonian (upper Famennian)–Upper Carboniferous (Bashkirian), ?Lower Permian:* southern China, *upper Famennian;* Europe, North America, Middle East, China, Australia, *Viséan–Bashkirian;* northeastern China, ?India, *?Lower Permian.*——FIG. 1015,*1a–b. *A. paradoxus,* Viséan, Kildare, Ireland; *a,* lectotype viewed

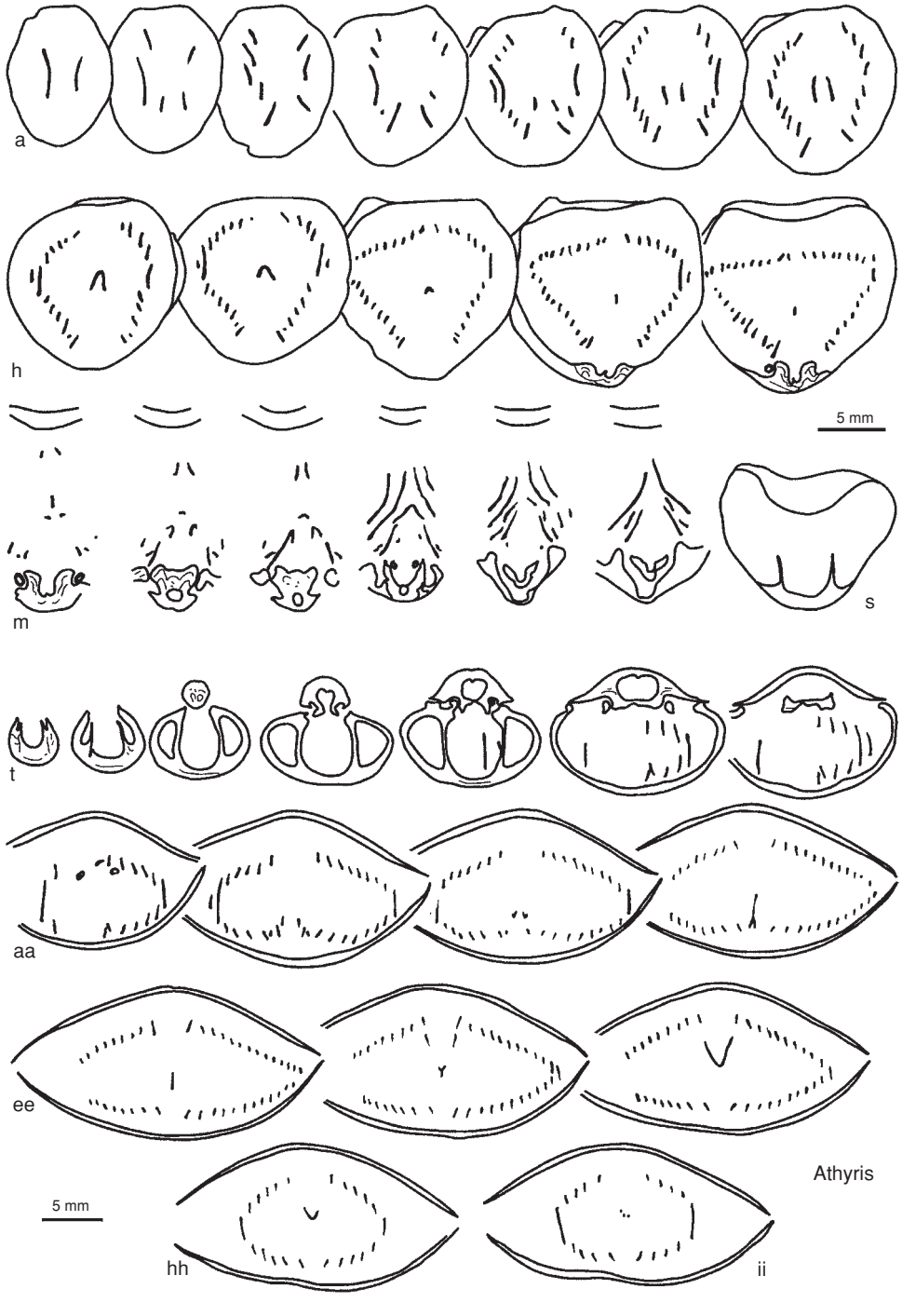


FIG. 1014. Athyrididae (p. 1497–1498).

dorsally, NMING: F6660, Griffith Collection; *b,* ventral view showing flanges, BMNH B5392, Davidson Collection, ×1.5 (Brunton, 1980; photographs courtesy of C. H. C. Brunton).——Fig. 1015,*1c–d. A. planosulcata* (Phillips), Lower Carboniferous, Yorkshire, England; ventral and lateral views showing jugum (Glass in Davidson, 1882). [See also Fig. 1002.5, p. 1477, in introduction.]

Alvarezites Struve, 1992, p. 559 [**Athyris (Alvarezites) wolfarti;* OD]. Large to very large, dorsibiconvex, slightly wider than long; hinge line almost straight, slightly shorter than maximum width, subtriangular to transversely subelliptical shells with fold and sulcus distinct in anterior half of adult shell; growth lamellae irregular, densely crowded, delicate, rarely coarse; lateral apical cavities commonly infilled with secondary shell material; ventral muscle field fan shaped, distinctly depressed only posteriorly; myophragm weakly developed. *Middle Devonian (Eifelian):* Germany (Eifel).——Fig. 1015,*2a–c. *A. wolfarti,* middle Eifelian; holotype, dorsal, ventral, and anterior views, SMF 54650, Struve Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

Atrythyris Struve, 1965, p. 218 [**A. atryplicata;* OD]. Similar to *Athyris,* but biconvex, with fine radial ornamentation somewhat similar to that of some atrypids; hinge plate slightly depressed medially. [The plicate exterior and umbonal interiors of Chinese specimens assigned to this genus are typically athyrisinin.] *Middle Devonian:* Germany, France, ?China.——Fig. 1015,*4a–d. *A. atryplicata,* middle Eifelian, Eifel, Germany, SMF 18946, Struve Collection; *a–c,* holotype, dorsal, ventral, and anterior views, ×1.5; *d,* detail of ornamentation, ×10 (Struve, 1965).

Brimethyris Alvarez, Rong, & Boucot, 1998, p. 842 [**Terebratula subconcentrica* de Verneuil & d'Archiac, 1845, p. 463; OD]. Medium to large, biconvex, slightly wider than long, rounded subpentagonal shells, with imbricate, widely spaced growth lamellae on any of which are up to 8 growth lines; papillose microornamentation affecting both primary layer and apparently most superficial secondary fibers; shallow ventral sulcus and flat, or slightly depressed medianly, dorsal fold beginning in posterior third of shell; internally essentially as in *Athyris* with reduced outer hinge plates and cardinal flanges, hinge plate almost flat with gentle longitudinal crest. *Lower Devonian (Emsian):* Spain.——Fig. 1016*a–g. *B. subconcentrica* (de Verneuil & d'Archiac), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, D855, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* ornamentation, ×9; *g,* ornamentation, DPO 17925, ×10 (Alvarez, 1990).——Fig. 1017*a–cc. *B. subconcentrica* (de Verneuil & d'Archiac), upper Emsian; transverse serial sections 1.15, 1.65, 1.85, 2.15, 2.75, 2.95, 3.35, 3.70, 4.15, 4.40, 4.65, 4.80, 5.35, 5.60, 6.35, 6.65, 6.90, 7.70, 8.25, 8.50, 8.80, 9.00, 9.35, 9.70, 9.90, 10.45, 10.85, 11.90, 12.00 mm from ventral umbo, DPO 17831 (adapted from Alvarez, 1990).

Bruntonites Struve, 1992, p. 559 [**Athyris (Bruntonites) mellingeni;* OD]. Similar to *Athyris,* but strongly biconvex, subcircular to broadly ovate in outline, fold and sulcus slightly developed only anteriorly; delthyrial cavity rather wide; myophragm very weak, commonly absent. *Middle Devonian (Eifelian):* Germany (Eifel).——Fig. 1015,*3a–c. *B. mellingeni* (Struve), middle Eifelian, Gondelsheim; holotype, dorsal, ventral, and anterior views, SMF 54700, Struve Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

Eifyris Struve, 1992, p. 561 [**Terebratula eifliensis* Schnur, 1853, p. 192; OD]. Similar to *Athyris,* but ventribiconvex, longer than wide, subovate, moderately to strongly rostrate; sinus mostly shallow with median groove, fold mostly low or indistinct, more or less short; delthyrial cavity wide; myophragm long. *Middle Devonian (Eifelian):* Germany (Gerolstein).——Fig. 1018,*3a–b. *E. eifliensis* (Schnur), middle Eifelian; lectotype, dorsal and ventral views, GPIBo S10, Schnur Collection, ×1 (Alvarez, Brunton, & Struve, 1996).

?Gonathyris Baranov, 1994, p. 30 [**G. ovata;* OD]. Shells resembling *Protathyris* but with hinge plate reportedly massive, pierced in its anterior part and serving as base for denticulate cardinal process; spiralia and jugum poorly known. [This genus requires revision.] *Lower Devonian (Pragian):* eastern Siberia, Yakutsk.——Fig. 1018,*1a–d. *G. ovata;* holotype, dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/17, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov).

Imacanthyris Grunt, 1991, p. 71 [**I. bortegensis;* OD]. External shape as in *Pachyplax* with bigger size and regular, thinner lamellose extensions covered with fine radial striations; internally resembling *Athyris;* jugum unknown. *Lower Devonian (Lochkovian):* Mongolia.——Fig. 1015,*5a–d. *I. bortegensis;* holotype, dorsal, ventral, lateral, and anterior views, PIN 3385/2071, ×1 (Grunt, 1991).

Johnsonathyris Savage, Eberlein, & Churkin, 1978, p. 381 [**J. adrianensis;* OD]. Small, strongly biconvex, subglobular, subcircular to subpentagonal; beaks incurved, foramen minute; weak dorsal fold and ventral sulcus developed anteriorly; commissure strongly uniplicate; fine growth lamellae crossed by regularly developed fine costellae; dental plates dorsally convergent, lateral apical cavities narrow; cardinal plate thin, flat, small, imperforate, medially crested; myophragm absent; jugum placed anterior of midlength, without saddle, stem, or accessory lamellae. *Upper Devonian (Famennian):* USA (Alaska).——Fig. 1018,*2a–n. *J. adrianensis; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 223913, ×2 (Savage, Eberlein, & Churkin, 1978); *f–m,* transverse serial sections 0.4, 0.5, 0.7, 0.8, 0.9, 3.4, 4.9, 5.4 mm from ventral umbo (adapted from Savage, Eberlein, & Churkin, 1978); *n,* ventral view showing reconstructed spiralium with jugum, USNM 223915 (Savage, Eberlein, & Churkin, 1978).

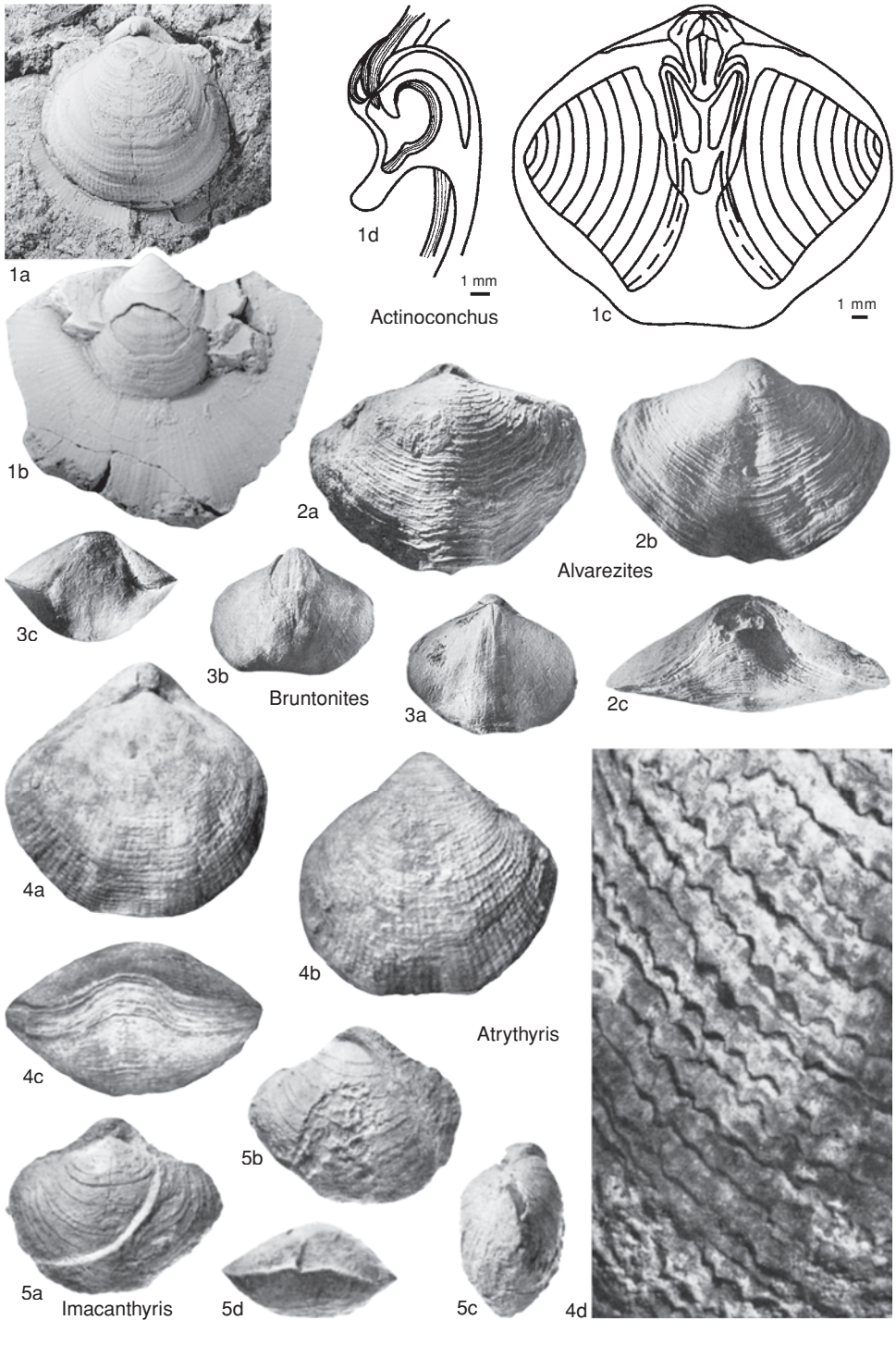


FIG. 1015. Athyrididae (p. 1498–1500).

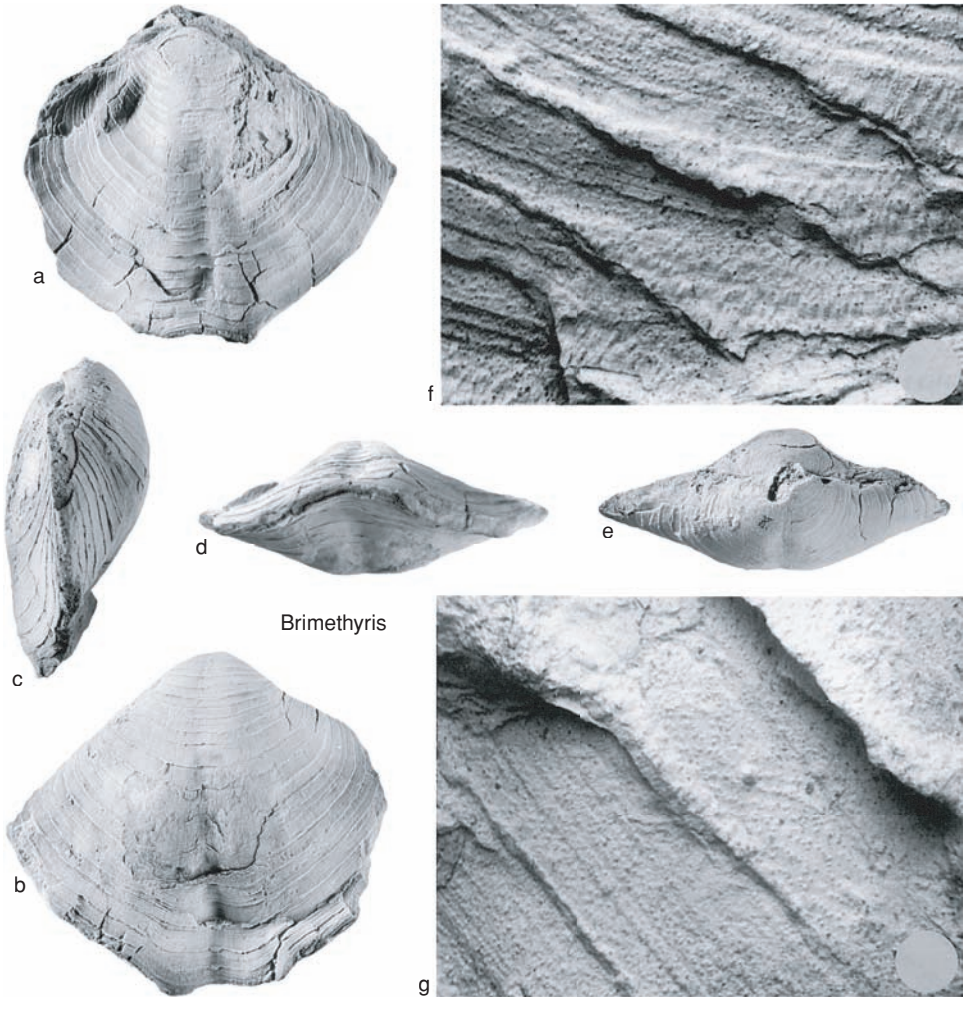


FIG. 1016. Athyrididae (p. 1500).

Lamellosathyris JIN & FANG, 1983, p. 147 [**Spirifer lamellosus* LEVEILLE, 1835, p. 39; OD]. Large, biconvex, subcircular to transversely elliptical shells, with long, radially corrugated shell flanges extending from rugae of both valves, with ventral sulcus and low dorsal fold with or without shallow median groove; dental plates slightly divergent dorsally, may become partially buried by secondary shell thickening during ontogeny; dorsal foramen small; cardinal flanges, more or less developed, projecting posteroventrally; low myophragm present; jugum, located at about midlength of first whorl of spiralia, essentially as in *Athyris* but accessory jugal lamellae shorter or absent. *Upper Devonian (Famennian)–Lower Carboniferous (Viséan):* ?Armenia, North America, *Famennian;* Elbourz, southwestern China (Yunnan), Europe, North America, *middle Tournaisian–Viséan.*——FIG. 1019,*2a–r.* **L. lamellosa* (LEVEILLE); *a–d,* neotype, dorsal, ventral, anterior, and posterior views, upper Tournaisian, Tournai, Belgium, BMNH B20138, Piret Collection, ×1; *e,* interior of silicified specimen, upper Tournaisian, Tournai, Belgium, BMNH BB62961, Piret Collection, ×3 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *f–r,* transverse serial sections 2.2, 3.5, 3.7, 4.3, 4.7, 5.7, 6.9, 8.5, 12.5, 15.2, 15.7, 15.9, 17.9 mm from ventral umbo, lower Viséan, western Yunnan, China (adapted from Jin & Fang, 1983). [See also Fig. 1002.4, p. 1477, and Fig. 1008.1, p. 1485, in introduction.]

?Meristospira GRABAU in GRABAU & SHERZER, 1910, p. 158 [**M. michiganensis;* OD]. Small to medium, subcircular or transversely oval biconvex shells; with or without faintly developed dorsal fold and ventral

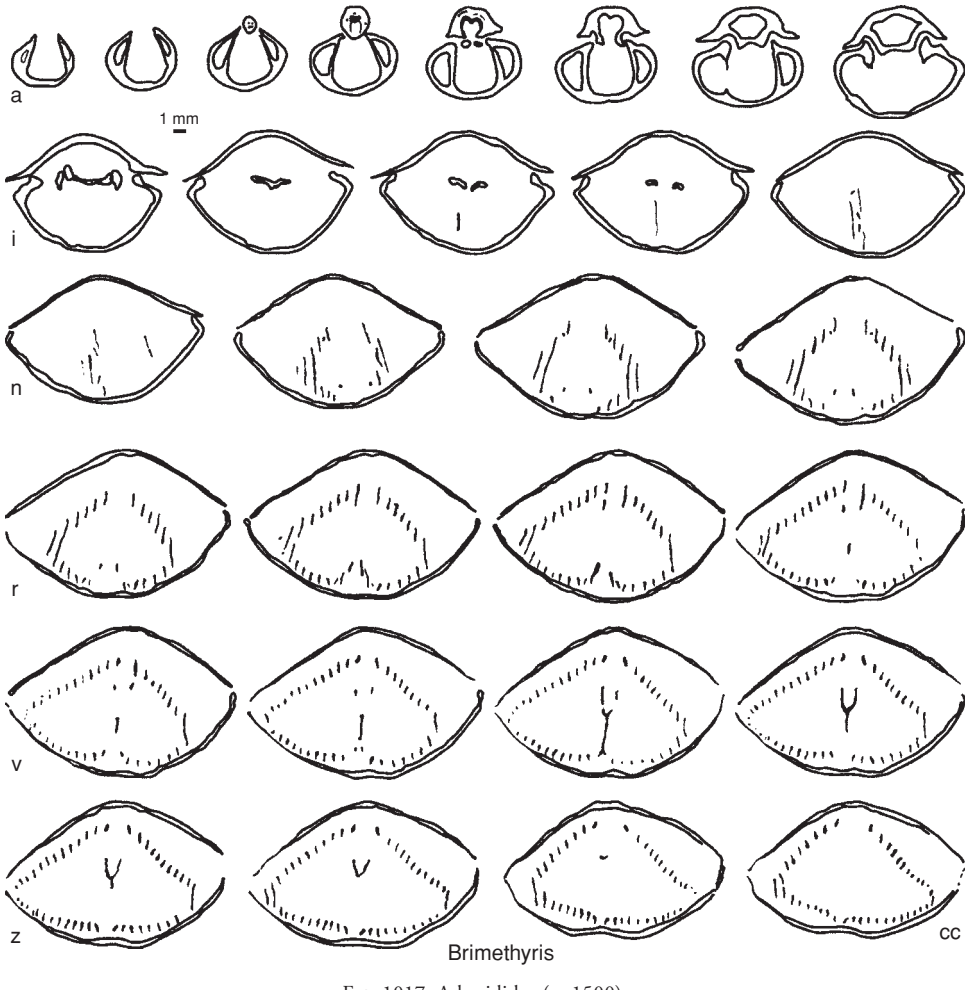


FIG. 1017. Athyrididae (p. 1500).

sulcus; growth lines not lamellose; a few low lateral plications may be present; dental plates subparallel, of moderate length; cardinal plate flat; dorsal myophragm present; spiralia and jugum unknown. [This genus requires revision.] *Middle Devonian:* USA (Michigan, Ohio), Canada (Ontario), ?China.——FIG. 1019,*1a–c.* **M. michiganensis,* Michigan; *a,* posterior internal mold both valves, ×3; *b–c,* lateral and ventral views of internal mold, ×2 (Grabau & Sherzer, 1910).

Pachyplax ALVAREZ & BRUNTON, 1990a, p. 31 [**P. transversa;* OD]. Resembling *Athyris* with small-sized, biconvex, rectimarginate to slightly uniplicate shells; valve surface covered by numerous, irregular, and very thick concentric lamellose extensions, formed by many layers of secondary fibers. *Lower Devonian (upper Emsian):* northwestern Spain.——FIG. 1020*a–v.* **P. transversa,* León; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, DPO 18642, ×1.5; *f–u,* transverse serial sections 0.70, 1.70, 2.00, 2.20, 2.70, 3.05, 3.80, 4.20, 4.55, 5.20, 5.60, 6.20, 6.50, 7.00, 8.95, 9.00 mm from ventral umbo, DPO 21154 (adapted from Alvarez & Brunton, 1990a); *v,* jugum, DPO 21154 (Alvarez & Brunton, 1990a).——FIG. 1020*w–x. P. gyralea* ALVAREZ & BRUNTON, Asturias; *w,* dorsal interior, DPO 25015, ×8; *x,* ventral interior, DPO 25010, ×9 (Alvarez & Brunton, 1990a). [See also Fig. 1003.2, 1003.4, p. 1478, and Fig. 1007.2, p. 1484, in introduction.]

Protathyris KOZLOWSKI, 1929, p. 223 [**P. praecursor;* SD GRABAU, 1932b, p. 90]. Similar to *Greenfieldia* externally and to *Athyris* internally, but shell wall thin, dental plates thin and very short; cardinal plate triangular, delicate, trilobed anteriorly, the central lobe being the largest and most concave, dorsal foramen large, cardinal flanges absent; dorsal myophragm may be present. *Silurian (?Wenlock,*

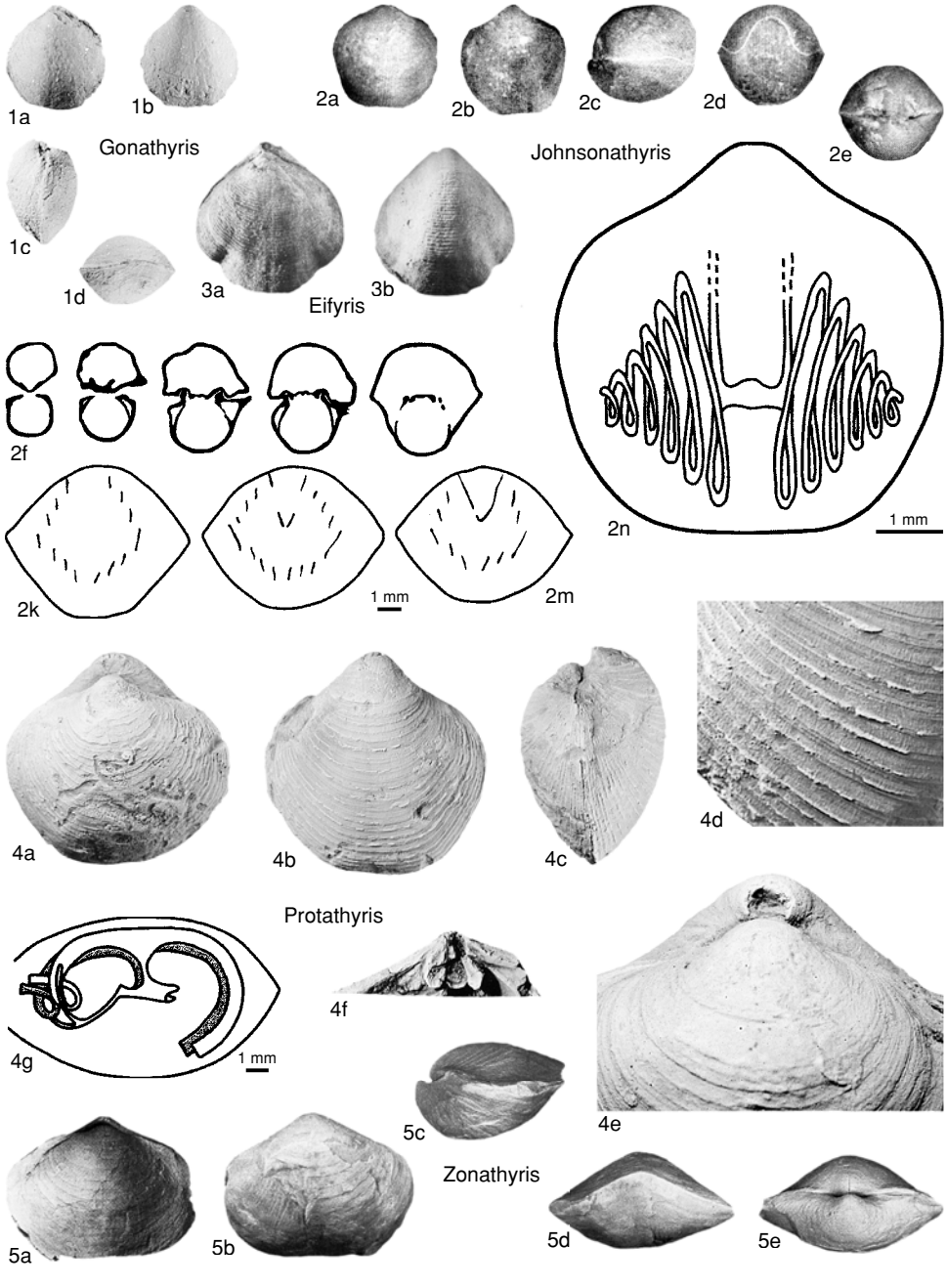


FIG. 1018. Athyrididae (p. 1500–1505).

Ludlow)–Lower Devonian (Emsian): North America, Europe, Asia, Australia.——FIG. 1018,*4a–g. *P. praecursor,* Lochkovian, Podolia, Russia; *a–c,* neotype, dorsal, ventral, and lateral views, CNIGR 125/11475, ×2; *d,* enlargement of ornament of ventral valve, CNIGR 125/11475, ×5; *e,* posterior part of conjoined valves showing foramen, CNIGR 68/11475; *f,* cardinalia, CNIGR 8/10001, ×6 (Nikiforova, Modzalevskaya, & Bassett, 1985; photographs courtesy of T. L. Modzalevskaya); *g,* lateral

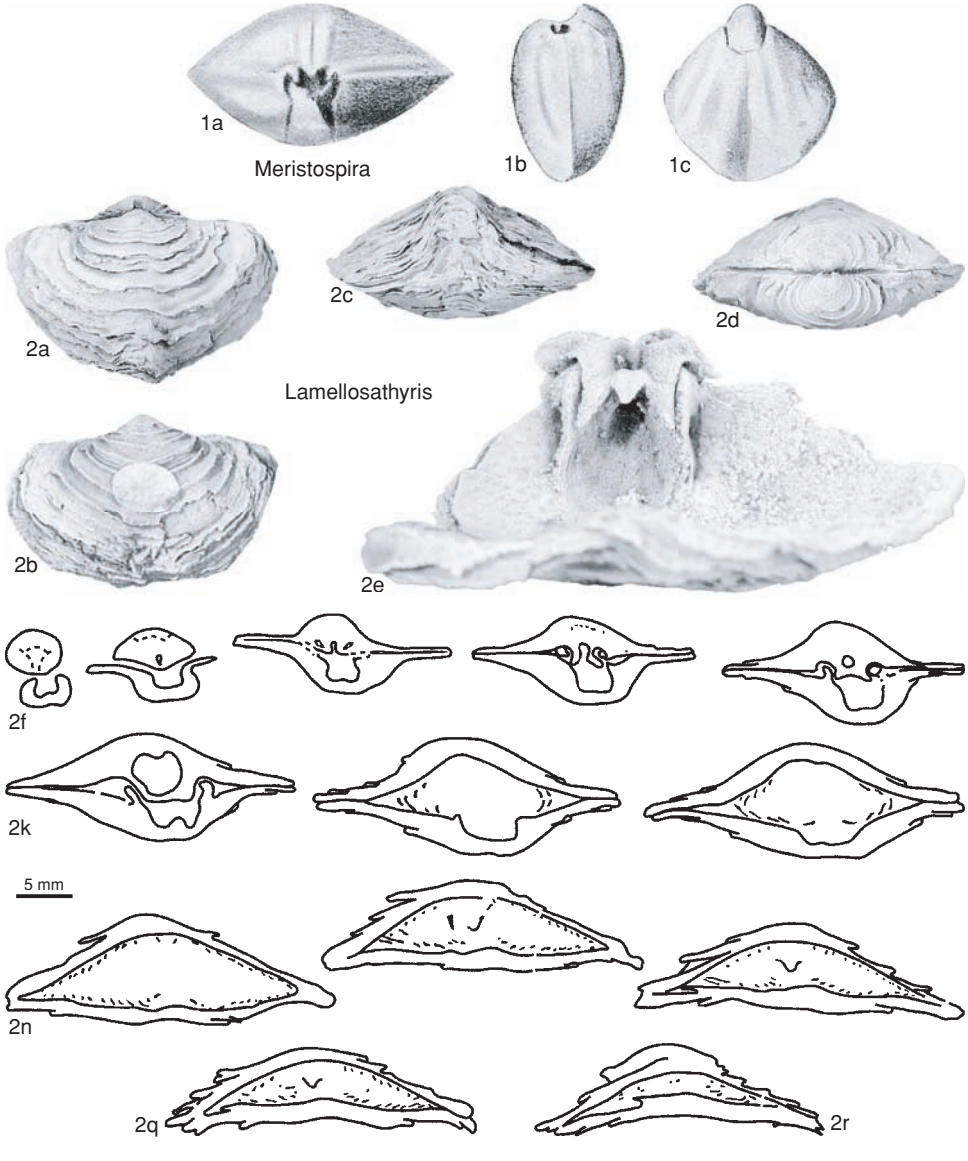


FIG. 1019. Athyrididae (p. 1502–1503).

view of jugum (adapted from Modzalevskaya, 1985).

Zonathyris STRUVE, 1992, p. 563 [**Terebratula cassidea oculta* QUENSTEDT, 1871 in 1868–1871, p. 460; OD]. Similar to *Alvarezites,* but biconvex, fold very faint, sinus weak to moderately developed, restricted to anterior part; growth lamellae delicate, regular, conspicuously spaced, on any of which are several weak growth lines. *Middle Devonian (Eifelian–Givetian):* Germany (Gerolstein).——FIG. 1018,*5a–e. *Z. oculta* (QUENSTEDT); holotype, dorsal, ventral, lateral, anterior, and posterior views, IMGPT 3/51/95, ×1 (Alvarez, Brunton, & Struve, 1996).

Subfamily ATHYRISININAE Grabau, 1931

[Athyrisininae GRABAU, 1931a, p. 509]

Shell small to large, moderately to strongly rostrate, ribbed or costate; growth

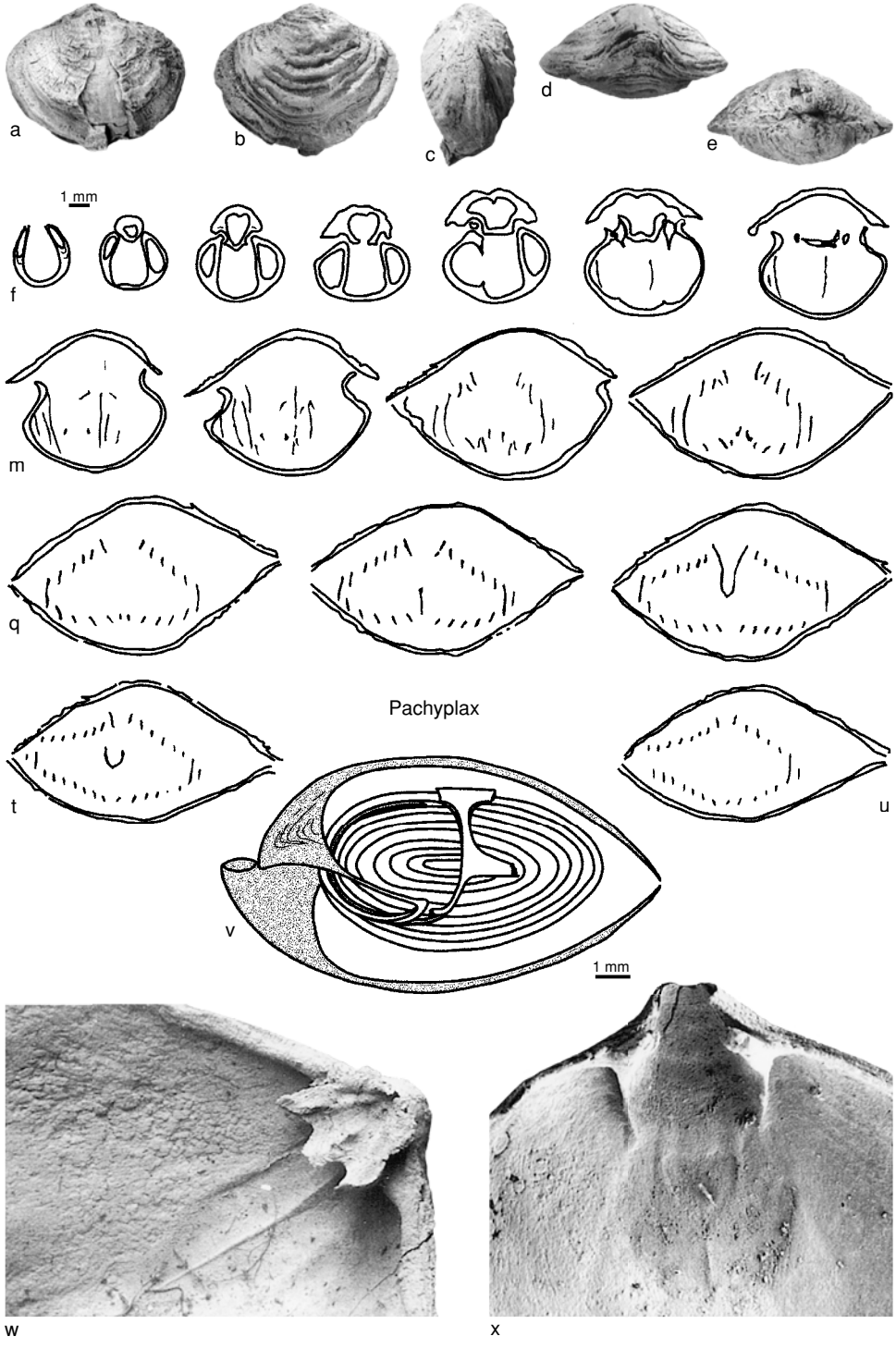


FIG. 1020. Athyrididae (p. 1503).

lamellae variably developed, may be squamose; fold and sulcus variably developed or absent; dental plates, when present, commonly short, converging dorsally; dorsal myophragm poorly developed, commonly absent; cardinal plate and jugum essentially as in *Athyris. Silurian (upper Ludlow)–Middle Devonian (Givetian).*

Athyrisina Hayasaka in Yabe & Hayasaka, 1920, p. 176 [**A. squamosa;* OD] [=*Kwangsia* Grabau, 1931a, p. 204 (type, *K. yohi,* OD); *Plectospirifer* Grabau, 1931a, p. 379 (type, *P. heimi,* OD); *Kwangsiella* Grabau, 1932a, p. 82 (type, *K. yohi,* OD); *Pseudoathyrisina* Chen, 1979, p. 17 (type, *P. fasciata,* OD); *Athyrisinopsis* Zhang Yan, 1983a, p. 354 (type, *A. uniplicata,* OD)]. Medium to large, rounded to transversely elliptical, ventribiconvex shell; ventral sulcus and dorsal fold usually well developed; pauciplicate to costellate, radial elements may bifurcate; concentric lamellae usually well developed; dental plates thin, short, dorsally convergent; lateral apical cavities very narrow; cardinal plate perforated apically by minute foramen, low myophragm may be present; lateral branches of jugum inclined anteriorly, starting posterior to mid-dorsal valve length, accessory jugal lamellae short. *Lower Devonian (lower Emsian)–Middle Devonian (Givetian):* southern China (Sichuan, Guizhou, Guangxi, Yunnan), northwestern China (Western Qinling, southeastern Gansu, western Shaanxi).——Fig. 1021,*4a–jj. *A. squamosa,* upper Emsian, Shuimogou, northern Sichuan; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, ×1 (new; photographs courtesy of the late Chen Yuan-ren); *f–jj,* serial sections 1.7, 2.4, 2.6, 2.8, 3.0, 3.4, 3.8, 4.05, 4.6, 5.1, 6.7, 7.6, 8.6, 9.8, 9.9, 11.4, 11.8, 12.5, 13.0, 13.9, 15.4, 15.7, 16.0, 16.25, 16.7, 17.3, 17.9, 18.25, 18.4, 18.7, 19.1 mm from ventral umbo (new).

Homeathyris Modzalevskaya, 1997, p. 209 [**H. insularis;* OD] [=*Homeathyris* Modzalevskaya in Modzalevskaya & others, 1994, p. 66, *nom. nud.; Homeathyris* Modzalevskaya, 1994b, p. 147, *nom. nud.*]. Similar to *Squamathyris* but bigger, with sulcus in both valves and without growth lamellae. Silurian (Ludfordian): Russia (Arctic Russia, southern island of Novaya Zemlya, Dolgii Island, western slopes of Central Urals).——Fig. 1021,*2a–b. **H. insularis,* Dolgii; holotype, ventral and lateral views, CNIGR 2/12918, ×1 (Modzalevskaya, 1997).

?Ikella Tiazheva, 1972, p. 205 [**I. numerosa;* OD]. Small to medium, costate shells; elongate subelliptical, biconvex, fold and sulcus commonly absent; costae rounded, bifurcating or not, in corresponding position on each valve; delthyrium with narrow deltidial plates; dental plates absent; cardinal plate present; myophragm absent; spiralium and jugum unknown. [Insufficiently described and figured.] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* Russia (Bashkirkostan, western slopes of Southern Urals).

Parathyrisina Wang in Wang, Yu, & Wu, 1974, p. 41 [**P. bella;* OD; =*Athyrisina tangnae* Hou, 1963, p. 416] [=*Athyrisinoides* Chen & Wan, 1978, p. 351 (type, *A. typica,* OD); *Athyrisinoidea* Chen & Wan in Wan, 1980, p. 105 (type, *A. typica,* OD); *Neoathyrisina* Chen, 1988b, p. 36, obj.]. Small to medium, transverse subelliptical to subcircular outline; pedicle opening large; ventral sulcus and dorsal fold rounded, well developed, without radial elements; lateral slopes bearing 3 or more round costae; interior and jugum essentially as in *Athyrisina. Lower Devonian (upper Pragian–lower Emsian):* northwestern China (western Qinling), southern China (Guangxi, Sichuan).——Fig. 1022*a–x. *P. tangnae* (Hou), Guangxi; *a–d,* dorsal, ventral, lateral, and anterior views, NIGP 23624, ×2 (new); *e–x,* transverse serial sections 1.0, 2.1, 2.5, 2.9, 3.2, 3.5, 3.8, 4.3, 5.2, 5.8, 6.2, 7.25, 9.6, 10.5, 10.9, 11.3, 11.9, 12.3, 12.7, 14.5 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Wang & Rong, 1986).

Pseudohomeospira Nikiforova, 1970, p. 139 [**P. polaris;* OD]. Small, biconvex, elongate oval, costate shells; ventral sulcus and dorsal fold weakly developed anteriorly; costae subangular, bifurcating in fold and sulcus; hypothyridid pedicle opening may be partially closed by deltidial plates; pedicle collar present; short ventral septum may be present apically; dental plates and dorsal interior essentially as in *Athyrisina;* spiralia directed laterally, jugum unknown. *Silurian (Přídolí):* Russia (Arctic Russia, Vaigatch, southern island of Novaya Zemlya, western Polar and Central Urals).——Fig. 1021,*1a–b. **P. polaris,* Vaigatch; holotype, dorsal and ventral views, TsNIGRA 159/10331, ×2 (Nikiforova, 1970; photographs courtesy of T. L. Modzalevskaya).

Squamathyris Modzalevskaya, 1981, p. 153 [**S. glacialis;* OD]. Medium size, biconvex, subpentagonal to longitudinally oval, ribbed shells; ventral sulcus and dorsal fold moderately developed; squamose surface of growth lamellae; ventral valve moderately to strongly rostrate; hypothyridid pedicle opening restricted laterally by deltidial plates; ventral interior as in *Didymothyris;* spiralia directed laterally, jugum unknown. *Silurian (Ludfordian):* Russia (Arctic Russia, Vaigach, Dolgii Island, southern island of Novaya Zemlya).——Fig. 1021,*3a–d. **S. glacialis,* Novaya Zemlya; *a–c,* holotype, dorsal, ventral, and lateral views, TsNIGRA 9/12011, ×1; *d,* ventral valve internal mold, ×3 (Modzalevskaya, 1981; photographs courtesy of T. L. Modzalevskaya).

