

ATRYPIDA

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INTRODUCTION

Atrypida are articulated brachiopods identified by a pair of medially to dorsally directed spiralia, which are in the form of mirror image, logarithmic spiral cones. They include the oldest known spire-bearing brachiopods.

Spiralia arise from crura along the inner socket ridges, then splay as primary lamellae to the sides of the shell, and are finally coiled anterodorsally into ever thinner and narrower lamellae terminating at the apex of the cone. Their spiralian orientation is diametrically opposed to the inside-out direction that characterizes the Spiriferida and Athyridida, which have laterally to ventrally directed spiralia and are thus assumed to have evolved independently from the ancestral spire-bearing stock(s) in Caradoc and Ashgill times. In complex, derived Siluro-Devonian taxa the spiralian whorls of atrypides increased in number and size until they almost filled the shell interior, becoming D-shaped in outline and dorsomedially to dorsally directed. The major evolutionary trends of the Atrypida are defined by the development of these calcified spiral lophophore supports and the jugum or jugal processes connecting them. They normally possess a jugum (primitive forms) or jugal processes (derived forms), which connect or nearly touch in the midlength of the shell, extending from the primary lamellae of the spiralia toward each other (Fig. 931).

Some common characteristics of the lamellae (whorls) of the spiralia follow.

(1) Primitive types of spiralia have whorls coiled in the plane of symmetry and are medially directed; derived spiralia have cones rotated into a mediadorsal to dorsal direction with the spiral lamellae roughly parallel to the commissural plane or partly tilted toward the plane of symmetry.

(2) The basal parts of the spiranium have the widest and thickest calcite lamellae; the apex, in contrast, has thin and delicate lamellae. (The thickness of lamellae varies from side to center, but lamellar width thins apically.)

(3) The spiral lamellae are thickest on the interior of the cones and thin out to very delicate flanges on the lateral sides of the cones. (Spiral lamellae are not evenly thick in cross section: they are convex dorsally, flat to concave ventrally.)

(4) Apical parts of the spiranium or small spiralia are always circular in plan view.

(5) The connection between the crura and primary lamellae of the spiralia is continuous in primitive Ordovician and Silurian taxa, but generally, in derived Siluro-Devonian taxa, the crura end in a zone of loosely disconnected fibers of calcite (feathery crura), or there may be no calcite connection. (The spiralia presumably were always connected by soft tissue.)

(6) Stratigraphically oldest taxa have small spiralia, with few whorls (fewer than 5 to 8), which may occupy only a portion of the shell; advanced forms have many spiralian whorls (up to about 20) that crowd the expanded dorsal valve interior.

(7) The spiralia in small and primitive shells tend to be circular in plan view; in large shells, the basal coils are commonly D-shaped in plan view or outline so as to face the opposing spiranium and to maximize space within the shell cavity.

(8) Some spiral lamellae appear to have possessed an outer fringe of spines, but in others this is absent.

(9) In some atrypides (glassiids) the medially directed spires are barrel shaped, instead of cone shaped, reaching their maximum whorl diameter in the center of the spire.

(10) In the flat-shelled Davidsoniidae and Carinatinidae, the spiralia form low cones

accommodated in grooves on the opposing ventral valve.

The first definitive atrypide spire bearers are known from lower Caradoc strata, but some forms appear to have been already present in late Llandeilo time. These early forms, with limited spiral coils, were very small shells (less than 5 mm wide) with relatively fine ribs or were partly smooth with simple corrugations. The coils of the spiralia were derived from elongated crura that were extended into the first ascending lamella, then coiled parallel to the plane of symmetry into the center of the shell (in a plane at right angles to the commissural plane). Some appear to have had less than one spiral whorl, and the space taken up by the spiral lamellae inside the shell was limited. The crura in these early shells were directed ventroanteriorly and laterally, then geniculated dorsally. Medially directed spiralia were lost in the later, advanced atrypides (e.g., the suborders Atrypidina, Davidsoniida, and later Lissatrypidina). Dorsally directed spiral lophophores are developed in living rhynchonellides, but these lack a calcified lophophore support.

Secreting the calcite support of the spiral lophophores of Atrypida required the expenditure of metabolic energy, i.e., the constant secretion and resorption of calcite, for which the atrypides must have paid a price. (The group were the first spire-bearers to die out, although this may have had little or nothing to do with the spiralia.) The mechanism of secretion of the calcite lamellae of the spiralia is disputed. One proposed mechanism consists of a corkscrew system (SAMTLEBEN, 1972, 1975) in which the spiralia were generated around and from the ends of the crura at the base of the spiralia, the oldest part of the calcite spiralia being the tip of the spiralia. The other proposed mechanism, called the mushroom system (MACKINNON, 1991), consists of constant growth from the apex of the spiralia toward the crura, with the apex thus representing the youngest secretion of calcite (the whole spiralia, or at least the apex, is the generative zone in this

case). Both systems required simultaneous secretion and resorption of calcite, particularly where the spiralia were large, crowded much of the shell interior, and show a noncircular or D-shaped spiral base. The corkscrew system would have been more efficient, it seems, in the sense that resorption was required only in later ontogenetic stages and only toward the plane of symmetry. The mushroom system required constant secretion at one side and resorption at the other, over the complete length of the spiralia.

The oldest, late Llandeilo to early Caradoc spire-bearing taxa possessed medially directed atrypoid spiralia, with or without a jugum. These are assigned either to the Anazygidina or else to the primitive Lissatrypidina, e.g., the Protozyginae. One subfamily of smooth atrypides, the Late Ordovician Idiospirinae, and one early Silurian lissatrypidinid (*Cerasina*), are known to have retained a simple jugum, strikingly also in a primitively dorsal position within the shell. One subfamily, the late Caradoc to Ashgill Cyclospirinae, retained the medially directed spiralia and lacked the jugum; whether this was by loss of a partial jugum or whether this group acquired one only later is not clear. For example, the Ashgill to Llandovery genus *Xysila*, with medially directed spiralia, is a homeomorph of *Cyclospira* but developed a jugum probably by acquisition via *Cyclospira* (or derivation from a *Protozyga* stock with a jugum). The earliest type of jugum, as seen in early Caradoc *Manespira*, arose near the anterior commissure from the ascending lamella of the first spiral whorl. This was developed variably among species: sometimes it did not stretch all the way across to meet the opposing jugal branch and thus was incomplete. In early Caradoc *Anazyga* and *Protozyga*, the complete jugum was a broad band located in an anterior and dorsal position (Fig. 931), and the spiralia were medially directed. By late Caradoc time the genus *Zygospira* had a jugum that had migrated into a medial position in the shell, and the spiralia began to be oriented partially toward the dorsal valve. The last survivors of the

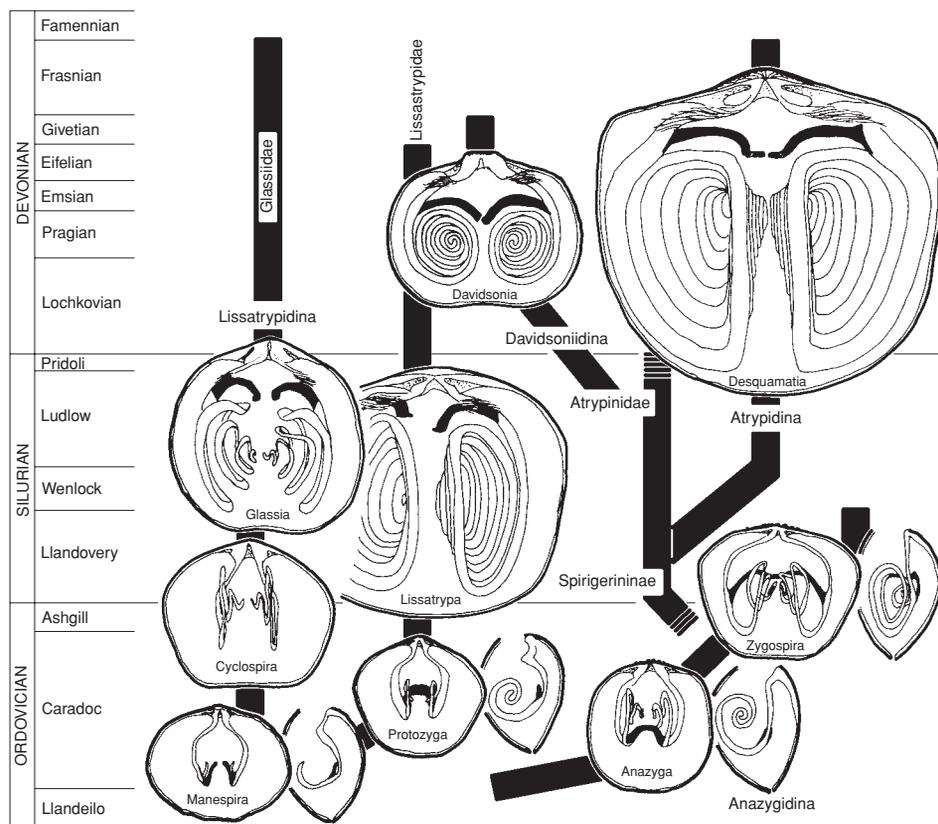


FIG. 931. Generalized evolution of the brachidia in atrypid brachiopods; jugum or jugal processes are shown in black; scale variable, approximately $\times 1.5$ to $\times 4$ (new).

anazygines were early Wenlock *Zygatrypa*, in which the jugum had moved almost into a posterior position. The migration of the jugum from an anterodorsal to postero-central position and the eventual loss of a jugum, with replacement by jugal processes, are two key early evolutionary trends. No jugate atrypides are known from the Wenlock onward. Later forms that were said to have had a complete jugum have been inspected and determined to be nonjugate. Even neanic growth stages of large atrypide shells of Siluro-Devonian age have no jugum. Perhaps with enlargement of the spiralia, a complete jugum was liable to breakage in large, adult shells, with separate jugal processes allowing greater flexibility in the spiralia.

The first atrypides to develop separate jugal processes were the subfamily Spirigerininae: these belonged to the Asian and Australian, late Caradoc to Ashgill genus *Sulcatospira*, and related taxa, that evolved jugal processes located in a posterior position more or less in the commissural plane (and which, concomitantly, increased the number of spiral whorls in the spiralia by up to about 50 percent). Such spirigerinid shells are superficially similar to the anazyginids, except that the anterior commissure is plicate instead of sulcate. In Silurian (Wenlock and younger) and Devonian atrypides of the suborders Lissatrypidina, Atrypidina, and Davidsoniina the jugum was normally split into two separate jugal processes, many of which are curved away from each other in

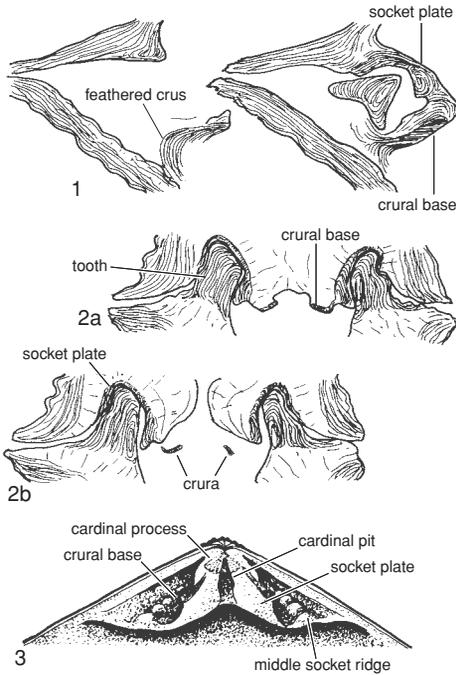


FIG. 932. Crura in Atrypida; 1, *Desquamatia* (*Seratrypa*), variatrypinid; 2a–b, *Mimatrypa*, karpinskiinid; 3, reconstruction of dorsal hinge plate in *Planatrypa* (Eifelian), approximately $\times 5$ (new).

the center of the shell (Fig. 931). The jugal processes, particularly the ends, were the thickest and strongest brachidial structures. In many advanced taxa, the jugal processes terminated in jugal plates consisting of hooklike, half ring, or spoon-shaped structures or a spinose boss. Spines are also a common feature along the jugal processes or the jugal plates in many unrelated Siluro-Devonian genera. The jugal processes were always in a posterior location and either in the commissural plane or toward the ventral valve side. Little is yet known about the details of the jugal processes in many poorly described genera, and new structures are bound to be discovered here.

The jugum and jugal processes of atrypids grew in tandem with the spiralia during ontogeny, suggesting that their growth was coordinated and contained within the same bauplan. The tips of the jugum almost

always terminate in the commissural plane (i.e., the plane separating the two valves) and in a central position between the two cones of the spiralia. In advanced forms the position of the jugal processes shifted toward the hinge axis and toward the ventral valve, but this was probably a reflection of the fact that advanced forms often had a more convex dorsal valve to accommodate more spiralia coils. Whether the jugal processes also contained the filaments and cilia of the lophophore is unknown. The lophophore function of the jugal processes is unclear. Their position within the shell suggests that the jugal ends supported the mouth parts and that food particles were canalized along the spiralia coils toward the base of the spiralia then to the jugum or jugal processes. If so, then the jugal processes or jugum probably were lined with cilia or tentacles, providing an analogue with the lophophore function of the loop in terebratulides. The terebratulide loop, however, is unlikely to have developed from separated jugal processes that are present in Early Devonian atrypids but may have developed from the complex jugum of Athyridida. Whether the jugal processes also were muscle-attachment sites, permitting some mobility of the spiralia, is equally unclear. Some jugal processes possess spines, but this is a feature also not unknown in the spiral lamellae.

The brachidial apparatus in the Atrypida was connected to the dorsal hinge via the crura. This connection is known as the crural base and was derived from the inner portion of the socket plate, i.e., the inner socket ridges (Fig. 932). The crural bases in early neanic stages are visible and traceable almost from the inner apex of the dorsal valve, even in mature shells where these are buried in later secondary shell fibers. The primary lamellae of the spiralia are continuous from the crural extensions in the earlier atrypide taxa. Commonly there is a groove at the side of the opposing ventral valve to accommodate these lamellae. A typical development in Siluro-Devonian taxa, however, is the distal disintegration of the crura into loose

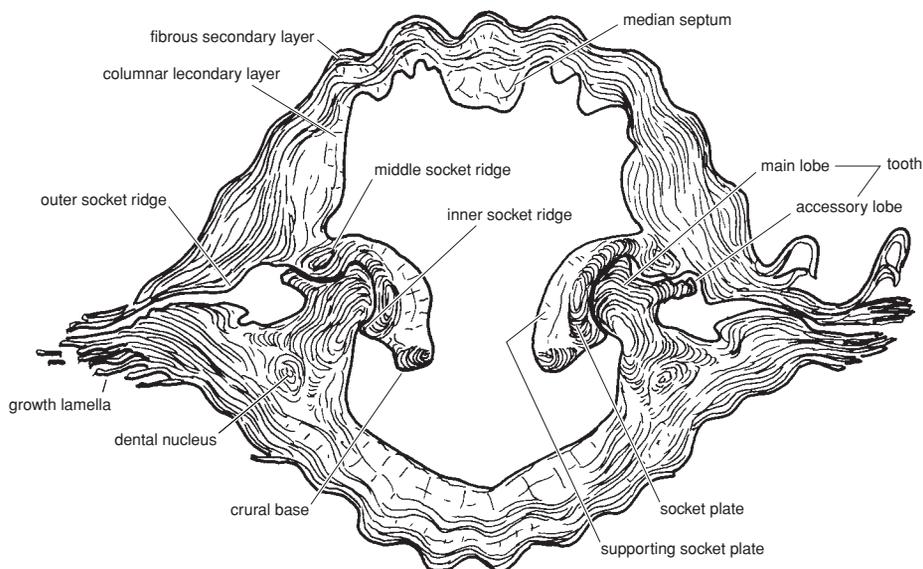


FIG. 933. Serial section view of tooth and socket structures in *Spinatrypa curvirostra* (lower Givetian), demonstrating common features in the Atrypida, approximately $\times 4$ (new).

bunches of calcite fibers with a feathery appearance (COPPER, 1965a). This occurs in the Variatrypinae and Spinatrypinae particularly but also in Silurian Lissatrypinae (COPPER, 1973a). In some atrypides there was therefore no direct or solid connection of the primary lamellae, hence the spiralia, to the socket plate. In fact, in some taxa, the spiralia appear to sit loose in the shell, a feature not recognizably due to breakage. The primary lamellae and jugal processes begin nearly simultaneously as solid, thick structures at the sides of the shell, often with the jugal processes appearing first, a few millimeters away from their initiation in crural fibers. Such features are not known to be present in athyridides or spiriferides, although some Ashgill Hindellinae (Athyridida) also lack any calcite connection between crura and spiralia.

The reasons for the common lack of connection between crura and spiralia in the atrypides are not directly evident. It is possible that this juncture represents the generative zone of the atrypide spiraliium. Alternatively, it may represent a structural advantage, providing greater flexibility or

maneuverability for large atrypide spiralia and less liability of breakage. It may not be a coincidence that this occurs only in forms that have disconnected jugal processes, possibly indicating that the jugal processes may have been attached to muscles that allowed the spiral lophophores some movement, as in living rhynchonellides. If this is correct, the feathery crura may have evolved simultaneously with splitting of the jugum into two separate processes in the three remaining atrypide suborders. The Anazygidina thus may have become extinct in competition with larger atrypides having more efficient, larger, and flexible lophophores.

The socket plate in atrypides lines the sockets and consists of densely packed fibers of the secondary layer, which acted as a support for the teeth from the opposing valve (Fig. 933). Socket plates may be relatively thin, as in many earlier Ordovician atrypides, in the thin-walled Silurian Septatrypinae, or in some of the Devonian Vagraniinae and Karpinskiinae. In the last two subfamilies the very thin socket plate was supported by the massive, coarsely fibrous secondary layer of the hinge plate. In

taxa with thin socket plates the crura were generally also thin and delicate. The middle socket ridge in many later atrypides is composed of a radial row of small knobs that probably constrained the accessory lobes of the teeth; indeed, these seem to be present only in forms that have accessory tooth lobes, which rested on these middle socket ridges. Toward the apex of the shell, the inner socket ridges and the middle part of the cardinal pit were the attachment sites for the diductors. This is evident in the presence of a small cardinal process, which in the atrypides seems to be variably developed, being prominent in gerontic shells but absent in neanic stages. There is little evidence of a cardinal process in the Ordovician Anazygidina, and there is only minimal development of these in many of the Lissatrypidae. The Atrypidina and Davidsoniidina, however, commonly feature a well-developed cardinal process that shows up as a series of striated, often irregular to knoblike or comb-like ridges lining the inner socket ridges and cardinal pit. Size of the shell seems to be important: large shells are more likely to have a cardinal process than small shells. Possibly this is related to increasing size and strength of the diductor muscles required in larger shells. As a rule, there is little evidence of secondary shell fibers in the cardinal process; the calcite growths of the cardinal process appear to consist of a granular layer.

Atrypides had an impunctate shell wall with a relatively thin, granular, primary layer underlain by an impunctate secondary layer. No punctate nor pseudopunctate shell wall has been confirmed. One carinatinid subgenus from Novaya Zemlya, *Biconostrophia (Cherkesoena)*, is said to have a pseudopunctate shell (CHERKESOVA, 1980); this needs corroboration. In terms of macro-

ornamentation, Caradoc atrypides had generally small, thin-walled shells that were either finely ribbed or smooth. By Ashgill time, the ribbed atrypides began to develop sharp breaks or growth interruptions in the primary and secondary layers, which ultimately led to growth lamellae freed from the shell surface in Silurian time. As the shell continued to expand in volume, the growth of such lamellae led to expansive frills or spines, especially in Devonian atrypides. The secondary layer consists of bundles of overlapping, flat, bladeliike crystals that usually radiate from the shell apex in ribbed shells (Fig. 934). In smooth shells (Lissatrypinae), these radial bundles of secondary fibers tend to be cross layered with bundles that are oblique and nonradiate, especially at the posterolateral shell margins. In *Lissatrypa* the surface calcite fibers may also flex upward, providing the shell surface with concentric layers of fine structures with a spinelike appearance. This is also known in the early Silurian Chinese subgenus *Gracianella (Guangyuania)*, where the secondary fibers form curved feathery structures that are evident as concentric ridges on the shell surface. This seems to have reinforced the shell wall and is typical of the smooth forms of atrypides, perhaps with a strengthening function in lieu of the existence of ribs. Early forms of atrypides usually had a thin shell wall, but this was thickened in more advanced taxa and provided additional strength for the shell wall and for muscle attachment.

Atrypides typically lack microornamentation. The shell surface is usually relatively smooth and with scanning magnification ($\times 100$ or more) has a granular to pebbly appearance (Fig. 934). Several Silurian and Devonian ribbed atryptide taxa belonging to different subfamilies, however, show highly

FIG. 934. Microornamentation in Atrypida, as seen under SEM; 1, growth lamellae of upper Llandovery *Gotatrypa bedei* STRUVE, 1966, with only primary layer visible on surface, $\times 30.6$; 2, growth lamellae of Givetian *Spinatrypa spinosa* (HALL, 1861), showing the granular primary outer layer overlying the fibrous secondary layer, $\times 151.6$; 3, primary layer of Wenlock *Endrea tubulosa* (BASSETT & COCKS, 1974), showing concentric microfilae, $\times 22.8$; 4, microfilae and fine radial ornament in primary layer of Ludlow *Spirigerina quinquecostata* (MUNTHE, 1911), $\times 43$; 5a–b, middle Llandovery *Lissatrypa atheroidea* TWENHOFEL, 1914; a, growth interruptions and secondary layer, $\times 228$; b, detached fibrous secondary layer at shell margins, $\times 457$ (new).

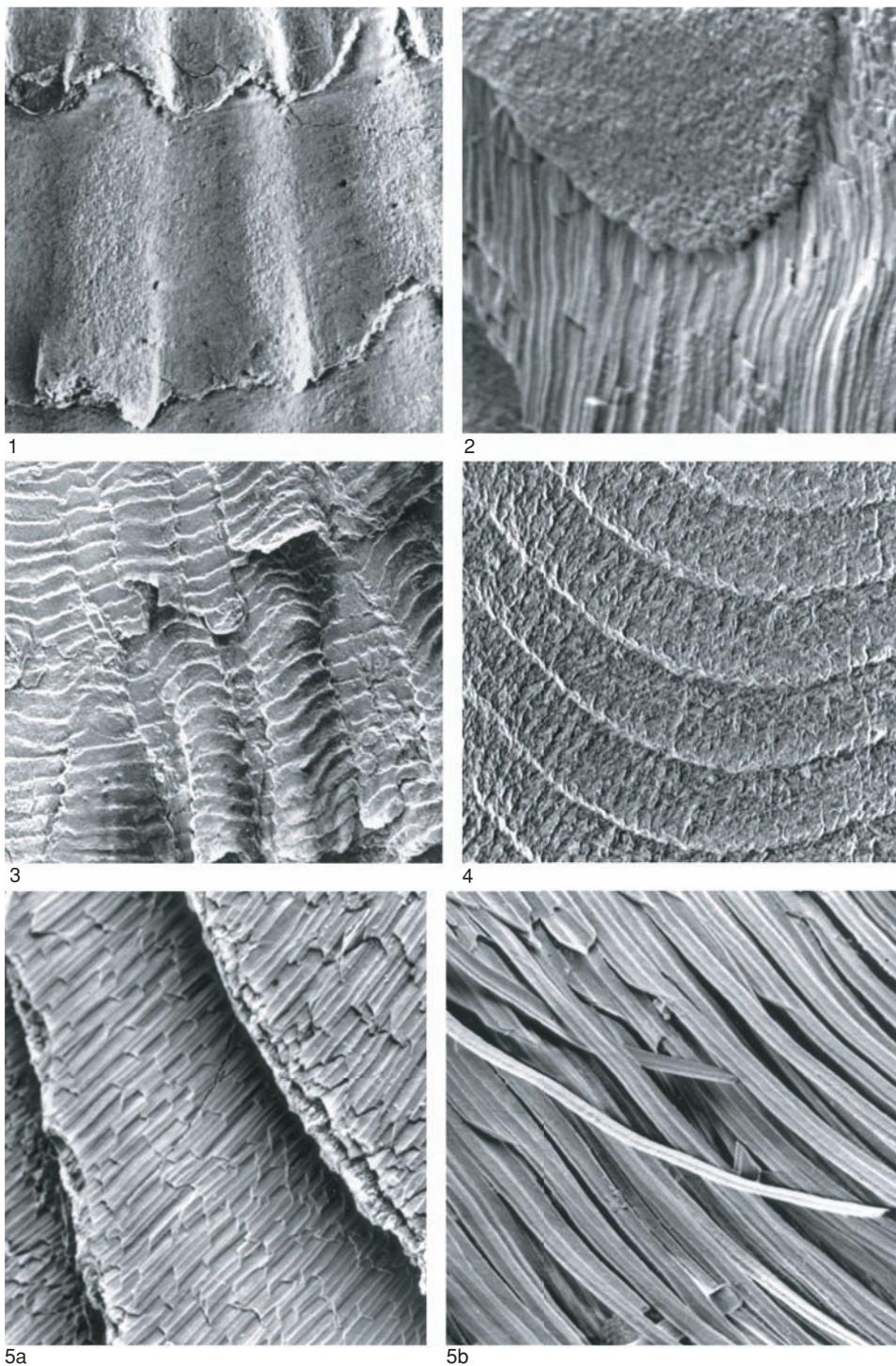


FIG. 934. For explanation, see facing page.

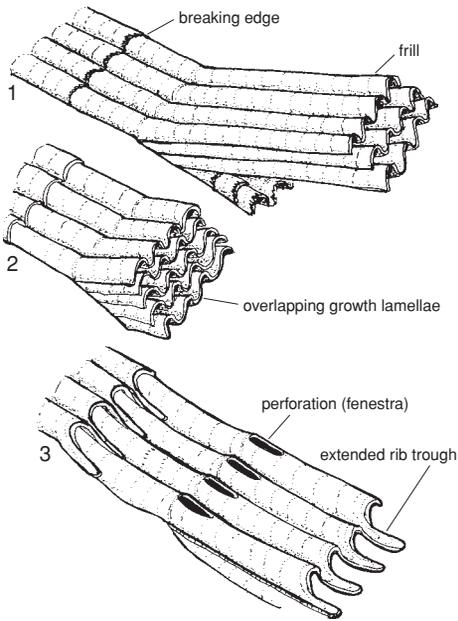


FIG. 935. Idealized growth lamellae and frills in Atrypida; 1, *Desquamatia*; 2, *Gotatrypa*; 3, *Atrypa*, showing perforations facilitating the detachment of frills, approximately $\times 10$ (new).

regular, very fine filae (concentric growth ridges) that are spaced at a density of 5 to 10 per millimeter. These are more evident in the troughs of ribs, where they have a better chance of preservation. The earliest such filae appear in Llandovery Atrypidae. Other variations of these filae show zigzag microornament and some carinatidids appear to have had a pustulose microornament. Since such microornament is often not preserved, it is difficult to evaluate its taxonomic significance; however, it has sometimes been used as a generic character when well developed.

Early shell forms had ribbed or smooth macroornamentation or a combination of these, and the shell had nearly continuous growth. Although growth interruptions were present, such early shells had no retraction of the mantle edge. Growth lamellae, extensions of secondary and primary layer beyond the normal shell wall, are a common feature of the Atrypidina (Fig. 935.2). The growth lamellae could extend evenly from the shell, irregularly, or more rapidly along the troughs

than along rib crests. Later forms of shells in the Atrypidina (especially Atrypinae and Variatrypinae) show considerable growth of the shell beyond the shell wall to produce frills. The first frills evolved in late Llandovery atrypides. Very wide, multiple, overlapping frills could double or triple shell width, with the widest shells of *Desquamatia* (*Independatrypa*) in the Givetian reaching an overall width of nearly 150 mm without a significant change in internal shell volume. The frills of many atrypides are broken naturally during ontogeny with only the last grown frills serving a function and the earlier frills broken off, demonstrating repair of the surface suture. The frills broke off episodically at the crest of each concentric wave (Fig. 935.1). Spines were the result of extensions of shell wall where the crests of ribs grew more rapidly, then curved together to form a hollow tube, unfused on the underside. Spines were often irregular in their extension and of various lengths over the shell surface (Fig. 936.5). Another sort of spine was formed by sharp protrusion of the rib troughs, as seen in early Silurian Atrypinae.

Some Silurian *Atrypa* possess elongate perforations at regular concentric intervals normally along the rib crests (but also along the rib troughs), very much like perforations in sheets of postage stamps (Fig. 935.3). These perforations undoubtedly facilitated the deliberate breakage of frills during life, with retention of only the last few frills at the commissure. Although these perforations are somewhat comparable to the fenestrae seen in the Punctatrypinae, they do not penetrate the shell interior and are entirely exterior to the shell cavity. (They are absent on the inner shell surface.) The secondary and primary layers of the Punctatrypinae are penetrated by small, elongated or rounded, concentrically aligned pores called fenestrae (about 0.1 to 0.3 mm in diameter), located along the shell commissure. These were successively closed, filled, or plugged posteriorly as the shell grew (Fig. 936.7–936.8). Fenestrae normally developed along rib crests (monofenestrate forms), but more than one fenestra may be present along each rib

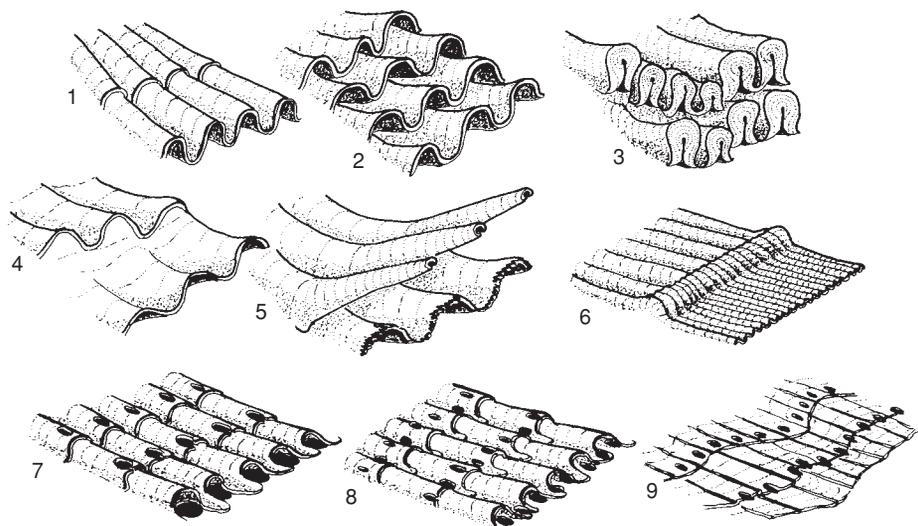


FIG. 936. Macroornamentation in Atrypida, demonstrating various features seen in different groups; 1, *Desquamatia*, corrugate; 2, *Plectatrypa*, imbricate; 3, *Gumia*, capidulate; 4, *Atrypa*, undulose; 5, *Spinatrypa*, spinose; 6, *Carinatina*, trailed; 7, *Punctatrypa*, monofenestrate; 8, *Sinopunctatrypa*, multifenestrate; 9, *Crassipunctatrypa*, platyfenestrate; approximately $\times 10$ (new).

(multifenestrate forms). In the middle of adult shells and posteriorly, these fenestrae are completely sealed off by calcite overgrowth, a process that began as the mantle retreated from the commissure. The function of these is not known. Since the holes penetrate the shell interior they could not have facilitated detachment of the frills, and are more likely to have had either a sensory or feeding-respiratory function. Moreover, such shells do not normally have frills, except for the short, grooved, flat frills of *Crassipunctatrypa*, which commonly cover the fenestrae during growth (Fig. 936.9). This genus also has narrow radial grooves along its extended growth lamellae.

Atrypides were usually attached by a pedicle that protruded through a pedicle opening located at the apex of the delthyrium and flanked by two triangular deltidial plates. (The ordinal name is therefore somewhat of a misnomer for the Greek *a* and *trypa*, meaning without a hole.) A typical example here is the genus *Spirigerina*, which had two hollow deltidial plates partially surrounding the pedicle opening (Fig. 937.1). Atrypides lacked a dorsal area and

possessed neither notothyrium nor chilidium. Some atrypides lost a pedicle opening by progressive incurvature of the beak, placing the area in orthocline through anacline positions until the area was pressed against the dorsal umbo in a position called hypercline. Among other atrypides (particularly those related directly to the type genus *Atrypa*) a pedicle opening is missing, usually, although not invariably, even in the earliest growth stages. The two valves then meet umbo-to-umbo in a position better called adpressed (since the area is not hypercline in this case, and the beak not incurved). The pedicle, however, may still have been squeezed into the remaining gap between the two valves despite the lack of a formal pedicle opening. The pediculate nature of such Atrypinae during life is unsettled. Moreover, the ventral umbo is often pierced or resorbed in such forms (Fig. 937). Loss of the pedicle was often accompanied by modification of the ventral valve into a flat shape (convexoplane) or by growth of spinose or frilly ornamentation, which stabilized the shell on soft substrates. Another method of pedicle loss occurred in

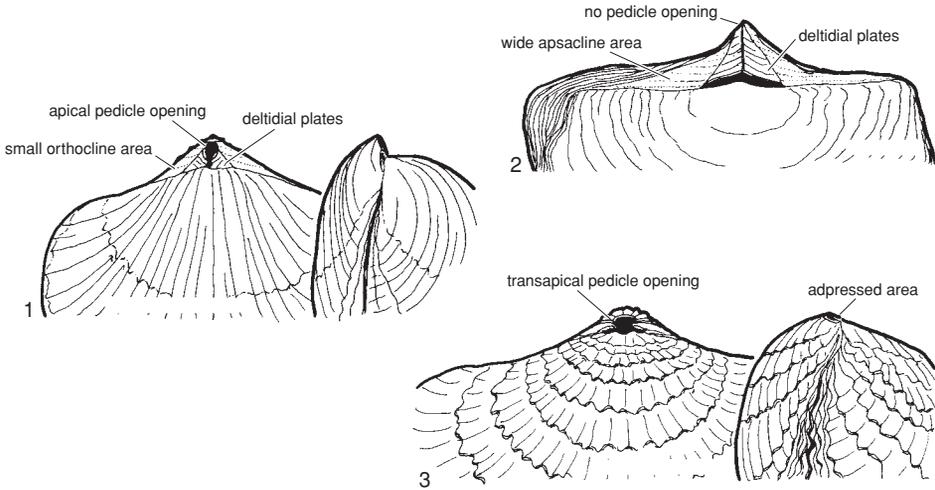


FIG. 937. External view of delthyrial structures in Atrypida; 1, *Spirigerina marginalis*; 2, *Davidsonia*; 3, *Atrypa reticularis*; from camera lucida drawings, $\times 3$ (new).

fixosessile, cementing atrypides such as the Davidsoniinae. Here the delthyrium is usually completely filled in by two deltidial plates and the foramen is closed (Fig. 937.2). In atrypide shells with a short pedicle muscle or a proportionally large pedicle opening and deltidial plates, the area may be curved backward ventrally into an apsacline to procline position, the most extreme excurvature seen in the atrypides. This suggests that a strong pedicle muscle affected the growth of the beak, pedicle opening, and deltidial plates. Many such shells grew in a skewed fashion, and a number of such affected brachiopods were coral-sponge-thicket or reef dwellers.

Internal delthyrial structures in the Atrypida may be quite complex (Fig. 938). Simplest forms have extremely small, hollow deltidial plates flanking a small pedicle opening or no discernible pedicle callist or deltidial plates. The deltidial plates may retreat from the outer margin of the delthyrium to a position inside the pedicle cavity. The development of a pedicle callist, thick layers of calcite in the pedicle cavity, is especially striking in taxa that have an addressed or hypercline area with loss or reduction of a pedicle opening. The pedicle callist may almost completely fill the pedicle cavity, be

layered, and sometimes also have a structure raised above the shell floor as a pedicle collar. These structures are extremely variably developed even within species from one locality and stratigraphic horizon. A pedicle callist or pedicle collar is common in such diverse taxa as the Lissatrypinae (*Lissatrypa*), Atrypinae (*Atrypa*), Variatrypinae (*Desquamatia*), Vagraniinae (*Vagrana*), and Palaferellinae (*Gruenewaldtia*). In some forms, the pedicle collar is consistently fused with the deltidial plates (Karpinskiidae, Palaferellidae), and in others the deltidial plates were kept separate from the pedicle collar (e.g., in *Iowatrypa*, *Desquamatia*). The presence of deltidial plates may be of familial importance in taxonomy, but this requires caution in identification; e.g., in *Lissatrypa* perfectly preserved material must be sectioned so that these are visible in peels. In loose valves any trace of deltidial plates is difficult to find. Pedicle callist and pedicle collar are highly variable even within species and thus not very reliable indicators of taxonomic affinity in many groups. The fusion of pedicle collar with deltidial plates, however, is characteristic and consistent within the Karpinskiidae and Palaferellidae and thus of diagnostic value.

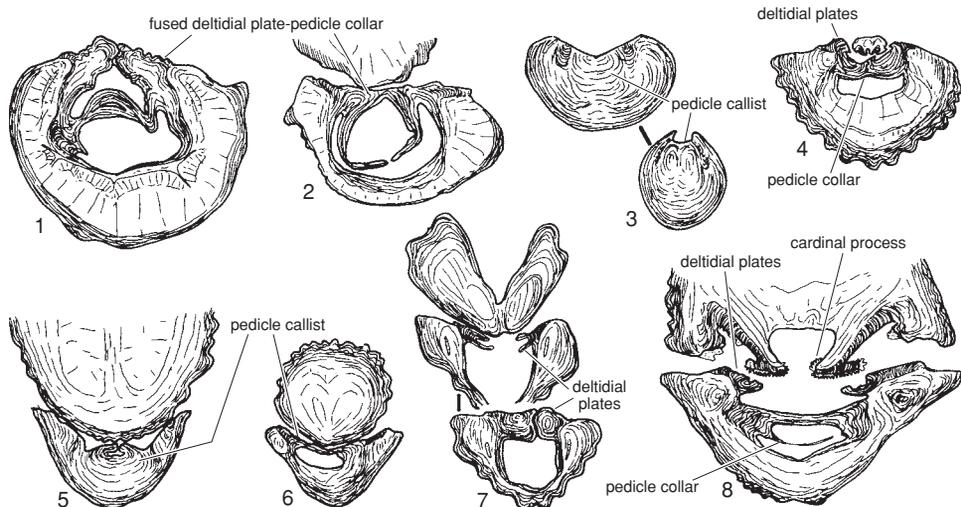


FIG. 938. Internal delthyrial structures in Atrypida as seen in serial section views, showing pedicle callists, pedicle collars, and deltidial plates; 1, *Gruenewaldtia*; 2, *Desatrypa*; 3, *Lissatrypa*; 4, *Iowatrypa*; 5, *Atryparia*; 6, *Atrypa*; 7, *Spirigerina*; 8, *Desquamatia*; approximately $\times 7$ (new).

The typical atrypide shell has a small, orthocline cardinal area, the margins of which may be slightly rounded (palintropelike, astrophic) to almost square edged, as in a true strophic shell. True strophic shells seem to occur only in the Davidsonioidea, but in some Variatrypinae the area widened, the delthyrium enlarged, and the shell approached a nearly strophic condition. Thus atrypide shells straddle the boundary between astrophic and strophic shells, with the latter evolving from the former, since the earliest shells were rhynchonelliform and astrophic.

Atrypides generally have a hinge mechanism composed of tightly fitting cyrtomatodont teeth, normally with accessory lobes. (This means that the teeth needed to be broken to allow valve detachment.) Some but not all of the flat atrypide shells (Davidsoniidae, Carinatininae) had teeth with a more deltidiodont nature; i.e., they appear to have been relatively easily detached and loose fitting at death. The teeth fit into sockets on the dorsal valve that were lined by socket plates, sometimes with accessory middle socket ridges used to constrain the teeth (see Fig. 933). The inner part of the socket plates

is defined by inner socket ridges, usually separated in the middle of the shell by a cardinal pit and on the outer side by a weak ridge or a slope leading to the side of the shell. In some taxa a cardinal pit is absent in adult shells and replaced by a low boss (e.g., in *Lissatrypa* and *Tuvaella*). The cardinal pit, which is only a slight depression in some atrypides and a relatively narrow, deep trough in others, is lined by a distinctive, comblike cardinal process in a number of independently derived Siluro-Devonian forms (e.g., Atrypinae, Variatrypinae, Carinatininae, Vagraniinae). This cardinal process may line not only the cardinal pit but spill over onto the inner socket ridges of the socket plates. The cardinal process, however, is relatively insignificant in atrypides and is highly variably developed even within species and during ontogeny: gerontic shells feature well-preserved cardinal processes in a number of Devonian taxa, but this feature is not evident in primitive Ordovician taxa and in relatively few Silurian forms.

Muscle scars consist of three types, including attachment for the pedicle muscle (the pedicle callist), the adductors, and the diductors. These are variably but not

consistently developed within different groups. The ventral adductor scars occur in the center of a depression toward the shell apex, are bean shaped and relatively narrow, and are sometimes difficult to discern from the diductor scars, which surround them on both sides. A low median septum rarely separates the ventral adductor scars. The diductors are larger, flabellate, and depressed on the ventral valve but rarely occupy more than one-quarter to one-third of the shell length. The dorsal adductors were modestly developed and attached to rounded depressions, commonly separated by a weak median septum (myophragm). When globose, gerontic dorsal valves are serially sectioned, this myophragm may often show up deceptively as a septalium, but a true septalium of the sort present in rhynchonellides is absent (see, for example, the misnamed genus *Septatrypa*, which lacks a septalium and where in some shells the median dorsal septum is barely detectable). Muscle scars may also be raised from the shell floor; in some globose Silurian and Devonian taxa (e.g., *Joviatrypa*, *Gotatrypa*, *Iowatrypa*) the scars have a lip elevated above the shell floor at the anterior margin of the scar. In only one family of atrypides, the Palaferellidae (represented by a single Middle Devonian genus *Gruenewaldtia*), are the dorsal and ventral muscle platforms raised above the shell floor by means of septa. In the earlier Eifelian species of *Gruenewaldtia* these muscle platforms are supported by numerous short septa; by late Eifelian to Givetian time, the supporting septa were reduced to two in each valve.

Raised vascular canals and gonadal pits are evident in thicker or gerontic atrypide shells but are generally not visible in thin-shelled taxa. They are rarely preserved in Ordovician shells, except for the genus *Catazyga*. Vasculae normally consist of curved, mirror-image branches that bifurcate or trifurcate frequently near the shell commissure and are most similar to those of living rhynchonellides. They are stronger on the ventral than the dorsal valve. Vasculae flank the muscle scars laterally and leave a gap between the

muscle scars anteriorly. Vascular canals are highly variably developed within species; they are most obvious in gerontic specimens. The taxonomic and evolutionary significance of the vasculae is not yet clearly established in the Atrypida. In the late Silurian-Devonian Vagraniinae and in Devonian Karpinskiinae, very striking raised vascular ridges, almost like irregular septa, are highly characteristic of most genera. In most other groups, however, the vasculae are weakly displayed and require further investigation.

Order ATRYPIDA Rzhonsnitskaia, 1960

[Atrypida RZHONSNITSKAIA, 1960a, p. 257; *emend.*, COPPER, herein]
[=Procampyli QUENSTEDT, 1882, p. 723, *nom. oblit.*]

Shell wall impunctate, rarely fenestrate; macroornamentation ranging from smooth to ribbed to divaricate, lamellose, spinose, or fenestrate; microornamentation of primary layer usually absent, or with filae, capillae. Shell usually rounded, biconvex to dorsibiconvex, usually astrophic, less commonly flat, strophic; ventral valve rarely partly or wholly cemented; small, flat or rounded ventral area; foramen apical to transapical, dividing 2 triangular deltidial plates; pedicle callist or collar common, perhaps fused with overlying deltidial plates; ventral diductor muscle field large, usually incised, less commonly raised; ventral adductors small; dorsal adductors rounded, separated by weak median septum; small, bushy cardinal process normally located in cardinal pit; weak to prominent ventral vasculae branched around muscle field, saccate to lemniscate, weaker on dorsal valve; faint to strong gonadal pits flanking all muscle fields; crura arising from inner socket ridges, laterally to dorsovertically directed, merging into primary lamellae at sides of shell, may be feathered; medially to dorsally directed, conical spiralia, arising laterally, connected by simple jugum or jugal processes, rarely ajugate. [RZHONSNITSKAIA (1960a, p. 257) was the first to raise the group to ordinal status, using as criteria that the spiralia were dorsally or medially directed, based on the evolution of these

character states in the Atrypida. She also included the planoconvex *Coelospira* and *Dayia* shells, as did the 1965 brachiopod *Treatise* (BOUCOT, JOHNSON, & STATON, 1965; but see suborder Uncertain, p. 1604 herein), based ostensibly on serial sections that appear to demonstrate a dorsal direction for spiralia. When these latter taxa are examined, it is evident that they possess laterally directed spiralia and complex juga with jugal stems, as known only from the order Athyridida, and thus cannot be assigned to the Atrypida. MOORE (1952, p. 221) defined the "suborder Atrypacea" as impunctate shells with a short hinge and the negative character "spiralia not directed toward cardinal extremities." A number of Atrypida have a long strophic hinge and lack cardinal extremities; moreover, *Cyrtia* (Spiriferida) have spiralia not directed to lateral extremities (and would thus have to be accommodated in his definition of the Atrypacea), so that the only character of MOORE's 1952 definition that remains is an impunctate shell. This is impractical, and does not reflect the nature of the Atrypida fossil record. RZHONSNITSKAIA's 1960 definition is thus accepted as the first reasonably accurate description of the order Atrypida, including the Cyclospiridae, Anazygidae, and Atrypidae, as defined by her (but excluding her Coelospiracea and Dayiaceae). This attribution has been almost universally adopted in the last 25 years.] *Ordovician (Llandeilo)–Upper Devonian (Frasnian)*.

Suborder ATRYPIDINA Moore, 1952

[*nom. correct.* BOUCOT, JOHNSON, & STATON, 1965, p. 632, *pro* suborder Atrypoidea MUIR-WOOD, 1955, p. 77, *nom. correct. pro* suborder Atrypacea MOORE, 1952, p. 221; *emend.*, COPPER, herein]

Ribbed, tubular, lamellose, wavy, spinose, fenestrate, or secondarily smooth-shelled atrypoids; generally rectimarginate to plicate commissure; spiralia dorsomedial to dorsal in direction, with up to 25 whorls; separated jugal processes in a posteromedial and ventral position toward hinge. *Ordovician (lower Caradoc)–Upper Devonian (Frasnian)*.

Superfamily ATRYOIDEA Gill, 1871

[*nom. correct.* COPPER, herein, *pro* superfamily Atrypacea SCHUCHERT & LEVENE, 1929a, p. 19, *nom. transl. ex* Atrypidae GILL, 1871, p. 25; *emend.*, COPPER, herein]

Ribbed atrypides, commonly with concentric growth lamellae or frills; spiralia dorsally or dorsomedially directed; jugal processes posteroventrally located. *Ordovician (lower Caradoc)–Upper Devonian (Frasnian)*.

Family ATRYPIDAE Gill, 1871

[Atrypidae GILL, 1871, p. 25, *partim; emend.*, COPPER, herein]

Small to very large, ribbed atrypoids, lacking carination; characterized by strong development of extended, concentric growth lamellae, sometimes as expansive frills, skirts, or spines (expanding shell width to more than 150 mm); pedicle callist variably developed; weak to strong, comblike cardinal process developed in cardinal pit; spiralia usually with more than 8 whorls, up to 25 whorls in large shells, jugal processes posteroventral; jugal plates attached to ends of processes. *Silurian (Llandovery)–Upper Devonian (Frasnian)*.

Subfamily ATRYPINAE Gill, 1871

[*nom. transl.* COPPER, herein, *ex* Atrypidae GILL, 1871, p. 25; *emend.*, COPPER, herein]

Atrypides with short, concentric, usually wavelike growth lamellae, to very wide overlapping or imbricate lamellae extended as frills; ribs discontinuous, commonly wavelike at frill breakage points; beak small; area varying from small, orthocline (rare) to hypercline (common), to absent; foramen and deltidial plates commonly lost in adult shells; usually small to wide, thick pedicle callist; teeth solid, but dental nucleus or small dental cavity in some taxa; weak to strong cardinal process spilling over cardinal pit; crura delicate to strong; spiralia with many whorls; relatively thick jugal processes terminating in gently curved to spatulate jugal plates. *Silurian (Llandovery)–Upper Devonian (Frasnian)*.

Atrypa DALMAN, 1828, p. 127 [**Anomia reticularis* LINNAEUS, 1758, p. 702; OD]. Medium to large,

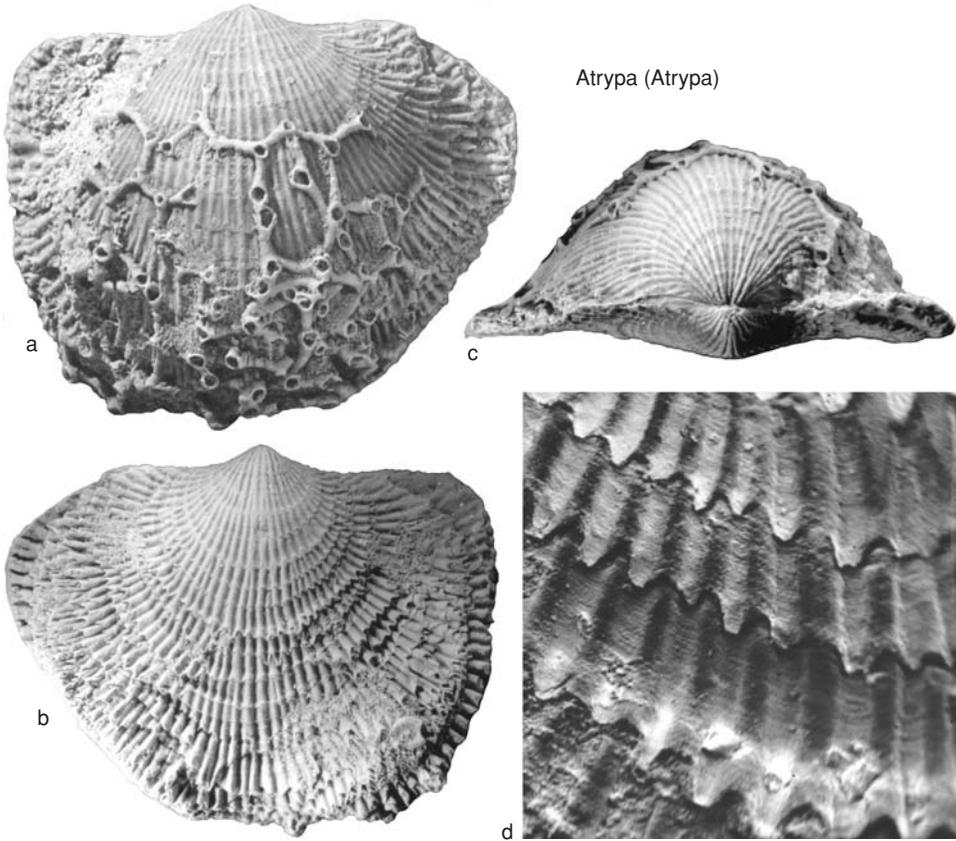


FIG. 939. Atrypidae (p. 1390).

broadly convexoplane to dorsibiconvex adult shell, ventral valve from very weakly convex apically; dorsal valve usually strongly convex; area generally absent; beak adpressed; foramen transapical or obscured; deltidial plates absent; ribs medium to coarse; regular, concentric, undulose to wavelike growth lamellae, usually expanded as prominent, multiple frills; commissure rectimarginate to plicate; thick pedicle callist; teeth massive, with dental nuclei, accessory lobes (dental cavities in neanic shells); muscle field depressed; vascular ridges weakly to strongly developed around muscle areas; hinge socket plates strong; comblike cardinal process lining cardinal pit; sockets with accessory ridges; crural bases large, bulbous; crura commonly feathered; spiralia dorsal, up to 20 whorls in large shells; jugal processes thick, terminating in long, dorsally directed spatulate jugal plates. [Differs from ancestral *Gotatrypa* in convexoplane shell, development of frills; from *Atryparia* in more imbricate ribs, lack of dental nuclei in adult teeth.] *Silurian* (upper Llandovery)—*Middle Devonian* (lower Givetian): worldwide.

A. (*Atrypa*). Description as for genus. Medium to large, broadly convexoplane shell, with ventral valve from very weakly convex apically, to planar, to resupinate; area absent or minute; foramen obscured; deltidial plates absent except in earliest growth stages; ribs fine to medium sized; multiple frills sometimes broken during life by seam of perforations; commissure plicate. [Differs from *A. (Planatrypa)* in weakly convex ventral umbo, possessing numerous frills, dental nuclei (and dental cavities in neanic stages).] *Silurian* (upper Llandovery)—*Lower Devonian* (Emsian): worldwide.—FIG. 939a–d. *A. (*A. reticularis*) (LINNAEUS), lower Ludlow, Gotland; a–c, dorsal, ventral, posterior views, $\times 2$; d, SEM detail of macroornament, $\times 12$ (new).—FIG. 940a–d. *A. (*A. reticularis*) (LINNAEUS), lower Ludlow, Gotland; a–c, serial sections, $\times 4$; d, reconstruction from serial sections, $\times 3.5$ (new).

A. (*Planatrypa*) STRUVE, 1966, p. 143 [*A. (*P. collega*); OD] [= *Mikrothyris* QUENSTEDT, 1871 in 1868–1871, p. 30, *nom. oblit.*, no type designated; *Planatrypa* COPPER, 1967a, p. 237 (type,

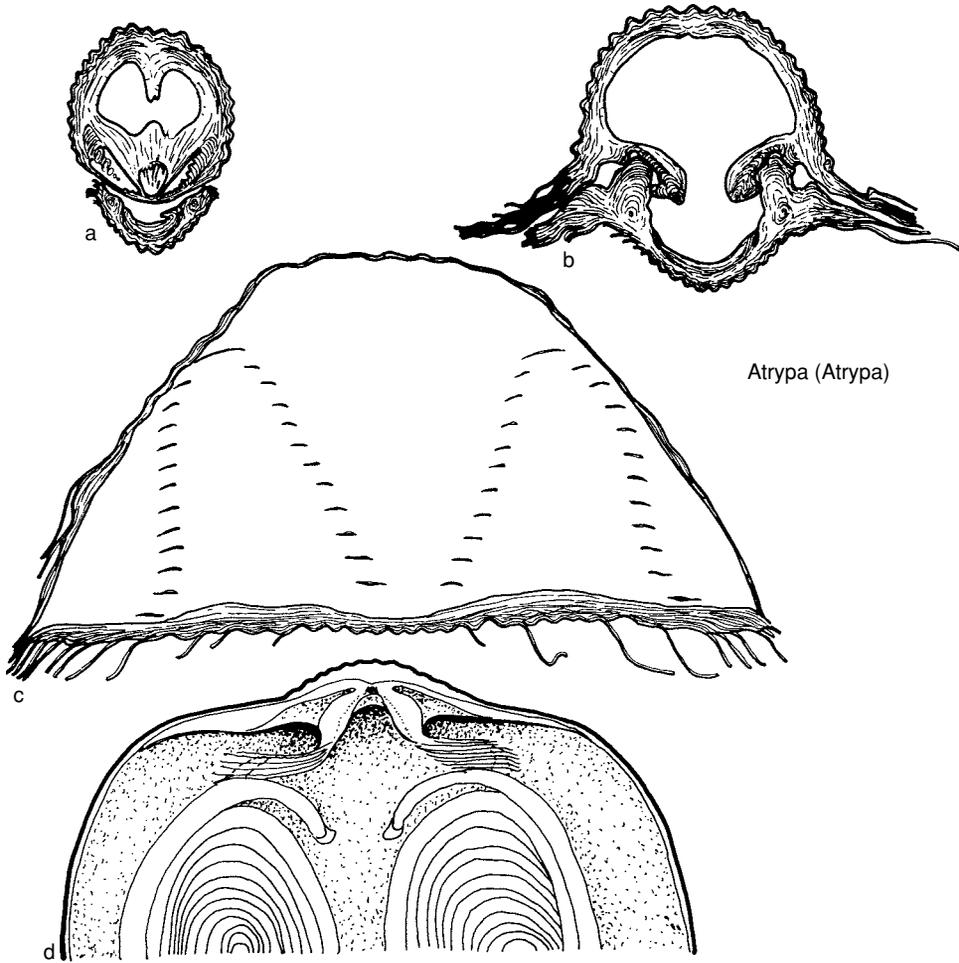
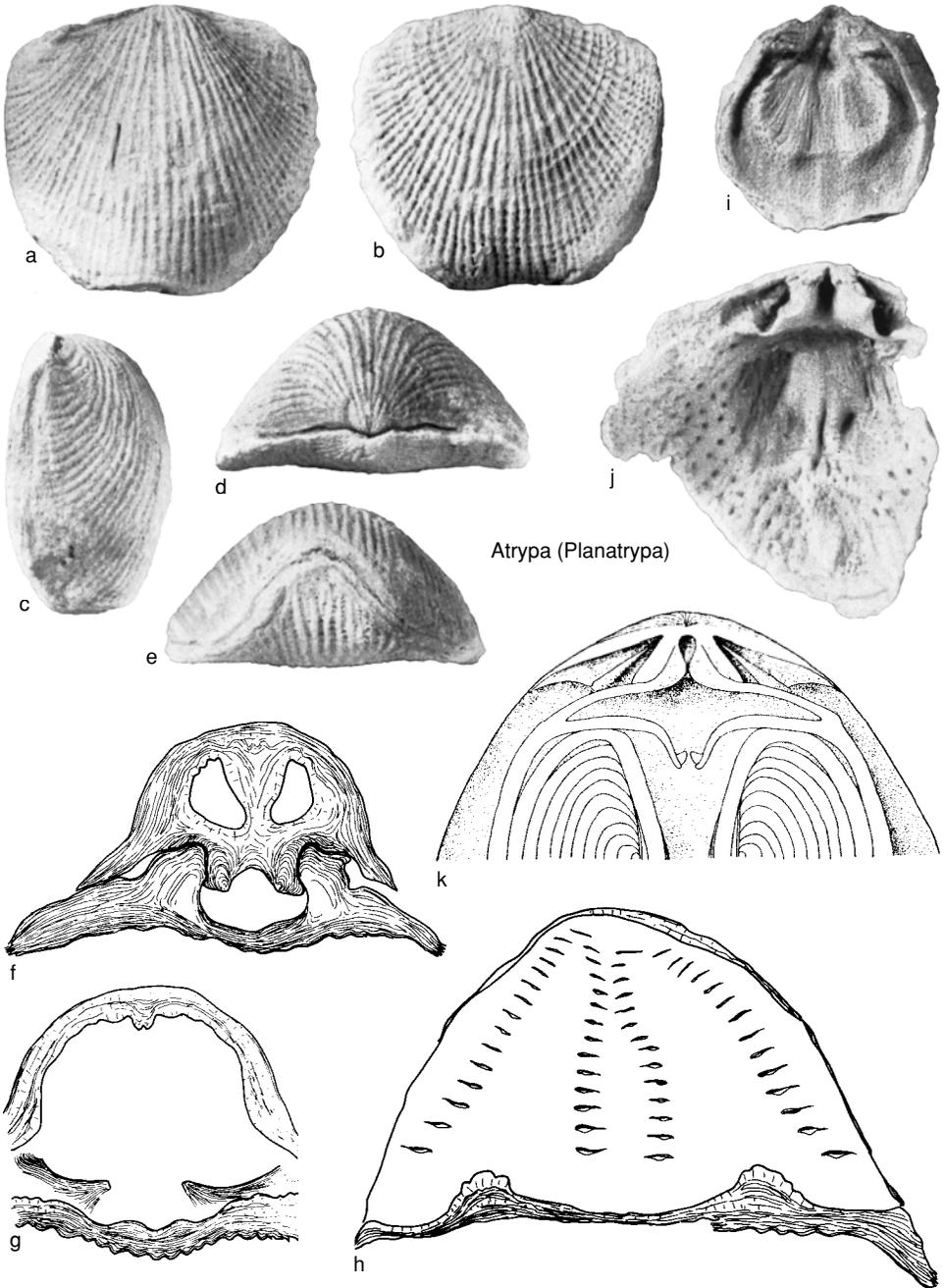


FIG. 940. Atrypidae (p. 1390).

