CRANIIFORMEA

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Subphylum CRANIIFORMEA Popov & others, 1993

[*nom. transl. et correct.* WILLIAMS & others, 1996, p. 1192, *pro* subclass Craniformea POPOV & others, 1993, p. 2]

Brachiopods with calcitic or possibly aragonitic inarticulated shells with laminar (tabular) secondary layers; posterior body wall complete, inner mantle lobes not developed at valve margins, pedicle not developed, shell free lying or with encrusting ventral valve cemented by larval epithelium; muscle system with a single pair of internal oblique and with paired outside lateral muscles attached anteriorly to the body wall; alimentary tract more or less axial with anus medially on posterior body wall; lophophore initially with median tentacle lost during growth, tentacles in double row in posttrocholophous growth stages only; nervous system in base of epidermis with paired subenteric ganglia; mantle canal systems with *vascula terminalia* peripheral only, normally pinnate, containing gonads; larva lecithotrophic without shell. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Holocene.*

So far as is known, the unique feature of craniiforms is the tabular nature of the laminar secondary layer of the shell, which could also have been characteristic of the presumed aragonitic shells of trimerellides. Other features, which in combination are diagnostic of the subphylum Craniiformea, include the orthodoxly inarticulated condition of the shell (and its attendant muscle system) and the presence of an anus, which are typical of the linguliforms; shell composition and a single row of tentacles on the trocholophous lophophore, on the other hand, are shared with the rhynchonelliforms.

CRANIATA

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Class CRANIATA Williams & others, 1996

[Craniata WILLIAMS & others, 1996, p. 1192]

Characters as for subphylum. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Holocene.*

The classification of the calcareous-shelled inarticulated brachiopods has long been problematical; the trimerellides were assigned to the Lingulida and the craniides to the Acrotretida by ROWELL (1965a), while HELMCKE (1939) and HENNIG (1966) proposed that the morphology and anatomy of Holocene craniides indicate that they are more closely related to the articulated stocks now comprising the rhynchonellate and strophomenate members of the Rhynchonelliformea. The craniopsides have been referred by some authors to the Cranioidea (GORJANSKY, 1960; WILLIAMS, 1963) and by others to the Linguloidea (ROWELL, 1965a); COOPER (1956) placed them in the Paterulidae (within the Trimerelloidea). This confusing array of conflicting interpretations is probably due to the fact that it has been difficult previously to interpret the muscle scars on the extinct craniopsides and trimerellides, which have distinctive muscle platforms somewhat resembling those of some lingulide taxa such as *Lingulasma* and *Lingulops.* Moreover, the earliest evolutionary record of the three carbonate-shelled groups has been obscure; the earliest known true craniides, craniopsides, and trimerellides were long accepted as being from the Ordovician, making it possible to assume that they were derived from organophosphate-

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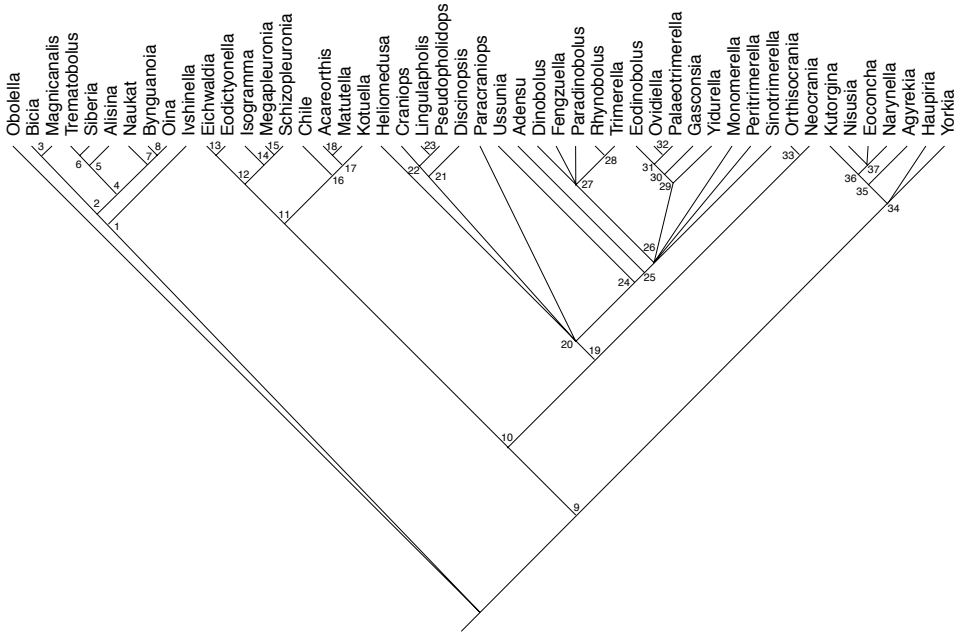

FIG. 88. Consensus tree (fifty-percent majority rule of 720 equally most parsimonious cladograms); numbered nodes supported by character states listed in Table 13 (new).

shelled ancestors at about that time (e.g., WILLIAMS & ROWELL, 1965b, fig. 141). A further problem has been the comparatively poor understanding of the ontogeny of the only surviving Holocene carbonate-shelled stock, the Craniida.

GORJANSKY and POPOV (1985, 1986), POPOV and others (1993), HOLMER and others (1995), and POPOV, HOLMER, and BASSETT (1996) proposed a classification in which the craniides, trimerellides, and craniopsides are sister groups within a monophyletic clade. Notwithstanding the equivocal relationships of the craniides as highlighted by some analyses (CARLSON, 1995; WILLIAMS & others, 1996), there is now a consensus of support for this model derived from a growing body of evidence (HOLMER & others, 1995; WILLIAMS & others, 1996). Support for this model now comes from a growing body of evidence: (1) the range of the nonpediculate, carbonate-shelled stocks has been extended down into the Lower Cambrian, through the discovery of the craniopside-like *Heliomedusa* from China (JIN & WANG, 1992); the problematical *Discinopsis* from the Middle Cambrian of Canada may also belong this group (POPOV, HOLMER, & BASSETT, 1996, p. 210); (2) the biochemistry of Holocene Craniida indicates that they may be quite unrelated to discinides and other organophosphate-shelled inarticulated brachiopods (JOPE, 1986; TUROSS & FISHER, 1989); (3) *Neocrania* lacks all trace of a pedicle throughout ontogeny, and the larva has no similarity to that of lingulides and discinides but is more similar to that of the articulated brachiopods in being lecithotrophic and lacking a protegulum and larval shell (NIELSEN, 1991); it is also clear that there is no trace of a larval shell and pedicle in the extinct trimerellides and craniopsides; (4) new, well-preserved material of trimerellides now shows that it is possible to interpret the muscle scars using Holocene craniides as a model (GORJANSKY & POPOV, 1985, 1986). It is also difficult to explain why the evolutionary transition from a phosphate-shelled

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TABLE 13. List of coded characters used in cladistic analysis (Fig. 88) of carbonate-shelled inarticulated brachiopods (new).

1. outline: subcircular (0); elongate oval (1); transversely oval (2); elongate semioval (3); transversely semioval (4); transversely subrectangular (5).
2. profile: equibiconvex (0); dorsibiconvex (1); ventribiconvex (2); planoconvex (3); convexoplane (4).
3. anterior commissure: rectimarginate (0); sulcate (1); uniplicate (2); bisulcate (3).
4. radial ornamentation: smooth (0); smooth apically, costellate peripherally (1); costate (2); coarsely costellate (3); finelly costellate (4); striated (5).
5. concentric ornamentation: fila (0); fine rugae (1); strong rugae (2).
6. growth lamellae: absent (0); present (1).
7. pustulose-spinose ornamentation: absent (0); pustulose (1); spinose (2).
8. pitted ornamentation: absent (0); present (1).
9. posterior commissure: straight wide (0); straight short (1); broadly convex; (2); short, convex (3).
10. delthyrial-notothyrial opening: narrow delthyrium (0); wide delthyrium and notothyrium (1); absent (2).
11. growth of dorsal valve: hemiperipheral (0); holoperipheral or mixoperipheral (1).
12. concave homeodeltidium: absent (0); narrow (1); wide (2).
13. pseudodeltidium: absent (0); apical (1); large, convex (2); concave (3).
14. chilidium: absent (0); forming single plate (1); forming two plates (2).
15. trimerellid ventral cardinal area: absent (0); low (1); high (2); vestigial (3).
16. inclication of trimerellid ventral cardinal area: orthocline or anacline (0); apsacline (1).
17. ventral interarea (width-length): absent (0); low, less than 50% (1); high, more than 50% (2).
18. inclination of ventral interarea: anacline (0); orthocline (1); apsacline (2); procline to catacline (3).
19. dorsal interarea (width-length): absent (0); low, less than 50% (1); high, more than 50% (2).
20. inclination of dorsal interarea: anacline (0); orthocline (1).
21. ventral pseudointerarea: absent (0); poorly defined laterally (1); well defined laterally (2).
22. dorsal pseudointerarea: absent (0); poorly defined laterally (1); well defined laterally (2).
23. pedicle opening: absent (0); delthyrial (1); posterior to apex (2); apical (3); anterior to apex (4).
24. ventral umbonal perforation: absent (0); small, apical (1); enlarged through resorption (2).
25. paired denticles: absent (0); consisting of secondary shell, located on delthyrial margins (1); located on anterise (2); consisting partly of primary shell, located on delthyrial margins (3).
26. sockets: absent (0); on sides of notothyrial cavity (1).
27. furrows along lateral sides of pseudodeltidium: absent (0); present (1).
28. hinge socket: absent (0); vestigial (1); well developed (2).
29. hinge plate: absent (0); vestigial (1); well developed (2).
30. kutorginid articulation: absent (0); present (1).
31. sockets and socket ridges composed partly of primary shell: absent (0); present (1).
32. oblique lateral muscles: absent (0); present (1).
33. internal oblique muscles: attached posterolaterally to dorsal valve (0); attached posteromedianly, but not serving as diductors (1); attached posteromedianly, serving as diductors (2).
34. *levator ani*: absent (0); present (1).
35. ventral muscle platform: absent (0); solid (1); free anteriorly (2); slightly vaulted anteriorly (3); strongly vaulted anteriorly (4).
36. dorsal muscle platform: absent (0); solid (1); slightly vaulted anteriorly (2); strongly vaulted anteriorly (3).
37. umbonal cavities: absent (0); vestigial (1); well defined (2).
38. cardinal process: absent (0); present (1).
39. ventral median structure: absent (0); ridge (1); septum (2); groove (3).
40. dorsal median structure: absent (0); ridge (1); septum (2); groove (3).
41. notothyrial platform: absent (0); present (1).
42. ventral median ridge or septum anterior to visceral area: absent (0); present (1).
43. dorsal median ridge or septum anterior to visceral area: absent (0); present (1).
44. ventral mantle canals: pinnate (0); bifurcate (1); baculate (2).
45. ventral *vascula lateralia:* absent (0); present (1).
46. ventral *vascula media:* absent (0); present (1).
47. dorsal mantle canals: pinnate (0); bifurcate (1); baculate (2).
48. dorsal *vascula lateralia:* absent (0); present (1).
49. dorsal *vascula media:* absent (0); present (1).
50. dorsal secondary shell layer: laminar (0); fibrous (1); shell aragonitic (2).
51. endopunctation: absent (0); simple pores (1); bifurcating pores.
52. attachment scar: absent (0); cicatrix (1); encrusting (2).
53. colleplax: absent (0); present (1).
54. dorsal adductors: dispersed (0); radial (1); quadripartite (2).

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ancestor to a carbonate shell in each of the three groups should have involved the repeated loss of a pedicle and larval shell; the change to an encrusting or free-lying mode of life occurred several times within the organophosphatic acrotretoids (*Eoconulus*) and linguloids (*Volborthia*), and in each of these groups traces of a pedicle and larval shell persist through ontogeny.

An analysis of 49 genera of carbonate-shelled brachiopods, including 23 trimerellides, craniopsides, and craniides, was performed using 54 unweighted, unordered characters, using the Obolellida as the root (Table 13, 15); these include the oldest known carbonate-shelled inarticulated brachiopods (PELMAN, 1977; POPOV, HOLMER, & BASSETT, 1996). Seven hundred twenty equally parsimonious trees 209 steps long were generated with a consistency index of 0.507 (heuristic search option, with character transformations following ACCTRAN optimization using PAUP 3.1.1; SWOFFORD, 1993). The consensus tree (Fig. 88; Table 14) is highly unresolved but gives support to the identity of the Trimerellida and Craniida as monophyletic orders. The Craniopsida as defined here, however, is not supported as a monophyletic group in our cladistic analysis; it possibly represents a paraphyletic stem-group.

Using the model proposed by GORJANSKY and POPOV (1985), the musculature of the craniopsides and trimerellides may have been closely similar to that of Holocene *Neocrania,* consisting of paired anterior and posterior adductors, oblique internal, and an unpaired median muscle (*levator* and *protrusor ani*); the oblique lateral muscles attached dorsally to the anterior body wall. In most craniiforms, the latter muscles may have served as a diductor by creating hydrostatic pressure in the body cavity, comparable with the model proposed erroneously by GUTMANN, VOGEL, and ZORN (1978) for the lingulides. Only the trimerellides seem to have developed a system with a diductor muscle analogous with that in rhynchonelliform articulated brachiopods (GORJANSKY & POPOV, 1985).

TABLE 14. Synapomorphy scheme for internal nodes of cladogram shown in Figure 88 (new).

Node	Character states						
1	25:3	35:1					
2	40:1						
3	1:1						
4	13:3	23:2	25:1	26:1	39:0		
5	2:2	6:1	23:3	54:2			
6	4:0	35:0	39:3				
7	1:2	4:2	25:2				
8	2:1						
9	4:0	39:0	41:0	44:0	46:1	47:0	50:1
10	19:0	20:0	32:1	51:1			
11	1:4	9:0	24:2	53:1			
12	32:0	38:2	40:2	43:1			
13	1:3	9:3	13:3	39:2			
14	2:3	5:2	18:0				
15	1:5	4:2	41:1				
16	2:1	11:0	33:1				
17	1:5	3:2					
18	4:2	53:0					
19	10:2	17:0	23:0	33:0	34:1	50:0	54:0
20	1:1	9:3	44:2	47:2	51:0		
21	35:1	36:1					
22	6:1						
23	21:1	22:1					
24	9:2	12:2	15:1	28:1	29:1	33:1	50:2
25	2:1	28:2	29:2	33:2	39:1		
26	12:1	35:3	36:2	43:1			
27	37:1	39:0	42:1				
28	12:2	35:4	36:1				
29	1:2	36:1					
30	6:1	35:1	43:0				
31	16:0	39:0	49:0				
32	1:0	15:2	44:1	47:1			
33	40:1	46:0					
34	9:2	10:1	13:2	27:1	30:1	45:0	48:0
35	17:2	20:1					
36	1:5	2:2	7:1	24:1			
37	3:1	4:4	7:2	9:0	31:1	41:1	

The mantle canal system of many craniiforms is relatively poorly known; it has been described from most craniides and a few trimerellides, but with the exception of the problematical *Heliomedusa* it is completely unknown for the craniopsides. Holocene craniides have only a single pair of main trunks in both valves, corresponding to the *vascula lateralia,* but some Lower Paleozoic forms (e.g., *Pseudocrania;* Fig. 89) have a dorsal *vascula media.* The trimerellides appear to have a mantle canal system similar to that of

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TABLE 15. Character-state matrix used in PAUP analysis (Fig. 88) of characters as listed in Table 13. Missing, polymorphic, or not applicable data coded as 9 (new).

Character no.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Obolella	0	0	0	5	0	1	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	0	0	0
Bicia	1	0	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	3	0	0
Ivshinella	0	1	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	3	0	0
Magnicanalis	1	0	0	5	0	0	0	0	1	0	1	0	0	0	0	9	1	2	1	1	0	0	1	0	9	0	0
Trematobolus	0	2	0	0	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	4	0	1	1	0
Alisina	0	2	0	5	0	1	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	3	0	1	1	0
Siberia	0	2	0	0	0	1	0	0	1	0	1	0	3	0	0	9	1	3	1	1	0	0	3	0	1	1	0
Naukat	2	0	2	2	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	2	0	2	1	0
Bunguanoia	2	1	1	2	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	2	0	2	1	0
Oina	2	1	0	0	0	0	0	0	1	0	1	0	3	0	0	9	1	2	1	1	0	0	0	0	2	1	0
Eichwaldia	3	0	0	0	0	0	0	0	3	0	1	0	3	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Dictyonella	3	0	0	0	0	1	0	1	3	0	1	0	3	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Isogramma	4	3	0	0	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Megapleuronia	5	3	0	2	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Schizopleuronia	5	3	1	2	2	0	0	0	0	0	1	0	0	0	0	9	1	0	0	9	0	0	1	2	0	0	0
Chile	4	2	0	1	0	0	0	0	0	0	0	0	1	0	0	9	1	1	0	9	0	0	1	2	0	0	0
Acareorthis	5	3	3	2	0	1	0	0	0	0	0	0	2	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Matutella	5	1	2	4	0	0	0	0	0	0	0	0	0	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Kotuella	5	1	2	0	0	0	0	0	0	0	0	0	0	0	0	9	1	2	0	9	0	0	1	2	0	0	0
Kutorgina	6	2	0	0	2	1	1	0	2	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Yorkia	0	0	0	0	0	0	0	0	2	1	1	0	2	0	0	9	1	2	1	1	0	0	1	1	0	0	1
Haupiria	0	0	0	0	0	0	0	0	2	1	1	0	2	0	0	9	1	2	1	1	0	0	1	0	0	0	1
Agyrekia	0	0	0	5	1	0	0	0	2	1	1	0	2	1	0	9	2	3	2	0	0	0	1	0	0	0	1
Nisusia	5	2	0	4	0	0	2	0	0	1	1	0	2	0	0	9	2	3	1	0	0	0	1	1	0	0	1
Eoconcha	5	2	1	3	0	0	0	0	0	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Narynella	5	2	1	4	0	0	2	0	0	1	1	0	2	0	0	9	2	2	1	0	0	0	1	1	0	0	1
Heliomedusa	0	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	0	0	0	0	0	9
Craniops	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Discinopsis	0	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Lingulapholis	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	1	0	0	0	0	9
Paracraniops	1	0	0	0	0	0	0	0	3	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Pseudopholidops	1	0	0	0	0	1	0	0	3	2	1	0	9	9	0	9	0	9	0	9	1	1	0	0	0	0	9
Ussunia	1	0	0	0	0	0	0	0	2	2	1	2	9	9	3	1	0	9	0	9	0	0	0	0	0	0	9
Adensu	1	1	0	0	0	0	0	0	2	2	1	2	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Dinobolus	0	0	0	0	0	1	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Eodinobolus	2	1	0	0	0	1	0	0	2	2	1	1	9	9	1	0	0	9	0	9	0	0	0	0	0	0	9
Fengzuella	0	1	0	0	0	0	0	0	2	2	1	1	9	9	1	9	0	9	0	9	0	0	0	0	0	0	9
Gasconsia	2	4	0	0	0	1	0	0	0	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Monomerella	1	1	0	0	0	1	0	0	2	2	1	2	9	9	2	1	0	9	0	9	0	0	0	0	0	0	9
Ovidiella	0	1	0	0	0	1	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Palaeotrimerella	1	1	0	0	0	1	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Paradinobolus	1	1	0	0	0	0	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Peritrimerella	0	4	0	0	0	0	0	0	2	2	1	2	9	9	1	9	0	9	0	9	0	0	0	0	0	0	9
Rhynobolus	1	1	0	0	0	0	0	0	2	2	1	2	9	9	2	1	0	9	0	9	0	0	0	0	0	0	9
Sinotrimerella	1	1	0	0	0	0	0	0	2	2	1	1	9	9	2	0	0	9	0	9	0	0	0	0	0	0	9
Trimerella	1	1	0	0	0	0	0	0	2	2	1	2	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Yidurella	2	0	0	0	0	0	0	0	2	2	1	1	9	9	1	1	0	9	0	9	0	0	0	0	0	0	9
Orthisocrania	0	0	0	3	0	0	0	0	1	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9
Neocrania	0	4	0	0	0	0	0	0	1	2	1	0	9	9	0	9	0	9	0	9	0	0	0	0	0	0	9

the craniides, but it differs in some genera (*Palaeotrimerella*) that have *vascula media* in the ventral valve, while others (*Monomerella* and *Gasconsia*) appear to have *vascula media* in both valves (HOLMER & POPOV in WILLIAMS, BRUNTON, & MACKINNON, 1997, fig. 386.2).

Heliomedusa is characterized by the presence of dorsal *vascula media* and *vascula lateralia;* the ventral mantle canals are poorly known, but apparently the *vascula lateralia* are developed (JIN & WANG, 1992).

Marginal mantle setae were long thought to be absent in craniides, but NIELSEN (1991) has now demonstrated their presence in juvenile *Neocrania.* Firm evidence of setae is generally lacking for most fossil craniiformeans, but they have been described from *Helio-*

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TABLE 15. *(Continued).*

Character no.	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54
Obolella	0	0	0	0	9	1	0	0	0	0	0	3	0	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Bicia	0	0	0	0	9	2	0	1	0	0	0	3	1	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Ivshinella	0	0	0	0	9	2	0	1	0	0	0	3	0	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Magnicanalis	0	0	0	0	9	2	0	1	0	0	0	1	1	1	0	0	2	1	0	2	1	1	9	0	0	0	1
Trematobolus	0	0	0	0	9	2	0	0	0	0	0	3	1	1	0	0	2	1	0	2	1	1	0	0	0	1	2
Alisina	0	0	0	0	9	2	0	1	0	0	0	0	1	1	0	0	2	1	0	2	1	1	9	0	0	0	2
Siberia	0	0	0	0	9	2	0	0	0	0	0	3	1	1	0	0	2	1	0	2	1	1	9	0	0	0	2
Naukat	0	0	0	0	0	2	0	1	1	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Bunguanoia	0	0	0	0	0	2	0	1	0	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Oina	0	0	0	0	0	2	0	2	0	0	0	0	1	1	0	0	9	9	9	9	9	9	9	9	0	0	1
Eichwaldia	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	1	9	9	9	9	9	9	9	9	0	1	9
Dictyonella	0	0	0	0	0	2	0	0	0	0	1	2	2	0	0	1	9	9	9	9	9	9	1	1	0	1	9
Isogramma	0	0	0	0	0	2	0	0	0	0	1	0	2	0	0	1	9	9	9	9	9	9	9	9	0	1	9
Megapleuronia	0	0	0	0	0	2	0	9	3	0	1	9	1	1	0	1	9	9	9	0	9	9	9	9	0	1	9
Schizopleuronia	0	0	0	0	0	2	0	0	0	0	1	0	2	1	0	1	9	9	9	9	9	9	9	9	0	1	9
Chile	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	9	9	9	1	9	9	9	0	1	1
Acareorthis	0	0	0	0	9	1	0	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	9
Matutella	0	0	0	0	9	9	0	0	0	0	0	0	0	0	0	0	0	9	9	0	9	9	9	9	0	0	9
Kotuella	0	0	0	0	9	9	0	0	9	0	9	0	0	9	0	9	9	9	9	9	9	9	1	1	0	1	9
Kutorgina	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	9	9	9	9	9	9	9	0	0	1
Yorkia	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	9	0	1	0	0	9	9	9	0	0	9
Haupiria	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	9
Agyrekia	0	0	1	0	9	2	0	0	0	0	0	0	1	0	0	0	9	9	9	0	9	9	9	9	0	0	1
Nisusia	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0	9	9	0	9	9	1	0	0	0	1
Eoconcha	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	9	9	9	9	9	9	9	0	0	0	9
Narynella	0	0	1	1	0	2	0	0	0	0	0	0	0	1	0	0	0	9	9	0	9	9	1	0	0	0	1
Heliomedusa	0	0	9	9	1	0	9	0	0	0	0	0	0	0	0	0	2	1	9	2	1	1	9	9	0	0	0
Craniops	0	0	9	9	1	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	9	0	0	1	0
Discinopsis	0	0	9	9	9	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	9	9	0	0	0
Lingulapholis	0	0	9	9	1	0	9	1	1	0	0	0	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Paracraniops	0	0	9	9	1	0	9	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Pseudopholidops	0	0	9	9	1	0	9	0	0	0	0	1	0	0	0	0	9	9	9	9	9	9	0	0	0	0	0
Ussunia	1	1	9	9	1	1	1	0	0	0	0	0	0	0	0	0	9	9	9	9	9	9	2	9	0	0	0
Adensu	2	2	9	9	0	2	1	0	0	0	0	1	0	0	0	0	0	1	1	9	9	9	2	9	0	0	0
Dinobolus	2	2	9	9	1	2	1	4	2	1	0	0	0	0	1	1	9	9	9	2	1	9	2	9	0	0	0
Eodinobolus	2	2	9	9	1	2	1	1	1	0	0	0	0	0	0	0	2	1	1	2	1	0	2	9	0	0	0
Fengzuella	2	2	9	9	9	2	9	3	2	1	0	1	1	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Gasconsia	1	1	9	9	1	2	1	1	1	0	0	1	0	0	0	0	2	1	9	2	1	1	2	9	0	0	0
Monomerella	2	2	9	9	1	2	1	1	2	2	0	1	0	0	0	1	2	1	1	9	9	9	2	9	0	0	0
Ovidiella	2	2	9	9	1	2	1	1	1	0	0	0	0	0	0	0	1	1	1	1	1	0	2	9	0	0	0
Palaeotrimerella	2	2	9	9	1	2	1	1	1	0	0	1	1	0	0	1	1	1	1	1	1	0	2	9	0	0	0
Paradinobolus	2	2	9	9	9	2	9	3	2	1	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Peritrimerella	2	2	9	9	9	2	9	3	2	0	0	0	0	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Rhynobolus	2	2	9	9	9	2	9	4	1	1	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Sinotrimerella	2	2	9	9	9	2	9	3	2	0	0	9	0	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Trimerella	2	2	9	9	1	2	1	4	3	2	0	0	0	0	1	1	9	9	9	9	9	9	2	9	0	0	0
Yidurella	2	2	9	9	9	2	9	3	1	0	0	1	1	0	0	1	9	9	9	9	9	9	2	9	0	0	0
Orthisocrania	0	0	9	9	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	1	0	1	0	0	0
Neocrania	0	0	9	9	1	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0	0	2	2	0	0

medusa (JIN & WANG, 1992). JIN and WANG (1992) concluded that *Heliomedusa* might be an early representative of a lineage of nonpediculate brachiopods independent from that of the lingulides. With the model adopted here it is likely that the morphology of such a craniopside-like brachiopod may have been close to that of the earliest common ancestor of the craniiforms.

The main radiation of the craniiforms apparently took place during the Early Ordovician, although their origin remains obscure. The Trimerellida tend to form large, heavy shells that appear to have been aragonitic in composition (JAANUSSON, 1966). This group also has a unique articulatory structure, consisting of a dorsal hinge plate fitting tightly into a ventral cardinal socket.

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This type of morphology is present already in the earliest trimerellides, the Ussuniidae of Llandeilo age; these shells are among the largest known Ordovician brachiopods. According to GORJANSKY and POPOV (1986) the Ussuniidae may be related closely to the craniopsides, and although the former can be over ten times larger than the latter, they show similarities in the shape of the pseudointerareas as well as the development of the visceral areas and main muscle scars.

CRANIOPSIDA

L. E. POPOV and L. E. HOLMER
[VSEGEI, St. Petersburg; and University of Uppsala]

Order CRANIOPSIDA Gorjansky & Popov, 1985

[Craniopsida GORJANSKY & POPOV, 1985, p. 12]

Shell biconvex, elongate oval to subcircular; visceral area of both valves extending anterior to midvalve; scars of dorsal oblique internal muscles situated posterolaterally; cemented at apical region of ventral valve, or free lying; shell calcitic, impunctate. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

The morphology of craniopsides is simple, and taxa within the order can be defined only on characters such as the presence or absence of pseudointerareas, visceral platforms, median ridges, position of the umbo, and presence of attachment scar (cicatrix). The shell is usually equally biconvex, with the umbo situated marginally or posteriorly. Only some craniopsids (*Lingulapholis, Pseudopholidops*) have well-developed pseudointerareas.

The craniopside muscle system is here modeled after that of the Craniida (Fig. 90); however, alternative reconstructions, based mainly on the pattern of muscles present in lingulides, have also been proposed. MERGL (1986), for example, suggested that the unpaired posteromedian scar might correspond to the lingulide umbonal muscle, but with the view adopted here it corresponds to the unpaired median muscle (*levator* and *protrusor ani*) of craniides (Fig. 90). According to MERGL, the remaining three paired dorsal and four ventral muscle scars can be correlated with the lingulide transmedian, anterior lateral, middle lateral, and central muscle scars; but the transmedian and central scars are also comparable with the craniide anterior and posterior adductors; the dorsal middle lateral scars may correspond to the craniide internal oblique muscles that were attached to the anterior part of the ventral median ridge. The ventral anterior lateral scars may have represented the oblique lateral muscles that were attached to the anterior body wall, while the dorsal anterior lateral may be similar to the brachial protractor muscles of craniides (Fig. 90).

Superfamily CRANIOPSOIDEA Williams, 1963

[*nom. transl.* HARPER in HARPER & others, 1993, p. 430, *ex* Craniopsidae WILLIAMS, 1963, p. 346]

Characters as for order. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

Family CRANIOPSIDAE Williams, 1963

[Craniopsidae WILLIAMS, 1963, p. 346] [=Pholidopsidae GORJANSKY, 1960, p. 177]

Characters as for superfamily. *Lower Cambrian (?Botomian), Middle Cambrian, Ordovician–Lower Carboniferous (Tournaisian).*

Craniops HALL, 1859b, p. 84 [**?Orbicula squamiformis* HALL, 1843a, p. 108; OD] [=*Pholidops* HALL, 1859a, p. 489, obj.]. Shell subequally biconvex, elongate oval, lamellose; both valves with growth holoperipheral, umbones posterior to center; visceral areas of both valves elevated anteriorly, forming low platforms; both valves with limbus; attached apically by cementation. *Ordovician (Caradoc)–Lower Carboniferous (Tournaisian):* Canada, *?Upper Ordovician, Silurian–Devonian;* USA, *?Upper Ordovician, Silurian–Tournaisian;* Poland, *Caradoc–Silurian;* China, Australia, Brazil, *Silurian–*

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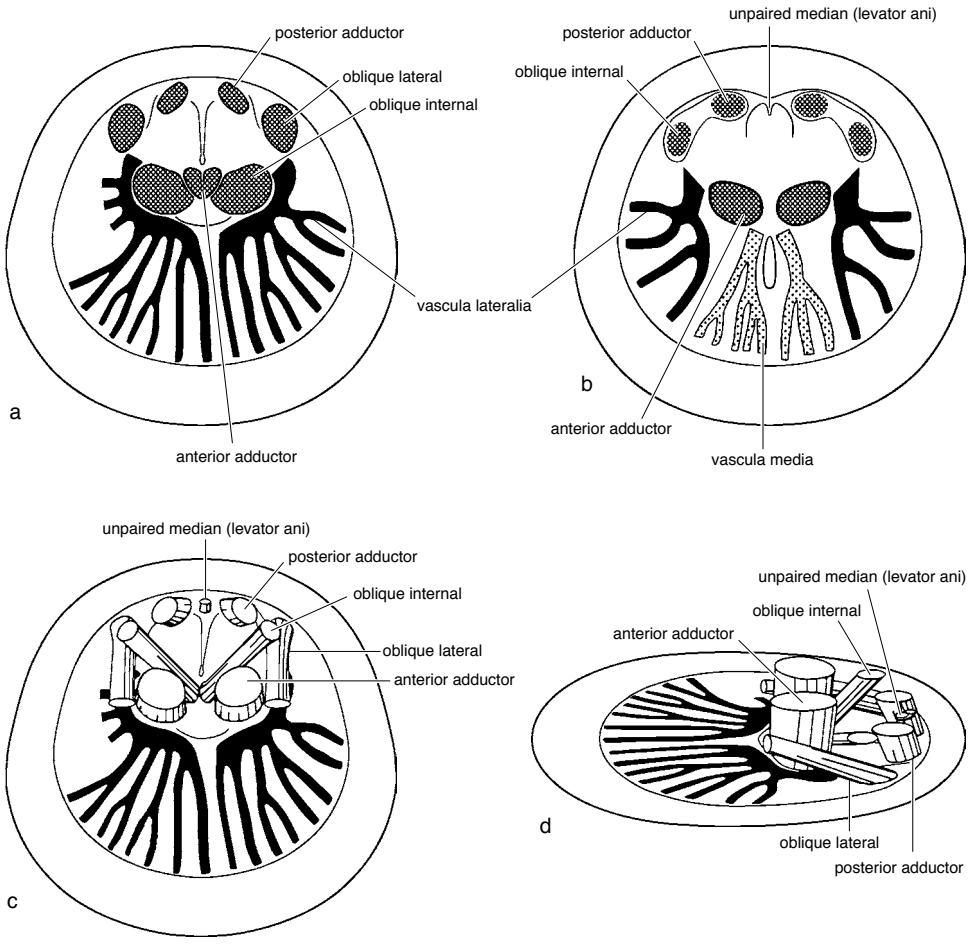

FIG. 89. Schematic illustration of musculature and mantle canal system of *Pseudocrania; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (Bassett, new).

Devonian; Portugal, Great Britain, Sweden, Bohemia, Estonia, *Silurian;* Colombia, *Devonian.* ——FIG. 91,*3a–e. C. implicata* (SOWERBY), Wenlock, Mulde beds, Fröjel, Gotland, Sweden; *a,* dorsal valve exterior, RM Br 24306a, ×15; *b,* lateral view of both valves, RM Br 24306b, ×25; *c,* ventral valve interior, ×19.2; *d,* oblique lateral view of ventral interior, RM Br 24306c, ×37.5; *e,* dorsal valve interior, RM Br 24306d, ×26.7 (new).

?Discinopsis MATTHEW in HALL & CLARKE, 1892, p. 105 [**?Acrotreta gulielmi* MATTHEW, 1886, p. 37; OD]. Genus inadequately known; shell probably biconvex, flattened, subcircular; growth apparently holoperipheral in both valves, umbones posterior to center; interiors of both valves poorly known, but with low visceral platforms bounded laterally by ridges. *Middle Cambrian:* Canada (New Brunswick).——FIG. 91,*1a–c. *D. gulielmi* (MATTHEW), Seely Limestone, New Brunswick (St. John), Canada, paralectotypes; *a,* internal mold, ROM 642CM(D); *b,* external mold, ROM 642CM(F); *c,* internal mold, ROM 642CM(E), ×8.3 (new).

?Heliomedusa SUN & HOU, 1987, p. 261[269] [**H. orienta;* OD]. Shell biconvex, inequivalved, subcircular; mixoperipheral growth in ventral valve, with beak marginal, and well-defined pseudointerarea; holoperipheral growth in dorsal valve, apex placed posterior to center; visceral area of both valves thickened slightly anteriorly, extending anterior to center; mantle canal system of both valves baculate; dorsal mantle canals with *vascula media* and *vascula lateralia. Lower Cambrian (?Botomian):* China (Yunnan).——FIG. 92,*1a–d. *H. orienta,* Chiungchussu Formation, Chengjiang; *a,* internal cast of both valves, NIGP 113927, ×2.5; *b,* dorsal internal mold, NIGP 100301, ×6.7; *c,* dorsal internal mold, NIGP 113930, ×6.7; *d,* setae around the margin of dorsal and ventral valves, NIGP 100282, ×6.7 (Jin & Wang, 1992).

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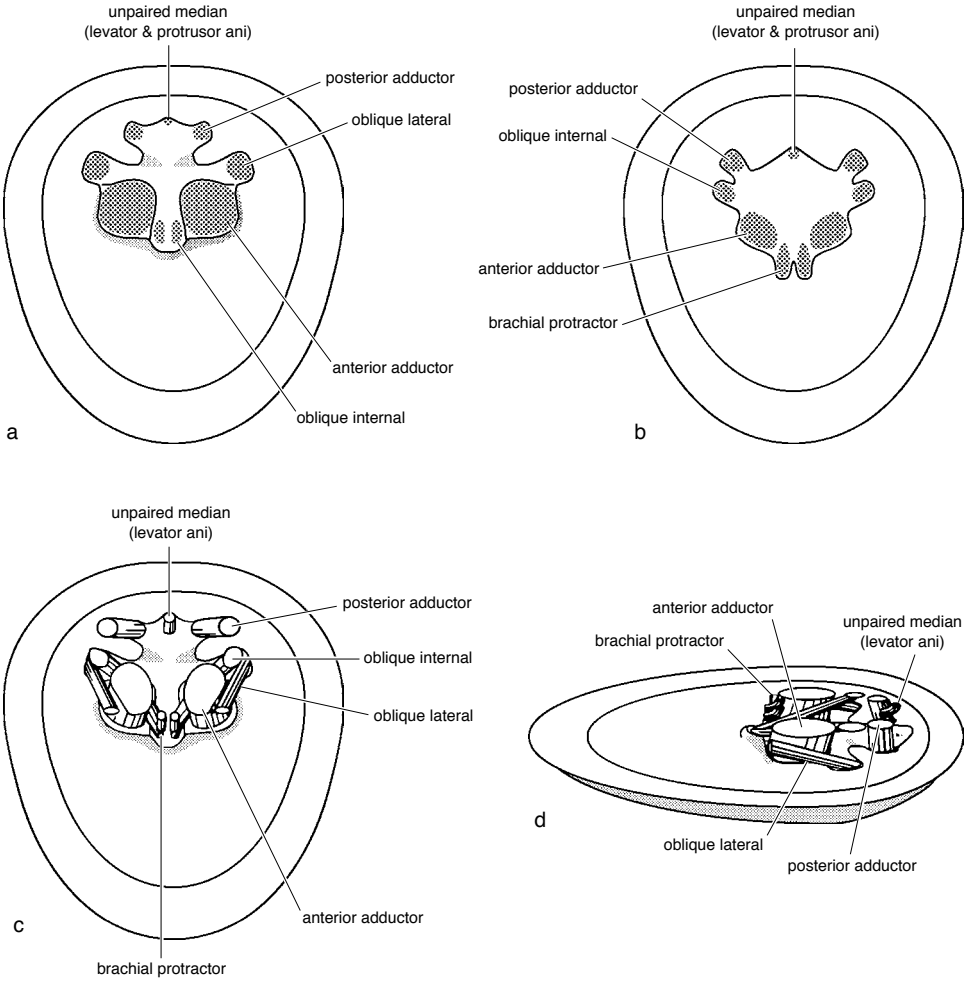

FIG. 90. Schematic illustration of musculature of *Craniops; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

Lingulapholis SCHUCHERT, 1913b, p. 295 [**Pholidops terminalis* HALL, 1859a, p. 490; OD]. Shell subequally biconvex, elongate oval, lamellose; mixoperipheral growth in both valves, marginal beaks, and well-developed pseudointerareas; visceral areas of both valves elevated anteriorly, forming low platforms; both valves with limbus; free lying. *Devonian:* USA, Colombia.——FIG. 91,*2a. *L. terminalis* (HALL), Becraft Mountain, New York (Hudson), USA; cast of dorsal internal mold, NYSM 1745, ×4.2 (new).——FIG. 91,*2b–f. L. calceola* (HALL & CLARKE), Camden Chert Quarry, Tennessee, USA; *b,* ventral valve exterior, USNM 459665c, ×8.3; *c,* ventral valve interior, USNM 459665d, ×10; *d,e,* dorsal valve exterior, oblique lateral view, USNM 459665a, ×10; *f,* dorsal valve interior, USNM 459665b, ×10 (new).

Paracraniops WILLIAMS, 1963, p. 346 [**Craniops pararia* WILLIAMS, 1962, p. 88; OD]. Externally similar to *Craniops,* but lacking cicatrix and dorsal visceral platform; dorsal interior with two low ridges. *Ordovician (Caradoc)–Silurian (Llandovery):* Turkey, China, *Caradoc;* Kazakhstan, *Caradoc–Llandovery;* Great Britain, *Caradoc–?Llandovery;* Sweden, Russia (Taimyr), *Ashgill;* Canada (Nova Scotia), *Llandovery.*——FIG. 92,*2a–c. *P. pararia* (WILLIAMS), Lower Ardmillan Series, Girvan, Scotland; *a,* paratype, ventral internal mold, BMNH BMNH 29799, ×8.3; *b,* paratype, dorsal external mold, ×8.3; *c,* holotype, dorsal internal mold, BMNH BB 26709, ×8.3 (Williams, 1962).

Pseudopholidops BEKKER, 1921, p. 64 [**Pholidops scutellata;* OD] [=*Sanxiaella* RONG & CHANG in CHANG, 1981, p. 558[565] (type, *Paracraniops*

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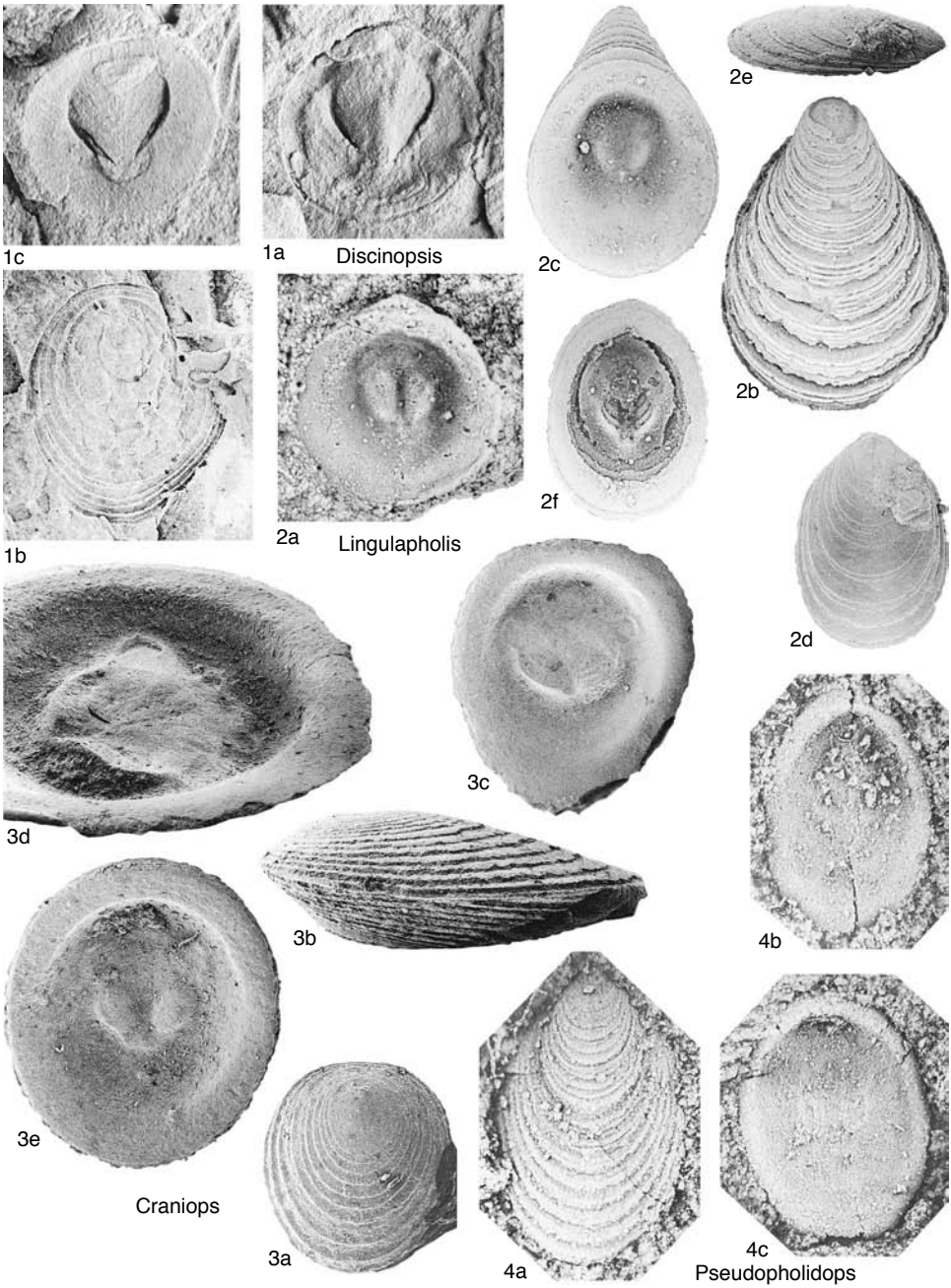

FIG. 91. Craniopsidae (p. 164–167).

partibilis RONG, 1979, p. 2)]. Externally like *Lingulapholis,* but with ventral median ridge and less thickened visceral areas. *Ordovician (Llandeilo–Ashgill):* Estonia, Lithuania, Bohemia, China.——FIG. 91,*4a–c. *P. scutellata* (BEKKER), Kohtla-Järve, Estonia; *a,* dorsal valve exterior, TAGI BR 3507, ×17.5; *b,* dorsal valve interior, TAGI BR 3508, ×15.8; *c,* ventral valve interior, TAGI BR 3509, ×16.7 (new).

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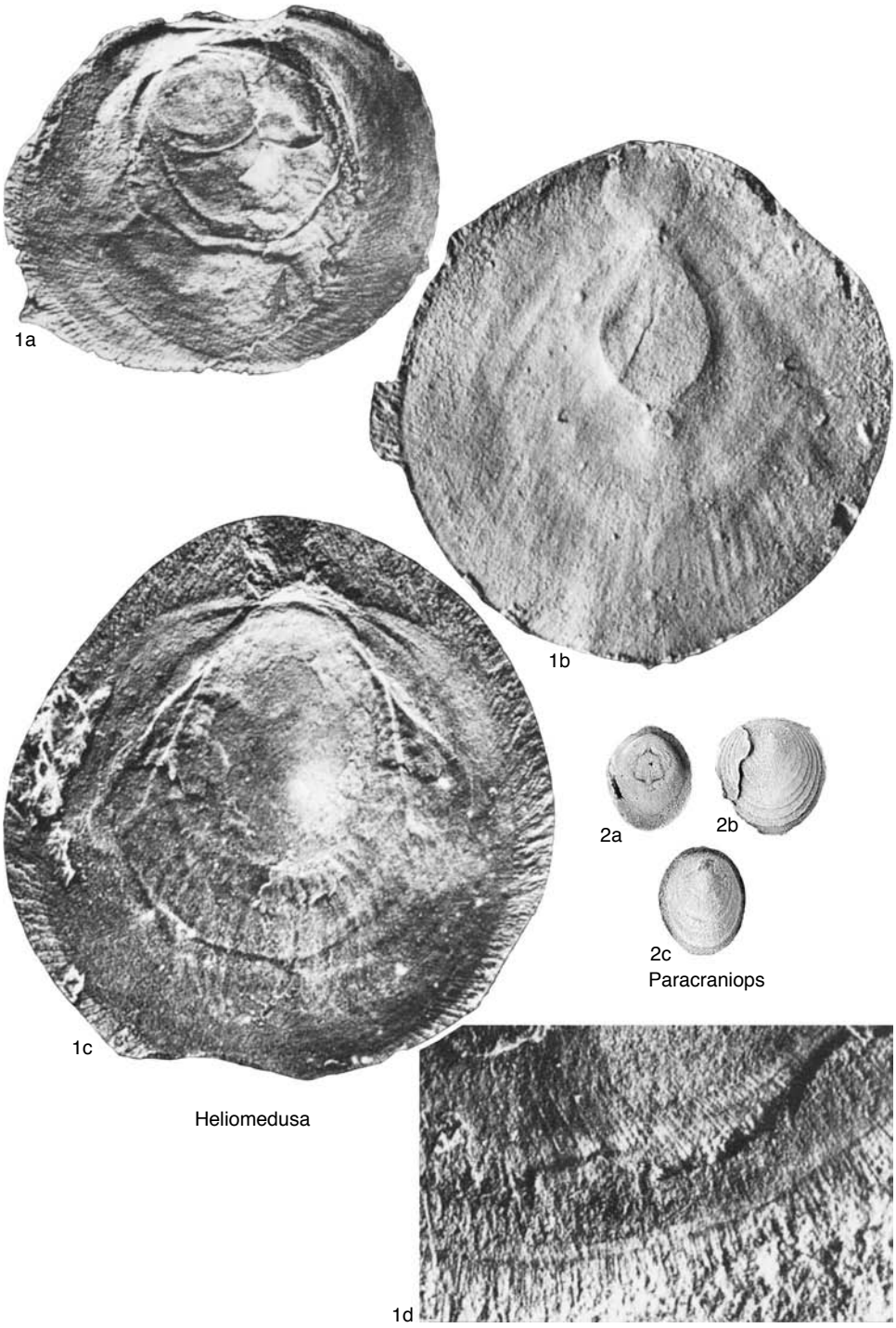

FIG. 92. Craniopsidae (p. 165–166).

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CRANIIDA

MICHAEL G. BASSETT
[National Museum of Wales]

Order CRANIIDA Waagen, 1885

[*nom. transl. et correct.* KUHN, 1949, p. 99, *ex* suborder Craniacea WAAGEN, 1885, p. 744] [=Gasteropegmata WAAGEN, 1885, p. 744, *partim;* Gastropegmata HALL & CLARKE, 1894a, p. 326, *partim;* Craniidina ROWELL, 1965a, p. 288, *partim*]

Dorsal valve invariably calcified, punctate; ventral valve in some taxa without secondary shell or entirely periostracal; mantle setae present in recent forms; shell growth generally holoperipheral, rarely mixoperipheral; dorsal valve convex to subconical, ventral valve plane to convex or encrusting; dorsal body wall of recent forms attached to dorsal valve in five separate areas; attachment scars of dorsal internal oblique muscles situated posterolaterally; mantle canal system pinnate, only rarely with *vascula media. Ordovician (upper Arenig)–Holocene.*

The earlier record of a single species of craniide from the Middle Cambrian (*?Crania columbiana* WALCOTT, 1889) is now known to be unfounded (BASSETT, unpublished). In the oldest known genus (*Pseudocrania*) from the Lower Ordovician, the pattern of the musculature and vascular system (Fig. 93) already heralds that of recent *Neocrania* and indicates a remarkably stable anatomical organization throughout the preserved history of the group.

Similar stability is recorded in the structural evolution of the dorsal valve, composed of primary acicular and secondary laminar calcitic layers permeated by punctae, and whose fabric is probably close to that of the craniide ancestor (WILLIAMS & WRIGHT, 1970). By contrast, the history of ventral shell secretion displays considerable variation, including the loss of punctation in one genus (*Petrocrania*). Such variation was initiated following the loss of a pedicle in the craniide prototype and the subsequent adoption of a ventrally cemented or encrusting mode of life by some genera (WILLIAMS & WRIGHT, 1970, p. 48; see also below).

NIELSEN's (1991) study of larval development in *Neocrania* confirms that a pedicle is

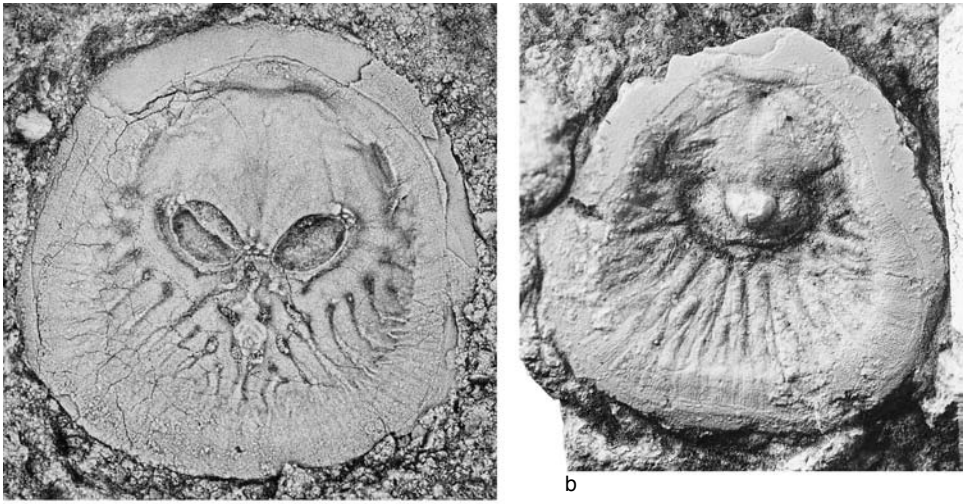

FIG. 93. Dorsal and ventral musculature and vascular systems of *Pseudocrania petropolitana* (PANDER); *a,* dorsal interior, Volkhov, Ordovician, Hälluden, Öland, Sweden, RM Br15082, ×2.7 (new); *b,* ventral interior, Volkhov, Ordovician, Voronino, Ingria, Russia, VSEGEI 113/9960, ×3 (Gorjansky, 1969).

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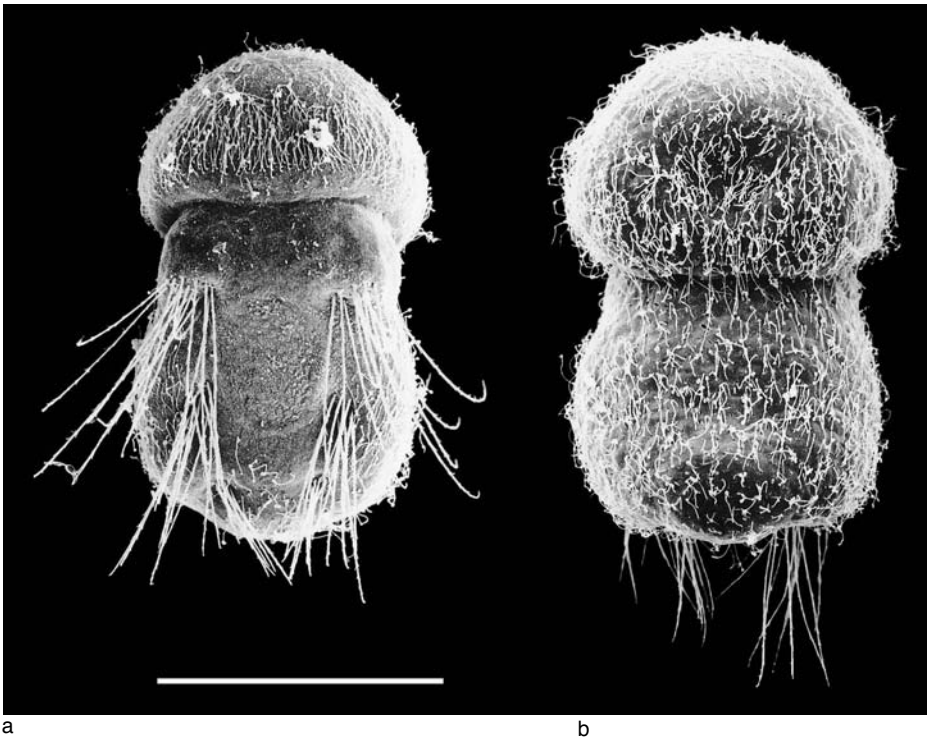

FIG. 94. Fully grown larvae of *Neocrania anomala* (MÜLLER) in *a,* dorsal and *b,* ventral views, showing setae and absence of larval shell; Holocene, off west coast of Sweden, scale bar: 100 mm (Nielsen, 1991).

lacking throughout ontogeny, and that, as in articulated brachiopods, no larval shell is developed (Fig. 94). His identification of marginal larval setae (Fig. 95) gives strong support to the view of brachiopod monophyly. The complex metamorphosis involved in larval development and settlement includes some change in direction of alignment of the setae, which suggests that some kind of mantle reversion takes place and which also supports a close relationship between the craniides and articulated rhynchonelliform stocks.

Superfamily CRANIOIDEA Menke, 1828

[*nom. correct.* HARPER in HARPER & others, 1993, p. 431, *pro* Craniacea SCHUCHERT, 1896, p. 310, *nom. imperf.; nom. transl. ex* Craniidae KING, 1846, p. 28; *nom. correct. pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*]

Characters as for order. *Ordovician (upper Arenig)–Holocene.*

Classification of the craniides within a single family is further recognition of their evolutionary stability. The Eoconulidae, previously assigned provisionally to this group (ROWELL, 1965a, p. 288), have organophosphatic shells and are now included in the Acrotretoidea (ROWELL & KRAUSE, 1973, p. 798; HOLMER, 1989b, p. 147). The establishment of a separate family to accommodate the free-lying *Pseudocrania* and *Orthisocrania* (POPOV in POPOV & PUSHKIN, 1986, p. 16) is unwarranted; although both these genera have a fully developed secondary laminar shell layer in the ventral valve, unlike that of encrusting taxa (WILLIAMS & WRIGHT, 1970, p. 42), the secretory regime of the dorsal valve is identical to that of all other craniides. Modifications of ventral shell fabric reflect accommodation to a cementing or encrusting life strategy that took place a number of times in the history of the craniides; this life strategy has no taxonomic significance.

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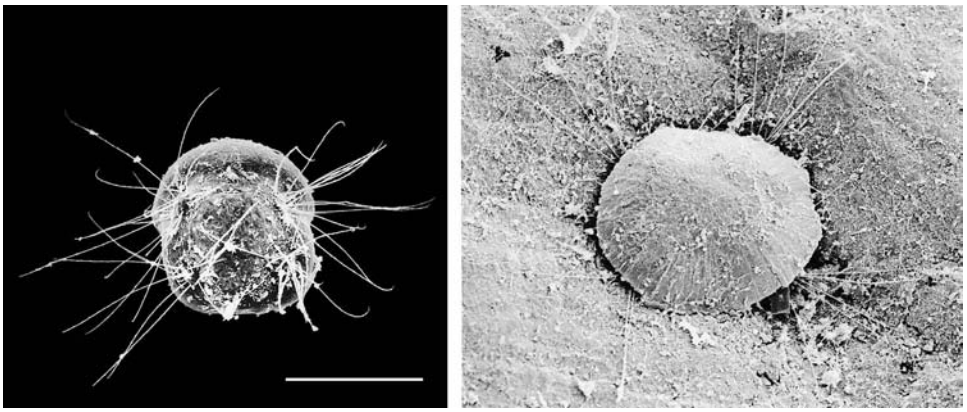

a b

FIG. 95. Development of setae in early ontogentic stages of *Neocrania anomala* (MÜLLER), showing *a,* early larval stage of dorsal valve, and *b,* juvenile with early shell about three days after settling; Holocene, off west coast of Sweden, scale bar: 100 mm (Nielsen, 1991).

Family CRANIIDAE Menke, 1828

[*nom. correct.* GRAY, 1840, p. 155, *pro* Craniaceae MENKE, 1828, p. 56, *nom. imperf.*] [=family Craniacea MENKE, 1830, p. 96; Craniadae FORBES, 1838, p. 38] [*incl.* Valdiviathyridae, *nom. correct.* ROWELL, 1965a, p. 289, *pro* Valdiviathyridae HELMCKE, 1940, p. 235, *nom. imperf.;* Pseudocraniidae POPOV in POPOV & PUSHKIN, 1986, p. 16]

Characters as for order. *Ordovician (upper Arenig)–Holocene.*

Crania RETZIUS, 1781, p. 72 [**Anomia craniolaris* LINNAEUS, 1758, p. 700; SD SCHMIDT, 1818, p. 71]. Dorsal valve subconical to conical; ventral valve convex, attached posteriorly at large cicatrix; beaks posterocentral; dorsal posterior face steep; pseudointerarea commonly developed; dorsal posterior margin straight; smooth with only faint growth laminae; ventral musculature deeply incised, posterior scars marginal, directed posteriorly, often perforating the valve externally; anterior scars central, united across rounded median ridge, with bounding rim; dorsal posterior adductors large, thickened, weak myophragm extending into anterior half of valve; well-developed, thickened, pustulose limbus. *Upper Cretaceous (Campanian–Maastrichtian):* Sweden, Denmark, France, Netherlands, Belgium, western Russia.——FIG. 96,*1a–k.* **C. craniolaris* (LINNAEUS); *a–c,* paralectotype, dorsal valve interior, exterior, lateral, lower Campanian chalk, Ivö, Scania, southern Sweden, LS 183C, ×3 (Lee & Brunton, 1986); *d,e,* ventral valve interior, exterior, lower Campanian chalk, Kristianstad, Scania, southern Sweden, PM Sk96, ×3; *f,g,* ventral valve interior, exterior with musculature perforating the posterior tip of the valve, lower Campanian chalk, Kristianstad, PM Sk97, ×3; *h,i,* ventral valve interior, exterior with large cicatrix, lower Campanian chalk, Ivö, RM Br 102250, ×3; *j,k,* dorsal valve interior, lateral, Senonian, Barnakälla, Scania, RM Br 94816, ×3 (new).

Acanthocrania WILLIAMS, 1943, p. 71 [**Crania spiculata* ROWLEY, 1908, p. 74; OD] [=?*Choniopora* VON SCHAUROTH, 1854, p. 546 (type, *C. radiata*); ?*Punctopatella* GRUBBS, 1939, p. 559 (type, *P. corallifera*); *Celidocrania* LIU, ZHU, & XUE, 1985, p. 9[40] (type, *C. luohoensis*)]. Dorsal valve convex to subconical; ornament of fine papillae disposed concentrically with coarser, hollow spines; beak excentric; posterior face normally steep; anterior adductor scars generally larger than posterior pair; muscle field bisected by weak myophragm; valve margin not thickened; limbus developed rarely; encrusting; ventral valve unknown. *Ordovician (Caradoc [upper Champlainian])–Lower Carboniferous:* cosmopolitan.——FIG. 97,*1a–c. A. spinosa* RODRIGUEZ & GUTSCHICK, Sappington Formation, unit E (lower Mississippian), Antelope Valley, western Montana; *a,b,* holotype, dorsal valve exterior, lateral, UND 352, ×3; *c,* paratype, dorsal valve exterior, UND 353, ×3 (Rodriguez & Gutschick, 1967).——FIG. 97,*1d–g. A. papillifera* (ROEMER), Ashgill, near Llanfyllin, North Wales; *d–f,* latex cast of dorsal valve exterior, internal mold, lateral, ×3; *g,* detail of ornamentation on anterolateral surface, BMNH BB34089, ×5 (Wright, 1972).

Ancistrocrania DALL, 1877, p. 13, *nom. subst. pro Cranopsis* DALL, 1871b, p. 27, *non* ADAMS, 1860 [**Crania parisiensis* DEFRANCE, 1818, p. 313; OD]. Ventral valve attached across entire surface and commonly simulating ornament of host; dorsal beak central; anterior face convex; posterior face long, concave; anterior dorsal adductors borne partly on two widely divergent, posterlaterally directed processes separated by short, high septum extending anteriorly as slender ridge; ventral anterior scars central, deeply incised; ventral rim commonly thickened, elevated as crest. *Upper Cretaceous (Coniacian–Maastrichtian), lower Paleogene (?Danian):* France, Belgium, Netherlands, Sweden,

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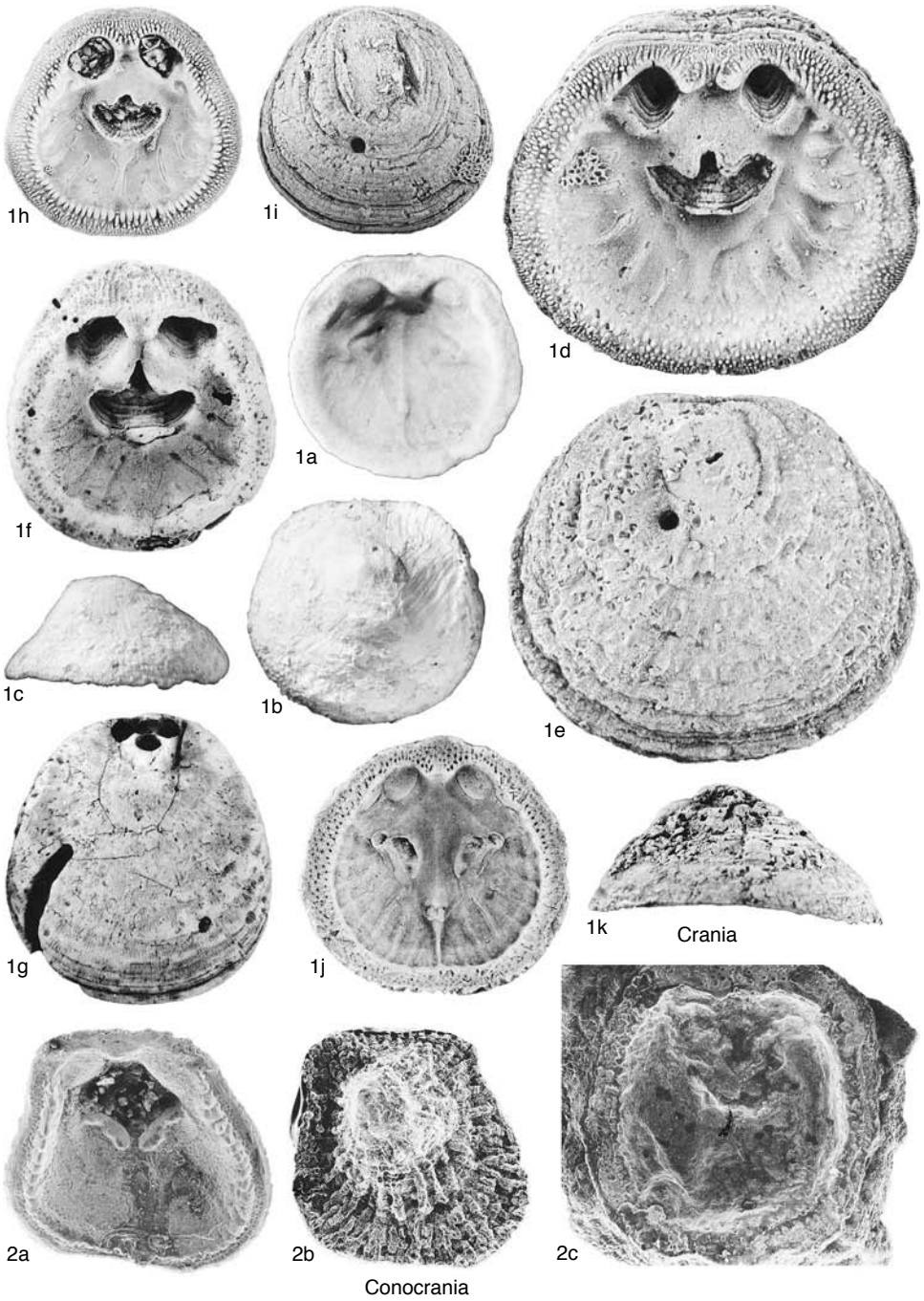

FIG. 96. Craniidae (p. 171–174).

England, North America.——FIG. 97,*2a–f.* **A. parisiensis* (DEFRANCE), upper Chalk, Senonian, England; *a,b,* dorsal valve exterior, lateral, Trimingham, Norfolk, SM B34482, ×2; *c,d,* dorsal valve interior, oblique posterolateral showing processes, Trimingham, Norfolk, SM B34483b, ×2; *e,* ventral valve interior, Norwich, SM B1067, ×2; *f,* ventral valve interior, Gravesend, Kent, SM B807, ×2 (new).

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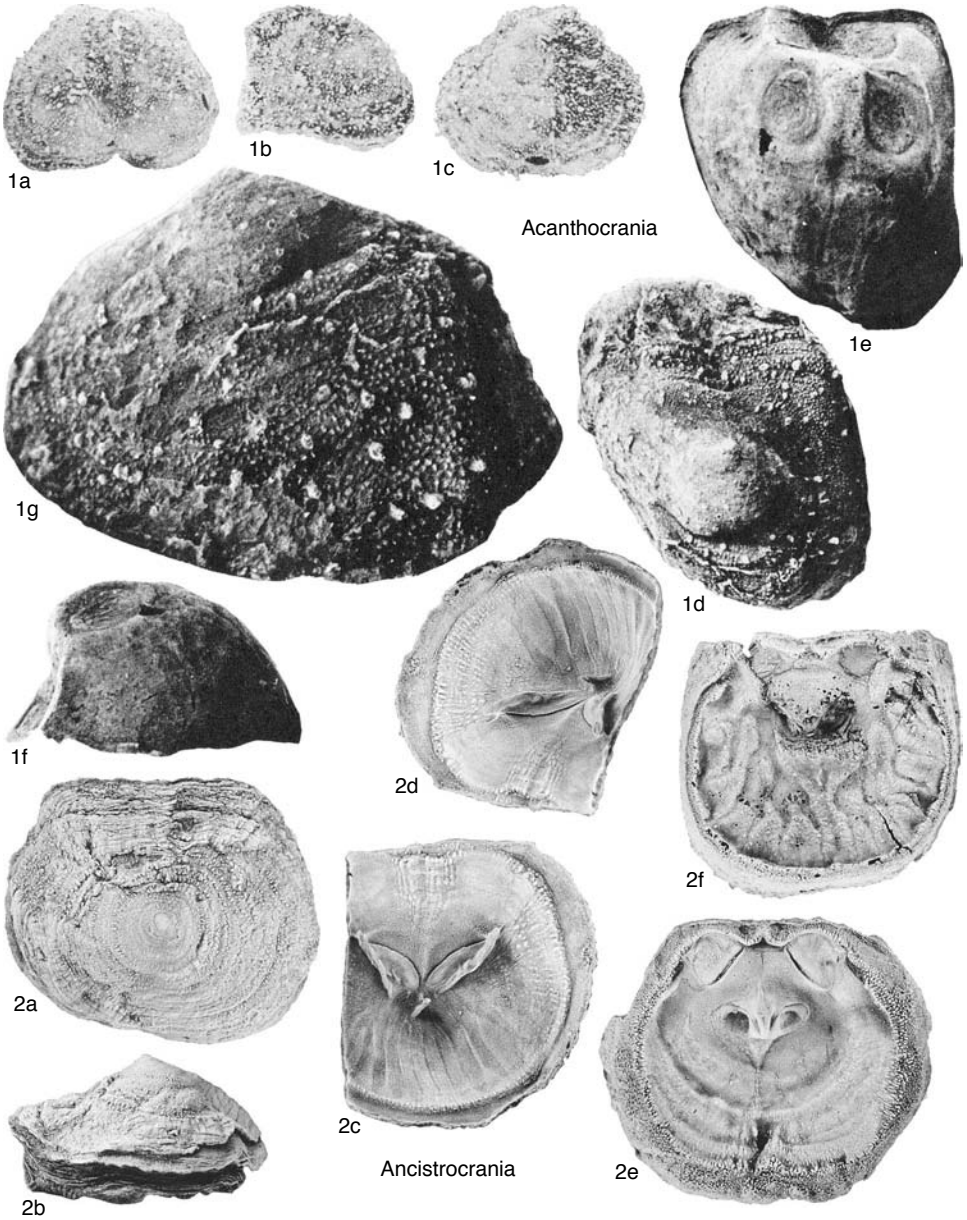

FIG. 97. Craniidae (p. 171–172).

Craniscus DALL, 1871b, p. 27 [**Crania tripartita* VON MÜNSTER, 1840, p. 297; OD]. Dorsal valve weakly to strongly convex; beak excentric; ventral valve of type species unknown, flat in other species, attached by entire surface; smooth with fine growth laminae; ventral musculature unknown; dorsal anterior adductor scars raised on two strong ridges, united with a medium septum or ridge to divide valve into three chambers; valve margins not thickened. *Upper Jurassic (lower Oxfordian)–Holocene:* Europe, Australia, Japan, Indo-Pacific seas.——FIG. 98,*1a–c.* **C. tripartita* (VON MÜNSTER), lower Oxfordian limestone (loose pebble), Thurnau, northern Bavaria, Germany; *a,* lectotype, dorsal valve interior, BSM AS VII 171, ×5; *b,c,* paralectotype, dorsal valve exterior, lateral, BSM AS VII 172, ×5 (Rowell, 1965a).

Conocrania SMIRNOVA, 1996, p. 262 [**Craniscus spinacostatum* SMIRNOVA, 1972, p. 23; OD]. Micromorphic; dorsal valve strongly convex to

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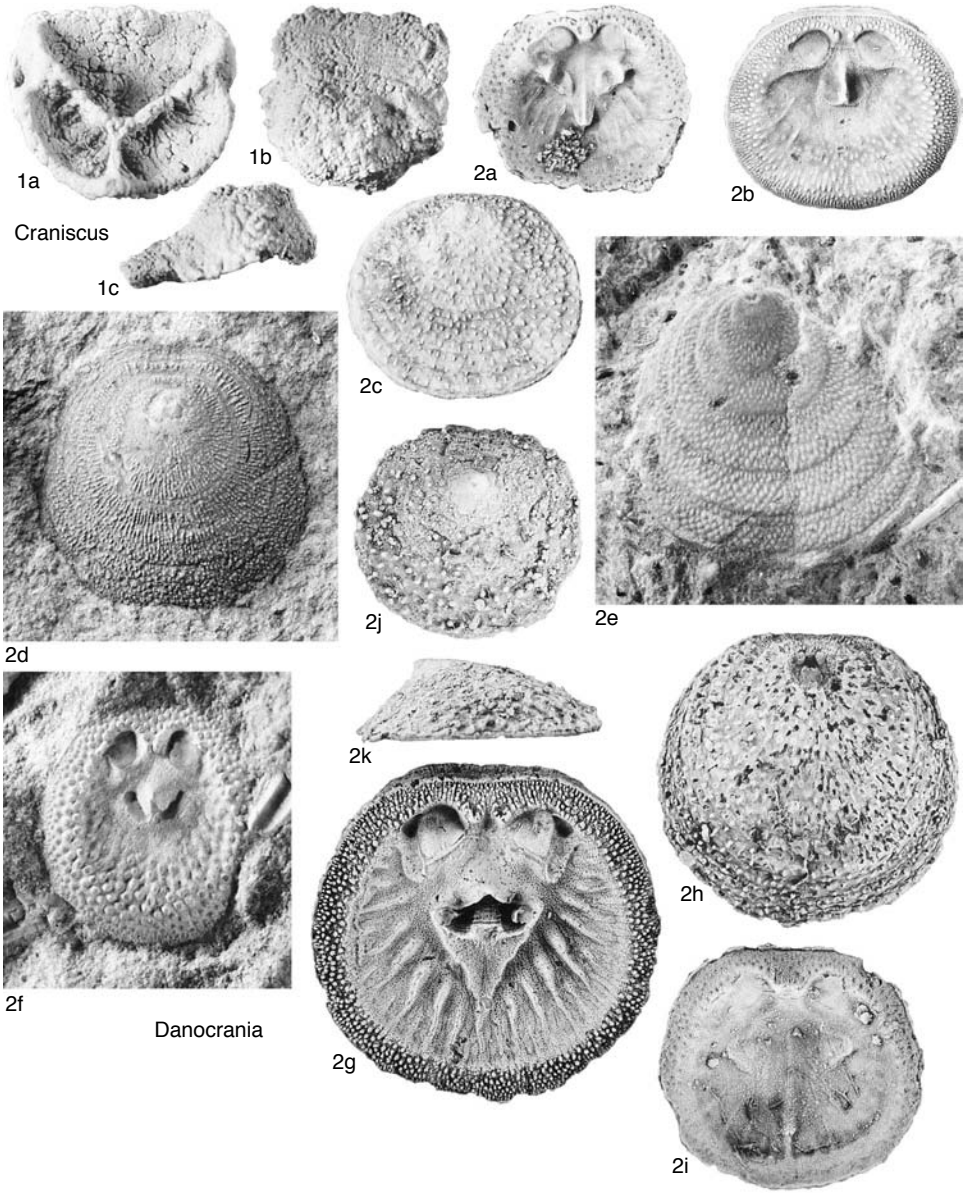

FIG. 98. Craniidae (p. 173–176).

subconical; beak close to straight posterior margin; ventral valve weakly convex, cemented across entire surface; coarsely costellate ribs elevated distally at thickened valve margins; dorsal posterior adductor scars large, abutting valve margin; anterior scars raised, crescentic to oval; ventral muscle scars small, slender with weak platform in front of anterior pair; subperipheral rim tuberculate; limbus flat to concave. *Lower Cretaceous (Berriasian–upper Valanginian):* Ukraine, Czech Republic.——FIG. 96,*2a–c*. **C. spinacostata* (SMIRNOVA), Berriasian sponge reef, Kuchki, Burulcha river, Crimea, Ukraine, topotypes; *a,* dorsal valve interior, CNIGR N168/12942, ×20; *b,* dorsal valve exterior, CNIGR N169/12942, ×20; *c,* ventral valve interior, CNIGR N174/12942, ×20 (Smirnova, 1996).

Danocrania ROSENKRANTZ, 1964, p. 515 [**Crania tuberculata* NILSSON, 1826, p. 326; OD; *nom. conserv.,* ICZN, 1988c, p. 63, Opinion 1469, *pro Craniolites brattenburgicus* SCHLOTHEIM, 1820, p. 246] [=*Westralicrania* COCKBAIN, 1967, p. 119 (type, *W. allani*)]. Convexiplane; dorsal valve rarely

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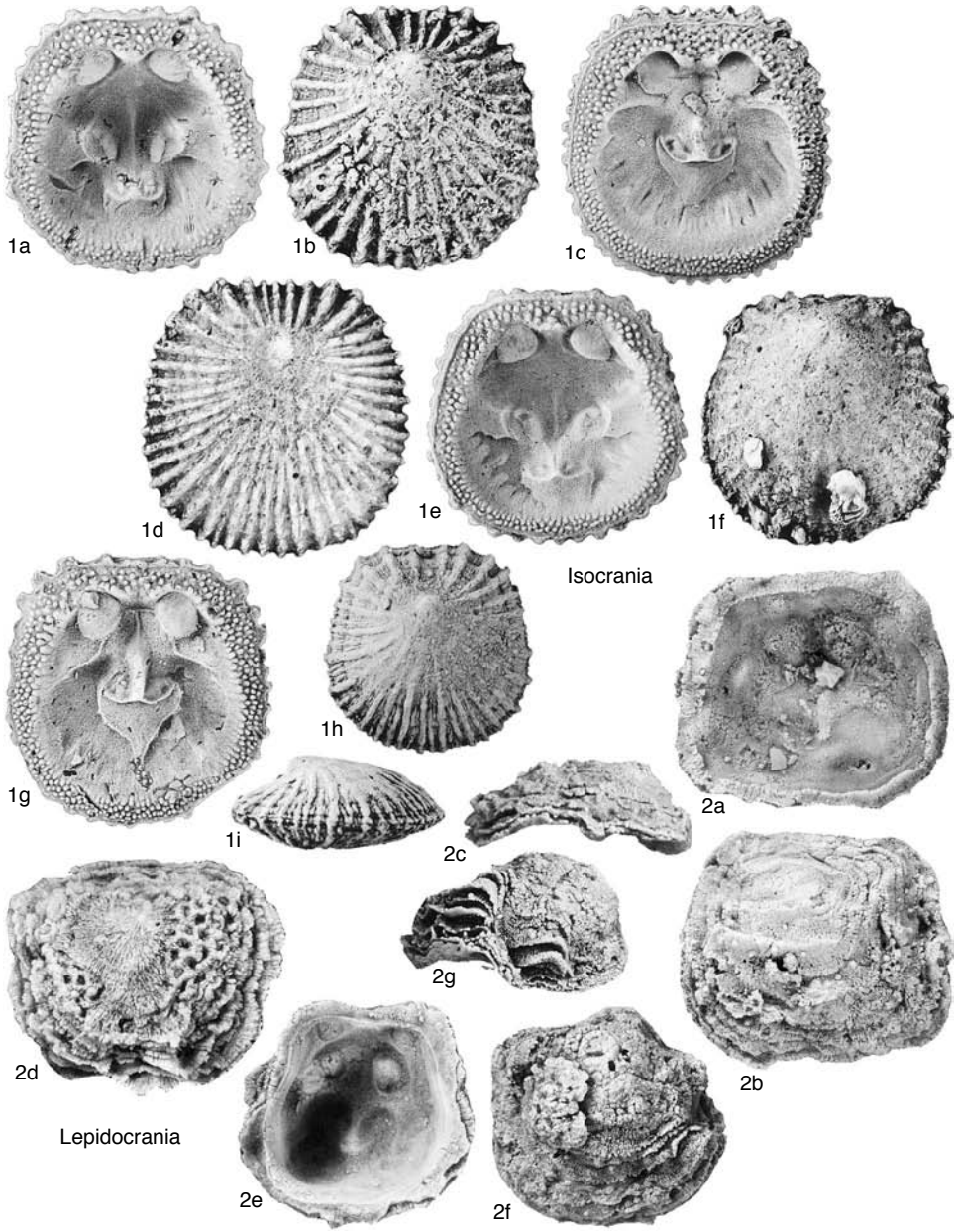

FIG. 99. Craniidae (p. 176–178).

subconical; ventral valve sometimes weakly concave; ornament pustulose to spinose; beaks set posteriorly; cicatrix at ventral umbo; pseudointerarea generally present; interiors commonly tuberculate; dorsal interior with articulatory ridge separating large, marginal posterior adductors; anterior scars widely separated, borne on low converging plates; short broad ridge extending anteriorly; short septum divides small anterior ventral scars; marginal rim rounded or as limbus. *Upper Cretaceous (Maastrichtian)–lower Paleogene (Danian, ?Thanetian):* Sweden, Denmark, Belgium, Netherlands, Austria, Ukraine, Crimea, western Australia.——FIG. 98,*2a–f.* **D. tuberculata* (NILSSON), Danian, Denmark; *a,* dorsal valve interior, Faxe, BMNH BD3367, ×3; *b,c,* ventral valve interior, exterior, Faxe, BMNH BD3366, ×3; *d,* dorsal valve exterior, Saltholm Limestone, Copenhagen, BMNH

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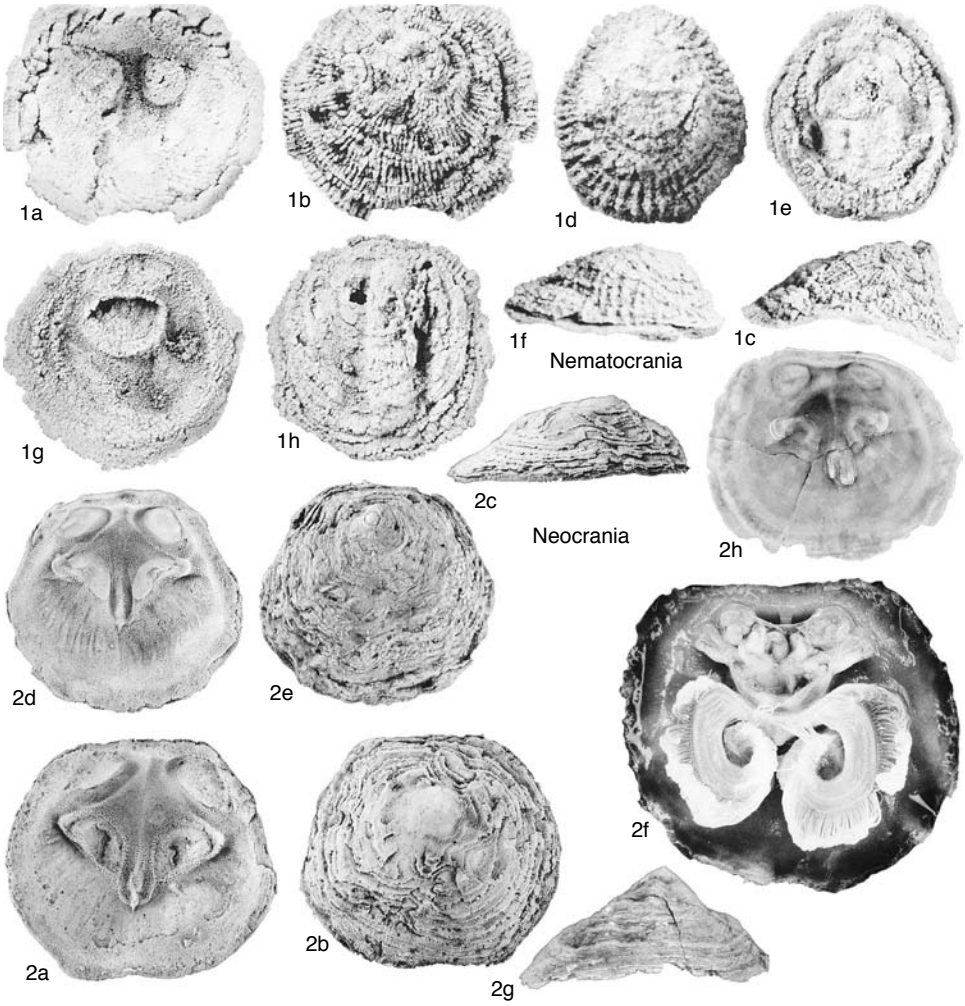

FIG. 100. Craniidae (p. 178–180).

B80856, ×3; *e,* ventral valve exterior, Saltholm Limestone, Copenhagen, BMNH B80850, ×3; *f,* ventral valve interior, Saltholm Limestone, Copenhagen, BMNH B80858, ×3 (Lee & Brunton, 1986).——FIG. 98,*2g–k. D. spinulosa* NILSSON, Senonian, Kjugestrand, Scania, southern Sweden; *g,h,* ventral valve interior, exterior, PM Sk110, ×3; *i–k,* dorsal valve interior, exterior, lateral, PM Sk111, ×3 (new).

Isocrania JAEKEL, 1902, p. 1062 [**Crania egnabergensis* RETZIUS, 1781, p. 75; SD SCHUCHERT & LEVENE, 1929, p. 69]. Subequally biconvex to subconical, dorsal curvature generally stronger; beaks excentric or well toward commonly straight posterior margin; attached at umbonal cicatrix in early growth, mostly free lying as adults; coarsely costellate; dorsal posterior adductors large, separated by broad articulatory ridge; anterior scars smaller, paired, broad median ridge extending well toward anterior margin; ventral posterior adductors large, well separated; anterior scars small, alongside short septum extending anteriorly as tapering ridge; limbus wide, coarsely pustulose. *Upper Cretaceous (lower Campanian)–lower Paleogene (Danian):* Sweden, Denmark, Netherlands, England, Africa, Asia.——FIG. 99,*1a–i. *I. egnabergensis* (RETZIUS), lower Campanian chalk, southern Sweden; *a,b,* dorsal valve interior, exterior, Ignaberga, Scania, PM Sk115, ×4; *c,d,* ventral valve interior, exterior, Ignaberga, Scania, PM Sk116, ×4; *e,f,* dorsal valve interior, exterior, Ignaberga, Scania, PM Sk117, ×4; *g,* ventral valve interior, Ignaberga, Scania, PM Sk118, ×4; *h,i,* ventral, lateral views of complete shell, Maltesholm, Scania, RM Br 97732, ×4 (new).

Lepidocrania COOPER & GRANT, 1974, p. 246 [**L. tardispinosa;* OD]. Dorsal valve gently convex to

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FIG. 101. Craniidae (p. 178–179).

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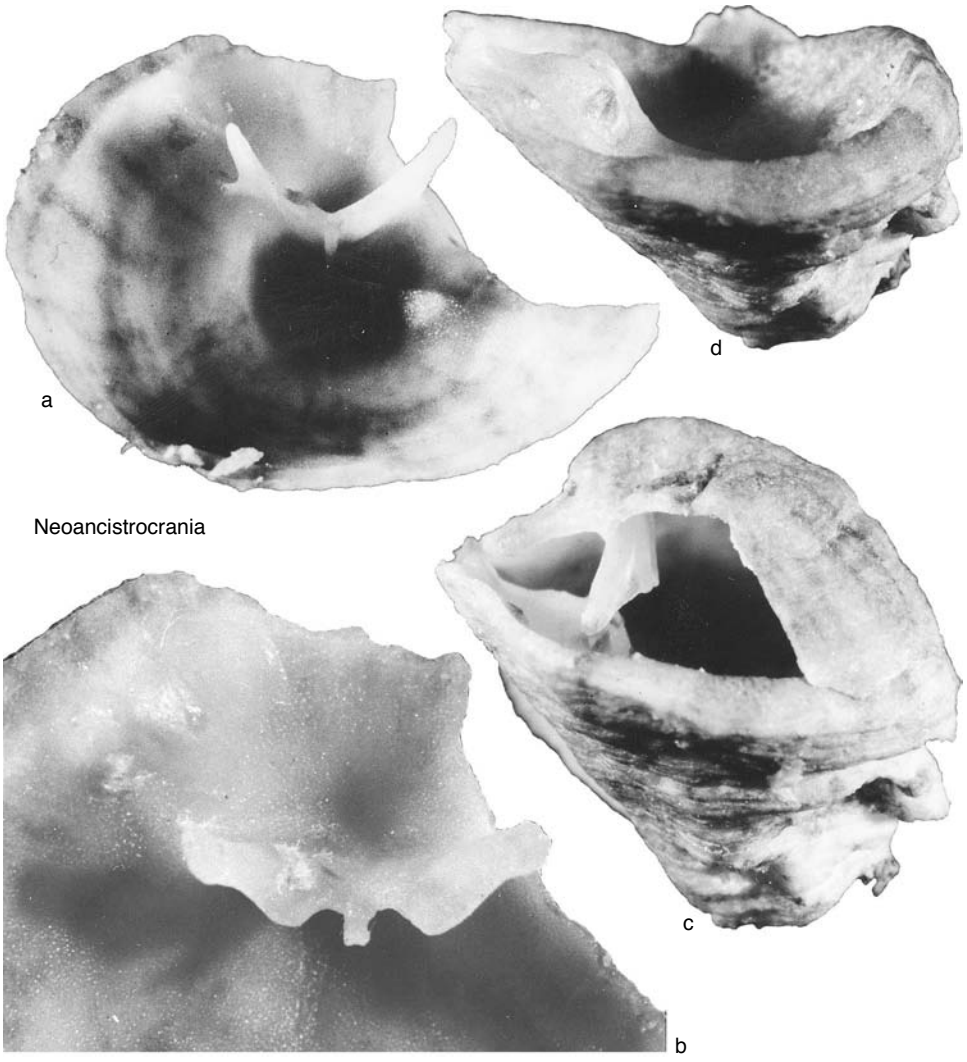

FIG. 102. Craniidae (p. 178–179).

conical, strongly lamellose or scaly with scattered, stout spines; beak excentric; posterior adductor scars marginal; oblique laterals, anterior adductors commonly subequal, thickened; limbus variably wide, thickened; encrusting; ventral valve unknown. *Lower Permian:* USA (western Texas).——FIG. 99,*2a–g.* **L. tardispinosa,* Road Canyon Formation, Wolfcampian, western Texas; *a–c,* holotype, dorsal valve interior, exterior, lateral, USNM 152582a, ×4; *d,* paratype, dorsal valve exterior, USNM 151395a, ×6; *e–g,* paratype, dorsal valve interior, exterior, lateral, USNM 152583, ×4 (Cooper & Grant, 1974).

Nematocrania GRANT, 1976, p. 31 [**N. crassa;* OD]. Ventral valve calcified, cemented posterocentrally at cicatrix, plane or simulating substrate morphology; dorsal valve convex to low conical with posterocentral beak, steep posterior face; costellate with widely spaced growth laminae; dorsal anterior adductors large, thickened; posterior scars small, marginal; ventral anterior adductors deeply incised with bounding rim; limbus narrow, finely pustulose. *Lower Permian (upper Artinskian):* southern Thailand.——FIG. 100,*1a–h.* **N. crassa,* Rat Buri Limestone, upper Artinskian, Ko Muk; *a–c,* holotype, dorsal valve interior, exterior, lateral, USNM 211603, ×4; *d–f,* paratype, dorsal exterior, ventral exterior, lateral, USNM 211595, ×5.5; *g,h,* paratype, ventral valve interior, exterior, USNM 211612, ×4 (Grant, 1976).

Neoancistrocrania LAURIN, 1992, p. 344 [**N. norfolki;* OD]. Biconical, inequivalved, ventral apex flattened

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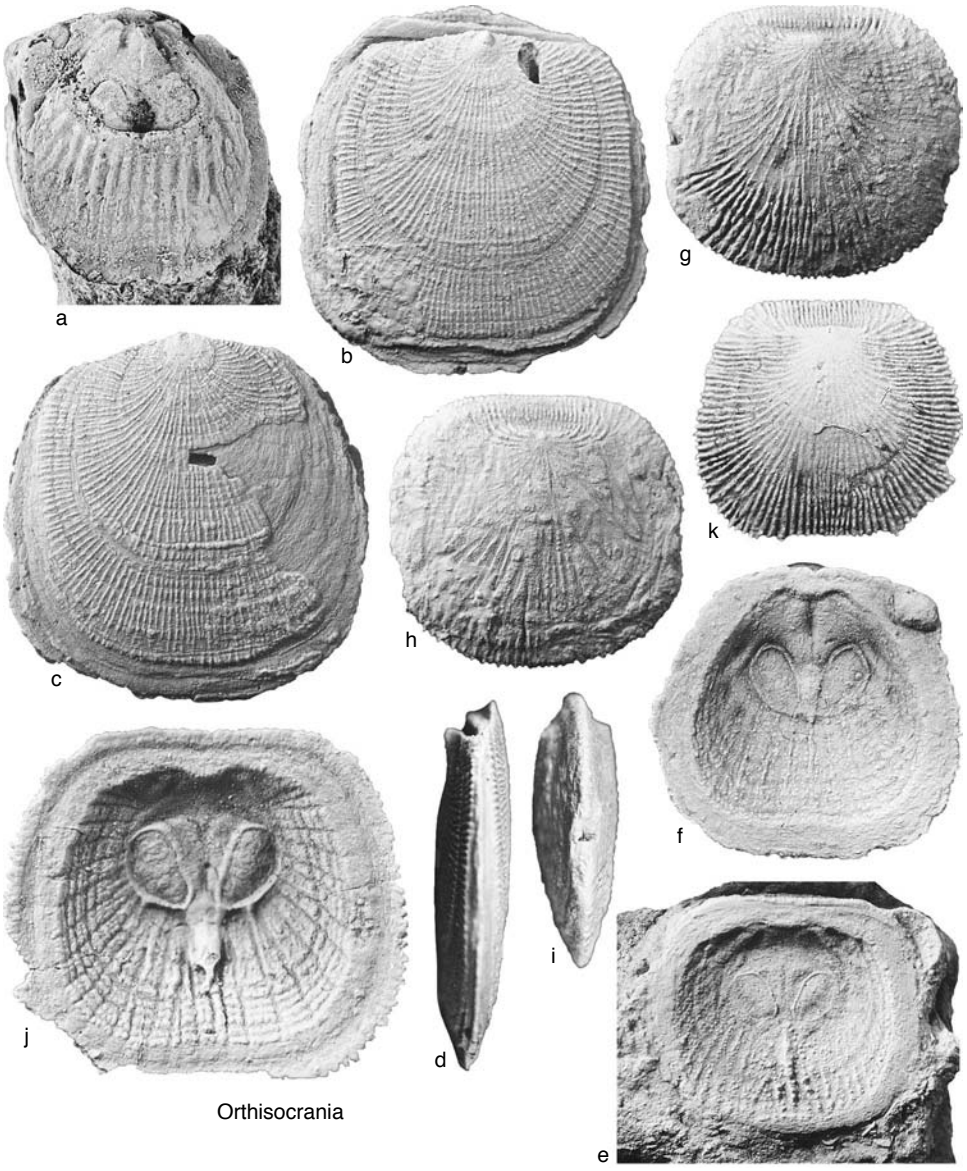

FIG. 103. Craniidae (p. 180–181).

as attachment cicatrix; dorsal beak posterocentral, smooth with faint growth laminae; ventral posterior muscle scars large, marginal, separated by a stout rounded swelling; dorsal interior with pair of rounded knobs alongside posterior adductors, bearing oblique muscles, extending up into ventral valve; otherwise resembling *Ancistrocrania* but with reduced septum between processes; marginal rim not thickened. [Precise affinities of this genus, known only from two specimens, remain unclear; it is possibly a mature *Valdiviathyris* or a synonym of *Ancistrocrania*]. *Holocene:* South Pacific.——FIG. 101*a–d.* **N. norfolki,* Holocene, Norfolk Ridge, South Pacific (233 m); holotype, posterior, lateral, ventral interior, dorsal interior, MNHN, ×4.5 (Laurin, 1992).——FIG. 102*a–d.* **N. norfolki,* Holocene, Norfolk Ridge, South Pacific (233 m); paratype, dorsal valve interior, anterior vertical view of processes, lateral view of conjoined valves showing disposition of dorsal processes, oblique view of ventral valve illustrating height of posterior knobs, UD, ×5 (Laurin, 1992).

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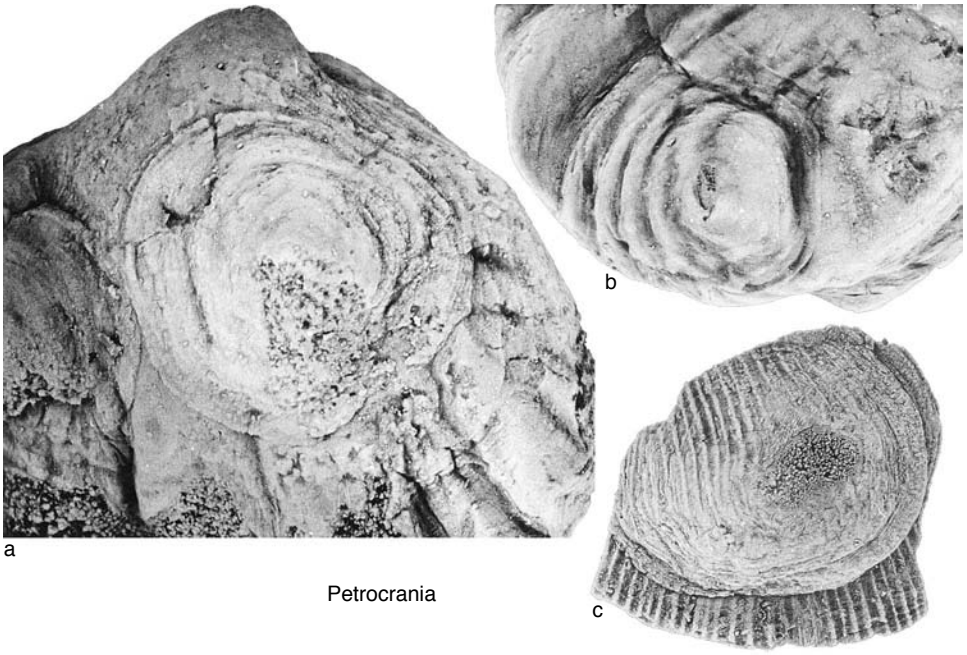

FIG. 104. Craniidae (p. 181–182).

Neocrania LEE & BRUNTON, 1986, p. 150 [**Patella anomala* MÜLLER, 1776, p. 237; OD; ICZN plenary powers, 1988b, p. 62, Opinion 1468] [=*Criopus* POLI, 1791, p. 34 (type, *C. fimbriatus* POLI, 1795, p. 189), ICZN plenary powers, 1988a, p. 61, opinion 1467; *Criopoderma* POLI, 1795, p. 255, ICZN plenary powers, 1988a, p. 61, opinion 1467; *Orbicula* CUVIER, 1798, p. 435, obj., ICZN plenary powers, 1988b, p. 62, opinion 1468; *Orbicularius* DUMÉRIL, 1806, p. 170; *Cryopus* DESHAYES in LAMARCK, 1836, p. 314, ICZN plenary powers, 1988a, p. 61, opinion 1467; *Criopododerma* AGASSIZ, 1848, p. 301, ICZN plenary powers, 1988a, p. 61, opinion 1467]. Dorsal valve convex to conical; beak subcentral to posterocentral, smooth, finely pustulose or rarely finely costellate; posterior margin commonly straight; recent species with dendroid shell punctation; dorsal posterior adductor scars large, rounded, thickened, widely separated; anterior scars commonly crescentic, raised above valve floor; weak myophragm bisects muscle field; encrusting; ventral valve uncalcified in recent species, otherwise sometimes thin; ventral posterior adductor scars large, anterior scars united medially; marginal mantle setae observed in recent forms; valve margins variably thickened, with limbus or faint submarginal rim. *Paleogene (Eocene)–Holocene:* cosmopolitan.——FIG. 100,*2a–h. *N. anomala* (MÜLLER), Holocene; *a–c,* dorsal valve interior, exterior, lateral, off western coast of Sweden, north of Hunnebostrand (60 to 120 m), NMW 98.10G.1, ×3; *d,e,* dorsal valve interior, exterior, off western coast of Sweden, north of Hunnebostrand (60 to 120 m), NMW 98.10G.2, ×3; *f,* dorsal interior with body preserved, off southwestern Yttre Vattenholmen, Kosterfjorden, western Sweden (40 to 65 m), NMW 98.11G.1, ×4 (new); *g,h,* lateral view of conical dorsal valve, dorsal interior with asymmetrical protractor scar, Øresund, Denmark, BMNH ZB3955a, ×2 (Lee & Brunton, 1986).

Orthisocrania ROWELL, 1963, p.39 [**Pseudocrania divaricata* M'COY, 1851, p. 388; OD]. Free lying; biplanate to weakly biconvex, beaks initially marginal, growth mixoperipheral, may become holoperipheral through ontogeny; ventral pseudointerarea apsacline to catacline; dorsal pseudointerarea anacline; multicostellate; anterior adductor scars usually considerably larger than posterior scars in both valves; mantle canal system includes paired *vascula media;* limbus wide, smooth. *Ordovician (Llandeilo–Ashgill):* England, Sweden, Estonia, Russia (Ingria), Kazakhstan.——FIG. 103*a. *O. divaricata* (M'COY), Caradoc Series, Longvillian, Bryn Melyn, Bala, North Wales; syntype, ventral valve internal mold, SM A41949, ×2 (new).——FIG. 103*b–f. O. planissima* (VON EICHWALD), middle Ordovician, Ingria; *b–d,* dorsal, ventral, lateral, CNIGR 114/9960, ×3; *e,f,* dorsal, ventral interiors, CNIGR 116/9960, 115/9960, ×2 (Gorjansky, 1969).——FIG. 103*g–k. O. depressa* (VON EICHWALD), middle Ordovician; *g–i,* ventral, dorsal, lateral, Estonia, CNIGR 118/9960, ×2; *j,* dorsal inte-

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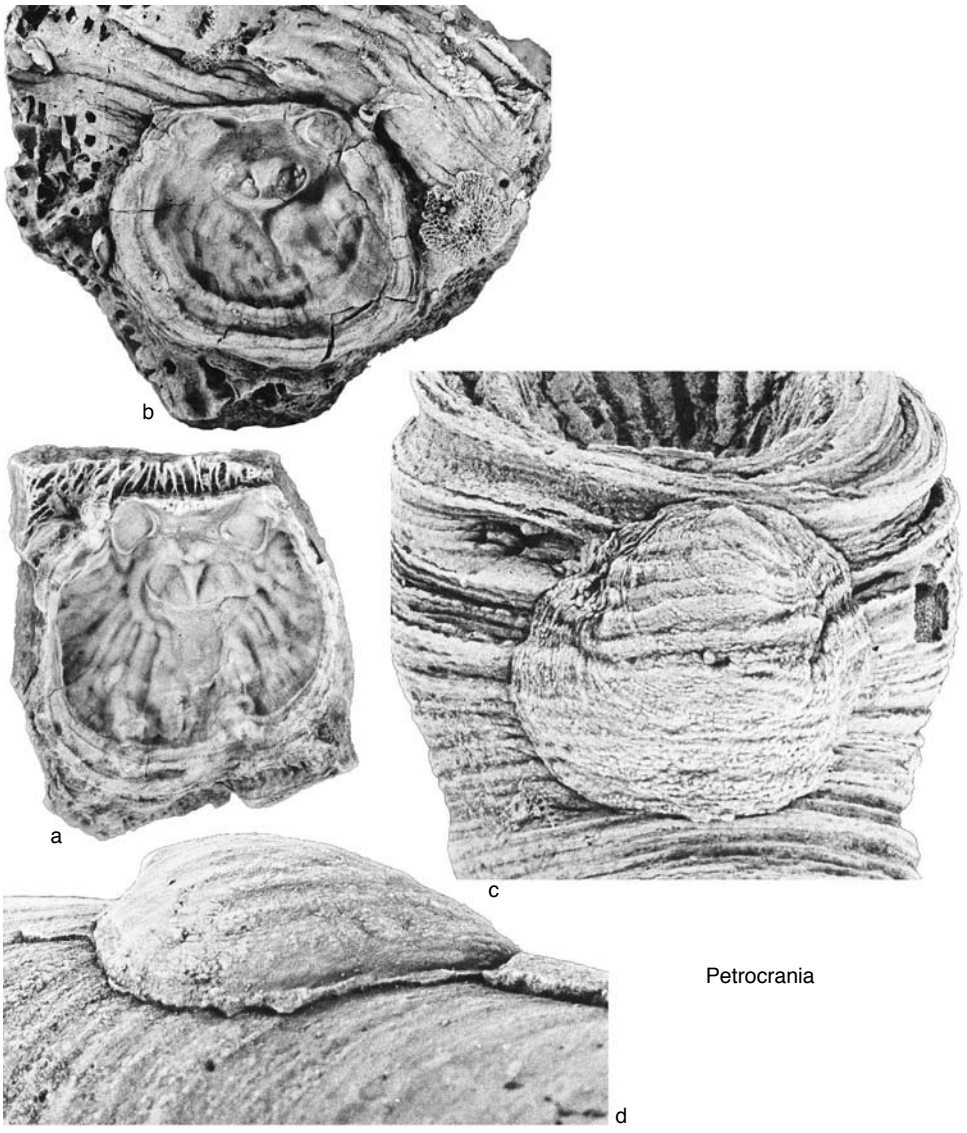

FIG. 105. Craniidae (p. 181–182).

rior, Ingria, CNIGR 119/9960, ×3; *k,* dorsal exterior, Ingria, CNIGR 119/9960, ×2 (Gorjansky, 1969).

Petrocrania RAYMOND, 1911, p. 229, *nom. subst. pro Craniella* OEHLERT, 1888, p. 101, *non* VON SCHLOTHEIM, 1820 [**Craniella meduanensis* OEHLERT, 1888, p. 102; OD] [=*Philhedrella* KOZŁOWSKI, 1929, p. 28 (type, *Philhedra (Philhedrella) mimetica*); *Lissocrania* WILLIAMS, 1943, p. 71 (type, *Crania dodgei* ROWLEY, 1908, p. 73); *Petrocraniella* PETROV, 1968, p. 74 (type, *P. grandissima*)]. Dorsal valve convex to subconical; beak subcentral to posterocentral; ornament only of concentric growth laminae or simulating morphology of the host; dorsal posterior adductor scars typically larger than anterior scars, but not exclusively; *vascula lateralia* commonly prominent, sigmoidal; valve margin not thickened, limbus narrow when developed; encrusting; ventral valve not known. *Lower Ordovician (upper Arenig)–Lower Carboniferous:* cosmopolitan.——FIG. 104*a–c. P. mimetica* (KOZŁOWSKI), Borshchov horizon, Lochkovian, Podolia, Ukraine; *a,b,* dorsal valves on host rhynchonelloidean shell, USNM 84331, ×4; *c,* dorsal valve, NMW 80.14G.3, ×3 (new).——FIG. 105*a–d. P.* sp., Wenlock, Gotland, Sweden; *a,b,* dorsal interiors, Halla

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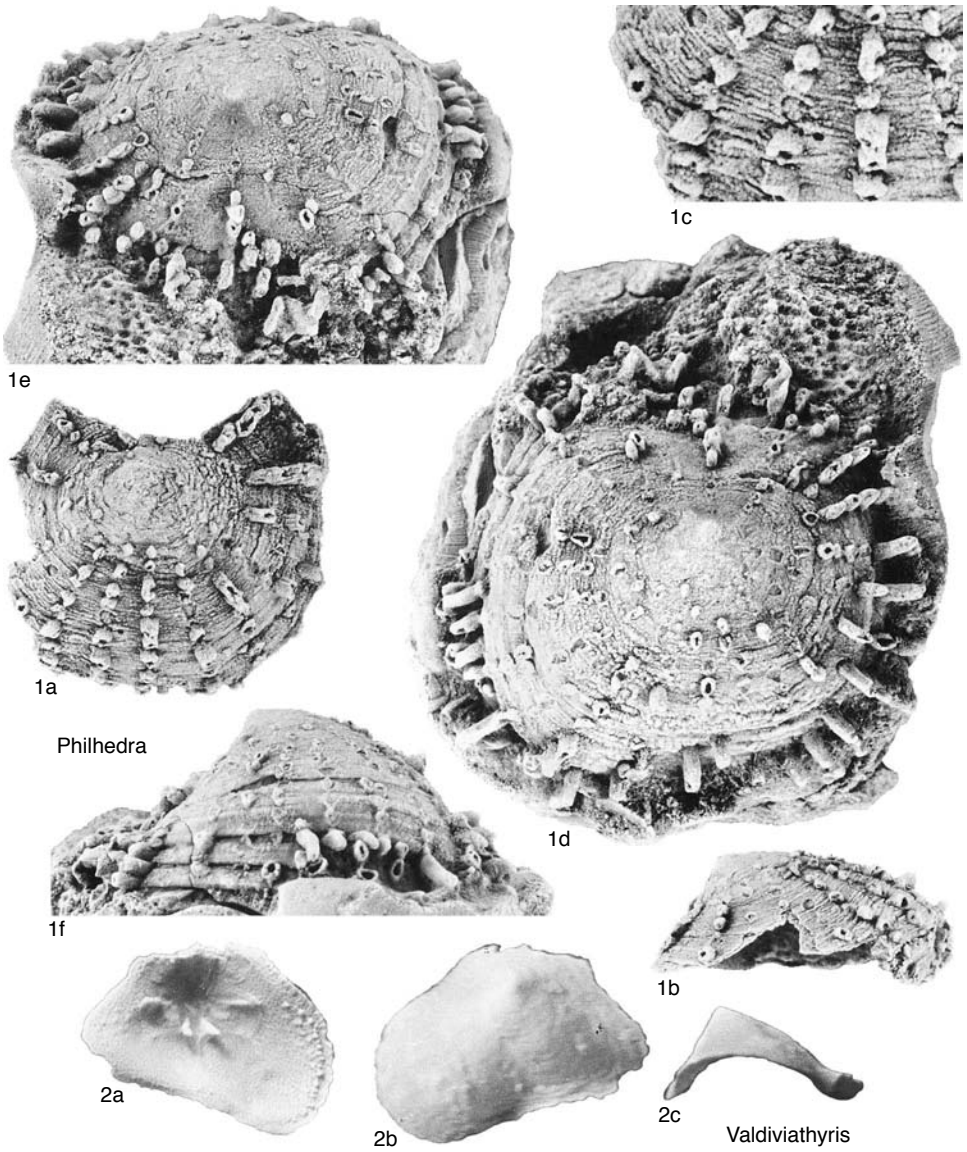

FIG. 106. Craniidae (p. 182–183).

Formation, SGU Type Collection, ×3; *c,* dorsal view, upper Visby Formation, RM Br 108374, ×3; *d,* lateral view, upper Visby Formation, RM Br 108240, ×3 (new).

Philhedra KOKEN, 1889, p. 465, *non Philhedra* SCHMIDT, 1939 [**P. baltica;* OD] [=*Philedra* BEKKER, 1921, p. 34]. Dorsal valve subconical; beak well posterior with steep, concave posterior face; ornament of thick, radially aligned hollow spines, concentric growth laminae; musculature unknown; encrusting; ventral valve unknown. *Ordovician (Llanvirn–Caradoc):* eastern Baltic (Ingria, Estonia).——FIG 106,*1a–f.* **P. baltica,* Viruan, Kukruse horizon, Kohtla-Järve, Kuttjejõu, northern Estonia; *a,b,* dorsal valve exterior, lateral, ×4; *c,* detail of ornament, TAGI BR 1311, ×6; *d–f,* dorsal valve exterior, posterior, lateral, TAGI BR 1313, ×4 (new).

