SPIRIFERINOIDEA

J. L. CARTER

[retired from Carnegie Museum of Natural History]

Superfamily SPIRIFERINOIDEA Davidson, 1884

[*nom. correct.* CARTER in CARTER & others, 1994, p. 370, *pro* superfamily Spiriferinacea IVANOVA, 1959, p. 57, *nom. transl. ex* subfamily Spiriferinidae DAVIDSON, 1884, p. 354]

Reticulariiform and subequally biconvex; cardinal extremities well rounded; ventral beak incurved; fold and sulcus usually weakly developed; lateral slopes smooth or obscurely ribbed, rarely with moderately developed ribbing; ventral septum invariably present. *Middle Triassic–Lower Jurassic.*

Family SPIRIFERINIDAE Davidson, 1884

[*nom. transl.* IVANOVA, 1959, p. 57, *ex* subfamily Spiriferinidae DAVIDSON, 1884, p. 354]

Lateral slopes smooth or obscurely ribbed. *Middle Triassic–Lower Jurassic.*

Subfamily SPIRIFERININAE Davidson, 1884

[*nom. correct.* SCHUCHERT, 1929, p. 21, *pro* subfamily Spiriferinidae DAVIDSON, 1884, p. 354] [=Spiriferellinae PAECKELMANN, 1931, p. 25; Spiriferininae SCHUCHERT, 1929, p. 21]

Reticulariiform; dental adminicula discrete. *Middle Triassic–Lower Jurassic.*

Spiriferina D'ORBIGNY, 1847, p. 268 [**Spirifer walcotti* J. DE C. SOWERBY, 1823 in 1823–1825, p. 106; SD DALL, 1877a, p. 64]. Small to medium size; unequally biconvex, ventral valve usually much thicker than dorsal; outline variable from transversely to longitudinally subelliptical; cardinal extremities rounded; ventral umbonal region usually inflated, beak incurved; ventral interarea narrow, concave, apsacline, usually low to moderately high; beak ridges rounded; delthyrium restricted by rarely preserved stegidial plates; fold and sulcus smooth, subangular, moderately wide, moderately developed, moderately well delimited; lateral slopes with few, subangular plicae; dental adminicula short; ventral median septum long; ctenophoridium stout, supported by median septum forming septalium with crural bases in type species; jugum unknown; microornament of dense, fine spinules; punctae moderately fine, not densely spaced. [DAVIDSON (1884) proposed the subfamily Spiriferinidae. SCHUCHERT (1929) proposed a subfamily Spiriferininae as a unit in DAVIDSON's family. PAECKELMANN (1931) proposed Spiriferellinae (an incorrect spelling) to replace SCHUCHERT's Spiriferininae for unknown reasons.] *Lower Jurassic:* Europe, North Africa, Saudi Arabia, USA (Alaska).——FIG. 1286,*3a–b.* **S. walcotti* (SOWERBY), Liassic, British Islands; dorsal and anterior views, ×1 (Pitrat, 1965).

Calyptoria COOPER, 1989, p. 65 [**C. extensa;* OD] [=*Cingolospiriferina* POZZA, 1992, p. 211 (type, *C. cingolana,* OD)]. Fold and sulcus well developed; lateral slopes with obscure plicae; spinules or other microornament absent; punctae fine; dorsal median septum extending to midvalve; jugum unknown in type species; otherwise similar to *Spiriferina. Lower Jurassic:* Saudi Arabia.——FIG. 1287,*1a–e.* **C. extensa;* holotype, anterior, lateral, dorsal, posterior, and ventral views, ×1 (Cooper, 1989).

Liospiriferina ROUSSELLE, 1977, p. 164 [**Terebratulites rostratus* SCHLOTHEIM, 1822, p. 260; OD]. Small to medium; flanks and sulcus not ribbed, smooth; fold and sulcus weakly to moderately developed, often only discernable at anterior commissure; ctenophoridium stout, supported by median septum forming short septalium with crural bases in some specimens of type species; jugum complete, high, and rounded; microornament of anteriorly directed, fine, hollow spinules arranged in quincunx; punctae large and densely spaced. *Lower Jurassic:* Europe, North Africa, Saudi Arabia.——FIG. 1286,*1a–g.* **L. rostrata* (SCHLOTHEIM), Germany; *a–e,* holotype, ventral, dorsal, lateral, anterior, and posterior views, ×1 (Logan, 1964); *f–g,* transverse sections, approximately ×1.8 (Rousselle, 1977).

Mentzelioides DAGYS, 1974, p. 130 [**Mentzeliopsis meridialis* DAGYS, 1963, p. 76; OD]. Medium to large; outline transversely subovate; cardinal extremities well rounded; subequally biconvex; ventral beak acute, slightly incurved; ventral interarea high, nearly catacline; fold poorly developed; sulcus produced anteriorly, smoothly rounded, shallow; anterior margin slightly emarginate; macroornament lacking; microornament of numerous irregularly arranged, hollow spinules that penetrate secondary layer; dental adminicula short, divergent; ventral median septum long, moderately thick apical callus present; short callus suporting ctenophoridium; jugum unknown. *Upper Triassic:* Caucasus, ?Alps, Carpathians.——FIG. 1286,*4a–h.* **M. meridialis* (DAGYS), Caucasus; *a–c,* holotype, posterior, ventral, and lateral views, ×1; *d,* microornament, enlarged (new); *e–h,* transverse sections, approximately ×1.5 (Dagys, 1963).

Qinghaispiriferina SUN & YE, 1982, p. 159 [**Q. obovata;* OD]. Medium size; outline subovate; cardinal extremities well rounded; valves subequally

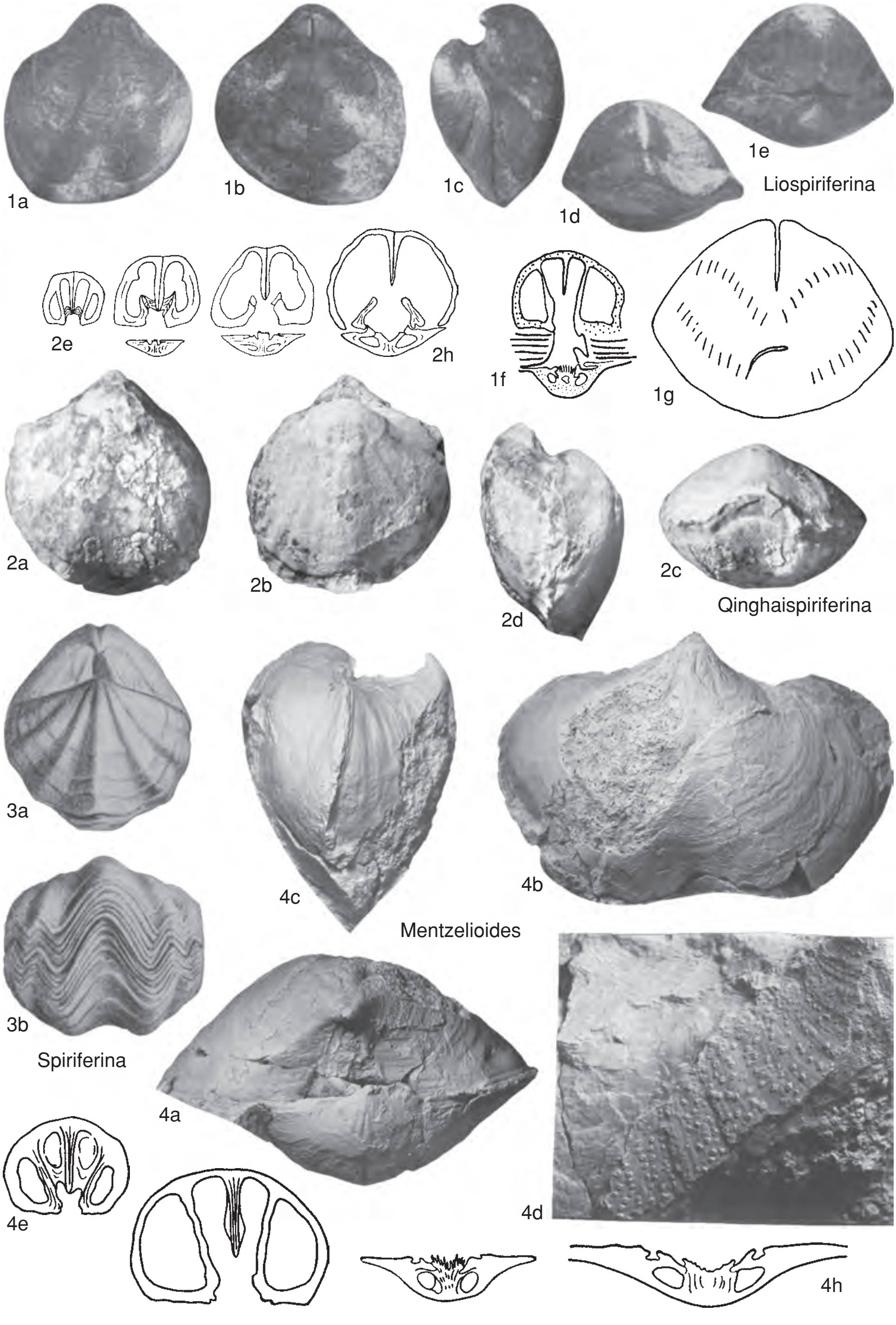

FIG. 1286. Spiriferinidae (p. 1930–1933).

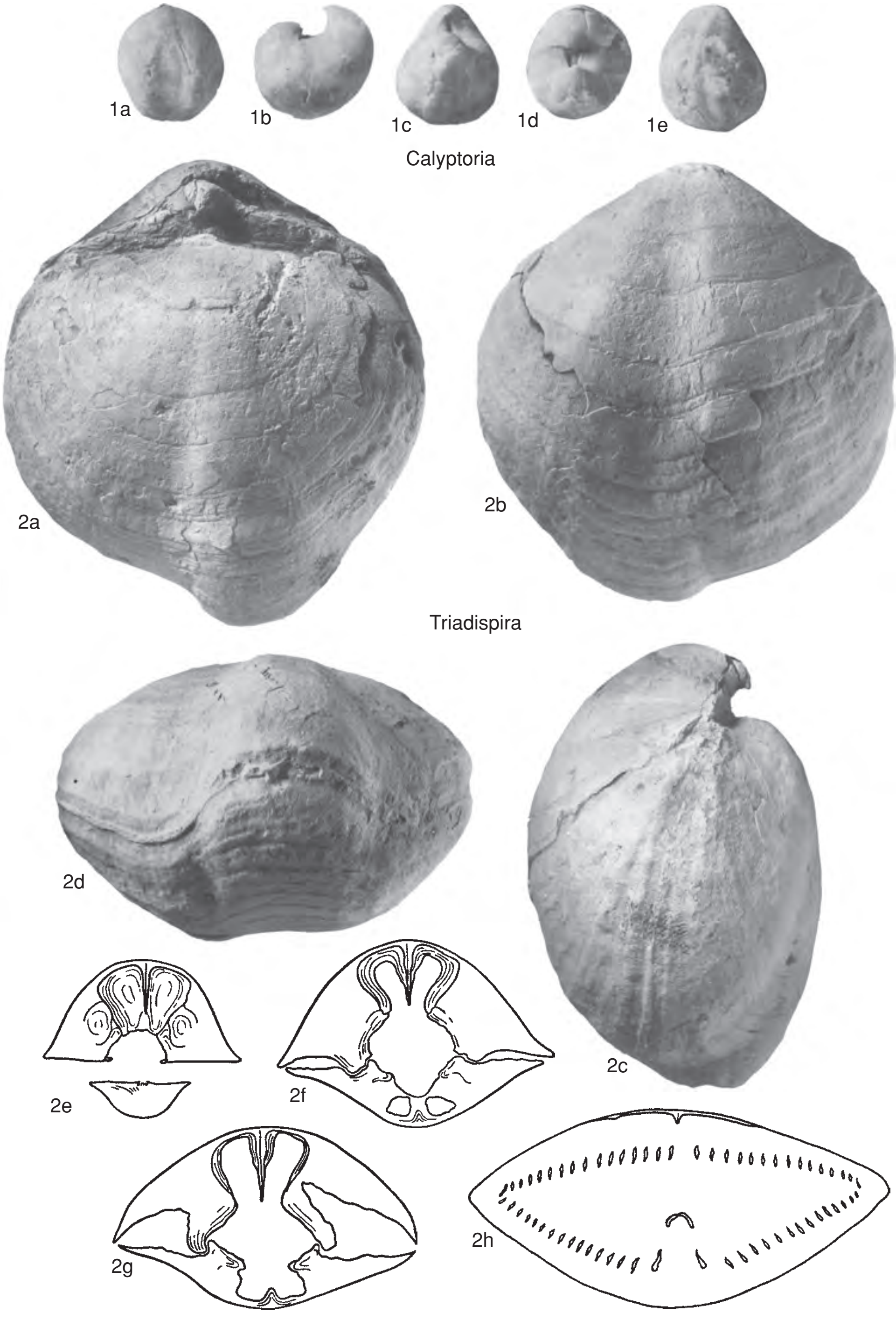

FIG. 1287. Spiriferinidae (p. 1930–1933).

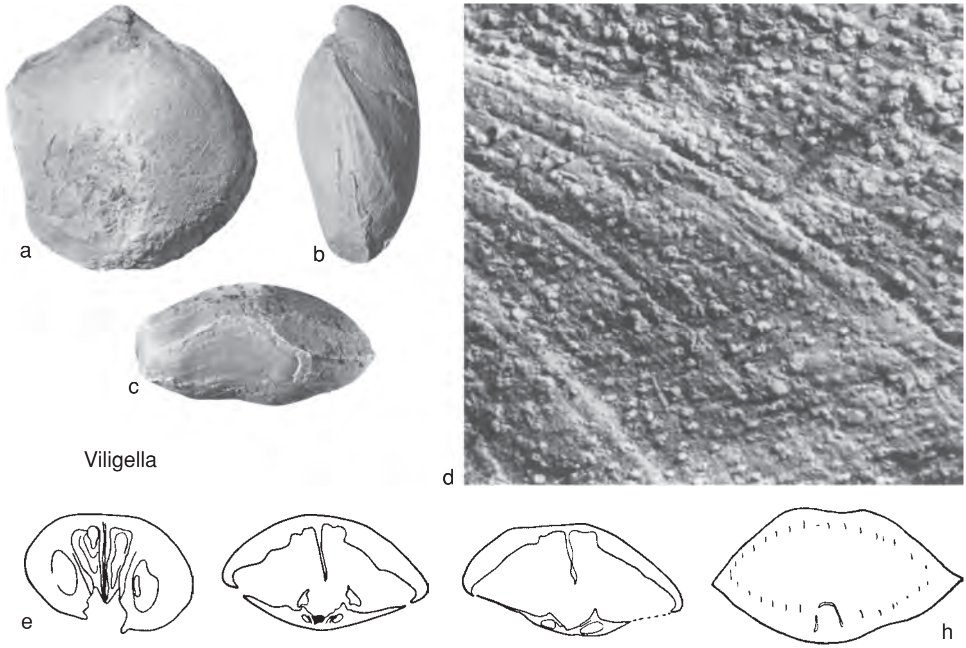

Fig. 1288. Spiriferinidae (p. 1933).

biconvex, ventral valve slightly thicker; ventral beak short, incurved; ventral interarea narrow, concave, apsacline; delthyrium open; fold and sulcus weakly developed, rounded, smooth; anterior commissure uniplicate; lateral slopes with few faint, low ribs; strong growth varices irregularly developed; microornament finely and regularly reticulate; dental adminicula short, stout; stout, high median septum united with dental flanges by short, transverse callus deposit; spondylium absent; dorsal interior posteriorly thickened with callus; ctenophoridium and converging crural bases supported by thick, low median septum or callus; jugum indistinct, apparently broadly V-shaped. *Middle Triassic:* China (Qinghai).——Fig. 1286,*2a–h.* **Q. obovata; a–d,* holotype, ventral, dorsal, anterior, and lateral views, ×2 (new); *e–h,* transverse sections, ×1.7 (Sun & Ye, 1982).

Triadispira Dagys, 1961, p. 457 [**T. caucasica;* OD]. Large; outline subovate; subequally biconvex; cardinal extremities well rounded, hinge line short; ventral interarea low, concave, strongly apsacline to orthocline; ventral umbonal region broadly inflated, beak incurved; fold and sulcus moderately narrow, rounded, smooth, well defined; macroornament lacking; microornament of fine spinules; both valves with thick apical callus; dental adminicula short, divergent, buried in callus with long, massive median septum; cardinalia supported by short median septum; jugum complete; spiralia with numerous whorls. *Upper Triassic (Norian–Rhaetian):* Georgia (Caucasus Mountains).——Fig. 1287,*2a–h.* **T. caucasica; a–d,* holotype, dorsal, ventral, lateral, and anterior views, ×1 (new); *e–h,* transverse sections, approximately ×1 (Dagys, 1963).

Viligella Dagys, 1965, p. 116 [**Mentzelia rotunda* Tuchkov, 1956, p. 180; OD]. Medium size; weakly inflated; outline ovate; fold and sulcus obscurely developed, smooth; hinge line narrow, cardinal extremities well rounded; ventral umbo reduced, broad, beak small, slightly incurved; ventral interarea narrow, low, strongly apsacline; macroornament absent or lateral slopes very obscurely plicate; microornament of fine, dense spinules; dental adminicula very short, with long median septum and thick apical callus; crural bases broadly converging, extending to valve floor; jugum complete, rounded, free. *Upper Triassic (Norian):* northeastern Siberia.——Fig. 1288*a–h.* **V. rotunda* (Tuchkov); *a–c,* dorsal, lateral, and anterior views, ×1; *d,* microornament, ×10 (new); *e–h,* transverse sections, approximately ×1.2 (Dagys, 1965).

