Family ISOGRAMMIDAE Schuchert & LeVene, 1929

[Isogrammidae SCHUCHERT & LEVENE, 1929, p. 18]

Shells transversely suboval in outline. Cardinal process with well-developed shaft, dental sockets relatively small, lateral to cardinal process (180). *Carb.-Perm.*

Isogramma MEEK & WORTHEN, 1870, p. 36 [**Chonetes? millipunctatus* MEEK & WORTHEN, 1870, p. 35; OD] [=*Aulacorhynchus* DITTMAR, 1872, p. 2 (*non* GOULD, 1834); *Aulacorhyna* STRAND, 1928, p. 37 (*nom. subst. pro Aulacorhynchus* DITTMAR, 1872 (*non* GOULD, 1834) (type, *Aulacorhynchus pachti* DITTMAR, 1872, p. 2)]. Large, concavo-convex; strong concentric ornament of elevated fila. Myophore strong, shaft bifurcating around dorsal median ridge; musculature of brachial valve obscure, in pedicle valve adductor scars on inner surface of umbonal plate, subflabellate diductor scars lateral to plate (5). *Carb.-Perm.*, N.Am.-Eu.-Asia.——FIG. 230,*2a-c. I. texanum* COOPER, Penn.(Gaptank F.), USA(Tex.); *2a*, latex replica ped.v. ext., ×1; *2b*, ped.v. int. impression, ×2; *2c*, brach.v. ext. mold, ×1 (180). ——FIG. 230,*2d,e, I. renfrarum* COOPER, Penn. (Gonzales Sh.); USA(Tex.); *2d,e*, detail of cardinal process, post., dors., both ×2 (180).

Megapleuronia COOPER, 1952, p. 117 [**Productus fabianii* GRECO, 1947, p. 1; OD]. Biconvex or concavo-convex; costate, with concentric ornament of discontinuous, raised lines. Ventral interior unknown, dorsal interior with muscle platform supported by median septum. *Perm.*, Eu.——FIG. 230, *1a. *M. fabianii* (GRECO), Italy; brach.v. int., ×1 (180).——FIG. 230,*1b,c. M. grecoi* COOPER, Italy; *1b*, ped.v. ext., ×2; *1c*, brach.v. ext., ×3 (180).

STROPHOMENIDA

By HELEN MUIR-WOOD and ALWYN WILLIAMS

[British Museum (Natural History) and Queen's University of Belfast]

Order STROPHOMENIDA Öpik, 1934

[*nom. transl.* MOORE *in* MOORE, LALICKER & FISCHER, 1952, p. 221 (*ex* suborder Strophomenoidea ÖPIK, 1934, p. 75); emended H. M. MUIR-WOOD & ALWYN WILLIAMS, herein] [Diagnosis prepared by ALWYN WILLIAMS]

Articulate brachiopods with plano- to concavo-convex, less commonly biconvex, resupinate or geniculated, shells; interareas lacking or vestigial to extravagantly developed, hinge lines rarely reduced; pseudodeltidium rarely absent, mostly strongly developed or continuous with ventral interarea, chilidium variably developed or indistinguishable from dorsal interarea; pedicle foramen, with sheath, supra-apical probably in all brephic shells but rarely open in adult shells, or attachment effected by cementation of pedicle valve with or without aid of open, tubular spines; spines may be present on brachial as well as pedicle valve, less commonly limited to margin of ventral interarea. Cardinal process rarely absent, elaborated from median partition or more commonly from pair of discrete lobes; socket ridges rarely strongly developed, commonly vestigial or absent; lophophore inferred to vary from schizolophous to spirolophous and attached plectolophous dispositions, less commonly supported by dorsal platforms or ridges, very rarely by calcareous spires. Ventral muscle field commonly expanded well beyond umbonal cavity, rarely borne on elevated structures; dorsal adductor field normally quadripartite rarely elevated. Shell substance pseudopunctate, very rarely impunctate. *L.Ord.-L.Jur.*

The Strophomenida constitute the largest ordinal group within the Brachiopoda, for the order embraces nearly 400 genera (including the largest and thickest shells known) distributed among nine superfamilies and four suborders. A taxonomic assemblage of this size inevitably includes a great variety of forms, but the morphological diversity displayed by members of the order is unprecedented, mainly because of the widespread adoption of an attached mode of life by cementation or spinous anchorage following the loss of a functional adult pedicle early in the evolutionary history of the group. Chonetidina and Productidina, for example, independently acquired spines or perforations containing outer epithelial strands by means of which support, through attachment to, or ramification within the substratum, was effected. A minority of strophomenaceans, most davidsoniaceans and all lyttoniaceans, on the other hand, remained attached for varying parts of their lives solely by cementation of the pedicle valves. Inflexible anchorage of this nature was probably the principal cause for repeated bizarre modifications in shell shape. Thus, conical shells were typical of late

davidsoniaceans as well as richthofenaceans; but, whereas those of the former involved an exaggerated growth of the ventral interarea, those of the latter were the result of holoperipheral increase in the pedicle valve subsequent to loss of the interarea.

Despite this extraordinary variation in shell form, the order is basically a homogeneous group. With the discovery that pedicle sheaths were also developed in at least some young Productidina (BRUNTON, 1965) the supra-apical location of the functional foramen, commonly ventral of a well-developed pseudodeltidium, becomes the chief diagnostic feature of the Strophomenida, although it is also characteristic of some members of the Orthida. The attendant implication that the embryonic pedicle developed directly from the ventral body wall indicates, if correct, how primitive the Strophomenida were relative to most other articulate brachiopods. The pseudopunctate nature of the shell is not as invariably developed nor as exclusive to the order as is generally believed. The shells of a few plectambonitaceans and of early davidsoniaceans are impunctate, whereas *Estlandia* and other related Clitambonitidina are pseudopunctate, so that this particular condition of the test must have arisen polyphyletically.

Simple socket ridges are also typical of the Strophomenida, although they were lost in a minority of the Strophomenidina and in most Productidina, in which group they were commonly replaced by lateral ridges. In only a few plectambonitaceans and davidsoniaceans did elaboration of the ridges entail the growth of dorsally directed apophyses which may have been connected with the mouth segment of the lophophore in the manner of crura. Indeed, only the spiralia of *Thecospira* can be confidently compared with the more orthodox lophophore structures of other articulate orders. It is therefore not surprising to find that in plectambonitaceans, a few strophomenaceans, and many species of Productidina and Chonetidina, dorsal platforms, ridges, and endospines which are so arranged as to suggest their functioning as supports to the lophophore (the problems involved in interpreting the Oldhaminidina shell are discussed as an introduction to the systematics of that suborder). The endospines of Productidina probably also functioned as strainer devices.

Other features are less convincingly diagnostic of the order, although a few of them are still noteworthy. All variations of the plectambonitacean cardinal process, which include bifid and trifid structures, arose through modification of a simple median partition. In contrast, cardinal processes of the remaining Strophomenida, which may be extravagantly developed and greatly elaborated, were derived from a pair of ridge-like myophores that flanked a vestigial median partition only in the primitive, earlier strophomenaceans. Differences in the shell profile are also significant at the superfamilial level. The brephic shell of all Strophomenida was either biconvex or rarely convexo-plane (as in some strophalosiids) but this relationship was retained throughout later stages of growth only by members of the Davidsoniacea and an aberrant productacean *(Septarinia)*. In all other Strophomenida are given below in the introductions to concavo-convex and was modified solely by resupination with or without geniculation; and in this respect most members of the order are immediately distinguishable from other articulate brachiopods.

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

Suborder STROPHOMENIDINA Öpik, 1934

[*nom. correct.* WILLIAMS, herein (*pro* suborder Strophomenoidea ÖPIK, 1934, p. 75] [Materials for this suborder prepared by ALWYN WILLIAMS]

Biconvex to concavo-convex or resupinate, smooth to unequally parvicostellate, wide-hinged articulate brachiopods, commonly with well-developed pseudodeltidium and chilidium; shell substance pseudopunctate, rarely impunctate. Teeth simple, rarely supplemented by accessory teeth and denticles or replaced by denticular plates; muscle bases rarely elevated above floor of valves; cardinal process commonly bilobed but also consisting of simple median ridge, rarely absent; mantle canal system in both valves saccate to lemniscate. *Ord.-Trias.*

The Strophomenidina brachiopods include a diverse host of stocks, mainly characteristic of the Paleozoic era, which, de-

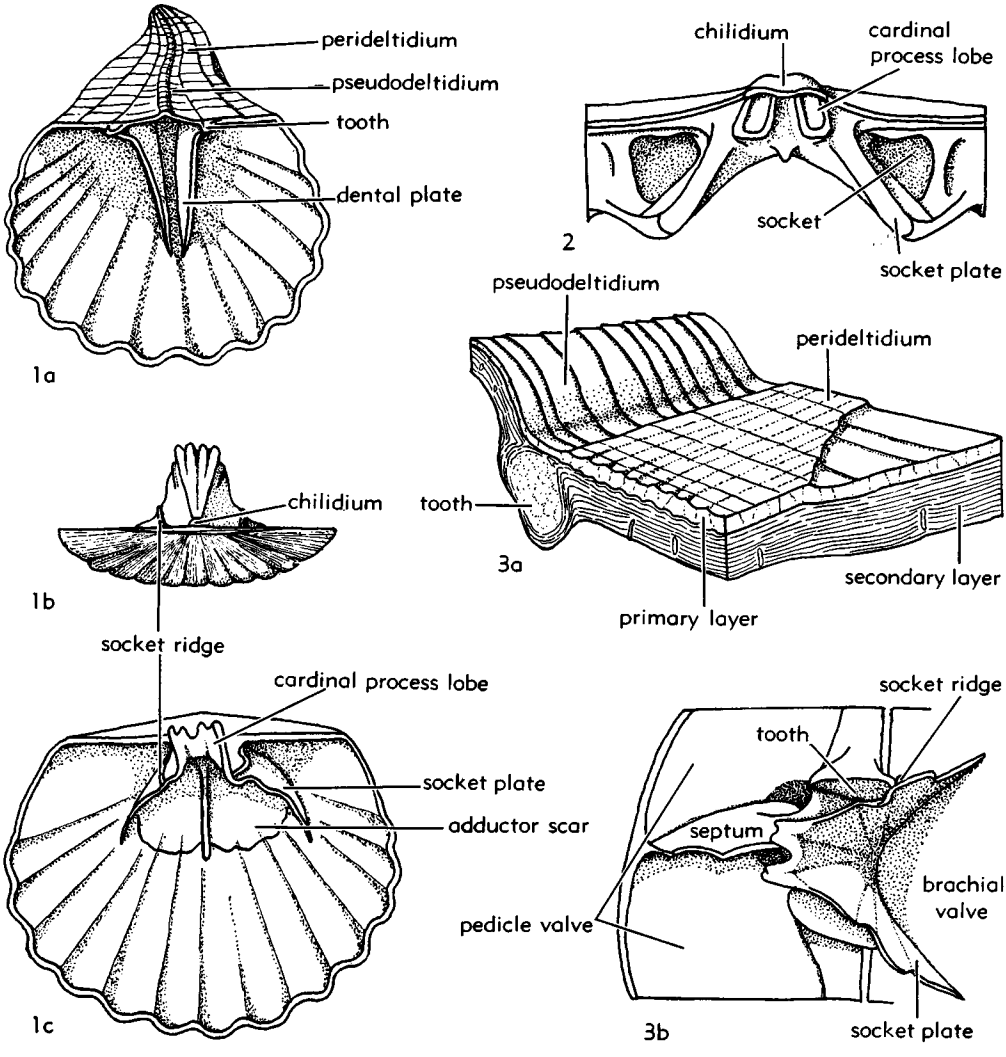

FIG. 231. Morphological features of davidsoniacean strophomenides (Williams, n). *1. Meekella*; *1a,* pedicle valve interior; *1b,* posterior view of brachial valve; *1c,* interior of brachial valve.——*2. Schuchertella,* showing chilidium and adjacent structures of brachial valve.——*3. Derbyia*; *3a,* oblique 3-dimension diagram showing structure of part of interarea; *3b,* view from inside shell looking toward beak.

spite a great deal of morphological variation, have a number of features indicative of common ancestry and collectively distinguishing them from the Productidina and Chonetidina.

The protegulum and brephic shells of all Strophomenidina, as far as known, are biconvex, a disposition maintained throughout the ontogeny of the davidsoniaceans, except for a minority (like some Schellwienella) in which the pedicle valve becomes concave in adult stages of growth. In contrast, the shell of all strophomenaceans and plectambonitaceans is concavo-convex in neanic stages at least, a relationship that never is eliminated completely even in resupinate stocks. The strophomenoid shell is typically widest at the hinge line and equipped with well-developed interareas, but among the davidsoniaceans a tendency toward reduction in width of the hinge line and in length of the dorsal interarea is seen.

The strophomenoid shell is ornamented in a variety of ways. The radial ornamenta-

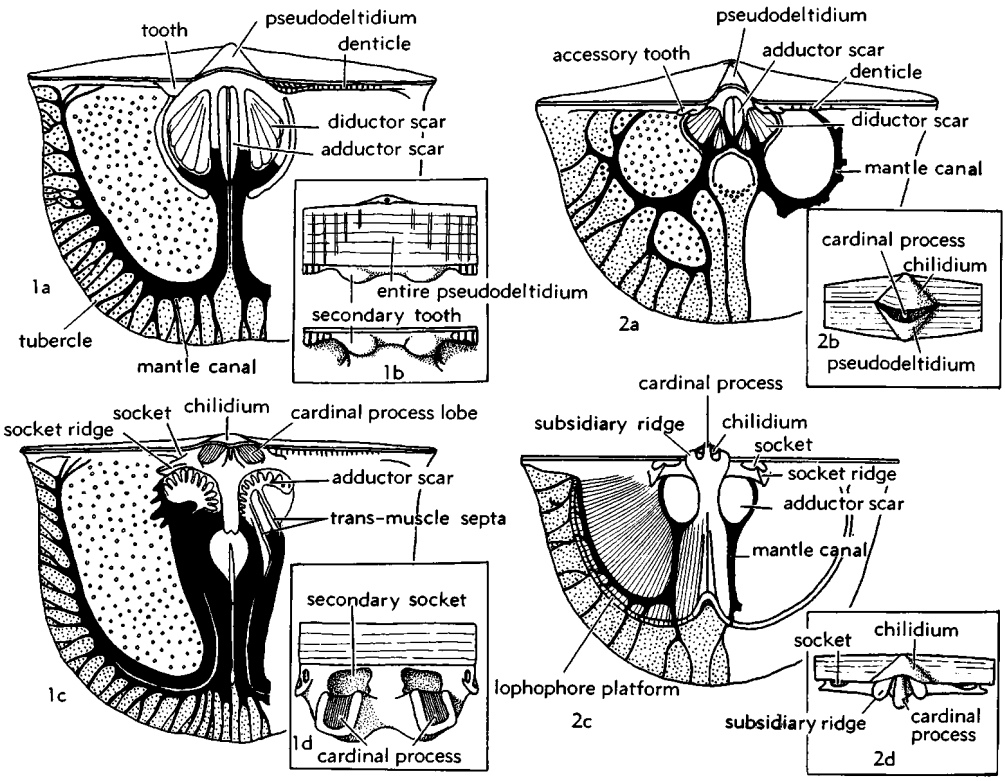

FIG. 232. Morphological features of earlier, less specialized strophomenide stocks (Williams, n).——*1.* Strophomenaceans; *1a,* stylized pedicle valve interior showing muscle scars and mantle canal pattern as developed in *Strophomena; 1b,* enlargements of median part of stropheodontid interarea; *1c,* brachial valve interior showing mantle canal pattern of *Strophomena*; *1d,* enlargement of median part of stropheodontid interarea.——*2.* Plectambonitaceans; *2a,* stylized pedicle valve interior showing mantle canal pattern as in *Leptestiina*; *2b,* enlargement of central part of interarea showing both valves; *2c,* stylized brachial valve interior showing mantle canal pattern as in *Leptestiina*; *2d,* enlargement showing chilidium and associated structures. The subsidiary ridges indicated in *2c* and *2d* also may be referred to as "notothyrial walls" or "chilidial plates" according to their origin.

tion is typically unequally parvicostellate but it disappears in such unrelated stocks as *Christiania, Bimuria, Pholidostrophia,* and *Thecospira,* and in late species of *Strophodonta* it is replaced by coarse secondary costellation. The shell may also be ornamented by fine lamellae or comae (as in many plectambonitaceans) and by concentric or impersistent rugae, as in most plectambonitaceans and strophomenaceans. All davidsoniaceans are characterized by a pair of triangular surfaces (perideltidium) forming part of the interarea of the pedicle valve and lying lateral to the pseudodeltidium, although not necessarily adjacent to it (Fig. 231, *1a, 3a*). Each surface is slightly elevated above the rest of the interarea, and in addition to being ornamented by growth lines parallel to the hinge line, is also feebly striated at right angles to the hinge line, the striations lying oblique to the perideltidial boundaries and not radiating from the umbo. Serial sections show that the perideltidial boundaries are represented by sharp deflections of both primary and secondary shell layers, the striations representing crenulations of the primary layer and part of the underlying secondary layer. No function has as yet been ascribed to the perideltidium.

In all plectambonitaceans, most strophomenaceans, and early davidsoniaceans, the pseudodeltidium and chilidium are well developed and they fit together so snugly that an exaggerated growth of one was matched by a complementary reduction of the other.

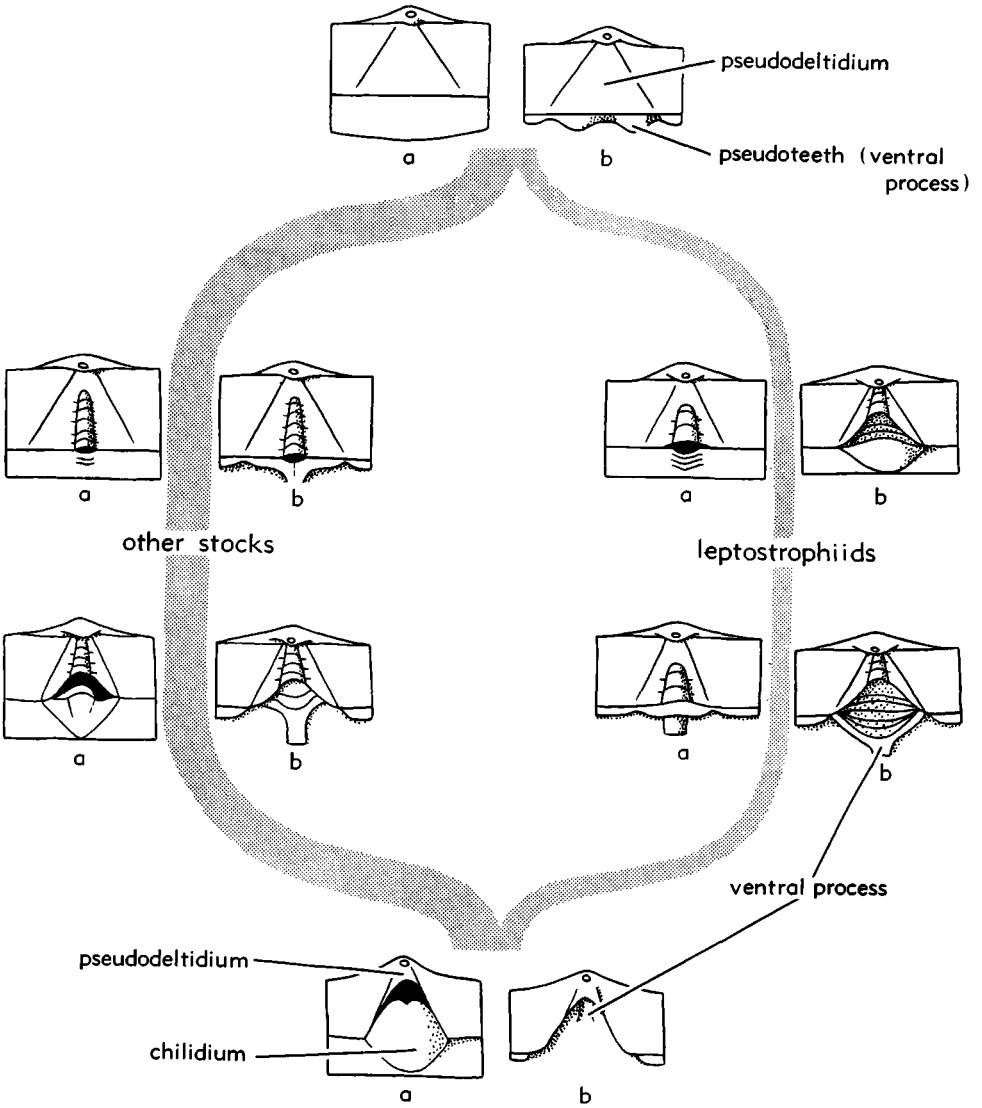

FIG. 233. Closure of delthyrium and loss of chilidium during evolution of stropheodontids (Williams, n). In most stocks, the delthyrium eventually was closed entirely by dorsal growth of the pseudodeltidium and ventral process on its inner side, without any pronounced concavity on the posterior surface of the ventral process. Among leptostrophiids, however, an evolutionary stage is seen in which the ventral process may be decidedly concave, simulating a spondylium, although certainly not homologous to it.

In early Strophomenidina (Fig. 232, *1c*) the chilidium, which usually is very much larger than the pseudodeltidium, probably functioned as a protective covering for the bases of the diductor muscles implanted on the notothyrial floor or on the cardinal process. It is therefore not surprising to find that among the stropheodontids the growth of the lobes of the cardinal process away from the hinge line was accompanied by a progressive elimination of the chilidium (871), so that in most Devonian representatives of the family the interarea of the brachial valve is entire, without a differentiated chilidium (Fig. 233). Concomitantly, the delthyrium ultimately became covered by an entire pseudodeltidium extending to the hinge line and disposed posteriorly in the

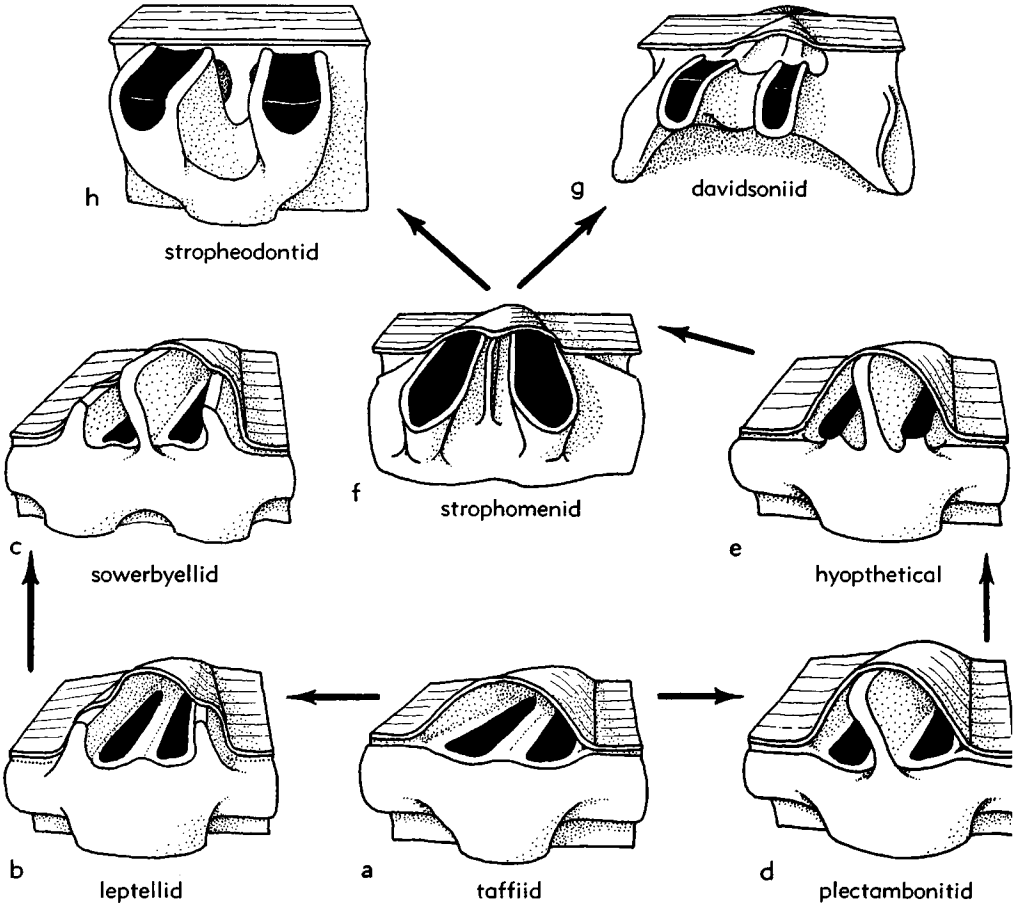

FIG. 234. Morphogeny of strophomenide cardinal process, with lines of presumed development indicated by arrows (black areas represent inferred seats of diductor muscle attachments) (Williams, n).

same plane as the interarea of the pedicle valve. In this ultimate stage the secondary shell deposit of the pseudodeltidium was fashioned into a pair of protuberances (secondary teeth) (Fig. 232, *1b*) which fit into the concave surfaces (secondary sockets, etc.) separating the cardinal process lobes from the interarea of the brachial valve.

A similar complementary growth of the pseudodeltidium and chilidium also apparently was connected with ventral growth of the cardinal process lobes and, accelerated by reduction in the interarea of the brachial valve, characterizes the davidsoniaceans (Fig. 231, *1*). Except for a few forms (e.g., *Thecospira*), however, the pseudodeltidium is never entire and usually it is sharply arched medianly to accommodate both a vestigial chilidium and the elevated posterior face of the cardinal process.

Modification of the notothyrial floor for attachment of the dorsal diductor muscle bases was diversely effected among the Strophomenidina (Fig. 234). In some early plectambonitaceans (e.g., *Taffia*), the diductor muscle bases must have been attached directly to the floor of the notothyrium, for no outgrowths which could have accommodated them are found on it.

A simple departure from this unspecialized condition consists of the growth of a median partition which usually extends from the notothyrial floor to the chilidium (as among the plectambonitids), thus dividing the notothyrium into two deep narrow chambers. This septum is conveniently

referred to as a simple cardinal process but in all probability the diductor bases were attached to the notothyrial floor on either side of the septum. Further elaboration included the infilling of the notothyrium by the growth of lateral ridges subsidiary to the median septum and subtending with it a pair of grooves for the reception of the dorsal diductor bases.

A similar development is seen in other plectambonitaceans but it was accompanied by the posterior and ventral growth of the notothyrial walls as a pair of prominent ridges more or less continuous with the socket ridges. These are commonly referred to as chilidial plates, although it is noteworthy that their formation was in no way related to the growth of the chilidium, which normally covers their dorsal ends. In early members (e.g., *Leptella*), the chilidial plates simply acted as high lateral boundaries to the notothyrium or to a notothyrium containing a median cardinal process (e.g., *Bimuria*). Among sowerbyellids, however, the plates, together with the median septum, are not only firmly ankylosed to the notothyrial floor but also considerably elevated above the hinge line and prolonged ventrally to it, and since the muscle bases probably were inserted within the narrow slots formed by the median septum and the chilidial plates, the entire structure is analogous to a bilobed cardinal process with the lobes ankylosed to each other along the median plane.

The strophomenacean and davidsoniacean arrangement is quite distinct from that of the plectambonitacean, for the diductor muscles were attached not to the notothyrial floor but to a pair of outgrowths from it (bilobed cardinal process), each of which bore the muscle bases on its posterior face. Öpik (618, p. 61) has commented on the presence of a fine ridge lying medianly between the lobes of the cardinal process of many strophomenaceans and his suggestion that this ridge is a degenerate homologue of the plectambonitacean median partition is probably correct. Despite subsequent modification of the strophomenoid cardinal process, the fundamental bilobed pattern is maintained (e.g., stropheodontids and most davidsoniaceans, in which the notothyrium, as well as the chilidium, is vestigial or absent and in which the cardinal process lobes project for some distance into the umbonal region of the pedicle valve).

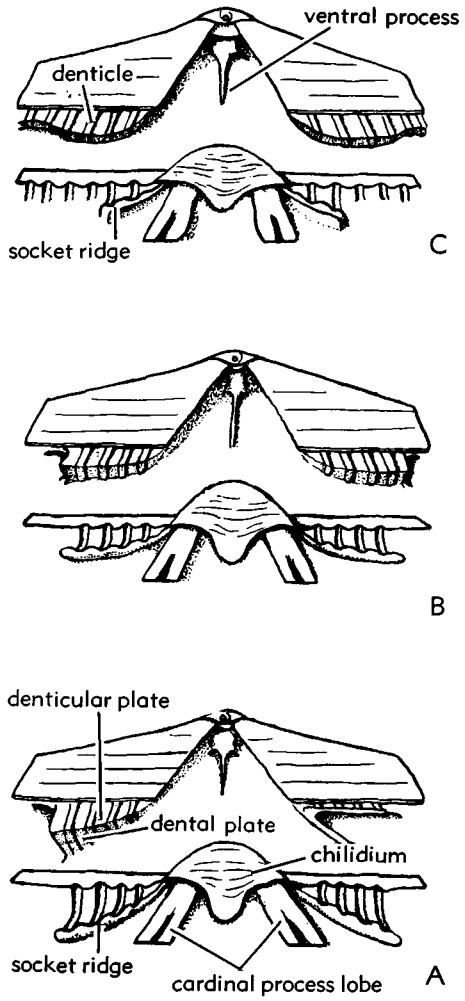

Fig. 235. Evolution of stropheodontid denticular structure associated with loss of dental plates, illustrated in sequence *A-C* (based on various Lower Silurian species of *Strophonella* (Williams, n).

A considerable variation in the articulatory devices also is displayed by the Strophomenidina. The simplest and seemingly the most primitive consisted of a pair of simple teeth, generally supported by dental plates in the pedicle valve, and a complementary pair of sockets in the brachial valve (Fig. 232, *1a,c*). In a number of plectambonitaceans, the teeth are flanked by a pair of similar protuberances (accessory teeth, Fig. 232, *2a*) which also are provided with accessory socket accommodation. In the earliest stropheodontids (871) the simple

teeth consist of a pair of obtusely triangular plates which are fused along their dorsal edges to a pair of widely divergent dental plates to form a pair of hollow cones with the dorsal edges corrugated by as many as seven ridges (denticles). The sockets of the brachial valve are corrugated in a like manner. As the stocks evolved, so the dental plates migrated to the hinge line and finally fused with the teeth to form a thick, wide, denticular plate on either side of the delthyrium (Fig. 235). Subsequent to fusion, the remainder of the hinge line became progressively denticulate in all strophoedontid stocks, although with varying tempo. A denticulate hinge line is also characteristic of some plectambonitaceans, but in this group it is not preceded by any modification of the teeth and dental plates which persisted.

The development of deep conical pedicle valves among the davidsoniaceans was accompanied by the exaggerated growth of the dental plates, which became a pair of long deep blades sweeping down from the anterior faces of the teeth to the floor of the valve (Fig. 231, *1a*). They may be divergent (e.g., *Schellwienella*), parallel (e.g., *Meekella*), or in various stages of coalescence leading to the formation of a spondylium which may be sessile (e.g., *Sicelia*), supported by a median septum (e.g., *Geyerella*), or even free for most of its length (e.g., *Orthotetella*). Small chambers found in the umbo of *Orthotetes* by fusion of the posterior end of the ventral median septum with the anterior edges of unsupported teeth are in no way homologous with these muscle-bearing spondylia.

Another important feature of strophomenoid organization is the apparent, and in many stocks the undoubted, absence of any specialized structures associated with the cardinalia which gave support to the lophophore. Thus, in the strophoedontids, the pair of ridges forming the inner boundary of the sockets in early members have been referred to as "brachiophores." With the progressive spread of denticles along the hinge line in later stocks, the teeth-and-socket arrangement became vestigial and the ridges either disappeared entirely or, exceptionally (e.g., leptostrophias), became modified to form ankylosed buttresses to the cardinal process lobes (Fig. 236). It seems, then, that the ridges are nothing more than internal walls of the sockets and the function of lophophore support cannot be ascribed to them. This is equally true for Strophomenidina generally which are equipped with weak ridges (e.g., early strophoedontids). Within the davidsoniacean group also, no evidence is found to suggest that specialized structures supported the lophophore. The presence of strong, large teeth, the loss of the interarea of the convex brachial valve, and the pronounced ventral growth of the cardinal process all contributed to the development of a pair of socket plates extending from the floor of the valve to the sides of the cardinal process and bearing a pair of concave socket surfaces bounded laterally by socket ridges (Fig. 231, *1b,c 2, 3b*). Even in *Thecospira* the calcareous spires are not attached to any structures associated with the socket ridges but were supported by a pair of very short, scarcely differentiated outgrowths from the bases of the cardinal process lobes.

Öpik (619, p. 44) has come to a similar conclusion in his investigation of *Leangella,* in which the ridges defining the teeth sockets are especially prominent; and in the plectambonitaceans generally, it is highly likely that the so-called crural processes, or brachiophores, functioned only as socket-bounding ridges (Fig. 232, *1c,d, 2c,d*).

Little evidence as to the form of the strophomenacean lophophore can be adduced but some preserved impressions (e.g., *Leptaenisca*) indicate that it consisted of a pair of depressed spirally coiled brachia, a disposition compatible with the shell configuration. Impressions suggestive of a spirolophe are also found in certain species of the plectambonitacean *Titambonites.*

A spirolophous lophophore was apparently also characteristic of the davidsoniaceans; impressions of depressed coiled brachia are found in *Davidsonia,* and the brachia of *Thecospira* were evidently strengthened by the development of a pair of spirally coiled calcareous ribbons. These spires form a pair of high cones extending well into the interior of the pedicle valve and it is probable that the lophophore of those davidsoniaceans, in which the depth of the shell was greatly increased by the exceptional growth of the pedicle valve, was similarly disposed.

Kozlowski (487), Öpik (619), and Wil-

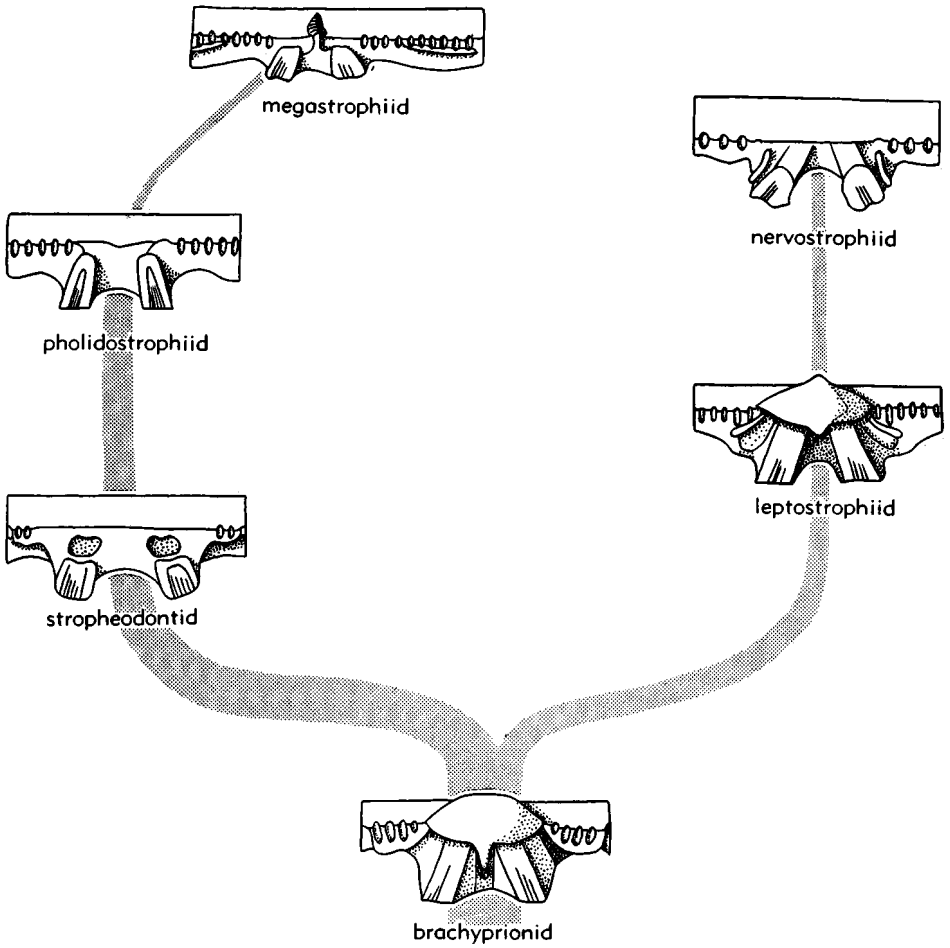

FIG. 236. Modification of socket ridges of brachial valve during evolution of stropheodontids (Williams, n). Most stocks show brachyprionid to pholidostrophiid patterns, with ultimate loss of ridges; megastrophiid forms are judged to belong in this group, for the articulatory ridges of Devonian members are secondary structures. The divergent branch of leptostrophiid and nervostrophiids is characterized by ankylosis of socket ridges to the cardinal process lobes.

LIAMS (875) have concluded that the strongly elevated and striated ridge often found in the plectambonitacean brachial valve (Fig. 232, *2c*) completely surrounding the posteromedian area (lophophore platform) represent the zone of attachment for the lophophore in a manner analogous to the lophophore-supporting structure of the thecideaceans. This interpretation is certainly the most plausible explanation for the development of such an extraordinary feature, and if it is correct, the supported lophophores were probably schizolophous or ptycholophous.

Elevated ridges are also found in the brachial valve of the strophomenacean *Christiania* and are strongly reminiscent of the plectambonitacean lophophore platform. In this stock, however, the partitions are disposed in two discrete loops and if the functional interpretation of these structures is correct, the lophophore was schizolophous.

Most of the morphogenetic trends outlined above, such as the complementary development of the pseudodeltidium and chilidium and the development of various types of cardinal processes, were important

features of strophomenoid evolution but the main one was undoubtedly the loss of a functional pedicle in postneanic stages of growth of most stocks. It is probable that in all Strophomenidina the pedicle rudiment was differentiated sufficiently to function as an organ of attachment during early stages of development and at least in the majority of the strophomenaceans was provided with a calcareous protective sheath. In a number of adult plectambonitaceans and strophomenaceans, the persistence of an apical foramen suggests that the rudiment did, in fact, give rise to a pedicle which functioned throughout the life of the individual. But all adult strophеodontids, together with certain other strophomenaceans and many plectambonitaceans in which the foramen was sealed off by the secretion of secondary shell within the umbonal cavity of the pedicle valve, must have rested unattached in or on the sediments of the sea floor.

In terms of stock longevity, this specialized mode of existence does not seem to have been entirely successful; the strophеodontids originated, proliferated, and suffered extinction well within the time range of the pedicle-bearing *Leptaena*. It is also significant that the plectambonitaceans and strophomenaceans were replaced by the davidsoniaceans, for although the supposed ancester of this group, *Fardenia*, lost a functional pedicle in adult shells of all but the earliest species, the remainder retained an attached mode of life by cementation of the pedicle valve to a foreign body. Attachment by cementation was not restricted to the davidsoniaceans; it was also a feature of the strophеodontid *Lilljevallia*, and the strophomenids *Leptaenoidea* and *Leptaenisca*, although none of these flourished on the davidsoniacean scale.

Superfamily PLECTAMBONITACEA Jones, 1928

[*nom. transl.* Cooper & Williams, 1952, p. 332 (*ex* Plectambonitinae Jones, 1928, p. 394)]

Concavo-convex to resupinate Strophomenidina with cardinalia consisting of well-developed socket ridges and cardinal process, which, when present, is essentially a simple median ridge, with or without subsidiary lateral ridges and rarely expanded as a bulbous myophore; pseudodeltidium and chilidium present in variable degree; pedicle presumably functional in adult shells with persistent apical foramen, more commonly lost during ontogeny, so that mature shells were unattached; brachial valve generally equipped with elevated lobate platform presumed to have given support to a ptycholophous or schizolophous lophophore. *Ord.-Dev.*

Family PLECTAMBONITIDAE Jones, 1928

[*nom. transl.* Kozlowski, 1929, p. 108 (*ex* Plectambonitinae Jones, 1928, p. 394]

Median cardinal process growing from notothyrial floor and ankylosed posteriorly to convex chilidium; pseudodeltidium large; apical foramen sporadically persistent in adult shells. Pedicle valve with pair of accessory teeth lying anterolaterally to 2 simple teeth; brachial valve without elevated lophophore platform, socket ridges flat-lying, subparallel with hinge line; subperipheral rims, possibly representing boundaries of brachial cavity, usually well developed in both valves; mantle canal systems poorly known but probably saccate in both valves. *L.Ord.-M.Ord.*

Subfamily PLECTAMBONITINAE Jones, 1928

[Plectambonitinae Jones, 1928, p. 394] [=Plectellinae Schuchert & Cooper, 1931, p. 245 (assigned to Clitambonitidae)]

Hinge line denticulate; pedicle valve with divergent diductor scars separated anteriorly by low broad plate or ridge and flanked by pair of variably developed, divergent ridges; adductor scars of brachial valve associated with variable number of low septa. *L.Ord.-M.Ord.*

Plectambonites Pander, 1830, p. 90 [**P. planissimus*; SD Hall & Clarke, 1892, p. 296]. Concavo-convex, unequally parvicostellate, with widely spaced accentuated costellae and strong concentric ridges breaking finer costellae into radial rows of tubercles, apical foramen persistent in adult shells. Dorsal adductor scars splayed about single pair of submedian septa and 3 pairs of radiating ridges. *M.Ord.*, Baltic.——Fig. 237,2. **P. planissimus*, C1; *2a,b*, ped.v. and post views of conjoined valves, ×1.5 (Williams, n); *2c*, brach.v. int., ×2; *2d*, ped.v. int., ×3 (Rõõmusoks, n).

Ingria Öpik, 1930, p. 57 [**Orthisina nefedywi* Eichwald, 1860; OD] [=*Palinorthis* Ulrich & Cooper, 1936, p. 625 (type, *P. cloudi*)]. Resupinate, unequally parvicostellate, with narrow seg-

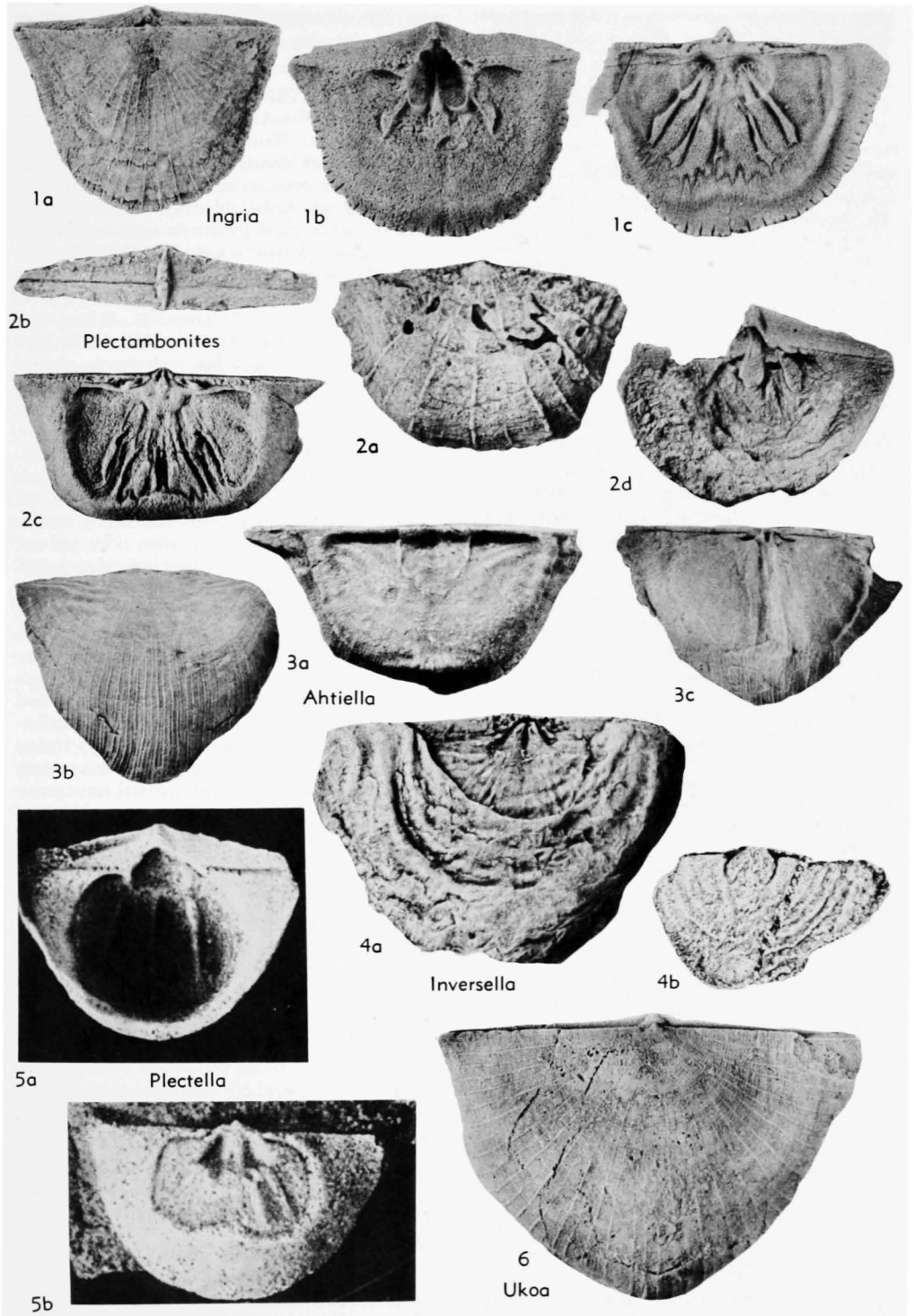

FIG. 237. Plectambonitidae (Plectambonitinae) *(1-2, 5)*, (Ahtiellinae) *(3, 4, 6)* (p. *H*370, *H*372).

ments defined by accentuated costellae, without apical foramen; brachial valve interior like that of *Plectella*. *L.Ord.*, Eu.-N.Am.——Fig. 237,*1*. *I. cloudi* (Ulrich & Cooper), Whiterock, USA (Nev.); *1a*, brach.v. view of conjoined valves, ×2; *1b,c*, ped.v. int., brach.v. int., ×2 (189).

Plectella Lamansky, 1901, p. 156 [**Plectambonites uncinata* Pander, 1830, p. 91; OD]. Like *Plectambonites* but without apical foramen and with median ridge in brachial valve commonly bifurcating to contain another median ridge which extends forward flanked by 2 pairs of low or indistinct ridges. *L.Ord.*(B$_I$), Baltic.——Fig. 237,*5*. **P. uncinata* (Pander), Est.; *5a*, ped.v. int., ×3; *5b*, brach.v. int. mold, ×3 (618).

Subfamily AHTIELLINAE Öpik, 1933

[Ahtiellinae Öpik, 1933, p. 19]

Resupinate, with smooth hinge lines and without elaborate septal apparatus in brachial valve. *L.Ord.-M.Ord.*

Ahtiella Öpik, 1932, p. 37 [**A. lirata*; OD]. Unequally parvicostellate, impersistently rugate, with dorsal sulcus and without apical foramen. Ventral muscle scar quadrate in outline, dorsal adductor scars impressed on either side of strong median septum. *L.Ord.*(B$_{III}$)-*M.Ord.*(C$_I$), Baltic.——Fig. 237,*3a*. **A. lirata*, M.Ord.(C$_I$); *3a*, ped.v. int., ×2 (Rõõmusoks, n).——Fig. 237,*3b,c*. *A. jaanussoni* (Hessland), L.Ord., Sweden; *3b,c*, brach.v. ext. and int. mold, ×1 (Williams, n).

Inversella Öpik, 1933, p. 21 [**I. borealis*; OD]. Like *Ahtiella* but strongly geniculate and persistently rugate; without median septum in brachial valve. *L.Ord.*(B$_{III}$)-*M.Ord.*(C$_I$), Baltic-Wales.——Fig. 237,*4a*. *I.* sp. cf. *I. borealis*, (B$_{III}$), Est.; *4a*, brach.v. ext. dissolved away posteromedianly to show mold of cardinalia, ×1.5 (Williams, n).——Fig 237,*4b*. *I.* sp., L.Ord., Wales; *4b*, ped.v. int., ×1.5 (Bates, n).

Ukoa Öpik, 1932, p. 33 [**U. ornata*; OD]. Differs from *Ahtiella* in being impunctate and having apical foramen and triangular muscle scar in pedicle valve. *L.Ord.*(B$_{III}$)-*M.Ord.*(C$_I$), Baltic.——Fig. 237,*6*. **U. ornata*, M.Ord.(C$_I$), Est.; brach.v. view of conjoined valves, ×1 (Rõõmusoks, n).

Family TAFFIIDAE Ulrich & Cooper, 1936

[Taffiidae Ulrich & Cooper, 1936, p. 625]

Subquadrate, faintly sulcate, unequally parvicostellate. Musculature and cardinalia orthoid-like; notothyrium covered completely by convex chilidium; teeth simple, supported by short dental plates; cardinal process absent or present as median ridge, exceptionally differentiated into myophore; pseudodeltidium variable in development, apical foramen small, only sporadically persistent in adult shells; subperipheral rims variably developed; mantle canal systems poorly known and variable: *L.Ord.(U. Canad.-Whiterock)*.

Taffia Ulrich, 1926, p. 99 [**T. planoconvexa* Butts in Ulrich, 1926, p. 100; OD]. Plano- to concavo-convex. Ventral muscle scar small, subtriangular, with diductor lobes not enclosing median adductor scar; socket ridges rodlike, cardinal process absent, dorsal subperipheral rim present; ventral mantle canal pattern saccate, dorsal probably digitate. *L.Ord.(U.Canad.)*, N.Am.——Fig. 238,*1*. **T. planoconvexa* Butts, USA(Ala.); *1a,b*, brach.v. ext. and int., ×1.5; *1c*, brach.v. view of conjoined valves, ×2; *1d*, ped.v. int., ×1.5 (189).

Aporthophyla Ulrich & Cooper, 1936, p. 625 [**A. typa*; OD]. Like *Taffia* but with simple cardinal process and without subperipheral rims inside margins of valves. *L.Ord.(Whiterock)*, N.Am.——Fig. 238,*2*. **A. typa*, USA(Nev.); *2a*, brach.v. post. view, ×3; *2b*, ped.v. int. mold, ×1 (189).

Pelonomia Cooper, 1956, p. 699 [**Orthis delicatula* Billings, 1865, p. 217; OD]. Like *Taffia* but with rudimentary pseudodeltidium, small median cardinal process and dorsal median ridge replaced by 2 submedian rows of strong tubercles. *L.Ord. (Whiterock)*, E.N.Am.(Newf.).

Toquimia Ulrich & Cooper, 1936, p. 626 [**T. kirki*; OD]. Shallowly concavo-convex with brachial valve becoming flat or gently convex anteriorly. Ventral muscle scar subflabellate, with diductor lobes enclosing median adductor scar and ending anterolaterally in pair of subdued callosities; socket ridges in form of short, flat blades; cardinal process consisting of short median shaft and trilobed myophore; subperipheral rims prominent in both valves; dorsal mantle canal pattern lemniscate. *L.Ord.(Whiterock)*, N.Am.——Fig. 238,*3*. **T. kirki*, USA(Nev.); *3a*, ped.v. int. mold, ×1; *3b*, brach.v. int. cast, ×2 (189).

Family LEPTESTIIDAE Öpik, 1933

[*nom. transl.* Williams, 1953, p. 6 (*ex* Lepestiinae Öpik, 1933, p. 24)]

Simple teeth supplemented by pair of variably developed accessory teeth and with variable number of septa associated with dorsal adductor field; pseudodeltidium commonly narrow, arched, pedicle foramen persistent in adult shells of one stock only; socket ridges short, divergent and commonly pointed distally; dorsal and ventral mantle canal systems commonly saccate or digitate but lemniscate exceptionally. *L.Ord.-U.Ord.*

Subfamily LEPTESTIINAE Öpik, 1933

[Leptestiinae Öpik, 1933, p. 24]

Unequally parvicostellate, with massive trilobed cardinal process differentiated posteriorly into high median crest flanked by

pair of lower lateral ridges and continuous anteriorly with median septum. *L.Ord.-U.Ord.*

Leptestia BEKKER, 1922, p. 362 [**L. musculosa*; OD] [=*Leptestia (Leptoptilum)* ÖPIK, 1930, p. 130 (type, *L. (L.) bekkeri*)]. Concavo-convex, commonly with strong concentric lamellae distally; ventral muscle scar suboval with wide adductor field not enclosed by diductor scars; dorsal median septum strong, dividing oval adductor field. *M.Ord.*, Baltic-Eire.——FIG. 239,*6*. **L. musculosa*, CII, Est.; *6a,b*, ped.v. and brach.v. int., ×1.5 (Williams, n).

Apatomorpha COOPER, 1956, p. 709 [**Rafinesquina pulchella* RAYMOND, 1928, p. 296; OD]. Concavo- or plano-convex, impersistently rugate posterolaterally. Ventral muscle scar large, bilobed, with diductors extending beyond median adductor; cardinal process bulbous, dorsal median septum strong, flanked by up to 3 pairs of narrowly divergent ridges. *M.Ord.(Porterfield)*, E.USA.——FIG. 239,*7*. **A. pulchella* (RAYMOND), Tenn.; *7a*, brach.v. view of conjoined valves, ×2;*7b,c*, brach. v. and ped.v. int. molds, ×3 (189).

Glyptambonites COOPER, 1956, p. 712 [**G. musculosus*; OD]. Like *Apatomorpha* but strongly rugate posterolaterally and even anteriorly, commonly with widely spaced accentuated costellae. Long, narrow, slightly divergent diductor scars in pedicle valve. *M.Ord.-U.Ord.*, E.N.Am.-Eu.(Scot.).——FIG. 239,*8*. **G. musculosus*, U.Ord.(Wilderness), USA(Va.); *8a*, ped.v. ext., ×2; *8b*, ped.v. int., ×1; *8c*, brach.v. int. cast, ×1.5 (189).

Goniotrema ULRICH & COOPER, 1936, p. 626 [**G. perplexum*; OD]. Like *Sowerbyites* but without callosities anterior to diductor scars in pedicle valve and strong submedian septa in brachial valve; pedicle foramen persistent in adult shells. *L.Ord.(Canad.)*, USA(Nev.).

Grorudia SPJELDNAES, 1957, p. 61 [**G. grorudi*; OD]. Like *Apatomorpha* but with poorly defined ventral muscle scar and short elevated platform for dorsal adductor scars flanking short median septum and pair of subparallel submedian septa. *M.Ord. (4aβ-4bα)*, Norway, Eire.——FIG. 239,*1*. **G. grorudi, 4aβ*, Norway; *1a*, brach.v. int., ×4.5; *1b*, ped.v. int. mold, ×5 (Williams, n).

Hesperomena COOPER, 1956, p. 744 [**H. leptellinoidea*; OD]. Like *Leptestia* but with large ventral muscle scar including long, slender diductors, trilobed cardinal process projecting as shelf over notothyrial platform; dorsal adductor scars obscure; median septum low. *L.Ord.(Whiterock)*, USA(Nev.).——FIG. 239,*2*. **H. leptellinoidea*; brach.v. int., ×2 (189).

Palaeostrophomena HOLTEDAHL, 1916, p. 43 [**Strophomena concava* SCHMIDT, 1958, p. 217; OD]. Like *Apatomorpha* but resupinate and commonly with widely spaced accentuated costellae. *M.Ord.*, Eu.-N.Am.——FIG. 239,*3*. **P. concava* (SCHMIDT), CII, Est.; *3a,b*, brach.v. ext., ped.v. int., ×1.5 (619).

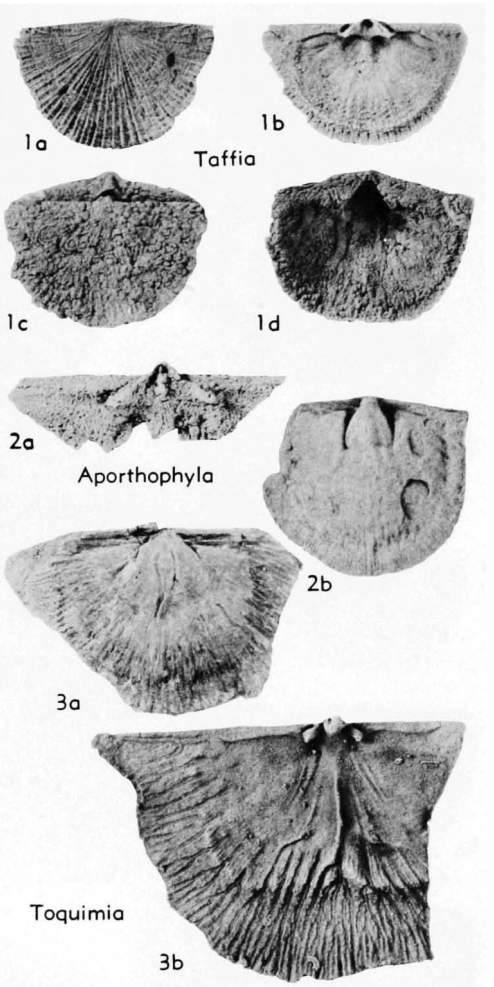

FIG. 238. Taffiidae (p. *H372*).

?Paucicostella COOPER, 1956, p. 711 [**P. canadensis*; OD]. Like *Glyptambonites* but with subdued posterolateral rugae and widely spaced accentuated costellae; cardinal process possibly absent. [The taxonomic position of this genus is uncertain.] *L.Ord.*, N.Am.(E.Can.).——FIG. 239,*4*. **P. canadensis*, Whiterock, Que.; *4*, ped.v. ext., ×2 (189).

Sowerbyites TEICHERT, 1937, p. 66 [**S. mediosepta*; OD]. Posterolateral rugae sporadically developed, accentuated costellae narrowly spaced, thickened concentric lamellae common distally. Ventral adductor scar small and within delthyrial cavity, diductor scars long, broad, divergent and ending in callosities; dorsal interior with strong median septum, submedian septa slightly divergent, weaker. *M.Ord., ?U.Ord.*, N.Am.-Greenl.-?Eu.——FIG. 239,*5*. *S. triseptatus* (WILLARD), M.Ord.,

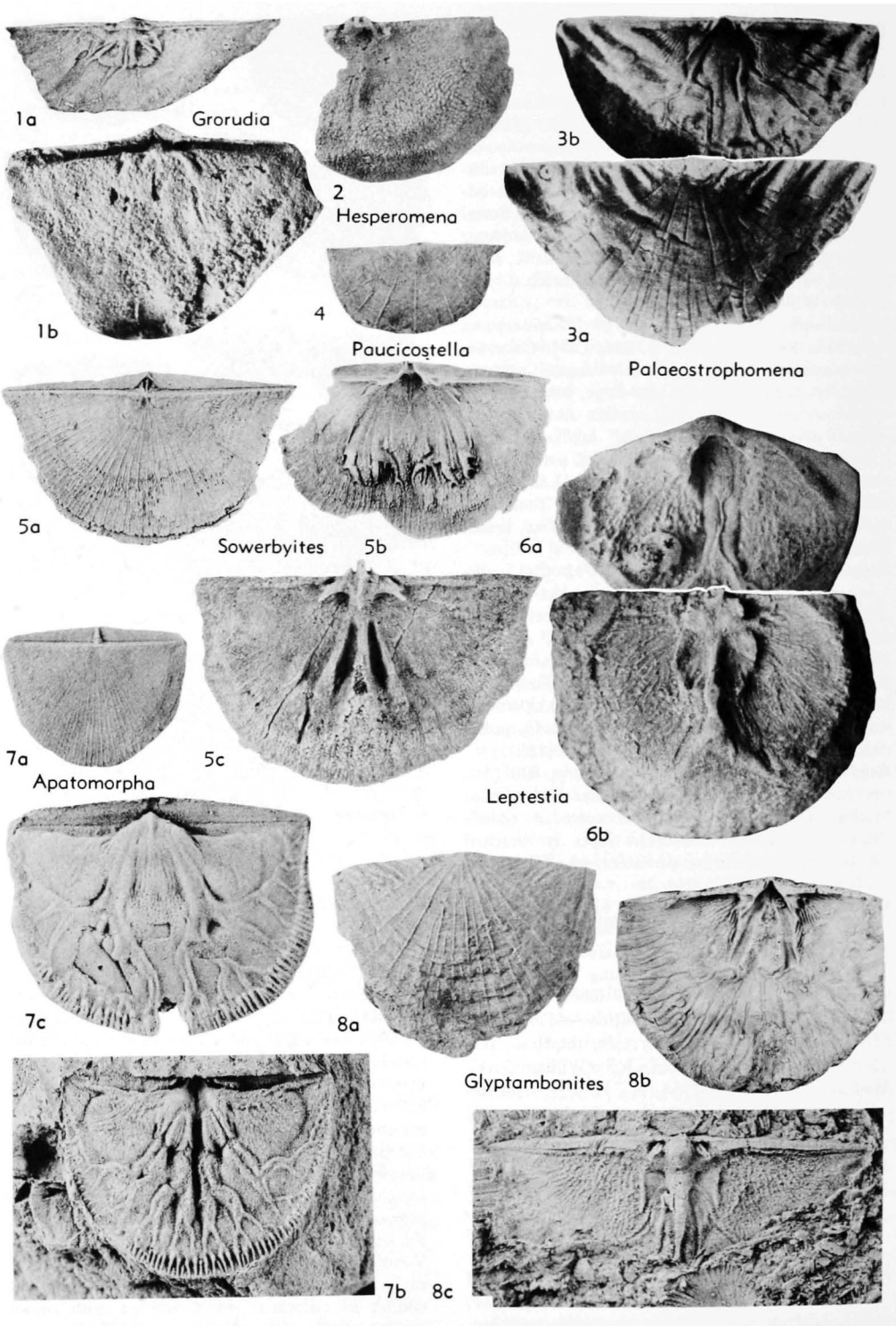

FIG. 239. Leptestiidae (Leptestiinae) (p. *H372-H373*).

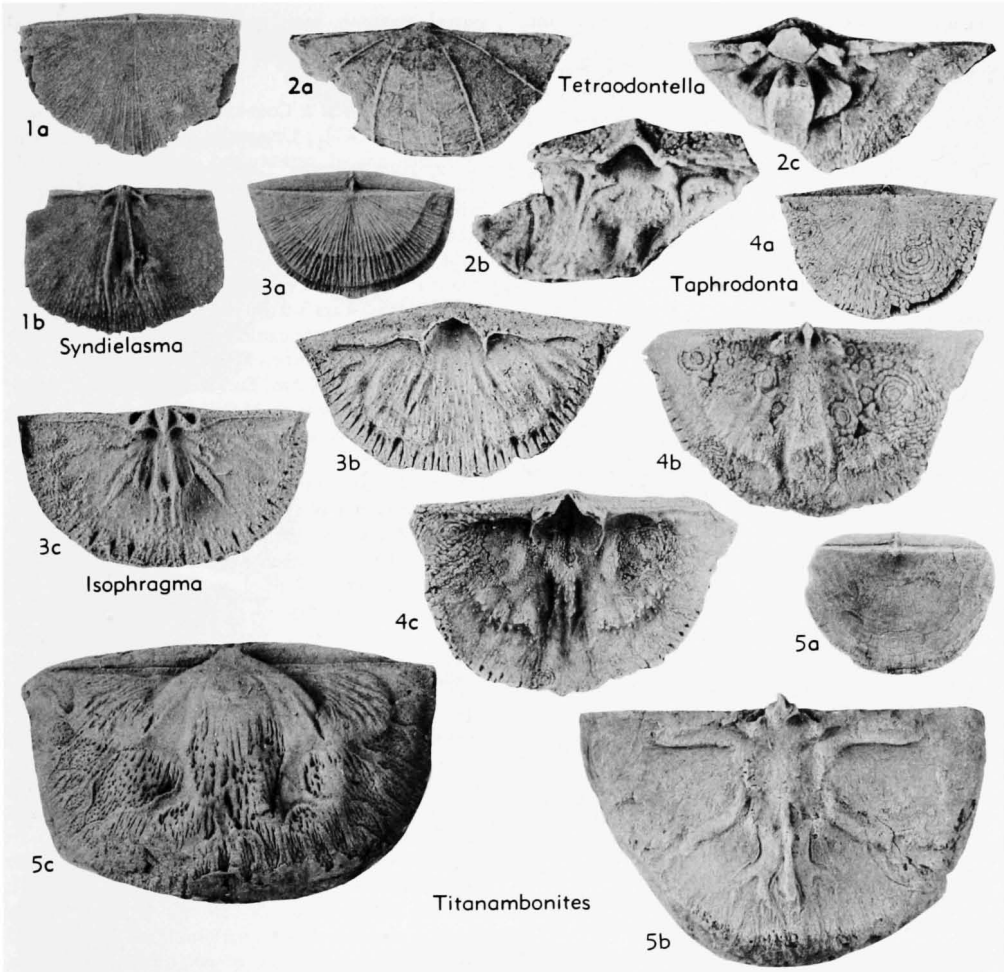

FIG. 240. Leptestiidae (Leptestiinae) *(5)*, (Isophragmatinae) *(1-3)*, (Taphrodontinae) *(4)* (p. *H*375-*H*376).

USA(Tenn.); *5a,* brach.v. view of conjoined valves, ×2; *5b,* ped.v. int., ×2; *5c,* brach.v. int., ×3 (189).

Spanodonta PRENDERGAST, 1935, p. 13 [**S. hoskingiae*; OD]. Like *Leptestia* but socket ridges united with trilobed cardinal process so as to project ventral of notothyrial platform. *M.Ord.,* W.Australia.

Titanambonites COOPER, 1956, p. 717 [**T. medius*; OD]. Like *Sowerbyites* but with finer parvicostellae crossed by regular concentric lamellae. Cardinal process bulbous; dorsal median ridge becoming strong anteriorly, dorsal submedian septa absent; strong ridges of secondary shell, parallel with and anterior to hinge line, conspicuous in both valves. *M.Ord.,* E.USA-Scot.——FIG. 240,*5*. **T. medius,* Porterfield, Tenn.; *5a,* brach.v. view of conjoined valves, ×1; *5b,* brach.v. int., ×1.5; *5c,* ped.v. int. mold, ×1.5 (189).

Subfamily ISOPHRAGMATINAE Cooper, 1956

[*nom. correct.* WILLIAMS, herein (*pro* Isophragminae COOPER, 1956, p. 733)] [=Syndielasmatidae COOPER, 1956, p. 742]

Costellate to unequally parvicostellate, with bulbous cardinal process generally not well differentiated into trilobed posterior face and pair of high, subparallel septa in brachial valve. *L.Ord.-M.Ord.*

Isophragma COOPER, 1956, p. 733 [**I. ricevillense*; OD]. Resupinate, with shallow dorsal sulcus replaced by fold in adult shells, costellate and commonly with widely spaced accentuated costellae. Dental plates short; ventral muscle scar subquadrate, with wide adductor trace; ventral subperipheral rim divided into several discrete callosities; suboval adductor field raised, divided by high submedian septa. *M.Ord.,* E.USA-Br.I.——FIG. 240,*3*. **I. ricevillense,* Porterfield, Tenn.; *3a,* brach.v.

view of conjoined valves, ×2; *3b,c,* ped.v. int., brach.v. int., ×3 (189).

Syndielasma COOPER, 1956, p. 742 [**S. biseptatum*; OD]. Concavo-convex unequally parvicostellate with narrowly spaced accentuated costellae, impersistent posterolateral rugae. Dental plates absent; ventral muscle scar indistinct; cardinal process bulbous, with trilobed posterior face; submedian septa long, slender. *L.Ord.(Whiterock),* USA (Nev.).——FIG. 240,*1.* **S. biseptatum*; *1a,* brach. v. view of conjoined valves, ×2; *1b,* brach.v. int., ×3 (189).

Tetraodontella JAANUSSON, 1962, p. 1 [**T. biseptata*; OD]. Like *Isophragma* but concavo-convex, with fine parvicostellae and widely spaced accentuated costellae, definite trilobed cardinal process, and smaller bilobed ventral muscle scar. *M.Ord.*(CII), Baltic.——FIG. 240,*2.* **T. biseptata,* Viruan, Sweden; *2a,* ped.v. ext., ×4; *2b,* post. portion of ped.v. int., ×5; *2c,* post. portion of brach.v. int., ×4 (Williams, n).

Subfamily TAPHRODONTINAE Cooper, 1956

[*nom. transl.* WILLIAMS, herein (*ex* Taphrodontidae COOPER, 1956, p. 740)]

Unequally parvicostellate, with bladelike cardinal process and wide median ridge in brachial valve built up from 2 submedian septa. *L.Ord.*

Taphrodonta COOPER, 1956, p. 740 [**T. parallela*; OD]. Concavo-convex, ventral muscle scar cordate, diductor scars wide but not completely enclosing small adductors; subperipheral thickened ridge, interrupted by median sulcus, well developed in pedicle valve, with corresponding ridge in brachial valve. *L.Ord.(Whiterock),* USA(Nev.). ——FIG. 240,*4.* **T. parallela; 4a,* brach.v. view of conjoined valves, ×2; *4b,* brach.v. int., ×2; *4c,* ped.v. int., ×3 (189).

Family LEPTELLINIDAE Ulrich & Cooper, 1936

[*nom. transl.* WILLIAMS, herein (*ex* Leptellininae ULRICH & COOPER, 1936, p. 626)]

Concavo-convex, with simple teeth supplemented by variably developed accessory teeth and undercut platform, which probably gave support to lophophore in brachial valve; socket ridges commonly short, divergent and commonly sharp-edged distally. *L.Ord.-U.Sil.*

Subfamily LEPTELLININAE Ulrich & Cooper, 1936

[Leptellininae ULRICH & COOPER, 1936, p. 626]

Strong cardinal process differentiated into sharp median crest and lower lateral ridges on posterior face; lophophore platform wide, extending to posterolateral margins, with high median crest; ventral mantle canal pattern saccate to lemniscate, dorsal mantle canal pattern, digitate or lemniscate. *L.Ord.-L.Sil.*

Leptellina ULRICH & COOPER, 1936, p. 626 [**L. tennesseensis*; OD]. Unequally parvicostellate, with variably spaced accentuated costellae; commonly impersistently rugate posterolaterally, comae well developed distally in some species; apical foramen sealed in adult shells, pseudodeltidium large. Ventral muscle scar short, transversely bilobed, commonly with raised callosity between anterior lobes of diductor scars which do not enclose wide median adductor scar; cardinal process broad, set low relative to hinge line. *L.Ord.(Whiterock)-M.Ord. (Wilderness),* N.Am.-Eu.(Scot.).——FIG. 241,*1.* **L. tennesseensis,* M.Ord.(Porterfield), USA (Tenn.); *1a,* brach.v. view of conjoined valves, ×2; *1b,c,* normal, post. views of brach.v. int., ×3; *1d,* ped.v. int., ×3 (189).

Anoptambonites WILLIAMS, 1962, p. 170 [**Leptaena grayae* DAVIDSON, 1883, p. 171; OD]. Finely multicostellate, with accentuated costae, pseudodeltidium unknown. Ventral muscle scar small, cordate about low median ridge which is continuous apically with small "pedicle" chamber; cardinal process massive, differentiated posteriorly into median ridge and up to 6 lower lateral ridges, fused laterally with pair of curved plates to form semicircular structure projecting ventrally between socket ridges. *M.Ord.,* Scot.-W.USSR.——FIG. 241, *6.* **A. grayae* (DAVIDSON), Caradoc., Scot.; *6a,* brach.v. view of conjoined valves, ×2.5; *6b,c,* ped.v. and brach.v. int., ×2.5 (877).

Leptelloidea JONES, 1928, p. 388 [**Plectambonites schmidti* TORNQUIST var. *leptelloides* BEKKER, 1921, p. 68; OD]. Like *Leptellina* but with widely spaced accentuated costellae, high trilobed cardinal process with median depression on its ventral face, and long bilobed ventral muscle scar consisting of subcircular adductor scar enclosed by diductor lobes. *M.Ord.,* Baltic.——FIG. 241,*5.* **L. leptelloides* (BEKKER), CIC-II, Est.; *5a,* brach.v. int., ×2; *5b,c,* ped.v. int., ext., ×2 (Williams, n).

Merciella LAMONT & GILBERT, 1945, p. 655 [**Leptella (Merciella) vesper*; OD] [=*Leptestiina (Benignites)* HAVLÍČEK, 1952, p. 409 (type, **Strophomena primula* BARRANDE, 1879, p. 101)]. Like *Leptellina* but with widely spaced accentuated costellae and small ventral adductor scar enclosed by diductors, giving subcordate outline to small ventral muscle field. *U.Ord.(Ashgill.)-L.Sil. (Llandover.),* Eu.——FIG. 241,*4.* **L. vesper,* Llandov.(C_6), Eng.; *4a,b,* brach.v. and ped.v. int. molds, ×2 (Williams, n).

Subfamily LEPTELLINAE Williams, n. subfam.

Smooth(?) or delicately unequally parvicostellate, with transversely subtriangular ventral muscle scar including wide adductor scar not enclosed by diductor lobes; socket

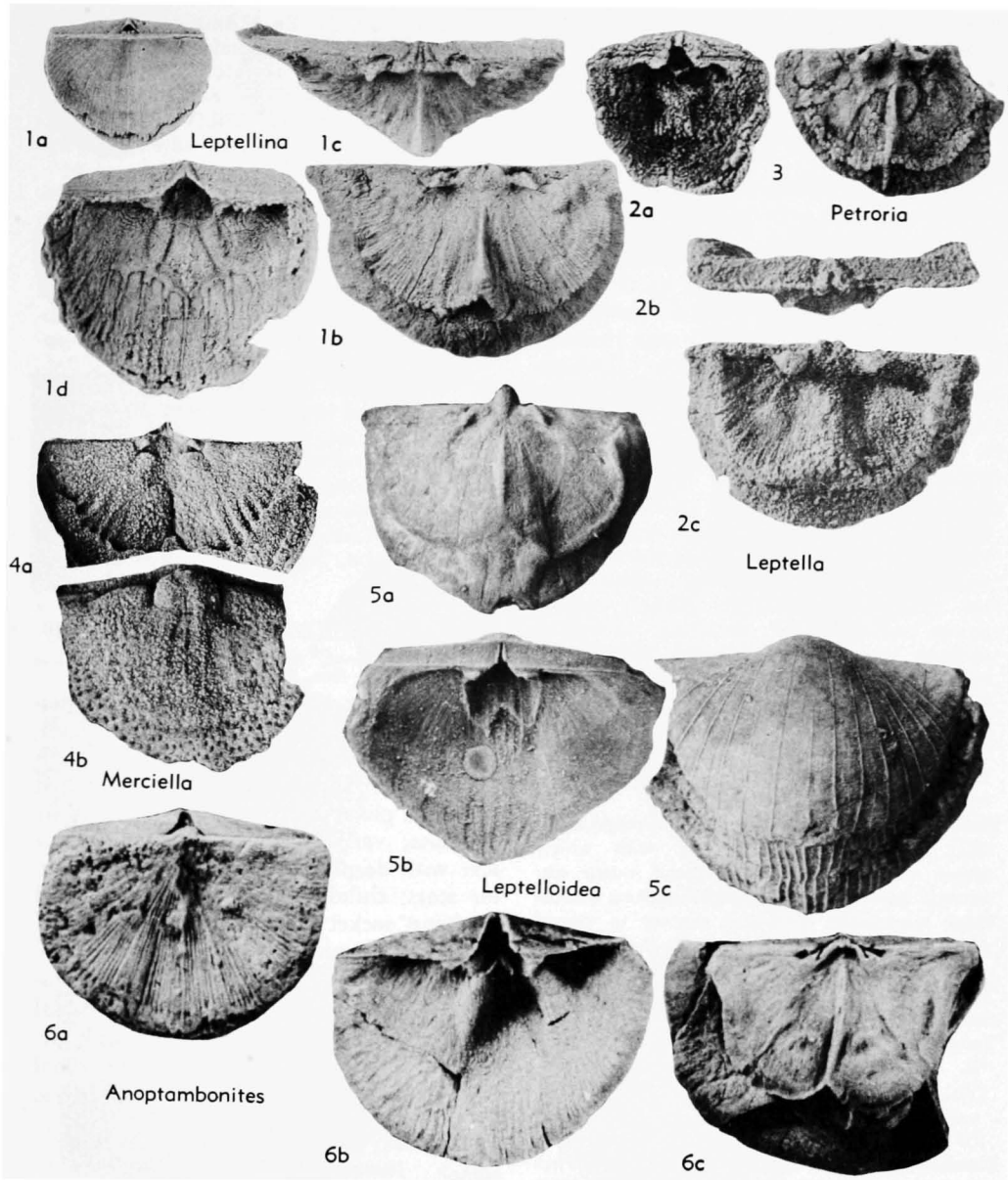

FIG. 241. Leptellinidae (Leptellininae) *(1, 4, 5, 6)*, (Leptellinae) *(2-3)* (p. *H376-H377*).

ridges short, curved, continuous with pair of chilidial plates which are covered posteriorly by chilidium, socket ridges bounding median hollow underlain by thickened notothyrial platform; lophophore platform wide, extending to posterolateral margins, not greatly elevated medianly; ventral mantle canal pattern saccate. *L.Ord.*

Leptella HALL & CLARKE, 1892, p. 293 [*non* CARUS, 1880, p. 625 (incorrect subs. spelling *pro Lepetella* VERRILL, 1880)] [**Leptaena sordida* BILLINGS, 1862, p. 74; OD] [*non Leptella* REUTER, 1893]. Dorsal median ridge wide, ending anteriorly as median indentation of lophophore platform; dental plates short, ventral muscle scar limited anteriorly by broad median callosity. *L.Ord.(Whiterock)*, N. Am.——FIG. 241,*2*. **L. sordida* (BILLINGS), Can. (Que.); *2a*, ped.v. int., ×3; *2b,c*, post., int. views of brach.v., ×6 (825).

Petroria WILSON, 1926, p. 27 [**P. rugosa*; OD]. Like *Leptella* but lacking ventral median callosity; dorsal median septum sharp, extending anteriorly of lophophore platform and dividing raised oval adductor area. *L.Ord.*, W.Can.-Eire.——FIG. 241, *3*. **P. rugosa*; brach.v. int., ×3 (189).

Subfamily LEPTESTIININAE Havlíček, 1961

[*nom. transl.* WILLIAMS, herein (*ex* Leptestiinidae HAVLÍČEK, 1961, p. 447)]

Strong cardinal process differentiated posteriorly into median crest and up to 3 pairs of lower lateral ridges; ventral muscle scar small, with median adductor scar enclosed by diductor lobes; lophophore platform small, originating just in front of socket ridges and strongly bilobed anteriorly; mantle canal patterns saccate to lemniscate. *M. Ord.-U.Sil.*

Leptestiina HAVLÍČEK, 1952, p. 409 [**L. prantli*; OD] [=*Dulankarella* RUKAVISHNIKOVA, 1956, p. 135 (type, **D. magna*)]. Unequally parvicostellate, with variably spaced accentuated costellae. Ventral muscle scar transversely bilobed; cardinal process squat, trilobed posteriorly, lophophore platform transversely to elongately bilobed, culminating medianly in wide ridge. *M.Ord.-U.Ord.*, Eu.——FIG. 242,*4a,b*. **L. prantli*, U.Ord.(Ashgill.), Czech.; *4a,b*, ped.v. and brach.v. int., ×2 (Havlíček, n).——FIG. 242,*4c,d*. *L. oepiki* (WHITTINGTON), M.Ord.(Caradoc.), Wales; *4c,d*, ped.v. and brach.v. int., ×4.5 (Williams, n).

Bilobia COOPER, 1956, p. 759 [**B. hemisphaerica*; OD]. Unequally parvicostellate, with widely spaced accentuated costellae; ventral muscle scar strongly bilobed, with divergent diductors; median ridge sporadically developed anterior to ventral scar, generally as coalescent tubercles; cardinal process high, trilobed, but with cleft median crest; lophophore platform of 2 elongate pointed or rounded lobes separated by discrete median septum. *M.Ord.-U.Ord.*, Eu.-N.Am.——FIG. 242,*1*. **B. hemisphaerica*, M.Ord.(Wilderness), E.USA (Va., *1a,b*-Pa., *1c*); *1a*, brach.v. view of conjoined valves, ×2; *1b,c*, ped.v. and brach.v. int. molds, ×3 (189).

Diambonia COOPER & KINDLE, 1936, p. 356 [**Plectambonites gibbosa* WINCHELL & SCHUCHERT, 1895, p. 416; OD]. Like *Leangella* but with strong median septum anterior to muscle scar on pedicle valve. *M.Ord.-U.Ord.*, N.Am.-Eu.

Leangella ÖPIK, 1933, p. 42 [**Plectambonites scissa* SALTER var. *triangularis* HOLTEDAHL, 1916, p. 84; OD]. Unequally parvicostellate, with widely spaced accentuated costellae. Ventral muscle scar transversely bilobed; cardinal process high, commonly with 2 pairs of ridges flanking median crest on its posterior face; lophophore platform small, bilobed, culminating medianly in wide ridge; rounded or medianly pointed, sharp, subperipheral rim defining brachial cavity in brachial valve. *M.Ord.-U.Sil.*, Eu.-N.Am.——FIG. 242,*2a-c*. **L. scissa* (SALTER), L.Llandover., Wales; *2a,b*, ped.v. int. mold and cast, ×5; *2c*, brach.v. int. cast, ×5 (Williams, n).——FIG. 242,*2d*. *L. segmentum* (LINDSTRÖM), U.Sil.(Wenlock), Eng.; *2d*, brach.v. view of conjoined valves, ×5 (Williams, n).

Sampo ÖPIK, 1933, p. 35 [**S. hiiuensis*; OD]. Unequally parvicostellate, with widely spaced accentuated costellae; hinge line denticulate. Ventral muscle scar bilobed; cardinal process high, trilobed posteriorly with indentation along ventral face of median crest; lophophore platform elongately bilobed, commonly with 2 boundaries anteriorly and culminating in median ridge. *U.Ord.*, Eu.——FIG. 242,*5*. **S. hiiuensis*, Fia, Est.; *5a*, brach.v. view of conjoined valves, ×3; *5b,c*, ped. v. and brach.v. int., ×5 (619).

Tufoleptina HAVLÍČEK, 1961, p. 447 [**T. tufogena*; OD]. Like *Leangella* but with subperipheral rim in pedicle valve as well as brachial valve. *U.Sil. (Wenlock)*, Czech.——FIG. 242,*3*. **T. tufogena*; *3a*, brach.v. int., ×4; *3b*, ped.v. int. mold, ×4 (Havlíček, n).

Family SOWERBYELLIDAE Öpik, 1930

[*nom. transl.* COOPER, 1956, p. 774 (*ex* Sowerbyellinae ÖPIK, 1930, p. 144)]

Semicircular to semioval, unequally parvicostellate, with small pseudodeltidium, apical foramen rarely if ever persistent in adult shells. Simple teeth rarely supported by dental plates and rarely supplemented by denticles; variably bilobed ventral muscle scar with deeply inserted lanceolate adductor scars; chilidial plates fused with small flat-lying socket ridges and median ridge-like cardinal process to form inverted V which overhangs subcircular deep depression in place of notothyrial platform; dorsal septa and lophophore platform variably developed; ventral and dorsal mantle canal patterns digitate to lemniscate. *Ord.-M.Dev.*

Subfamily SOWERBYELLINAE Öpik, 1930

[Sowerbyellinae ÖPIK, 1930, p. 144]

Concavo-convex, with impersistent rugae commonly developed posterolaterally at acute angles to hinge line and with variable number of septa in brachial valve surrounding or associated with suboval raised areas which probably gave support to anterior portion of lophophore, as well as dorsal adductor bases. *Ord.-M.Dev.*

Sowerbyella JONES, 1928, p. 384 [**Leptaena sericea* SOWERBY, 1839, p. 636; OD]. Parvicostellae either smooth or slightly beaded and variably segregated; ventral muscle scar small and bilobed, bounded

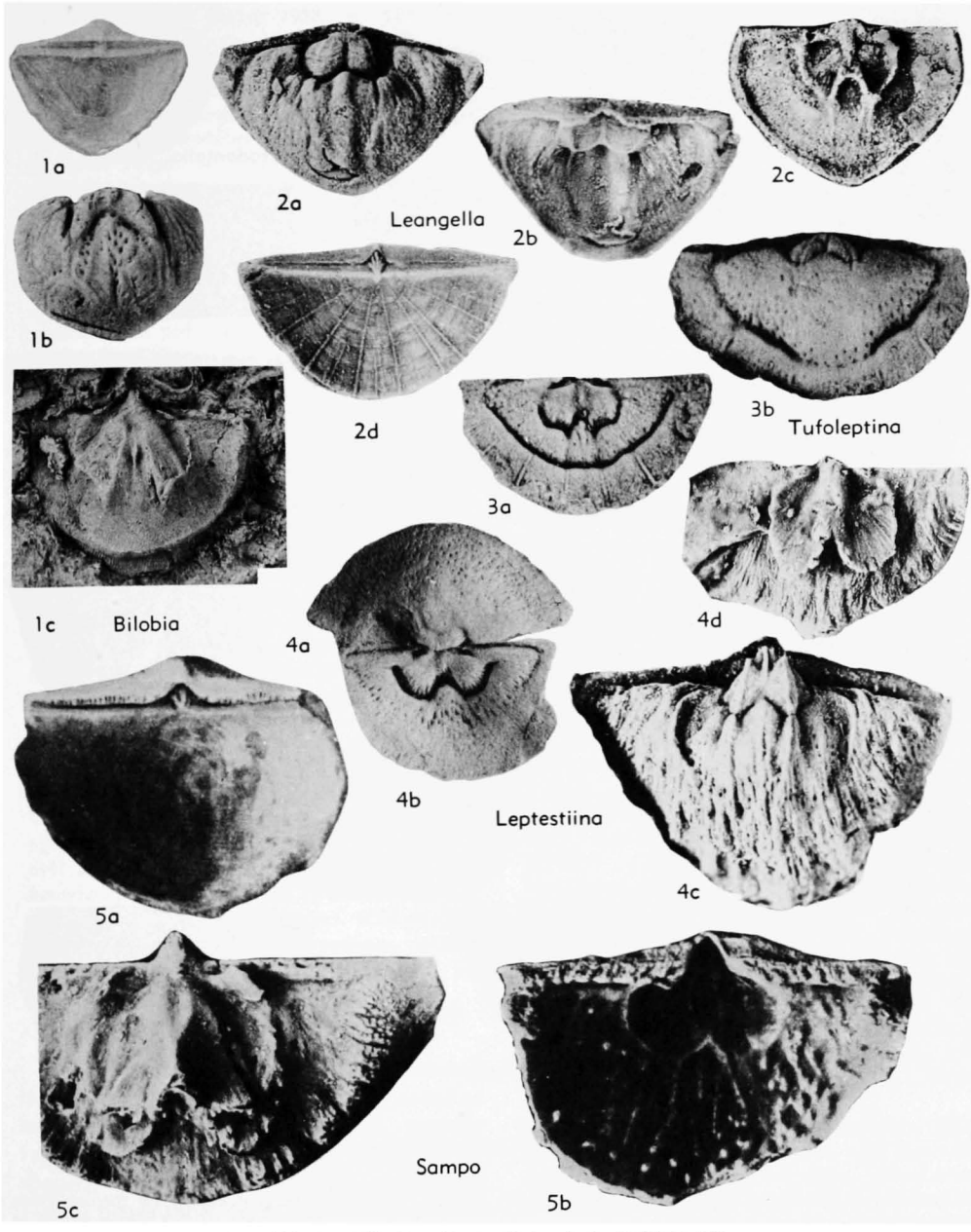

FIG. 242. Leptellinidae (Leptestiininae) (p. *H*377-*H*378).

posterolaterally by short dental plates and anteromedianly by pair of divergent ridges bifurcating from short median ridge bearing adductor scars; brachial valve with pair of strong submedian septa flanked by raised suboval areas, median ridge variably developed. *Ord.-L.Sil.*, cosmop.

S. ***(Sowerbyella)***. Parvicostellae segregated into narrow segments by many accentuated costellae; median ridge in brachial valve weak or absent. *Ord.-L.Sil.*, cosmop.——FIG. 243,*1*. **S. (S.) sericea* (SOWERBY), M.Ord.(Caradoc), Eng.; *1a,b*, brach.v. ints., ×3.5, ×2; *1c,d*, brach.v. int. and ext., ×3; *1e*, ped.v. int. mold, ×3; *1f*, brach.v. ext., ×2.5 (Williams, n).

S. ***(Viruella)*** RÕÕMUSOKS, 1959, p. 43 [**Sowerbyella liliifera* ÖPIK, 1930, p. 148; OD]. Like *S. (Sowerbyella)* but with small number of accentuated costellae dividing radial ornamentation

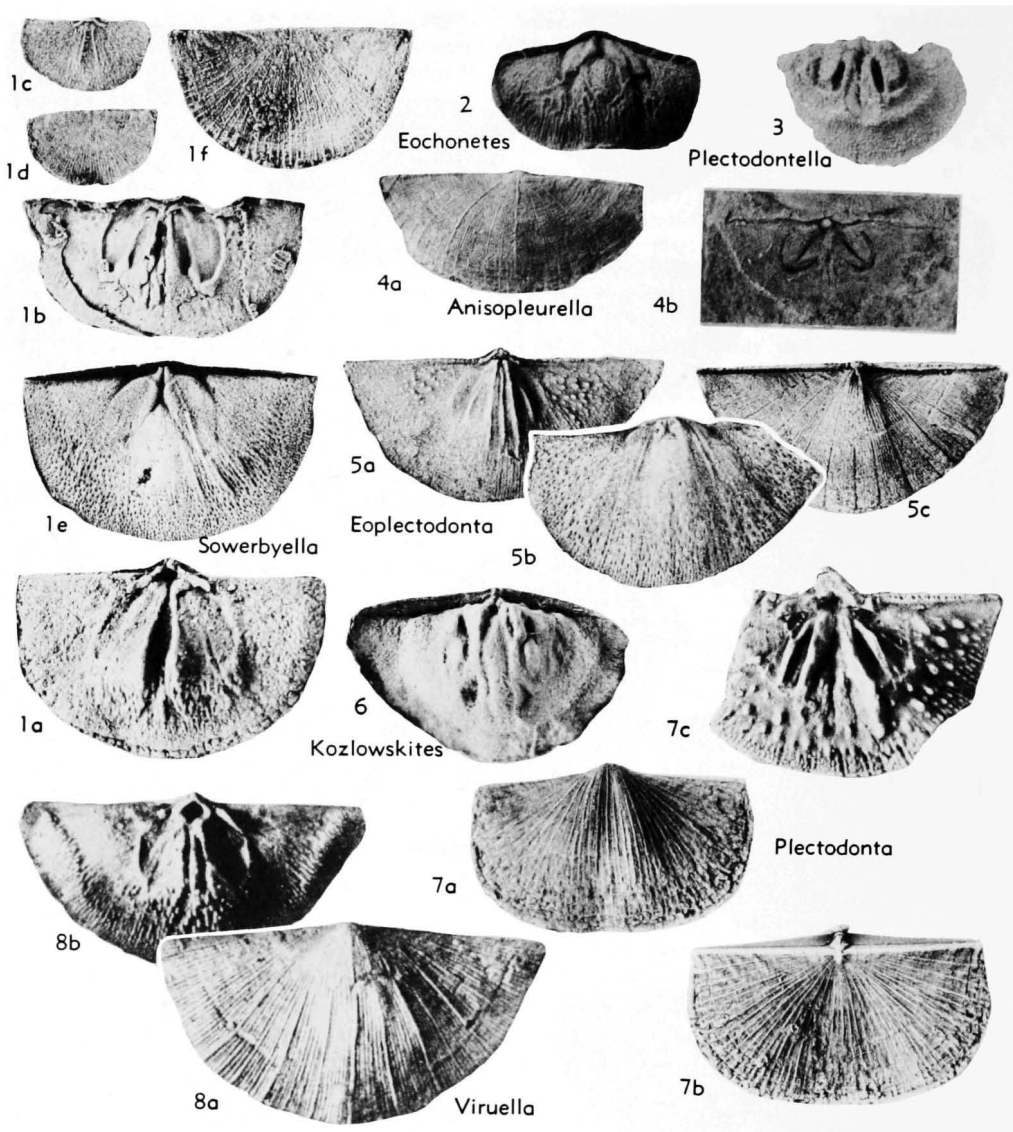

FIG. 243. Sowerbyellidae (Sowerbyellinae) (p. *H*378-*H*381).

into wide segments and strong median ridge in brachial valve standing high above flanking submedian septa. *L.Ord.(Llandeil.,* C_{1a}*)-M.Ord.(Caradoc.,* C_{III}), Eu.——FIG. 243,*8*. **S. (V.) liliifera* (ÖPIK), M.Ord.(Kukruse $C_{II\alpha}$), Est.; *8a,* ped.v. ext., ×3.5; *8b,* brach.v. int., ×3 (676).

Anisopleurella COOPER, 1956, p. 804 [**A. inaequistriata*; OD]. Finely and unequally parvicostellate, with 3 accentuated costellae arising near umbo and disposed medianly and laterally, supplemented by few shorter ones. Ventral muscle scar bilobed, with divergent diductors and adductors borne on low median ridge; in brachial valve, submedian septa, narrowly divergent about low median ridge and continuous with outer pair of sublateral ridges to define 2 suboval areas each divided by divergent septum. *M.Ord.(Caradoc.)-U.Ord.(Ashgill.),* Eu.-Am.——FIG. 243,*4*. **A. inquequistriata,* M.Ord. (Porterfield), USA(Tenn.); *4a,* ped.v. ext., ×4; *4b,* brach.v. int. mold, ×4 (189).

Eochonetes REED, 1917, p. 916 [**E. advena*; OD]. Like *Sowerbyella (Sowerbyella)* but with interarea of pedicle valve pierced by about 6 oblique narrow canals. *U.Ord.(Ashgill.),* Scot.——FIG. 243,*2*. **E. advena*; ped.v. int. mold, ×1 (Williams, n).

Eoplectodonta KOZLOWSKI, 1929, p. 113 [**Sower-*

byella praecursor JONES, 1928, p. 437; OD] [=*Thaerodonta* WANG, 1949, p. 19 (type, *T. aspera*)]. Like *Sowerbyella (Viruella)* but with variably denticulate hinge line and with oval areas flanking dorsal submedian septa, well defined by raised lateral boundaries and containing pair of divergent ridges. *M. Ord. (Caradoc) - L. Sil. (Llandover.)*, cosmop.

E. (Eoplectodonta). Ventral muscle field divided by narrow median ridge that bifurcates to form anteromedian boundaries of divergent diductor scars. *M.Ord.-L.Sil.*, cosmop.——FIG. 243,*5*. **E. (E.) praecursor* (JONES), L.Llandov., Wales; *5a,b*, brach.v. and ped.v. int. molds, ×3; *5c*, brach.v. ext., ×3 (Williams, n).

E. (Kozlowskites) HAVLÍČEK, 1952, p. 406 [**Strophomena nuncia* BARRANDE, 1879, pl. 49, fig. III; OD]. Ventral adductor scars inserted on high short platform not dividing anteriorly, diductor scars subparallel. *U.Ord.(Ashgill.)*, Eu. (Czech.).——FIG. 243,*6*. **E. (K.) nuncia* (BARRANDE), ped.v. int. mold, ×3.5 (Williams, n).

Plectodonta KOZLOWSKI, 1929, p. 112 [**P. mariae*; OD] [=*Dalejodiscus* HAVLÍČEK, 1961, p. 449 (type, *Strophomena comitans* BARRANDE, 1879, p. 101)]. Like *Eoplectodonta (Eoplectodonta)* but without dorsal median septum and with hinge line more or less entirely denticulate. *U.Sil.-M.Dev.*, cosmop.——FIG. 243,*7*. **P. mariae*, U.Sil.(Ludlov.), Pol.; *7a,b*, ped.v. and brach.v. views of conjoined valves, ×4; *7c*, brach.v. int., ×6 (Williams, n).

Plectodontella HAVLÍČEK, 1953, p. 9 [**P. redunca*; OD] [=*Ygera* HAVLÍČEK, 1961, p. 449 (type, Y. *ygerens*)]. Like *Plectodonta* but with elevated suboval areas in brachial valve contained by high boundaries formed by fusion of submedian septa with strong curved lateral ridges. *U.Sil.-M.Dev.*, cosmop.——FIG. 243,*3*. **P. redunca*, M.Dev. (Eifel.), Czech.; brach.v. int., ×3 (Havlíček, n).

Subfamily PTYCHOGLYPTINAE Cooper, 1956

[Ptychoglyptinae COOPER, 1956, p. 815]

Concavo-convex, unequally parvicostellate, with strongly accentuated costellae breaking concentrically disposed, narrow rugae into segments which may be chevron-shaped, or even strips oblique to costellae. Dental plates short, receding, ventral muscle scar small, slightly bilobed and without median ridge; median and submedian septa in brachial valve poorly developed. *Ord.*

Ptychoglyptus WILLARD, 1928, p. 283 [**P. virginiensis*; OD]. Commonly alate and thin-shelled, rarely geniculate. *Ord.(Whiterock-Porterfield)*, N.Am.-Eu.——FIG. 244,*6*. **P. virginiensis* M.Ord.(Porterfield), USA(Va.); *6a-c*, ped.v., brach.v., post. views of conjoined valves, ×2; *6d,e*, ped.v. int. and ext., ×3; *6f*, brach.v. int., ×4 (189).

Subfamily XENAMBONITINAE Cooper, 1956

[Xenambonitinae COOPER, 1956, p. 813]

Concavo-convex, finely costellate, brachial valve sulcate and geniculate anteriorly toward pedicle valve; dental plates vestigial, ventral muscle scar transversely bilobed; lophophore platform short, narrow, undercut and pointed anteromedianly. *M.Ord.-U. Ord.*

Xenambonites COOPER, 1956, p. 813 [**X. undosus*; OD]. Alate, accentuated costellae rarely developed and mainly as boundaries to ventral fold and in dorsal sulcus, posterolateral rugae parallel with hinge line. *M.Ord.(Porterfield)-U.Ord.(Trenton.)*, E.USA-Scot.——FIG. 244,*1*. **X. undosus*, M.Ord. (Porterfield), USA(Ala.); *1a*, ped.v. ext., ×4; *1b*, ant. view of conjoined valves, ×5; *1c*, brach.v. int., ×6; *1d*, ped.v. int., ×4 (189).

Subfamily AEGIROMENINAE Havlíček, 1961

[Aegiromeninae HAVLÍČEK, 1961, p. 450]

Plano- to concavo-convex, with short, narrow tract in brachial valve which probably gave support to lophophore as well as dorsal adductor bases, defined either by septules arranged in arc(s) or as elevated undercut platform; dorsal median septum always present. *M.Ord.-L.Sil.*

Aegiromena HAVLÍČEK, 1961, p. 450 [**Leptaena aquila* BARRANDE, 1848, p. 76; OD]. Concavo-convex, unequally parvicostellate but not well segregated into distinct segments. Dental plates short, receding, ventral muscle scar bilobed, with divergent diductor scars extending anterolaterally into raised, pustulose areas, contained posteromedianly by pair of ridges bifurcating from median ridge supporting adductor scars; lophophore platform in brachial valve bilobed but weakly defined by incomplete fusion of septule arcs. *M.Ord.-U.Ord.(Ashgill.)*, Czech. —— FIG. 244,*7*. **A. aquila* (BARRANDE), M.Ord.(Llandeil.-Caradoc.), Czech.; *7a,b*, ped.v. and brach.v. int. molds, ×2; *7c*, brach.v. view of conjoined valves, ×2 (Havlíček, n).