Pseudocrania M'COY, 1851, p. 387 [**Orbicula antiquissima* VON EICHWALD, 1840, p. 169; =*Crania petropolitana* PANDER, 1830, p. 100, subj.; SD DAVIDSON, 1853, expl. pl. 9] [=*Palaeocrania* VON EICH-

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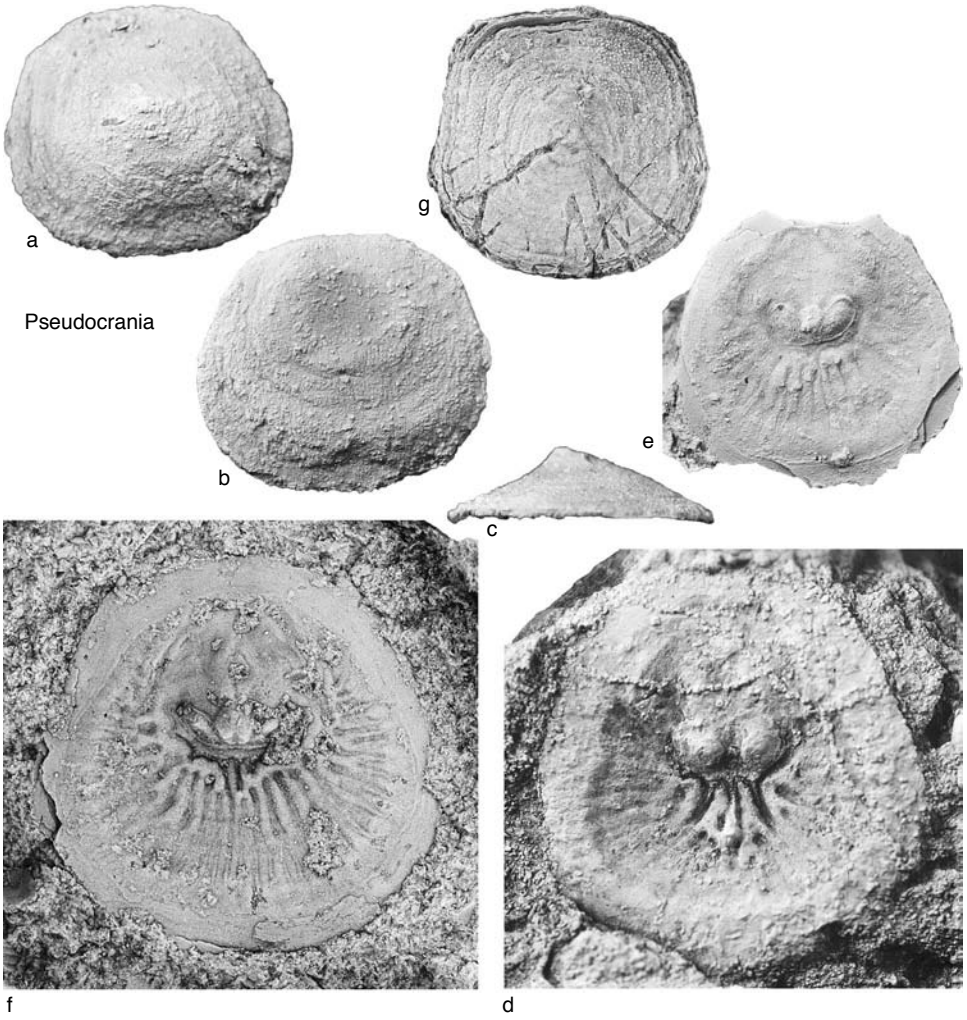

FIG. 107. Craniidae (p. 182–183).

WALD, 1854, p. 20, obj.]. Free lying; dorsal valve convex to subconical; ventral valve plane to subconical; beaks subcentral; growth holoperipheral; ornament of randomly spaced fine papillae, growth laminae; internally similar to *Orthisocrania,* including development of *vascula media. Lower Ordovician (upper Arenig):* Sweden, Russia (Ingria), Estonia, northern Germany.——FIG. 107*a–g.* **P. petropolitana,* Volkhov; *a–c,* dorsal, ventral, lateral views of conjoined valves, Ingria, CNIGR 108/9960, ×2; *d,* dorsal valve interior, Ingria, CNIGR 109/9960, ×2; *e,* ventral valve interior, Ingria, CNIGR 112/9960, ×2 (Gorjansky, 1969); *f,* ventral interior, Öland, Sweden, RM Br 15016, ×2; *g,* ventral valve exterior, Hälludden, Öland, SGU Type Collection, ×1.5 (new).

Valdiviathyris HELMCKE, 1940, p. 237 [**V. quenstedti;* OD]. Ventral valve unknown; dorsal valve thin-shelled, conical; beak posterocentral with steep posterior face; ornament of fine growth laminae only; internally similar to *Ancistrocrania* but lacking septum, with processes less divergent, more ventrally directed. [*Valdiviathyris* remains imperfectly known from a single, probable juvenile valve (ROWELL, 1962b); it is not unlikely that it could be a synonym of *Ancistrocrania,* and until more material of the type species is found it is recommended that the generic name should not be used for other taxa]. *Holocene:* southern Indian Ocean.——FIG. 106,*2a–c.* **V. quenstedti;* holotype, dorsal valve interior, exterior, lateral, MB 198, ×8 (Rowell, 1962b).

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TRIMERELLIDA

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[VSEGEI, St. Petersburg; and University of Uppsala]

Order TRIMERELLIDA Gorjansky & Popov, 1985

[Trimerellida GORJANSKY & POPOV, 1985, p. 12]

Shell thick, unusually large, probably aragonitic; free lying; unequally biconvex, growth mixoperipheral in both valves; usually smooth; ventral cardinal interarea commonly well developed, articulatory structure comprising ventral cardinal socket and dorsal hinge plate (apart from Ussuniidae); mantle lobes probably not fused along posterior margin; musculature apparently composed of paired posterior and anterior adductors, and outside lateral muscles; paired internal oblique muscles attached to posterior end of dorsal hinge plate (except in *Gasconsia*); mantle canal system baculate, bifurcate, or pinnate, sometimes with *vascula lateralia* and *vascula media* in both valves. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Trimerellides are characterized by inequibiconvex, sometimes almost spheroidal, thick shells, with mixoperipheral growth in both valves; they are among the largest known Early Paleozoic brachiopods and probably had an aragonitic shell (JAANUSSON, 1966). They adopted a free-living mode of life, lacking all evidence of a pedicle throughout ontogeny. Trimerellides are commonly found in massive reeflike accumulations of numerous individuals of the same species, vertically inclined, umbo downward; a typical such occurrence of *Eodinobolus* was described by WEBBY and PERCIVAL (1983) from the Upper Ordovician of Australia.

The shells of most trimerellides are usually almost smooth, and only *Costitrimerella* has radial ornamentation. The shape of the shell probably correlates strongly with the unique type of articulation, which consists of a dorsal hinge plate that fits tightly into a cardinal socket in the ventral valve, with a concave homeodeltidium in the center of the ventral interarea (Fig. 108); these structures effectively fixed the axis of rotation in a manner analogous to that of the articulated brachiopods.

The trimerellides also have unusual muscle scars; it is unlikely that the muscle system is comparable with that of the lingulides as proposed originally by DAVIDSON and KING (1872). NORFORD and STEELE (1969) showed that the muscle scars on some unusually well-preserved *Eodinobolus* are completely different from those of lingulides; they reconstructed a musculature consisting mainly of two paired large adductors and two smaller diductors working behind the axis of rotation. GORJANSKY and POPOV (1985, 1986) described the muscle system from *Eodinobolus, Ovidiella,* and *Palaeotrimerella* and proposed an alternative reconstruction based mainly on the craniide muscle system (Fig. 108); they also recognized that the trimerellides might have had a shell-opening mechanism with directly working diductors, but in contrast to NORFORD and STEELE (1969) they proposed that the oblique internal muscles may have been attached to the dorsal hinge plate, which is placed behind the axis of rotation (Fig. 108).

The muscle system of *Gasconsia* seems to have been slightly different; it is the only strophic trimerellide with a wide posterior margin, and the dorsal hinge plate is apparently situated anterior to the rotation axis. As noted by HANKEN and HARPER (1985) and MERGL (1988) this indicates that a diductor muscle could not function in the manner proposed for other trimerellids. MERGL (1988) proposed that it had a hydraulic shell opening mechanism with the outside lateral muscles attached to the anterior body wall.

Most trimerellids have muscle platforms in the anterior region of the visceral area of one or both valves. In most Ordovician genera (such as *Eodinobolus* and *Ovidiella*) these platforms are simple thickenings beneath the anterior muscle fields, while most Silurian

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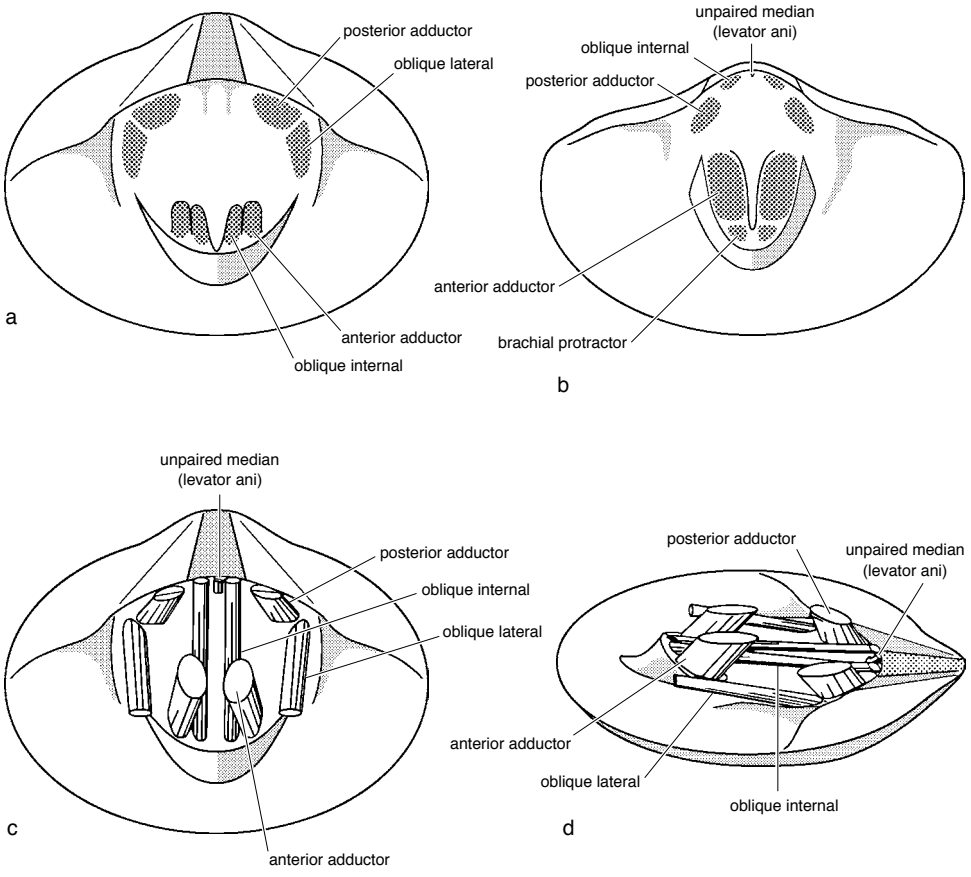

FIG. 108. Schematic illustration of musculature of *Eodinobolus; a,* ventral; *b,* dorsal; *c,d,* reconstructed muscle system viewed dorsally, laterally (new).

forms have distinctly raised, vaulted platforms that are hollow anteriorly.

Superfamily TRIMERELLOIDEA Davidson & King, 1872

[*nom. correct.* HARPER & others, 1993, p. 430, *pro* Trimerellacea SCHUCHERT & LEVENE, 1929, p. 12, *nom. imperf.; nom. transl. ex* Trimerellidae DAVIDSON & KING, 1872, p. 442]

Characters as for order. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Family TRIMERELLIDAE Davidson & King, 1872

[Trimerellidae DAVIDSON & KING, 1872, p. 442]

Shell with well-developed visceral platforms in one or both valves; lateral oblique muscle scars commonly present in ventral valve; mantle canal system bifurcate or baculate. *Ordovician (Llandeilo)–Silurian (Ludlow).*

Trimerella BILLINGS, 1862c, p. 166 [**T. grandis;* SD DALL, 1870, p. 160] [=*Gotlandia* DALL, 1870, p. 160 (type, *G. lindstroemi;* OD); *Machaerocolella* LI & HAN, 1980, p. 15 (type, *M. zhoujiashanensis;* OD); *Prosoponella* LI, 1984, p. 778[780] (type, *P. jiangshanensis;* OD)]. Shell dorsibiconvex, elongate triangular; ventral valve flattened; ventral interarea high, triangular, apsacline, with deep concave homeodeltidium occupying more than half of interarea; dorsal valve strongly convex, beak incurved; ventral umbonal cavities small or vestigial; both valves with distinctly raised visceral platforms, extending anterior to center; visceral platforms with deep vaults, separated by median partition, extending anterior to platform; dorsal hinge plate high, strongly incurved; dorsal *vascula lateralia* broad, slightly divergent, lacking trace of bifurcation.

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Ordovician (Ashgill)–Silurian (Wenlock): China, *Ashgill;* Kazakhstan, *Llandovery;* USA, Canada, Sweden (Gotland), Australia, Russia (Altai), *Wenlock.*——Fig. 109,*1a,b. *T. grandis,* Guelph Limestone, Hespeler, Ontario, syntypes, GSC 2803; *a,* dorsal view of internal mold of both valves, ×0.6; *b,* oblique posterior view of both valves, ×0.7 (new).——Fig. 109,*1c–e. T. lindstroemi* Dall, Högklint beds, Gotland, Sweden; *c,* detail of articulatory structure of both valves, Visby, Galgberget, RM Br 24466, ×1.2; *d,e,* ventral valve interior, exterior, BMNH B 5958, ×0.8 (new).——Fig. 109,*1f. T. acuminata* Billings, Guelph Limestone, Hespeler, Ontario; cast of ventral internal mold, BMNH B 14308, ×0.8 (new).——Fig. 109,*1g. T. ohioensis* Meek, Niagara Group, Otwa County, Ohio; posterior view of internal mold of both valves, BMNH B 5959, ×0.8 (new).

Costitrimerella Rong & Li, 1993, p. 131[138] [**C. costellata;* OD]. Shell subcircular, costellate; ventral valve unknown; dorsal visceral platform solid, transversely oval, extending anteriorly to midvalve. *Ordovician (Ashgill):* China (Zhejiang).——Fig. 109,*3a–c. *C. costellata,* Huangnekang Formation, Jiangshan, NIGP 119155; *a,* holotype, latex cast of dorsal external mold, NIGP 119155, ×4.2; *b,* latex cast of dorsal internal mold, ×3.3; *c,* holotype, lateral view, NIGP 119155, ×4.2 (Rong & Li, 1993).

Dinobolus Hall, 1871a, p. 4 [**Obolus conradi* Hall, 1867b, p. 368; OD] [=*Conradia* Hall, 1872b, p. 107, obj.]. Shell subequally biconvex, subcircular; lamellose peripherally; ventral pseudointerarea widely triangular with narrow homeodeltidium; ventral umbonal cavities vestigial; ventral visceral platform rhomboidal, somewhat hollow anteriorly, extending to midvalve and supported anteriorly by short median septum; dorsal visceral platform extending somewhat anteriorly to midvalve, supported anteriorly by short median septum; dorsal hinge plate short, low, slightly incurved. *Silurian (Llandovery–Wenlock):* USA, Canada, Great Britain, Ireland, Sweden (Gotland), Estonia, Russia (Siberia), Kazakhstan, China.——Fig. 109,*2a,b. *D. conradi* (Hall), Cedarville, Ohio; *a,b,* ventral view of internal mold of both valves, lateral view, USNM 459666, ×0.8 (new).——Fig. 109,*2c. D. davidsoni* (Salter); lectotype, dorsal view of internal mold of both valves, BMNH B 16510, ×1.2 (new).

Eodinobolus Rowell, 1963, p. 37 [**Obolellina magnifica* Billings, 1871c, p. 329; OD]. Shell subequally biconvex to weakly dorsibiconvex, subtriangular to transversely suboval; lamellose peripherally; ventral pseudointerarea orthocline, triangular, of variable height, with widely triangular, narrow homeodeltidium; visceral platforms of both valves massive, low elongated suboval, extending to or somewhat anterior of midvalve, sometimes with weak median ridge; ventral umbonal cavities absent; mantle canal system baculate; *vascula lateralia* of both valves short, subparallel or slightly convergent, lacking evidence of bifurcation; ventral *vascula media* subparallel. *Ordovician (Caradoc–Ashgill):* USA, Canada, Ireland, Great Britain, Estonia, Kazakhstan, Russia (Siberia, Urals), ?Uzbekistan, Australia.——Fig. 109,*4a–e. *E. magnificus* (Billings), Rockland Formation, Ontario; *a,* ventral valve exterior, USNM 116800a, ×1.2; *b,* ventral valve interior, USNM 116800d, ×1.2; *c,d,* dorsal valve exterior, oblique lateral view, USNM 116800b, ×1 (new); *e,* dorsal valve interior, GSC 1161b, ×1.2 (Cooper, 1956).

Fengzuella Li & Han, 1980, p. 17 [**F. zhejiangensis;* OD]. Shell subpentagonal, dorsibiconvex; ventral pseudointerarea moderately high, with widely triangular, shallow, narrow homeodeltidium; ventral umbonal cavities poorly developed; ventral visceral platform broadly rhomboidal, bisected by low median ridge, slightly vaulted anteriorly, extending anteriorly to midvalve, supported anteriorly by short median septum; shallow cardinal socket bounded anteriorly by broad cardinal buttress, supported by low median ridge; dorsal interior with widely triangular, short, slightly vaulted anteriorly visceral platform, not extending to midvalve; supported by long median ridge that extends to anterior margin. *Ordovician (Ashgill):* China (Zhejiang).——Fig. 110,*1a,b. *F. zhejiangensis;* Huangnekang Formation, Jiangshan, holotype, FD 144; *a,* ventral internal mold, ×3; *b,* dorsal internal mold, ×2.5 (Li & Han, 1980).

Gasconsia Northrop, 1939, p. 161 [**G. schucherti;* OD]. Shell convexiplane to convexiconcave; transversely suboval with long, straight posterior margin; ornament of indistinct low radial ribs, fine, concentric rugae; may be lamellose peripherally; ventral cardinal interarea low, apsacline, with narrow, poorly defined homeodeltidium; visceral platforms of both valves low, solid; median ridges of both valves vestigial or absent; dorsal hinge plate broad, low, bounded posteriorly by transverse furrow; mantle canal systems of both valves baculate with dorsal *vascula media. Ordovician (Ashgill)–Silurian (Ludlow):* Norway, Sweden, Kazakhstan, *Ashgill;* USA, *Wenlock;* Canada, Bohemia, *Ludlow.*——Fig. 110,*2a. *G. schucherti,* Gascons and Bouleaux Formations, Quebec; paralectotype, dorsal internal mold, YPM 13312, ×1.7 (Hanken & Harper, 1985).——Fig. 110,*2b,c. G. worsleyi* Hanken & Harper, Bønsnes Formation, Rawtheyan, Ringerike, Oslo; *b,* holotype, ventral valve interior, PMO 13091, ×0.8, *c,* latex cast of dorsal internal mold, PMO 104.000, ×0.8 (Hanken & Harper, 1985).——Fig. 110,*2d. G.* sp., Delphi, Indiana, USNM 62258; latex cast of dorsal internal mold, ×0.7 (new).

?Gyroselenella Li, 1985, p. 581, *nom. nov. pro Selenella* Li, 1984, p. 779, *non Selenella* Hall & Clarke, 1894a [**Selenella circularis* Li, 1984, p. 779]. Genus poorly understood; known only from one valve, described as ventral but probably dorsal. *Ordovician (Ashgill):* China (Zhejiang).

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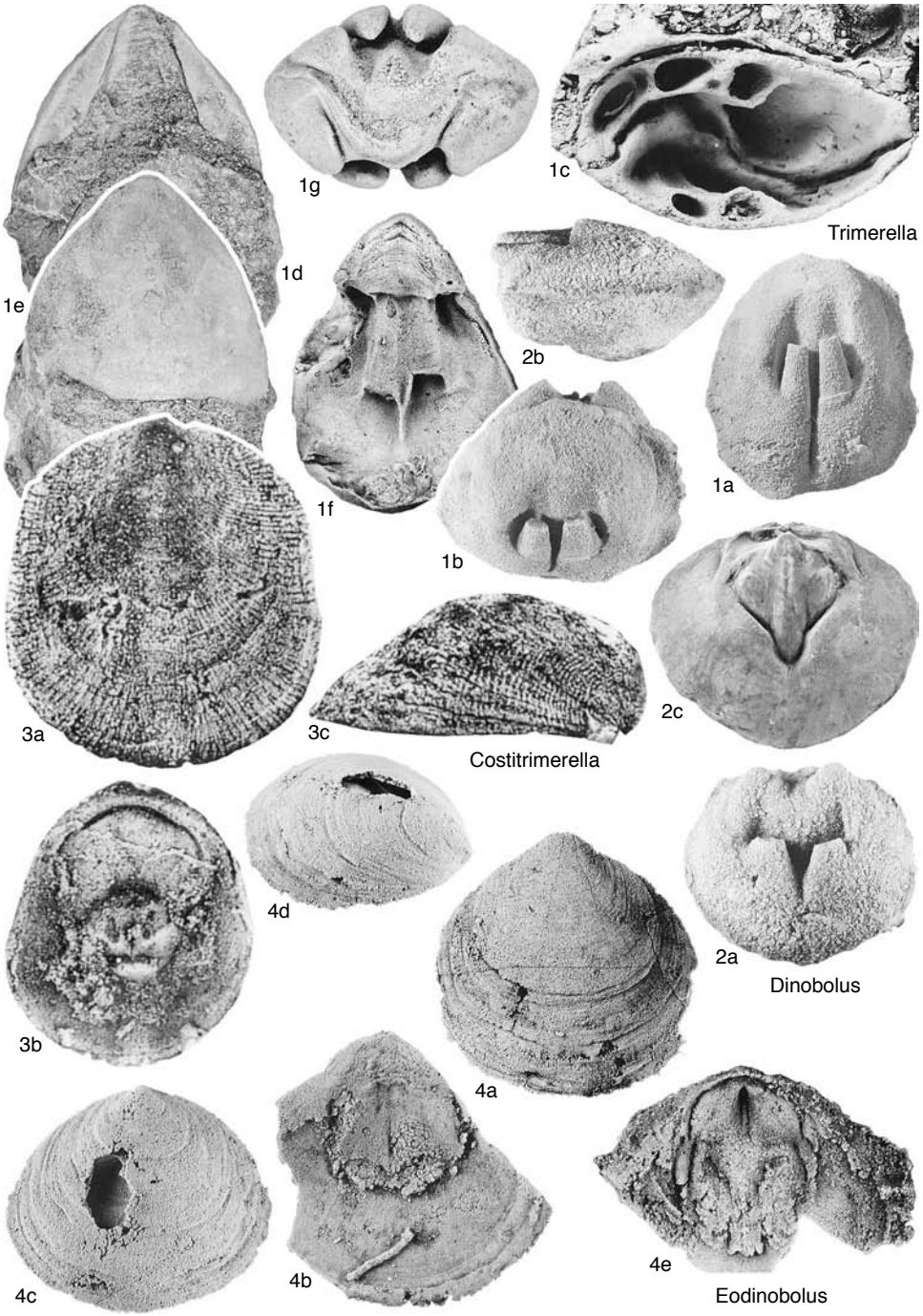

FIG. 109. Trimerellidae (p. 185–186).

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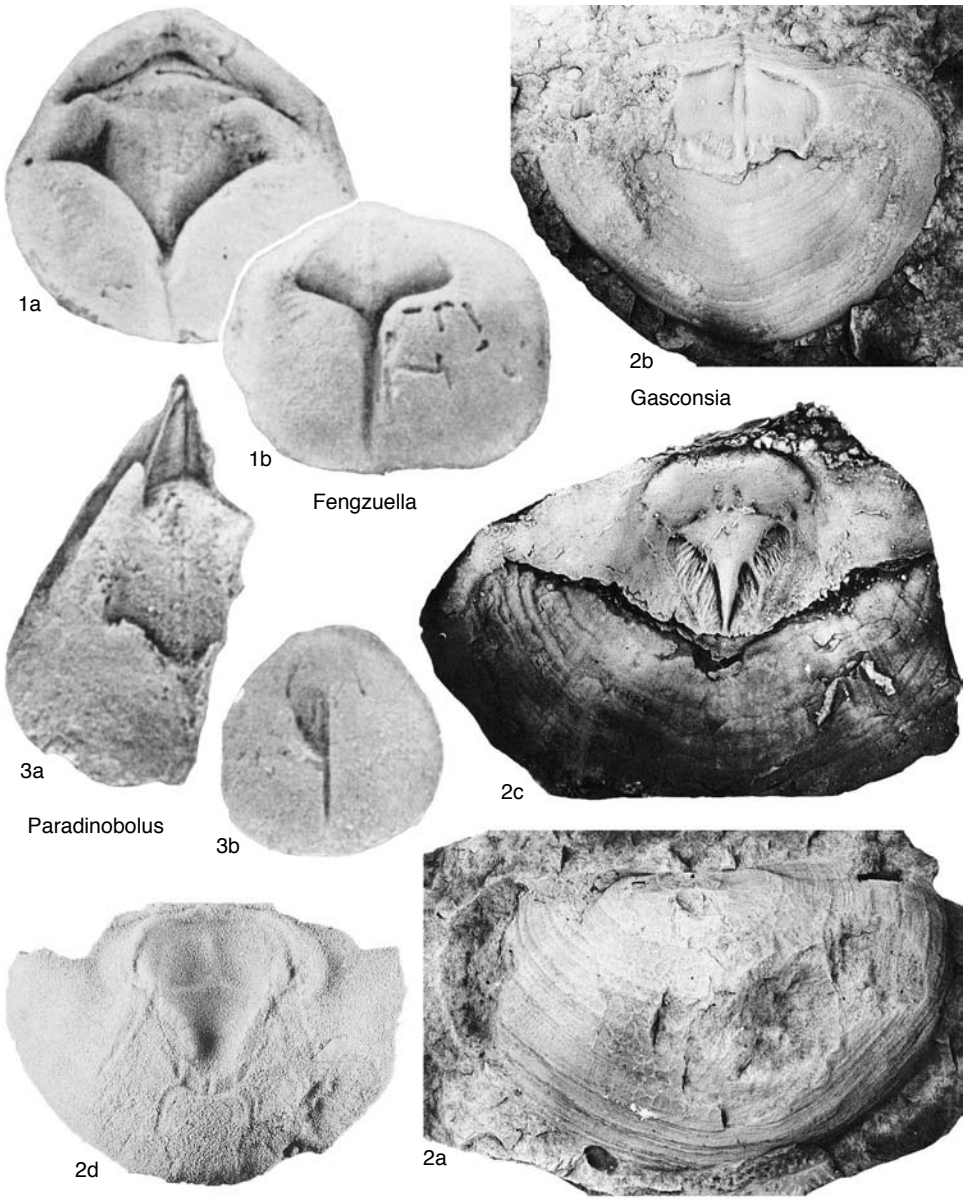

FIG. 110. Trimerellidae (p. 186–190).

Monomerella BILLINGS, 1871b, p. 220 [**M. prisca;* SD DAVIDSON & KING, 1874, p. 155]. Shell elongate subtriangular; sometimes ornamented by fine, concentric rugae; may be lamellose peripherally; ventral cardinal interarea apsacline, high, triangular, with broad, shallow homeodeltidium; dorsal valve moderately convex with incurved beak; ventral interior with deep umbonal cavities; ventral visceral platform slightly vaulted to solid, extending anteriorly to midvalve, bisected by median ridge that may be transformed anteriorly into high septum; dorsal visceral platforms vaulted anteriorly, supported by variably developed median ridge; ventral mantle canals baculate with well-defined *vascula media* and *vascula lateralia. Ordovician (Caradoc)–Silurian (Wenlock):* Australia, *Caradoc;* ?Kazakhstan, China, *Ashgill;* eastern USA, Canada, Sweden (Gotland), Estonia, *Wenlock.*——FIG. 111,*1a,b. *M. prisca,*

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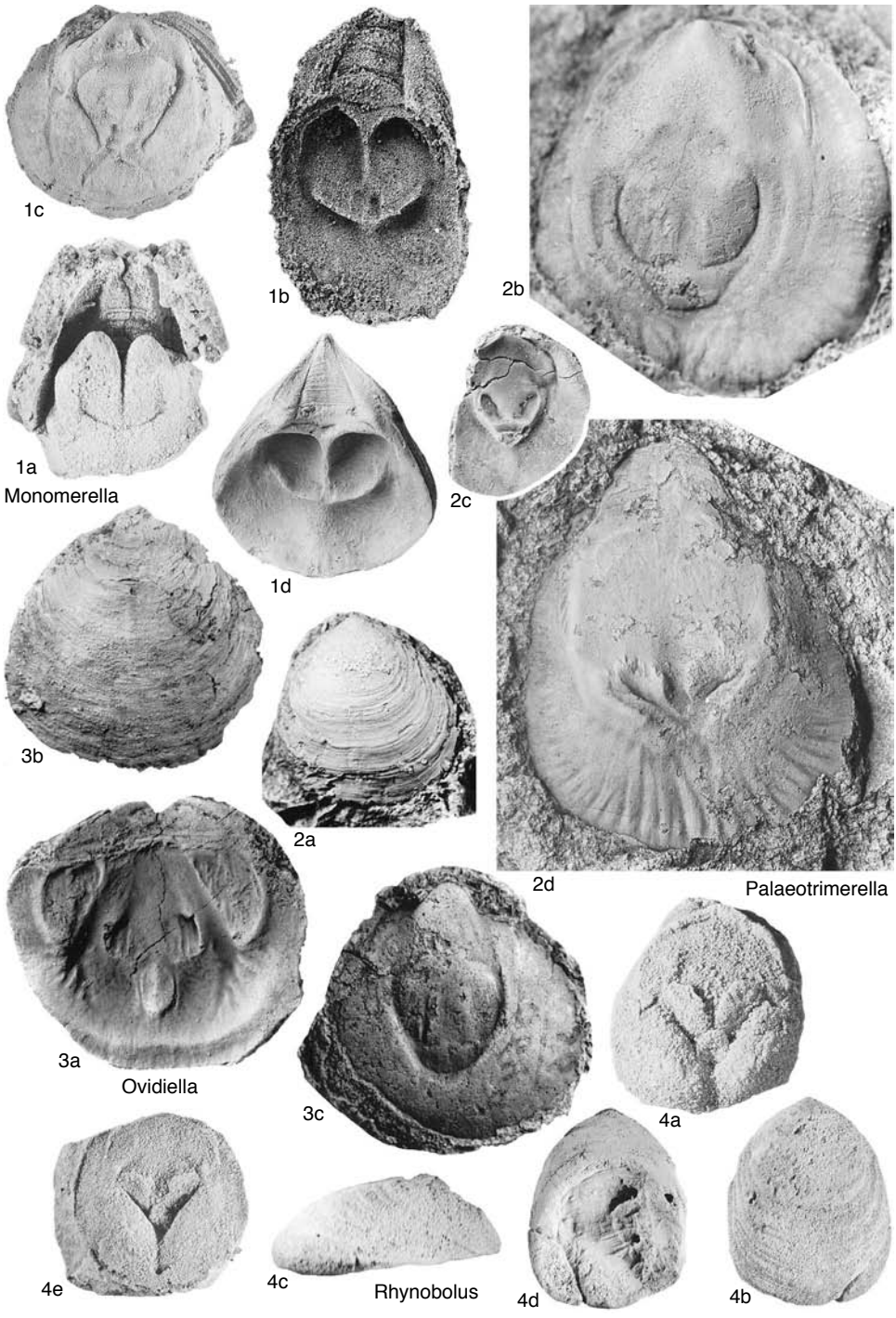

FIG. 111. Trimerellidae (p. 188–191).

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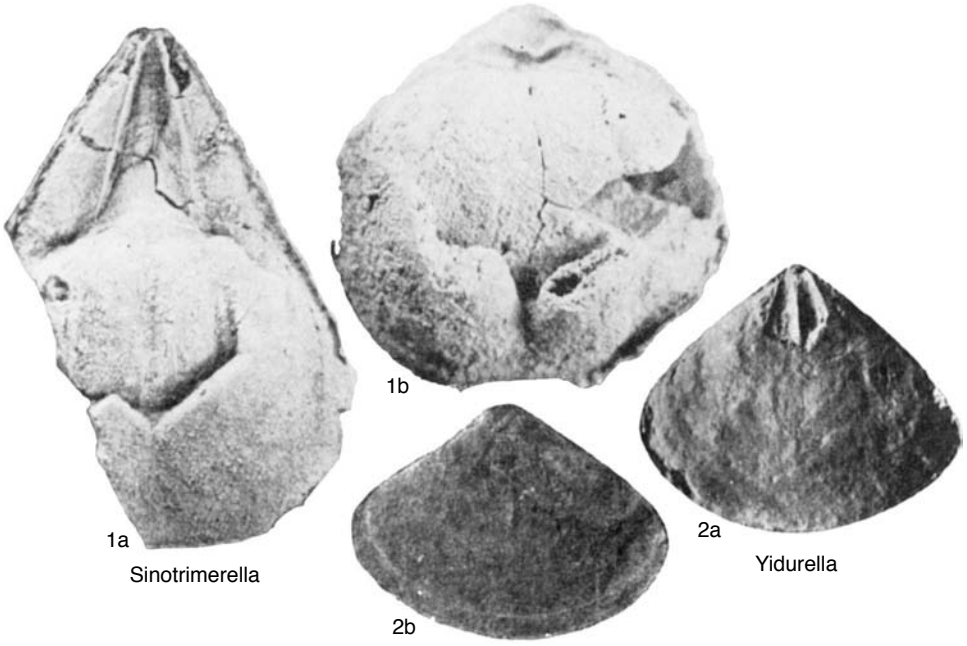

FIG. 112. Trimerellidae (p. 191).

Guelph Formation, Hespeler, Ontario; *a,* syntype, ventral internal mold, GSC 2811d, ×0.8; *b,* latex cast of ventral internal mold, USNM 67179, ×0.8 (new).——FIG. 111,*1c. M. greeni* HALL & CLARKE, Niagara Limestone, Rising Sun, Ohio; holotype, dorsal internal mold, OSU 7322, ×0.8 (new).——FIG. 111,*1d. M. walmstedti* DAVIDSON & KING, 1872, Slite beds, Fårön, Lanså, Gotland; ventral valve interior, RM Br 24443, ×0.8 (new).

Ovidiella NIKITIN & POPOV, 1984, p. 130 [**O. plana;* OD]. Shell dorsibiconvex with wide, straight posterior margin; subcircular; lamellose peripherally; ventral cardinal interarea moderately high, orthocline with very broad homeodeltidium and reduced propareas; dorsal valve moderately convex, beak slightly incurved; ventral interior with low, solid visceral platform, extending far anteriorly to midvalve; ventral scars of outside lateral and posterior adductor muscles on thickened, elongate semioval platforms; dorsal interior with solid, elongate oval visceral platform; ventral *vascula lateralia* with vestigial bifurcation; ventral *vascula media* short, subparallel; dorsal *vascula lateralia* bifurcate, with anterior branches slightly arcuate, convergent. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan.——FIG. 111,*3a–c. *O. plana,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,* holotype, ventral valve interior, CNIGR 15/12095, ×1.4; *b,* ventral valve exterior, CNIGR 17/12095, ×1.4; *c,* dorsal internal mold, CNIGR 19/12095, ×1.4 (Nikitin & Popov, 1984).

Palaeotrimerella LI & HAN, 1980, p. 10 [**P. orientalis;* OD]. Shell dorsibiconvex, elongate subtriangular; ornamented by irregular concentric rugellae, lamellose peripherally; ventral cardinal interarea high, orthocline, with shallow, relatively narrow homeodeltidium; dorsal valve moderately convex; ventral interior lacking umbonal cavities; visceral platforms of both valves low, solid, extending anteriorly to center, bisected by fine median ridges; dorsal visceral platform supported anteriorly by median septum; hinge plate low, thickened; mantle canal system bifurcate in both valves, with short subparallel *vascula media* in ventral valve. *Ordovician (Llandeilo–Ashgill):* Kazakhstan, China (Zhejiang).——FIG. 111,*2a–d. P. superba* NIKITIN & POPOV, Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,* dorsal valve exterior, CNIGR 13/12095, ×1.7; *b,* dorsal internal mold, CNIGR 8/12095, ×1.7; *c,* dorsal valve interior, CNIGR 8a/12095, ×1.7; *d,* ventral internal mold, CNIGR 1/11921, ×1.7 (Nikitin & Popov, 1984).

Paradinobolus LI & HAN, 1980, p. 19 [**P. sinensis;* OD]. Shell elongate oval; ventral cardinal interarea triangular, moderately high with narrow homeodeltidium; ventral interior without umbonal cavities; visceral platforms of both valves long, narrow, vaulted anteriorly, extending slightly anteriorly to midvalve, supported anteriorly by median septum. May be juvenile *Sinotrimerella. Ordovician (Ashgill):* China (Zhejiang).——FIG. 110,*3a,b. *P. sinensis,* Huangnekang Formation, Jiangshan, Zhejiang, holotype, FD 152; *a,* ventral internal mold, ×2.5; *b,* dorsal internal mold, ×2.5 (Li & Han, 1980).

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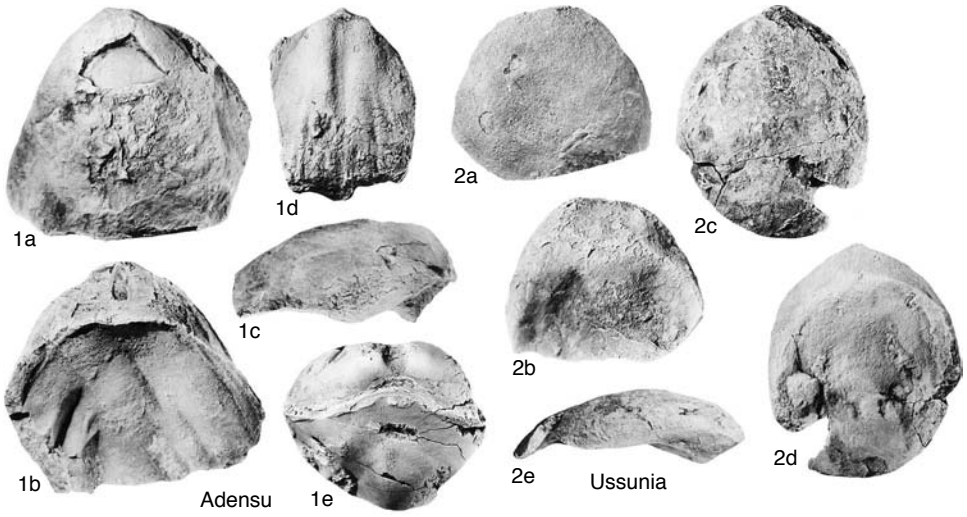

FIG. 113. Adensuidae and Ussuniidae (p. 191–192).

Peritrimerella LIANG, 1983, p. 257 [**P. chunanensis;* OD]. Similar to *Fengzuella* but convexoplane, lacking ventral umbonal cavities and median septum or ridge; short visceral platforms of both valves not extending to midvalve. *Ordovician (Ashgill):* China (Zhejiang).

Rhynobolus HALL, 1871a, p. 5 [**Obolus galtensis* BILLINGS, 1862c, p. 168; SD DALL, 1877, p. 61] [=*Obolellina* BILLINGS, 1871b, p. 222, obj.; *Rhinobolus* HALL & CLARKE, 1892, p. 44]. Shell elongate oval; ventral cardinal interarea high, triangular with broad homeodeltidium; ventral umbonal cavities vestigial; ventral visceral platform very low, solid; dorsal hinge plate small, slightly convex, bounded posteriorly by transverse furrow; dorsal visceral platform moderately high, slightly vaulted anteriorly; visceral platforms in each valve may be supported by weak median ridge. *Silurian (Wenlock):* USA, Canada, Sweden (Gotland).——FIG. 111,*4a–e. *R. galtensis* (BILLINGS), Guelph Limestone, Ontario; *a,* holotype, dorsal view of internal mold of both valves, Galt, Canada, GSC 2818a, ×0.8; *b–d,* dorsal valve exterior, lateral view, interior, GSC 2820a, ×0.8; *e,* dorsal internal mold, Durham, Hespeler, GSC 2820b, ×0.8 (new).

Sinotrimerella LI & HAN, 1980, p. 13 [**S. jiangshanensis;* OD]. Shell elongate oval to subtriangular, dorsibiconvex; ventral cardinal interarea high, triangular, with broad, shallow to moderately deep homeodeltidium; visceral platforms of both valves extending anteriorly to midvalve, slightly vaulted, each bisected medially by fine ridge; dorsal visceral platform supported anteriorly by short median septum. *Ordovician (Ashgill):* China (Zhejiang).——FIG. 112,*1a,b. *S. jiangshanensis,* Huangnekang Formation, Jiangshan; *a,* holotype, ventral internal mold, FD 149, ×1.3; *b,* paratype, dorsal internal mold, FD 148, ×1.5 (Li & Han, 1980).

Yidurella ZENG, 1987, p. 210 [**Y. yiduensis;* OD]. Shell subequally biconvex, transversely oval; ventral cardinal interarea short, triangular; ventral interior with an elongate, solid visceral platform bisected by fine median ridge, supported anteriorly by short septum; dorsal interior with long median septum anterior to narrow, solid visceral platform. *lower Silurian:* China.——FIG. 112,*2a,b. *Y. yiduensis,* Shamao Formation, Tizikou, Yidu; *a,* paratype, ventral internal mold, IV 45872, ×0.8; *b,* paratype, dorsal internal mold, IV 45876, ×0.8 (Zeng, 1987).

Family ADENSUIDAE Popov & Rukavishnikova, 1986

[Adensuidae POPOV & RUKAVISHNIKOVA, 1986, p. 58]

Shell strongly biconvex to spheroidal; elongate oval; ventral pseudointerarea low; both valves thickened posteriorly, lacking visceral platforms; lateral oblique muscles absent; ventral mantle canal system pinnate, ventral *vascula media* well developed. *Ordovician (upper Caradoc–lower Ashgill).*

Adensu POPOV & RUKAVISHNIKOVA, 1986, p. 58 [**A. monstratum;* OD]. Shell slightly ventribiconvex; ventral valve with strongly incurved posterior margin; ventral interior with broad, low median ridge bisecting visceral field; dorsal hinge plate massive, semielliptical, strongly incurved; dorsal anterior, posterior adductor muscles separated by deep, broad, widely divergent furrows; ventral *vascula lateralia, vascula media* very short. *Ordovician (upper Caradoc–lower Ashgill):* Kazakhstan.——FIG. 113,*1a–e. *A. monstratum,* Dulankara Formation, Adensu River, Chu-Ili Range; *a–c,* holotype, dorsal valve exterior, interior, lateral view, CNIGR 1/

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11544, ×0.4; *d,* paratype, ventral internal mold, CNIGR 9/11544, ×0.4; *e,* paratype, posterior view of internal mold of both valves, CNIGR 6/11544, ×0.4 (Popov & Rukavishnikova, 1986).

Family USSUNIIDAE Nikitin & Popov, 1984

[Ussuniidae Nikitin & Popov, 1984, p. 127]

Posterior margin rounded; articulatory structures poorly developed; visceral platforms absent in both valves; ventral pseudointerarea vestigial. *Ordovician (Llandeilo–lower Caradoc).*

Ussunia Nikitin & Popov, 1984, p. 127 [**U. incredibilis;* OD]. Shell subequally biconvex, elongate oval; both valves thickened posteriorly; ventral interior with shallow, broad, median depression along posterior margin; ventral visceral field poorly defined, with two broad depressions diverging anteriorly; dorsal hinge plate vestigial; dorsal visceral field extending anteriorly to midvalve. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan.——Fig. 113,*2a–e.* **U. incredibilis,* Bestamak Formation, *Nemagraptus gracilis* Biozone, Bestamak, Chingiz Range; *a,b,* paratype, dorsal valve exterior, interior, CNIGR 3/12095, ×0.8; *c–e,* paratype, ventral valve exterior, interior, lateral view, CNIGR 2/12095, ×0.8 (Nikitin & Popov, 1984).

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RHYNCHONELLIFORMEA

ALWYN WILLIAMS,[1] SANDRA J. CARLSON,[2] and C. HOWARD C. BRUNTON[3]
[[1]The University of Glasgow; [2]The University of California, Davis; and [3]formerly of the Natural History Museum, London]

Subphylum RHYNCHONELLIFORMEA Williams & others, 1996

[Rhynchonelliformea WILLIAMS & others, 1996, p. 1192]

Brachiopods with articulated calcitic shells, secondary layer basically fibrous; outer mantle lobe variably indented by periostracal slot between vesicular and lobate cells; hinge formed by margins of posterior interareas secreted by fused mantle lobes; articulatory structures essentially a pair of ventral teeth and dorsal sockets on either side of median indentations (delthyrium and notothyrium respectively) of interareas; pedicle of later groups developing from rudiment and occupying delthyrial area, filled with connective tissue, controlled by adjustor muscles; adductor muscles normally located posteromedially, diductor muscles flanking adductors ventrally, inserted in notothyrial region dorsally; alimentary tract without anus in living species; lophophore without median tentacle, tentacles double in post-trocholophous stages of growth; lophophore supported in later groups by calcitic extensions from dorsal hinge in form of crura, spiralia, or loops; mantle canal systems variable in branching, containing gonads, without marginal sinuses; larvae lecithotrophic, without shell, embryonic mantle in later groups undergoing reversal. *Lower Cambrian (Atdabanian)–Holocene.*

The rhynchonelliforms are the largest group of brachiopods and have been the dominant subphylum since Late Cambrian times, although only one of the five constituent classes is represented by living species. The definitive synapomorphy is the fibrous, secondary layer in a calcitic shell. The development of interareas, notched by a delthyrium and notothyrium, is shared with the linguliform paterinates. Similarly there is evidence to suggest that a functional anus persisted within the rhynchonelliforms at least to the emergence of the kutorginates and that the development of a pedicle from a rudiment is a synapomorphy of the only extant class, the Rhynchonellata.

CHILEATA

LEONID E. POPOV and LARS E. HOLMER
[VSEGEI, St. Petersburg; and University of Uppsala]

Class CHILEATA Williams & others, 1996

[Chileata WILLIAMS & others, 1996, p. 1192]

Shell strophic (with exception of Eichwaldiidae), ventral valve with mixoperipheral growth, dorsal valve with hemiperipheral growth; mantle lobes possibly fused posteriorly; ventral valve with cardinal interarea; ventral umbo with perforation enlarged anteriorly by resorption, usually covered posteriorly by colleplax; mantle canals pinnate. *Lower Cambrian (Botomian)–Permian.*

Order CHILEIDA Popov & Tikhonov, 1990

[Chileida POPOV & TIKHONOV, 1990, p. 39]

Strophic shell lacking hinge structures; ventral interarea flattened, widely triangular with delthyrium open or covered by variably developed convex pseudodeltidium; ventral umbonal perforation large subtriangular, sometimes covered posteriorly by colleplax; visceral fields in both valves placed close to posterior shell margin; musculature with posterior and anterior adductors; internal oblique muscles attached to apical part of

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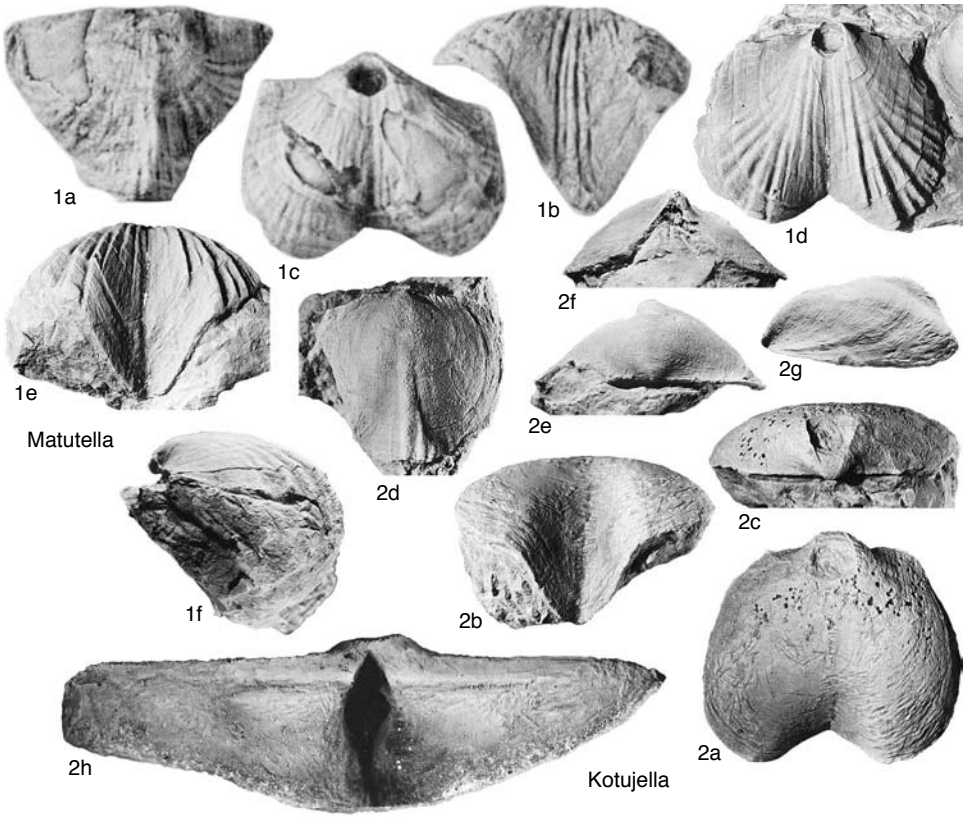

FIG. 114. Matutellidae (p. 195–196).

dorsal valve. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

The chileides first appeared in the Botomian and include the earliest known calcitic brachiopods with a strophic shell. Chileides lack any trace of articulatory structures along the posterior margin, and it is possible that the axis of rotation was fixed entirely by fused mantle lobes (POPOV & TIKHONOV, 1990; POPOV, 1992; HOLMER & POPOV, 1996b). Chileides also have an unusually large ventral umbonal perforation, which is enlarged by resorption and sometimes covered posteriorly by a plate. The plate is more or less identical in morphology to the colleplax described by WRIGHT (1981) in eichwaldioids. The function of the ventral perforation is not understood fully, but it is unlikely that it served as a pedicle opening, both because of its anterior position and due to the fact that the chileides also have a delthyrium. If it is homologous with a colleplax, it is possible that it was the site of an organic pad secreted by the outer epithelium, as proposed by WRIGHT (1981). POPOV and TIKHONOV (1990) and POPOV (1992) speculated that the perforation may have served as part of an hydraulic shell-opening mechanism. Chileide shell structure is known only from *Kotujella,* and according to WILLIAMS (1990) this may represent the oldest known endopunctate brachiopod with a fibrous secondary layer. The muscle system of the chileides is poorly understood; according to POPOV and TIKHONOV (1990), a set of internal oblique muscles may have attached posteromedially to the dorsal valve. Their location suggests that they are possibly ho-

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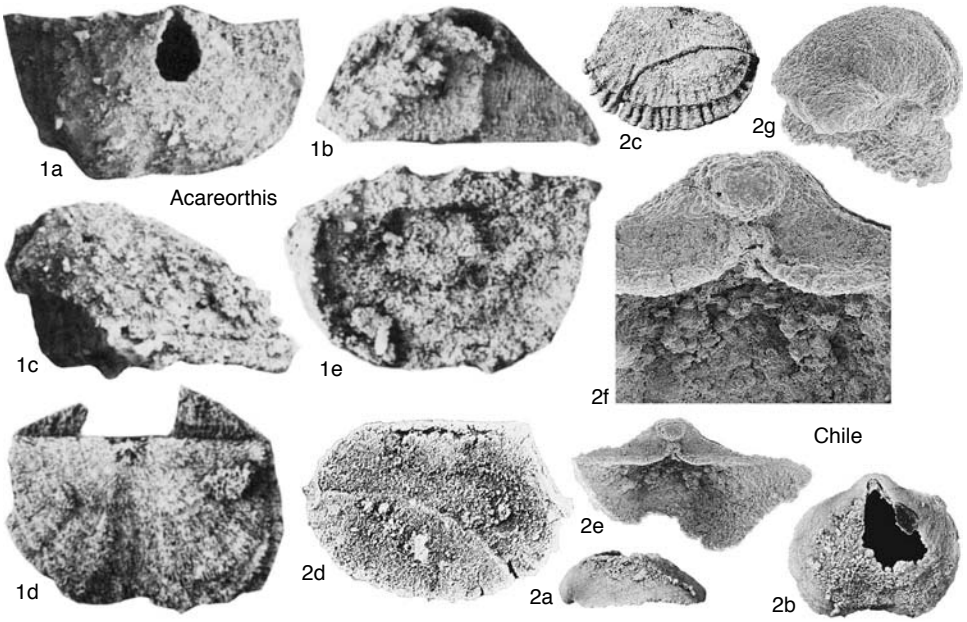

FIG. 115. Chileidae (p. 196).

mologous with the diductors of articulated brachiopods including obolellides, but because they are situated anterior to the axis of rotation they cannot have aided in shell opening. It is probable that chileides opened their shell by contraction of outside lateral muscles attached anteriorly to the body wall, comparable with the arrangement in recent craniides. In the Matutellidae, both valves have pinnate mantle canals; in *Chile* there are three pairs of main trunks in the ventral valve and only one pair in the dorsal valve.

Superfamily MATUTELLOIDEA Andreeva, 1962

[*nom. correct.* HOLMER & POPOV, herein, *pro* Matutellacea ANDREEVA, 1987, p. 33, *nom. transl. ex* Matutellidae ANDREEVA, 1962, p. 90]

Characters as for order. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

Family MATUTELLIDAE Andreeva, 1962

[Matutellidae ANDREEVA, 1962, p. 90]

Shell dorsibiconvex, anterior commissure uniplicate; ventral valve with sulcus, open triangular delthyrium, which may be covered apically by convex pseudodeltidium; broad triangular opening anterior to beak not extending to midvalve, covered posteriorly by small concave plate; dorsal valve with strong median fold; mantle canal system of ventral valve pinnate. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian).*

Matutella COOPER, 1951, p. 6 [**M. clarki;* OD]. Shell subquadrate in outline, costellate, sporadically imbricate; homeodeltidium small, apical. *Lower Cambrian (Botomian)–Middle Cambrian (Amgaian):* USA, Russia (Siberia, Altai).——FIG. 114,*1a–c. *M. clarki,* Shady Formation, northeast of Austinville, Virginia; *a,* dorsal valve exterior, USNM 111689k, ×1.7; *b,* anterior view of ventral valve, USNM 111689d, ×1.7; *c,* holotype, ventral valve exterior, USNM 111689n, ×1.7 (Cooper, 1951).——FIG. 114,*1d–f. M. grata* ANDREEVA, Toyonian, Rassokha River, Siberia; ventral valve exterior, anterior view, lateral view, CNIGR 8202, ×1.7 (new).

Kotujella ANDREEVA, 1962, p. 94 [**K. calva;* OD]. Shell externally similar to *Matutella,* but smooth and lacking pseudodeltidium. *Lower Cambrian (Toyonian):* Russia (Siberia).——FIG. 114,*2a–h. *K. calva,* Rassokha River, Siberia; *a–c,* ventral valve exterior, anterior view, posterior view, CNIGR 8202, ×1.7; *d–g,* dorsal valve exterior, posterior view, anterior view, lateral view, CNIGR 8202,

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×1.7 (new); *h,* ventral valve interior, CNIGR 24/8202, ×5 (Andreeva, 1962).

Family CHILEIDAE Popov & Tikhonov, 1990

[Chileidae Popov & Tikhonov, 1990, p. 39]

Shell inequibiconvex, or planoconvex; anterior commissure rectimarginate; pseudodeltidium commonly present; large, subtriangular perforation anterior to beak extending to midvalve. *Lower Cambrian (Botomian)–Middle Cambrian (lower Amgaian).*

Chile Popov & Tikhonov, 1990, p. 39 [**C. mirabilis;* OD]. Shell ventribiconvex, semielliptical; smooth apically, costellate peripherally; ventral interarea low, orthocline; delthyrium small, covered apically by convex pseudodeltidium; large, elongate triangular perforation extending anteriorly to midvalve, covered apically by colleplax; ventral mantle canals with two or three pairs of main trunks; dorsal *vascula lateralia* widely divergent. *Lower Cambrian (Botomian):* south Kirghizia.——Fig. 115,*2a–g.* **C. mirabilis,* southern Tien Shan Range, Chachme River; *a,b,* holotype, lateral view of ventral valve exterior, exterior, CNIGR 3/12589, ×3.3; *c,* dorsal valve exterior, ×3.3; *d,* paratype, dorsal valve interior, CNIGR 7/12589, ×4.2 (Popov & Tikhonov, 1990); *e,* ventral valve interior, ×7.5; *f,* paratype, detail of ventral interarea, delthyrium, RMS Br 136454, ×22.9; *g,* paratype, lateral view of ventral valve exterior, RMS Br 136455, ×12.5 (new).

Acareorthis Roberts in Roberts & Jell, 1990, p. 268 [**A. jelli;* OD]. Shell planoconvex, bisulcate, subrectangular; ornament of costae and concentric lamellae; ventral interarea high triangular, catacline to apsacline, bisected by narrow, convex pseudodeltidium; dorsal interior with transverse ridge along posterior margin, divided medially by thickened internal oblique muscle scars; dorsal posterior, anterior adductor scars deeply impressed. *Lower Cambrian (Toyonian)–Middle Cambrian (lower Amgaian):* Greenland, *Toyonian;* Australia (New South Wales), *lower Amgaian.*——Fig. 115,*1a–e.* **A. jelli,* Coonigan Formation, Mootwingee area, New South Wales; *a,* holotype, ventral valve exterior, AMF 79654, ×12.5; *b,* paratype, ventral valve, posterior view, AMF 79657, ×10; *c,* paratype, ventral valve, lateral view, AMF 79658, ×12.5; *d,* paratype, dorsal valve exterior, AMF 79659, ×12.5; *e,* paratype, dorsal valve interior, AMF 79663, ×15 (Roberts & Jell, 1990).

DICTYONELLIDA

Lars E. Holmer
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Order DICTYONELLIDA Cooper, 1956

[*nom. transl.* Holmer, herein, *ex* Dictyonellidina Rowell, 1965b, p. 359, *nom. correct. pro* suborder Dictyonelloidea Cooper, 1956, p. 947]

Ventral interarea variably developed; ventral perforation extending anterior to umbo through resorption and covered by colleplax; delthyrium open or covered by concave pseudodeltidium; dorsal valve with cardinal process, high median septum; dorsal mantle canals pinnate. *Upper Ordovician (Caradoc)–Lower Permian (Artinskian).*

The systematic position of the Eichwaldiidae and Isogrammidae has long remained uncertain (Rowell, 1965b; Wright, 1981); they have been considered to be closely related to each other and this is also supported by our cladistic analysis (see Fig. 89). The inferred relationship between the eichwaldiids and isogrammids is based mainly on the presence of a smooth, triangular area at the umbo, which is enlarged by shell resorption and covered posteriorly by a plate, having a slitlike opening to the interior (Fig. 116.2a, 116.3a). This peculiar structure was termed the colleplax by Wright (1981) and was known previously only from the dictyonellides; however, a similar structure is now also known to be present in the Chileida (Fig. 116.1a). If it is homologous, the dictyonellides may form a monophyletic group together with the Cambrian Chileida, as suggested by cladistic analysis (see Fig. 89). Wright (1981) assumed that the colleplax was the site of an organic pad secreted by the outer epithelium, rather than serving as a passage for the pedicle. The isogrammids and eichwaldiids differ from each other in other aspects of their morphology; the Eichwaldiidae has a nonstrophic shell with a concave pseudodeltidium, while the Isogram-

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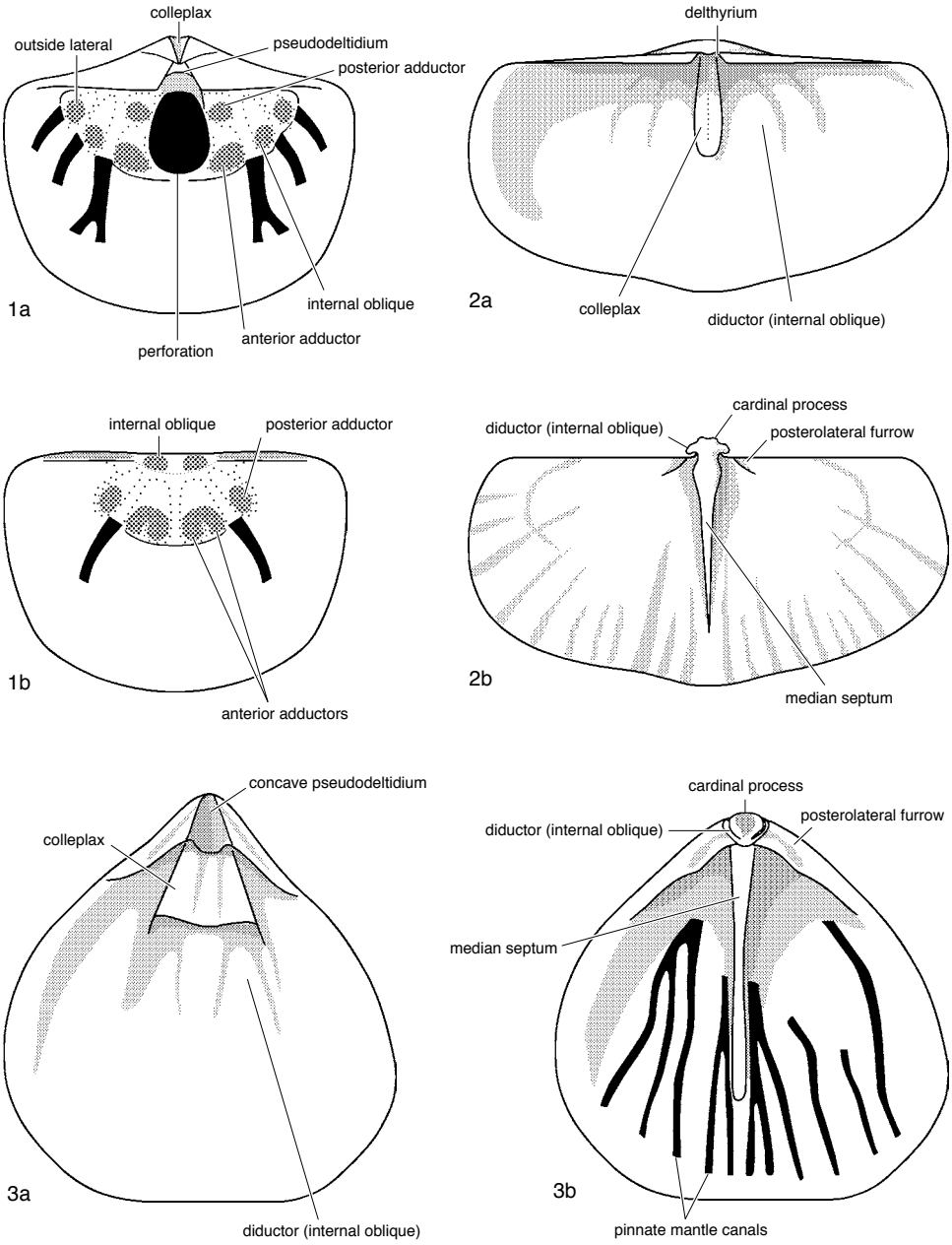

FIG. 116. Schematic illustration of musculature, mantle canal system, and articulation of Dictyonellida and Chileida; *1a,b,* ventral, dorsal valve of *Chile; 2a,b,* ventral, dorsal valve of *Isogramma; 3a,b,* ventral, dorsal valve of *Eodictyonella* (new).

midae is characterized by a strophic shell with a triangular delthyrium (Fig. 116.2–116.3). The muscle system is inadequately known in both families, but the presence of a cardinal process in both groups (Fig. 116.2b, 116.3b) suggests that they may have had diductor muscles as in articulated brachiopods (ROWELL, 1965a); in some

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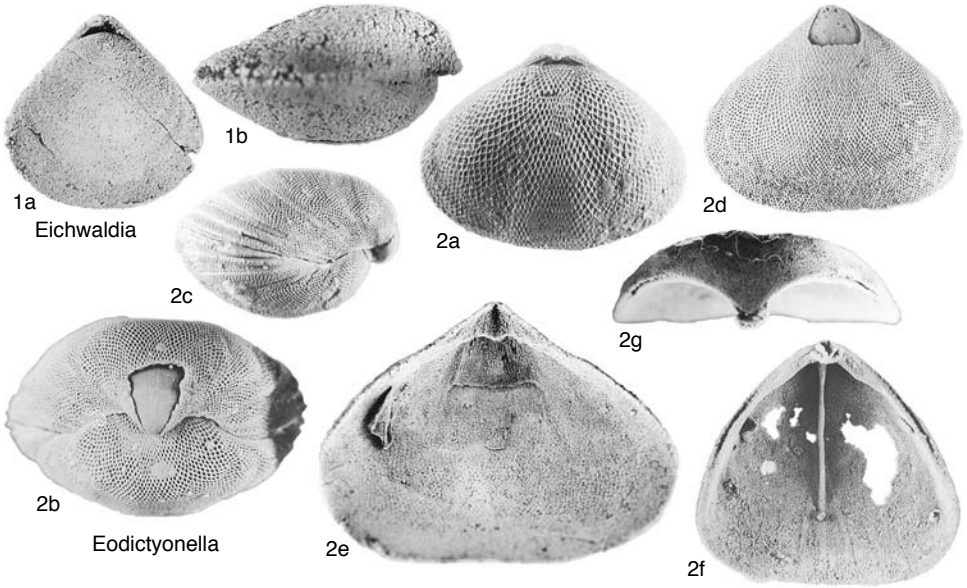

FIG. 117. Eichwaldiidae (p. 198–200).

isogrammids (*Megapleuronia*), the dorsal attachment of the diductor muscle is located on a high platform. They differ from the articulated brachiopods, however, in having a different type of articulation; in the Eichwaldiidae, the lateral movements of the valves are restricted both by furrows on the posterolateral margins of the dorsal valve as well as an incurved dorsal beak, fitting tightly into the concave pseudodeltidium (Fig. 116.2ab). In the Isogrammidae, the articulatory structures include small posterolateral furrows located lateral to the cardinal process (Fig. 116.3ab). The shell of eichwaldiids is endopunctate and has a fibrous secondary layer (WRIGHT, 1981), while the original shell structure in the Isogrammidae is unknown. It would seem that the latter are preserved invariably as internal molds and casts or have become silicified; this type of preservation may suggest that the shell of isogrammids was originally aragonitic, but further work is needed to clarify this problem. The mantle canals of isogrammids are poorly known and known only from the dorsal valve of *Megapleuronia,* which has a pinnate condition. In the Eichwaldiidae, the dorsal mantle canals of *Eodictyonella* also appear to be pinnate (Fig. 116.2b).

Superfamily EICHWALDIOIDEA Schuchert, 1893

[*nom. correct.* HARPER & others, 1993, p. 435, *pro* Eichwaldiacea ROWELL, 1965b, p. 359, *nom. transl. ex* Eichwaldiidae SCHUCHERT, 1893, p. 155]

Characters as for order. *Upper Ordovician (Caradoc)–Lower Permian (Artinskian).*

Family EICHWALDIIDAE Schuchert, 1893

[Eichwaldiidae SCHUCHERT, 1893, p. 155]

Shell biconvex, triangular; ventral interarea high, subtriangular with reduced propareas; pseudodeltidium broad, concave; dorsal posterolateral margins with long, oblique furrows, serving as articulatory structures; shell punctate with fibrous secondary layer. *Upper Ordovician (Caradoc)–Lower Devonian.*

Eichwaldia BILLINGS, 1858, p. 190 [**E. subtrigonalis;* OD]. Ornament of fine fila; dorsal median septum prominent, extending close to anterior margin, with cardinal process forming boss at posterior end of septum; musculature unknown. *Ordovician*

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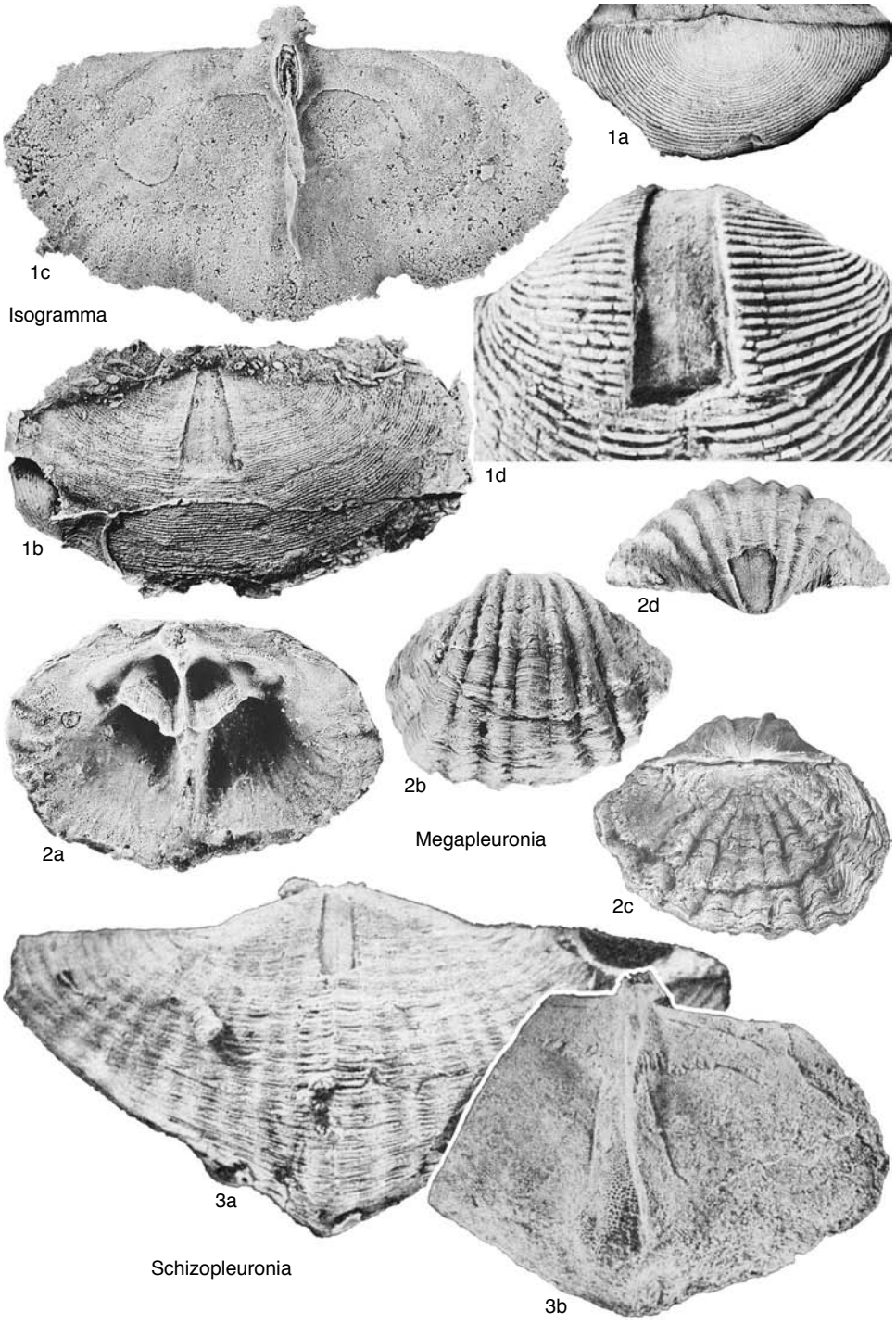

FIG. 118. Isogrammidae (p. 200).

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(Caradoc): Canada (Ontario, Quebec).——Fig. 117,*1a,b.* **E. subtrigonalis,* Ottawa Formation, Allumette Island, Quebec; *a,* dorsal view of both valves, ×1.7; *b,* oblique lateral view of both valves, GSC 1145, ×3.3 (new).

Eodictyonella Wright, 1994a, p. 908, *nom. nov. pro Dictyonella* Hall, 1867a, p. 274, *non Dictyonella* Schmidt, 1868, p. 10 [**Atrypa coralifera* Hall, 1852, p. 281; OD] [=*Dyctionella* Oehlert, 1887b, p. 1267]. Similar to *Eichwaldia,* but with ornament of coarse pits, formed by intersecting, offset radiating rows of narrow ridges. *Ordovician (Ashgill)–Lower Devonian:* USA, Canada, *Ashgill–Silurian;* Great Britain, Sweden, Estonia, Bohemia, Russia (Altai), Ukraine (Podolia), China, *Silurian;* Kazakhstan, *Silurian–Lower Devonian.*——Fig. 117,*2a–c. D. reticulata* (Hall), Waldron Shale, Silurian, Waldron, Indiana; *a,* dorsal view of both valves, AMNH 36636, ×2.5; *b,* posterior view of both valves, ×2.7; *c,* lateral view of both valves, USNM 303732, ×2.1 (new).——Fig. 117,*2d–g. D. gibbosa* (Hall), Decatur Formation, Silurian, Linden, Tennessee; *d,* ventral valve exterior, USNM 459702a, ×2.9; *e,* ventral valve interior, USNM 459702b, ×4.7; *f,* dorsal valve interior, ×2.5; *g,* posterior view, dorsal valve interior, USNM 459702c, ×2.8 (new).

Family ISOGRAMMIDAE Schuchert, 1929

[Isogrammidae Schuchert, 1929, p. 18] [*incl.* Megapleuroniinae Liao, 1983, p. 637]

Shells transversely suboval; ventral interarea wide, flattened; delthyrium open, triangular; cardinal process with well-developed shaft; posterolateral furrows small, located lateral to cardinal process. *Carboniferous–Permian.*

Isogramma Meek & Worthen, 1870, p. 36 [*?*Chonetes millipunctatus* Meek & Worthen, 1870, p. 35; OD] [=*Aulacorhynchus* von Dittmar, 1872, p. 2, *non* Gould, 1834; *Aulacorhyna* Strand, 1928, p. 37, *nom. nov. pro Aulacorhynchus* von Dittmar, 1872 (type, *Aulacorhynchus pachti* von Dittmar, 1872, p. 2), *non* Gould, 1834]. Large, concavoconvex; ornament of strong, concentric, elevated fila; myophore strong; shaft bifurcating around dorsal median ridge. *Carboniferous–Permian:* Great Britain, Austria, Germany, Spain, Poland, Kazakhstan, Uzbekistan, *Carboniferous;* USA, European Russia, Ukraine, China, *Carboniferous–Permian;* Japan, *Permian.*——Fig. 118,*1a,b. I. texanum* Cooper, Gaptank Formation, Carboniferous, Marathon, western Texas; *a,* dorsal external mold, ×1.1; *b,* holotype, ventral external mold, USNM 111688a, ×1.1 (Cooper, 1952a).——Fig. 118,*1c. I. lobatum* Cooper & Grant, Cathedral Mountain Formation, Permian, western Texas; dorsal interior, USNM 151384, ×0.8 (Cooper & Grant, 1974).——Fig. 118,*1d. I. salteri* Brand, Hotwells Limestone, Carboniferous, Compton Martin, Somerset; detail of colleplax, BGS Zo1525, ×5 (Wright, 1981).

Megapleuronia Cooper, 1952a, p. 117 [**Productus fabianii* Greco, 1947, p. 1; OD]. Biconvex or concavoconvex; costate, with discontinuous, raised fila; ventral interior unknown; dorsal muscle platform free, supported by median septum. *Permian:* Italy (Sicily).——Fig. 118,*2a.* **M. fabianii* (Greco), Sosio Limestone, Pietra di Salamone, Sosio Valley; dorsal valve interior, USNM 116346, ×1.2 (Cooper, 1952a).——Fig. 118,*2b–d. M. grecoi* Cooper, Sosio Limestone, Pietra di Salamone, Sosio Valley; holotype, ventral view, dorsal view, posterior view of both valves, USNM 116347b, ×1.2 (Cooper, 1952a).

Schizopleuronia Liao, 1983, p. 637 [**S. grandis;* OD]. Externally similar to *Megapleuronia,* but sulcate, lacking dorsal muscle platform. *Permian:* China.——Fig. 118,*3a,b.* **S. grandis,* Heshan Formation, Guangxi; *a,* holotype, ventral view, NIGP 70460, ×0.8; *b,* paratype, dorsal valve interior, NIGP 70462, ×0.8 (Liao, 1983).

OBOLELLATA

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[VSEGEI, St. Petersburg; and University of Uppsala]

Class OBOLELLATA Williams & others, 1996

[Obolellata Williams & others, 1996, p. 1192]

Shell biconvex, foliated, impunctate; both valves with hemiperipheral growth and well-defined interareas; ventral interarea with delthyrium, usually covered by concave pseudodeltidium, rarely open; articulatory structures variably developed; musculature probably with internal oblique muscles attached to dorsal valve posteromedianly. *Lower Cambrian–Middle Cambrian (Amgaian).*

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Order OBOLELLIDA Rowell, 1965

[Obolellida Rowell, 1965a, p. 291]

Anterior commissure rectimarginate or slightly sulcate; ventral interarea low and relatively short; delthyrium open, or covered by convex pseudodeltidium; paired denticles, if present, lacking supporting structures; mantle canal system baculate in both valves, with ventral and dorsal *vascula lateralia* and dorsal *vascula media;* impunctate with laminar secondary layer. *Lower Cambrian–Middle Cambrian (Amgaian).*

The obolellides were usually united previously with the siphonotretoids, but Rowell (1962a, 1965a) recognized them as a separate superfamily and order. The possible monophyly of the order could not be confirmed by our cladistic analysis, where they were used as an outgroup; the same analysis suggests that the Naukatidina forms a monophyletic group within the Obolellida as well as the Trematobolidae (see Fig. 89). The obolellides include the earliest known calcitic brachiopods and are known from the lower Atdabanian (Pelman, 1977); the poorly known late Tommotian obolellide *Nochoroiella* (Grigorieva, Melnikova, & Pelman, 1983) is here considered to be of problematic affinity. The group includes both forms that lack articulation, as well as those that have primitive articulation, consisting of paired ventral denticles and dorsal sockets (Fig. 119). The denticles are first known from forms within the Obolellidae, where they are composed partly of primary shell, while the Trematobolidae and Naukatida have denticles consisting entirely of secondary shell (Popov, Holmer, & Bassett, 1996). The denticles lack supporting structures in all Obolellida, but in Naukatida they are supported by an arcuate plate below the interarea, the anterise (Fig. 119.3a). An open delthyrium is present only in the Obolellidae; in all other obolellides the delthyrium is covered by a concave pseudodeltidium (Fig. 119). According to Gorjansky and Popov (1985, 1986), the muscle system in the Obolellida is closely comparable with that of other articulated brachiopods in having anterior and posterior adductor scars, which form a quadripartite muscle field in the dorsal valve; and a single pair of oblique muscles, the internal oblique muscles, attached dorsally to a small area at the bottom of the notothyrial cavity (Fig. 119). In *Obolella,* the ventral muscle scars are located peripherally within the visceral area, but in most genera they form a single muscle field, with the adductor scars located medially. In articulated obolellides, the attachment scar of the internal oblique muscles is located posterior to the axis of rotation, suggesting that they may have served as diductors (Fig. 119).

Superfamily OBOLELLOIDEA Walcott & Schuchert, 1908

[*nom. correct.* Harper in Harper & others, 1993, p. 431, *pro* Obolellacea Gorjansky, 1960, p. 180, *nom. imperf., nom. transl. ex* Obolellidae Walcott & Schuchert in Walcott, 1908, p. 145]

Characters as for order. *Lower Cambrian–Middle Cambrian (Amgaian).*

Family OBOLELLIDAE Walcott & Schuchert, 1908

[Obolellidae Walcott & Schuchert in Walcott, 1908, p. 145]

Ornament of fine, radial capillae; ventral valve with open delthyrium; articulation lacking or vestigial, with paired denticles on delthyrial margins, composed partly of primary shell; dorsal adductor scars radially arranged; ventral *vascula lateralia* submedian, divergent; dorsal *vascula lateralia* submarginal. *Lower Cambrian.*

Obolella Billings, 1861b, p. 6 [**O. chromatica;* SD Dall, 1870, p. 163]. Shell weakly biconvex, subcircular or elongate oval; ornament of fine striae, lamellose peripherally; ventral interarea low, narrow, apsacline to catacline; ventral beak marginal; dorsal interarea low, orthocline; ventral visceral field forming low, solid platform, bisected by shallow median groove. *Lower Cambrian (Atdabanian, ?Botomian):* USA, Canada, Greenland, Russia (Siberia, Altai), ?Norway, China, Spain, Australia.——Fig. 120,*2a–c.* **O. chromatica,* Labrador, Canada; *a,* ventral valve interior, GSC 395i, ×4.2 (new); *b,* dorsal valve exterior, USNM 14891c, ×3.3 (Rowell, 1962a); *c,* dorsal interior, GSC 395m, ×4.2 (new).——Fig.

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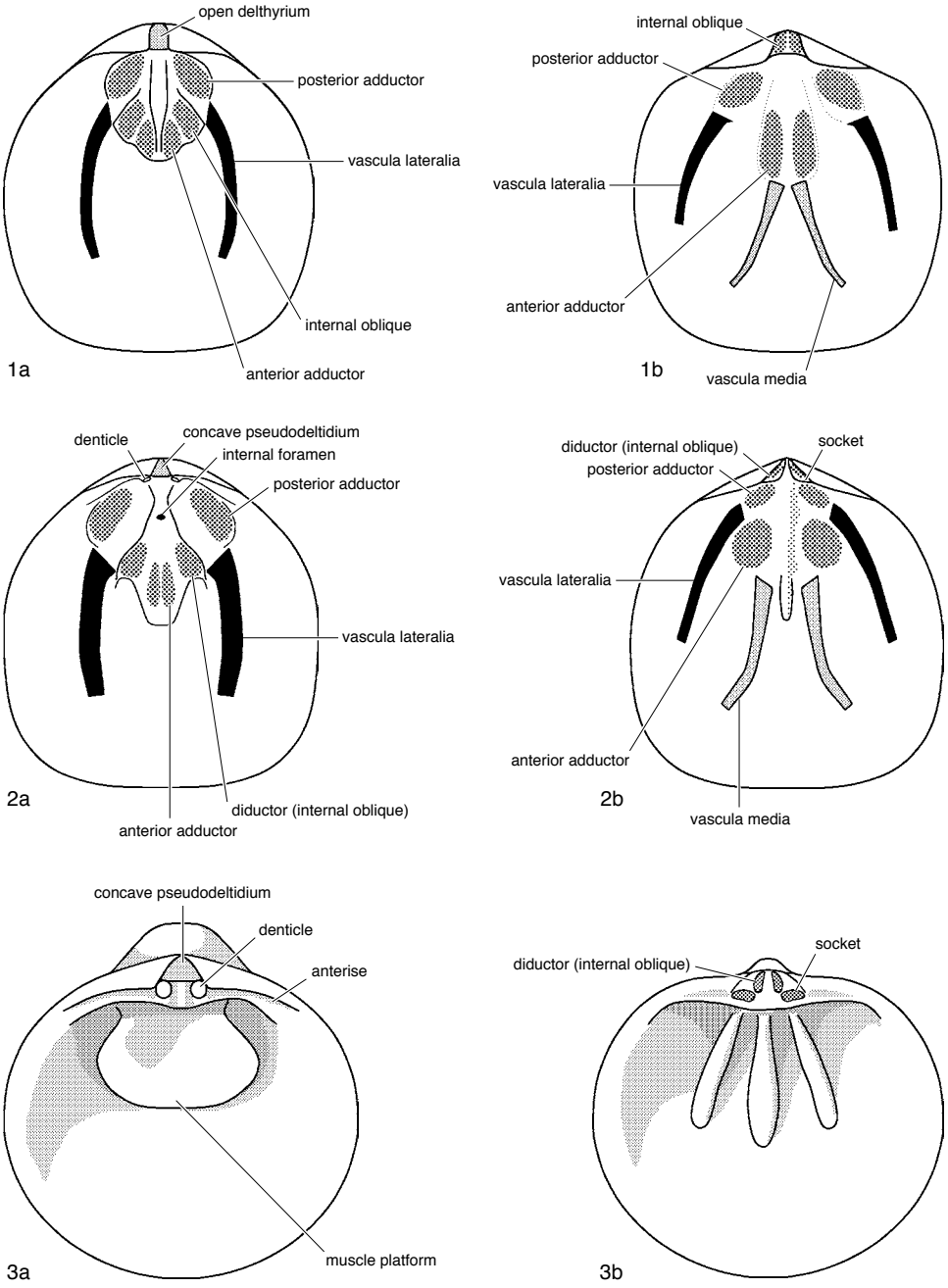

FIG. 119. Schematic illustration of musculature, mantle canal system, and articulation of Obolellida; *1a,b,* ventral, dorsal valve of *Obolella; 2a,b,* ventral, dorsal valve of *Trematobolus; 3a,b,* ventral, dorsal valve of *Oina* (new).

120,*2d–f. O. crassa* (HALL), Troy, New York; *d,* ventral valve interior, USNM 51951f, ×3.3; *e,* dorsal internal mold, USNM 51951, ×3.3; *f,* ventral valve exterior, USNM 14691, ×2.5 (new).

Bicia WALCOTT, 1901, p. 676 [**Obolella gemma* BILLINGS, 1871b, p. 218; OD]. Shell subtriangular or ovate; ornament of weak, radial striae; ventral beak subacuminate; ventral interarea relatively high,

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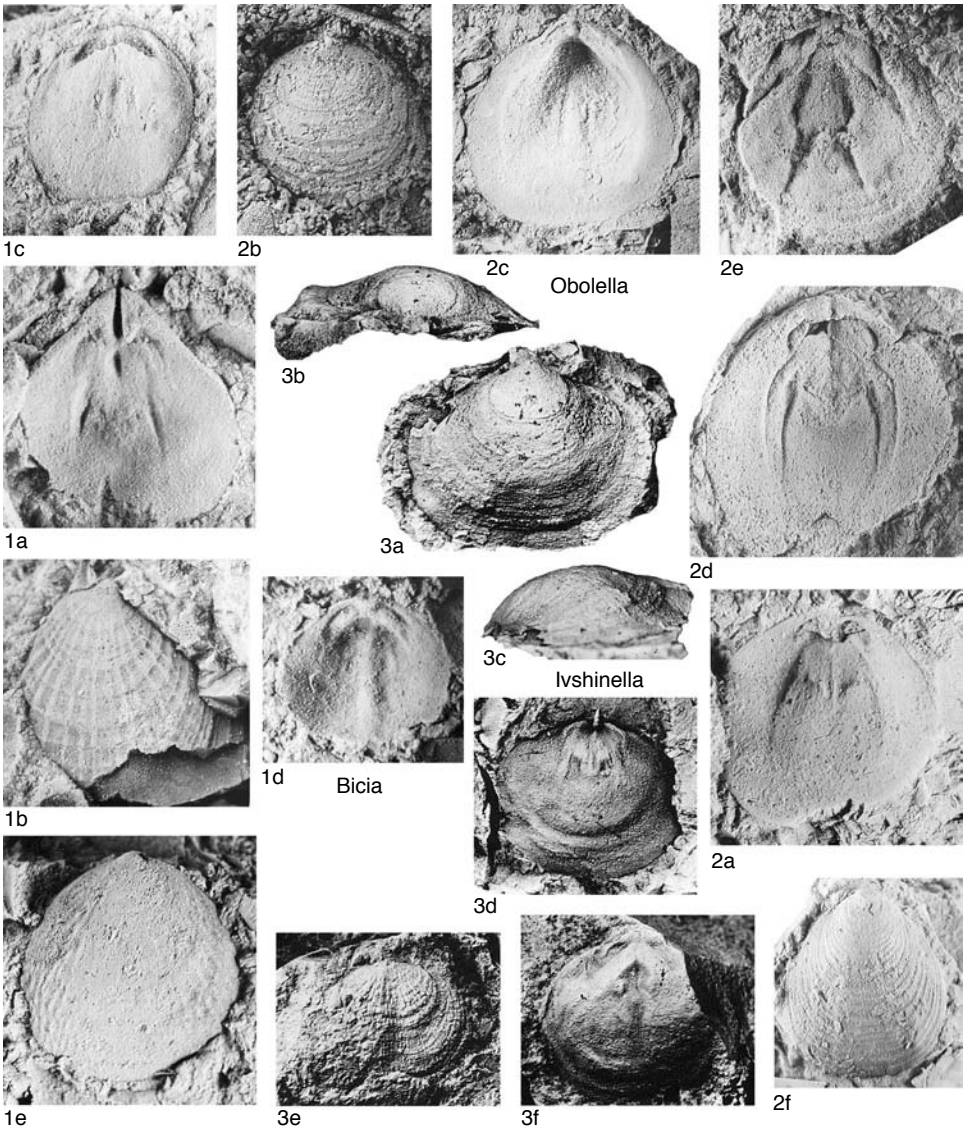

FIG. 120. Obolellidae (p. 201–204).

orthocline, triangular, with delthyrium, bearing small denticles; dorsal pseudointerarea low, orthocline; ventral visceral field thickened, extending to midvalve, with median depression; dorsal median ridge broad, extending from beak; ventral *vascula lateralia* submedian, widely divergent. *Lower Cambrian:* USA, Russia (southeastern Siberia).——FIG. 120,*1a–e.* **B. gemma* (BILLINGS), Troy, New York; *a,* ventral valve interior, GSC 387d, ×6.7; *b,* ventral valve exterior, USNM 51900, ×6.1; *c,* dorsal internal mold, USNM 51900d, ×5; *d,* dorsal valve interior, USNM 14889f, ×5; *e,* dorsal valve exterior, GSC 387, ×6.7 (new).

Brevipelta GEYER, 1994, p. 996 [**B. chouberti* GEYER, 1994, p. 997; OD]. Ventral valve with deep delthyrial opening; ventral visceral field poorly defined; dorsal median septum poorly defined; dorsal adductor scars poorly defined; ventral *vascula lateralia* submedian, divergent. *Lower Cambrian:* Morocco, *Choubertella* and *Daguinaspis* Zones.——FIG. 121,*1a–d.* **B. chouberti,* Lower Cambrian, Amouslek Formation, western Anti-Atlas

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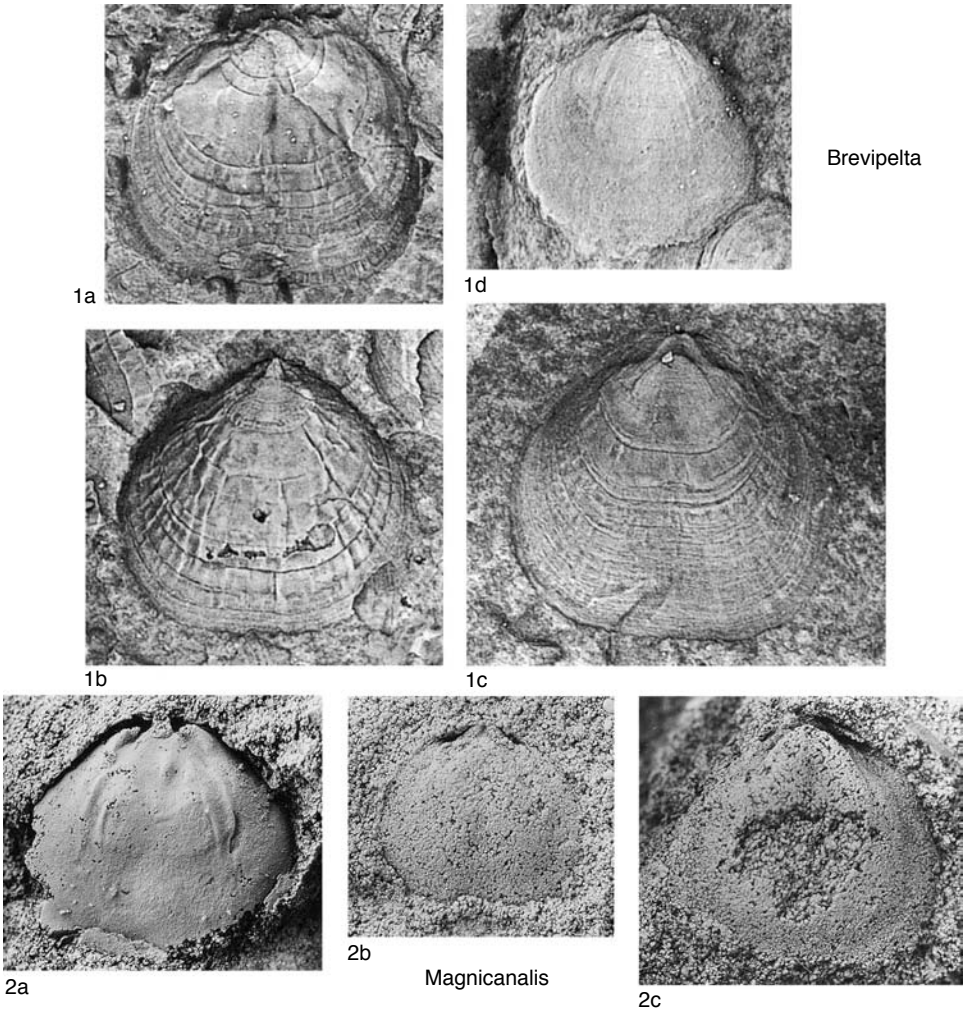

FIG. 121. Obolellidae (p. 203–205).

Mountains; *a,* dorsal valve exterior, IGR 19994g, ×6; *b,* ventral valve exterior, PIW 93119b, ×6; *c,* dorsal internal mold, PIW 93119q, ×6; *d,* ventral internal mold, PIW 93118a, ×6 (Geyer, 1994).

Ivshinella KONEVA, 1979, p. 54 [**I. modesta;* OD]. Shell almost equibiconvex, subcircular, or transversely oval; ornament of radial striae; ventral interarea orthocline, with low, triangular delthyrium, bearing small denticles; dorsal valve slightly sulcate; dorsal interarea low, orthocline; ventral visceral field moderately thickened, extending anteriorly to midvalve; dorsal visceral field broad, elongate oval, slightly thickened, extending to midvalve; ventral *vascula lateralia* submedian, slightly divergent. *Lower Cambrian (Botomian):* central Kazakhstan.——FIG. 120,*3a–f.* **I. modesta,* Edrej Beds, Edrej Mountains; *a–c,* holotype, ventral valve exterior, posterior view, lateral view, MANK 2138/198, ×3.3; *d,* ventral internal mold, MANK 2138/204, ×3.3; *e,* dorsal valve exterior, MANK 2138/211, ×3.3; *f,* dorsal internal mold, MANK 2138/210, ×3.3 (Koneva, 1979).

Magnicanalis ROWELL, 1962a, p. 140 [**Obolella mobergi* WALCOTT, 1901, p. 673; OD]. Shell gently biconvex, elongate to transversely oval; ornament of fine radial striae; ventral interarea low, apsacline, with delthyrium; dorsal interarea orthocline; ventral visceral field slightly thickened in posterior third, bisected by median groove; dorsal visceral field poorly defined, bisected by low median ridge; dorsal internal oblique muscles scars on strongly elevated notothyrial platform, bisected by low, median plication; dorsal posterior adductor scars on two widely divergent, ridgelike elevations; ventral

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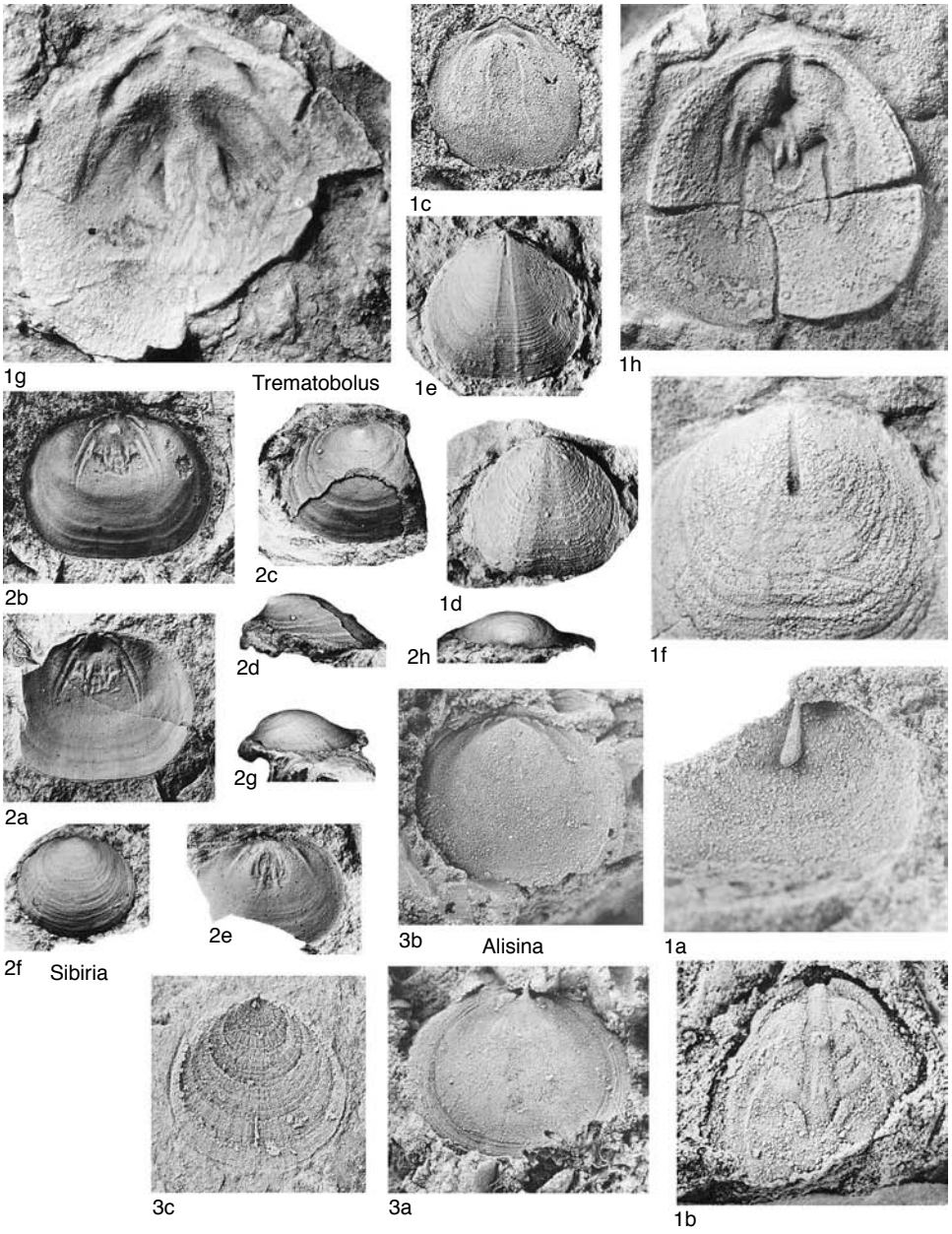

FIG. 122. Trematobolidae (p. 206).

vascula lateralia submedian, subparallel. *Lower Cambrian:* Sweden, Russia (southeastern Siberia).——FIG. 121,*2a–c. *M. mobergi* (WALCOTT), Lingulid Sandstone, Sularp, Scania; *a,* ventral internal mold, LO 6575t, ×3.3; *b,* dorsal internal mold, LO 6576t, ×2.9; *c,* dorsal internal mold, LO 6577t, ×4.2 (new).

Family TREMATOBOLIDAE new family

[Trematobolidae POPOV & HOLMER, herein]

Strophic articulation with paired, ventral denticles, composed of secondary shell; sometimes with dorsal sockets; delthyrium

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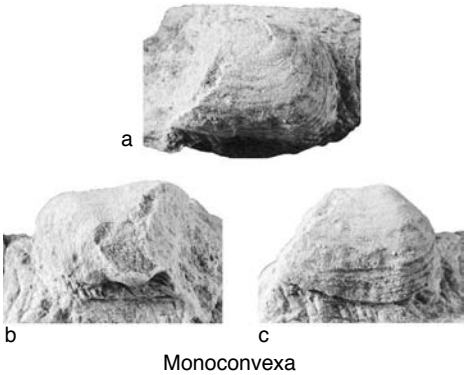

FIG. 123. Uncertain (p. 206).

covered by concave pseudodeltidium; pedicle emerging through foramen, located apical or anterior to beak. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian).*

Trematobolus MATTHEW, 1893, p. 276 [**T. insignis;* OD] [=*Protosiphon* MATTHEW, 1897, p. 70 (type, *P. kempanum*); *Protosyphon* GORJANSKY, 1960, p. 181; *Lamellodonta* VOGEL, 1962, p. 216 (type, *L. simplex*)]. Shell almost equibiconvex to somewhat dorsibiconvex, elongate or transversely oval; ventral interarea low; apsacline, with narrow, concave pseudodeltidium; pedicle foramen small, rounded, anterior to beak; pedicle track narrow, triangular, covered by concave plate; dorsal interarea low, orthocline or gently anacline; ventral visceral area strongly thickened, with broad median furrow posterior to foramen; notothyrial cavity sometimes with small sockets; dorsal diductor scars sometimes bisected by low median ridge; ventral *vascula lateralia* submedian, subparallel; dorsal *vascula lateralia* straight, widely divergent. *Lower Cambrian (Toyonian)–Middle Cambrian (Amgaian):* USA, Canada, Spain, Morocco, Russia (Siberia, Altai).——FIG. 122,*1a–c. T. kempanum* (MATTHEW), Lower Cambrian, Long Island, New Brunswick; *a,* ventral external mold, USNM 52212n, ×3.3; *b,* ventral internal mold, USNM 52212c, ×3.6; *c,* dorsal internal mold, USNM 52212k, ×1.7 (Rowell, 1962a).——FIG. 122,*1d–h. T. pristinus bicostatus* GORJANSKY, Toyonian, Rassokha River, Siberia; *d,* paratype, dorsal valve exterior, CNIGR 11/8362, ×1.7; *e,* holotype, ventral valve exterior, CNIGR 1/8362, ×1.7; *f,* detail of ventral umbonal area, CNIGR 5/8362, ×5 (Gorjansky, Egorova, & Savitskii, 1964); *g,* dorsal valve interior, CNIGR 15/8362, ×4.2; *h,* paratype, ventral valve interior, CNIGR 9/8362, ×4.2 (Gorjansky & Popov, 1986).

Alisina ROWELL, 1962a, p. 141 [**Obolella atlantica* WALCOTT, 1890, p. 36; OD]. Shell gently ventribiconvex, subcircular, sometimes with fine striae; ventral interarea apsacline to catacline; concave pseudodeltidium with median plication; foramen rounded, apical; dorsal valve sometimes gently sulcate; dorsal interarea low, triangular, orthocline, with open notothyrium, bearing sockets, bounded by low ridges; ventral visceral field thickened anteriorly; dorsal adductor scars arranged radially, with smaller posterior scars; ventral *vascula lateralia,* submedian subparallel, or slightly divergent; dorsal *vascula lateralia* submarginal, widely divergent; dorsal *vascula media* long, widely divergent. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian):* USA, Canada, Russia (Siberia, Altai), Great Britain.——FIG. 122,*3a–c. *A. atlantica* (WALCOTT), Lower Cambrian; *a,* ventral internal mold, Conception Bay, Newfoundland, USNM 18322a, ×5; *b,* dorsal internal mold, Bristol County, Massachusetts, USNM 143123, ×5; *c,* ventral external mold, Trinity Bay, Newfoundland, USNM 51998b, ×3.3 (Rowell, 1962a).

Sibiria GORJANSKY in PELMAN, 1977, p. 47 [**S. magna;* OD]. Shell ventribiconvex, subcircular, smooth apically, lamellose peripherally; ventral valve subconical; ventral interarea procline to catacline, with deep, concave pseudodeltidium with median plication; beak anterior to margin; pedicle foramen small, apical; dorsal valve may be slightly sulcate; dorsal interarea low, orthocline; ventral visceral field somewhat thickened; notothyrial platform low, broadly triangular, bearing small sockets on its lateral sides; dorsal visceral area sightly raised, extending anteriorly to midvalve; ventral *vascula lateralia* submedian, straight, slightly divergent; dorsal *vascula lateralia* submarginal, widely divergent; *vascula media* long, divergent. *Lower Cambrian (Atdabanian):* Russia (eastern Siberia).——FIG. 122,*2a–e. *S. magna,* Kotuy River; *a,b,* paratype, ventral valve interior, internal mold, CNIGR 2/10933, ×1.7; *c,d,* holotype, ventral valve exterior, lateral view, CNIGR 1/10933, ×1.7; *e,* paratype, dorsal internal mold, CNIGR 3/10933, ×1.7 (Gorjansky, 1977).——FIG. 122,*2f–h. S. glabra* GORJANSKY, Kotuy River; paratype, dorsal exterior, lateral view, posterior view, CNIGR 7/10933, ×1.7 (Gorjansky, 1977).

Superfamily UNCERTAIN

Monoconvexa PELMAN, 1977, p. 49 [**M. monoconvexa;* OD]. Shell ventribiconvex, transversely suboval; beaks of both valves marginal; interareas, internal characters of both valves unknown. *Lower Cambrian (upper Atdabanian):* Russia (Siberia).——FIG. 123*a–c. *M. monoconvexa,* Lena River; ventral exterior, posterior view, anterior view, IGiG 392/31, ×3 (new).

Nochoroiella PELMAN in GRIGORIEVA, MELNIKOVA, & PELMAN, 1983, p. 54 [**N. isitica;* OD]. Shell small, biconvex, transversely elliptical to subtriangular; both valves with marginal beaks, lacking interareas.

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Genus poorly known, may be an operculum. *Lower Cambrian (upper Tommotian):* Russia (Siberia).

Order NAUKATIDA Popov & Tikhonov, 1990

[Naukatida Popov & Tikhonov, 1990, p. 40]

Shell biconvex, smooth or with radial ornament; ventral interarea with concave pseudodeltidium, which may be perforated apically by elongate oval foramen; ventral visceral platform high, may be free peripherally; articulation with pair of closely spaced, ventral denticles, located on anterise, dorsal sockets on lateral sides of notothyrial platform; dorsal adductor scars arranged radially. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

In the Naukatida, the ventral muscle field is located on a high platform, and in some genera, like *Oina,* this platform is free distally (see Fig. 119.3a), thus making it comparable with the ventral spondylium-like structure of protorthoids, like *Arctohedra* and *Glyptoria* (Popov, 1992).

Superfamily NAUKATOIDEA Popov & Tikhonov, 1990

[*nom. transl.* Harper in Harper & others, 1993, p. 431, *ex* Naukatidae Popov & Tikhonov, 1990, p. 41]

Characters as for suborder. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

Family NAUKATIDAE Popov & Tikhonov, 1990

[Naukatidae Popov & Tikhonov, 1990, p. 41]

Characters as for superfamily. *Lower Cambrian–Middle Cambrian (lower Amgaian).*

Naukat Popov & Tikhonov, 1990, p. 41 [**N. proprium;* OD]. Shell dorsibiconvex, transverse oval, smooth apically, coarsely costellate peripherally; anterior commissure uniplicate; ventral interarea apsacline; pseudodeltidium concave, perforated apically by elongate-oval pedicle foramen; ventral visceral platform small, strongly thickened anteriorly; dorsal interior with median septum, anterior adductor scars located on high, broad ridges lateral to septum. *Lower Cambrian (Botomian):* southern Kirghizia.——Fig. 124,*3a–d.* **N. proprium,* Chachme River, southern Tien Shan Range; *a,* oblique posterior view of both valves, ×22.9; *b,* dorsal view of both valves, ×19.6; *c,* holotype, oblique lateral view of both valves, CNIGR 10/12589, ×22.9 (new); *d,* paratype, ventral exterior, CNIGR 11/12589, ×16.7 (Popov & Tikhonov, 1990).

Bojarinovia Aksarina in Aksarina & Pelman, 1978, p. 106 [**B. levigata;* OD]. Shell ventribiconvex, transversely oval; anterior commissure rectimarginate; ventral interarea low, narrow, apsacline; pedicle opening, interior poorly known; dorsal valve (described originally as ventral) with anterior and posterior adductor scars forming elevated tripartite platform, divided by two deep furrows; *vascula media* straight, widely divergent. *upper Lower Cambrian:* Russia (Altai). Satisfactory material not available for illustration.

Bynguanoia Roberts in Roberts & Jell, 1990, p. 281 [**B. perplexa;* OD]. Shell ventribiconvex, subcircular; anterior commissure sulcate; ornament of coarse, radial costae; ventral interarea low, narrow, apsacline; concave pseudodeltidium perforated apically by elongate-oval pedicle foramen; dorsal valve with vestigial interarea and shallow sulcus; ventral interior with strongly thickened anterior visceral platform; notothyrial platform narrow, strongly elevated; dorsal posterior adductor scars forming separate elevated platforms close to posterior margin. *Middle Cambrian (lower Amgaian):* Australia (New South Wales).——Fig. 124,*1a–g.* **B. perplexa,* Coonigan Formation, Mootwingee area; *a–e,* paratype, ventral, dorsal, posterior, anterior, lateral views of both valves, AMF 79714, ×3.3; *f,* holotype, ventral valve interior, AMF 79716, ×3.3; *g,* paratype, dorsal valve interior, AMF 79718, ×3.3 (Roberts & Jell, 1990).

Oina Popov & Tikhonov, 1990, p. 42 [**O. rotunda;* OD]. Shell subequibiconvex, transverse oval; anterior commissure rectimarginate; ventral interarea low, short, apsacline; delthyrium completely closed by concave pseudodeltidium; dorsal interarea small, orthocline; ventral visceral platform strongly elevated, free distally; notothyrial platform strongly elevated; dorsal interior with three broad, high septa not extending to midvalve. *Lower Cambrian (Botomian):* southern Kirghizia.——Fig. 124,*2a–g.* **O. rotunda,* Chachme River, southern Tien Shan Range; *a,* holotype, ventral valve interior, CNIGR 14/12589, ×3.3; *b,* paratype, ventral valve exterior, CNIGR 18/12589, ×3.3 (Popov & Tikhonov, 1990); *c,* dorsal valve exterior, CNIGR 17/12589, ×3.3; *d,* paratype, oblique lateral view of ventral valve interior, RMS Br 136451, ×13.8; *e,* oblique lateral view of ventral valve exterior, ×6.2; *f,* paratype, oblique posterior view of ventral valve exterior, RMS Br 136452, ×8.3; *g,* paratype, dorsal valve interior, RMS Br 136453, ×13.8 (new).

?Swantonia Walcott, 1905, p. 296 [**Camerella antiquata* Billings, 1861b, p. 10; OD]. Shell subtriangular, with rectimarginate anterior commissure; ornament of coarse, rounded ribs; ventral interarea with concave pseudodeltidium; other characters unknown. *Lower Cambrian:* USA (Nevada, Vermont).

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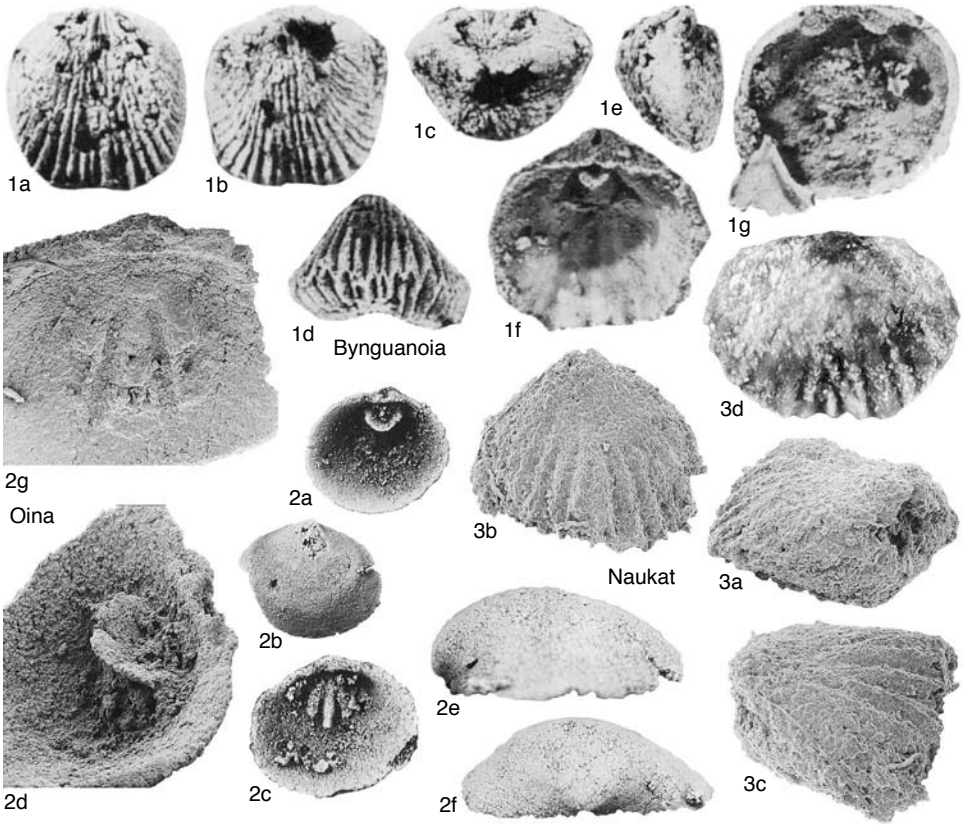

FIG. 124. Naukatidae (p. 207).

