PRODUCTIDA

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Order PRODUCTIDA Sarytcheva & Sokolskaya, 1959

[Productida Sarytcheva & Sokolskaya, 1959, p. 182]

This large and diverse order includes the biggest and most unusual brachiopods known. Characterization can, therefore, be difficult, but the order is described as follows.

Small to gigantic strophomenates with dorsal valves markedly smaller than ventral; corpus cavity in profile commonly concavo-convex to planoconvex, rarely conical or even resupinate; ears and trails commonly prominent, in some the latter elaborated into bordering structures, such as gutters; spines tubular and normally covering ventral valves, but may be restricted to hinge line; may also be present on dorsal valves, rarely absent, as in lyttonioids and some richthofenioids; radial ribbing common, rugae less so; dental plates absent; cardinal process normally present, prominent, some with a proximal shaft, bilobed with posteriorly facing recessed myophores; brachial ridges or more elaborate brachial structures variably present; anderidia present in chonetidines and earliest true productides; mantle canal markings rare; internal surfaces commonly endospinose; shell structure crested to cross-bladed laminar with pseudopunctae having taleolae, fine internal tuberculation common; in some large-sized taxa shell thickening produced a prismatic appearance in section. *Upper Ordovician (Cautleyan)–Upper Permian, ?Lower Triassic.*

Within the Productida are included those strophomenates that developed tubular spines. These developed at valve margins but continued growth after being left behind the margin. Some remained alive, containing growth tissue, during long periods of ontogeny. These spines are unlike those found in some rhynchonellides or other orders. We include chonetidines, true productidines, strophalosiidines, which include aulostegoids and richthofenioids, and the lyttoniidines. Rarely the spines were lost, especially in cemented species during the Permian.

PRODUCTIDA EXCLUDING THE CHONETIDINA

History

Classification of this group has always been problematical, with specialists such as Thomas Davidson (1861) commenting on the existing confusion and Girty (1909, p. 230) remarking upon "the abundant intermediate stages" to be found between what would be considered as distinct species. In 1918 Janischewsky's opinion was that productids were the most complex of brachiopods and incapable of being clearly classified. In 1928, however, Muir-Wood gathered 41 species and varieties together and discussed the use of 8 genera within what would today probably be recognized as 4 different families, but only representing a small proportion of the Productida. Sarytcheva (1937, 1949), Sokolskaya (1948), Sarytcheva and Sokolskaya (1952), and Sarytcheva and others (1963) published descriptive works. Sarytcheva, Licharew, and Sokolskaja (1960) wrote the Productida section of the Russian *Treatise on Brachiopods and Bryozoans* (*Osnovy*), which provided a classification of the whole of the Productida, including the Chonetacea. The *Osnovy* included lyttonioids but not the few genera based on *Gemmellaroia,* which Williams (1953b) had placed with the orthotetaceans. Also in 1960, however, and a few months prior to publication of the Russian *Osnovy,* Muir-Wood and Cooper (1960) published a monograph on the Productoidea, a superbly illustrated book, thanks to Cooper's photographic expertise, and one that described 167 genera, divided between 11 families within the Productacea and 8 within the Strophalosiacea, including the conical Richthofeniidae and Scacchinellidae. They reintroduced the Gemmellaroiinae into the

Richthofeniidae because of their anchoring spines. Their work formed the basis, presented by MUIR-WOOD, for the Productidina section of the brachiopod *Treatise on Invertebrate Paleontology* (WILLIAMS & others in MOORE, 1965). At that time the suborder was divided into two superfamilies, following the 1960 pattern, and WILLIAMS added the Oldhaminidina (including the Lyttonioidea). Not surprisingly the *Treatise* and its forerunner (MUIR-WOOD & COOPER, 1960) stimulated a spate of studies so that by the early 1990s the number of nominal genera had risen to about 500, many of which could not easily be fitted into either the Russian (SARYTCHEVA, LICHAREW, & SOKOLSKAJA, 1960) or international (MOORE, 1965) published classifications.

The uncertain taxonomic position of the gemmellaroiids has again been challenged by GRANT (1993a), who usefully pointed out the normal operation of the dorsal valve in *Gemmellaroia* but assigned the group of four genera back to the orthotetides, believing them to lack spines and have koskinoid perforations. GRANT (1993a) stressed the taxonomic importance of koskinoid ventral umbonal perforations, but their true nature has been questioned by WILLIAMS and BRUNTON (1993), who suggest they are secondary borings. Further study reveals that *Loczyella* belongs with the Permianellinae of the Lyttonioidea, while the probable spinose exterior of *Gemmellaroia* means it should remain in the Richthofenioidea. The fate of the remaining two genera is unclear, but for the time being we retain *Tectaria* and *Cyndalia* in the Productida, although the latter only questionably.

Various problems attended previous classifications. First, the early evolution of the group, in the Early and Middle Devonian, was poorly known, so it was impossible to determine clear lineages. Second, and partly because of the above, groupings were the result of similar morphologies rather than lineages or the study of variations in morphological features in time and space. Although in the 1965 *Treatise* homeomorphy was featured and the similarities between some Carboniferous and Permian genera were listed, the separation of genera to different families lacked clear explanation. Third, some of the characters selected as important in the 1965 classification have proven to be variable and hence difficult to use; for example, the cardinal process changed during ontogeny and by adulthood is also variable in detail. On the other hand the shape and depth of the corpus cavity (see below) were rejected as a useful character. This was because in grouping genera with superficial similarities, without considering ancestry, taxa of different lineages were brought together that had different adult corpus cavity depths. Here we find corpus cavity depth a valuable characteristic when considered in conjunction with other characters of the shell and its evolution.

Much excellent descriptive work has been published during the last 30 years, and this, together with the earlier monographs, has allowed us to take a new look at the classification of the Productida. We accept the importance of corpus shape and the forms of growth stressed by Russian brachiopod specialists but also the value of internal and external features such as ribbing, rugation, spine distributions and styles, lamellae, the various ridges bounding the corpus cavity internally or positions of muscle scars, as well as the basic adult form of the cardinal process.

Since the 1965 edition of the brachiopod *Treatise* there have been few attempts to reclassify productides, and those of COOPER and GRANT (1975) or WATERHOUSE (1978), based largely on Permian faunas, made some changes. The former retained the Productidina with four superfamilies (Strophalosiacea, Aulostegacea, Richthofeniacea, and Productacea). WATERHOUSE (1978) raised the group to ordinal level with two suborders, the Productidina (divided into Productellacea, Productacea, and Linoproductacea) and Strophalosiidina (divided into Strophalosiacea, Richthofeniacea, and Aulostegacea, into which he included some genera assigned here to the Echinoconchoidea in the Productidina). LIANG (1990), also studying Permian brachiopods, proposed a classification

for the phylum that, like COOPER (1944), divided the inarticulated and articulated brachiopods into impunctate and punctate divisions, including two orders of productides, in the belief that they too included an endopunctate group; this scheme has not gained support, and it is felt (in the absence of any direct electron-microscopic study) that his punctate structures in productides are a form of pseudopunctation.

Present situation

The number of pre-Frasnian, Devonian productidine genera has increased from about 3, described in 1965, to 11 by 1993. This information has allowed the reconstruction of three major lines of evolution in the Productidina: the Linoproductoidea, Productoidea, and Echinoconchoidea, all of which proliferated near the Devonian to Carboniferous boundary into many more families and subfamilies. This evidence allows a phylogenetic classification by building lineages of species and genera. This technique led to the recognition of many homeomorphic parallel lineages with different origins, and in consequence some large groups have been divided into smaller taxa. For example, the Margiferidae of the 1965 *Treatise* involved 4 subfamilies and a total of about 21 genera united by somewhat similar morphologies, namely, tendencies toward smallness, sparse but symmetrically situated spines, and internal marginal ridges. In detail, however, diagnoses within subfamilies proved to be inconsistent. We now recognize that those 21 genera are distributed in taxa having their origins in 4 different subfamilies and 2 families of the new classification (see BRUNTON, LAZAREV, & GRANT, 1995).

Studies of the brachiopod genome by COHEN and GAWTHROP in the first volume of the revision of the brachiopod *Treatise* (1997, p. 189) indicate that the genome is small as compared to some other invertebrates, implying that it is probably not rich in repetitive sequences. The relationship between genome size and diversity of morphology, however, remains to be established; so for the present we can only speculate on any direct relationship between a small genome size and tendency toward repetitions of morphological features through time. In practice a consequence of the recognition of many reintroductions of morphologies in the same or different lineages is that we cannot fit our identified suprageneric taxa within the 4 levels of classification available between the suborder and subfamily while maintaining anything close to a phylogenetic structure. For instance one of the longest ranging and most diverse groups in the Productoidea is the Productellidae, starting in the Early Devonian and becoming extinct at the end of the Permian; it consists of 5 subfamilies, all probably with independent origins from the Productellinae stem group, and then about 20 subgroups ranging from 3 to about 20 genera (in a total of over 100 genera), which we cluster into tribes (see BRUNTON, LAZAREV, & GRANT, 1995, and BRUNTON & LAZAREV, 1997). This category has been used occasionally in the past for brachiopods and, more commonly, in other organisms for subfamilial generic groupings; it is recognized by the International Commission on Zoological Nomenclature with the termination -ini.

Morphology

Depth and shape of the corpus and its relationship to ears and trails are useful characters. Definitions of terms, however, such as visceral disk, body or visceral cavity, and trail, have been used differently by authors and lack precision (but see Morphological and Anatomical Terms Applied to Brachiopods, WILLIAMS, BRUNTON, & others, 1997, p. 423). Growth studies of deep productidines demonstrate that ventral and dorsal valves grew at different speeds, that ventral trails correspond in a stable relationship only with dorsal trails in adulthood, and that the former originated posteriorly at the anterior margin of what has been called the ventral visceral disk. It is important to be able to define unequivocally the complete shell cavity exclusive of its peripheral cavities, where the ears and trails are located, so as to provide a measure of its depth. Thus the corpus (Fig. 230, and see BRUNTON, LAZAREV, & GRANT,

1995) includes the body (or visceral) cavity plus the mantle cavity. The term can be used for the description of external surfaces or this cavity between the valves. Peripheral cavities are marginal to and commonly partially separated from the corpus by marginal structures, usually ridges of secondary shell material.

The ventral trail, *sensu lato,* started growth on the ventral corpus at a point marked on the shell lateral profile (commonly best seen in median section) by a tightening of the spiral growth curve that, in different species, produced anything from a slight change in curve to a true geniculation. At this geniculation point the ventral surface ornamentation commonly changed to one that continued to the anterior margin. As adults the ventral and dorsal trails grew more or less parallel to each other, forming the slitlike gape through which seawater was circulated to the mantle cavity. The ventral trail can be differentiated into two regions: posteriorly the region of preadult growth, which started at the geniculation point and was confined to the corpus; and the true adult functional ventral trail extending beyond the corpus. The dorsal and ventral visceral disks become specifically defined as those areas of the corpus posterior to the origins of trails. Normally, in deep shells, the anterior margin of the ventral visceral disk can be defined by a radius of curvature centered on the hinge axis equal to the dorsal visceral disk length (Fig. 230). The situation differs in shallow, strongly concavoconvex shells, because the two valves follow closely similar growth curves and in consequence are approximately equal in surface length. Any change in their growth spiral, seen in lateral profile, was slight and occurred at about the same position on both valves; consequently the visceral and trail areas of these shells are poorly differentiated and of similar curved lengths.

As in living brachiopods, the corpus cavity of productides can be divided into the posterior body cavity containing the body organs of the animal, and the anteriorly placed mantle cavity containing the lophophore. All evidence indicates the presence of a normal, anterior body wall composed of inner mantle epithelium (Williams, 1956), which in all probability was ciliated where it lined the mantle cavity. The disposition of the anterior body wall, separating the two cavities and in all probability accommodating the median mouth section of the lophophore, has been questioned for over a century. Until recently there has commonly been an assumption that this body wall extended posterolaterally toward the hinge extremities (e.g., Brunton, 1982). Lazarev (1985) suggested a more centrally confined position for the body cavity in buxtoniids. This interpretation was based on the presence of paired ridges anterior to the cardinal process, which possibly supported the body wall, and the rather similar microornamentation of the dorsal valve interior both anterior and posterior to the brachial ridges (widely accepted as areas from which the lophophore was suspended), perhaps indicating that both areas accommodated the mantle cavity. This microornamentation is a mixture of small pits and tubercles, which have been likened to shagreen, and occurs also in some ventral valve umbos, as in some productids. Since then, study of other productides and strophomenides supports the view that the body cavity was confined closely around the cardinalia and dorsal muscle scars, with lateral and anterior regions of the body wall connecting across the corpus cavity just

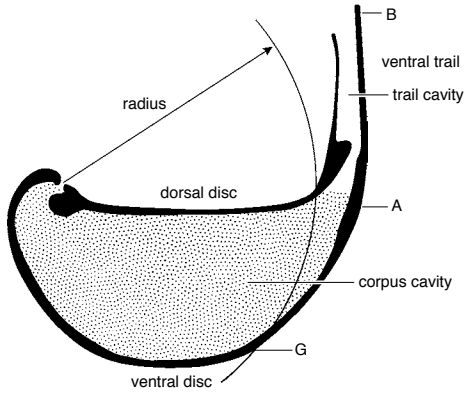

Fig. 230. Median section of adult productidine with deep corpus cavity; from points *A* to *B,* adult ventral trail; from *G* to *A,* anterior region of corpus from point of geniculation (*G*), representing earlier ventral trail growth; the region posterior to *G* is ventral disc; radius from hinge axis representing dorsal disc length prior to geniculation (new).

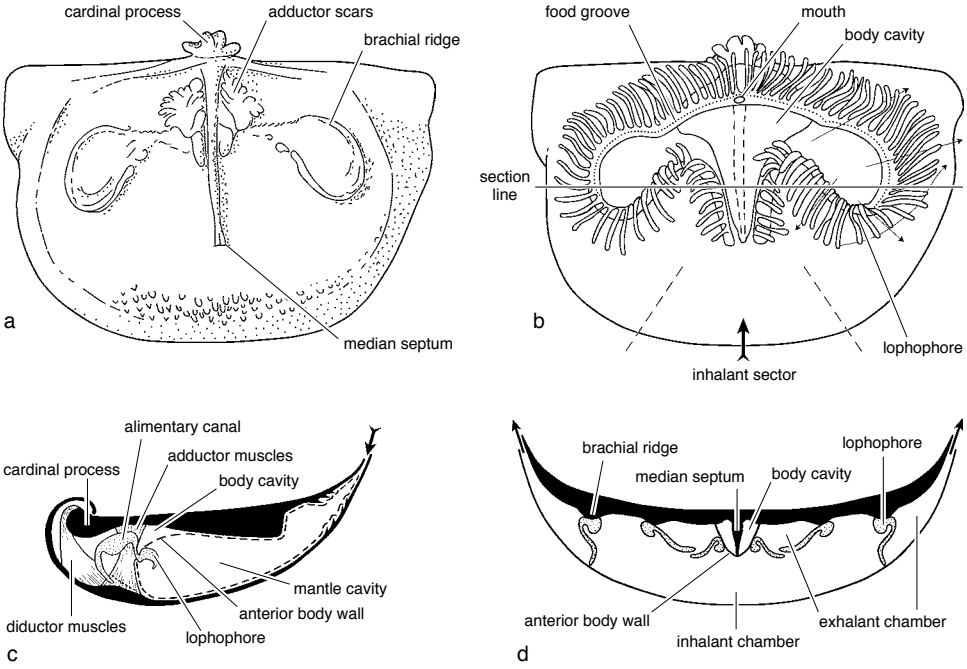

FIG. 231. *a,* dorsal valve interior of productoid, based on *Reticulatia; b,* stylized reconstruction of lophophore and body cavity region (*shaded*); *c,* median longitudinal section of shell showing inferred main musculature, mantle epithelium, and body wall with lophophore and alimentary canal; *d,* cross section of shell indicating ventromedian inhalant and more dorsally situated exhalant water chambers separated by lophophore. Inhalant *arrows* have tails; water current entered anteromedianly, down narrow trail region, into ventral part of mantle cavity from where it passed between tentacles, from food groove side, to exhalant chamber and lateral margins of shell (new).

anterior to the positions of the diductor muscles (Fig. 231a,b). This disposition of the body cavity leaves more space posterolaterally for extensions of the mantle cavity behind the posterodorsal attachment areas of the lophophore, thus allowing the posterior elements of the lophophore to have passed water posteriorly between their tentacles in the same direction (relative to the tentacles) as in all known living brachiopods. This position of the body wall implies that the mantle epithelium formed much of the posterior hinge margin. These surfaces probably were not fused, leaving the posterior margin potentially open to the sea, especially as the valves moved relative to each other during growth, tending to leave gaps at the posterior margin. These were closed by the growth of a variety of shelly ridges, such as cardinal ridges, the ginglymus or interarea, the lophidium, and modifications of the external surface of the cardinal process within the delthyrium of some strophalosiidines. Many of these structures helped articulate the valves as well as provide better seals at the hinge line.

The concept of the mantle cavity extending posteriorly has been applied in other possible strophomenates, such as clitambonitaceans (WRIGHT, 1994b), in which mantle canal-like markings were recognized on internal surfaces of the interareas.

Mantle canals are rarely, poorly, or questionably preserved in productides. In chonetidines, traces of vascular trunks were described by MUIR-WOOD (1962) in the middle of ventral valves of *Neochonetes;* and, although these ridges are unlike the depressions left by mantle canals in well-authenticated genera, similar structures can be found in several Carboniferous and Permian genera. In productidines ROBERTS (1971) described fragmentary traces of canals in the dorsal

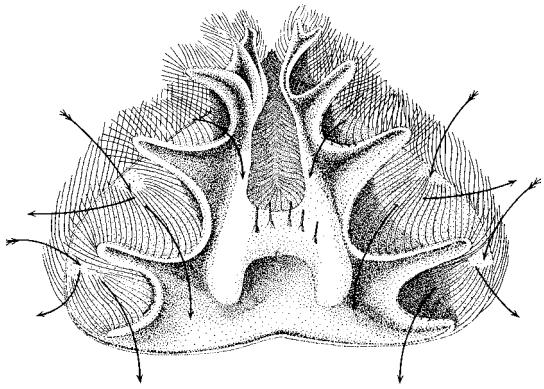

FIG. 232. Falafer calcified brachidium and reconstructed lophophore of small Permian aulostegid lacking trails; shells probably opened as in living thecideidines, capable of raising dorsal valves widely to expose lophophore and able to create a lateral inhalant water current (adapted from Grant, 1972).

valves of *Lomatiphora,* but these may be the internal representations of external ribbing in these thin-shelled specimens. BRUNTON (1966), in a general discussion on productoid morphology, wrote of a possible pinnate system associated with the marginal ribbing of adult shells. In more recent years the internal disk areas of many productidines, characteristically patterned by minute tubercles and pits, are interpreted as underlying the positions of gonadal tissue in the mantles. If so, at least some productidines had spreading saccate canal systems, which may have terminated distally in fine radiating canals between the radially aligned endospines and tubercles commonly seen at visceral disk margins and on trails. There seems to be no evidence for median canals or canals surrounding the gonocoel. The remaining groups of Productida have even less evidence of mantle canal systems.

In the Productida the form of the lophophore and pattern of water circulation within the mantle cavity remained enigmatical for a long time; even the function of the brachial ridges was questioned. Now it is generally agreed that these ridges reflect the attachment areas of a simple schizolophe or the basal course of a more strongly folded ptycholophous falafer type of lophophore, as described by GRANT (1972). The falafer style of lophophore is known in small, deep corpus strophalosiids and was supported on a calcified brachidium (Fig. 232). Whether this type of lophophore was universal in all productides with deep corpus cavities is unclear, but there is no direct evidence in pre-Permian species; and it may be that it was confined to small attached species lacking long trails. In these small species an efficient water circulation system would have entered laterally with the main exhalant current anteromedianly. Currently there is no universal agreement on the possible water circulation systems in productides. In chonetids and productides with a shallow corpus, however, (perhaps also in other deep species with trails) the shallow cavity could not have accommodated a falafer lophophore; and a simple schizolophe, following the brachial ridges, is more likely (Fig. 231b). Assuming that fossil brachiopod lophophores worked as do all those in living species, that is, with water passed between the lophophore tentacles from the brachial (food) groove surface to the outer surface, the disposition of tentacles around the schizolophe requires the inhalant current to have been anteromedian with the exhalant currents laterally positioned, as suggested by BRUNTON for chonetids (1972) and some productides (1982; Fig. 231d). A water circulation system like this is seen in living juvenile species during their schizolophous growth stage, although by adulthood the circulation changed to the median exhalant current typical of plectolophous species. The alternative view, with a median exhalant current, has been

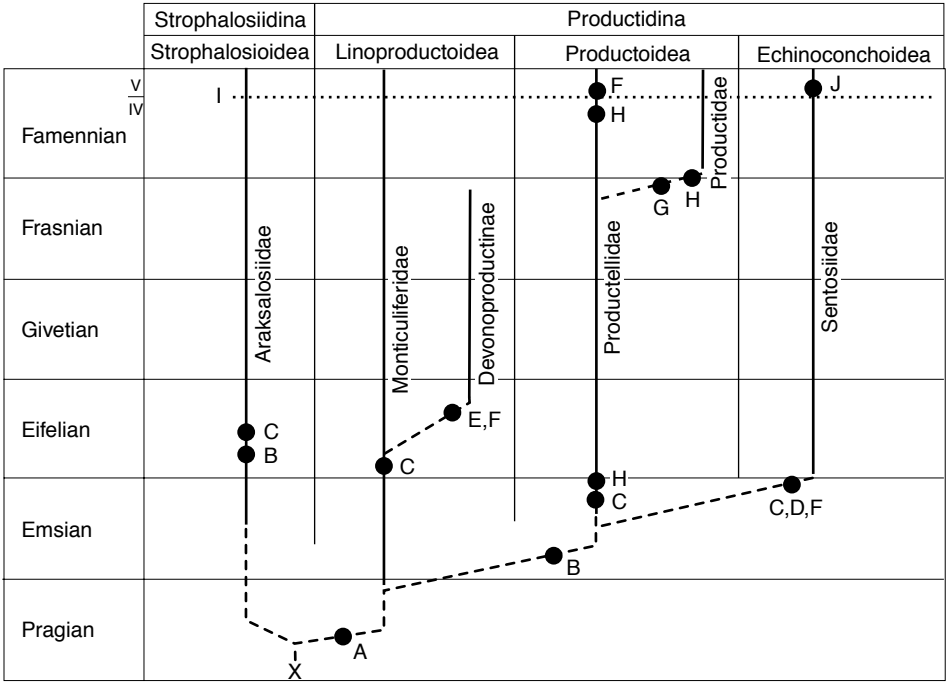

FIG. 233. Major morphological changes during Devonian of Productida, giving rise to Productidina and Strophalosiidina and their superfamilies and families; character changes identified by letters *A* to *J; A,* loss of interareas; *B,* loss of fine, chonetid-like ribbing; *C,* loss of anderidia; *D,* development of dorsal spines (unimportant in strophalosiidines); *E,* development of serial dorsal lamellae; *F,* development of marginal structures; *G,* development of deep corpus cavity; *H,* introduction of anterior ribbing; *I,* loss of toothed articulation in Productidina; *J,* first differentiation of spines into bands; *X,* chonetidine ancestor from which spread of spines over ventral valve gave rise to Productidina and Strophalosidina (new).

suggested by LAZAREV (1996) in the Yakovleviini. (For development and function of lophophores, see the lophophore section of the chapter on anatomy in the first volume of the Brachiopoda revision, WILLIAMS & others, 1997, p. 110–120.)

Recently differences between the cardinal processes of productides and some other strophomenates as compared to the cardinal processes of many other rhynchonelliforms were discussed by BRUNTON, ALVAREZ, and MACKINNON (1996). An important characteristic of the cardinal process of productides is the traces, commonly preserved on their external (dorsal) faces, of relic myophores indicating the dorsal attachment positions of paired diductor muscles during ontogeny.

Morphological changes

Early Devonian productides retained some chonetidine characteristics, such as anderidia found in *Ralia, Eoproductella,* and *Chattertonia* in the Strophalosioidea, Linoproductoidea, and Productoidea respectively and a fine radial ribbing that persisted throughout most of the linoproductoids (Fig. 233). These shared characters indicate a common ancestry (monophyly in the sense of SIMPSON, 1961) for the whole group. Spines were restricted to the hinge line in chonetidines, but spread to the rest of the ventral valve in true productides. At an early stage, probably within the Lochkovian or Pragian, loss of the interarea differentiated the Productidina from the Strophalosiidina. This separation was further marked by the tendencies for the cardinal process in productidines to grow posterodorsally, curving into the ventral umbo, while that of strophalosiidines grew posteroventrally (Fig. 234). In the Emsian (e.g., *Chattertonia,* an early productellid in the Productoidea) the

ancestral fine radial ribbing was lost and anterior ribbing developed, which became coarse in the latest Emsian (e.g., *Spinulicosta*). Specimens in the late Famennian developed ribbing that started more posteriorly, and by the middle Tournaisian it originated near the umbo, as in some lineages of the Productidae. By the Eifelian spines had developed on dorsal valves and *Caucasiproductus* (in the Sentosiidae) introduced the Echinoconchoidea. LAZAREV (1989) described the systematics of Devonian Strophalosiidina, and in 1990 he published details of the evolution and systematics of the Productidina.

Late in the Famennian, between the European Zones IV and V, important changes occurred. Until then productidines retained a toothed articulation, similar to that of the strophalosiidines, but from then on teeth and sockets were lost from all productidine lineages (Fig. 233). Early in the Famennian, within the diverse Productoidea, the Productidae arose from their stem group, the Productellinae, by a deepening of the corpus cavity in the relatively smooth leioproductines, which evolved in the Early Carboniferous into the ribbed and reticulate genera of the Dictyoclostinae and Productinae. Early in the Early Carboniferous some of these deep productids, the Buxtoniinae, also developed spinose dorsal valves. These trends toward spinose dorsal valves and deeper corpus cavities are also seen in some Early Carboniferous Productellinae, in some Plicatiferinae, and in Marginiferinae. At much the same time corpus depth increased in the Echinoconchoidea and slightly later (Viséan) in the Linoproductoidea, but although it was a widespread trend in the former, in the linoproductoids shallow genera of the Monticuliferidae continued through the Permian. Similar trends are seen in the Productellidae and Productidae.

By the Early Carboniferous most characteristics had been introduced into the Productidina. More varied and widespread ecological conditions in the Viséan and again in the Early Permian seem to have resulted in a proliferation of diversity, commonly resulting from recombinations of characters, character evolution, or loss. In most lineages these changes occurred several times, leading to much parallelism. Within Carboniferous and Permian Productidina a few novelties arose, such as nasute or tubiform trails, gigantism, external monticules, or the direct evidence for the acquisition of a complex ptycholophe suspended from the falafer brachidium in some Permian species with deep corpus cavities. These changes in development of the lophophore were probably in response to the need for greater capacity in the food- and oxygen-capturing mechanism

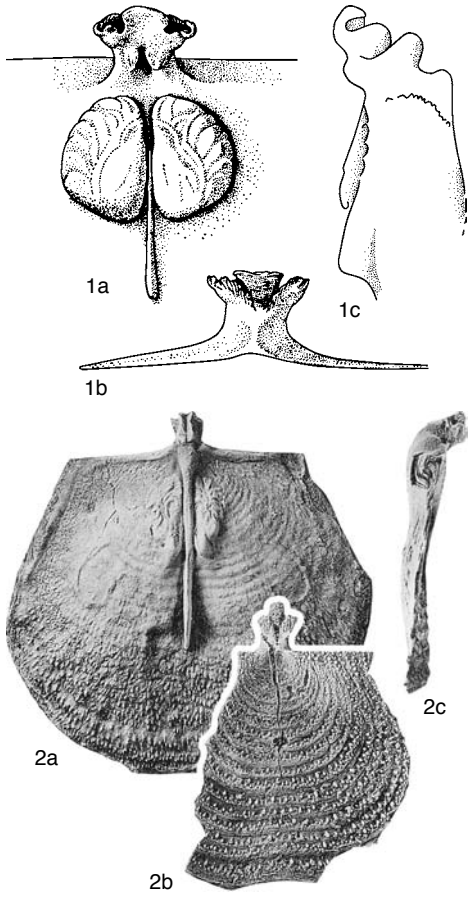

FIG. 234. Cardinalia showing dispositions of cardinal processes; *1a,* internal, *1b,* external (adapted from Muir-Wood & Cooper, 1960), and *1c,* lateral views (new), typical of strophalosiidines, based on *Edriosteges,* with posteroventrally directed cardinal process; *2a,* internal, *2b,* external, and *2c,* lateral views typical of productidines, based on *Echinaria,* with posterodorsally directed cardinal process (adapted from Muir-Wood & Cooper, 1960).

of the lophophore. This depends on cilia covering the tentacles, so the greater number of tentacles capable of being housed on the lophophore, the greater its food-gathering capacity. In order to increase feeding area the tentacles had to lengthen or the lophophore had to lengthen to accommodate more tentacles and become folded within the mantle cavity. This required a deepening of the shell. The unresolved question is whether a simple schizolophe, perhaps with long tentacles, persisted in deep shells with the falafer type of lophophore restricted to its known occurence in small Permian strophalosiidine species, or whether an unsupported ptycholophe could have evolved along with the deepening of the corpus cavity in the latest Devonian?

It is in the Strophalosiidina and lyttoniidines that the most unusual and extreme morphologies are found. The Strophalosioidea remained relatively conservative from their Early Devonian origin; interareas were reduced in many of the Araksalosiidae and in the Chonopectidae, in which spine cover was also reduced, but for the rest there were variations in spine cover and style, radial and concentric ornamentation. The Aulostegoidea, with its origin in the early Carboniferous, lost its toothed articulation, developed shallow and deep species, and some developed elaborated trails as flanges, gutters, and even complex needlelike spinose margins, such as in the Lower Permian *Chonosteges.*

Richthofenioids, characterized by their conical shapes in which the dorsal valve commonly was positioned within the ventral cone, seem to have had their origin in a mid-Carboniferous aulostegoid (Sutherland, 1996; refer to the section on the Richthofenioidea, herein, p. 610). Diversity in the form of ventral valve marginal growth is also seen in some richthofeniids that developed a characteristic meshwork covering the aperture of the cone, called the coscinidium. This structure created a protected area of sea water into which the lophophore was extended while feeding and is characteristic of several later genera in most families. A consistent feature within the superfamily is the form of articulation in which knobs (tegula) at the lateral extremities of narrow dorsal hinge lines fit into corresponding cavities at the dorsal edge of the posterior margin of the ventral corpus cavity. Associated with their conical shape is the myocoelidium in ventral valves of the Richthofeniidae, which probably accommodated the ventral ends of the diductor and adductor muscles (Rudwick & Cowen, 1968). In other families this structure is replaced by a median septum or muscle platform.

In the Late Carboniferous the most extreme modifications occurred, probably in a strophalosiidine, giving rise to the Lyttoniidina. The relationships of this group were discussed by Grant (1972) where it was noted that the late Triassic Bactryniidae was unrelated to the lyttoniids and removed to the Thecideidina. Thus now it is almost certain that few, if any, post-Permian productides existed (but see Shen & Shi, 1996). The morphology and phylogeny of the lyttoniidines are outlined by Williams, Harper, and Grant in the introduction to that suborder (herein, p. 619).

We recognize many problems remaining in the classification of the Productida, and in particular the Strophalosiidina has yet to be studied phylogenetically in order to unravel the lineages from homeomorphic groupings.

Terminology

Terms herein emended or added since 1965, in the first edition of the brachiopod *Treatise,* follow.

Bordering structures. An informal general term covering any structure developed at the valve or trail margins in adulthood, such as flanges (Morphological and Anatomical Terms, Williams, Brunton, & others, 1997, p. 430) or gutters.

Cardinal ridge (Morphological and Anatomical Terms, Williams, Brunton, & others, 1997, p. 426). Ridge extending along the dorsal valve posterior margin from the cardinal process base (Fig. 235.2), as compared to lateral ridges, which diverge from the hinge line (Fig. 235.1).

Corpus (Morphological and Anatomical

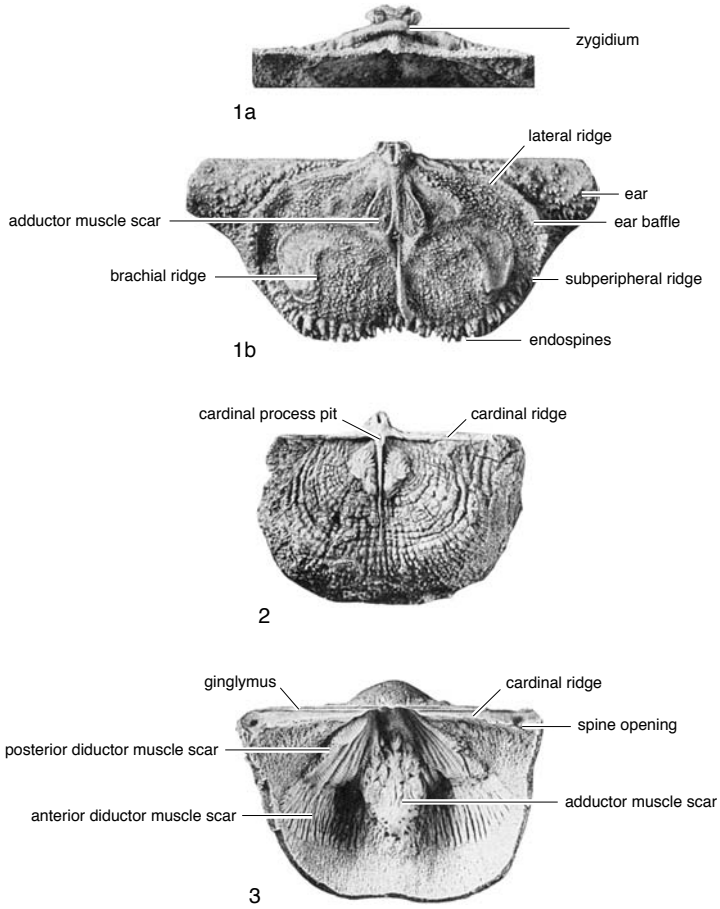

FIG. 235. Productidine internal morphology; *1a, Paucispinifera* dorsal valve, exterior of cardinal process, *1b,* interior; *2, Buxtonia* dorsal valve interior; *3, Inflatia* ventral valve interior; ginglymus here weakly developed; ear baffle and subperipheral ridge form marginal structures of dorsal valve corpus (new).

Terms, WILLIAMS, BRUNTON, & others, 1997, p. 427). Those areas of the valves enclosing the corpus cavity, the area occupied by the body cavity (p. 425) and mantle (p. 433) cavities, but excluding the peripheral cavities separating the dorsal and ventral ears and trails (Fig. 230).

Marginal structures. An informal description including structures forming part of the margins to the corpus cavity, helping to differentiate it from the ears and trails. Such structures are not at the valve edges. The term includes lateral ridges, ear baffles, and any marginal or subperipheral ridges or structures such as cinctures.

Peripheral cavities. A general informal description for any cavity distal to the corpus cavity and narrowly enclosed by ears and trails in productides and some strophomenoids or by other shell extensions in groups such as athyridids.

Many productide features are linked: strongly developed lateral ridges and ear baffles commonly correlate with well-differentiated corpus and peripheral cavities; prominent dorsal lateral ridges correlate with lines of external ventral spines diverging from the hinge line or marking the posterior limit of spines on the ventral valve.

In diagnoses we use size terms as general indicators in some taxa. These relate to the maximum width of the corpus, not including

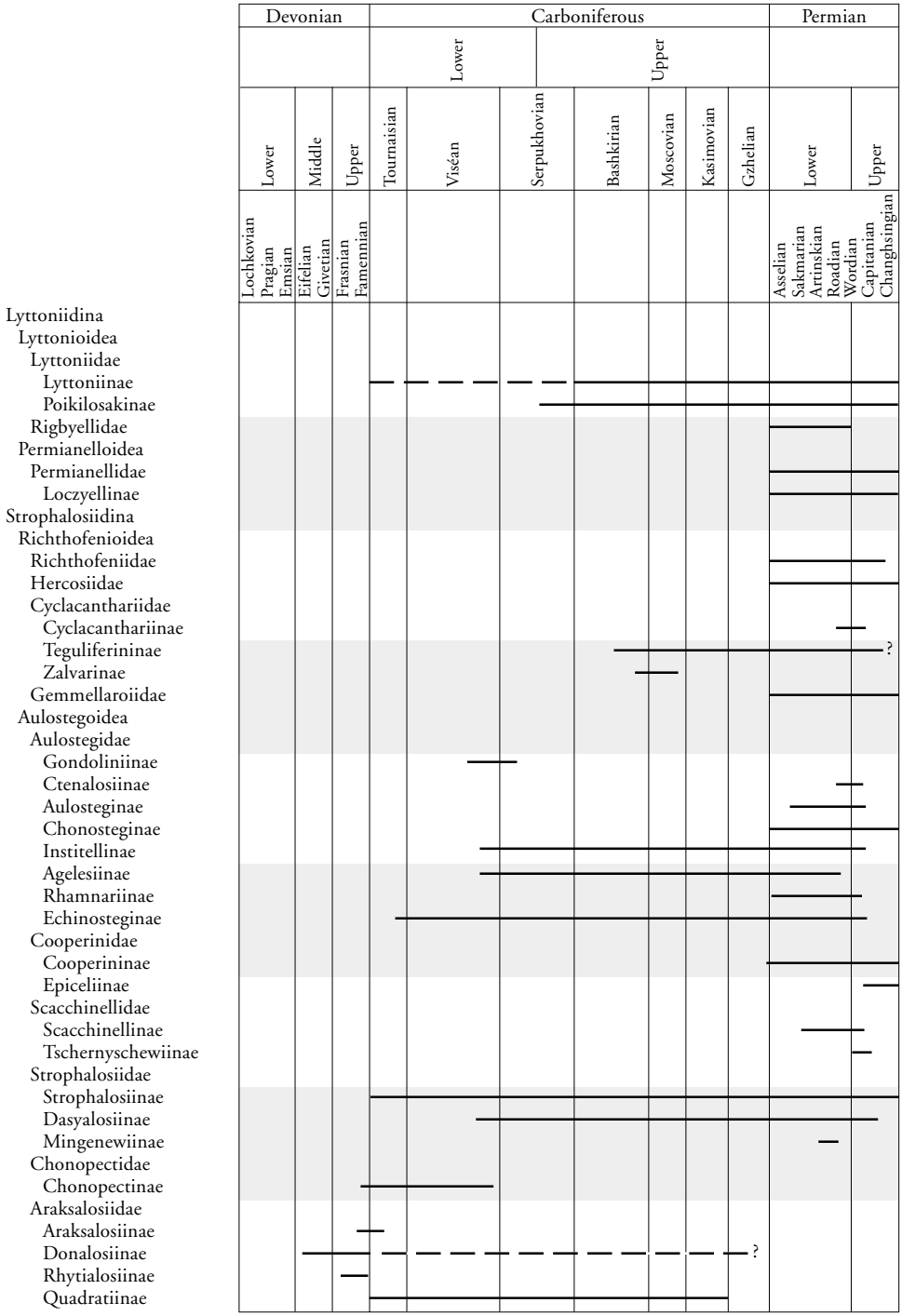

FIG. 236. Resume of classification of non-chonetidine Productida to subfamily levels and their stratigraphic distributions; *, Productininae ranges questionably into the Triassic (new).