Subfamily CLEIOTHYRIDININAE Alvarez, Rong, & Boucot, 1998

[Cleiothyridininae Alvarez, Rong, & Boucot, 1998, p. 842]

Shell medium to large, moderately rostrate; numerous, concentric, imbricate, very close growth lamellae projecting anteriorly

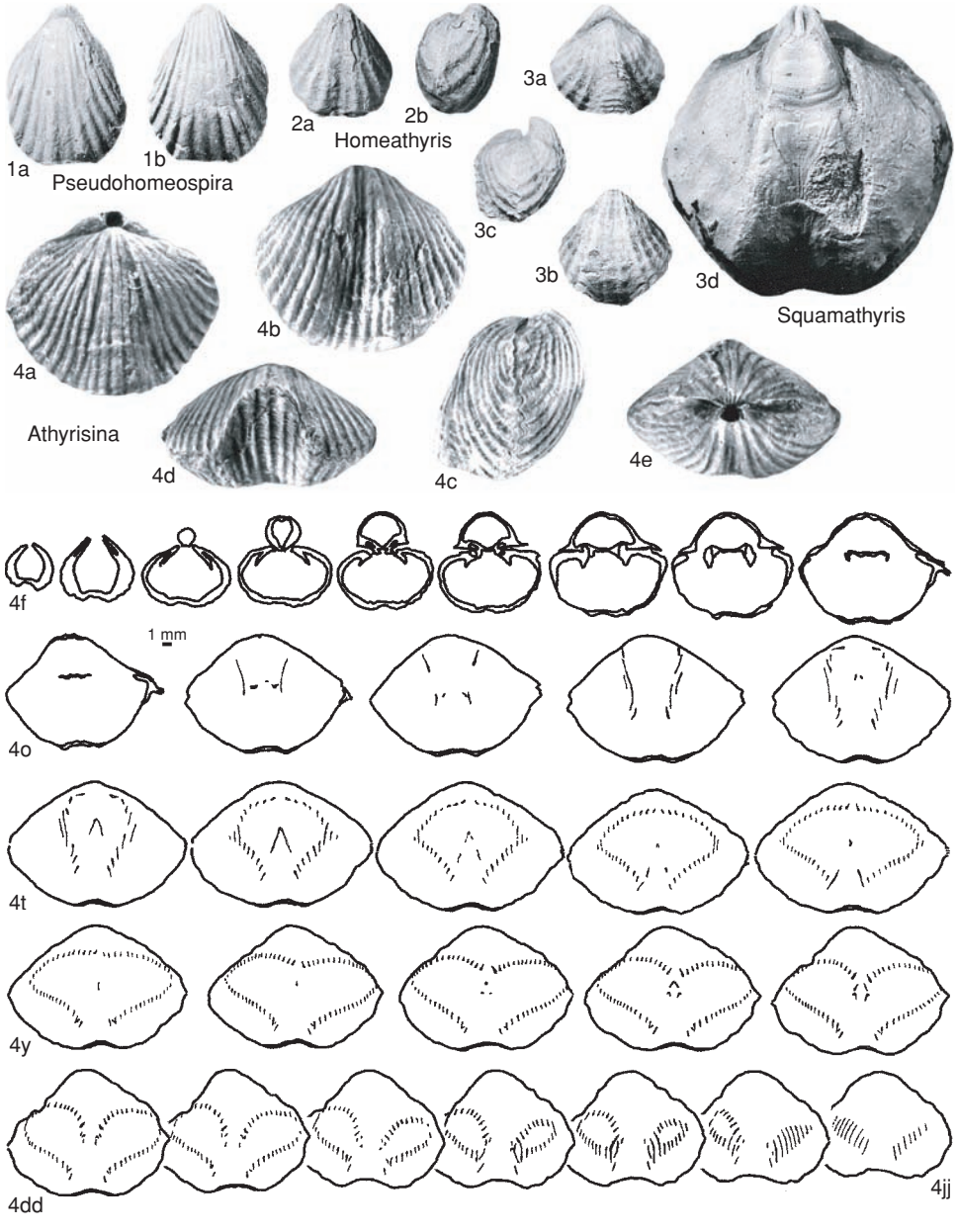


FIG. 1021. Athyrididae (p. 1507).

and anterolaterally as flat, solid spines; faint dorsal fold and ventral sulcus developed anteriorly; dental plates short, low, dorsally divergent, may become partially buried by secondary shell thickening; cardinal plate subtriangular; outer hinge plates well developed and ventrally concave, conjunct inner hinge plates subtrapezoidal, short, wide, and

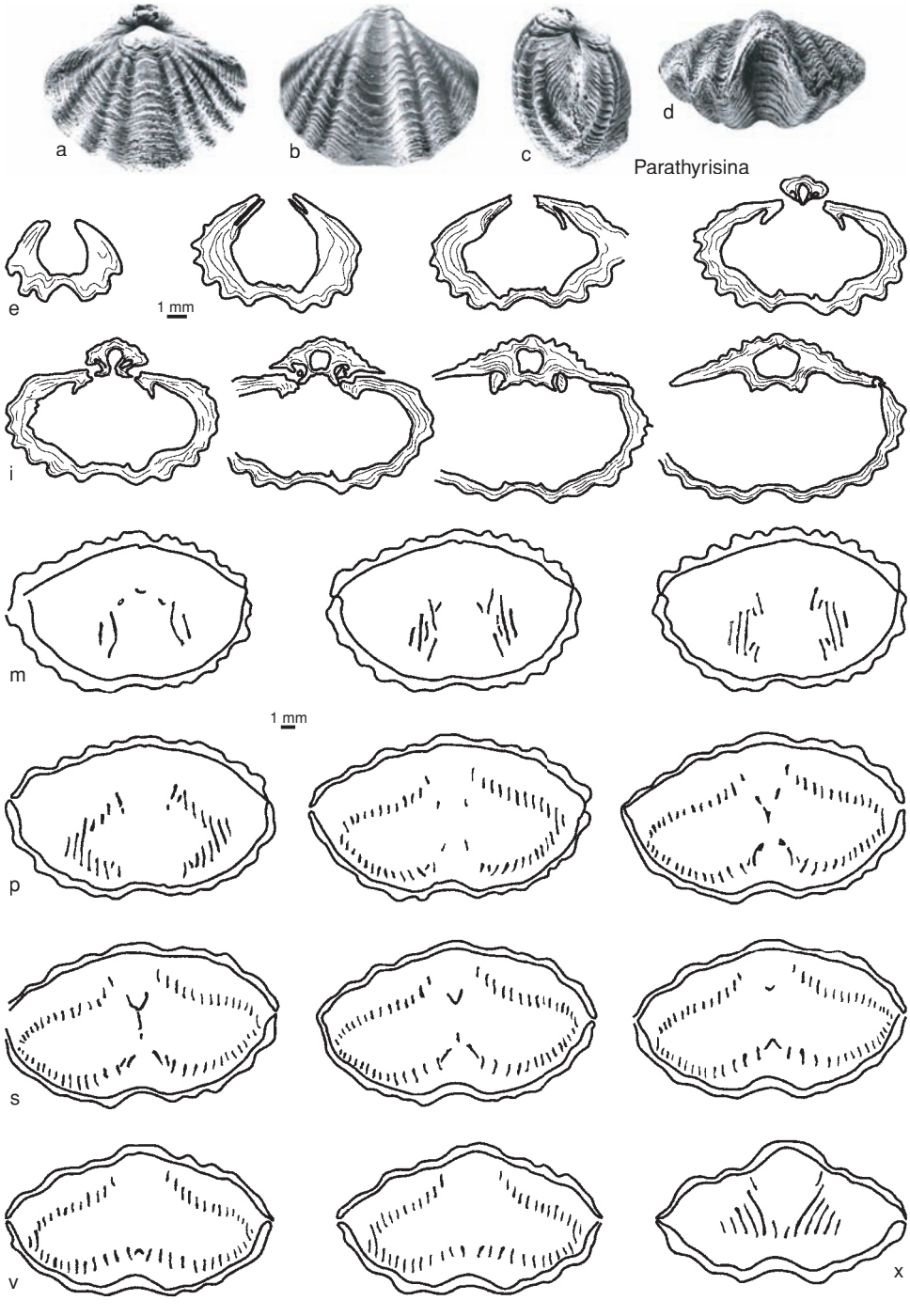


FIG. 1022. Athyrididae (p. 1507).

usually flat and situated more dorsally than outer hinge plates; posteroventrally projecting striate cardinal flanges variously developed; low myophragm present; jugum essentially as in *Athyris* with longer accessory jugal lamellae commonly terminating anterior to lateral branches; tertiary layer may be present. *Upper Devonian (Famennian)–Upper Permian (Kazanian, ?Tatarian).*

Cleiothyridina Buckman, 1906, p. 324, *nom. nov. pro Cleiothyris* King, 1850, p. 137 [**Atrypa pectinifera* J. de C. Sowerby, 1840 in 1840–1846, p. 14; validated by ICZN Opinion 1041, 1976, p. 210] [=*Cliothyris* Hall & Clarke, 1893, p. 90, obj., *non* Agassiz, 1846; *Cleiothyridellina* Waterhouse, 1978, p. 82 (type, *C. accoliformis,* OD); *Gerankalasiella* Gretchishnikova, 1996, p. 423 (type, *G. gerankalasiensis,* OD); *Kjarkiella* Gretchishnikova, 1996, p. 424 (type, *K. kjarkiensis,* OD)]. Medium-sized, transversely elliptical to longitudinally ovate, subequally biconvex shells. [*Cleiothyridellina,* from the Upper Permian of Nepal, is said to differ by having swollen shells, flat cardinal plate, and very short and low median septum, usually absent at maturity; *Gerankalasiella* and *Kjarkiella* from the Tournaisian of Transcaucasia are said to differ by having wider growth lamellae and spiral brachidium having a higher number of whorls (*Gerankalasiella*), while *Kjarkiella* has a larger size, high shell convexity, and very dense, narrow growth lamellae, weakly divided at margins.] *Upper Devonian (Famennian)–Upper Permian (Kazanian, ?Tatarian):* cosmopolitan.——Fig. 1023*a–e.* **C. pectinifera* (Sowerby), Kazanian, ?Tatarian, Durham, United Kingdom; *a–d,* lectotype, dorsal, ventral, lateral, and posterior views, BMNH B61055, Sowerby Collection, ×2 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *e,* jugum, approximately ×4.5 (Davidson, 1857).——Fig. 1023*f–g. C. seriata* Grant, Artinskian, southern Thailand; *f,* cardinalia, USNM 497424, ×16.5; *g,* anterior view into articulated umbones showing cardinalia and articulation, USNM 497425, ×14 (new). [See also Fig. 1002.3, p. 1477, Fig. 1004.1, p. 1479, and Fig. 1007.1, p. 1484, in introduction.]

Bajtugania Grunt, 1980, p. 97 [**B. netschaevi;* OD]. Similar to *Cleiothyridina,* but with thick shell; dental plates absent; more or less prominent ridge joining thick cardinal plate at posterodorsal end; dorsal foramen may be overgrown. *Upper Permian (Kazanian):* Russian Platform, Verkhoyansk, Mongolia.——Fig. 1024,*1a–bb.* **B. netschaevi,* Russian Platform; *a–b,* holotype, dorsal and ventral views, PIN 1511/2695, ×1 (Grunt, 1980); *c–k,* transverse serial sections 1.3, 1.7, 2.6, 2.8, 3.1, 3.2, 3.4, 3.7, 4.4 mm from ventral umbo, PIN 3599/105; *l–bb,* tangential serial sections, parallel to commissural plane, 1.6, 2.7, 3.4, 3.7, 4.7, 5.3, 5.9, 6.1, 7.1, 7.2, 7.4, 7.5, 7.6, 7.7, 7.9, 8.0, 8.1 mm from dorsal valve, PIN 3599/829 (adapted from Grunt, 1986).

Carteridina Alvarez, Rong, & Boucot, 1998, p. 842 [**Spirigera prouti* Swallow, 1860, p. 649; OD]. Very large, transverse, dorsibiconvex shells resembling *Cleiothyridina,* with large growth lamellae; without dental plates and myophragm. *Lower Carboniferous (Tournaisian–Viséan):* USA (Missouri, New Mexico, Texas).——Fig. 1025,*1a–e.* **C. prouti* (Swallow), Tournaisian, Texas; dorsal, ventral, lateral, anterior, and posterior views, USNM 154774, ×2 (Carter, 1967).

Crinisarina Cooper & Dutro, 1982, p. 92 [**Cleiothyridina reticulata* Stainbrook, 1947, p. 326; OD]. Similar to *Cleiothyridina* with pentagonal outline, strongly uniplicate anterior commissure. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America.——Fig. 1025,*4a–k.* **C. reticulata* (Stainbrook), Famennian, New Mexico, USA; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 200928, ×1; *f,* spines, ×4 (Cooper & Dutro, 1982); *g–k,* transverse serial sections 2.4, 2.8, 3.2, 3.6, 8.1 mm from ventral umbo, USNM 341941 (adapted from Cooper & Dutro, 1982).

?Deltachania Waterhouse, 1971, p. 217 [**D. acanthatia;* OD]. Similar to *Cleiothyridina,* but reportedly without hinge plate; spiralium and jugum unknown. [This genus requires revision.] *Upper Carboniferous (Moscovian):* Canada (northern Yukon).——Fig. 1024,*2a–d.* **D. acanthatia; a–b,* holotype, dorsal and ventral views of internal mold, GSC 26422, ×1; *c,* dorsal view, GSC 26418, ×1; *d,* rubber mold of cardinalia articulated with fragment of ventral valve, anterior view, GSC 26422, ×2 (Waterhouse, 1971).

?Himathyris Waterhouse, 1986b, p. 214 [**Athyris gerardi* Diener, 1899, p. 56; OD]. Large shells with almost flat ventral valve, growth lamellae similar to those on *Actinoconchus,* with fine radial ribs and reportedly flat, small, erratically developed spines on only some lamellae; interior poorly known. [This genus requires revision. Date on publication is 1985, but volume 3 of *Contributions to Himalayan Geology* was published in 1986.] *Upper Permian (Tatarian):* India, Spiti.——Fig. 1025,*3.* **H. gerardi* (Diener); lectotype, ventral view, GSI 6295, ×1 (Diener, 1899).

Leiothycridina Grunt, 1980, p. 64 [**L. okensis;* OD]. Similar to *Cleiothyridina* but with poorly differentiated dental plates; very flat cardinal plate with longer inner hinge plates and thicker shell with well-developed tertiary layer; spiralia and jugum unknown. *Lower Carboniferous (Viséan–lower Namurian):* Belgium, England, France, Russia, Tian Shan, southern China, Japan.——Fig. 1025,*2a–i.* **L. okensis,* Viséan, Moscow syncline, Russia; *a–d,* holotype, dorsal and ventral valves viewed externally and internally, PIN 544/468, ×1 (Grunt, 1980); *e–i,* transverse serial sections 2.2, 2.5, 2.7, 3.7, 3.9 mm from ventral umbo, PIN 544/288 (adapted from Grunt, 1980).

Pinegathyris Grunt, 1980, p. 88 [**Terebratula royssiana* von Keyserling, 1846, p. 237; OD]. Similar to *Cleiothyridina,* but bigger, frequently

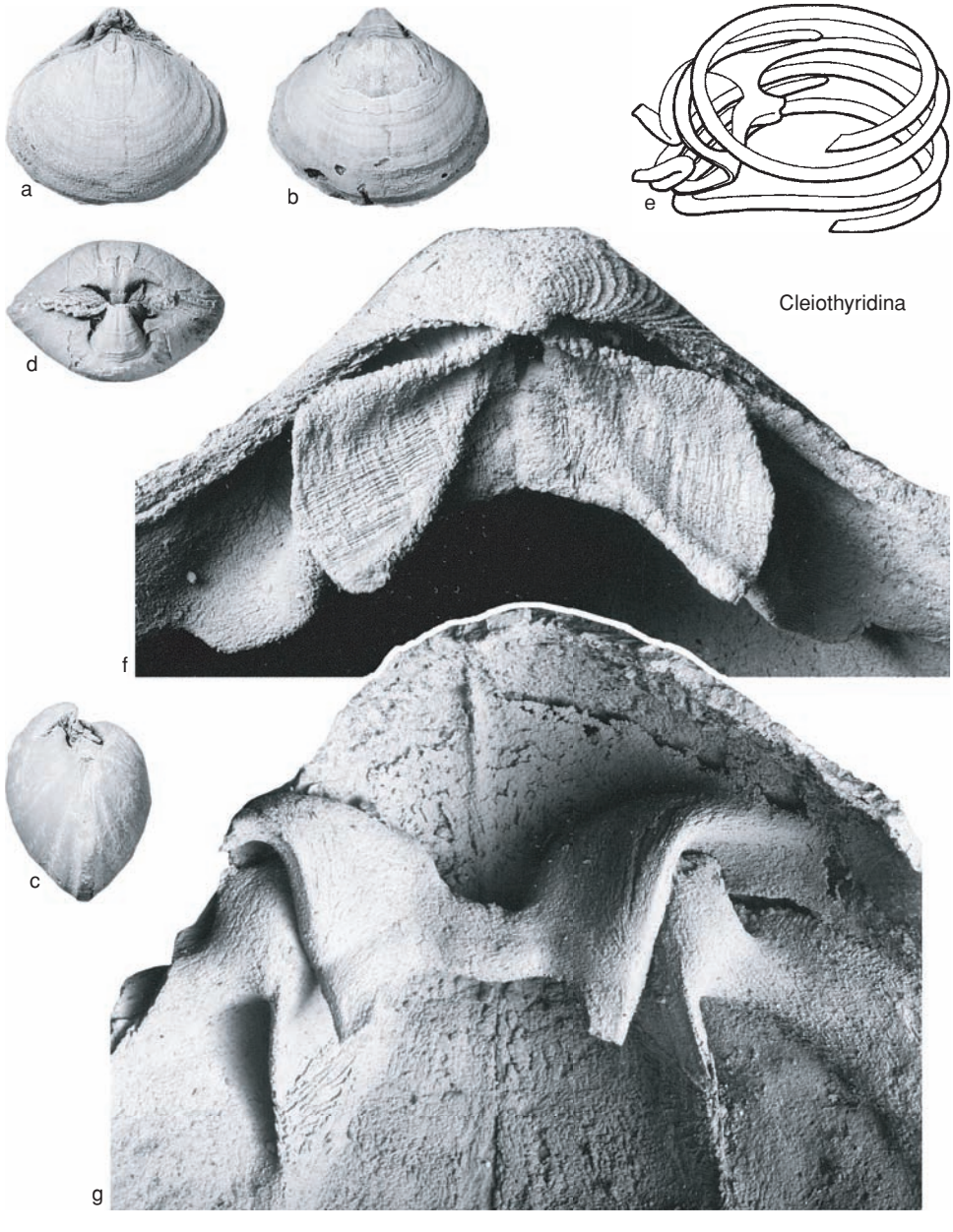


FIG. 1023. Athyrididae (p. 1510).

with winged overall aspect, well-defined subtrapezoidal ventral palintrope, almost straight hinge line equal or slightly shorter than maximum width; internally similar to *Bajtugania* but with low myophragm. *Lower Permian (Kungurian)–Upper Permian (Kazanian):* Kanin Peninsula, Spitzbergen, *Kungurian–Kazanian;* Russian Platform, *Kazanian.*——FIG. 1026,*2a–l.* **P. royssiana* (VON KEYSERLING), Kazanian, Russian Platform; *a–c,* dorsal, ventral, and anterior views, PIN 1120/845, ×1 (Grunt, 1980); *d–l,* transverse serial sections 8.9, 10.5, 11.9, 13.6, 14.2, 16.1, 16.2, 17.9, 18.8 mm from ventral umbo, PIN 1511/2302 (adapted from Grunt, 1986).

?Rawdonia PEOU, 1979, p. 190 [**R. nasharae;* OD]. Ventral valve exterior similar to *Cleiothyridina;*

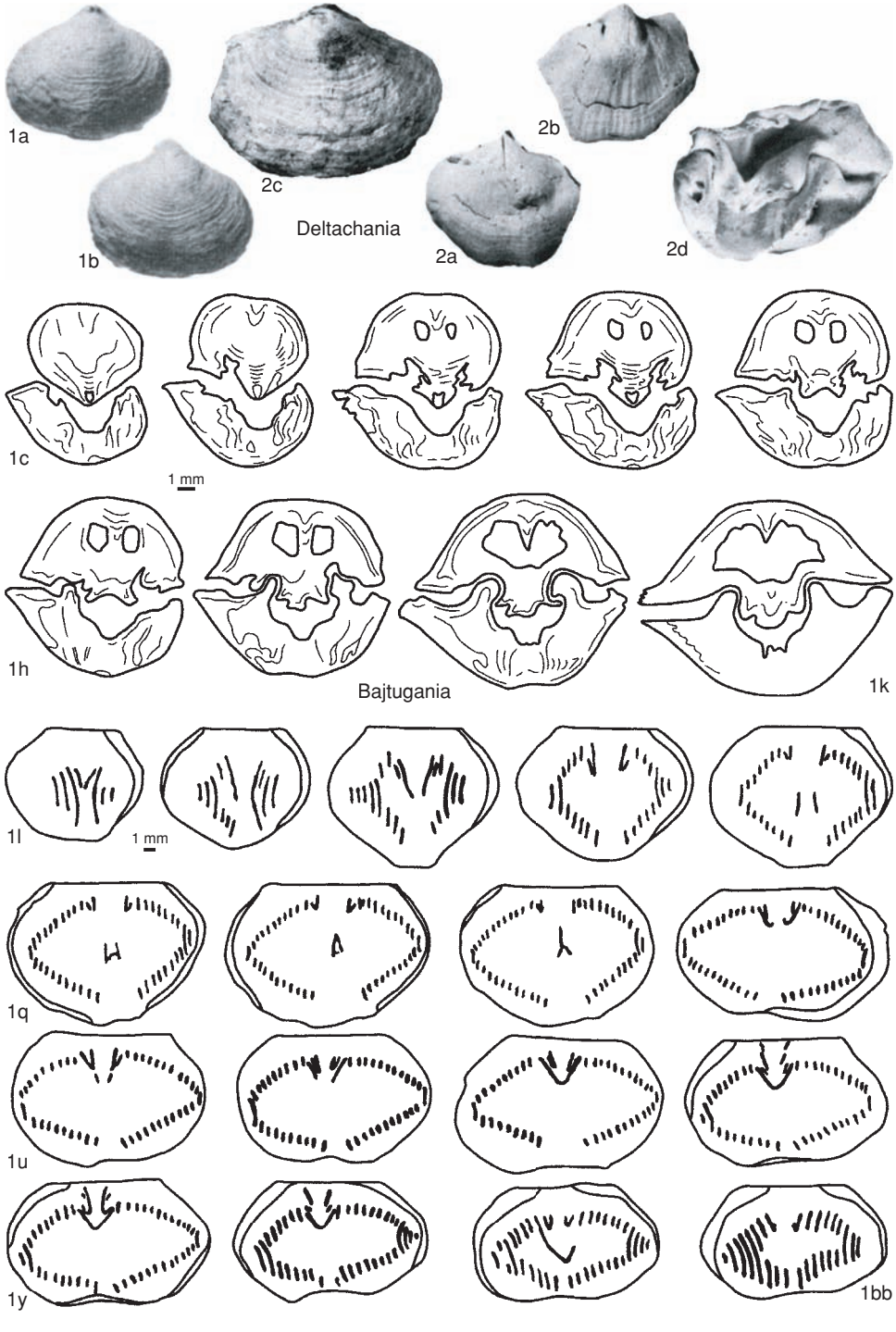


FIG. 1024. Athyrididae (p. 1510).

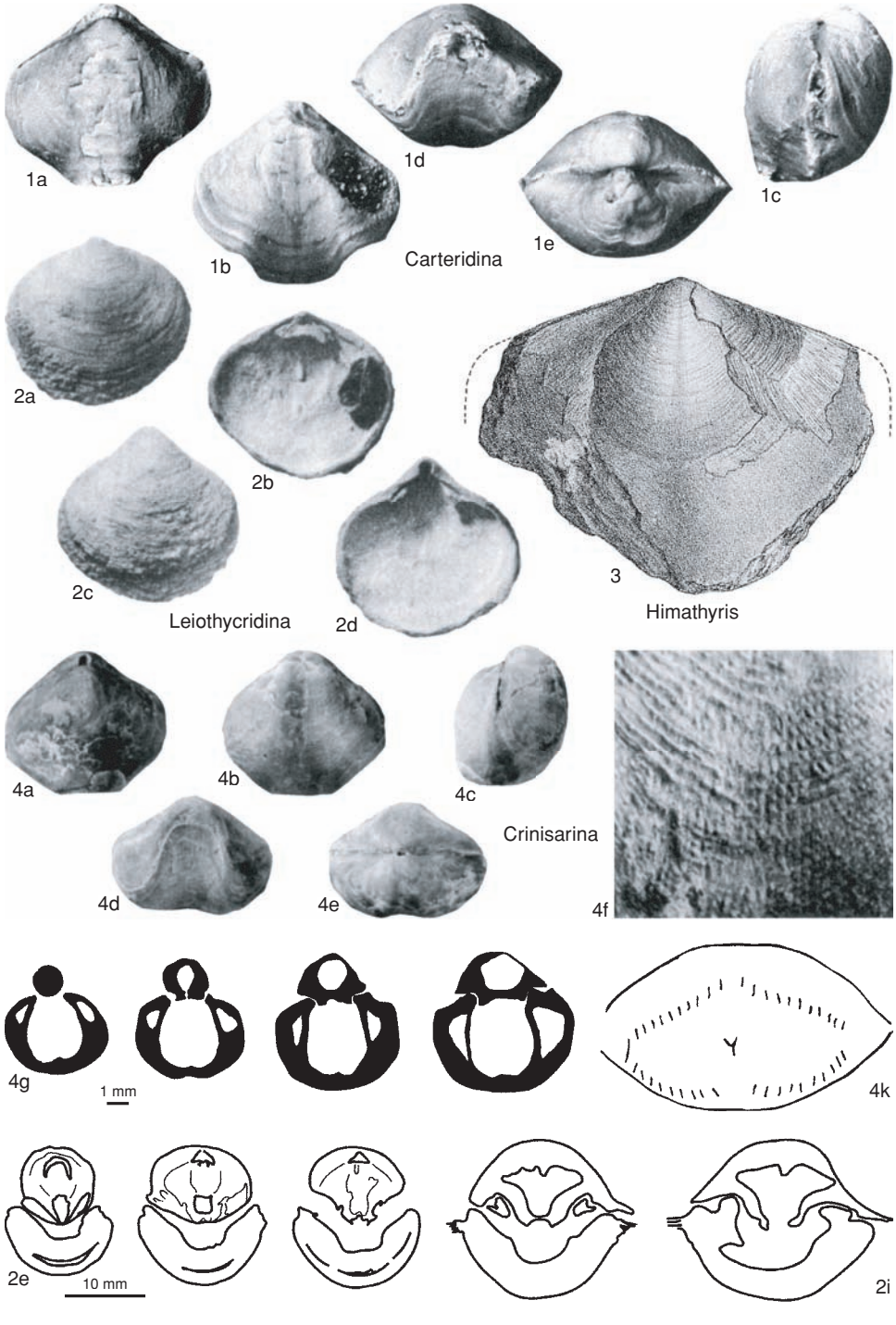


FIG. 1025. Athyrididae (p. 1510).

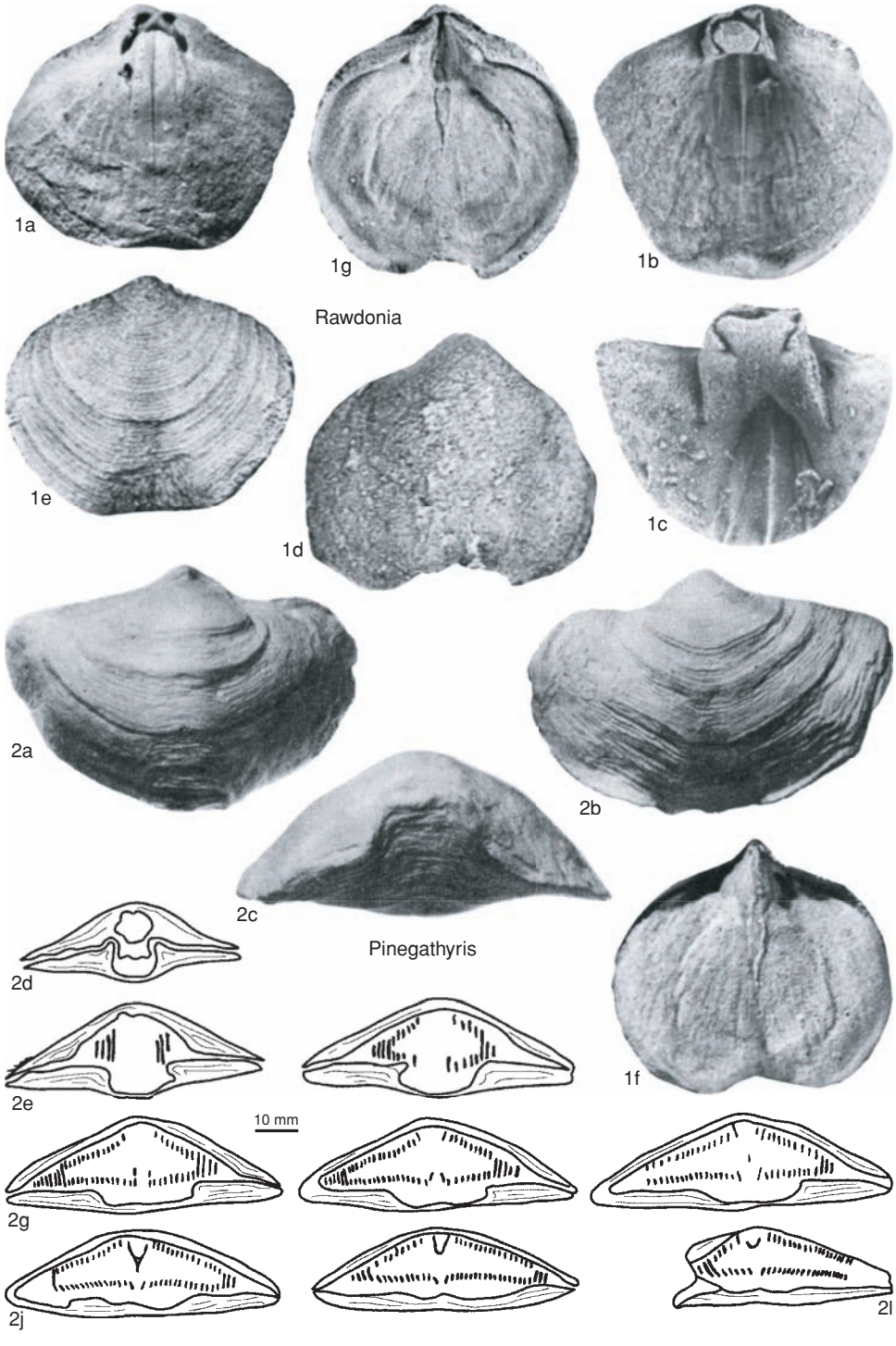


FIG. 1026. Athyrididae (p. 1510–1515).

dorsal valve smooth (?); poorly known. [Although the shells were found in the same beds, they were not conjoined. There is therefore the possibility that the smooth dorsal valves and the ornamented ventral valves do not belong to the same genus. This genus requires revision.] *Lower Carboniferous (Viséan):* Australia (New South Wales).——Fig. 1026,*1a–g.* **R. nasharae; a,* holotype, internal mold of dorsal valve, NUF 4128, ×2.5; *b,* holotype, ventral view of rubber mold, ×3; *c,* anterior view of rubber mold, ×5.7; *d,* exterior of dorsal valve (?), NUF 4116; *e,* exterior of ventral valve, ×2.5, NUF 4113; *f–g,* internal mold of ventral valve and rubber mold, NUF 4123, ×2.5 (Peou, 1979).

Subfamily COMELICANIINAE Merla, 1930

[*nom. correct.* Posenato, 1989, p. 385, *pro* Comelicaniidae Merla, 1930, p. 22, *nom. imperf.*]

Shell large to extremely large, smooth, with fine growth lines, commonly with 2 pairs of folds, more or less developed, on each valve; transverse, with greatest shell width at hinge margin; hinge line almost straight; ventral palintrope moderate to extensive, hypothyridid pedicle opening without deltidial plates, commonly obscured by beak of dorsal valve; pedicle supports absent; dental plates faintly developed or absent, low dental flanges may support teeth; cardinal plate triangular to subquadrangular and thick; cardinal flanges well developed; dorsal foramen infilled; median septum absent, but low dorsal myophragm may develop; jugum essentially as in *Athyris. Upper Permian (Changhsingian).*

Comelicania Frech, 1901, p. 551 [*?*Spirifer megalotis* Stache, 1878, p. 139; SD Schuchert & LeVene, 1929a, p. 43] [=*Spitispirifer* Waterhouse & Gupta, 1986, p. 48 (type, *S. bisulcata,* OD); *Alatothyris* Waterhouse & Gupta, 1986, p. 51 (type, *Spirifer Haueri* Stache, 1878, p. 140, OD)]. Externally similar to *Anathyris;* dental plates thin and short; ventral and dorsal muscle fields deeply impressed, may be divided by low myophragm; cardinal plate subrectangular, rather thick, commonly with shallow longitudinal depression. *Upper Permian (Changhsingian):* southern Alps.——Fig. 1027,*1a–c.* **C. megalotis* (Stache); *a,* holotype, ventral view of plaster replica, Monte Croce di Comelico, MGBW 3780, Stache Collection, ×1 (Posenato, 1998; photograph courtesy of R. Posenato); *b–c,* dorsal and posterior views, Sass de Putia, MDSGF PK1, ×1 (Posenato, 1989; photographs courtesy of R. Posenato).——Fig. 1028*a–m. C.* sp.; transverse serial sections 2.6, 4.6, 5.6, 9.0, 10.9, 11.7, 14.5, 15.5, 17.0, 20.2, 22.8, 24.5, 27.2 mm from ventral umbo, Val Brutta, MDSGF VB110 (adapted from Posenato, 1998).——Fig. 1027,*1d–e. C.* sp.; ventral and lateral views of reconstructed jugum, Val Brutta, MDSGF VB110 (Posenato, 1998).

Gruntallina Waterhouse & Gupta, 1986, p. 51 [**Comelicania triangularis* Grunt, 1965, p. 252; OD]. Similar to *Comelicania,* but much smaller; internally with very low dental flanges supporting teeth, transverse, smaller and flatter cardinalia with underlying median ridge. Jugum unknown. *Upper Permian (Changhsingian):* Transcaucasus.——Fig. 1027,*2a–g.* **G. triangularis* (Grunt); *a–b,* holotype, dorsal and ventral views, Dzhul'fa Gorge, PIN 2073/551, ×1 (Grunt, 1965); *c–g,* transverse serial sections 0.8, 1.2, 1.5, 2.0, 2.5 mm from ventral umbo, PIN 2073/551 (adapted from Grunt, 1965).

Subfamily DIDYMOTHYRIDINAE Modzalevskaya, 1979

[Didymothyridinae Modzalevskaya, 1979, p. 50]

Small to medium, strongly convex, moderately to strongly rostrate; growth lines weak, commonly without frills; dorsal fold and ventral sulcus commonly weak and narrow; dental plates thin and commonly short; ventral muscle field weakly impressed; cardinal plate commonly thin, flat, triangular, apically perforated by large foramen; cardinal process absent or rudimentary; jugal saddle moderately developed or absent; jugal arch may project posteroventrally as thin jugal stem, bifurcating into short accessory jugal lamellae, or as short horizontal and posteriorly directed stemlike process; shell thin valved, without tertiary layer. *Silurian (Wenlock)–Middle Devonian (Givetian), Upper Devonian (?Famennian).*

Didymothyris Rubel & Modzalevskaya, 1967, p. 238 [**Terebratula? didyma* Dalman, 1828, p. 146; OD]. Small to medium, unequally biconvex, elongate oval to rounded pentagonal smooth shells, sometimes with fine growth lines; ventral valve sulcate, dorsal valve with flat or slightly depressed median fold; anterior margin faintly emarginate; ventral beak high, slightly curved; hypothyridid pedicle opening partially closed by deltidial plates; low dorsal beak does not conceal delthyrium. Dental plates converging dorsally, anteriorly only dental flanges support teeth; large delthyrial chamber with 2 variably developed curved plates, formed of secondary layer, medially and apically situated, parallel to dental plates and joined with them at their posterodorsal end; very low dorsal myophragm may be present; cardinal plate and jugum essentially as in

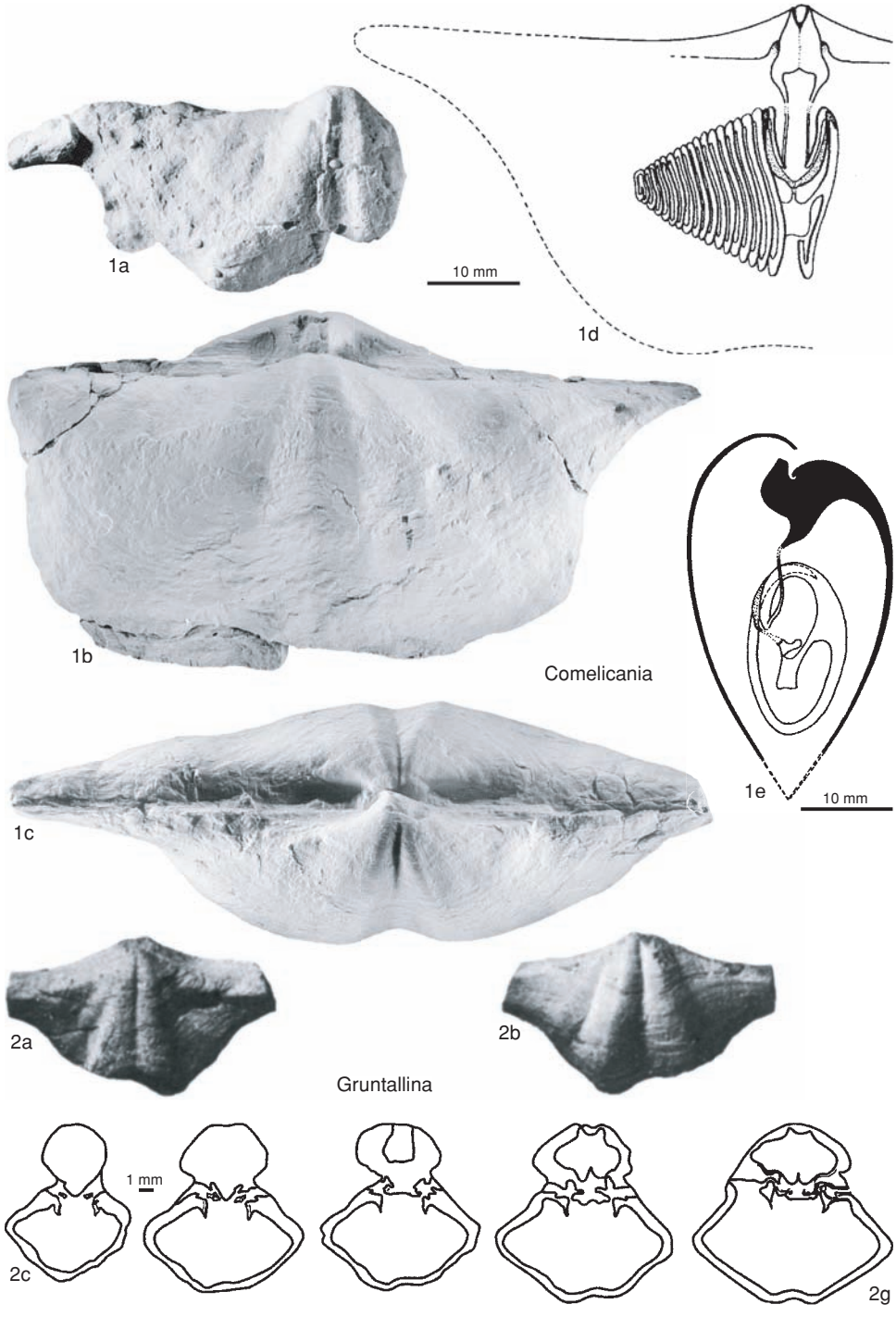


FIG. 1027. Athyrididae (p. 1515).

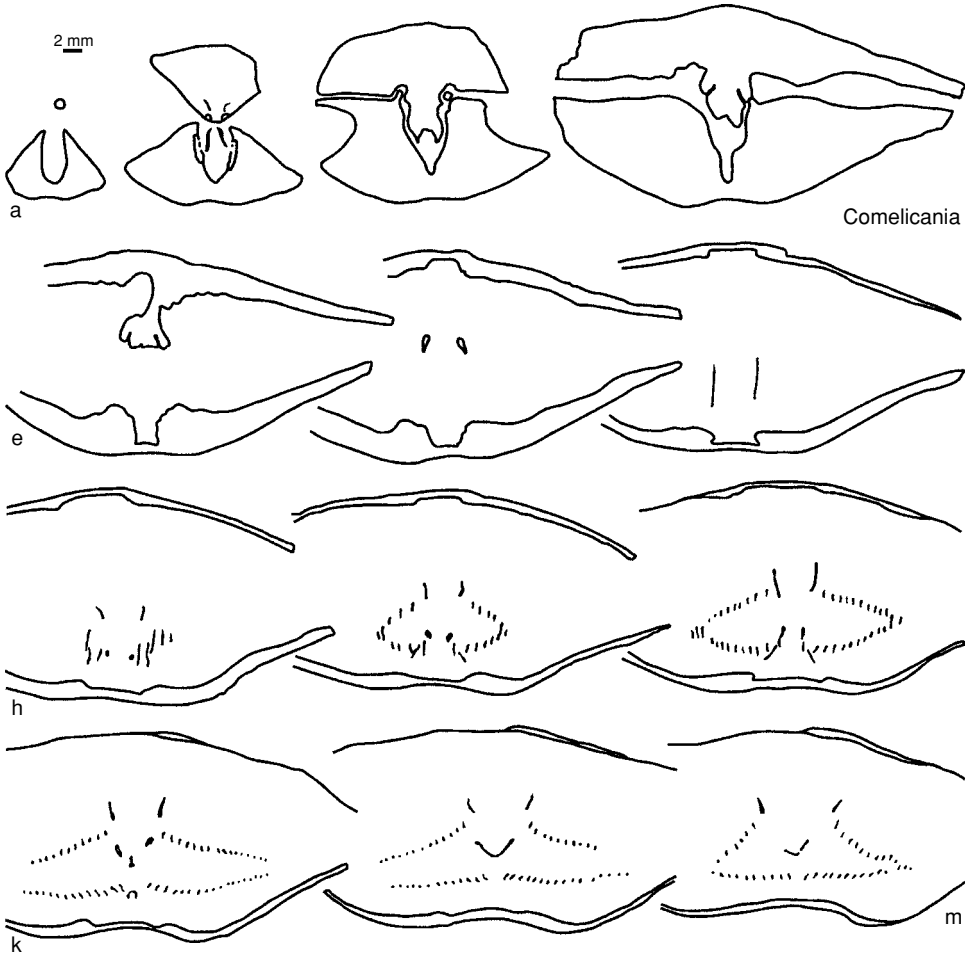


FIG. 1028. Athyrididae (p. 1515).

Athyris. Silurian (Wenlock–Ludlow, ?Přídolí): Estonia, ?Sweden, *Wenlock–Ludlow;* Gotland, Latvia, Podolia, Novaya Zemlya, Vaigach, Dolgii, Kotelmi, Chernova uplift, western circumpolar, northern, and central Urals, western Saian, ?Yukon, *Ludlow;* Salair, Altay, *Ludlow, ?Přídolí.*——FIG. 1029,*1a–w.* **D. didyma* (DALMAN), Ludlow, Estonia; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, TAGI BR 2629, ×2; *f,* ventral valve prepared to show dental and median plates, TAGI BR 2584, ×3; *g,* specimen polished to show ventral umbo structures, CNIGR 4/9742, ×1.5 (Rubel & Modzalevskaya, 1967; photographs courtesy of T. L. Modzalevskaya); *h–v,* transverse serial sections 0.7, 1.2, 1.5, 2.0, 2.4, 2.6, 3.0, 3.6, 4.0, 4.2, 5.1, 6.4, 7.8, 8.7, 9.1 mm from ventral umbo, distance from ventral umbo to first section approximate, CNIGR 69/11964; *w,* lateral view of jugum (adapted from Modzalevskaya, 1985).

Buchanathyris TALENT, 1956, p. 36 [**B. westoni;* OD]. Medium shell, subequally biconvex, subcircular to subelliptical in outline; with or without faintly developed dorsal fold and ventral sulcus; dental plates of medium length, medially concave; dorsal median septum or myophragm absent; lateral branches of jugum beginning posterior to middorsal valve length, inclined slightly anteriorly, united in acute jugal arch (without saddle), situated at middorsal valve length, pointed backward as short stemlike process, without bifurcations. *Lower Devonian (Pragian–lower Emsian):* Australia (Victoria, New South Wales), ?China.——FIG. 1029,*2a–n.* **B. westoni,* lower Emsian, Victoria; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, NMV P127838, ×1.5 (new; photographs courtesy of A. Sandford); *f–m,* transverse serial sections 0.50, 1.25, 1.50, 1.75, 2.00, 2.25, 2.50, 3.00 mm from ventral umbo, distance from ventral umbo to first

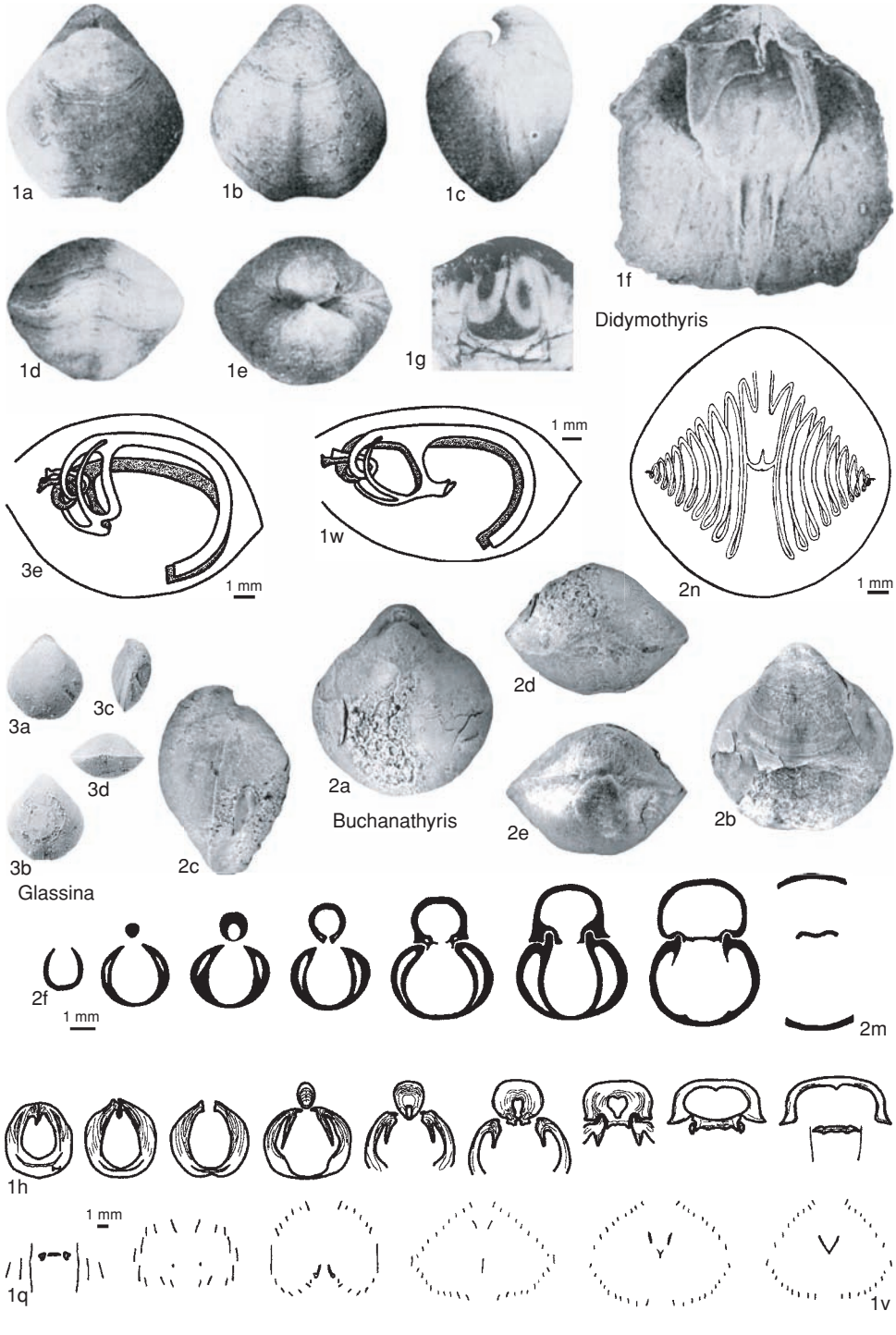


FIG. 1029. Athyrididae (p. 1515–1519).

section approximate (adapted from Talent, 1956); *n,* brachidium (Talent, 1956).

Collarothyris Modzalevskaya, 1970, p. 155 [**Meristella canaliculata* Veniukov, 1899, p. 143; OD]. Similar to *Didymothyris* but having dorsally convex delthyrial plate, instead of apically situated curved plates, parallel to dental plates. *Silurian (Přídolí):* Podolia, Estonia, Latvia, Novaya Zemlya, Dolgii, Vaigach, Chernyshev uplift, Bol'shezeml'skaia Tundra, western circumpolar, northern, and central Urals.——Fig. 1030,*1a–e.* **C. canaliculata canaliculata* (Veniukov), Podolia; *a–d,* lectotype, dorsal, ventral, lateral, and anterior views, IGN 367/165, ×2 (Modzalevskaya, 1994a; photographs courtesy of T. L. Modzalevskaya); *e,* dorsal view of ventral beak of articulated specimen showing deltidial plates and pedicle support, CNIGR 15/9742, ×6 (Rubel & Modzalevskaya, 1967; photograph courtesy of T. L. Modzalevskaya).——Fig. 1030,*1f–w. C. canaliculata lata* (Chernyshev & Iakovlev), Bol'shezeml'skaia Tundra, Russia; *f–m,* transverse serial sections illustrating the development of cardinalia, 1.1, 1.3, 2.3, 2.4, 2.5, 2.8, 3.1, 3.4 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Modzalevskaya, 1970); *n–v,* transverse serial sections illustrating development of brachidium, 3.7, 4.5, 5.4, 5.8, 6.2, 6.6, 7.2, 7.3, 7.6 mm from ventral umbo, distance from ventral umbo to first section approximate, CNIGR 77/11964; *w,* lateral view of jugum (adapted from Modzalevskaya, 1985).

Dogdathyris Baranov, 1994, p. 31 [**D. horridula;* OD]. Similar to *Leptathyris* but reportedly with low median septum in ventral valve; jugum with long stem and short accessory jugal lamellae. *Lower Devonian (Emsian):* eastern Siberia, Yakutsk.——Fig. 1031,*1a–m.* **D. horridula; a–d,* holotype, dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/15, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov); *e–m,* transverse serial sections 0.4, 1.6, 2.7, 3.6, 4.7, 6.2, 6.7, 7.0, 8.0 mm from ventral umbo, GM YaRGTs 208/32 (adapted from Baranov, 1994).

Glassina Hall & Clarke, 1893, p. 98 [**Terebratula laeviuscula* J. de C. Sowerby, 1839, p. 631; OD]. Small, elongate subelliptical to subpentagonal, subequally moderately biconvex shells; slight median depression near front in ventral valve; anterior margin truncated or slightly emarginate; ventral beak small, incurved with minute oval foramen; hinge plate supported by median septum extending about one-third length of shell; jugum backward inclined X with upper tips curved outward, without jugal stem and saddle. *Silurian (Wenlock–Ludlow):* United Kingdom, Podolia, Gotland, Novaya Zemlya, Vaigach, ?Ontario.——Fig. 1029,*3a–d.* **G. laeviuscula* (Sowerby), Wenlock, Shropshire, England; *a–d,* dorsal, ventral, lateral, and anterior views, BMNH B5389(3), Davidson collection, ×2 (new; photographs courtesy of S. Long).——Fig. 1029,*3e. G. pentagona* Modzalevskaya, Ludlow, Podolia; lateral view of reconstructed jugum (adapted from Modzalevskaya, 1979).

Greenfieldia Grabau in Grabau & Sherzer, 1910, p. 148 [**G. whitfieldi;* OD]. Medium, subequally biconvex, elongate trigonal to subpentagonal shells, with or without faint sulcus on both valves; cardinal plate with narrow outer hinge plates and short, inner plates commonly fused medianly; dorsal median septum or myophragm absent; jugum as in *Buchanathyris. Silurian (Ludlow):* USA (Ohio, Michigan), Novaya Zemlya, Vaigach, Dolgii, Bol'shezemlia Tundra, China (?Yunnan).——Fig. 1031,*2a–b.* **G. whitfieldi,* Michigan, USA; dorsal and ventral interior molds, ×1 (Grabau & Sherzer, 1910).——Fig. 1031,*2c. G.* sp., Michigan, USA; jugum, USNM 487828, ×10 (Boucot, Alvarez, & Leibold, 1997).