A. (P.) petasa, OD)]. Medium to large, convexo-plane; beak adpressed; foramen transapical or obscured; deltidial plates absent; ribs medium size, interrupted by numerous, flat, weakly imbricate growth lamellae; frills absent; anterior commissure rectimarginate to weakly plicate; crura curved, feathery; spiralia with more than 8 whorls; posteroventral jugal processes terminating in curved, short, spatulate jugal plates. [Similar to *A. (Atrypa)*, except that in early mature shell, the pedicle valve is flat, anterior fold weakly developed to absent, frills not known to be present, jugal processes more ventrally located. QUENSTEDT stated for *Atrypa*, "und *Atrypa*

(besser wäre es *Mikrothyris*)," but no type was designated]. Middle Devonian (Eifelian-lower Givetian): worldwide.—FIG. 941*a–h*. **A. (P.) collega*, middle Eifelian, Germany; *a–e*, dorsal, ventral, lateral, posterior, anterior views, $\times 2$; *f–h*, serial sections, $\times 5$ (Copper, 1967b).—FIG. 941*i–k*. *A. (P.) petasa* COPPER, upper Eifelian, Germany; *i*, ventral interior, $\times 2$; *j*, dorsal interior, $\times 4$; *k*, reconstruction of brachidia, $\times 3$ (Copper, 1967b).

Atryparia COPPER, 1966a, p. 982 [**A. instita* COPPER, 1966a, p. 983; OD] [= *Hyponeatrypa* STRUVE, 1966, p. 137 (type, *Atrypa (Hyponeatrypa) aureolata* STRUVE, 1966, p. 140, OD)]. Medium to very large, dorsibiconvex-convexo-plane; ventral valve inflated posteriorly, commonly keel-like; very coarse to fading ribs intersected by flat, relatively widely spaced growth lamellae extended into broad, multiple



Atrypa (*Planatrypa*)

FIG. 941. Atrypidae (p. 1390–1391).

overlapping frills; thick, wide pedicle callist, commonly with narrow central groove; teeth possessing dental nuclei; fewer than 15 relatively widely spaced spiral whorls; jugal processes terminating in long, downturned plates. [Distinguished from *Atrypa* and

Kyrtatrypa by coarse, flattened ribs and growth lamellae showing smoothed, distally expanding ribs, wide multiple frills, internally in having dental nuclei.] Lower Devonian (*Emsian*)–Upper Devonian (*Frasnian*): worldwide.

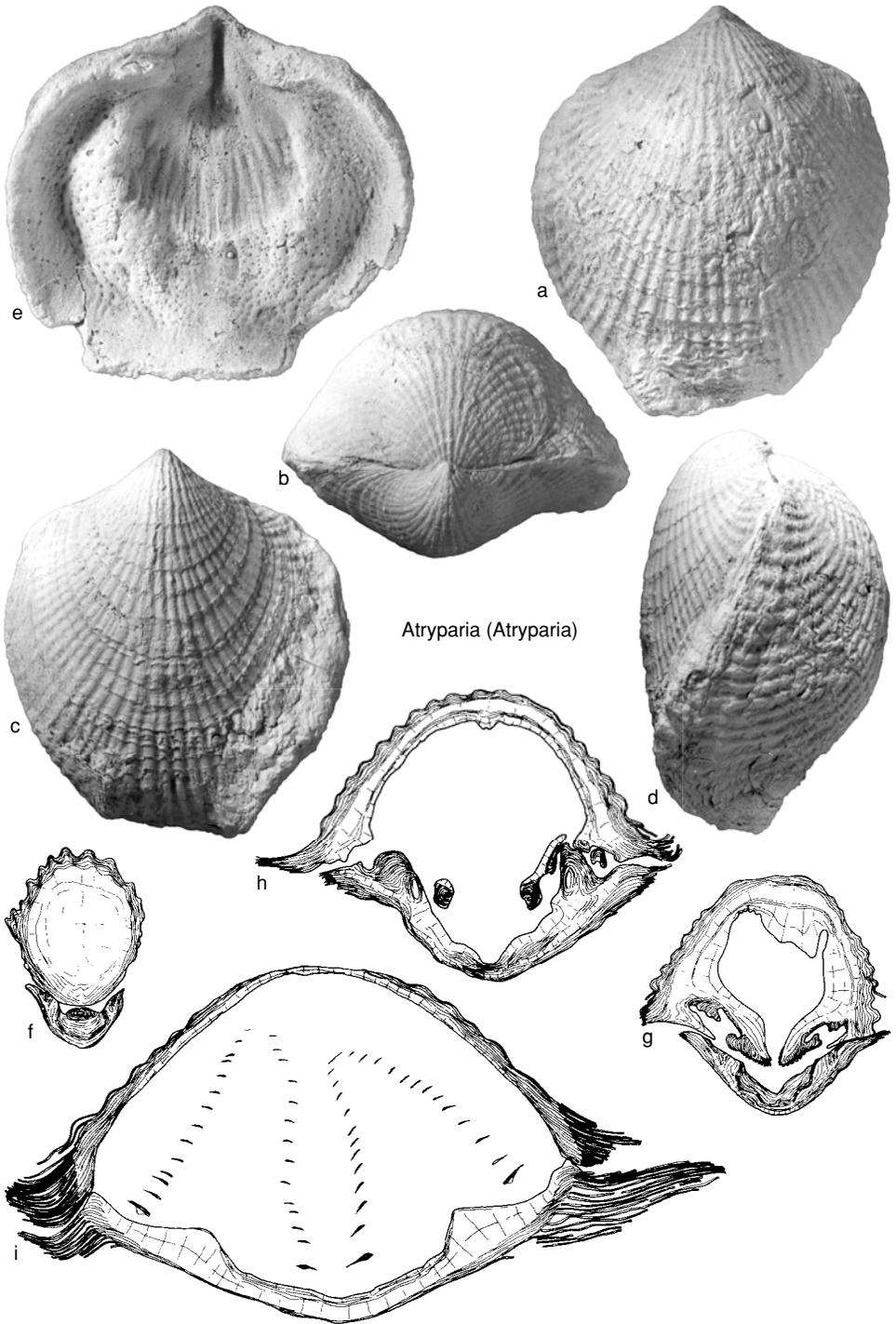
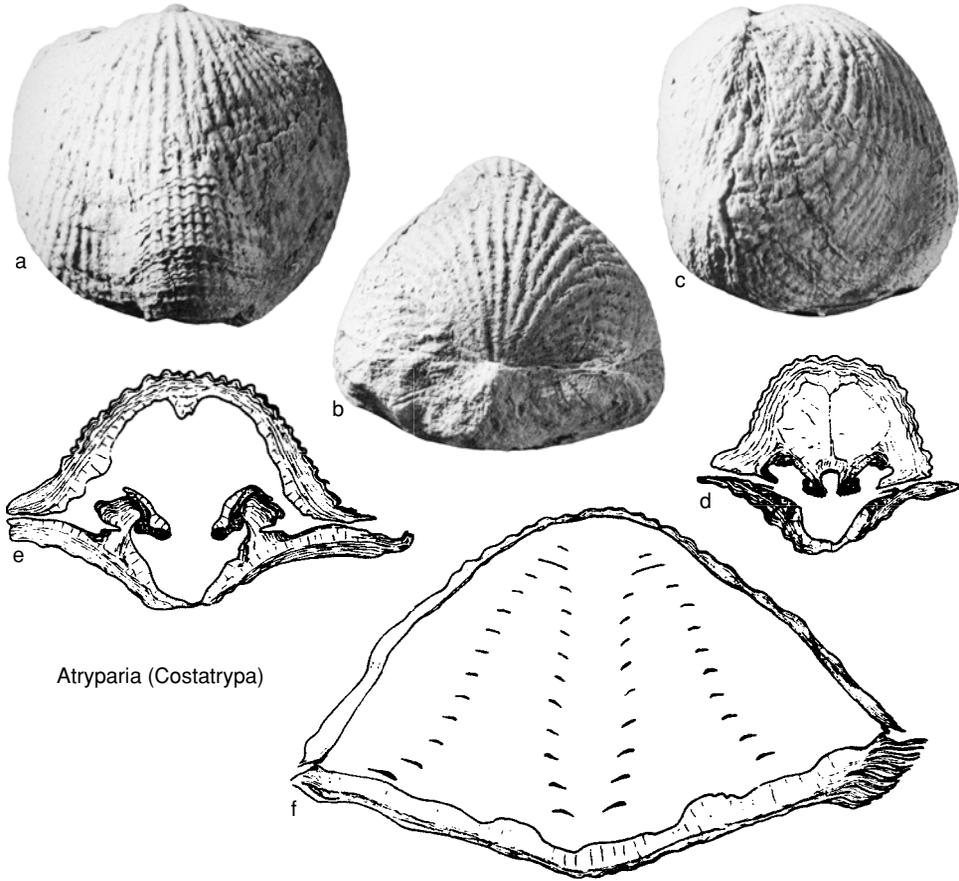


FIG. 942. Atrypidae (p. 1394).



Atryparia (Costatrypa)

FIG. 943. Atrypidae (p. 1394).

- A. (Atryparia). Description as for genus, but medium to very large, dorsibiconvex. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Eurasia, northern Africa, North America.—FIG. 942*a–i*. *A. (*A.*) *instita*, upper Eifelian, Germany; *a–e*, dorsal, posterior, ventral, lateral, interior of ventral valve, $\times 2$; *f–i*, serial sections, $\times 5$ (new).
- A. (Costatrypa) COPPER, 1973c, p. 494 [**Atrypa varicostata* STAINBROOK, 1945, p. 47; OD]. Medium to large, dorsibiconvex-convexoplane, shield shaped to subquadrate; generally relatively long hinge; adpressed area; small beak, lacking apical foramen; ribs shallow, medium size, coarser ribs on frills; prominent frills up to about 15 mm long; moderate to strongly plicate commissure; moderate pedicle callist; large teeth; minute dental nuclei; crural bases thick, rounded; crura feathered; dorsomedial spiralia with fewer than 15 whorls; curved jugal processes terminating in hook-shaped plates. [Differentiated from *A. (Atryparia)* by more clearly

defined ribs, flatter, wider, shield-shaped shell, less prominent frills.] *Upper Devonian (Frasnian)*: worldwide.—FIG. 943*a–c*. *A. (*C.*) *varicostata* (STAINBROOK), Iowa, USA; dorsal, posterior, lateral views, $\times 2$ (Copper, 1973c). —FIG. 943*d–f*. A. (*C.*) *variabilis* GODEFROID, Belgium; serial sections, $\times 3$ (new).

- Dihelictera* COPPER, 1995, p. 855 [**D. acrolopha*; OD]. Small to medium, planar to weakly biconvex; posterior ventral valve weakly carinate; small, orthocline area; apical foramen flanked by deltidial plates; relatively straight ribs posteriorly; short growth interruptions or lamellae anteriorly; regular concentric filae; rectimarginate to weakly plicate commissure; pedicle callist absent; teeth with moderate dental cavities; small, distinct cardinal pit lined by minute cardinal process; spiralia dorsomedial, fewer than 6 whorls; jugal processes simple, terminating in small, hooklike jugal plates. [Similar externally to *Procarinatina*, but possessing fine, concentric filae, ribs straight to tubular posteriorly, lacking wavelike imbrication; differs from

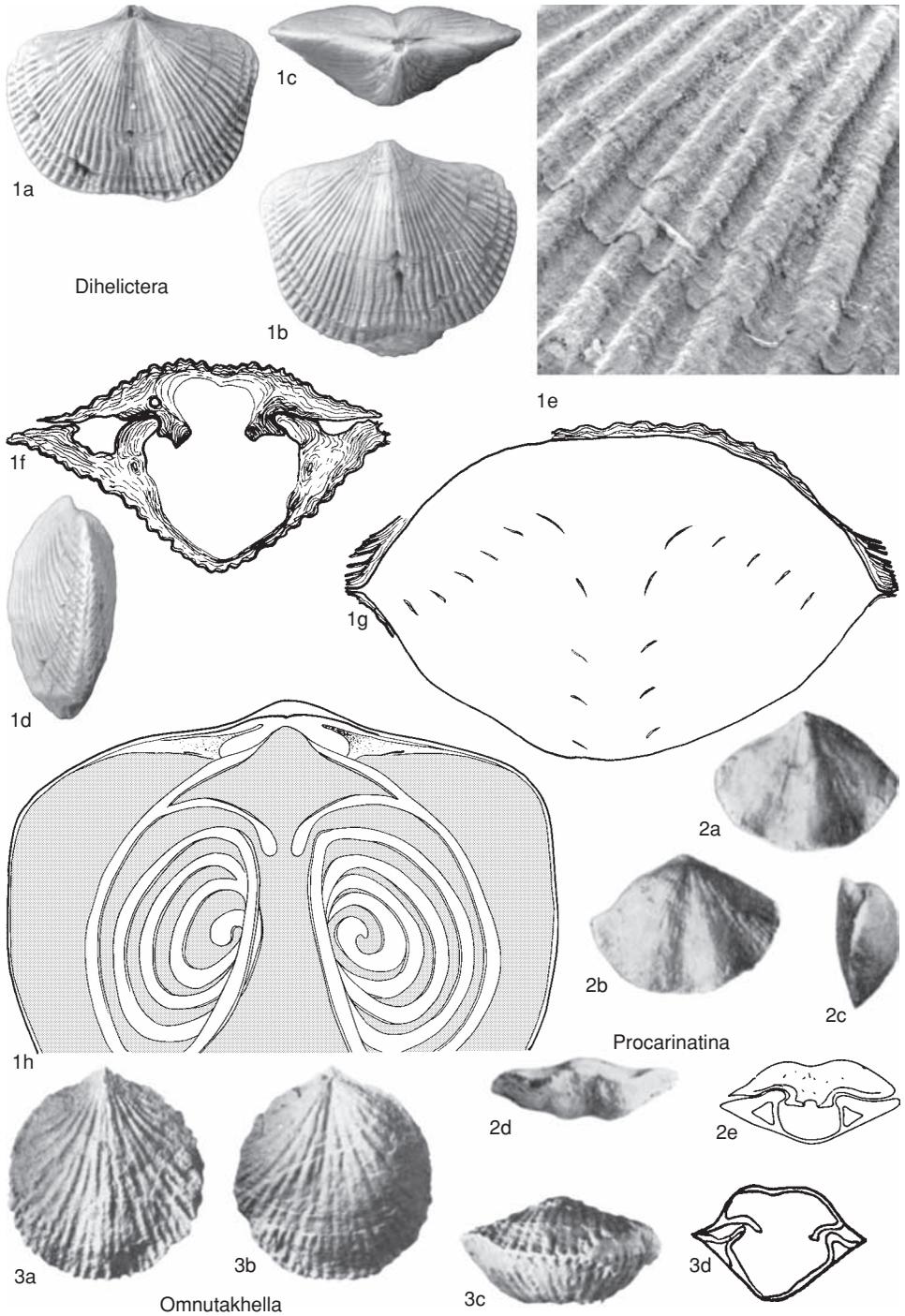


FIG. 944. Atrypidae (p. 1394–1400).

- Protatrypa* by nature of hinge plate, ornamentation, teeth with dental cavities.] *Silurian (middle Llandovery–upper Llandovery)*: North America, Siberia.—FIG. 944, 1a–b. **D. acrolopha*, Aeronian, Anticosti, Canada; a–d, dorsal, ventral, posterior, lateral views, $\times 3$; e, SEM detail of ornament, $\times 13$; f–h, serial sections and reconstruction of brachidia, $\times 5$ (Copper, 1995).
- Endrea** COPPER, 1996b, p. 919 [**E. echoica*; OD]. Medium to large, biconvex-dorsibiconvex, rarely convexoplane, shield shaped; small orthocline-anacline area, apical foramen surrounding small deltidial plates even in adult shells; highly arched, tubular-imbriate ribs, short frills or frills lacking, fine concentric filose microornament; commissure weakly to strongly folded; pedicle callist very thin to lacking; teeth with small dental cavities; spiralia with fewer than 10 whorls; jugal processes terminating in small, weakly curved jugal plates. [Distinguished from *Atrypa* by tubular-imbriate ribs, very short frills or no frills, filose microornament (where preserved), small deltidial plates, dental cavities, lack of pedicle callist; rib structure *Spinatrypina*-like, but shells have short frills; *Rugosatrypa* is most similar, but has finer, more *Atrypa*-like, flatter ribs, convexoplane shell.] *Silurian (Wenlock–Ludlow)*: western Europe, North America.—FIG. 945, 2a–d. **E. echoica*, lower Wenlock, Gotland; a–b, ventral, lateral views, $\times 2$; c–d, serial sections, $\times 5$ (Copper, 1996b).
- Gotatrypa** STRUVE, 1966, p. 130 [**Atrypa (Gotatrypa) hedei*; OD]. Small to medium, globose, ventribiconvex to biconvex to weakly dorsibiconvex; minute, adpressed area; foramen transapical or obscured; deltidial plates absent, except in neanic stages; fine ribs intersected by closely spaced, weak, wavelike growth lamellae, projected less than 2 to 3 mm, commonly pointed as spines and longer in rib troughs; frills absent; pedicle callist moderate; teeth with dental nuclei; crura thin, rarely bushy; spiralia dorsomedial, fewer than 8 to 12 whorls; short, centroposterior jugal processes with small jugal plates. [Differs from *Atrypa* in convexity, globose shape, closely spaced, overlapping growth lamellae, lack of frills. Distinguished from *Oglupes* by small size, very fine ribs, very short frills.] *Silurian (Aeronian–Telychian, ?Wenlock)*: worldwide.—FIG. 945, 1a–g. **G. hedei*, Telychian, Gotland; a–d, dorsal, ventral, posterior, lateral views, $\times 2$; e–g, serial sections, $\times 5$ (new).
- Joviatrypa** COPPER, 1995, p. 858 [**J. brabyla* COPPER, 1995, p. 859; OD]. Medium to large, ovoid, globose, ventribiconvex-biconvex; small, hypercline area; foramen transapical-apical; deltidial plates absent; ribs fine to medium, interrupted by numerous, closely spaced (less than 1 mm), short growth interruptions, projecting growth lamellae; frills lacking; weakly plicate commissure; thick pedicle callist bisected by narrow groove; strong teeth with minute dental nuclei; rounded cardinal pit; weak cardinal process on bulbous inner socket ridges; crura stout, fibrous; dorsomedial spiralia with fewer than 15 whorls; jugal processes terminated in thick, blocky jugal plates. [Differs from *Gotatrypa* and *Atrypa* in lacking growth lamellae and frills, presence of anteriorly raised, ventral muscle platform; resembles *Nalivkinia* externally, but lacks dental cavities, dental plates, has ventral muscle platform.] *Silurian (middle Llandovery–upper Llandovery)*: North America, ?Siberia.—FIG. 946a–i. **J. brabyla*, Aeronian, Anticosti, Canada; a–e, dorsal, posterior, anterior, lateral views, internal of ventral valve, $\times 2$; f–h, serial sections, $\times 3.5$; i, reconstruction of serial sections, $\times 2.5$ (Copper, 1995).
- Kyrtatrypa** STRUVE, 1966, p. 133 [**Atrypa (Kyrtatrypa) culminigera* STRUVE, 1966, p. 135; OD] [= *Anulatrypa* HAVLÍČEK, 1987a, p. 73 (type, *A. anulata*, OD)]. Small to large, biconvex to strongly dorsibiconvex, globose; narrow, hypercline to adpressed area; transapical foramen; deltidial plates lacking, except possibly in some neanic specimens; ribs medium size, intersected by numerous overlapping growth lamellae, commonly expanded into long, wide frills; moderately to strongly plicate commissure; thick pedicle callist, with deep central groove; pedicle collar common; prominent, large, solid teeth; hinge plates bulbous; crural bases round, large; spiralia with fewer than 20 whorls, dorsomedially directed; jugal processes tipped by small jugal plates. [Differs from *Atrypa* in strong biconvexity, presence of wide frills over shell surface, plicate commissure; differs from *Atryparia* in finer, rounded, wavelike ribs, absence of ventral keel, thick pedicle callist.] *Lower Devonian (Lochkovian)–Upper Devonian (middle Frasnian, ?upper Frasnian)*: worldwide.—FIG. 947a–g. **K. culminigera*, middle Eifelian, Germany; a–d, dorsal, ventral, lateral, posterior views, $\times 2$; e–g, serial sections, $\times 3$ (new).
- Oglupes** HAVLÍČEK, 1987b, p. 239 [**O. scarabeus* HAVLÍČEK, 1987b, p. 240; OD] [= *Kantinatrypa* HAVLÍČEK, 1995, p. 58 (type, *K. gambrina* HAVLÍČEK, 1995, p. 59, OD)]. Small to large, biconvex-dorsibiconvex; hypercline-adpressed, obscured area; small beak; foramen absent; ribs relatively coarse; surface bearing distinctive, fine concentric filae, with concentric growth lamellae, frills, or trail; anterior commissure rectimarginate to weakly plicate; pedicle callist moderate; deltidial plates absent; teeth with possible dental nuclei; cardinal process minute to absent; socket plates thin, with strong inner socket ridges; spiralia, jugal processes undescribed. [Distinguished from *Gotatrypa* by coarser ribs, distinct concentric filae, commonly prominent growth lamellae, frills.] *Silurian (upper Llandovery–Wenlock)*: Eurasia.—FIG. 945, 3a–c. **O. scarabeus*, Wenlock, Czech Republic; dorsal, ventral, posterior views, $\times 2.6$ (Havlíček, 1987b).
- ?Omnutakhella** LOPUSHINSKAYA, 1976, p. 66 [**O. bazhenovae*; OD]. Small, rounded, dorsibiconvex, noncarinate; protruding beak; small, orthocline area; transapical foramen; possible deltidial plates; weak, broadly plicate commissure; ribs fine to medium, weakly undulose; growth lamellae, frills absent; small teeth with dental cavities; delicate hinge plate with cardinal pit; thin socket plates; fewer

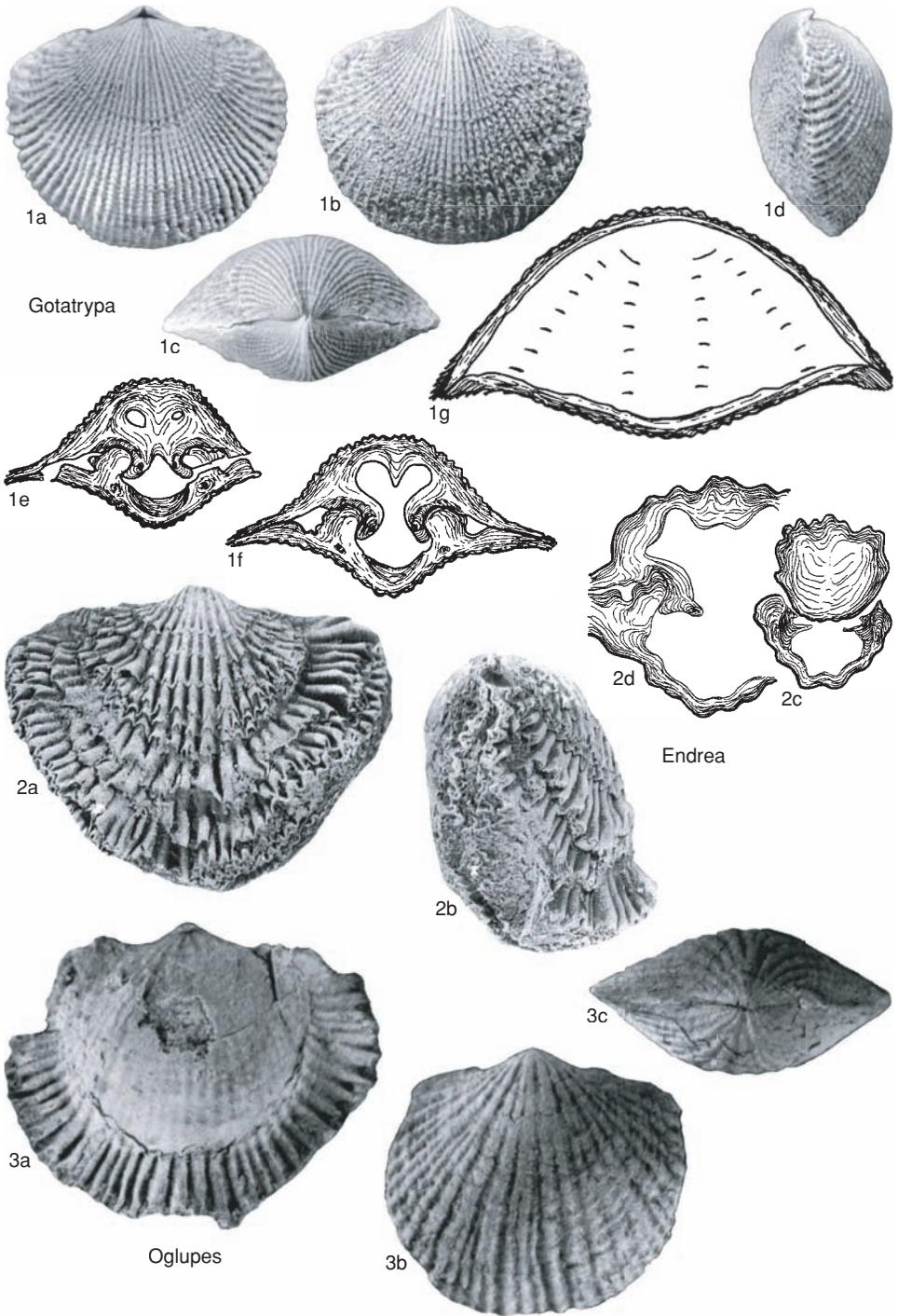


FIG. 945. Atrypidae (p. 1396).

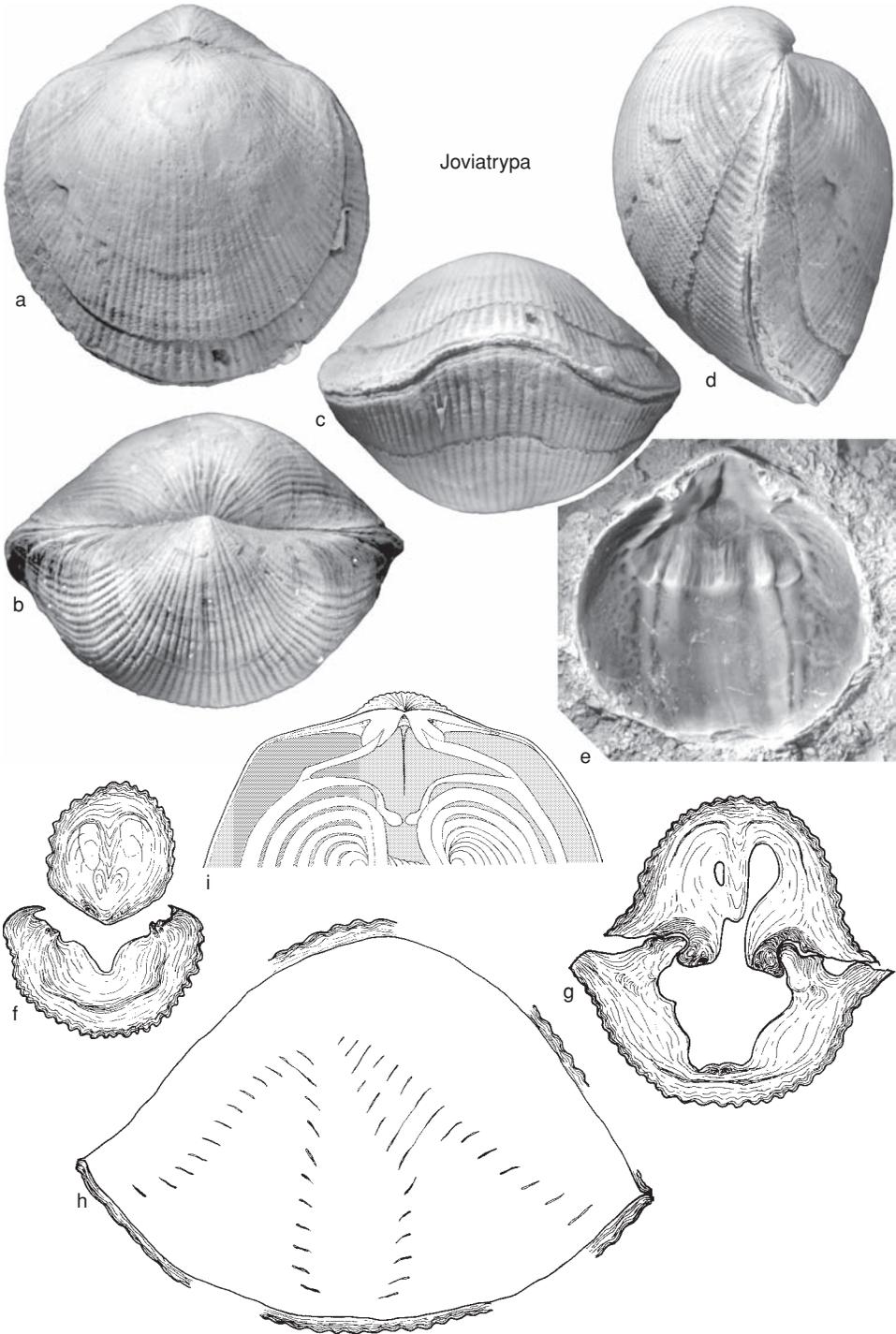


FIG. 946. Atrypidae (p. 1396).

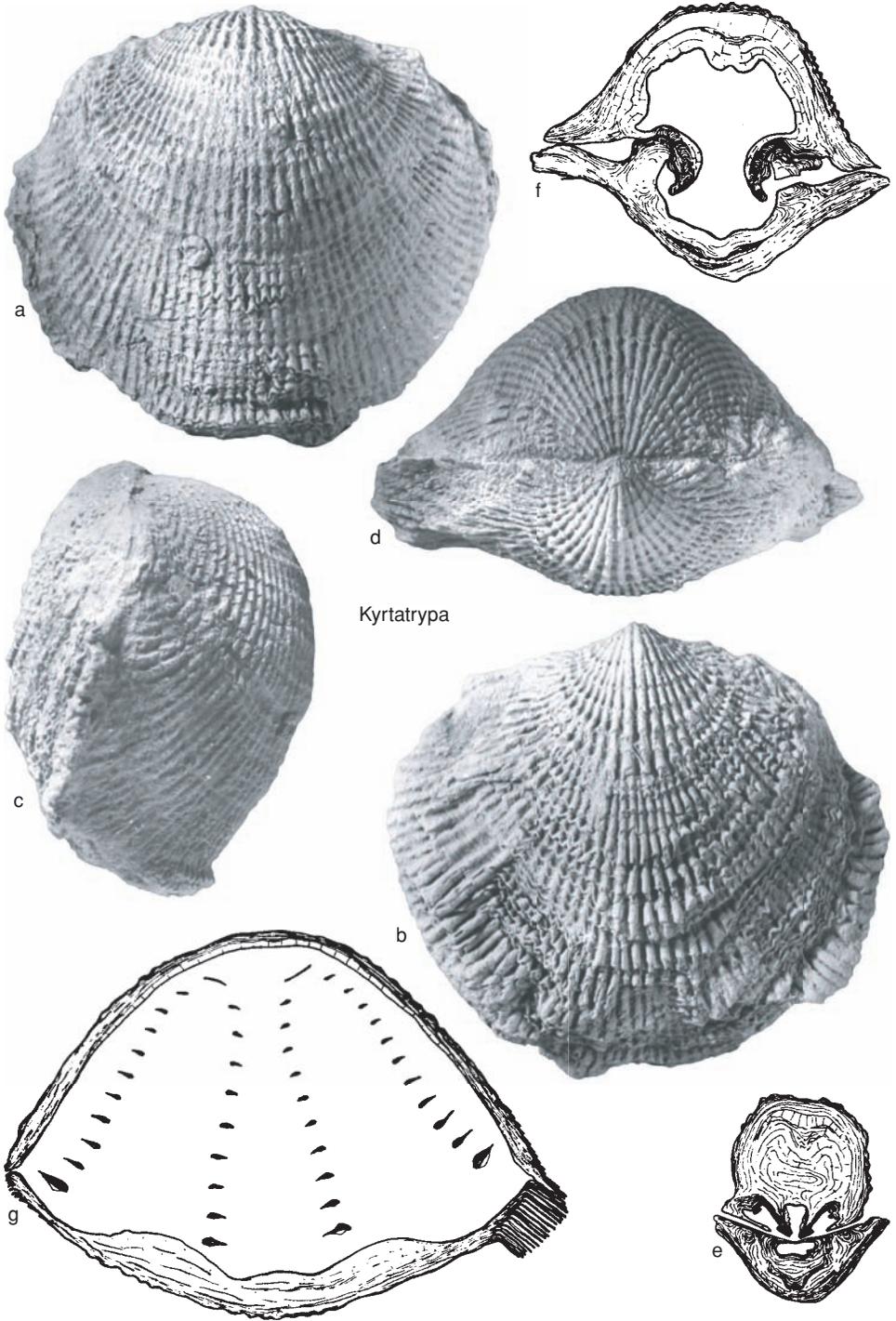


FIG. 947. Atrypidae (p. 1396).

- than 5 to 6 dorsomedial spiralia whorls; crura, jugal processes undescribed. [Possible synonym of *Gotatrypa*, but for prominent dental cavities, lack of pedicle callist; similar to *Procarinatina* and *Dihelictera*, except in rounded shell, short hinge, weakly undulate ribs, lacking carination; differs from *Protatrypa* in small size, round outline, dorsibiconvex shape, dental cavities, short hinge, lacking carination; differs from *Sypharotrypa* in lacking growth lamellae, strong anterior fold.] *Silurian* (Wenlock): Siberian Platform.—FIG. 944,3a–d. **O. bazhenovae*, northern Siberia; a–c, dorsal, ventral, anterior views, $\times 3$; d, serial section, $\times 7$ (Lopushinskaya, 1976).
- Procarinatina** MIZENS & SAPELNIKOV, 1982, p. 18 [**Carinatina silurica* SAPELNIKOV, 1964, p. 9; OD]. Small to medium, biconvex, shield shaped to somewhat wide, flat; ventral valve strongly carinate; dorsal valve with widening median groove; protruding beak; small, apsacline-orthoclinal area; apical foramen; small deltidial plates; ribs fine to medium; ventral midribs raised; ribs interrupted by wavelike, closely spaced, short growth lamellae or interruptions; commissure rectimarginate to bilobate, or weakly sulcinate; pedicle callist absent; short, wide teeth; relatively large dental cavities; hinge plate thick; crura, jugal processes, and spiralia undescribed. [Similar to *Protatrypa* in carination, but differing in having dental cavities, thin hinge plate with cardinal pit, sulcinate commissure; differs from *Dihelictera* in strong carination, nature of growth lamellae, sulcinate commissure.] *Silurian* (Wenlock–Ludlow): Urals.—FIG. 944,2a–e. **P. silurica* (SAPELNIKOV), lower Ludlow, eastern Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 1$; e, serial section, $\times 6.5$ (Mizens & Sapelnikov, 1982).
- Protatrypa** BOUCOT, JOHNSON, & STATON, 1964, p. 809 [**P. malmoeyensis* BOUCOT, JOHNSON, & STATON, 1964, p. 810; OD]. Medium size, biconvex-ventribiconvex; relatively flat, carinate ventral valve; small, distinct orthoclinal area; apical foramen; small deltidial plates; ribs weakly undulate to continuous; absent or very short growth lamellae; frills absent; commissure broadly rectimarginate; internally lacking thick pedicle callist; strong teeth with dental nucleus or minute dental cavities; hinge plates thick, low; cardinal pit lacking; prominent, bushy cardinal process in center of hinge plate; spiralia dorsomedial, fewer than 10 whorls; jugal processes tipped by small jugal plates. [Differs from *Atrypa* in flat, wide shape, orthoclinal area, strong cardinal process, and lacking frills, pedicle callist, and cardinal pit.] *Silurian* (lower Llandovery): North America, Europe, Siberia.—FIG. 948,2a–g. **P. malmoeyensis*, Rhuddanian, Norway; a–d, dorsal, ventral, anterior, lateral views, $\times 2$; e–f, serial sections; g, reconstruction of brachidia, $\times 2.5$ (Copper, 1995).
- Rugosatrypa** RZHONSNITSKAIA, 1975, p. 98 [**R. tschernyschewi* RZHONSNITSKAIA, 1975, p. 99; OD; vid. *Spinatrypa tschernyschewi* RZHONSNITSKAIA, 1964, p. 101, *nom. nud.*, no description]. Small to medium, usually shield shaped, dorsibiconvex to convexoplane; small, distinct orthoclinal area; protruding beak; apical foramen, deltidial plates in all growth stages; ribs relatively fine, *Atrypa*-like with undulose, short, growth lamellae in regular concentric rows; frills absent; commissure rectimarginate to weakly plicate; shell relatively thin; pedicle callist thin to absent; teeth moderately strong; prominent dental cavities; hinge plate modest; socket plates thin; crura delicate; spiralia, jugal processes undescribed. [Shell generally *Atrypa*-like in shape, rib structure, growth lamellae, but possessing orthoclinal area, deltidial plates, dental cavities, lacking thick pedicle callist, frills; similar to *Endrea* externally, but more finely ribbed, smaller sized.] *Silurian* (?Ludlow), Lower Devonian (Lochkovian–Emsian): Eurasia, North America.—FIG. 948,1a–e. **R. tschernyschewi*, Emsian, southern Siberia; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e, detail of ornamentation, $\times 4$ (Rzhonsnitskaia, 1975).
- ?**Togatrypa** HAVLÍČEK, 1987a, p. 76 [**T. fantomas*; OD]. Small to medium, moderately dorsibiconvex; beak adpressed; area absent; foramen transapical or absent; deltidial plates lacking; ribs coarse, undulose, *Spinatrypa*-like; interrupted by wavelike concentric lamellae extended as less than 5-mm-wide commissural frills; rectimarginate commissure; thick pedicle callist; short, solid teeth with lateral processes, lacking nuclei or cavities; socket plates thin, subvertically oriented; crura small; spiralia and jugal processes undescribed. [Possibly synonymous with or ancestral to *Atryparia*; may be mistaken for *Spinatrypa*, but spines absent, with short frills, pedicle callist; similar to *Atrypa* and *Gotatrypa* internally, especially in pedicle callist, hinge plate, teeth, but with very coarse ribs.] Lower Devonian (Lochkovian–Pragian): Czech Republic.—FIG. 948,3a–f. **T. fantomas*, Lochkovian; a–d, dorsal, ventral, posterior, lateral views, $\times 2$; e–f, serial sections, $\times 5$ (Havlíček, 1987a).
- Zygospiraella** NIKIFOROVA, 1961, p. 237 [**Terebratula duboisi* DE VERNEUIL, 1845, p. 97; OD] [= *Megumatrypa* HARPER, 1973, p. 72 (type, *M. glencoensis*, OD); *Cryptospira* LAURIE, 1991, p. 100 (type, *C. intraplicata* LAURIE, 1991, p. 101, OD)]. Small, planoconvex to ventribiconvex, lacking distinct carination; small orthoclinal area; apical-transapical foramen; ribs continuous, anteriorly interrupted by short growth interruptions; frills absent; rectimarginate to weakly sulcate commissure; short teeth; small dental cavities; hinge plate shallow; wide cardinal pit; small crural bases; partly feathered crura; mediadorsal spiralia with fewer than 6 whorls; jugal processes tipped by small jugal plates. [Hinge plates, jugal processes, and crura as in *Protatrypa*, but differing in small size, convexity, lack of carination, presence of cardinal pit.] *Silurian* (lower Llandovery): Eurasia, North America, Tasmania.—FIG. 949a–d. **Z. duboisi* (DE VERNEUIL), Rhuddanian, Estonia; serial sections, and reconstruction of brachidia, $\times 5$ (Copper, 1982).—FIG. 949e–j. *Z. planoconvexa* (HALL), Rhuddanian,

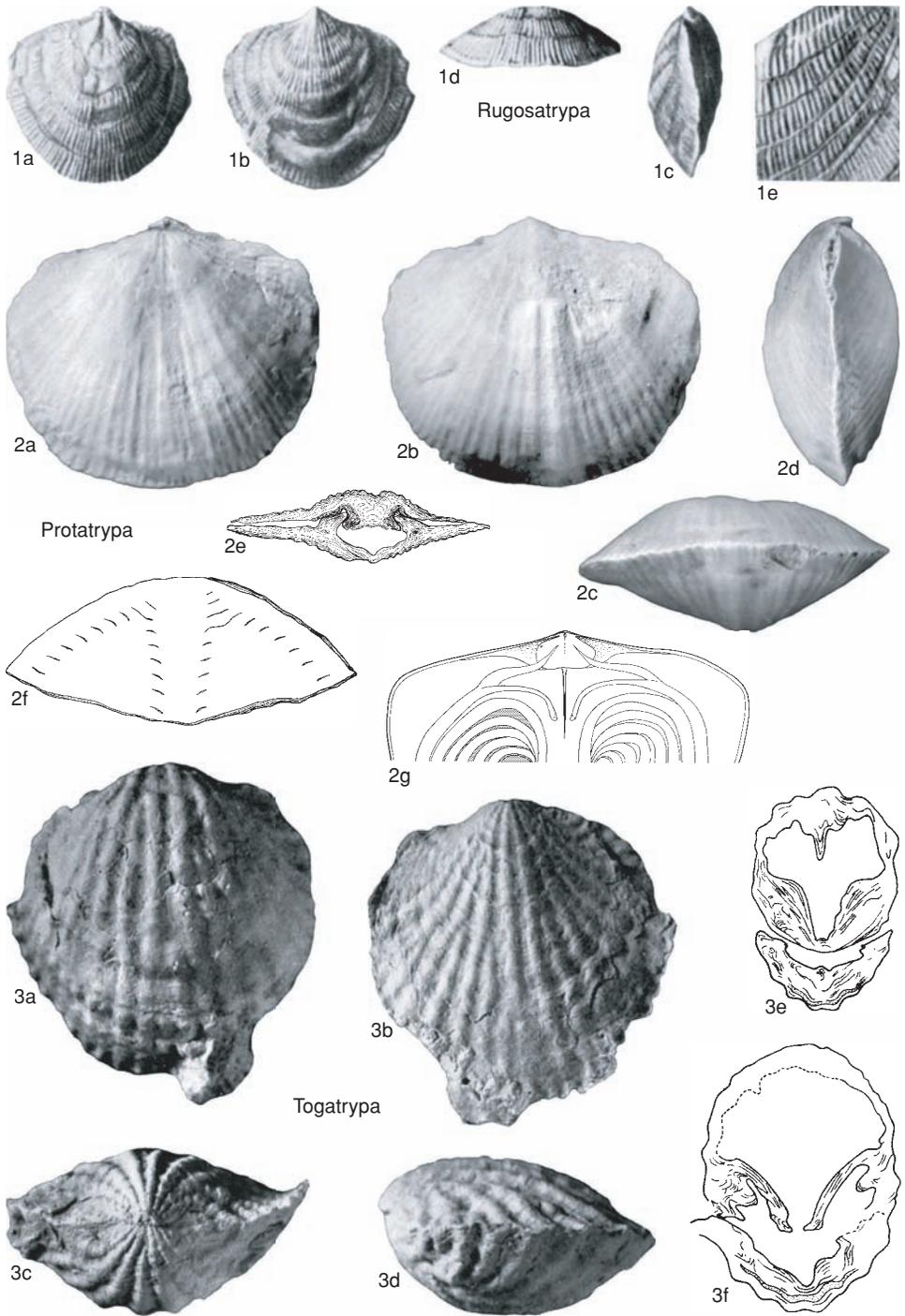


FIG. 948. Atrypidae (p. 1400).

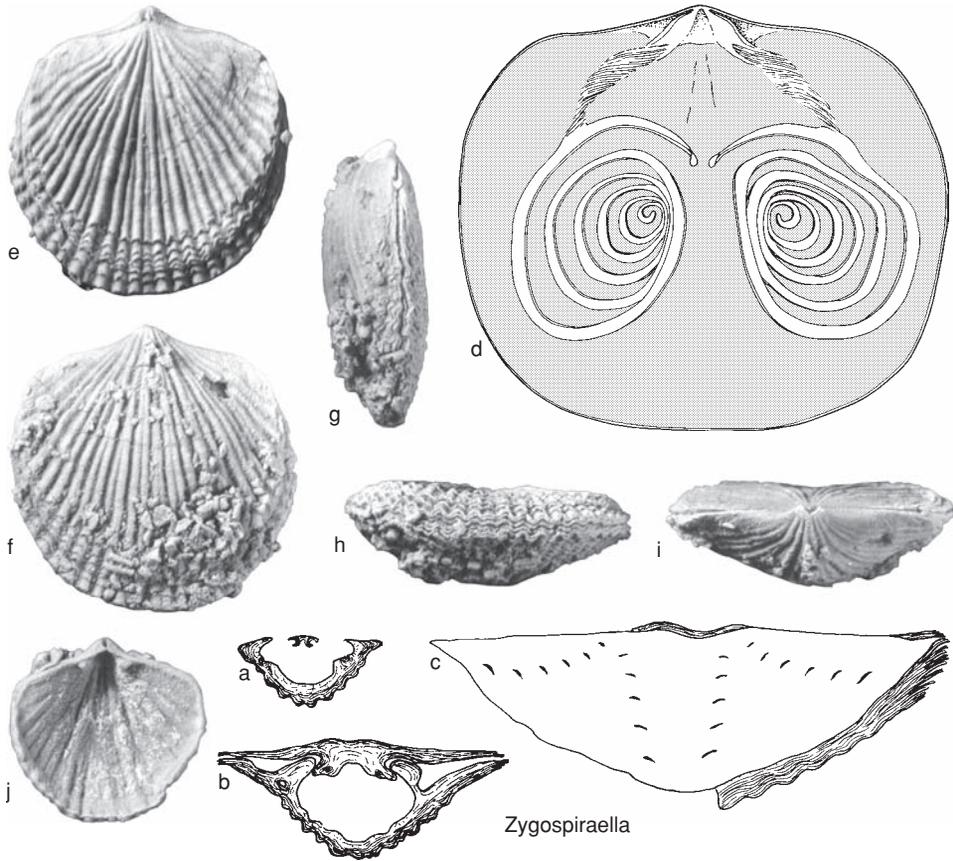


FIG. 949. Atrypidae (p. 1400–1402).

eastern Canada; dorsal, ventral, lateral, anterior, posterior views, internal ventral valve, $\times 2$ (Copper, 1982).

Subfamily INVERTININAE Copper & Chen, 1995

[Invertininae COPPER & CHEN, 1995, p. 251]

Small to medium, fine, tubular to imbricately ribbed, lacking carination; short growth lamellae; frills absent; prominent orthocline-procline area; valves commonly asymmetrical, fixosessile-cemented via ventral valve apex; pedicle callist normally well developed, commonly with pedicle collar pressed against thick deltidial plates; teeth strong, solid, lacking dental cavities; muscle field commonly raised on solid platform; hinge plates thick, spiralia mediodorsal; jugal

processes small. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*.

Invertina COPPER & CHEN, 1995, p. 254 [**Atrypa aspera* var. *sinensis* VON RICHTHOFEN, 1883, p. 83; OD]. Small to medium, elongate, planoconvex-ventribiconvex (weakly convex ventral valve); orthocline-anacline area; apical-transapical foramen; small deltidial plates; ribs fine to medium, imbricate, intersected by numerous, closely spaced, short growth lamellae (spines absent); internally moderate pedicle callist integrated with deltidial plates; teeth solid, strong, with lateral lobes; small cardinal process in cardinal pit overlapping inner socket ridges; crura short, partly fibrous, extended from long inner socket ridges; dorsomedial spiralia with fewer than 8 whorls; jugal processes terminating in small, stubby jugal plates. [Externally similar to *Spinatrypa* but planoconvex, with solid teeth, pedicle callist, lacking dental cavities; differs from *Falsatrypa* and *Kerpina* in normal bilateral symmetry, smaller area, coarser ribs; differs from *lowatrypa*

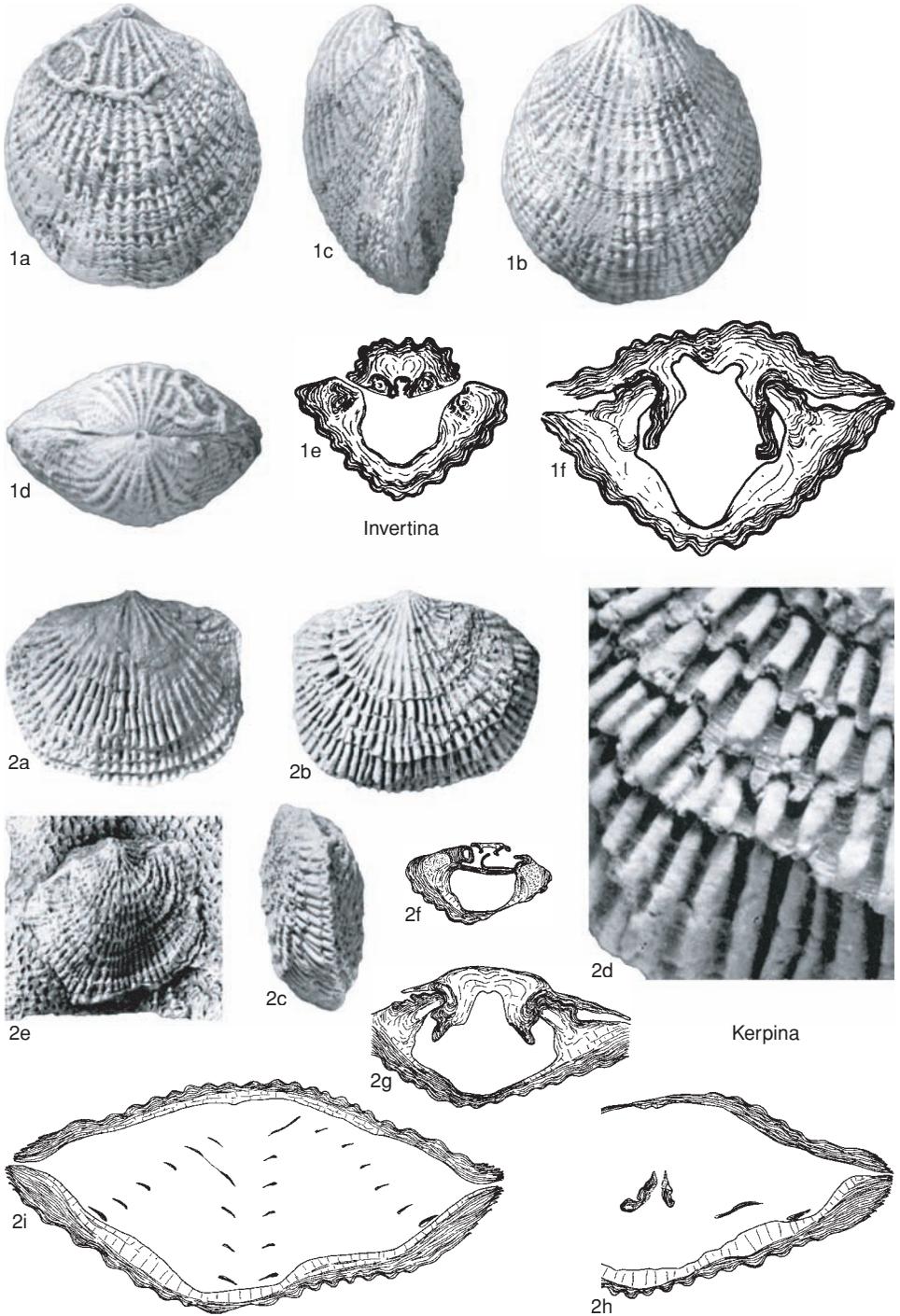


FIG. 950. Atrypidae (p. 1402–1404).

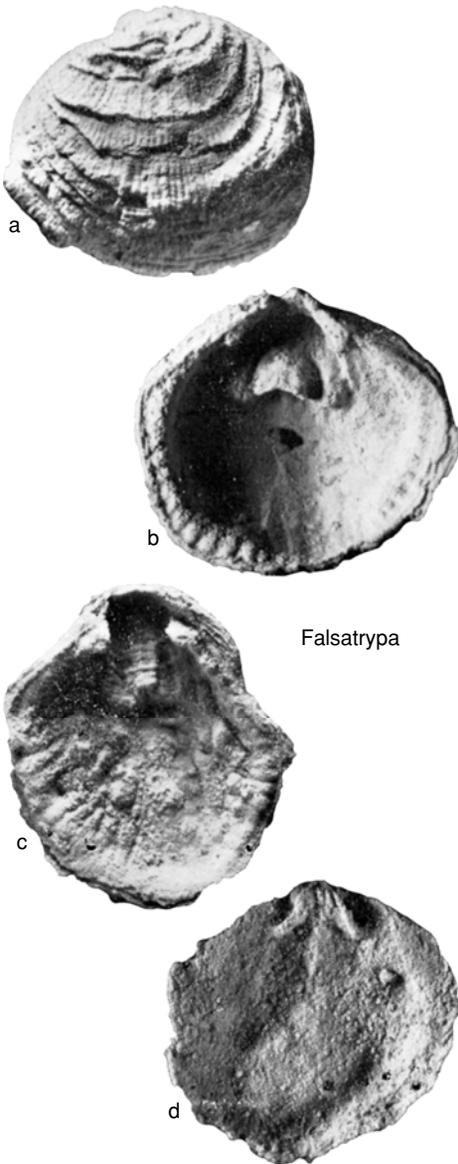


FIG. 951. Atrypidae (p. 1404).

in imbricate-tubular ribs.] *Middle Devonian (Givetian)*: China, North Africa.—FIG. 950, 1a–f. **I. sinensis* (VON RICHTHOFEN), lower Givetian, Sichuan; a–d, dorsal, ventral, lateral, posterior views, $\times 2$; e–f, serial sections, $\times 5$ (new).