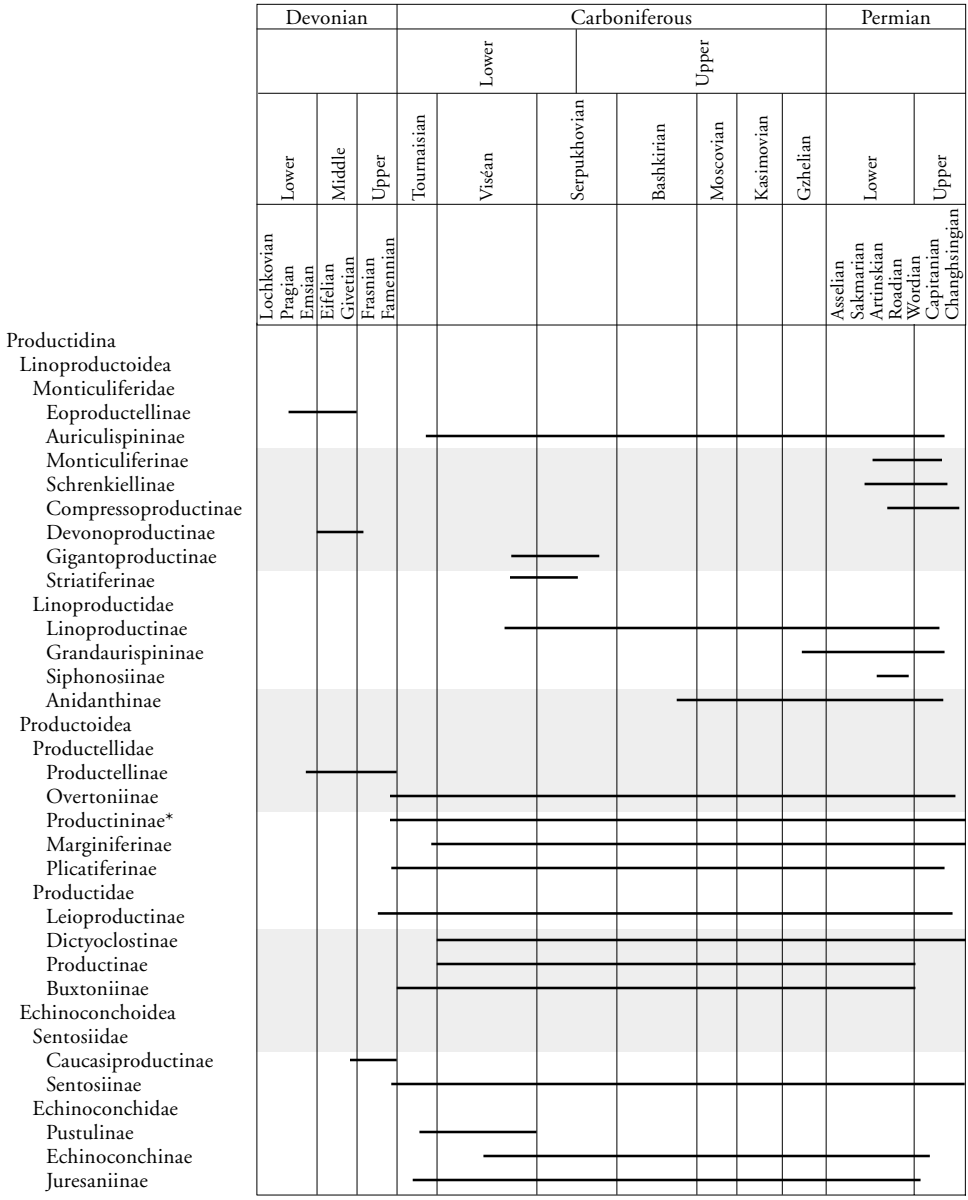

FIG. 236. *Continued.*

ears. We find this measure to be the most consistent, and it can be used on broken shells even when their peripheral cavities have been lost. The size terms used are: small: shells up to 20 mm wide; medium: shells more than 20 mm and up to 50 mm wide; large: shells more than 50 mm and up to 100 mm wide; and gigantic: shells over 100 mm wide. Corpus depth is assessed as the maximum dorsal corpus length divided by the maximum depth; where this ratio is less than 3 the shell is termed deep, if about 3 it is moderate, if the ratio is over 3 the corpus cavity is shallow.

Using the Classification

Generic diagnoses commonly make reference to another long-established genus,

usually the taxon name bearer. In some a genus may be described as similar to another genus, in which case it is felt that the two are closely similar and likely, with added information, to prove to be subjective synonyms. When translations from Russian or Chinese to English are readily available, the English translation pages are included and enclosed in brackets.

At the onset of work on the Productida, genera were assigned so that RACHEBOEUF took charge of all chonetidines; regarding the Productidina and Strophalosiidina, BRUNTON and LAZAREV took charge of the pre-Permian; and GRANT dealt with Permian genera, his speciality for about thirty years. Although this apportionment was not conducive to phylogenetic analysis, at a meeting in London in 1993 an outline classification was discussed and agreed upon. In December 1994 the sudden death of GRANT necessitated all Permian genera going to the assignment of BRUNTON and LAZAREV, who found much remaining to be investigated in these less familiar taxa. Consequently, and in order to minimize delay in publication of this volume of the *Treatise,* some of the more obscure Permian genera are not treated as fully as we would wish.

Generic stratigraphic ranges follow the IUGS (see Fig. 236) chart despite the increasingly common practice of considering the Roadian as the basal stage of the Upper Permian, coming between the Kungurian and the Kazanian.

ACKNOWLEDGMENTS

Grateful thanks are due to Sarah Long (Natural History Museum, London) for preparing the list of references and maintaining the computer-based files and without whose considerable support this contribution would have been delayed. We thank Bruce Wardlaw (USGS, Denver) and Alwyn Williams for accepting the tasks of completing the Richthofenioidea and Lyttoniidina respectively, following Richard Grant's death. Tom Dutro (Smithsonian, Washington) kindly sent to London various files and illustrations of Permian genera. Colleagues, too numerous to name, have helped in providing valuable information, and CHCB is grateful to the Natural History Museum, London, for facilities provided since his retirement.

CHONETIDINA

PATRICK R. RACHEBOEUF
[Université Claude Bernard-Lyon 1, France]

Suborder CHONETIDINA Muir-Wood, 1955

[*nom. correct.* MUIR-WOOD, 1965a, p. 420, *pro* suborder Chonetoidea MUIR-WOOD, 1955, p. 68]

Productides with concavoconvex to planoconvex profiles, resupinate in some; spines tubular, posteriorly directed, or spine apertures only, on ventral valves posterior margin only; shell surface with radial costae, and costellae, or smooth, rarely lamellose in some; interareas present; toothed articulation or denticulate hinge line; cardinal process bilobed, directed posteriorly, supported by a median septum or anteriorly bounded by a cardinal process pit; accessory septa in some; anderidia present, faint to strongly developed; brachial ridges absent or weakly developed. *Upper Ordovician (Cautleyan)–Permian, ?Lower Triassic.*

The suborder Chonetidina, as here constituted, is an extinct Paleozoic group of articulated brachiopods. The range of the suborder is from Late Ordovician (Ashgill, Cautleyan to Rawtheyan) to Late Permian and possibly the earliest Triassic, a period of about 200 million years, during which they had a worldwide distribution (Fig. 237). They were especially prolific during Devonian to Permian times. The external morphology of the chonetidine shell is highly conservative from the uppermost Ordovician to the Upper Permian, and most of the morphological innovations and evolutionary tendencies among characters were developed as early as the

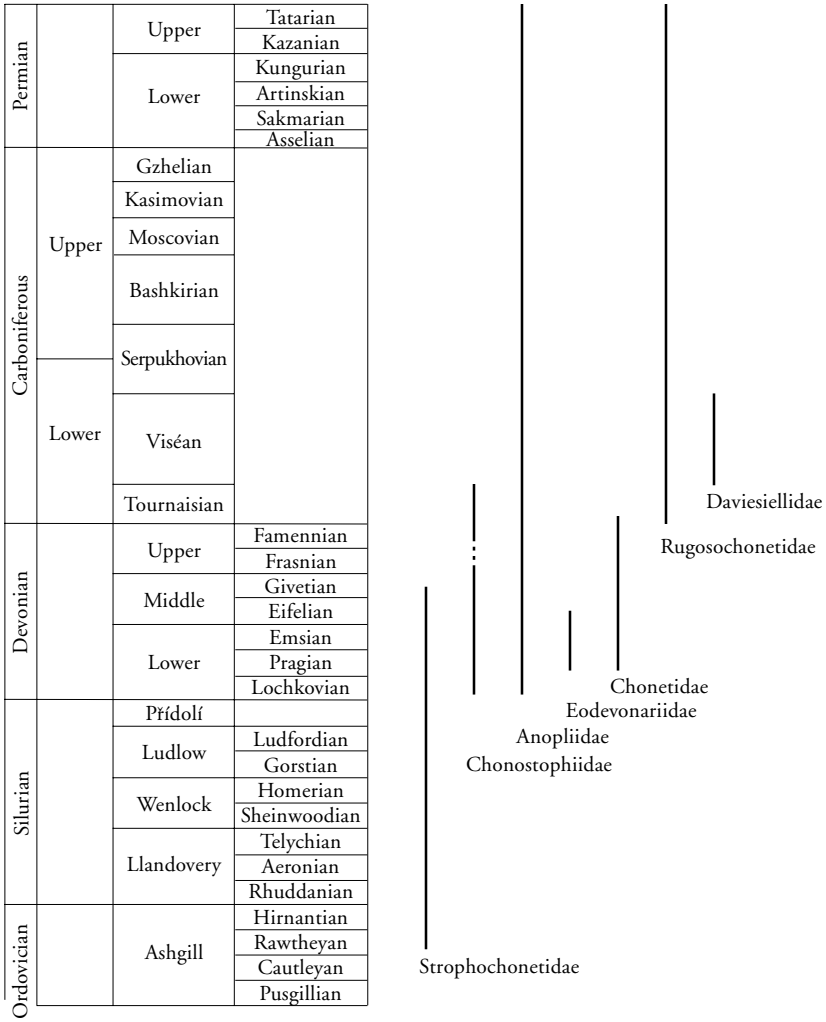

FIG. 237. Chronostratigraphic range of chonetoidean families (new).

Early Devonian (Emsian). They can be found in rocks deposited in all types of marine environments other than reefs; they evolved rapidly; and they are usually abundant. Such characters make them very useful for biostratigraphic purposes and paleogeographic reconstructions.

Known as early as 1820, the chonetidines have been studied more intensively during the last 30 years than ever before. In the first edition of the Brachiopoda *Treatise* (MOORE, 1965) the suborder Chonetidina included two superfamilies: Chonetacea and Cadomellacea. The order to which the superfamily Cadomellacea belongs is now uncertain. The first edition of the *Treatise* listed 32 genera assigned to 11 subfamilies (Cadomellacea excluded) and 4 families. After the revision of the genus *Semenewia* (Semenewiidae), now assigned to the suborder Strophalosiidina, the suborder included more than 1,200 species belonging to 162 genera assigned to 15 subfamilies and 7 families, namely Strophochonetidae, Chonostrophiidae, Anopliidae, Eodevonariidae, Chonetidae, Rugosochonetidae, and Daviesiellidae (Fig. 237).

The exterior of a typical member of the Chonetidina exhibits a concavoconvex strophic shell, subrectangular in outline with a maximum width at or just anterior to the hinge line, with a row of oblique spines, symmetrically inserted on the posterior edge of the ventral valve, and a weakly curved, commonly apsacline ventral interarea that is longer than the usually hypercline dorsal interarea (Fig. 238). A pseudodeltidium and chilidium are present, with variably developed cardinal crests below the chilidium. The shell surface is usually costellate. Variations include convexity, the planoconvex profile of strophochonetids as well as the convexoconcave, resupinate profile of the chonostrophiids; the outline varies, with length:width ratios usually between 0.6 and 1.0; the reduced or mucronate hinge lines of *Chonetes* and *Dyoros* respectively; the rectimarginate or sulcate anterior commissure; the ventral sulcus of *Dagnachonetes,* associated with the dorsal median fold of *Dyoros,* with its superimposed median plication of *Mesolobus;* and the size of radial ornamentation, with or without median enlarged costae, or the absence of radial ornamentation in *Anoplia* and *Tornquistia.* The most important external difference, however, is the morphology of spines, their orientation, and their distribution along the posterior edge of the ventral valve (Fig. 239). Spines are commonly straight, oblique, posterolaterally directed, and symmetrically arranged as in *Protochonetes;* they are orthomorph perpendicular (*Ctenochonetes*), oblique, or parallel (*Longispina*). They can, however, also be variably curved, cyrtomorph intraversed or extraversed (*Renaudia, Eodevonaria* respectively), or even geniculated (*Devonochonetes*); their angle with the hinge line varies from 0° to 90°. Moreover, spines can be asymmetrically inserted during juvenile stages, as in *Ctenochonetes,* or even at adult stages (*Asymmetrochonetes, Chlupacina, Semicaplinoplia*). Spine characters have been described previously (Racheboeuf, 1981b).

The largest species occur in the Lower Carboniferous, and they belong to the genus *Delepinea.* They may attain a width of 30 cm and rival the gigantoproductid productidines. During the Early Devonian (Emsian) a first tendency toward relative gigantism developed with shells attaining a width of about 5 cm (*e.g., Ctenochonetes, Loreleiella, Pleurochonetes*). Shell size decreased at the end of the Devonian. Shell size is better referred to as the length of the shell, which is often better preserved, rather than to the width of the shell. Specimens are referred to as very small when they are less than 5 mm long, small when between 5 and 10 mm, medium-sized between 10 and 20 mm, large between 20 and 30 mm, and very large when the length exceeds 30 mm, which corresponds to a width of about 50 mm. Most shells are between 5 and 20 mm long, with a corresponding width between 5 and 30 mm, according to their outline. The length is measured along the longitudinal axis from the most posterior part of the ventral umbo to the anterior margin. The width is the maximum width of the shell. It is measured along the hinge or anterior to the hinge line. Thickness is measured along an axis at right angles to length and width. Convexity is expressed by the length to thickness ratio. The spine implantation on the posterior margin of the ventral valve is described by the distance of each spine from the umbo in millimeters (Racheboeuf, 1981b). In dorsal valve interiors, the angles (in degrees) between inner socket ridges, anderidia, and accessory septa are often used to provide diagnoses.

The shell structure is typically pseudopunctate. Internally, an important morphological feature common to most of the chonetidine shells is the presence of a pair of anderidia in the dorsal valve interior; they are interpreted as lophophore supports. In the earliest representatives (*Archeochonetes*) anderidia may be absent or imperceptible.

The ventral muscle impressions of the chonetidines are confined to the posterior half of the ventral valve and are longitudinally divided by a myophragm (Fig. 238). Adductor scars are relatively small,

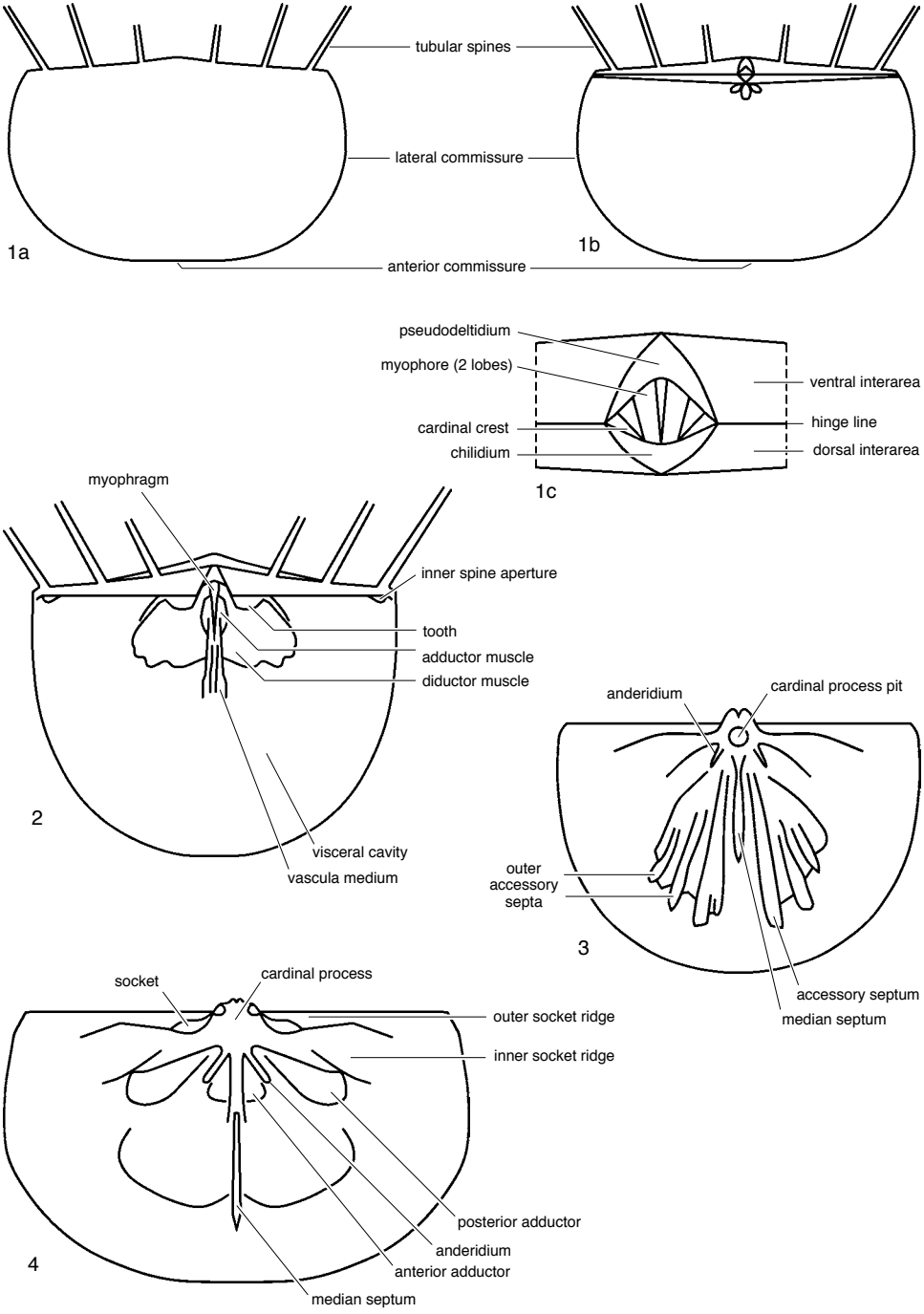

FIG. 238. Diagrammatic representation of morphology of chonetoidean shell; *1,* external morphology of complete articulated shell; *1a,* ventral view; *1b,* dorsal view; *1c,* detail of dorsal view; *2–4,* internal morphology; *2,* ventral valve interior; *3,* dorsal valve interior of anopliid type; *4,* dorsal valve interior of strophochonetid type (new).

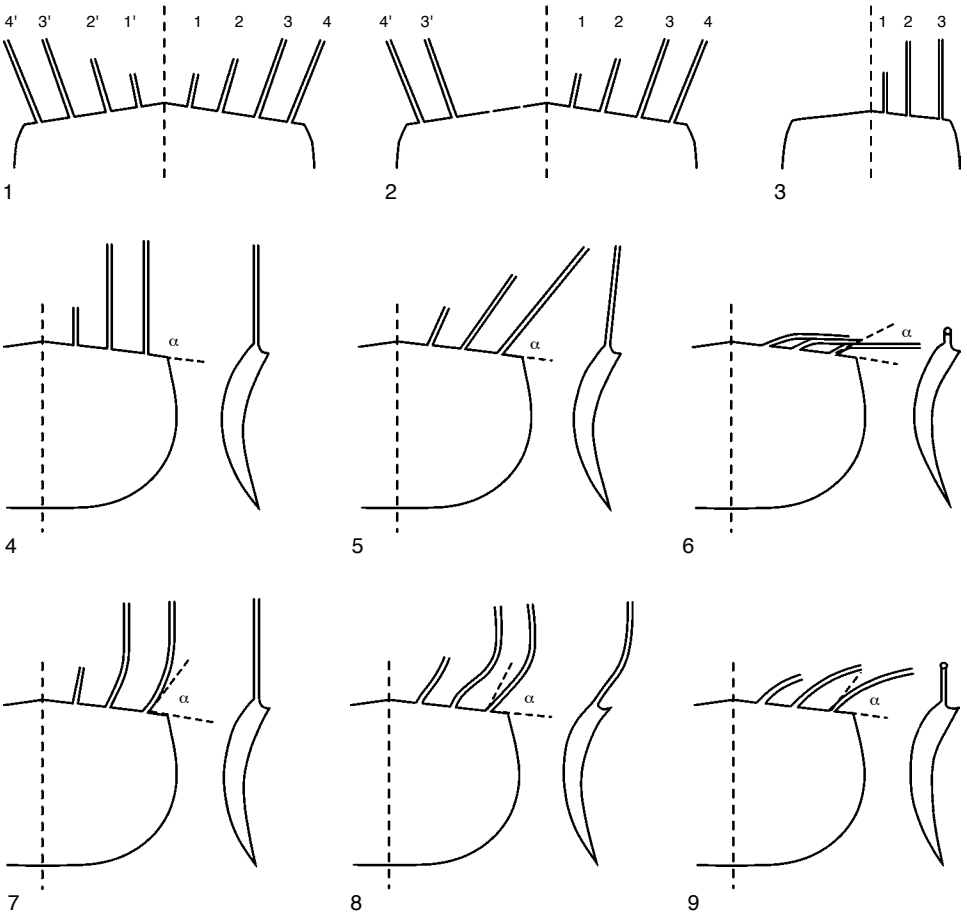

FIG. 239. *1–3,* Distribution of spines along posterior margins and corresponding formulae; *4–9,* descriptions of spine morphology and orientations; *4,* orthomorph perpendicular; *5,* orthomorph oblique; *6,* orthomorph parallel; *7,* cyrtomorph intraversed; *8,* cyrtomorph geniculate intraversed; *9,* cyrtomorph extraversed (new).

subrounded, elliptical or subtriangular, narrow, elongate, and adjacent to the myophragm. They are surrounded by diductor scars, usually subtriangular in outline, anteriorly rounded, and may be radially grooved. The mantle canal system is reduced to one pair of variably developed *vascula media* originating anterior of the adductors. The hinge is usually smooth, but denticles, probably reminiscent of a plectambonitoid ancestor, are developed in several genera. A denticulate hinge line characterizes the family Eodevonariidae, but it sporadically occurs in other families such as the Middle Devonian genus *Devonaria* (Anopliidae) and the Permian *Striochonetes.*

The dorsal valve interior exhibits two main types of morphological features (Fig. 238). The first one shows a median septum, and the second shows one or several pairs of accessory septa, commonly without a median septum, or with a reduced median septum or a breviseptum. Variations affect both morphological types. The median septum is commonly absent or very reduced in primitive forms in juveniles and in such paedomorphic shells as *Strophochonetes, Ctenochonetes,* and *Chlupacina* respectively. When developed, the median septum may support the cardinal process as in *Ctenochonetes;* in *Dagnachonetes* this is not so. In the latter genus, a cardinal process pit commonly developed between the

cardinal process and the median septum. The median septum is sometimes reduced to a breviseptum. Accessory septa characterize the families Anopliidae and Chonetidae. They are variable in number, size, and morphology and are commonly bladelike, smooth, or variably spinose. The cardinal process morphology is a constant feature among chonetidines and is invariably bilobed. Variations affect size, outline, and morphology of the two lobes of the myophore, which are narrow and medially coalescent or posterolaterally widened and deeply separated as in *Chonetes* and *Loreleiella* respectively. A quadrilobate myophore is commonly described but refers only to the paired outer walls of each lobe of the myophore.

The strophochonetids are one of the most homogenous groups among chonetidines and undoubtedly represent one of the ancestral stocks. They range from the Upper Ordovician to the Middle Devonian (Eifelian). Externally, they are mainly characterized by a fine radial ornament, the presence of a variably developed ventral median enlarged costa (*e.g., Ctenochonetes*), or several radially arranged enlarged costae (*e.g., Archeochonetes, Strophochonetes*), associated with a planoconvex to moderately concavoconvex longitudinal profile (an exception being the markedly concavoconvex shell of *Leptochonetes*). The lack of enlarged costae and the development of coarser radial costellae allow differentiation of the Protochonetinae from the Strophochonetinae. Additional diagnostic features of both subfamilies are high-angled to perpendicular spines and primitive features in interiors of both valves; the interior of the dorsal valve with a weakly developed median septum and inner socket ridges during the Silurian, becoming usually well developed from the Lower Devonian, except for small, paedomorphic forms such as *Chlupacina;* and interior of the ventral valve with a similar progressive development of muscle scars, myophragm, and *vascula media.* The sporadic appearance of small forms, commonly with asymmetrically arranged spines, related with environmental changes during the Devonian and corresponding to intra-Devonian biotic events, is interpreted in terms of heterochrony.

The chonostrophiids may also exhibit one or several enlarged costae (*Chonostrophia*), but they are easily distinguished from strophochonetids, to which they are probably closely allied, by their resupinate, convexoconcave, longitudinal profile. Except for the Lower Carboniferous *Tulcumbella,* they range from Lower to Middle Devonian (Givetian).

The family Anopliidae is commonly regarded as a group with very small, smooth or costate shells with one or several pairs of accessory septa in the interior of the dorsal valve. There are two subfamilies, Anopliinae with smooth exteriors, and Caenanopliinae with radial ornament, but such a definition is not satisfactory because it is purely phenetic. The shell size is not a reliable character at the family level. The large size of *Airtonia* was considered to preclude its assignment to the family Anopliidae, but size increase between the Lower Devonian *Plicanoplia* and the Lower Carboniferous *Airtonia* is no more than a factor of 12, *i.e.,* almost the same as that between the smallest Silurian and the largest Lower Devonian Strophochonetinae (factor of 11). It is likely that some small Devonian shells included within the family Anopliidae are paedomorphic derivatives of the Chonetidae.

The family Eodevonariidae is typically restricted to Lower and Middle Devonian (Pragian to Eifelian). The main characteristics of its representatives are the denticulate nature of the hinge line and the variable development of accessory septa. Both features are probably reminiscent of the plectambonitoids. A denticulate hinge line, however, may also occur in such other families as anopliids (*Devonaria*) and possibly rugosochonetids (*Striochonetes*).

The Devonian family Chonetidae includes the subfamilies Chonetinae, Dagnachonetinae, Retichonetinae, Devonochonetinae, and Notiochonetinae. The family is externally characterized by the development of concentric fila, which appear by Middle Devonian times, and, internally, by usually

weakly divergent anderidia in the dorsal valve interior. Except for the oldest group, the chonetines, the dorsal valve inner features are commonly reduced to a median septum or breviseptum. Accessory septa are, as a rule, poorly developed, bladelike, spinose accessory septa, often developed in the anterior half of the shell only (*Chonetes, Longispina*). Accessory septa tended to diminish in size during the Early Devonian and have disappeared by the Middle Devonian.

Rugosochonetidae represents the largest family among chonetidines, but phyletic relationships are not evident within the family, which will probably have to be divided. The family ranges from the Lower Carboniferous to Upper Permian and includes the subfamilies Rugosochonetinae, Capillomesolobinae, Plicochonetinae, Delepineinae, Svalbardiinae, Undulellinae, Lamellosiinae, and Quinquenellidae. This group is characterized by a global common tendency to develop a ventral sulcus associated with a corresponding dorsal fold, sometimes complicated by the development of a ventral median ridge. The exterior of the shell may be radially ornamented, smooth, or lamellose (*Lamellosia*). Internally rugosochonetids lack dorsal accessory septa; anderidia are usually relatively large and prominent, and the cardinal process is anteriorly bounded by a pit.

Following MUIR-WOOD (1962, 1965a), the family Daviesiellidae is restricted to the Carboniferous large shells of *Daviesiella.* The family is herein retained within chonetidines only questionably because its representatives exhibit several characters that make them apparently more closely allied to productidines than to chonetidines. Among these characters are the thickened ventral valve with reduced interarea, as well as the lack of a spine row, pseudodeltidium, and anderidia.

After early attachment by means of the pedicle, most of the chonetidine shells rested on the sea bottom with the dorsal valve uppermost, the extremities of the hinge spines serving for attachment by cementation with mucopolysaccharides to particles. It seems likely that many juveniles and some paedomorphic forms had an epiplanktonic mode of life, such as the Early Devonian representatives of the family Strophochonetidae.

The conservative morphology of the chonetidine shell leads to a number of homeomorphs characterized by similar external form, spines, and ornament associated with dissimilar internal structures mainly in the dorsal valve (*e.g., Chonetes, Dagnachonetes,* and *Devonochonetes*).

The classification employed here is based on external characters, including shell form, convexity, ornament, morphology, orientation, and implantation of spines; internally, the main characters are the morphology of the muscle field and hinge teeth in the ventral valve, and the morphology of the dorsal valve interior.

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The author is greatly indebted to G. A. Afanas'eva, N. W. Archbold, A. Balinski, M. G. Bassett, D. B. Blake, A. J. Boucot, C. H. C. Brunton, J. L. Carter, L. R. M. Cocks, F. Collier, R. E. Doescher, R. M. Feldmann, J.-C. Fischer, J. L. Garcia-Alcalde, V. Havlíček, J. G. Johnson, M. Lagabrielle, F. Langenstrassen, J. Pečar, J. Roberts, Rong Jia-Yu, Su Yang-Zhen, K. Vogel, and J. B. Waterhouse for providing needed references or data and for lending type specimens, molds, and photographs.

Superfamily CHONETOIDEA Bronn, 1862

[*nom. transl.* RACHEBOEUF, herein, *ex* Chonetacea SCHROCK & TWENHOFEL, 1953, p. 317, *nom. transl. ex* Chonetidae BRONN, 1862, p. 301]

Shell very small (3 mm) to very large (200 mm), concavoconvex to resupinate, with hollow spine row normally developed along posterior margin of ventral valve only; when spines not externally developed, canal apertures visible; when spines absent, corresponding canal apertures also absent; spines vary in number, orientation, morphology, and disposition on both sides of posterior ventral margin; sulcus and fold absent or variably developed; anterior commissure rectimarginate, sulcate, or parasulcate; functional pedicle in early growth stages only;

shell smooth, sometimes lamellose, usually costellate with branching or intercalating costellae; enlarged costae present in some genera; interarea present in both valves with variably developed pseudodeltidium and chilidium, more rarely with chilidial plates; ventral interior with variably developed myophragm dividing relatively large muscle field with small adductors and large, smooth or flabellate diductors; *vascula media* sporadically preserved; hinge with a pair of variably developed hinge teeth, sometimes longitudinally striate, or hinge line denticulate with or without vestigial hinge teeth; dorsal interior typically with a pair of variably developed anderidia; cardinal process always present, variable in shape and size, more or less strongly bilobed internally; myophore with two lobes, variably developed but always longitudinally grooved, and medianly adjacent or distinctly separated; median septum often absent in juveniles, developing with growth as longitudinal ridge or breviseptum or lacking; accessory septa developed in some families, bladelike or formed by fused pustules; cardinal process anteriorly limited by pit or supported by median septum; inner socket ridges variably developed, always supporting cardinal process; lophophore possibly of trocholophe, ptycholophe, spirolophe, or mesolophe type, supported by anderidia; brachial ridges absent or variably developed; shell structure laminar, pseudopunctate. *Upper Ordovician (Cautleyan)–Permian, ?Lower Triassic.*

Family STROPHOCHONETIDAE Muir-Wood, 1962

[*nom. transl.* Racheboeuf, 1981b, p. 45, *ex* Strophochonetinae Muir-Wood, 1962, p. 40]

Shell small to large, transverse, finely costellate, planoconvex to markedly concavoconvex; median enlarged costa restricted to beak or reaching anterior margin, rarely absent; growth lines usually ill defined; interareas flat with well-developed pseudodeltidium, chilidium; hinge spines long, high-angled, commonly orthomorph perpendicular, sometimes cyrtomorph intraverse or orthomorph oblique; spines symmetrically or variously asymmetrically inserted on posterior ventral margin, sometimes lacking on one side of valve; ventral valve interior with short myophragm; relatively stout hinge teeth; dorsal valve interior with strong cardinal process, usually wider than long, deeply bilobed; myophore posteriorly displayed, two lobes being laterally flanked by short chilidial crests fusing anteriorly with shaft of cardinal process; cardinal process pit present during Silurian, persisting in juvenile and paedomorphic Devonian taxa; sockets anteriorly bounded by variably developed inner socket ridges, short and posteriorly curved, long and parallel to hinge line or anteriorly highly divergent at about 150°; sockets sometimes overhung in their mesial part by lateral horizontal expansions of cardinal process; dorsal median septum absent or well developed; no accessory septa; anderidia usually relatively small, anteriorly divergent at 35° to 90° and not posteriorly fused to cardinal process in oldest forms; brachial ridges commonly not developed. *Upper Ordovician (Cautleyan)–lower Middle Devonian.*

Subfamily STROPHOCHONETINAE Muir-Wood, 1962

[Strophochonetinae Muir-Wood, 1962, p. 40]

Strophochonetids with ventral median enlarged costa always present but variably developed; spines orthomorph perpendicular or cyrtomorph intraverse, symetrically or asymmetrically arranged. *Upper Ordovician (Cautleyan)–Middle Devonian (Eifelian).*

Strophochonetes Muir-Wood, 1962, p. 40 [**Chonetes cingulatus* Lindström, 1861, p. 374; OD]. Shell small, plano- to moderately concavoconvex; well-developed median enlarged costa; long, symmetrically arranged high-angled spines varying from intraverse cyrtomorph proximally to orthomorph vertical distally; cardinal process strongly bilobed internally, anteriorly bounded by cardinal process pit; no median septum; anderidia long, narrow, anteriorly divergent at 60° and isolated on valve floor; inner socket ridges short, thin, as two rounded ridges almost parallel to hinge. *lower Silurian (upper Llandovery–Wenlock):* Sweden, Bohemia, Spain, Great Britain, Anticosti, Algeria.——Fig. 240,*3a–c.* **S. cingulatus* (Lindström), Silurian, Baltic; ventral view, dorsal view, dorsal valve interior, ×4 (Muir-Wood, 1962).

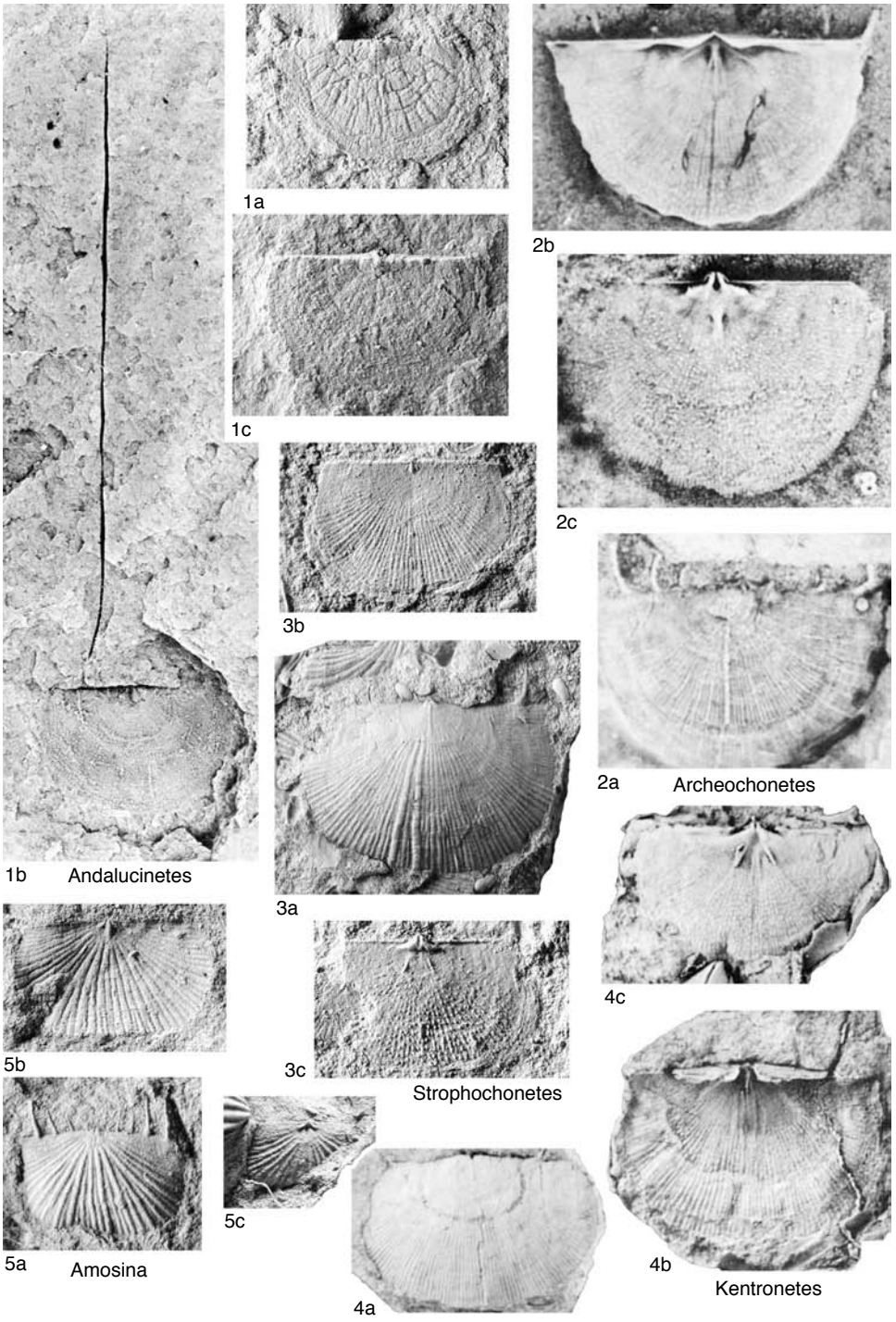

FIG. 240. Strophochonetidae (p. 369–374).

Amosina Boucot, 1975, p. 359 [**Chonetes fuertensis* Kayser, 1897, p. 300; OD]. Shell small, almost planoconvex to concavoconvex transversely elongate to subrectangular in outline; ventral sulcus present or absent, with or without longitudinal ridge; median enlarged costa absent or reaching anterior commissure; orthomorph symmetrically arranged spines, vertical or high-angled; no dorsal median septum; inner socket ridges poorly developed, supporting wide, short cardinal process; reduced anderidia anteriorly divergent at 90°, not fused posteriorly. *upper Silurian (Ludlow)–Lower Devonian (Lochkovian):* Argentina, Bolivia.——Fig. 240,*5a–c. *A. fuertensis* (Kayser), Ludlow–Přídolí, Argentina; ventral view, dorsal view, dorsal valve interior, ×4 (Benedetto & others, 1992).

Andalucinetes Racheboeuf, 1985, p. 660 [**A. hastatus;* OD]. Very small, thin, almost planoconvex shell; median enlarged costa restricted to posteromedian part of ventral valve; anteriorly, surface of shell becoming parchmentlike; very long vertical spines, either on right or left side; hinge teeth laterally elongated, parallel to hinge line; myophragm long, thin; dorsal interior with low, narrow inner socket ridges, narrow, elongate cardinal process pit; anderidia reduced, widely spaced, anteriorly divergent at 90°; no median septum. *Lower Devonian (Pragian):* Spain.——Fig. 240,*1a–c. *A. hastatus; a,* ventral valve exterior; *b,* external mold of complete shell; *c,* dorsal valve exterior, ×4 (Racheboeuf, 1985).

Archeochonetes Racheboeuf & Copper, 1986, p. 1303 [**Chonetes (Eodevonaria) primigenius* Twenhofel, 1914, p. 26; OD]. Shell small; median enlarged costa present with several variably developed secondary enlarged costae; spines cyrtomorph intraverse to orthomorph, high-angled, symmetrically arranged and progressively infilled during growth, then not connected with shell interior; teeth, anterior wall of sockets longitudinally crenulated; anderidia poorly developed, anteriorly divergent at 35°; cardinal process deeply bilobed internally; median septum low, short. *Upper Ordovician (Cautleyan)–Silurian (Wenlock):* Anticosti Island, New Brunswick.——Fig. 240,*2a–c. *A. primigenius* (Twenhofel), Ashgill, Anticosti; ventral valve exterior, ventral valve interior, dorsal valve interior, ×4 (Racheboeuf & Copper, 1986).

Asymmetrochonetes Smith, 1980, p. 49 [**A. spinalonga;* OD]. Shell small with variably developed median enlarged costa; orthomorph perpendicular spines on right side of pedicle valve only, very rarely on left side only; inner socket ridges, median septum, anderidia faintly developed but present. *Lower Devonian (Lochkovian–Pragian):* Canadian Arctic Archipelago, southern France, Spain, Bohemia, Australia (New South Wales).——Fig. 241,*3a–c. *A. spinalonga,* Lochkovian, Canadian Arctic Archipelago; ventral valve, ventral valve interior, dorsal valve interior, ×4 (Smith, 1980).

Australostrophia Caster, 1939, p. 83 [**Leptostrophia?? mesembria* Clarke, 1913, p. 286; OD]. Medium, plano- to concavoconvex shell; maximum width at midlength; radial ornamentation parvicostellate, crossed by dense fila; median enlarged costa present in early stages only; spines orthomorph oblique, symetric and low-angled. *Lower Devonian (Lochkovian–Emsian):* Brazil, Argentina, Bolivia, Guinea.——Fig. 241,*1a–c. A. clarkei* Racheboeuf & Herrera, Pragian, Bolivia; *a,* ventral valve, ×4; *b,* dorsal side of an articulated shell, ×3; *c,* dorsal valve interior, ×3 (Racheboeuf & Herrera, 1994).

Babinia Racheboeuf & Branisa, 1985, p. 1435 [**B. parvula;* OD]. Shell small, transversely elongate, weakly concavoconvex; orthomorph vertical, symmetrically arranged spines; no dorsal median septum; narrow, elevated rounded ridgelike inner socket ridges anteriorly divergent at 160°, supporting wide, short cardinal process anteriorly bounded by weak cardinal process pit; thin anderidia isolated on valve floor, anteriorly divergent at 70°. *Lower Devonian (upper Emsian)–Middle Devonian (lower Eifelian):* Bolivia, Argentina, Brazil, Quebec.——Fig. 241,*4a,b. *B. parvula,* Emsian, Bolivia; ventral valve exterior, interiors of articulated specimen, ×4 (Racheboeuf & Branisa, 1985).