?Jarovathyris Havlíček, 1987b, p. 241 [**Atrypa canaliculata* Barrande, 1879b, p. 89; OD]. Similar to *Glassina* but with narrow sulcus starting on dorsal umbo and unisulcate anterior commissure; internally with low myophragm, spiralia and jugum unknown; interior poorly known. [This genus requires revision.] *Silurian (Ludlow)–Lower Devonian (Lochkovian):* Czech Republic (central Bohemia).——Fig. 1030,*2a–d.* **J. canaliculata* (Barrande), upper Ludlow; lectotype, dorsal, ventral, lateral, and anterior views, L 23357, ×2 (Havlíček, 1990d).

Leptathyris Siehl, 1962, p. 212 [**L. gryphis;* OD]. Subequally biconvex, small to medium size, subcircular, elongate or transverse shell; ventral beak suberect; open delthyrium and minute foramen; commonly faintly bisulcate; few, widely spaced growth lines; shell thick in umbonal region; lateral apical cavities narrow, dental plates of medium length, subparallel; cardinal plate depressed, medially crested; stout myophragm may be developed; jugum as in *Buchanathyris. Lower Devonian (Emsian)–Middle Devonian (Givetian), Upper Devonian (?Famennian):* Germany, Bohemia, Salair, southern Siberia, southern China, USA (Nevada, Alaska), Canada, *Emsian–Givetian;* ?Poland, *Famennian.*——Fig. 1032*a–j.* **L. gryphis,* Eifelian, Eifel, Germany; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GIB Nr23, ×1.5; *f–j,* transverse serial sections 1.6, 1.7, 1.8, 2.0, 2.1 mm from ventral umbo, distance from ventral umbo to first section approximate (Siehl, 1962).——Fig. 1032*k–w. L. salaraica* Iazikov, Emsian, Salair; transverse serial sections 6.3, 7.8, 10.3, 10.9, 11.8, 13.1, 13.9, 15.2, 15.8, 16.1, 17.0, 17.2, 17.5 mm from ventral umbo, TSGM 839-15 (adapted from Iazikov, 1988).

Pseudoprotathyris Modzalevskaya, 1979, p. 59 [**Protathyris infantile* Kozlowski, 1929, p. 230; OD]. Small, subpentagonal, ventribiconvex shell; anteriorly faint sulcus in both valves; anterior margin may be slightly emarginate; dental plates subparallel; myophragm absent; inner hinge plates fused medially and dorsally concave; outer plates and crural bases projecting ventrally at right angle at anterior end of cardinal plate; lateral branches of

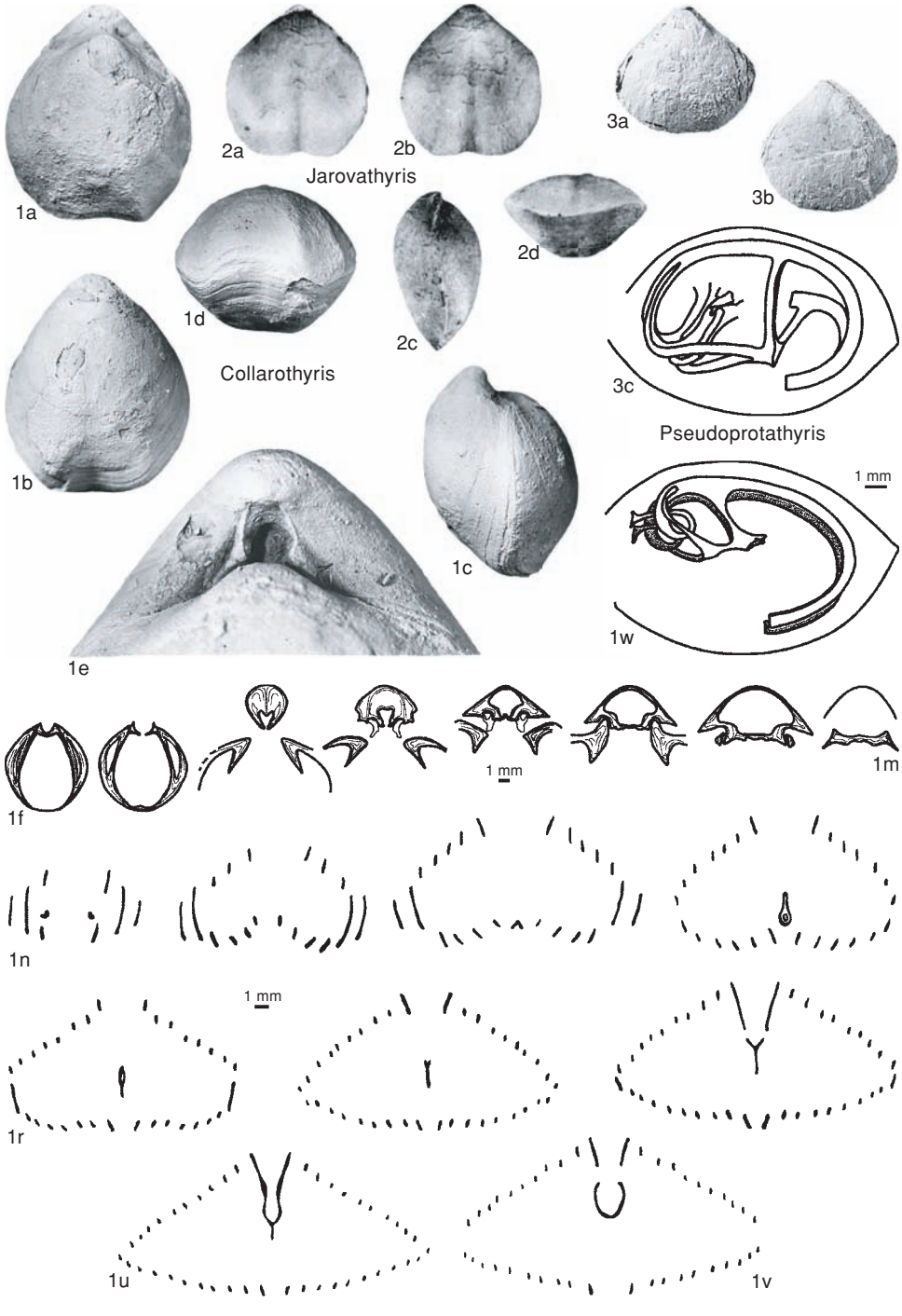


FIG. 1030. Athyrididae (p. 1519–1522).

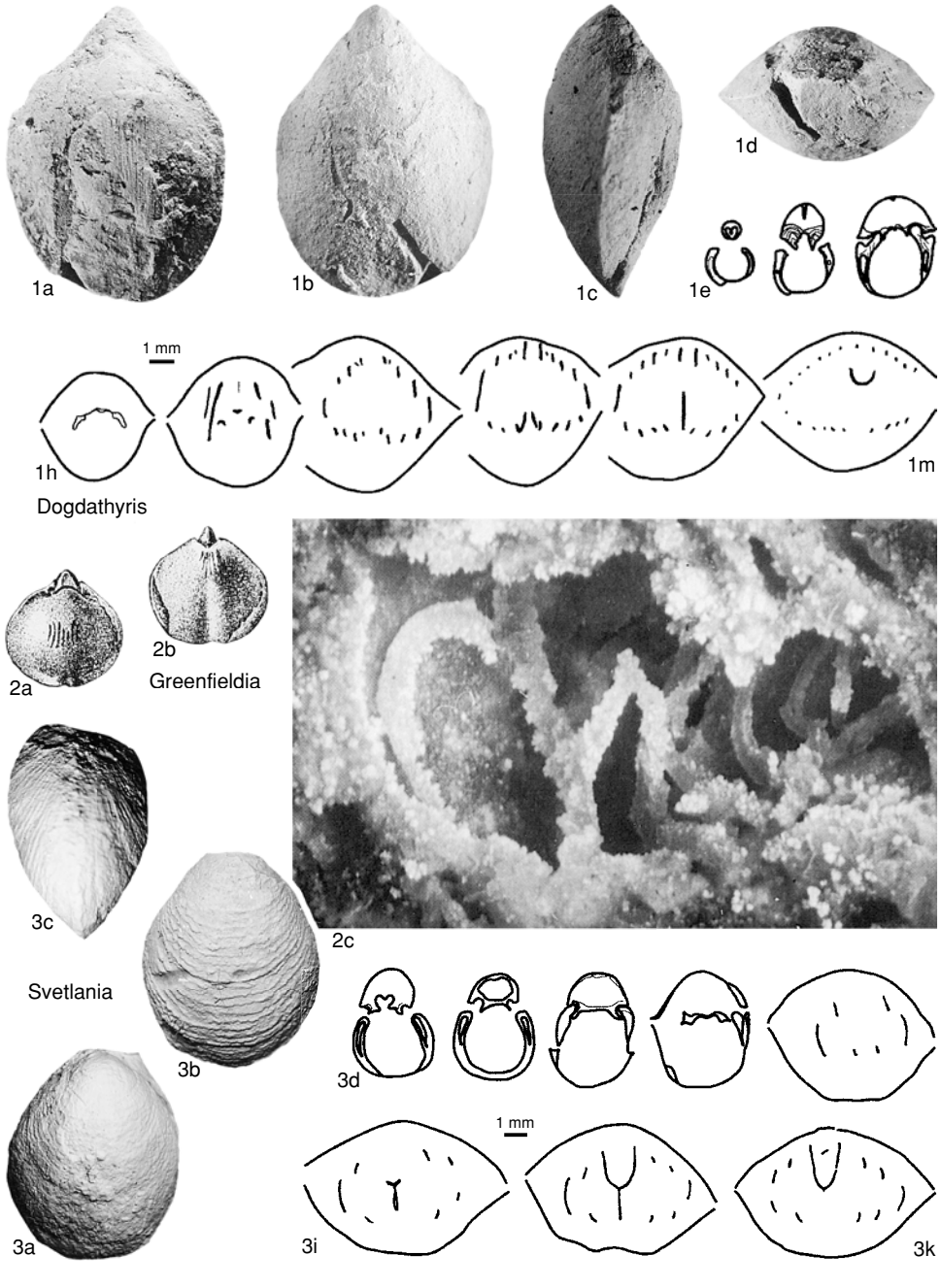


FIG. 1031. Athyrididae (p. 1519–1522).

jugum vertical; jugum anteriorly situated, without saddle and stem, projecting posteriorly up to dorsal valve midlength, there dividing into 2 accessory jugal lamellae posteriorly and dorsally directed, between primary and secondary lamellae, to end quite posteriorly to lateral branches of jugum. *Silurian (Wenlock)–Lower Devonian (Lochkovian):* Russia (Podolia), Bohemia, USA (Maryland), Arctic Canada.——FIG. 1030,*3a–c.* **P. infantilis* (KOZLOWSKI), Přídolí, Podolia; *a–b,* neotype, dorsal and

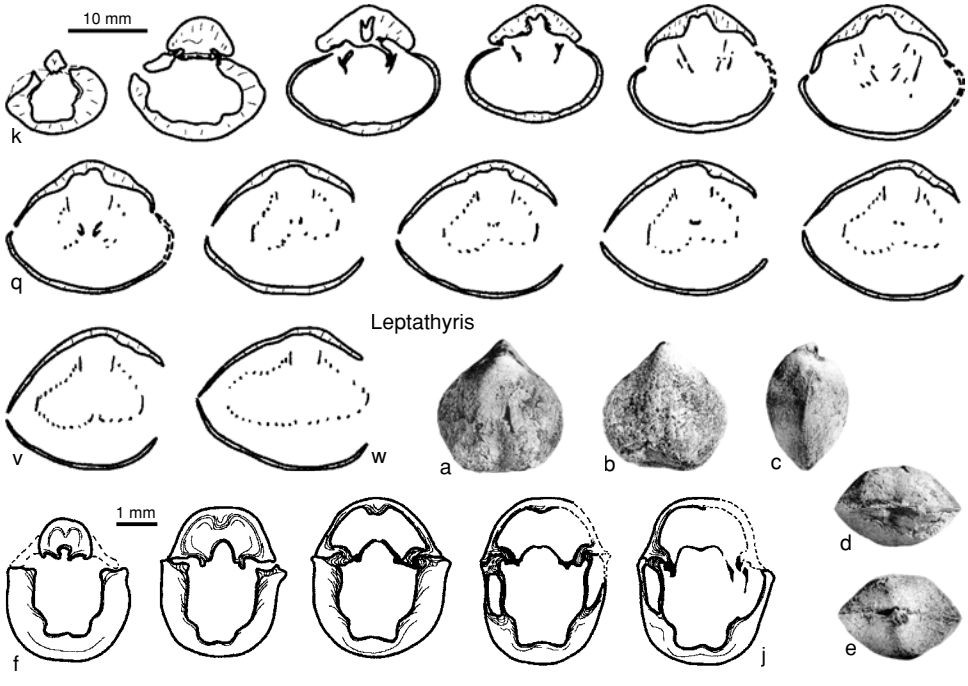


FIG. 1032. Athyrididae (p. 1519).

ventral views, CNIGR 14/11712, ×4 (Modzalevskaya, 1979; photographs courtesy of T. L. Modzalevskaya); *c,* lateral view showing reconstructed jugum, CNIGR 25/11712, approximately ×8 (adapted from Modzalevskaya, 1979).

Svetlania BARANOV, 1982, p. 48 [**S. rara;* OD]. Medium, elongate subelliptical, ventribiconvex shell; rectimarginate or with anterior faint sulcus in ventral valve; numerous lamellose growth lines; dental plates dorsally convergent; myophragm absent; cardinal plate with anterior median ridge; jugum with vertical lateral branches, long vertical stem, and reportedly short accessory jugal lamellae. *Lower Devonian–Middle Devonian:* eastern Siberia (Yakutsk). ——FIG. 1031,*3a–k. *S. rara,* lower Emsian; *a–c,* holotype, dorsal, ventral, and lateral views, ventral umbo cut, YaTGU Museum 142/23, ×3 (Baranov, 1982; photographs courtesy of V. V. Baranov); *d–k,* transverse serial sections 1.2, 1.4, 1.6, 2.0, 3.2, 3.7, 3.8, 4.1 mm from ventral umbo, distance from ventral umbo to first section approximate, YaTGU Museum 142/26 (adapted from Baranov, 1982).

Subfamily HELENATHYRIDINAE Dagys, 1974

[Helenathyridinae DAGYS, 1974, p. 154]

Shell small, slightly rostrate, numerous growth lines; dorsal fold and ventral sulcus commonly absent; ventral beak short, suberect, with hypothyridid pedicle opening, with (*Eobiernatella, Sphaerathyris*) or without narrow deltidial plates; ventral area small, commonly orthocline; dental plates short to medium length, subparallel, or converging slightly ventrally, present until latest Givetian; cardinal plate apically perforate in Early Devonian, absent in Late Devonian; cardinal process absent; without dorsal septum or myophragm; lateral branches of jugum almost vertical, starting middorsal valve length; jugal saddle commonly absent, poorly developed and spiny when present; short, posteroventrally directed stem may be present; accessory jugal lamellae branching from ventral side of jugum, extending posterodorsally, and intercalating with spiralial loops to apex; thick shelled after Early Devonian. *Lower Devonian–Upper Devonian (Frasnian).*

Helenathyris ALEKSEEVA, 1969, p. 1157 [**H. plana;* OD]. Subcircular, weakly biconvex; growth plates covered with very fine fimbriae; dental plates short; cardinal plate apically perforate, inner sockets ridges and outer hinge plates projecting ventrolaterally.

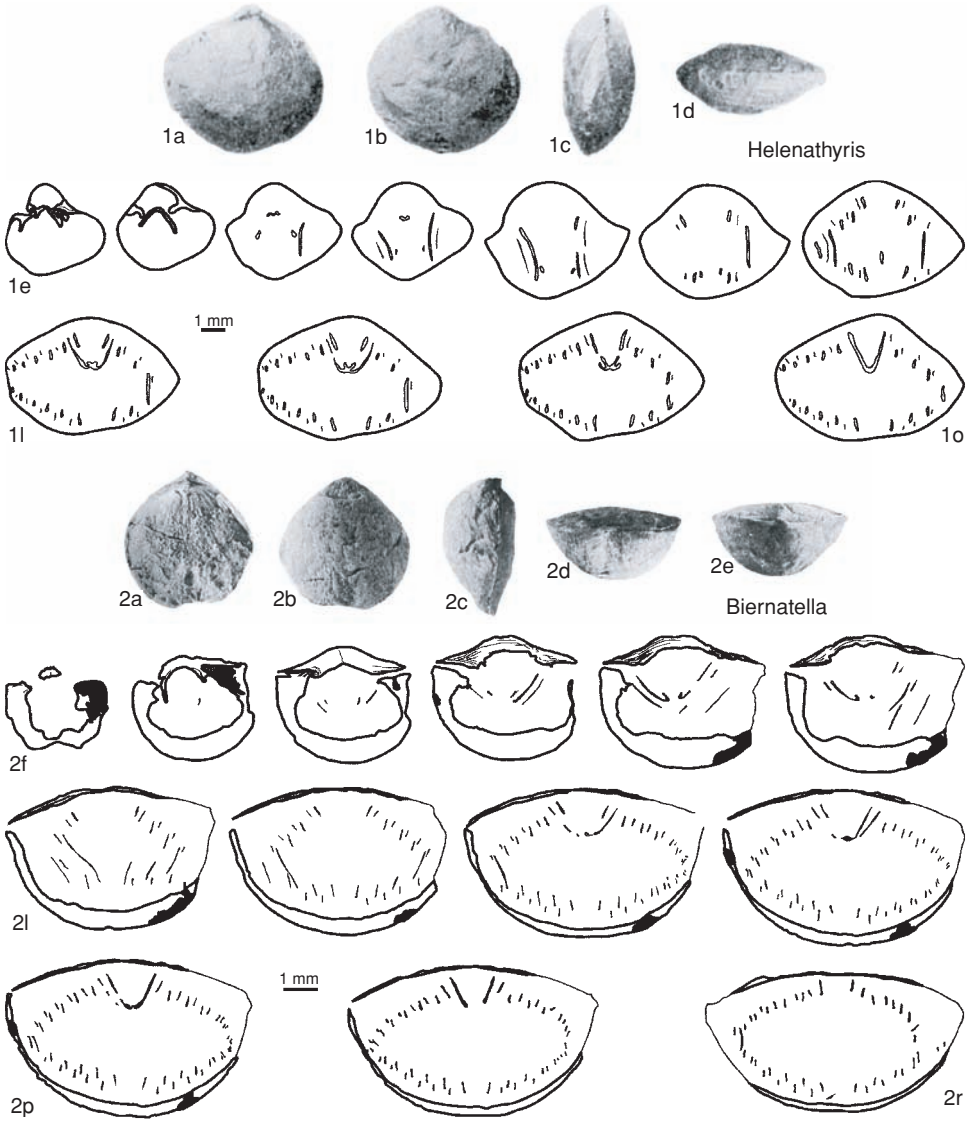


FIG. 1033. Athyrididae (p. 1522–1523).

Lower Devonian: northeastern Russia (Cherskogo Mountains).——FIG. 1033,*1a–o. *H. plana; a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 340/1, ×2 (Alekseeva, 1969); *e–o,* transverse serial sections 1.7, 1.8, 1.9, 2.2, 2.4, 3.0, 3.8, 4.2, 4.3, 4.5, 4.6 mm from ventral umbo, IGiG 340/2 (adapted from Alekseeva, 1969).

Biernatella BALINSKI, 1977, p. 179 [**B. polonica;* OD] [=*Sedjulina* LIASCHENKO, 1985, p. 17 (type, *S. timanica,* OD)]. Elongate oval to subcircular, ventribiconvex; smooth, concentric lines weak, numerous; weak median sulcus may be present anteriorly; thick shelled. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Poland, western Russia.——FIG. 1033,*2a–r. *B. polonica,* Frasnian, Kraków area, Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ZPAL Bp XXIII/31g, ×2 (Balinski, 1977); *f–r,* transverse serial sections 0.6, 0.8. 1.0, 1.15, 1.35, 1.5, 2.0, 2.3, 2.8, 2.9, 3.0, 3.15, 3.4 mm from ventral umbo, ZPAL Bp XXIII/30e (adapted from Balinski, 1977).

Eobiernatella BALINSKI, 1995b, p. 138 [**E. rackii;* OD]. Similar to *Biernatella* externally and to

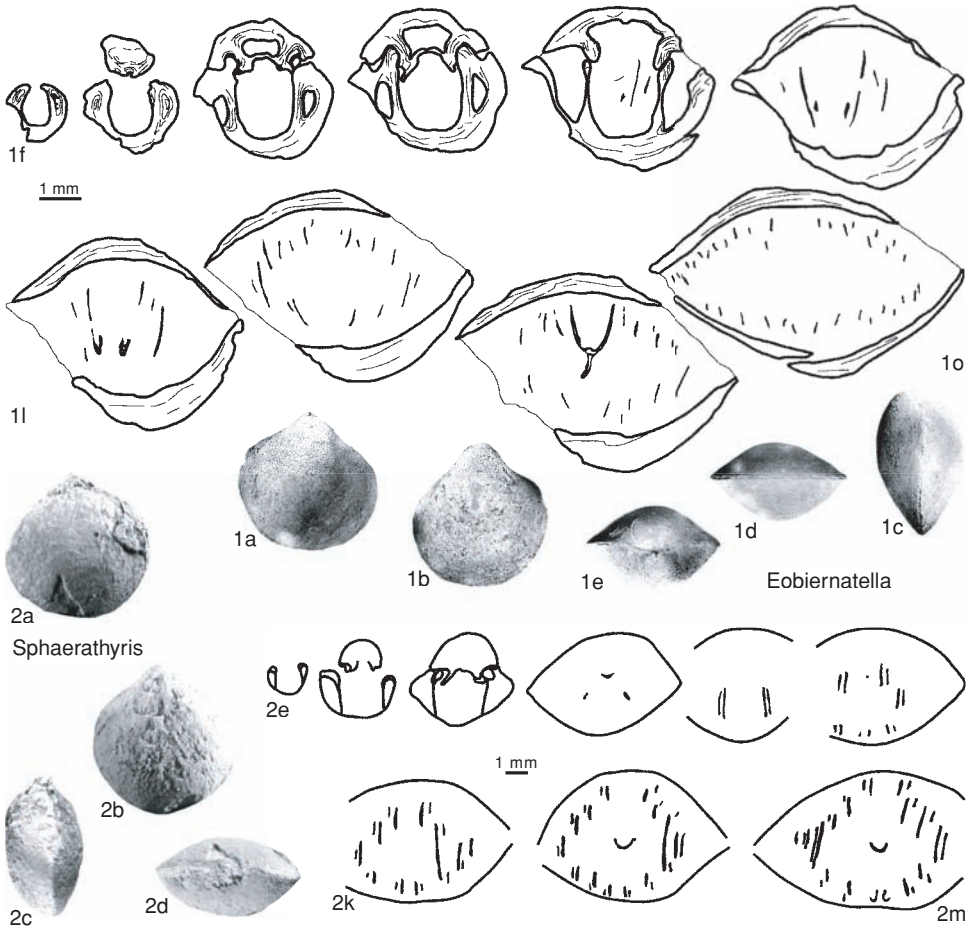


FIG. 1034. Athyrididae (p. 1523–1524).

Helenathyris internally; thick shelled. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* Poland, Russia, ?Pyrenees.——FIG. 1034,*1a–o.* **E. rackii,* Givetian, Holy Cross Mountains, Poland; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, ZPAL Bp XXXVIII/7, ×2 (Balinski, 1995b); *f–o,* transverse serial sections 0.4, 0.6, 1.2, 1.4, 1.8, 2.1, 2.3, 2.9, 3.1, 4.1 mm from ventral umbo (adapted from Balinski, 1995b).

Sphaerathyris BARANOV, 1994, p. 34 [**S. repentina*; OD]. Similar to *Helenathyris* but differing in smooth exterior, delthyrium reportedly covered by deltidial plates, longer dental plates, and lack of stem in jugum. *Lower Devonian (upper Pragian–Emsian):* eastern Siberia, Yakutsk.——FIG. 1034,*2a–m.* **S. repentina,* Emsian; *a–d,* dorsal, ventral, lateral, and anterior views, GM YaRGTs 208/20, ×2 (Baranov, 1994; photographs courtesy of V. V. Baranov); *e–m,* transverse serial sections 0.1, 0.4, 0.8, 1.3, 1.8, 2.1, 2.8, 3.3, 3.5 mm from ventral umbo, GM YaRGTs 208/42 (adapted from Baranov, 1994).

Subfamily LOCHENGIINAE Ching & Yang, 1977

[*nom. transl.* ALVAREZ, RONG, & BOUCOT, 1998, p. 842, *ex* Lochengiidae CHING & YANG, 1977, p. 412]

Shell very large, slightly to moderately rostrate; growth lines fine or lamellose, commonly plicate or costate; dorsal fold and ventral sulcus poorly developed or absent; dental plates short or absent; cardinal plate subtrapezoidal; cardinal flanges variably developed when present; jugum essentially as in *Athyris. Lower Carboniferous (Viséan)–Lower Permian.*

Lochengia Yoh, 1929, p. 70 [**L. lochengensis* Ching & Yang, 1977, p. 412; SD Jin, 1983, p. 227; =*Lochengia holoensis* Grabau, 1931a, p. 478, *nom. nud.; Cryptospirifer lochengensis* Grabau, 1931c, p. 405, *nom. nud.*] [=*Flexathyris* Grunt, 1980, p. 61 (type, *F. prokofjevi,* OD)]. Ventribiconvex to planoconvex or slightly concavoconvex, transversely oval, thick shells; dorsal fold faintly developed or absent, shallow ventral sulcus present from umbo; surface commonly with numerous, simple, round plicae variably developed; growth lines lamellose, closely and regularly spaced; very fine ribbing may be present in sulcus; ventral beak thick, strongly curved, foramen in meso- to permesothyridid position; dental plates moderately thick, short, low, converging slightly dorsally; cardinal plate thin, almost flat. [The genus is usually credited to Grabau (1931a, p. 478) although Yoh (1929, p. 70) should be considered its author (see Alvarez & Rong, 1995, p. 604).] *Lower Carboniferous (Viséan, ?Serpukhovian):* southern China (Guangxi), Russia (eastern Urals), Ukraine (Donetsk).——Fig. 1035,*1a–c. *L. lochengensis* (Ching & Yang), Guangxi; holotype, dorsal, ventral, and lateral views, NIGP 70738, ×1 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Cryptospirifer Grabau, 1931c, p. 405 [**C. omeishanensis* Huang, 1933, p. 44; SD Wang, Ching, & Fang, 1964, p. 512]. Biconvex, transverse to subcircular or elongate oval, massive shells; without dorsal fold and ventral sulcus; few growth lines irregularly spaced; ventral beak short, strongly curved concealing small foramen; cardinal plate ventrally concave; cardinal flanges well developed; dorsal myophragm present. [The genus was credited by some authors to Huang (1933) although Grabau (1931b, p. 405) should be considered as author (see Alvarez & Rong, 1995, p. 604–605).] *Lower Permian:* southern China, Iran, Turkey, Armenia.——Fig. 1035,*4a–b. *C. omeishanensis* Huang, Sichuan, southern China; holotype, ventral and posterior views, NIGP 4708, ×0.5 (Huang, 1933; photographs courtesy of Jin Yu-gan).

Galeatathyris Jin, 1983, p. 230 [**G. galeata;* OD]. Similar to *Lochengia* but clearly concavoconvex, with low ventral fold and wide and flat ears. *Lower Carboniferous (Viséan, ?Serpukhovian):* southern China.——Fig. 1035,*2a–c. *G. galeata,* Guangxi; holotype, dorsal, ventral, and lateral views, NIGP 70750, ×0.5 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Titanothyris Ching & Hu, 1982, p. 253 [**T. subplicata;* OD]. Biconvex, subcircular to transversely oval shells, without dorsal fold and ventral sulcus; numerous coarse costae increasing in number anteriorly by bifurcation or intercalation; growth lines fine, growth lamellae stronger, more widely and randomly spaced; ventral beak short, strongly curved, concealing foramen; dental plates absent; cardinal flanges more or less developed; jugum unknown. *Lower Permian:* southern China.——Fig. 1035,*3a. *T. subplicata,* western Sichuan; holotype, dorsal view, NIGP 70753, ×0.5 (Jin, 1983).——Fig. 1035,*3b. T. striata,* northwestern Hunan; detail of external ornamentation of ventral valve, NIGP 707555, ×0.5 (Jin, 1983; photographs courtesy of Jin Yu-gan).

Subfamily PLICATHYRIDINAE Alvarez, 1990

[Plicathyridinae Alvarez, 1990, p. 93]

Shell medium to very large; anterior margin emarginate; moderately to strongly rostrate; ventral cardinal area (palintrope) moderate to extensive, covered by numerous, fine, and very closely spaced growth lines; dorsal cardinal area reduced; valve surfaces covered by numerous, concentric, fine, imbricate lamellae projecting outwardly; folding mixed (opposite medially and laterally, alternate between these zones); dental plates commonly of medium length, thin, slightly concave medianly, subparallel or converging dorsally; hinge plate rather wide, concave, and commonly with the median part projecting anteroventrally, giving plate a generally lobate aspect; outer hinge plates reduced; cardinal flanges moderately developed (well developed in *Anathyrella*); dorsal myophragm commonly present; jugum essentially as in *Athyris* with lateral branches of jugum starting in posterior third of primary lamellae, almost perpendicular to them, to a point at which they curve abruptly laterally or anterolaterally; they then project anteroventrally at a low angle before joining as jugal arch; anterior edge of jugal saddle spiny; jugal stem vertical. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian), ?Lower Carboniferous.*

Plicathyris Khalfin, 1946, p. 56 [**Terebratula Ezquerra* de Verneuil & d'Archiac, 1845, p. 467; OD]. Large, elongate to transverse shells, outline palmate; hinge line almost straight, rather shorter than maximum width; with median and outer lateral folds of dorsal valve and inner median and lateral folds of ventral valve starting at apex, well defined, sometimes carinate; inner lateral folds poorly developed or absent; outer median folds gentle and rounded; ventral cardinal area reduced. [The genus *Plicathyris* Khalfin, 1946 was placed in subjective synonymy with *Anathyris* von Peetz, 1901, by Boucot, Johnson, & Staton, 1965, p. 662. For validation of *Plicathyris* Khalfin, 1946 and discussion of its type species see Alvarez, 1990, p. 93–94]. *Lower Devonian (Pragian)–Upper Devonian*

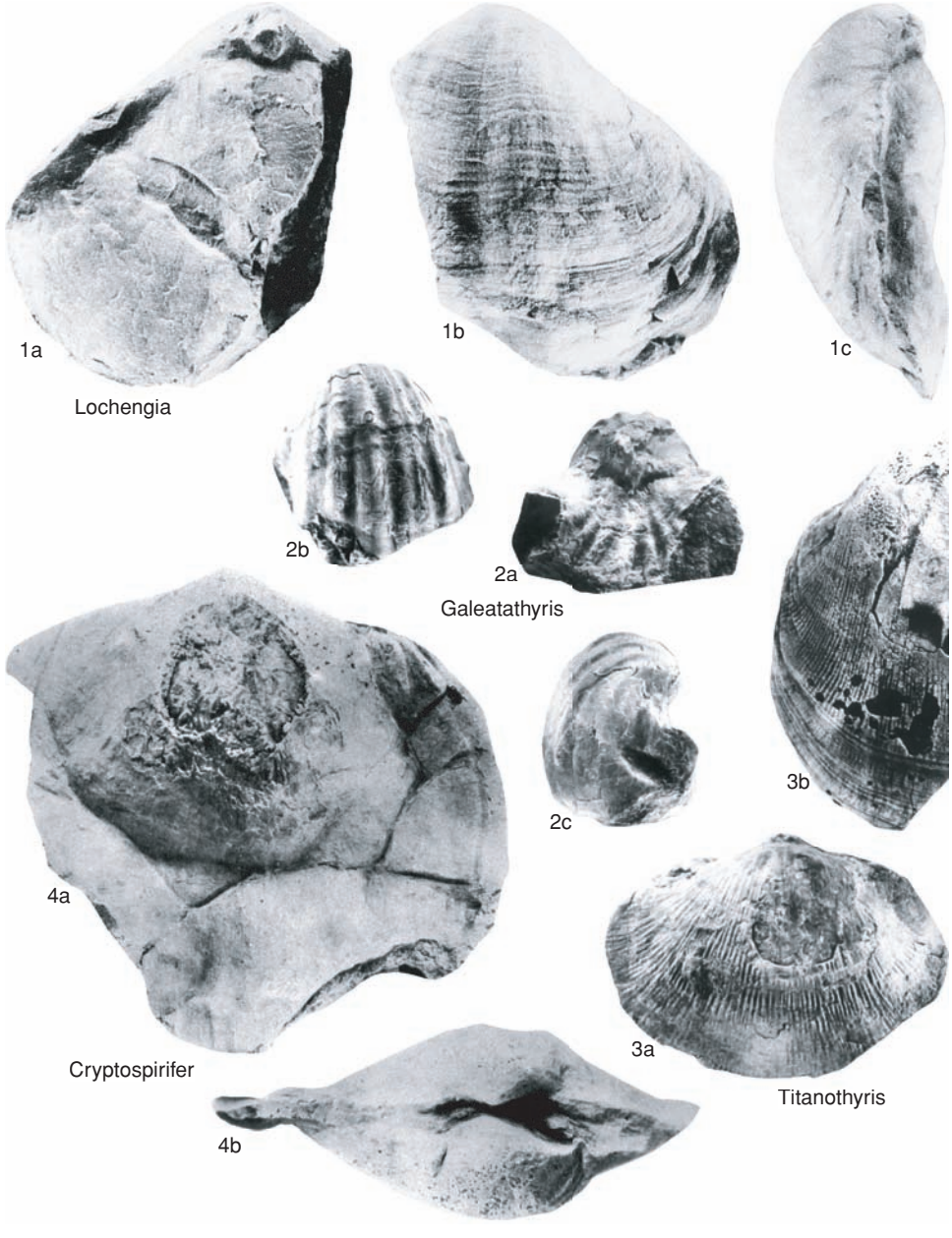


FIG. 1035. Athyrididae (p. 1525).

(lower Frasnian): northwestern Spain, France, Belgium, *Pragian–Emsian;* Kuznetsk, Altay, Salair, *upper Givetian–lower Frasnian.*——FIG. 1036*a–v.* **P. ezquerrai* (DE VERNEUIL & D'ARCHIAC), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Asturias, Spain, EM 20109, de Verneuil Collection, ×1; *f,* growth lamellae in posterior area, Asturias, Spain, EM 20109, de Verneuil Collection, ×7; *g,* growth lamellae in posterior area, Asturias, Spain, EM 20109, de Verneuil Collection, ×17 (Alvarez, 1990); *h–v,* transverse serial sections 1.15, 1.35, 2.00, 2.30, 2.60, 3.25,

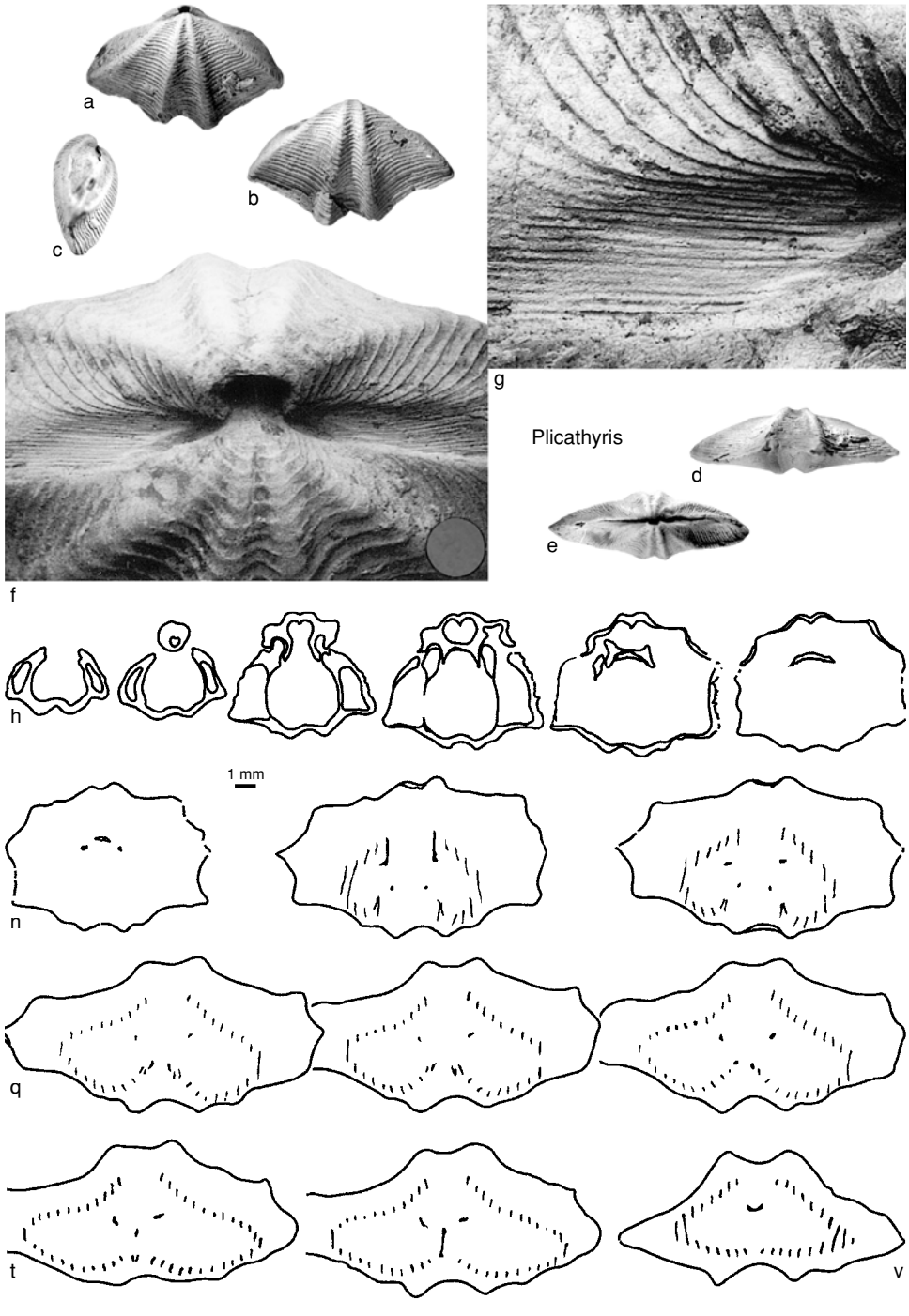


FIG. 1036. Athyrididae (p. 1525–1528).

3.85, 5.80, 6.30, 7.70, 7.80, 7.90, 8.45, 8.60, 10.30 mm from ventral umbo, León, Spain, DPO 19444 (adapted from Alvarez, 1990).——Fig. 1037*a–q. *P. ezquerrai* (de Verneuil & d'Archiac), upper Emsian; *a–p,* tangential serial sections, parallel to commissural plane, 1.60, 1.90, 2.30, 2.40, 2.60, 2.85, 3.30, 3.75, 3.90, 4.05, 4.35, 4.45, 4.60, 4.85, 4.90, 5.00 mm from ventral valve, León, Spain, DPO 19442; *q,* lateral view of reconstructed jugum, León, Spain, approximately ×5 (adapted from Alvarez, 1990). [See also Fig. 1002.6, p. 1477, in introduction.]

Anathyrella Khalfin in Gratsianova, Sinchenko, & Kul'kov, 1961, p. 476 [**Anathyris ussoffi* Khalfin, 1933, p. 112; OD]. Medium to large, transverse shells with widely flaring flanks; dorsal fold and ventral sulcus well developed, sometimes hypertrophically; hinge line almost straight, equal or slightly shorter than maximum width; ventral cardinal area rather high, subtrapezoidal, concave; thick-shelled ventral valve with poorly differentiated dental plates; may have pedicle support resembling that of early didymothyridins; stout subquadrate cardinal plate with dorsal foramen reportedly present, filled late in growth; thick cardinal flanges projecting strongly into delthyrial cavity; jugum unknown. [According to Gratsianova & Dagys (1983) all athyridid descriptions in Gratsianova, Sinchenko, & Kul'kov (1961) were made by the editor of the volume, L. L. Khalfin, although this does not appear in the table of contents; the date on the publication is 1960, but Gratsianova (1975, p. 72) cites this publication as 1960 (1961) and *Nomenclator Zoologicus* (Edwards & Vevers, 1975) also lists *Anathyella* [*sic*] as 1961. Note that *ussovi* is deemed to be an incorrect subsequent spelling for *ussoffi*.] *Upper Devonian (Frasnian):* northeastern Kuznetsk basin, Gorno-Altay.——Fig. 1038,*1a–d. *A. ussoffi* (Khalfin), northeastern Kuznetsk basin; dorsal, ventral, anterior, and posterior views, ×1 (new; photographs courtesy of T. L. Modzalevskaya).——Fig. 1038,*1e–m. A. peetzi* (Khalfin), Gorno-Altay; transverse serial sections, distances for serial sections not indicated, TsGM 470-21b (adapted from Gratsianova & Dagys, 1983).

Anathyris von Peetz, 1901, p. 134 [**Spirifera phalaena* Phillips, 1841, p. 71; SD Schuchert & LeVene, 1929a, p. 29]. Medium to very large transverse shells with overall winged outline; hinge line almost straight, equal to or slightly shorter than maximum width; folding almost opposite and anterior commissure straight in juveniles, passing during ontogeny to develop a clearer mixed folding; ventral cardinal area well defined, rather high, subtrapezoidal, concave, ranging from apsacline to almost catacline in lateral regions to strongly curved anacline centrally; area covered by numerous, close and horizontal, well-marked growth lines; foramen in permesothyridid position; delthyrium wide, triangular, open or partially restricted laterally by narrow deltidial plates; internally similar to *Plicathyris* but with thicker teeth and dental plates; in late growth stages of some specimens dorsal foramen filled. [For discussion of its type species and other species included, see Alvarez, 1990, p. 206–207. The inclusion of *A. rhomboidalis* from the Lower Carboniferous of Hunan, China, may extend the range from the Upper Devonian, Frasnian, but assignment uncertain.] *Lower Devonian (Emsian)–Upper Devonian (Frasnian), ?Lower Carboniferous:* northwestern Spain, France, northern Africa, Saudi Arabia, *Emsian;* England, Czech Republic, Timan, Kuznetsk Basin, North America, *Middle Devonian;* Timan, Urals, Kuznetsk basin, Afghanistan, *Frasnian;* ?Hunan, *?Lower Carboniferous.*——Fig. 1039*a–x. *A. phalaena* (Phillips); *a,* lectotype, ventral view, Middle Devonian, Devon, United Kingdom, GSM 6866, Phillips Collection, ×1 (Alvarez, 1990; photograph courtesy of D. E. Butler); *b–f,* dorsal, ventral, lateral, anterior, and posterior views, upper Emsian, Asturias, Spain, EM 20142, de Verneuil Collection, ×1 (Alvarez, 1990); *g–w,* transverse serial sections 0.80, 1.40, 1.70, 3.00, 3.40, 4.00, 5.75, 6.20, 8.25, 8.75, 9.00, 9.70, 11.00, 11.50, 12.80, 15.50, 18.85 mm from ventral umbo, upper Emsian, Asturias, Spain, DPO 24481, ×1.5 (adapted from Alvarez, 1990); *x,* dorsal view of winged specimen, upper Emsian, León, Spain, DPO 24777, ×1.5 (Alvarez, 1990). [See also Fig. 1003.3, p. 1478, in introduction.]

Hexarhytis Alvarez, 1990, p. 157 [**H. bonarensis;* OD]. Medium to large, equidimensional to elongate shells with generally lobate outline; slightly curved hinge line, rather narrower than maximum width; both valves with 6 unequal bifurcating folds; ventral cardinal area poorly defined, not very high, triangular, concave; internally similar to *Plicathyris* but dental plates thinner and shorter. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* Spain, France, Transcaucasus, Saudi Arabia.——Fig. 1040*a–bb. *H. bonarensis,* upper Emsian, León, Spain; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, DPO 23838, ×1 (Alvarez, 1990); *f–bb,* transverse serial sections 0.20, 0.60, 1.15, 1.45, 1.50, 1.55, 1.95, 2.15, 2.45, 2.80, 3.45, 3.55, 3.80, 4.20, 4.55, 4.65, 4.80, 4.85, 5.25, 5.55, 6.05, 6.75, 7.15 mm from ventral umbo, DPO 23839 (adapted from Alvarez, 1990). [See also Fig. 1001, p. 1476, and Fig. 1003.1, p. 1478, in introduction.]

Sulcathyris Dürkoop, 1970, p. 190 [**S. periplicata;* OD]. Medium to large, ventribiconvex, strongly rostrate, subcircular to subpentagonal shells; anterior margin slightly emarginate; ventral sulcus starting at apex, dorsal median fold flat or divided by narrow, shallow furrow, 2 wide folds may develop anterolaterally in both valves, parasulcate folding with anterior and lateral commissures in same plane; internally similar to *Athyris* but with deep, narrow sulcus in posteriormost part of cardinal plate, dorsal foramen reportedly present. *Middle Devonian (Eifelian):* western Afghanistan, Iran.——Fig. 1038,*2a–p. *S. periplicata,* western Afghani-

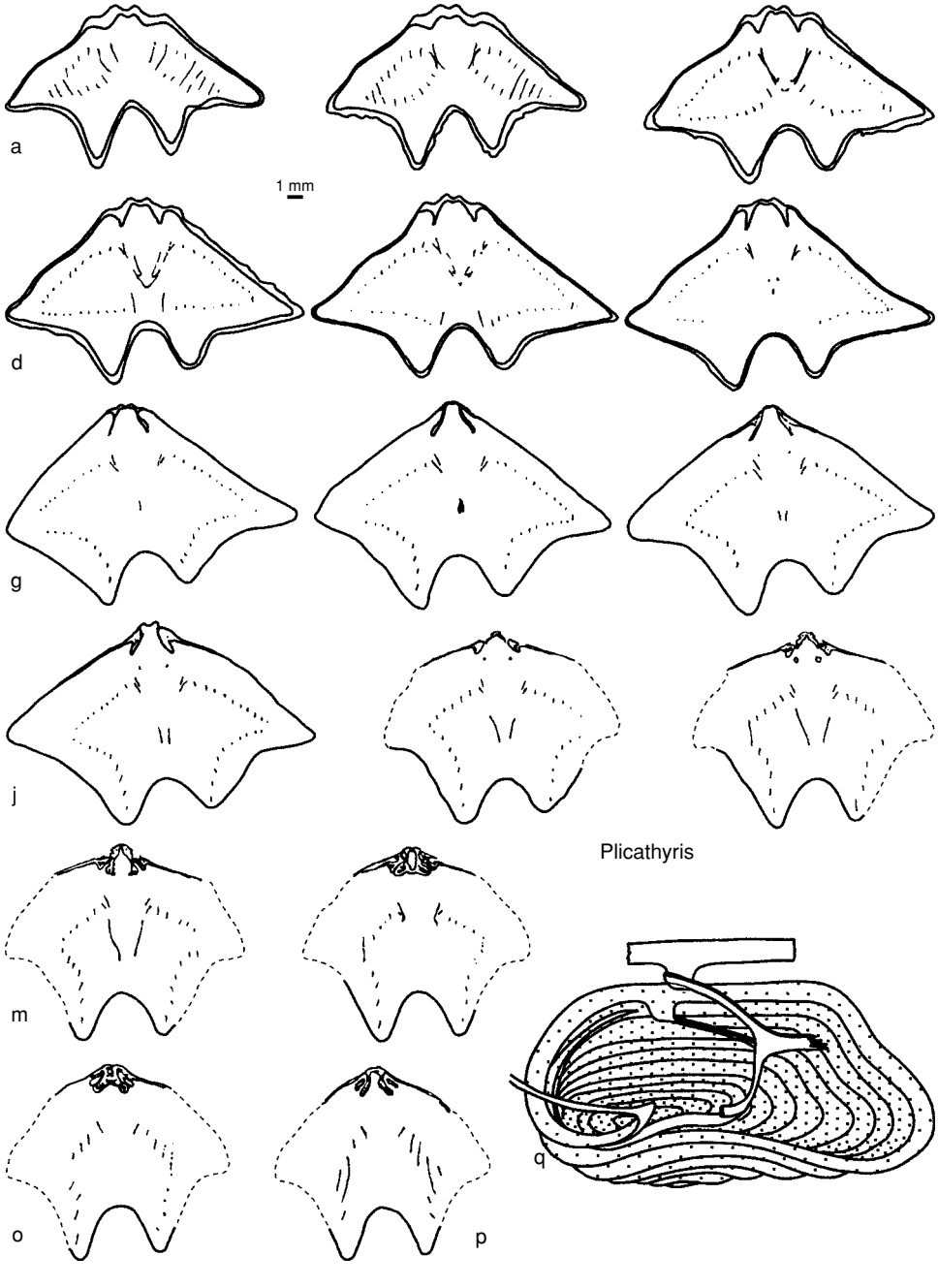


FIG. 1037. Athyrididae (p. 1525–1528).

stan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GPIBo 91, ×1.5 (Dürkoop, 1970); *f–k,* transverse serial sections showing cardinalia, 1.9, 2.6, 2.7, 3.1, 3.4, 4.0 mm from ventral umbo, GPIBo 93; *l–o,* transverse serial sections showing spiralium, 6.8, 8.6, 10.0, 10.4 mm from ventral umbo, GPIBo 95; *p,* jugum, approximately ×10 (adapted from Dürkoop, 1970).