KUTORGINATA

LEONID E. POPOV and ALWYN WILLIAMS
[VSEGEI, St. Petersburg; and The University of Glasgow]

Class KUTORGINATA Williams & others, 1996

[Kutorginata WILLIAMS & others, 1996, p. 1193]

Shell strophic, ventribiconvex; anterior margin rectimarginate, rarely sulcate; posterior margin wide, straight, with large median opening; delthyrium widely triangular, covered by convex pseudodeltidium, bounded laterally by furrows; beak with small, rounded apical foramen; dorsal interarea divided by wide notothyrium; both valves with slightly thickened, weakly defined visceral area situated close to posterior margin; dorsal adductor scars radially disposed, dorsal diductor scars impressed on floor of notothyrial cavity; cardinal process absent; articulation by edges of interareas, without teeth and dental sockets; mantle canal systems pinnate; digestive tract probably open with anus placed posteromedianly between valves; shell structure fibrous impunctate. *Lower Cambrian–Middle Cambrian.*

The strophic, articulated shells of the Kutorginata rotated on simple hinge mechanisms that are different from those of other rhynchonelliforms. The hinge mechanisms of *Nisusia* and *Kutorgina* (Fig. 125), which

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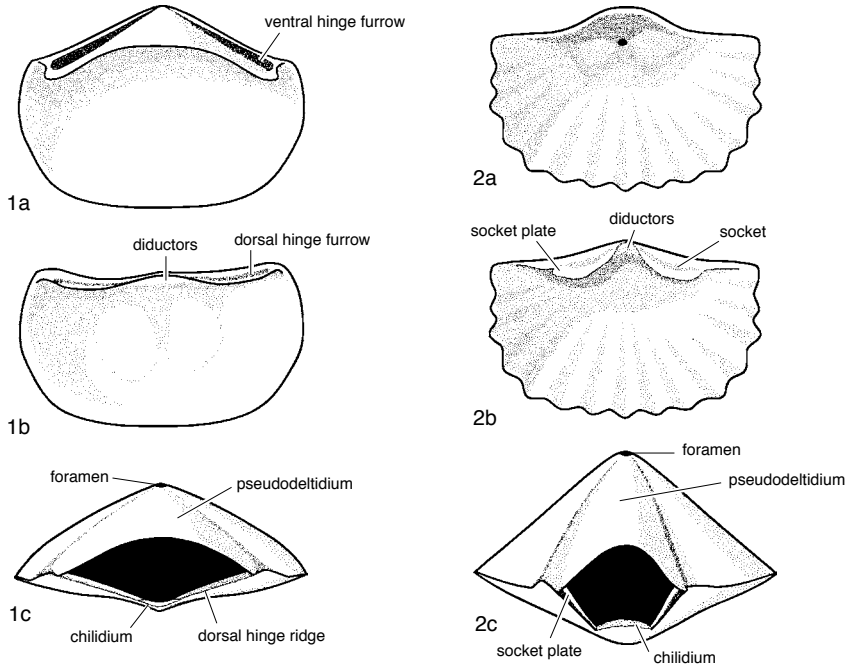

FIG. 125. Diagrammatic representation of kutorginide articulation; *1a–c, Kutorgina,* interiors of ventral and dorsal valves and posterior view of shell; *2a–c, Nisusia,* interiors of ventral and dorsal valves and posterior view of shell (adapted from Holmer & Popov, 1996).

are best known (ROWELL & CARUSO, 1985; POPOV & TIKHONOV, 1990; ROBERTS & JELL, 1990; POPOV and others, 1997), illustrate the variability of these primitive devices. In *Nisusia,* the lateral margins of the pseudodeltidium fit into deep sockets at the ends of a groove separating the dorsal interarea from a narrow socket plate continuous with the chilidium. In *Kutorgina,* a deep groove (ventral hinge groove) also separates the ventral interarea from the pseudodeltidium. This furrow accommodated the ends of the narrow lateral sectors of the dorsal interarea, which was also separated by a hinge furrow from a dorsal hinge ridge continuous with a chilidium. The differences between these two interlocking devices are minor as they merely reflect the strength of flexuring developing between the delthyrial and notothyrial covers and their respective interareas. Indeed the discovery by POPOV and TIKHONOV (1990) of a rudimentary kutorginid hinge device in juvenile specimens of *Nisusia* confirms the homology of the mechanisms.

With respect to brachiopod phylogeny, the discovery by ROWELL and CARUSO (1985) of silicified specimens of their *Nisusia sulcata*

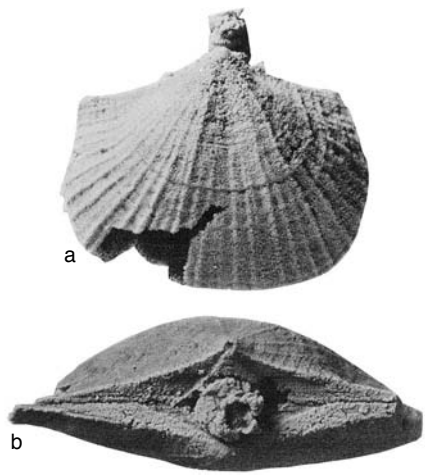

FIG. 126. *a,* Ventral and *b,* posterior views of complete shells of *Nisusia sulcata* ROWELL & CARUSO, 1985, showing assumed lithified fecal material in relation to shell and delthyrium and notothyrium, ×4 (Rowell & Caruso, 1985).

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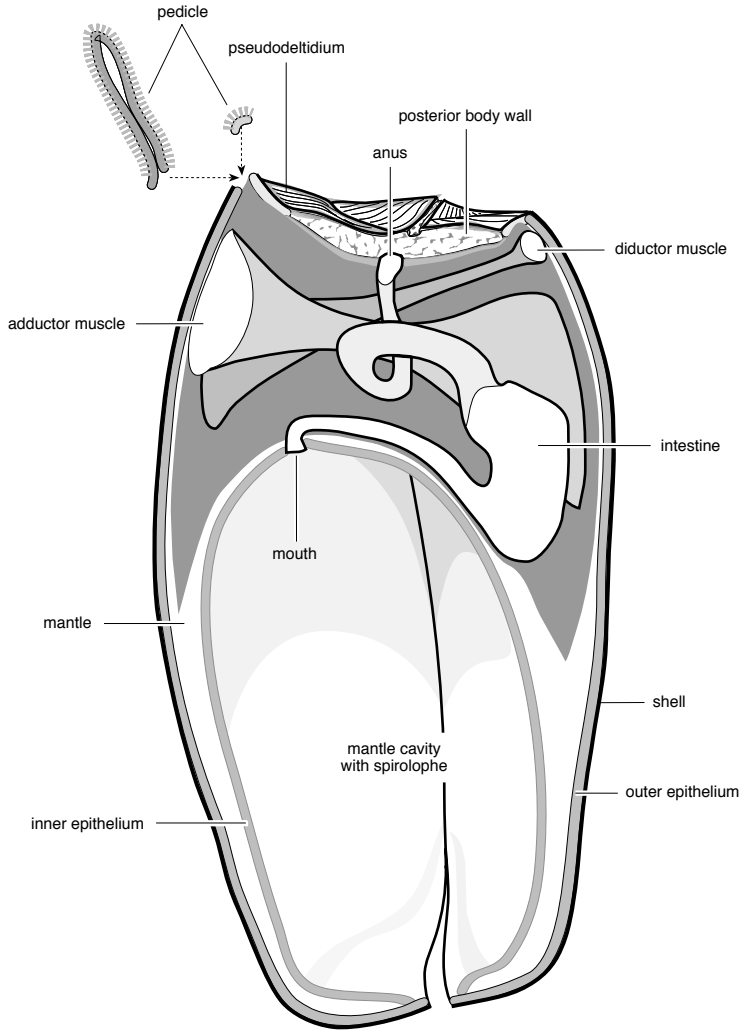

FIG. 127. Diagrammatic reconstruction of integument, pedicle, musculature, and intestine of nisusiids based on interpretation of *Nisusia sulcata* by ROWELL and CARUSO (1985); pedicle shown as varying from fully functional organ with chitinous cuticle to vestigial patch of poorly differentiated pedicle epithelium secreting chitinomucus cementing cover resulting in deformation of some kutorginid shells (new).

with cylindroid structures emerging from the opening subtended by the delthyrium and notothyrium (Fig. 126), is highly significant. The presence of a supra-apical foramen in the ventral valve precludes these structures from being pedicles and there are compelling reasons for accepting the authors' interpretation of them as fossilized feces. This would be consistent with the kutorginates having an anus located on a posterior body wall in the manner characteristic of living discinids and craniids (Fig. 127).

The secondary layer of *Nisusia* (Fig. 128) is typically fibrous; and this fabric is assumed to be characteristic of the kutorginates as a whole.

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Order KUTORGINIDA Kuhn, 1949

[*nom. transl.* Gorjansky, 1960, p. 181, *pro* order Kutorginacea Kuhn, 1949, p. 99] [=Paleotremata Thomson, 1927, p. 118; *incl.* order Rustellida Kuhn, 1949, p. 99]

Characters as for class. *Lower Cambrian–Middle Cambrian.*

Superfamily KUTORGINOIDEA Schuchert, 1893

[*nom. correct.* Popov & Williams, herein, *pro* Kutorginacea Walcott & Schuchert in Walcott, 1908, p. 144, *nom. transl. ex* Kutorginidae Schuchert, 1893, p. 151] [*incl.* Rustellacea Walcott, 1908, p. 143, *partim*]

Shell with articulation characterized by two triangular plates formed by dorsal interarea, bearing oblique ridges on the inner sides, which fit into deep furrows formed by ridges along inner sides of ventral interarea and lateral extensions of pseudodeltidium. *Lower Cambrian–Middle Cambrian.*

Family KUTORGINIDAE Schuchert, 1893

[Kutorginidae Schuchert, 1893, p. 151] [*incl.* Rustellidae Walcott, 1908, p. 143; ?Schuchertinidae Walcott, 1908, p. 145; Yorkiidae Rowell, 1962a, p. 144; Agyrekiidae Koneva, 1979, p. 59]

Shell ventribiconvex; ventral interarea narrow, poorly defined laterally; dorsal valve with marginal beak; notothyrium open; mantle canal system with two principal canals on both valves, radiating anteriorly. *Lower Cambrian–Middle Cambrian.*

Kutorgina Billings, 1861b, p. 8 [**K. cingulata;* OD] [=*Koturgina* Billings, 1861b, p. 8, *nom. imperf.; ?Rustella* Walcott, 1905, p. 311 (type, *R. edisoni*)]. Shell slightly elongate to transverse oval in outline with irregular ventral profile; strongly lamellose peripherally, with granular microornament; ventral cardinal area strongly apsacline to anacline. *Lower Cambrian (Atdabanian)–Middle Cambrian (Amgaian):* Canada, USA, Greenland, Sardinia, Russia (Siberia, southern Urals), Kazakhstan, Kirghizia, Israel, Australia (New South Wales).——Fig. 129,*1a–g. K. catenata* Koneva, Lower Cambrian, Botomian, right side of Chachme River, southern Kirghizia; *a,* ventral valve exterior, ×10; *b,* posterior view, ×11; *c,* lateral view, RM 137376, ×11; *d,* dorsal valve exterior, ×9; *e,* posterior view, RM 137377, ×10; *f,* dorsal valve interior, RM 137378, ×10; *g,* incomplete ventral valve interior, RM 137379, ×10 (new).

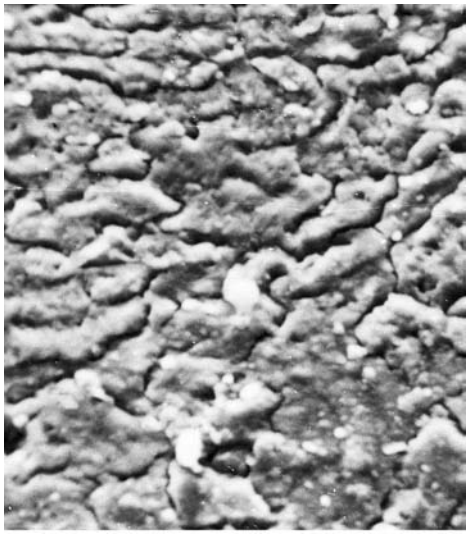

Fig. 128. SEM micrograph of polished and etched section of secondary layer of the shell of *Nisusia* sp. cf. *N. kotujensis* Andreeva (1962, p. 87) showing variably recrystallized fibers, ×1200 (new).

Agyrekia Koneva, 1979, p. 60 [**A. alta;* OD]. Shell biconvex ornamented by fila and radial striations; ventral interarea high, triangular, catacline, or procline; beak slightly incurved, pseudodeltidium broad, gently convex; dorsal valve moderately to strongly convex with broad open notothyrium, short triangular interarea; ventral interior with short median septum near apex. *Lower Cambrian (Botomian)–Middle Cambrian (lower Amgaian):* Kazakhstan, Australia (New South Wales), Russia (southwestern Siberia), Greenland.——Fig. 129,*2a–f. *A. alta,* Botomian, Kazakhstan, Agyrek Mountains; *a–c,* ventral valve exterior, lateral view, posterior view, KAS 2138/257, ×3; *d–f,* ventral valve (illustrated as a dorsal valve by Koneva, 1979) exterior, posterior view, lateral view, KAS 2138/258, ×3 (Koneva, 1979).

Haupiria MacKinnon, 1983, p. 101 [**H. tasmani;* OD]. Similar to *Yorkia,* but lacking apical foramen and internal tube. *Middle Cambrian:* New Zealand. Illustrated specimens not as informative as diagnosis.

Schuchertina Walcott, 1905, p. 323 [**S. cambria;* OD]. Genus poorly known; shell subequally biconvex, smooth or filate; interarea, interior of ventral valve unknown; dorsal interior with short median ridge and pinnate mantle canals. *Middle Cambrian:* North America.

Yorkia Walcott, 1897, p. 714 [**Y. wanneri;* OD] [=*Quebecia* Walcott, 1905, p. 320 (type, *Obolella circe* Billings, 1871b, p. 219)]. Shell subcircular or

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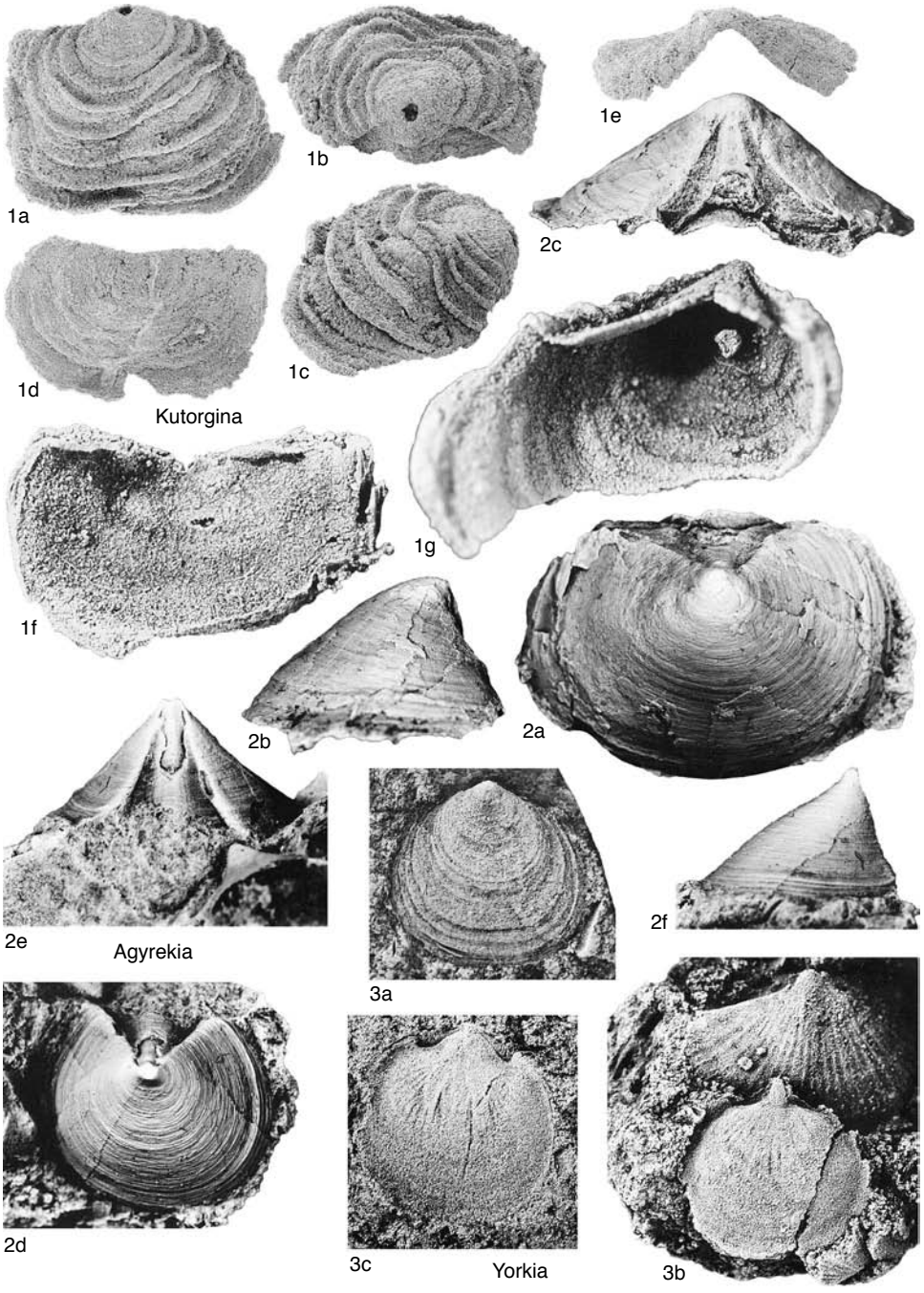

FIG. 129. Kutorginidae (p. 211–213).

subtriangular in outline, smooth; ventral interarea low, apsacline, or rarely catacline; ventral beak small, perforated by minute foramen extending internally as subconical tube; dorsal valve with broad notothyrium, narrow triangular propareas; muscle scars, mantle canals in both valves imperfectly known. *Lower Cambrian:* USA (New York, Pennsylvania), eastern Canada, Russia (Altai).——FIG.

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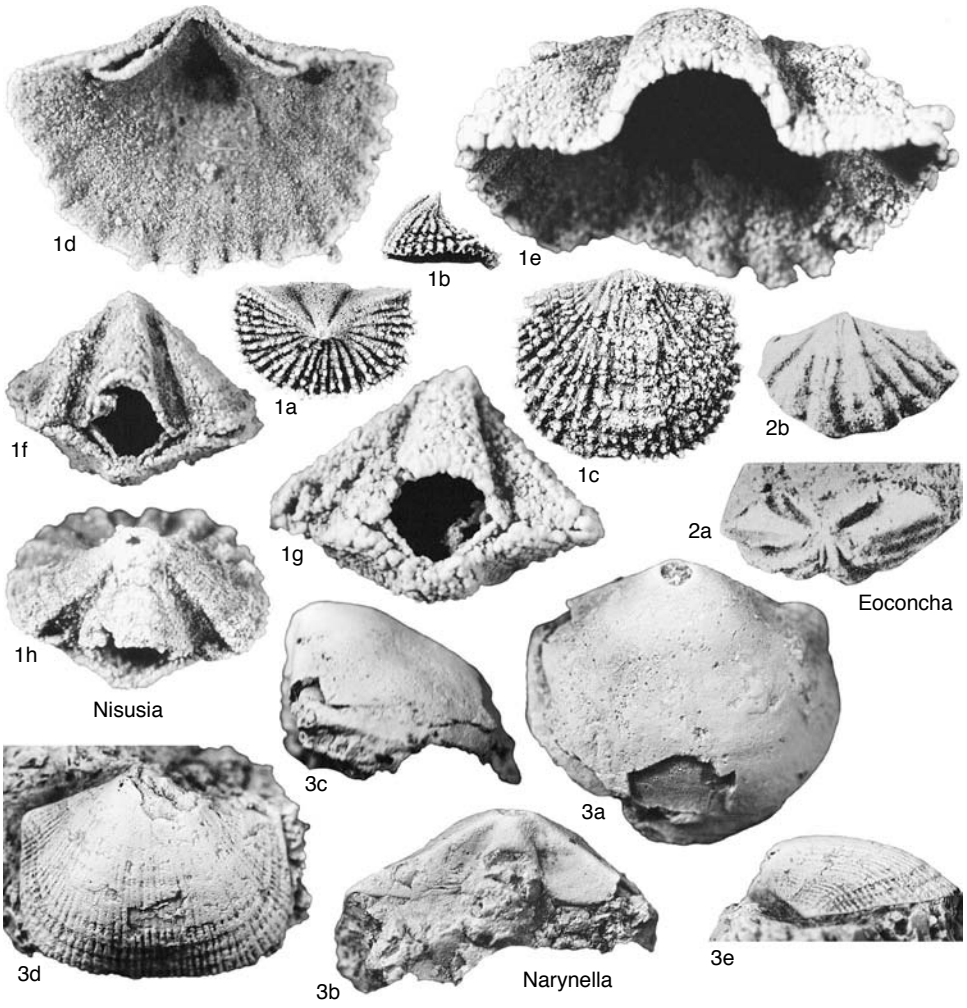

FIG. 130. Nisusiidae (p. 213–214).

129,*3a–c.* **Y. wanneri,* Lower Cambrian; *a,* ventral valve exterior, latex cast, Codorus Creek near Emigsville, Pennsylvania, USNM 26433a, ×2; *b,* ventral internal mold, 3 miles northwest of York, Pennsylvania, USNM 139470, ×2; *c,* dorsal internal mold, Codorus Creek near Emigsville, Pennsylvania, USNM 26433h, ×2 (Rowell, 1962a).

Superfamily NISUSIOIDEA Walcott & Schuchert, 1908

[*nom. correct.* POPOV & WILLIAMS, herein, *pro* Nisusiacea ANDREEVA, 1987, p. 32, *nom. transl. ex* Nisusiidae SCHUCHERT & COOPER, 1931, p. 242; *nom. transl. ex* Nisusiinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147]

Articulation effected by two lateral plates bounding elongate dorsal sockets into which the dorsal edges of ventral interarea fit; diductor muscles attached dorsally to elevated notothyrial platform; mantle canal system of both valves pinnate. *Lower Cambrian–Middle Cambrian.*

Family NISUSIIDAE Walcott & Schuchert, 1908

[*nom. transl.* SCHUCHERT & COOPER, 1931, p. 242, *ex* Nisusiinae WALCOTT & SCHUCHERT in WALCOTT, 1908, p. 147]

Characters as for superfamily. *Lower Cambrian–Middle Cambrian.*

Nisusia WALCOTT, 1905, p. 247 [**Orthisina festinata* BILLINGS, 1861b, p. 10; OD]. Shell ventribiconvex; transverse rectangular or semioval in outline; ornamented by costellae normally bearing numerous

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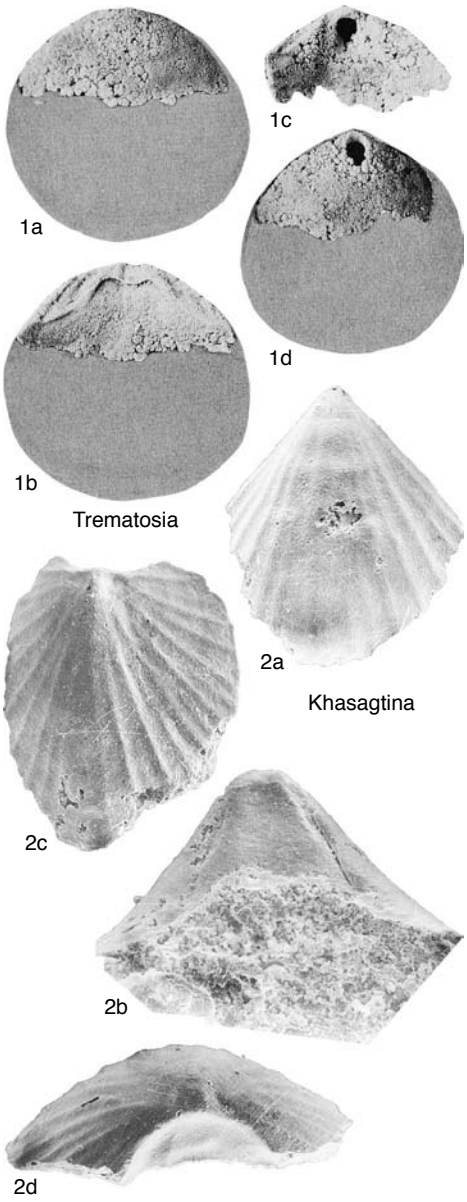

FIG. 131. Nisusiidae (p. 214–215).

small, hollow spines; anterior margin rectimarginate or slightly sulcate; interarea high, triangular, procline to apsacline; dorsal interior with transverse, elevated notothyrial platform; dorsal adductor muscle scars may be discretely impressed on two pairs by prominent ridges. *Lower Cambrian (Botomian)–Middle Cambrian:* USA, Canada, Greenland, Russia (Siberia), Kazakhstan, Australia.——FIG.130,*1a–h. N. alaica* POPOV & TIKHONOV; Botomian, right side of Chachme River, southern Kirghizia; *a,b,* ventral valve exterior, lateral view, CNIGR 31/12589, ×3; *c,* dorsal valve exterior, CNIGR 18/12589, ×3 (Popov & Tikhonov, 1990); *d,* dorsal valve, interior, ×10; *e,* ventral valve, posterior view, RM, no number, ×15 (new); *f,* complete shell of juvenile specimen, posterior view, CNIGR 34/12589, ×10 (Popov & Tikhonov, 1990); *g,* complete shell of juvenile specimen, posterior view, RM, no number, ×15 (new); *h,* complete shell of juvenile specimen, posterior view, CNIGR 33/12589, ×15 (Popov & Tikhonov, 1990).

Eoconcha COOPER, 1951, p. 4 [**E. austini;* OD]. Shell coarsely costellate, with ventral median sulcus, dorsal fold; no spines; ventral interarea apsacline; interior of both valves imperfectly known. *Lower Cambrian–Middle Cambrian:* USA (Virginia).——FIG. 130,*2a,b. *E. austini,* Lower Cambrian, Virginia; *a,* dorsal valve exterior, posterior view, ×1.5; *b,* ventral internal mold, ×2 (Cooper, 1951).

Narynella ANDREEVA, 1987, p. 34 [**Nisusia ferganensis* ANDREEVA, 1962, p. 89; OD]. Shell finely costellate, with variably developed median sulcus, dorsal fold, similar to *Nisusia,* but lacking spines. *Lower Cambrian (Toyonian)–Middle Cambrian:* USA, Uzbekistan, Australia.——FIG. 130,*3a–e. *N. ferganensis* (ANDREEVA), Amgaian, Madygen, Fergana Valley, Uzbekistan; *a–c,* ventral valve exterior, posterior view, lateral view, CNIGR 7/8202, ×3; *d,e,* dorsal valve, exterior, lateral view, CNIGR 9/8202, ×3 (Andreeva, 1962).

Khasagtina USHATINSKAYA, 1987, p. 66 [**K. primaria;* OD]. Shell ventribiconvex, elongate suboval in outline, costellate, with narrow, slightly incurved posterior margin; ventral valve with apical foramen, narrow apsacline interarea occupied mainly by convex pseudodeltidium; dorsal valve with orthocline interarea and two pairs of muscle scars. [This genus is provisionally assigned to the Kutorginida until more is known about its internal features]. *Lower Cambrian (?Tommotian, Atdabanian):* Mongolia, France.——FIG. 131,*2a–d. *K. primaria,* Atdabanian, Bajangol Formation; Salany-Gol Rivulet, western Mongolia; *a,* holotype, ventral internal mold, PIN 3302/5007, ×15; *b,* ventral internal mold, posterior view, PIN 3302/5005, ×54; *c,* dorsal internal mold, PIN 3302/5001, ×13; *d,* dorsal internal mold, posterior view, PIN 3302/5007, ×20 (Ushatinskaya, 1987).

Trematosia COOPER, 1976, p. 276 [**Obolus radifer* RICHTER & RICHTER, 1941, p. 22; OD]. Shell biconvex, elongate oval to subcircular in outline, with rectimarginate anterior margin; smooth, lamellose peripherally; ventral valve with large subcircular foramen placed anteriorly to beak and narrow pseudodeltidium; dorsal valve with narrow, divided interarea bounding widely diverging furrows; internal characters of both valves poorly known. [This

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genus is doubtfully assigned to the Kutorginata. The holotype and several syntypes of *Trematosia radifer* (Cooper, 1976, pl. 3, fig. 1–6, 32) are characterized by a large foramen anterior to the ventral beak, a poorly defined ventral interarea, and a different kind of dorsal interarea with distinctive hinge structures. Such features are unknown in kutorginids. Other specimens also assigned to *T. radifer* are those identified as *Trematosia* sp. 1 (Cooper, 1976, pl. 1, fig. 39–41), probably better identified as *Yorkia*]. *Lower Cambrian:* Israel, Jordan.——Fig. 131,*1a–d.* **T. radifer* (Richter & Richter), Nimra Formation, Ghor-es-Safi, Jordan; *a,b,* incomplete dorsal valve exterior, interior, BMNH BB 61421, ×2; *c,d,* incomplete ventral valve interior, exterior, BMNH BB 61422, ×2 (Cooper, 1976).

STROPHOMENATA

Alwyn Williams,[1] C. Howard C. Brunton,[2] and L. R. M. Cocks[3]
[1]The University of Glasgow; [2]formerly of The Natural History Museum, London; and [3]The Natural History Museum, London]

Class STROPHOMENATA Williams & others, 1996

[Strophomenata Williams & others, 1996, p. 1193]

Rhynchonelliform brachiopods with secondary shell composed preeminently of cross-bladed laminae but also of fibers or laminar laths in older groups; impunctate in early stocks but typically pseudopunctate with or without taleolae or rarely extropunctate; shell outline and profile variable, but essentially planar to weakly concavoconvex in strophomenides; strophic hinge line, commonly with high ventral interarea and reduced dorsal interarea; delthyrium and notothyrium variably covered by pseudodeltidium and chilidium; supra-apical foramen normally developed in larval shells but becoming lost in adults; some species cemented at the umbo; tubular spines uniquely developed in productides; deltidiodont teeth simple, transverse or peglike, lost in strophodontids and post-Famennian productidines, dental sockets commonly defined by low, flat-lying ridges parallel with hinge line; dorsal bases of diductor muscles inserted on notothyrial platform or normally on prominent cardinal process of varied morphology; ventral bases attached laterally of medially placed adductor scars; lophophore supports rare, posteriorly as brachiophores or medially as raised dorsal ridges; mantle canal systems saccate to pinnate, poorly known in later groups. *Middle Cambrian (Amgaian)–Upper Permian (Tatarian).*

More than 1,500 genera, ranging throughout the Paleozoic era, have been assigned to the Strophomenata and are major constituents of many faunas, some in rock-forming quantities. They include some of the most bizarre species of the phylum so that the class embraces a number of groups characterized by autapomorphies meriting suprafamilial recognition as in the Lyttoniidina and Richthofenioidea.

The most inclusive morphological feature of the Strophomenata is a supra-apical or apical foramen, at least in juveniles, that became sealed in adult valves of many later groups. It is assumed that such a foramen accommodated an apically situated peduncular outgrowth of the ventral mantle that acted solely as an adhesive anchor and, in the absence of adjustor scars, never as an axis of rotation for the shell. The outgrowth is regarded as homologous with that inferred for the Obolellata and Kutorginata.

Articulatory devices are also widely used in strophomenate classification; but the deltidiodont teeth and socket ridge apparatus, found in all older stocks, is not greatly different from that of early rhynchonellates (orthides) except in one respect. Early strophomenate socket ridges are weak and flat lying, a synapomorphic condition precursory to taxonomically significant transformations like the loss of dentition in the later productides or its secondary elaboration in the later orthotetidines.

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Shell structure and pseudopunctation have previously played a crucial taxonomic role in distinguishing strophomenates from other brachiopods. Cross-bladed lamination, however, is demonstrably homoplastic with, for example, the chonetidine fabric of lath-like secondary fibers appearing some time after its development in Early Ordovician strophomenoids, triplesiidines, and orthotetidines, all in contrast to the more orthodox fibrous secondary layers of plectambonitoids. This contrast is also true of the laminar-shelled billingselloids and the fibrous-shelled clitambonitidines, both of which have been provisionally assigned to the same order (Billingsellida). Similarly, pseudopunctation, so characteristic of plectambonitoids and strophomenoids, was not fully established in the orthotetidines until Devonian times, although sporadic traces of a form of pseudopunctation have been found in the otherwise impunctate triplesiidines and older orthotetidines (chilidiopsoids).

Such variability, which is matched in the elaboration of cardinalia, the distribution of spinose outgrowths on the shell and so on, suggests that homoplasy is a serious handicap to a phylogenetic classification of the Strophomenata.

STROPHOMENIDA

L. R. M. Cocks and Rong Jia-yu
[The Natural History Museum, London; and Academia Sinica, Nanjing]

Order STROPHOMENIDA Öpik, 1934

[*nom. transl.* Moore, 1952, p. 221, *ex* suborder Strophomenoidea Öpik, 1934, p. 75]

Strophomenate brachiopods with pseudopunctate shell structure, normally with taleolae; spines absent; shell outline normally with relatively wide hinge line, variable profile from concavoconvex to convexoconcave, also biconvex; delthyrium and notothyrium variably covered by pseudodeltidium and chilidium; some species cemented at the umbo; teeth usually present but sometimes absent and replaced in function by hinge line denticles; cardinal process bifid or trifid; mantle canal systems saccate to pinnate where seen. *Lower Ordovician (Tremadoc)–Carboniferous (Namurian).*

Since the revision of the supraordinal classification of the Brachiopoda (Williams & others, 1996), the order Strophomenida is now much more restricted than in the previous *Treatise* (Moore, 1965), in which it also included the chonetids, productids, davidsonids, oldhaminids, and lyttoniids as well as the strophomenids. The order is here restricted to two central superfamilies, the Strophomenoidea and the Plectambonitoidea, neither of which has any external spines (unlike the chonetidines and productidines) and both of which invariably have pseudopunctate shell structure (unlike the orthotetidines). The irregular shapes of the oldhaminids and lyttoniids are very different from the general bilateral symmetry of the Strophomenida. The key variables within the order are discussed under the two superfamilies below. The Strophomenoidea were derived from the Plectambonitoidea, probably in early Arenig time, and the Plectambonitoidea probably evolved from the Billingselloidea at about the Cambro-Ordovician boundary. Both the included superfamilies were abundant and diverse during Ordovician and early Silurian times, but the Plectambonitoidea dwindled as the Silurian progressed, with a small number lingering into the Eifelian. The Strophomenoidea also flourished during most of the Devonian but were badly depleted by the Frasnian-Famennian extinction, with the few remaining representatives becoming extinct near the end of the Namurian.

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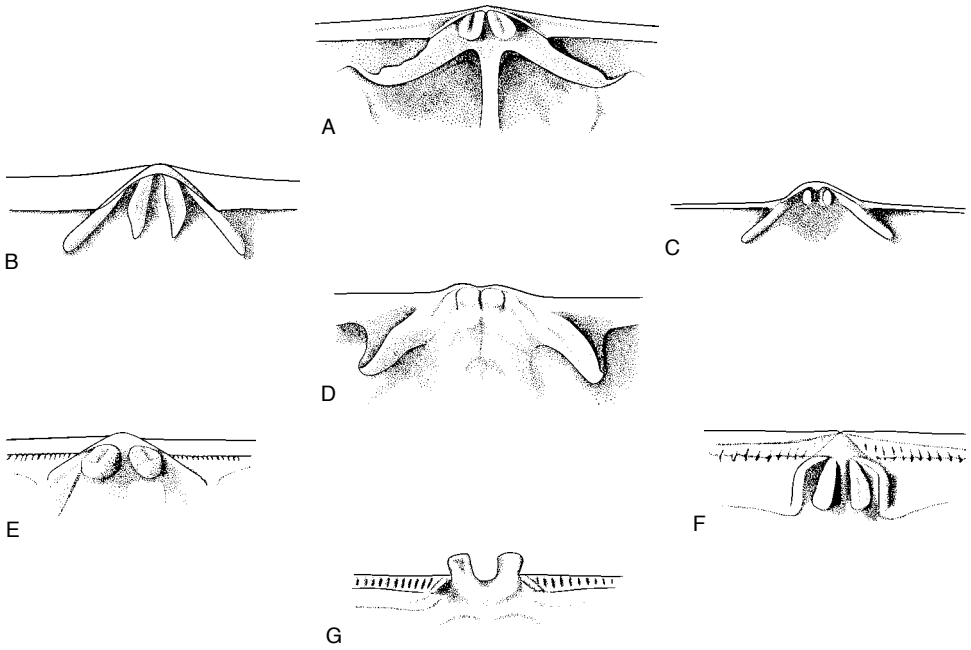

FIG. 132. Differing cardinalia types among Strophomenoidea; *A,* based on *Strophomena* (Strophomenidae); *B,* based on *Kjerulfina* (Rafinesquinidae); *C,* based on *Bystromena* (Glyptomenidae); *D,* based on *Christiania* (Christianiidae); *E,* based on *Amphistrophia* (Amphistrophiidae); *F,* based on *Leptostrophia* (Leptostrophiidae); *G,* based on *Strophodonta* (Strophodontidae) (new).

Superfamily STROPHOMENOIDEA King, 1846

[*nom. correct.* COCKS & RONG, herein, *pro* Strophomenacea SCHUCHERT, 1896, p. 312, *nom. transl. ex* Strophomenidae KING, 1846, p. 28]

Outline semicircular with greatest width usually at hinge line; external spines absent; slender profile varying from concavoconvex to convexoconcave, sometimes geniculate; supra-apical foramen open or closed in adults, pedicle tube sometimes present in juveniles; interareas, pseudodeltidium, and chilidium present in most stocks; articulation either of teeth and sockets or denticulations, occasionally both; bifid cardinal process. An undescribed Arenig genus in family Strophomenidae (RONG & COCKS, 1994) extends the stratigraphic range of this superfamily and family. *Ordovician (Arenig)–Carboniferous (Namurian).*

This superfamily differs chiefly from the other superfamily in the suborder, the Plectambonitoidea (below) in possessing bifid rather than single or trifid cardinal process lobes. Some previous authors, although not in the previous edition of the *Treatise* (MOORE, 1965), have subdivided the group into two superfamilies; one, the Strophomenoidea (previously termed the Strophomenacea) with smooth hinge lines and the other (often termed Stropheodontacea) with denticulate hinge lines. After close analysis, RONG and COCKS (1994) determined that denticulation arose independently and polyphyletically in at least three stocks of the Strophomenoidea, and thus the stropheodontids have been subsumed as a number of separate families within the Strophomenoidea here. Apart from the presence or absence of denticulated hinge lines, the key feature for familial differentiation within the superfamily has again been the form of the cardinal process (Fig. 132). RONG and COCKS (1994) defined four types, which they termed A to D, for the nondenticulate

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families and a further three types (E to G) for the denticulate families. A complication is that during the later Silurian and Devonian history of the denticulate families, the cardinal process changed and evolved within the various stocks, as originally described by WILLIAMS (1953a). In earlier classifications much familial weight was attributed to the valve profile, *e.g.,* the normal convexity of the Rafinesquinidae, the resupinate Strophomenidae, and the geniculate Leptaenidae; however, the valve profile is now considered to be a merely generic or occasionally a subfamilial character.

The development of the hinge line denticulation is of great importance, both for phylogeny and for classification. After the differentiation of the cardinalia, some of the Strophomenidae underwent early experimentation in the development of denticulation. There are many Caradoc-Ashgill taxa that bear crenulations and even denticles. Weakness, irregularity, and instability of development of the denticles and crenulations in the Strophomenidae indicate that their adaptive experimentation in this feature was unsuccessful, and no taxon of the family Strophomenidae gave rise to any strophodontoids. Within the Rafinesquinidae crenulations can be developed sporadically in the same population: sometimes the crenulations are quite strong, but usually they are weak. Despite the development of crenulations in several genera, however, the development of true denticulation in the *Leptaena* subgroup was also unsuccessful, and no strophodontoids were derived from the Leptaeninae.

The earliest known strophomenoids with crenulations (mainly pits) on the anteromedian faces of the teeth and on the posterior faces of the socket ridges are known in rocks of Llanvirn age, for example "*Macrocoelia*" *llandeiloensis elongata,* which is a rafinesquinid. Thus the rafinesquinids were possibly the first family to experiment in the development of denticulation, and this occurred in a very early stage of their evolutionary history. During the first stage of denticular development denticles are present only in the ventral valve and are usually regular but weak.

In the second stage, during late Caradoc and Ashgill times, there was a stable development of both crenulations and denticles in the rafinesquinid ventral valve, emerging from beneath the lamellar layer on either side of the delthyrium. Both denticles and crenulations are seen in the ventral valves on the denticular plates and the median anterior part of the teeth. These should have counterparts in the dorsal valve. Although there are counterpart crenulations on the posterior face of the socket ridge in the dorsal valve, however, there are no counterpart denticles to those on the ventral valve denticular plate.

The third stage in the evolution of denticulation was mainly in early and middle Llandovery times, when many taxa evolved that bear true denticles on the hinge lines of both valves for the first time, although others bear denticles only in the ventral valve and they are absent in the dorsal valve apart from crenulated socket ridges. There are three stocks in which denticles occur in both valves: *Eopholidostrophia, Eostrophonella,* and *Palaeoleptostrophia.* Establishment of denticulation is usually associated with an open delthyrium, loss of dental plates, a faintly impressed muscle field with no bounding ridges in the ventral valve, and a weakly impressed muscle field lacking any traces of transmuscle septa in the dorsal valve.

In the fourth stage (mainly in the late Llandovery), the establishment of denticulation was completed and almost all taxa of the denticulate families bear denticles in both ventral and dorsal valves. As time went by, denticular plates became larger in general, with more denticles on them, and the denticles started to spread gradually and progressively along the hinge line. The general trend in evolution of denticulation in the Silurian was that the more denticles present, the younger the age of the taxon in the same stock, assuming that the absolute size was comparable. We do not put any great systematic value on the absolute number of the denticles or on the proportion of the hinge line occupied by them at any time in the history

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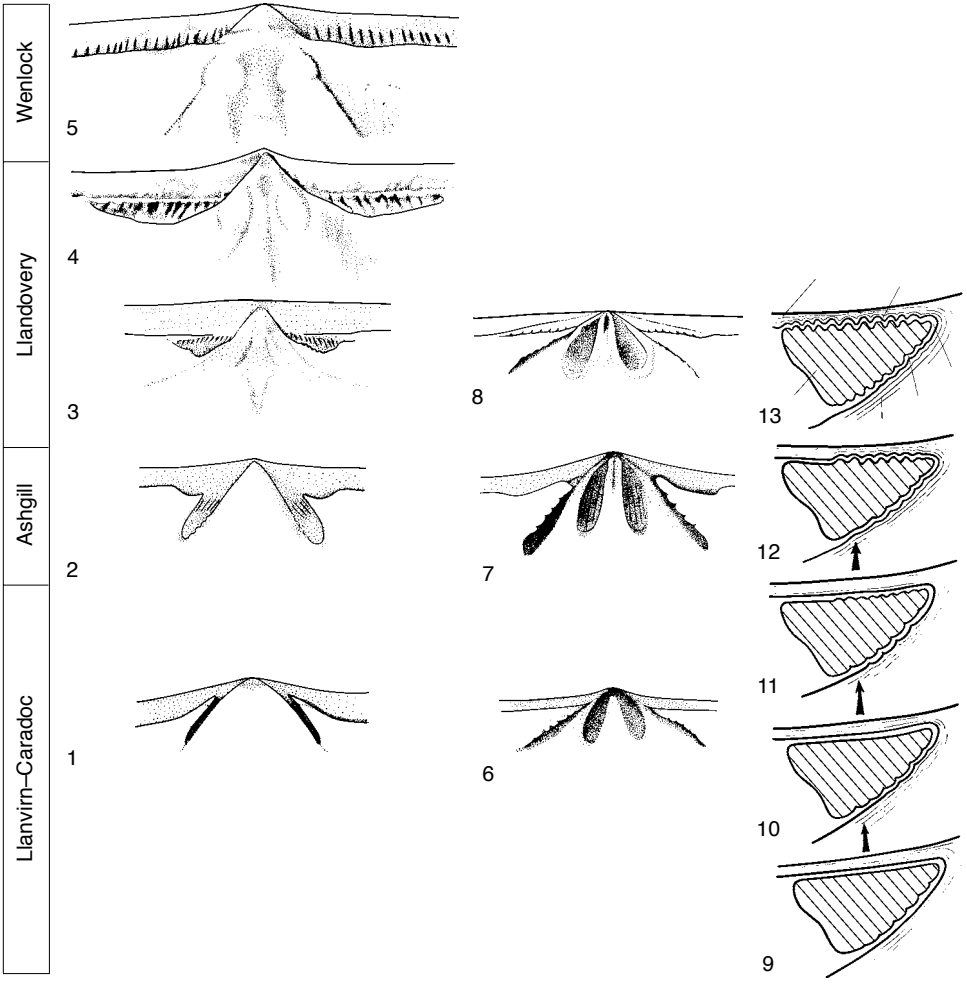

FIG. 133. Evolution of articulation in Strophomenoidea in Late Ordovician and early Silurian; *1–8,* internal molds; *1,6, Macrocoelia; 2,7, Eostropheodonta; 3,8, Palaeoleptostrophia; 4, Brachyprion; 5, Mesoleptostrophia filosa; 9–13,* schematic sections through strophomenoidean ventral hinge line, socket ridge, and dental plate showing development first of crenulations and subsequently denticles (Rong & Cocks, 1994).

of the stock, since, as noted by WILLIAMS (1953a), the increasing denticulation of the hinge line was progressive ontogenetically as well as phylogenetically. It is a general evolutionary trend, however, that early forms have fewer denticles in adult stages and later forms more numerous denticles.

The order Strophomenida (including plectambonitoids and strophomenoids) possess deltidiodont rather than the cyrtomatodont hinge teeth, which are more efficient in articulation than deltidiodont teeth (JAANUSSON, 1971). To have the function of keeping the position of the axis of rotation fixed along a long hinge line in strophomenoid evolutionary history, it was necessary to form accessory structures, such as crenulations and denticles, which were developed to fulfill the same function when the teeth became reduced. Thus the denticles functioned as interlocking devices to prevent the valves from skewing sideways. Almost no group with cyrtomatodont teeth possesses denticles along the hinge line. The establishment of denticulation, which seems to have been a new advantageous construction, led to a

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radiation in the Silurian and Devonian. Although the denticulate families survived the latest Ordovician ice age, however, they did not escape the Frasnian-Famennian mass extinction. This was perhaps because either (1) in the early stage of their evolutionary history they had great vitality and their novelties, especially the establishment of denticulation, were very favorable to their life habits; or (2) in the later stages of their history they did not adjust to the changing environments and, although they developed existing structures, such as strong forked, posteriorly directed cardinal process lobes, there was not enough space between the two valves for a more developed cardinal process.

The loss of dental plates in different denticulate stocks also occurred at different times, but mostly before the Wenlock. The earliest known taxon lacking dental plates is *Origostrophia*. The loss of dental plates, which progressed by simple shortening (rather than by a flaring toward and subsequent merger with the denticular plates and then the hinge line), may be considered an important trend in strophodontoid evolutionary history (WILLIAMS, 1953a; see also Fig. 133). The evolution and stratigraphical ranges of the families within the Strophomenoidea are shown in Figure 134 (RONG & COCKS, 1994).

Family STROPHOMENIDAE King, 1846

[Strophomenidae KING, 1846, p. 28]

Outline semicircular to transverse; cardinal process lobes robust and often subcircular, situated on the posterior end of a notothyrial platform; discrete, strong socket ridges often curved around laterally at their ends. *Ordovician (Arenig)–Silurian (Ludlow).*

Subfamily STROPHOMENINAE King, 1846

[*nom. transl.* GILL, 1871, p. 26, *ex* Strophomenidae KING, 1846, p. 28]

Differs from Furcitellinae in that muscle-bounding ridges in dorsal valve and side septa absent or very weak. *Ordovician (Llanvirn–Ashgill).*

Strophomena RAFINESQUE in DE BLAINVILLE, 1824, p. 302 [**Leptaena planumbona* HALL, 1847, p. 112; SD ICZN Opinion 1671, 1992] [=*Rugomena* RÕÕMUSOKS, 1993b, p. 115 (type, *R. adilensis*)]. Profile gently resupinate; ornament variable from parvicostellate to costellate; prominent pseudodeltidium; small chilidium; teeth strong, sometimes with irregular denticles, crenulations; dental plates extending into elevated bounding ridges largely surrounding the subcircular to rhomboidal ventral muscle field; adductor scars not enclosed by diductor scars; ventral myophragm sometimes present; socket ridges sometimes crenulated; strong, short median ridge coming from the posterior edge of notothyrium; ridge sometimes forked anteriorly; dorsal muscle field gently impressed, with weak bounding ridges sometimes present laterally; occasional weak transmuscle ridges sometimes present, often absent. *Ordovician (Caradoc–Ashgill):* North America, Europe.

S. (Strophomena). Similar to *S. (Keilamena)* but with squatter, more triangular cardinal process lobes and dorsal side septa often weakly developed; similar to *S. (Tetraphalerella)* but generally larger, with flaring although small ventral adductor muscle scars and more anterolaterally directed socket plates rather than recurving back to the hinge line. *Ordovician (Caradoc–Ashgill):* North America, Scotland.——FIG. 135,*1a–f.* **S. (S.) planumbona* (HALL), Trenton Group, Caradoc, Cincinnati, Ohio; *a–c,* lectotype, ventral, posterior, lateral views of conjoined valves, AMNH 30247, ×1.5; *d,e,* ventral, anterior views of ventral interior, AMNH 30248, ×1.5; *f,* dorsal interior, AMNH 918/5, ×1.5 (Rong & Cocks, 1994).——FIG. 135,*1g. S. adilensis* (RÕÕMUSOKS), ventral interior, Adila Formation, Pirgu Stage, Ashgill, Vardi, Estonia, TAGI BR 1531, ×1.5 (Rõõmusoks, 1993b).

S. (Keilamena) RÕÕMUSOKS, 1993b, p. 114 [**Actinomena occidens* MANNIL in ORASPOLD, 1956, p. 59; OD]. Similar to *S. (Strophomena),* but with erect cardinal process lobes, no hint of dorsal side septa. *Ordovician (Caradoc):* Baltic. ——FIG. 135,*3a–c.* **S. (K.) occidens* (MANNIL), Keila Stage, middle Caradoc; *a,* ventral exterior, Jälgimägi, Estonia, TAGI BR 2387, ×1; *b,* holotype, ventral interior, Keila, Estonia, TAGI BR 3091, ×1; *c,* dorsal interior, Kulna, Estonia, TAGI BR 2380, ×1.5 (Rõõmusoks, 1993b).

S. (Tetraphalerella) WANG, 1949, p. 28 [**T. cooperi;* OD]. Similar to *S. (Strophomena),* but with small ventral adductor muscle scars completely enclosed by diductor scars; socket plates more recurved laterally back toward the hinge line; dorsal transmuscle ridges not known. *Ordovician (Ashgill):* North America.——FIG. 135,*2a–c.* **S.*

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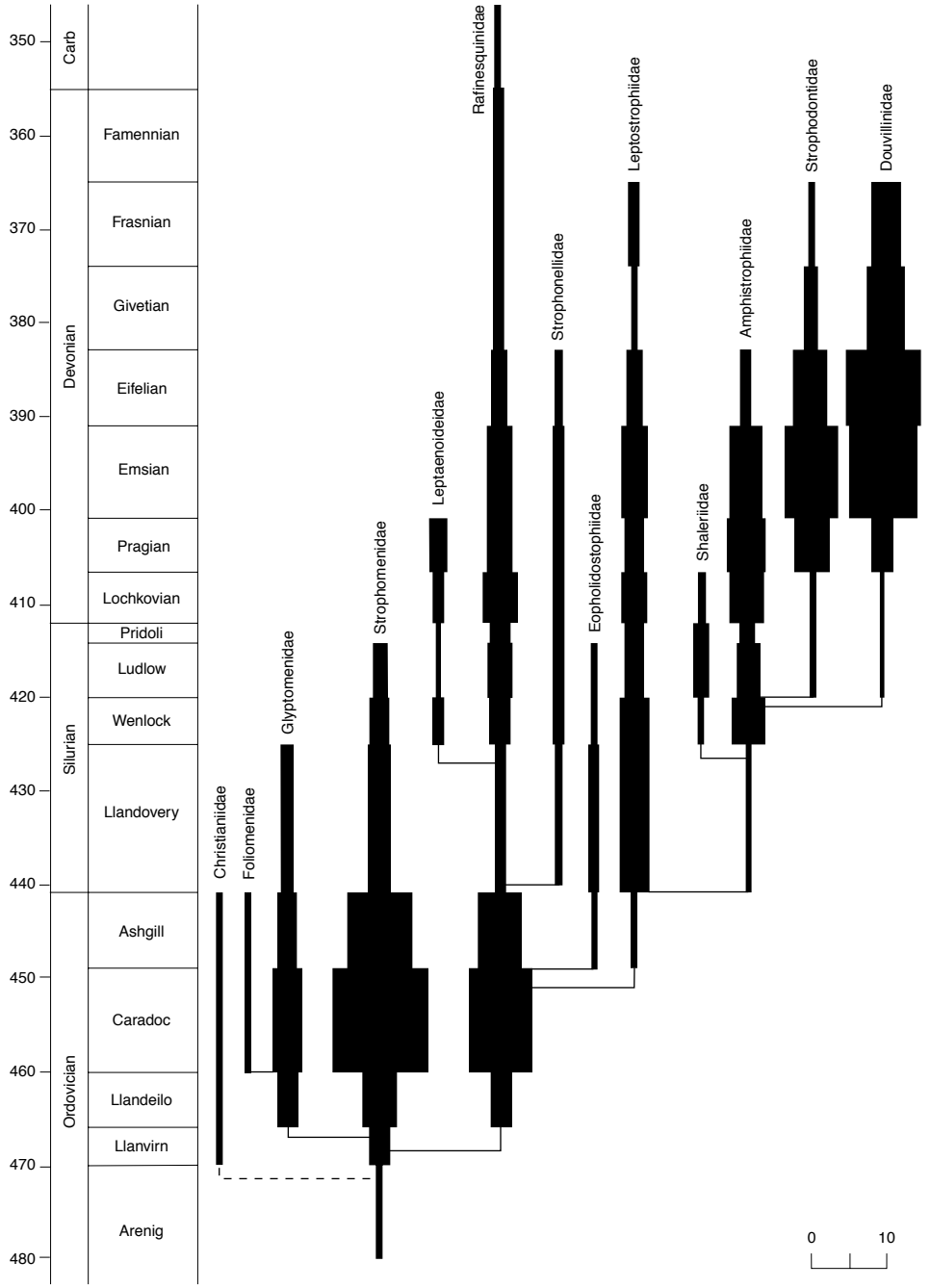

FIG. 134. Stratigraphic ranges and postulated relationship of families of Strophomenoidea; absolute ages in million years shown on left; widths of column representing each family indicate relative number of genera in each series (Ordovician and Silurian) or stage (Devonian) (Rong & Cocks, 1994).

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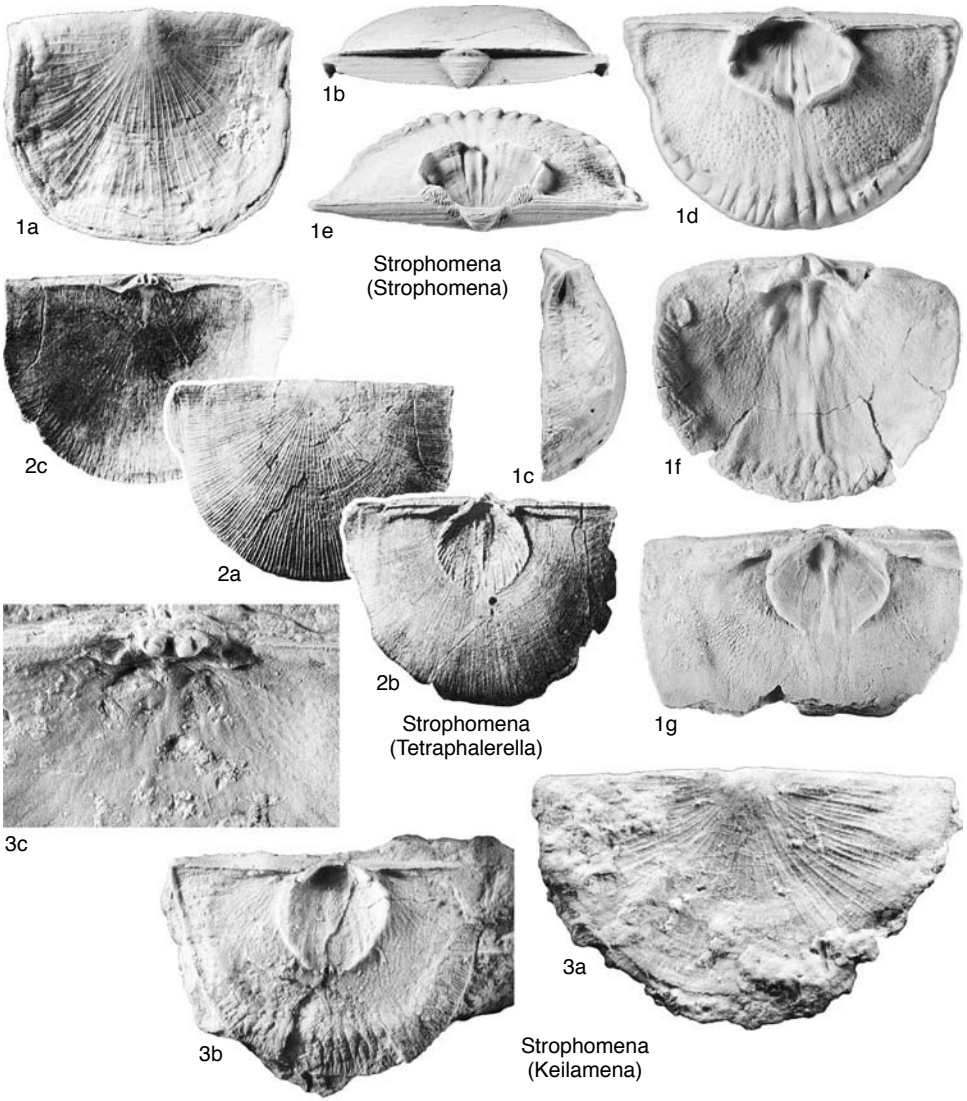

FIG. 135. Strophomenidae (p. 220–222).

(T.) cooperi, upper Elgin Limestone, lower Ashgill, Orleans, Winneshiek County, Iowa; holotype, dorsal exterior, ventral interior, dorsal interior, SUI 1860, ×1 (Wang, 1949).

Actinomena ÖPIK, 1930, p. 166 [**Strophomena (A.) orta;* OD]. Profile gently resupinate; ornament unequally parvicostellate with rugae only posterolaterally; with pseudodeltidium, chilidium; prominent teeth with irregular denticles on dorsal face; thick dental plates continuous anteriorly with curved to straight bounding ridges on lateral parts of subquadrate to subcircular ventral muscle field; faint dorsal transmuscle ridges; muscle-bounding ridges, side septa weakly developed in some species. *Ordovician (Llandeilo–Caradoc):* Europe.——FIG. 136,*1a–d. *A. orta,* Kukruse Formation C2β, upper Llandeilo; *a,* dorsal exterior, Käva, TAGI BR 201, ×1.5; *b,* ventral interior, Kukers, northwest of Jewe, Estonia, BMNH B 10881, ×1.5; *c,* ventral interior, Käva, TAGI BR 1504, ×1.5; *d,* dorsal interior, Käva, ×1.5 (new).

Drummuckina BANCROFT, 1949, p. 11 [**Stropheodonta donax* REED, 1917, p. 892; OD]. Profile concavo-convex; ornament costellate; small deltidial plates;

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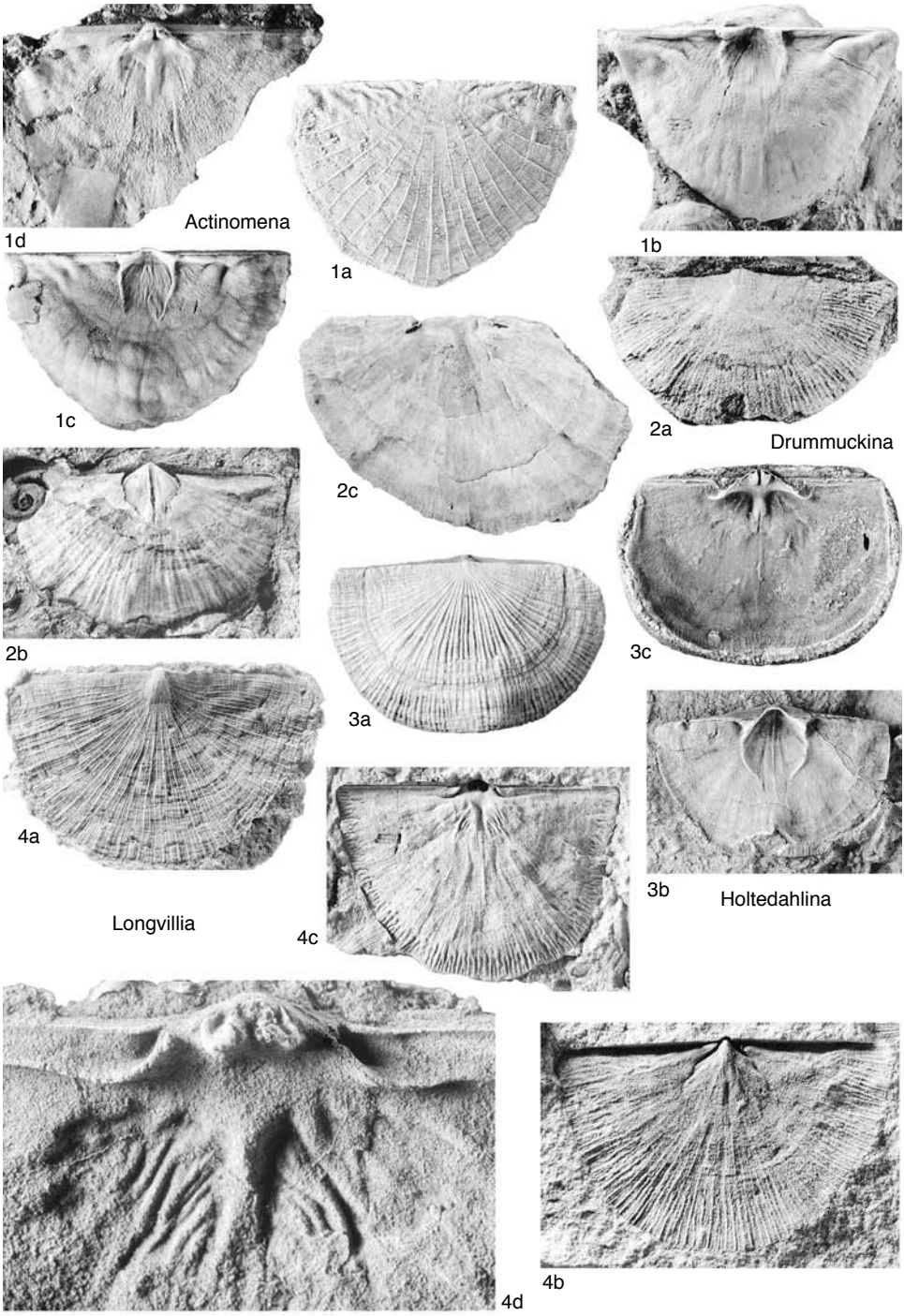

FIG. 136. Strophomenidae (p. 222–224).

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large chilidium; teeth with weak, irregular denticles; short dental plates continuous with elevated bounding ridges nearly enclosing trapezoidal ventral muscle field; myophragm present; socket ridges flaring laterally subparallel to hinge line; dorsal muscle field poorly impressed; small thin dorsal median ridge. *Ordovician (Ashgill):* Scotland.——Fig. 136,*2a–c.* **D. donax* (Reed), Starfish Bed, Drummuck Group, Rawtheyan, Thraive Glen, Girvan, Strathclyde, Scotland; *a,* ventral exterior, BMNH B 72915, ×1.5; *b,* lectotype, ventral internal mold, BMNH B 72906, ×1.5; *c,* dorsal internal mold, BMNH B 72916, ×1.5 (new).

Esilia Nikitin & Popov, 1985, p. 38 [**E. tchetvericovae;* OD]. Profile biconvex, with strong dorsal fold, ventral sulcus; ornament unequally costellate, with bifurcation, intercalation; strong pseudodeltidium, chilidium; dental plates continuous with elongate elliptical bounding ridges enclosing ventral muscle field except anteriorly; cardinal process robust, with lobes close together, situated on strong notothyrial platform; socket ridges fused to base of cardinal process lobes curving posteriorly, extending laterally very close to hinge line; dorsal muscle field faint; dorsal median ridge present. *Ordovician (Llandeilo–Caradoc):* Kazakhstan.——Fig. 137,*3a–e.* **E. tchetvericovae,* ?Andriushenskaya Formation, middle Ordovician, Ishim River, ?North Kuprianovka, central Kazakhstan; *a,* latex cast of dorsal exterior, CNIGR 32/12209, ×2; *b,c,* dorsal, lateral views of dorsal exterior, BMNH BC 12930, ×1.5; *d,* latex cast of ventral interior, CNIGR 17/12209, ×2; *e,* latex cast of dorsal interior, CNIGR 21/12209, ×2 (new).

Holtedahlina Foerste, 1924, p. 122 [**Leptaena sulcata* de Verneuil, 1848b, p. 350; OD]. Profile gently dorsibiconvex with strong ventral sulcus, dorsal fold anteriorly; ornament of unequal costellae; large pseudodeltidium; small chilidial plates; interior as in *Strophomena,* but dorsal transmuscle ridges weakly developed. *Ordovician (upper Llandeilo–lower Ashgill):* North America, Baltic, Kazakhstan, China.——Fig. 136,*3a–c.* **H. sulcata* (de Verneuil), Whitewater Formation, upper Caradoc–lower Ashgill, Camden, Ohio; *a,* dorsal view of conjoined valves, USNM 117747a, ×1.5; *b,* ventral interior, USNM 117744, ×1.5; *c,* dorsal interior, USNM 117747b, ×1.5 (Cooper, 1956).

Infurca Percival, 1979a, p. 185 [**I. tessellata;* OD]. Profile convexoplanar to dorsibiconvex; ornament multicostellate with conspicuous growth lamellae; small pseudodeltidium, chilidium; crenulate teeth supported by divergent dental plates with short bounding ridges to pentagonal muscle field, which is open anteriorly; cardinalia as in *Strophomena;* thin dorsal median ridge. *Ordovician (Caradoc):* Australia.——Fig. 137,*2a–c.* **I. tessellata,* Sandstone in Goonumbla Volcanoes, upper Caradoc, Currajong Park Homestead, Gunningbland, New South Wales, Australia; *a,* latex of ventral exterior mold, SUP 62566, ×3; *b,* latex of ventral internal mold, SUP 62564, ×2; *c,* holotype, latex of dorsal internal mold, SUP 62560, ×2 (Percival, 1979a).

Longvillia Bancroft, 1933, p. 3 [**Orthis grandis* J. de C. Sowerby, 1839, p. 638; OD]. Profile very gently resupinate; unequally parvicostellate ornament; small pseudodeltidium, chilidium; short divergent dental plates continuous with short bounding ridges only posterolateral to muscle field, which is open anteriorly; strong cardinal process with lobes close together; short thin socket ridges curving anteriorly, then laterally subparallel with hinge line; short dorsal median ridge present. *Ordovician (Llandeilo–Ashgill):* Europe, Asia.——Fig. 136,*4a–d.* **L. grandis* (J. de C. Sowerby), Cheney Longville Flags, Caradoc, Marsh Wood, Marshbrook, Shropshire, England; *a,b,* latex casts of ventral external, internal molds, BMNH B 8528, ×1 (new); *c,* dorsal internal mold, ×1; *d,* magnification of latex cast of cardinalia, BMNH BB 30638, ×5 (Rong & Cocks, 1994).

Pseudostrophomena Rõõmusoks, 1963, p. 237 [**P. reclinis;* OD]. Profile resupinate as in *Strophomena;* ornament unequally costellate; small pseudodeltidium, chilidium; differs from *Strophomena* in short straight bounding ridges only posterolaterally to ventral muscle field,which is open anterolaterally, anteriorly; distinctive recurved socket plates; dorsal muscle field poorly impressed. *Ordovician (Caradoc):* Baltic.——Fig. 137,*4a–d.* **P. reclinis,* Rägavere Formation, upper Caradoc; *a,* dorsal exterior, Voore, Estonia, BMNH BB 91298, ×1.5; *b,* ventral interior, Rägavere, Estonia, BMNH BC 12945, ×1.5; *c,* ventral interior, Voore, BMNH BB 91296, ×1.5; *d,* dorsal interior, Voore, BMNH BB 91297, ×1.5 (new). [Note added in proof: not orthotetidine, see page 674.]

Trotlandella Neuman in Neuman & Bruton, 1974, p. 95 [**T. loki;* OD]. Profile dorsibiconvex; multicostellate ornament; pseudodeltidium large; chilidium small; dental plates extending anteriorly to bound short oval ventral muscle field; cardinal process lobes delicate, but socket ridges short, strong, curved laterally subparallel to hinge line; dorsal muscle field poorly impressed. *Ordovician (Llanvirn):* Baltic.——Fig. 137,*1a–d.* **T. loki,* Whiterock, Llanvirn, siltstone block, Trotland Farm, Hølonda area, Trøndelag, Norway; *a,b,* ventral, posterior views of latex cast of conjoined valves, PMO 89083, ×1.5; *c,* ventral internal mold, PMO 89088, ×1.5; *d,* holotype, latex cast of dorsal interior, PMO 89080, ×1 (Neuman & Bruton, 1974).

Subfamily FURCITELLINAE Williams, 1965

[Furcitellinae Williams, 1965d, p. 384]

Dorsal valve muscle field with muscle-bounding ridges; dorsal side septa often developed, although can be weak in some members of population. *Ordovician (Llanvirn)–Silurian (Ludlow).*

Furcitella Cooper, 1956, p. 875 [**F. plicata;* OD]. Profile dorsibiconvex with deeper dorsal valve; ventral valve often flat to concave anteriorly; ornament

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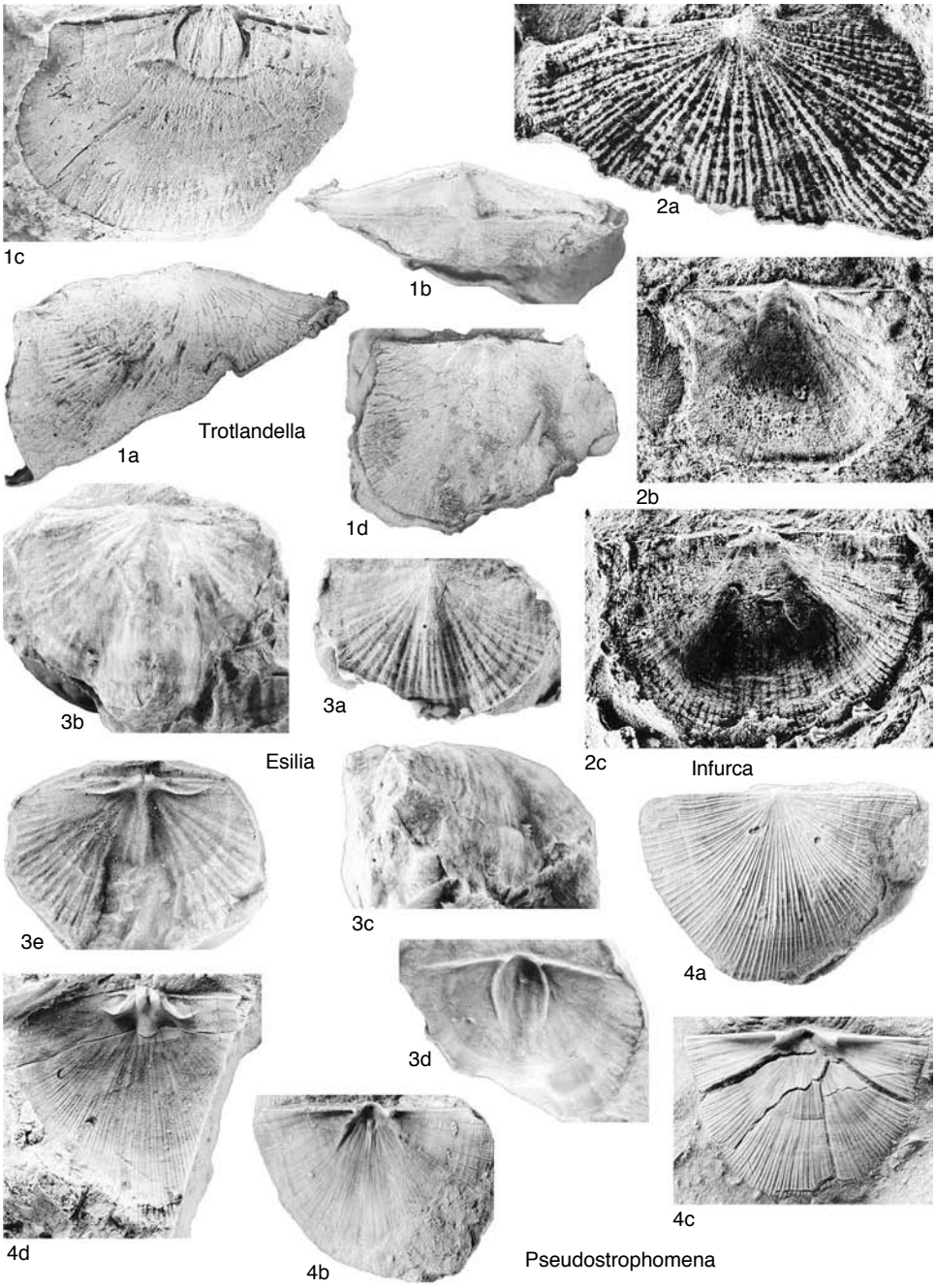

FIG. 137. Strophomenidae (p. 224).

costellate; strongly convex pseudodeltidium, chilidium; short but stout dental plates extending into curved bounding ridges enclosing trapezoidal ventral muscle field except anteriorly; cardinal process lobes united with dorsal median ridge; transmuscle ridges well developed, close to socket

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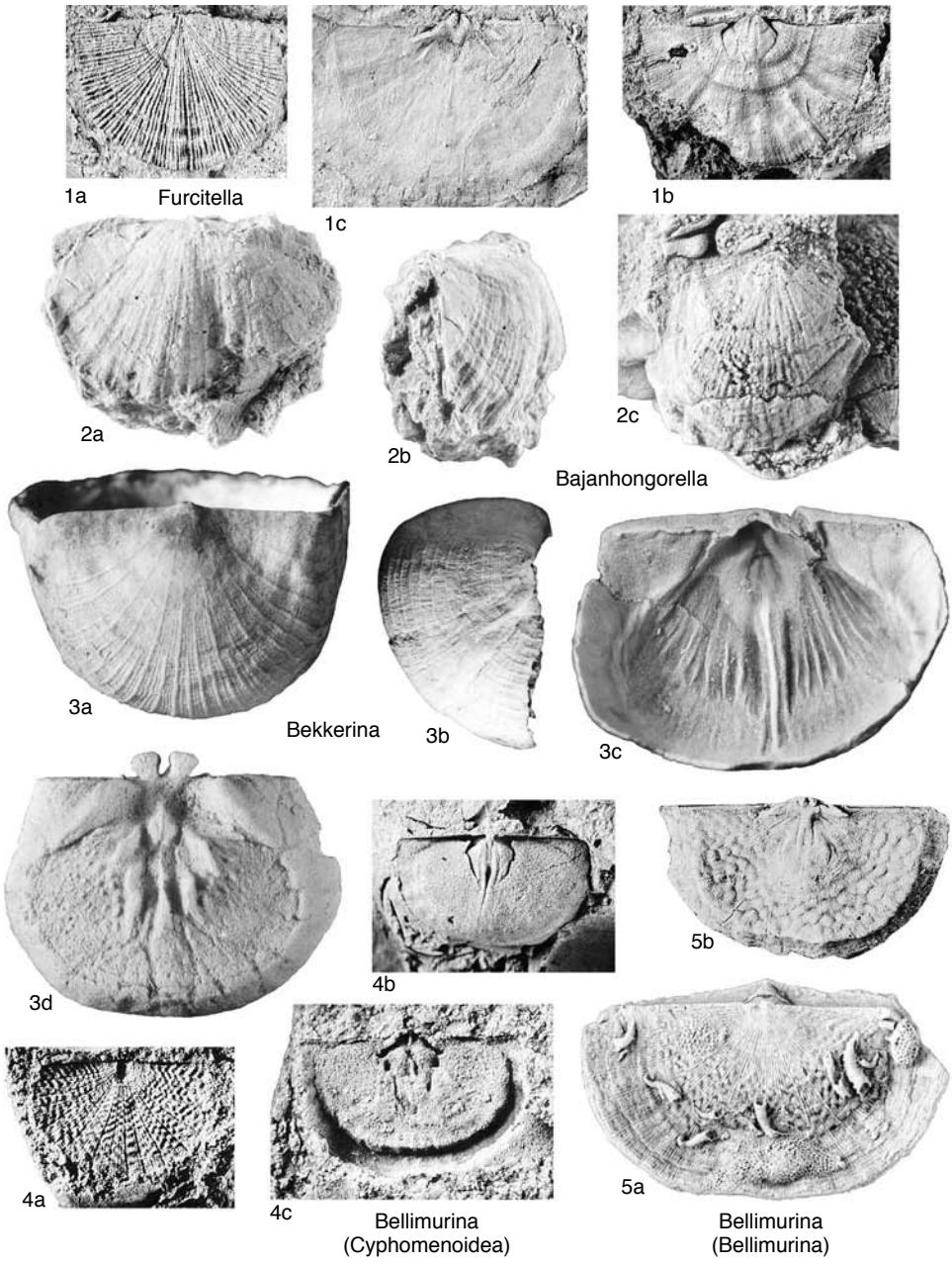

FIG. 138. Strophomenidae (p. 224–227).

ridges; small thin median ridge variably developed in valve center bifurcating anteriorly; side septa variably developed, but often absent. *Ordovician (Caradoc–Ashgill):* North America.——FIG. 138,*1a–c.* **F. plicata,* Oranda Formation, Caradoc, Linville Station, Virginia; *a,* plasticine cast of ventral exterior, USNM 117750d, ×2; *b,* ventral internal mold, USNM 117750c, ×2; *c,* plasticine cast of dorsal interior, USNM 117751c, ×2 (Cooper, 1956).

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?Bajanhongorella ROZMAN, 1977, p. 124 [**B. bajanhongorica;* OD]. Small; subcircular outline, profile strongly dorsibiconvex; fasciculate ornament; interior poorly known, apart from strong dental plates, dorsal median septum; hence family uncertain. *Ordovician (Ashgill):* Mongolia.——FIG. 138,*2a–c.* **B. bajanhongorica,* lower Ashgill, Bayan Khongor, Mongolia; *a,b,* dorsal, lateral views of dorsal exterior, BMNH BB 75086, ×3; *c,* partly exfoliated ventral valve, BMNH BB 75087, ×3 (new).

Bekkerina RÕÕMUSOKS, 1993a, p. 50 [**Rafinesquina dorsata* BEKKER, 1921, p. 73; OD]. Ventral valve profile strongly convex; dorsal profile flat, geniculate; unequally parvicostellate ornament; pseudodeltidium vestigial; chilidium small; flaring dental plates extending anterolaterally into edge of large, distinctive ventral muscle field without bounding ridges but impressed into valve floor, with radial striae; long narrow ventral median septum; prominent cardinal process lobes directed ventroposteriorly; discrete thin socket plates; anterior dorsal side septa high, long; dorsal subperipheral rim present. *Ordovician (Llandeilo–Caradoc):* Baltic. ——FIG. 138,*3a–d.* **B. dorsata* (BEKKER), Kukruse Stage, Llandeilo–Caradoc, Kohtla-Järve, Estonia; *a,b,* ventral, lateral views of conjoined valves, TAGI BR 227, ×4; *c,* ventral interior, TAGI BR 236, ×4; *d,* dorsal interior, TAGI BR 229, ×4 (Rõõmusoks, 1993a).

Bellimurina COOPER, 1956, p. 854 [**Leptaena charlottae* WINCHELL & SCHUCHERT, 1892, p. 288; OD]. Profile biconvex centrally, concavoconvex in adults, gently geniculate dorsally; distinctive ornament of small concentric rugae interrupted by costellae; large pseudodeltidium; smaller chilidium; short divergent dental plates extending into curved bounding ridges to ventral muscle field, open anteriorly; cardinalia as in *Furcitella;* short dorsal median ridge often forked anteriorly, but variably developed; variably developed dorsal transmuscle ridges. *Ordovician (Caradoc)–Silurian (Telychian):* cosmopolitan.

B. (**Bellimurina**). Similar to *B. (Cyphomenoidea)* but with continuous dorsal transmuscle ridges and lower dorsal subperipheral rim. *Ordovician (Caradoc):* North America, Kazakhstan, China.——FIG. 138,*5a,b.* **B. (B.) charlottae* (WINCHELL & SCHUCHERT), Decorah Formation, Guttenberg Member, Caradoc, St. Paul, Minnesota; *a,* dorsal view of conjoined valves, YPM S3620a, ×2; *b,* dorsal interior, YPM S3619, ×2 (Cooper, 1956).

B. (**Cyphomenoidea**) COCKS, 1968, p. 316 [**Leptaena wisgoriensis* LAMONT & GILBERT, 1945, p. 660; OD]. Similar to *B. (Bellimurina)* but dorsal transmuscle ridges vestigial to dotlike; dorsal side septa strong, high subperipheral rim present. *Silurian (Aeronian–Telychian):* Europe, North America.——FIG. 138,*4a–c.* **B. (C.) wisgoriensis* (LAMONT & GILBERT), Wych Beds, upper Llandovery, Coneygore Coppice, Alfrick, Worcestershire, England; *a,* dorsal external mold, OUM C5612, ×2; *b,* ventral internal mold, OUM C5638, ×2; *c,* dorsal internal mold, OUM C5631, ×2 (Cocks, 1968).

Biparetis AMSDEN, 1974, p. 54 [**B. paucirugosus;* OD]. Profile concavoconvex, with strong dorsal geniculation; ornament unequally parvicostellate with weak, irregular rugae sometimes developed; large pseudodeltidium; small chilidium; teeth strong with occasional irregular denticles, crenulations; flaring dental plates with pair of short transverse ridges connecting them with hinge line; strong curved elevated bounding ridges to ventral muscle field except anteriorly; diductor scars enclosing adductor scars; distinctive curved pair of united side septa, dorsal muscle-bounding ridges extending anteriorly from anterolateral end of socket ridges. *Ordovician (Ashgill):* North America.——FIG. 139,*1a–d.* **B. paucirigosus,* Leemon Formation, upper Ashgill, Cape Girardeau County, Missouri; *a,b,* holotype, dorsal, lateral views of conjoined valves, OKGS 6707, ×1.5; *c,* ventral interior, OKGS 6703, ×1.5; *d,* dorsal interior, OKGS 6716, ×1.5 (new).

Dactylogonia ULRICH & COOPER, 1942, p. 623 [**D. geniculata;* OD] [=*Blyskavomena* HAVLÍČEK, 1976, p. 369 (type, *D. blyskavensis* HAVLÍČEK, 1967, p. 85; OD); *Cyphomena* COOPER, 1956, p. 840 (type, *Leptaena homostriata* BUTTS, 1942, p. 110; OD)]. Profile concavoconvex, dorsally geniculate; ornament finely costellate to parvicostellate; large pseudodeltidium; small chilidium; short dental plates with curved muscle-bounding ridges variably developed from strong to absent in some specimens; short myophragm present or absent; cardinal process lobes ventrally directed; socket ridges widely divergent; dorsal median ridge variably developed; dorsal transmuscle ridges, side septa well developed; dorsal subperipheral rim. *Ordovician (Caradoc):* North America, Europe.——FIG. 139,*2a–c.* **D. geniculata,* Little Oak Formation, Caradoc, Cahaba Valley, Alabama; *a,* dorsal view of conjoined valves, USNM 117588a, ×2; *b,* ventral interior, ×1; *c,* dorsal interior, USNM 108202, ×3 (Cooper, 1956). ——FIG. 139,*2d,e. D. homostriata* (BUTTS), Oranda Formation, Caradoc, Strasburg, Virginia; *d,* ventral view of conjoined valves, USNM 117623a, ×3; *e,* dorsal interior, USNM 117624, ×3 (Cooper, 1956).——FIG. 139,*2f,g. D. blyskavensis* (HAVLÍČEK), Letná Formation, lower Caradoc, Blyskava Hill, Chrustenice, Czech Republic; *f,* ventral internal mold, ×2; *g,* holotype, dorsal internal mold, OMR VH 337a, ×1.5 (Havlíček, 1976).

?Dzhebaglina MISIUS, 1986, p. 169 [**D. kelpensis;* OD; Ichkebash Formation (Middle Ordovician), Orto-Nura River, Nura Mountains, northern Kirghizia]. Profile biconvex, with slight dorsal fold, ventral sulcus; ornament unequally parvicostellate; small interarea; small subparallel dental plates posterolaterally bounding small ventral muscle field with elevated bounding ridges uniting anteriorly to form a spondylium-like structure; cardinal process obscure, thus family assignment uncertain; short

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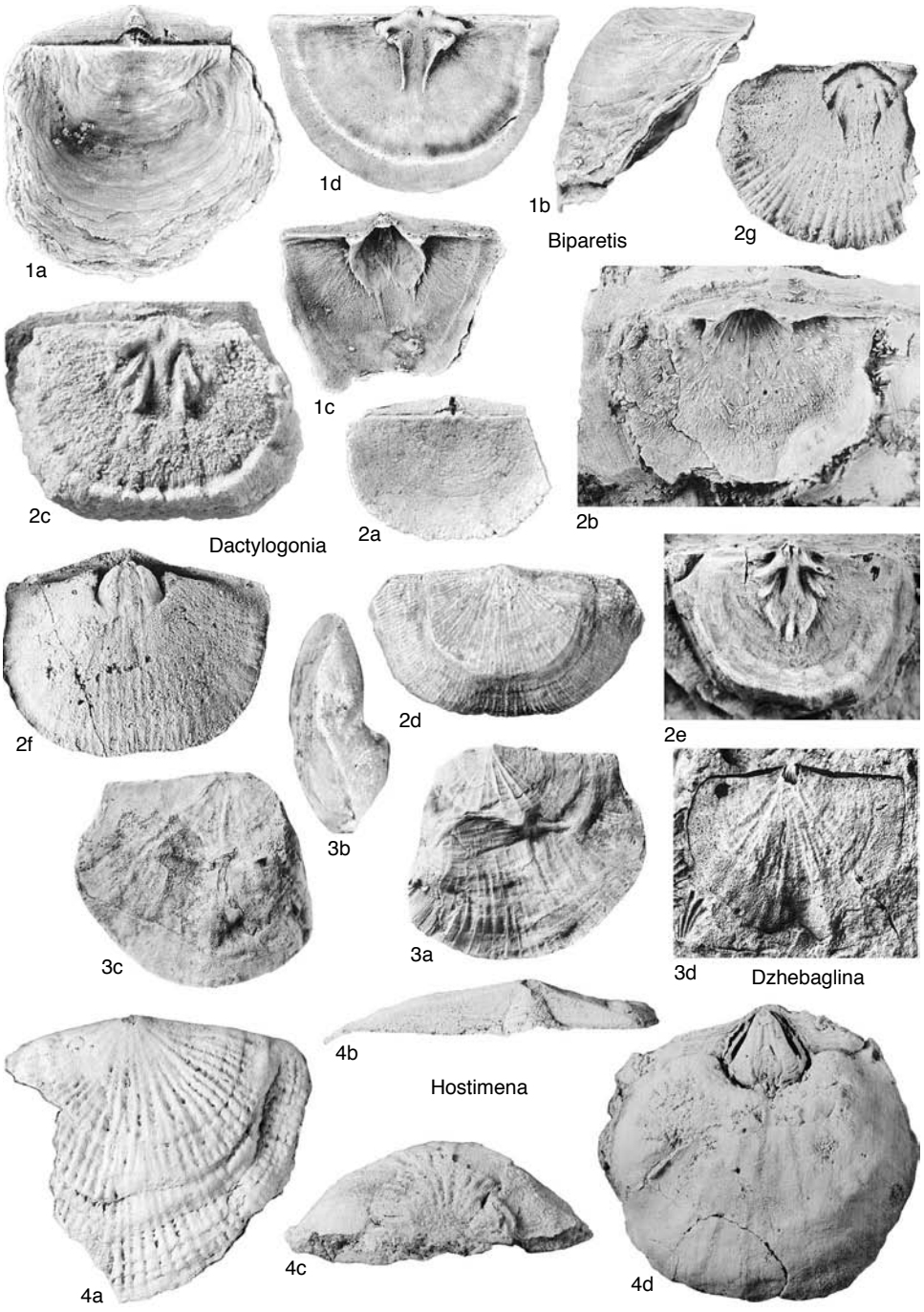

FIG. 139. Strophomenidae (p. 227–229).

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socket ridges, relatively small dorsal muscle field with side septa; short central dorsal median septum poorly developed. *Ordovician (Caradoc–Ashgill):* Asia.——Fig. 139,*3a–d. D.* sp., Dulankara Formation, lower Ashgill, Dulankara, Kazakhstan; *a–c,* ventral, lateral, dorsal views of conjoined valves, ×2; *d,* ventral internal mold, ×2 (Popov, new).

Geniculina Rõõmusoks, 1993a, p. 53 [**Strophomena pseudoalternata* Schmidt, 1858, p. 214; OD]. Transverse outline; gently concavoconvex profile, geniculate anteriorly with a trail of variable length; unequally parvicostellate ornament with irregular oblique wrinkles posterolaterally; prominent pseudodeltidium, chilidium; subcircular to trapezoidal ventral muscle field with bounding ridges; short ventral myophragm; ventroposteriorly directed robust cardinal process lobes; socket plates curving laterally to become subparallel with hinge line, crenulate posteriorly in center; one strong pair of dorsal side septa with other minor pairs variably developed; thin dorsal median septum extending anteriorly from myophragm; subperipheral rim present. *Ordovician (Ashgill):* Baltic, North America.——Fig. 140,*1a–c. *G. pseudoalternata* (Schmidt), Pirgu Stage, middle Ashgill, Estonia; *a,* ventral exterior, Piirsalu, TAGI BR 1463, ×1.5; *b,* ventral internal mold, Röa, TAGI BR 1539, ×1.5; *c,* lectotype, dorsal interior, Vardi, TAGI BR 1460, ×1.5 (Rõõmusoks, 1993a).

?Hostimena Havlíček in Havlíček & Štorch, 1990, p. 69 [**Strophomena hirundo explanans* Barrande, 1879, pl. 47, fig. 11.3–11.5, 11.7–11.9; OD]. Profile strongly dorsibiconvex, with ventral valve flat posteriorly, moderately convex anteriorly; geniculate dorsally in some adult specimens; large pseudodeltidium; ventral muscle field relatively small, completely bounded by ridges; dorsal interior unknown. *Silurian (Telychian–Sheinwoodian):* Europe.——Fig. 139,*4a–d. *H. explanans* (Barrande), Tuffaceous limestone in Motol Formation, Wenlock, Listice, near Beroun, Bohemia, Czech Republic; *a,b,* ventral, posterior views of ventral exterior, OMR VH 4280a, ×1.5; *c,* posterior view of dorsal exterior, OMR VH 4280b, ×1.5; *d,* ventral internal mold, OMR VH 1945, ×1.5 (Havlíček & Štorch, 1990).

Iberomena Villas, 1985, p. 97 [**Strophomena sardoa* Vinassa, 1927, p. 481; OD]. Profile flat to gently resupinate; ornament mainly unequally parvicostellate; pseudodeltidium small; chilidium reduced or absent; short thick dental plates joined to weak bounding ridges only developed in posterolateral part of subspherical to pentagonal ventral muscle field; short myophragm; short dorsal transmuscle ridges well developed, sometimes united with thin side septa. *Ordovician (Caradoc–Ashgill):* Europe.——Fig. 140,*2a–e. *I. sardoa* (Vinassa); *a,* latex cast of ventral exterior, Fombuena Formation, upper Caradoc, Luesma, Cadenas Ibéricas Orientales, Spain, DP 2300, ×1.5; *b,c,* ventral internal mold, latex cast, Portixeddu Formation, upper Caradoc–lower Ashgill, Portixeddu, Sardinia, Italy, ×1.5; *d,e,* dorsal internal mold, ×1.5, enlargement of latex cast of cardinalia, Fombuena Formation, upper Caradoc, Luesma, Cadenas Ibéricas Orientales, Spain, DB 2309, ×6 (Villas, 1985).

Katastrophomena Cocks, 1968, p. 293 [**Strophomena antiquata woodlandensis* Reed, 1917, p. 902; OD]. Resupinate with variable ventral geniculation, dorsal fold, ventral sulcus often developed anteriorly; irregularly and variably costellate ornament; large pseudodeltidium, chilidium; teeth with irregular denticles, crenulations sometimes developed; short dental plates merging with curved bounding ridges to relatively small subcircular ventral muscle field, not joined anteriorly; myophragm variably developed; short dorsal transmuscle ridges usually present, side septa often present; short dorsal median ridge present posteriorly; additional small central ridge sometimes developed between side septa. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.

K. (**Katastrophomena**)**.** Similar to *K. (Costistrophomena)* but with finer (but still irregular) radial costellae. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.——Fig. 141,*1a–d. *K. (K.) woodlandensis* (Reed), Woodland Formation, Llandovery, Rhuddanian, Woodland Point, Girvan, Strathclyde, Scotland; *a,* dorsal exterior, BMNH B 73012, ×1.5; *b,c,* lectotype, ventral interior, latex cast, BMNH B 54490, ×1.5; *d,* dorsal internal mold, BMNH BB 31425, ×1.5 (Cocks, 1968).

K. (**Costistrophomena**) Sheehan, 1987, p. 41 [**C. costata;* OD]. Similar to *K. (Katastrophomena)* except with coarser radial ornament, with strong, widely spaced growth lines. *Ordovician (Ashgill):* Europe.——Fig. 141,*2a–e. *K. (C.) costata,* Lower Fosse Formation, Ashgill, Vitrival-Bruyère, Ardennes, Belgium; *a,* ventral external mold, IRScNB 1608, ×1.5; *b,* ventral internal mold, IRScNB 1612, ×2; *c,* ventral internal mold, IRScNB 1615, ×2; *d,* holotype, dorsal internal mold, IRScNB 1610, ×2; *e,* dorsal internal mold, IRScNB 1613, ×2 (Sheehan, 1987).

Kirkina Salmon, 1942, p. 598 [**K. millardensis;* OD]. Profile gently concavoconvex; ornament of fine parvicostellae; ventral interior unknown apart from dental plates present; socket ridges widely divergent, curving posterolaterally; dorsal muscle field diamond shaped with two or more pairs of side septa; poorly defined weak, broad myophragm present, but no dorsal median septum. *Ordovician (Llanvirn–Llandeilo):* North America.——Fig. 142,*2a,b. *K. millardensis,* Pogonip Group,

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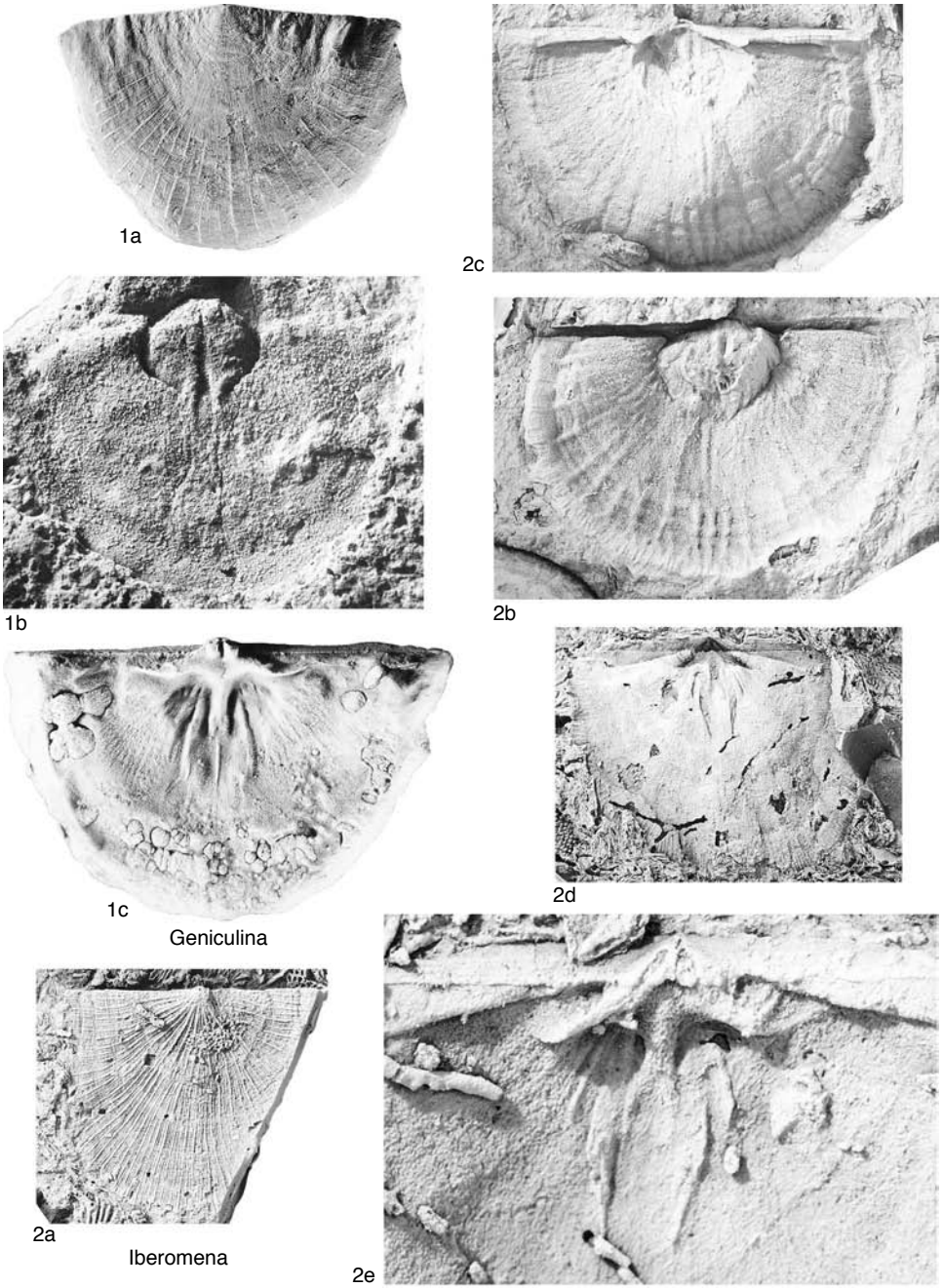

FIG. 140. Strophomenidae (p. 229).

Llanvirn, Point of Rocks, Millard County, Utah; *a,* partly exfoliated ventral exterior, AMNH CU 25918, ×1.5; *b,* holotype, dorsal interior, AMNH CU 25917, ×2 (new).

Laevicyphomena COCKS, 1968, p. 317 [**Cyphomena (L.) feliciter;* OD]. Outline transverse, profile dorsibiconvex, geniculate; radial ornament absent; small pseudodeltidium, chilidium; muscle-

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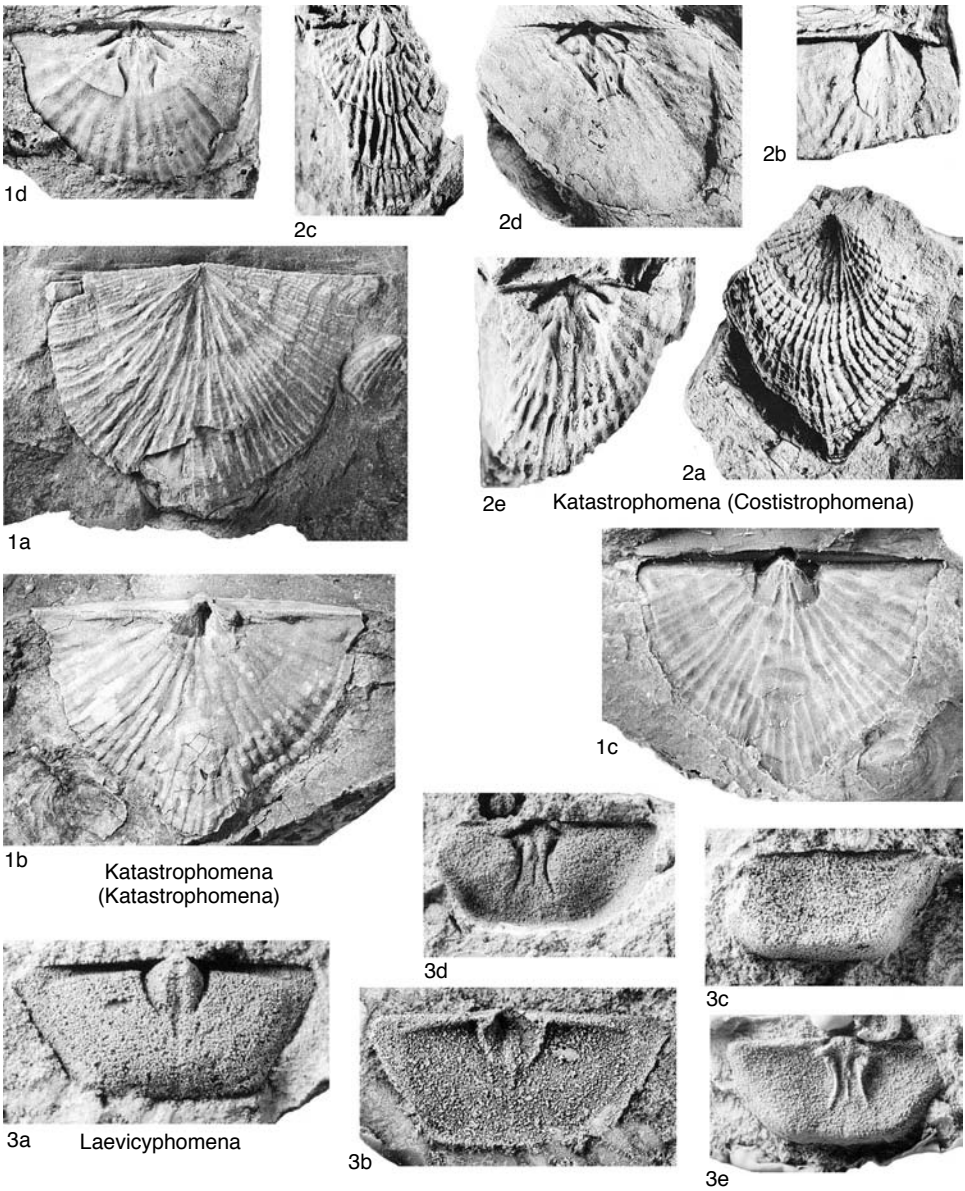

FIG. 141. Strophomenidae (p. 229–231).

bounding ridges enclosing small, often bilobed ventral muscle field; myophragm often present; erect cardinal process; short straight socket plates; distinctive pair of concave dorsal side septa as in *Biparetis,* united posteriorly with short muscle-bounding ridges. *Silurian (Aeronian):* Europe.—— FIG. 141,*3a–e.* **L. feliciter,* Bog Quartzite, Aeronian, Bog Mine, Shropshire, England; *a,b,* holotype, ventral internal mold, latex cast, BMNH BB 31346, ×3; *c–e,* dorsal external, internal molds, latex cast of dorsal interior, BMNH BB 31352, ×2 (new).

Luhaia RÕÕMUSOKS, 1956, p. 1091 [**L. vardi;* OD]. Profile convexoconcave, geniculate in ventral direction; rugae irregular, variably developed but sometimes over whole shell, not broken by irregular parvicostellae; large pseudodeltidium; smaller chilidium; strong teeth uniting anterolaterally with

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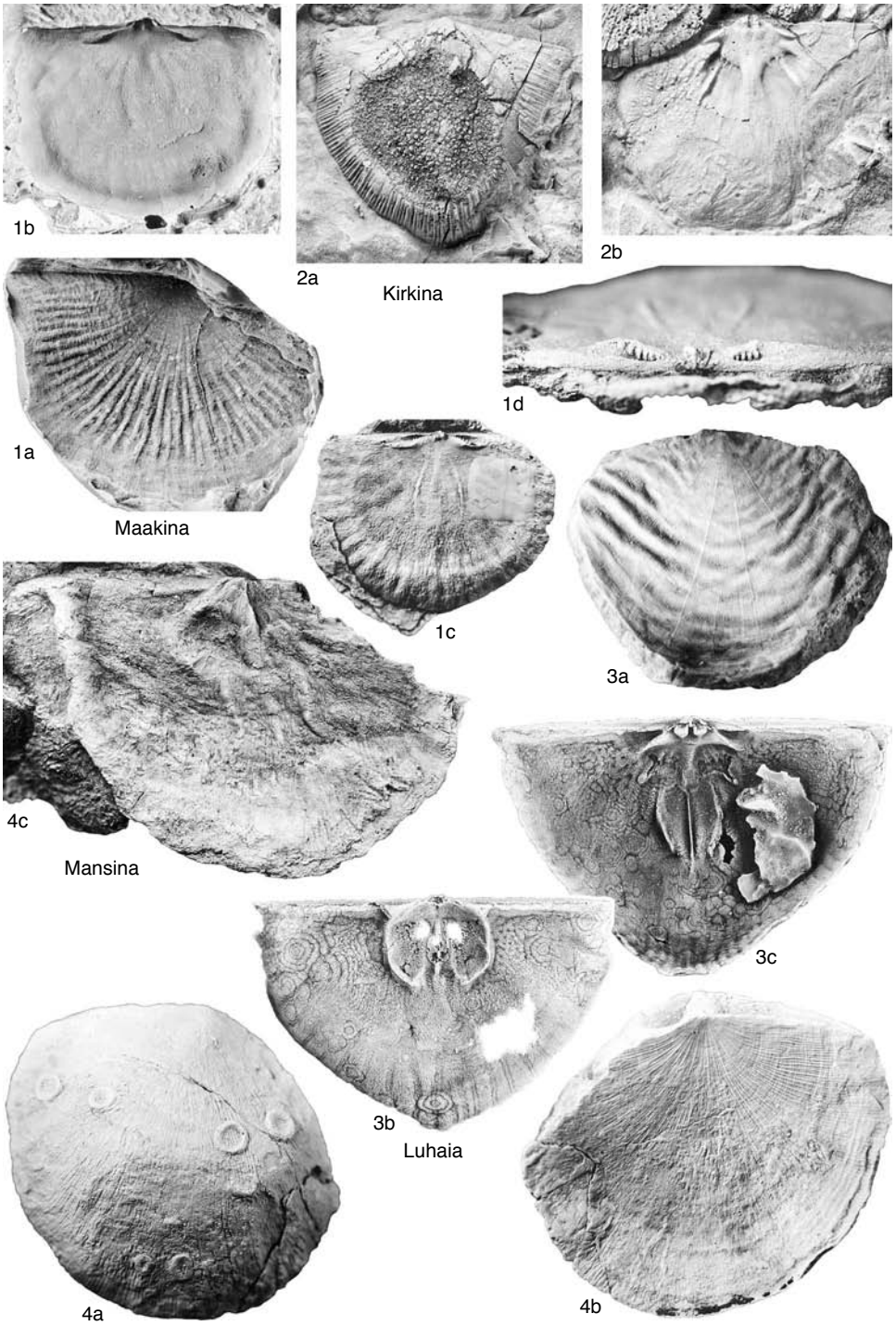

FIG. 142. Strophomenidae (p. 229–233).

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pronounced muscle-bounding ridges that curve around subquadrangular ventral muscle field, progress posteriorly before merging with valve floor without uniting; short ventral median septum; socket ridges short, stout, small notothyrial platform developed; pair of curved side septa in dorsal valve center, as well as thin central median septum anterior of short, broad myophragm. *Ordovician (Ashgill):* Baltic.——Fig. 142,*3a–c.* **L. vardi; a,* ventral exterior, Pirgu Formation, Ashgill, Khoskholm, Estonia, TAGI BR 1607, ×2 (Rõõmusoks, new); *b,* ventral interior, Ashgill, Estonia, PM 1010a, ×2; *c,* dorsal interior, Ashgill, Estonia, PM 1010b, ×2 (Jaanusson, new).

Maakina Andreeva in Nikiforova & Andreeva, 1961, p. 170 [**Oepikina (M.) kulinnensis;* OD]. Semicircular outline; ventral valve with gently convex profile; dorsal valve flat with gentle geniculation anteriorly; distinctive ornament of strong to median rounded costellae; small pseudodeltidium; large chilidium; ventral interior poorly known; very divergent crenulated socket ridges curving laterally subparallel with hinge line; dorsal muscle field poorly impressed, but with thin, curved side septa, no median septum. *Ordovician (Caradoc):* northern Asia.——Fig. 142,*1a–d.* **M. kulinnensis,* Baksansk Horizon, Mangazei Stage, Caradoc, Siberian Platform, Russia; *a,* holotype, latex cast of ventral exterior, CNIGR 7453/420, ×2; *b,* latex cast of dorsal internal mold, CNIGR 7453/416, ×2 (new); *c,* dorsal view of dorsal interior, CNIGR 7453/418, ×2; *d,* posterior view of dorsal interior, CNIGR 7453/418, ×5 (Popov, new).

?Mansina Andreeva, 1977, p. 116 [**M. uralica;* OD]. Large with concavoconvex profile, subcircular outline; unequally parvicostellate ornament; large chilidium; ventral interior unknown; cardinal process poorly known, hence family uncertain; short socket ridges, small notothyrial platform; pair of dorsal side septa variably developed, curved posteriorly, subparallel anteriorly; small dorsal median septum poorly developed for short distance centrally. *Ordovician (Caradoc):* Russia.——Fig. 142,*4a–c.* **M. uralica,* Shchygoisk Formation, middle Ordovician, River Khosin, subpolar Urals, Russia; *a,b,* holotype, ventral, dorsal views of conjoined valves, CNIGR 24/10852, ×1.5; *c,* dorsal interior, CNIGR 25/10852, ×2 (Popov, new).

Molongcola Percival, 1991, p. 153 [**M. variabilis;* OD]. Profile planoconvex to unequally biconvex, not geniculate; ornament coarsely multicostellate; strong pseudodeltidium; very small chilidium; dental plates continuous anteriorly with bounding ridges that are sometimes short, sometimes curved to enclose most of muscle field; cardinalia prominent with ventral facing cardinal process lobes; dorsal median ridge short, small, sometimes absent; distinctive dorsal transmuscle ridges connected anteriorly to anterior ends of curved muscle-bounding ridges, continuing anteriorly as side septa, between which is small central ridge. *Ordovician (Caradoc):* Australia.——Fig. 143,*1a–c.* **M. variabilis,* Trilobite Hill Limestone Member, Cliefden Caves Limestone, Caradoc, Licking Hole Creek, New South Wales, Australia; *a,* dorsal exterior, SUP 68569, ×2; *b,* ventral interior, SUP 68562, ×1.5; *c,* oblique view of dorsal interior, SUP 68563, ×2 (Percival, 1991).