Borealinetes Racheboeuf & Lespérance, 1995, p. 21 [**B. comestus;* OD]. Shell small to medium; spines cyrtomorph intraverse, symmetrically arranged; median enlarged costa reaching anterior margin of ventral valve; ventral valve interior with semicircular to semielliptical adductor scars; dorsal valve interior with inner socket ridges typically overhanging sockets posteriorly. *Lower Devonian (Pragian–Emsian):* Quebec.——Fig. 241,*2a–d. *B. comestus,* Pragian, Quebec; *a,* ventral valve, ×4; *b,* ventral valve interior, ×4; *c,d,* articulated shell, dorsal side, dorsal valve interior, ×4 (Racheboeuf & Lespérance, 1995).

Chlupacina Havlíček & Racheboeuf, 1979, p. 86 [**C. longispina;* OD] [=*Hemichonetes* Havlíček & Racheboeuf, 1979, p. 83, *nom. nud.; Hemichonetes* Racheboeuf, 1981b, *non* Li, Gu, & Su, 1980, p. 343, obj.; *Philippotia* Racheboeuf, 1982, p. 1024; obj.]. Very small plano- to concavoconvex shell; radial ornamentation often restricted to periphery of valves; median enlarged costa well developed; two to three long spines on one side only; usually oblique in their proximal part, then becoming orthomorph vertical; dorsal valve interior without median septum; cardinal process short, wide, supported by narrow, rounded ridgelike inner socket ridges anteriorly divergent at about 145°; anterior margin of cardinal process, socket ridges almost vertical above valve floor; cardinal process pit variably developed, often longitudinally elongate; anderidia short, thin, isolated on valve floor, anteriorly divergent at 50°. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Bohemia, Armorican Massif, Spain, Canadian Arctic Archipelago, Australia, ?China.——Fig. 242,*4a–d. C. belairensis* (Racheboeuf), Emsian, southwestern Europe; *a,* ventral valve exterior, ×5; *b,* dorsal valve interior, ×5; *c,* detail of

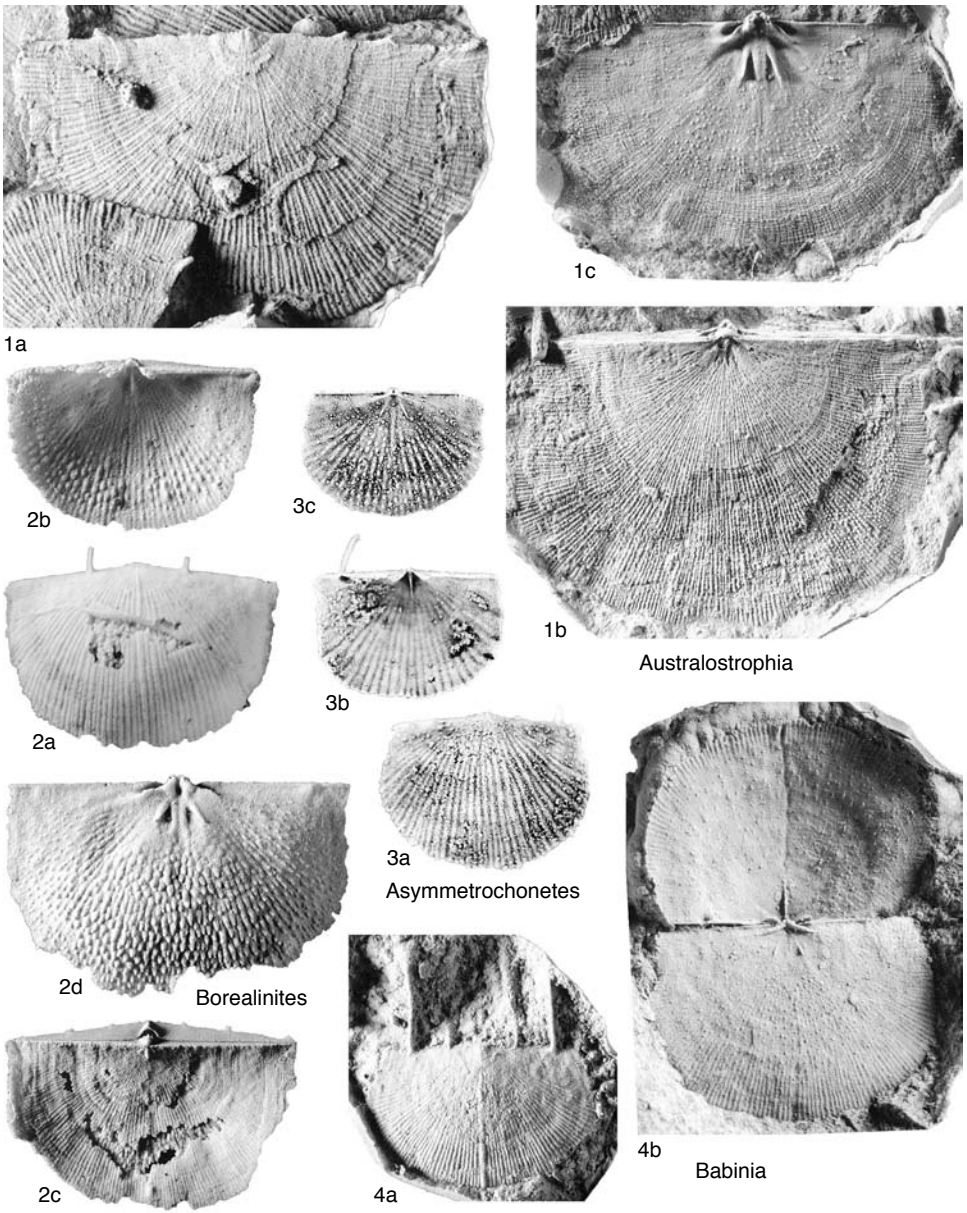

FIG. 241. Strophochonetidae (p. 371).

cardinal process, ×12; *d,* ventral valve with spines, ×5 (Racheboeuf, 1982).

Ctenochonetes RACHEBOEUF, 1976, p. 52 [**Chonetes tenuicostata* OEHLERT, 1877, p. 599; OD]. Shell small to medium, weakly to markedly concavoconvex; variably developed median enlarged costa; spines orthomorph perpendicular; juveniles spines asymmetrically arranged, then symmetrical in adults, two spines closest from umbo always lacking on one side (commonly the left one, Fig. 243); inner socket ridges, dorsal septum and anderidia well developed, fusing posteriorly and supporting cardinal process; median wall of sockets overhung by two horizontal, platelike expansions. *Lower Devonian (upper Lochkovian–lower Emsian):* Germany, France, Spain, Morocco.——FIG. 242,*1a–d.* **C. tenuicostatus* (OEHLERT), Pragian, Armorican Massif ; *a,* ventral valve; *b,* articulated shell in dorsal view; *c,*

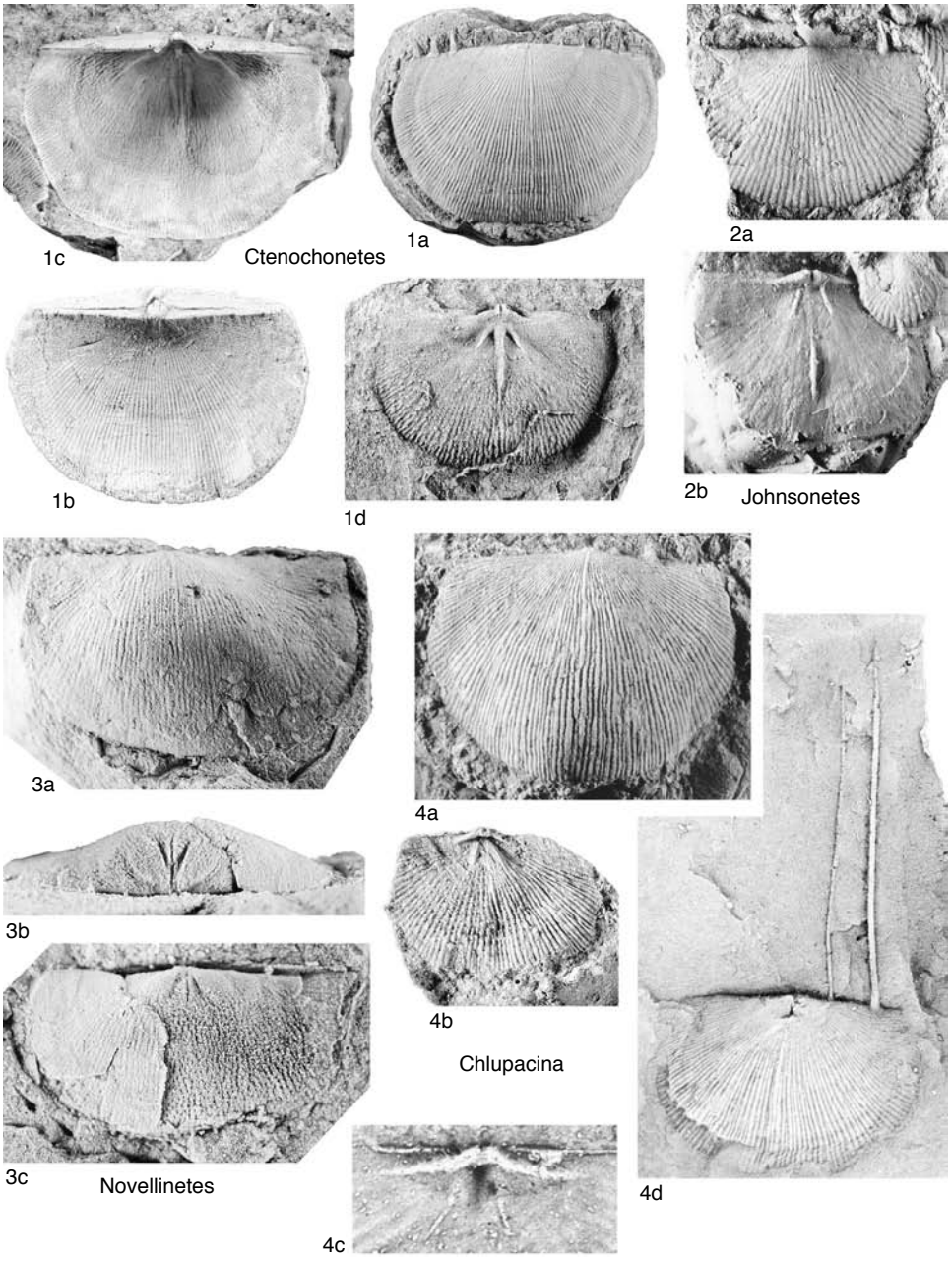

FIG. 242. Strophochonetidae (p. 371–376).

ventral valve interior; *d,* dorsal valve interior, ×2 (Racheboeuf, 1976).

Dawsonelloides BOUCOT & HARPER, 1968, p. 165 [**Chonetes canadensis* BILLINGS, 1874, p. 17; OD]. Shell medium to large, almost plano- to gently concavoconvex; surface finely costellate with narrow median enlarged costa; ventral interarea apsacline; dorsal interarea anacline to hypercline; pseudodeltidium, chilidial plates; orthomorph high-angled to perpendicular spines; dorsal interior with long, prominent median septum supporting cardinal process; anderidia variably developed; long, narrow inner socket ridges parallel to hinge line; interior of ventral, or both valve interiors, with radial grooves.

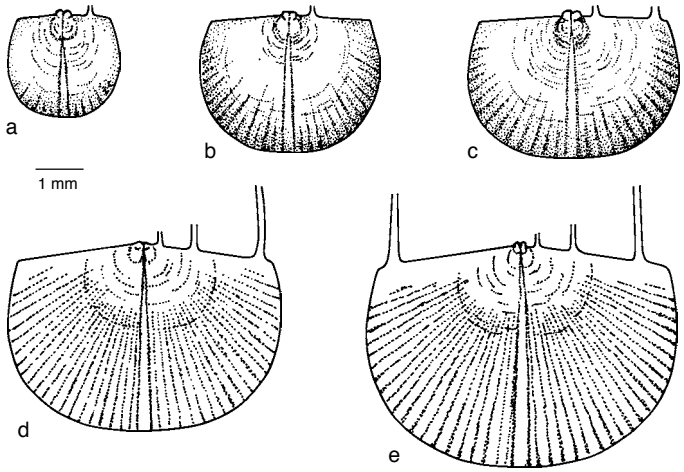

FIG. 243. Strophochonetidae (Strophochonetinae); *a–e,* ontogenetic development of spines on ventral valve of *Ctenochonetes tenuicostatus* (OEHLERT) (new).

upper Silurian (Ludlow)–Lower Devonian (Pragian): Maine, Quebec.——FIG. 244,*1a–c. *D. canadensis* (BILLINGS), Pragian, Quebec; *a,* ventral valve, ×1.5 (Racheboeuf & Lespérance, 1995); *b,* ventral valve interior, ×1.5 (Boucot & Harper, 1968); *c,* dorsal valve interior, ×1.5 (Racheboeuf & Lespérance, 1995).

Johnsonetes RACHEBOEUF, 1987, p. 7 [**Chonetes filistriata* WALCOTT, 1884, p. 127; OD]. Shell small to medium, markedly concavoconvex, transverse in outline; when present, median enlarged costa developed on beak only; spines orthomorph vertical, asymmetrically arranged, more spines on one side; homologous spines appearing first on opposite side; long, thin dorsal median septum supporting stout, short, wide cardinal process; inner socket ridges low, rounded, anteriorly divergent at 130° to 140°; anderidia short, anteriorly divergent at 45° to 50°, posteriorly fused with cardinal process. *Lower Devonian (Pragian–Emsian):* Canadian Arctic Archipelago, Australia (New South Wales).——FIG. 242,*2a,b. *J. filistriata* (WALCOTT), Pragian, Canadian Arctic Archipelago; *a,* ventral valve exterior, ×3; *b,* dorsal valve interior, ×4 (Racheboeuf, 1987).

Kentronetes RACHEBOEUF & HERRERA, 1994, p. 552 [**Chonetes rücki* ULRICH, 1893, p. 79; OD]. Shell medium; median enlarged costa commonly reduced to posterior part of ventral valve; spines cyrtomorph intraverse, symmetrically arranged; ventral valve interior with long *vascula media;* posterior muscle bounding ridges bending anteriorly; well-differentiated muscle scars with typically droplike adductors; dorsal valve interior with isolated anderidia; variably developed median septum not supporting cardinalia; short, curved inner socket ridges supporting lobes of deeply bilobed cardinal process. *Lower Devonian (Pragian–Emsian):* Bolivia, Argentina, South Africa.——FIG. 240,*4a–c. *K. ruecki* (ULRICH), Pragian, Bolivia; ventral exterior, ventral interior, dorsal interior, ×2 (Racheboeuf & Branisa, 1985).

Leptochonetes HAVLÍČEK & RACHEBOEUF, 1979, p. 89 [**Chonetes tardus* BARRANDE, 1879, pl. 46; OD]. Shell small, strongly concavoconvex, very thin, maximum width at hinge line; long median enlarged costa; orthomorph oblique spines, low to medium angled, symmetrically arranged; interareas linear; ventral muscle field small, ill defined; dorsal interior without median septum; inner socket ridges relatively well developed, supporting small cardinal process; anderidia isolated on valve floor, anteriorly divergent at 40°. *Lower Devonian (Pragian–Emsian):* Bohemia.——FIG. 244,*2a,b. *L. tardus* (BARRANDE), Pragian, Bohemia; *a,* ventral valve, ventral view, ×4; *b,* lateral view, ×5 (Havlíček & Racheboeuf, 1979).——FIG. 244,*2c. L. hostinensis* (BARRANDE), Emsian, Bohemia; dorsal valve internal mold, ×5 (Havlíček & Racheboeuf, 1979).

Novellinetes HAVLÍČEK & RACHEBOEUF, 1979, p. 87 [**Chonetes novellus* BARRANDE, 1879, pl. 46; OD]. Shell small to medium size, transversely elongate, subrectangular in outline; ornamentation very fine with weak median enlarged costa; spines orthomorph almost vertical; two spines on one side, one on other; ventral muscle field wide, well impressed with nonadjacent adductors; inner socket ridges long, narrow, almost parallel to hinge line; anderidia very small; no median septum; small cardinal process anteriorly bounded by deep, narrow cardinal process pit. *Lower Devonian (Emsian):* Bohemia.

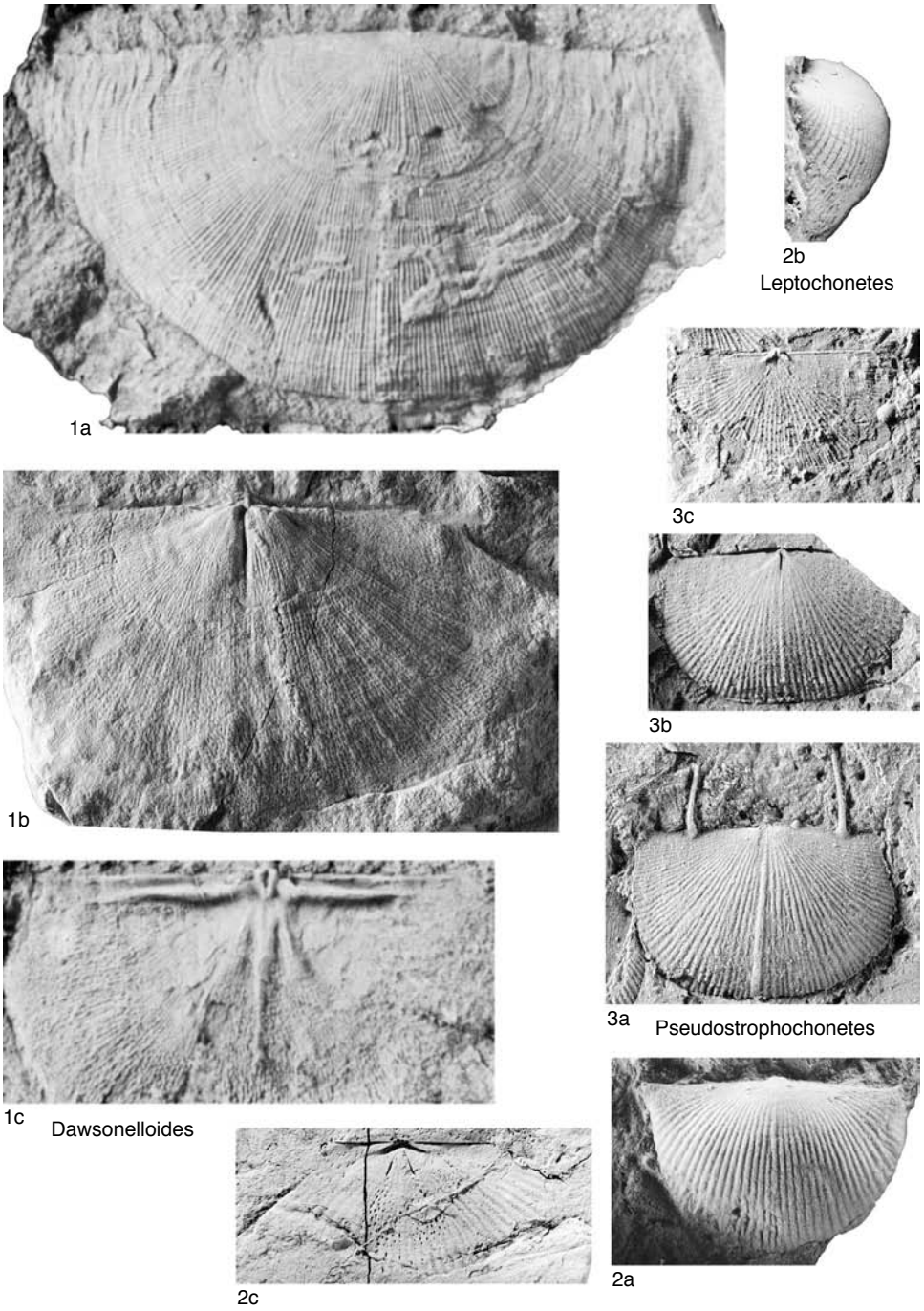

FIG. 244. Strophochonetidae (p. 373–376).

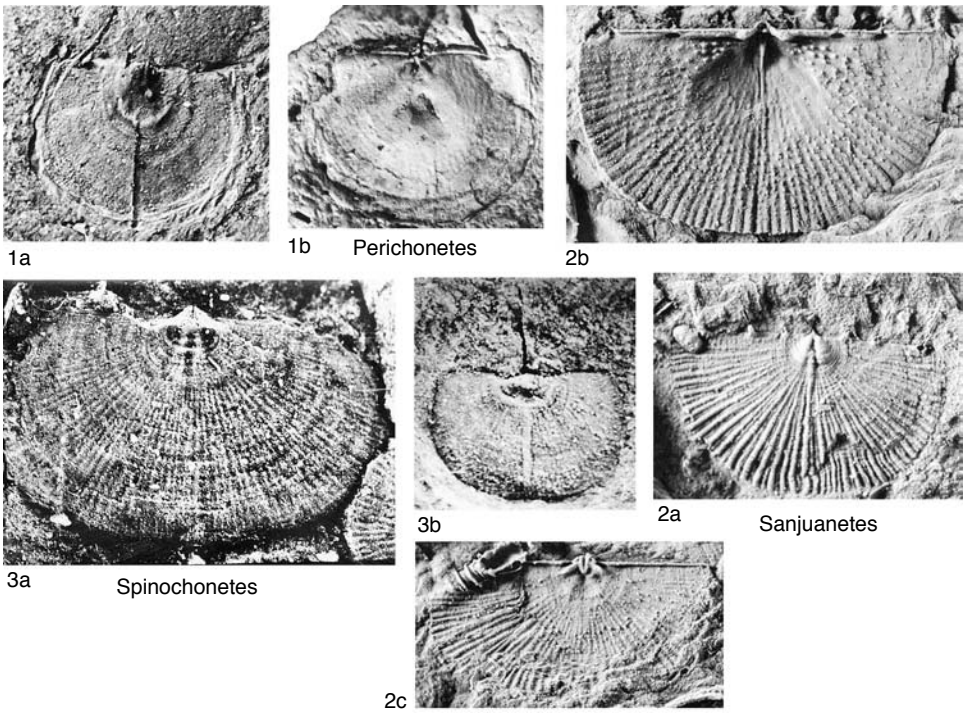

FIG. 245. Strophochonetidae (p. 376–377).

——FIG. 242,*3a–c. *N. novellus* (BARRANDE), Emsian, Bohemia; *a,* ventral valve exterior; *b,c,* ventral valve interior, posterior and ventral views, ×5 (Havlícek & Racheboeuf, 1979).

Perichonetes XU, 1979, p. 372[380] [**P. mirabilis;* OD]. Very small, almost planoconvex thin shell, subquadrate to weakly transverse in outline; prominent median enlarged costa; fine radial costellae crossed by concentric growth lines; one or two, orthomorph vertical spines, usually on right side only; ventral interior with narrow ridge surrounding muscle field and anteriorly fusing with myophragm; dorsal interior without median septum; long, narrow socket ridges coalescing with small cardinal process. [*Perichonetes* differs from *Chlupacina* in the presence of a narrow ridge surrounding the ventral muscle only. This feature may be no more than an artefact due to the flattening of specimens, and possibly related to an ontogenetic discontinuity in the shell fabric. *Perichonetes* is retained as a distinct genus, awaiting further data about the ventral valve interior.] *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* southern China (Guangxi), northeastern Vietnam.——FIG. 245,*1a,b. *P. mirabilis;* ventral valve external mold, dorsal valve external mold, ×10 (Xu, 1979).

Pseudostrophochonetes RACHEBOEUF, 1981b, p. 40 [**Chonetes mediocostalis* KOZŁOWSKI, 1929, p. 120; OD]. Externally similar to *Strophochonetes* except in spine morphology, arrangement; orthomorph vertical spines, two first juvenile spines lacking on one side of valve; internally close to *Strophochonetes* but with narrow elongate cardinal process pit, anteriorly divergent inner socket ridges. *Lower Devonian (Lochkovian):* Podolia.——FIG. 244,*3a–c. *P. mediocostalis* (KOZŁOWSKI), Lochkovian, Podolia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×4 (Racheboeuf, 1981b).

Sanjuanetes RACHEBOEUF & HERRERA, 1994, p. 543 [**S. dalenzae;* OD]. Shell transverse, plano- to weakly concavoconvex; ventral interarea steeply apsacline to catacline; dorsal interarea catacline; pseudodeltidium, chilidium large, prominent; spines high angled, weakly cyrtomorph intraverse, symmetrically arranged; radial costae, costellae rounded, intercalating ventrally, bifurcating dorsally, crossed by fila; ventral valve interior with long pad parallel to hinge; anderidia not fused posteriorly with cardinal process; no median septum; deeply bilobed cardinal process supported by short inner socket ridges subparallel to hinge. *Silurian (Ludlow)–Devonian (Lochkovian):* Argentina, Bolivia.——FIG. 245,*2a–c. *S. dalenzae,* Lochkovian, Bolivia; ventral valve exterior, ventral valve interior, dorsal valve interior, ×5 (Racheboeuf & Herrera, 1994).

Spinochonetes RONG, XU, & YANG, 1974, p. 203 [**S. notata;* OD][=*Shiqianella* XIAN in XIAN & JIANG, 1978, p. 272, obj.; *Megaspinochonetes* YANG &

RONG, 1982, p. 434, obj.]. Shell small, gently to strongly concavoconvex; only one orthomorph vertical spine originating from ventral umbo; median enlarged costa well developed; ventral, dorsal muscle field more or less impressed with variably developed surrounding ridges. *lower Silurian (upper Llandovery–lower Wenlock):* southern China (Sichuan, Guizhou, Hunan, Hubei).——FIG. 245,*3a. *S. notata,* Telychian, central China; ventral valve internal mold, ×6 (Rong, Xu, & Yang, 1974).——FIG. 245,*3b. S. subrectangularis* (YANG & RONG), Telychian, central China; dorsal valve interior, ×5 (Rong, Xu, & Yang, 1974).

Subfamily PROTOCHONETINAE new subfamily

[Protochonetinae RACHEBOEUF, herein]

Small to medium, plano- to concavoconvex shell; pseudodeltidium, chilidium, or chilidial plates present; median enlarged costa usually absent or weakly developed; spines symmetrically arranged, orthomorph oblique, low to high angled; dorsal interior with median septum, weakly divergent anderidia; inner socket ridges varying from short, curved to long, narrow, parallel to hinge line. *Silurian (Wenlock)–Lower Devonian (Emsian).*

Protochonetes MUIR-WOOD, 1962, p. 50 [**P. ludloviensis;* OD]. Shell small to medium, transverse, almost plano- to concavoconvex; surface costellate; pseudodeltidium, chilidium present; long, variably developed dorsal median septum supporting cardinal process; short curved inner socket ridges; cardinal process internally deeply bilobed; short, free anderidia anteriorly divergent at 40° to 45°. *Silurian (Wenlock–Přídolí):* England, Sweden, Russia, Quebec, USA (New York).——FIG. 246,*6a,b. *P. ludloviensis,* Wenlock, England; ventral valve, dorsal valve interior, ×3 (Muir-Wood, 1962).

Eoplicanoplia BOUCOT & HARPER, 1968, p. 168 [**Chonetes colliculus* FOERSTE, 1909c, p. 24; OD]. Shell small, strongly concavoconvex; surface costellate; ventral interarea orthocline with pseudodeltidium; dorsal interarea unknown; dorsal interior with long inner socket ridges slightly divergent from hinge line, well-developed anderidia, faint median septum. *upper Silurian (Ludlow–Přídolí):* northeastern USA.——FIG. 246,*2a–c. *E. collicula* (FOERSTE), Ludlow, North America; ventral valve, ventral, posterior views, ventral valve interior, ×4 (Boucot & Harper, 1968).

Hypselonetes RACHEBOEUF, 1981b, p. 43 [**Strophochonetes (Hypselonetes) vinearum;* OD]. Shell small; median enlarged costa often ill developed; inner socket ridges, median septum, anderidia posteriorly fused, supporting stout cardinal process. *upper Silurian (Ludlow–Přídolí):* France, Spain.——FIG. 246,*1a–c. *H. vinearum,* Přídolí, Spain; ventral valve exterior, ventral valve interior, dorsal valve exterior, ×4 (Racheboeuf, 1981b).——FIG. 246,*1d. H. arauzensis* RACHEBOEUF, Přídolí, Spain; dorsal valve interior, ×5 (Racheboeuf, 1981b).

Nabarredia HAVLÍČEK & RACHEBOEUF, 1979, p. 96 [**Chonetes minor* BARRANDE, 1879, pl. 46; OD]. Shell small, subrectangular in outline, with ventral valve longitudinally weakly depressed; radial ornamentation of rounded costellae; median enlarged costa restricted to posterior half of juvenile shells only; visceral disk surrounded by wide, low, rounded ridge; dorsal interior with short anderidia anteriorly divergent at 35° to 40°, reduced inner socket ridges posteriorly overhanging sockets, anteriorly divergent at 115° to 125°; no cardinal process pit; median septum lacking or reduced to low, narrow ridge. *upper Silurian (Přídolí)–Lower Devonian (Lochkovian):* Bohemia, China.——FIG. 246,*5. *N. minor* (BARRANDE), Lochkovian, Bohemia; partly exfoliated ventral valve, ×4.5 (Havlíček & Racheboeuf, 1979).

Quadrikentron BOUCOT & GAURI, 1966, p. 1023 [**Chonetes hudsonica camdenensis* DUNBAR, 1920, p. 131; OD]. Shell small to medium, concavoconvex; ornamentation finely costellate; no median enlarged costa; ventral interior with subcircular muscle field posteriorly bounded by curved ridges; adductors well developed; *vascula media* wide, long; dorsal interior with stout, internally deeply bilobed cardinal process; median septum wide, low, commonly longitudinally grooved, sometimes extending anteriorly as high, narrow breviseptum; anderidia relatively small but well differentiated, anteriorly divergent at 55° to 70°; inner socket ridges variably developed, laterally widening, tapering, anteriorly divergent at 130° to 150°; no cardinal process pit but depressed area between cardinal process and median septum. *Lower Devonian (Pragian–Emsian):* USA (Maine, Tennessee, New York), Argentina, Bolivia.——FIG. 246,*4a,b. *Q. camdenensis* (DUNBAR), Emsian, North America; ventral valve, dorsal valve interior, ×4 (Boucot & Gauri, 1966).

Shagamella BOUCOT & HARPER, 1968, p. 167 [**S. ludloviensis;* OD]. Shell very small, moderately to markedly concavoconvex; surface looking smooth but generally faintly costellate at periphery of shell, with variably developed median enlarged costa; dorsal interior with strong anderidia, cardinal process pit; breviseptum rarely developed; no accessory septa. *Silurian (Wenlock–Ludlow):* Great Britain, Bohemia.——FIG. 246,*3a–c. *S. ludloviensis,* Ludlow, Great Britain; ventral valve exterior, ventral valve interior, dorsal valve interior, ×5 (Boucot & Harper, 1968).

Subfamily PARACHONETINAE Johnson, 1970

[Parachonetinae JOHNSON, 1970a, p. 135]

Shell medium to large, robust; radial ornamentation costate, often sinuous, irregular; posterolateral costae originating along

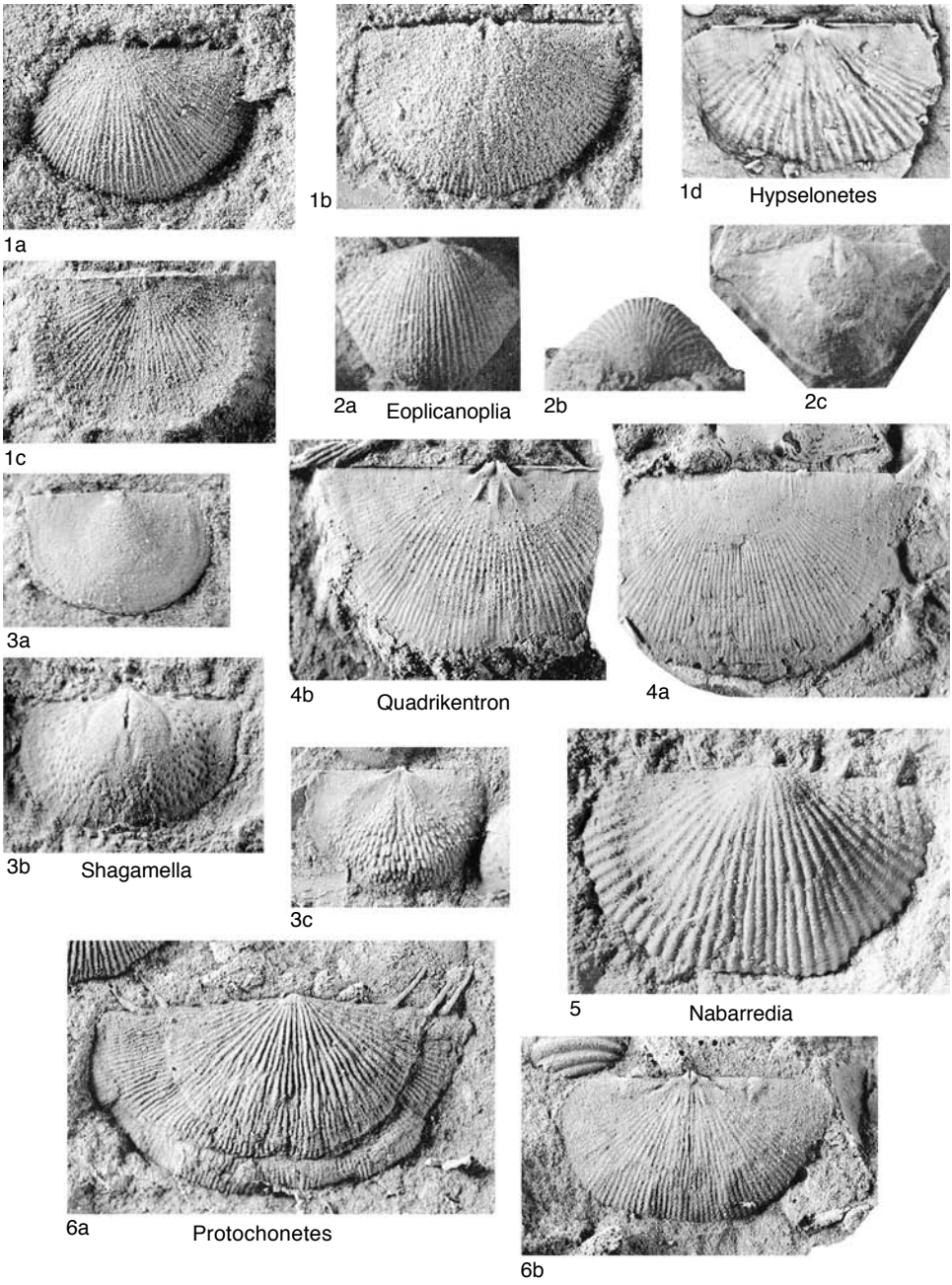

FIG. 246. Strophochonetidae (p. 377).

posterior margin of valves; orthomorph spines high-angled to perpendicular; large, deep dorsal cardinal process pit; anderidia long, slightly divergent anteriorly; variably developed median septum; no accessory septa. *Silurian (Ludlow)–Middle Devonian.*

Parachonetes JOHNSON, 1966b, p. 365 [**Chonetes macrostriata* WALCOTT, 1884, p. 126; OD]. Shell

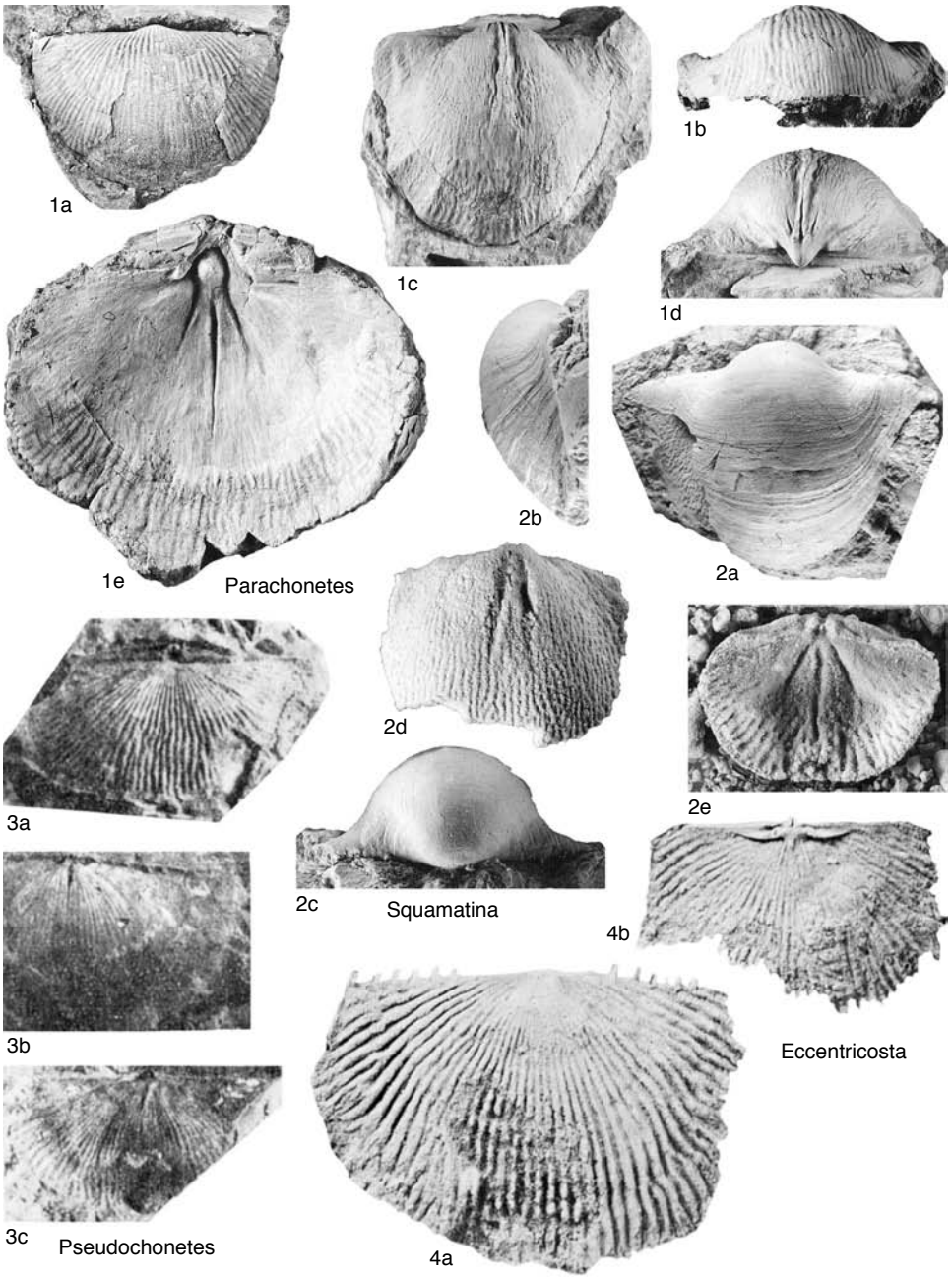

FIG. 247. Strophochonetidae (p. 378–380).

medium to large, strongly concavoconvex; radial rounded, irregular costae; spines orthomorph, high angled to perpendicular, symmetrically arranged; dorsal valve interior with wide, more or less deep cardinal process pit between bases of two lobes of cardinal process; long anderidia anteriorly divergent at 35°, posteriorly fused with cardinal process lobes; well-developed median septum; low, ill-defined inner socket ridges anteriorly divergent at 100° to 130°. *Lower Devonian (Pragian–Emsian):* USA

(Nevada, Alaska), Canadian Arctic Archipelago, Australia (New South Wales), ?France, Bohemia, Russian platform, northeastern China, Vietnam. ——FIG. 247,*1a–e. *P. macrostriatus* (WALCOTT), Emsian, Nevada; *a,b,* ventral valve exterior, ventral, anterior views, ×1; *c,d,* ventral valve interior, ventral, posterior views, ×1.5; *e,* dorsal valve mold, ×2 (Johnson, 1966b).

Eccentricosta BERDAN, 1963, p. 254 [**Chonetes jerseyensis* WELLER, 1900, p. 8; OD]. Shell medium, transverse, moderately concavoconvex; spines orthomorph perpendicular, symmetrically arranged; radial ornamentation of costae, posterolateral costae originating along posterior margin; ventral interior with short, wide hinge teeth; stout, short median septum; dorsal interior with small internally bilobed cardinal process; inner socket ridges narrow, rounded, weakly curved posteriorly, extending along hinge line; median septum low, short; anderidia long, low, narrow, anteriorly divergent at 35° to 40°. *Silurian (Ludlow–Přídolí):* North America.——FIG. 247,*4a,b. * E. jerseyensis* (WELLER), Přídolí, North America; ventral valve, dorsal valve interior, ×3 (Berdan, 1972).