?*Falsatrypa* HAVLÍČEK, 1956, p. 584 [**F. admiranda*; OD]. Small, usually asymmetric (possibly fixosessile), ventribiconvex-planoconvex; wide, deformed orthocline-apsacline area; apical foramen; deltidial plates; fine, tubular-imbricate ribs;

rectimarginate commissure; short, overlapping growth lamellae; teeth solid, lacking dental cavities; crura, spiralia, jugal processes undescribed. [Poorly preserved, rare genus of problematic affinity (*vid.* HAVLÍČEK, 1967a), assigned by HAVLÍČEK (1987a) to Lissatrypidae; possibly synonymous with *Kerpina*, but more finely ribbed, smaller.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Czech Republic.—FIG. 951a–d. **F. admiranda*, Emsian; a–c, ventral external, internal, internal views, approximately $\times 4$; d, dorsal internal view, approximately $\times 6$ (Havlíček, 1987a).

Kerpina STRUVE, 1961, p. 333 [**K. vineta vineta*; OD] [= *Adaptatrypa* STRUVE, 1980, p. 412 (type, *A. heckeri*, OD)]. Small to medium, usually with asymmetric growth (commonly fixosessile), variable convexity from ventribiconvex-concavoconvex; proportionally large, very wide, sharp edged, often twisted, procline-orthocone area; large apical foramen; relatively wide deltidial plates; fine to medium tubular-imbricate ribs; overlapping, short growth lamellae; rectimarginate to weakly plicate commissure; pedicle collar conjunct to thick deltidial plates; teeth solid, lacking dental cavities; spiralia dorsomedial, with fewer than 8 whorls; jugal processes curved together in V-shape, tipped by jugal plates. [Possibly synonymous with *Falsatrypa*, but brachidia for *Falsatrypa* undescribed.] *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian, ?lower Givetian)*: western Europe, Urals (western slopes).—FIG. 950, 2a–i. **K. vineta vineta*, upper Eifelian, Germany; a–c, dorsal, ventral, lateral views, $\times 2$; d, enlarged detail ornament, $\times 8$; e, specimen fixed to alveolitic coral, $\times 2$; f–i, serial sections, $\times 4$ (Copper, 1967e).

Subfamily

PSEUDOGRUENEWALDTIINAE

Rzhonsnitskaia, Yudina, & Sokiran, 1997

[*nom. correct.* COPPER, herein, *pro* Pseudogruenewaldtiinae RZHONSNITSKAIA, YUDINA, & SOKIRAN, 1997, p. 57]

Ventribiconvex to planoconvex, small to large shells, ribbing as in Atrypinae, lacking carination and with no frills or only short growth lamellae (less than 1 mm); beak orthocline-anacline; pedicle callist to collar variably developed, teeth strong, lacking dental cavities, muscle field normally raised on thick platform, thick hinge plates; spiralia mediodorsal, small jugal processes. *Upper Devonian (Frasnian)*: worldwide.

Pseudogruenewaldtia RZHONSNITSKAIA, 1960b, p. 48 [**P. tschernyschewi*; OD]. Medium to large, inflated ventribiconvex-biconvex, rounded to elongate; small, hypercline area, obscuring deltidial plates; large transapical foramen, beak anacline-hypercline; ribs fine, interrupted by numerous, closely spaced growth lamellae; shell wall thick; pedicle callist

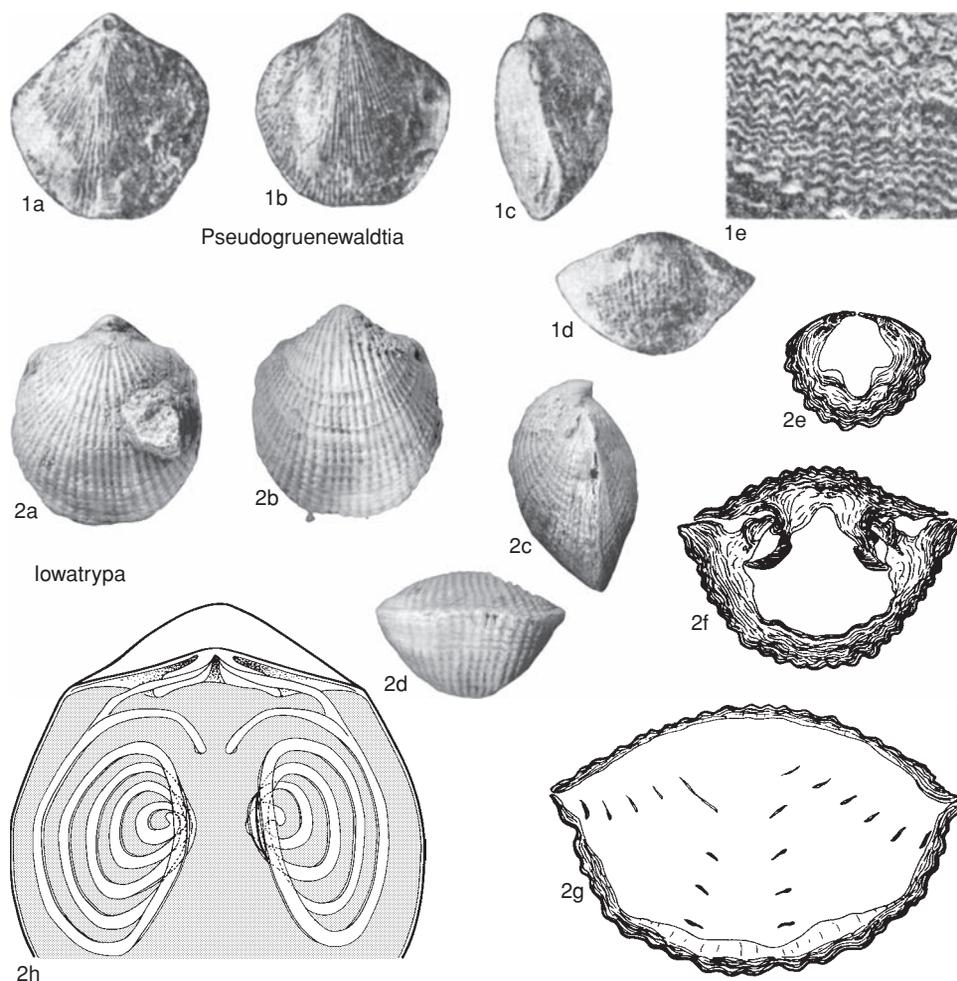


FIG. 952. Atrypidae (p. 1404–1405).

divided by central groove; hinge plate strong; cardinal pit small; socket plates thin; spiralia mediodorsal; crura, jugal processes undescribed. [Differs from closely related *Iowatrypa* in larger shell, hypercline area with large transapical foramen, lack of deltidial plates, raised muscle platform; distinguished from *Anatrypa* by microornament of overlapping growth lamellae; distinguished from *Gruenewaldtia* by lack of septally raised muscle platform.] *Upper Devonian (Frasnian)*: northern Urals, Poland, Germany. — FIG. 952, 1a–e. **P. tschernyschewi*, Timan, Russia; a–d, dorsal, ventral, lateral, anterior views, $\times 1$; e, detail of macroornament, $\times 4$ (Rzhonsnitskaia, 1964).

Iowatrypa COPPER, 1973c, p. 495 [**Atrypa owenensis* WEBSTER, 1921, p. 14; OD]. Small, elongate to equidimensional, planoconvex-ventribiconvex; commonly with short, straight hinge; small, orthocline-anacline area; apical foramen; minute

deltidial plates; ribs relatively fine, *Atrypa*-like; numerous, tightly spaced, non-deflected, very short growth lamellae; commissure rectimarginate; interior with relatively thick ventral valve; usually thick pedicle callist or collar; short teeth with notch for crura; small dental cavities or nuclei; incised muscle scars; prominent, thickened ventral muscle platform; crural bases Z-shaped; crura short, stubby; spiralia dorsomedial, fewer than 8 whorls; jugal processes thick, ending in minute jugal plates. [Similar to *Pseudogruenewaldtia*, but smaller, ventribiconvex-planoconvex shell, possessing apical foramen, deltidial plates, and raised ventral muscle platform.] *Upper Devonian (Frasnian)*: North America, Europe, Urals, China. — FIG. 952, 2a–h. **I. owenensis* (WEBSTER), upper Frasnian, Iowa; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e–g, serial sections; h, reconstruction of brachidia, $\times 5$ (new).

Subfamily SPINATRYPINAE
Copper, 1978

[Spinatrypinae COPPER, 1978, p. 297]

Atrypides with ribs disrupted into waves, commonly producing nodular surface macroornament; commonly spinose or imbricate; growth lamellae short, may be projected up to about 10 mm as irregular spines from rib crests; ventral valve noncarinate; usually small beak; small orthocline-anacline area; deltidial plates reduced or covered; apical-transapical foramen; rectimarginate to plicate commissure; pedicle callist thin to moderate; pedicle collar rarely developed; teeth with dental cavities, lateral lobes; small cardinal process in cardinal pit; spiralia dorsomedial, about 15 whorls in large shells; jugal processes normally terminating in stubby, short jugal plates. [Considerable infrageneric and infraspecific variability in convexity and spinosity for Wenlockian to Emsian forms suggests that such ancestral taxa as *Eospinatrypa*, *Punctspinatrypa*, and *Oglu* may be synonymous or should be considered as subgenera; ancestry of subfamily lies with Plectatrypinae.] *Silurian* (?*Telychian*, *Wenlock*)—*Upper Devonian* (*Frasnian*).

Spinatrypa STAINBROOK, 1951, p. 196, *nom. nov. pro Hystericina* STAINBROOK, 1945, p. 49, *non* MALLOCH, 1932 [**Atrypa hystrix* var. *occidentalis* HALL, 1858a, p. 515; OD] [= *Plicispinatrypa* RZHONSNITSKAIA in RZHONSNITSKAIA & others, 1998, p. 322 (type, *Spinatrypa plicata* RZHONSNITSKAIA, 1975, p. 124, OD, *vid. Spinatrypa plicata* RZHONSNITSKAIA, 1964, p. 108, *nom. nud.*)]. Medium to large, dorsibiconvex to convexoplane; small orthocline-hypercline area; foramen apical-transapical; deltidial plates commonly lost or obscured by beak incurvature; ribs coarse to very coarse, rarely becoming almost smooth; strong, wavelike growth lamellae developing into coarse, irregular spines up to 15 mm long; moderately to strongly plicate commissure; interior with thin pedicle callist or collar; teeth large, with accessory lobes; dental cavities small to prominent (i.e., strong dental plates); hinge plates strong; crura curved, feathered; dorsal spiralia with 8 to 15 widely spaced whorls; long jugal processes terminating in large, spatulate jugal plates. [Distinguished from *Isospinatrypa* and *Spinatrypa* by large size, very coarse, undulose ribs, long spines, more prominent area, deltidial plates, larger dental cavities. STAINBROOK first described the genus as *Hystericina* (1945), which turned out to be preoccupied, so he substituted *Spinatrypa* (1951). When he

cited the type he indicated *Atrypa aspera* var. *occidentalis*, for he misread the original HALL description that said *Atrypa hystrix* var. *occidentalis* (corrected, but not by STAINBROOK). In 1938, moreover, STAINBROOK had already raised *occidentalis* to species rank, which he had forgotten about by 1945. RZHONSNITSKAIA described *Plicispinatrypa* as part of a wider paper by her and others in 1998 (she alone is listed as author of the genus). The type of *Plicispinatrypa* is cited as *Spinatrypa plicata* RZHONSNITSKAIA, 1964; unfortunately in 1964 she never described the species and just published a single figure. She finally described the species *plicata* in 1975, which then validates the species.] *Middle Devonian* (*Upper Eifelian*, *Givetian*)—*Upper Devonian* (*Frasnian*): worldwide.—FIG. 953a–c. **S. occidentalis* (HALL), Iowa, USA; dorsal, posterior, lateral views, $\times 2$ (new).—FIG. 953d–e. *S. spinosa* (HALL), Givetian, New York, USA; internal views of ventral, dorsal valves, $\times 2$ (new).—FIG. 953f–g. *S. curvirostra* COPPER, lower Givetian, Germany; serial sections, $\times 3$ (Copper, 1967d).

?*Catatrypa* MIZENS, 1993, p. 3 [**C. schemachensis*; OD]. Small, convexoconcave to questionably convexoplane, ventral valve almost flat; protruding beak, catacline-apsacline area; small apical foramen; ribs coarse, with concentric lamellae, spines; internal structures undescribed except for massive crura, lack of dental cavities. [Distinguished from other spinatrypids by flattened ventral valve, prominent area with catacline-apsacline beak; similar to *Oglu* in convexity, but lacks hypercline beak of *Oglu*, and has apsacline area with apical foramen; possibly a synonym of davidsoniid ?*Rugodavidsonia*, with comparable asymmetry, ribs, area, and foramen; may also be aberrant ?*Kerpina*.] *Middle Devonian* (*Eifelian*): western slopes of Urals.—FIG. 954, 1a–c. **C. schemachensis*; ventral, dorsal, lateral views, $\times 3$ (Mizens, 1993).

Eospinatrypa COPPER, 1973c, p. 496 [**Atrypa nodostriata* HALL, 1852, p. 272; OD] [= *Morinatrypa* HAVLÍČEK in HAVLÍČEK & STORCH, 1990, p. 165 (type, *M. mergli*, OD)]. Small to medium, round to elongate or shield shaped, biconvex; small, orthocline area; apical (rarely transapical) foramen; minute deltidial plates; weak anterior fold; ribs few, coarse, bifurcating ventrally, intercalating dorsally, weakly raised ventral midrib pair; spines absent, rarely capidulate; short, weakly deflected, undulose growth lamellae; thin wall; pedicle callist thin or lacking; small, delicate teeth; small dental cavities; hinge plates thin; crural bases rounded; crura short; dorsomedial spiralia, fewer than 8 whorls; nodose jugal processes; thin, scooplike jugal plates. [Distinguished from *Spinatrypa* by small size, lack of spines, delicate tooth and socket structure, fewer spiralia whorls.] *Silurian* (?*Telychian*, *Wenlock*—*Přídolí*): North America, Eurasia.—FIG. 955, 1a–c. **E. nodostriata* (HALL), Wenlock, New York; a–c, dorsal, ventral, posterior views, $\times 2$ (Copper, 1973c).—FIG. 955, 1d–g. *Eospinatrypa* sp., upper Wenlock, Gotland; d–f, serial sections; g, reconstruction of brachidia, $\times 5$ (new).

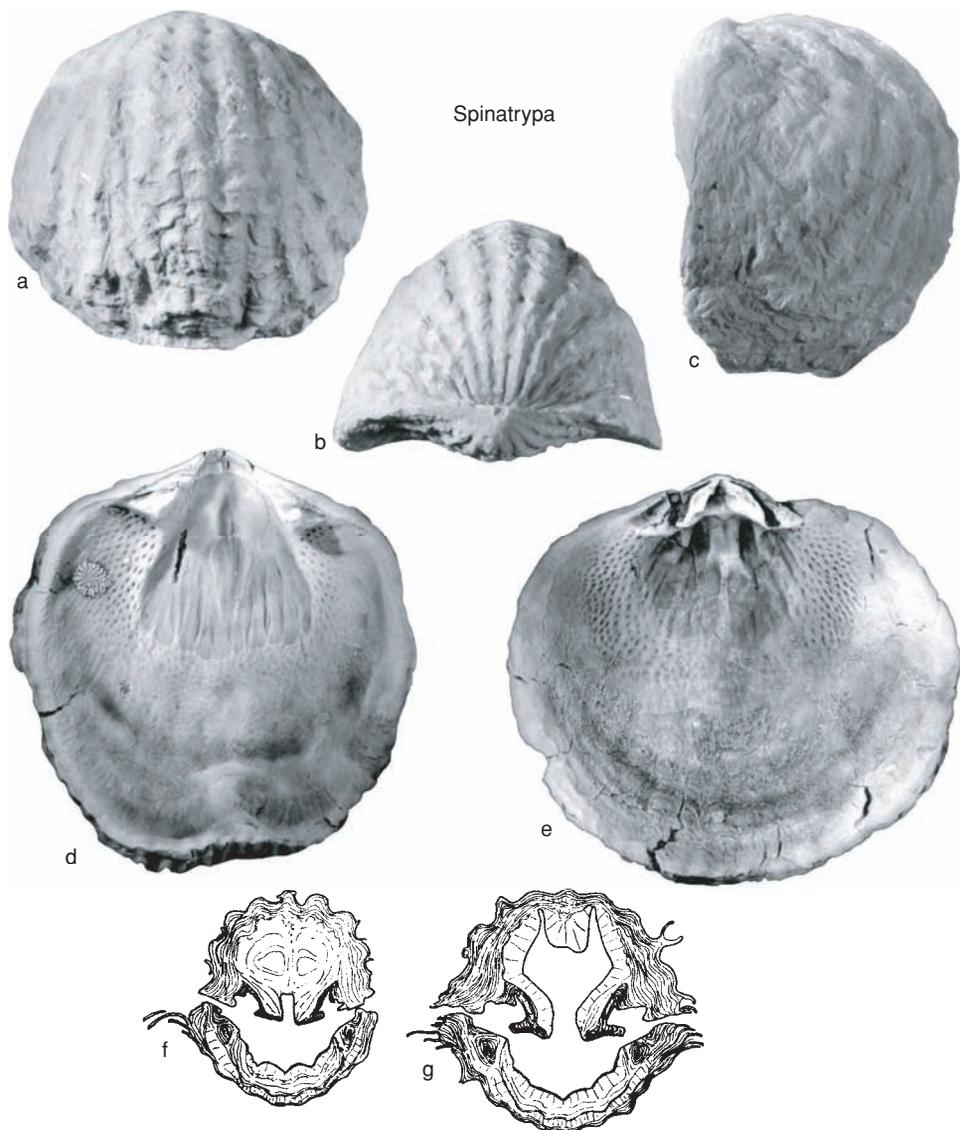


FIG. 953. Atrypidae (p. 1406).

?*Gibberosatrypa* MARKOVSKII & RZHONSNITSKAIA in RZHONSNITSKAIA & others, 1998, p. 316 [**Atrypa gibberosa* MARKOVSKII, 1989, p. 90; OD]. Medium size, relatively coarsely ribbed; subquadrate to subcircular shell, subcarinate ventrally, with broad, flat fold anteriorly; interior unknown. [Coarser ribs suggest *Spinatrypa* derivation, with some external similarities to *Carinatrypa* and *Mogoliella*; original material described by MARKOVSKII (1989) resembles spinatrypid; assignment unclear.] *Upper Devonian (Frasnian)*: Urals, Russian Platform.—FIG. 956, 1a–d. **G. gibberosa* (MARKOVSKII), upper

Frasnian, southwestern Urals; dorsal, ventral, lateral, anterior views, $\times 2$ (Rzhonsnitskaia & others, 1998).

Inverttrypa STRUVE, 1961, p. 334 [**Spinatrypa kelusiana* STRUVE, 1956, p. 385; OD]. Small to medium, ventribiconvex-planoconvex-concavoconvex; small, hypercline area; foramen transapical; deltidial plates absent or minute, obscured by beak; anterior commissure rectimarginate, rarely weakly sulcate; ribs coarse, undulose to nearly flat, ending in 4 to 5 mm long, straight spines, especially on ventral valve; strongly developed ventral midrib keel

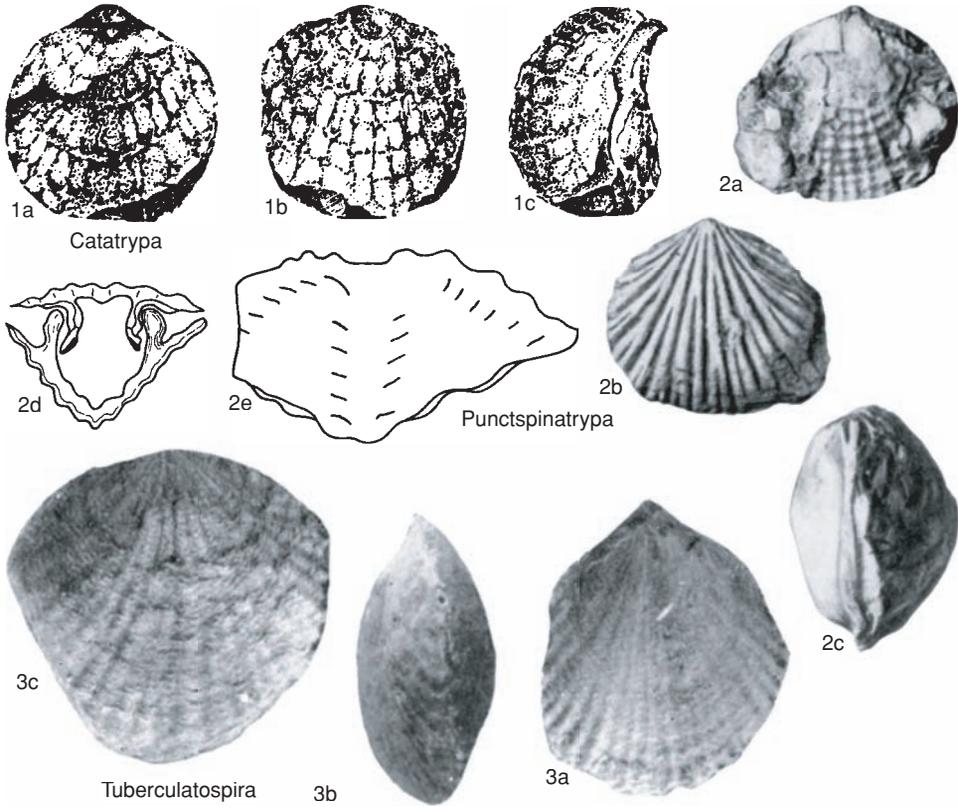


FIG. 954. Atrypidae (p. 1406–1412).

from 2 ribs; internally shell relatively thick; teeth short; small dental cavities; crura feathered; spiralia dorsomedial, fewer than 10 whorls; jugal processes with minute jugal plates. [Distinguished from *Spinatrypa* by small size, reversed convexity, rectimarginate commissure, relatively strong ventral midrib plan, obscured hypercline area; distinguished from *Iso-spinatrypa* by almost flat ribs, hypercline area, absence of deltidial plates, enlarged ventral midrib pair; distinguished from *Oglu* by reversed convexity.] *Middle Devonian* (upper Eifelian–lower Givetian): Europe, northwestern Canada. —FIG. 955, 2a–b. **I. kelusiana* (STRUVE), upper Eifelian, ?lower Givetian, Germany; a–d, ventral, lateral, ventral, dorsal views of 2 specimens, $\times 2$; e–g, serial sections, $\times 4$ (Copper, 1967d); b, reconstruction of brachidia, $\times 4$ (Copper, 1967b).

Iso-spinatrypa STRUVE, 1966, p. 155 [**Terebratulites asper* VON SCHLOTTHEIM [sic], 1813, pl. 1, fig. 7 (description, VON SCHLOTTHEIM, 1820 in 1820–1823, p. 263); OD; modified to *aspera* by KOENIG, 1825, p. 3] [= ?*Hanusitrypa* HAVLÍČEK, 1967a, p. 443 (type, *H. hanusi*, OD)]. Small to medium; bi-convex to weakly dorsibiconvex, shield shaped to

elongate; small orthocline-anacline area; blunt beak; minute deltidial plates flanking apical-transapical foramen; ribs medium sized, well defined; ventral midribs only slightly raised; short, wavy growth lamellae ending in short, irregular spines on both valves; rectimarginate to weakly plicate commissure; thin pedicle callist; stubby teeth; small dental cavities; spiralia dorsomedial, fewer than 12 closely spaced whorls; jugal processes short, tipped by small, blunt jugal plates. [Distinguished from *Spinatrypa* by small size, finer, well-defined ribs, short spines; distinguished from *Invertrypa* by bi-convexity; possibly synonymous with *Oglu* but with reduced pedicle callist, clearly defined ribs.] *Lower Devonian* (?Lochkovian, Emsian)–*Middle Devonian* (lower Givetian): worldwide. —FIG. 956, 3a–i. **I. aspera* (VON SCHLOTTHEIM), upper Eifelian, Germany; a–d, dorsal, ventral, posterior, posterior views, $\times 2$; e–f, internal view dorsal, ventral valve, $\times 2$; g–i, serial sections, $\times 4$ (Copper, 1967d).

?**Oglu** HAVLÍČEK, 1987a, p. 81 [**Terebratulata semiorbis* BARRANDE, 1847, p. 454; OD]. Small to medium, elongate-equidimensional, dorsibiconvex-convexoplane; hypercline area; deltidial plates lacking;

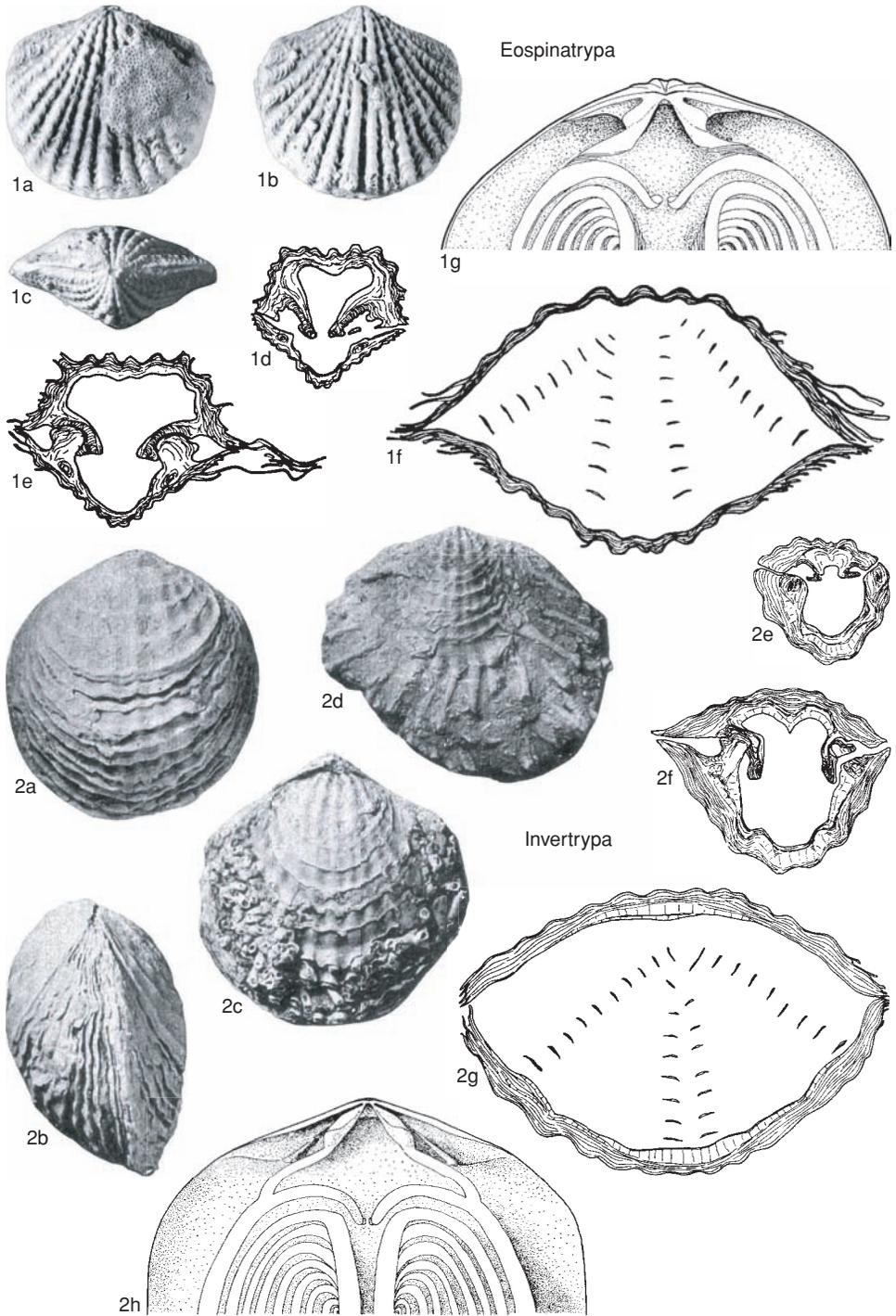


FIG. 955. Atrypidae (p. 1406–1408).

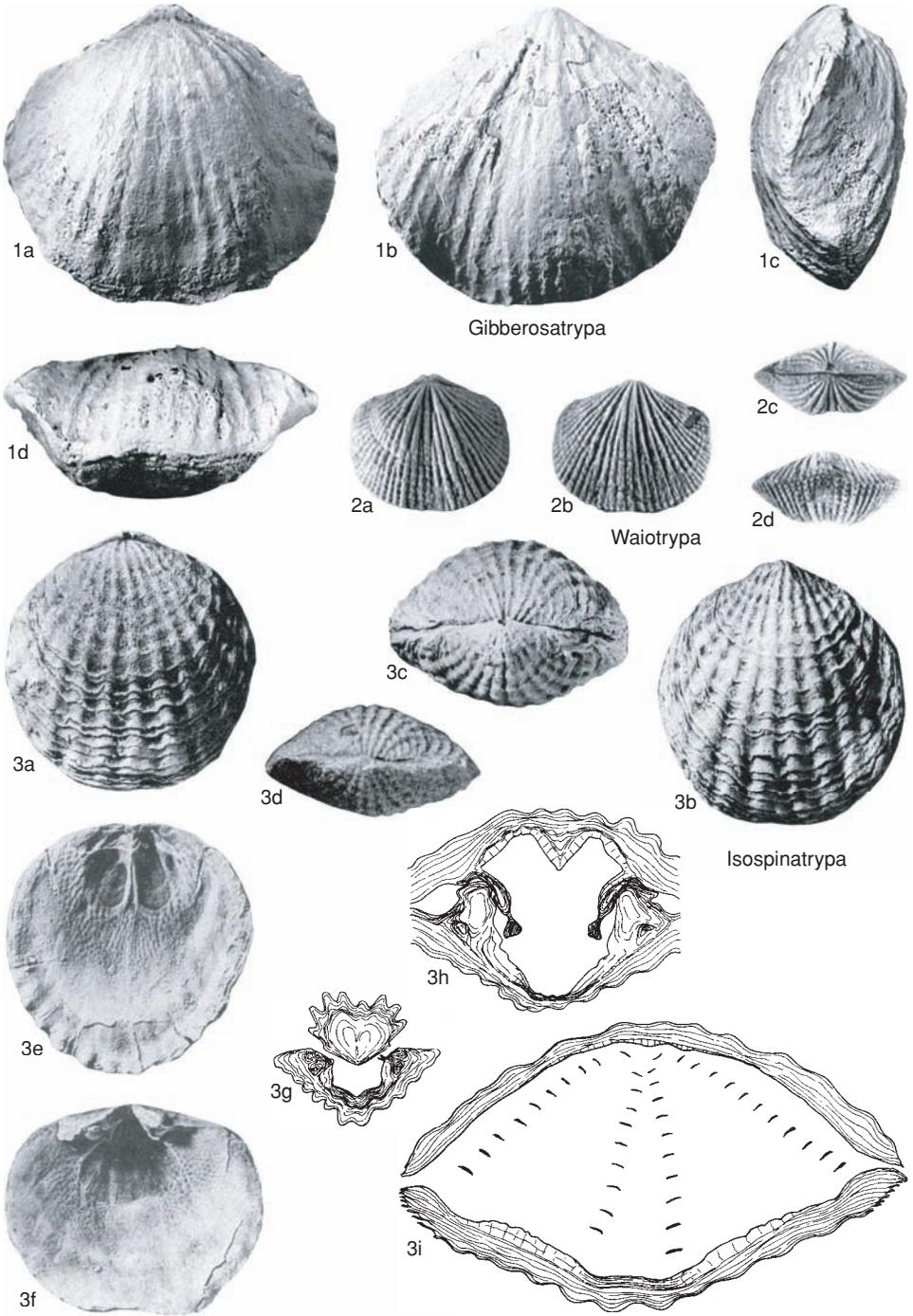


FIG. 956. Atrypidae (p. 1407–1412).

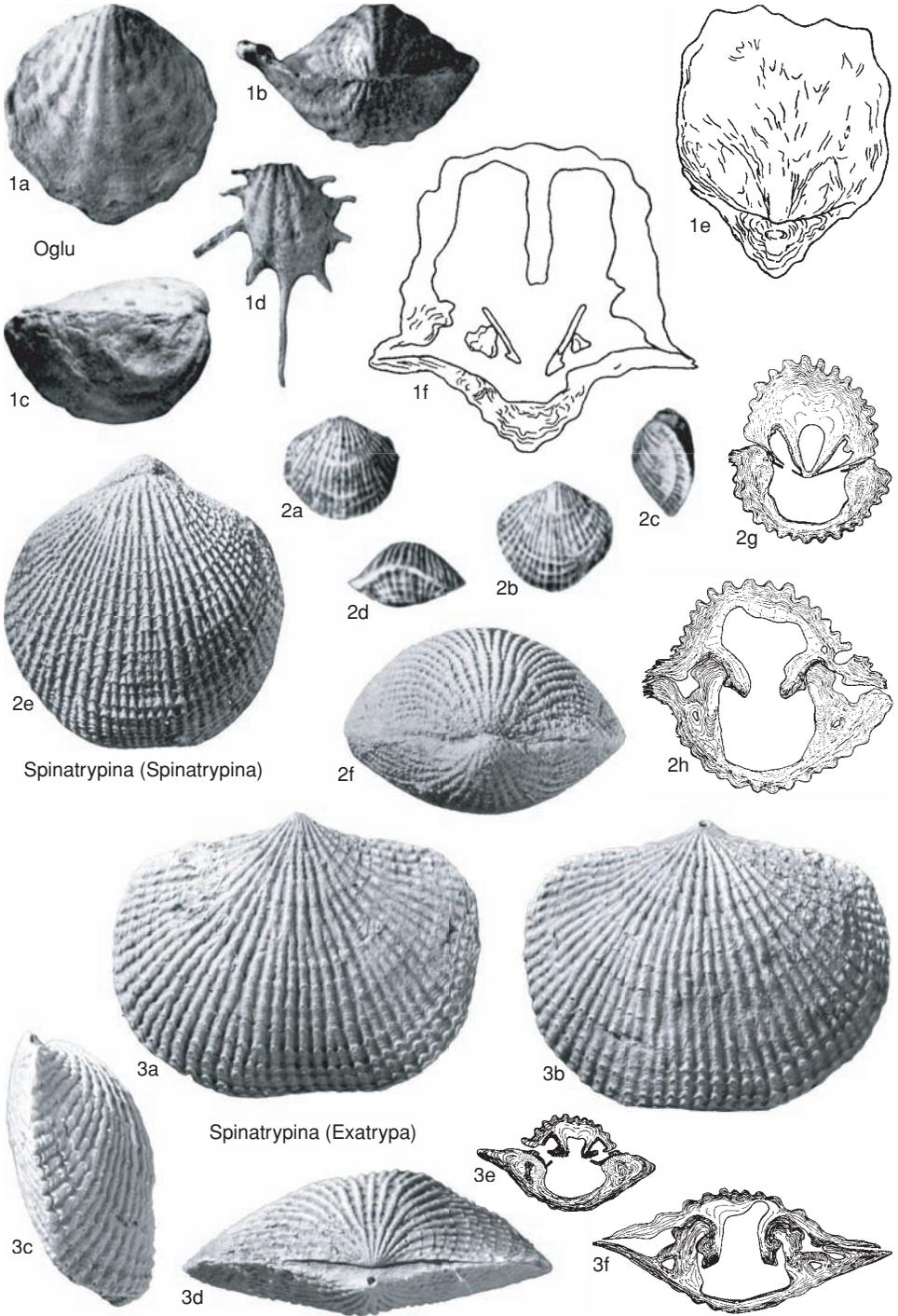


FIG. 957. Atrypidae (p. 1408-1412).

- foramen transapical or lacking; relatively few, expanding, rarely bifurcating, undulose ribs, strong ventral midrib pair; simple growth lamellae on ventral valve; short spines possibly limited to dorsal valve; rectimarginate commissure; thick pedicle callist; solid teeth; crura strongly arcuate; spiralia, jugal processes undescribed. [Possible synonym of *Eospinatrypa* or *Punctspinatrypa*, differing in reversed convexity; distinguished from *Isospinatrypa* and *Eospinatrypa* by thick pedicle callist, possible restriction of spines to brachial valve, hypercline area, convexoplane shell; lack of deltidial plates. Differences between *Isospinatrypa*, *Oglu*, and *Punctspinatrypa* are relatively minor, and may not be sufficient to allow even subgeneric distinction.] *Lower Devonian (Pragian–Emsian)*: Europe, northern Africa, Urals.—FIG. 957,1a–f. **O. semiorbis* (BARRANDE), Pragian, Czech Republic; a–c, ventral, posterior, lateral views, approximately $\times 3.7$; d, dorsal valve, $\times 1.5$; e–f, serial sections, $\times 5$ (Havlíček, 1987a).
- ?**Punctspinatrypa** RZHONSNITSKAIA, 1975, p. 116 [**Atrypa rejenis* KHODALEVICH, 1951, p. 79; OD] [= *Atrypunculus* HAVLÍČEK, 1987a, p. 94 (type, *A. hians* HAVLÍČEK, 1987a, p. 95, OD)]. Medium, ventribiconvex–planoconvex, rounded to elongate; hypercline area; concealed deltidial plates, foramen; well-developed ventral midrib pair forming weak carination; ribs coarse, posteriorly relatively straight, interrupted by regular, short growth lamellae along commissure, lacking wavelike interruptions; spines undescribed (shell nonfenestrate); commissure rectimarginate to very weakly plicate; slender, vertically oriented teeth; small dental cavities; slender socket plates; spiralia, jugal processes undescribed. [Fenestrae or punctae attributed to genus absent in topotype specimens of type species, are possibly borings. Convexity, midrib pair as in *Invertrypa*, but internal comparison unavailable; possibly synonymous with *Oglu*, but for convexity, which may be variable.] *Lower Devonian (Pragian–Emsian)*: Europe, Urals, central Asia.—FIG. 954,2a–e. **P. rejenis* (KHODALEVICH), Pragian, eastern slopes, Urals; a–c, dorsal, ventral, lateral views, $\times 1$; d–e, serial sections, approximately $\times 3$ (Rzhonsnitskaia, 1975).
- Spinatrypa** RZHONSNITSKAIA, 1964, p. 101 [**S. margaritoides*; OD] [= *Sibirispira* ALEKSEVA, 1968, p. 198 (type, *S. inflata* ALEKSEVA, 1968, p. 200, OD)]. Small to medium, rounded, globose, biconvex to planar; short to longer hinge; small, orthocline area; protruding beak; apical foramen; deltidial plates; fine to medium-sized, tubular-imbricate ribs; spines lacking; short deflected, rhythmic growth lamellae producing strong imbrication; weakly plicate commissure; thin shell wall, lacking pedicle callist or collar; delicate, long teeth; small to large dental cavities; hinge and socket plates thin, delicate; crura straight or partly feathered; dorsomedial spiralia with fewer than 10 whorls; jugal processes tipped by small plates. [Distinct from *Spinatrypa* in fine, tubular-imbricate ribbing, delicate teeth with wide dental cavities; differs from *Atrypinella* and *Reticulatrypa* in larger size, short growth lamellae, coarser ribs, presence of dental cavities.] *Silurian (?Ludlow, Přídolí)–Upper Devonian (Frasnian)*: worldwide.
- S. (Spinatrypa)**. Diagnosis as for genus, but smaller shells, biconvex to weakly dorsibiconvex; short hinge; small to medium dental cavities. *Silurian (?Ludlow, Přídolí)–Upper Devonian (Frasnian)*: worldwide.—FIG. 957,2a–d. **S. (S.) margaritoides*, Pragian, Siberia; dorsal, ventral, lateral, anterior views, $\times 1$ (Rzhonsnitskaia, 1975).—FIG. 957,2e–b. *S. (S.) soetenica* (STRUVE), lower Givetian, Germany; e–f, dorsal, posterior views, $\times 2$; g–h, serial sections, $\times 3$ (Copper, 1967d).
- S. (Exatrypa)** COPPER, 1967c, p. 123 [**Terebratulites explanatus* VON SCHLOTHEIM, 1820 in 1820–1823, p. 263; OD; modified to *explanata*, QUENSTEDT, 1871 in 1868–1871, explanation to pl. 42]. Similar to *Spinatrypa*, except for normally relatively flat, wide shell, long hinge, wide orthocline-apsacline area, long deltidial plates, rectimarginate commissure. *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian)*: worldwide.—FIG. 957,3a–f. **S. (E.) explanata* (VON SCHLOTHEIM), lower Frasnian, Germany; a–d, ventral, dorsal, lateral, posterior views, $\times 2$; e–f, serial sections, $\times 3$ (Copper, 1967c).
- ?**Tuberculatospira** XIAN, p. 223 [**T. elegans*; OD]. Small, ovoid, ventribiconvex; protruding orthocline area; apical foramen flanked by deltidial plates; ribs medium; short growth lamellae; finely wrinkled flose microornament; inner shell wall tuberculate; weakly plicate commissure; thin pedicle callist; teeth with possible dental cavities; brachidia undescribed. [Enigmatic genus, doubtful atrypid (synonymous with ?*Neocoelia*), or possibly synonymous with *Spinatrypa*, except for external microornament of wrinkled filae.] *Lower Devonian (Emsian)–Middle Devonian (lower Eifelian)*: southwestern China (Sichuan).—FIG. 954,3a–c. **T. elegans*, lower Eifelian; dorsal, lateral views, detail of ornament, $\times 5.5$ (Xian, 1988).
- Waiotrypa** BALINSKI, 1997, p. 429 [**W. sulcicarina* BALINSKI, 1997, p. 430; OD]. Small, biconvex, ventrally weakly carinate, dorsally sulcate; commissure rectimarginate to weakly sulcate; small orthocline area, apical foramen, deltidial plates. Surface finely, imbricately ribbed, slightly raised ventral midrib pair. Interior with prominent dental cavities; muscle scars deeply impressed, not raised; spiralia, jugal processes undescribed. [Ribbing, biconvexity, impressed muscle scars, and large dental cavities suggest assignment to *Spinatrypa* species-group, particularly the finely ribbed type of *Exatrypa*.] *Upper Devonian (Frasnian)*: western Europe, North America.—FIG. 956,2a–d. **W. sulcicarina*, Poland; dorsal, ventral, posterior, anterior views, $\times 2$ (Balinski, 1997).

Subfamily VARIATRYPINAE
Copper, 1978

[Variatrypinae COPPER, 1978, p. 292]

Medium to large shells; long, straight ribs, commonly interrupted by widely spaced growth lamellae (expansive frills may produce shells more than 150 mm wide); rarely weakly carinate; normally projecting beak; distinct orthocline-anacline area; prominent, hollow, wrinkled deltidial plates; apical foramen; variably developed pedicle callist, sometimes leading to pedicle collar; teeth with small to large dental cavities; weak to strong, comblike cardinal process in cardinal pit and inner socket ridges; dorsally to dorsomedially directed spiralia in large shells, often with many whorls; long, posteroventral jugal processes tipped by central to ventral, inwardly curved jugal plates. *Lower Devonian (Pragian)*—*Upper Devonian (Frasnian)*.

Variatrypa COPPER, 1966b, p. 12 [**Desquamatia ajugata* COPPER, 1965a, p. 316; OD] [= *Peetzatrypa* RZHONSNIŤSKAIA, 1975, p. 95 (type, *Dentatrypa? tschumyschensis* RZHONSNIŤSKAIA, 1968e, p. 142, OD); *Pesterevatrypa* RZHONSNIŤSKAIA, 1975, p. 93 (type, *P. malosalairica*, OD); *Lichnatrypa* WANG & RONG, 1986, p. 144 (type, *L. decora* WANG & RONG, 1986, p. 146, OD)]. Medium to large, usually shield shaped, dorsibiconvex; relatively long hinge; pointed beak; prominent orthocline area; apical foramen; large deltidial plates commonly corrugated, interlocking; ribs fine to medium, continuous, lacking growth lamellae, may be extended beyond shell margin as single trail; fine concentric filae microornament; commissure gently to strongly plicate; thin pedicle callist; rare pedicle collar; hollow deltidial plates separated from pedicle callist-collar; strong teeth with large dental cavities; thin hinge socket plates; cardinal pit lined by comblike cardinal process; crura highly feathered; spiralia with fewer than 15 whorls; jugal processes hook shaped. [Differs from *Desquamatia* by continuous, uninterrupted ribs, lack of frills, large dental cavities, thin hinge socket plates; differs from *Anatrypa* in dorsibiconvexity, nature of deltidial plates, pedicle callist.] *Lower Devonian (Emsian)*—*Middle Devonian (Givetian)*, *Upper Devonian (?Frasnian)*: worldwide.—FIG. 958, 1a–b. **V. ajugata* (COPPER), lower Givetian, Germany; a–e, dorsal, ventral, lateral, posterior, anterior views, $\times 1$; f–h, serial sections, $\times 4$ (Copper, 1965a).

Anatrypa NALIVKIN, 1941, p. 172 [**Orthis micans* VON BUCH, 1840, p. 56; OD]. Medium, ventribiconvex-planconvex, rounded outline; protruding beak,

orthocline area; large apical foramen; prominent deltidial plates; finely ribbed; growth lamellae, frills, trail absent; rectimarginate commissure; pedicle callist absent; slender teeth, with accessory lobes; large dental cavities; thin shell wall; delicate hinge plates; crura feathered; spiralia dorsomedial, fewer than 10 whorls; jugal processes terminating in V-shaped plates. [Distinguished from *Variatrypa* and *Radiatrypa* in convexity, lack of projecting trail, nature of deltidial plates inside pedicle cavity.] *Upper Devonian (Frasnian)*: Europe, Urals, North America.—FIG. 958, 2a–f. **A. micans* (VON BUCH), Syas River, Russian Platform; a–d, dorsal, ventral, posterior, anterior views, $\times 2$; e–f, serial sections, $\times 5$ (new).

Desquamatia ALEKSEEVA, 1960a, p. 421 [**Atrypa (Desquamatia) khavae* ALEKSEEVA, 1960a, p. 423; OD] [= *Cleiothyris* PHILLIPS, 1841, p. 55, *nom. oblit.*, no type species described; *Desquamatia (Synatrypa)* COPPER, 1966b, p. 10 (type, *Desquamatia subzonata* BIERNAT, 1964, p. 319, OD); *Carinatinella* GRATSIANOVA, 1967, p. 97 (type, *C. concentrica*, OD); *Tenuiatrypa* RZHONSNIŤSKAIA, 1975, p. 91 (type, *T. subsalairica*, OD); *Peshiatrypa* XIAN in XIAN & JIANG, 1978, p. 298 (type, *Atrypa peshiensis* GRABAU, 1931b, p. 181, OD)]. Small to large, ovoid to shield shaped, biconvex to dorsibiconvex; beak small to medium; orthocline-hypercline area; small, commonly obscured foramen; minute deltidial plates; ribs fine to medium, in some coarsening distally, interrupted by regular, concentric growth lamellae; frills short to wide, concentrated around commissure, rarely preserved; commissure weakly to strongly plicate; thin pedicle callist separated from deltidial plates; teeth with small to large dental cavities; hinge plate weak to strong; crura feathered; dorsal spiralia with up to 20 whorls; jugal processes terminating in hooklike jugal plates. [Distinguished from other variatrypinids by nature of growth lamellae and rib size.] *Lower Devonian (Pragian)*—*Upper Devonian (Frasnian)*: worldwide.

D. (Desquamatia). Small to medium, ovoid, rounded outline, inflated, biconvex-weakly dorsibiconvex; relatively short hinged; beak small; short, orthocline-hypercline area; ribs fine to very fine, interrupted by regular, densely spaced concentric growth lamellae; frills short, concentrated around commissure, rarely preserved; commissure weakly plicate; thin pedicle callist separated from deltidial plates; teeth with distinct dental cavities; hinge plate strong; dorsal spiralia with about 10 to 12 whorls. [Distinguished from *D. (Independatrypa)* and *D. (Seratrypa)* in smaller size, inflated, more biconvex shape, finer ribs, closely spaced growth lamellae, absence of large frills.] *Lower Devonian (Pragian)*—*Middle Devonian (Givetian)*, *Upper Devonian (?Frasnian)*: worldwide.—FIG. 959, 2a–c. **D. (D.) khavae* (ALEKSEEVA), lower Eifelian, eastern slopes, Urals; a–b, dorsal, ventral views, $\times 1$; c, serial section, $\times 1.6$ (Aleksseeva, 1960a).

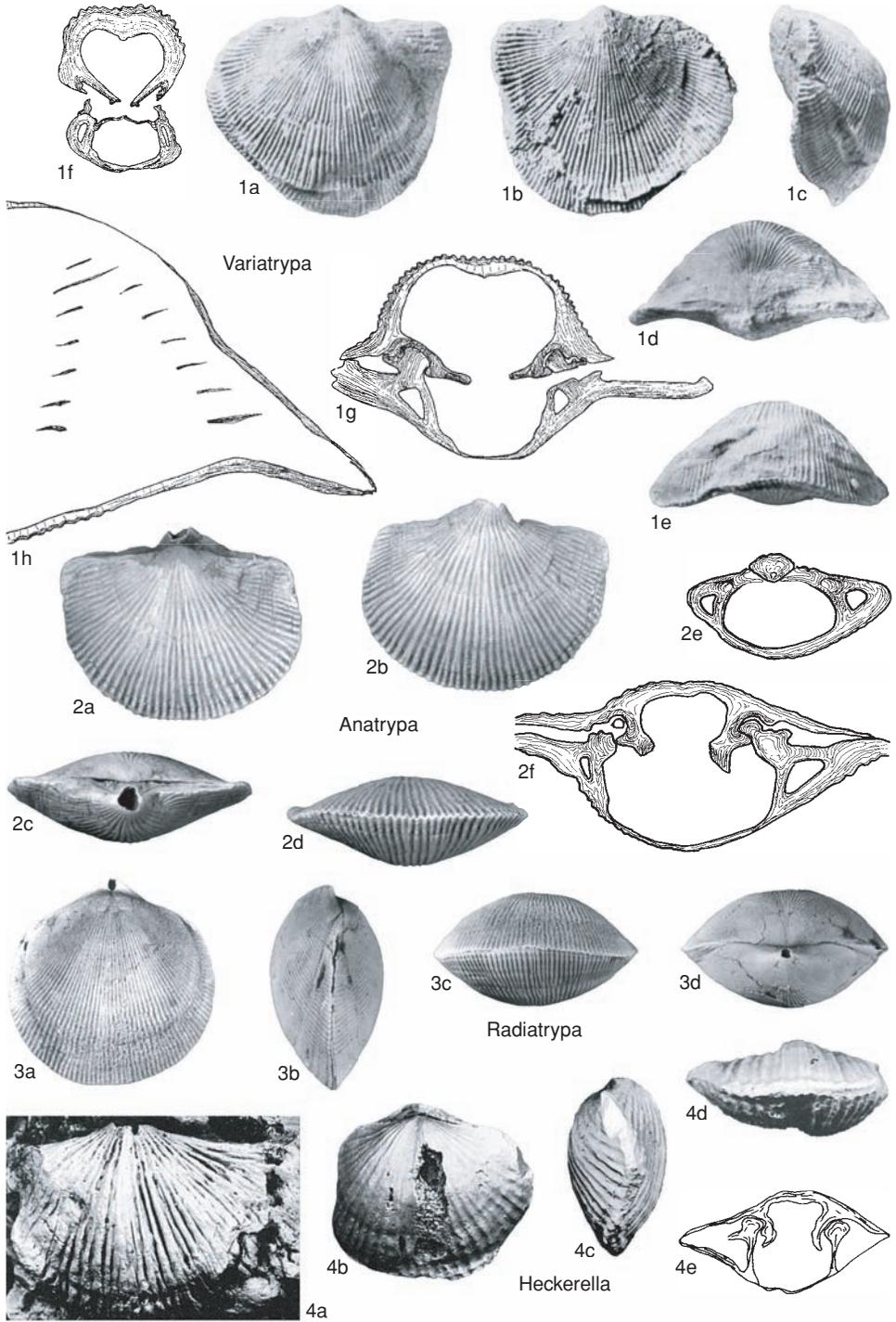


FIG. 958. Atrypidae (p. 1413–1419).

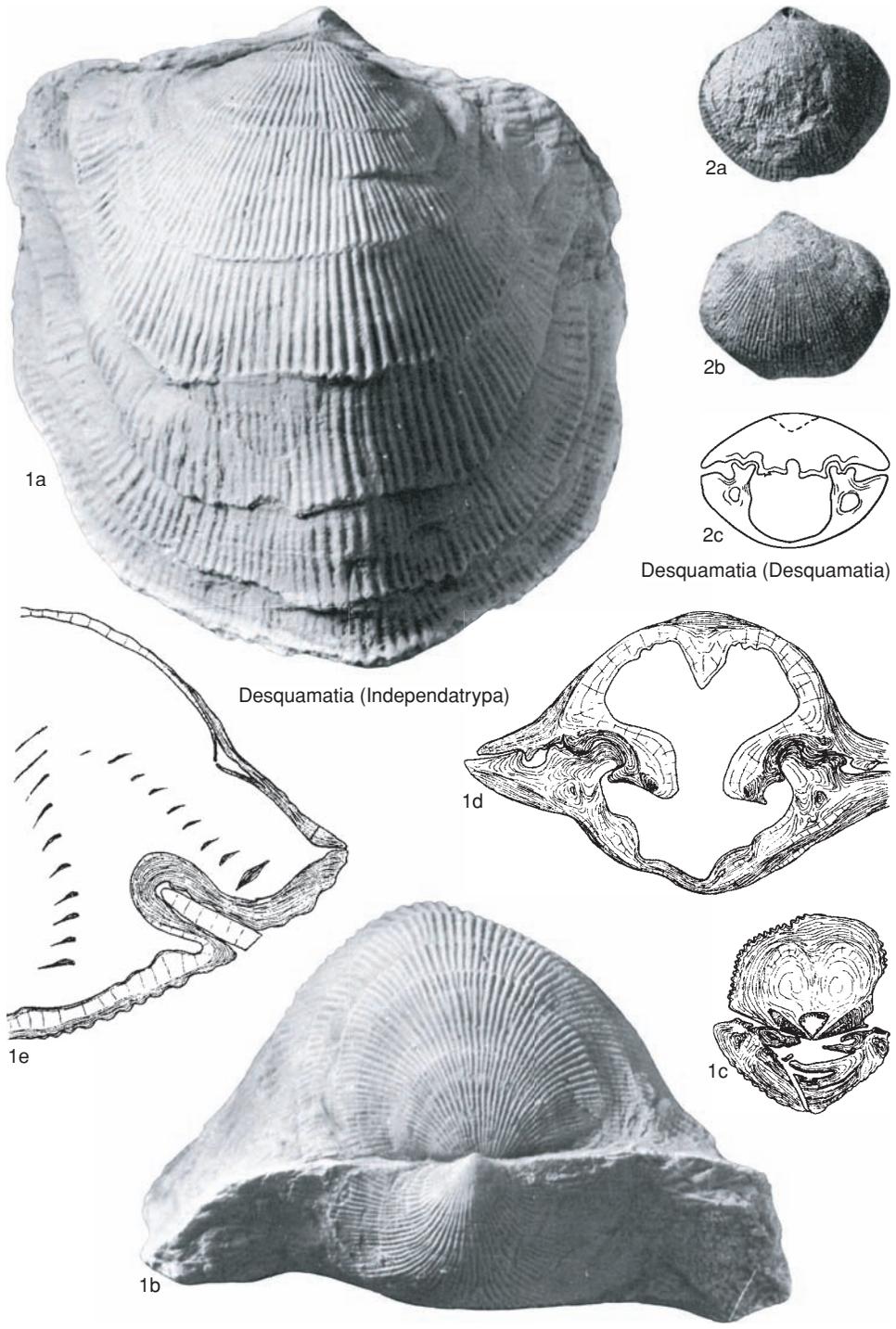


FIG. 959. Atrypidae (p. 1413-1416).