Murinella Cooper, 1956, p. 844 [**M. partita;* OD]. Planoconvex but variably biconvex to concavoconvex profile; costellate to unequally parvicostellate ornament; large interarea, pseudodeltidium, very small discrete chilidial plates; ventral muscle field short, subcircular with variably developed muscle-bounding ridges; adductors separated by median septum extending anteriorly beyond muscle field; short stout socket ridges, strong notothyrial platform; thin central dorsal median septum, one or two pairs of subparallel side septa weakly developed; elevated subperipheral rim in dorsal valve, sometimes with variably developed corresponding subperipheral groove in ventral valve. *Ordovician (Llandeilo–Caradoc):* North America.——Fig. 143,*3a,b.* **M. partita,* Mountain Lake Member, Bromide Formation, Llandeilo–Caradoc, Sulphur, Murray County, Oklahoma; *a,* ventral interior, BMNH BC 12841, ×2; *b,* dorsal interior, BMNH BC 12842, ×2 (new).

Oepikina Salmon, 1942, p. 589 [**O. septata;* OD] [=*Oepikinella* Wilson, 1944, p. 199 (type, *O. affinis;* OD)]. Transverse outline; concavoconvex profile with weak geniculation developed in older specimens; unequally parvicostellate ornament; small pseudodeltidium; vestigial chilidium; crenulate teeth; dental plates short, weak; ventral muscle field poorly impressed; notothyrial platform well developed, extending anteriorly into variably developed, usually prominent dorsal median septum; two or more pairs of strong transmuscle septa; distinctive dorsal subperipheral rim. *Ordovician (Llandeilo–lower Ashgill):* North America, Baltic.——Fig. 143,*2a–e.* **O. septata, Doleroides* Zone, Lebanon Formation, Caradoc, Knox Brook, near Murfreesboro, Tennessee; *a,b,* ventral, dorsal views of conjoined valves, USNM 117828, ×2; *c,* ventral interior, USNM 117829b, ×2 (Cooper, 1956); *d,* holotype, dorsal interior, USNM 117829c, ×2 (new); *e,* ventral interior, USNM 117827b, ×2 (Cooper, 1956).

?Oslomena Spjeldnaes, 1957, p. 161 [**O. osloensis;* OD]. Small shells with strongly concavoconvex profile; parvicostellate ornament; large pseudodeltidium, chilidium; ventral muscle field bounded posterolaterally by dental plates merging anteriorly with curved muscle-bounding ridges not uniting anteriorly; cardinal process poorly known, hence family uncertain; widely divergent socket plates; poorly impressed dorsal muscle field with weak median septum, side septa. *Ordovician (Caradoc):* Baltic.——Fig. 143,*5a,b.* **O. osloensis,* Arnestad Formation, lower Caradoc; *a,* dorsal view of conjoined valves, Skien, Norway, PMO L153, ×2; *b,* lateral view of ventral valve, BMNH BC 13036, Billingstad, Norway, ×2 (new).

Panderites Rõõmusoks, 1993a, p. 49 [**Plectambonites imbrex* Pander, 1830, p. 91; OD]. Concavoconvex

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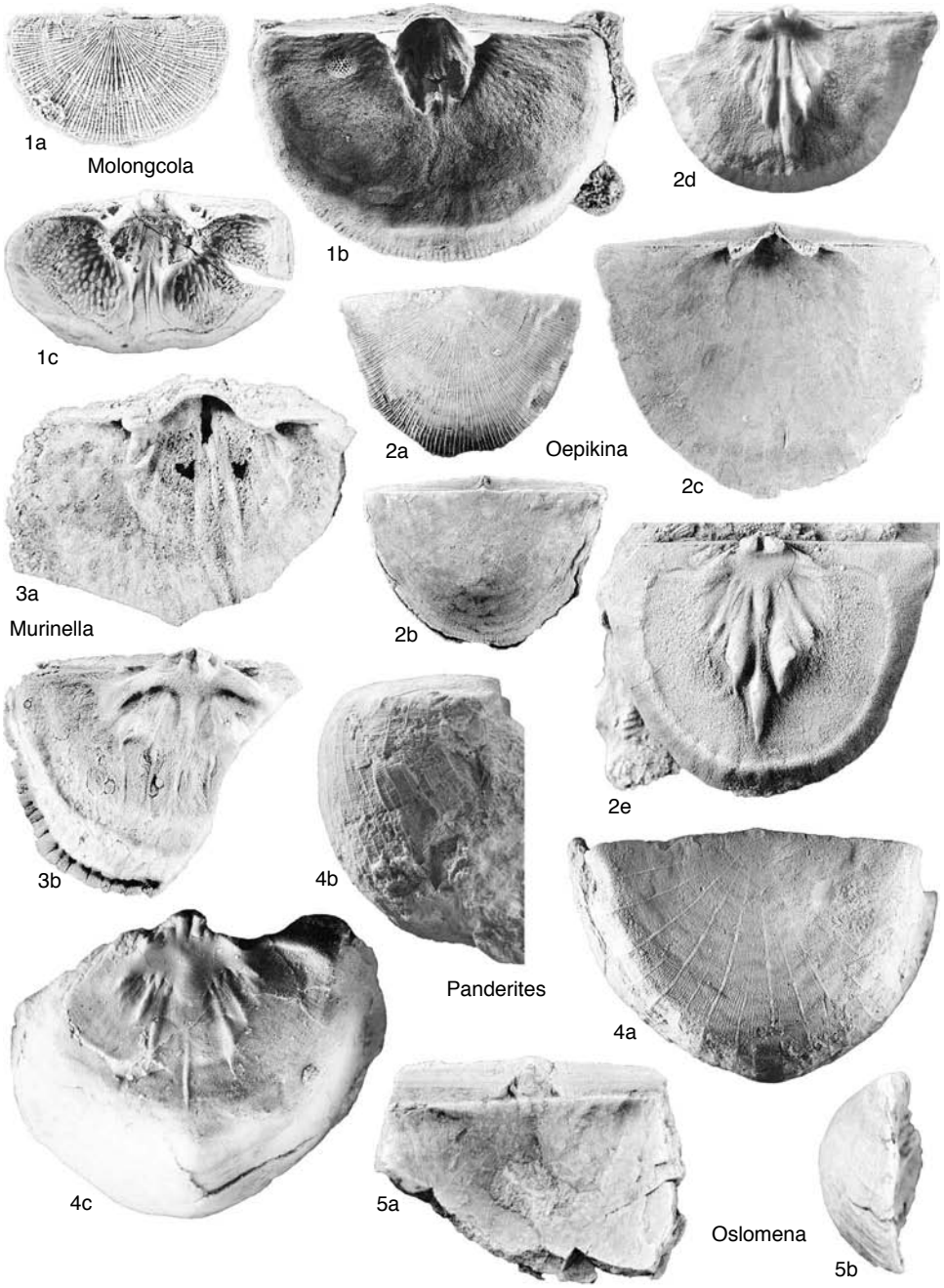

FIG. 143. Strophomenidae (p. 233–235).

profile with sharp dorsal geniculation, long trail; unequally parvicostellate ornament; small pseudodeltidium; large chilidium; subcircular ventral muscle field, faintly impressed, with no bounding ridges; erect, ventroposteriorly directed, relatively small cardinal process lobes; broad low myophragm extending anteriorly into thin dorsal median septum; two or more pairs of thin transmuscle septa. *Ordovician (Llanvirn):* Baltic.——FIG. 143,*4a–c. *P. imbrex* (PANDER), Aseri Stage, upper Llanvirn,

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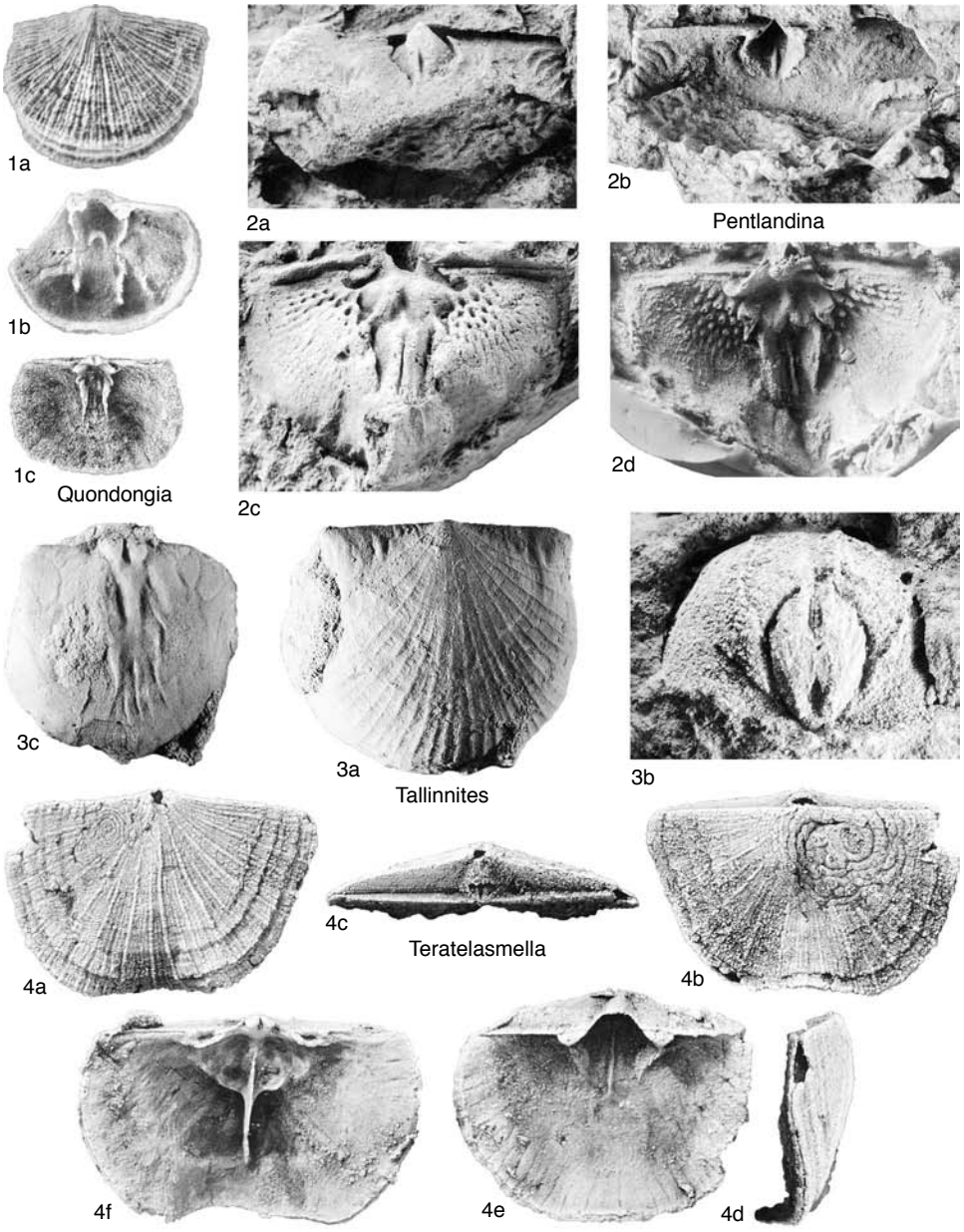

FIG. 144. Strophomenidae (p. 235–237).

Pavlovsk, St. Petersburg, Russia; *a,* ventral view of conjoined valves, ×2; *b,* lateral view of conjoined valves, BMNH B 3959, ×1.5 (new); *c,* dorsal interior, RMS Br 131660, ×2 (Rõõmusoks, 1993a).

Pentlandina BANCROFT, 1949, p. 13 [**Strophomena (P.) tartana;* OD]. Transverse to subtriangular outline; biconvex profile with strong dorsal fold, ventral sulcus; parvicostellate ornament that breaks distinctive small, regular rugae; open delthyrium with small pseudodeltidial plates, vestigial chilidium; strong teeth, dental plates merging with elevated muscle-bounding ridges not quite uniting anteriorly; strong, short, curved socket ridges, short notothyrial platform; prominent dorsal side septa, small central median ridge. *Silurian (Telychian–Wenlock):* Europe, North America, China.——FIG. 144,*2a–d.* **P.*

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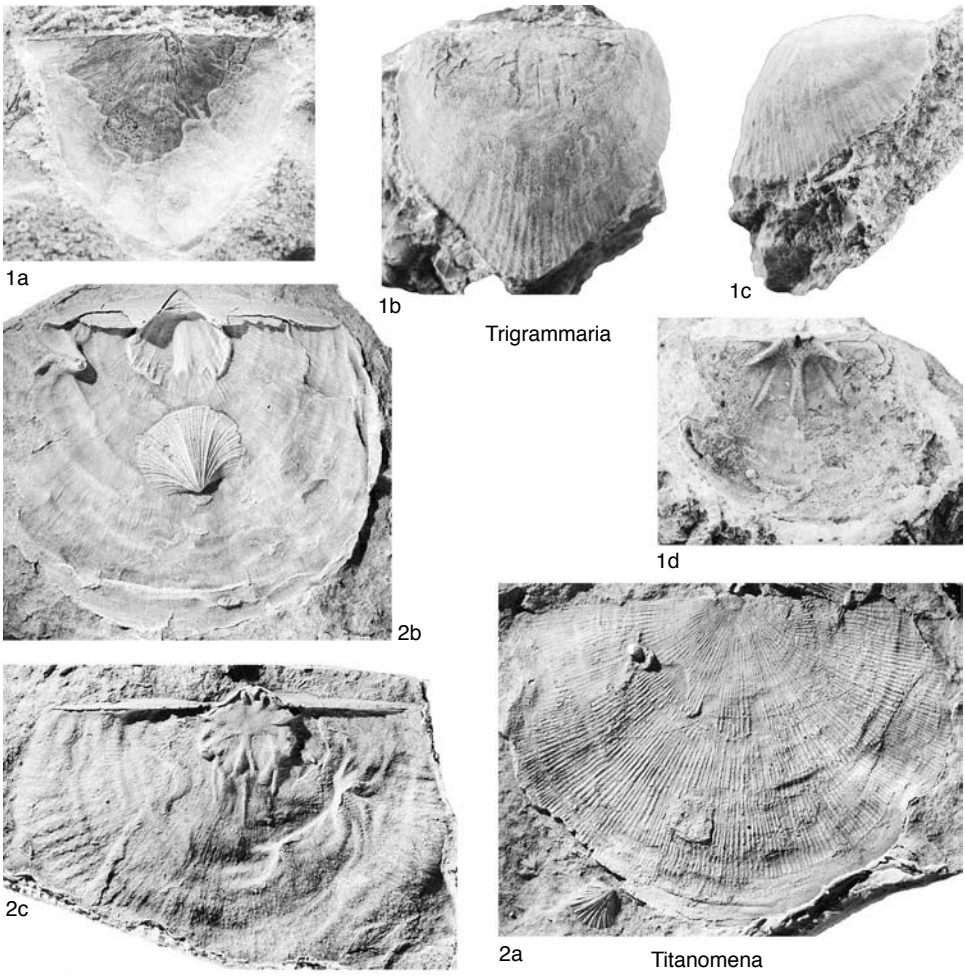

FIG. 145. Strophomenidae (p. 237).

tartana, Llandovery (Telychian) Beds, North Esk Inlier, Pentland Hills, Borders region, Scotland; *a,b,* ventral internal mold, latex cast, BMNH B 8485, ×2; *c,d,* dorsal internal mold, latex cast, BMNH BB 31450, ×3 (new).

Quondongia PERCIVAL, 1991, p. 151 [**Q. alitis;* OD]. Small shells with planoconvex to biconvex profile, occasional rounded plications anteriorly; unequally parvicostellate ornament; prominent pseudodeltidium, small chilidium; thin dental plates merging with anteriorly directed muscle-bounding ridges; ventral muscle field open anteriorly; short socket ridges; prominent elevated curved dorsal side septa; thin short central median ridge. *Ordovician (Caradoc):* Australia.——FIG. 144,*1a–c.* **Q. alitis,* Quondong Limestone, Caradoc, Bowan Park, New South Wales, Australia; *a,* ventral exterior, SUP 68595, ×4; *b,* ventral interior, SUP 68596, ×4; *c,* dorsal interior, SUP 69478, ×4 (Percival, 1991).

Tallinnites RÕÕMUSOKS, 1993a, p. 50 [**Oepikina? imbrexoidea* SOKOLSKAYA, 1954, p. 51; OD]. Subrectangular to semicircular outline; ventral valve evenly, strongly convex, dorsal valve more gently concave; unequally parvicostellate ornament; pseudodeltidium small; chilidium large; long elliptical ventral muscle field with bounding ridges not quite uniting anteriorly; ventroposteriorly directed, prominent cardinal process lobes; weak socket ridges; broad notothyrial platform posteriorly; centrally, anteriorly in dorsal valve there are variably developed, rather irregular but generally weak side septa, median ridge. *Ordovician (Llanvirn–Llandeilo):* Baltic.——FIG. 144,*3a–c.* **T. imbrexoidea* (SOKOLSKAYA), Uhaku Stage, lower Llandeilo, Estonia; *a,* ventral exterior, Kohtla-Järve, TAGI BR 1572, ×1.5; *b,* ventral internal mold, Loo, ×2; *c,* dorsal interior, Lasnamägi, TAGI BR 1574, ×1.5 (Rõõmusoks, 1993a).

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Teratelasmella LAURIE, 1991, p. 84 [**T. plicata;* OD]. Planoconvex to biconvex profile with ventral sulcus, dorsal fold; relatively large ventral interarea with well-developed pseudodeltidium; pair of small chilidial plates; unequally parvicostellate ornament; stout teeth; stout dental plates; poorly impressed ventral muscle field laterally bounded by short muscle-bounding ridges; small ventral median septum; widely divergent curving socket ridges; relatively small dorsal muscle field with bounding ridges, short transmuscle ridges; thin but prominent, relatively long, dorsal median septum. *Ordovician (Llandeilo):* Australia.——FIG. 144,*4a–f.* **T. plicata,* Upper Cashions Creek Limestone, Llandeilo, Settlement Road, Tasmania, Australia; *a–d,* holotype, ventral, dorsal, posterior, lateral views of conjoined valves, UTGD 99641, ×4; *e,* ventral interior, UTGD 99648, ×5; *f,* dorsal interior, UTGD 99669, ×4 (Laurie, 1991).

?Titanomena BERGSTRÖM, 1968, p. 16 [**T. grandis;* OD]. Large, with compressed plano- to concavoconvex profile; equally parvicostellate ornament; small pseudodeltidium, chilidium; short dental plates merging anteriorly with bounding ridges to diamond-shaped ventral muscle field; relatively small, erect cardinal process lobes as in some glyptomenids, thus family position uncertain; chilidium present; dorsal muscle field with poorly developed, thin median, transmuscle septa. *Ordovician (Ashgill):* Baltic.——FIG. 145,*2a–c.* **T. grandis,* upper *Dalmanitina* Beds, Ashgill, Allebergsände, Västergötland, Sweden; *a,* latex cast of dorsal exterior, RMS Br 10929, ×1.5; *b,* latex cast of ventral internal mold, RMS Br 10944, ×1; *c,* holotype, latex cast of dorsal internal mold, LO 4257, ×1.5 (Bergström, 1968).

Trigrammaria WILSON, 1945, p. 140 [**T. trigonalis;* OD] [=*Microtrypa* WILSON, 1945, p. 144 (type, *M. altilis;* OD)]. Resupinate profile, with variably developed dorsal fold, ventral sulcus near anterior margin; ornament usually parvicostellate; ventral interior poorly known; socket ridges divergent; fine dorsal side septa, median septum variably developed; median septum sometimes bifurcating anteriorly as in *Furcitella. Ordovician (Llandeilo):* North America.——FIG. 145,*1a–c.* **T. trigonalis,* Ottawa Limestone, Llanvirn, Ottawa, Ontaria, Canada; *a,* partially exfoliated conjoined valves, GSC 7614b, ×1.5; *b,c,* holotype, dorsal, lateral views of dorsal internal mold, GSC 7614, ×1.5 (new).——FIG. 145,*1d. T. altilis* (WILSON), Ottawa Limestone, Llanvirn, Rockland, Ontario, Canada; holotype, dorsal interior, GSC 7649, ×2 (new).

Family RAFINESQUINIDAE Schuchert, 1893

[*nom. transl.* POPE, 1976, p. 151, *ex* Rafinesquininae SCHUCHERT, 1893, p. 153] [=Elliptostrophiidae HAVLÍČEK, 1967, p. 111; Leptaenidae HALL & CLARKE, 1894a, p. 354]

Outline usually transverse; cardinal process lobes usually elongate or platelike in shape, entirely discrete throughout ontogeny; notothyrial platform variably developed; socket ridges straight, often thinner, smaller than in the Strophomenidae. *Ordovician (Llanvirn)–Carboniferous (Namurian).*

Subfamily RAFINESQUININAE Schuchert, 1893

[Rafinesquininae SCHUCHERT, 1893, p. 153]

Rafinesquinids lacking dorsal geniculation, often lacking rugae (except posterolaterally in gerontic specimens). *Ordovician (Llandeilo)–Silurian (Ludlow).*

Rafinesquina HALL & CLARKE, 1892, p. 281 [**Leptaena alternata* CONRAD, 1838, p. 115; OD]. Concavoconvex profile, with dorsal valve initially very gently concave but with increased curvature anteriorly; unequally parvicostellate ornament; pseudodeltidium, larger chilidium filling delthyrium; relatively short, divergent dental plates; ventral muscle field flabellate, with no bounding ridges; ponderous triangular cardinal process lobes in adults flanked by short delicate socket ridges often with crenulations; weak dorsal median septum present, merging posteriorly with low myophragm. *Ordovician (Caradoc–Ashgill):* cosmopolitan.——FIG. 146,*2a–e.* **R. alternata* (CONRAD), Hudson River Group, Caradoc, Cincinnati, Ohio; *a,* dorsal view of conjoined valves, BMNH BC 56160, ×1; *b,* ventral interior, BMNH BC 13035, ×1; *c,* dorsal interior, BMNH BC 13549, ×1 (new); *d,* latex cast of cardinal area, muscle field, BMNH B 39912, ×2; *e,* enlarged view of cardinal area, BMNH B 39912, ×4 (Cocks, new).

Colaptomena COOPER, 1956, p. 889 [**C. leptostrophoidea;* OD] [=*Macrocoelia* COOPER, 1956, p. 890 (type, *M. obesa;* OD)]. Large, with compressed plano- to concavoconvex profile; vestigial pseudodeltidium; small chilidium; dental plates rudimentary or obsolescent; flabellate ventral muscle field well impressed, but without bounding ridges; triangular, lobate cardinal process lobes; thin, small, divergent socket plates; short thin dorsal median septum extending anteriorly from myophragm; transmuscle septa poorly developed. *Ordovician (Llandeilo–Caradoc):* North America, Europe, Asia.——FIG. 147,*1a–c.* **C. leptostrophoidea,* Martinsburg formation, Caradoc, Green Mount Church, Broadway Quadrangle, Virginia; *a,* ventral exterior, USNM 117763a, ×1; *b,* ventral internal mold, USNM 117762a, ×1; *c,* dorsal interior, USNM 117763b, ×1 (Cooper, 1956).——FIG. 147,*1d–f. C. obesa,* Arline Formation, Llandeilo–Caradoc, Friendsville, Concord, Tennessee; *d,* holotype, ventral exterior, USNM 117783a, ×1; *e,* ventral interior, USNM 117782b, ×1; *f,* dorsal interior, USNM 117782a, ×2 (Cooper, 1956).

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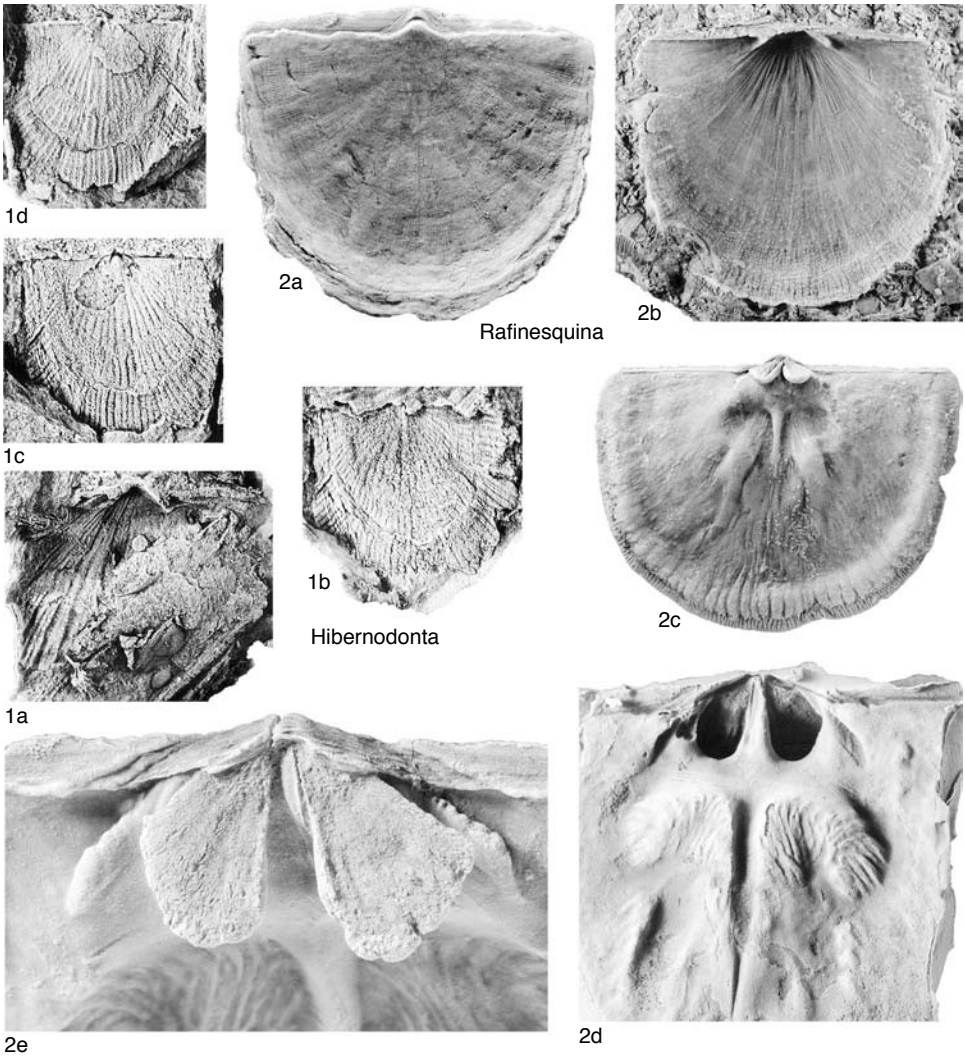

FIG. 146. Rafinesquinidae (p. 237–239).

Hedstroemina BANCROFT, 1929, p. 58 [**H. fragilis;* OD] [=*Rakverina* RÕÕMUSOKS, 1993c, p. 161 (type, *?Oepikina inaequiclina* ALICHOVA, 1951, p. 58)]. Concavoconvex profile, weakly geniculate anteriorly; relatively fine, irregularly parvicostellate ornament with impersistent concentric wrinkles; vestigial pseudodeltidium; small chilidium; strong, divergent dental plates, but poorly impressed muscle fields with no bounding ridges; robust, narrowly divergent cardinal process lobes, but short, weak socket ridges; faint myophragm, but no dorsal septa. *Ordovician (Caradoc):* Europe.——FIG. 148,*2a–c. *H. fragilis,* Cheney Longville Flags, Caradoc, Woolston House, Shropshire, England; *a,* dorsal external mold, BMNH BB 69460, ×1.5; *b,* lectotype, ventral internal mold, BMNH BB 14380, ×1.5; *c,* dorsal internal mold, BMNH BB 73550, ×3 (new).——FIG. 148,*2d,e. H. inaequiclina* (ALICHOVA), Rägavere Formation, Caradoc, Rägavere, Estonia; *d,* ventral exterior, GMUT Br 1560, ×2; *e,* dorsal interior, GMUT Br 1630, ×2 (Rõõmusoks, 1993c).

?Hibernodonta HARPER & MITCHELL in HARPER & others, 1985, p. 300 [**H. praeco;* OD]. Small, planoconvex profile; relatively coarse parvicostellate ornament; no pseudodeltidium; with chilidium; no denticles on hinge line, but crenulations on teeth; intermediate between rafinesquinids, leptostrophiids, hence family position uncertain; thin, widely divergent dental plates present; poorly impressed

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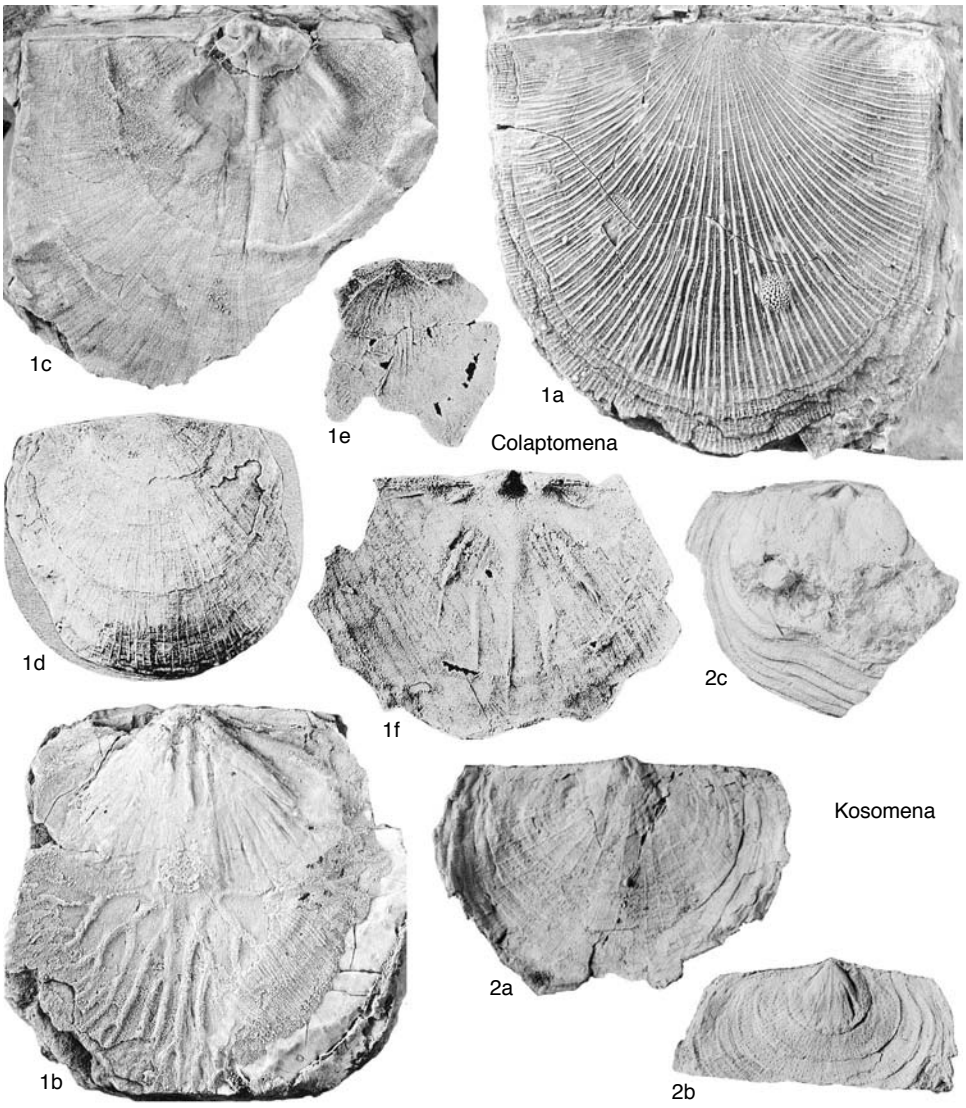

FIG. 147. Rafinesquinidae (p. 237–242).

ventral muscle field with no bounding ridges; small, discrete cardinal process lobes; short, slender crenulated socket ridges; dorsal muscle field poorly impressed. *Ordovician (Caradoc):* Ireland.——FIG. 146,*1a–d. *H. praeco,* Clashford House Formation, middle Caradoc, Herbertstown, County Meath, Ireland; *a,* holotype, latex of ventral interior, BMNH BC 9197, ×4; *b–d,* exterior, internal mold, latex of dorsal valve, BMNH BC 9195, ×4 (Harper & others, 1985).

Kjaerina BANCROFT, 1929, p. 43 [**K. typa;* OD]. Gently concavoconvex profile with occasional dorsal geniculation posteriorly; parvicostellate ornament with accentuated median costella, often with posterolateral rugae; vestigial pseudodeltidium; small chilidium; prominent dental plates anterolaterally leading to muscle-bounding ridges enclosing weakly impressed triangular ventral muscle field; delicate cardinalia with dorsal socket ridges present but separate from elongate cardinal process lobes; weakly impressed dorsal muscle field with transmuscle septa absent. *Ordovician (Caradoc):* Britain.——FIG. 149,*1a–d. *K. typa,* Cheney Longville Flags, Caradoc, Burrell's Coppice, Cheney Longville, Shropshire, England; *a,* ventral external mold, BMNH BB 30650, ×1.5; *b,* lectotype,

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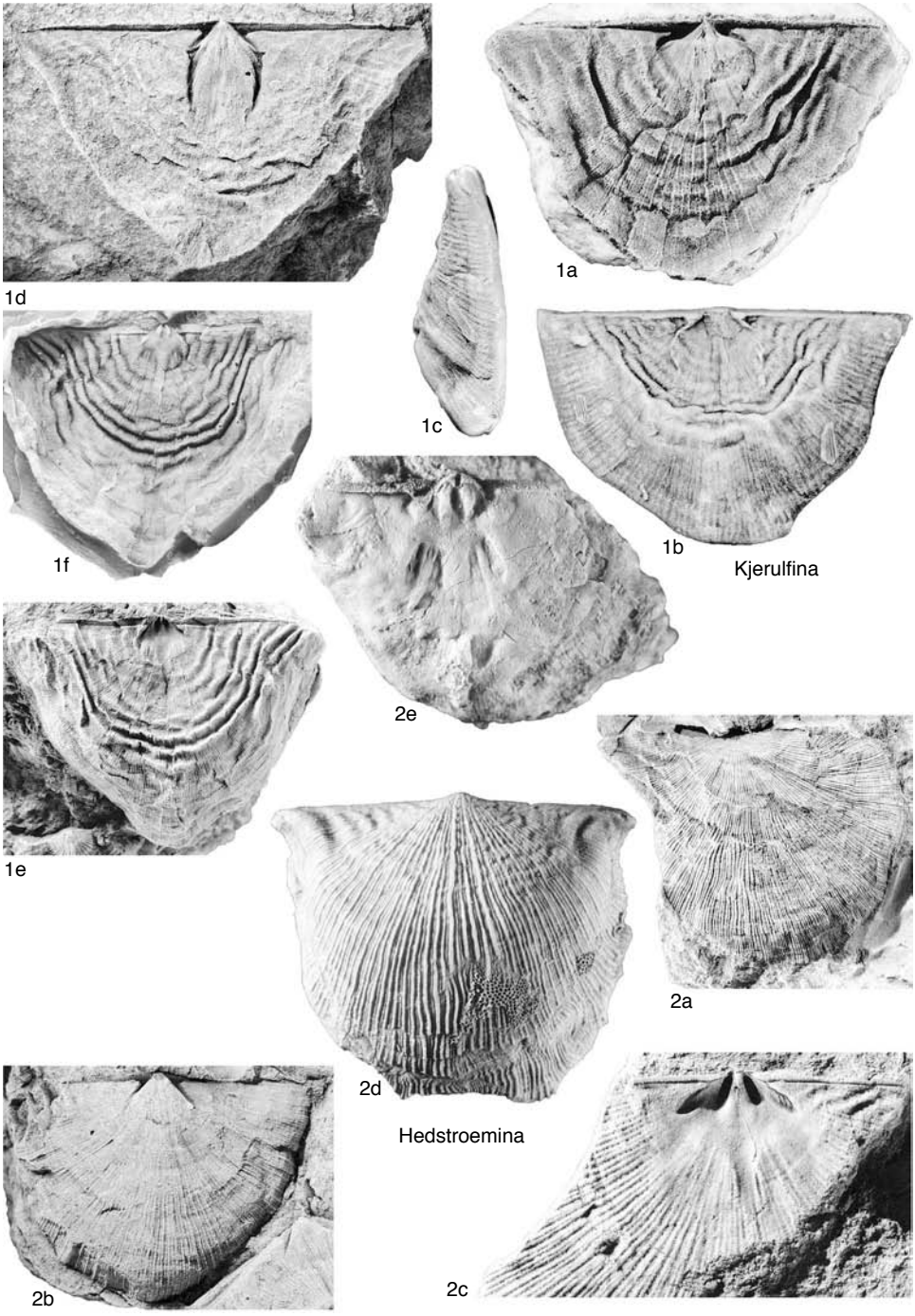

FIG. 148. Rafinesquinidae (p. 239–241).

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ventral internal mold, BMNH BB 14383, ×1.5; *c,* dorsal internal mold, ×2; *d,* enlargement of latex cast of cardinal area, BMNH BC 13405, ×8 (new).

Kjerulfina Bancroft, 1929, p. 59 [**K. trigonalis;* OD]. Posterior part of ventral valve with convex profile, dorsal valve flat or gently concave, then both valves anteriorly geniculate in a ventral direction; ornament usually unequally parvicostellate with fine to coarse irregular rugae; small pseudodeltidium, chilidium; short, thin flaring dental plates; ventral muscle field elongate to subcircular, muscle-bounding ridges variably developed; cardinal process lobes elongate; socket ridges widely divergent; dorsal muscle field poorly defined. *Ordovician (Caradoc–Ashgill):* Europe.——Fig. 148,*1a–f. *K. trigonalis,* Cheney Longville Flags, Caradoc, Marsh Wood, Marshbrook, Shropshire, England; *a,* ventral internal mold, BMNH BB 9148, ×2; *b,* ventral view of plaster cast of ventral interior, BMNH BB 73908, ×1.5; *c,* lateral view of plaster cast of ventral interior, BMNH BB 73908, ×1.5; *d,* lectotype, ventral internal mold, BMNH BB 73834, ×1.5; *e,* dorsal internal mold, ×1.5; *f,* latex cast, BMNH BB 73901, ×1.5 (new).

Kosomena Havlíček in Havlíček & Štorch, 1990, p. 71 [**K. kosia;* OD]. Ventral valve with gently convex profile posteriorly, but resupinate anteriorly; dorsal valve posteriorly planar but anteriorly convex; dental plates present, but no muscle-bounding ridges; muscle fields poorly impressed; divergent cardinal process lobes, short socket ridges; dorsal median septum absent. *Silurian (Ludlow):* Europe.——Fig. 147,*2a–c. *K. kosia,* Upper Kopininá Formation, upper Ludlow, Kosov Quarry, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 4227, ×1.5; *b,* ventral internal mold, OMR VH 4229, ×1.5; *c,* dorsal internal mold, OMR VH 4228, ×1.5 (Havlíček & Štorch, 1990).

Megamyonia Wang, 1949, p. 32 [**M. knighti;* OD]. Small; concavoconvex profile, with dorsal valve initially very gently concave but with increased curvature anteriorly; finely costellate, sometimes with prominent central costa; pseudodeltidium small; chilidium large; with dental plates; relatively large, very impressed ventral muscle field distinctive from all other Rafinesquinidae, flabellate, with irregular transmuscle septa; socket ridges faint, short; dorsal myophragm prominent but no median septum. *Ordovician (Ashgill):* North America.——Fig. 149,*4a–c. *M. knighti,* Fort Atkinson Member, Maquoketa Shale, Ashgill, Ossian, Winneshiek County, Iowa; *a,* dorsal exterior, SUI 1868, ×2; *b,* holotype, ventral interior, SUI 1869, ×2; *c,* dorsal interior, SUI 1870, ×2 (Wang, 1949).

Odoratus Zhu, 1985, p. 39[51] [**O. wangi;* OD]. Profile gently concavoconvex, but geniculation ventrally directed; ornament unequally parvicostellate; dental plates short; rounded ventral muscle field with low bounding ridges posterolaterally; dorsal median ridge well developed. *Ordovician (Caradoc–Ashgill):* China.——Fig. 149,*3a,b. *O. wangi,* Maimushan Member, Wulongtun Formation, upper Caradoc–lower Ashgill, Wulongtun, Huma County, eastern Greater Khingan Mountains, Heilongjiang Province, northeastern China; *a,* latex cast of ventral internal mold, SIGM 70167, ×2; *b,* latex cast of dorsal internal mold, SIGM 70178, ×2 (Rong & Zhu, new).

Rhipidomena Cooper, 1956, p. 866 [**Strophomena tennesseensis* Willard, 1928, p. 285; OD]. Profile initially convexoconcave but resupinate anteriorly; low pseudodeltidium; small chilidial plates; abbreviated divergent dental plates, strongly impressed large flabellate ventral muscle field without bounding ridges; large lobate cardinal process lobes; short socket ridges; broad myophragm extending short distance anteriorly; two or three pairs of fine united dorsal transmuscle, side septa sometimes present. *Ordovician (Llandeilo–Caradoc):* North America.——Fig. 149,*2a–e. *R. tennesseensis* (Willard), Benbolt Formation, Llandeilo; *a,b,* ventral, lateral views of conjoined valves, New Harmony, Heiskell, Virginia, BMNH BC 12840, ×1.5 (new); *c,* posterior view of conjoined valves, Rye Cove, Clinchport, Virginia, USNM 117683a, ×1 (Cooper, 1956); *d,* ventral interior, New Harmony, Heiskell, BMNH BC 12838, ×1.5 (new); *e,* dorsal interior, Mount Eager Church, Tennessee, USNM 117692a, ×2 (Cooper, 1956).

Subfamily LEPTAENINAE Hall & Clarke, 1894

[*nom. transl.* Cocks & Rong, herein, *ex* Leptaenidae Hall & Clarke, 1894a, p. 354] [=Elliptostrophiidae Havlíček, 1967, p. 111]

Rafinesquinids with dorsal geniculation; usually with concentric rugae over whole shell. *Ordovician (Llanvirn)–Carboniferous (Namurian).*

Leptaena Dalman, 1828, p. 94 [**L. rugosa;* SD King, 1846, p. 28] [=*Astamena* Rõõmusoks, 1989, p. 114 (type, *A. inaequalis;* OD); *Kurnamena* Rõõmusoks, 1989, p. 114 (type, *L. taxilla* Oraspõld, 1956, p. 51; OD); *Leptaenella* Fredericks, 1918, p. 89 (type, *L. rhomboidalis ventricosa* Hall & Clarke, 1892, pl. 15A, fig. 43; OD; Oriskany Sandstone (Lower Devonian), Cumberland, Maryland, USA); *Leptaenopoma* Marek & Havlíček, 1967, p. 282 (type, *L. trifidum;* OD); ?*Leptaenulopsis* Haupt, 1878, p. 31 (type, *L. simplex;* SD Hall & Clarke, 1892, p. 294; Wenlock, Germany); *Oandumena* Rõõmusoks, 1989, p. 116 (type, *L. fluviatilis* Oraspõld, 1956, p. 54; OD; Oandu Series (upper Caradoc), Rakvere, Estonia); *Orhoria* Havlíček in Havlíček & Štorch, 1990, p. 73 (type, *O. provellerosa;* OD; Kopaninà Formation (Ludfordian), Bohemia, Czech Republic); *Schmidtomena* Rõõmusoks, 1989, p. 115 (type, *L. acuteplicata* Schmidt, 1908, p. 726; OD); *Similoleptaena* Rõõmusoks, 1989, p. 114 (type, *S. paucirugata;* OD); ?*Turgenostrophia* Alekseeva in Alekseeva & Erlanger, 1983, p. 29 (type, *T. rara;* OD; upper

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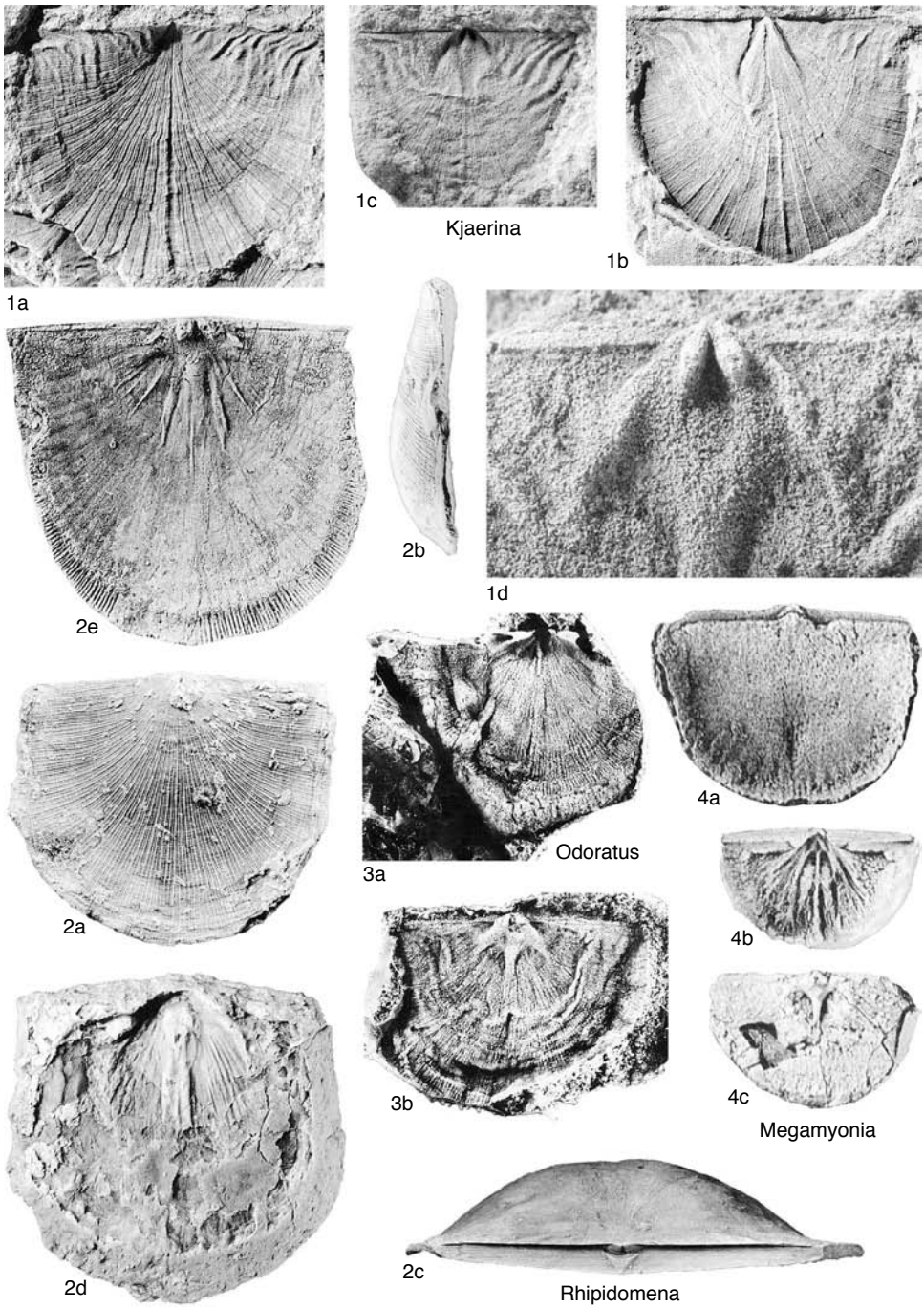

FIG. 149. Rafinesquinidae (p. 239–242).

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Silurian, Yamatu-Gol river, northwestern Mongolia)]. Outline usually transverse, rounded anteriorly; profile concavoconvex with sharp anterior dorsal geniculation; ornament costellate to unequally parvicostellate; concentric rugae variable but usually well developed; small pseudodeltidium; large chilidium; short dental plates; ventral muscle field varies from subcircular to elongate with bounding ridges usually developed posterolaterally, sometimes curving round anteriorly; cardinal process lobes elongate, ventrally directed; socket ridges present but usually weak, sometimes with crenulations; dorsal muscle field variably impressed with median ridge often present; transmuscle ridges, diaphragm variably developed in dorsal valve. *Ordovician (Llanvirn)–Devonian (Pragian, ?Emsian).*

L. (Leptaena). Similar to *L. (Septomena)* but lacking the distinctive two pairs of dorsal transmuscle ridges. *Ordovician (Caradoc)–Devonian (Pragian, ?Emsian):* cosmopolitan.——Fig. 150,*1a–e.* **L. (L.) rugosa, Dalmanitina* Beds, Ashgill, Alleberg, Västergötland, Sweden; *a,b,* ventral, lateral views of ventral internal mold, BMNH B 13594, ×1.5; *c,d,* dorsal internal mold, ×1.5, latex cast of it, BMNH BB 67944, ×1.5; *e,* latex cast of juvenile dorsal internal mold, BMNH BB 67946, ×2 (new).——Fig. 150,*1f.* *L. (L.) inaequalis* (Rõõmusoks), Johvi Beds, lower Caradoc, Anija, Estonia; holotype, ventral exterior, TAGI BR 1346, ×1.5 (Rõõmusoks, 1989).——Fig. 150,*1g.* *L. (L.) taxilla* Oraspõld, Johvi Stage, lower Caradoc, Alliku, Estonia; dorsal interior, ×2 (Rõõmusoks, 1989).——Fig. 150,*1h.* *L. (L.) acuteplicata* Schmidt, Porkuni Stage, upper Ashgill, Estonia; ventral interior, TAGI BR 1335, ×1.7 (Rõõmusoks, 1989).——Fig. 150,*1i,j.* *L. (L.) paucirugata* (Rõõmusoks), Vormsi Stage, Ashgill, Kõrgessaare, Estonia; holotype, ventral, lateral views of ventral valve, TAGI BR 1349, ×1.5 (Rõõmusoks, 1989).——Fig. 150,*1k.* *L. (L.) trifidum* (Marek & Havlíček), Kosov Formation, Ashgill, Bechovice, Czech Republic; dorsal internal mold, OMR VH 354e, ×3 (Havlíček, new).

L. (Septomena) Rõõmusoks, 1989, p. 115 [**L. juvenilis* Öpik, 1930, p. 173; OD]. Similar to *L. (Leptaena)* but with two well-developed pairs of transmuscle ridges in dorsal valve, outer pair divergent, inner pair subparallel, united with side septa, continuing anteriorly for over half valve length. *Ordovician (Llanvirn–Caradoc):* Baltic.——Fig. 150,*2a–c.* **L. (S.) juvenilis* (Öpik), Viivikonna Formation, Kukruse Stage C2β, upper Llandeilo, Estonia; *a,* holotype, ventral exterior, Käva, TAGI BR 207, ×2; *b,* ventral interior, Kohtla-Järve, TAGI BR 212, ×2; *c,* dorsal interior, Küttejõu, TAGI BR 1319, ×2 (Rõõmusoks, 1989).

?Bracteoleptaena Havlíček, 1963, p. 224 [**Strophomena bracteola* Barrande, 1879, pl. 45, fig. 17, 18, 20–24, pl. 53, fig. 1; OD]. Costellate; profile gently geniculate dorsally with regular or irregular rugae; small interarea with pseudodeltidium, chilidium; short, thin, widely divergent dental plates; weak muscle-bounding ridges leading to relatively small subcircular ventral muscle field; cardinal process lobes small, rather obscure (thus could be glyptomenid if lobes posterior to hinge line, rather than rafinesquinid); socket ridges small, widely divergent, subparallel to hinge line; dorsal muscle field ill defined. *Silurian (Wenlock–Ludlow):* Europe.——Fig. 151,*1a,b.* **B. bracteola* (Barrande), Liten Formation, Wenlock; *a,* ventral, dorsal internal molds, Mezoun, OMR VH 380b, ×2; *b,* lectotype, ventral internal mold, Borek, Suchomasty, Czech Republic, NM CE 236, ×2 (Havlíček, 1967).

Glossoleptaena Havlíček, 1967, p. 115 [**Strophomena emarginata* Barrande, 1879, pl. 45, fig. 8–9; OD] [=*Ludfordina* Kelly, 1967, p. 599 (type, *L. pixis;* OD)]. Outline subquadrate; profile as in *Rugoleptaena,* with anterior margin concave; ornament of faint costellae, weak rugae; lacks dental plates; small oval ventral muscle field bounded posterolaterally by low curved ridges; cardinal process lobes delicate, slightly elongate, directed ventrally; socket ridges short, well developed. *Silurian (Ludlow)–Devonian (Lochkovian–Eifelian):* Europe.——Fig. 152,*3a,b.* **G. emarginata* (Barrande), Lochkov Limestone, Lochkovian, Karlík, Bohemia, Czech Republic; ventral external, internal molds, OMR VH 385, ×2.6 (Havlíček, 1967).

Harjumena Rõõmusoks, 1993c, p. 162 [**Strophomena schmidti* Gagel, 1890, p. 42; OD]. Similar to *Leptaena* in profile, but more subtriangular in outline; ornament unequally parvicostellate with irregular concentric corrugations on disc; vestigial pseudodeltidium, large chilidium; elongate ventral muscle field open anteriorly; long cardinal process lobes, short dental plates; dorsal muscle field poorly impressed. *Ordovician (Ashgill):* Baltic.——Fig. 151,*2a–c.* **H. schmidti* (Gagel), Saunja Formation, Nabala Stage, lower Ashgill, glacial boulders, Estonia; *a,* partly exfoliated dorsal valve, ×1; *b,* ventral internal mold, ×1; *c,* dorsal interior, RMS Br 13609, ×3 (Rõõmusoks, 1993c).

Hingganoleptaena Zhu, 1985, p. 41 [**Leptaena nenjiangensis* Su, 1980, p. 274; OD]. Similar to *Leptaena* in profile, ornamentation, but with concave pair of long dorsal valve side septa prominent, originating from just anterior of pair of very short muscle-bounding ridges. *Ordovician (Caradoc–Ashgill):* China.——Fig. 151,*3a–d.* **H. nenjiangensis* (Su), Wulongtun Formation, upper Caradoc–lower Ashgill, Wulongtun, Huma County, Heilongjiang Province, China; *a,* dorsal external mold, SIGM 70130, ×3; *b,* ventral internal mold, SIGM 70140, ×3; *c,d,* dorsal internal molds, SIGM 70126-7, ×3 (Su, new).

Hollardina Racheboeuf & Garcia-Alcade in Racheboeuf, Carls, & Garcia-Alcade, 1982, p. 46 [**H. plana;* OD]. Profile concavoconvex, geniculate; multicostellate ornament; rugae absent except weak near hinge line; small pseudodeltidium; large

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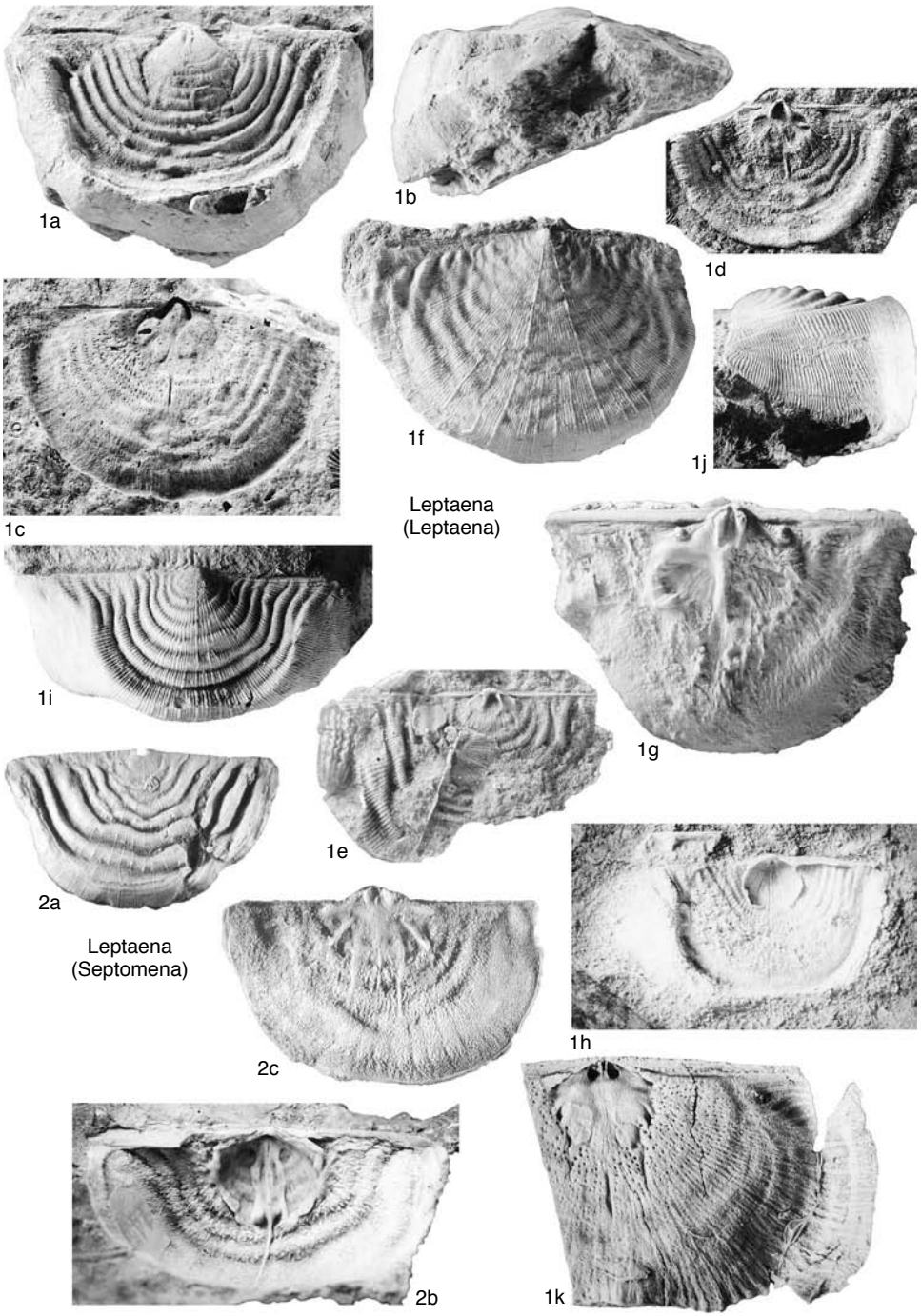

FIG. 150. Rafinesquinidae (p. 242).

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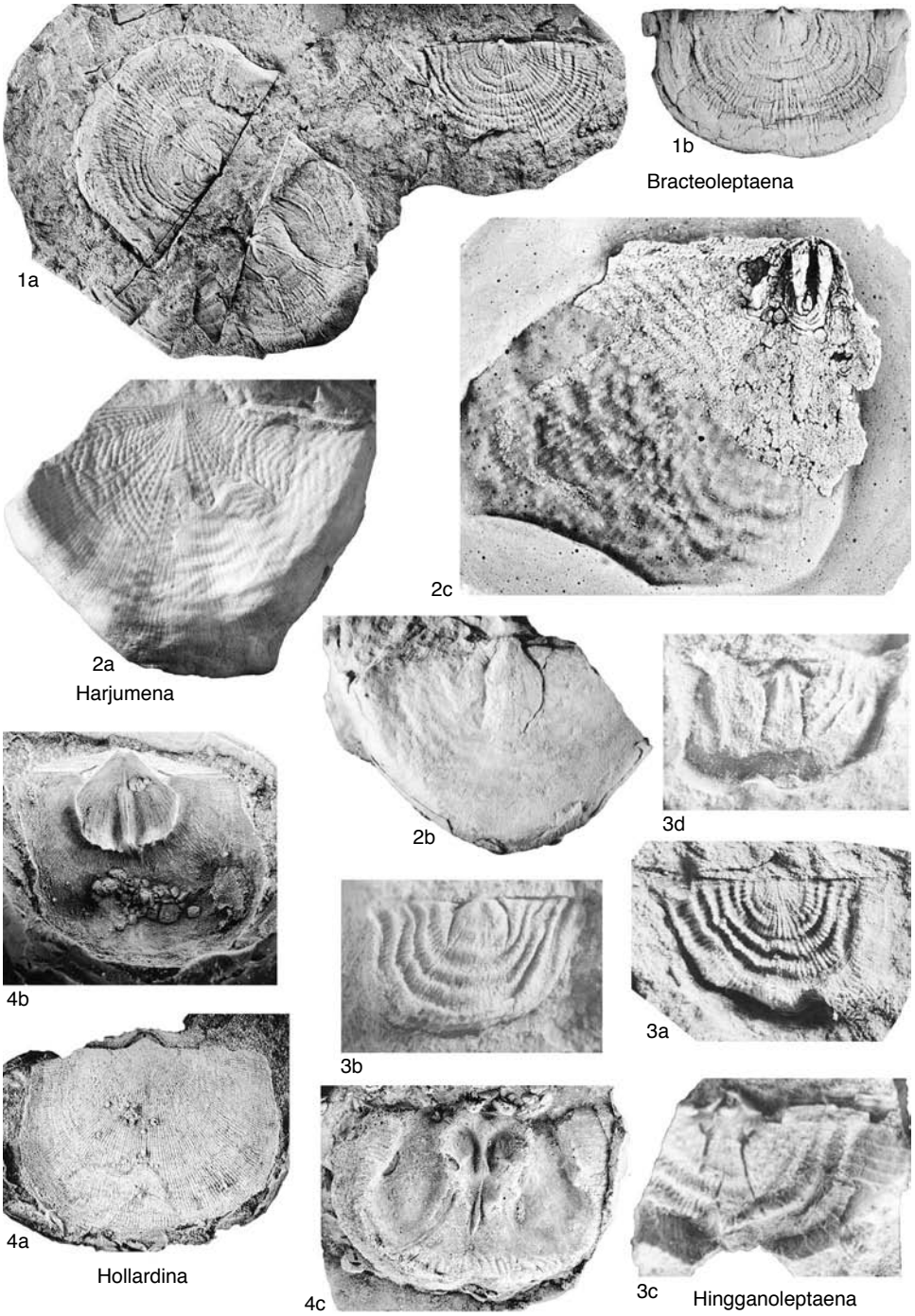

FIG. 151. Rafinesquinidae (p. 243–246).

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chilidium; ventral muscle platform completely surrounded by ridges, partly elevated; dorsal muscle-bounding ridges also developed; thin dorsal median septum. *Devonian (Lochkovian):* Europe.——Fig. 151,*4a–c. *H. plana,* Kerdéniel Member, Landévennec Formation, Lochkovian, Pointe du Corbeau, Finistère, Brittany, France; *a,* dorsal view of conjoined valves, LPB 8918, ×1; *b,* latex cast of ventral internal mold, LPB 8919, ×1; *c,* latex cast of dorsal internal mold, LPB 8917, ×1 (Racheboeuf, new).

Kiaeromena Spjeldnaes, 1957, p. 183 [**Leptaena kjerulfi* Holtedahl, 1916, p. 72; OD] [=*Estonomena* Rõõmusoks, 1989, p. 113 (type, *Leptaena estonensis* Bekker, 1921; OD)]. Gentle geniculation; unequally parvicostellate, rugate ornament; pseudodeltidium, chilidium large; dental plates leading to posterolateral muscle-bounding ridges; ventral valve muscle field subcircular; cardinalia as in *Kjerulfina;* dorsal transmuscle ridges variably developed. *Ordovician (Llandeilo–Ashgill).*

K. (Kiaeromena). Similar to *K. (Bekkeromena),* but without elevated muscle-bounding ridges and with subcirular rather than elongate ventral muscle field. *Ordovician (Llandeilo–Caradoc):* Baltic.——Fig. 152,*1a–d. *K. (K.) kjerulfi* (Holtedahl), Frognerkiln Formation, middle Caradoc, Norway; *a,b,* ventral, lateral views of ventral internal mold, Lindøya, Oslo, PMO 66964, ×1; *c,* lectotype, dorsal interior, Gasøya, Oslo-Asker district, PMO L128, ×1; *d,* dorsal internal mold, Lindøya, PMO 67014, ×1 (new).——Fig. 152,*1e,f. K. (K.) estonensis* (Bekker), Kukruse Formation, Llandeilo, Estonia; *e,* ventral exterior, Kukruse, BMNH BB 5220, ×1 (new); *f,* dorsal interior, Vanamõisa, TAGI BR 219, ×1 (Rõõmusoks, 1989).

K. (Bekkeromena) Rõõmusoks, 1963, p. 235 [**Strophomena semipartita* Roemer, 1861, pl. 1, fig. 5–9; OD]. Similar to *K. (Kiaeromena)* but with elevated muscle-bounding ridges encircling ventral valve muscle field elongate rather than subcircular; dorsal transmuscle ridges usually absent. *Ordovician (Ashgill):* Baltic.——Fig. 152,*2a,b. *K. (B.) semipartita* (Roemer), Pirgu Formation, Ashgill, Pirgu, Estonia; *a,* ventral exterior, TAGI BR 1295, ×1.5 (Rõõmusoks, 1963); *b,* ventral exterior, BMNH BB 91342, ×1.5 (new).——Fig. 152,*2c,d. *K. (B.)* sp. aff. *K. (B.) semipartita* (Roemer), Kuti, Estonia; *c,* ventral interior, TAGI BR 1297, ×1.5; *d,* partially exfoliated conjoined valves showing cardinalia, dorsal muscle field, TAGI BR 1296, ×1.5 (Rõõmusoks, 1963).

Lepidoleptaena Havlíček, 1963, p. 224 [**Strophomena rhomboidalis lepidula* Barrande, 1879, pl. 41, fig. 10; OD]. Transverse outline; similar to *Leptaena* but with strong ridges bounding visceral area in both valves, merging with valve hinge line lateral to vestigial dental plates, well-developed socket ridges. *Silurian (Ludlow)–Devonian (Emsian):* Europe.——Fig. 153,*1a–d. *L. lepidula* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* dorsal external mold, NM L6657, ×1; *b,c,* ventral, anterior views of ventral internal mold, OMR VH 373a, ×1; *d,* dorsal internal mold, OMR VH 374, ×1 (Havlíček, 1967).

Leptaenopyxis Havlíček, 1963, p. 224 [**Leptaena bouei* Barrande, 1848, p. 237; OD] [=*Yujiangia* Xu, 1991, p. 314 (type, *Leptaenopyxis intermedia* Hou & Xian, 1975, p. 20; OD)]. Transverse, subquadrate outline; concavoconvex profile with anterior margin usually concave, lateral margins raised ventrally above disc before dorsal geniculation; costellate ornament with well-developed rugae; short pseudodeltidium, chilidium; ventral muscle field subcircular, bounded by ridges; dorsal muscle field bounded by variably developed ridges; dorsal median septum usually present; diaphragm variable. *Devonian (Pragian–Emsian):* Europe, Asia.

L. (Leptaenopyxis). More transverse than *L. (Hefengia)* but with relatively smaller ventral muscle field and with no ventral median septum anterior of the muscle field. *Devonian (Pragian–Emsian):* Europe.——Fig. 153,*2a–d. *L. (L.) bouei* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,b,* dorsal, anterior views of conjoined valves, NM CF385, ×1; *c,* ventral internal mold, OMR VH 372b, ×1; *d,* dorsal internal mold, OMR VH 372a, ×1 (Havlíček, 1967).——Fig. 153,*2e. L. (L.) intermedia* (Hou & Xian), Yukiang Formation, lower Emsian, Liujiang, Heng Xian County, southern Guangxi Province, China; dorsal view of conjoined valves, NIGP 87820, ×1 (Xu, 1991).

L. (Hefengia) Xu, 1991, p. 313 [**L. (H.) hefengensis;* OD]. Similar to *L. (Leptaenopyxis),* but with larger ventral muscle field occupying more than half disc; dorsal median septum very long, extending to anterior margin of disc. *Devonian (Emsian):* China.——Fig. 153,*3a–d. *L. (H.) hefengensis,* Mangkelu Formation, Emsian, Mangkelu, Hoboksar County, western Junggar, Xingjiang Province, China; *a,b,* holotype, ventral, lateral views of internal mold of conjoined valves, NIGP 111514, ×1; *c,d,* ventral, dorsal views of internal mold of conjoined valves, NIGP 111512, ×1 (new).

Leptagonia M'Coy, 1844, p. 116 [**Producta analoga* Phillips, 1836, p. 215; OD] [?=*Adiaphragma* Xian in Xu, Wan, & Chen, 1978, p. 299 (type, *A. ganxiensis;* M; Xian gives "*Adiaphragma yukiangensis* Xian (MS)" as type species, but it is a *nomen nudum* and *Adiaphragma ganxiensis* Wan is only species described within new genus; however, interiors are unknown; Ganxi Formation (lower Emsian), Ganxi, Beichuan County, northern Sichuan, China); *Pseudoleptaena* Miloradovich, 1947, p. 96

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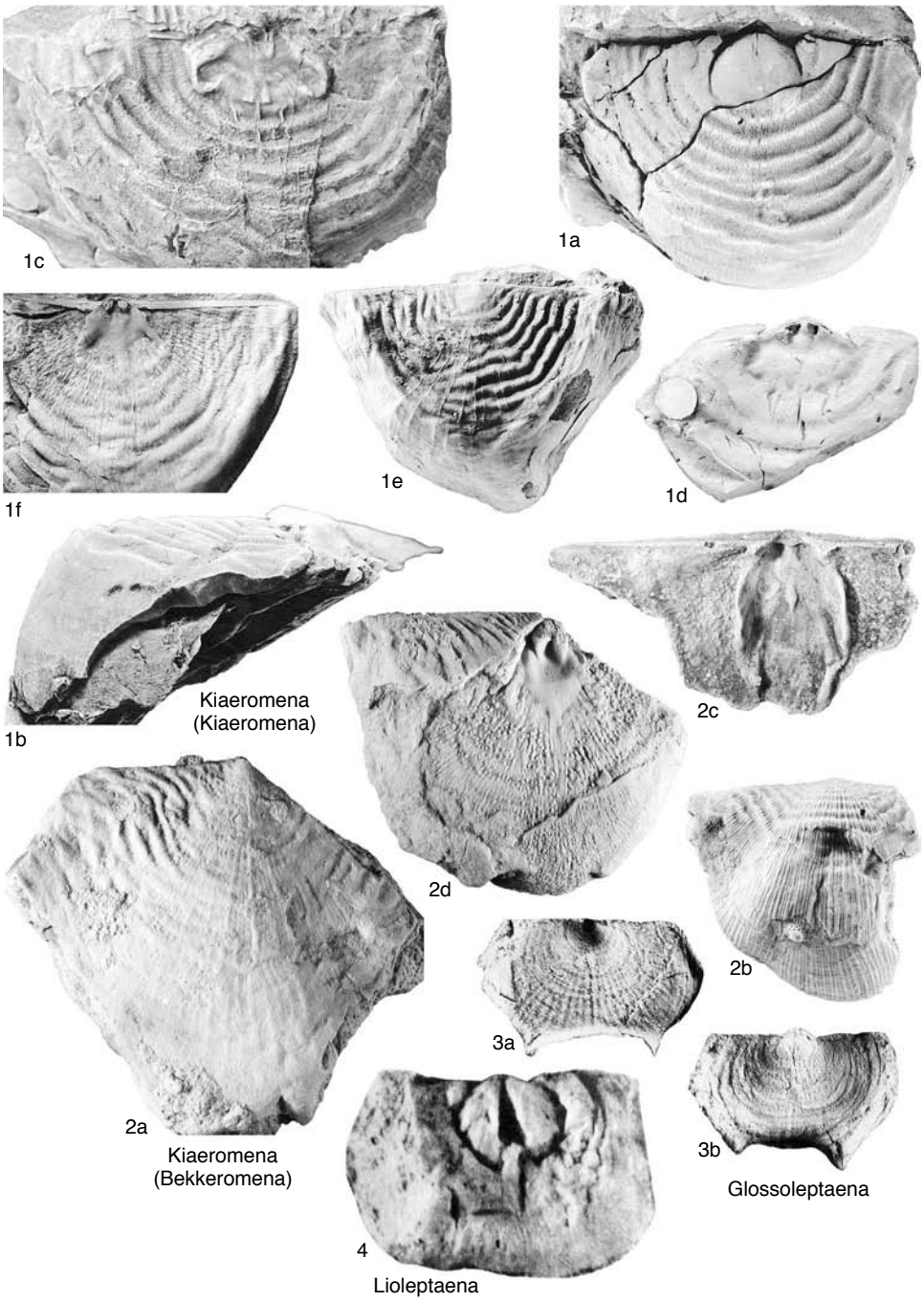

FIG. 152. Rafinesquinidae (p. 243–250).

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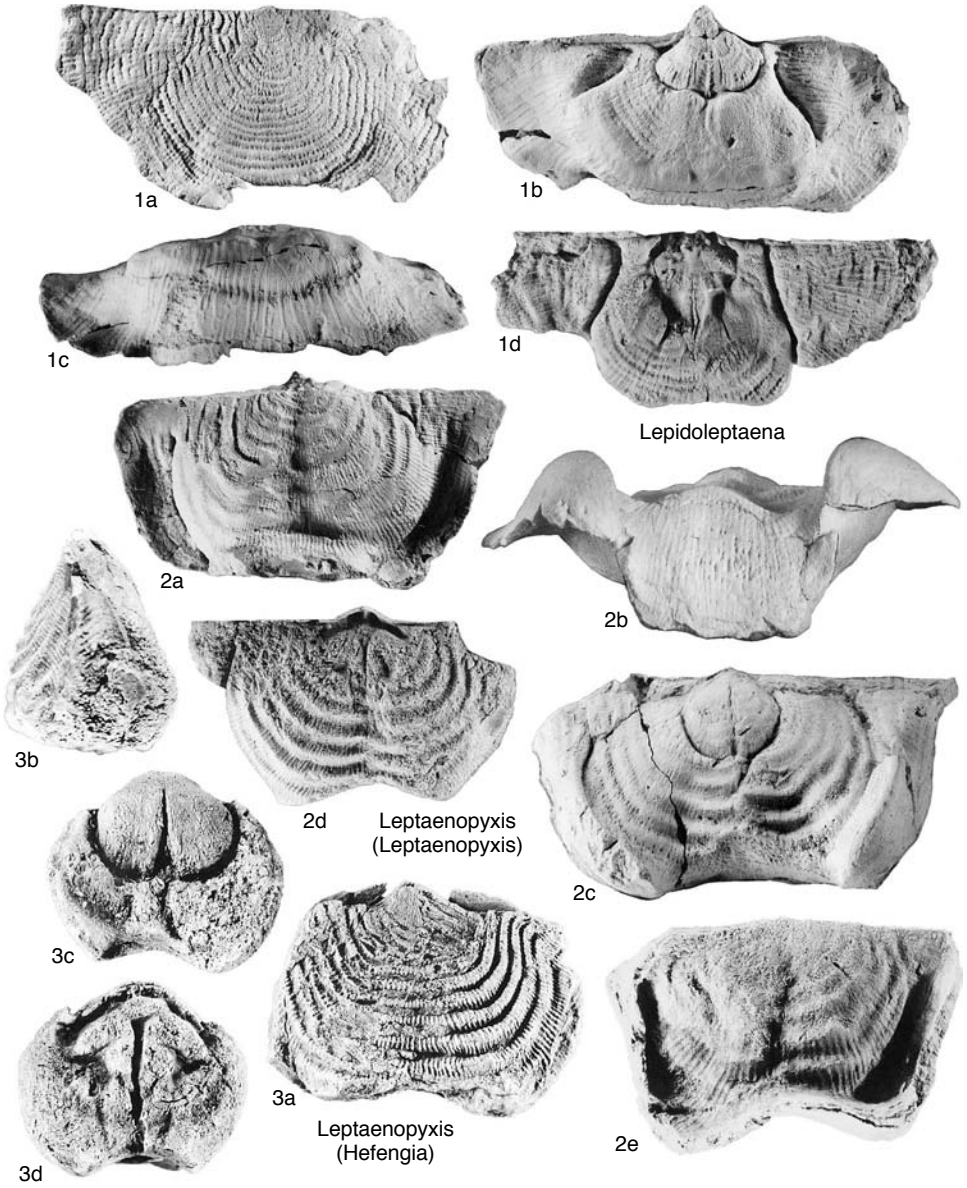

FIG. 153. Rafinesquinidae (p. 246).

(type, *Leptaena distorta* J. DE C. SOWERBY, 1840 in 1840–1846, p. 10); ?*Semileptagonia* KARAPETOV, 1971, p. 60 (type, *S. pamirica;* OD; upper Famennian, Pamir Mountains, Tadzhikistan)]. Similar to *Leptaena,* but with both ventral, dorsal muscle field platforms elevated clear of valve floor; more substantial cardinal process. *Devonian (Emsian)–Carboniferous (Namurian):* cosmopolitan.——FIG. 154,*1a–d.* **L. analoga* (PHILLIPS); *a,b,* lectotype, ventral, lateral views of conjoined valves, Carboniferous Limestone, Viséan, Bolland, Yorkshire, BMNH B 8936, ×1.5; *c,* ventral interior, Redesdale Formation, Viséan, Redesdale, Cumbria, England, BMNH B 46524, ×2; *d,* dorsal interior,

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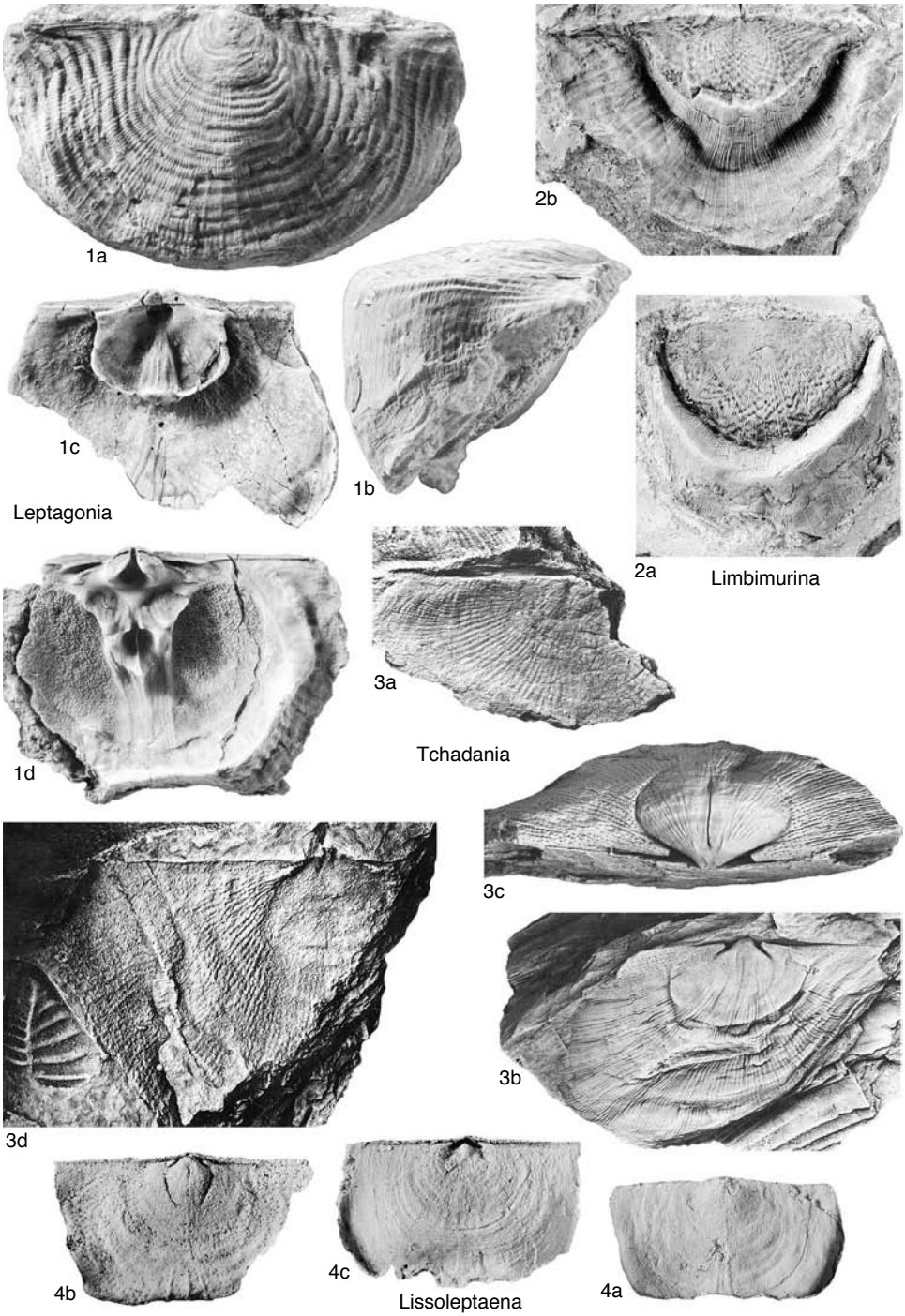

FIG. 154. Rafinesquinidae (p. 246–252).

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Redesdale Formation, Viséan, Redesdale, Cumbria, England, BMNH B 43708, ×1.5 (new).

Limbimurina Cooper, 1956, p. 851 [**L. insueta;* OD]. Profile gently biconvex posteriorly with ventral geniculation followed by dorsal geniculation; distinctive ornament of small rugae interrupted by costellae, sometimes achieving interference pattern; strong divergent dental plates, leading to elevated bounding ridges surrounding subcircular ventral muscle field divided by low median ridge; thin widely diverging socket ridges; dorsal transmuscle ridges. *Ordovician (Caradoc–lower Ashgill):* North America, Scotland, Kazakhstan.——Fig. 154,*2a,b.* **L. insueta,* Rodman Member, Nealmont Formation, Caradoc, Holidaysburg, Pennsylvania; *a,* holotype, ventral exterior, USNM 117659a, ×2; *b,* dorsal exterior, USNM 117660b, ×2 (Cooper, 1956).

?Lioleptaena Xian in Xian & Jiang, 1978, p. 264 [**L. kailiensis;* OD]. Similar to *Leptaena* but without ornament on disc; dorsal interior unknown, thus family uncertain. *Silurian (Llandovery):* China.——Fig. 152,*4. *L. kailiensis,* Wengxiang Formation, upper Telychian, Wengxiang, Kaili County, Guizhou Province, southwestern China; holotype, ventral internal mold, GB 354, ×1 (Xian & Jiang, 1978).

Lissoleptaena Havlíček, 1992, p. 171 [**L. lissodermis;* OD]. Ornament of radial costellae absent except near median plane; similar to *Leptaena* but with no radial ornament laterally, small number of faint median costellae, faint rugae. *Devonian (Lochkovian):* Europe.——Fig. 154,*4a–c. *L. lissodermis,* Kotys Limestone, Lochkovian, Lobolitová strán, Reporyje, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 5166a, ×2; *b,* ventral internal mold, OMR VH 4696a, ×2; *c,* dorsal internal mold, OMR VH 5163a, ×2.5 (Havlíček, 1992).

Mackerrovia Cocks, 1968, p. 319 [**Brachyprion arenaceus lobatus* Lamont & Gilbert, 1945, p. 667; OD]. Concavoconvex profile with dorsal geniculation varying from sharp to more gentle; faint ornament of unequal parvicostellae, fine, irregular rugae weakly developed; teeth, dental plates continuous with long distinctive subparallel muscle-bounding ridges more than half valve length; cardinal process lobes elongate, erect; short flaring socket ridges with fine crenulations; dorsal muscle field faintly impressed with pair of long parallel side septa; central median ridge developed in central part of valve. *Silurian (Telychian):* Europe.——Fig. 155,*3a–d. *M. lobata* (Lamont & Gilbert); *a,b,* external, internal molds of dorsal valve, Hughley Shales, Telychian, Devil's Dingle, Shropshire, England, BMNH BC 50573, ×1.5 (new); *c,* ventral internal mold, Damery Beds, Telychian, Tortworth, Avon, England, BUM 12180, ×1.5; *d,* latex cast of ventral interior, Damery Beds, Telychian, Tortworth, Avon, England, BUM 12159, ×1.5 (Cocks, 1968).

Notoleptaena Gill, 1951, p. 191 [**N. linguifera;* OD]. Ventral profile planar, dorsal convex, but with substantial dorsally directed sulcus, fold; similar to *Leptaenopyxis* but lateral margins flat, not raised ventrally; dorsally geniculate anteriorly, laterally; no pseudodeltidium; small chilidium; ventral muscle field elevated, enclosed by muscle-bounding ridges; ventral peripheral rim developed; dorsal muscle field small, enclosed posterolaterally; thin but prominent dorsal median septum. *Devonian (?Emsian):* Australia.——Fig. 155,*1a–c. **N. linguifera,* Mount Ida Beds, Lower Devonian, Dargile Parish, Heathcote district, Victoria, Australia; *a,* latex of ventral exterior, NMVP P59527, ×1.5; *b,* holotype, latex of ventral interior, NMVP P59523, ×1; *c,* latex of dorsal interior, NMVP P59526, ×1 (new).

Rugoleptaena Havlíček, 1956, p. 558 [**R. hornyi;* OD] [?=*Elliptostrophia* Havlíček, 1963, p. 225 (type, *E. elliptica*); *Yunnanoleptaena* Jahnke & Shi, 1989, p. 153 (type, *Y. shidianensis;* OD)]. Transverse outline with shell raised ventrally at lateral margin; dorsal geniculation, short trail developed only in adults; similar to *Glossoleptaena* except radial ornament lacking apart from single median costella; small pseudodeltidium; large chilidium; dental plates very short or absent leading to muscle-bounding ridges posterolaterally defining small subcircular ventral muscle field; socket ridges, dorsal valve muscle field weakly developed. *Devonian (Pragian–Emsian):* Europe, China.——Fig. 155,*2a–d. *R. hornyi; a,* dorsal exterior, Zlíchov Limestone, Emsian, Hlubocepy, Prague, Czech Republic, OMR VH 101a, ×2; *b,* ventral internal mold, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 35, ×2; *c,* latex cast of ventral interior, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 34, ×2; *d,* dorsal internal mold, Dvorce-Prokop Limestones, Pragian, Dvorce, Czech Republic, OMR VH 32, ×2 (Havlíček, 1967).——Fig. 155,*2e,f. R. elliptica* Havlíček, Daleje Shales, Emsian, Hlubocepy, Prague, Czech Republic; *e,* ventral internal mold, OMR VH 381c, ×2; *f,* dorsal internal mold, OMR VH 381a, ×2 (Havlíček, 1967).——Fig. 155,*2g,h. R. shidianensis* (Jahnke & Shi), Xiangyangsi Formation, Pragian, Dazhaimen, Yunnan, China; *g,* holotype, ventral internal mold, CIGMR 919-68, ×2; *h,* dorsal internal mold, CIGMR 919-107, ×2 (Jahnke & Shi, 1989).

Scamnomena Bassett, 1977, p. 134 [**Strophomena rugata* Lindström, 1861, p. 371; OD]. Small, with geniculation weak or absent; prominent apical foramen; radial ornament absent or very weak; concentric rugae variably developed or absent; large pseudodeltidium; small chilidium; teeth relatively large; low median ventral ridge; cardinal process lobes stout, divergent; socket ridges widely divergent. *Silurian (Wenlock):* Europe.——Fig. 155,*4a–d. **S. rugata* (Lindström), upper Visby Beds,

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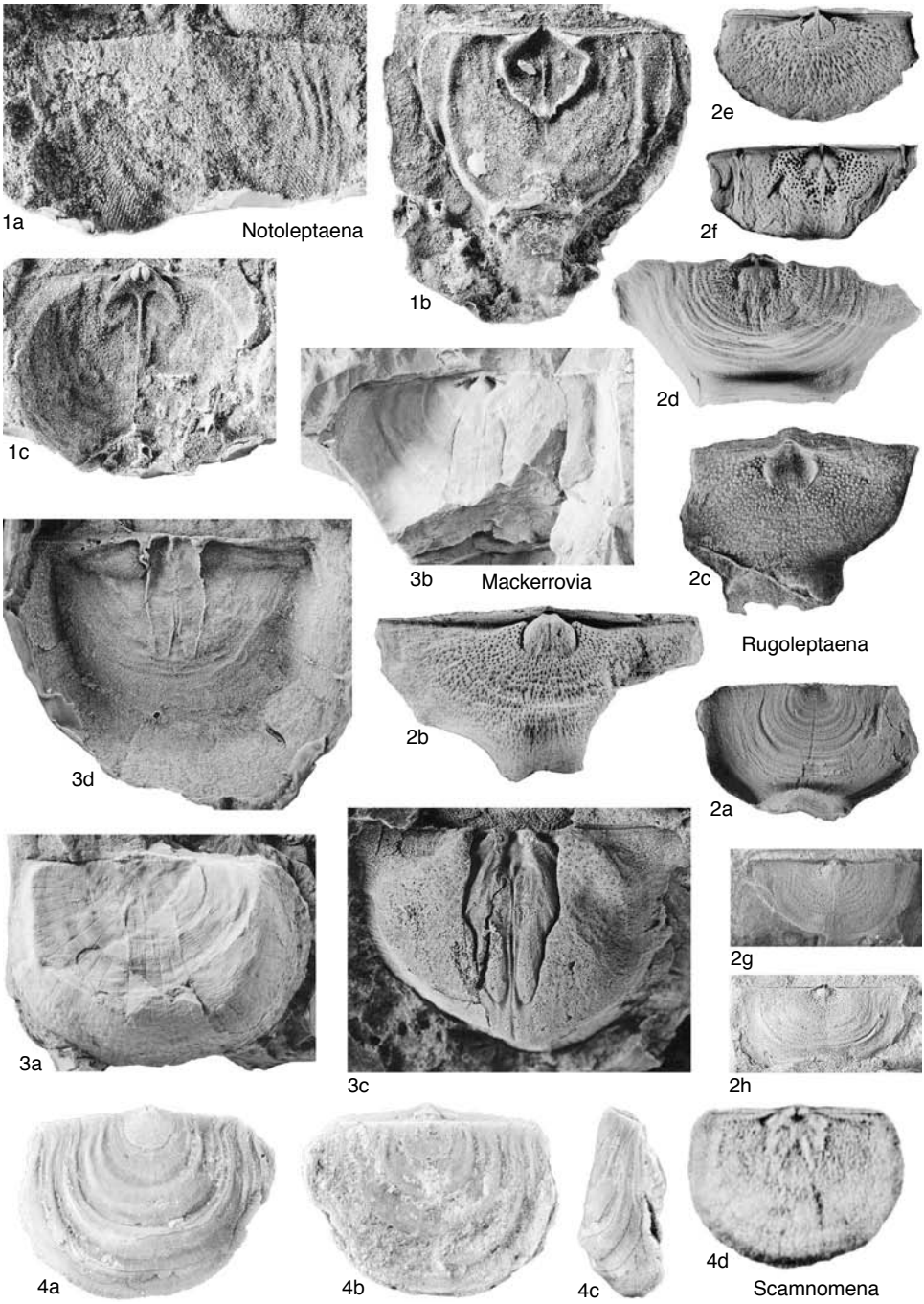

FIG. 155. Rafinesquinidae (p. 250–252).

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Sheinwoodian, Visby, Gotland, Sweden; *a–c,* ventral, dorsal, side views of conjoined valves, BMNH B13498, ×4 (new); *d,* dorsal interior, RMS Br 102333, ×4 (Bassett, 1977).

?Tchadania Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 85 [**T. insignis;* OD]. Profile convexoconcave; ornament multicostellate; pseudodeltidium, chilidium small; with dental plates, curved muscle-bounding ridges laterally, but poorly impressed ventral muscle field open anteriorly; short, variably developed ventral median ridge; cardinal process lobes small, position obscure (and thus may be glyptomenid rather than rafinesquinid); poorly impressed dorsal muscle field; no dorsal median septum or side septa. *Silurian (Ludlow):* Russia.——Fig. 154,*3a–d. *T. insignis,* Pichishuysk Formation, Ludlow, Pichi-Shuy, Tuva, Russia; *a,* dorsal external mold, IGiG 35/6884, ×2; *b,* holotype, ventral internal mold, IGiG 34/6884, ×1.5; *c,* holotype, ventral internal mold, IGiG 34a/6884, ×1.5; *d,* dorsal internal mold, IGiG 37/6884, ×2 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Family GLYPTOMENIDAE Williams, 1965

[*nom. transl.* Rong & Cocks, 1994, p. 664, *ex* Glyptomeninae Williams, 1965d, p. 388]

Outline usually transverse; small cardinal process lobes at or largely posterior to hinge line; socket ridges fused directly onto lateral bases of cardinal process lobes; notothyrial platform usually absent; concave area variably occurs immediately anterior to cardinal process lobes. *Ordovician (Llanvirn)–Silurian (Llandovery).*

Subfamily GLYPTOMENINAE Williams, 1965

[Glyptomeninae Williams 1965d, p. 388]

Lacking side septa; lacking dorsal median septum. *Ordovician (Llanvirn)–Silurian (Llandovery).*

Glyptomena Cooper, 1956, p. 881 [**G. sculpturata;* OD]. Profile gently concavoconvex; ornament unequally parvicostellate; small pseudodeltidium; short dental plates; poorly defined small subcircular ventral muscle field open anteriorly; widely divergent, prominent socket ridges; notothyrial platform weak; dorsal muscle field poorly impressed, with usually absent but sometimes sporadic, faint transmuscle septa; faint dorsal central median septum variably developed. *Ordovician (Llandeilo–Caradoc):* North America, Scotland, Kazakhstan, China.——Fig. 156,*3a–c. *G. sculpturata,* Chatham Hill Formation, Llandeilo, Sharon Springs, Burkes Garden Quadrangle, Virginia; *a,b,* exterior, interior views of ventral valve, USNM 117856a, ×3; *c,* dorsal interior, USNM 117856b, ×3 (Cooper, 1956).

Bystromena Williams, 1974, p. 146 [**B. perplexa;* OD]. Small, concavoconvex profile; ornament of variably developed, sometimes unequal parvicostellae; large protegulum, foramen truncating ventral beak; large arched chilidium; small pseudodeltidium; short divergent dental plates; ventral muscle field poorly impressed, open anteriorly; delicate cardinalia; short, very divergent socket ridges; poorly impressed dorsal muscle field with short faint transmuscle septa; thin dorsal central median septum present in some specimens, absent in others. *Ordovician (Caradoc):* England.——Fig. 156,*5a–c. *B. perplexa,* Spy Wood Grit, Costonian, Shelve, Shropshire, England; *a,b,* dorsal external, internal molds, BMNH BB 35367, ×5; *c,* holotype, ventral internal mold, BMNH BB 35363, ×3 (new).

?Hesperinia Cooper, 1956, p. 822 [**H. kirki;* OD]. Plano- to slightly concavoconvex outline; parvicostellate ornament; substantial pseudodeltidium; small chilidium; oblique dental plates present; ventral muscle field unknown; cardinal process obscure, thus familial position uncertain; very divergent socket plates curving laterally to run parallel to hinge line. Irregular notothyrial platform developed; hint of valve thickening on platform, but no dorsal septa clearly developed; dorsal subperipheral rim present. *Ordovician (Llanvirn–Llandeilo):* North America.——Fig. 156,*2a,b. *H. kirki,* Tank Hill Formation, Llanvirn–Llandeilo, Monument Canyon, Nevada; *a,* holotype, dorsal exterior of conjoined valves, USNM 117626a, ×3; *b,* dorsal interior, USNM 117627a, ×3 (Cooper, 1956).

Linostrophomena Rong, Xu, & Yang, 1974, p. 203 [**L. convexa;* OD]. Ventral valve convex profile, dorsal valve initially convex, then concave anterolaterally; parvicostellate ornament; small pseudodeltidium; vestigal chilidium; teeth strong; true dental plates absent, well-defined elevated ventral muscle field with curved bounding ridges; cardinal process lobes separate, fused to widely divergent but short curved socket ridges; two pairs of adductor scars differentiated in relatively small dorsal muscle field. *Silurian (Telychian):* China.——Fig. 157,*1a–c. *L. convexa,* upper Xiushan Formation, upper Telychian, Rongxi, Xiushan County, Sichuan Province; *a,b,* latex casts of ventral internal molds, NIGP 22344-5, ×2, *c,* holotype, latex cast of dorsal internal mold, NIGP 22347, ×1.5 (new).

?Mjoesina Spjeldnaes, 1957, p. 137 [**Rafinesquina mjoesensis* Holtedahl, 1916, p. 19; OD]. Profile concavoconvex; ornament unequally parvicostellate; strong but short dental plates extending into lateral curved muscle-bounding ridges; dorsal valve interior, hence familial assignment unknown. [Types untraced in PMO; Spjeldnaes figures too poor to

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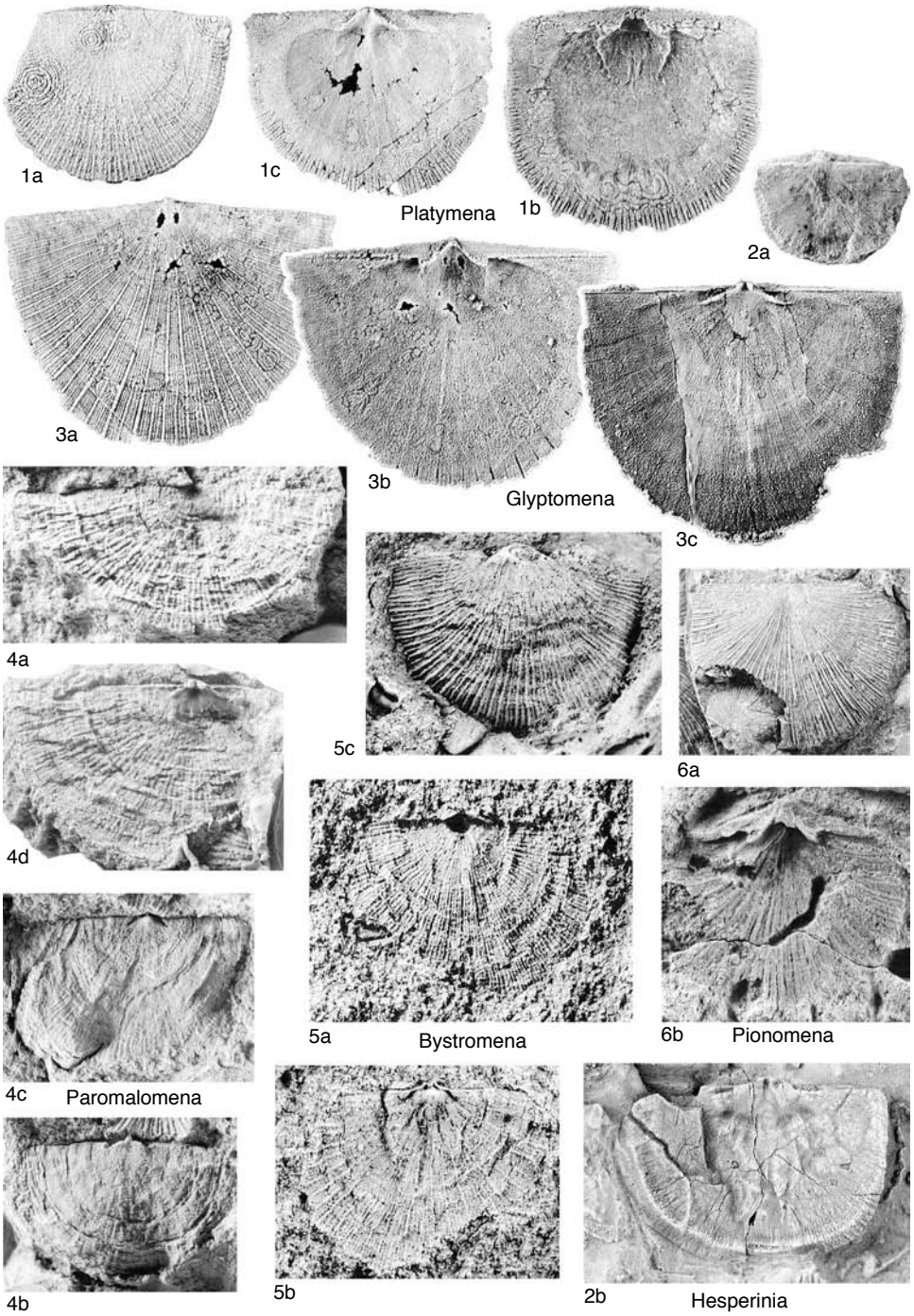

FIG. 156. Glyptomenidae (p. 252–255).

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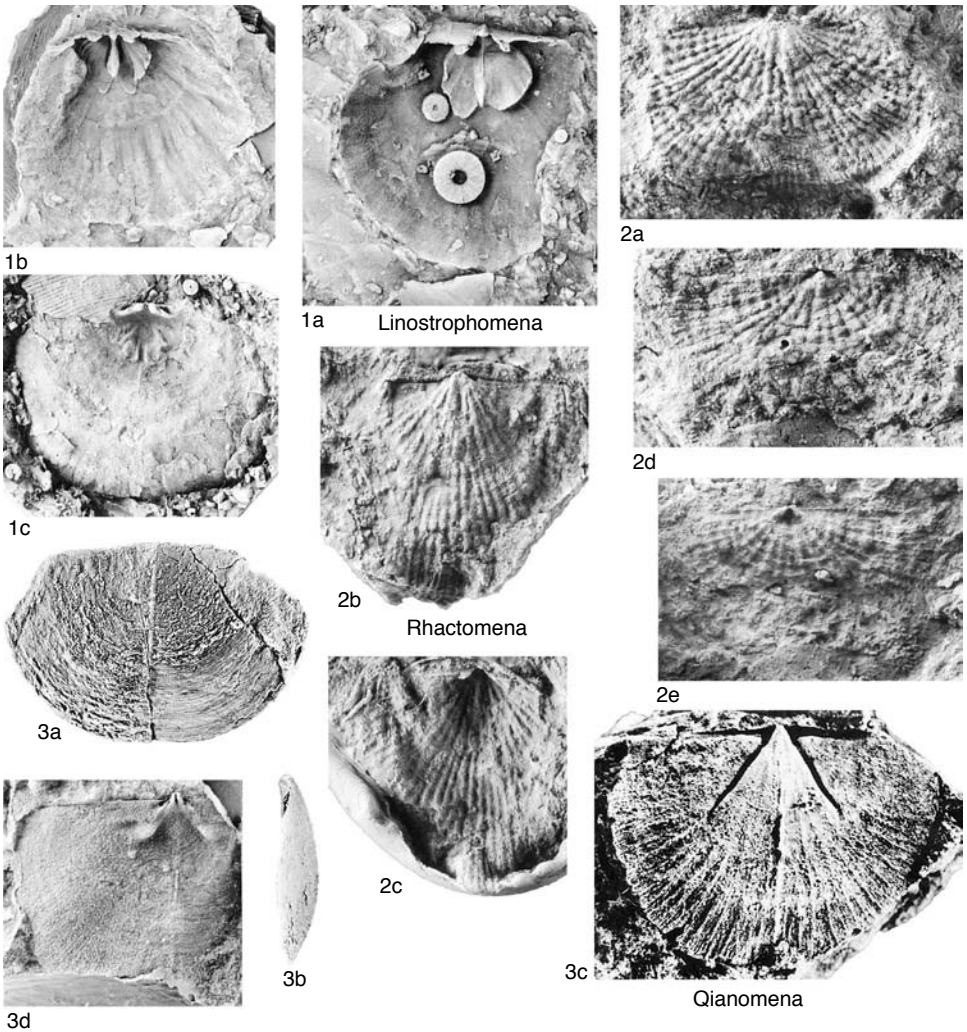

FIG. 157. Glyptomenidae (p. 252–256).

illustrate; could be *nomen dubium.*] *Ordovician (Caradoc):* Baltic, Upper Mjøsa Limestone, upper Caradoc, Helgøya, Hamar-Nes district, Norway.

Paromalomena RONG, 1984, p. 150 [**Platymena polonica* TEMPLE, 1965, p. 407; OD]. Relatively wide outline; planoconvex profile, with anterior fold, sulcus; finely costellate ornament; small pseudodeltidium; large chilidium; short, widely divergent dental plates; poorly impressed small ventral muscle field; small, short but widely divergent socket ridges; small, poorly impressed dorsal muscle field with no septa, although pair of short transmuscle ridges sometimes present. *Ordovician (Ashgill):* cosmopolitan.——FIG. 156,*4a–d.* **P. polonica* (TEMPLE), Dalmanitina Beds, Ashgill, Stawy, near Kagow, Holy Cross Mountains, Poland; *a,* ventral external mold, BMNH BB 29216, ×3; *b,* ventral internal mold, BMNH BB 30010, ×3; *c,* holotype, dorsal internal mold, BMNH BB 30009, ×3; *d,* latex cast of dorsal internal mold, BMNH BB 29216, ×3 (new).

?Pionomena COOPER, 1956, p. 901 [**P. neumani;* OD]. Similar to *Glyptomena,* but gently biconvex, with shorter, more obsolescent dental plates; small pseudodeltidium, larger chilidium; dorsal interior, hence family assignment, poorly known. *Ordovician (Llandeilo–Caradoc):* North America, Scotland. ——FIG. 156,*6a,b.* **P. neumani,* New Market Formation, Llandeilo–Caradoc, Williamsport, Maryland; *a,* dorsal exterior, USNM 117756c, ×2; *b,*

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ventral interior, USNM 117755, ×3 (Cooper, 1956).

Platymena Cooper, 1956, p. 879 [**P. plana;* OD]. Planoconvex to slightly concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium, chilidium small; stout teeth leading anteriorly to thin dental plates flaring laterally, coalescing with curved muscle-bounding ridges directed inward, merging anteriorly with valve floor; short, stout socket ridges merging with prominent thick but short notothyrial platform; dorsal muscle field poorly impressed with no septa; faint subperipheral ventral, dorsal rims poorly developed in some adults. *Ordovician (Caradoc–lower Ashgill):* North America, Kazakhstan.——Fig. 156,*1a–c. *P. plana,* Arline Formation, Caradoc, Friendsville, Tennessee; *a,* dorsal exterior, USNM 117759c, ×2; *b,* ventral interior, USNM 117759a, ×2; *c,* dorsal interior, USNM 117759e, ×2 (Cooper, 1956).

Pomeromena Mitchell, 1977, p. 112 [**P. transversa;* OD]. Small with transverse outline, concavoconvex profile; pronounced ventral sulcus, smaller dorsal fold; faint parvicostellate ornament; small pseudodeltidium; larger chilidium; small ventral process; no dental plates; faint muscle-bounding ridges defining small bilobed ventral muscle field; widely divergent socket ridges, weak notothyrial platform; dorsal muscle field poorly impressed; no dorsal median septum or side septa. *Ordovician (Ashgill):* Ireland.——Fig. 158,*2a–e. *P. transversa,* Killey Bridge Formation, Ashgill, Killey Bridge, Pomeroy, County Tyrone, Northern Ireland; *a–c,* holotype, latex cast of ventral external mold, ventral internal mold, latex cast, BGS NIG 887, ×2.5; *d,* latex of ventral internal mold, BGS GU 1041, ×2.5; *e,* dorsal internal mold, BGS GU 1093, ×3 (new).

?Proboscisambon Havlíček & Mergl, 1982, p. 44 [**Strophomena quaesita* Barrande, 1879, p. 101; OD]. Transverse outline, biplanar to very gently concavoconvex profile; very faint parvicostellate ornament, with accentuated median costella; small pseudodeltidium, chilidium; very short, thin widely divergent dental plates; poorly impressed muscle fields in both valves; cardinal process lobes delicate, widely separated, on hinge line; socket ridges not visible. *Ordovician (Ashgill):* Europe.——Fig. 158,*1a,b. *P. quaesita* (Barrande), Králuv Dvur Formation, Ashgill, Jezerka, Bohemia, Czech Republic; *a,* ventral internal mold, MM 039, ×6; *b,* dorsal internal mold, MM 041, ×6 (Mergl, new).

Qianomena Rong & Yang, 1981, p. 173 [**Q. unicosta;* OD]. Profile moderately concavoconvex; radial ornament absent or very faint apart from single prominent central costa; no true dental plates but very prominent, straight ventral muscle-bounding ridges posterolaterally to ventral muscle field, open anteriorly; cardinal process lobes projected posteriorly; socket ridges short; dorsal muscle field poorly impressed. *Silurian (Llandovery):* China.——Fig. 157,*3a–d. *Q. unicosta,* lower Xiangshuyuan Formation, upper Rhuddanian–

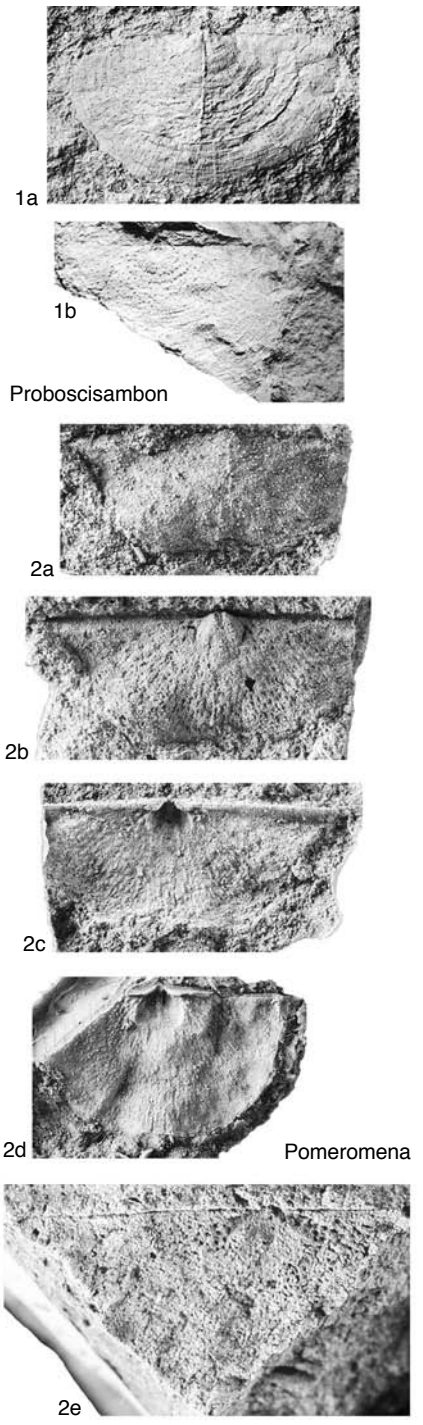

Fig. 158. Glyptomenidae (p. 255).

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lower Aeronian; *a,b,* holotype, ventral, lateral views of conjoined valves, Yingwuxi, Sinan County, NIGP 43873, ×2; *c,* ventral internal mold, Hongyan reservoir, Sinan County, northeastern Guizhou Province, China, NIGP 43870, ×2; *d,* latex cast of dorsal internal mold, Hongyan Reservoir, Sinan County, northeastern Guizhou Province, China, NIGP 43868, ×3 (new).

Rhactomena Mitchell, 1977, p. 111 [**R. splendens;* OD]. Planoconvex profile with ventral sulcus, weaker dorsal fold; distinctive ornament of relatively strong costae forming small nodes where strong growth lines cross them; weak rugae; small convex chilidium with median groove; small teeth, no dental plates; both muscle fields poorly impressed; short divergent socket ridges; no dorsal median septum or side septa. *Ordovician (Ashgill):* Ireland.——Fig. 157,*2a–e. *R. splendens,* Killey Bridge Formation, Ashgill, Killey Bridge, Pomeroy, County Tyrone, Northern Ireland; *a,* dorsal exterior, BGS GU 1076, ×6; *b,c,* internal mold, latex of ventral interior, BGS GU 1071, ×6; *d,e,* internal mold, latex of dorsal interior, BGS GU 1070, ×6 (new).

Subfamily TERATELASMINAE Pope, 1976

[*nom. transl.* Rong & Cocks, 1994, p. 664, *ex* tribe Teratelasmini Pope, 1976, p. 153]

Similar to the Glyptomeninae but differs in possessing muscle-bounding ridges, or united transmuscle ridges and side septa; high dorsal median septum. *Ordovician (Llandeilo–Ashgill).*

Teratelasma Cooper, 1956, p. 823 [**T. neumani;* OD]. Profile planoconvex to gently biconvex, with dorsal median sulcus; unequally parvicostellate ornament; short flaring dental plates posterolaterally bounding short, bilobed ventral muscle field, poorly impressed; short curved socket ridges; dorsal muscle field poorly impressed but with posterolateral muscle-bounding ridges; prominent but short elevated dorsal side septa, with lateral protrusions in older specimens; very large elevated dorsal median septum extending for four-fifths of valve length. *Ordovician (Llandeilo–Caradoc):* North America.——Fig. 159,*1a–d. *T. neumani,* Sevier Formation, Llandeilo–Caradoc, Old Kagley Church, Binfield Quadrangle, Tennessee; *a,* plasticine cast of dorsal exterior, USNM 117938a, ×3; *b,* plasticine cast of ventral interior, USNM 117938l, ×3; *c,d,* dorsal internal mold, latex cast, USNM 117938m, ×4 (Cooper, 1956).