Aegiria ÖPIK, 1933, p. 55 [**A. norvegica*; OD]. Concavo-convex, finely costellate, and generally sulcate; dental plates short, receding, ventral muscle scar small, bilobed with adductor scars impressed on median ridge that bifurcate anteriorly to define anteromedian boundaries of divergent diductor scars, suboval lophophore platform well developed, undercut, median septum high. *L.Sil.*, Eu.——FIG. 244,*4*. **A. norvegica*, M.Llandover., Norway; *4a,b*, ped.v. and brach.v. int. molds, ×4 (Williams, n).

Alwynella SPJELDNAES, 1957, p. 85 [**A. osloensis*; OD]. Like *Aegiria* but with fine parvicostellae segregated into narrow segments by accentuated costellae, denticulate hinge line and without me-

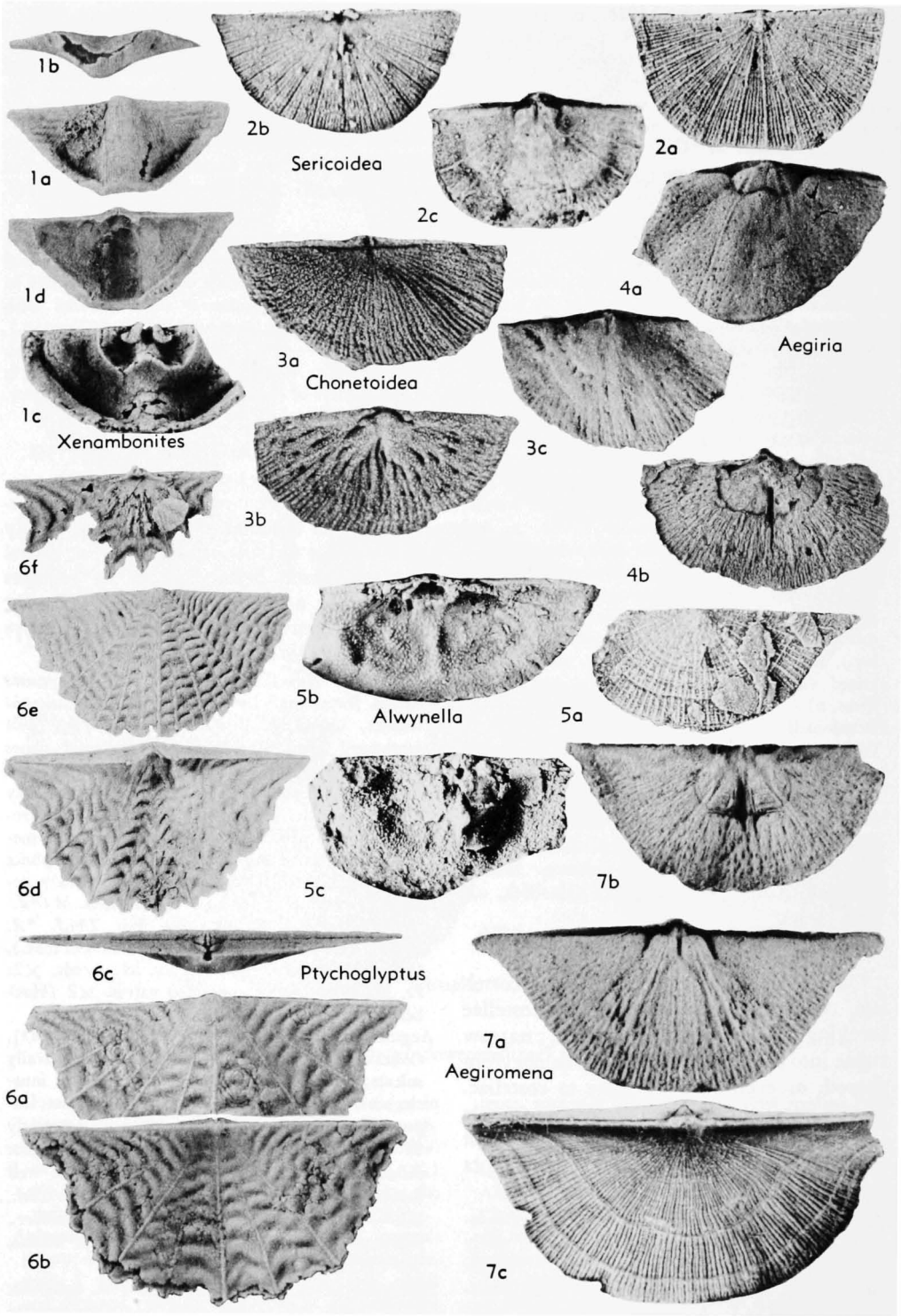

FIG. 244. Sowerbyellidae (Ptychoglyptinae) *(6)*, (Xenambonitinae) *(1)*, (Aegiromeninae) *(2-5, 7)* (p. *H*381, *H*383).

dian ridge dividing ventral muscle scar. *M.Ord. (4aα-β)*, Scand.——Fig. 244,*5*. **A. osloensis*, *4aβ*, Nor.; *5a,b*, ped.v. ext. and int., ×4; *5c*, brach.v. int., ×4.5 (Williams, n).

Chonetoidea Jones, 1928, p. 393 [**Plectambonites papillosa* Reed, 1905, p. 45; OD]. Like *Aegiria* but with lophophore platform weakly defined by series of discrete or coalescing elongate tubercles usually disposed arcuately about median septum. *U.Ord.(Caradoc.)-L.Sil.(Llandover.)*, Eu.——Fig. 244,*3*. **C. papillosa* (Reed), Ashgill., Br.I.; *3a-c*, brach.v. ext., brach.v. and ped.v. int. molds, ×4 (Williams, n).

Kassinella Borissiak, 1956, p. 50 [**K. globosa*; OD]. Like *Aegiromena* but plano-convex and with pair of posterolateral processes in each valve. *M. Ord.*, USSR(Kazakh.).

Sericoidea Lindström, 1953, p. 473 [**Leptaena sericea* var. *restricta* Hadding, 1913, p. 62; OD]. Like *Chonetoidea* but with radial ornamentation unequally parvicostellate and segregated into well-defined segments by accentuated costellae; dorsal tubercles discrete. *M.Ord.-U.Ord.(Caradoc.)*, Eu.-N.Am.——Fig. 244,*2*. **S. restricta* (Hadding), M.Ord., Sweden; *2a,b*, brach.v. ext. and int., ×7; *2c*, ped.v. int., ×7 (Williams, n).

Family BIMURIIDAE Cooper, 1956

[Bimuriidae Cooper, 1956, p. 764]

Radial ornamentation lacking but with concentric lamellae commonly grossly thickened into comae; pedicle foramen persistent in adult shells. Teeth simple, dental plates obsolete; ventral muscle field not clearly impressed but probably large; ventral mantle canal pattern pinnate; socket ridges strong, widely divergent and continuous with high chilidial plates bounding notothyrium; cardinal process simple; chilidium apical or absent; brachial valve interior with 3 long, high median septa flanked by elongately oval callosites or subtriangular, elevated platforms, dorsal mantle canal pattern lemniscate or pinnate. *M.Ord.*

Bimuria Ulrich & Cooper, 1942, p. 622 [**B. superba*; OD]. Concavo-convex, with elongately oval callosities in brachial valve commonly contained laterally by pair of ridges which converge anteriorly toward outer median septa. *M.Ord.(Porterfield-Wilderness)*, N.Am.-Eu.——Fig. 245,*2*. **B. superba*, Porterfield, USA(Tenn.); *2a*, brach.v. view of conjoined valves, ×1; *2b*, ped.v. int., ×1.5; *2c*, brach.v. int., ×2; *2d*, post. view of brach.v. tilted to show cardinalia, ×3 (189).

Craspedelia Cooper, 1956, p. 772 [**C. marginata*; OD]. Like *Bimuria* but with anterior margin geniculate ventrally and elevated triangular platforms flanking median septa of brachial valve; median ridge or line of tubercles commonly developed in pedicle valve. *M.Ord.(Porterfield-Wilderness)*, N.Am.-Scot.——Fig. 245,*1*. **C. marginata*, Porterfield, USA(Ala.); *1a*, brach.v. ext., ×5; *1b-d*, ext., int., ant. views of ped.v., ×4; *1e*, tilted view of brach.v. int., ×4 (189).

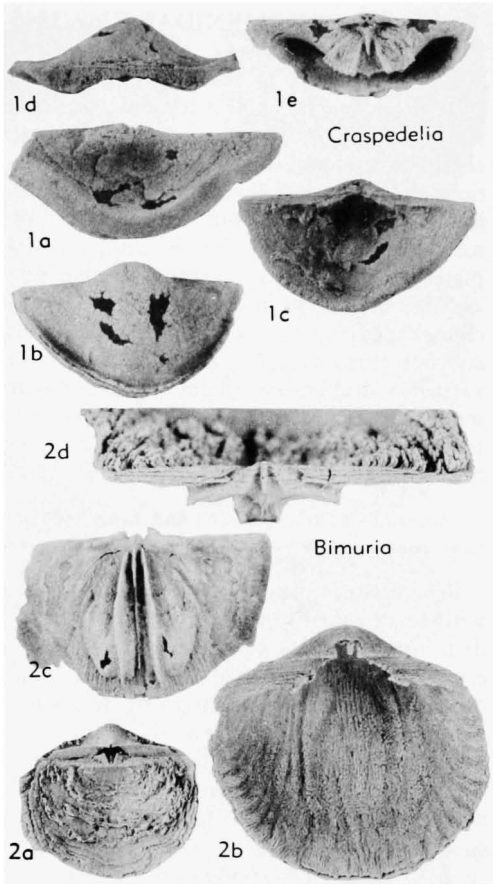

Fig. 245. Bimuriidae (p. *H383*).

Superfamily STROPHOMENACEA King, 1846

[*nom. transl.* Schuchert, 1896, p. 312 (*ex* Strophomenidae King, 1846, p. 28)]

Concavo-convex to resupinate, with cardinalia consisting of strong to obsolescent socket ridges and bilobed cardinal process; delthyrium covered apically to completely by pseudodeltidium, chilidium well developed to absent; apical foramen sealed in some later stocks so that adult shells were unattached or exceptionally cemented by part of pedicle valve to substratum; brachial valve rarely equipped with raised supports for schizolophous or spirolophous lophophore. *Ord.-Carb.*

Family STROPHOMENIDAE King, 1846

[Strophomenidae King, 1846, p. 28]

Concavo-convex to resupinate, rarely geniculate or rugate; apical foramen in adult shells small or (less commonly) closed, shells exceptionally attached by cementation; chilidium well developed, pseudodeltidium usually present but exceptionally resorbed in adult shells. Teeth simple, dental plates usually present; ventral muscle scar variable in outline; notothyrial platform anchor-shaped, dorsal adductor impressions subcircular to oval, traversed by 2 pairs of variable developed ridges (trans-muscle septa); mantle canal systems poorly preserved, but probably saccate in both valves of many genera. *M.Ord.-L.Dev.*

Subfamily STROPHOMENINAE King, 1846

[*nom. transl.* Gill, 1871, p. 26 (*ex* Strophomenidae King, 1846, p. 28)]

Resupinate, unequally parvicostellate, with small apical foramen and large pseudodeltidium. Dental plates short to obsolescent; ventral muscle scar subcircular to subquadrate, commonly with strong bounding ridges; notothyrial platform short but well developed, trans-muscle septa variably defined. Shell substance commonly finely and densely pseudopunctate. *M.Ord.-U.Sil.*

Strophomena Rafinesque in de Blainville, 1825, p. 513 [**S. rugosa* Rafinesque in de Blainville, 1825 (?conspecific with *Leptaena planumbona* Hall, 1847); SD King, 1846, p. 28] [=*Longvillia* Bancroft, 1933, p. 3 (type, *Strophomena grandis* Sowerby, 1839); *Öpikinella* Wilson, 1946, p. 199 (type, *O. affinis*); *S. (Drummuckina)* Bancroft, 1949, p. 12 (type, *S. (D.) agrestis*)]. Variably unequally parvicostellate. Teeth smooth or striated, dental plates obsolescent, ventral muscle scar subcircular to suboval, with strong lateral bounding ridges not united with strong median adductor ridge; trans-muscle septa variably developed. *M.Ord.-U.Ord.*, cosmop.——Fig. 246,*3*. *S. planumbona* (Hall), U.Ord.(Cincinnati.), USA (Ohio); *3a*, brach.v. int., ×1 (189); *3b,c*, brach.v. ext., lat. view of conjoined valves, ×1; *3d*, ped.v. int., ×2 (851).

Actinomena Öpik, 1930, p. 166 [**Strophomena (Actinomena) orta*; OD]. Gently resupinate and strongly unequally parvicostellate, with strong posterolateral rugae. Ventral muscle scar short, subquadrate, with high subparallel lateral bounding ridges and broad median adductor ridge; trans-muscle septa present. *M.Ord.*, Eu.(Est.-Eire).——Fig. 246,*5*. **A. orta* (Öpik), Cii, Est.; *5a*, ped.v. int., ×1.5; *5b,c*, brach.v. ext. and int., ×1.5 (617).

Gunnarella Spjeldnaes, 1957, p. 149 [**Strophomena (Gunnarella) delta*; OD]. Like *Strophomena* but rarely geniculate and with strong concentric rugae interrupted by widely spaced accentuated costellae. *M.Ord.-U.Ord.*, N. Am.-N. Eu.——Fig. 246,*1*. *G. regulifera* (Wang), U.Ord.(Richmond.), USA(Iowa); *1a,b*, ped.v. and ant. views of complete shell, ×2 (851).

Luhaia Rõõmusoks, 1956, p. 1091 [**L. vardi*; OD]. Like *Strophomena* but strongly geniculate in ventral direction and with concentric rugae not broken by accentuated costellae; trans-muscle septa present. *U.Ord.*(Fig), W.USSR.——Fig. 246,*6*. **L. vardi*, Est.; *6a*, ped.v. view of conjoined valves, ×2; *6b*, brach.v. int. mold, ×2; *6c*, ped.v. ext., ×2 (Rõõmusoks, n).

Microtrypa Wilson, 1945, p. 144 [**M. altilis*; OD]. Like *Strophomena* but with submedian pair of trans-muscle septa well developed and lateral of forked medium extension of notothyrial platform. *M.Ord.*, N.Am.-Eu.

Pentlandina Bancroft, 1949, p. 11 [**Strophomena (Pentlandina) tartana;* OD]. Like *Luhaia* but lacking geniculation and with strong median fold in brachial valve; trans-muscle septa well developed, *L.Sil.-U.Sil.*, G.Brit.

Rhipidomena Cooper, 1956, p. 866 [**Strophomena tennesseensis* Willard, 1928, p. 285; OD]. Like *Tetraphalerella* but with large ventral muscle field occupying nearly half of internal area of pedicle valve, not enclosed by strong bounding ridges, dental plates absent, cardinalia small, trans-muscle septa subdued. *M.Ord.*, E.USA.——Fig. 246,*7*. **R. tennesseensis* (Willard), Porterfield, Va. *(7a,b)*, Tenn. *(7c)*; *7a*, ped.v. int., ×1; *7b*, brach.v. int., ×2; *7c*, lat. view of conjoined valves, ×1 (189).

Tetraphalerella Wang, 1949, p. 19 [**T. cooperi*; OD]. Like *Strophomena* but with small suboval adductor scar in ventral muscle field divided by short thin ridge and enclosed anteriorly by diductor scars; trans-muscle septa not developed; shell substance coarsely and densely pseudopunctate. *U.Ord.*, N.Am.——Fig. 246,*4*. **T. cooperi*, Richmond., USA(Iowa); *4a,b*, brach.v. int. and ext., ×1; *4c*, ped.v. int., ×1 (851).

Trigrammaria Wilson, 1945, p. 140 [**T. trigonalis*; OD]. Like *Strophomena* but with rounded dorsal median fold and with submedian pair of trans-muscle septa well developed in addition to median prolongation from notothyrial platform. *M. Ord.*, N. Am.——Fig. 246,*2*. *T. wilsoni* (Cooper), Wilderness, USA(N.Y.); *2a,b*, ped.v. and brach.v. ext., ×2 (189).

Subfamily FURCITELLINAE Williams, n. subfam.

Biconvex to concavo-convex or resupinate, costellate, with large foramen and pseudodeltidium. Ventral muscle scar small, subcircular to trapezoidal in outline, notothyrial platform and trans-muscle septa well de-

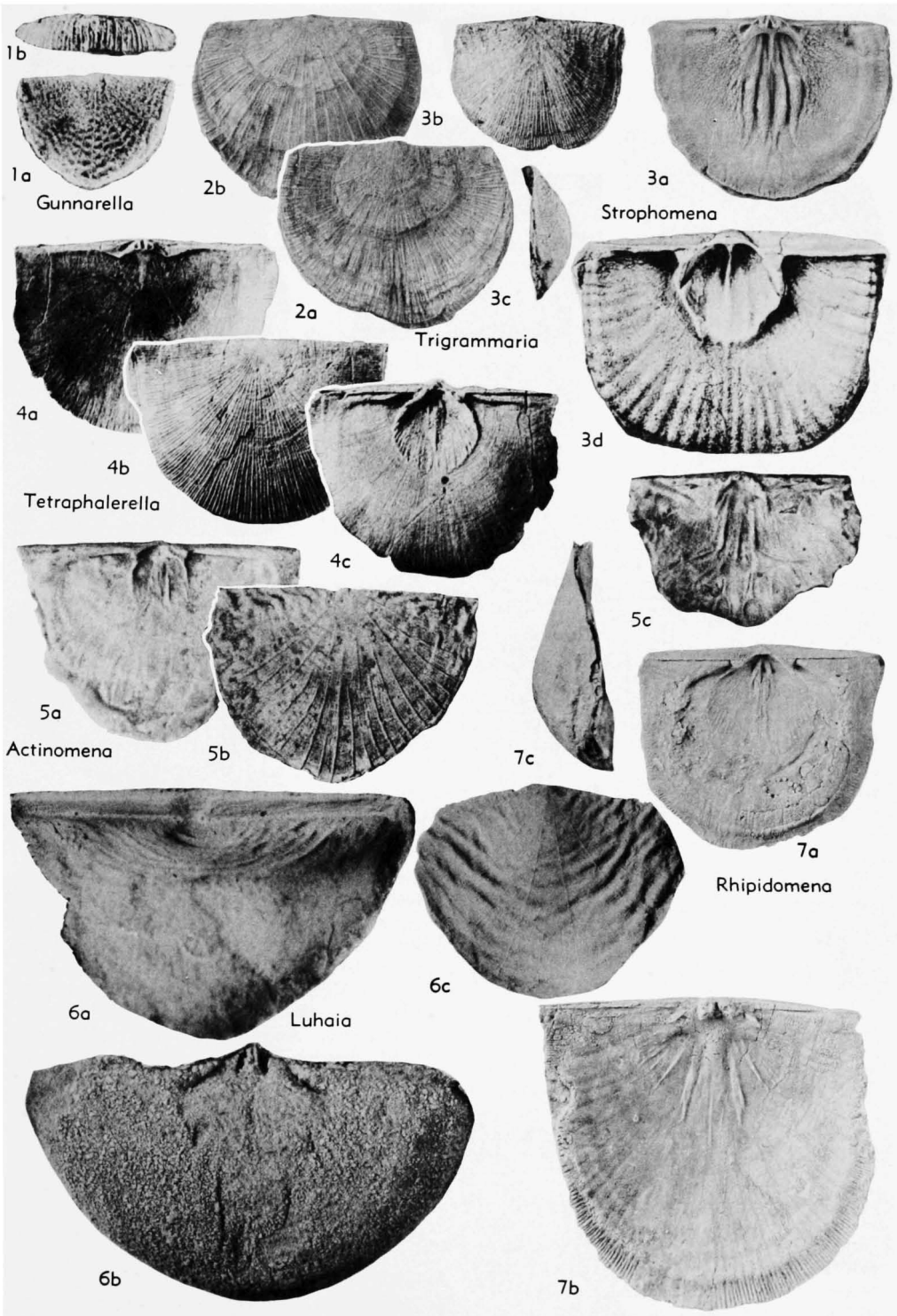

FIG. 246. Strophomenidae (Strophomeninae) (p. *H*384).

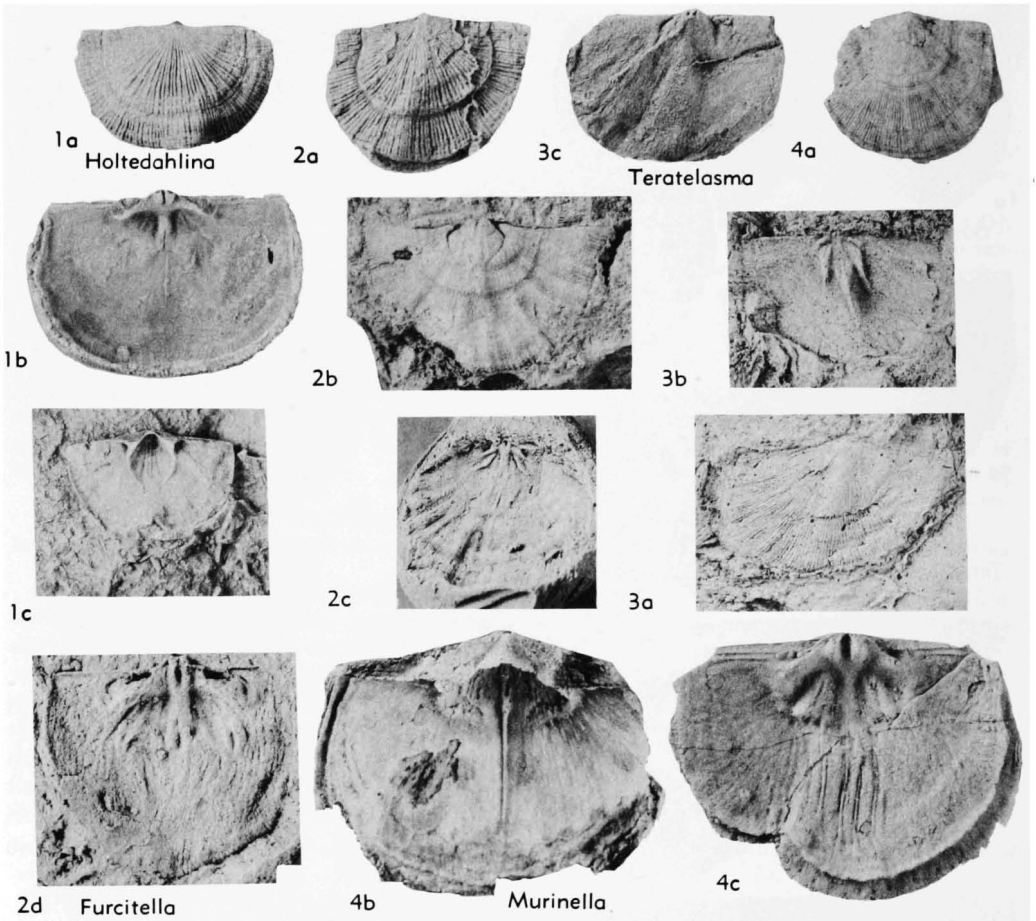

FIG. 247. Strophomenidae (Furcitellinae) (p. *H*384, *H*386).

veloped. Shell substance finely and densely pseudopunctate. *M.Ord.-L.Sil.*

Furcitella COOPER, 1956, p. 875 [**F. plicata*; OD]. Biconvex, with deeper brachial valve and pedicle valve commonly flattened to concave anteriorly; ventral muscle field trapezoidal, with strong bounding ridges; median ridge of notothyrial platform divided, trans-muscle septa normally well developed, with curved submedian septa. *M.Ord.-L.Sil.*, N.Hemis.——FIG. 247,*2*. **F. plicata*, M. Ord.(Wilderness), USA(Va.); *2a,c*, plasticene casts of ped.v. ext. and brach.v. int., ×2; *2b*, ped.v. int., ×2; *2d*, plasticene cast of brach.v. int. mold, ×3 (189).

Holtedahlina FOERSTE, 1925, p. 122 [**Leptaena sulcata* DE VERNEUIL, 1848, p. 350; OD]. Like *Furcitella* but unequally biconvex, with dorsal median fold; trans-muscle septa poorly developed. *U.Ord.*, N.Am.——FIG. 247,*1*. **H. sulcata* (DE VERNEUIL), Richmond., USA(Ohio); *1a*, brach.v. view of conjoined valves, ×1; *1b*, brach.v. int., ×1.5; *1c*, ped.v. int., ×1 (189).

Murinella COOPER, 1956, p. 844 [**M. partita*; OD]. Biconvex but also concavo-convex in late growth stages of some species, costellate to unequally parvicostellate. Ventral muscle field subcircular, with strong bounding ridges, adductors separated by median ridge continuing anteriorly beyond muscle field; trans-muscle septa present, with long submedian pair; dorsal interior with strongly elevated subperipheral band. *M.Ord.*, N.Am.——FIG. 247,*4*. **M. partita*, Porterfield, USA(Okla.); *4a*, ped.v. ext., ×1; *4b,c*, ped.v. and brach.v. int., ×2 (189).

Teratelasma COOPER, 1956, p. 823 [**T. neumani*; OD]. Gently biconvex, with narrow dorsal median sulcus. Ventral muscle field short and bilobed about median fold in ventral interior; trans-muscle septa well developed, with median septum, extending almost to anterior margin, pointed and strongly elevated posteriorly, and strong submedian septa. *M.Ord.*, N.Am.(USA).——FIG. 247, *3*. **T. neumani*; *3a,b*, plasticene casts of ped.v. ext., and brach.v. int., ×3; *3c*, ped.v. int. mold, ×3 (189).

Subfamily RAFINESQUININAE Schuchert, 1893
[Rafinesquininae SCHUCHERT, 1893, p. 153]

Concavo-convex, or rarely resupinate and geniculate, unequally parvicostellate, with small apical foramen and vestigial or resorbed pseudodeltidium; rugae concentric or impersistent posterolaterally. Ventral muscle scar subquadrate to subcircular,

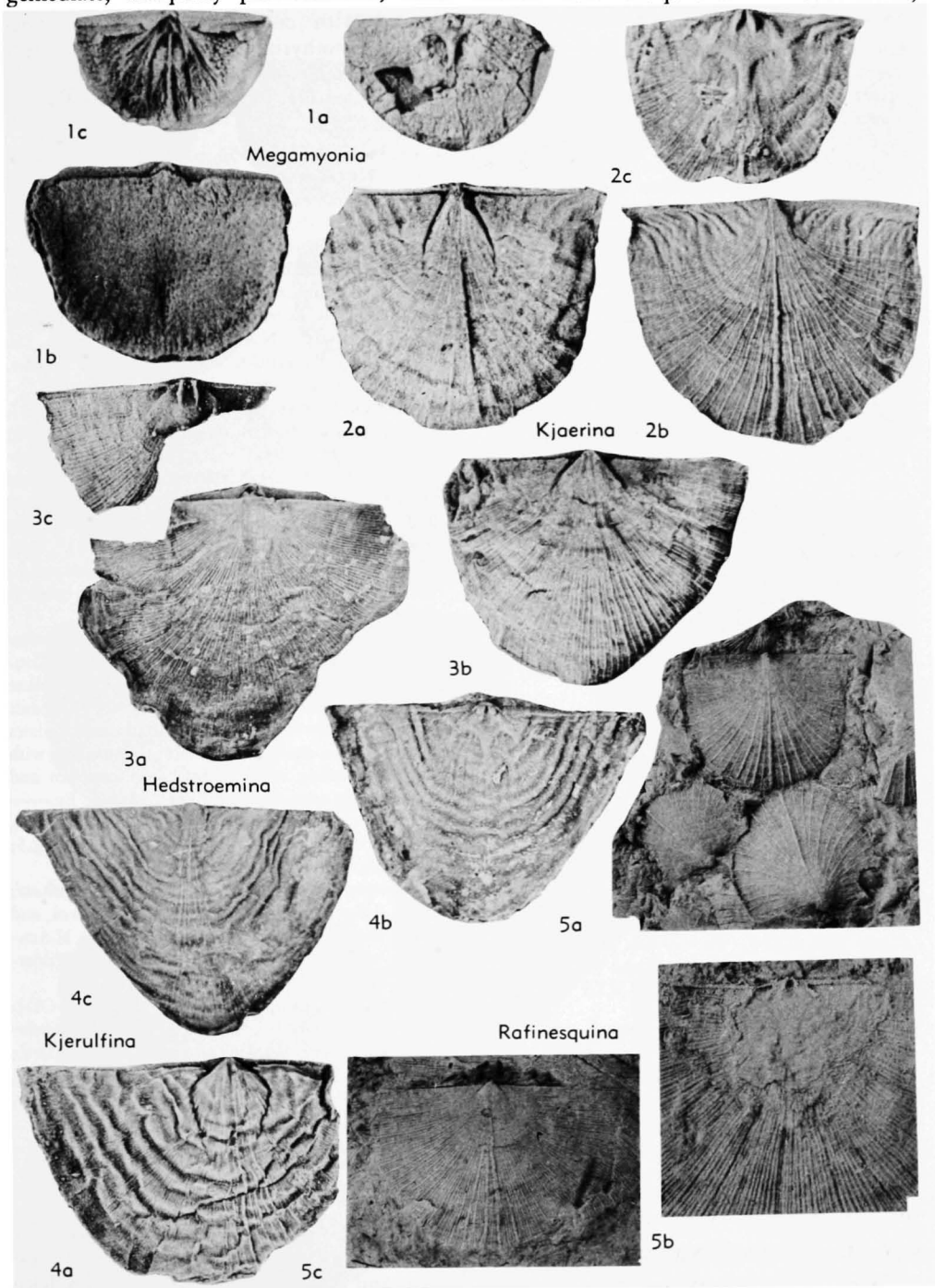

FIG. 248. Strophomenidae (Rafinesquininae) (p. *H*386-*H*388).

bounding ridges weak or absent; notothyrial platform small, cardinalia commonly delicate, trans-muscle weakly defined or absent; shell substance regularly and coarsely pseudopunctate. *M.Ord.-U.Ord.*

Rafinesquina HALL & CLARKE, 1892, p. 281 [**Leptaena alternata* CONRAD, 1838, p. 115; OD] [=*Playfairia* REED, 1917, p. 866 (type, *Strophomena deltoidea* CONRAD, 1839, p. 63)]. Concavo-convex, unequally parvicostellate, commonly with thickened, conspicuous median costa, posterolateral rugae feeble, pseudodeltidium vestigial. Ventral muscle scar small, subcircular, weakly impressed, and without bonding ridges except for extensions of divergent dental plates; cardinalia delicate; notothyrial platform weak; trans-muscle septa not preserved. *M.Ord.-U.Ord.*, N.Hemis.——FIG. 248, *5a. R. trentonensis* (CONRAD), M.Ord.(Wilderness-Trenton.), USA(N.Y.); *5a*, ext. views of 3 ped. valves, ×1 (189).——FIG. 248,*5b,c. R. planulata* (COOPER), M.Ord.(Wilderness), USA(Va.); *5b*, brach.v. int., ×3; *5c*, ped.v. int., ×2 (189).

Kjaerina BANCROFT, 1929, p. 43 [**K. typa*; OD]. Like *Rafinesquina* but with strong posterolateral rugae and lightly impressed, triangular ventral muscle scar, with low, subparallel bounding ridges. *M.Ord.-U.Ord.*, Eu.

K (Kjaerina). Brachial valve plane to shallowly concave; pedicle valve convex to geniculately convex; thickened median costae on pedicle valve conspicuous. *M.Ord.*, Eu.——FIG. 248,*2. *K. (K.) typa*, Caradoc., Eng.; *2a*, ped.v. int., ×1.5; *2b*, ped.v. ext., ×2; *2c*, brach.v. int., ×2 (Williams, n).

K. (Hedstroemina) BANCROFT, 1929, p. 56 [**H. fragilis*; OD]. Concavo-convex valves commonly geniculate dorsally; thickened median costae rare. *M.Ord.-U.Ord.*, Eu.——FIG. 248,*3. *K. (H.) fragilis*, Caradoc., Eng.; *3a*, brach.v. view of conjoined valves, ×1.5; *3b*, ped.v. int., ×1.5; *3c*, brach.v. int., ×2.5 (Williams, n).

Kjerulfina BANCROFT, 1929, p. 59 [**K. trigonalis*; OD]. Like *Kjaerina* but resupinate, with ventrally directed geniculation and concentrically rugate disc. *U.Ord.*, Eu.——FIG. 248,*4. K. polycyma* (BANCROFT), Caradoc., Eng.; *4a*, ped.v. int., ×1.5; *4b,c*, brach.v. int., ext., ×1.5 (Williams, n).

Megamyonia WANG, 1949, p. 32 [**M. knighti*; OD]. Concavo-convex, with sharp dorsal geniculation, thick median costa commonly well developed, posterolateral rugae weak. Dental plates absent; ventral muscle field large subcircular; trans-muscle septa commonly absent, rarely variably and feebly developed. *U.Ord.*, N.Am.——FIG. 248,*1. *M. knighti*, Richmond., USA(Iowa); *1a,b*, brach.v. int., ext., ×2; *1c*, ped.v. int., ×2 (851).

Subfamily GLYPTOMENINAE Williams, n. subfam.

Biconvex to concavo-convex, unequally parvicostellate, with apical foramen and moderately large pseudodeltidium; dental plates short to obsolescent, ventral muscle scar small, cordate to subcircular in outline; cardinal process lobes small, commonly united with curved socket ridges above weak notothyrial platform; trans-muscle septa variably developed. Shell substance mainly densely and finely pseudopunctate. *L.Ord.-M.Ord.*

Glyptomena COOPER, 1956, p. 881 [**G. sculpturata*; OD] [=*Oslomena* SPJELDNAES, 1957, p. 161 (type, *O. osloensis*)]. Concavo-convex, commonly with strong short rugae posterolaterally. Teeth commonly tuberculate, dental plates short; ventral muscle field subcordate, with lateral bounding ridges; notothyrial platform weak; trans-muscle septa variably developed, submedian pair slightly curved. *M.Ord.*, N.Am.-Eu.——FIG. 249,*1. *G. sculpturata*, Porterfield, USA(Va.); *1a,b*, brach.v. int., ext., ×2; *1c*, ped.v. int., ×2 (189).

?Hesperinia COOPER, 1956, p. 822 [**H. kirki*; OD]. Plano- to slightly concavo-convex, parvicostellate; dental plates present, ventral muscle field unknown; notothyrial platform and trans-muscle septa poorly developed. Shell substance coarsely pseudopunctate. [The taxonomic position of this genus is uncertain.] *L.Ord.(Whiterock)*, USA (Nev.).——FIG. 249,*2. *H. kirki; 2a,b*, ped.v., lat. views of conjoined valves, ×3; *2c*, brach.v. int., ×3 (189).

Mjoesina SPJELDNAES, 1957, p. 137 [**Rafinesquina mjoesensis* HOLTEDAHL, 1916, p. 19; OD]. Concavo-convex, with brachial valve initially plane or slightly concave, but geniculate dorsally in adult stages of growth. Teeth striated; dental plates short; ventral muscle scar short, rhomboidal, with lateral bounding ridges; notothyrial platform and trans-muscle septa faint or absent. *M.Ord.*, Eu.——FIG. 249,*3. M. rugata* WILLIAMS, Scot.; *3a*, brach.v. int. cast, ×3; *3b*, ped.v. int. mold, ×2.5; *3c*, brach.v. ext. cast, ×2 (877).

Pionomena COOPER, 1956, p. 901 [**P. neumani*; OD]. Like *Glyptomena* but gently biconvex and with obsolescent dental plates. *M.Ord.*, N.Am.-Scot.——FIG. 249,*5. P. pulchra* (COOPER), Wilderness, USA(Pa.); ped.v. ext., ×2 (189).

Platymena COOPER, 1956, p. 879 [**P. plana*; OD]. Like *Glyptomena* but plano- to slightly concavo-convex and with obsolescent dental plates. *M.Ord.*, N.Am.——FIG. 249,*4. *P. plana*, Porterfield, USA (Tenn.); *4a,b*, ped.v. int. and ext., ×2; *4c*, brach.v. int., ×2 (189).

Subfamily OEPIKINAE Sokolskaya, 1960

[*nom. correct.* WILLIAMS, herein (*pro* Öpikinae SOKOLSKAYA, 1960, p. 211)]

Concavo-convex, unequally parvicostellate, rarely costellate, with small apical foramen and variably developed pseudodeltidium; impersistent rugae common postero-

laterally. Ventral muscle scar large, subcircular, with flabellate diductor scars enclosing adductor scars on either side of variably developed median ridge, bounding ridges weak or absent; notothyrial platform, cardinalia and trans-muscle septa commonly strongly developed. Shell substance densely and finely pseudopunctate. *M.Ord.-U.Ord.*

Oepikina SALMON, 1942, p. 589 [**Öpikina septata*; OD]. Concavo-convex, with convex or gently

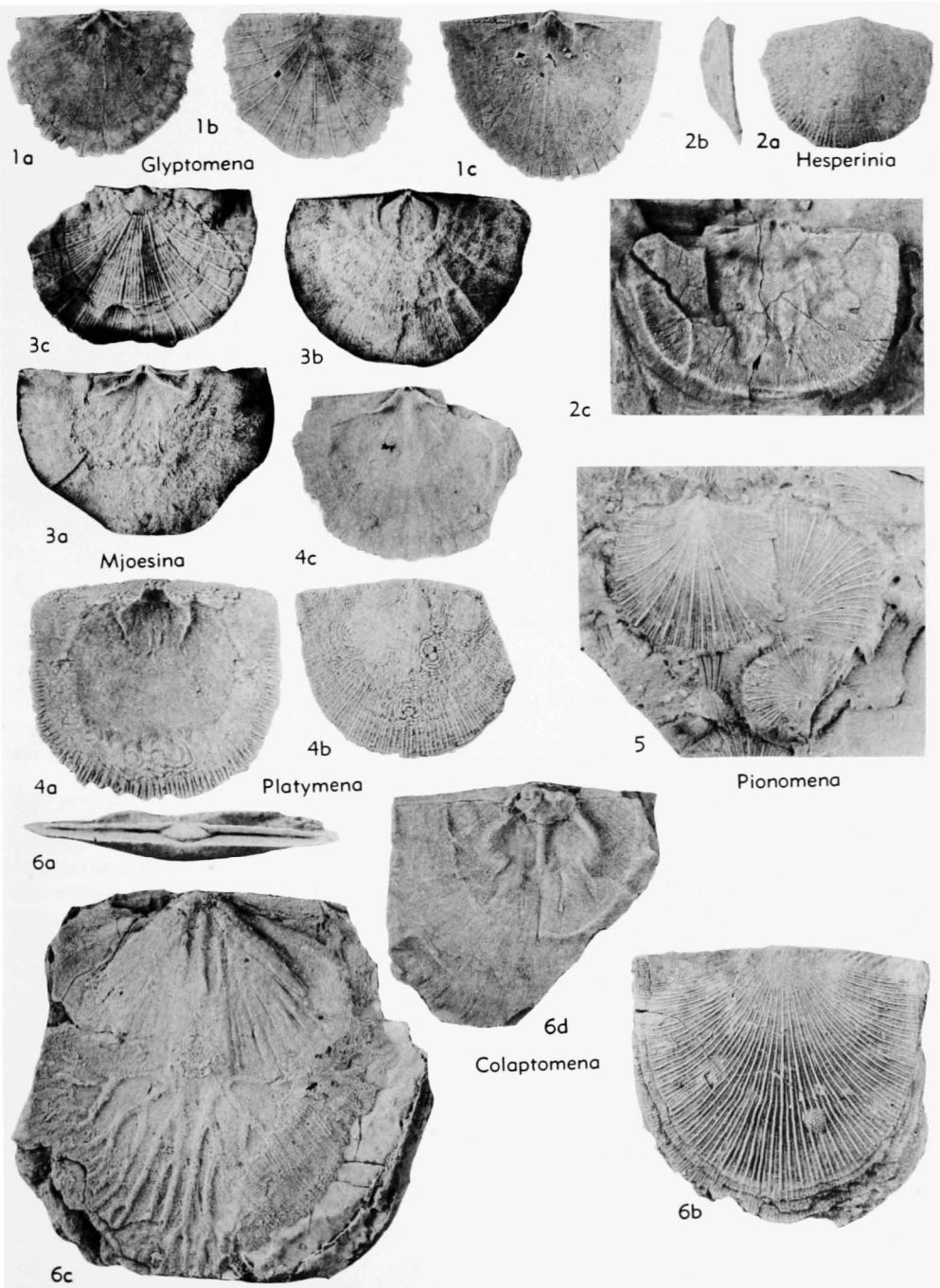

FIG. 249. Strophomenidae (Glyptomeninae) *(1-5)*, (Oepikinae) *(6)* (p. *H*388-*H*390).

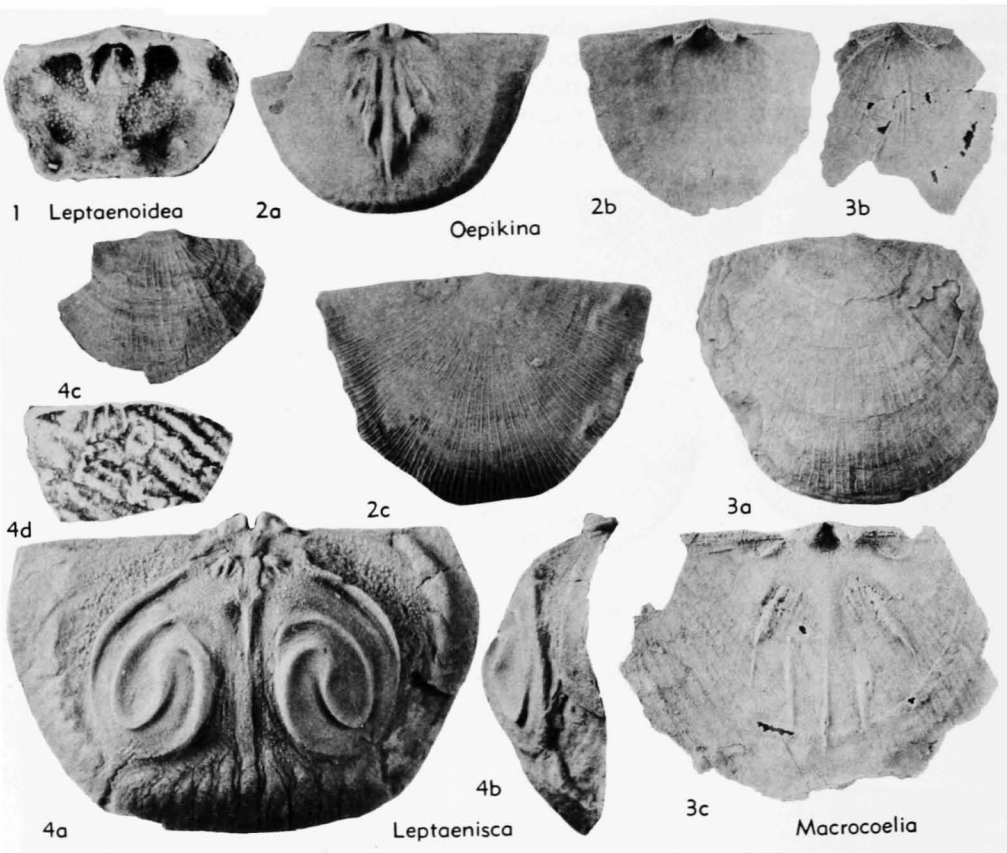

FIG. 250. Strophomenidae (Oepikinae) *(2-3)*, (Leptaenoideinae) *(1,4)* (p. *H*388-*H*390).

geniculate pedicle valve and dorsally geniculate brachial valve; unequally parvicostellate, pseudodeltidium small. Teeth commonly crenulate or tuberculate, dental plates widely divergent; trans-muscle septa strongly developed and high anteriorly, dorsal subperipheral rim conspicuous. *M.Ord.-U.Ord.*, cosmop.——FIG. 250,*2*. **O. septata*, M. Ord.(Wilderness), USA(Tenn.); *2a,b*, brach.v. and ped.v. int., ×2; *2c*, ped.v. view of conjoined valves, ×2 (189).

Colaptomena COOPER, 1956, p. 889 [**C. leptostrophoidea*; OD]. Like *Oepikina* but large, with compressed plano- to concavo-convex profile and resorbed pseudodeltidium; dental plates obsolescent, trans-muscle septa faint. *M.Ord.*, E.N.Am.-G.Brit.——FIG. 249,*6*. **C. leptostrophoidea*, Trenton., USA(Va.); *6a*, post. view of conjoined valves, ×1; *6b*, ped.v. ext., ×1; *6c*, ped.v. int. mold, ×1.5; *6d*, brach.v. int., ×1 (189).

Kirkina SALMON, 1942, p. 598 [**K. millardensis*; OD]. Concavo-convex, subequally parvicostellate, median and submedian septa in dorsal trans-muscle set, poorly developed; pedicle valve unknown. *L.Ord.*, W.USA(Nev.).

Maakina ANDREEVA, 1961, p. 170 [*Öpikina (M.) kulinnensis*; OD]. Like *Oepikina* but with costellate radial ornamentation. *M.Ord.*, USSR.

Macrocoelia COOPER, 1956, p. 890 [**M. obesa*; OD]. Like *Oepikina* but evenly concavo-convex, with small pseudodeltidium rarely resorbed, rudimentary or obsolescent dental plates and subdued trans-muscle septa. *M.Ord.*, N.Hemis.——FIG. 250, *3*. **M. obesa*, Porterfield, USA(Tenn.); *3a*, ped.v. view of conjoined valves, ×1;*3b*, ped.v. int., ×1; *3c*, brach.v. int., ×2 (189).

Subfamily LEPTAENOIDEINAE Williams, 1953

[Leptaenoideinae WILLIAMS, 1953, p. 8]

Parvicostellate, attached to foreign body by cementation of umbonal area of pedicle valve; shell substance coarsely pseudopunctate. *U.Sil.-L.Dev.*

Leptaenoidea HEDSTRÖM, 1917, p. 2 [**L. silurica*; OD]. Finely costellate, plano-convex; pedicle valve with short broad muscle scar, adductors borne on median ridge; interior of brachial valve unknown. *U.Sil.(Wenlock)*, Eu.——FIG. 250,*1*. **L.* sp. aff. *L. silurica*, Sweden; ped.v. int., ×4 (Williams, n).

Leptaenisca BEECHER, 1890, p. 239 [**Leptaena concava* HALL, 1857, p. 47; SD HALL & CLARKE, 1892, p. 300]. Unequally parvicostellate, concavo-convex, attached in young stages of growth only. Ventral muscle field longer than that of *Leptaenoidea*; dorsal interior bearing a par of planospiral ridges. *U.Sil.-L.Dev.*, N.Am.——FIG. 250,*4a-c*. **L. concava* (HALL), L.Dev.(Haragan), USA(Okla.); *4a,b*, int., lat. views of brach.v. int., ×1.5; *4c*, ped.v. ext., ×1.5 (Cooper, n).——FIG. 250,*4d*. *L.* sp. cf. *L. concava* (HALL); *4d*, brach.v. int., ×4 (Williams, n).

Family FOLIOMENIDAE Williams, n. fam.

Plano-convex, lacking radial ornamentation; condition of apical foramen unknown, pseudodeltidium and chilidium well developed. Teeth simple, unsupported; ventral muscle field bilobed, with divergent diductors separated medianly by short median ridge and completely enclosing posteriorly located adductor scars; socket ridges subparallel with hinge line; submedian trans-muscle septa strong, median ridge faint; ventral mantle canal system probably digitate with divergent *vascula media*. *U.Ord.*

Foliomena HAVLÍČEK, 1952, p. 17 [**Strophomena folium* BARRANDE, 1879, p. 55, figs. 11-13; OD]. Transversely semioval in outline, shell surface ornamented by impersistent concentric rugae. *U. Ord.*, Czech.——FIG. 251,*2*. **F. folium* (BARRANDE); *2a,b*, brach.v. ext. and int., ×3; *2c*, ped. v. int., ×3 (Havlíček, n).

Family CHRISTIANIIDAE Williams, 1953

[Christianiidae WILLIAMS, 1953, p. 9]

Pseudodeltidium and chilidium, well developed, apical foramen persistent throughout ontogeny; some early species possibly impunctate, majority coarsely pseudopunctate. Teeth simple, supported by receding dental plates; ventral muscle field transversely bilobed; brachial valve with strong socket ridges and pair of long, discrete U-shaped ridges, presumably comprising supports for schizolophous lophophore; mantle-canal pattern digitate. *Ord.*

Christiania HALL & CLARKE, 1892, p. 298 [**Leptaena subquadrata* HALL, 1883, pl. 46, figs. 32, 33; OD]. Elongately oval in outline, smooth or with faint fine costellae. Dorsal muscle field defined within posterior parts of loops either by obliquely or transversely directed ridges. *Ord.*, N.Hemis.——FIG. 251,*1*. **C. subquadrata* (HALL), M.Ord.(Porterfield), USA(Appalach.); *1a*, brach. v. view of conioined valves, ×2; *1b,c*, int., post., views of brach.v. ×2; *1d,e*, int., post. views of ped.v., ×2 (189).

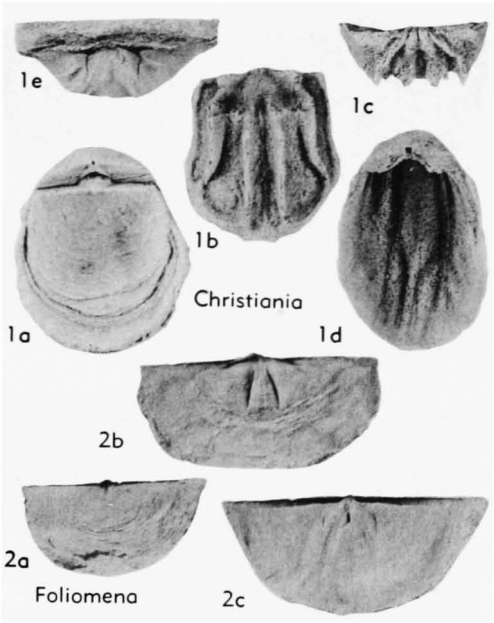

FIG. 251. Foliomenidae *(2)*; Christianiidae *(1)* (p. *H*390-*H*391).

Family LEPTAENIDAE Hall & Clarke, 1894

[Leptaenidae HALL & CLARKE, 1894, p. 354]

Concavo-convex to biconvex, with variably developed geniculation directed dorsally or (rarely) ventrally; concentric rugae almost invariably present on disc; apical foramen large, persistent throughout ontogeny or rarely plugged by secondary shell, pseudodeltidium commonly present but exceptionally resorbed in adult shells, chilidium well developed. Teeth simple, supported by receding dental plates, ventral muscle scar suboval to subcircular with strong bounding ridges; cardinal process lobes strong and with socket ridges, supported by anchor-shaped extension of notothyrial platform embracing posterior ends of dorsal adductor scars; trans-muscle septa variably developed; mantle canal systems saccate to lemniscate; shell substance coarsely pseudopunctate. *M.Ord.-L.Carb.*

Leptaena DALMAN, 1828, p. 93 [**L. rugosa* DALMAN, 1828; SD KING, 1846, p. 28] [=*Leptaenella* FREDERIKS, 1917, p. 89 (type, *Leptaena rhomboidalis ventricosa* HALL) (*non* SARYCHEVA & SOKOLSKAYA, 1952); *Leptaenulopsis* HAUPT, 1878, p. 59 (type, indeterminate young *Leptaena*)].

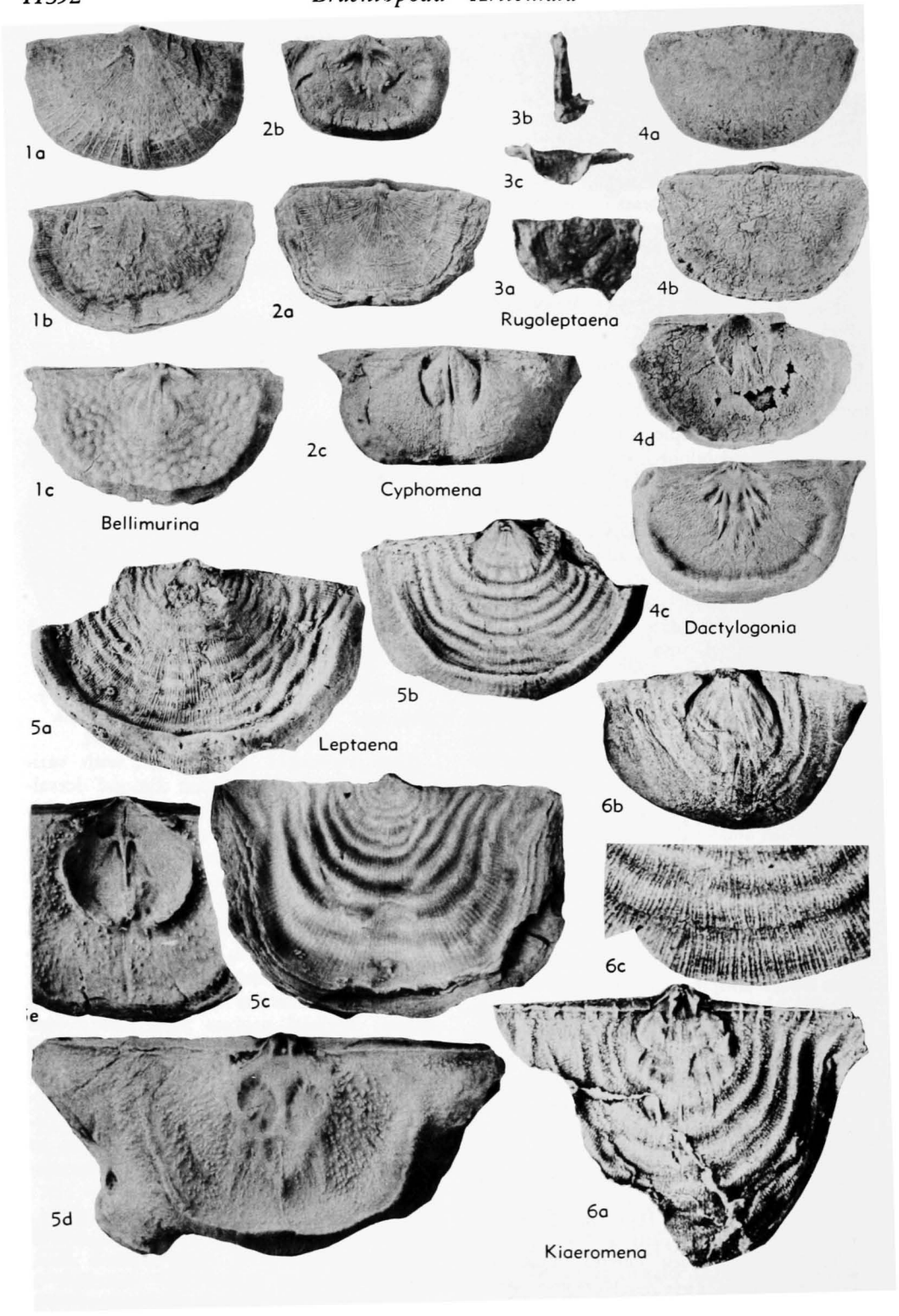

FIG. 252. Leptaenidae (p. *H*391, *H*393-*H*394).

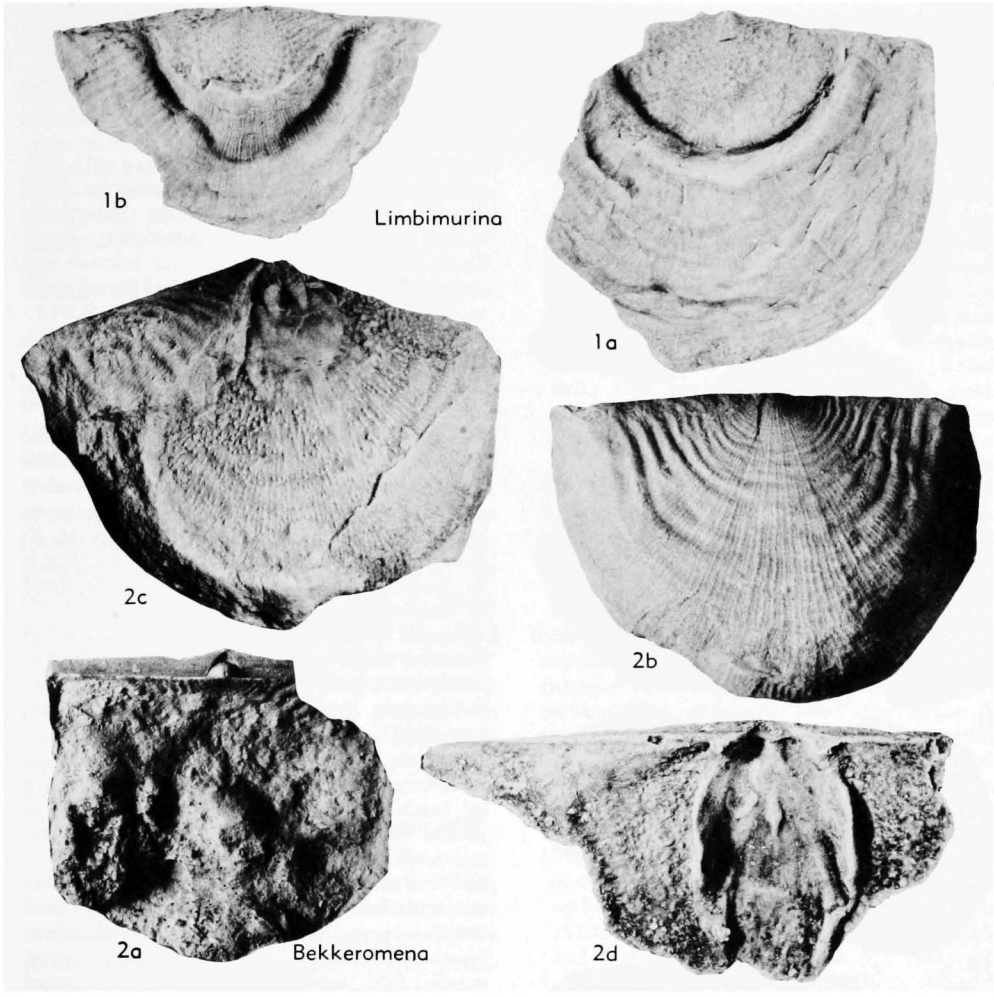

FIG. 253. Leptaenidae (p. *H*391, *H*393-*H*394).

Sharply geniculate with narrow ventrally projecting ridge separating disc from trail; finely and evenly costellate, concentric rugae strong; pseudodeltidium present or resorbed. Teeth smooth or crenulated, ventral muscle scar suboval to subcircular surrounded by ridges; dorsal trans-muscle septa including variably developed median septum, 2 long, curved submedian septa and 2 shorter, lateral septa. *M.Ord.-Dev.*, cosmop. ——FIG. 252,*5a,b*. **L. rugosa*, U.Ord., Sweden; *5a,b*, brach.v. ext., ped.v. int. mold, ×1.5 (Williams, n).——FIG. 252,*5c-e*. *L. rhomboidalis* (WILCKENS), U.Sil., Eng.; *5c*, brach.v. ext., ×1.5; *5d,e*, brach.v. and ped.v. int., ×1.5 (Williams, n).

Bekkeromena RÕÕMUSOKS, 1963, p. 235 [**Strophomena semipartita* ROEMER, 1861, pl. 1, figs. 5-9, text-figs. 2-3; OD]. Like *Leptaena* but with unequally parvicostellate ornamentation, elongately subquadrate ventral muscle field, rounded geniculation without ventrally projecting ridge, and without trans-muscle septa. *U.Ord., E.Eu.*——FIG. 253,*2*. **B. semipartita* (ROEMER), Flab-d, Est.; *2a*, brach.v. view of conjoined valves, ×1.5; *2b,c*, ped.v. ext., brach.v. int., ×1.5; *2d*, ped.v. int., ×2 (RÕÕMUSOKS, n).

Bellimurina COOPER, 1956, p. 854 [**Leptaena charlottae* WINCHELL & SCHUCHERT, 1892, p. 288; OD]. Gently geniculate in dorsal direction, unequally parvicostellate with stronger costellae breaking up rugae into short zigzag sets. Ventral muscle scar short and wide; trans-muscle septa variably developed. *M.Ord.*, N.Am.-Eu.——FIG. 252,1. **B. charlottae* (WINCHELL & SCHUCHERT), Wilderness, USA (Minn.); *1a,b*, ped.v. and brach.v. views of conjoined valves, ×2; *1c*, brach.v. int., ×2 (189).

Cyphomena COOPER, 1956, p. 840 [**Leptaena homostriata* BUTTS, 1942, p. 110; OD]. Sharply geniculate in dorsal direction, finely costellate, impersistent rugae developed only posterolaterally;

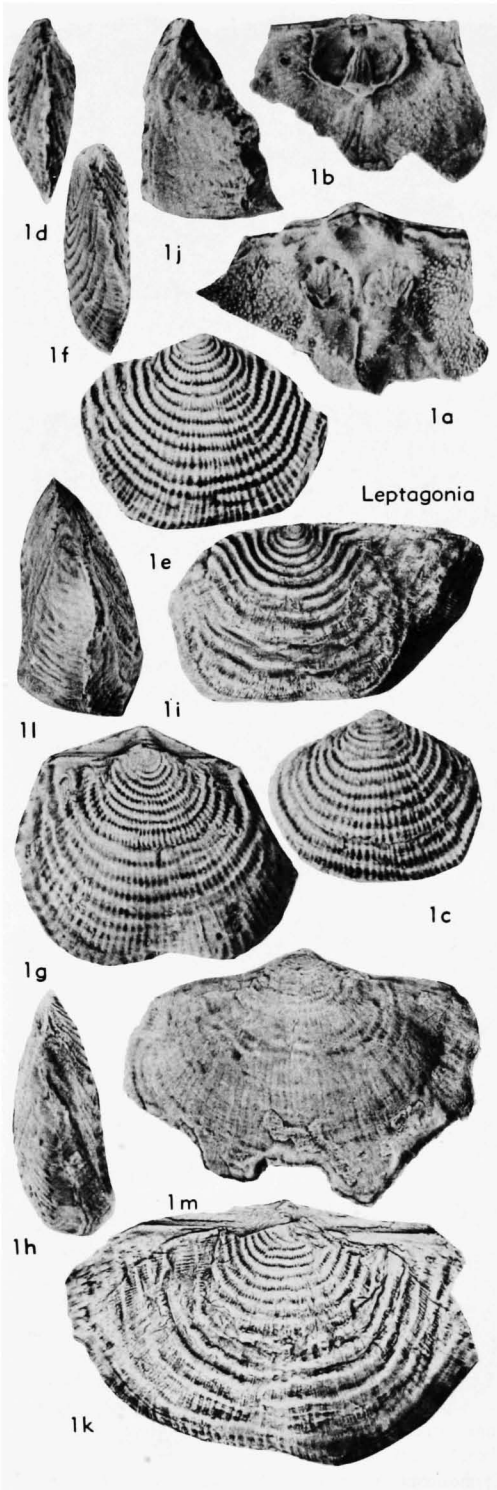

FIG. 254. Leptaenidae (p. *H*394).

ventral muscle scar small, elongately oval; trans-muscle septa strong. *M.Ord.*, USA-Scot.——FIG. 252,*2*. *C. angulata* (COOPER), Porterfield, Va. (*2a*), Pa. (*2b*), Md. (*2c*); *2a*, brach. v. view of conjoined valves, ×2; *2b*, brach.v. int., ×2; *2c*, ped.v. int. mold, ×3 (189).

Dactylogonia ULRICH & COOPER, 1942, p. 623 [**D. geniculata;* OD]. Sharply geniculated in dorsal direction, unequally parvicostellate, impersistent rugae posterolaterally, pseudodeltidium large. Teeth smooth, ventral muscle scar suboval normally with strong bounding ridges; dorsal trans-muscle septa well developed. *M.Ord.*, E.USA.-Scot.——FIG. 252,*4*. **D. geniculata*, Porterfield, USA(Tenn.); *4a,b*, ped.v. and brach.v. views of conjoined valves, ×2; *4c,d*, brach.v. and ped.v. int., ×2 (189).

Kiaeromena SPJELDNAES, 1957, p. 183 [**Leptaena kjerulfi* HOLTEDAHL, 1916, p. 72; OD]. Like *Bekkeromena* but with subcircular ventral muscle field and weakly developed trans-muscle septa. *M.Ord.-U.Ord.* Eu.——FIG. 252,*6*. *K.* sp. cf. *K. kjerulfi* (HOLTEDAHL), M.Ord.(4bβ), Eu.(Nor.); *6a*, brach.v. int., ×3; *6b*, ped.v. int., 2; *6c*, detail of ornamentation, ×4 (Williams, n).

Leptagonia M'COY, 1844, p. 116 [**Producta analoga* PHILLIPS, 1836, p. 215; SD SCHUCHERT & LEVENE, 1929, p. 74] [=*Pseudoleptaena* WILLIAMS, herein (*pro Leptaenella* SARYCHEVA & SOKOLSKAYA, 1952, *non* FREDERIKS, 1917)]. Initially biconvex through resupination but with biconvexity accentuated in adult shells by ventral geniculation in brachial valve and dorsal geniculation in pedicle valve to give shelflike anterior margin commonly indented medianly or even laterally, and less commonly prolonged dorsally as a narrow trail; finely costellate, rarely with accentuated costellae, concentric rugae strong; pseudodeltidium present or resorbed. Teeth crenulated, ventral muscle field subcircular, impressed on raised cup of secondary shell suported by median ridge; dorsal adductor field impressed posteriorly on subtriangular elevation culminating in high median septum. *L.Carb.*, Eurasia.——FIG. 254,*1*. **L. analoga* (PHILLIPS), Carb., Wales; *1a,b*, fragments of brach.v. and ped.v. ints., ×1.5; *1c,d*, ped.v. ext., lat., ×1.5; *1e,f*, ped.v. ext. lat., ×1.5; *1g,h*, brach.v. ext., lat., ×1.5; *1i,j*, ped.v. ext., lat., ×1; *1k,l*, brach.v. ext., lat. ×1; *1m*, brach.v. ext., ×1, views of 6 complete specimens (Williams, n).

Limbimurina COOPER, 1956, p. 851 [**L. insueta;* OD]. Ventrally directed ridge surrounding disc greatly exaggerated to give ventral, then dorsal direction to geniculation; surface ornamentation like that of *Bellimurina;* interiors like those of *Leptaena*. *M.Ord.*, USA.——FIG. 253,*1*. **L. insueta*, Wilderness, USA(Penn.); *1a,b;* ped.v. and brach.v. ext., ×2 (189).

Notoleptaena GILL, 1951, p. 191 [**N. linguifera;* OD]. Like *Leptaena* but geniculate in ventral direction and with anteromedian zone of ventral

trail projecting dorsally to fit into deep, complementary incision in brachial valve. *L.Dev.*, Australia.

Rugoleptaena HAVLÍČEK, 1956, p. 24 [**Rugoleptaena hornyi;* OD]. Like *Notoleptaena* but with anteromedian parts of both ventral and dorsal trails deflected dorsally as tongue. *U.-Sil-L.Dev.*, Eu.——FIG. 252,*3*. *R. emarginata* (BARRANDE), U.Sil., Pol.; *3a-c*, brach.v. ext., lat., ant. views of brach.v., ×1 (487).

Family STROPHEODONTIDAE Caster, 1939

[Stropheodontidae CASTER, 1939, p. 26]

Lacking functional pedicle and with simple teeth and dental plates replaced by denticles subsequently spreading along hinge line; socket ridges abbreviated subsequent to loss of dental plates becoming obsolescent or disappearing completely, exceptionally forming buttresses to cardinal process lobes; pseudodeltidium initially small, apical, becoming progressively larger and in some stocks ultimately closing delthyrium completely; chilidium initially massive becoming degenerate and in some stocks ultimately completely lost; mantle canal patterns in both valves probably lemniscate; shell substance densely pseudopunctate. *U.Ord.-U. Dev.*

Subfamily STROPHEODONTINAE Caster, 1939

[Stropheodontinae CASTER, 1939, p. 28]

Unattached, concavo-convex or resupinate, with parvicostellate radial ornamentation commonly modified or even supplanted by secondary plicate or costellate patterns, concentric rugae rare; ventral muscle scar subcircular to subquadrate; dorsal adductor scars commonly impressed on elevated platforms in late stocks. *U.Ord.-U.Dev.*

Strophodonta HALL, 1850, p. 348 [**Leptaena demissa* CONRAD, 1842, p. 258; OD] [=*Stropheodonta* HALL, 1852, p. 63 *(nom. van.)*]. Concavo-convex, ventral muscle field elongately oval, with diductor scars anterolateral to lanceolate adductor scar. *U.Ord.-U.Dev.*, cosmop.

S. (Strophodonta). Finely costellate, also secondarily ornamented by plicae or costellae; pseudodeltidium complete, no chilidium; no dental plates, socket-ridge obsolescent; strong muscle scars. *Dev.*, cosmop.——FIG. 255,*4*. *S. (S.)* sp. aff. *S. (S.) demissa* (CONRAD), M.Dev., USA (Mich.); *4a,b*, ped.v. ext., ×2, ×1.5; *4c,d*, ped.v. and brach.v. int., ×1.5 (871).

S. (Brachyprion) SHALER, 1865, p. 63 [**Strophomena leda* BILLINGS, 1860, p. 55; OD]. Parvicostellate; delthyrium progressively closed by pseudodeltidium, chilidium degenerate; no dental plates, socket ridges abbreviated. *L.Sil.-L.Dev.*, cosmop.——FIG. 255,*1*. *S. (B.)* sp., L.Dev.(Haragan), USA(Okla.); *1a,b*, ped.v. int. and ext., ×1.5; *1c*, brach. v. int., ×1.5 (871).

S. (Eostropheodonta) BANCROFT, 1949, p. 9 [**Orthis hirnantensis* M'COY, 1851, p. 395; OD]. Finely parvicostellate to fascicostellate; delthyrium open, chilidium massive; dental plates short, socket ridges strong; muscle scars faint. *U.Ord.-L.Sil.*, Eu.——FIG. 255,*3a-c*. **S. (E.) hirnantensis* (M'COY), U.Ord.(Ashgill.), Wales; *3a*, ped. v. int. mold, ×2.5; brach.v. int., ×3; *3c*, ped.v. ext., ×1.5 (Williams, n).——FIG. 255,*3d,e*. *S. (E.) siluriana* (DAVIDSON), U.Ord., Br.I.; *3d,e*, brach.v. ext. and ped.v. int. molds, ×2.5, ×10 (conical mold of hollow between expanded tooth and dental plate figured on left of ped.v. umbonal mold removed on right to show denticulate nature of both tooth and plate) (870).

S. (Rhenostrophia) BOUCOT, 1960, p. 483 [**Orthis subarchnoidea* D'ARCHIAC & DE VERNEUIL, 1842, p. 372; OD]. Like *S. (Strophodonta)* but strongly geniculate in dorsal direction. *L.Dev.*, E.Can.-Eu.

Cymostrophia CASTER, 1939, p. 48 [**Leptaena stephani* BARRANDE, 1879, p. 308; OD] [=*Corrugatella* KHALFIN, 1948, p. 236 (obj.)]. Finely parvicostellate segregated into wide sectors by strongly developed costellae that also interrupt close concentric rugation; ventral muscle field subcircular with well-developed posterolateral ridges; dorsal interior unknown. *U.Sil.-L.Dev.*, N.Hemis.

C. (Cymostrophia). Pseudodeltidium almost complete, with slight median fold, hinge line almost entirely denticulate. *L. Dev.*, N.Hemis.——FIG. 255,*2*. **C. (C.) stephani* (BARRANDE), Czech.; *2a,b*, ped.v. ext. and int. mold, ×1 (871).

C. (Idioglyptus) NORTHROP, 1939, p. 172 [**I. stigmatus;* OD] [=*Pioglyptus* ST. JOSEPH, 1941, p. 8 *(nom. null.)*]. Hinge line denticulate for less than half of its length; interiors unknown. *U.Sil.*, E.N.Am.

Megastrophia CASTER, 1939, p. 36 [**Strophomena (Strophodonta) concava* HALL, 1857, p. 140; OD] [=*Dictyostrophia* CASTER, 1939, p. 40 (type, *D. cooperi*)]. Large concavo-convex, unequally parvicostellate. Ventral muscle field transversely oval, diductor scars lying laterally to adductor. *Sil.-M.Dev.*, N.Hemis.

M. (Megastrophia). Pseudodeltidium entire but with sharp median fold, chilidium vestigial. Dorsal adductor scars borne on foliaceous platforms. *M.Dev.*, N.Hemis.——FIG. 255,*5*. *M. (M.)* sp. aff. **M. (M.) concava* (HALL), USA (N.Y.); *5a*, brach.v. view of conjoined valves, ×1; *5b*, ped.v. int., ×1; *5c*, brach.v. int., ×1.5 (871).

M. (Protomegastrophia) CASTER, 1939, p. 36 [**Leptaena profunda* HALL, 1852, p. 61; OD]. Pseudodeltidium progressively developed but not

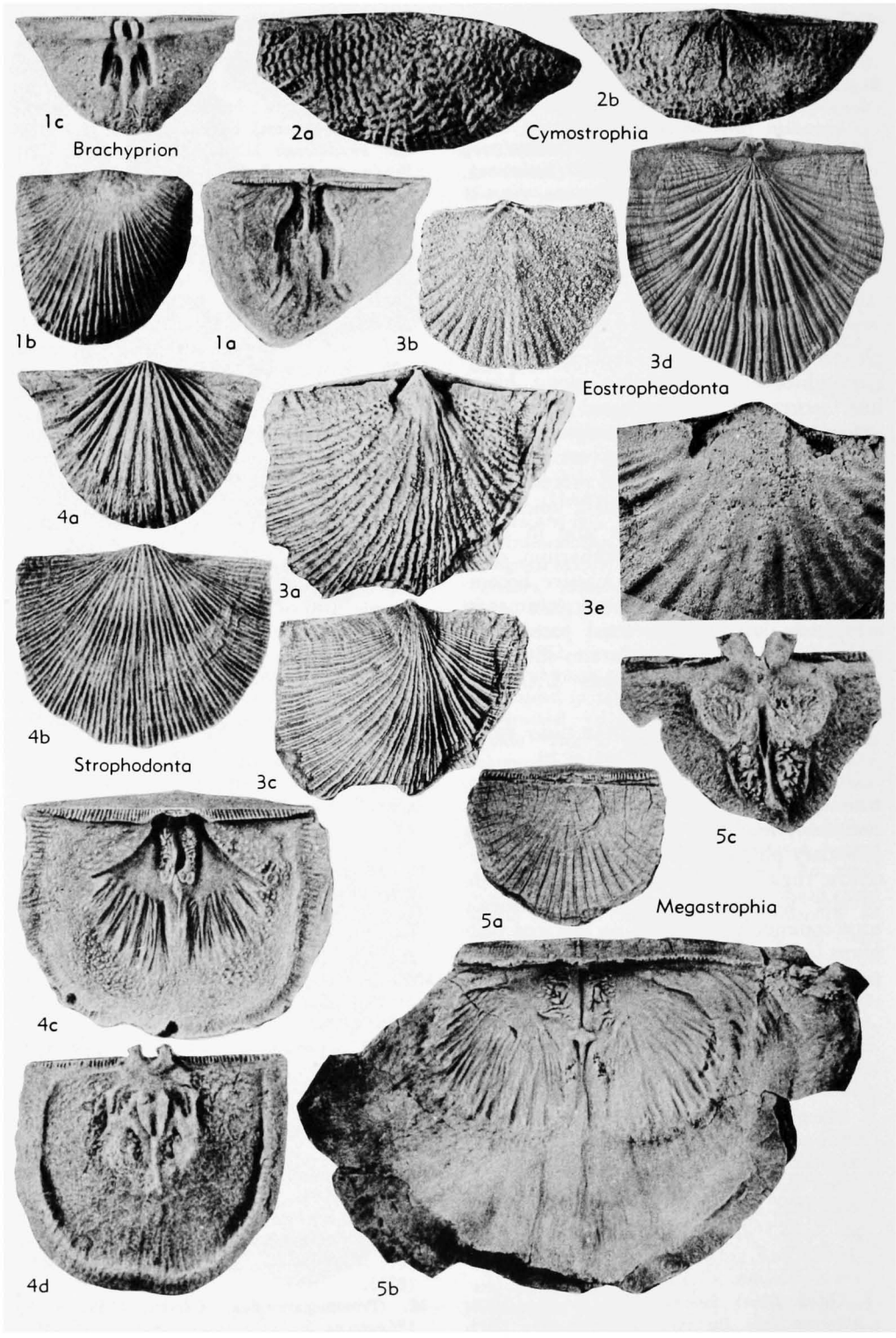

FIG. 255. Stropheodontidae (Stropheodontinae) (p. *H*395).

completely filling delthyrium, chilidium strong to obsolescent. Dorsal adductor scars faintly impressed on valve floor. *L.Sil.-L.Dev.*, Eu.-N.Am. ——Fig. 256,*4*. **M. (P.) profunda* (Hall), M.Sil.(Racine), USA(Wis.); *4a*, ped.v. int. mold, ×1; *4b*, brach.v. int. mold, ×1.5 (871).

Plicostropheodonta Sokolskaya, 1960, p. 214 [**Orthis murchisoni* D'Archiac & de Verneuil, 1842, p. 371; OD]. Like *Megastrophia (Megastrophia)* but with secondary ornament of strong coarse costae and subperipheral rim in brachial valve. *L.Dev.-M.Dev.*, Eurasia-N.Afr.

Radiomena Havlíček, 1962, p. 471 [**Orthis irregularis* Roemer, 1844, p. 75; OD]. Like *Megastrophia (Megastrophia)* but strongly geniculate in dorsal direction and with accentuated

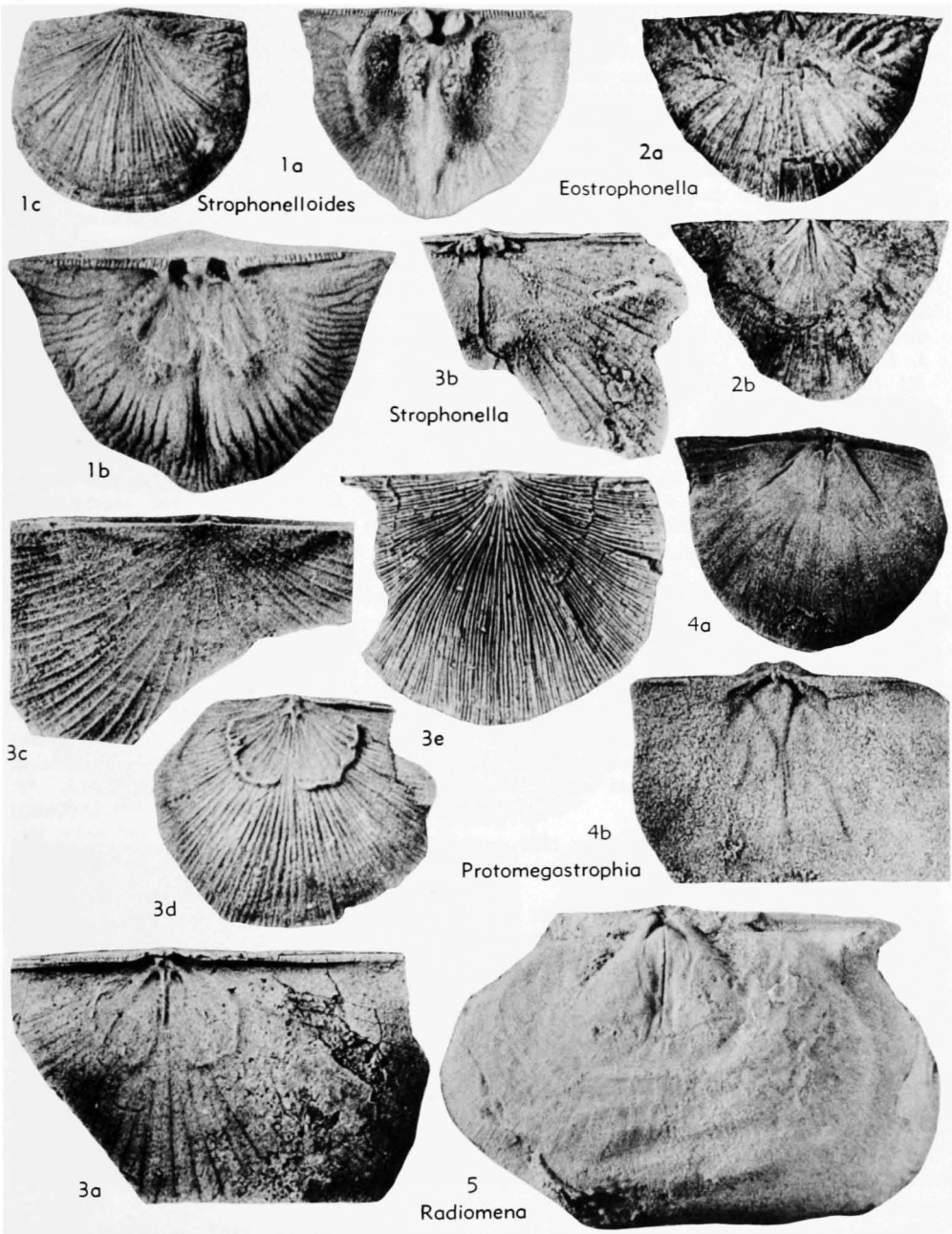

Fig. 256. Stropheodontidae (Stropheodontinae) (p. *H*395, *H*397-*H*398).

costellae dying away on trail to give undifferentiated parvicostellate ornamentation anteriorly; pseudodeltidium without median fold. *M.Dev.*, C.Eu.——FIG. 256,*5*. **R. irregularis* (ROEMER); ped.v. int. mold, ×1 (Havlíček, n.).

Strophonella HALL, 1879, p. 153 [**Strophomena semifasciata* HALL, 1863, p. 210; SD HALL & CLARKE, 1892, p. 291] [=*Strophoprion* TWENHOFEL, 1914, p. 25 (type, *Brachyprion geniculatum* SHALER, 1865, p. 63)]. Resupinate, radial ornament unequally parvicostellate with superimposed secondary costellation in some late stocks, rugae impersistent posterolaterally; pseudodeltidium progressively degenerate; ventral muscle scar subcircular to subquadrate. *L.Sil.-L.Dev.*, N.Hemis.

S. (Strophonella). Pedicle valve without dental plates, ventral muscle scar subquadrate, bounded laterally and anteriorly by low interrupted ridges with petaloid appearance. *U.Sil.-L.Dev.*, N.Hemis.——FIG. 256,*3a-c*. **S. (S.) semifasciata* (HALL), U.Sil., USA(Tenn.); *3a,b,* ped.v. and brach.v. int., ×1.5; *3c,* brach.v. view of incomplete shell, ×1.5 (871).——FIG. 256,*3d*. *S. (S.)* sp., L.Dev., USA(Tenn.); ped.v. int., ×1 (871).——FIG. 256,*3e*. *S. (S.)* sp. cf. *S. (S.) cavumbona* (HALL), L.Dev., USA(Tenn.); brach.v. ext., ×1 (871).

S. (Eostrophonella) WILLIAMS, 1950, p. 281 [**Strophonella davidsoni* HOLTEDAHL, 1916, p. 64; OD]. Pedicle valve with dental plates; ventral muscle scar subcircular. *L.Sil.*, Eu.——FIG. 256,*2*. *S. (E.) eothen* (BANCROFT), L.Sil., Wales; *2a,b,* brach.v. and ped.v. int. mold, ×1 (871).

Strophonelloides CASTER, 1939, p. 106 [**Strophodonta reversa* CALVIN, 1878, p. 728; OD] [=*Chemungia* CASTER, 1939, p. 106 (type, *Strophodonta caelata* HALL, 1867, p. 112)]. Like *S. (Strophodonta)* but resupinate. *U.Dev.*, N.Am.——FIG. 256,*1*. **S. reversa* (CALVIN), Cerro Gordo, USA(Iowa); *1a,b,* brach.v. and ped.v. int., ×1; *1c,* brach.v. view of conjoined valves, ×1 (871).

Subfamily LEPTOSTROPHIINAE Caster, 1939

[*nom. transl.* WILLIAMS, herein (*ex* tribe Leptostrophiini CASTER, 1939, p. 73)]

Unattached, concavo-convex, biplanate or rarely resupinate, with costellate to unequally parvicostellate radial ornamentation, less commonly broken at irregular intervals to give subspinose (nervate) appearance; rugae impersistent posterolaterally or rarely concentric. Ventral muscle scar subtriangular and commonly splayed; dorsal adductor scars impressed on floor of brachial valve with variably developed posterolateral bounding ridges. *L.Sil.-U.Dev.*

Leptostrophia HALL & CLARKE, 1892, p. 288 [**Stropheodonta magnifica* HALL, 1857, p. 54; OD] [=*Rhytistrophia* CASTER, 1939, p. 86 (type, *Stropheodonta beckii* HALL, 1859, p. 191)]. Gently concavo-convex to biplanate, parvicostellate, subdued concentric rugae generally present posterolaterally and rarely covering entire shell; pseudodeltidium never complete, chilidium becoming degenerate. Socket ridges initially widely divergent, later adjacent to cardinal process lobes. *Sil.-Dev.*, cosmop.——FIG. 257,*6*. *L.* sp., *L.Dev.*, USA(Tenn.); *6a,* brach.v. int., ×1.5; *6b,* ped.v. int., ×2 (Williams, n).

Gamphalosia STAINBROOK, 1946, p . 33 [**G. tenuissima;* OD]. Like *Nervostrophia* but resupinate. *U.Dev.*, N.Am.(Iowa).

Maoristrophia ALLAN, 1947, p. 440 [**M. neozelanica;* OD]. Costellate, plano-subconvex, with narrow median fold in pedicle valve, hinge line incompletely denticulate. Ventral muscle scar subtriangular; socket ridges short, stout, dorsal median ridge flanked anteriorly by pair of low curved ridges. *L.Dev.*, N.Z.——FIG. 257,*5*. **M. neozelanica; 5a-c,* rubber casts of brach.v. int., brach.v. ext., ped.v. int., ×1 (27).

Nervostrophia CASTER, 1939, p. 79 [**Strophomena nervosa* HALL, 1843, p. 266; OD] [=*Sulcatostrophia* CASTER, 1939, p. 81 (type, *Leptostrophia camerata* FENTON & FENTON, 1924, p. 96); *Pseudodouvillina* STAINBROOK, 1945, p. 26 (type, *P. euglyphea*)]. Concavo-convex, rarely sulcate, unequally parvicostellate with stronger costellae irregularly broken into several short lengths (nervate); pseudodeltidium complete, with or without median fold, chilidium vestigial or absent. Socket ridges parallel to sides of cardinal process lobes and fused with them. *M.Dev.-U.Dev.*, cosmop.——FIG. 257,*3*. *N. rockfordensis* (FENTON & FENTON), *U.Dev.*, USA(Iowa); *3a,* brach.v. int., ×2; *3b,* ped.v. ext., ×1; *3c,* ped.v. int., ×1.5 (871).

Protoleptostrophia CASTER, 1939, p. 75 [**Strophomena blainvillii* BILLINGS, 1874, p. 28; OD]. Like *Leptostrophia* but without socket ridges in brachial valve. *M.Dev.*, N.Am.——FIG. 257,*1a,b*. **P. blainvillii* (BILLINGS), Silica Sh., USA(Ohio); *1a,b,* plasticene casts of brach.v. and ped.v. int., ×1 (871).——FIG. 257,*1c*. *P.* sp., Silica Sh., USA(Ohio); *1c,* ped.v. ext., ×1 (871).

Subfamily DOUVILLININAE Caster, 1939

[*nom. transl.* WILLIAMS, herein (*ex* tribe Douvillinini CASTER, 1939, p. 70)]

Unattached concavo-convex to resupinate, with unequally parvicostellate radial ornamentation. Ventral muscle scar suboval to transversely subquadrate, with well-developed bounding ridges; socket ridges short to obsolescent, dorsal adductor scars variably impressed on floor of brachial valve posterior to pair of narrowly divergent ridges. *U.Sil.-U.Dev.*

Douvillina OEHLERT, 1887, p. 1282 [**Orthis dutertrei* MURCHISON, 1839, p. 253; OD]. Con-

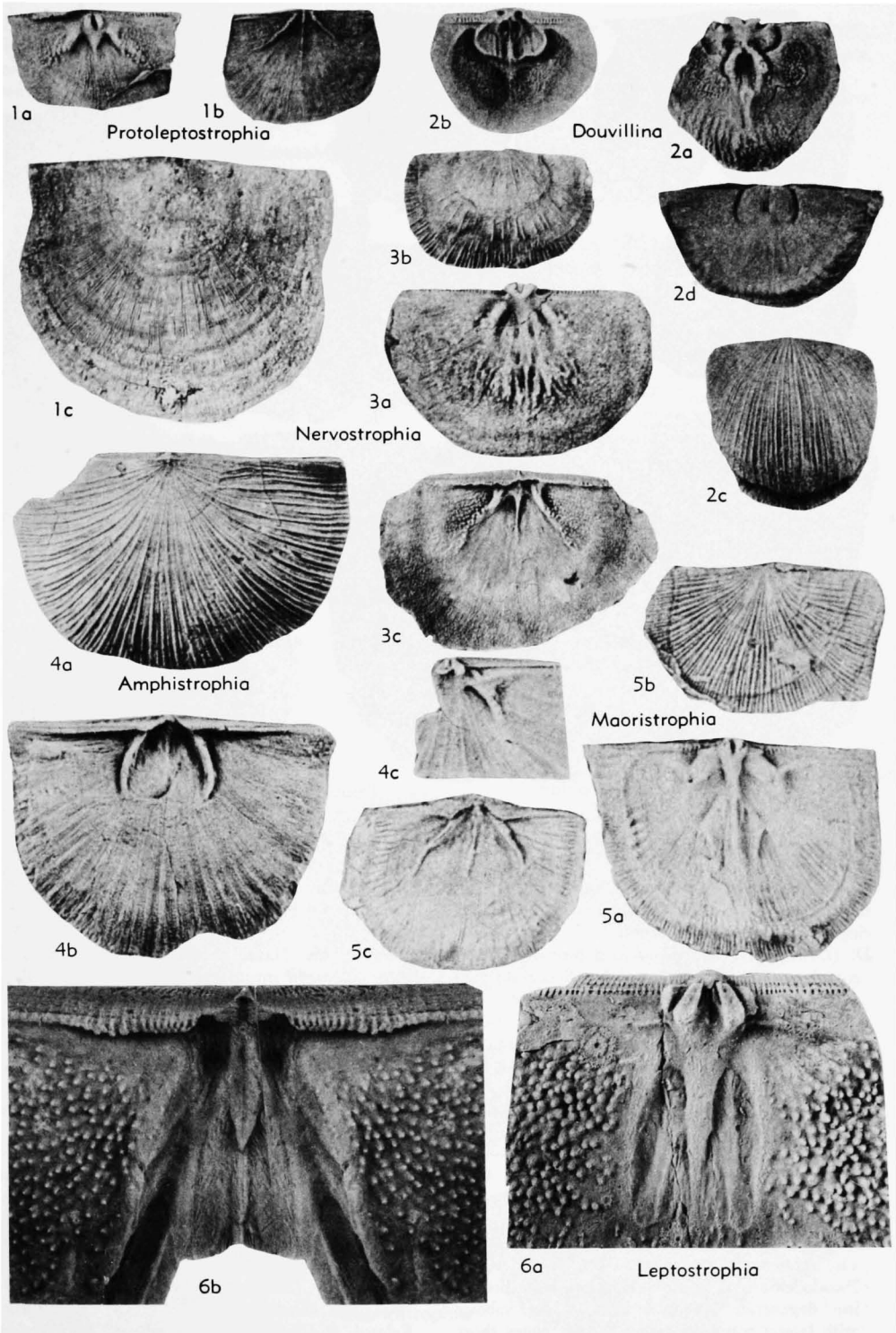

FIG. 257. Stropheodontidae (Leptostrophiinae) *(1, 3, 5, 6)*, (Douvillininae) *(2, 4)* (p. *H*398, *H*400).

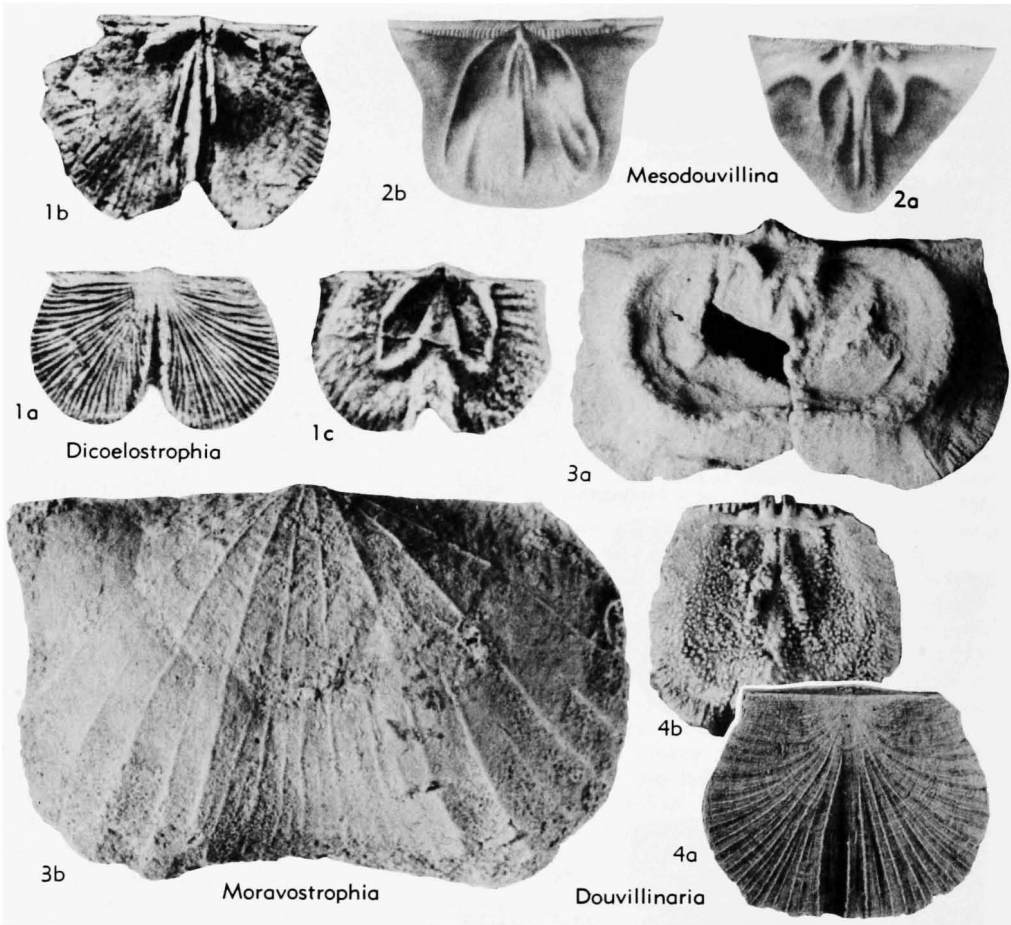

FIG. 258. Stropheodontidae (Douvillininae) (p. *H*400-*H*401).

cavo-convex, unequally parvicostellate. Ventral muscle scar ultimately completely bounded by ridges. *U.Sil.-U.Dev.*, N.Hemis.

D. (Douvillina). Medianly folded pseudodeltidium complete, chilidium vestigial. Socket ridges obsolescent; ventral muscle scar transversely subquadrate, bounded anteriorly by raised ridges commonly to form a raised cup; ridges anterior to dorsal adductor scars, tuberculate, strong, and curving toward each other. *Dev.*, N.Hemis.——FIG. 257,*2a-c*. *D. (D.) arcuata* (HALL), U.Dev.-(Hackberry), USA(Iowa); *2a-c*, brach.v. int., ped.v. int., ped.v. ext., ×1.5 (871).——FIG. 257,*2d*. *D. (D.)* sp., M.Dev.(Hamilton), USA (Va.), *2d*, ped.v. int. mold, ×1 (871).

D. (Mesodouvillina) WILLIAMS, 1950, p. 281 [**Stropheodonta (Brachyprion) subinterstrialis* var. *seretensis* KOZLOWSKI, 1929, p. 97; OD]. Pseudodeltidium incomplete, chilidium becoming degenerate. Ventral muscle scar suboval with lateral bounding ridges; socket plates short, ridges anterior to dorsal adductor scars low. *U.Sil.*, N.Hemis.——FIG. 258,*2*. **D* (*M.*) *subinterstrialis seretensis* (KOZLOWSKI), U.Sil. (Czortkov), Pol.; *2a,b*, brach.v. int., ped.v. int., ×2 (487).

Amphistrophia HALL & CLARKE, 1892, p. 292 [**Strophomena striata* HALL, 1843, p. 104; OD]. Resupinate, with incompletely developed pseudodeltidium and massive chilidium. Ventral muscle scar suboval, bounded by strong, curved lateral ridges. *U.Sil.*, cosmop.——FIG. 257,*4*. **A. striata* (HALL), Waldron, USA(Ind.); *4a-c*, brach.v. view of conjoined valves, ped.v. int., incomplete brach.v. int., ×2 (871).

Dicoelostrophia WANG, 1955, p. 350 [**D. punctatum*, OD]. Like *Douvillina (Douvillina)* but with resupinate, emarginate shell ornamented by branching costellae. *M.Dev.*, China.——FIG. 258,*1*. **D. punctata*; *1a*, ped.v. ext., ×1.5; *1b,c*, brach.v. int., ped.v. int., ×2 (852).

Douvillinaria STAINBROOK, 1946, p. 24 [**Stropheodonta variabilis* CALVIN, 1878, p. 727; OD]. Related to *Douvillina (Douvillina)* but having resupinate shell reverting in adult forms to concavo-convex habit. *U. Dev.*, N.Am.——FIG.

258,*4*. **D. variabilis* (CALVIN), USA(Iowa); *4a*, brach.v. view of conjoined valves, ×2; *4b*, brach.v. int., ×2 (Williams, n).

Douvillinella SPRIESTERSBACH, 1925, p. 432 [**Strophodonta filifer* SCHMIDT, 1912, p. 313; OD]. Like *Douvillina* (*Douvillina*) but resupinate. *M.Dev.-U.Dev.*, N.Hemis.