- D. (Independatrypa)** COPPER, 1973c, p. 493 [*Atrypa independensis* WEBSTER, 1921, p. 15; OD] [= *Puanatrypa* XIAN in XIAN & JIANG, 1978, p. 302 (type, *P. guanziyaoensis*, OD)]. Large to very large, dorsibiconvex to convexoplane, shield shaped; orthocline-anacline area; pointed beak; inflated umbo; apical foramen flanked by hollow deltidial plates; ribs medium, but coarsening slightly distally; widely spaced (2 to 15 mm) growth lamellae with fine concentric filae; wide, multiple frills commonly expanding shell to about 150 mm width; commissure moderately to strongly plicate; interior with thick callist or free pedicle collar; deltidial plates separated from pedicle callist; strong teeth with lateral lobes, prominent dental cavities; socket plates relatively thin; hinge plate thick; comblike cardinal process lining cardinal pit, inner socket ridges; crural bases thick, ball-like; crura feathered; spiralia dorsomedial, up to 20 whorls; jugal processes long, tipped by V-shaped jugal plates. [Distinct from *D. (Desquamatia)* by larger size, dorsibiconvexity, shield shape, widely spaced, large frills; differs from *D. (Seratrypa)* by shield-shape, less inflated shell, prominent pedicle callist, sturdy hinge socket plates.] *Middle Devonian (Eifelian–Givetian)*: worldwide.—FIG. 959, 1a–b. **D. (I.) independensis* (WEBSTER), middle Givetian, Iowa, USA; dorsal, posterior views, $\times 2$ (Copper, 1973c).—FIG. 959, 1c–e. *D. (I.) zonata* (SCHNUR), middle Eifelian, Germany; serial sections, $\times 3$ (Copper, 1966b).
- D. (Seratrypa)** COPPER, 1967c, p. 132 [*Terebratulasp. pectinatas* SCHRÖTER, 1777, p. 382; OD] [= *Filiatrypa* CHEN Yuan-ren, 1983, p. 309 (type, *F. typica*, OD)]. Medium to large, ovoid-rounded outline, globose, biconvex-dorsibiconvex; ventral valve inflated posteriorly; very small anacline-hypercline area; short hinge; foramen and deltidial plates small or obscured; fine ribs apically, flattening, coarsening and expanding anteriorly; wide, 5- to 10-mm-spaced, concentric growth lamellae, upturned and overlapping distally, commonly producing large, coarsely ribbed frills; concentric filae absent; commissure gently plicate; moderately sized teeth; small dental cavities, may be reduced to dental nuclei; socket plate thin, slender; crura delicate; spiralia with more than 10 whorls; long jugal processes posterocentrally located, large; hook-shaped jugal plates. [Distinguished from other *Desquamatia* by ovoid instead of shield shape, short hinge, coarsening ribs lacking concentric filae, lack of pedicle callist-collar, slender cardinalia.] *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian)*: Eurasia, North America.—FIG. 960a–g. **D. (S.) pectinata* (SCHRÖTER), lower Frasnian, Germany; a–d, dorsal, ventral, lateral, posterior views, $\times 2$; e–f, serial sections, $\times 3$ (Copper, 1967c); g, reconstruction of brachidia, $\times 3$ (Copper, 1967b).
- Devonatrypa** RZHONSNITSKAIA, 1964, p. 93 [*Atrypa waterlooensis* WEBSTER, 1921, p. 18; OD] [= *Desquamatia (Neatrypa)* STRUVE, 1966, p. 137 (type, *D. (N.) europaea* STRUVE, 1966, p. 140, OD, = *Terebratulites priscus* VON SCHLOTHEIM, 1820 in 1820–1823, p. 262, SD COPPER, 1967c, p. 134); *Sibiratrypa* RZHONSNITSKAIA, 1975, p. 100 (type, *S. vassinensis*, OD)]. Medium to large, convexoplane, subquadrate to elongate; beak blunt; small, hypercline area; transapical foramen; deltidial plates reduced to lost in ontogeny; ribs coarse, rarely bifurcating-intercalating; growth lamellae widely spaced; frills absent; pedicle callist thin; shell strong, blunt, with dental nuclei; dental cavities unknown; crural bases knoblike; crura feathered; dorsally directed spiralia, fewer than 13 to 15 whorls; jugal processes tipped by small, blunt jugal plates. [Distinguished from *Desquamatia* by convexoplane shell, coarse ribs, lack of concentric filae, adult deltidial plates, dental cavities, frills.] *Upper Devonian (Frasnian)*: Eurasia, North America.—FIG. 961a–e. **D. prisca* (VON SCHLOTHEIM), lower Frasnian, Germany; a–c, dorsal, lateral, posterior views, $\times 2$; d–e, serial sections, $\times 3$ (Copper, 1967c).
- Heckerella** RZHONSNITSKAIA & SOKIRAN, 2000, p. 426 [*Anatrypa heckeri* NALIVKIN, 1941, p. 173; OD]. Medium size, moderately biconvex, rectimarginate; ventral valve weakly carinate from 2 midribs, dorsal valve slightly sulcate; commissure broadly rectimarginate to weakly paraplicate; small protruding beak, orthocline area, apical foramen and small deltidial plates; ribs fine, tubular, with weak growth interruptions, lacking growth lamellae, frills, or trail; large dental cavities, moderately slender teeth; weak hinge plate, small crural bases; spiralia and jugal processes undescribed. [Presence of filae in rib troughs suggest affinity with *Desquamatia* group, but shell is also broadly similar to *Gibberosatrypa*, from which it differs by a more elongate hinge, dorsal sulcus, and narrower ribs; overall affinity uncertain.] *Upper Devonian (lower Frasnian, ?middle Frasnian)*: Europe.—FIG. 958, 4a–e. **H. heckeri* (NALIVKIN), lower Frasnian, Shelon River, Russian Platform; a–d, ventral, dorsal, lateral, anterior views, $\times 1.5$; e, serial section, $\times 3$ (Rzhonsnitskaia & Sokiran, 2000).
- Pseudoatrypa** COPPER, 1973c, p. 492 [*Atrypa devoniana* WEBSTER, 1921, p. 19; OD]. Medium size, convexoplane, weakly convex to anteriorly weakly resupinate ventral valve, subrounded outline; small anacline-hypercline area; apical-transapical foramen; small deltidial plates reduced to lost in adult shell; fine tubular ribs interrupted by closely spaced, regular growth lamellae, crowded anteriorly; frills unknown; commissure weakly to moderately plicate; interior with thin or no pedicle callist; teeth small; dental cavities reduced; hinge socket plates delicate; crura feathered; spiralia dorsal, with fewer than about 12 whorls; jugal processes tipped by small jugal plates. [Distinguished from *Desquamatia* by rounded, ovoid shape, smaller size, closely spaced, less rhythmic growth lamellae, lack of frills, reduction of area, deltidial plates; from *Atrypa* by its minimal pedicle callist, *Desquamatia*-

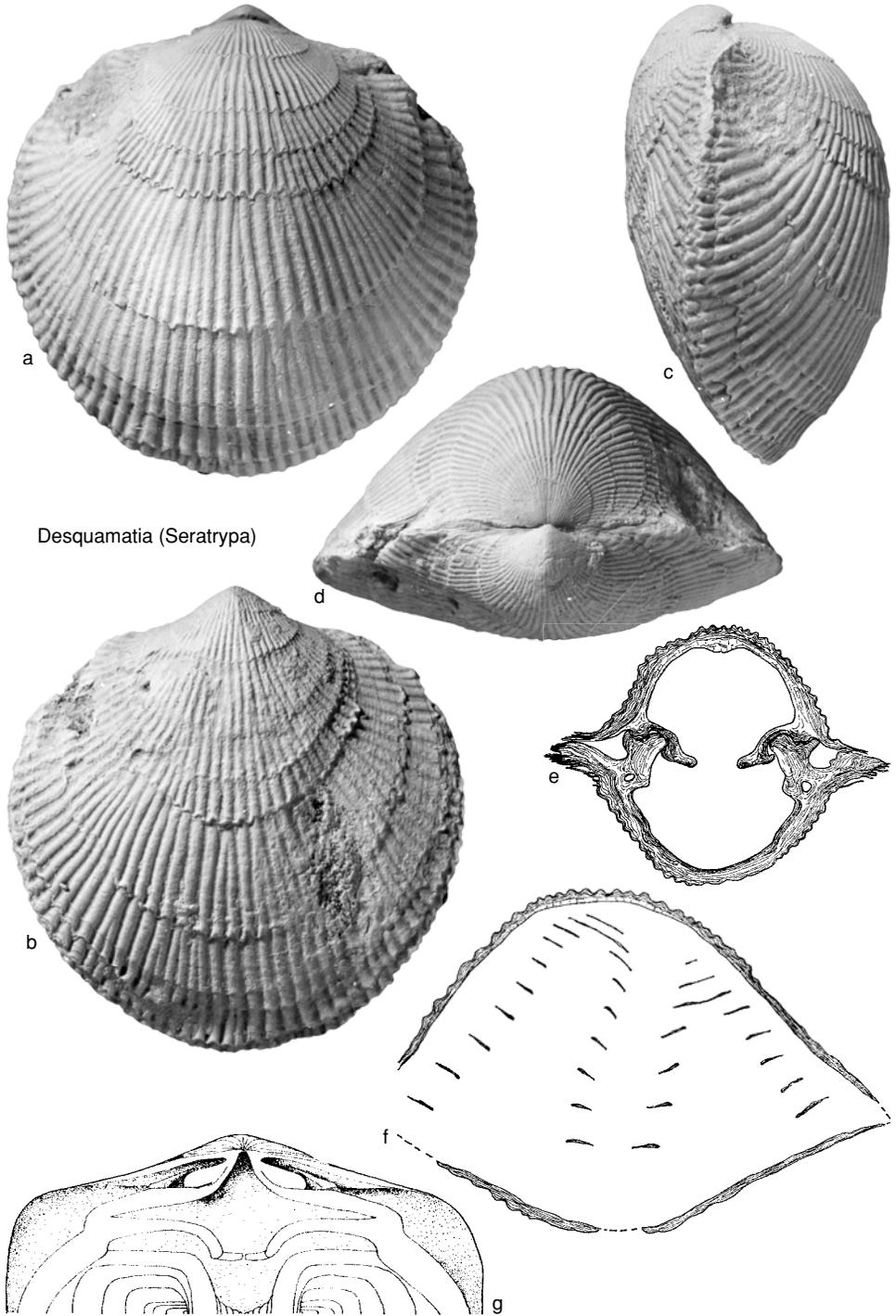


FIG. 960. Atrypidae (p. 1416).

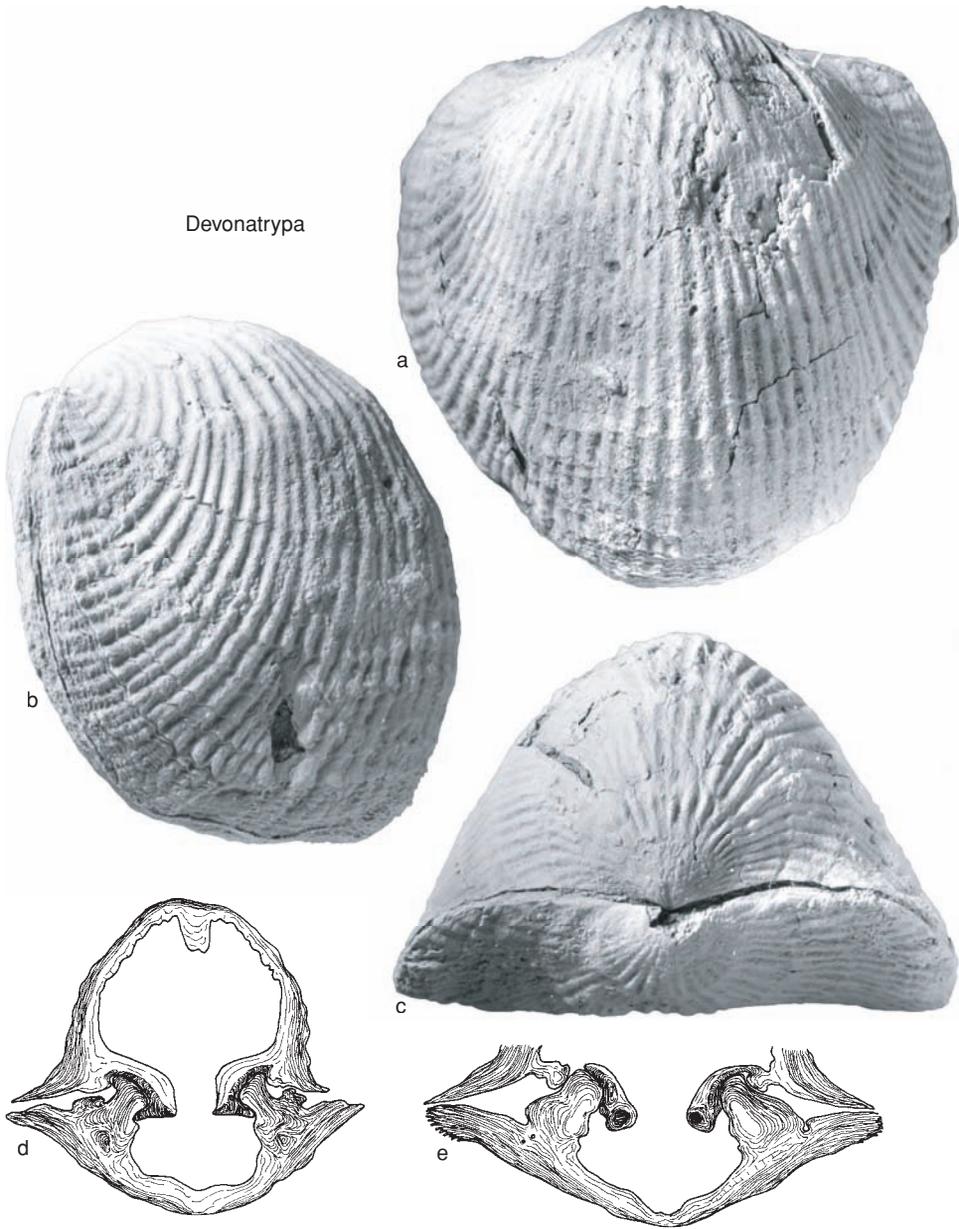


FIG. 961. Atrypidae (p. 1416).

like ribs in early growth stages, teeth with dental cavities, nature of hinge socket plates, brachidia.] *Middle Devonian (upper Givetian)—Upper Devonian (Frasnian)*: North America, Eurasia, Australia. — FIG. 962, 1a–d. **P. devoniana* (WEBSTER), Frasnian, Iowa, USA; dorsal, ventral, posterior, lateral views, $\times 2$ (Copper, 1973c).

Radiatrypa COPPER, 1978, p. 293 [**Atrypa gregeri* ROWLEY, 1900, p. 264; OD] [= *Paratrypa* L. I. MIZENS in G. A. MIZENS & L. I. MIZENS, 1997, p. 21 (type, *P. orbi* G. A. MIZENS & L. I. MIZENS, 1997, p. 21, OD)]. Small to medium, rounded to ovoid, biconvex to weakly dorsibiconvex; orthocline area; minute apical foramen; distinct deltidial

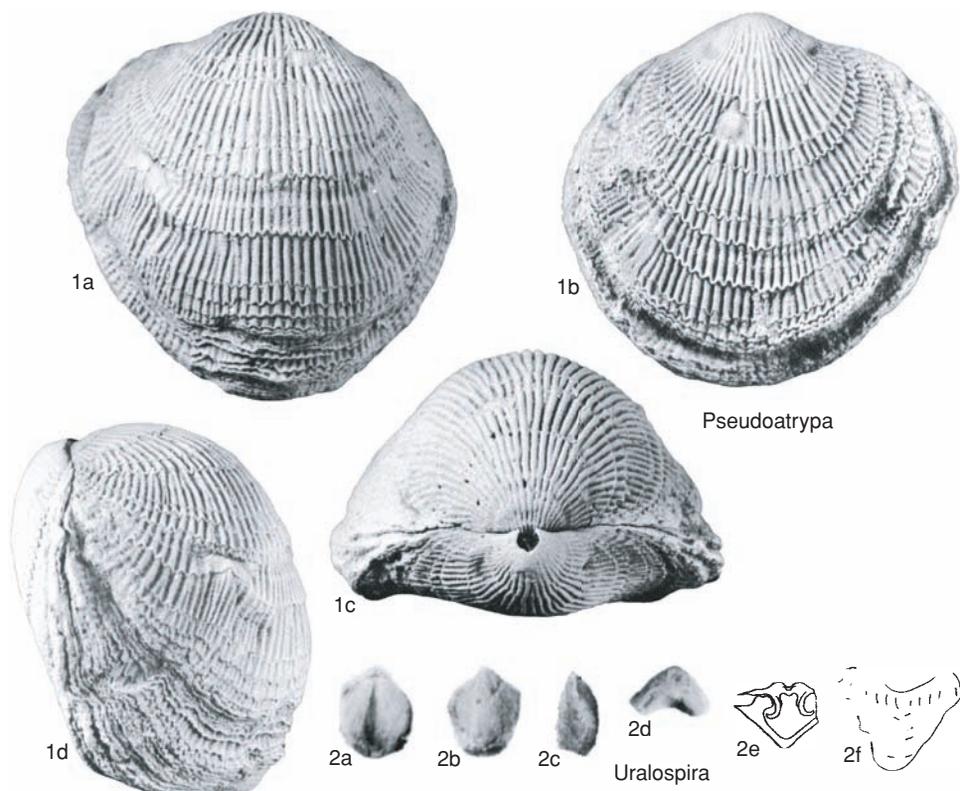


FIG. 962. Atrypidae (p. 1416–1419).

plates; ribs ultrafine, continuous; growth lamellae or frills lacking; rectimarginate to weakly plicate commissure; interior with short teeth; small dental cavities; delicate hinge plates; jugal processes and spiralia undescribed. [Similar to *Anatrypa*, but for biconvexity, smaller globose shell, nature of pedicle callist, deltidial plates. Material ascribed to *Paratrypa* by MIZENS & MIZENS lacks internal characters of karpinskiiniids.] *Middle Devonian (upper Givetian)*—*Upper Devonian (Frasnian)*: North America, Urals, Russian Platform.—FIG. 958, 3a–d. **R. gregeri* (ROWLEY), lower Frasnian, Missouri, USA; dorsal, lateral, anterior, posterior views, $\times 2$ (new).

Uralospira MIZENS, 1977b, p. 82 [**U. tenuicostata*; OD]. Small, planoconvex-concavoconvex, elongate; ventrally subcarinate, dorsally deeply sulcate; prominent orthocline area; protruding beak; apical foramen; small deltidial plates; very fine continuous ribs to nearly smooth appearance; growth lamellae, frills absent; V-shaped sulcate commissure; deeply incised ventral muscle field; short, blunt teeth; slender socket plates; cardinal pit; crura arched laterally; mediodorsal spiralia with fewer than 5 whorls; jugal processes curved. [Differing from *Variatrypa* and *Desquamatia* by small size, sulcate commissure,

subcarinate ventral valve, lack of frills.] *Lower Devonian (Pragian–Emsian)*: Urals, central Asia, Altai-Salair.—FIG. 962, 2a–f. **U. tenuicostata*, Pragian, eastern slopes, Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e–f, serial sections, $\times 3.6$ (Mizens, 1977b).

Family ATRYPINIDAE McEwan, 1939

[Atrypinidae McEWAN, 1939, p. 619, *partim*; *emend.*, COPPER, herein]

Shells small to medium, plicate or rarely sulcate, commonly carinate ventrally; ribbed, less commonly secondarily smooth; ribs interrupted by short growth lamellae or growth lines; frills lacking; usually small orthocline area; distinct deltidial plates surrounding apical foramen; teeth solid or with small dental cavities; small dorsomedial spiralia with relatively few whorls; strong, short jugal processes, generally lacking terminal jugal plates. *Ordovician (lower Caradoc)*—*Lower Devonian (Emsian)*.

Subfamily ATRYPININAE
McEwan, 1939

[*nom. transl.* COPPER, herein, ex Atrypinidae MCEWAN, 1939, p. 619]
[=Gracianellinae JOHNSON, 1973b, p. 1013]

Small, ventribiconvex to planoconvex shells; relatively few coarse ribs, less commonly smooth; usually strongly carinate apically, with raised ventral midribs; short growth lamellae, sometimes slightly imbricate; commissure weakly sulcate to weakly plicate; small but distinct area with deltidial plates; small apical foramen; teeth solid or with small dental cavities; spiralia dorso-medial, few whorls; jugal processes strong, thick. *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian)*.

Atrypina HALL in HALL & CLARKE, 1893, p. 161 [**Lepocoelia imbricata* HALL, 1859b, p. 246; OD; *vid.* HALL, 1894, p. 815]. Small, suboval to subquadrate; planoconvex to subconcavoconvex to ventribiconvex; short hinge; minute orthocline to anacline area; beak small, projecting; apical foramen flanked by small triangular deltidial plates; relatively few, coarse expanding ribs, rarely bifurcating or intercalated, with strong ventral midrib pair; sulcus usually lined by strong dorsal midrib; anterior concentric growth lamellae very short or absent, apically lacking or missing in small shells, may have strong concentric ridges; commissure weakly sulcate to rectimarginate to weakly plicate. [Distinct from *Gracianella* by its stronger ribs, strong plicate commissure, roofed-over cardinal pit and fused hinge plate, externally by small size, very coarse ribs.] *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian)*: North America, Eurasia.

A. (*Atrypina*). External description as for genus except in having plicate commissure, strongly defined ventral fold; internally pedicle cavity lined with thin callist continuous with deltidial plates; small teeth; distinct dental cavities; hinge plate strong, raised, divided by small cardinal pit, roofed over anteriorly by conjunct to fused inner socket plates; crura minute; spiralia mediodorsally directed, fewer than 6 thick, wide whorls; central jugal processes ending in small, ringed to crescentic jugal plates. *Upper Ordovician (upper Ashgill)–Lower Devonian (Emsian)*: North America, Eurasia.—FIG. 963, 1a–c. **A. (A.) imbricata* (HALL), lectotype, Emsian, New York, USA; dorsal, ventral, and anterior views, $\times 2$ (new).—FIG. 963, 1d–g. *A. (A.)* sp. cf. *A. (A.) barrandii*, Wenlock, United Kingdom; serial sections showing hinge plate, jugal processes, and reconstruction of brachidia, $\times 5$ (new).

A. (*Atrypinopsis*) RONG & YANG, 1981, p. 232 [**A. biconvexa*; OD]. Similar to *Atrypina* except for stronger dorsal midrib producing more strongly

plicate to plicosulcate commissure. [Some *Atrypina* also with weakly plicate commissure from dorsal midrib; brachidia undescribed.] *Silurian (lower Llandovery)*: China, ?northwestern Canada.—FIG. 963, 2a–d. **A. (A.) biconvexa*, China; a–c, dorsal, ventral, and anterior views, $\times 2$; d, serial section, $\times 3.2$ (Rong & Yang, 1981).

Gracianella JOHNSON & BOUCOT, 1967, p. 868 [**G. lissumbra* JOHNSON & BOUCOT, 1967, p. 871; OD] [= *Claratrypa* HAVLÍČEK, 1987b, p. 240 (type, *C. clarula*, OD)]. Very small to small, rounded to lenticular outline, relatively flat, roughly biconvex shell; hinge short; small, flat apsacline-orthocline area; apical foramen flanked by small deltidial plates; variable surface ornament from ribbed to nearly entirely smooth, sometimes capillose; weak to strong concentric growth lines, with or without growth lamellae; ventrally weakly to strongly carinate, with carina consisting of single or double, normally fused midrib pair; sulcus dorsal, weak to strong, narrow; weakly sulcate-rectimarginate commissure; interior with small, raised, ventral muscle platform; minute crura; dorsomedial spiralia of fewer than 7 whorls; jugal processes ending in ring-shaped jugal plates. *Silurian (middle Llandovery)–Lower Devonian (Lochkovian)*: North America, Eurasia, Australia.

G. (*Gracianella*). Description as for genus, but relatively flat shell; ribbed variably to nearly entirely smooth; ribs continuous; weak concentric growth lines, lacking growth lamellae; ventrally weakly to strongly carinate, with carina consisting of single or double, fused midrib pair; spiralia and jugal processes undescribed. [Some *G. (Gracianella)* species appear to intergrade with *G. (Sublepidia)*.] *Silurian (Wenlock)–Lower Devonian (Lochkovian)*: North America, Eurasia, Australia.—FIG. 963, 5a–g. **G. (G.) lissumbra*, Ludlow, Nevada, USA; a–e, dorsal, ventral, lateral, posterior, anterior views; f–g, ventral, dorsal valve interiors, $\times 5$ (Johnson & Boucot, 1967).

G. (*Guangyuania*) SHENG, 1975, p. 81 [**Quangyuania* [sic] *ovalia*; OD; *nom. correct.* COPPER, herein, *pro Quangyuania*]. Small, rounded, planoconvex-ventribiconvex; distinct ventral keel, dorsal sulcus; prominent orthocline area; deltidial plates parted by apical foramen; shell surface apically usually partly ribbed, carinate, but smooth distally, ornamented by rhythmic, concentric, capillose ridges on shell surface; commissure weakly sulcate; teeth with minute apical dental cavities, solid distally; hinge plates thick, with narrow V-shaped cardinal pit lined by small cardinal process; thick crura; 4 to 5 thick, mediodorsal spiralia whorls; jugal processes ending in small, ringlike jugal plates. [Similar to *G. (Gracianella)* in interior structure of hinge, orthocline area, and apical ribs, but differing in strong, bushy, concentric, capillate ridges on shell surface, similar to capillae in

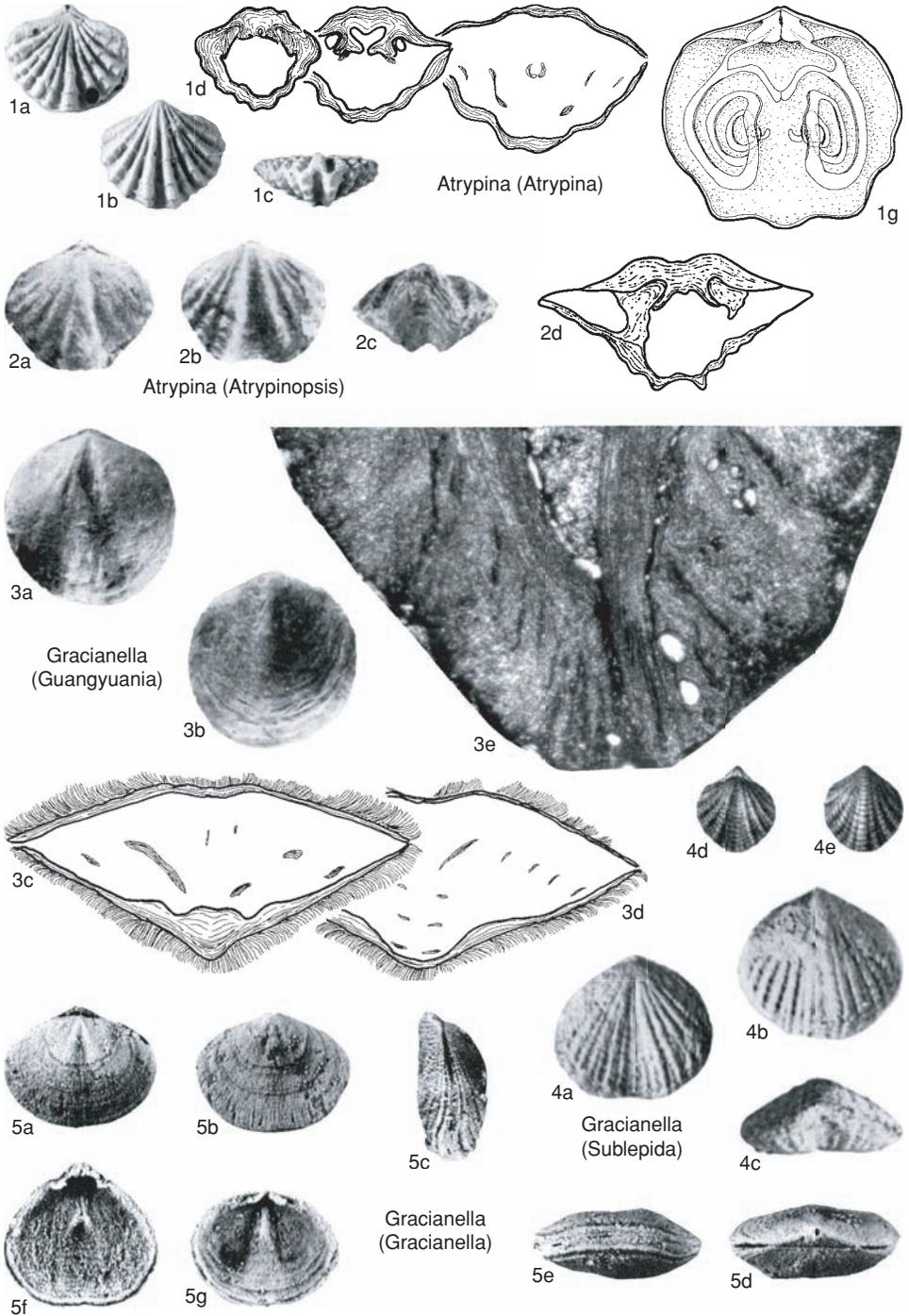


FIG. 963. Atrypinidae (p. 1420–1422).

Lissatrypa; differs from *G.* (*Sublepada*) in loss of ribs, presence of cardinal pit on hinge plate.] *Silurian* (middle Llandovery–Wenlock): southwestern China (Sichuan, Guizhou, southern Shaanxi).—FIG. 963,3a–e. **G.* (*G.*) *ovalia*, middle Llandovery, northern Sichuan; a–b, dorsal and ventral views, ×2 (Sheng, 1975); c–d, serial sections, ×5; e, peel photograph of capillose shell microornament, ×30 (new).

- G. (*Sublepada*) MIZENS & SAPELNIKOV, 1982, p. 16 [**Terebratula sublepada* DE VERNEUIL, 1845, p. 96; OD]. Small, weakly ventribiconvex–planoconvex; ventrally carinate; dorsally sulcate; small orthocline–anacline area; apical foramen; deltidial plates; completely covered by ribs intersected by short, overlapping growth lamellae; commissure sulcate; interiorly thick ventral shell; raised muscle field; teeth solid, lacking dental cavities; hinge plate thick, lacking cardinal pit; dorsomedial spiralia with 4 to 6 thick whorls; ring- to hook-shaped jugal plates terminating processes. [Differs from *G.* (*Gracianella*) and *G.* (*Guangyuania*) in presence of ribs, short growth lamellae completely covering shell.] *Silurian* (Ludlow–Přidolí): southern and central Urals, central Asia, North America.—FIG. 963,4a–e. **G.* (*S.*) *sublepada* (DE VERNEUIL), Přidolí, southern and central Urals; a–c, dorsal, ventral, and anterior views, ×3 (Mizens & Sapelnikov, 1982); d–e, lectotype, dorsal and ventral views, ×2 (de Verneuil, 1845).

Subfamily CLINTONELLINAE Poulsen, 1943

[Clintonellinae POULSEN, 1943, p. 40, *partim; emend.*, COPPER, herein]

Small to medium-sized, rarely large, rounded, biconvex, often rhynchonelliform shell, lacking carination; weakly sulcate to moderately plicate commissure; ribs fine to very fine, evenly sized, continuous, lacking concentric growth lamellae or frills; shell thinly walled, lacking pedicle callist; dental cavities distinct to large; hinge plate thin to modest; spiralia with fewer than 8 to 11 whorls; ventroposterior jugal processes, possibly lacking jugal plates. [Although some genera commonly reported in upper Ashgill from Russia, definitive taxa unknown; neanic specimens may be confused with Rhynchonellida, or with some Spirigerinae.] *Silurian* (Llandovery)—Lower Devonian (*Emsian*).

- Clintonella* HALL in HALL & CLARKE, 1893, p. 159 [**C. vagabunda* HALL in HALL & CLARKE, 1893, p. 160; OD; *vid.* HALL, 1894, p. 160] [= *Pronalivkinia* RUKAVISHNIKOVA, 1977, p. 134 (type, *Nalivkinia*

(*Pronalivkinia*) *numerosa*, OD); ?*Dabashanospira* FU, 1982, p. 170 (type, *Pentlandella sinicus*, SD FU, 1975, p. 107); *Dabashanospira* FU, 1984, p. 379 (type, *Pentlandella sinicus* FU, 1975, p. 107, OD)]. Small to medium, elongate to rounded, globose, biconvex, noncarinate; small beak; anacline area with apical foramen, minute deltidial plates; ribs fine to medium, continuous; rib troughs ornamented by concentric filae; growth lamellae lacking; commissure roughly rectimarginate to weakly plicate; interior with thin wall; teeth delicate; prominent dental cavities; hinge plate thin, divided by small cardinal pit; crura laterally arched; spiralia and jugal processes undescribed. [Differs from *Alispira* in generally elongate, globose shell, weakly plicate–rectimarginate commissure, lack of carination.] *Silurian* (middle Llandovery–Wenlock): North America, Siberia, Kazakhstan, China.—FIG. 964,2a–b. **C. vagabunda*, upper Llandovery, New York, USA; exterior ventral valve, interior dorsal valve, ×4 (Boucot & Johnson, 1970).—FIG. 964,2c–j. *C. anticostiana* (TWHENHOFEL), middle Llandovery, Anticosti, Canada; c–g, dorsal, ventral, posterior, lateral, anterior views, ×2; h–i, serial sections, ×5; j, enlargement of microfilae ornament, ×38 (new).

- Alispira* NIKIFOROVA, 1961, p. 243 [**Zygospira* (*Alispira*) *gracilis* NIKIFOROVA, 1961, p. 244; OD]. Small; rounded to subtriangular outline; ventribiconvex–biconvex; ventrally weakly carinate; small orthocline area; apical foramen flanked by minute deltidial plates; ribs fine, continuous; sulcate–rectimarginate commissure; interior with thin shell; short teeth; small dental cavities; hinge plate with minute cardinal pit; inner socket ridges nearly touching; small, fibrous, laterally directed crura; dorsomedial spiralia with fewer than 6 whorls; jugal processes subhorizontal, terminating in center of shell. [Similar internally to *Clintonella*, externally finely ribbed, smaller in size, shield shaped, with weak carination, sulcate commissure, lacking globose–elongate shape.] *Silurian* (Llandovery–Wenlock): Siberia, China, ?North America.—FIG. 965,1a–g. **A. gracilis* (NIKIFOROVA), Llandovery, western Siberia; a–c, dorsal, ventral, and anterior views, ×2; d–f, serial sections, ×5; g, dorsal apex, ×12 (new).

- Anabaria* LOPUSHINSKAYA, 1965, p. 27 [**Catazyga rara* NIKIFOROVA, 1961, p. 248; OD]. Small to medium, rounded outline, biconvex–dorsibiconvex; orthocline–anacline area; small beak; apical foramen; minute deltidial plates; ribs fine, continuous, posterolateral shell flanks almost smooth; growth interruptions rare; moderately U-shaped, plicate commissure; interior with thin shell; small teeth with large lateral cavities; delicate hinge plates leading to feathery crura; dorsal spiralia with fewer than 8 whorls; jugal processes undescribed. [Differs from *Clintonella* in finer ribs, rounded, dorsibiconvex shape, and wide, U-shaped anterior fold; similar to *Beitaia*, except in coarser ribs, lower anterior fold.] *Silurian* (upper Llandovery, Wenlock): Siberia.—FIG. 964,1a–g. **A. rara* (NIKIFOROVA), ?upper

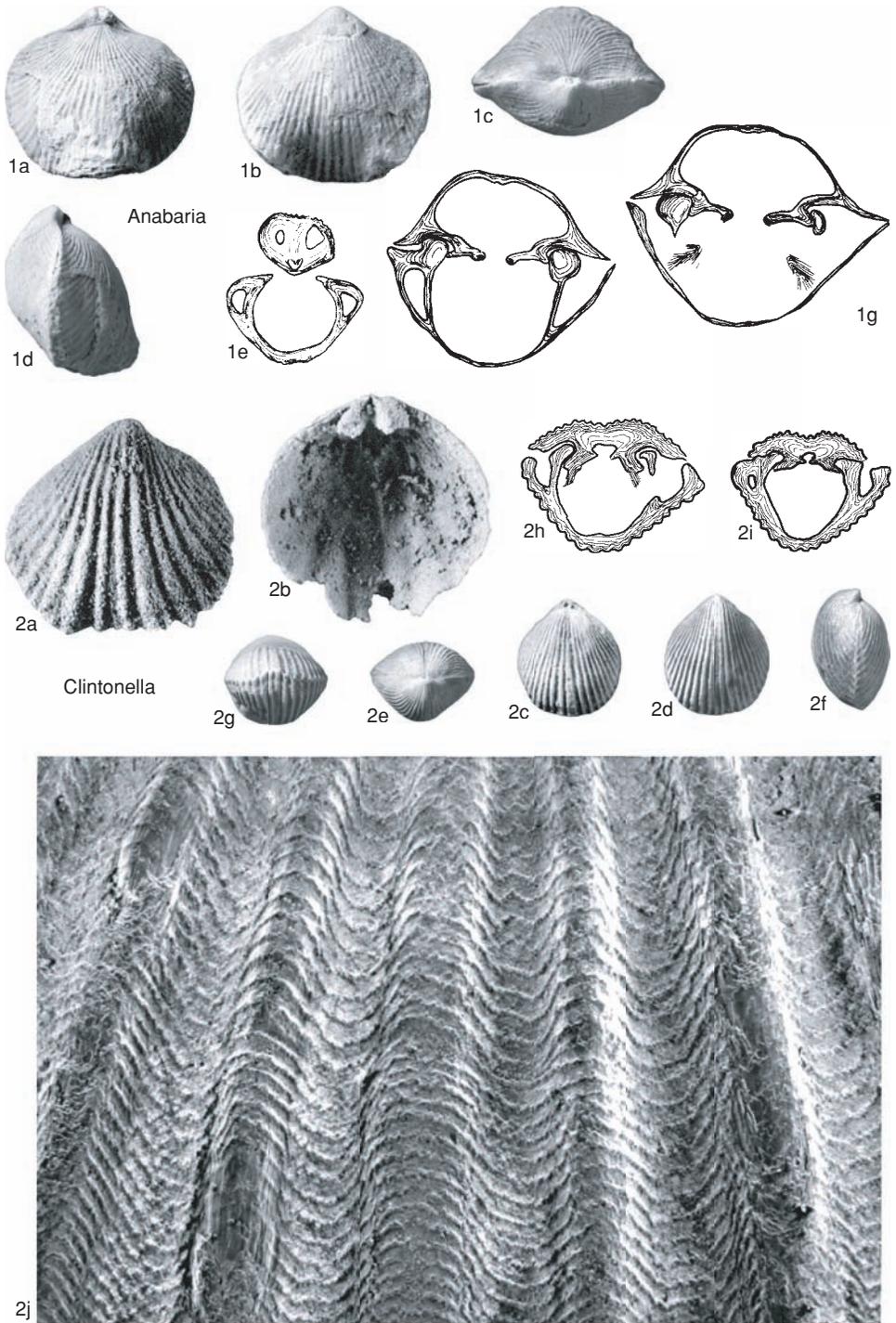


FIG. 964. Atrypinidae (p. 1422–1425).

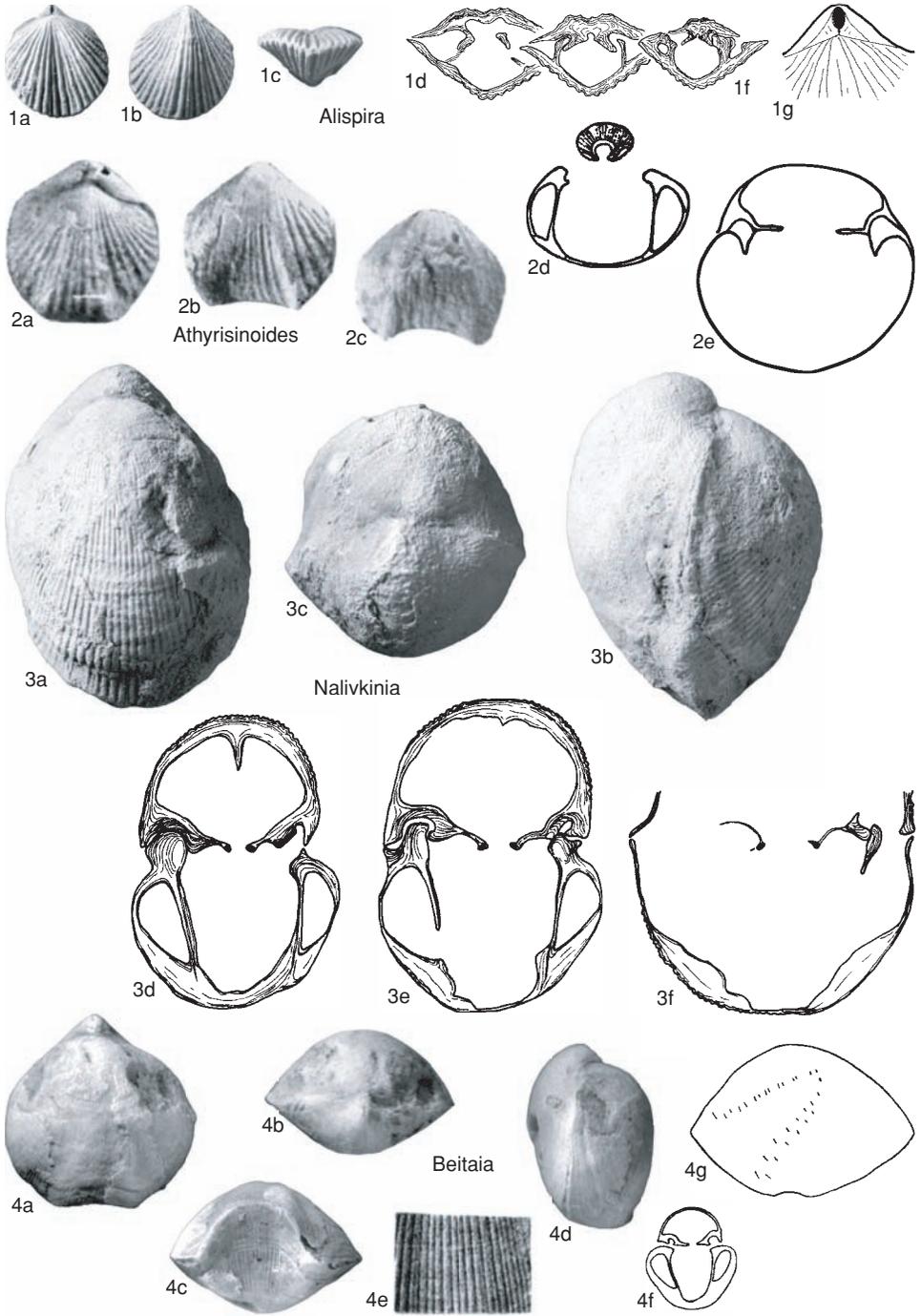


FIG. 965. Atrypinidae (p. 1422–1425).

- Llandoverly; *a-d*, dorsal, ventral, posterior, lateral views, $\times 2$; *e-g*, serial sections, $\times 5$ (Copper, 1977a).
- Athyrisinoides** JIANG in XIAN & JIANG, 1978, p. 303, non *Athyrisinoides* CHEN & WAN in CHEN, 1979, p. 18 (type, *A. typica* CHEN & WAN in CHEN, 1979, p. 20, OD), =*Athyrisinoidea* CHEN & WAN, 1980, p. 105, obj.; *Neoathyrisina* CHEN, 1990, p. 14, obj. [**A. shiqianensis*; OD] [=*Kritorhynchia* RONG & YANG, 1981, p. 215 (type, *K. seclusa*, OD)]. Small to medium; rounded to subquadrate, rhychnelliform outline; small anacline area, obscuring apical foramen, deltidial plates; ribs medium size, coarsening distally; ribs defining sharp fold with flanking troughs on both valves; short, overlapping growth lamellae may be present; squared to U-shaped strongly plicate commissure; internally modest dental cavities; dental plates; cardinal pit lined by weak cardinal process; crura lateral; spiralia with fewer than 6 whorls, dorsomedial; jugal processes undescribed. [Distinguished from *Anabaria* by coarser ribs, sharply defined, *Plectatrypa*-like fold, and presence of very short growth lamellae; genus is homeomorphic with some athyrisinids (Athyridida), but distinguished by dorsally directed atrypoid spiralia. Regarding the synonymy of this genus, *Athyrisinoides* JIANG, 1978, an atrypid, has priority. *Athyrisinoides* CHEN & WAN, 1979, an athyridid, is a junior homonym. CHEN & WAN renamed their athyridid *Athyrisinoidea*, but since there is only one letter difference in the names, they renamed it again as *Neoathyrisina*.] *Silurian* (middle Llandoverly—upper Llandoverly): southwestern China (Guizhou).—FIG. 965,2*a-c*. **A. shiqianensis*, middle Llandoverly; dorsal, ventral, and anterior views, $\times 1$ (Jiang, 1978).—FIG. 965,2*d-e*. *A. seclusa* (RONG & YANG), middle Llandoverly; serial sections, $\times 5$ (Rong & Yang, 1981).
- Beitaita** RONG, XU, & YANG, 1974, p. 199 [**B. modica*; OD]. Small to medium, ventribiconvex to nearly convexoplane, very finely ribbed to almost smooth septatrypiform shell; orthocline-anacline area; protruding beak; small apical foramen; deltidial plates; ribs very fine (costellate) to nearly invisible, lacking growth interruptions; distinct concentric growth filae; commissure with high, wide, U-shaped fold; interior with large dental cavities, long dental plates; delicate hinge plates; dorsally directed spiralia with fewer than 11 whorls; jugal processes delicate. [Differs from *Clintonella* in very fine ribs, high dorsal fold, and broader shell; from *Anabaria* by septatrypid shape, large and wide fold, very fine ribs; worn shells may be mistaken for *Septatrypa*.] *Silurian* (middle Llandoverly): southern China (Guizhou, Hubei, Sichuan).—FIG. 965,4*a-g*. **B. modica*, middle Llandoverly, Guizhou; *a-d*, dorsal, posterior, anterior, lateral views, $\times 2$; *e*, enlargement of fine ribs, $\times 4$ (Rong, Xu, & Yang, 1974); *f-g*, serial sections, $\times 2.5$ (Rong & Yang, 1981).
- Nalivkinia** BUBLICHENKO, 1927, p. 982 [**Atrypa gruenewaldtiaeformis* VON PEETZ, 1901, p. 147; OD]. Medium to large, globose, strongly biconvex; small, hypercline area; foramen transapical or obscured, absent; deltidial plates absent in adult shell;

ribs fine; abundant, very short, growth lamellae or growth interruptions; commissure rectimarginate to weakly plicate; interior with large dental cavities; short, dorsoventrally oriented teeth; delicate socket plates; small bushy crura; spiralia dorsomedial, fewer than 6 whorls, jugal processes straight, nearly touching. [Distinguished from other clintonellinids by large size, incurved beak, presence of short concentric growth lamellae; distinguished from *Tibetatrypa* by large dental cavities, thinner shell, delicate socket plates, absence of strong anterior fold.] *Silurian* (upper Llandoverly—Ludlow): southern Siberia, Altai.—FIG. 965,3*a-f*. **N. gruenewaldtiaeformis* (VON PEETZ), Wenlock, Kuznetsk basin; *a-c*, dorsal, lateral, posterior views, $\times 2$; *d-f*, serial sections, $\times 5$ (Copper, 1977a).

- Tibetatrypa** COPPER & HOU, 1986, p. 287 [**T. xainzaensis* COPPER & HOU, 1986, p. 289; OD]. Large to very large, rotund, elongate, ventribiconvex to biconvex; hypercline area; narrow beak; foramen and deltidial plates absent or obscured in adult shell; ribs fine; intersected at relatively wide intervals by growth interruptions, lacking growth lamellae; rectimarginate to weakly plicate commissure; internally thick shell wall, pedicle callist; deep pedicle groove; teeth with long, narrow, reduced dental cavities; thin socket plates; short crura; spiralia dorsal, 8 to 10 whorls; jugal processes delicate, tapering into small, flat jugal plates. [Differs from closely related *Nalivkinia* in its much larger size, minute dental cavities, and deep pedicle groove.] *Lower Devonian* (Lochkovian—Emsian): Tibet.—FIG. 966,2*a-g*. **T. xainzaensis*, Emsian; *a-c*, dorsal, lateral, posterior views, $\times 2$; *d-f*, serial sections, $\times 5$; *g*, reconstruction from serial sections, $\times 3$ (Copper & Hou, 1986).

- ?Ucitispira** FU, 1982, p. 150 [**U. sinica*; OD]. Small, rounded; orthocline area; strongly protruding beak; apical foramen, deltidial plates; ribs fine, continuous; lacking growth lamellae; rectimarginate to weakly plicate commissure; interior with thin wall; small teeth; large dental cavities; hinge plate short and sturdy; small cardinal pit; dorsomedially directed spiralia with about 6 whorls; crura; jugal processes undescribed. [Possible synonym of *Anabaria*, or *Clintonella*, but with strongly pointed, extended beak.] *Silurian* (upper Llandoverly): northwestern China (Gansu).—FIG. 966,1*a-d*. **U. sinica*; *a-c*, dorsal, lateral, anterior views, $\times 3$; *d*, polished section, $\times 3$ (Fu, 1982).

Subfamily PLECTATRYPINAE Copper, 1996

[Plectatrypinae COPPER, 1996b, p. 914]

Small- to medium-sized shells; small orthocline-hypercline area; apical-transapical foramen; highly imbricate, highly arched ribs, may be terminated by blunt caps (capidulae), nonspinose; ventral valve usually strongly carinate with enlarged, diverging

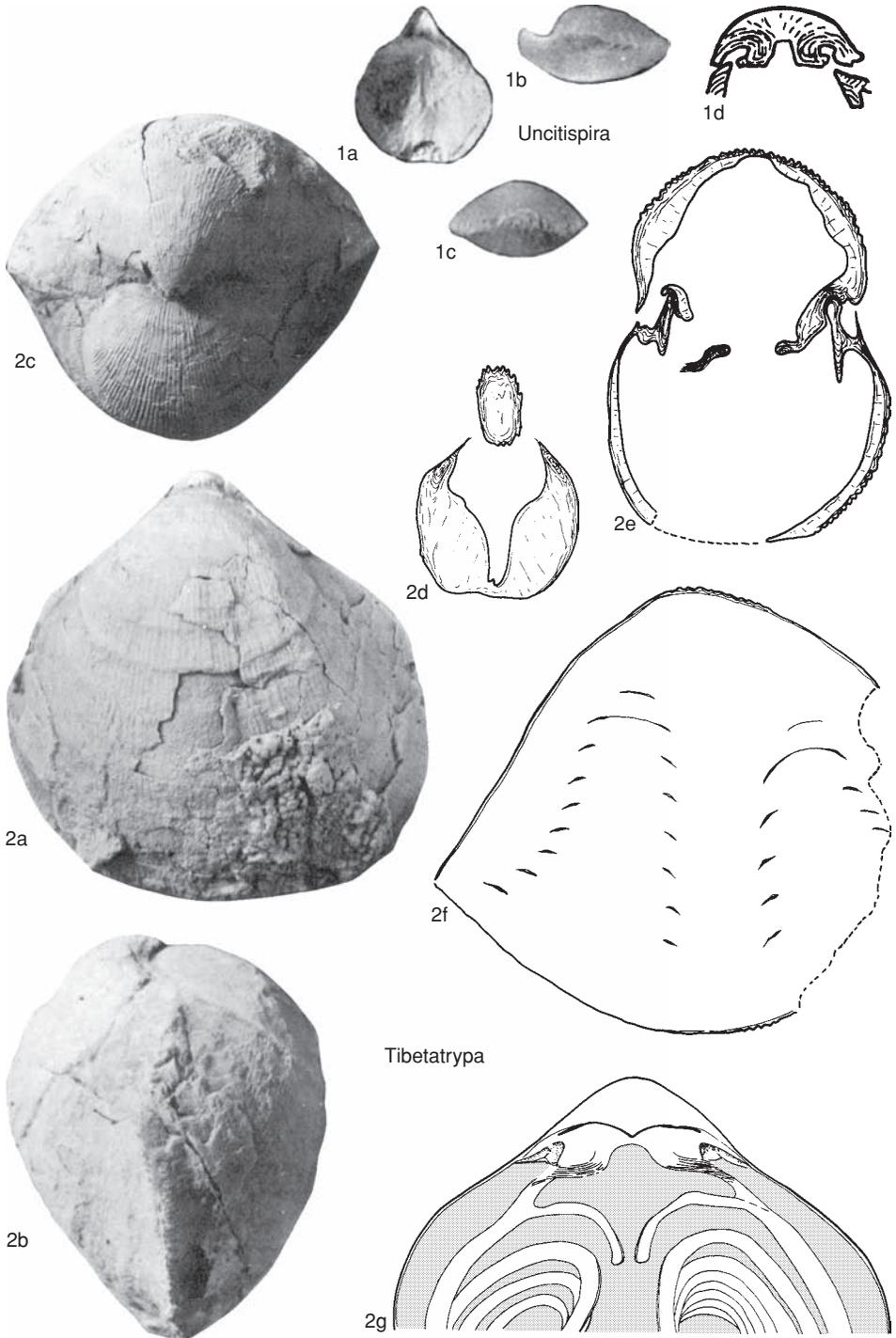


FIG. 966. Atrypinidae (p. 1425).

midribs separated by smaller ribs; short, overlapping, imbricate growth lamellae; frills absent; strongly plicate commissure; pedicle callist absent to very thin; teeth usually lacking dental cavities, but with nuclei; dorsomedial spiralia with fewer than 10 whorls; jugal processes far apart, terminated by small blunt jugal plates. *Ordovician* (?Ashgill), *Silurian* (Llandovery–Ludlow, ?Přidolí).

Plectatrypa COOPER, 1930, p. 278 [**Terebratula imbricata* J. de C. SOWERBY, 1839, p. 624; OD] [= *Imbricatospira* FU, 1982, p. 149 (type, *I. decora*, OD); *Imbricatospira* FU, 1985, p. 96 (type, *I. decora*, OD)]. Small to medium size, rounded, biconvex-dorsibiconvex; small pointed beak; anacline-hypercline area; apical-transapical foramen; deltidial plates normally not exposed; ribs medium to coarse, highly imbricate, with sharply projecting growth lamellae; strongly divergent, enlarged ventral midrib sets separated by wide sulcus, producing carination; strong, U-shaped anterior fold; internally thin to thick shell apically; pedicle callist thin to absent; deltidial plates extended into pedicle cavity as thin lining; teeth short, thick, medially directed, lacking dental cavities; delicate crural bases, fine crura; fewer than 8 dorsomedial, relatively widely spaced spiralia whorls; fine jugal processes curved laterally, terminating in delicate plates. [Distinct from *Syphartrypa* in rib imbrication; distinct from *Xanthea* in finer ribs, lack of microornament.] *Silurian* (Llandovery–Ludlow, ?Přidolí): North America, Eurasia.

P. (Plectatrypa). Diagnosis as for genus, but includes only medium to coarsely ribbed, imbricate forms lacking capidulae; shell wall thin, hinge plate weak. *Silurian* (Llandovery–Ludlow, ?Přidolí): North America, Eurasia.—FIG. 967, 1a–g. **P. (P.) imbricata* (SOWERBY), upper Wenlock, United Kingdom; a–e, dorsal, ventral, posterior, anterior, lateral views; f–g, serial sections, $\times 4$ (new).—FIG. 967, 1b. *P. (P.)* sp. cf. *P. (P.) imbricata*, upper Wenlock, Gotland; reconstruction of brachidia, $\times 4$ (new).

P. (Gutnia) COPPER, 1996b, p. 915 [**G. capidula* COPPER, 1996b, p. 917; OD]. Small to medium, rounded outline; orthocline-anacline area; small, protruding beak; apical-transapical foramen; minute deltidial plates; ribs fine to very fine, evenly sized over shell surface; closely spaced imbricate growth lamellae; rib crests terminated by bulbous caps (capidulae); gently to strongly plicate anterior commissure; shell wall thick apically; deltidial plates hollow, distally retreating to sides of pedicle cavity; teeth short, anteriorly accommodating groove for crura; hinge plate sturdy; socket plates thin; crura very delicate; spiralia, jugal processes undescribed. [Differs from *Plectatrypa* in much finer ribs, presence of capidulae, lack of strong ventral midrib pair,

lack of carination; internally similar but thick walled.] *Silurian* (Wenlock): western Europe, North America.—FIG. 967, 2a–g. **P. (G.) capidula*, upper Wenlock, Gotland; a–c, dorsal, ventral, lateral views, $\times 3$; d–f, serial sections, $\times 5$; g, capidulae, $\times 20$ (Copper, 1996b).

Syphartrypa COPPER, 1982, p. 690 [**S. honora* COPPER, 1982, p. 692; OD]. Small to medium, biconvex-dorsibiconvex; protruding beak; small apacline-orthocline area; rimmed apical foramen; small deltidial plates; ribs interrupted by relatively widely spaced, wavy, short growth lamellae, projecting 1 to 2 mm, subparallel to shell surface; rounded, plicate commissure; thin or no pedicle callist; small teeth; small dental cavities; dorsomedial spiralia with fewer than 6 whorls, jugal processes undescribed. [Externally similar in shape to *Eospirigerina* and *Schachriomonia*, but lacking carination and possessing wavelike, extended, short growth lamellae; differs from *Plectatrypa* in having coarser, wider ribs, without well-defined carination, rib imbrication.] *Ordovician* (?Ashgill), *Silurian* (lower Llandovery–middle Llandovery): eastern North America, western Europe.—FIG. 968a–e. **S. honora*, Rhuddanian, Manitoulin Island, Canada; a–c, dorsal, lateral, anterior views, $\times 2$; d, dorsal view of large specimen showing growth lamellae, $\times 2$; e, detail of dorsal beak, $\times 12$ (new).