Subfamily PARALABALLINAE
Carter, 1994

[Paralaballinae Carter in Carter & others, 1994, p. 370]

Cyrtiniform; fold and sulcus weakly developed; ornament absent; dental adminicula discrete, thin, short, subparallel. *Upper Triassic.*

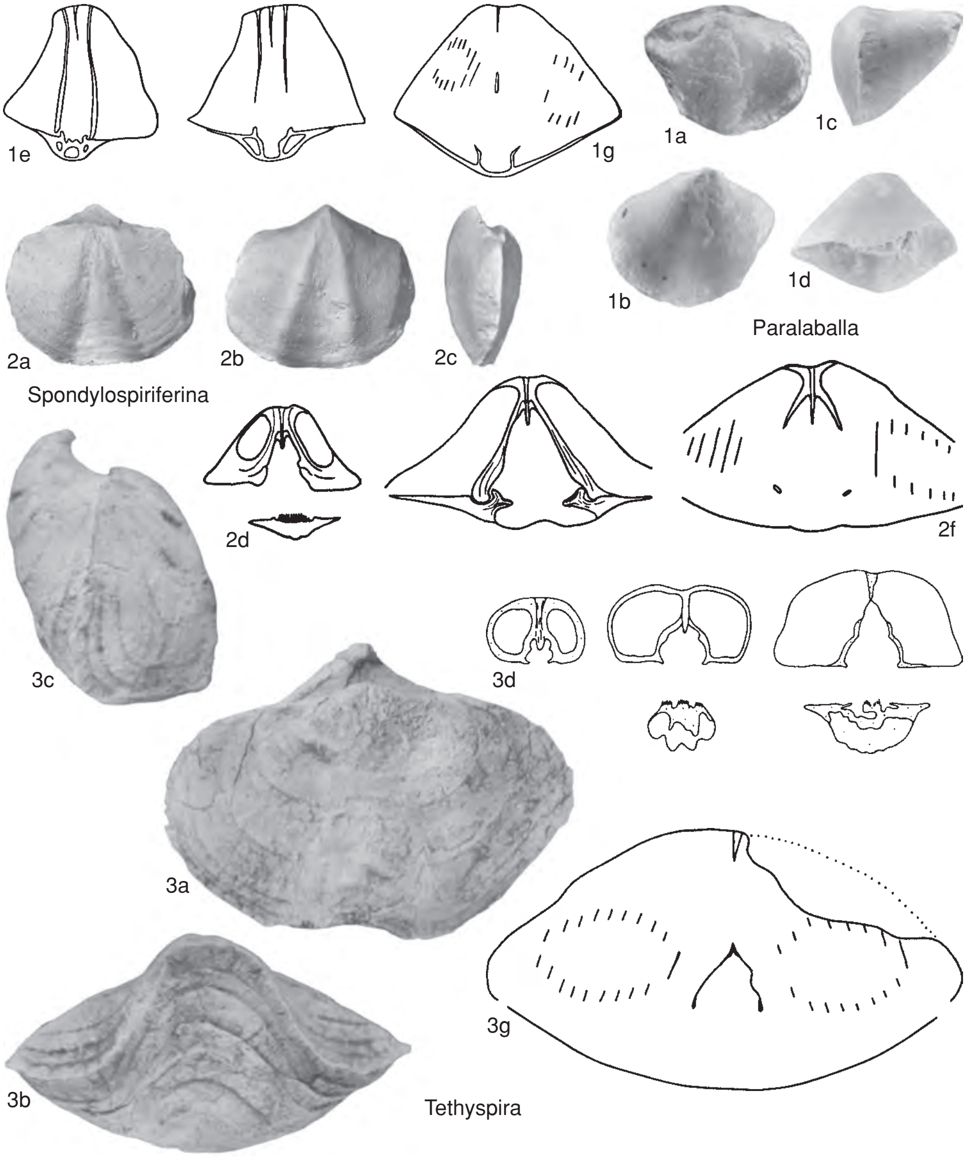

FIG. 1289. Spiriferinidae (p. 1934–1936).

Paralaballa SUN, 1981, p. 204 [**P. zangbeinensis;* OD]. Medium size; roundly rhomboidal in outline, semipyramidal in lateral profile; fold and sulcus weakly developed; hinge line shorter than maximum width, cardinal extremities obtusely rounded; ventral interarea high, flat, catacline; delthyrium open, narrow; dorsal interarea very low; ornament absent; dental adminicula thin, short, subparallel, with high median septum; hinge plate complete with subparallel dorsal adminicula fused to crural bases; ctenophoridium low; jugum unknown. *Upper Triassic:* Tibet.——FIG. 1289,*1a–g.* **P. zangbeinensis; a–d,* dorsal, ventral, lateral, and anterior views, ×1 (new); *e–g,* transverse sections, approximately ×1.5 (Sun, 1981).

Subfamily MENTZELIINAE
Dagys, 1974

[Mentzeliinae DAGYS, 1974, p. 138]

Dental adminicula absent. *Middle Triassic–Upper Triassic.*

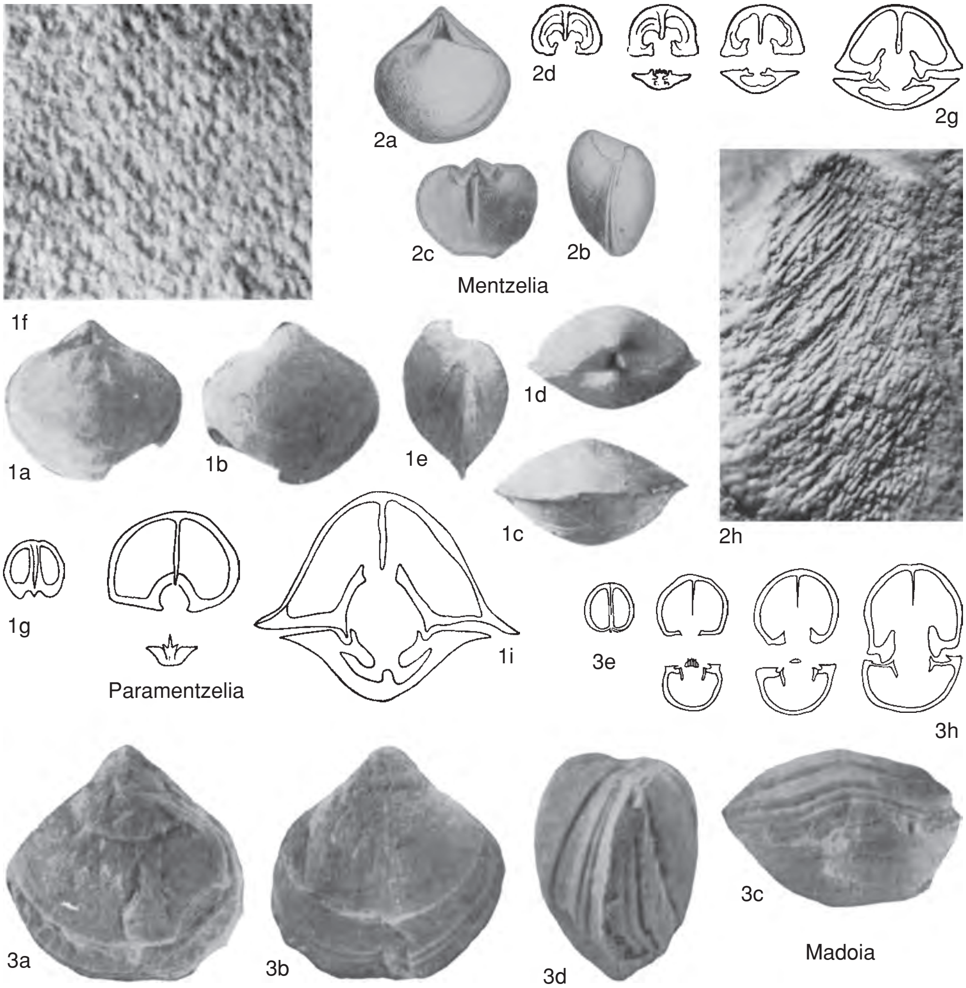

FIG. 1290. Spiriferinidae (p. 1935–1936).

Mentzelia QUENSTEDT, 1871 in 1868–1871, p. 522 [**Spirifer medianus* QUENSTEDT, 1852 in 1849–1875, p. 482; OD; =*Spirifer mentzeli* DUNKER, 1851, p. 287]. Medium size; subequally biconvex; outline subovate, cardinal extremities well rounded; ventral umbonal region slightly compressed, beak incurved; ventral interarea low to moderately high, smooth, concave, apsacline; fold and sulcus lacking or variably developed, smooth and rounded, if present; macroornament usually lacking, rarely with few obscure plicae; microornament of very dense, fine spinules; high median septum apically fused with short dental flanges forming false spondylium; jugum incomplete. *Middle Triassic–Upper Triassic:* Tethyan geosyncline.——FIG. 1290,*2a–h*. **M. mentzeli* (DUNKER), Middle Triassic, Germany; *a–c,* dorsal, lateral, and ventral interior views, approximately ×1 (Quenstedt, 1871 in 1868–1871); *d–g,* transverse sections, approximately ×2 (Dagys, 1963); *h,* microornament, ×12 (new).

Madoia SUN & YE, 1982, p. 162 [**M. rostrata;* OD]. Small to medium size; outline subovate to rounded subpentagonal; cardinal extremities well rounded; valves equally biconvex; hinge line narrow; ventral interarea narrow, concave, low, delthyrium open; ventral umbonal region broad, short, slightly compressed, beak incurved; fold and sulcus lacking posteriorly, poorly developed anteriorly, anterior commissure weakly uniplicate; surface smooth except for strong subimbricate growth varices; microornament absent; dental adminicula and true spondylium absent; small, false spondylium formed in beak by fusion of median septum and dental flanges; median septum long, thick; ctenophoridium with discrete, vertically inclined crural bases; jugum unknown. *Middle Triassic:* China

(Qinghai).——FIG. 1290,*3a–h.* **M. rostrata; a–d,* dorsal, ventral, anterior, and lateral views, ×2; *e–h,* transverse sections, ×3.3 (Sun & Ye, 1982).

Paramentzelia XU, 1978, p. 293 [**P. ovata;* OD]. Medium size; fold and sulcus absent or weakly developed anteriorly; microornament densely papillose; false spondylium very short, high, shallow; dental adminicula absent; moderately long, stout median septum supporting cardinalia; cardinal process bladelike; jugum unknown; otherwise similar to *Mentzelia. Upper Triassic:* China.——FIG. 1290,*1a–i.* **P. ovata; a–e,* dorsal, ventral, anterior, posterior, and lateral views, ×1; *f,* microornament, ×10; *g–i,* transverse sections, approximately ×2 (Xu, 1978).

Subfamily TETHYSPIRINAE
Carter, 1994

[Tethyspirinae CARTER in CARTER & others, 1994, p. 370]

Spondylium present. *Middle Triassic (Ladinian)–Upper Triassic (Carnian).*

Tethyspira SIBLÍK, 1991, p. 167 [**T. persis;* OD]. Medium to large; moderately and subequally biconvex; outline transversely subelliptical, cardinal extremities well rounded; ventral beak small, incurved; ventral interarea apsacline, sharply delimited; fold and sulcus well developed, moderately wide, rounded; macroornament generally lacking except for strong growth varices; very faint costae may be present on whole surface in some specimens; microornament absent; spondylium long, deep, moderately elevated, bisected by very long median septum; ctenophoridium and complete V-shaped jugum present. *Middle Triassic (Ladinian):* Iran.——FIG. 1289,*3a–g.* **T. persis; a–c,* holotype, dorsal, anterior, and lateral views, ×1; *d–g,* transverse sections, approximately ×1.4 (Siblík, 1991).

Spondylospiriferina DAGYS, 1972a, p. 38, *nom. transl.* CARTER, herein, *ex Pennospiriferina (Spondylospiriferina)* DAGYS, 1972a, p. 38 [**Pennospiriferina (Spondylospiriferina) glabra;* OD]. Medium size; unequally biconvex, ventral valve moderately inflated, dorsal valve flattened; slightly wider than long, outline subovate; cardinal extremities weakly rounded or rarely subangular; fold and sulcus well defined, rounded, smooth; ventral interarea low, concave, smooth; lateral slopes smooth; microornament absent; converging dental adminicula bisected by median septum slightly above floor of valve, forming low, deep spondylium; wide, low ctenophoridium supported by callus; jugum, if any, unknown. *Middle Triassic (Ladinian)–Upper Triassic (Carnian):* northeastern Siberia, Japan, New Zealand.——FIG. 1289,*2a–f.* **S. glabra,* Carnian, northeastern Siberia; *a–c,* holotype, dorsal, ventral, and lateral views, ×1 (new); *d–f,* transverse sections, approximately ×2 (Dagys, 1972a).

Family SINUCOSTIDAE
Xu & Liu, 1983

[*nom. transl.* CARTER in CARTER & others, 1994, p. 370, *ex* Sinucostinae XU & LIU, 1983b, p. 112]

Lateral slopes ribbed; dental adminicula discrete. *Middle Triassic–Upper Triassic, ?Lower Jurassic.*

Subfamily SINUCOSTINAE
Xu & Liu, 1983

[Sinucostinae XU & LIU, 1983b, p. 112]

Dorsal septum absent. *Middle Triassic–Upper Triassic, ?Lower Jurassic.*

Sinucosta DAGYS, 1963, p. 104 [**Spirifer emmrichi* SUESS, 1854, p. 52; OD] [?=*Guseriplia* DAGYS, 1963, p. 107 (type, *G. multicostata,* OD)]. Small; outline subovate; cardinal extremities rounded, hinge line narrow; unequally biconvex, ventral valve strongly inflated, subconical; ventral interarea high, concave, smooth; fold and sulcus very weakly developed, poorly differentiated; entire surface multicostate, ribs numerous, mostly simple; microornament of densely spaced, short spinules; dental adminicula short; median septum long, high, with anterior process; cardinalia sessile with nearly vertical, short dorsal adminicula; jugum complete, flattened, fimbriate. *Middle Triassic–Upper Triassic, ?Lower Jurassic:* Tethyan geosyncline.——FIG. 1291,*2a–g.* **S. emmrichi* (SUESS); *a–c,* dorsal, ventral, and lateral views, ×1 (new); *d–g,* transverse sections, approximately ×2 (Dagys, 1963).

Mentzeliopsis TRECHMANN, 1918, p. 229 [**M. spinosa;* OD]. Small to medium size; outline subovate; cardinal extremities rounded, hinge line less than maximum width; ventral interarea low, delthyrium open; fold and sulcus well delineated, moderately wide, rounded; lateral slopes with few weak to moderately strong, low, rounded plicae; growth varices strong, irregularly spaced, moderately lamellose; microornament of concentrically arranged, coarse, hollow spinules; dental adminicula stout, divergent, with strong median septum; jugum unknown. *Middle Triassic (Ladinian):* New Zealand.——FIG. 1291,*1a–e.* **M. spinosa; a–b,* dorsal and ventral valves; *c,* dorsal view of internal mold, ×1 (Trechmann, 1918); *d,* dorsal valve, ×1; *e,* ventral valve, ×0.75 (Marwick, 1953).

Qispiriferina XU & LIU, 1983b, p. 117 [**Q. subrotunda;* OD]. Medium size; outline subovate; subequally biconvex, moderately inflated; cardinal extremities well rounded, hinge line narrow; ventral beak incurved, interarea apsacline, delthyrium open; fold and sulcus weakly to moderately developed and delineated, smooth; sulcus shallow, bottom flattened; fold low, flattened; lateral slopes with

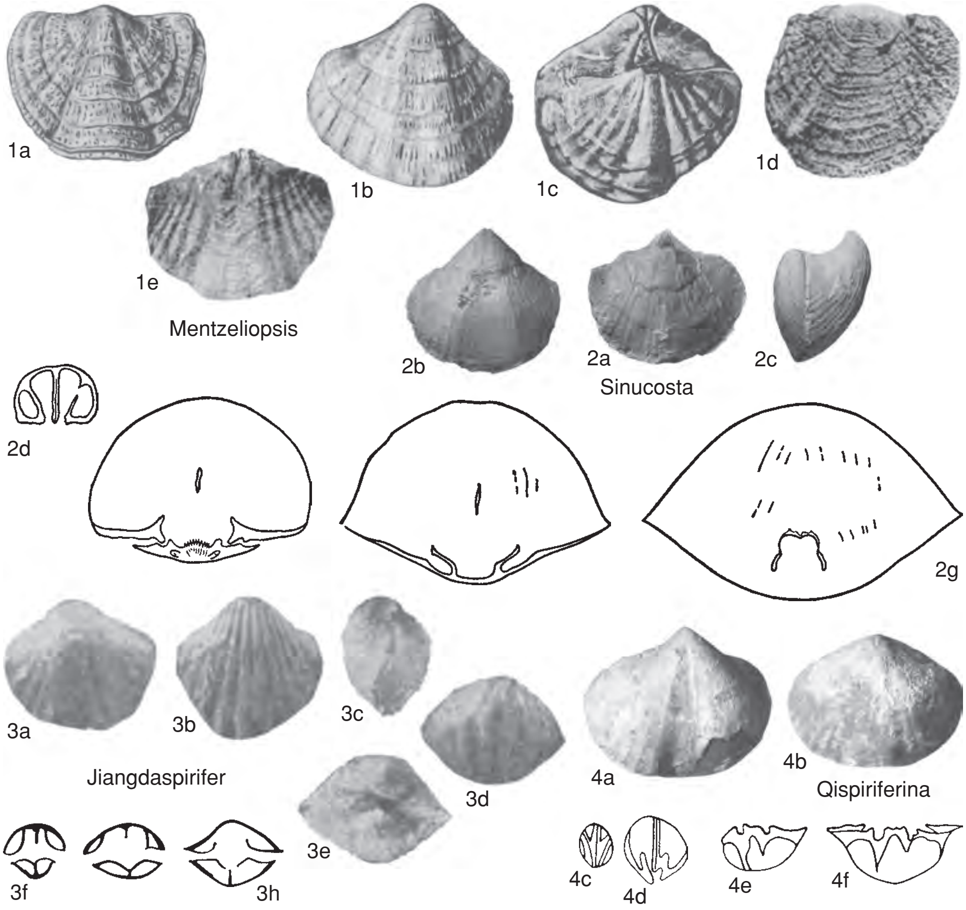

FIG. 1291. Sinucostidae (p. 1936–1937).

moderately numerous, weak, low, rounded costae; microornament unknown; dental adminicula very short with long, high median septum and short apical callus; cardinalia supported by thin callus, with variably developed short, vertical dorsal adminicula; jugum unknown. *Middle Triassic:* China (Qinghai).——FIG. 1291,*4a–f.* **Q. subrotunda; a–b,* syntypes, ventral and dorsal valves, ×1 (new); *c–f,* transverse sections, magnification unknown (Xu & Liu, 1983b).