Moravostrophia HAVLÍČEK, 1962, p. 471 [**Stro-*

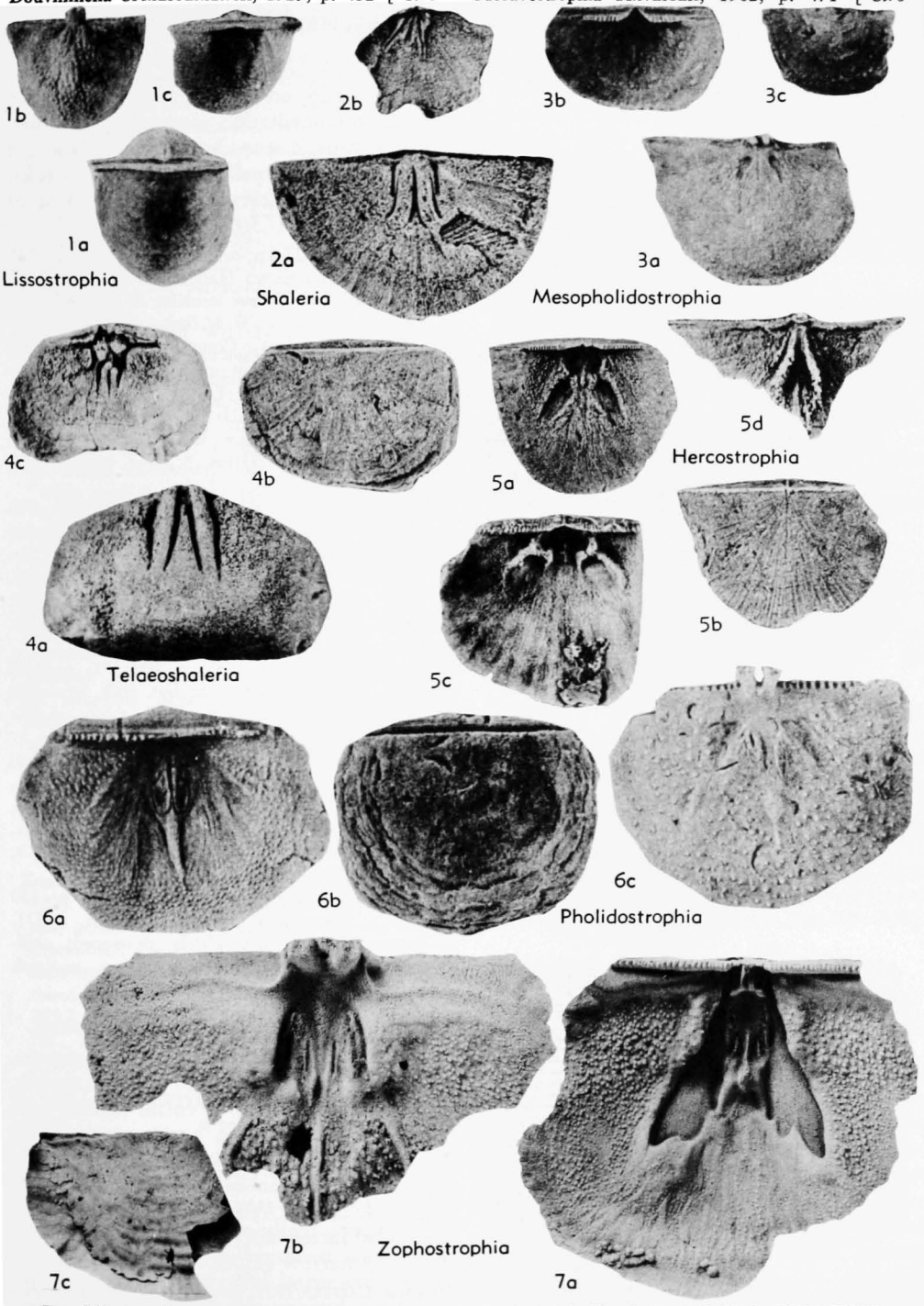

FIG. 259. Stropheodontidae (Pholidostrophiinae) *(1, 3, 6)*, (Shaleriinae) *(2, 4, 5, 7)* (p. *H*401-*H*403).

phomena interstrialis moravica SMYČKA, 1897, p. 41; OD]. Like *Douvillina (Douvillina)* but with widely spaced accentuated parvicostellae, high subperipheral rim, and short, anteriorly located, median septum in brachial valve. *M.Dev.*, Czech. ——FIG. 258,*3*. **M. moravica* (SMYČKA); *3a*, brach.v. int., ×2; *3b*, ped.v. ext., ×2 (Havlíček, n).

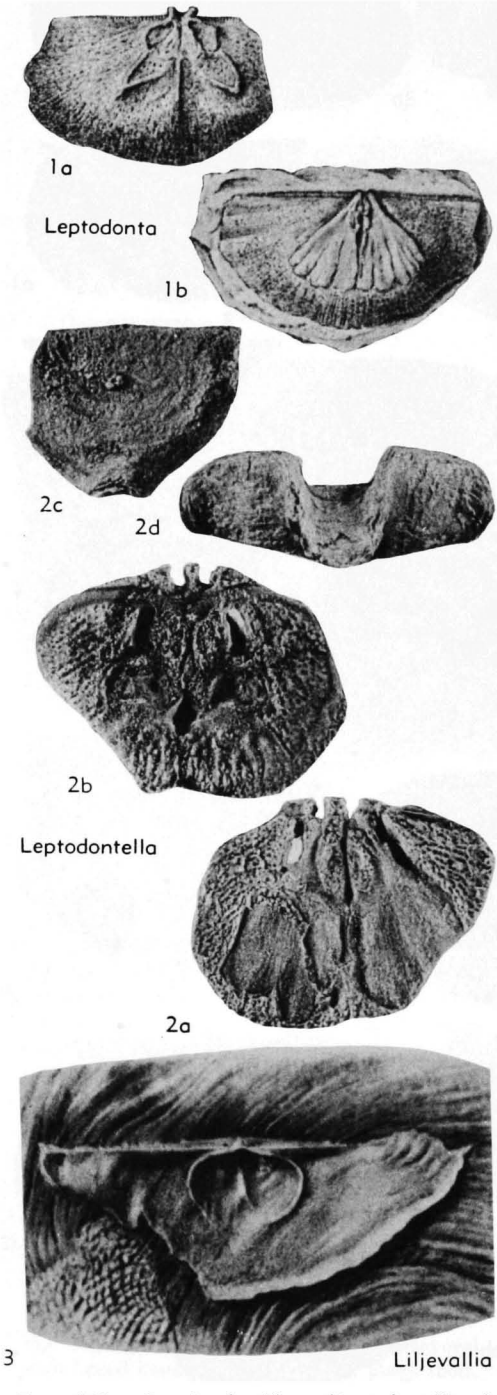

FIG. 260. Stropheodontidae (Leptodontellinae) *(1-2)*, (Liljevalliinae) *(3)* (p. *H*403).

Subfamily PHOLIDOSTROPHIINAE Stainbrook, 1943

[Pholidostrophiinae STAINBROOK, 1943, p. 44]

Unattached, concavo-convex, lacking any surface ornamentation except growth lines. Ventral muscle scar elongately oval; socket ridges initially small, lost in later stocks, dorsal adductor scars impressed on floor of brachial valve. *U.Sil.-M.Dev.*

Pholidostrophia HALL & CLARKE, 1892, p. 287 [**Strophomena nacrea* HALL, 1857, p. 144; OD]. Shell composed of thin lamellae of calcite giving nacreous sheen. *U.Sil.-M.Dev.*, N.Hemis.

P. (Pholidostrophia). Complete pseudodeltidium, no chilidium; socket ridges absent. *L.Dev.-M.Dev.*, N.Hemis.——FIG. 259,*6*. *P. (P.)* sp. aff. **P. (P.) nacrea* (HALL), M.Dev.(Hamilton), USA(N.Y.); *6a*, ped.v. int., ×2; *6b*, brach.v. view of conjoined valves, ×2; *6c*, brach.v. int., ×3 (871).

P. (Mesopholidostrophia) WILLIAMS, 1950, p. 278 [**P. (Mesopholidostrophia) nitens;* OD]. Pseudodeltidium incompletely developed, chilidium becoming degenerate, socket ridges abbreviated. *U.Sil.*, Eu.——FIG. 259,*3*. **P. (M.) nitens*, Gotl.; *3a,b*, brach.v. and ped.v. int., ×3; *3c*, ped.v. ext., ×2 (871).

Lissostrophia AMSDEN, 1949, p. 202 [**L. cooperi;* OD]. Like *Pholidostrophia* but with secondary layer of shell composed of fibrous calcite. *L.Sil.-L.Dev.*, N.Hemis.

L. (Lissostrophia). Complete pseudodeltidium; chilidium and socket ridges absent. *U.Sil.-L.Dev.*, N.Hemis.——FIG. 259,*1*. **L. (L.) cooperi*, U.Sil.(Henryhouse), USA(Okla.); *1a*, brach.v. view of conjoined valves, ×3; *1b,c*, brach.v. and ped.v. int., ×3 (871).

L. (Mesolissostrophia) WILLIAMS, 1950, p. 280 [**L. (Mesolissostrophia) pellucida;* OD]. Pseudodeltidium incompletely developed; chilidium and socket ridges becoming vestigial. *U.Sil.*, N.Hemis.

Subfamily SHALERIINAE Williams, n. subfam.

Unattached, concavo-convex to biplanate, with parvicostellate radial ornamentation, concentric rugae rare. Ventral muscle field including pair of long narrow, subparallel to divergent diductor scars, each bounded by more or less continuous ridges, rarely meeting above floor of valve to form narrow ring; dorsal adductor scars impressed posteriorly to 3 or 4 narrow ridges. *L.Sil.-Dev.*

Shaleria CASTER, 1939, p. 33 [**Strophomena gilpini* DAWSON, 1881, p. 341; OD] [=*Mclearnites*

CASTER, 1945, *pro Mclearnia* CASTER, 1939, p. 34 (type, *Brachyprion mertoni* MCLEARN, 1924, p. 61) *(non McLearnites* CRICKMAY, 1930)]. Concavo-convex, unequally parvicostellate. Ventral muscle scar bounded by pair of high lateral ridges and divided by bifurcated median ridge; socket ridges small, applied to sides of cardinal process lobes in late forms, dorsal adductor scar borne on 4 parallel ridges. *L.Sil-M.Dev.*, N.Hemis.

S. (Shaleria). Pseudodeltidium progressively developed but incomplete, chilidium progressively obsolescent; ventral muscle scar bounded by parallel lateral ridges and divided by median ridge which bifurcates at anterior end. *L.Sil.-L.Dev.*, N.Hemis.——FIG. 259,*2*. **S. (S.) gilpini* (DAWSON), U.Sil., N.Scot.; *2a*, ped.v. int. mold, ×2; *2b*, plasticene cast of brach.v. int., ×2 (871).

S. (Telaeoshaleria) WILLIAMS, 1950, p. 281 [**S. (Telaeoshaleria) sulcata;* OD]. Pseudodeltidium entire, folded medianly, chilidium vestigial. Ventral muscle scar divided into 2 narrow, divergent parts by median ridge which bifurcates anteriorly; in brachial valve outer pair of ridges obsolescent, inner pair fused posteriorly, short median ridge anterior of dorsal adductor scars. *M.Dev.*, Eu.——FIG. 259,*4*. **S. (T.) sulcata*, Ger.(Eifel); *4a*, ped.v. int. mold, ×2; *4b*, brach.v., view of conjoined valves, ×2; *4c*, brach.v. int. mold, × 1.5 (871).

Hercostrophia WILLIAMS, 1950, p. 277 [**H. alpenensis*; OD]. Differs from *Shaleria (Telaeoshaleria)* especially in encirclement of divergent diductor scars by pair of rings formed by apices of bounding ridges, vestigial widely divergent socket ridges and persistence of outer pairs of divergent ridges in brachial valve. *M.Dev.*, N.-Am.——FIG. 259,*5a,b*. **H. alpenensis*, USA-(Mich.); *5a*, ped.v. int., ×2; *5b*, brach.v. view of conjoined valves, ×2 (871).——FIG. 259,*5c,d*. *H.* sp., USA(N.Y.); *5c,d*, ped.v. and brach.v. int., ×2 (871).

Zophostrophia VEEVERS, 1959, p. 63 [**Z. ungamica;* OD]. Like *Shaleria (Telaeoshaleria)* but dorsally geniculate, equally parvicostellate and weakly concentrically rugate externally. Ventral diductor scars strongly divergent, median adductor scar on raised platform. *U.Dev.*, W.Australia.——FIG. 259,*7*. **Z. ungamica; 7a,b*, ped.v. and brach.v. int., ×3.5; *7c*, ped.v. view of conjoined valves, ×1 (838).

Subfamily LEPTODONTELLINAE Williams, n. subfam.

Concavo-convex or resupinate, with unequally parvicostellate radial ornamentation. Ventral muscle scar triangular; socket ridges short, flanking cardinal process lobes; dorsal adductor scars bounded laterally by strong, raised ridges and impressed posterior to high median septum and curved or deflected brachial ridges defining slightly elevated areas. *L.Dev.-M.Dev.*

Leptodontella KHALFIN, 1948, p. 253 [**Leptaena caudata* SCHNUR, 1854, p. 224; OD] [=*Glossostrophia* WILLIAMS, 1950, p. 282 (obj.) (type, *Leptaena caudata*); *Altaestrophia* BUBLICHENKO, 1956 (type, *Leptodontella acuta* KHALFIN, 1948)]. Resupinate by sharp, ventrally directed geniculation, with narrow median zone of trail projecting beyond profile of brachial valve like tongue. Dorsal median septum ending anteriorly in raised boss, brachial ridges curved. *L.Dev.-M.Dev.*, Eurasia.——FIG. 260,*2*. **L. caudata* (SCHNUR); *2a,b*, ped.v. and brach.v. int. molds, ×1.5; *2c*, brach.v. view of conjoined valves, ×1; *2d*, ant. view of conjoined valves, ×1.5 (871).

Leptodonta KHALFIN, 1955, p. 237 [*pro Oehlertia* KHALFIN, 1948 (*non* PERNER, 1907)] [**Leptaena? leblanci* ROUAULT, 1851, p. 393; OD]. Like *Leptodontella* but concavo-convex and with sharply deflected brachial ridges. *M.Dev.*, Eurasia.——FIG. 260,*1*. **L. leblanci* (ROUAULT), Fr.; *1a*, brach.v. int., ×2; *1b*, ped.v. int. mold, ×1 (610).

Parastrophonella BUBLICHENKO, 1956, p. 93 [**Strophomea anaglypha* KAYSER, 1871, p. 628; OD]. Like *Leptodontella* but without dorsally projecting tongue. *M.Dev.*, Eurasia.

Subfamily LILJEVALLIINAE Williams, 1953

[*nom. correct.* WILLIAMS, herein (*pro* Liljevallinae WILLIAMS, 1953, p. 9)]

Attached to foreign body throughout ontogeny by cementation of pedicle valve. *M. Sil.*

Liljevallia HEDSTRÖM, 1917, p. 9 [**L. gotlandica;* OD]. Pseudodeltidium arched, incompletely developed, ventral process low; hinge line denticulate for less than half of its length. Dental plates absent; ventral muscle scar subcircular, enclosed by bounding ridges except anteriorly; brachial valve unknown but cardinal process lobes inferred to be disjunct from position of accommodating holes drilled into ventral interarea. *M.Sil.*, Sweden.——FIG. 260,*3*. **L. gotlandica;* ped.v. int., ×2 (419).

Superfamily DAVIDSONIACEA King, 1850

[*nom. transl.* WILLIAMS, herein (*ex* Davidsoniinae KING, 1850, p. 81)]

Functional pedicle present only in earliest known species; pedicle valve usually modified and cemented by umbo or greater part of shell surface to substratum, brachial valve invariably convex in young growth stages; pseudodeltidium commonly forming complete cover to delthyrium, chilidium well developed to obsolescent; cardinal process bilobed, in many forms greatly extended ventrally, ankylosed with variably disposed

socket plates; lophophore probably spirolophous in all stocks, rarely impressed or supported by spirally coiled calcareous ribbons; mantle canal systems poorly known, probably saccate to lemniscate in both valves; shell substance commonly pseudopunctate but impunctate in older stocks. *M.Ord.-Trias.*

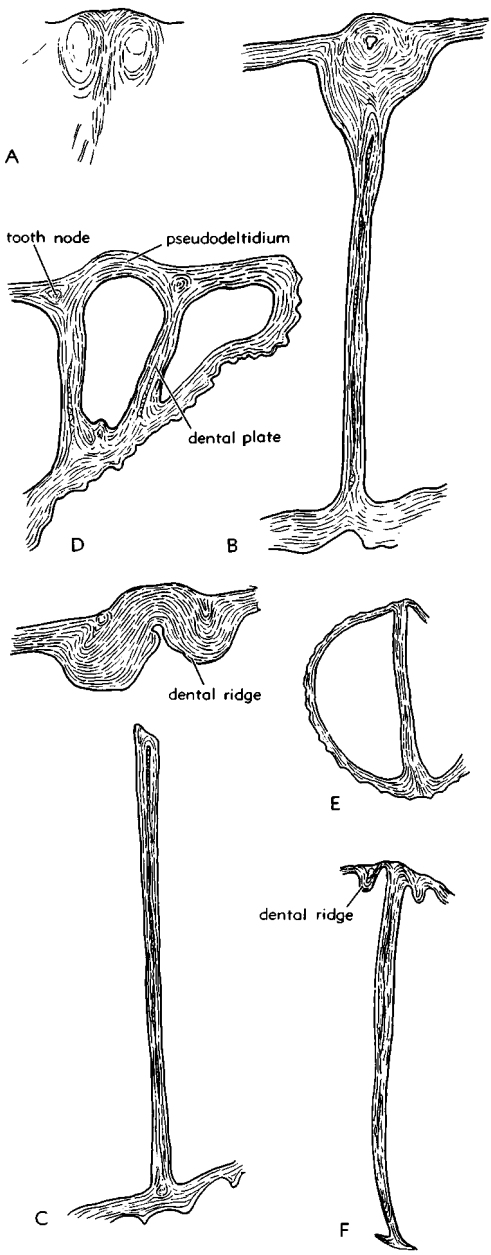

FIG. 261. Sections through the umbonal regions of davidsoniacean pedicle valve; *A-C*, *Orthotetes radiata* (FISCHER), M.Carb.(C_2^{pd}), USSR, ×7; *D*, *Meekella* sp., Penn. (La Salle Ls.), USA, ×7; *E-F*, *Derbyia* sp. cf. *D. cymbula* HALL & CLARKE, Perm., USA(Tex.), ×4.

Although the davidsoniaceans constitute a homogeneous group of brachiopods which is immediately distinguishable from other Strophomenida, they have never been satisfactorily classified. Many attempts have been made (DUNBAR & CONDRA, 1932, 270; WILLIAMS, 1953, 872; STEHLI, 1954, 773; and THOMAS, 1958, 802) to arrange the increasing number of genera assigned to the superfamily into subordinate taxonomic groups that reflect the course of evolution and at the same time provide a workable basis for ready generic identification. All of them have been unsuccessful, owing mainly to persistent misinterpretation of the ventral interior of *Orthotetes* FISCHER DE WALDHEIM, the first davidsoniacean genus to be recognized. The specimens on which the type-species, *O. radiata*, was founded, were lost during the last century and, until recently, systematists have had to rely exclusively on an original illustration of a partially weathered pedicle valve to ascertain the main ventral features. This showed a tiny cavity, immediately anterior of the pseudodeltidium and contained by the teeth and the median septum apparently fused into a single unit, which has always been taken to be a spondylium. Accordingly, *Orthotetes* has been classified with davidsoniaceans possessing strongly developed dental plates which may or may not join just above the floor of the valve (Fig. 261). True dental plates, however, invariably formed the lateral boundaries of the ventral muscle field even when they converged high above the valve floor, as in *Ombonia*, whereas the ventral muscle scars of *Orthotetes* are impressed on the valve floor on either side of the median septum. The subpseudodeltidial cavity of *Orthotetes* is therefore in no way homologous with the spondylium of the meekellids, because it is formed not by the median fusion of dental plates but by secondary shell joining the median septum with a pair of ridges representing the anterior edges of unsupported teeth (Fig. 261). In this respect *Orthotetes* is much more like *Derbyia*, a fact recorded

by SOKOLSKAYA in 1954 (755), although unfortunately ignored by her in the classification of the davidsoniaceans which she gave for the Russian Treatise (1960). Through the kindness of Dr. SOKOLSKAYA it has been possible to obtain specimens of *Orthotetes,* believed to be conspecific with *O. radiata,* and these have been used for sectioning. Comparisons of thin sections of *Orthotetes, Derbyia,* and *Meekella* show the fundamental difference between the dental ridges of the first two and the long dental plates of the last. These differences have furnished the basis for the classification given below.

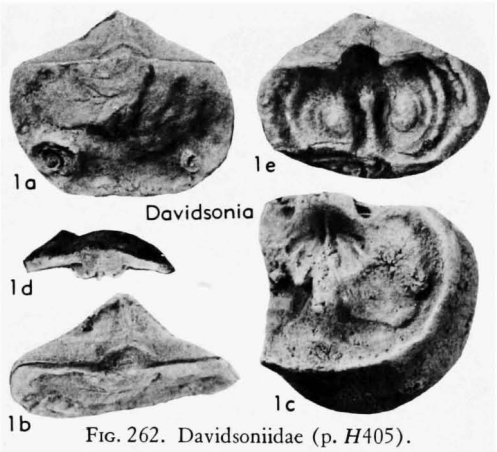

FIG. 262. Davidsoniidae (p. H405).

Family DAVIDSONIIDAE King, 1850

[*nom. correct.* WILLIAMS, herein (*pro* Davidsonidae KING, 1850, p. 81)]

Pseudodeltidium and chilidium well developed; teeth unsupported, ventral muscle scar small, suboval, restricted laterally and anteriorly by low ridges; socket plates recurved, united with dorsal posterior margin and with low cardinal process lobes that join anteriorly to form low median ridge; quadripartite dorsal adductor scars small, subcircular, divided by low median ridge; both valves with impressions of pair of brachia spirally coiled into about 6 convolutions forming 2 very low cones with apices directed dorsally; shell substance pseudopunctate. *L.Dev.-M.Dev.*

Davidsonia BOUCHARD, 1849, p. 92 [**D. verneuili;* OD]. Brachial valve convex, pedicle valve irregular, cemented to substratum by most of external surface throughout life; radial ornamentation lacking. *M.Dev.,* Eu.——FIG. 262,*1*. **D. verneuili,* Ger.; *1a,b,* brach.v., post. views of conjoined valves, ×1.5; *1c,d,* brach.v. int., post., ×1.5; *1e,* ped.v. int., ×1.5 (Cooper, n).

Biconostrophia HAVLÍČEK, 1956, p. 562 [**B. spirifera;* OD]. Like *Davidsonia* but with flat or slightly concave pedicle valve not attached to substratum except in very early growth stages and with coarsely costate radial ornamentation. *L.Dev.,* Eu.(Czech.).

Prodavidsonia HAVLÍČEK, 1956, p. 564 [**P. dalejensis;* OD]. Unattached, like *Biconostrophia* but with convex pedicle valve and without radial ornamentation as in *Davidsonia. M.Dev.,* Eu. (Czech.).

Family MEEKELLIDAE Stehli, 1954

[*nom. transl.* WILLIAMS, herein (*ex* Meekellinae STEHLI, 1954, p. 303)]

Teeth in pedicle valve supported by variably disposed dental plates; ventral muscle field subcircular to elongately oval, with flabellate diductor and posteromedian lanceolate adductor scars impressed either on floor of valve between dental plates or to varying degree on dental plates in their convergence toward spondylium; chilidium well developed to obsolescent. *M.Ord.-Perm.*

Subfamily MEEKELLINAE Stehli, 1954

[Meekellinae STEHLI, 1954, p. 303] [=Omboniinae SOKOLSKAYA, 1960, p. 218]

Cemented by ventral umbo, with socket plates ankylosed to cardinal process lobes and prolonged anterolaterally as pair of widely divergent supporting plates arising from floor of brachial valve, enclosing posteriorly dorsal adductor field; shell substance pseudopunctate. *Dev.-Perm.*

Meekella WHITE & ST. JOHN, 1867, p. 120 [**Plicatula striatocostata* COX in OWEN, 1857, p. 568; OD]. Unequally biconvex, with deeply conical pedicle valve, finely costellate and radially plicate; dorsal interarea linear, chilidium vestigial; dental plates long, subparallel; cardinal process high. *Carb.-Perm.,* cosmop.——FIG. 263,*4*. *M. attenuata* (GIRTY), Perm.(Leonard.), USA(Tex.); *4a,* brach.v. view of conjoined valves; *4b,c,* ped.v. int., brach.v. int., all ×1.5 (Williams, n).

Geyerella SCHELLWIEN, 1899, p. 4 [**G. gemmellaroi;* OD] [=*Turriculum* DE GREGORIO, 1930, p. 26 (type, *T. imperans*)]. Like *Meekella* but with dental plates converging and coalescing toward middle of pedicle valve as narrow spondylium supported by median septum. *U.Carb.-Perm.,* cosmop. ——FIG. 263,*1*. *G.* sp., Perm., N.Am.; lat. view of conjoined valves, ×1.5 (Williams, n).

Ombonia CANEVA, 1906, p. 54 [**O. dieneri* LIKHAREV, 1932, p. 30; SD LIKHAREV, 1932, p. 26]. Like *Geyerella* but finely costellate and without radial plicae. *Perm.,* N.Hemis.——FIG. 263,*3*. *O.* sp., Perm.(Lamar), USA(N.Mex.); *3a,b,* 2 views of ped.v. int., ×2 (Williams, n).

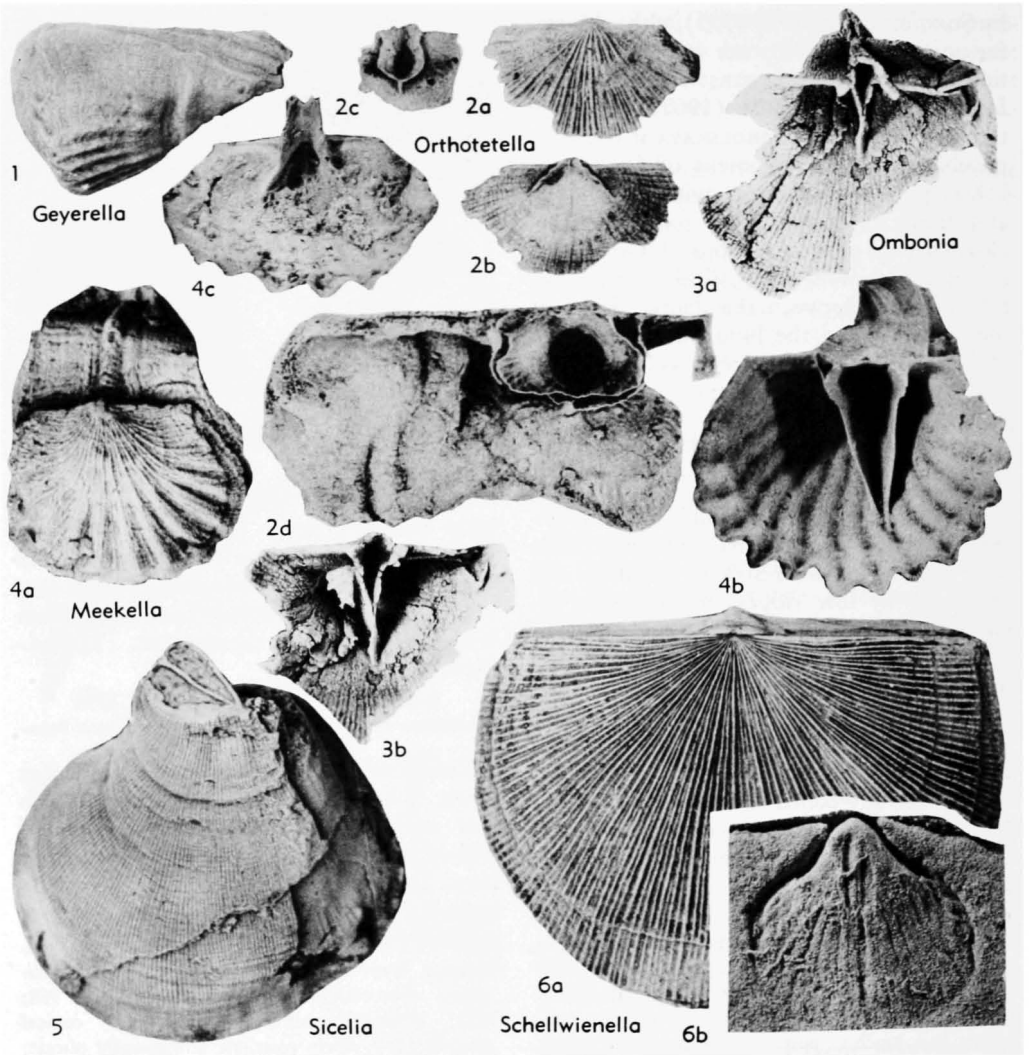

FIG. 263. Meekellidae (Meekellinae) (p. *H*405-*H*407).

Orthotetella R. E. KING, 1931, p. 51 [**O. wolfcampensis;* OD]. Biconvex to plano-convex, costellate; dorsal interarea and chilidium vestigial; dental plates strongly convergent to form deep conical spondylium supported posteriorly by short median septum; cardinal process low. *L. Perm.*, USA.——FIG. 263,2. **O. wolfcampensis*; USA (Tex.); *2a,b,* brach.v. ext., int., ×1; *2c,d,* fragments of ped.v. ints., ×1 (773).

Orthothetina SCHELLWIEN, 1900, p. 8 [**Orthotetes persicus* (SCHELLWIEN); SD SCHUCHERT & LEVENE, 1929, p. 91] [=*Hamletella* HYASAKA, 1953, p. 92 (type, **Streptorhynchus altus* HAMLET, 1928)]. Like *Meekella* but without radial plicae. *Carb.-Perm.*, cosmop.

Perigeyerella WANG, 1955, p. 346 [**P. costellata;* OD]. Biconvex, with conical pedicle valve, finely costellate, dorsal interarea and chilidium vestigial; dental plates becoming less convergent with growth so that spondylium with supporting median septum is characteristic of young pedicle valve and sessile spondylium or discrete dental plates typical of adult valves. *U.Perm.*, China.——FIG. 264,*1*. **P. costellata; 1a,* brach.v. view of conjoined valves, ×1; *1b-d,* serial secs. at intervals indicated on *1a,* ×2 (852).

Pseudoderbyia LIKHAREV, 1934, p. 213 [**P. netschajewi; OD*]. Costellate, ventral interior with sessile spondylium like that of *Sicelia,* containing independently developed short, median ridge; dorsal interior unknown. *L.Perm.*, USSR.

Schellwienella I. THOMAS, 1910, p. 92 [**Spirifera crenistria* PHILLIPS, 1836, pl. 9, fig. 6; OD]. Biconvex to resupinate, pedicle valve commonly

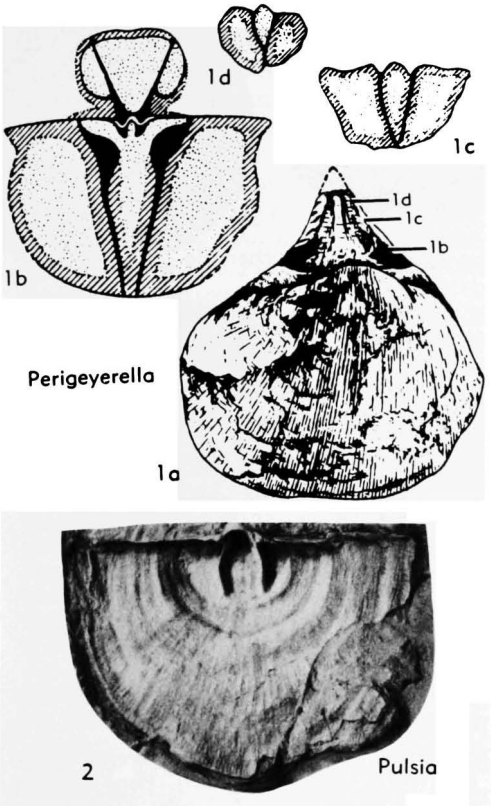

FIG. 264. Meekellidae (Meekellinae) (p. *H*406-*H*407).

less convex than brachial valve and distorted umbonally due to cementation; costellate; pseudodeltidium well developed, chilidium obsolescent; dental plates short, reaching to floor of pedicle valve; cardinal process low with discrete lobes. *Dev.-Carb.*, cosmop.

S. (Schellwienella) [=*Carlopsina* REED, 1954, p. 183 (type, *Spirifera radialis* PHILLIPS, 1836)]. Dental plates divergent. *Dev.-Carb.*, cosmop.—— FIG. 263,6. *S. (S.)* sp. cf. *S. (S.) aspis* (SMYTHE), L.Carb., G.Brit.; *6a*, brach.v. view of complete shell, ×1.5; *6b*, mold of posteromedian region of ped.v. int., ×1.5 (Williams, n).

S. (Pulsia) IVANOV, 1925, p. 113 [**P. mosquensis;* OD]. Dental plates, subparallel, *Carb.*, USSR.—— FIG. 264,2. **S. (P.) mosquensis*, U.Carb., ped.v. int., ×0.5 (755).

Sicelia GORTANI & MERLA, 1934, p. 284 [*pro Canavaria* MERLA, 1928 (*non* OPPENHEIM, 1899; *nec* GEMMELLARO, 1866)] [**Canavaria acropedion* MERLA, 1928, p. 70; OD] [=*Gemmellaria* FABIANI & RUIZ, 1933 (*non* MUNIER-CHALMAS, 1873)]. Unequally biconvex, with deep, distorted pedicle valve, finely costellate; dorsal interarea and chilidium vestigial; dental plates long, convergent, uniting with floor of pedicle valve to form elongately oval spondylium. *Perm.*, Eurasia.——

FIG. 263,5. **S. acropedion* (MERLA), Perm.(Sosio), Italy; ped.v. ext. showing dental plates in partly dissected post. portion, ×2 (Williams, n).

Subfamily FARDENIINAE Williams, n. subfam.

Uncemented, rarely with functional pedicle in adult shells; socket plates short, divergent, cardinal process lobes low, discrete; pseudodeltidium and chilidium variably developed; shell substance impunctate. *M. Ord.-U.Sil.*

Fardenia LAMONT, 1935, p. 310 [**F. scotica;* OD] [=*Coolinia* BANCROFT, 1949, p. 7 (type, **Orthis? applanata* SALTER, 1846, p. 72); *Saughina* BANCROFT, 1949, p. 7 (type, *Strophomena pertinax* REED, 1917, p. 907); *Chilidiopsis* BOUCOT, 1959 (type, *Fardenia reedsi* AMSDEN, 1951, p. 84)]. Subequally biconvex to resupinate, costellate; pseudodeltidium variably developed, pedicle foramen rarely persistent in adult shells; dorsal interarea short, chilidium varying even in type-species from complete convex cover to one extending beyond apical areas only as lateral partitions flanking cardinal process lobes; dental plates and socket plates short, divergent. *M.Ord.-U.Sil.*,

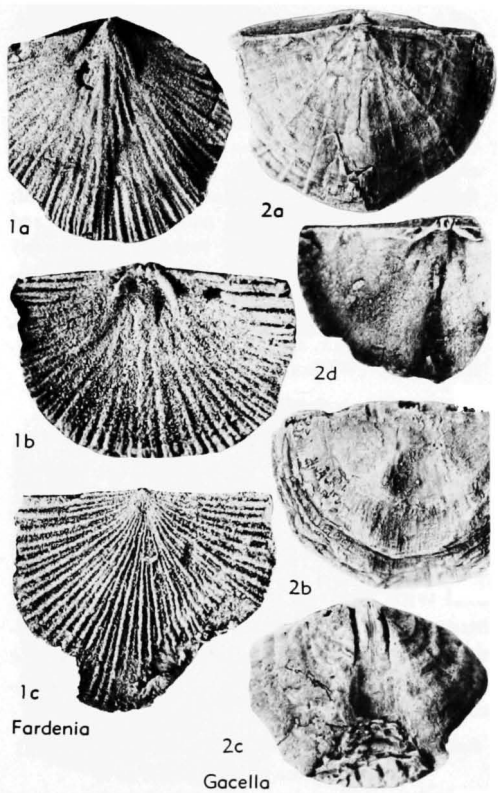

FIG. 265. Meekellidae (Fardeniinae) (p. *H*407-*H*408).

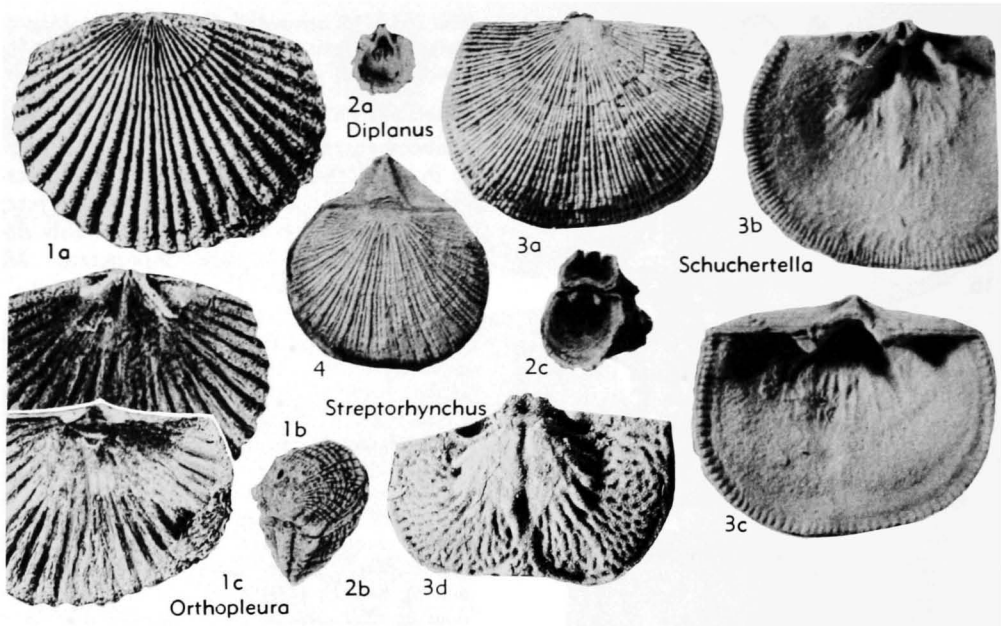

FIG. 266. Schuchertellidae (Schuchertellinae) *(1-3)*, (Streptorhynchinae) *(4)* (p. *H*408-*H*409).

cosmop.——FIG. 265,*1*. **F. scotica*; U.Ord.(Ashgill.), Scot.; *1a*, ped.v. int. mold, ×2.25; *1b*, brach.v. int., ×3.6; *1c*, brach.v. ext., ×2.7 (Williams, n).

Gacella WILLIAMS, 1962, p. 222 [**G. insolita*; OD]. Biconvex, with strong dorsal median fold, unequally parvicostellate, pseudodeltidium and chilidium well developed, pedicle foramen open throughout life; dental plates long, subparallel; ventral muscle field with narrow diductor and lanceolate adductor scars; socket plates widely divergent, subparallel with hinge line. *M.Ord.*, Scot.-SE.USA.——FIG. 265,*2*. **G. insolita*, Scot.; *2a,b*, brach.v., ped.v. views of conjoined valves, ×2.25; *2c*, ped.v. int. mold, ×2.25; *2d*, brach.v. int., ×2.25 (Williams, n).

Family SCHUCHERTELLIDAE Williams, 1953

[*nom. transl.* STEHLI, 1954 (*ex* Schuchertellinae WILLIAMS, 1953, p. 9)]

Cemented by ventral umbo and with pair of unsupported teeth in pedicle valve; ventral muscle field subcircular to elongately oval with large flabellate diductor scars and more posteriorly located elongately oval adductor scars impressed on floor of pedicle valve; chilidium well developed to obsolescent. *Dev.-Perm.*

Subfamily SCHUCHERTELLINAE Williams, 1953

[Schuchertellinae WILLIAMS, 1953, p. 9]

Socket plates recurved, ankylosed to cardinal process lobes and dorsal posterior margin; dorsal adductor field variably impressed. *Dev.-Perm.*

Schuchertella GIRTY, 1904, p. 734 [**Streptorhynchus lens* WHITE, 1862, p. 28; OD]. Plano-convex to biconvex, costellate, with costellae added by intercalation during shell growth; dorsal interarea linear; cardinal process lobes low, not united posteromedianly; median ridge dividing dorsal adductor field variably developed; shell substance impunctate. *L.Dev.-Perm.*, cosmop.——FIG. 266,*3*. *Schuchertella* sp. cf. *S. parva* (HALL), U.Dev.(Hackberry), USA(Iowa); *3a-c*, brach.v. ext., int., ped.v. int., ×1.5; *3d*, ped.v. int. mold, ×3 (Williams, n).

Diplanus STEHLI, 1954, p. 229 [**Streptorhynchus lamellatum* R. E. KING, 1930, p. 49; OD]. Like *Schuchertella* but with small, developed dorsal interarea and costate radial ornamentation interrupted by strong, irregular imbrication; shell substance pseudopunctate. *L.Perm.*, USA.——FIG. 266,*2*. **D. lamellatum* (KING); *2a*, brach.v. int.; *2b*, sublat. view of complete shell; *2c*, ped.v. int., all ×1 (773).

Orthopleura IMBRIE, 1959, p. 391 [**O. rhipis*; OD]. Like *Schuchertella* but biconvex with deeper pedicle valve, radial ornamentation costate, shell substance pseudopunctate. *M.Dev.*, N.Am.——FIG. 266,*1*. **O. rhipis*, M.Dev.(Onesquethaw-Taghanic), USA(Mich.); *1a-c*, brach.v. ext., int., ped.v. int., ×3 (445).

Schuchertellopsis MAILLIEUX, 1939, p. 3 [**S. durbutensis*; OD]. Small, like *Schuchertella* but with pedicle valve completely cemented to foreign body throughout life. *U.Dev.*, Eu.

Subfamily STREPTORHYNCHINAE Stehli, 1954

[Streptorhynchinae STEHLI, 1954, p. 299]

Socket plates ankylosed to cardinal process lobes and prolonged anterolaterally as pair of widely divergent plates arising from floor of brachial valve and enclosing posteriorly dorsal adductor field; shell substance pseudopunctate. *Carb.-Perm.*

Streptorhynchus KING, 1850, p. 107 [**Terebratulites pelargonatus* VON SCHLOTHEIM, 1816, p. 28; OD] [=*Lepsius* DE GREGORIO, 1930, p. 24 (type, *L. favoritus*); *Mammosum* DE GREGORIO, 1930, p.25 (type, *M. ipsium*)]. Unequally biconvex, with conical pedicle valve, costellate, with variable texture; cardinal process lobes high, not united posteromedianly above low median ridge; chilidium vestigial. *Carb.-Perm.*, cosmop.——FIG. 266,*4*. **S. pelargonatus* (VON SCHLOTHEIM), Perm.(Zechstein), Ger.; brach.v. view of conjoined valves, ×2 (802).——FIG. 267,*1*. *S.* sp. cf. *pelargonatus* (SCHLOTHEIM), U.Perm. (Liveringa F.), W.Australia(Fitzroy Basin); incompl. brach.v. showing cardinal process, ant., ×2 (802).

?Irboskites BEKKER, 1924, p. 48 [**I. fixatus*; OD]. Brachial valve with dorsally deflected margin; pedicle valve irregularly convex, cemented to substratum by most of external surface throughout life, radial ornamentation lacking; teeth unsupported, ventral muscle field large, subcircular, commonly with raised adductor scars; cardinal process lobes high, socket plates divergent, arising from floor of brachial valve, dorsal median ridge strong and long, dividing deeply impressed subcircular dorsal adductor field. [The taxonomic position of this genus is uncertain but provisionally it is best accommodated within the Streptorhynchinae.] *M.Dev.*, USSR.——FIG. 267,*2*. **I. fixatus*, Est.; *2a*, ped.v. int., ×2; *2b*, brach.v. int., ×2; *2c*, ped.v. attached, ×1 (60).

Kiangsiella GRABAU & CHAO, 1927, p. 103 [*Orthotetes tingi* GRABAU, 1924, p. 359; OD]. Like *Streptorhynchus* but with strong secondary plications like coarse costae. *U.Carb.-Perm.*, cosmop. ——FIG. 267,*3*. *K. condoni* (THOMAS), Perm. (Artinsk.), Australia; brach.v. view of conjoined valves, ×1 (802).

Family ORTHOTETIDAE Waagen, 1884

[*nom. transl.* MCEWAN, 1939 (*ex* Orthotetinae WAAGEN, 1884, p. 576)]

Cemented by ventral umbo, with pair of unsupported teeth in pedicle valve; ventral muscle field subcircular to elongately oval, with larger flabellate diductor scars flanking lanceolate adductor scars and divided by variably developed median septum commonly continuous with inner surface of pseudodeltidium or less commonly ankylosed to short dental ridges forming anterior edges of teeth; shell substance pseudopunctate. *Carb.-Perm.*

Subfamily ORTHOTETINAE Waagen, 1884

[Orthotetinae WAAGEN, 1884, p. 576] [=Derbyoidinae THOMAS, 1958, p. 21]

Recurved socket plates ankylosed to cardinal process lobes and dorsal posterior margin; dorsal adductor field subcircular generally weakly impressed; dorsal interarea and chilidium mostly obsolescent. *Carb.-Perm.*

Orthotetes FISCHER DE WALDHEIM, 1829, p. 375 [**O. radiata* FISCHER DE WALDHEIM, 1850, p. 491; SD GIRTY, 1908, p. 186] [=*Werriea* CAMPBELL,

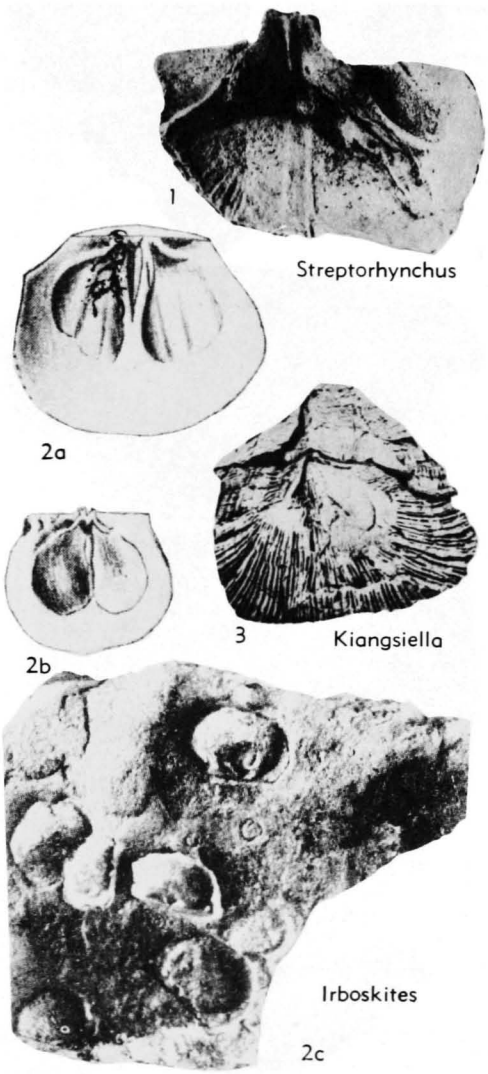

FIG. 267. Schuchertellidae (Streptorhynchinae) (p. H409).

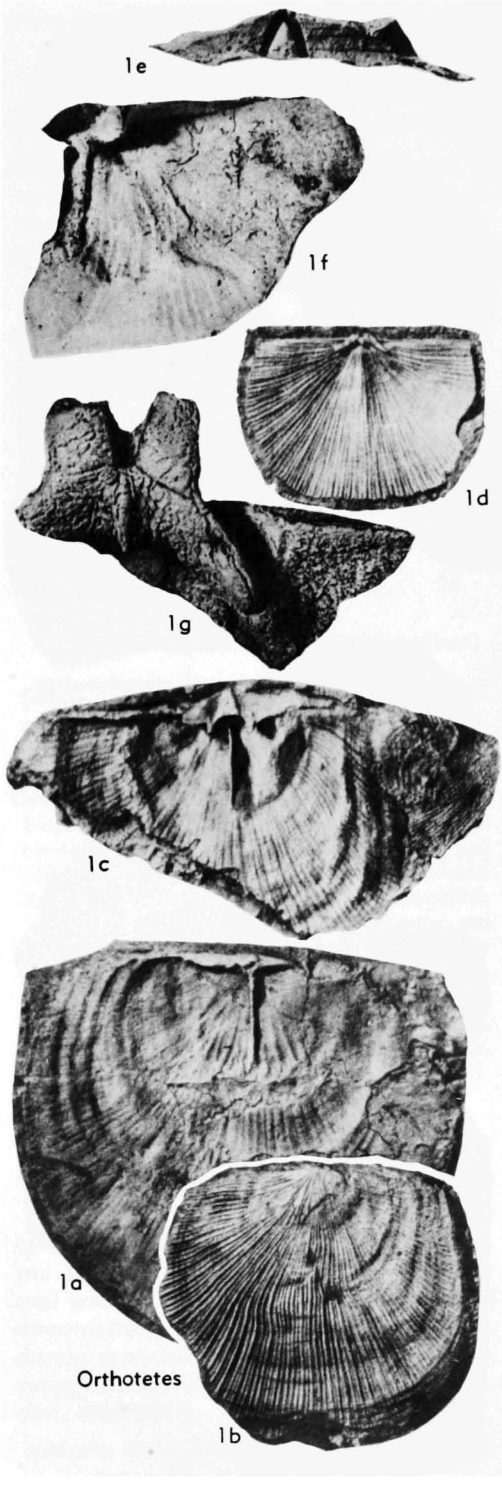

FIG. 268. Orthotetidae (Orthotetinae) (p. H409-H410).

1957, p. 44 (type, *W. australis*); *Permorthotetes* G. A. THOMAS, 1958, p. 82 (type, *P. callytharrensis*); *Pseudoorthotetes* SOKOLSKAYA, 1963, p. 96 (type, *P. borodencovensis*)]. Subequally biconvex to resupinate, finely costellate; dental ridges united by secondary shell substance to posterior edge of ventral median septum to define small delthyrial chamber commonly filled with secondary shell substance and less commonly extending anteromedianly for entire length of ventral interarea; cardinal process lobes fairly low, separate posteriorly but united into median ridge anteriorly. *M.Carb.-Perm.*, cosmop.——FIG. 268,*1a,b*. **O. radiata* (FISCHER DE WALDHEIM), M.Carb. (C_2^{pd}), USSR; *1a,b*, ped.v. int., ext., ×1 (755).——FIG. 268,*1c,d*. *O. plana* (IVANOV), U.Carb. (C_3^{ks}), USSR; *1c,d*, ped.v. int., brach.v. int., ×1 (755).——268,*1e-g*. *O. callytharrensis* (THOMAS), Perm., Aus.; *1e*, post. view of ped.v. int. mold, ×1; *1f*, ped.v. int., ×1; *1g*, post. view of detached cardinal process, ×2 (802).

Derbyoides DUNBAR & CONDRA, 1932, p. 114 [**D. nebrascensis;* OD]. Biconvex, with variable depth to pedicle valve; finely costellate; ventral median septum fused posteriorly with inner surface of pseudodeltidium; cardinal process lobes like those of *Orthotetes;* chilidium and dorsal interarea relatively well developed. *Penn.*, N.Am.——FIG. 269,*1*. **D. nebrascensis*, USA(Kans.-Neb.); *1a,b*, brach.v. int., ext., ×1; *1c*, vent. view of brach.v. cardinal region, ×1.5 (270).

Hipparionyx VANUXEM, 1842, p. 124 [**H. proximus* VANUXEM, 1842; SD HALL & CLARKE, 1892, p. 258]. Unequally biconvex, with gently convex pedicle valve, subcircular in outline, finely costellate; ventral muscle scar large with strong bounding ridges, median septum low, united umbonally with dental ridges; cardinal process lobes high, strongly divergent. *L.Dev.*, N.Am.——FIG. 269,*3*. **H. proximus* (VANUXEM), Oriskany; *3a*, brach.v. int., ×1; *3b*, ped.v. int. mold, ×1 (740).

Tapajotia DRESSER, 1954, p. 149 [**Streptorhynchus tapajotensis* DERBY, 1874, p. 37; OD]. Like *Derbyoides* but with weaker median septum in pedicle valve and with more strongly recurved socket plates parallel to dorsal hinge line and widely divergent cardinal process lobes. *U.Carb.-L.Perm.*, USSR-Brazil.——FIG. 269,*2*. **T. tapajotensis* (DERBY), U.Carb.(Penn.), Brazil; *2a*, brach.v. ext., ×1; *2b*, ped.v. int., ×1; *2c*, brach.v. int., ×2 (266).

Subfamily DERBYIINAE Stehli, 1954

[Derbyiinae STEHLI, 1954, p. 300]

Socket plates ankylosed to high cardinal process lobes and prolonged anterolaterally as pair of widely divergent supporting plates arising from floor of brachial valve and enclosing posteriorly dorsal adductor field; dorsal interarea and chilidium obsolescent. *Carb.-Perm.*

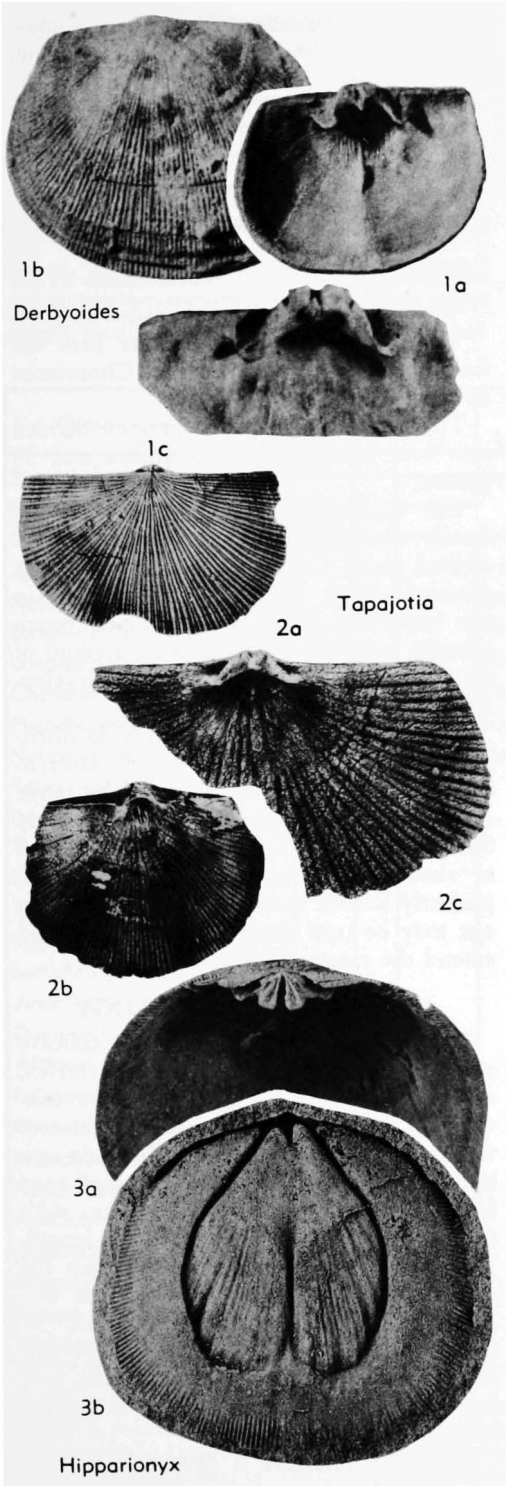

FIG. 269. Orthotetidae (Orthotetinae) (p. *H*410).

Derbyia WAAGEN, 1884, p. 576 [**P. regularis;* SD HALL & CLARKE, 1892, p. 262] [=*Derbyaeconcha* LIKHAREV, 1934, p. 507 (type, *Derbyia anomata* LIKHAREV, 1932, p. 20); *Grabauellina* LIKHAREV, 1934, p. 507 (type, *Derbyia mongolica* GRABAU, 1931, p. 259), *pro Derbyina* GRABAU, 1931 (*non* CLARKE, 1913)]. Biconvex, with variable depth of pedicle valve, finely costellate; ventral median septum strong, fused posteriorly with inner surface of pseudodeltidium; cardinal process lobes high, divergent posteriorly. *Carb.-Perm.*, cosmop.——FIG. 270,*1*. *D.* sp., Perm.(Leonard.), N.Am.(Tex.); *1a-c*, ped.v. int., brach.v. int., ext., ×1.5 (Williams, n).——FIG. 270,2. *D. cymbula* HALL & CLARKE, Perm., USA; post. view of conjoined valves, ×1.5 (Williams, n).

Licharewiella SOKOLSKAYA, 1960, p. 219 [**Derbya magnifica* LIKHAREV, 1939, p. 80; OD]. Like *Derbyia* but with median septum of pedicle valve continuous anteriorly with high transverse ridge. *L.Perm.*, USSR-Asia.

Plicatoderbya H. D. THOMAS, 1937, p. 14 [*Orthotetes magnus* BRANSON, 1930, p. 26; OD]. Like *Derbyia* but with shell additionally ornamented by broad radial plicae. *L.Perm.*, N.Am.

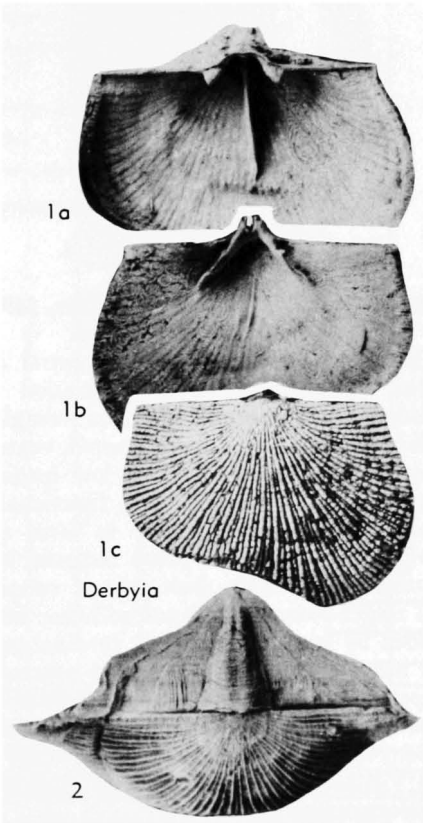

FIG. 270. Orthotetidae (Derbyiinae) (p. *H*410-*H*411).

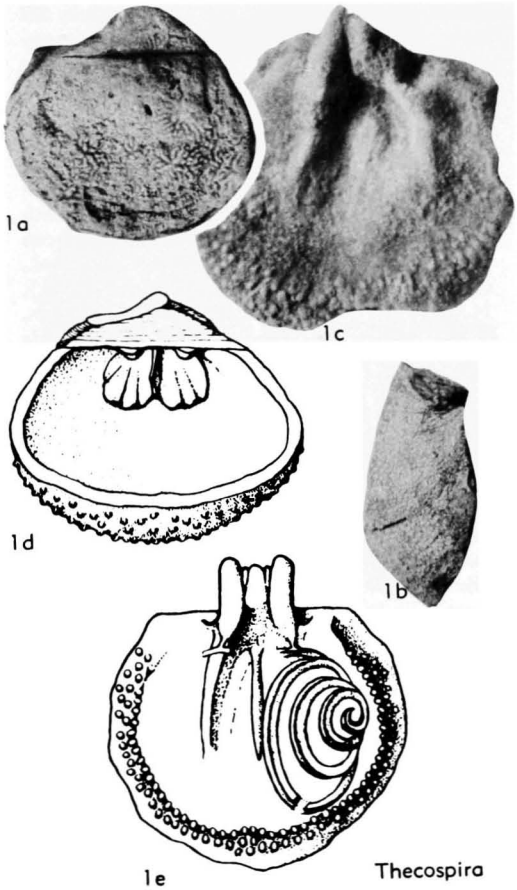

FIG. 271. Thecospiridae (p. *H*412).

Family THECOSPIRIDAE Bittner, 1893

[Thecospiridae BITTNER, 1890, p. 310]

Cemented by ventral umbo, ventral interarea entire, without differentiation of pseudodeltidium; dorsal interarea vestigial, chilidium absent; teeth unsupported, ventral muscle scar small, divided by low median septum; cardinal process high, functionally bilobed but united medianly to form tripartite structure, socket plates recurved but continuous anteriorly with pair of subparallel ridges containing dorsal adductor field divided by low median ridge; cardinal process bases prolonged into 2 short processes supporting pair of spirally coiled calcareous ribbons directed ventrolaterally; brachial ribbons sharply folded throughout length to give V-shaped cross section; shell substance pseudopunctate. *Trias.*

Thecospira ZUGMAYER, 1880, p. 152 [**Thecidea haidingeri* SUESS, 1854, p. 15; OD]. Exterior tuberculate, sporadically and impersistently rugate but without radial ornamentation. *Trias.*, Eu. ——FIG. 271,*1*. **T. haidingeri* (SUESS), Alps; *1a,b*, brach.v., lat. views of conjoined valves, ×2; *1c*, brach. v. int., ×3; *1d,e*, brach.v., ped.v., ints., ×3 (Williams, n).

CHONETIDINA

[Materials for this suborder prepared by HELEN M. MUIR-WOOD]

[Appreciation and cordial thanks are expressed to the Trustees of the British Museum (Natural History) for permission to use numerous illustrations published in the MUIR-WOOD monograph on the Chonetoidea (586)]

The suborder Chonetidina as here defined includes the superfamilies Chonetacea and Cadomellacea.

The Chonetacea are at present divided into four families, 11 subfamilies and 30 genera.

The Cadomellacea comprise the single family Cadomellidae, containing one described genus, *Cadomella*. Although it lacks pseudopunctate shell structure, except in the innermost layer, it is grouped provisionally with the Chonetacea on account of its supra-apical foramen and the development of chilidial plates.

The Chonetacea have world-wide distribution, though many genera (e.g., *Daviesiella*) are only locally developed. The range of the superfamily is definitely from Early Silurian through Late Permian, a period of about 210 million years, but two imperfectly known species of Late Ordovician age may be true chonetids and this would extend the range still further (Fig. 272).

EXTERNAL MORPHOLOGY

The brachial valve is plane or concave and the pedicle valve more or less convex, except in *Chonostrophia,* where the convexity is reversed. In *Megachonetes* the two valves may be almost flat and the body cavity reduced to a minimum. The shell may be semicircular, alate, or quadrate, with the width normally exceeding the length. The hinge may be equal or less than the greatest width of the shell, with the cardinal extremities angular, rounded, or spinelike. The ears are more or less flattened, triangular, and slightly convex, and demarcated from the flanks by a shallow sulcus.

A narrow **interarea** is developed in each valve, that of the pedicle valve usually being twice the height of that of the brachial valve. The two interareas taper laterally

and lie in the same plane or are set at an angle to one another. In some upper Paleozoic forms the dorsal interarea may be reflexed or bent anteriorly owing to development medianly of a secondary interarea in the pedicle valve. This serves to force the two umbones apart and make room for the growing external face of the cardinal process.

The **notothyrium** may be closed by the **chilidium**, a trigonal or subtrigonal, commonly medianly notched plate, developed at the base of the exterior of the cardinal process of some chonetoids (e.g., *Daviesiella*) (see Fig. 292,*1c*). The chilidium may be replaced by two narrow **chilidial plates** which are fused anteriorly and extend along the lateral margin of the triangular external face of the cardinal process. The latter serves to close part of the triangular **delthyrium** in the conjoined valves, the **pseudodeltidium** being as a rule a small crescentic or subtrigonal plate occupying the apex of the delthyrium. The delthy-

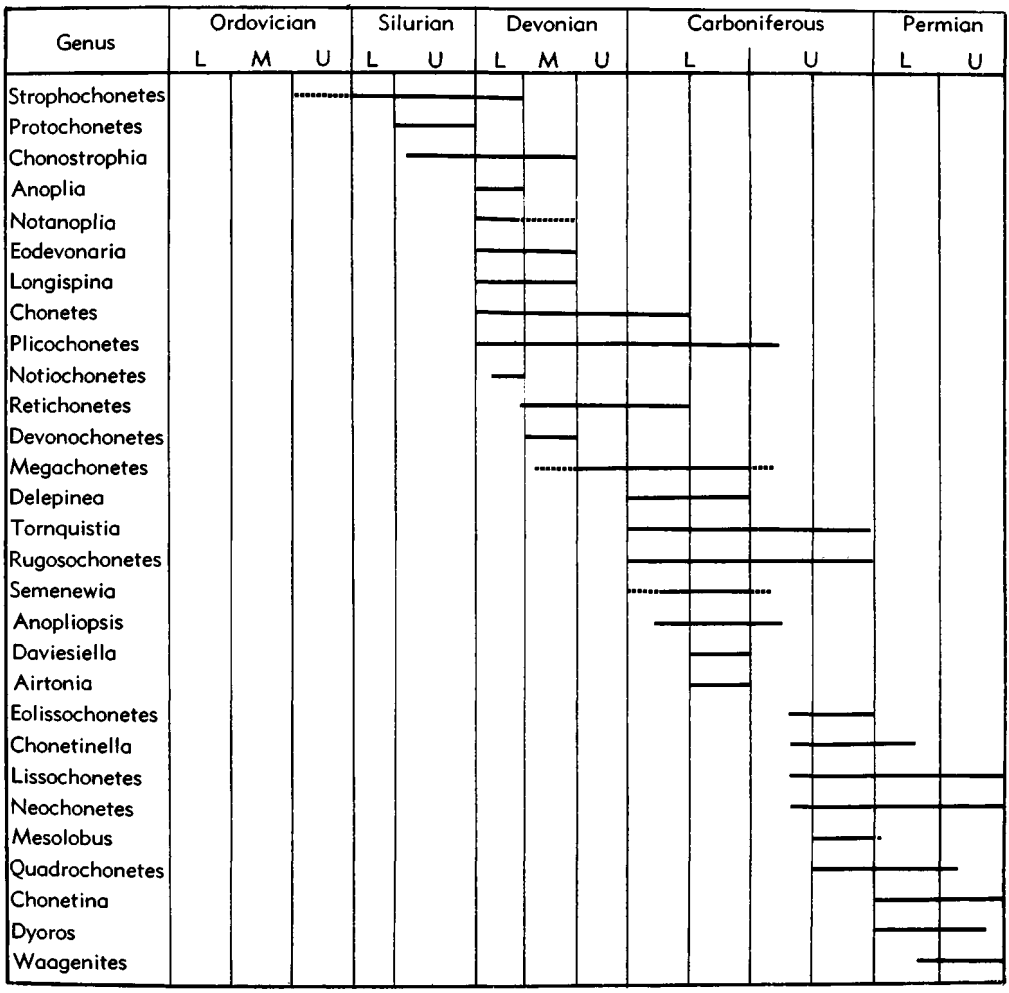

FIG. 272. Ranges of presently known chonetoid genera, with indicated duration of geologic-time divisions plotted in accordance with latest figures published by A. HOLMES (1959) (horizontal scale, 1 mm.=2.6 million years). Letters L, M, and U denote Lower, Middle, and Upper; in Silurian, L=Llandovery, U=Wenlock+Ludlow; in Devonian, L=Gedinnian+Siegenian+Emsian, M=Eifelian (Couvinian)+Givetian, U=Frasnian+Famennian; in Carboniferous, L=Tournaisian+Visean, U=Namurian+Westphalian (Mississippian corresponding to L+part of Namurian, and Pennsylvanian to U less part of Namurian) (Muir-Wood, n).

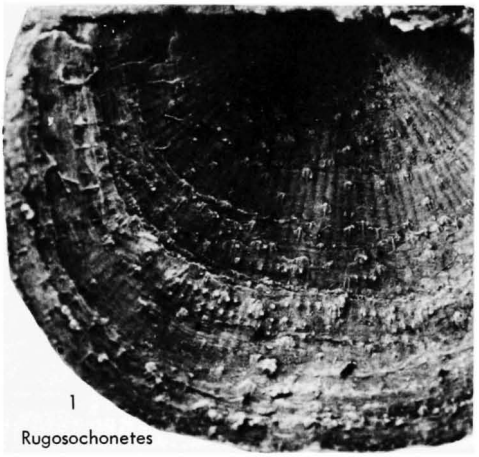

FIG. 273. Spinules in place of exterior of brachial valve of *Rugosochonetes hindi* MUIR-WOOD, U. Carb.(Namur.), Eng., ×6 (Muir-Wood, n).

rium is not occupied by a pedicle, but as in *Leptaena* and some stropheodontids, a supraapical foramen may be developed, at least in some Silurian and Devonian forms, anterior to the ventral umbo in early growth stages, and this serves for the passage of a pedicle. A pedicle pipe is rarely preserved. The young chonetoid shell was probably attached by the pedicle to some external object and is, therefore, quite unlike young productoids. In the latter an attachment ring has been observed in the pedicle valve of very young shells in several genera, serving to attach the shell to a spine or some other small cylindrical object.

The ornament of chonetacean shells may be radial, or concentric, or both combined to give a netlike structure (e.g., *Retichonetes*), or the shell may be smooth, with only growth lines or lamellae (e.g., *Tornquistia, Lissochonetes*). The radial ornament consists of longitudinal ridges separated by intercostal sulci. Intercalated costae may occur on one valve and bifurcations on the other, but normally both occur on each valve.

When there are fewer than 15 ridges in a breadth of 10 mm. the ridges are referred to as **costae** (e.g., *Plicochonetes, Waagenites*); where 15 to 25 ridges occur in 10 mm. they are called **costellae** (e.g., *Daviesiella*); when more than 25 ridges are counted in 10 mm. they are termed **capillae** (e.g., *Chonetes*). The latter term replaces "striae," since these are incisions and not ridges.

The primary capillae and costellae usually extend from the umbo, and rarely from the hinge when they correspond in position to the spine bases. Most chonetids have radial ornament, and smooth forms may be derived from them by loss of ornament, usually first seen on the anterior third or half of the shell. More rarely, costellae are developed anteriorly in a posteriorly smooth species. Decorticated shells of smooth forms may appear capillate. The ears may be smooth and the remainder of the shell capillate.

Semenewia has concentric rugae and no radial ornament, and *Chonostrophia* has fine capillae inserted between slightly coarser costellae, as in some strophomenoids. Spines occur in a row on each side of the ventral umbo. The spines, ranging in number from 4 to 20, are set along the posterior edge of the interarea and are absent from the body of the shell and from the brachial valve. The form of the spines, whether straight or curved, their length, diameter, and angle of emergence—whether high-angled, oblique, or parallel to the hinge—is found to be more or less constant in a single species, and in species belonging to the same genus, and is of considerable importance in classification. The spines are tubular and they contained extensions of the mantle, but unlike productoid spines, were probably closed at the tip. They may exhibit growth lines. The roots of the spines extend through the interarea, in some shells at an angle to the externally projecting spine. In some species the roots may be curved instead of geniculated, whereas in other forms the spines extend straight through the interarea. The spine roots are not as a rule parallel, but in *Delepinea* the roots appear as parallel incisions when the interarea is decorticated. The inner openings of the roots can be seen as rounded apertures near the anterior margin of the interarea.

Fine spinules, a few millimeters in length, leave a trace of their existence in the elongated apertures on the summit of the capillae or scattered over the shell of smooth forms (Fig. 273). The spinules are seldom preserved in place but can often be detected as minute hairlike spines in the matrix enclosing a chonetid shell. They are very numerous on both valves in upper

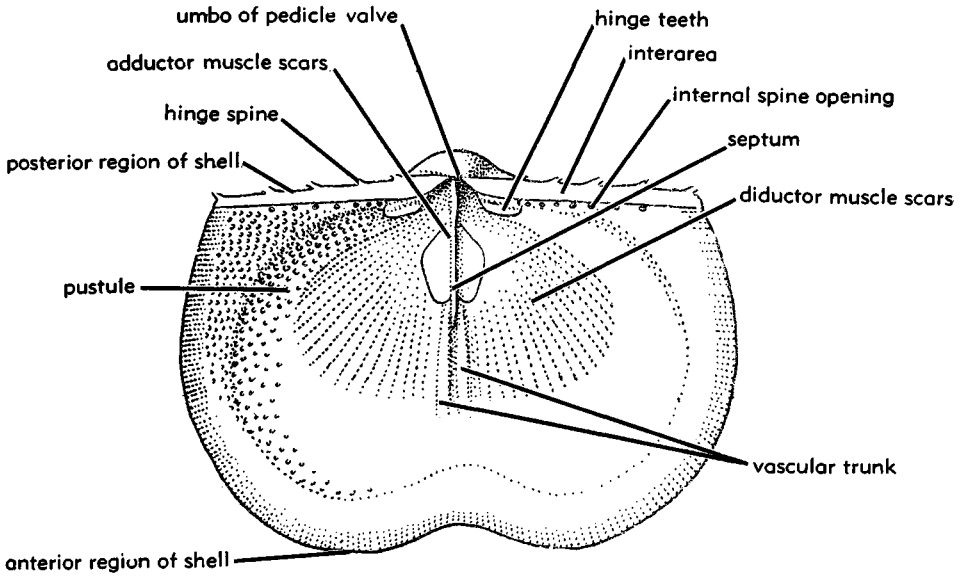

FIG. 274. Diagrammatic representation of internal morphology of pedicle valve of *Neochonetes pratti* (T. DAVIDSON), L.Perm., W.Australia, approx. ×2.5 (copyright, Trustees of British Museum, by permission).

Paleozoic forms. The spinules penetrate the outer, but not the inner shell layers, and when first formed at the shell margin each spinule would be filled with a small outgrowth of mantle and would be in communication with the shell interior. It was later sealed off by inner fibrous deposits. A median sulcus may be developed in the pedicle valve and a fold in the brachial valve (e.g., *Chonetina, Chonetinella*). An additional fold in the ventral median sulcus and a sulcus in the dorsal median fold may be developed in *Mesolobus*.

DIMENSIONS

The largest species all belong to the family Daviesiellidae and occur in the Lower Carboniferous, mostly in the Visean, and one genus extends its range into the Namurian. Species of *Delepinea* may attain a width of 8 to 10 inches and rival the Gigantoproductidae with their massive, thickened pedicle valve.

Specimens are referred to as small when their width is less than 0.75 in. or 20 mm., medium-sized when width is between 0.75 and 2 in., or 20 and 50 mm., large when the width exceeds 2 in. or 50 mm. Many chonetids are less than 20 mm. wide.

The length is measured along a vertical axis from the most posterior part of the ventral umbo to the anterior margin. The width is measured along the hinge or along the region of greatest width. The thickness is measured along an axis at right angles to length and width.

INTERNAL MORPHOLOGY

PEDICLE VALVE

The **hinge teeth** are developed as two bosses, one on each side of the anterolateral margin of the delthyrium (Fig. 274). They are usually elongated laterally and grooved longitudinally or transversely. A groove may separate the tooth from the anterior edge of the interarea and may articulate with the inner or outer ridges bounding the **hinge socket.** In *Eodevonaria* a denticulate hinge occurs and the hinge teeth and sockets are reduced.

Dental plates are normally absent but may be represented in some genera by ridges diverging from the umbo and extending as a raised rim along the outer margin of the diductor scars.

A ventral **median septum** is normally developed as a low ridge about one-third or one-half of the length of the pedicle valve. In *Protochonetes* the septum bifurcates posteriorly; in some genera it becomes more prominent and bladelike or fimbriate anteriorly.

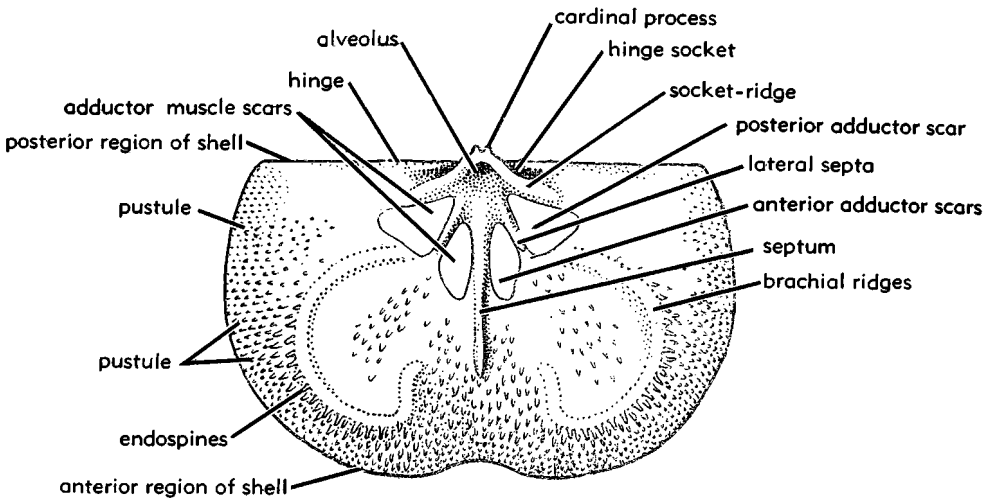

FIG. 275. Diagrammatic representation of internal morphology of brachial valve of *Neochonetes pratti* (T. DAVIDSON), L.Perm., W.Australia, approx. ×2.5 (copyright, Trustees of British Museum, by permission).

Articulation is effected by **adductor and diductor muscles,** in addition to hinge teeth and sockets. In the pedicle valve the diductor scars are usually pear-shaped, commonly ridged or furrowed, and in contact with the adductor scars along their inner margins. The adductor scars, usually four in number, are medianly placed and separated by the median septum. In smaller chonetoids the adductors are smooth. In *Daviesiella* the adductor scars are large and dendritic, and in part attached to the stout median septum. Small rounded accessory adductor scars are developed in genera belonging to the Daviesiellidae.

BRACHIAL VALVE

In the brachial valve the diductors are attached to grooves between the lobes of the outer face of the **cardinal process** (Fig. 275). The inner face of this process in larger chonetoids is short and bilobed or quadrilobed, but the outer face is large, trigonal, and lobed, with four, five, or six lobes. The dorsal adductor scars are commonly smooth and obscure but may be divisible into posterior (outer) and anterior (inner) scars. No pedicle muscle scars have been observed.

The inner face of the cardinal process may be separated from the median septum or **breviseptum** by a circular pit or **alveolus** (Fig. 276). The function of this pit, which also occurs in the Productellidae and Aulostegidae, is unknown. It may be a muscle pit, but as it appears to have been in open communication with the exterior, at least in early growth stages, it has been thought by some authors to be a visceral foramen, though no evidence is found to indicate that such exists in Recent articulate genera. In *Devonochonetes* and *Notiochonetes* the cardinal process is massive, trilobed, and supported by the septum.

The dental sockets are inserted at the base of the cardinal process and may be bounded by outer, as well as by inner, **socket ridges**

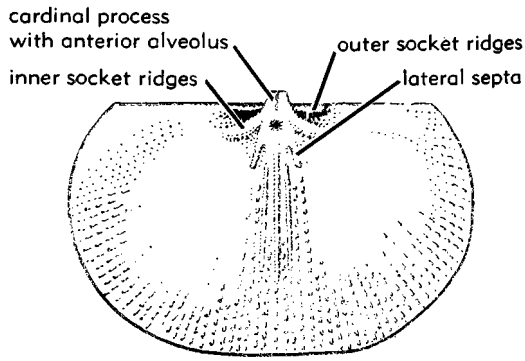

FIG. 276. Diagrammatic representation of internal morphology of brachial valve of *Chonetes sarcinulatus* (VON SCHLOTHEIM), L.Dev.(Ems.), Ger., showing three fine parallel septa and bilobate cardinal process with anterior alveolus, ×1.75 (copyright, Trustees of British Museum, by permission).

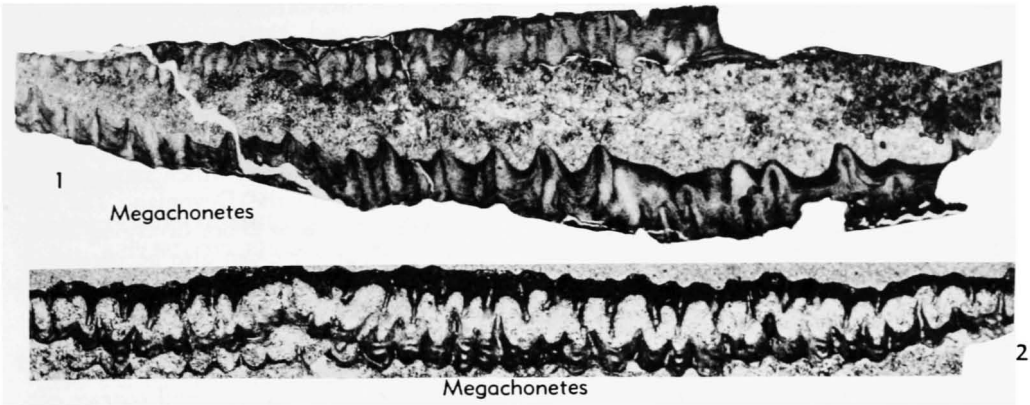

FIG. 277,*1,2*. Shell structure of *Megachonetes siblyi* (I. THOMAS), L.Carb.(U.Visean), G. Brit.; *1*, thin section through two valves showing taleolae as thin peaks with central canal clearly visible, ×10; *2*, thin section showing taleolae alternating with those of opposite valve and appearing as toothlike projections with central cavity, ×10 (Muir-Wood, n).

(Fig. 275, 276). The inner ridges are in contact with the cardinal process, and both inner and outer socket ridges probably assist in articulation of the shell.

In addition to the median septum there are usually two lateral septa, often referred to as **brachiophores.** These may have served as seat of attachment of the brachia, which may have been schizolophes or low spirolophes. Two additional septa, medially placed from the two lateral septa in some species, are referred to as **accessory septa.** Two or more diverging septa may replace the single dorsal median septum (e.g., *Chonetes s.s., Tornquistia, Anoplia*). In *Chonetina* and *Airtonia* a number of platelike ridges are present.

The brachial ridges are seldom seen in Silurian and Devonian forms but in Carboniferous and Permian chonetoids they appear as low coiled, generally endospinose ridges.

SHELL STRUCTURE

The shell of chonetoids is pseudopunctate. It is composed of a thin, lamellar, outer layer and a thicker, fibrous, inner layer with rods **(taleolae)** formerly called spicules, or pseudopunctae, composed of nonfibrous calcite (Fig. 277, 278). The taleolae are perforated medianly and in the live animal were filled with outgrowths of mantle. They appear to be closely related to the external spines and spinules. They are commonly of two diameters and variable in length, and some taleolae may project into the shell cavity as rounded pustules or as endospines. The shell tends to be much thickened posteriorly, especially in the pedicle valve of the Daviesiellidae. The mode of formation of pseudopunctate shells and their relationship, if any, to true punctate shells (e.g., Mesozoic *Spiriferina,* in which external pustules are perforate) is not perfectly understood. The subject is at present under investigation.

LIFE HABITS

After early attachment by means of the pedicle, at least in Silurian and Devonian species, chonetid shells probably rested on the sea bottom with the brachial valve uppermost, the spines along the hinge serving as balancers, or for entanglement or attachment of the normally small, light shell. It has been suggested that the smaller forms may have floated.

The surface spinules may have served as strainers across the anterior gape of the valves, like the setae in Recent brachiopods. The endospines developed in both valves would serve the same purpose and help to keep out large particles or predators.

EVOLUTION

The superfamily Chonetacea is probably polyphyletic and derived from the Plectambonitacea and Strophomenacea. The Productidina are not thought to be derived from the Chonetidina.

Strophochonetes, the earliest chonetoid

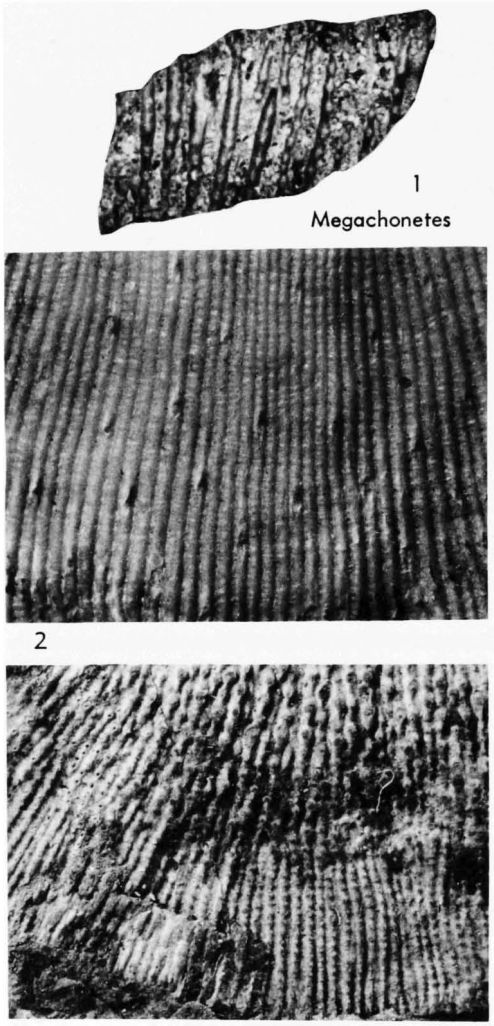

FIG. 278,*1-3*. Shell structure of *Megachonetes siblyi* (I. THOMAS), L.Carb.(U.Visean), Eng.(Derbys.); *1*, tang. sec. through shell showing rows of taleolae-like rows of beads, ×8.5; *2*, unweathered shell surface showing spinule apertures, ×7; *3*, weathered shell surface showing rows of taleolae, some with median perforation visible, ×7 (Muir-Wood, n).

now known, is capillate and has an enlarged median capilla, suggesting plectambonitid ancestry, although its musculature and the development of a median septum in each valve are chonetoid characters. Some species of *Anoplia* have oblique hollow tubes that penetrate the interarea, suggesting those of *Eochonetes* from the Upper Ordovician (Ashgillian) of Scotland (Ayrshire). *Eochonetes* has plectambonitacean musculature and external ornament and appears to be an offshoot of the Plectambonitacea.

The denticulate hinge of *Eodevonaria* is reminiscent of that of the plectambonitacean genus *Plectodonta,* which ranges from the Ordovician to the Devonian. The development of two or more diverging septa in the brachial valve can also be paralleled in the Plectambonitacea, but the ventral median septum is mainly a chonetoid character.

Chonostrophia, with reversed convexity of its valves, finer capillae and coarser costellae, as well as lobate diductor scars, suggests a strophomenoid ancestor, whereas *Devonoproductus* has spines developed as triangular projections from the hinge without any roots.

In spite of their long range small species of the Chonetacea remain practically unchanged. Except in number of spinules per capilla and better development of interareas and brachial ridges, Permian chonetoids are little more advanced or specialized than Silurian forms. This subject has been fully discussed by me elsewhere (586).

HOMEOMORPHY

A number of pairs of homeomorphs characterized by similar external form and ornament associated with dissimilar internal structures occur in the Chonetacea, as in other brachiopod superfamilies. For example, the large convex genus *Daviesiella* has been confused with *Airtonia,* the small capillate genus *Chonetes* with *Protochonetes*, the smooth genus *Anoplia* with *Tornquista* and *Lissochonetes,* and the sulcate genus *Chonetina* with *Chonetinella.* All these genera are easily distinguished by differences in their internal structure.

CLASSIFICATION

The classification employed here is based on external characters, including shell form, convexity, ornament, number of hinge spines and especially the angle of emergence of the spines, as well as on internal morphology, especially that of the brachial valve. A discussion of the present classification, as well as a history of the classification of the Chonetidina, is given by MUIR-WOOD (586).

TERMINOLOGY

Morphological terms applicable to the Chonetidina are partly the same as are employed for brachiopods generally, but others are largely or entirely restricted to this group. It is convenient to list and define the terms here.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO CHONETIDINA

accessory septa. Two septa in brachial valve situated between median septum and lateral septa in some genera.

adductor muscle scars. Muscles serving to close valves and forming 2 or 4 scars of attachment in each valve, centrally or posteriorly located on each side of median septum.

adductor scars (accessory). Two subcircular muscle scars in *Daviesiella, Delepinea,* and *Megachonetes,* interpreted by WAAGEN (1884) as adductors and by COPE (1940) as diductors.

alveolus. Circular pit in some species at base of cardinal process separating it from median septum, and interpreted as visceral foramen in early growth stages or serving as muscle pit.

angle of spines. Angle formed by external hinge spines with hinge line or interarea.

bifurcation. Forking of capillae or costellae.

brachial bases. Term used by IMBRIE (1959) for low ridgelike structures at base of cardinal process and thought by him to be homologous with orthoid brachiophores. A comparable structure observed in *Notiochonetes* was not interpreted as a brachiophore.

brachial ridges. Curved ridges extending from adductor muscle scars and possibly region of attachment of lophophore.

breviseptum. Septum not supporting cardinal process and anteriorly placed in some shells.

capillae. Fine radial ridges (more than 25 in 10 mm.) comprising external ornament of most chonetoid species.

chilidial plates. Two narrow diverging plates fused apically and in some shells developed along lateral margins of external face of cardinal process.

chilidium. Trigonal or subtrigonal plate developed in chonetoids at base of external face of cardinal process, and partly closing notothyrium; may be replaced by chilidial plates.

costae. Radial ridges on exterior of shell, broader than costellae (fewer than 15 in 10 mm.).

costellae. Radial ridges intermediate in width between capillae and costae (15 to 25 in 10 mm.).

delthyrium. Triangular opening in interarea of pedicle valve not serving for passage of pedicle, partly closed by pseudodeltidium and partly or wholly by exterior face of cardinal process.

dendritic. Having branched leaflike pattern; term used in connection with adductor muscle scars.

dental sockets. Hollows on each side of cardinal process serving for reception of hinge teeth, bounded on anterior margin by inner socket ridges, and in some shells by outer ridges along hinge margin.

diductor muscle scars. Opening muscles attached to cardinal process in brachial valve and forming large flabellate scars in pedicle valve.

endospines. Internal spines developed on interior of both valves, usually small papillae with central cavity in chonetoids (*see* taleolae).

fibrous layer. Inner shell layer formed of fine fibers commonly set at angle to shell surface, serving to thicken valves.

fold. Elevation in either valve, generally median and corresponding to sulcus in opposite valve.

hinge spines. Spines developed in row along posterior margin of pedicle-valve interarea on either side of umbo; roots of spines extending through ventral interarea generally at angle to external spines.

hinge teeth. Two peglike projections situated on anterior lateral margin of delthyrium and articulating with sockets in brachial valve.

imbricate. Having ornament consisting of overlapping lamellae.

interarea. Smooth or striated region along hinge of each valve bisected by delthyrium in pedicle valve and in some shells by notothyrium in brachial valve; formerly called cardinal area.

intercalation. Costella or capilla inserted between 2 other costellae or capillae.

lamellar layer. Outer shell layer, usually thin.

lateral septa. Short diverging ridges that tend to be anteriorly prominent and separated by median septum of brachial valve, but not as a rule in contact with it, possibly serving for attachment of lophophore; referred to by some authors as brachiophores, and by IMBRIE (1959) as adductor dividing ridges.

notothyrium. Triangular opening in interarea of brachial valve, similar to delthyrium of pedicle valve.

papillae. Short, spinelike projections (endospines) which tend to be regularly arranged in interior of both valves.

protegulum. First-formed chitinous shell, only exceptionally preserved.

pseudopunctae. *See* taleolae.

reflexed interarea. Anterior curvature of interarea of brachial valve due to secondary growth along interarea of pedicle valve, forcing umbones of valves apart to permit growth of exterior face of cardinal process.

reticulate. Having netlike enlargements formed at point of intersection of rugae or growth-lines and radial capillae or costellae.

rugae. Concentric folds, rarely developed ornament in chonetids, except in *Semenewia.*

septum. Median vertical ridge in either valve, may support cardinal process in brachial valve.

socket ridges. Ridges extending laterally from cardinal process, commonly parallel to hinge and

bounding anterior margin of hinge sockets; referred to by other authors as dental lamellae or brachiophores and by IMBRIE (1959) as prosocket ridges. Outer socket ridges extend along hinge and posterior margin of sockets; these occur in *Chonetes s.s.* but are rarely developed in other genera.

spine apertures. Internal opening of spine bases on interior of pedicle valve just below interarea.

spinules. Minute spines of fine diameter and approximately 1 or 2 mm. in length, rarely preserved *in situ*.

spinule bases, or apertures. Small oval perforations usually seen on summit of costellae or capillae and only penetrating external shell layer; represent bases of fine spinules.

squamose. Having irregular and ragged margins; often used in referring to margins of concentric lamellae.

striae. Fine radial depressions or incisions.

sulcus. Depression in either valve, commonly deep and medianly placed, dividing valve into 2 parts; shallow sulcus may separate ears from venter.

supra-apical foramen. Pedicle foramen situated outside delthyrium and generally on ventral side of umbo.

taleolae. Nonfibrous calcite rods with central cavity which are developed in fibrous shell layer and may emerge into shell cavity as endospines.

Suborder CHONETIDINA Muir-Wood, 1955

[*nom. correct.* MUIR-WOOD, herein (*pro* suborder Chonetoidea MUIR-WOOD, 1955, p. 68)]

Articulate brachiopods with functional pedicle present in all growth stages or in early stages only, foramen supra-apical and outside delthyrium. Lophophore probably schizolophous or spirolophous. Valves normally concavo-convex except in one genus. Spine row normally developed along margin of pedicle-valve interarea; spinules represented by fine apertures on shell, or spines and spinules absent. Shell composed of thin outer lamellar layer and inner fibrous layer, with hollow pseudopunctae (taleolae) present, except in Cadomellacea. Endospines commonly in radial rows. *?U.Ord., L.Sil.-L.Jur.(U.Lias.).*

Superfamily CHONETACEA Bronn, 1862

[*nom. transl.* SHROCK & TWENHOFEL, 1953, p. 317 (*ex* Chonetidae BRONN, 1862, p. 301)]

Small to large Chonetidina with functional pedicle only in early growth stages, and foramen rarely preserved. Interareas in each valve may be reflexed in brachial valve. Pseudodeltidium, chilidium, or chilidial plates and lobate cardinal process normally present. Brachial ridges and vascular markings preserved in some genera. Median septum in each valve, lateral septa in brachial valve probably acting as brachiophores. Adductor scars normally smooth, rarely dendritic, accessory adductors in one family. Shell substance lamellar and pseudopunctate. *?U.Ord., L.Sil.-U.Perm.*

Family CHONETIDAE Bronn, 1862

[Chonetidae BRONN, 1862, p. 301]

Small to medium in size; shell rarely thickened, externally smooth, capillate, costellate or lamellose, rarely rugose, spine row and spinules usually developed. Adductor scars smooth, no accessory adductors. One or more septa in brachial valve. *?U.Ord., L.Sil.-U.Perm.*

Subfamily CHONETINAE Bronn, 1862

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

Three or more fine, diverging septa in brachial valve, brachial ridges normally absent, cardinal process bilobed or quadrilobed, alveolus present; spine angle oblique (45 degrees). *L.Dev.-L.Carb.*

Chonetes FISCHER DE WALDHEIM, 1830, pl. 26, fig. 8,9 [**Terebratulites sarcinulatus* VON SCHLOTHEIM, 1820, p. 256; SD DE VERNEUIL, 1845, p. 240]. Shell small, semicircular; valves plano- or slightly concavo-convex; pseudodeltidium present; shell capillate, commonly becoming smooth or lamellose anteriorly; hinge sockets with curved inner and short outer socket ridges, no brachial ridges developed. *L.Dev.-U.Dev.*, Eu.(G.Brit.-Fr.-Ger.)-N. Am.-?Asia-N. Afr.-Australia; *L. Carb.*, Eu. (G. Brit.-Ger.).——FIG. 279,*1*. **C. sarcinulatus* (VON SCHLOTHEIM), L.Dev. (Ems.), Ger.(Eifel.); *1a*, ped.v. and brach.v. ext., ×2; *1b*, ped.v. int. mold, ×1.5; *1c*, ped.v. int. (reconstr.) showing adductor scars *(ad)*, diductor scars *(did)*, ridge bounding post. margin of diductors *(r)*, long median septum *(s)*, ×1.75; *1d*, brach.v. (lectotype) int., ×2.5 (586).——FIG. 279,*2*. *C. plebejus* SCHNUR, L.Dev.(Ems.), Ger.(Eifel.); *2a*, ped.v. ext. and brach.v. int., ×2; *2b,c*, brach.v. int., ×3, ×2 (586).

Subfamily STROPHOCHONETINAE Muir-Wood, 1962

[Strophochonetinae MUIR-WOOD, 1962, p. 40]

Dorsal median septum short or absent, prominent lateral septa, alveolus sometimes developed, spinules present, spines long, vertical. *?U.Ord., L.Sil.-L.Dev.*

Strophochonetes MUIR-WOOD, 1962, p. 40 [**Chonetes cingulatus* LINDSTRÖM, 1860, p. 374; OD]. Small, hemispherical; valves plano- or slightly concavo-convex, pseudodeltidium and chilidial plates present, capillate, commonly smooth posteriorly and lamellose anteriorly, with median en-

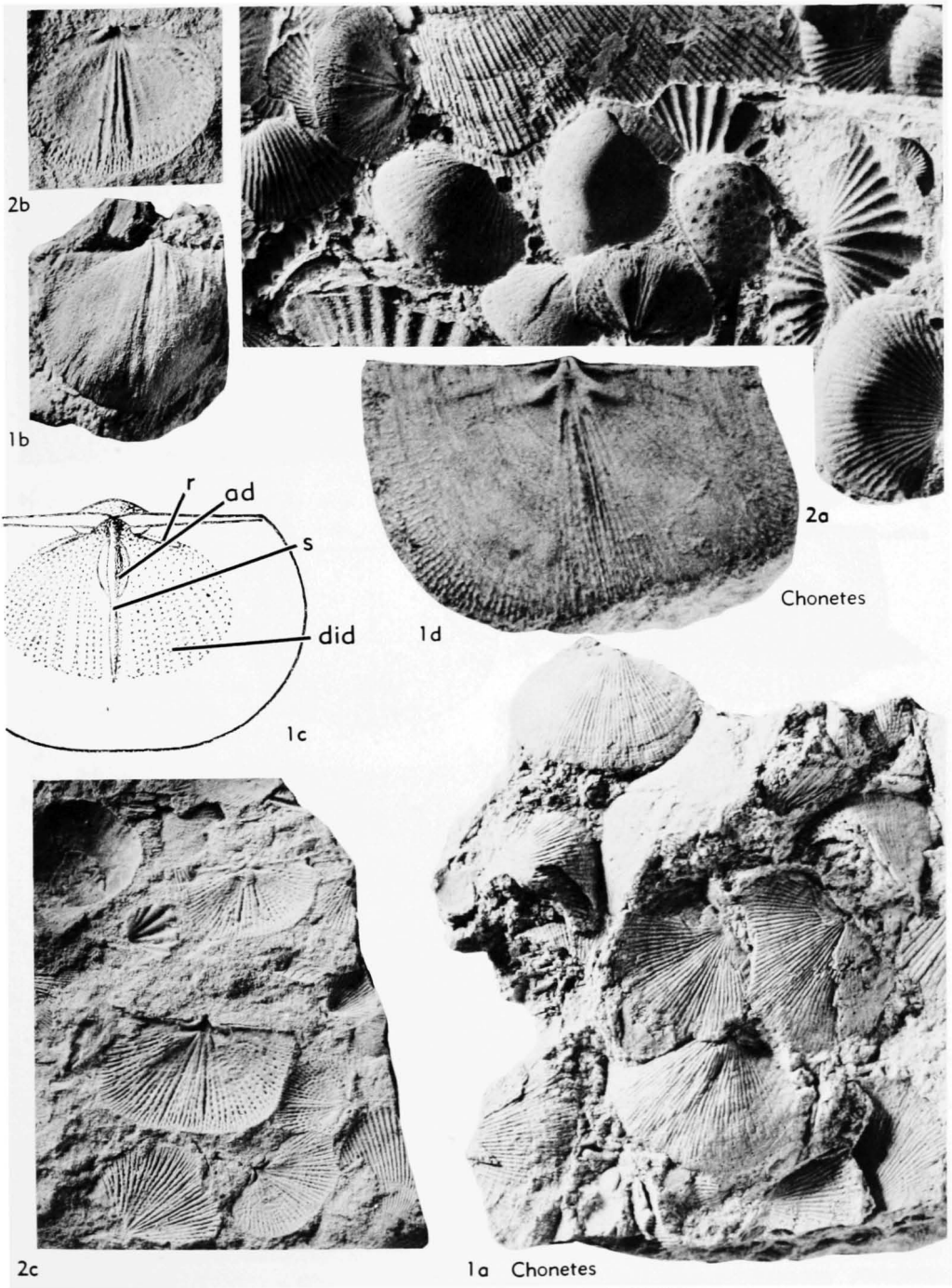

FIG. 279. Chonetidae (Chonetinae) (p. H420).

larged capilla in pedicle valve, socket ridges along hinge margin, no brachial ridges. *?U.Ord.*, N.Am. (Anticosti Is.)-Eu.(G.Brit.); *Sil.-L.Dev.*, Eu.-N. Am.(USA-Can.).——FIG. 280,*1*. *S. tenuicostatus* (OEHLERT), L.Dev., Fr.(Mayenne); brach.v. int., ×4 (586).——FIG. 280,*2*. **S. cingulatus* (LINDSTRÖM), U.Sil.(Wenlock.), Sweden(Gotl.); *2a*, ped.v. ext., ×2; *2b,c*, ped.v. ext. with long spines and prominent median capilla, brach.v. ext. showing capillae without strong median one, ×5; *2d*, slab with both ped.v. and brach.v. ext., ×3 (586).