Xanthea COPPER, 1996b, p. 917 [**Atrypa imbricata* var. *lamellosa* LINDSTRÖM, 1861, p. 363; OD]. Small to medium, dorsibiconvex, wider than long or equidimensional; small orthocline-anacline area; protruding beak; apical to transapical foramen; small deltidial plates; ribs coarse, thicker apical midrib pair diverging rapidly, outlining sharp ventral sulcus; 2 to 4 ribs lining crest of strong, sharp dorsal fold; growth lamellae widely spaced, non-imbricate; microornament of zigzag fliae; sharply plicate commissure; internally thick deltidial plates lining inside of pedicle cavity; pedicle callist absent; teeth solid, short, stubby; thick hinge plate; inner socket ridges expanded, globose; crura delicate; spiralia dorsomedial, fewer than 9 whorls; jugal processes delicate, terminating without touching. [Differs from *Plectatrypa* in very coarse ribs, widely spaced growth lamellae, zigzag, microornamental fliae, larger size.] *Silurian* (Telychian–Wenlock): Europe.—FIG. 969a–h. **X. lamellosa* (LINDSTRÖM), lower Wenlock, Gotland; a, dorsal view, $\times 4$; b–d, ventral, posterior, lateral views, $\times 2$; e–g, serial sections, $\times 5$; h, reconstruction of brachidia, $\times 5$ (Copper, 1996b).

Subfamily SPIRIGERININAE

Rzhonsnitskaia, 1974

[Spirigerininae RZHONSNITSKAIA, 1974, p. 57] [=Schachriomoniinae RUKAVISHNIKOVA, 1982, p. 46; Pectenospirinae POPOV, NIKITIN, & SOKIRAN, 1999, p. 646]

Small to medium size, inflated biconvex-dorsibiconvex; short hinge; small apacline-anacline area; protruding beak; continuous

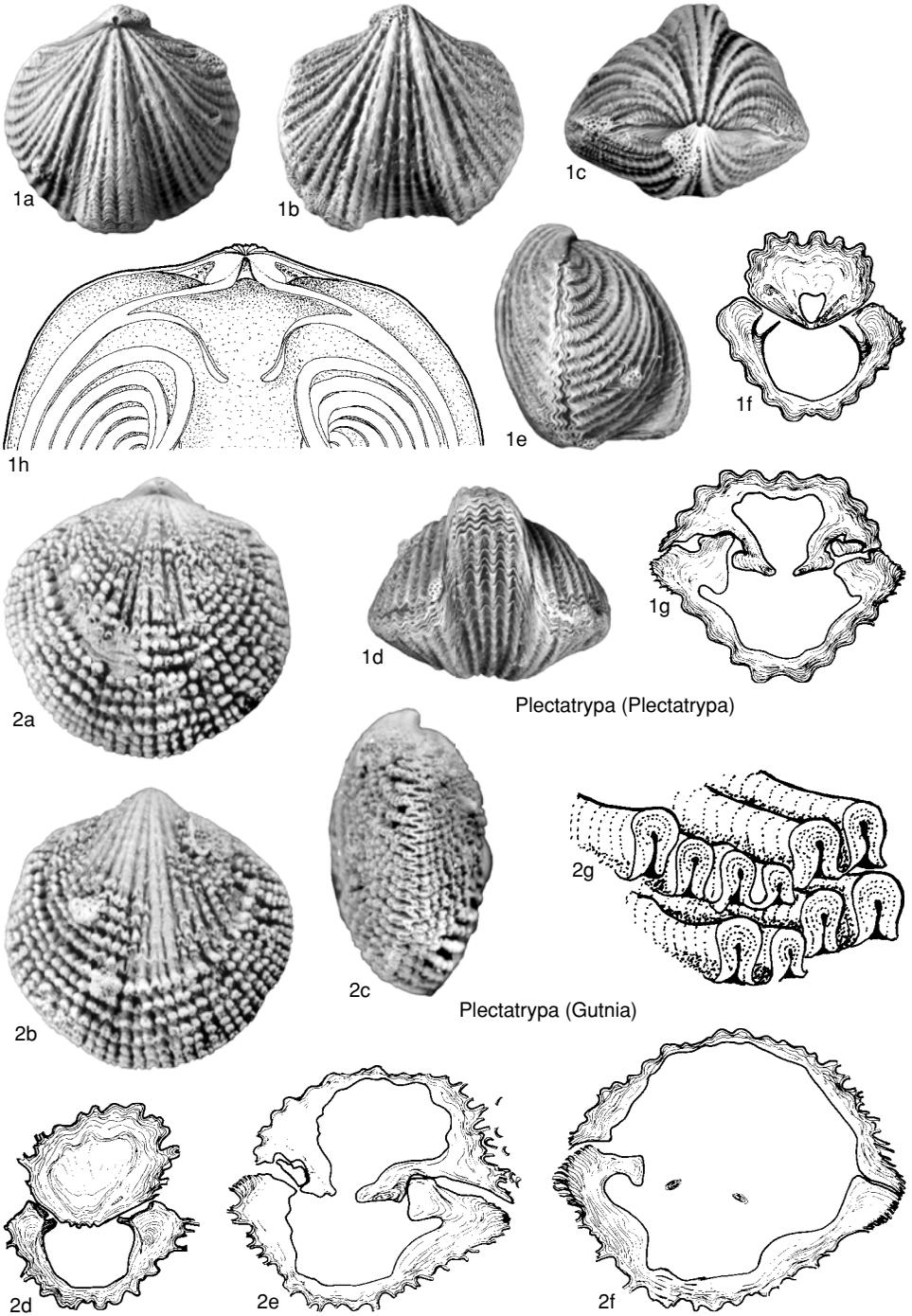


FIG. 967. Atrypinidae (p. 1427).

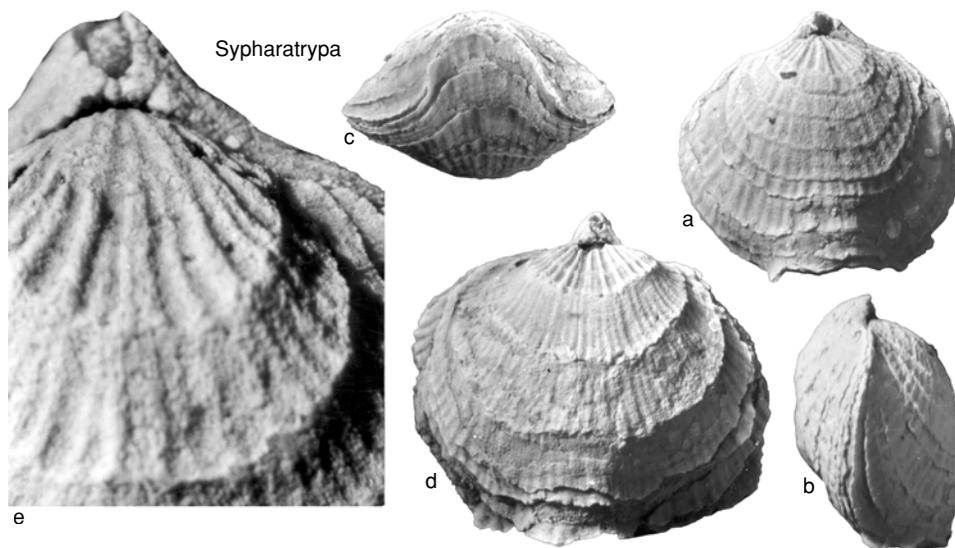


FIG. 968. Atrypinidae (p. 1427).

ribs, usually with strongly diverging ventral midrib pair producing pronounced carination; median sulcus on ventral valve; rarely weak concentric growth lamellae, rarely with trail, lacking frills; moderately to strongly plicate commissure; teeth solid or with small, rounded to slitlike dental cavities; feathery crura unknown; spiralia dorsomedially directed, fewer than 8 to 10 whorls; centroventral jugal processes recurved, with or without small jugal plates. *Ordovician (lower Caradoc)–Lower Devonian (Emsian)*.

Spirigerina D'ORBIGNY, 1847, p. 268 [**Terebratula marginalis* DALMAN, 1828, p. 143; SD ALEKSEVA, 1960b, p. 64, *vid.* D'ORBIGNY, 1850 in 1849–1852, p. 42] [= *Paraplectatrypa* ZENG & others, 1993, p. 375, *nom. nud.*, lacking description, only figures]. Medium size, subquadrate to pentagonal, dorsibiconvex; sharply pointed beak; triangular, orthocline area; apical foramen prominent; deltidial plates well developed; corrugate medium to coarse ribs, expanding distally, ventral midrib pair bi- to trifurcating with intervening sulcus filled by ribs; dorsal strongly bifurcating midrib; ribs ornamented by fine concentric filae, radial capillae; strong, angular-rounded, plicate commissure; internally thin pedicle callist; prominent hollow deltidial plates; strong, wide teeth; slitlike dental nucleus expanding to dental cavity anteriorly; thick central hinge plate; narrow cardinal pit; very thin socket plates; bulbous inner socket ridges; small, delicate crura; dorsal

spiralia of fewer than 6 whorls, spiral lamellae widely spaced; jugal processes recurved in center, lacking jugal plates. *Silurian (middle Llandovery)–Lower Devonian (Emsian)*: worldwide.—FIG. 970, 2a–i. **S. marginalis* (DALMAN), Wenlock, Gotland; a–e, dorsal, ventral, lateral, posterior, anterior views, $\times 2$; f–h, serial sections, $\times 5$; i, reconstruction of left brachidium, $\times 5$ (new).

?**Australispira** PERCIVAL, 1991, p. 169 [**A. disticha*; OD]. Medium size, globose-rounded, dorsibiconvex; broadly diverging ventral midribs separated by sulcus and numerous fine ribs; ribs tubular, continuous, expanding anteriorly to coarse; broadly plicate commissure; interior with blunt teeth; small dental cavities; spiralia dorsomedial, with about 7 whorls; possibly with posteroventrally located jugal processes. Smaller shells similar to *Sulcatospira*, but some gerontic shells with more robust shell, thicker shell wall. [PERCIVAL (1991) showed simple ventroposterior jugum, but silicification probably hides disconnected jugal processes. Similar to *Schachriomonina* but more finely ribbed, differing in strong globosity; neanic growth stages very similar to *Eospirigerina*.] *Ordovician (upper Caradoc)*: Australia.—FIG. 970, 1a–h. **A. disticha*, New South Wales; a–d, dorsal, ventral, lateral, anterior views; e, internal of dorsal valve; f–g, serial section; h, reconstruction of brachidia, $\times 2$ (Percival, 1991).

Eospirigerina BOUCOT & JOHNSON, 1967a, p. 90 [**Zygospira putilla* HALL in HALL & CLARKE, 1895, p. 365, *vid.* HALL, 1894, p. 653; SD AMSDEN, 1974, p. 72; = *Atrypa praemarginalis* SAVAGE, 1913a, p. 84, OD, *vid.* AMSDEN, 1974, p. 72] [= *Zanclorhyncha* XU, 1979a, p. 96 (type, *Z. gentilis*, OD); *Eorhynchula* LIANG, 1983a, p. 284 (type, *E. yulangensis*, OD); *Neorhynchula* LIANG, 1983b, p.

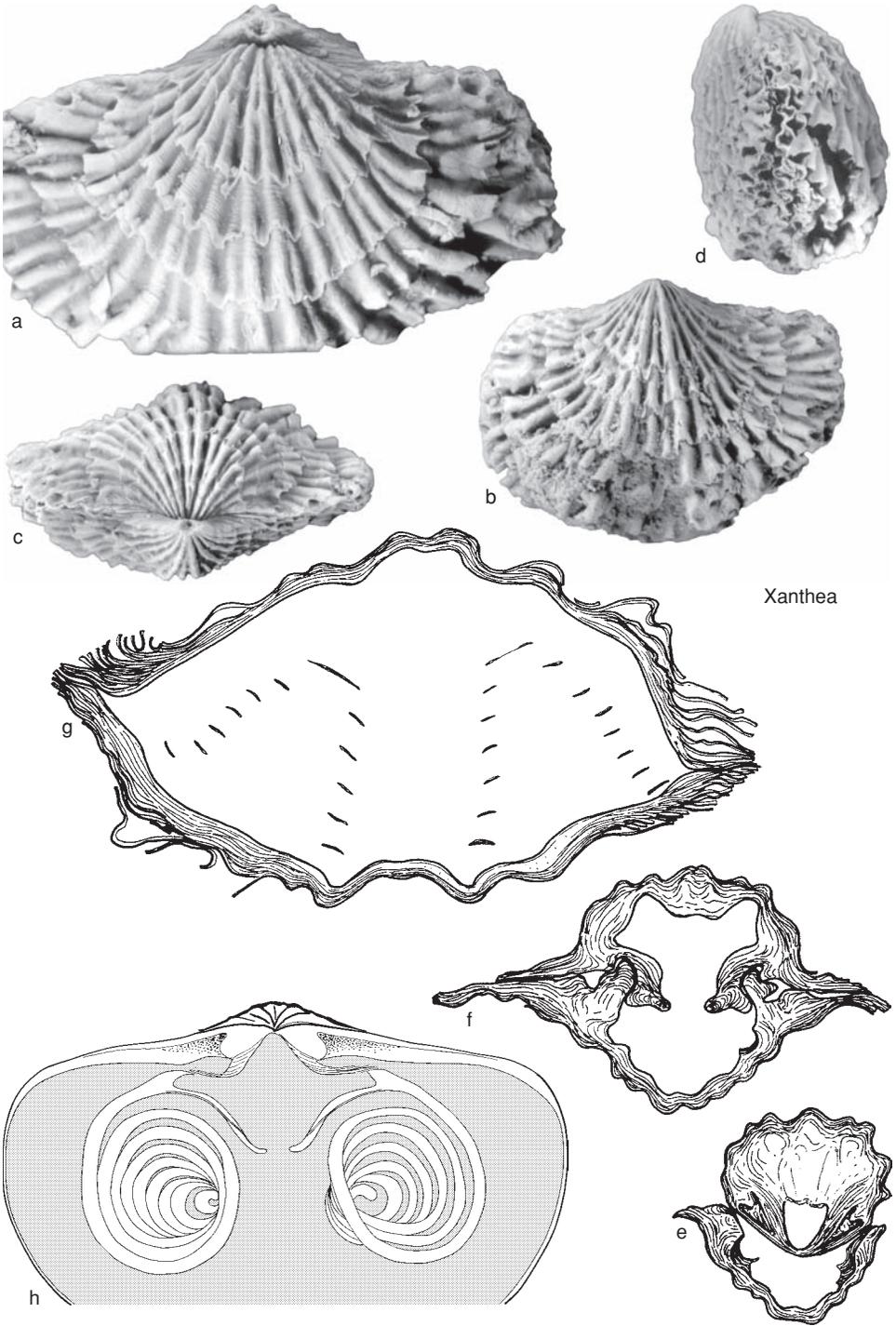


FIG. 969. Atrypinidae (p. 1427).

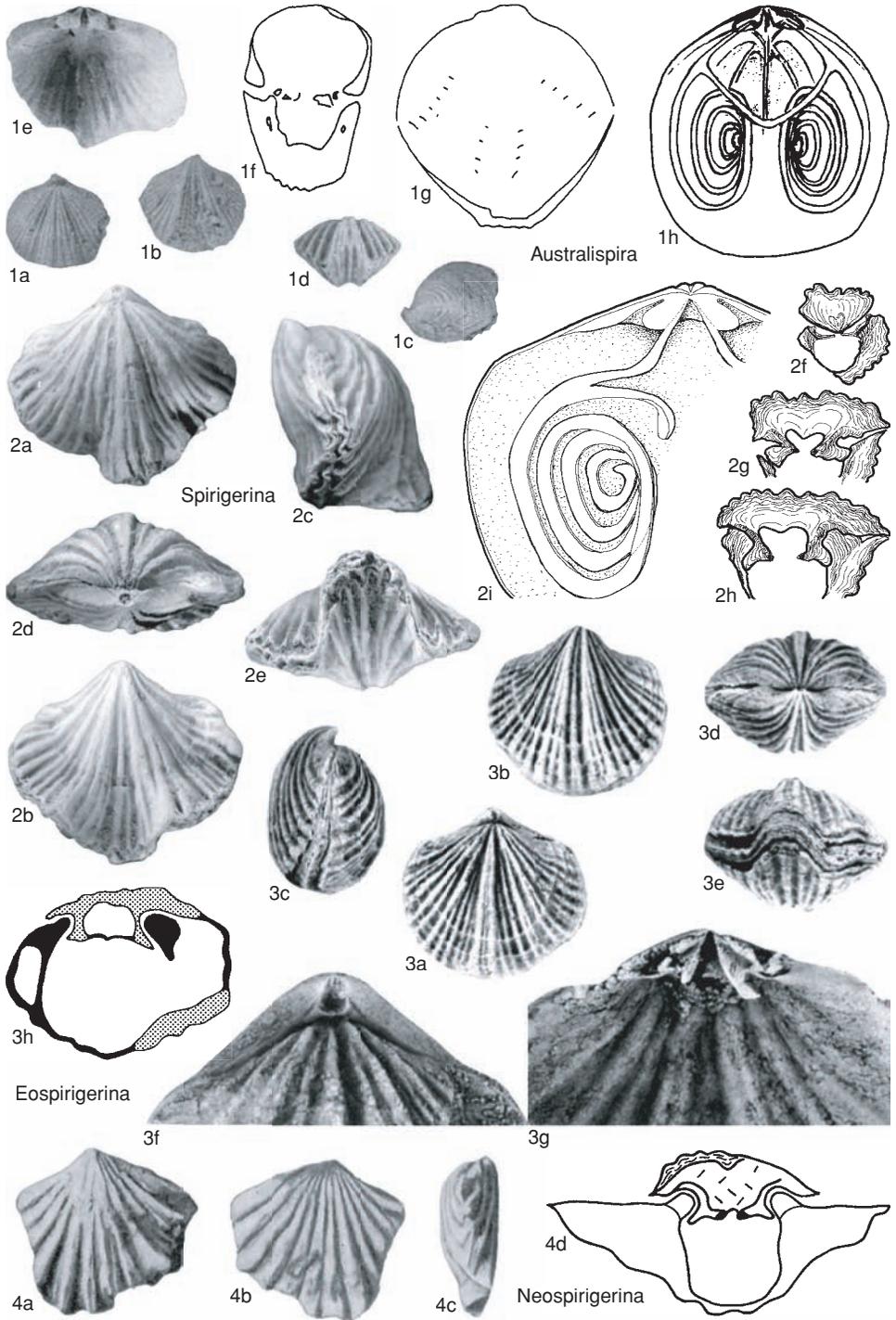


FIG. 970. Atrypinidae (p. 1429-1432).

- 284 (type, *N. jianglutangensis*, OD)]. Subquadrate to shield shaped, dorsibiconvex; small orthoclinae-anacline area; apical to transapical foramen, flanked by small deltidial plates; ribs fine to medium size, to fading laterally to sometimes nearly smooth, expanding and coarsening anteriorly; ventral diverging, furcating raised midrib clusters forming weak margins to ventral sulcus; ribs continuous or with partly developed growth lamellae anteriorly; strong, U-shaped anterior fold; short, stout teeth; small, subhorizontal, slitlike dental cavities; crura strong; dorsomedial spiralia with fewer than 12 whorls; jugal processes delicate. [Distinguished from *Spirigerina* by generally finer ribs, poorly defined midribs along fold margins, lacking microfilae, very short growth lamellae or growth interruptions commonly present, thin hinge plates; distinguished from *Qilianotryma* by coarser ribs, and rib-defined anterior fold; neanic specimens may be mistaken for *Atrypina*.] Ordovician (middle Ashgill)—Silurian (Llandovery): worldwide.—FIG. 970,3a–h. **E. putilla* (HALL), upper Ashgill, Missouri, USA; a–e, dorsal, ventral, lateral, posterior, and anterior views, $\times 2$; f–g, dorsal interior, exterior, $\times 5$; h, serial section, $\times 3$ (Amsden, 1974).
- Neospirigerina** RZHONSNITSKAIA, 1975, p. 72 [*Plectatrypa ossa* NALIVKIN, 1960, p. 381; OD]. Medium size, weakly dorsibiconvex to flat, rhynchonelliform shell; protruding strong beak; small, apsacline-orthoclinae area; prominent deltidial plates, apical foramen; ribs coarse, nonbifurcating, with weakly defined midrib pair; rectimarginate to weak, broadly plicate commissure; internally broad, blunt teeth, possibly lacking dental cavities; massive hinge plate; slender socket plates with small inner socket ridges; spiralia and jugal processes undescribed. [Differentiated from *Spirigerina* by its very coarse, nondividing ribs, flat shell, weak anterior fold, lack of dental cavities; possibly synonymous with *Plesicarinata*.] Lower Devonian (Lochkovian—Emsian): Siberia, Urals, Kazakhstan, central Asia.—FIG. 970,4a–d. **N. ossa* (NALIVKIN), Pragian, Urals; a–c, dorsal, ventral, lateral views, $\times 2$ (Nalivkin, 1960); d, serial section at hinge plate, $\times 2$ (Rzhonsnitskaia, 1975).
- ?**Ogilviella** LENZ, 1968, p. 180 [**O. rotunda* LENZ, 1968, p. 181; OD] [=?*Arctispina* SMITH, 1980, p. 66 (type, *A. canadensis*, OD)]. Small, rotund, biconvex-ventribiconvex, carinate ventrally; small orthoclinae area; minute deltidial plates; apical foramen; continuous ribs expanding distally; growth lamellae absent; ventral carina produced by raised midrib pair(s) matched by sulcus on brachial valve; rectimarginate to sulcate commissure; interior with thin shell wall; small teeth, minute dental cavities; thin hinge plates; crura, jugal processes, and spiralia undescribed. [Differs from *Spirigerina* by small size, lack of wide anterior fold, absence of ribs between raised ventral midrib pair, lack of ventral sulcus, sulcate-rectimarginate commissure; internal structure of brachidia unknown.] Lower Devonian (Lochkovian—Pragian): northern Canada, Australia.—FIG. 971,1a–f. **O. rotunda*, Pragian, Yukon, Canada; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e–f, dorsal, ventral interiors, $\times 3.5$ (Lenz, 1968).
- ?**Otarella** RUKAVISHNIKOVA, 1982, p. 46 [**O. multicostata*; OD; nom. nud.]. No known published description nor figures of genus or type species. Ordovician (upper Ashgill)—Silurian (lower Llandovery): Kazakhstan.
- Pectenospira** POPOV, NIKITIN, & SOKIRAN, 1999, p. 648 [**P. pectenata*; OD]. Small, ventribiconvex, acuminate shell, plicate with anterior, dorsal, smooth fold expressed as small posterior sulcus on ventral valve; high apical angle with narrow orthoclinae beak; ventral valve with 2 divergent main ribs flanked by smaller ribs; interior with large dental cavities, spiralia simple with fewer than 2 whorls, dorsomedially directed; centrodorsal, short jugal processes. [Earliest known spirigerinid, defined from others by small size and simple spirulum directed dorsomedially.] Ordovician (lower Caradoc—middle Caradoc): Kazakhstan, northwestern China (Qinghai).—FIG. 971,2a–d. **P. pectenata*, Anderken Formation, Kazakhstan; a–c, dorsal, ventral, anterior views, $\times 4$; d, reconstruction of brachidia, approximately $\times 12$ (Popov, Nikitin, & Sokiran, 1999).
- Qilianotryma** XU Hankui, 1979b, p. 97 [**Q. mirabile*; OD] [=*Euroatrypa* ORADOVSKAYA in NIKIFOROVA, ORADOVSKAIA, & POPOV, 1982, p. 63 (type, *E. tajmyrica* NIKIFOROVA, 1982, p. 65, OD); *Ovalospira* (*Orthocarina*) FU, 1982, p. 158 (type, *O. carinatiformis*, OD)]. Medium size, wide, subquadrate to subrounded, spirifer shaped; relatively long hinge; small, protruding, orthoclinae area; deltidial plates; apical foramen; broad, U-shaped anterior fold; ribs fine to very fine, evenly sized, bifurcating and intercalating; interior with short, broad teeth; slitlike to rounded dental cavity; dorsomedial-dorsal spiralia with fewer than 8 whorls; posteroventral jugal processes almost touching. [Similar to *Eospirigerina*, but relatively wide shell with very fine ribs, i.e., costellate ornamentation; ribbing as in *Beitaia* (Clintonellinae), but with *Eospirigerina*-like shell, small dental cavities, and sturdy teeth.] Ordovician (upper Caradoc)—Silurian (Llandovery): China (Qinghai), Urals, Kazakhstan, central Asia, upper Caradoc; Estonia, China (Qinling Mountains), Llandovery.—FIG. 971,3a–c. **Q. mirabile*, Ashgill, Qinghai; a–b, dorsal and posterior views, $\times 2$; c, polished section, $\times 2.5$ (Xu, 1979b).—FIG. 971,3d. *Q. tajmyrica* NIKIFOROVA, Ashgill, Taimyr, Russia; detail of shell surface, $\times 4$ (Nikiforova, 1982).
- Schachriomonina** NIKIFOROVA, 1978, p. 118 [**S. schachriomonica* NIKIFOROVA, 1978, p. 119; OD]. Medium size; medium to coarsely ribbed; rounded to subquadrate outline; lacking strong midribs, but slightly carinate, with weak, concentric growth lamellae; small orthoclinae-anacline area; protruding beak; small deltidial plates; apical foramen; weakly plicate to rectimarginate commissure; thick walled; teeth with small dental cavities; spiralia dorso-medial; separated jugal processes. [Differs from

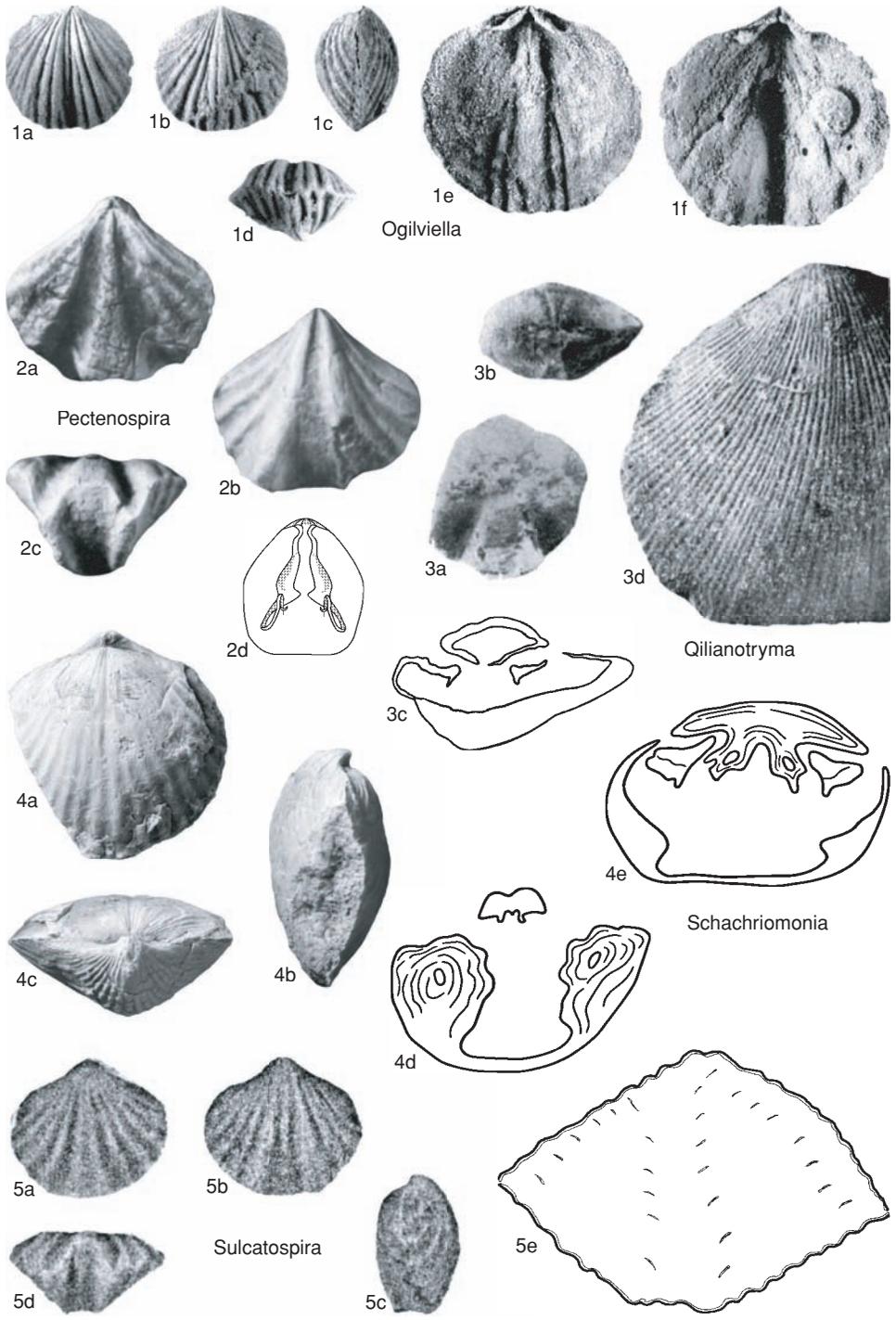


FIG. 971. Atrypinidae (p. 1432-1434).

Eospirigerina in coarser ribs, lack of strong carination, wider area; very similar to ?*Australispira*, except in convexity and lack of strong carination.] Ordovician (Ashgill), Silurian (?Llandovery): Kazakhstan, central Asia, Altai.—FIG. 971,4a–e. **S. schachriomonica*, Ashgill, Shakhriomon, Uzbekistan; a–c, dorsal, lateral, posterior views, ×2 (new); d–e, polished sections, ×3.5 (Nikiforova, 1978).

Sulcatospira XU, 1979c, p. 109 [**Zygospira* (*Sulcatospira*) *plicata* XU, 1979c, p. 110; OD] [= *Antizygospira* FU, 1982, p. 146 (type, *A. liquanensis*, OD); *Ovalospira* FU, 1982, p. 157 (type, *O. ovalis*, OD); *Taoquospira* FU, 1982, p. 159 (type, *T. dichotoma*, OD); *Kuzgunia* MISIUS, 1969 (ms.) in KLENINA, 1984, p. 113 (type, *Zygospira parva* RUKAVISHNIKOVA, 1956, p. 162, OD); *Kuzgunia* MISIUS, 1986, p. 186 (type, *K. asiatica*, OD)]. Small, rounded to subquadrate, weakly carinate; minute orthocline area; triangular beak; small deltidial plates flanking apical foramen; tubular, expanding coarse ribs with ventral, diverging midrib pair, producing carination; plicate-sulciple commisure; short teeth; small, rounded dental cavities; small, bulbous hinge plates; dorsomedial spiralia with fewer than 8 whorls; slender, long jugal processes posteromedial, lacking jugal plates. [Differs from superficially similar *Zygospira* in being plicate instead of sulcate, with jugal processes instead of jugum; differs from *Eospirigerina* and *Spirigerina* in small size, expanding coarse ribs.] Ordovician (?middle *Caradoc*, upper *Caradoc*–Ashgill): China, Kazakhstan, Altai, central Asia, Australia.—FIG. 971,5a–d. **S. plicata*, Ashgill, Qinghai, northwestern China; dorsal, ventral, lateral, anterior views, ×3 (XU, 1979c).—FIG. 971,5e. **S. parva* (RUKAVISHNIKOVA), Ashgill, Kazakhstan; serial section of spiralia, ×5 (new).

Superfamily PUNCTATRYPOIDEA Rzhonsnitskaia, 1960

[*nom. transl.* COPPER, herein, ex Punctatrypinæ RZHONSNITSKAIA, 1960a, p. 262; *emend.*, COPPER, herein]

Ribbed atrypoids, with imbricate growth lamellae or short lamellae with fine grooves, ranging from ancestral, finely ribbed, nodose forms with short growth lamellae, lacking fenestrae, to shells with anterior fenestrae developed in concentric rows, open along actively growing anterior commisure, sealed posteriorly; dorsomedially directed spiralia with fewer than 10 whorls; jugal processes

with short jugal plates. *Silurian* (Aeronian)–*Middle Devonian* (Eifelian).

Family PUNCTATRYPIDAE Rzhonsnitskaia, 1960

[*nom. transl.* COPPER, herein, ex Punctatrypinæ RZHONSNITSKAIA, 1960a, p. 262]

Diagnosis as for superfamily. *Silurian* (Aeronian)–*Middle Devonian* (Eifelian).

Subfamily PUNCTATRYPINAE Rzhonsnitskaia, 1960

[Punctatrypinæ RZHONSNITSKAIA, 1960a, p. 262] [=Crassipunctatrypinæ WANG, COPPER, & RONG, 1983, p. 1085]

Punctatrypids with secondary layer modified to develop concentrically, radially aligned, round to oval fenestrae, open around commissure, posteriorly sealed off during growth, penetrating primary and secondary shell layers to shell interior; fenestrae (not punctae) oriented oblique or normal to shell surface (fenestrae absent in teeth, hinge, and socket plates); short growth lamellae may protrude as ribbed or smooth frills with angular narrow grooves, partly covering fenestrae; teeth solid; hinge plate usually thick. *Lower Devonian* (middle *Lochkovian*)–*Middle Devonian* (Eifelian).

Punctatrypa HAVLÍČEK, 1953, p. 8 [**P. naliivkini*; OD].

Small, elongate to rounded, biconvex, non-carinate; narrow hinge; protruding beak; small orthocline area; apical foramen flanked by triangular deltidial plates; finely ribbed; short, imbricate growth lamellae, closely spaced along commissure; single, vertical fenestra on each rib crest; weak, small dorsal sulcus posteriorly; rectimarginate commissure; solid, strong, short teeth, lacking dental cavities; thick hinge plate; narrow cardinal pit; large inner socket ridges; short crura; spiralia, jugal processes undescribed. [Distinguished by small, rounded, biconvex shell, evenly developed, fine ribs.] *Lower Devonian* (middle *Lochkovian*)–*Middle Devonian* (Eifelian): Eurasia, North America.—FIG. 972,2a–g. **P. naliivkini*, Emsian, Czech Republic; a–d, dorsal, ventral, posterior, anterior views, ×3.5; e, interior of ventral valve, ×3.7 (Havlíček, 1987a); f, SEM view of ventral valve interior, ×25.5 (new); g, external view of shell with fenestrae, ×30 (Wang, Copper, & Rong, 1983).

Crassipunctatrypa MIZENS & RZHONSNITSKAIA, 1979, p. 63 [**Punctatrypa crassiconcentrica* MIZENS, 1977b, p. 93; OD]. Small to medium, rounded,

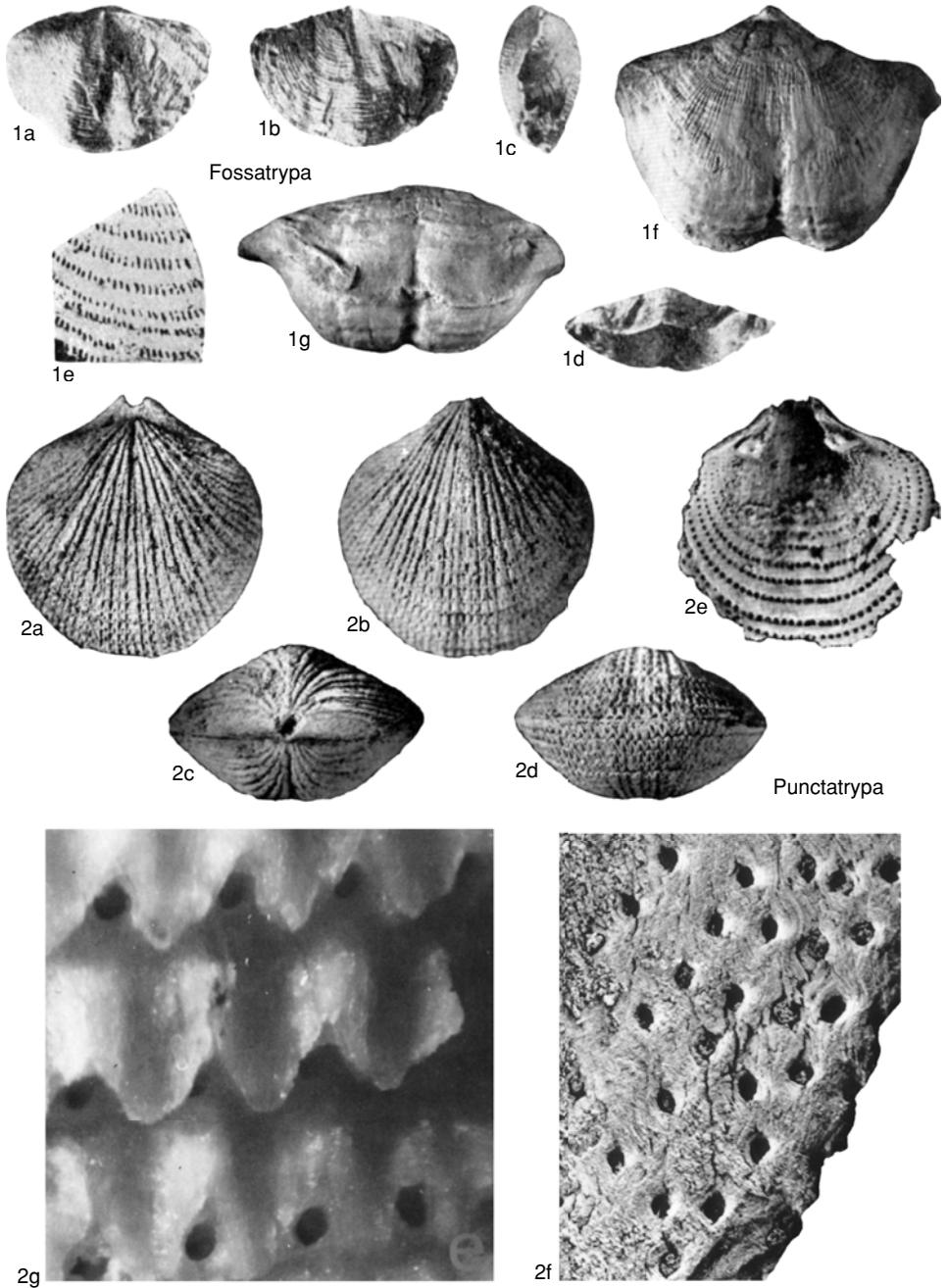


FIG. 972. Punctatrypidae (p. 1434–1437).

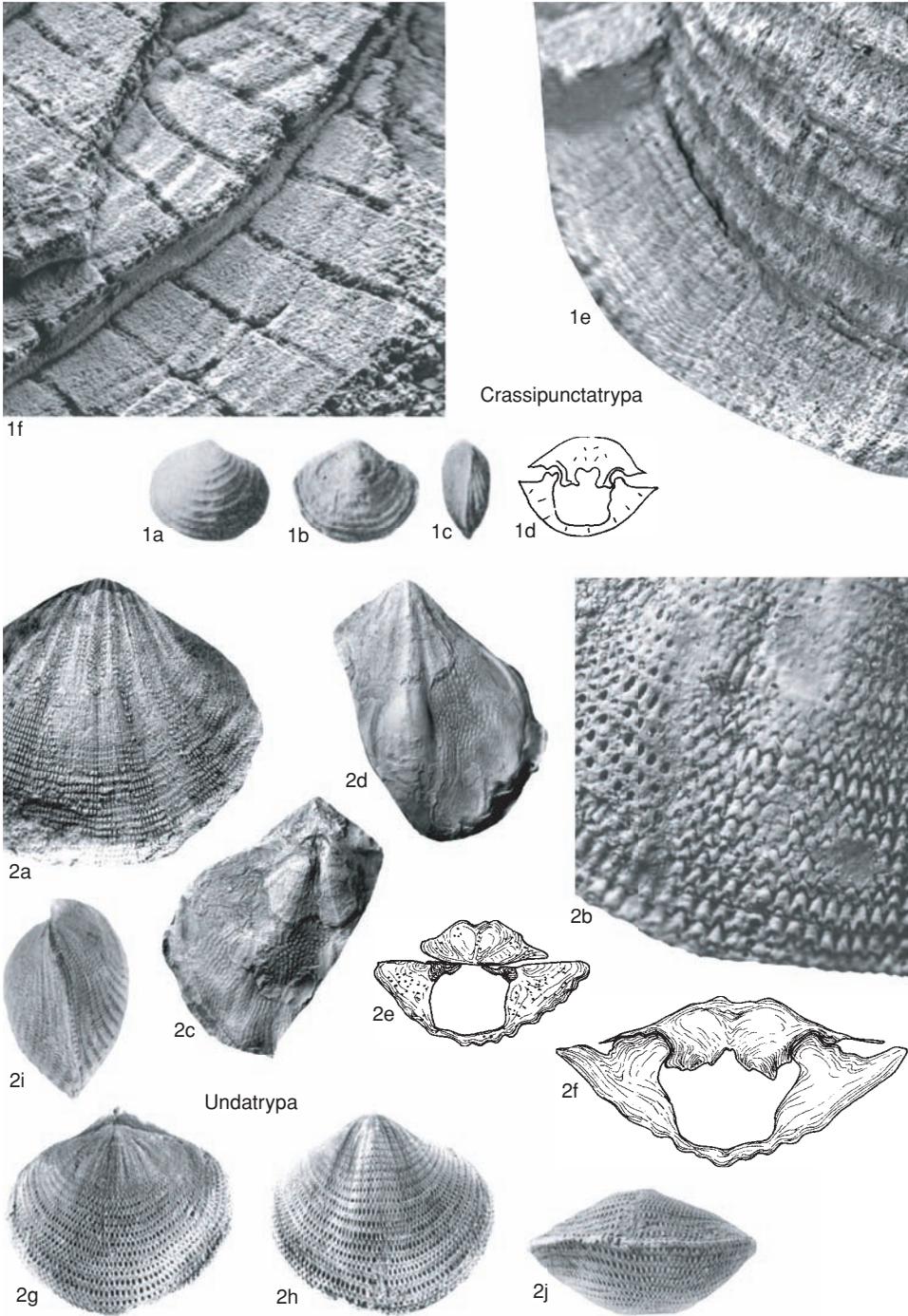


FIG. 973. Punctatrypidae (p. 1434–1438).

biconvex; small beak; minute anacline-orthocline area; apical foramen bisecting deltidial plates; surface covered by very fine ribs posteriorly, tending to fade anteriorly, ribbing absent on growth lamellae; concentric, flat, weakly deflected growth lamellae protruding as overlapping, flat frills, possessing narrow, radial, linear grooves; concentric anterior fenestrae partially roofed over by growth lamellae; commissure rectimarginate to weakly plicate; solid teeth; hinge plates delicate; spiralia, jugal processes undescribed. [Distinguished from *Punctatrypa* and others by its unique, flat growth lamellae with radiating linear grooves, rib loss anteriorly, hidden fenestrae.] Lower Devonian (upper Pragian)—Middle Devonian (middle Eifelian): Urals, central Asia, Tian Shan.—FIG. 973, 1a–f. **C. crassiconcentrica* (MIZENS), Emsian, Turkestan; a–c, dorsal, ventral, lateral views, $\times 1$; d, serial section, $\times 2.5$ (Mizens, 1984); e, SEM view of growth lamellae, $\times 14$; f, SEM view of fenestrae, $\times 43$ (new).

Fossatrypa MIZENS & RZHONSNIJSKAIA, 1979, p. 62 [**Punctatrypa fossa* BREIVEL, 1959, p. 56; OD] [= *Araneatrypa* HAVLÍČEK, 1987a, p. 90 (type, *Terebratula arachne* BARRANDE, 1847, p. 457, OD)]. Medium, biconvex, wider than long, long hinged, weakly carinate posteroventrally; hypercline-anacline area; beak incurved, obscuring foramen, deltidial plates; ribs fine, not overprinted by coarser ribs; short, concentric lamellae creating appearance of granules at rib crests, overlying oval fenestrae beneath; anterior fenestrae diagonal to shell surface; frills absent; commissure ligate or rectimarginate; interior with solid teeth; laterally arched crura; dorsomedial spiralia with about 6 whorls, jugal processes undescribed. [Differs from other punctatrypinids by its long hinge, wide spiriferoid shell, lack of overprinted ribs. "*Terebratula granulifera* BARRANDE, 1847, lacks fenestrae and cannot be assigned to this genus.] Lower Devonian (Pragian–Emsian), Middle Devonian (Eifelian): eastern Urals, Carnic Alps, Czech Republic.—FIG. 972, 1a–e. **F. fossa* (BREIVEL), ?lower Eifelian, ?middle Eifelian, eastern slopes, Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 3$; e, enlarged view of macroornament, approximately $\times 10$ (Breivel, 1959).—FIG. 972, 1f–g. *F. arachne* (BARRANDE), Pragian, Czech Republic; dorsal, posterior views, $\times 1.4$ (Havlíček, 1987a).

Sinopunctatrypa WANG, COPPER, & RONG, 1983, p. 1081 [**Punctatrypa* (*Sinopunctatrypa*) *saetulosa*; OD]. Small, ventribiconvex-planoconvex; weakly keeled or unkeeled; apsacline-orthocline area; small beak; apical foramen; wrinkled deltidial plates; fine ribs completely covering shell, intersected by short growth lamellae; ventral midrib pair raised; 2 or more vertical small fenestrae per rib; commissure sulcate to weakly plicate; interior with solid teeth; hinge plates broad; wide cardinal pit; dorsomedial spiralia with fewer than 8 whorls; jugal processes undescribed. [Distinct from other punctatrypinids in having 2 or more fenestrae per rib, instead of

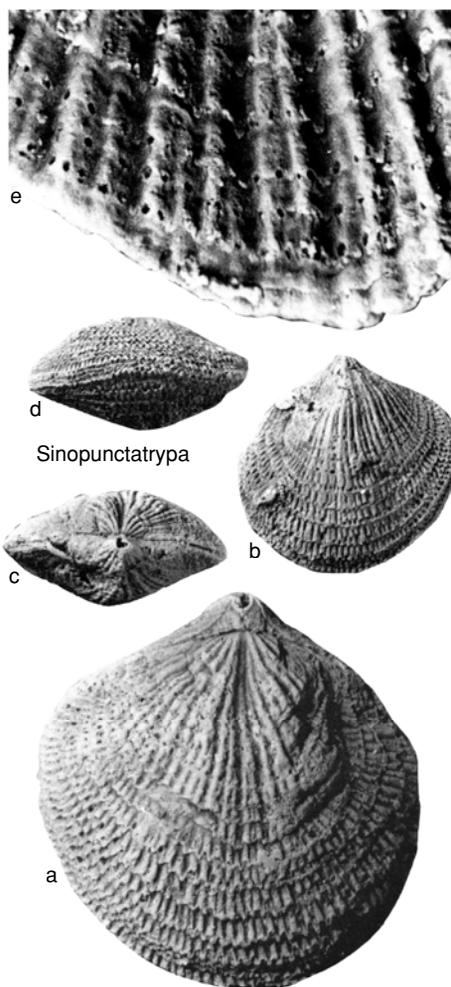


FIG. 974. Punctatrypidae (p. 1437).

single fenestra on each rib crest.] Lower Devonian (Emsian): southern China (Guangxi).—FIG. 974a–e. **S. saetulosa* (WANG, COPPER, & RONG), lower Emsian; a, dorsal view, $\times 5$; b–d, ventral, posterior, anterior views, $\times 3$; e, detail of ventral valve, $\times 15$ (Wang, Copper, & Rong, 1983).

Undatrypa COPPER, 1978, p. 302 [**Terebratula munieri* GRUENEWALDT, 1854, p. 581[13]; OD] [= *Munieratrypa* (*Munieratrypa*) MIZENS & RZHONSNIJSKAIA, 1979, p. 60 (type, *Punctatrypa munieri dichotomoplicata* RZHONSNIJSKAIA, 1960a, pl. 56, 4ab, nom. nud., no description, OD, vid. RZHONSNIJSKAIA, 1975, p. 156)]. Small to medium, flattened, biconvex; carinate posteroventrally, sulcate dorsally; moderately long hinge; small orthocline area; protruding beak; apical foramen flanked by deltidial plates; ribs

fine, posteriorly overprinted by coarse, strong ribs, fading anteriorly; ventral midribs producing keel; anterior, diagonal fenestrae at intersections of growth lamellae and finer ribs; commissure rectimarginate to weakly plicate; thick shell wall; solid teeth; hinge plates strong; spiralia dorsomedial, fewer than 10 whorls; jugal processes undescribed. [Distinguished from other Punctatrypininae by having fine ribs overprinted with coarse ribs.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Urals, southwestern Europe, China, northern Canada.—FIG. 973,2a–f. **U. munieri* (GRUENEWALDT), Emsian, eastern slopes, Urals; *a*, ventral view, $\times 2.5$; *b*, macroornament, fenestrae, $\times 12$; *c–d*, dorsal, ventral interiors, $\times 2.5$; *e–f*, serial sections, $\times 5$ (Copper, 1978).—FIG. 973,2g–j. *U. bellatula* (WANG, COPPER, & RONG), Emsian, Guangxi, China; dorsal, ventral, lateral, anterior views, $\times 3$ (Wang, Copper, & Rong, 1983).

Subfamily ATRYPINELLINAE

new subfamily

[Atrypinellinae COPPER, herein]

Finely ribbed, small to medium, biconvex, sometimes bilobate shells, commonly ventrally subcarinate; finely ribbed; short, evenly spaced, slightly imbricate growth lamellae; fenestrae absent; narrow to wide hinge; orthocone beak; distinct deltidial plates; apical foramen; thin shell, small dental cavities or nuclei. [Taxa resembling *Punctatrypa*, but lacking fenestrae, e.g., *Atrypinella granulifera* (BARRANDE, 1879b), may be assigned here.] *Silurian (Aeronian)–Lower Devonian (Emsian)*.

Atrypinella KHODALEVICH, 1939, p. 45 [**Atrypa (Atrypinella) biloba*; OD]. Small to medium, rounded, globose, bilobate to biconvex; both valves normally sulcate, ventral valve subcarinate posteriorly; finely ribbed, with decorticated shell giving granulose appearance; closely spaced, flat, short growth lamellae; ligate to rectimarginate commissure; short teeth, possessing nuclei or small dental cavities; hinge socket plates thick; dorsal spiralia with fewer than 6 whorls; jugal processes thin, ventromedial to medial, almost touching. [Differs from *Reticulatrype* in subcarinate, bisulcate shell; includes well-known *A. granulifera* (BARRANDE, 1879b).] *Silurian (Přídolí)–Lower Devonian (Emsian)*: Urals, central Asia, western Europe, arctic Canada.—FIG. 975,1a–d. **A. biloba* (KHODALEVICH), Lochkovian, Urals; dorsal, ventral, lateral, anterior views, $\times 1$ (Khodalevich, 1939).—FIG. 975,1e–f. *A. losvensis* (KHODALEVICH), upper Lochkovian–lower Pragian, eastern slopes, Urals; serial sections, $\times 2$ (Mizens, 1984).

?*Istokina* BREIVEL & BREIVEL, 1988, p. 81 [*?*Spinatrypa bobrovkensis* MIZENS, 1977a, p. 50; OD]. Small, biconvex-ventribiconvex, rounded, subcarinate; moderately long, straight hinge; area orthocone; apical foramen; small deltidial plates; fine, imbricate-undulose ribs; bifurcating midrib pair producing weak keel on ventral valve; median sulcus on dorsal valve; very short, less than 2 mm, deflected growth lamellae; rectimarginate to weakly plicate commissure; pedicle callist absent; solid teeth; vertically oriented, long crura; spiralia, jugal processes undescribed. [Affinity uncertain; possibly synonymous with *Atrypinella* from which it differs in more wavy ribs, carination, apparent absence of dental cavities or nuclei; similar to finely ribbed *Plectatrypa* in sculpture, but lacking strong ventral carination.] *Silurian (Přídolí)*: Urals.—FIG. 975,3a–e. **I. bobrovkensis* (MIZENS), eastern slopes; *a–d*, dorsal, ventral, lateral, anterior views, $\times 1$ (Mizens, 1977a); *e*, enlarged view of dorsal macroornamentation, $\times 3$ (Breivel & Breivel, 1988).

Limbatrype COPPER, 1982, p. 700 [**L. leptostriata*; OD]. Relatively flat, weakly biconvex, ventrally weakly carinate; wide hinge; small, pointed beak; prominent orthocone area; apical foramen; deltidial plates; very finely ribbed; growth lamellae right-angled, short, less than 5 mm; rectimarginate commissure; teeth with dental cavities; crura, spiralia, jugal processes silicified, undescribed. [Similar to *Atrypinella* in rib fineness, granulose appearance at growth lamellae, but with relatively flat, wide shell, sharply deflected (about 90°), short lamellae, lack of bisulcation; affinities with Atrypinae, Variatrypininae, or Atrypinellinae uncertain.] *Silurian (Aeronian–Wenlock)*: North America, Urals, central Asia.—FIG. 975,4a–e. **L. leptostriata*, Telychian, Manitoulin, eastern Canada; *a–d*, dorsal, ventral, posterior, lateral views, $\times 2$ (Copper, 1982); *e*, detail of dorsal macroornamentation, $\times 5$ (new).

Reticulatrype SAVAGE, 1970, p. 663 [**R. fairhillensis*; OD]. Rounded, subcircular to ovate, globose, biconvex, weakly carinate or noncarinate; small orthocone area; apical foramen; minute deltidial plates; finely ribbed; imbricate ornamentation produced by less than 1-mm-spaced, short growth lamellae; rectimarginate to flat, widely plicate commissure; shell wall thin; teeth with possible dental cavities; muscle scars weakly incised; hinge plate delicate; spiralia of fewer than 6 whorls, dorsally directed; jugal processes undescribed (from silicified type material). [Ornamentation similar to possibly congeneric *Atrypinella*, but lacking strong bisulcation of type species; differs from *Limbatrype* in imbricate ornamentation; affinities with Atrypinellinae uncertain, possibly referable to Atrypinae.] *Silurian (?Přídolí)*, *Lower Devonian (Lochkovian–Pragian)*: Australia, ?Europe, ?Urals, ?northwestern Canada.—FIG. 975,2a–e. **R. fairhillensis*, Pragian, New South Wales; *a–d*, dorsal, ventral, posterior, anterior views; *e*, lateral view of spirillum, $\times 3$ (Savage, 1970).

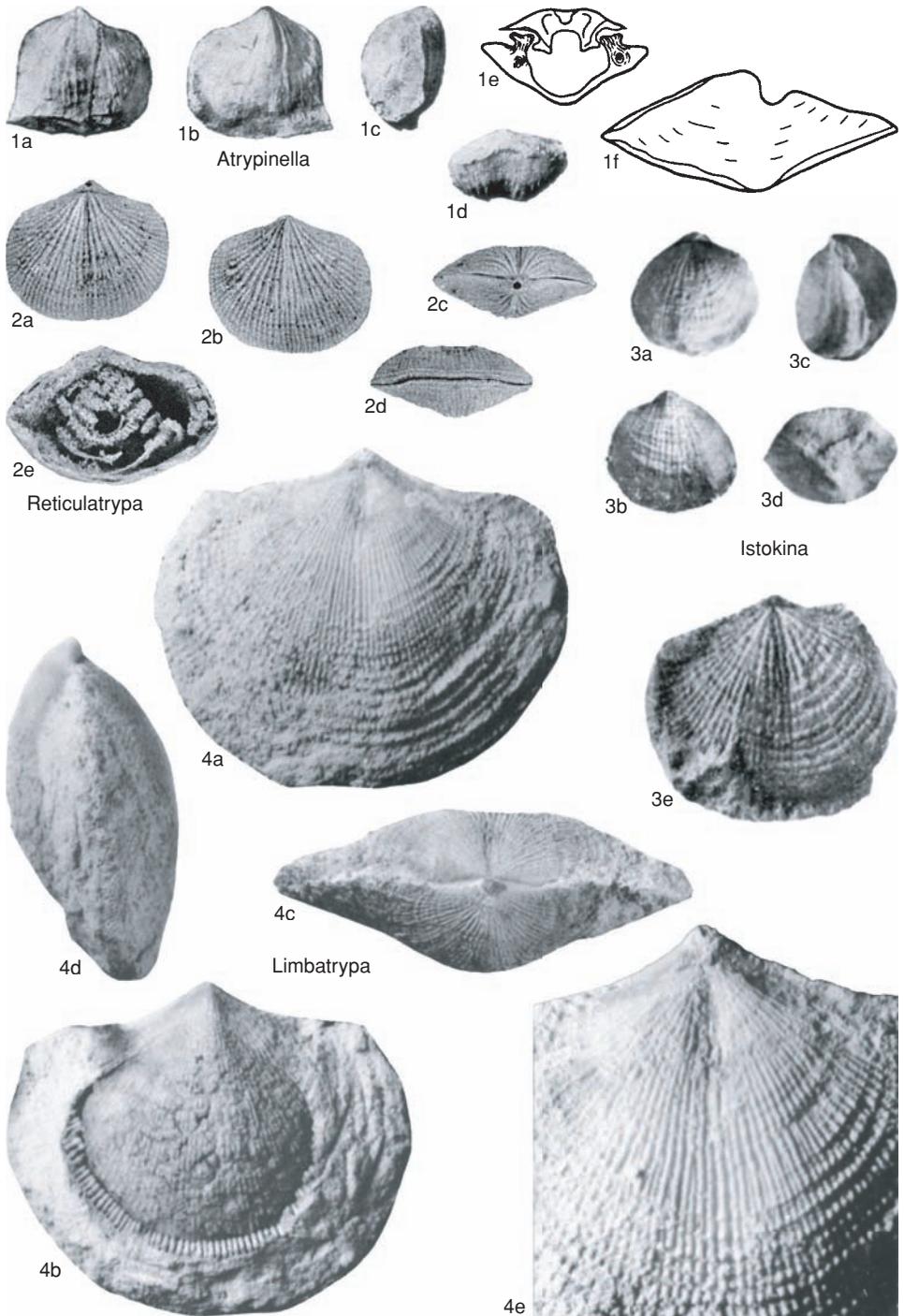


FIG. 975. Punctatrypidae (p. 1438).