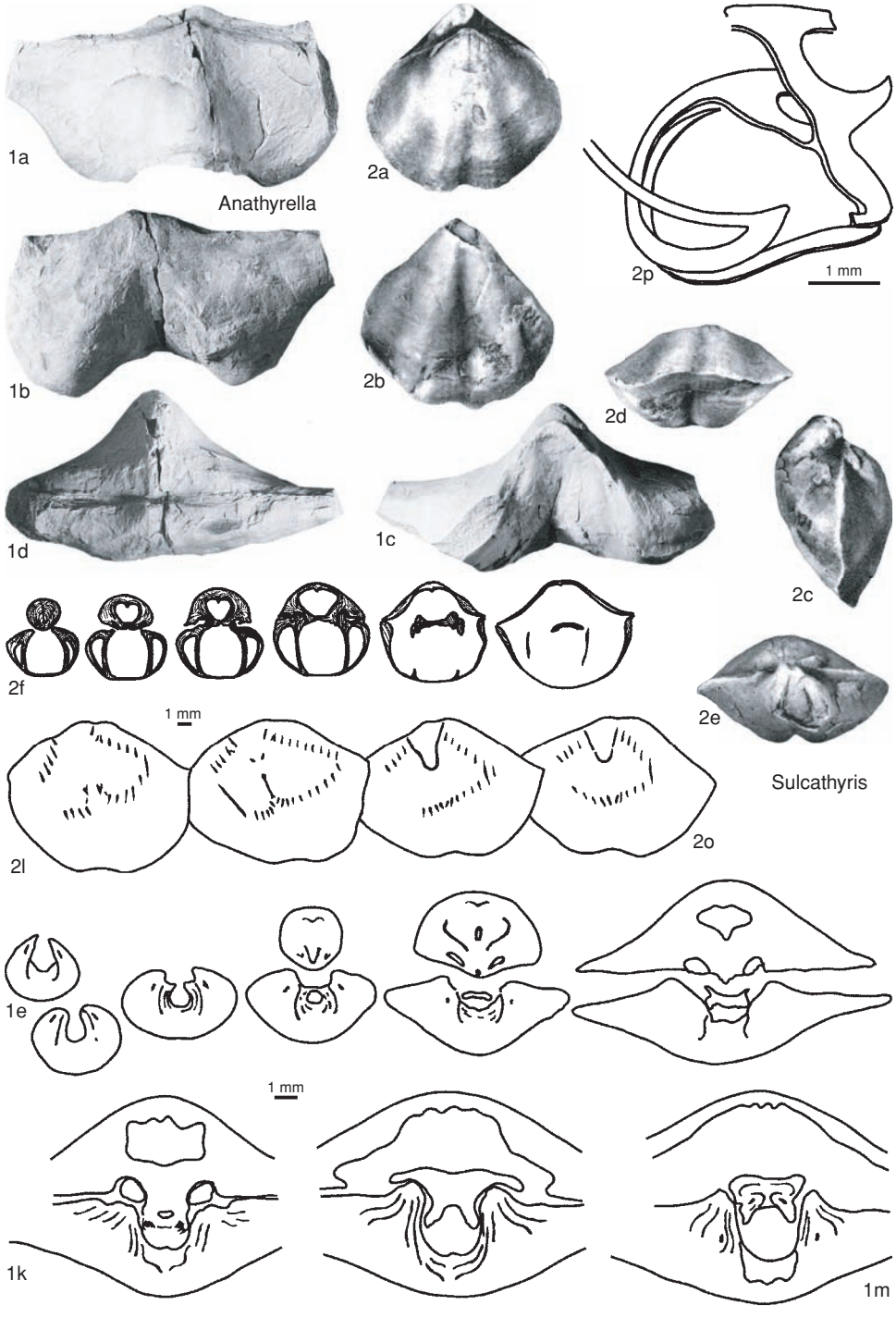


FIG. 1038. Athyrididae (p. 1528–1529).

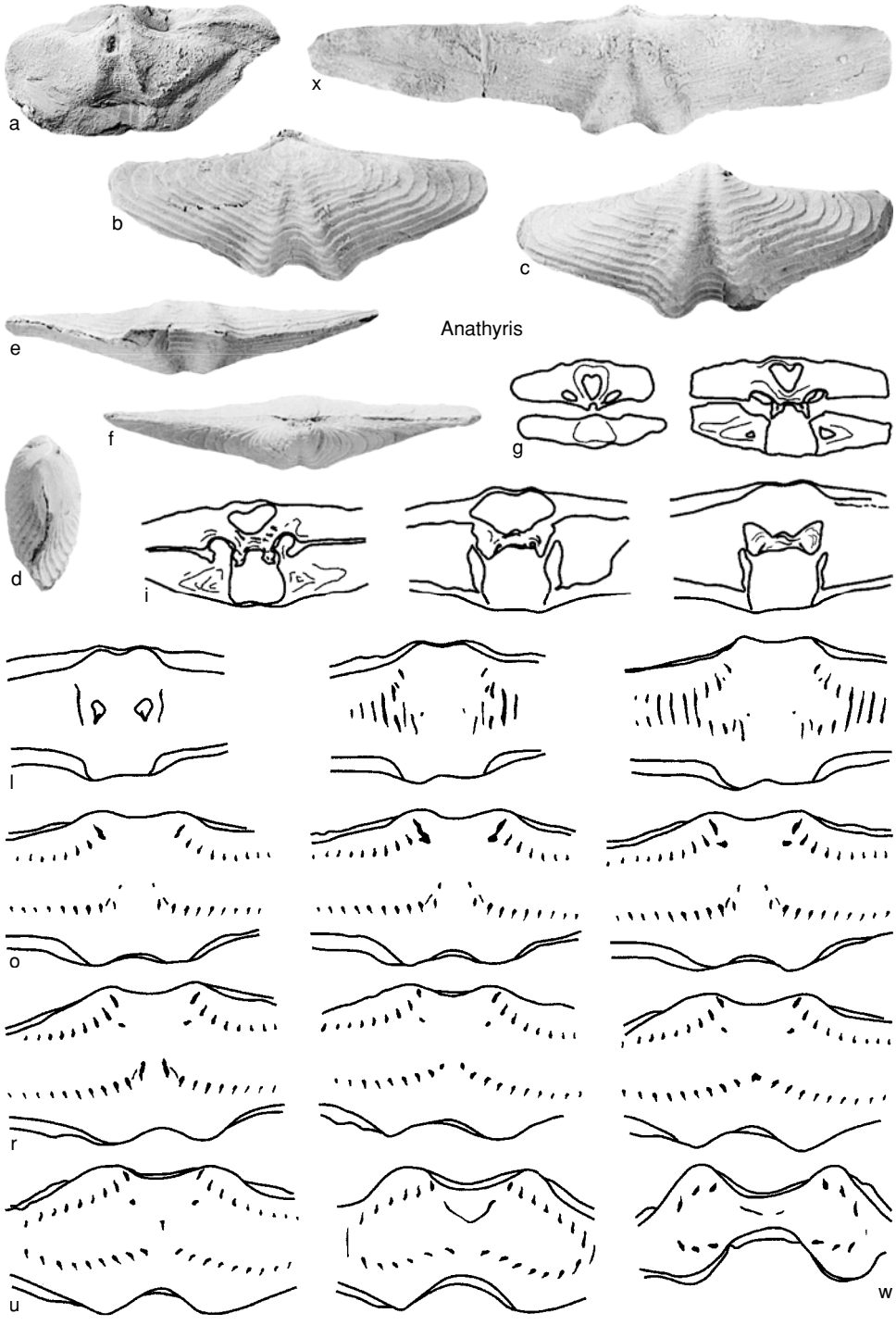


FIG. 1039. Athyrididae (p. 1528).

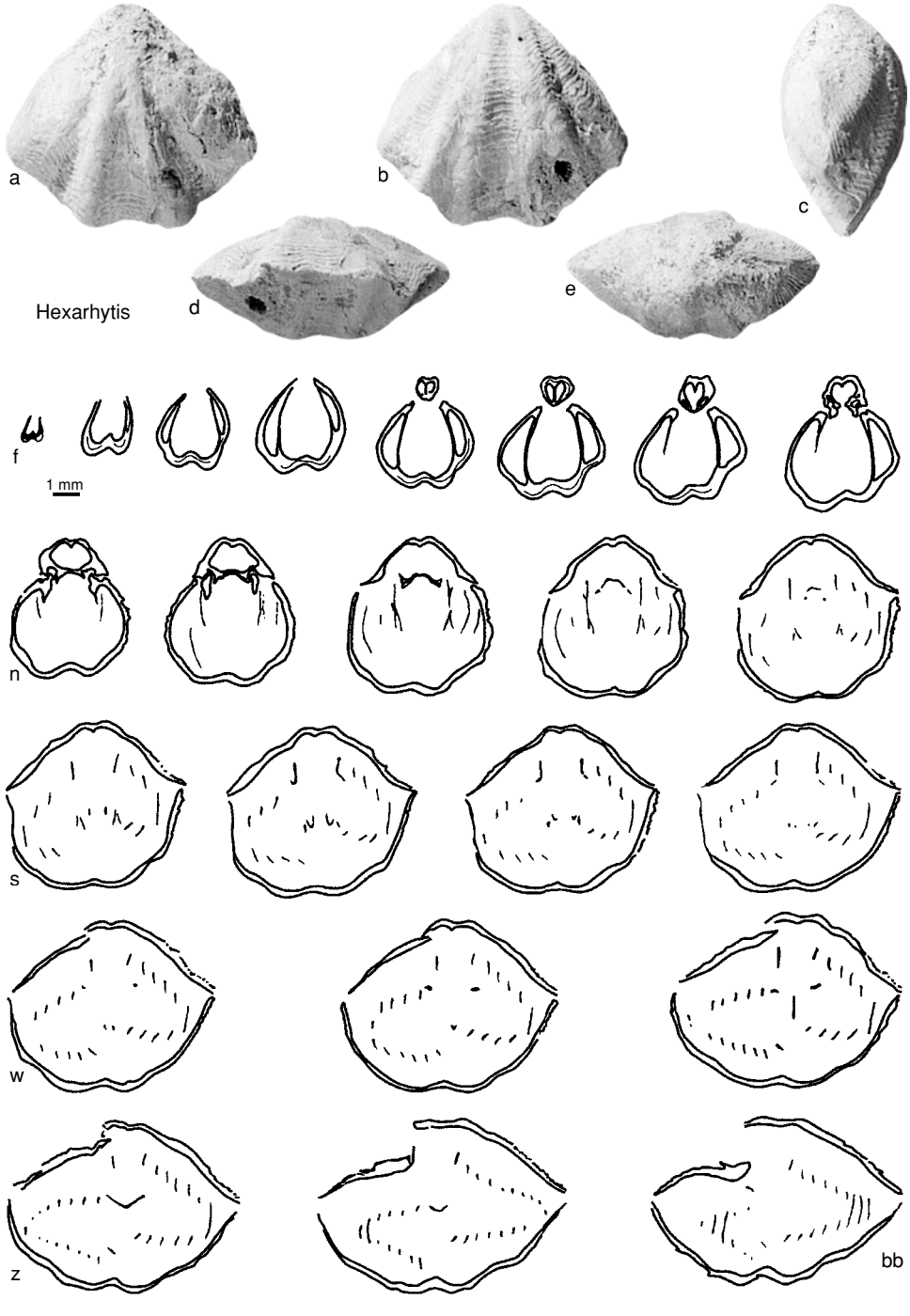


FIG. 1040. Athyrididae (p. 1528).

Subfamily PRADOIINAE García-Alcalde, 1986

[Pradoiinae García-Alcalde, 1986, p. 65]

Shell medium to large, slightly rostrate, ventral umbo moderately curved; median sulcus in both valves and opposite folding; anterior margin emarginate; lateral profile commonly compressed anteriorly; exterior with fine delayed costation progressively developed medially and few, weak, growth lines, without frills; wedgelike microornament usually present; interior as in Plicathyridinae but commonly with very narrow lateral apical cavities and very short accessory jugal lamellae. *Lower Devonian (Lochkovian)–Middle Devonian (lower Eifelian, ?Givetian).*

Pradoia Boucot, Johnson, & Staton, 1965, p. 665 [**Terebratula toreno* de Verneuil & d'Archiac, 1845, p. 469; OD]. Elongate subpentagonal with faint sulcus, starting in umbo, in both valves; dorsal profile bilobate; fine delayed costation and wedgelike microornament with narrowest part directed anteriorly, commonly quincuncially disposed. [Authorship of this genus is usually credited to Comte (1938, p. 43); however, he did not designate a type for the genus. The first unequivocal designation of the type species seems to be that of Boucot, Johnson, & Staton, 1965; thus they validated the name in their publication.] *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian, ?Givetian):* Spain, *upper Emsian–lower Eifelian;* Armenia, *?Givetian.*——Fig. 1041*a–t.* **P. torenoi* (de Verneuil & d'Archiac), upper Emsian; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Asturias, Spain, D866, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f–r,* transverse serial sections 1.7, 3.1, 4.2, 5.0, 5.3, 6.6, 7.1, 7.6, 7.9, 8.5, 8.7, 9.0, 9.9 mm from ventral umbo, Asturias, Spain, DPO 424 (adapted from García-Alcalde, 1971); *s,* detail of external microornamentation, León, Spain, DPO F24244, ×18; *t,* detail of external microornamentation, León, Spain, DPO F24244, ×44 (new).

?Dichozygopleura Renouf, 1972, p. 121 [**D. dichozygopleura;* OD]. Elongate subelliptical; faint sulcus in anterior two-thirds of both valves; few growth lines usually present; strong ribs in posterolateral region of shell, curving anterolaterally; cardinal plate flat, with small dorsal foramen apically, dental cavities ventrally covered posteriorly; jugum unknown. [This genus requires revision.] *Lower Devonian:* France.——Fig. 1042,*2a–b.* **D. dichozygopleura,* Brittany; *a,* rubber impression of dorsal exterior mold, LPB 1186; *b,* rubber impression of ventral exterior mold, LPB 1161, ×2 (Renouf, 1972).

Guaxa García-Alcalde, 1986, p. 67 [**G. iberica;* OD]. Similar to *Pradoia* externally but with ribs stronger, present over entire valve and curving anterolaterally; ventral interior and cardinalia essentially as in *Athyris;* jugum poorly known. *Lower Devonian (Lochkovian–Pragian):* Spain.——Fig. 1042,*1a–d.* **G. iberica,* Teruel; holotype, dorsal, ventral, lateral, and anterior views, DPO 112.096, ×1 (García-Alcalde, 1986).

Quadriloba Alvarez, Rong, & Boucot, 1999, p. 547, *nom. nov. pro Tetraloba* Alvarez, Rong, & Boucot, 1998, p. 843, *non Tetraloba* Lee, 1983, Collembola [**Terebratula collettii* de Verneuil, 1850, p. 173; OD]. Resembles elongate *Plicathyris* but without lamellose growth lines; surface ornamentation similar to that of *Pradoia;* interior as in *Plicathyris* but with very narrow lateral apical cavities. [The names *colletei* and *colletti* are incorrect subsequent spellings of *collettii.*] *Lower Devonian (Emsian):* northwestern Spain.——Fig. 1042,*3a–r.* **Q. collettii* (de Verneuil), upper Emsian, León; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, D867, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* detail of external microornamentation, DPO F24245, ×11; *g,* detail of external microornamentation, DPO F24245, ×44 (new); *h–r,* transverse serial sections 1.7, 2.9, 4.2, 4.7, 5.6, 6.1, 6.2, 6.6, 6.8, 7.0, 7.4 mm from ventral umbo (adapted from García-Alcalde, 1971).

Subfamily SPIRIGERELLINAE Grunt, 1965

[Spirigerellinae Grunt, 1965, p. 237; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 843]

Small to extremely large, subpentagonal, subtrigonal, elongate or transversely oval in outline; bi- to dorsibiconvex with convexity moderate to strong; moderately rostrate; ventral sulcus and dorsal fold variably developed; lateral plications may develop; growth lines very fine, closely and regularly spaced; growth laminae stronger, more widely and randomly spaced; pedicle supports absent (delthyrial plate may be present in *Spirigerella*); dental plates thin and short (may form spondylium, e.g., *Araxathyris, Rectambitus*); cardinal plate commonly subquadrangular, thick in late Carboniferous and Permian taxa; inner hinge plate triangular, slightly lowered to plane of outer hinge plates in oldest species; well-developed

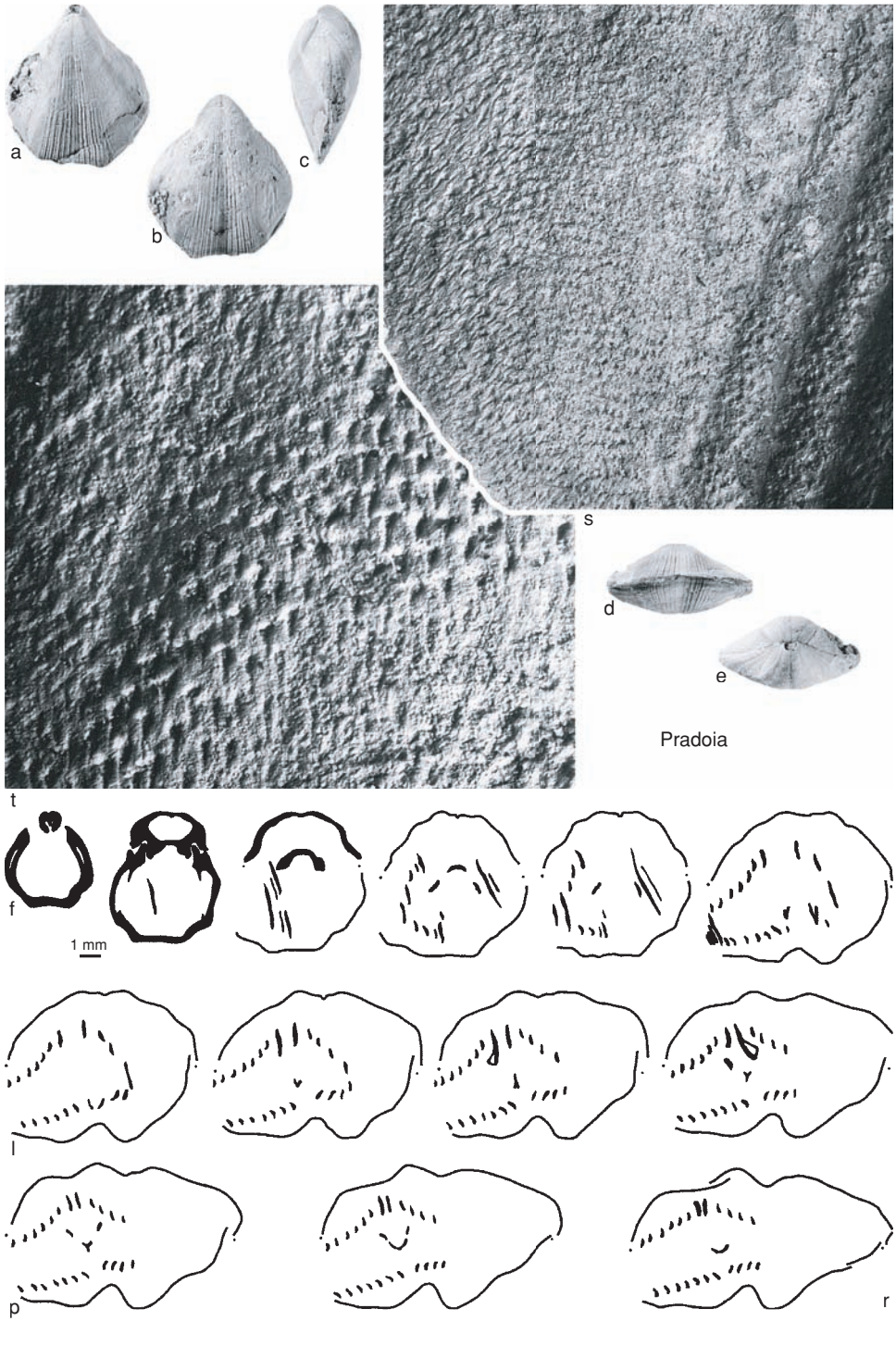


FIG. 1041. Athyrididae (p. 1533).

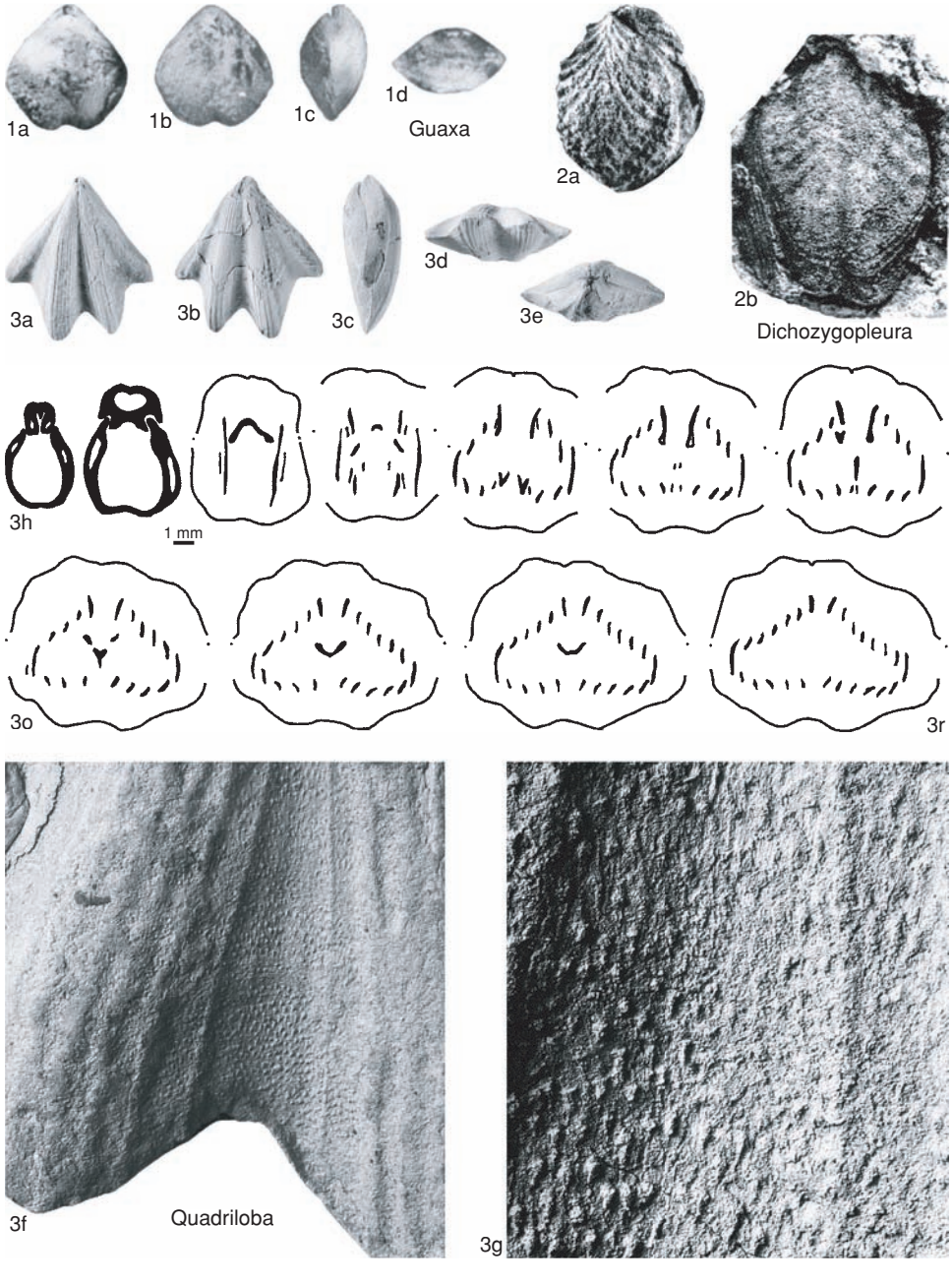


FIG. 1042. Athyrididae (p. 1533).

divergent crural bases; concave, serrated cardinal flanges moderately to strongly developed mainly in Permian species; dorsal foramen commonly small, may be infilled in latest stocks; dorsal myophragm may be present; jugum essentially as in *Athyris;* tertiary layer may be present. *Lower Devonian (Pragian)–Upper Triassic.*

Spirigerella WAAGEN, 1883, p. 450 [**S. derbyi;* SD OEHLERT, 1887a, p. 1300] [=*Juxathyris* LIANG, 1990, p. 270 (type, *J. apionucula,* OD)]. Bi- to dorsibiconvex or convexiplane, isometric or subovate massive shells commonly widest anterior to midlength; strong, broad dorsal fold and ventral sulcus; uniplicate or parasulcate anterior commissure; ventral beak short, strongly incurved, concealing small foramen; nearly flat palintrope; dental plates, if present, buried in secondary shell material that is strongly developed in umbonal cavities; more or less developed delthyrial plate may be present; high, massive, cardinal plate; outer hinge plates reduced; cardinal flanges may be unified, strongly developed, serrated, ventrally concave, with deeply impressed pair of diductor pits; dorsal myophragm commonly present; jugum essentially as in *Athyris,* but lateral branches of jugum originating before valve midlength, projecting anteroventrally; median bladelike elevation on saddle extending backward as far as jugal stem; tertiary layer may be present apically. [*Juxathyris,* from Middle to Upper Permian of southern China, is said to differ by having inner socket ridges superseded by high and large processes that take the shape of phoenix coronet (*sic*).] *Upper Carboniferous–Upper Permian:* Slovakia, Croatia, Hungary, Italy, Turkey, Iran, Pakistan, Nepal, Kashmir, western Malaysia, Timor, northeastern and southern China, Western Australia, Argentina.——FIG. 1043,*1a–g. *S. derbyi,* Kazanian, Salt Range, Pakistan; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, GSI 3407, Waagen collection, ×1 (new; photographs courtesy of R. K. Biswas); *f,* ventral interior, USNM 212888, ×2 (Grant, 1976); *g,* lateral view of jugum, approximately ×4 (Waagen, 1883). [See also Fig. 1002.2, p. 1477, and Fig. 1008.2, p. 1485, in introduction.]

Araxathyris GRUNT, 1965, p. 240 [**Spirigera protea* ABICH, 1878, p. 55; OD]. Medium to large, moderately to strongly biconvex, transversely oval to subpentagonal, inflated shells; ventral sulcus and dorsal fold wide and flat anteriorly, bearing distinct median groove starting at apex; 2 poorly developed lateral plications may bound sulcus; anterior commissure para- to bisulcate; growth laminae widely and irregularly spaced; short, thin, medially concave dental plates forming narrow sessile spondylium; cardinal plate thin, narrow, subtriangular, apically perforated by small foramen; cardinal flanges well developed; tertiary layer present. *?Lower Permian, Upper Permian:* ?northern China, *?Lower Permian;* southern Alps, Transcaucasus, Iran, southern China (Sichuan, Shaanxi), northwestern China (Qinghai), Thailand.——FIG. 1044*a–c. *A. protea* (ABICH), Transcaucasus; lectotype, dorsal, ventral, and anterior views, LGI 66/99, ×1 (Grunt, 1965).——FIG. 1044*d–p. A. felina* (ARTHABER), Transcaucasus; transverse serial sections, 6.7, 6.9, 7.2, 7.7, 8.2, 8.9, 9.7, 10.6, 11.8, 12.2, 12.9, 13.4, 17.5 mm from ventral umbo, PIN 2073/547 (adapted from Grunt, 1965).——FIG. 1044*q–x. A. abichi* (ARTHABER), Transcaucasus; tangential serial sections, parallel to commissural plane, 3.1, 4.8, 5.7, 6.5, 7.0, 7.3, 8.1, 8.7 mm from dorsal valve, PIN 3599/833 (adapted from Grunt, 1986).

Cardiothyris ROBERTS, 1971, p. 178 [**C. bisulcata;* OD]. Medium, subcircular to subpentagonal or elongate oval, subequally biconvex, thin shells; poorly rostrate, bearing small pedicle foramen in epithyridid position; sinus on each valve of equal depth, resulting in rectimarginate commissure; emarginate outline; external ornament of prominent, simple, widely spaced capillae crossed by few, fine, concentric growth lines; dental plates short, thin, subparallel; muscle scars weakly defined; cardinal plate subquadrate, robust, divided into 2 concave portions by median furrow and pierced apically, close to dorsal umbo, by minute dorsal foramen; cardinal flanges moderately developed; dorsal myophragm very low or absent; spiralia and jugum unknown. *Lower Carboniferous (Tournaisian):* northwestern Australia, USA (Missouri, Illinois).——FIG. 1045,*1a–o. *C. bisulcata,* northwestern Australia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, CPC 8245, ×1.5; *f–o,* transverse serial sections 0.3, 0.5, 0.8, 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.7 mm from ventral umbo, CPC 11102 (Roberts, 1971).

Composita BROWN, 1845, p. 131 [**Spirifer ambiguus* SOWERBY, 1822 in 1821–1822, p. 105; OD] [=*Seminula* HALL & CLARKE, 1893, p. 93, *non* M'COY, 1844, p. 158; *Gruntathyris* GRETCHISHNIKOVA, 1996, p. 417 (type, *G. innae,* OD)]. Moderately to strongly biconvex, subovate, subpentagonal or subtrigonal shells, commonly widest near midlength, dorsal fold and ventral sulcus variably developed, may extend to umbonal region or be restricted to anterior part, fold may be flat or slightly depressed medianly; anterior commissure uniplicate to parasulcate; ventral beak thick, rounded, foramen large, ovate, in epi- to permesothyridid position; delthyrium completely filled by dorsal umbo without deltidial plates; dorsal foramen infilled other than in early forms. [Date on BROWN's publication is 1849, but parts 24–28 (p. 117–136) containing *Composita* (p. 131) were published in 1845 (see C. D. SHERBORN, 1905, p. 359).] *Upper Devonian (Famennian)–Upper Permian:* cosmopolitan.——FIG. 1043,*2a–c. *C. ambigua* (SOWERBY), Viséan, Derbyshire, England; *a–b,* lectotype, dorsal and ventral views, BMNH B 61041, ×1.5 (Brunton, 1980; photographs courtesy of C. H. C. Brunton); *c,* ventral view of dorsal interior showing jugum, approximately ×3 (Davidson, 1861). [See also Fig. 1007.3, p. 1484, in introduction.]

Densalvus CARTER, 1991, p. 88 [**Athyris crassicardinalis* WHITE, 1860, p. 229; OD]. Similar to *Planalvus* but with strongly inflated ventral valve and weakly convex dorsal valve; dorsal fold and ventral sulcus absent; without ridges defining areas on either side of delthyrium; surface weakly and finely capillate; dorsal valve thick shelled; spiralia and

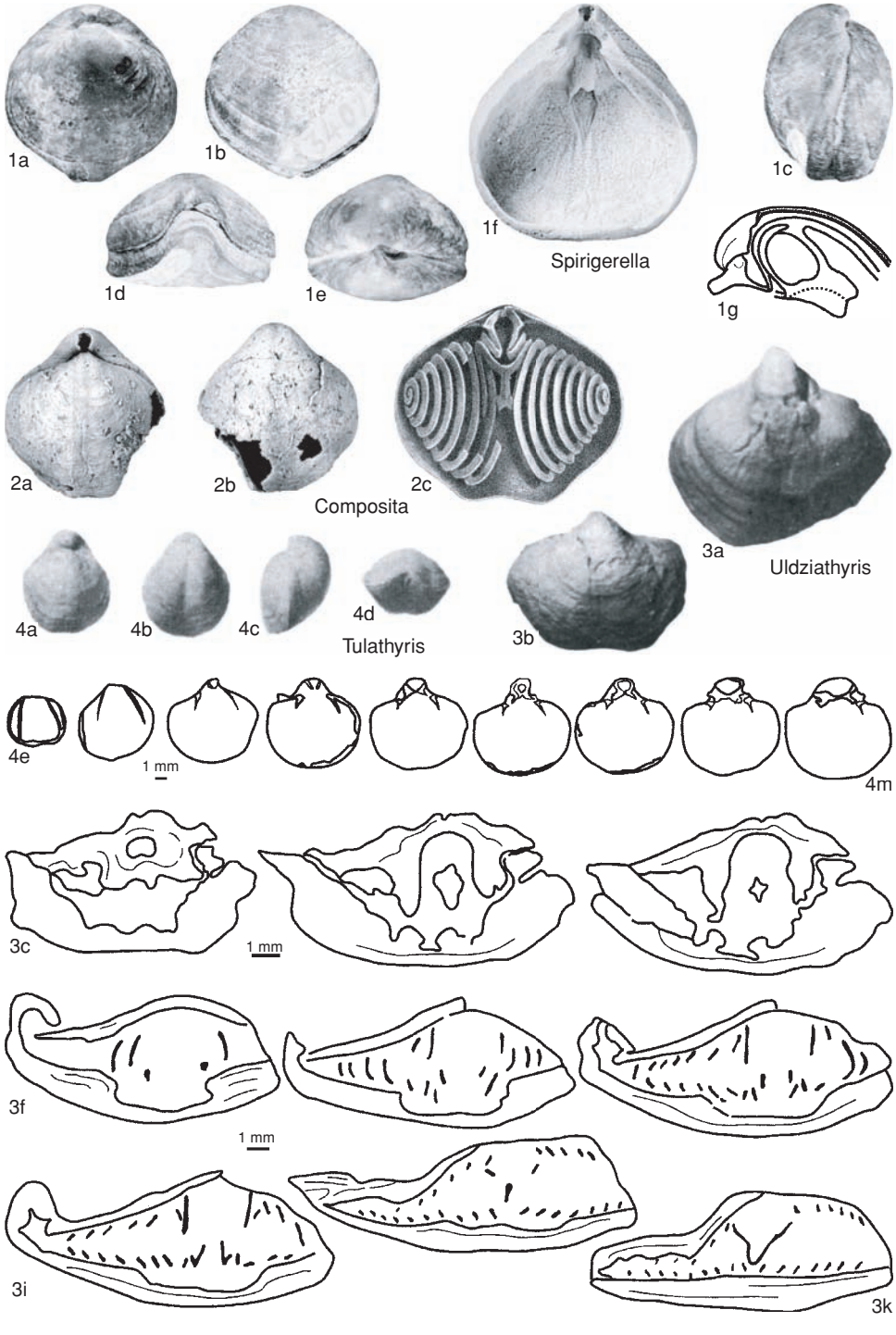


FIG. 1043. Athyrididae (p. 1536–1544).

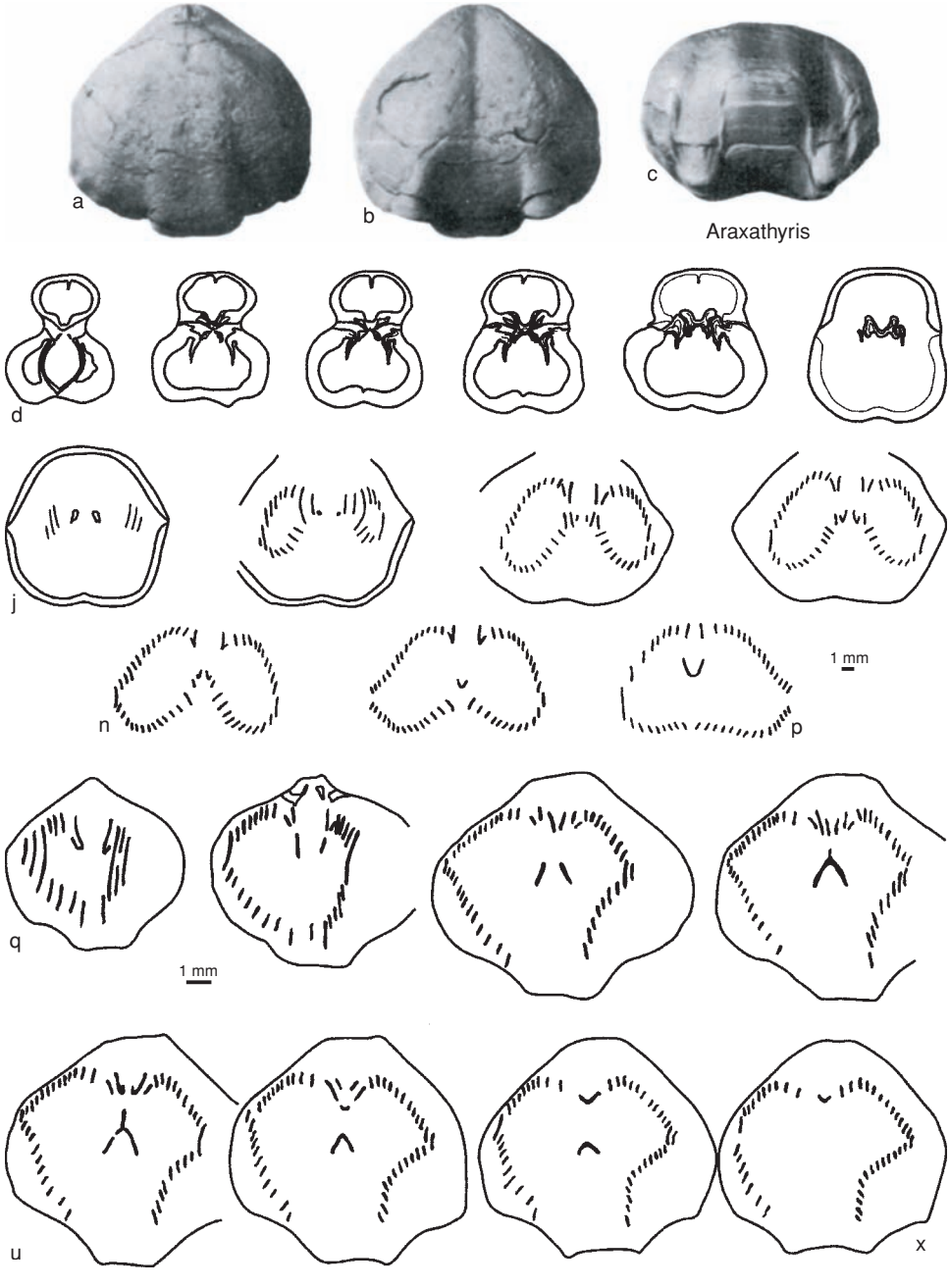


FIG. 1044. Athyrididae (p. 1536).

jugum unknown. *Lower Carboniferous (lower Tournaisian):* USA (Iowa, Missouri).——FIG. 1046,*1a–g.* **D. crassicardinalis* (WHITE); *a–d,* lectotype, ventral valve with dorsal cardinalia attached, ventral, dorsal, lateral, and posterior views, Iowa, UM 66073, White Collection, photographs courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA; *e,* posterior view, Iowa, UM

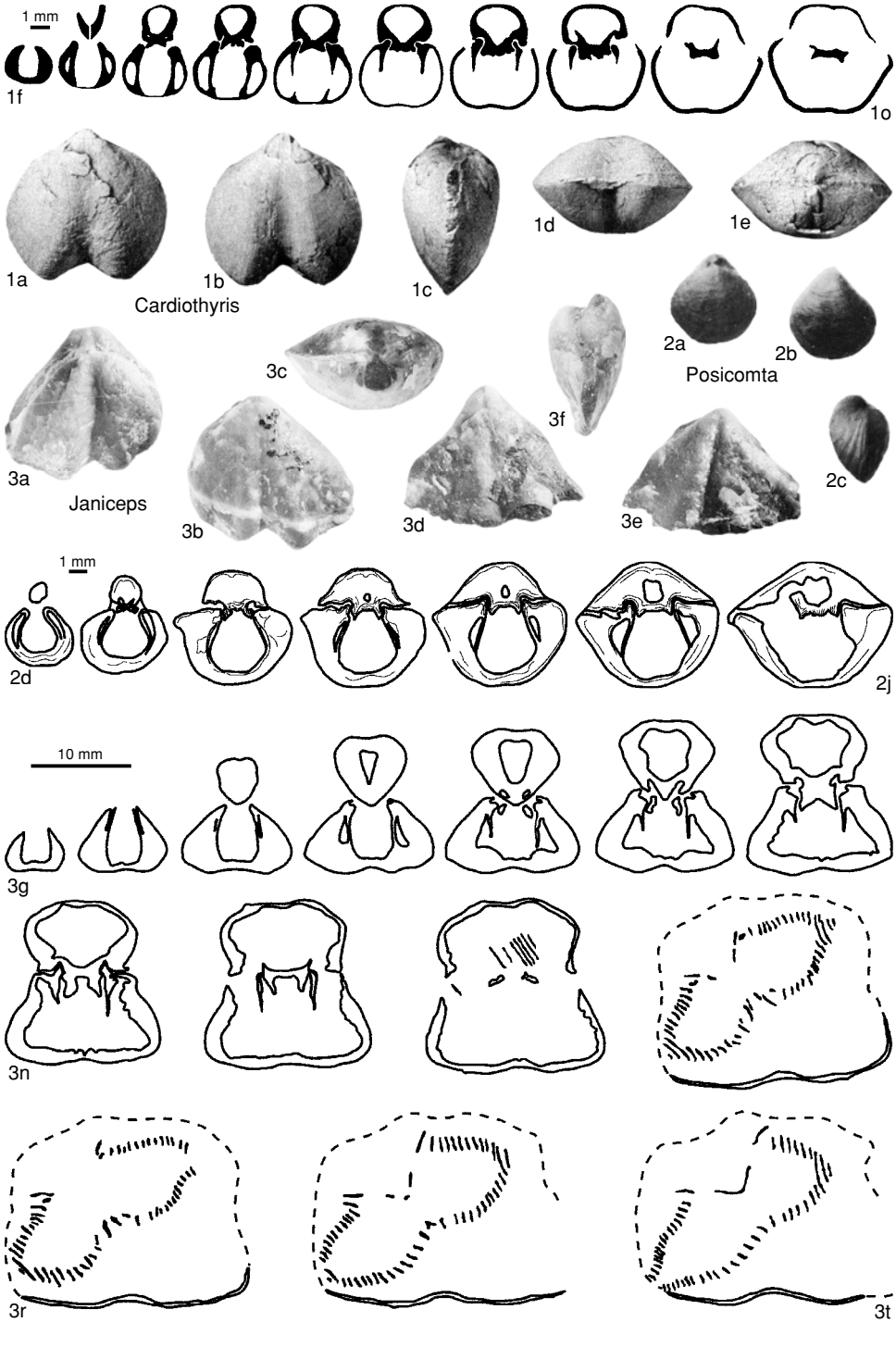


FIG. 1045. Athyrididae (p. 1536–1540).

66075, White Collection, photograph courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA; *f–g,* dorsal valve, external and internal views, Missouri, UC 9817, Weller Collection, ×3 (Carter, 1991; photographs courtesy of J. L. Carter).

Iniathyris Beznosova, 1963, p. 312 [**I. topkensis;* OD]. Externally similar to *Composita;* ventral interior, dental plates, and greatly thickened umbonal region as in *Nordathyris,* but without prismatic layer and having less impressed muscle field; dorsal interior and spiralium poorly known. *Lower Carboniferous (Tournaisian):* Russia (Kuznetsk basin), Kazakhstan, China, USA (Iowa).——Fig. 1047,*1a–d. *I. topkensis,* Kuznetsk basin; holotype, dorsal, ventral, lateral, and posterior views, PIN 760/4470, ×1 (Beznosova, 1963).

Janiceps Frech, 1901, p. 551 [**Spirigera peracuta* Stache, 1878, p. 152; SD Schuchert & LeVene, 1929a, p. 70]. Medium to large, subequally biconvex, usually triangular shells with maximum width at anterior third of shell, very close to front, more rarely subrhomboidal to pentagonal; each valve usually bearing 2 pair of rounded unequal folds starting at apex and widening moderately anteriorly; ventral cardinal area more or less defined; dental plates thin and short, may be buried in secondary shell material that is strongly developed in umbonal cavities, low dental flanges may support teeth anteriorly. [The outline of some *Janiceps* species resembles that of young *Comelicania* (e.g., Posenato, 1998). But, until better preserved specimens of *Janiceps* can be studied, this genus is provisionally included in the Spirigerellinae due to its adult external morphology and internal characters. The relationship between *Janiceps* and *Comelicania* and their taxonomic position within the Athyrididae requires revision.] *Upper Permian (Changhsingian):* Italy (southern Alps), Armenia.——Fig. 1045, *3a–t. *J. peracuta* (Stache), upper Changhsingian, southern Alps; *a–c,* dorsal, ventral, and posterior views, Monte Croce di Cornelico, MGBW 3797-b, Stache Collection; *d–f,* dorsal, ventral, and lateral views, Monte Croce di Cornelico, MGBW 3797-a, Stache Collection, ×2; *g–t,* transverse serial sections 0.50, 1.55, 3.55, 4.50, 4.95, 5.30, 5.55, 5.80, 6.40, 7.45, 10.70, 11.25, 12.55, 14.05 mm from ventral umbo, Val Brutta, MDSGF J06 (new; photographs and serial sections courtesy of R. Posenato).

Nordathyris Grunt, 1977a, p. 73 [**N. bulkanensis;* OD]. Medium to large, subequally biconvex, transverse subelliptical to subpentagonal massive shell; narrow sulcus extending from ventral beak, widening considerably toward anterior margin; dorsal fold may be divided by narrow and shallow furrow, variably developed, lateral folds may be present; lateral apical cavities narrow and minute; ventral muscle field moderately to deeply impressed in thick umbonal region; high, massive cardinal plate; cardinal flanges well developed; tertiary layer present. *Upper Carboniferous (Bashkirian):* northeastern Russia (Kolyma-Omolonsk massif).——Fig. 1046,*3a–q. *N. bulkanensis; a–c,* holotype, dorsal, ventral, and anterior views, PIN 2840/461, ×1 (Grunt, 1977a); *d–i,* transverse serial sections 0.6, 2.3, 2.5, 2.6, 3.8, 3.9 mm from ventral umbo, PIN 2840/460 (adapted from Grunt, 1977a); *j–q,* tangential serial sections, parallel to commissural plane, 1.1, 2.0, 3.2, 5.5, 6.6, 7.1, 7.4, 7.6 mm from dorsal valve, PIN 2840/465 (Grunt, 1986).

Planalvus Carter, 1971, p. 248 [**P. gibberosa;* OD]. Small to medium size, longitudinally to transversely ovate, dorsibiconvex shells, ventral valve almost flat; broad, shallow sulcus originating in posterior third of ventral valve, dorsal valve with high median fold, but poorly defined laterally; surface lamellose, lamellae finely striated and apparently fringed with minute solid spines; gently curved beak, not prominent, truncated by circular meso- to permesothyridid foramen; beak ridges subangular, defining areas on either side of open delthyrium; ventral valve with thick shell, without dental plates; subtrapezoidal cardinal plate, imperforate apically; variably developed cardinal flanges project slightly posteroventrally within delthyrial cavity; wide, conjunct inner hinge plates flat or slightly concave ventrally; outer hinge plates reduced, difficult to distinguish from inner socket ridges, which slightly overhang sockets; posteriormost part of cardinal plate resting on short, thin median ridge extending as low myophragm to midshell. [The brachidium of the type species seems to be different from those of French species; if subsequent investigations show that their morphology is different, the French species must be separated into a new genus externally homeomorphic with *Planalvus.*] *Lower Devonian (Pragian)–Lower Carboniferous (Viséan):* France, *Pragian, ?lower Emsian;* Spain, *Famennian;* North America, *Tournaisian–Viséan.*——Fig. 1048*a–t. *P. gibberosa,* Tournaisian, Iowa, USA; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, UI X-3435; *f,* dorsal interior, UI X-3441-2, ×3 (Carter, 1971); *g–t,* transverse serial sections 0.2, 0.6, 1.4, 1.8, 2.0, 3.4, 3.6, 4.0, 4.4, 4.6, 5.0, 5.4, 5.8, 6.2 mm from ventral umbo, USNM 176844 (adapted from Carter, 1972).——Fig. 1048*u–dd. P. rufus* Racheboeuf, Copper, & Alvarez, Pragian, Armorican Massif, France; transverse serial sections 1.6, 1.9, 2.0, 2.4, 2.7, 3.4, 3.6, 3.8, 4.4, 4.8 mm from ventral umbo, IGR 10298 (adapted from Racheboeuf, Copper, & Alvarez, 1994).