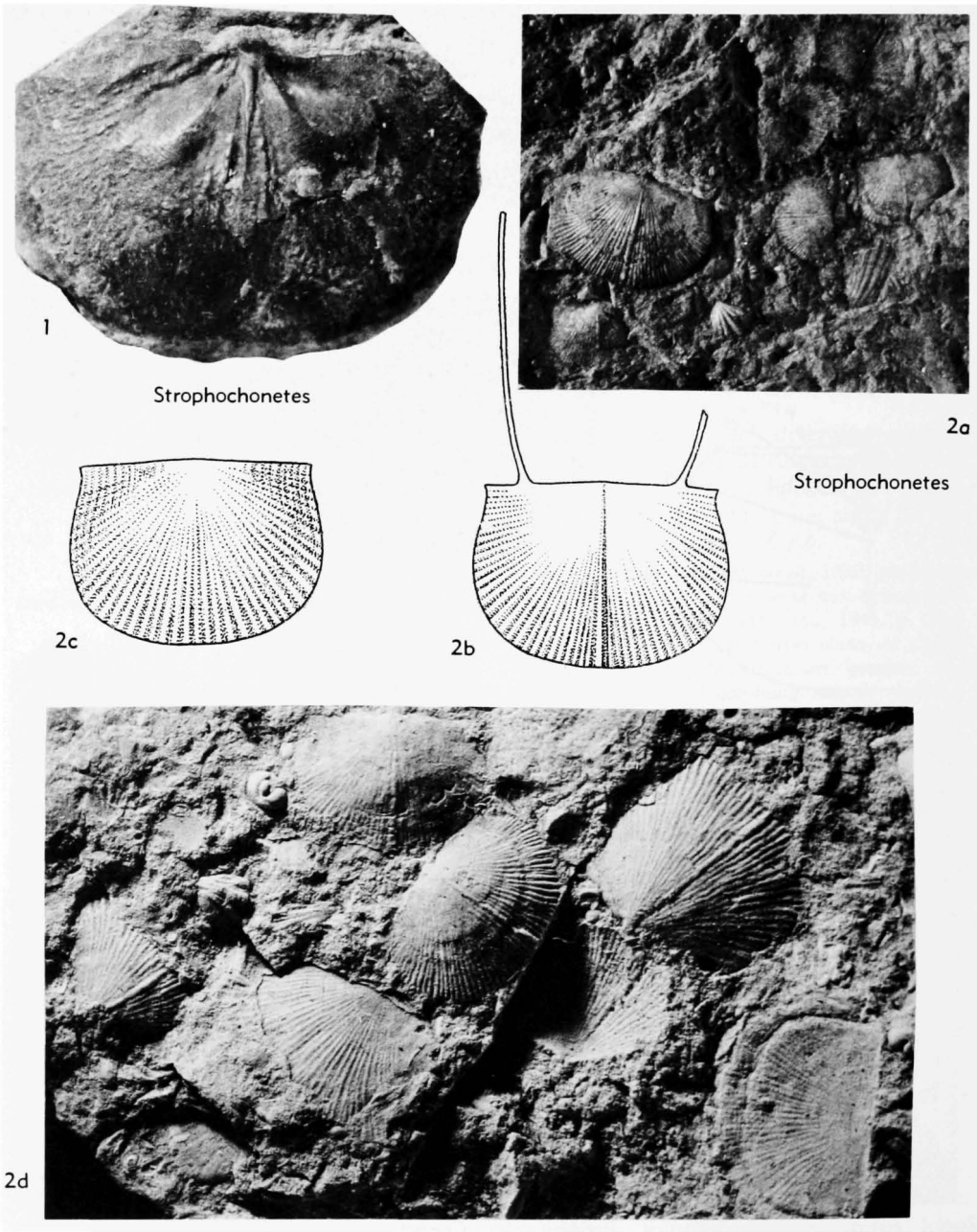

FIG. 280. Chonetidae (Strophochonetinae) (p. *H*420-*H*422).

Subfamily DEVONOCHONETINAE Muir-Wood, 1962

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

Dorsal median septum supporting large prominent bilobate or trilobate cardinal process, breviseptum in one genus, lateral septa developed, brachial ridges rarely seen; spinules developed, spines low-angled. *M. Sil.-M.Dev.*

Devonochonetes Muir-Wood, 1962, p. 43 [**Strophomena carinata* Conrad, 1842, p. 257 (*non* Conrad, 1839, p. 64) (=*Chonetes coronatus* Hall, 1857, p. 146); OD]. Shell small or medium in size; valves moderately concavo-convex, pseudodeltidium and chilidium usually present, shell costellate or capillate, spinules not numerous, spine angle low, curved inner and short outer socket ridges present. *M.Dev.(Hamilton)*, N.Am.-N.Afr.——Fig. 281,*1*. **D. coronatus* (Hall), Hamilton(Kashong Sh.), USA(N.Y.); *1a-c*, ped. v. vent., lat., ant. views, ×2.5; *1d*, brach.v. view, ×2.5; *1e*, brach.v. int., ×2.5 (586).

Longispina Cooper, 1942, p. 230 [**Chonetes emmetensis* Winchell, 1866, p. 92; OD]. Small, subquadrate; valves strongly concavo-convex, pseudodeltidium and chilidium may be present, costellate or capillate, spines long, parallel to hinge, projecting from cardinal extremities, inner socket ridges short, brachial ridges rare. *L. Dev.-M.Dev.*, N. Am.(Can.-USA)-S. Am.——Fig. 282,*1*. **L. emmetensis* (Winchell), M.Dev. (Hamilton), USA(Mich.); *1a,b*, slab showing ped. v. ext., ×1, ×2; *1c*, brach.v. int. (reconstr.) showing faint brach. ridges *(br)*, knoblike card. process *(cp)*, median septum *(s)*, and short socket ridges *(sr)*, ×4; *1d*, ped.v. int. (reconstr.) showing long spines parallel to hinge, hinge teeth *(ht)*, and short median septum, ×4 (586).

Notiochonetes Muir-Wood, 1962, p. 48 [**Chonetes skottsbergi* Clarke, 1913, p. 29; OD]. Medium-sized; brachial valve flat, pedicle valve slightly convex, pseudodeltidium and ?chilidial plates present; shell finely costellate, with spine roots but external spines rarely preserved, cardinal process large, projecting ventrally, strong inner and outer socket ridges, breviseptum and strong lateral septa present, brachial ridges rare. *Up.L.Dev.*, E.Falkland Is.——Fig. 282,*2*. **N. skottsbergi* (Clarke); *2a*, ped.v. ext. mold showing capillation and spinule bases, ×2; *2b,c*, ped.v. int., with reconstr. showing small adductor scars *(ad)*, longitud. ridged diductor scars *(did)*, hinge teeth *(ht)*, and spine openings *(so)* near hinge, ×1 ×1.5; *2d,e*, wax squeeze of brach.v. int. mold, with reconstr. showing 2 pairs of adductor scars *(ad)*, broad card. process *(cp)*, inner socket ridges *(isr)*, lateral septa *(ls)*, and outer socket ridges *(osr)*, ×1, ×1.25; *2f*, post. view of card. process showing chilidial plates, each side of card. process *(chp)*, card. process *(cp)*, inner socket ridges *(isr)*, and outer socket ridges *(osr)*, ×4 (586).

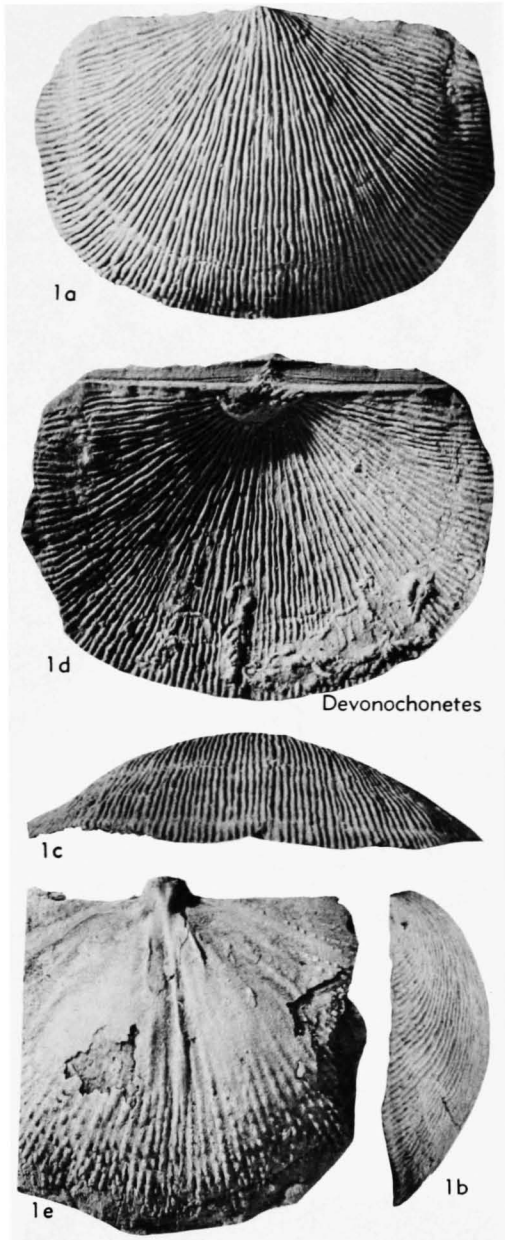

Fig. 281. Chonetidae (Devonochonetinae) (p. *H*423).

Protochonetes Muir-Wood, 1962, p. 50 [**P. ludloviensis*; OD]. Small to medium-sized; valves plano- to concavo-convex, pseudodeltidium small, chilidium may be present; shell capillate, spines oblique; ventral septum bifurcating posteriorly, dorsal septum long, anteriorly elevated, inner

socket ridges short, curved. *Sil.(Wenlock.-Ludlov.),* Eu.-N.Am.——Fig. 283,*1*. **P. ludloviensis,* U.Sil.(U.Ludlov.), Eng.(Shrops.-Herefords.); *1a,b,* ped.v. ext. (*1a,* holotype), ×3, ×4; *1c,* ped.v. int. mold showing post. bifurcating septum, ×3; *1d,e,* brach.v. int. (reconstr.) showing card. process *(cp),* lateral septa *(ls),* and socket ridges *(sr),* ×2.5 (586).——Fig. 283,*2*. *P. striatellus* (Dalman), U.Sil., Sweden(Gotl.); *2a,* ped.v. ext.; *2b,* part of brach.v. view showing interarea; *2c,* ped.v. int. showing post. bifurcating median septum; all ×3 (586).

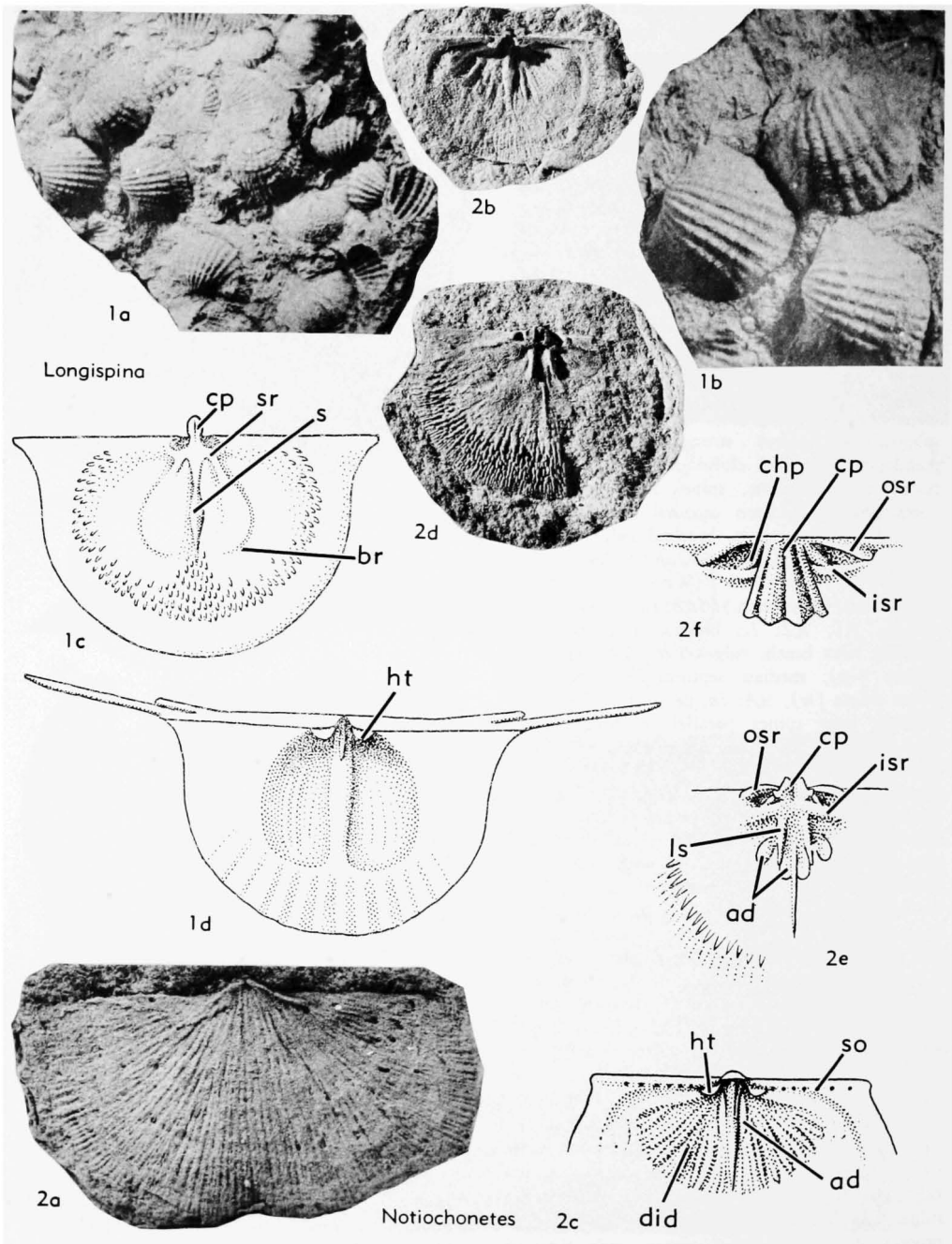

Fig. 282. Chonetidae (Devonochonetinae) (p. *H*423).

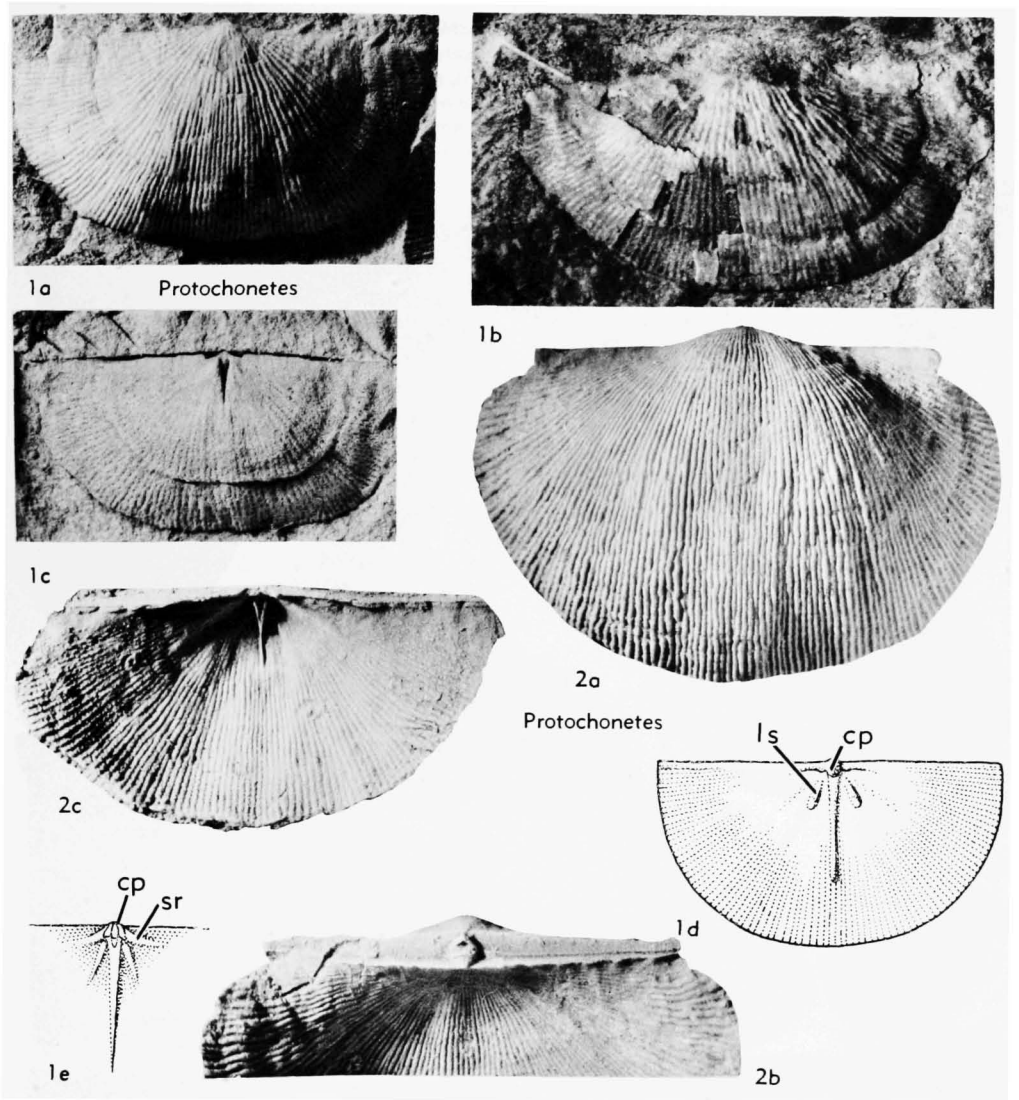

FIG. 283. Chonetidae (Devonochonetinae) (p. *H*423-*H*424).

Subfamily ANOPLIINAE Muir-Wood, 1962

[Anopliinae MUIR-WOOD, 1962, p. 53]

Two or more diverging plates or septa in one or both valves, dorsal median septum reduced or absent, no brachial ridges, cardinal process small, usually bilobed; shell normally smooth, external spines high-angled or spine roots only. *L.Dev.-L.Perm.*

Anoplia HALL & CLARKE, 1892, p. 309 [**Leptaena? nucleata* HALL, 1857, p. 47; OD(M)]. Small in size, semicircular; valves highly concavo-convex, interareas linear, pseudodeltidium present; shell smooth with growth lamellae, no spinules, spines usually absent, roots may be present; brachial valve with 2 diverging septa and short lateral septa, socket ridges long, crenulated. *L.Dev.*, N. Am. (USA-Can.) - Eu. (Belg. - Ger.) - N. Afr.-Australia(Victoria).——FIG. 284,*1*. **A. nucleata* (HALL), L.Dev.(Camden Chert), USA(Tenn.); *1a,b*, ped.v. vent., lat., ×4; *1c*, brach.v. view, ×4; *1d*, brach.v. int., ×4; *1e,f*, ped.v. and brach. v. int. (reconstr.) showing card. process *(cp)*, median septa *(s)*, socket ridges *(sr)*, ×6, ×8 (396).

Anopliopsis GIRTY, 1938, p. 281 [**Chonetina subcarinata* GIRTY, 1926, p. 27; OD]. Small trigonal shells, slightly concavo-convex; shell smooth with

few lamellae, spines at high angle, brachial valve interior with median sulcus; pedicle valve with septum, both valves with radial platelike septa from umbo to anterior margin; socket ridges short curved. *L.Miss.-U.Miss.*, N.Am.(Tex.-Tenn.-Okla.).——Fig. 284,*2*. **A. subcarinata* (Girty), L.Miss.(Ft.Payne), USA(Tenn.); *2a*, ped.v. int. cast, ×5; *2b,c*, brach.v. int. with lamellae, ×5; *2d*, ped.v. int. cast, ×5 (351).

Chonetina Krotow, 1888, p. 500 [*pro Chonetella* Krotow, 1885, p. 274, 309 (*non* Waagen, 1884, p. 613) (obj.)] [**Chonetella artiensis* Krotow,

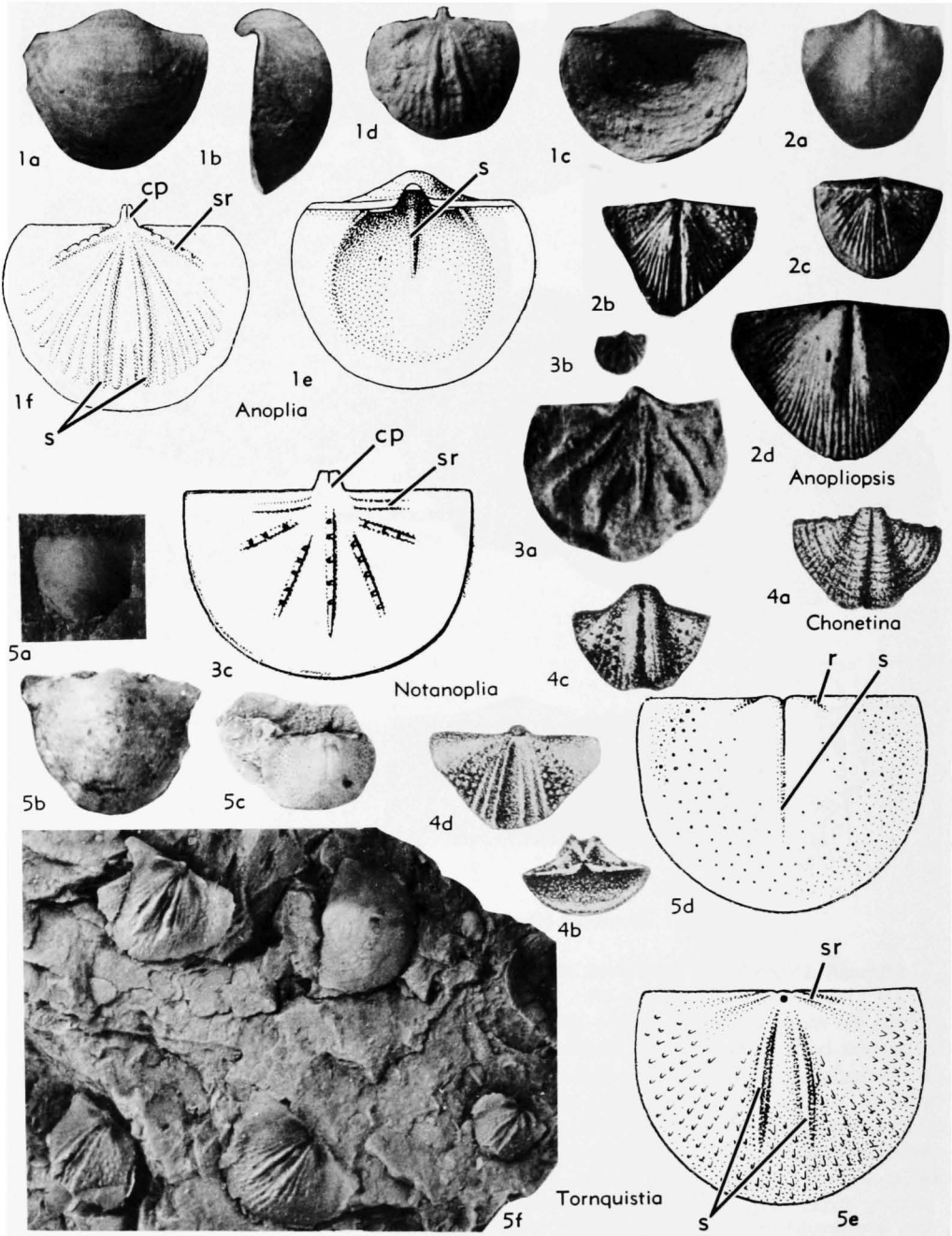

Fig. 284. Chonetidae (Anopliinae) (p. *H*425-*H*428).

1885, p. 275; OD]. Shell small, highly concavo-convex with dorsal median fold, and deep ventral sulcus; shell smooth, with growth lines, external spine row developed; brachial valve interior with several platelike septa formed from fused papillae, no true median septum. *L.Perm-U.Perm.*, Eu.-Asia.——Fig. 284,*4*. **C. artiensis* (Krotow), USSR(Urals); *4a,c,* ped.v. vent. and int. cast;

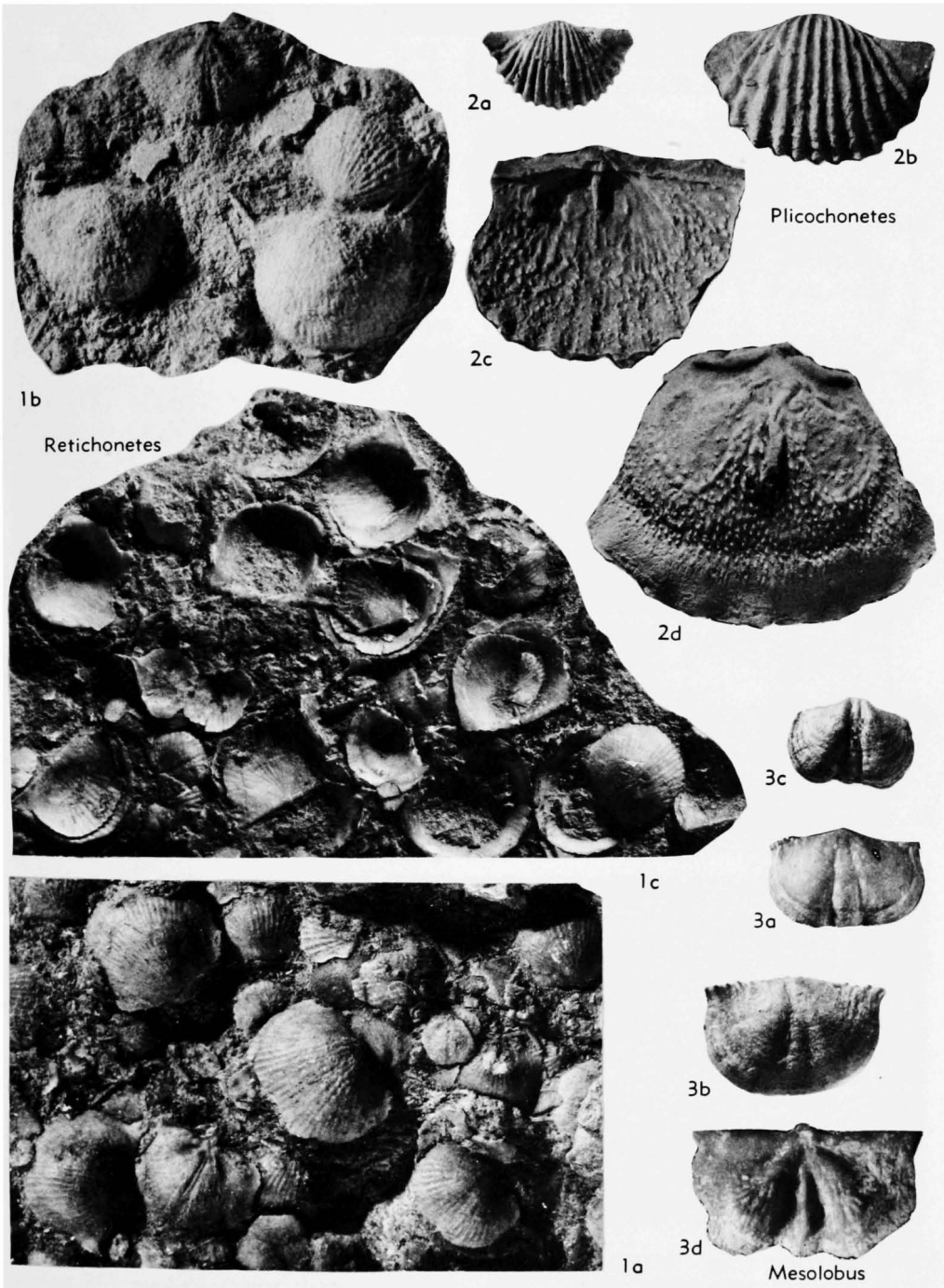

Fig. 285. Chonetidae (Retichonetinae) *(1)*, (Rugosochonetinae) *(2, 3)* (p. *H*428, *H*430).

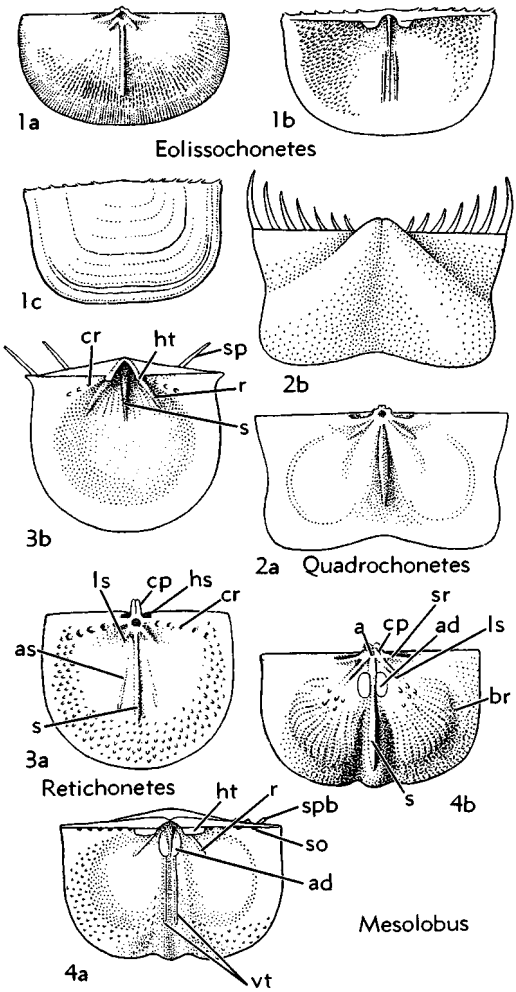

FIG. 286. Chonetidae (Retichonetinae) *(3)*, (Rugosochonetinae) *(1, 2, 4)* (p. *H*428, *H*430).

4b, ped.v. view showing interarea and umbo; *4d*, brach.v. int. cast showing int. plates; all ×3 (491).

Notanoplia GILL, 1950, p. 249 [**N. pherista*; OD]. Small, plano- or concavo-convex, shell smooth, with growth lines and rare capillae, no spine row present, both valves with long median septum and 2 or more accessory septa with row of pits along each septum, socket ridges extending along hinge. *L.Dev., ?M.Dev.*, Australia(Vict.-Tasm.). ——FIG. 284,*3a,b*. *N. loyolensis* GILL, L.Dev. (base of Yeringian), Vict.; *3a,b*, ped.v. int., ×3.5, ×1 (338).——FIG. 284,*3c*. *N.* sp., L.Dev., Vict.; brach.v. int. (reconstr.) showing card. process *(cp)*, socket ridges *(sr)* and diverging septa with pits on top, ×5 (338).

Tornquistia PAECKELMANN, 1930, p. 227 [**Leptaena (Chonetes) polita* M'COY, 1855, p. 456; OD] [=*Paeckelmannia* LIKHAREV, 1934, p. 509 (obj.)]. Small, valves highly concavo-convex, ears well demarcated, shell smooth or faintly capillate when decorticated, spinules scattered, row of spines at high angle; brachial valve interior with 2 long diverging septa, median septum rare, alveolus present, socket ridges parallel to hinge. *L. Carb.-U. Carb.*, Eu.(G.Brit.-Eire-Ger.).——FIG. 284,*5*. **T. polita* (M'COY), L.Carb., Scot.(Stirlings.); *5a,b*, ped.v. vent. showing spine row, ×4; *5c*, ped.v. int. cast, ×3; *5d,e*, ped.v. int. cast and brach.v. int. (reconstr.) showing ridges diverging from hinge *(r)*, socket ridges *(sr)*, and septa *(s)*, in ped.v. represented by slit, ×8; *5f*, slab with 4 brach.v. int. and ped.v. cast, ×3 (632).

Subfamily RETICHONETINAE Muir-Wood, 1962

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

Median septum, lateral and accessory septa and alveolus present in brachial valve; hinge longitudinally ridged when decorticated, or crenulate; brachial ridges absent, spines oblique or high-angled (45 to 60 degrees). *L.Dev.-L.Carb.(Miss.)*.

Retichonetes MUIR-WOOD, 1962, p. 62 [**Chonetes armatus* BOUCHARD-CHANTEREAUX in DE VERNEUIL, 1845, p. 241; OD]. Shell small, semicircular to subquadrate; valves moderately to highly concavo-convex, pseudodeltidium and chilidium developed, shell capillate or costellate, with growth lines or lamellae causing reticulation, spinules developed, socket ridges short, diverging from hinge. *L. Dev.-L. Carb.(Miss.)*, Eu.(G. Brit.-Fr.-Belg.-Ger.-USSR)-Asia(Burma-Tibet)-W.Australia-N. Am.(Iowa-Md.-N. Y.).——FIG. 285,*1*; 286,*3*. **R. armatus* (BOUCHARD-CHANTEREAUX), U.Dev. (Frasn.), Fr.(Boulonnais); 285,*1a*, slab with several ped.v. ext. and single brach.v. int., ×2.5; 285,*1b*, ped.v. ext. (one with long spines) and brach.v. int., ×3; 285,*1c*, slab with brach.v. ext. and ped.v. int., ×2; 286,*3a*, brach.v. int. (reconstr.) showing alveolus separating median septum *(s)* from card. process *(cp)*, accessory septa *(as)*, rounded crenulations *(cr)*, hinge sockets *(hs)*, and lateral septa *(ls)*, ×2.7; 286, *3b*, ped.v. int. (reconstr.) showing hinge teeth *(ht)*, ridges along outer margin of diductor scar *(r)*, spines *(sp)*, crenulations *(cr)* and septum *(s)*, ×2.7 (586).

Subfamily RUGOSOCHONETINAE Muir-Wood, 1962

[Rugosochonetinae MUIR-WOOD, 1962, p. 64]

Median septum, lateral, and commonly accessory septa and alveolus developed in brachial valve; cardinal process bilobate or quadrilobate, brachial ridges prominent, dorsal interarea may be reflexed; shell capillate or smooth; median fold and sulcus variably developed; spines oblique (35 to 45 degrees) or high-angled. *L.Dev.-U.Perm.*

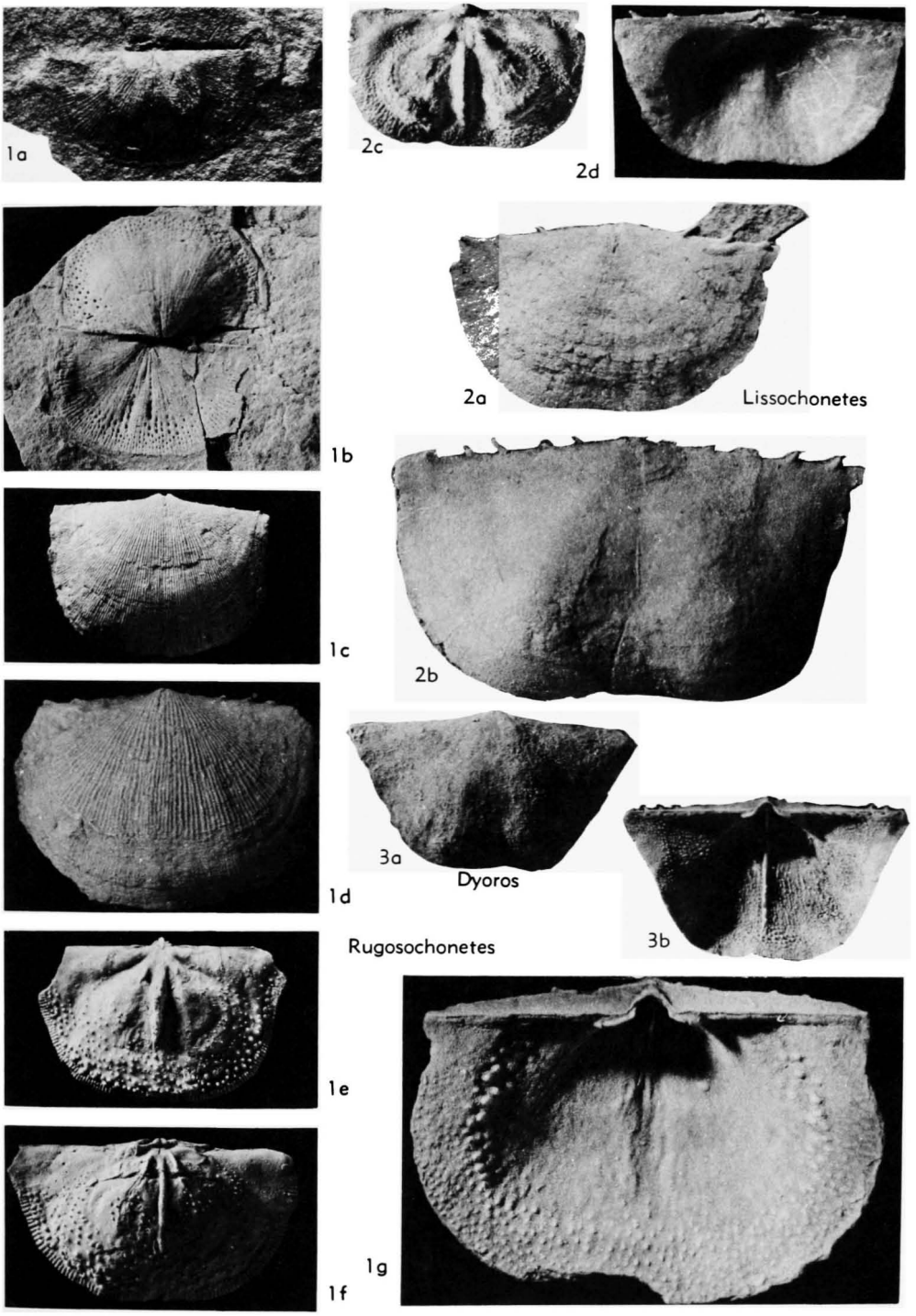

FIG. 287. Chonetidae (Rugosochonetinae) (p. *H*430).

Rugosochonetes SOKOLSKAYA, 1950, p. 23 [**Orthis hardrensis* PHILLIPS, 1841, p. 138; OD]. Shell small, plano- to slightly concavo-convex, dorsal interarea reflexed, pseudodeltidium and chilidium developed. Shell capillate, spinules numerous, dorsal median septum half of valve length, spines at angle of 45 to 60 degrees, socket ridges curved. *L. Carb.-U. Carb.*, Eu.-Asia-Australia-N.Am.-?Afr. ——FIG. 287,*1a,b*. **R. hardrensis* (PHILLIPS), L. Carb.(Visean), Eng.(Yorks.); *1a*, ped.v. ext. with impression of spines along hinge, ×2; *1b*, ped.v. and brach.v. int. molds in contact along hinge, ×2 (586).——FIG. 287,*1c-g*. *R. celticus* MUIR-WOOD, U.Carb.(Namur.), Scot.; *1c,d*, ped.v. ext., ×1.5, ×3; *1e,f*, brach.v. int., ×2; *1g*, ped.v. int., ×4 (586).

Dyoros STEHLI, 1954, p. 312 [**Chonetes consanguineus* GIRTY, 1929, p. 409; OD]. Shell small to medium-sized, slightly concavo-convex, with median fold and sulcus; pseudodeltidium vestigial or absent, shell smooth except for growth lines, capillate if decorticated, spines oblique (30 to 45 degrees), dorsal septum long, socket ridges diverging from hinge. *L.Perm.-U.Perm.*, N.Am.-?Eu.——FIG. 287,*3*; 288,*2*. *D. subliratus* (GIRTY), Perm.(Word), USA(Tex.); 287,*3a,b*, ped.v. ext., int., ×1.5; 288,*2a,b*, brach.v. int., ×4, ×1.5; 288,*2c,d*, ped.v. int., ×4, ×6.5 (773).

Eolissochonetes HOARE, 1960, p. 220 [**Chonetes laevis* KEYES, 1888, p. 229 (*non* DAVIDSON, 1866) =**E. keyesi* MUIR-WOOD, 1962, p. 76; OD]. Differs from *Lissochonetes* in its smaller dimensions and less marked ventral median sulcus, by development of long dorsal median septum and less defined brachial ridges. *M.Penn.(Desmoines.)*, N. Am.——FIG. 286,*1a*. **E. keyesi* MUIR-WOOD, USA (Mo.); brach.v. int., ×1.8 (429).——FIG. 286, *1b,c*. *E. bilobatus* HOARE, USA(Mo.); *1b,c*, ped.v. int., ext., ×1.8 (429).

Lissochonetes DUNBAR & CONDRA, 1932, p. 169 [**Chonetes glaber* GEINITZ, 1866, p. 60 (*non* HALL, 1857, p. 117)=*Chonetes geinitzianus* WAAGEN, 1884, p. 621; OD]. Small to medium-sized; valves slightly concavo-convex with ill-defined fold and sulcus, pseudodeltidium present; shell smooth with fine growth lines and spinules, capillate if decorticated, spines long, at angle of about 40 degrees, dorsal septum may be anterior only or absent, socket ridges along hinge. *U.Carb.*, Eu.-Asia-N.Afr.-Australia; *Penn.-Perm.*, N.Am.-Asia.——FIG. 287,*2*. *L. geinitzianus* (WAAGEN), U.Penn.(Virgil.), Neb. (*2a,b,d*), Ill. (*2c*); *2a,b*, ped.v. ext. with spine row, ×3.5; *2c,d*, brach.v. int., ext., ×3 (270).

Mesolobus DUNBAR & CONDRA, 1932, p. 134, 159 [**Chonetes mesolobus* NORWOOD & PRATTEN, 1855, p. 27; OD]. Small, valves moderately concavo-convex, normally with ventral sulcus bearing median fold, and dorsal fold bearing median sulcus; pseudodeltidium and chilidium present; shell capillate or smooth, commonly lamellose; spines oblique, spinules numerous; dorsal median septum long, anteriorly elevated and serrated, inner socket ridges parallel to hinge. *Penn.*, N.Am.; *?L.Perm.*, Eu.——FIG. 285,*3*; 286,*4*. **M. mesolobus* (NORWOOD & PRATTEN), M.Penn. (Desmoines.), USA (Ill.); 285,*3a-c*, ped.v. ext., ×2.5, ×2, ×2; 285, *3d*, brach.v. int., ×4; 286,*4a*, ped.v. int. (reconstr.), showing adductor scar (*ad*), hinge teeth (*ht*), ridge along post. margin of diductor scars (*r*), int. spine openings (*so*), spine bases (*spb*), and vascular trunks (*vt*), ×4; 286, *4b*, brach.v. int. (reconstr.) showing alveolus (*a*), adductor scars (*ad*), brachial ridges (*br*), card. process (*cp*), lateral septa (*ls*), median septum (*s*), and socket ridges (*sr*), ×4 (270).

Plicochonetes PAECKELMANN, 1930, p. 222, 306, 311 [**Chonetes buchianus* DEKONINCK, 1843, p. 208; OD]. Small to medium-sized, concavo-convex, pedicle valve medianly arched, pseudodeltidium small or absent; shell costate or costellate, rarely bifurcating, numerous growth lines, spines at high angle (55 to 70 degrees), spinules developed; septum in brachial valve extending half of its length or absent, inner socket ridges short, curved. *L.Dev.-U.Dev.*, Eu.(Eng.-Fr.-Ger.)-Asia; *L.Carb. (Miss.)*, Eu. - Asia - N. Afr.-Australia-N. Am.; *U. Carb.(Namur.)*, Eu.(Eng.-Czech.).——FIG. 285, *2*. **P. buchianus* (DEKONINCK), L.Carb.(U.Visean) or U.Carb.(Namur.), Eng.(Yorks.); *2a,b*, ped.v. ext., ×1, ×1.5; *2c*, ped.v. int., ×3; *2d*, brach.v. int., ×3 (483).

Quadrochonetes STEHLI, 1954, p. 309 [**Chonetes quadratus* GIRTY, 1929, p. 407 (*non C. uralica quadratus* BOLKHOVITINOVA & MARKOV, 1926, p. 26, *non* NIKITIN, 1890)=*Q. girtyi* STEHLI, 1954; OD]. Small, quadrate, strongly concavo-convex, with prominent dorsal fold and deep ventral sulcus, ears large; shell smooth, with spines at angle of 75 degrees; median septum of brachial valve low, extending about half of its length, brachial ridges obscure or absent, socket ridges short, curved. *Penn.-L.Perm.*, N.Am.; *L.Perm.*, Eu. (USSR).——FIG. 286,*2*. *Q. girtyi*, L.Perm. (Leonard), USA(Tex.); *2a,b*, brach.v. int., ped. v. ext., ×2.7 (773).

Subfamily CHONETINELLINAE Muir-Wood, 1962

[Chonetinellinae MUIR-WOOD, 1962, p. 85]

Internally near to Rugosochonetinae, but no accessory septa; median fold and sulcus usually strong; dorsal interarea commonly reflexed; shell capillate to costate; spinules numerous; spines parallel to hinge. *U.Carb. (Penn.)-U.Perm.*

Chonetinella RAMSBOTTOM, 1952, p. 13 [**Chonetes flemingi* NORWOOD & PRATTEN, 1855, p. 26; OD]. Small, bilobate, highly concavo-convex, with deep median sulcus and high fold, pseudodeltidium and chilidium rudimentary or absent; shell capillate, with spinules; cardinal process small, bilobed,

with alveolus, median septum long, anteriorly elevated; socket ridges long, parallel to hinge, brachial ridges prominent. *U.Carb.(Penn.)*, Eu.-N.Am.-S.Am.; *L.Perm.*, N.Am.-Asia.——Fig. 288,*1*. **C. flemingi* (Norwood & Pratten), Penn., Tex. *(1a-e)*, Ill. *(1f)*; *1a,b*, ped.v. ext., brach.v. ext., ×3; *1c,d*, ped.v. ext. with spines, brach.v. ext. and interarea, ×8; *1e,f*, ped.v. int., brach.v. int., ×3 (654).

Neochonetes Muir-Wood, 1962, p. 87 [**Chonetes dominus* R. H. King, 1938, p. 259; OD] [=*Quadranetes* Sadlick, 1963, p. 721 (obj.)].

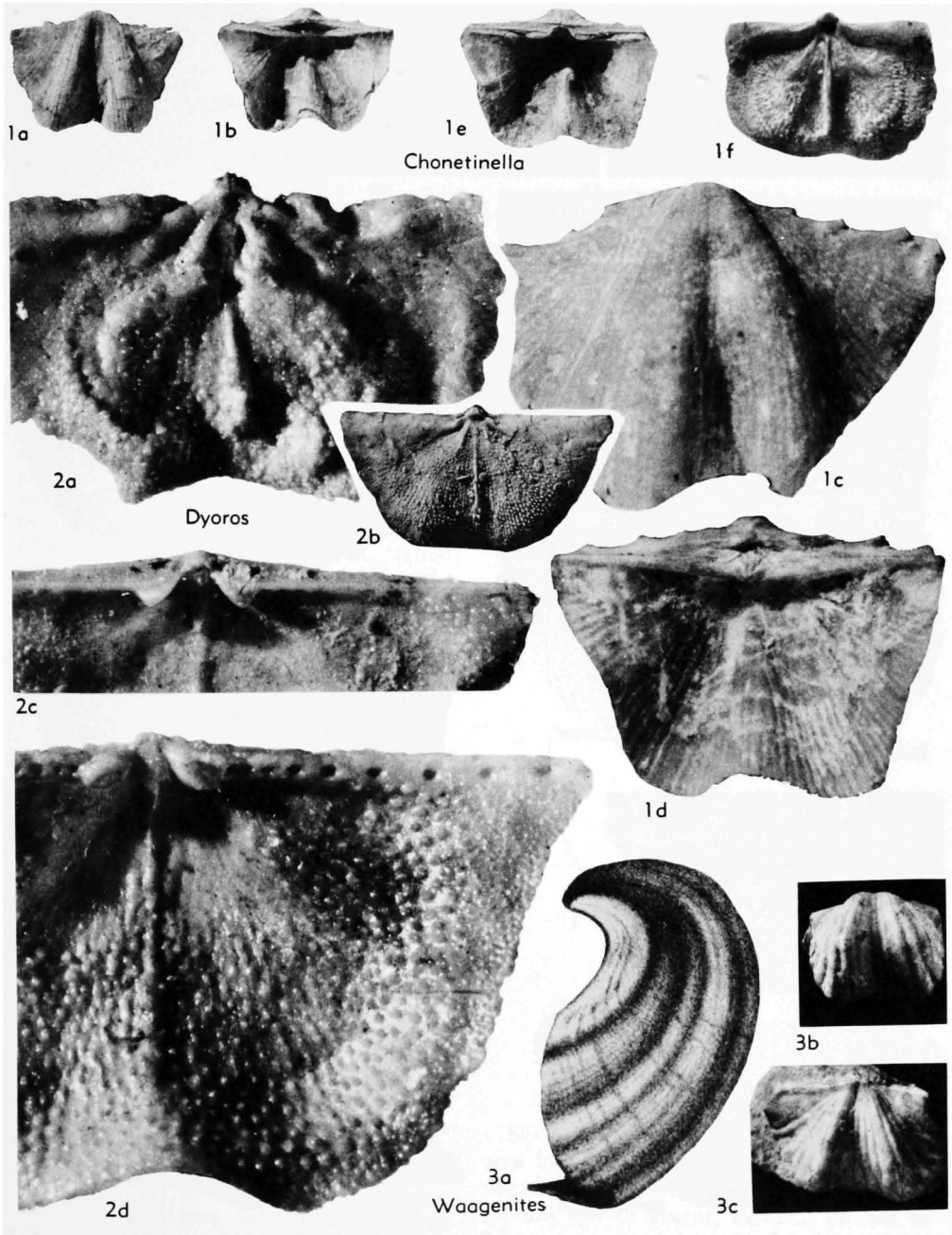

Fig. 288. Chonetidae (Rugosochonetinae) *(2)*, (Chonetinellinae) *(1, 3)* (p. *H*430-*H*433).

Small to medium-sized, plano- to slightly concavo-convex, ventral valve may be sulcate; pseudodeltidium vestigial or absent, chilidium present; capillate or smooth anteriorly, many spinules, hinge spines numerous; median septum anteriorly elevated, with inner socket ridges and commonly outer ones also. *U.Carb.(Penn.)-U.Perm.*, cosmop. ——Fig. 289,*1a,b*. *N. transversalis* (Dunbar & Condra), U.Penn., USA(Neb.); *1a,b,* ped.v. ext., brach.v. int., ×2 (471).——Fig. 289,*1c*. *N. granulifer* (Owen), Penn., USA(Ala.); ped.v. int., ×2 (471).——Fig. 289,*1d-g*. **N. dominus*

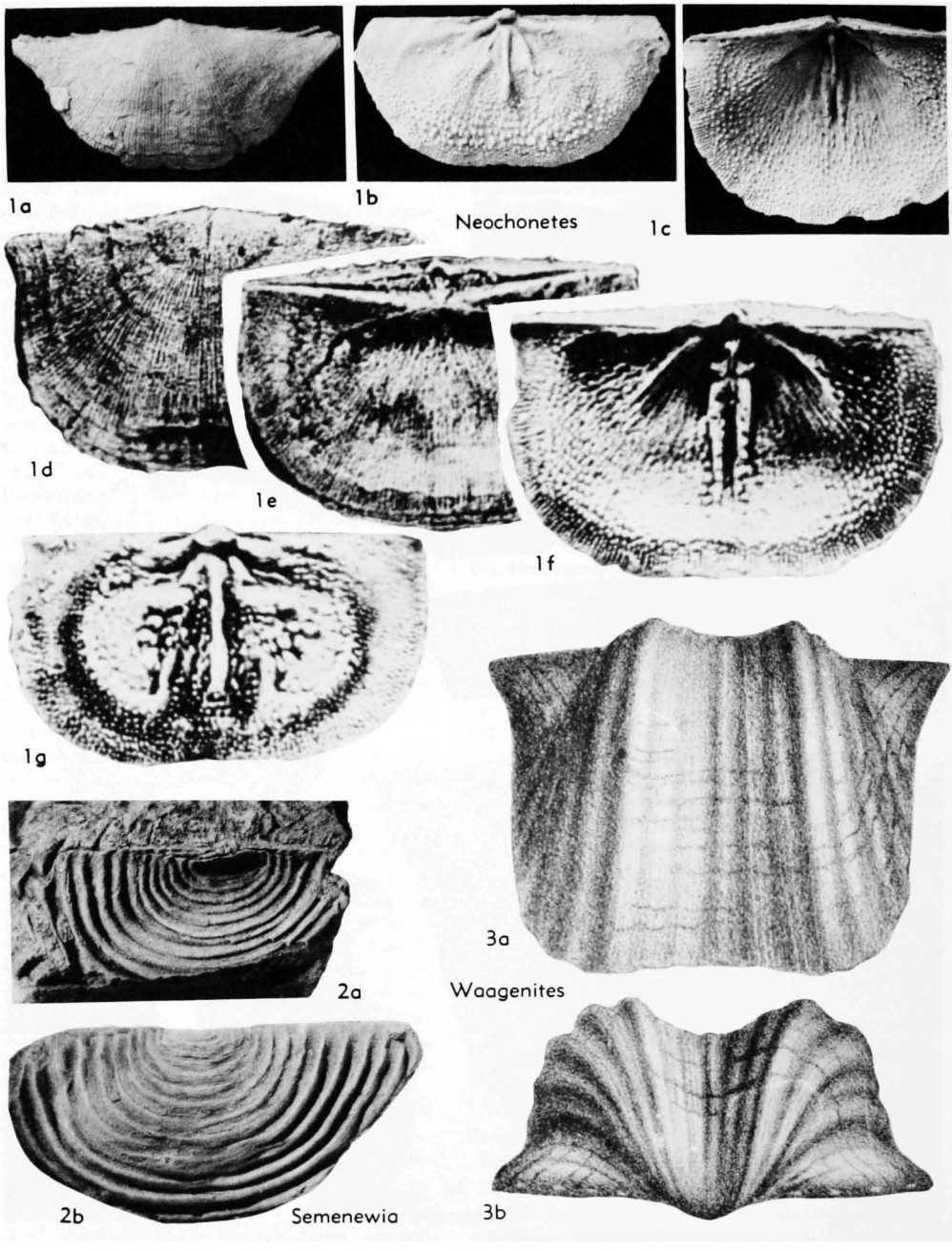

Fig. 289. Chonetidae (Chonetinellinae) *(1, 3)*, (Semenewiinae) *(2)* (p. *H*431-*H*433).

(R. H. KING), Penn., USA(Tex.); *1d,e,* ped.v. ext., brach.v. ext., ×3; *1f,g,* ped.v. int., brach.v. int., ×3 (471).

Waagenites PAECKELMANN, 1930, p. 223 [**Chonetes grandicostus* WAAGEN, 1884, p. 638; OD] [=*Dienerella* REED, 1931, p. 18 (obj.)]. Small, quadrate, pedicle valve highly convex, with deep median sulcus, no pseudodeltidium, umbo much incurved; valves with few coarse costae, or costellate, rarely capillate; ears large, smooth, dorsal septum medianly developed, socket ridges short. *U.Perm.,* Asia(Pak.-Timor)-?N.Am.-Arctic (Spitz.).——FIG. 288,*3*; 289,*3*. **W. grandicostus* (WAAGEN), U.Perm.(U.Productus Ls.), Pak.(Punjab); 288,*3a,* ped.v. lat., ×4; 288,*3b,c,* ped.v. ext., ×1.5, ×2; 289, *3a,b,* ped.v. ext., post., ×4 (845) (288,*3a,* 289,*3a,b,* after Waagen).

Subfamily SEMENEWIINAE Muir-Wood, 1962

[Semenewiinae MUIR-WOOD, 1962, p. 91]

Median septum in each valve, valves ornamented by concentric rugae, spines vertical. *L.Carb.(Tournais.-Visean).*

Semenewia PAECKELMANN, 1930, p. 217, 224 [**Chonetes concentricus* DEKONINCK, 1874, p. 186; OD]. Small to medium-sized, semicircular, slightly concavo-convex, interareas low, pseudodeltidium present; shell with concentric rugae and no radial ornament, spinules developed; internal characters imperfectly known. *L.Carb. (Tournais.-Visean),* Eu.——FIG. 289,*2*. **S. concentrica* (DEKONINCK), Visean, Belg.; *2a,b,* ped.v. ext. with curved erect spines, ×2 (483).

[Subfamily Uncertain.—Eccentricosta, Nix, *see* p. *H*904.]

Family EODEVONARIIDAE Sokolskaya, 1960

[Eodevonariidae SOKOLSKAYA, 1960, p. 223]

Hinge denticulate, hinge teeth and sockets reduced; with long curving inner socket ridges, alveolus absent, strong dorsal septum and lateral septa, spines low-angled. *L.Dev.-M.Dev.*

Eodevonaria BREGER, 1906, p. 534 [**Chonetes arcuatus* HALL, 1857, p. 76; SD, SCHUCHERT & LEVENE, 1929, p. 57]. Small to medium-sized, laterally extended, strongly concavo-convex, with incurved ventral umbo, pseudodeltidium developed; shell capillate, spinules rare; cardinal process bilobate or quadrilobate. *L.Dev.-M.Dev.,* Eu.-N.Afr.-S.Afr.-N.Am.-S.Am.——FIG. 290,*1*. *E. dilatata* (RÖMER), L.Dev.(Emsian), Ger.; *1a,* brach.v. int., ×1; *1b,* ped.v. int. with denticulate hinge, ×1; *1c,d,* squeeze of brach.v. int. with post. view showing card. process, ×2; *1e,* decorticated ped.v., ×1.5; *1f,* ped.v. int. (reconstr.) showing adductor scars *(ad),* denticulate hinge *(dh),* diductor scars *(did),* and median septum *(s),* ×1.25 (117).

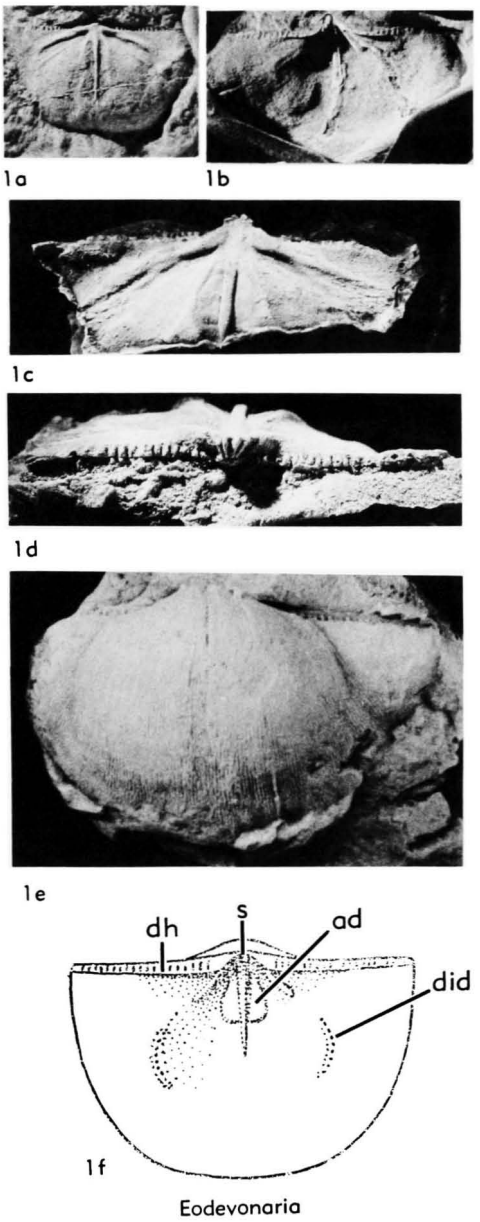

FIG. 290. Eodevonariidae (p. *H*433).

Family CHONOSTROPHIIDAE Muir-Wood, 1962

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

Shell convexity reversed; ventral muscle area lobed, with raised rim, as in strophomenoids; ventral septum present, dorsal septum low or absent; cardinal process bilobate, supported laterally by short socket ridges. *U.Sil.-M.Dev.*

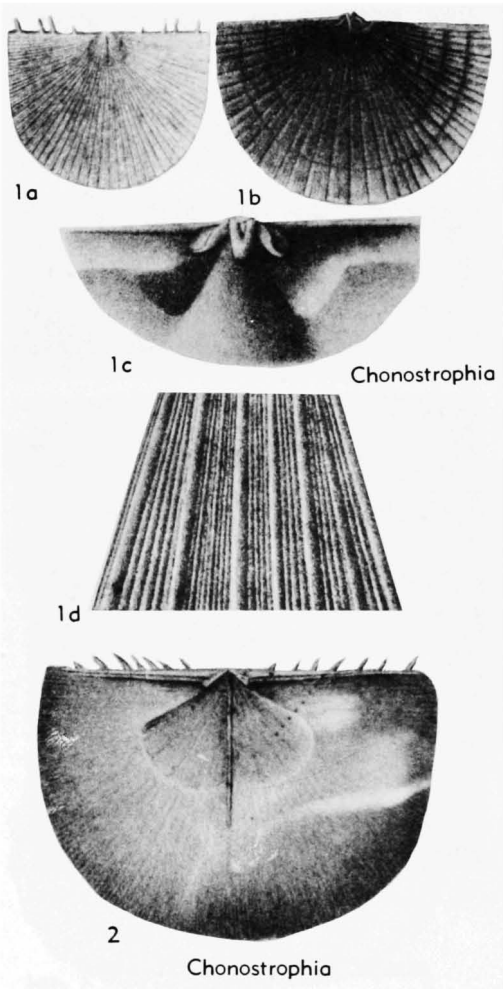

FIG. 291. Chonostrophiidae (p. *H*434).

Chonostrophia HALL & CLARKE, 1892, p. 310 [**Chonetes reversa* WHITFIELD, 1882, p. 213; OD (M)]. Medium-sized, semicircular, thin-shelled, pedicle valve resupinate, brachial valve slightly convex, interareas linear, pseudodeltidium present; valves costellate, with intervening capillae, spines long, vertical. *U.Sil.-M.Dev.*, N.Am.(Can.-USA)-S. Am.(Colombia-Bolivia-Argentina). —— FIG. 291,*1*. **C. reversa* (WHITFIELD), L.Dev.(U. Helderberg.), N.Am., Can.(Ont.) *(1a)*, USA (Ohio) *(1b-d)*; *1a,b*, ped.v. ext., ×2.5; *1c*, brach.v. int. showing card. process, ×9; *1d*, ext. ornament, ×9 (396).——FIG. 291,*2*. *C. complanata* (HALL), L.Dev.(Oriskany), USA(N.Y.); ped.v. int., ×1 (396).

Chonostrophiella (*see* p. *H*904).

Tulcumbella (*see* p. *H*905).

Family DAVIESIELLIDAE Sokolskaya, 1960

[Daviesiellidae SOKOLSKAYA, 1960, p. 223]

Medium-sized to large, pedicle valve usually thickened; median septum in each valve, cardinal process bilobate or quadrilobate; brachial ridges may be developed, adductor scars wholly or partly dendritic or striated, detached rounded accessory adductor scars present; rarely row of oblique or high-angled spines. *?M.Dev., U.Dev.-L. Carb., ?U.Carb.(Namur.)*.

Subfamily DAVIESIELLINAE Sokolskaya, 1960

[*nom. transl.* MUIR-WOOD, 1962, p. 96 (*ex* Daviesiellidae SOKOLSKAYA, 1960, p. 223)]

Dorsal septum massive, supporting cardinal process, without alveolus, brachial ridges anteriorly directed, adductor scars dendritic; interareas low. *L.Carb. (Visean)*.

Daviesiella WAAGEN, 1884, p. 613 [**Productus llangollensis* T. DAVIDSON, 1863, p. 277; SD OEHLERT, 1887, p. 1280]. Large, highly concavo-convex, pedicle valve massive, much thickened; pseudodeltidium lacking, chilidium present; capillate or costellate, external spine row not observed. *L.Carb.(Visean)*, Eu.(Eng.-Wales).——FIG. 292,*1*. **D. llangollensis* (DAVIDSON), Wales(Denbighs.); *1a,b*, ped.v. vent., lat., ×1; *1c*, interareas showing hinge teeth and chilidium of damaged specimen, ×2; *1d,e*, ped.v. int., brach.v. int., ×1 (201).

Subfamily DELEPINEINAE Muir-Wood, 1962

[Delepineinae MUIR-WOOD, 1962, p. 99]

Dorsal median septum fine, not supporting cardinal process, alveolus present, lateral septa short, brachial ridges not observed; pseudodeltidium and chilidium present, ventral interarea high, with spine roots as parallel incisions, some forms with external row of oblique spines. *?M.Dev., U.Dev.-L.Carb., ?U.Carb.(Namur.)*.

Delepinea MUIR-WOOD, 1962, p. 99 [**Productus comoides* J. SOWERBY, 1822, p. 31; OD]. Large, moderately concavo-convex; pedicle valve posteriorly thickened, layers weathering characteristically; capillate or costellate, spinules present, spine row rarely preserved. *L.Carb.(Tournais.-Visean)*, Eu.(G. Brit.-Fr.-Belg.-Ger.-USSR-N.Afr.-Asia.——FIG. 293,*1*. **D. comoides* (J. SOWERBY), Visean, Eng.(Westmorland); *1a,b*, ped.v. ext., brach.v. view, ×1 (586).——FIG. 293,*2*. *D. destinezi* (VAUGHAN), Visean, N.Ire.(Fermanagh); *2a,b*, ped.v. int. showing spine roots in interarea and accessory adductor scars, ×1 (586).——FIG. 293,*3*. *D. carinata* (GARWOOD), Visean, Eng.(Westmorland); *3a*, ped.v. ext., ×1; *3b*, brach.v. int., ×1 (586).

Megachonetes SOKOLSKAYA, 1950, p. 42 [**Chonetes compressa* SIBLY, 1908 (*non* WAAGEN, 1884, p. 630) =*C. siblyi* I. THOMAS, 1919, p. 612 (also PAECKELMANN, 1930, p. 274); OD]. Medium-sized to large, plano- to slightly concavo-convex, pedicle valve slightly thickened, interareas commonly high, shell finely capillate, spinules numerous, spines curved, extending at angle of 45 to 60 degrees. *?M.Dev.*, Eng.; *U.Dev.-L.Carb. (Tournais.-U.Visean), ?U.Carb.(Namur.)*, Eu.(G. Brit.-Eire-Fr.-Belg.-Ger.-USSR)-?Asia-N.Afr. —— FIG. 294,*1. M. siblyi* (I. THOMAS), L.Carb. (Visean), Eng.(Yorks.-Derbys.); *1a-c,* ped.v. vent., brach.v. ext. and lat. views, ×1.25; *1d,* brach.v. view showing interarea, ×2; *1e,* ped.v. post. with interarea and pseudodeltidium, ×1;

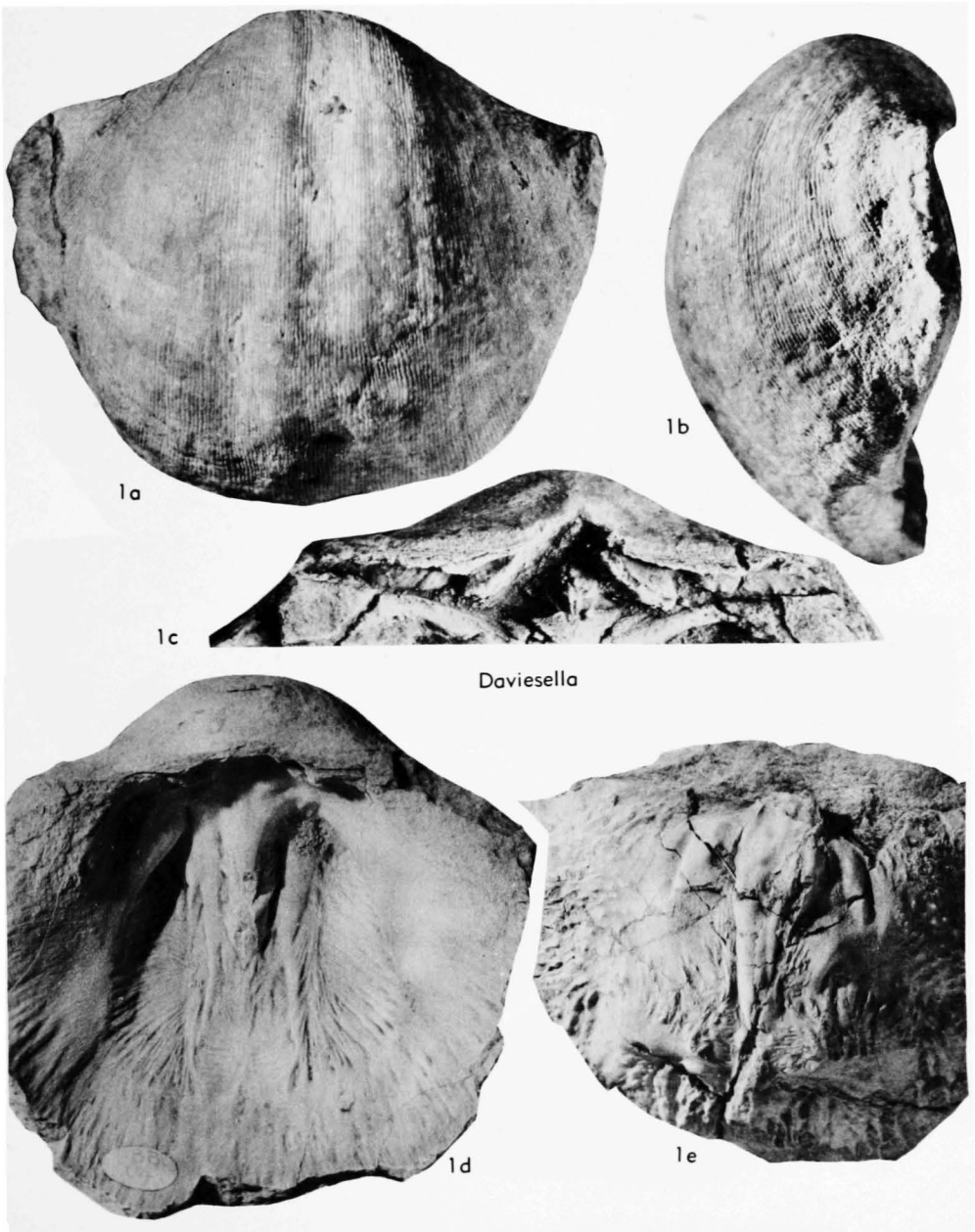

FIG. 292. Daviesiellidae (Daviesiellinae) (p. *H*434).

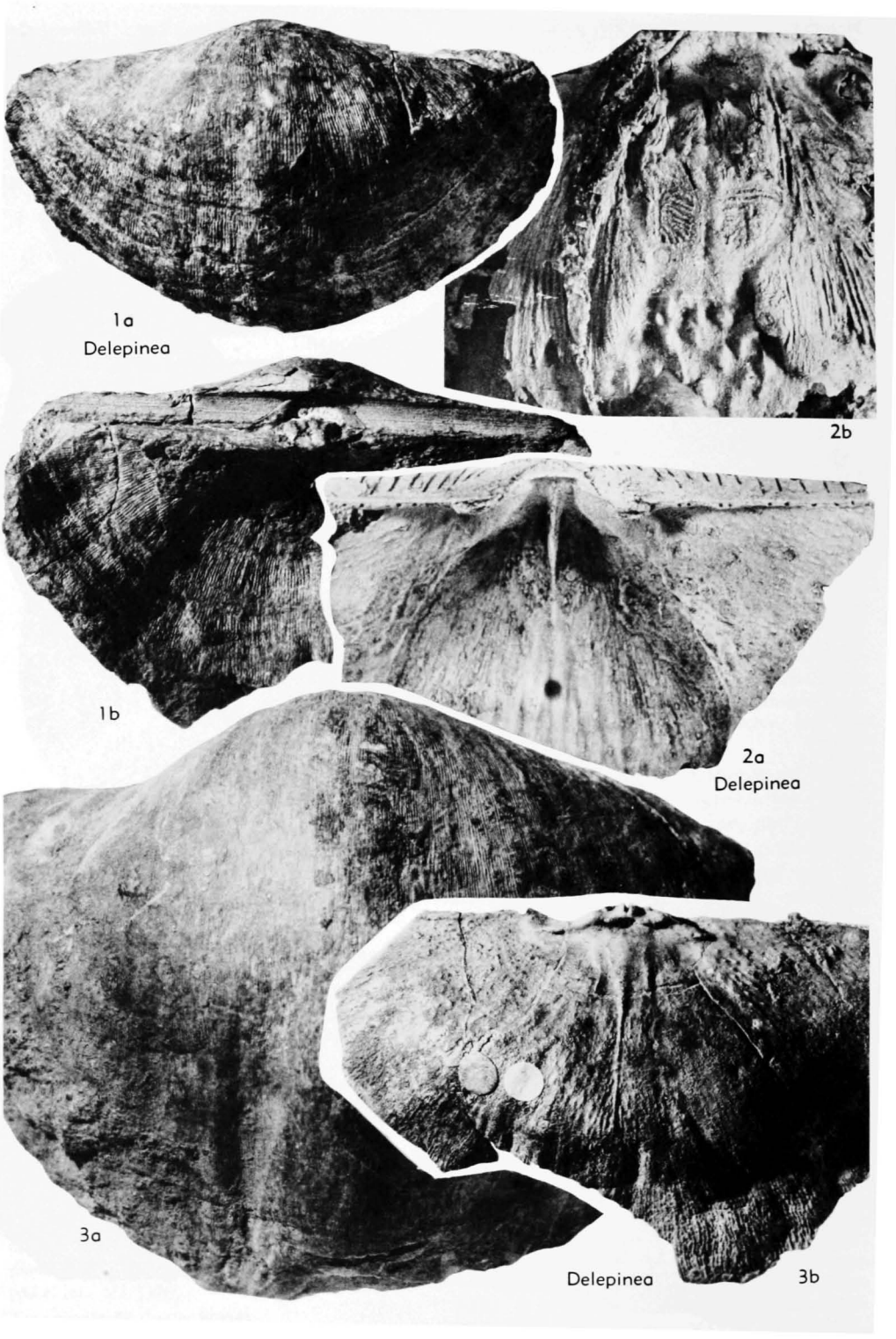

FIG. 293. Daviesiellidae (Delepineinae) (p. *H*434).

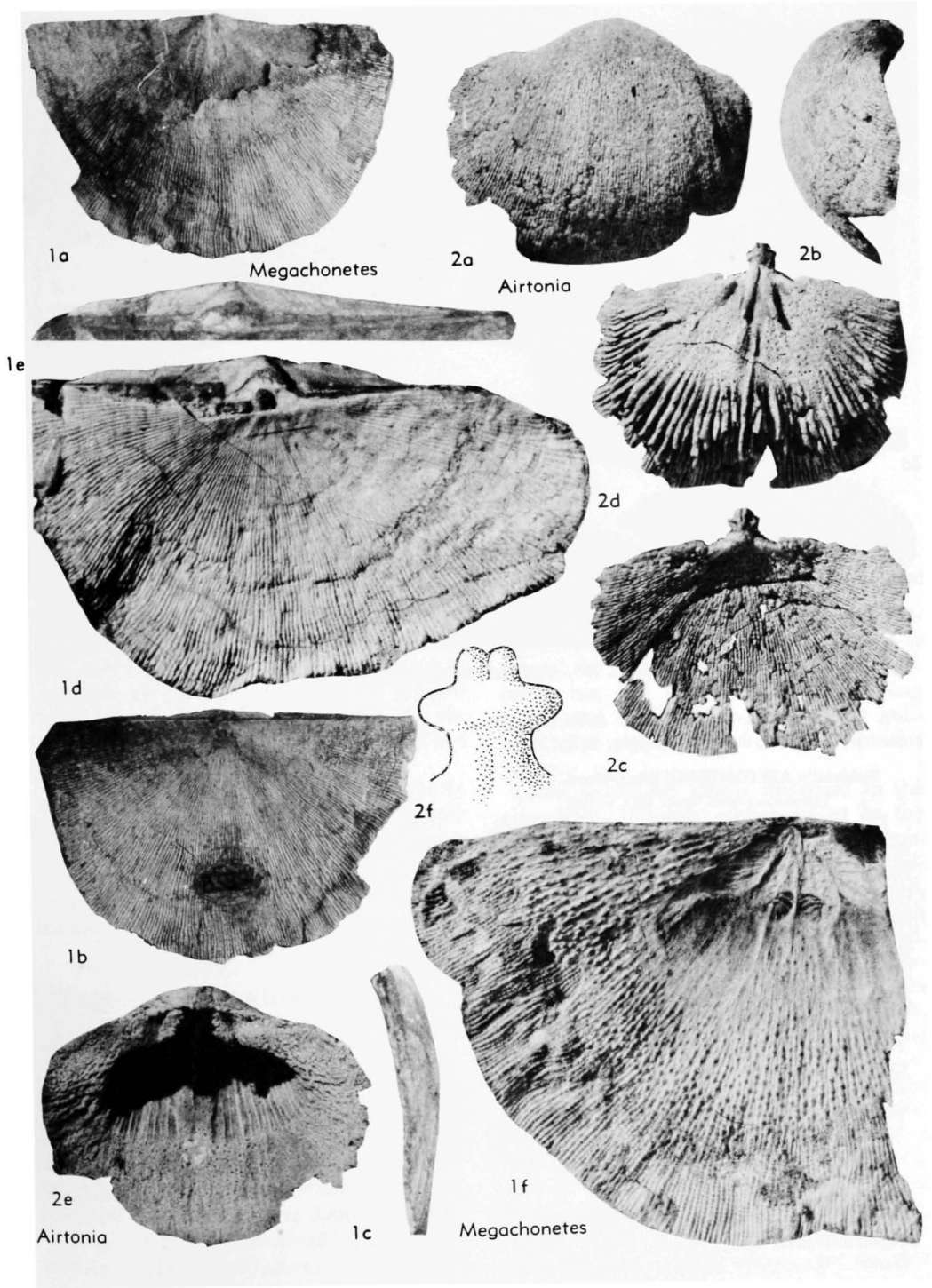

FIG. 294. Daviesiellidae (Delepineinae) *(1)*, (Airtoniinae) *(2)* (p. *H*435, *H*438).

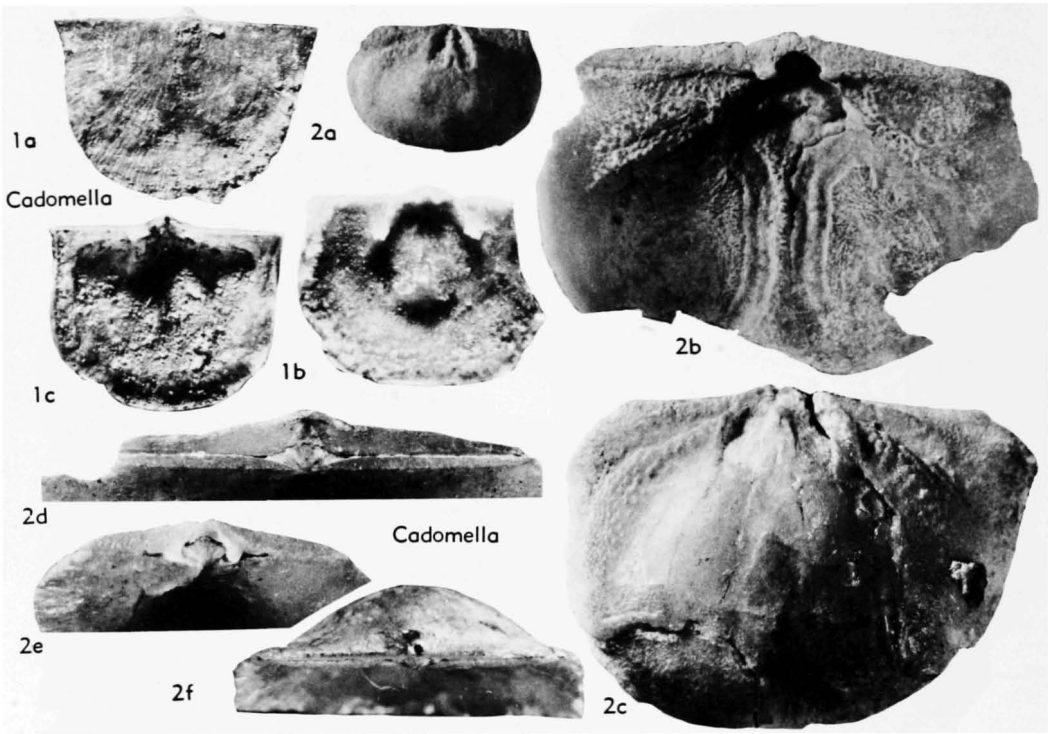

FIG. 295. Cadomellidae (p. *H438-H439*).

1f, ped.v. int. showing accessory adductor scars and pseudopunctate shell structure, ×2 (586).

Subfamily AIRTONIINAE Muir-Wood, 1962

[Airtoniinae MUIR-WOOD, 1962, p. 107]

Dorsal breviseptum and two strong diverging lateral septa extending from prominent trilobate or quadrilobate cardinal process; anterior ridges platelike; brachial ridges laterally directed, adductor scars not dendritic, ventral interarea low, no dorsal interarea. *L.Carb.(Visean).*

Airtonia COPE, 1934, p. 273 [**A. hudsoni*; OD]. Medium-sized, highly concavo-convex, small pseudodeltidium or posterior callosity; shell finely capillate, spine row along hinge. *L.Carb.(L.Visean)*, Eu.(Eng.-Belg.-Fr.).——FIG. 294,*2*. **A. hudsoni*, Eng.(Yorks.); *2a,b*, ped.v. vent., lat., ×1; *2c,d*, brach.v. ext., int., showing prominent card. process, ×1; *2e*, ped.v. int., ×1; *2f*, card. process, ×5 (199).

Suborder and Family UNCERTAIN

Reticulatochonetes BUBLICHENKO, 1956, p. 97 [**R. lautus*]. Imperfectly known, possibly a productoid. Said to have concavo-convex valves with interareas and spines on ventral valve, reticulate ornament and bilobate cardinal process. *L.Carb.(Tournais.)*, Asia(Kazakh.) (126).

Superfamily CADOMELLACEA Schuchert, 1893

[*nom. transl.* MUIR-WOOD, 1955, p. 90 (*ex* Cadomellinae SCHUCHERT, 1893, p. 153, *non* MUNIER-CHALMAS MS)]

Small forms having functional pedicle throughout life with apical foramen, interarea in each valve and hinge teeth and sockets; hinge spines not developed; shell structure lamellar, fibrous, with internal layer pseudopunctate. *L.Jur.(U.Lias).*

Family CADOMELLIDAE Schuchert, 1893

[*nom. transl.* MUIR-WOOD, 1955, p. 90 (*ex* Cadomellinae SCHUCHERT, 1893, p. 153)]

Median septa, brachial ridges and vascular markings variably developed, muscle area wholly or partly surrounded by raised rim, delthyrium closed by small triangular pseudodeltidium and by external face of lobate cardinal process, possibly bordered by chilidial plates. *L.Jur.(U.Lias).*

Cadomella OEHLERT in FISCHER, 1887, p. 1285 (*non* MUNIER-CHALMAS MS) [**Leptaena moorei* DAVIDSON, 1850, p. 17; OD]. Valves slightly concavo-convex, laterally elongated with greatest width along hinge, finely capillate or smooth:

low anterior septum in each valve, brachial ridges obscure. *L.Jur.(U.Lias.)*, Eu.(Eng.-Fr.).——Fig. 295,*1*. **C. moorei* (Davidson), Fr.; *1a-c*, brach.v. ext. and int., ped.v. int., ×10 (Muir-Wood, n). ——Fig. 295,*2*; 296,*1*. *C. davidsoni* (Eudes-Deslongchamps), Fr.; 295,*2a*, brach.v. int., ×2; 295, *2b*, ped.v. int. with teeth and mantle-canal markings, ×4; 295,*2c*, brach.v. int. showing papillae and brachial ridges, ×4; 295,*2d*, interarea showing pseudodeltidium, ×4; 295,*2e*, hinge of both valves showing teeth, sockets, and exterior part of cardinal process, ×4; 295,*2f*, ped.v. foramen, ×4; 296,*1a*, brach.v. view of shell showing interareas, foramen, and ext. card. process, ×3; 296, *1b*, ped.v. view of shell, ×3 (224).

PRODUCTIDINA

[Materials for this suborder prepared by Helen M. Muir-Wood]

The suborder Productidina includes the largest, as well as the most bizarre and aberrant, brachiopods known at present. Owing to its world-wide distribution and range of about a hundred and fifty million years, a very considerable number of genera and species have been recognized. The ancestors of this remarkable group, as well as the relationship of the various families, are still uncertain. It has been cited as an example of explosive evolution on account of the rapid increase in numbers after the first appearance of the Strophalosiacea and Productacea in the Lower Devonian.

The suborder Productidina, as here defined, includes the superfamilies Strophalosiacea, Richthofeniacea, and Productacea. These are at present subdivided into 20 families and 39 subfamilies, and 179 genera.

RANGE AND DISTRIBUTION

The Productidina have a world-wide distribution, but are especially abundant in the Mississippian, Pennsylvanian, and Permian of North America.

The range of the two superfamiiles Strophalosiacea and Productacea is from Lower Devonian through Permian. The Richthofeniacea range from Pennsylvanian to Permian (Fig. 297).

The earliest strophalosiacean genus at present known is *Devonalosia* from an equivalent of the Onondaga Limestone of Gaspé Peninsula, Quebec, while *Spinulicosta* from the Onondaga of Ohio is the earliest productacean. In both these genera teeth and sockets are developed. An interarea occurs in each valve, with pseudodeltidium but no chilidium. The ornament is spinose in both *Devonalosia* and *Spinulicosta*, but the development of clasping spines and a cicatrix in *Devonalosia* indicates close attachment of the shell in this genus.

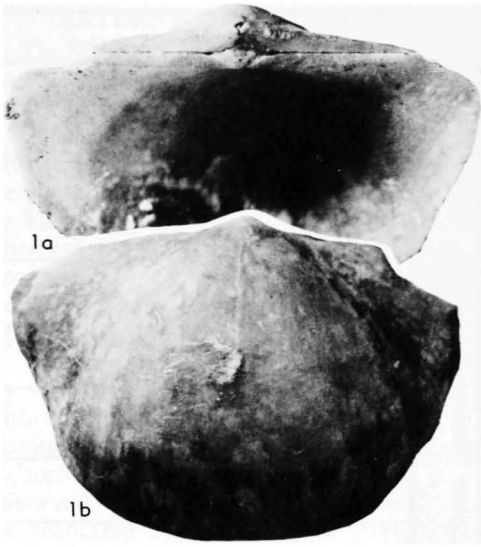

Fig. 296. Cadomellidae (p. *H*438-*H*439).

Both stocks are clearly unrelated to the chonetoids, formerly considered to be the ancestors of the productoids, and it is probable that they were derived from some Silurian or early Devonian strophomenoid, such as the genus *Leptaenisca*, in which brachial ridges are prominently developed.

The strophalosiaceans were not numerous in Devonian and Carboniferous times but were locally abundant in the Permian.

The productaceans abounded from the Upper Devonian onward, showing considerable variation in size and ornament. The largest brachiopods known—*Gigantoproductus* and *Titanaria*, from 12 to 15 inches in width—occurred in the upper part of the Lower Carboniferous, the former genus having an almost world-wide distribution, but both having a short duration.

In the Upper Carboniferous the number of genera declined somewhat, but a great increase occurred in the Permian when a multiplicity of new genera appeared, many

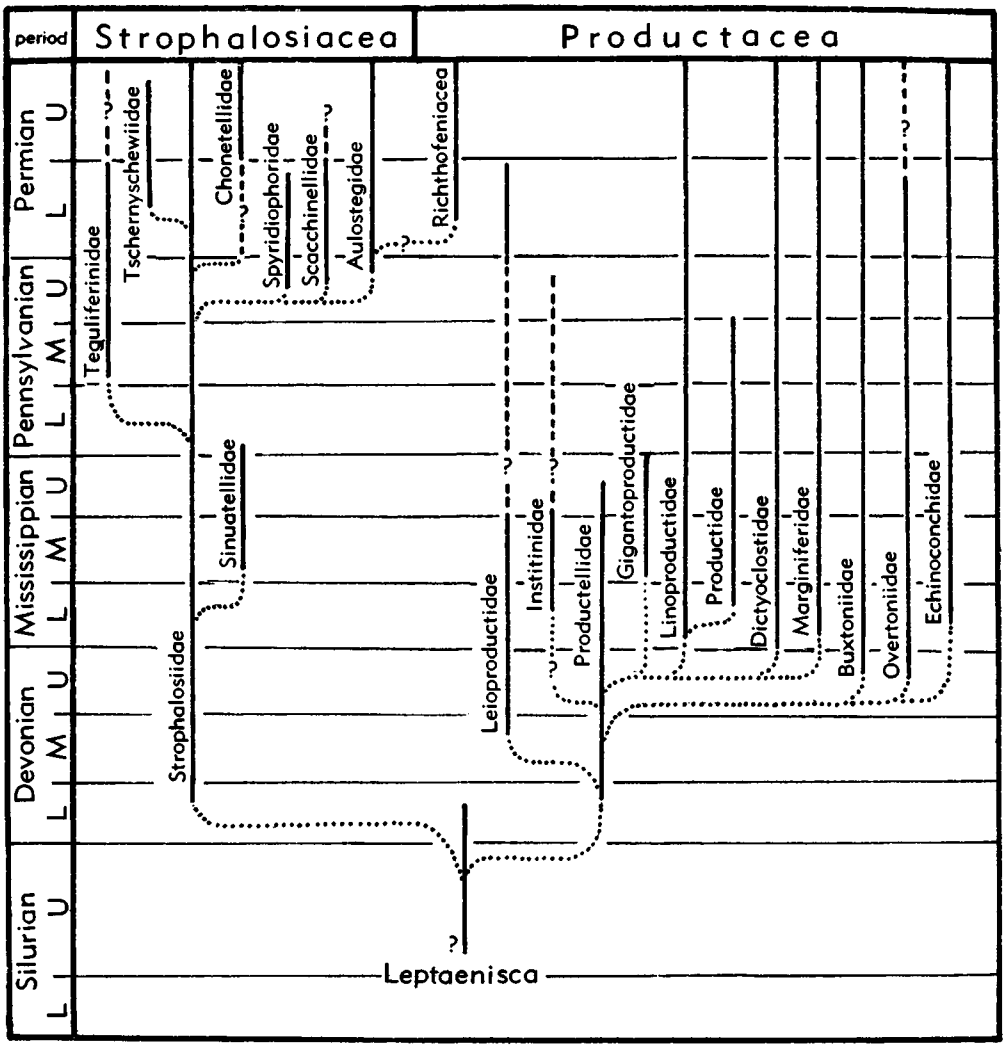

FIG. 297. Stratigraphic distribution and inferred phylogeny of productoid family assemblages (587).

of bizarre type, such as the richthofeniids and scacchinellids, with conical shells and rootlet spines, and other genera with extravagant development of spines and frills.

The productoids died out in the Permian, though some of the Triassic spiriferoids, such as *Koninckina* and *Koninckella,* with calcified dorsoventral spiralia, and *Thecospira,* with a pseudopunctate shell, may have been derived from the Productidina.

LIFE HABITS

No pedicle was developed in the productoids, and many species lived free and unattached. Such forms frequently had long, symmetrically placed spines to support the shell, so that the anterior margin was kept free from the mud of the sea bottom. Some species were attached to a foreign body by cementation of the umbo of the pedicle valve in the early growth stages, often assisted by clasping or attachment spines.

Examples of the young of a Mississippian productellid, *Orbinaria pyxidata* (HALL), have a ringlike structure on the umbo of the pedicle valve (Fig. 298), and it is suggested that this served to attach the young

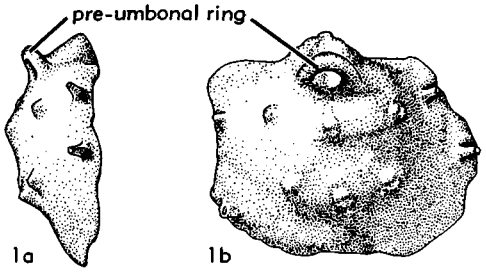

FIG. 298. Lateral and ventral views of juvenile *Orbinaria pyxidata* from the Louisiana Limestone (U.Dev. or L.Miss.) of Missouri, showing attachment ring on umbo, ×15 (587).

shell to a spine, possibly one on a parent's shell. A similar structure has been observed in young forms of *Megousia* and in some British forms and it may have been of common occurrence. In some small unnamed Permian shells from Texas the spines along the hinge are inclined toward the umbo, forming a ring which probably served for attachment in early growth stages, and a similar ringlike development of hinge spines has been observed in a number of adult forms.

The long creeping spines, in well-preserved specimens of *Antiquatonia*, certainly served to steady the shell and to attach it to some foreign object, while the large brush of rhizoid spines preserved in silicified specimens from the Texas Permian reefs must have served for entanglement and support.

Many specimens have been observed in what must have been their original position of growth, with the brachial valve uppermost, and the anterior margin lifted free of the sea-bottom mud.

Straining devices to prevent foreign particles or attacking organisms from entering the shell are elaborately developed, and consist of rims, frills, and anterior gutter-like or tubelike development of the trail, or the development of prostrate spines from the anterior margin, which would project across the anterior gape of the shell like a sieve. The interior or endospines in the two valves also tend to interlock in a mesh, and this is especially well developed in the richthofeniids and forms a sievelike strainer in *Coscinarina* from the Permian of Sicily.

EXTERNAL MORPHOLOGY

The shell consists of a flat or concave, or rarely, convex brachial valve, and a convex pedicle valve. Both valves may be geniculated and develop a long or short trail. The **trail** of one or both valves may develop flattened rims, or may be recurved to form a gutter or coil (Fig. 299). In the aberrant forms belonging to the Richthofeniidae and Scacchinellidae, the pedicle valve is conical and the brachial valve opercular, forming a lid.

The median part of the valve is known as the **venter** and this slopes down on either side to join the **lateral slopes** or **flanks.** The pedicle valve tapers posteriorly to form the **umbo,** which terminates in a more or less acute **beak.** The umbo may be truncated by a **cicatrix** of attachment of variable size and development. A corresponding rounded swelling may occur in the brachial valve.

The two valves are united along the **hinge,** which may be the widest part of the shell. The lateral extremities of the hinge, usually trigonal in outline, are known as **ears.** In some of the more primitive families (e.g., Productellidae, Strophalosiidae) an **interarea** is developed in each valve. In the Aulostegidae only the pedicle valve has an interarea. The **delthyrium** and **notothy-**

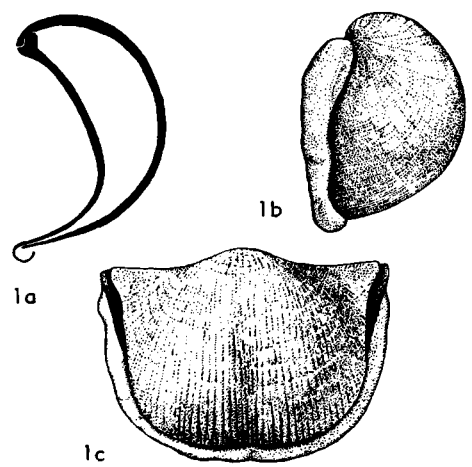

FIG. 299. *Auloprotonia aulacophora* MUIR-WOOD & COOPER (U.Miss., Okla.), showing specialized gutter formed by reflexed margin of brachial valve; *1a,* long. sec., ×0.75; *1b,c,* lat. and vent. views, latter showing openings of gutter near ears of shell, ×0.75 (587).

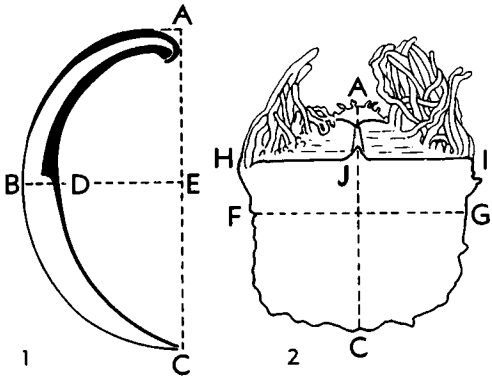

FIG. 300. Directions of measurement of productid *(1)* and aulostegid *(2)* brachiopods. [Explanation: *AC,* length of shell; *AJ,* length of interarea; *ABC,* surface length of pedicle valve; *BD,* thickness; *BDE,* height; *FG,* mid-width; *HI,* width of hinge or interarea (587).]

rium are closed in some shells by a **pseudodeltidium** and **chilidium.** The latter structure occurs only in the Strophalosiidae. The pseudodeltidium, however, tends to be replaced by the external face of the cardinal process or an extension of it called the **lophidium.** In the Aulostegidae the delthyrium is closed by a convex puckered plate known as the **elytridium,** and the interarea on either side of the delthyrium, known as the **perideltidial area,** is demarcated by distinct ornament in some genera. In some Visean, Pennsylvanian, and Permian shells, a secondary area **(ginglymus)** may be developed in the pedicle valve, and serves to close the shell or to articulate with ridges in the brachial valve.