Suborder ANAZYGIDINA Copper, 1996

[Anazygidina COPPER in COPPER & GOURVENNEC, 1996, p. 82]
[=Zygospiridae WAAGEN, 1883, p. 449, *partim*]

Ribbed, small shells with sulcate-rectimarginate commissure; astrophic to strophic hinge; small orthocline area, beak; apical foramen; deltidial plates lacking or minute; teeth solid or with small dental cavities; simple spiralia medially to dorsomedially directed, normally fewer than 10 whorls; complete U- or W-shaped jugum. *Ordovician* (?*Llandeilo*, *Caradoc*)–*Silurian* (*Ludlow*, ?*Přídolí*).

Superfamily ANAZYGOIDEA Davidson, 1883

[*nom. transl.* COPPER, *herein*, *ex* Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim*; *emend.* COPPER, *herein*] [=Zygospiroidea WAAGEN, 1883, p. 446, *partim*; *emend.*, MUIR-WOOD, 1955, p. 91]

Characters as for suborder. *Ordovician* (?*Llandeilo*, *Caradoc*)–*Silurian* (*Ludlow*, ?*Přídolí*).

Family ANAZYGIDAE Davidson, 1883

[Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim*; *emend.*, COPPER, *herein*] [=Zygospiroidea WAAGEN, 1883, p. 446, *partim*; *emend.*, MUIR-WOOD, 1955, p. 91]

Small, ventribiconvex to planoconvex, ribbed shells; astrophic hinge; small area; sulcate to rectimarginate commissure; spiralia directed medially to dorsomedially with few whorls; simple jugum located dorsally to centrally. *Ordovician* (?*Llandeilo*, *Caradoc*)–*Silurian* (*Ludlow*, ?*Přídolí*).

Subfamily ANAZYGINAE Davidson, 1883

[*nom. transl.* COPPER, *herein*, *ex* Anazygidae DAVIDSON, 1882 *in* DAVIDSON, 1883, p. 136, *partim*; *emend.*, COPPER, *herein*] [=Zygospiridae WAAGEN, 1883, p. 446, *partim*; *emend.*, MUIR-WOOD, 1955, p. 91]

Small, weakly to strongly carinate, ventribiconvex to planoconvex anazygids with sulcate commissure; simple medially to dorsomedially directed spiralia with few whorls, central to anterodorsal jugum arising anterolaterally. *Ordovician* (?*Llandeilo*, *Caradoc*)–*Silurian* (*Sheinwoodian*).

Anazyga DAVIDSON, 1882, p. 128 [**Atrypa recurvirostra* HALL, 1847, p. 140; OD] [=Hallina WINCHELL & SCHUCHERT, 1892, p. 291 (type, *H. saffordi*, OD); *Nuria* MISIUS, 1986, p. 199 (type, *N. mediasiatica*,

OD)]. Small, ventribiconvex, rounded to elongate, noncarinate; short hinge; protruding beak; small orthocline area; minute apical foramen; deltidial plates minute or lacking; ribs fine, anteriorly slightly expanding, bifurcating-intercalating; sulcate commissure; interior thin shelled; small, medially directed teeth with minute dental cavities; small, delicate hinge plate; crura vertical; spiralia medially directed, normally fewer than 5 whorls, occupying only part of shell interior; jugum flat, dorsomedially located, near shell anterior. [Distinguished from *Zygospira* by rounded-elongate shape, lack of carination, fine ribs, short hinge, medially oriented spiralia.] *Ordovician* (?*Llandeilo*, *Caradoc*, ?*middle Ashgill*); worldwide.—FIG. 976, 2*a*–*i*. **A. recurvirostra* (HALL), *Caradoc*, New York, USA; *a*–*d*, dorsal, ventral, anterior, lateral views, $\times 3$; *e*–*h*, serial sections, $\times 5$; *i*, reconstruction of brachidium, $\times 5$ (new).

Zygotrypa COPPER, 1977a, p. 307 [**Zygospira paupera* BILLINGS, 1866, p. 46; OD]. Small, strongly carinate, ventribiconvex-planoconvex; narrow hinge; beak minute, pinched; small anacline to hypercline area; minute deltidial plates; apical-transapical foramen; shell almost smooth to partly ribbed, ribs coarsening distally, shell generally smooth on lateral flanks; where present, 6 to 8 ribs occupying ventral carina; broadly sulcate commissure; interior relatively thick walled; short teeth with dental nuclei, dental cavities lacking; hinge plate stout; crura short, laterally directed; spiralia dorsomedial, fewer than 5 whorls; jugum curved, posterodorsal, almost resting on dorsal valve floor. [Distinguished from *Zygospira* by its thick shell wall, trend toward lateral or total rib loss, fine ribs on ventral carina, lack of dental cavities, and posteriorly located jugum.] *Silurian* (*Llandovery*–*Sheinwoodian*): North America, western Europe.—FIG. 976, 3*a*–*b*. **Z. paupera* (BILLINGS), Telychian, Anticosti, Canada; *a*, ventral view, $\times 4$; *b*–*c*, dorsal, anterior views, $\times 3$; *d*–*e*, serial sections, $\times 5$; *f*–*g*, camera lucida drawings, $\times 6$; *h*, reconstruction of brachidia, $\times 5$ (Copper, 1977a).

Zygospira HALL, 1862, p. 154 [**Producta modesta* SAY in HALL, 1847, p. 141; OD] [=Pusillagutta MISIUS, 1986, p. 210 (type, *P. gibbera* MISIUS, 1986, p. 211, OD)]. Small, ventribiconvex-planoconvex; ventral valve strongly to weakly carinate; weakly sulcate dorsal valve; long hinge; small orthocline-anacline area; minute beak; apical-transapical foramen; deltidial plates minute to absent; ribs medium (coarse ribs on ventral carina), expanding distally, generally nonbifurcating; growth interruptions common, rare, slightly overlapping anterior growth lamellae; commissure sulcate; interior thinly walled; minute, medially directed teeth with dental cavities; brachidia delicate; crura small, laterally directed; spiralia dorsomedially directed with fewer than 8 whorls, filling much of shell interior; jugum posteromedial to dorsal, in mid-anterior of shell. [Distinguished from *Anazyga* by wider hinge line, carination, coarser ribs, dorsomedially directed spiralia.] *Ordovician* (*Caradoc*–*Ashgill*); worldwide.—FIG. 976, 1*a*–*b*. **Z. modesta* (SAY), middle

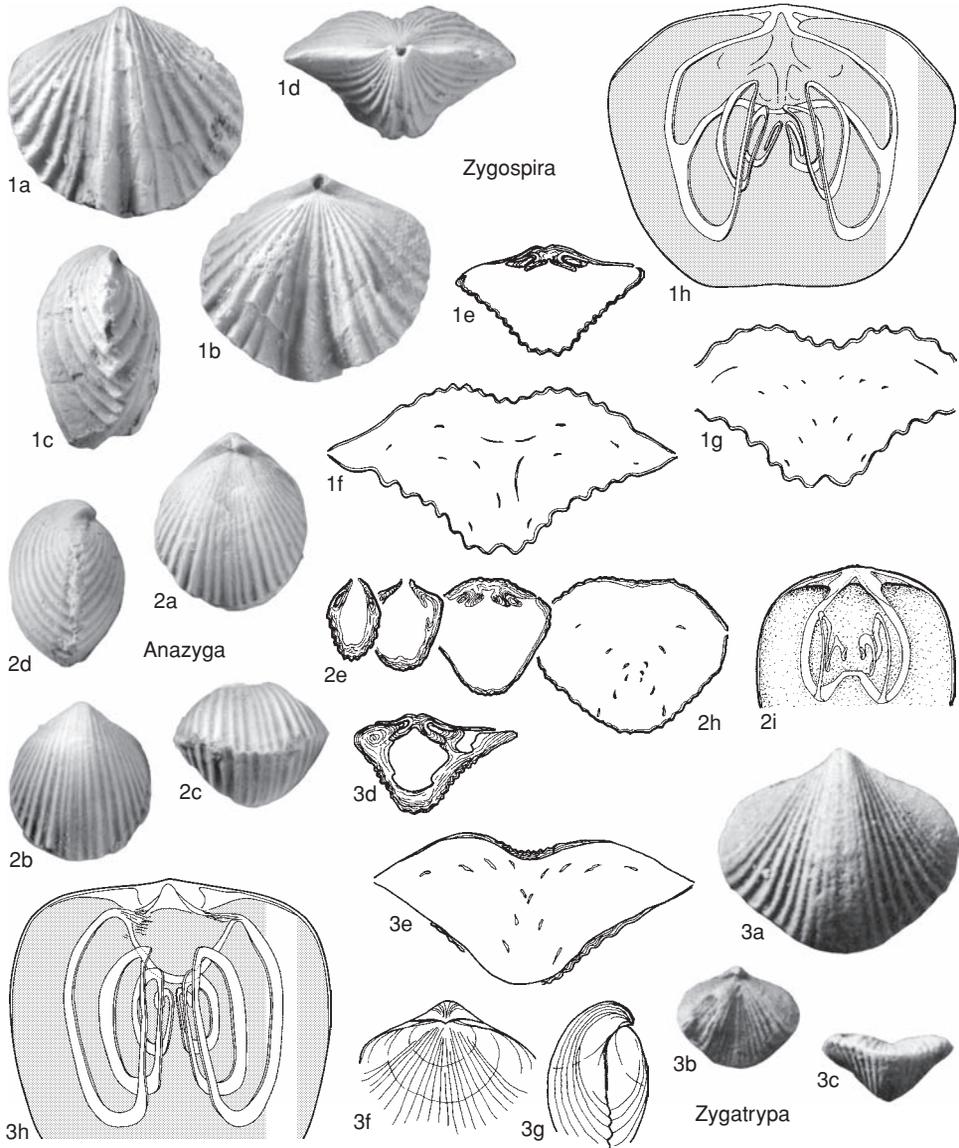


FIG. 976. Anazygidae (p. 1440).

Ashgill, Ohio, USA; *a-d*, ventral, dorsal, lateral, posterior views, $\times 3$; *e-g*, serial sections with jugum, spiralia, $\times 5$; *h*, reconstruction of brachidium, $\times 5$ (Copper, 1977a).

Subfamily CATAZYGINAE Copper, 1977

[Catazyginae COPPER, 1977a, p. 311]

Ribbed, elongate to rounded, biconvex to dorsibiconvex, lacking ventral carination;

rectimarginate commissure; small, narrow, ananeline-hypercline area; minute foramen; deltidial plates obscured to absent; thick shell wall; prominent pedicle callist; dental cavities small to absent; dorsomedial to dorsal spiralia; simple central to ventrocentral jugum. *Ordovician (upper Caradoc)–Silurian (Llandovery)*.

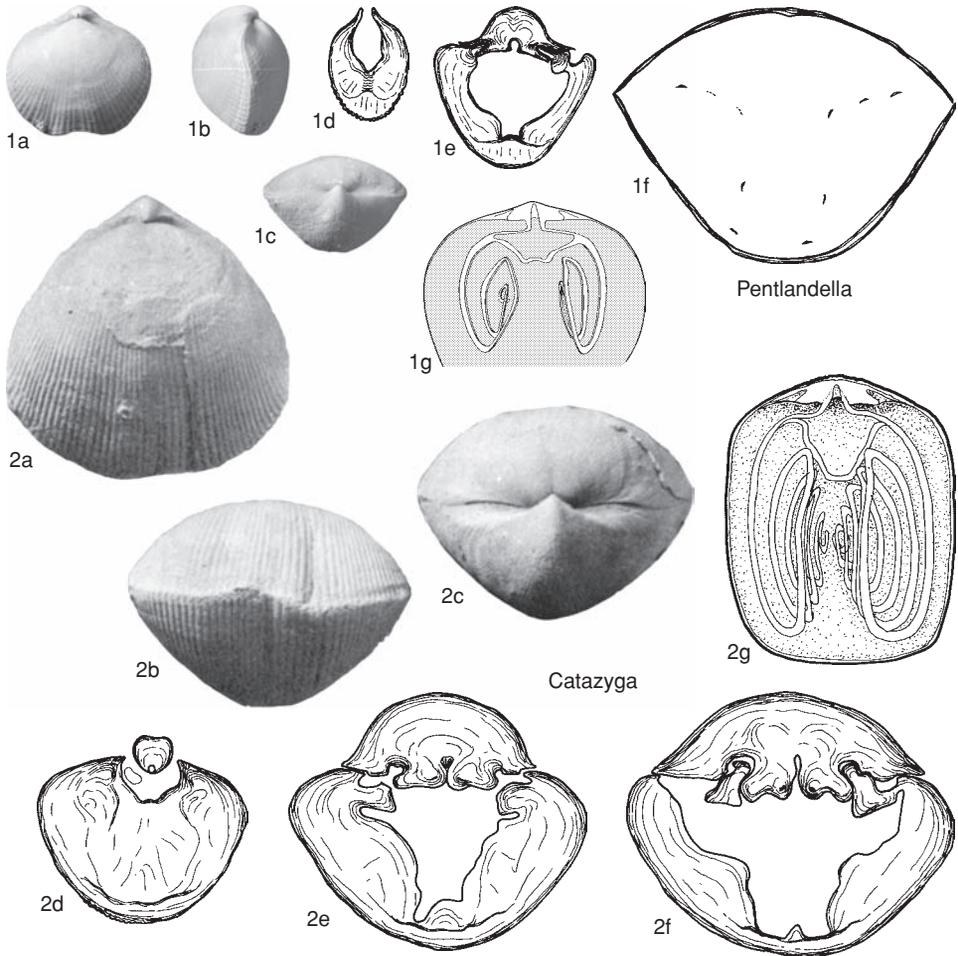


FIG. 977. Anazygidae (p. 1442–1443).

Catazyga HALL in HALL & CLARKE, 1893, p. 157 [**Athyris beadi* BILLINGS, 1862, p. 147; OD; *vid.* HALL, 1894, p. 601] [= *Orithonoma* HALL in HALL & CLARKE, 1893, p. 159 (type, *Orthis ?erratica* HALL, 1847, p. 288, OD, *vid.* HALL, 1894, p. 601); *Septacatazyga* DISTLER, 1972, p. 194, *nom. nud.* (type, *Catazyga homeospiroides* ROSS & DUTRO, 1966, p. 19, OD); *Salairella* SEVERGINA, 1984, p. 45 (type, *Catazyga salairica* SEVERGINA, 1960a, p. 403, OD); *Eonalivkinia* VLADIMIRSKAYA, 1985, p. 155 (type, *E. hondelensis*, OD)]. Small to medium, globose-elongate, biconvex-ventribiconvex; short, narrow hinge; small anacline to hypercline area; obscured pedicle opening; minute deltidial plates; finely ribbed; rarely fine concentric growth filae; weakly sulcate-rectimarginate to weakly plicate commissure; thick pedicle callist; muscle scars strongly incised; teeth stubby, curved, with or without dental cavity; hinge plate massive; bulbous cru-

ral bases; crura short; mediodorsal spiralia with fewer than 10 whorls; simple, posteromedial, U-shaped jugum. [Distinguished from *Anazyga* by large size, thick shell wall, nature of hinge plate, posterior location of jugum.] *Ordovician* (upper *Caradoc–Ashgill*): North America, Eurasia.—FIG. 977, 2a–g. **C. beadi* (BILLINGS), middle Ashgill, Québec, Canada; a–c, dorsal, posterior, anterior views, $\times 2$; d–f, serial sections, $\times 5$ (Copper, 1977a); g, reconstruction of brachidia, $\times 3$ (new).

Pentlandella BOUCOT, 1964b, p. 104 [**Rhynchonella* [sic] *pentlandicus* HASWELL, 1865, p. 31; OD]. Small, ventribiconvex, subpentagonal outline; small, hypercline area; beak minute; apical-transapical foramen; deltidial plates lost; very fine ribs; fine to almost smooth shell; commissure rectimarginate to weakly plicate; interior with thick shell wall; partly raised ventral muscle field; short, solid teeth; hinge plate small, with central cardinal

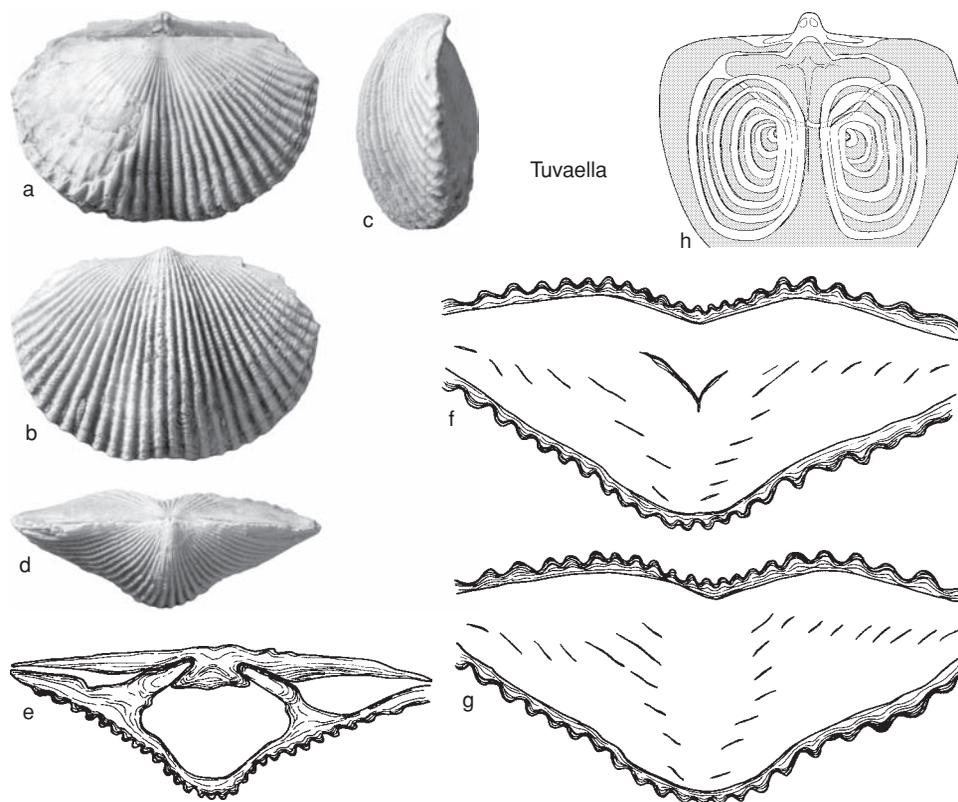


FIG. 978. Anazygidae (p. 1443).

pit; delicate crura; posteromedial to mediodorsal spiralia with fewer than 5 whorls; W- to U-shaped, ventroposterior jugum. [Distinguished from *Catazyga* by small, pentagonal shell, very fine ribs, weak hinge plate, raised ventral muscle field, reduced number of spiralia whorls. Holotype and paratypes preserved as molds in sandstones.] *Silurian* (*Llandovery*): Europe, North America.—FIG. 977, 1a–g. *P. tenuistriata* RUBEL, Telychian, Estonia; a–c, dorsal, lateral, posterior views, $\times 2$; d–f, serial sections, $\times 5$; g, reconstruction of brachidium, $\times 3.5$ (Copper, 1977a).

Subfamily TUVSELLINAE Alikhova, 1960

[*nom. transl.* COPPER, herein, ex *Tuvaellidae* ALIKHOVA, 1960, p. 190; *emend.*, COPPER, herein]

Medium to large, relatively flat, orthoid to spiriferoid shape, ribbed; wide, flat ventral area; sulcate commissure; long, strophic hinge; delthyrium with deltidial plates, apical foramen; notothyrium, chilidium lacking; teeth solid; dorsomedial spiralia with

fewer than 10 whorls; jugum large, dorsomedial. *Silurian* (*upper Llandovery–Ludlow*, ?*Pridoli*).

Tuvaella CHERNYSHEV, 1937, p. 12 [**T. rackovskii*; OD]. Medium to large, long hinged, flat, ventribiconvex-planoconvex-dorsibiconvex; ventral valve carinate, dorsal sulcate; large, wide orthocline-anacline area; small, slitlike apical foramen, or foramen may be absent; prominent deltidial plates; continuous ribs expanding anteriorly, lacking raised, ventral midribs; distinct concentric growth filae; commissure sulcate; interior with solid, broad teeth, lacking accessory projections; hinge plate massive; cardinal pit absent; raised, but flat cardinal process; crura laterally directed; postero- to mediodorsally directed spiralia of fewer than 10 whorls; jugum dorsomedial, V-shaped, possessing ventrally directed crest. [Differs from other anazygids in large size, spiriferoid shape, solid teeth, V-shaped jugum.] *Silurian* (*upper Llandovery–Ludlow*, ?*Pridoli*): Tuva, Altai, Mongolia, Xinjiang, north-eastern China.—FIG. 978a–b. **T. rackovskii*, upper Llandovery, Tuva; a–d, dorsal, ventral, lateral, posterior views, $\times 2$; e–g, serial sections, $\times 5$; b, reconstruction of brachidium, $\times 2.5$ (Copper, 1977a).

Suborder DAVIDSONIIDINA Copper, 1996

[Davidsoniidina COPPER, 1996a, p. 593]

Ribbed or smooth atrypoids, lacking growth lamellae; rarely with wide single frill (trail); strophic-astrophic hinge; relatively prominent, wide orthocline-apsacline area; deltidial plates with apical foramen, or foramen lost by total closure of delthyrium; dorsomedially directed spiralia with fewer than 10 whorls; ventroposterior jugal processes commonly terminating in large boss. *Silurian (Ludlow)–Middle Devonian (Givetian)*.

Superfamily DAVIDSONIOIDEA King, 1850

[*nom. transl. et correct.* COPPER, 1996a, p. 593, ex Davidsonidae KING, 1850, p. 81; *emend.*, COPPER, 1996a, p. 593]

Generally wide, flat, biconvex to dorsibiconvex, strophic shell, with wide area, deltidial plates, and apical foramen, usually liberossessile or cemented by pedicle valve (pedicle opening fully sealed by deltidial plates); rarely with commissural trail; multiple frills, growth lamellae absent; muscle scars, vascular canals atrypod, dorsomedially to dorsally directed spiralia, commonly impressed as grooves in ventral valve; jugal processes ventroposterior, may terminate in jugal boss. *Silurian (?Ludlow, Přídolí)–Middle Devonian (Givetian)*.

Family DAVIDSONIIDAE King, 1850

[*nom. correct.* COPPER, 1978, p. 306, *pro* Davidsonidae KING, 1850, p. 81; *emend.*, COPPER, 1978, p. 306]

Smooth, rarely radially corrugate or concentrically wrinkled shell; cemented or free-living, convex ventral valve; commonly flat to concave dorsal valve; trail absent; strophic hinge; teeth solid; spiralia dorsally directed, usually centered over spiral grooves on raised cones of ventral valve; jugal processes touching. *Silurian (Přídolí)–Middle Devonian (Givetian)*.

Davidsonia BOUCHARD-CHANTEREAUX, 1849, p. 92 [**D. Verneuillii*; OD]. Medium to large, commonly

asymmetrical, wider than long, subquadrate to rounded in outline, smooth, flat to ventribiconvex-planoconvex; cemented ventral valve thick in gerontic stages, usually cemented to hard substrates from apex to commissure, rarely free; dorsal valve flat to weakly concave; enlarged, flat, normally apsacline area; pointed, triangular beak; delthyrial cavity normally completely sealed by conjunct deltidial plates (foramen, deltidium, chilidium absent); surface smooth to concentrically wrinkled; rectimarginate commissure; pedicle collar lining apical cavity; teeth solid; hinge plate short, thick, lacking cardinal pit, capped by prominent, bushy cardinal process; crura projected from inner socket ridges; spiralia, rarely preserved, impressed in grooves of raised cones on ventral valve, fewer than 6 whorls, dorsally directed; jugal processes undescribed (except as fragments). [Distinct from other davidsoniids in fixosessile cementation of ventral valve, common asymmetry, lack of foramen.] *Lower Devonian (Emsian)–Middle Devonian (upper Givetian)*: Europe, central Asia, China, USA (Nevada).—FIG. 979, 1a–f. **D. verneuillii*, upper Eifelian, Germany; a–c, exterior dorsal view, interior ventral valve (cemented to alveolitic coral), interior dorsal valve, $\times 2$ (new); d–f, serial sections, $\times 5$ (Copper, 1978).

Prodauidsonia HAVLIČEK, 1956, p. 564 [**P. dalejensis*; OD] [= *Quasidavidsonia* HAVLIČEK, 1987a, p. 106 (type, *Prodauidsonia vicina* HAVLIČEK, 1967b, p. 215, OD)]. Symmetrical, wider than long, flat, planoconvex to weakly concavoconvex to weakly ventribiconvex; weakly carinate, weakly convex ventral valve; weakly convex, flat, posteriorly sulcate dorsal valve; shell liberossessile; wide apsacline-orthocline area; slightly projecting beak; apical foramen flanked by deltidial plates; smooth to weakly concentrically ornamented surface; commissure rectimarginate to weakly sulcate; teeth solid; hinge plate *Davidsonia*-like with small cardinal process; spiralia grooves impressed in raised cones of ventral valve; spiralia, jugal processes undescribed. [Spiralia grooves in ventral valve, muscle scars as in *Davidsonia*, but more weakly impressed; differs in having apical foramen, liberossessile ventral valve (uncemented to substrate), bilateral symmetry, wider than long shape.] *Lower Devonian (?Pragian, Emsian)–Middle Devonian (lower Givetian)*: western Europe, Urals.—FIG. 979, 2a–e. **P. dalejensis*, Emsian, Czech Republic; a–d, dorsal, ventral, anterior, posterior views, $\times 2$ (new); e, interior ventral valve, $\times 3$ (Havlíček, 1987a).

Rugodavidsonia COPPER, 1996a, p. 597 [**Davidsonia woodwardiana* DE KONINCK, 1855, p. 284; OD]. Small to medium, planoconvex-concavoconvex, rounded to ovoid outline, usually asymmetrical; short hinge line; ventral valve apex flattened, cemented or liberossessile apically; strongly protruding beak; large, flat area; deltidial plates narrow, high, completely sealing delthyrium; foramen absent; rectimarginate commissure; smooth apically, coarsely ribbed ornamentation distally; ventral valve

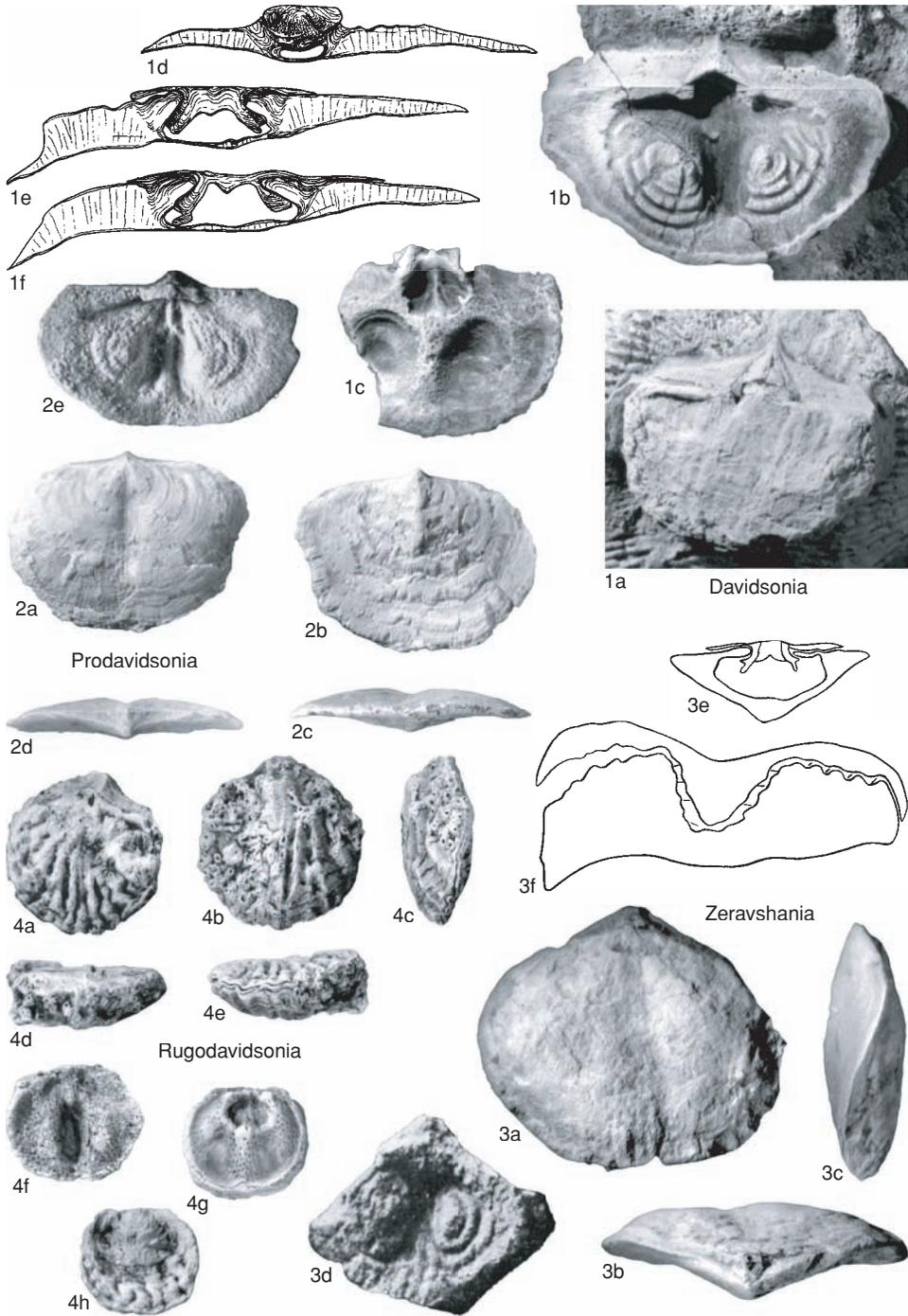


FIG. 979. Davidsoniidae (p. 1444–1446).

with central cones accommodating dorsally directed spiralia from opposing valve, lacking spiralia grooves; muscle scars, gonadal pits atrypoid; short hinge plate, protruding partially into delthyrial cavity; crura, spiralia, jugal processes undescribed. [Differs from *Davidsonia* in presence of coarse radial ribs, rounded-elongate shape, liberossessile ventral valve, lack of spiralia grooves in ventral valve; homeomorphic with Permian orthotetids, but differing in lack of notothyrium, chlidium.] *Middle Devonian (upper Eifelian–Givetian)*: Europe, USA (Nevada), southern China.—FIG. 979, 4a–b. **R. woodwardiana* (DE KONINCK), upper Eifelian, Belgium; a–e, dorsal, ventral, lateral, posterior, anterior views, $\times 2$; f–h, interior ventral valve, interior and exterior of same dorsal valve, $\times 2$ (new).

Zeravshania MENAKOVA, 1983, p. 66 [**Z. pachyvalvata* MENAKOVA, 1983, p. 68; OD]. Small, smooth, flat, weakly biconvex to planoconvex; relatively short hinge line; ventrally strongly carinate, dorsally sulcate; protruding beak; small apsacline area; minute apical foramen at apex of deltidial plates; commissure weakly sulcate to rectimarginate to weakly plicate to ligate; thick shell wall; strong ventral, dorsal median septa; spiralia grooves weakly to strongly impressed into conical thickenings of ventral valve; teeth solid; spiralia dorsally directed, fewer than 4 whorls; jugal processes touching. [Most similar to *Prodauidsonia*, but differing in smaller size, reduced area, strong carination, sulcate-ligate commissure.] *Silurian (Přídolí)–Lower Devonian (Lochkovian)*: central Asia, Urals (eastern slopes).—FIG. 979, 3a–f. **Z. pachyvalvata*, Přídolí, Zeravshan, Tadzhikistan; a–c, dorsal, posterior, lateral views, $\times 2$ (new); d, interior of ventral valve, $\times 2$; e–f, serial sections with spiralia, $\times 5$ (Menakova, 1983).

Family CARINATINIDAE Rzhonsnitskaia, 1960

[*nom. transl.* COPPER, 1996a, p. 600, ex Carinatinae RZHONSNITSKAIA, 1960a, p. 261] [=Davidsoniatrypidae HAVLIČEK, 1987a, p. 100]

Usually relatively flattened, commonly carinate (secondary loss of carination), biconvex-dorsibiconvex, mostly strophic shells, with prominently enlarged area (not anacline-hypercline), foramen, continuous ribs, wide trail (where preserved). Relatively thick hinge plates, jugal processes commonly with enlarged ends, spiralia nearly always dorsally directed, may or may not be impressed into ventral valve. *Silurian (?Ludlow), Lower Devonian (Pragian)–Middle Devonian (Givetian)*.

Carinatina NALIVKIN, 1930a, p. 104 [**Orthis arimaspus* EICHWALD in VON BUCH, 1840, p. 108; OD; *vid.* D'EICHWALD, 1861, p. 216] [=Zejszneria SIEM-

IRADZKI, 1920, p. 172, *nom. oblit.* (type, *Orthisina davyi* BARROIS, 1886, p. 194); ?*Salairina* ALEKSEEVA, 1970, p. 131 (type, *S. misera*, OD); *Kaplicona* HAVLIČEK, 1987a, p. 101 (type, *Biconostrophia confifera* HAVLIČEK, 1967b, p. 209, OD); ?*Kluk-atrypa* HAVLIČEK, 1987a, p. 95 (type, *K. klukovensis*, OD)]. Medium to large, flat, biconvex, strongly carinate; strophic hinge; wide apsacline-orthocline area; apical foramen, deltidial plates; coarsely ribbed, with 2 to 4 raised ventral midribs forming carina; broad, flat fold to rectimarginate commissure; broad, ventral rim surrounded by wide trail (5 to 15 mm) with ribs replaced by fine costellae; pedicle collar fused into deltidial plates; teeth with prominent dental cavities; thick hinge plate with bushy cardinal process; crura laterally divergent; spiralia dorsal, only rarely, weakly impressed as grooves into ventral valve, fewer than 10 whorls; jugal processes undescribed. [Differs from *Biconostrophia* in having dental cavities, spiralia normally not impressed into ventral valve; differs from *Eifelatrypa* in possessing ventral carination, teeth with dental cavities. Possibly occurs in the Frasnian in Timan.] *Lower Devonian (Pragian)–Middle Devonian (lower Givetian)*: Eurasia, North America, *Pragian–lower Givetian*.—FIG. 980, 1a–g. **C. arimaspa* (EICHWALD), middle Eifelian, Urals; a–e, ventral, ventral (smaller shell), dorsal, lateral, anterior views, $\times 2$ (Copper, 1978); f–g, serial sections, $\times 2$ (Rzhonsnitskaia, 1975).

Biconostrophia HAVLIČEK, 1956, p. 562 [**B. spirifera* HAVLIČEK, 1956, p. 563; OD] [=Davidsoniatrypa LENZ, 1968, p. 182 (type, *D. johnsoni*, OD)] [?Biconostrophia (*Cherkesovaena*) HAVLIČEK, 1987a, p. 103 (type, *B. sinelkovaensis* CHERKESOVA, 1980, p. 171, OD)]. Medium to large, semicircular outline, flat to weakly biconvex, ventrally carinate to weakly resupinate; wide, long, strophic hinge; shell widest at hinge; apsacline-orthocline beak; apical foramen; wide deltidial plates; ribs coarse distally, tubular, expanding, rarely bifurcating; single or double ventral midrib pair producing keel; trail unknown; muscle scars incised in ventral valve, slightly raised on platform in dorsal valve; solid teeth; raised cardinal process; cardinal pit absent; spiralia strongly impressed into cones on ventral valve, fewer than 6 whorls; jugal processes undescribed. [Similar to and possibly synonymous with *Carinatina*, but lacking dental cavities, spiralia impressed into ventral grooves as in *Davidsonia*. *Cherkesovaena* is possibly pseudopunctate (CHERKESOVA, 1980), otherwise identical to *Biconostrophia*.] *Lower Devonian (Pragian–Emsian)*: Europe, Urals, Australia, North America.—FIG. 981, 3a–d. **B. spirifera* (HAVLIČEK), Emsian, Czech Republic; a–b, dorsal, ventral views; c–d, internal views of dorsal, ventral valves, $\times 1.5$ (Havliček, 1967b).

Carinatrypa COPPER, 1973c, p. 496 [**Spinatrypa dysmorphostrota* CRICKMAY, 1960, p. 13; OD] [=Hergetatrypa HAVLIČEK, 1987a, p. 97 (type, *Carinatina minuta* SIEHL, 1962, p. 188, OD)].

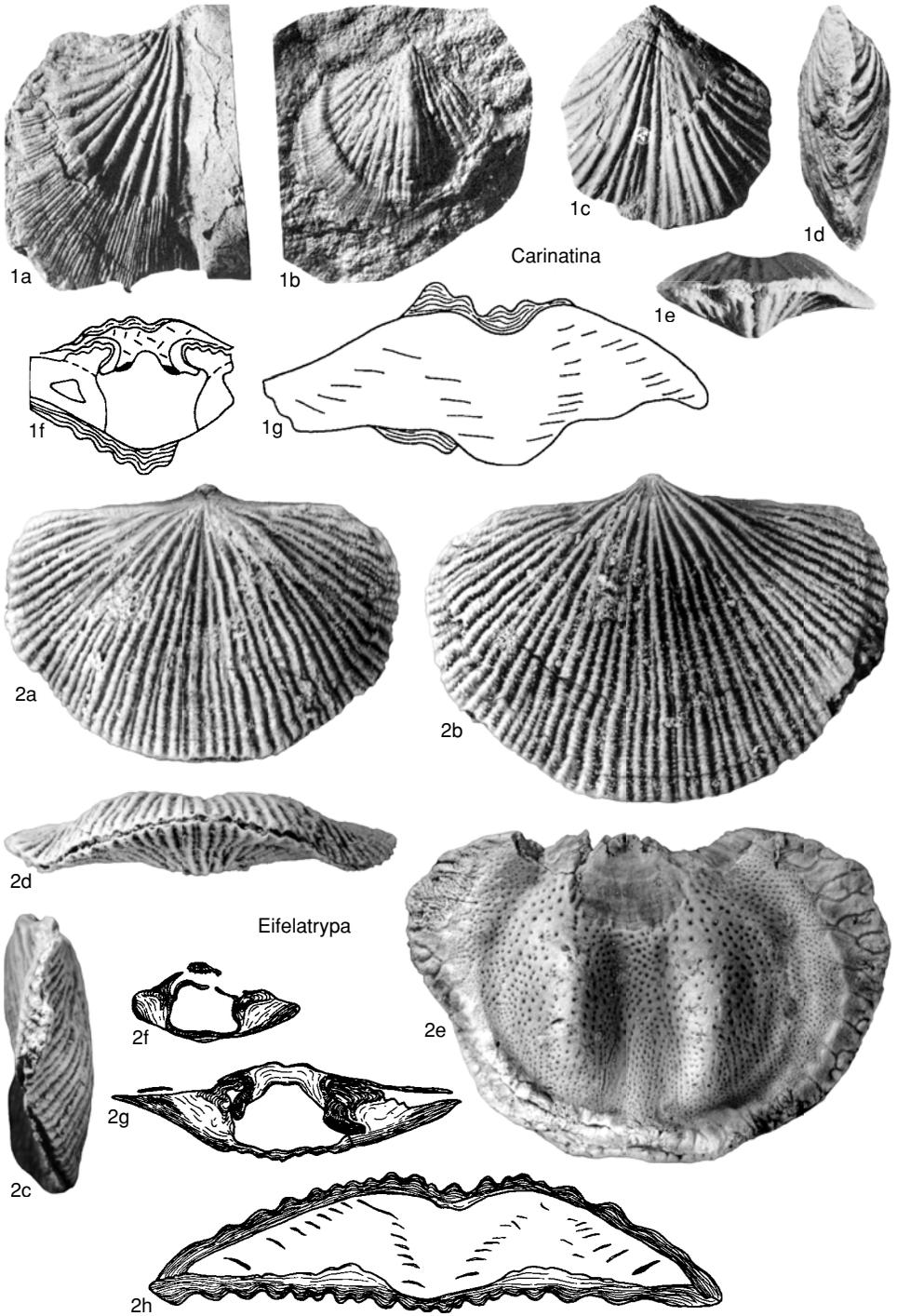


FIG. 980. Carinatinae (p. 1446–1450).

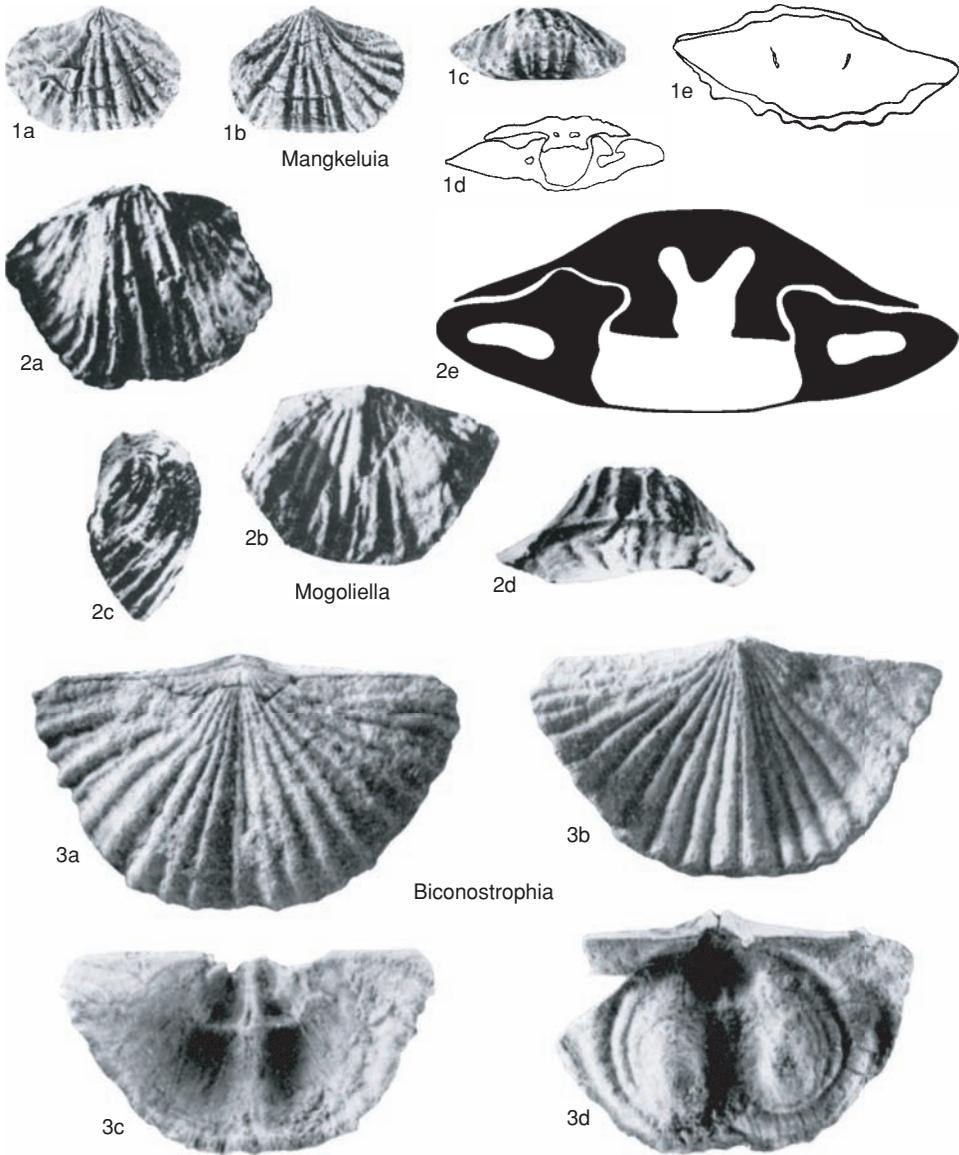


FIG. 981. Carinatinidae (p. 1446–1450).

Medium to large, dorsibiconvex, ventroapically carinate; small protruding beak; apsacline-orthocline area; apical foramen, deltidial plates; coarse tubular ribs, usually with concentric growth lamellae; trail with rib coarsening; moderately to strongly plicate commissure; thin shell; pedicle collar absent; teeth with large dental cavities; thin hinge, socket plates; crura delicate; dorsal spiralia with fewer than 10 whorls (not impressed into ventral valve); jugal processes with small, hooked jugal plates. [Differs from *Carinatina* and *Bicono-*

strophia in strong dorsal convexity (expansion of spiralia), high anterior fold, skirt with rib coarsening (instead of fine costellae), hinge plate divided by cardinal pit; possibly synonymous with *Mogoliella*.] *Middle Devonian* (?upper Eifelian, Givetian): northwestern Canada, USA (Michigan), western Europe, Russian Platform.—FIG. 982, 1a–e. *C. dysmorphostrota* (CRICKMAY), lower Givetian, Northwest Territories; a–d, dorsal, ventral, lateral, posterior views, $\times 2$; e, internal ventral valve, $\times 2$ (Copper, 1978).

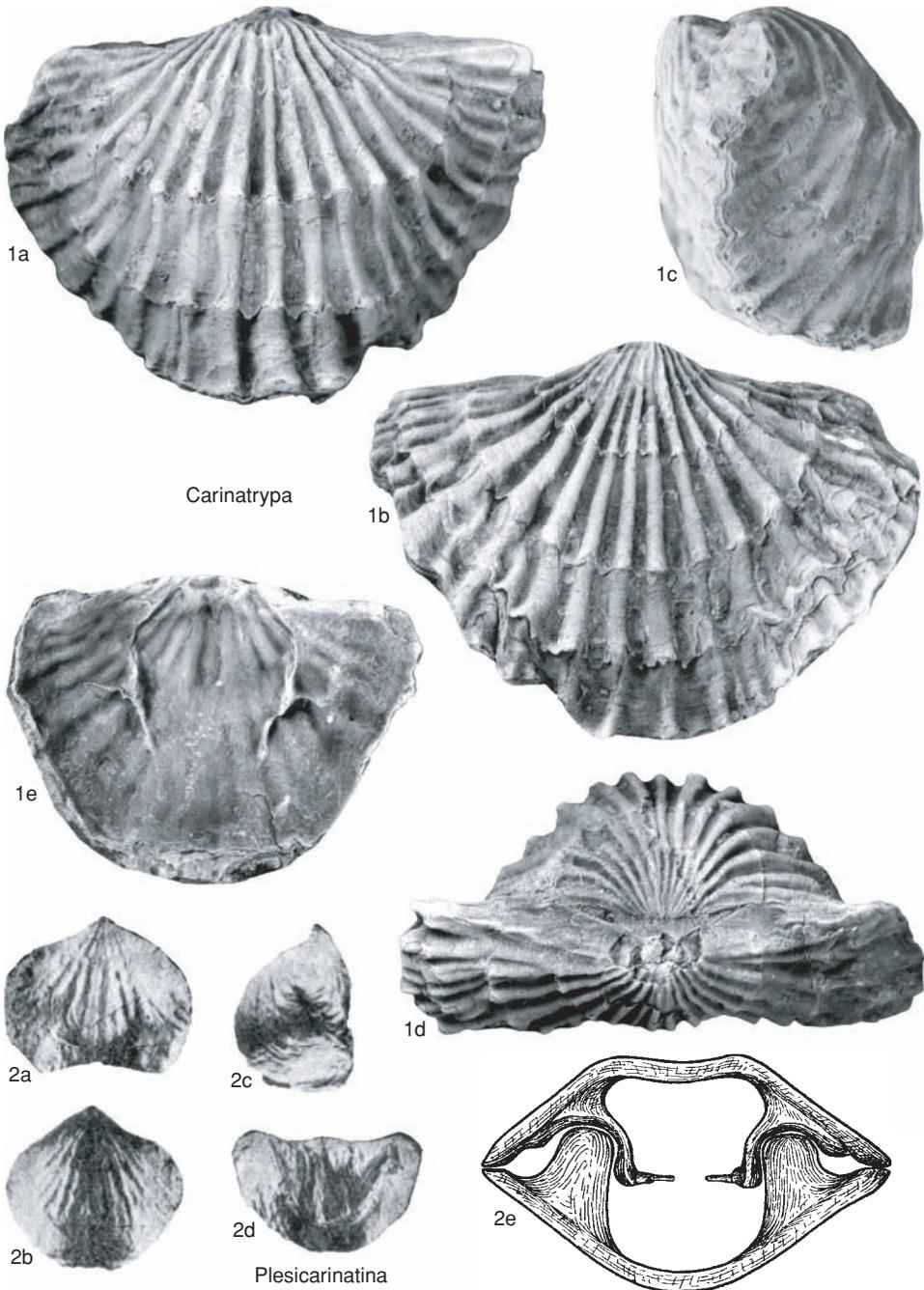


FIG. 982. Carinatinidae (p. 1446–1450).

Eifelatrypa COPPER, 1973c, p. 497 [*Atrypa reticularis* var. *plana* KAYSER, 1871, p. 545; OD]. Medium to large, widest between hinge and midshell; round hinge corners; biconvex, strophic, lacking ventral

carination (except neanic shells); area apsacline-orthocline; prominent apical foramen; wide deltidial plates; ribs fine, tubular, even over whole shell; trail with fine ribs continuing from main

- shell; rectimarginate; interior pedicle collar continuous with deltidial plates; solid teeth; hinge plate wide, thick, lacking cardinal pit, capped by large, bushy cardinal process; crural bases large, extended from bulbous inner socket ridges; spiralia weakly incised into cones on thickened ventral valve; dorsal spiralia with about 8 to 10 whorls; thick jugal processes with large, bosslike jugal plates. [Differs from *Carinatina* and *Biconostrophia* by loss of carination, finer ribs, lack of costellae on trail, nature of hinge socket plates, crura, jugal boss.] *Middle Devonian (Eifelian–Givetian)*: Europe, Urals, southern China.—FIG. 980,2a–b. **E. plana* (KAYSER), upper Eifelian, Germany; a–e, dorsal, ventral, lateral, anterior views, internal view ventral valve, $\times 2$ (new); f–h, serial sections, $\times 4$ (Copper, 1978).
- ?**Mangkeluia** XU Hankui, 1991, p. 318 [**M. extensa*; OD]. Small to medium, wider than long, round, dorsibiconvex, globose; ventral valve weakly carinate; small, orthocline area; protruding beak; apical foramen, deltidial plates; ribs expanding anteriorly, tubular; widely spaced, partly imbricate growth lamellae; low, broadly plicate commissure; stout, broad teeth; distinct dental cavities; hinge plate thick; crural bases stout; crura slender; spiralia, jugal processes undescribed. [Similar to small forms of *Carinatrypa* or *Mogoliella*, differing in small shell, hinge plates; possible rhynchonellid, lack of data on brachidia makes identification as atrypid doubtful.] *Lower Devonian (Emsian)*: northwestern China (Xinjiang).—FIG. 981,1a–e. **M. extensa*; a–c, dorsal, ventral, anterior views, $\times 1.5$; d–e, serial sections, $\times 1$ (Xu Hankui, 1991).
- Mogoliella** ISHNAZAROV, 1972, p. 69 [**M. sukokentica* ISHNAZAROV, 1972, p. 72; OD] [= *Sulcificatarypa* ZHANG Fengming, 1983, p. 336 (type, *Spinatrypa (Sulcificatarypa) xinjiangensis* ZHANG Fengming, 1983, p. 337, OD)]. Large, widest at hinge, dorsibiconvex, ventral valve weakly carinate; orthocline-apsacline area; protruding beak; prominent apical foramen; deltidial plates; strongly divergent, coarse ribs, ventrally raised midrib pairs; weak, short concentric growth lamellae partly developed; broad anterior fold; stout teeth; wide dental cavities; crural bases thick; dorsal spiralia with 10 to 12 whorls; jugal processes undescribed. [Externally very similar, possibly synonymous with *Carinatrypa*.] *Middle Devonian (Givetian)*: Uzbekistan, China (Xinjiang).—FIG. 981,2a–e. **M. sukokentica*, Uzbekistan; a–d, dorsal, ventral, lateral, anterior views, $\times 1.5$; e, sketch of polished view, $\times 4$ (Ishnazarov, 1972).
- ?**Plesicarinatina** MIZENS, 1977b, p. 89 [**Plectatrypa? carpulenta* BREIVEL, 1959, p. 65; OD]. Equidimensional, inflated dorsibiconvex-convexoplane, carinate posteriorly; coarsely ribbed; fine concentric filae; trail present; narrow, protruding beak; apsacline-orthocline area; large apical foramen; deltidial plates; strong, U-shaped anterior fold; solid teeth; thick hinge plate, lacking cardinal pit; dorsally directed spiralia of fewer than about 7 whorls; jugal processes undescribed. [Possible junior synonym of *Neospirigerina*, but with weak carination and trail indicating carinatid affinities.] *Silurian (?Ludlow, Přídolí)–Middle Devonian (lower Eifelian)*: Urals.—FIG. 982,2a–e. **P. carpulenta* (BREIVEL), lower Eifelian; a–d, ventral, dorsal, lateral, anterior views, $\times 3$; e, serial section, $\times 4$ (Breivel, 1959).

Superfamily PALAFERELLOIDEA Priestersbach, 1942

[*nom. transl.* COPPER, 1996a, p. 599, ex Palafereinae SPRIESTERSBACH, 1942, p. 187; *emend.*, COPPER, 1996a, p. 599]

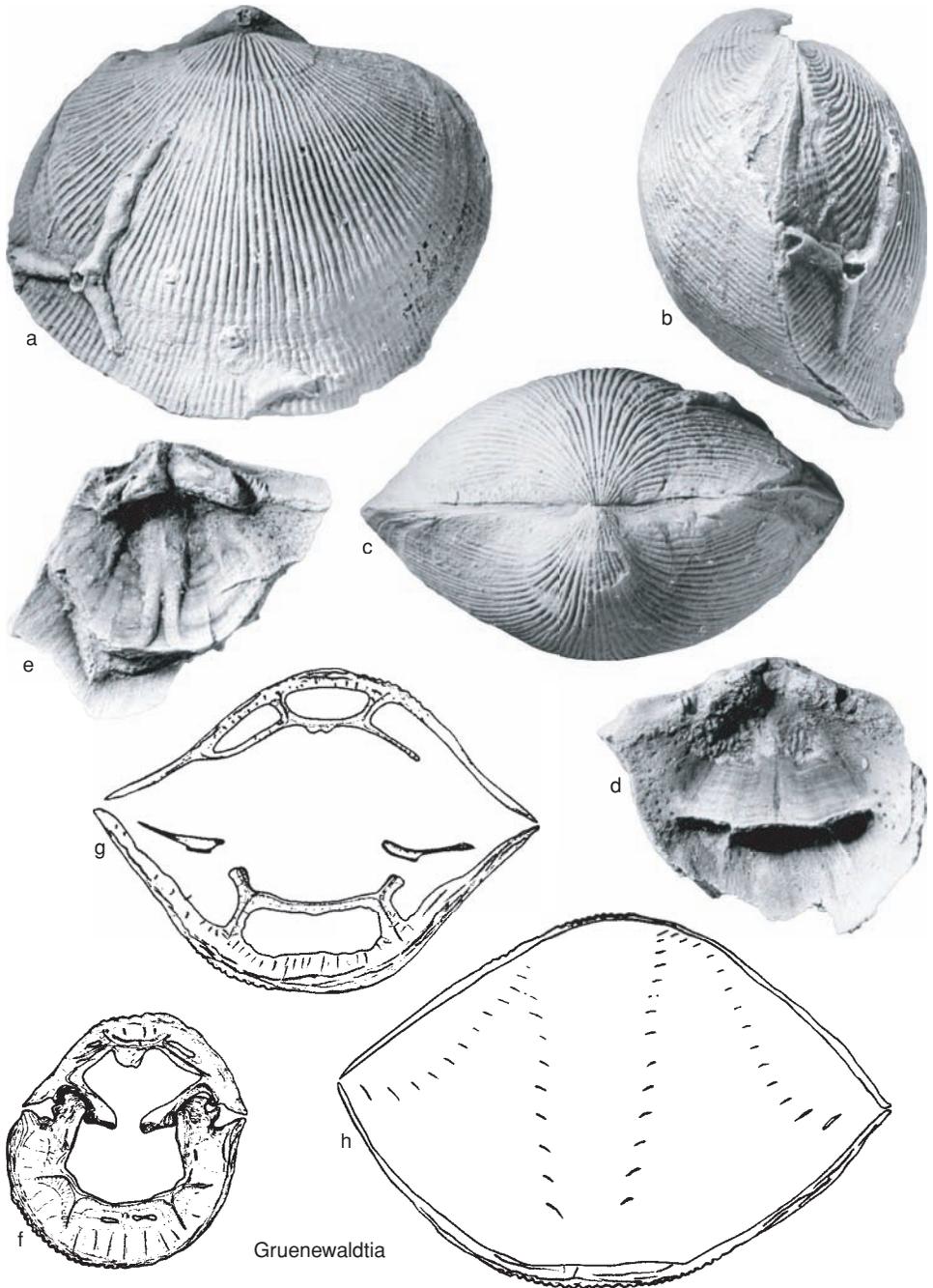
Ventribiconvex to dorsibiconvex, rectimarginate to weakly plicate; ribbed shells, lacking growth lamellae, frills; rarely with fringing commissural skirt; distinct area, deltidial plates, apical foramen; relatively thick shell wall, pedicle callist continuous with deltidial plates; strong teeth, hinge plates; spiralia dorsal-dorsomedial; jugal processes. *Silurian (Ludlow)–Middle Devonian (Givetian)*.