Posicomta Grunt, 1986, p. 120 [**P. gundarensis;* OD]. Shells resembling *Composita* with smaller size, dorsal fold and ventral sulcus poorly developed, possibly with narrow groove and much thicker shell; spiralia and jugum unknown. *Upper Permian:* Pamir, Tajikistan, southern Thailand.——Fig. 1045,*2a–j. *P. gundarensis,* Darvaz, Tajikistan; *a–c,* holotype, dorsal, ventral, and lateral views, PIN 3599/814-382, ×1 (Grunt, 1986); *d–j,* transverse serial sections 0.8, 1.6, 2.6, 3.0, 3.3, 3.6, 3.9 mm from ventral umbo, PIN 3599/835 (adapted from Grunt, 1986).

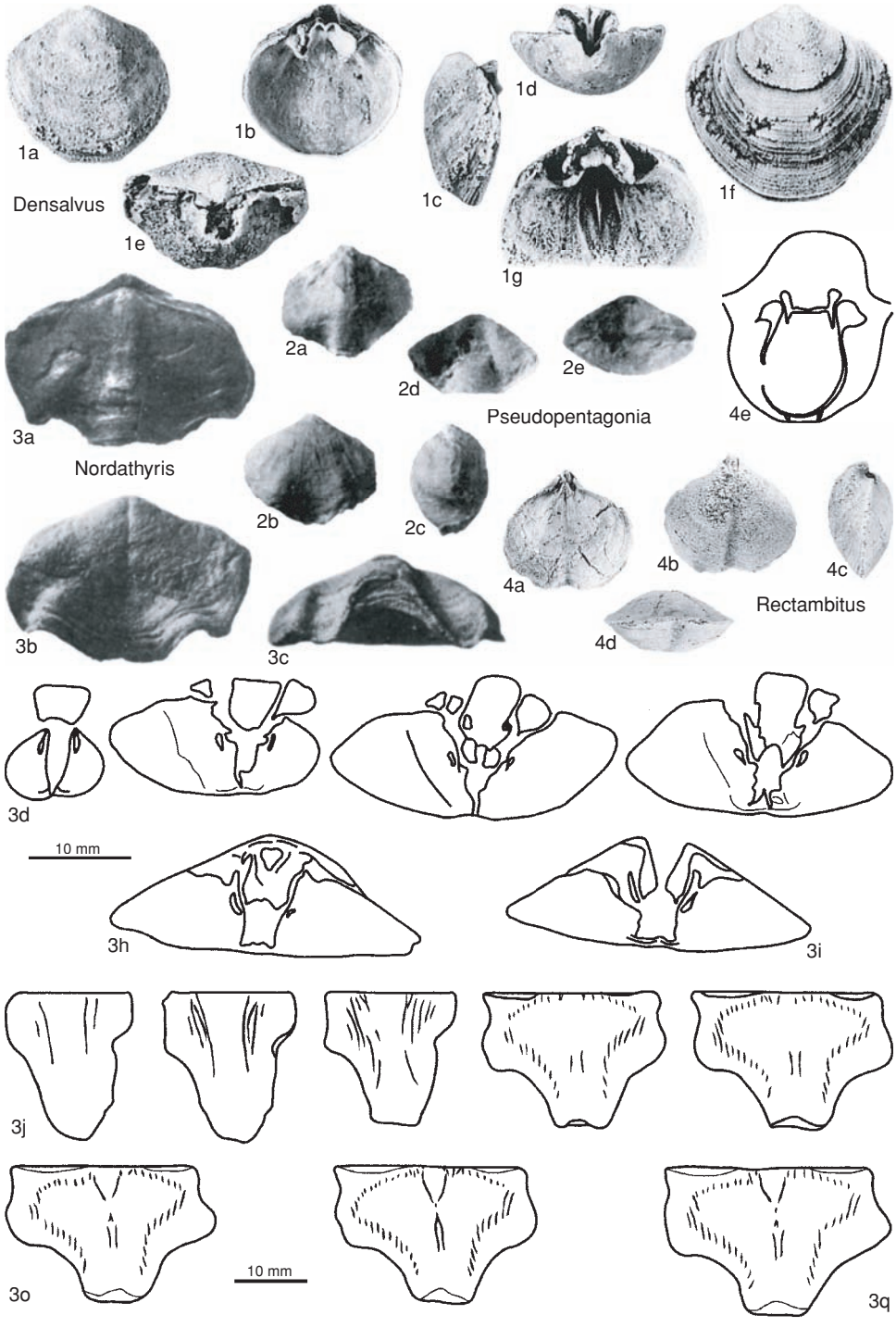


FIG. 1046. Athyrididae (p. 1536–1544).

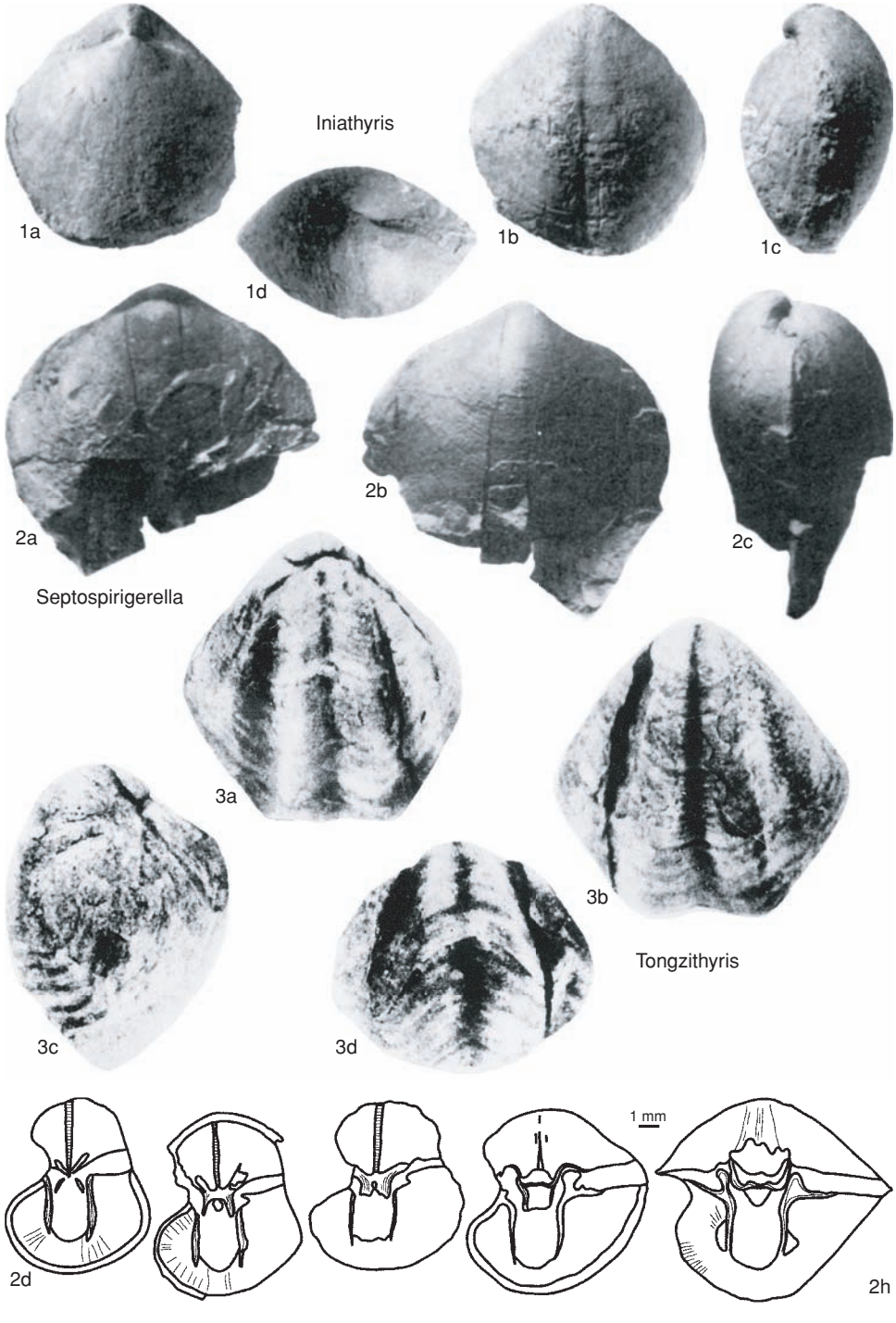


Fig. 1047. Athyrididae (p. 1540–1544).

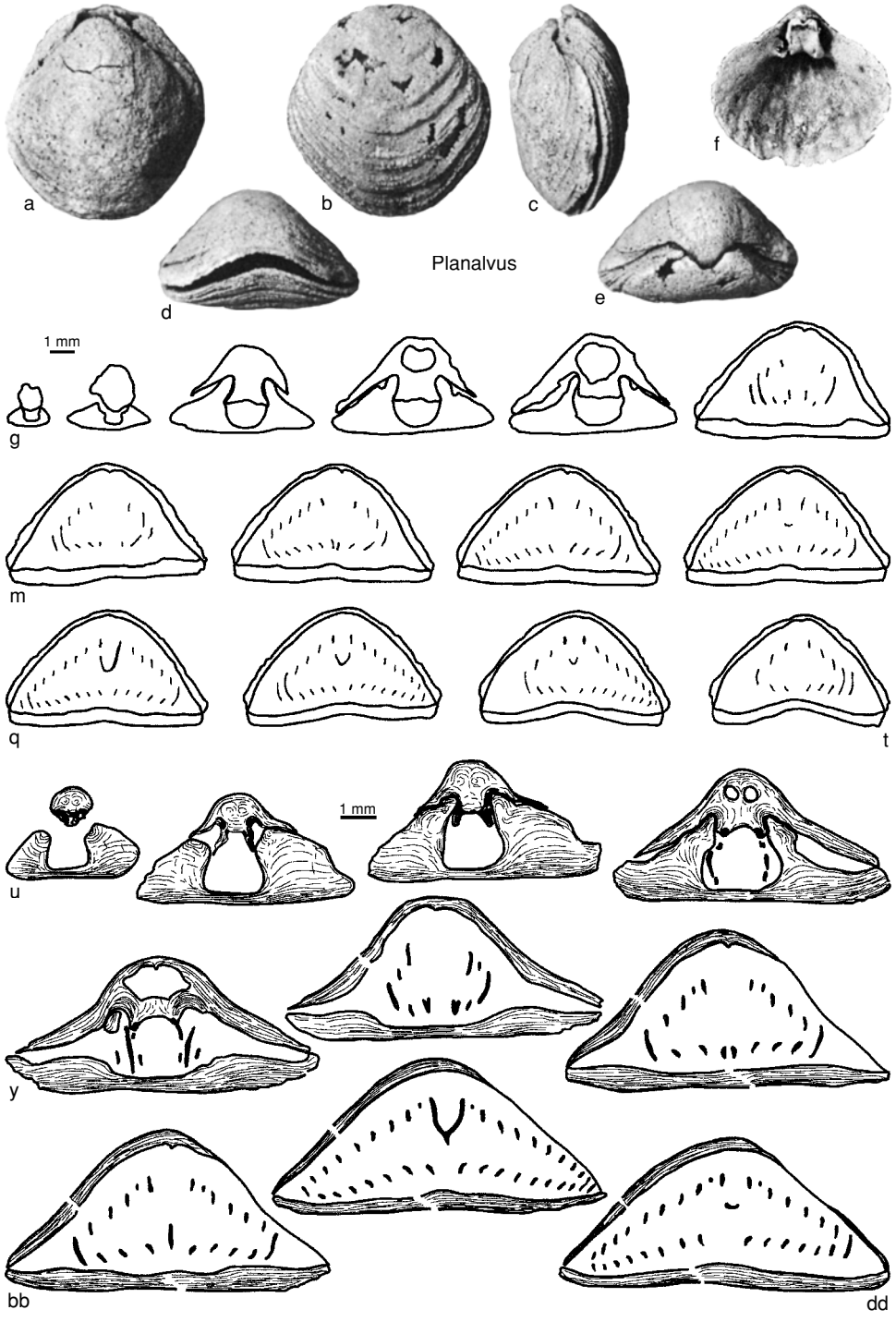


FIG. 1048. Athyrididae (p. 1540).

Pseudopentagonia Beznosova, 1963, p. 315 [**P. injensis;* OD]. Dorsibiconvex shell, similar to *Nordathyris* but with dental plates delicate, without apical thickening in both valves and without prismatic layer. *Lower Carboniferous (Tournaisian):* Kazakhstan, Russia (Kuznetsk basin).——Fig. 1046,*2a–e.* **P. injensis,* Kuznetsk basin; holotype, dorsal, ventral, lateral, anterior, and posterior views, PIN 760/4485, ×1 (Beznosova, 1963).

?Rectambitus Xu & Grant, 1994, p. 50 [**Araxathyris bisulcata* Liao, 1980, p. 268; OD]. Small to medium with rectimarginate, slightly emarginate, anterior commissure; spondylium supported anteriorly by low, broad median septum; jugum unknown. [May be synonymous with *Araxathyris*.] *Upper Permian (Changhsingian):* southern China (Guizhou, Shaanxi).——Fig. 1046,*4a–e.* **R. bisulcatus* (Liao), Guizhou; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Liao, 1980; photographs courtesy of Liao Zhuo-ting); *e,* transverse serial section showing spondylium supported by low, broad septum, USNM 456173, approximately ×3 (adapted from Xu & Grant, 1994).

Septospirigerella Grunt, 1965, p. 237 [**S. baissalensis;* OD]. Similar to *Spirigerella* without dorsal fold and ventral sulcus, ventral beak moderately curved; more or less prominent short ridge joining thick cardinal plate at posterior end; spiralia and jugum unknown; tertiary layer present. *Upper Permian–Upper Triassic:* Armenia, Iran, Transcaucasus, Thailand, *Upper Permian;* China (Sichuan), *Upper Triassic.*——Fig. 1047,*2a–h.* **S. baissalensis,* Upper Permian, Transcaucasus; *a–c,* holotype, dorsal, ventral, and lateral views, PIN 2073/626, ×1 (Grunt, 1965); *d–h,* transverse serial sections 3.9, 4.3, 4.4, 4.9, 5.4 mm from ventral umbo, PIN 2073/485 (adapted from Grunt, 1965).

Tongzithyris Ching, Liao, & Fang, 1974, p. 313 [**T. episulcata;* OD]. Similar to *Araxathyris* but larger and thick shelled, bearing 1 or 2 folds on lateral slopes; dorsal foramen absent; dorsal myophragm may be present; jugum unknown. *Upper Permian (Changhsingian):* southern China.——Fig. 1047, *3a–d.* **T. episulcata,* Tongzi, northern Guizhou; holotype, dorsal, ventral, lateral, and anterior views, NIGP 22501, ×1 (Ching, Liao, & Fang, 1974; photographs courtesy of Jin Yu-gan).

Tulathyris Grunt, 1976, p. 78 [**Athyris vogdti* von Peetz, 1893, p. 59; OD]. Shells resembling *Composita* with smaller size and thinner-shelled valves; cardinal plate subtriangular, cardinal flanges poorly developed; spiralia and jugum unknown. *Lower Carboniferous (Tournaisian):* Moscow syncline, Donets basin, northern Kyrgyzstan, Kuznetsk Basin, ?Kazakhstan, ?Verkhoyansk.——Fig. 1043, *4a–m.* **T. vogdti* (von Peetz), Tula, Russia; *a–d,* dorsal, ventral, lateral, and anterior views, PIN 544/150(9), ×1 (Grunt, 1980); *e–m,* transverse serial sections 0.9, 1.9, 2.0, 2.2, 2.3, 2.4, 2.5, 2.7, 3.0 mm from ventral umbo, PIN 544/1375 (adapted from Grunt, 1980).

Uldziathyris Grunt, 1977b, p. 82 [**U. tikhonovi;* OD]. Similar to *Composita* with coarse lamellae projecting slightly outwardly in anterior part of shell, dental plates very short, ventral muscle field moderately to deeply impressed in thick umbonal region; cardinal plate thick, with median, ridgelike process directed ventrally, dorsal foramen absent. *Lower Carboniferous:* western Mongolia.——Fig. 1043,*3a–k.* **U. tikhonovi; a,* holotype, internal mold of ventral valve, PIN 3158/85; *b,* ventral view, PIN 3158/87, ×1 (Grunt, 1977b); *c–e,* transverse serial sections 3.1, 3.5, 4.1 mm from ventral umbo, PIN 3158/93 (adapted from Grunt, 1977b); *f–k,* transverse serial sections 5.5, 6.6, 7.7, 8.8, 11.7, 14.8 mm from ventral umbo, PIN 3158/93 (adapted from Grunt, 1986).

Subfamily XENOSARIINAE Cooper & Grant, 1976

[*nom. transl.* Grunt, 1984, p. 70, *pro* Xenosariidae Cooper & Grant, 1976a, p. 2170]

Shell small, slightly rostrate; lenslike outline, with narrow sulcus extending from beak in both valves; anterior margin bisulcate; smooth, with only regular, fine, infrequent, growth lines; frills absent; beak of ventral valve small, pointed, straight; ventral area narrow, apsacline; hypothyridid pedicle opening without deltidial plates; valves thin shelled; dental plates wholly absent; teeth small; no septum in either valve, no dorsal myophragm; socket ridges prominent, short, thick, defining wide sockets; outer hinge plates very narrow or absent, hinge plate short, inconspicuous, ventrally concave, triangular, with small, oval foramen; crura short, stout, projecting ventrally at high angle at anterior end of cardinal plate; cardinal flanges absent; jugum poorly known, seemingly as in *Glassina. Lower Permian (Artinskian–Kungurian).*

Xenosaria Cooper & Grant, 1976a, p. 2170 [**X. exotica;* OD]. Moderately dorsibiconvex shells with swollen umbonal regions; anterior commissure rectimarginate; narrowly notched anterior margin; flanks bounding sulcus moderately swollen, lateral slopes gentle in ventral, moderate in dorsal valve. *Lower Permian (Artinskian–Kungurian):* USA (western Texas).——Fig. 1049*a–g.* **X. exotica,* Bell Canyon Formation, Hegler Member; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, USNM 153459e, ×2; *f,* dorsal interior, USNM 153459g; *g,* ventral interior, USNM 153459c, ×4 (Cooper & Grant, 1976a; photographs courtesy of the late G. A. Cooper & the late R. E. Grant).

Family DIPLOSPIRELLIDAE Schuchert, 1894

[*nom. transl.* GRUNT, 1980, p. 51, *ex* Diplospirellinae SCHUCHERT, 1913, p. 418, *nom. correct. pro* Diplospirinae SCHUCHERT, 1894, p. 106, *nom. imperf.; emend.,* ALVAREZ, RONG, & BOUCOT, 1998, p. 844]

Small to large, commonly small shells; foramen commonly small, in permesothyridid position; dorsal fold and ventral sulcus commonly faint or absent, shallow sulcus may develop in both valves; costae may be present; dental plates commonly short; median septum and pedicle support may be present; cardinal plate subquadrate, not pierced apically, commonly thick; moderately to strongly developed cardinal flanges, commonly serrated; low myophragm usually present. *Lower Permian (Artinskian)–Upper Triassic (Norian), ?Upper Jurassic.*

Subfamily DIPLOSPIRELLINAE Schuchert, 1894

[*nom. correct.* SCHUCHERT, 1913, p. 418, *pro* Diplospirinae SCHUCHERT, 1894, p. 106, *nom. imperf.*]

Commonly small; dorsal fold and ventral sulcus variably developed, commonly faint, more or less rounded plications may be present in both valves; growth lines weak, growth lamellae absent; delthyrium commonly concealed by beak of dorsal valve, rarely by symphytium; dental plates short, fused with lateral wall of valve or absent; median septum may be present; cardinal plate robust, inner socket ridges high and thick; cardinal flanges moderately to well developed; dorsal myophragm may be present; accessory jugal lamellae long, commonly continuing intercoiled with primary volutions of spiralia to ends. *Middle Triassic (Anisian)–Upper Triassic (Norian).*

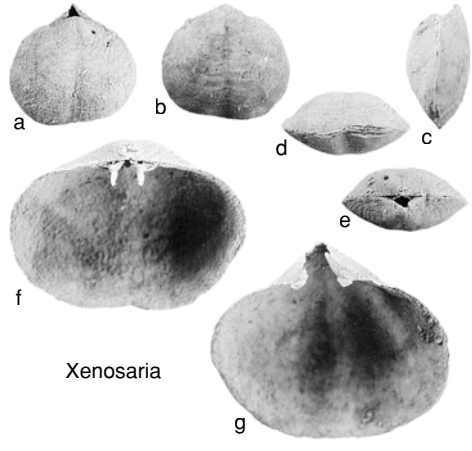


FIG. 1049. Athyrididae (p. 1544).

Diplospirella BITTNER, 1890, p. 297 [**Terebratula wissmanni* MÜNSTER, 1841, p. 64; OD]. Elongate to transversely oval or subpentagonal, anterior commissure rectimarginate or weakly uniplicate or sulcate; ventral median septum extending for two-thirds length of valve; hinge plate thin, steeply inclined posterodorsally; cardinal flanges moderately developed; myophragm extending to half length of valve, distally flanked by short ridges; jugum posteriorly situated, projecting posteroventrally as long stem from which accessory jugal lamellae lead off, jugal saddle thick, with spiny apophysis. *Upper Triassic (Carnian):* Alps, Sicily, Carpathians, Caucasus, southeastern Pamir.——FIG. 1050,*1a–x.* **D. wissmanni* (MÜNSTER), Cortina d'Ampezzo area; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, MPUM 5823/9, ×2; *f,* cardinalia, ×20 (Benigni & Ferliga, 1990; photographs courtesy of C. Benigni); *g–w,* transverse serial sections 1.1, 2.0, 2.9, 3.3, 3.6, 3.95, 4.2, 4.3, 4.5, 4.65, 4.85, 5.1, 5.35, 5.7, 6.05, 6.22, 6.35 mm from ventral umbo, MPUM 5819/20 (adapted from Benigni & Ferliga, 1990); *x,* lateral view of reconstructed jugum, ×12 (Benigni & Ferliga, 1990).——FIG. 1050,*1y. D. sufflata* (MÜNSTER), Cortina d´Ampezzo area; spiny jugal saddle, MPUM 5827/29, ×40 (Benigni & Ferliga, 1990).

?Amphitomella BITTNER, 1890, p. 298 [**Terebratula hemisphaeroidica* VON KLIPSTEIN, 1845, p. 222; OD]. Similar to *Diplospirella,* but with strongly developed median septum in dorsal valve and single spiralium. [Although all other features are typically diplospirelline, the development of short accessory jugal lamellae makes the subfamily assignment uncertain. Further study of Triassic athyridoids is necessary to understand their affinities (see also comments in BENIGNI & FERLIGA, 1995).] *Upper Triassic (Carnian):* Alps.——FIG. 1051,*1a–x.* **A. hemisphaeroidica* (VON KLIPSTEIN), Cortina d'Ampezzo area; *a–d,* ventral, lateral, anterior, and posterior views, MPUM 5863/42, ×4; *e,* dorsal interior, MPUM 5858/74, ×7.5; *f,* ventral interior, MPUM 5858/75, ×11 (Benigni & Ferliga, 1995; photographs courtesy of C. Benigni); *g–i,* transverse serial sections of posterior part of cardinalia, 1.15, 1.20, 1.35 mm from ventral umbo, MPUM 5858/61; *j–w,* transverse serial sections showing development of internal structures, 1.20, 1.30, 1.35, 1.50, 1.60, 1.70, 1.95, 2.30, 2.70, 2.85, 3.05, 3.35, 3.80, 4.70 mm from ventral umbo, MPUM 5858/63 (adapted from Benigni & Ferliga, 1995); *x,* lateral view of

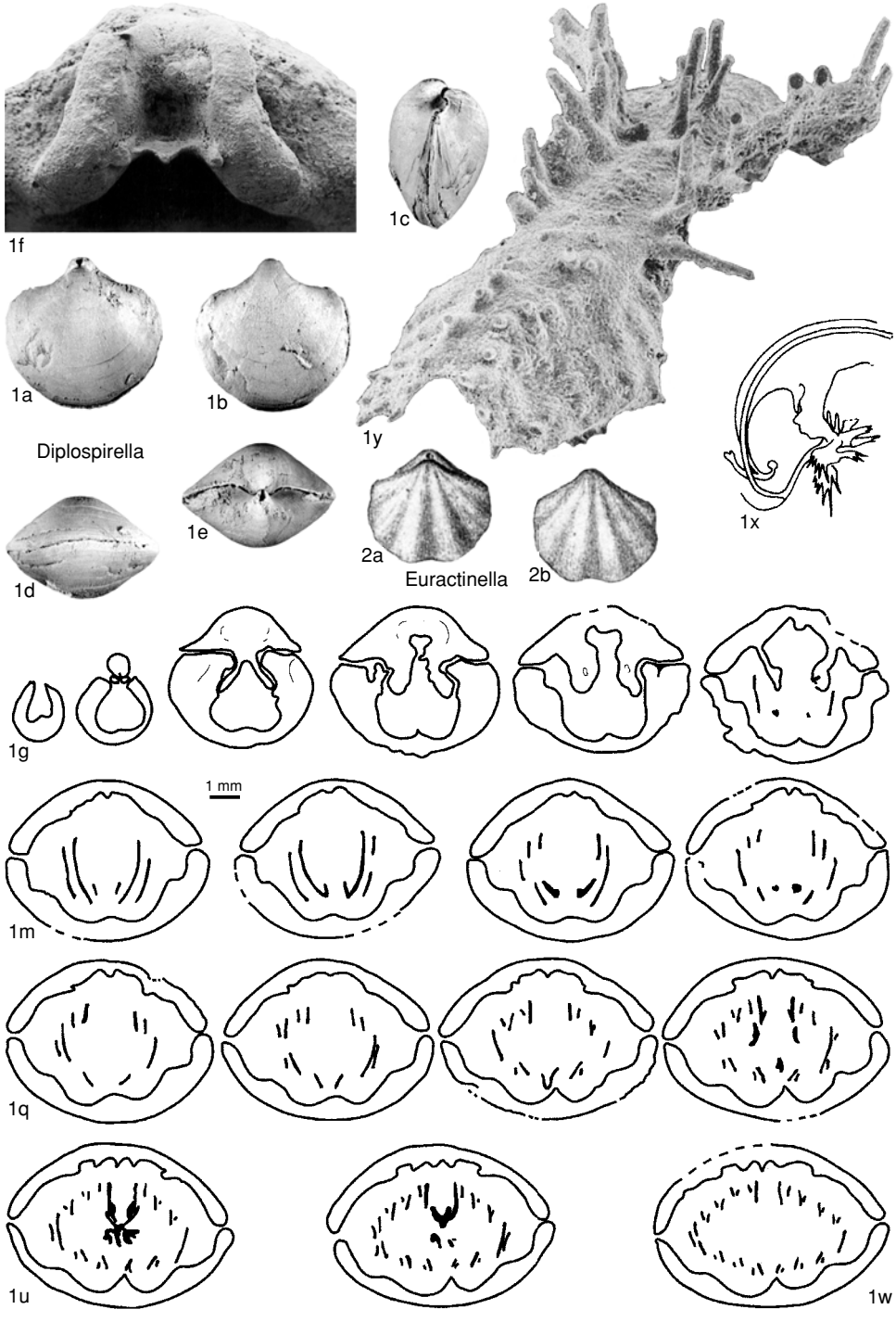


FIG. 1050. Diplospirellidae (p. 1545–1548).

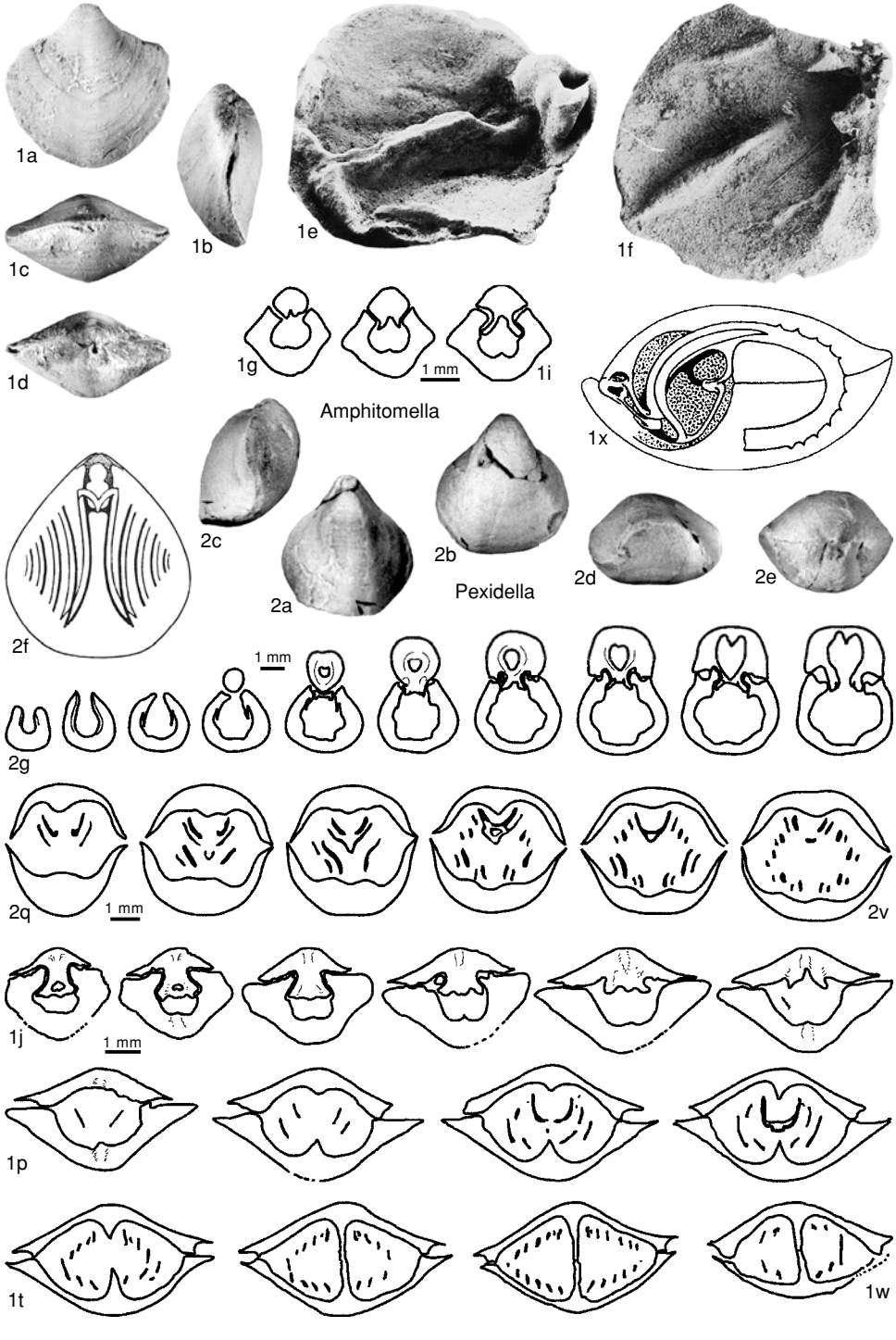


FIG. 1051. Diplospirellidae (p. 1545–1548).

reconstructed jugum, approximately ×6.5 (Benigni & Ferliga, 1995).

Anisactinella Bittner, 1890, p. 302 [**Terebratula quadriplecta* Münster, 1841, p. 58; OD]. Small to medium, subtrapezoidal to subpentagonal shells; hinge line almost rectilinear; plicate ventral sulcus and dorsal fold defined laterally by sharp plicae, lateral surfaces commonly smooth; ventral cardinal area well defined, rather high, triangular, slightly concave, orthocline; delthyrium partially covered by symphytium (arcuate to flat); foramen supra-apical; ventral low median septum may be present; cardinal plate subtrapezoidal, ventrally concave, with median ridge; cardinal flange well developed, semicircular to subrectangular, projecting strongly into delthyrial cavity; jugum as in *Pexidella.* [The number and development of plicae shows a high degree of variability in the assigned specimens.] *Middle Triassic (Anisian)–Upper Triassic (Carnian):* Dinarides, Southern Alps, Lucania, Bakony Mountains, Carpathians, northwestern China (Qinghai).——Fig. 1052*a–u. *A. quadriplecta* (Münster); *a–e,* dorsal, ventral, lateral, anterior, and posterior views, Ladinian, Cortina d'Ampezzo area, MPUM 5847/9, ×3; *f,* posterior view, showing cardinal flange, Ladinian, Cortina d'Ampezzo area, MPUM 5849/4, ×6; *g,* posterior view, showing cardinal flange, Triassic, Cortina d'Ampezzo area, MPUM 5847/20, ×13 (Benigni & Ferliga, 1992; photographs courtesy of C. Benigni); *h–u,* transverse serial sections 0.8, 0.9, 1.1, 1.2, 1.3, 1.4, 1.5, 1.6, 1.7, 1.8, 1.95, 2.05, 2.15, 2.45 mm from ventral umbo, distance from ventral umbo to first section approximate, Carnian, Hungary (adapted from Dagys, 1974).——Fig. 1052*v–ff. A. maurensis* Taddei Ruggiero, Ladinian, Lucania, Italy; transverse serial sections 0.76, 1.12, 1.22, 1.47, 1.60, 1.84, 2.50, 3.36, 5.10, 5.30, 5.70 mm from ventral umbo (Taddei Ruggiero, 1968).

Euractinella Bittner, 1890, p. 302 [**Terebratula contraplecta* Braun in Münster, 1841, p. 59; OD]. Suboval shells, without fold and sulcus; low rounded plications may be developed in corresponding positions on each valve; interior poorly known. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* southern Alps.——Fig. 1050,*2a–b. *E. contraplecta* (Braun); holotype, dorsal and ventral views, ×2 (Münster, 1841).

Pexidella Bittner, 1890, p. 300 [**Spirifer strohmayeri* Suess, 1855, p. 27; OD]. Elongate oval; commonly with dorsal fold and ventral sulcus; posterior part of both valves may be strongly thickened by secondary shell material; jugum, posteriorly situated, originates from very wide umbonal blades, giving rise directly to accessory jugal lamellae. *Middle Triassic (Anisian)–Upper Triassic (Norian):* Carpathians, Alps, Dinarides, Balkans, Caucasus, Nepal, Pamir, *Anisian–Norian;* USA (southeastern Alaska), ?Chile, *Upper Triassic.*——Fig. 1051,*2a–v. *P. strohmayeri* (Suess), Norian; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, Mühltal, Austria, USNM 497419, ×1.5 (new); *f,* ventral view showing brachidium, Mühltal, Austria, ×2 (Bittner, 1890); *g–v,* transverse serial sections 0.6, 0.9, 1.1, 1.3, 1.4, 1.6, 1.8, 1.9, 2.1, 2.3, 2.7, 2.9, 3.0, 3.2, 3.4, 3.5 mm from ventral umbo, distance from ventral umbo to first section and between sections *p* and *q* approximate, northwestern Caucasus, IGiG 394/275 (adapted from Dagys, 1974).

Subfamily CLAVIGERINAE Waterhouse, 1975

[*nom. transl.* Grunt, 1984, p. 70, *ex* Clavigeridae Waterhouse, 1975, p. 14]

Large, subpentagonal to subtrapezoidal; commonly with long straight hinge line and cardinal areas more or less well defined in both valves; dorsal fold and ventral sulcus faintly developed, or shallow sulcus may develop in both valves; surface with growth laminae; dental plates short, subparallel, slightly separated from thick lateral walls; pedicle support present, commonly complex; cardinal plate massive; cardinal flanges strongly developed; myophragm commonly present; jugum essentially as in *Athyris* with lateral branches of jugum originating before valve midlength, projecting anteroventrally; accessory jugal lamellae commonly very short and anteriorly serrated; shell massive, tertiary layer usually thick. *Upper Triassic.*

Clavigera Hector, 1879, p. 538 [**C. bisulcata* Hector in Thomson, 1913, p. 50; SD Thomson, 1919, p. 412] [=*Hectoria* Trechmann, 1918, p. 233, OD, obj.; *Hectorina* Finlay, 1927, p. 533, *nom. nov. pro Hectoria* Trechmann, 1918, p. 233, *non Hectoria* Castelnau, 1873, Pisces, *nec Hectoria* Tepper, 1889, Orthoptera; *Clavigerina* Marwick, 1946, p. 30, *lapsus pro Clavigera*]. Transverse shell with shallow median sulcus in both valves, bordered by more or less rounded ridge on either side; anterior commissure rectimarginate to faintly uniplicate; hinge line straight, almost equal to maximum width; ventral cardinal area low and wide, concave, apsacline to anacline, faintly striated; foramen small, in meso- to permesothyridid position, closed at maturity; dental plates diverging slightly dorsally, very short ventral median septum may support apically situated delthyrial plate; divergent muscle scars strongly marked; very high cardinal plate commonly with shallow longitudinal depression; accessory jugal lamellae very short. *Upper Triassic (Norian–Rhaetian):* New Caledonia, New Zealand, Chile.——Fig. 1053,*1a–f. *C. bisulcata* Hector, Rhaetian, New Zealand; *a,* holotype, dorsal view, ×1 (Thomson, 1913); *b–f,* transverse serial sections 11.0, 14.0, 16.5, 18.5, 21.5 mm from ventral

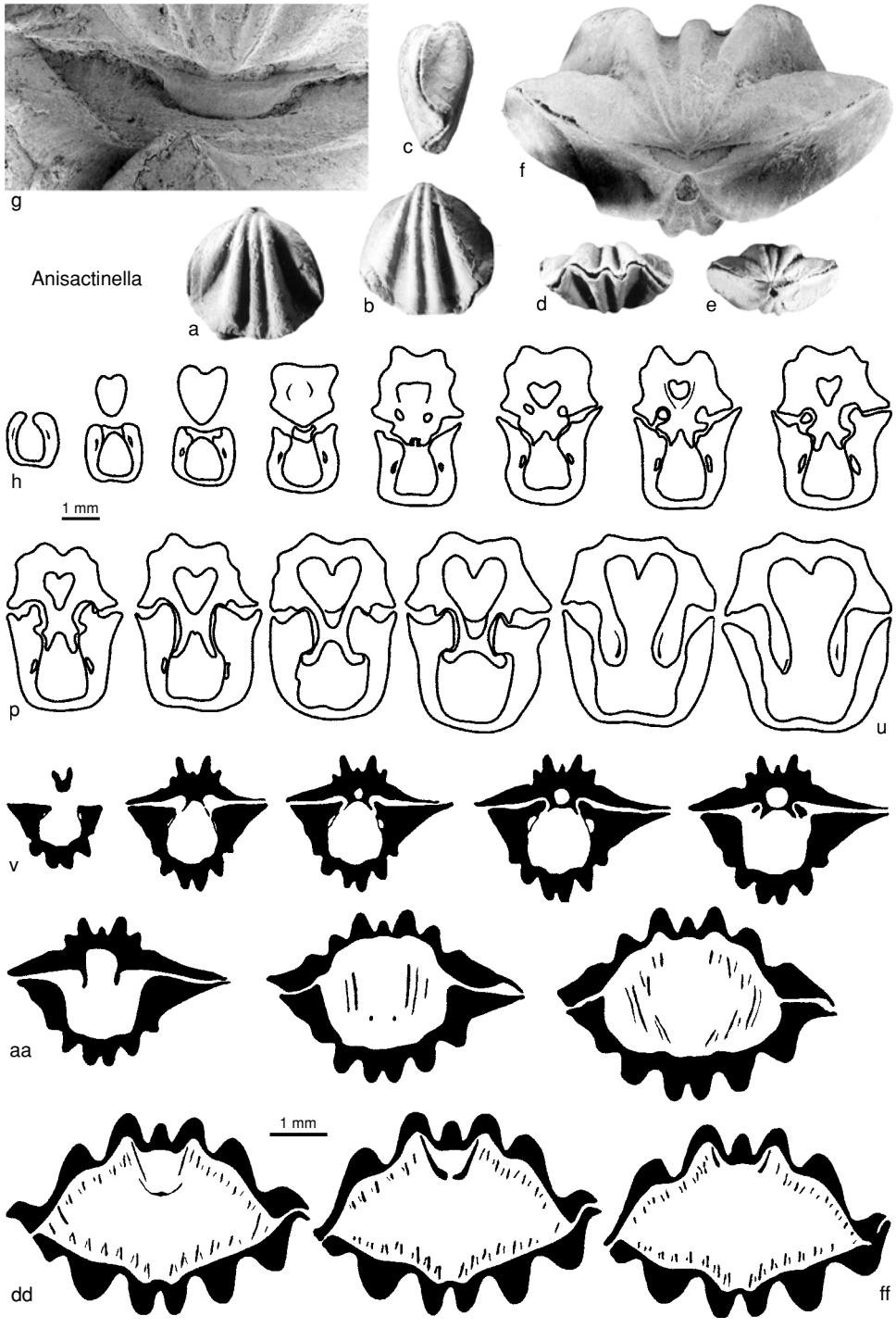


FIG. 1052. Diplospirellidae (p. 1548).

umbo, NZGS br1297 (adapted from Waterhouse, 1975).——Fig. 1053,*1g–k. C.* sp.; posterodorsal, ventral, lateral, anterior, and posterior views of internal mold, DPO F24246, ×1 (new).

Majkopella Moisseiev in Dagys, 1962, p. 61 [**Athyris worobievi* Moisseev, 1947a, p. 76; OD]. Subequally biconvex, rounded subpentagonal to transverse semielliptical shells; hinge line nearly straight, equal or slightly shorter than maximum width; ventral cardinal area low, long, with almost parallel margins; pedicle collar complex, almost completely filling delthyrial cavity; cardinal plate as in *Oxycolpella.* [The name *Majkopella* is commonly credited to Dagys (1962). We agree with Dagys (1962, 1974) and accept Moisseiev (in Dagys, 1962) as author.] *Upper Triassic:* Crimea, Carpathians, Balkans, Turkey, Caucasus, ?southern China (Sichuan).——Fig. 1053,*2a–o. *M. worobievi* (Moisseiev), Rhaetian, northern Caucasus; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, IGiG 166/101, ×1 (Dagys, 1962; photographs courtesy of the late A. S. Dagys); *f–o,* transverse serial sections 0.6, 1.2, 1.7, 2.1, 2.6, 3.2, 4.3, 4.8, 6.2, 7.2 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Dagys, 1962).

Oxycolpella Dagys, 1962, p. 68 [**Spirigera oxycolpos* Suess, 1854, p. 45[17]; OD; =*Spirigera oxycolpos* Suess, 1853, p. 287, *nom. nud.*] [=*Dictyonathyris* Xu, 1978, p. 287 (type, *D. lanaensis,* OD)]. Round to rounded pentagonal; growth laminae irregular; large foramen; thick delthyrial plate; sessile pedicle collar may be present; cardinal plate massive, subquadrate; cardinal flanges strongly developed, serrated, ventrally concave, projecting into delthyrial cavity. [Type species is usually credited to Emmrich, 1853, p. 356; however he gave no description or figure. The first to fulfill the conditions of availability was Suess (1854) who therefore has been credited with authorship (Pearson, 1977).] *Upper Triassic:* Slovakia, Bavaria, southern Austria, Hungary, Romania, Turkey, Iran, Himalayas, Pamir, southern and northwestern China, New Caledonia, New Zealand, northern Chile.——Fig. 1054*a–bb.* **O. oxycolpos* (Suess), Rhaetian, Austria; *a–d,* lectotype, dorsal, lateral, anterior, and posterior views, MGBW 1074, ×1 (Pearson, 1977); *e–q,* transverse serial sections 2.3, 3.1, 3.9, 4.5, 11.6, 12.8, 15.0, 15.5, 16.0, 16.3, 16.9, 17.7, 19.3 mm from ventral umbo, MGBW PC.Nr.69 (adapted from Pearson, 1977); *r–bb,* transverse serial sections 0.8, 2.4, 3.6, 5.0, 6.1, 6.6, 7.7, 8.5, 9.2, 10.0, 11.1 mm from ventral umbo, distance from ventral umbo to first section approximate, northern Caucasus (adapted from Dagys, 1962).

Subfamily MISOLIINAE Dagys, 1996

[Misoliinae Dagys, 1996, p. 89]

Commonly small, rarely large, elongate oval, costate; fold and sulcus faint or absent; growth lines commonly numerous and weak; dental plates poorly developed; cardinal plate slightly concave ventrally; swollen cardinal flanges moderately to strongly developed; jugum without jugal stem, short accessory jugal lamellae extend posterodorsally directly from anteriorly pointed jugal saddle. *Lower Permian (Artinskian)–Upper Triassic (Norian).*

Misolia von Seidlitz, 1913, p. 172 [**M. misolica;* OD]. Large, moderately to strongly biconvex, elongate-oval; costae may bifurcate anteriorly; foramen large, in meso- to permesothyridid position; deltidial plates conjunct. *Upper Triassic (Norian):* Indonesia, Moluccas, Timor, Oman, ?India, ?China, northwestern Australia.——Fig. 1055,*1a–g. *M. misolica,* Indonesia; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, ×1; *f–g,* ventral and lateral views of jugum, ×2 (von Seidlitz, 1913).

?Anomactinella Bittner, 1890, p. 300 [**Terebratula flexuosa* Münster, 1841, p. 59; OD]. Small, circular to elongate oval or pentagonal shells; umbones smooth, anterior half of valves prominently costate, with costae in corresponding position on each valve, commissure denticulate in dorsal view; ventral interior, cardinalia, and brachidium poorly known. [This genus requires revision.] *Middle Triassic (?Ladinian), Upper Triassic (Carnian):* southern Alps.——Fig. 1055,*2a–b. *A. flexuosa* (Münster); dorsal and ventral views, ×1 (Bittner, 1890).

?Pentactinella Bittner, 1890, p. 300 [**Terebratula quinquecostata* Münster, 1841, p. 59; SD Hall & Clarke, 1894, p. 977]. Small, oval to subcircular or rhomboidal; each valve with 5 to 16 coarse costae in corresponding position; costae may bifurcate anteriorly; commissure strongly denticulate in dorsal view; foramen small, in permesothyridid position; structure of jugum unknown. [This genus requires revision.] *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* southern Alps, southern Italy, Slovakia, Romania.——Fig. 1055,*5a–b. *P. quinquecostata* (Münster), Carnian, San Cassiano, Italy; dorsal and ventral views, ×2.5 (Taddei Ruggiero, 1968).——Fig. 1055,*5c–g. P. scandonei* Taddei Ruggiero, Ladinian, Lucania, Italy; transverse serial sections 0.68, 0.9, 1.06, 1.2, 1.62 mm from ventral umbo (Taddei Ruggiero, 1968).

?Stolzenburgiella Bittner, 1903, p. 508 [**S. bukowskii;* OD]. Medium, elongate or transverse subpentagonal; costae in corresponding position on each valve; foramen dotlike; ventral interior, cardinalia, and brachidium poorly known. [This genus requires revision.] *Triassic:* Dinaric Alps, *Anisian;* Slovakia, *Ladinian;* Malaysia, *Triassic.*——Fig. 1055,*3a–c. *S. bukowskii,* Anisian, Bosnia; dorsal, ventral, and anterior views, ×2 (Bittner, 1903).