Tashanomena Zhan & Rong, 1994, p. 418 [**T. variabilis;* OD]. Concavo- to planoconvex profile; thin dental plates merging anteriorly into curved bounding ridges enclosing small ventral muscle field except anteriorly; small cardinal process lobes united with short, thin socket ridges; dorsal muscle field with posterolateral oblique curved bounding ridges, elevated anteriorly; elongated dorsal side septa, prominent median septum in dorsal valve center only. *Ordovician (Ashgill):* China.——Fig. 159,*2a–d. *T. variabilis,* Xiazhen Formation, middle Ashgill, Tashan, Yushan, Jiangxi Province, China; *a,* dorsal external mold, NIGP 121549, ×10; *b,* ventral internal mold, NIGP 121542, ×10; *c,* holotype, dorsal internal mold, NIGP 121550, ×10; *d,* holotype, dorsal internal mold, NIGP 121553, ×10 (Zhan & Rong, 1994).

Family FOLIOMENIDAE Williams, 1965

[Foliomenidae Williams, 1965d, p. 391]

Without radial ornament, lacking dental plates, with small, bilobed ventral muscle field; cardinal process as in Glyptomenidae, but with pair of close, narrowly divergent dorsal valve side septa. *Ordovician (Caradoc–Ashgill).*

Foliomena Havlíček, 1952, p. 413 [**Strophomena folium* Barrande, 1879, pl. 55; OD] [=*Jielingia* Zeng, 1987, p. 235 (type, *J. jielingensis;* OD)]. Transverse outline, biplanar to very gently concavoconvex profile; pedicle sheath often prominent; small interarea with very small pseudodeltidium; ventral muscle field bilobed, weakly impressed; short myophragm; bladelike socket ridges broadly divergent to become subparallel to hinge line. *Ordovician (Caradoc–Ashgill):* cosmopolitan.——Fig. 160,*1a–c. *F. folium* (Barrande), Králuv Dvur Formation, Ashgill, Králuv Dvur, Czech Republic; *a,* ventral external mold, NM CD1566, ×2; *b,* lectotype, ventral internal mold, NM CD1565a, ×2.5; *c,* dorsal internal mold, NM CD1565b, ×2 (Havlíček, 1967).——Fig. 160,*1d. F. jielingensis* (Zeng), Miaopo Formation, lower Caradoc, Jieling, Yichang County, Hubei Province, China, dorsal internal mold, YIGM IV45822, ×5 (Zeng, new).

Family CHRISTIANIIDAE Williams, 1953

[Christianiidae Williams, 1953b, p. 9]

Low cardinal process with lobes very close together, fused at their bases; socket plates often elevated anteriorly from valve floor; two pairs of distinctive large dorsal side septa. *Ordovician (Llanvirn–Ashgill).*

Christiania Hall & Clarke, 1892, p. 298 [**Leptaena subquadrata* Hall, 1883, pl. 46, fig. 32, 33; OD] [=*Christianella* Liang in Liu, Xu, & Liang, 1983, p. 277 (type, *C. zhitangensis;* OD)]. Outline usually elongate in adults; concavoconvex profile with

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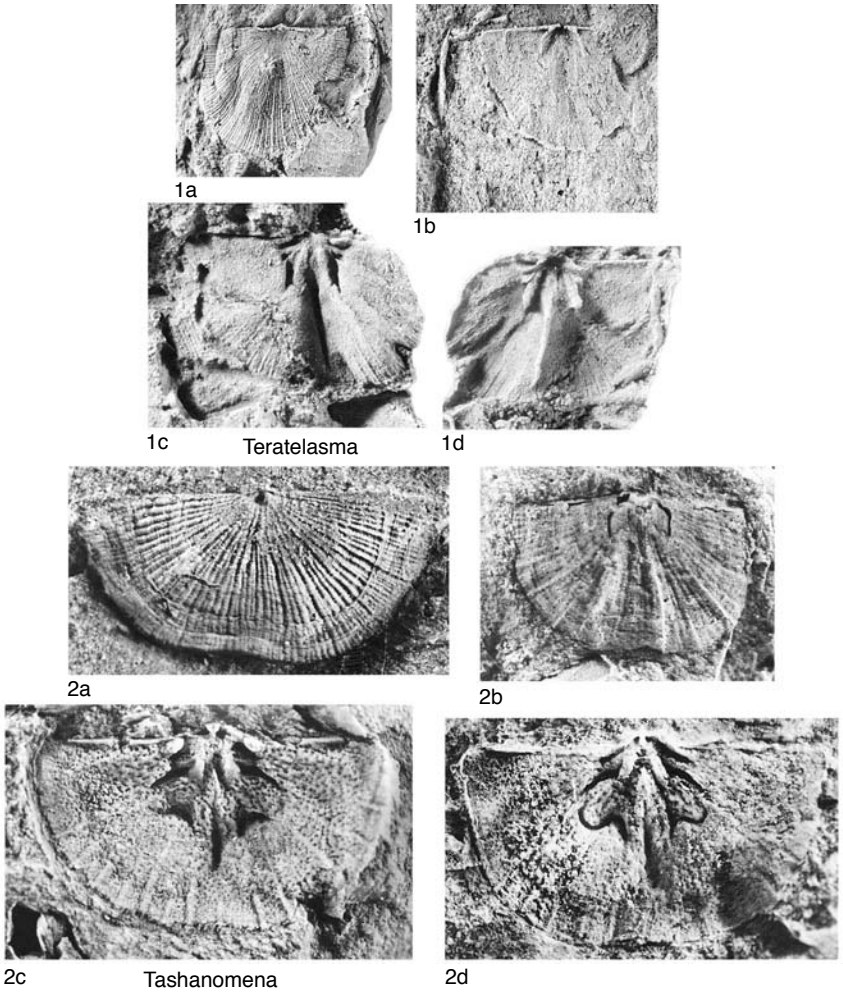

FIG. 159. Glyptomenidae (p. 256).

strong convexity, especially near umbo; apical foramen persistent throughout ontogeny; no radial ornament; largely open delthyrium, but with small pseudodeltidium, chilidium; teeth simple, supported by receding dental plates; well-impressed bilobed ventral muscle field bounded laterally by weak low ridges; anterior part of muscle field continuous with vascula media leading to digitate mantle canals; small transverse plates sometimes developed between two prominent pairs of dorsal valve side septa. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.——FIG. 160,*2a–d. *C. subquadrata* (HALL), Caradoc; *a,b,* dorsal, lateral views of conjoined valves, Lenoir Formation, Friendsville, Tennessee, BMNH B 78727, ×3; *c,d,* dorsal, posterior views of dorsal interior, Athens Formation, Perry County, Tennessee, AMNH 37883, ×3 (new).——FIG. 160,*2e–g. C. zhitangensis* (LIANG), Huangnikang Formation, lower Ashgill, Zhitang, Quxian County, Zhejiang Province, eastern China; *e,* dorsal external mold, HIGS 2703, ×3; *f,* holotype, ventral internal mold, HIGS 2701, ×3; *g,* dorsal internal mold, HIGS 2702, ×3 (Liu, Xu, & Liang, 1983).

Nubialba NEUMAN, 1994, p. 1231 [**N. forbesi;* OD]. Similar to *Christiania,* but with ornament of fine, widely spaced costae, one medially located. *Ordovician (Ashgill):* North America.——FIG. 160,*3a–c. *N. forbesi,* Pyle Mountain Argillite, Ashgill, Aroostook County, Maine, USA; *a,* dorsal external mold, USNM 465231, ×5; *b,* ventral internal mold, USNM 465242, ×5; *c,* holotype, dorsal internal mold, USNM 455231, ×5 (Neuman, 1994).

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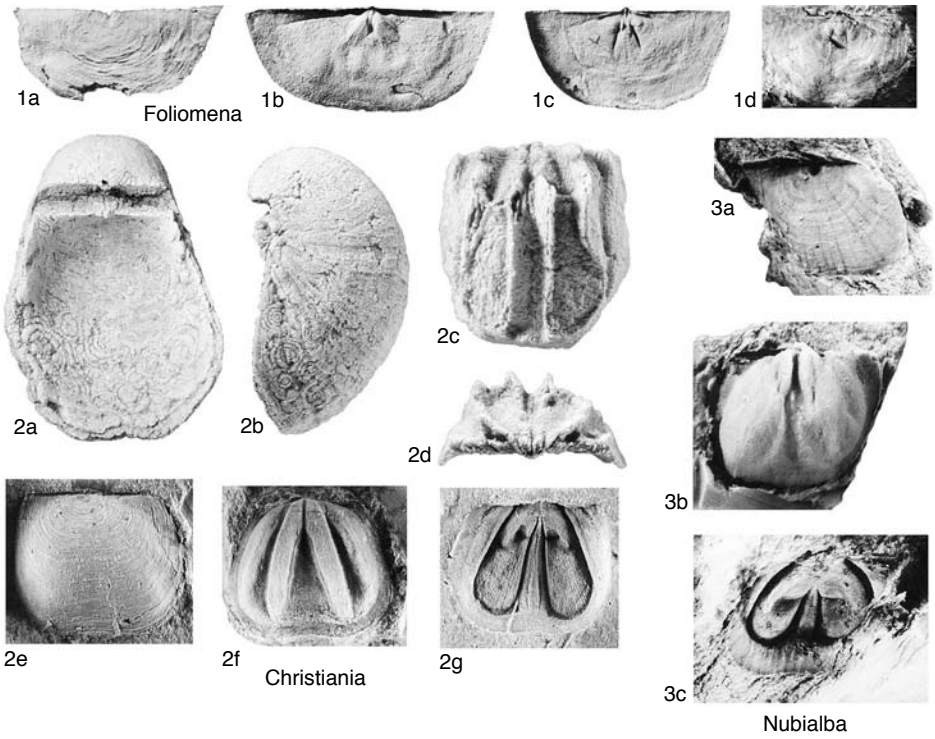

FIG. 160. Foliomenidae and Christianiidae (p. 256–257).

Family LEPTAENOIDEIDAE Williams, 1953

[*nom. transl.* RONG & COCKS, 1994, p. 665, *ex* Leptaenoideinae WILLIAMS, 1953b, p. 8] [=Liljevallinae WILLIAMS, 1953b, p. 9]

Bizarre forms with ventral valve attached to substrate by cementation; dorsal interiors only known in *Leptaenisca,* which has strong, ventrally directed cardinal process lobes. *Silurian (upper Llandovery)–Devonian (Emsian).*

Leptaenoidea HEDSTROM, 1917, p. 2 [**L. silurica;* OD]. Ventral valve cemented over complete disc prior to geniculation; ornament finely costellate, rugose; ventral muscle field short, broad with strong elevated lateral bounding ridges; myophragm present; dorsal valve unknown. *Silurian (Wenlock):* Baltic.——FIG. 161,*1. *L. silurica,* Halla Beds, Wenlock, Horsne Canal, Gotland, Sweden; lectotype, ventral interior, Swedish Geological Survey, ×4 (Bassett & Cocks, 1974).

Leptaenisca BEECHER, 1890a, p. 239 [**Leptaena concava* HALL, 1857, p. 47; OD]. Ventral valve attached in umbonal area in younger growth stages only; profile concavoconvex with unequally parvicostellate ornament; elongate bilobed ventral muscle field bounded laterally by strong plates; ventral median septum; strong cardinal process lobes posteroventrally directed; thin low short socket ridges present close to cardinal process; distinctive planospiral brachial ridges originating anterolateral to cardinalia. *Devonian (Pragian–Emsian):* North America.——FIG. 161,*2a–e. *L. concava* (HALL), lower Helderburg Group, Lower Devonian, Albany County, New York; *a–c,* ventral, lateral, internal views of ventral valve, YPM 28116, ×2; *d,* dorsal internal mold, YPM 24859, ×2; *e,* dorsal interior showing cardinalia, YPM 28115, ×2 (Bassett, new).

Leptaenomendax GARCÍA-ALCALDE in GARCÍA-ALCALDE & MARTÍNEZ-CHACÓN, 1978, p. 255 [**L. chaconae;* OD]. Asymmetrically cemented by ventral umbo, otherwise regular outline; ornament of costellae, rugae; elevated ventral muscle field bounded anteriorly, laterally by united bounding ridges; cardinal process lobes high, delicate, directed posteroventrally; low socket ridges straight, narrow; dorsal muscle field elevated; dorsal subperipheral rim. *Devonian (Emsian):* Europe.——FIG. 161,*3a–d. *L. chaconae,* Grupo la Vid, upper Emsian, Colle Church, Sabero, Spain; *a,b,* holotype, conjoined valves, dorsal, ventral views, with ventral valve cemented to bryozoan, DPO 431, ×2; *c,* ventral interior, DPO 433, ×2; *d,* dorsal interior, DPO

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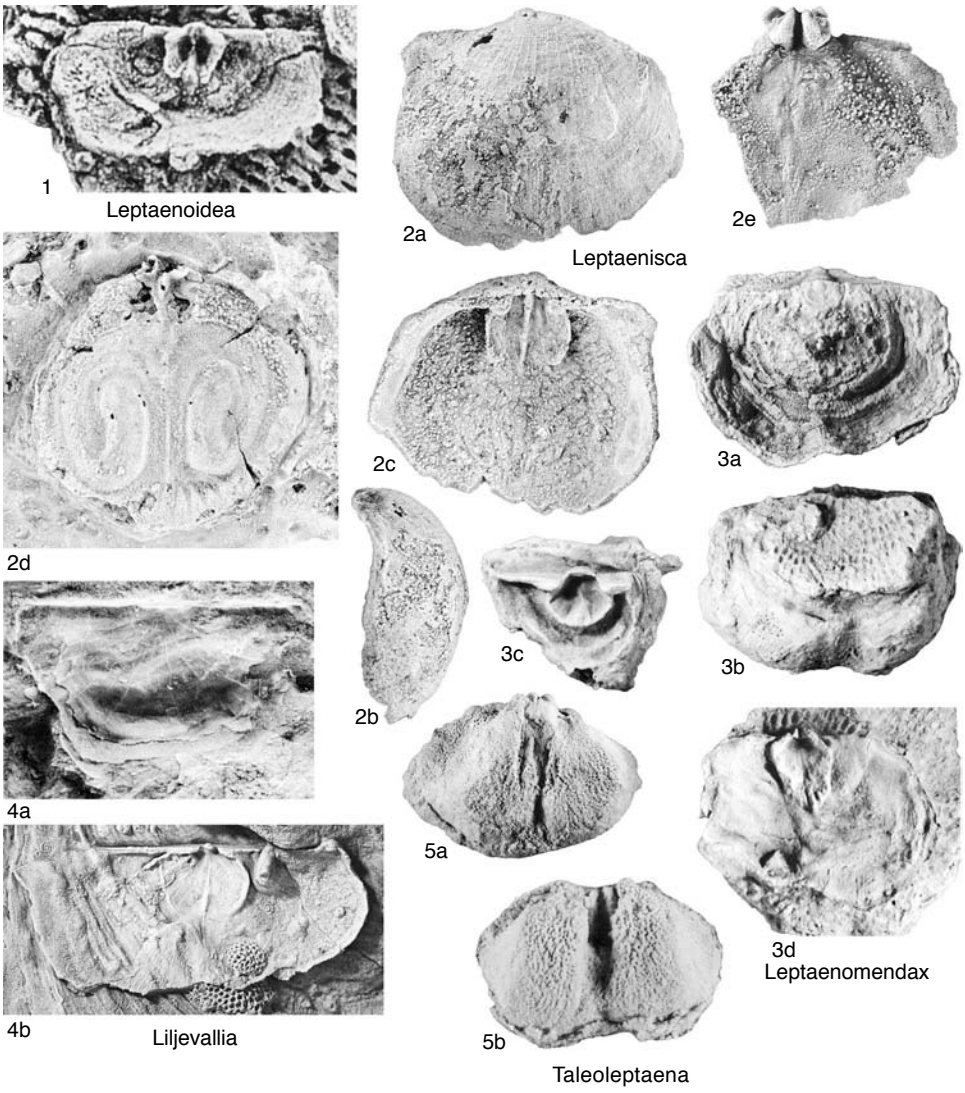

FIG. 161. Leptaenoideidae (p. 258–259).

6259, ×2 (García-Alcalde & Martínez-Chacón, 1978).

Liljevallia HEDSTROM, 1917, p. 9 [**L. gotlandica;* OD]. Irregular profile, outline with cementation to match substrate, but usually transverse; unequally parvicostellate ornament; irregular oblique denticles present on dorsal facets of teeth; dental plates continuous with curved high bounding ridges around ventral muscle field; myophragm variably developed; dorsal interior unknown. *Silurian (upper Llandovery–lower Wenlock):* Baltic.——FIG. 161,*4a,b. *L. gotlandica,* upper Visby Beds, lower Wenlock; *a,* dorsal exterior, Stenkwrkehuks Fyr, ×2 (new); *b,* lectotype, ventral interior encrusted on stromatoporoid, Nygardsback, Gotland, Sweden, Swedish Geological Survey, ×2 (Bassett & Cocks, 1974).

?Taleoleptaena HAVLÍČEK, 1967, p. 121 [**T. taleolata;* OD]. Profile strongly convex but irregular; attachment scar not known; thick shelled, lacking ornament; dental plates parallel, close together; ventral median septum; dorsal valve unknown, thus familial position uncertain. *Devonian (Emsian):* Europe.——FIG. 161,*5a,b. *T. taleolata,* Zlichov Limestones, Emsian, Praha-Hlubocepy, Czech Republic; *a,* partly exfoliated ventral valve, OMR VH 497b, ×3; *b,* holotype, ventral internal mold, OMR VH 497e, ×5 (Havlíček, 1967).

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Family AMPHISTROPHIIDAE Harper, 1973

[*nom. transl.* Harper & Boucot, 1978, p. 154, *ex* Amphistrophiinae Harper, 1973, p. 36] [=Maoristrophiidae Ushatinskaya & Alekseeva, 1983, p. 37]

Hinge line denticulate; lacking dental plates; ventral valve muscle field semi-elliptical in outline, bounded laterally by curved muscle-bounding ridges (except *Eoamphistrophia*); variable cardinal process; dorsal muscle field bounded posterolaterally by low ridges extending anteriorly from socket ridges; no dorsal side septa. *Silurian (Telychian)–Devonian (Eifelian).*

Subfamily AMPHISTROPHIINAE Harper, 1973

[Amphistrophiinae Harper, 1973, p. 36]

Differs from Mesodouvillininae in having resupinate profile. *Silurian (Telychian)–Devonian (Emsian).*

Amphistrophia Hall & Clarke, 1892, p. 292 [**Strophomena striata* Hall, 1843a, p. 104; OD] [=*Strophonellites* Havlíček, 1967, p. 184 (type, *Leptaena patricia* Barrande, 1848, p. 245; OD)]. Resupinate, with curved to geniculate profile; ornament unequally parvicostellate to costellate; strong bounding ridges posterior, lateral to suboval ventral muscle field; weak ventral median septum; cardinal process lobes short, posteroventrally directed, situated on hinge line; weakly impressed dorsal muscle field. *Silurian (Telychian)–Devonian (Lochkovian).*

A. (Amphistrophia). Similar to *A. (Pembrostrophia)* but with unequally costellate to finely costellate ornament; similar to *A. (Amphistrophiella)* but with relatively gentle and evenly curved geniculation. *Silurian (Telychian–Ludfordian):* cosmopolitan.——Fig. 162,*1a–c. *A. (A.) striata* (Hall), Wenlock; *a,* syntype, dorsal exterior, Niagara Group, Lockport, New York, AMNH 31255, ×1.5; *b,* ventral interior, Waldron Shale, Waldron, Indiana, AMNH 40780, ×1.5; *c,* dorsal interior, Waldron Shale, Waldron, Indiana, AMNH 40779, ×1.5 (new).——Fig. 162,*1d–f. A. (A.) patricia* (Barrande), Motol Formation, Wenlock, Svaty Jan pod Skalou, Bohemia, Czech Republic; *d,* dorsal exterior mold, ×1.5; *e,* ventral internal mold, OMR VH 457b, ×2; *f,* dorsal internal mold, OMR VH 457a, ×1.5 (Havlíček, 1967).

A. (Amphistrophiella) Harper & Boucot, 1978, p. 157 [**Orthis funiculata* M'Coy, 1846, p. 30; OD] [=*Amphistrophiella (Amsdenostrophiella)* Harper & Boucot, 1978, p. 158 (type, *Strophonella prolongata* Foerste, 1909a, p. 85; OD)]. Similar to *A. (Amphistrophia)* but with more sharply geniculate profile. *Silurian (Telychian)–Devonian (Lochkovian):* cosmopolitan.——Fig. 162,*3a–e. *A. (A.) funiculata* (M'Coy), Much Wenlock Limestone Formation, Homerian, Dudley, western Midlands, England; *a–c,* exterior of conjoined valves, *a,* ventral view, *b,* oblique dorsal view, ×1.5, *c,* center of interarea, BMNH B 5692, ×8; *d,* ventral interior, BMNH BC 13419, ×2; *e,* dorsal interior, BMNH BC 13420, ×2 (new).

A. (Pembrostrophia) Bassett, 1971, p. 325 [**A. (P.) freshwaterensis;* OD]. Similar to *A. (Amphistrophia),* but with ornament stronger and more uniformly costellate. *Silurian (Wenlock):* Europe.——Fig. 162,*2a–e. *A. (P.) freshwaterensis,* Gray Sandstone Group, lower Wenlock, Freshwater East Bay, Dyfed, Wales; *a,* latex of ventral exterior; *b,c,* ventral internal mold, latex cast, BMNH BC 41356, ×1.5; *d,e,* dorsal internal mold, latex cast, BMNH BC 41362, ×1.5 (new).

Devonamphistrophia Harper & Boucot, 1978, p. 159 [**Strophodonta alveata* Hall, 1863a, p. 36; OD]. Gently resupinate profile; uniformly costellate ornament; cardinal process lobes strongly posteriorly directed; straight posterolateral bounding ridges to subtriangular, bilobed ventral muscle field; possible dorsal median septum; faint myophragm; dorsal muscle field weakly impressed. *Devonian (?Lochkovian, Pragian–Emsian):* North America.——Fig. 163,*1a–c. *D. alveata* (Hall), Schoharie Grit, Emsian, Clarkesville, Albany County, New York; *a,b,* ventral internal mold, latex cast, NYSM 2053, ×1.5; *c,* latex cast of dorsal interior, NYSM 2054, ×2 (new).

Eoamphistrophia Harper & Boucot, 1978, p. 154 [**Amphistrophia whittardi* Cocks, 1967, p. 261; OD]. Profile gently resupinate with anterior rounded geniculation; unequally parvicostellate ornament; weakly impressed muscle fields in both valves; no ventral valve muscle-bounding ridges; cardinal process ventrally directed, but short. *Silurian (Telychian):* Europe.——Fig. 163,*2a,b. *E. whittardi* (Cocks), Hughley Shale, Telychian, Domas, Shropshire; *a,* ventral internal mold, OUM C13514, ×2.5; *b,* dorsal internal mold, OUM C13536, ×2.5 (Cocks, 1967).

Subfamily MESODOUVILLININAE Harper & Boucot, 1978

[Mesodouvillininae Harper & Boucot, 1978, p. 124]

Similar to Amphistrophiinae, but concavoconvex profile. *Silurian (?Telychian, Sheinwoodian)–Devonian (Eifelian).*

Mesodouvillina Williams, 1950, p. 281 [**Strophe-odonta subinterstrialis seretensis* Kozłowski, 1929, p. 96; OD] [=*Mesodouviella* Harper & Boucot, 1978, p. 124 (type, *Mclearnites invasor* Johnson, 1970a,

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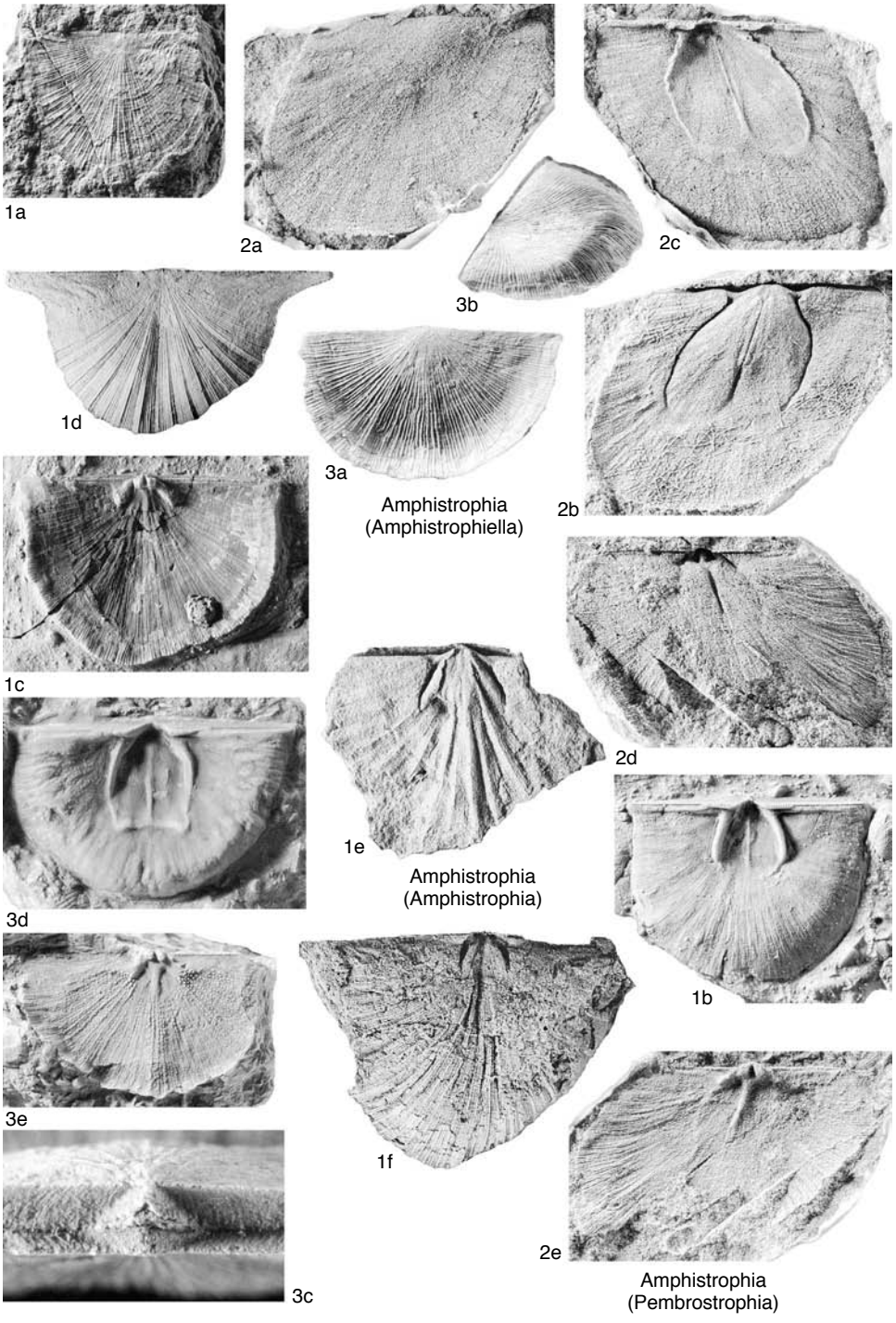

FIG. 162. Amphistrophiidae (p. 260).

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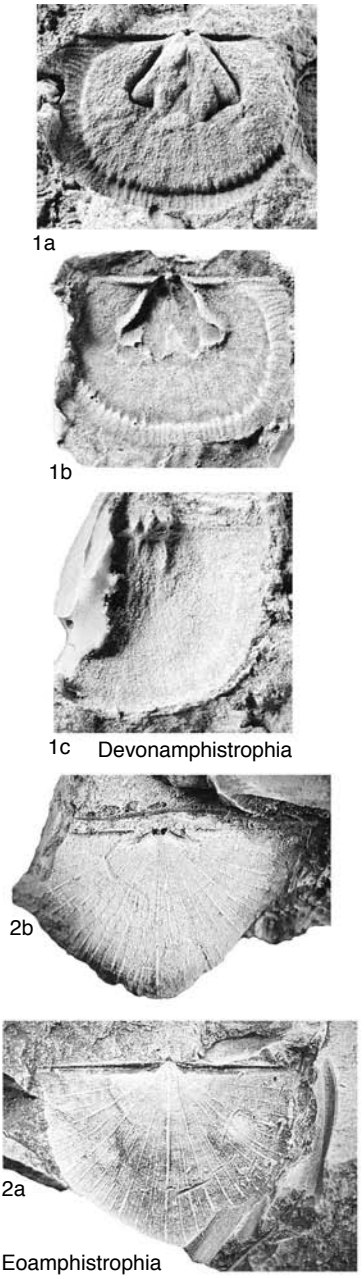

FIG. 163. Amphistrophiidae (p. 260).

p. 118; OD); ?*Planodouvillina* HARPER & BOUCOT, 1978, p. 145 (type, *P. cortezi;* OD; *Eurekaspirifer pinyonensis* Zone (Emsian), Cortez Mountains, Nevada)]. Strongly to gently concavoconvex profile; unequally parvicostellate ornament; small interarea with pseudodeltidium, small chilidium; denticles along half to two-thirds of hinge line; straight or slightly curved muscle-bounding ridges to subtriangular ventral muscle field, open anteriorly; cardinal process posteroventrally to posteriorly directed; short thin divergent socket plates; weak curved dorsal muscle-bounding ridges; dorsal side septa usually absent; dorsal subperipheral rim variably developed. *Silurian (Sheinwoodian)–Devonian (Eifelian):* cosmopolitan.——FIG. 164,*1a–d. *M. subinterstrialis seretensis* (KOZŁOWSKI), Bogdanovka Beds, Bogdanovka, Podolia, Ukraine; *a–c,* neotype, ventral, dorsal, lateral views of conjoined valves, CNIGR 33/11475, ×1.5; *d,* ventral interior, CNIGR 32/11475, ×1.5 (Bassett, new).——FIG. 164,*1e. M. s. subinterstrialis,* Mitkov Beds, Borshchov Stage, Lochkovian, Lanovtsy, Podolia, Ukraine; dorsal interior, CNIGR 30/11475, ×1.5 (Bassett, new).——FIG. 164,*1f–h. M. invasor* (JOHNSON), *Acrospirifer kobehana* Zone, Emsian, Sulphur Spring Range, Great Basin, Nevada; *f,g,* holotype, ventral exterior, interior, USNM 156938, ×1.5; *h,* dorsal interior, USNM 156941, ×1.5 (Johnson, new).

Desistrophia TALENT in GRATSIANOVA, SHISHKINA, & TALENT, 1988, p. 94 [**Maoristrophia papilio* STRUSZ, 1983, p. 165; OD]. Transverse outline; concavoconvex profile with large ventral fold, dorsal sulcus; similar to *Maoristrophia* but with parvicostellate ornament, narrower triangular ventral muscle field with shorter, smaller socket ridges which, with cardinal process lobes, situated on notothyrial platform; dorsal muscle-bounding ridges more sharply developed, pair of short transmuscle ridges present in gerontic specimens. *Silurian (Wenlock, ?Ludlow):* Australasia.——FIG. 165,*2a–c. *D. papilio* (STRUSZ), Canberra Formation, Wenlock, Canberra, Australian Capital Territory, Australia; *a,* latex cast of ventral exterior, CPC 21488, ×4; *b,* latex cast of ventral interior, CPC 21480, ×4; *c,* holotype, latex cast of dorsal interior, CPC 21485, ×4 (Strusz, new).

Eomaoristrophia USHATINSKAYA in USHATINSKAYA & ALEKSEEVA, 1983, p. 38 [**E. kobdensis;* OD]. Similar to *Maoristrophia* but with cardinal process on posterior part of notothyrial plate between two socket ridges, with no trace of dorsal transmuscle septa or subperipheral ridge. *Silurian (?Wenlock, Ludlow):* Mongolia.——FIG. 164,*3a,b. *E. kobdensis,* Wenlock–Ludlow, Buliantu-Gol River, western Mongolia; *a,* holotype, internal mold of ventral valve, PIN 3950/1, ×2; *b,* internal mold of dorsal valve, PIN 3950/3, ×1 (Ushatinskaya & Alekseeva, 1983).

Gladiostrophia HAVLÍČEK, 1967, p. 141 [**Leptaena verneuili* BARRANDE, 1848, p. 219; OD]. Large; strongly concavoconvex profile; strong, coarse, uniform costellate ornament; subtriangular ventral muscle field with strong straight bounding ridges posterolaterally only; erect cardinal process lobes directed ventroposteriorly; prominent curved dorsal muscle-bounding ridges posterolaterally; weak dorsal median septum. *Silurian (Ludlow)–Devonian*

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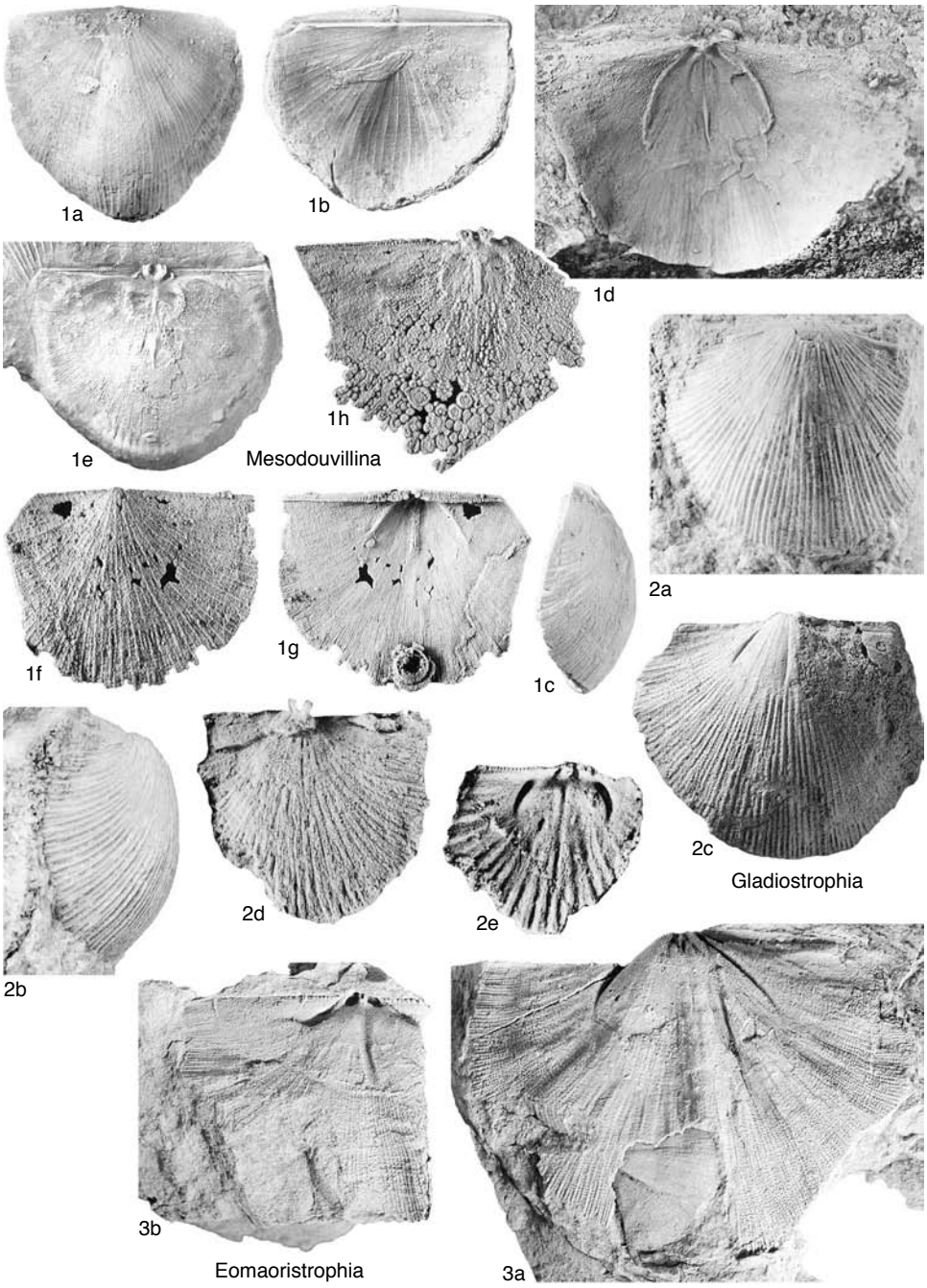

FIG. 164. Amphistrophiidae (p. 260–264).

(Emsian): Europe, Asia.——FIG. 164,*2a–e. *G. verneuili* (BARRANDE), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,b,* ventral, lateral views of ventral exterior, BMNH BB 54620, ×1 (new); *c,* ventral interior, OMR VH 411a, ×1; *d,* dorsal external mold, OMR VH 410a,

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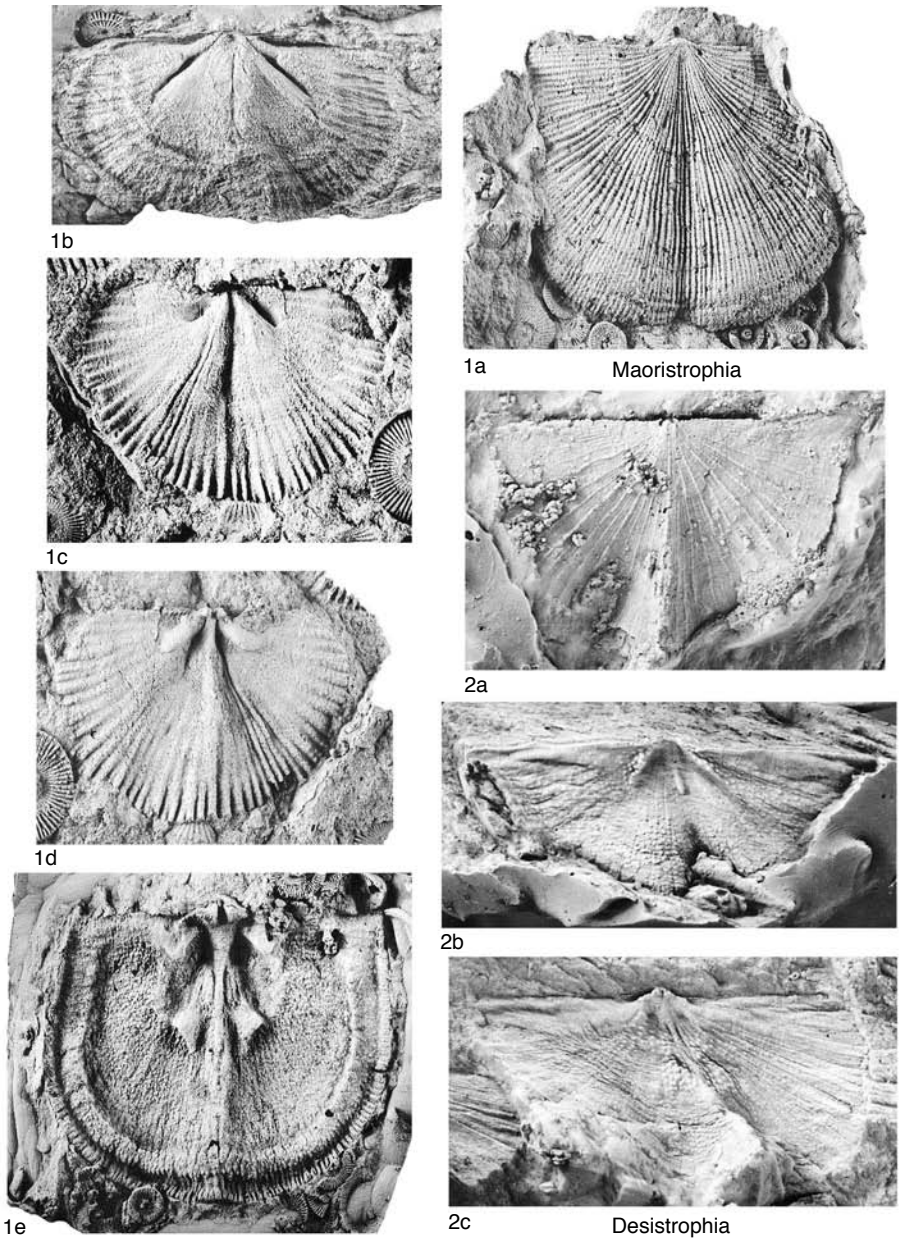

FIG. 165. Amphistrophiidae (p. 262–266).

×1.5; *e,* dorsal internal mold, OMR VH 410c, ×2 (Havlíček, 1967).

?Jakutostrophia MANANKOV, 1991, p. 65 [**J. undata;* OD]. Distinctive ornament of strong raised costellae with fine radial costellae, with rugae interrupted by primary costellae; interiors poorly known, thus familial position uncertain. *Devonian (Eifelian):* Asia.——FIG. 166,*4a,b.* **J. undata,* Middle Sakin Formation, Eifelian, River Khobochalo, eastern Yakutia, Russia; *a,* partly exfoliated

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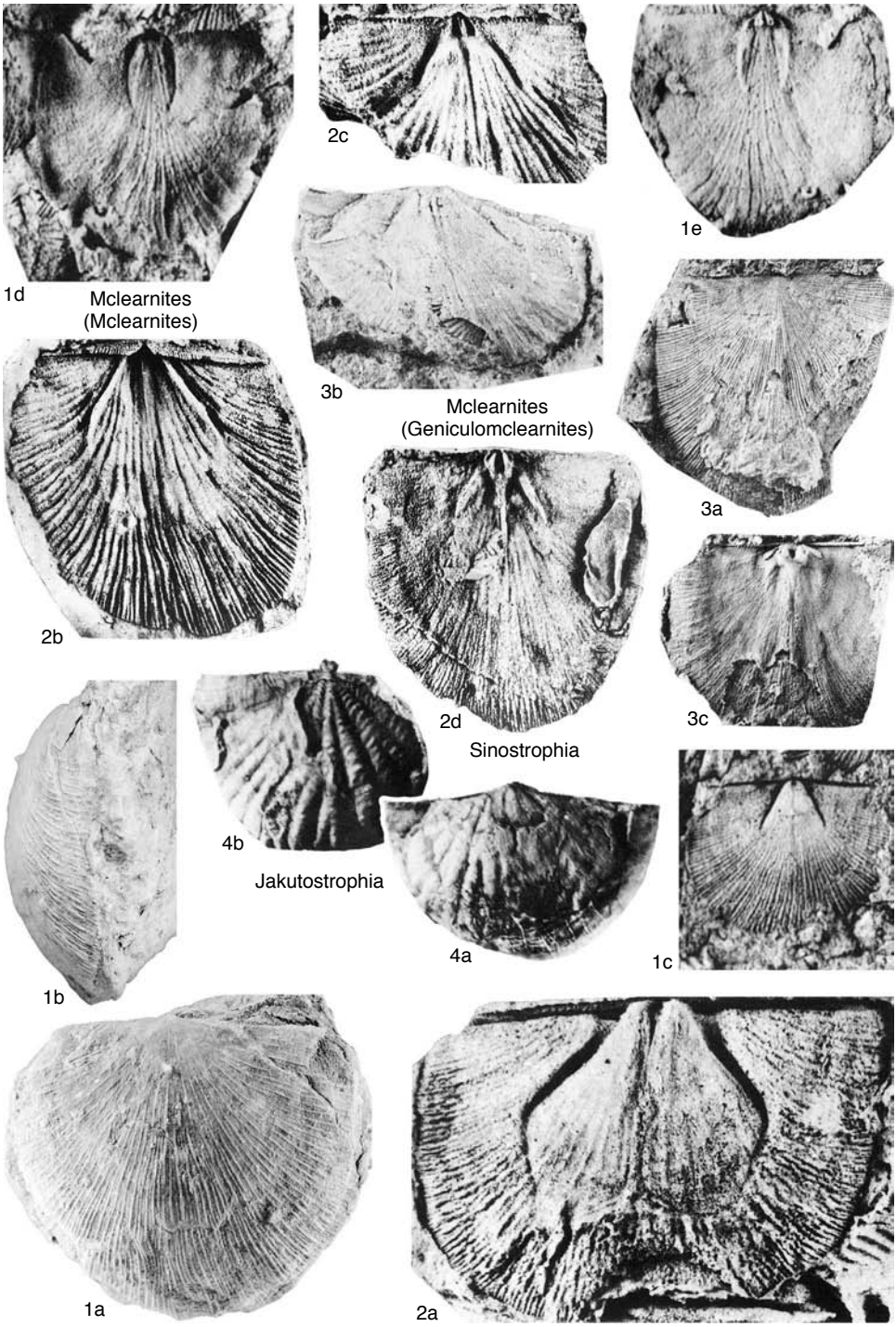

FIG. 166. Amphistrophiidae (p. 264–266).

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ventral valve, CNIGR 4114/634, ×1.5; *b,* holotype, partly exfoliated dorsal valve, CNIGR 4114/633, ×1 (Manankov, 1991).

Maoristrophia Allan, 1947, p. 440 [**M. neozelanica;* OD]. Semielliptical, planoconvex profile with ventral fold, dorsal sulcus; ornament costellate; denticles along less than half hinge line; triangular ventral muscle field bounded posterolaterally with largely straight ridges that curve around a short distance anteriorly; muscle field poorly impressed anteriorly; cardinal process on hinge line, strong, ventrally directed, joined to posterior end of median ridge, which extends for at least half valve length; strong socket ridges that curve, extending laterally for variable distance; dorsal transmuscle ridges, subperipheral ridge variably developed in both valves, more common in gerontic specimens. *Devonian (Emsian):* Australasia, Mongolia.——Fig. 165,*1a–e. *M. neozelanica,* Reefton Beds, Emsian, Lankey Creek, Reefton, New Zealand; *a,* latex cast of dorsal exterior, USNM 153136, ×1.5; *b,* internal mold of ventral valve, USNM 153137, ×1.25; *c,d,* internal mold of dorsal valve, latex cast, USNM 153138, ×2; *e,* latex cast of dorsal internal mold, USNM 153135, ×1.25 (Johnson, new).

Mclearnites Caster, 1945, p. 319, *nom. nov. pro Mclearnia* Caster, 1939, p. 28, *non* Crickmay, 1930 [**Brachyprion mertoni* McLearn, 1924, p. 61; OD] [=*Mclearnitesella* Harper & Boucot, 1978, p. 131 (type, *Mclearnites (M.) hickoxi;* OD)]. Concavoconvex profile similar to *Mesodouvillina;* ornament usually uniformly costellate; denticles along one-third to one-half of hinge line; subtriangular ventral muscle field with strong bounding ridges posterolaterally only; open anteriorly; relatively small, erect cardinal process; strong, slightly curved dorsal valve muscle-bounding ridges. *Silurian (?Telychian, Wenlock)–Devonian (Lochkovian):* cosmopolitan.

M. (Mclearnites). Similar to *M. (Geniculomclearnites)* but without dorsal geniculation. *Silurian (?Telychian, Wenlock)–Devonian (Lochkovian):* cosmopolitan.——Fig. 166,*1a–c. *M. (M.) mertoni* (McLearn), Stonehouse Formation, Přídolí–Lochkovian, Arisaig, Nova Scotia, Canada; *a,* ventral internal mold, GSC 19341, ×1; *b,c,* dorsal internal mold, latex cast, GSC 19344, ×1.5 (Harper & Boucot, 1978).——Fig. 166,*1d,e. M. (M.) newsomensis* (Foerste), Waldron Shale, Wenlock, Newsom, Nashville, Tennessee; ventral, lateral views of ventral exterior, BMNH BB 31482, ×1.5 (new).

M. (Geniculomclearnites) Harper & Boucot, 1978, p. 133 [**M. (G.) genicularia;* OD]. Similar to *M. (Mclearnites)* but with dorsally directed geniculate anterior margins; denticles slightly more than halfway along hinge line. *Devonian (Lochkovian):* North America.——Fig. 166,*3a–c. *M. (G.) genicularia,* Dalhousie Formation equivalent, Lochkovian, New Brunswick, Canada; *a,* dorsal external mold, USNM 220606, ×1.5; *b,* ventral internal mold, USNM 220607, ×1.5; *c,* latex cast of dorsal internal mold, USNM 220605, ×1.5 (Harper & Boucot, 1978).

Sinostrophia Hamada, 1971, p. 52 [**S. kondoi;* OD]. Moderately concavoconvex profile; ornament coarsely costellate (although can become abruptly fine near valve margin); denticulate along entire hinge line; prominent straight bounding ridges posterolateral to bilobed ventral muscle field, open anteriorly; relatively small erect cardinal process lobes; socket ridges abbreviated, located posterolateral to cardinal process lobes; dorsal muscle-bounding ridges mostly straight posterolaterally. *Devonian (Pragian–Emsian):* China.——Fig. 166,*2a–d. *S. kondoi,* Huolongmen Formation, lower Emsian, Jinshui, Lesser Khingan District, Heilongjiang, northeastern China; *a,* holotype, ventral interior mold, 130KE1, repository unknown, ×1.5; *b,* latex cast of ventral interior, 220KG1, repository unknown, ×1; *c,* dorsal interior mold, O56HF3, repository unknown, ×1; *d,* latex cast of dorsal interior, 223KGI, repository unknown, ×1 (Hamada, new).

Family DOUVILLINIDAE Caster, 1939

[*nom. transl.* Sokolskaya, 1960, p. 214, *ex* Douvillininae Stainbrook, 1945, p. 20, *nom. transl. ex* tribe Douvillinini Caster, 1939, p. 70] [=Telaeoshaleriidae Harper & Boucot, 1978, p. 153]

Hinge line denticulate; lacking dental plates [except *Douvillinella (Crinistrophia)*]; ventral muscle field variable, subcircular to bilobed, well impressed, usually with bounding ridges laterally, anteriorly; cardinal process lobes directed ventroposteriorly, posteriorly; socket ridges present but small; dorsal side septa. *Silurian (Ludlow)–Devonian (Frasnian).*

Subfamily DOUVILLININAE Caster, 1939

[*nom. transl.* Stainbrook, 1945, p. 20, *ex* Douvillinini Caster, 1939, p. 70]

Relatively transverse ventral muscle field elevated, with prominent overhanging muscle-bounding ridges meeting anteriorly; dorsal median septum bifurcates anteriorly. *Devonian (?Eifelian–Frasnian).*

Douvillina Oehlert, 1887b, p. 1282 [**Orthis dutertrei* Murchison, 1840, p. 253 (attributed to de Verneuil by Oehlert); OD]. Strongly concavoconvex profile; ornament parvicostellate; denticles over most of hinge line; elevated, very curved bounding ridges surrounding distinctive subcircular but relatively small ventral muscle field; erect cardinal process lobes; diverging dorsal side septa with cavity between them anteriorly. *Devonian (Frasnian):* cosmopolitan.——Fig. 167,*1a–d. *D. dutertrei* (Murchison), Ferques Limestone Forma-

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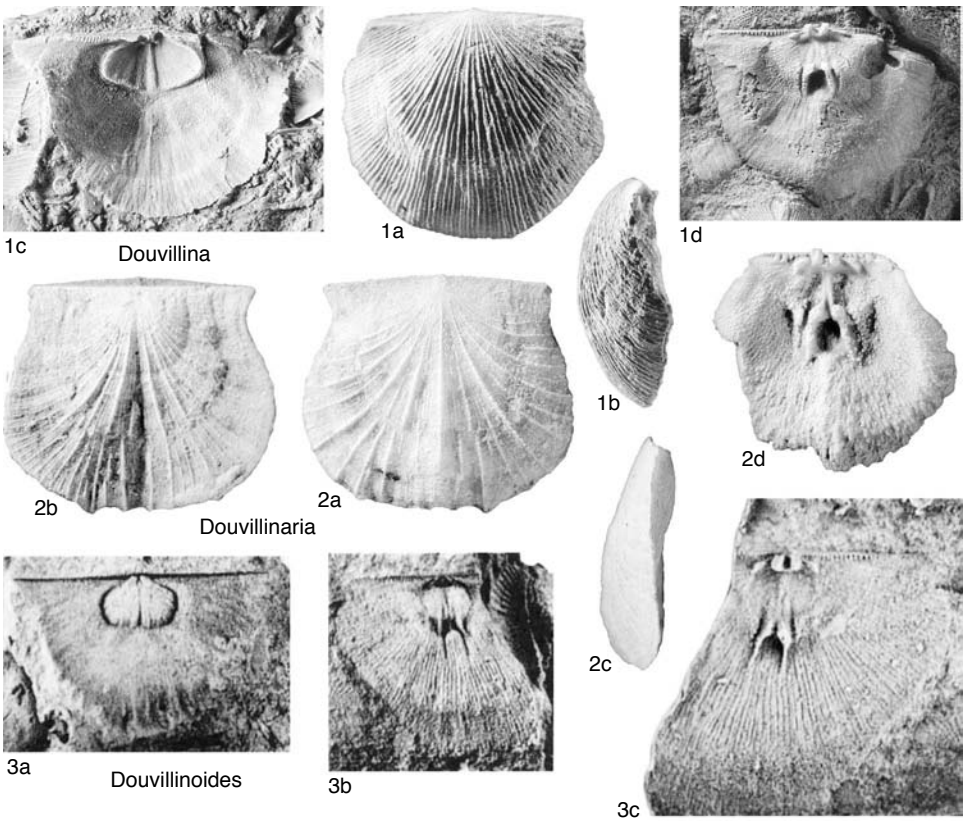

FIG. 167. Douvillinidae (p. 266–267).

tion, Frasnian, Ferques, Boulonnais, France; *a,b,* ventral, lateral views of conjoined valves, BMNH BC 13416, ×1.5; *c,* ventral interior, BMNH BC 13417, ×1.5; *d,* dorsal interior, BMNH BC 13418, ×1.5 (new).

Douvillinaria STAINBROOK, 1945, p. 22 [**Strophedonta variabilis* CALVIN, 1878, p. 727; OD]. Biconvex profile, but with ventral fold, dorsal sulcus; ornament of curving unequal parvicostellae to uniform costellae; denticles along entire hinge line; elevated bounding ridges around relatively small subcircular to bilobed ventral muscle field; erect ventrally, posteriorly directed cardinal process lobes; dorsal myophragm bifurcating anterior to two septa with hollow between them. *Devonian (?Eifelian, Givetian–Frasnian):* North America, ?Spain.——FIG. 167,*2a–d.* **D. variabilis* (CALVIN), Independence Shale, Frasnian, Middle Amana, Iowa; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH BB 57970, ×3; *d,* dorsal interior, BMNH BB 57971, ×3 (new).

Douvillinoides HARPER & BOUCOT, 1978, p. 152 [**Douvillinella? crickmayi* PEDDER, 1960, p. 212; OD]. Similar to *Douvillinaria* but profile thin, gently resupinate without fold or sulcus; ornament usually uniformly costellate. *Devonian (Frasnian):* North America.——FIG. 167,*3a–c. D.* sp., Chemung Group, Frasnian, Nichols, New York; *a,* ventral internal mold, USNM 220633, ×1; *b,* ventral internal mold, ×1; *c,* ventral latex cast, USNM 220634, ×1.5 (Harper & Boucot, 1978).

Subfamily PROTODOUVILLININAE Harper & Boucot, 1978

[Protodouvillininae HARPER & BOUCOT, 1978, p. 138] [=Douvinellinellinae HARPER & BOUCOT, 1978, p. 146; Teichostrophiinae HARPER & BOUCOT, 1978, p. 43]

Maximum width of dorsal muscle field near posterior of valve, in contrast to Leptodontellinae; ventral muscle field strongly impressed, usually semielliptical, but with tendency to elongation in some genera, bounded laterally by muscle-bounding ridges in most genera, however, these bounding ridges not elevated, unlike Douvillininae; dorsal side septa mostly straight but

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sometimes diverging anteriorly; second pair of side septa rarely developed. *Silurian (Ludlow)–Devonian (Frasnian).*

Protodouvillina HARPER & BOUCOT, 1978, p. 138 [**Strophomena inaequistriata* CONRAD, 1842, p. 254; OD]. Profile strongly concavoconvex; unequally parvicostellate ornament; ventral muscle field bounded by short but strong curved ridges posterolaterally, with anterior margin open; small erect cardinal process lobes; dorsal myophragm continuous with base of cardinal process continuing anteriorly, bifurcating into pair of short but prominent side septa that may be relatively straight or may curve inward. *Silurian–Devonian (Přídolí–Givetian):* cosmopolitan.——FIG. 168,*1a–c.* **P. inaequistriata* (CONRAD), Hamilton Group, Eifelian, Moscow, Livingston, New York; *a,* ventral exterior, AMNH 37215, ×2; *b,* ventral interior, AMNH 37218, ×2; *c,* dorsal interior, AMNH 37217, ×2 (new).

Bojodouvillina HAVLÍČEK, 1967, p. 171 [**Leptaena phillipsii* BARRANDE, 1848, p. 226; OD]. Profile moderately concavoconvex; unequally parvicostellate ornament; denticles along two-thirds of hinge; ventral diductor field separated by well-developed median septum; muscle-bounding ridges poorly developed around bilobed muscle field; erect, posteriorly directed cardinal process; dorsal interior relatively simple, with pair of short, straight side septa; curved dorsal muscle-bounding ridges weakly developed; no dorsal median septum. *Devonian (Pragian–Emsian):* Europe, ?Mongolia.——FIG. 168,*2a–d.* **B. phillipsii* (BARRANDE), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* lectotype, ventral interior, NM L6747, ×1.5; *b,* conjoined valves showing dorsal internal mold, OMR VH 444a, ×1.5; *c,* damaged conjoined valves, including cardinal process, OMR VH 444b, ×1.5; *d,* ventral internal mold, Zlíchov Limestones, Emsian, U kaplicky, Praha-Hlubocepy, Bohemia, Czech Republic, OMR VH 93a, ×1.5 (Havlíček, 1967).

?Contradouvillina GRATSIANOVA, 1975, p. 48 [**C. salairica;* OD]. Transverse, gently planoconvex profile, anteriorly geniculate ventrally; elongate ventral muscle field with diductors close together, enclosing adductor scars; dorsal interior poorly known, hence generic status and family position uncertain. *Devonian (Pragian):* Asia, Malobachat Beds, Mount Gurevska region, northeastern Salair, Altai-Sayan, Russia.

Cymostrophia CASTER, 1939, p. 39 [**Leptaena stephani* BARRANDE, 1848, p. 230; OD] [=*Corrugatella* KHALFIN, 1948, p. 236, obj.]. Variable outline; variably convex profile, geniculate ventral valve; dorsal valve initially flat, geniculate anteriorly; distinctive ornament of rugae interrupted by primary costellae; relatively large, suboval ventral muscle field bounded by low ridges posterolaterally only; ventral myophragm developed; small, erect cardinal process lobes; dorsal muscle field bounded posterolaterally by low ridges; one pair of low dorsal side septa, small median ridge in valve center. *Silurian (Ludlow)–Devonian (Givetian):* cosmopolitan.

C. (Cymostrophia). Transverse outline; strongly convex profile; ornament of very pronounced interrrupted rugae. *Devonian (Lochkovian–Givetian):* cosmopolitan.——FIG. 168,*3a–c.* **C. (C.) stephani* (BARRANDE), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* ventral exterior, NM CF382, ×1 (Havlíček, 1967); *b,* ventral interior, BMNH BC 13007, ×1.5 (new); *c,* dorsal interior, OMR VH 398a, ×1 (Havlíček, 1967).

C. (Protocymostrophia) HARPER & BOUCOT, 1978, p. 127 [**Strophomena ivanensis* BARRANDE, 1879, pl. 52, fig. IV 1–4, 9–12; OD]. Similar to *C. (Cymostrophia)* but having suboval rather than transverse outline, gently concavoconvex profile, less pronounced interrupted rugae in ornament. *Silurian (Ludlow)–Devonian (Eifelian):* cosmopolitan.——FIG. 168,*4a–c.* **C. (P.) ivanensis* (BARRANDE), Kotys Limestone, Lochkovian, Svaty Jan pod Skalou, Bohemia, Czech Republic; *a,* ventral exterior, OMR VH 439a, ×1.5; *b,* ventral interior, OMR VH 439d, ×2; *c,* dorsal internal mold, OMR VH 439c, ×1.5 (Havlíček, 1967).

Douvillinella SPRIESTERSBACH, 1925, p. 432 [**Stropheodonta filifer* SCHMIDT, 1913, p. 313; OD; locality: *cultrijugatus* zone (Eifelian), ?Attendorn-Elsper, Doppelmulde, Germany] [=*Fibulistrophia* GARCÍA-ALCALDE, 1972, p. 43 (type, *F. fibula;* OD)]. Profile gently resupinate to gently concavoconvex; ornament uniformly costellate; denticulate along most of hinge line; bilobed ventral diductor muscle field widely separated by broad triangular space, bounded laterally by faint muscle-bounding ridges that are sometimes also present anteriorly; socket ridges long, widely divergent, not joined to cardinal process lobes; pair of long, thin, curved dorsal side septa; short dorsal median ridge may be developed centrally; subperipheral rims variably present in both valves. *Devonian (Emsian–Eifelian):* Europe.

D. (Douvillinella). Similar to *D. (Crinistrophia)* but with muscle-bounding ridges always developed, although sometimes faint. *Devonian (Emsian–Eifelian):* Europe.——FIG. 169,*1a–d.* **D. (D.) fibula* (GARCÍA-ALCADE), Moniello Formation, Emsian, Les Areñes, Avilés, Asturias, Spain; *a,b,* holotype, ventral, dorsal views of conjoined valves, DPO 2489, ×1.5; *c,* ventral interior, DPO 2546, ×2; *d,* dorsal interior, DPO 2563, ×2 (García-Alcade, 1972).

D. (Crinistrophia) HAVLÍČEK, 1967, p. 134 [**C. crinita;* OD]. Similar to *D. (Douvillinella)* but gently concavoconvex profile; ornament unequally parvicostellate to costellate; short dental plates may be developed; relatively large bilobed ventral muscle field without bounding ridges;

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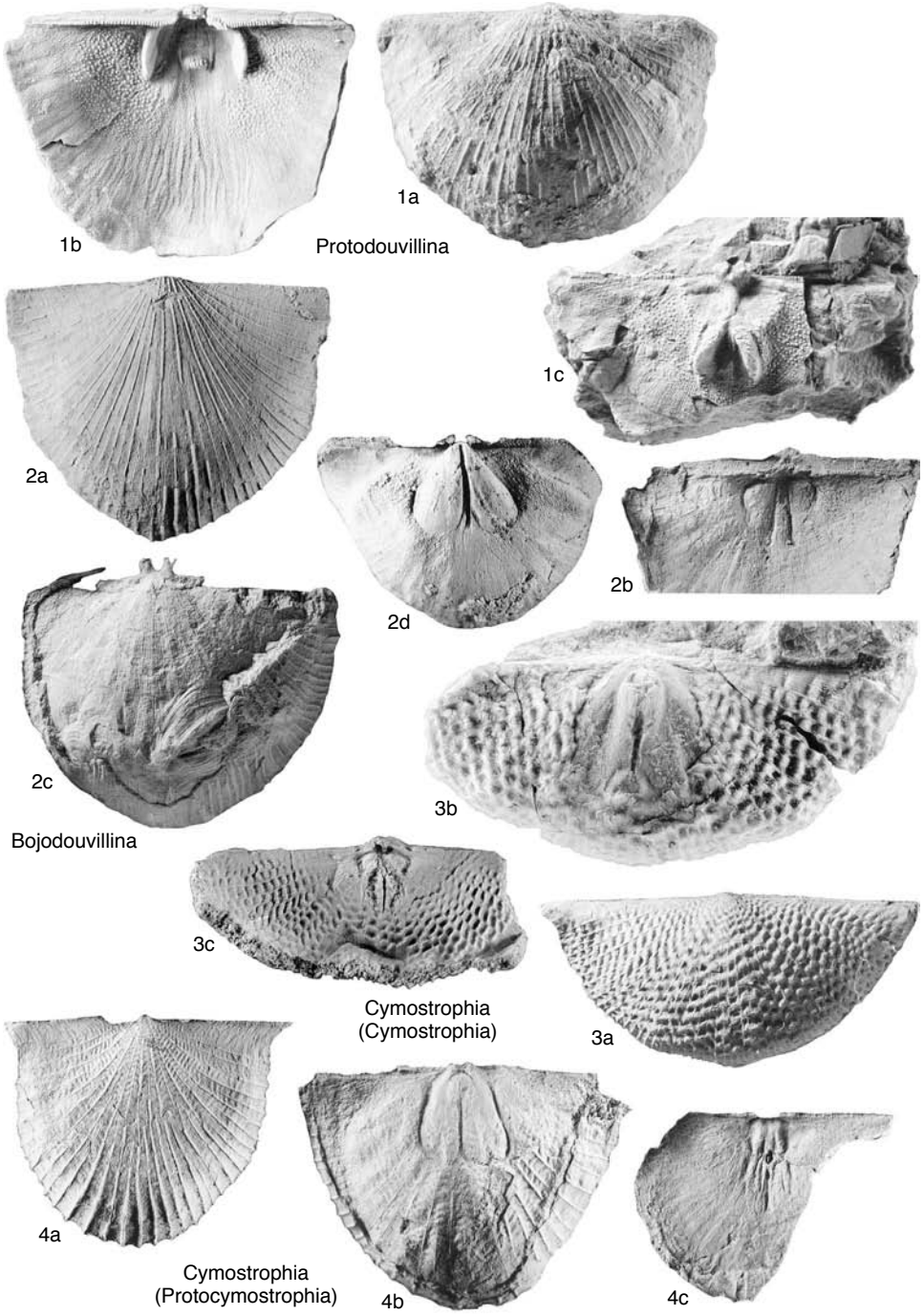

FIG. 168. Douvillinidae (p. 268).

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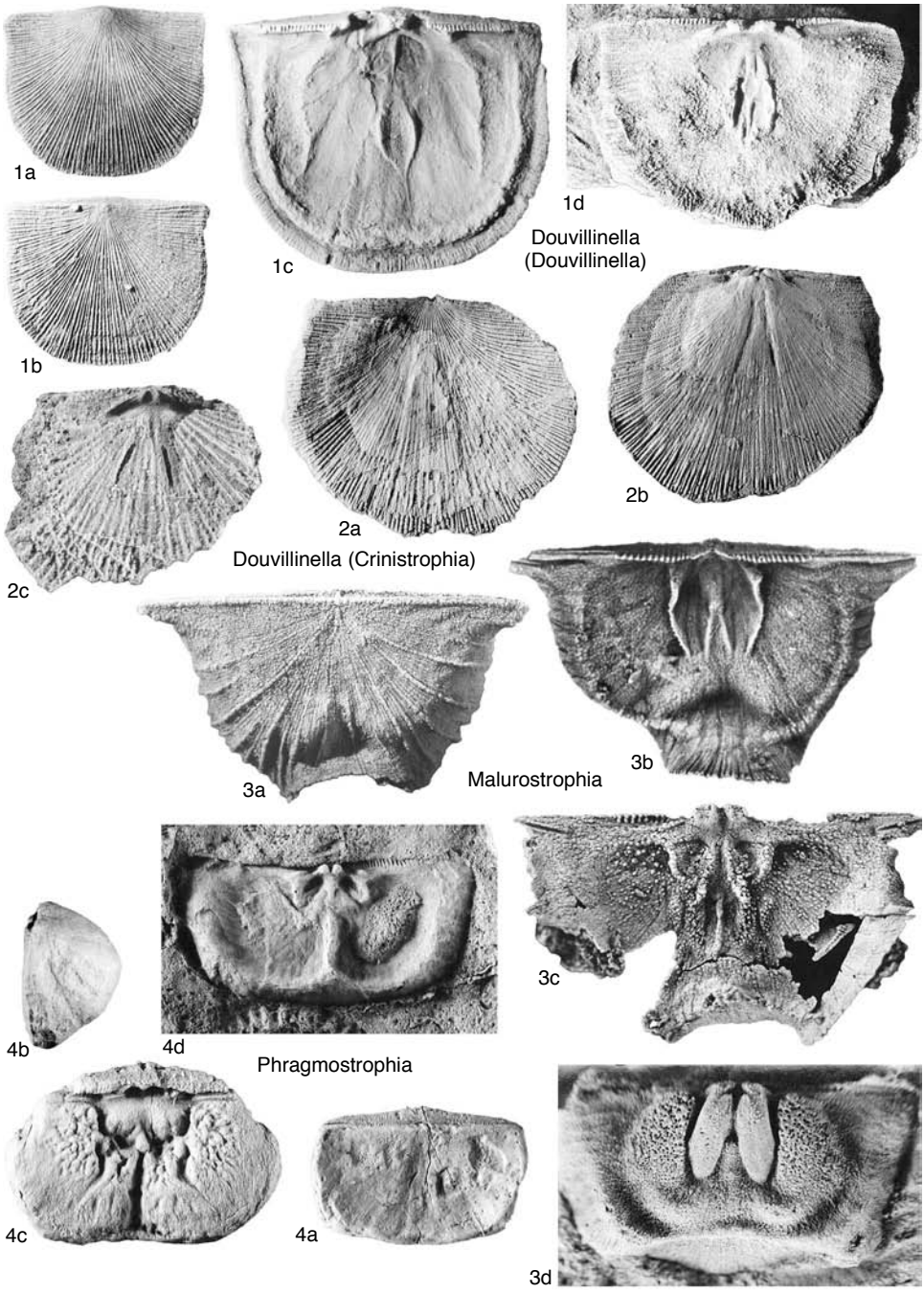

FIG. 169. Douvillinidae (p. 268–274).

short erect cardinal process with prominent socket ridges flaring anterolaterally; short, straight dorsal transmuscle septa variably developed. *Devonian (Emsian):* Europe.——FIG. 169,*2a–c. *D. (C.) crinita,* Zlíchov Limestone, Emsian, Praha-Hlubocepy, Bohemia, Czech Re-

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public; *a,b,* ventral interior, exterior molds, OMR VH 405c, ×1.5; *c,* dorsal interior mold, OMR VH 406b, ×3.7 (Havlíček, 1967).

Hercostrophia Williams, 1950, p. 277 [**H. alpenensis;* OD]. Gently to moderately concavoconvex profile; unequally parvicostellate ornament; bilobed to subtriangular ventral muscle field bounded by two pairs of lateral, median bounding ridges sometimes united posteriorly to form arch; dorsal muscle field not situated on elevated platform, bounding ridges absent; pair of strong dorsal side septa. *Devonian (Givetian–Frasnian):* North America, Australia.——Fig. 170,*1a,b. *H. alpenensis,* Alpena Limestone, Givetian, Alpena, Michigan; *a,* ventral interior, USNM 116017, ×2; *b,* dorsal view of conjoined valves, USNM 116018, ×2 (Williams, 1953a).——Fig. 170,*1c. H.* sp., Givetian, New York; dorsal interior, ×2 (Williams, 1953a).

Malurostrophia Campbell & Talent, 1967, p. 309 [**M. flabellicauda;* OD] [=*Sinoshaleria* Xian in Xian & Jiang, 1978, p. 268 (type, *S. guangshunensis;* OD)]. Profile gently resupinate, geniculate; quadrate outline, indented anterior margin; ornament unequally parvicostellate; ventral muscle field bilobed, elongate, bounded laterally by subparallel but slightly curved ridges; myophragm well developed, bifurcating anteriorly; ventral subperipheral rim; large, erect, posteriorly directed cardinal process lobes; dorsal muscle field bounded laterally, posteriorly by ridges; one pair of dorsal side septa, additional pair sometimes developed laterally; short dorsal median ridge developed centrally, sometimes extending anteriorly. *Devonian (Emsian–Givetian):* Australia, China.——Fig. 169,*3a–c. *M. flabellicauda, Receptaculites* Limestone, Emsian–Eifelian, Bloomfield Station, Taemas, New South Wales, Australia; *a,* holotype, dorsal view of conjoined valves, ANU 14620, ×4; *b,* ventral interior, ANU 14987, ×4; *c,* dorsal interior, ANU 14983, ×4 (Campbell & Talent, 1967).——Fig. 169,*3d. M. guangshunensis* (Xian), Dushan Formation, Givetian, Tianqibao, Guangshun, Changshung County, Guizhou Province, China; holotype, ventral internal mold, GB 371, ×2 (Xian & Jiang, 1978).

Megastrophiella Harper & Boucot, 1978, p. 19 [**Stropheodonta iddingsi* Merriam, 1940, p. 79; OD]. Profile strongly concavoconvex; parvicostellate to costellate ornament; ventral muscle field bilobed to oval with weak bounding ridges mainly developed posterolaterally; central ventral median ridge present; cardinal process lobes posteriorly directed, not joined at their bases; socket ridges widely divergent, separate from cardinal process lobes; dorsal muscle field elevated on platform, with well-developed transmuscle septa, bounding ridges; central dorsal median septum extended anteriorly. *Devonian (Emsian–Eifelian):* North America.——Fig. 170,*2a–f. *M. iddingsi* (Merriam), *Spirifer pinyonensis* Zone, lower Nevada Formation, Emsian, Lone Mountain, Roberts Mountains, Nevada; *a,b,* holotype, ventral, posterior views of conjoined valves, USNM 96370, ×1.5; *c,d,* ventral, posterior views of ventral internal mold, USNM 156961, ×1.5; *e,f,* dorsal internal mold, latex cast, USNM 156962, ×2 (Johnson, new).

?Moravostrophia Havlíček, 1962, p. 471 [**Strophomena interstrialis moravica* Šmycka, 1897, p. 19; OD]. Small shell with subrectangular outline; concavoconvex profile; parvicostellate ornament, sometimes with fine rugae between costellae; ventral interior unknown, hence queried familial assignment; cardinal process lobes separate, strongly posteriorly directed; socket ridges small, widely divergent; dorsal adductor muscle field weakly impressed with strong bounding ridges curved inward; short central dorsal median septum, with pair of short side septa between it and muscle field; dorsal subperipheral rim well developed. *Devonian (Givetian):* Europe.——Fig. 170,*4a–e. *M. moravica* (Šmycka), Givetian Beds, Celechovice na Hané, Moravia, Czech Republic; *a,* lectotype, ventral exterior, Brno 10939, ×2; *b,c,* dorsal, ventral views of conjoined valves, OMR VH 522a, ×2; *d,* dorsal interior, Figner collection, ×2; *e,* enlargement of cardinalia, OMR VH 522b, ×4.5 (Havlíček, 1967).

Nadiastrophia Talent, 1963, p. 62 [**N. superba;* OD] [?=*Xenostrophia* Wang in Wang, Yu, & Wu, 1974, p. 37 (type, *Shaleria yukiangensis* Wang, 1956, p. 149; OD)]. Profile gently concavoconvex, sharply geniculate in both valves; ornament unequally parvicostellate; hinge line denticulate along most of width; bilobed ventral muscle field chiefly elongate; muscle-bounding ridges present laterally, sometimes weakly anteriorly; ventral subperipheral rim developed in gerontic specimens; erect, posteriorly directed cardinal process lobes; myophragm variably developed; dorsal side septa vary from strong to very weak; dorsal muscle field on elevated platform with short bounding ridges present posterolaterally; dorsal median septum variably developed centrally, occasionally anteriorly, but sometimes absent; variably developed dorsal subperipheral rim. *Devonian (Emsian–Eifelian):* Australasia, China, Canada.——Fig. 170,*3a,b. *N. superba,* Kilgower Member, Tabberabbera Formation, Emsian, Mitchell River, south of Tabberabbera, Victoria, Australia; *a,* ventral internal mold, GSV 5889a, ×3; *b,* dorsal internal mold, GSV 56578a, ×3 (Harper & Boucot, 1978).——Fig. 170,*3c–f. N. yukiangensis* (Wang), Liujing Member, Yukiang Formation, lower Emsian, Liujing railway station, Hengxian County, southern Guangxi, China; *c,d,* dorsal, lateral views of conjoined valves, BMNH BC 12833, ×2; *e,* ventral interior, BMNH BC 12834, ×2; *f,* dorsal interior, NIGP 23618, ×2 (new).

Paucistrophia Wang & Zhu, 1979, p. 23 [**Radiomena concinnusa* Wang in Wang, Yu, & Wu, 1974, p. 38; OD]. Profile concavoconvex, geniculate; ornament unequally parvicostellate; hinge line denticulate over most of valve width; large bilobed ventral muscle field, with strong bounding ridges anterior from dental plates surrounding entire field; dorsal valve similar to *Nadiastrophia. Devonian (Emsian):* China.——Fig. 172,*2a,b. *P. concinnusa* (Wang),

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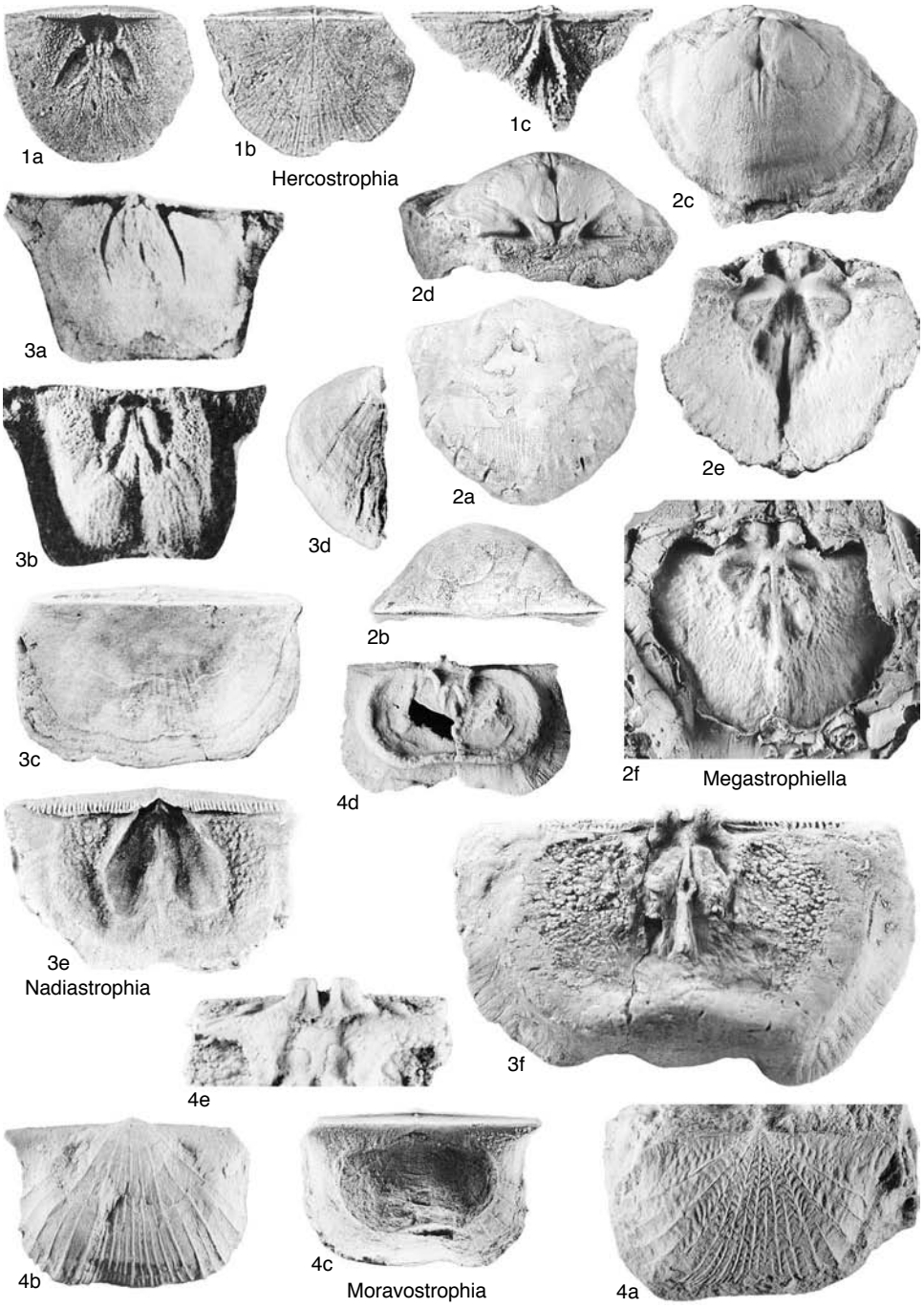

FIG. 170. Douvillinidae (p. 271).

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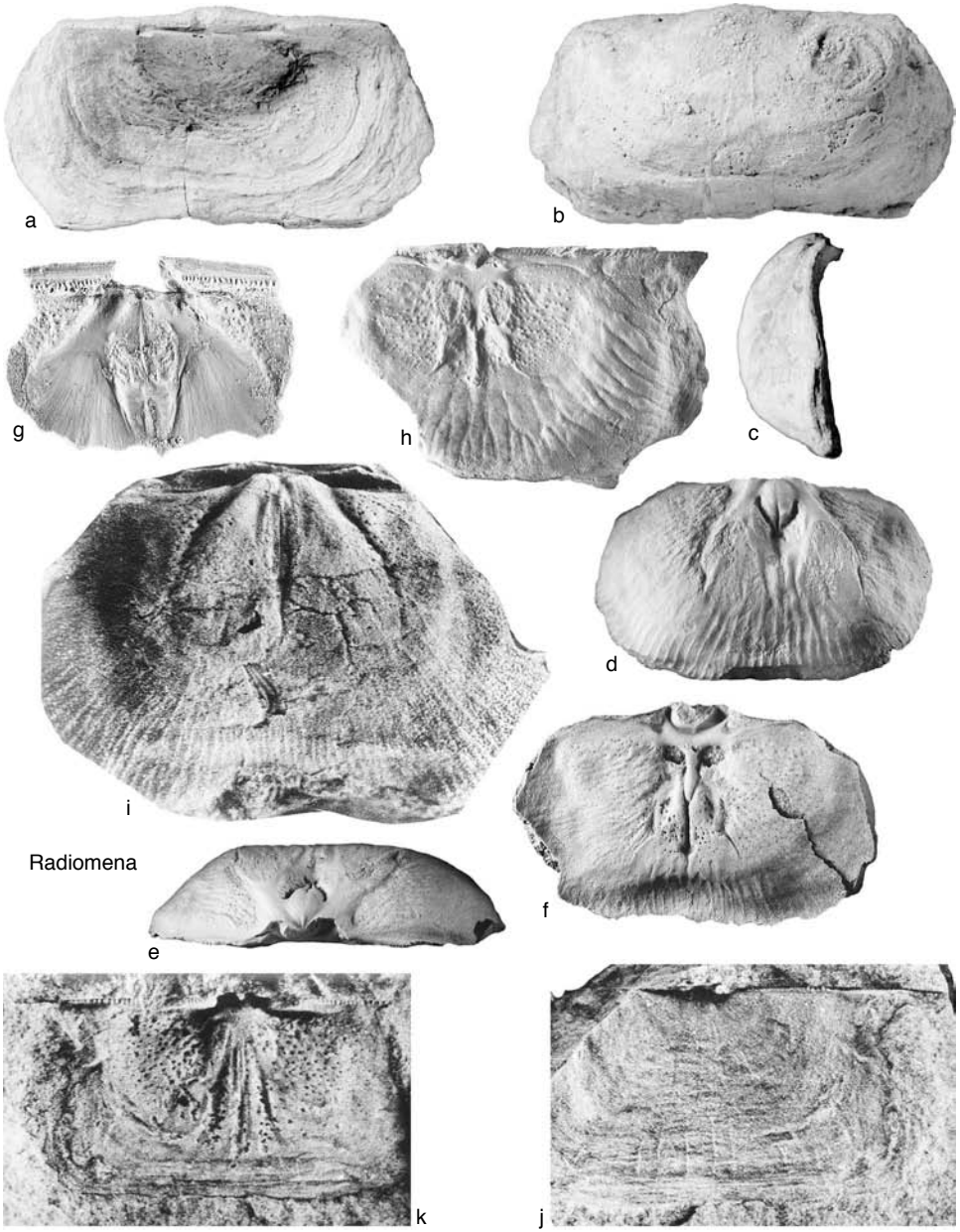

FIG. 171. Douvillinidae (p. 274).

Sipai Formation, upper Emsian, Sipai Village, Luzhai, Guangxi Province, China; holotype, ventral, dorsal views of internal mold of conjoined valves, NIGP 23657, ×1.5 (new).

Phragmostrophia HARPER, JOHNSON, & BOUCOT, 1967, p. 428 [**P. merriami;* OD]. Ventral valve strongly convex profile, dorsal valve flat; fine, unequally parvicostellate ornament; denticles along

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most of valve width; ventral muscle field bounded laterally by ridges; dorsal muscle field raised on elevated platform with bounding ridges; one or two pairs of dorsal side septa present; ventral dorsal median septum relatively strong, sometimes extending anteriorly to join subperipheral rim. *Devonian (Emsian–Eifelian):* North America, Russia.——Fig. 169,*4a–d. *P. merriami, Eurekaspirifer pinyonensis* Zone, Emsian; *a,* dorsal view of conjoined valves, Sulphur Spring Range, ×2; *b,* lateral view of conjoined valves, northern Roberts Mountains, Eureka County, Nevada, USNM 140410, ×1.5; *c,* holotype, dorsal internal mold, Sulphur Spring Range, USNM 140409, ×2; *d,* latex cast of dorsal internal mold, Sulphur Spring Range, ×2 (Harper, Johnson, & Boucot, 1967).

Radiomena Havlíček, 1962, p. 471 [**Orthis irregularis* Roemer, 1844, p. 75; OD] [=*Chuanostrophia* Xian in Xian & others, 1988, p. 207 (type, *C. scitula;* OD)]. Ventral valve moderately to strongly convex profile, dorsal valve first flat but geniculate anteriorly; unequally parvicostellate weak ornament; denticles along most of valve width; ventral muscle field weakly impressed anteriorly, bilobed diductor scars separated by low, wide myophragm; erect, posteriorly directed cardinal process lobes; dorsal muscle field bounded by low ridges; one pair of dorsal side septa present, anterior ends sometimes curve out laterally; weak dorsal median ridge developed centrally. *Devonian (Emsian–Givetian):* Europe, Asia.——Fig. 171*a–h. *R. irregularis* (Roemer); *a–c,* dorsal, ventral, lateral views of conjoined valves, Eifelian Beds, Gerolstein, BMNH BC 12831, ×2 (new); *d–f,* ventral, posterior, dorsal views of conjoined valves, Eifelian Beds, Eifel, Germany, SMF 19119, ×1 (Johnson, new); *g,* interior of incomplete ventral valve, Givetian, Celechovice na Hané, Moravia, Czech Republic, OMR VH 402a, ×1.6; *h,* dorsal interior, Givetian, Celechovice na Hané, Moravia, Czech Republic, OMR VH 404c, ×1.7 (Havlíček, 1967).——Fig. 171*i–k. R. scitula* (Xian), Shiliangzi Member, Yangmaba Formation, upper Emsian, Jiangyou, Beichuan County, northern Sichuan Province, China; *i,* ventral internal mold, ×1; *j,k,* holotype, internal, external mold of dorsal valve, ×1.5 (Xian & others, 1988).

Taemostrophia Chatterton, 1973, p. 43 [**T. patmorei;* OD]. Alate, subquadrate outline; flat profile but with sharply geniculate margin; unequally parvicostellate ornament; variable ventral muscle field with bounding ridges directed toward center at first, then anteriorly flare out laterally before curving back to unite anteriorly; other specimens simply curving laterally, open anteriorly; adductor muscles entirely enclosed by diductors; erect cardinal process lobes directed ventrally or posteroventrally; dorsal muscle-bounding ridges strong both laterally and anteriorly; central dorsal median ridge present; one pair of dorsal side septa variably developed; similar to *Malurostrophia* but ventral muscle field less bilobed. *Devonian (Emsian–Eifelian):* Australia.——Fig. 172,*3a–c. *T. patmorei,* Warroo Limestone, Emsian, Hume Park, Yass, New South Wales, Australia; *a,b,* holotype, ventral exterior, interior, ANU 18922, ×1.5; *c,* dorsal interior, ANU 18923e, ×2 (Campbell, new).

Teichostrophia Harper, Johnson, & Boucot, 1967, p. 420 [**Strophomena lepis* Bronn, 1837, p. 87; OD] [?=*Ancylostrophia* Harper, Johnson, & Boucot, 1967, p. 423 (type, *A. kondelensis;* OD)]. Outline subquadrate; ventral valve strongly convex profile, dorsal valve flat posteriorly, sharply geniculate, with raised interior subperipheral rim; ornament smooth or very faint unequal parvicostellae; bilobed ventral muscle field strongly impressed but without raised muscle-bounding ridges; socket ridges very small; dorsal muscle field impressed onto elevated platform with encircling muscle-bounding ridges, variably developed side septa; short dorsal median septum sometimes developed anteriorly. *Devonian (Emsian–Givetian):* Europe, Asia.——Fig. 172,*1a–d. *T. lepis* (Bronn), Siegenian, Emsian Beds, Gerolstein, Eifel, Germany; *a,* ventral view of conjoined valves, BMNH BC 12830, ×2; *b,* dorsal view of conjoined valves, BMNH BC 12828, ×2; *c,* internal mold of ventral valve, BMNH BC 12829, ×2 (new); *d,* internal mold of conjoined valves, USNM 145566, ×2 (Harper & Boucot, 1978).

Telaeoshaleria Williams, 1950, p. 281 [**Shaleria (T.) sulcata;* OD] [?=*Kinelina* Ljaschenko, 1969, p. 35 (type, *K. eifelensis;* OD)]. Ventral valve strongly convex profile, dorsal valve flat posteriorly, geniculate anteriorly; unequally parvicostellate ornament; ventral muscle field with long, parallel-sided diductor scars bounded laterally by strong bounding ridges, divided by myophragm that forks anteriorly; dorsal muscle field on elevated but relatively small, low platform; central pair of dorsal side septa always present, sometimes additional pair also developed laterally; short dorsal median ridge centrally. *Devonian (Eifelian–Givetian):* Europe, Asia, Algeria.——Fig. 172,*4a–c. *T. sulcata,* Calceola beds, Eifelian, Lissingen, Eifel, Germany; *a,* interior mold of ventral valve, USNM 116031, ×2; *b,* holotype, dorsal view of conjoined valves, USNM 116030, ×2; *c,* interior mold of dorsal valve, USNM 116032, ×1.5 (Williams, 1953a).

Tsaganella Oleneva, 1994, p. 50 [**T. plana;* OD]. Ventral valve weakly convex profile, dorsal valve nearly flat; relatively fine unequally parvicostellate ornament; denticles along half valve width; ventral muscle field bilobed, surrounded by well-developed bounding ridges; small ventral process; cardinal process erect; flaring, medium-sized socket ridges; small side septa variably developed within relatively small dorsal muscle field; fine dorsal median septum sometimes present centrally. *Devonian (Givetian):* Asia.——Fig. 172,*5a–d. *T. plana,* Khatygolsk Formation, Givetian, Khar-Tolgoi, Altai Mountains, Mongolia; *a,* dorsal external mold, PAN 4427/146, ×1.5; *b,c,* holotype, ventral internal mold, latex cast, PAN 4427/210, ×1.5; *d,* dorsal internal mold, PAN 4427/188, ×1.3 (Oleneva, 1994).

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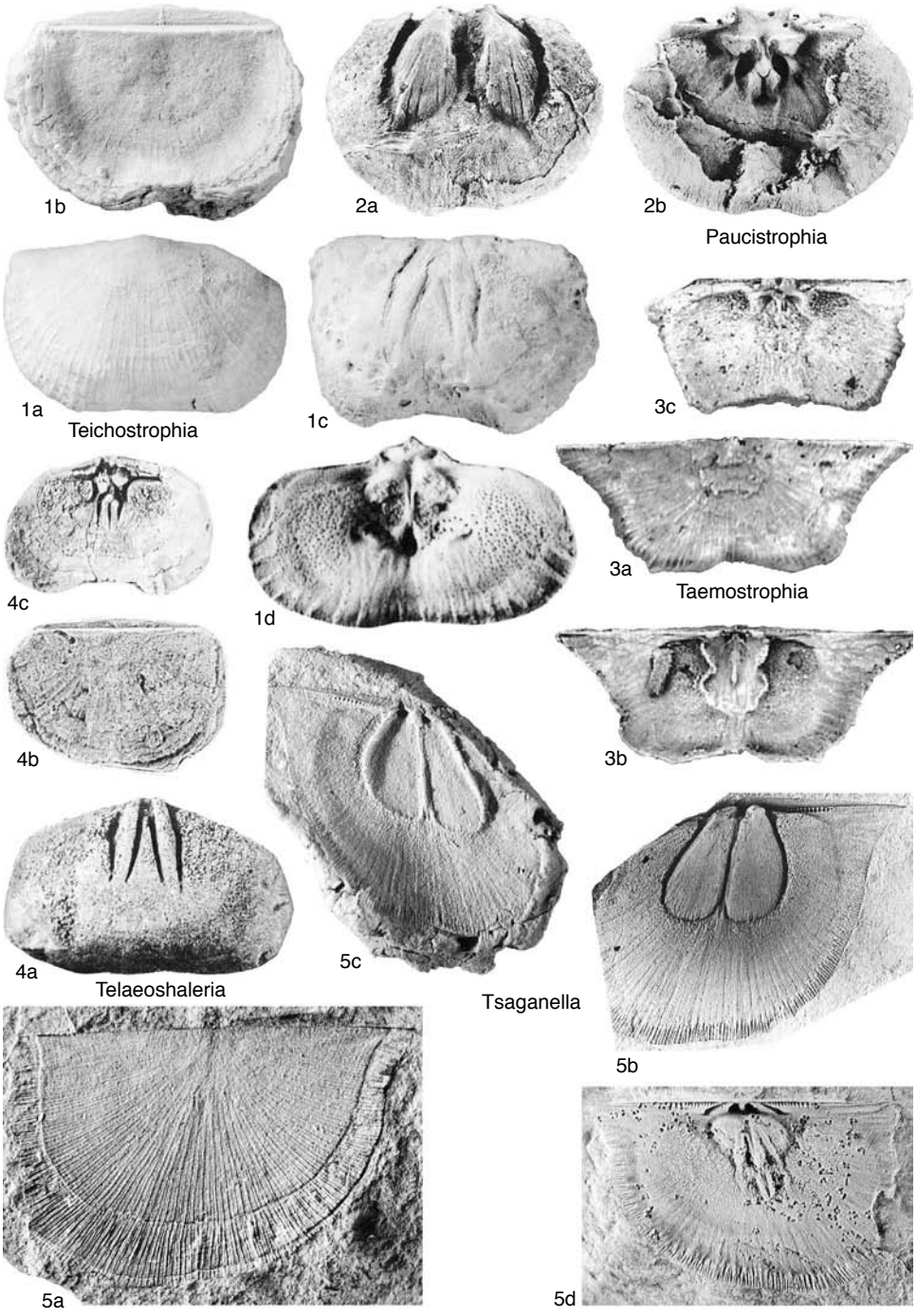

FIG. 172. Douvillinidae (p. 271–274).

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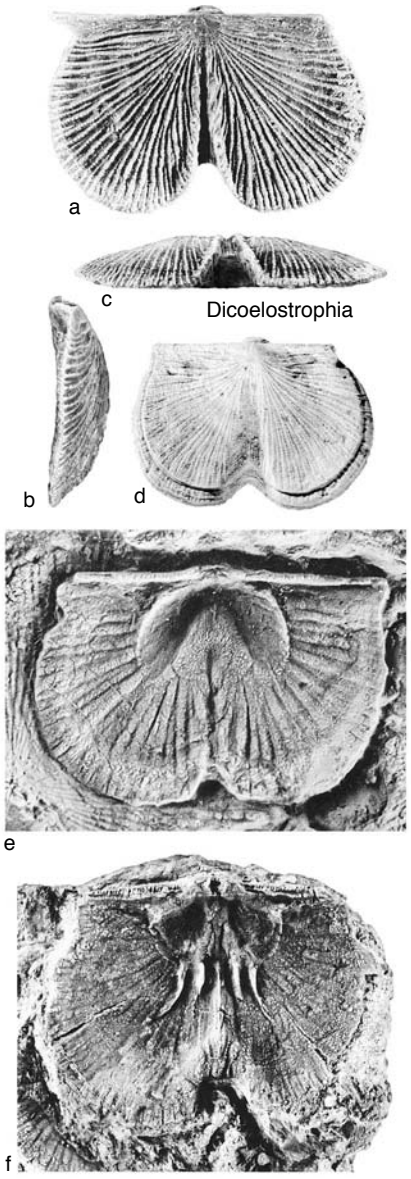

FIG. 173. Douvillinidae (p. 276).

Subfamily DICOELOSTROPHIINAE Wang & Rong, 1986

[Dicoelostrophiinae WANG & RONG, 1986, p. 98]

Characters same as for Douvillinidae, with sharply indented, bilobed anterior commissure due to prominent long narrow sulcus in each valve; two pairs of dorsal side septa. *Devonian (Emsian).*

Dicoelostrophia WANG, 1955a, p. 104 [**D. punctatum;* OD]. Profile mostly gently resupinate to shallowly biconvex; ornament variable, ranging from unequally parvicostellate to fascicostellate, usually costellate; denticles along most of hinge width; bilobed ventral muscle field with strong bounding ridges posterolaterally, separated anteriorly by broad central area; dorsal muscle field bounded laterally, posteriorly by ridges; two pairs of high, strong dorsal side septa, median septum. *Devonian (Emsian):* China.——FIG. 173*a–f.* **D. punctatum,* Yukiang Formation, lower Emsian, Liujing, Hengxian, Guangxi Province, China; *a–c,* holotype, dorsal, lateral, anterior views of conjoined valves, ×1.5; *d,* dorsal view of conjoined valves, BMNH BC 12848, ×1.5; *e,* ventral valve interior, NIGP 87917, ×2; *f,* dorsal valve interior, NIGP 23611, ×2 (new).

Subfamily LEPTODONTELLINAE Williams, 1965

[Leptodontellinae WILLIAMS, 1965d, p. 403]

Profile gently to strongly concavoconvex, usually geniculate in varying degrees; ventral muscle field long, bilobed, separated by relatively broad flat area anterior to diductor scars; cardinal process lobes directed posteriorly; distinct short socket ridges almost parallel with lateral margins of cardinal process lobes, turning laterally to form low ridges parallel to hinge line; differs from Douvillininae in general absence of dorsal valve side septa and in widest part of dorsal muscle field, occurring anteriorly rather than posteriorly. *Devonian (Emsian–Frasnian).*

Leptodontella KHALFIN, 1948, p. 253 [**Leptaena caudata* SCHNUR, 1854, p. 224; OD] [=*Glossostrophia* WILLIAMS, 1950, p. 282, obj.; *Altaestrophia* BUBLICHENKO, 1956, p. 96 (type, *Leptodontella acuta* KHALFIN, 1948, p. 255; OD]. Profile biplanar in central disc, then gently resupinate, sharply geniculate ventrally; fold, sulcus present in concave anterior margin; unequally parvicostellate ornament; large, bilobed, weakly impressed ventral muscle field; strong dorsal muscle-bounding ridges; dorsal side septa absent or weakly developed; thin dorsal median septum with prominent thickening centrally. *Devonian (Eifelian–Givetian):* Europe, Africa, Asia.——FIG. 174,*4a–e.* **L. caudata* (SCHNUR), Eifelian; *a,b,* internal molds of ventral, dorsal interiors, Blankenheim Limestone, Gerolstein, Eifel, Germany, USNM 116391a, ×1.5; *c,d,* dorsal, ×1, and anterior views, ×1.5, of conjoined valves, Blankenheim Limestone, Gerolstein, Eifel, Germany, USNM 116391b (Williams, 1953a); *e,* dorsal interior, Padaukpin Limestone, Padaukpin, near Maymyo, northern Shan States, Burma, SM 2654, ×1.25 (Johnson, new).——FIG. 174,*4f. L. acuta,*

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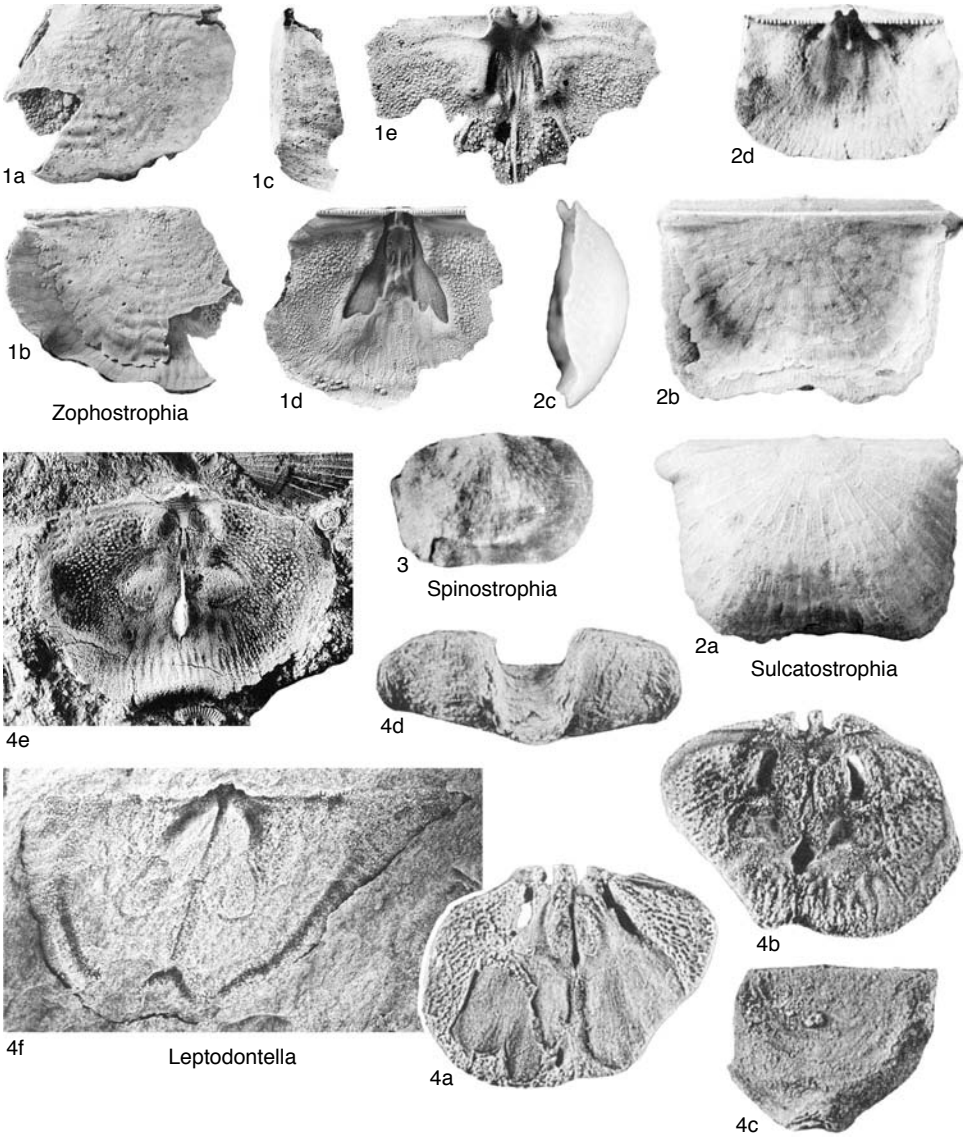

FIG. 174. Douvillinidae (p. 276–278).

Medvedev Formation, upper Emsian, Medvedev, Gorny Altai, Russia; dorsal internal mold, PAN 1/244, ×2 (Gratsianova, new).

Parastrophonella BUBLICHENKO, 1956, p. 93 [**Strophomena anaglypha* KAYSER, 1871, p. 628; OD]. Planoconvex to gently resupinate profile; similar to *Leptodontella,* but without anterior fold, sulcus; unequally parvicostellate ornament; triangular, bilobed ventral muscle field, well impressed but without bounding ridges; erect, ventrally directed cardinal process lobes; dorsal muscle field well impressed posteriorly, open anteriorly; weak dorsal myophragm posteriorly only; dorsal side septa absent. *Devonian (Emsian–Givetian):* Europe, northern Africa.——FIG. 175*a–d.* **P. anaglypha* (KAYSER), Rommersheimer Shale, Eifelian, Eifel, Germany; *a,* latex of ventral exterior, Gees, SMF 19154, ×3; *b,* ventral interior, Rommersheim, Prümer Mulde, SMF 19154, ×3; *c,d,* mold, latex cast of dorsal interior, Rommersheim, Prümer Mulde, SMF 19160, ×3 (Johnson, new).

?Spinostrophia JIANG in XIAN & JIANG, 1978, p. 267 [**S. ellipsoidea;* OD]. Ornament of interrupted costellae as in *Nervostrophia,* but profile strongly

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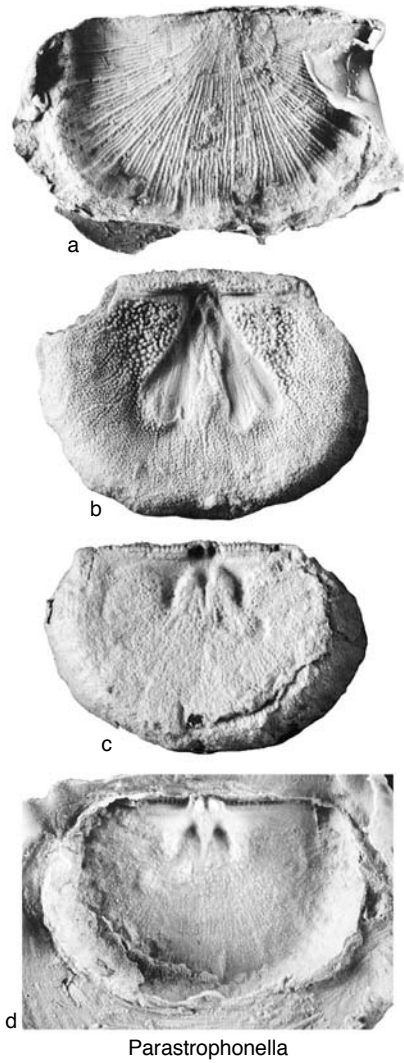

FIG. 175. Douvillinidae (p. 277).

concavoconvex, dorsally geniculate (unlike *Nervostrophia*); ventral muscle field bilobed; dorsal interior unknown, hence queried assignment to this subfamily. *Devonian (Eifelian):* China.——FIG. 174,*3. *S. ellipsoidea,* Longdongshui Formation, Eifelian, Pinghuangshan, Dushan County, Guizhou Province; holotype, ventral exterior, GB 127, ×1 (Xian & Jiang, 1978).

Sulcatostrophia CASTER, 1939, p. 81 [**Leptostrophia camerata* FENTON & FENTON, 1924, p. 96; OD] [=*Pseudodouvillina* STAINBROOK, 1945, p. 26 (type, *P. euglyphea;* OD)]. Quadrate outline; profile strongly concavoconvex; ventral valve sulcus occasionally present; costellate to unequally parvicostellate ornament, with some individual ventral valve costellae occasionally variably strong along their length, as in *Nervostrophia;* poorly impressed ventral muscle field, but with prominent short flaring muscle-bounding ridges posteroventrally only, mimicking dental plates; short ventral median septum posteriorly only; dorsal side septa absent or sometimes faintly developed. *Devonian (Frasnian):* North America, Russia.——FIG. 174,*2a–d. *S. camerata* (FENTON & FENTON), Hackberry Formation, Frasnian, Mason City, Iowa; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH B 18905, ×3 (new); *d,* ventral valve interior, USNM 220529, ×2 (Harper & Boucot, 1978).

Zophostrophia VEEVERS, 1959, p. 63 [**Z. ungamica;* OD]. Profile dorsally geniculate; ornament uniformly costellate with weak rugae; deeply impressed bilobed ventral muscle field with short ventral median septum; dorsal muscle field strongly impressed, especially posteriorly; thin dorsal median septum centrally only. *Devonian (Frasnian):* Australia.——FIG. 174,*1a–e. *Z. ungamica,* Sadler Formation, Frasnian, Sadler Ridge, Fitzroy basin; *a–c,* holotype, ventral, dorsal, lateral views of conjoined valves, CPC 2942, ×1; *d,* ventral interior, CPC 2941, ×1.23; *e,* dorsal interior, CPC 2940, ×1.77 (Strusz, new).

Family LEPTOSTROPHIIDAE Caster, 1939

[*nom. transl.* SOKOLSKAYA, 1960, p. 215, *ex* Leptostrophiinae CASTER, 1939, p. 27] [=Eostropheodontidae HAVLÍČEK, 1967, p. 80; Nervostrophiinae HARPER & BOUCOT, 1978, p. 89; Mesoleptostrophiinae HARPER & BOUCOT, 1978, p. 66; Brachyprioninae HARPER & BOUCOT, 1978, p. 13]

Profile biplanate or gently concavoconvex; hinge line usually denticulate; triangular ventral muscle field, bounded posterolaterally by ridges (sometimes lacking in older forms) sometimes partitioned by radial ridges (unique in Strophomenoidea), open anteriorly; cardinal process lobes usually ventrally directed, although rarely posteriorly or posteroventrally directed; socket ridges usually present; side septa in dorsal valve generally absent. *Ordovician (Ashgill)–Devonian (Frasnian).*

Leptostrophia HALL & CLARKE, 1892, p. 288 [**Stropheodonta magnifica* HALL, 1857, p. 54; OD] [=*Magniventra* HARPER & BOUCOT, 1978, p. 77 (type, *Strophomena magniventra* HALL, 1857, p. 54; OD)]. Semicircular outline; profile biplanate to gently concavoconvex; ornament usually unequally costellate; hinge line entirely denticulate; ventral valve with distinctive ventral process or tubular

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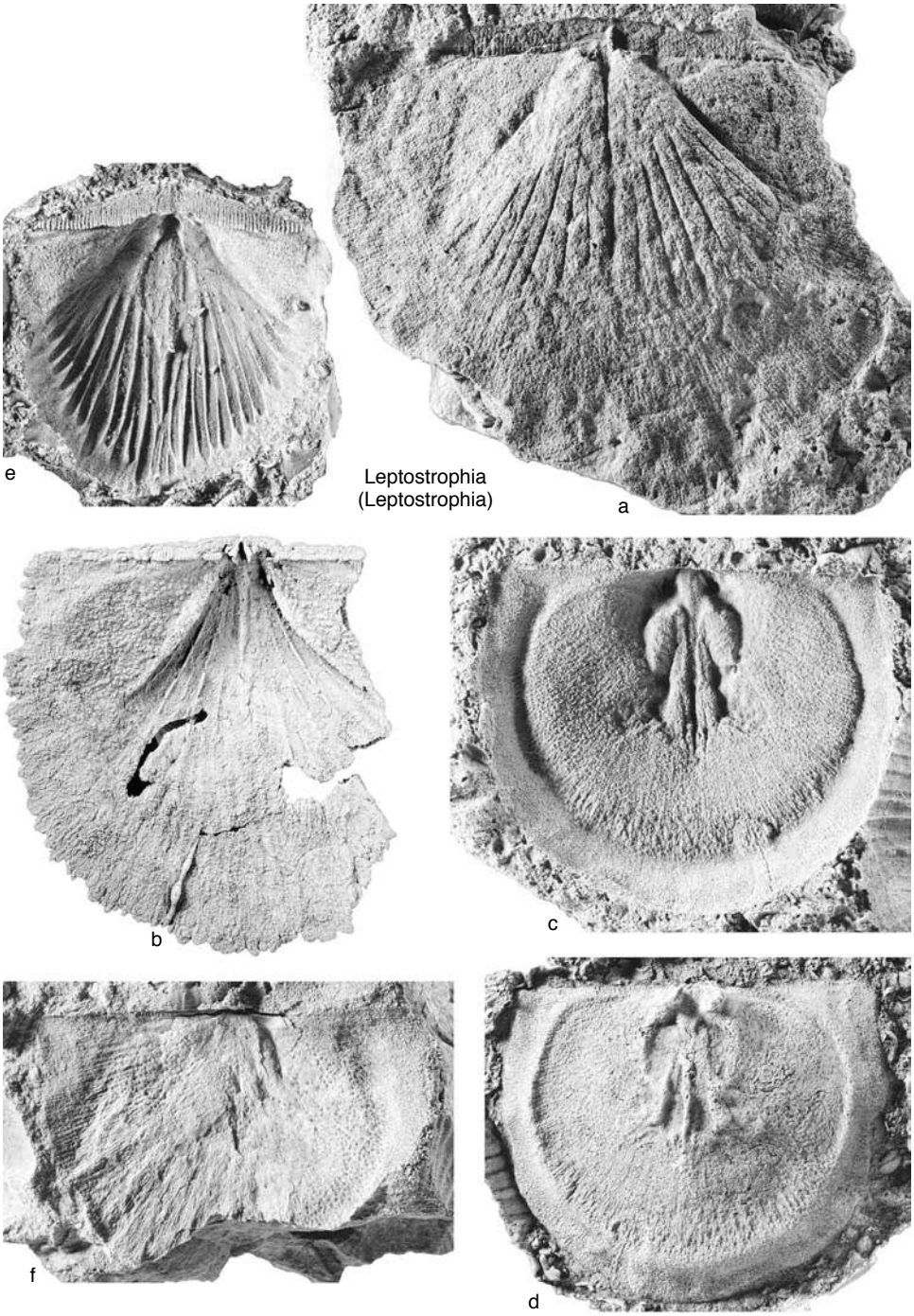

FIG. 176. Leptostrophiidae (p. 280).