Every productoid shell is more or less spinose, but may otherwise be smooth with growth lines, or bear radial ridges of varying size, known as **costae** (less than 15 in 10 mm.), **costellae** (15 to 25 in 10 mm.) or **capillae** (more than 25 in 10 mm.). Concentric wrinkles or **rugae** may be developed posteriorly near the hinge or cover the entire valve. Concentric bands bearing rows of small **spines** occur in some species, or spines may be set on **spine ridges** or rounded nodes known as **monticules.** Different ornament may occur on the posterior and anterior parts of one valve, or dorsal and ventral valve may be dissimilar (e.g., *Dev-onoproductus,* which has a capillate spinose pedicle valve and a lamellose brachial valve).

Productoid **spines** are of several distinct types which have been described as (1) **rhizoid or rootlike spines,** serving for attachment by entanglement, including also the clasping spines of strophalosiids; (2) **halteroid spines,** usually extending at right angles to the shell surface, serving as struts to steady or balance the shell and prevent it from sinking in the mud; (3) **vermiform or wormlike spines** of some strophalosiids; (4) **prostrate spines,** straight or slightly curved and extending along the shell surface, and serving as a protective coat for stopping foreign bodies from boring into or attaching themselves to either valve or acting as a strainer at the anterior margin. Spines of two or more types or series may be developed on a single valve. Spines are developed in great profusion and almost endless variety in Permian species and have been studied in the marvelously preserved silicified specimens from western Texas. Spines up to 9 or 10 inches in length have been observed and may fork or unite with neighboring spines. The spines vary considerably in diameter, but all are hollow and open at the distal end. They were originally lined by outgrowths of the mantle, but the internal aperture of the spines tended to become blocked by deposition of secondary calcareous layers on the shell interior as the valves elongated. The rows of spines near the hinge and the four or six symmetrically placed halteroid or strutlike supporting spines remained in contact with the shell interior throughout the life of the animal.

In systematic descriptions the specimens are said to be of **small size** when they are less than 0.75 inch (20 mm.) wide; **medium size** when 0.75 to 2 inches (20 mm. to 50 mm.) wide; **large size** when above 2 inches (50 mm.) wide; and **gigantic size** when above 6 inches (150 mm.) wide.

The **width** is measured parallel to the hinge, which is commonly the widest part of the shell. The **length** is measured from the umbo to the anterior margin at right angles to the width and thickness. The **thickness** is measured along an axis at right angles to the width and length (Fig. 300).

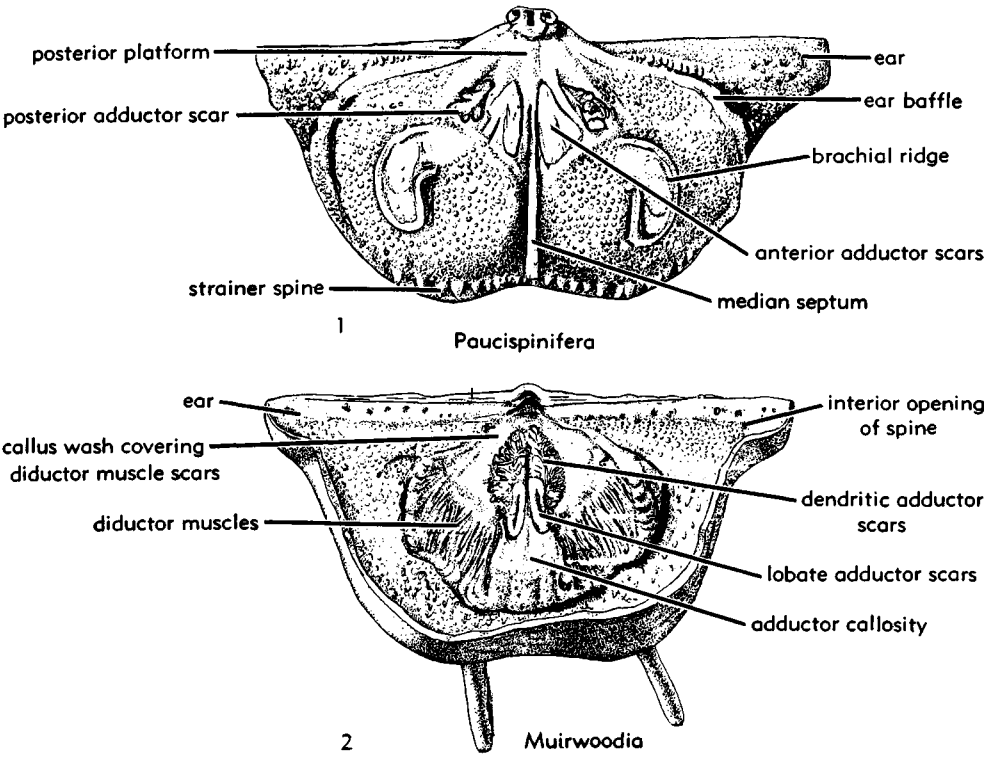

FIG. 301. Brachial valve interior *(1, Paucispinifera)* and pedicle valve interior *(2, Muirwoodia)* showing morphological features (587).

INTERNAL MORPHOLOGY

BRACHIAL OR DORSAL VALVE

In the more primitive genera the two valves articulate by means of small **hinge teeth** in the pedicle valve which fit into **sockets** in the brachial valve (Fig. 301,*1*, 302). In some of the more bizarre genera the position of the teeth and sockets may be reversed, but in others it is replaced by a number of teeth or **denticulations** which fit into corresponding depressions in the opposite valve. The sockets are bounded anteriorly by **socket ridges.** In most productoids without teeth and sockets, the cardinal process and lateral ridges, which extend from it more or less along the hinge margin of the brachial valve, aid in articulation. The **lateral ridges** may extend across the ears and be continued along the lateral margin of the visceral disc as marginal ridges, or they may unite on the dorsal side of the cardinal process as a **zygidium** which functions like the lophidium.

The **cardinal process** varies in type and size and has been used by MUIR-WOOD & COOPER (1960) in family classification. The most primitive type is bilobate, the two lobes remaining in contact, divided only by a median furrow. The lobes tend to become separated from one another or to be united only by a minute median lobe developed posteriorly. This median lobe may be inclined dorsally (exteriorly) in some genera, and may be more prominent than the two lateral lobes. The external face of the process, commonly triangular in outline, consists of three or four anteriorly converging lobes, and in some genera it is enlarged into a triangular boss or **lophidium.** Some of the various types of cardinal processes are figured (Fig. 303). The cardinal process consists of the lobed **myophore** and the **shaft** or stalk. When the stalk is absent the process is said to be **sessile.**

The cardinal process may be supported by the **median septum** or be separated from

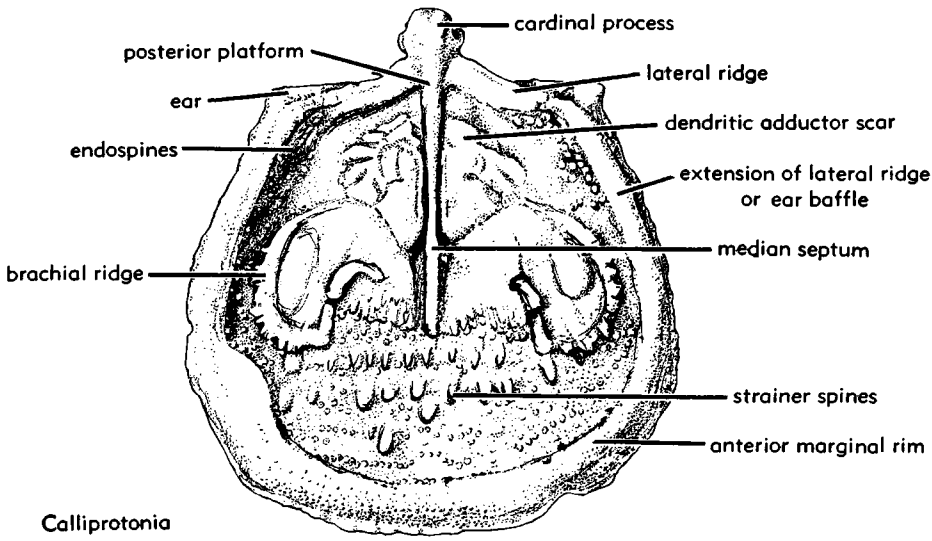

FIG. 302. Interior of brachial valve of *Calliprotonia,* echinoconchid, from Finis Shale (Penn.) of Texas, showing morphological features, ×3 (587).

it by a rounded pit or **alveolus.** In the latter case the median ridge is known as the **breviseptum.** In some genera (e.g., *Juresania*) two vertical or converging ridges called **buttress plates** extend anteriorly from the cardinal process and may unite with the median septum, in some shells leaving a median hollow known as the **antron.** The anterior part of the septum may become prominent and bulbous or bladelike and probably it served to divide the internal shell cavity into two parts and to regulate food currents.

The internal shell surface is more or less papillose, granular or endospinose, the **endospines** attaining several millimeters in length, and commonly forming an anterior mesh or strainer across the gape in the valves with comparable spines in the pedicle valve (e.g., richthofeniids). **Brachial ridges,** more or less spirally curved, extend from the line of junction of the anterior and posterior adductor muscle scars. These ridges vary in form in different families and are obscure or not distinguishable in some genera. They are given off at varying angles, from horizontal in the Dictyoclostidae and Aulostegidae, to nearly vertical, in *Overtonia* and the strophalosiids.

Mantle-canal markings, which are a feature of the interior of both valves of strophomenoids, cannot as a rule be distinguished in the Productidina, probably on account of the papillose or endospinose internal surface. **Genital markings** were not observed.

In *Productus, Diaphragmus,* and other genera, a thin crescentic plate, called the **diaphragm,** may be developed around the **visceral disc** of the brachial valve to close the gap between the two valves.

The valves are attached to one another by means of the **adductor and diductor muscles,** the former serving to close and the latter to open the shell. The diductors are attached to the cardinal process and leave roughened areas showing attachment to the sulci between the lobes, and in some shells to the lobes themselves. The attachment of these muscles to the pedicle valve leaves large flabellate scars, which may be radially ridged or provided with a bounding rim. The adductors are attached to the brachial valve on either side of the median septum, forming two anterior and two posterior scars, or rarely six scars which may be smooth, lobate or dendritic. The adductor scars are commonly set on a platform. In the pedicle valve the adductors form two or four scars situated within or anterior to the diductors. Additional scars interpreted as **accessory diductors** are attached to the shaft of the cardinal process

in some aulostegids, but the position of their attachment to the pedicle valve is uncertain. Rounded and detached accessory adductor scars are developed in the pedicle valve of the chonetoid family Daviesiellidae but are not found in the Productidina.

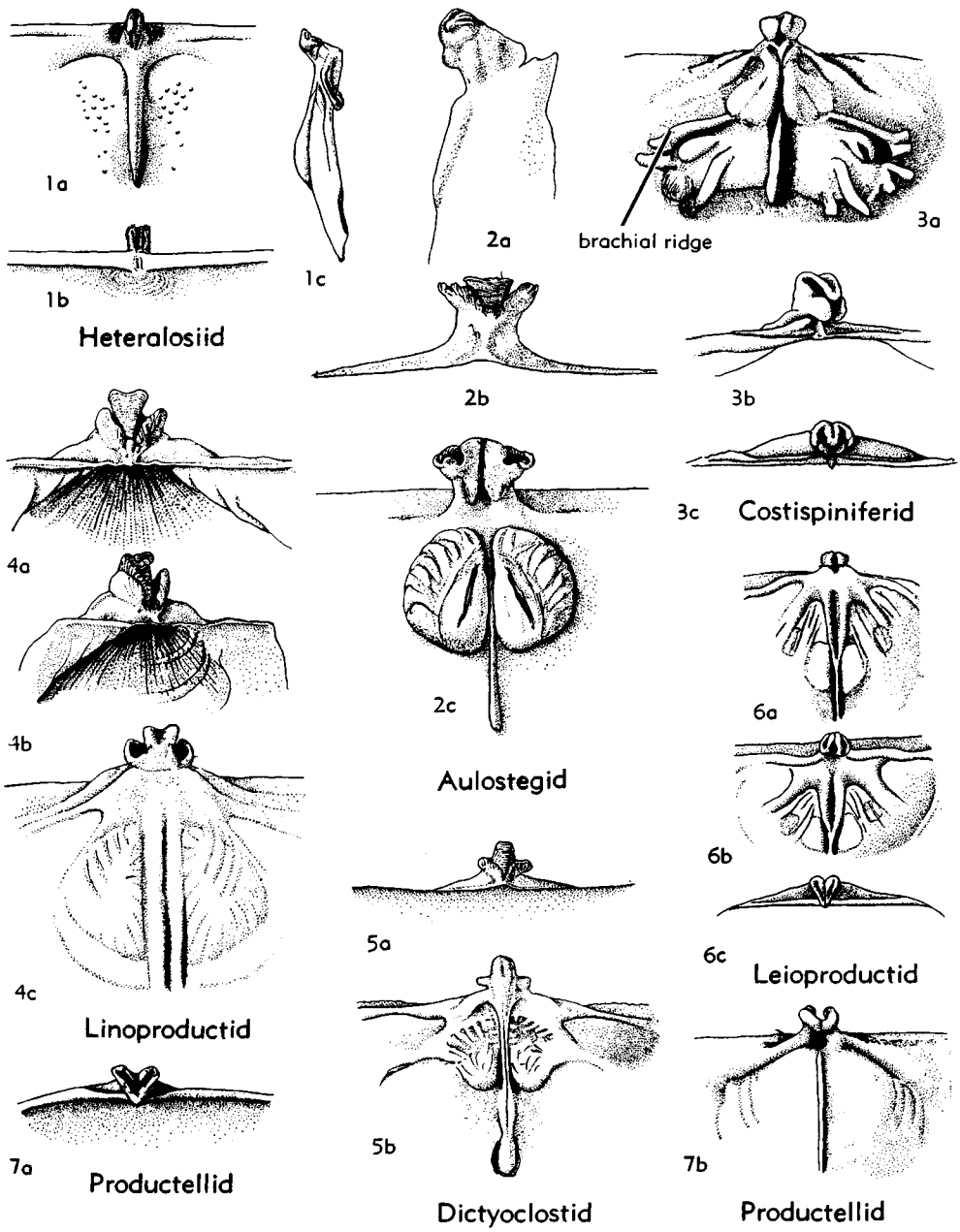

FIG. 303. Types of productoid cardinal processes showing associated morphological features (587).——*1.* Heteralosiid *(Heteralosia)*; *1a-c,* int., post., lat. views, ×3.——*2.* Aulostegid *(Edriosteges)*; *2a-c,* lat., ext., int. views, ×1.5.——*3.* Costispiniferid *(Costispinifera)*; *3a-c,* int., oblique lat., post. views, ×2.——*4.* Linoproductid *(Linoproductus)*; *4a-c,* ext., oblique lat., int. views, ×2.25.——*5.* Dictyoclostid *(Penicularis)*; *5a,b,* ext., int. views, ×0.75.——*6.* Leioproductid *(Leioproductus)*; *6a-c,* int., oblique int.-post., post. views, ×2.——*7.* Productellid *(Spinulicosta)*; *7a,b,* post., int. views, ×2.

PEDICLE OR VENTRAL VALVE

Hinge teeth are developed in some of the more primitive genera of the Productellidae, in the Strophalosiidae and Sinuatellidae (Fig. 301,*2*). **Dental plates** are very rarely developed. The teeth are situated on the anterior outer margin of the delthyrium, and vary in form and prominence. A short **median septum** is developed in *Rhamnaria, Septarinia,* and *Chonetipustula.* In *Tschernyschewia* the septum is high and platelike and a comparable septum occurs in *Scacchinella.*

The **lophophore** is assumed to have been spirolophous, with the apices of the two spirals projecting into the mantle cavity of the pedicle valve. Traces of these spirals can be seen as elevated cones in specimens of *Gigantoproductus* and *Levitusia.* The spirals were probably attached to the spirally curved brachial ridges developed in the brachial valve of many genera.

Marginal or submarginal ridges are developed in some pedicle valves (e.g., *Alifera, Paramarginifera, Eomarginifera*). In some genera (e.g., *Kozlowskia, Marginifera, Costispiniferina*) the ridges may be crenulated.

In the richthofeniids the thickening on the interior of the conical valve, against which the brachial valve rested when the shell was closed, is known as the **aulacoterma.** The chamber, similar to a spondylium, but not derived from dental plates, to which muscles were attached in the Richthofeniidae, is called the **myocoelidium,** while the cuplike attachment surface for the adductors in the Spyridiophoridae is known as the **spyridium.**

SHELL STRUCTURE

The shell consists of a thin external lamellose layer and an inner fibrous layer which seems to vary in different genera and is commonly of considerable thickness. The inner layer is said to be **pseudopunctate** on account of nonfibrous calcite rods or **taleolae** (formerly called **pseudopunctae** or **spicules).** These may be of more than one diameter and extend for a varying distance through the fibrous layer, and may project as pustules or **endospines** into the internal shell cavity. The spines are also composed of two shell layers, the "spines within spines" described by Young (1891) being taleolae.

In richthofeniids and *Scacchinella,* the conical shell may be partly filled by cystose shell, which consists of small or large curved calcareous plates, of which the method of formation is uncertain. It is suggested that fluid was secreted by the mantle between the mantle and the shell, and that this liquid was sealed within a thin layer of shell. This process was continued gradually, pushing the body upward as the cone increased in depth.

CLASSIFICATION

Classification of the productoids has been based largely on external shell ornament. This consists of spines, in some shells accompanied by radial costae or costellae and concentric rugae or lamellae. The arrangement of spines, whether scattered over the shell, arranged in rows or groups near the hinge or on the flanks, borne on the costae or rugae, or set on tubercles or spine ridges, has been found to be of first importance. Spines developed in any one species have been found to have a fairly constant arrangement and to be of uniform type, and of more than one series in some genera.

The present classification is also based on internal morphology, especially type of the cardinal process; the adductor scars, whether smooth or dendritic, length and position of the lateral ridges; length and form of the dorsal median septum, and its rare development in the pedicle valve, and the angle of emergence of the brachial ridges.

Some structures, such as marginal ridges and diaphragm, formerly thought to be a characteristic of a single genus, are now found to be repeated in a number of genera.

Earlier classifications attached considerable importance to shell contour and size of the body cavity. This has been found to be somewhat variable and important only as a specific character.

A history of the classification of the Productidina has been given by Muir-Wood and Cooper (1960, 587).

HOMEOMORPHY

The number of possible ornament patterns in productoids is limited and may be

repeated two or more times, thus giving external similarity, accompanied by different internal morphology. Such pairs of homeomorphs may occur in beds of the same age (e.g., *Sphenalosia, Sphenosteges,* from the Permian of USA), or in beds of widely differing age (e.g., *Dictyoclostus,* from the Lower Carboniferous, and *Reticulatia,* from the Permian). Many species formerly placed together in one genus on account of superficial similarity in ornament have now been separated as distinct genera and placed in different families. For example, *Productus mesolobus* (J. PHILLIPS) and *Productus humerosus* (J. SOWERBY) were formerly grouped together in the genus *Plicatifera. Productus mesolobus* is now the type-species of *Acanthoplecta,* and *P. humerosus* is now assigned to the genus *Levitusia*; the two genera are separated, *Acanthoplecta* being placed in the family Leioproductidae and *Levitusia* in the Dictyoclostidae.

GLOSSARY OF MORPHOLOGICAL TERMS APPLIED TO PRODUCTIDINA

[Abbreviations used in figure descriptions are given in parentheses.]

adductor muscle scars. Attachment impressions of muscles serving to close valves, comprising four or six scars in brachial valve; anterior adductor scars anterior to or on inner side of posterior adductors; in pedicle valve two or four scars between diductor scars.

adductor platform. Platform or broad ridge to which adductors are attached.

alae. Winglike extensions of ears or cardinal extremities.

alveolus. Pit anterior to internal face of cardinal process (e.g., Productellidae).

antron. Triangular gap due to incomplete fusion of cardinal process buttress plates and breviseptum (e.g., *Buxtonia*).

aulacoterma. Thickening on inside wall of Richthofeniidae against which brachial valve rested when shell was closed.

beak. Extremity of umbo, commonly pointed and incurved.

brachial ridges. Ridges originating between anterior and posterior adductor scars in brachial valve and extending laterally or anteriorly forming open loop.

brachial valve *(brach.v.)*. Dorsal valve.

breviseptum. Median ridge not supporting cardinal process.

buttress plates. Two vertical or converging plates extending from cardinal process and in some shells uniting with breviseptum. (*See* antron.)

callus. Secondary deposit composed of fibrous layer, thickening shell and covering up internal structures.

capillae. Fine raised radial lines on exterior of valves (more than 25 in width of 10 mm.).

cardinal process *(card. process)*. Boss, more or less elevated, serving for attachment of diductor muscles, and also assisting in articulation; consists of shaft and lobate myophore, or shaft may be lacking when myophore is sessile.

chilidium. Flat or convex plate closing notothyrium (e.g., Strophalosiidae).

cicatrix of attachment. Flattening of pedicle umbo representing place of cementation of shell to foreign object.

cincture. External concentric incision in either valve, usually corresponding to an internal ridge or diaphragm.

costae. Radial ridges on exterior of shell (less than 15 in 10 mm.).

costellae. Radial ridges on exterior of shell and finer than costae (about 15 to 25 in width of 10 mm.).

crenulations. Alternating elevations and depressions usually serving as accessory form of articulation of shell.

cystose shell. Blister-like deposits formed in conical shells (e.g., Richthofeniidae, Scacchinellidae) to fill up shell as result of dorsal migration of body during growth.

delthyrium. Triangular opening in interarea under umbo of pedicle valve.

dendritic muscle scars. Branching or leaflike pattern of adductor scars in some genera.

diaphragm. Thin crescentic place developed as secondary deposit around visceral disc of brachial valve and bridging gap between brachial valve and trail of pedicle valve (e.g., *Productus*).

diductor muscle scars. Muscles serving to open valves and attached to cardinal process myophore in brachial valve, and forming large flabellate scars in pedicle valve. Accessory diductor muscle scars are situated between diductor scars in pedicle valve, and are attached to cardinal process shaft in brachial valve.

ear. Lateral extremity of hinge, usually trigonal in outline.

elytridium. Convex puckered cover of delthyrium in Aulostegidae.

endospines. Fine spines or protruding ends of taleolae in interior of both valves, possibly serving as strainers and preventing access to interior.

erect spines. Spines extending at high angle (75°-90°) to shell surface.

flanks. Lateral slopes on each side of venter.

fold. Major radial plication.

geniculate. Bent at an angle (e.g., trail in *Sinuatella* which extends at an angle to visceral disc).

ginglymus. Secondary interarea in pedicle valve of some Visean, Pennsylvanian, and Permian spe-

cies, serving to close gap between valves and to assist in articulation of shell.

gutter. Anterior recurvature of trail of one or both valves, to form a gutter (e.g., Aulostegidae), and possibly serving as strainer or stabilizer.

halteroid spines. Long spines, commonly four or six in number and symmetrically placed, acting as strutlike supports (e.g., *Muirwoodia, Eomarginifera*).

hinge. Posterior line of valve junction.

imbricate. Overlapping (e.g., lamellae).

interarea. Formerly called cardinal area.

lateral ridges. Ridges in interior of brachial valve extending laterally from cardinal process, probably serving to strengthen shell and assisting in articulation.

lophidium. Inverted V-shaped projection of median posterior part of brachial valve or of external face of cardinal process, helping to close gap in delthyrium.

marginal ridges. Thickening along internal lateral margin of visceral disc, usually in brachial valve.

monticules. Small rounded nodes, commonly bearing spines.

myocoelidium. Chamber similar to spondylium but not formed by dental plates, serving for attachment of muscles (e.g., Richthofeniidae).

myophore. *See* cardinal process.

myophragm. Median shell ridge, probably formed of secondary shell matter secreted between muscles and not extending beyond muscle field.

notothyrium. Triangular opening in interarea of brachial valve (e.g., Strophalosiidae).

opercular. Lidlike, referring to brachial valve in some genera (e.g., Richthofeniidae).

pedicle valve *(ped.v.)*. Ventral valve.

perideltidium. Triangular area forming part of interarea, marked by vertical as well as horizontal lines and bounding pseudodeltidium (e.g., some aulostegids).

prostrate spines. Usually straight spines that lie prone on shell surface.

pseudodeltidium. Single flat or convex plate covering part of delthyrium.

pseudopunctae. *See* taleolae.

recumbent spines. Slightly curved spines extending at low angle (less than 45°) to shell surface.

reticulation. Nodelike enlargement formed by intersection of concentric rugae with radial costae or costellae.

rhizoid spines. Spines resembling rootlets serving for attachment either by entanglement or by extending along and cementing themselves to some foreign surface.

rugae (rugose). Concentric folds or wrinkles (e.g., *Dictyoclostus*).

septum. Median ridge extending from umbo of pedicle valve or from cardinal process of brachial valve.

shaft. *See* cardinal process.

spine ridge. Elongated ridge bearing spine at anterior end.

spyridium. Structure formed by union of adductor platforms and supporting plates to form cuplike adductor attachment surface (e.g., *Spyridiophora*).

squamose. Ragged margin, e.g., of overlapping lamellae at anterior end of trail.

strainer spines. *See* endospines.

suberect spines. Spines inclined to shell surface at angle of about 45°-75°.

submarginal ridge. Thickening of interior of either valve parallel to anterior margin of visceral disc.

sulcus. Major depression in either valve, generally median in position.

taleolae. Nonfibrous calcite rods, commonly with median perforation and embedded in fibrous shell layer or protruding into shell interior as endospines in a pseudopunctate shell; on weathered surface may appear as pits (formerly called spicules or pseudopunctae).

trail. Extension of shell in either valve anterior to visceral disc.

umbo. Region just anterior to beak.

umbonal slopes. Region about umbo.

venter. Median region of shell between lateral slopes or flanks.

visceral cavity. Term used in fossils to include body cavity which was occupied by stomach, intestine, liver, etc., posterior to mouth, and mantle or brachial cavity which housed lophophore.

visceral disc. Posterior part of shell in both valves including umbones and venter and corresponding externally to visceral cavity.

zygidium. Collar-like structure uniting lateral ridges on dorsal side of cardinal process, and functioning like lophidium.

Suborder PRODUCTIDINA Waagen, 1883

[*nom. correct.* Muir-Wood, herein (*pro* suborder Productacea Waagen, 1883, p. 447)]

Specialized, and in some instances degenerate brachiopods having pseudopunctate shell composed of inner fibrous layer with taleolae, and thin outer lamellar layer. Pedicle valve convex, brachial valve flat or concave, rarely convex, or one or both valves geniculated, with development of trail. Pedicle valve invariably, and brachial valve commonly, provided with open tubular spines. Brachial valve interior, with lobate cardinal process and hook-shaped brachial ridges. Socket ridges obsolete; adductor muscle scars smooth, lobate or dendritic in both valves. Pedicle absent. Pedicle valve with ringlike structure for attachment in early stage. *L.Dev.-U.Perm.*

Superfamily STROPHALOSIACEA Schuchert, 1913

[*nom. transl.* Muir-Wood & Cooper, 1960 (*ex* Strophalosiinae Schuchert, 1913)]

Commonly cemented by beak of pedicle valve and anchored by clasping or attachment (rhizoid) spines; interareas present in both valves, in pedicle valve only, or absent; delthyrium closed by pseudodeltidium, or (when teeth are absent) by elytridium or partly by lophidium; notothyrium and chilidium, teeth and sockets developed in one family; cardinal process usually prominent, initially bilobed, becoming trilobed; alveolus commonly present. *L.Dev.-U.Perm.*

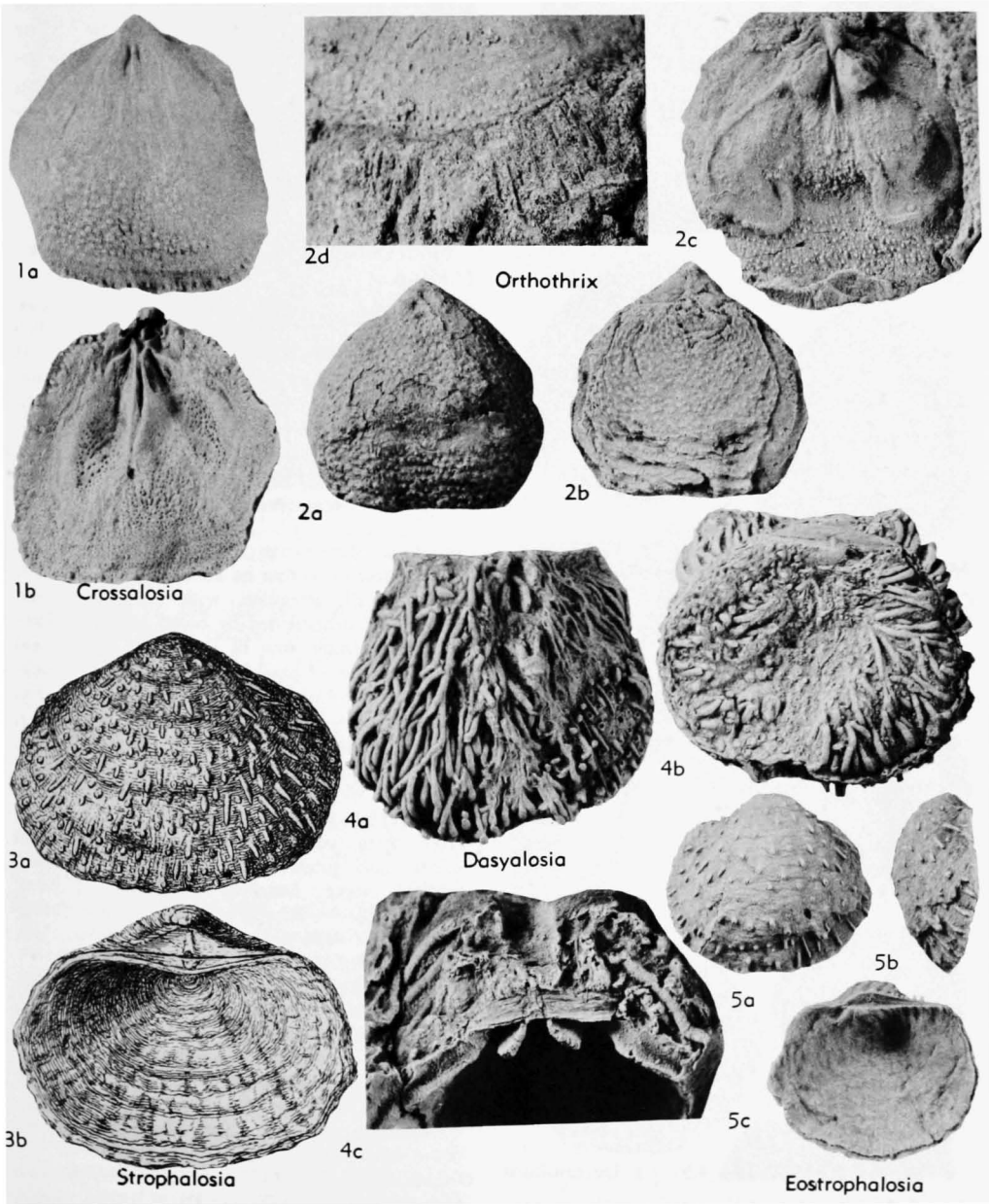

Fig. 304. Strophalosiidae (Strophalosiinae) (p. H450-H451).

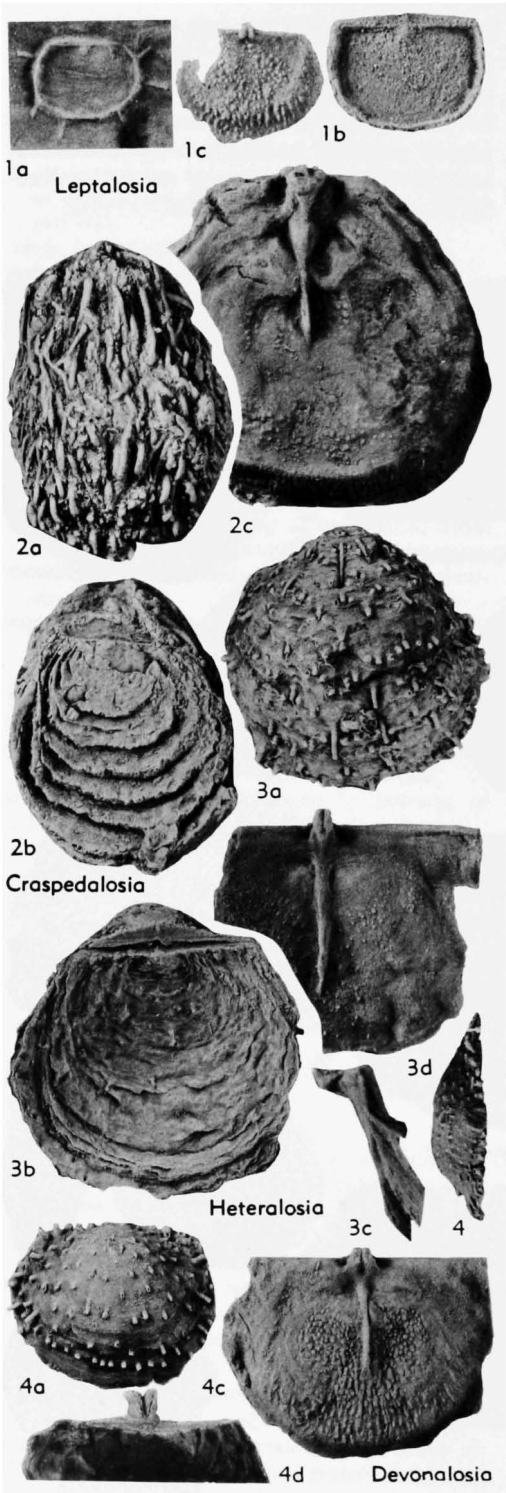

FIG. 305. Strophalosiidae (Heteralosiinae) (p. *H*451).

Family STROPHALOSIIDAE Schuchert, 1913

[*nom. transl.* STEHLI, 1954, p. 328 (*ex* Strophalosiinae SCHUCHERT, 1913, p. 391)]

Primitive Strophalosiacea with hinge teeth and sockets; both valves with short interarea; delthyrium closed by pseudodeltidium and notothyrium closed by chilidium; pedicle valve usually cemented by umbo and anchored by clasping spines on ears and near hinge. Brachial valve with or without spines; cardinal process bilobed, trilobed, or bulbous; brachial ridges long, sharply descendent. Alveolus normally absent; adductors not dendritic. *L.Dev.-U. Perm.*

Subfamily STROPHALOSIINAE Schuchert, 1913

[Strophalosiinae SCHUCHERT, 1913, p. 391]

Spines developed on both valves. *M.Dev.-U.Perm.*

Strophalosia KING, 1844, p. 313 [**S. gerardi* KING, 1846, p. 92; SD MUIR-WOOD & COOPER, 1960 (ICZN)] [=*Leptaenalosia* KING, 1850, p. 93 *(nom. nud.)*]. Medium-sized, with low interareas; pedicle valve ornament of prostrate and suberect clasping spines; brachial valve lamellose, few spines; cardinal process trilobed. *Perm.*, Asia-Australia.——FIG. 304,*3*. **S. gerardi,* Asia(Himalayas); *3a,b,* holotype, ped.v. and brach.v. views, ×1 (472).

Crossalosia MUIR-WOOD & COOPER, 1960, p. 75 [**Productus buchianus* DE KONINCK, 1847, p. 129; OD]. Small, irregular, by short interareas; both valves ornamented by broad concentric lamellae with single row of recumbent spines, and spines on ears of brachial valves; teeth and sockets and alveolus present. *L.Carb.(Visean)*, Eu. ——FIG. 304,*1*. **C. buchiana* (DE KONINCK), Belg.; *1a,b,* int. mold., ped.v. and brach.v. views, ×2 (587).

Dasyalosia MUIR-WOOD & COOPER, 1960, p. 76 [**Spondylus goldfussi* MÜNSTER, 1839, p. 43; OD]. Both valves with recurving vermiform spines, also prostrate spines in pedicle valve; brachial valve lamellose anteriorly. *U.Perm. (Zech.)*, Eu.——FIG. 304,*4*. **D. goldfussi* (MÜNSTER), Ger.; *4a,b,* ped.v. and brach.v. views, ×2; *4c,* ped.v. int., ×3 (587).

Eostrophalosia STAINBROOK, 1943, p. 58 [**Strophalosia rockfordensis* HALL & CLARKE, 1893, p. 316; OD]. Small; pedicle valve with rugae or lamellae and scattered recumbent spines and erect spines along hinge. *M.Dev.-U.Dev.*, N.Am.——FIG. 304, *5*. **E. rockfordensis* (HALL & CLARKE), U.Dev., USA(Iowa); *5a-c,* ped.v., lat., and brach.v. views, ×2 (766).

Orthothrix GEINITZ, 1847, p. 84 [**Orthis excavata* GEINITZ, 1842, p. 578; SD DALL, 1877]. Small, trigonal, with high ventral interarea; both valves

Devonalosia

FIG. 306. Strophalosiidae (Heteralosiinae) (p. H451).

ornamented by fine hairlike recumbent spines and narrow rugae; cardinal process long-shafted, bilobed. *U.Perm.(Zech.)*, Eu.——FIG. 304,*2*. **O. excavata* (GEINITZ), Ger.; *2a,b*, ped.v. and brach. v. views, ×2; *2c*, brach.v. int., ×2; *2d*, recumbent spines (impressions), ×4 (327).

Subfamily HETERALOSIINAE Muir-Wood & Cooper, 1960

[Heteralosiinae MUIR-WOOD & COOPER, 1960, p. 80]

Spines absent on brachial valve. *L.Dev.-U.Perm.*

Heteralosia R. H. KING, 1938, p. 278 [**H. slocomi*; OD]. Pedicle valve with concentric lamellae, fine recumbent and erect clasping spines; brachial valve dimpled, lamellose, rarely capillate; brachial ridges ill-defined, cardinal process bilobate or quadrilobate. *L.Miss.-L.Perm.* N.Am.-Eu.-Australia.——FIG. 305,*3*. **H. slocomi*, Penn., USA (Tex.); *3a,b*, ped.v. and brach.v. views, ×2; *3c*, lat. view of card. process, ×2; *3d*, brach.v. int., ×3 (471).

Craspedalosia MUIR-WOOD & COOPER, 1960, p. 82 [**Orthothrix lamellosus* GEINITZ, 1848, p. 86; OD]. Like *Dasyalosia* but brachial valve with squamose overlapping lamellae and obscure capillation. *U.Perm.(Zech.)*, Eu.——FIG. 305,*2*. **C. lamellosa* (GEINITZ), Ger.; *2a,b*, ped.v. and brach.v. views, ×2; *2c*, brach.v. int., ×3 (587).

Devonalosia MUIR-WOOD & COOPER, 1960, p. 83 [**D. wrightorum*; OD]. Small, subcircular; flat pseudodeltidium, no chilidium; pedicle valve ornament of prostrate and coarser recumbent spines; brachial valve rugose, dimpled; no brachial ridges, cardinal process small, bilobed; alveolus developed. *L.Dev.-M.Dev.*, N.Am.(USA-Can.).——FIG. 305,*4*. **D. wrightorum*, Arkona Sh., Ont.; *4a,b*, ped.v. (holotype) ext., post., ×2; *4c*, brach.v. int., ×3; *4d*, brach.v. ext., post. dors. view of card. process, ×4 (587).——FIG. 306,*1*. *D. radicans* (WINCHELL), M.Dev., USA(Mich.); shells attached to base of *Hexagonaria* colony, ×2 (587).

Leptalosia DUNBAR & CONDRA, 1932, p. 260 [**Strophalosia scintilla* BEECHER, 1890, p. 243; OD]. Small; pedicle valve wholly attached with prostrate spines; brachial valve smooth or with concentric lamellae; no median septum or brachial ridges. *U. Dev.* or *L.Miss., ?Penn.*, N. Am.——FIG. 305,*1*. **L. scintilla* (BEECHER), U. Dev. or L. Miss., Louisiana Ls., USA(Mo.); *1a,b*, attached brach.v. ext., ×4, ×8; *1c*, brach.v. int., ×8 (270).

Lialosia MUIR-WOOD & COOPER, 1960, p. 86 [**Strophalosia Kimberleyensis* PRENDERGAST, 1943, p. 47; OD]. Valves subcircular, some with short trail; lamellose, faintly capillate; spines near hinge of pedicle valve, possibly absent elsewhere. *L. Perm.(Artinsk.)*, Australia.——FIG. 307,*4*. **L. kimberleyensis* (PRENDERGAST); *4a,b*, ped.v. and brach.v. views, ×1; *4c*, brach.v. int., ×1.5; *4d*, ped.v. int., ×1.5 (647).

Oligorachis IMBRIE, 1959, p. 403 [**O. oligorachis*; OD]. Subelliptical, small, with small cicatrix and small, narrow, convex pseudodeltidium, hinge narrow; pedicle valve convex with stout scattered spines; brachial valve irregularly ridged, no spines, cardinal process small, bilobed, less prominent than in *Heteralosia*. *M.Dev.*, N.Am.——FIG. 307,*2*. **O. oligorachis*, USA(Mich.); *2a-d*, holotype, ped.v., brach.v., lat., and post. views, ×3 (445).

Sphenalosia MUIR-WOOD & COOPER, 1960, p. 87 [**S. smedleyi*; OD]. Trigonal, with high ventral interarea and narrow pseudodeltidium; pedicle valve with recumbent and also erect clasping spines; brachial valve smooth, operculiform; cardinal process ventrally elongated, 2-pronged, long septum. *L.Perm.*, N.Am.——FIG. 308,*1*. **S. smedleyi*, Phosphoria F., USA(Wyo.); *1a,b*, holotype, ped.v. lat., int., ×1; *1c*, brach.v. int., oblique lat. view showing card. process, ×2 (587).

Truncalosia IMBRIE, 1959, p. 401 [**T. gibbosa*; OD]. Differs from *Heteralosia* in having large cicatrix of attachment truncating umbo, more delicate recumbent spines and smaller cardinal process, prominent diverging socket ridges, alveolus developed. *M.Dev.*, N.Am.——FIG. 307,*1*. **T.*

gibbosa, USA(Mich.); *1a,b*, holotype, ped.v. and brach.v. views, ×2; *1c*, brach.v. int., ×3 (445).

Wyndhamia Booker, 1929, p. 24 [**W. dalwoodensis*; OD] [=*Branxtonia* Booker, 1929 (type, *B. typica*), Perm., Australia]. Like *Strophalosia* but with more concentrically arranged spine ridges and finer prostrate spines in pedicle valve, brachial valve dimpled, usually nonspinose. *L.Perm.*, Australia.——Fig. 307,*3*. **W. dalwoodensis*; *3a,b*, brach.v. view, brach.v. int., ×1; *3c*, ped.v. ext. showing ornament, ×2 (89).

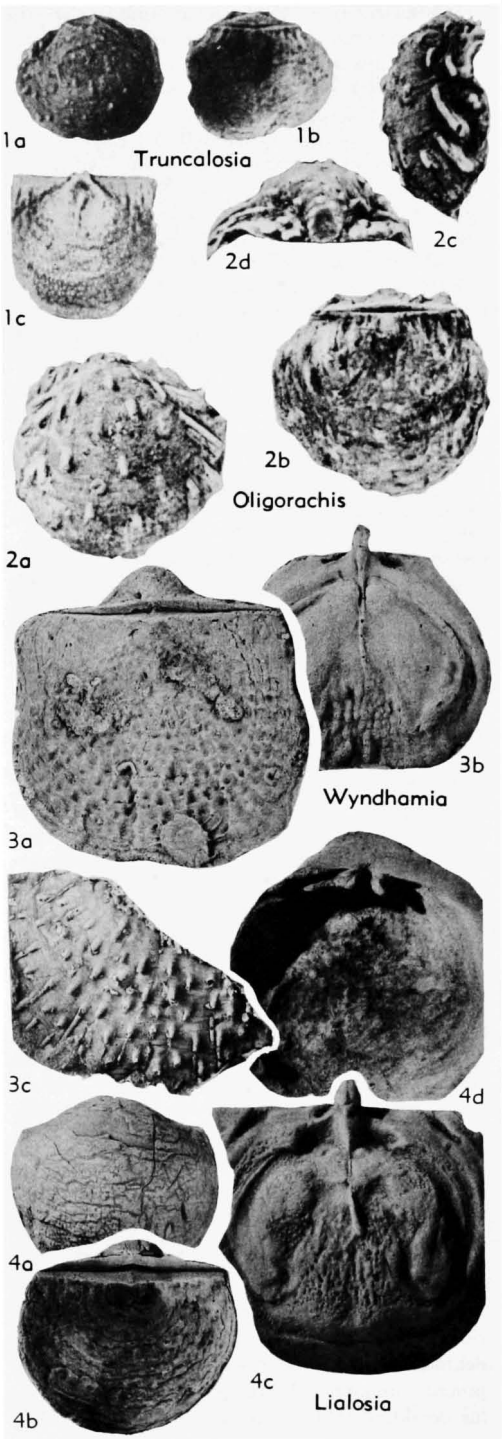

Fig. 307. Strophalosiidae (Heteralosiinae) (p. *H*451-*H*452).

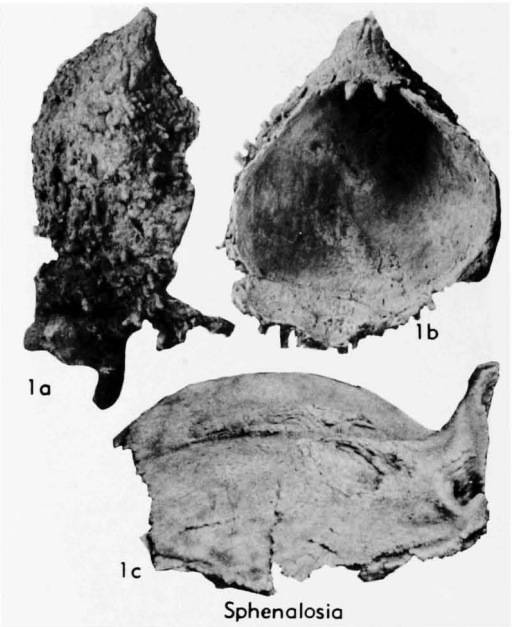

Fig. 308. Strophalosiidae (Heteralosiinae) (p. *H*451).

Subfamily CTENALOSIINAE Muir-Wood & Cooper, 1960

[Ctenalosiinae Muir-Wood & Cooper, 1960, p. 91]

Small irregular forms, brachial valve opercular; hinge of pedicle valve with numerous minute teeth and corresponding sockets in brachial valve; cardinal process with long bifid shaft; brachial ridges strophalosiid. *L.Perm.*

Ctenalosia Cooper & Stehli, 1955, p. 470 [**C. fixata*; OD]. Pedicle valve with interarea; valves smooth or obscurely costate, attachment spines in row near hinge, rare elsewhere; brachial valve rugose and dimpled, no spines. *L.Perm.*, N.Am. ——Fig. 309,*1*. **C. fixata*, USA(W.Tex.); *1a,b*, ped.v. ant. and int., ×3; *1c*, holotype, brach.v. view, ×3; *1d*, brach.v. int., ×3 (196).

Family TEGULIFERINIDAE Muir-Wood & Cooper, 1960

[Teguliferinidae Muir-Wood & Cooper, 1960 (November), p. 92] [=Teguliferidae Likharev, 1960 (December)]

Shell with obliquely conical pedicle valve

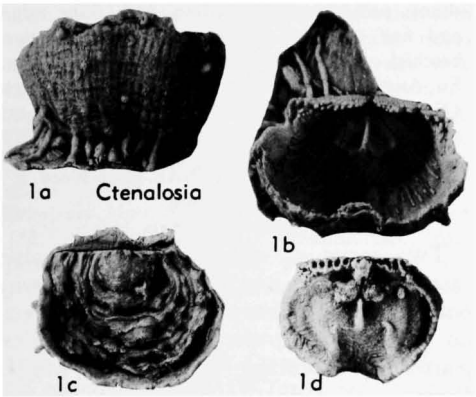

FIG. 309. Strophalosiidae (Ctenalosiinae) (p. *H*452).

attached by apex and anchored by rhizoid spines; no interareas or pseudodeltidium; brachial valve opercular; cardinal process bilobate, long-shafted and resembling Strophalosiidae, no alveolus. *U.Carb.(Penn.)-L.Perm., ?U.Perm.*

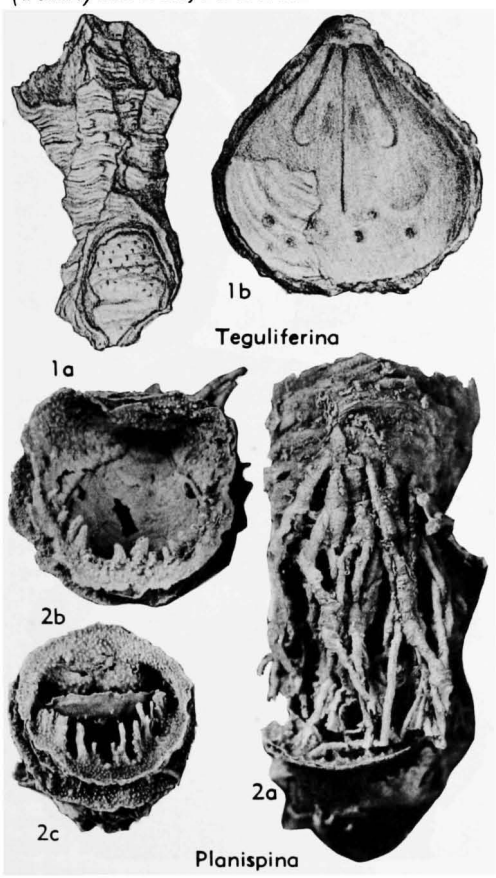

FIG. 310. Teguliferinidae (p. *H*453).

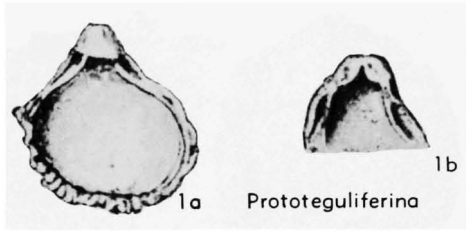

FIG. 311. Teguliferinidae (p. *H*453).

Teguliferina SCHUCHERT & LEVENE, 1929, p. 121 [*pro Tegulifera* SCHELLWIEN, 1898, p. 362 (*non* SAALMÜLLER, 1880)] [**Tegulifera deformis* SCHELLWIEN, 1898, p. 362; OD]. Pedicle valve an irregular cone; brachial valve operculiform, external in young shells but deep within pedicle valve in adult; pedicle valve with large spines, rugae and obscure capillae. *U.Carb.(Penn.)-L. Perm., ?U.Perm.*, Eu.(USSR-Yugosl.)-Asia(Japan-USSR,Ferghana).——FIG. 310,*1*. **T. deformis* (SCHELLWIEN), Perm., Yugosl.; *1a*, brach.v. view, elongate ped.v. above, ×1; *1b*, brach.v. int., ×2 (712).

Planispina STEHLI, 1954, p. 331 [**P. conida*; OD]. Like *Teguliferina*, but attachment spines fused together and to sides of cup by flat webs, and anterior margin of cup with long strainer spines. *Penn.-L.Perm.*, N.Am.——FIG. 310,*2a,b*. *P. boesei* (R. E. KING), L.Perm., USA(W.Tex.); *2a*, ped.v. lat. view showing long spines, ×2; *2b*, brach.v. ext., in place in cup, ×2 (773).——FIG. 310,*2c*. **P. conida*, L.Perm., USA(W.Tex.); ped.v. aperture, showing spines, ×1 (773).

Prototeguliferina LIKHAREV, 1960, p. 236 [**Tegulifera rossica* IVANOV, 1925, p. 111; OD]. Similar to *Teguliferina* but with spines along periphery of both valves, rudimentary interarea covered by hoodlike protuberance, brachial valve less deeply inserted. *U.Carb.-L.Perm.*, Eu.(USSR, Moscow & Donetz Basins), ?N.Am.——FIG. 311,*1*. **P. rossica* (IVANOV); *1a,b*, ped.v. and brach.v. in contact with hood concealing interarea, interarea exposed by removal of protuberance, ×1 (446).

Family AULOSTEGIDAE Muir-Wood & Cooper, 1960

[Aulostegidae MUIR-WOOD & COOPER, 1960, p. 94]

Shell attached by umbo and anchored by spines, and having gutter-like extension of both valves; interarea in pedicle valve only, delthyrium closed by convex elytridium (formerly pseudodeltidium) and lophidium. No teeth, sockets, or chilidium. Cardinal process trilobate or quadrilobate, alveolus present; adductor scars dendritic, accessory diductor scars on cardinal process shaft; brachial ridges given off horizontally. *U. Penn.-U.Perm.*

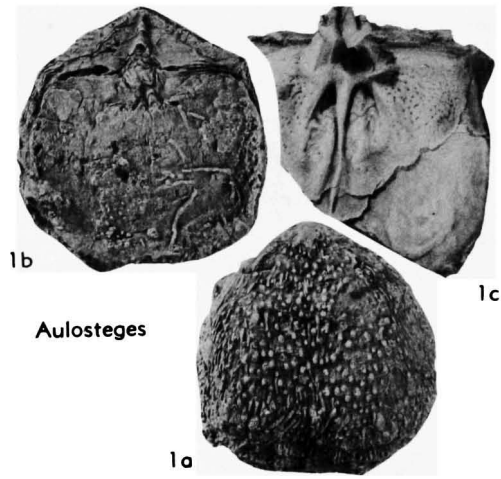

FIG. 312. Aulostegidae (Aulosteginae) (p. *H*454).

Subfamily AULOSTEGINAE Muir-Wood & Cooper, 1960

[Aulosteginae MUIR-WOOD & COOPER, 1960, p. 95]

Spines of two series present on both valves, otherwise smooth or lamellose; secondary area usually developed as perideltidium. Dorsal adductor scars not set on platforms. *L.Perm.-U.Perm.*

Aulosteges VON HELMERSEN, 1847, p. 330 [**A variabilis* (=**Orthis wangenheimi* DEVERNEUIL, 1845, p. 194); OD]. Medium-sized, commonly distorted, tapering to umbo; both valves with prostrate and suberect attachment spines encroaching on interarea; brachial valve adductors deeply inserted. *L.Perm.-U.Perm.*, Eu.-Asia-Arctic-Australia.——FIG. 312,*1*. **A. wangenheimi* (DE VERNEUIL), USSR; *1a-c*, ped.v. and brach.v. views, brach.v. int., ×1 (426).

Taeniothaerus WHITEHOUSE, 1928, p. 281 (*emend.* PRENDERGAST, 1943, p. 27) [**Productus subquadratus* MORRIS, 1845, p. 284; OD]. Large, with low interarea and no perideltidium; both valves with numerous elongate, regularly arranged spine ridges, prostrate and suberect spines projecting as thick brush, lamellose anteriorly; cardinal process trilobate, with elongated shaft and well-defined accessory diductor scars. *L.Perm.*, Asia-Australia-Tasm.——FIG 313,*1*. **T. subquadratus* (MORRIS), Australia; *1a,b*, ped.v. post., lat.; *1c*, brach.v. view; *1d*, brach.v. int. showing card. process; all ×0.75 (647).

Wyatkina FREDERIKS, 1931, p. 211 [**Aulosteges gigas* NECHAEV, 1894, p. 155; OD]. Large, elongate, subquadrate; interarea high, with elytridium and transversely striated perideltidium, no lophidium; pedicle valve lamellose, with spine ridges and fine prostrate spines resembling capillation; brachial valve smooth, lamellose anteriorly. *Perm.*, Eu.-Asia-Australia. —— FIG. 314,*1*. **W. gigas* (NECHAEV), Eu.(USSR); *1a,b*, ped.v. int., ext. showing spines, ×1; *1c*, brach.v. int., ×1 (597).

Subfamily ECHINOSTEGINAE Muir-Wood & Cooper, 1960

[Echinosteginae MUIR-WOOD & COOPER, 1960, p. 101]

Two series of spines on pedicle valve, rare spines on brachial valve, otherwise both valves capillate, lamellose or costate; no perideltidium; dorsal adductors set on platforms obscuring septum. *U.Penn.-L. Perm.*

Echinosteges MUIR-WOOD & COOPER, 1960, p. 101 [**Aulosteges tuberculatus* R. E. KING, 1931, p. 95; OD]. Large, asymmetrically subpentagonal, with high transversely striated interarea; elytri-

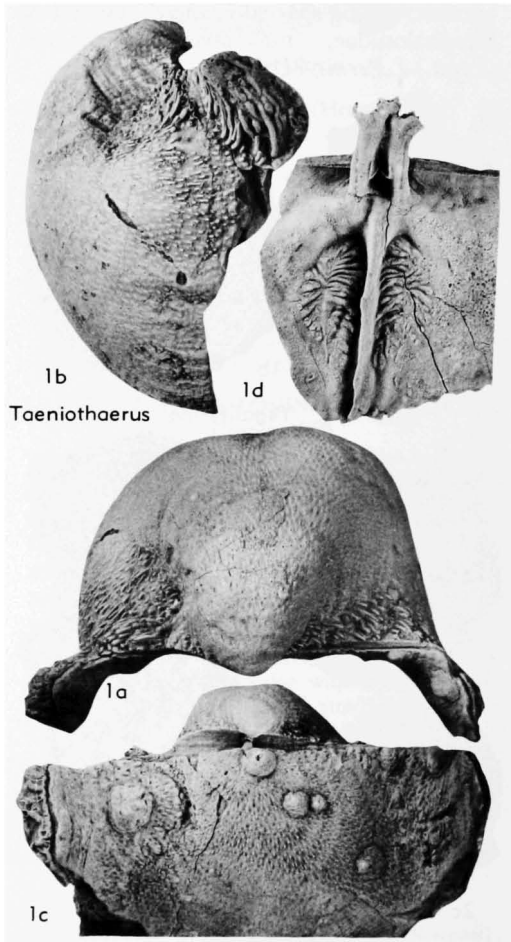

FIG. 313. Aulostegidae (Aulosteginae) (p. *H*454).

dium and lophidium present; pedicle valve with rugae, rhizoid spines posteriorly, spine ridges medianly, costate anteriorly; brachial valve with honeycomb ornament, rare spines. *L.Perm.*, N. Am.——Fig. 315,*2*. **E. tuberculatus* (R. E. King), USA(W.Tex.); *2a,b,* ped.v. ext., brach.v. ext., ×1; *2c,d,* brach.v. int., ped.v. interarea with spines, ×2 (587).

Edriosteges Muir-Wood & Cooper, 1960, p. 103 [**E. multispinosus*; OD]. Medium-sized, subpentagonal to subquadrate, with low interarea; pedicle valve with short recumbent spines, dense brush of rhizoid spines on ears and flanks; brachial valve faintly capillate, dimpled, no spines. *L. Perm.*, N.Am.-Asia(Pak.-China).——Fig. 315,*1*. **E. multispinosus,* USA(W.Tex.); *1a,b,* holotype, ped.v. view, brach.v. int., ×1; *1c,d,* ped.v. lat., brach.v. view, ×1 (587).

Girlasia de Gregorio, 1930, p. 21 [**Strophalosia (G.) superelegans*; OD]. Small, elongate-oval; lophidium present, no elytridium; pedicle valve lamellose with fine prostrate spines, row of coarser rhizoid spines near interarea; brachial valve with rare fine spines, cardinal process bilobate; hinge of both valves minutely crenulated. *L.Perm.*, Sicily. ——Fig. 316,*1*. **G. superelegans,* Sosio Ls.; *1a,b,* ped.v. and brach.v. views, ×3 (370).

Limbella Stehli, 1954, p. 329 [**Aulosteges wolfcampensis* R. E. King, 1931, p. 95; OD]. Differs from *Edriosteges* in having both valves capillate; elytridium absent; gutter developed in all growth stages. *U.Penn.-L.Perm.*, N.Am.——Fig. 317,*2*. **L. wolfcampensis* (R. E. King), L.Perm., USA (W.Tex.); *2a,b,* ped.v., brach.v. views, ×0.7; *2c,* ped.v. int., ×0.7; *2d,e,* brach.v., showing card. process with lophidium, ×2 (773).

Sphenosteges Muir-Wood & Cooper, 1960, p. 108 [**Aulosteges hispidus* Girty, 1920; OD]. Medium-sized, trigonal outline, commonly asymmetrical; interarea high, lophidium and elytridium present; pedicle valve with few rugae, prostrate and erect clasping spines, faintly capillate; brachial valve capillate, rare spines. *L.Perm.*, N.Am.(Wyo.-Utah).——Fig. 316,*3*. **S. hispidus* (Girty), Phosphoria F., USA(Wyo.); *3a,b,* ped.v. and brach.v. views, ×3 (587).

Spirisosium de Gregorio, 1930, p. 23 [**S. primarium* (=**Aulosteges Karpinskyi* Gemmellaro, 1892); OD]. Large, elongate-trigonal; very high interarea with narrow median ridge; pedicle valve with spine bases of 2 series, curved attachment spines along edge of interarea; brachial valve with rare spines. *L.Perm.*, Sicily.——Fig. 317,*1*. **S. karpinskyi* (Gemmellaro), Sosio Ls.; *1a,b,* ped.v. and brach.v. views, ×0.7 (370).

Strophalosiella Likharev, 1935, p. 372 [**S. coraeformis*; OD]. Pentagonal, tapering, elytridium present; both valves finely costellate, spines on flanks and near interarea in pedicle valve, absent in brachial valve. *L.Perm.*, Eu.(USSR).

Xenosteges Muir-Wood & Cooper, 1960, p. 111

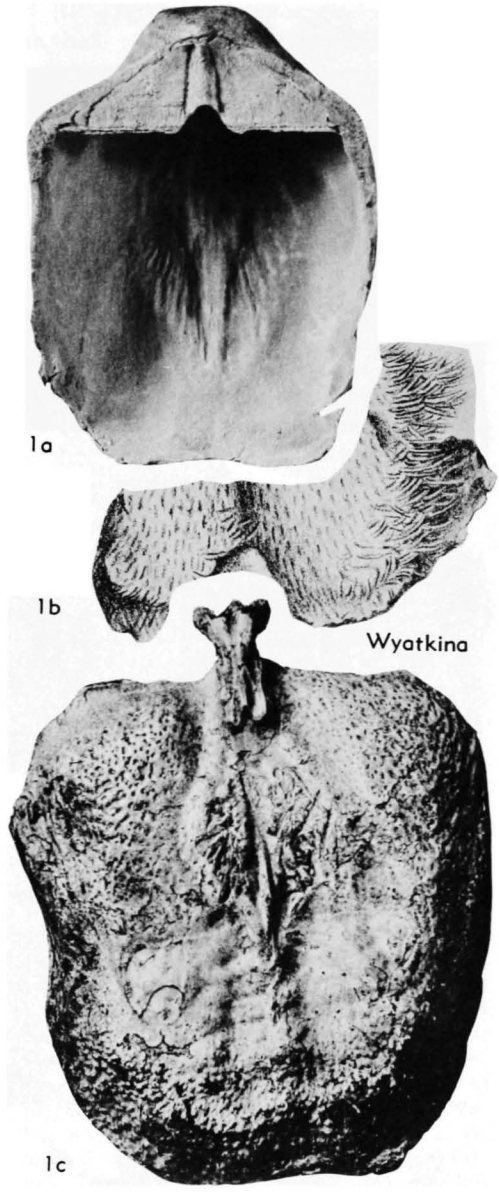

Fig. 314. Aulostegidae (Aulosteginae) (p. *H*454).

[**X. adherens*; OD]. Small, asymmetrical; edge of narrow interarea articulating with slot in brachial valve; both valves rugose or lamellose; spines near hinge margin in pedicle valve, absent in brachial valve. *L.Perm.(Leonard.-Word.)*, N. Am.——Fig. 316,*2*. **X. adherens,* USA(W.Tex.); *2a,b,* ped.v., ×3, ×2; *2c,* brach.v. view, ×4; *2d,* brach.v. int., ×4 (587).

Subfamily CHONOSTEGINAE Muir-Wood & Cooper, 1960

[Chonosteginae Muir-Wood & Cooper, 1960, p. 113]

Specialized, posteriorly rugose and anteriorly costate; pedicle valve with anterior projecting ledge, bearing row of erect attachment spines, another spine row along hinge margin. *U.Carb* or *L.Perm., ?U.Perm.*

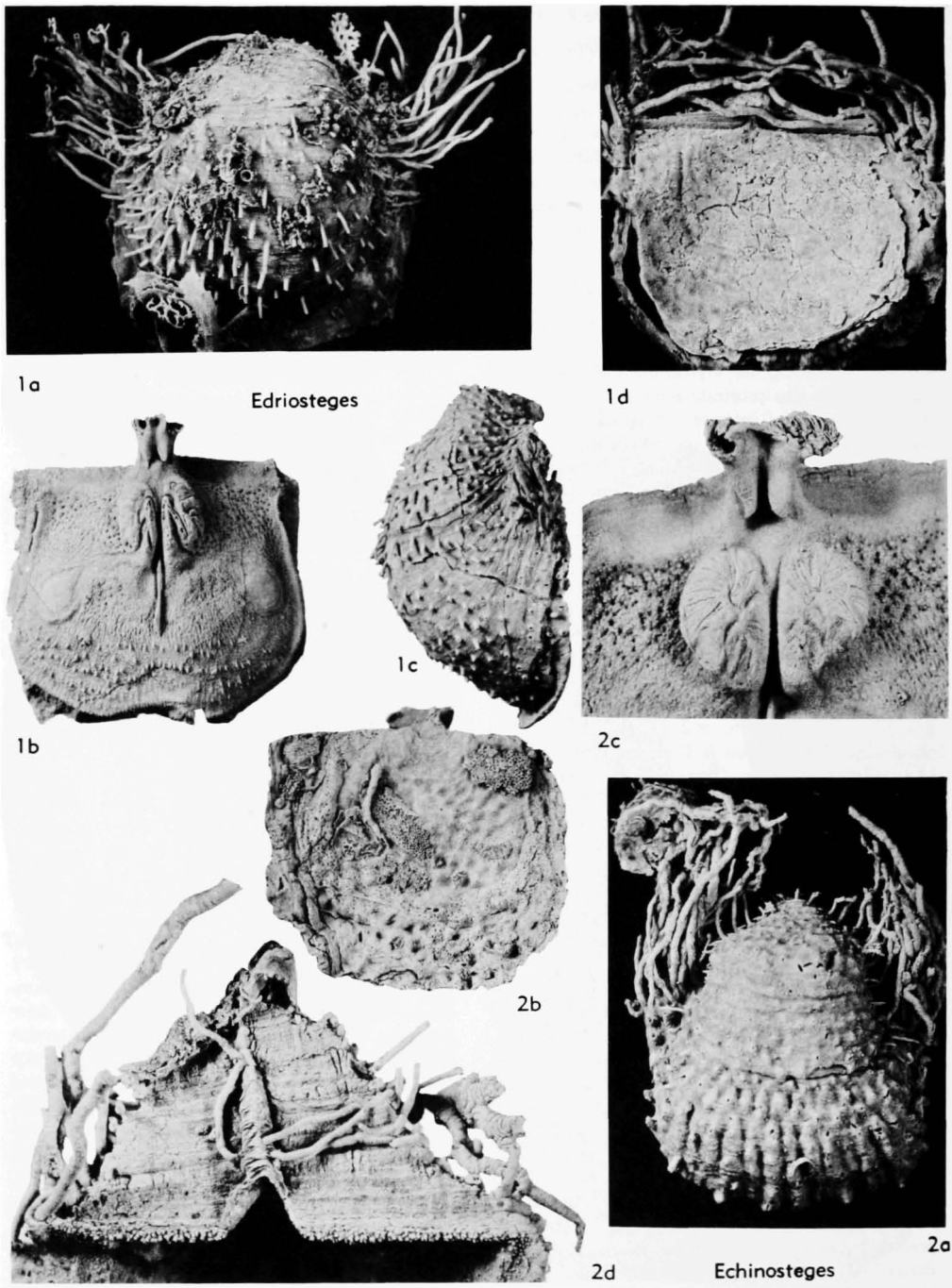

Fig. 315. Aulostegidae (Echinosteginae) (p. *H*454, *H*455).

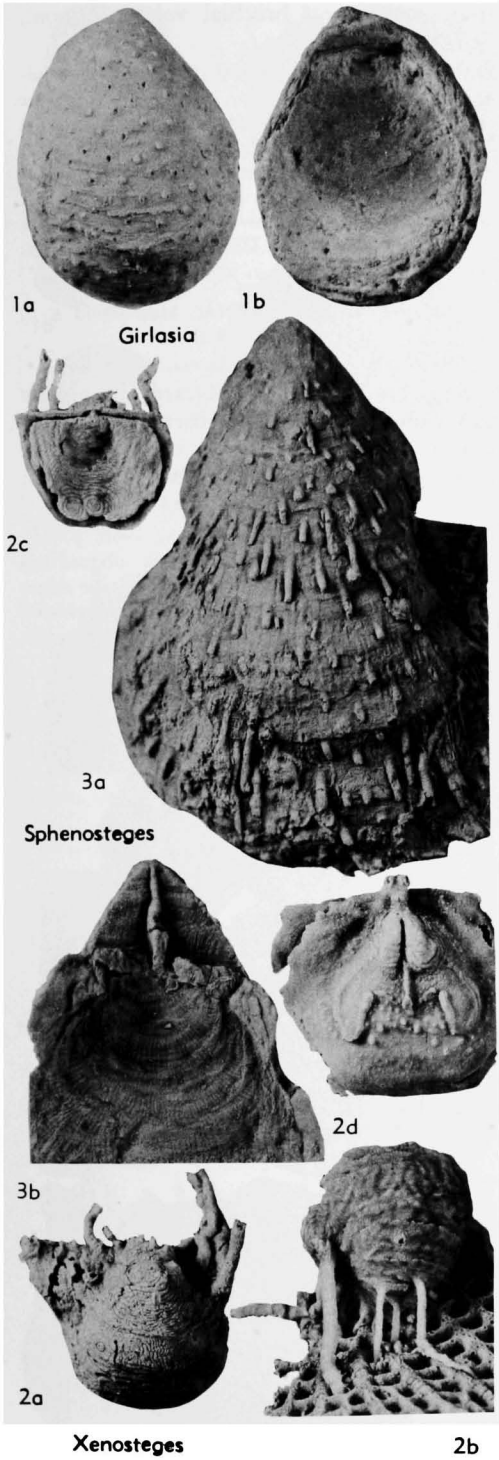

FIG. 316. Aulostegidae (Echinosteginae) (p. *H*455).

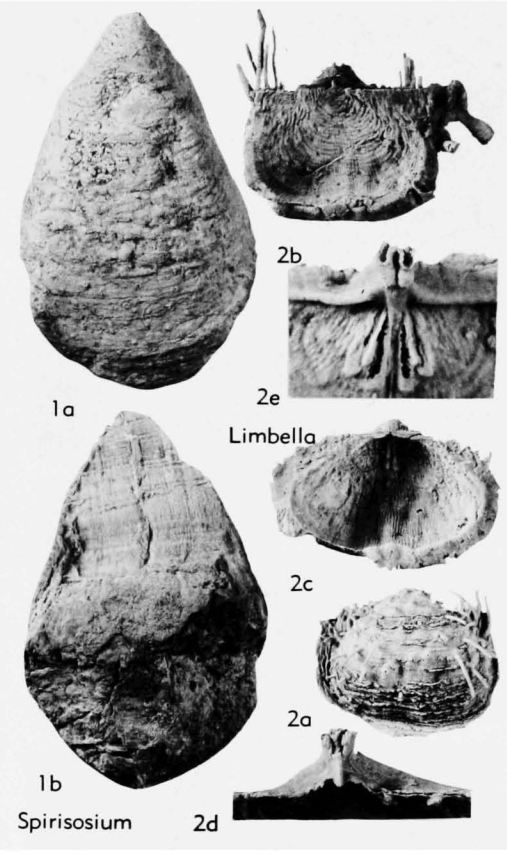

FIG. 317. Aulostegidae (Echinosteginae) (p. *H*455).

Chonosteges MUIR-WOOD & COOPER, 1960, p. 113 [**Aulosteges magnicostatus* GIRTY, 1909, p. 278; OD]. Pedicle valve geniculated, with short trail, elytridium and lophidium present, anterior ledge in pedicle valve with erect spines on costae and interior openings on intercostal sulci, 2 series of spines on rugose visceral disc; brachial valve costae terminating in anterior row of spines or funnels; complex internal system of strainer spines and pluglike fillings. *L.Perm.*, N.Am.——FIG. 318,*1*. **C. magnicostatus* (GIRTY), USA(W.Tex.); *1a*, brach.v. views showing attachment spines and funnels, ×2; *1b*, ant. margin with funnels, ×4; *1c*, ped.v. ant. view showing spines, ×1.35; *1d*, ant. view of both valves showing rim and stoppers, ×2; *1e*, brach.v. int., ×2 (587).

Strophalosiina LIKHAREV, 1935, p. 369 [**Aulosteges tibeticus* DIENER, 1897, p. 35; OD]. Resembles *Chonosteges* in external form and ornament but lacks spines on anterior ledge; brachial valve lacking spines or funnels. *(?U.)Perm.*, Eu.(Caucasus)-Asia.——FIG. 318,*2*. **S. tibetica* (DIENER), Tibet; *2a,b*, ped.v. ext., lat., ×0.7; *2c*, brach.v. view, ×0.7 (257).

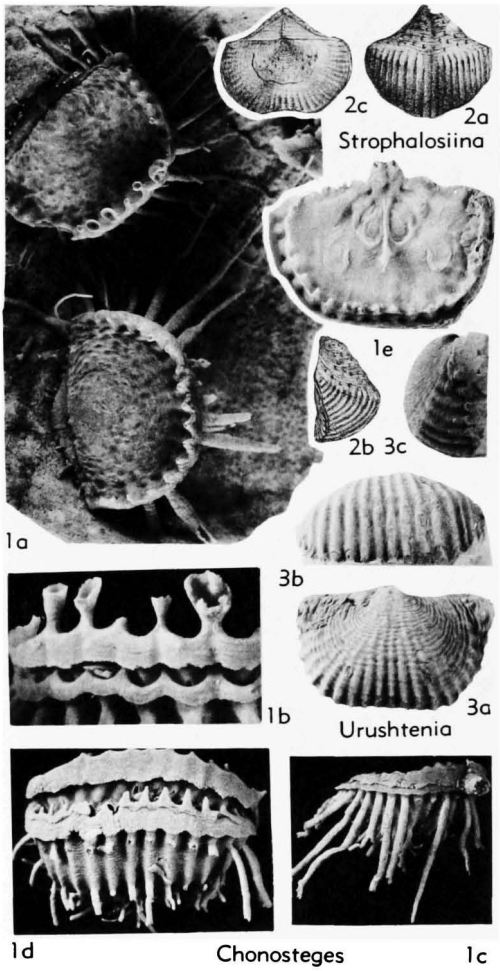

FIG. 318. Aulostegidae (Chonosteginae) (p. *H*457-*H*458).

Urushtenia LIKHAREV, 1935, p. 370 [**Productus pseudomedusa* CHERNYSHEV, 1902; OD]. Like *Strophalosiina* externally but interarea rarely developed; anterior ledge or ledges bearing erect spines as in *Chonosteges*, but no openings on intercostal sulci; brachial valve without funnels or spines. *L.Perm.*, Eu.(USSR).——FIG. 318,*3*. **U. pseudomedusa* (CHERNYSHEV); *3a-c*, ped.v., ext., ant., lat., ×1.3 (514).

Subfamily INSTITELLINAE Muir-Wood & Cooper, 1960

[Institellinae MUIR-WOOD & COOPER, 1960, p. 117]

Ornament costellate and rugose, visceral disc reticulate; pedicle valve with long attachment spines on ears and near hinge; spines absent on brachial valve. *L.Perm., ?U.Perm.*

Institella COOPER, 1942, p. 230 [**Productus leonardensis* R. E. KING, 1931, p. 70; OD]. Both valves geniculated, cicatrix of attachment present; low interarea without elytridium, lophidium present; trail with elaborate marginal gutter in both valves with median tonguelike extension. *L.Perm., ?U. Perm.*, Eu.-Asia-N.Am.——FIG. 319,*1*. **I. leonardensis* (R. E. KING), USA(W.Tex.); *1a*, ped.v. ext., ×1.5; *1b,c*, brach.v. ext., int., ×1 (587).

Subfamily RHAMNARIINAE Muir-Wood & Cooper, 1960

[Rhamnariinae MUIR-WOOD & COOPER, 1960, p. 119]

Aberrant, with low interarea in pedicle valve, elytridium usually absent, attachment cicatrix developed; both valves spinose. Small septum in pedicle valve. *L.Perm.-U. Perm.*

Rhamnaria MUIR-WOOD & COOPER, 1960, p. 119 [**R. kingorum*; OD]. Medium-sized, subquadrate, with low interarea; pedicle valve with spine ridges bearing fine prostrate or larger erect spines, rhizoid spines near hinge and on ears, brush of spines

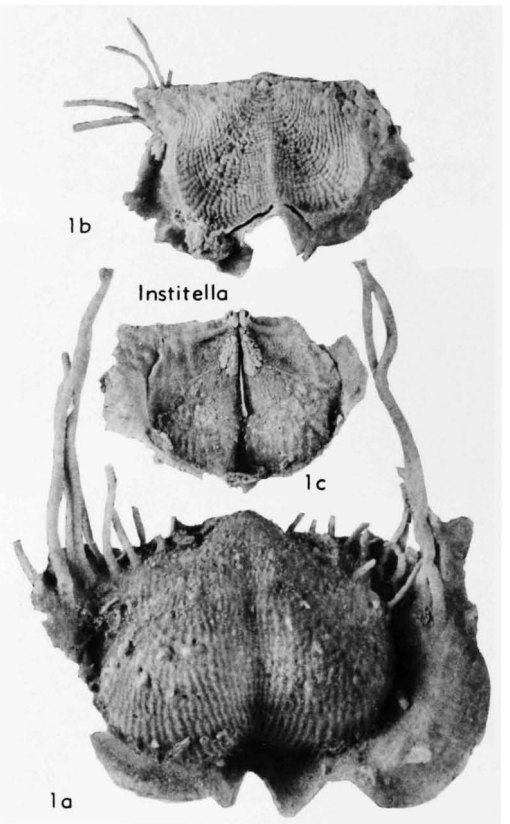

FIG. 319. Aulostegidae (Institellinae) (p. *H*458).

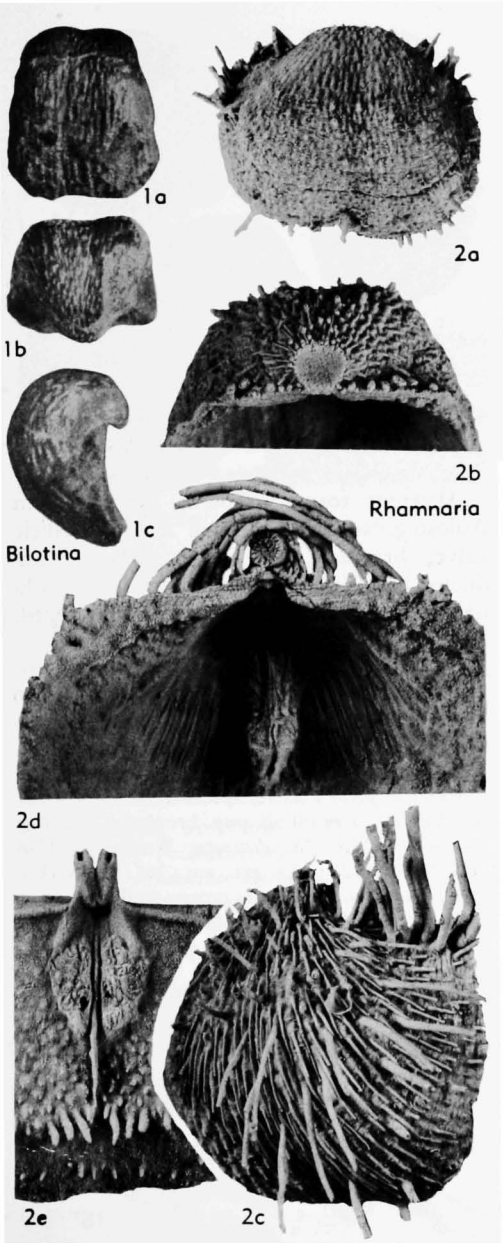

FIG. 320. Aulostegidae (Rhamnariinae) (p. *H*458-*H*459).

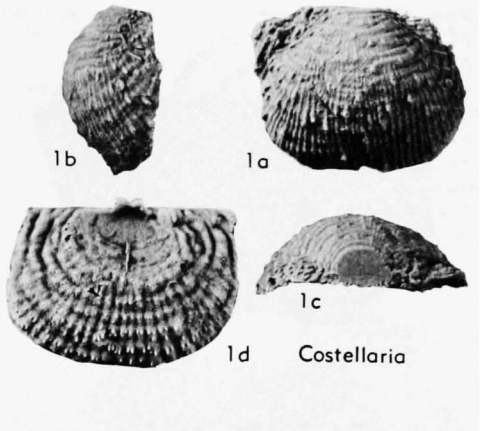

FIG. 321. Aulostegidae (Costellariinae) (p. *H*459).

extending laterally from flanks, anteriorly lamellose; brachial valve rugose, with fine, prostrate spines. *L.Perm.-U.Perm.*, N.Am.——FIG. 320,*2*. **R. kingorum*, L.Perm., USA(W.Tex.); *2a,b*, holotype, ped.v. ext., post., ×1, ×2; *2c,d*, ped.v., ext., int., ×2; *2e*, brach.v. int., ×2 (587).

Bilotina F. R. C. REED, 1944, p. 109 [**B. subtecta*; OD]. Medium-sized, elongate, with low interarea; pedicle valve with spine ridges posteriorly, irregularly costate anteriorly, large spines on ears and flanks, short ventral median septum; brachial valve spinose and pitted, internally with long median septum and 2 buttress plates. *L.Perm.*, Asia(Pak.).——FIG. 320,*1*. **B. subtecta*; *1a-c*, ped.v. vent., post., lat., ×1 (664).

Subfamily COSTELLARIINAE Muir-Wood & Cooper, 1960

[Costellariinae MUIR-WOOD & COOPER, 1960, p. 123]

Pedicle valve with low interarea, no elytridium, teeth or sockets, its exterior posteriorly rugose and finely costellate with 2 series of spines; brachial valve similar but lacking spines. *L.Perm.*

Costellaria MUIR-WOOD & COOPER, 1960, p. 123 [**C. costellata*; OD]. Growth habit strophalosiid, with cicatrix truncating umbo, but ornamented like *Cancrinella*; cardinal process bilobate, sessile, closing delthyrium anteriorly. *L.Perm.*, N.Am.——FIG. 321,*1*. **C. costellata*, USA(Tex.); *1a-c*, ped. v. ext., lat., post., ×2; *1d*, brach.v. int., ×4 (587).

Family SINUATELLIDAE Muir-Wood & Cooper, 1960

[Sinuatellidae MUIR-WOOD & COOPER, 1960, p. 124]

Strongly geniculated, anchored by attachment spines; ventral interarea with pseudodeltidium; teeth and sockets rarely developed; cardinal process posteriorly quadrilobate, alveolus present; diductor scars with lobate bounding ridges, adductors smooth. *L.Carb.-U.Carb.(Namur.)*.

Sinuatella MUIR-WOOD, 1928, p. 37 [**Leptaena sinuata* DE KONINCK, 1851, p. 654; OD]. Both valves with rugae and costae posteriorly, commonly reticulate; trail costate; spines long, curving near hinge, and on ears of pedicle valve. *L. Carb.(Visean) - U. Carb.(Namur.)*, Eu.-Asia. ——

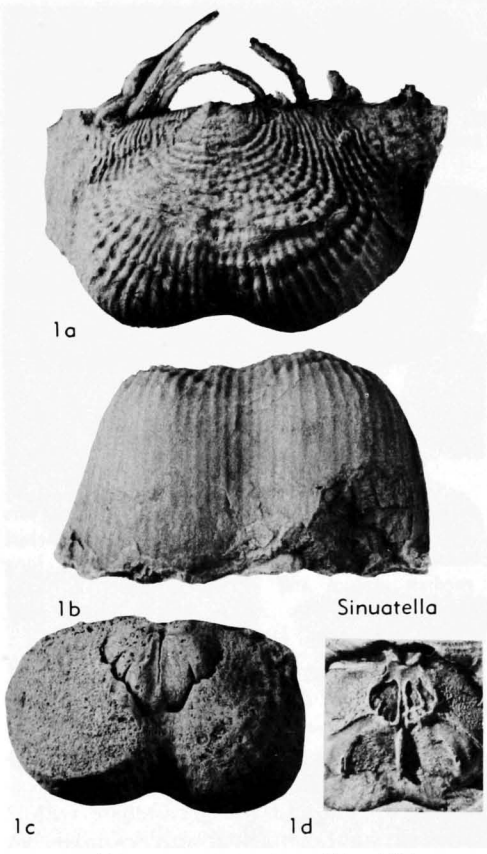

FIG. 322. Sinuatellidae (p. *H*459-*H*460).

FIG. 322,*1*. **S. sinuata* (DE KONINCK), L.Carb., Eng.; *1a-c,* ped.v. post. with overlapping spines, ant., mold of int. showing muscle field impression, ×2; *1d,* brach.v. int., ×2 (574).

Family CHONETELLIDAE Likharev, 1960

[Chonetellidae LIKHAREV, 1960, p. 226]

Externally resembling chonetoids, but with surface spines; interarea in each valve, small teeth and sockets; cardinal process large, bilobate, no alveolus; adductors smooth; brachial ridges well defined. *?L. Perm., U.Perm.*

Chonetella WAAGEN, 1884, p. 613 [**C. nasuta*; M] [*non Chonetella* KROTOV, 1885 (=*Chonetina* KROTOV, 1888)]. Small, valves highly concavo-convex, both valves costellate; pedicle valve with notched trail or with V-shaped extension, spines scattered and in row near interarea and on flanks of pedicle valve. *?L.Perm., U.Perm.,* Eu.(USSR)-Asia(Pak.)-Arctic.——FIG. 323,*1*. **C. nasuta,* Pak.; *1a-c,* ped.v. ext., post., ant., ×2; *1d,* brach. v. int., ×2 (587).

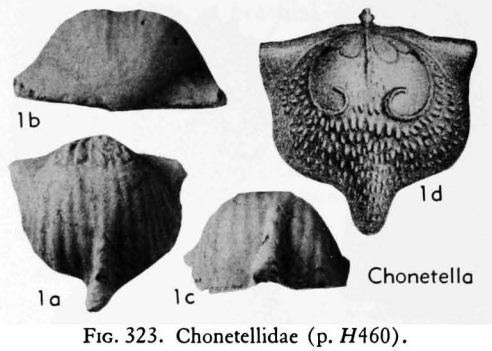

FIG. 323. Chonetellidae (p. *H*460).

Family SPYRIDIOPHORIDAE Muir-Wood & Cooper, 1960

[Spyridiophoridae MUIR-WOOD & COOPER, 1960, p. 144]

Aberrant forms probably derived from Aulostegidae but interarea lost in pedicle valve; brachial valve with elaborate adductor platforms forming spyridium, cardinal process bilobed, with alveolus developed. *U.Penn.-L.Perm.*

Spyridiophora COOPER & STEHLI, 1955, p. 471 [**S. distincta*; OD] [=*Spiridiophora* SARYCHEVA, 1960 *(nom. null.)*]. Medium-sized, transverse, both valves geniculated, posteriorly rugose and costate, trail costate; spines in row near hinge, and group on ears of pedicle valve, absent on brachial valve. *U. Penn.-L. Perm.(Wolfcamp.-Leonard.),* N. Am. ——FIG. 324,*1*. **S. distincta,* Wolfcamp., USA (W.Tex.); *1a,b,* ped.v. ext., ant., ×1; *1c,* brach.v. post. view showing card. process and spyridium, ×3; *1d,,* brach.v. view, ×1 (196).

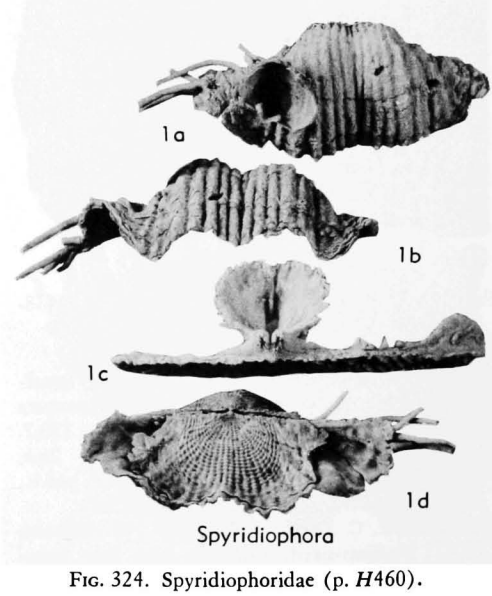

FIG. 324. Spyridiophoridae (p. *H*460).

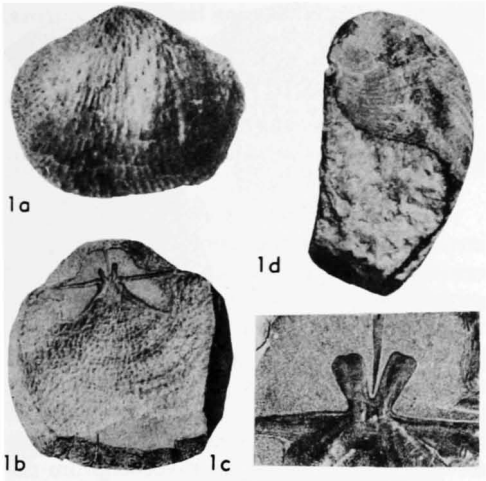

FIG. 325. Tschernyschewiidae (p. *H*461).

Family TSCHERNYSCHEWIIDAE Muir-Wood & Cooper, 1960

[Tschernyschewiidae MUIR-WOOD & COOPER, 1960, p. 126]

Aberrant forms with high platelike septum in pedicle valve fitting between 2 lobes of cardinal process; no teeth and sockets; adductors nondendritic. *L.Perm.-U.Perm.*

Tschernyschewia STOYANOW, 1910, p. 853 [**T. typica*; OD] [=*Septoproductus* FRECH, 1911, p. 75 (type, *Productus abichi* WAAGEN, 1884, p. 697)]. Medium-sized, externally resembling *Waagenoconcha,* with spine ridges medianly and fine spines on flanks; pedicle valve with low interarea, umbo commonly truncated by attachment cicatrix. *L.Perm.-U.Perm.,* Eu.-Asia.——FIG. 325,*1*. **T. typica,* Armenia; *1a,* ped.v. ext., ×1; *1b,c,* brach.v. view with beaks ground showing ped.v. septum and card. process, ×1, ×2; *1d,* ped.v. long. sec. showing septum, ×1 (785).

Family SCACCHINELLIDAE Likharev, 1928

[*nom. transl.* A. WILLIAMS, 1953, p. 12 (*ex* Scacchinellinae LIKHAREV, 1928, p. 265)]

Aberrant, specialized forms probably derived from Aulostegidae, characterized by conical pedicle valve cemented at apex and anchored by numerous rhizoid spines; pedicle valve interior with long median septum, distal end fitting between prongs of cardinal process; dorsal growth of body accompanied by deposition of abundant cystose or blister-like plates forming partitions; adductor scars dendritic, set on muscle platforms. *U.Penn.-L.Perm., ?U.Perm.*

Scacchinella GEMMELLARO, 1891, p. 22 [**S. variabilis* GEMMELLARO, 1897; SD SCHUCHERT & LEVENE, 1929, p. 110]. Medium-sized to large; interarea very large, longitudinally striated, elytridium not distinguishable; pedicle valve spinose except on interarea; brachial valve finely spinose, no interarea. *U.Penn.-L.Perm., ?U.Perm.,* N.Am.; *Perm.,* Eu. (Sicily-Alps-Caucasus)-Asia(Ferghana-Japan).——FIG. 326,*2*. **S. americana* STEHLI, L. Perm.(Leonard.), USA(W.Tex.); *2a,b,* ped.v.,

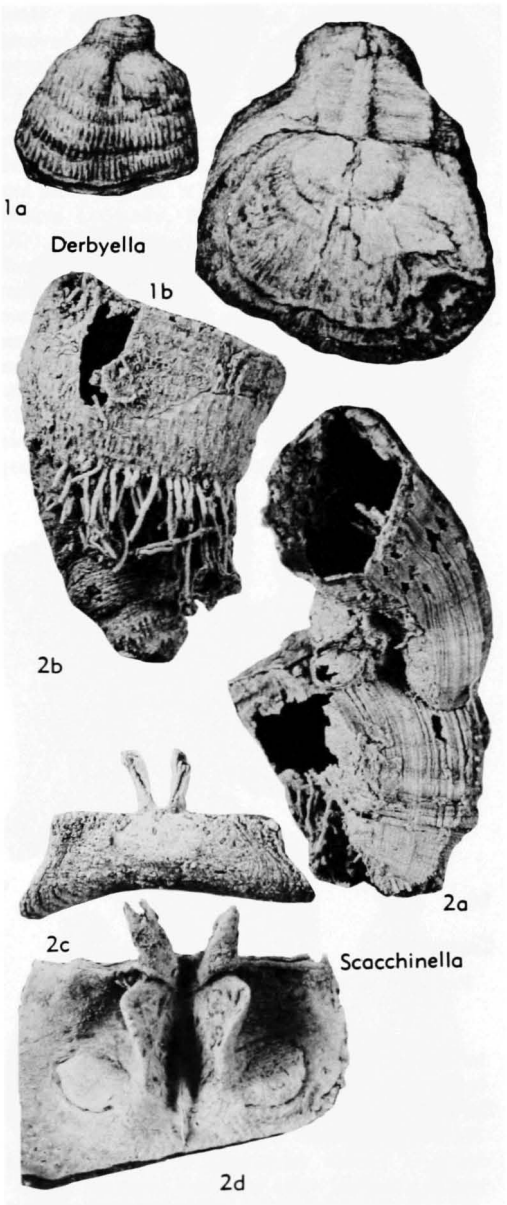

FIG. 326. Scacchinellidae (p. *H*461-*H*462).

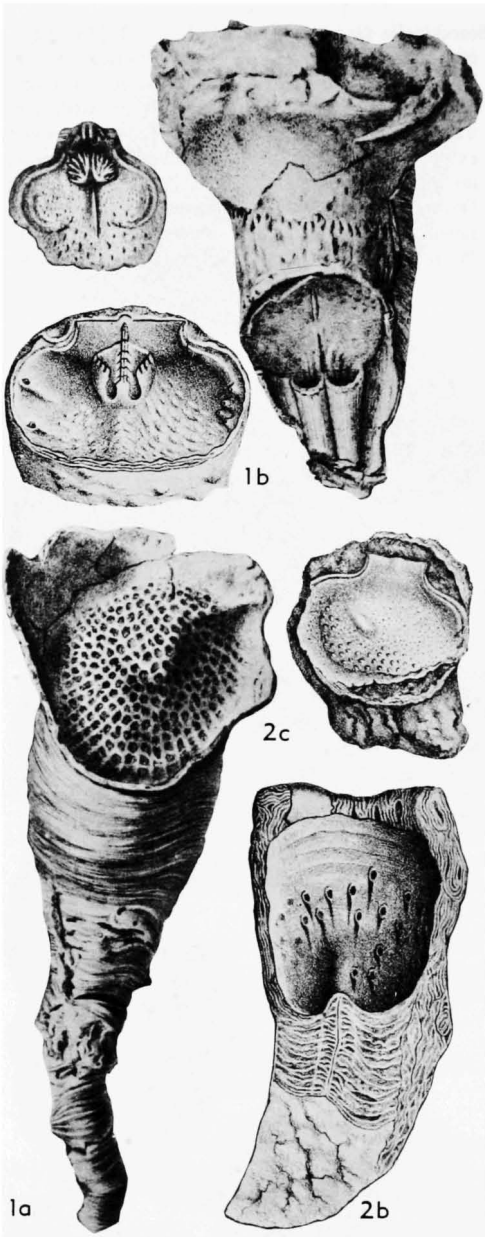

FIG. 327. Richthofeniidae (Richthofeniinae) (p. *H462*).

lat. views showing attachment spines, ×1; *2c,d,* brach.v. ext., int., ×1, ×2 (470).

Derbyella GRABAU, 1931, p. 269 [**D. bureri*; OD]. Medium-sized, with high ventral interarea; interior of pedicle valve with myocoelidium and septum; brachial valve with low interarea, otherwise imperfectly known. *L.Perm.*, Asia(Mongolia). ——FIG. 326,*1*. **D. bureri*; *1a,b,* holotype, ped.v. ext., brach.v. view showing large ped.v. interarea, ×1, ×2 (360).

Superfamily RICHTHOFENIACEA Waagen, 1885

[*nom. correct.* MUIR-WOOD, herein (*pro* Richthofenacea MUIR-WOOD, 1955; *nom. transl. ex* Richthofenidae WAAGEN, 1885, p. 729)]

Aberrant productoids specialized for reef environment, having conical pedicle valve cemented by apex and anchored by rhizoid spines; brachial valve opercular, commonly inserted deeply in cone and resting in closed position on ridge or aulocoterma; 2-shafted small bilobed cardinal process and laterally placed brachial ridges present; aperture of cone with strainer spines or mesh-forming sieve; muscle chamber of myocoelidium developed. *L.Perm.-U.Perm.*

Family RICHTHOFENIIDAE Waagen, 1885

[*nom. correct.* SCHUCHERT & LEVENE, 1929, p. 17 (*pro* Richthofenidae WAAGEN, 1885, p. 729)]

Pseudodeltidium exposed, or enclosed by outer shell layer, interarea absent; pedicle valve with muscles partially or completely enclosed within myocoelidium or myocoelidium absent in adult; dorsal adductor scars dendritic; teeth situated in brachial valve and sockets in pedicle valve. *L.Perm.-U. Perm.*

Subfamily RICHTHOFENIINAE Waagen, 1885

[*nom. correct.* MUIR-WOOD & COOPER, 1960 (*pro* Richthofeninae, *nom. transl.* STOYANOW, 1915, p. 30, *ex* Richthofenidae WAAGEN, 1885)]

Pseudodeltidium enclosed by outer shell layer; myocoelidium with single septum or 3 septa. *L.Perm.-U.Perm.*

Richthofenia KAYSER, 1881, p. 352 [**Anomia lawrenciana* DE KONINCK, 1863, p. 18; OD]. Aperture spines unknown but possibly similar to those of *Prorichthofenia*; myocoelidium with 3 septa. *L. Perm.-U. Perm.*, Eu. (Sicily-USSR)-Asia (China-Japan-Pak.-Timor). —— FIG. 327,*2*. **R. lawrenciana* (DE KONINCK), Pak.; *2a,* ped.v. int. with myocoelidium; *2b,* ped.v. long. sec. showing vesiculose shell structure; *2c,* brach.v. view, all ×0.85 (845).

Coscinarina MUIR-WOOD & COOPER, 1960, p. 138 [**Richthofenia communis* GEMMELLARO, 1894, p. 7; OD]. Large, with cone much elongated, aperture covered by arched reticulated meshwork of spines; myocoelidium with single septum, extending length of cup. *L.Perm.*, Eu.——FIG. 327,*1*. **C. communis* (GEMMELLARO), Sosio Ls., Sicily; *1a-c,* ext. of cup with meshwork, specimen showing brach.v. and myocoelidium, brach.v. int., all ×0.85 (772).