Family PALAFERELLIDAE Priestersbach, 1942

[*nom. transl.* COPPER, 1996a, p. 599, ex Palafereinae SPRIESTERSBACH, 1942, p. 187]

Strongly biconvex to ventribiconvex, ribbed shells, lacking growth lamellae, frills; small apsacline-hypercline area, apical foramen; deltidial plates fused with pedicle callist-collar complex; thickened muscle platforms raised above shell floor by 2 or more septa in both valves. *Lower Devonian (?upper Emsian), Middle Devonian (Eifelian–Givetian)*.

Gruenewaldtia CHERNYSHEV, 1885, p. 46 [**Terebratula latilinguis* SCHNUR, 1851, p. 7; OD] [= *Palafarella* SPRIESTERSBACH, 1942, p. 187 (type, *P. rhenana*, OD)]. Medium to large, rounded, globose, biconvex-ventribiconvex; umbo inflated; orthocline-anacline, rarely hypercline area; small apical foramen, deltidial plates; fine-medium ribs; concentric filae; rectimarginate to weakly plicate commissure; thick shell wall; pedicle callist or collar continuous with deltidial plates; interior of inner part of deltidial plates forming flange alongside foramen; muscle platforms on both valves raised above shell floor by 2 or more septa; ventral muscle platform larger than dorsal; hinge plate strong; crural bases small; crura laterally directed; dorsomedially directed spiralia with fewer than 15 whorls; disjunct, posteroventral jugal processes, terminating in spinose boss. [Distinct from homeomorphic *Desatrypa*



Gruenewaldtia

FIG. 983. Palaferelloidea (p. 1450–1452).

and probably ancestral *Neokarpinskia* in septally raised muscle platforms. Early species have more septa supporting muscle platform, are smaller, more coarsely ribbed.] *Lower Devonian* (?upper Emsian),

Middle Devonian (Eifelian–Givetian): Europe, Urals, Novaya Zemlya, Armenia, Uzbekistan, Siberia, arctic Canada.—FIG. 983a–h. **G. latilinguis* (SCHNUR), middle Eifelian, Germany; a–c, dorsal,

lateral, posterior views; *d–e*, interior of ventral, dorsal valves with muscle platforms; *f–h*, serial sections, $\times 2$ (new).

Family KARPINSKIIDAE
Poulsen, 1943

[*nom. transl.* COPPER, 1996a, p. 600, ex Karpinskiinae POULSEN, 1943, p. 40; *emend.*, COPPER, herein]

Dorsibiconvex-convexoplane, thick shell wall, weakly apsacline-orthocone area (never anacline-hypercline), beak prominent, apical foramen large; ribs fine to coarse, always fine apically; commissure rectimarginate or very weakly plicate; muscle scars incised posteriorly with raised anterior edges, vascular canals strongly raised as prominent ridges; spiralia dorsally directed, jugal processes poorly known. *Silurian (Ludlow)–Middle Devonian (Givetian)*.

Subfamily KARPINSKIINAE
Poulsen, 1943

[Karpinskiinae POULSEN, 1943, p. 40; *emend.*, COPPER, 1996a, p. 600]

Elongate, commonly laterally compressed shells, biconvex to strongly dorsibiconvex to convexoplane; narrow apsacline-orthocone area; prominent apical foramen, deltidial plates; rectimarginate commissure; ribs fine posteriorly, usually coarser anteriorly, less commonly bifurcating-intercalating, rarely partly smooth shell; pedicle callist-collar common; commonly prominent ventral vascular ridges; teeth solid or with dental cavities; spiralia dorsally directed, jugal processes poorly known. *Silurian (Ludlow)–Middle Devonian (Givetian)*.

Karpinskia CHERNYSHEV, 1885, p. 48 [**K. conjugula*; OD]. Medium to large, highly elongate, narrow, rectangular to triangular, laterally compressed, roughly squared in anterior view, dorsibiconvex, convexoplane; protruding beak; short hinge; acute hinge angle; apsacline-orthocone area; prominent apical foramen; thick deltidial plates; ribs fine apically, nonbifurcating, to very coarse anteriorly, zigzag at commissure; wide, high, subrectangular, plicate commissure; thick shell wall; weak vascular ridges; medium to thick pedicle callist-collar; long, narrow teeth; elongated dental cavities; thick hinge plate; long, thin socket plates; small crural bases, crura; dorsally directed spiralia with fewer than 13 whorls; jugal processes undescribed. [Pedicle callist,

deltidial plates, and hinge structure as in *Vagrana* and *Mimatrypa* but differentiated by highly elongate shell, squared shape in transverse section, fine ribs posteriorly changing to very coarse ribs along commissure.] *Lower Devonian (Emsian)*: southern Europe, Urals, central Asia, China (Xinjiang).—FIG. 984, 1a–g. **K. conjugula*, Emsian, western slopes, Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 1$; e–g, serial sections, $\times 2.5$ (Mizens, 1984).

Crassatrypa MIZENS, 1977a, p. 54 [**Atrypa diversa* SAPELNIKOV, 1968, p. 128; OD]. Small, triangulate to elongate, narrow hinge angle, biconvex to weakly dorsibiconvex, rhynchonelliform shape; highly protruding beak; apsacline-orthocone area; prominent apical foramen and deltidial plates; 8 to 10 coarse expanding ribs, rarely bifurcating or intercalating; anterior growth interruptions; rectimarginate to weakly plicate commissure; interior with long, solid teeth; narrow hinge plates with deep cardinal pit; small, delicate socket plates, crura; spiralia dorsally directed, fewer than 10 whorls; jugal processes undescribed. [Differentiated from *Karpinskia* by small size, coarser ribs posteriorly, rhynchonelliform shape; differs from *Vagrana* by its elongate outline, anteriorly coarse ribs.] *Silurian (Ludlow–Přídolí)*: Urals (eastern slopes).—FIG. 984, 2a–e. **C. diversa* (SAPELNIKOV), lower Ludlow; a–c, dorsal, ventral, lateral views, $\times 1$; d–e, serial sections, $\times 5.5$ (Mizens & Sapelnikov, 1982).

Eokarpinskia RZHONSNISSKAIA, 1964, p. 103 [**Karpinskia nalivkini* NIKIFOROVA, 1937b, p. 23; OD]. Small, elongate to subtriangulate, inflated (rounded in cross section), biconvex, laterally weakly compressed, maximum width anteriorly; narrow, acute hinge angle; narrow area with smooth curved flanks; apical-transapical foramen; surface with smooth appearance, very finely ribbed; rectimarginate-bisulcate commissure; thin pedicle callist; long teeth with elongated dental cavities; thin, curved dental plates; socket plates thin, curved; crura, spiralia, jugal processes undescribed. [Distinguished from *Neokarpinskia*, *Karpinskia*, and *Crassatrypa* by very fine ribs leading to nearly smooth appearance, biconvexity, rounded cross section; differs from similarly shaped *Tectatrypa* (Lissatrypinae) by possessing fine ribs, dental cavities, thin socket plates.] *Silurian (Přídolí)–Lower Devonian (Lochkovian)*: Kazakhstan, Urals, ?arctic Canada.—FIG. 984, 3a–d. **E. nalivkini* (NIKIFOROVA), Přídolí, Kazakhstan; a–c, dorsal, ventral, lateral views, $\times 2$; d, serial section, $\times 5$ (Nikiforova, 1937b).

Mimatrypa STRUVE, 1964a, p. 436 [**Terebratula prisca* var. *flabellata* ROEMER, 1844, p. 66; OD] [= *Toquimaella* JOHNSON, 1967, p. 876 (type, *T. kayi*, OD); ?=*Megaplectatrypa* ZHANG Yan, 1981a, p. 386 (type, *M. simplex*, OD)]. Small to large, convexoplane-dorsibiconvex; flat adult ventral valve, weakly convex apically; shell outline rounded to subelongate, narrow hinge angle; apsacline-orthocone area; large apical-transapical foramen; fine ribs apically,

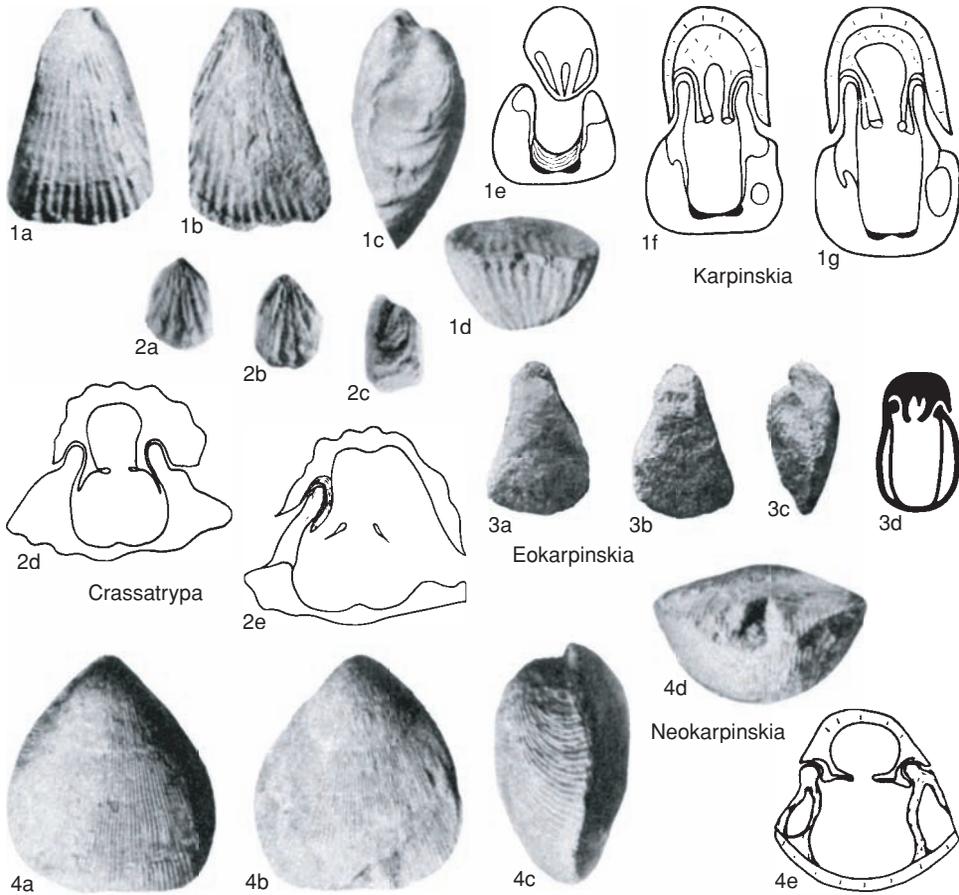
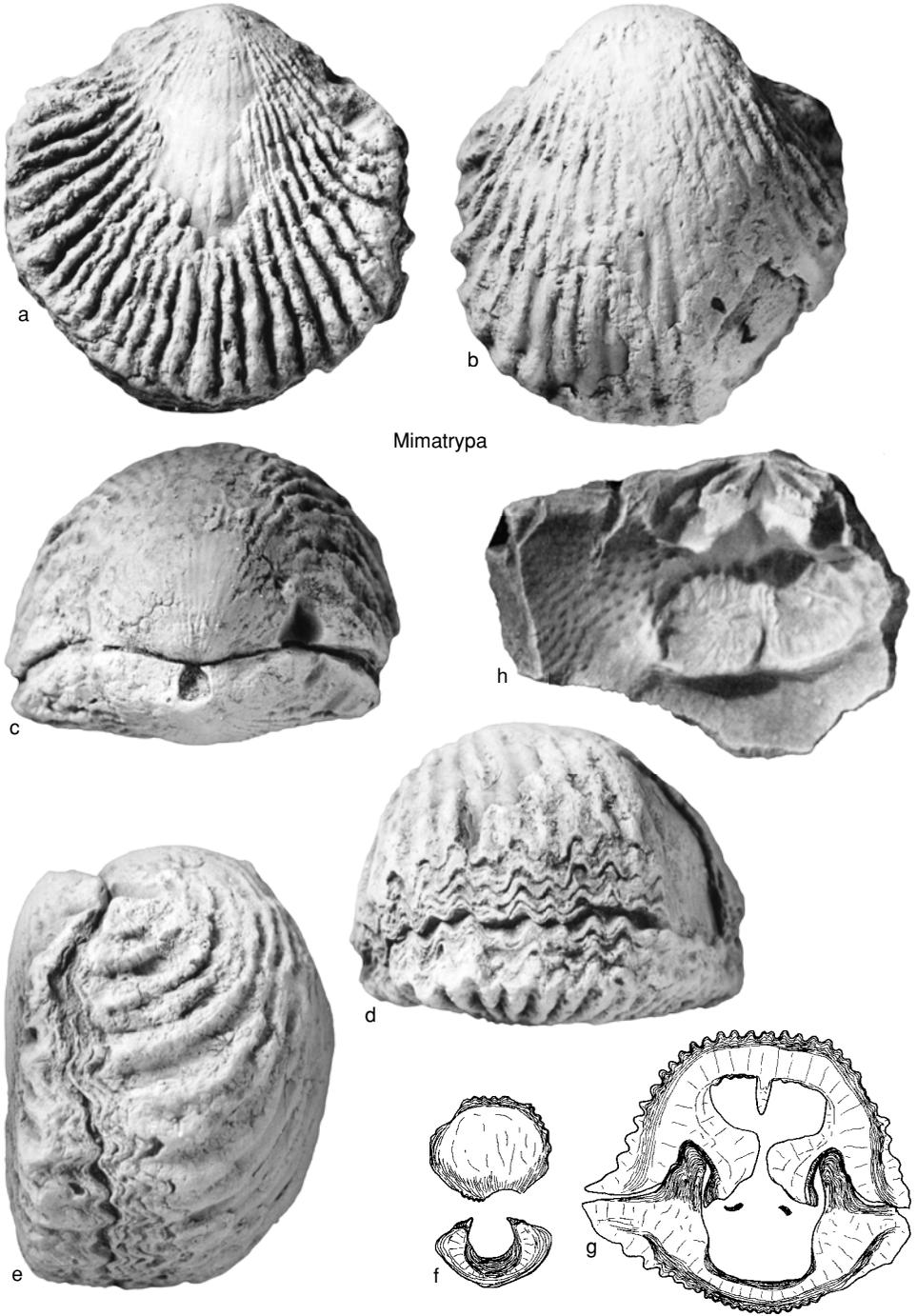


FIG. 984. Karpinskiidae (p. 1452–1456).

coarsening distally, rarely bifurcated or intercalated; microornament of fine concentric filae, growth interruptions; rectimarginate commissure; thick shell wall; hollow deltidial plates fused with pedicle callist or collar; muscle scars posteriorly incised but raised anteriorly; ventral vascular ridges prominently raised; teeth solid; hinge plate thickly reinforced by secondary layer; socket plates thin; small, rounded cardinal pit; minute, delicate crural bases, crura; dorsomedially directed spiralia, up to 21 closely spaced whorls; jugal processes undescribed. [Distinguished from *Karpinskia* by its wide, broader shell (neanic shells difficult to distinguish from *Karpinskia*), ovate cross section, solid teeth lacking dental cavities, distinct vascular ridges; differs from *Vagrana* by its flat ventral valve, apically highly angular beak, narrow hinge angle, anteriorly very coarse ribs.] *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Eurasia, North America.—FIG.

985a–b. **M. flabellata* (ROEMER), upper Eifelian, Germany; a–e, dorsal, ventral, posterior, anterior, lateral views, $\times 2$; f–g, serial sections, $\times 2$ (new); h, internal dorsal valve, $\times 2$ (Struve, 1964a).

Neokarpinskia MIZENS, 1977b, p. 95 [**Karpinskia fedorovi* var. *ivdeli* KHODALEVICH, 1937, p. 67; OD] [= *Parakarpinskia* ZHANG Yan, 1983b, p. 589 (type, *P. striata*, OD); *Parakarpinskia* ZHANG Yan, 1985, p. 347 (type, *P. striata*, OD, *nom. duplic.*)]. Medium to large, dorsibiconvex, triangular hinge angle; elongate, pear shaped, rounded in cross section; small apsacline area; narrow beak; apical-transapical foramen; small deltidial plates; ribs fine, continuous, lacking clear growth interruptions; commissure rectimarginate to weakly plicate; pedicle callist absent; teeth with long, elongate dental cavities; cardinal pit lined by bushy process; small delicate socket plates; medium dorsal septum lacking; crura minute, dorsal to laterodorsal spiralia, fewer than



Mimatrypa

FIG. 985. Karpinskiidae (p. 1452–1453).

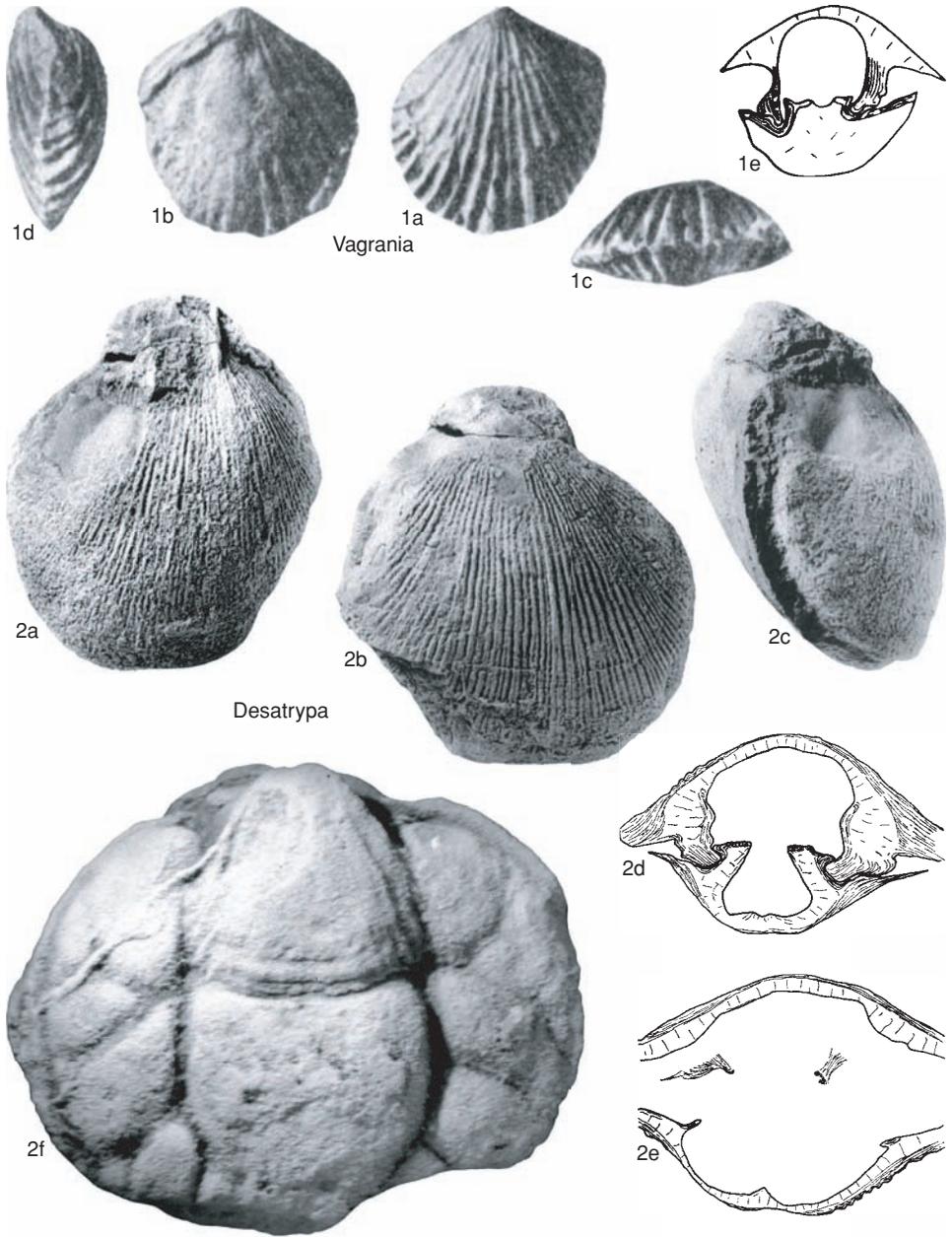


FIG. 986. Karpinskiidae (p. 1456–1457).

16 whorls; jugal processes undescribed. [Distinguished from *Karpinskia* by very fine ribs covering entire shell surface, rounded cross section, lack of lateral compression, numerous spiral whorls; from

superficially similar *Gruenewaldtia* by lack of septally raised muscle platforms.] Lower Devonian (?lower Pragian, middle Pragian–Emsian): Urals (eastern slopes), central Asia, China (Gansu).—

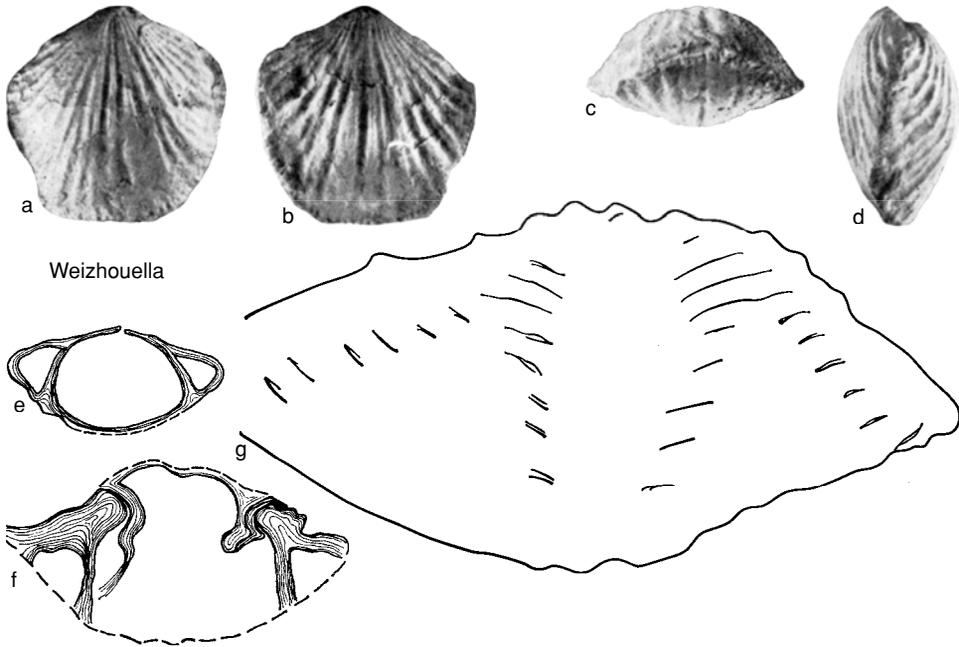


FIG. 987. Karpinskiidae (p. 1457).

FIG. 984, 4a–e. **N. ivdeli* (KHODALEVICH), Emsian, eastern slopes, Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 1$ (Mizens, 1984); e, serial section, $\times 2.5$ (Mizens, 1977b).

Subfamily VAGRANIINAE Aleksееva, 1995

[Vagraniinae ALEKSEEVA, 1995, p. 49; *emend.*, COPPER, 1996a, p. 600]

Biconvex-dorsibiconvex, rounded shells; prominent beak, area, deltidial plates, apical foramen; tubular ribs normally bifurcating or intercalating; usually fine concentric flae; frills, growth lamellae lacking; thick hinge plates, usually strongly raised vascular ridges, incised muscle scars. *Lower Devonian (Lochkovian)–Middle Devonian (Givetian)*.

Vagrani ALEKSEEVA, 1959, p. 389 [**Atrypa kolymensis* NALIVKIN, 1936, p. 17; OD] [= *Dentatrypa* BREIVEL, 1959, p. 57, obj.; *Totia* RZHONSNIJSKAIA & MIZENS, 1977, p. 20 (type, *Atrypa intermediafera* KHODALEVICH, 1951, p. 62, OD)]. Small to medium, rounded, biconvex; prominent apsacline-orthocone area; apical foramen; ribs medium to coarse, consistently spaced, bifurcating ventrally, intercalating dorsally; rectimarginate to weakly plicate commissure; large deltidial plates fused into collar; teeth

with prominent dental cavities; strong ventral vascular ridges; hinge plate thick; crural bases, crura delicate; spiralia dorsomedial, fewer than 20 whorls; jugal processes terminating in jugal plates curving away from each other. [Distinguished from *Mimatrypa* by its convexity, bifurcating and intercalating coarser ribs, dental cavities; differs from *Desatrypa* by having dental cavities (dental plates), coarser ribs. *Totia* has been distinguished from *Vagrani* by its somewhat finer ribs and the presence of microornamental tubercles, but these characters appear to be variable.] *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: Europe, Urals, arctic Canada, southern China.—FIG. 986, 1a–e. **V. kolymensis* (NALIVKIN), upper Emsian, ?lower Eifelian, Kolyma, northeastern Siberia; a–d, dorsal, ventral, anterior, lateral views, $\times 1$; e, serial section, $\times 2$ (Rzhonsnitskaia & Mizens, 1977).

Desatrypa COPPER, 1964, p. 363 [**Atrypa desquamata* SOWERBY, 1840b, explanation to pl. 56, fig. 19–20; OD] [= *Lixatrypa* HAVLIČEK, 1987a, p. 78 (type, *L. ponderosa* HAVLIČEK, 1987a, p. 80, OD)]. Medium to large, moderately biconvex-dorsibiconvex, rounded outline; prominent beak; orthocone area; large apical foramen surrounded by deltidial plates; fine to medium, even, bifurcating or intercalating ribs; commissure rectimarginate to weakly plicate; pedicle callist or collar continuous from deltidial plates; posteriorly incised muscle scars raised anteriorly on solid platform; distinctive ventral vascular

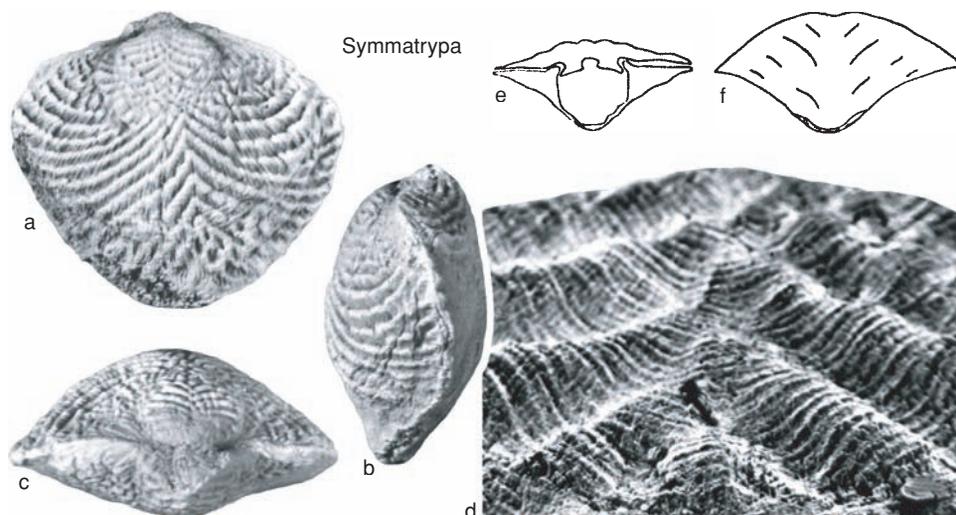


FIG. 988. Symmatrypidae (p. 1457).

ridges; solid teeth; hinge plates thick, massive; crura small, delicate; dorsal spiralia with about 15 whorls; jugal processes undescribed. [Identical to *Vagrana* in strongly raised vascular ridges, pedicle callist and deltidial plate complex, hinge plates, crura, brachidia, but with larger, more finely ribbed shell, solid teeth lacking dental cavities. Genus commonly homeomorphic with *Variatrypa* (Variatrypinae).] Lower Devonian (Pragian)—Middle Devonian (upper Givetian): western Europe, ?China.—FIG. 986, 2a–f. **D. desquamata* (SOWERBY), upper Givetian; a–c, dorsal, ventral, lateral views, $\times 1$; d–e, serial sections, United Kingdom, $\times 2$ (Copper, 1965a); f, internal mold of ventral valve, Germany, $\times 2$ (new). ?*Weizhouella* CHEN Yuanren, 1983, p. 322 [**W. shuimoensis*; OD]. Medium to large, dorsibiconvex; prominent orthocline-anacline area, beak; apical-transapical foramen; wide deltidial plates; ribs coarse, expanding distally; moderately plicate commissure; shell wall thin; pedicle callist absent; pallial sinuses weak; teeth strong with large dental cavities; crura long, fibrous; spiralia dorsal, about 12 whorls; ventral jugal processes ending in small stubby plates. [Problematic genus, similar to *Vagrana* externally in ribs, shape, but lacking vascular ridges, pedicle callist-deltidial plate complex, thick hinge plate; possibly synonymous with *Carinatrypa* or *Mogoliella* (Carinatinae) in thin shell wall, lack of pedicle callist, nature of hinge plate, dental cavities, but lacks carination, trail.] Middle Devonian (Eifelian—Givetian): southern China (Sichuan).—FIG. 987a–g. **W. shuimoensis*, Givetian; a–d, dorsal, ventral, anterior, lateral views, $\times 1$; e–g, serial sections, approximately $\times 4$ (Chen Yuanren, 1983).

Family SYMMATRYPIDAE Mizens, 1989

[nom. transl. COPPER, herein, ex Symmatrypinae MIZENS, 1989, p. 48]

Shell surface with strong, diagonal, divaricate rib structure; lacking concentric growth lamellae, frills; small orthocline area; protruding beak; deltidial plates; apical foramen; teeth solid; hinge plate thick; spiralia dorsomedial; disjunct jugal processes. *Silurian* (Ludlow—Pridoli).

Symmatrypa MIZENS & SAPELNIKOV, 1975, p. 43 [**S. piceaplicata*; OD]. Small to medium, weakly to moderately biconvex, ovoid to shield shaped; small orthocline area; apical foramen, deltidial plates; ribs subradially diverging from plane of symmetry to produce divaricate, subconcentric growth undulations; rectimarginate commissure; thin pedicle callist, deltidial plates possibly fused; solid teeth; thick hinge plate; spiralia dorsomedial, with 4 to 5 widely spaced whorls; crura, jugal processes undescribed. [Affinities of this exotic genus appear to lie with Davidsoniina and Palaferelloidea, possibly derived from *Gracianella*; superficially homeomorphic with *Kulumbella* (Pentamerida), but with area, deltidial plates, spiralia.] *Silurian* (Ludlow—Pridoli): Urals (eastern slopes).—FIG. 988a–f. **S. piceaplicata*, lower Ludlow; a–c, dorsal, lateral, posterior views, $\times 3$; d, SEM detail of divaricate ornament, $\times 44$ (new); e–f, serial sections, $\times 5.5$ (Mizens, 1989).

Suborder LISSATRYPIDINA Copper, 1996

[Lissatrypidina COPPER in COPPER & GOURVENNEC, 1996, p. 81]

Shell smooth, rarely corrugated or undulose, may be covered with fine, projecting capillae or fibers of secondary shell; spiralia medially to dorsomedially directed; jugum complete to incomplete or absent in most Ordovician forms; jugal processes and plates in most Siluro-Devonian taxa. *Ordovician (Llandeilo)–Upper Devonian (Frasnian)*.

Superfamily LISSATRYPOIDEA Twenhofel, 1914

[*nom. transl.* COPPER, herein, ex Lissatrypinae TWENHOFEL, 1914, p. 31; *emend.*, COPPER, herein]

Diagnosis as for suborder, but excludes forms assigned to superfamily Protozygoidea, i.e., those possessing medially directed spiralia, lacking a jugum or with incomplete jugum. [Excludes Glassiidae with medial spiralia; the internal structure of many lissatrypoids is unknown and requires description.] *Ordovician (Caradoc)–Middle Devonian (Eifelian)*.

Family LISSATRYPIDAE Twenhofel, 1914

[*nom. transl.* COPPER, herein, ex Lissatrypinae TWENHOFEL, 1914, p. 31; *emend.*, COPPER, herein]

Smooth or covered by fine radial and concentric capillose ornament, biconvex-dorsibiconvex, with variably thick shell wall, small ventral beak, minute apical foramen, rectimarginate to plicate commissure; solid teeth lacking dental cavities; normally separate jugal processes with simple to complex, curved terminal jugal plates, rarely jugum; spiralia dorsomedially to dorsally directed. *Silurian (Llandovery)–Middle Devonian (Eifelian)*.

Lissatrypa TWENHOFEL, 1914, p. 31 [**L. atheroidea* TWENHOFEL, 1914, p. 33; OD] [= *Spondylobolus* M'COY, 1851, p. 407, *nom. oblit.* (type, *S. craniolaris*, OD); ?*Loilemia* REED, 1936, p. 116 (type, *L. proxima*, OD); *Nanospira* AMSDEN, 1949a, p. 203 (type, *N. parvula*, OD); *Lissatrypoidea* BOUCOT & AMSDEN, 1958, p. 159 (type, *Nucleospira concentrica* HALL, 1859b, p. 223, OD); *Buceqia*

HAVLIČEK, 1984, p. 109 (type, *Terebratula obolina* BARRANDE, 1847, p. 404, OD); *Solitudinella* GODEFROID, 1991, p. 108 (type, *S. hollardi* GODEFROID, 1991, p. 110, OD)]. Small to medium, biconvex-dorsibiconvex-planoconvex; usually smooth (shells may preserve fine, concentrically aligned, radial capillae); apical to transapical foramen; small deltidial plates (commonly resorbed or covered by beak in adult shells); rectimarginate to gently plicate commissure; thick shell wall, pedicle callist, distinct collar; muscle scars commonly deeply incised, may be separated by septum, with V-shaped ventral adductors; short, solid teeth; thickened to bulbous hinge plate; cardinal pit commonly lost, overgrown or suppressed by massive crural bases in adult shells, covered by small cardinal process; dorsomedial spiralia with fewer than 7 to 8 whorls; short, bulky, posterior jugal processes terminating in thick, ringlike jugal plates. [Differs from *Australina* in thick shell, nature of hinge plate, pedicle callist-collar. The name *Spondylobolus* has not been used in more than 140 years and is abandoned.] *Silurian (middle Llandovery)–Middle Devonian (Eifelian)*: worldwide.—FIG. 989, 5a–h. **L. atheroidea*, middle Llandovery, Anticosti, Canada; a–d, dorsal, ventral, posterior, lateral views, ×3 (Copper, 1973a); e–g, serial sections, ×5; h, reconstruction of brachidia, ×3 (new).

Atrypellina MENAKOVA & NIKIFOROVA, 1986, p. 66 [**Lissatrypa caudata* NIKIFOROVA, 1949, p. 16; OD]. Small, dorsibiconvex, subquadrate-pentagonal outline; maximum width near hinge; narrow anacline area; small apical foramen separating deltidial plates; ventral, angular V-shaped sulcus, dorsal V-shaped fold; sharp, angular, plicate commissure; interior with short, small solid teeth; small hinge plate separated by cardinal pit; jugal processes posteromedial; spiralia dorsomedial, fewer than 7 whorls. [Distinct from *Meifodia*, *Cerasina*, and other lissatrypids by its subquadrate-pentagonal shape, very sharp, V-shaped fold-sulcus.] *Silurian (Pridoli)*: central Asia, Urals.—FIG. 989, 3a–g. **A. caudata* (NIKIFOROVA), Turkestan; a–d, dorsal, ventral, lateral, anterior views, ×3; e–f, serial sections, ×3.7; g, reconstruction of brachidia, ×5.5 (Menakova & Nikiforova, 1986).

Atrypoidea MITCHELL & DUN, 1920, p. 271 [**Meristina(?) australis* DUN, 1904, p. 318; OD] [= *Atrypella* KOZLOWSKI, 1929, p. 173 (type, *Atrypa prunum* DALMAN, 1828, p. 133, OD); *Lingatrypa* MIZENS, 1985, p. 10 (type, *Terebratula linguata* VON BUCH, 1834, p. 101, OD); *Globatrypa* MIZENS & SAPELNIKOV, 1985, p. 10 (type, *Merista globus* CHERNYSHEV, 1885, p. 5, OD)]. Medium to large, globose, wide to elongate, convexoplane-dorsibiconvex; shell smooth, may be partly corrugate on anterior fold; small apical-transapical foramen; deltidial plates in neanic shells; orthocline-anacline area in small shells, hypercline area in large shells; weak to strongly plicate commissure; thick shell wall with muscle scars weakly incised; solid teeth; relatively delicate hinge, socket plates; small crural bases;

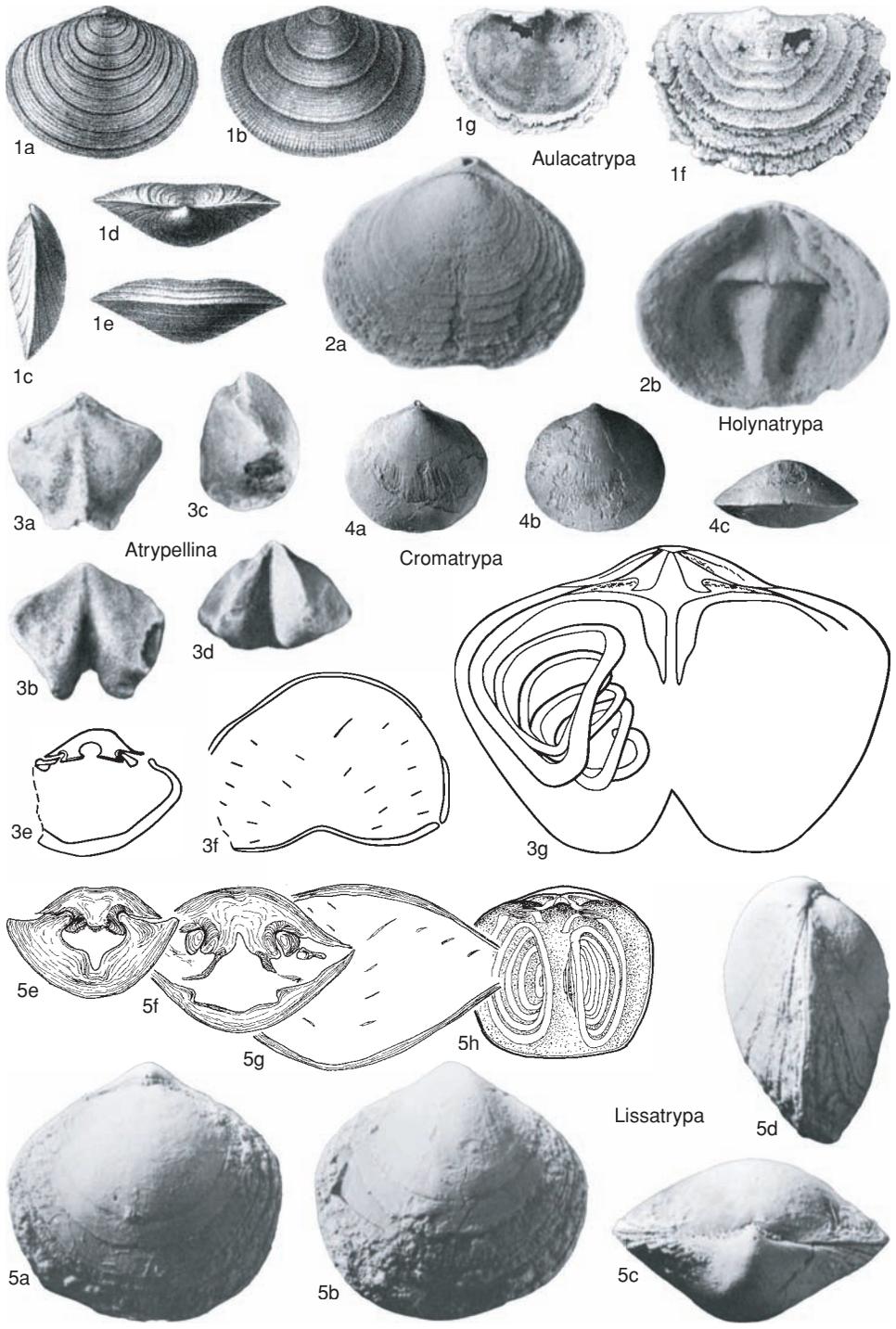


FIG. 989. Lissatrypidae (p. 1458–1463).

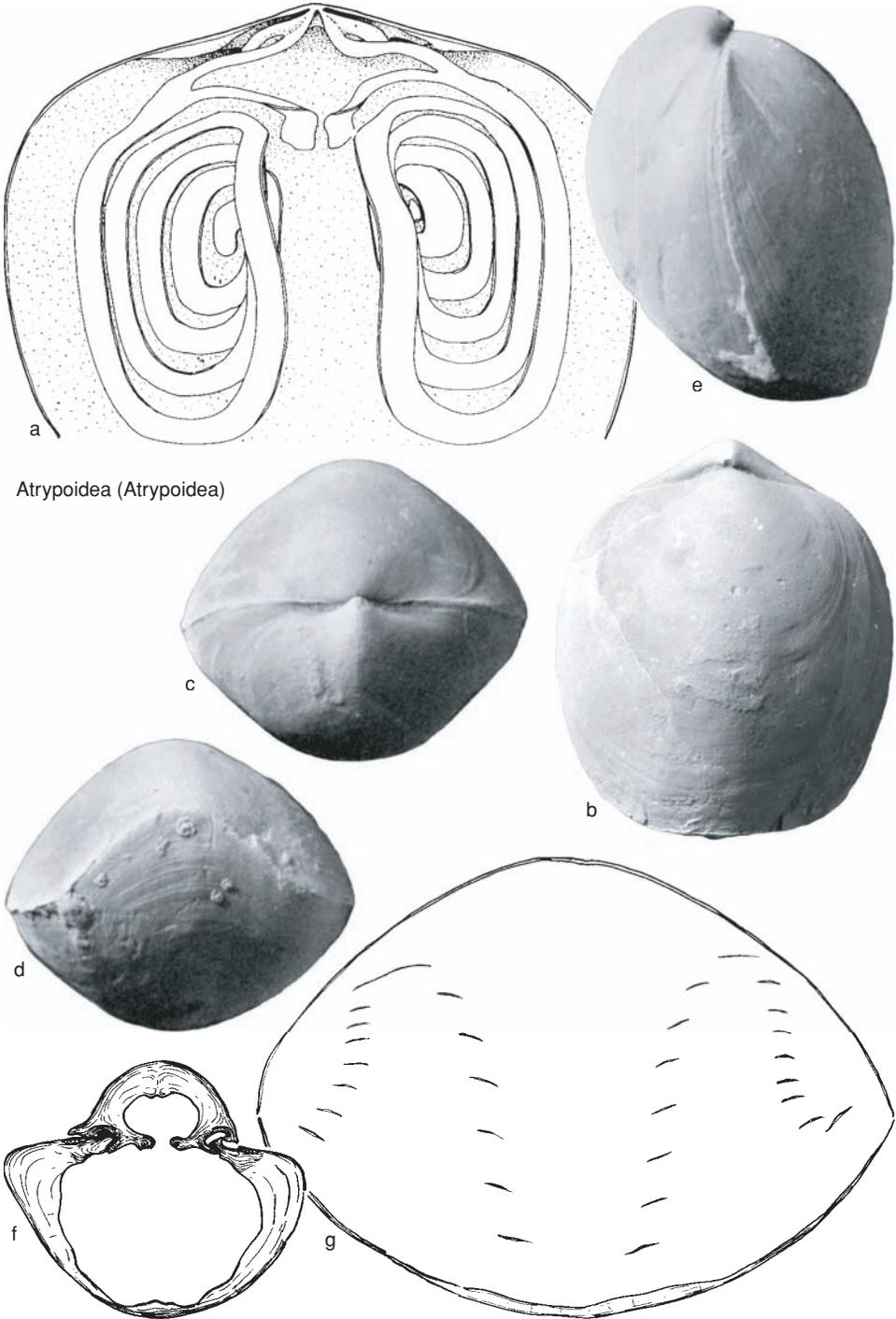


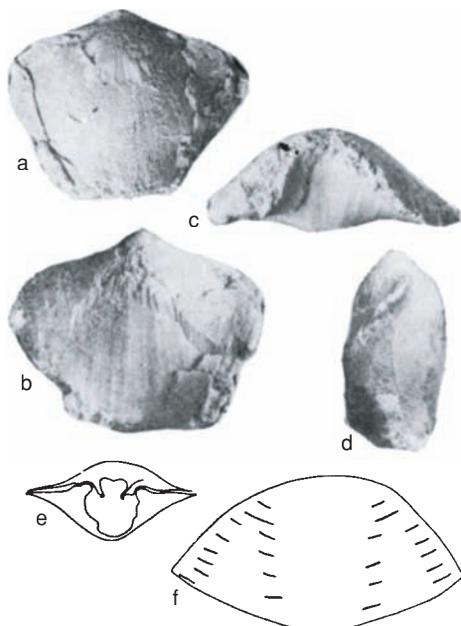
FIG. 990. Lissatrypidae (p. 1461).

dorsal-dorsolateral spiralia; ventrally positioned jugal processes with bulky jugal plates. [Differs from *Lissatrypa* and *Meifodia* in inflated size, elongate shape, hinge plates, stumpy jugal processes.] *Silurian* (?middle Llandovery, Wenlock–Prídolí), *Lower Devonian* (?Lochkovian): China, Urals, ?Aeronian; worldwide, Wenlock–Prídolí; Czech Republic, ?Lochkovian.

A. (Atrypioidea). Description as for genus, but biconvex-dorsibiconvex; broad, U-shaped to subangular, plicate commissure; thick shell wall, with muscle scars lobate, weakly incised; dorsal-dorsolateral spiralia with fewer than 14 whorls; posteroventral jugal processes with bulky jugal plates. [Differs from *Lissatrypa* in size, shape, outline, hinge plates, stumpy jugal processes; differs from *A. (Lissatrypella)* by convex ventral valve; intrapopulation variability encompasses wide shape variation in *Lingatrypa* and *Globatrypa*.] *Silurian* (?middle Llandovery, Wenlock–Prídolí), *Lower Devonian* (?Lochkovian): China, Urals, ?Aeronian; worldwide, Wenlock–Prídolí; Czech Republic, ?Lochkovian (Havlíček, 1987a).—FIG. 990a. **A. (A.) australis* (DUN), Ludlow, New South Wales, Australia; reconstruction from serial sections, $\times 4$ (Copper, 1977b).—FIG. 990b–g. *A. (A.) prunum* (DALMAN), middle Ludlow, Gotland; b–e, dorsal, posterior, anterior, lateral views, $\times 2$; f–g, serial sections, $\times 4$ (Copper, 1977b).

?**A. (Lissatrypella)** SAPELNIKOV & MIZENS, 1982, p. 30 [**Atrypa kuschvensis* CHERNYSHEV, 1893, p. 60; OD]. Medium, round outline, flat ventral valve; convexoplane to weakly dorsibiconvex; small, anacline-hypercline area; apical foramen; small, obscured deltidial plates; broadly plicate commissure; interior with solid teeth, straight hinge plate, long slender jugal processes, dorsomedial spiralia with about 8 whorls. [Possibly synonymous with *A. (Atrypioidea)*, distinguished only by variable characters such as broad, flattened, convexoplane shape, low anterior fold, possible deltidial plates in adult shells; possibly synonymous with *Tectatrypa*, except in plicate commissure. CHERNYSHEV's types are small, *Lissatrypa*-like, round shells, not corresponding to the description of the subgenus.] *Silurian* (upper Wenlock–Prídolí), *Lower Devonian* (?Lochkovian): eastern Urals, central Asia, northern Canada, upper Wenlock–Prídolí; Czech Republic, ?Lochkovian (Havlíček, 1987a, p. 107).—FIG. 991a–f. **A. (L.) kuschvensis* (CHERNYSHEV), lower Ludlow, eastern slopes, Urals; a–d, dorsal, ventral, anterior, lateral views, $\times 1$; e–f, serial sections, $\times 3.5$ (Sapelnikov & Mizens, 1982).

?**Aulacatrypa** HAVLÍČEK, 1987b, p. 241 [**Atrypa squama* BARRANDE, 1879b, pl. 82; OD; *emend.*, HAVLÍČEK, 1990c, p. 203] [= *Johnsoniatrypa* ZHANG Ning, 1989b, p. 8 (type, *J. imbricata*, OD)]. Very small (less than 5 mm), weakly biconvex-planoconvex; widest at long, straight hinge;



Atrypioidea (*Lissatrypella*)

FIG. 991. Lissatrypidae (p. 1461).

orthocline-apsacline area; open delthyrium, possibly lacking deltidial plates; slightly overlapping, concentric growth lamellae with fine capillae (spinulose); weakly sulcate to rectimarginate commissure; teeth solid; cardinal pit dividing hinge plate; crura, spiralia, and jugal processes undescribed. [Similar to ?*Lissatrypa* in possessing concentrically aligned capillae, but differing in very small size, thin shell, convexity, long hinge, large area, delicate hinge plate; possibly synonymous with *Australina*, with which it shares convexity, hinge plate structure.] *Silurian* (Wenlock): Czech Republic, arctic Canada.—FIG. 989, 1a–e. **A. squama* (BARRANDE), Czech Republic; dorsal, ventral, lateral, posterior, anterior views, approximately $\times 6$ (Barrande, 1879b).—FIG. 989, 1f–g. *A. imbricata* (ZHANG), arctic Canada; dorsal valve exterior, interior, $\times 6$ (Zhang Ning, 1989b).

Australina CLARKE, 1913, p. 348 [**A. jachalensis*; OD; *emend.*, COPPER, HÜNICKEN, & BENEDETTO, 1988, p. 533]. Small to medium; planoconvex-concavoconvex; long, narrow sulcus on dorsal valve; rounded outline; surface smooth, capillae unknown; beak adpressed; minute area; transapical foramen obscured; deltidial plates possibly absent; rectimarginate to weakly sulcate commissure; internally, weak pedicle callist; teeth stubby, medially directed, solid; socket plates strong, separated by distinct cardinal pit; cardinal process absent; dorsomedial spiralia with fewer than 5 whorls; jugal processes undescribed. [Distinguished from

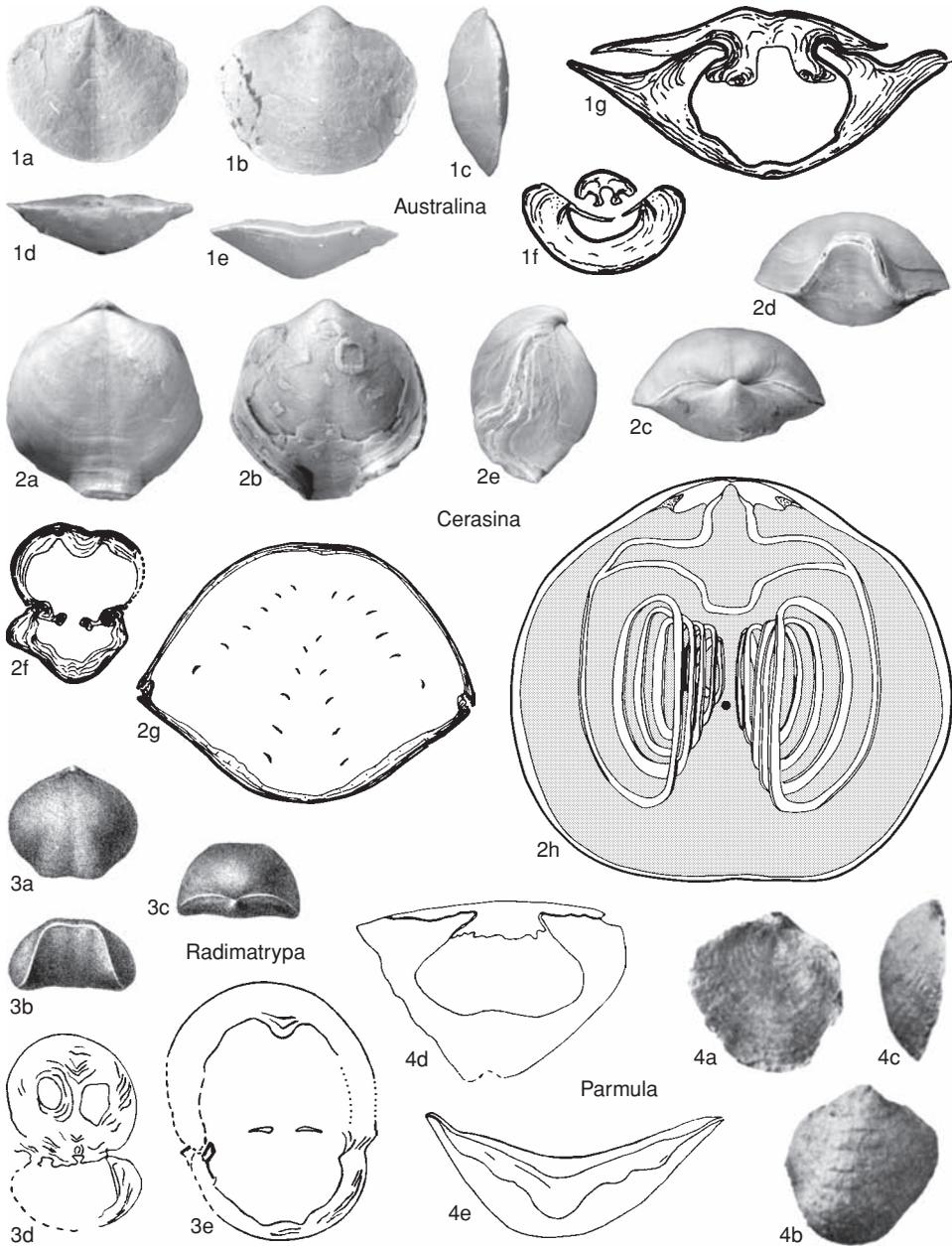


FIG. 992. Lissatrypidae (p. 1461–1463).

Lissatrypa by convexity, hinge plate with cardinal pit, lack of thick pedicle callist or collar; similar to *Aulacatrypa*, but larger, lacking straight hinge line.] *Silurian* (Copper Wenlock, Ludlow–Přidoli): South America, ?northern Africa, Australia, Czech Republic, ?China.—FIG. 992, 1a–g. **A. jachalensis*, Ludlow, Argentina; a–c, dorsal, ventral, lateral, pos-

terior, anterior views, $\times 2$; f–g, serial sections, $\times 5$ (Copper, Hünicken, & Benedetto, 1988).