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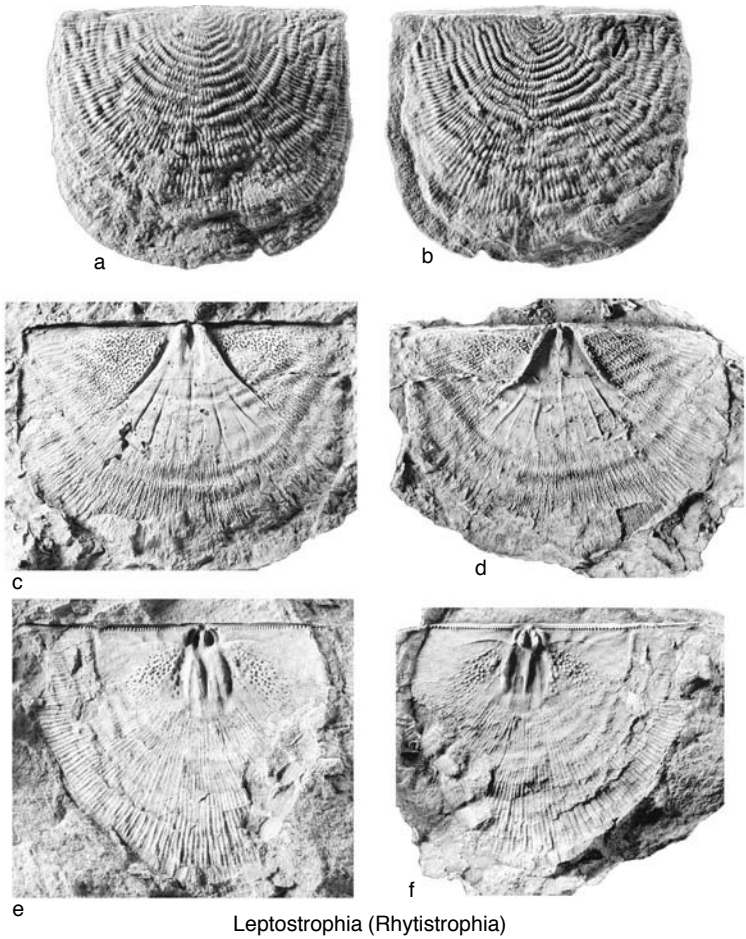

FIG. 177. Leptostrophiidae (p. 280–281).

chamber; ventral muscle field with bounding ridges posterolaterally only, partitioned by low radial ridges; cardinal process lobes elongate to ponderous but separated at their base, ventrally to posteroventrally directed; socket plates small, situated posterolaterally, close to cardinal process lobes, often curved subparallel with lobes; dorsal muscle-bounding ridges may be present laterally, posteriorly; small central dorsal septum variably developed; dorsal subperipheral rim variably present. *Devonian (Pragian–Emsian):* cosmopolitan.

L. (Leptostrophia). Similar to *L. (Rhytistrophia)* but lacking rugae except minimally at alae; distinctive tubular chamber in place of ventral process. *Devonian (Pragian–Emsian):* North America.——FIG. 176*a–d.* **L. (L.) magnifica* (HALL), Oriskany Sandstone, Pragian; *a,* lectotype, internal mold of ventral valve, Schoharie County, New York, AMNH 34789, ×0.75; *b,* ventral interior, Cumberland, Maryland, AMNH 34794, ×1; *c,d,* internal mold, latex cast of dorsal valve, Schoharie County, New York, BMNH BC 13063, ×1 (new).——FIG. 176*e,f. L. (L.) magniventra* (HALL), Oriskany Sandstone, Pragian, Schoharie, Schoharie County, New York; *e,* syntype, latex cast of mold of ventral valve, AMNH 34780, ×1; *f,* partly exfoliated dorsal valve, showing mold of cardinal process, AMNH 34782, ×1 (new).

L. (Rhytistrophia) CASTER, 1939, p. 86 [**Strophеodonta beckii* HALL, 1859a, p. 191; OD]. Similar to *L. (Leptostrophia),* but with ornament of variably developed, discontinuous concentric rugae; ventral process instead of tubular chamber. *Silurian (Ludlow)–Devonian (Emsian):* North America, Europe, Mongolia.——FIG. 177*a–f.* **L. (R.) beckii* (HALL), Helderberg Group, Pragian; *a,b,* lectotype, ventral, dorsal views of

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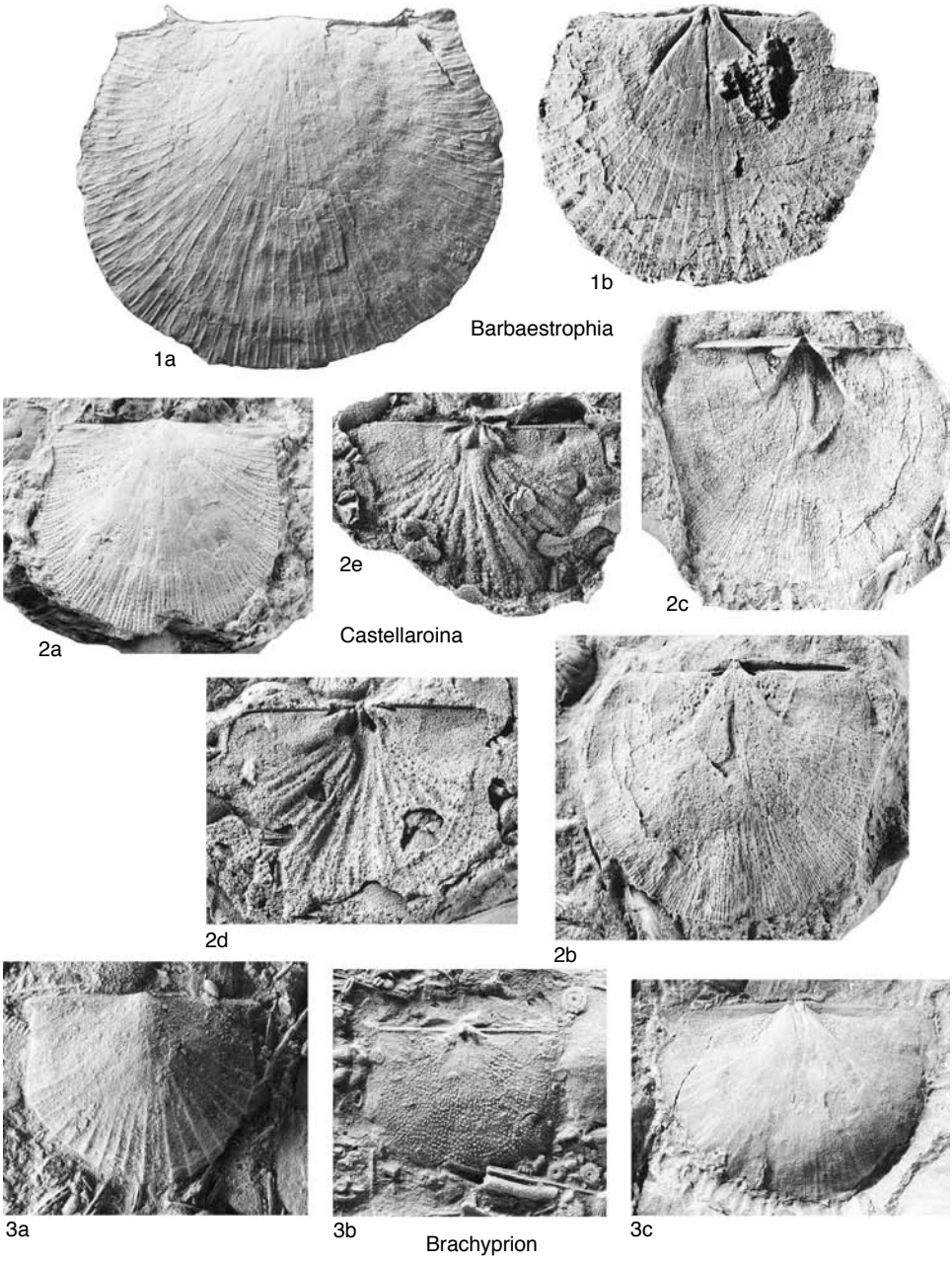

FIG. 178. Leptostrophiidae (p. 282).

conjoined valves, Schoharie, New York, AMNH 33162, ×1; *c,d,* ventral internal mold, latex cast, Becraft's Mountain, Columbia, New York, AMNH 33166, ×1; *e,f,* dorsal internal mold, latex cast, Becraft's Mountain, Columbia, New York, AMNH 33167, ×1 (new).

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?Barbaestrophia Havlíček, 1965a, p. 7 [**Strophomena praestans* Barrande, 1879, pl. 51–IV, fig. 1–7; OD]. Two to three pairs of curved spines extending posterolaterally from hinge line; family designation uncertain because dorsal interior unknown, but ventral muscle field typically leptostrophiid in its posterolateral bounding ridges and in its triangularity. *Devonian (Lochkovian):* Europe.——Fig. 178,*1a,b.* **B. praestans* (Barrande), Kotys Limestones, Lochkovian, Svaty Jan pod Skalou, Czech Republic; *a,* lectotype, ventral exterior, NM L6672, ×1.5; *b,* internal mold of ventral interior, OMR VH 427, ×1.5 (Havlíček, 1967).

Brachyprion Shaler, 1865, p. 63 [**Strophomena leda* Billings, 1860, p. 55; OD]. Profile gently to moderately concavoconvex; ornament mainly unequally parvicostellate, but may be costellate; denticles on denticular plates in ventral valve, small number on dorsal hinge line; dental plates absent; ventral muscle field usually triangular, but may be gently curved posterolaterally; muscle-bounding ridges weak or absent; cardinal process lobes erect, small, suboval, not united at their base; socket ridges thin, widely divergent; dorsal muscle field poorly impressed. *Silurian (Aeronian–Ludlow):* cosmopolitan.——Fig. 178,*3a,b.* **B. leda* (Billings), Jupiter Formation, Telychian, Anticosti Island, Quebec, Canada; *a,* lectotype, ventral exterior, ×2; *b,* dorsal interior, GSC 2442, ×2 (new).——Fig. 178,*3c. B.* sp., Vik Formation, Telychian, Porsgrunn, Norway; ventral internal mold, BMNH BC 6894, ×1.5 (new).

Castellaroina Boucot in Amos, 1972, p. 11 [**Tropidoleptus fascifer* Kayser, 1897, p. 291; OD]. Profile gently concavoconvex; unequally parvicostellate ornament; strong teeth with crenulations fused to vestigial dental plates; very finely denticulate for up to half hinge width; muscle-bounding ridges weak or absent although triangular ventral muscle field well impressed posterolaterally; strong cardinal process lobes positioned completely anterior to hinge line, not united at their base; short flaring socket ridges; dorsal muscle field poorly impressed. *Silurian (Ludlow, ?Přídolí):* Argentina.——Fig. 178,*2a–e.* **C. fascifer* (Kayser), Los Espejos Formation, Ludlow, Agua Negra, San Juan, Argentina; *a,* ventral exterior, BAU 7693, ×1.5; *b,c,* ventral internal mold, latex cast, BAU 7694, ×1.5; *d,e,* dorsal internal mold, latex cast, BAU 7700, ×2 (new).

Chynistrophia Havlíček, 1977b, p. 301 [**C. foliola;* OD]. Small subrectangular outline; planoconvex profile; similar to *Leptostrophia* apart from narrower diductor scars, no radial ridges in ventral muscle field, dorsal muscle field relatively small. *Devonian (Pragian):* Europe.——Fig. 179,*1a–c.* **C. foliola,* Chotec Limestone, Pragian, Chynice, Bohemia, Czech Republic; *a,* holotype, ventral exterior, OMR VH 2601, ×3.5; *b,* ventral internal mold, ×3.5; *c,* dorsal internal mold, ×4 (Havlíček, 1977b).

Eomegastrophia Cocks, 1967, p. 260 [**Megastrophia (E.) ethica;* OD]. Profile concavoconvex; ornament from unequally parvicostellate to uniformly costellate; dental plates present in parts or all of population; denticular plates with small number of denticles; ventral muscle field moderately impressed, muscle-bounding ridges absent; cardinal process lobes narrow, ventrally directed, not joined at bases; short anterolateral socket plates present; dorsal muscle field weakly impressed. *Silurian (Aeronian):* Europe, ?North America.——Fig. 180,*2a–c.* **E. ethica,* Pentamerus Beds, Aeronian, Morrellswood, Shropshire, England; *a,* holotype, mold of ventral interior, GSM 102715, ×1; *b,* mold of dorsal interior, GSM 102717, ×1; *c,* mold of dorsal interior, BMNH BC 13415, ×1.5 (Cocks, 1967).

Eostropheodonta Bancroft, 1949, p. 9 [**Orthis hirnantensis* M'Coy, 1851, p. 395; OD] [=*Aphanomena* Bergström, 1968, p. 13 (type, *A. schmalenseei;* OD); *Eoleptostrophia* Harper & Boucot in Amos, 1972, p. 11, *nom. nud.; Neokjaerina* Levy & Nullo, 1974, p. 191 (type, *Kjaerina (N.) florentina*); *Pirgumena* Rõõmusoks, 1993c, p. 163 (type, *P. martnai;* OD)]. Planoconvex to gently concavoconvex profile; ornament variable from unequally parvicostellate to fascicostellate, sometimes in same population; small denticular plates with few denticles; no denticles on hinge line; short but strong dental plates present, with crenulations; ventral process generally absent; muscle field in both valves obscure or faintly impressed; erect cardinal process lobes elongate, separated at their bases; socket ridges widely divergent; dorsal septa absent. *Ordovician (Ashgill)–Silurian (Wenlock):* cosmopolitan.——Fig. 181*a–d.* **E. hirnantensis* (M'Coy), Ashgill; *a,* latex of dorsal exterior, Husbergøya Formation, Rambergøya, Oslo, Norway, BMNH BB 93972, ×1.5; *b,c,* dorsal internal mold, latex cast, Husbergøya Formation, Rambergøya, Oslo, Norway, BMNH BB 94003, ×2; *d,* ventral internal mold, Hirnant Formation, Aber Hirnant, near Bala, Gwynedd, Wales, BMNH B 89573, ×1.5 (new).——Fig. 181*e–g. E. schmalenseei* (Bergström), lower *Dalmanitina* Beds, Ashgill; *e,* latex cast of external mold of conjoined valves, Stommen, Västergötland, Sweden, LO 4249, ×1.5 (Bergström, 1968); *f,* ventral internal mold, Stommen, BMNH B 90684, ×1 (new); *g,* holotype, latex cast of dorsal internal mold, Allebergsände, Västergötland, Sweden, LO 4248, ×1 (Bergström, 1968).——Fig. 181*h,i. E. martnai* (Rõõmusoks), Adila Formation, Pirgu Stage, Ashgill, Härküla, Aruküla, Estonia; *h,* ventral external mold, GMUT Br 1492, ×1; *i,* dorsal internal mold, GMUT Br 1477, ×1 (Rõõmusoks, 1993c).——Fig. 181*j,k. E. florentina* (Levy & Nullo), Don Braulio Formation, Ashgill, Villicun Range, San Juan Province, Argentina; *j,* holotype, latex cast of ventral exterior, DNGM 14994, ×2; *k,* latex cast of ventral exterior,

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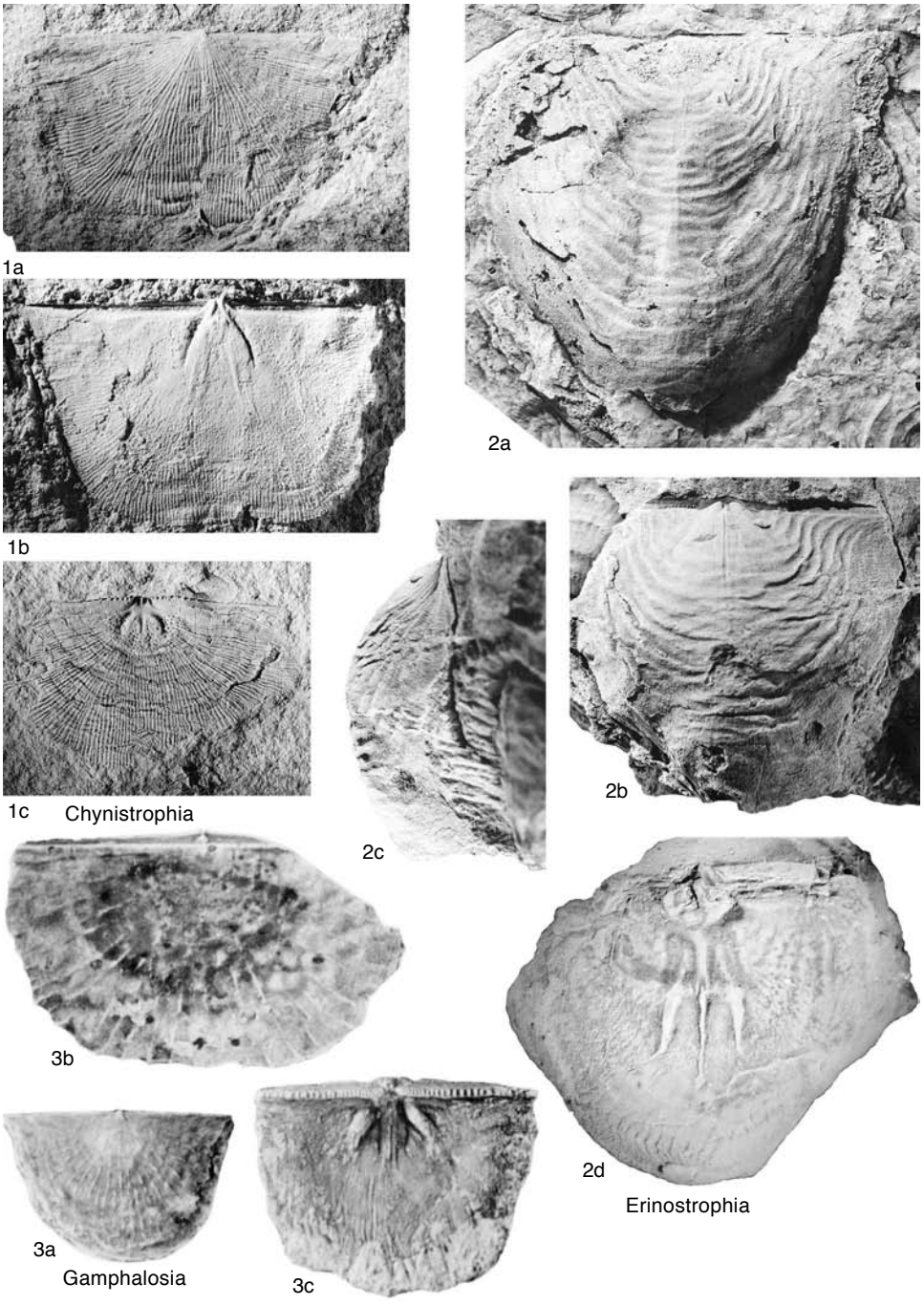

FIG. 179. Leptostrophiidae (p. 282–286).

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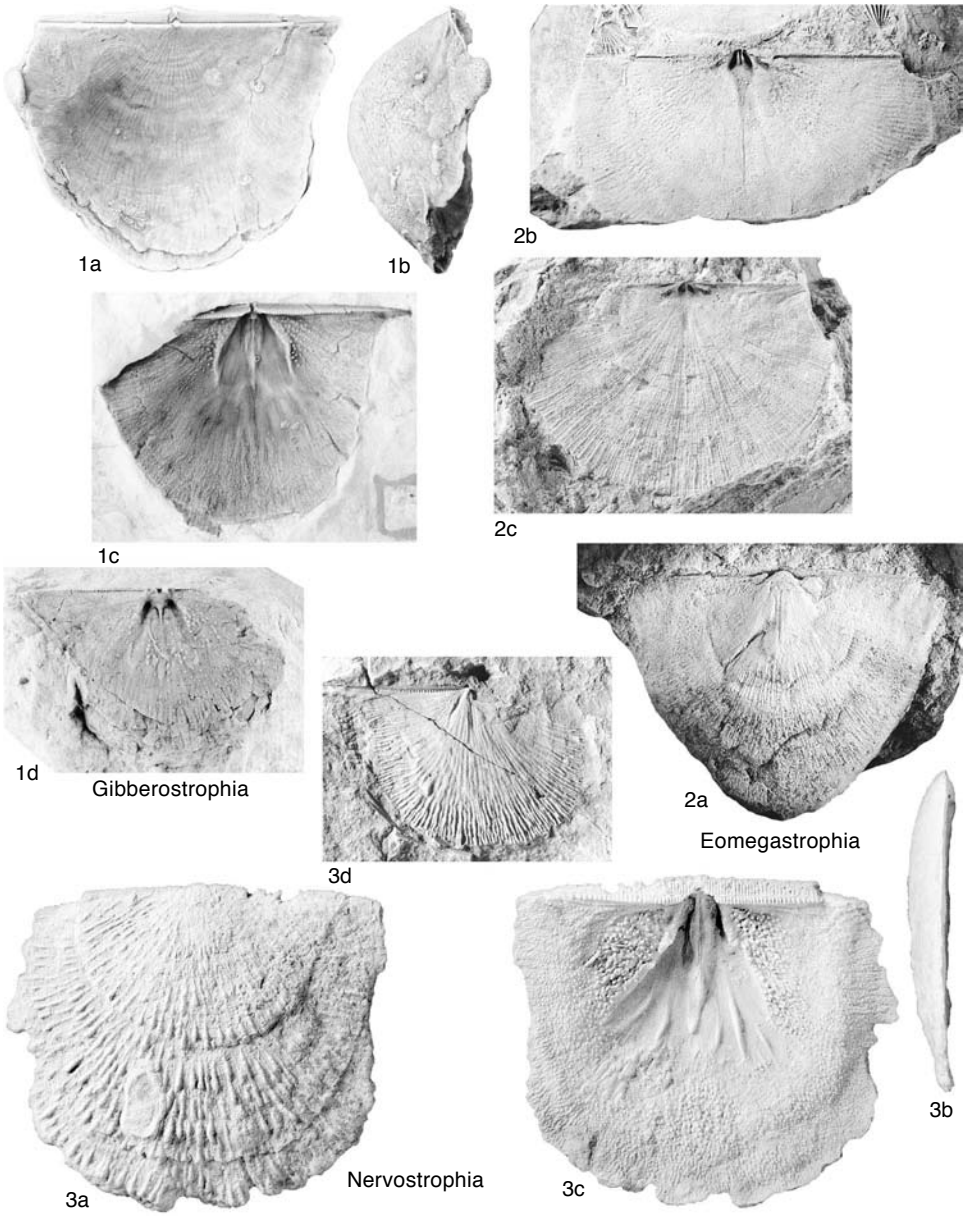

FIG. 180. Leptostrophiidae (p. 282–286).

dorsal interior, *ex* DNGM 14995, ×5 (Benedetto, new).

Erinostrophia COCKS & WORSLEY, 1993, p. 44 [**Orthis undata* M'COY, 1846, p. 36; OD]. Strongly concavoconvex profile; similar to *Protomegastrophia,* but with pronounced but discontinuous rugae over whole shell; rounded rather than bladelike cardinal process lobes. *Silurian (Telychian):* Europe.——FIG. 179,*2a–d. *E. undata,* Telychian; *a,* external mold of dorsal valve, Porsgrunn Formation, Skien, Norway, BMNH BC 6806, ×1.5; *b,c,* ventral, lateral views of ventral internal mold, Bruflat Formation, Sogn, Hadeland, Norway, BMNH BC 6686, ×1.5; *d,* dorsal interior, lower Visby Beds, Visby, Gotland, Sweden, BMNH B 13611, ×1 (Cocks & Worsley, 1993).

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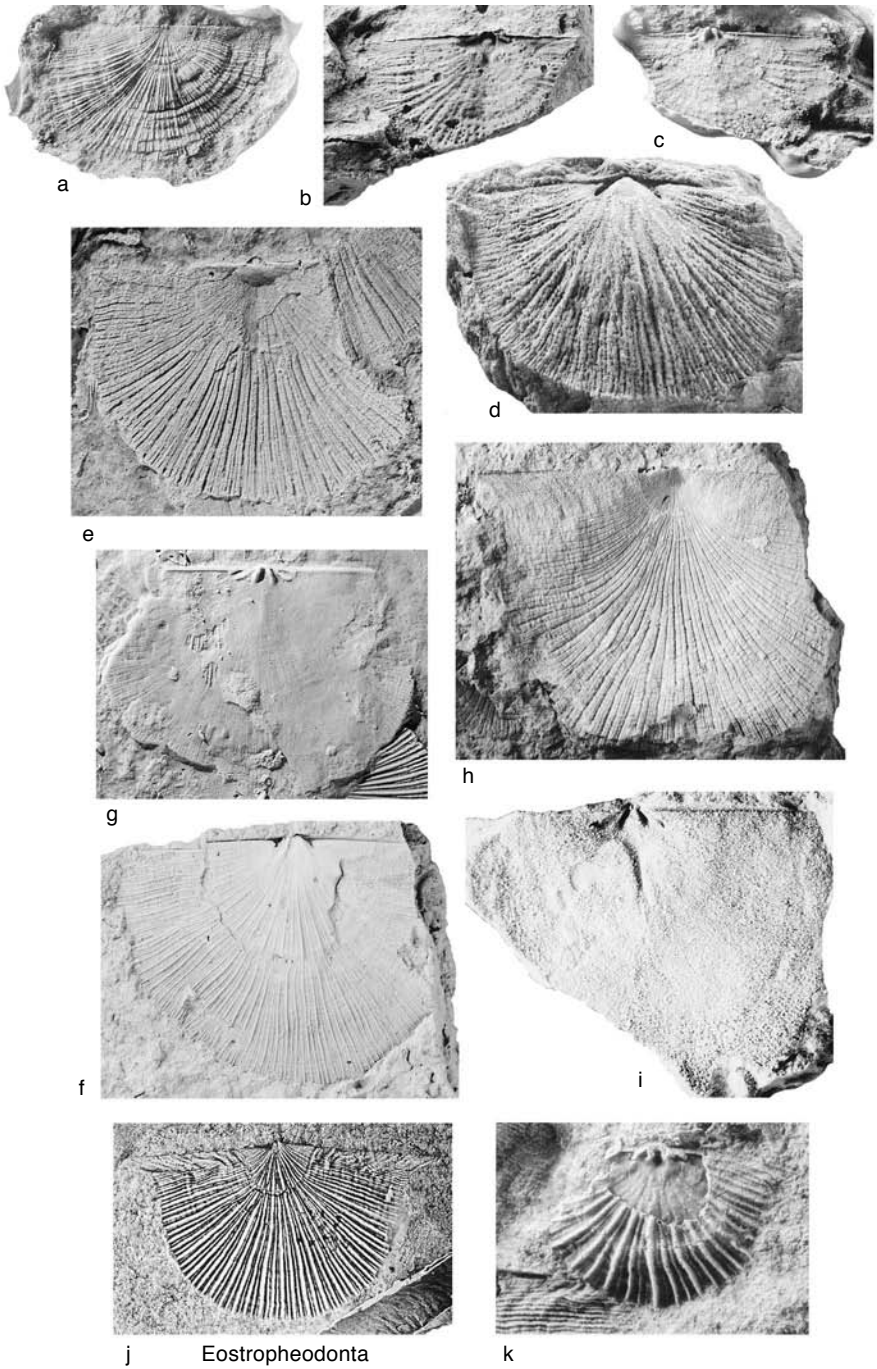

FIG. 181. Leptostrophiidae (p. 282).

Gamphalosia STAINBROOK, 1945, p. 33 [**G. tenuissima;* OD]. Profile gently resupinate; ornament with costellae of variable strength as in *Nervostrophia* but more pronounced on ventral than dorsal valve; weak rugae also developed sporadically. *Devonian (Frasnian):* North America, Europe.——FIG.

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179,*3a–c.* **G. tenuissima,* Independence Shale, Frasnian, Brandon, Iowa; *a,* ventral valve exterior, SUI MAS 858b, ×2; *b,* dorsal view of exterior of conjoined valves, SUI MAS 859B, ×3; *c,* ventral valve interior, SUI MAS 859, ×3 (Harper & Boucot, 1978).

Gibberostrophia Harper & Boucot, 1978, p. 79 [**Strophеodonta gibbera* Amsden, 1958, p. 73; OD]. Profile strongly concavoconvex; ornament uniformly costellate; denticulation over most of hinge line; muscle field deeply impressed in both valves laterally, posteriorly, becoming fainter anteriorly; with slightly curved bounding ridges posterolaterally in ventral valve; ventral process well developed; myophragm present in both valves; cardinal process lobes elongate, close together but not united; socket ridges abbreviated, close to but separate from cardinal process lobes. *Devonian (Lochkovian):* North America.——Fig. 180,*1a–d.* **G. gibbera* (Amsden), Haragan Formation, Lochkovian, Hunton, Arbuckle Mountains, Oklahoma; *a,b,* holotype, dorsal, lateral views of conjoined valves, OKGS 930, ×1.5; *c,* ventral interior, OKGS 927, ×1.5; *d,* dorsal interior, OKGS 924, ×1.5 (new).

Mesoleptostrophia Harper & Boucot, 1978, p. 68 [**M. kartalensis;* OD, *nom. nov. pro Strophеodonta (Leptostrophia) explanata* Paeckelmann & Sieverts, 1932, *non* Sowerby, 1842 in 1840–1846, p. 40; Kartal-schichten (Emsian), Turkey] [=*Leptostrophiella* Harper & Boucot, 1978, p. 74 (type, *Leptaena explanata* Sowerby, 1842, p. 409; OD); *Mitchellella* Strusz, 1984, p. 126 (type, *Strophеodonta quadrata* Mitchell, 1923, p. 469; OD)]. Outline semicircular to subquadrate; profile biplanate to gently concavoconvex; ornament unequally parvicostellate to uniformly costellate; denticulate over most of valve width; small ventral process present; subtriangular to bilobed ventral muscle field with bounding ridges variably developed posterolaterally; variable, usually small, cardinal process lobes. *Silurian (Telychian)–Devonian (Eifelian):* cosmopolitan.

M. (Mesoleptostrophia). Relatively small cardinal process lobes, ventroposteriorly directed, close posteriorly, convergent anteriorly, continuous with median ridge. *Silurian (Telychian)–Devonian (Emsian):* cosmopolitan.——Fig. 182,*2a–c. M. (M.) quadrata* (Mitchell), Bowning Beds, Ludlow, Bowning Railway Station, New South Wales, Australia; *a,b,* latex cast of external, internal molds of ventral valve, CPC 24006, ×2; *c,* latex cast of dorsal internal mold, AMF 28820, ×5 (Strusz, new).——Fig. 182, *2d,e. M. (M.) explanata* Sowerby, Coblenzian, Emsian; *d,* internal mold of ventral valve, Daun, BMNH B 42798, ×1; *e,* internal mold of dorsal valve, Grünbach, Germany, BMNH B 24570, ×1 (new).

M. (Paraleptostrophia) Harper & Boucot, 1978, p. 70 [**Leptostrophia clarkei* Chatterton, 1973, p. 58; OD]. Ventral valve as in *M. (Mesoleptostrophia),* but cardinal process lobes strongly posteriorly directed with thin socket ridges parallel to lateral margins of cardinal process lobes, turning to extend laterally as low ridges subparallel to hinge line; dorsal median septum present; curved bounding ridges posterolateral to dorsal muscle field. *Devonian (Emsian–Eifelian):* Australia, Burma.——Fig. 182,*1a–c.* **M. (P.) clarkei* (Chatterton), Warroo Limestone, Emsian, Yass, New South Wales, Australia; *a,b,* holotype, exterior, interior views of ventral valve, ANU 18934, ×1; *c,* dorsal interior, ANU 18935e, ×1.5 (Campbell, new).

Nervostrophia Caster, 1939, p. 79 [**Strophomena nervosa* Hall, 1843a, p. 266; OD]. Profile gently concavoconvex to planoconvex; distinctive ornament of radial costellae that are intermittently discontinuous over whole shell; hinge line completely denticulate; triangular ventral muscle field similar to *Leptostrophia* with some radial ridges, open anteriorly; ventral process continuous with myophragm; ponderous but short cardinal process lobes ventrally, posteriorly directed, short socket plates subparallel with cardinal process lobes; prominent dorsal muscle-bounding ridges. *Devonian (?Givetian, Frasnian):* cosmopolitan.——Fig. 180,*3a–d.* **N. nervosa* (Hall), Frasnian; *a–c,* external, lateral, internal views of ventral valves, Hackberry Formation, Frasnian, Rockford, Iowa, BMNH B 41544, ×1.5; *d,* syntype, ventral internal mold, Chemung Group, Bath, New York, AMNH 37205, ×1 (new).

Palaeoleptostrophia Rong & Cocks, 1994, p. 683 [**Strophеodonta jamesoni* Reed, 1917, p. 893; OD]. Profile biplanate to gently concavoconvex; ornament of gently curved unequal parvicostellae; no dental plates; denticles confined to small denticular plates in ventral valve interlocking with corresponding denticles on dorsal hinge line; muscle field poorly impressed in both valves, bounding ridges absent; ventral process weakly developed; thin short myophragm present; cardinal process lobes anteroventrally directed, divergent; thin platelike socket ridges with crenulations on posterior facets. *Silurian (Rhuddanian–Aeronian):* Europe, ?North America.——Fig. 183,*4a–c.* **P. jamesoni* (Reed), Woodland Formation, Rhuddanian, Woodland Point, near Girvan, Strathclyde, Scotland; *a,* ventral internal mold, BMNH BC 2454, ×1.5; *b,c,* dorsal internal mold, latex cast, BMNH BC 2471, ×1.5 (Rong & Cocks, 1994).

Protoleptostrophia Caster, 1939, p. 75 [**Strophomena blainvillii* Billings, 1874, p. 28; OD] [=*Siberistrophia* Astashkina, 1970, p. 131 (type, *Brachyprion speranskii* Khalfin, 1948, p. 274; OD); *Tastaria* Havlíček, 1965a, p. 6 (type, *Leptostrophia tasta* Rukavishnikova, 1961, p. 52; OD)]. Similar to *L. (Leptostrophia),* but with strong ventral process, without radial ridges in ventral muscle field; socket ridges absent in most specimens, although very faint in few members of populations. *Devonian (Lochkovian–Frasnian):* cosmopolitan.——Fig.

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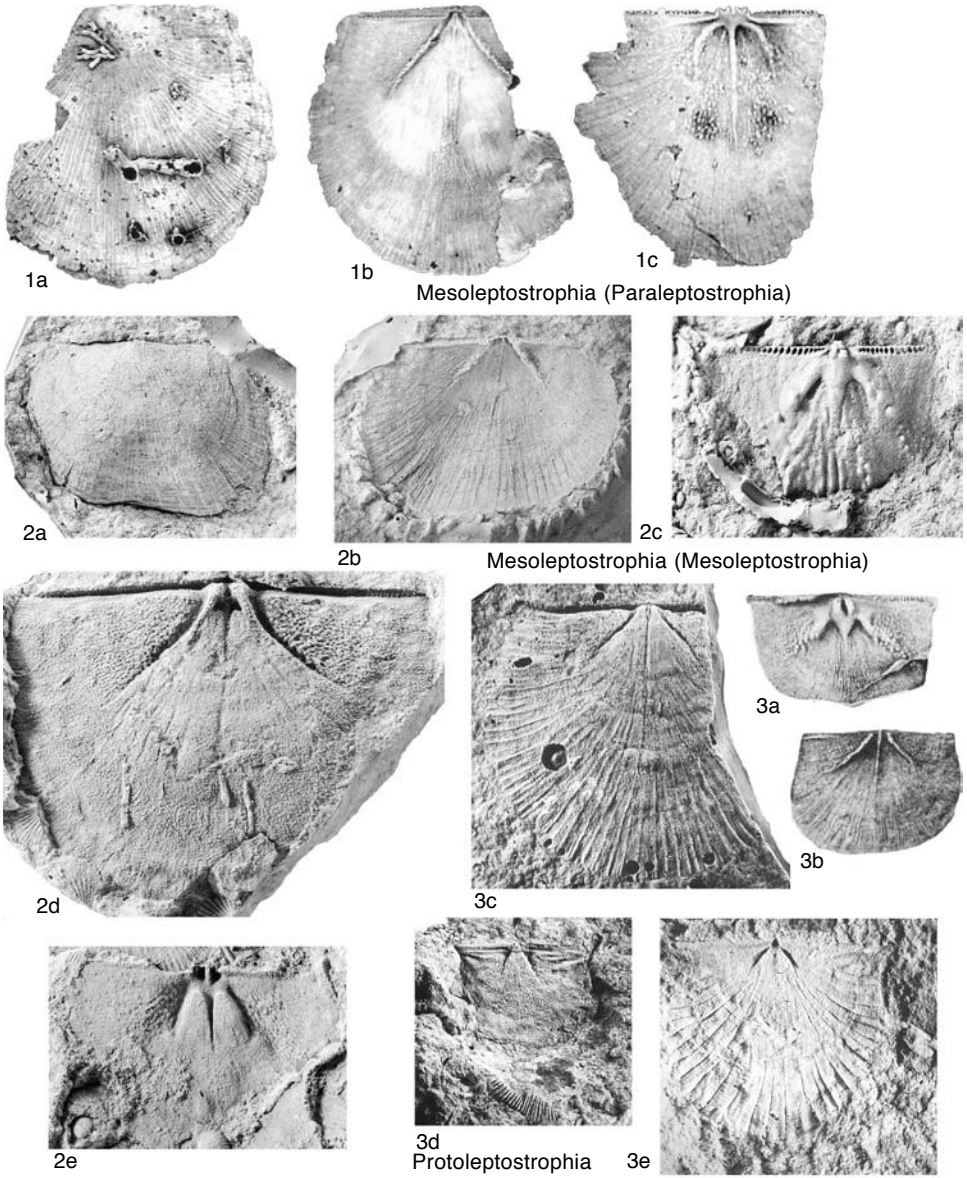

FIG. 182. Leptostrophiidae (p. 286–287).

182,*3a,b.* **P. blainvillii* (BILLINGS), Gaspé Sandstones (Devonian), St. John River, York Township, Gaspé, Quebec, Canada; *a,* plasticine cast of mold of dorsal interior, USNM 112091a, ×1; *b,* plasticine cast of mold of ventral interior, USNM 112091b, ×1 (Williams, 1953a).——FIG. 182,*3c–e. P. tasta* (RUKAVISHNIKOVA), Karazhirik Formation, Lochkovian; *c,* holotype, ventral internal mold, Tastuibulak well, MANK 67/9, ×1; *d,* ventral internal mold, Kogan well, north Pribalkash, Kazakhstan, MANK 67/13, ×1; *e,* dorsal internal mold, Tastuibulak well, MANK 67/17, ×1 (Rukavishnikova, 1961).

Protomegastrophia CASTER, 1939, p. 36 [**Leptaena profunda* HALL, 1852, p. 61; OD]. Profile moderately to strongly concavoconvex; ornament usually parvicostellate but rarely subuniformly costellate; denticles on denticular plates may stretch laterally

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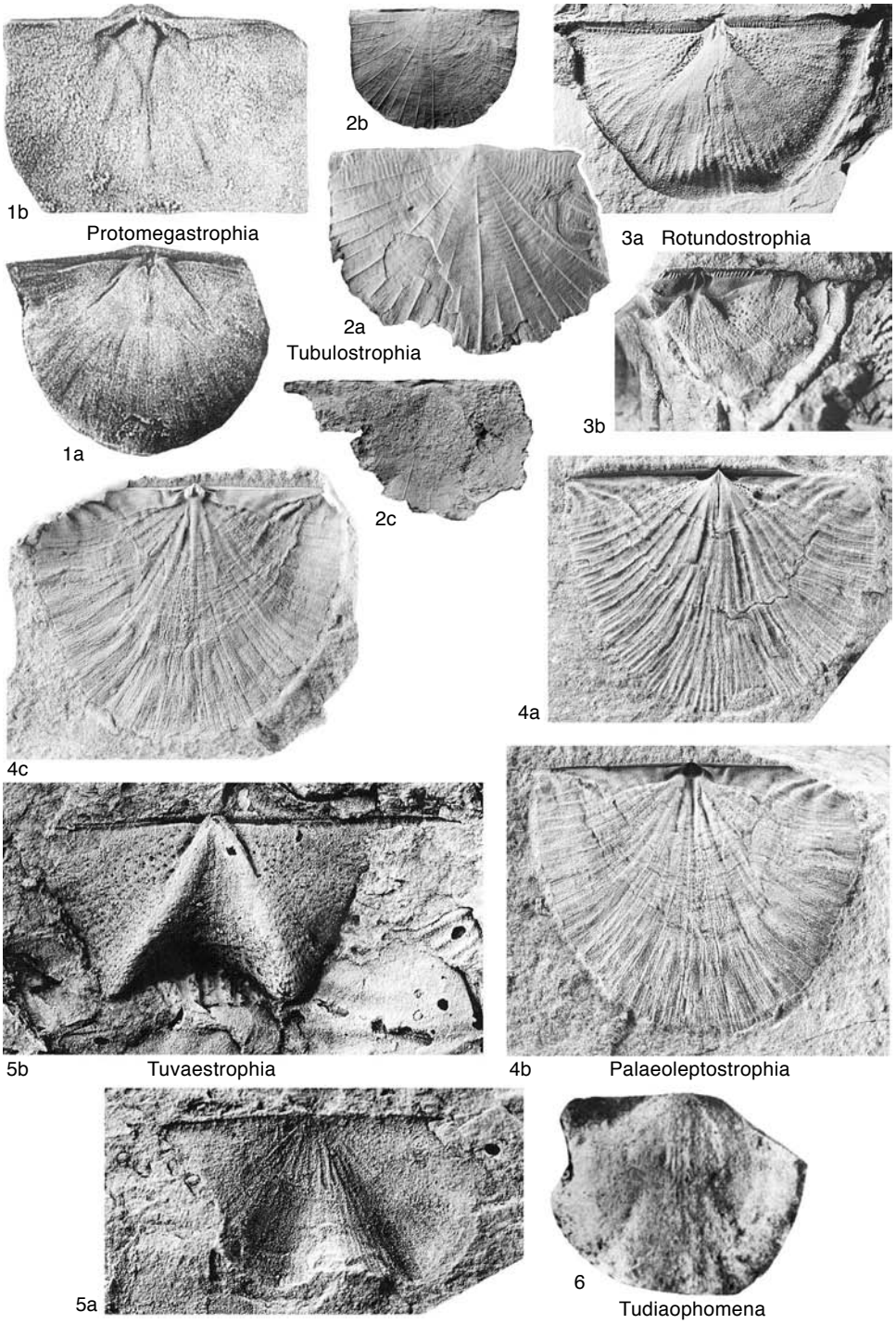

FIG. 183. Leptostrophiidae (p. 286–289).

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up to one-third of hinge line; ventral muscle field bounding ridges developed for short distance posterolaterally; small but distinct ventral process, myophragm present; strong cardinal process lobes divergent, separated at base, directed ventrally; cardinal process pit present; socket ridges short; dorsal muscle field with faint bounding ridges posterolaterally. *Silurian (Telychian)–Devonian (Lochkovian):* cosmopolitan.——Fig. 183,*1a,b. *P. profunda* (Hall), Racine Formation, Wenlock, Racine, Wisconsin; *a,* ventral internal mold, USNM 11637a, ×0.75; *b,* dorsal internal mold, USNM 116372b, ×1.5 (Williams, 1953a).

Rotundostrophia Gratsianova in Gratsianova, Zinchenko, & Kul'kov, 1960, p. 439 [**Leptodontella rotundata* Khalfin, 1948, p. 278; OD]. Similar to *Leptostrophia* but more transverse outline, no ventral muscle field radial ridges, ventrally geniculate near anterior margin; cardinal process lobes ventrally directed; dorsal muscle-bounding ridges strong for short distance posterolaterally. *Devonian (Emsian):* Russia.——Fig. 183,*3a,b. *P. rotundata* (Khalfin), Kondratev Formation, lower Emsian, Kondratev, Altai Mountains, Russia; *a,* internal mold of ventral valve, TsGM 377/29, ×2; *b,* internal mold of dorsal valve, TsGM 377/26, ×3 (Gratsianova, new).

?Tubulostrophia Havlíček, 1967, p. 139 [**Leptaena fugax* Barrande, 1848, p. 233; OD]. Profile flat to gently concavoconvex; semicircular outline; ornament unequally parvicostellate, sometimes with fine rugae developed posteriorly; delicate pedicle tube preserved; small, very fine cardinal process lobes, but ventral interior poorly known and family uncertain, although hinge line denticulate for about one-third of its width; poorly impressed muscle fields. *Devonian (Pragian–Emsian):* Europe.——Fig. 183,*2a–c. *T. fugax* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Bohemia, Czech Republic; *a,* ventral valve exterior, OMR VH 448a, ×1.5; *b,* internal mold of ventral valve, OMR VH 449b, ×1.5; *c,* brachial valve internal mold, OMR VH 499a, ×1.5 (Havlíček, 1967).

?Tudiaophomena Xian in Xian & Jiang, 1978, p. 266 [**T. plicata;* OD]. Interiors poorly known, perhaps leptostrophiid due to outline, profile, but treated here as a *nomen dubium. Silurian (Telychian):* China.——Fig. 183,*6. *T. plicata,* Xiushan Formation, upper Telychian, Tudi-ao, Yanhe County, Guizhou Province, China; ventral valve internal mold, GB 353, ×1 (Xian & Jiang, 1978).

Tuvaechonetes Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 114 [**T. insolitus;* OD]. Triangular ventral muscle field, lack of spines, clear denticulation reveal its leptostrophiid rather than chonetid affinities; ornament unequally costellate; long lateral hinge line extensions. *Silurian (Přídolí):* Russia.——Fig. 184,*2a,b. *T. insolitus,* Přídolí beds, Pichi-Shuy, Tuva, Russia; *a,* internal mold of ventral valve, IGiG SO 116, ×3; *b,* internal mold of dorsal valve, IGiG SO 117, ×2 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Tuvaestrophia Kulkov in Kulkov, Vladimirskaya, & Rybkina, 1985, p. 100 [**T. elegantula;* OD]. Transverse outline with extended alae, distinctive triangular ventral sulcus, dorsal fold; ornament of fine costellae; triangular ventral muscle field with strong posterolateral bounding ridges, open anteriorly; dorsal valve interior poorly known. *Silurian (Ludlow, ?Přídolí):* Russia.——Fig. 183,*5a,b. *T. elegantula,* Pichishuysk Formation, Ludlow, Pichi-Shuy, Tuva, Russia; *a,* mold of ventral exterior, IGiG SO N78a, ×4; *b,* holotype, mold of ventral interior, IGiG SO N78, ×4 (Kulkov, Vladimirskaya, & Rybkina, 1985).

Velostrophia Havlíček, 1965a, p. 7 [**Strophomena insolita* Barrande, 1879, pl. 52, fig. 1, pl. 128, fig. 3, pl. 143, fig. VI–3; OD]. Distinctive outline of spinelike projections curving posterolaterally from lateral extremities, also irregular plications around anterior commissure; variably geniculate profile; ventral muscle field narrowly divergent for family, with small muscle-bounding ridges, open anteriorly; myophragm present; cardinalia as in *Mesoleptostrophia;* curved dorsal muscle-bounding ridges posterolaterally. *Devonian (Pragian–Emsian):* Europe.——Fig. 184,*1a–c. *V. insolita* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* lectotype, ventral exterior, NM L6459, ×1.5; *b,* ventral interior, OMR VH 426a, ×1.5; *c,* dorsal internal mold, OMR VH 429c, ×2 (Havlíček, 1967).

Viodostrophia Villas & Cocks, 1996, p. 579 [**V. alcaldei;* OD]. Planoconvex to gently concavoconvex profile; uniformly parvicostellate ornament; no dental plates, with denticles restricted to denticular plates in ventral valve, posterior edge of divergent socket ridges in dorsal valve; subtriangular ventral muscle field with short straight posterolateral bounding ridges; open anteriorly; similar to *Palaeoleptostrophia,* but with muscle-bounding ridges; similar to *Eostropheodonta,* but no dental plates. *Silurian (Telychian):* Spain.——Fig. 184,*3a–e. *V. alcaldei,* El Castro Formation, Telychian, Viodo, Asturias, Spain; *a–c,* holotype, latex, internal mold, latex of ventral interior, DPO 29362, ×3; *d,e,* internal mold, latex of dorsal interior, DPO 29368, ×3 (Villas & Cocks, 1996).

Family EOPHOLIDOSTROPHIIDAE Rong & Cocks, 1994

[Eopholidostrophiidae Rong & Cocks, 1994, p. 690]

Profile moderately to strongly concavoconvex; denticles on hinge line or denticular plates; triangular ventral muscle field very weakly impressed, open anteriorly, with no muscle-bounding ridges except for short distance posterolaterally; no radial ridges in muscle field, unlike some Leptostrophiidae; cardinal process lobes small, separate,

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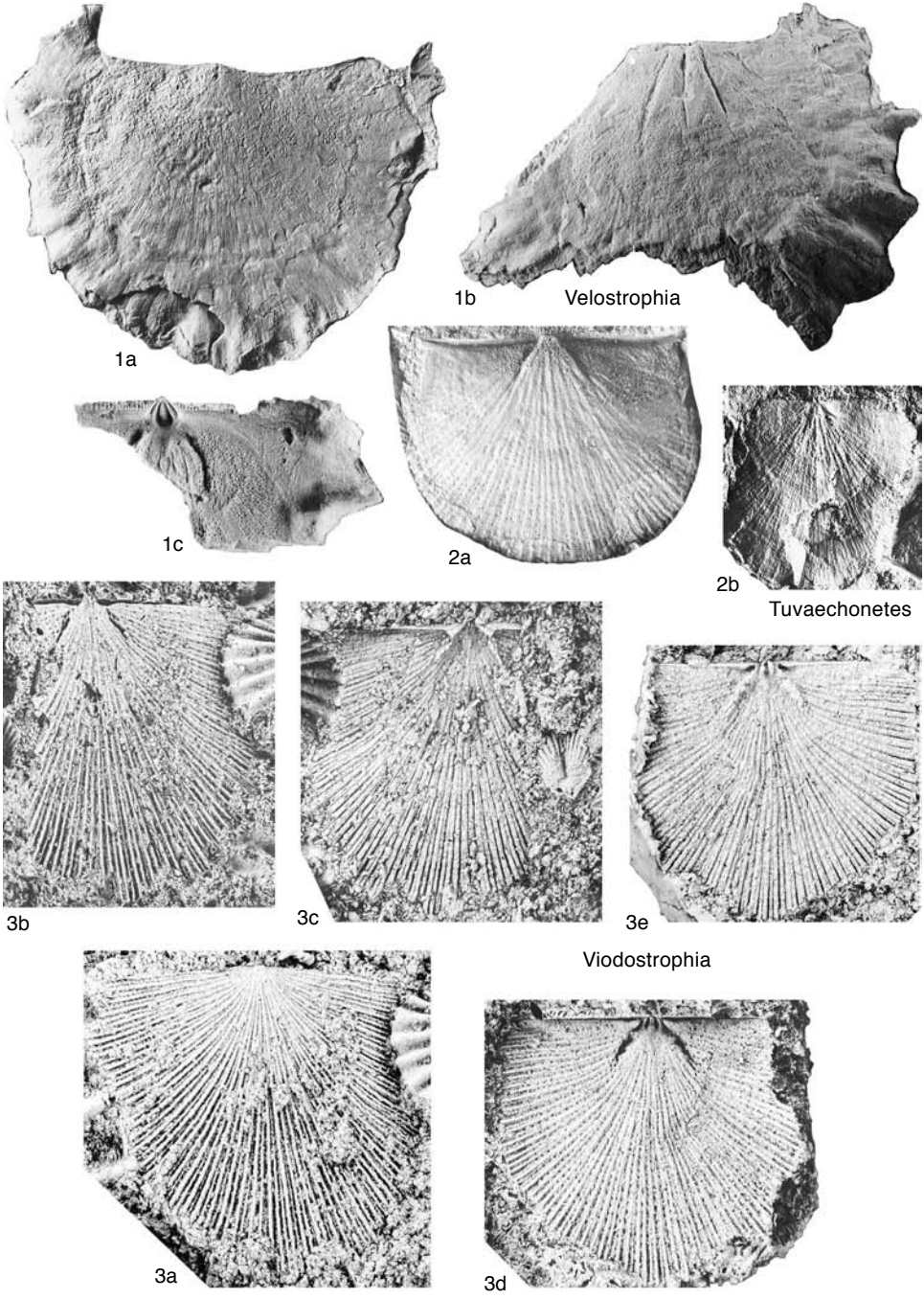

FIG. 184. Leptostrophiidae (p. 289).

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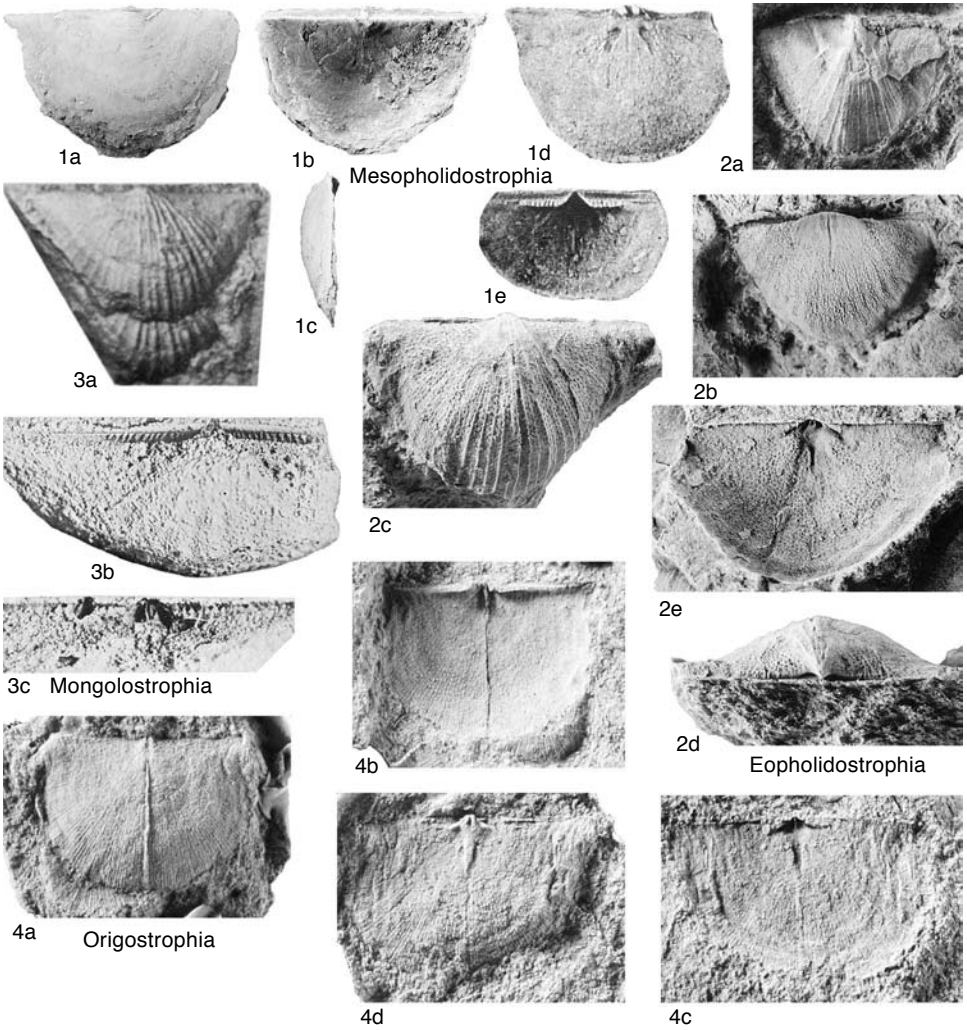

FIG. 185. Eopholidostrophiidae (p. 291–292).

ventrally directed; short thin socket ridges; dorsal side septa absent. *Ordovician (Ashgill)–Silurian (Ludlow).*

Eopholidostrophia HARPER, JOHNSON, & BOUCOT, 1967, p. 411 [**Stropheodonta sefinensis* WILLIAMS, 1951, p. 124; OD]. Profile concavoconvex, usually transverse, with thin body cavity; ornament finely costellate to unequally parvicostellate, sometimes with accentuated median rib; denticles on denticular plate; few denticles may be present along short distance of dorsal hinge line near umbo; ventral muscle field weakly impressed, without bounding ridges; cardinal process lobes elongate, ventrally directed, situated between thin, short socket ridges; dorsal muscle field very weakly impressed; weak dorsal myophragm posteriorly only. *Ordovician (Ashgill)–Silurian (Telychian):* cosmospolitan.——FIG. 185,*2a–e. *E. sefinensis* (WILLIAMS), Rhydings Formation, Aeronian, River Sefin, Llandovery, Dyfed, Wales; *a,* partly exfoliated ventral exterior,

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BMNH BB 95809, ×3; *b,* holotype, internal mold of ventral valve, SM 30051, ×2; *c,d,* ventral, posterior views of ventral internal mold, BMNH BB 95813, ×3; *e,* internal mold of dorsal valve, BMNH BB 95790, ×3 (new).

Mesopholidostrophia Williams, 1950, p. 278 [**Pholidostrophia (M.) nitens;* OD] [=*Mesolissostrophia* Williams, 1950, p. 280 (type, *Lissostrophia (M.) pellucida;* OD, from same type locality as *P. (M.) nitens*)]. Similar to *Eopholidostrophia* in outline, profile, but ornament weak or almost absent; pedicle tube often preserved; nacreous shell often developed; denticulation spread along one-third to half of hinge line; ventral process present; cardinal process small, erect; dorsal muscle field weakly impressed posteriorly, open anteriorly; weak dorsal myophragm. *Silurian (Telychian–Ludlow):* cosmopolitan.——Fig. 185,*1a–e. *M. nitens* (Williams), Mulde Marl, Homerian, Klintehamn, Gotland, Sweden; *a–c,* ventral, dorsal, lateral views of conjoined valves, BMNH BC 12836, ×3 (new); *d,* ventral interior, USNM 116024b, ×3; *e,* dorsal interior, USNM 116024c, ×3 (Willliams, 1953a).

Mongolostrophia Rozman & Rong, 1993, p. 39 [**?Leptodonta ludmilae* Rozman, 1992, p. 19; OD]. Similar to *Origostrophia,* but with ornament of coarse wavy costellae with wide interspaces, prominent growth lines. *Silurian (Llandovery):* Mongolia.——Fig. 185,*3a–c. *M. ludmilae* (Rozman), Baidarik Formation, Aeronian, Gobi Altai, Mongolia; *a,* ventral exterior, PAN 3980/1343, ×2; *b,* ventral internal mold, PAN 3980/1850, ×5; *c,* dorsal internal mold, PAN 3980/1847, ×10 (Rozman & Rong, 1993).

Origostrophia Mitchell, 1977, p. 115 [**O. fragilis;* OD]. Transverse outline, gently concavoconvex profile; fine parvicostellate ornament with single enhanced median costella; hinge line bearing narrow but very wide denticular plates, each bearing 5 to 16 denticles, extending along hinge line for up to half its width; no dental plates; dorsal interior as in *Eopholidostrophia. Ordovician (Ashgill):* Ireland.——Fig. 185,*4a–d. *O. fragilis,* Killey Bridge Formation, Ashgill, Pomeroy, Northern Ireland; *a,b,* holotype, latex casts of ventral exterior, interior, GSM GU998-9, ×4; *c,d,* internal mold of dorsal valve, latex cast, GSM GU1007, ×4 (new).

Family STROPHODONTIDAE Caster, 1939

[*nom. correct.* Rong & Cocks, 1994, p. 666, *pro* Stropheodontidae Caster, 1939, p. 26] [=Pholidostrophiidae Sokolskaya, 1960, p. 215, *nom. transl. pro* Pholidostrophiinae Stainbrook, 1943, p. 44; Lissostrophiidae Harper & Boucot, 1978, p. 38]

Hinge line denticulate; ventral muscle field strongly impressed, but muscle-bounding ridges absent anteriorly, usually laterally; ventral muscle field subcircular to suboval; dorsal muscle field subelliptical, usually elevated on platform with bounding ridges; central dorsal median ridge or septum often present; dorsal side septa usually, but not always, developed. *Silurian (Ludlow)–Devonian (Frasnian).*

Strophodonta Hall, 1850, p. 348 [**Strophomena demissa* Conrad, 1842, p. 258; OD] [=*Cymbistropheodonta* Harper & Boucot, 1978, p. 38 (type, *Strophodonta cymbiformis* Swallow, 1860, p. 635; OD)]. Profile moderately to strongly concavoconvex; uniformly costellate ornamentation, varying from fine to coarse; entire hinge line denticulate; ventral muscle field moderately impressed, bilobed, but with no bounding ridges; adductor, diductor scars clearly differentiated; radial ridges variably developed in anterior part of diductor scars; cardinal process lobes strong, posteriorly directed, usually joined at their bases to form U-shaped structure; socket ridges very small, divergent; variably elevated dorsal muscle field with two pairs of adductor scars, lateral pair larger than median pair; prominent muscle-bounding ridges; short central dorsal median septum, short dorsal side ridges variably developed; subperipheral rim usually present. *Silurian (Přídolí)–Devonian (Frasnian):* North America, Europe.

- **S. (Strophodonta).** Similar to *S. (Asturistrophia)* but with weaker socket ridges and elevated dorsal muscle field. *Silurian (Přídolí)–Devonian (Frasnian):* North America, Europe.——Fig. 186,*2a–e. *S. (S.) demissa* (Conrad); *a–c,* ventral, dorsal, lateral views of conjoined valves, Hamilton Group, Eifelian–Givetian, Arkona, Ontario, Canada, BMNH B 75070, ×1.5; *d,* ventral interior, Hamilton Group, Eifelian–Givetian, Sylvania, Ohio, BMNH BB 23316, ×1; *e,* dorsal interior, Upper Ferron Point Formation (Givetian), Alpena County, Michigan, BMNH BB 16568, ×1.5 (new).——Fig. 186,*2f,g. S. (S.) cymbiformis* (Swallow), Hamilton Group, Frasnian, Fulton, Missouri; *f,g,* ventral, lateral views of ventral exterior, BMNH B 39797, ×1.5 (new).
- **S. (Asturistrophia)** García-Alcade, 1992, p. 72 [**A. insolita;* OD]. Similar to *S. (Strophodonta)* but stronger socket ridges, dorsal muscle field not elevated; dorsal subperipheral rim more marked. *Devonian (Emsian)*: Europe.——Fig. 186,*1a–c. *S. (A.) insolita,* La Ladrona Formation, upper Emsian, La Vela, Arnao, Avilés, Asturias, Spain; *a,* dorsal exterior, DPO 26399, ×1; *b,* ventral interior, DPO 27119, ×2; *c,* dorsal interior, DPO 26400, ×1 (García-Alcade, 1992).

Arbizustrophia García-Alcalde, 1972, p. 57 [**A. diaphragmata;* OD]. Small size; concavoconvex to planoconvex profile; evenly parvicostellate ornament; convex pseudodeltidium; weakly curved ventral muscle-bounding ridges posterolaterally; muscle field open anteriorly; dorsal interior as in

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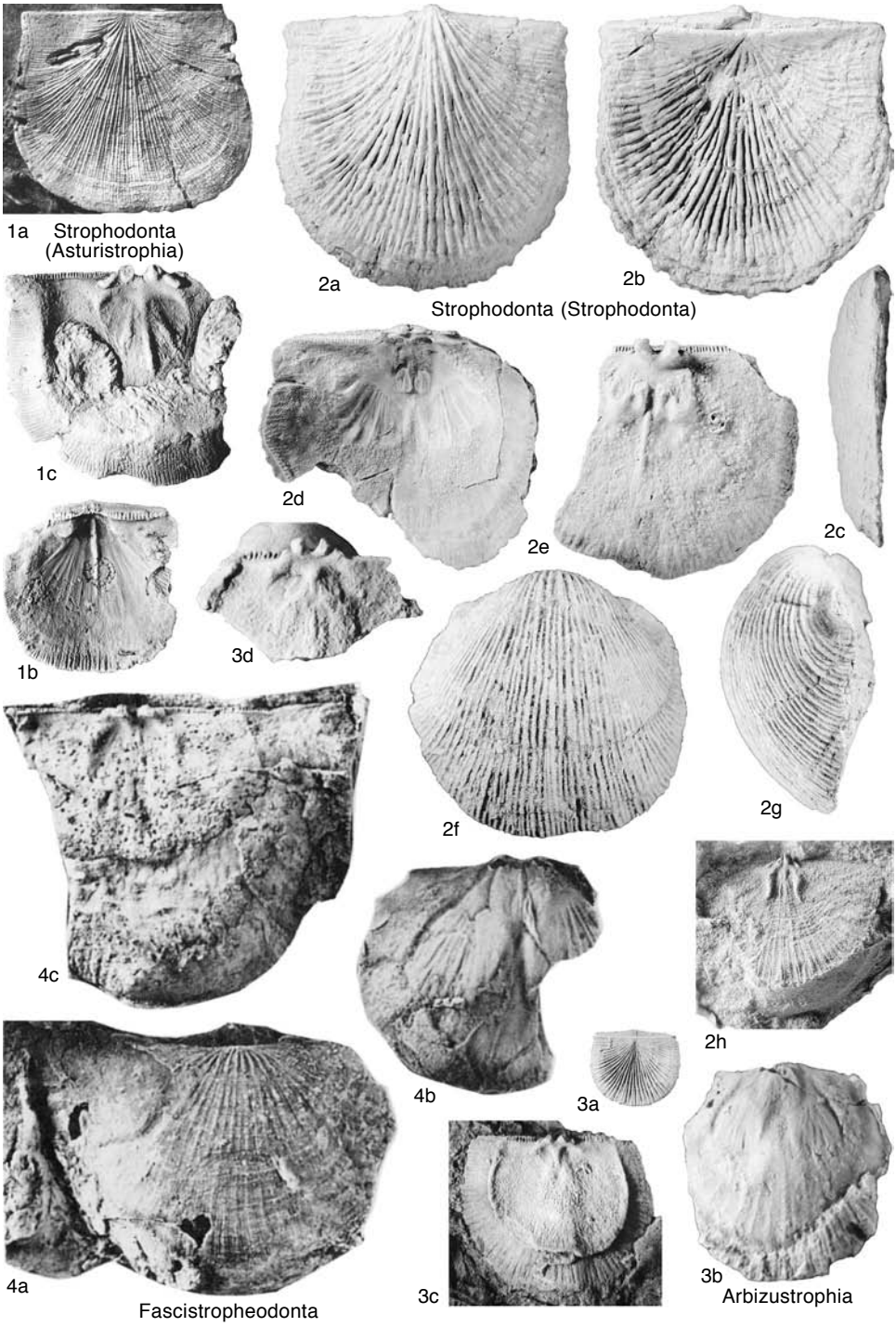

FIG. 186. Strophodontidae (p. 292–294).

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Strophodonta except denticles extending only half valve width, dorsal muscle-bounding ridges scarcely developed, diaphragm more pronounced. *Devonian (Emsian):* Europe.——Fig. 186,*3a–d. *A. diaphragmata,* Aguion Formation, Emsian; *a,* holotype, dorsal view of conjoined valves, Avilés, DPO 2622, ×1; *b,* ventral internal mold, Avilés, DPO 2663, ×2; *c,* dorsal interior, Luanco, Asturias, Spain, DPO 26563, ×2; *d,* fragment of dorsal interior showing cardinalia, Avilés, DPO 26747, ×3 (García-Alcalde, 1972).

Boucotstrophia Jahnke, 1981, p. 150 [**Stropheodonta herculea* Dreverman, 1904, p. 276; OD]. Profile concavoconvex, weakly dorsally geniculate; ornament unequally parvicostellate to finely costellate; denticles half valve width; ventral muscle field circular, with weak bounding ridges laterally, posteriorly, prominent radial ridges present within muscle field; cardinal process lobes large, close together, ventrally directed; small socket ridges flaring anterolaterally from near cardinal process lobes; elevated, elongate dorsal muscle field with prominent bounding ridges; central dorsal median ridge, faint side septa present. *Devonian (Pragian–Emsian):* Europe.——Fig. 187,*1a–c. *B. herculea* (Dreverman), Seifener Shale, Emsian, Altenkirchen, Germany; *a,* latex cast of dorsal exterior, SMF 66/424, ×1; *b,* ventral internal mold, SMF 72/43, ×0.75; *c,* latex cast of dorsal internal mold, SMF 163/4, ×1 (Jahnke, 1981).

Dictyostrophia Caster, 1939, p. 40 [**D. cooperi;* OD]. Strongly concavoconvex profile, sometimes weakly geniculate; ornament of coarse angular plications imposed on finer unequal parvicostellae; hinge line entirely denticulate; small short ventral median ridge present; cardinal process lobes posteriorly directed, joined at their bases; socket ridges thin, widely separated from cardinal process lobes; muscle-bounding ridges well developed in dorsal valve; variable muscle platform. *Devonian (Pragian–Eifelian):* cosmopolitan.

D. (Dictyostrophia). Similar to *D. (Plicostropheodonta),* but without elevated dorsal muscle platform, dorsal subperipheral rim. *Devonian (Emsian):* South America.——Fig. 187,*3a,b. *D. (D.) cooperi,* beds of Emsian age, Floresta, Colombia; *a,* dorsal exterior mold, USNM 220648, ×1; *b,* dorsal view of internal mold of conjoined valves, USNM 220649, ×1 (Harper & Boucot, 1978).

D. (Plicostropheodonta) Sokolskaya, 1960, p. 214 [**Orthis murchisoni* de Verneuil & d'Archiac in d'Archiac & de Verneuil, 1842, p. 371; OD]. Similar to *D. (Dictyostrophia),* but stronger plications, stronger dorsal muscle platform, dorsal subperipheral rim. *Devonian (Pragian–Eifelian):* Europe, Africa, New Zealand.——Fig. 187,*4a,b. *D. (P.) murchisoni* (de Verneuil & d'Archiac), Siegenian Beds, Humerich, Oberstadfeld, Eifel, Germany; posterior, ventral views of ventral internal mold, BMNH B 40574, ×1.5 (new).

Fascistropheodonta Harper & Boucot, 1978, p. 24 [**Orthis sedgwicki* d'Archiac & de Verneuil, 1842, p. 371; OD]. Strongly concavoconvex profile; ornament of angular plications, commonly forming fascicostellate bundles, superimposed on fine uniform costellae; large bilobed ventral muscle field with bounding ridges posterolaterally; interior as in *Dictyostrophia* but dorsal muscle field not raised, except posterolaterally, bounding ridges weaker; central dorsal median ridge variably present. *Devonian (Pragian–Eifelian):* Europe.——Fig. 186,*4a–c. *F. sedgwicki* (d'Archiac & de Verneuil), Wiltzer Schichten, upper Emsian, Daleiden, Eifel, Germany; *a,b,* dorsal external mold, ventral view of internal mold of conjoined valves, USNM 220753, ×1.5; *c,* latex cast of dorsal internal mold, USNM 220757, ×1.5 (Harper & Boucot, 1978).

Galateastrophia Harper & Boucot, 1978, p. 25 [**Stropheodonta galatea* Billings, 1874, p. 20; OD]. Strongly concavoconvex profile; distinctive ornament of strong plications on central part of both valves, anteriorly, laterally weaker, with fine parvicostellae present; hinge line entirely denticulate; variably impressed, large bilobed ventral muscle field, ventral median septum; cardinal process lobes posterior to hinge line, directed posteriorly; divergent socket ridges faint, short; dorsal muscle field small with distinctive transmuscle ridges and muscle-bounding ridges; central dorsal median ridge; dorsal side ridges. *Devonian (Emsian–Givetian):* North America.——Fig. 188,*1a–c. *G. galatea* (Billings), Grande Grève Limestone, lower Emsian, Indian Cove, Gaspé Bay, Quebec, Canada; *a,* dorsal view of conjoined valves, USNM 220705, ×3; *b,* ventral interior, USNM 220708, ×3; *c,* dorsal interior, USNM 220701, ×3 (Harper & Boucot, 1978).

Gorgostrophia Havlíček, 1967, p. 136 [**Leptaena neutra* Barrande, 1848, p. 231; OD]. Moderately concavoconvex profile; uniformly costellate or unequally parvicostellate ornamentation; denticulation over two-thirds valve width; ventral muscle field large, extending to two-thirds length; diductor, adductor scars separated by narrow myophragm that bifurcates anteriorly; short, wide cardinal process lobes posteroventrally directed; dorsal muscle field weakly impressed; long narrow, dorsal median septum extending anteriorly from near cardinal process. *Devonian (Pragian–Emsian):* Europe.——Fig. 187,*2a–d. *G. neutra* (Barrande), Pragian, Koneprusy, Czech Republic; *a,* ventral exterior, Vinarice Limestone, Pragian, Certovy schody, OMR VH 416, ×1.4; *b,* ventral interior, Koneprusy Limestone, NM L6743, ×1.5; *c,* ventral internal mold, Koneprusy Limestone, OMR VH 415a, ×1.5; *d,* dorsal internal mold, Vinarice Limestone, Certovy schody, OMR VH 416b, ×2 (Havlíček, 1967).

Khangaestrophia Mendbajar, 1994, p. 40 [**K. raissae;* OD]. Strongly concavoconvex profile; ornament of coarse costellae with sharp crests interspersed with fine parvicostellae; very small dental plates; ventral muscle field bilobed to subcircular; lateral muscle-bounding ridges that only originate near hinge line separately from and lateral to dental plates; very fine ventral median septum; weak myophragm devel-

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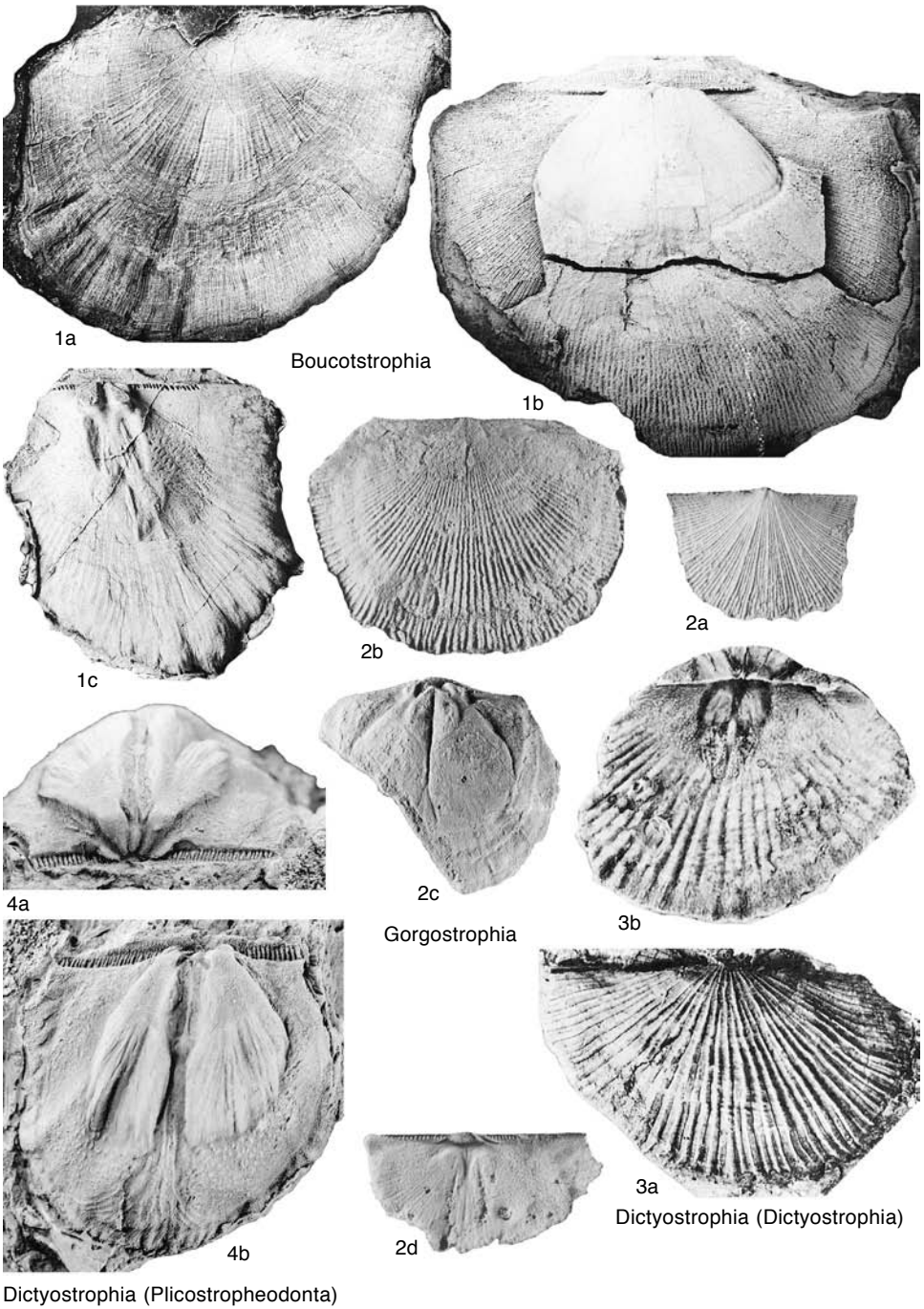

FIG. 187. Strophodontidae (p. 294).

oped posteriorly; cardinal process lobes erect, directed posteroventrally; dorsal muscle field with lateral curved bounding ridges, bisected by median septum reaching to half valve length. *Devonian (Emsian):* Mongolia.——FIG. 188,*2a–d. *K. raissae,* Chulinsk Formation, Emsian, Terchin-Tsagaan-Nuur, Mongolia; *a,* ventral exterior mold, PAN 4131/13, ×1.5; *b,* enlarged to show ornament, PAN

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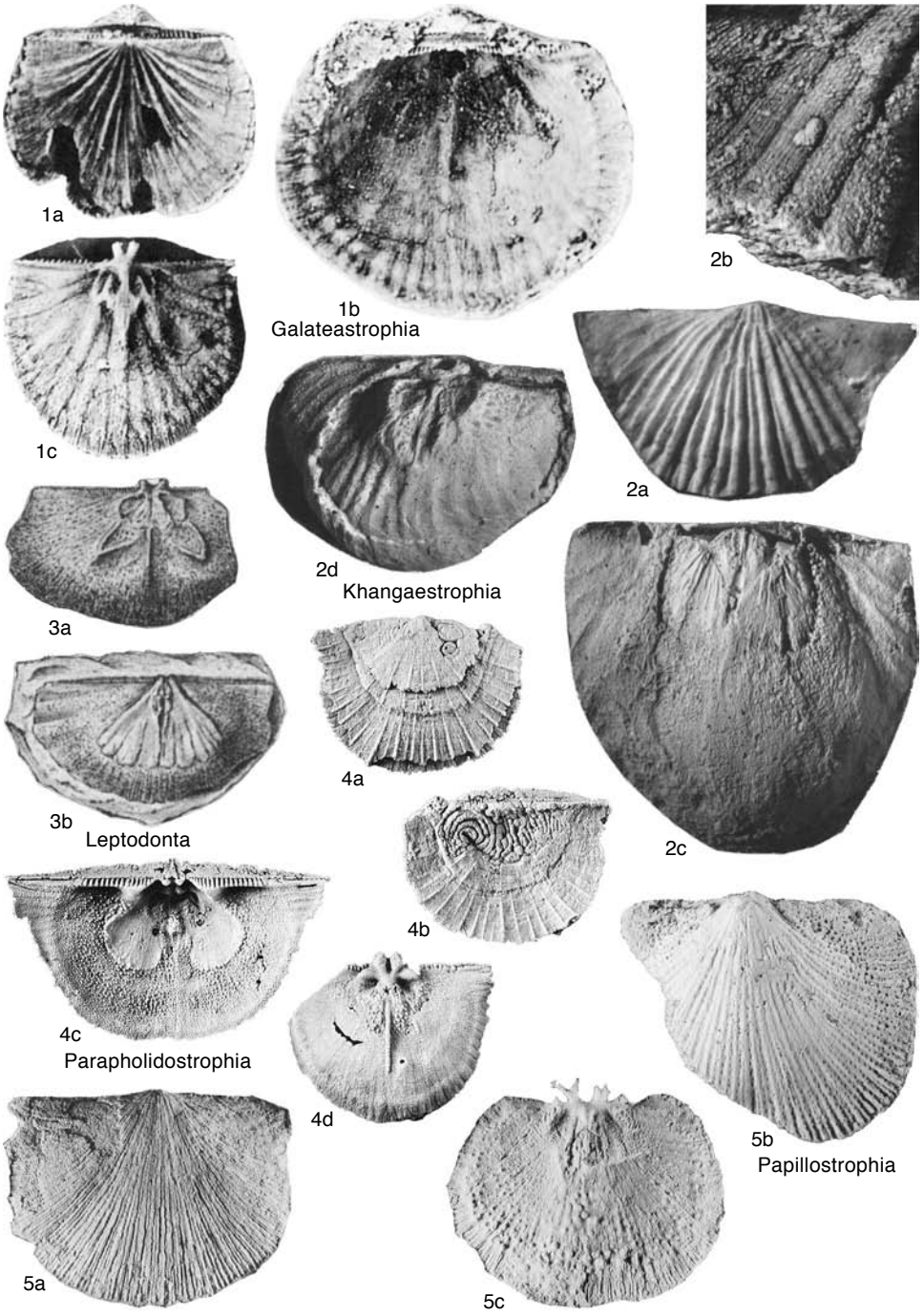

FIG. 188. Strophodontidae (p. 294–297).

4131/10, ×7; *c,* ventral internal mold, PAN 4131/14, ×1.5; *d,* holotype, latex cast of dorsal internal mold, PAN 4131/12, ×1.5 (Alekseeva, new).

?Leptodonta KHALFIN, 1955, p. 237, *nom. nov. pro Oehlertia* KHALFIN, 1948, p. 256, *non* PERNER, 1907 [**?Leptaena leblanci* ROUAULT, 1851, p. 393; OD].

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Strongly concavoconvex profile; ornament of uniform coarse costellae; ventral muscle field strongly impressed posteriorly but not anteriorly; muscle-bounding ridges absent; cardinal lobes posteriorly directed, extended posterior to hinge line; socket ridges absent; dorsal muscle field weakly impressed; central dorsal median ridge variably developed; weak side ridges present; topotype material not located, so revision is needed; hence queried family assignment. *Devonian (Pragian–Eifelian):* Europe, Turkey.——Fig. 188,*3a,b. *L. leblanci* (Rouault), Emsian beds, Izé, Rennes, France; *a,* ventral internal mold, ×2; *b,* dorsal interior, ×1 (Oehlert, 1886).

Lissostrophia Amsden, 1949, p. 202 [**L. cooperi;* OD]. Minute; strongly concavoconvex profile shells with conspicuous ventral umbo; subcircular in outline; no ornament; ventral muscle field small, slightly divergent; cardinal process lobes pronglike, united at base, posteriorly directed beyond hinge line; socket ridges absent; dorsal muscle field weakly impressed, with thick bounding ridges posterolaterally; thick pair of dorsal transmuscle ridges slightly divergent. *Silurian (Ludlow):* North America.——Fig. 189,*2a–d. *L. cooperi,* Henryhouse Formation, Ludlow, Ada, Pontotoc County, Oklahoma; *a,b,* dorsal, lateral views of conjoined valves, BMNH BC 13001, ×3 (new); *c,* ventral interior, USNM 115379, ×3; *d,* dorsal interior, USNM 115382, ×3 (Williams, 1953a).

Megastrophia Caster, 1939, p. 37 [**Stropheodonta concava* Hall, 1857, p. 140; OD]. Large shells, with strongly concavoconvex profile; ornament costellate to unequally parvicostellate; denticulate along two-thirds of hinge line; ventral muscle field varying from elongate to transverse, muscle-bounding ridges absent except in few gerontic individuals; cardinal process lobes massive, wide, joined at their base to form U-shaped structure, projecting posterior to hinge line; socket ridges small, thin, widely divergent; elevated dorsal muscle field with strong bounding ridges; small central dorsal septum; two very short dorsal side septa. *Devonian (Emsian–Givetian):* North America, Asia (Altai-Sayan).——Fig. 189,*1a–e. *M. concava* (Hall), Givetian; *a,b,* ventral, lateral views of conjoined valves, Hamilton Group, York, AMNH 37197, ×1; *c,* ventral interior, Hamilton Group, Canandaigua Lake, AMNH 37196, ×1; *d,* dorsal interior, Hamilton Group, Darien, New York, BMNH B 9580, ×1; *e,* partial dorsal interior showing cardinal process, Silica Shale, Travers Group, Sylvania, Ohio, BMNH BB 16709, ×1.5 (new).

Minutostropheodonta Harper & Boucot, 1978, p. 30 [**Leptaena subtransversa* Schnur, 1854, p. 223; OD]. Small shells with transverse outline; profile strongly concavoconvex; distinctive ornament of widely spaced costellae separated by broad arched or flat areas on ventral valve, corresponding slightly concave areas on dorsal valve; dorsal valve may have superimposed coarse plications centrally but not anteriorly; denticles over half valve width; ventral muscle field not bounded by ridges, strongly impressed, extending up to two-thirds valve length; cardinal process lobes posteriorly directed, overhanging hinge line; socket ridges widely divergent; dorsal muscle field elevated on prominent platform; central dorsal median septum extends from platform to subperipheral ridge. *Devonian (Eifelian):* Germany.——Fig. 190,*2a–d. *M. subtransversa* (Schnur), Rommersheimer Schichten, Eifelian, Gerolstein, Eifel, Germany; *a,b,* ventral, lateral views of conjoined valves, BMNH B 39638, ×4 (new); *c,* ventral interior, USNM 220822, ×3; *d,* dorsal interior, USNM 220802, ×5 (Harper & Boucot, 1978).

?Neumanella Harper & Boucot, 1978, p. 29 [**N. varimya;* OD]. Similar to *Leptodonta* in outline, profile, ornament, but with narrower ventral muscle field; lacking central dorsal median septum, dorsal side septa; family uncertain. *Silurian (Ludlow, ?Přídolí):* North America.——Fig. 191,*2a–c. *N. varimya,* Přídolí beds, Scraggly Lake, Maine; *a,* latex of external mold of conjoined valves, USNM 220732, ×3; *b,* latex of ventral internal mold, USNM 220725, ×3; *c,* latex of dorsal internal mold, USNM 220736, ×1.5 (Harper & Boucot, 1978).

Papillostrophia Havlíček, 1967, p. 132 [**Leptaena consobrina* Barrande, 1848, p. 218; OD]. Concavoconvex profile with geniculation; similar to *Gorgostrophia,* but with dental plates, distinctive papillae on dorsal median, subperipheral ridges. *Devonian (Emsian):* Europe.——Fig. 188,*5a–c. *P. consobrina* (Barrande); *a,* ventral exterior, Koneprusy Limestone, Pragian, Koneprusy, NM CF395; *b,* ventral internal mold, Koneprusy Limestone, Pragian, Koneprusy, OMR VH 407b, ×2.4; *c,* lectotype, dorsal interior, Zlíchov Limestone, Emsian, U kaplícky, Praha-Hlubocepy, Bohemia, Czech Republic, NM CF395, ×1.5 (Havlíček, 1967).

Parapholidostrophia Johnson, 1971, p. 309 [**P. harperi;* OD]. Outline semicircular; profile concavoconvex; unequally parvicostellate ornament; denticulate over more than half width; bilobed, well-impressed ventral muscle field; similar to *Pholidostrophia,* but shell not nacreous; short socket plates fused to lateral bases of cardinal process lobes; prominent thin dorsal median septum. *Devonian (Emsian–Eifelian):* North America.——Fig. 188,*4a–d. *P. harperi, Warrenella kirki* Zone of Denay Limestone, Eifelian, Roberts Creek Ranch, southern Roberts Mountains, Nevada; *a,b,* ventral, dorsal views of conjoined valves, USNM 157355, ×2; *c,* holotype, ventral interior, USNM 157354, ×2; *d,* dorsal interior, USNM 157366, ×2 (Johnson, new).

Pholidostrophia Hall & Clarke, 1892, p. 287 [**Strophomena nacrea* Hall, 1857, p. 144; OD]. Transverse, semielliptical outline, moderately concavoconvex profile; commonly smooth, but some specimens with faint traces of radial ornament; distinctive nacreous shell; hinge line denticulate over half valve width; bilobed ventral muscle field impressed, but with no bounding ridges; cardinal process lobes united at their bases, posteriorly directed; socket ridges absent; dorsal muscle field

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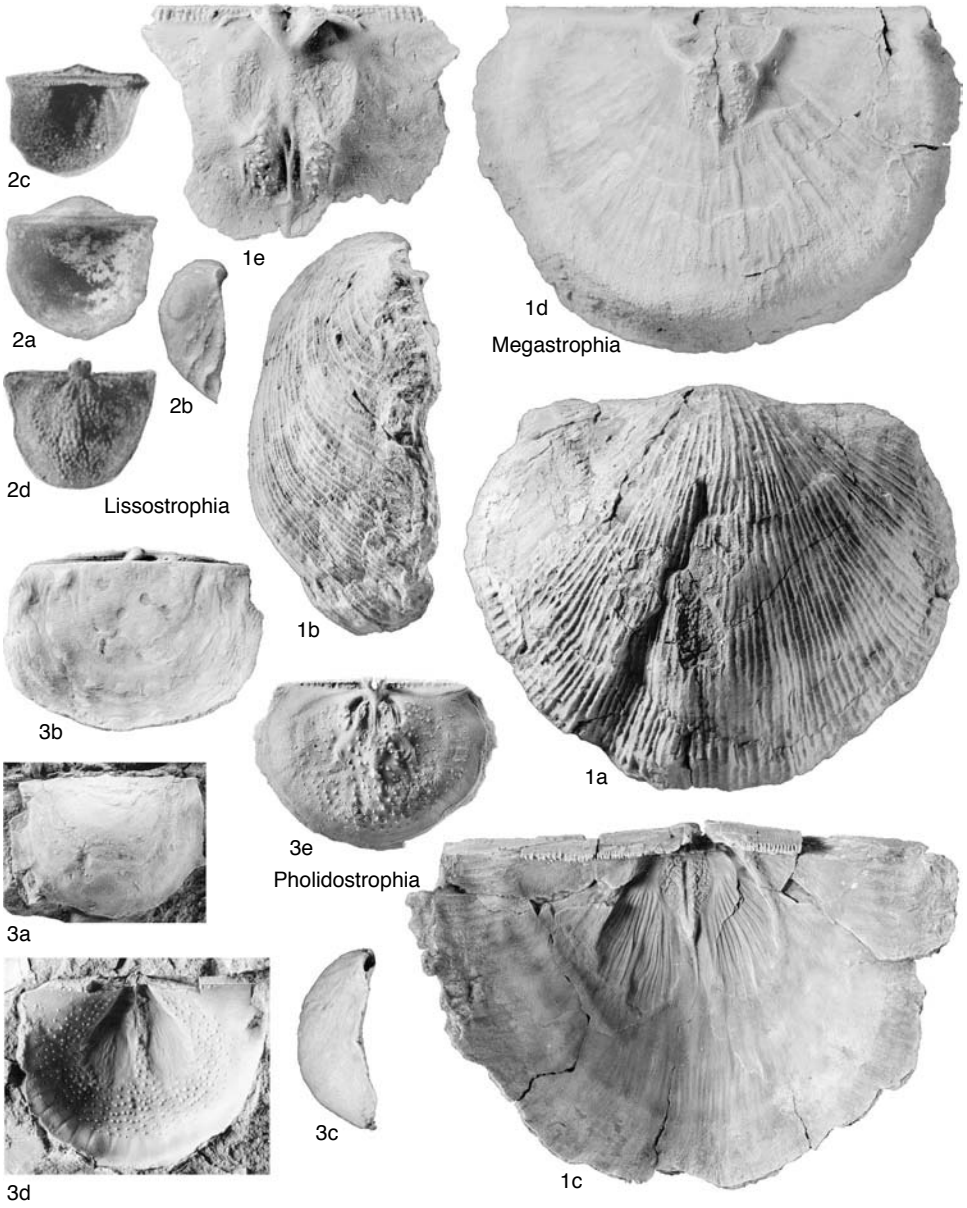

FIG. 189. Strophodontidae (p. 297–298).

differentiated into two pairs; central dorsal median ridge; side ridges variably developed. *Devonian (Emsian–Frasnian):* North America, Europe.——FIG. 189,*3a–e.* **P. nacrea* (HALL), Hamilton Group, Givetian; *a,* ventral exterior, Gennessee Valley, AMNH 37211, ×2; *b,c,* dorsal, lateral views of conjoined valves, York, BMNH B 9579, ×2; *d,* ventral interior, Canandaigua Lake, New York, AMNH 37213, ×2; *e,* dorsal interior, Gennessee Valley, AMNH 37211, ×2 (new).

Pterostrophia GARRATT, 1985, p. 523 [**P. carinatus;* OD]. Strongly convex profile with sharply deflected trail; distinctive parvicostellate ornament with weak small interrupted rugae between primary costellae; denticulate over two-thirds of hinge line; small dental plates; subtriangular to bilobed ventral muscle

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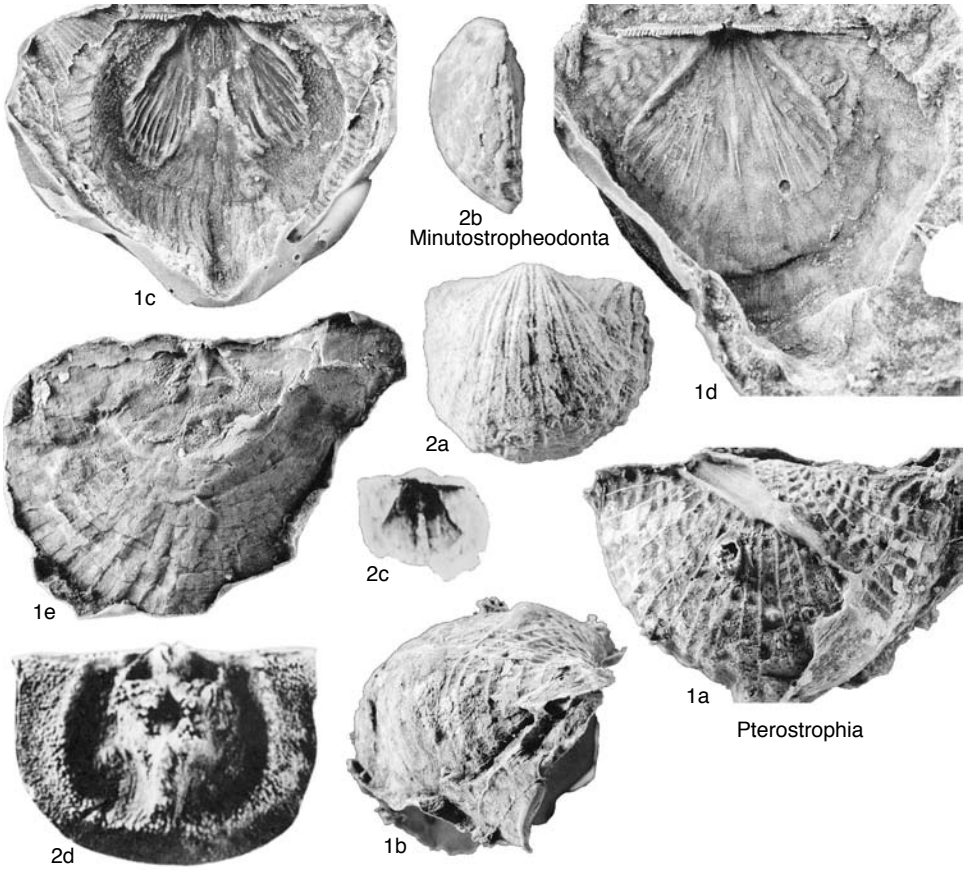

FIG. 190. Strophodontidae (p. 297–299).

field large, flabellate, but variably impressed, particularly centrally; dorsal muscle field faintly impressed, with rare muscle-bounding ridges; short dorsal myophragm; dorsal side septa absent. *Lower Devonian:* Australasia.——FIG. 190,*1a–e. *P. carinatus,* Humevale Formation, Lower Devonian, Mooroolbark, Lilydale, Victoria, Australia; *a–c,* holotype, external, lateral, internal views of latexes of ventral valve, NMVP P1474, ×1.5; *d,* latex of ventral interior, NMVP P49770, ×1.5; *e,* latex of dorsal interior, NMVP P49496, ×1.5 (new).

Strophonelloides CASTER, 1939, p. 106 [**Strophodonta reversa* HALL, 1858a, p. 494; OD] [?=*Chemungia* CASTER, 1939, p. 106 (type, *Stropheodonta caelata* HALL, 1867c, p. 112; OD)]. Profile resupinate, ventrally gently geniculate except in young individuals (only resupinate genus in family); costellate ornament; denticulate over almost entire hinge line width; ventral muscle field as in *Strophodonta* but with muscle-bounding ridges varying from strong, elevated to absent; weak central furrow developed in ventral subperipheral rim corresponding with median ridge in anterior part of dorsal valve; dorsal muscle field elevated on platform with bounding ridges; weak dorsal subperipheral rim. *Devonian (Frasnian):* North America.——FIG. 191,*1a–e. *S. reversa* (HALL), Hackberry Formation, Frasnian, Rockford, Iowa; *a,* ventral view of conjoined valves, NYSM 2092, ×1.5; *b,* lateral view of conjoined valves, BMNH B 41670, ×1; *c,* ventral interior, NYSM 2095, ×1.5; *d,* ventral interior, BMNH B 41456, ×2; *e,* dorsal interior, NYSM 2094, ×2 (new).——FIG. 191,*1f–h. S. caelata* (HALL), Chemung Group, Frasnian; *f,* latex cast of ventral internal mold, Blossburg, Pennsylvania, AMNH 37220, ×1; *g,h,* dorsal internal mold, latex cast, Waverly, New York, NYSM 2088, ×1.5 (new).

?Trilobostrophia SHISHKINA, 1983, p. 1229 [*Megastrophia bobilevi* SHISHKINA in GRASIANOVA & SHISHKINA, 1977, p. 34; OD]. Outline transverse, strongly concavoconvex profile, trilobate with anterior fold, sulcus; costellate ornament; large ventral muscle field with bounding ridges posterolaterally; ventral median ridge present; massive cardinal

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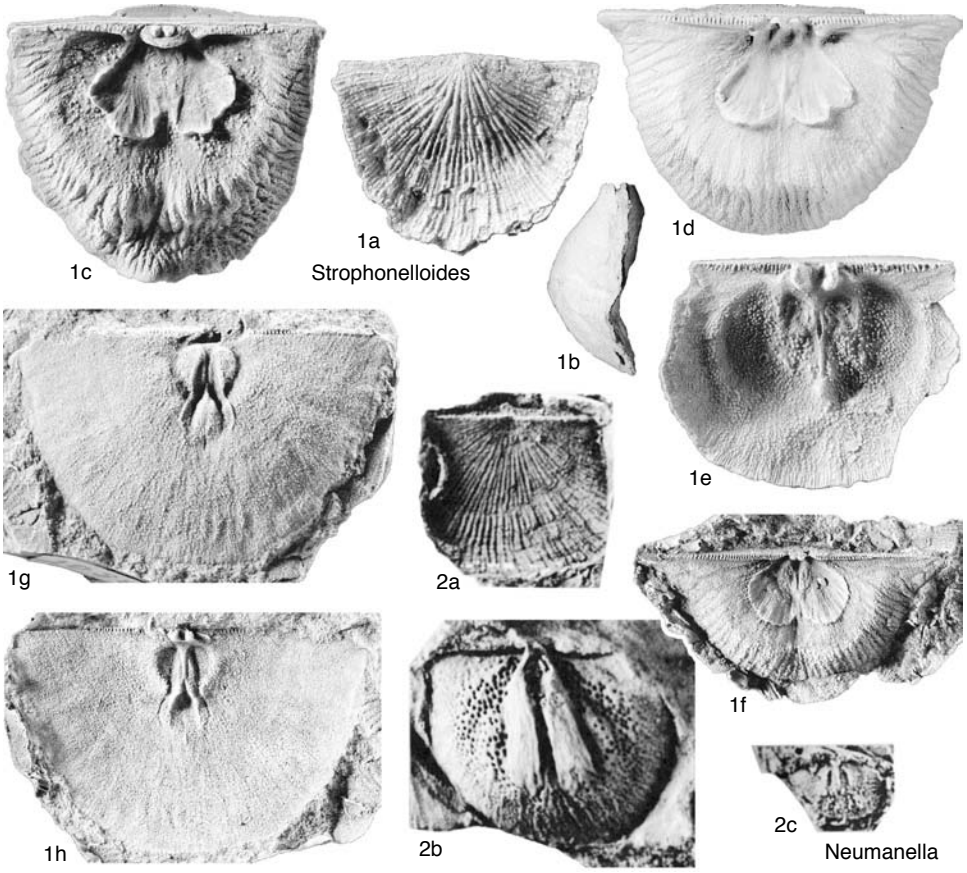

FIG. 191. Strophodontidae (p. 297–299).

process lobes; socket ridges flaring laterally subparallel with hinge line; strongly impressed dorsal muscle field with two pairs of adductor scars differentiated; short central dorsal median septum; requires revision. *Devonian (Emsian):* Siberia.

Family SHALERIIDAE Williams, 1965

[*nom. transl.* HAVLÍČEK, 1967, p. 174, *ex* Shaleriinae WILLIAMS, 1965d, p. 402]

Denticulate hinge line; parallel-sided, elongate diductor muscle scars in ventral valve, bounded laterally by ridges; dorsal median ridge (myophragm) usually present, commonly bifurcating anteriorly. *Silurian (Wenlock)–Devonian (Lochkovian).*

Shaleria CASTER, 1939, p. 33 [**Strophomena gilpeni* DAWSON, 1881, p. 336; OD] [=*Shaleria (Protoshaleria)* HARPER & BOUCOT, 1978, p. 162 (type, *Strophomena ornatella* DAVIDSON, 1871, p. 309; OD)]. Gently concavoconvex profile; not geniculate; ornament unequally parvicostellate, often with small rugae within parvicostellae; denticulate along half valve width; prominent ventral muscle-bounding ridges posterolaterally only, with additional oblique muscle ridges, small ventral process; erect to anteriorly facing cardinal process lobes; short, flaring socket ridges; one or two pairs of dorsal side septa. *Silurian (Ludlow)–Devonian (Lochkovian):* North America, Europe.

S. (Shaleria). Similar to *S. (Janiomya)* but with two pairs of relatively large dorsal side septa. *Silurian (Ludlow)–Devonian (Lochkovian):* North America, Europe.——FIG. 192,*3a–d. *S. (S.) gilpeni* (DAWSON), Stonehouse Formation, Přídolí–Lochkovian, Arisaig, Nova Scotia, Canada; *a,b,* mold, latex cast of ventral interior, USNM 10201, ×2; *c,d,* mold, latex cast of dorsal interior, GSC 19355, ×2 (Harper, 1973). ——FIG. 192,*3e–h. S. (S.) ornatella* (DAVIDSON), Ludfordian; *e,f,* latex casts of ventral exterior, interior, Llangibby Formation, near Usk, Gwent,

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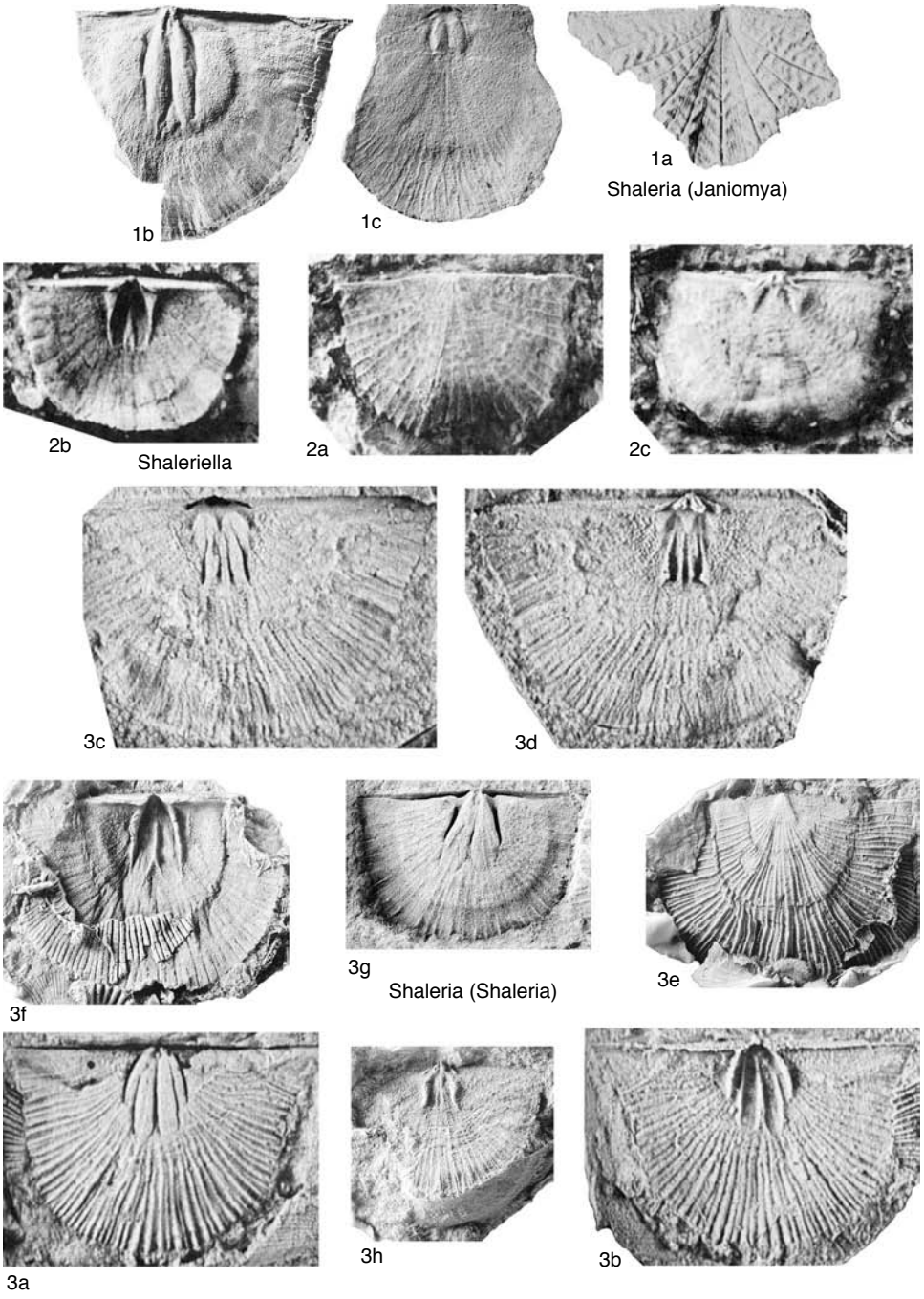

FIG. 192. Shaleriidae (p. 300–302).

Wales, BMNH BC 13115, ×2; *g,* internal mold of ventral valve, Whitcliffe Formation, Ludlow, Shropshire, England, BMNH B 842, ×2; *h,* latex cast of dorsal interior, Llangibby Formation, near Usk, Gwent, Wales, BMNH BC 13112, ×2 (new).

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S. (Janiomya) Havlíček, 1967, p. 174 [**J. parallelomya;* OD]. Ornament unequally parvicostellate to uniformly costellate; similar to *S. (Shaleria)* but with only single pair of weak, abbreviated lateral dorsal side septa. *Silurian (Ludlow–Přídolí):* Europe.——Fig. 192,*1a,b.* **S. (J.) parallelomya,* Pozary Formation, Přídolí, Svaty Jan pod Skalou, Bohemia, Czech Republic; *a,* holotype, ventral internal mold, OMR VH 445b, ×1.5; *b,* dorsal internal mold, OMR VH 445a, ×1.5 (Havlíček, 1967).——Fig. 192,*1c. S. (J.) flexa* (Havlíček); ventral external mold, Kopaniná Formation, Ludlow, Morina, OMR VH 4230, ×4 (Havlíček, 1967).

Shaleriella Harper & Boucot, 1978, p. 160 [**S. delicata;* OD]. Ornament of distinctive zigzag rugae interrupted by primary costellae over most of central area of valve, but often absent anteriorly; similar to *S. (Shaleria)* but dorsal side septa absent, gently geniculate dorsally. *Silurian (Wenlock–Přídolí):* cosmopolitan.——Fig. 192,*2a–c.* **S. delicata,* Hemse Marl, Gorstian, Hemse Station, Gotland, Sweden; *a,* holotype, ventral exterior, USNM 220911, ×3; *b,* ventral interior, USNM 220913, ×3; *c,* dorsal interior, USNM 220914, ×3 (Harper & Boucot, 1978).

Family STROPHONELLIDAE Caster, 1939

[*nom. transl.* Sokolskaya, 1960, p. 215, *ex* Strophonellinae Caster, 1939, p. 98]

Resupinate profile; hinge line denticulate; ventral muscle field subquadrate, with muscle-bounding ridges well developed except in *Eostrophonella. Silurian (Rhuddanian)–Devonian (Emsian).*

Strophonella Hall, 1879, p. 153 [**Strophomena semifasciata* Hall, 1863b, p. 210; OD] [=*Costistrophonella* Harper & Boucot, 1978, p. 99 (type, *Strophomena punctulifera* Conrad, 1838, p. 117; OD); *Strophoprion* Twenhofel, 1914, p. 25 (type, *Brachyprion geniculatum* Shaler, 1865, p. 63; OD)]. Ornament variably costellate; hinge line denticulate over most of valve width; no dental plates; ventral muscle field subquadrate, usually with well-developed muscle-bounding ridges except anteriorly at valve center; cardinal process lobes short, swollen, directed posteroventrally; dorsal muscle field weakly impressed. *Silurian (Wenlock)–Devonian (Emsian):* cosmopolitan.

S. (Strophonella). Similar to *S. (Quasistrophonella),* but with finely costellate or parvicostellate ornament not separated by smooth interspaces. *Silurian (Wenlock)–Devonian (Emsian):* cosmopolitan.——Fig. 193,*2a.* **S. (S.) semifasciata* (Hall), Niagara Group, Wenlock, Waldron, Indiana; lectotype, dorsal exterior, AMNH 1932, ×1 (new).——Fig. 193,*2b–e. S. (S.) punctulifera* (Conrad), Lochkovian; *b,c,* dorsal, lateral views of partly exfoliated dorsal valve, lower Helderberg Group, Port Colburn, Ontario, Canada, AMNH 33070, ×1; *d,* internal mold of ventral valve, lower Helderberg Group, Schoharie, New York, BMNH B 9290, ×1; *e,* dorsal interior, BMNH B 74973, ×1 (new).

S. (Quasistrophonella) Harper & Boucot, 1978, p. 98 [**Leptaena bohemica* Barrande, 1848, p. 243; OD]. Similar to *S. (Strophonella),* but with broad smooth interspaces between costellae. *Silurian (Ludlow)–Devonian (Emsian):* Europe.——Fig. 193,*1a,b.* **S. (Q.) bohemica* (Barrande), Koneprusy Limestone, Pragian, Koneprusy, Czech Republic; *a,* dorsal exterior, NM L6686, ×1; *b,* internal mold of dorsal valve, OMR VH 508, ×1 (Havlíček, 1967).

Eostrophonella Williams, 1950, p. 281 [**Strophonella davidsoni* Holtedahl, 1916, p. 64; OD]. Outline, profile as in *Strophonella;* dental plates; denticles confined to denticular plates in ventral valve, variably developed on posterior margins of sockets in dorsal valve; muscle field faintly impressed in both valves; cardinal process lobes elongate as in *Kjerulfina. Silurian (Rhuddanian–Aeronian):* Europe.——Fig. 193,*3a–e. E. eothen* (Bancroft), Haverford Mudstone Formation, Rhuddanian, Gasworks, Haverfordwest, Dyfed, Wales; *a,b,* exterior, interior dorsal molds, BMNH BB 771016, ×1; *c,* ventral internal mold, BMNH BB 71005, ×1; *d,* latex cast of dorsal internal mold, ×1.5; *e,* enlargement of cardinalia, BMNH BC 50617, ×6 (new).