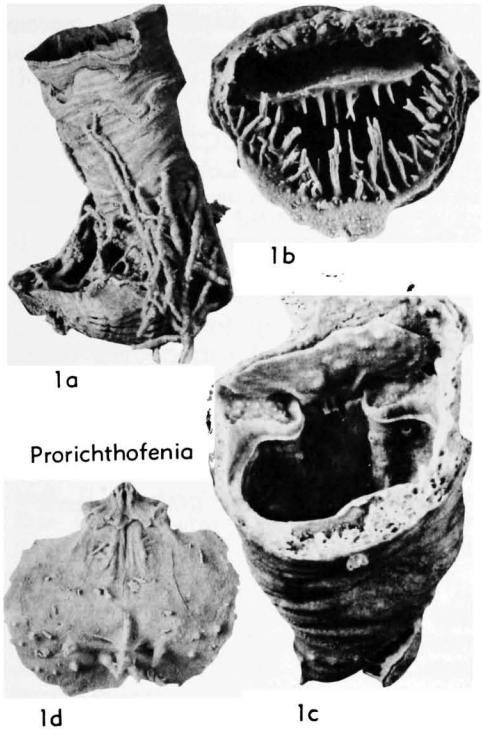

FIG. 328. Richthofeniidae (Prorichthofeniinae) (p. *H*463).

Subfamily PRORICHTHOFENIINAE Muir-Wood & Cooper, 1960

[Prorichthofeniinae MUIR-WOOD & COOPER, 1960, p. 139]

With rudimentary myocoelidium developed only in early growth stages and later covered by cystose shell; pseudodeltidium enclosed by outer shell layer. *L.Perm.*

Prorichthofenia R. E. KING, 1931, p. 97 [**Crania permiana* SHUMARD, 1859, p. 395; OD]. Anterior part of pedicle-valve aperture with long, commonly forked spines forming mesh with endospines on interior of brachial valve; brachial ridge not developed; median septum reduced. *L.Perm.*, Eu.(USSR)-N. Am.(Tex.-N. Mex.-Mex.).——FIG. 328,*1*. **P. permiana* (SHUMARD), Word., USA(W. Tex.); *1a*, ped.v. lat. view with attachment spines, ×0.85; *1b*, apertural view of cup showing brach. v. (above) with spines on int., ×1.7; *1c*, oblique view of cup showing lidlike brach.v. in place, resting on aulacoterma, ×1.7; *1d*, brach.v. int., ×1.7 (587).

Subfamily GEMMELLAROIINAE A. Williams, 1953

[*nom. transl.* MUIR-WOOD & COOPER, 1960, p. 140 (*ex* Gemmellaroiidae A. WILLIAMS, 1953, p. 10)]

Conical, attached by umbo and anchoring spines but having brachial valve as lid over aperture; pseudodeltidium exposed; no vesiculose shell; myocoelidium long; cardinal process massive, extending into myocoelidium. *L.Perm.*

Gemmellaroia COSSMANN, 1898 [*pro Megarhynchus* GEMMELLARO, 1894, p. 7 (*non* DE LAPORTE, 1832)] [**Megarhynchus marii* GEMMELLARO, 1894, p. 7; SD MABUTI, 1937, p. 16] [=*Megalorhynchus* DE GREGORIO, 1930, p. 23 *(errore pro Megarhynchus)*; *Gemmellaroiella* MABUTI, 1937, p. 16 (type, *G. ozawai*)]. Exterior rugose and finely spinose; myocoelidium long, anteriorly grooved and having internal median septum; internal margins of both valves denticulate. *L.Perm.*, Eu-Asia.——FIG. 329,*1*. **G. marii* (GEMMELLARO), Sosio Ls., Sicily; *1a*, post. view showing conical ped.v. with pseudodeltidium and lidlike brach.v., ×1; *1b*, brach.v. int. with card. process and pitted margin, ×2 (331).

Tectarea LIKHAREV, 1928, p. 268 [**T. robinsoni*; OD]. Probably attached by umbo; exterior usually decorticated, probably capillate with intervening radially arranged pits; myocoelidium long, without septum or anterior groove, may be filled with secondary deposit; each valve with toothlike process and socket articulating with similar structures on other valve. *L.Perm.*, Eu.(Caucasus).——FIG. 329,*2*. **T. robinsoni*; *2a,b*, ped.v. and brach.v. views, ×3; *2c*, transv. sec. showing card. process and myocoelidium, ×3 (509).

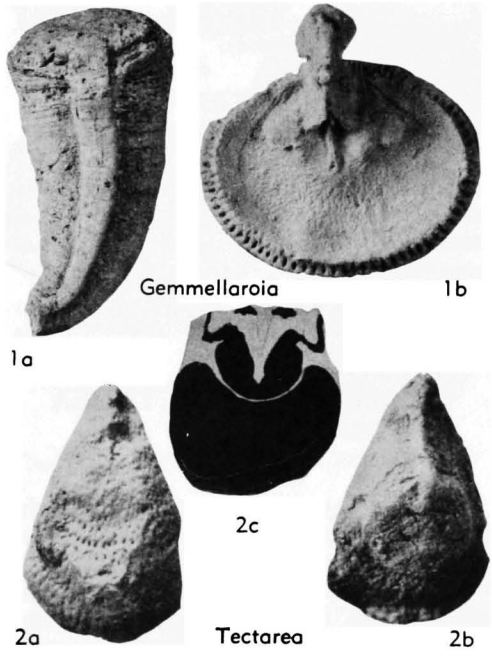

FIG. 329. Richthofeniidae (Gemmellaroiinae) (p. *H*463).

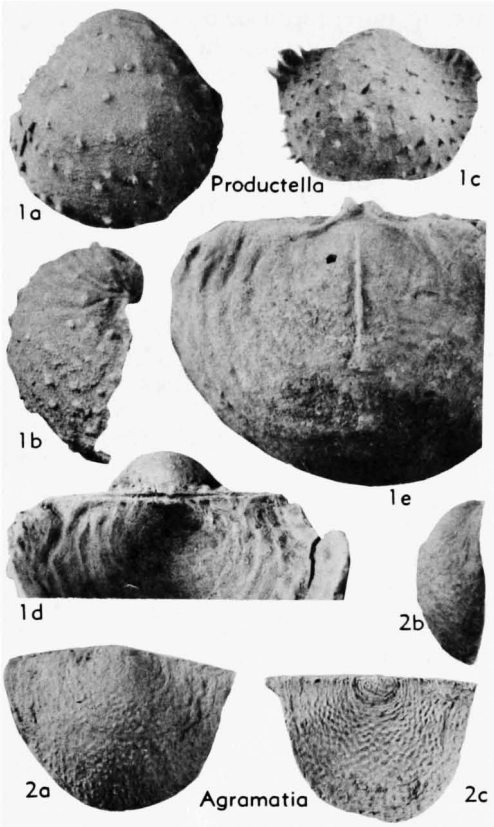

FIG. 330. Productellidae (Productellinae) (p. *H*464).

Family UNCERTAIN

Subfamily LOCZYELLINAE Likharev, 1937

[Loczyellinae LIKHAREV, 1937, p. 83]

Shovel-shaped, probably attached by umbo; valves concavo-convex; external surface with growth lines; internal characters unknown. *Perm.*

Loczyella FRECH, 1901, p. 503 [**L. nankinensis*; OD]. Characters of subfamily. *Perm.*, Eu.-Asia (China).

Superfamily PRODUCTACEA Gray, 1840

[*nom. transl.* MAILLIEUX, 1941, p. 7 (*ex* Productidae GRAY, 1840, p. 151)]

Generally attached by ringlike attachment spines in early growth stages, and rarely cemented by umbo, living free in later growth stages and supported by halteroid spines, interareas, teeth and sockets weakly developed in primitive forms only; ginglymus in gerontic stages of some genera; cardinal process bilobate or trilobate, rarely quadrilobate; diaphragm in brachial valve and crenulated marginal ridges in one or both valves in some genera. *L.Dev.-U. Perm.*

Family PRODUCTELLIDAE Schuchert & LeVene, 1929

[*nom. transl.* MUIR-WOOD & COOPER, 1960, p. 145 (*ex* Productellinae SCHUCHERT & LEVENE, 1929, p. 17)]

Primitive productoids with variably developed interareas and pseudodeltidium; chilidium absent in one subfamily; teeth and sockets varying from strongly developed to weak or absent; cardinal process small, bilobed internally, quadrilobate externally, alveolus developed with breviseptum; adductors smooth or dendritic. *Up.L. Dev.-U.Miss.*

Subfamily PRODUCTELLINAE Schuchert & LeVene, 1929

[Productellinae SCHUCHERT & LEVENE, 1929, p. 17]

Without cicatrix of attachment, pseudodeltidium, or chilidium; scattered spines on pedicle valve, rare on brachial valve; adductors smooth. *L.Dev.-L.Miss.*

Productella HALL, 1867, p. 153 [**Productus subaculeatus* MURCHISON, 1840, p. 255; SD OEHLERT, 1887, p. 1279]. Small or medium in size, subquadrate or hemispherical; interareas commonly linear, pseudodeltidium usually absent; small hinge teeth and sockets; pedicle valve with scattered pustules bearing recumbent or suberect spines, row of spines near hinge, growth lines prominent, rare rugae; brachial valve similar to pedicle valve, with few spines. *M.Dev.-U.Dev.*, Eu.-Asia-N.Am. ——FIG. 330,*1*. **P. subaculeata* (MURCHISON), U. Dev., Fr.; *1a,b*, ped.v. ext., lat., ×2; *1c*, ped.v. with spines, ext., ×2; *1d*, brach.v. view, ×3; *1e*, brach.v. int., ×4 (589).

Agramatia SOKOLSKAYA, 1948, p. 39 [**Productus agramati* NALIVKIN, 1934, p. 21; OD]. Shell semicircular in outline, cicatrix of attachment present; teeth and sockets and interareas developed, no pseudodeltidium; pedicle valve with row of spines near hinge, rugae and spine ridges developed over whole valve, latter possibly bearing fine curving spines. *U.Dev.*, Eu.(USSR)-N.Am. ——FIG. 330,*2*. **A. agramati* (NALIVKIN), Famenn., USSR; *2a,b*, ped.v. ext., lat., ×2; *2c*, brach.v. ext., ×2 (753).

Helaspis IMBRIE, 1959, p. 400 [**H. luma*; OD]. Small, subquadrate, with narrow interarea in both valves; spine bases and elongate spine ridges crowded on pedicle valve only; brachial valve dimpled, without spines; small convex apical pseudodeltidium present; hinge teeth strong. *M. Dev.*, N.Am.——FIG. 331,*1*. **H. luma*, USA (Mich.); *1a-c*, ped.v. ext., brach.v. view, brach.v. int., ×2 (445).

Orbinaria MUIR-WOOD & COOPER, 1960, p. 149 [**Productella pyxidata* HALL, 1858, p. 498; OD]. Shell hemispherical; pedicle valve with interarea, no pseudodeltidium; small teeth and sockets; pedicle valve with rugae and lamellae, spine ridges and small erect spines, row of spines near hinge, ringlike attachment in young (Fig. 298); brachial valve with concentric ornament and no spines, alveolus rarely developed. *U.Dev.* or *L. Miss.*, N.Am.——FIG. 331,*2*. **O. pyxidata* (HALL), Louisiana Ls., USA(Mo.); *2a,b,* ped.v. and brach. v. views, ×2; *2c,* brach.v. int., ×3 (587). [Attachment ring in young shell, Fig. 298.]

Praewaagenoconcha SOKOLSKAYA, 1948, p. 132 [**Productus orelianus* MÖLLER, 1871, p. 389; OD]. Hemispherical, interareas linear; pedicle valve medianly arched or with low vertical spinose ridge, rugae and long suberect spines near hinge; brachial valve finely spinose; teeth and sockets small. *U.Dev.*, Eu.-Asia.——FIG. 331,*4*. **P. orelianа* (MÖLLER), Famenn., USSR; *4a,b,* ped.v. views (*4b* with median spinose ridge), *4c,* brach. v. view, ×2 (753).

Productellana STAINBROOK, 1950, p. 373 [**P. bifaria*; OD]. Small, subcircular; pedicle valve with low interarea, ornament of rugae posteriorly, erect spines may occur on short spine ridges; brachial valve more rugose, with scattered spines, cardinal process closing delthyrium; other internal characters unknown. *L.Miss.*, N.Am.——FIG. 331, *3*. **P. bifaria,* Kinderhook., USA(Iowa); *3a,b,* ped.v. and brach.v. views, ×1 (587).

Sinoproductella WANG, 1955, p. 349 [**Productella hemispherica* TIEN, 1938, p. 19; OD] [?=*Praewaagenoconcha* SOKOLSKAYA, 1948, p. 132]. *U. Dev.*, China(Hunan).——FIG. 332,*1*. **S. hemispherica* (TIEN); ped.v. view, ×1 (852).

Spinulicosta NALIVKIN, 1937, p. 49 [**Productella spinulicosta* HALL, 1857, p. 173; OD]. Subcircular to elongate, interareas linear or absent; pedicle valve with concentric lamellae, long curved spines on flanks and near hinge, spine ridges, and obscure costae; brachial valve dimpled with concentric ornament and rare spines; teeth and sockets developed. *L.Dev.-U.Dev.*, cosmop.——FIG. 332, *3a,b*. *S.* sp., cf. **S. spinulicosta* (HALL), L.Dev., USA(Ohio); *3a,b,* ped.v. post., vent., ×2 (587). ——FIG. 332,*3c,d*. *S.* sp., aff. *S. navicella* (HALL), M.Dev., USA(Nev.); *3c,* brach.v. int., ×3; *3d,* group of shells with spines preserved, ×1 (587).

Stelckia (*see* p. *H*904).

Strophoproductus NALIVKIN, 1937, p. 46 [**Productella hystricula* HALL, 1867, p. 178; OD]. Small, orbicular; pedicle valve with narrow interarea; ornament of concentric lamellae, rugae, and prostrate spines on spine ridges, 2 rows of spines near hinge and down flanks; brachial valve with concentric ornament and spines; teeth and sockets developed. *U.Dev.*, N.Am.-Eu.-Asia.——FIG. 332, *2*. **S. hystriculus* (HALL), USA(N.Y.); *2a,b,* ped. v. views, ×2; *2c,* brach.v. int., ×2 (587).

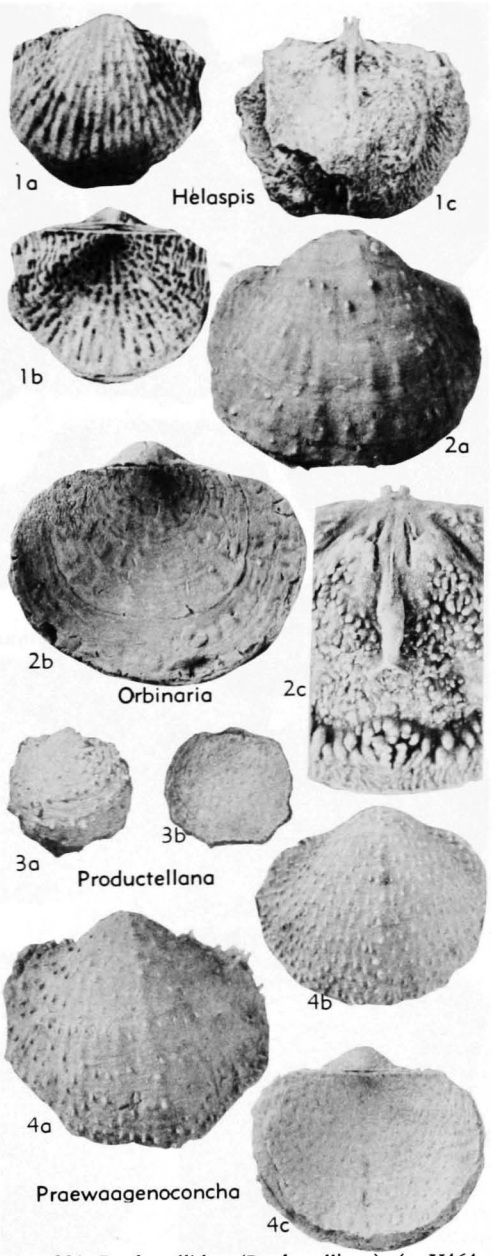

FIG. 331. Productellidae (Productellinae) (p. *H*464-*H*465).

Subfamily CHONOPECTINAE Muir-Wood & Cooper, 1960

[Chonopectinae MUIR-WOOD & COOPER, 1960, p. 156]

Commonly with cicatrix of attachment; pedicle valve slightly convex; body cavity narrow, pseudodeltidium and chilidium; teeth and sockets present; interareas in both valves or pedicle valve only; adductors

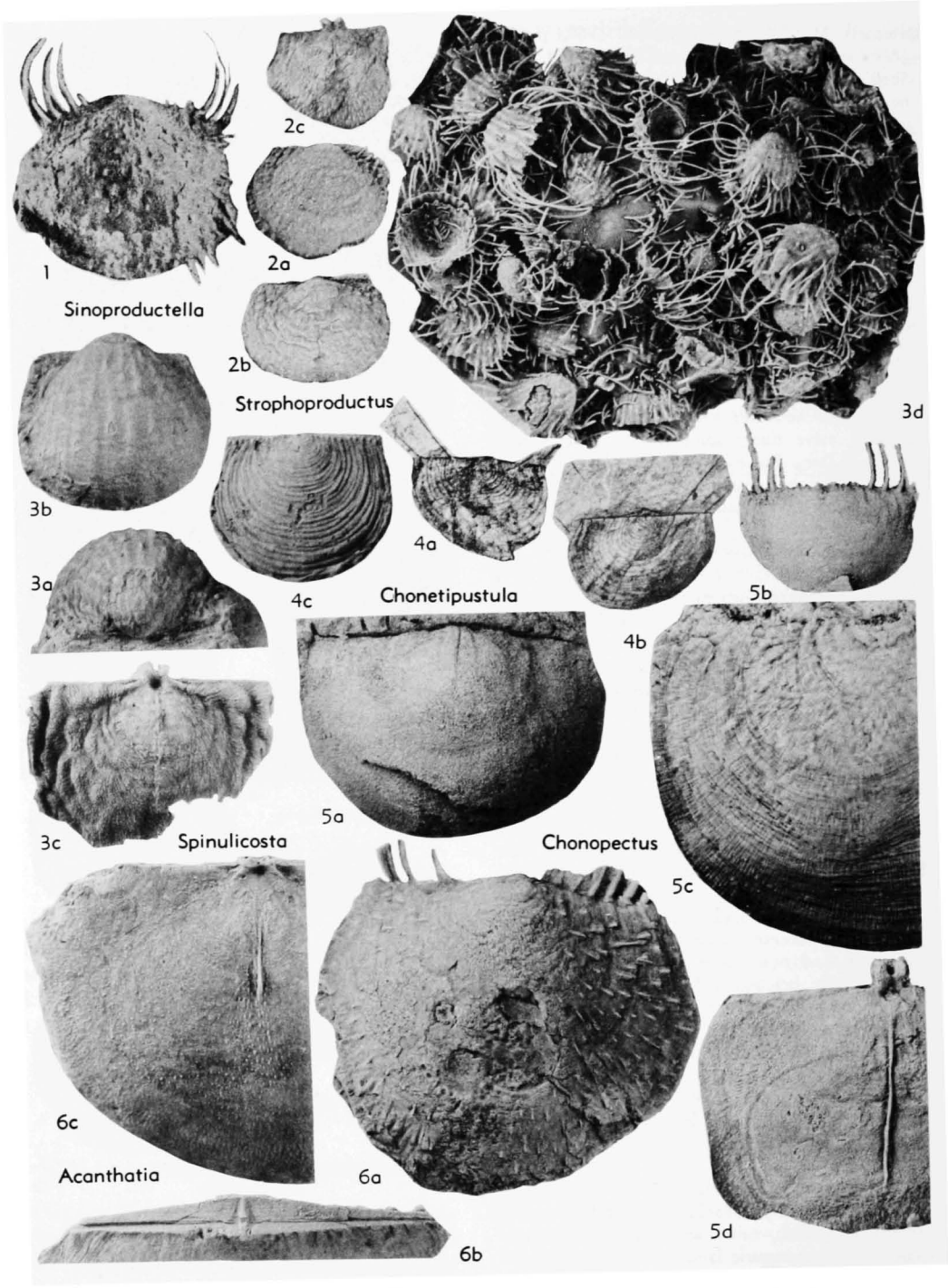

FIG. 332. Productellidae (Productellinae) *(1-3)*, (Chonopectinae) *(4-6)* *(p. H465, H467)*.

smooth or posterior scars dendritic; cardinal process bilobed, lobes separate, short septum rarely in pedicle valve. *U.Dev.-L.Carb. (L.Miss.-U.Miss.).*

Chonopectus HALL & CLARKE, 1893, p. 312 [**Chonetes fischeri* NORWOOD & PRATTEN, 1855, p. 25; OD]. Cicatrix of attachment present or absent; pedicle valve with radial capillae and oblique eccentric ornament when decorticated; erect spine row near hinge, spines rare elsewhere; brachial valve ornament similar, no spines; short septum in pedicle valve. *U.Dev.-L.Miss.*, N.Am. ——FIG. 332,*5a-c*. **C. fischeri* (NORWOOD & PRATTEN), L.Miss.(Kinderhook.), USA(Iowa); *5a,b*, ped.v. views; *5b*, with spines preserved, ×2, ×1; *5c*, ped.v. ext. showing ornament, ×3 (396).——FIG. 332,*5d*. *C.* sp., U.Dev., USA(N.Y.); brach.v. int. showing hollow card. process, ×2 (396).

Acanthatia MUIR-WOOD & COOPER, 1960, p. 158 [**Heteralosia nupera* STAINBROOK, 1947, p. 309; OD]. Medium-sized, subcircular, cicatrix of attachment present, interarea in each valve; pedicle valve with vertical attachment spines along hinge, fine prostrate spines elsewhere; brachial valve rugose posteriorly, with rare spines. *U.Dev.*, N. Am.——FIG. 332,*6*. **A. nupera* (STAINBROOK), USA(N.Mex.); *6a*, ped.v. ext.; *6b*, interareas of both valves; *6c*, brach.v. int.; all ×2 (769).

Chonetipustula PAECKELMANN, 1931, p. 31 [**Productus plicatus* SARRES, 1857, p. 20; OD]. Semicircular, with narrow interareas; cardinal process closing delthyrium; no chilidium; small septum in pedicle valve; ornament of both valves rugose; pedicle valve with fine, long straight spines in row along hinge margin, procumbent spines elsewhere; spines rare on brachial valve. *L.Carb. (Visean-Culm.)*, Eu.——FIG. 332,*4a,b*. **C. plicata* (SARRES), Culm., Ger.; *4a,b*, ped.v. ext. and int. molds, ×1 (633).——FIG. 332,*4c*. *C. carringtoniana* (DAVIDSON), Visean, Eng.; brach.v. ext. mold, ×1.5 (633).

Hamlingella REED, 1943, p. 78 [**Productella goergesi* PAECKELMANN, 1931, p. 56; OD]. Subelliptical, medium-sized; ventral interarea narrow, ornament on both valves of numerous fine, hairlike spines, brush of long curving spines from hinge margin, fine rugae posteriorly; cardinal process lobes medianly grooved; posterior adductors dendritic, with bounding ridge, anterior scars smooth. *U.Dev.-L.Carb.*, Eu.——FIG. 333, *1a,b*. **H. goergesi* (PAECKELMANN), L.Carb. (Etroeungt.), Ger.; *1a,b*, partly decort. ped.v., brach.v. int., ×1 (663).——FIG. 333,*1c*. *H. capillaris* REED, U.Dev., Eng.(Devon.); ped.v. ext. showing spines, ×1.5 (663).

Quadratia MUIR-WOOD & COOPER, 1960, p. 161 [**Productus hirsutiformis* WALCOTT, 1884, p. 133; OD]. Subrectangular, interareas present; cardinal process closing delthyrium; pedicle valve with rugae and small spines concentrically arranged,

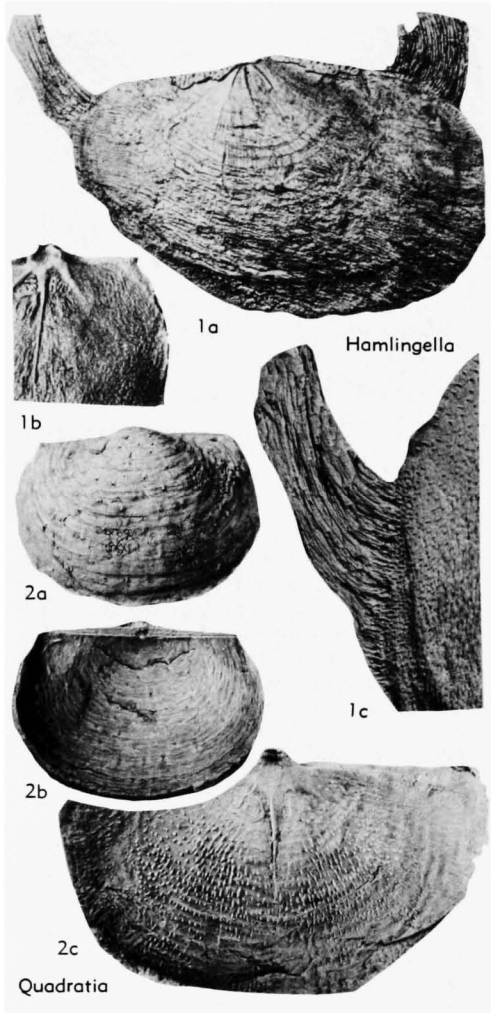

FIG. 333. Productellidae (Chonopectinae) (p. *H*467).

row of spines near hinge extending laterally; brachial valve with fine rugae and rare spines; adductors smooth. *U.Miss.*, USA(Ark.-Okla.-Tex.-Wyo.-Nev.).——FIG. 333,*2*. **Q. hirsutiformis* (WALCOTT), Okla.; *2a,b*, ped.v. and brach.v. views, ×1; *2c*, brach.v. int., ×2 (587).

Steinhagella GOLDRING, 1957, p. 223 [**Leptaena membranacea* PHILLIPS, 1841, p. 60; OD]. Like *Whidbornella* but rugae more numerous and undulating, recumbent spines in pedicle valve, more erect spines in brachial valve. *U.Dev.*, Eu.——FIG. 334,*2*. **S. membranacea* (PHILLIPS), Eng.; holotype, ped.v. ext., ×1 (354).

Whidbornella REED, 1943, p. 71 [**Leptaena caperata* J. DE C. SOWERBY, 1840, pl. 53, fig. 4; OD]. Medium-sized, semielliptical, no cicatrix or pseu-

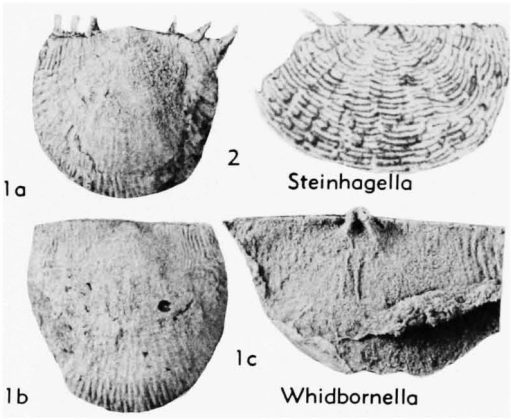

FIG. 334. Productellidae (Chonopectinae) (p. *H467-H468*).

dodeltidium; ornament on both valves of rugae and overlapping spine ridges with fine prostrate spines, which may be aligned, forming costellae; row of long straight spines in pedicle valve at high angle to hinge; pedicle valve with short septum; adductors dendritic. *U.Dev.*, Eu.——FIG. 334,*1*. **W. caperata* (J. DE C. SOWERBY), Eng. (Devon.); *1a,b*, ped.v. ext., brach.v. ext. mold, ×1; *1c*, brach.v. int., ×2 (663).

Family INSTITINIDAE Muir-Wood & Cooper, 1960

[Institinidae MUIR-WOOD & COOPER, 1960, p. 164]

Small, with or without interarea in pedicle valve, one or more cinctures developed; pseudodeltidium, teeth and sockets absent; cardinal process bilobate, with 2 separated lobes; adductors smooth; brachial ridges long, given off horizontally. *L.Carb.(Visean), ?U.Carb.*

Institina MUIR-WOOD & COOPER, 1960, p. 164 [**Productus marginalis* DE KONINCK, 1847, p. 238; OD]. Subquadrate, with ventral interarea; visceral disc separated from trail by deep cincture; pedicle valve rugose posteriorly, irregularly plicated on trail, spines scattered, also in row near cincture, row up flanks and near hinge; brachial valve rugose. *L.Carb.(Visean), ?U.Carb.*, Eu.——FIG. 335,*1*. **I. marginalis* (DE KONINCK), Belg.; *1a-c*, ped.v. vent., ant., and lat. views showing ant. plicated margin, ×2; *1d*, brach.v. int., ×3 (483).

Cinctifera MUIR-WOOD & COOPER, 1960, p. 165 [**Productus medusa* DE KONINCK, 1842, p. 166; OD]. Transversely oblong; valves geniculated, with short trail; 3 or 4 cinctures in each valve; small attachment cicatrix; interarea absent, both valves costate, pedicle valve with rugae and scattered spines, prostrate spine row from trail margin, row of spines near hinge; brachial valve trail smooth. *L.Carb.(Visean)*, Eu.——FIG. 335,*2*. **C. medusa* (DE KONINCK), Belg.; *2a,b*, ped.v. ant. and lat. views showing spines, ×3; *2c,d*, ped.v. vent. and post. views showing cinctures, ×2, ×3 (483).

Rugicostella MUIR-WOOD & COOPER, 1960, p. 166 [**Productus nystianus* DE KONINCK, 1842, p. 202; OD]. Subcircular, no interareas, both valves rugose and having cincture that separates visceral disc from trail; pedicle valve geniculated, with smooth or costate trail rarely produced into one or more tubes, spines on rugae and attachment spines along hinge, fringe of spines on flanks; brachial valve lacking spines. *L.Carb.(Visean)*, Eu.——FIG. 335,*3*. **R. nystiana* (DE KONINCK), Belg.; *3a-c*, ped.v. post. and lat. views showing spines, wrinkled visceral disc, and cincture, ×3; *3d*, brach.v. int. mold, ×4 (587).

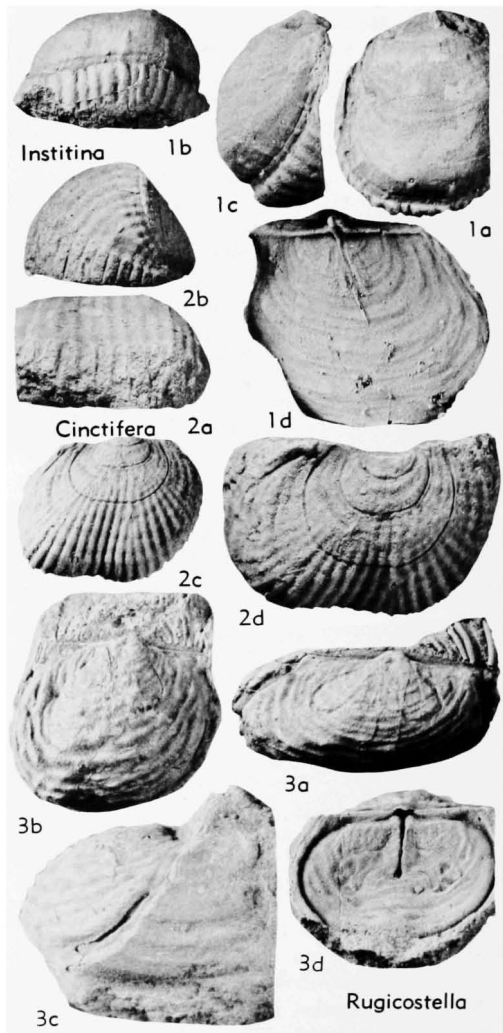

FIG. 335. Institinidae (p. *H468*).

Family LEIOPRODUCTIDAE Muir-Wood & Cooper, 1960

[Leioproductidae Muir-Wood & Cooper, 1960, p. 167]

Progressive Productacea with bilobed sessile cardinal process, but median halves of lobes tending to fuse to form trilobed process; alveolus developed; hinge teeth and sockets and interareas normally absent; adductors slightly dendritic. *M.Dev.-L.Perm.*

Subfamily LEIOPRODUCTINAE Muir-Wood & Cooper, 1960

[Leioproductinae Muir-Wood & Cooper, 1960, p. 168]

Cardinal process bilobed, or rarely trilobed; pedicle valve rugose and spinose; commonly with median longitudinal spine-bearing ridge, spines absent on brachial valve. *U.Dev.-L.Perm.*

Leioproductus Stainbrook, 1947, p. 307 [**Productella coloradoensis* var. *plicatus* Kindle, 1909, p. 18; OD] [=*Bispinoproductus* Stainbrook, 1947, p. 311 (type, *B. varispinosus*)]. Small to medium-sized, geniculated, with short trail on each valve; pedicle valve rugose or lamellose, with scattered spines or spine ridges and median longitudinal spine-row or spine-bearing ridge, spines in row up flanks and near hinge; brachial valve lamellose, dimpled, septum posteriorly bifid. *U.Dev.*, N.Am.-Asia.——Fig. 336,*1*. **L. plicatus* (Kindle), USA(N.Mex.); *1a,b*, ped.v. vent. and lat. views, ×2; *1c*, brach.v. view, ×1; *1d*, brach.v. int., post. part, ×3 (769).

Acanthoplecta Muir-Wood & Cooper, 1960, p. 170 [**Producta mesoloba* J. Phillips, 1836, p. 215; OD]. Medium-sized, both valves geniculated, with long trail, body cavity small, both valves rugose or smooth, valves costellate when decorticated; pedicle valve with longitudinal median spine-bearing ridge, spines scattered and in row near hinge and on flanks; cardinal process bilobed, alveolus developed, slender breviseptum. *L.Carb. (Visean)*, Eu.——Fig. 336,*2*. **A. mesoloba* (Phillips), Visean; *2a-c* (Eng.), ped.v. post. and lat., brach.v. views, ×1; *2d,e* (Belg.), ped.v. with median ridge bearing spines, brach.v. int., ×1, ×2 (587).

Ericiatia Muir-Wood & Cooper, 1960, p. 172 [**Productus newberryi* Hall, 1857, p. 180; OD]. Medium-sized, valves moderately concavo-convex, geniculated, both valves with fine overlapping spine-ridges bearing recumbent spines; spines in rows near hinge of pedicle valve and on ears; cardinal process bilobed, without alveolus; septum posteriorly notched; adductors dendritic. *L.Miss.*, N.Am.——Fig. 337,*1*. **E. newberryi* (Hall), USA(Ohio); *1a,b*, ped.v. and brach.v. views, ×1; *1c*, brach.v. int., ×2 (396).

Galeatella Muir-Wood & Cooper, 1960, p. 173 [**G. galeata*; OD]. Small, both valves geniculated,

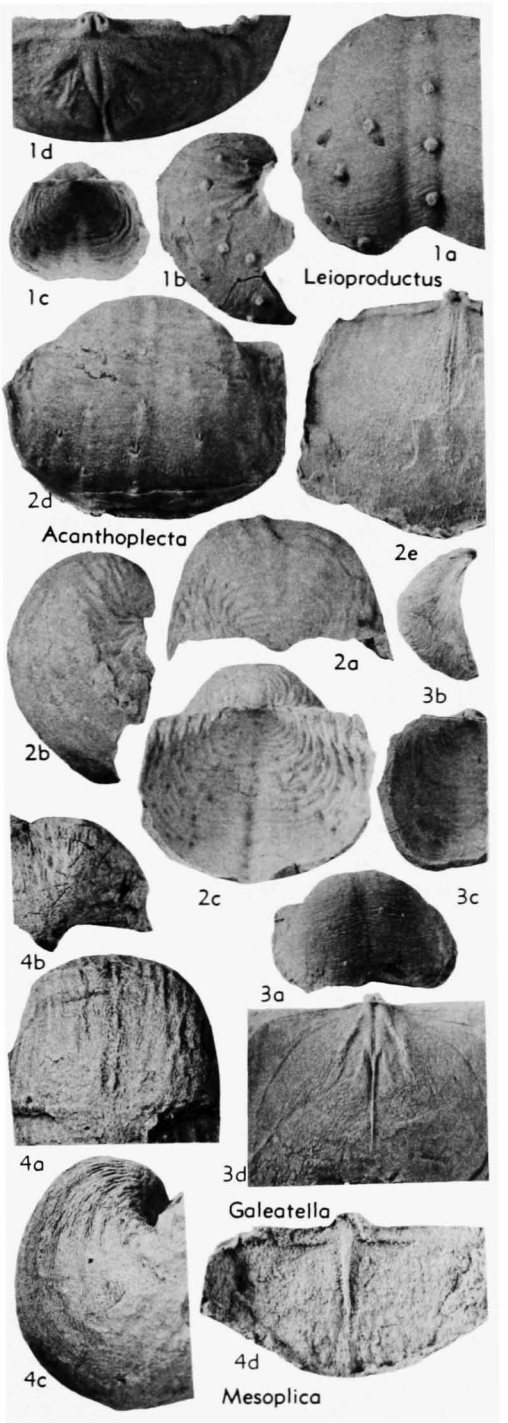

Fig. 336. Leioproductidae (Leioproductinae) (p. *H*469-*H*470).

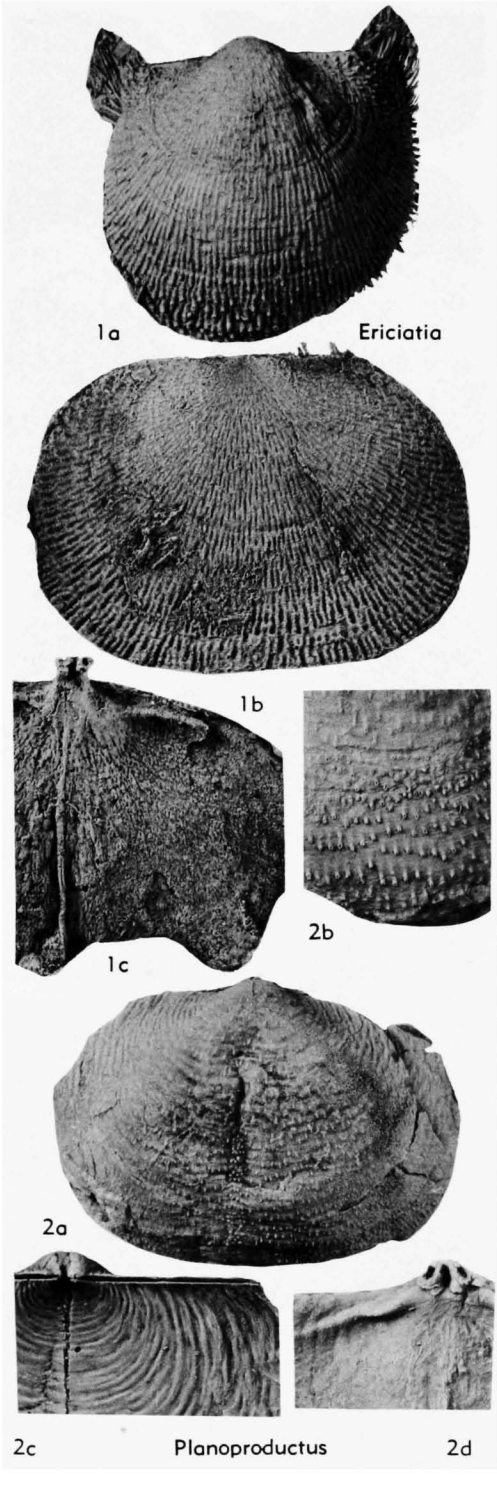

FIG. 337. Leioproductidae (Leioproductinae) (p. *H*469-*H*470).

trails short; linear interarea in pedicle valve, both valves smooth or with faint rugae; spines scattered, or in row near hinge of pedicle valve; cardinal process trilobed on internal face, quadrilobate externally, septum posteriorly bifid. *U.Dev.*, N.Am.——FIG. 336,*3*. **G. galeata*, USA(N.Mex.); *3a,b*, ped.v. vent., lat., ×1; *3c,d*, brach.v. ext. int., ×1, ×2 (587).

Jakutoproductus KASHIRTSEV, 1959, p. 70 [**Marginifera verchoyanica* FREDERIKS, 1931, p. 211; OD]. Medium-sized, laterally extended, concavo-convex, rarely geniculated; ornament of rugae over entire shell and quincuncially arranged spines, row along hinge; cardinal process bilobed, sessile; septum smooth, broad and medianly sulcate posteriorly becoming thin anteriorly, adductors smooth. *L.Perm.*, Asia(USSR-Siberia, Novaya Zemlya-China).

Mesoplica REED, 1943, p. 97 [**Leptaena praelonga* J. DE C. SOWERBY, 1840, pl. 53, fig. 29; OD]. Medium-sized, both valves geniculated, with short trail; median longitudinal spine-bearing ridge or median row of spines in pedicle valve; both valves rugose posteriorly, anteriorly costate; spines in group on ears, one spine on each flank of pedicle valve; row of spines in brachial valve near hinge. *U.Dev.*, Eu.-Asia.——FIG. 336,*4*. **M. praelonga* (J. DE C. SOWERBY), Famenn., Eng.; *4a-c*, ped.v. int. mold, ant., post., lat. views, ×1; *4d*, brach.v. int., ×2 (663).

Planoproductus STAINBROOK, 1947, p. 310 [**Productella hillsboroensis* KINDLE, 1909, p. 19; OD]. Medium-sized, nongeniculated; pedicle valve depressed, convex, ventral interarea developed; surface rugose and abundant spines and spine ridges, 2 rows of spines near hinge and on ears extending at high angle to hinge; brachial valve rugose, spines absent, cardinal process internally trilobate; adductors dendritic. *U.Dev.*, N.Am.——FIG. 337, *2*. **P. hillsboroensis* (KINDLE), USA(N.Mex.); *2a,b*, ped.v. ext., ×1, ×2; *2c,d*, brach.v. ext., int., ×2, ×4 (769).

Subfamily DEVONOPRODUCTINAE Muir-Wood & Cooper, 1960

[Devonoproductinae MUIR-WOOD & COOPER, 1960, p. 177]

Cardinal process interiorly bilobate and exteriorly quadrilobate; minute hinge teeth and sockets; linear interarea in pedicle valve; lateral ridges with posterior surface denticulate. *M.Dev.-U.Dev.*

Devonoproductus STAINBROOK, 1943, p. 55 [**Productella walcotti* FENTON & FENTON, 1924, p. 119 (=*Productus dissimilis* HALL, 1858, p. 497, *non* DEKONINCK, 1847, p. 255) (=*P. (Productella) hallana* WALCOTT, 1884, p. 130, *partim*); OD] [=*Striatoproductus* NALIVKIN, 1947, p. 75 (type, *Orthis sericea* VON BUCH, 1838, p. 68)]. Small, semicircular, nongeniculate, cicatrix of attachment present or absent; pedicle valve with obscure nodose costellae, rugose posteriorly, spines scat-

tered and row of erect spines near hinge; brachial valve lamellose and finely capillate. *M.Dev.-U. Dev.*, Eu.-Asia-N.Am.——FIG. 338,*3*. **D. walcotti* (FENTON & FENTON), U.Dev., USA(Iowa); *3a*, ped.v. ext., ×2; *3b,c*, brach.v. ext., int., ×3 (766).

Chonopectoides (*see* p. *H*904).

Productellina F. R. C. REED, 1943, p. 99 [**P. fremingtonensis*; OD]. Genus imperfectly known. *U.Dev.*, Eng.(Devon).

Subfamily PRODUCTININAE Muir-Wood & Cooper, 1960

[Productininae MUIR-WOOD & COOPER, 1960, p. 181]

Cardinal process small, bilobate or trilobate with two lobes well separated, and posteriorly incised, short breviseptum, adductors smooth or dendritic. *L.Miss.-L.Carb. (Visean)*.

Productina SUTTON, 1938, p. 551 [**Productus sampsoni* WELLER, 1909, p. 300; OD]. Small, subcircular to elongate-oval, not geniculated; pedicle valve costate and lamellose, spines rare, erect, row of spines from hinge down flanks; brachial valve lamellose; lateral ridges diverging from hinge, cardinal process bilobate, extending dorsally, adductors smooth. *L.Miss.-L.Carb.(Visean)*, N.Am.-Asia.——FIG. 338,*2*. **P. sampsoni* (WELLER), L.Miss.(Kinderhook.), USA(Tex.) *(2a-c)*, USA(N.Mex.) *(2d)*; *2a-c*, ped.v. vent., lat., ant., ×2; *2d*, brach.v. int., ×3 (795).

Argentiproductus COOPER & MUIR-WOOD, 1951, p. 195 [**Producta margaritacea* PHILLIPS, 1836, p. 215; OD] [=*Thomasia* FREDERIKS, 1929, p. 790 (*non* POCHE, 1908; *nec* RUEBSAAMEN, 1910; *nec* WILSON, 1910; *nec* LAMBERT, 1918); *Thomasina* PAECKELMANN, 1931, p. 181 (*non* NEWSTEAD & CARTER, 1911); *Thomasella* PAUL, 1942, p. 191 (*non* FREDERIKS, 1928)]. Hemispherical, geniculate, with small body cavity, both valves costate, lamellose, commonly lustrous; spines rare, prostrate, row of spines near hinge and on flanks of pedicle valve; cardinal process sessile, trilobate, lateral ridges not strongly divergent from hinge; adductors faintly dendritic. *L.Carb.(Visean)*, Eu. ——FIG. 338,*1*. **A. margaritaceus* (PHILLIPS), N.Wales *(1a,b)*, Belg. *(1c)*; *1a,b*, ped.v. and brach.v. views, ×1; *1c*, brach.v. int., ×2 (587).

Family OVERTONIIDAE Muir-Wood & Cooper, 1960

[Overtoniidae MUIR-WOOD & COOPER, 1960 (November), p. 183] [=Avoniidae SARYCHEVA, 1960 (December), p. 226 *(partim)*]

Cardinal process sessile, bilobed, with lobes posteriorly incised or separated by deep sulcus, rarely trilobed, with minute sulcate median lobe; alveolus usually absent; brachial ridges spoon-shaped, oblique; adductors smooth or partly dendritic; exterior spinose, rugose or lamellose, rarely anteriorly costate. *U.Dev.-L.Perm., ?U. Perm.*

Subfamily OVERTONIINAE Muir-Wood & Cooper, 1960

[Overtoniinae MUIR-WOOD & COOPER, 1960, p. 183]

Exterior spinose, rugose, or lamellose, rarely costate anteriorly. *U.Dev.-L.Perm., ?U.Perm.*

Overtonia I. THOMAS, 1914, p. 259 [**Productus fimbriata* J. DE C. SOWERBY, 1824, p. 85; OD]. Medium-sized, subcircular; umbo much incurved; trail rarely developed, both valves with rugae or broad bands bearing single row of elongated

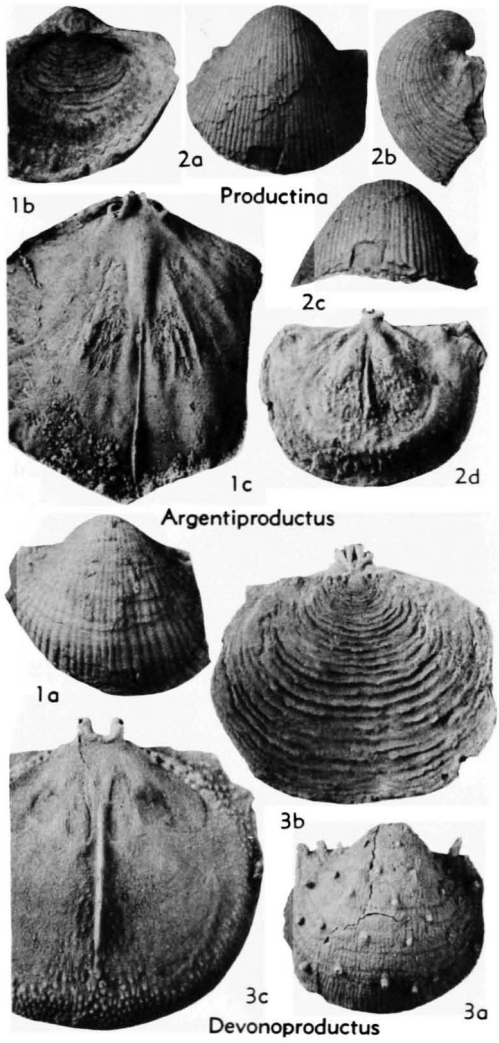

FIG. 338. Leioproductidae (Devonoproductinae) *(3)*, (Productininae) *(1-2)* (p. *H*470-*H*471).

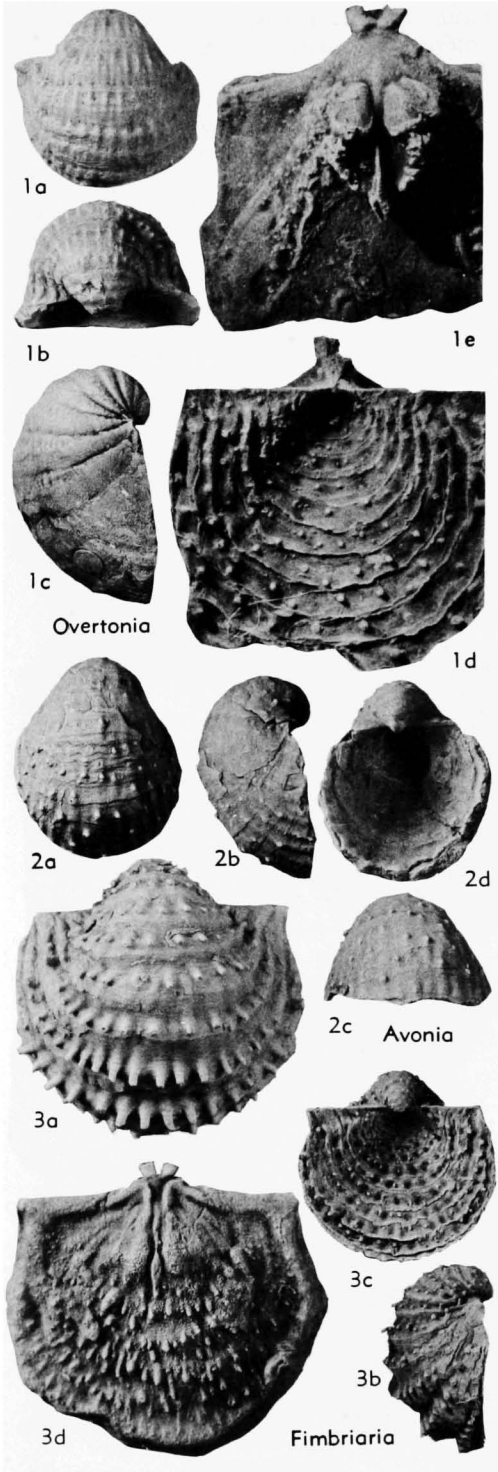

FIG. 339. Overtoniidae (Overtoniinae) (p. *H*471-*H*472).

spine-ridges, and rarely costate anteriorly; cardinal process bilobed or trilobed, no alveolus, lateral ridges marginal. *L.Carb.(Visean)*, Eu.-Asia-Arctic. ——FIG. 339,*1*. **O. fimbriata* (J. DE C. SOWERBY), Scot. *(1a,b)*, Eire *(1c)*, Eng. *(1d,e)*; *1a,b*, ped.v. vent., post., ×1; *1c*, ped.v. lat., ×1; *1d,e*, brach. v. ext., int., ×5 (805).

Avonia I. THOMAS, 1914, p. 259 [**Productus youngianus* DAVIDSON, 1860, p. 45; OD]. Small, orbicular, or elongate-oval, both valves with irregularly placed spines posteriorly, spine ridges radially arranged forming costae anteriorly, concentric lamellae numerous, interrupting costae, spines erect; brachial valve with lateral ridges curving away from margin, cardinal process bilobed. *L.Miss.-U.Miss.*, N.Am.; *L.Carb.(Tournais.-Visean)-U.Carb.(Namur.)*, Eu.-Asia.——FIG. 339, *2*. **A. youngiana* (DAVIDSON), Visean, Scot.; *2a-c*, ped.v. vent., lat., ant., ×2; *2d*, brach.v. view, ×2 (574).

Fimbriaria MUIR-WOOD & COOPER, 1960, p. 186 [**Overtonia plummeri* R. H. KING, 1938, p. 276; OD]. Small, strongly concavo-convex; ornament of broad, prominent, lamellose bands with single row of stout recumbent spines; dorsal interior with elevated rim around shell; lateral ridges medianly recurved anteriorly, forming 2 ridges that enclose end of breviseptum. *U.Penn.(U.Carb)-L.Perm.*, N.Am.-S.Am.——FIG. 339,*3*. **F. plummeri* (R. H. KING), U.Penn., USA(Tex.); *3a,b*, ped.v. vent., lat., ×3, ×2; *3c*, brach.v. view, ×2; *3d*, brach.v. int., ×4 (471).

Geniculifera MUIR-WOOD & COOPER, 1960, p. 187 [**Avonia boonensis* E. B. BRANSON, 1938, p. 40; OD]. Small, valves geniculated, with short trails and steep flanks, both valves rugose on visceral disc and costate anteriorly, spines scattered on rugae and costae, absent on brachial valve; cardinal process minute, bilobate, sloping dorsally. *L.Miss.*, N.Am.——FIG. 340,*1*. **G. boonensis* (BRANSON), USA(N.Mex.); *1a-c*, ped.v. vent., lat., post., ×2; *1d*, brach.v. int., ×3 (116).

Grandaurispina MUIR-WOOD & COOPER, 1960, p. 305 [**G. kingorum*; OD]. Medium-sized, nongeniculate; pedicle valve rugose near hinge, with small elongated spine ridges quincuncially arranged over whole valve, spines in 2 or more series, larger diameter spines in group on flanks extending laterally; brachial valve more rugose and commonly capillate, with numerous suberect or hooklike spines medianly or posteriorly directed, cardinal process trilobed, with sulcate dorsally recurved median lobe; adductors dendritic, lateral ridges short, divergent. *L.Perm.*, N.Am.——FIG. 341,*1*. **G. kingorum*, Word., USA(W.Tex.); *1a*, ped.v. vent., spines attached, ×0.8; *1b* (holotype), brach. v. view, ×1.6; *1c,d*, brach.v. ext. showing capillae, int., ×1.6 (587).

Krotovia FREDERIKS, 1928, p. 779 [**Productus spinulosus* J. SOWERBY, 1814, p. 155; OD]. Small, thin-shelled, highly concavo-convex valves; umbo

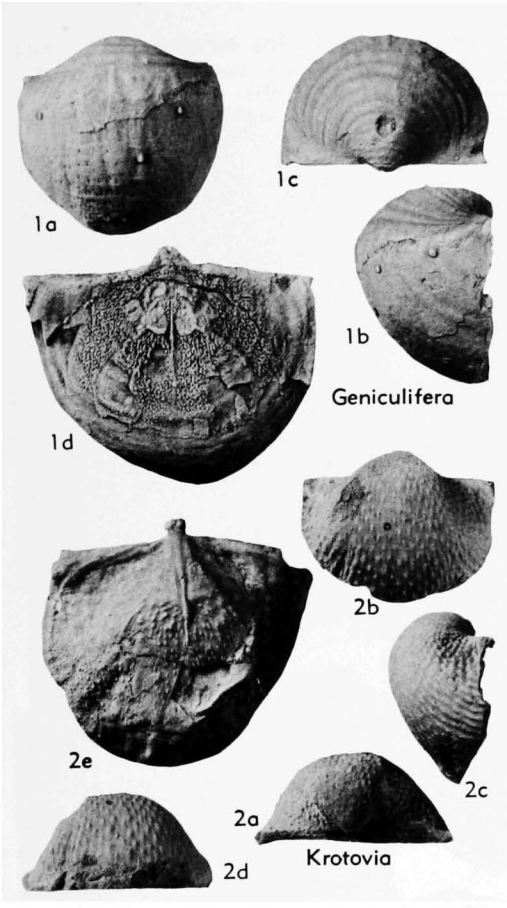

FIG. 340. Overtoniidae (Overtoniinae) (p. *H*472-*H*473).

much incurved, ears large; pedicle valve with quincuncially arranged spine tubercles bearing small suberect spines, rugae near hinge; brachial valve more rugose, numerous spines; lateral ridges along hinge and extending as vertical ridges parallel to septum. *L.Carb.-L.Perm., ?U.Perm.*, cosmop.——FIG. 340,*2*. **K. spinulosa* (J. SOWERBY), L.Carb.(Visean), Eng.; *2a-d*, ped.v. post., vent., lat., ant., ×1; *2e*, brach.v. int., ×2 (587).

Laminatia MUIR-WOOD & COOPER, 1960, p. 189 [**Productella laminata* KINDLE, 1909, p. 18; OD]. Small, subquadrate, valves slightly concavo-convex, cicatrix of attachment present; ornament in both valves of lamellose, commonly stepped bands with 2 series of fine spine ridges, which may alternate, larger extending across band, smaller more anteriorly developed; spines prostrate, tapering; cardinal process erect, bilobate. *U.Dev.*, N. Am.——FIG. 342,*1*. **L. laminata* (KINDLE), USA(N.Mex.); *1a*, ped.v. vent., ×2; *1b,c*, brach. v. ext., ×2, ×3; *1d*, brach.v. int., ×3 (587).

Levipustula MAXWELL, 1951, p. 10 [**L. levis*; OD]. Medium-sized, subcircular, moderately concavo-convex valves; ornament of quincuncially arranged, elongate spine ridges bearing prostrate spines, row of erect spines along hinge and on ears; brachial valve with dimples, prominent growth lines and no spines; cardinal process bilobate internally; 2 ridges enclosing alveolus, breviseptum developed. *U.Carb.(Moscov.)*, Australia.——FIG. 342,*5*. **L. levis*, New S.Wales; *5a,b*, ped.v. ext., brach.v. int., ×2 (538).

Rhytiophora MUIR-WOOD & COOPER, 1960, p. 192 [**Productus blairi* MILLER, 1891, p. 689; OD] [=?*Semiproductus* BUBLITSCHENKO, 1956, p. 99 (type, *S. minax*)]. Medium-sized, subquadrate, both valves with short trails and anterior rim; ornament of irregular rugae posteriorly, spine ridges commonly aligned radially; spines numerous, prostrate or erect, in rows near hinge, and on ears and flanks; brachial valve rugose, spines rare, cardinal process bilobate internally; adductors slightly dendritic or smooth. *L.Miss.*, N.Am.——FIG. 342,*3*. **R. blairi* (MILLER), Kinderhook., USA(Mo.); *3a,b*, ped.v. vent., lat., ×1; *3c,d*, brach.v. ext., int., ×2 (587).

Rugauris MUIR-WOOD & COOPER, 1960, p. 193 [**R. paucispina*; OD]. Medium-sized, subquadrate, valves slightly concavo-convex; ornament of numerous rugae with small spine ridges bearing fine prostrate or recumbent spines; pedicle valve with row of spines along hinge margin; cardinal process trilobate, brachial ridges given off at angle

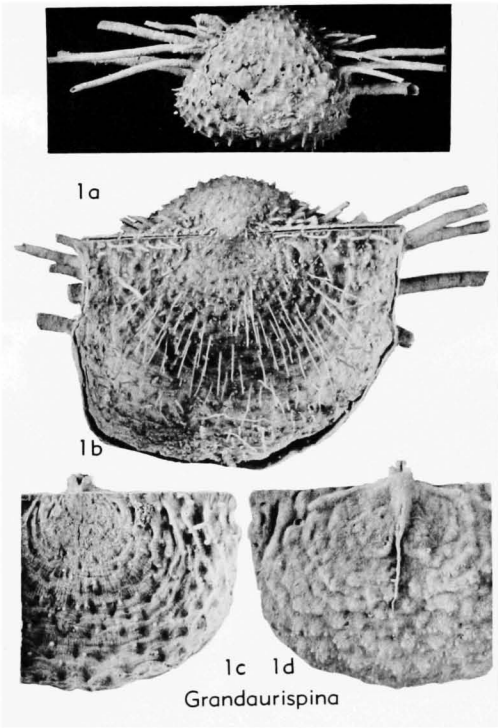

FIG. 341. Overtoniidae (Overtoniinae) (p. *H*472).

of 25 degrees to horizontal; adductors dendritic or smooth. *L.Miss.*, N.Am.——Fig. 342,*2*. **R. paucispina*, Kinderhook., USA(Iowa); *2a,b* (holotype), ped.v. vent., lat., ×1; *2c,d*, brach.v. ext., int., ×1 (587).

Scutepustula (*see* p. *H*904).

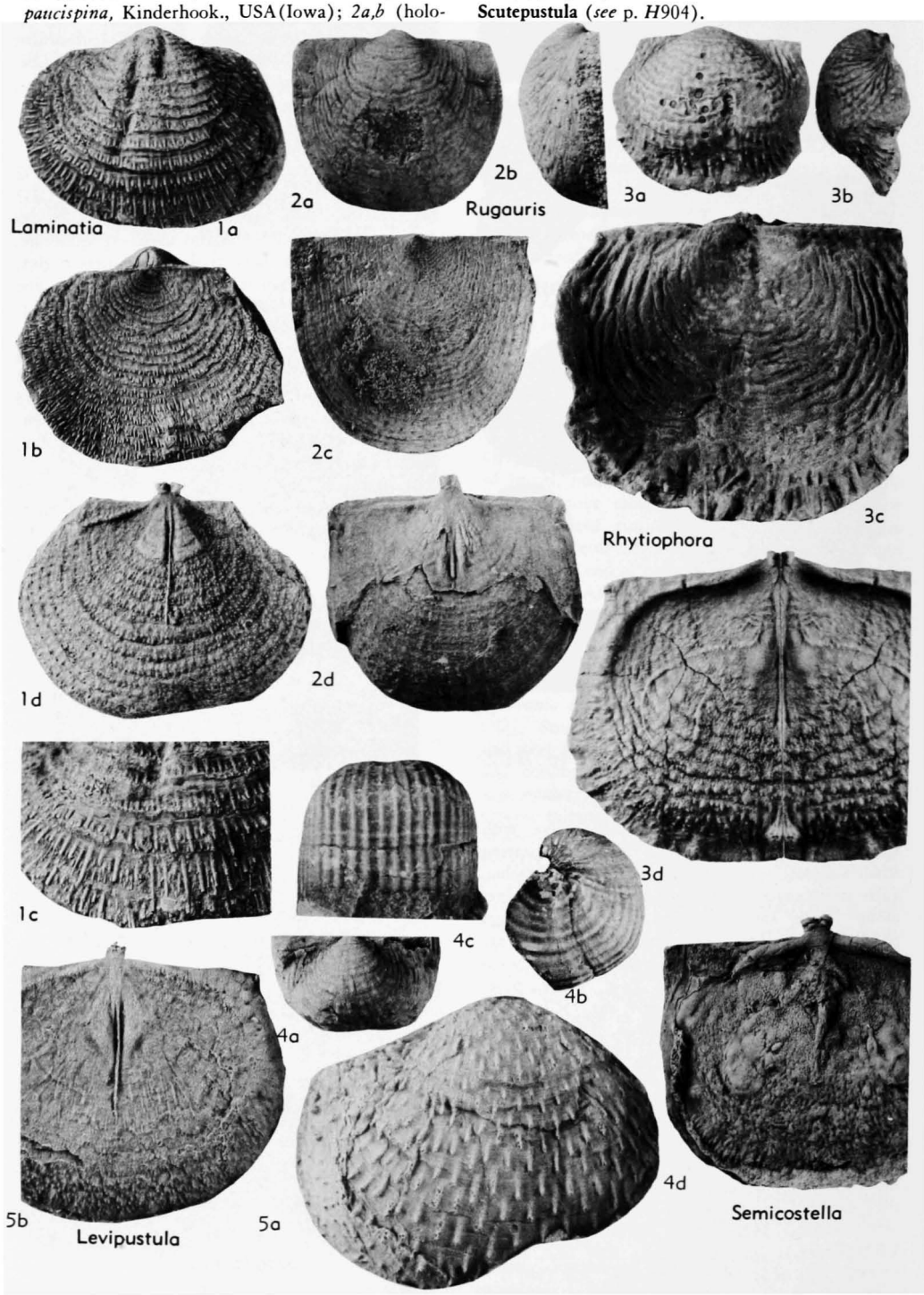

Fig. 342. Overtoniidae (Overtoniinae) (p. *H*473-*H*475).

Semicostella MUIR-WOOD & COOPER, 1960, p. 195 [**Avonia oklahomensis* SNIDER, 1915, p. 83; OD]. Medium-sized, subquadrate, valves concavo- or plano-convex with short trails; cincture in pedicle valve; pedicle valve ornament posteriorly of rugae and spine ridges, trail with broad costae bearing few spines; spines in row up flanks and near hinge; brachial valve rugose and spinose, costae absent or obscure, cardinal process bilobate. *U.Miss.*, N.Am.——FIG. 342,*4*. **S. oklahomensis* (SNIDER), USA(Okla.); *4a-c*, ped.v. post., lat., ant., ×1; *4d*, brach.v. int., ×2 (587).

Semiproductus BUBLITSCHENKO, 1956, p. 9 [**S. minax*; OD]. Both valves geniculated, ornamented

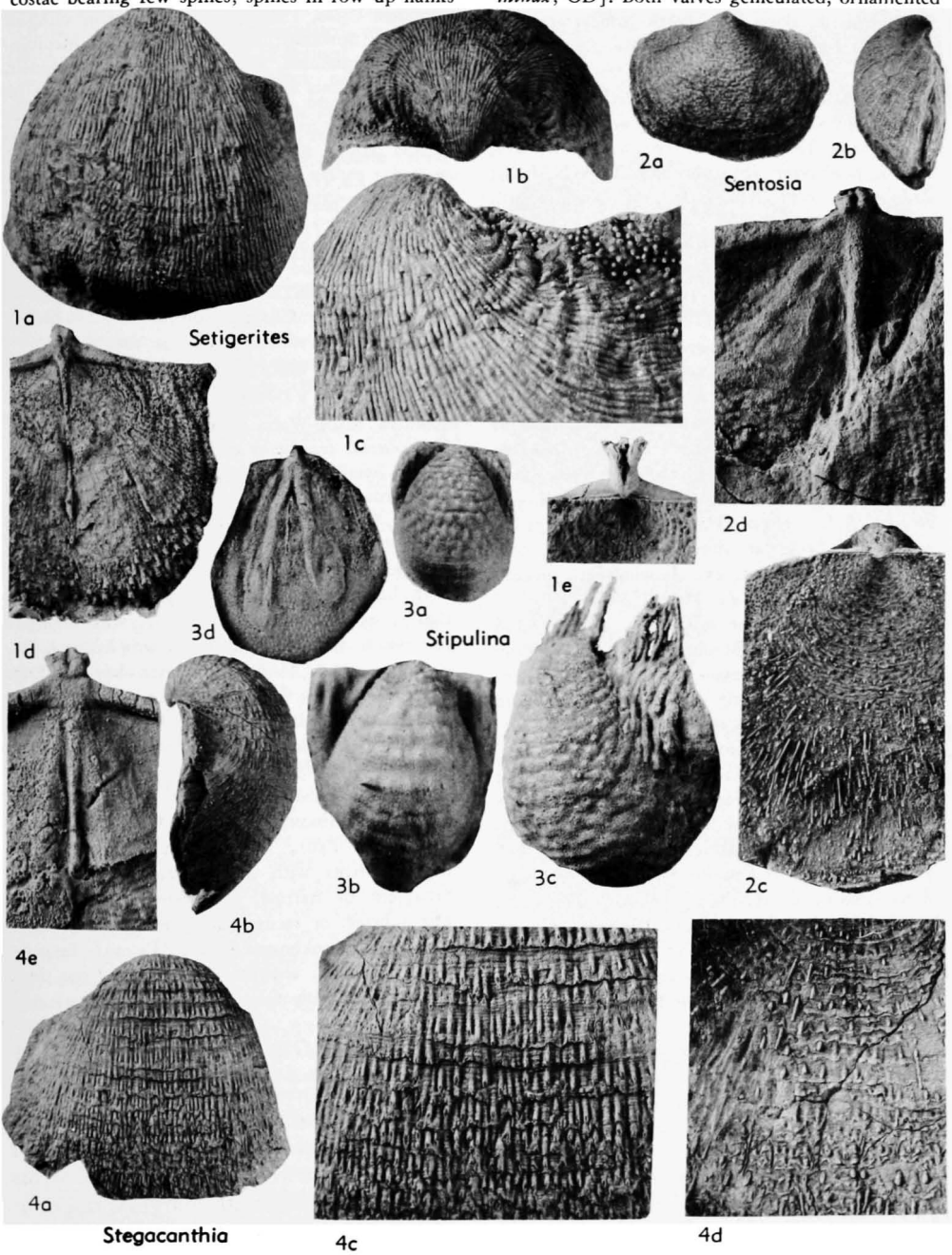

FIG. 343. Overtoniidae (Overtoniinae) (p. *H*476).

on visceral disc by concentric rugae and elongated spine ridges, and anteriorly by costae and rare spines. Interior as in *Pustula*. [Possibly a senior synonym of *Rhytiophora*.] *U.Dev.-L.Carb.*, Eu.-Asia.

Sentosia MUIR-WOOD & COOPER, 1960, p. 196 [**Krotovia praecursor* STAINBROOK, 1947, p. 313; OD]. Small, plano- to slightly concavo-convex; ornament finely rugose and spinose; spines long, prostrate, roughly arranged in rows; cardinal process bilobate, with lobes fused posteriorly, process not supported by narrow septum; adductors obscure, lobate. *U.Dev.*, N.Am.——FIG. 343, *2*. **S. praecursor* (STAINBROOK), USA(N.Mex.); *2a,b*, ped.v. vent., lat., ×1; *2c,d*, brach.v. ext., int., ×2 (769).

Setigerites GIRTY, 1939, p. 141 [*pro Setigerella* GIRTY, 1938, p. 434 (*non* EHRENBERG, 1872)] [**Productus setigerus* HALL, 1858, p. 638 (=*P. setiger, nom. correct.* MUIR-WOOD & COOPER, 1960, p. 197; OD]. Medium-sized, subquadrate; ornament of fine costae with spines, both valves with gutter-like extension of trail, rugae posteriorly; pedicle valve with spine rows near hinge and in group on ears and flanks; cardinal process bilobate or trilobate projecting dorsally; adductors dendritic. *L. Miss.(Osag.) - U .Miss.(Meramec.)*, N.Am.——FIG. 343,*1*. **S. setiger* (HALL), USA; *1a-c*, ped.v. vent., post., post. lat. showing spines, ×1, ×1, ×2; *1d,e*, brach.v. int., ext. showing card process, ×1, ×2 (*1a-c*, Ind; *1d,e*, Mo.) (587).

Stegacanthia MUIR-WOOD & COOPER, 1960, p. 198 [**S. bowsheri*; OD]. Medium-sized, subquadrate; valves moderately concavo-convex; nongeniculated; pedicle valve posteriorly rugose, medianly with elongate spine ridges on lamellose bands, anteriorly bands narrow and squamose; spines fine, prostrate, in rows near hinge and on spine ridges; brachial valve more lamellose with numerous spines, cardinal process bilobed or trilobed; adductors obscurely dendritic. *L.Miss.(Osag.), ?U. Miss.(Meramec.)*, N.Am.——FIG. 343,*4*. **S. bowsheri*, L.Miss., USA(N.Mex.); *4a,b*, ped.v. vent., lat., ×1; *4c,d*, ped.v. ext., brach.v. ext., ×2; *4e*, brach.v. int., ×3 (*4a-d*, holotype) (587).

Stipulina MUIR-WOOD & COOPER, 1960, p. 200 [**Productus deshayesianus* DE KONINCK, 1842, p. 193; OD]. Small, elongate-oval, valves slightly concavo-convex, cicatrix of attachment rare; ornament of concentric convex bands bearing single row of spine tubercles, spines crowded anteriorly, and arranged in row along hinge extending vertically, elsewhere prostrate; brachial valve with concentric bands and dimples, no spines, cardinal process bilobate. *L.Carb.(Visean)*, Eu.(Eng.-Belg.). —— FIG. 343,*3*. **S. deshayesiana* (DE KONINCK), Belg.; *3a-c*, ped.v. vent., post., lat., ×4, ×5, ×5; *3d*, brach.v. int.,×4 (483).

Subfamily PLICATIFERINAE Muir-Wood & Cooper, 1960

[Plicatiferinae MUIR-WOOD & COOPER, 1960, p. 201]

Geniculated, with large body cavity; posteriorly rugose and trail smooth, adductor scars dendritic. *L.Carb.(Visean)*.

Plicatifera CHAO, 1927, p. 25 [**Productus plicatilis* J. DE C. SOWERBY, 1824, p. 85; OD]. Medium-sized, subquadrate; rugae prominent, subangular, more numerous on brachial valve; spines rare on brachial valve, scattered on pedicle valve and in erect row near hinge; cardinal process trilobate with minute median lobe. *L.Carb.(Visean-U. Miss.)*, Eu. (Eng.-Belg.)-N. Am.(Calif.).——FIG. 344,*1*. **P. plicatilis* (J. DE C. SOWERBY), Eng. (*1a-c*), Belg. (*1d*); *1a,b*, ped.v. ant., post., ×1; *1c,d*, brach.v. ext., int., ×2 (153).

Subfamily INSTITIFERINAE Muir-Wood & Cooper, 1960

[Institiferinae MUIR-WOOD & COOPER, 1960, p. 203]

Small, with elaborate marginal flanges or frills. *L.Carb.(Visean)*.

Institifera MUIR-WOOD & COOPER, 1960, p. 203 [**Productus tessellatus* DEKONINCK, 1847, p. 110; OD]. Small, valves nongeniculate, cicatrix present; pedicle valve with anterior flattened, finely costate flange, with rugae posteriorly, and costae anteriorly, lamellae intersecting costae causing enlarged tubercles bearing spines; brachial valve with lateral and anterior margins recurved medianly, exterior costate, lamellose, with capillate or smooth marginal flanges. *L.Carb.(Visean)*, Eu. ——FIG. 344,*2*. **I. tessellata* (DEKONINCK), Eng. (Yorks.) (*2a,b*), Eire (*2c-e*); *2a,b*, ped.v. vent., lat., ×2; *2c-e*, brach.v. views showing recurved ped.v. and brach.v. margins, developed as flanges, ×2, ×3, ×3 (483).

Thomasella FREDERIKS, 1928, p. 778 [**Productus wrighti* DAVIDSON, 1861, p. 162; OD] [*non Thomasella* PAUL, 1942]. Minute; pedicle valve highly convex with anterior flat costellate rim; ornament of narrow, prominent rugae bearing fine suberect or recumbent spines; brachial valve and interior unknown. *L.Carb.(Visean)*, Eu.—— FIG. 344,*3*. **T. wrighti* (DAVIDSON), Eire; *3a,b*, ped.v. vent. with frill, ×3, ×4 (229).

Family MARGINIFERIDAE Stehli, 1954

[*nom. transl.* MUIR-WOOD & COOPER, 1960, p. 205 (*ex* Marginiferinae STEHLI, 1954, p. 321)]

Small or medium-sized, commonly with symmetrically arranged spines; interior of pedicle valve with marginal ridges across ears, brachial valve with marginal ridges or anterior rows of endospines, cardinal process trilobed with median lobe bent dorsally (toward exterior). *L.Carb.-U.Perm.*

Subfamily MARGINIFERINAE Stehli, 1954

[Marginiferinae Stehli, 1954, p. 321]

With externally crenulated marginal ridges around visceral disc of brachial valve; adductor scars smooth, lobate, or dendritic. *L.Carb.-U.Perm.*

Marginifera Waagen, 1884, p. 713 [**M. typica*; OD]. Small, both valves geniculated, trails short, flanks steep, ornament of ill-defined costae with rugae posteriorly; spines erect, scattered over pedicle valve, in 1 or 2 rows on flanks, absent from brachial valve; pedicle valve with crenulated ridges across ears, articulating with brachial valve; no anterior thickening in either valve; adductors smooth. [Although Waagen did not explicitly designate a type-species by formal statement, in adopting the name *typica* for one of the forms described by him he automatically fixed the type-species (Zool. Code, 1961, Art. 68,b); Oehlert's (1887, p. 1277) action in stating that the type-species is *M. typica* is superfluous and does not constitute a subsequent designation, as construed by some.] *?L.Perm., U.Perm.*, Eu.-Asia. ——Fig. 345,*2*. **M. typica*, Pak.; *2a-c*, ped.v. vent., lat., ant., ×1; *2d-f*, brach.v. views, ×1 (845).

Alifera Muir-Wood & Cooper, 1960, p. 207 [**Productus expansus* deKoninck, 1842, p. 159 (*non* Pander, 1830) (=**A. koninckí* Muir-Wood & Cooper, 1960, p. 208; OD]. Small or medium-sized, externally like small dictyoclostid but with cincture in pedicle valve corresponding to internal diaphragm; spines rare, erect, 1 from cardinal extremities and 1 or 2 on flanks; absent from brachial valve; adductors nondendritic. *L.Carb. (Visean)*, Eu.——Fig. 345,*3*. **A. koninckí* Muir-Wood & Cooper, Belg.; *3a-c*, ped.v. post., ant., lat., ×2; *3d*, brach.v. int., ×2 (483).

Duartea Mendes, 1959, p. 58 [**Productus batesianus* Derby, 1874, p. 54; OD]. Resembling *Eomarginifera* in outline and small ears, fine costellae and faintly reticulate ornament, and 6 major spines and no row along hinge, but has narrow interarea (ginglymus), large cardinal process, and ventral adductors set on ridge. *M.Penn.*, S.Am.——Fig. 346,*1*. **D. batesiana* (Derby), Itaituba Ser., Brazil; *1a,b*, ped.v. vent., post., ×1; *1c*, brach.v. ext., ×1.35 (555).

Eomarginifera Muir-Wood, 1930, p. 103 [**Productus longispinus* J. Sowerby, 1814, p. 154; OD]. Small or medium-sized, both valves geniculated, costellate and rugose, with slight reticulation posteriorly, costellate on trail; spines on pedicle valve only and rare except for 6 symmetrical spines; brachial valve commonly thickened or with overlapping laminae representing successive trails; adductors dendritic and lobate; pedicle valve without marginal ridge. *L.Carb.(Visean)*, Asia-Afr.; *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.——Fig. 345,*1*. *E. setosa* (Phillips), L.Carb.(Visean), Eng. *(1a-d)*, Scot. *(1e-g)*; *1a-c*, ped.v. vent., post., lat., ×2; *1d*, brach.v. view, ×2; *1e,f*, brach. v. int., ×3, ×4; *1g*, card. process, ×4 (574). [*See* p. *H*904.]

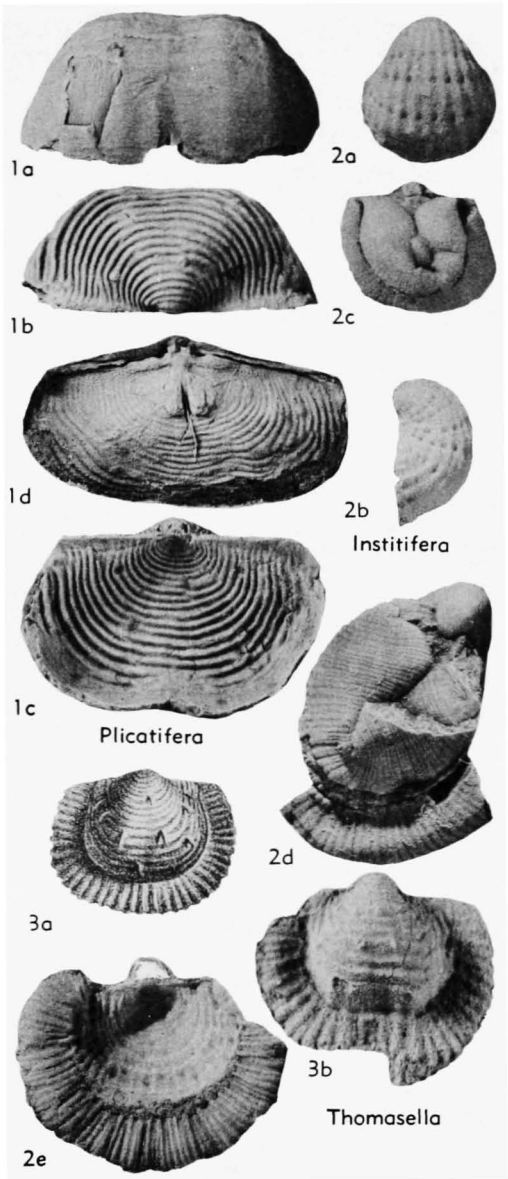

Fig. 344. Overtoniidae (Plicatiferinae) *(1)*, (Institiferinae) *(2-3)* (p. *H*476).

Hystriculina Muir-Wood & Cooper, 1960, p. 210 [**H. texana*; OD]. Like *Eomarginifera* externally but with no anterior thickening in brachial valve, lamellose ornament anteriorly, and scattered spines on pedicle valve with row up flanks; pedicle valve with crenulated ridge across ears; adductors smooth; brachial ridges obscure; endospines large and numerous in rows. *Penn.-L.Perm.*, N.Am.-S.

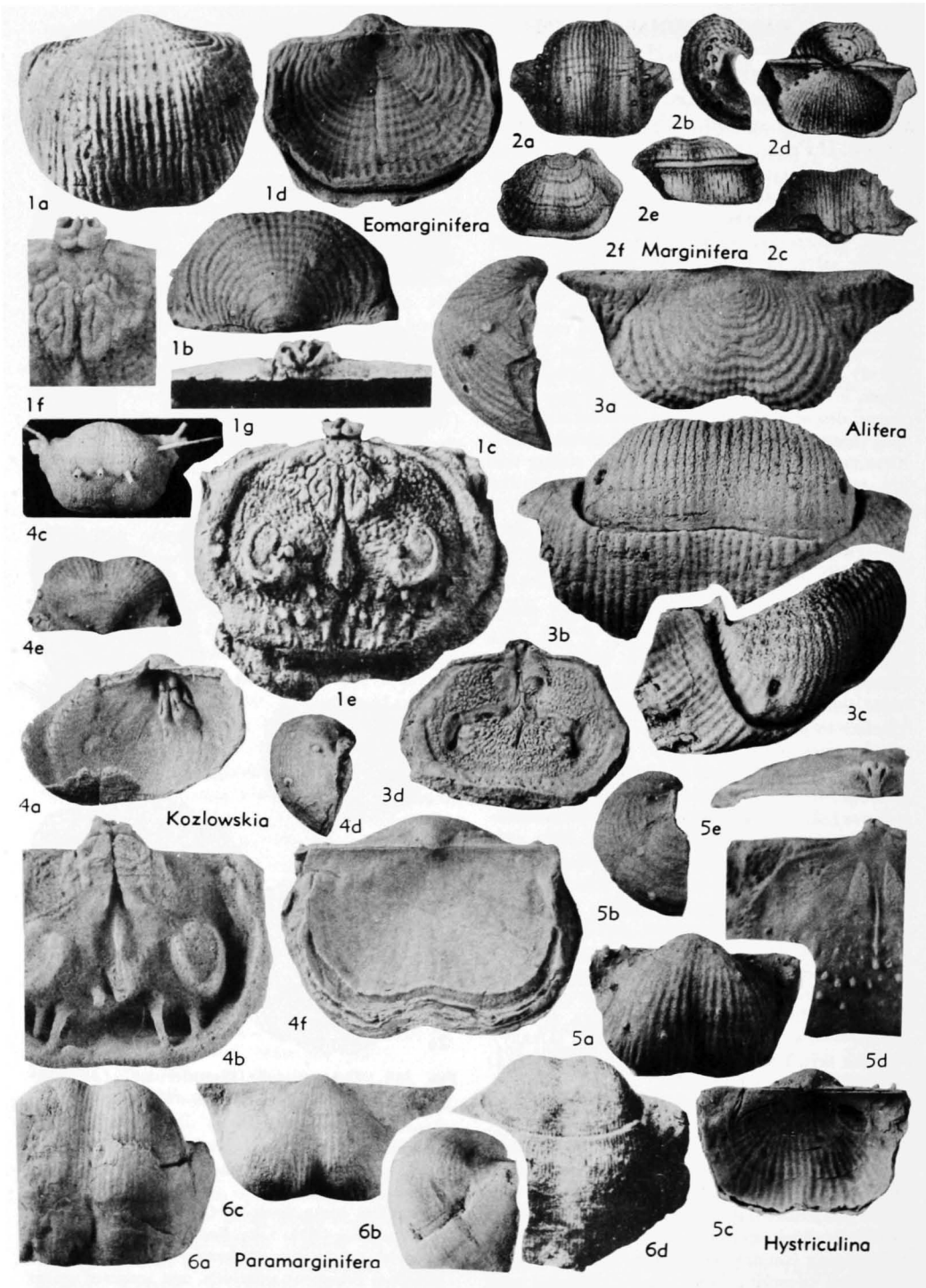

FIG. 345. Margniferidae (Marginiferinae) (p. *H*477, *H*479).

Am.——Fig. 345,5. **H. texana,* Penn., USA (Tex.); *5a,b,* ped.v. vent., lat., ×2; *5c,* brach.v. view, ×2; *5d,e,* brach.v. int., card. process in post. view, ×3 (587).

Kozlowskia Frederiks, 1933, p. 29 [**Productus capaci* d'Orbigny, 1842, p. 50; OD]. Like *Eomarginifera* externally and having broken off trails as overlapping lamellae in brachial valve but spine row near hinge, as well as 6 symmetrical spines; crenulated marginal ridges in both valves; smooth anterior rim in brachial valve interior; adductors in part dendritic. *M.Penn.-L.Perm.,* N.Am.-S.Am.; *U.Carb.,* Eu.-Asia.——Fig. 345,*4a.* **K. capaci* (d'Orbigny), L.Perm., Bolivia; ped.v. int. showing marginal ridge, ×2 (485).——Fig. 345,*4b.* *K. haydenensis* (Girty), M.Penn., USA(Okla.); brach.v. int. with endospines, ×3 (485).——Fig. 345,*4c-f.* *K. splendens* (Norwood & Pratten), U.Penn., USA(N.Mex.-Tex.); *4c-e,* ped.v. vent., lat., post., ×1; *4f,* brach.v. view showing thickened margins, ×2 (485).

Paramarginifera Frederiks, 1916, p. 61 [**Marginifera clarkei* Chernyshev, 1902, p. 328; OD]. Medium-sized, subpentagonal; pedicle valve with cincture demarcating ears, probably corresponding to internal ridge or diaphragm, trail tending to form tube; ornament costate and rugose, spine row along hinge and 6 symmetrical spines; brachial valve unknown. *U.Carb.* or *L.Perm.,* Eu.——Fig. 345,*6.* **P. clarkei* (Chernyshev), Perm., USSR; *6a-c,* ped.v. vent., lat., post.; *6d,* ped.v. (syntype) vent. with cincture; all ×1 (158).

Spinomarginifera Huang, 1932, p. 16 [**S. kueichowensis*; OD]. Small or medium-sized, valves geniculated, rugose, long spines on spine ridges, or tubercles quincuncially or radially arranged in pedicle valve, also spine row near hinge and on ears; brachial valve without spines, adductors dendritic. *?U.Carb., L.Perm.-U.Perm.,* Asia.——Fig. 346,*2.* **S. kueichowensis,* Perm., China; *2a-c,* ped.v. vent., post., lat.; *2d,f,* ped.v. ext., with spines, int.; *2e,* brach.v. int.; all ×0.9 (435).

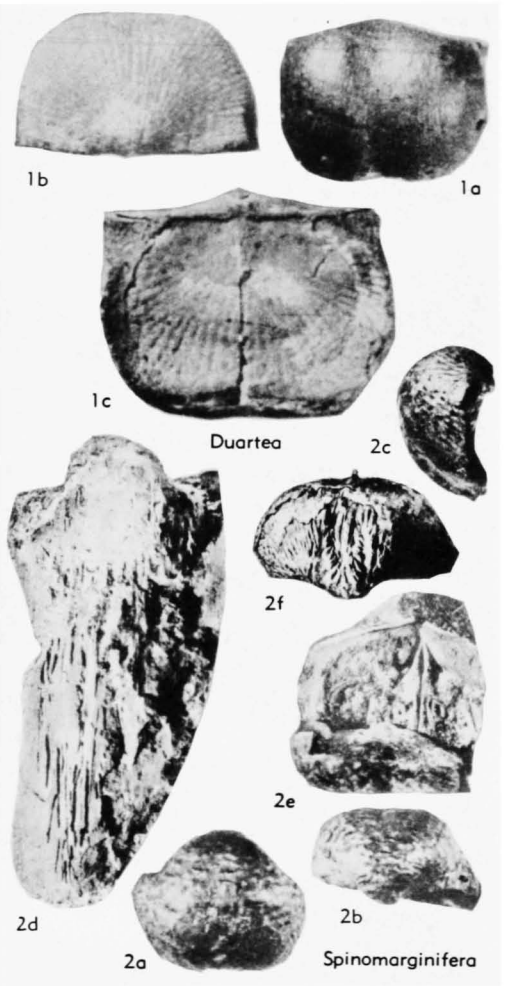

Fig. 346. Marginiferidae (Marginiferinae) (p. *H*477, *H*479).

Subfamily COSTISPINIFERINAE Muir-Wood & Cooper, 1960

[Costispiniferinae Muir-Wood & Cooper, 1960, p. 217]

Ridges extending across ears of both valves internally, prominent endospines in row anterior to septum, and set on outer margin of brachial ridges. *U.Miss.-U.Perm.*

Costispinifera Muir-Wood & Cooper, 1960, p. 217 [**C. texana*; OD]. Like *Avonia* superficially; pedicle valve irregularly rugose and spinose posteriorly, becoming costate and lamellose anteriorly; spines erect on trail, in row near hinge and on flanks; brachial valve similar, with numerous erect or suberect spines and in row, commonly centripetal, near hinge; adductors smooth. *L. Perm.,* N.Am.(USA-Mex.).——Fig. 347,*1.* **C. texana,* Perm., USA(Tex.); *1a-c,* ped.v. vent., lat., post., ×1; *1d,e,* brach.v. views, ×1, ×2; *1f,* brach.v. int., ×2; *1g,* card. process, ext., ×4 (*1a-e,* holotype) (587).

Desmoinesia Hoare, 1960, p. 226 [**Productus muricatus* Norwood & Pratten, 1855, p. 14 (*non* Phillips, 1838), =**Marginifera muricatina* Dunbar & Condra, 1932, p. 222; OD] [=*Rudinia* Muir-Wood & Cooper, 1960, p. 229 (obj.)]. Small, moderately concavo-convex, body cavity narrow; pedicle valve posteriorly rugose and spinose, becoming costate, thickened with lamellae, bearing spines anteriorly, spine row near hinge and up flanks; brachial valve more rugose, obscurely costate, fewer spines, adductors faintly dendritic. *M.Penn.,* N.Am.(Okla.-Mo.-Ill.-Tex.).——Fig. 347,*2.* **D. muricata* (Norwood & Pratten), USA(Okla.); *2a-c,* ped.v. vent., post., int., ×2; *2d,* brach.v. view, ×2; *2e,f,* brach.v. int., post., ×3 (429).

Echinauris Muir-Wood & Cooper, 1960, p. 221 [**E. lateralis*; OD]. Small to medium-sized, both valves with short trails; pedicle valve with irregularly distributed curving recumbent spines, group of straight spines on flanks and 2 rows at angle to hinge; brachial valve posteriorly rugose, and with scattered spines, commonly centripetal; adductors smooth, *L.Perm.(Word.)*, N.Am.—— Fig. 347,*3*. **E. lateralis*, USA(W.Tex.); *3a*, ped.v. (holotype) vent., with spines attached, ×1; *3b*, juv. ped.v. vent., with converging spines, ×4; *3c,d*, brach.v. ext., int., ×2, ×3; *3e*, card. process ext., ×4 (587).

Elliottella Stehli, 1955, p. 711 [*pro Psilonotus* Stehli, 1954, p. 323 (*non* Walker, 1834)] [**Psilonotus transversalis* Stehli, 1954, p. 324; OD]. Like *Costispinifera* but visceral disc of pedicle valve less convex and shell less elongate,

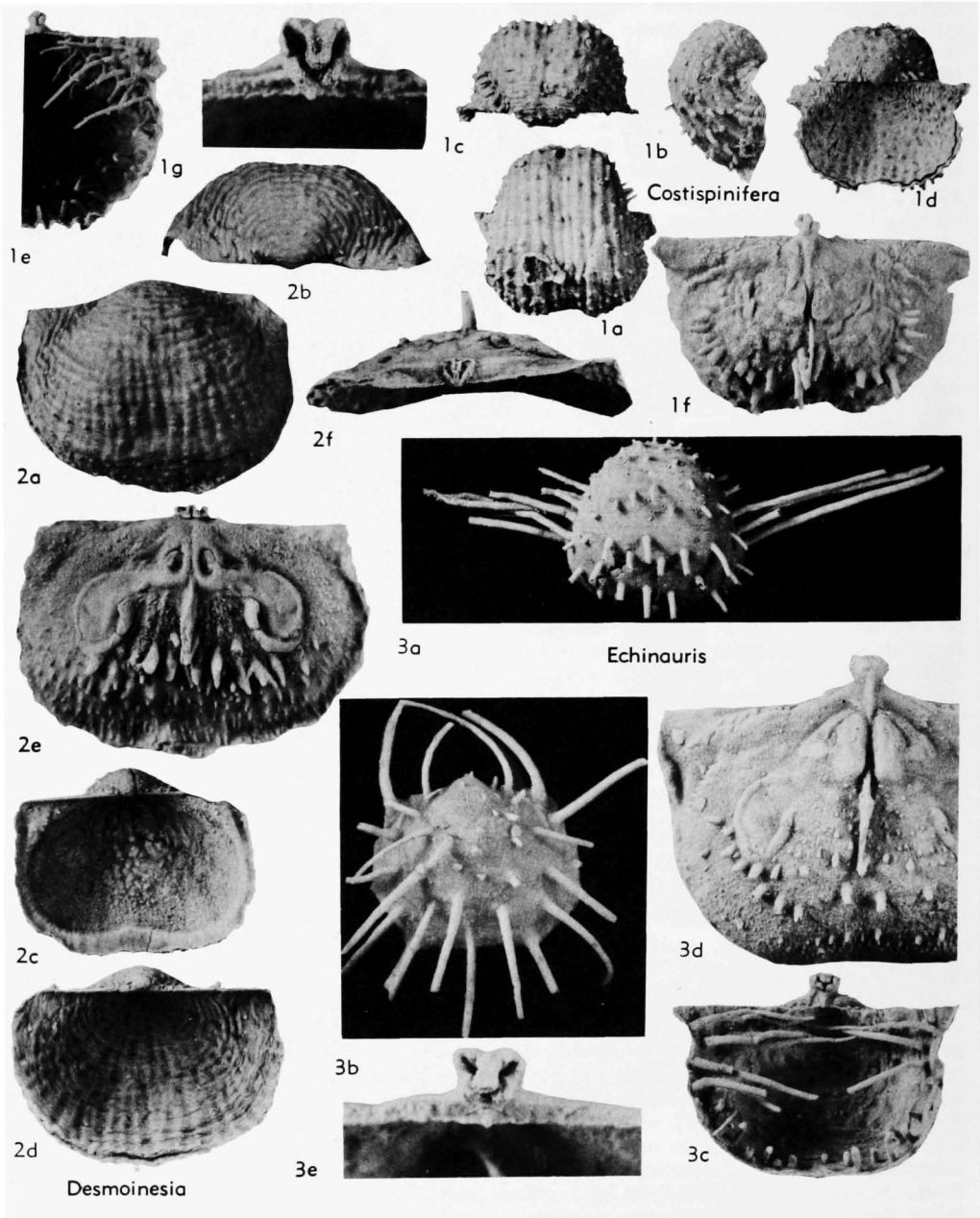

Fig. 347. Marginiferidae (Costispiniferinae) (p. *H*479-*H*480).

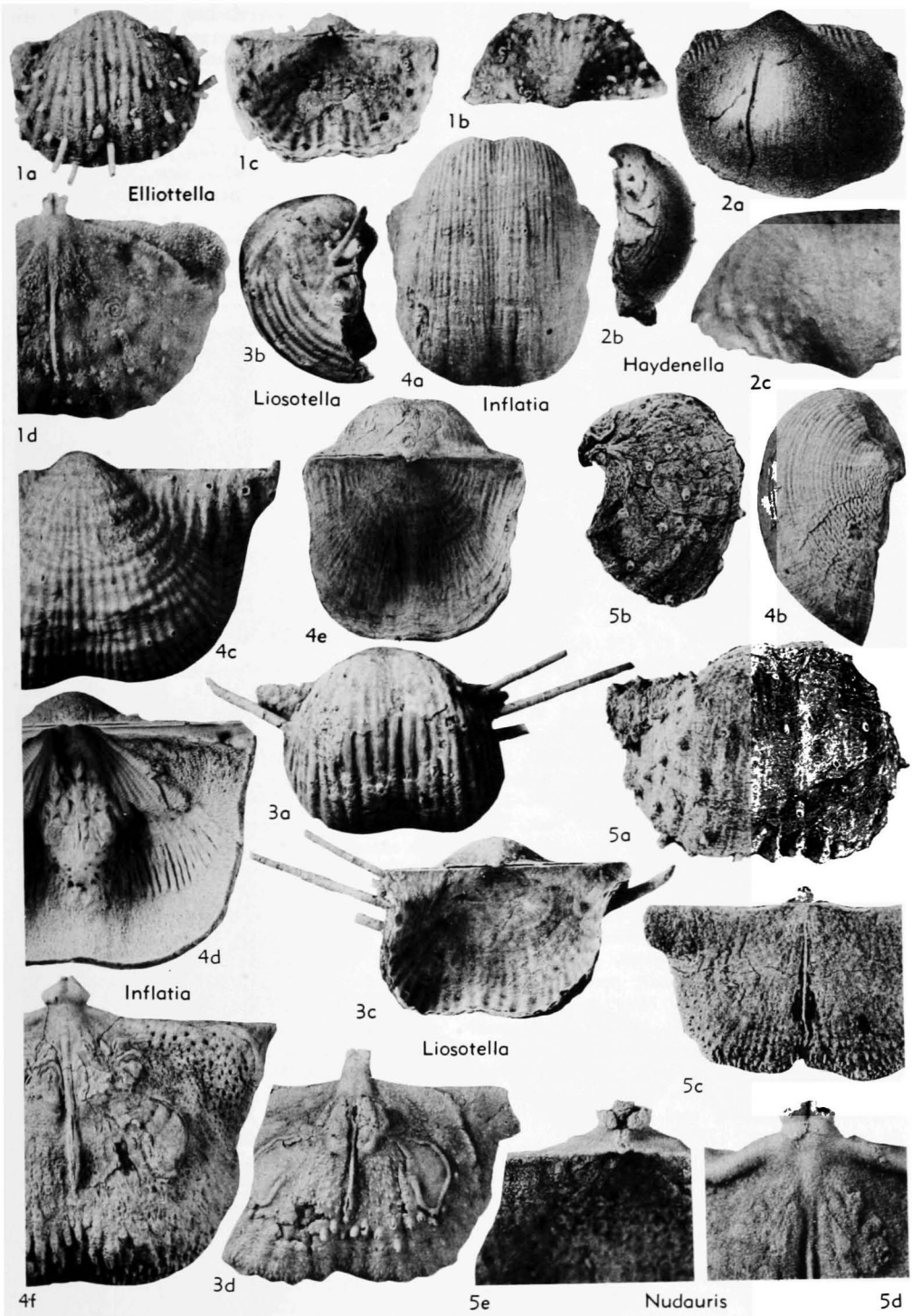

FIG. 348. Margineferidae (Costispiniferinae) (p. *H*480, *H*482).