Pseudochonetes SU, 1976, p. 183 [**P. flexoplicatus;* OD]. Medium to large, moderately concavoconvex; radial rounded, sinuous, irregular costellae; ventral valve interior with short myophragm; muscle field large, well impressed, radially striate; dorsal valve interior without cardinal process pit; median septum posteriorly low, wide, narrowing, tapering anteriorly; low, narrow, ill-defined inner socket ridges anteriorly divergent at about 150°. *?Lower Devonian, Middle Devonian:* Inner Mongolia.——FIG. 247,*3a–c. *P. flexoplicatus; a,* dorsal side of an articulated shell, ×2; *b,* ventral valve internal mold, ×2; *c,* dorsal valve internal mold, ×2 (Su, 1976).

Squamatina HAVLÍČEK & RACHEBOEUF, 1979, p. 109 [**Chonetes squamatula* BARRANDE, 1848, p. 249; OD]. Small, thick, strongly concavoconvex shell with depressed flanks, well-differentiated ears; maximum width at hinge line; ventral interarea apsacline, flat; dorsal interarea weakly hypercline; pseudodeltidium, chilidium not observed; shell surface lamellose, without radial ornamentation; symmetrically arranged orthomorph oblique, high-angled spines; ventral muscle field posteriorly situated; very short myophragm; pair of strong, long, poorly divergent vascular trunks; long, wide dorsal median septum supporting small bilobed cardinal process; very long, stout anderidia anteriorly divergent at 55°; low, long inner socket ridges. [Although smooth, *Squamatina* is herein questionably placed within the Parachonetinae due to its inner features: the morphology of ventral muscle scars and *vascula media;* and the stout dorsal median septum and anderidia]. *Lower Devonian (Pragian):* Czech Republic.——FIG. 247,*2a–e. *S. squamatula* (BARRANDE), Pragian, *Nowakia acuaria* Zone, Bohemia; *a–c,* ventral valve, ventral, lateral, posterior views; *d,* ventral valve interior; *e,* dorsal valve interior, ×3 (Havlíček & Racheboeuf, 1979).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

[Chonostrophiidae MUIR-WOOD, 1962, p. 95]

Shell small to large, resupinate; ventral valve concave to almost flat; dorsal valve moderately convex; outline moderately to strongly transverse, subsemicircular to suboval; ventral interarea flat, anacline to strongly catacline with variably developed, but present, wide pseudodeltidium; dorsal interarea flat, strongly anacline, with chilidium or chilidial plates; numerous spines orthomorph perpendicular or oblique, high-angled, symmetrically arranged; radial ornamentation costellate or parvicostellate with very fine concentric fila; ventral interior with stout oblique hinge teeth; muscle field relatively large, variably impressed in valve floor, divided by short to long myophragm; dorsal interior with faint to long, well-differentiated anderidia; median septum absent or strongly developed; inner socket ridges straight, parallel to hinge line, or short, bending posteriorly, or short, anteriorly divergent; cardinal process wide, short, not extending beyond posterior margin, always elevated above valve floor; cardinal process internally bilobed but lobes adjacent medianly; myophore with two triangular, wide, longitudinally deeply grooved lobes directed posteriorly. *Lower Devonian (Lochkovian)–Lower Carboniferous (Tournaisian).*

Chonostrophia HALL & CLARKE, 1892, p. 310 [**Chonetes reversa* WHITFIELD, 1882, p. 213; OD]. Shell small to medium; radial ornamentation parvicostellate, with low, narrow costellae; spines orthomorph oblique, symmetrically arranged; chilidium present; no dorsal median septum; anderidia ill defined; inner socket ridges short, bending posteriorly, surrounding sockets. *upper Lower Devonian (upper Emsian)–Middle Devonian (Eifelian):* North America (Appalachian Mountains), South America (Bolivia, Argentina).——FIG. 248,*2a. *C. reversa* (WHITFIELD), ventral valve exterior, original of HALL & CLARKE, 1892, NYSM 1241, ×10 (Racheboeuf & Lespérance, 1995).——FIG. 248,*2b–d. C. dawsoni* (BILLINGS), Emsian, Québec; *b,* dorsal valve interior, ×3; *c,* ventral valve exterior, ×2; *d,* ventral valve interior, ×2 (Racheboeuf & Lespérance, 1995).

Chonostrophiella BOUCOT & AMSDEN, 1964, p. 881 [**Chonetes complanata* HALL, 1857, p. 56; OD].

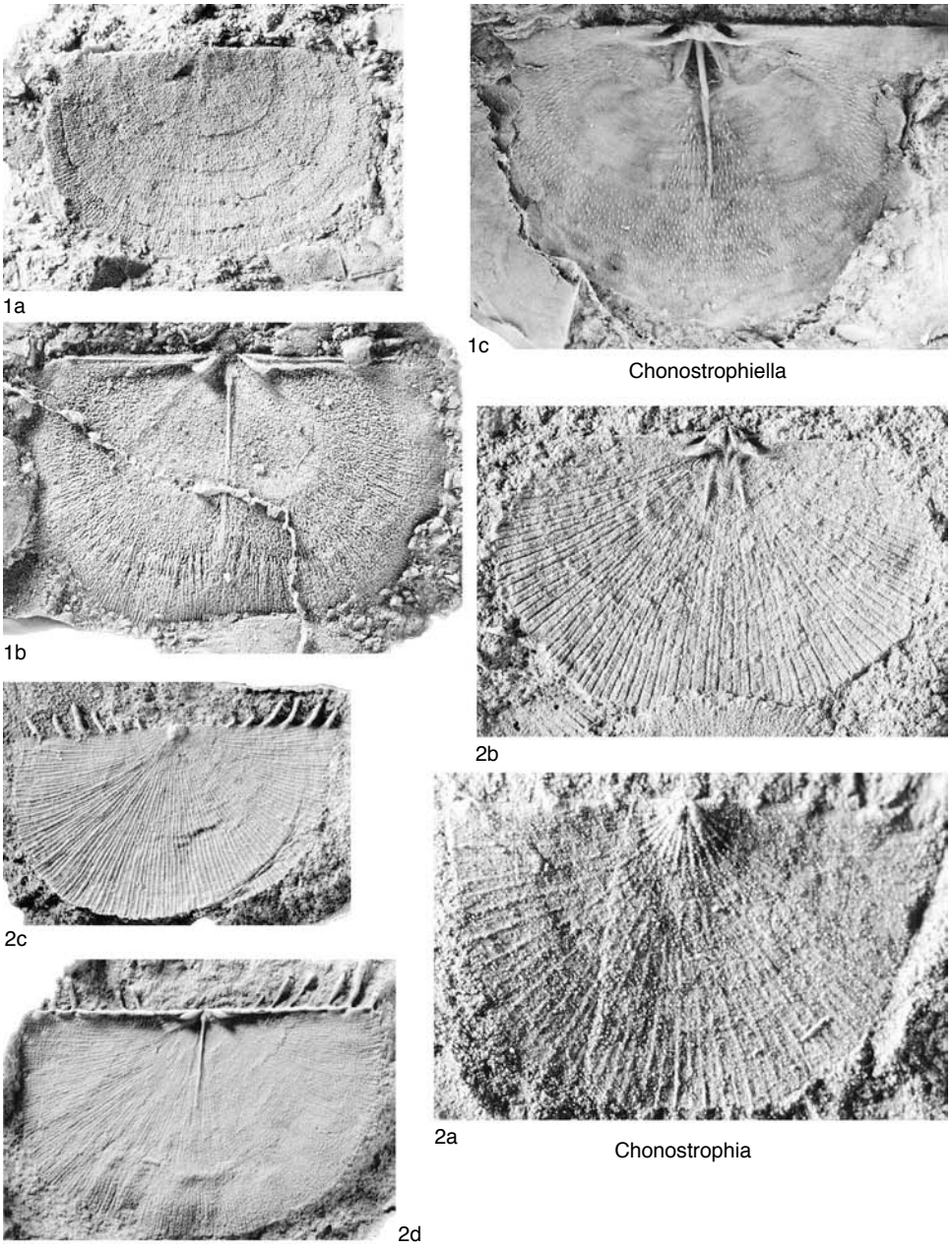

FIG. 248. Chonostrophiidae (p. 380–382).

Shell small to large; radial ornamentation finely costellate; spines orthomorph perpendicular, symmetrically arranged; dorsal interior with long median septum; long elevated anderidia anteriorly divergent at 50°; anterior margin of cardinal process, anterior edge of inner socket ridges almost vertical above valve floor; inner socket ridges short, narrow, rounded. *Lower Devonian (upper Lochkovian–lower Emsian):* North America (Appalachian Mountains, Canadian Arctic Archipelago), northeastern

China.——Fig. 248,*1a,b.* **C. complanata* (Hall), originals of Hall; ventral valve exterior, ventral valve interior, ×2 (Boucot & Amsden, 1964).——Fig. 248,*1c. C. briceae* Racheboeuf, Emsian, Canadian Arctic; dorsal valve interior, ×2 (Racheboeuf, 1987).

Tulcumbella Campbell in Campbell & Engel, 1963, p. 68 [**T. microstriata;* OD]. Shell small to medium, slightly resupinate; similar to *Chonostrophiella,* but with very short ventral median septum; dorsal interior with short, narrow median septum; inner socket ridges long, straight, parallel to hinge line; anderidia unknown. *Lower Carboniferous (Tournaisian):* Australia (New South Wales). Material not suitable for illustration.

Family ANOPLIIDAE Muir-Wood, 1962

[*nom. transl.* Boucot & Harper, 1968, p. 167, *ex* Anopliinae Muir-Wood, 1962, p. 32]

Shell very small to small, commonly as long as wide, usually strongly concavoconvex; shell surface smooth, capillate or costellate; pseudodeltidium and chilidium present; ventral area commonly concave; spines lacking or present, low-angled to vertical, always orthomorph, symmetrically or asymmetrically arranged; ventral muscle field usually deeply impressed in valve floor; hinge line denticulate in one genus; dorsal interior with pair of generally high-angled anderidia; one or several pairs of bladelike accessory septa sometimes replaced by sinuous irregular crests, or by stout, radially arranged, more or less fused endospines; median septum usually less well developed than accessory septa, lacking or replaced by breviseptum; cardinal process pit commonly present. [The classification adopted herein is still classical, purely phenetic, and without any phylogenetical implication. Due to their small size (among other characters), most genera included in this family seem likely to be no more than paedomorphic forms evolved from the family Chonetidae during the Devonian or from the family Rugosochonetidae during the Carboniferous, for example. A complete and detailed revision of the family Anopliidae is urgently needed.] *Devonian (Lochkovian)–Permian (Tatarian).*

Subfamily ANOPLIINAE Muir-Wood, 1962

[Anopliinae Muir-Wood, 1962, p. 32]

Small, strongly concavoconvex anopliids possessing smooth external shell. *Devonian (Lochkovian)–Permian (Tatarian).*

Anoplia Hall & Clarke, 1892, p. 309 [**Leptaena nucleata* Hall, 1857, p. 47; OD]. Shell very small, strongly concavoconvex; outline subtriangular to elongate; profile strongly arched transversely; spines not developed; spine apertures symmetrically arranged on posterior margin of ventral valve; dorsal interior with one to four pairs of variably developed accessory septa; median septum supporting cardinal process in oldest forms; cardinal process pit present in younger forms as in juveniles; in any case, median septum short, not extending beyond half valve length; anderidia relatively small, anteriorly divergent at 70°. *Lower Devonian (Lochkovian–upper Emsian):* USA, Europe.——Fig. 249,*1a–d.* **A. nucleata* (Hall), Camden Chert, USA; ventral valve exterior, dorsal valve exterior, ventral valve interior, dorsal valve interior, ×3.5 (Hall & Clarke, 1892).

Anopliella Racheboeuf, 1998, p. 52, *nom. nov. pro Tuberella* Vogel, Xu, & Langenstrassen, 1989, p. 36, *non Tuberella* Lee, 1987, echinoconchoid productid [**Tuberella tangxiangensis* Vogel, Xu, & Langenstrassen, 1989, p. 36; OD]. Shell very small, semicircular, and markedly concavoconvex; surface smooth; spines unknown; ventral interior without dental plates and septum; dorsal interior without median and lateral septa, but with numerous elongate, fusing tubercles in the midportion of the valve. *Lower Devonian (upper Emsian):* southern China.——Fig. 250,*1a,b.* **A. tangxiangensis* (Vogel, Xu, & Langenstrassen), upper Emsian, southern China; dorsal valve interiors, ×15 (Vogel, Xu, & Langenstrassen, 1989).

Anopliopsis Girty, 1938a, p. 281 [**Chonetina subcarinata* Girty, 1926, p. 27; OD]. Shell very small, subtriangular in outline with usually well-developed ears; profile deeply concavoconvex longitudinally; ventral valve with narrow, shallow sulcus; surface smooth with few prominent growth lines; spines orthomorph oblique, high-angled, symmetrically arranged; ventral interior with short median septum continued anteriorly by row of pustules that may coalesce; dorsal interior without median septum; several pairs of variably developed accessory septa; cardinal process small, anteriorly bounded by relatively large cardinal process pit; anderidia small. *Carboniferous (Viséan–Namurian):* USA.——Fig. 249,*2a,b.* **A. subcarinata* (Girty), lower Viséan, USA; dorsal valve interior, ventral valve internal mold, ×5 (Girty, 1938a).

Chonetina Krotow, 1888, p. 500, *nom. nov. pro Chonetella* Krotow, 1885, p. 274, 309, *non*

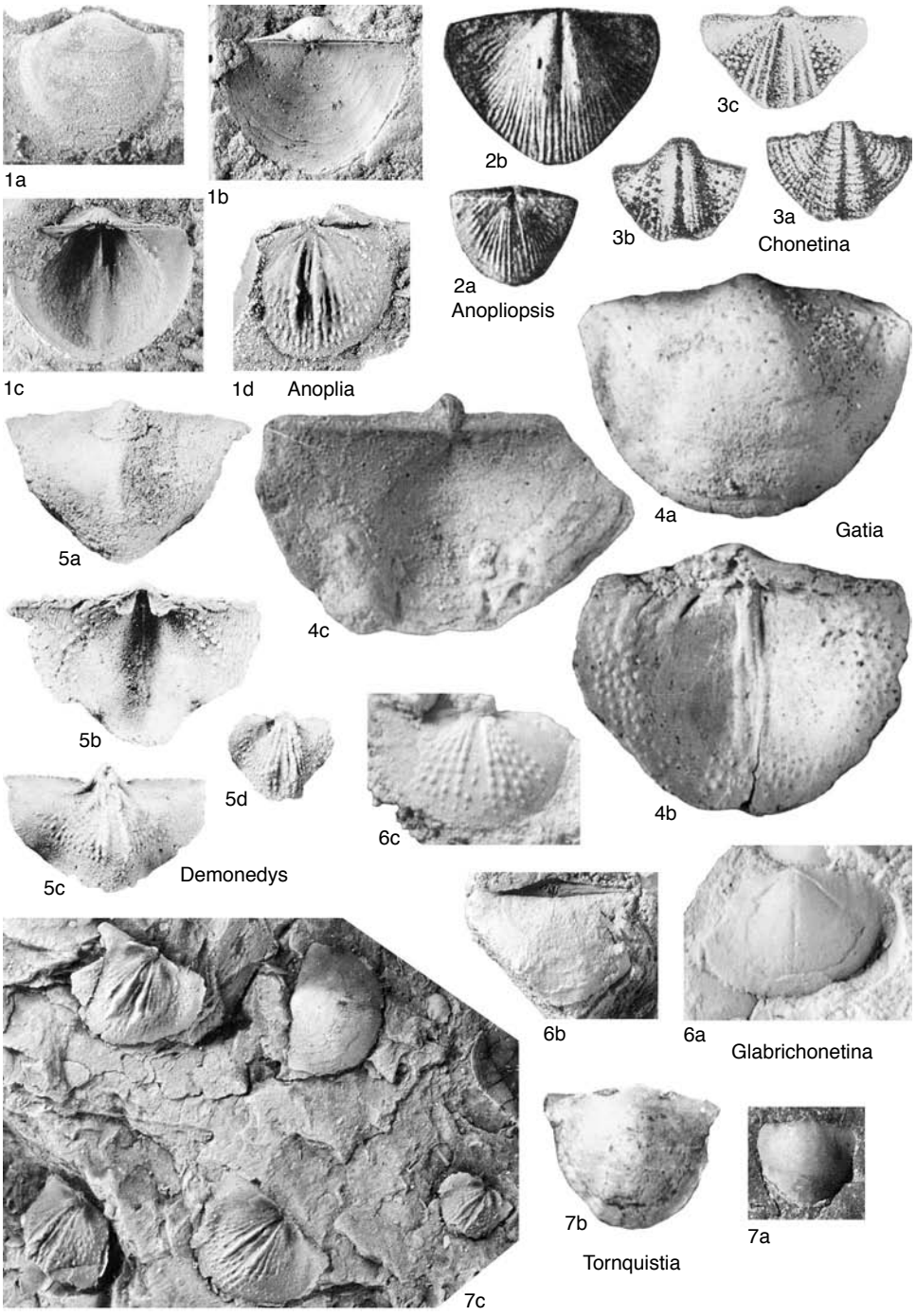

FIG. 249. Anopliidae (p. 382–385).

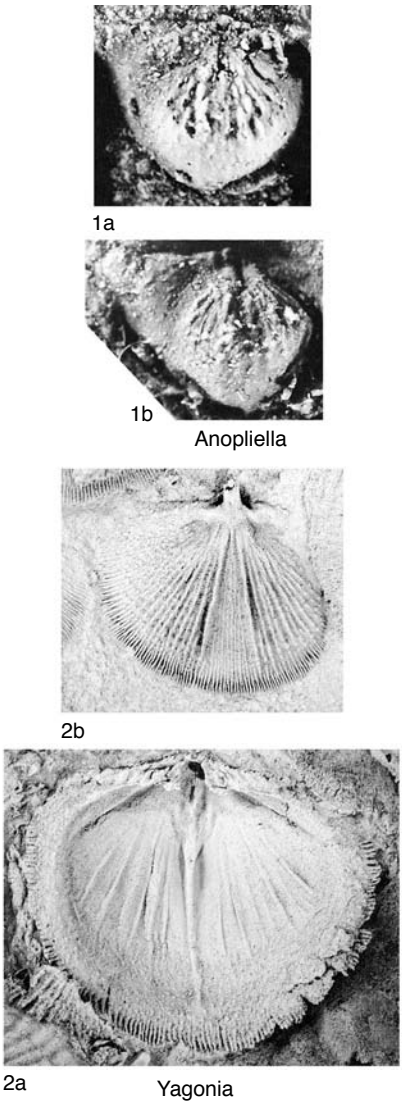

FIG. 250. Anopliidae (p. 382–385).

WAAGEN, 1884, p. 613, obj. [**Chonetella artiensis* KROTOW, 1885, p. 275; OD]. Shell small, highly concavoconvex with dorsal median fold, deep ventral sulcus; shell smooth with growth lines; spines developed; dorsal valve interior with several platelike septa formed from fused papillae; no median septum. *Upper Carboniferous (Stephanian)–Permian (Kazanian):* Europe, Asia.——FIG. 249,*3a–c. *C. artiensis* (KROTOW), Russia, Urals; ventral valve, ventral valve internal mold, dorsal valve interior, ×3 (Krotow, 1885).

Demonedys GRANT, 1976, p. 66 [**D. fastigiata;* OD]. Shell small, typically transversely subtrigonal in outline; shell strongly concavoconvex, almost trilobate with large median ventral fold, corresponding dorsal sulcus; surface smooth, pseudocapillate, with few lamellose concentric growth lines; spines orthomorph oblique, symmetrically arranged; ventral interior with short median septum; dorsal interior medianly folded with short anderidia, pair of long divergent accessory septa; cardinal process wide, posteriorly elevated above valve floor, supported by straight, narrow inner socket ridges anteriorly divergent at 100° to 105°, deep anterior pit. *Permian (Artinskian–Tatarian):* Thailand, Nepal, Western Australia.——FIG. 249,*5a–d. *D. fastigiata,* Permian, Thailand; ventral valve exterior, interior, dorsal valve interior, juvenile dorsal interior, ×4 (Grant, 1976).

Gatia ARCHBOLD, 1993, p. 4 [**G. superba;* OD]. Large, smooth anopliid-shaped shells, widest at hinge; ventral valve interior with short myophragm posteriorly, parallel vascular trunks extending to valve anterior on either side of myophragm; dorsal valve interior with short anderidia extending to form rounded, club-shaped brachiophores; short median septum arising anterior to shallow cardinal process pit, separated from short median septum by narrow depressed region; short accessory septa (or ridges) developed anterior to median septum, apparently by fusion of row of papillae. *Permian (Artinskian):* Western Australia.——FIG. 249,*4a–c. * G. superba,* Artinskian, Carnarvon basin, Western Australia; ventral valve exterior, interior, dorsal valve interior, ×3.5 (Archbold, 1993).

Glabrichonetina WATERHOUSE, 1978, p. 130 [**G. kuwaensis;* OD]. Shell small, moderately concavoconvex, with almost flat dorsal valve, ventral valve slightly swollen medianly; no fold nor sulcus; ventral interarea short, concave; dorsal interarea almost linear; no radial ornamentation; surface covered with very fine concentric lamellae; about ten pairs of spines orthomorph oblique, symmetrically arranged; ventral interior with low, long median septum; dorsal interior without median septum, accessory septa, but with several radial, anteriorly divergent rows of pustules. *Upper Permian (Tatarian):* northwestern Nepal.——FIG. 249,*6a–c. *G. kuwaensis,* Tatarian, Nepal; *a,* partly exfoliated ventral valve; *b,* dorsal exterior of articulated shell; *c,* dorsal valve interior, ×6 (Waterhouse, 1978).

Tornquistia PAECKELMANN, 1930, p. 227 [**Leptaena (Chonetes) polita* M'COY, 1855, p. 427; OD] [=*Paeckelmannia* LICHAREW, 1934b, p. 509, obj.]. Very small to small, highly concavoconvex medianly; greatest width along hinge line with well-differentiated ears; shell surface smooth, pseudocapillate when decorticated; few growth lines; spines orthomorph oblique, symmetrically arranged; ventral interior with long, narrow septum; dorsal interior with short, ill-defined anderidia anteriorly divergent at 40° to 50°; pair of long, narrow accessory

septa anteriorly divergent at 25° to 35°; median septum absent or reduced to short anteriorly placed median ridge; inner socket ridges short, straight, narrow; cardinal process small, anteriorly bounded by cardinal process pit. *Upper Devonian–Permian:* Great Britain, Ireland, France, Spain, Germany, Thailand.——Fig. 249,*7a–c. *T. polita* (M'Coy), Lower Carboniferous, Scotland; *a,b,* ventral valves showing spine row, ×4; *c,* slab with four dorsal valve interiors, ventral valve cast, ×4 (Paeckelmann, 1930).

Yagonia Roberts, Hunt, & Thompson, 1976, p. 210 [**Y. gibberensis;* OD]. Shell medium, moderately concavoconvex; no radial ornamentation; surface pseudocapillate when decorticated; narrow concentric growth lines; ventral interarea apsacline; dorsal interarea linear; pseudodeltidium, chilidium small; spines unknown; ventral interior with long median septum, flabellate diductors; dorsal interior with strong median septum supporting elongate cardinal process in largest shell, no pit; small anderidia anteriorly divergent at 60°; usually two pairs of long, spinose accessory septa and variably developed additional septa formed by fused endospines. *Carboniferous (upper Viséan–Westphalian):* eastern Australia.——Fig. 250,*2a,b. *Y. gibberensis,* Viséan, eastern Australia; ventral valve interior, dorsal valve interior, ×2 (Roberts, Hunt, & Thompson, 1976).

Subfamily CAENANOPLIINAE Archbold, 1980

[Caenanopliinae Archbold, 1980a, p. 189]

Small to medium-sized, concavoconvex anopliids with costate or costellate exterior. *Devonian (Lochkovian)–Permian (Kungurian).*

Caenanoplia Carter, 1968, p. 1143 [**C. burlingtonensis;* OD]. Shell small, strongly concavoconvex, subsemicircular to subtriangular in outline; ears well differentiated; spines orthomorph oblique, high-angled, symmetrically arranged; ventral interarea apsacline, flat to curved, with small pseudodeltidium; dorsal interarea hypercline, with chilidium; radial ornamentation of low rounded costellae crossed by lamellose growth lines; long, narrow ventral median septum; dorsal interior with large cardinal process pit, no median septum nor accessory septa; anderidia long, narrow, anteriorly divergent at 80°; surface covered with sparse endospines arranged in radial rows. *Lower Carboniferous (Tournaisian–Namurian):* North America.——Fig. 251,*1a–d. *C. burlingtonensis,* Burlington Limestone, Missouri; *a–c,* articulated shell, ventral, lateral, dorsal views; *d,* dorsal valve interior, ×4 (Carter, 1968).

Arcuaminetes Bizzarro, 1995, p. 158 [**Chonetes scitula* Hall, 1857, p. 107; OD]. Shell small, strongly concavoconvex, elliptical in outline with maximum width toward midline; radial ornamentation costellate; spines cyrtomorph intraversed, symmetrically arranged; dorsal valve interior with low median septum supporting low cardinal process; accessory septa low angled; anderidia well developed, high angled at 70°. *Middle Devonian (upper Eifelian–Givetian):* USA, France, Spain, Niger, Mauritania.——Fig. 251,*3a,b. *A. scitulus* (Hall), Hamilton Group, Givetian, USA; ventral valve exterior, dorsal valve interior, ×6.6 (Bizzarro, 1995).

Caplinoplia Havlíček & Racheboeuf, 1979, p. 102 [**C. pragensis;* OD]. Shell very small, strongly concavoconvex; spines orthomorph perpendicular, symmetrically arranged; dorsal interior with cardinal process pit, well-developed anderidia anteriorly divergent at 60° to 70°; two pairs of strong, bladelike accessory septa; external septa shorter, lengthening anderidia; well-developed breviseptum originating at midlength of valve. *Lower Devonian (Pragian–Emsian):* France, Spain, Bohemia, Russia, Canadian Arctic Archipelago.——Fig. 251,*2a–c. *C. pragensis,* Koneprusy Limestone, Pragian, Bohemia; *a,* ventral valve exterior; *b,* ventral valve internal mold; *c,* dorsal valve internal mold, ×10 (Havlíček & Racheboeuf, 1979).

Celtanoplia Racheboeuf, 1981b, p. 95 [**Chonetes boblayei* de Verneuil, 1850, p. 783; OD]. Shell very small, strongly concavoconvex; radial costellae tending to increase symmetrically both by bifurcation and intercalation; spines orthomorph oblique, symmetrically arranged, middle to high angled; cardinal process pit present in juveniles; short median septum supporting cardinal process in adults; anderidia relatively small but stout, anteriorly divergent at 80°; two or three pairs of well-developed, bladelike accessory septa. *Lower Devonian (Pragian–lower Emsian):* Rhenish Slate Mountains, Armorican Massif, Spain, Morocco, Algeria.——Fig. 251,*4a–e. *C. boblayei* de Verneuil, Saint Céneré Formation, Pragian, Armorican Massif; *a,* ventral valve exterior; *b,* dorsal side of articulated shell; *c,* ventral valve internal mold; *d,* ventral valve interior; *e,* dorsal valve interior, ×4 (Racheboeuf, 1981b).

Corbicularia Ljaschenko, 1973, p. 29 [**Chonetes menneri* Ljaschenko, 1958b, p. 119; OD]. Shell very small, ornamented with small fine costae; structure of shell with strongly concentrically wrinkled layers; spines symmetrically arranged, almost perpendicular; dorsal valve interior with well-developed cardinal process pit; median septum, accessory septa absent or reduced to low, almost indistinct structures. *Upper Devonian:* northern Europe, Russian Platform. Material not suitable for illustration (Ljaschenko, 1973).

Costachonetes Waterhouse, 1975, p. 2 [**Chonetes uralica* Möller var. *pygmaea* von Loczy, 1897, p. 64; OD]. Caenanopliids with swollen ventral valve with narrow ventral sulcus at least posteriorly; dorsal interior with thin median septum, small anderidia. *Upper Carboniferous (Kasimovian)–Lower Permian (Sakmarian):* Thailand. Material not suitable for illustration (Waterhouse, 1975).

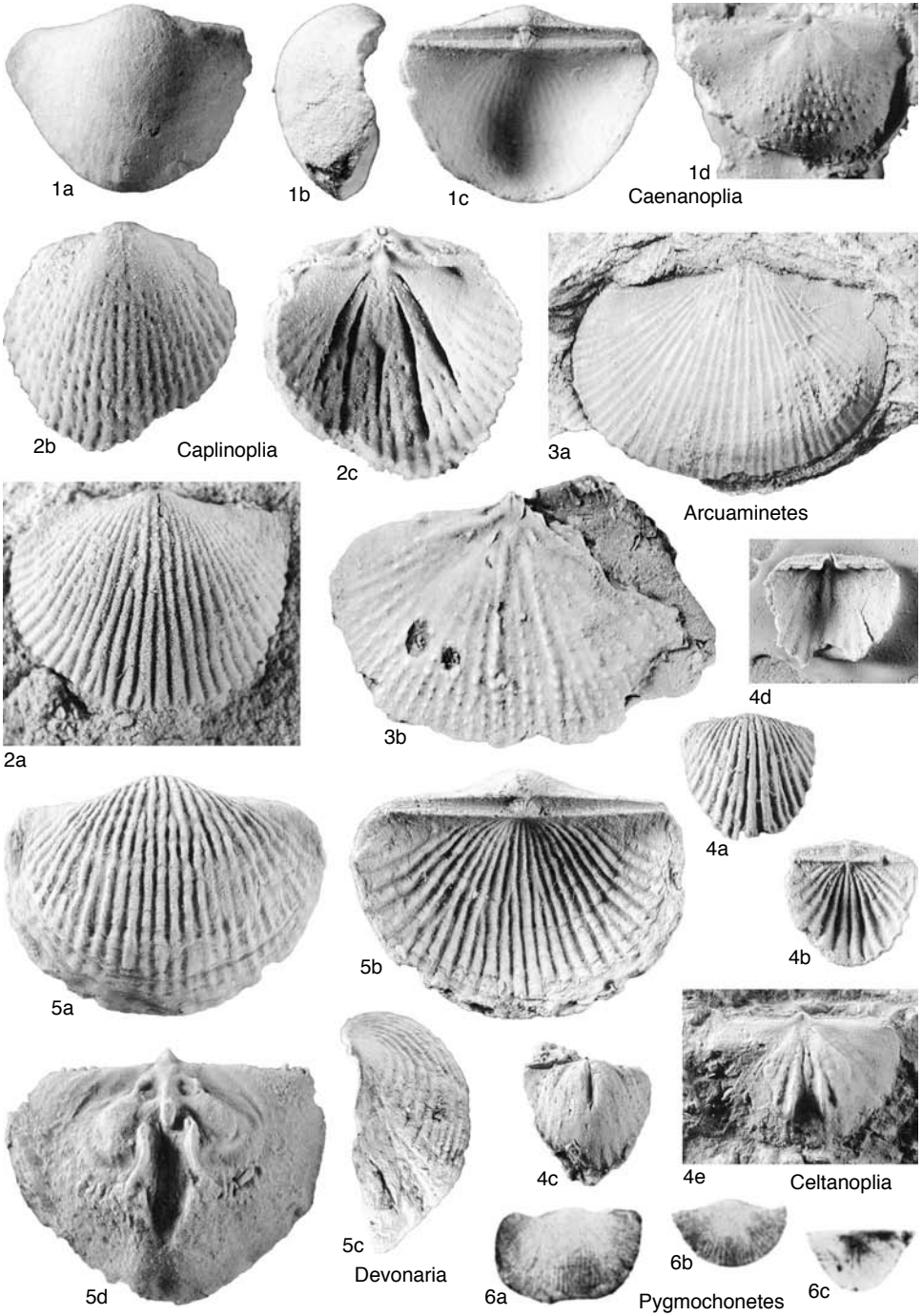

FIG. 251. Anopliidae (p. 385–387).

Costachonetina WATERHOUSE, 1981, p. 63 [**C. krotowi;* OD][=*Chonetina* sp. GRANT, 1976, p. 65]. Small subtriangular shell with arched ventral valve bearing sulcus; dorsal valve with corresponding fold; ears large; shell surface ornamented by strong costae; no spines developed but few spine apertures on posterior margin of ventral valve; dorsal median septum short, anteriorly elevated, with 2 to 4 pairs of spinose accessory septa. [AFANAS'EVA (1988, p. 89) regarded *Costachonetina* as a junior synonym of *Chonetinella* RAMSBOTTOM, 1952. The relatively strong radial ribbing, the development of the short, anteriorly elevated dorsal median septum, as well as the development of 2 to 4 spinose accessory septa, all characters lacking in *Chonetinella,* preclude such a synonymy.] *Lower Permian (Artinskian–Kungurian):* southern Thailand. Material not suitable for illustration (Waterhouse, 1981).

Devonaria BIERNAT, 1966, p. 77 [**Chonetes zeuschneri* SOBOLEV, 1909, p. 444; OD][=*Plicodevonaria* BOUCOT & HARPER, 1968, p. 162, obj.]. Shell small, rounded or weakly elongate in outline, usually strongly concavoconvex; surface costellate; no spines developed but canal apertures alternating on each side of umbo; hinge denticulate; cardinal process internally ventrally gibbous; short median septum supporting cardinal process; anderidia posteriorly fusing with septum, anteriorly divergent at 80°; one pair of long, narrow, bladelike accessory septa usually longitudinally curved medianly. *Middle Devonian (Eifelian–Givetian):* Poland, Nakichevan, Rhenish Slate Mountains, Armorican Massif, northern Africa (Tindouf syncline).——FIG. 251,*5a–d. *D. zeuschneri* (SOBOLEV), Skaly beds, Givetian, Poland; ventral valve exterior, dorsal exterior, lateral profile, dorsal valve interior, ×3 (Racheboeuf, new).

Globosochonetes BRUNTON, 1968, p. 48 [**G. parseptus;* OD]. Shell very small, strongly concavoconvex; strong radial ornamentation; ventral interarea orthocline with small pseudodeltidium; dorsal interarea almost linear; spines cyrtomorph bending medianly, disymmetrically arranged with two more spines on left side; ventral interior with short laterally elongated hinge teeth parallel to hinge line; dorsal interior showing short lobate median breviseptum in gerontic shells; long, narrow inner socket ridges supporting small cardinal process with small pit; anderidia reduced, anteriorly divergent at about 90°; accessory septa long, bladelike, anteriorly divergent at 10° to 15°. *Upper Devonian (Famennian)–Carboniferous (Moscovian):* Europe.——FIG. 252,*1a–d. *G. parseptus,* Viséan, Fermanagh, Ireland; *a,b,* ventral valve, exterior, interior; *c,* lateral profile; *d,* dorsal valve interior, ×7.5 (Brunton, 1968).

Klocinetes BIZZARRO, 1995, p. 162 [**Chonetes lepidus* HALL, 1857, p. 108; OD]. Shell small with flattened cardinal extremities; ornamentation of fine, angular costellae, with two enlarged costellae originating at beak of ventral valve; ventral valve interior with longitudinally divided myophragm; dorsal valve interior with pair of accessory septa; anderidia well developed, anteriorly divergent at 60°, not connected with cardinal process; short breviseptum, cardinal process pit present. *Middle Devonian (Eifelian):* USA.——FIG. 252,*3a–c. *K. lepidus* (HALL), Eifelian, Marcellus Formation of Hamilton Group; *a,* ventral valve exterior, ×7; *b,* articulated shell, dorsal view, ×5.4; *c,* dorsal valve interior, ×7.5 (Bizzarro, 1995).

Permochonetes AFANAS'EVA, 1977a, p. 148 [**P. pamiricus;* OD]. Shell relatively large for family; exterior finely costellate; spines orthomorph oblique, low angled; dorsal valve interior without accessory septa, median septum; anderidia reduced; rows of radial papillae present. *Permian (Artinskian):* Pamirs.——FIG. 252,*4a–c. *P. pamiricus,* Artinskian, Pamirs; ventral valve exterior, ventral valve internal cast, dorsal valve interior, ×3 (Afanas'eva, 1977a).

Plicanoplia BOUCOT & HARPER, 1968, p. 169, *non Plicanoplia* HAVLÍČEK, 1973, p. 337, obj. [**Chonetes fornacula* DUNBAR, 1920, p. 130; OD] [=*Cyrtoniscus* BOUCOT & HARPER, 1968, p. 172, subj.]. Shell very small, commonly strongly concavoconvex; radial costellae or costae relatively strong for shell size; no spines developed but symmetrically arranged canal apertures along posterior margin of ventral valve; dorsal interior with elevated anderidia anteriorly divergent at 90°; median septum fusing posteriorly with inner cristae, supporting cardinal process; accessory septa well developed. *Lower Devonian (Pragian–Emsian):* eastern North America, Armorican Massif, Spain, northern Africa.——FIG. 252,*2a–d. *P. fornacula* (DUNBAR), Camden Chert, Tennessee; juvenile dorsal valve interior, adult dorsal valve interior, ventral valve exterior, ventral valve interior, ×5 (Boucot & Harper, 1968).

Pygmochonetes JING & HU, 1978, p. 111[126] [**P. jingxianensis;* OD]. Shell small, subsemicircular, strongly concavoconvex; shell surface costellate; costellae bifurcating, intercalating laterally; spines orthomorph oblique, symmetrically arranged; ventral valve interior with low myophragm, radial rows of coarse endospines; dorsal valve interior with cardinal process pit, reduced breviseptum, at least one pair of accessory septa sometimes reaching anterior margin. *Lower Permian:* southern China.——FIG. 251,*6a–c. *P. jingxianensis,* Lower Permian, southern China; ventral valve exterior, ventral valve interior, dorsal valve internal mold, ×3 (Jing & Hu, 1978).

Semicaplinoplia RACHEBOEUF, 1995, p. 555 [**Plicanoplia sotoi* GARCIA-ALCALDE & RACHEBOEUF, 1978, p. 852; OD]. Externally similar to *Caplinoplia* but without spines on one side (usually left one) of ventral valve; dorsal valve interior with accessory septa displayed as in *Celtanoplia. Lower*

Devonian (Lochkovian): Spain, France, Algeria.——Fig. 252,*7a,b. *S. sotoi* (Garcia-Alcalde & Racheboeuf), Lochkovian, Nieva Formation, northwestern Spain; ventral valve exterior, dorsal valve interior, ×4 (Racheboeuf, 1995).

Songzichonetes Yang Xue-chang, 1984, p. 210[332] [**S. sanxiaensis;* OD]. Differs externally from *Pygmochonetes* by its less arched longitudinal profile, radial costellae bifurcating in middle part of shell, development of growth lines; internally, dorsal valve interior exhibits long inner socket ridges, but no median septum. *Permian:* southern China.——Fig. 252,*6a–c. *S. sanxiaensis,* Permian, southern China; ventral valve exterior, lateral profile, dorsal valve interior, ×5 (Yang Xue-chang, 1984).

Subglobosochonetes Afanas'eva, 1976, p. 67 [**C. (Rugosochonetes) malevkensis* Sokolskaya, 1950, p. 23; OD]. Similar to *Globosochonetes,* but dorsal valve interior without accessory septa; anderidia anteriorly divergent at 40° to 50°; no median septum. *Lower Carboniferous (Tournaisian):* Russian Platform.——Fig. 252,*5a–e. *S. malevkensis* (Sokolskaya), Tournaisian, Malevkian Horizon, Russian Platform; *a,b,* articulated shell, ventral, lateral views, ×6; *c,* ventral valve interior, ×3; *d,* ventral valve with preserved spines, ×3; *e,* dorsal valve interior, ×3 (Afanas'eva, 1976).

Subfamily HOLYNETINAE Racheboeuf, 1981

[Holynetinae Racheboeuf, 1981b, p. 109]

Small shell weakly concavoconvex to strongly arched; tranverse, subequidimensional to semicircular in outline; shell surface costate to costellate; spines orthomorph oblique to vertical, symmetrically or asymmetrically arranged; ventral valve interior with short, wide, transversely elongated teeth; dorsal valve interior with cardinal process pit, no median septum and one, or several, pair of accessory septa; anderidia low, short, not fused posteriorly; inner socket ridges short, poorly developed. *Devonian (Emsian)–Lower Carboniferous (Viséan).*

Holynetes Havlíček & Racheboeuf, 1979, p. 97 [**H. holynensis;* OD]. Shell weakly to strongly concavoconvex, transversely elongate; spines orthomorph perpendicular on right side of ventral valve only; dorsal interior without median septum; cardinal process pit small, deep, narrow; usually one pair of narrow, bladelike accessory septa extending from cardinal process pit almost to anterior margin; anderidia isolated on valve floor, anteriorly divergent at 50° to 60°. *Middle Devonian (Eifelian, Givetian):* Armorican Massif, Rhenish Slate Mountains, Spain, Bohemia.——Fig. 253,*4a. *H. holynensis,* Eifelian, Europe; ventral valve exterior, ×6.5 (Havlíček & Racheboeuf, 1979).——Fig. 253,*4b–d. H. stephaniae* Racheboeuf, Givetian, Kersadiou Formation, Armorican Massif; ventral valve exterior, ventral valve interior, dorsal valve interior, ×6 (Racheboeuf, 1981b).