Family UNCERTAIN

Douvinella Ljaschenko, 1985, p. 12 [**D. parva;* OD]. Concavoconvex profile, unequally parvicostellate ornament; ventral interior with denticulate hinge line, muscle field expanded anteriorly as in *Parastrophonella;* dorsal interior unknown. *Devonian (Frasnian):* Timan, Russia.

Gunnarella Spjeldnaes, 1957, p. 149 [**Strophomena (G.) delta;* OD]. Resupinate; ornament of rugae interrupted by costellae; dorsal valve interior unknown, but possibly within Strophomenidae. *Ordovician (Caradoc):* Baltic.——Fig. 194,*2a,b.* **G. delta,* Solvang Formation, upper Caradoc, Gasøya, Oslo district, Norway; dorsal, lateral views of dorsal valve, PMO L63, ×1.5 (new).

Idioglyptus Northrop, 1939, p. 172 [**I. stigmatus;* OD]. Exteriors of type specimens have ornament of interrupted rugae as in *Cymostrophia,* but interiors unknown, thus genus considered *nomen dubium. middle Silurian:* West Point Formation, middle Silurian, West Point, Port Daniel region, Chaleur Bay, Gaspé Peninsula, Quebec, Canada.

Playfairia Reed, 1917, p. 866 [**Strophomena deltoidea* Conrad, 1839, p. 64; OD]. Profile concavoconvex, with parvicostellate ornament; dorsal valve interior unknown, but possibly within Rafinesquinidae. *Ordovician (Caradoc):* North America.——Fig. 194,*3a,b.* **P. deltoidea* (Conrad), Trenton Group, Caradoc, Trenton Falls, New York; *a,* lectotype, dorsal exterior, AMNH 701A, ×1.5; *b,* partly exfoliated ventral exterior, AMNH 701B, ×1.5 (new).

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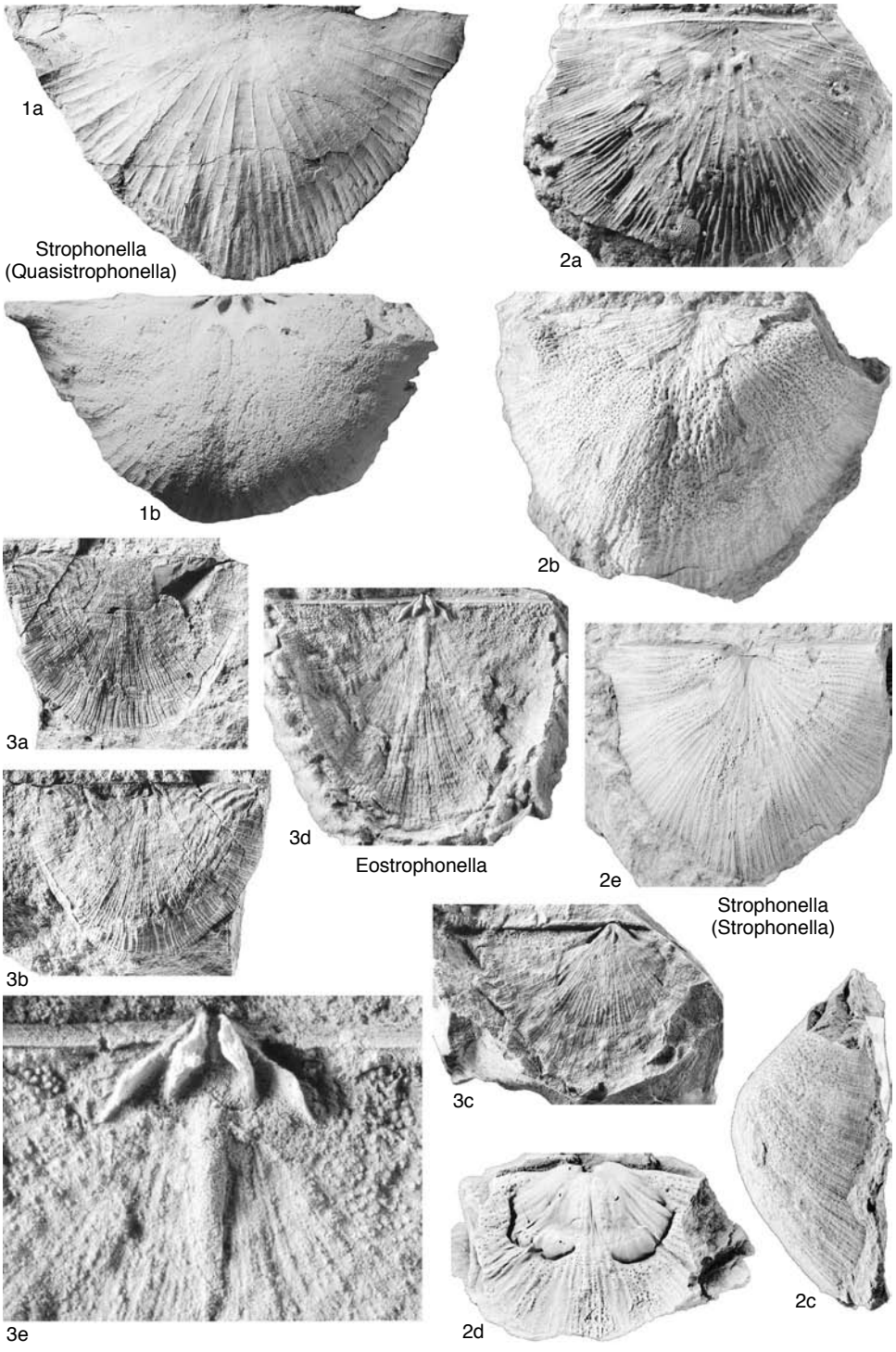

FIG. 193. Strophonellidae (p. 302).

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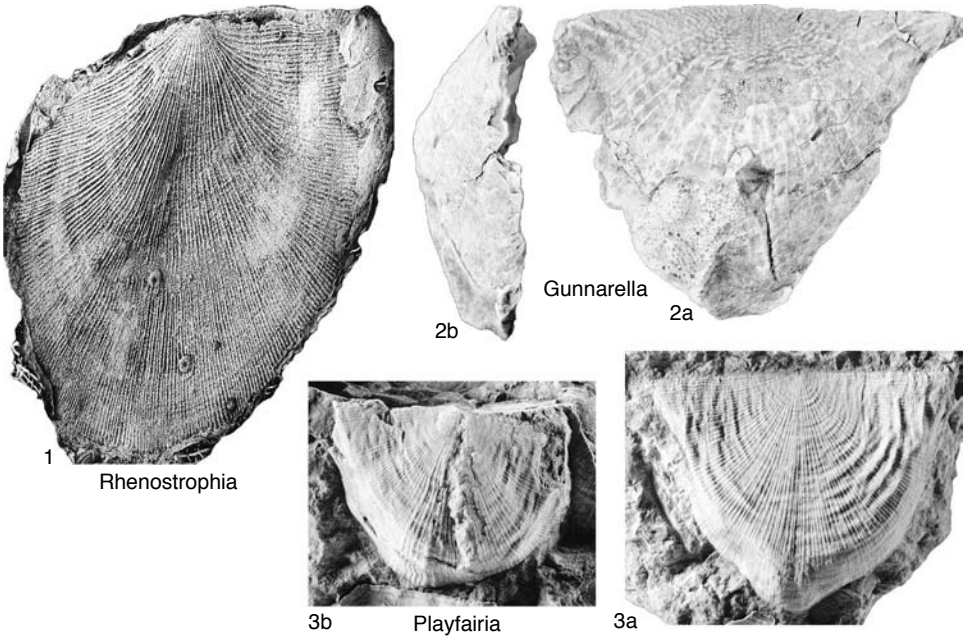

FIG. 194. Uncertain (p. 302–304).

Rhenostrophia BOUCOT, 1960b, p. 483 [**Orthis subarachnoidea* D'ARCHIAC & DE VERNEUIL, 1842, p. 372; OD]. Only holotype, exterior of ventral valve, known; although undoubtedly strophomenoid, without knowledge of interior must remain a *nomen dubium. Lower Devonian (Emsian):* Germany.—— FIG. 194,*1. *R. subarachnoidea* (D'ARCHIAC & DE VERNEUIL), Laubacher Schichten, upper Emsian, Kemmenau, near Ems, Nassau, Germany; holotype, ventral exterior, École de Mines, Orsay, ×1 (Jahnke, new).

Syntrophodonta STRUVE, 1982, p. 198 [**S. paeckelmanni;* OD]. Although hinge line denticulate, uncertain if genus (known only from single ventral valve internal mold) is within Strophomenida since shell structure unknown; ventral muscle field elevated, bounded anterolaterally by pair of raised plates not quite meeting centrally; even if strophomenoid, family unknown. *Devonian (Givetian):* Grossilbeck Member, Mergelsberg Formation, Gross-Illbeck, Ratingen, Germany.

Superfamily PLECTAMBONITOIDEA Jones, 1928

[*nom. transl.* COOPER & WILLIAMS, 1952, p. 332, *ex* Plectambonitinae JONES, 1928, p. 394]

Shell fibrous, pseudopunctate; shell outline generally semicircular with straight hinge line; profile normally concavoconvex, occasionally resupinate; ornamentation variable, but generally unequally parvicostellate; external spines absent; supra-apical pedicle foramen present, although usually closed, nonfunctional in adults; pseudodeltidium and chilidium present to variable degrees; articulation chiefly of simple teeth (usually supported by short dental plates), sockets, hinge line denticles rarely developed; ventral muscle field usually bilobed with muscle-bounding ridges varying from strong to absent; cardinal process with simple median ridge, sometimes with subsidiary lateral ridges to become trifid, never bifid (although there are a few genera with no cardinal process); dorsal valve including variably developed or absent median septum, paired side septa; dorsal muscle field often on elevated bema (originating posterocentrally) or platform (originating posterolaterally); mantle canals often present but variable in form. *Ordovician (Tremadoc)–Devonian (Eifelian).*

Revision of this superfamily has revealed a relatively limited range of morphologies within it. The valve profile, for example, varies between concavoconvex and convexo-

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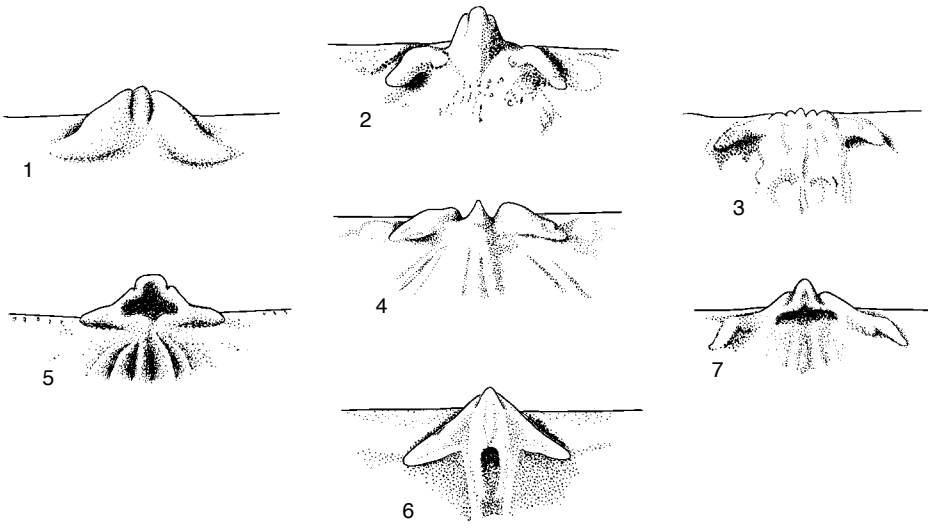

FIG. 195. Cardinal processes of various Plectambonitoidea; *1,4,* simple, ankylosed anteriorly to valve floor (*1,* Taffiidae: *Spanodonta,* ×6; *4,* Bimuriidae: *Bimuria,* ×4); *2,3,* trifid, ankylosed anteriorly to valve floor (Leptellinidae: *2, Leptelloidea,* ×6; *3, Leptellina,* ×6); *5–7,* trifid, undercut anteriorly (Sowerbyellidae: *5, Eoplectodonta,* ×6; *6, Gunningblandella,* ×7; *7, Sowerbyella,* ×7) (new).

concave (resupinate) and can determine differences only between genera, and ornament too is very repetitive. Similarly the presence or absence of a pseudodeltidium in the ventral valve or a chilidium in the dorsal valve, even though sometimes difficult to determine with the vagaries of preservation, seems of little classificatory value above generic rank. The ventral valve interior is also relatively conservative, with, in many stocks, a bilobed muscle field confined posterocentrally by the space between the simple teeth. The presence or absence of dental plates in the superfamily is only of significance at the generic level, and not always then. It is only in the dorsal valve that a variety of structures can be found that are useful for suprageneric classification and identification. Chief is the cardinal process, which varies from family to family between being simple, with a ridge growing from the notothyrial floor, to trifid, *i.e.,* with an extra pair of ridges on either side of the central ridge, and finally what is termed here trifid and undercut, in which the central ridge and its partners are not ankylosed anteriorly to the valve floor, but supported laterally (FIG. 195). Another key feature is the presence or absence of a bema, a thickened pad of secondary shell originating posterocentrally, sometimes as an extension of socket ridges, and upon which the dorsal valve muscle field and other structures are located. The bema is not to be confused with the platform, which in contrast originates posterolaterally and is much closer to the anterior valve margin than the bema. Some plectambonitoids, e.g., *Leangella* (FIG. 196) have both bema and platform. Thus the platform represents chiefly the area occupied by the lophophore, while the bema serves as the area for attachment and elevation of the dorsal muscle field. The dorsal muscle field may be transversely or obliquely divided. The final feature used to distinguish between families is the presence or absence of dorsal side septa, which are paired septa running obliquely across the interior of the dorsal valve.

Family PLECTAMBONITIDAE Jones, 1928

[*nom. transl.* KOZŁOWSKI, 1929, p. 108, *ex* Plectambonitinae JONES, 1928, p. 394]

Transverse outline, width always greatest at cardinal extremities; concavoconvex to gently resupinate profile; dental plates

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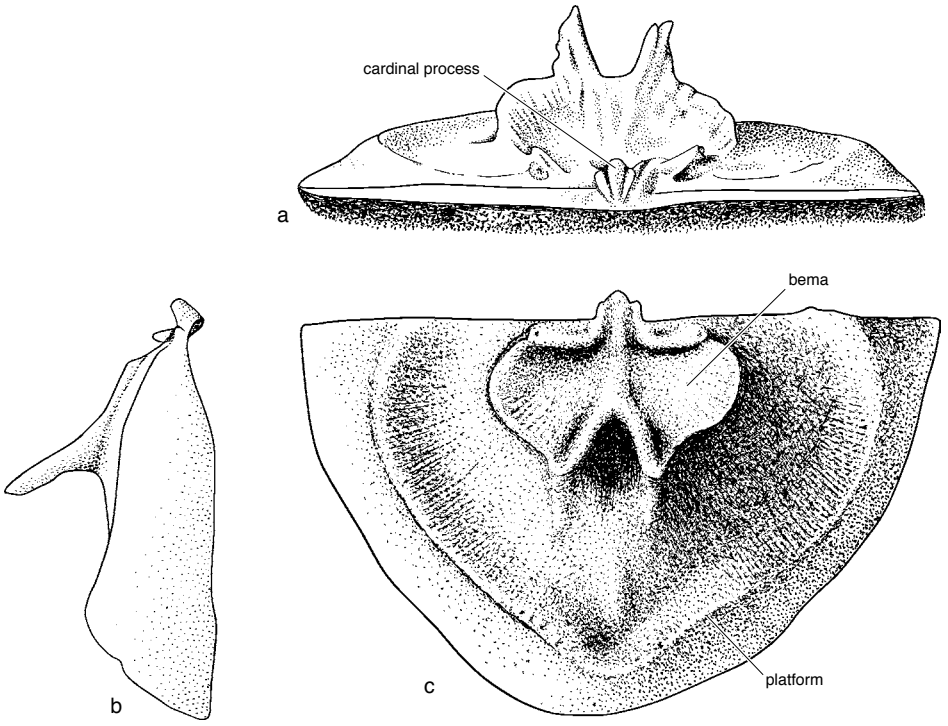

FIG. 196. Dorsal interior of *Leangella (L.) gibbosa* showing trifid cardinal process ankylosed anteriorly to valve floor, elevated bema, and edge of prominent platform; *a–c,* posterior, lateral, dorsal views, ×9 (Cocks & Rong, 1989).

usually present; simple cardinal process, not undercut; no bema; side septa usually present. *Ordovician (Tremadoc–lower Caradoc).*

Subfamily PLECTAMBONITINAE Jones, 1928

[Plectambonitinae JONES, 1928, p. 394] [=Plectellinae SCHUCHERT & COOPER, 1931, p. 245, assigned to Clitambonitidae]

Differs from Taphrodontinae in possessing hinge line denticles and in having simple dorsal median septum. *Ordovician (Tremadoc–Llandeilo).*

Plectambonites PANDER, 1830, p. 90 [**P. planissimus;* SD HALL & CLARKE, 1892, p. 296]. Concavoconvex profile; distinctive unequally parvicostellate ornament but not with granular texture; small chilidium, pseudodeltidium not filling delthyrium; denticles over half valve width; dental plates present, confining posterolateral part of ventral muscle field that is flabellate, open anteriorly; similar to *Plectella* but more convex (sometimes geniculate), with side septa in dorsal valve more pronounced, more numerous, more complex; weak dorsal platform present. *Ordovician (Llanvirn–Llandeilo):* Baltic.——FIG. 197,*1a–e. *P. planissimus,* Aseri Horizon, upper Llanvirn; *a–c,* ventral, dorsal, lateral views of conjoined valves, Pavlovsk, TAGI BR 345, ×3; *d,* ventral interior, Pavlovsk, TAGI BR 346, ×3; *e,* dorsal interior, Putilovo, St. Petersburg, Russia, BMNH BC 13030, ×3 (new).

?Akelina SEVERGINA, 1967, p. 133 [**A. akelina;* OD] [=*Humaella* ZHU, 1982, p. 53 (type, *H. huangbanjiensis*)]. Concavoconvex to planoconvex profile; reticulate ornamentation; no dental plates; faintly impressed bilobed ventral muscle field; strong dorsal median septum, with ridges in dorsal valve interpreted as side septa; familial assignment uncertain due to variable morphology in the few assigned specimens. *Ordovician (Tremadoc):* Asia.——FIG. 197,*3a–d. *A. akelina,* Algan Formation, upper Tremadoc, River Akel, Kusnetz Alatau, Altai Mountains, Russia; *a,* ventral interior, CNIGR 424/1323, ×4; *b,* ventral exterior, CNIGR 1030/11323, ×3; *c,* dorsal interior, CNIGR 1027/1323, ×3; *d,* dorsal interior, CNIGR 427/1323, ×4 (Cocks & Rong, 1989).——FIG. 197,*3e,f. A. huangbanjiensis,* Huangbanjishan Formation, Tremadoc, Fulintun, west of Xinglong, Huma County, Heilongjiang Province, China; *e,* ventral internal mold, SIGM LBr 81047, ×4; *f,* dorsal internal mold, SIGM LBr 81041, ×4 (Zhu, 1982).

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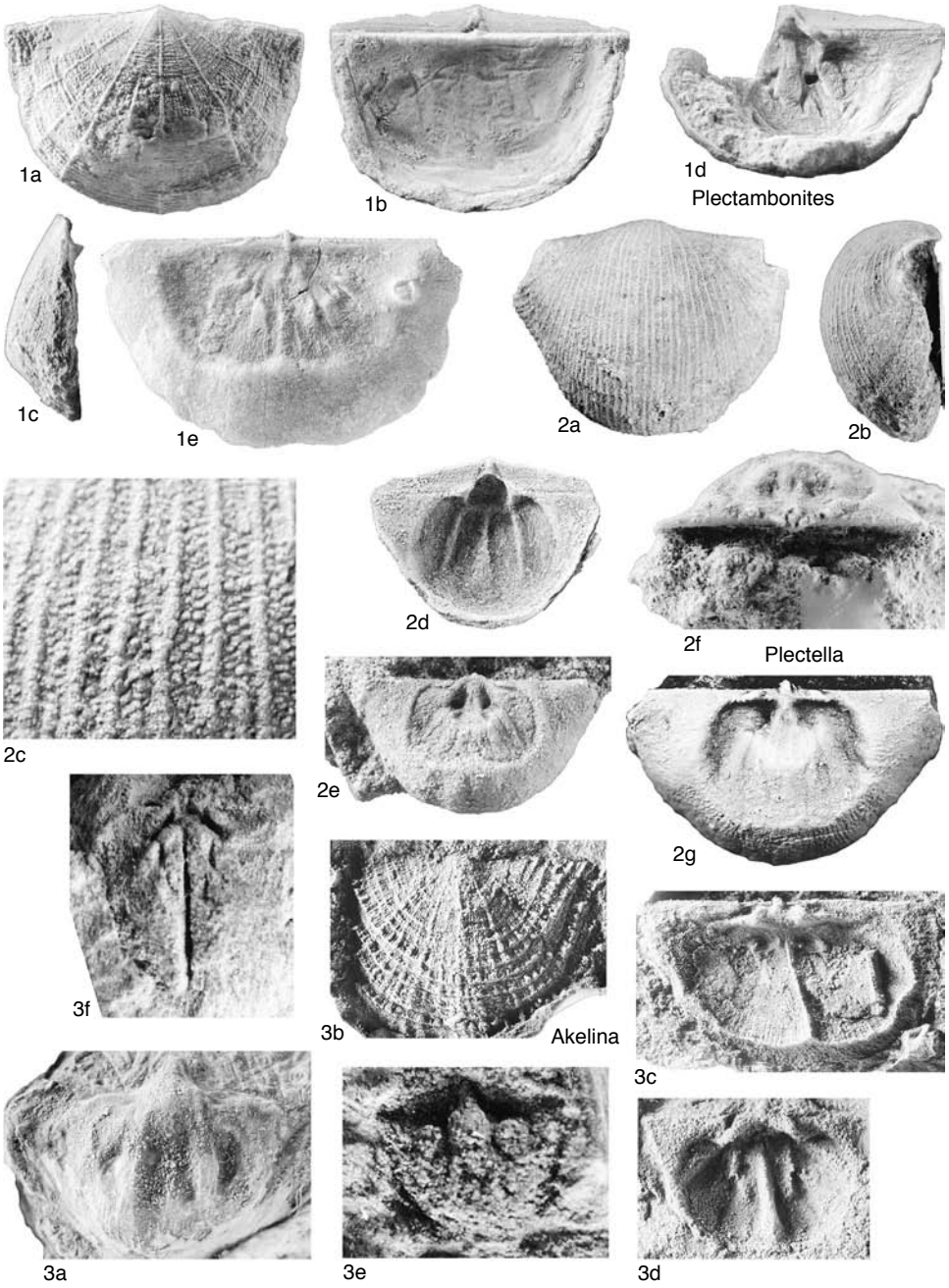

FIG. 197. Plectambonitidae (p. 306–308).

Ingria ÖPIK, 1930, p. 57 [**Orthisina nefedyevi* VON EICHWALD, 1855, pl. 36, fig. 13; OD] [=*Palinorthis* ULRICH & COOPER, 1936b, p. 625 (type, *P. cloudi;* OD)]. Flat to gently resupinate profile; unequally parvicostellate ornament; narrow chilidium, pseudodeltidium not filling delthyrium; denticles over half valve width; dental plates present with short straight or slightly curved ventral muscle-

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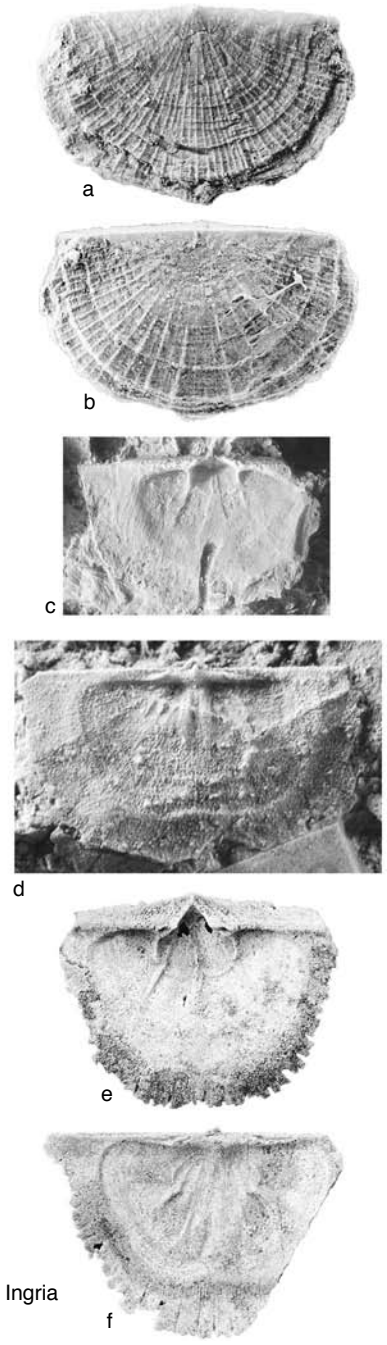

FIG. 198. Plectambonitidae (p. 307–308).

bounding ridges laterally only; muscle field poorly impressed anteriorly; socket plates short, ridgelike, widely divergent, subparallel with hinge line; complex side septa similar to *Plectambonites;* weak dorsal platform present. *Ordovician (Arenig–Llanvirn):* Baltic, North America, Tuva, northern Asia.——FIG. 198*a–d. *I. nefedyevi* (VON EICHWALD); *a,b,* ventral, dorsal views of conjoined valves, Volkhov Horizon, upper Arenig, Obukova Village, St. Petersburg, Russia, BMNH BC 12876, ×2; *c,* ventral interior, Jagala-Joa, Estonia, ×2.5; *d,* dorsal interior, Kunda Stage, upper Arenig, Ingria, Russia, TAGI BR 314, ×4 (new).——FIG. 198*e,f. I. cloudi, Orthidiella* Zone, lower Llanvirn, Frenchman's Flat, Nevada; *e,* ventral interior, BMNH BC 10310, ×2; *f,* dorsal interior, BMNH BC 10306, ×2 (new).

Plectella LAMANSKY, 1905, p. 156 [**Plectambonites uncinata* PANDER, 1830, p. 91; OD]. Concavoconvex profile with incurved beak; equally parvicostellate, granular ornament; small pseudodeltidium, small chilidium; short dental plates; ventral median septum anterior of muscle field, pair of ventral side septa extending from anterior edge of dental plates; pronounced ventral diaphragm, dorsal platform; similar to *Plectambonites* but with distinctive granular ornament, less pronounced side septa. *Ordovician (Arenig):* Baltic.——FIG. 197,*2a–g. *P. uncinata* (PANDER), Leetse Formation, lower Arenig; *a,b,* ventral, lateral views of ventral exterior, ×2.5; *c,* enlargement of ornament, Popovka river, St. Petersburg, Russia, BMNH BC 12854, ×10; *d,* ventral interior, Mäeküla, Estonia, TAGI BR 336, ×2; *e,* dorsal view of dorsal interior, Mäeküla, Estonia, TAGI BR 338, ×2; *f,* posterior view of dorsal interior, St. Zakluha River, St. Petersburg, Russia, BMNH BC 12855, ×3; *g,* dorsal view of dorsal interior, Popovka River, St. Petersburg, Russia, KIGLGU 155/691. 693, ×2 (new).

Subfamily TAPHRODONTINAE Cooper, 1956

[*nom. transl.* WILLIAMS, 1965d, p. 376, *ex* Taphrodontidae COOPER, 1956, p. 740] [=Isophragminae COOPER, 1956, p. 733]

Differs from Plectambonitinae in possessing prominent pair of fused septa centrally in dorsal valve and in lacking hinge line denticles. *Ordovician (Llanvirn–Caradoc).*

Taphrodonta COOPER, 1956, p. 740 [**T. parallela;* OD]. Concavoconvex profile; unequally parvicostellate ornament; similar to *Isophragma* but with no resupination, smaller, more subcircular ventral valve muscle field; subperipheral thickened ridge variably developed in ventral valve, with corresponding platform in dorsal valve, both anteriorly interrupted by central fused septa; cardinal process narrow, high; two small plates between cardinal process and interarea; side septa vestigial, often absent, except for strong central pair fused together along length, homologizing wide medium septum. *Ordovician (Llanvirn, ?Llandeilo, ?Caradoc):* North America, Asia.

T. (Taphrodonta). Similar to *T. (Nanambonites),* but with no chilidium in dorsal valve. *Ordovi-*

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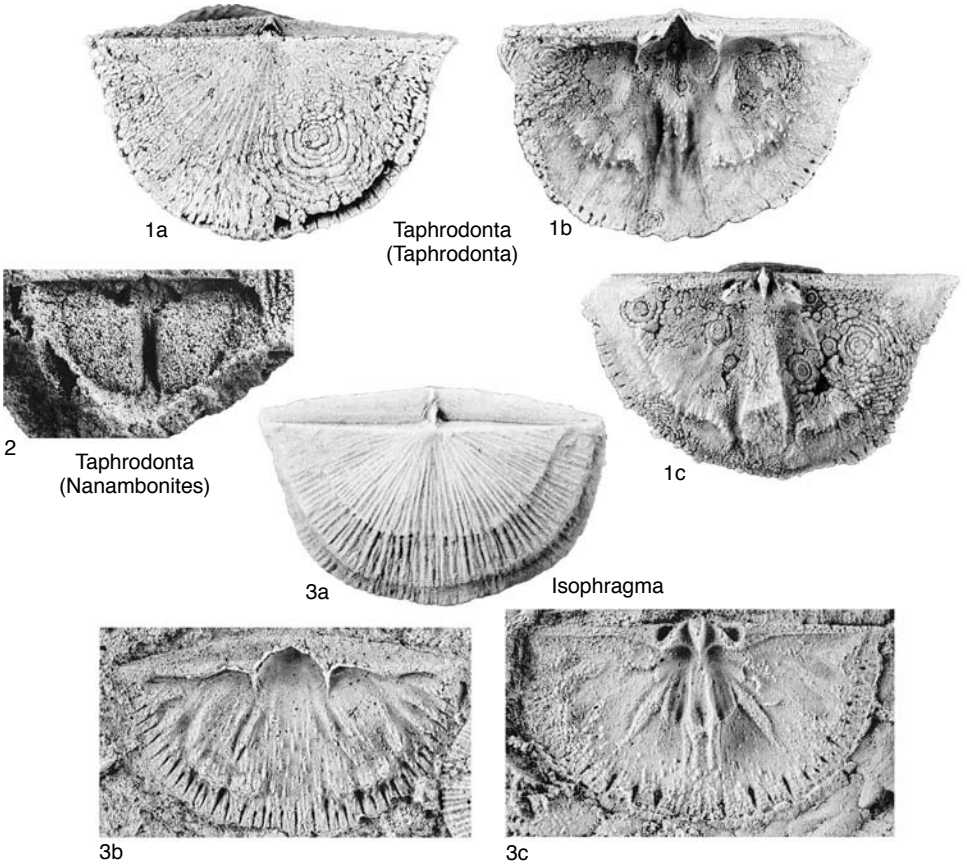

FIG. 199. Plectambonitidae (p. 308–309).

cian (Llanvirn, ?Llandeilo, ?Caradoc): North America, Kazakhstan.——FIG. 199,*1a–c. *T. (T.) parallela,* Antelope Valley Formation, upper Llanvirn, Ikes Canyon, Nevada; *a,* holotype, dorsal view of conjoined valves, USNM 117562e, ×3; *b,* ventral interior, USNM 117562g, ×3; *c,* dorsal interior, USNM 117562f, ×3 (Cooper, 1956).

T. (Nanambonites) LIU, 1976, p. 145 [**N. paucus;* OD]. Similar to *T. (Taphrodonta)* but with chilidium in dorsal valve. *Ordovician (Llanvirn):* Asia.——FIG. 199,*2. *T. (N.) paucus,* lower formation of Jiacun Group, Llanvirn, Mount Jolmo Lungma area, Tibet, China; holotype, dorsal internal mold, NIGP 23173, ×3 (Liu, 1976).

Isophragma COOPER, 1956, p. 733 [**I. ricevillense;* OD]. Flat to slightly resupinate profile; finely costellate to unequally parvicostellate ornament; dental plates short; ventral muscle field subquadrate with wide adductor traces; faint ventral subperipheral rim variably present; strong, low, wide cardinal process; no accessory plates between cardinal process, interarea; side septa variably developed, usually absent apart from strong, centrally fused pair. *Ordovician (Llanvirn–Caradoc):* North America, Scotland, Tuva, Kazakhstan.——FIG. 199,*3a–c. *I. ricevillense,* Athens Formation, lower Caradoc, Riceville, Tennessee; *a,* holotype, dorsal view of conjoined valves, USNM 110918a, ×3; *b,* ventral interior, USNM 110923a, ×4; *c,* dorsal interior, USNM 110923b, ×4 (Cooper, 1956).

Family TAFFIIDAE Schuchert & Cooper, 1931

[*nom. transl.* ULRICH & COOPER, 1936b, p. 625, *ex* Taffiinae SCHUCHERT & COOPER, 1931, p. 243]

Outline quadrate to transverse; profile concavoconvex to resupinate; variable ornament from multicostellate to unequally parvicostellate; short dental plates usually present; simple cardinal process ankylosed anteriorly to valve floor (occasionally absent);

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no bema; weak dorsal median septum variably developed, but no side septa. *Ordovician (?Tremadoc, Arenig–Llandeilo).*

Subfamily TAFFIINAE Schuchert & Cooper, 1931

[Taffiinae Schuchert & Cooper, 1931, p. 243] [=Aporthophylinae Liu, 1976, p. 143; Spanodontinae Cocks & Rong, 1989, p. 98]

Profile concavoconvex; with platform. *Ordovician (Arenig–Llandeilo).*

Taffia Butts, 1926, p. 99 [**T. planoconvexa;* OD] [=*Chaloupskia* Neuman in Neuman & Bruton, 1989, p. 61 (type, *C. scabrella;* OD)]. Planoconvex profile; parvicostellate ornament; large apsacline interarea, large pseudodeltidium, small chilidium also present; ventral muscle scar small, open anteriorly; usually without simple cardinal process (but rarely present); weak myophragm developed to half valve length; weak subperipheral rim variably developed. *Ordovician (Arenig–Llanvirn):* North America, Argentina, Norway, Australia.——Fig. 200,*1a–d. *T. planoconvexa,* Odenville Formation, lower Arenig; *a,* dorsal view of conjoined valves, St. Clair County, USNM 71461b, ×4; *b,c,* holotype, dorsal exterior, interior, St. Clair County, USNM 91586, ×3; *d,* ventral interior, Vandiver, Alabama, USNM 91590a, ×3 (Cooper, 1956).——Fig. 200,*1e–h. T. scabrella* (Neuman), Hølonda Limestone, Arenig–Llanvirn, Katugleåsen, Trondheim, Norway; *e,* ventral exterior, PMO 116659, ×2; *f,* ventral internal mold, PMO 116661, ×2; *g,h,* dorsal internal mold, latex cast, PMO 116664, ×2 (Neuman & Bruton, 1989).

Aporthophyla Ulrich & Cooper, 1936b, p. 625 [**A. typa*; OD]. Gently concavoconvex to planoconvex profile; differs from *Taffia* in its unequally parvicostellate ornament, smaller interarea; chilidium present, pseudodeltidium reduced or absent; strong dental plates, short ventral muscle-bounding ridges; cardinal process always present; dorsal muscle field weak: short dorsal myophragm to quarter valve length. *Ordovician (Arenig–Llanvirn):* North America, Asia, Australia.——Fig. 200,*3a–d. *A. typa,* Antelope Valley Formation, Llanvirn, Ikes Canyon, Nevada; *a–c,* latex cast of dorsal exterior, dorsal internal mold, latex cast, USNM 92866e, ×1.5; *d,* ventral internal mold, USNM 117566, ×1.5 (Cooper, 1956).

Aporthophylina Liu, 1976, p. 144 [**A. intermedia;* OD]. Similar to *Aporthophyla* but lacking dental plates in ventral valve, with stronger subperipheral rim in both valves. *Ordovician (Arenig–Llanvirn):* China.——Fig. 200,*2a–c. *A. intermedia,* Jiacun Formation, Llanvirn, Zhaya, Dingri County, southern Tibet, China; *a,* ventral external mold, NIGP 23171, ×1; *b,* ventral internal mold, NIGP 23170 ×2; *c,* holotype, dorsal internal mold, NIGP 23169, ×1 (Liu, 1976).

Spanodonta Prendergast, 1935, p. 12 [**S. hoskingiae;* OD] [=*Archambona* Cooper, 1988, p. 186 (type, *A. floweri;* OD)]. Concavoconvex profile; fine unequally parvicostellate ornament; ventral interarea apsacline, dorsal hypercline; pseudodeltidium, chilidium apparently vestigial; short dental plates, muscle-bounding ridges mostly surrounding bilobed ventral muscle field; cardinal process not trilobed (*contra* Williams, 1965d, p. 375), consists of simple ridge; prominent socket ridges curved anterolaterally; distinctive dalmanelloid-like dorsal muscle field, with median septum, transverse ridge separating two pairs of muscle scars; prominent dorsal subperipheral rim. *Ordovician (Llanvirn–Llandeilo):* Australia, Malaya.——Fig. 201,*3a–d. *S. hoskingiae,* Gap Creek Formation, Llanvirn–Llandeilo, Gap Spring, Price's Creek, Emmanuel Range, Western Australia; *a,* ventral exterior, BMNH BC 10604, ×4; *b,* conjoined valves showing ventral interior, BMNH BC 7242, ×4; *c,d,* dorsal interior, BMNH BC 10605, ×3 (Cocks & Rong, 1989).

Tourmakeadia Williams & Curry, 1985, p. 252 [**T. fimbriata;* OD]. Concavoconvex profile; costellate to parvicostellate ornament; prominent apsacline interarea, open notothyrium; short divergent dental plates; small, thin cardinal process; very divergent socket plates; with distinctive elevated, striated, bilobed platforms in both valves. *Ordovician (Arenig–Llanvirn):* North America, Europe.

T. (**Tourmakeadia**). Similar to *T. (Bockelia)* but with open delthyrium, less prominent dorsal myophragm, and stronger ventral subperipheral rim. *Ordovician (Arenig):* North America, Ireland.——Fig. 201,*1a–c. *T. (T.) fimbriata,* Tourmakeady Formation, upper Arenig, County Mayo, Ireland; *a,* ventral exterior, BMNH BB 95539, ×4; *b,* ventral interior, BMNH BB 95542, ×4; *c,* holotype, dorsal interior, BMNH BB 95538, ×5 (Williams & Curry, 1985).

T. (**Bockelia**) Neuman in Neuman & Bruton, 1989, p. 63 [**B. angusticostata;* OD]. Similar to *T. (Tourmakeadia)* but with pseudodeltidium, more prominent dorsal myophragm merging anteriorly with bilobed platform; ventral subperipheral rim only weakly developed. *Ordovician (Arenig–Llanvirn):* Baltic.——Fig. 201,*2a–d. *T. (B.) angusticostata,* Hølanda Formation, Arenig–Llanvirn, Trondheim, Norway; *a–c,* latex cast of dorsal exterior, dorsal internal mold, latex cast of dorsal valve, PMO 116671, ×2; *d,* ventral internal mold, PMO 116674, ×2 (Neuman & Bruton, 1989).

Subfamily AHTIELLINAE Öpik, 1933

[Ahtiellinae Öpik, 1933a, p. 19]

Resupinate profile; with platform (or diaphragm). *Ordovician (Arenig–Llanvirn).*

Ahtiella Öpik, 1932, p. 37 [**A. lirata;* OD]. Profile resupinate, geniculate; unequally parvicostellate, often unequally rugate ornament; catacline ventral interarea; anacline dorsal interarea; widely spaced ventral dental plates, muscle-bounding ridges con-

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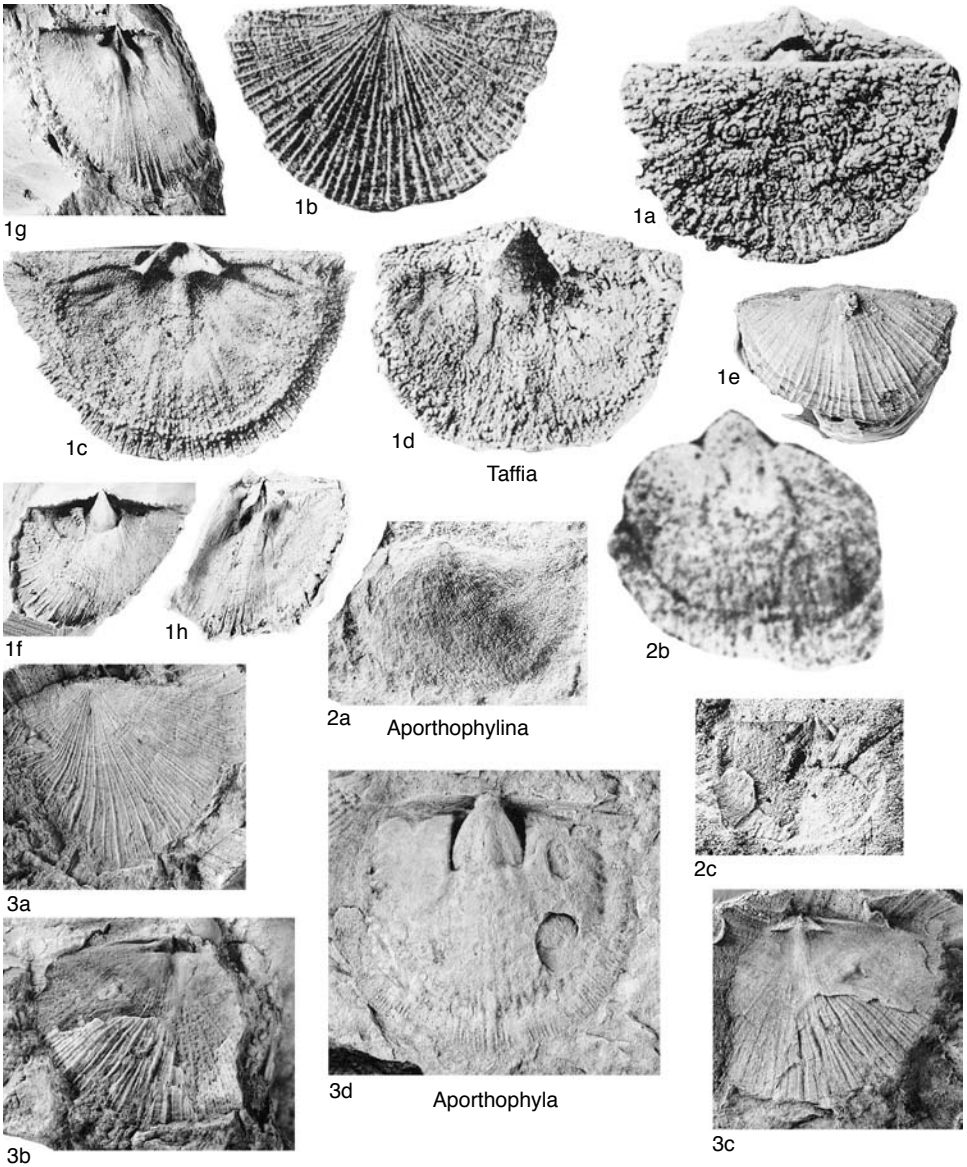

FIG. 200. Taffiidae (p. 310).

verging anteriorly before merging with valve floor; small thin cardinal process, relatively fine socket plates posteriorly that are more robust anteriorly; dorsal myophragm weak to absent; no dorsal median septum. *Ordovician (Arenig–Llanvirn):* northwestern Europe, North America, South America. ——FIG. 202,*1a,b.* **A. lirata,* Kunda Stage, Llanvirn, Tsitri, Estonia; *a,* ventral interior, ×2 (Williams, 1965d); *b,* dorsal interior, ×1.8 (Rõõmusoks, new).——FIG. 202,*1c,d. A. jaanussoni* (HESSLAND), Arenig–Llanvirn, Sweden; dorsal exterior, internal mold, ×1 (Williams, 1965d).

Borua WILLIAMS & CURRY, 1985, p. 250 [**B. modesta;* OD]. Smooth apart from faint peripheral parvicostellae, occasional impersistent rugae in some specimens; ventral interarea apsacline to orthocline; dorsal interarea anacline; arched pseudodeltidium, chilidium not covering entire delthyrium; short dental plates, very weak ventral muscle-bounding ridges; elevated ventral subperipheral rim; low small

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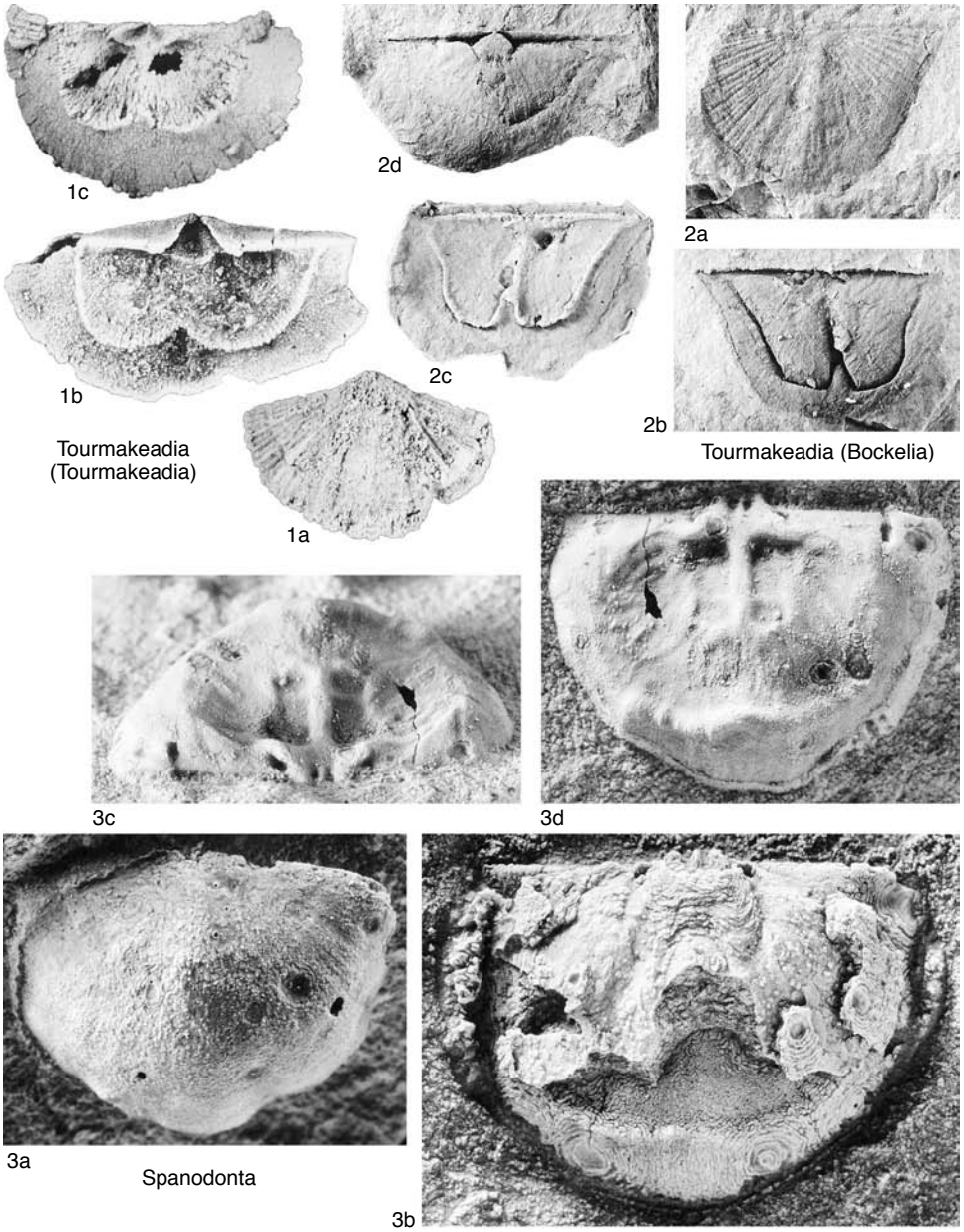

FIG. 201. Taffiidae (p. 310).

cardinal process; elevated small socket plates; short myophragm in dorsal valve, but no dorsal valve median septum; dorsal valve diaphragm present. *Ordovician (Arenig):* North America, Ireland.—— FIG. 202,*3a–d.* **B. modesta,* Tourmakeady Limestone, upper Arenig, Srah Bridge, County Mayo, Ireland; *a,* dorsal exterior, BMNH BB 95537, ×4; *b,* ventral interior, BMNH BB 95532, ×3; *c,* holotype, dorsal interior, BMNH BB 95531, ×3; *d,* dorsal interior, BMNH BB 95533, ×3 (Williams & Curry, 1985).

Guttasella NEUMAN, 1976, p. 31 [**G. gutta;* OD]. Doubly geniculate profile as in *Inversella (Reinversella);* fine unequally parvicostellate ornament; no

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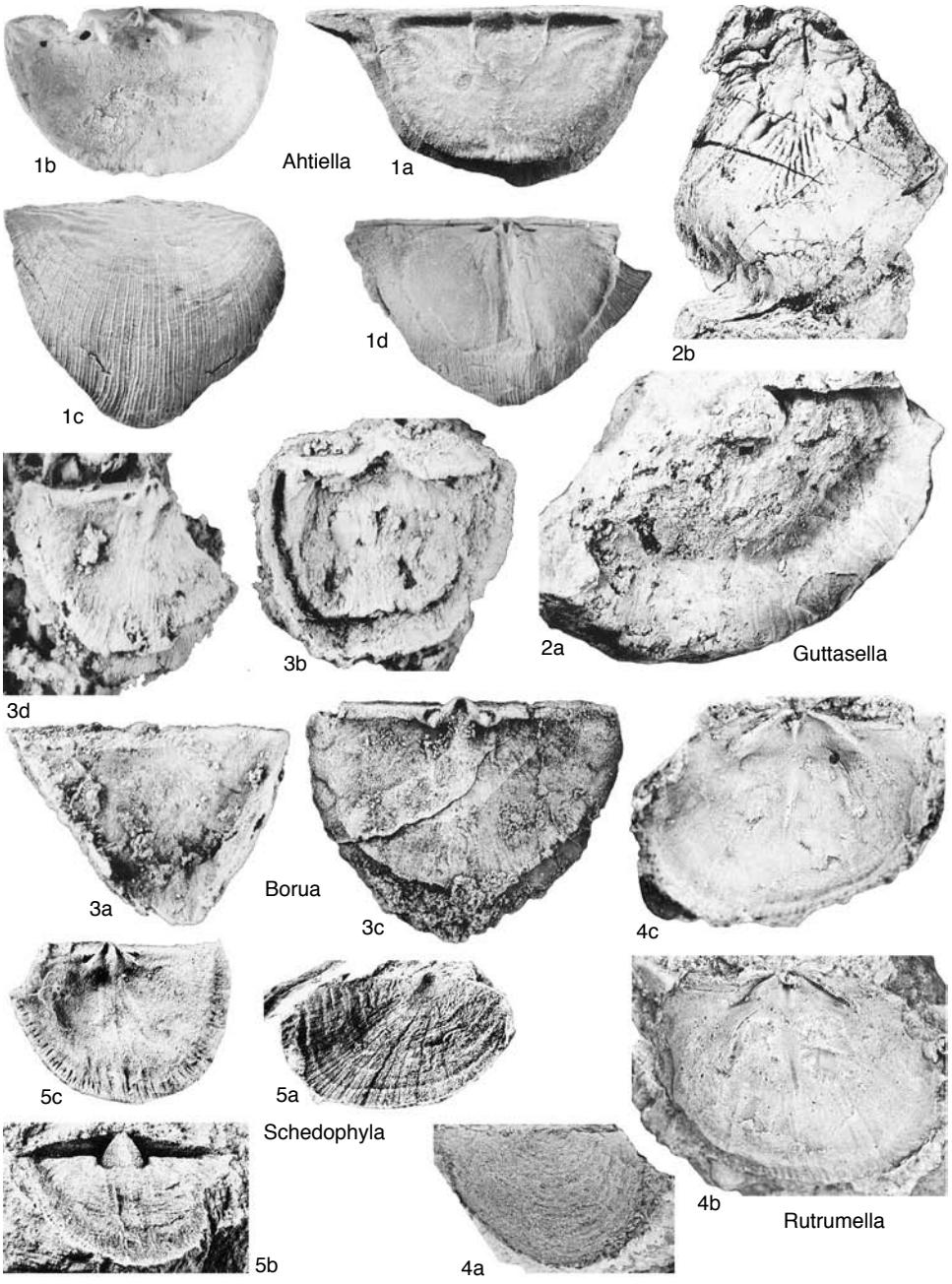

FIG. 202. Taffiidae (p. 310–314).

rugae; apsacline ventral interarea; short dental plates posterolateral to weakly impressed bilobed ventral muscle field; prominent but narrow bladelike cardinal process; variably impressed irregular dorsal muscle-bounding ridges; no dorsal median septum; subperipheral rims absent (apart from double geniculation). *Ordovician (Llanvirn):* North America.——FIG. 202,*2a,b.* **G. gutta,* Virgin Arm Tuffs, Llanvirn, Virgin Arm, Newfoundland, Canada; *a,* ventral internal mold, GSC 35059,

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×1.5; *b,* holotype, dorsal internal mold, GSC 35058, ×1.5 (Neuman, 1976).

Inversella Öpik, 1933a, p. 21 [**I. borealis;* OD]. Strongly geniculate in ventral direction, sometimes with more than one deflection; unequally parvicostellate ornament with persistent rugae over valve; small interarea; short dental plates leading anteriorly to muscle-bounding ridges define relatively small bilobed ventral muscle field; prominent bladelike cardinal process, socket plates; no dorsal median septum. *Ordovician (Arenig–Llanvirn):* Europe, South America, North America.

I. (Inversella). Similar to *I. (Reinversella)* but with only one deflection at anterior and lateral valve borders and less continuous rugae. *Ordovician (Llanvirn):* Baltic, North America.——Fig. 203,*1a–c. *I. (I.) borealis,* Echinosphaeriten Limestone, Aseri Stage, upper Llanvirn, Eesti, Estonia; *a,* dorsal exterior, BMNH BC 12877, ×1.5 (new); *b,* ventral internal mold, ×1.5; *c,* dorsal exterior, dissolved away posteromedianly to show mold of cardinalia, ×1.5 (Williams, 1965d).

I. (Reinversella) Bates, 1968, p. 169 [**R. monensis;* OD]. Similar to *I. (Inversella)* but with an extra second deflection of anterior, lateral borders, with more continuous rugae. *Ordovician (Arenig–Llanvirn):* Wales, South America.——Fig. 203,*2a–d. *I. (R.) monensis,* Treiorwerth Formation, Arenig, Ffynnon-y-mab, Anglesey, Wales; *a–c,* holotype, latex of dorsal exterior, internal mold, latex cast, BMNH BB 30574, ×2; *d,* latex cast of ventral interior, BMNH BB 30575, ×2 (new).

?Rutrumella Harper in Bruton & Harper, 1981, p. 163 [**R. implexa;* OD]. Resupinate profile; subquadrate outline, not geniculate; differs from *Schedophyla* in having discontinuous rugae but no radial ornament; ventral interior unknown, familial assignment uncertain; relatively large socket plates, low dorsal median septum to half valve length; dorsal muscle field poorly impressed. *Ordovician (Llanvirn):* Baltic.——Fig. 202,*4a–c. *R. implexa,* clasts in Otta Conglomerate, lower Llanvirn, Otta, Norway; *a,* holotype, dorsal exterior, PMO 105.803, ×1; *b,c,* mold, latex of dorsal interior, PMO 105.804, ×2 (Bruton & Harper, 1981).

Sanjuanella Benedetto & Herrera, 1987, p. 103 [**S. plicata;* OD]. Biconvex to planoconvex profile; similar to *Borua* but with marked parvicostellate ornament; prominent pseudodeltidium; short dental plates, curved muscle-bounding ridges nearly encircling relatively small ventral muscle field; small bladelike socket ridges; myophragm, but no dorsal valve median septum; dorsal muscle field poorly impressed; no dorsal platform. *Ordovician (Llanvirn):* South America.——Fig. 203,*3a–e. *S. plicata,* upper San Juan Formation, Llanvirn, Quebrada Honda, Cerro Viejo, San Juan Province, Argentina; *a,b,* ventral, dorsal views of conjoined valves, CORD-PZ 8760, ×1.5; *c,* ventral internal mold, CORD-PZ 8766, ×1.5; *d,* dorsal internal mold, ×1.4; *e,* latex cast, ×3 (Benedetto & Herrera, 1993).

Schedophyla Neuman, 1971, p. 120 [**S. potteri;* OD]. Similar to *Aporthophyla* but resupinate profile; differs from *Rutrumella* in having radial ornamentation, no rugae; large apsacline ventral interarea, with low-arched pseudodeltidium; short stout dental plates, small curved muscle-bounding ridges nearly enclosing short subcircular ventral muscle field; bulbous cardinal process; bladelike socket ridges; median septum absent; subperipheral rim weakly developed. *Ordovician (Arenig–Llanvirn):* North America, China.——Fig. 202,*5a–c. *S. potteri,* Tuffaceous Sandstone, ?Llanvirn, Hayden Brook, York County, New Brunswick, Canada; *a,* ventral exterior, GSC 24796, ×2; *b,* ventral internal mold, GSC 24795, ×2; *c,* holotype, latex cast of dorsal interior, GSC 24793, ×2 (Neuman, 1971).

Subfamily PELONOMIINAE Cocks & Rong, 1989

[Pelonomiinae Cocks & Rong, 1989, p. 98]

Not resupinate, although fairly flat profiles; no platform. *Ordovician (Llanvirn).*

Pelonomia Cooper, 1956, p. 699 [**Orthis delicatula* Billings, 1865 in 1861–1865, p. 217; OD]. Subrectangular outline; profile planoconvex with slight ventral fold with corresponding dorsal sulcus; unequally parvicostellate ornament; small interareas with rudimentary pseudodeltidium but larger chilidium; short dental plates posterolaterally bounding small ventral muscle field; small cardinal process; bladelike socket ridges; median ridge absent but larger pseudopunctae developed on dorsal sulcus. *Ordovician (Llanvirn):* North America.——Fig. 204,*1a–c. *P. delicatula* (Billings), Table Head Formation, Llanvirn, Table Head, Newfoundland, Canada; *a,* ventral exterior, ×4 (new); *b,c,* dorsal internal mold, latex cast, USNM 117557, ×3 (Cooper, 1956).

Subfamily LEPTELLINAE Williams, 1965

[Leptellinae Williams, 1965d, p. 376]

Characters as for family, but without cardinal process. *Ordovician (?Tremadoc–Llanvirn).*

Leptella Hall & Clarke, 1892, p. 293 [**Leptaena sordida* Billings, 1862 in 1861–1865, p. 74; OD] [=*Leptella (Eosericoidea)* Zeng, 1987, p. 228 (type, *L. hubeiensis* Zeng, 1977, p. 57; OD); *Niquivilia* Benedetto & Herrera, 1993, p. 50 (type, *N. extensa*)]. Concavoconvex profile; unequally parvicostellate ornament; large interareas with small pseudodeltidium, chilidium; relatively small, but well-impressed bilobed ventral muscle field between

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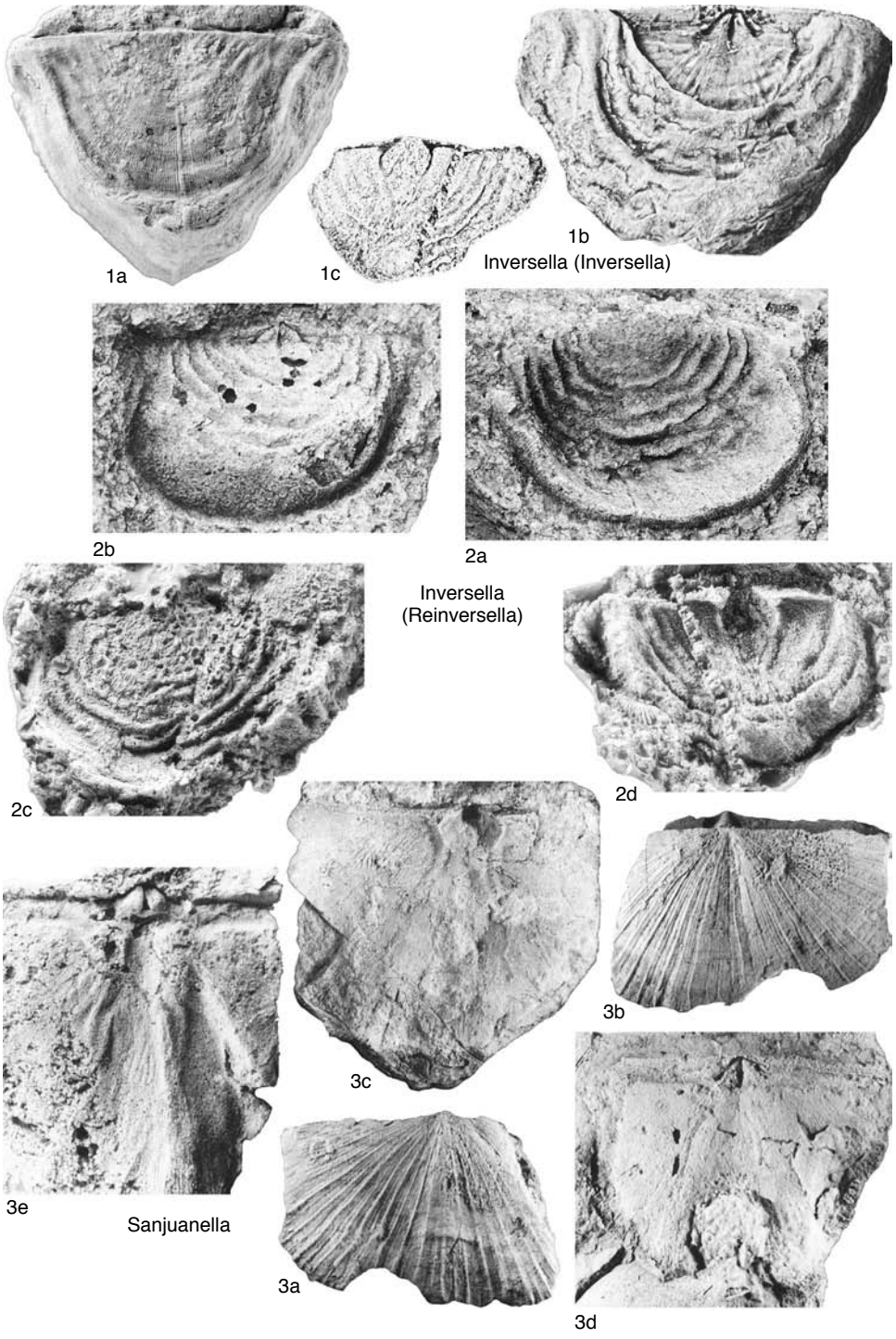

FIG. 203. Taffiidae (p. 314).

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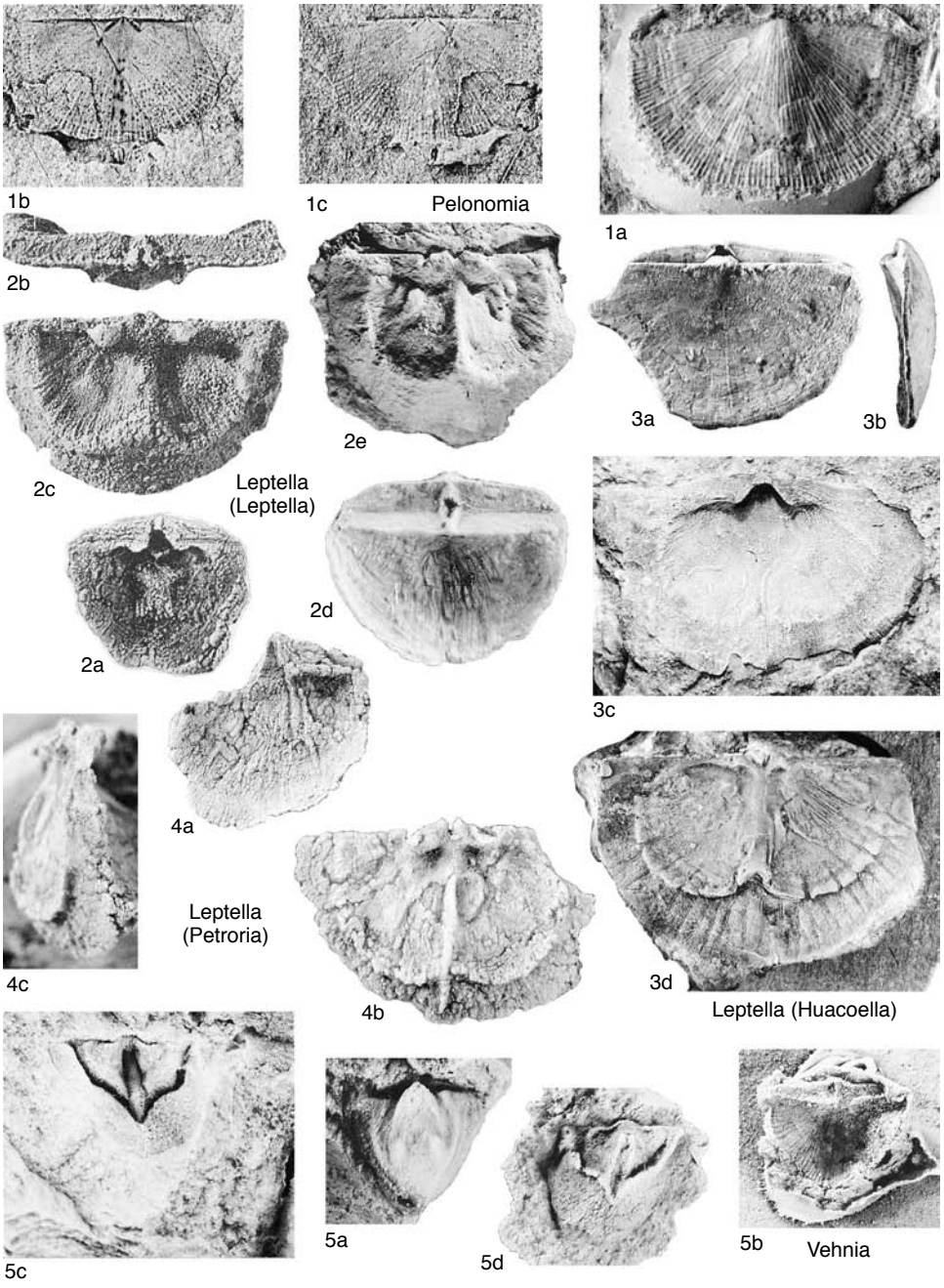

FIG. 204. Taffiidae (p. 314–317).

short dental plates; field limited anteriorly by variably developed broad median callosity; robust socket ridges curving posterolaterally; dorsal median septum merging anteriorly with bilobed platform but may continue anterior to it; may possess one or two pairs of short lateral ridges at posterolateral margin of platform. *Ordovician (?Tremadoc, Arenig–Llanvirn):* cosmopolitan.

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L. (Leptella). Diagnosis as for genus, but more convex than *L. (Huacoella)* and with hypercline dorsal interarea. Differs from *L. (Petroria)* in the median septum being confined by platform anteriorly and in possessing a median ventral callosity. *Ordovician (?Tremadoc, Arenig–Llanvirn):* North America, South America, Ireland, China.——Fig. 204,*2a–c. *L. (L.) sordida* (Billings), Lévis Shale, Arenig–Llanvirn, Point Lévis, Quebec, Canada; *a,* ventral interior, GSC 9069, ×3; *b,c,* posterior, dorsal views of dorsal interior, USNM 90752b, ×6 (Ulrich & Cooper, 1938). ——Fig. 204,*2d,e. L. (L.) hubeiensis* Zeng, Dawan Formation, Arenig, Yichang, western Hubei Province, China; *d,* dorsal view of conjoined valves, YIGM IV45222, ×3; *e,* dorsal interior, YIGM IV46023, ×3 (Zeng, 1977).

L. (Huacoella) Benedetto & Herrera, 1993, p. 46 [**H. radiata;* OD]. Similar to *L. (Leptella),* but larger, less convex in profile, with orthocline rather than hypercline dorsal interarea, less robust teeth, socket plates. *Ordovician (Arenig):* Argentina.——Fig. 204,*3a–d. *L. (H.) radiata,* San Juan Limestone, upper Arenig, Huaco, San Juan, Argentina; *a,b,* dorsal, lateral views of conjoined valves, CORD-PZ UNC 288, ×1.5; *c,* ventral interior, CORD-PZ UNC 287, ×1.5; *d,* holotype, dorsal interior, CORD-PZ UNC 281, ×1.5 (Benedetto & Herrera, 1993).

L. (Petroria) Wilson, 1926, p. 27 [**P. rugosa;* OD]. Similar to *L. (Leptella)* but lacking median ventral callosity, with median septum continuing anteriorly of raised platform in dorsal valve. *Ordovician (Arenig–Llanvirn):* North America, South America, Kazakhstan.——Fig. 204,*4a–c. *L. (P.) rugosa,* Beaverfoot Formation, Arenig, Palliser Pass, British Columbia, Canada; *a,* ventral interior, ×3; *b,c,* dorsal, lateral views of dorsal interior, GSC 6754a, ×4 (Cooper, 1956).

Vehnia Neuman in Neuman & Bruton, 1989, p. 65 [**Chonetoidea triangularis* Reed, 1932a, p. 137; OD]. Very concavoconvex profile; finely costellate ornament; interareas coplanar, pseudodeltidium, chilidial plates developed; very short dental plates, weak muscle-bounding ridges defining short bilobed ventral muscle field; cardinal process variably developed, often absent; widely flaring thin socket ridges; median septum bifurcating, with two halves running subparallel anteriorly, but not beyond high elevated platform extending anteriorly. *Ordovician (Arenig–Llanvirn):* Norway.——Fig. 204,*5a–d. *V. triangularis* (Reed), Hølanda Formation, Arenig–Llanvirn, Damtjern, Trondheim, Norway; *a,* ventral internal mold, PMO 116690, ×5; *b,* latex cast of conjoined valves, PMO 11681, ×5; *c,d,* dorsal internal mold, latex cast, PMO 116689, ×5 (Neuman & Bruton, 1989).

Family BIMURIIDAE Cooper, 1956

[Bimuriidae Cooper, 1956, p. 764, *partim*] [=Craspedeliinae Cocks & Rong, 1989, p. 145]

Strongly concavoconvex profile; dental plates poorly developed or absent; cardinal process simple, not undercut, sometimes fused with socket ridges; with bema, side septa. *Ordovician (Llandeilo–middle Ashgill).*

Bimuria Ulrich & Cooper, 1942, p. 622 [**B. superba;* OD]. Concavoconvex profile with incurved beak; no ornament, but comae sometimes developed; small pseudodeltidium, chilidium absent; widely spaced, very divergent teeth, curved socket plates; ventral muscle field poorly impressed, open anteriorly; cardinal process varies from wedgelike to absent; widely flaring socket plates varying from straight, stout to curving anterolaterally; dorsal side septa varying from one to two pairs; long dorsal median septum. *Ordovician (Llandeilo–middle Ashgill):* cosmopolitan.

B. (Bimuria). Differs from *B. (Cooperea)* in its less elongate outline and in its elongate, divided bema in adults. *Ordovician (Llandeilo–middle Ashgill):* cosmopolitan.——Fig. 205,*1a–e. *B. (B.) superba,* Arline Formation, Llandeilo, Friendsville, Tennessee; *a,b,* ventral, dorsal views of conjoined valves, BMNH BC 7270, ×2; *c,* ventral interior, BMNH BC 13421, ×2; *d,e,* posterior, dorsal views of dorsal interior, BMNH BC 7269, ×2 (Cocks & Rong, 1989).

B. (Cooperea) Cocks & Rong, 1989, p. 147 [**B. siphonata* Cooper, 1956, p. 770; OD]. Profile concavoconvex; outline very laterally elongate; pedicle tube sometimes present; differs from *B. (Bimuria)* in its bilobed subcircular bema in adults, often elevated anteriorly, laterally. *Ordovician (Llandeilo–Caradoc):* North America.——Fig. 205,*2a–c. *B. (C). siphonata* (Cooper), Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* holotype, external view of conjoined valves (specimen also shows pedicle tube), USNM 117470a, ×10 (Cooper, 1956); *b,* ventral interior, BMNH BC 10303, ×10 (Cocks & Rong, 1989); *c,* dorsal interior, USNM 117470e, ×10 (Cooper, 1956).

Craspedelia Cooper, 1956, p. 772 [**C. marginata;* OD]. Similar to *Bimuria,* but with geniculate profile with additional anterior deflection; fold, sulcus; no ornament known; bema sometimes elevated anteriorly. *Ordovician (Llandeilo–Caradoc):* North America, Scotland, Kazakhstan.——Fig. 205,*3a–d. **C. marginata,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,b,* ventral exterior, interior, USNM 117474a, ×6; *c,* dorsal exterior, USNM 117474e, ×5; *d,* dorsal interior, USNM 117474d, ×7 (Cooper, 1956).

Family SYNDIELASMATIDAE Cooper, 1956

[Syndielasmatidae Cooper, 1956, p. 742]

Concavoconvex to planoconvex profile; dental plates poorly developed, often absent; trifid cardinal process; no bema; side septa usually developed. *Ordovician (Llanvirn–Caradoc).*

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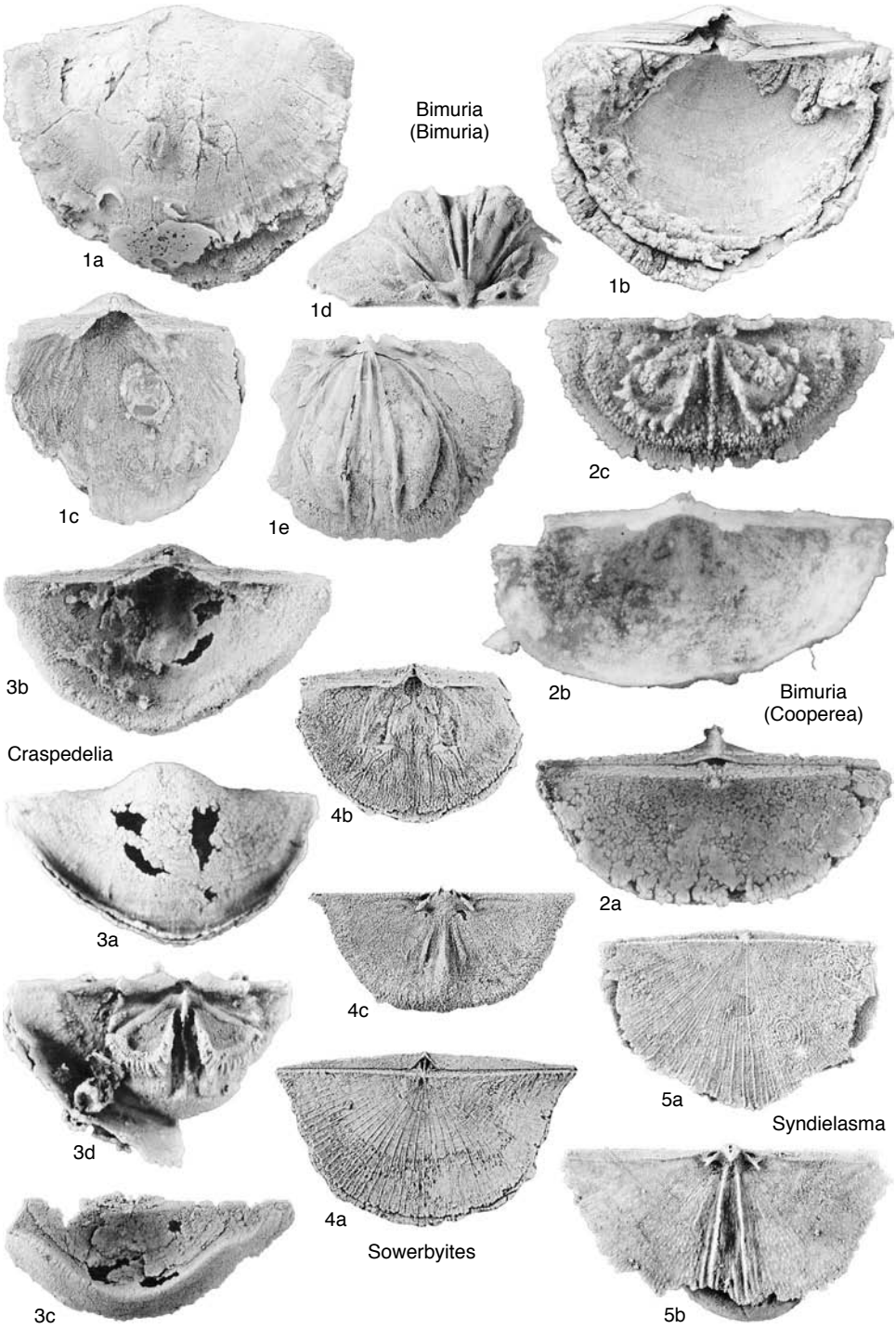

FIG. 205. Bimuriidae and Syndielasmatidae (p. 317–319).

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Syndielasma Cooper, 1956, p. 742 [**S. biseptatum;* OD]. Gently concavoconvex to planoconvex profile; unequally parvicostellate ornament; interarea small; pseudodeltidium reduced or absent; ventral interior poorly known, but without dental plates; muscle fields poorly impressed; bulbous cardinal process not fused anterolaterally to thin socket plates; very short thin dorsal median septum developed posteriorly in some specimens only; two prominent long side septa; similar to *Sowerbyites* but without dorsal median septum. *Ordovician (Llanvirn):* North America.——Fig. 205,*5a,b.* **S. biseptatum,* upper Pogonip Group, Llanvirn, Ikes Canyon, Nevada; *a,* dorsal view of conjoined valves, USNM 117565e, ×3; *b,* dorsal interior, USNM 117565h, ×4 (Cooper, 1956).

Sowerbyites Teichert, 1937, p. 66 [**S. medioseptatus;* OD]. Concavoconvex profile; unequally parvicostellate ornament with accentuated costellae narrowly spaced; thickened concentric lamellae common distally; delthyrium largely open, but small pseudodeltidium, small chilidial plates; ventral adductor scar small, within delthyrial cavity; diductor scars long, broad, divergent, ending in callosities; cardinal process fused with brachiophore bases; similar to *Syndielasma,* but median septum present in dorsal valve; side septa variably developed. *Ordovician (Llandeilo–Caradoc):* North America, Ireland, Mongolia, Australia.——Fig. 205,*4a–c. S. triseptatus* (Willard), Lincolnshire Formation, Caradoc, Clinch Valley, Tennessee; *a,* dorsal view of conjoined valves, USNM 117415b, ×2; *b,* ventral interior, USNM 117415j, ×2; *c,* dorsal interior, USNM 117415a, ×2 (Cooper, 1956).

Family LEPTELLINIDAE Ulrich & Cooper, 1936

[*nom. transl.* Cooper, 1956, p. 744, *ex* Leptellininae Ulrich & Cooper, 1936b, p. 626] [=Titanambonitidae Laurie, 1991, p. 55]

Profile concavoconvex to resupinate; dental plates present; trifid cardinal process fused anteriorly to valve floor (not undercut); no side septa present; no bema present (although clear muscle-bounding ridges occasionally seen). *Ordovician (upper Arenig)–Silurian (upper Llandovery).*

Subfamily LEPTELLININAE Ulrich & Cooper, 1936

[Leptellininae Ulrich & Cooper, 1936b, p. 626]

Restricted ventral valve muscle field. *Ordovician (?Arenig, Llanvirn)–Silurian (Telychian).*

Leptellina Ulrich & Cooper, 1936b, p. 626 [**L. tennesseensis;* OD] [=*Urbimena* Havlíček, 1976, p. 367 (type, *U. mareki;* OD); *Qianjiangella* Liang in Liu, Xu, & Liang, 1983, p. 274 (type, *Q. qianjiangensis;* OD]. Concavoconvex profile; unequally parvicostellate ornament, sometimes with comae; relatively large interarea; small pseudodeltidium in apex of delthyrium; chilidium absent; small dental plates, bounding ridges posterolateral to bilobed ventral valve muscle field (often less than quarter valve length); subperipheral rims sometimes present; thin central ridge to cardinal process set low relative to hinge line, with lateral components less prominent (only thin central process projecting posteriorly from hinge line; even this is sometimes entirely anterior to hinge line); median septum elevated anteriorly to merge with variably elevated platform. *Ordovician (?Arenig, Llanvirn)–Silurian (Telychian):* cosmopolitan.

- **L. (Leptellina).** Similar to *L. (Merciella)* but with narrower cardinal process, less elevated and narrower platform and a single dorsal subperipheral rim. *Ordovician (?Arenig, Llanvirn–Ashgill):* cosmopolitan.——Fig. 206,*1a–c.* **L. (L.) tennesseensis,* Arline Formation, Llandeilo, Friendsville, Tennessee; *a,* dorsal view of conjoined valves, USNM 117453b, ×4 (Cooper, 1956); *b,* posterior view of dorsal interior, BMNH BB 1228, ×4; *c,* lateral view of dorsal interior, BMNH BB 1228, ×3.5 (Cocks & Rong, 1989).——Fig. 206,*1d,e. L. (L.) mareki* (Havlíček), Liben Formation, lower Caradoc, Motol, Prague, Czech Republic; *d,* ventral internal mold, ×5; *e,* dorsal internal mold, ×5 (Havlíček, 1976).——Fig. 206,*1f–i. L. (L.) qianjiangensis* (Liang), Changwu Formation, middle Ashgill, Jianglütang, Chunan County, western Zhejiang Province, China; *f,* dorsal view of external mold of conjoined valves, showing interarea, HIGS 04351, ×2; *g,h,* holotype, internal mold of ventral valve, HIGS 04312, ×2; *i,* dorsal view of internal mold of conjoined valves, HIGS 04322, ×1.8 (Liu, Xu, & Liang, 1983).
- **L. (Merciella)** Lamont & Gilbert, 1945, p. 655 [**Leptella (Merciella) vesper;* OD]. Concavoconvex profile; unequally parvicostellate ornament; differs from *L. (Leptellina)* in having broader cardinal process, in having more elevated, wider platform, with an extra subperipheral rim in dorsal valve. *Silurian (Llandovery):* Europe, China.——Fig. 206,*2a–d.* **L. (M.) vesper,* Wych Formation, Telychian, Alfrick, Worcestershire, England; *a,* partially exfoliated ventral valve, showing ornament to left, interior to right, BU 373, ×3; *b,* ventral interior mold, BU 368, ×3; *c,d,* mold, latex cast of dorsal interior, BU 370, ×3 (new).

Acculina Misius in Misius & Ushatinskaya, 1977, p. 113 [**A. acculica;* OD]. Gently resupinate profile; unequally parvicostellate ornament; pseudodeltidium over more than half ventral delthyrium; dental plates leading to muscle-bounding ridges surrounding bilobed ventral muscle field not enclosed anteriorly; no ventral valve myophragm; short, prominent socket ridges; myophragm elevated

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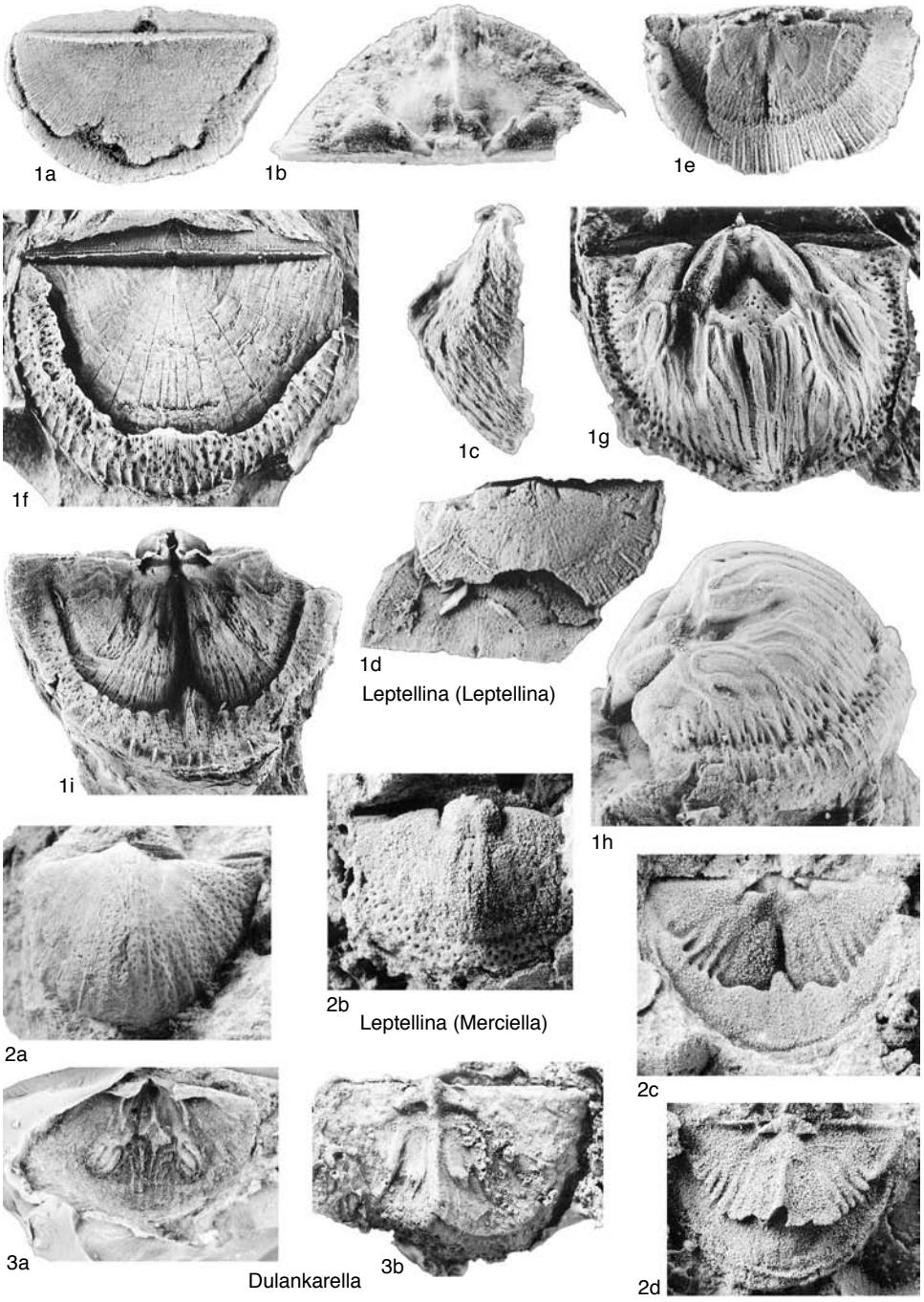

FIG. 206. Leptellinidae (p. 319–322).

anterior to dorsal median septum leading to quadrate dorsal platform, bilobed anteriorly. *Ordovician (Llandeilo–Caradoc):* Central Asia.——FIG. 207,*1a–f. *A. acculica; a,* dorsal view of conjoined valves, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia,

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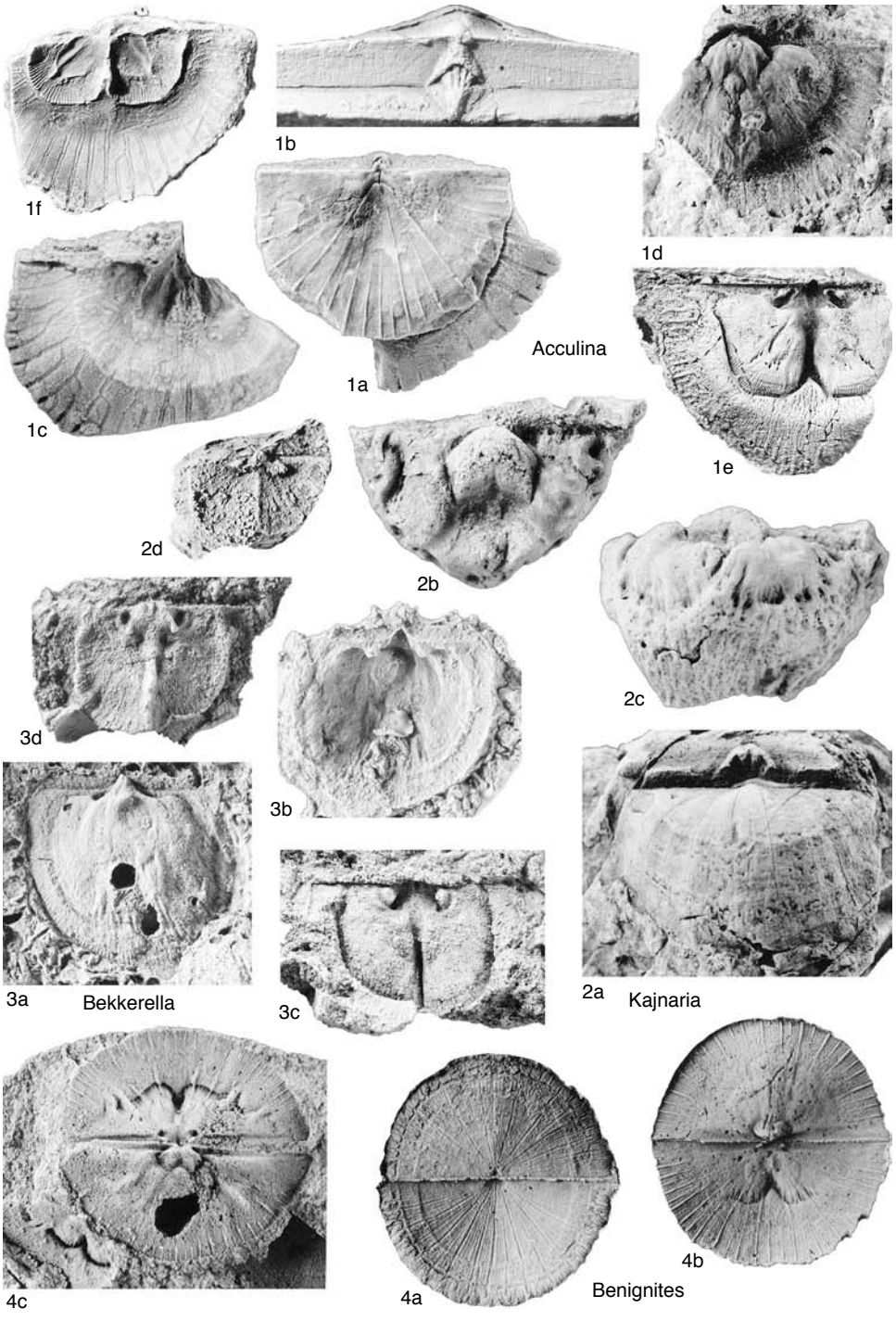

FIG. 207. Leptellinidae (p. 319–322).

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BMNH BC 12907, ×3 (new); *b,* interarea of conjoined valves, Anderken Formation, Caradoc, Burultas, Kazakhstan, ×5 (Popov, new); *c,* ventral interior, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia, BMNH BC 12903, ×2; *d,* internal mold, Tabilgatinsk Formation, middle Ordovician, Moldo-Too Mountains, northern Kirghizia, BMNH BC 12896, ×2 (new); *e,f,* dorsal internal mold, dorsal interior, Anderken Formation, Caradoc, Burultas, Kazakhstan, ×2 (Popov, new).

Bekkerella Reed, 1936, p. 38 [**Orthis subcrateroides* Reed, 1906, p. 63; OD]. Concavoconvex profile; fine radial ornament; pseudodeltidium, chilidium not known; prominent teeth with minimal dental plates; ventral muscle scars divergent, restricted by variably developed muscle-bounding ridges; weak ventral subperipheral ridge; small simple cardinal process; short, stout, curved socket ridges; prominent dorsal median septum developed anteriorly from myophragm, dividing prominent quadrate platform anteriorly. *Ordovician (Caradoc):* Burma.——Fig. 207,*3a–d. *B. subcrateroides* (Reed), Naungkangyi Beds, Caradoc, Chaungzon, Northern Shan States, Burma; *a,b,* ventral internal mold, latex cast, SM 3128, ×2.5; *c,d,* dorsal internal mold, latex cast, BMNH BB 37750, ×2 (new).

Benignites Havlíček, 1952, p. 412 [**Strophomena primula* Barrande, 1879, pl. 52, fig. 3; OD]. Transverse outline; gently concavoconvex profile; unequally parvicostellate ornament; small bilobed ventral muscle field enclosed anteriorly; no ventral valve median septum; simple cardinal process, small socket ridges; wide but relatively small bilobed platform in posterior of center of dorsal valve, interrupted by mantle canals. *Ordovician (Llandeilo):* Europe.——Fig. 207,*4a–c. *B. primula,* Dobrotivá Shales, Llandeilo, Malé Prílepy, Bohemia, Czech Republic; *a,b,* external, internal molds of conjoined valves, ×4; *c,* internal mold of conjoined valves, ×3 (Havlíček, 1976).

Dulankarella Rukavishnikova, 1956, p. 135 [**D. magna;* OD]. Concavoconvex profile; exterior, ventral interior as in *Leptellina,* except for larger bilobed ventral muscle field extending to half valve length or more; dorsal interior with striated lateral lobes of cardinal process distinct from brachiophores; pronounced socket ridges, muscle-bounding ridges; prominent dorsal median septum not extending anteriorly of diaphragm. *Ordovician (Caradoc–Ashgill):* Kazakhstan.——Fig. 206,*3a,b. *D. magna; a,* latex cast of ventral internal mold, Otarsky Horizon, Caradoc, CNIGR 12375/200, ×1.5; *b,* latex cast of dorsal interior, Dulankara Formation, upper Caradoc, Dulankara, Chu-Ili Mountains, Kazakhstan, ×2 (new).

Kajnaria Nikitin & Popov in Klenina, Nikitin, & Popov, 1984, p. 144 [**K. derupta;* OD] [=*Pseudoleptellina* Andreev, 1992, p. 112 (type, *P. similis;* OD)]. Strongly concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium, no chilidium; massive teeth, no dental plates; strong muscle-bounding ridges in ventral valve, with two curved ridges variably developed anteriorly (the diaphragm of Nikitin & Popov, 1984); variably developed ventral valve myophragm; dorsal interior with robust dental plates, prominent median septum, platform. *Ordovician (Llandeilo–Ashgill):* Kazakhstan.——Fig. 207,*2a–d. *K. derupta,* upper Bestamakskaya Formation, Erkebidaikski Horizon, middle Ordovician, New Archal Hill, Chinghiz Mountains, Kazakhstan; *a,* dorsal external mold, BMNH BC 12931, ×3; *b,c,* ventral internal mold, BMNH BC 12932, ×3 (new); *d,* latex cast of dorsal internal mold, CNIGR 110/12095, ×2 (Klenina, Nikitin, & Popov, 1984).

Leptelloidea Jones, 1928, p. 385 [**Plectambonites schmidti* var. *leptelloides* Bekker, 1921, p. 68; OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; very small deltidial plates, small chilidium; distinctive articulation including pits, accessory teeth in ends of dental plates, corresponding structures in dorsal valve; large bilobed ventral muscle scars extending to about half valve length (much longer than *Leptellina* but not so wide as in *Dulankarella*), adductor scars enclosed by diductor scars; large cardinal process projecting posteriorly from hinge line, but cardinal process separate from socket plates; dorsal median septum merging with bilobed elevated platform. *Ordovician (Llanvirn–Caradoc):* Europe, Burma.——Fig. 208,*1a–f. *L. leptelloides* (Bekker), Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia; *a,* dorsal view of conjoined valves, USNM 84257c, ×3 (Cooper, 1956); *b,c,* ventral interior, viewed ventrally, from anterior, TAGI BR 93, ×3 (new); *d–f,* dorsal interior viewed laterally, ×3, dorsally, ×3, posteriorly, ×5, BMNH BB 5169 (Cocks & Rong, 1989).

Mabella Klenina in Klenina, Nikitin, & Popov, 1984, p. 69 [**Leptellina (M.) semiovalis;* OD] [=*Wiradjuriella* Percival, 1991, p. 138 (type, *W. halis;* OD)]. Very convex ventral profile, slightly concave dorsal profile; very fine parvicostellate ornament; pseudodeltidium filling most of delthyrium; chilidium absent; stout flaring teeth; vestigial dental plates leading to bounding ridges lateral to bilobed ventral muscle field; prominent cardinal process, flaring socket ridges; dorsal interior as in *Leptellina* but with prominent median septum anteriorly enlarging, tubular, sometimes bifurcating, but not extending anteriorly from platform rim; platform may be elevated. *Ordovician (Caradoc–Ashgill):* Kazakhstan, Australia, ?Burma.——Fig. 208,*2a–e. M. multicosta* (Rukavishnikova), lower Kulunbulak Formation, Dulankara Horizon, lower Ashgill, Kulunbulak River, Kazakhstan; *a,b,* ventral internal mold, latex cast, BMNH BC 12935a, ×5; *c,d,* dorsal internal mold, latex cast, BMNH BC 12935b, ×5; *e,* latex cast of dorsal interior, BMNH BC 12934, ×5 (new).——Fig. 208,*2f–i. M. halis* (Percival), Billabong Limestone, middle Caradoc, Parkes, New South Wales, Australia; *f,g,* dorsal, posterior views of conjoined valves, SUP 67527, ×3; *h,* ventral inte-

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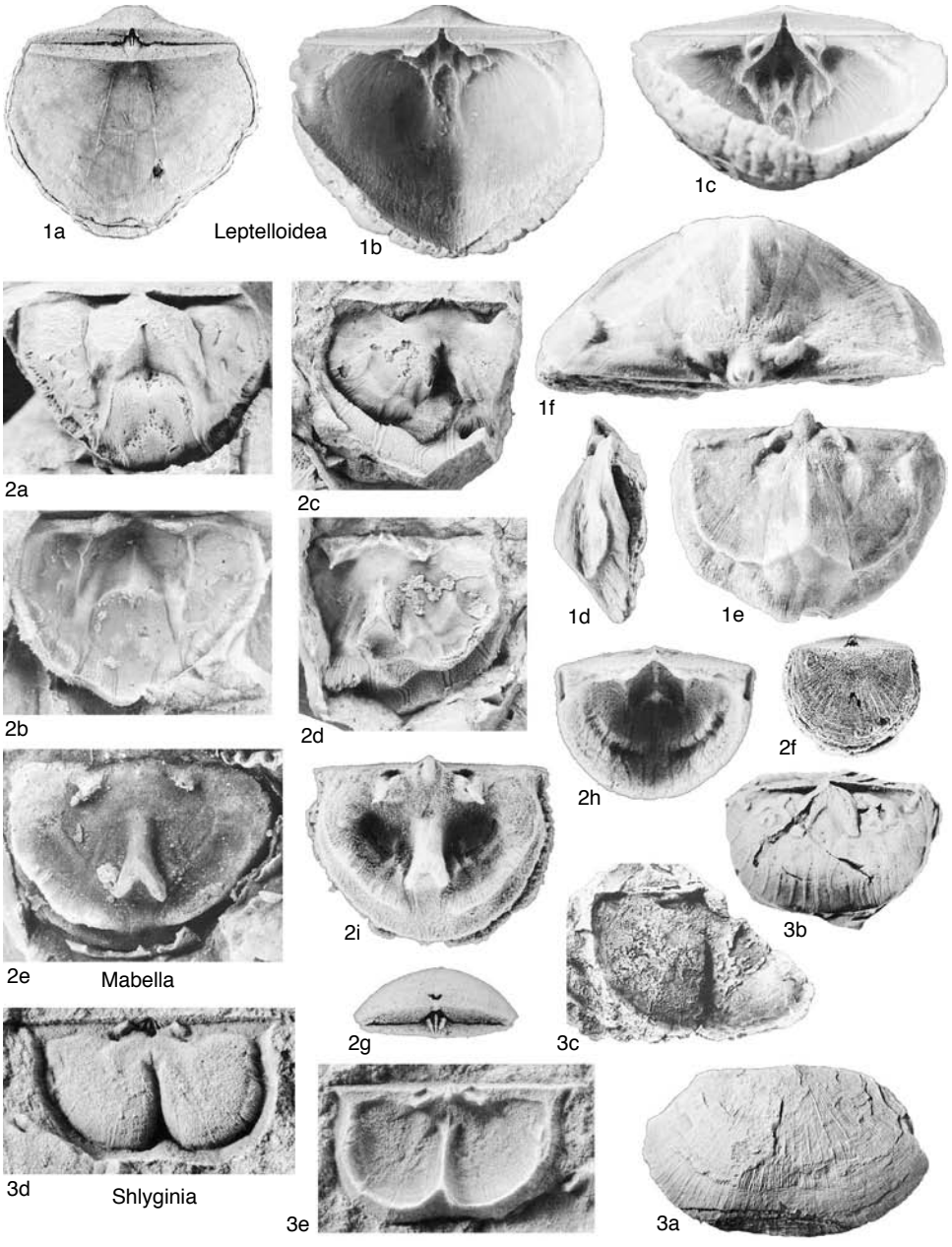

FIG. 208. Leptellinidae (p. 322–324).

rior, SUP 67512, ×5; *i,* holotype, dorsal interior, SUP 67491, ×5 (Percival, 1991).

Reversella LIANG in LIU, XU, & LIANG, 1983, p. 274 [**R. trigonoformis;* OD]. Profile resupinate, strongly geniculate ventrally; unequally parvicostellate ornament; teeth, dental plates posterior to ventral muscle field with strong bounding ridges, meeting anteriorly, with central strong myophragm within muscle field; prominent cardinal process, socket plates, large median septum extending anteriorly to

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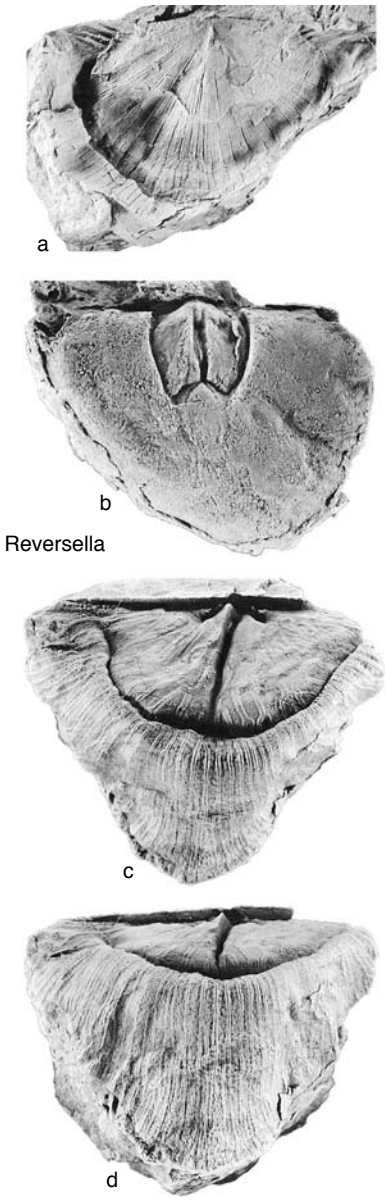

FIG. 209. Leptellinidae (p. 323–324).

merge with platform; dorsal platform with diaphragm, not bilobed anteriorly. *Ordovician (Ashgill):* China.——FIG. 209*a–d. *R. trigonoformis,* Changwu Formation, middle Ashgill, Jianglütang, Chunan County, western Zhejiang, China; *a,* dorsal external mold, HIGS 04332, ×1; *b,* ventral internal mold, HIGS 04328, ×1.4; *c,d,* holotype, dorsal internal mold viewed obliquely, anteriorly, HIGS 04327, ×1 (Liu, Xu, & Liang, 1983).

Shlyginia NIKITIN & POPOV, 1983, p. 237 [**S. declivis;* OD]. Concavoconvex profile; differs from *Leptellina* in possessing large muscle field in ventral valve to about half valve length or more; adductor muscle scars usually enclosed by diductor scars in ventral valve; cardinal process projecting slightly or not at all posteriorly from hinge line as in *Leptellina. Ordovician (Llandeilo–lower Ashgill):* Kazakhstan.——FIG. 208,*3a–c. *S. declivis,* Andryushinka Formation, Llandeilo–Caradoc, Ishim River, Kazakhstan; *a,* holotype, ventral exterior, CNIGR 31/11990, ×3; *b,* ventral internal mold, CNIGR 34/11990, ×3; *c,* dorsal internal mold, CNIGR 35/11990, ×3 (Nikitin & Popov, 1983).——FIG. 208,*3d,e. S. extraordinaria* (RUKAVISHNIKOVA), Dulankara Formation, Caradoc, Dulankara, Kazakhstan; dorsal internal mold, latex cast, BMNH BC 12897, ×3 (new).

Subfamily PALAEOSTROPHOMENINAE Cocks & Rong, 1989

[Palaeostrophomeninae COCKS & RONG, 1989, p. 107]

Profile concavoconvex to resupinate; large open ventral valve muscle field; usually with deeply impressed mantle canal markings in both valves. *Ordovician (Arenig–Caradoc).*

Palaeostrophomena HOLTEDAHL, 1916, p. 43 [**Strophomena concava* SCHMIDT, 1858, p. 215; OD]. Gently resupinate profile; unequally parvicostellate ornament with posterolateral rugae common; small pseudodeltidium, larger chilidium; small teeth with reduced dental plates leading to posterolateral bounding ridges around triangular ventral muscle field open anteriorly; prominent cardinal process, small socket ridges; central myophragm becoming striated anteriorly; platform absent; dorsal interior as in *Apatomorpha. Ordovician (Llanvirn–Caradoc):* cosmopolitan.——FIG. 210,*1a–c. *P. concava* (SCHMIDT), Llanvirn; *a,* dorsal exterior, Hunduum Formation, Tallinn, BMNH BB 91269, ×2 (new); *b,c,* ventral and dorsal interiors, Uhaku Stage, Erra, Estonia, ×2 (Rõõmusoks, new).

Apatomorpha COOPER, 1956, p. 709 [**Rafinesquina pulchella* RAYMOND, 1928, p. 296; OD]. Concavoconvex to planoconvex profile; unequally parvicostellate ornament; narrow pseudodeltidium developed; widely divergent teeth; dental plates present; large prominent ventral muscle field with short muscle-bounding ridges, muscle scars flabellate anteriorly; prominent cardinal process, small socket ridges; prominent but divided dorsal myophragm; small dorsal muscle field with oblique ridges; no platform. *Ordovician (Llanvirn–Caradoc):* North America, Australia.——FIG. 210,*2a–d. *A. pulchella* (RAYMOND), Athens Formation, upper Llandeilo–lower Caradoc, Tennessee; *a,* dorsal view of exterior of conjoined valves, USNM 110895c, ×3; *b,* ventral internal mold, BMNH BC 12849, ×2; *c,* ventral interior, USNM 110896a, ×3 (Cooper, 1956); *d,* dorsal interior, USNM 110896c, ×3 (new).

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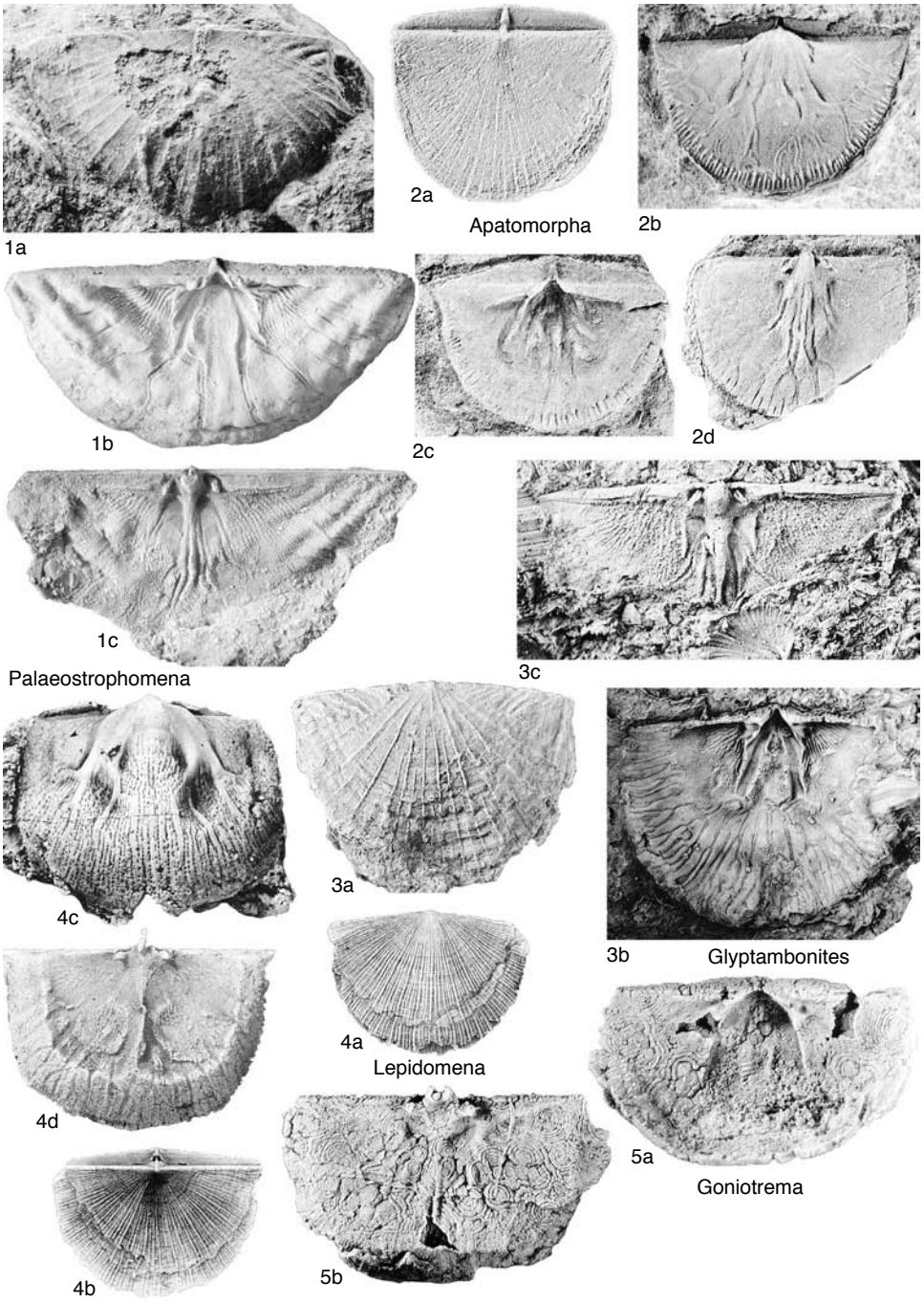

FIG. 210. Leptellinidae (p. 324–326).

Glyptambonites COOPER, 1956, p. 712 [**G. musculosus;* OD]. Gently concavoconvex profile; unequally parvicostellate ornament with much accentuated costellae, posterolateral rugae common; small pseudodeltidium, moderate chilidium; small teeth, dental plates leading to strong lateral muscle-

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bounding ridges; bilobed ventral muscle field relatively open anteriorly; bulbous cardinal process; very small socket ridges; large myophragm leading anteriorly to relatively small dorsal median septum; posterolateral dorsal muscle-bounding ridges in adults; no platform (although no entire dorsal valve yet illustrated); similar to *Apatomorpha* but with ventral valve muscle field narrower, longer muscle-bounding ridges. *Ordovician (Llanvirn–Caradoc):* North America, Scotland, Kazakhstan.——Fig. 210,*3a–c.* **G. musculosus,* Oranda Formation, lower Caradoc, Linville Station, Virginia; *a,* ventral exterior, USNM 117391, ×2; *b,* latex cast of ventral internal mold, USNM 117390a, ×1; *c,* latex cast of dorsal interior, USNM 117388c, ×2 (Cooper, 1956).

?Goniotrema Ulrich & Cooper, 1936b, p. 626 [**G. perplexum;* OD]. Concavoconvex profile; ornament uncertain; strong teeth; strong muscle-bounding ridges, triangular ventral muscle field open anteriorly; prominent erect cardinal process but very small socket ridges; weak myophragm; no bema but faint traces of possible side septa (and thus possible inclusion in Syndielasmatidae); weak platform present; not certainly leptellinid. *Ordovician (Llanvirn):* North America.——Fig. 210,*5a,b.* **G. perplexum,* upper Pogonip Group, upper Llanvirn, Ikes Canyon, Nevada; *a,b,* holotype, ventral, dorsal interiors, USNM 92872, ×2 (Cooper, 1956).