2 rows of spines near hinge; brachial valve without spines, and small internal differences. *L.Perm.*, N.Am.——FIG. 348,*1*. *E. minima* (STEHLI), USA (W.Tex.); *1a,b*, ped.v. vent., post., ×2; *1c*, brach.v. view, ×2; *1d*, brach.v. int., ×4 (773).

Haydenella F. R. C. REED, 1944, p. 78 [**Productus kiangsiensis* KAYSER, 1883, p. 185; OD]. Small to medium-sized; pedicle valve globose, with short interarea; both valves capillate, smooth when decorticated, rugose near hinge, spines rare and in curved row up pedicle valve flanks; adductors smooth. *L.Perm.-U.Perm.*, Asia(China-Pak.).——FIG. 348,*2*. **H. kiangsiensis* (KAYSER), China *(2a,b)*, Pak. *(2c)*; *2a,b*, ped.v. vent., lat., ×1; *2c*, ped.v. post., ×2 (460).

Inflatia MUIR-WOOD & COOPER, 1960, p. 226 [**Productus inflatus* MCCHESNEY, 1860, p. 40; OD]. Medium-sized, elongate-quadrate; pedicle valve spirally curved; narrow ginglymus; both valves rugose posteriorly and costate, lamellose anteriorly, spines suberect or erect, scattered, and in row near hinge of pedicle valve, absent on brachial valve; adductors dendritic and lobate, large ventral muscle area. *U.Miss.(Chester.)*, N.Am.——FIG. 348,*4*. **I. inflata* (MCCHESNEY), USA (Okla.); *4a,b*, ped.v. vent., lat., ×1; *4c,d*, ped.v. post., int., ×2; *4e*, brach.v. view, ×1; *4f*, brach. v. int., ×2 (587).

Liosotella COOPER, 1953, p. 227 [**L. rugosa*; OD]. Small to moderately large; pedicle valve with strongly convex visceral disc and curved trail; minute ginglymus; marginiferid ridges in each valve; both valves posteriorly smooth, costate on trail; spines scattered and in row up flanks, rare on brachial valve; adductors slightly dendritic. *L. Perm.*, N. Am.-Arctic (Greenl.-Spitz.).——FIG. 348,*3a-c*. **L. rugosa*, Mex.; *3a-c*, ped.v. vent., lat., and brach.v. views (holotype), ×1 (182).——FIG. 348,*3d*. *L.* sp., L.Perm., USA(W.Tex.); brach.v. int., ×2 (182).

Nudauris STEHLI, 1954, p. 317 [**N. diabloensis*; OD]. Medium-sized, both valves geniculated, trails short; ginglymus present, pedicle valve costellate, ears smooth, rugose posteriorly, scattered stout spines, row near hinge; brachial valve smooth or costellate, spines absent; no internal ridges across ears; adductors faintly dendritic. *L. Perm.*, N.Am.——FIG. 348,*5*. **N. diabloensis*, USA(W.Tex.); *5a,b*, ped.v. vent., lat., ×1; *5c,d*, brach.v. int. showing card. process, ×1, ×2; *5e*, brach.v. ext., ×2 (773).

Subfamily RETARIINAE Muir-Wood & Cooper, 1960

[Retariinae MUIR-WOOD & COOPER, 1960, p. 230]

Valves geniculate, visceral disc reticulate, trail long, commonly tubuliform; brachial valve with ridge across ears; some shells with lateral flange; anterior row of endospines. *U.Carb.(Moscov.-Ural.)-L.Perm.*

Retaria MUIR-WOOD & COOPER, 1960, p. 230 [**R. umbonata*; OD]. Medium-sized, trails tending to split off from visceral disc, both valves finely rugose and costate, spines erect or suberect, scattered, and in row near hinge and up flanks, few spines in brachial valve; adductors dendritic and lobate; lateral flange in brachial valve. *U.Penn.-L.Perm.*, N.Am.-?Asia.——FIG. 349,*1*. **R. umbonata*, USA(W.Tex.); *1a,b*, ped.v. (holotype) vent., lat., ×1; *1c*, brach.v. view, ×1; *1d*, brach. v. int., ×3; *1e*, post. view of brach.v. int. showing flanges, ×2 (587).

Alexenia IVANOVA in IVANOV, 1935, p. 89 [**A. reticulata*; OD]. Medium-sized, with short trails and cicatrix of attachment, both valves rugose and costate, reticulate, ears smooth; spines scattered, in row near hinge and up flanks; adductors nondendritic, set on platforms supported by vertical ridges from cardinal process; dorsal marginal ridge corrugated anteriorly. *U.Carb.(Moscov.-Ural.)*, Eu.——FIG. 349,*4*. **A. reticulata* (IVANOVA), USSR; *4a,b*, ped.v. vent., post., ×1; *4c*, brach.v. int., ×2.5 (711).

Kutorginella IVANOVA, 1951, p. 329 [**K. mosquensis*; OD] [=*Neoproboscidella* IVANOVA, 1949 *(nom. nud.)*]. Medium-sized; pedicle valve posteriorly rugose, costate and reticulate, spines scattered and in row near hinge, trail funnel-shaped; brachial valve exterior unknown; marginal ridge in brachial valves, laterally flangelike, and spinose anteriorly; adductors partly dendritic. *U.Carb. (Moscov.-Ural.)-L.Perm.*, Eu.——FIG. 349,*5*. **K. mosquensis*, U.Carb., USSR; *5a,b*, ped.v. ant., vent., ×1; *5c*, brach.v. int., ×2 (711).

Rugivestis MUIR-WOOD & COOPER, 1960, p. 235 [**Proboscidella? carinata* MUIR-WOOD & COOPER in COOPER, 1957, p. 36; OD]. Small to medium-sized; pedicle valve trail carinate or with incipient tube; cincture present in each valve; flattened rim anterior to cincture in pedicle valve; internal marginal ridge corresponding to cincture; ornament of irregular costae, rugose and reticulate posteriorly; spines rare, possible 6 symmetrically placed. *L.Perm.*, N.Am.-Eu.——FIG. 349,*3*. **R. carinata* (MUIR-WOOD & COOPER), USA(Ore.); *3a-c*, ped.v. (holotype) vent., lat., ant., ×2 (192).

Tubaria MUIR-WOOD & COOPER, 1960, p. 236 [**Productus genuinus* KUTORGA, 1844, p. 93; OD]. Small or medium-sized, posteriorly fusiform; trail of pedicle valve forming incomplete tube, open anteriorly; ears large, merging into flanks; cincture present; both valves posteriorly rugose, costate and reticulate, tube finely costate; spines in pedicle valve only on visceral disc and ears. Interior unknown. *L.Perm.*, Eu.——FIG. 349,*2*. **T. genuina* (KUTORGA), USSR; *2a,b*, ped.v. ext. with ant. tube, lat. view, ×1; *2c*, same shell with ped.v. removed, ×1 (158).

Subfamily PROBOLIONIINAE Muir-Wood & Cooper, 1960

[Probolioniinae MUIR-WOOD & COOPER, 1960, p. 237]

Thickened submarginal rim resembling diaphragm in brachial valve interior, but with long subparallel trails springing from

exterior surface; pedicle valve with crenulated ridges across ears. *L.Perm.*

Probolionia Cooper, 1957, p. 27 [**P. posteroreticulata*; OD]. Small or medium-sized, both valves geniculated, posteriorly rugose, costellate and reticulate, trail costellate, pedicle valve with sulcate trail, spines scattered and in row up flanks and 6 spines symmetrically placed, spines absent in brachial valve. *L.Perm.*, N.Am.-Asia(China). ——Fig. 350,*1*. **P. posteroreticulata*, USA(Ore.); *1a-c*, ped.v. post., vent., lat., ×2; *1d*, long. sec. of shell showing trails, ×2 (192).

Family PRODUCTIDAE Gray, 1840

[Productidae Gray, 1840, p. 151]

Costellate shells with long trail in pedicle valve and one or more trails in brachial valve; visceral disc of brachial valve with one or several diaphragms as thin crescent-shaped plate, closing gap between valves; sessile bilobate or trilobate cardinal process inclined dorsally (externally); adductors dendritic or partly dendritic. *L.Carb.(Visean)-U.Carb.(Westphal.)*.

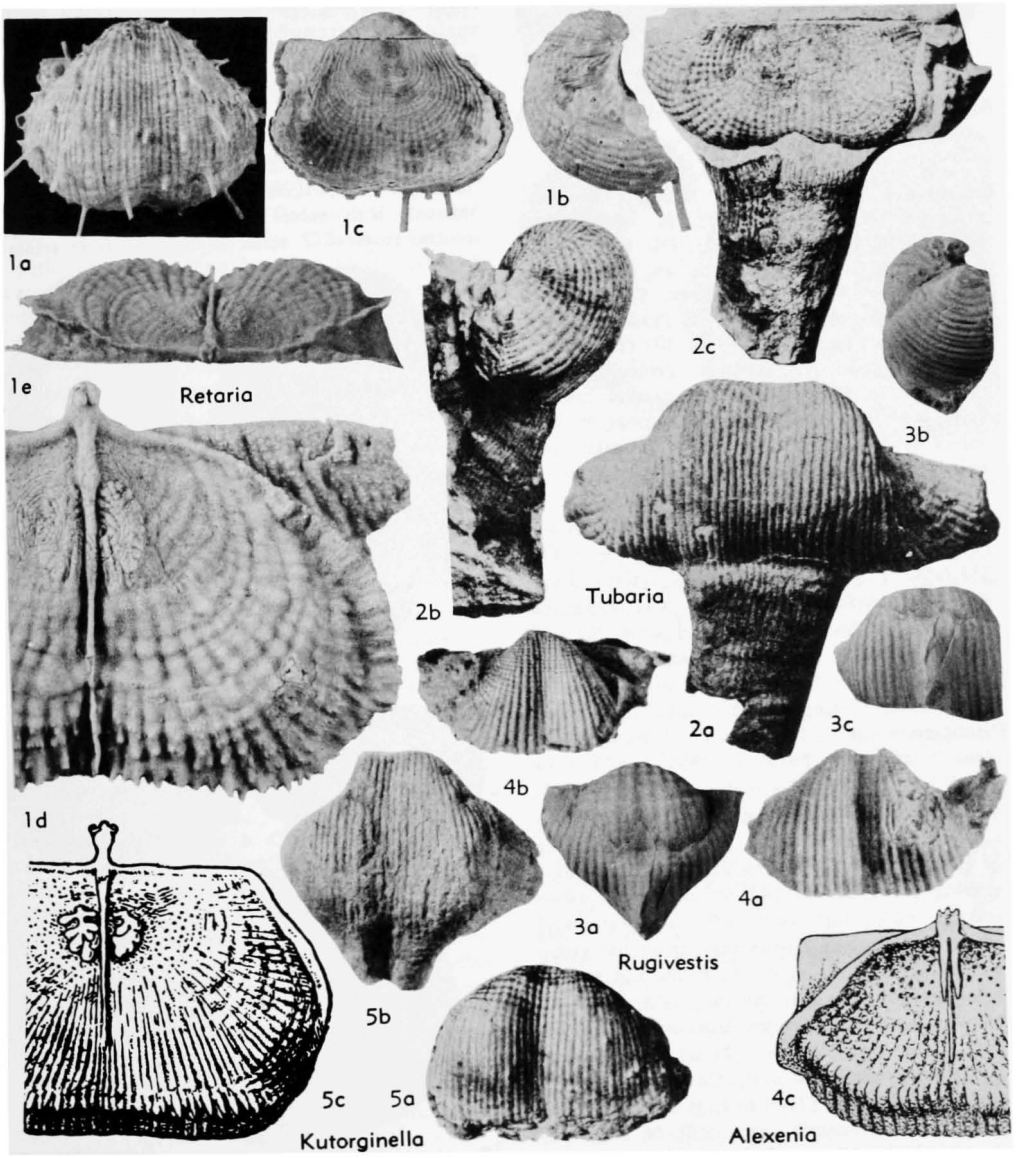

Fig. 349. Marginiferidae (Retariinae) (p. *H*482).

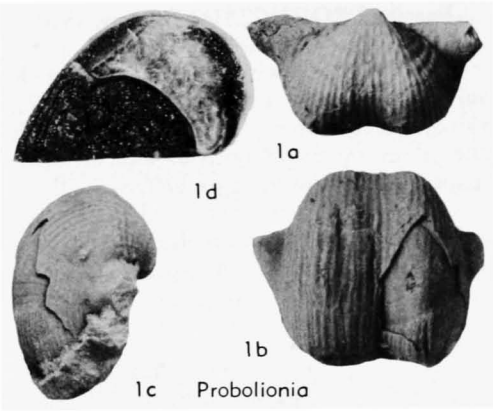

FIG. 350. Marginiferidae (Probolioniinae) (p. *H*483).

Productus J. SOWERBY, 1814, p. 153 [**Anomites productus* W. MARTIN, 1809, p. 9 (validated ICZN, 1956, Opin. 419, p. 75); OD (abs. taut.)] [=*Producta* CONYBEARE & PHILLIPS, 1822, p. 357 (no type-species); *Protonia* LINK, 1830, p. 449 (*non* RAFINESQUE, 1814) (obj.); *Pyxis* CHEMNITZ in MARTIN & CHEMNITZ, 1784, p. 301 (nonbinominal)]. Medium-sized to large, geniculated, visceral disc of pedicle valve and part of brachial valve tending to split off along diaphragm, both valves costate, rugose and slightly reticulate posteriorly, unevenly costate on spreading trail; spines scattered and in 2 rows near hinge margin on pedicle valve, absent on brachial valve. *L.Carb.(Visean)-U.Carb.(Westphal.)*, Eu.-Asia. —— FIG. 351,*1a-d*. **P. productus* (MARTIN), L.Carb., Eng.; *1a,b*, ped.v. with trail, vent., lat., ×1; *1c*, visceral disc detached from trail in dorsal view, ×1; *1d*, brach.v. ext. mold showing diaphragm, ×1 (574). ——FIG. 351,*1e*. *P. carbonarius* DEKONINCK, U. Carb.(Namur.), Eng.; brach.v. int., ×2 (574).

Diaphragmus GIRTY, 1910, p. 217 [**Productus elegans* NORWOOD & PRATTEN, 1855, p. 13 (*non* M'COY, 1844) (=**P. cestriensis* WORTHEN, 1860, p. 570); OD]. Small or medium-sized, commonly elongate, cincture variably developed, repetition of thin-shelled trails in brachial valve, diaphragm tending to be curved and repeated, both valves costate, rugose and faintly reticulate posteriorly; spines on costae, in 2 rows near hinge and group on flanks in pedicle valve, on flanks and trail in brachial valve; cardinal process bilobate, dorsally inclined; adductors obscurely dendritic and smooth. *U.Miss.(Meramec.-Chester.)*, N.Am.——FIG. 352, *1. **D. cestriensis* (WORTHEN), Chester., Ill. *(1a-c)*, Okla. *(1d,e)*, Ala. *(1f)*; *1a-c*, ped.v. vent., lat., post., ×1; *1d*, brach.v. view, ×1; *1e*, long. sec. showing both valves, ×2; *1f*, brach.v. int., ×3 (346).

Family ECHINOCONCHIDAE Stehli, 1954

[Echinoconchidae STEHLI, 1954, p. 326]

Body cavity large, greatly developed umbo in pedicle valve; cardinal process posteriorly trilobed, long-shafted and dorsally curved; brachial ridges generally obscure. *L.Carb.(Miss.)-U.Perm.*

Subfamily ECHINOCONCHINAE Stehli, 1954

[*nom. transl.* MUIR-WOOD & COOPER, 1960, p. 243 (*ex* Echinoconchidae STEHLI, 1954, p. 326)]

Spines of two or more series, or spine ridges bearing spines, either scattered over surface or arranged on concentric bands or rugae. *L.Carb.(Miss.)-L.Perm.*

Echinoconchus WELLER 1914, p. 138 [**Anomites punctatus* W. MARTIN, 1809, pl. 37, fig. 6-8 (invalid ICZN, 1948), =*Productus punctatus* J. SOWERBY, 1822, p. 22; SD CHAO, 1927]. Small to large, concavo-convex or brachial valve geniculated, both valves with bands bearing concentric rows of 2 series of fine prostrate spines

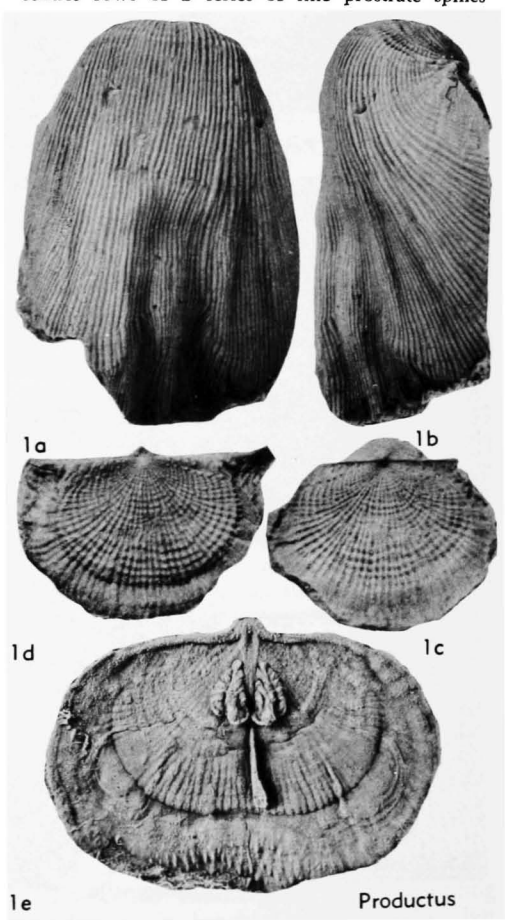

FIG. 351. Productidae (p. *H*484).

forming dense coat; adductors smooth. *L.Carb. (Miss.)*, Eu.-N.Afr.-Asia-N.Am.——FIG. 353,*1a-d*. **E. punctatus* (J. SOWERBY), Visean, Eng.; *1a,b*, ped.v. vent., lat., ×1; *1c*, brach.v. view, ×1; *1d*, brach.v. ext. showing spines, ×2 (858).——FIG. 353,*1e,f*. *E. alternatus* (NORWOOD & PRATTEN), Chester., Ky. *(1e)*, Okla. *(1f)*; *1e*, brach.v. int., ×1; *1f*, lat. view of card. process, ×2 (858).

Bathymyonia MUIR-WOOD & COOPER, 1960, p. 244 [**Productus nevadensis* MEEK, 1877, p. 64; OD]. Large, valves thickened, brachial valve geniculated; pedicle valve with overlapping spine ridges posteriorly, broad bands on trail with prostrate spines of 2 series in several rows, and in rows on ears and near hinge; brachial valve similar, fewer spines, anteriorly lamellose; adductors dendritic; cardinal process massive, trilobed, dorsally recurved. *L.Perm.*, N.Am.——FIG. 353,*3*. **B. nevadensis* (MEEK), Nev. *(3a-c)*, Utah *(3d)*, Wyo. *(3e)*; *3a-c*, ped.v. (lectotype) vent., post., lat.; *3d*, brach.v. view; *3e*, brach.v. int. showing massive card. process; all ×1 (587).

Calliprotonia MUIR-WOOD & COOPER, 1960, p. 246 [**C. renfrarum*; OD]. Like *Echinoconchus* but with more imbricating lamellose bands, up to 8 rows of spines of 2 series in pedicle valve; concentric laminae in brachial valve with single spine row; lateral ridges continued down lateral margin as prominent flange; adductors part-dendritic; cardinal process sessile, trilobed; brachial ridges prominent. *U.Penn., ?L.Perm.*, N.Am.-S.Am.——FIG. 354,*2*. **C. renfrarum*, U.Penn., USA(Tex.); *2a,b*, ped.v. (holotype) vent., lat., ×1; *2c*, brach. v. view, ×2; *2d,e*, brach.v. ext., int., ×3 (587).

Echinaria MUIR-WOOD & COOPER, 1960, p. 248 [**Productus semipunctatus* SHEPARD, 1838, p. 153; OD]. Like *Echinoconchus* but with more tapering visceral disc, narrower hinge, massive tapering incurved umbo; bands developed over whole shell bearing prostrate spines of 3 series; adductors partly dendritic; cardinal process more massive, less recurved, with sulcate shaft. *U.Carb.(M.Penn.-U.Penn.)*, N.Am.-Asia.——FIG. 354,*1*. **E. semipunctata* (SHEPARD), Tex. *(1a,c,e)*, Kan. *(1b)*, Ill. *(1d)*; *1a,b*, ped.v. vent., lat., ×1; *1c,d*, brach. v. view, brach.v. int., ×1; *1e*, brach.v. ext. with card. process, ×2 (587).

Pulchratia MUIR-WOOD & COOPER, 1960, p. 249 [**Productus symmetricus* MCCHESNEY, 1860, p. 35; OD]. Medium-sized to large, subcircular; pedicle valve rugose with spine ridges posteriorly; concentric bands wtih erect and prostrate spines, becoming lamellose anteriorly; brachial valve rather similar; adductor scars partly dendritic; cardinal process trilobed, extending dorsally, shaft with median sulcus. *U.Penn.*, N.Am.——FIG. 353, *2*. **P. symmetrica* (MCCHESNEY), USA(Tex.); *2a,b*, ped.v. vent., lat., ×1; *2c*, brach.v. view, ×1; *2d*, brach.v. int., ×2; *2e*, card. process lat. view, ×1 (587).

Pustula I. THOMAS, 1914, p. 259 [**Producta pustulosa* PHILLIPS, 1836, p. 216; OD]. Medium-sized to large, nongeniculated; pedicle valve rugose with spine ridges, tending to be quincuncially arranged on rugae, spines prostrate or suberect in rows near hinge, brachial valve rugose and spinose; cardinal process posteriorly trilobate, long shaft; adductors dendritic; brachial ridges well defined. *L.Carb.(Tournais.-Visean)*, Eu.-?Asia-N.Afr.——FIG. 355,*1*. **P. pustulosa* (PHILLIPS), Visean, Eng.; *1a,c*, ped.v. (holotype) vent., ×1, ×2; *1b*, brach.v. view, ×1; *1d*, brach.v. int., ×1; *1e*, lat. view of card. process, ×3 (805).

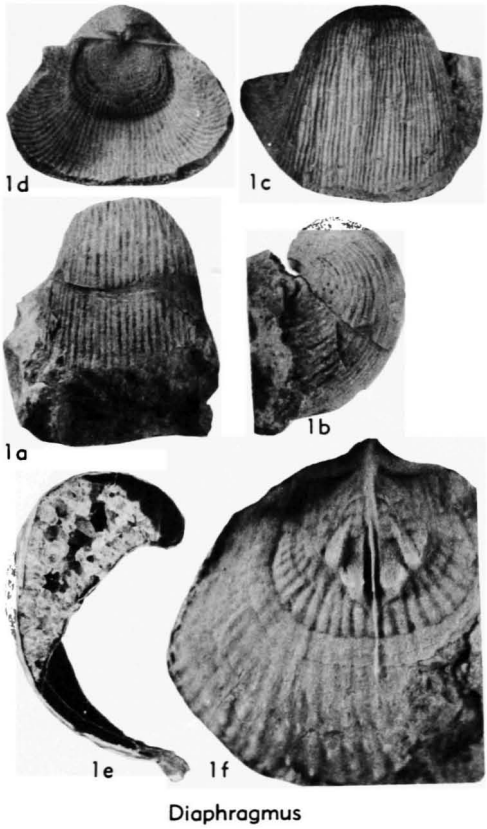

FIG. 352. Productidae (p. *H*484).

Septarinia MUIR-WOOD & COOPER, 1960, p. 251 [**Productus leuchtenbergensis* DEKONINCK, 1847, p. 226; OD]. Large, both valves convex in lateral contour; ornament of rugae posteriorly with spine ridges bearing prostrate spines, lamellae anteriorly with 1 or 2 rows of spines of 2 series; brachial valve similar but dimpled; median septum in pedicle valve with V-shaped chamber posteriorly; long-shafted trilobed cardinal process, curved dorsally; adductors obscurely dendritic. *L. Carb.(Visean)*, Eu.——FIG. 356,*1*. **S. leuchtenbergensis* (DEKONINCK), Belg.; *1a,b,d*, ped.v. vent., lat., ant., ×1; *1c*, ped.v. int. mold showing septum, ×1; *1e*, brach.v. int. mold, ×1 (483).

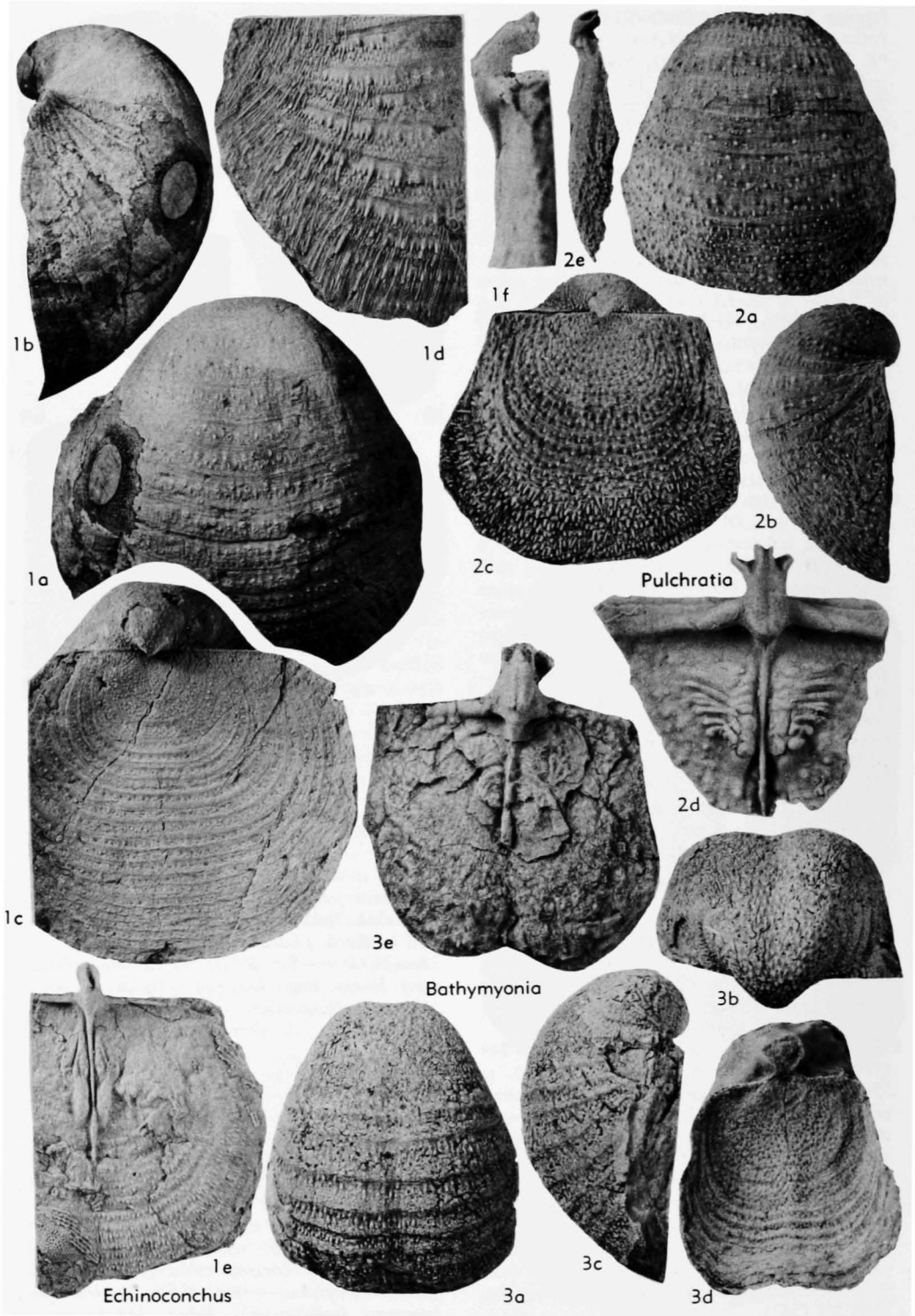

FIG. 353. Echinoconchidae (Echinoconchinae) (p. *H*484-*H*485).

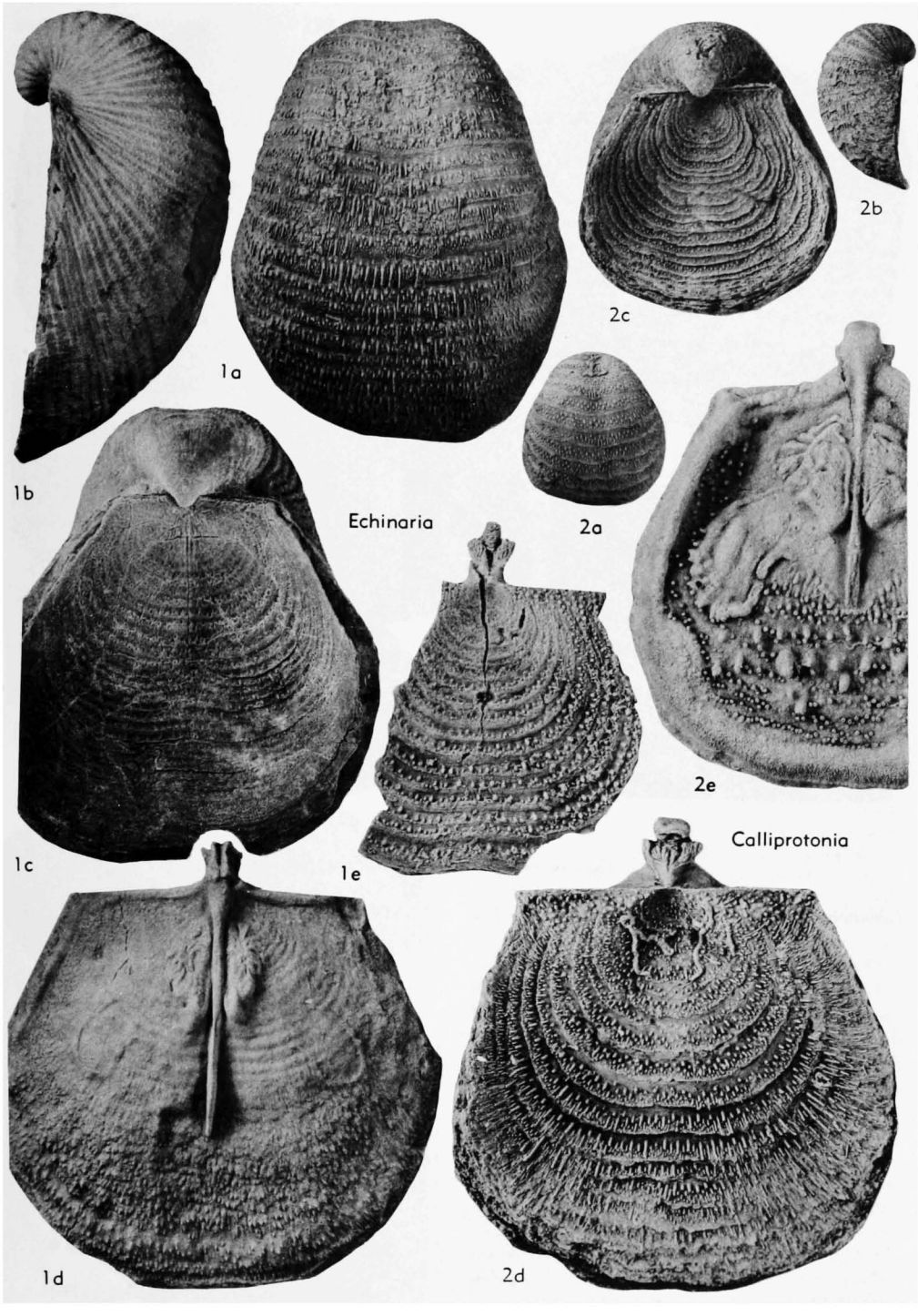

FIG. 354. Echinoconchidae (Echinoconchinae) (p. *H*485).

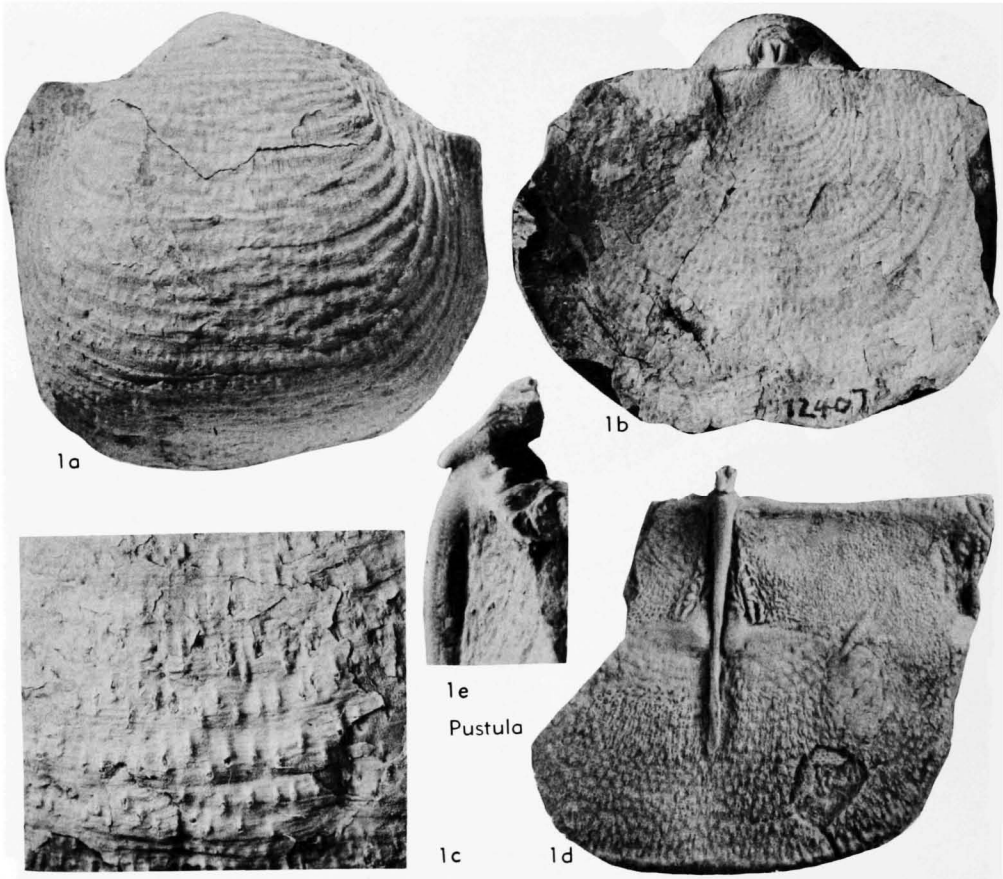

FIG. 355. Echinoconchidae (Echinoconchinae) (p. *H*485).

Subfamily WAAGENOCONCHINAE Muir-Wood & Cooper, 1960

[Waagenoconchinae MUIR-WOOD & COOPER, 1960, p. 252]

Delicate spines arranged in quincunx, in some forms springing from spine ridges and diminishing in diameter anteriorly. *U. Penn.-U.Perm.*

Waagenoconcha CHAO, 1927, p. 24 [**Productus humboldti* D'ORBIGNY, 1842, p. 54; OD] [=*Ruthenia* FREDERIKS, 1928, p. 789 (type, *Productus irginae* STUCKENBERG, 1898, p. 340)]. Medium-sized to large, valves not geniculated; cardinal process trilobate on long shaft, inclined dorsally, brachial ridges obscure; adductors dendritic. *U. Penn.-U.Perm.*, N.Am.-S.Am.-Eu.-Arctic-Asia-Australia. —— FIG. 356,*2a,b*. **W. humboldti* (D'ORBIGNY), Perm., Bolivia; *2a,b*, ped.v. and brach.v. views, ×1 (152).——FIG. 356,*2c,d*. *W.* sp., cf. *W. irginae* (STUCKENBERG), U.Penn., USA (Tex.); *2c,d*, ped.v. vent., ×1, ×2 (152).—— FIG. 357,*1*. *W. montpelierensis* (GIRTY), L.Perm., USA(W.Tex.); *1a,b*, brach.v. ext., int., ×1.5; *1c*, lat. view of card. process, ×1.5 (152).

Family BUXTONIIDAE Muir-Wood & Cooper, 1960

[Buxtoniidae MUIR-WOOD & COOPER, 1960, p. 255]

Cardinal process dorsally recurved, bilobate or trilobate, with supporting buttress plates in youth, or buttress plates fusing with septum leaving cavity (antron) at posterior end of septum; costate or lamellose ornament with anterior spinose bands or rims. *U.Dev.-U.Perm.*

Subfamily BUXTONIINAE Muir-Wood & Cooper, 1960

[Buxtoniinae MUIR-WOOD & COOPER, 1960, p. 255]

Antron present except in older growth stages, ornament rugose, costate, and spinose, with anterior bands or rims. *U. Dev.-U.Perm.*

Buxtonia I. THOMAS, 1914, p. 259 [**Anomites scabriculus* W. MARTIN, 1809, p. 8; OD] (but species declared invalid, ICZN, 1956); =**Productus scabriculus* J. SOWERBY, 1814, p. 157; SD ICZN (Op. 420), 1956, p. 143]. Medium-sized or large, not geniculated externally; rugose posteriorly and costate, costae decreasing in width anteriorly and terminating in spines or replaced by rows of spines forming bands; spines numerous, prostrate on costae, and more erect spines in rows near hinge, on spine ridges on flanks; adductors dendritic. *U.Dev.-U.Carb.*, cosmop.—— FIG. 358,*1*. **B. scabricula* (J. SOWERBY), L.Carb., Eng.; *1a-c*, ped.v. vent., post., lat., ×1.25; *1d*, brach.v. int. showing septum and antron, ×1.6; *1e,f*, card. process post., lat., ×1.25 (574).

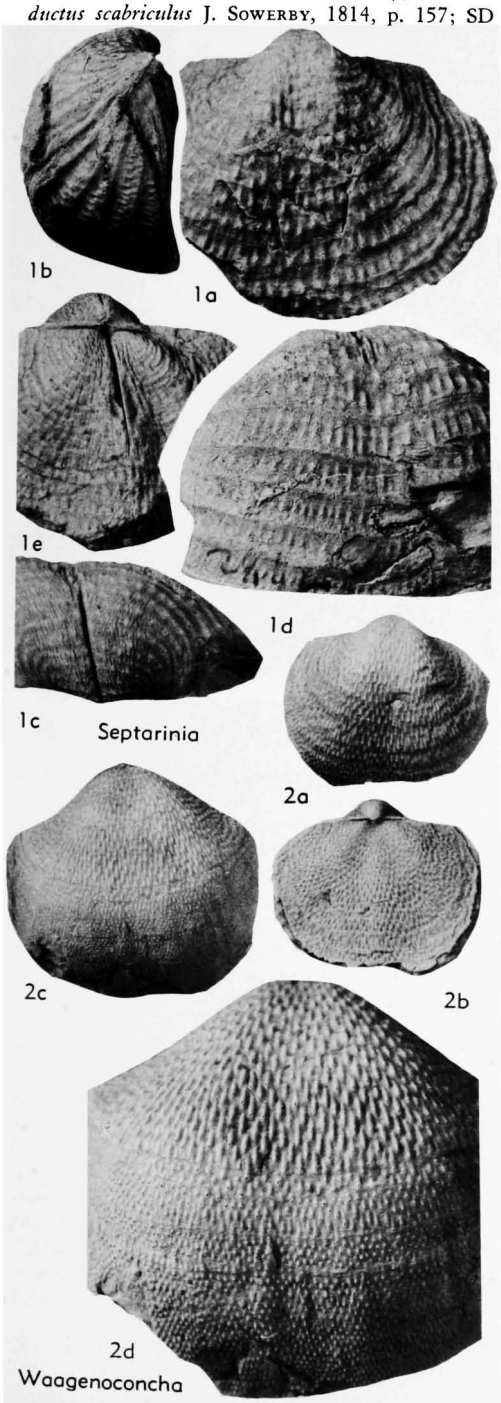

FIG. 356. Echinoconchidae (Echinoconchinae) *(1)*, (Waagenoconchinae) *(2)* (p. *H*485, *H*488).

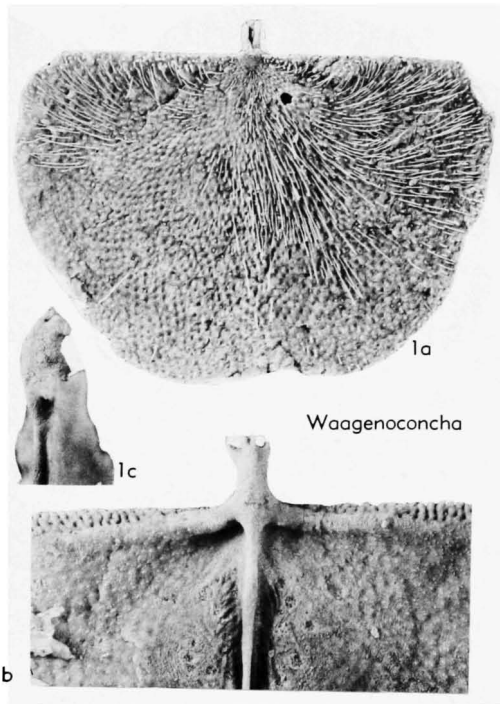

FIG. 357. Echinoconchidae (Waagenoconchinae) (p. *H*488).

Buxtonioides MENDES, 1959, p. 43 [**Productus amazonicus* KATZER, 1903, p. 264; OD]. Resembling *Buxtonia* externally but without spinose bands and having trilobed cardinal process and septum without antron or buttress plates. *M.Penn.*, S.Am.——FIG. 359,*1*. **B. amazonicus* (KATZER), Itaituba Ser., Brazil; *1a,b*, ped.v. vent., ×1, ×5; *1c*, brach.v. ext., ×1; *1d*, ped.v. ext. with spines on ears, ×1.25 (555).

Etheridgina OEHLERT, 1887, p. 1278 [**Productus complectens* R. ETHERIDGE JR., 1876, p. 462; OD]. Small, depressed, attached to foreign bodies by clasping spines, at least in early growth stages, no interareas, teeth or sockets; ornamented by angular rugae or overlapping lamellae with rare spines; row of long clasping spines along hinge and lateral margins; cardinal process sessile, bilobate, supported by 2 buttress plates that com-

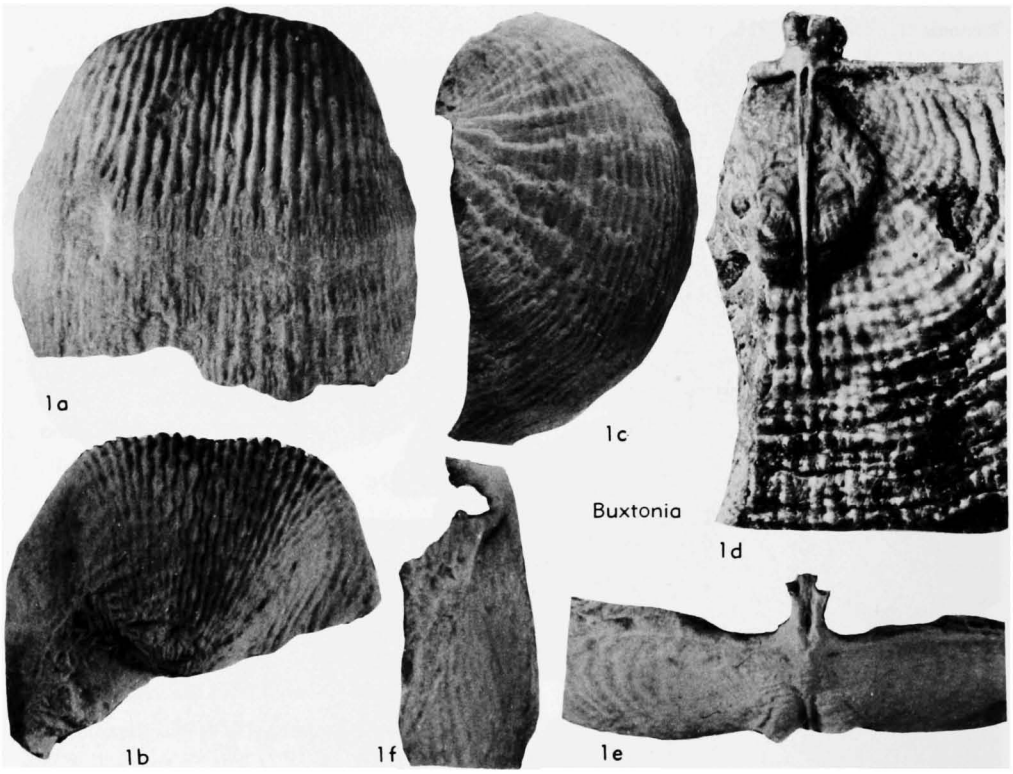

FIG. 358. Buxtoniidae (Buxtoniinae) (p. *H*489).

monly converge and unite with septum. *L.Carb. (Visean),* Eu.——FIG. 360,*1*. **E. complectens* (R. ETHERIDGE), Visean, Scot.; *1a,* shell with spines clasping crinoid stem, ×14; *1b,* ped.v. vent., ×5; *1c,d,* brach.v. int., ×5 (290).

Flexaria MUIR-WOOD & COOPER, 1960, p. 258 [**Productus arkansanus* GIRTY, 1910, p. 216; OD]. Like *Setigerites* in external form but without anterior rims or troughs, and with more prominent costae, replaced by spine ridges on flanks; interior of brachial valve geniculated, concave posteriorly; cardinal process almost at right angles to septum; adductors dendritic. *U.Miss. (Chester.),* N.Am.——FIG. 360,*2*. **F. arkansana* (GIRTY), Mo. *(2a-d),* Okla. *(2e-g)*; *2a-c,* ped.v. vent., lat., post., ×1; *2d,* brach.v. view, ×1; *2e,f,* brach.v. int., ×1, ×2; *2g,* brach.v. lat. showing card. process, ×2 (346).

Kochiproductus DUNBAR, 1955, p. 107 [*pro Tschernyschewiella* FREDERIKS, 1924, p. 20 (*non* VON TOLL, 1899)] [**Productus porrectus* KUTORGA, 1844, p. 96; SD MUIR-WOOD & COOPER, 1960, p. 260, for *Tschernyschewiella* and hence for *Kochiproductus,* DUNBAR's original designation of *K. flexicostatus* as type-species being invalid]. Large, commonly geniculated, both valves with anterior rim; costate, rugose, slightly reticulate, becoming lamellose without spinose bands anteriorly; spines numerous, recumbent, from swollen nodes posteriorly, more erect on ears and on trail; low septum in pedicle valve; cardinal process trilobed on long shaft; antron on brachial valve septum; adductors dendritic. *L.Perm.-U.Perm.,* N. Am.-S. Am.-Arctic-Eu.-Asia. —— FIG. 361,*1*. *K. peruvianus* (D'ORBIGNY); USA(W.Tex.); *1a-c,* ped.v. vent., lat., post., ×0.7; *1d,* brach.v. view, ×0.7; *1e,* brach.v. int., ×1.3 (269).

Labriproductus COOPER & MUIR-WOOD, 1951, p. 195 [*pro Worthenella* GIRTY, 1938, p. 442 (*non* WALCOTT, 1911)] [**Productus wortheni* HALL, 1858, p. 638; OD]. Medium-sized, both valves geniculated; cincture demarcating anterior thickened ridge in pedicle valve, rugae near hinge, costae replaced anteriorly by spine rows, spines scattered and in rows near hinge, and group on ears and flanks; brachial valve with antron, cardinal process small, bilobate, extending dorsally; adductors smooth. *L.Miss.(Osag.),* N.Am.——FIG. 361,*2*. **L. wortheni* (HALL), USA(Mo.); *2a-c,* ped.v. vent., lat., ant., ×1.3; *2d,* brach.v. int., ×1.3 (795).

Marginatia MUIR-WOOD & COOPER, 1960, p. 262 [**Productus fernglenensis* WELLER, 1909, p. 299; OD]. Medium-sized to large, valves geniculated, no rims or troughs; ornament dictyoclostid but with few spines on trail and on or near ears, rare

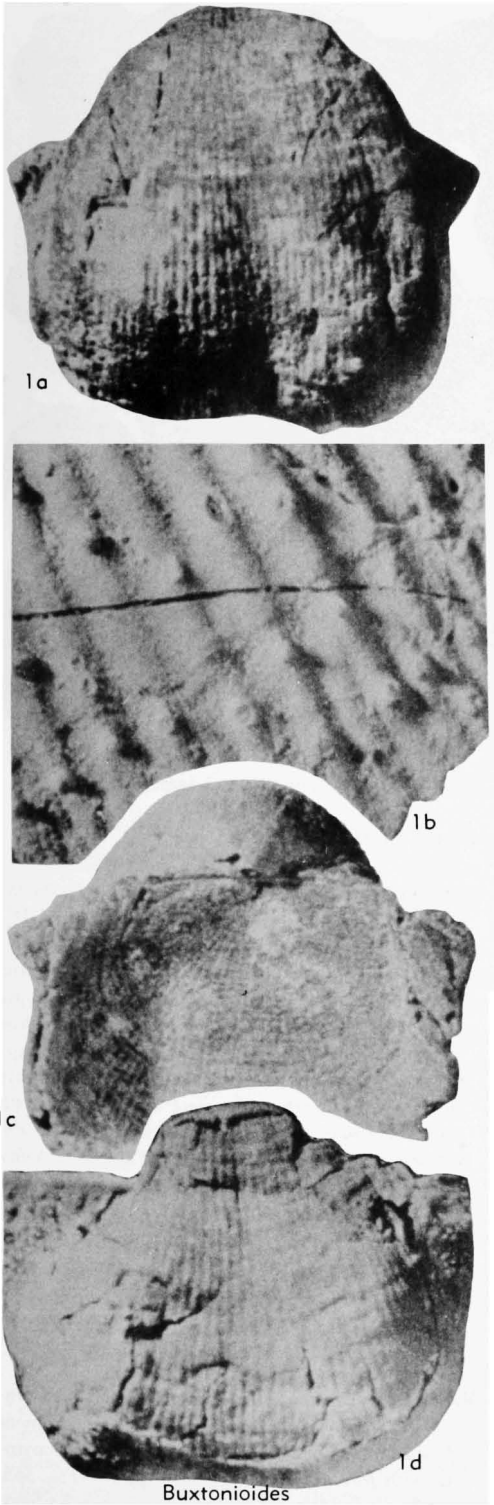

FIG. 359. Buxtoniidae (Buxtoniinae) (p. *H*489).

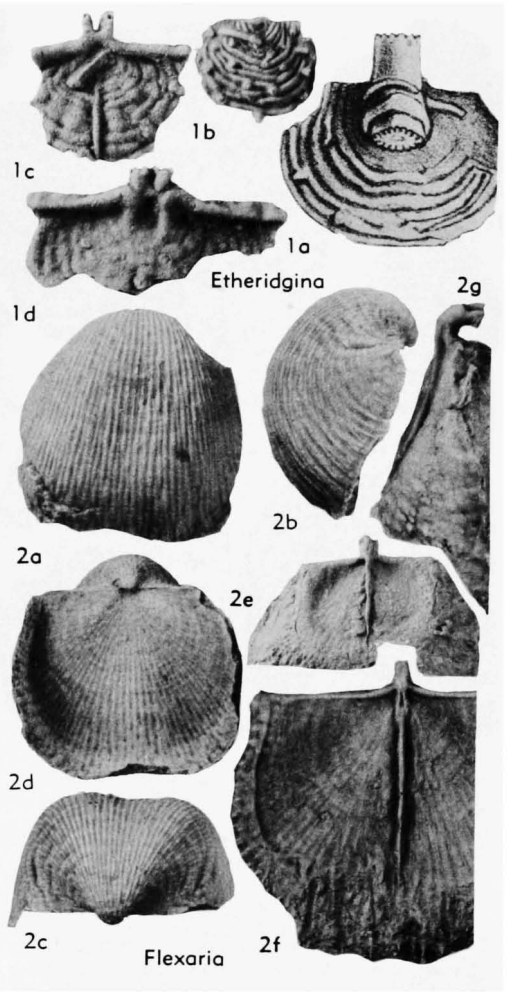

FIG. 360. Buxtoniidae (Buxtoniinae) (p. *H*489-*H*490).

in brachial valve; brachial valve septum with antron, accessory socket behind lateral ridges, internal posterior or posterolateral margin of brachial valve with thickened rim; adductors dendritic. *L.Miss.(Osag.)*, N.Am.——FIG. 361,*3*. **M. fernglenensis* (WELLER), USA(Mo.); *3a-c*, ped.v. vent., lat., post., ×0.7; *3d*, brach.v. int., ×1.3 (587).

Marginicinctus SUTTON, 1938, p. 561 [**Productus marginicinctus* PROUT, 1857, p. 43; OD]. Like *Labriproductus* in having *Buxtonia*-like ornament but with anterior flattened or curving ledge in each valve demarcated by cincture and ornamented by costae and spines or spine row; cardinal process bilobed, with buttress plates enclosing end of breviseptum; adductors dendritic. *L.Carb.(Miss.)*, Eu.-N.Am.——FIG. 362,*2*. **M. marginicinctus* (PROUT), U.Miss.(Meramec.), Mo. *(2a,b)*, Iowa *(2c,d)*, Tenn. *(2e)*; *2a,b*, ped.v.

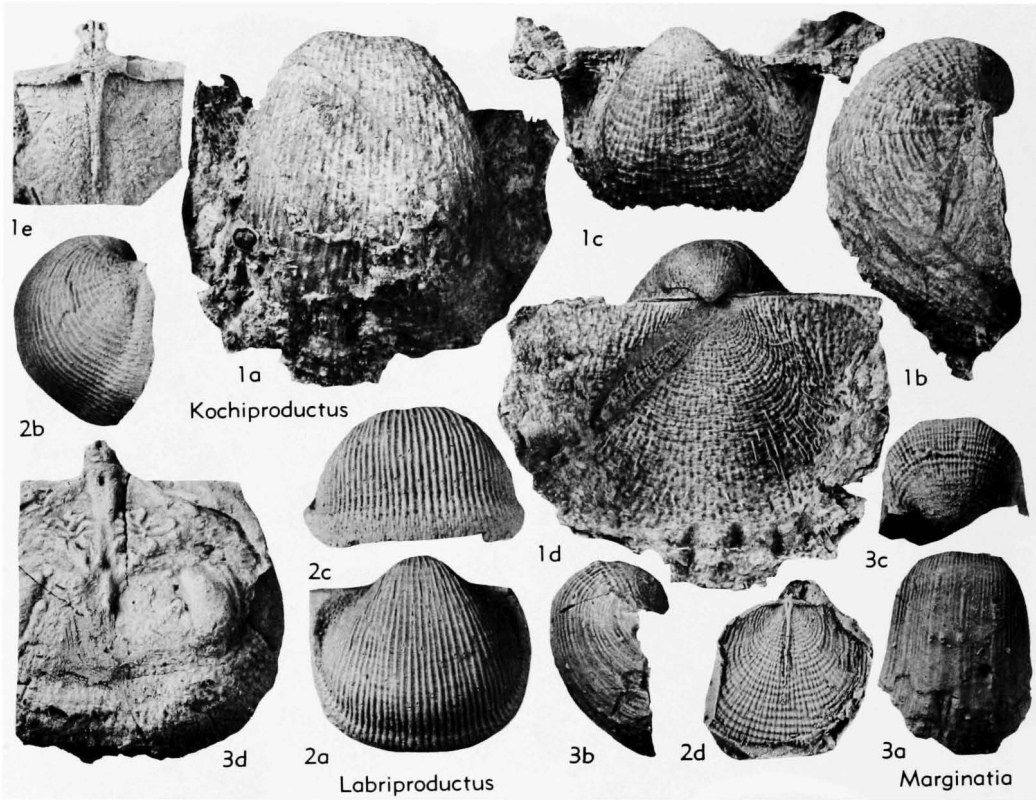

FIG. 361. Buxtoniidae (Buxtoniinae) (p. *H*490-*H*491).

vent., lat., ×1; *2c,d,* ped.v. ant., oblique lat., ×2; *2e,* brach.v. int., ×2 (795).

Protoniella BELL., 1929, p. 110 [**P. beedei*; OD]. Small; pedicle valve with short trail, cicatrix rare; faintly rugose, with spines posteriorly, costate and lamellose anteriorly; spines on costae, in row near hinge and down flanks; brachial valve costate and lamellose, septum with antron, cardinal process internally bilobate. *U. Miss.(Meramec.-Chester.), ?L.Penn.(Morrow.),* N.Am.——FIG. 362,*1.* **P. beedei,* U.Windsor, Nova Scotia; *1a,* ped.v. vent., ×1; *1b,* brach.v. view, ×1; *1c,* brach.v. int., ×1 (64).

Tomilia (*see* p. *H*904).

?Tomiproductus (*see* p. *H*905).

Subfamily JURESANIINAE Muir-Wood & Cooper, 1960

[Juresaniinae MUIR-WOOD & COOPER, 1960, p. 266]

Shell with cicatrix of attachment; ornament of lamellae, spine ridges and 2 or more series of spines, buttress plates enclosing end of breviseptum or fusing with it; cardinal process variably developed, bilobate, trilobate, or quadrilobate externally. *U.Carb. (L.Penn.-U.Penn.)-L.Perm.*

Juresania FREDERIKS, 1928, p. 786 [**Productus juresanensis* CHERNYSHEV, 1902, p. 276; OD]. Medium-sized, valves geniculated, minute ginglymus; pedicle valve posteriorly rugose, with spine ridges concentrically arranged, ridges overlapping or radially aligned medianly, becoming lamellose or banded on trail; spines suberect or prostrate, in rows near hinge; brachial valve posteriorly rugose with prostrate or erect spines, trail with prostrate spines of 2 series, antron may be developed; adductors dendritic. *U.Carb.(L.Penn.-U.Penn.)-L.Perm.,* Eu.-Asia-N.Am.——FIG 363, *1a-f. J. nebrascensis* (OWEN), L.Perm., USA (Kan.); *1a-c,* ped.v. vent., ant., lat., ×1; *1d,* brach.v. view, ×1; *1e,f,* brach.v. int. showing separated and joined card. process lobes, ×2 (158).——FIG. 363,*1g. J. rectangularia* R. H. KING, U.Penn., USA(Tex.); brach.v. view showing cicatrix, ×2 (158).

Ramavectus STEHLI, 1954, p. 327 [**R. diabloensis;* OD]. Only brachial valve known; ornament of prostrate spines of 2 series. [Possibly synonymous with *Juresania.*] *L.Perm.,* N.Am.——FIG. 363, *2.* **R. diabloensis,* USA(Tex.); *2a,b,* brach.v. ext. with prostrate spines, int., ×1 (773).

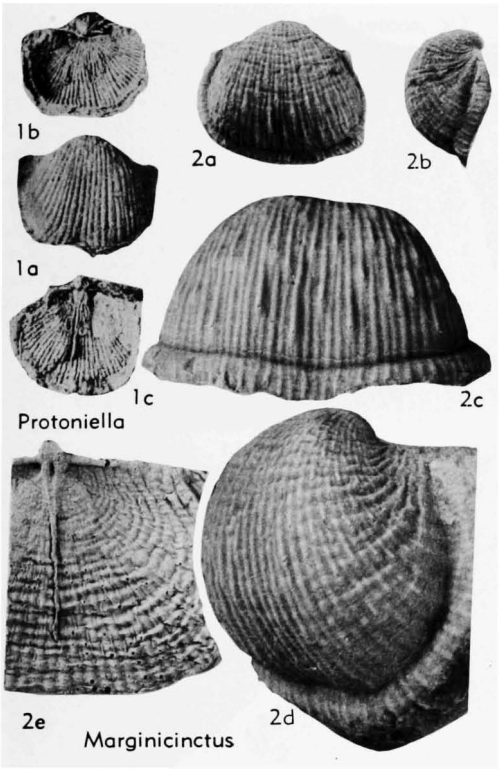

FIG. 362. Buxtoniidae (Buxtoniinae) (p. *H*491-*H*492).

Family DICTYOCLOSTIDAE Stehli, 1954

[Dictyoclostidae STEHLI, 1954, p. 316]

Valves usually large, costate, and geniculated, with reticulated visceral discs and long trail; cardinal process sessile, or short-shafted, trilobed, with large median lobe; dendritic adductors; brachial ridges given off horizontally. *L.Carb.(Tournais.-Visean)-U.Perm.*

Subfamily DICTYOCLOSTINAE Stehli, 1954

[Dictyoclostinae STEHLI, 1954, p. 316]

Posterior region reticulate and trail costate. *L.Carb.(Tournais.-Visean)-U.Perm.*

Dictyoclostus MUIR-WOOD, 1930, p. 103 [**Anomites semireticulatus* MARTIN, 1809, p. 7 (validated ICZN); OD]. Large, quadrate, concavo-convex, rarely geniculated; rugae posteriorly or extending over whole shell, reticulation prominent; fine erect spines in group on flanks and on venter, in row near hinge; brachial valve similar, fewer spines; massive cardinal process with short shaft, lophidium developed, lateral ridges along hinge margin. *L.Carb.(Tournais.-Visean)*, Eu.——FIG. 364,*1a-c*. **D. semireticulatus* (MARTIN), Eng.;

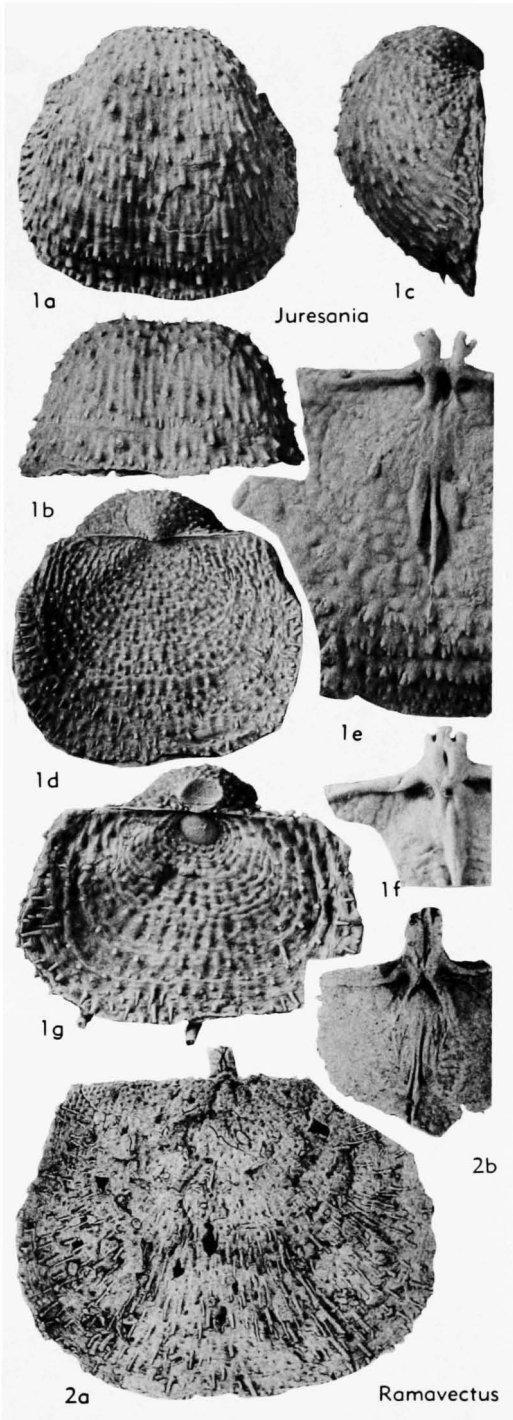

FIG. 363. Buxtoniidae (Juresaniinae) (p. *H*492).

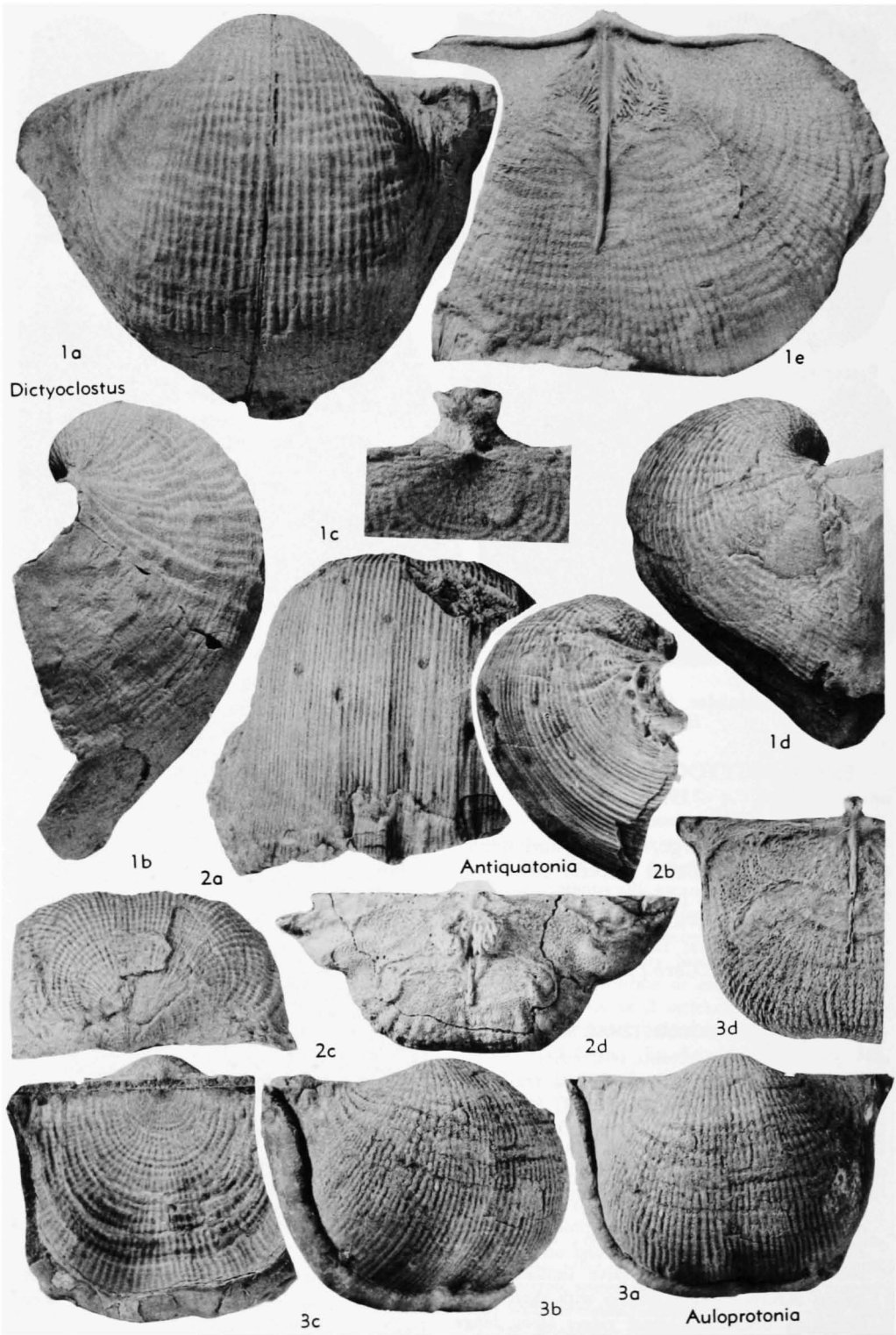

FIG. 364. Dictyoclostidae (Dictyoclostinae) (p. *H*493, *H*495).

1a,b, ped.v. vent., lat., ×1; *1c*, card. process, ×2 (574).——FIG. 364,*1d*. *D. multispiniferus* (MUIR-WOOD), Eng.; ped.v. lat. showing fine spines, ×1 (574).——FIG. 364,*1e*. *D. pinguis* (MUIR-WOOD), Eng.; brach.v. int., ×1 (574).

Antiquatonia MILORADOVICH, 1945, p. 496 [**Productus antiquatus* J. SOWERBY, 1821, p. 15; OD]. Small to large, both valves geniculated; costate and rugose, prominently reticulate posteriorly, spines scattered, row near hinge, and up flanks commonly on curved ridge, rare on brachial valve; median lobe of small cardinal process dorsally directed, spinelike lophidium; lateral ridges diverging from hinge, not extending down lateral margin. *L.Carb.(Visean)*, Eu.-Asia-Afr.-Australia; *U. Carb.*, Eu.-Asia-Australia.——FIG. 364,*2a-c*. *A. wettonensis* (MUIR-WOOD), L.Carb.(U. Visean), Eng.; *2a-c*, ped.v. ant., lat., post., ×1 (711).——FIG. 364,*2d*. *A. costata* (J. DE C. SOWERBY); U. Carb.(Namur.), Scot.; brach.v. int., ×1 (711).

Auloprotonia MUIR-WOOD & COOPER, 1960, p. 273 [**A. aulacophora*; OD]. Like *Dictyoclostus* but with brachial valve geniculated, trail recurved in tubelike coil around anterior margin enclosing end of trail of pedicle valve; reticulation less prominent; spines rare, scattered, in row near hinge margin and single spine from each cardinal extremity; absent on brachial valve; cardinal process bilobate; lateral ridges continued down posterolateral margin of visceral disc. *U.Miss. (Meramec.)*, N.Am.——FIG. 364,*3*. **A. aulocophora*, Moorefield, USA(Okla.); *3a,b*, ped.v. (holotype) vent., oblique lat., showing ant. coil, ×1; *3c,d*, brach.v. ext., int., ×1 (587). [See Fig. 299 for additional illustrations.]

Brasilioproductus MENDES, 1959, p. 48 [**Productus chandlessi* DERBY, 1874, p. 51; OD]. Resembling *Squamaria* in quadrate shell outline but having coarser costation usually over whole shell and single oblique row of spines near hinge in pedicle valve, and row near hinge in brachial valve. *M. Penn.(Itaituba Ser.)*, S.Am.(Brazil).——FIG. 365, *1*. **B. chandlessi* (DERBY); *1a-c*, ped.v. vent., lat., post.; *1d*, brach.v. ext. (*1a,b,d*, ×1; *1c*, ×1.8) (555).

Chaoiella FREDERIKS, 1933, p. 31 [**Productus gruenewaldti* KROTOV, 1888, p. 546; OD]. Medium-sized to large, subquadrate, geniculated; attachment cicatrix present; both valves finely costate and rugose posteriorly with slight reticulation; lamellose anteriorly; spines in pedicle valve only, few, scattered and in row near hinge; cardinal process trilobate, sessile, curved dorsally with broad median lobe; adductors obscurely dendritic; lateral ridges extending along hinge. *U. Carb.(Penn.) - L. Perm.*, Eu. (Alps - USSR) - Asia (China)-N.Am.-S.Am.——FIG. 366,*2*. **C gruenewaldti* (KROTOV), U.Carb.(Moscov.), USSR; *2a-c*, ped.v. vent., post., lat.; *2d*, ped.v. ear with spines; *2e*, brach.v. ext.; all ×0.7 (492).

Costiferina MUIR-WOOD & COOPER, 1960, p. 277 [**Productus indicus* WAAGEN, 1884, p. 687; OD].

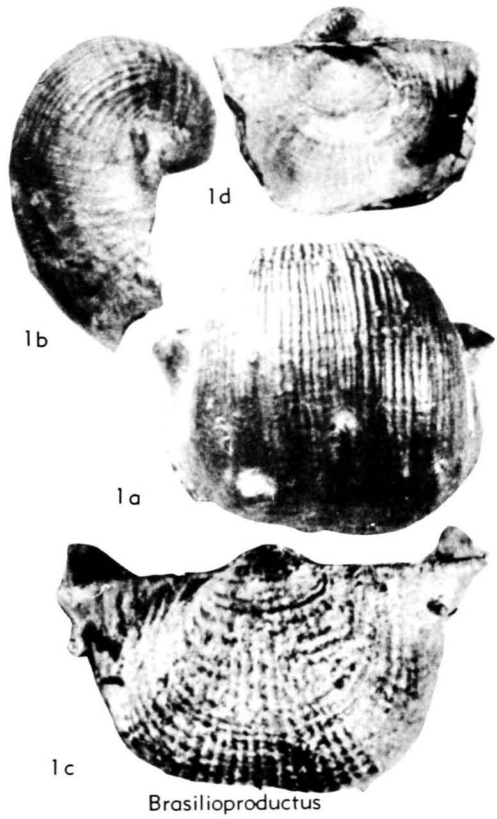

FIG. 365. Dictyoclostidae (Dictyoclostinae) (p. *H*495).

Like *Dictyoclostus* but shell thickened, valves geniculated, visceral disc strongly reticulated; spines few, coarse, erect, scattered, in row near hinge and near ears, absent on brachial valve; cardinal process sessile, trilobed, dorsally inclined; lateral ridges extending down lateral margin of visceral disc. *L.Perm.-U.Perm.*, Asia(Pak.-Himalayas).——FIG. 366,*1*. **C. indica* (WAAGEN), Pak.; *1a-d*, ped.v. vent., ant., lat., post.; *1e,f*, brach.v. int., lat.; all ×0.7 (845).

Peniculauris MUIR-WOOD & COOPER, 1960, p. 278 [**Productus ivesi* R. E. KING, 1931, p. 69 (*non* NEWBERRY, 1861) (=**Peniculauris mckeei* MUIR-WOOD & COOPER, 1960, p. 280; OD]. Like *Dictyoclostus* but valves geniculated, visceral disc slightly reticulate; costae nodose, replaced by overlapping laminae, possibly representing successive trails anteriorly; spines numerous, fine, erect, or suberect, scattered, and in rows along hinge and group on ears; brachial valve with spines, cardinal process trilobate, median lobe with pit; lateral ridges extending across ears. *L.Perm.*, N.Am.-S.Am.——FIG. 366,*4*. **P. mckeei*, L.Perm. (Leonard.), USA(W.Tex.); *4a-c*, ped.v. vent., post., lat., ×0.7; *4d,e*, brach.v. ext., int., ×0.7 (470).

Pugilis Sarycheva, 1949, p. 104 [**Producta pugilis* Phillips, 1836, p. 215; OD] [=*Pugilus* Sarycheva in Sarycheva & Sokolskaya, 1952, p. 77 (obj.)]. Medium-sized to large, nongeniculated; ornament of irregular costae, rugose posteriorly with slight reticulation; brachial valve similar, anteriorly lamellose with broken-off ends of successive trails; spines in pedicle valve scattered, large diameter, 2 rows on ears, longitudinal fluting below spines on trail; lateral ridges extending down lateral margin of visceral disc. *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.——Fig. 366,*3*. **P. pugilis* (Phillips), Visean; Eng. *(3a-c,e)*, Namur., Scot. *(3d)*; *3a-c*, ped.v. vent., post., lat.; *3d*, brach.v. view; *3e*, brach.v. int.; all ×0.7 (574).

Reticulatia Muir-Wood & Cooper, 1960, p. 284 [**Productus huecoensis* R. E. King, 1931, p. 68;

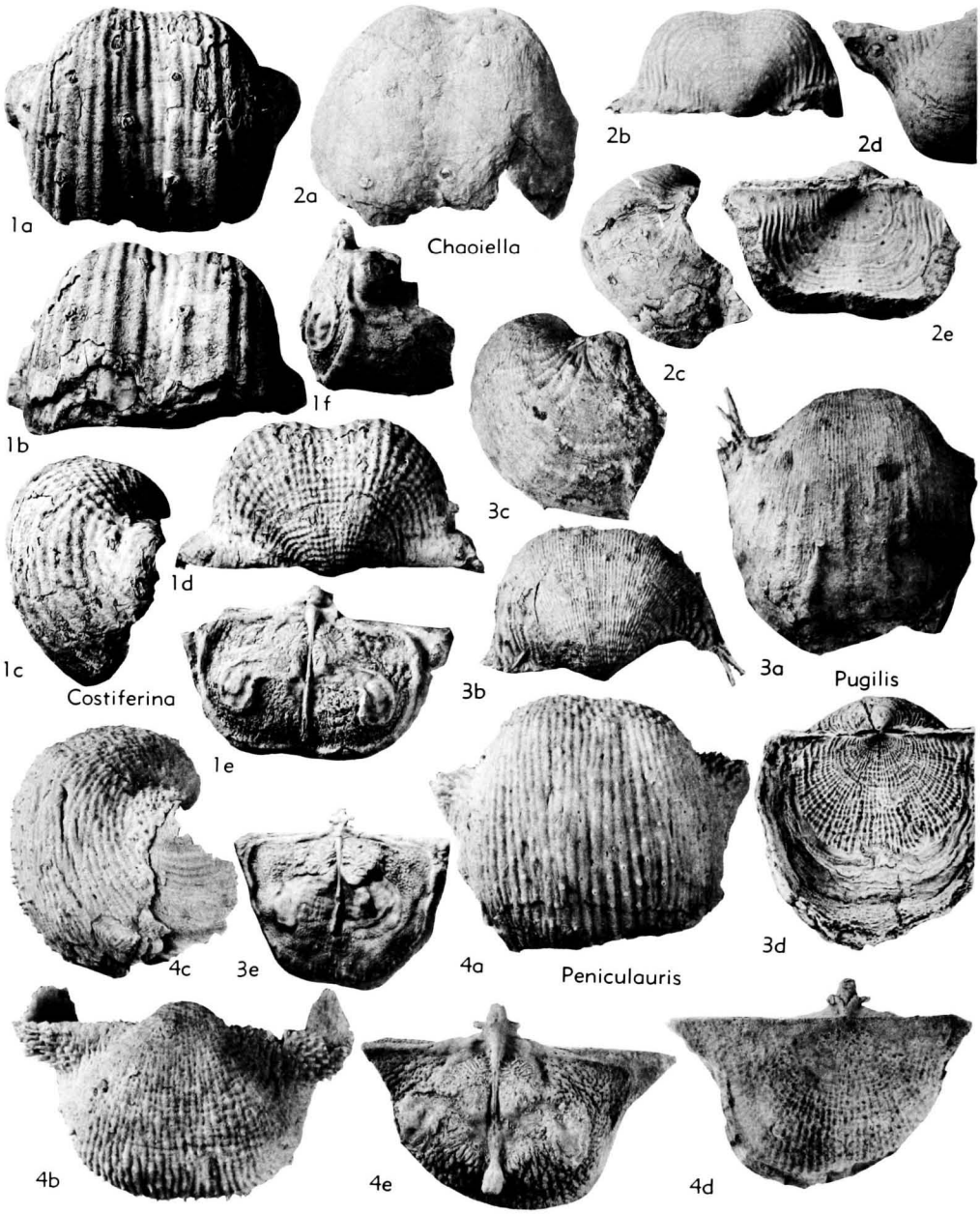

Fig. 366. Dictyoclostidae (Dictyoclostinae) (p. *H*495-*H*496).

OD]. Like *Dictyoclostus* but with valves geniculated, body cavity narrow, ginglymus developed, reticulation prominent on visceral disc, overlapping lamellae on pedicle valve trail; spines small, scattered, in row near hinge and row up flanks; brachial valve with rare spines; cardinal process trilobed with broad median lobe, V-shaped lophidium; lateral ridges short, slightly diverging from hinge. *U.Penn.-L.Perm.*, N.Am. ——Fig. 367,*1*. **R. huecoensis* (King), L.Perm., USA(W.Tex.); *1a-c,* ped.v. vent., post., lat., ×0.8; *1d,* brach.v. view showing ginglymus, ×0.8; *1e,* brach.v. int., ×1.2 (470).

Rugatia Muir-Wood & Cooper, 1960, p. 285 [**Productus paraindicus* McKee, 1938, p. 241; OD]. Medium-sized to large, both valves geniculated, ginglymus present; costae ill-defined, rugae faint posteriorly; spines scattered, and 1 or 2 rows near hinge, in group on ears; brachial valve costate, dimpled, no spines; cardinal process with median sulcate lobe, small lophidium; lateral ridges short, slightly curved. *L.Perm.*, N.Am.—— Fig. 368,*1*. **R. paraindica* (McKee), L.Perm. (Leonard.), USA(W.Tex.); *1a-c,* ped.v. vent. view of 2 specimens, ant.; *1d,* brach.v. view; *1e,* brach.v. int.; all ×1 (548).

Spinifrons Stehli, 1954, p. 318 [**S. quadratus*; OD]. Like *Antiquatonia* in external form but with ginglymus developed, costae more irregular, spines erect, in group on ears near hinge and numerous on trail; brachial valve with fine erect spines; small trilobate cardinal process; fine, short, slightly curving lateral ridges. *L.Perm.*, N.Am. ——Fig. 369,*1*. **S. quadratus,* Leonard., USA(W. Tex.); *1a-c,* ped.v. vent., post., lat.; *1d,* brach.v. view; *1e,* brach.v. int.; all ×1 (773).

Squamaria Muir-Wood & Cooper, 1960, p. 287 [**S. moorei*; OD]. Like *Pugilis* in external form but with ginglymus; no repetition of trails in brachial valve but successive laminae in pedicle valve anteriorly replacing costae; rugae narrow, spines numerous, scattered, and in rows near hinge and group on ears; numerous spines on brachial valve; cardinal process sessile, inclined dorsally, with broad median and diverging lateral lobes; lateral ridges extending inside ears. *L. Perm.*, N.Am.——Fig. 370,*1*. **S. moorei,* USA (Tex.); *1a-d,* ped.v. vent., ant., post., lat., ×1; *1e,* brach.v. view, ×1; *1f,* brach.v. int., ×1; *1g,* ped.v. int., ×1.5 (*1b,e,* holotype; others paratypes) (587).

Tolmatchoffia Frederiks, 1933, p. 28 [**Productus robustus* Tolmachev, 1924, p. 230; OD]. [May be synonym of *Dictyoclostus.*] *L.Carb.(Tournais.),* Eu.(USSR)-Asia(Sib.).

Tyloplecta Muir-Wood & Cooper, 1960, p. 290 [**Productus scabriculus* mut. *nankingensis* Frech, 1911; OD]. Medium-sized to large, subquadrate; pedicle valve with strongly curved trail; ginglymus present; large body cavity; costae coarse, irregular, rugae numerous, prominently reticulate; spines rare anteriorly, in row near

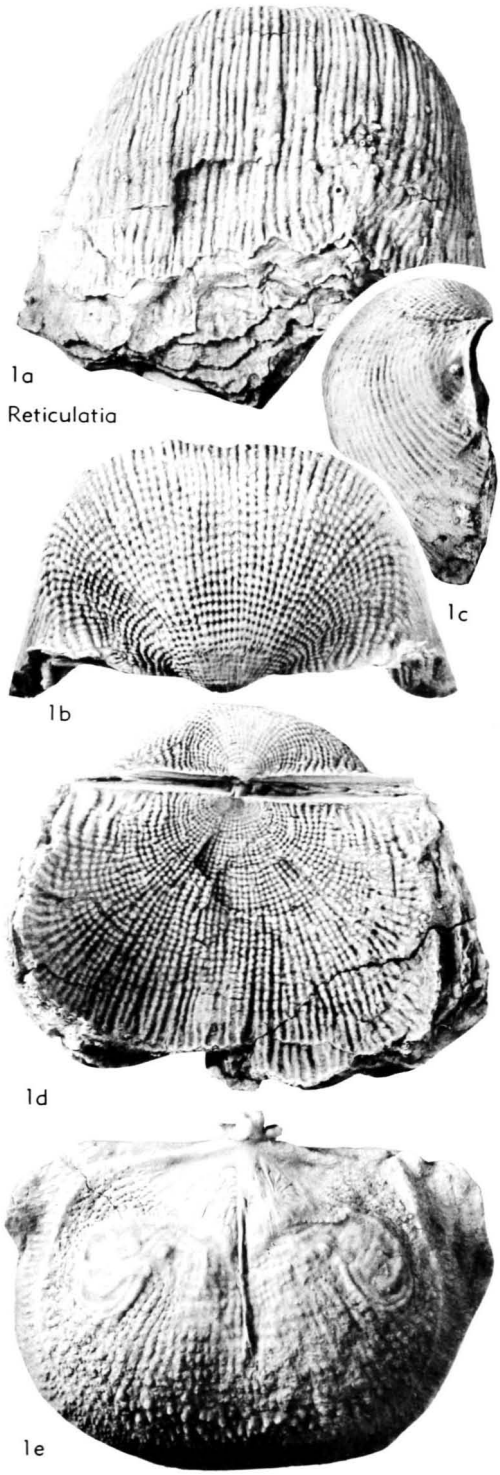

Fig. 367. Dictyoclostidae (Dictyoclostinae) (p. H496-*H*497).

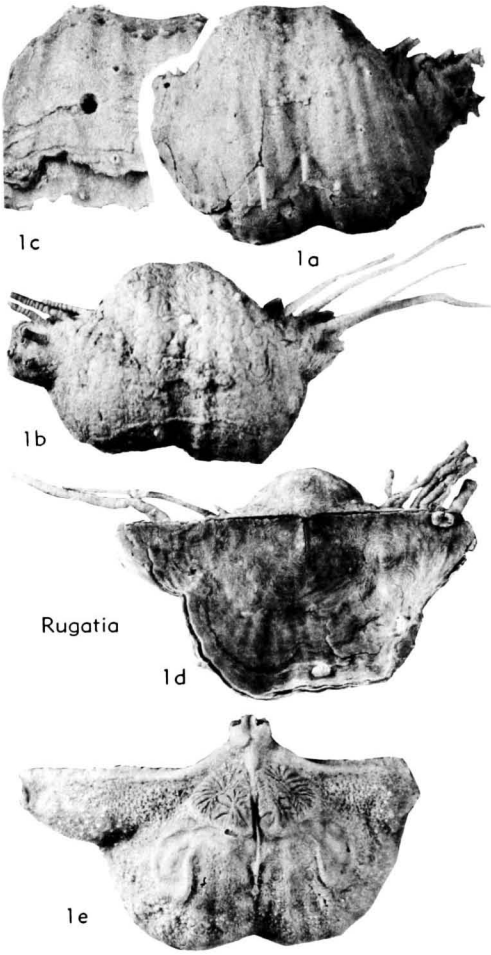

FIG. 368. Dictyoclostidae (Dictyoclostinae) (p. *H*497).

hinge, curved row inside ears and scattered; brachial valve similar in reverse, rare spines and valve capillate; cardinal process sessile, dorsally deflected, trilobate; lateral ridges extending to lateral margin. *L.Perm.-U.Perm.*, Asia(Sumatra-China); U.Perm., Eu.(USSR-Yugosl.). —— FIG. 370,*2*. **T. nankinensis* (FRECH), Perm., China; *2a,b*, ped.v. vent., post., ×1; *2c*, brach.v. view, ×1; *2d,e*, brach.v. int., lat., ×1; *2f*, brach.v. ext. showing capillate ornament, ×2 (313).

Subfamily HORRIDONIINAE Muir-Wood & Cooper, 1960

[Horridoniinae MUIR-WOOD & COOPER, 1960 (November), p. 292] [=Horridoniidae SARYCHEVA, 1960 (December), p. 234]

Costae and rugae usually lacking, spine rows near hinge in both valves; adductors dendritic, posteriorly placed. *Perm.*

Horridonia CHAO, 1927, p. 24 [**Productus horridus* J. SOWERBY, 1822, p. 17; SD SCHUCHERT & LEVENE, 1929, p. 68] [=*Sowerbina* FREDERIKS, 1928, p. 789 (type, *Productus timanicus* STUCKENBERG, 1875, p. 86); *Pleurohorridonia* DUNBAR, 1955 (type, *P. scoresbyensis*)]. Medium-sized to large; pedicle valve strongly curved, brachial valve slightly concave, anteriorly geniculated; valves smooth with numerous growth lines or pedicle valve rarely costate anteriorly; spines scattered in pedicle valve and in 2 or 3 rows near hinge and on ears, spines in single row on brachial valve and 1 or 2 spines on ears, rare elsewhere; cardinal process large, trilobate; lateral ridges short, divergent. *L. Perm.-U. Perm.*, Eu.-Arctic-Asia-Australia. ——FIG. 371,*1*. **H. horrida* (J. SOWERBY), U. Perm., Ger. *(1a-f)*, Eng. *(1g)*; *1a-d*, ped.v. vent., post., lat., ant., ×1; *1e*, brach.v. view, ×2; *1f*, ped.v. p st. showing spines, ×1; *1g*, brach.v. int., ×1 (587).

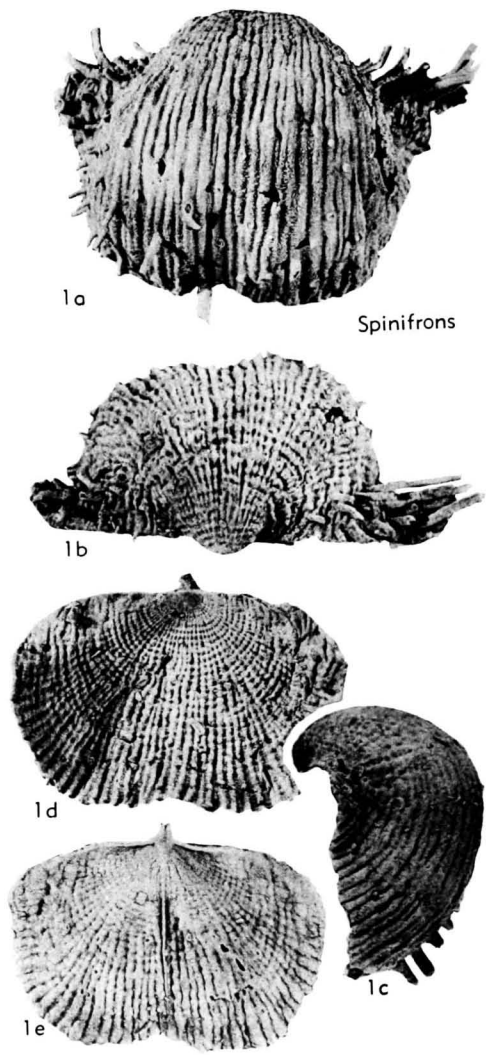

FIG. 369. Dictyoclostidae (Dictyoclostinae) (p. *H*497).

Subfamily LEVITUSIINAE Muir-Wood & Cooper, 1960

[Levitusiinae Muir-Wood & Cooper, 1960, p. 295]

Valves faintly costellate and posteriorly rugose, with few spines; deep cavities in pedicle valve representing position of lophophore spirals; brachial ridges given off obliquely, cardinal process large, trilobate with tapering lateral lobes. *L.Carb.(Visean).*

Levitusia Muir-Wood & Cooper, 1960, p. 295 [**Productus humerosus* J. Sowerby, 1822, p. 21; OD]. Large, each valve with long trail, pedicle

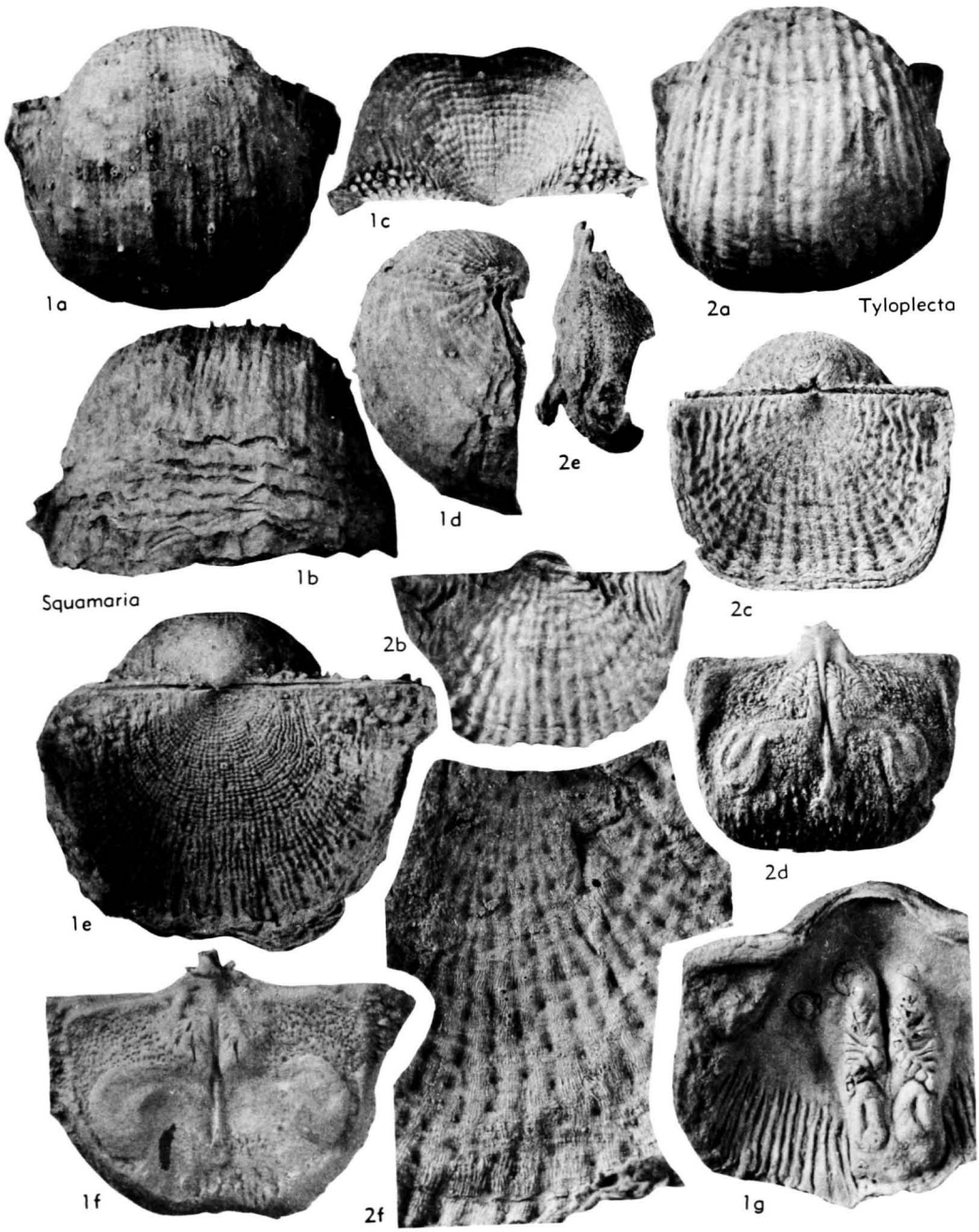

Fig. 370. Dictyoclostidae (Dictyoclostinae) (p. *H*497-*H*498).

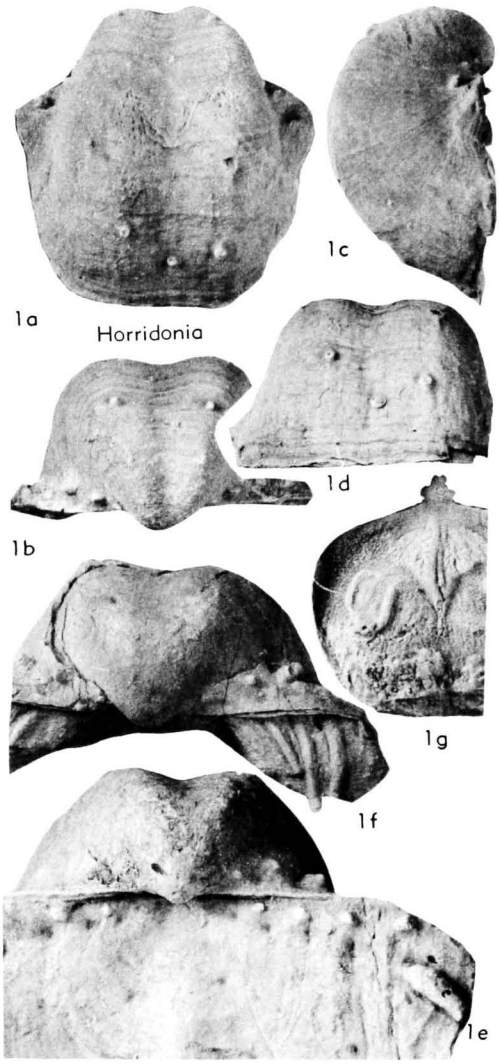

FIG. 371. Dictyoclostidae (Horridoniinae) (p. H498).

valve thickened, may bear median longitudinal fold; costellae appearing as striations or pits if shell is decorticated, lamellose on trail; spines rare, scattered, in row on median ridge, in row in sulcus demarcating ears and rarely on ears; brachial valve without spines. *L.Carb.(Visean)*, Eu.(Eng.-Belg.-Fr.)-Asia.——FIG. 372,*1*. **L. humerosa* (J. SOWERBY), Visean, Belg. *(1a-c)* and Eng. *(1d,e)*; *1a-c*, ped.v. oblique vent., lat., post.; *1d,e*, brach.v. int., post. and ant. views; all ×1 (483).

[**Subfamily Uncertain—Rugoclostus**, *see* p. H904.]

Family LINOPRODUCTIDAE Stehli, 1954

[*nom. transl.* MUIR-WOOD & COOPER, 1960, p. 296 (*ex* Linoproductinae STEHLI, 1954, p. 319)]

Valves costellate and rugose, with rows of fine spines near hinge; trilobate sessile cardinal process with widely separated lobes; small body cavity; dendritic adductors posteriorly placed; obscure brachial ridges. *L. Carb.(L.Miss.-U.Miss.)-U.Perm.*

Subfamily LINOPRODUCTINAE Stehli, 1954

[Linoproductinae STEHLI, 1954, p. 319]

Hinge wide, trail normally long. *L.Carb. (L.Miss.)-U.Perm.*

Linoproductus CHAO, 1927, p. 25 [**Productus cora* D'ORBIGNY, 1842, p. 55; OD] [=*Cora* FREDERIKS, 1928, p. 781 (obj.); *Euproductus* WHITEHOUSE, 1928, p. 281 (obj.)]. Small to large, geniculated; both valves irregularly costellate, rugae as broad wrinkles on flanks and ears, better developed in brachial valve; spines scattered, prostrate or suberect, and in 1 or 2 rows at high angle to hinge, rare in brachial valve; prominent lamellae interrupting costellae in brachial valve and representing internal diaphragms and broken off ends of trails; cardinal process trilobate, with sulcate median lobe; alveolus present; lateral ridges short, diverging from hinge; second pair of ridges bounding posterior part of adductors. *?L.Carb. (L.Miss.-U.Perm.)*, N.Am.-S.Am.-Eu.-Asia-N.Afr.-Australia.——FIG. 373,*2a-d*. **L. cora* (D'ORBIGNY), L.Perm., Bol.; *2a-c*, ped.v. vent., lat., post., ×1; *2d*, brach.v. view, ×1 (485).——FIG. 373, *2e*. *L. prattenianus* (NORWOOD & PRATTEN), U. Penn., USA(Tex.); brach.v. int., ×1 (485).——FIG. 373,*2f*. *L.* sp., U.Penn., USA(N.Mex.); brach. v. view, ×2 (485). [See Fig. 303. *L.* sp.; diagrams of card. process, int., oblique ext., ext., ×2 (485).]