Herrerella Racheboeuf, 1995, p. 559 [**H. zarelae;* OD]. Very small, transversely elongate, moderately concavoconvex; radial ornamentation of very low, almost indistinct costellae crossed by concentric, faint growth lines; erect, dissymmetrically arranged spines; ventral myophragm reduced; teeth laterally elongate, parallel to ventral interarea; dorsal valve interior with short, wide cardinal process, with pit, but no median septum; long inner socket ridges anteriorly divergent at 150°; anderidia almost imperceptible; no accessory septa, but two radial rows of strong endospines. *Upper Devonian (Famennian):* Morocco (Tafilalt).——Fig. 253,*5a–c. *H. zarelae,* Famennian, Tafilalt, Morocco; *a,* ventral valve exterior, ×18; *b,* holotype, ventral valve interior, FLS 413819, ×18; *c,* dorsal valve interior, ×18 (Racheboeuf, 1995).

Malayanoplia Hamada, 1969, p. 255 [**M. demiluna;* OD]. Shell transverse, gently concavoconvex; shell surface capillate; spines orthomorph vertical; dorsal valve interior with faint anderidia; no median septum; inner socket ridges narrow, parallel to hinge; one pair of prominent, high accessory septa; several pairs of less developed accessory septa on either side of first pair. *Upper Devonian:* Malayan Peninsula.——Fig. 253,*2. *M. demiluna;* dorsal valve interior, ×5 (Hamada, 1969).

Saharonetes Havlíček, 1984, p. 84 [**S. saharensis;* OD]. Shell gently concavoconvex; radial ornamentation costellate; costellae increase by bifurcation on ventral valve, by implantation in dorsal valve; spines orthomorph oblique, symmetrically arranged; ventral interarea flat, apsacline; dorsal one flat, almost linear, hypercline; pseudodeltidium present; chilidium unknown; small, oblique hinge teeth; interior dorsal without median septum; anderidia reduced, isolated on valve floor, anteriorly divergent at 90°; cardinal process longitudinally depressed ventrally; inner socket ridges short, strongly bending posteriorly to fuse with cardinal process; pair of long, thin accessory septa, low, gently divergent at 25° to 45°, extending about two-thirds valve length. *Lower Carboniferous (Tournaisian–Viséan):* Libya, Ghana.——Fig. 253,*1a,b. S. ghanaensis* Racheboeuf & others, ?Tournaisian, Ghana; ventral valve exterior, dorsal valve interior, ×5 (Havlíček, 1984).

Septachonetes Chatterton, 1973, p. 76 [**S. melanus;* OD]. Shell very small, transversely elongate; surface capillate; two orthomorph perpendicular spines on right side of ventral valve only; dorsal interior with deep cardinal process pit, faint anderidia anteriorly divergent at 70° to 80°; no median septum; three to five pairs of irregular sinuous accessory septa developed in anteromedian part of valve only. *Devonian*

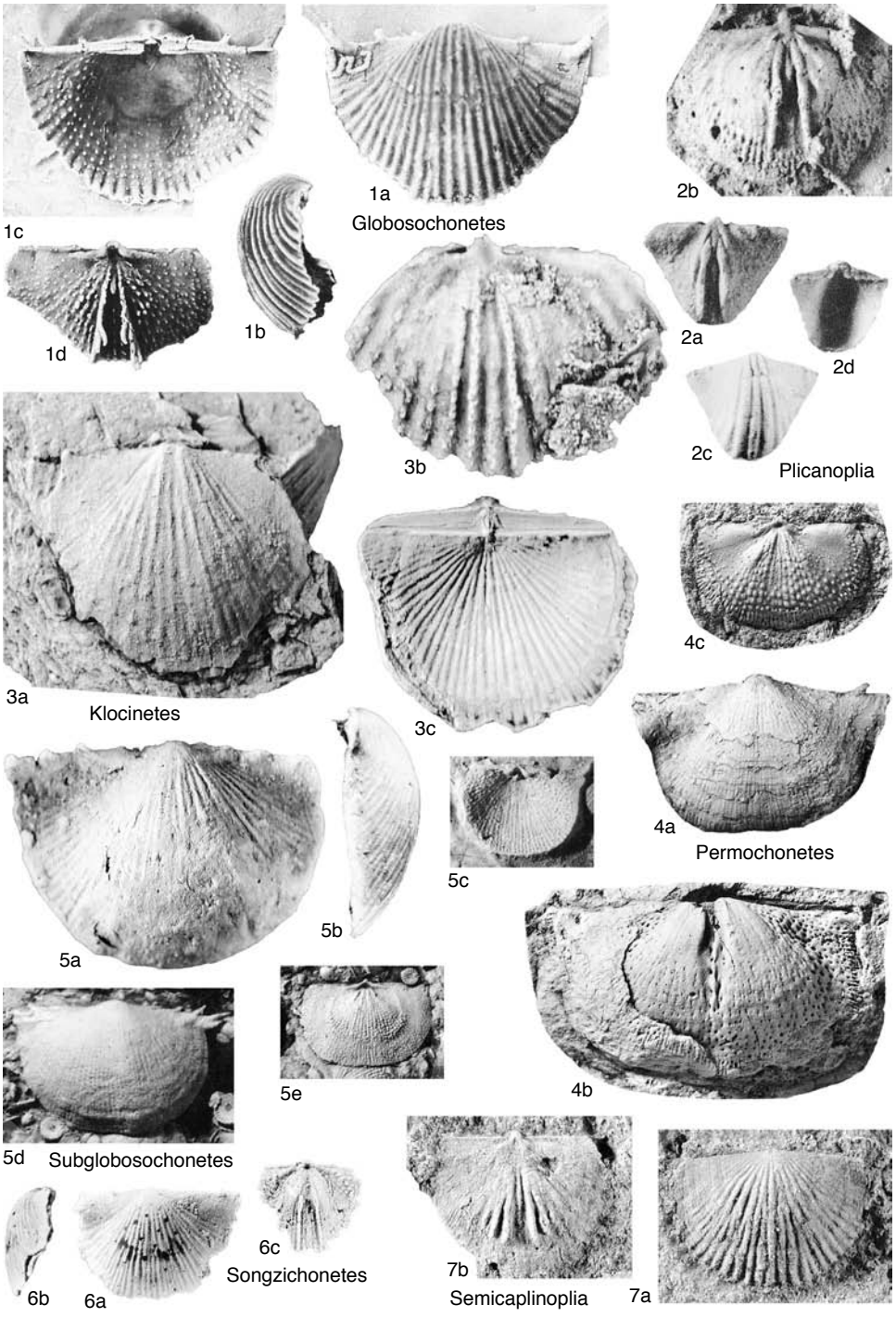

FIG. 252. Anopliidae (p. 387–388).

(?upper Emsian, ?lower Eifelian): Australia (New South Wales).——Fig. 253,*6a–c.* **S. melanus,* upper Emsian, Australia, New South Wales; *a,b,* ventral valve, exterior, interior, ×5.7; *c,* dorsal valve interior, ×10 (Chatterton, 1973).

Trichochonetes Roberts, 1976, p. 22 [**T. perpendicularis;* OD]. Similar to *Saharonetes,* but with orthomorph perpendicular spines; radial ornamentation capillate; dorsal interior with narrow inner socket ridges extending laterally almost parallel to posterior margin. *Lower Carboniferous (Viséan):* Australia (New South Wales).——Fig. 253,*3a,b.* **T. perpendicularis,* Viséan, Australia, New South Wales; ventral valve exterior, interior of an articulated shell, ×3 (Roberts, 1976).

Subfamily AIRTONIINAE Muir-Wood, 1962

[Airtoniinae Muir-Wood, 1962, p. 107]

Shell with thickened ventral valve; ventral interarea low; no dorsal interarea; adductor scars not dendritic; dorsal valve interior with breviseptum, strong anderidia posteriorly fused with strong, posteriorly projected cardinal process. *Lower Carboniferous (Viséan).*

Airtonia Cope, 1934, p. 273 [**A. hudsoni;* OD]. Shell medium, markedly concavoconvex, finely capillate; pseudodeltidium reduced or posterior callosity; cardinal process lobes widely divergent posterolaterally; periphery of brachial platform with strong radial accessory septalike ridges. *Lower Carboniferous (Viséan):* England, ?Belgium, ?France.——Fig. 254*a–e.* **A. hudsoni,* Viséan, England, Yorkshire; *a–c,* ventral valve, ventral, lateral, interior, ×1; *d,e,* dorsal valve, interior, exterior, ×1 (Cope, 1934).

Family EODEVONARIIDAE Sokolskaja, 1960

[Eodevonariidae Sokolskaja in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 223]

Shell small to large, capillate to rarely costate, moderately to markedly concavoconvex; ventral valve sometimes weakly sulcate; ventral interarea flat to more or less concave, weakly apsacline to anacline; dorsal interarea usually short, flat, hypercline; pseudodeltidium, chilidium present; spines inserted on posterior ventral margin, either symmetrically or not; spines closest to umbo sometimes lacking on one side; spines absent or variably developed, short, almost orthomorph perpendicular or long and cyrtomorph, bending medianly or laterally; ventral interior with myophragm, muscle field usually well developed; hinge line typically denticulate but variably developed; denticles extending all along hinge of both valves, or restricted to median part of both valves, or well developed on ventral valve only; vestigial hinge teeth present especially when hinge line not completely denticulate; dorsal median septum usually long, low, variably developed, supporting cardinal process; anderidia well differentiated, anteriorly divergent between 40° and 90°; inner socket ridges long, narrow, widely divergent anteriorly from 130° to 165°; accessory septa ill-defined, often reduced to low ridges in anteromedian part of valve, sometimes bending laterally; cardinal process variably developed in shape, size; short, small with posteriorly directed myophore, or internally geniculated with dorsally directed myophore, or strongly bilobed, widened posteriorly. *Lower Devonian (Pragian)–Middle Devonian (Eifelian).*

Eodevonaria Breger, 1906, p. 534 [**Chonetes arcuatus* Hall, 1857, p. 76; SD Schuchert & LeVene, 1929, p. 57]. Shell small to medium, variably concavoconvex in profile, moderately transverse in outline; radial ornamentation capillate to costate; spines symmetrically arranged, cyrtomorph bending laterally; ventral interarea flat to very weakly concave, apsacline; cardinal process short, subtriangular in ventral view, weakly bilobed internally; anderidia slightly divergent anteriorly at 40° to 50°; inner socket ridges at about 130° to 145°; accessory septa restricted to anterior part. *Lower Devonian (Pragian–Emsian):* North America (Appalachian Mountains).——Fig. 255,*1a–c.* **E. arcuata* (Hall), Camden Chert, Tennessee, USA; ventral internal mold, ventral valve exterior, dorsal valve interior, ×2 (Breger, 1906).

Davoustia Racheboeuf, 1976, p. 68 [**Chonetes davousti* Oehlert, 1887a, p. 66; OD]. Shell small, strongly concavoconvex, more or less transversely elongate; spines always very short, orthomorph almost perpendicular; spines asymmetrically arranged; hinge line denticulate with two vestigial hinge teeth; denticles always present in median part of ventral valve, sometimes lacking in dorsal valve of oldest species; dorsal interior with long median septum supporting cardinal process, ill-defined, variably developed accessory septa; cardinal process ventrally connected with swollen callus; anderidia long,

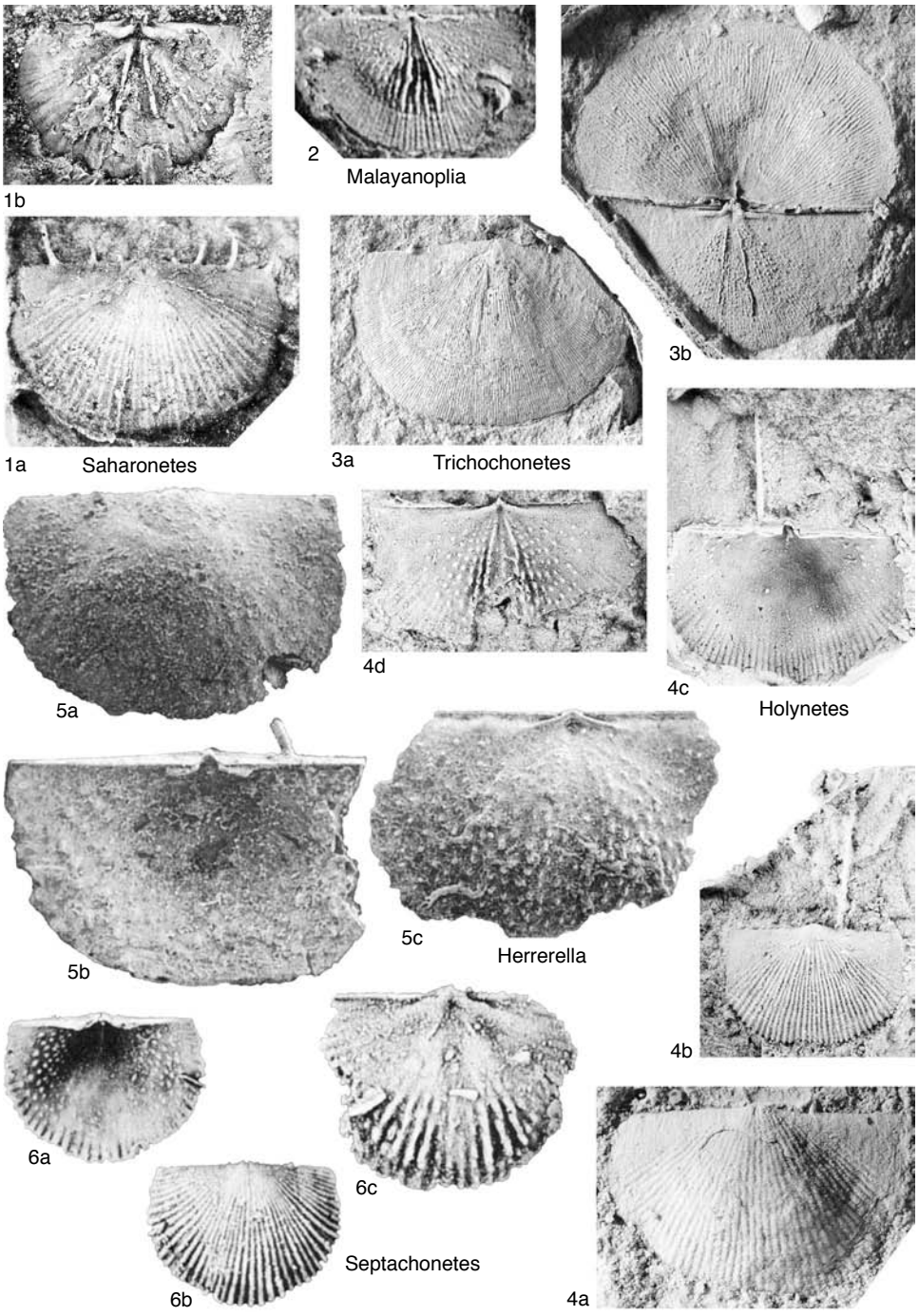

FIG. 253. Anopliidae (p. 388–390).

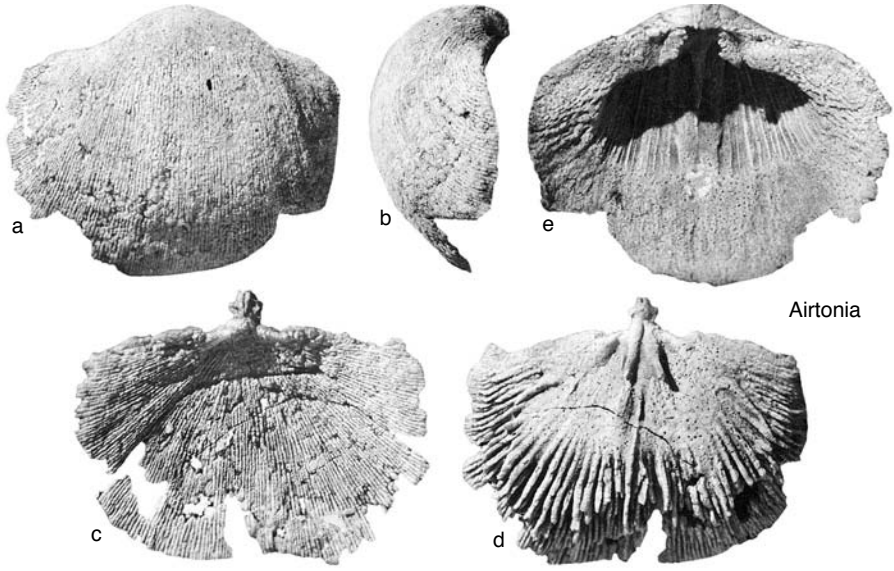

FIG. 254. Anopliidae (p. 390).

elevated, anteriorly divergent at 80° to 90°; cardinal process geniculated, bending dorsally, with myophore directed dorsally. *Lower Devonian (Pragian):* Armorican Massif, Spain, Morocco.——FIG. 255,*3a–c. *D. davousti* (OEHLERT), Pragian, Saint Céneré Formation, Armorican Massif; juvenile ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×6 (Racheboeuf, 1976).

Lomaella HERRERA, 1995, p. 127 [**L. primoris;* OD]. Medium to large, transverse shell, resembling *Loreleiella* in its posterolaterally widened cardinal process lobes, but without developed spines. *Lower Devonian (Pragian–Emsian):* Argentine Precordillera (Herrera, 1995).

Loreleiella RACHEBOEUF, 1986, p. 643 [**Eodevonaria jahnkei* RACHEBOEUF, 1981b, p. 192; OD]. Similar to *Eodevonaria* but shell often larger, transversely elongate; maximum width at hinge line, ears triangular, often well developed; cardinal process stout, deeply bilobed; lobes massive, widening, diverging posterolaterally, deeply grooved longitudinally; myophore directed posteriorly, sticking out of posterior margin. *Lower Devonian (Pragian)–Middle Devonian (Eifelian):* Armorican Massif, Rhenish Slate Mountains, Spain, Morocco, Algeria.——FIG. 255,*4a,b. *L. jahnkei* (RACHEBOEUF), Emsian, Spain; ventral valve exterior, dorsal valve interior, ×2 (Racheboeuf, 1986).

Renaudia RACHEBOEUF, 1976, p. 71 [**Eodevonaria (Renaudia) mainensis;* OD]. Similar to *Eodevonaria* but shell medium, transversely elongate, strongly arched longitudinally; ventral valve more or less sulcate; spines cyrtomorph bending medianly, symmetrically arranged; interareas relatively short. *Lower Devonian (upper Pragian–lower Emsian):* Armorican Massif, Spain, Morocco.——FIG. 255,*2a–d. *R. mainensis* (RACHEBOEUF), upper Pragian, Montguyon Formation, Armorican Massif; *a,* ventral valve exterior; *b,* dorsal side of articulated shell with spines; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Racheboeuf, 1976).

Family CHONETIDAE Bronn, 1862

[Chonetidae BRONN, 1862, p. 301]

Shell small to large, usually transverse, planoconvex to variably concavoconvex; shell surface smooth to costate; radial ornamentation sometimes restricted to posteromedian part of shell; concentric undulating fila present in some genera; spines commonly oblique, often numerous, high-angled to parallel to hinge line, symmetrically or asymmetrically arranged; ventral valve interior with well-developed, often transversely elongate, longitudinally striate hinge teeth; long, thin myophragm dividing large, variably impressed muscle field; *vascula media* weak or indistinct; dorsal valve interior with cardinal process anteriorly bounded by cardinal process pit, or elevated above valve floor, or

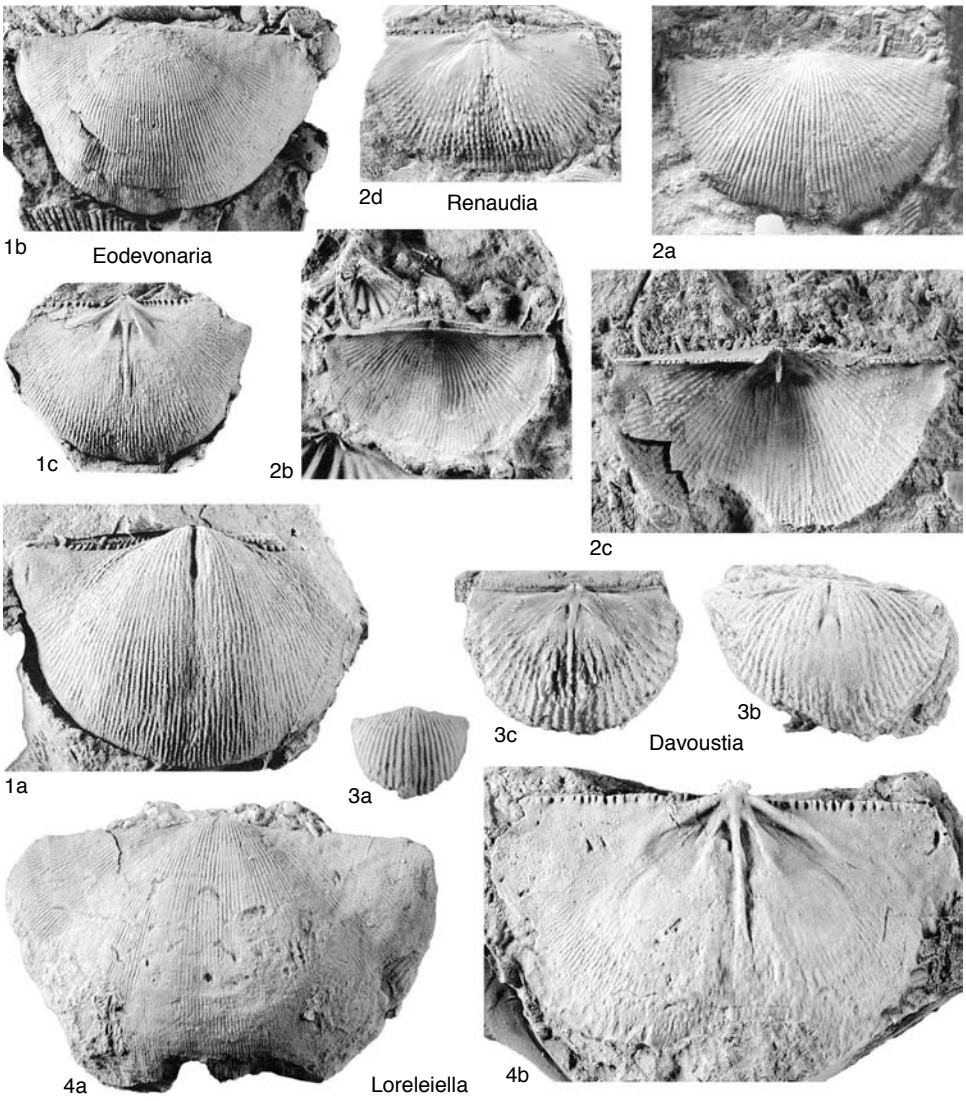

FIG. 255. Eodevonariidae (p. 390–392).

supported by median septum; cardinal process laterally flanked by commonly short, narrow, posteriorly bent inner socket ridges; median septum variably developed, sometimes reduced to breviseptum; pair of spinose or bladelike accessory septa developed in subfamily Chonetinae; anderidia usually weakly divergent anteriorly. *Lower Devonian (Pragian)–Upper Devonian (Frasnian, ?Famennian).*

Subfamily CHONETINAE Bronn, 1862

[*nom. transl.* WAAGEN, 1884, p. 612, *ex* Chonetidae BRONN, 1862, p. 301]

Small to medium chonetids, costate to capillate, without concentric fila; spines numerous, short, symmetrically arranged;

dorsal valve interior with short, low cardinal process, variably developed cardinal process pit; median septum ill developed, low, narrow, with one pair of variably differentiated accessory septa, usually spinose; long, low anteriorly weakly divergent anderidia. *Lower Devonian (Pragian–Emsian).*

Chonetes Fischer de Waldheim, 1830, pl. 26, fig. 8–9 [**Terebratulites sarcinulatus* von Schlotheim, 1820, p. 256; SD de Verneuil, 1845, p. 238]. Shell small to medium, transversely elongate; profile from almost planoconvex to moderately concavoconvex; beak small, narrow; ventral interarea apsacline, dorsal interarea hypercline; pseudodeltidium, chilidium present; spines low angled, orthomorph oblique geniculate, symmetrically arranged; radial ornamentation capillate or costellate originating at umbo, tapering toward margins looking smooth or finely lamellose; ventral interior with long, narrow median septum; strong laterally elongate hinge teeth obliquely placed; teeth, sockets longitudinally striate; dorsal interior with long, narrow median septum supporting cardinal process; short, posteriorly curved inner socket ridges; anderidia long, anteriorly divergent at 40°, posteriorly fused; shaft of cardinal process sometimes depressed medianly, but no true cardinal process pit; long, usually ill-defined accessory septa formed by fused endospines, anteriorly divergent at about 20°. *Lower Devonian (Pragian–Emsian):* Europe.——Fig. 256,*1a–d.* **C. sarcinulatus* (von Schlotheim), Emsian, Rhenish Slate Mountains; *a,* ventral valve exterior; *b,* dorsal valve interior; *c,* incomplete ventral valve exterior with spine bases; *d,* ventral valve internal mold, ×2 (Fischer de Waldheim, 1830).

Boicinetes Havlíček & Racheboeuf, 1979, p. 73 [**Chonetes bohemicus* Barrande, 1879, pl. 46, fig. II, 1–5; OD] [=*Chalimochonetes* Baranov, 1980, p. 142, obj.]. Shell medium, weakly concavoconvex; spines orthomorph oblique at about 70° to 80°, symmetrically arranged; ventral interarea apsacline, weakly concave, with small pseudodeltidium; dorsal interarea hypercline, flat, short, with inconspicuous chilidium; radial ornamentation very finely capillate (about 10 per mm); lamellose concentric growth lines; ventral interior with short myophragm; dorsal interior with long median septum, cardinal process pit, long anderidia anteriorly divergent at 35° to 45°; inner socket ridges high, narrow. *Lower Devonian (Pragian–Emsian):* Czech Republic, northeastern Russia.——Fig. 256,*2a–d.* **B. bohemicus* (Barrande), Pragian, Koneprusy Limestone, Czech Republic; *a,b,* ventral valve exterior, lateral profile; *c,* ventral valve internal mold; *d,* partly exfoliated dorsal valve interior, ×2 (Havlíček & Racheboeuf, 1979).

Plebejochonetes Boucot & Harper, 1968, p. 159 [**Chonetes plebeja* Schnur, 1854, p. 226; OD]. Resembles *Chonetes,* but shell usually smaller, more strongly concavoconvex; radial ornamentation of costellae or costae, posterolateral costae crossing posterior margin of valves; spines orthomorph oblique, symmetrically arranged; ventral valve interior with short myophragm, anteriorly rounded teeth; dorsal valve with short median septum; cardinal process pit developed in oldest representatives; cardinal process deeply bilobed internally; several pairs of ill-defined accessory septa in oldest forms, one pair of bladelike accessory septa in last representatives. *Lower Devonian (Pragian–Emsian):* Europe.——Fig. 256,*3a–d.* **P. semiradiatus* (Sowerby), Emsian, Rhenish Slate Mountains; *a,b,* ventral valve exterior, lateral profile; *c,* ventral valve internal mold; *d,* dorsal valve external mold, ×2 (Boucot & Harper, 1968).

Subfamily DAGNACHONETINAE Racheboeuf, 1981

[Dagnachonetinae Racheboeuf, 1981b, p. 153]

Small to large chonetids with numerous undulating fila crossing radial ornamentation; dorsal valve interior with large, posteriorly widened cardinal process not supported by median septum; breviseptum often well developed; no accessory septa; anderidia usually long, well developed, weakly divergent anteriorly. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Dagnachonetes Afanas'eva, 1978b, p. 66 [**D. caucasius;* OD]. Shell medium, weakly to moderately concavoconvex, transversely elongate; ventral sulcus, dorsal fold sometimes poorly developed in more arched species; spines orthomorph oblique, symmetrically arranged; ventral interarea apsacline, with wide pseudodeltidium; dorsal interarea catacline, with chilidium; radial ornamentation of numerous low costellae increasing rapidly in number, mainly by bifurcation in ventral valve; costellae narrowing toward periphery of shell when their numbers increase, crossed by very fine concentric fila; ventral interior with umbonal thickening, narrow, high median septum extending to midlength; hinge teeth laterally elongate, semioval; wide, internally bilobed cardinal process anteriorly bounded by cardinal process pit; inner socket ridges variable in length, extending almost parallel to hinge line; long, low, rounded median septum; anderidia long, straight or slightly bending medianly, anteriorly divergent at 50° to 70°; adductors usually well delimited. *Middle Devonian (Eifelian–Givetian):* Poland, Russia, France, Spain, China.——Fig. 257,*1a,b.* **D. caucasius,* Eifelian, Russia; ventral valve, dorsal valve interior, ×3 (Afanas'eva, 1978b).

Frankiella Racheboeuf, 1983, p. 607 [**F. drewitzi;* OD]. Shell small, transverse with leptaenoid morphology; longitudinal profile regularly concavo-

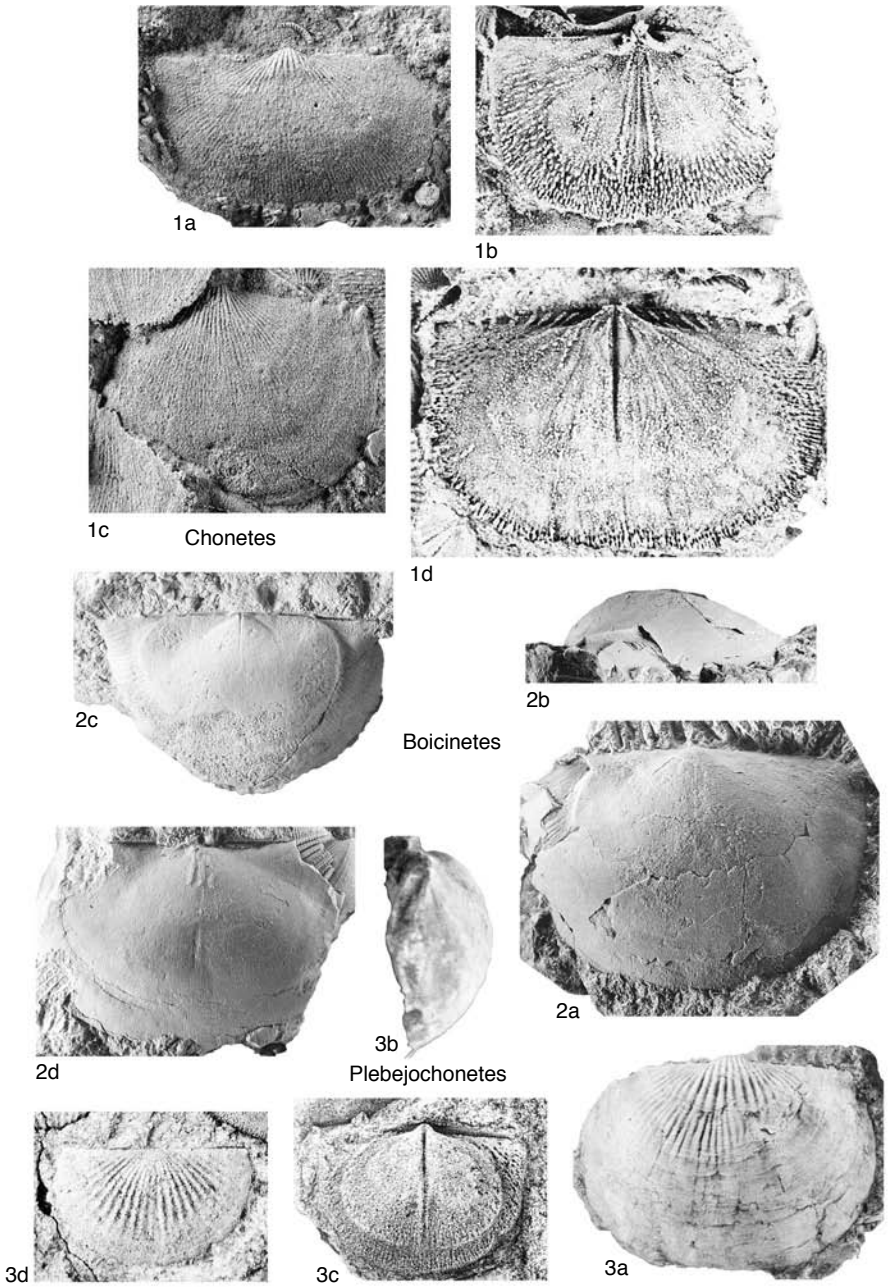

FIG. 256. Chonetidae (p. 394).

convex; from umbo, profile becoming anterolaterally planoconvex then resupinate, determining trail in anterior view; margin of both valves bending dorsally; ventral interarea flat, apsacline with wide delthyrium covered by pseudodeltidium; dorsal interarea flat, hypercline; chilidium unknown; radial

ornamentation costellate; costellae increasing ventrally by implantation, dorsally by bifurcation; spines orthomorph oblique, symmetrically arranged; ventral interior with short median septum; hinge teeth stout but small, anteriorly rounded; dorsal interior with wide, short, internally deeply bilobed cardinal process anteriorly bounded by large cardinal process pit; anderidia relatively long; breviseptum present; inner socket ridges low, widening laterally, supporting cardinal process medianly. *Middle Devonian (Eifelian):* Armorican Massif, Rhenish Slate Mountains.——Fig. 257,*2a,b.* **F. drewitzi,* Eifelian, Saint-Fiacre Formation, Armorican Massif; well-preserved ventral valve exterior, ventral valve with spines, ×3 (Racheboeuf, 1983).

Luanquella Garcia-Alcalde & Racheboeuf, 1978, p. 847 [**L. cantabriensis;* OD] [=*Dagnachonetes (Luanquella)* Racheboeuf, 1981b, p. 155]. Differs from *Dagnachonetes* by its radial ornamentation with costellae anteriorly widening, or not, crossed by few perceptible concentric fila; dorsal interarea always hypercline instead of catacline; inner socket ridges narrower, anteriorly less divergent. *Lower Devonian (Emsian):* France, Spain.——Fig. 257,*3a–d.* **L. cantabriensis,* Emsian, Cantabrian Mountains, Spain; *a–c,* ventral valve, exterior, profile, interior; *d,* dorsal valve interior, ×1.5 (Garcia-Alcalde & Racheboeuf, 1978).

Mamutinetes Havlíček, 1990, p. 132 [**M. latipleura;* OD]. Small, moderately concavoconvex shell with wide, very low radial costellae originating anterior of beak, widening anteriorly; orthomorph oblique, symetrically arranged hinge spines; deep elongate-oval cardinal process pit; long, low, narrow breviseptum; no accessory septa; anderidia ill defined; long, straight inner socket ridges parallel to hinge line. *Lower Devonian (Emsian):* Bohemia.——Fig. 258,*1.* **M. latipleura,* Eifelian, Czech Republic; ventral valve exterior, ×4 (Havlíček, 1990).

Nurochonetes Ushatinskaya, 1977, p. 42 [**Chonetes akkultukensis* Ushatinskaya, 1966, p. 92; OD]. Shell medium to large, transverse; gentle ventral sulcus, weak dorsal fold usually present; radial ornamentation of bifurcating costellae; spines orthomorph, almost vertical, symmetrically arranged; pseudodeltidium, widely separated chilidial plates; ventral valve interior with short myophragm, massive lamellar teeth; dorsal valve interior with narrow median septum supporting cardinal process; anderidia anteriorly divergent at 40° to 50°; strong, curved, inner socket ridges. *Lower Devonian (Emsian):* Kazakhstan.——Fig. 257,*4.* **N. akkultukensis* (Ushatinskaya), Emsian, Kazakhstan; ventral, dorsal valve internal molds, ×3 (Ushatinskaya, 1977).

Pradochonetes Pardo & Garcia-Alcalde, 1984, p. 104 [**P. muelleri;* OD]. Shell small, weakly transverse, moderately concavoconvex; radial ornamentation of rounded costellae regularly dichotomizing ventrally, intercalating dorsally; spines orthomorph, high angled, symmetrically arranged; ventral valve interior with very short myophragm, strong endospines in posterolateral areas; dorsal valve interior with breviseptum in juveniles, stout median septum supporting cardinal process in largest shells; anderidia long, narrow, widely divergent anteriorly, not fusing posteriorly; inner socket ridges thickening, elevating during ontogeny, almost parallel to hinge. *Upper Devonian (Frasnian):* Spain.——Fig. 258,*2a–c.* **P. muelleri,* Frasnian, southern Spain; *a,b,* ventral valve exterior, dorsal valve interior; *c,* ventral valve exteriors, dorsal valve interiors, ×3 (Pardo & Garcia-Alcalde, 1984).

Rhyssochonetes Johnson, 1970b, p. 2095 [**R. aurora solox;* OD] [=*Cedulia* Racheboeuf, 1979, p. 256, obj.]. Shell small, transversely elongate, moderately concavoconvex; radial ornamentation of rounded costellae crossed by fine, closely spaced fila; orthomorph oblique, high-angled, symmetrically arranged spines; periphery of ventral interior ornamented with concentric undulating ridges, corresponding to fila; variably developed cardinal process pit; inner socket ridges variably elongate, almost parallel to hinge line; anderidia relatively short, anteriorly divergent at 60° to 70°; septum poorly developed, sometimes absent or extending anteriorly as breviseptum; no accessory septa. *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* North America, northern France.——Fig. 257,*5a–d.* **R. solox,* Givetian, Nevada; *a,b,* ventral valve exterior, interior; *c,d,* dorsal valve interiors, ×4 (Johnson, 1970b).

Sinochonetes Wang, Boucot, & Rong, 1981, p. 288[293] [**Chonetes minutisulcatus* Hou & Xian, 1975, p. 25; OD]. Shell small to medium, often uniplicate; ventral sulcus, dorsal fold variably developed; ventral interarea apsacline, flat; dorsal interarea narrow, hypercline; pseudodeltidium, chilidium present; orthomorph oblique symmetrically arranged spines; radial ornamentation capillate to costellate; ventral myophragm very short; hinge teeth massive; dorsal interior with long median septum often elevated anteriorly, supporting cardinal process ventrally connected with swollen callus; anderidia anteriorly divergent at 60°; inner socket ridges long, variably developed, anteriorly divergent at 150° to 160°. *Lower Devonian (Pragian–Emsian):* southern China, Canadian Arctic Archipelago.——Fig. 258,*3a–c.* **S. minutisulcatus* (Hou & Xian), upper Pragian, southern China; *a,b,* ventral valve, exterior, profile; *c,* dorsal valve interior, ×3 (Wang, Boucot, & Rong, 1981).