Ishimia Nikitin, 1974, p. 59 [**I. ishimensis;* OD]. Large with convex ventral valve, flat dorsal valve becoming concave anteriorly; unequally parvicostellate ornament, sometimes with comae; pseudodeltidium, chilidium present; substantial teeth but dental plates short or absent; well-impressed triangular ventral muscle field with no bounding ridges, open anteriorly; prominent cardinal process, socket plates curving anterolaterally; prominent dorsal median septum merging anteriorly with elevated platform; similar to *Toquimia,* but with concavoconvex profile, stronger median septum, stronger dorsal platform. *Ordovician (Llanvirn–lower Caradoc):* Asia.——Fig. 211,*1a,b.* **I. ishimensis,* Andryshenskaya Formation, Llandeilo, Ishim River, Kazakhstan; *a,* latex cast of ventral interior, CNIGR 1614/14, ×1; *b,* holotype, latex cast of dorsal interior, CNIGR 1614/15, ×1 (new).

Lepidomena Laurie, 1991, p. 55 [**L. pulchra;* OD]. Concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium, chilidium; ventral interarea orthocline or apsacline; dorsal interarea hypercline; dental plates absent; ventral muscle field bilobed; similar to *Apatomorpha* but high bladelike cardinal process, delicate bladelike socket ridges free distally; dorsal median septum, low dorsal platform rim developed. *Ordovician (Caradoc):* Australia.——Fig. 210,*4a–d.* **L. pulchra,* lower Benjamin Limestone, Caradoc, Settlement Road, Florentine Valley, Tasmania, Australia; *a,b,* ventral, dorsal views of conjoined valves, UTGD 99913, ×2; *c,* ventral internal mold, UTGD 99911, ×2; *d,* holotype, dorsal interior, UTGD 99906, ×2 (Laurie, 1991).

Onegia Andreev, 1993, p. 51 [**O. vitrea;* OD]. Small transverse shells with concavoconvex profile; unequally parvicostellate ornament with anterior extensions of three major costellae; poorly impressed ventral muscle field; ventral subperipheral rim; stubby socket plates; dorsal median septum leading to elevated bilobed dorsal valve platform. *Ordovician (Arenig):* Russia.——Fig. 211,*2a.* **O. vitrea,* uppermost Volkhov Formation, upper Arenig, Volkhov River, St. Petersburg, Russia; dorsal interior, PAN 4459/4, ×9 (Andreev, 1993).——Fig. 211,*2b–d. O. geometrica* (Kutorga), uppermost Volkhov Formation, upper Arenig, River Lava, St. Petersburg, Russia; *b,c,* ventral, dorsal views of conjoined valves, BMNH BC 51234, ×10; *d,* ventral interior, BMNH BC 51235, ×10 (Popov, new).

Titanambonites Cooper, 1956, p. 717 [**T. medius;* OD]. Concavoconvex profile; ornament unequally parvicostellate, but with finer parvicostellae crossed by regular concentric lamellae; ventral muscle field flabellate; interior as in *Apatomorpha* but with variably developed platform; cardinal process bulbous; posterior dorsal valve adductor scars separated by transverse rather than oblique ridges leading to *vascula myaria. Ordovician (Llandeilo–Caradoc):* North America, Kazakhstan.——Fig. 211,*3a–d.* **T. medius,* Athens Formation, Llandeilo–Caradoc, Christiansburg, Tennessee; *a,* dorsal view of conjoined valves, USNM 117429c, ×1; *b,* ventral internal mold, USNM 117429f, ×2; *c,d,* latex cast, natural mold of dorsal interior, USNM 117429g, ×2 (Cooper, 1956).

Toquimia Ulrich & Cooper, 1936b, p. 626 [**T. kirki;* OD]. Gently concavoconvex to planoconvex profile initially, but resupination develops anteriorly in larger specimens; unequally parvicostellate ornament; large pseudodeltidium, small chilidium variably developed; large but poorly impressed ventral muscle field; ventral subperipheral rim; bulbous cardinal process with massive central component, small lateral processes; short, erect socket ridges; weak myophragm extending anteriorly into thin, low median septum; mantle canals often well impressed; similar to *Apatomorpha* but with weak platform. *Ordovician (Llanvirn–Llandeilo, ?Caradoc):* cosmopolitan.——Fig. 212,*2a–c.* **T. kirki,* upper Pogonip Group, Llanvirn, Ikes Canyon, Nevada; *a,* interarea of conjoined valves, USNM 117567h, ×3; *b,* latex of ventral internal mold, USNM 117567a, ×1.5; *c,* latex of dorsal internal mold, USNM 117567d, ×2 (Cooper, 1956).

Ujukites Andreeva, 1985, p. 41 [**U. altaicus;* OD]. Profile planoconvex to slightly resupinate; very upright interarea with small pseudodeltidium, chilidium; very short dental plates, no bounding ridges to triangular, flabellate weakly impressed ventral muscle field; cardinal process weak, but definitely leptellinid (i.e., trifid, not undercut); short dorsal median septum developed in valve center only; very weakly developed dorsal platform. *middle Ordovician:* Tuva, Russia.——Fig. 212,*1a–d.* **U. altaicus,* ?Stretinski Formation, middle Ordovician, River Tuloi, Altai Mountains, Russia; *a,b,* holotype, con-

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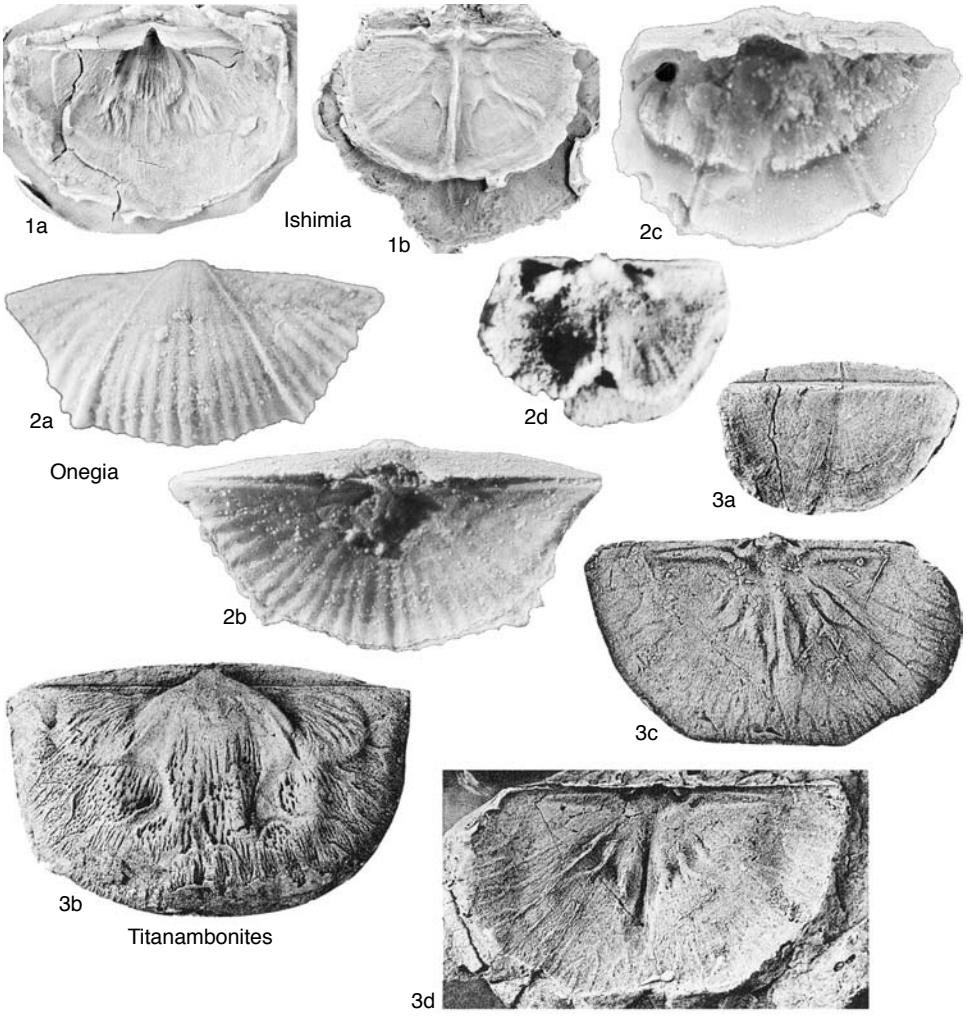

FIG. 211. Leptellinidae (p. 326).

joined valves, CNIGR 70/11865, ×4; *c,* ventral interior, CNIGR 76/11865, ×4; *d,* dorsal internal mold, CNIGR 74/11865, ×4 (Popov, new).

Family GRORUDIIDAE Cocks & Rong, 1989

[Grorudiidae COCKS & RONG, 1989, p. 112]

Concavoconvex profile; dental plates present; cardinal process trifid, not undercut; bema present; side septa present, but sometimes merged or weakly developed; platform variably developed. *Ordovician (lower Llanvirn–upper Caradoc).*

Grorudia SPJELDNAES, 1957, p. 61 [**G. grorudi;* OD] [=*Alwynella* SPJELDNAES, 1957, p. 85 (type, *A. osloensis;* OD)]. Very transverse outline; gently concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidium unknown; small teeth; poorly impressed ventral muscle field with no bounding ridges; prominent bulbous cardinal process with very small socket ridges; similar to *Tetraodontella, Calyptolepta* but with no platform, side septa not extending beyond small but elevated bema; short strong median septum also present, but not anterior of bema. *Ordovician (Caradoc):* Baltic.——FIG. 213,*3a–c.* **G. grorudi,* Zone 4aβ, lower Caradoc, Tåsen Station, Oslo, Norway; *a,* latex cast of dorsal exterior, PMO 66940, ×4; *b,c,* holotype, dorsal internal mold, latex cast, PMO 66940, ×6 (Cocks & Rong, 1989).

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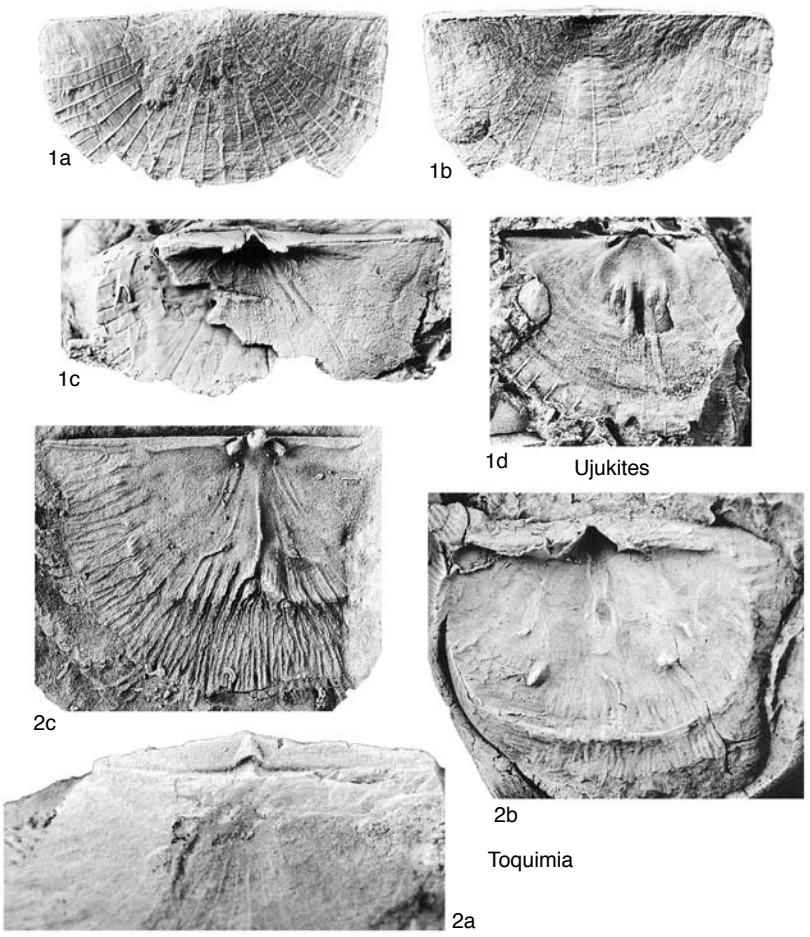

FIG. 212. Leptellinidae (p. 326–327).

Calyptolepta NEUMAN, 1976, p. 35 [**C. diaphragma;* OD] [=*Anechophragma* NEUMAN, 1976, p. 37 (type, *A. rarum;* OD); *Ujukella* ANDREEV, 1993, p. 52 (type, *U. alexandrae;* middle Malinovsk Formation (Llanvirn), Tevel-tal, Tuva, Russia); *Yuanbaella* FU, 1982, p. 116 (type, *Tetraodontella truncata* FU, 1975, p. 108; OD)]. Small; strongly concavoconvex profile; ventral interarea apsacline with small pseudodeltidium; dorsal interarea catacline to hypercline with small chilidium; short wide teeth with dental plates absent or reduced to slight thickening at sides of muscle field; short bilobed ventral muscle field; ventral subperipheral rim; simple bladelike cardinal process; flaring socket ridges; dorsal myophragm elevated anteriorly into median septum rising anteriorly to merge with elevated platform; similar to *Tetraodontella* but with two distinct side septa in median part of dorsal valve although with some variability; in some specimens septa nearly merged into median septum. *Ordovician (Llanvirn):* North America, Tuva, China.——FIG. 214*a–e.* **C. diaphragma,* Virgin Arm Formation, Llanvirn, Virgin Arm, New World Island, Newfoundland, Canada; *a,* dorsal view of conjoined valves, GSC 35067, ×2; *b,c,* latex cast of internal mold, ventral interior, GSC 35071, ×2 (Neuman, 1976); *d,e,* latex cast of internal mold, dorsal interior, GSC 35068a, ×3 (Cocks & Rong, 1989).——FIG. 214*f–i. C. rarum,* Virgin Arm Formation, Llanvirn, Virgin Arm, New World Island, Newfoundland, Canada; *f,g,* molds of ventral, dorsal exteriors, GSC 35078, ×3; *h,i,* holotype, latex cast of dorsal interior, GSC 35077, ×3 (Neuman, 1976).——FIG. 214*j–m. C. truncata,* Xiliangsi Formation, lower Llanvirn, Dangmengou, Yuanba, Nanzheng County, southern Shaanxi Province, China; *j,k,* exterior of ventral, dorsal valves, GB 141, GB 142, ×12; *l,* internal mold of ventral valve, GB 143, ×9; *m,* internal mold of dorsal valve, GB 145, ×12 (Fu, 1982).

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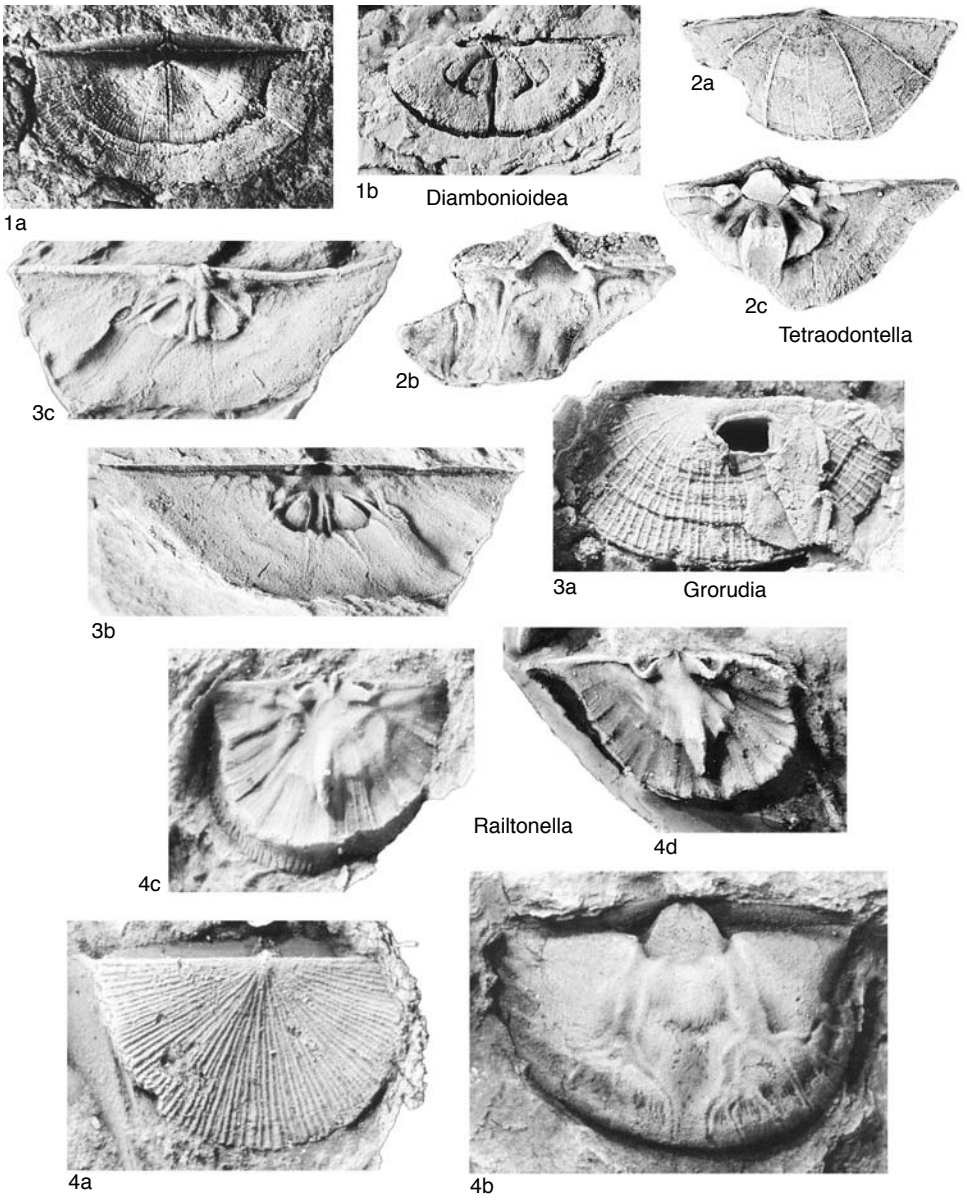

FIG. 213. Grorudiidae (p. 327–331).

Diambonioidea ZENG, 1987, p. 230 [**D. transversa;* OD]. Concavoconvex profile; unequally parvicostellate ornament; deltidial plates covering only small part of delthyrium; similar to *Calyptolepta,* but dorsal valve flat, with wider dorsal valve muscle field; short side septa constrained within muscle field; prominent dorsal median septum merging anteriorly with platform. *Ordovician (Llandeilo–Caradoc):* China.——FIG. 213,*1a,b. *D. transversa,* Miaopo Formation, upper Llandeilo–lower Caradoc, Huanghuachang, Yichang County, western Hubei, China; *a,* external mold of conjoined valves, YIGM IV45808, ×4; *b,* dorsal internal mold, YIGM IV45807, ×4 (Zeng, 1987).

Railtonella LAURIE, 1991, p. 63 [**R. scanloni;* OD]. Ventral valve convex; dorsal valve flat but concave anteriorly; small pseudodeltidium, chilidium; large teeth with vestigial dental plates, poorly impressed

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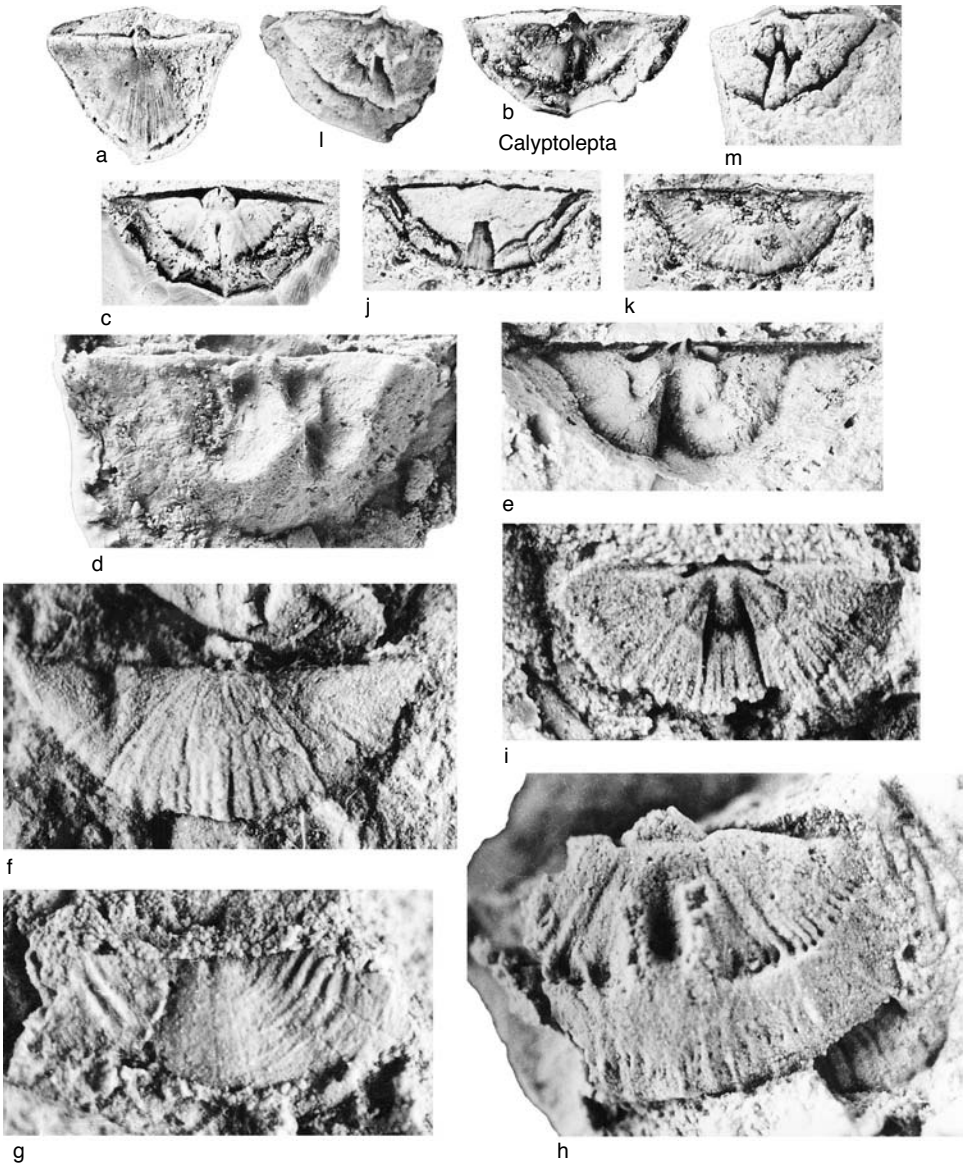

FIG. 214. Grorudiidae (p. 328).

ventral muscle field; prominent saccate ventral mantle canals; variable but relatively small bladelike cardinal process; similar to *Calyptolepta,* but with thick, well-developed dorsal median septum extending beyond bema; prominent variably elevated dorsal platform. *Ordovician (Llanvirn):* Australia.——FIG. 213,*4a–d. *R. scanloni,* Karmberg Limestone, Llanvirn, Railton, Tasmania, Australia; *a,* dorsal view of latex cast of conjoined valves, UTGD 99822, ×6; *b,* ventral internal mold, UTGD 99837, ×6; *c,* holotype, latex cast of dorsal valves, UTGD 99825, ×6; *d,* latex cast of dorsal valves, UTGD 120293, ×6 (Laurie, 1991).

Tetraodontella JAANUSSON, 1962, p. 1 [**T. biseptata;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; small teeth, dental plates; relatively small ventral muscle field; dorsal interior as in *Calyptolepta* but with strong central pair of septa fused together along their length, homologizing a wide median

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septum, except where they divide anteriorly; further short side septa constrained within muscle field, bema; weak platform present. *Ordovician (Llanvirn–Caradoc):* Baltic, China.——Fig. 213,*2a–c.* **T. biseptata,* Dalby Limestone, middle Caradoc, Böda Hamn borehole, Öland, Sweden; *a,* holotype, ventral exterior, RMS Öl 1040, ×5; *b,* ventral interior, RMS Öl 1037, ×7; *c,* dorsal interior, ×4 (Williams, 1965d).

Family LEPTESTIIDAE Öpik, 1933

[*nom. transl.* Williams, 1953b, p. 6, *ex* Leptestiinae Öpik, 1933a, p. 24]

Concavoconvex profile; dental plates present; with bema, no side septa; trifid cardinal process not undercut. *Ordovician (?Arenig, Llanvirn)–Silurian (Ludlow).*

Leptestia Bekker, 1922, p. 362 [**L. musculosa;* OD]. Concavoconvex profile; fine, unequally parvicostellate ornament; with pseudodeltidium, chilidium; teeth small, dental plates lacking; ventral muscle field subcircular, well impressed though without raised muscle-bounding ridges; erect cardinal process, small socket ridges, variably developed myophragm leading anteriorly to weak dorsal median septum; with elongate bema; median septum through bema merging anteriorly with lobes of platform. *Ordovician (?Arenig, Llanvirn–Caradoc):* Europe, Asia.——Fig. 215,*1a–d.* **L. musculosa; a,* ventral exterior, Uhaku Stage, Llandeilo, Uhaku, Estonia, BMNH BB 33356, ×1.5 (new); *b,* ventral interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, ×2 (Rõõmusoks, new); *c,* dorsal view of dorsal interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, BMNH BB 5189, ×1.5; *d,* posterior view of dorsal interior, Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia, BMNH BB 5189, ×2 (Cocks & Rong, 1989).

Bilobia Cooper, 1956, p. 759 [**B. hemisphaerica;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium short or absent; thin chilidium present; stubby bilobed teeth, obsolescent dental plates; ventral muscle field strongly bilobed with divergent diductors; broad median ridge sporadically developed anterior to ventral scar, generally as coalescent tubercles; cardinal process erect; divided, elevated bema, undercut anteriorly, separated centrally by small discrete median septum; variably developed platform with diaphragm or peripheral rim. *Ordovician (Caradoc):* cosmopolitan.——Fig. 216,*2a–d.* **B. hemisphaerica,* Oranda Formation, lower Caradoc, Strasburg Quadrangle, Virginia; *a,* holotype, dorsal view of exterior of conjoined valves, USNM 111099b, ×4; *b,* ventral internal mold, USNM 111099d, ×5; *c,* conjoined valves, including mold of dorsal interior, USNM 111099c, ×4; *d,* dorsal interior, USNM 111099f, ×5 (Cooper, 1956).——Fig. 216,*2e,f.* **B. musca* (Öpik) Kukruse Formation (lower Caradoc), Kohtla-Järve, Estonia; *e,f,* posterior, ×7, lateral views of dorsal interior, ×5, BMNH BB 5202 (Cocks & Rong, 1989).

Leangella Öpik, 1933a, p. 42 [**Plectambonites scissa* (Davidson, 1871) var. *triangularis* Holtedahl, 1916, p. 84; OD] [=*Diambonia* Cooper & Kindle, 1936, p. 356 (type, *Plectambonites gibbosa* Winchell & Schuchert, 1892, p. 288; OD); *Opikella* Amsden, 1968, p. 48 (type, *L. (O.) dissiticostella;* OD); *Tufoleptina* Havlíček, 1961, p. 447 (type, *T. tufogena;* OD)]. Strongly concavoconvex profile; unequally parvicostellate ornament; large orthocline interarea; strong teeth with small dental plates; ventral muscle field small, bilobed, with pronounced muscle-bounding ridges; subperipheral rim variably present in ventral valve; ventral median septum varying from strong to absent; erect cardinal process, laterally flaring socket ridges; weak myophragm; dorsal median septum absent; elevated bema bilobed, undercut anteriorly; platform or discontinuous row of enhanced septules; diaphragm or peripheral rim near valve margin. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.

L. (Leangella). Similar to *L. (Leptestiina)* but with discrete platform. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.——Fig. 216,*3a–d.* **L. (L.) scissa* (Davidson), upper Haverford Mudstone Formation, Rhuddanian, Gasworks, Haverfordwest, Dyfed, Wales; *a,* latex of conjoined valves, BMNH BB 70996, ×5; *b,* dorsal exterior latex, BMNH BB 31826, ×5 (new); *c,d,* mold, latex of dorsal interior, BMNH BB 32167, ×6 (Cocks & Rong, 1989).——Fig. 216,*3e,f. L. (L.) tufogena,* Liten Formation, Homerian, Hlinik, Svaty Jan pod Skalou, Bohemia, Czech Republic; *e,* ventral internal mold, OMR VH 290, ×5; *f,* dorsal internal mold, OMR VH 285, ×5 (Havlíček, 1967).——Fig. 216,*3g. L. (L.) gibbosa,* Stewartville Formation, lower Ashgill, Stewartville, Minnesota; dorsal interior, BMNH BC 7272, ×5 (Cocks & Rong, 1989).

L. (Leptestiina) Havlíček, 1952, p. 412 [**Benignites (Leptestiina) prantli;* OD]. Similar to *L. (Leangella)* except that dorsal valve platform is made up anteriorly of discrete septules not merged to form typical continuous platform. *Ordovician (Caradoc–Ashgill):* Europe, ?China.——Fig. 216,*1a,b.* **L. (L.) prantli* Havlíček, Králův Dvur Formation, middle Ashgill, Králův Dvur, Bohemia, Czech Republic; *a,b,* internal mold of conjoined valves, external mold of dorsal valve, NM CD 1557, ×5 (Havlíček, 1967).

Rurambonites Cocks & Rong, 1989, p. 118 [**Plectambonites ruralis* Reed, 1917, p. 879; OD]. Concavoconvex profile; unequally parvicostellate ornament; delthyrium largely open, with small pseudodeltidium, pair of chilidial plates; strong teeth, denticulate hinge line; ventral muscle field relatively small; bilobed with encircling muscle-bounding ridges; strong erect cardinal process; bladelike, widely divergent socket ridges; bema transverse, not bilobed, in contrast to bilobed elongate bema of *Sampo;* small dorsal median septum

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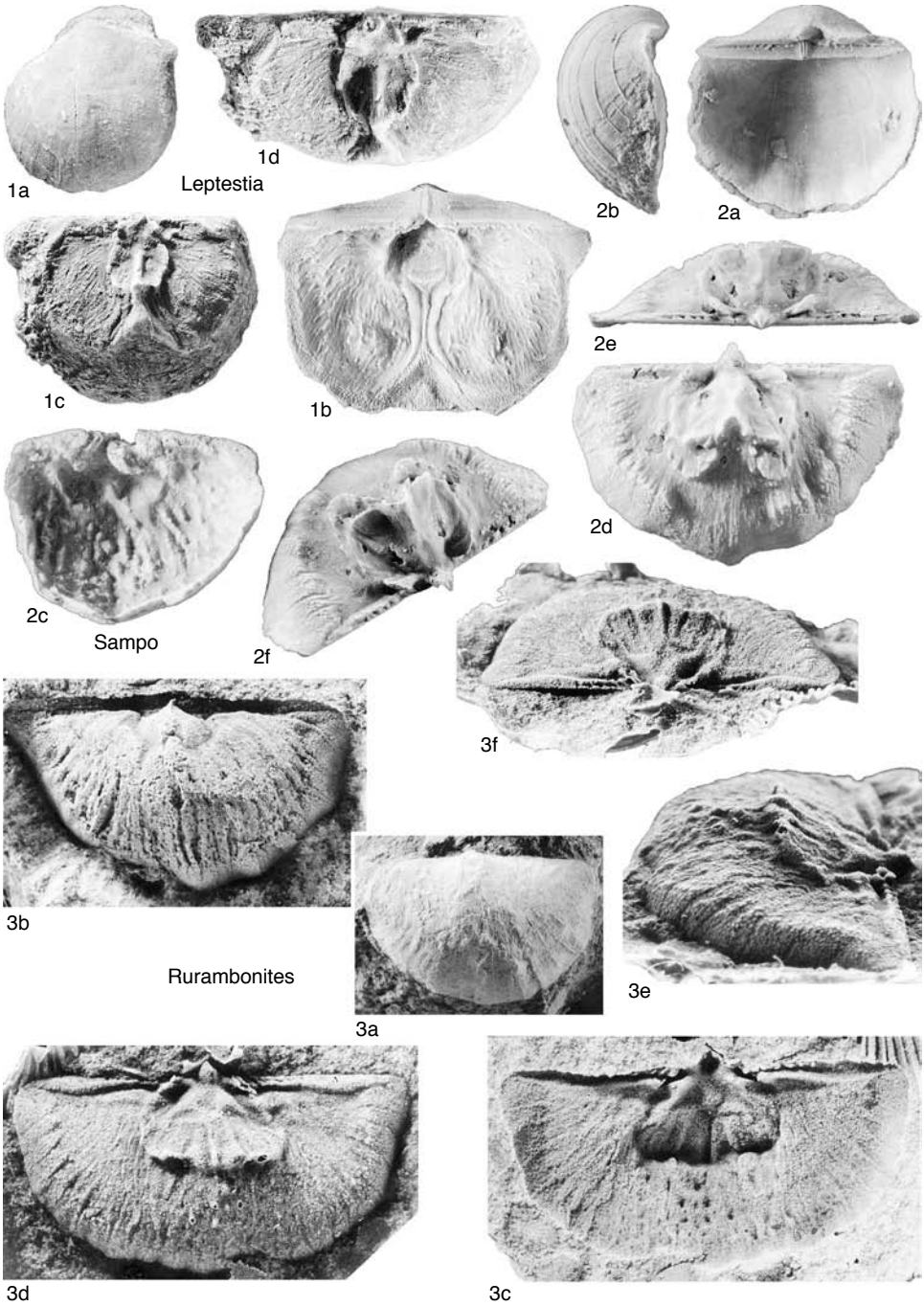

FIG. 215. Lepestiidae (p. 331–334).

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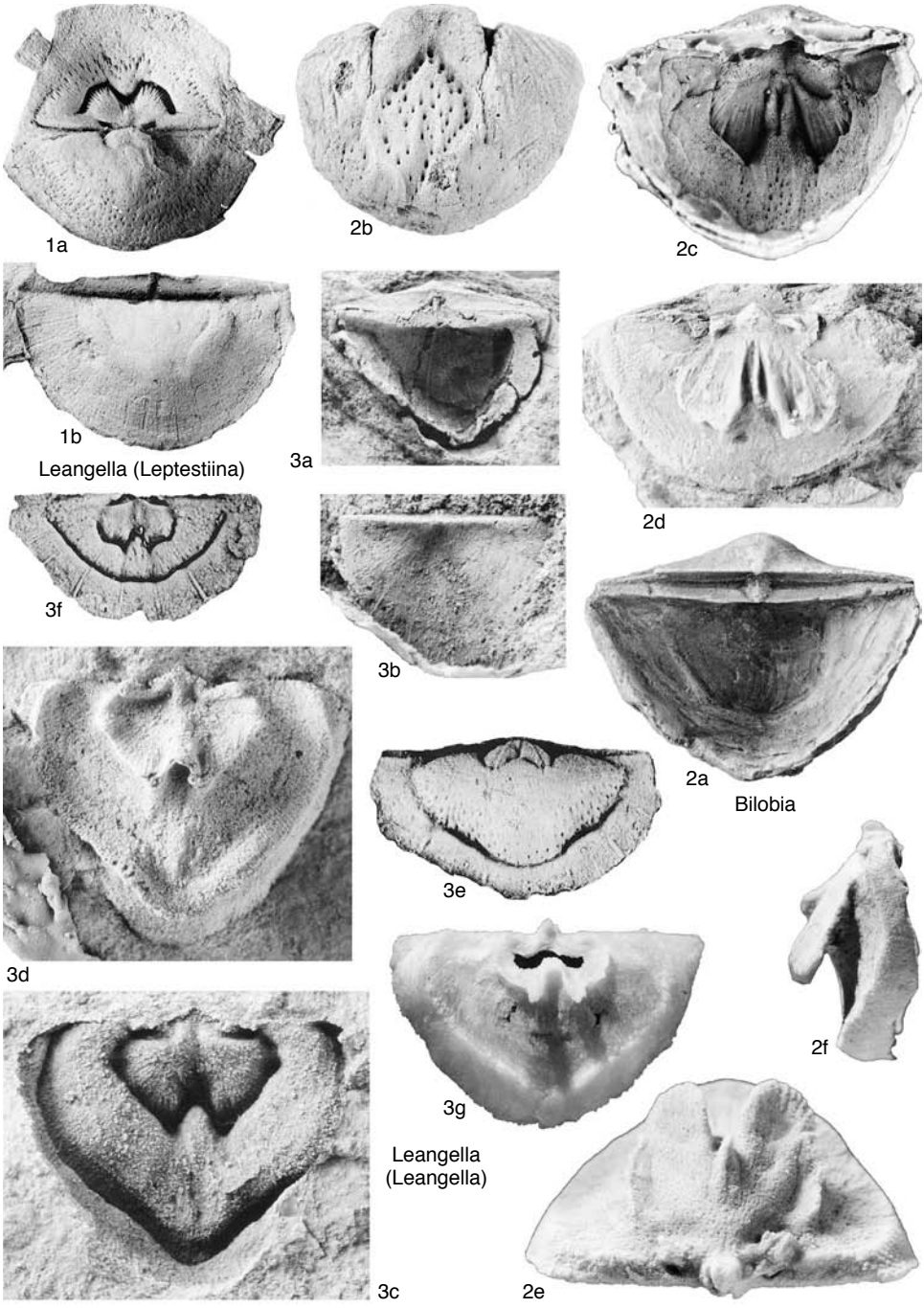

FIG. 216. Leptestiidae (p. 331).

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confined to bema. *Ordovician (Ashgill):* Scotland, North America.——Fig. 215,*3a–f.* **R. ruralis* (Reed), southern Threave Formation, Rawtheyan, Starfish Bed, Girvan, Strathclyde, Scotland; *a,* ventral exterior, BMNH BC 50914, ×2; *b,* ventral internal mold, BMNH BC 7202, ×3; *c–f,* dorsal internal mold, dorsal, lateral, posterior views of latex cast, BMNH BC 7200, ×3 (Cocks & Rong, 1989).

Sampo Öpik, 1933a, p. 35 [**S. hiiuensis;* OD]. Concavoconvex profile; unequally parvicostellate ornament; hinge line denticulate; ventral muscle field bilobed; cardinal process erect; bema elongate (in contrast to *Rurambonites*), bilobed, undercut; similar to *Bilobia* apart from denticulate hinge line. *Ordovician (Caradoc–Ashgill):* Baltic.——Fig. 215,*2a–f.* **S. hiiuensis,* Vormsi Stage, lower Ashgill; *a,b,* dorsal, lateral views of conjoined valves, Hiiuma, TAGI BR 1235, ×2; *c,* ventral interior, Kõrgessaare, Estonia, TAGI BR 1236, ×3; *d–f,* dorsal interior viewed dorsally, posteriorly, obliquely, Kõrgessaare, Estonia, TAGI BR 361, ×3 (new).

Family XENAMBONITIDAE Cooper, 1956

[*nom. transl.* Cocks & Rong, 1989, p. 120, *ex* Xenambonitinae Cooper, 1956, p. 813]

Concavoconvex to planoconvex profile; with dental plates; cardinal process undercut; variably developed bema; no side septa. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Subfamily XENAMBONITINAE Cooper, 1956

[Xenambonitinae Cooper, 1956, p. 813]

Similar to Aegiromeninae, but with platform; bema elevated. *Ordovician (Llandeilo–Ashgill).*

Xenambonites Cooper, 1956, p. 813 [**X. undosus;* OD]. Strongly concavoconvex profile with ventral fold, dorsal sulcus; parvicostellate ornament with occasional stronger costellae; geniculate anteriorly in ventral direction; apparently open delthyrium; strong teeth; vestigial dental plates; small bilobed ventral valve muscle field, elevated except at posterior ends of mantle canals, ventral subperipheral rim; small cardinal process lobes; substantial but short curved socket plates; short elevated myophragm, too broad to be termed septum, confined within elevated bema; weak platform mirroring ventral subperipheral rim. *Ordovician (Llandeilo–Caradoc):* North America, Scotland.——Fig. 217,*2a–c.* **X. undosus,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* ventral exterior, USNM 117468-l, ×6; *b,* ventral interior, USNM 117468a, ×6; *c,* holotype, dorsal interior, USNM 117468h, ×7 (Cooper, 1956).

Metambonites Zhan & Rong, 1995, p. 552 [**M. meritus;* OD]. Dorsibiconvex profile; unequally parvicostellate ornament with no rugae; teeth small, dental plates absent; ventral denticles, dorsal fossettes irregularly developed; distinctive ventral platform, elevated in most specimens, surrounding bilobed muscle field, short stout ventral myophragm; cardinal process massive, projecting posteroventrally; socket ridges short, thick, high; bema strongly elevated, undercut, significantly smaller than ventral platform. *Ordovician (Ashgill):* China, Kazakhstan.——Fig. 217,*1a–d.* **M. meritus,* Xiazhen Formation, middle Ashgill, Daqiao, Jiangshan County, Zhejiang Province, China; *a,b,* ventral internal mold, ×5, latex cast, ×5, NIGP 124512; *c,d,* holotype, dorsal internal mold, ×4, latex cast, ×5, NIGP 124515 (Zhan & Rong, 1995).

Synambonites Zhan & Rong, 1995, p. 552 [**S. biconvexus;* OD]. Ventribiconvex profile with elevated ventral marginal deflection and trough, corresponding narrow, high dorsal rim; fine multicostellate ornament, irregular rugae; similar to *Xenambonites* but differs in profile, in lacking fold, sulcus; elongated, bilobed, relatively small ventral muscle field, with strong teeth, dental plates; massive cardinal process projecting ventrally; elevated bema; subperipheral rim in ventral valve, corresponding dorsal trough. *Ordovician (Ashgill):* China.——Fig. 217,*3a–d.* **S. biconvexus,* Xiazhen Formation, middle Ashgill, Daqiao, Jingshan County, Zhejiang Province; *a,* latex cast of dorsal exterior, NIGP 124511, ×6; *b,* ventral internal mold, NIGP 124514, ×4; *c,d,* holotype, dorsal internal mold, latex cast, NIGP 124515, ×5 (Zhan & Rong, 1995).

Subfamily AEGIROMENINAE Havlíček, 1961

[Aegiromeninae Havlíček, 1961, p. 450]

Similar to Xenambonitinae, but without platform; variably developed bema, sometimes represented merely by line of enlarged septules, but never elevated. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Aegiromena Havlíček, 1961, p. 450 [**Leptaena aquila* Barrande, 1848, p. 228; OD]. Gently concavoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; small teeth, dental plates; weak muscle-bounding ridges posterolateral only to elongate, bilobed ventral muscle field; widely flaring short socket ridges, bema variably developed, absent in some specimens; weakly impressed dorsal muscle field; similar to *Aegiria,* but with dental plates. *Ordovician (Llanvirn–Ashgill):* Europe, northern Africa, Bolivia.——Fig. 218,*1a–d.* **A. aquila* (Barrande), Zahorany Formation, middle Caradoc, Bohemia, Czech Republic; *a,* latex cast of ventral exterior, BMNH BB 3340, ×3; *b,c,* ventral internal mold, latex cast, BMNH BB 13658, ×3; *d,* dorsal internal mold, BMNH BC 7212, ×4 (new).

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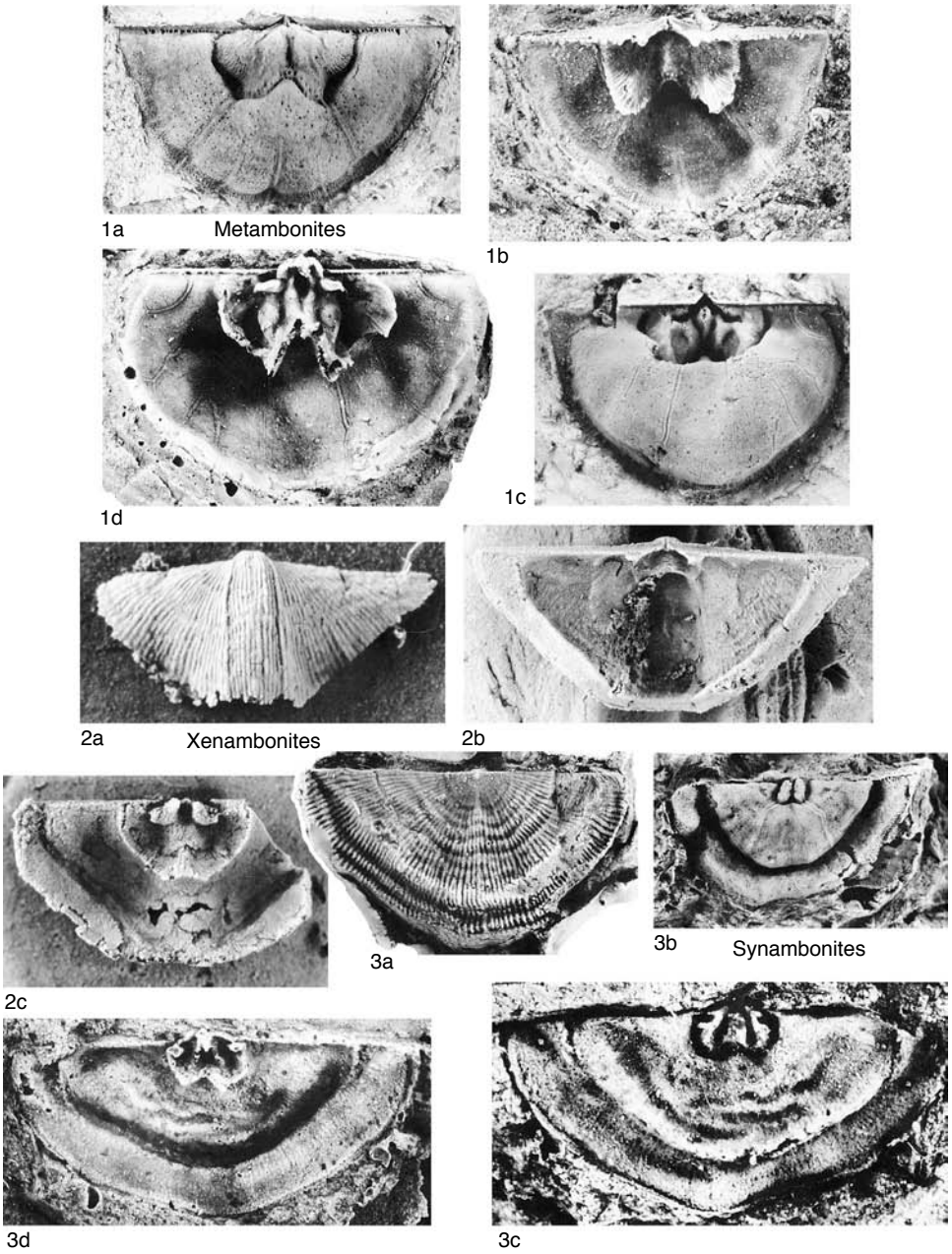

FIG. 217. Xenambonitidae (p. 334).

Aegiria ÖPIK, 1933a, p. 55 [**A. norvegica;* OD] [=*Aegironetes* HAVLÍČEK, 1967, p. 46 (type, *Strophomena tristis* BARRANDE, 1879, pl. 70, fig. 6.1; OD)]. Gently concavoconvex profile; parvicostellate ornament; delthyrium closed by large pseudodeltidium, chilidium; relatively short, variably impressed, bilobed ventral muscle field; erect cardinal process; differs from *Mezounia* in relatively transverse bema, not bilobed anteriorly; bema always present; short central median septum transecting anterior end of bema; platform sometimes indicated merely by elongate pseudopunctae. *Ordovician (Ashgill)–Silurian (Llandovery):* Europe, China.——FIG. 218,*3a–e. *A. norvegica,* Solvik Formation,

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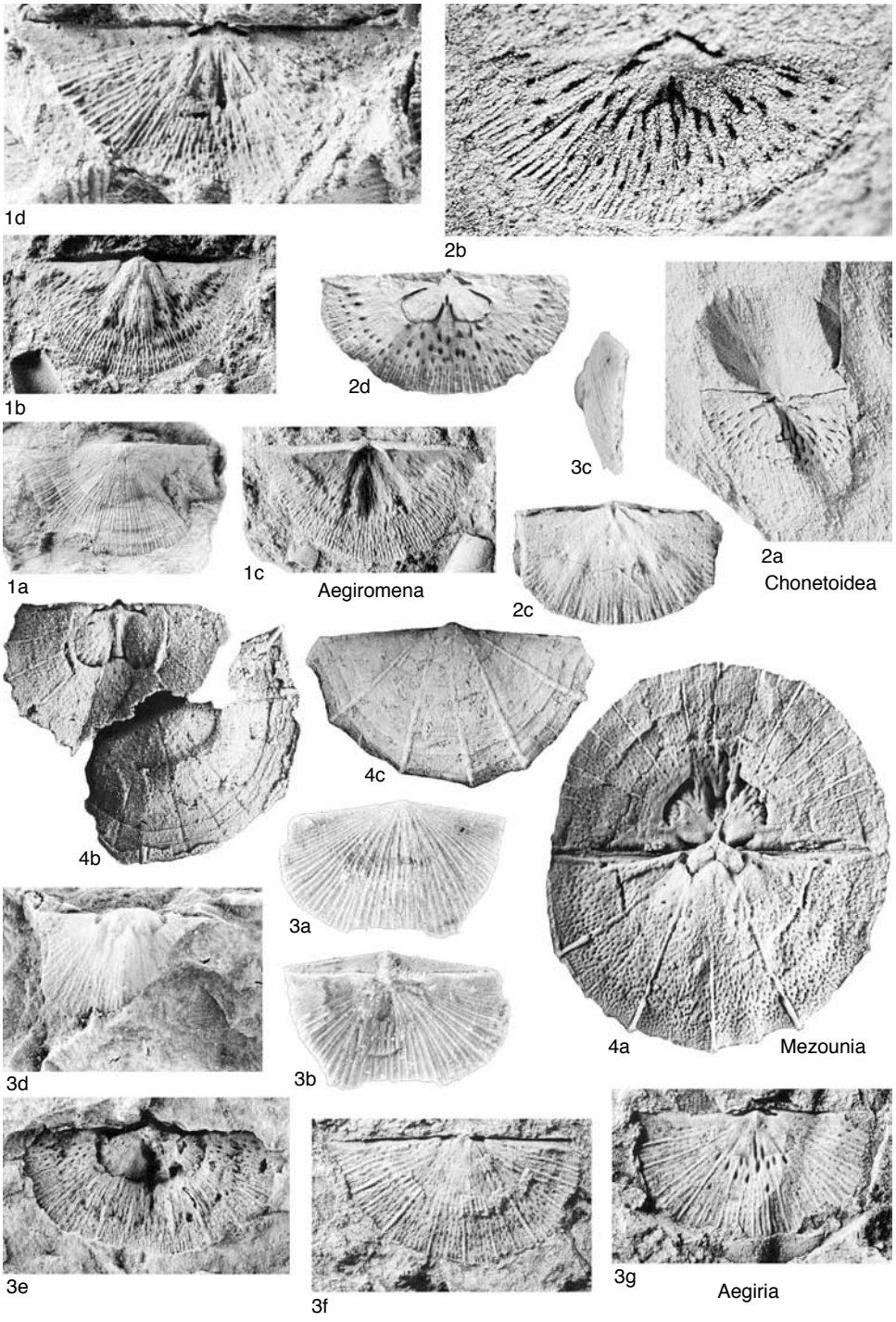

FIG. 218. Xenambonitidae (p. 334–337).

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Rhuddanian, Leangen, Asker, Norway; *a–c,* ventral, dorsal, lateral views of conjoined valves, PMO 40690, ×4; *d,* ventral internal mold, PMO 40689, ×4; *e,* dorsal internal mold, PMO 40688, ×4 (new).——Fig. 218,*3f,g. A. tristis,* Králuv Dvur Formation, lower–middle Ashgill, Jezerka, Michli, Prague, Czech Republic; *f,* ventral internal mold, ×7; *g,* dorsal internal mold, ×7 (Mergl, new).

Chonetoidea Jones, 1928, p. 393 [**Plectambonites papillosa* Reed, 1905, p. 451; OD] [=*Sericoidea* Lindström, 1953, p. 134 (type, *Leptaena sericea* var. *restricta* Hadding, 1913, p. 62; OD); ?*Sentolunia* Havlíček, 1967, p. 53 (type, *S. senta;* OD)]. Gently concavoconvex profile; parvicostellate ornament, sometimes with unequal parvicostellae; small interarea; small arched pseudodeltidium; no chilidium; widely divergent teeth, socket plates; bilobed but weakly impressed ventral muscle field; similar to *Jonesea,* but with elongated septules, rather than circular papillae; bema sometimes present, sometimes delineated only by larger septules. *Ordovician (Llandeilo–Ashgill):* cosmopolitan.——Fig. 218,*2a,b. *C. papillosa* (Reed), Slade, Redhill Mudstone Formation, middle Ashgill, Upper Slade, near Haverfordwest, Dyfed, Wales; *a,* internal mold of conjoined valves, SM A11313, ×4; *b,* lectotype, dorsal internal mold, SM A11311, ×10 (Cocks & Rong, 1989).——Fig. 218,*2c,d. C. senta,* Králuv Dvur shales, lower–middle Ashgill, Králuv Dvur, Czech Republic; holotype, ventral, dorsal internal molds, OMR VH 276, ×4 (Havlíček, 1967).

Epelidoaegiria Strusz, 1982, p. 115 [**Aegiria (E.) chilidifera;* OD]. Similar to *Aegiria* but with unequally parvicostellate ornament, hinge line denticulate, small pseudodeltidium, chilidium. *Silurian (Wenlock, ?Ludlow):* Australia, Japan.——Fig. 219,*3a–d. *E. chilidifera,* Walker Volcanics, Wenlock, Canberra, A.C.T., Australia; *a,* dorsal view of latex cast of conjoined valves, CPC 20365, ×4; *b,* magnified view of latex cast of interarea, CPC 20387, ×10; *c,* latex cast of ventral interior, CPC 20359, ×4; *d,* latex cast of dorsal interior, CPC 20949, ×4 (Strusz, 1982).

Jonesea Cocks & Rong, 1989, p. 127 [**Leptaena grayi* Davidson, 1849, p. 271; OD] [=*Dionaegiria* Havlíček in Havlíček & Štorch, 1990, p. 65, obj.]. Gently concavoconvex profile; distinctive sharply crested parvicostellate ornament; vestigial dental plates, bilobed ventral muscle field; sometimes septules with pair of prominent tubercles posterolaterally inside ventral valve; similar to *Chonetoidea,* but with circular papillae rather than elongated; bema sometimes suggested by raised tubercles but not always developed. *Ordovician (Ashgill)–Silurian (Ludlow):* cosmopolitan.——Fig. 220*a–d. *J. grayi* (Davidson); *a,* latex cast of external molds of conjoined valves, lower Bringewood Beds, upper Ludlow, Ludlow, Shropshire, England, BMNH BC 10343, ×12; *b,c,* dorsal internal mold, latex cast, lower Bringewood Beds, upper Ludlow, Ludlow, Shropshire, England, BMNH BC 10375, ×12; *d,* upper Leintwardine Beds, Ludlow, Ludlow, Shropshire, England, ventral internal mold, BMNH BC 10340, ×12 (Cocks & Rong, 1989).

Mezounia Havlíček, 1967, p. 31 [**Strophomena bicuspis* Barrande, 1879, pl. 128, fig. 1–5; OD]. Gently concavoconvex profile; semicircular outline; unequally parvicostellate ornament; prominent flaring teeth, bounding ridges around relatively small bilobed ventral muscle field; similar to *Aegiria* but with small bema bilobed anteriorly; no dorsal median septum. *Silurian (Wenlock):* Europe.——Fig. 218,*4a–d. *M. bicuspis* (Barrande), Motol Formation, Wenlock, Borek, Mezoun, Bohemia, Czech Republic; *a,* internal mold of conjoined valves, OMR VH 514, ×7.3; *b,c,* internal, external molds of two dorsal valves, OMR VH 513d, ×7.7; *d,* ventral exterior, ×5.5 (Havlíček, 1967).

Multiridgia Zeng, 1987, p. 234 [**M. elegans;* OD]. Gently concavoconvex to planoconvex profile; unequally parvicostellate ornament; dental plates lacking; row of septules developed, enclosing poorly impressed muscle fields in both valves; dorsal valve septules as in *Chonetoidea,* but without anterior bilobation; short dorsal median septum. *Ordovician (Llandeilo–Caradoc):* China.——Fig. 219,*2a,b. *M. elegans,* Miaopo Formation, upper Llandeilo–lower Caradoc; *a,* holotype, ventral internal mold, Jieling, YIGM IV45746, ×7; *b,* dorsal internal mold, Huanhuachang, Yichang County, Hubei Province, YIGM IV45740, ×9 (Zeng, 1987).

Nabiaoia Xu, 1979, p. 370 [**N. pusilla;* OD]. Planoconvex profile; thin shelled; almost imperceptable parvicostellate radial ornament with irregular rugae; short, flaring teeth, socket ridges; no bema, platform, or side septa; dorsal muscle field of elevated pustules in irregular but subradial rows; dorsal median septum variably present, stronger posteriorly, centrally. *Devonian (Eifelian):* China.——Fig. 219,*1a–d. *N. pusilla,* Tangxiang Formation, Eifelian, Luofu of Nandan, Guangxi Province; *a,b,* ventral internal mold, latex cast, NIGP 81012, ×10 (Xu, new); *c,d,* holotype, dorsal internal mold, latex cast, NIGP 41251, ×7 (Xu, 1979).

Family HESPEROMENIDAE Cooper, 1956

[*nom. transl.* Cocks & Rong, 1989, p. 127, *ex* Hesperomeninae Cooper, 1956, p. 744] [=Anoptambonitidae Rõõmusoks, 1963, p. 231]

Concavoconvex to resupinate profile; dental plates weakly present or absent; cardinal process undercut; no bema; no side septa; with platform. *Ordovician (Llanvirn–Ashgill).*

Hesperomena Cooper, 1956, p. 744 [**H. leptellinoidea;* OD]. Concavoconvex profile; unequally parvicostellate ornament; pseudodeltidium, but no chilidium known; short flaring teeth; large, wide but poorly impressed ventral muscle field; large erect cardinal process; short socket ridges; weak

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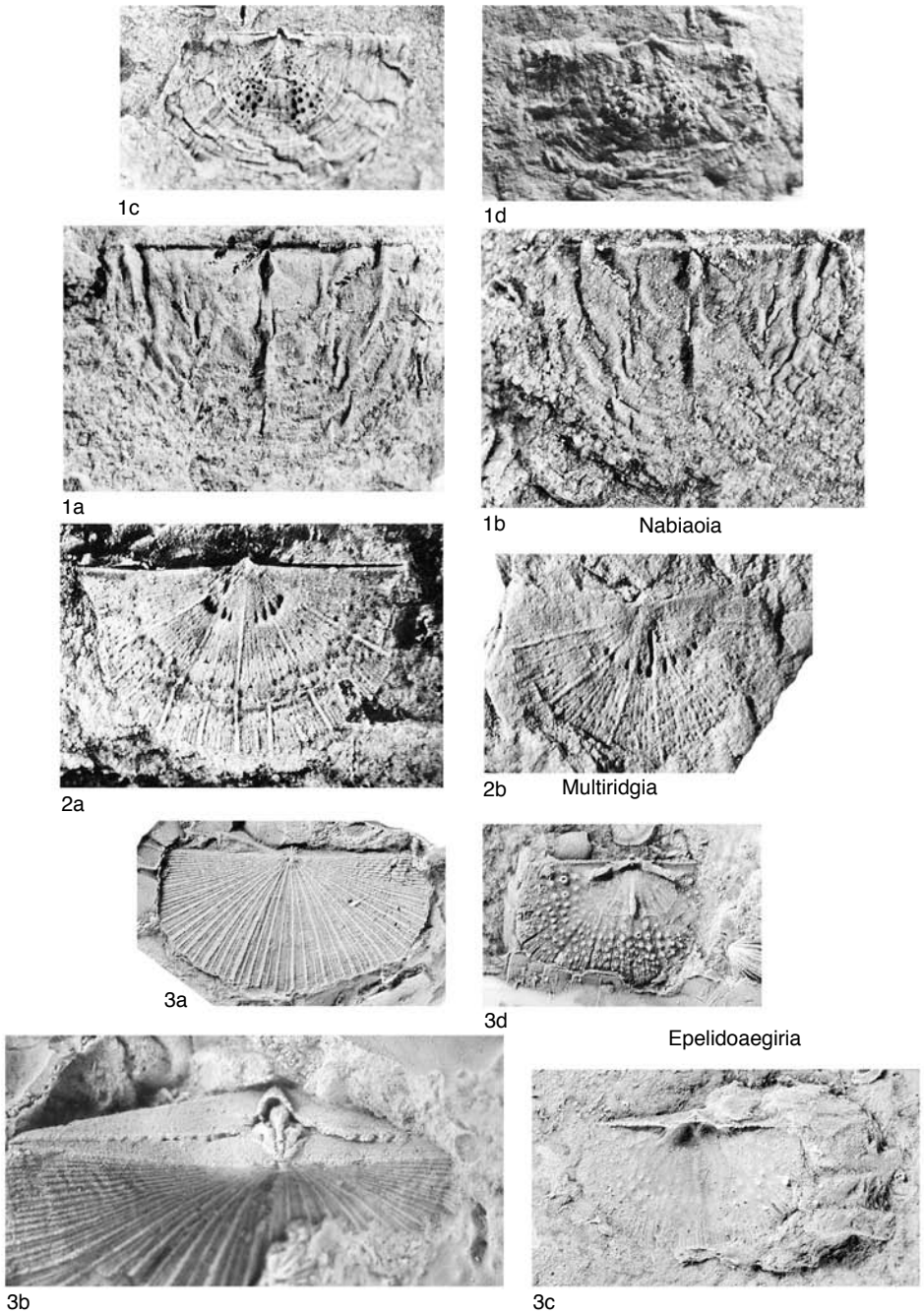

FIG. 219. Xenambonitidae (p. 337).

dorsal median septum bifurcating anteriorly to unite with weak platform. *Ordovician (Llanvirn):* North America.——FIG. 221,*1a–c. *H. leptellinoidea,* Antelope Valley Limestone, Pogonip Group, upper Llanvirn, Ikes Canyon, Roberts Mountains, Nevada; holotype, dorsal exterior, ventral interior,

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dorsal interior views of conjoined valves, USNM 117560, ×3 (Cooper, 1956).

Anoptambonites Williams, 1962, p. 170 [**Leptaena grayae* Davidson, 1883, p. 171; OD] Concavoconvex profile; parvicostellate ornament; large rectimarginate to procline interarea; open delthyrium; variable, sometimes large, chilidium; prominent teeth; short dental plates; small ventral muscle field restricted by bilobed muscle-bounding ridges; no ventral median septum; no posterolateral tubercles in ventral valve; large cardinal process striated posteriorly; flaring socket ridges; strong median septum merging anteriorly with elevated bilobed platform. *Ordovician (Llandeilo–Ashgill):* North America, Scotland, Ireland, Asia.——Fig. 221,*2a–e.* **A. grayae* (Davidson), Craighead Limestone, upper Caradoc, Craighead, Girvan, Strathclyde, Scotland; *a,b,* lectotype, dorsal, lateral views of conjoined valves, BMNH B 73408, ×4 (new); *c,d,* posterior, downward views of ventral interior, BMNH BB 15868, ×3 (Cocks & Rong, 1989); *e,* dorsal interior, BMNH BB 15869, ×3.5 (new).

Aulie Nikitin & Popov in Klenina, Nikitin, & Popov, 1984, p. 148 [**A. convexa;* OD]. Strongly concavoconvex profile; unequally parvicostellate ornament; similar to *Anoptambonites* but with pseudodeltidium present, ventral valve muscle-bounding ridges semicircular, not bilobed, with dorsal valve median septum extending a little anteriorly of platform. *Ordovician (Caradoc):* Kazakhstan.——Fig. 222,*1a–d.* **A. convexa,* middle Erkebidaiski Horizon, Caradoc, Chinghiz Mountains; *a,b,* latex cast of exterior of conjoined valves with enlargement of interarea, CNIGR 104/12095, ×2, ×5; *c,* ventral internal mold, CNIGR 99/12095, ×3; *d,* dorsal internal mold, CNIGR 100/12095, ×3 (Popov, new).

Chaganella Nikitin, 1974, p. 65 [**C. chaganensis;* OD] [=*Tylambonites* Percival, 1991, p. 143 (type, *T. speciosa;* OD)]. Similar to *Anoptambonites* but biconvex to weakly resupinate profile anteriorly; unequally parvicostellate ornament; open delthyrium, large discrete chilidial plates; ventral muscle field bilobed; prominent callosities in ventral interior; erect cardinal process; flaring socket plates; weakly impressed bema; strong dorsal median septum merging anteriorly with bilobed platform. *Ordovician (Llandeilo–lower Caradoc):* Kazakhstan, Australia.——Fig. 222,*2a–d.* **C. chaganensis,* lower Bestamak Formation, Llandeilo, Chagan River, Chinghiz Mountains, Kazakhstan; *a,* holotype, ventral exterior, CNIGR 1614/45, ×2; *b,* ventral internal mold, KAS 1614/41, ×2; *c,* dorsal internal mold, KAS 1614/43, ×2 (Nikitin, 1974); *d,* latex cast of dorsal interior, CNIGR 133/12095, ×2.5 (new).——Fig. 222,*2e–h. T. speciosa,* Cliefden Caves Limestone, Caradoc, Walli, New South Wales, Australia; *e,* posterior view of conjoined valves, SUP 68483, ×5; *f,g,* holotype, ventral exterior, interior, SUP 68462, ×2; *h,* dorsal interior, SUP 68469, ×3 (Percival, 1991).

Kassinella Borissiak, 1956, p. 50 [**K. globosa;* OD] [=*Durranella* Percival, 1979b, p. 96 (type, *D. septata;* OD)]. Concavoconvex to planoconvex profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; posterolateral tubercles usually present in ventral interior; short ventral median septum always present; similar to *Aulie* but with peripheral rim developed, ventral muscle-bounding ridges very elongate, bilobed; no dental plates; erect cardinal process with laterally flaring socket ridges; dorsal septum; dorsal peripheral rim

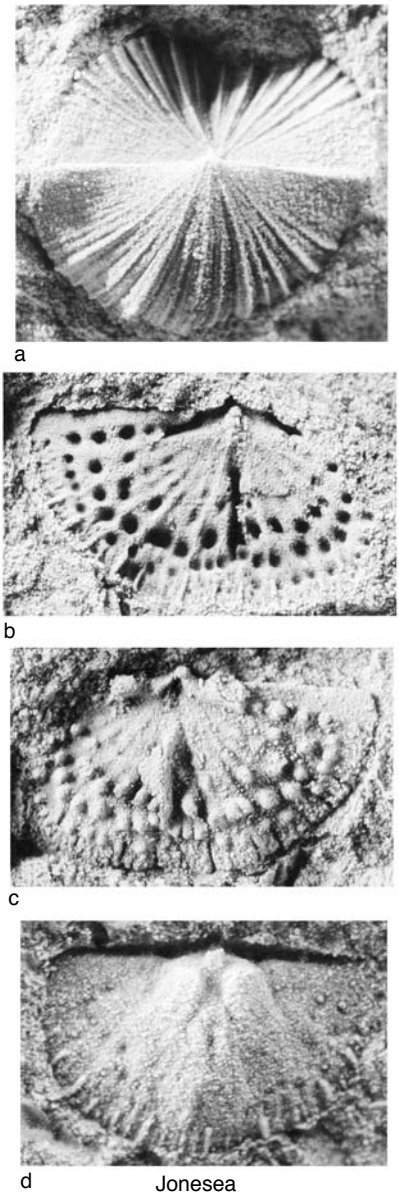

Fig. 220. Xenambonitidae (p. 337).

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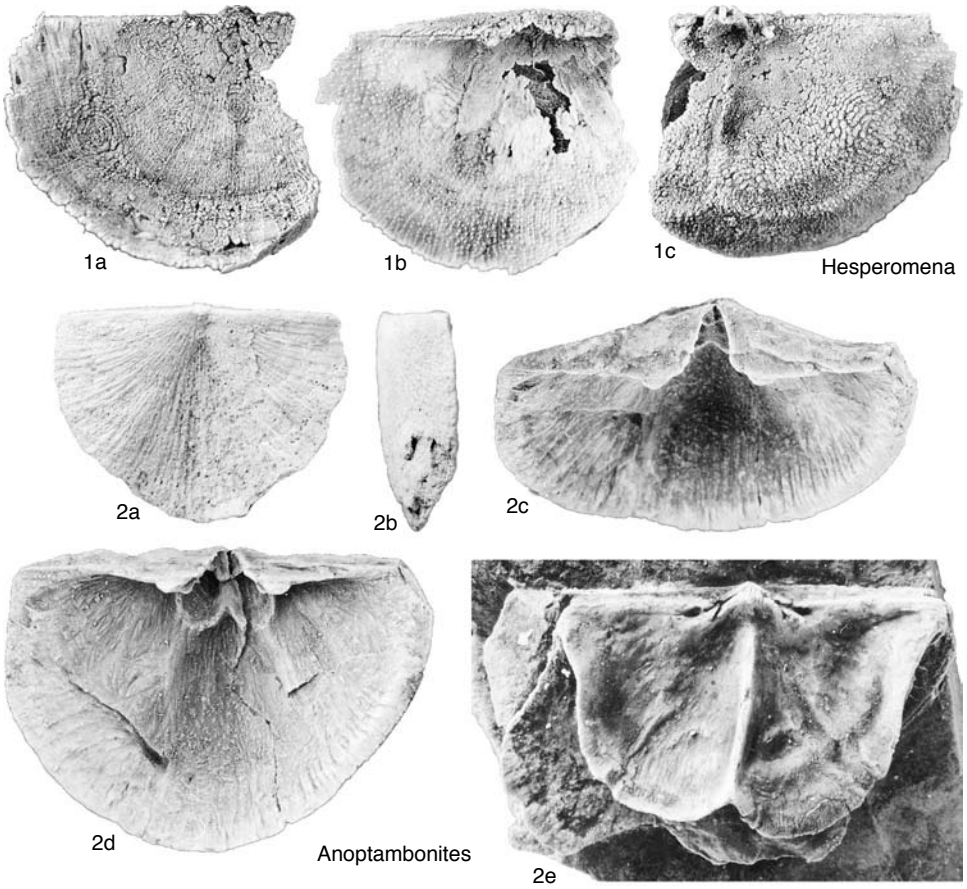

FIG. 221. Hesperomenidae (p. 337–339).

variably developed. *Ordovician (Caradoc–Ashgill):* Kazakhstan, China, Australia, Europe.

K. (Kassinella). Similar to *K. (Trimurellina)* but with dorsal median septum not extending anteriorly of platform. *Ordovician (Caradoc–Ashgill):* Asia, Australia, Europe.——FIG. 223,*1a. *K. (K.) globosa,* Kulunbulak Formation, Dulankara Horizon, lower Ashgill, Kulunbulak River, Tarbagatai Range, Kazakhstan; ventral internal mold, BMNH BC 12934, ×5 (new).——FIG. 223,*1b. K. (K.)* sp., Changwu Formation, middle Ashgill, Jiangshan County, Zhejiang Province, China; dorsal internal mold, NIGP 101834, ×10 (Cocks & Rong, 1989).——FIG. 223,*1c,d. K. (K.) septata,* Goonumbla Volcanics, upper Caradoc, Gunningbland, New South Wales, Australia; *c,* latex cast of dorsal interior, SUP 61570, ×5; *d,* dorsal internal mold, SUP 61562, ×5 (Percival, 1979b).

K. (Trimurellina) MITCHELL, 1977, p. 74 [**T. superba;* OD]. Concavoconvex profile; semicircular outline; similar to *K. (Kassinella)* but with dorsal valve median septum extending anteriorly of platform (but not of peripheral rim). *Ordovician (Ashgill):* Ireland, Scotland.——FIG. 223,*2a–d. *K. (T.) superba,* Killey Bridge Formation, middle Ashgill, Pomeroy, County Tyrone, Northern Ireland; *a,* dorsal external latex, GSM GU 1112, ×15; *b,* ventral internal mold, GSM GU 1113, ×15; *c,* dorsal internal mold, GSM GU 1124, ×15; *d,* holotype, dorsal internal latex, GSM GU 1109, ×15 (new).

Family SOWERBYELLIDAE Öpik, 1930

[*nom. transl.* COOPER, 1956, p. 744, *ex* Sowerbyellinae ÖPIK, 1930, p. 60] [=Dubioleptinidae HAVLÍČEK, 1967, p. 70]

Concavoconvex to resupinate profile; weak dental plates usually developed, sometimes absent; undercut cardinal process; side septa; bema usually developed. *Ordovician (Llanvirn)–Devonian (Eifelian).*

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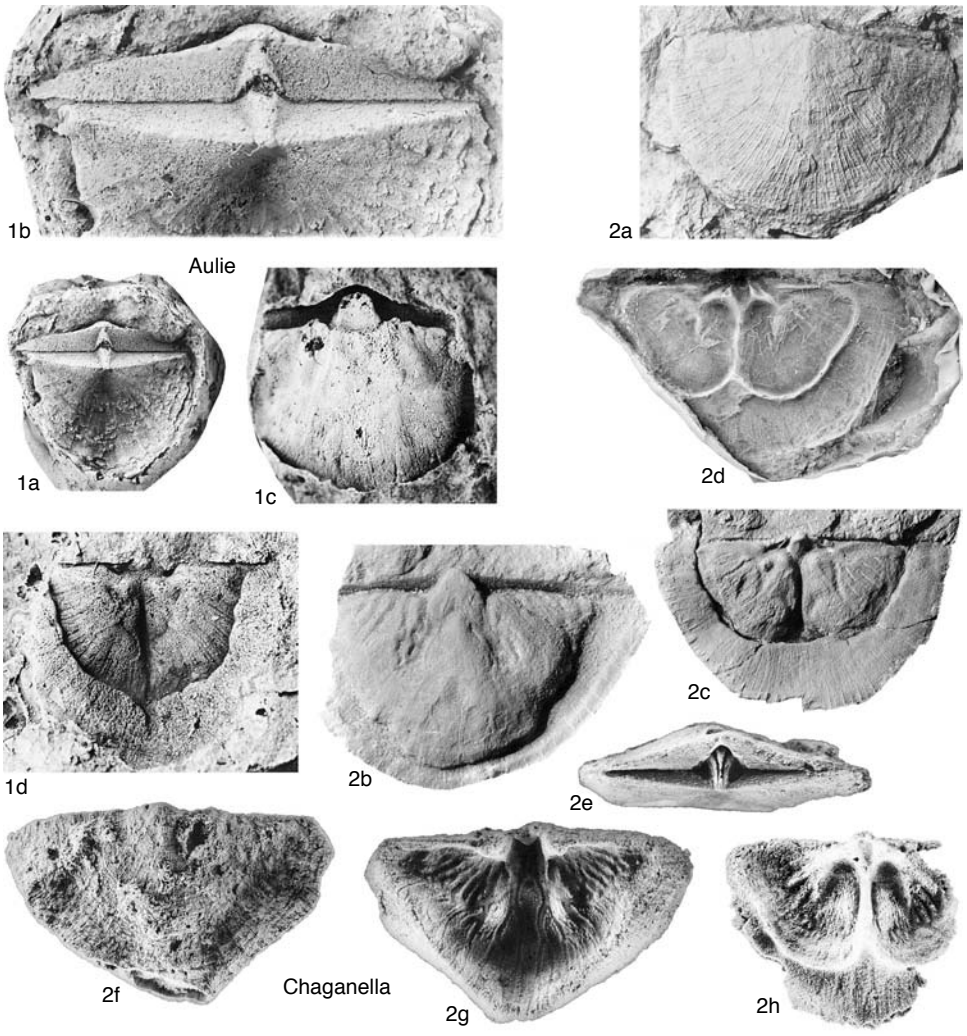

FIG. 222. Hesperomenidae (p. 339).

Subfamily SOWERBYELLINAE Öpik, 1930

[Sowerbyellinae ÖPIK, 1930, p. 60]

Bema divided; cardinal process differentiated. *Ordovician (Llanvirn)–Devonian (Eifelian).*

Sowerbyella JONES, 1928, p. 384 [**Leptaena sericea* J. DE C. SOWERBY, 1839, p. 636; OD] [=*Sowerbyella (Viruella)* RÕÕMUSOKS, 1959, p. 14 (type, *S. liliifera* ÖPIK, 1930, p. 148; OD)]. Concavoconvex profile; parvicostellate to unequally parvicostellate ornament; small arched pseudodeltidium; no chilidium; short teeth; no denticles on hinge line; short but widely diverging dental plates; bilobed ventral muscle field open anteriorly, with posterolateral muscle-bounding ridges; thin short ventral median septum posteriorly; small cardinal process; wide flaring socket plates; bema variable, usually present but occasionally absent; median septum in dorsal valve variably developed, usually absent; similar to *Anisopleurella* but with prominent pair of central side septa, which sometimes form edge of bema and are sometimes developed above it. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.

S. (Sowerbyella). Similar to *S. (Rugosowerbyella),* but rugae absent or confined to simple rugae at cardinal extremities. *Ordovician (Llanvirn–Ashgill):* cosmopolitan.——FIG. 224,*1a–d.* **S. (S.) sericea* (J. DE C. SOWERBY), Horderley Sandstone Formation, Longvillian, Onny Valley, Shropshire, England; *a,* ventral internal mold,

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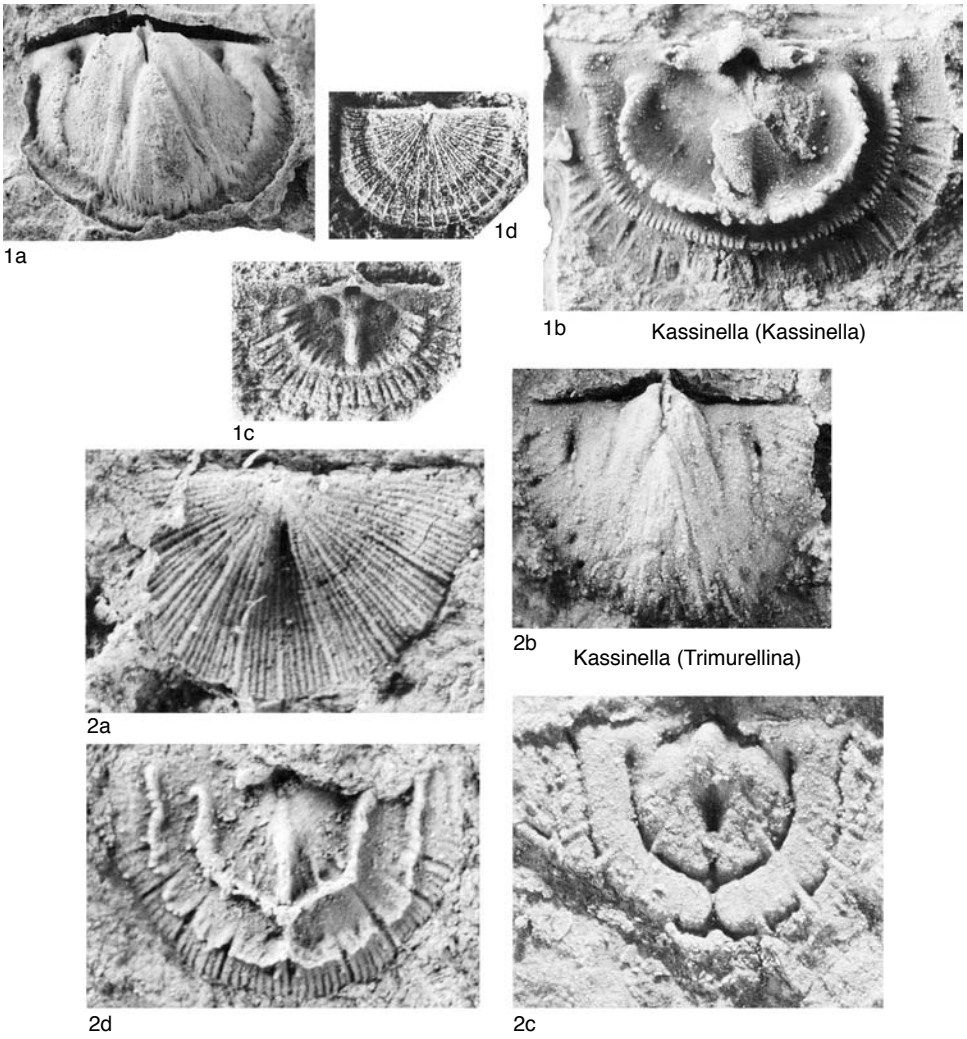

FIG. 223. Hesperomenidae (p. 340).

BMNH BC 7302, ×3; *b,* latex cast of dorsal interior, BMNH BC 6052, ×5; *c,d,* posterior, oblique lateral views of latex cast of dorsal interior, BMNH BC 6051, ×4 (Cocks & Rong, 1989).——FIG. 224,*1e–h. S. (S.) liliifera,* Kukruse Formation, lower Caradoc, Kohtla-Järve, Estonia; *e,* dorsal view of conjoined valves, BMNH BB 5147, ×5; *f,* ventral exterior, BMNH BB 5148, ×3; *g,* ventral interior, BMNH BB 5151, ×4; *h,* dorsal interior, BMNH BB 5149, ×5 (Cocks & Rong, 1989).

S. (**Rugosowerbyella**) MITCHELL, 1977, p. 83 [**Ptychoglyptus ambiguus* REED, 1952, p. 56; OD; =*Plectambonites subcorrugatella* REED, 1917, p. 886; OD]. Similar to *S. (Sowerbyella)* but with distinctive ornament of concentric rugae truncated, offset by accentuated costae. *Ordovician (?Llanvirn, Ashgill):* cosmopolitan.——FIG. 224,*2a–c. *S. (R.) subcorrugatella,* Killey Bridge Formation, lower Ashgill, Pomeroy, County Tyrone, Northern Ireland; *a,* external mold of conjoined valves, BMNH BC 12219, ×4; *b,* ventral internal mold, BMNH BB 67729, ×4; *c,* dorsal internal mold, BMNH BB 67728, ×4 (new).

Anisopleurella COOPER, 1956, p. 804 [**A. tricostellata;* OD] [=*Pseudoanisopeurella* WANG in WANG & YAN, 1978, p. 222 (type, *P. aletheta;* OD; upper Miaopo Formation (lower Caradoc), Fenxiang, Yichang County, western Hubei Province, China)]. Wide outline; gently concavoconvex profile; unequally parvicostellate ornament often with only three

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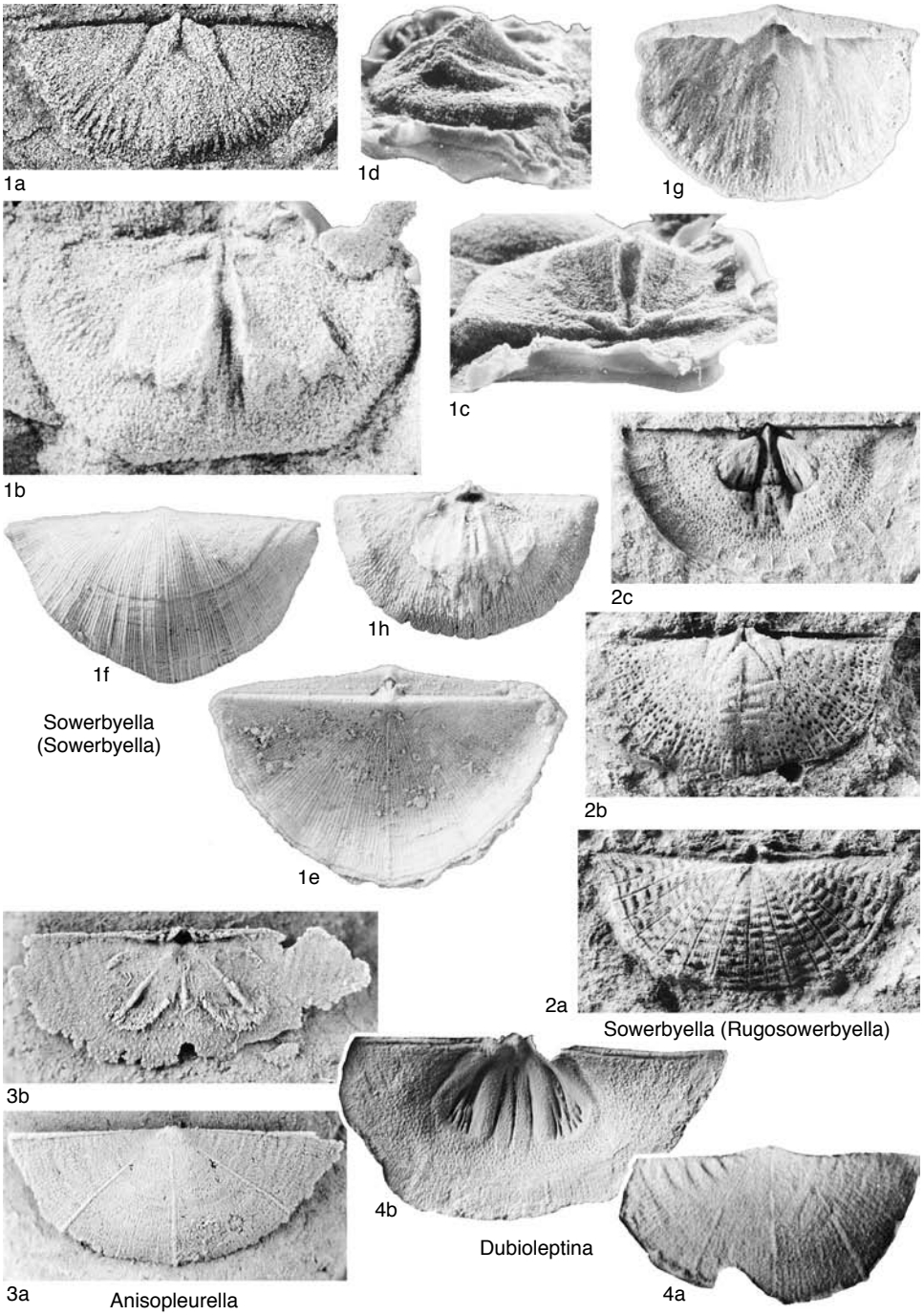

FIG. 224. Sowerbyellidae (p. 341–344).

prominent costellae; with pseudodeltidium, chilidium; teeth small, no denticles on hinge line; ventral muscle field small, bilobed, with divergent diductors, adductors borne on low median ridge; small cardinal process with laterally elongate socket ridges; prominent lateral side septa confined within

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bilobed, suboval bema; dorsal median septum; similar to *Sowerbyella* but no prominent paired central side septa developed. *Ordovician (Llandeilo)–Silurian (Llandovery):* cosmopolitan.——Fig. 224,*3a,b. *A. tricostellata,* Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama; *a,* holotype, ventral exterior, USNM 117475b, ×9; *b,* dorsal interior, USNM 117475a, ×9 (Cooper, 1956).

Dubioleptina Havlíček, 1967, p. 70 [**Strophomena expulsa* Barrande, 1879, pl. 53, fig. 4; OD]. Concavoconvex profile; unequally parvicostellate ornament; hinge line not denticulate; similar to *Sowerbyella* but with no teeth or socket plates. *Silurian (Wenlock):* Europe.——Fig. 224,*4a,b. *D. expulsa,* Liten Formation, Wenlock, Lodenice, Bohemia, Czech Republic; *a,* ventral exterior, NM L6476, ×6; *b,* dorsal internal mold, OMR VH 332, ×4 (Havlíček, 1967).

Eochonetes Reed, 1917, p. 916 [**Chonetes (Eochonetes) advena* Reed, 1917, p. 915; OD] [=*Thaerodonta* Wang, 1949, p. 19 (type, *T. aspera;* OD]. Similar to *Sowerbyella* but with denticles on lateral parts of dorsal valve hinge line only, opposing small sockets on ventral valve hinge line; canals in ventral valve hinge line variably developed, usually absent. *Ordovician (Caradoc–Ashgill):* Scotland, North America, Baltic, northern Africa.——Fig. 225,*1a–d. *E. advena,* Starfish Bed, South Threave, upper Rawtheyan, Girvan, Strathclyde, Scotland; *a,* ventral internal mold, BMNH BC 10817, ×5; *b,* dorsal internal mold, BMNH B 73919, ×3; *c,d,* dorsal internal mold obliquely tilted to show lateral denticles, latex cast, BMNH BC 10291, ×5 (Cocks & Rong, 1989).

Eoplectodonta Kozłowski, 1929, p. 112 [**Sowerbyella precursor* Jones, 1928, p. 437; OD; =*Leptaena duplicata* J. de C. Sowerby, 1839, p. 636 (Cocks, 1970, p. 166)] [=*Ygera* Havlíček, 1961, p. 449 (type, *Y. ygerens;* OD; =*Leptaena transversalis sowerbyana* Barrande, 1848, p. 225)]. Transverse outline; concavoconvex profile with incurved beak; parvicostellate to unequally parvicostellate ornament; open delthyrium, chilidial plates usual, but sometimes an entire chilidium; similar to *Sowerbyella* but with denticulate hinge line in central area of ventral valve, corresponding fossettes in dorsal valve hinge line; flaring bilobed ventral muscle field with strong dental plates, bounding ridges posterolaterally; variably developed, thin, short, ventral median septum posteriorly; erect cardinal process, socket plates; bilobed bema often raised off valve floor laterally, with from one to three pairs of prominent side septa; fine small dorsal median septum variably present in valve center only. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.

E. (Eoplectodonta). Differs from *E. (Kozlowskites)* in ventral muscle scars that touch centrally (although they are partly divided by the thin, short median septum) and from *E. (Ygerodiscus)* in lack of shell undulations. *Ordovician (Caradoc)–Silurian (Ludlow):* cosmopolitan.——Fig. 225,*3a. *E. (E.) duplicata,* upper Haverford Mudstone Formation, Rhuddanian, Haverfordwest, Dyfed, Wales; *a,* ventral internal mold, BMNH BB 31674, ×3 (Cocks, 1970).——Fig. 225,*3b–d. E. (E.) transversalis* (Wahlenberg), lower Visby Marl, Telychian, Nyhamn, Visby, Gotland, Sweden; *b,* dorsal view of conjoined valves, BMNH BB 34820, ×3; *c,* ventral interior, BMNH BB 34829, ×3; *d,* dorsal interior, BMNH BB 32425, ×3 (Cocks, 1970).——Fig. 225,*3e,f. E. (E.) sowerbyana,* Liten Formation, Wenlock, Svaty Jan pod Skalou, Bohemia, Czech Republic; *e,* ventral internal mold, OMR VH 324, ×1.8; *f,* dorsal internal mold, OMR VH 320, ×2 (Havlíček, 1967).

E. (Kozlowskites) Havlíček, 1952, p. 406 [**Strophomena nuntia* Barrande, 1879, pl. 49, fig. 3; OD]. Similar to *E. (Eoplectodonta)* but ventral muscle scars not united centrally; ventral valve mantle canal markings simple, subparallel; bilobed dorsal muscle field less than half valve length, unlike *E. (Eoplectodonta). Ordovician (Caradoc–Ashgill):* Europe, China.——Fig. 225,*4a–c. *E. (K.) nuntia* (Barrande), Králuv Dvur Formation, Ashgill, Králuv Dvur, Bohemia, Czech Republic; *a,* external mold of conjoined valves, NM CD 1568, ×4; *b,* ventral internal mold, NM CH 314, ×4; *c,* dorsal internal mold, NM CD 1557, ×4 (Havlíček, 1967).

E. (Ygerodiscus) Havlíček, 1967, p. 62 [**Leptaena transversalis* var. *undulata* Salter in Phillips & Salter, 1848, p. 372; OD] [=*E. (Paranisopleurella)* Zhang, 1989b, p. 102 (type, *E. (P.) cooperi;* OD)]. Similar to *E. (Eoplectodonta)* but with distinctive shell undulations and with less massive bema. *Silurian (Llandovery–Wenlock):* Europe, North America.——Fig. 225,*2a–d. *E. (Y.) undulata* (Salter), V_2C Beds, Rhuddanian, Mathyrafal, Meifod, Wales; *a,* dorsal external mold, BMNH BB 31925, ×3; *b,* ventral internal mold, BMNH BB 32109, ×3; *c,d,* dorsal internal mold, latex cast, BMNH BB 31917, ×5 (new).

Gunningblandella Percival, 1979b, p. 111 [**G. resupinata;* OD]. Similar to *Sowerbyella* but resupinate in profile; unequally parvicostellate ornament; small pseudodeltidium; chilidial plates; hinge line not denticulate; short dental plates; bilobed ventral muscle field divided by short thin median septum posteriorly; erect cardinal process, flaring socket plates; bema less than half valve length; dorsal side septa weakly developed. *Ordovician (Caradoc):* Australia, ?Norway.——Fig. 226,*2a–e. *G. resupinata,* Goonumbla Volcanics, upper Caradoc, Gunningbland, New South Wales, Australia; *a,* latex cast of dorsal exterior, SUP 61490, ×2.5; *b,* latex cast of ventral interior, SUP 61510, ×2.5; *c,* holotype, dorsal internal mold, ×2.5; *d,* latex cast, SUP 61487, ×3; *e,* latex cast of dorsal interior, SUP 61503, ×5 (Percival, 1979b).

Plectodonta Kozłowski, 1929, p. 112 [**P. mariae;* OD]. Quadrate outline; gently concavoconvex

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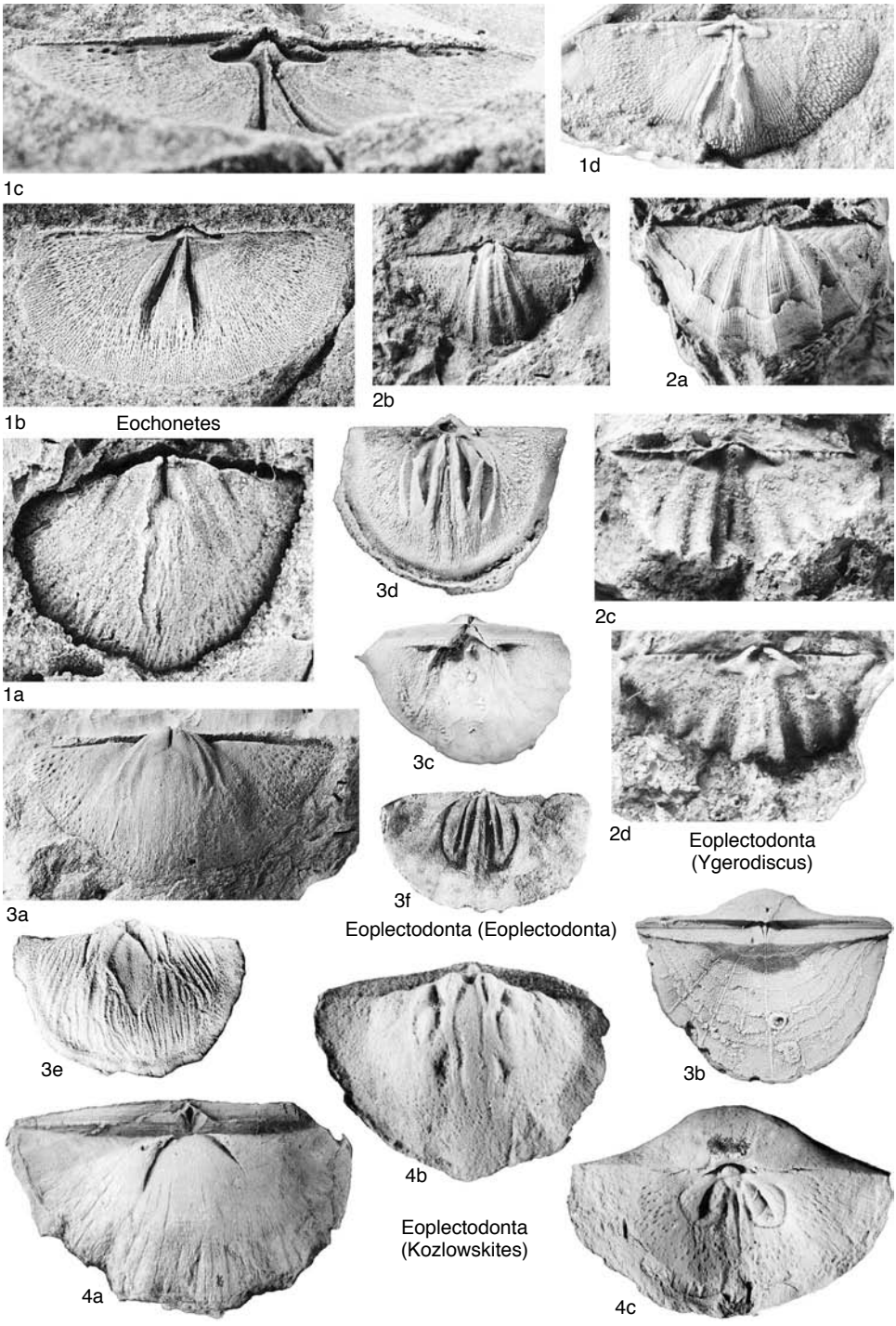

FIG. 225. Sowerbyellidae (p. 344).

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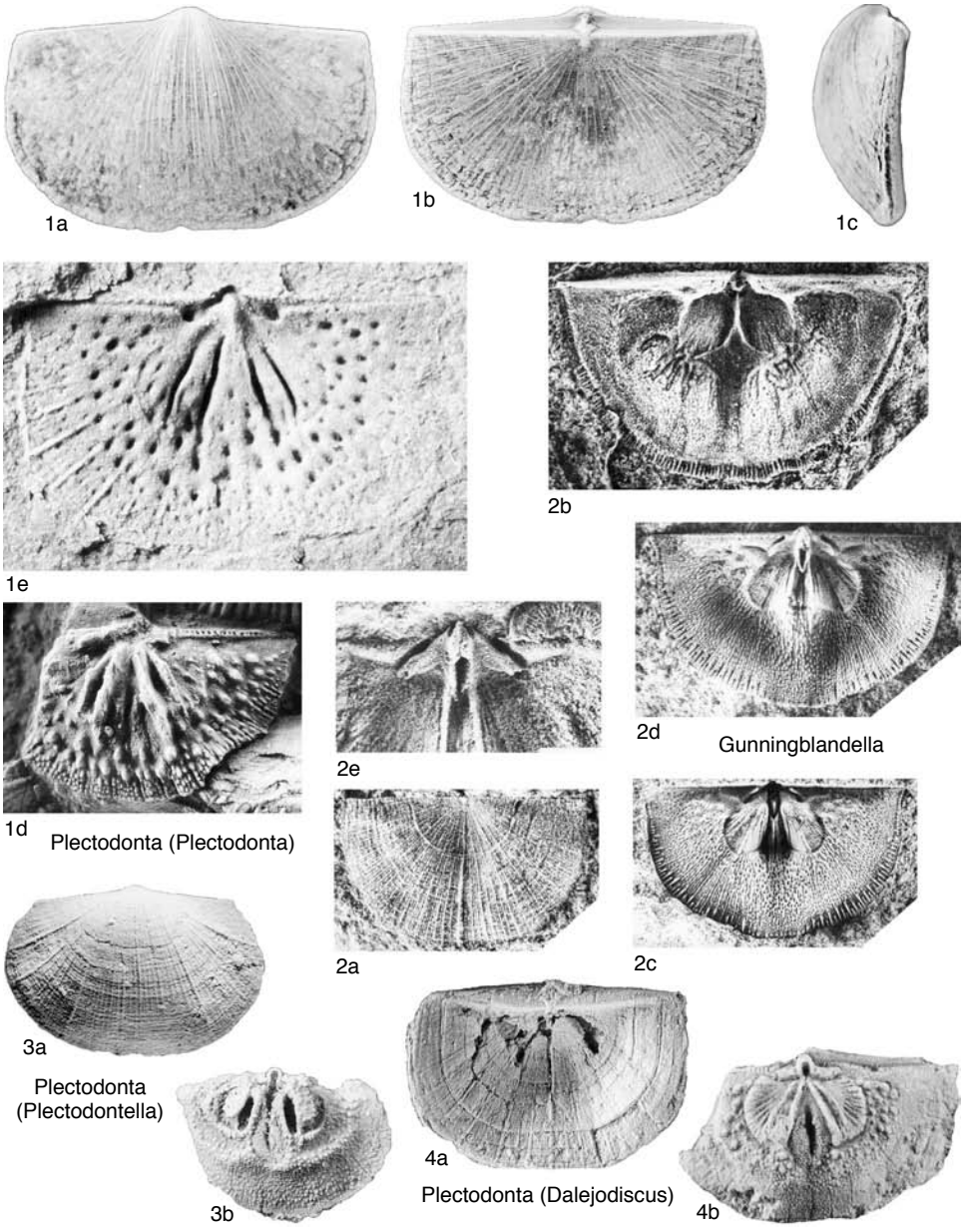

FIG. 226. Sowerbyellidae (p. 344–347).

profile; parvicostellate ornament; hinge line denticulate; small pseudodeltidium, chilidial plates; small teeth, stubby socket plates; small bilobed ventral muscle field; bema variably developed; dorsal median septum, platform absent; similar to *Eoplectodonta* except with stronger pseudodeltidium, less incurved beak, more quadrate, less alate valve extremities, coarse papillae on dorsal valve interior. *Silurian (Přídolí)–Devonian (Eifelian):* cosmopolitan.

P. (Plectodonta). Similar to *P. (Dalejodiscus)* but with bema weak or absent, and differing from *P. (Plectodontella)* in the absence of side septa. *Silurian (Přídolí)–Devonian (Eifelian):* cosmopolitan.——FIG. 226,*1a–e. *P. (P.) mariae,* Taina Formation, Borshchov Group, Lochkovian,

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Rukhotin, Krzywcze, Podolia, Ukraine; *a–c,* exterior views of conjoined valves, BMNH BB 81378, ×5 (new); *d,* dorsal interior, BMNH B 81370, ×6; *e,* dorsal internal mold, BMNH BB 65810, ×8 (Cocks & Rong, 1989).

P. (Dalejodiscus) Havlíček, 1961, p. 449 [**Strophomena comitans* Barrande, 1879, pl. 56; OD]. Similar to *P. (Plectodonta)* but with elevated, radially striated bema, short central dorsal median septum. *Devonian (Pragian–Eifelian):* Europe, ?Asia.——Fig. 226,*3a,b.* **P. (D.) comitans* (Barrande), Daleje Shales, Eifelian, Praha-Hlubocepy, Czech Republic; *a,* exterior of conjoined valves, OMR VH 318, ×4; *b,* dorsal interior, OMR VH 284, ×4 (Havlíček, 1967).

P. (Plectodontella) Havlíček, 1953, p. 8 [**P. redunca;* OD]. Similar to *P. (Plectodonta)* but with strong raised bema, distinctive pair of strong side septa posterior of valve center; weak platform present. *Devonian (Eifelian):* Europe. ——Fig. 226,*4a,b.* **P. (P.) redunca,* Trebotov Limestone Formation, lower Eifelian, Holyne, Prague, Czech Republic; *a,* ventral exterior, OMR VH 26, ×3.7; *b,* dorsal interior, OMR VH 25, ×3.5 (Havlíček, 1967).

Subfamily PTYCHOGLYPTINAE Cooper, 1956

[Ptychoglyptinae Cooper, 1956, p. 815]

Weak bema, not divided; cardinal process differentiated. *Ordovician (?Llandeilo, Caradoc–Ashgill).*

Ptychoglyptus Willard, 1928, p. 283 [**P. virginiensis;* OD]. Concavoconvex to planoconvex profile, shell often delicate; distinctive ornament of small rugae interrupted by costellae; small arched pseudodeltidium; chilidial plates; flaring teeth with short dental plates; poorly impressed muscle fields; small, erect cardinal process lobes; flaring socket plates; bema poorly impressed; one or two pairs of short weak side septa variably developed. *Ordovician (?Llandeilo, Caradoc–Ashgill):* cosmopolitan.—— Fig. 227*a–d.* **P. virginiensis; a,* ventral exterior, Edinburg Formation, Caradoc, Harrisonburg, Virginia, USNM 98231b, ×3; *b,* ventral interior, Edinburg Formation, Caradoc, Harrisonburg, Virginia, USNM 98231b1, ×3; *c,* dorsal interior, Effna-Rich Valley Formation, lower Caradoc, Porterfield Quarry, Virginia, USNM 111042b, ×4; *d,* dorsal interior, Pratt Ferry Formation, Llandeilo, Pratt Ferry, Blocton, Alabama, USNM 117398c, ×4 (Cooper, 1956).

PLECTAMBONITOIDEAN GENERA UNASSIGNED TO FAMILIES

Leptoptilum Öpik, 1930, p. 130 [**Leptestia (Leptoptilum) bekkeri;* OD]. Only broken fragments available showing merely pseudopunctate, convex ventral valve, parvicostellate ornament; perhaps synonym of *Leptestia,* but considered *nomen dubium* here. *Ordovician (Caradoc):* Kukruse Formation, Kohtla, Estonia.

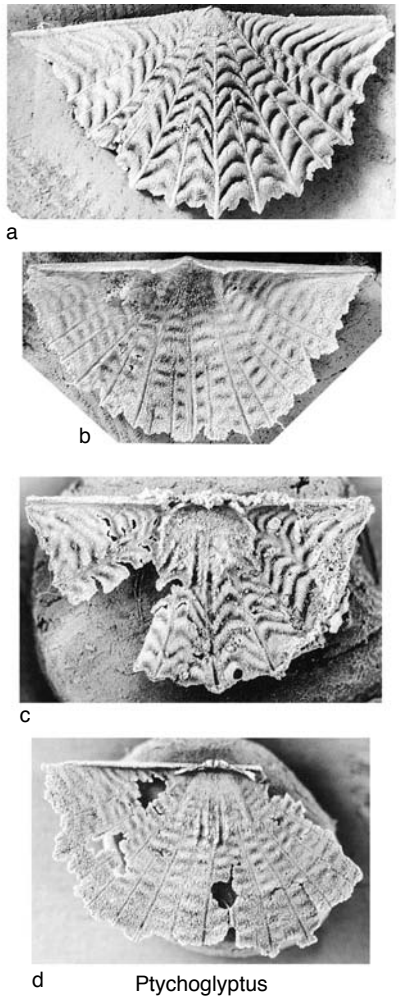

Fig. 227. Sowerbyellidae (p. 347).

Paucicostella Cooper, 1956, p. 711 [**P. canadensis;* OD]. Parvicostellate ornament, gently convex ventral valve, nearly flat dorsal valve; interior unknown, apart from short dental plates, relatively wide ventral muscle field; *nomen dubium. Ordovician (Arenig–Llanvirn):* Canada.——Fig. 228,*1.* **P. canadensis,* Mystic Conglomerate, Arenig–Llanvirn, Mystic, Quebec, Canada; ventral exterior, USNM 117395a, ×3 (Cooper, 1956).

Ukoa Öpik, 1932, p. 33 [**U. ornata;* OD]. Large; resupinate, weakly geniculate profile; unequally parvicostellate ornament; ventral muscle field triangular, open anteriorly; dorsal interior unknown,

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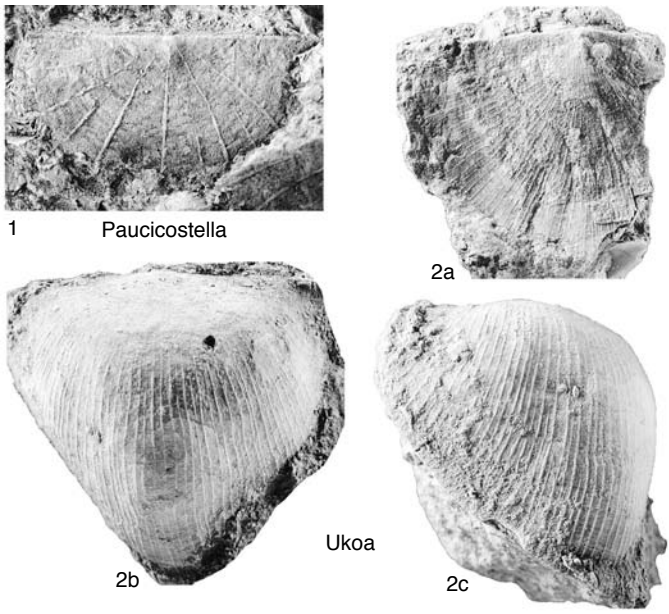

FIG. 228. Unassigned (p. 347–348).

thus may be strophomenine. *Ordovician (Arenig–Llanvirn):* Baltic.——FIG. 228,*2a–c. *U. ornata; a,* ventral exterior, Kunda Horizon, lower Llanvirn, Lava River, St. Petersburg, Russia, BMNH BC 12858, ×1; *b,c,* dorsal exterior, Kunda Horizon, upper Arenig, Lynna River, St. Petersburg, Russia, BMNH BC 12857, ×1 (new).

UNCERTAIN

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Suborder UNCERTAIN
Family EOCRAMATIIDAE Williams, 1974

[Eocramatiidae WILLIAMS, 1974, p. 127]

Subquadrate, costellate; apsacline ventral interarea with submesothyrid foramen and long, convex pseudodeltidium; narrow, hypercline dorsal interarea with small, convex chilidium; teeth unsupported, ventral muscle scar indistinct but more or less limited to delthyrial cavity; divergent chilidial plates filling notothyrium, ankylosed to socket ridges or plates parallel with hinge line, dorsal adductor scars quadripartite about low myophragm; shell impunctate. *Lower Ordovician (Llanvirn).*

Eocramatia WILLIAMS, 1974, p. 128 [**E. dissimulata;* OD]. Planoconvex, gently uniplicate, finely costellate by branching and intercalation. [This genus has many generalized features in common with the billingselloids and clitambonitoids. But the absence of dental plates and notothyrial platform and the presence of divergent plates filling the notothyrium (in a manner more reminiscent of the chilidial plates of the leptellids than the bilobed cardinal process of strophomenids) suggest that it belongs to the Strophomenida. Within that order, the Orthotetidina and the Plectambonitoidea are the most likely taxonomic repositories for *Eocramatia.* If the structures occupying the notothyrium prove to be the cardinal process lobes, the genus could be placed with the orthotetoids, although the profile of the

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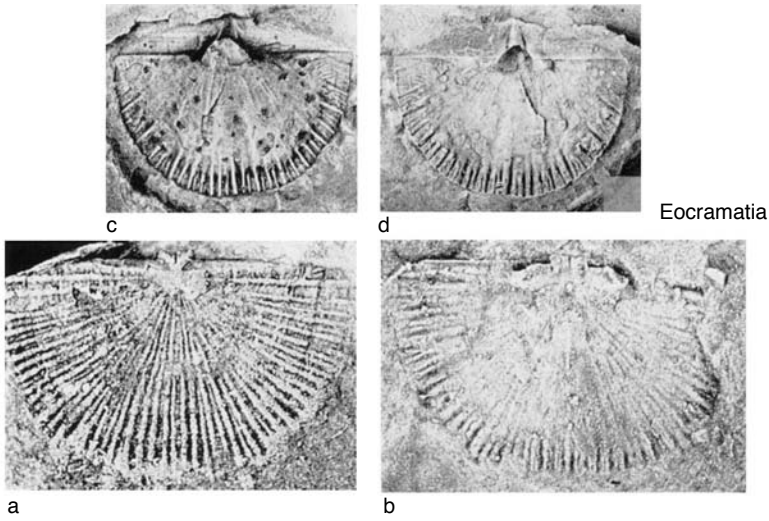

FIG. 229. Uncertain (p. 348–349).

dorsal valve would militate against such an assignment as would the attitude of the socket ridges and the absence of dental plates. The impunctate condition of the shell has been inferred from the condition of the molds of specimens, which are preseved in fine shale. In any event, both the Orthotetidina and the Plectambonitoidea accommodate impunctate stocks.] *Lower Ordovician (Llanvirn):* England.——FIG. 229*a–d. *E. dissimulata;* Hope Shales, Brithdir Farm, Shropshire, Llanvirn; *a,b,* paratype, latex casts of dorsal valve exterior, interior, BMNH BB35489a, BMNH BB35489b, ×5.8; *c,d,* holotype, latex mold, cast of ventral valve interior, BMNH BB35488a, ×3.5 (Williams, 1974).

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