Subfamily JIANGDASPIRIFERINAE Carter, 1994

[Jiangdaspiriferinae CARTER in CARTER & others, 1994, p. 371]

With dorsal median septum. *Upper Triassic.*

Jiangdaspirifer CHEN & others, 1986, p. 74 [**J. tongpuensis;* OD]. Very small, subovate, subequally biconvex; maximum width near midlength; maximum thickness attained slightly posterior to midlength; delthyrium open; hinge line short, interarea triangular; fold and sulcus weakly developed, sometimes indistinct; dental adminicula widely set, diverging, with long median septum; cardinal process indistinct; hinge plate complete, supported by thin, high median septum; spiralia with 3 to 4 whorls; jugum and microornament unknown. *Upper Triassic:* Tibet.——FIG. 1291,*3a–h.* **J. tongpuensis; a–e,* ventral, dorsal, lateral, anterior, and posterior views, ×4; *f–h,* three transverse sections, approximately ×1 (Chen & others, 1986).

THECIDEIDA

PETER G. BAKER

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Order THECIDEIDA Elliott, 1958

[*nom. transl.* WILLIAMS & others, 1996, p. 1,193, *ex* suborder Thecideidina ELLIOTT, 1965c, p. 858, *nom. correct. pro* Thecideoidea ELLIOTT, 1958, p. 373]

Small articulates, shell usually attached by cementation, without pedicle, rarely free, outline variable and irregular, cicatrix of variable size; valves hinged by unsupported cyrtomatodont teeth and sockets, permitting abnormally wide gape, usually smooth externally, commonly tuberculate internally; no obvious mantle canal markings or ovarian scars; ventral valve usually with well-developed, normally apsacline interarea with convex or flat pseudodeltidium, geniculation commonly sharp at anterior boundary of cicatrix, giving rise to well-developed, free ventral wall, 2 diductor muscle scars prominent, 2 median and 2 lateral, adductor muscle scars usually less conspicuous, sessile or raised hemispondylium commonly present, housing diductor and median adductor muscle scars; dorsal valve essentially lidlike, commonly with small, hypercline interarea with undifferentiated chilidium, square usually bilobed cardinal process, well-developed, inner socket ridges, crura usually converging and uniting to form bridge, subperipheral rim usually present and tuberculate, simple or divided median septum, or digitate, or exceptionally with spiralia, brachial lobes and lophophore grooves commonly present, lateral adductor muscle scars usually conspicuous; shell thick, sculptured internally by shell resorption, fibrous secondary shell forming a continuous lining in all early representatives, progressively replaced by granular shell in later representatives, usually with endopunctae. Mantle thin, outer mantle lobe with periostracal slot, without marginal setae in adult, spicules present or absent in mantle; lophophore thin, centripetal, schizolophous or ptycholophous (exceptionally trocholophous or spirolophous); muscles paired, not branching, muscle scars smooth. *Upper Triassic–Holocene.*

INTRODUCTION

The typical thecideide shell (Fig. 1292,*1–3*) is strongly ventribiconvex with clearly marked growth lines and a rectimarginate, anterior commissure. The ventral valve is characterized by a variably sized cicatrix of attachment and a well-developed, apsacline interarea with differentiated pseudodeltidium. The dorsal valve is essentially lidlike, commonly with a small interarea that is usually hypercline. Internally, the principal features of the ventral valve are unsupported cyrtomatodont teeth and sessile or raised hemispondylium (Fig. 1292,*4–5*). The dorsal valve (Fig. 1292,*6–9*) is characterized by a well-developed cardinal process, conspicuous, lateral, adductor muscle scars, subperiperal rim, and crura converging and uniting to form a bridge (or supporting exceptionally the spiralia in *Thecospira*) (Fig. 1292,*6*). Anteriorly, the mantle cavity is partitioned normally by a simple or divided median septum to form brachial cavities that house a schizolophous, ptycholophous, or exceptionally spirolophous lophophore. The lophophore is commonly confined to channels formed by the development of skeletal, brachial lobes. The brachial lobes are fragile and have considerable and often confusing variation in morphology resulting from both original form and damage due to transportation (Fig. 1292,*7–8*).

The full taxonomic potential of shell microstructure remains to be realized. The shell is thick, commonly tuberculate, and normally endopunctate. In most genera the shell microstructure differs in dorsal and ventral

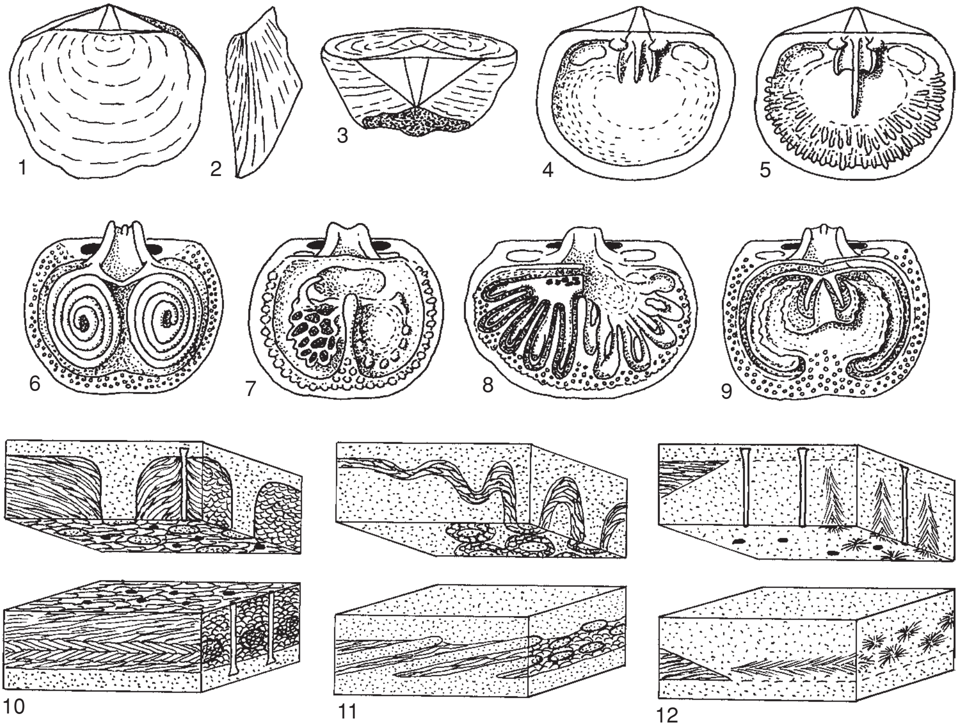

FIG. 1292,*1–12.* Various thecideide morphological and shell microstructural characters; *1–3,* dorsal, lateral, and posterior views of shell; *4–5,* ventral valve interiors showing *4,* sessile and *5,* raised hemispondylium; *6–9,* dorsal valve interiors showing *6,* crura supporting spiralium in *Thecospira; 7,* monoseptate condition with bridge and canopied brachial lobes, undamaged (left) and damaged (right) in *Eothecidellina; 8,* polyseptate condition with reticulum and undamaged brachial lobes interdigitating with septa (left) and typically preserved, damaged state (right) in *Thecidiopsis; 9,* ramulate condition with interdigitating brachial lobes in *Lacazella; 10–12,* block diagrams showing microstructure of dorsal and ventral valves; *10,* continuous lining of secondary shell, typical of Upper Triassic and Lower Jurassic genera; *11,* fibrous secondary shell partially suppressed but well represented in many Middle Jurassic to Lower Cretaceous genera; *12,* fibrous secondary shell sporadic in occurrence, almost completely replaced by granular calcite, typical of Upper Cretaceous to Holocene genera (new).

valves (Fig. 1292,*10–12*). Fibrous secondary shell formed a continuous lining in all early representatives of the group. Fibrous secondary shell was progressively replaced by granular cacite in all taxa from the Middle Jurassic to Early Cretaceous. By the Late Cretaceous fibrous secondary shell had been almost completely suppressed or reduced to vestigial patches associated with the hinge teeth and inner socket ridges. The changes proceeded at different rates and had been largely accomplished by the end of the Jurassic in the Lacazellinae and Thecideinae; but fibrous secondary shell layers persisted into the Early Cretaceous in the Moorellininae and to the end of the Cretaceous in the Thecidellininae.

Their small size, cemented habit, and strongly convergent, external morphological similarity have always posed problems for classification of thecideide brachiopods. The abnormally wide gape facilitates postmortem disarticulation of valves, and even limited transportation ensures the spatial separation of dorsal from attached ventral valves. Traditionally, therefore, classification relied heavily on the internal morphology of the more commonly available, separated dorsal valves (Fig. 1292,*6–9*) and, to a much lesser extent, on ventral valves (Fig. 1292,*4–5*).

Particular attention has always been paid to the lophophore skeletal supports preserved in the dorsal valve. Unfortunately, the brachial lobes almost always failed to survive transportation without damage but were described as diagnostic without reference to their damaged state. The confusion in thecideide taxonomy resulting from previous failure to differentiate between damaged and undamaged lophophore skeletal supports should not be underestimated. Diagnoses unsupported by evidence from sectioned, whole shells must always remain open to suspicion.

A number of studies, notably those of ELLIOTT (1948a, 1953a), BACKHAUS (1959), RUDWICK (1968), SMIRNOVA (1969a, 1984), WILLIAMS (1973), and BAKER (1990, 1991), enable us to establish the general course of evolution within the Thecideida, although major gaps in our knowledge of Early Triassic to Early Jurassic events remain. Because of their supposed neotenous origin, however, the sytematic position of thecideides has remained a matter of controversy, with the Terebratulida (ELLIOTT, 1965c), Spiriferida (WILLIAMS, 1973; BAKER, 1990) and Strophomenida (RUDWICK, 1968; BAKER, 1970a; PAJAUD, 1970; GRANT, 1972; DAGYS, 1972c; BENIGNI & FERLIGA, 1989) being favored as the main ordinal contenders. All the foregoing opinions were reviewed comprehensively by BAKER (1990, 1991). The assignment of the group to the Spiriferida derived from the more recent studies detailing comprehensively the morphology, ontogeny, and shell microstructure, which enabled us to see more clearly the general drift of genetic change within the group. Previous opinions regarding the systematic position of thecideides had focused too rigidly on the importance of cementation and the presence of a pseudodeltidium. The significance of cyrtomatodont teeth, fibrous secondary shell, and tubercles and the importance of shell resorption in sculpturing the broad configuration of lophophore supports had received too little consideration. The current assignment of ordinal status to the group (WILLIAMS & others, 1996) takes into account the recent understanding of the anatomy, molecular biology, shell morphology, ontogeny, and phylogeny of the phylum and avoids the difficulty of identifying which of the several widely recognized orders of spire bearers should contain thecideides included in a taxon of subordinal rank.

Recent investigations of thecideide origin have resurrected the historically favored idea of a terebratulide or strophomenate ancestor, but so far phylogenetic analyses using parsimony have failed to identify a sister group of the thecideides. This may be explained by the lack of fossils with the key morphological features preserved. Difficulties are exacerbated by the lack of a solid phylogenetic framework for the thecideides as a whole.

Molecular-sequence data using terebratulides (COHEN & GAWTHROP, 1997; COHEN, GAWTHROP, & CAVALIER-SMITH, 1998) tentatively identified thecideides as a sister group of the short-looped terebratulidines. Unfortunately, the results from 18S rDNA analysis failed to realize their early promise (B. L. COHEN, personal communication, in JAECKS, 2001, p. 243). Parsimony-based studies were conducted (JAECKS, 2001; JAECKS & CARLSON, 2001) using terebratulide, strophomenate, and spire-bearing outgroups. Although the outgroups used together or separately show thecideides to be consistently monophyletic, it has not proved possible to root specifically the thecideide tree. Most terebratulide-rooted trees have the Jurassic genus *Eudesella* basal and result in the stratigraphic inversion of many distal clades within the oldest members in derived positions. These problems together with doubt regarding the 18S rDNA analysis indicate that terebratulides and thecideides appear to share relatively little beyond fibrous shell structure and the possession of endopunctae. Endopunctae with perforated canopies, however, are characteristic of terebratulides throughout their geological history and also permeate the shells of thecideides and Jurassic spiriferinoids (MACKINNON, 1971), although being sporadically suppressed in some thecideides. It is considered that the cytological (as well as the microstructural) complexities of terebratulide and thecideide caeca and endopunctae rule out homoplasy. The coincidence of the uniqueness of character of endopunctae with perforated canopies suggests that terebratulides, thecideides, and some endopunctate spiriferides are monophyletic with a stem group of pre-Devonian age; and also that endopunctae with perforated canopies represent evidence of an ancestral link (WILLIAMS, 1973, 1997) between thecideides and spiriferides. Differences between strophomenate and spire-bearer rooted phylogenies are suprisingly minor and mainly infer differing synapomorphies. Choice of outgroup taxa seems to have relatively little effect on the first-order pattern of relationships, perhaps because these or any other outgroup taxa that might have been chosen share too few characters with the ingroup to afford them much power to polarize characters.

Parsimony-based phylogenies do, however, provide useful information regarding ingroup relationships and show that the general categorization of thecideides as paedomorphic is open to challenge. Although results support the traditional interpretation of decrease in body size and reduction or loss of fibrous secondary shell as paedomorphic patterns, other characters such as the evolution of more complex brachidia from smaller, more simple forms may be regarded as an example of peramorphosis. Typically thecideide characters such as the dorsal median septum do not appear with the origins of the Thecideida but appear later in its evolution. A narrow, bladelike septum (thecidelliniform) is broadly paraphyletic, but trees where it is paraphyletic with respect to the Thecideidae (lacazelliform) imply a large stratigraphic gap, although lacazelliform and thecidelliniform morphotypes have coexisted since the Jurassic.

Unweighted cladograms reveal clearly a complex mosaic of different evolutionary processes affecting thecideides since their appearance but unfortunately reveal little about their origin, possibly because early thecideides and their ancestors share too few characters to make the link possible. In the absence of a clear pointer from the evolution of thecideide shell fabric, basic shell microstructure again emerges as a critical factor. In all cladistic analyses, species nearest the root all retain a full complement of fibrous secondary shell, inferring that this represented the thecideide ancestral state and that the reduction or loss of the secondary layer is a derived feature. A comprehensive review of shell microstructure (WILLIAMS, 1997) clearly establishes the structural and functional differences between the pseudopunctae of strophomenides and the endopunctae of thecideides and also the essential differences between strophomenide and thecideide shell fabrics. Spiral arc growth patterns and the orthodox stacking (WILLIAMS, 1968a, 1968b; BAKER, 1970a) of calcitic fibers of fibrous secondary shell so characteristic of terebratulides, spire-bearing brachiopods, and early Mesozoic thecideides contrast sharply with the laminar secondary fabric of strophomenides in which the basic building blocks of laminae are sets of lath or blade-shaped crystallites contiguously aligned with their lateral junctions in various stages of amalgamation. Traces of blade sets may be disposed at acute angles to one another in successive laminae to form a cross-bladed fabric. Even so far as fibrous-shelled strophomenide plectambonitoids such as *Aegiromena* are concerned, the orthodoxly stacked fibers dominating the outer secondary shell fabric soon give way to an inner layer composed of lathlike fibers with their edges commonly overlapping in a way very similar to the Silurian chonetidine laminar sheet precursor (BRUNTON, 1972). In addition their wide geochronological separation offers little reassurance of the probability of a link between the shell microstructure of plectambonitoids and thecideides. In any event, forms such as *Aegiromena* indicate a progression toward laminar shell rather than progression toward the granular calcite shell seen in thecideides.

Pseudopunctae are an unmistakable feature of the strophomenide shell and resemble superficially thecideide tubercles, probably because both are initiated by a similar sort of spiral dislocation, i.e., spirally arranged laminae (or fibers) around a cylindroid core in the former and rosettes of spirally arranged fibers around a cylindroid core in the latter. A pseudopuncta typically appears as an anteriorly inclined trail of cone-in-cone deflections affecting the entire secondary laminar (or fibrous in plectambonitoids) fabric and emerging on the internal surface of the valve as a tubercle.

In early strophomenoids the rosettes of conically disposed laminae form a concentric layering around a core of solid calcite or of tilted fragments of discrete laminar sets (WILLIAMS & BRUNTON, 1993). In many other strophomenoids and especially in plectambonitoids, the pseudopunctae have a distinctive rod of calcite (taleola) with a calcified surface patina that sharply separates it from the surrounding laminae. Contrary to earlier belief, the taleola is not composed of crystalline calcite as etched taleolae are found to have a porous fabric permeating the entire structure.