Anidanthus HILL, 1950, p. 9 [**Linoproductus springsurensis* BOOKER, 1932, p. 67; OD] [=*Anidanthus* WHITEHOUSE, 1928, p. 282 *(nom. nud.)*; *?Pseudomarginifera* STEPANOV, 1934, p. 56 (type, *Productus ussuricus* FREDERIKS, 1924, p. 8)]. Medium-sized, geniculated; ornament of costellae, rugose posteriorly, spines rare, scattered, in row near hinge; brachial valve with lamellae interrupting costellae, possibly representing broken-off ends of successive trails; cardinal process sessile, quadrilobate; adductors smooth; lateral ridges extending to anterior margin of visceral disc. *U. Carb. - L. Perm.*, Asia-Arctic-Eu.-Australia-N. Am. ——FIG. 373,*4*. **A. springsurensis* (BOOKER), New S.Wales; *4a*, ped.v. vent., ×2; *4b,c*, brach.v. ext., int., ×2, ×3; *4d*, ped.v. int. mold, ×2 (861).

Balakhonia (*see* p. H903).

Cancrinella FREDERIKS, 1928, p. 784 [**Productus cancrini* DE VERNEUIL, 1845, p. 273; OD]. Small to medium-sized, brachial valve usually geniculated; costellate, rugose on flanks and ears; spines numerous, commonly quincuncially arranged on swollen costae and in group on flanks and ears; brachial valve without spines, dimpled, costellate and rugose; cardinal process sessile, in-

ternally bilobate; adductors obscurely dendritic, lateral ridges short, divergent from hinge. *U.Carb.(Penn.)-Perm.*, Eu.-Asia-Australia-N.Am.——FIG. 373,*1a-c*. *C. altissima* R. H. KING, U.Penn., USA (Tex.); *1a,b*, ped.v. vent., post., ×2, ×1; *1c*, brach.v. view, ×2 (483).——FIG. 373,*1d-f*. *C. boonensis* (SWALLOW), U.Penn., USA(Tex.); *1d,e*, ped.v. vent., lat., ×2; *1f*, brach.v. int., ×3 (483).

Cancrinelloides (*see* p. H903).

Fluctuaria MUIR-WOOD & COOPER, 1960, p. 303 [**Productus undatus* DEFRANCE, 1826, p. 354; OD]. Small or medium-sized; costellate and rugose, rugae prominent on entire valve; spines erect, rare, in 2 rows near hinge and group on ears, absent on brachial valve; cardinal process minute, sessile, bilobate; lateral ridges along hinge margin. *L.Carb.(Visean)*, Eu.(Eng.-Eire-Belg.-Fr.-USSR).——FIG. 373,*3*. **F. undata* (DEFRANCE), Belg.; *3a-c*, ped.v. vent., lat., post., ×2; *3d*, brach.v. view, ×2 (587).

Globiella MUIR-WOOD & COOPER, 1960, p. 304 [**Productus hemisphaerium* KUTORGA, 1844, p. 99; OD] [=*Stepanoviella* ZAVODOVSKY, 1960 (type, *S. paracurvata*) (possibly a senior synonym)]. Medium-sized, nongeniculate, costellate, rugose near hinge; spines rare, in row along hinge and on ears, absent on brachial valve; cardinal process small, sessile, trilobate, median lobe with central pit; adductors smooth; lateral ridges short, curving down from hinge; pedicle valve with low ridges extending from umbo to inside ears. *L. Perm.-U.Perm.*, Eu.(USSR)-Arctic-Asia(China-India-Armenia).——FIG. 374,*1*. **G. hemisphaerium* (KUTORGA), U.Perm.(Kazan), USSR; *1a,b*, ped.v. vent., lat., ×1; *1c,d*, ped.v. int., brach.v. int., ×1; *1e*, card. process post. view, ×2 (587).

Marginirugus SUTTON, 1938, p. 559 [**Productus magnus* MEEK & WORTHEN, 1862, p. 142; OD]. Large, brachial valve geniculated; costae irregularly developed, rugae near hinge, spines recumbent, scattered, in one or more rows extending at high angle to hinge margin, absent in brachial valve; cardinal process large, trilobate, broad sulcate median lobe; adductors dendritic; lateral ridges extending around ears. *L.Carb.(Miss.)*, N. Am.-Australia.——FIG. 375,*3*. **M. magnus* (MEEK & WORTHEN), L.Miss.(Osag.), Ill. *(3a-c,e,f)*, Mo. *(3d)*; *3a-c*, ped.v. vent. with spines along hinge, post., lat.; *3d*, brach.v. int.; *3e,f*, card. process, int. and ext. views; all ×1 (795).

Megousia MUIR-WOOD & COOPER, 1960, p. 309 [**M. auriculata*; OD]. Like *Anidanthus* but with larger ears, commonly with crescentic extensions in brachial valve and radial ornament on ears cutting across concentric lamellae of remainder of valve; cardinal process trilobate or quadrilobate on short massive shaft; adductors obscure; lateral ridges divergent, extending as flattened rims down lateral margin of visceral disc. *L.Perm.*, N.Am.-S.Am.——FIG. 375,*1a-d*. **M. auriculata*, USA(W. Tex.); *1a*, ped.v. vent., ×2; *1b,c*, brach.v. views showing alae, ×1, ×4; *1d*, brach.v. int., ×3

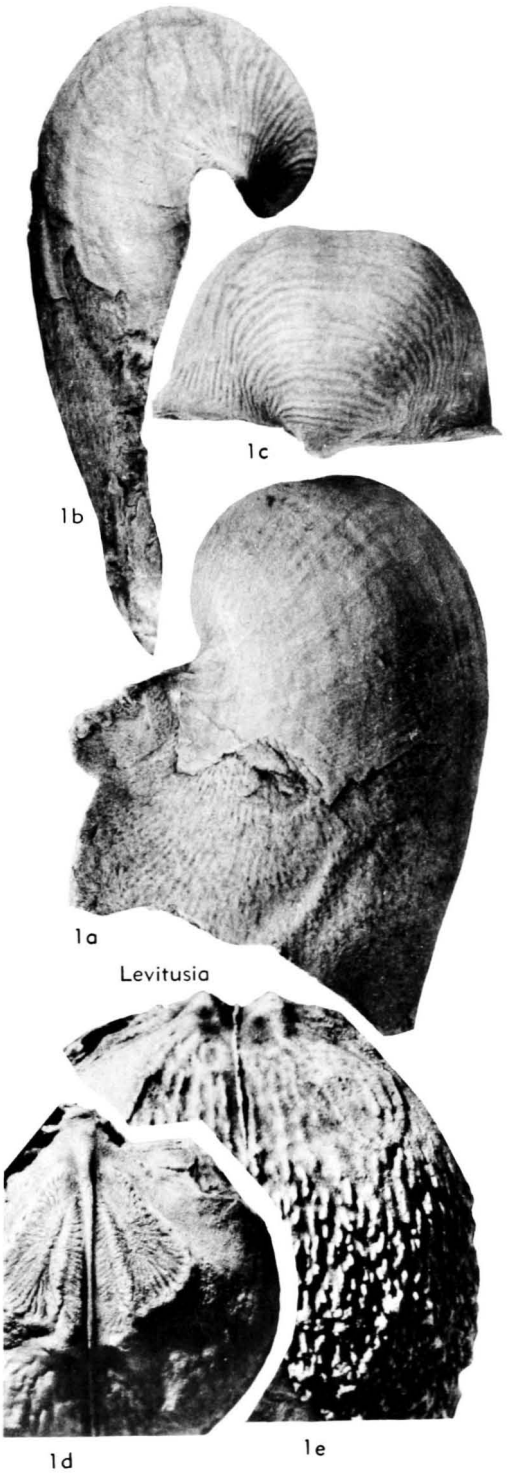

FIG. 372. Dictyoclostidae (Levitusiinae) (p. H499-H500).

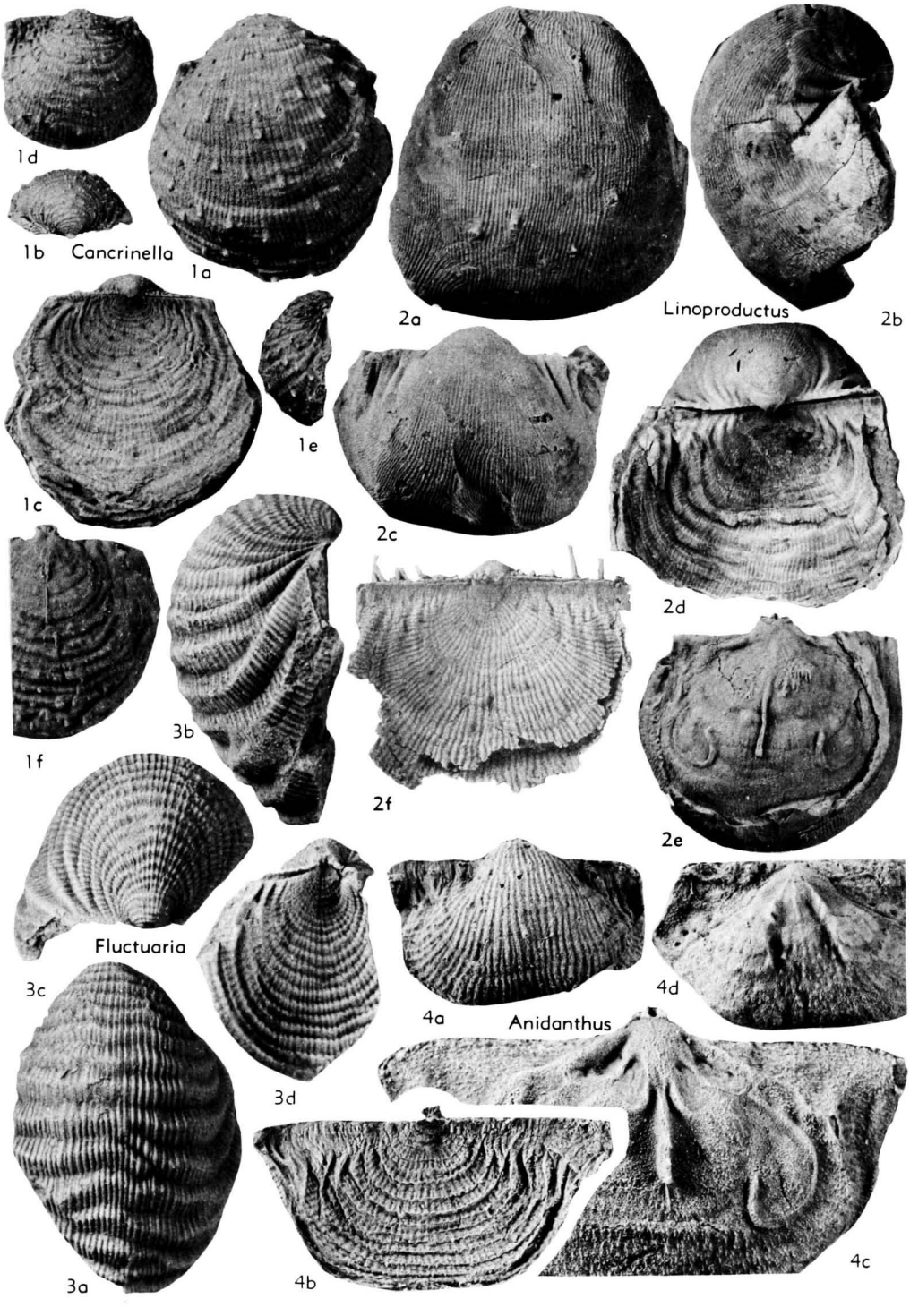

FIG. 373. Linoproductidae (Linoproductinae) (p. *H*500-*H*501).

(587).——FIG. 375,*1e,f. M. alata* (COOPER), Mex.; *1e*, ped.v. vent., ×4; *1f*, brach.v. view, ×3 (587).

Ovatia MUIR-WOOD & COOPER, 1960, p. 311 [**O. elongata*; OD]. Medium-sized to large, narrow body cavity, long trail; brachial valve with no repetition of trails or diaphragms; costellate, few rugae on flanks, spines rare, scattered, 1 or 2 rows near hinge, group on ears, absent or rare on brachial valve; cardinal process trilobate, minute median lobe; adductors part dendritic; lateral ridges short, slightly diverging from hinge. *L.Carb. (L.Miss.-U.Miss.)*, N. Am.-Eu.(USSR)-Asia (Kazakhstan).——FIG. 374,*2*. **O. elongata*, U.Miss. (Chester.), USA(Okla.); *2a-c*, ped.v. vent., lat., post. (*2a-c*, holotype), ×1; *2d*, brach.v. int. with card. process, ×1 (382).

Pseudomarginifera STEPANOV, 1934, p. 56 [**Productus ussuricus* FREDERIKS, 1924; OD]. [May be synonym of *Anidanthus*.] *L.Perm.*, Asia.

Terrakea BOOKER, 1930, p. 66 [**Productus brachythaerus* MORRIS, 1845, p. 284 (*non* G. B. SOWERBY, 1844, p. 158; SD MAXWELL, 1956, p. 333 (ICZN pend.)]. Medium-sized, may be geniculated; cicatrix of attachment present; irregularly costellate, obscure rugae, spines fine, long, prostrate, on costae, in group of more erect spines near hinge and on ears, scattered on brachial valve; cardinal process stout, erect, posteriorly quadrilobate; adductors finely dendritic, lateral ridges short extending along hinge margin. *L. Perm.*, Australia.——FIG. 375,*2a-d*. **T. brachythaerum* (MORRIS), Australia(New S.Wales); *2a,b*, ped.v. lat., post., ×1; *2c,d*, brach.v. views, ×1 (90).——FIG. 375,*2e,f*. *T. fragile* (DANA), Australia(New S.Wales); *2e*, brach.v. int., ×2; *2f*, ped.v. vent., with spines, ×1 (90).

Undaria MUIR-WOOD & COOPER, 1960, p. 317 [**U. manxensis*; OD]. Like *Fluctuaria* but more elongate and body cavity very narrow; rugae more numerous, flexuous and narrower, interrupting costellae, spines more numerous, scattered on rugae, 2 rows near hinge, spines represented in brachial valve by dimples; lateral ridges short, curved; cardinal process bilobate or quadrilobate. *L.Carb.(Visean)*, Eu.——FIG. 374,*3*. **U. manxensis*, Eng. (I. of Man); *3a*, ped.v. vent., ×2; *3b,c*, brach.v. with ext. layer removed, dors. and lat. views, ×2; *3d*, brach.v. int., ×4 (*3a,b,d*, holotype) (587).

Subfamily PROBOSCIDELLINAE Muir-Wood & Cooper, 1960

[Proboscidellinae MUIR-WOOD & COOPER, 1960, p. 325]

Trail of pedicle valve forming tube; cardinal process bilobate; external cincture in pedicle valve corresponding to low internal marginal ridge. *L.Carb.(Visean)*.

Proboscidella OEHLERT, 1887, p. 1277 [**Productus proboscideus* DE VERNEUIL, 1840, p. 259; OD]. Medium-sized; pedicle valve elongate, tubular;

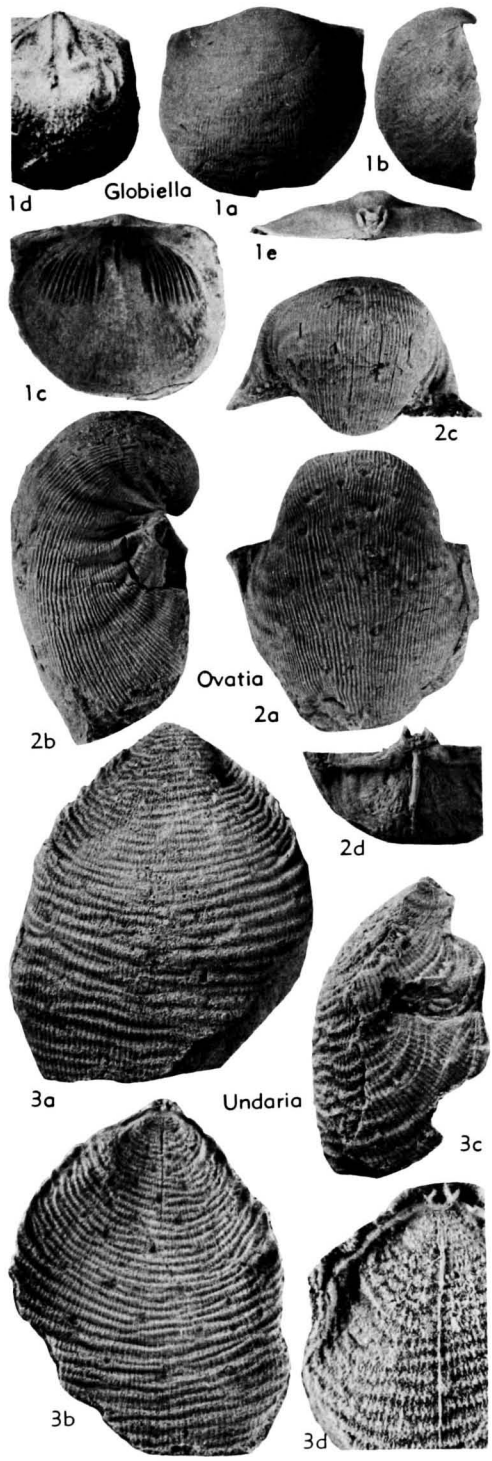

FIG. 374. Linoproductidae (Linoproductinae) (p. *H*501, *H*503).

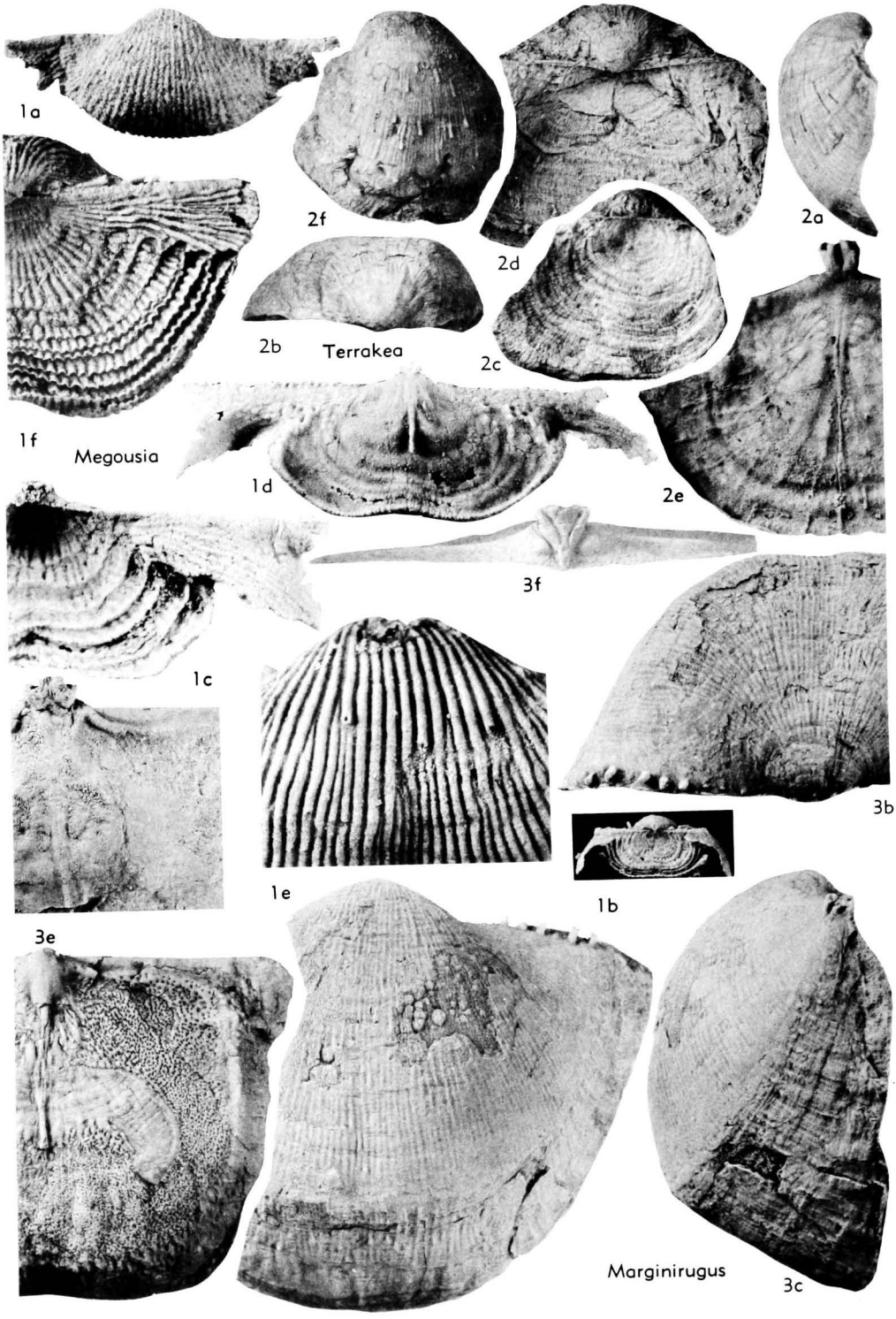

FIG. 375. Linoproductidae (Linoproductinae) (p. *H*501, *H*503).

cicatrix of attachment present; brachial valve opercular, rarely tubular, cincture around anterior margin; costellae and rugae on entire shell, spines on pedicle valve only, rarely on rugae, in row or group on flanks probably for attachment, and row at angle to hinge margin; cardinal process bilobate; lateral ridges short, diverging from hinge. *L.Carb.(Visean)*, Eu.-Asia.——Fig. 376,*1*. **P. proboscidea* (deVerneuil), Belg.; *1a*, ped.v. with cincture and long tube; *1b*, ped.v. lat. view with part of brach.v.; *1c*, lat. view of valves showing cincture; *1d*, ped.v. with clasping spines; *1e*, brach.v. int.; all ×3 (611).

Subfamily MONTICULIFERINAE Muir-Wood & Cooper, 1960

Valves with ornament of pustules (monticules) interrupting costellae or capillae; cardinal process short-shafted, trilobate, with minute lophidium. *L.Perm., ?U.Perm.*

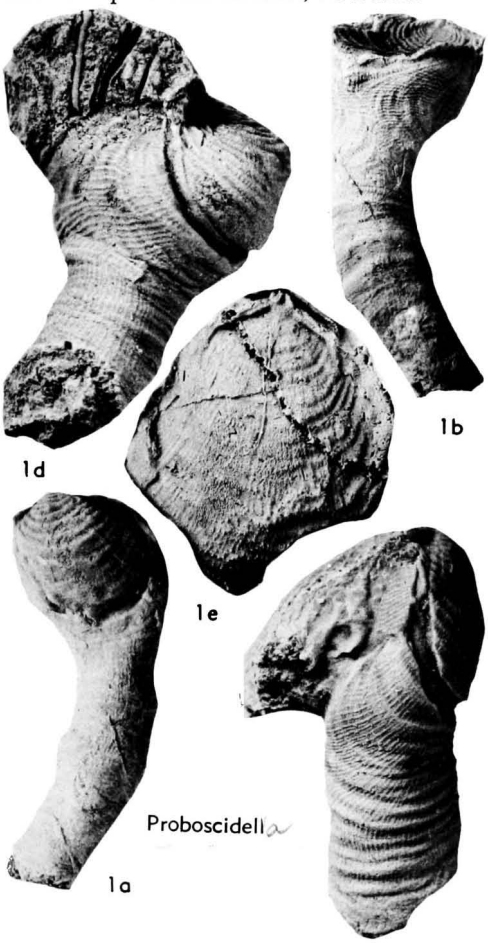

Fig. 376. Linoproductidae (Proboscidellinae) (p. *H*503, *H*505).

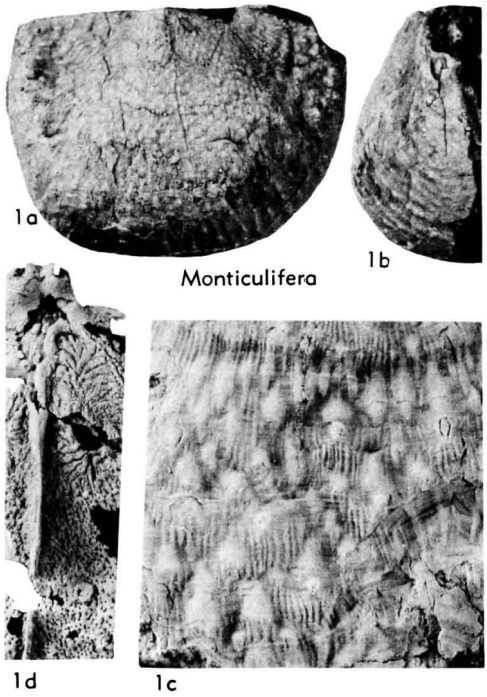

Fig. 377. Linoproductidae (Monticuliferinae) (p. *H*505).

Monticulifera Muir-Wood & Cooper, 1960, p. 327 [**Productus intermedius* Abich var. *sinensis* Frech, 1911, p. 176; OD]. Medium-sized to large, subquadrate in outline, geniculated; capillate with prostrate spines umbonally, monticules possibly bearing spines medianly, costellate anteriorly; spines prostrate scattered and more erect in row along hinge; brachial valve capillate with capillate monticules, no spines; adductors dendritic; lateral ridges extending along hinge. *L.Perm., ?U. Perm.*, Asia (Indo China - Manchuria - China). ——Fig. 377,*1*. **M. sinensis* (Frech), China; *1a,b*, ped.v. vent., lat., ×1; *1c*, ped.v. ext. ornament, ×3; *1d*, brach.v. int., ×2 (313). [*See* p. *H*904.]

Subfamily PAUCISPINIFERINAE Muir-Wood & Cooper, 1960

[Paucispiniferinae Muir-Wood & Cooper, 1960, p. 319]

Valves with ornament of costae or capillae, and 4 to 6 halteroid spines, cardinal process sessile, trilobate, dorsally recurved; zygidium present in some species. *U.Carb. (Penn.)-U.Perm.*

Paucispinifera Muir-Wood & Cooper, 1960, p. 319 [**P. auriculata*; OD]. Medium-sized, commonly alate, geniculated, with small ginglymus; obscurely costate, large halteroid spines symmetrically placed, row of small spines near ears, spines absent on brachial valve; adductors dendritic and

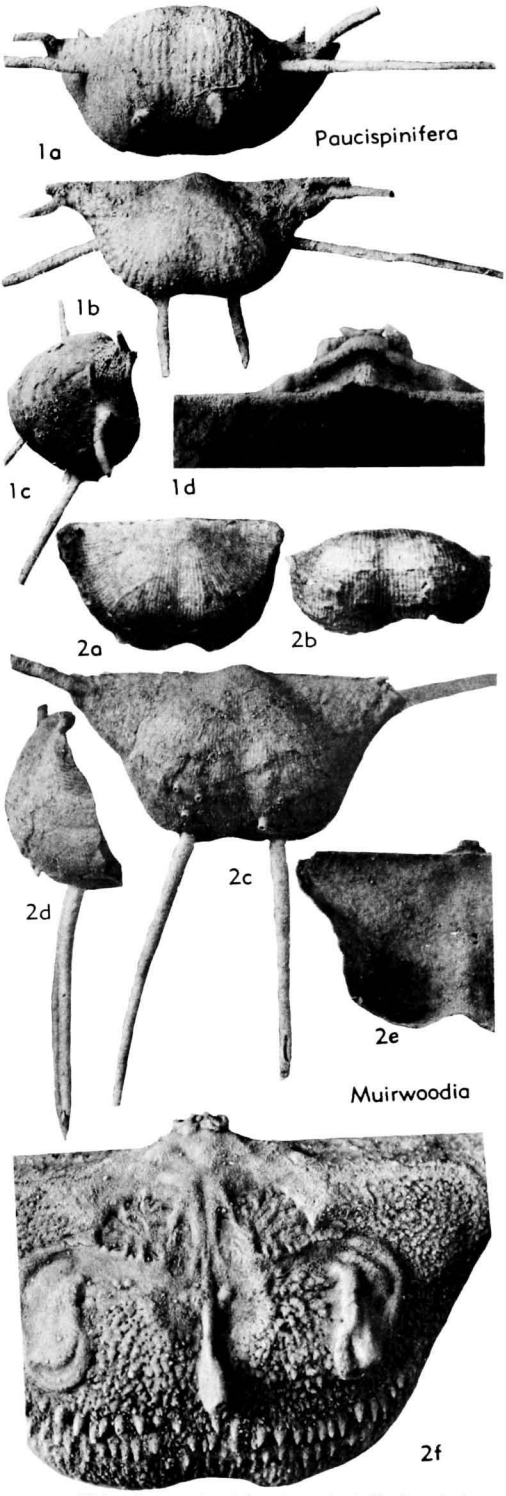

FIG. 378. Linoproductidae (Paucispiniferinae) (p. *H*505-*H*506).

lobate, lateral ridges united medianly by zygidium and extending down lateral margin of visceral disc. *L.Perm.*, N.Am.——FIG. 378,*1*. **P. auriculata*, USA(W.Tex.); *1a-c*, ped.v. with long spines vent., post., lat., ×1 (*1a,b*, holotype); *1d*, card. process and zygidium, ext. view, ×4 (587).

Muirwoodia LIKHAREV, 1947, p. 187 [**Productus mammatus* KEYSERLING, 1846, p. 206; OD]. Small or medium-sized; transverse, geniculated, rare ginglymus; both valves capillate; spines scattered, 4 or 6 symmetrically placed halteroid spines, row near hinge, spines absent in brachial valve; adductors smooth or lobate; lateral ridges parallel to hinge and demarcating accessory sockets. *U. Carb.(Penn.)*, Eu.-S.Am.; *L.Perm.-U.Perm.*, Eu.-Arctic-N.Am.-Asia.——FIG. 378,*2a,b*. **M. mammata* (KEYSERLING), L.Perm., USSR; *2a,b*, ped.v. vent., ant., ×1 (516).——FIG. 378,*2c-g*. *M.* sp. cf. *M. multistriata* (MEEK), L.Perm., USA(W. Tex.); *2c,d*, ped.v. with spines, vent., lat., ×1; *2e,f*, brach.v. ext., int., ×1, ×2 (516). [See Fig. 301 for additional illustrations.]

Yakovlevia FREDERIKS, 1925, p. 7 [**Y. kaluzinensis*; OD]. Large, concavo-convex; pedicle valve with striated interarea and apical callosity filling delthyrium; pedicle valve finely costellate, spine row along hinge, and single spine on ear; adductors smooth; cardinal process sessile, trilobate. *L.Perm., ?U.Perm.*, Arctic-Asia.——FIG. 379,*1a,b*. **Y. kaluzinensis*, L.Perm., Asia(Sib.); *1a,b*, ped. v. int. mold, vent., lat., ×0.7 (889).——FIG. 379,*1c-g*. *Y. impressa* (TOULA), Arctic; *1c,d*, ped. v. vent., lat.; *1e,g*, brach.v. ext., int.; *1f*, ped.v. int.; all ×0.7 (889).

Subfamily STRIATIFERINAE Muir-Wood & Cooper, 1960

[Striatiferinae MUIR-WOOD & COOPER, 1960, p. 328]

Aberrant linoproductids, commonly much elongated and narrow-hinged; cardinal process with single lobe, septum prominent, bladelike, adductors part dendritic. *L.Carb.(Visean)-Perm.*

Striatifera CHAO, 1927, p. 24 [**Mytilus striatus* FISCHER DE WALDHEIM, 1837, p. 181 (=**Pileopsis striatus* PHILLIPS, 1836, p. 224; OD]. Large, shell commonly tapering posteriorly, not geniculated; pedicle valve costellate, rugose near hinge; spines fine, numerous on costae, in group on ears and flanks; brachial valve costellate, no spines; lateral ridges and brachial ridges obscure. *L.Carb. (Visean)*, Eu.-Asia-N. Am.——FIG. 381,*1*. **S. striata* (PHILLIPS), *(1a-c)* Eng., *(1d-f)* USSR; *1a,b*, ped.v. vent., lat., ×0.7; *1c*, brach.v. view, ×0.7; *1d*, ped.v. with spine bases, lat., ×1.3; *1e,f*, brach.v. int., front and lat. views showing single-lobed card. process and adductor muscle scars, ×0.7 (587).

Compressoproductus SARYCHEVA, 1960, p. 231 [**Productus compressus* WAAGEN, 1884, p. 710; OD]. Trigonal in outline, tapering to umbo,

ornament of capillae and irregular rugae on both valves, spines fine on flanks of pedicle valve, and row near posterior commissure; cardinal process

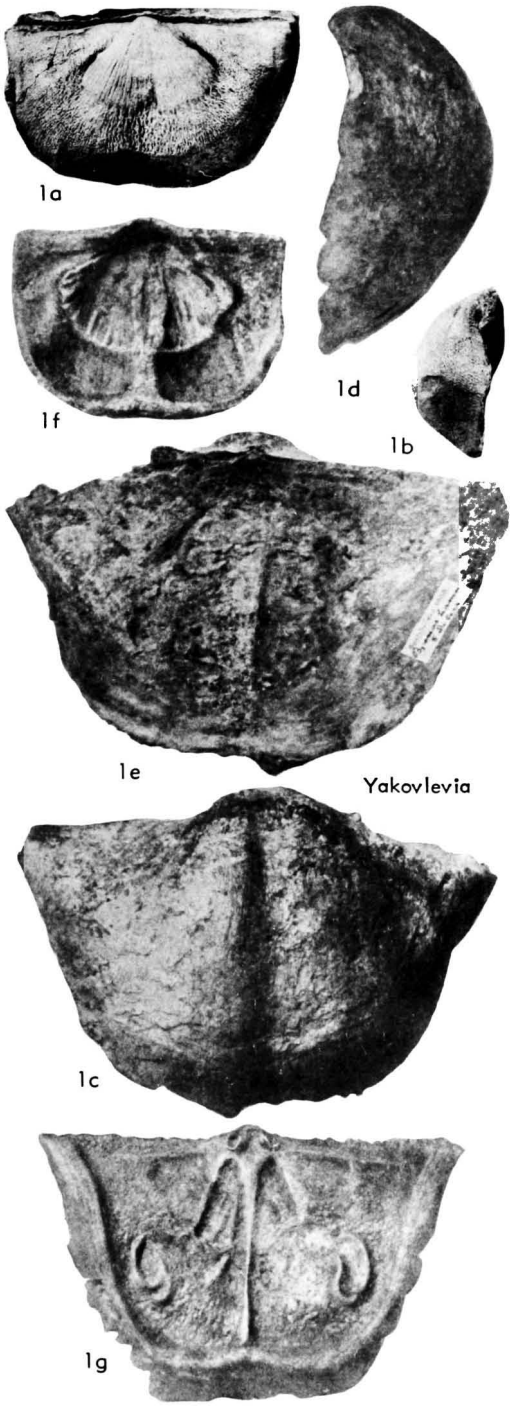

FIG. 379. Linoproductidae (Paucispiniferinae) (p. *H*506).

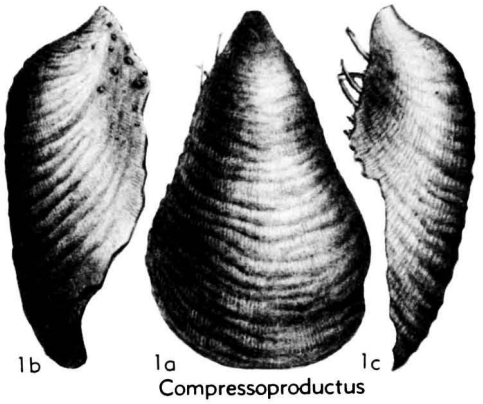

FIG. 380. Linoproductidae (Striatiferinae) (p. *H*506-*H*507).

one-lobed as in *Striatifera*. *Perm.*, Eu.-Greenl.-Asia-Australia-S.Am.——FIG. 380,*1*. **C. compressus* (WAAGEN), Pak.; *1a-c*, ped.v. vent., lat. from left, lat. from right showing spines, ×0.8 (845).

Family GIGANTOPRODUCTIDAE Muir-Wood & Cooper, 1960

[Gigantoproductidae MUIR-WOOD & COOPER, 1960, p. 330]

Large, usually thick-shelled, wide-hinged, with thin body cavity, interarea rare; cardinal process bilobed or trilobed, or modified with one lobe, lophidium present; adductors highly dendritic or smooth. *U.Dev.-U.Carb. (Namur.)*.

Subfamily GIGANTOPRODUCTINAE Muir-Wood & Cooper, 1960

[Gigantoproductinae MUIR-WOOD & COOPER, 1960, p. 330]

Pedicle valve rarely having ginglymus, adductors highly dendritic. *L.Carb.(Visean)*.

Gigantoproductus PRENTICE, 1950, p. 437 [*pro Gigantella* SARYCHEVA, 1928, p. 13 (*non* EKMAN, 1905)] [**Anomites giganteus* W. MARTIN, 1793, 1809 (declared invalid ICZN) =**Productus giganteus* J. SOWERBY, 1822, p. 19; SD MUIR-WOOD, 1951, p. 98 (species validated and SD confirmed, ICZN, 1956, Op. 420, p. 135)]. Large to gigantic, thick-shelled, not geniculated; irregularly costate, rugose near hinge, may be longitudinally fluted, spines scattered, row near hinge; adductors markedly dendritic; flattened rim replacing lateral ridges along hinge; rounded elevations in brachial valve and hollows in pedicle valve representing the position of the lophophore spirals; cardinal process trilobate or quadrilobate. *L.Carb.(Visean)*, cosmop., rare in N.Am.——FIG. 382,*1*. **G. giganteus* (J. SOWERBY), *(1a,b)* USSR; *(1c-f)* Eng.; *1a,b*, ped.v. int. mold, vent., post. showing mus-

culature; *1c,d,* ped.v. (decorticated) vent., post.; *1e,f,* ped.v. and brach.v. int. molds; all ×0.6 (*1a,b,* 587; *1c-f,* 587).

Titanaria MUIR-WOOD & COOPER, 1960, p. 334 [**T. costellata*; OD]. Like *Gigantoproductus* but with ginglymus in pedicle valve, no pseudodeltidium; costellate and with numerous fine spines in both valves, no rugae; cardinal process sessile with

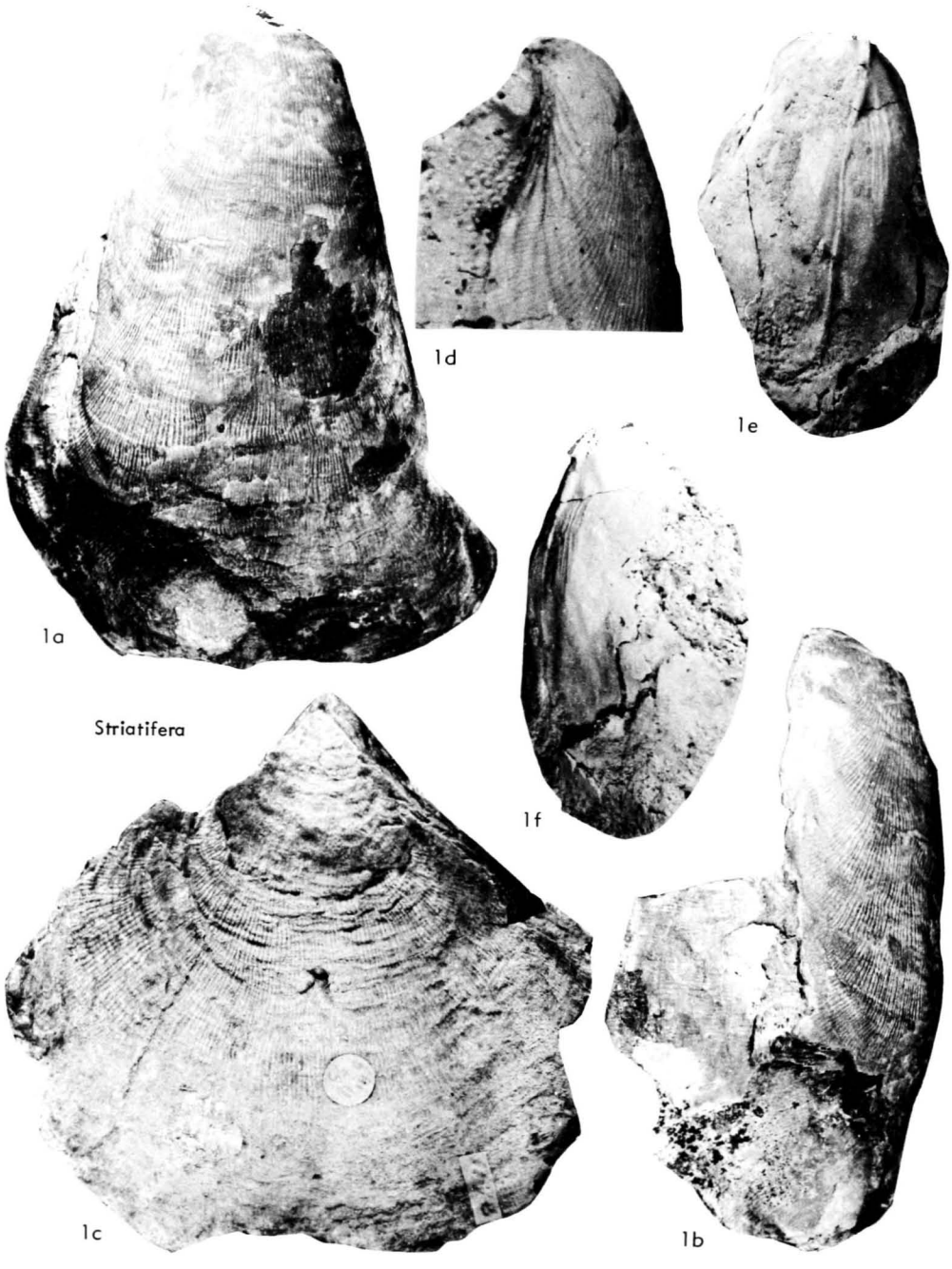

FIG. 381. Linoproductidae (Striatiferinae) (p. H506).

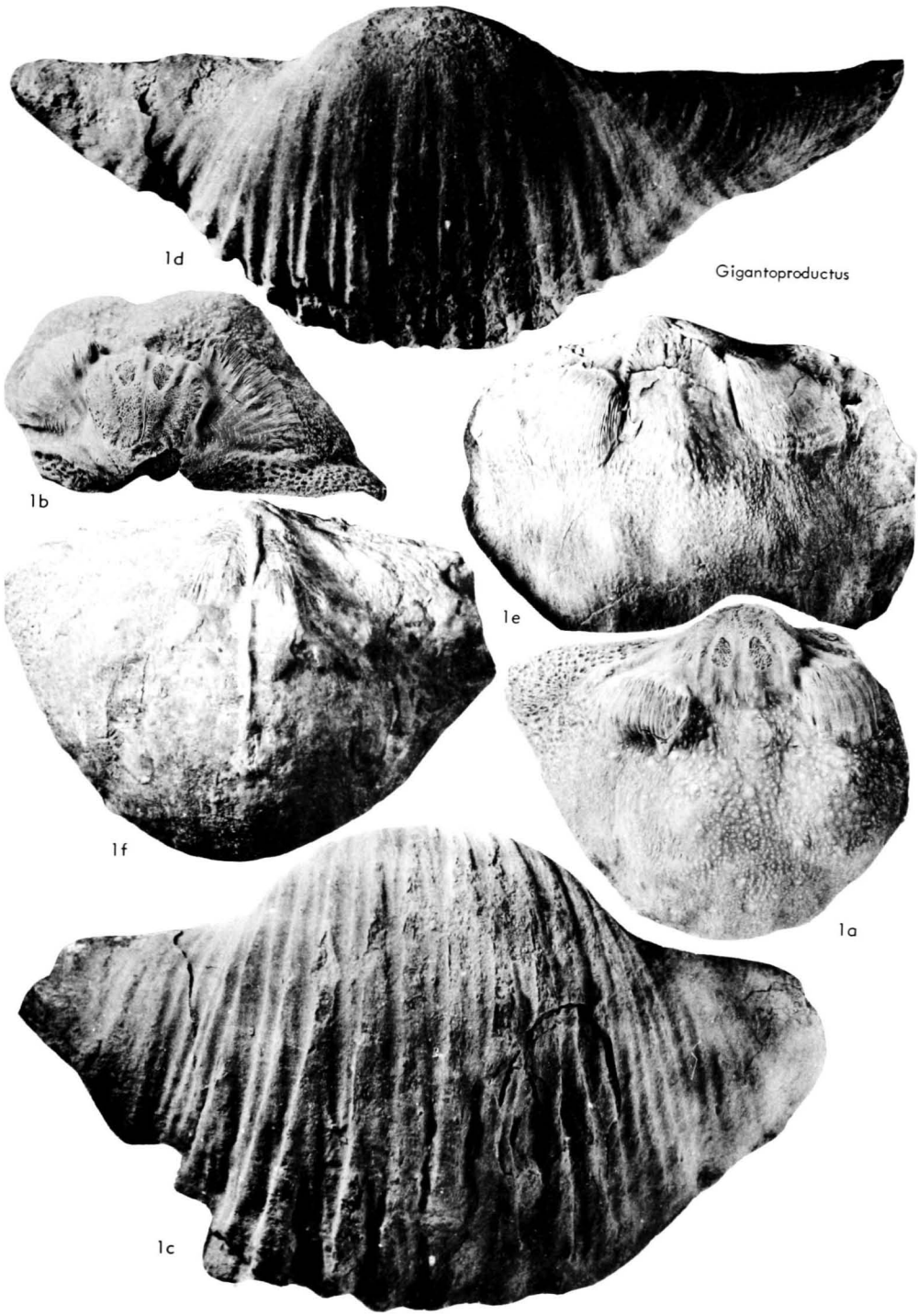

FIG. 382. Gigantoproductidae (Gigantoproductinae) (p. *H*507-*H*508).

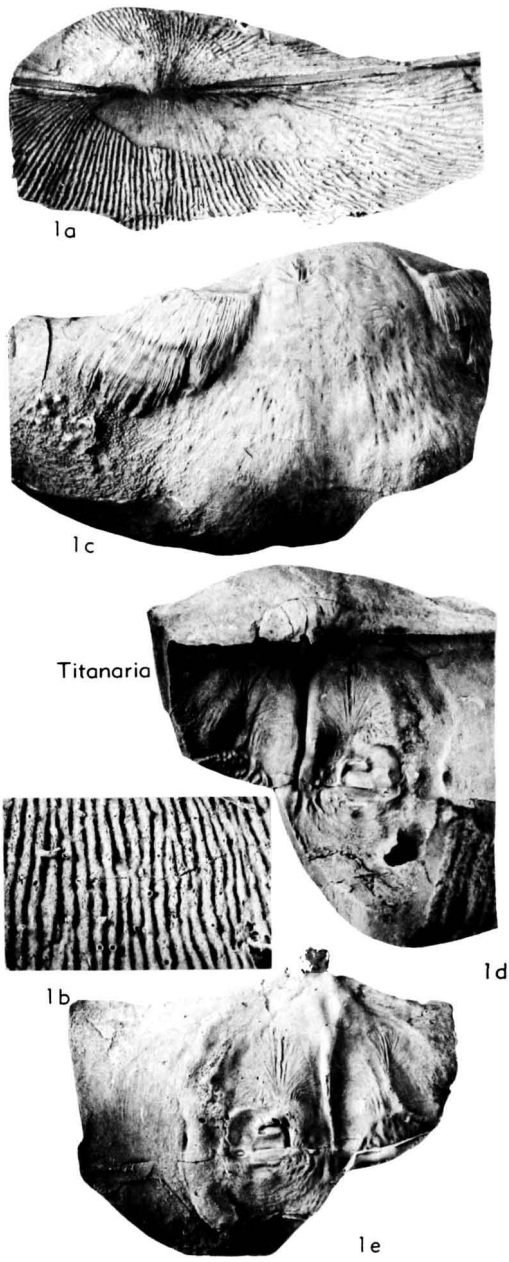

FIG. 383. Gigantoproductidae (Gigantoproductinae) (p. *H*508, *H*510).

single lobe; adductors finely dendritic; no trace of lophophore spirals. *U.Miss.*, N.Am.——FIG. 383,*1*. **T. costellata*, USA(Calif.); *1a*, brach.v. view, ×0.8; *1b*, costellae of brach.v., ×1.6; *1c,d*, ped.v. and brach.v. int. molds, ×0.8; *1e*, brach.v. int., ×0.8 (all, holotype) (587).

Subfamily SEMIPLANINAE Sarycheva, 1960

[*nom. transl.* MUIR-WOOD, herein (*ex* Semiplanidae SARYCHEVA, 1960, p. 231)]

Usually thin-shelled, laterally fusiform or elongate shells with much incurved umbo; no interareas or ginglymus; cardinal process small, sessile, bilobate, or quadrilobate; adductors smooth. *U.Dev.-U.Carb. (Namur.)*.

Semiplanus SARYCHEVA in SARYCHEVA & SOKOLSKAYA, 1952, p. 119 [**Productus semiplanus* SHVETSOV, 1922, p. 10 (=*?P. latissimus* J. SOWERBY, 1822); OD]. Ornament of costellae, numerous growth lines forming regular transverse ornament, and quincuncially arranged fine spines, row near hinge; hinge margin thickened internally and longitudinally grooved; cardinal process quadrilobate, septum long, medianly grooved, lateral ridges short. *L.Carb.(Visean)-U.Carb.(Namur.)*, Eu.(USSR)-Asia(Kazakhstan).——FIG. 384,*1a-c*. **S. semiplanus* (SHVETSOV); *1a-c*, ped.v. vent., post., profile, ×1 (587).——FIG. 384,*1d-f*. *S. latissimus*, Eng.; *1d,e*, ped.v. vent., post., ×1.5; *1f*, ped.v. int. mold, ×1 (587).

?Bagrasia NALIVKIN, 1960, p. 231 [**Productus chonetiformis* KRESTOVNIKOV & KARPYSHEV, 1948, p. 48; OD]. Elongated along hinge with no interareas; umbo scarcely projecting beyond hinge. Ornament of fine costellae with weakly swollen elongated tubercles, the bases of fine spines; cardinal process small, bilobate, median septum absent. *U.Dev.-L.Carb.* (Etroeungt beds), Eu.(USSR, S. Urals, Caucasus).

Subfamily KANSUELLINAE Muir-Wood & Cooper, 1960

[Kansuellinae MUIR-WOOD & COOPER, 1960, p. 336]

Interarea in each valve with pseudodeltidium and chilidium; cardinal process probably bilobate. *L.Carb.(Visean)*.

Kansuella CHAO, 1928, p. 67 [**Stratifera kansuensis* CHAO, 1927, p. 108; OD]. Imperfectly known and possibly composite; shell gigantic, transverse, pedicle valve thick-shelled, valves nongeniculate; irregularly costellate and rugose posteriorly, lamellose, spines scattered over pedicle valve, absent in brachial valve; adductors lobate or dendritic; indications of lophophore spirals; lateral ridges absent. *L.Carb.(Visean)*, Asia(China-Ferghana).——FIG. 385,*1*. **K. kansuensis* (CHAO), China; *1a*, brach.v. int. (post. part); *1b*, interareas of both valves; *1c*, brach.v. interarea, pseudodeltidium; and ornament; all ×0.55 (153).

Suborder OLDHAMINIDINA Williams, 1953

[*nom. correct.* WILLIAMS, herein (*pro* suborder Oldhaminoidea WILLIAMS, 1953, p. 286)] [Materials for this suborder prepared by ALWYN WILLIAMS]

Shell shape irregular, without radial orna-

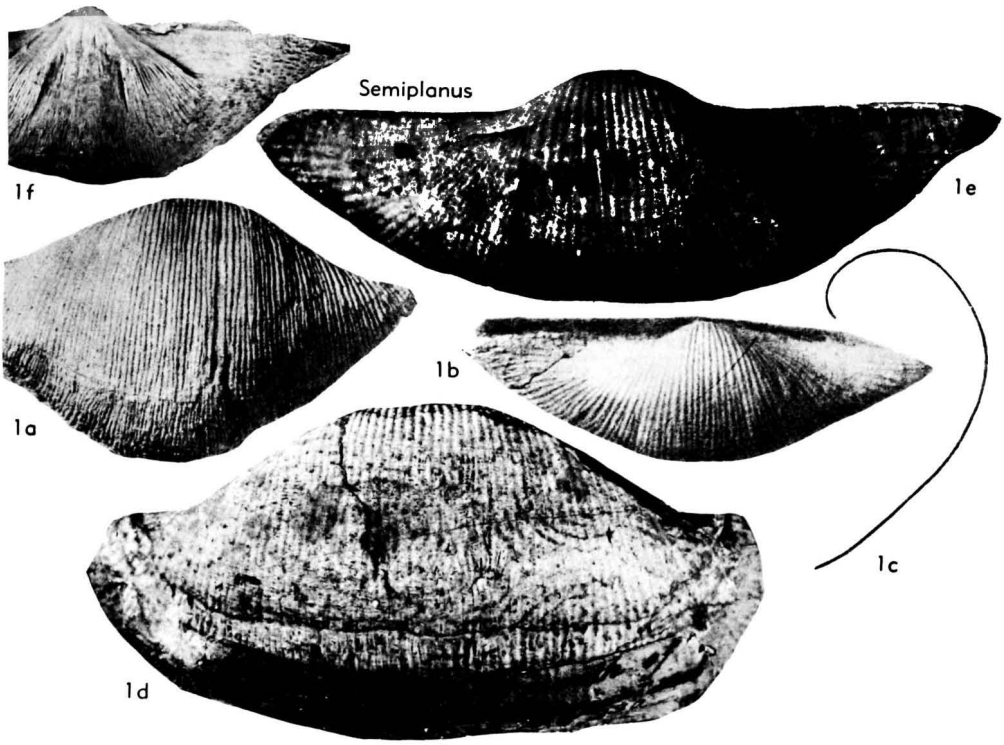

FIG. 384. Gigantoproductidae (Semiplaninae) (p. *H*510) .

mentation, pedicle opening, interareas or hinge lines; primary shell of brachial valve limited to small, triangular area forming posteromedian apex of large plate of secondary shell, presumed to have been deposited by infold of mantle as lophophore support, commonly symmetrically or asymmetrically highly lobate; pedicle valve extending dorsally of apex of brachial valve as posterior flap commonly everted for attachment to substratum or extending forward to transform pedicle valve into cone; articulation effected by pair of striated, convex dental areas on posteromedian floor of pedicle valve fitting into striated concave surfaces on either side of bilobed cardinal process in brachial valve; ventral muscle impressions symmetrical or unequally developed about median plane; ventral bounding ridge on floor of pedicle valve disposed as loops or septa coincident with outline of dorsal internal plate; shell substance pseudopunctate. *U.Carb.-U.Trias.*

The morphology of the Oldhaminidina brachiopods warrants a full discussion because, although vaguely suggestive of a productoid ancestry, it is so bizarre as to defy any confident interpretation of its details. This is true not only of certain features of both valves but also of the growth of the

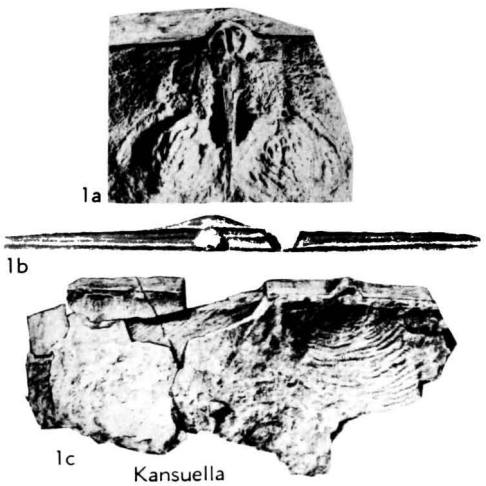

FIG. 385. Gigantoproductidae (Kansuellinae) (p. *H*510).

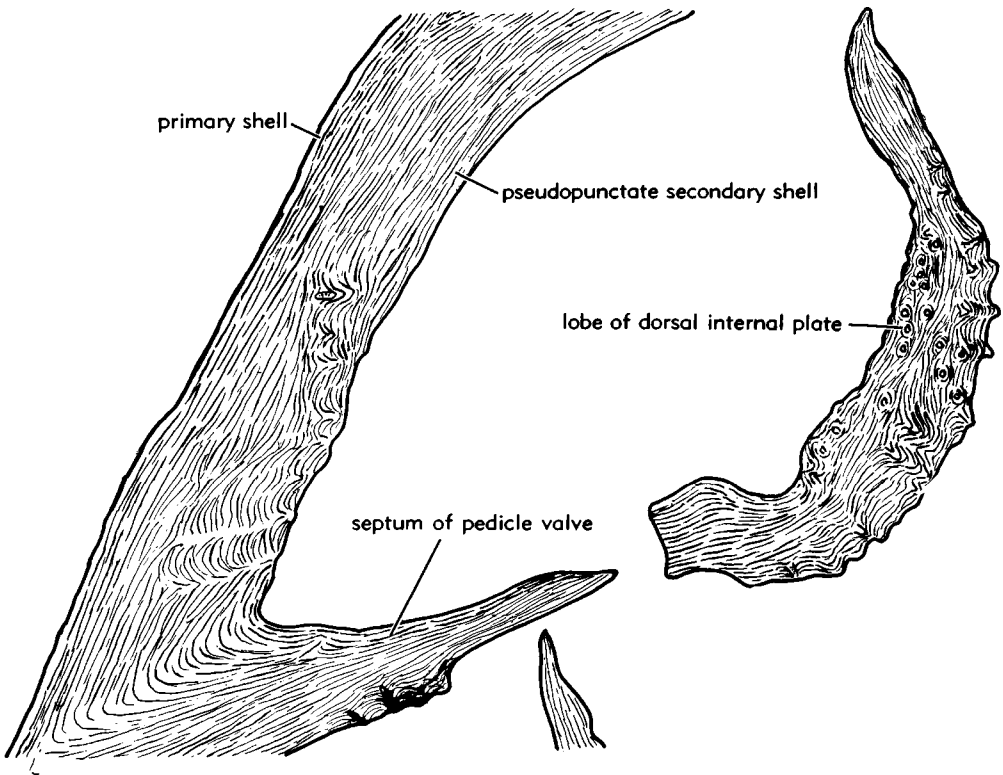

FIG. 386. Shell structure of *Oldhamina decipiens* (DE KONINCK) (×15).

valves themselves; hence, the following observations and even the proposed classification may ultimately require fundamental revision.

The shells are functionally bivalved, with the inner surface of the pedicle valve everywhere extending well beyond the periphery of the other valve so that much of the ventral mantle, despite evidence for retractability, must have been permanently exposed during life. The shell structure of the pedicle valve is pseudopunctate, with a thin but recognizable primary layer orthodoxly forming the entire outer surface of the valve (Fig. 386). In the structure generally identified as the brachial valve, however, the primary layer is absent for a small, posteriorly located, triangular area (Fig. 387). The rest of the "valve" is made up exclusively of pseudopunctate secondary calcite (Fig. 386) so that *both* external and internal surfaces are pierced by taleolae to give a finely tuberculate appearance identical with that of the ventral internal surface (WILLIAMS, 1953, 873). It can be demonstrated in other articulate brachiopods that structures, like lophophore supports, muscle platforms, etc., which are composed only of secondary shell, were secreted within invaginations of outer epithelium independent of the mantle edge. Consequently, it may be assumed that the part of the oldhaminoid brachial valve which is also composed only of secondary shell formed no part of the exoskeleton but was an internal skeletal support (internal plate) to a highly lobate mantle infold (WILLIAMS, 1953, 873). According to this interpretation, the true brachial valve is vestigial, being represented by the small, obtusely triangular, apical portion of the valve that consists of both outer primary shell and the inner secondary layer forming the cardinal process lobes and the posterior part of the dental sockets. STEHLI (1956, 777), on the other hand, prefers to ascribe the anomalous distribution of primary shell to a physiological malfunction in an otherwise normally growing valve. The mantle lobes that are ultimately responsible for the growth of the shell are, however, differen-

tiated from the same rudimentary mantle ring in living larvae and, if this were also true for the Oldhaminidina brachiopods, a fundamental difference in the shell structure of normally growing valves could hardly have arisen. Furthermore, the obtusely triangular area covered by primary shell, although reminiscent of an obsolescent interarea and chilidium, is not homologous with them because growth was in an anterodorsal direction away from the cardinal process in a manner which suggests that expansion was controlled by a mantle edge coincident with the base of the triangle.

By imparting rigidity to an investing infold of the mantle, the inferred internal plate could have given support to the lophophore. Immature specimens of the earliest-known Oldhaminidina, *Poikilosakos,* possess a subcircular internal plate with a median incision. Assuming the lophophore to have arisen from the inner epithelium just within the edge of such a plate, it would have resembled the schizolophe; and with the development of lateral lobes to the internal plate, the feeding apparatus would have been transformed into a ptycholophe (Fig. 388).

The morphology of the posterior part of the pedicle valve is, in some respects, as anomalous as the structure of the brachial valve. There is no interarea but the posterior part of the pedicle valve is extended anterodorsally as a flap to overlie the brachial valve, which is accommodated by a triangular impression (Fig. 389). This impression is also ornamented by growth lines parallel with the base and probably represents a zone of the posterior flap where secondary shell deposition was held in abeyance by the pressure of the heavily rutted periostracal cover to the brachial valve. The flap is almost invariably sharply reflexed just anterior of the base of the impression and its attitude and shape can vary considerably. Specimens attached to a regular surface possess a flap which resembles a pair of ears extending laterally from the median reflexed area (Fig. 390); in those which lay free on the sea floor throughout most of their lives the flap is greatly extroverted, so that the distal edge is usually in contact with the external surface of the pedicle valve (Fig. 391); in those attached

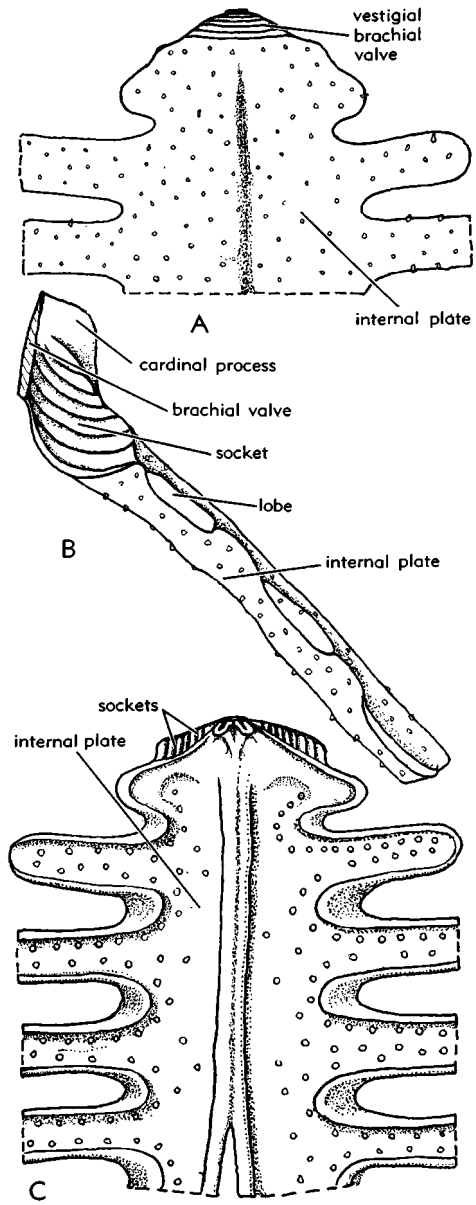

FIG. 387. Brachial valve and internal plate of *Leptodus* sp., M.Perm., Tex.; *(A)* internal, *(B)* lateral, and *(C)* external views (873).

to irregular surfaces or crinoid stems the flap is closely adherent and molded to the base (Fig. 389); and in at least three distinct stocks *(Adriana, Keyserlingina, Pirgulia)* the flap grew forward with the rest of the pedicle valve to form a deep cone (Fig. 392).

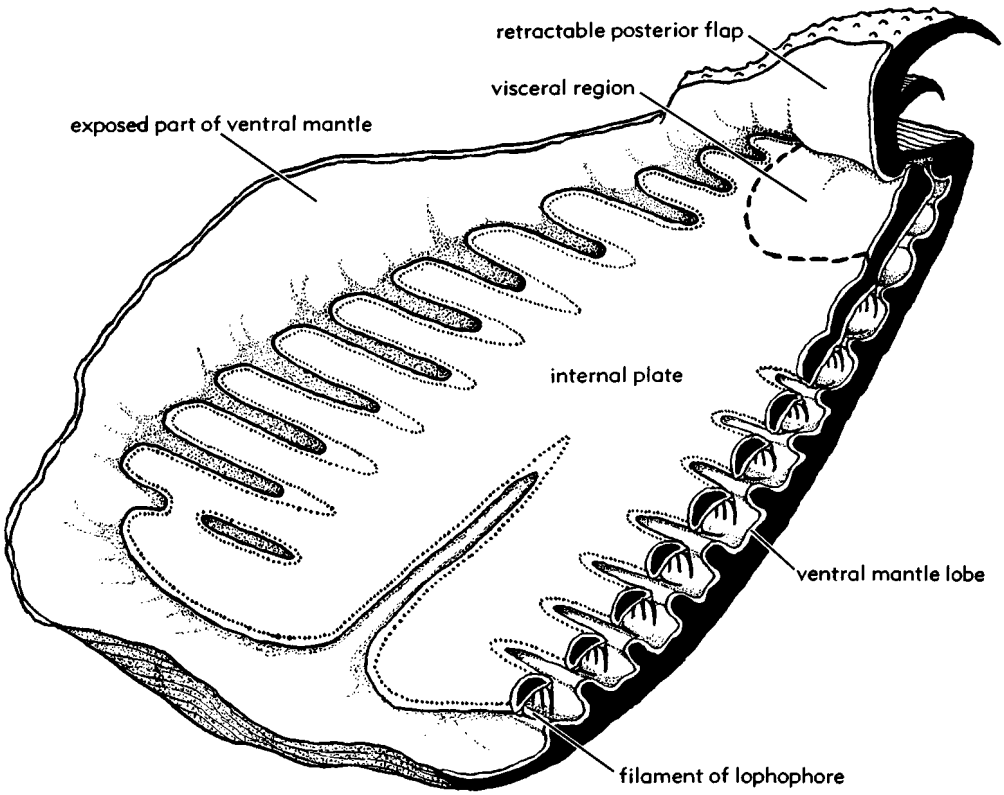

FIG. 388. Submedian view of *Leptodus* sp. (reconstr.), M.Perm., Tex., showing relationship between mantle lobes and shell (portrayed in solid block) (873).

Subsequent to the settling of spats, presumably by cementation of the apex of the pedicle valve, the posterior flap assisted in fixation, as is well seen in those oldhaminoids attached to crinoid stems. It is envisaged as having been laid down by a posterior extension of the mantle, capable of a rapid deposition of cementing shell material and disposed in such a way that the inner epithelial layer was invariably exposed. This posterior mantle flap must have molded itself closely to any surface available for attachment and must have been greatly retractable because paper-thin layers of shell, consisting of both primary and secondary calcite, were commonly plastered one on top of another (Fig. 391).

Apart from the cardinal process, which is bilobed in the strophomenoid fashion, the internal features also show noteworthy departures from arrangements typical of other articulate brachiopods. No teeth are found in the pedicle valve, but a pair of striated, convex surfaces (dental areas of WATSON, 854) occur in the apical region; and these articulate with a pair of similarly striated, oval concave surfaces (sockets) lying anterolaterally to the cardinal process lobes and extending down to the first pair of lateral lobes in the brachial valve. Muscle scars are only sporadically impressed but include a pair of variably defined dorsal adductor scars on either side of the median ridge. The ventral impressions, on the other hand, can be asymmetrically developed (853, 854), and according to STEHLI (777) the disposition of the ventral scars is indicative of two important groups. In the first group (e.g., *Coscinophora*), a pair of large elongate adductor scars located submedianly are flanked by a pair of smaller, elongate diductors; this symmetrical field is commonly associated with median and submedian ridges. In the second group, which includes forms like *Poikilosakos,* the right diductor is always larger than the left and is contained within

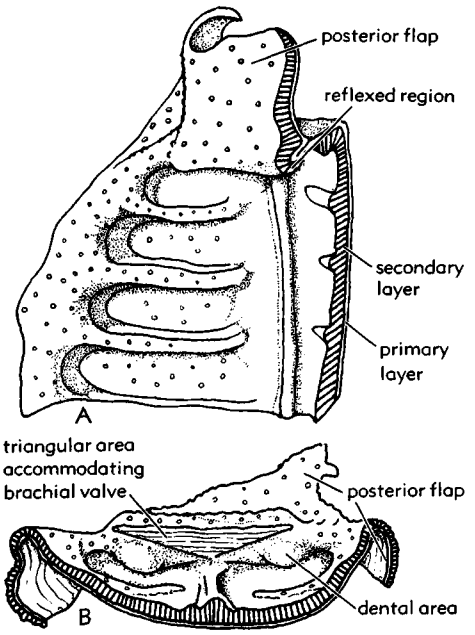

FIG. 389. Apical part of pedicle valve of *Leptodus* sp., *M.Perm.*, Tex.; submedian *(A)* and posterior *(B)* views (873).

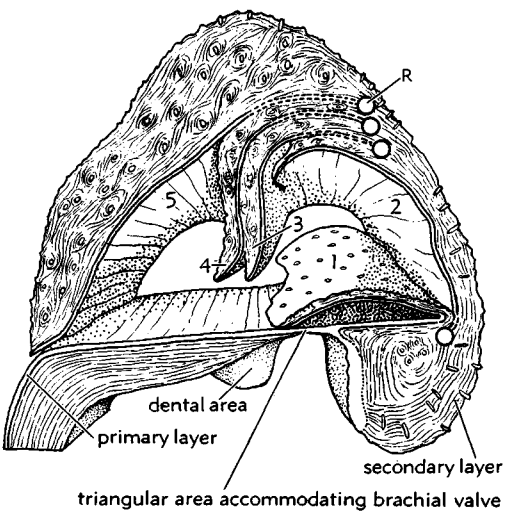

FIG. 391. Submedian portion of posterior flap of *Oldhamina decipiens* (DE KONINCK), Perm., Salt Range, Pak.; 1, 2, 3, 4, and 5 denote successive layers of shell deposited by posterior flap; circles represent points of minimum retractability of mantle flap necessary for deposition of each succeeding layer (873).

an elongately semiconical sheath, while the adductor scars are obscure or represented by inconspicuous asymmetrical hollows located posteromedianly. This asymmetry of scars probably reflected a degeneracy in the muscle system because the brachial valve was commonly so confined by the lateral walls of the pedicle that it could not have slewed in the plane of articulation as believed by WATSON (854). Furthermore, the close proximity of the cardinal process lobes to the floor of the pedicle valve and the physical constraint of the posterior flap immediately dorsal of the brachial valve precludes any considerable movement normal to the plane of articulation.

The most significant morphological changes seen in the Oldhaminidina resulted from development of the septal apparatus of the pedicle valve and the corresponding lobation of the internal plate.

In the earliest oldhaminoid, *Poikilosakos*, with a low bounding ridge (flange of WAT-

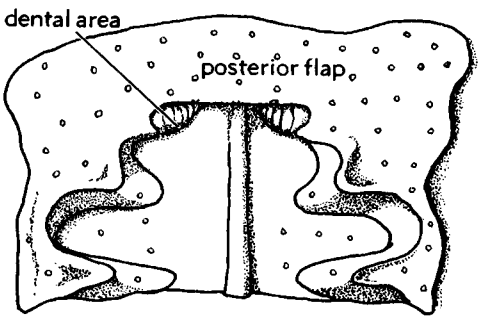

FIG. 390. Apical part of pedicle valve of *Leptodus* sp., M.Perm., Tex. (873).

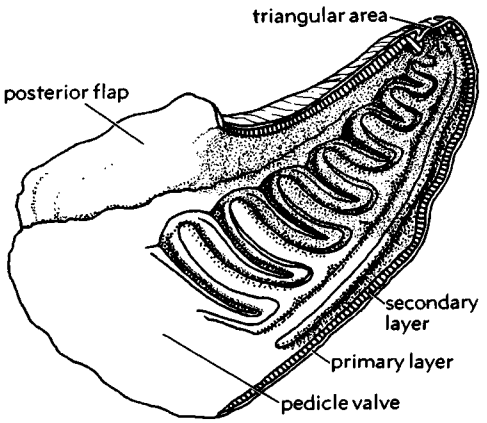

FIG. 392. Submedian view of interior of pedicle valve of *Pirgulia* sp., M. Perm., Tex. (873).

son, 854), lying well within the margin of the pedicle valve, completely surrounded the median area of the interior. In young shells, the bounding ridge was roughly subcircular in outline and was indented to form a median loop only; but during further growth involving resorption, the bounding ridge increased in size and became disposed as a small number of lateral loops in addition to the median one. Each loop was sufficiently open to include medianly a narrow strip of the valve floor bounded by an indented segment of the bounding ridge. The internal plate of the brachial valve corresponded in outline to the disposition of the bounding ridge, so that it was lobate and lay so close to the pedicle valve that each lobe was seemingly isolated distally from its neighbor by a loop of the bounding ridge.

In later Oldhaminidina (e.g., *Keyserlingina, Paralyttonia*), the loops began to close by an increase in the size of adjacent segments of the bounding ridge and their encroachment onto the intervening median strip of the valve floor until, in extreme forms like *Oldhamina* and *Leptodus*, the ridge boundaries to each loop were completely united into one solid septal structure. In this manner the looped bounding ridge of the earlier and more generalized Oldhaminidina was transformed into solid septa, the dorsal surfaces of which may be concave, bluntly convex or sharp; and a pair of notches, extending the length of the septa, commonly developed to accommodate the edges of lobes to the internal plate.

Other modifications associated with evolution of the septal apparatus included an increase in the number of septa disposed symmetrically or asymmetrically about the median line, the progressive closure of the median incision of the internal plate and the partial fusion of the lateral lobes by the growth of dissepiments. *Bactrynium* has been only provisionally assigned to the Oldhaminidina, but if this arrangement does reflect the true affinities of the stock, a remarkable reversion to a more normal kind of shell occurred within the group. Many features of *Bactrynium* are certainly reminiscent of the Oldhaminidina. But there is no posterior flap to the pedicle valve and the primary shell also extends over the entire outer surface of a normally developed brachial valve which bears internally an adnate lobate structure like the oldhaminoid internal plate.

The classification of the Oldhaminidina brachiopods is inevitably in a state of some confusion. All but one of the genera described below are clearly related to one another but display degrees of morphological differences that normally call for some kind of convenient familial grouping. Thus, Williams (1953, 873), recognized two families, the Poikilosakidae and the Oldhaminidae, based upon the symmetry of lobation. Stehli (1956, 777), has since claimed that the symmetry of the ventral muscle scars is more trustworthy for suprageneric segregation and his procedure has been adopted below although further radical revision will probably be necessary as more becomes known of these unique brachiopods. *Bactrynium,* on the other hand, is so distinct from the poikilosakids and oldhaminids that details of its morphological features have not been incorporated into the diagnosis of the suborder. Its resemblance to true Oldhaminidina may reflect affinity or homeomorphy and its retention within the suborder cannot be assured until its Triassic antecedents have been discovered.

A great deal of nomenclatorial confusion has also arisen through an unwarranted action of Waagen (1883, 845). The first described genus of the group was named *Leptodus* by Kayser (1882, 460) in the belief that the incomplete specimen he examined represented the remains of fish teeth. Shortly afterward, Waagen ascertained their true nature and because the name *Leptodus* perpetuated a serious misidentification, suppressed it in favor of *Lyttonia* Waagen, the type-species of which was subsequently designated by Hall & Clarke (396). In the same publication, Waagen erected another genus *(Oldhamina)* and a new subfamily, the Lyttoniinae. Since then most European paleontologists (Noetling, 605; Wanner & Sieverts, 853; Likharev, 511, etc.) have used the familial name Lyttoniidae, whereas Schuchert (726), presumably in recognition of the invalid procedure adopted by Waagen, proposed Leptodinae as a suprageneric

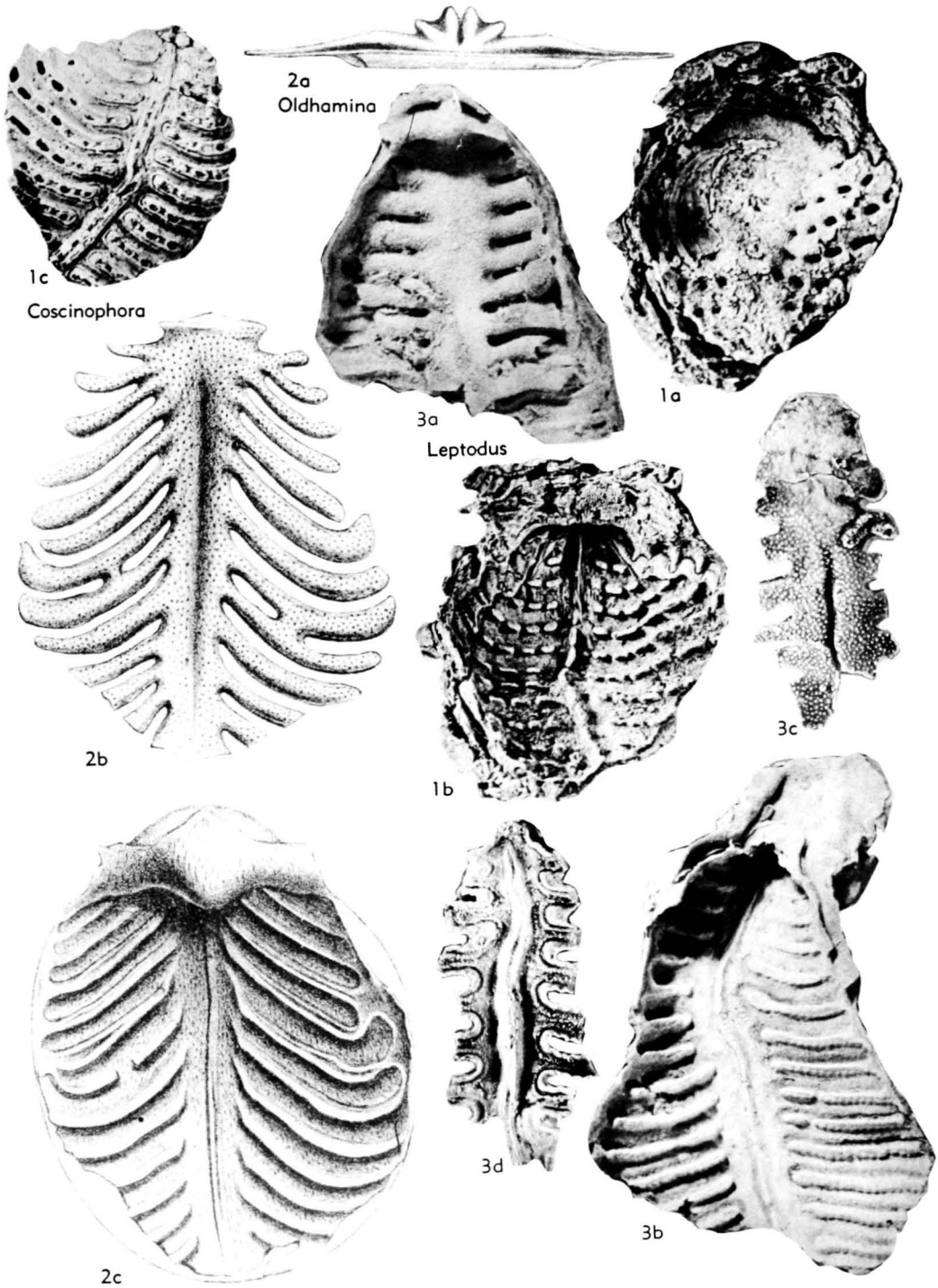

FIG. 393. Lyttoniidae (p. *H*518).

FIG. 394. Lyttoniidae (p. H518).

taxon in 1913, and (with LEVENE) Oldhaminidae in 1929 (730). In general, there is no doubt that the familial designation Lyttoniidae has been more widely employed by paleontologists than either Oldhaminidae or Leptodinae and therefore (Zool. Code, 1961, art. 40, a) is adopted below.

Superfamily LYTTONIACEA Waagen, 1883

[*nom. transl.* LIKHAREV, 1960, p. 237 (*ex* Lyttoniinae WAAGEN, 1883, p. 396)]

Characters of suborder. *U.Carb.-U.Trias.*

Family LYTTONIIDAE Waagen, 1883

[*nom. transl.* NOETLING, 1905, p. 129 (*ex* Lyttoniinae WAAGEN, 1883, p. 396)] [=Leptodinae SCHUCHERT, 1913, p. 387; Oldhaminidae SCHUCHERT & LEVENE, 1929, p. 18]

Ventral muscle field including large submedian adductor scars flanked by pair of smaller diductor impressions symmetrically developed about median ridge and two divergent submedian ridges of variable strength. *U.Carb.-Perm.*

Oldhamina WAAGEN, 1883, p. 403 [**Bellerophon decipiens* DE KONINCK, 1863, p. 8; OD] [=*Waagenopora* NOETLING, 1902, p. 647 (type, *Oldhamina decipiens* DE KONINCK, 1863); *Oldhamella* NOETLING, 1905, p. 129 (type, *Bellerophon decipiens* DE KONINCK) *pro Oldhamina* WAAGEN; *Oldhamia* ZITTEL, 1910 *(nom. null.)*]. Pedicle valve strongly convex, probably unattached in adult stages of growth with recurved posterior flap; septal apparatus symmetrical with many lateral pairs of high, sharp septa; median incision of internal plate of brachial valve, vestigial. *Perm.,* Asia.——FIG. 393,*2*. **O. decipiens* (DE KONINCK); Productus Ls., Pak.; *2a,b,* post., ext. views of brach.v., ×3; *2c,* ped.v. int., ×3 (845).

Coscinophora COOPER & STEHLI, 1955, p. 469 [**C. nodosa*; OD]. Like *Leptodus* but with median and lateral ridges of symmetrical septal apparatus broken into series of discrete beads; internal plate of brachial valve with lobes united by dissepiments to define series of holes complementary to ventral beads. *L.Perm.(Leonard.),* USA(Tex.).——FIG. 393,*1*. **C. nodosa*; *1a,* brach.v. view of conjoined valves, ×1; *1b,* same specimen with brach.v. removed, ×1; *1c,* brach.v. int., ×1 (196).

Eolyttonia FREDERIKS, 1923, p. 25 [**Oldhamia (Lyttonia) mira* FREDERIKS, 1916, p. 74; OD] [=*Uralina* SCHUCHERT & LEVENE, 1929, p. 27 (type, *U. tastubaensis* LIKHAREV, 1925) *pro Uralia* LIKHAREV, 1925, *non* MULSANT & VERREAUX, 1866]. Pedicle valve convex or flat, incompletely attached with everted posterior flap; ventral bounding ridge forming number of symmetrically disposed loops with incompletely fused sides forming septal apparatus of elevated ridges with concave dorsal surfaces; median incision of internal plate of brachial valve limited to anterior half. *U.Carb.(Ural.)-Perm.,* Asia.

Gubleria TERMIER & TERMIER, 1960, p. 241 [**G. disjuncta*; OD]. Like *Leptodus* but with median incision of internal plate of brachial valve incompletely closed by series of transverse bars of secondary shell. *Perm.,* SE.Asia(Cambodia).

Keyserlingina CHERNYSHEV, 1902, p. 55 [**K. schellwieni*; OD] [=*Parakeyserlingina* FREDERIKS, 1916, p. 14 (type, *Keyserlingina darvasica* CHERNYSHEV, 1914); *Chaoella* LIKHAREV, 1932, p. 161 (type, *C. caucasica*)]. Pedicle valve subconical through forward growth of posterior flap, attached umbonally; ventral bounding ridge as series of symmetrical loops with long median and up to 7 lateral pairs; internal plate of brachial valve correspondingly lobate. *U.Carb.(Ural.) - Perm.,* Eurasia.——FIG. 394,*1*. *K. filicis* (KEYSERLING); L.Perm.(Sakmar.), W.Urals; ped.v. int. mold, ×1 (710).

Leptodus KAYSER in RICHTHOFEN, 1882, p. 161 [**L. richthofeni*; OD] [=*Lyttonia* WAAGEN, 1883, p. 396 (type, *L. nobilis*); *Lyttonia (Digitia)* DE GREGORIO, 1930, p. 30 (type, *L. (D.) angustata*); *Lyttonia (Imperia)* DE GREGORIO, 1930, p. 31 (type, *L. (I.) princeps* var. *glomerata*); *Lyttonia (Irma)* DE GREGORIO, 1930, p. 32 (type, *L. (I.) bilobata*); *Lyttonia (Vincia)* DE GREGORIO, 1930, p. 31 (type, *L. (V.) asymmetrica*); *Lyttonia? (Prisca)* DE GREGORIO, 1930, p. 31 (type, *L. (P.) fasciculata*)]. Pedicle valve attached to variable extent, irregular in outline, commonly with great expansion of peripheral zone, posterior flap everted; septal apparatus symmetrical with up to 33 pairs of blunt septa; median incision of internal plate of brachial valve vestigial. *Perm.,* cosmop.——FIG. 393,*3*. *L.* sp. cf. *L. americanus* GIRTY; M.Perm.(Word), Tex.; *3a,* brach.v. view of fragment of conjoined valves, ×1.5; *3b,* ped.v. int., ×1.5; *3c,d,* brach.v. ext., int., ×2.5 (Williams, n).

Oldhaminella WANNER & SIEVERTS, 1935, p. 232 [**O. philocrina*; OD]. Pedicle valve strongly convex, attached, with everted posterior flap; septal apparatus symmetrical, median septum extending

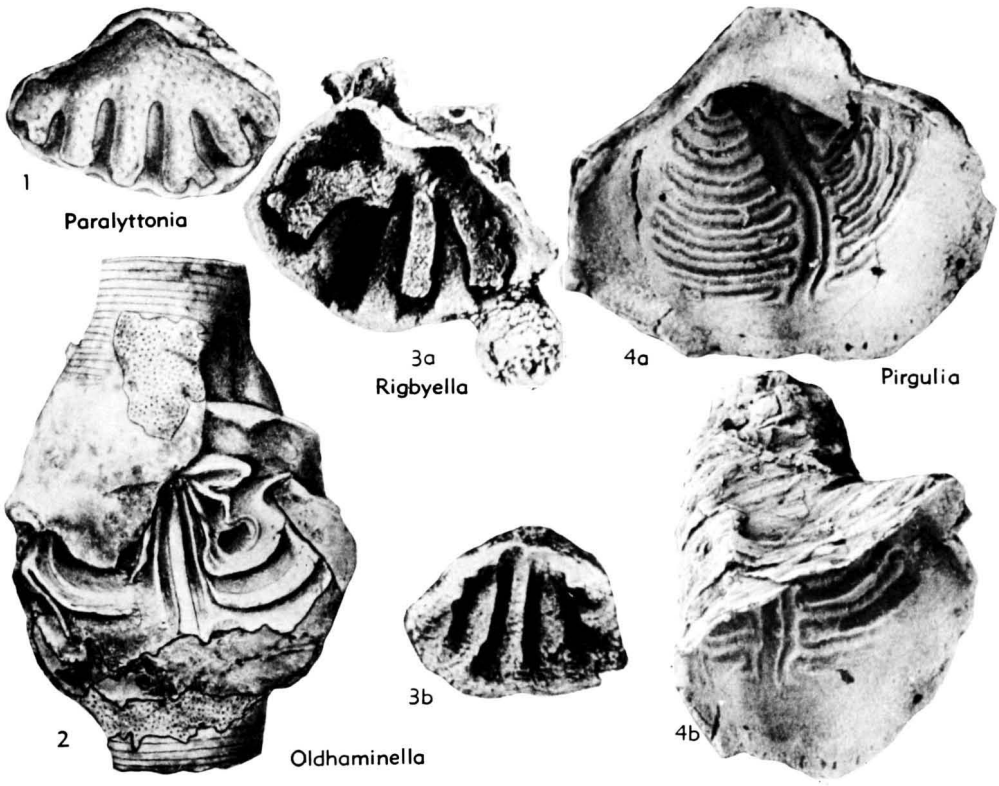

FIG. 395. Lyttoniidae (p. *H*518-*H*519).

almost to apex of valve, 3 or 4 pairs of convexly crested lateral septa formed by fusion of sides of loops with anterior sides strongly developed as fine ridges; median incision of internal plate of brachial valve, short to vestigial. *Perm.*, Timor. ——FIG. 395,*2*. **O. philocrina*; Perm., Timor; ped.v. int., attached to crinoid stem, ×1.5 (853).

Pirgulia COOPER & MUIR-WOOD, 1951, p. 195 [**Lyttonia? (Pirgula) pediculata* DE GREGORIO, 1930, p. 30; OD] [*pro Pirgula* DE GREGORIO, 1930 (*non Pirgula* TESSMAN, 1921)]. Like *Leptodus* but with subconical pedicle valve through forward growth of posterior flap. *Perm.*, Italy-USA(Tex.). ——FIG. 395,*4*. *P.* sp., Leonard., USA(Tex.); *4a,b,* int. and anterolat. views of ped.v., ×1.5 (Williams, n).

Paralyttonia WANNER & SIEVERTS, 1935, p. 207 [**P. permica*; OD]. Small, wide, pedicle valve completely attached; ventral muscle scar divided by median ridge; ventral bounding ridge disposed as up to six asymmetrical lobes parallel with median line; internal plate of brachial valve correspondingly lobate. *Perm.*, Timor.——FIG. 395, *1*. **P. permica*; Perm., Timor; dorsal view of conjoined valves, ×2 (853).

Rigbyella STEHLI, 1956, p. 310 [**Paralyttonia girtyi* WANNER & SIEVERTS, 1935, p. 209; OD]. Small, cup-shaped pedicle valve attached by apex; submedian ridges as well as median ridge commonly developed in ventral muscle field, ventral bounding ridge looped like that of *Paralyttonia*. *M.Perm.*, USA(N.Mex.).——FIG. 395,*3*. **R. girtyi* (WANNER & SIEVERTS); *3a,* view of conjoined valves, ×4; *3b,* ped.v. int., ×2 (777).

Family POIKILOSAKIDAE Williams, 1953

[Poikilosakidae WILLIAMS, 1953, p. 287]

Ventral muscle scars asymmetrically developed about median plane with long right diductor scar contained by partitions commonly forming subconical sheath. *U.Carb.-Perm.*

Poikilosakos WATSON, 1917, p. 212 [**P. petaloides*; OD] [=*?Prokeyserlingina* FREDERIKS, 1916, p. 64 (hypothetical genus)]. Pedicle valve completely attached, posterior flap everted; left diductor impression more widely divergent than right diductor sheath, left adductor scar obscurely impressed; ventral bounding ridge forming median loop and about 2 pairs of irregular lateral loops. *U.Carb.*, cosmop.——FIG. 396,*1*. **P. petaloides,*

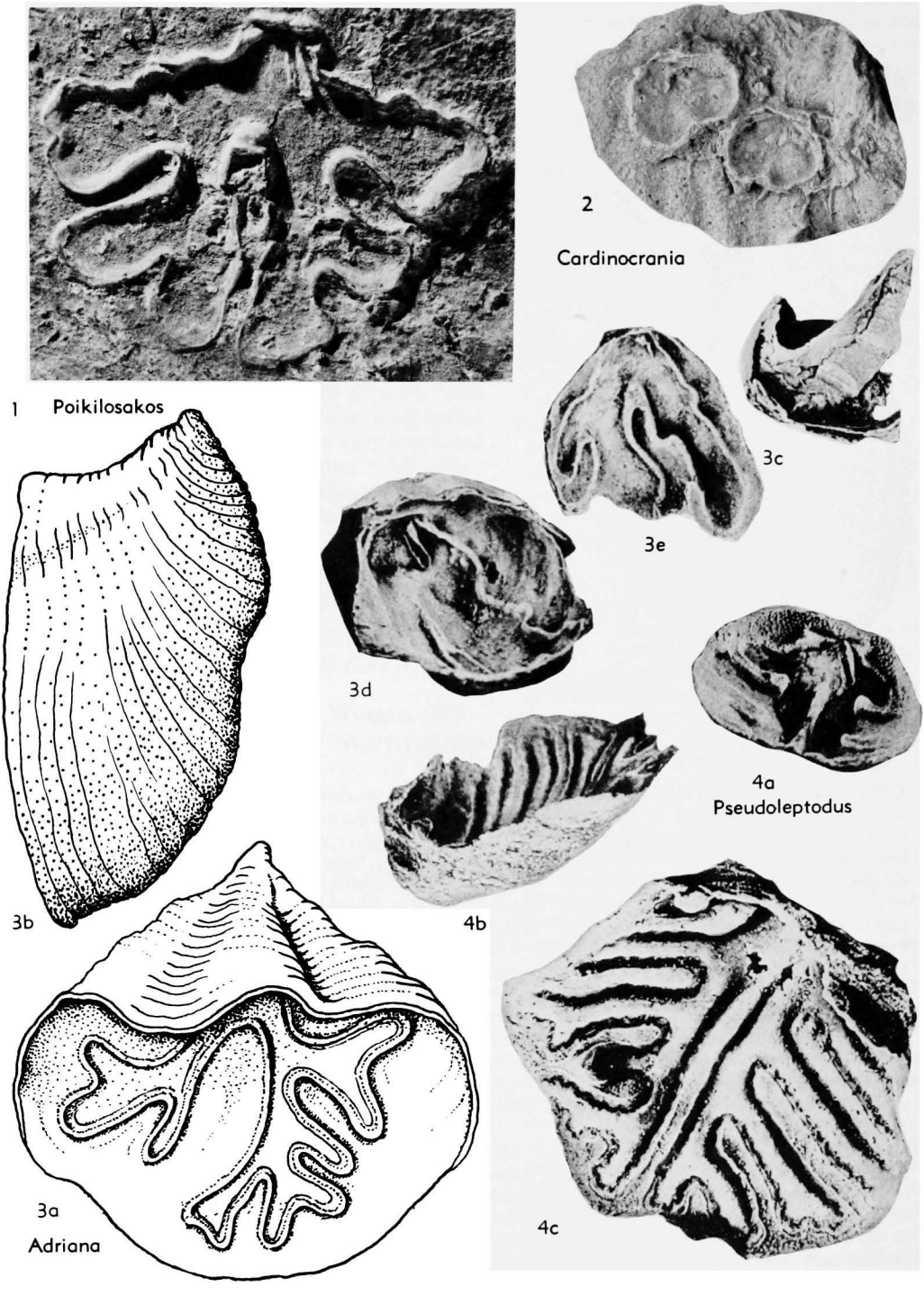

FIG. 396. Poikilosakidae (p. *H*519, *H*521).

Cisco Gr., USA(Tex.); ped.v. int., ×3 (Muir-Wood, n).

Adriana DE GREGORIO, 1930, p. 32 [**A. osiensis*; OD] [=*Stita* DE GREGORIO, 1930, p. 32 (type, *Lyttonia (Stita) paupera*; OD)]. Pedicle valve subconical through forward growth of posterior flap, attached apically; septal apparatus with asymmetrically disposed septa. *Perm.*, Sicily, ?N.Mex. ——FIG. 396,*3a,b*. **A. osiensis*; L.Perm.(Sosio Beds), Sicily; *3a,b*, int. and lat. views of ped.v., ×1 (reconstr.) (370).——FIG. 396,*3c-e*. *A.? guadalupensis* STEHLI, U.Perm.(Guadalup.), N. Mex.; *3c,d*, lat., int. views of ped.v., ×2; *3e*, ped. v. int., ×3 (777).

Cardinocrania WAAGEN, 1885, p. 745 [**C. indica*; OD] [=*?Pseudokeyserlingina* FREDERIKS, 1916, p. 64 (hypothetical genus)]. Small, subcircular pedicle valve with raised, medianly indented, anterior margin and everted posterior flap; raised median ridges normally developed posteriorly in ventral interior in addition to partitions containing right adductor scar; internal plate of brachial valve bilobed. *Perm.*, Pak.-Timor.——FIG. 396,*2*. **C. indica*; Productus Ls., Pak.; 2 ped. valves attached to productoid, ×2 (587).

Pseudoleptodus STEHLI, 1956, p. 311 [**P. getawayensis*; OD]. Pedicle valve subconical through forward growth of posterior flap, attached apically; septal apparatus symmetrical, with 5 or more pairs of wide, thick ridges, median ridge long; brachial valve and internal plate unknown. *U. Perm.*, USA(N.Mex.).——FIG. 396,*4*. **P. getawayensis*; *4a,b*, ped.v. int. and lat. views, ×2; *4c*, ped.v. int., ×2 (777).

Family BACTRYNIIDAE Williams, n.fam.

Concavo-convex shells attached by ventral apex, lacking interareas and radial ornamentation; pedicle valve without posterior flap; brachial valve normally developed but internally bearing adnate, symmetrical, medianly incised lobate apparatus with 8 to 10 pairs of lateral lobes complementary to lateral and long median ridges in pedicle valve; cardinal process possibly solid piece at apex to posterior boundaries of lobate apparatus that also define shallow sockets; muscle impressions obscure; shell substance pseudopunctate. *U.Trias.(Rhaet.)*.

Bactrynium EMMRICH, 1855, p. 449 [**B. bicarinatum*; OD] [=*Pterophloios* GÜMBEL, 1861, p. 411 (type, *Bactrynium bicarinata* EMMRICH, 1855)]. Pedicle valve highly convex, surface of both valves ornamented solely by well-developed, concentric growth lines. *U.Trias.(Rhaet.)*, Aus. ——FIG. 397,*1*. **B. bicarinatum; 1a,b*, post. and int. views of brach.v., ×4 (Cooper, n).

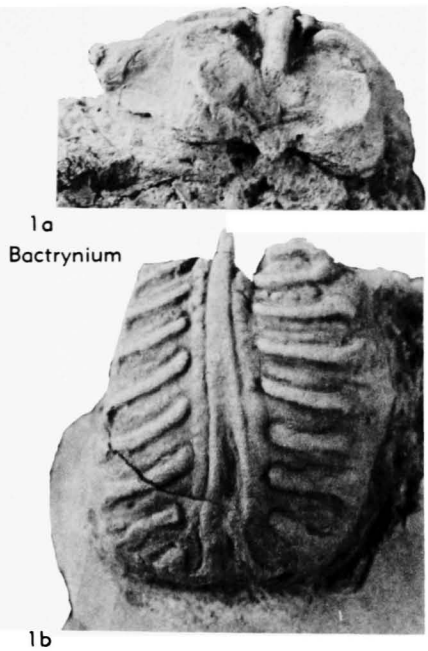

FIG. 397. Bactryniidae (p. *H*521).

Family SPINOLYTTONIIDAE Williams, n. fam.

Resembling *Leptodus* but with septal apparatus like that of *Oldhamina* and with spines on external posterolateral areas of pedicle valve. *Perm.*

Spinolyttonia SARYCHEVA, 1964, p. 69 [**S. arakeljani*; OD]. Characters of family. *U.Perm.*, USSR (Transcaucasus). [The presence of spines in *Spinolyttonia* is unique among the Oldhaminidina and calls for a thorough investigation of their inferred growth and habit. If the spines prove to be comparable with those of the Productidina, their development may prove to be either a late and independently acquired feature of certain lyttoniids or the retention in a hitherto unknown stock of an ancestral character which was lost in the great majority of Oldhaminidina. In either event, a new family seems justified.]