?Uncinella Waagen, 1883, p. 494 [**U. indica;* M]. Medium, biconvex, longitudinally subelliptical, ribbed shells commonly without fold and sulcus; foramen labiate in epithyridid position; delthyrium

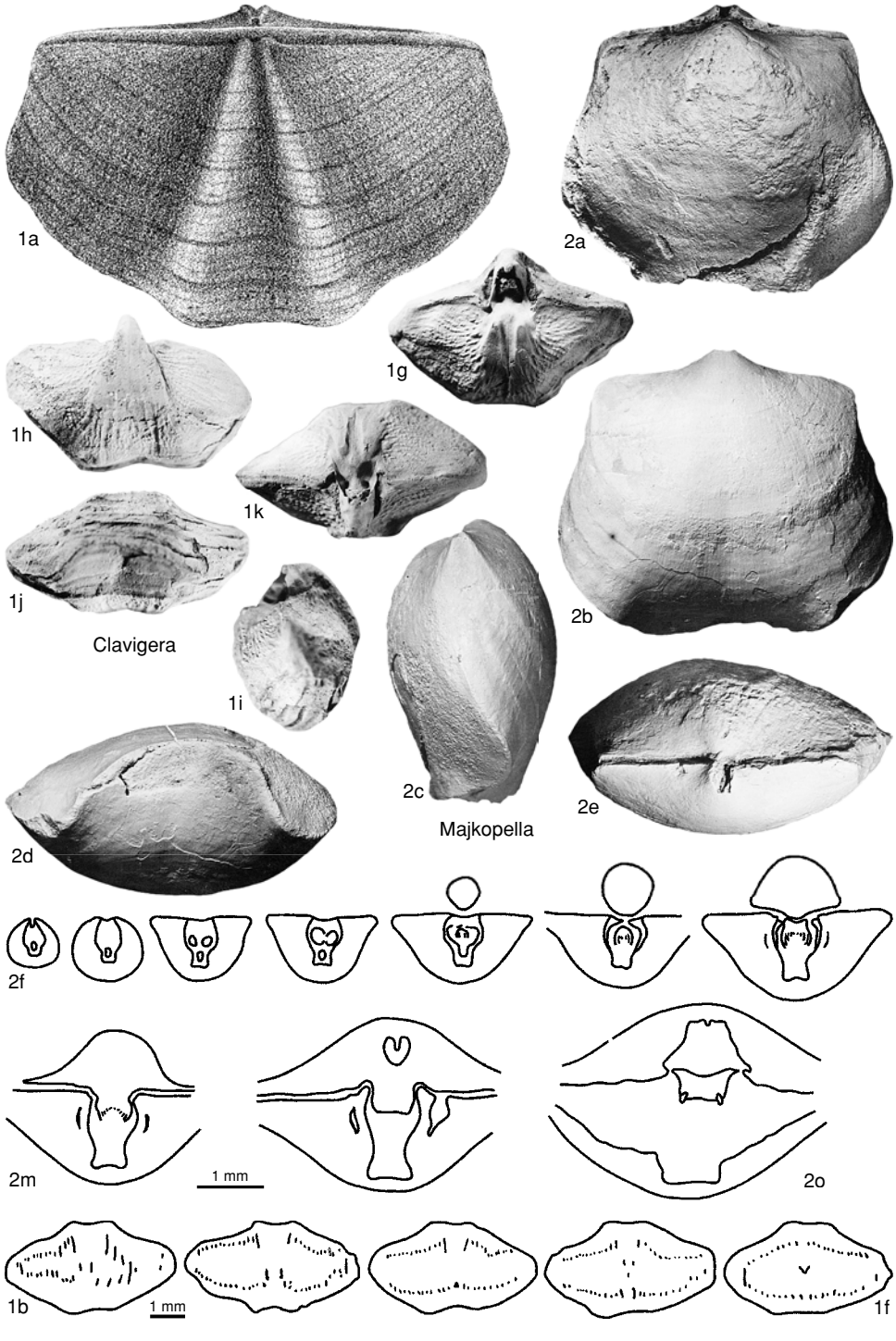


FIG. 1053. Diplospirellidae (p. 1548–1550).

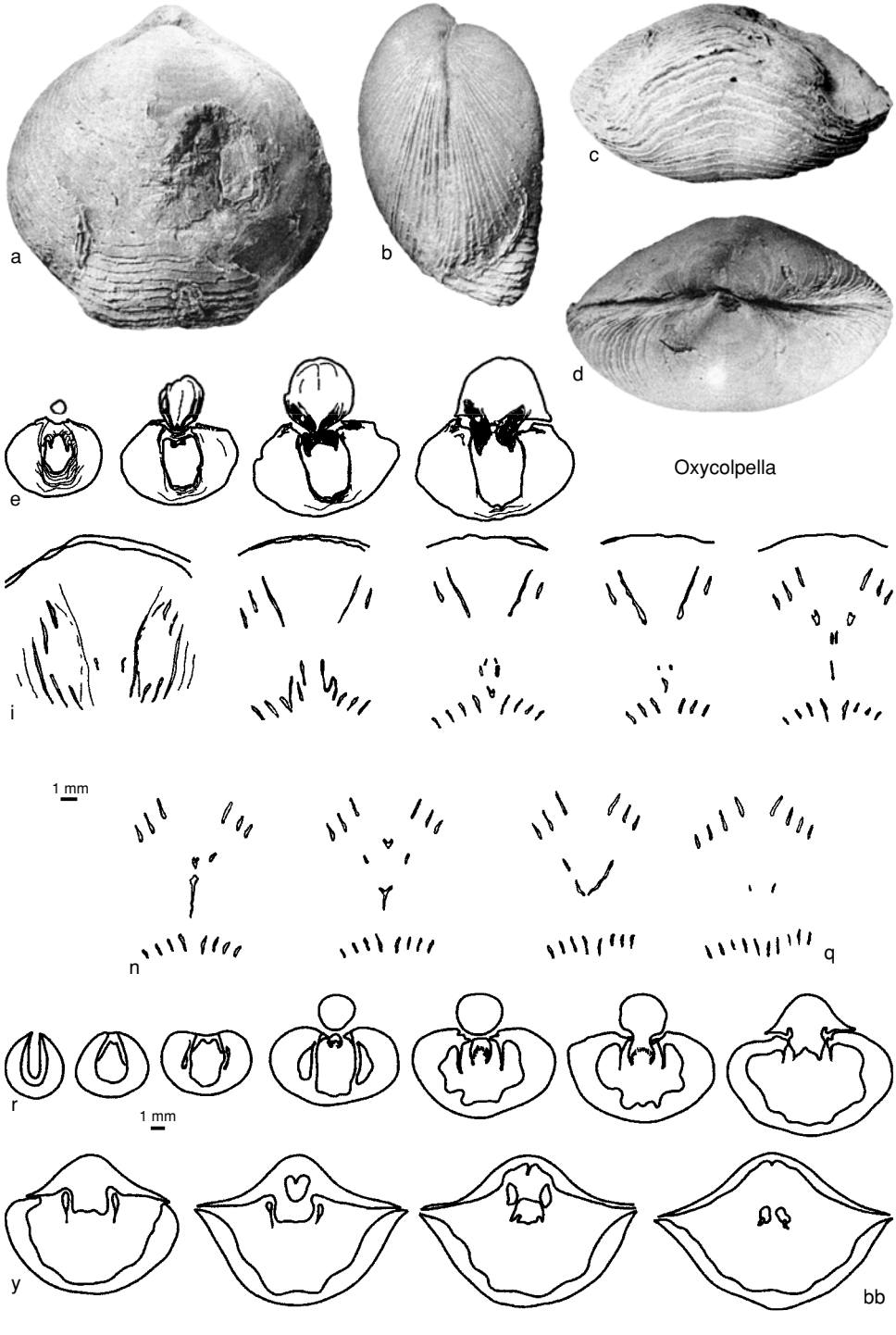


FIG. 1054. Diplospirellidae (p. 1550).

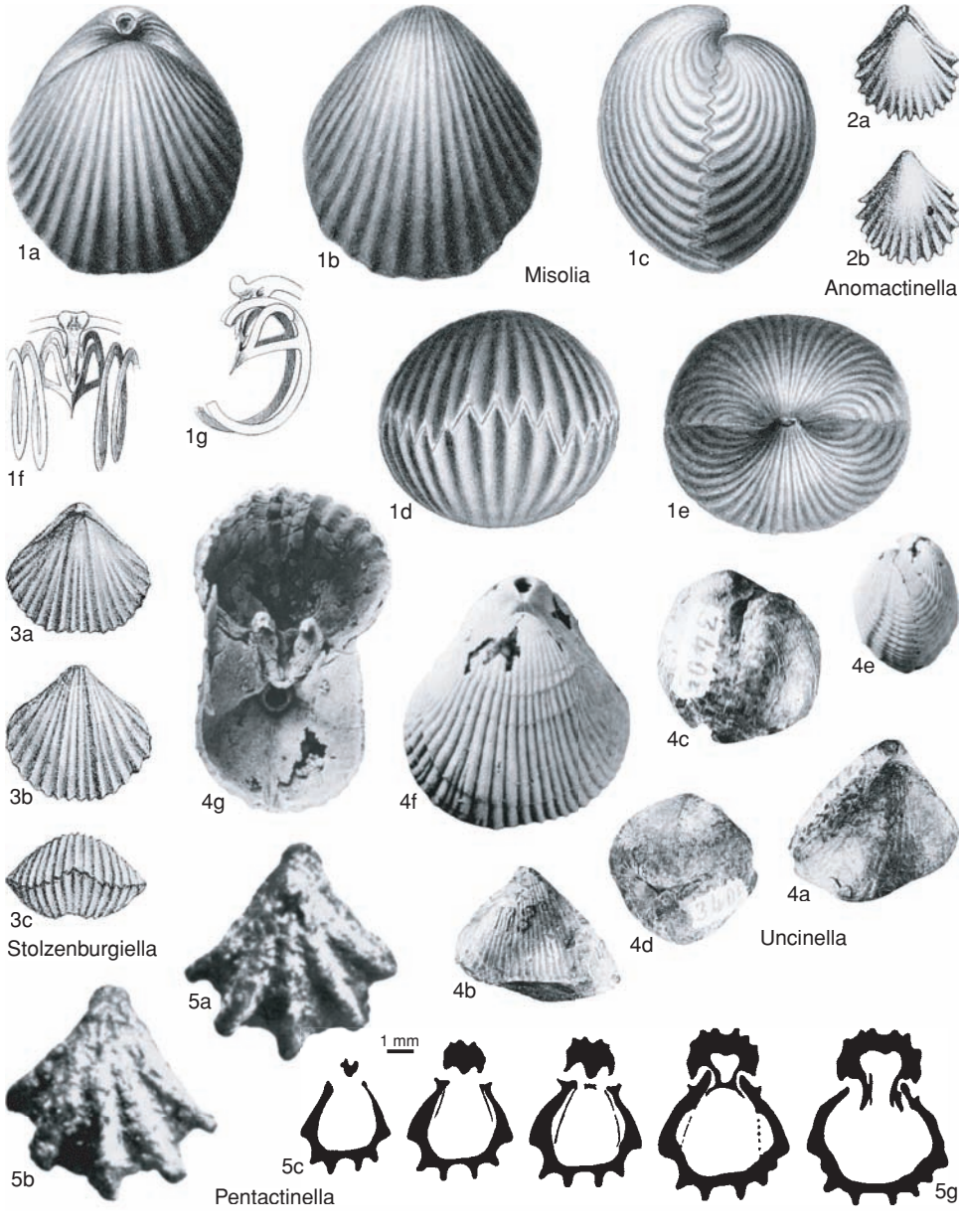


FIG. 1055. Diplospirellidae (p. 1050–1055).

with conjunct deltidial plates; dental plates absent, short pedicle collar may be present; hinge plate widely divided; cardinal process with large median knob and posteroventrally directed, well-developed cardinal flanges; crura ribbonlike, myophragm absent; spiral brachidium have been reported but not described or illustrated; jugum unknown. [Systematic position uncertain; this genus requires revision.] *Lower Permian (Artinskian):* Pakistan, southern Thailand, Cambodia, ?Vietnam, ?China.——FIG. 1055,*4a–f.* **U. indica,* Pakistan; *a–d,* holotype, dorsal, ventral, lateral, and posterior views, GSI 3405, Waagen collection, ×1 (new; photographs courtesy of R. K. Biswas); *e,* lateral view, ×1; *f,* dorsal view, USNM 212772, ×2 (Grant, 1976). ——FIG. 1055,*4g. U. siamestris* GRANT, Artinskian,

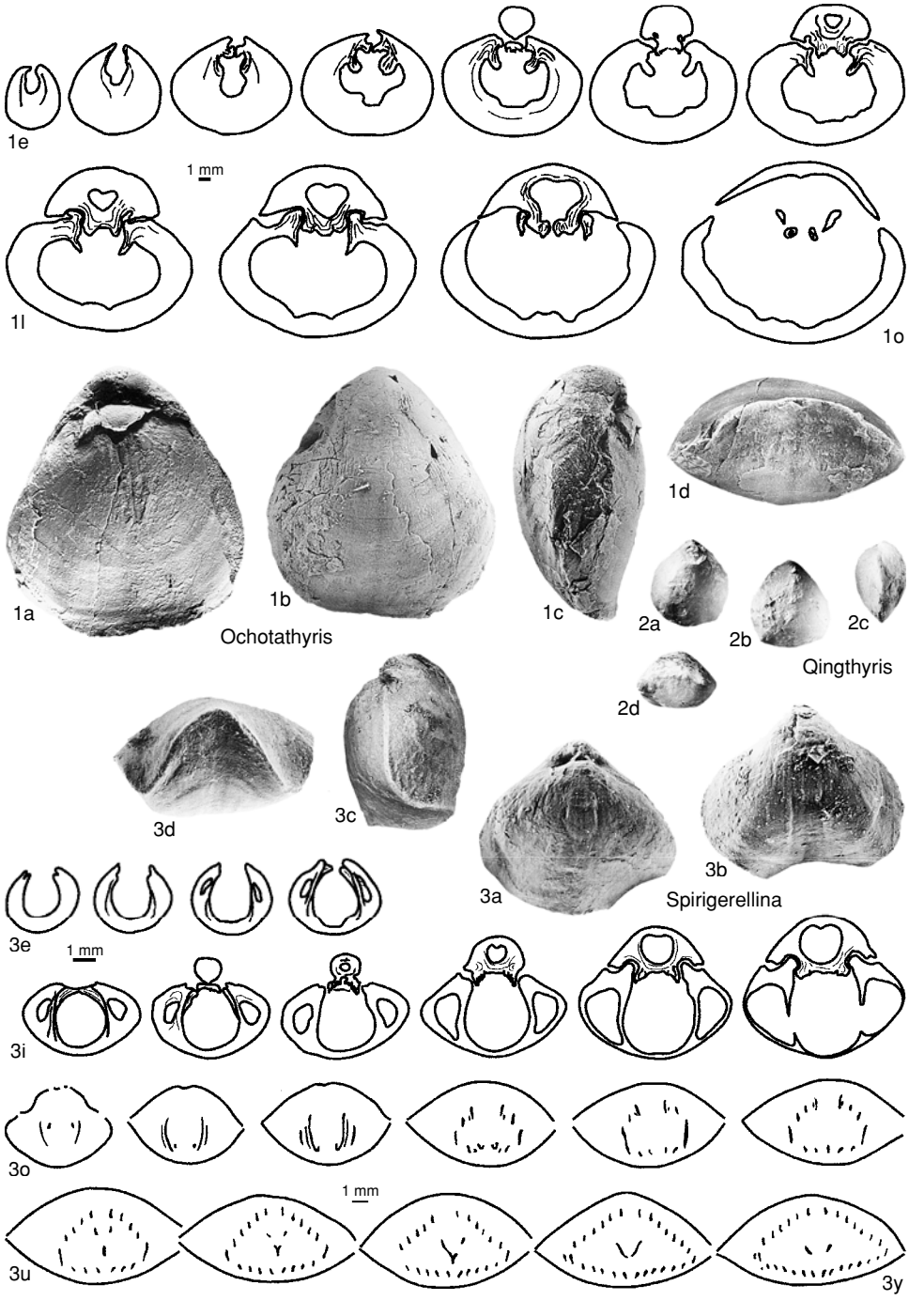


FIG. 1056. Diplospirellidae (p. 1555–1556).

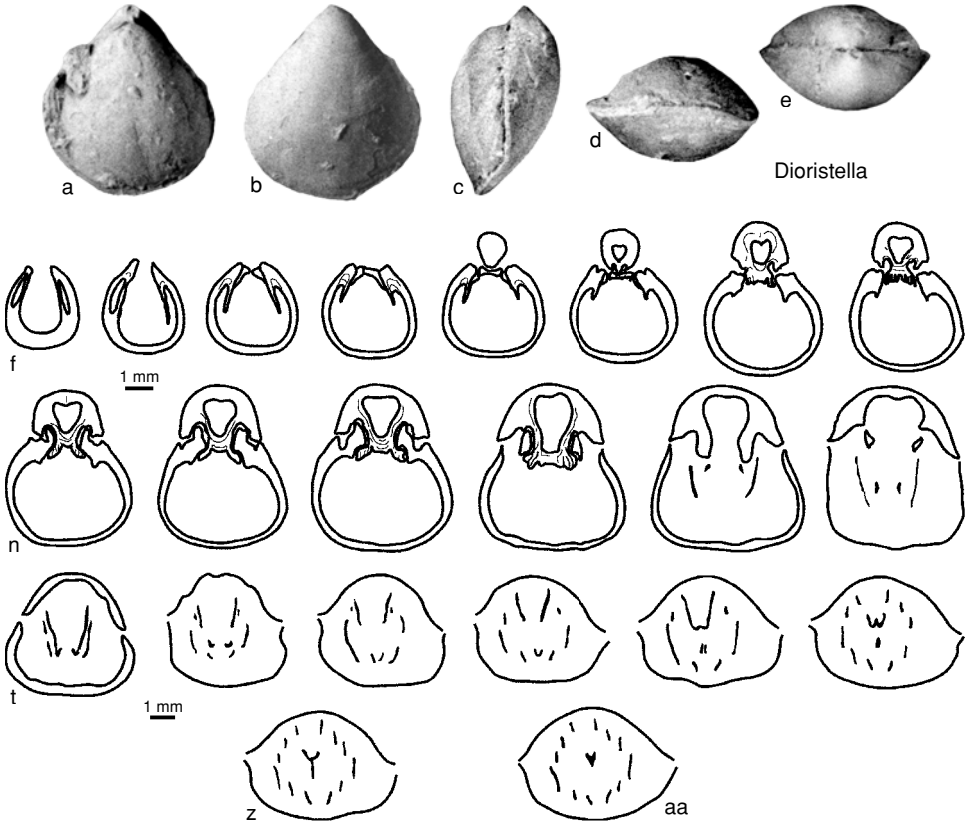


FIG. 1057. Diplospirellidae (p. 1555–1556).

Thailand; interior of articulated shell showing cardinalia and articulation, USNM 212770, ×2 (Grant, 1976).

Subfamily OCHOTATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Ochotathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 844]

Small to large, commonly elongate-oval; dorsal fold and ventral sulcus variably developed, commonly faint; growth lines faintly expressed, growth lamellae absent; dental plates short, converging dorsally, only dental flanges support massive teeth anteriorly; delthyrial plate present; cardinal plate commonly high and thick; cardinal flanges serrated, commonly well developed; low myophragm usually present; jugum essentially as in *Athyris* with short accessory jugal lamellae, jugal saddle poorly developed or absent; tertiary layer may be present. *Lower Triassic (Scythian)–Upper Triassic (Norian), ?Upper Jurassic.*

Ochotathyris DAGYS, 1974, p. 159 [**Oxycolpella ochotica* DAGYS, 1965, p. 132; OD]. Medium to large, oval to longitudinally triangular shells with dorsal fold and ventral sulcus faintly developed; beak thick, strongly incurved; faintly developed sessile pedicle collar may be present; tertiary layer thick. *Upper Triassic (Norian), ?Upper Jurassic:* Russia (Primorya, Siberia), USA (Arctic Alaska), *Norian;* northwestern China, Qinghai, *?Upper Jurassic.*——FIG. 1056,*1a–o.* **O. ochotica* (DAGYS), Norian, Primorya; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 290/118, ×1 (Dagys, 1974; photographs courtesy of the late A. S. Dagys); *e–o,* transverse serial sections 2.0, 3.2, 3.7, 4.2, 5.0, 5.7, 6.3, 7.0, 8.4, 8.9, 9.4 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Dagys, 1965).

Dioristella BITTNER, 1890, p. 299 [**Terebratula indistincta* BEYRICH, 1863, p. 34; SD HALL &

Clarke, 1894, p. 969]. Small, commonly nonsulcate, longitudinal furrows may be developed in both valves; lateral branches of jugum lead off from umbonal blades until joining anteroventrally, jugal stem long, projecting posteroventrally with low angle, accessory jugal lamellae normally free. *Upper Triassic (Carnian):* southern Alps, Carpathians, Caucasus, Pamir.——Fig. 1057*a–aa.* **D. indistincta* (Beyrich), St. Cassian, southern Tyrol; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497421, ×3 (new); *f–aa,* transverse serial sections 0.2, 0.5, 0.7, 0.9, 1.0, 1.1, 1.2, 1.4, 1.6, 1.7, 1.9, 2.1, 2.3, 2.4, 2.7, 3.0, 3.2, 3.4, 3.5, 3.7, 3.9, 4.2 mm from ventral umbo, distance from ventral umbo to first section and between sections *s* and *t* approximate, IGiG 394/265 (adapted from Dagys, 1974).

?Qingthyris Xu & Liu, 1983, p. 126 [**Q. variabilis;* OD]. Medium size with variable outline; interior poorly known, reportedly without dental plates but possibly with bilobed cardinal process and posterior median ridge in dorsal valve; spiralia and jugum unknown. [May be synonymous with *Dioristella.*] *Middle Triassic:* northwestern China (Qilian Mountains).——Fig. 1056,*2a–d.* **Q. variabilis;* holotype, dorsal, ventral, lateral, and anterior views, ×1 (Xu & Liu, 1983; photographs courtesy of Xu Guirong).

Spirigerellina Dagys, 1974, p. 160 [**S. pygmaea;* OD] [=*Compositella* Xu & Liu, 1983, p. 124 (type, *C. planosulcata,* OD)]. Small, rounded pentagonal to transversely oval shells with variably developed dorsal fold and ventral sulcus that may bear median furrow; anterior commissure uniplicate to parasulcate; cardinal flanges low; jugum without saddle. *Lower Triassic (Scythian)–Upper Triassic (Carnian):* Alps, Dinarids, Carpathians, Primorya, Caucasus, Nepal, Siberia, Kazakhstan, Mongolia, southern Qilian, Chaidam, northwestern China. ——Fig. 1056,*3a–y.* **S. pygmaea,* Scythian, Mangylschak, Kazakhstan; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 394/76, ×2.5 (Dagys, 1974; photographs courtesy of the late A. S. Dagys); *e–y,* transverse serial sections 1.0, 1.2, 1.4, 1.6, 1.8, 2.0, 2.1, 2.3, 2.5, 2.7, 3.0, 3.2, 3.4, 3.6, 4.1, 4.4, 4.7, 5.3, 5.6, 5.8, 6.0 mm from ventral umbo, distance from ventral umbo to first section and between sections *n* and *o* approximate, IGiG 394/84 (adapted from Dagys, 1974).

Subfamily TETRACTINELLINAE Grunt, 1986

[Tetractinellinae Grunt, 1986, p. 7]

Medium, externally resembling *Plicathyris;* dental plates of medium length, converging slightly dorsally; delthyrial plate present; cardinal plate thin, high; cardinal flanges serrated, moderately developed; short dorsal myophragm may be present; jugum essentially as in *Athyris* with short jugal saddle and accessory jugal lamellae terminating anteriorly of lateral branches of jugum. *Middle Triassic.*

Tetractinella Bittner, 1890, p. 300 [**Terebratulites trigonellus* von Schlotheim, 1820 in 1820–1823, p. 271; SD Hall & Clarke, 1894, p. 977]. Shell commonly with 4 narrow, cusplike plications in corresponding position on each valve, separated by wide, flat interspaces; anterior commissure straight or slightly deflected dorsally. *Middle Triassic:* Alps, Dinarids, Carpathians, Balkans, Caucasus, Pamir, ?China.——Fig. 1058*a–x.* **T. trigonella* (von Schlotheim); *a–e,* dorsal, ventral, lateral, anterior, and posterior views, southern Tyrol, USNM 497420, ×1.5 (new); *f,* lateral view of jugum, southern Tyrol, ×4 (Bittner, 1890); *g–x,* transverse serial sections 1.0, 1.4, 1.8, 2.1, 2.4, 2.6, 2.8, 3.3, 3.8, 4.0, 4.2, 5.2, 5.9, 6.4, 6.9, 7.3, 7.7, 8.1 mm from ventral umbo, distance from ventral umbo to first section approximate, Caucasus, IGiG 394/273 (adapted from Dagys, 1974).

Family HYATTIDINIDAE Sheehan, 1977

[*nom. transl.* Alvarez, Rong, & Boucot, 1998, p. 841, *ex* Hyattidininae Sheehan, 1977, p. 29; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 841]

Astrophic, medium, moderately to strongly convex and rostrate shell; with or without ventral sulcus and dorsal fold; growth lines weak, without frills; dental plates thin and short; pedicle supports absent; ventral muscle field impressed, without longitudinal striations; cardinal plate thin, flat, triangular, inner hinge plates separated by narrow fissure; no cardinal process; no dorsal median septum or myophragm; lateral branches of jugum originating before valve midlength, projecting backward and joining in narrow jugal arch; jugal saddle and stem absent; without tertiary layer. *Upper Ordovician (?Caradoc, Ashgill)–Silurian (Přídolí).*

Hyattidina Schuchert, 1913, p. 415, *nom. nov. pro Hyattella* Hall & Clarke, 1893, p. 61, *non* Lenendfeld, 1891 [**Atrypa congesta* Conrad, 1842, p. 265; OD]. Biconvex shells with pentagonal outline, covered with numerous growth lines; ventral sulcus and dorsal fold may be accentuated by bounding furrows; slightly divergent diductor scars enclose linear adductors. *Upper Ordovician (?Caradoc, Ashgill)–Silurian (Ludlow):* Scotland, Ireland, *?Caradoc, Ashgill;* North America, United Kingdom, Ireland, Norway, Russian Platform, Siberian Platform, *Ludlow.*——Fig. 1059,*1a–g.* **H. congesta* (Conrad), Ludlow, Clinton Group, New York, USA; *a–e,* neotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 31132, Hall

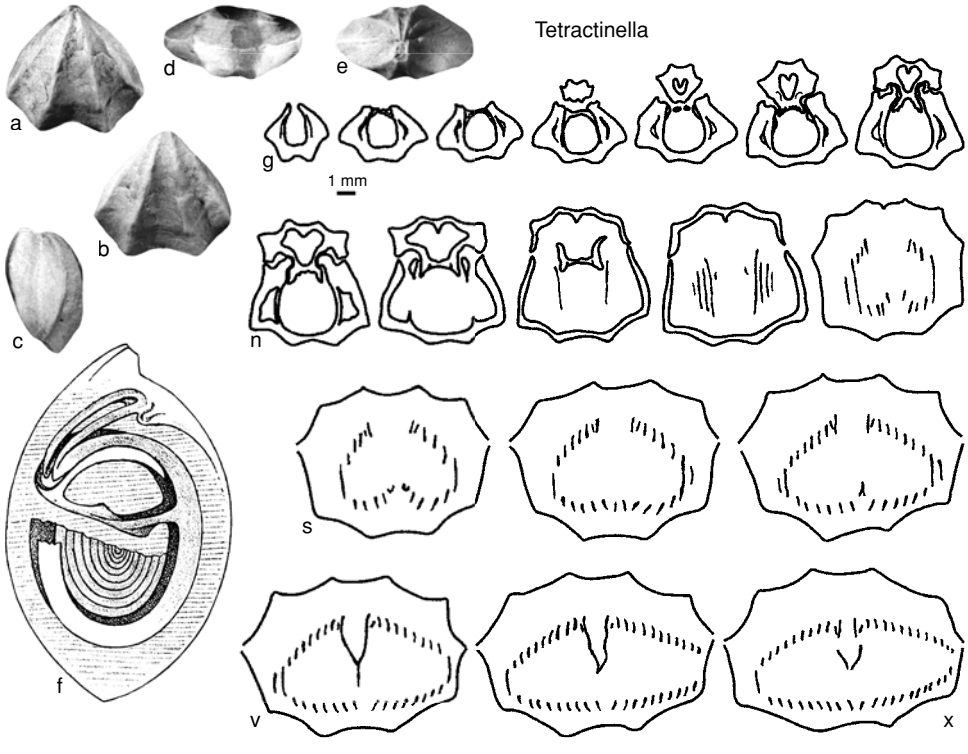


FIG. 1058. Diplospirellidae (p. 1556).

collection, ×2; *f,* cardinalia, I1420, Hall collection, ×17 (Alvarez & Brime, 2000); *g,* cardinalia, USNM 497423, ×20 (new).

?**Argella** MENAKOVA & NIKIFOROVA, 1986, p. 68 [**A. pirum;* OD]. Similar to *Hyattidina* but strongly inflated; base of delthyrium closed by short deltidial plates; crura ventrally directed. [*Argella* was identified by its authors as a meristelloid, presumably on the basis of the overall external morphology. Other features, such as the absence of septalium and dorsal septum, however, are more typically athyridoid. It has some similarities with the didymothyridins and the hyattidins. Revision of dorsal and ventral posterior internal structures is required to confirm its affinities.] *Silurian (Přídolí):* Tajikistan.——FIG. 1059,*2a–w.* **A. pirum; a–d,* holotype, dorsal, ventral, lateral, and anteroventral views, ×2 (Menakova & Nikiforova, 1986; photographs courtesy of T. L. Modzalevskaya); *e–u,* transverse serial sections 0.8, 1.2, 1.4, 1.8, 2.0, 2.05, 2.15, 2.2, 2.8, 3.2, 3.5, 3.6, 3.8, 4.0, 4.4, 4.9, 5.4 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 31/6228 (adapted from Menakova & Nikiforova, 1986); *v–w,* ventral and lateral views of jugum, TsNIGRA 31/6228 (Menakova & Nikiforova, 1986).

Superfamily MERISTELLOIDEA Waagen, 1883

[*nom. correct.* HARPER, 1993, p. 447, *pro* Meristellacea DAGYS, 1974, p. 231, *nom. transl. ex* Meristellinae WAAGEN, 1883, p. 449; *emend.*, ALVAREZ, RONG, & BOUCOT, 1998, p. 834]

Athyrididines commonly smooth; moderately to strongly rostrate, ventral umbo moderate to strongly curved; narrow and astrophic hinge line; concentric growth lamellae poorly developed or absent; dorsal fold and ventral sulcus commonly weak or absent; ventral cardinal area (palintrope) reduced; pedicle opening commonly present as foramen, in meso- to epithyridid position, and delthyrium open or partially covered by deltidial plates (completely in *Septathyris*); shell tending to be thick, particularly in the umbonal region; pedicle support absent; distinct dental plates commonly present, may be reinforced by mystrochial plates or shoelifter (meristids) or form spondylial structure

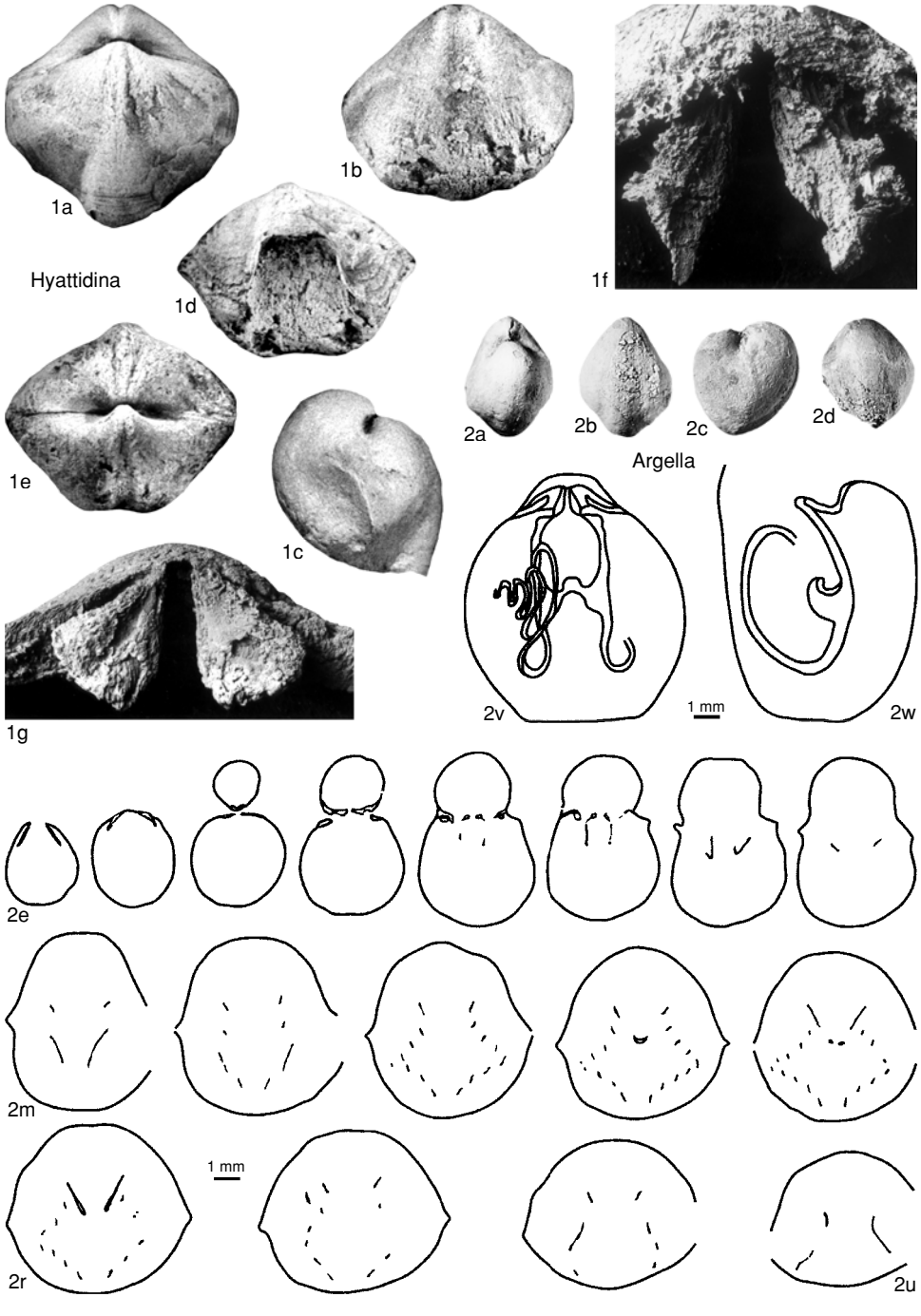


FIG. 1059. Hyattidinidae (p. 1556–1557).

(camarophorellins and rowleyellins); inner hinge plates present, forming septalium; long and high dorsal median septum commonly present; dorsal shoe-lifter may be present in some meristids; simple to complex jugum, jugal saddle absent, accessory jugal lamellae, when present, reunited with lateral branches of jugum or with jugal stem. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Family MERISTELLIDAE Waagen, 1883

[*nom. transl.* Hall & Clarke, 1894, p. 840, *ex* Meristellinae Waagen, 1883, p. 449; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 835]

Commonly large, strongly convex, with dorsal valve equally or less convex than ventral; dental plates subparallel, long (possibly extending anteriorly to flank muscle scars) in Ordovician and Silurian genera, short to obsolescent in Devonian genera; ventral muscle field commonly deeply impressed, fan shaped, widening anteriorly; bulbous pedicle callist with a short constriction anteriorly commonly present; septalium commonly deep and narrow, but wide and shallow in late forms; other structures strengthening the muscle system, or supporting dental plates, absent; tertiary layer may be present. *Upper Ordovician (Ashgill)–Upper Devonian (lower Frasnian).*

Subfamily MERISTELLINAE Waagen, 1883

[Meristellinae Waagen, 1883, p. 449; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 836]

Acute jugal arch projecting as long stem, moderately inclined posteriorly, may bifurcate into accessory jugal lamellae that may reunite with stem. *Upper Ordovician (Ashgill)–Upper Devonian (lower Frasnian).*

Meristella Hall, 1859a, p. 78 [**Atrypa laevis* Vanuxem, 1842, p. 120; SD Miller, 1889, p. 354; validated ICZN Opinion 1899, 1998a, p. 131]. Subequally biconvex shells, commonly longer than wide; ventral beak strongly incurved at maturity, frequently concealing foramen, with delthyrium commonly obscured by beak of dorsal valve; deltidial plates may be exposed in early growth stages; with or without dorsal fold and ventral sulcus that may affect only anterior commissure; dental plates short, obsolescent; ventral muscle field flaring widely laterally; broad and shallow supported septalium; septum extending anteriorly to about midvalve length; acute jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae then reuniting with stem; tertiary layer present. *Silurian (?upper Přídolí), Lower Devonian (Lochkovian)–Middle Devonian (Eifelian):* northeastern USA, *?upper Přídolí;* North America, Morocco, Mauritania, France, Belgium, Poland, Bohemia, Altay, Kazakhstan, eastern Urals, Chinese Altay, southeastern Australia, *Lochkovian;* Venezuela, *Pragian;* Spain, Bohemia, *Emsian;* Germany, *Eifelian.*——Fig. 1060*a–e.* **M. laevis* (Vanuxem), Lochkovian, Lower Helderberg Group, New York, USA; neotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33581, Hall collection, ×1.5 (Alvarez & Brime, 2000).——Fig. 1060*f–k. M. walcotti* Hall & Clarke, Lower Devonian, Ontario, Canada; *f–g,* dorsal and anterior views of specimen prepared to show spiralium and jugum, I1573, Hall collection, ×1.5 (Alvarez, Rong, & Boucot, 1998); *h–i,* ventral and posterior views of specimen prepared to show spiralium and jugum, I1573, Hall collection, ×1.5 (new); *j–k,* lateral and ventral views of jugum (Hall & Clarke, 1893).——Fig. 1060*l–m. M. arcuata* (Hall), Lochkovian, Lower Helderberg Group, New York, USA; ventral and lateral views showing jugum (Glass, 1882).——Fig. 1060*n. M. atoka* Girty, Haragan, Oklahoma, USA; detail of growth lines and faintly developed radial ornamentation on flat growth lamella, USNM 497422, ×18 (new). [See also Fig. 1006.2, p. 1481, in introduction.]

Arctomeristina Amsden, 1978, p. 33 [**A. compressa;* OD]. Similar to *Hindella* externally and to *Meristina* internally; dorsal valve with short septalium supported by high, bladelike septum extending forward for approximately one-half valve length on mature shells; jugum projecting posteriorly, jugal bifurcations unknown. *Silurian (Wenlock):* North America, ?Russia (Tuva).——Fig. 1061,*2a–j.* **A. compressa,* Wenlock, Oklahoma, USA; *a–d,* holotype, dorsal, ventral, lateral, and posteroventral views, OU 8505, ×1 (Amsden, 1978); *e–j,* transverse serial sections 4.0, 4.44, 4.9, 6.4, 6.7, 7.6 mm from ventral umbo (adapted from Amsden, 1978).

Charionella Billings, 1861, p. 148 [**Atrypa scitula* Hall, 1843, p. 171; OD]. Similar to *Meristella* but having a sessile septalium. *Lower Devonian (lower Emsian)–Upper Devonian (lower Frasnian):* North America.——Fig. 1062,*2a–f.* **C. scitula* (Hall); *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, Givetian, New York, USA, I1215, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f,* ventral view of septalium, Middle Devonian, Ontario, Canada, I1214, Hall collection, ×11 (new).

Charionoides Boucot, Johnson, & Staton, 1964, p. 817 [**Meristella doris* Hall, 1860a, p. 84; OD].

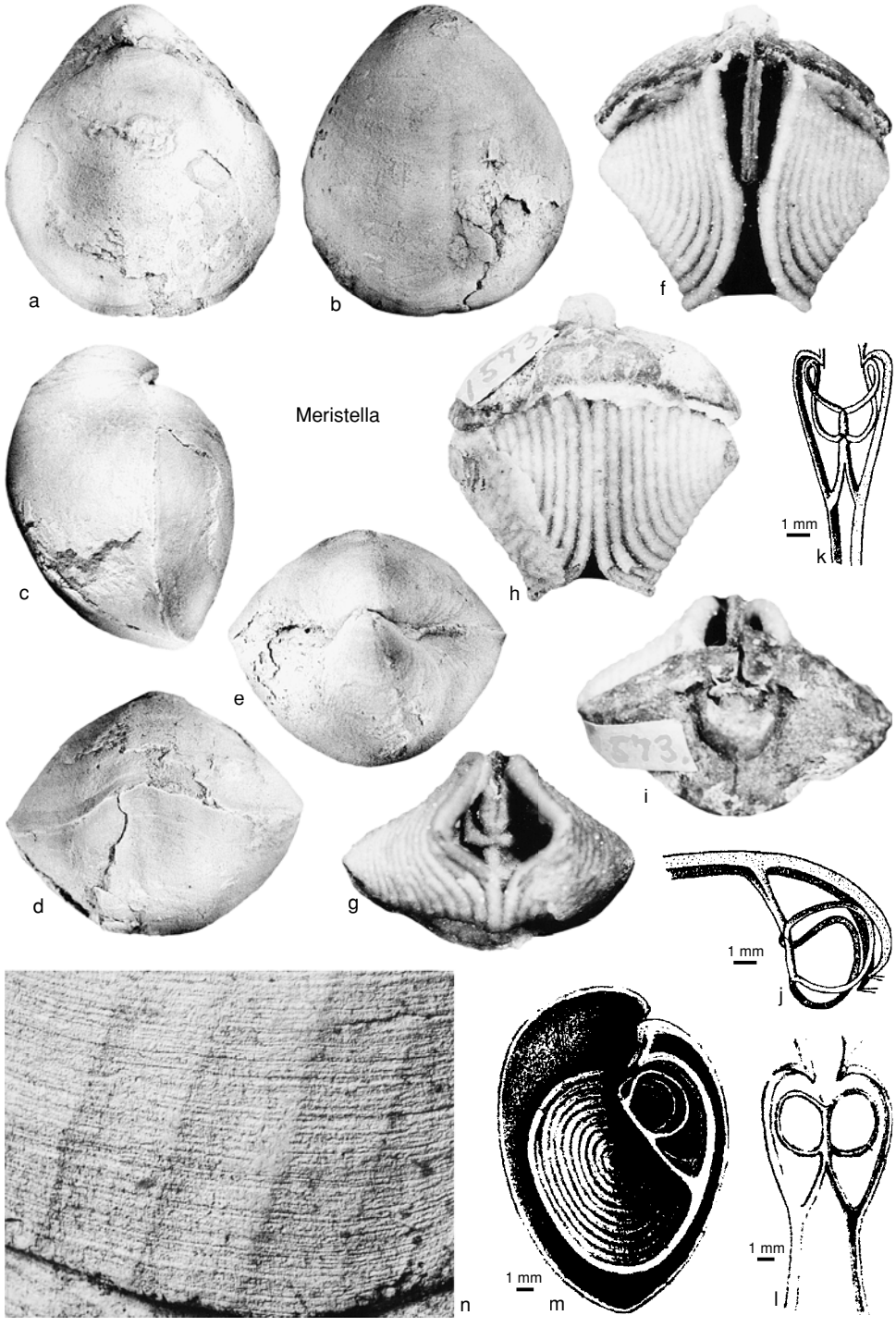


FIG. 1060. Meristellidae (p. 1559).

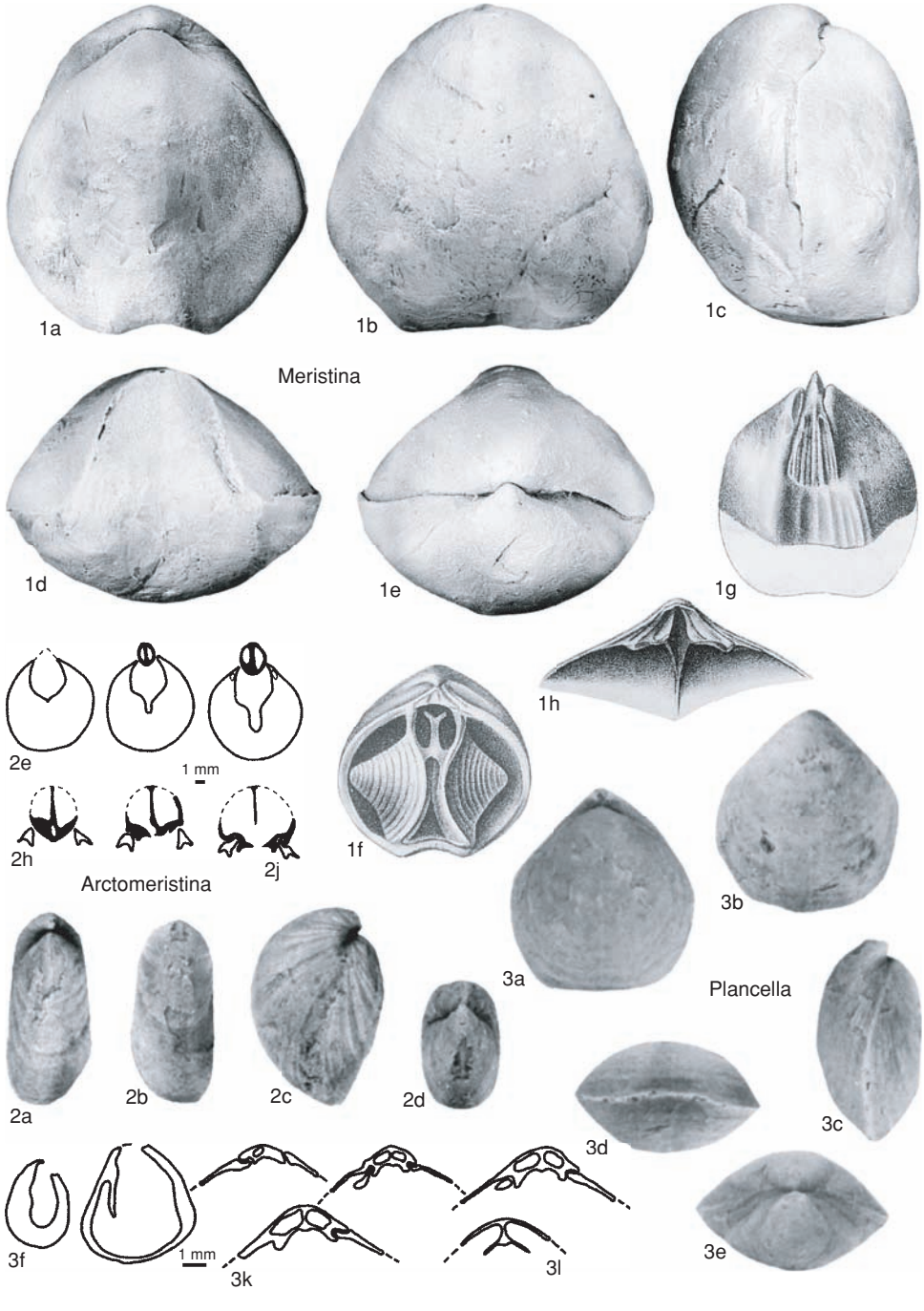


FIG. 1061. Meristellidae (p. 1559–1566).

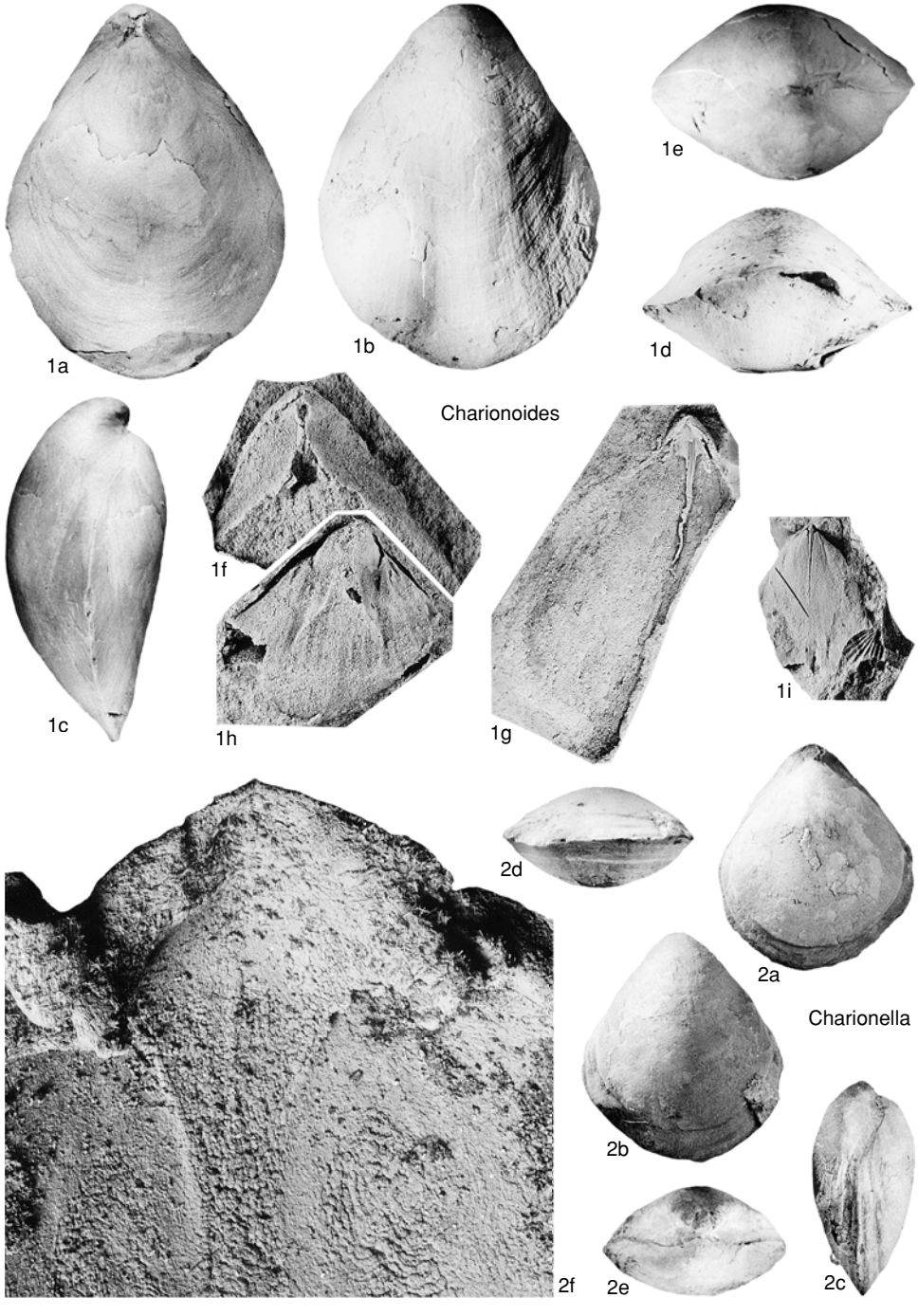


FIG. 1062. Meristellidae (p. 1559–1563).