Tubercle cores in thecideides and denticles in spiriferides are composed of granular calcite and are continguous with the granular primary layer. They may be considered to have arisen from small clusters of epithelial cells that continued to secrete (primary) granular calcite. Tubercles originate near the outer boundary of the subperipheral rim and deflect adjacent fibrous shell material. As the shell increases in size they are truncated by shell resorption and buried beneath subsequently deposited shell. Although it is probable that strophomenide pseudopunctae lacking taleolae originated on a thin, granular primary layer, pseudopunctae with taleolar cores show the taleola base resting unconformably on laminar shell (or fibrous in plectambonitoids; WILLIAMS & BRUNTON, 1993). As strophomenates lack the ability to resorb shell, taleolae are never truncated and continue to penetrate laminae as internal tubercles until they are overdraped by subsequently deposited laminae. As yet no thecideide with tubercle cores composed of perforated calcite has been discovered. Thus although the morphological expression of tubercles and taleolae is similar, tubercles are structurally and functionally different from psuedopunctae.

From the point of view of structure, location, and capacity for resorption, the internal tubercles of terebratelloid kraussinids and megathyrids are arguably homologous with those of thecideide thecospiroids (SMIRNOVA & POPIEL-BARCZYK, 1991). If the physiological implication is considered, thecideide tubercles and spire-bearer denticles are genetically much more similar to each other than either are to strophomenate taleolae. Leaving aside differences in shell microstructure and the fact that the secretory processes involved in the formation of tubercles and taleolae are fundamentally different, the actual fabrication of the whole shell needs to be considered. The strophomenate shell is fashioned principally by the process of accretion (as exemplified by the deltidiodont teeth). In thecideides, in addition to the sculpturing of cyrtomatodont teeth, the physiological processes involved in the simultaneous accretion and resorption of large tracts of shell in maintaining the relative position of the subperipheral rim during enlargement of the brachial cavities, the configuration of the brachial lobes, and the development and relative displacement of lateral septa must have been complex.

Identical processes appear to have operated in the fabrication of the shell and spiralia of spire-bearers. The main differences between strophomenates, thecideides, and spire-bearers therefore appear to lie in the basic shell microstructure pattern and the fabrication of the shell itself. The precisely controlled accretion-resorption regime operative during the fashioning of the thecideide and spire-bearer shells must be regarded as being far more sophisticated than the simple accretion regime adopted by strophomenates. Admittedly the mechanism and genetics of shell resorption remain unknown, but added to the established differences in shell microstructure, the complex physiological processes involved in fashioning their shells surely places thecideides closer to a cyrtomatodont fibrous-shelled spire-bearer than to a strophomenate ancestor.

Enallothecidea remains problematical as it tends to root with the rhynchonellate outgroups, and its inclusion in analyses affects the rooting position of *Thecospira.* Its exclusion is equally problematical because although trees are stabilized with *Thecospira* returned to a basal position, its removal to a rhynchonellate outgroup jeopardizes the view that cementation is diagnostic (GRANT, 1972) of strophomenates. *Enallothecidea* may be important as a link with the thecideide ancestor as current research shows that very early juvenile thecideides also lacked a median septum, and the subperipheral rim was initially confined to posterolateral sectors of the dorsal valve, indicating that *Enallothecidea* is probably paedomorphic (neotenous).

It may be concluded that the complex of contemporaneous paedomorphic and peramorphic patterns, complicated by homoplasy and heterotopy, which parsimony-based analyses reveal, must include a number of environmentally induced and geographically sustainable adaptations. Thecideides are possibly not an appropriate experimental group since, without doubt, niche constraints result in a high level of homoplasy both in contemporaneously associated and geographically isolated but stratigraphically concurrent populations. The addition of data on new genera will increase the coherence of ingroup evolutionary patterns.

In addition, new data on early ontogeny may result in a clearer picture of thecideide origin. It may be possible eventually to test the hypothesis that the emergence of thecideides resulted from a catastrophic late Permian or Early Triassic event during which a population (of juveniles) survived in a protected (cryptic) niche to subsequently evolve paedomorphically into a form that bore little resemblance to their adult ancestors. In any event, the paucity of our knowledge of the number of early thecideide representatives and the almost complete absence of information regarding their early ontogeny, together with, at best, a hazy recognition of diagnostic ancestral characters, means that establishing a link between Thecideida and its sister group remains a distant prospect.

THECOSPIROIDEA

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Superfamily THECOSPIROIDEA Bittner, 1890

[*nom. transl.* DAGYS, 1972c, p. 96, *ex* Thecospiridae BITTNER, 1890, p. 310]

Shell smooth, less frequently pustulose, cemented by ventral umbo, cicatrix relatively large; ventral interarea variably developed, variably inclined, commonly with undifferentiated pseudodeltidium; dorsal interarea not develped or vestigial, hemispondylium rarely developed, subperipheral rim thickened and commonly tuberculate, crura variably developed, median septum variably developed; lophophore supported by calcareous brachidia of variable structure, brachial lobes not developed, lophophore grooves present exceptionally, lateral adductor muscle scars not developed; fibrous secondary shell continuous or well represented in both valves. *Upper Triassic.*

Family THECOSPIRIDAE Bittner, 1890

[Thecospiridae BITTNER, 1890, p. 310]

Shell commonly with traces of pustulose ornament; ventral interarea moderate, orthocline to apsacline; pseudodeltidium undifferentiated; dorsal valve initially weakly convex, later shallowly concave; dorsal interarea vestigial, hypercline; ventral muscle scars small, separated by low myophragm; cardinal process high, functionally bilobed but united medianly to form tripartite structure; inner socket ridges recurved; subperipheral rim tuberculate; well-demarcated adductor muscle field divided by poorly developed, median septum; crura short, supporting a pair of spirally coiled, calcareous ribbons directed ventrolaterally, brachial ribbons sharply folded throughout length to give asymmetrically U-shaped cross section; commonly impunctate; fibrous secondary shell forming continuous lining in both valves; lophophore spirolophous. *Upper Triassic.*

Thecospira ZUGMAYER, 1880, p. 152 [**Thecidea haidingeri* SUESS, 1854, p. 43; OD] [=*Thecospiropsis* DAGYS, 1974, p. 75 (type, *Thecospira semseyi* BITTNER, 1912, p. 41)]. Outline transversely elliptical, pseudodeltidium usually precisely flush with interarea, ornament in form of small, tear-shaped pustules with faint traces of radial costellae commonly present on well-preserved specimens; subperipheral rim strongly thickened, spicules possibly associated with spiralia. [*Thecospiropsis* is morphologically inseparable from *Thecospira,* its separation being based solely on the absence of endopunctae in *Thecospiropsis* ("only pseudopunctate forms" of DAGYS, 1974, p. 75). In view of the known variation in the distribution of endopunctae in other thecideidine genera and the uncertainty regarding their occurrence in *Thecospira* species (BENIGNI & FERLIGA, 1989), it is considered that separation is unjustified. *Thecospiropsis* is therefore considered to be a synonym of *Thecospira.*] *Upper Triassic:* Europe.——FIG. 1293,*1a–f.* **T. haidingeri* (SUESS); *a–d,* dorsal, ventral, lateral, posterior views, Rhaetian, Kitsberg, Austria, ×3; *e,* oblique posterior view of spiral brachidium exposed by grinding and polishing, showing crus (*c*) and jugum (*j*), Rhaetian, Kitsberg, Austria, ×4.5 (Rudwick, 1968); *f,* dorsal valve interior, Carnian, Cortina D'Ampezzo, Italy, ×4 (Benigni & Ferliga, 1989).——FIG. 1293,*1g. T. tenuistriata* BITTNER, Carnian, Cortina D'Ampezzo, Italy; ventral valve interior, ×5 (Benigni & Ferliga, 1989).——FIG. 1293,*1h–i. T. semseyi* BITTNER, Carnian, Vesprem, Hungary; *h,* dorsal view of ventral valve showing detached spiral brachidium, ×4; *i,* possible spicules associated with brachidium, ×8 (Dagys, 1974).——FIG. 1293,*1j–p. T. tyrolensis* (LORETZ), Carnian, Cortina D'Ampezzo, Italy; serial transverse sections through posterior part of shell, 0.5, 1.05, 2.1, 3.4, 4.6, 6.6, 7.2 mm from umbo, ×7 (adapted from Benigni & Ferliga, 1989).

Family THECOSPIRELLIDAE Dagys, 1972

[Thecospirellidae DAGYS, 1972c, p. 97]

Shell markedly inequivalve; ventral valve very deep, pseudodeltidium convex, with ventral median septum extended posterodorsally to unite with pseudodeltidium; dorsal valve flattened or concave,

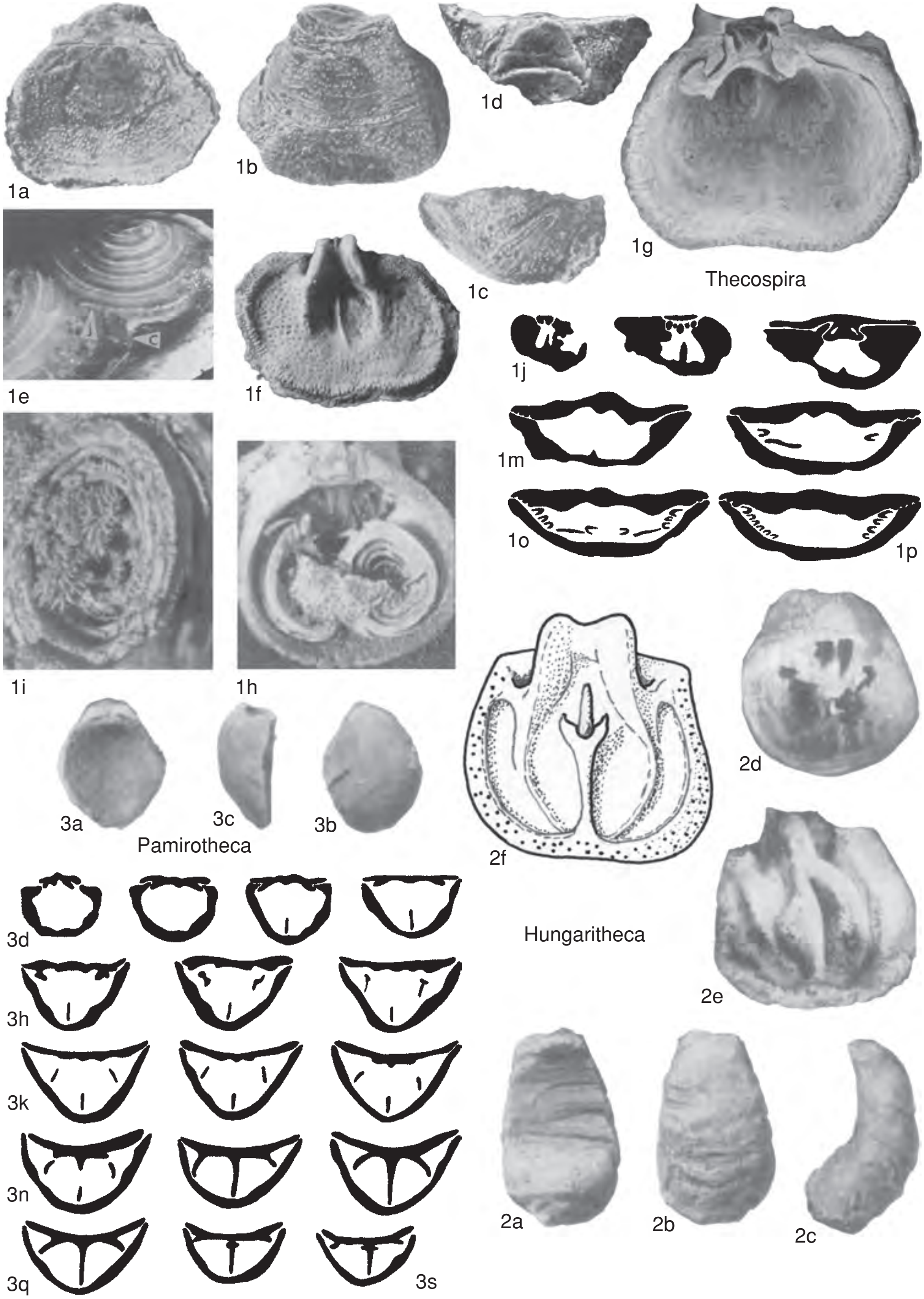

FIG. 1293. Thecospiridae and Hungarithecidae (p. 1944–1947).

without interarea, socket ridges short, subperipheral rim commonly with scalloped ornament, median septum low and divided, and relatively complex brachidium consisting essentially of pair of double, slightly divergent, slender, hamate structures connected by jugum and directed posteroventrally over body cavity; endopunctate; lophophore probably ptycholophous. *Upper Triassic.*

Thecospirella Bittner, 1912, p. 46 [**T. loczyi;* OD]. Shell elongate-pyriform, relatively small; ventral valve commonly with shallow, anterior sulcus; subperipheral rim with scalloped ornament; brachial apparatus consisting of pair of anterolaterally placed septa arising from subperipheral rim and of short, completely bifurcated, median septum (from walls of which hamate structures arise); regularly endopunctate. [Previous citations of *Thecospirella* as 1900 are erroneous. The 1912 citation is the first mention by Bittner of the genus.] *Upper Triassic (Carnian):* southern Alps, Hungary.——Fig. 1294,*1a–v.* **T. loczyi,* Vesprem, Hungary; *a–c,* dorsal, lateral views, ventral valve interior, ×5; *d,* lateral view of breached shell, showing partially preserved, brachial apparatus, ×6; *e,* young dorsal valve interior, showing partially preserved, brachial apparatus, ×10 (Dagys, 1974); *f,* dorsal valve interior, reconstruction, ×9 (adapted from Dagys, 1972c); *g–v,* serial transverse sections, 0.2, 0.6, 0.9, 1.2, 1.3, 1.5, 1.9, 2.1, 2.3, 2.6, 2.8, 2.9, 3.1, 3.4, 3.5, 3.6 mm from umbo, ×5 (adapted from Dagys, 1974).

Bittnerella Dagys, 1974, p. 77 [**B. bittneri;* OD]. Larger than *Thecospirella;* ventral valve almost conical without anterior sulcus, almost catacline interarea and pseudodeltidium clearly differentiated; brachial apparatus delicate without anterolateral elements, brachial supports arising from short, posteriorly bifurcating, median septum; endopunctae extensively branching. *Upper Triassic:* southern Alps, Hungary, Pamir.——Fig. 1294, *2a–q.* **B. bittneri,* Carnian, Shindy Gorge, Pamir; *a–d,* dorsal, anterior, lateral, posterior views, ×3 (Dagys, 1974); *e–q,* serial horizontal sections, 1.4, 1.7, 1.8, 2.1, 2.4, 2.6, 2.8, 2.9, 3.1, 3.2, 3.4, 3.6, 3.8 mm from origin, ×3.5 (adapted from Dagys, 1974).

Family HUNGARITHECIDAE
Dagys, 1972

[Hungarithecidae Dagys, 1972c, p. 97]

Shell inequivalve, ventral interarea and pseudodeltidium variable; ventral valve without median septum; dorsal valve normally without interarea, cardinal process relatively massive, brachidium consisting of possible crural plates of different height, fully or partly joined to floor of valve, extending from inner socket ridges and merging at anterior margin with high, median septum; endopunctate; lophophore probably schizolophous. *Upper Triassic (Carnian).*

Subfamily HUNGARITHECINAE
Dagys, 1972

[*nom. transl.* Dagys, 1974, p. 80, *pro* Hungarithecidae Dagys, 1972c, p. 97]

Shells ventribiconvex, ventral interarea high, pseudodeltidium flush with surface; structure resembling sessile hemispondylium present; brachidium in form of low plates united with valve floor for their entire length; possibly endopunctate; shell microstructure unknown. *Upper Triassic (Carnian).*

Hungaritheca Dagys, 1972c, p. 97 [**Thecospira andreaei* Bittner, 1912, p. 44; OD]. Elongate with hinge line approximately equal to maximum width; ventral valve strongly convex with relatively small cicatrix, ventral muscle field on platform slightly elevated anteriorly and divided by septal ridge; dorsal valve moderately convex, with low structure resembling interarea, median septum high, sometimes bifurcating along posterior, ventral edge, subperipheral rim ornamented by pits thought to represent endopunctae. *Upper Triassic (Carnian):* Hungary.——Fig. 1293,*2a–f.* **H. andreaei* (Bittner), Vesprem; *a–c,* dorsal, ventral, lateral views, ×3; *d–e,* ventral valve, dorsal valve interiors, ×4 (Dagys, 1974); *f,* dorsal valve interior, reconstruction, ×5 (adapted from Dagys, 1972c).