Subfamily DEVONOCHONETINAE Muir-Wood, 1962

[Devonochonetinae Muir-Wood, 1962, p. 43]

Small to large chonetids, weakly to markedly concavoconvex; shell surface with

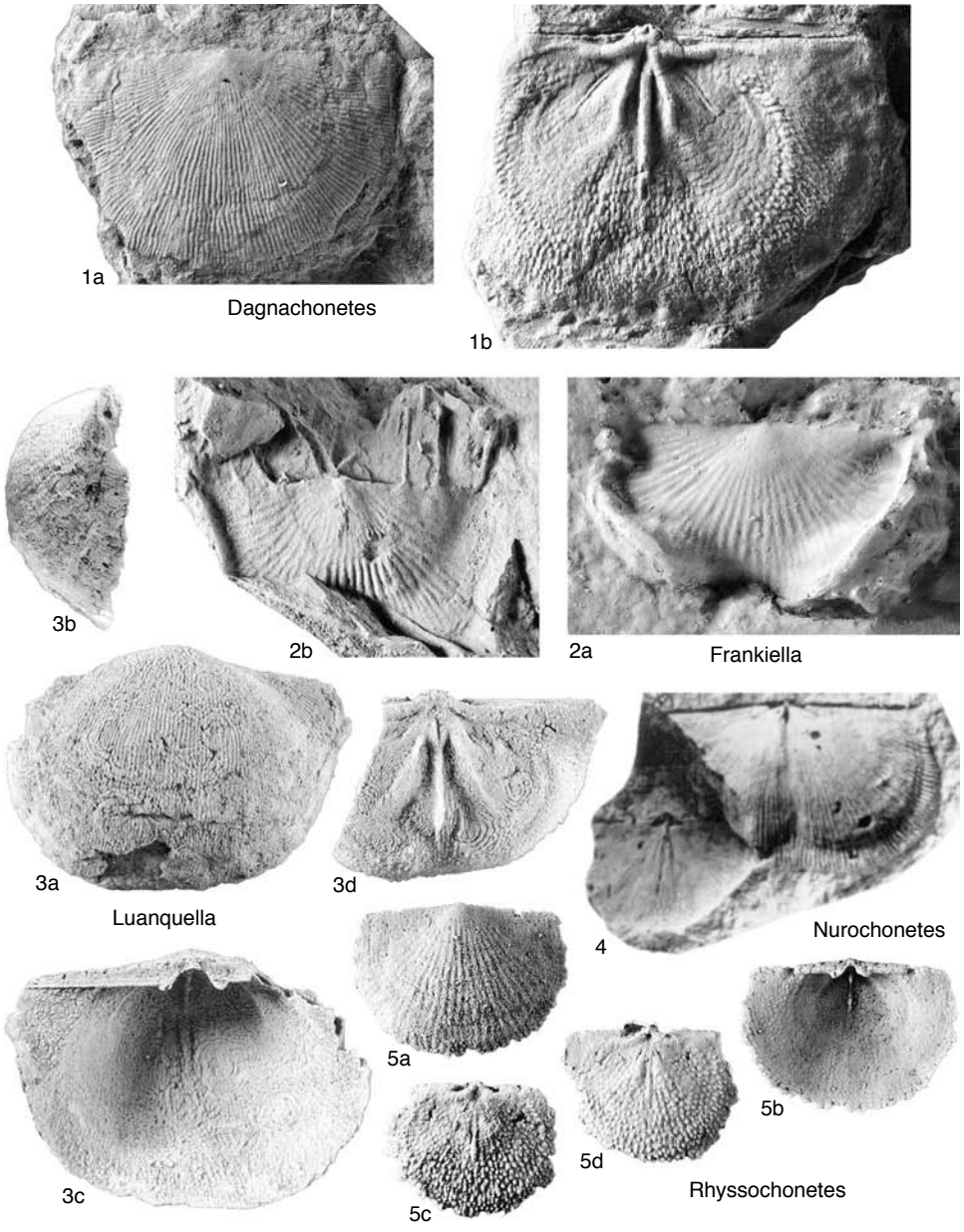

FIG. 257. Chonetidae (p. 394–396).

numerous costae or costellae without concentric fila; spines orthomorph oblique to cyrtomorph; large, weakly prominent pseudodeltidium; chilidium small; ventral valve interior with large, well-impressed muscle field; dorsal valve interior with long median septum supporting elevated, relatively long, narrow, cardinal process; no true

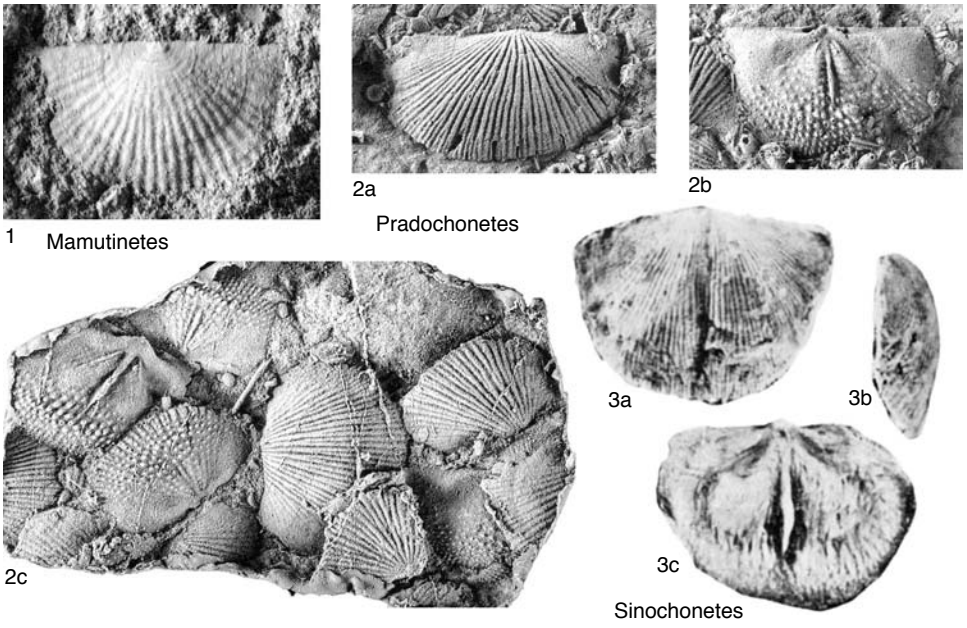

FIG. 258. Chonetidae (p. 396).

accessory septa; anderidia posteriorly fused with cardinal process; inner socket ridges relatively developed for family. *Lower Devonian (Emsian)–Upper Devonian (Frasnian).*

Devonochonetes MUIR-WOOD, 1962, p. 43 [**Chonetes coronatus* HALL, 1857, p. 146; OD; *nom. nov. pro Strophomena carinata* CONRAD, 1842, p. 257, *non* CONRAD, 1839, p. 64]. Shell small to medium, transverse, moderately concavoconvex; shell surface capillate to costellate; spines orthomorph oblique, low angled; dorsal valve interior with long median septum supporting the long, elevated cardinal process; anderidia weakly anteriorly divergent. *Middle Devonian (Eifelian–Givetian):* North America.——FIG. 259,*1a–e.* **D. coronatus* (HALL), Hamilton Group, Kashong Shales, New York; *a–c,* ventral valve, ventral, lateral, anterior views; *d,e,* dorsal valve exterior, interior, ×2.5 (Muir-Wood, 1962).

Aseptonetes ISAACSON, 1977, p. 177 [**A. boucoti;* OD]. Shell small to medium, moderately concavoconvex, equidimensional to weakly transverse; radial costellae, interspaces variably V-shaped in cross section; spines orthomorph oblique high angled to vertical, symmetrically arranged; juvenile dorsal valve interior with weak median septum, accessory septalike radial rows of strong endospines; adult dorsal valve interior with long, narrow median septum. *Middle Devonian (Eifelian–Givetian):* South America (Bolivia).——FIG. 259,*3a–e.* **A. boucoti,* Eifelian, uppermost Icla, Huamampampa Formations, Bolivia; *a,* internal mold of articulated shell; *b,* ventral valve; *c,d,* latex cast of both valves; *e,* ventral valve exterior, latex cast, ×2 (Racheboeuf & Branisa, 1985).

Hallinetes RACHEBOEUF & FELDMAN, 1990, p. 4 [**Strophomena lineata* CONRAD, 1839, p. 64; OD]. Shell small, markedly concavoconvex when adult; spines orthomorph perpendicular, disymmetrically arranged; radial ornamentation of low-rounded costellae often narrowing anteriorly as their numbers increase; ventral interarea apsacline, concave; dorsal interarea almost linear, hypercline; pseudodeltidium, chilidium not observed; ventral interior with long myophragm and large, deeply impressed muscle field; dorsal interior swollen with long median septum not supporting cardinal process; cardinal process pit in juveniles; posteromedian part of valve deeply depressed in adults; anderidia anteriorly divergent at 50° to 55°, posteriorly fused with wide, long inner socket ridges; no accessory septa; adductors deeply impressed. *Middle Devonian (Eifelian):* New York.——FIG. 259,*2a–c.* **H. lineatus* (CONRAD), Seneca Member, Onondaga Limestone, New York; ventral valve exterior, ventral valve interior, dorsal valve interior, ×3 (Racheboeuf & Feldman, 1990).

Huananochonetes WANG, BOUCOT, & RONG, 1981, p. 290[295] [**Parachonetes ovalis* HOU & XIAN, 1975, p. 27; OD]. Shell small, highly concavoconvex;

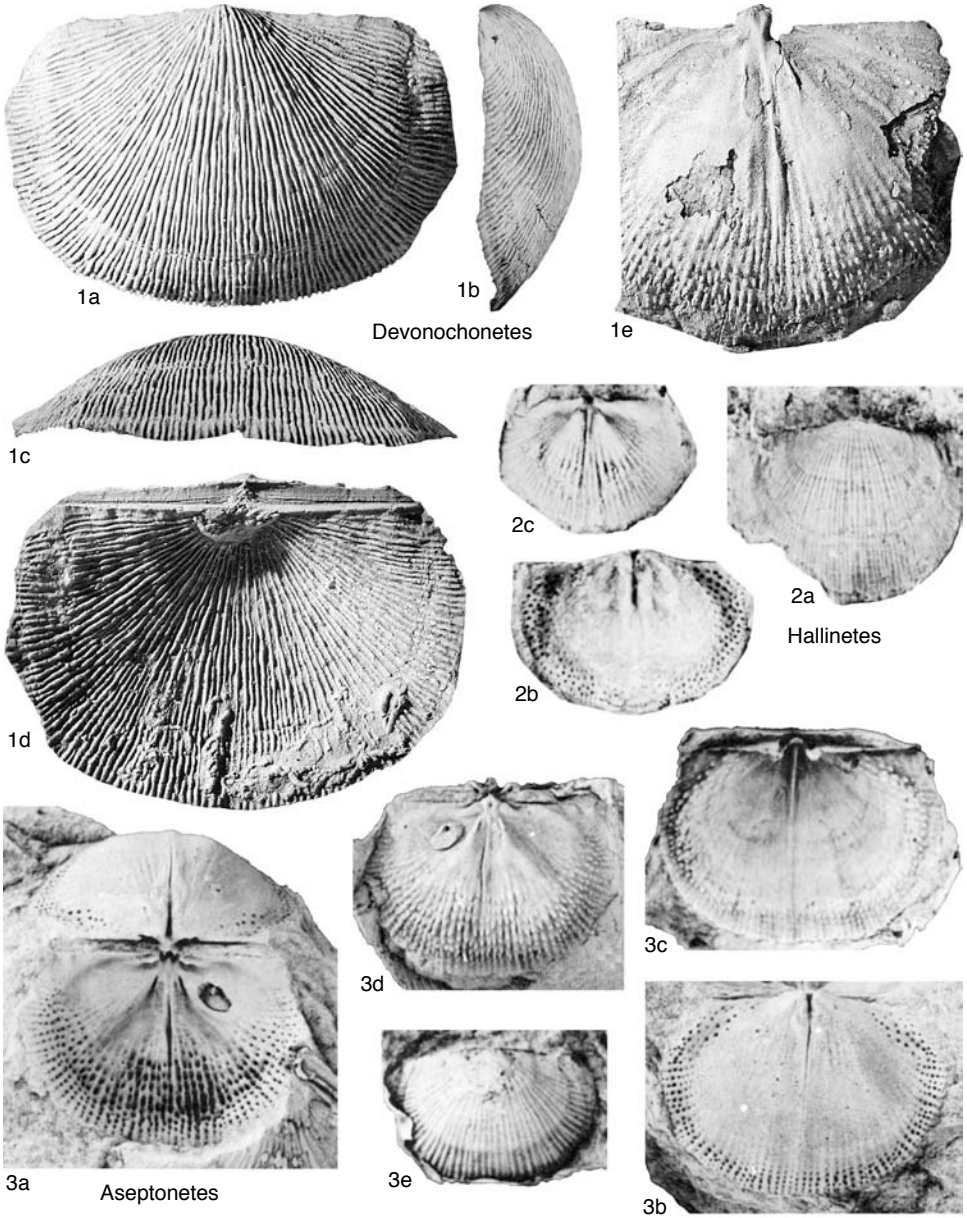

FIG. 259. Chonetidae (p. 398).

orthomorph oblique, high-angled spines at about 50°; radial ornamentation of narrow, rounded costellae; large, convex pseudodeltidium; chilidium reduced, almost indistinct; ventral interior with short myophragm, short, ill-developed hinge teeth; dorsal interior with long median septum supporting cardinal process; short anderidia anteriorly highly divergent at 80°; long, narrow inner socket ridges almost parallel to posterior margin. *Lower Devonian (Emsian):* southern China.——FIG. 260,*1a–c.* **H. ovalis* (HOU & XIAN), lower Emsian, Yukiang Formation, central Guangxi; *a,b,* ventral valve, ventral, lateral views; *c,* dorsal valve interior, ×3 (Wang, Boucot, & Rong, 1981).

Longispina Cooper, 1942, p. 230 [**Chonetes emmetensis* Winchell, 1866, p. 92; OD]. Shell small, usually strongly concavoconvex; anterior margin regularly rounded; small umbo prominent, often strongly curved posteriorly; ventral interarea concave, anacline; dorsal interarea more or less concave, hypercline; pseudodeltidium long, narrow; chilidium small; radial ornamentation costellate to costate; few strong growth lines usually present; spines orthomorph parallel to hinge line, symmetrically arranged; ventral interior with short, stout median septum; hinge teeth relatively small, anteriorly rounded; dorsal interior with variably developed median septum supporting long, narrow cardinal process; myophore long, narrow, dorsally directed; inner socket ridges low, short; anderidia small, anteriorly divergent at 50° to 70°; pair of variably developed accessory septa in anterior part of valve, anteriorly divergent at 20° to 30°. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian):* North America (Appalachian Mountains), Venezuela, Bolivia, Morocco, Algeria, Spain, France.——Fig. 260,*5a–d. *L. emmetensis* (Winchell), Middle Devonian, Hamilton Group, New York, USA; ventral valve internal mold, ventral valve exterior, articulated shell in dorsal view, dorsal valve interior, ×3 (Cooper, 1942).

Montsenetes Racheboeuf, 1992, p. 37 [**Devonochonetes notius* Benedetto, 1984, p. 60; OD]. Shell medium, subequidimensional or weakly transverse, strongly concavoconvex; radial ornamentation relatively strong; spines orthomorph oblique, symmetrically arranged; ventral valve interior with long myophragm dividing large, radially striate, muscle field with semielliptical adductors; dorsal valve interior with strong median septum, anteriorly elevated, supporting large, posteriorly elongated, elevated cardinal process; anderidia weakly divergent anteriorly. *Middle Devonian (Eifelian–Givetian):* North America (Appalachian Mountains), Venezuela, Bolivia, Sahara.——Fig. 260,*2a–c. *M. notius* (Benedetto), Middle Devonian, Caño del Oeste Formation, Sierra de Perija, Venezuela; ventral valve, ventral, lateral views, dorsal valve interior, ×2 (Benedetto, 1984).

Striatochonetes Mikrjukov, 1968, p. 90 [**Strophonema setigera* Hall, 1843a, p. 180; OD]. Shell very small, subsemicircular; shell surface finely costellate; spines cyrtomorph intraverse, symmetrically arranged; dorsal valve interior with shallow cardinal process pit, no median septum, one pair of narrow, low accessory septa; anderidia very reduced; inner socket ridges relatively strong. [When he described the new genus, Mikrjukov mentioned the concentric fila crossing the radial ribs and the intervals. This character could not be observed in the North American shells.] *Middle Devonian (Eifelian):* North America, Russia.——Fig. 260,*4a–c. *S. setigera* (Hall), Middle Devonian, Chemung Group, New York; ventral valve exterior, partly exfoliated ventral valve, dorsal valve interior, ×4 (Mikrjukov, 1968).

Xinjiangochonetes Xu, 1991, p. 317[330] [**X. pygmaeus;* OD]. Shell small to medium, moderately concavoconvex, subsemicircular in outline; shell surface costellate; spines low angled; ventral valve interior with large teeth, very long myophragm; dorsal valve interior with short, weak median septum. [Due to the preservation of the type material, this monospecific genus remains poorly known. The lack of dorsal accessory septa, however, makes likely its assignment to the Devonochonetinae.] *?Lower Devonian (Emsian), Middle Devonian (Eifelian):* China (northern Xinjiang).——Fig. 260,*3a,b. *X. pygmaeus,* ?upper Lower Devonian, Eifelian, northern Xinjiang; ventral valve internal molds, dorsal valve interior, ×1.5 (Xu, 1991).

Subfamily NOTIOCHONETINAE Racheboeuf, 1992

[Notiochonetinae Racheboeuf, 1992, p. 42]

Shell medium to large, transverse, nearly planoconvex to markedly concavoconvex; ventral interarea orthocline or apsacline, flat or weakly concave, with pseudodeltidium; dorsal interarea anacline, with strong, distinct chilidial plates; radial ornamentation costellate, without fila; spines orthomorph oblique, low angled, symmetrically arranged; ventral interior with strong, short, often laterally elongate hinge teeth; myophragm long, dividing large muscle field; diductors usually flabellate; dorsal interior with stout cardinal process, strongly bilobed internally, prominent above valve floor; myophore varying from posteriorly to dorsally oriented; strong anderidia anteriorly divergent at 20° to 45°; long, narrow median septum usually supporting cardinal process developing during ontogenesis; accessory septa distinct in juveniles, tapering with growth, often absent in largest shells. *Lower Devonian (Emsian)–Middle Devonian (Givetian).*

Notiochonetes Muir-Wood, 1962, p. 48 [**Chonetes skottsbergi* Clarke, 1913, p. 29; OD]. Shell medium to large, transverse, plano- to slightly concavoconvex; pseudodeltidium, disjunct chilidial plates; external spines unknown; ventral valve interior with large elongate teeth, large muscle field; large cardinal process, elevated, with myophore projecting ventrally; median septum low, narrow, pos-

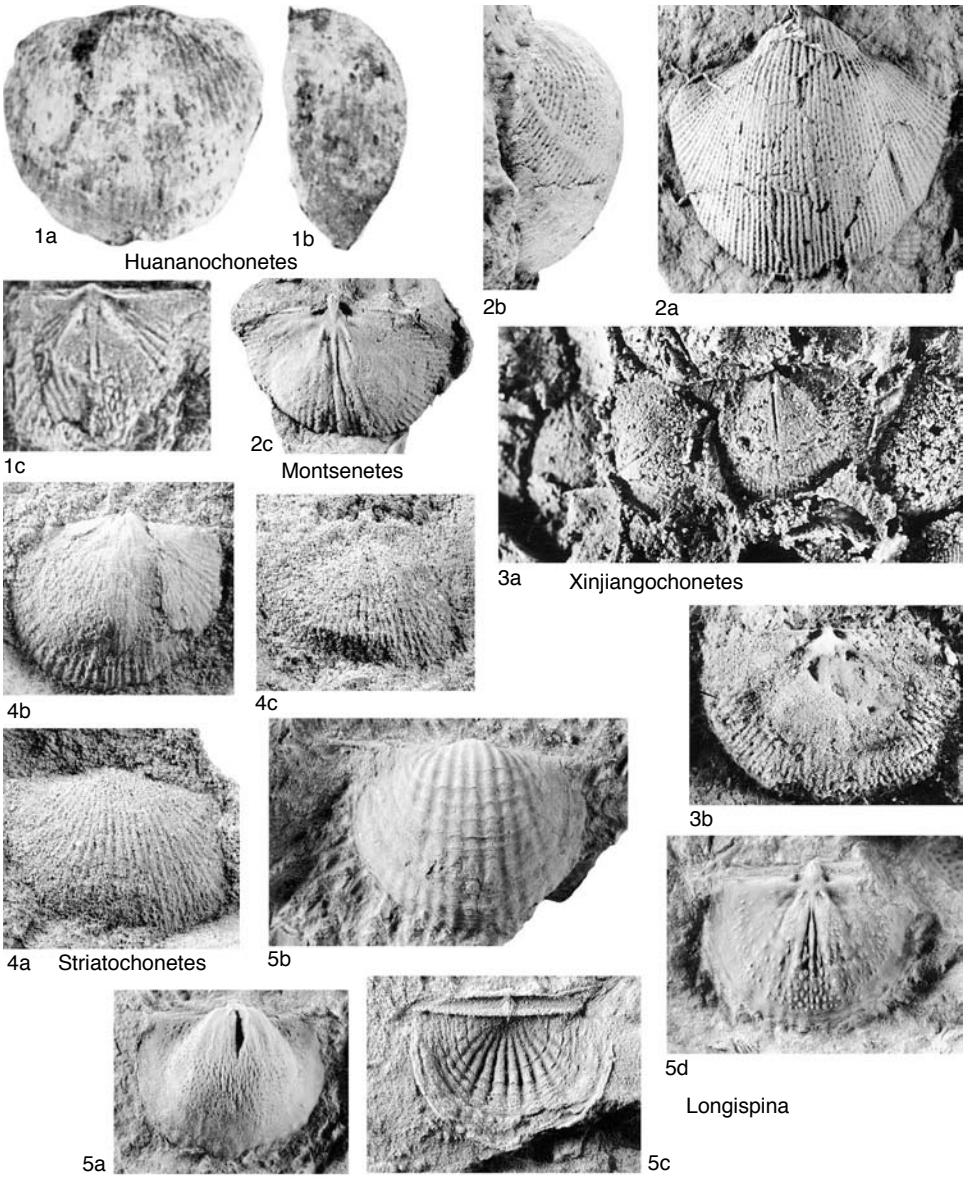

FIG. 260. Chonetidae (p. 398–400).

teriorly thickened; long, strong anderidia; inner socket ridges straight. *Middle Devonian (Eifelian):* Falkland Islands, ?Brazil, South Africa.——FIG. 261,*1a,b.* **N. skottsbergi* (CLARKE), western Cape, Bokkeveld Group, South Africa; ventral valve internal mold, dorsal valve interior, ×1.5 (Hiller, 1987).

Allanetes BOUCOT & JOHNSON, 1967, p. 142 [**A. neozelanica;* OD]. Shell medium to large, markedly concavoconvex; radial ornamentation of coarse costae, costellae; disjunct chilidial plates; few spines ?symmetrically arranged, orthomorph ?perpendicular; ventral myophragm high, bladelike; dorsal valve interior with median septum, stout anderidia;

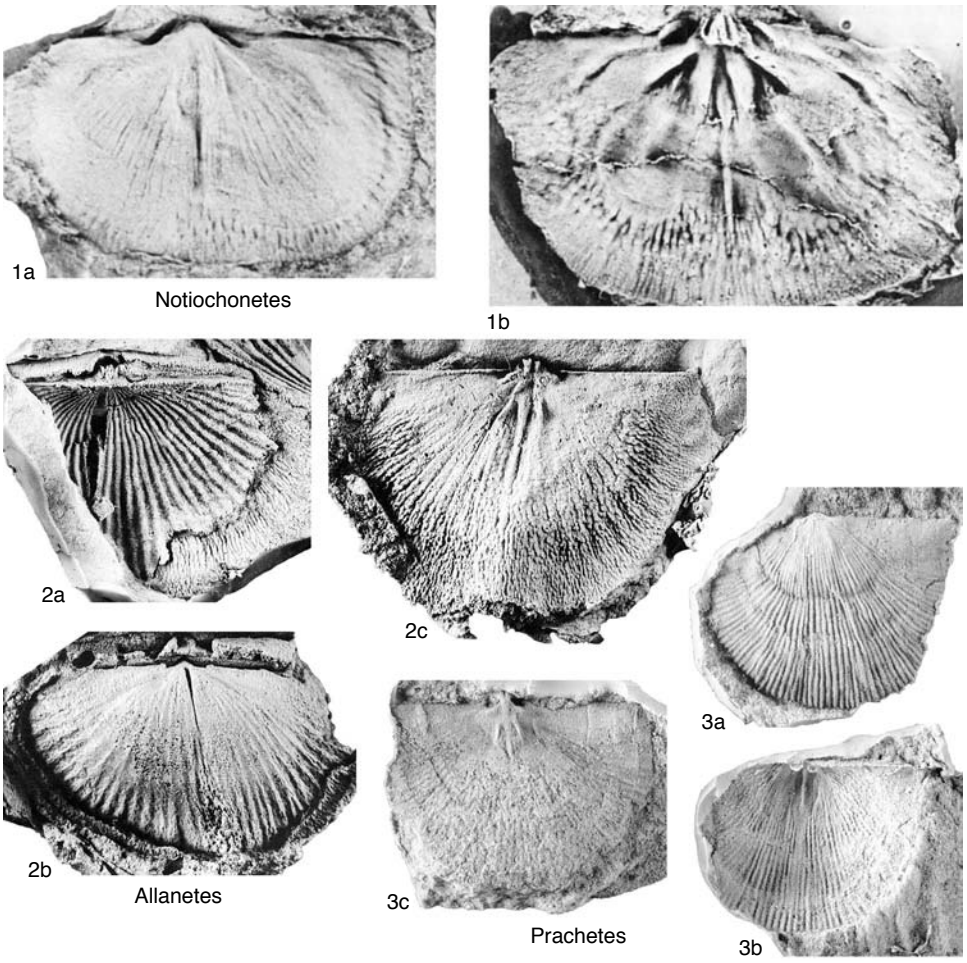

FIG. 261. Chonetidae (p. 400–403).

cardinal process deeply bilobed, elevated above valve floor, anteriorly bounded by cardinal process pit; inner socket ridges short, narrow. *Lower Devonian (Emsian):* New Zealand.——FIG. 261,*2a–c.* **A. neozelanica,* lower Emsian, Reefton beds, New Zealand; dorsal side of articulated shell, ventral valve internal mold, dorsal valve interior, ×2 (Boucot & Johnson, 1967).

Pleurochonetes ISAACSON, 1977, p. 175 [**Chonetes (Pleurochonetes) lauriata;* OD][=*Gamonetes* ISAACSON, 1977, p. 168, obj.; *Aseptonetes* ISAACSON, 1977, p. 177, obj.]. Differs from *Notiochonetes* in its dorsal valve interior; anderidia less developed, more divergent anteriorly; inner socket ridges shorter, posteriorly curved, more posteriorly situated, more divergent anteriorly; median septum supporting cardinal process; myophore projecting posteriorly; spines orthomorph oblique, symmetrically arranged. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* Bolivia, Argentina, South Africa.——FIG. 262*a. P. falklandicus* (MORRIS & SHARPE), Emsian, Falkland islands; dorsal valve interior, ×2 (Hiller, 1987).——FIG. 262*b–e. P. anteloi* (ISAACSON), Eifelian, upper Icla Formation, Bolivia; *b–d,* dorsal valve interior, ventral valve interior, adult dorsal valve interior; *e,* ventral valve exterior, ×2 (Racheboeuf, 1992).

Prachetes BIZZARRO, 1995, p. 175 [**Pleurochonetes? condori* RACHEBOEUF, 1992, p. 49; OD]. Shell medium, slightly transverse to equidimensional, moderately concavoconvex, with flattened cardinal extremities; maximum width at hinge line; spines symmetrical, orthomorph oblique; ornamentation of dense, narrow, angular costellae; ventral valve interior with posterior ridges anteriorly divergent at 70° to 80°; dorsal valve interior with small cardinal

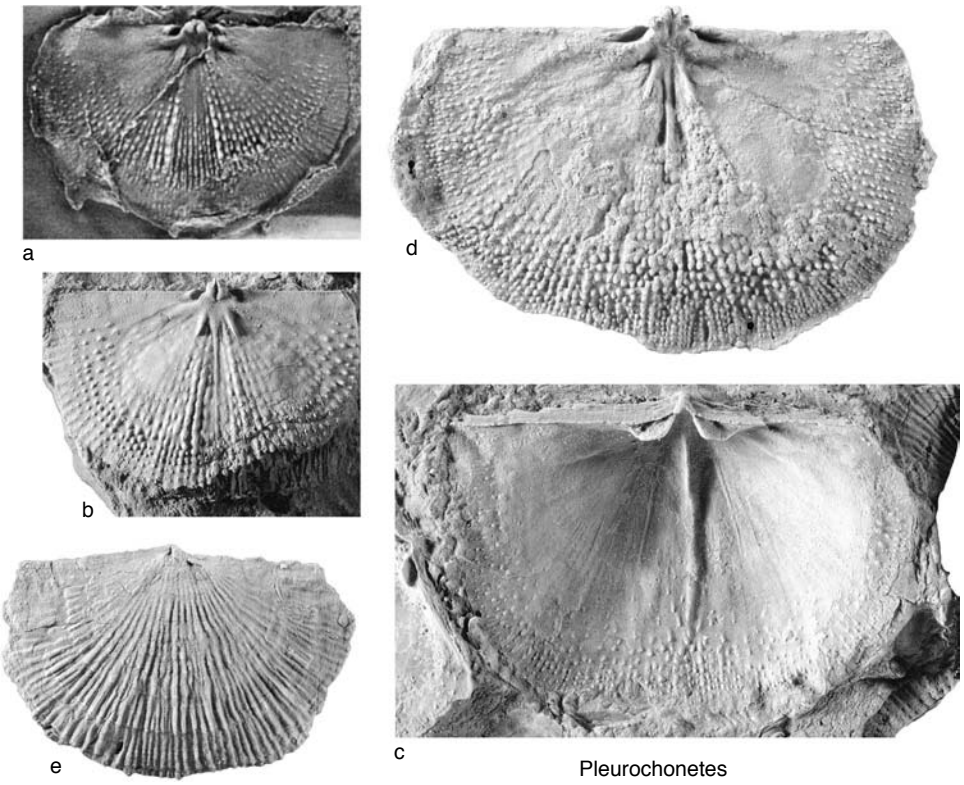

FIG. 262. Chonetidae (p. 402).

process, short median septum, anderidia anteriorly weakly divergent, less than 40°. *Middle Devonian (Givetian):* North America (Appalachian Mountains), Bolivia.——FIG. 261,*3a–c. *Prachetes condori* (RACHEBOEUF), Givetian, Cruz Loma Sandstone, Bolivia; ventral valve exterior, ventral valve interior, dorsal valve interior, ×2 (Bizzarro, 1995).

Subfamily RETICHONETINAE Muir-Wood, 1962

[Retichonetinae MUIR-WOOD, 1962, p. 62]

Shell small, subequidimensional; dorsal valve interior without cardinal process pit; median septum supporting cardinal process; inner socket ridges, anderidia reduced; no accessory septa; no brachial ridges. [This subfamily is retained herein to include genera for which the phylogenetic relationships are unclear. They can be provisionally regarded as neotenic forms; further investigations would possibly suggest their assignment to the subfamily Devonochonetinae.] *Upper Devonian (Frasnian, ?Famennian).*

Retichonetes MUIR-WOOD, 1962, p. 62 [**Chonetes armata* BOUCHARD-CHANTEREAUX in DE VERNEUIL, 1845, p. 241; OD]. Shell small, usually weakly transverse in outline, markedly concavoconvex; ventral interarea apsacline, posteriorly concave; dorsal interarea hypercline; small, convex pseudodeltidium, chilidium; radial ornamentation of low, narrow costellae; few lamellose concentric growth lines; spines orthomorph oblique, low to high angled from umbo to cardinal extremities; ventral interior with small rounded hinge teeth, short myophragm; posterolateral margins of visceral cavity with two radial rows of strong pustules; dorsal interior with stout median septum supporting cardinal process, no pit; small but strong anderidia anteriorly divergent at 80° to 90°; inner socket ridges relatively long, anteriorly divergent at 160°, bearing radial row of pits for articulation with posterior pustules of ventral valve. *Upper Devonian (Frasnian, ?Famennian):* Europe, Australia; USA (New Mexico), *?Famennian.*——FIG. 263,*1a–c. *R. armatus* (BOUCHARD-CHANTEREAUX), Frasnian,

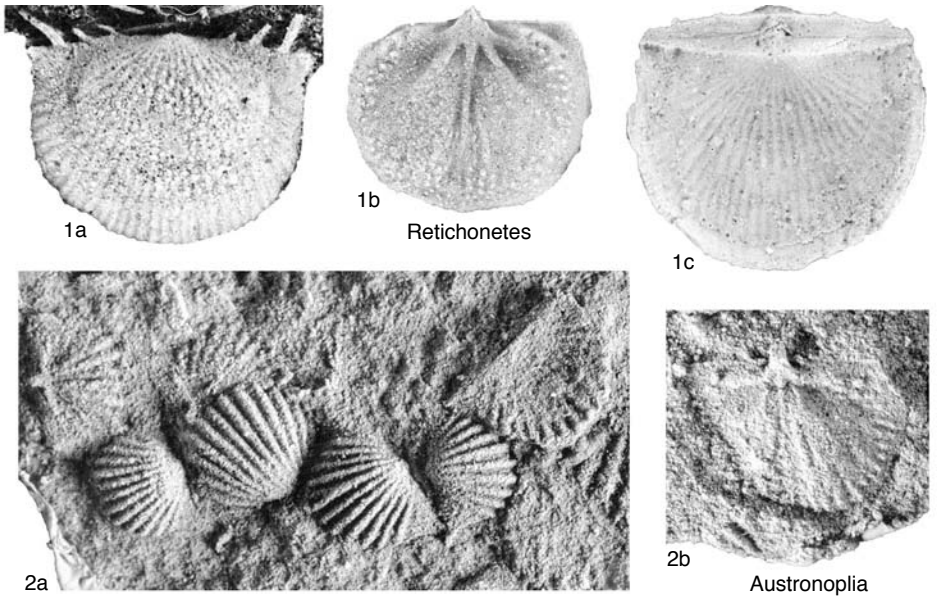

FIG. 263. Chonetidae (p. 403–404).

upper *Asymmetricus* Zone, northern France; ventral valve exterior, dorsal side of articulated shell, dorsal valve interior, ×5 (Racheboeuf, 1979).

Austronoplia ISAACSON, 1977, p. 178 [**Chonetes stuebeli* ULRICH, 1893, p. 80; OD]. Shell small, moderately concavoconvex, subsemicircular; shell surface with subtriangular to rounded costae; ventral valve exterior with median fold in largest shells; spines orthomorph oblique, symmetrically arranged; dorsal valve interior with median septum supporting posteriorly elongate cardinal process; no cardinal process pit; anderidia short, widely divergent anteriorly; inner socket ridges short, posteriorly curved; no accessory septa; interior of both valves with strong endospines. [The overall shell morphology and the lack of cardinal process pit and accessory septa make *Austranoplia* a member of the Retichonetinae rather than Costanopliinae.] *Upper Devonian (Frasnian):* Bolivia.——FIG. 263,*2a,b.* **A. stuebeli* (ULRICH), Frasnian, Bolivia; ventral valve exteriors, dorsal valve interior, ×5 (Racheboeuf, 1992).

Family RUGOSOCHONETIDAE Muir-Wood, 1962

[*nom. transl.* COOPER & GRANT, 1975, p. 1212, *ex* Rugosochonetinae MUIR-WOOD, 1962, p. 32]

Shell small to large, costate, capillate, smooth or lamellose, plano- to strongly concavoconvex; ventral sulcus absent to strongly developed, with corresponding dorsal fold; spines symmetrically arranged, orthomorph oblique to perpendicular; pseudodeltidium, chilidium usually present; variably developed ventral myophragm, always high posteriorly; dorsal interior with long median septum; no accessory septa; anderidia always prominent, anteriorly moderately divergent; internally bilobed cardinal process anteriorly bounded by cardinal process pit. *Carboniferous–Permian, ?Lower Triassic.*

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

[Rugosochonetinae MUIR-WOOD, 1962, p. 32]

Small to large rugosochonetids with radially capillate or costate external ornament; ventral sulcus weakly to strongly developed; dorsal fold present in several genera; spines usually orthomorph oblique, at low to moderate angle; brachial ridges often well developed. *Carboniferous–Permian, ?Lower Triassic.*

Rugosochonetes Sokolskaya, 1950, p. 23 [**Orthis hardrensis* Phillips, 1841, p. 138; OD] [=*Nix* Easton, 1962, p. 45, obj.]. Shell small, plano- to slightly concavoconvex; dorsal interarea reflexed; pseudodeltidium, chilidium developed; shell capillate; spines orthomorph oblique, at 45° to 60°, symmetrically arranged; dorsal median septum half of valve length, inner socket ridges curved. *Lower Carboniferous (Tournaisian)–Upper Carboniferous (Gzhelian):* Europe, Asia, Australia, North America, Africa.——Fig. 264,*1a–d. R. celticus* Muir-Wood, Namurian, Scotland; *a,* ventral valve exterior, ×3; *b,* ventral valve interior, ×4; *c,d,* dorsal valve interiors, ×2 (Muir-Wood, 1962).

Alatochonetes Liang, 1990, p. 144[460] [**A. alata;* OD]. Shell small, strongly transverse, subtrapezoidal, with acute to alate cardinal extremities; shell surface with coarse radial costae crossed by strong concentric rugae with prominent tubercles at junction; ventral valve interior with long, low myophragm; dorsal valve interior poorly known. *middle Permian:* southern China.——Fig. 264,*2. *A. alatus,* middle Permian, southern China; dorsal view of articulated shell, internal mold, ×3.5 (Liang, 1990).

Arctochonetes Ifanova, 1968, p. 29 [**Chonetina? postartiensis* Ustritsky, 1960, p. 112; OD]. Shell small, concavoconvex; ventral sulcus weak or absent; shell surface finely costellate; spines orthomorph oblique, symmetrically arranged; ventral valve interior with short myophragm, pair of strong vascular trunks, anteriorly divergent at 60°; dorsal valve interior with ill-defined median septum, pair of long, low accessory septa. *Lower Permian (Artinskian–Kungurian):* Pechora Basin.——Fig. 264,*3a–c. *A. postartiensis* (Ustritsky), Artinskian, Pechora Basin; ventral valve internal molds, ventral valve exterior, dorsal valve internal mold, ×2 (Ifanova, 1968).

Chonetinella Ramsbottom, 1952, p. 13 [**Chonetes flemingi* Norwood & Pratten, 1855b, p. 26; OD]. Small, bilobate, highly concavoconvex shell with deep median sulcus, high fold; pseudodeltidium, chilidium ill developed or absent; shell surface capillate; dorsal valve interior with small bilobed cardinal process, alveolus; long, anteriorly elevated median septum; long inner socket ridges, parallel to hinge. *Upper Carboniferous–Lower Permian (Kungurian):* Europe, North America, South America, *Pennsylvanian;* North America, Asia, *Wolfcampian–Leonardian.*——Fig. 264,*6a–d. *C. flemingi* (Norwood & Pratten), Pennsylvanian, Texas; *a,b,* articulated shell, ventral, dorsal views; *c,* ventral valve interior; *d,* dorsal valve interior, ×3 (Ramsbottom, 1952).

Fanichonetes Xu & Grant, 1994, p. 29 [**F. campigia;* OD]. Small to medium, transverse shell; shell surface strongly costellate; ventral sulcus and corresponding dorsal fold developed; numerous spine canals but outer spines not observed; ventral valve interior with short myophragm, coarse isolated endospines posterolaterally; dorsal valve interior poorly known, with cardinal process pit. [Among the diagnostic characters the authors quoted the ". . . spines mostly inclined toward midline." Judging from the specimens illustrated in their figure 16, it appears clearly that these features are not the spines but molds of the spine canals inside the posterior margin of the decalcified ventral valve. Their orientation toward midline conforms with all chonetoids and is only due to the growth process.] *Upper Permian (Tatarian):* southern China.——Fig. 264,*7a,b. *F. campigia,* Upper Permian, southern China; *a,* ventral valve exterior; *b,* holotype, ventral valve interior, ×3 (Xu & Grant, 1994).

Fusichonetes Liao in Zhao & others, 1981, p. 52[83] [**Plicochonetes nayongensis* Liao, 1980, p. 252; OD]. Shell small, transverse with ventral sulcus, dorsal fold; shell surface with strong simple costae; spines low angled; ventral valve interior with rows of endospines; dorsal valve interior with median septum. *Upper Permian, ?Lower Triassic:* China.——Fig. 264,*8a–c. *F. nayongensis* (Liao), uppermost Permian–?lowermost Triassic, southern China; ventral valve exterior, dorsal exterior of articulated shell, ventral valve interior, ×4 (Liao, 1981).

Isochonetes Aisenverg, 1985, p. 41 [**I. larinoensis;* OD]. Shell medium, transverse; ventral valve regularly convex; ornament of uniform, fine, regular costellae; spine bases medium angled, 45° to 60°; ventral valve interior with short myophragm, long vascular trunks; adductor scars small, oval; diductor scars large, triangular; dorsal valve interior with cardinal process pit, median septum, distinct brachial ridges. *Lower Carboniferous (lower Bashkirian):* Donets Basin.——Fig. 264,*4a–d. *I. larinoensis,* lower Bashkirian, western Donets Basin; *a,b,* articulated shell, ventral, dorsal views; *c,d,* ventral valve interior, dorsal valve interior, ×2 (Aisenverg, 1985).

Jakutochonetes Afanas'eva, 1977a, p. 31 [**J. jacuticus;* OD]. Shell large, transverse, without sulcus, but narrow furrow anteriorly developed in both valves; pseudodeltidium developed; surface ornamented by very thin, intercalating, branching costellae with prominent growth lines; spines low angled, posterolaterally oriented; ventral myophragm not extending beyond midlength; oval adductor scars; *vascula media* developed; hinge teeth laterally elongated; dorsal valve interior with relatively large cardinal process pit, laterally widened cardinal process, myophore; median septum stout in posterior half of valve; inner socket ridges high, narrow, posteriorly bent. *Upper Carboniferous:* Arctic Siberia.——Fig. 264,*5a–d. *J. jacuticus;* ventral valve internal mold, ventral valve external mold, dorsal valve internal mold, dorsal external mold of articulated shell, ×2 (Afanas'eva, 1977a).