Similar to *Charionella* but with ventral beak only slightly incurved; internally ventral valve with short dental plates, and muscle field less strongly impressed than in *Meristella;* dorsal valve septalium longer than in *Charionella,* being sessile posteriorly but elevated on short median septum anteriorly; spiralium and jugum unknown. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* eastern North America.——Fig. 1062,*1a–e.* **C. doris* (Hall), Emsian, New York, USA; lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 3071B, Hall collection, ×1.5 (Alvarez & Brime, 2000).——Fig. 1062,*1f–i. C.* sp. cf. *C. doris* (Hall), Emsian, Maine, USA; *f,* dorsal view of ventral beak, ×3; *g–h,* dorsal valve interior and ventral valve interior mold, ×2; *i,* dorsal interior mold, ×1 (Boucot, Johnson, & Staton, 1964).

Hindella Davidson, 1882, p. 130 [**Athyris umbonata* Billings, 1862, p. 144; OD] [=*Cryptothyrella* Cooper, 1942, p. 233 (type, *Whitfieldella quadrangularis* Foerste, 1906, p. 327, OD)]. Medium to large, elongate, subequally to ventribiconvex shells of variable outline commonly ranging from subrectangular to pyriform; ventral beak strongly incurved; dorsal fold and ventral sulcus absent or poorly developed, less frequently with narrow and shallow sulcus extending from umbo of ventral valve, and from about one-third posterior length of dorsal valve to anterior margin; few but strong growth lines; long, medially convex or dorsally convergent dental plates bounding deeply impressed muscle field; narrow, deep, and partially covered septalium, sessile or supported by median septum extending quite anteriorly as low ridge; lateral branches of jugum commonly originate well anteriorly, projecting backward at low angle, semicircular jugal arch projecting posteriorly as short, straight, and undivided stem; tertiary layer may be present. [*Cryptothyrella* Cooper differs only in minor changes in shell size and shape and in having longer, medially convex dental plates that bound a deeper, impressed muscle field (see Gauri & Boucot, 1970; Sheehan, 1977). The jugum of *Cryptothyrella* is more posteriorly placed, with jugal stem very long, posteroventrally directed, finally reaching a position close to crural ends. These differences are likely to reflect nothing more than specific variability and therefore the two genera are herein considered as synonoyms (see Rong, 1979; Rong & Yang, 1981; Wang Yu & others, 1984). Detailed revision of internal variability on species assigned to these two genera is needed.] *Upper Ordovician (Ashgill)–Silurian (Llandovery):* North America, Peru, Venezuela, Argentina, Sweden, Norway, Estonia, United Kingdom, Ireland, Czech Republic, southern Alps, Sardinia, Turkey, Altay-Sayan, Kazakhstan, Tuva, ?Thailand, southern and western China (Tibet), Burma.——Fig. 1063*a–v.* **H. umbonata* (Billings), Ashgill, Anticosti Island, Canada; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497418, ×1.5 (new); *f–u,* transverse serial sections 0.8, 1.1, 1.5, 1.7, 2.1, 2.9, 3.1, 3.4, 4.0, 4.4, 5.9, 6.6, 7.1, 7.4, 7.9, 8.0 mm from ventral umbo, BMNH BB94780 (new); *v,* dorsal valve interior and brachidium (Glass in Davidson, 1882).

?Imdentistella Grunt, 1991, p. 68 [**I. khabtagaica;* OD]. Similar to *Meristella* but differing in presence of axial groove in roof-shaped dorsal valve, complete absence of dental plates, and presence of incipient cardinal flanges; muscle field, spiralium, and jugum unknown. *Lower Devonian (lower Emsian):* Russia (Mongolia), eastern Gobi.——Fig. 1064,*1a–d.* **I. khabtagaica,* Mongolia; holotype, dorsal, ventral, lateral, and anterior views, PIN 3385/2055, ×1 (Grunt, 1991).

?Meristelloides Isaacson, 1977, p. 175 [**Meristella Riskowskyi* Ulrich, 1893, p. 64; OD]. Similar to *Meristella* but with stout and shorter dorsal median septum; diductor muscle scars weakly impressed on ventral valve; poorly known, hence generic status uncertain. [The name *Meristelloides* is commonly attributed to Branisa (1965) but this name was made available by Isaacson (1977). The authorship and date are his and not those of Branisa (1965) since in the latter paper the name was not accompanied by a description or definition that states in words characters that are purported to differentiate the taxon (Art. 13.1.1, ICZN, 1999).] *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Bolivia, Brazil, Peru, Argentina, South Africa.——Fig. 1064,*2a–t.* **M. riskowskyi* (Ulrich), Emsian, ?lower Eifelian, Bolivia; *a–c,* dorsal, lateral, and anterior views, USNM 209105, ×1.8; *d,* dorsal view, USNM 209104, ×1.5 (Isaacson, 1977); *e–t,* transverse serial sections 2.0, 4.0, 5.25, 7.0, 7.5, 8.25, 9.0, 9.75, 11.5, 13.0, 14.0, 16.0, 17.5, 18.5, 19.5, 20.0 mm from ventral umbo (adapted from Isaacson, 1977).

Meristina Hall, 1867b, p. 299 [**Meristella maria* Hall, 1863a, p. 212; SD Dall 1877, p. 49] [=*Whitfieldia* Davidson, 1881b, p. 156 (type, *Atrypa tumida* Dalman, 1828, p. 134, SD Davidson, 1882, p. 83; although the name *Whitfieldia* is commonly attributed to Davidson (1882, p. 107) this name was already made available by Davidson (1881b, p. 156)]. Externally and internally similar to *Meristella* but commonly with well-developed dental plates extending anteriorly as ridges, subparallel or slightly divergent, bounding a narrow, deep, and longitudinally striate muscle field; narrow and deep supported septalium, and jugal stem bifurcating into 2 short arms at its posteroventral end; tertiary layer may be present. [Fixation of type species is usually credited to Hall, 1867b by original designation. When *Meristina* was established by Hall (1867b, p. 299), however, no nominal species was explicitly designated as type species, and as there are two species, *M. maria* and *M. nitida,* included within the genus there is no type by indication (type by monotypy, Article 68.3, ICZN, 1999). According to Article 69.1.1 (ICZN,

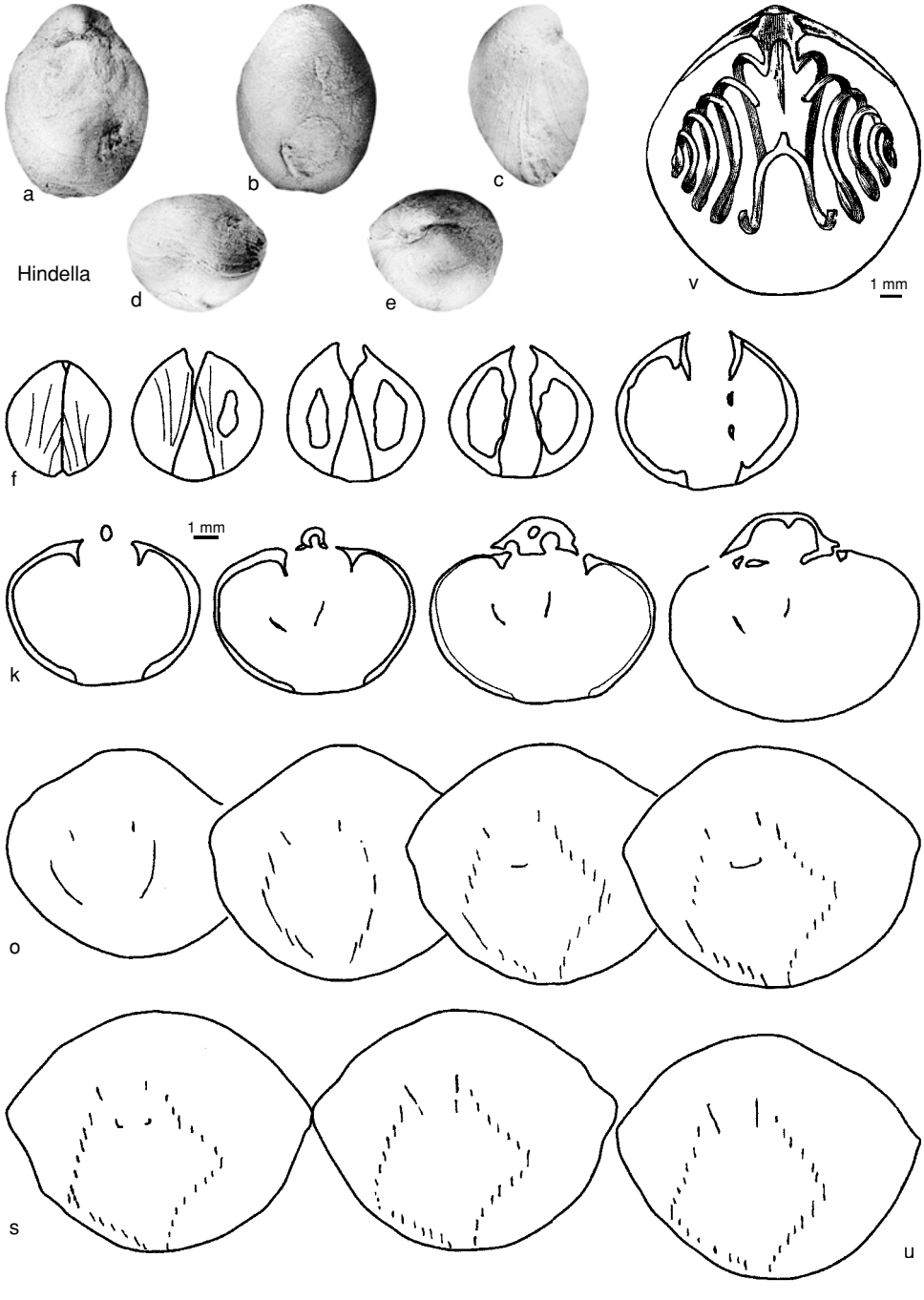


FIG. 1063. Meristellidae (p. 1563).

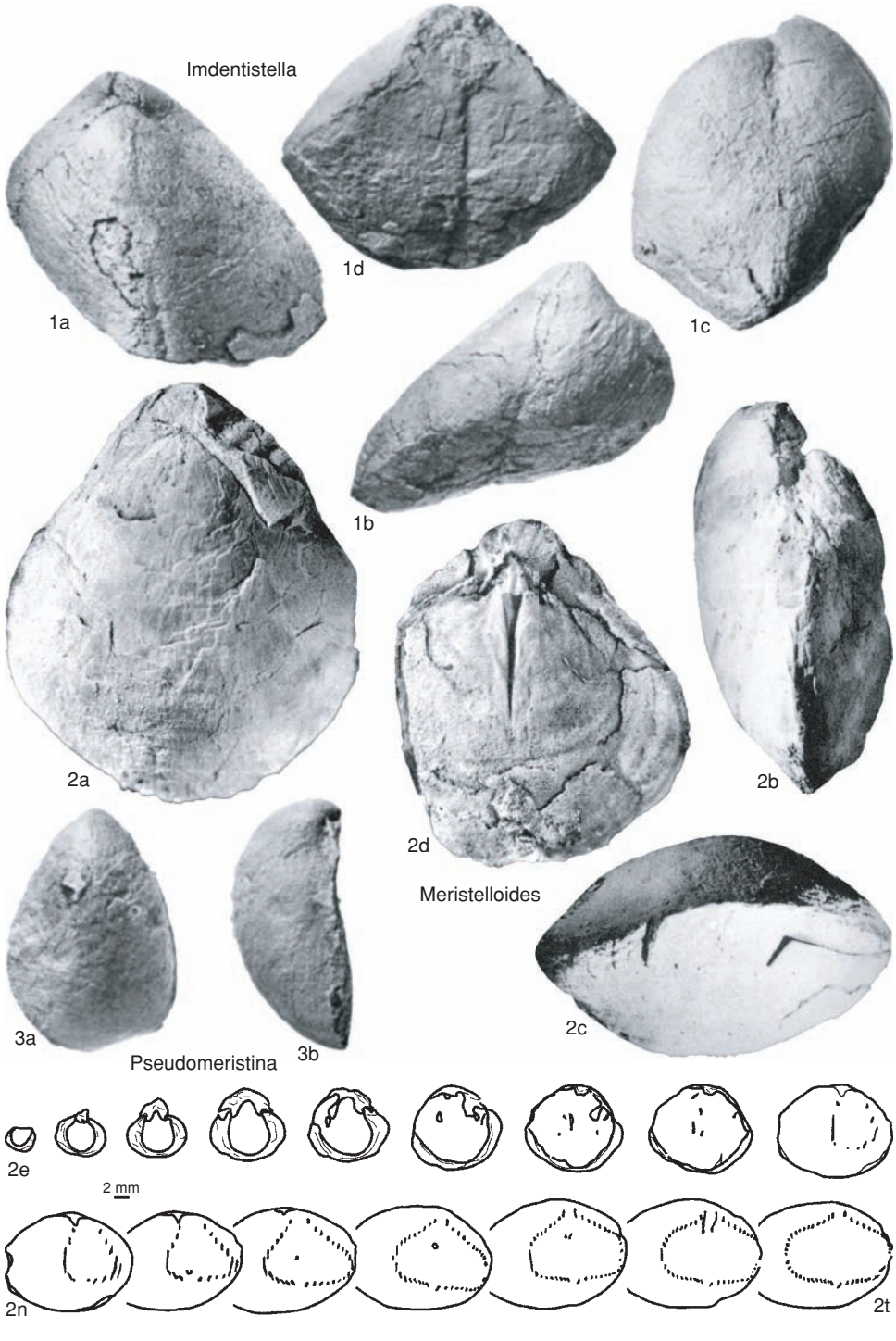


FIG. 1064. Meristellidae (p. 1563–1566).

1999), it is DALL (1877) who should be given the credit for the subsequent designation of *M. maria* as type species for *Meristina*.] *Silurian (Llandovery)–Middle Devonian (Givetian):* New Brunswick, Nova Scotia, Venezuela, Ireland, Novaya Zemlya, Siberia, *Llandovery;* North America, Podolia, Estonia, Lithuania, Bohemia, Gotland, United Kingdom, Ireland, southeastern Australia, *Wenlock;* Lithuania, northern China (Xinjiang, Heilongjiang), *Ludlow;* North America, *Lower Devonian–Middle Devonian (Givetian).*——FIG. 1061,*1a–h.* **M. maria* (HALL), Waldron, Indiana, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 36616, Hall collection, ×1.5 (Alvarez & Brime, 2000); *f–g,* interior showing brachidium, and ventral valve internal mold, ×1; *h,* dorsal interior showing septalium, ×2 (Hall & Clarke, 1895).

Pentagonia COZZENS, 1846, p. 158 [**P. peersii;* OD] [=*Goniocoelia* HALL, 1861, p. 101 (type, *Atrypa uniangulata* HALL, 1861, p. 101, =*Atrypa unisulcata* CONRAD, 1841, p. 56, OD)]. Bi- to dorsibiconvex shells, pentagonal to hexagonal outline; ventral valve with very broad sulcus bounded by angular divergent carinae, lateral slopes abrupt; dorsal valve with broad, rounded fold commonly with narrow medial groove, 2 narrow folds could develop in posterolateral region of dorsal valve; ventral muscle impression essentially as in *Meristella;* dental plates short; low dorsal median septum continuing posteriorly as faint median ridge on massive cardinal plate arising vertically from bottom of valve so as to present erect, concave anterior face, top of plate extended posteriorly as scoop-shaped concavity; jugal stem without bifurcations. *Lower Devonian (Emsian)–Middle Devonian:* North America, Colombia, Venezuela.——FIG. 1065*a–e.* **P. peersii,* Emsian, Kentucky, USA; dorsal, ventral, lateral, anterior, and posterior views, AMNH 37546, Hall collection, ×1.5 (new).——FIG. 1065*f–h. P. unisulcata* (CONRAD), Middle Devonian, New York, USA; *f,* anterior view of broken specimen showing part of spiralium and jugum, I1722, Hall collection, ×5 (new); *g,* ventral view of cardinalia, I1721, Hall collection, ×14 (new); *h,* ventral valve interior, ×1 (Hall & Clarke, 1895).

?Plancella AMSDEN, 1985, p. 11 [**P. turkiensis;* OD]. External features and ventral valve interior similar to *Whitfieldella;* wide and shallow supported septalium as in *Meristella;* spiralium and jugum unknown. [This genus requires revision.] *Lower Devonian (Pragian):* USA (Oklahoma).——FIG. 1061,*3a–l.* **P. turkiensis; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, OU 10276, ×2 (Amsden, 1985); *f–l,* transverse serial sections 0.7, 1.3, 3.2, 3.8, 4.2, 5.8, ? mm from ventral umbo (adapted from Amsden, 1985).

?Pseudomeristina GRUNT, 1991, p. 65 [**P. rozmanae;* OD]. Similar to *Meristina* but differing in shell wall and dental lamellae being composed of prismatic calcite; spiralium and jugum unknown. *Silurian (Wenlock–Ludlow):* Russia (Mongolia, Altay region), ?northeastern China.——FIG. 1064,*3a–b.* **P. rozmanae,* upper Wenlock–lower Ludlow, Mongolia; holotype, ventral and lateral views, PIN 3385/2002, ×1 (Grunt, 1991).

Subfamily WHITFIELDELLINAE Alvarez, Rong, & Boucot, 1998

[Whitfieldellinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Ventral umbo moderately curved; dental plates short and dorsally convergent; ventral muscle field weakly impressed, without longitudinal striations; septalium shallow, short, partially covered, supported by high and short median septum; jugal stem may be thick and spiny. *Upper Ordovician (Ashgill)–Silurian, Lower Devonian (?Lochkovian).*

Whitfieldella HALL & CLARKE, 1893, p. 58 [**Atrypa nitida* HALL, 1843, table 14,*5;* OD (note that the figure on p. 12 is erroneously numbered as 13 when it should be 14; see HALL figure explanations)]. Biconvex, elongate trigonal to subpentagonal; with or without faint sulcus on both valves; lateral branches of jugum originating at approximately midlength of dorsal valve, vertical or projecting backward at high angle. *Upper Ordovician (Ashgill)–Silurian, Lower Devonian (?Lochkovian):* south-central USA, Tadzhikistan, southwestern China (Guizhou), *Ashgill;* North America, Europe, Siberia, southern China, *Silurian;* North America, *?Lochkovian.*——FIG. 1066,*2a–s.* **W. nitida* (HALL), Silurian, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 31290, Hall collection, ×3; *f–h,* dorsal, ventral, and posterior views, AMNH 40799, Hall collection, ×1 (Alvarez & Brime, 2000); *i–r,* transverse serial sections 2.9, 3.1, 3.5, 4.6, 7.5, 7.6, 8.1, 8.4, 9.3, 10.5 mm from ventral umbo, GSC 98796 (adapted from Jin, Caldwell, & Norford, 1993); *s,* lateral view showing jugum (Glass, 1882).

Koigia MODZALEVSKAYA, 1985, p. 37 [**Hindella extenuata* RUBEL, 1970, p. 48; OD]. Biconvex, elongate-oval to rounded, medium shells; with or without faint sulcus on ventral valve; deltidial plates partially covering delthyrium; foramen in epithyridid position; internally similar to *Whitfieldella. Silurian (Llandovery):* Estonia, eastern Siberia.——FIG. 1067,*1a–dd.* **K. extenuata* (RUBEL), Estonia; *a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, TAGI BR2546, ×2 (Rubel, 1970; photographs courtesy of T. L. Modzalevskaya); *f,* dorsal umbo showing foramen and delthyrium partially covered by deltidial plates, TAGI BR 3859, ×6 (Modzalevskaya, 1985; photographs courtesy of T. L. Modzalevskaya); *g–cc,* transverse serial sections 0.2, 0.5, 0.7, 1.0, 1.1, 1.2,

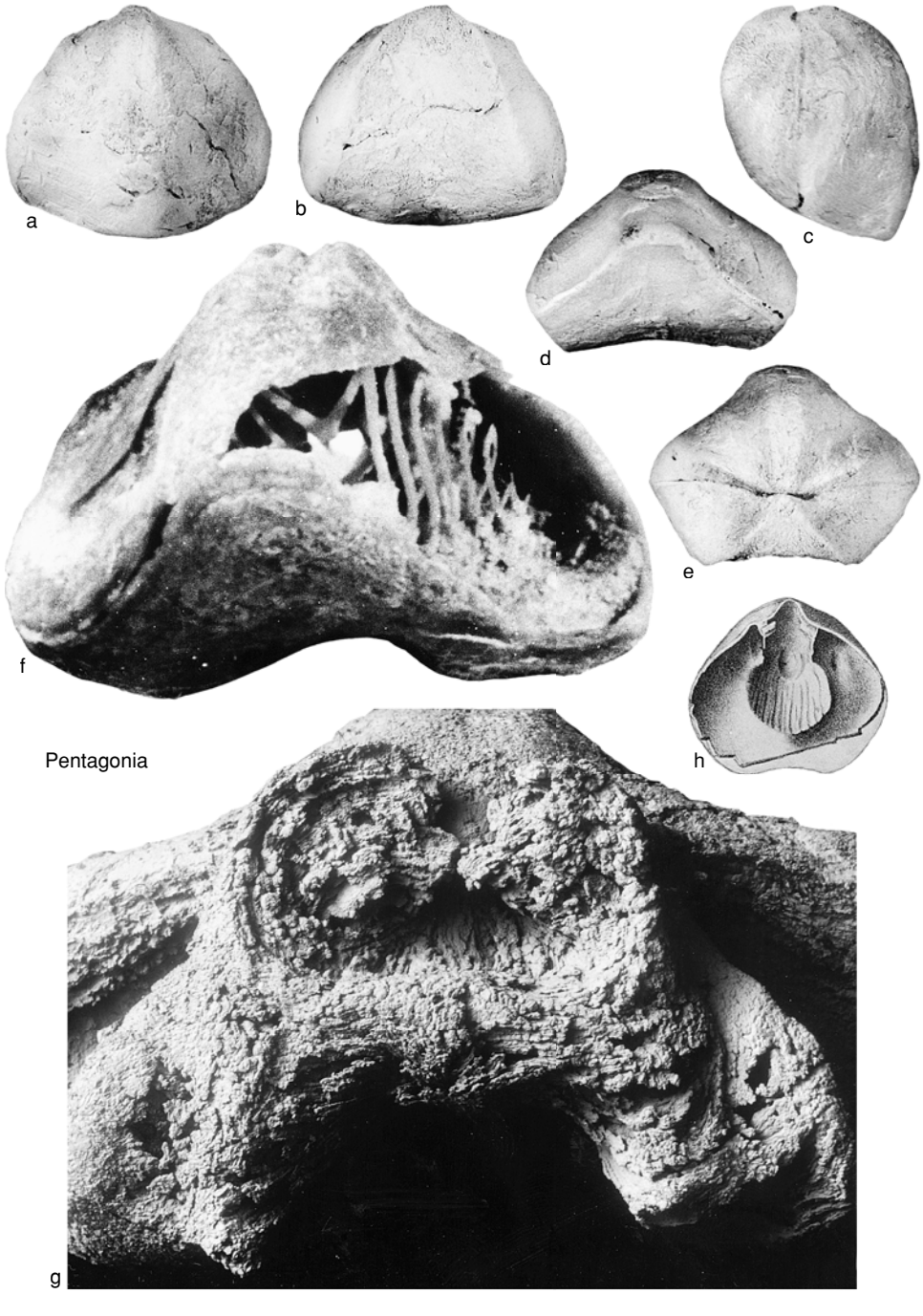


FIG. 1065. Meristellidae (p. 1566).

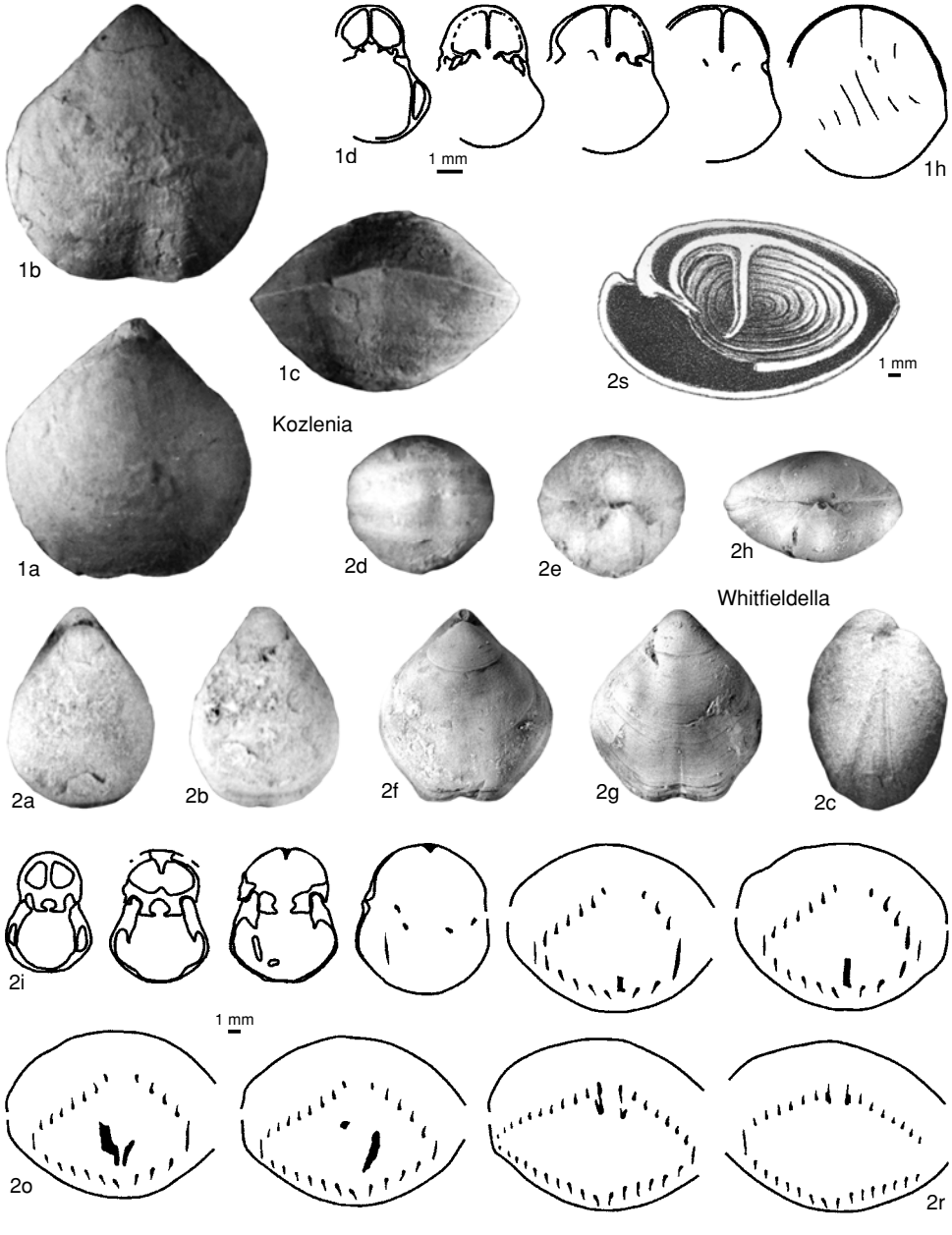


FIG. 1066. Meristellidae (p. 1566–1570).

1.4, 1.6, 1.8, 2.0, 2.2, 2.8, 3.4, 3.6, 4.0, 4.3, 4.5, 4.6, 4.8, 4.9, 5.2, 5.6, 6.9 mm from ventral umbo, distance approximate from ventral umbo to first section and to section *o,* TAGI BR 2545 (adapted from Rubel, 1970); *dd,* brachidium, approximately ×5.5 (Rubel, 1970).

Kozlenia HAVLÍČEK, 1987b, p. 241 [**K. kozlensis;* OD]. Similar to *Whitfieldella,* with short and shallow sulcus in ventral valves of mature specimens, dorsal fold absent; internally with thin and high median septum supporting septalium along entire length; jugum unknown. *Silurian (upper Llandovery–*

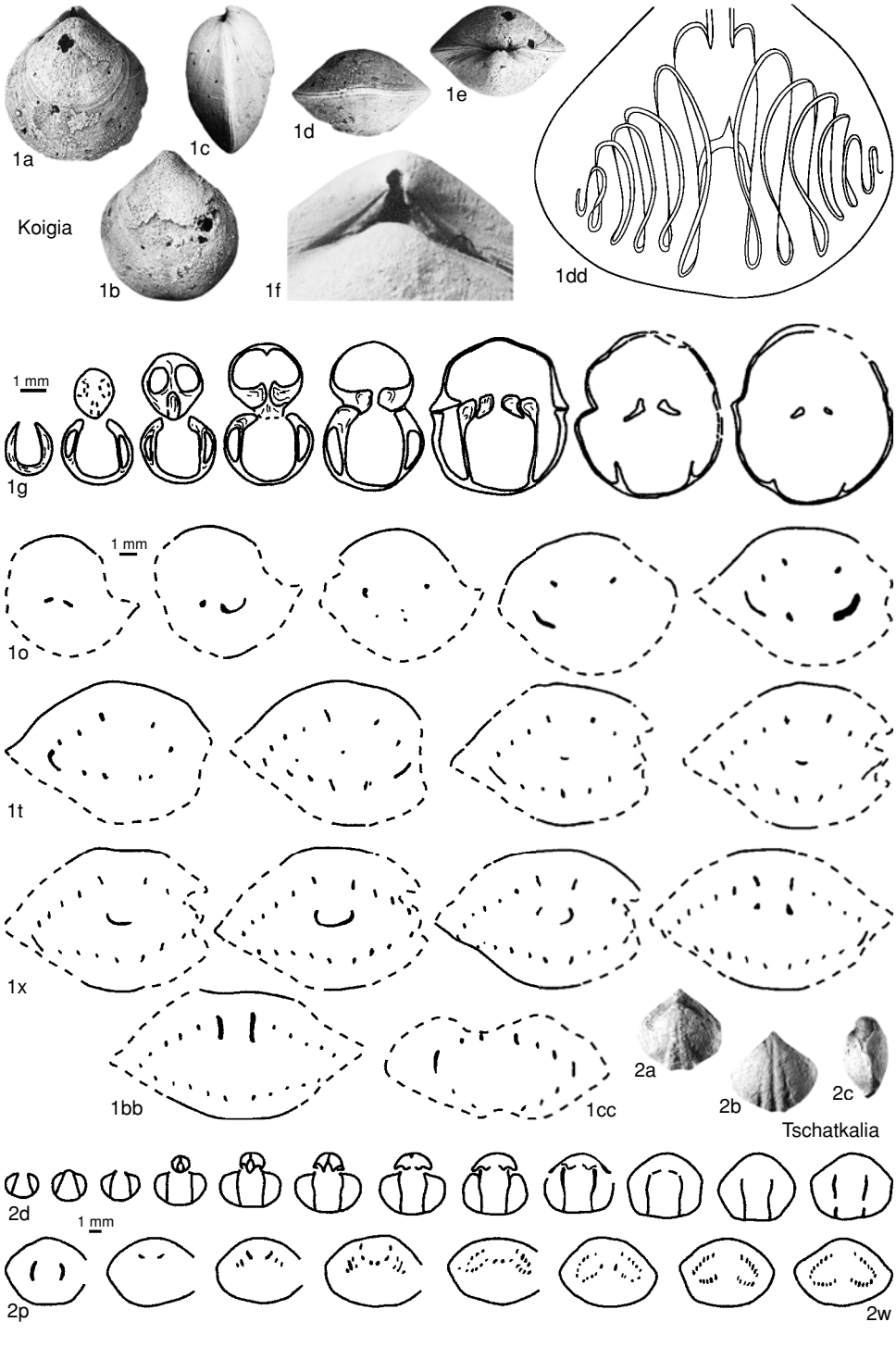


FIG. 1067. Meristellidae (p. 1566–1570).

Wenlock): Bohemia.——Fig. 1066,*1a–h. *K. kozlensis; a–c,* holotype, dorsal, ventral, and anterior views, VH 4138a, ×3.5 (Havlíček, 1987b); *d–h,* transverse serial sections 2.1, 2.2, 2.4, 2.7, 3.5 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Havlíček, 1990d).

Tschatkalia Nikiforova, 1964, p. 85 [**T. unica;* OD]. Small, ventribiconvex shells of triangular to pentagonal outline; ventral valve with narrow sulcus bounded by rounded plicae; rounded fold, extending from dorsal umbo, commonly with narrow medial groove; deltidial plates present; internally similar to *Koigia,* but with longer dental plates, often recurved in middle; jugum unknown. *Silurian (Llandovery–Wenlock):* Fergana, Kazakhstan.——Fig. 1067,*2a–w. *T. unica,* Llandovery, Fergana; *a–c,* holotype, dorsal, ventral, and lateral views, CNIGR 36/8201, ×1 (Nikiforova, 1964; photographs courtesy of T. L. Modzalevskaya); *d–w,* transverse serial sections 1.5, 2.0, 2.4, 3.2, 3.6, 3.7, 3.9, 4.0, 4.3, 4.5, 4.6, 4.7, 5.2, 5.6, 5.7, 5.8, 6.0, 6.3, 6.4, 6.7 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Nikiforova, 1964).

Family MERISTIDAE Hall & Clarke, 1895

[Meristidae Hall & Clarke, 1895, pl. 42]

Small to large size; biconvex; moderate to strong adult valve convexity; mystrochial plates and shoe-lifter possibly strengthening dental plates; spondylial structure, supported along entire length by septum, may be present; septalium shallow or deep and wide in late forms; other structures strengthening the dorsal muscle system may be present. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Subfamily MERISTINAE Hall & Clarke, 1895

[*nom. transl.* Schuchert, 1929, p. 22, *ex* Meristidae Hall & Clarke, 1895, pl. 42]

Shell small to large; dental plates possibly extending anteriorly as thickened ridges, shoe-lifter supporting dental plates, if not (as in *Amerista*), then very steeply, laterally inclined area for muscle attachment similar to that of *Merista,* mystrochial plates may be present; septalium shallow, narrow, supported by high and thin median septum; dorsal shoe-lifter may be present; acute jugal arch projecting as long stem, moderately inclined posteriorly, bifurcating into accessory jugal lamellae that reunite with lateral branches of jugum. *Upper Ordovician (Caradoc)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian).*

Merista Suess, 1851, p. 150 [**Terebratula herculea* Barrande, 1847, p. 26; SD Suess in Davidson, 1856, p. 85]. Biconvex, elongate or transverse shells of rounded subpentagonal outline, with dorsal fold and ventral sulcus commonly developed anteriorly; dental plates short or may be produced anteriorly as thickened ridges that unite with outer part of medially placed shoe-lifter process along its lateral edges, shoe-lifter process with form of posteriorly plunging roof-shaped plate; mystrochial plates present; small septalium supported by high and thin median septum; accessory jugal lamellae reunite with lateral branches of jugum. [No nominal species were assigned to *Merista* when the genus was erected by Suess (1851). No species was associated with *Merista* until 1854 when Suess (1854, p. 62–63) assigned 3 species to the genus: *T. herculea, T. passer,* and *T. tumida;* no type species was designated. The first indication of a type species is that of Suess (in Davidson, 1856, p. 85), who designated *T. herculea* as type species of *Merista.*] *Silurian (Llandovery)–Middle Devonian:* southern Siberia, Altay, Canada, *Llandovery;* Canada, *Wenlock;* Venezuela, Mexico, south-central USA (Oklahoma, Tennessee), *Ludlow;* northeastern USA (Maine), *Ludlow or Přídolí;* Bohemia, Poland, Kazahkstan, Altay, Inner Mongolia, *Lower Devonian;* Germany, ?Burma, *Middle Devonian.*——Fig. 1068,*1a–k. *M. herculea* (Barrande), Lower Devonian, Bohemia, Czech Republic; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, USNM 497417, ×1.5 (new); *f–i,* transverse serial sections 1.4, 2.2, 2.9, 3.6 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr70 (adapted from Siehl, 1962); *j–k,* ventral and lateral views of brachidium (Glass, 1882).

Amerista Boucot & Blodgett in Boucot, Blodgett, & Stewart, 1997, p. 287 [**A. carillobravoi;* OD]. Similar to *Merista* but with very steeply, laterally inclined area for muscle attachment in ventral valve instead of shoe-lifter. [The diagnosis is presently based on ventral valves because conjoined valves were not found; dorsal valves are only questionably assigned to *Amerista.*] *Silurian (upper Wenlock–Ludlow):* northeastern Mexico (Sierra Madre Oriental).——Fig. 1068,*2a–b. *A. carillobravoi;* holotype, impression and rubber replica of ventral valve interior, IGM 6938a, ×2 (Boucot, Blodgett, & Stewart, 1977; photographs courtesy of R. B. Blodgett & A. J. Boucot).

Aulidospira Williams, 1962, p. 252 [**A. trippi;* OD]. Ventribiconvex, small shell, with broad, shallow sulcus in dorsal valve and wide median ventral fold separated from pair of inconspicuous folds in

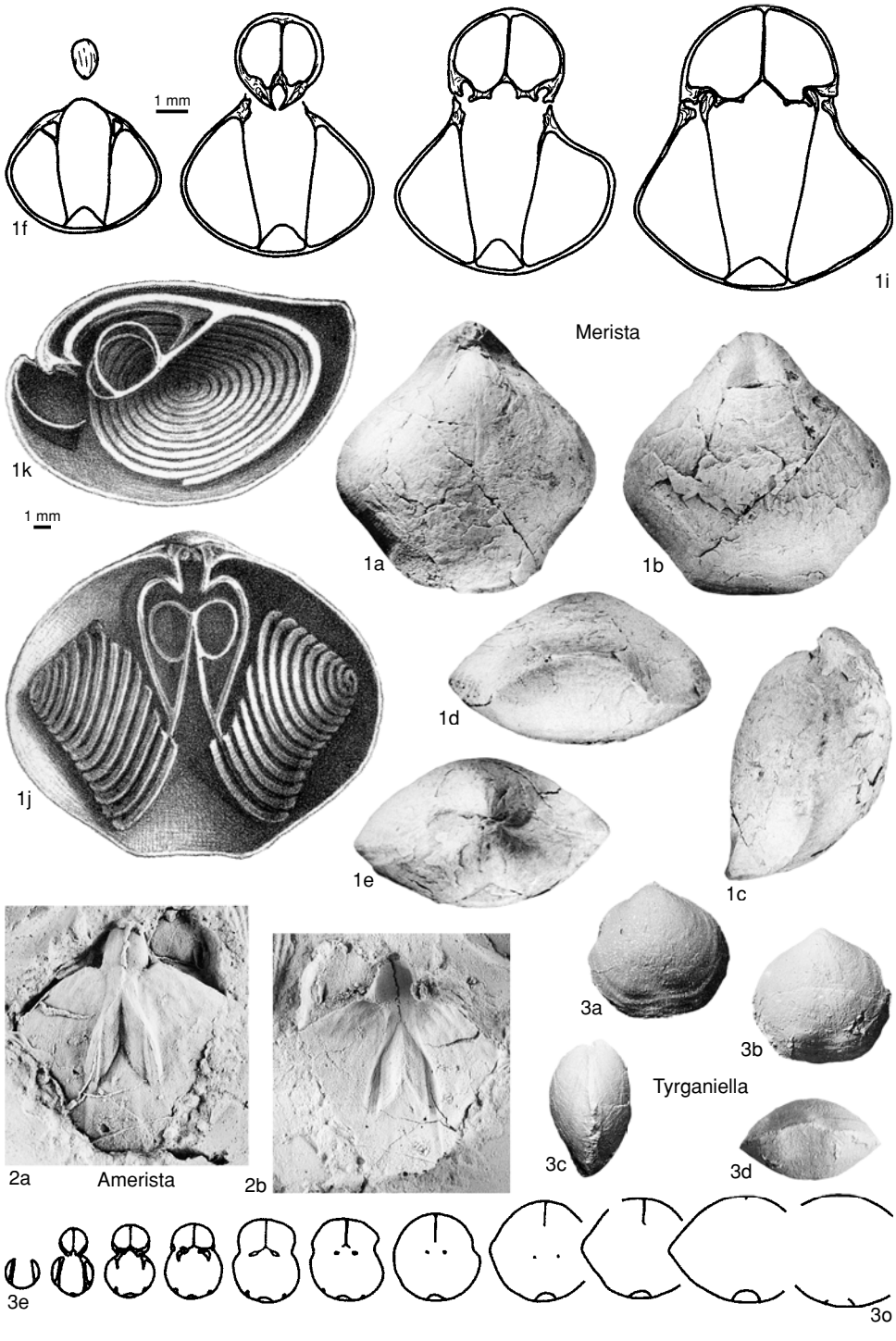


FIG. 1068. Meristidae (p. 1570–1572).

flattened posterolateral areas by pair of widely divergent and shallow, rounded sulci; dental plates attached to ventral side of small, nearly flat, shoe-lifter process; cardinalia poorly known; myophragm present, median septum absent; rudimentary spiralia coiled in plane parallel to median plane, jugal structure unknown. [The genus is also listed by P. COPPER, herein, p. 1472, as a junior synonym of *Cyclospira* HALL in HALL & CLARKE, 1893. This ambiguity should be resolved when the brachiojugal structure of *Aulidospira* is known.] *Upper Ordovician (Caradoc, ?Ashgill):* Great Britain, ?Bohemia, ?Quebec.——FIG. 1069,*1a–f. *A. trippi,* Great Britain; *a,* holotype, lateral view of ventral internal mold, BMNH BB 27653, ×6; *b,* rubber replica of dorsal exterior, BMNH BB 27656, ×4.5; *c–d,* ventral and lateral views of complete shell, BMNH BB 27655; *e,* dorsal view of internal mold, BMNH BB 27654; *f,* ventral view of internal mold, BMNH BB 27657, ×6 (Williams, 1962).

Camarium HALL, 1859, p. 42 [**C. typum;* OD]. Similar to *Merista* but without mystrochial plates. [The name *Camarium* was published by HALL (1859a) without designation of a type species, but as one of the originally included new nominal species (Art. 67.2.1, ICZN, 1999) was given the name *C. typum;* that species must be considered as the type species by original designation (Art. 68.2.2, ICZN, 1999; by indication according to the ICZN, 3rd ed., 1985). HALL (1860a, 1862) then listed this genus as being identical with *Merista* (subjective synonym; see also BOUCOT, JOHNSON, & STATON, 1965, p. 658). Later, AMSDEN (1968) validated *Camarium* HALL after discovering that it lacks the mystrochial plates present in *Merista* SUESS.] *Lower Devonian (Lochkovian)–Upper Carboniferous (upper Bashkirian, ?lower Moscovian):* USA (Maryland, New York), Germany, Bohemia, Gorno-Altay, *Lower Devonian–Middle Devonian;* Australia (New South Wales), USA (Texas), *Tournaisian;* Canadian Arctic Archipelago (Ellesmere), *upper Bashkirian or lower Moscovian.*——FIG. 1069,*2a–e. *C. typum,* Lochkovian, USA (Maryland); *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 34713, Hall collection, ×1.5 (Alvarez & Brime, 2000). [See also Fig. 1006.1, p. 1481, in introduction].

Dicamara HALL & CLARKE, 1893, p. 73 [**Atrypa plebeia* SOWERBY, 1840a, pl. 56,*12–13;* SD HALL & CLARKE, 1894, p. 966; =*Terebratula scalprum* ROEMER, 1844, p. 68]. Similar to *Merista* but without mystrochial plates and having shoe-lifter process, bisected by median septum in dorsal valve. [Fixation of type species is usually wrongly credited to HALL & CLARKE by original designation. The first unequivocal designation of the type species seems to be that of HALL & CLARKE, 1894, p. 966.] *Lower Devonian–Middle Devonian:* Poland, Czech Republic (Moravia), Germany, France, northwestern Spain, Salair, Kazakhstan, India, Algeria.——FIG. 1069,*4a–l. *D. plebeia* (SOWERBY), Middle Devonian, Eifel, Germany; *a,* dorsal view, USNM 497413, ×1.5 (Alvarez, Rong, & Boucot, 1998); *b–e,* ventral, lateral, anterior, and posterior views, USNM 497413, ×1.5 (new); *f–l,* transverse serial sections 0.6, 1.1, 1.4, 1.8, 2.3, 2.5, 3.2 mm from ventral umbo, distance from ventral umbo to first section approximate, GIB Nr71 (adapted from Siehl, 1962).

Dicamaropsis AMSDEN, 1968, p. 85 [**Merista parva* THOMAS, 1926, p. 400; OD]. Similar to *Dicamara* but having mystrochial plates and rather flat septalium with knob in center; spiralium and jugum unknown. *Silurian (upper Llandovery–Wenlock):* southwestern China (Sichuan), *upper Llandovery (upper Telychian);* southern and central USA, *Wenlock.*——FIG. 1069,*3a–j. *D. parva* (THOMAS), Wenlock, Arkansas, USA; *a–c,* lectotype, dorsal, ventral, and posterior views, YPM 25745, ×3 (Amsden, 1968); *d–j,* transverse serial sections 0.5, 0.6, 0.8, 1.0, 1.2, 1.5, 2.1 mm from ventral umbo (adapted from Amsden, 1968).

Tyrganiella KUL'KOV in ALEKSEEVA & others, 1970, p. 167 [**T. repentina;* OD] [=?*Paramerista* SU, 1976, p. 206 (type, *P. brevisepta,* OD)]. Externally similar to *Merista,* but differing internally in having more rounded shoe-lifter process not attached to very short dental plates; spiralium and jugum unknown. [The name of the type species of ?*Paramerista* was spelled as *brevisepta* and *breviseptata* in the work in which it was established; following Articles 24.2.2 and 32.2.1 (ICZN, 1999), the name of *brevisepta* is chosen in this revision. The inclusion of ?*Paramerista* from the Lochkovian and Pragian of Inner Mongolia, northern China, may extend the range from the Lochkovian; but interiors are poorly known and assignment uncertain.] *Lower Devonian (Lochkovian, ?Pragian):* Russia (western Siberia, northeastern Salair), northern China.——FIG. 1068,*3a–o. *T. repentina,* northeastern Salair; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, IGiG 326-104, ×2 (Alekseeva & others, 1970; photographs courtesy of T. L. Modzalevskaya); *e–o,* transverse serial sections 0.5, 0.7, 0.8, 1.0, 1.2, 1.3, 1.4, 1.6, 1.9, 2.1, 2.3 mm from ventral umbo, IGiG 326-106 (adapted from Alekseeva & others, 1970).