Subfamily PAMIROTHECINAE
Dagys, 1974

[Pamirothecinae Dagys, 1974, p. 79]

Shells concavoconvex, ventral interarea low, pseudodeltidium obscured, cicatrix strongly developed; brachidium in form of high, subhorizontal plates free posteriorly but coalescing with floor of valve anteriorly; endopunctate; fibrous secondary shell well represented in both valves. *Upper Triassic (Norian–Rhaetian).*

Pamirotheca Dagys, 1974, p. 79 [**P. aulacothyridiformis;* OD]. Shell elongately oval; ventral valve moderately convex; dorsal valve uniformly concave,

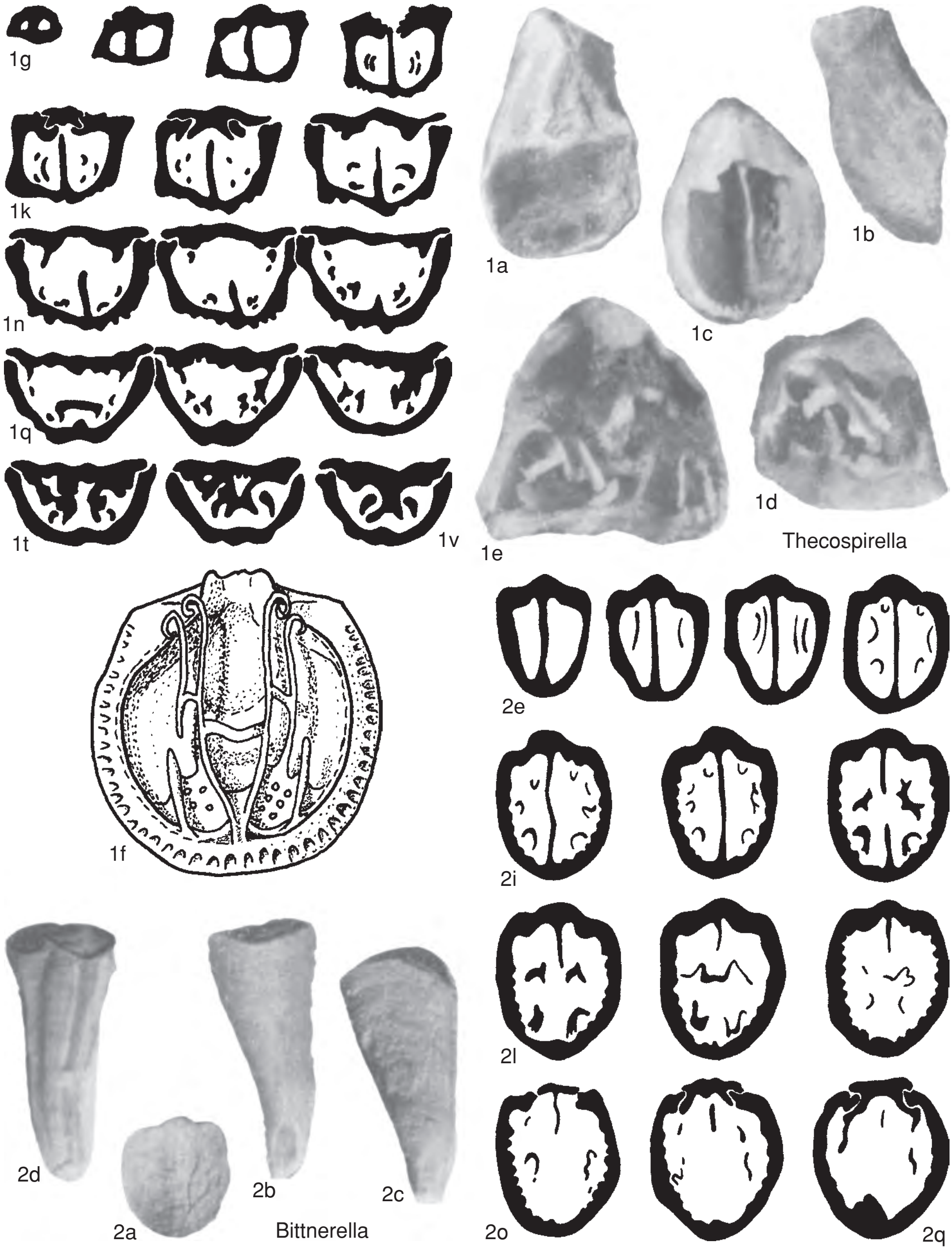

FIG. 1294. Thecospirellidae (p. 1946).

median septum very high, posteriorly free. *Upper Triassic (Norian–Rhaetian):* Pamir.——FIG. 1293,*3a–s.* **P. aulacothyridiformis; a–c,* dorsal, ventral, lateral views, ×3 (Dagys, 1974); *d–s,* serial transverse sections, 0.4, 0.55, 0.65, 0.75, 0.95, 1.15, 1.45, 1.65, 1.85, 2.25, 2.65, 3.15, 3.55, 4.15, 5.15, 5.55 mm from umbo, ×4 (adapted from Dagys, 1974).

THECIDEOIDEA

PETER G. BAKER

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Superfamily THECIDEOIDEA Gray, 1840

[*nom. transl.* TERMIER & TERMIER, 1949b, p. 59, *ex* Thecideidae GRAY, 1840, p. 151]

Typically smooth, ventribiconvex shells, ventral interarea normally well developed, normally apsacline with pseudodeltidium normally well differentiated, usually tuberculate internally; hemispondylium normally present, variably developed; dorsal valve normally weakly convex, dorsal interarea variably developed, sockets defined by pair of prominent inner socket ridges fused medially with undifferentiated wedge of shell material to form bilobed cardinal process, complete bridge over dorsal body cavity, absent exceptionally, median septum simple or divided or exceptionally lacking, with or without lateral septa extending from anterior margin to terminate posteriorly, brachial lobes and lophophore grooves usually present, lateral adductor muscle scars normally conspicuous; usually endopunctate; fibrous secondary shell forming continuous lining in Triassic and Lower Jurassic representatives, or rarely in Middle to Upper Jurassic representatives; lophophore schizolophous or ptycholophous or exceptionally trocholophous; marsupium present in some species. *Upper Triassic–Holocene.*

Family ENALLOTHECIDEIDAE Baker, 1983

[*nom. transl.* BAKER, herein, *ex* Enallothecideinae BAKER, 1983, p. 664]

Minute shells, strongly ventribiconvex, pyriform, with small, apical cicatrix, ventral interarea orthocline to anacline; interior undivided, without tubercles, ventral valve without hemispondylium; dorsal valve without interarea, crura, median septum, brachial lobes, or lophophore grooves, lateral adductor muscle scars inconspicuous; endopunctate; fibrous secondary shell continuous in both valves; lophophore probably trocholophous. *Middle Jurassic (upper Aalenian)–Upper Jurassic (middle Oxfordian).*

Enallothecidea BAKER, 1983, p. 664 [**Thecideum pygmaeum* MOORE, 1861, p. 96; OD]. Ventral valve with characteristic, ladle-shaped, lateral profile, cicatrix tuberose, ventral interarea poorly defined, pseudodeltidium small, not completely closing delthyrium anteriorly; subperipheral rim incomplete, confined to lateral and posterolateral regions of dorsal valve; densely endopunctate. *Middle Jurassic (upper Aalenian)–Upper Jurassic (middle Oxfordian):* southern England, *upper Aalenian.*——FIG. 1295*a–e.* **E. pygmaea* (MOORE), upper Aalenian, Cotswolds; *a–c,* dorsal, anterior, lateral views; *d–e,* dorsal valve, ventral valve interiors, ×50 (Baker, 1983).

Family THECIDELLINIDAE Elliott, 1958

[Thecidellinidae ELLIOTT, 1958, p. 373]

Small, monoseptate forms, ventral interarea apsacline, pseudodeltidum rarely convex, usually internally tuberculate, dorsal mantle cavity bilobed, arising from development of simple, bladelike median septum, persistent throughout ontogeny, brachial lobes with or without intrabrachial cavities; usually endopunctate; fibrous secondary shell usually forming continuous lining in Middle to Upper Jurassic representatives, well represented to heavily suppressed but present in both valves from Lower Cretaceous to Holocene; lophophore schizolophous; spicules present in mantle of some species. *Upper Triassic–Holocene.*

Subfamily THECIDELLININAE Elliott, 1953

[Thecidellininae ELLIOTT, 1953a, p. 700]

Ventral interarea anacline exceptionally; dorsal interarea absent exceptionally, tuberculate forms with brachial lobe skeletal elements arising from base of dorsal median septum and floor of valve usually anastomosing to form canopies over intrabrachial cavi-

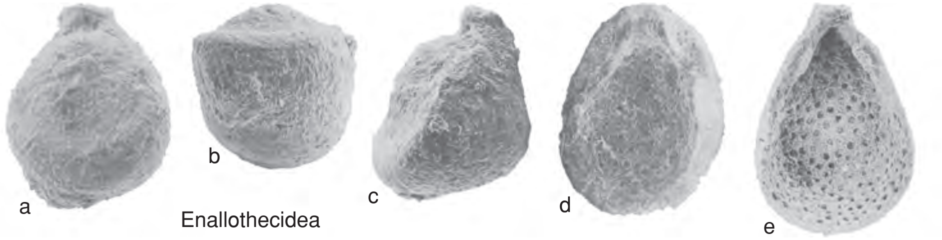

FIG. 1295. Enallothecideidae (p. 1948).

ties, brachial lobes exceptionally extended posteriorly as reticulum overarching body cavity; impunctate exceptionally. *Middle Jurassic (upper Bathonian)–Holocene.*

Thecidellina THOMSON, 1915d, p. 462 [**Thecidium barretti* DAVIDSON, 1864, p. 17; OD] [=*Thecidellella* HAYASAKA, 1938, p. 9 (type, *T. japonica*)]. Ventral interarea clearly developed with poorly differentiated pseudodeltidium, hemispondylium U-shaped sessile or raised without supporting septum; dorsal valve with wide, peripheral flange, long, relatively thick, median septum arching over body cavity, almost reaching bridge, bridge with posteriorly directed spur reaching base of cardinal process, brachial lobes elongate with brachial ridges secondarily elaborated by spiny processess that may anastomose to form canopies, fragile reticulum present, lophophore muscle scars present; fibrous secondary shell heavily suppressed in both valves with acicular crystallite tracts present; spicules present. [*Thecidellella* resembles *Thecidellina* except for the accessory shelly structure ("reversed spondylium" of HAYASAKA, 1938, p. 10) between the bridge and posterior end of the median septum in the dorsal valve. The distinction is slight and the structure also occurs in *Thecidellina* spp. (COOPER, 1954a); *Thecidellella* therefore is considered to be a synonym of *Thecidellina.*] *Paleogene (Eocene)–Holocene:* Alabama, *Eocene;* West Indies, southeastern North Atlantic (Cape Verde Islands), *Holocene;* Pacific Ocean, Indian Ocean, *Miocene–Holocene.*——FIG. 1296,*2a–h. *T. barretti* (DAVIDSON), Holocene, off Rio Bueno, north-central Jamaica; *a–c,* dorsal, anterior, lateral views; *d,* hypotype, posterior view, USNM 461945, ×10 (new); *e,* dorsal valve interior; *f,* dorsal valve anterior view; *g,* dorsal valve profile, lateral view; *h,* hypotype, dorsal valve, oblique posterior view, USNM 461946, ×10 (new).——FIG. 1296,*2i–j. T. blochmanni* (DALL), Holocene, Christmas Island; *i,* ventral valve interior; *j,* hypotype, ventral valve interior showing hemispondylium, BMNH BD9139, ×15 (new).

Bifolium ELLIOTT, 1948a, p. 2 [**Thecidium faringdonense* DAVIDSON, 1874, p. 23; OD]. Pyriform with small cicatrix, ventral interarea indistinct and curved laterally, pseudodeltidium weakly convex and flush with interarea, hinge line very short, hemispondylium sessile, formed from low median ridge flanked by parallel pair of higher lateral ridges; dorsal valve moderately convex without interarea, relatively strongly thickened, lateral adductor muscle scars constricted by root of prostrate, relatively massive cardinal process, bridge with posteriorly directed spur, females with marsupial notch, brachial ridges almost circular, brachial lobe skeletal elements forming loosely reticulate canopies; fibrous secondary shell strongly suppressed in both valves, acicular crystallite tracts present in dorsal valve. [Endopunctae, with scattered distribution, occur in juvenile dorsal valves only; adult shells are apparently impunctate.] *Lower Cretaceous (Hauterivian–upper Aptian):* southwestern Asia, *Hauterivian;* Europe, *upper Aptian.*——FIG. 1297,*2a–t. *B. faringdonense* (DAVIDSON), upper Aptian, Faringdon, southern England; *a,* dorsal view; *b,* oblique anterior view; *c,* oblique lateral view; *d,* posterior view; *e,* dorsal valve interior, ×13 (Baker, 1991); *f,* dorsal valve posterior view; *g,* hypotype, dorsal valve interior showing typical state of brachial lobe preservation, BMNH BD9134; *h,* ventral valve interior, ×13; *i,* hypotype, ventral valve interior showing profile view of hemispondylium, BMNH BD9135, ×25; *j–t,* serial horizontal sections showing morphology of brachial lobes, 0.375, 0.425, 0.475, 0.5, 0.55, 0.6, 0.625, 0.675, 0.7, 0.725, 0.75 mm from free ventral wall, ×9 (new).

Eothecidellina BAKER, 1991, p. 816 [**Thecidiopsis (Thecidiopsis) bohemica imperfecta* NEKVASILOVÁ, 1967, p. 115; OD]. Roughly pyriform with shallow, ventral, anterior sulcus, cicatrix rounded triangular, relatively large, free ventral wall well developed, giving characteristic triangular lateral profile, ventral interarea anacline to apsacline, well defined with flat pseudodeltidium; dorsal valve with interarea, cardinal process with pronounced dorsal deflection, brachial lobes similar to *Bifolium* but canopy anterior perforations sealed by subsequent thickening, lophophore muscle scars present; fibrous secondary shell continuous in ventral valve, heavily suppressed in dorsal valve. [In *Eothecidellina,* as in *Bifolium,* the brachial lobes are invariably broken in separated valves so that intrabrachial cavities are exposed as two roughly oval depressions, characteristically ringed by damaged canopy skeletal

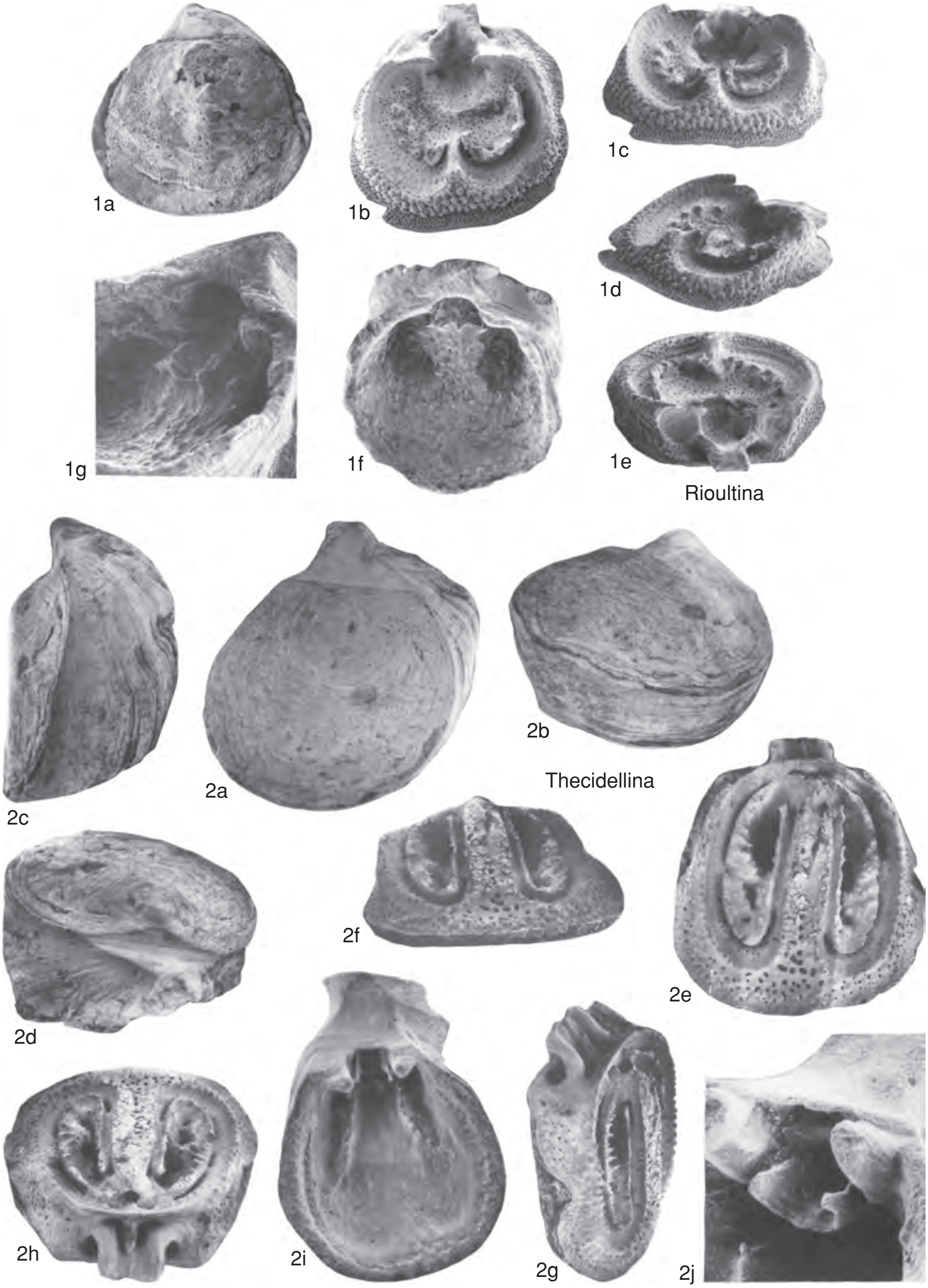

FIG. 1296. Thecidellinidae (p. 1949–1953).