Komukia Waterhouse, 1982b, p. 343 [**K. solita;* OD]. Shell thickened, transverse; surface ornamented by low capillae interrupted by low growth lines; spine bases symmetrical; ventral valve interior with strong, long myophragm, two long, broad

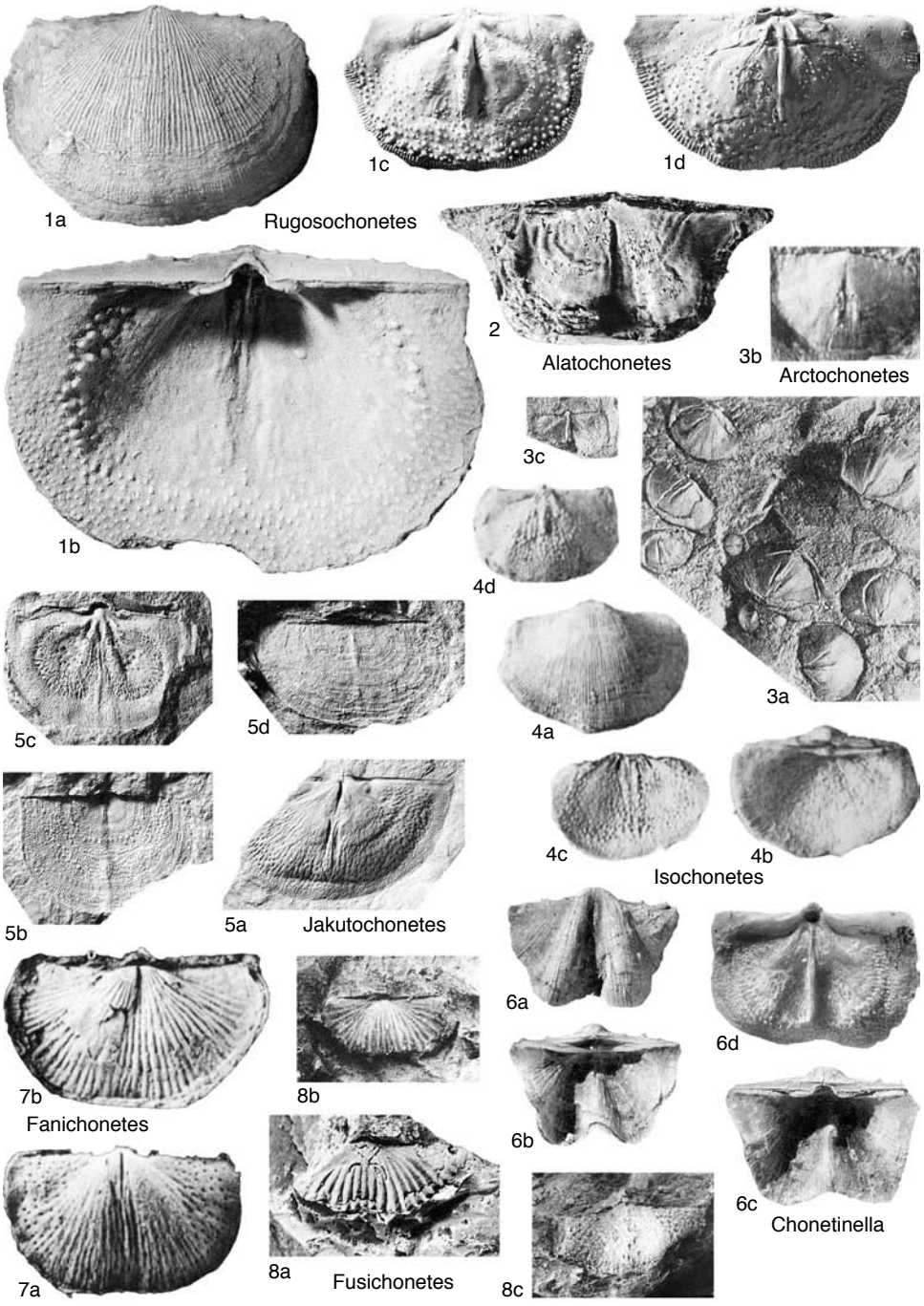

FIG. 264. Rugosochonetidae (p. 405).

vascular trunks; dorsal valve interior with cardinal process pit in largest shells; median septum well developed; strong inner socket ridges; brachial platform well delimited by spinose ridge. *Lower Permian:* Thailand.——FIG. 265,*1a–d. *K. solita,* Lower Permian, Thailand; *a,b,* articulated shells, dorsal view; *c,d,* ventral valve internal mold, dorsal valve internal mold, ×1.5 (Waterhouse, 1982b).

Neochonetes MUIR-WOOD, 1962, p. 87 [**Chonetes dominus* KING, 1938, p. 259; OD] [=*Quadranetes* SADLICK, 1963, p. 721, obj.]. Small to large sized, almost plano- to moderately concavoconvex rugosochonetids with finely capillate external ornament, feebly to distinctly developed sulcus; low to moderately angled spines; ventral valve interior with prominent myophragm; vascular trunks parallel, deeply impressed; dorsal interior with cardinal process pit, anderidia, median septum, brachial ridges; inner socket ridges well developed; outer socket ridges may be present. *Upper Carboniferous–Upper Permian.*

N. (Neochonetes) MUIR-WOOD, 1962, p. 87 [**Chonetes dominus* KING, 1938, p. 259; OD] [=*Quadranetes* SADLICK, 1963, p. 721, obj.]. Small- to medium-sized, slightly concavoconvex; ventral valve may be sulcate; pseudodeltidium vestigial or absent, chilidium present; exterior capillate or smooth anteriorly; spines numerous, oblique, symmetrically arranged; dorsal median septum anteriorly elevated; inner, outer socket ridges commonly developed. *Upper Carboniferous–Upper Permian:* cosmopolitan.——FIG. 265,*2a–d. *N. (N.) dominus* (KING), Pennsylvanian, Texas; *a,b,* articulated shell, ventral, dorsal views; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (King, 1938).

N. (Sommeriella) ARCHBOLD, 1982, p. 10 [**Chonetes pratti* DAVIDSON, 1859a, p. 116; OD] [=*N. (Sommeria)* ARCHBOLD, 1981b, p. 113; obj.]. Similar to *N. (Neochonetes)* but sulcus usually conspicuously developed, gentle fold often developed in dorsal valve, greater convexity in ventral valve, hinge spines at about 40° to 45°; maximum width of mature shells usually anterior of hinge; interiors as for *N. (Neochonetes). Lower Permian (Sakmarian–Kungurian):* Western Australia.——FIG. 265,*3a–e. *N. (S.) pratti* (DAVIDSON), Holmwood Shales, Irwin River, uppermost Sakmarian–Artinskian; *a,b,* ventral, dorsal sides of articulated shell; *c–e,* dorsal valve interiors, ×2 (Archbold, 1981b).

Paramesolobus AFANAS'EVA, 1975, p. 101 [**P. ivanovae;* OD]. Differs from *Mesolobus* by its shell surface ornamented with relatively strong bifurcating costellae. *Upper Carboniferous (Moscovian–Gzhelian):* Russia.——FIG. 265,*4a–d. *P. ivanovae,* Kasimovian, Russian Platform; *a,* ventral valve exterior; *b,c,* dorsal valves, exterior, interior; *d,* ventral valve interior, ×2 (Afanas'eva, 1975).

Schistochonetes ROBERTS, 1971, p. 54 [**S. abruptus;* OD]. Shell medium sized, auriculate, mainly characterized by its ornamentation; surface coarsely costate posteriorly, becoming finely or indistinctly costellate anteriorly; costae bifurcating, rarely trifurcating then intercalating from umbo to shell margin; spines symmetrically arranged, orthomorph oblique, low angled (25°); median septum not supporting cardinal process, pit shallow; anderidia anteriorly divergent at 60° to 70°; short, narrow inner socket ridges. *Lower Carboniferous (Viséan):* Australia.——FIG. 266,*1a–d. *S. abruptus,* Utting Calcarenite, Viséan, northwestern Australia; *a,b,* articulated shell, ventral, lateral views; *c,* ventral valve interior; *d,* dorsal valve interior, ×2 (Roberts, 1971).

Sokolskya AISENVERG, 1980, p. 55 [**S. calmiusensis;* OD]. Shell medium, thin walled, weakly concavoconvex, transverse, with maximum width at hinge line; shell surface capillate; spines not observed; ventral valve interior with narrow myophragm, small oval adductor scars, large, triangular diductor scars; dorsal valve interior with posteriorly curved short inner socket ridges; no cardinal process pit; short, low median septum, anderidia posteriorly fused with cardinalia. *Upper Carboniferous (lower Kinderscoutian):* Russia (Donets Basin).——FIG. 266,*3a–c. *S. calmiusiensis,* lower Kinderscoutian, Donets Basin, Russia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×2 (Aisenverg, 1980).

Waagenites PAECKELMANN, 1930, p. 223 [**Chonetes grandicostus* WAAGEN, 1884, p. 638; OD] [=*Dienerella* REED, 1931, p. 18, obj.]. Small, quadrate, ventral valve highly convex, with deep median sulcus; no pseudodeltidium; umbo much incurved; valves with very few coarse costae, or costellate, rarely capillate; ears large, smooth; dorsal septum medianly developed; short socket ridges. *Upper Permian:* Pakistan, Timor, ?North America, Arctic (Spitzbergen).——FIG. 265,*5a–d. *W. grandicostus* (WAAGEN), upper *Productus* Limestone, Pakistan; *a,* ventral valve exterior, ×1; *b–d,* enlarged ventral, posterior, lateral views, ×2 (Muir-Wood, 1962).

Waterhouseiella ARCHBOLD, 1983a, p. 70 [**Waagenites speciosus* WATERHOUSE & PIYASIN, 1970, p. 112; OD]. Small, distinctly concavoconvex, moderately transverse rugosochonetids with strongly developed, radial, costellate ornament; sulcus weakly developed or obsolescent; dorsal fold low; dorsal interior with strongly developed cardinal process pit, socket plates, lateral septa, median septum; ventral valve with myophragm, variably developed vascular trunks parallel to myophragm. *Permian:* Thailand, Indonesia, Pakistan, Afghanistan.——FIG. 266,*2a–d. *W. speciosus* (WATERHOUSE & PIYASIN), Kazanian, southern Thailand; *a,b,* ventral valve, ventral, lateral views, ×3; *c,* dorsal view of articulated shell, ×3; *d,*

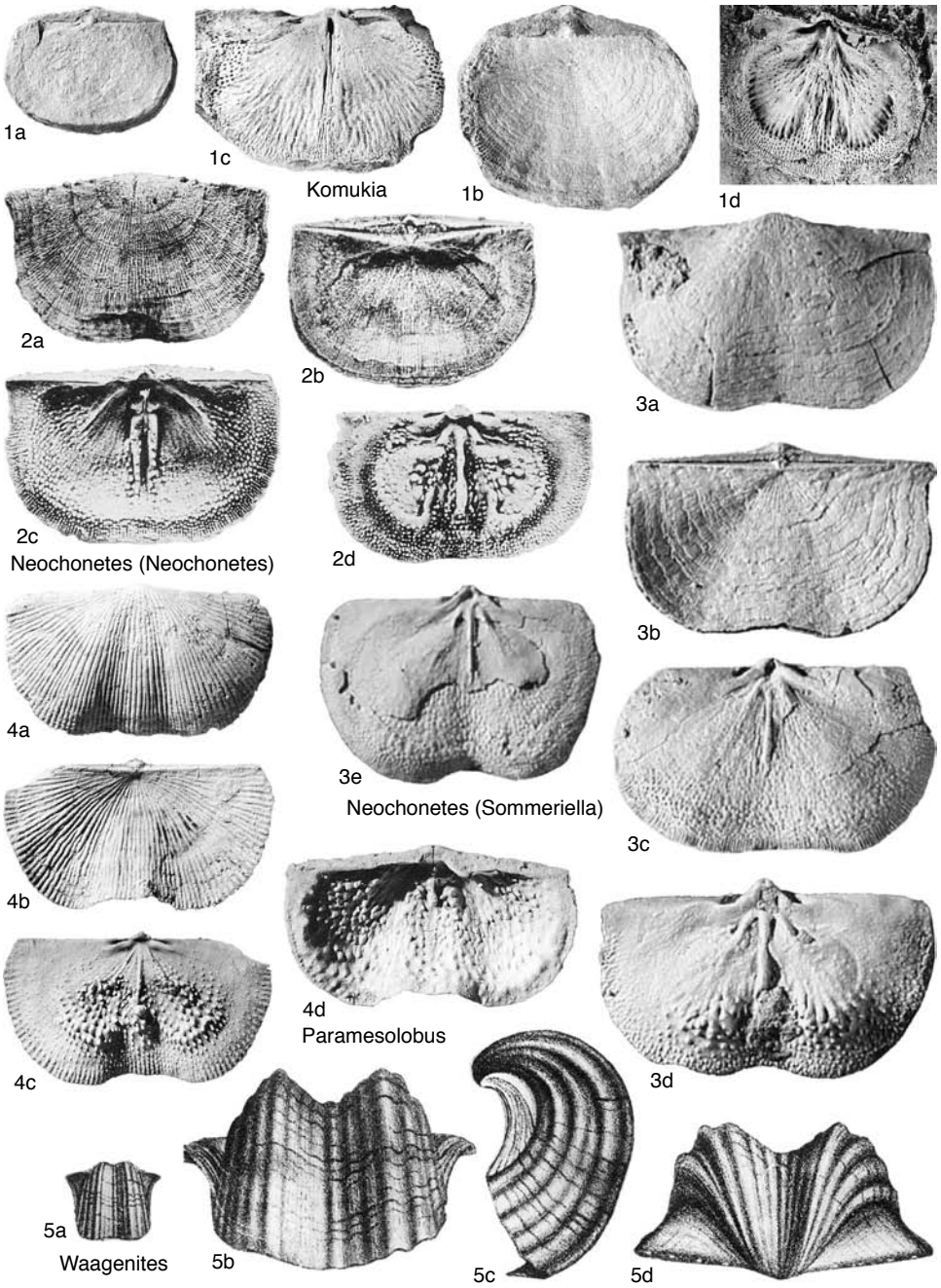

FIG. 265. Rugosochonetidae (p. 405–407).

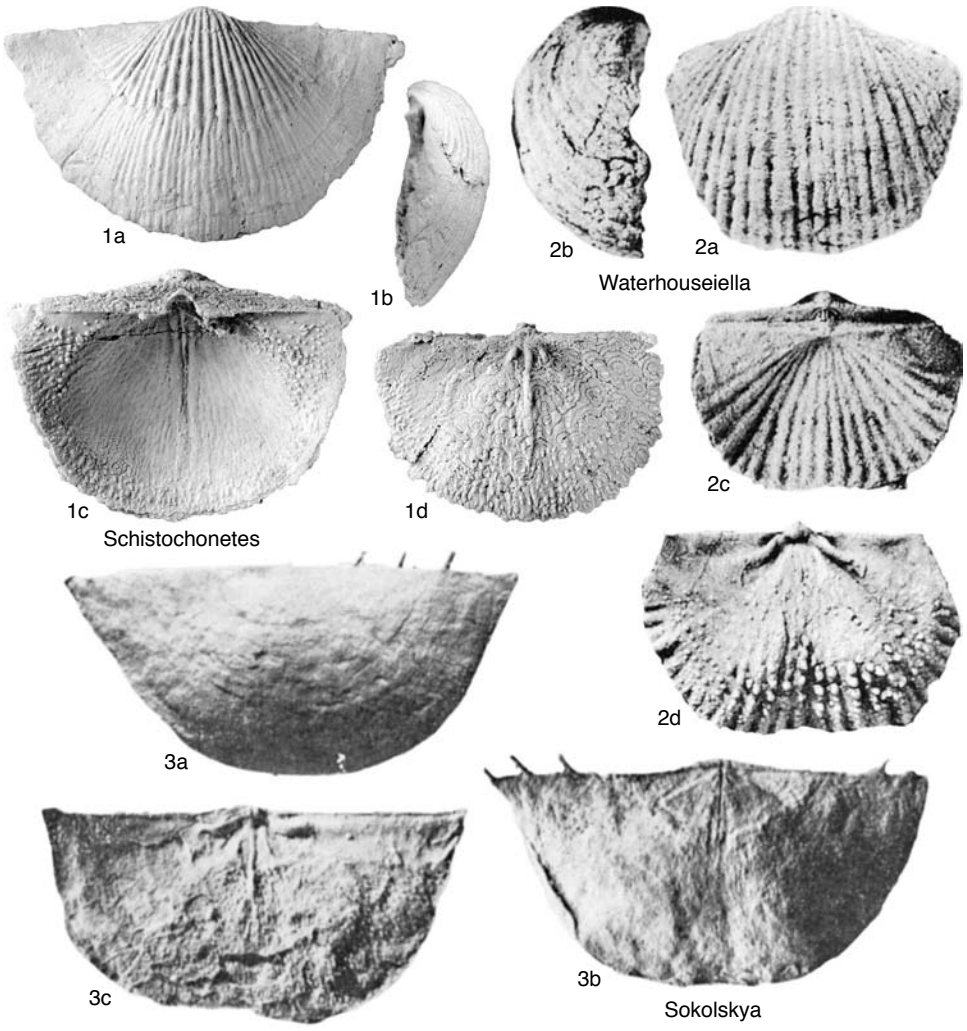

FIG. 266. Rugosochonetidae (p. 407–409).

dorsal valve interior, ×4 (Waterhouse & Piyasin, 1970).

Subfamily CAPILLOMESOLOBINAE Pečar, 1986

[Capillomesolobinae PEČAR, 1986, p. 16]

Small, capillate or smooth Rugosochonetidae; median lobe present or absent in ventral median sulcus. *Upper Carboniferous (Moscovian)–Permian.*

Capillomesolobus PEČAR, 1986, p. 18 [**C. karavankensis;* OD]. Small, finely capillate Rugosochonetidae; median lobe present or absent in ventral median sulcus; spines orthomorph oblique, high angled to vertical. *Upper Carboniferous (Moscovian)–Permian:* North America, Europe (Carnian Alps). ——FIG. 267,*1a–d. *C. karavankensis,* Gzhelian, Karavanke Mountains; *a,* ventral valve, ×2; *b,c,* ventral valve, exterior, interior, ×2; *d,* dorsal valve, internal mold, ×2 (Pečar, 1986).

Mesolobus DUNBAR & CONDRA, 1932, p. 134 [**Chonetes mesolobus* NORWOOD & PRATTEN, 1855b,

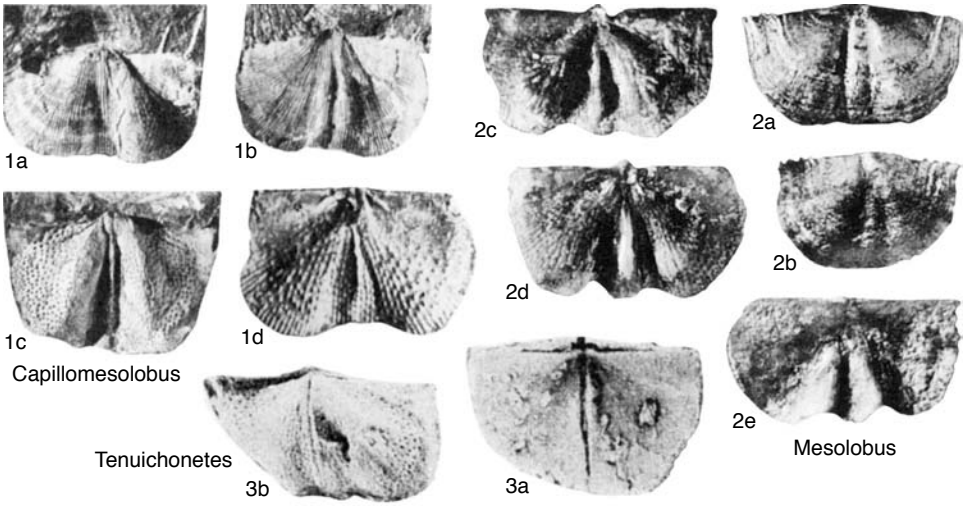

FIG. 267. Rugosochonetidae (p. 409–410).

p. 27; OD]. Small, valves moderately concavoconvex, normally with ventral sulcus bearing median fold, dorsal fold bearing median sulcus; pseudodeltidium, chilidium present; shell capillate or smooth, commonly lamellose; spines oblique, symmetrically arranged; dorsal median septum long, anteriorly elevated, serrated; inner socket ridges parallel to hinge. *Upper Carboniferous:* North America.——FIG. 267,*2a–e. *M. mesolobus* (NORWOOD & PRATTEN), Missouri; *a,b,* ventral valves, ×2; *c,* dorsal valve interior, ×2; *d,e,* dorsal valve, interior, exterior, ×2 (Muir-Wood, 1962).

Tenuichonetes JING & HU, 1978, p. 109[125] [**Chonetes tenuilirata* CHAO, 1928, p. 26; OD]. Shell medium, trapezoidal; shell surface capillate; ventral valve moderately convex; deep ventral sulcus originating at beak, with single plication in sulcus; spines orthomorph oblique, symmetrically arranged; ventral valve interior with long myophragm; dorsal valve interior with cardinal process pit; long median septum; long, straight inner socket ridges parallel to hinge, short anderidia; no brachial ridges. *Lower Permian:* China.——FIG. 267,*3a,b. *T. tenuilirata* (CHAO), Lower Permian, China; dorsal valve internal mold, ventral valve internal mold, ×2 (Jing & Hu, 1978).

Subfamily DELEPINEINAE Muir-Wood, 1962

[Delepineinae MUIR-WOOD, 1962, p. 33]

Shell medium to large, almost plano- to markedly concavoconvex, transverse in outline; ventral valve thickened; radial ornamentation capillate to costellate; ventral interarea flat, apsacline to orthocline; dorsal interarea hypercline; pseudodeltidium, chilidium present, usually wide; numerous, symmetrically arranged spine canals crossing posterior margin of ventral valve; spines usually poorly developed, orthomorph oblique or irregularly curved, low to medium angled; dorsal median septum long, narrow, widening, tapering posteriorly, not supporting cardinal process; cardinal process short, widened, with anterior margin almost vertical above valve floor, more or less concave anteriorly, bounded by cardinal process pit; short, weakly developed, slightly divergent anderidia; inner socket ridges short, posteriorly concave, almost parallel to hinge line. *Lower Carboniferous (Tournaisian)–Upper Permian.*

Delepinea MUIR-WOOD, 1962, p. 99 [**Productus comoides* J. SOWERBY, 1822 in 1821–1822, p. 31; OD]. Large, markedly transverse in outline, with posteriorly thickened ventral valve; longitudinal profile strongly arched posteriorly; radial ornamentation capillate to costellate; spines orthomorph oblique when preserved. *Lower Carboniferous (Tournaisian–Viséan):* France, Belgium, Germany, Great Britain, Russia, northern Africa, Asia, Australia.——FIG. 268*a,b. *D. comoides* (SOWERBY), Viséan, Westmorland, England; articulated shell,

ventral, dorsal views, ×1 (Muir-Wood, 1962).——Fig. 268*c,d. D. destinezi* (Vaughan), Viséan, Fermanagh, Northern Ireland; ventral valve interior, accessory adductor scars, ×1 (Muir-Wood, 1962).——Fig. 268*e,f. D. carinatus* (Garwood), Viséan, Westmorland, England; ventral valve exterior, dorsal valve interior, ×1 (Muir-Wood, 1962).

Gibbochonetes Aisenverg, 1971, p. 70 [**Delepinea (Gibbochonetes) forniculata;* OD]. Shell thin, medium to large, strongly concavoconvex; surface capillate with almost indistinct concentric fila; ventral valve interior with short myophragm, large diductors, poorly impressed adductors; dorsal valve interior with low cardinal process; median lobes of myophore higher than lateral ones; small cardinal process pit present; median septum, anderidia fairly well developed. [The author initially compared his new subgenus to *Delepinea,* and it is provisionally left here within the subfamily Delepineinae, but the presence of cardinal process pit would possibly imply a close relationship to the subfamily Rugosochonetinae.] *Lower Carboniferous (upper Tournaisian–lower Viséan):* Russian Platform.——Fig. 269,*1a–d. *G. forniculata,* upper Tournaisian, Donetz Basin, Russia; *a–c,* ventral valve exterior, ventral, lateral, posterior views, ×2; *d,* dorsal valve interior, ×2 (Aisenverg, 1971).

Megachonetes Sokolskaya, 1950, p. 42 [**Chonetes siblyi* Thomas, 1919, p. 612 (also Paeckelmann, 1930, p. 274); OD; *nom. nov. pro Chonetes compressa* Sibly, 1908, p. 78, *non* Waagen, 1884, p. 630]. Medium to large, almost plano- to moderately concavoconvex; ventral valve slightly thickened; surface finely capillate; irregularly curved spines, extending at 45 to 60°. *Lower Carboniferous (Tournaisian–upper Viséan):* Belgium, France, Germany, Great Britain, Ireland, Russia, northern Africa, Asia, Australia.——Fig. 269,*3a–e. *M. siblyi* (Thomas), Lower Carboniferous, Viséan, England; *a–c,* articulated shell, ventral, dorsal, lateral views, ×1.25; *d,* ventral valve posterior part with interarea, pseudodeltidium; *e,* ventral valve interior with accessory adductor scars, ×2 (Muir-Wood, 1962).

Mongolochonetes Afanas'eva, 1991, p. 98 [**M. inaequalis;* OD]. Differs from *Megachonetes* in its smaller size, its slightly concavoconvex longitudinal profile, development of ventral sulcus, dorsal fold, and lower-angled spines at 30° to 35°. *Upper Permian:* southern Mongolia. Material not suitable for illustration.

Petalochonetes Afanas'eva in Afanas'eva & others, 1988, p. 52 [**P. altaicus;* OD]. Large, with well-developed ventral sulcus; spines medium angled, at 50° to 60°; radial ornamentation of thin, dense costellae crossed by fila; dorsal valve interior without cardinal process pit; median septum not supporting cardinal process; no brachial ridges; anderidia not fused posteriorly, anteriorly divergent at 60° to 70°. [The development of the ventral sulcus would better fit with the subfamily Rugosochonetinae. The subfamilial assignment cannot be stated without detailed revision of the type species.] *Lower Carboniferous:* southern Mongolia.——Fig. 269,*2a–d. *P. altaicus; a,b,* ventral internal molds, ×2; *c,* dorsal valve internal mold, ×2; *d,* internal mold of the cardinalia, ×6 (Afanas'eva & others, 1988b).

Subfamily PLICOCHONETINAE Sokolskaja, 1960

[Plicochonetinae Sokolskaja in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 222]

Small, strongly cconcavoconvex, costellate to costate rugosochonetids; hinge spines oblique, high angled; fold, sulcus absent; interior generalized, often poorly known. *Carboniferous–Permian.*

Plicochonetes Paeckelmann, 1930, p. 222 [**Chonetes buchianus* de Koninck, 1843, p. 208; OD]. Shell small to medium; ventral valve medianly arched; pseudodeltidium small or absent; shell surface costate, rarely bifurcating, with numerous growth lines; spines high angled (55° to 70°); dorsal valve with well-developed median septum, or without; short, curved, inner socket ridges. *Lower Carboniferous–Upper Carboniferous (Namurian):* Europe, Asia, northern Africa, Australia, North America.——Fig. 270,*1a–c. *P. buchianus* (de Koninck), lower Namurian, Yorkshire; *a,* ventral valve exterior, ×1.5 (de Koninck, 1847b); *b,* ventral valve interior, ×3 (Muir-Wood, 1962); *c,* dorsal valve interior, ×3 (de Koninck, 1847b).

Hemichonetes Li, Gu, & Su, 1980, p. 343, *non Hemichonetes* Racheboeuf, 1981a [**H. hemipleura;* OD]. Differs externally from *Plicochonetes* by radial ornamentation restricted to posteromedian part of shell, and by development, or not, of low sulcus, fold; internally by short dorsal median septum, large cardinal process pit, long, parallel, inner socket ridges. *Lower Permian:* northeastern China.——Fig. 270,*5a,b. *H. hemipleura,* Lower Permian, northeastern China; dorsal valve internal mold, external mold, ×2 (Li, Gu, & Su, 1980).

Prorugaria Waterhouse, 1982a, p. 40 [**P. thailandica;* OD]. Small shell with moderately developed sulcus, fold; hinge wide; strong costae, costellae bifurcating on flanks of sulcus, fold; dorsal valve interior with short median septum, anderidia; inner surface with strong radially arranged endospines forming at least one pair of accessory septalike ridges. *Lower Carboniferous:* Thailand.——Fig. 270,*3a,b. *P. thailandica;* ventral valve exterior, incomplete dorsal valve interior, ×6 (Waterhouse, 1982a).

Rugaria Cooper & Grant, 1969, p. 4 [**Chonetes hessensis* King, 1931, p. 61; OD]. Small, strongly costate shell; spines oblique; dorsal valve interior with short, well-developed median septum; large cardinal process with deep cardinal process pit; broad, strongly endospinose anterior slope in dorsal

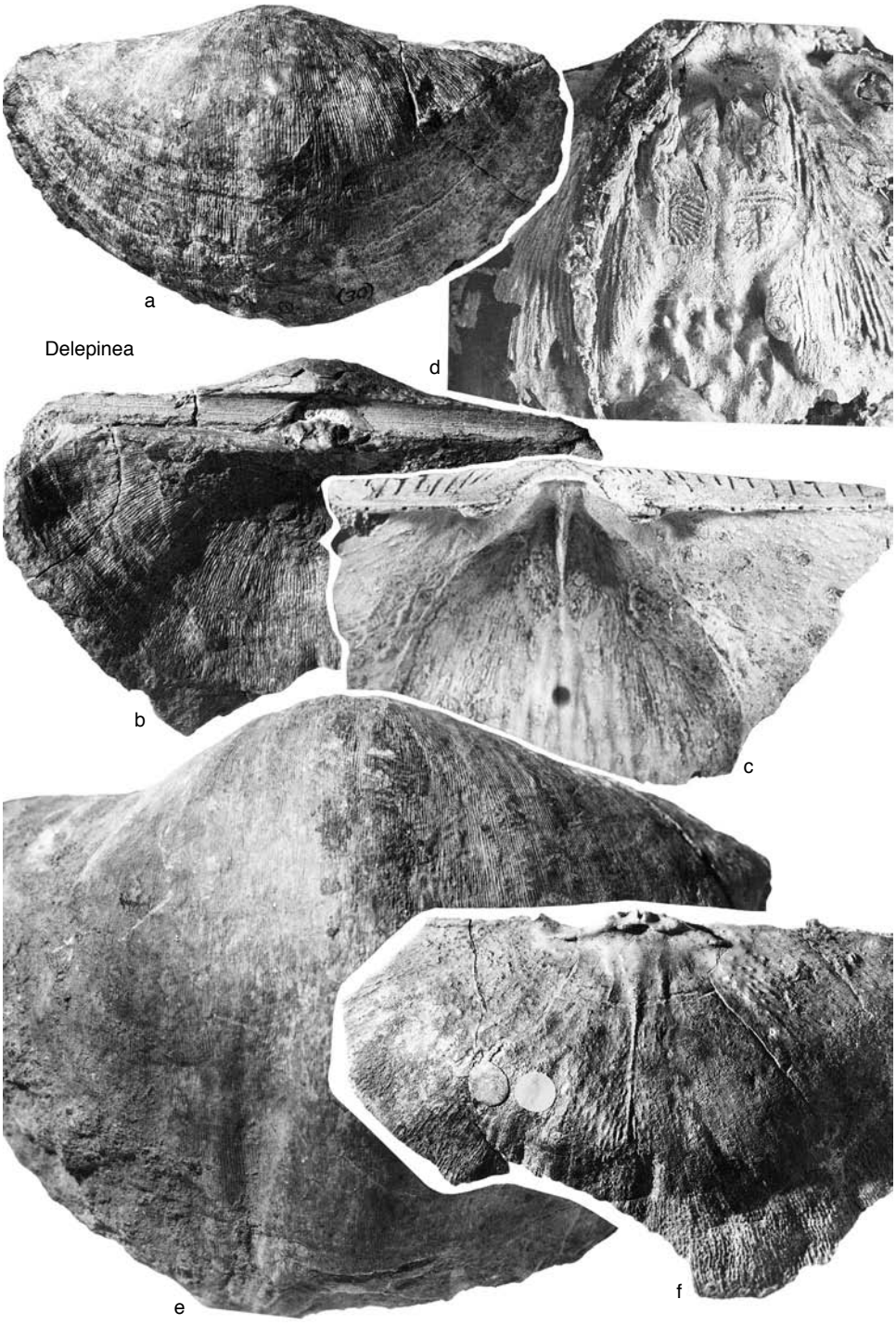

FIG. 268. Rugosochonetidae (p. 410–411).

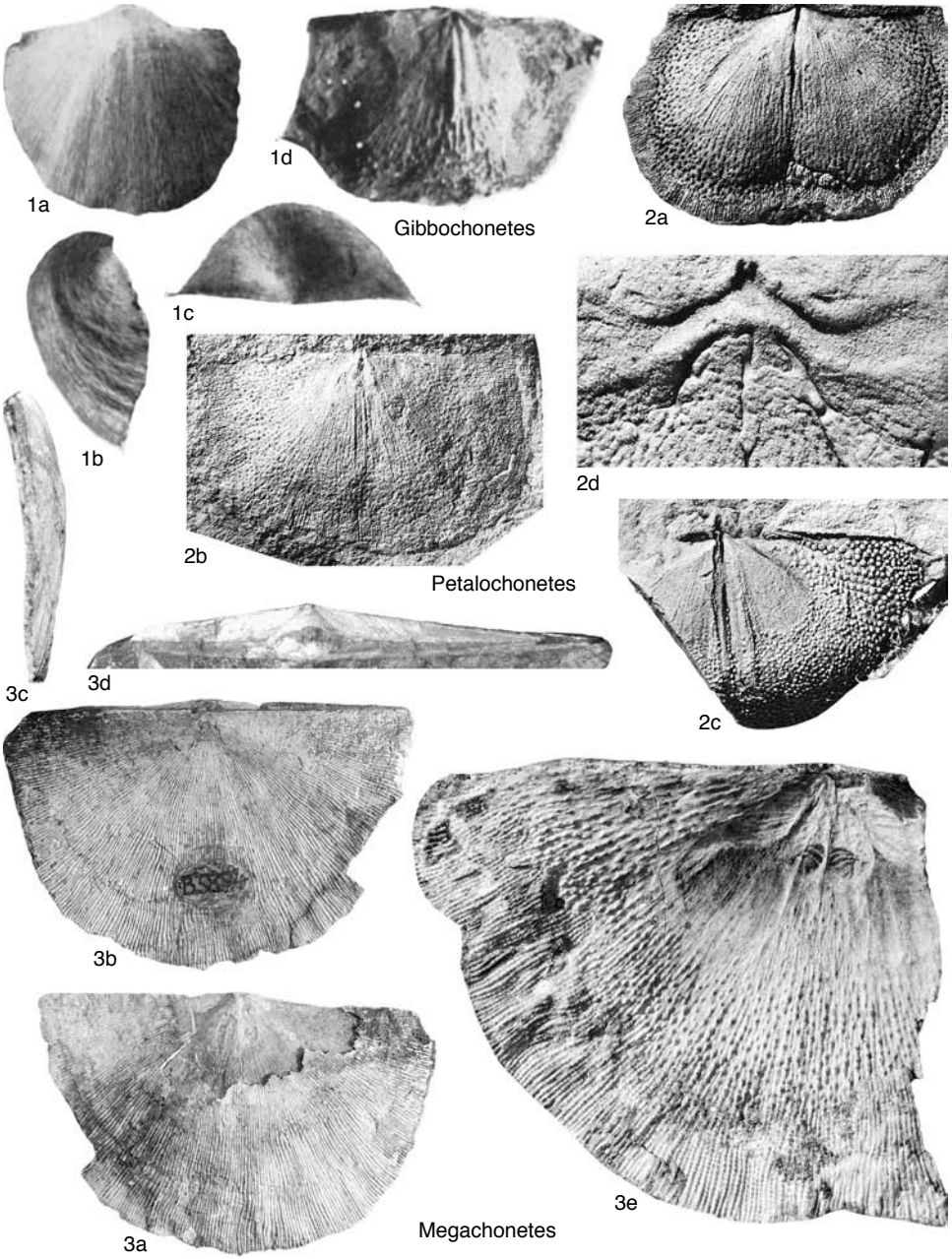

FIG. 269. Rugosochonetidae (p. 411).

valve. *Permian (Asselian):* USA (Texas).——FIG. 270,*2a–d. *R. hessensis* (KING), Asselian, Hess Canyon; *a,b,* articulated shell, ventral, dorsal views, ×4; *c,d,* dorsal valve interiors, ×4 (Cooper & Grant, 1969).

Sulcirugaria WATERHOUSE, 1983b, p. 112 [**S. transversa;* OD]. Shell transverse to subelongate with well-developed fold, sulcus; shell surface covered with strong bifurcating costellae; spines not observed; ventral valve interior with short

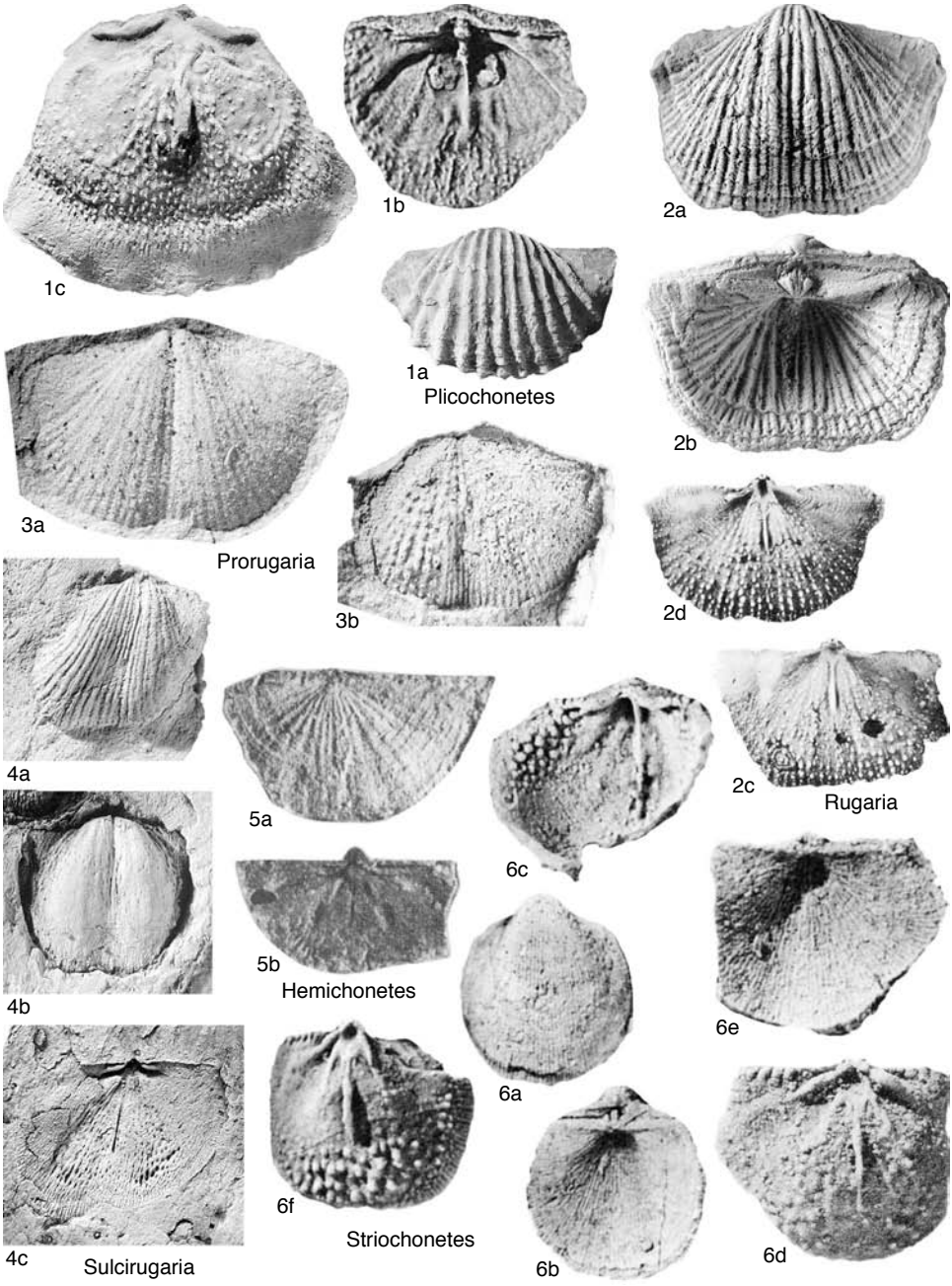

FIG. 270. Rugosochonetidae (p. 411–415).

myophragm, low vascular trunks; dorsal valve interior with low median septum, well-developed adductor scars. *Upper Permian (Tatarian):* Nepal.——FIG. 270,*4a–c.* **S. transversa;* ventral valve exterior, ventral valve internal mold, dorsal valve internal mold, ×2 (Waterhouse, 1983b).

Subfamily STRIOCHONETINAE Waterhouse & Piyasin, 1970

[Striochonetinae Waterhouse & Piyasin, 1970, p. 106]

Hinge denticulated chonetids; without sulcus, fold; ventral valve interior with long, bladelike myophragm; dorsal valve interior with cardinal process pit, median septum or breviseptum, strong anderidia, short, oblique inner socket ridges; no accessory septa. *middle Permian.*

Striochonetes Waterhouse & Piyasin, 1970, p. 106 [**S. scutella;* OD] [=*Ratburia* Yanagida, 1970, p. 85, obj.]. Small, markedly concavoconvex subcircular shell; shell surface capillate; spines developed in juvenile forms only; posterolateral parts of ventral valve interior with strong endospines; dorsal valve interior with small cardinal process, median septum arising anteriorly; strong anderidia; large anterior adductor scars. *middle Permian:* Thailand.——Fig. 270,*6a–f.* **S. scutella; a,b,* articulated shell, ventral, dorsal views, ×3; *c,* incomplete ventral valve interior, ×3; *d,e,* dorsal valve interior, exterior, ×4; *f,* dorsal valve interior, ×4 (Waterhouse & Piyasin, 1970).