Cerasina COPPER, 1995, p. 850 [**C. pycnata* COPPER, 1995, p. 851; OD]. Small to medium, elongate to equidimensional, rounded-subquadrate, dorsibi-convex-biconvex; narrow, hypercline area; foramen usually transapical; deltidial plates obscured by

- incurved beak, commonly lost; sharp, U-shaped anterior fold; interior with thick shell; dorsally directed solid teeth; thin hinge plate; small, apical, rounded ventral septum; broad dorsal septum; small crura; spiralia dorsomedial, about 8 whorls; dorsally positioned, simple jugum. [*Septatrypa*-like shape, but lacking dental cavities, delicate cardinalia internally; most similar to *Meifodia*, but distinguished by dorsally located, primitive jugum instead of separated jugal processes and a smaller, narrower shell with more sharply defined anterior fold.] *Silurian* (lower Llandovery—middle Llandovery): North America.—FIG. 992,2a–b. **C. pycnata*, lower Llandovery, Anticosti; a–e, dorsal, ventral, posterior, anterior, lateral views, $\times 2$; f–g, serial sections, $\times 5$; h, reconstruction of brachidia, $\times 5$ (Copper, 1995).
- ?**Cromatrypa** HAVLÍČEK, 1987b, p. 240 [**C. orbis*; OD]. Small, smooth, rounded outline, biconvex to weakly dorsibiconvex; minute orthocline area; small deltidial plates with apical foramen; rectimarginate commissure; ventral *vascula media* long, straight, diverging; massive hinge plate with cardinal pit; probably dorsomedial spiralia; jugal processes undescribed. [Problematic genus; possibly synonymous with *Levispira* except in rounded shape, convexity; possibly synonymous with *Lissatrypa*, but adult shells possess exposed deltidial plates, apical foramen, small orthocline area; dorsomedial spiralia, but spiralia undescribed (HAVLÍČEK, personal communication, 1990).] *Silurian* (Ludlow): Czech Republic.—FIG. 989,4a–c. **C. orbis*; dorsal, ventral, anterior views, $\times 3.2$ (Havlíček, 1987b).
- ?**Holynatrypa** HAVLÍČEK, 1973, p. 339 [**H. crucifera*; OD]. Similar to *Lissatrypa*, but generally very small shell, planoconvex; ventral valve with triangular, raised muscle platform, supported by raised median septum; brachidia undescribed. [Affinities unknown, possibly not atrypide.] *Lower Devonian* (Emsian): Czech Republic.—FIG. 989,2a–b. **H. crucifera*, upper Emsian; dorsal view, interior ventral valve, $\times 5.5$ (Havlíček, 1998a).
- Levispira** MIZENS, 1975b, p. 47 [**L. eifeliensis*; MIZENS, 1975b, p. 48; OD]. Small to medium, elongate, planoconvex-ventribiconvex; keeled ventral valve; strongly protruding beak; small orthocline area; apical foramen; minute deltidial plates; rectimarginate to weakly sulcate commissure; solid teeth; dorsal hinge plate thick; small cardinal pit; mediadorsal spiralia with fewer than about 6 whorls; jugal processes touching medially. [Possibly synonymous with *Cromatrypa* except in elongate shape, convexity, sulcate commissure; distinguished from *Lissatrypa* by keeled, elongate, sulcate shell, convexity, orthocline area, exposed deltidial plates; possibly synonymous with *Shrockia*.] *Lower Devonian* (upper Emsian)—*Middle Devonian* (Eifelian): Urals.—FIG. 993,2a–f. **L. eifeliensis*, upper Emsian—lower Eifelian, eastern slopes; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e–f, serial sections, $\times 3$ (Mizens, 1975b).
- Meifodia** WILLIAMS, 1951, p. 106 [**Hemithyris subundata* M'COY, 1851, p. 394; OD] [= *Tyrothyris* ÖPIK, 1953, p. 15 (type, *T. tyro*, OD)]. Medium, equally wide as long or wider than long, dorsibiconvex; straight hinge; small anacline-hypercline area usually obscuring apical-transapical foramen; deltidial plates commonly lost in adult shells; prominent, broad, angular, anterior fold on commissure; solid teeth; ventral valve with long, slightly arcuate, subparallel vascular canals; hinge plate divided by cardinal pit; straight, horizontal inner socket ridges; dorsomedially directed spiralia with fewer than 10 whorls; long, simple, posteroventrally located jugal processes, with hooklike jugal plates. [Distinct from *Cerasina* in the possession of ventral jugal processes (instead of dorsal jugum), wide shell with broad fold; differs from *Australina* by its convexity, strong anterior fold; may be confused with septatrypinids, but for solid teeth lacking dental cavities.] *Silurian* (Llandovery): Eurasia, North America.—FIG. 993,1a–b. **M. subundata* (M'COY), Rhuddanian, United Kingdom; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e–g, serial sections, $\times 5$; h, reconstruction of brachidia, $\times 5$ (Copper, 1995).
- ?**Parmula** MENAKOVA & BREIVEL, 1987, p. 110 [**P. orbis* NIKIFOROVA & MENAKOVA, 1987, p. 112; OD]. Very small to small, concavoconvex-planoconvex; smooth or with numerous weak, overlapping concentric growth lamellae; minute anacline-hypercline area; obscured, small foramen; deltidial plates absent; thick shell wall; long, straight, median ventral septum almost to commissure; teeth solid; possibly dorsomedial spiralia with 2 to 4 whorls; jugal processes said to be present. [Homeomorphic with the athyridids *Dayia* or *Dnestrina*, with which it shares long ventral septum, but said to have atrypoid spiralia (original types lack intact brachidia); possibly synonymous with dwarfed *Lissatrypa*, *Levispira*, or *Shrockia*.] *Silurian* (upper Llandovery—Přídolí): Turkestan, Tian Shan, Urals, Hudson Bay Lowlands, Canada.—FIG. 992,4a–e. **P. orbis* NIKIFOROVA & MENAKOVA, Přídolí, Zeravshan Range, Turkestan; a–c, dorsal, ventral, lateral views, $\times 3$; d–e, serial sections, $\times 6.5$ (Menakova & Breivel, 1987).
- ?**Radimatrypa** HAVLÍČEK, 1990c, p. 161 [**R. zelaria*; OD]. Small to medium, dorsibiconvex, smooth; small, hypercline area, lacking (or obscuring) foramen, deltidial plates; broadly plicate commissure; thick shell wall; solid teeth, probably lacking dental cavities; crura, spiralia, jugal processes undescribed. [Problematic genus; externally homeomorphic with *Septatrypa* or *Cerasina*; internally apparently similar to *Lissatrypa* in solid teeth, but dental cavities may be infilled.] *Lower Devonian* (Emsian), *Middle Devonian* (?Eifelian): Czech Republic.—FIG. 992,3a–e. **R. zelaria*, upper Emsian; a–c, dorsal, anterior, posterior views, $\times 1$ (Barrande, 1879b); d–e, serial sections, $\times 5$ (Havlíček, 1990c).
- ?**Shrockia** BOUCOT & SMITH, 1978, p. 268 [**S. tuenhofeli* BOUCOT & SMITH, 1978, p. 271; OD]. Large, smooth, elongate, planoconvex-ventribiconvex; obscured hypercline area; deltidial plates unknown; sulcate commissure; brachidia unknown.

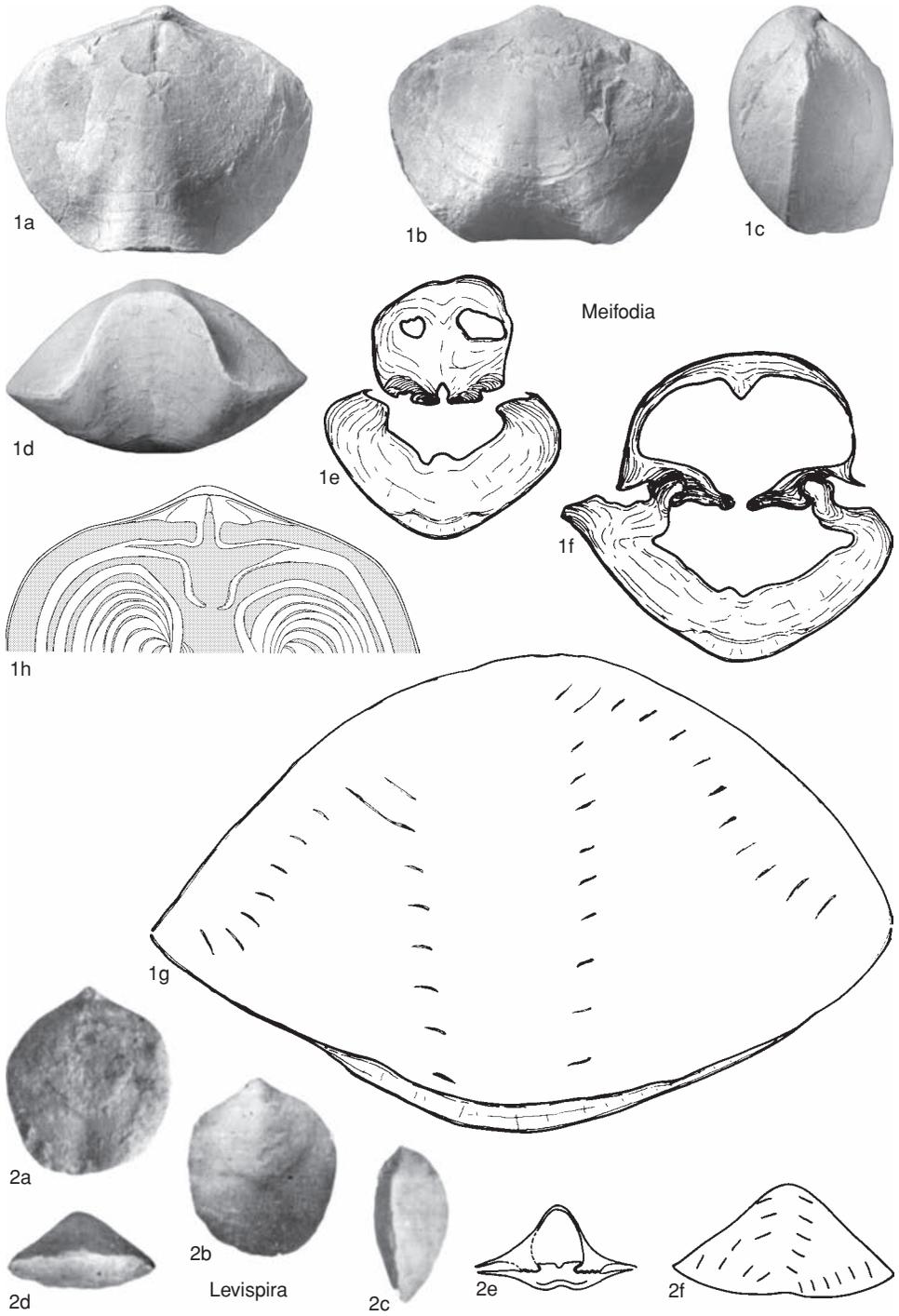


FIG. 993. Lissatrypidae (p. 1463).

[Externally like *Dayia* but with much larger shell; questionable atrypid since internal structure of poorly preserved shell unknown, shell may be deformed; elongate outline as in *Atrypoides*, except for reversed convexity, sulcate commissure; possibly synonymous with *Levispira* or *Parmula*, but much larger in size.] *Silurian* (Ludlow): Newfoundland. —FIG. 994, 2a–e. **S. twenhofeli*; a–c, dorsal, posterior, ventral views, $\times 1$; d, serial section, $\times 1.8$; e, serial section, $\times 1.6$ (Boucot & Smith, 1978).

?*Tectatrypa* MIZENS, 1973, p. 44 [**Merista tectiformis* CHERNYSHEV, 1893, p. 44; OD]. Small to medium, convexoplane, elongate to subtriangulate, laterally compressed; narrow beak; anacline area; possible small deltidial plates; apical foramen; high, broad, rounded, U-shaped anterior fold; interior with thick shell; solid, inwardly directed teeth; hinge plate slender; dorsally directed spiralia of fewer than 8 whorls; jugal processes undescribed. [Possibly synonymous with *Atrypoides* (*Lissatrypella*), but with smaller, more globose, elongate shell; differs from smooth *Eokarpinskia* in hinge plate, lack of dental cavities.] *Silurian* (upper Wenlock–Ludlow): Urals. —FIG. 994, 1a–f. **T. tectiformis* (CHERNYSHEV), upper Wenlock, eastern slopes; a–d, dorsal, ventral, lateral, anterior views, $\times 1$; e–f, serial sections, $\times 4$ (Sapelnikov & Mizens, 1982).

Family SEPTATRYPIDAE

Kozłowski, 1929

[*nom. transl.* COPPER, herein, ex Septatrypinae KOZŁOWSKI, 1929, p. 30; *emend.*, COPPER, herein]

Small to medium, smooth, rarely corrugated, dorsibiconvex shells, generally with high anterior fold; large dental cavities with or without dental plates; thin, delicate hinge, socket plates; spiralia dorsomedially directed, with fine, narrow lamellae; spiralia dorso-medial; central to ventral jugum (Ordovician forms), or jugal processes (Siluro-Devonian forms). *Ordovician* (*Caradoc*)–*Lower Devonian* (*Emsian*), *Middle Devonian* (?*Eifelian*).

Subfamily SEPTATRYPINAE

Kozłowski, 1929

[Septatrypinae KOZŁOWSKI, 1929, p. 30] [=Atrypopsinae POULSEN, 1943, p. 40]

Smooth, thinly shelled, dorsibiconvex; may possess anterior corrugations (ribs); usually weakly to strongly plicate; large dental cavities; fragile hinge plates; dorsal septum very short to nearly absent; dorsomedially directed spiralia; delicate, long, ventrally to centrally located jugal processes. *Silurian* (*Llandovery*)–*Lower Devonian* (*Emsian*), *Middle Devonian* (?*Eifelian*).

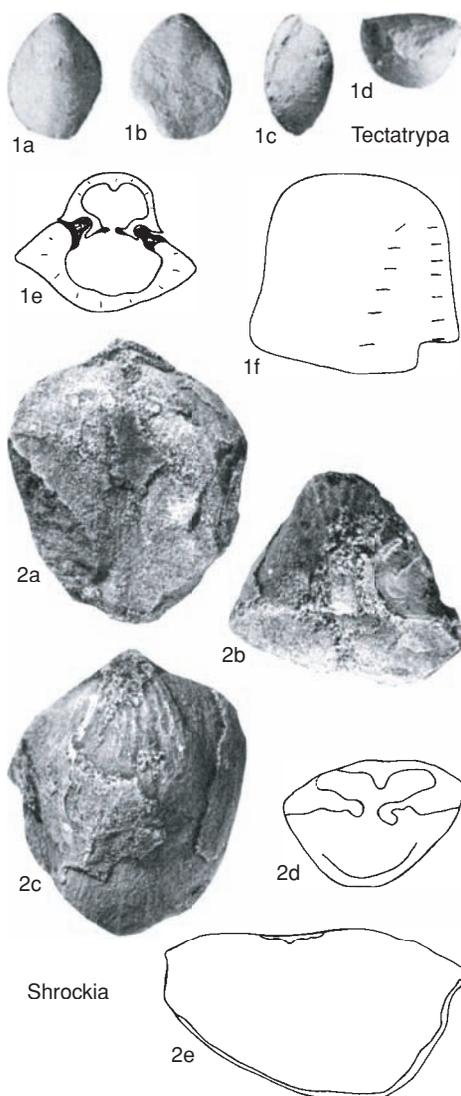


FIG. 994. Lissatrypidae (p. 1463–1465).

Septatrypa KOZŁOWSKI, 1929, p. 176 [**S. secreta*; OD] [=*Dubaria* TERMIER, 1936, p. 1266 (type, *D. lantenoisi*, OD); *Atrypopsis* POULSEN, 1943, p. 44 (type, *A. varians*, OD); *Rhynchatrypa* STEHL, 1962, p. 199 (type, *Terebratula thetis* BARRANDE, 1847, p. 349, OD); *Barkolia* ZHANG Quan, 1981, p. 97 (type, *B. typica*, OD)]. Medium, rounded to subtriangulate-subquadrate, dorsibiconvex; ventral valve relatively flat to concave posteriorly in specimens with high fold; shell smooth or corrugated; pinched beak; small anacline-hypercline area; minute apical-transapical foramen, obscuring small deltidial plates; shell smooth to corrugated; high, strongly defined, U-shaped plicate commissure;

- thin shell wall; delicate teeth with large dental cavities flanked by thin dental plates; hinge, socket plates delicate, subhorizontal; distinct cardinal pit; variable weak, short dorsal septum [septalium-like structure in specimens with strong dorsal convexity]; crura delicate; dorsal spiralia with fewer than 8 whorls; posteromedial jugal processes ending in long, delicate jugal plates. [Differs from *Idiospira* in presence of ventrally located jugal processes. Contrary to published literature, Llandovery species externally, internally indistinguishable from later forms]. *Silurian (Aeronian)*–*Lower Devonian (Pragian)*: worldwide.
- S. (*Septatrypa*)**. Description as for genus, but only smooth species included. [Differs from *S. (Hircinisca)* in absence or rare appearance of anterior corrugations; differs from *Idiospira* in presence of jugal processes.] *Silurian (Aeronian)*–*Lower Devonian (Pragian)*: worldwide.—FIG. 995,1a–d. **S. (S.) secreta*, Lochkovian, Podolia, Ukraine; dorsal, ventral, lateral, anterior views, $\times 2$ (Nikiforova, Modzalevskaya, & Bassett, 1985).—FIG. 995,1e–h. *S. (S.)* sp., Wenlock, Gotland; e–g, serial sections; h, reconstruction of brachidia, $\times 5$ (new).
- S. (*Hircinisca*)** HAVLÍČEK, 1960, p. 241 [**Atrypa Sappho* [sic] var. *hircina* BARRANDE, 1879b, pl. 90, fig. IV; OD; no original description of types]. Identical to *S. (Septatrypa)* internally, but variably up to 7 or 8 anterior corrugations along fold-sulcus producing rhynchonelliform shape, appearance of anterior ribs; population variants of *Septatrypa sensu stricto* also possess weak corrugations. *Silurian (middle Wenlock)*–*Lower Devonian (Lochkovian)*: Europe, Morocco, North America, Urals, central Asia, ?southern China.—FIG. 995,2a–g. **S. (H.) hircina* (BARRANDE), upper Wenlock, Czech Republic; a–e, dorsal, ventral, lateral, posterior, anterior views, $\times 1$; f–g, serial sections, $\times 4.6$ (Havlíček & Plodowski, 1974).
- Bescia** COPPER, 1995, p. 853 [**B. scissura*; OD]. Small, smooth, biconvex; 2 strong, divergent ventral corrugations separated by sulcus; commonly 1 or 2 lateral corrugations; small orthocline-anacline area; apical foramen; minute deltidial plates; multiplicate commissure; shell wall thin; teeth delicate; large, elongate dental cavities; inner socket ridges fused over cardinal pit; thin hinge, socket plates; mediiodorsal spiralia with fewer than 4 whorls; centrodorsally located jugal processes. [Differs from *Hircinisca* in its prominent ventral, divergent pair of corrugations, producing *Atrypina*-like form, internally by fused inner socket ridges; differs from *Atrypina* in lack of growth lamellae or imbrication, centrodorsal jugal processes, large dental cavities.] *Silurian (Llandovery)*: North America, ?United Kingdom, Urals.—FIG. 995,3a–h. **B. scissura*, Rhuddanian, Anticosti; a–e, dorsal, ventral, lateral, posterior, anterior views, $\times 3$; f–g, serial sections; h, reconstruction of brachidia, $\times 5$ (Copper, 1995).
- ?**Cerberatrypa** HAVLÍČEK, 1990c, p. 162 [**C. cerberus* HAVLÍČEK, 1990c, p. 163; OD]. Small to medium, cordate to pentagonal outline, biconvex; small, orthocline-anacline area; apical foramen; small deltidial plates; rectimarginate-plicate commissure; delicate hinge plates; large dental cavities; crura, spiralia, jugal processes unknown. [Problematic genus similar to *Septatrypa* but cordate shape, weak dorsal fold: may possibly be athyridid.] *Lower Devonian (Emsian), Middle Devonian (?Eifelian)*: Czech Republic.—FIG. 995,4a–c. **C. cerberus*, Emsian; dorsal, ventral, anterior views, $\times 2$ (Havlíček, 1990c).—FIG. 995,4d. *C. dissidens* (BARRANDE), Emsian; serial section, $\times 6$ (Havlíček, 1990c).

Subfamily IDIOSPIRINAE

new subfamily

[Idiospirinae COPPER, herein]

Septatrypidae with posterodorsally located jugum. *Ordovician (Caradoc–Ashgill)*, *Silurian (?Llandovery)*.

Idiospira COOPER, 1956a, p. 690 [**Camerella panderi* BILLINGS, 1859b, p. 302; OD]. Small to medium, ovoid, biconvex-dorsibiconvex, smooth to weakly corrugated anteriorly; small, orthocline-hypercline area; apical foramen; deltidial plates obscured, minute; usually corrugated, subangular to rounded, plicate commissure; teeth with large dental cavities; weak dorsal septum; thin socket plates; spiralia dorsomedial with fewer than 6 whorls; posterodorsal jugum. [Externally similar to *Septatrypa* or *Hircinisca*, but smaller shell, possessing jugum instead of jugal processes, thicker hinge plate.] *Ordovician (middle Caradoc–Ashgill)*, *Silurian (?Llandovery)*: North America, Eurasia.—FIG. 996,1a–h. **I. panderi* (BILLINGS), middle Caradoc, Ontario, Canada; a–e, dorsal, ventral, lateral, anterior, posterior, $\times 3$; f–g, serial sections; h, reconstruction of brachidia, $\times 4$ (Copper, 1986b).

?**Webbyspira** PERCIVAL, 1991, p. 163 [**W. principalis*; OD]. Medium size, wide, dorsibiconvex-biconvex, smooth, only rarely corrugate; small, anacline area; foramen, deltidial plates unknown; broadly plicate commissure; thick walled; long, narrow dental cavities; moderate to strong dorsal septum; dorsomedial spiralia with fewer than 8 whorls; nature of discrete jugal processes or jugum unknown. [Differs from externally similar *Meifodia* in having dental cavities; differs from *Septatrypa* in broad shell, low anterior fold, narrow dental cavities, socket plates, jugal processes; differs from *Idiospira* in larger size, broad shell. Original description cites jugal processes; if correct, *Webbyspira* should be assigned to the Septatrypinae.] *Ordovician (Caradoc)*: Australia.—FIG. 996,2a–g. **W. principalis*, New South Wales; a–d, dorsal, posterior, lateral, anterior views, $\times 2$; e–f, serial sections, $\times 2$; g, reconstruction of brachidia, $\times 2$ (Percival, 1991).

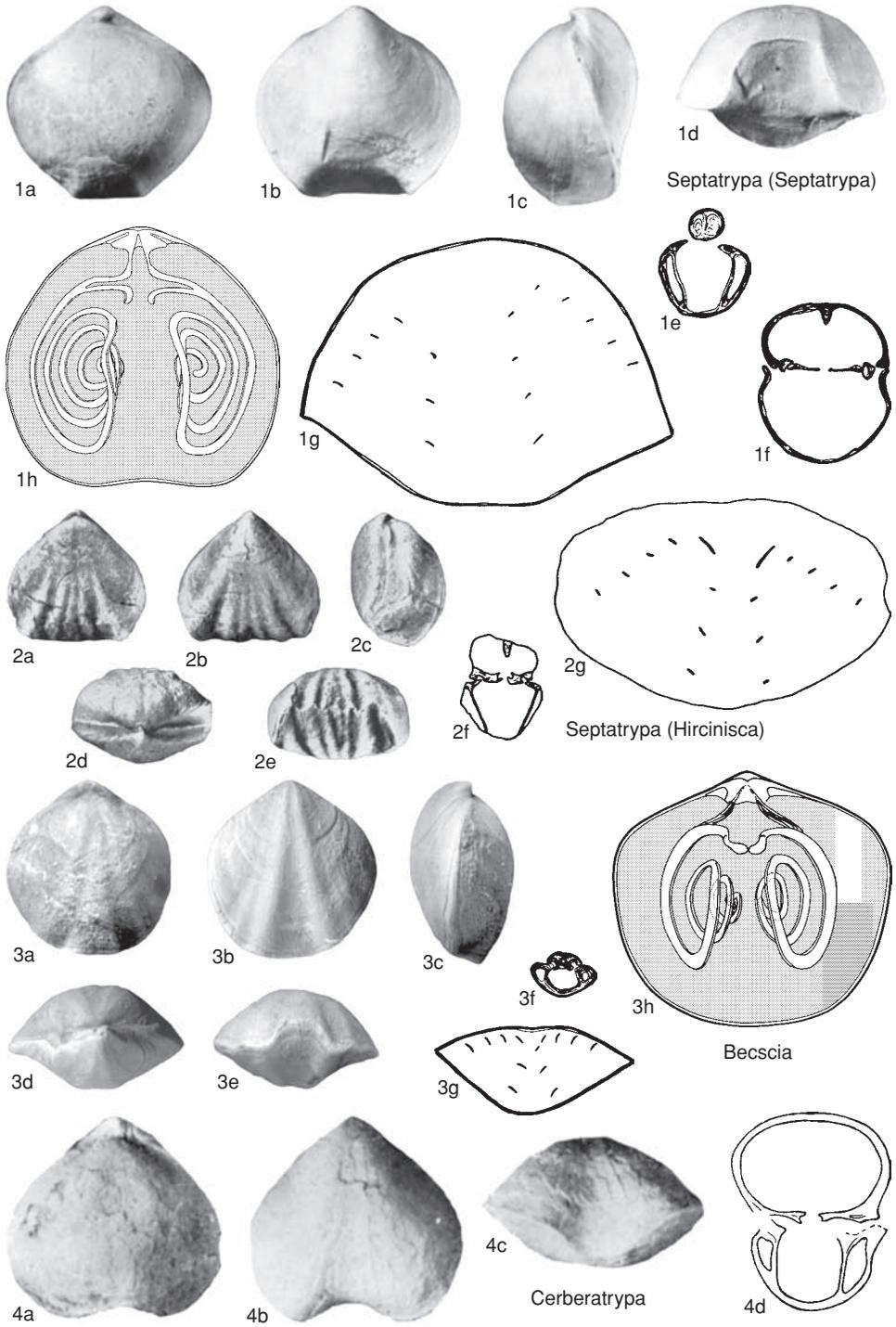


FIG. 995. Septatrypidae (p. 1466).

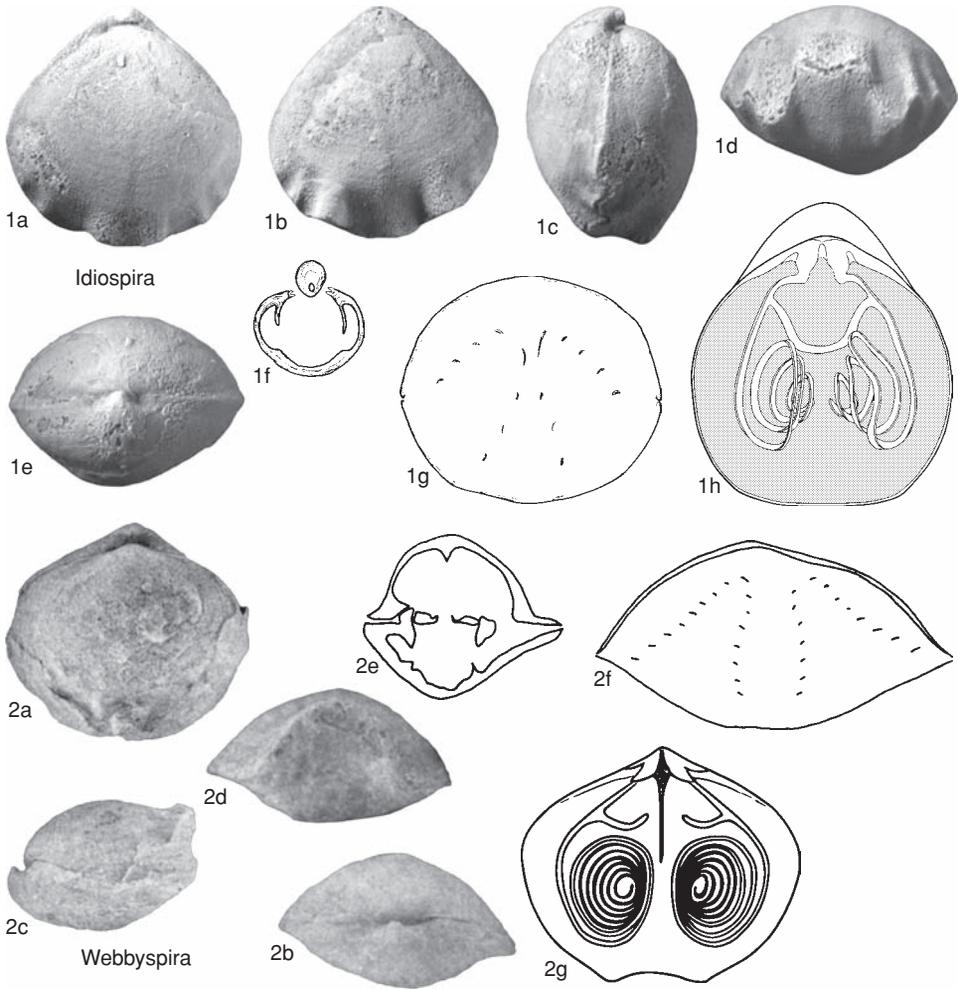


FIG. 996. Septatrypidae (p. 1466).

Superfamily GLASSIOIDEA
Schuchert & LeVene, 1929

[*nom. transl.* COPPER, herein, ex Glassiinae SCHUCHERT & LEVENE, 1929a, p. 20; *emend.*, COPPER, 1986b, p. 852]

Small to medium, smooth, biconvex, commonly ligate shells; thick walled; sturdy hinge socket plates, solid teeth usually reinforced by exposed or buried dental plates; dental cavities in later taxa; spiralia medially directed, barrel shaped, scooped toward jugal processes; jugal processes terminated by

small to large jugal plates. *Silurian* (?upper Llandovery, Wenlock)—*Upper Devonian* (Frasnian).

Family GLASSIIDAE
Schuchert & LeVene, 1929

[*nom. transl.* COPPER, herein, ex Glassiinae SCHUCHERT & LEVENE, 1929a, p. 20; *emend.*, COPPER, 1986b, p. 852]

Diagnosis as for superfamily. *Silurian* (?upper Llandovery, Wenlock)—*Upper Devonian* (Frasnian).

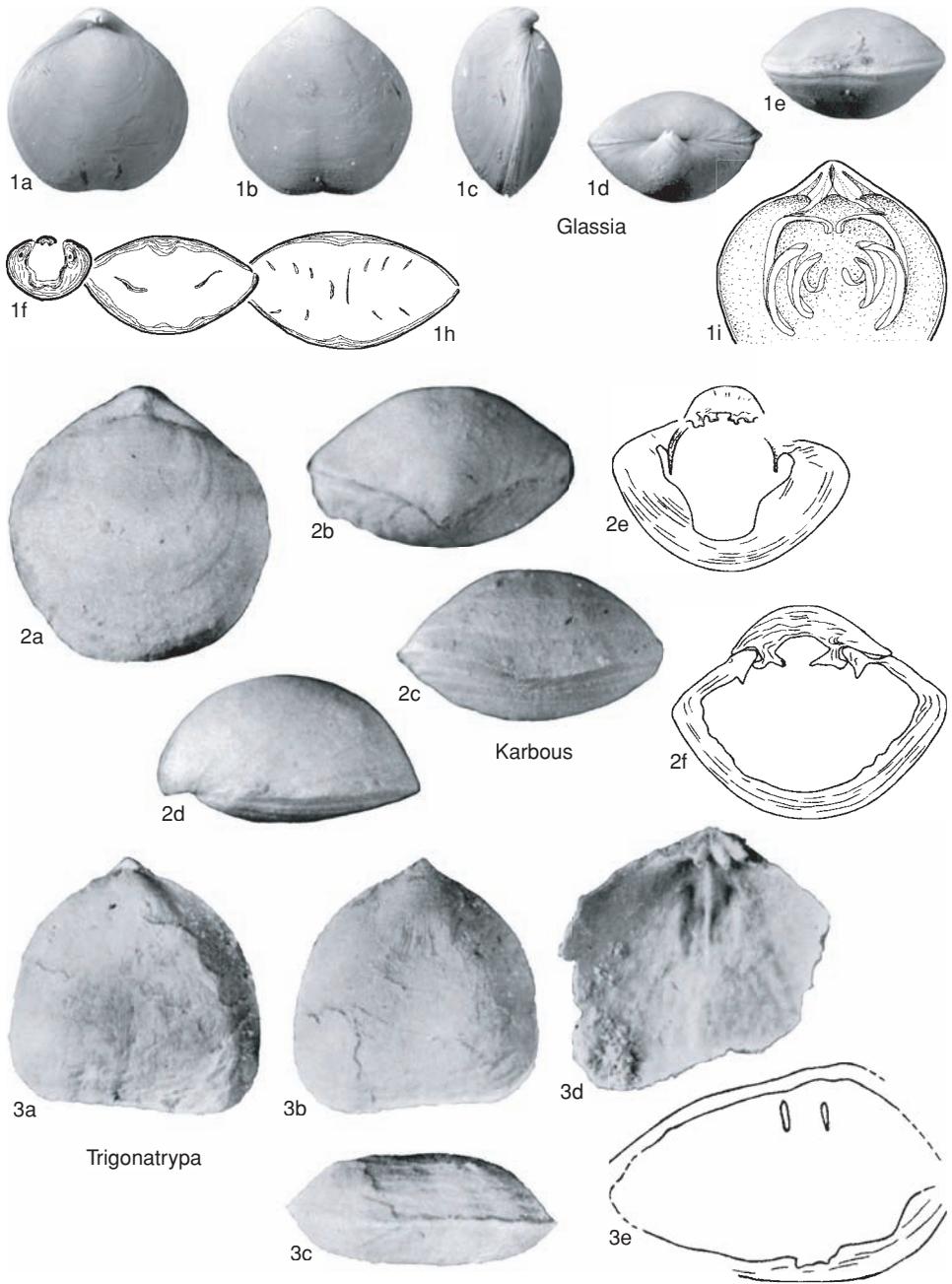


FIG. 997. Glassiidae (p. 1469–1470).

Glassia DAVIDSON, 1881a, p. 11 [**Atrypa obovata* J. de C. SOWERBY, 1839, p. 618; OD; *typum invalidum*, belongs to *Lissatrypa*; *ergo*, type revised to *Glassia elongata* DAVIDSON, 1881b, p. 148; *vid.* COPPER, 2001] [= *Cryptatrypa* SIEHL, 1962, p. 196 (type,

Terebratula philomela BARRANDE, 1847, p. 387, OD)]. Small, biconvex to weakly ventribiconvex, rounded to elongate; small anacline-hypercline area; beak obscuring minute apical-transapical foramen; deltidial plates minute or absent; commissure ligate

- (both valves sulcate) to rectimarginate; thick shell wall; medium septum common in both valves; teeth distally solid or with minute apical dental cavities; buried dental plates; thick, squared hinge plate divided by narrow cardinal pit; spiralia barrel shaped, medially directed, fewer than 6 whorls; ventro-posterior jugal processes terminating in hooks. [The originally and unfortunately designated type species of *Glossia*, *G. obovata* (SOWERBY), is a species of *Lissatrypa* (family Lissatrypidae), with dorsally directed spiralia; DAVIDSON (1881b) correctly identified *Glossia elongata* with medially directed spiralia, typical of the family Glossiidae as defined by SCHUCHERT and LEVENE (1929a) and used by DAVIDSON in his diagnosis of the genus. This species was then selected as type (COPPER, 1996b).] *Silurian* (?upper Llandovery, Wenlock–Ludlow, ?Přídolí): western Europe, Urals, ?northern Canada.—FIG. 997, 1a–e. **G. sp. cf. G. elongata* (DAVIDSON), Wenlock, Gotland; dorsal, ventral, lateral, posterior, anterior views, $\times 3$ (new).—FIG. 997, 1f–i. **G. elongata* (DAVIDSON), Wenlock, United Kingdom; f–h, serial sections, $\times 5$; i, reconstruction of brachidium, $\times 5$ (new).
- Karbous** HAVLIČEK, 1985a, p. 236 [**K. aperinus*; OD]. Small to medium, smooth, rounded to elongate to subrectangular outline, ventribiconvex; beak inflated; small, anacline-hypercline area; apical foramen flanked by minute deltidial plates; rectimarginate to weakly plicate commissure; squared pedicle cavity; teeth with dental cavities, dental plates; hinge plate with cardinal pit, lacking process; inner socket ridges flat; crura, spiralia, jugal processes unknown. [Similar to *Glossia* internally but differing in larger size, ventribiconvex-planoconvex shape, lack of sulci on either valve, expanded anacline-hypercline area, foramen, small dental cavities outlining dental plates; distinguished from *Peratos* by small dental cavities, small area; distinguished from *Lissatrypa* by hinge plate with distinct cardinal pit, straight inner socket ridges, prominent dental cavities. HAVLIČEK (1990c, p. 159) stated that spiralia are dorsal, providing no figures; this is contradicted by *Glossia*-like hinge plate, tooth structure, but brachidia need confirmation.] *Lower Devonian* (Lochkovian–Emsian): western Europe, Urals, central Asia, ?China.—FIG. 997, 2a–f. **K. aperinus*, upper Emsian, Czech Republic; a–d, dorsal, posterior, anterior, lateral views, $\times 3.5$; e–f, serial sections, $\times 5.2$ (Havliček, 1985a).
- ?**Nanatrypa** SAPELNIKOV & MIZENS, 1982, p. 12 [**Lissatrypa* (Nanatrypa) *bisinuata* SAPELNIKOV & MIZENS, 1982, p. 13; OD]. Small, globose, rounded, biconvex; ventral, dorsal valve with well-developed median sulcus; minute, anacline area; small beak; minute apical foramen; deltidial plates undescribed; anterior commissure ligate, rectimarginate; internally thick shell apically; solid teeth, no dental cavities described; hinge plate divided by rounded cardinal pit; inner socket ridges *Glossia*-like; spiralia, jugal processes undescribed. [Homeomorphic with *Glossia*, which is occasionally ligate, i.e., bisinuate; lack of data on brachidia precludes comparison with Lissatrypinae or Glossiinae.] *Silurian* (Ludlow): Urals (eastern slopes), Czech Republic.—FIG. 998, 2a–e. **N. bisinuata* (SAPELNIKOV & MIZENS), eastern slopes, Urals; a–d, dorsal, ventral, lateral, anterior views, $\times 2$; e, polished section, $\times 5$ (Sapelnikov & Mizens, 1982).
- Peratos** COPPER, 1986b, p. 856 [**P. arrectus* COPPER, 1986b, p. 859; OD]. Medium to large, rounded to subquadrate outline, weakly biconvex; prominent orthocline area; strong protruding beak; apical foramen; prominent deltidial plates; rectimarginate commissure; thick shell wall; median septa lacking in either valve; large, subpyramidal dental cavities; long, straight dental plates; medially directed, barrel-shaped spiralia with 4 to 6 whorls; jugal processes posteromedial, terminating in large, spoon-shaped, incurved jugal plates. [Distinguished from *Karbous* by its large, orthocline area, biconvexity, internally by large dental cavities, free, straight dental plates; distinguished from *Glossia* in larger size, prominent orthocline area, lack of sulci, wide dental cavities, jugal processes.] *Middle Devonian* (Eifelian)–*Upper Devonian* (Frasnian): Europe, Urals (western slopes).—FIG. 998, 1a–h. **P. arrectus*, upper Eifelian, Germany; a–d, dorsal, lateral, anterior, posterior views, $\times 3$; e–g, serial sections, $\times 4$; h, reconstruction of brachidia, $\times 4$ (Copper, 1986b).
- ?**Trigonatrypa** HAVLIČEK, 1990c, p. 154 [**Meristella holynensis* HAVLIČEK, 1956, p. 613; OD]. Small to medium, triangulate-spatulate outline, widest anteriorly; weak anterior sulcus on dorsal valve; narrow, angular, apsacline-orthocone area; minute deltidial plates flanking apical foramen; rectimarginate commissure; thick shell wall; distally distinct dental cavities; possible dental plates; hinge socket plates delicate; jugal processes, spiralia undescribed. [Unusual for its triangulate shape, differentiating it from *Glossia* and *Karbous*, but spiralia undescribed; comparable in shape to *Tectatrypa*, which is more elongate; lack of data for brachidia makes assignment to Lissatrypidina or Atrypida questionable (possible rhynchonellide).] *Lower Devonian* (Emsian)–*Middle Devonian* (Eifelian): Czech Republic.—FIG. 997, 3a–e. **T. holynensis* (HAVLIČEK), Emsian; a–d, dorsal, ventral, anterior views, internal dorsal valve, $\times 3$; e, serial section, $\times 10$ (Havliček, 1990c).

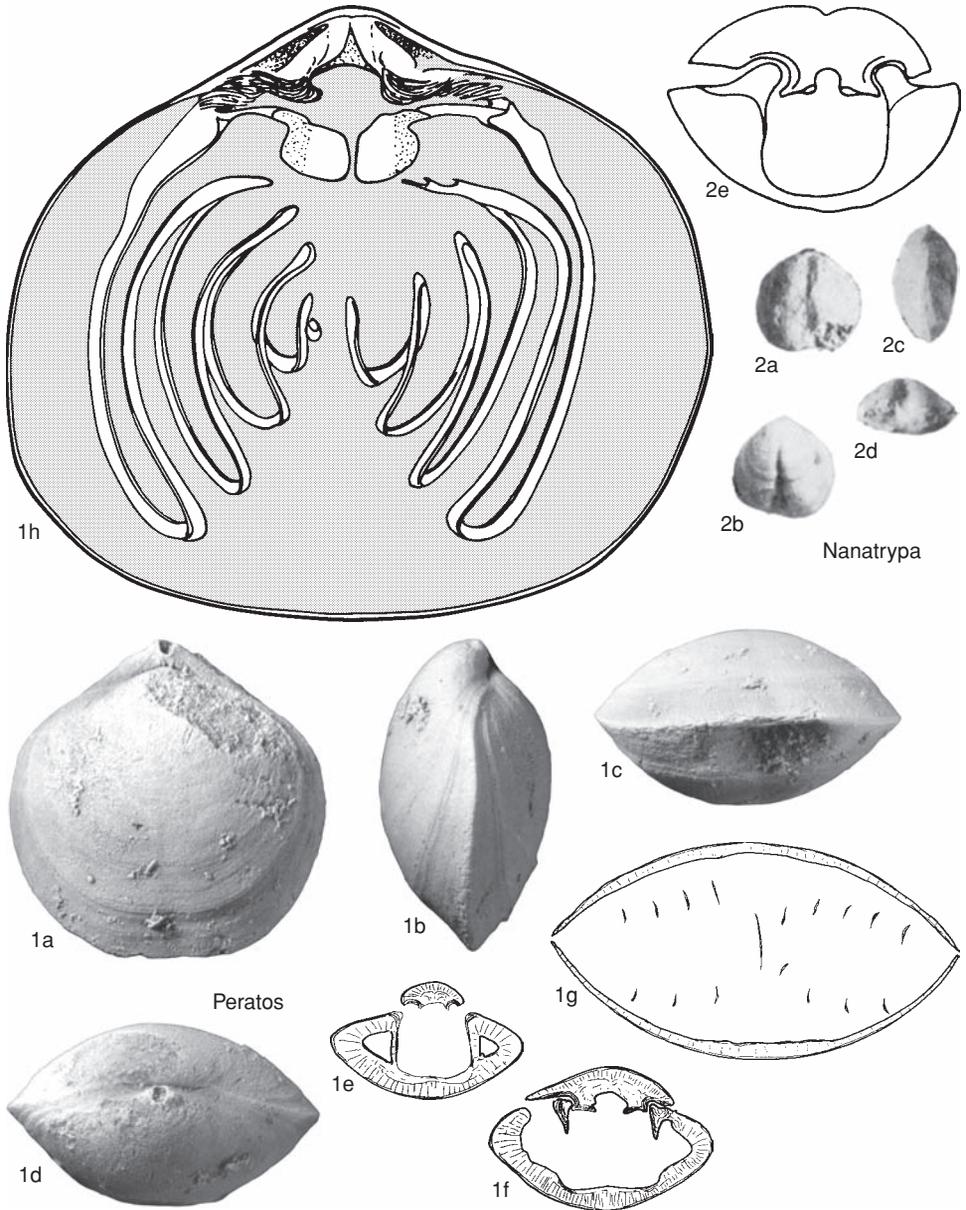


FIG. 998. Glassiidae (p. 1470).

Superfamily PROTOZYGOIDEA Copper, 1986

[*nom. transl.* COPPER, herein, ex Protozyginae COPPER, 1986b, p. 834; *emend.*, COPPER, herein]

Small shelled, smooth Lissatrypidina with medially directed spiralia of few whorls or less than 1 whorl, jugum, partial jugum, or no jugum. *Ordovician* (*Llandeilo–Ashgill*), *Silurian* (?*Llandovery*).

Family PROTOZYGIDAE Copper, 1986

[*nom. transl.* COPPER, 1995, p. 848, ex Protozyginae COPPER, 1986b, p. 834]

Protozygoids with small, ventribiconvex-planiconvex, thin-walled shell; sulcate to rectimarginate commissure; may be smooth to weakly corrugate or weakly ribbed; planar to conical spiralia with few whorls, or less than 1 whorl; jugum complete or incomplete, anterodorsal to medial. *Ordovician* (*Llandeilo–Ashgill*), *Silurian* (?*Llandovery*).

Protozyga HALL in HALL & CLARKE, 1893, p. 141 [**Atrypa exigua* HALL, 1847, p. 141; OD]. Small, rounded, normally smooth or slightly corrugate anteriorly, planoconvex-ventribiconvex; small, anacline-hypercline area; minute apical foramen; deltidial plates minute or absent; sulcate commissure; thin shell wall; teeth with large dental cavities; small cardinalia; crura delicate, ventrolateral; medially to mediadorsally directed spiralia, usually fewer than 3 whorls; ventrocentral, U-shaped jugum. [Differs from *Manespira* in spiralia of multiple whorls, complete jugum, posterior absence of corrugations.] *Ordovician* (*Caradoc*): worldwide.—FIG. 999,3*a–i*. **P. exigua* (HALL), lower Caradoc, New York, USA; *a–e*, dorsal, ventral, lateral, anterior, posterior views, $\times 5$; *f–g*, serial sections, $\times 5$ (Copper, 1986b); *h–i*, dorsal, lateral reconstruction of brachidium, $\times 10$ (new).

Manespira COPPER, 1986b, p. 839 [**Hallina nicolleti* WINCHELL & SCHUCHERT, 1892, p. 293; OD]. Small, rounded outline, ventribiconvex-biconvex-planiconvex; commonly weakly ventrocarinate; neanic shell smooth, adult corrugated anteriorly; weak, diverging midrib pair on ventral valve; commonly with small fold developed on dorsal sulcus; area minute; very small beak; minute foramen; deltidial plates unknown; unisulcate to bisulcate commissure; thin shell wall; minute teeth; small dental cavities; thin, narrow hinge plates; medially directed spiralia with 1 whorl or part whorl; anterior to central, complete or incomplete jugum. [Distinct from *Protozyga* in its very simple spiralia (usually 1 whorl or fewer), incomplete jugum, commonly more frequent corrugations along adult

commissure.] *Ordovician* (*Llandeilo–Caradoc*): North America, Europe.—FIG. 999,1*a–i*. **M. nicolleti* (WINCHELL & SCHUCHERT), lower Caradoc, Minnesota, USA; *a–e*, dorsal, ventral, lateral, anterior, posterior views, $\times 4$; *f–g*, serial sections, $\times 6$ (Copper, 1986b); *h–i*, reconstruction of brachidium, $\times 10$ (new).

Xysila COPPER, 1995, p. 848 [**X. astaca* COPPER, 1995, p. 849; OD]. Small, elongate, ventribiconvex, globose, noncarinate; hypercline area; small, inflated beak; transapical foramen; deltidial plates unknown; smooth shell lacking corrugations or ribs; commissure weakly sulcate to ligate; both valves usually with narrow median sulcus; interior with thick shell apically; minute teeth with dental cavities; strong dorsal septum; crura sharply laterally geniculated; medially directed spiralia; jugum beginning anteriorly, joining dorsocentrally. [Similar to *Cyclospira* in shape and medially directed spiralia, but possessing simple jugum, lacking corrugations along commissure. *Xysila* could be assigned to Cyclospiridae, if alternately derived from *Cyclospira* via later addition of jugum, but ancestry seems more probable with Protozygidae. *Xysila* probable ancestor to Glassiidae.] *Ordovician* (*Ashgill*), *Silurian* (?*Llandovery*): North America, *Ashgill*; western Europe, ?*Llandovery*.—FIG. 999,2*a–i*. **X. astaca*, Ashgill, Anticosti, Canada; *a–e*, dorsal, ventral, lateral, anterior, posterior views, $\times 3$; *f–g*, serial sections, $\times 5$; *h–i*, reconstruction of brachidia, $\times 5$ (Copper, 1995).

Family CYCLOSPIRIDAE Schuchert, 1913

[Cyclospiridae SCHUCHERT, 1913, p. 410; *emend.*, COPPER, herein]

Small, smooth or weakly corrugated, planoconvex-ventribiconvex-biconvex; sulcate to rectimarginate; medially directed spiralia of fewer than 4 whorls; jugum absent. *Ordovician* (?*Llandeilo*, *Caradoc–Ashgill*).

Cyclospira HALL in HALL & CLARKE, 1893, p. 146 [**Orthis bisulcata* EMMONS, 1842, p. 396; OD] [= *Triplecella* WILSON, 1932, p. 399 (type, *T. duplicata*, OD); *Aulidospira* WILLIAMS, 1962, p. 252 (type, *A. trippi*, OD); ?*Cyclorhynchia* BARANOV, 1994, p. 29 (type, *Cyclospira globosa* ROZMAN, 1964a, p. 189)]. Small, ventribiconvex-planiconvex, subtriangulate to elongate; strongly convex ventral valve, weakly convex to planar dorsal valve; small area anacline-hypercline; apical-transapical foramen; sulcate-bisulcate commissure; shell thickly walled; teeth solid or with small, slitlike dental cavities or nuclei; medially directed spiralia with normally fewer than 4 whorls; jugum or jugal processes absent. [Distinguished from homeomorphic protozyginids by absence of jugum; distinguished from *Rozmanospira* by presence of more than 1

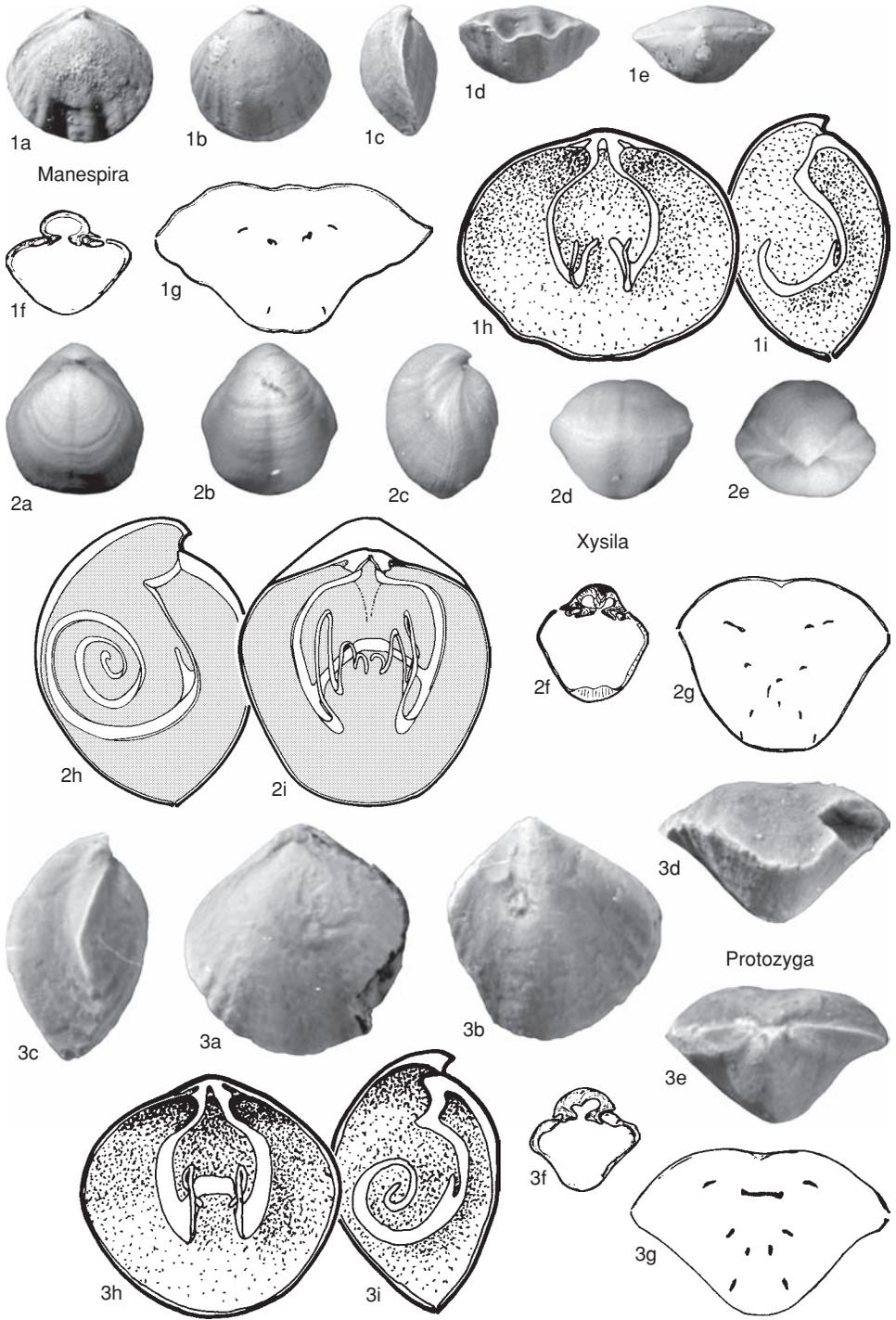


FIG. 999. Protozygidae (p. 1472).

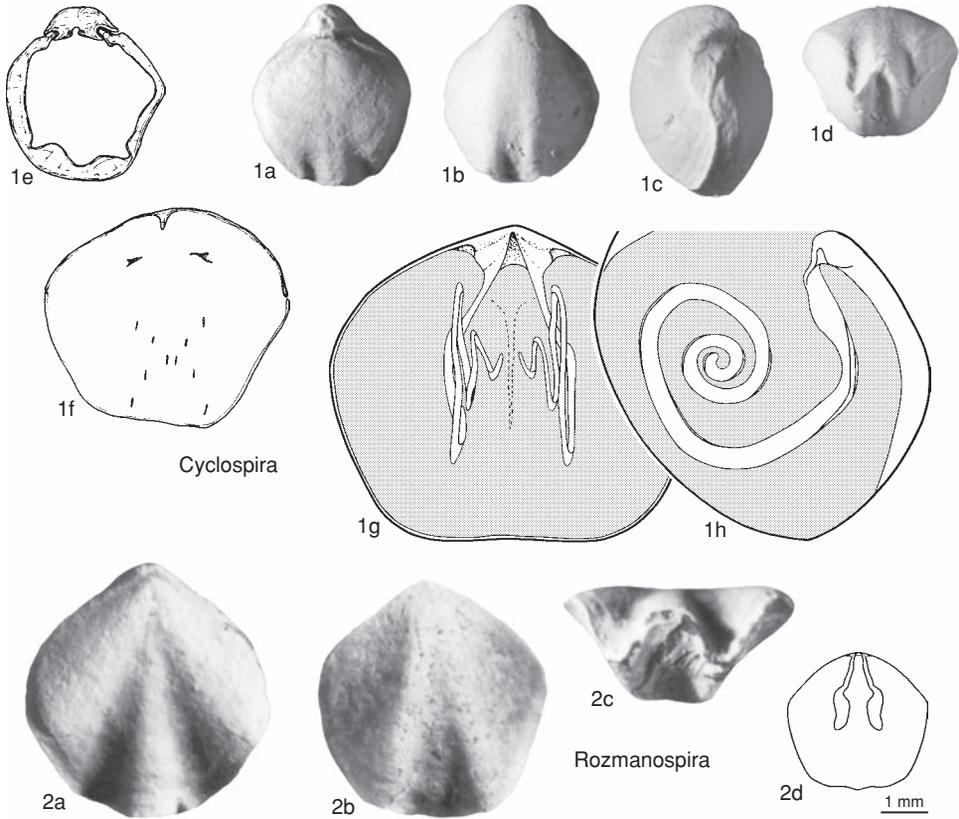


FIG. 1000. Cyclospiridae (p. 1472–1474).

spiral whorl. The synonym *Aulidospira* is also listed by ALVAREZ & RONG, herein, p. 1570, as a genus in the subfamily Meristinae, family Meristidae. See discussion of examination of type specimen in COPPER, 1986b, p. 849.] *Ordovician (Caradoc–Ashgill)*: North America, Eurasia.—FIG. 1000, 1a–h. **C. bisulcata* (EMMONS), upper Caradoc, New York, USA; a–d, dorsal, ventral, lateral, anterior views, $\times 3$; e–f, serial sections, $\times 5$; g–h, dorsal and lateral reconstruction of brachidia, $\times 5$ (Copper, 1986b).

Rozmanospira POPOV, NIKITIN, & SOKIRAN, 1999, p. 645 [**Oligorhynchia mica* NIKITIN & POPOV, 1984, p. 156; OD]. Cyclospirinid with minute, smooth

ventribiconvex shell, moderate to angular, dorsal anterior fold; small, incurved beak, minute pedicle opening; interior with short teeth, small dental cavities; divergent crura leading to medially directed, less than single revolution spiral whorl aligned in plane of symmetry; no jugum or jugal processes. [Differs from *Cyclospira* in its smaller shell, very simple partial spiral whorl.] *Ordovician (?Llandeilo, lower Caradoc–middle Caradoc)*: Kazakhstan.—FIG. 1000, 2a–d. **R. mica* (NIKITIN & POPOV), lower Caradoc; a–c, dorsal, ventral, and anterior views, $\times 10$; d, reconstruction of brachidium, $\times 12$ (Popov, Nikitin, & Sokiran, 1999).