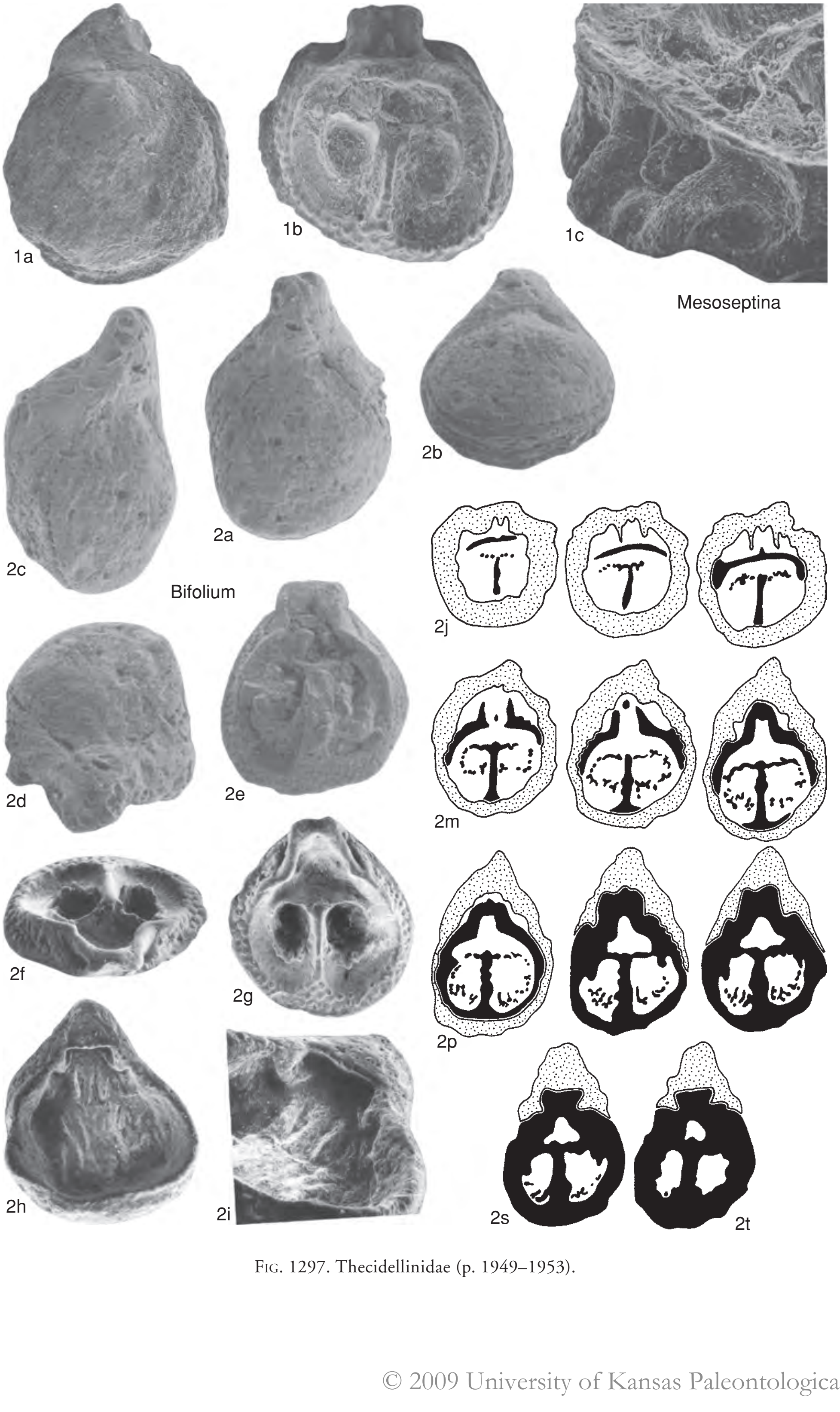

FIG. 1297. Thecidellinidae (p. 1949–1953).

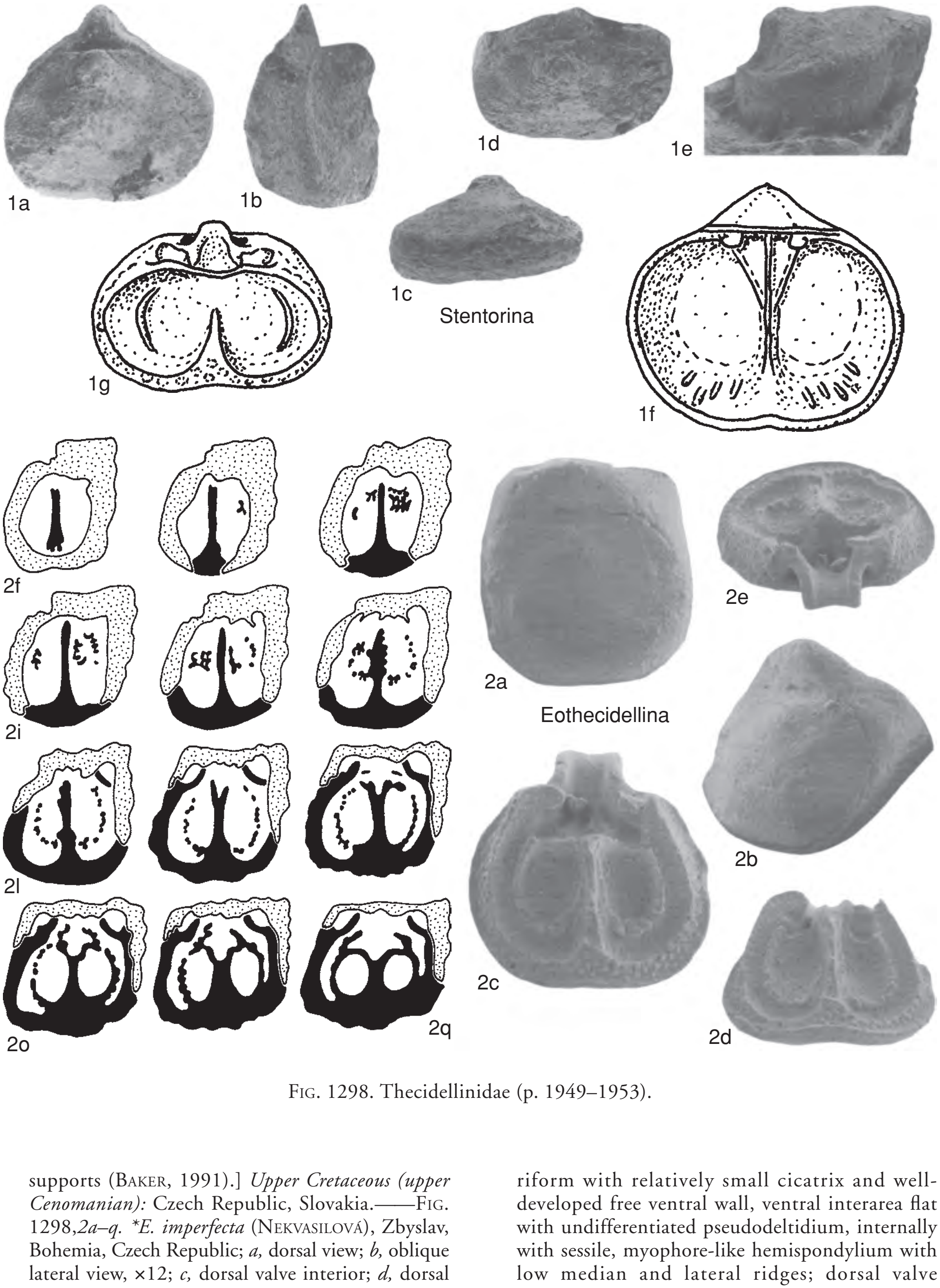

FIG. 1298. Thecidellinidae (p. 1949–1953).

supports (BAKER, 1991).] *Upper Cretaceous (upper Cenomanian):* Czech Republic, Slovakia.——FIG. 1298,*2a–q. *E. imperfecta* (NEKVASILOVÁ), Zbyslav, Bohemia, Czech Republic; *a,* dorsal view; *b,* oblique lateral view, ×12; *c,* dorsal valve interior; *d,* dorsal valve anterior view; *e,* dorsal valve posterior view, ×13 (Baker, 1991); *f–q,* serial horizontal sections showing morphology of brachial lobes, 0.18, 0.22, 0.26, 0.28, 0.32, 0.34, 0.38, 0.42, 0.46, 0.48, 0.52, 0.56 mm from free ventral wall, ×10 (new).

Mesoseptina MUÑOZ, 1994, p. 167 [**M. minima;* OD] [=*Midiseptina* MUÑOZ, 1989, *nom. nud.*]. Pyriform with relatively small cicatrix and well-developed free ventral wall, ventral interarea flat with undifferentiated pseudodeltidium, internally with sessile, myophore-like hemispondylium with low median and lateral ridges; dorsal valve subcircular with small, hypercline interarea exceptionally, cardinal process incipiently trilobed, bridge with well-developed, dorsal, posteriorly directed apophysis, brachial lobes superficially similar to *Bifolium* but ridgelike without tuberculate elaboration, intrabrachial cavities not developed or vestigial, anteriorly placed depressions exceptionally, lophophore muscle scars present; fibrous secondary shell heavily suppressed, restricted to inner socket ridges of dorsal valve, possibly endopunctate. *Upper Cretaceous (Santonian–lower Maastrichtian):* northeastern Spain, *Santonian.*——FIG. 1297,*1a–c.* **M. minima,* Santonian, Serra del Montsec, south central Pyrenees; *a,* dorsal view; *b,* dorsal valve interior, ×30; *c,* dorsal valve interior, oblique posterior view showing apophysis, ×60 (Muñoz, 1994).

Rioultina PAJAUD, 1966b, p. 631 [**Thecidea triangularis* D'ORBIGNY, 1847 in 1847–1851, p. 316; OD]. Small, rounded triangular, hinge line relatively short, ventral interarea clearly demarcated, flat, acutely triangular, pseudodeltidium undifferentiated, hemispondylium wide, sessile, relatively massive; dorsal valve subcircular, cardinal process relatively large, brachial lobes small, auriform, each consisting of ring of spiny, often connected processes with nearest being obliquely divergent from base of median septum; fibrous secondary shell continuous in both valves. *Middle Jurassic (upper Bathonian)–Upper Jurassic (upper Oxfordian):* England, France, Germany, *upper Bathonian.*——FIG. 1296,*1a–g.* **R. triangularis* (D'ORBIGNY), upper Bathonian, Luc-sur-Mer, Normandy, France; *a,* hypotype, dorsal view, BMNH BD9131, ×13 (new); *b,* dorsal valve interior; *c,* dorsal valve, oblique anterior view; *d,* dorsal valve, oblique lateral view; *e,* hypotype, dorsal valve, oblique posterior view, BMNH BD9132, ×13 (new); *f,* ventral valve interior; *g,* hypotype, ventral valve, oblique anterior view showing hemispondylium, BMNH BD9133, ×20 (new).

Stentorina BAKER & WILSON, 1999, p. 887 [**S. sagittata;* OD]. Small, hinge line relatively short, ventral interarea small, flat, poorly defined, pseudodeltidium indistinct, relatively large attachment scar, shallow anterior sulcus commonly developed; ventral valve with sessile hemispondylium with pronounced median ridge; dorsal valve with prominent umbo, cardinal process small, brachial lobes represented by low, curved ridges; fibrous secondary shell continuous in both valves. *Middle Jurassic (Bajocian or lower Bathonian):* USA (Utah).——FIG. 1298,*1a–g.* **S. sagittata,* Washington County, southwestern Utah, BMNH BD9372; *a–d,* dorsal, lateral, anterior, posterior views; *e,* holotype, three-quarters profile, lateral view, ×20 (Baker & Wilson, 1999); *f,* ventral valve interior, reconstruction; *g,* dorsal valve interior, reconstruction, ×20 (new).

Subfamily MOORELLININAE Pajaud, 1966

[Moorellininae PAJAUD, 1966a, p. 618]

Forms with ridgelike, lateral extensions from posterior end of dorsal median septum, usually with tuberculate, brachial lobes; endopunctate. *Upper Triassic–Lower Cretaceous.*

Moorellina ELLIOTT, 1953a, p. 693 [**Thecideum duplicatum* MOORE, 1854, p. 118; OD] [=*Elliottina* PAJAUD, 1963, p. 996 (type, *Thecidea deslongchampsii* DAVIDSON, 1852b, p. 258)]. Typically rounded triangular, cicatrix commonly triangular, geniculation producing low to high, free, ventral wall, ventral interarea flat, with pseudodeltidium flush with surface; dorsal valve typically with small, hypercline interarea, median septum relatively short with lateral ridges arranged in Y-shaped configuration, brachial lobes varying from incomplete arcuate lines to tuberculate ridges surrounding shallow, intrabrachial depressions; fibrous secondary shell continuous in both valves. [Distinction between *Elliottina* and *Moorellina* rests essentially on shape of ventral interarea, which does not merit taxonomic distinction.] *Upper Triassic–Middle Jurassic:* western Europe, *Middle Jurassic.*——FIG. 1299,*3a–e.* **M. duplicata* (MOORE), Cotswolds, southern England; *a,* dorsal valve interior, upper Aalenian; *b,* dorsal valve, oblique lateral view, upper Aalenian; *c,* hypotype, dorsal valve, oblique posterior view, upper Aalenian, BMNH BD9129, ×10; *d,* hypotype, juvenile dorsal valve interior, upper Aalenian, BMNH BD9130, ×25 (new); *e,* ventral valve interior, Bajocian, ×10 (Moore, 1854).

Bosquetella SMIRNOVA, 1969a, p. 83 [**Thecidium campichei* DE LORIOL in PICTET, 1872, p. 146; OD]. Elongately semioval, markedly ventribiconvex, cicatrix variable but never large, ventral interarea poorly developed with undifferentiated pseudodeltidium; dorsal valve without interarea, cardinal process with median protruberance giving incipiently trilobed appearance, brachial lobes in form of tuberculate ridges, asymmetrically pyriform with apices curving toward body cavity, median septum long with lateral ridges in T-shaped configuration; fibrous secondary shell partially suppressed in ventral valve, heavily suppressed in dorsal valve. *Lower Cretaceous:* Crimea, Switzerland.——FIG. 1299,*1a–d.* **B. campichei* (DE LORIOL); *a,* dorsal view, Valanginian, Crimea, ×10.5 (Smirnova, 1969a); *b,* dorsal valve interior, upper Valanginian, Auberson, Switzerland; *c,* dorsal valve, profile lateral view, upper Valanginian, Auberson, Switzerland; *d,* dorsal valve, posterior view, upper Valanginian, Auberson, Switzerland, ×9 (Baker, 1991).

Pachymoorellina BAKER, 1989a, p. 56 [**Thecideum bouchardii* MOORE, 1854, p. 116, *non* DAVIDSON, 1851; OD; =*Thecidea (Davidsonella) dundriensis* ROLLIER, 1915, p. 53]. Ventral interarea well developed, convex pseudodeltidium, relatively large cicatrix and conspicuously thickened, free, ventral wall, internally with deeply impressed, diductor muscle scars forming an inverted V; dorsal interarea not developed or vestigial, valve with fragile, very wide, peripheral flange usually not preserved and high, median septum separating brachial cavities devoid of brachial lobes, lateral ridges weakly developed, lophophore grooves shallow and indistinct; fibrous secondary shell strongly suppressed in both valves, acicular crystallite tracts well developed in ventral

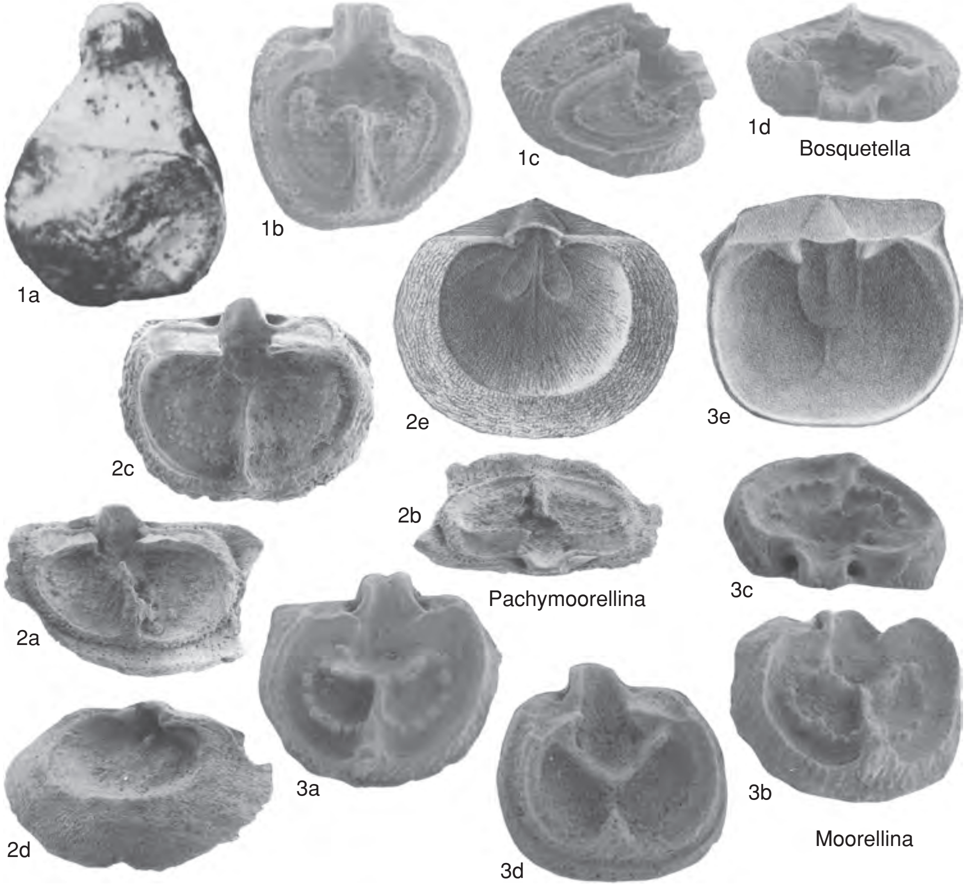

FIG. 1299. Thecidellinidae (p. 1953–1954).

valve. *Middle Jurassic (upper Aalenian–Bajocian):* southern England, *upper Aalenian.*——FIG. 1299,*2a–e.* **P. dundriensis* (ROLLIER), Cotswolds; *a–b,* dorsal valve interior, dorsal valve posterior view, upper Aalenian; *c,* dorsal valve showing typical destruction of peripheral flange, upper Aalenian, ×10; *d,* immature ventral valve profile, interior view, upper Aalenian, ×8.5 (Baker, 1989a); *e,* ventral valve interior, Bajocian, ×8 (Moore, 1854).