Subfamily SVALBARDIINAE Archbold, 1982

[Svalbardiinae Archbold, 1982, p. 4]

Small to medium sized, externally smooth rugosochonetids; dorsal exterior pseudocapillate when worn; spines orthomorph oblique at low to moderate angle. *Lower Carboniferous–Upper Permian (Tatarian).*

Svalbardia Barchatova, 1970, p. 78 [**Chonetes capitolinus* Toula, 1875; OD]. Small, planoconvex to weakly concavoconvex; short, orthomorph oblique, low-angled spines; ventral valve coarsely pseudopunctate; dorsal interior with anteriorly prominent median septum, anderidia posteriorly fusing anterior to cardinal process pit; brachial ridges well defined; recurved anterior portions raised in mature individuals. *Permian (Kungurian–Kazanian):* Russia, Spitzbergen, Canadian Arctic, Australia.——Fig. 271,*1a–d. S. thomasi* Archbold, Baker Formation, Kungurian, Western Australia; *a,b,* articulated shell, dorsal, ventral views, ×3.5; *c,* ventral valve interior, ×4; *d,* dorsal valve interior, ×4.5 (Archbold, 1981c).

Capillonia Waterhouse, 1973, p. 37 [**Lissochonetes brevisulcus* Waterhouse, 1964, p. 21; OD]. Shell medium; ventral valve smooth, dorsal valve capillate; spines orthomorph oblique, symmetrically arranged; dorsal valve interior with thin median septum, short anderidia; brachial ridges with raised recurved anterior portions. [Archbold (1982, p. 4) interpreted the original illustrations of Waterhouse (1964) and thought that the dorsal valve was smooth instead of capillate, although Waterhouse (1973) concluded that the ornament was original and not worn. Without further information the description of capillate dorsal valve is maintained here.] *middle Permian:* New Zealand.——Fig. 271,*2a–c.* **Capillonia brevisulcus* (Waterhouse), Arthurton Group, ?Kazanian, South Island, New Zealand; articulated shell, dorsal side, ventral valve interior, incomplete dorsal valve interior, ×2 (Waterhouse, 1964).

Chonetinetes Cooper & Grant, 1969, p. 3 [**C. reversus;* OD]. Small, smooth, alate, dorsally deeply concave, anteriorly tapering shell; ventral sulcus, dorsal fold better developed in the umbonal region; dorsal valve interior with short median septum; erect cardinal process having deep cardinal process pit; anderidia reduced but anterior slope of dorsal valve deeply sulcate, lateral regions elevated. *Upper Permian (Kazanian–Tatarian):* USA (Texas).——Fig. 271,*5a–e.* **C. reversus,* Road Canyon Formation, upper Artinskian, Texas; *a,* ventral valve exterior, ×3; *b,* articulated shell, dorsal side, ×4; *c,* ventral valve interior, ×3; *d,e,* dorsal valve interiors, ×3 (Cooper & Grant, 1975).

Dyoros Stehli, 1954, p. 312 [**Chonetes consaguineus* Girty, 1929, p. 409; OD] [=*Stauromata* Hoover, 1981, p. 51, obj.]. Wide-hinged smooth shells with sulcus varying from deep to barely visible; ventral valve interior, visceral region usually strongly fringed by spines on anterolateral side. *Lower Permian (Sakmarian)–Upper Permian (Kazanian).*

D. (Dyoros) Stehli, 1954, p. 312 [**Chonetes consanguineus* Girty, 1929, p. 409; OD]. Strong angular ears, deep ventral sulcus. *Permian:* USA (Texas).——Fig. 272,*1a–c.* **D. (D.) consanguineus* (Girty), Bone Spring and Skinner Ranch Formations, Asselian, Texas; *a,* articulated shell, dorsal side, ×2; *b,* ventral valve interior, ×2; *c,* dorsal valve interior, ×4 (Cooper & Grant, 1975).

D. (Lissosia) Cooper & Grant, 1975, p. 1241 [**D. (L.) concavus;* OD]. Wide hinge, strong ears but sulcus conspicuously developed in late adult stages. *Permian (Artinskian–Kazanian):* USA (Texas).——Fig. 273*a–c.* **D. (L.) concavus,* Word Formation, Kazanian, Texas; ventral valve exterior, ventral valve interior, dorsal valve interior, ×4 (new).

D. (Tetragonetes) Cooper & Grant, 1975, p. 1246 [**D. (T.) quadrangulatus;* OD]. Relatively narrow hinged, reduced ears, rectangular outline, strong sulcus, moderately developed interior details. *Permian (Artinskian–Kazanian):* USA (Texas).——Fig. 272,*2a–d.* **D. (T.) quadrangulatus,* Word Formation, Kazanian, Texas; *a–c,* ventral valve, exterior, anterior, internal view, ×3; *d,* dorsal valve interior, ×3 (new).

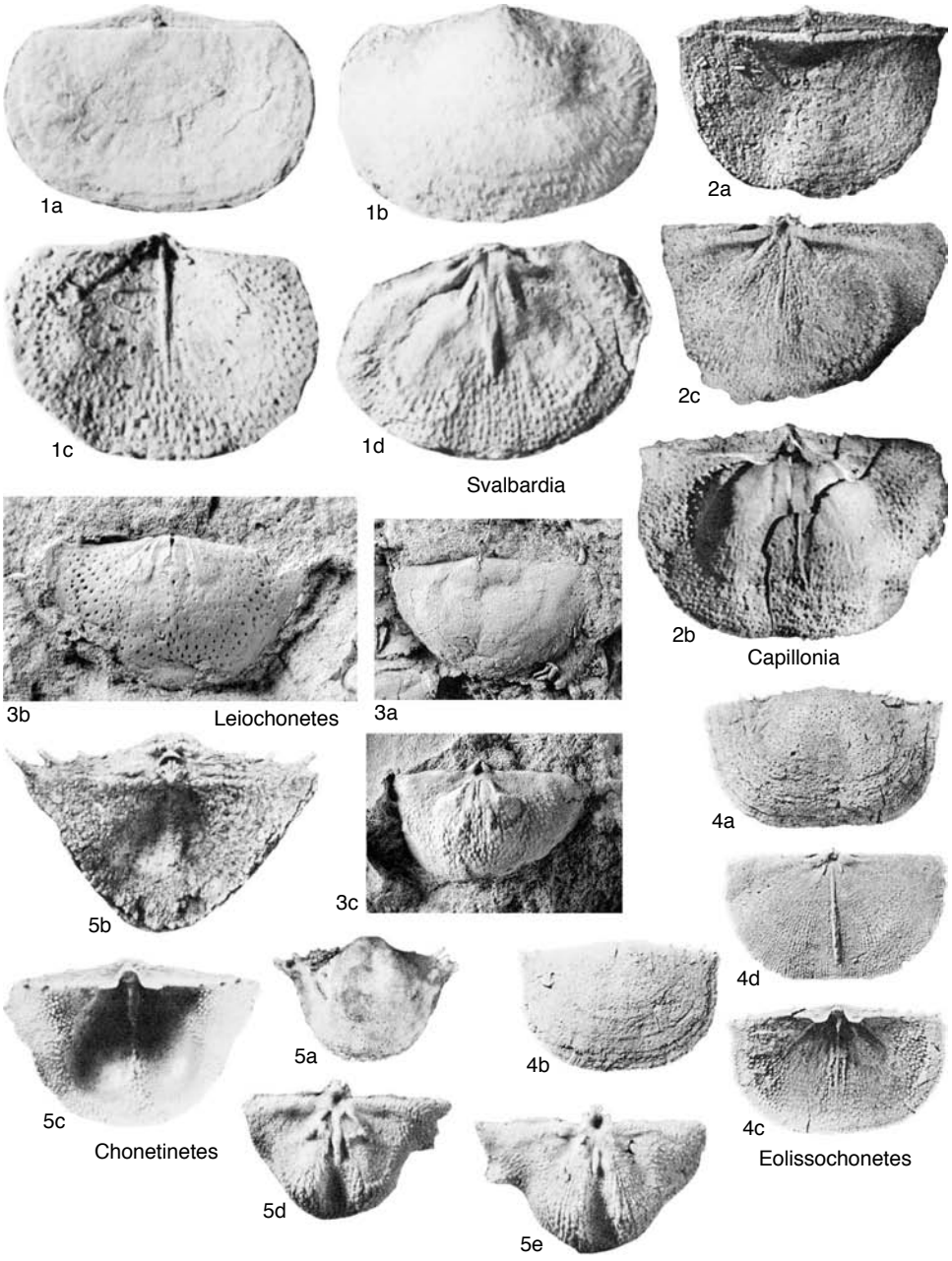

FIG. 271. Rugosochonetidae (p. 415–417).

Eolissochonetes HOARE, 1960, p. 220 [**Chonetes laevis* KEYES, 1888, p. 229, *non* DAVIDSON, 1866; OD; =*Eolissochonetes keyesi* MUIR-WOOD, 1962, p. 76; OD]. Differs from *Svalbardia* by the very short anderidia that usually do not fuse with median septum posteriorly, and by poorly developed brachial ridges; dorsal valve interior with long, anteriorly elevated median septum. *Lower Carboniferous (Namurian):* North America.——FIG. 271,*4a–d.* **E. keyesi* (MUIR-WOOD), Namurian, Missouri; *a,b,*

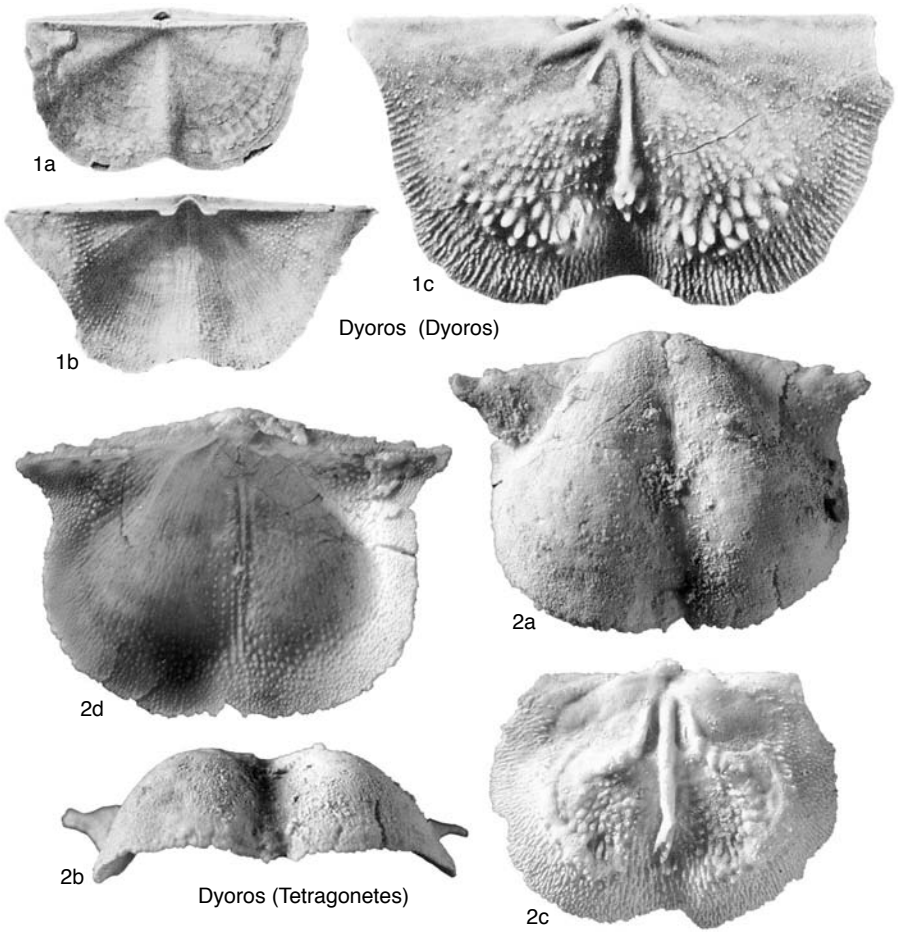

FIG. 272. Rugosochonetidae (p. 415).

ventral valve exteriors, ×2; *c,* ventral valve interior, ×2; *d,* dorsal valve interior, ×2 (Hoare, 1960).

Komiella BARCHATOVA, 1970, p. 62 [**Chonetes omolonensis* LICHAREW, 1934c, p. 11; OD]. Differs from *Lissochonetes* by its stout anderidia, strong median septum fused anteriorly of deep cardinal process pit; shell subquadrate; dorsal valve interior with poorly defined brachial ridges. [ARCHBOLD (1981c, p. 3) discussed the relationships between *Svalbardia* and *Komiella.* AFANAS'EVA (1988) regarded *Komiella* as junior synonym of *Lissochonetes,* but the author follows ARCHBOLD's 1982 opinion, considering *Komiella* useful for separating a group of species with strongly developed dorsal internal structures from *Lissochonetes.* To synonymize these genera would be premature.] *Upper Carboniferous (Moscovian)–Permian (Kazanian):* Russia.

Leiochonetes ROBERTS, 1976, p. 26 [**L. salisburyensis;* OD]. Small, moderately to strongly concavoconvex; spines orthomorph oblique, almost perpendicular, symmetrically arranged; dorsal valve interior with short median septum; cardinal process pit well developed; anderidia widely divergent anteriorly. *Lower Carboniferous (Viséan):* eastern Australia.——FIG. 271,*3a–c.* **L. salisburyensis,* Viséan, eastern Australia; ventral valve exterior, ventral valve internal mold, dorsal valve interior, ×3 (Roberts, 1976).

Leurosina COOPER & GRANT, 1975, p. 1260 [**L. marginata;* OD]. Small, widely rectangular in outline; anterior commissure unfolded or broadly deflected dorsally; spines orthomorph oblique. *Lower Permian (Sakmarian–Kungurian):* USA (Texas).——FIG. 274,*1a–d.* * *L. marginata,* Word Formation, Kazanian, Texas; *a–c,* ventral valve, exterior, interior, anterior view, ×3; *d,* dorsal valve interior, ×3 (Cooper & Grant, 1975).

Lissochonetes DUNBAR & CONDRA, 1932, p. 169 [**Chonetes geinitzianus* WAAGEN, 1884, p. 621; OD; *nom. nov. pro Chonetes glabra* GEINITZ, 1866, p. 60, *non* HALL, 1857, p. 117]. Shell transverse, slightly

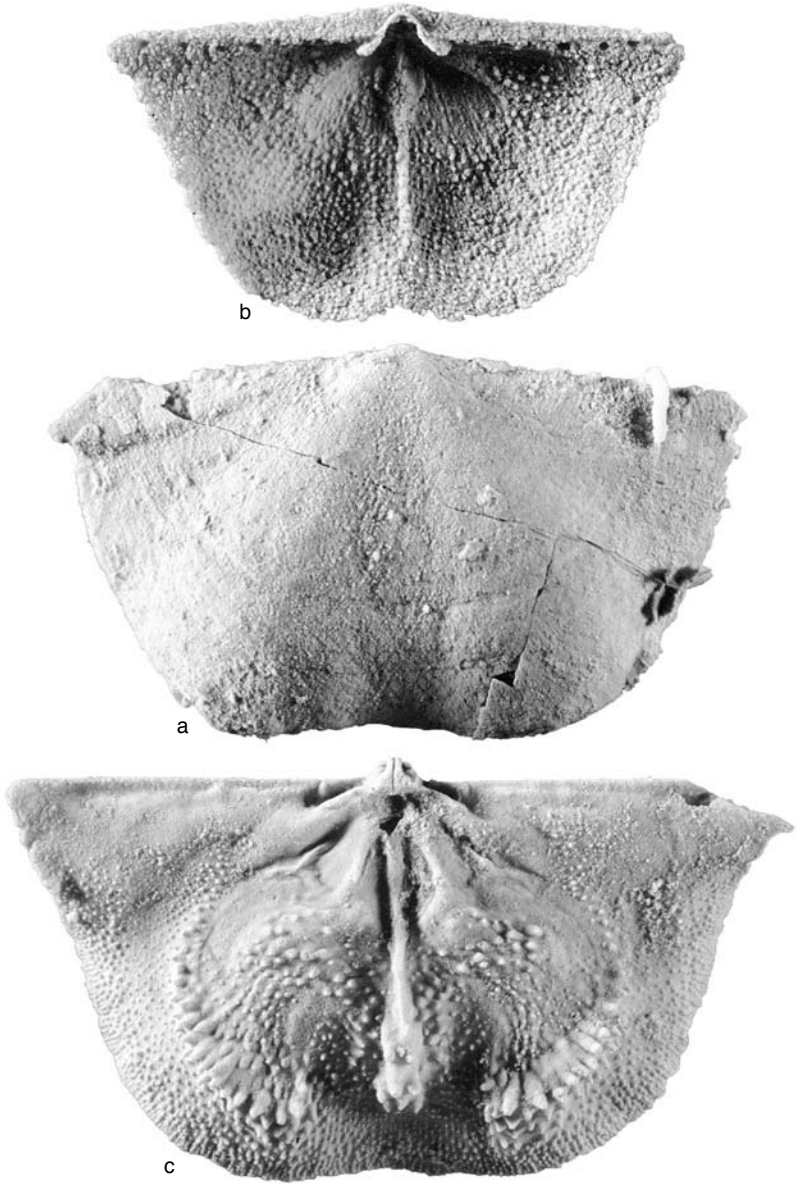

FIG. 273. Rugosochonetidae (p. 415).

concavoconvex, weakly sulcate; spines orthomorph oblique (40°), symmetrically arranged; delicate dorsal valve internal structures with low, narrow median septum, or breviseptum, and anderidia not fusing posteriorly; cardinal process pit present. *Upper Carboniferous (Namurian)–Permian:* Europe, Asia, northern Africa, North America, Asia; Australia, *Namurian–Permian.*——FIG. 274,*2a–c. *L. geinitzianus* (WAAGEN), upper Pennsylvanian, Nebraska; *a,* ventral valve exterior, ×3.5; *b,* articulated shell, dorsal side, ×3; *c,* dorsal valve interior, ×3 (Dunbar & Condra, 1932).

Quadrochonetes STEHLI, 1954, p. 309 [**Q. girtyi;* OD; *nom. nov. pro Chonetes quadratus* GIRTY, 1929, p.

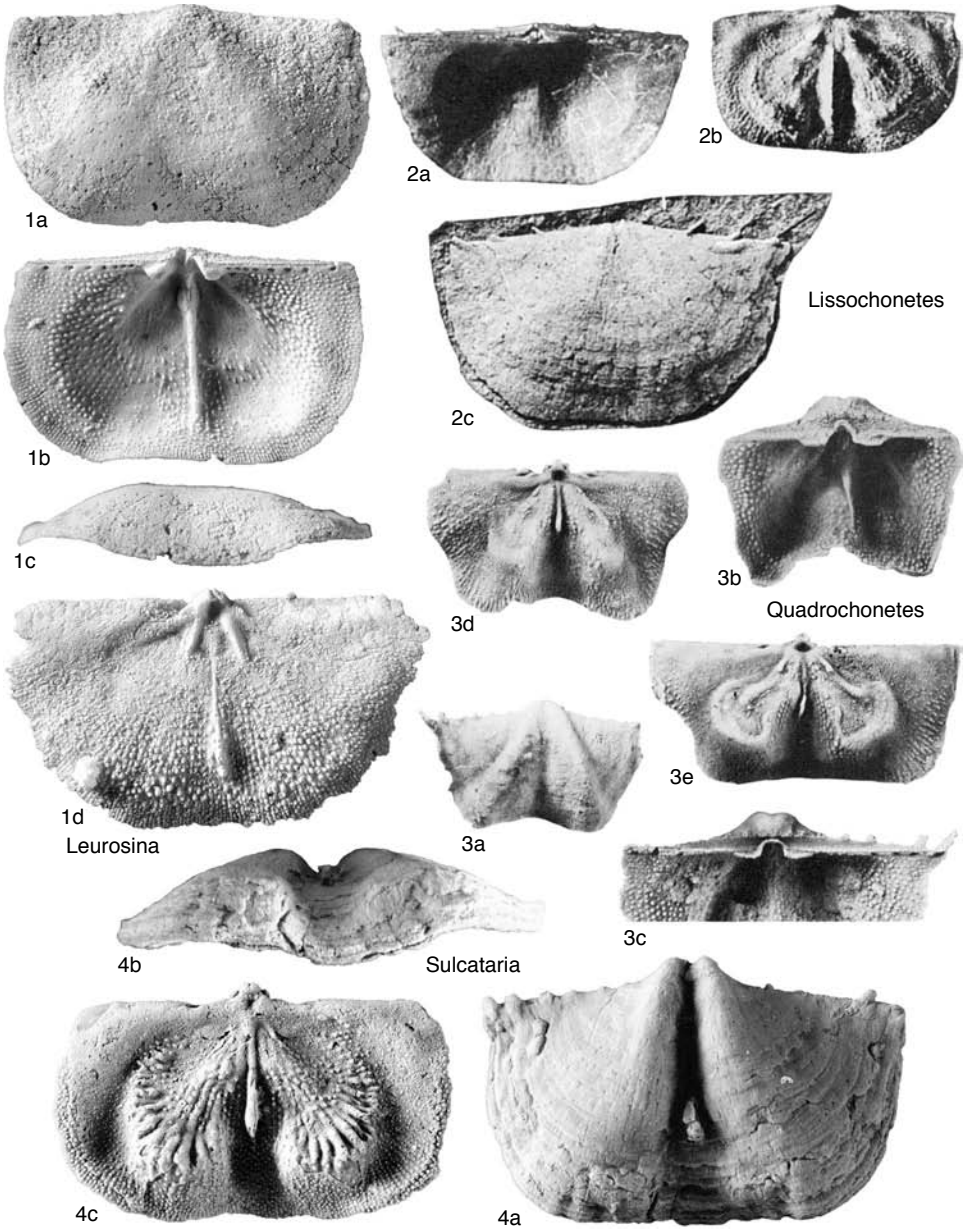

FIG. 274. Rugosochonetidae (p. 417–420).

407, *non Chonetes uralica quadratus* BOLKHOVITINIVA & MARKOV, 1926, p. 26, *nec* NIKITIN, 1890]. Small, quadrate, strongly concavoconvex, smooth shell; prominent dorsal fold, deep ventral sulcus; ears large; spines orthomorph oblique, high angled; dorsal valve interior with low, short median septum; brachial ridges obscure or absent; short, curved inner socket ridges; anderidia anteriorly widely divergent. *Carboniferous–Lower Permian:* USA.——FIG. 274,*3a–e.* **Q. girtyi*, Bone Spring Formation, Artinskian, Texas; *a,* ventral valve exterior, ×2; *b,* ventral valve interior, ×3; *c,* posterior part of ventral valve, ×4; *d,e,* dorsal valve interiors, ×3 (Cooper & Grant, 1975).

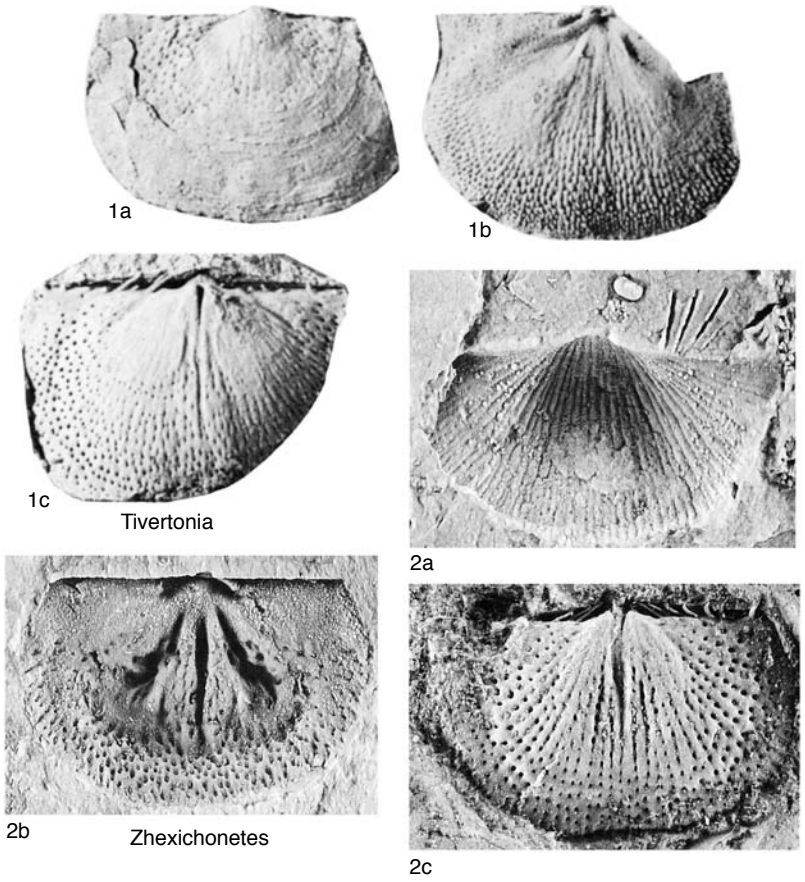

FIG. 275. Rugosochonetidae (p. 420).

Sulcataria COOPER & GRANT, 1969, p. 5 [**Chonetina? rostrata* DUNBAR & CONDRA, 1932, p. 150; OD]. Small, smooth shell with deeply sulcate ventral valve; dorsal valve weakly concave with strong median fold; ventral valve interior with broad, elevated adductor ridge, flattened margins; dorsal valve interior with thick median septum, strongly lobed anterior visceral region. *Lower Permian (Asselian):* USA (Texas).——FIG. 274,*4a–c. *S. rostrata* (DUNBAR & CONDRA), Graham Formation, Asselian, Texas; *a,b,* ventral valve, ventral, anterior views, ×4; *c,* dorsal valve interior, ×4 (Cooper & Grant, 1969).

Tivertonia ARCHBOLD, 1983a, p. 71 [**Lissochonetes yarrolensis* MAXWELL, 1954a, p. 35; OD]. Shell smooth, gently concavoconvex; ventral valve with short, thin spines at moderate angle to hinge; mature dorsal valve interior with distinct cardinal process pit, lateral septa, long median septum; maximum width of shell of immature individuals at midlength of valves, lending semicircular outline to shell; sulcus absent or ill defined. *Lower Permian (Sakmarian):* eastern Australia, Argentina.——FIG. 275,*1a–c. *T. yarrolensis* (MAXWELL), Yarrol Formation, Queensland; *a,* ventral valve exterior, ×4; *b,* dorsal valve interior, ×3.25; *c,* ventral valve internal mold, ×3.75 (Archbold, 1983a).

Zhexichonetes LIANG, 1982, p. 201 [**Z. longispina;* OD]. Small, costellate shell without sulcus, fold; spines long, vertical near umbo, posterolaterally directed near angles; dorsal valve interior with stout median septum not supporting cardinal process; strongly developed anderidia, high, anteriorly thickened. *Lower Permian:* China (Zhejiang).——FIG. 275,*2a–c. *Z. longispina,* Jia Shan Formation, Lower Permian; ventral valve external mold, dorsal valve internal mold, ventral valve internal mold, ×4.7 (Liang, 1990).

Subfamily UNDULELLINAE Cooper & Grant, 1975

[Undulellinae COOPER & GRANT, 1975, p. 1286]

Small smooth rugosochonetids; exterior of dorsal valve pseudocapillate when worn;

spines orthomorph, oblique or perpendicular, symmetrically arranged; brachial ridges, dorsal median septum prominent; cardinal process small. *Permian (Sakmarian–Kungurian).*

Undulella Cooper & Grant, 1969, p. 5 [**U. undulata;* OD]. Small, slightly concavoconvex, subrectangular in outline with cardinal extremities at 90°; anteromedian margin of shell deflected dorsally; spines orthomorph, almost perpendicular. *Lower Permian (Artinskian–Kungurian):* USA (Texas).——Fig. 276,*1a–c. *U. undulata,* Word Formation, Texas; ventral valve exterior, interior, dorsal valve interior, ×4 (Cooper & Grant, 1969).

Micraphelia Cooper & Grant, 1969, p. 4 [**M. scitula;* OD]. Small, unfolded, narrow-hinged rugosochonetids with orthomorph oblique spines; interior with thickened, spinose anterolateral visceral region. *Lower Permian (Sakmarian–Artinskian):* USA (Texas).——Fig. 276,*2a–c. *M. scitula,* Bell Canyon Formation, Texas; ventral valve exterior, interior, dorsal valve interior, ×4 (Cooper & Grant, 1969).

Subfamily LAMELLOSIINAE Cooper & Grant, 1975

[Lamellosiinae Cooper & Grant, 1975, p. 1270]

Concentrically lamellose rugosochonetids without radial ornament; pseudocapillate shell when worn. *Permian.*

Lamellosia Cooper & Grant, 1975, p. 1270 [**L. lamellosa;* OD]. Small, subtrapezoidal; spines orthomorph oblique, symmetrically arranged. *Upper Permian (Kazanian–Tatarian):* USA (Texas).——Fig. 276,*4a,b. *L. lamellosa;* Guadalupian, Texas; ventral valve exterior, interior, ×3 (Cooper & Grant, 1975).

Parademonedys Yang Xue-chang, 1984, p. 208[332] [**P. huananensis;* OD]. Small, subtrapezoidal, strongly concavoconvex; spines present but not described; interiors unknown. [The author compared this new genus with *Demonedys* and placed it within the Anopliinae, but it seems provisionally better placed within the Lamellosiinae because of the nature of its ornamentation, which is similar to that of *Lamellosia.*] *Lower Permian:* southern China.——Fig. 276,*3. *P. huananensis,* southern China; ventral valve exterior, ×3 (Yang Xue-chang, 1984).

Subfamily QUINQUENELLINAE Archbold, 1981

[Quinquenellinae Archbold, 1981a, p. 205]

Small, subquadrate, with smooth exterior; shell surface not pseudocapillate when worn; ventral sulcus absent or ill defined; spines symmetrically arranged; dorsal interior with short anderidia, pair of long accessory septa, variably developed median septum. *Permian.*

Quinquenella Waterhouse, 1975, p. 2 [**Q. glabra;* OD]. Transverse, subquadrate to subtrapezoidal, with maximum width at hinge line; orthomorph oblique spines; dorsal valve interior with variably developed, thin median septum, long, thin accessory septa, short, strong anderidia usually fused posteriorly; cardinal process pit variably developed. *Permian (Artinskian–Tatarian):* Australia, Indonesia, Himalaya, ?Burma, ?Malaysia, ?Afghanistan.——Fig. 276,*5a–d. Q. magnifica* Archbold, Aifat Formation, Irian Jaya, Permian, Indonesia; *a,* dorsal side of articulated shell, latex, ×4; *b,* ventral valve internal mold, ×4; *c,* dorsal valve internal mold, ×4.5; *d,* juvenile dorsal valve internal mold, ×8 (Archbold, 1981d).

Sandrella Waterhouse, 1985, p. 212 [**S. platina;* OD]. Smaller medium, smooth shell, almost planoconvex; spines not observed; ventral valve interior with short, narrow myophragm; dorsal valve interior with cardinal process pit, low, ill-developed median septum, long anderidia, five pairs of low, narrow accessory septa. *Permian:* Himalayas, *Lamnimargus himalayaensis* Zone.——Fig. 276,*6a–c. **S. platina, Gungri formation, Permian, *Lamnimargus himalayensis* Zone, western Himalayas; *a,* ventral valve internal mold, ×1.5; *b,* dorsal valve interior, latex, ×2; *c,* dorsal valve interior, latex, ×3 (Waterhouse, 1985).

Family DAVIESIELLIDAE Sokolskaja, 1960

[Daviesiellidae Sokolskaja in Sarytcheva, Licharew, & Sokolskaja, 1960, p. 223]

Large shell with thickened ventral valve; very low interareas; no spine row; adductor scars partly or wholly dendritic; detached rounded accessory adductor scars present; dorsal valve interior without cardinal process pit; brachial ridges anteriorly directed. *Lower Carboniferous (Viséan).*

Daviesiella Waagen, 1884, p. 613 [**Productus llangollensis* Davidson, 1863, p. 277; SD Oehlert, 1887b, p. 1280]. Large, highly concavoconvex shell; ventral valve massive, much thickened; pseudodeltidium lacking, chilidium present; ventral valve interior with dendritic adductor scars; dorsal valve interior with massive median septum supporting cardinal process. [*Daviesiella* differs from all other chonetoidean genera in its shell shape (much thickened ventral valve, very low interareas), as well as in the lack of spine row, pseudodeltidium and anderidia. Moreover the adductor scars are typically dendritic. In this sense the position of *Daviesiella* within the Chonetoidea remains uncertain and it would probably be better assigned to the superfamily Productoidea.] *Lower Carboniferous*

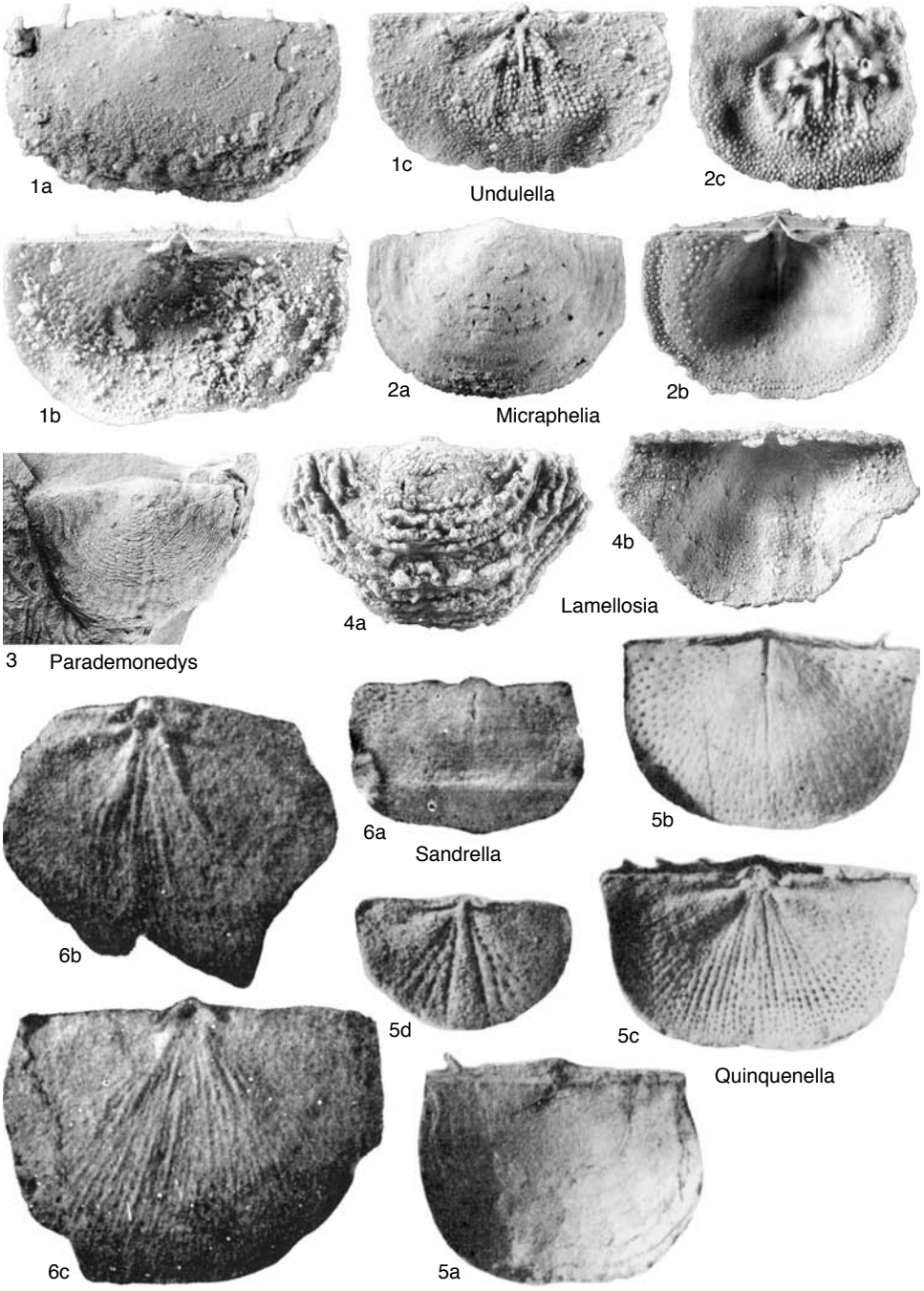

FIG. 276. Rugosochonetidae (p. 421).

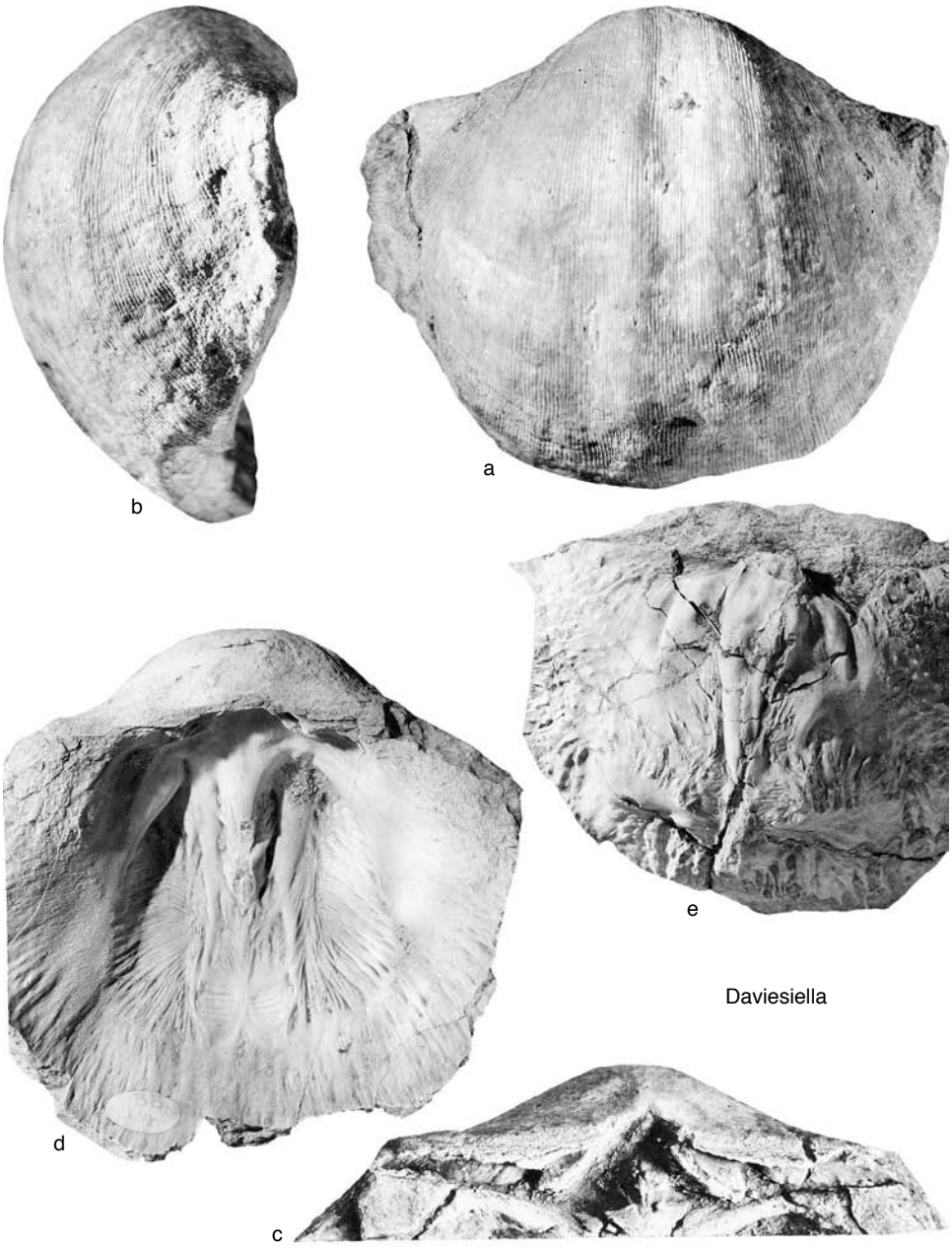

FIG. 277. Rugosochonetidae (p. 421–423).

(Viséan): England, Wales.——FIG. 277*a–e.* **D. llangollensis* (DAVIDSON), Wales (Denbighshire); *a,b,* ventral valve, ventral, lateral views, ×1; *c,* interarea showing hinge teeth, chilidium of damaged specimen, ×2; *d,* ventral valve interior, ×1; *e,* dorsal valve interior, ×1 (Muir-Wood, 1962).