Subfamily CAMAROPHORELLINAE Schuchert, 1929

[Camarophorellinae SCHUCHERT, 1929, p. 22]

Medium-sized meristids with spondylium; mystrochial plates may be present; septalium deeply concave, supported by long, high median septum; dorsal shoe-lifter may be present; jugum posteriorly situated, consisting of complex, inverted, troughlike structure with small saddle, resting on

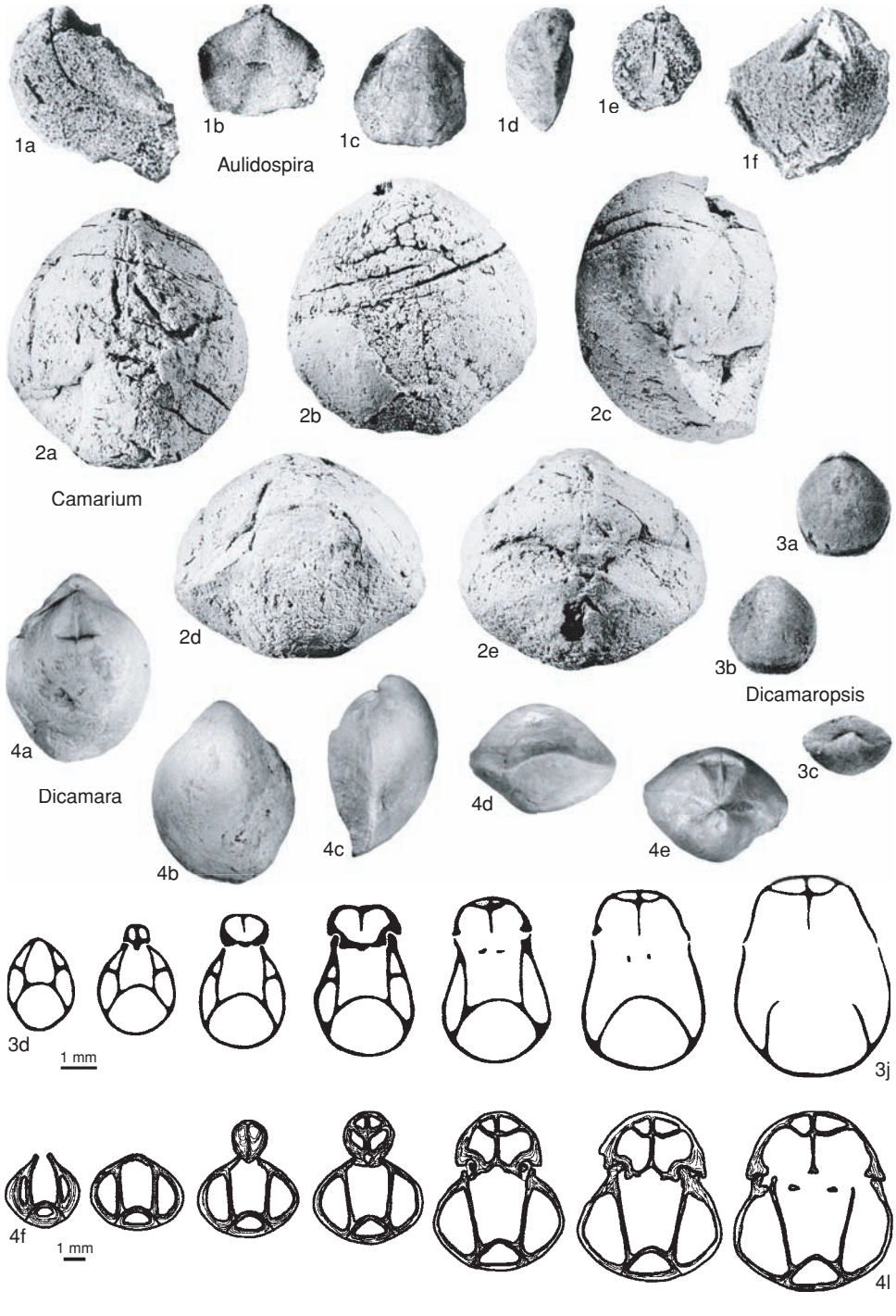


FIG. 1069. Meristidae (p. 1570–1572).

median septum, projecting backward as complex stem with lateral expansions that bifurcate into 2 spiny accessory jugal lamellae recurving dorsally, then anteriorly rejoining lateral branches of jugum near base. *Silurian (upper Llandovery)–Lower Carboniferous (Tournaisian).*

Camarophorella Hall & Clarke, 1893, p. 215 [**Pentamerus lenticularis* White & Whitfield, 1862, p. 295; OD]. Transversely subovate, subcircular or elongate biconvex shells with dorsal fold and ventral sulcus poorly developed or absent; fine growth lines may be crossed by irregular, fine radial lines; well-developed dental plates, laterally buttressed by mystrochial plates, converging to form spondylium duplex rising slightly on long, low median septum; dorsal shoe-lifter present; inner shell surfaces of both valves finely and densely papillose. *Upper Devonian (Famennian)–Lower Carboniferous (Tournaisian):* North America.——Fig. 1070*a–b.* **C. lenticularis* (White & Whitfield), middle Tournaisian, Iowa, USA; *a,* view of internal cast of ventral valve, ×3; *b,* view of internal cast of dorsal valve, UM1356a–b, ×3 (new; photographs courtesy of J. L. Carter).——Fig. 1070*c–f.* *C. mutabilis* Hyde, lower upper Tournaisian, Ohio, USA; *c,* posterior view of internal cast, ×2 (Carter, 1991); *d,* detail of external ornamentation and papillose inner surface, CMNH 69571a–b, ×10 (new; photographs courtesy of J. L. Carter); *e–f,* ventral and lateral views of jugum (Hyde, 1908).——Fig. 1070*g–w.* *C. buckleyi* (Rowley), upper Famennian, Missouri, USA; transverse serial sections 0.6, 0.8, 1.0, 1.2, 1.4, 1.6, 1.8, 2.2, 2.6, 3.0, 3.6, 3.8, 4.0, 5.0, 5.4, 6.0, 6.6 mm from ventral umbo, CMNH 34950 (adapted from Carter, 1991; courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA).

Camarospira Hall & Clarke, 1893, p. 82 [**Camarophoria eucharis* Hall, 1867b, p. 368; OD]. Externally similar to *Merista;* internally similar to *Camarophorella* but without mystrochial plates and dorsal shoe-lifter process; jugum unknown. *Middle Devonian:* North America, ?China.——Fig. 1071,*1a–e.* **C. eucharis* (Hall), Givetian, Ontario, Canada; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, I1174, Hall collection, ×1.5 (Alvarez & Brime, 2000).

?Liocoelia Schuchert & Cooper, 1931, p. 248 [**Pentamerus proximus* Barrande, 1879b, p. 96; OD]. Similar to *Camarospira* but with mystrochial plates and much higher septum supporting spondylium; dorsal interior and spiralium poorly known; jugum unknown. [This genus requires revision.] *Silurian (upper Llandovery–Ludlow):* Bohemia.——Fig. 1071,*2a–e.* **L. proxima* (Barrande), upper Llandovery–Wenlock; *a–b,* lectotype, dorsal and ventral views, L24919 Barrande collection, ×1.4 (Havlíček, 1990d); *c–e,* transverse serial sections 1.7, 2.8, 3.0 mm from ventral umbo, distance from ventral umbo to first section approximate (adapted from Havlíček, 1990d).

Subfamily ROWLEYELLINAE Alvarez & Brunton, 1995

[Rowleyellinae Alvarez & Brunton, 1995, p. 606]

Small-sized meristids with spondylium, supported by median septum, and mystrochial plates; dorsal valve with shallow septalium, short shoe-lifter, and long cruralium supported by long, high median septum; jugum unknown. *Lower Carboniferous (upper Tournaisian).*

Rowleyella Weller, 1911, p. 447 [**Terebratula fabulites* Rowley, 1900, p. 265; OD]. Externally and internally similar to *Camarophorella* but also with cruralium. [The genus *Rowleyella* Weller, 1911 was placed in subjective synonymy with *Camarospira* Hall & Clarke, 1893, by Boucot, Johnson, & Staton, 1965, p. 658. Later, Carter (1991) validated *Rowleyella* Weller, 1911 after noting internal dorsal shoe-lifter, similar to the one present in *Camarophorella* Hall & Clarke, 1893 (see also Alvarez & Brunton, 1995 for discussion).] *Lower Carboniferous (upper Tournaisian):* USA (eastern Missouri and eastern Oklahoma).——Fig. 1072*a–m.* **R. fabulites* (Rowley), Missouri; *a–b,* lectotype, dorsal and ventral views, RX 165A, Rowley Collection, ×5; *c,* posterior view of silicified natural internal mold showing mystrochial plates and very short dorsal shoe-lifter process, CMNH 34945, ×8 (Carter, 1991; photographs courtesy of J. L. Carter); *d–m,* transverse serial sections 0.2, 0.45, 0.6, 0.65, 0.75, 0.9, 1.0, 1.3, 1.8, 2.0 mm from ventral umbo, CMNH 34949 (adapted from Carter, 1991; courtesy of Carnegie Museum of Natural History, Pittsburgh, PA, USA).

Family TRIATHYRIDIDAE Alvarez, Rong, & Boucot, 1998

[Triathyrididae Alvarez, Rong, & Boucot, 1998, p. 836]

Medium to very large meristelloids; moderately rostrate; subequally biconvex; moderate to strong adult valve convexity; ornament consisting of delayed costation progressively developed medially or fine lines folded in chevronlike pattern that follows outline of shell, growth lines weak or absent, not developed into frills; dental plates commonly short; ventral muscle field weakly impressed; septalium long, uncovered, deep and wide, supported by long, bladelike to robust, commonly high median septum; jugum thick,

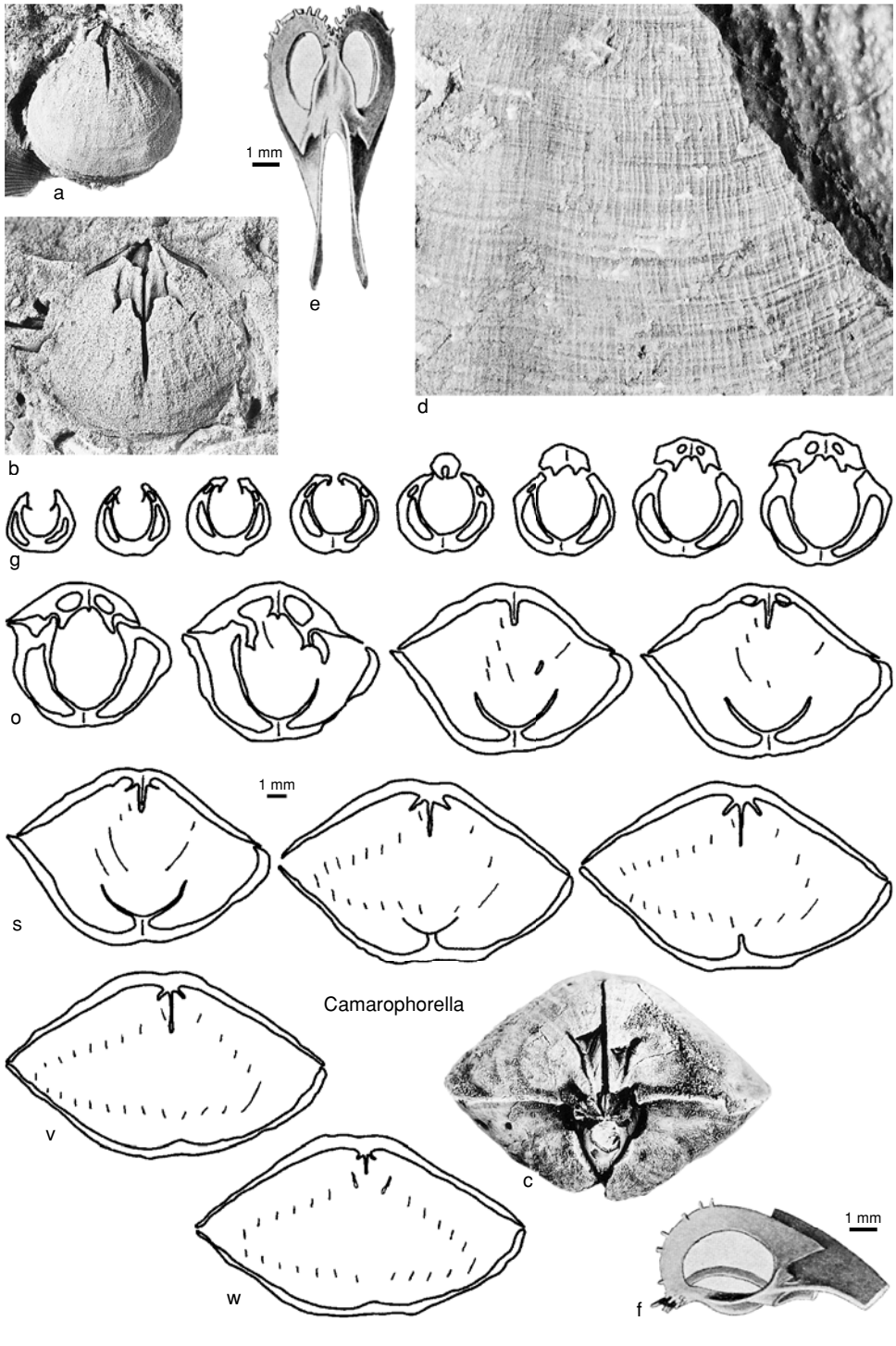


FIG. 1070. Meristidae (p. 1574).

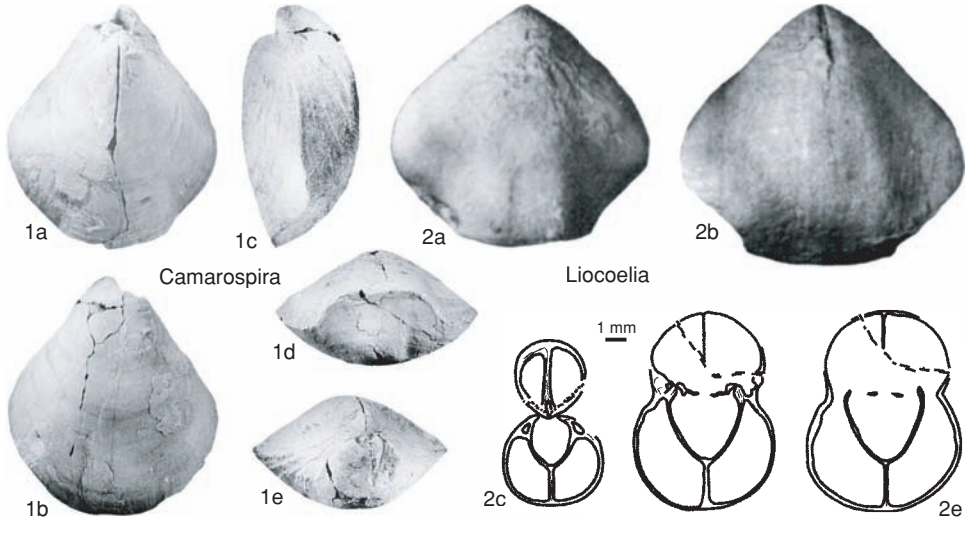


FIG. 1071. Meristidae (p. 1574).

accessory jugal lamellae reuniting with stem like that of some meristellins. *Lower Devonian (Pragian–upper Emsian).*

Subfamily TRIATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Triathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

External ornament of delayed costation progressively developed medially. *Lower Devonian (upper Emsian).*

Triathyris BOUCOT, JOHNSON, & STATON, 1965, p. 663 [**Terebratula mucronata* DE VERNEUIL, 1850, p. 171; OD]. Medium to large; equidimensional to elongate; commonly of rhomboidal outline; ventribiconvex with moderate adult valve convexity, compressed anterolaterally; clearly astrophic, short hinge line; ventral cardinal area reduced apsacline to orthocline; foramen in epithyridid position, delthyrium partially covered; growth lines weak and closely spaced; median plication on each valve raised to form anterior projection; anterior commissure almost straight; dental plates short, thin, medially concave; dorsal median septum very high. [Authorship of this genus is usually credited to COMTE (1938, p. 45); however, he did not designate a type for the genus. The first unequivocal designation of the type species seems to be that of BOUCOT, JOHNSON, & STATON, 1965 and thus they validated the name in their publication.] *Lower Devonian (upper Emsian):* Spain, ?France, ?Morocco.——FIG. 1073*a–v.* **T. mucronata* (DE VERNEUIL), Colle, León, Spain; *a–e,* lectotype, dorsal, ventral, lateral,

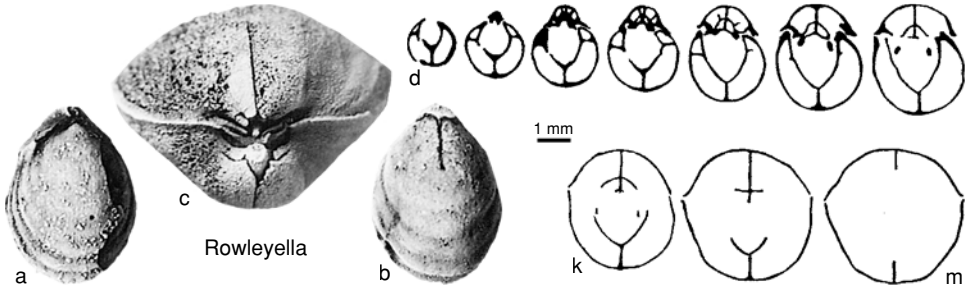


FIG. 1072. Meristidae (p. 1574).

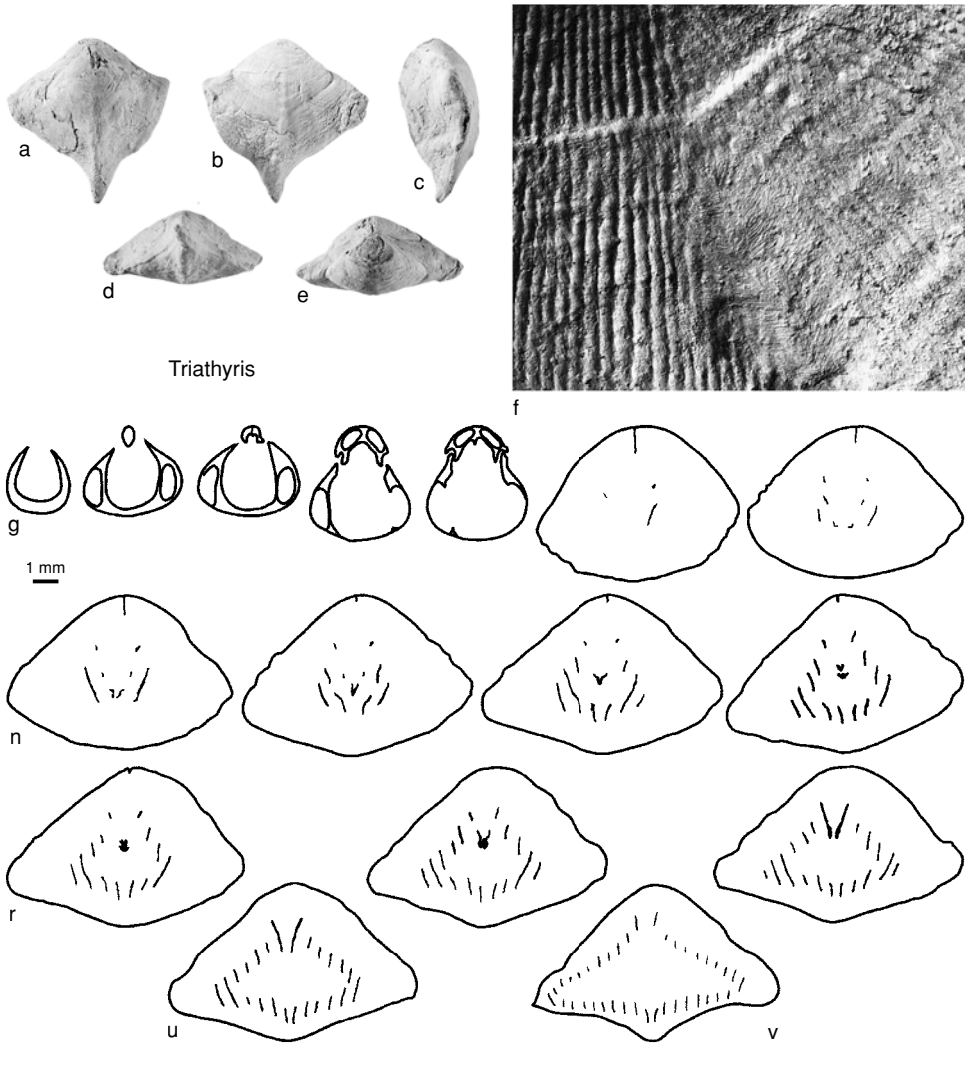


FIG. 1073. Triathyrididae (p. 1576–1577).

anterior, and posterior views, D868, de Verneuil collection, ×1 (new; photographs courtesy of N. Podevigne); *f,* external ornament on ventral valve, DPO F24240, ×13 (new); *g–v,* transverse serial sections 0.2, 0.9, 1.4, 2.4, 2.55, 6.5, 7.0, 7.2, 7.45, 7.8, 8.0, 8.2, 8.3, 8.6, 8.8, 9.8 mm from ventral umbo, DPO F24235 (Alvarez, Rong, & Boucot, 1998).

Subfamily SEPTATHYRIDINAE Alvarez, Rong, & Boucot, 1998

[Septathyridinae ALVAREZ, RONG, & BOUCOT, 1998, p. 836]

Ornament of fine lines folded in chevron-like pattern with angles directed in postero-anterior direction. *Lower Devonian (Pragian–Emsian).*

Septathyris BOUCOT, JOHNSON, & STATON, 1964, p. 819 [**Athyris aliena* DREVERMANN, 1904, p. 258; OD]. Resembling *Anathyris* in external configuration but without lamellose growth lines; foramen in meso- to permesothyridid position, delthyrium completely covered by deltidial plates; dental plates thick, medially concave, not extending as ridges along muscle scars; dorsal median septum moderately high. *Lower Devonian (Pragian–Emsian):* Germany, Spain, northern Africa.——FIG. 1074*a–c.* **S. aliena* (DREVERMANN), Pragian, Germany; *a,* mold of exterior of dorsal valve, ×3; *b,* dorsal interior mold, ×1; *c,* rubber impression of dorsal interior

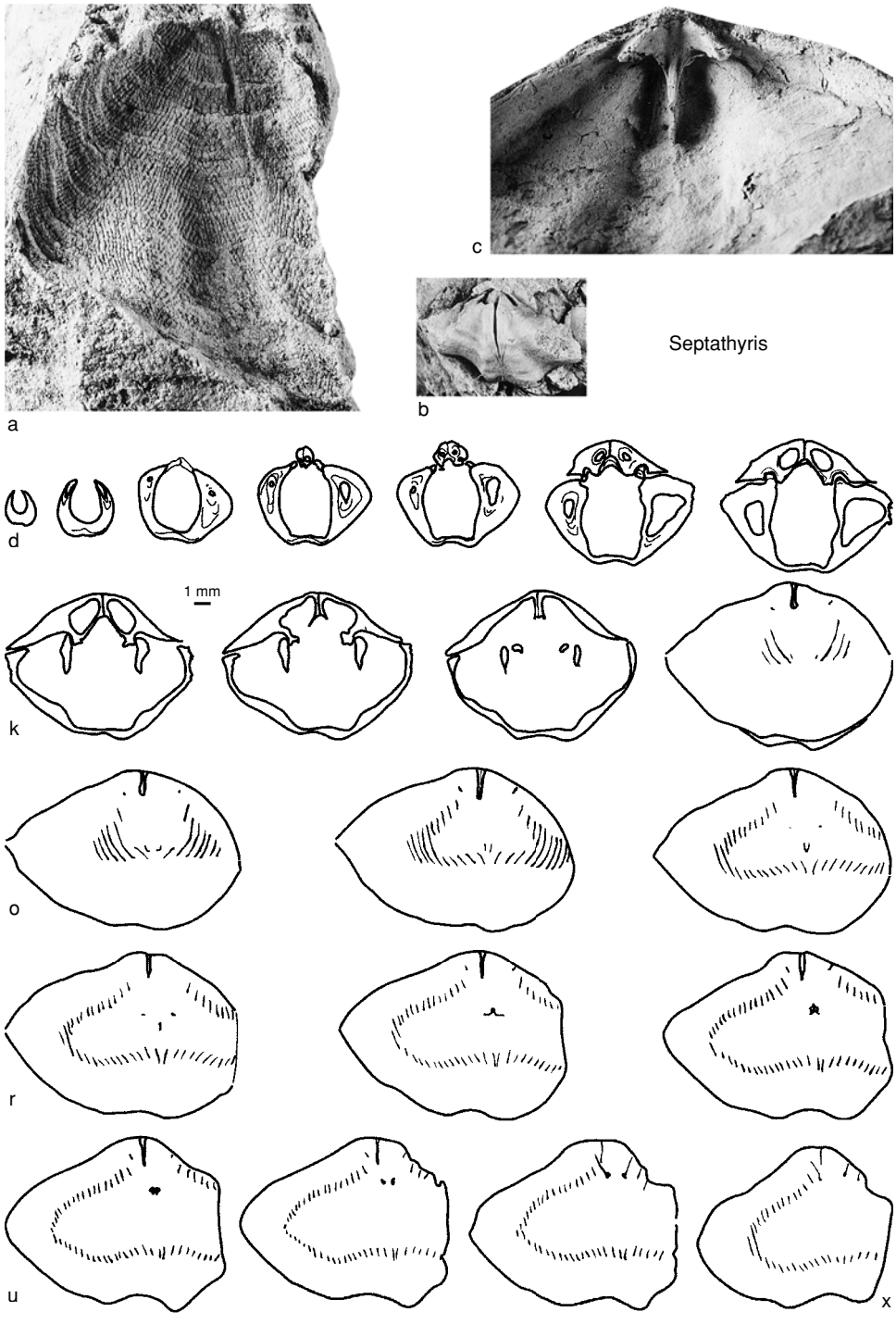


FIG. 1074. Triathyrididae (p. 1577–1579).

mold, ×2 (Boucot, Johnson, & Staton, 1964; photographs courtesy of the late J. G. Johnson).——Fig. 1074*d–x*. *S. cabrugnanensis* Alvarez, Rong, & Boucot, Emsian, Asturias, Spain; transverse serial sections 0.2, 1.4, 2.9, 3.7, 4.1, 5.2, 6.2, 7.4, 7.6, 7.9, 11.4, 12.1, 13.1, 14.0, 14.5, 15.4, 16.4, 17.1, 18.0, 19.3, 20.4 mm from ventral umbo, DPO F24236 (Alvarez, Rong, & Boucot, 1998).

Superfamily NUCLEOSPIROIDEA Davidson, 1881

[*nom. correct.* Harper, 1993, p. 448, *pro* Nucleospiracea Grunt, 1984, p. 70, *nom. transl. ex* Nucleospiridae Davidson, 1881a, p. 4; *emend.,* Alvarez, Rong, & Boucot, 1998, p. 844]

Smooth athyrididines with irregularly and commonly anteriorly concentrated lamellose growth lines and concentrically arranged fine, solid spines covering entire shell and projecting radially at different angles from valve surface; hinge line from astrophic (very short in Permian species) to almost strophic, foramen small (e.g., Permian species), commonly absent; delthyrium commonly completely covered apically by concave plate; dental plates absent but delthyrial margins commonly thickened; low, long median ridge present in both valves, less developed in ventral valve of Permian species; cardinalia without inner hinge plates, strongly developed cardinal flange extending posteroventrally into ventral umbo; simple, acute jugum posteriorly situated, without jugal saddle but having long stem, accessory jugal lamellae absent; without tertiary layer. *Silurian (Llandovery)–Lower Permian (Sakmarian).*

Family NUCLEOSPIRIDAE Davidson, 1881

[Nucleospiridae Davidson, 1881a, p. 4]

Characters as for superfamily. *Silurian (Llandovery)–Lower Permian (Sakmarian).*

Nucleospira Hall in Davidson, 1858, p. 412 [**Spirifer ventricosus* Hall, 1857a, p. 57; M]. Small, moderately to strongly biconvex, subcircular to transversely broadly elliptical shells; ventral valve commonly with shallow median sulcus forming weakly uniplicate anterior commissure, or both valves shallowly sulcate, producing slight emargination of anterior outline; ventral cardinal area, apsacline, concave, nearly equilaterally triangular, commonly obscured by small incurved ventral beak; ventral diductor scars flabellate, feebly impressed, enclosing elongate adductor scars, restricted to umbonal cavity. [Authorship is usually credited to Hall (1859a); however the first to publish the name was Davidson (1858), who included *Nucleospira* Hall with an existing species, *N. ventricosa* Hall. This is adequate to make the generic name *Nucleospira* available with *N. ventricosa* as type species by monotypy; therefore, under Article 50.1 of the *Code* (ICZN, 1999), authorship of *Nucleospira* is Hall in Davidson, 1858.] *Silurian (Llandovery)–Lower Permian (Sakmarian):* cosmopolitan.——Fig. 1075*a–f*. **N. ventricosa* (Hall), Lochkovian, Lower Helderberg Group, New York, USA; *a–e,* lectotype, dorsal, ventral, lateral, anterior, and posterior views, AMNH 33416, Hall collection, ×2.5 (Alvarez & Brime, 2000); *f,* lateral view of jugum, approximately ×7 (Hall & Clarke, 1893).——Fig. 1075*g*. *N. cunctata* Cooper & Grant, Sakmarian, western Texas, USA; anterior oblique view of shell interior showing jugum and spires, USNM 154393g, ×8 (Cooper & Grant, 1976a; photograph courtesy of the late G. A. Cooper and the late R. E. Grant). [See also Fig. 1004.2, p. 1479, and Fig. 1008.3, p. 1485, in introduction.]

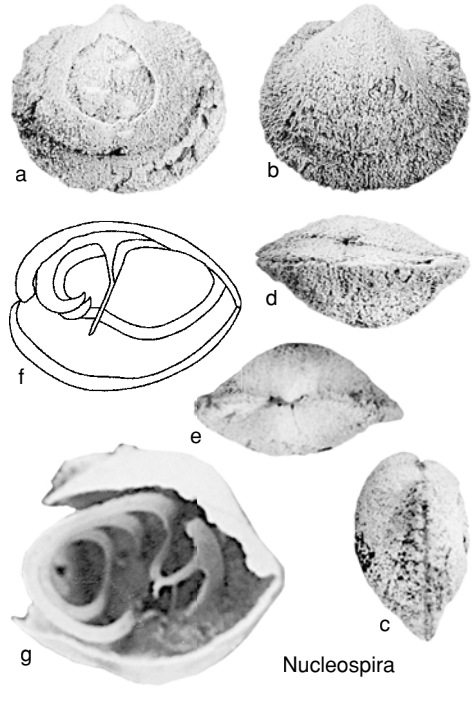


Fig. 1075. Nucleospiridae (p. 1579).

Superfamily RETZIELLOIDEA Rzhonsnitskaya, 1974

[*nom. correct.* Alvarez, Rong, & Boucot, 1998, p. 845, *pro* Retziellioidea Modzalevskaya, 1996, p. 179, *nom. transl. ex* Retziellinae Rzhonsnitskaya, 1974, p. 54]

Plicate or costate rhynchonelliform athyrididines of small to medium size; short and astrophic hinge line; bi- to ventribiconvex shells with moderate convexity in adult valves; fold and sulcus variably developed (sulcus may develop in both valves) commonly with ribs less developed than those on flanks, concentric growth lamellae may be present anteriorly; ventral cardinal area (palintrope) moderately developed; pedicle opening in meso- to permesothyridid position, delthyrium commonly open (completely covered by deltidial plates in *Gissarina*); pedicle support absent; short, dorsally convergent dental plates; outer hinge plates variably developed, inner hinge plates absent or forming short and shallow septalium partially covered by long, platelike, crural bases, supported by moderately high median septum; other structures strengthening the muscle system absent; jugum simple, medially or anteriorly situated, lateral branches vertical, very short jugal saddle and vertical stem may be present, accessory jugal lamellae absent; tertiary layer absent. *Silurian (upper Aeronian)–Lower Devonian (lower Emsian).*

Family RETZIELLIDAE Rzhonsnitskaya, 1974

[*nom. transl.* Rong & others, 1994, p. 546, *ex* Retziellinae Rzhonsnitskaya, 1974, p. 59] [=Retzielinae Rzhonsnitskaya, 1974, p. 59, *nom. imperf., nom. correct.* Rong & others, 1994, p. 547]

Characters as for superfamily. *Silurian (upper Aeronian)–Lower Devonian (lower Emsian).*

Retziella Nikiforova, 1937a, p. 57 [**Retzia (Retziella) weberi;* OD] [=*Protathyrisina* Chu, 1974, p. 457 (type, *P. kütsingensis,* OD, =*Athyrisina minor* Hayasaka in Yabe & Hayasaka, 1920, p. 183); *Stegospira* Fu, 1982, p. 167 (type, *S. nucleola,* OD), see also Fu, 1984, p. 374; *Gannania* Fu, 1982, p. 168 (type, *G. spiriferoides,* OD); *Gannania* Fu, 1984, p. 376 (type, *G. spireferoidea,* OD]. Shell with variably developed ventral sulcus and dorsal fold, both usually ribbed or plicate; well-developed apical septalium, shallow and partially covered by platelike crural bases and supported by short septum. *Silurian (upper Wenlock)–Lower Devonian (lower Lochkovian):* Kyrgyzstan, Tajikistan, China (Jilin, Inner Mongolia, Gansu, Sichuan, Yunnan, Guangxi), northern Vietnam, southwestern Tian Shan, ?North Korea, ?central Pamir, ?Afghanistan, ?eastern Iran, ?New Zealand.——Fig. 1076*a–w.* **R. weberi* (Nikiforova), Přídolí, central Asia, southern Tian Shan, Fergana; *a–d,* holotype, dorsal, ventral, lateral, and anterior views, VSEGEI W2456/50327, V. N. Weber Collection, 1885, ×2 (Nikiforova, 1937a; photographs courtesy of T. L. Modzalevskaya); *e–l,* serial sections, NIGP 121423-1; *m,* lateral view of sectioned specimen showing approximate position of serial sections; *n–v,* serial sections, NIGP 121423-1; *w,* lateral view of sectioned specimen showing approximate position of serial sections (adapted from Rong & others, 1994).——Fig. 1076*x–y. R. minor* (Hayasaka), upper Ludlow–lower Přídolí, Yunnan; ventral and lateral views of reconstructed jugum, approximately ×3 (Rong & others, 1994). [See also Fig. 1006.3, p. 1481, in introduction.]

?Argorhynx Havlíček, 1992, p. 110 [**Monticola prokopensis* Havlíček, 1956, p. 541; OD]. Paucicostate rhynchonelliform shell with smooth umbonal regions; internally similar to *Gissarina*; spiralia poorly preserved, jugum unknown. [This genus requires revision.] *Lower Devonian (upper Pragian):* Prague basin (Bohemia).——Fig. 1077,*6a–c.* **A. prokopensis* (Havlíček); holotype, ventral, lateral, and anterior views, VH 3667, ×1.7 (Havlíček, 1956).

Gissarina Menakova & Nikiforova, 1986, p. 71 [**Parazyga ? argensis* Nikiforova, 1949, p. 19; OD]. Similar to *Retziella* but sulcus may develop in both valves; delthyrium covered by deltidial plates; septalium and median septum extremely short or absent. *Silurian (Přídolí):* Tajikistan.——Fig. 1077,*7a–s.* **G. argensis* (Nikiforova); *a–d,* holotype, dorsal, ventral, lateral, and anterior views, TsNIGRA 4/8639, ×2 (Nikiforova, 1949; photographs courtesy of T. L. Modzalevskaya); *e–j,* transverse serial sections showing umbonal regions 0.2, 0.55, 0.80, 0.95, 1.00, 1.45 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 19/6228; *k–q,* transverse serial sections showing cardinalia and brachidium 0.6, 1.2, 1.5, 2.25, 3.50, 4.90, 5.30 mm from ventral umbo, distance from ventral umbo to first section approximate, TsNIGRA 20/6228 (adapted from Menakova & Nikiforova, 1986); *r–s,* ventral and lateral views of reconstructed jugum (Menakova & Nikiforova, 1986).

Metathyrisina Rong & Yang, 1981, p. 246 [**M. merita;* OD]. Similar to *Retziella* with shorter and lower septalium arising somewhat forward of apex, outer hinge plates short. *Silurian (upper Aeronian):* southwestern China (northeastern Guizhou).——

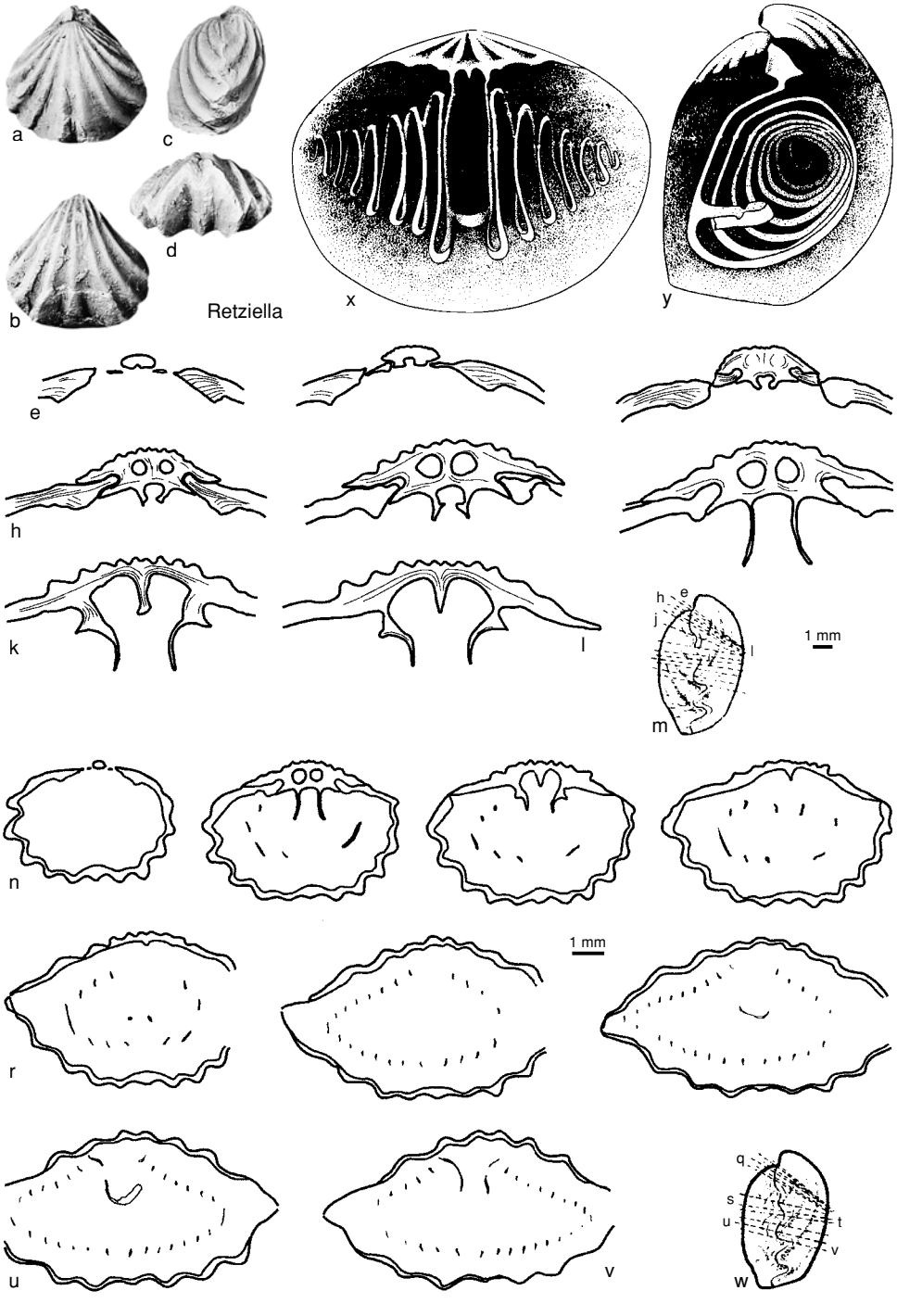


FIG. 1076. Retziellidae (p. 1580).

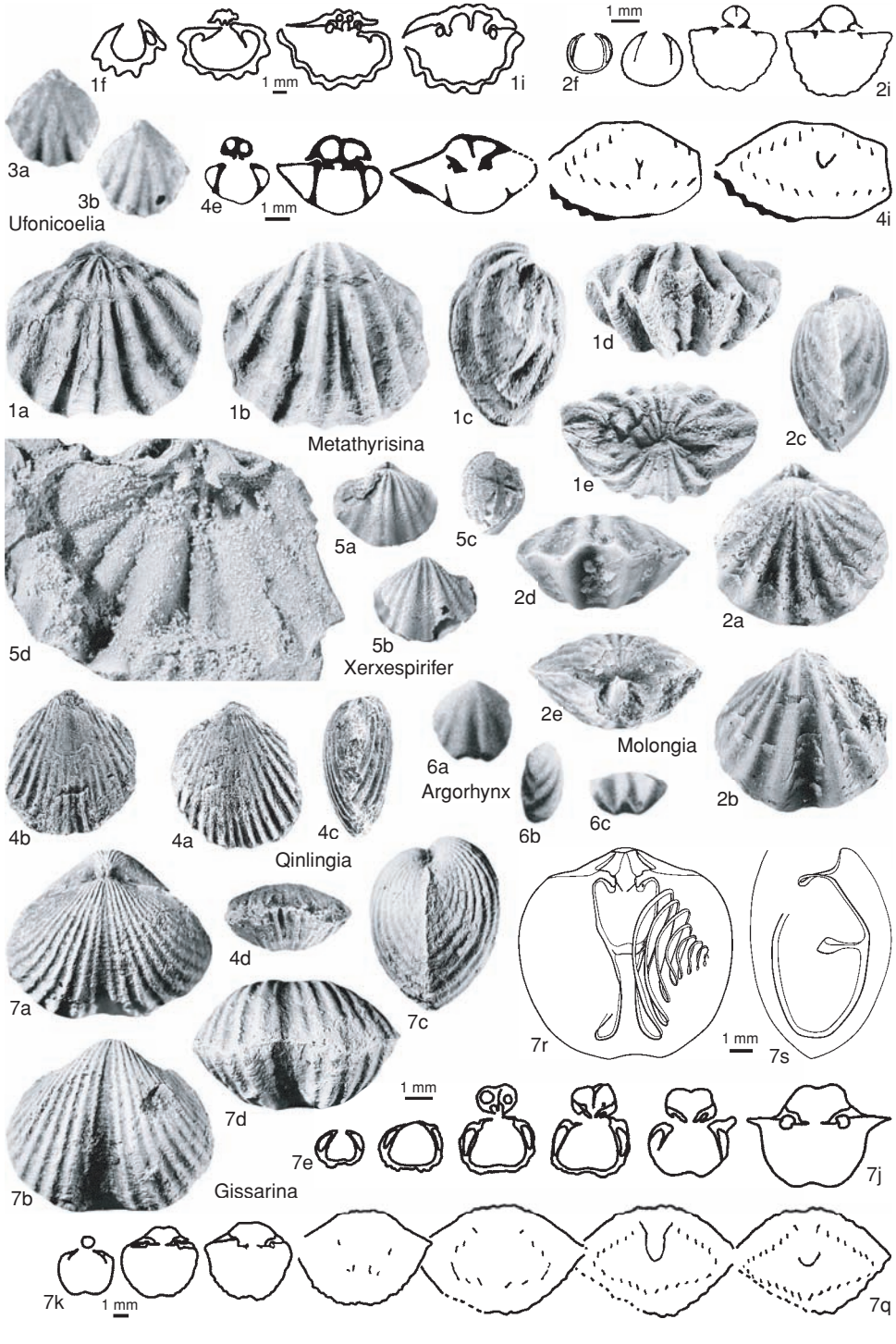


FIG. 1077. Retziellidae (p. 1580–1583).

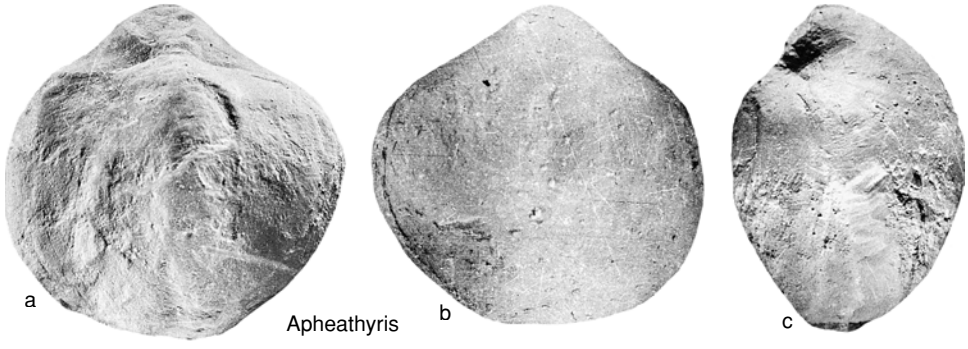


FIG. 1078. Uncertain (p. 1583).

FIG. 1077,*1a–i. *M. merita; a–e,* holotype, dorsal, ventral, lateral, anterior, and posterior views, NIGP 44075, ×2.3 (Rong & Yang, 1981); *f–i,* transverse serial sections 0.5, 1.2, 1.9, 2.2 mm from ventral umbo (adapted from Rong & Yang, 1981).

Molongia MITCHELL, 1921, p. 546 [**M. elegans;* OD]. Shell with variably developed ventral sulcus and dorsal fold that may be plicate but is usually smooth; without dorsal median septum and septalium; short myophragm commonly present. *Silurian (Wenlock)–Lower Devonian (Lochkovian):* Australia (New South Wales, Victoria, Queensland).——FIG. 1077,*2a–i. *M. elegans,* ?Wenlock, Ludlow, Molong, New South Wales; *a–e,* dorsal, ventral, lateral, anterior, and posterior views, NIGP 121425, ×3 (Rong & others, 1994); *f–i,* transverse serial sections 0.3, 0.5, 0.8, 1.15 mm from ventral umbo (adapted from Rong & others, 1994).

Qinlingia RONG, ZHANG, & CHEN, 1987, p. 71 [**Q. bisulcata;* OD]. Similar to *Retziella* but having weak sulcus on each valve and jugal stem. *Lower Devonian (lower Lochkovian):* China (northwestern Sichuan).——FIG. 1077,*4a–i. *Q. bisulcata; a–d,* holotype, dorsal, ventral, lateral, and anterior views, XAGM B108, ×2 (Rong, Zhang, & Chen, 1987); *e–i,* transverse serial sections 0.3, 0.6, 1.1, 4.2, 4.9 mm from ventral umbo (adapted from Rong, Zhang, & Chen, 1987).

?Ufonicoelia HAVLÍČEK, 1992, p. 112 [**Monticola torleyi* HAVLÍČEK, 1956, p. 576; OD]. Similar to *Argorhynx* but with ribs starting in umbo and having median costa in ventral valve; poorly known. [This genus requires revision.] *Lower Devonian (upper Pragian–lower Emsian):* Prague basin (Bohemia).——FIG. 1077,*3a–b. *U. torleyi* (HAVLÍČEK); holotype, dorsal and ventral views, VH 177, ×4 (Havlíček, 1956).

?Xerxespirifer COCKS, 1979, p. 40 [**X. iranicus;* OD]. Shell with small but distinctive median rib in sulcus of ventral valve and corresponding trough in dorsal valve fold; concentric ornament of fine growth lines; cardinal process small; no inner hinge plates, no median septum; spiralium and jugum unknown. [This genus was erected by COCKS (1979) as an acrospiriferinine and was rejected from the spiriferidines by CARTER and others (1994), suggesting a rhynchonellid or leptocoeliid affiliation for the genus. Based mainly on external similarities it was placed herein within the retzielloids. While in proofs, BRICE (1999) placed part of the specimens illustrated by COCKS (1979) of *X. iranicus (*type species of *Xerxespirifer*), in the synonymy of *S. procerum (*type species of *Stegocornu* DÜRKOOP, 1970), therefore *Xerxespirifer* is also listed herein as a synonym of *Stegocornu* (rhynchonelloid) by N. SAVAGE, p. 1050. Careful revision of internal morphology is required to solve this ambiguity.] *Silurian (?Wenlock):* Iran.——FIG. 1077,*5a–d. *X. iranicus,* Elburz; *a–c,* holotype, dorsal, ventral, and lateral views, BMNH BB 93453, ×1; *d,* dorsal interior and fragment of ventral valve above, BMNH BB 93462, ×3 (Cocks, 1979; photographs courtesy of L. R. M. Cocks).

Superfamily and Family UNCERTAIN

Apheathyris FU, 1982, p. 172 [**A. guyuanensis;* OD]. Poorly known. Large, elliptical to round pentagonal, ventribiconvex, smooth shell; with low dorsal fold and shallow ventral sulcus; interior poorly known, dental plates absent, outer hinge plates short and small, inner hinge plate absent, crura long, spiralia laterally directed. [When erected, this genus was included in the Athyrididina, Athyrididae; this genus needs revision.] *Upper Ordovician (lower Caradoc):* northern China (Shijiezigou, Guyuan, Ningxia).——FIG. 1078,*2a–c. *A. guyuanensis;* holotype, dorsal, ventral, and lateral views, XAGM B993, ×1.5 (Fu, 1982).