Family BACTRYNIIDAE Williams, 1965

[Bactryniidae WILLIAMS, 1965, p. 521]

Concavoconvex, elongate-oval shells attached by ventral apex, ventral interarea and pseudodeltidium variably developed, internally tuberculate; dorsal valve with small, indistinctly bilobed cardinal process, inner socket ridges low, defining shallow sockets, lateral adductor muscle scars present, other muscle impressions obscure, long, low, median septum divided by shallow sinus, dorsal mantle cavities occupied by pustulose brachial lobes; impunctate; fibrous secondary shell forming continuous lining in both valves; lophophore ptycholophous or incipiently ptycholophous. *Upper Triassic (Rhaetian)–Upper Jurassic (upper Oxfordian).*

Subfamily BACTRYNIINAE Williams, 1965

[*nom. transl.* BAKER, herein, *ex* Bactryniidae WILLIAMS, 1965, p. 521]

Dorsal valve with long, low, possibly catacline interarea, subperipheral rim with numerous pairs of weakly developed, lateral septa, dorsal mantle cavities shallow, brachial lobes interdigitating with lateral septa, brachidium digitate; lophophore ptycholophous. *Upper Triassic (Rhaetian).*

Bactrynium Emmrich, 1855, p. 449 [**B. bicarinatum;* OD] [=*Pterophloios* Gumbel, 1861, p. 411, obj.]. Ornamented by fine growth lines, hinge line approximately equal to maximum width of shell, ventral interarea obscure, possibly apsacline, pseudodeltidium obscure; dorsal valve longitudinally semioval with low, plane interarea, bridge possibly present, strongly thickened subperipheral rim with 8 to 10 pairs of lateral septa, median septum ridgelike, extending posteriorly over body cavity, septa complementary to lateral and long, median ridges in ventral valve. *Upper Triassic (Rhaetian):* Austria.——Fig. 1300,*1a–f.* **B. bicarinatum,* Kossener Schichten; *a,* dorsal valve interior; *b,* dorsal valve posterior view, ×3 (Williams, 1965); *c,* dorsal valve, lateral view, ×3; *d,* dorsal valve fragment, interior view showing pustulose brachial lobes; *e,* dorsal valve fragment, interior view showing lateral adductor muscle scar to left of cardinal process; *f,* posterior view of view *e,* ×6 (Rudwick, 1968).

Subfamily DAVIDSONELLINAE Pajaud, 1966

[Davidsonellinae Pajaud, 1966a, p. 618]

Dorsal interarea absent or vestigial, relatively broad median septum divided by an anterior sinus for much of its length; lophophore incipiently ptycholophous (extended schizolophe functionally equivalent to ptycholophe). *Upper Triassic (Rhaetian)–Upper Jurassic (upper Oxfordian).*

Davidsonella Munier-Chalmas, 1880, p. 279, *non* Waagen, 1885, *nec* Frederiks, 1926 [**Thecidea sinuata* Eudes-Deslongchamps, 1853, p. 242; OD]. Small, longitudinally subrectangular, emarginate, ventral interarea flat, almost orthocline, acutely triangular, pseudodeltidum convex, relatively large; ventral valve deep with relatively pronounced anterior sulcus continuous with well-defined, broad, median ridge, hemispondylium raised thickened and supported by lateral connections with valve wall; dorsal valve with small, prostrate cardinal process and anterior sulcus continuous with shallow sinus dividing median septum for almost entire length, brachial lobes may form fragile reticulum, lophophore grooves conspicuous. *Upper Triassic (Rhaetian)–Lower Jurassic (Toarcian):* Austria, *Rhaetian;* Wales, *Hettangian;* Normandy, southern England, *Toarcian.*——Fig. 1300,*3a–h.* **D. sinuata* (Eudes-Deslongchamps), Toarcian, May-sur-Orne, Normandy, France; *a,* dorsal view; *b,* hypotype, lateral view, BMNH BD9356, ×8; *c,* dorsal valve interior; *d,* dorsal valve anterior view; *e,* dorsal valve, oblique lateral view; *f,* hypotype, dorsal valve, oblique posterior view, BMNH BD9357, ×9; *g,* ventral valve interior; *h,* hypotype, ventral valve tilted showing hemispondylium, BMNH BD9358, ×12 (new).

Agerinella Patrulius in Pajaud & Patrulius, 1964, p. 582 [**A. lyrata* Patrulius in Pajaud & Patrulius, 1964, p. 583; OD]. Small; ventral valve with large cicatrix giving sharply triangular lateral profile, interarea reduced, pseudodeltidium undifferentiated, hemispondylium relatively massive, formed from 3 nearly touching columns united by transverse bar; dorsal valve subcircular with pronounced convexity at umbo, internal characters imperfectly known but brachial apparatus simple and apparently similar to *Davidsonella. Upper Jurassic (upper Oxfordian):* Romania.——Fig. 1300,*2a–c.* **A. lyrata,* Visterna Valley; *a,* dorsal view of damaged shell showing internal characters; *b,* drawing of *a; c,* drawing of frontal view of *a,* ×8 (Pajaud & Patrulius, 1964).

Family THECIDEIDAE Gray, 1840

[Thecideidae Gray, 1840, p. 151]

Small to larger forms, secondarily free exceptionally, ventral interarea normally not well defined, with clearly convex pseudodeltidium, dorsal interarea variably developed, usually tuberculate internally; in ontogeny brachial supports developing from thickened, triangular plate at anterior margin of dorsal valve, commonly leading to much divided brachial interiors, brachial lobes commonly with reticulum, intrabrachial cavities not developed; impunctate exceptionally; fibrous secondary shell normally suppressed, continuous lining in only Jurassic representatives, present or absent in one or both valves in Lower Cretaceous to Holocene representatives; lophophore ptycholophous. *Lower Jurassic–Holocene.*

Subfamily THECIDEINAE Gray, 1840

[Thecideinae Gray, 1840, p. 151]

Shell with costellate ornament exceptionally, rarely with ridged and grooved, internal ornament; polyseptate, without anterior sinus, median septum repeatedly divided during growth to form lateral septa or divided anterolaterally to form septules, commonly a combination of both; Jurassic forms digitate, usually without brachial lobes or lophophore

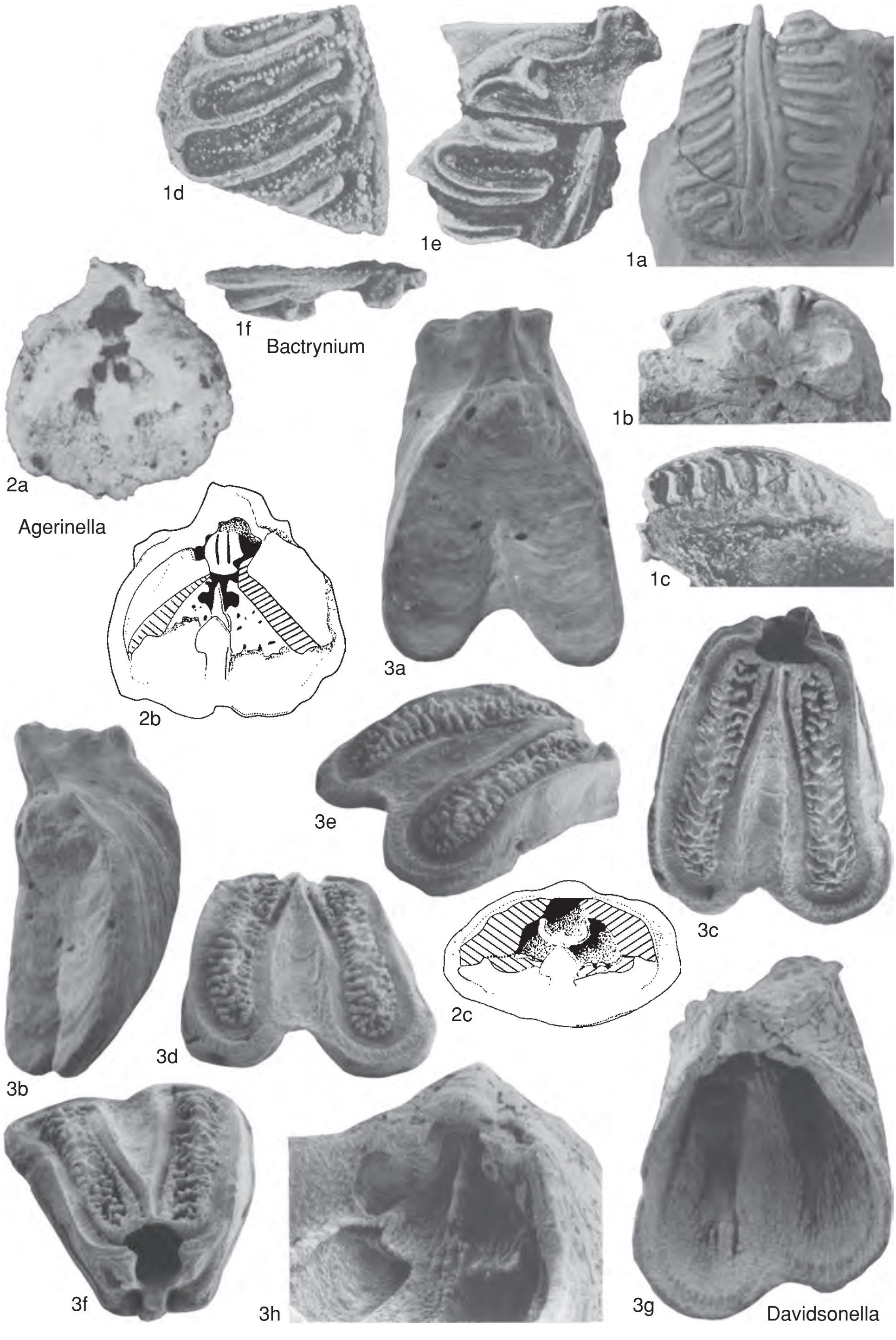

FIG. 1300. Bactryniidae (p. 1955).

grooves; Cretaceous forms with brachial lobes interdigitating with lateral septa and septules, lophophore grooves well developed. *Lower Jurassic (Toarcian)–Neogene (Tortonian).*

Thecidea DEFRANCE, 1822, p. 325 [**Terebratulites papillatus* SCHLOTHEIM, 1813, p. 113; OD; =*Thecidea radians* DEFRANCE, 1822, p. 325] [=*Thecidium* G. B. SOWERBY, 1823, p. 248, *nom. null.; Thecidaea* KEFERSTEIN, 1829, p. 82, *nom. null.; Thecideum* FISCHER DE WALDHEIM, 1834, p. 279, *nom. null.; Thecedea* D'ORBIGNY, 1847 in 1847–1851, p. 249, *nom. null.*]. Relatively large, symmetrical, with minute cicatrix at rostral extremity, high ventral interarea with clear growth lines and narrow convex pseudodeltidium with longitudinal ridge on ventral surface, costellate radial ornament; ventral valve thick with densely tuberculate border, internal median ridge, supported hemispondylium and conspicuous lateral adductor muscle scars; dorsal valve almost circular with wide, densely tuberculate border and small, acutely triangular, longitudinally grooved interarea, cardinal process, small, square, obscurely bilobed, with longitudinal groove extended on dorsal surface, complementing ridge on underside of pseudodeltidium, bridge with marsupial notch, median septum divided into regularly incurving septules, brachial lobes interdigitating with septules, reticulum weakly developed; fibrous secondary shell completely suppressed, acicular crystallite tracts in ventral valve. *Upper Cretaceous (upper Maastrichtian):* Denmark, The Netherlands, Germany, Belgium, France, Spain.——FIG. 1301,*4a–i.* **T. papillata* (SCHLOTHEIM), Ciply, Belgium; *a,* dorsal view; *b,* oblique lateral view; *c,* hypotype, oblique posterior view, BMNH BD9402; ×6.5; *d,* dorsal valve interior; *e,* dorsal valve anterior view; *f,* dorsal valve, oblique lateral view; *g,* hypotype, dorsal valve, oblique posterior view, BMNH BD9403, ×7; *h,* ventral valve interior, ×6.5; *i,* hypotype, ventral valve interior showing hemispondylium, BMNH BD9404, ×12 (new).

Backhausina PAJAUD, 1966d, p. 125 [**Thecidea rugosa* D'ORBIGNY, 1847 in 1847–1851, p. 153; OD]. Medium size, outline subtrigonal, cicatrix well developed, ventral interarea indistinct with convex pseudodeltidium; ventral valve interior ornamented by tuberculate ridges; dorsal valve subcircular but with longer hinge line than *Thecidea,* 1 or 2 lateral septa, median septum divided to form almost straight septules, brachial lobes interdigitating, reticulum depressed. *Lower Cretaceous (Albian)–lower Paleogene (Paleocene):* France, Switzerland, Germany, *Albian;* Sweden, Germany, *Campanian;* Denmark, Germany, Belgium, France, *Paleocene.* ——FIG. 1301,*1a–b.* **B. rugosa* (D'ORBIGNY), Cenomanian, Le Mans, France; *a,* dorsal valve interior, ×7.5 (Pajaud, 1970); *b,* ventral valve interior, ×6 (Backhaus, 1959).

Eudesella MUNIER-CHALMAS, 1880, p. 279 [**Thecidea mayalis* EUDES-DESLONGCHAMPS, 1853, p. 234; OD]. Medium size, transversely oval with long hinge line, ventral interarea large with well-developed, convex pseudodeltidium; dorsal valve characteristically transverse, without interarea, with relatively small cardinal process and variable number of septa, commonly more than 8, extending from valve margin to terminate near body cavity, brachial lobes pustulose, interdigitating with septa and occasionally forming reticulum united with posterior termination of median septum; fibrous secondary shell continuous in both valves. *Lower Jurassic (Toarcian):* France (Normandy).——FIG. 1301,*3a–c.* **E. mayalis* (EUDES-DESLONGCHAMPS), May-sur-Orne; *a,* dorsal view, ×4 (Elliott, 1965c); *b,* dorsal valve interior, ×6.5 (Pajaud, 1970); *c,* ventral valve interior, ×3 (Elliott, 1965c).

Glazewskia PAJAUD, 1964, p. 259 [**G. demarcqui;* OD]. Medium size, rounded outline, ventral interarea clearly differentiated with broad, convex pseudodeltidium; dorsal valve wider than long with relatively large cardinal process, 2 or 3 septa in frontal position, brachial lobes irregularly developed. *Neogene (?lower Burdigalian, upper Burdigalian–Tortonian):* southeastern France.——FIG. 1301,*2a–b.* **G. demarcqui,* Serravallian, Saint Fons; *a,* dorsal valve interior; *b,* ventral valve interior, ×6 (Pajaud, 1970).

Konstantia PAJAUD, 1970, p. 189 [**Glazewskia* sp. GLAZEWSKI & PAJAUD, 1964, p. 263; OD; *nom. nov. pro Eudesella podolica ex* GLAZEWSKI MS, 1938] [=genus *X* PAJAUD, 1966d, p. 124 (type, genus *X* sp. *A,* OD)]. Small, subtrigonal, ventral interarea flat with undifferentiated pseudodeltidium; dorsal valve subcircular to transversely elliptical, cardinal process prostrate, usually 4 lateral septa with the most centrally placed being commonly bifid, brachial cavities with a few nodelike tubercles, without brachial lobes. [The genus is known only from a collection of 135 shells, later destroyed or lost, described and figured in an unpublished manuscript. Subsequently transferrred incorrectly to *Glazewskia* sp. and then temporarily to genus *X,* the form was finally assigned to *Konstantia,* validated by the publication of a figure (graphotype) and a photograph (phototype) from the original manuscript.] *Upper Jurassic (Tithonian):* Podolia. ——FIG. 1302,*4a–b.* **K. podolica* (GLAZEWSKI MS), Bukowna; *a,* dorsal valve exterior; *b,* dorsal valve interior, ×10 (Glazewski & Pajaud, 1964).

Mimikonstantia BAKER & ELSTON, 1984, p. 778 [**M. sculpta;* OD]. Shell larger than *Konstantia,* wider than long, outline transversely elliptical, ventral interarea ill defined, pseudodeltidium weakly convex; ventral valve with relatively large cicatrix and characteristic marginal rim with tuberculate inner and smooth outer zones, hemispondylium supported by septum; dorsal valve with wide, peripheral flange, without interarea, interior with septum in an approximately median position and usually 4

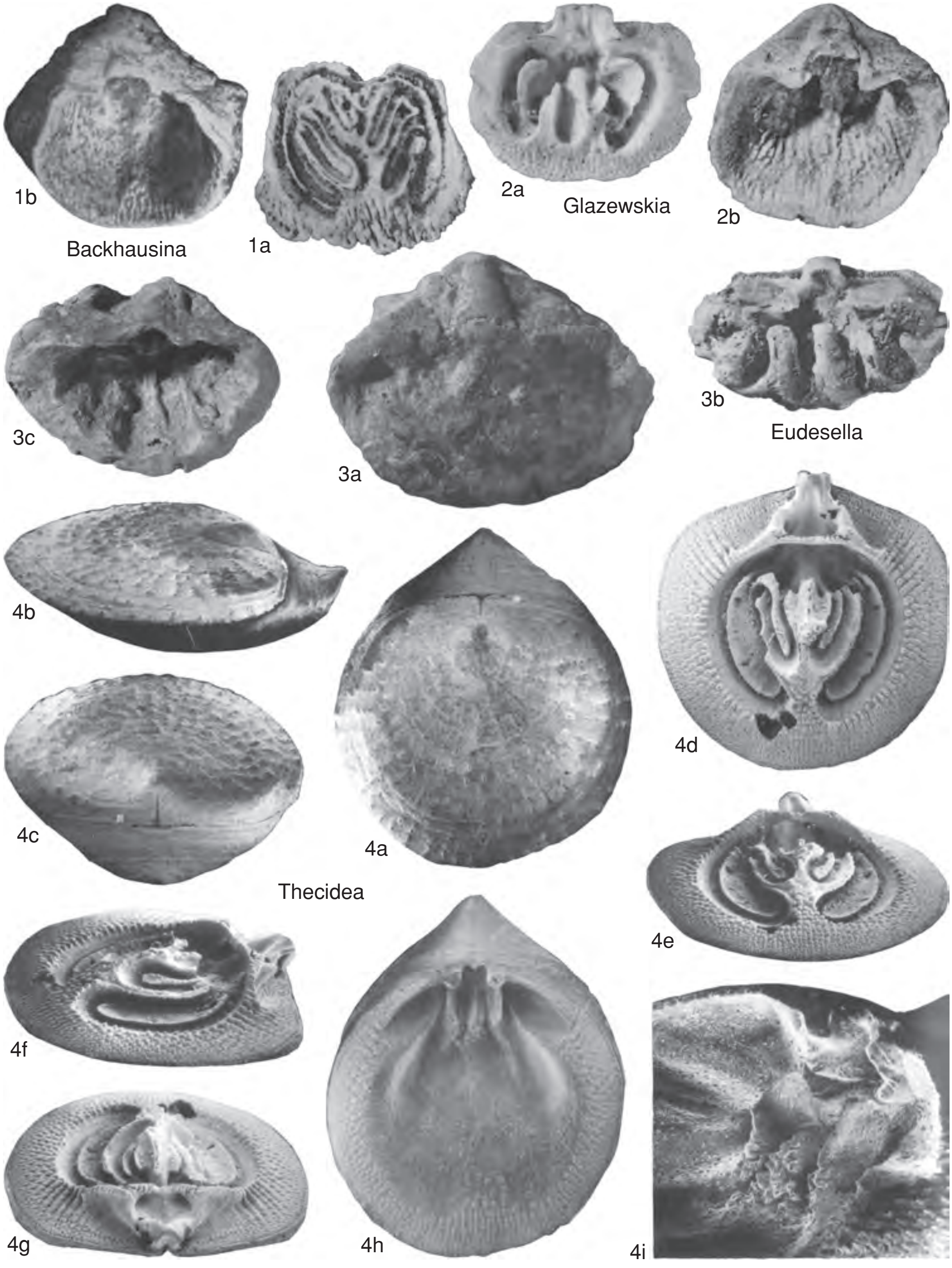

FIG. 1301. Thecideidae (p. 1957).

lateral septa, without brachial lobes; fibrous secondary shell partially suppressed in both valves; impunctate. *Middle Jurassic (Aalenian):* southern England.——FIG. 1302,*3a–e.* **M. sculpta,* Stroud, Cotswolds; *a,* complete shell, dorsal view; *b,* dorsal valve interior showing usual state of preservation; *c,* dorsal valve, anterior oblique view, ×12.5; *d,* dorsal valve interior showing undamaged septa, ×15; *e,* ventral valve interior, ×12.5 (Baker & Elston, 1984).

Parathecidea BACKHAUS, 1959, p. 55 [**Thecidea hieroglyphica* GOLDFUSS, 1840, p. 290; OD].

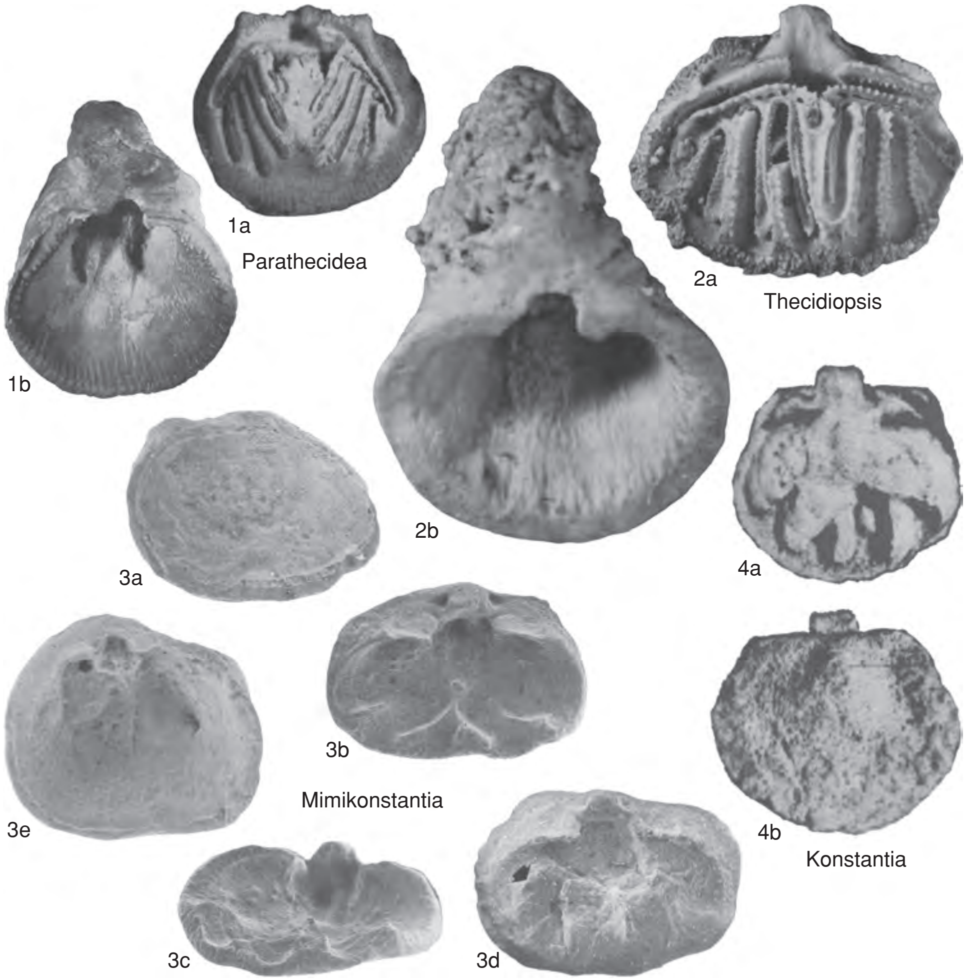

Fig. 1302. Thecideidae (p. 1957–1959).

Medium size to large; ventral valve with several irregular, longitudinal-radial, internal ridges, adductor muscle scars deeply impressed, and hemispondylium supported by thin septum; dorsal valve with wide border commonly ornamented by short, radial grooves, median septum divided to form long, approximately straight septules, 3 or 4 lateral septa, brachial lobes interdigitate with septa and septules, narrow reticulum present in some. *Upper Cretaceous (upper Campanian–upper Maastrichtian):* Sweden, *upper Campanian;* Germany, The Netherlands, Switzerland, *upper Maastrichtian.*——Fig. 1302,*1a–b.* **P. hieroglyphica* (Goldfuss), upper Maastrichtian, Maastricht, The Netherlands; *a,* dorsal valve interior; *b,* ventral valve interior, ×3 (Backhaus, 1959).

Thecidiopsis Munier-Chalmas, 1887, p. 40 [**Thecidium digitatum* G. B. Sowerby, 1823, p. 249; OD]. Size variable, commonly large; normally transversely elliptical with ventral and dorsal interareas clearly developed; ventral valve with large hemispondylium with robust supporting septum; dorsal valve with up to 12 (usually 8 to 10) lateral septa and median septum more or less divided to form septules, brachial lobe interdigitations bordered by spinules, narrow reticulum; fibrous secondary shell strongly suppressed in both valves, acicular crystallite tracts present in both valves. *Lower Cretaceous (Valanginian)–Upper Cretaceous (Maastrichtian):* Switzerland, France, Russia, *Valanginian;* Germany, *Barremian;* Czech Republic, Slovakia, *Cenomanian–Turonian;* The Netherlands, *Maastrichtian.*——Fig. 1302,*2a–b.* **T. digitata* (Sowerby), upper Maastrichtian, Maastricht, The Netherlands; *a,* dorsal valve interior; *b,* ventral valve interior, ×4.5 (Elliott, 1965c).

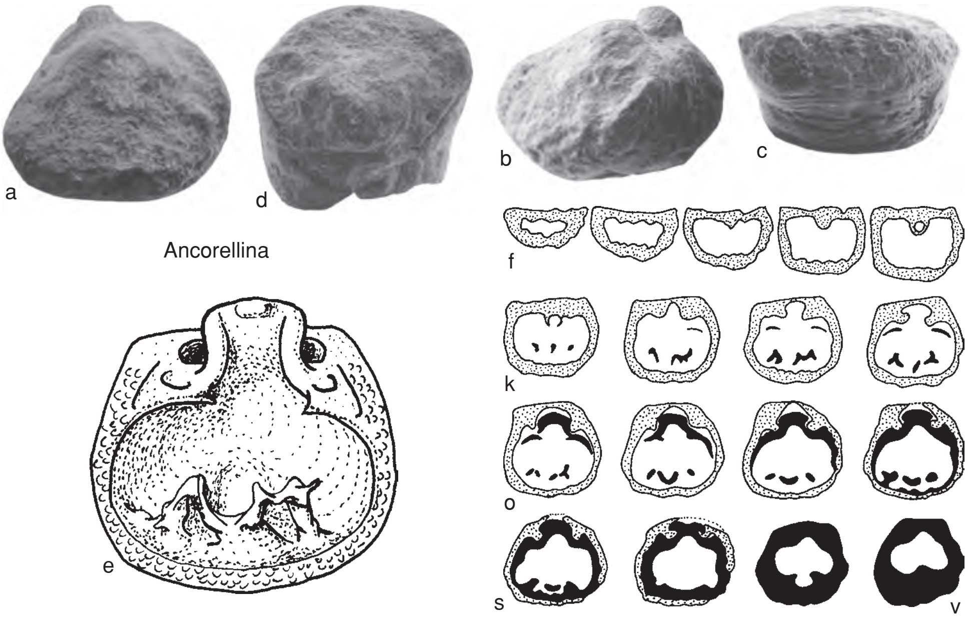

FIG. 1303. Thecideidae (p. 1960).

Subfamily ANCORELLININAE
Baker & Manceñido, 1997

[Ancorellininae BAKER & MANCEÑIDO, 1997, p. 192]

Median septum resorbed posteriorly, brachidium consisting of anterior, distally bifurcated, median column supported by pair of anterolaterally placed pillars and directed posteroventrally; lophophore grooves not developed; endopunctate; fibrous secondary shell continuous in both balves. *Lower Jurassic.*

Ancorellina MANCEÑIDO & DAMBORENEA, 1990, p. 89 [**A. ageri;* OD]. Small, subcircular, cicatrix relatively large, free ventral wall well developed, ventral interarea reduced, pseudodeltidium indistinct, hinge line short; hemispondylium sessile, anteriorly raised to form spoonlike termination, diductor muscle scars impressed posteriorly; cardinal process relatively massive, incipiently trilobed, crura possibly not uniting to form bridge, median septum reduced to anteroposteriorly flattened, distally bifurcated column, each limb united laterally with pillar arising from anterior of brachial cavities. *Lower Jurassic:* Argentina.——FIG. 1303*a–v.* **A. ageri,* upper Pliensbachian, Neuquén, Piedra Pintada area, west-central Argentina; *a–d,* dorsal, lateral, anterior, posterior views, ×15; *e,* dorsal valve interior, reconstruction, ×20; *f–v,* hypotype, serial horizontal sections 0.280, 0.392, 0.448, 0.504, 0.560, 0.588, 0.644, 0.672, 0.700, 0.756, 0.784, 0.840, 0.868, 0.896, 0.952, 1.064, 1.092 mm from free ventral wall, MLP PB3257, ×6 (new).

Subfamily LACAZELLINAE
Backhaus, 1959

[Lacazellinae BACKHAUS, 1959, p. 19]

Commonly with ridged and grooved, internal ornament; anterior sinus developed to divide median septum longitudinally, commonly with posterior convolution to form ramuli, jugal pillar present or absent, brachial lobes usually with interdigitation, lophophore grooves present in most; spicules present in mantle of some species. *Lower Jurassic (Toarcian)–Holocene.*

Lacazella MUNIER-CHALMAS, 1880, p. 279 [**Thecidea mediterranea* RISSO, 1826, p. 394; OD]. Relatively small, irregular with convex pseudodeltidium; interior of ventral valve papillose to spinose except over muscle scars, hemispondylium projecting anteriorly as two spurs; dorsal valve with hypercline interarea, bridge with marsupial notch, median septum divided to form trifurcating structure consisting of pair of lateral ramuli and posterior median ridge uniting with jugal pillar, brachial lobes interdigitating with ramuli; shell granular except for superficial

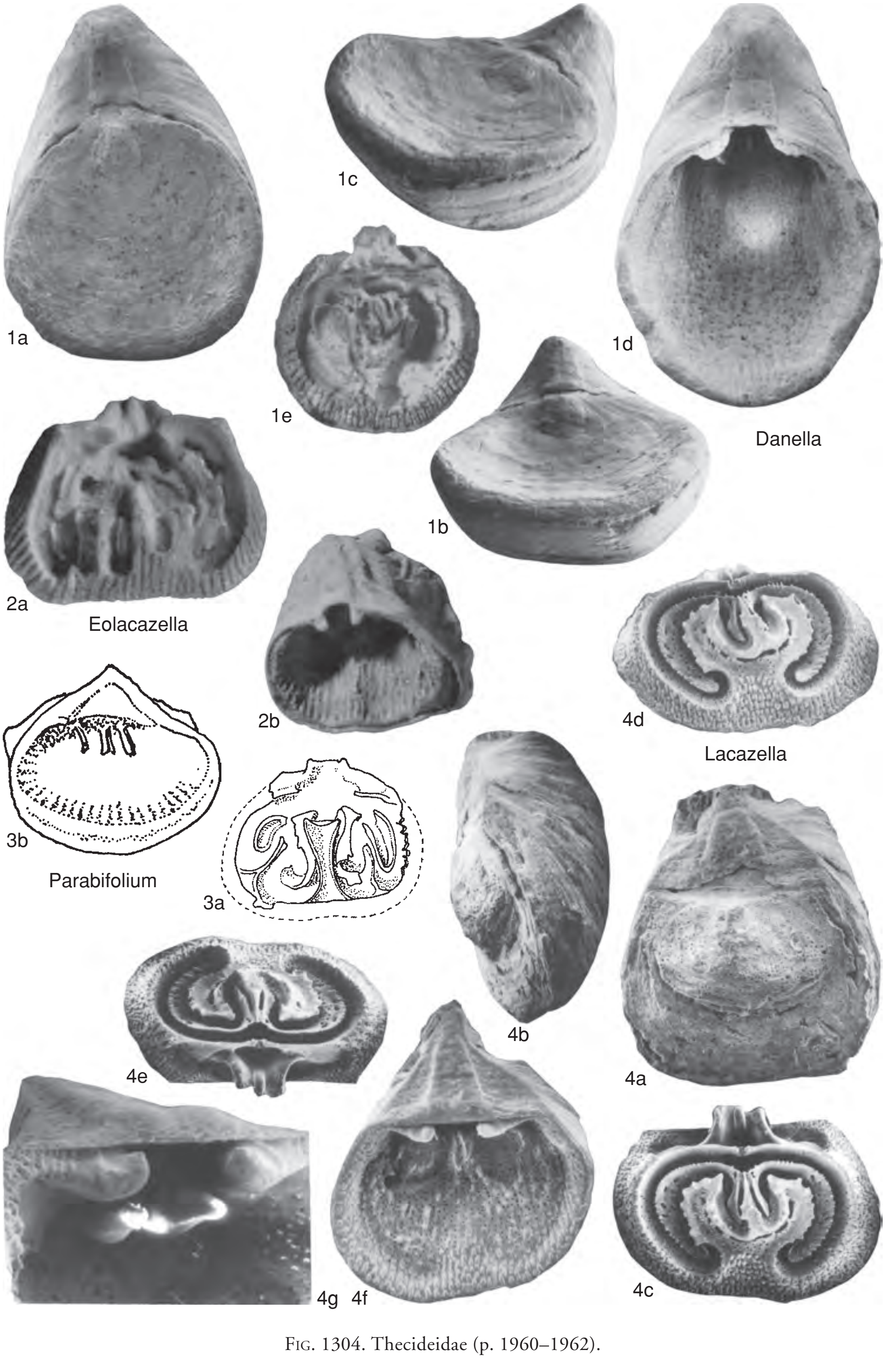

FIG. 1304. Thecideidae (p. 1960–1962).

traces of fibrous secondary shell on dorsal surface of teeth; mantle thin, coarsely spicular. *Eocene–Holocene:* Europe, ?Australia, *Eocene;* Mediterranean, West Indies, Mauritius, Pacific, *Holocene.*——FIG. 1304,*4a–g.* **L. mediterranea* (RISSO), Holocene, La Calle, Mediterranean, Algeria; *a,* dorsal view; *b,* hypotype, lateral view, BMNH BD9399; *c,* dorsal valve interior; *d,* dorsal valve, oblique anterior view; *e,* hypotype, dorsal valve, oblique posterior view, BMNH BD9400; *f,* ventral valve interior, ×8; *g,* hypotype, ventral valve, oblique anterior view showing hemispondylium, BMNH BD9401, ×15 (new).

Danella PAJAUD, 1966c, p. 70 [**D. fragilis;* OD]. Small to medium size, outline commonly pyriform, externally smooth, cicatrix small to minute, rostral extremity strongly recurved in some species, ventral interarea obscure, pseudodeltidium clearly convex; hemispondylium sessile with low median and very high lateral ridges; dorsal valve convex at umbo, otherwise shallowly concave with narrow, acute, almost procline interarea, circular with relatively wide border ornamented by fine ribbing, median septum folded into 4 to 6 ramuli with spinose borders, brachial lobes large with well-developed reticulum and elaborate interdigitation with ramuli. [Preservation of detail in the type material is poor. Generic characters are more clearly illustrated in the species figured herein.] *Upper Cretaceous (upper Campanian)–Paleogene (middle Danian):* England, France, The Netherlands, Denmark, Belgium, Germany, *upper Campanian.*——FIG. 1304,*1a–d. D. recurvirostris* (DEFRANCE), ?upper Maastrichtian, Nehou, France; *a,* dorsal view; *b,* anterior view; *c,* hypotype, oblique lateral view, BMNH BD9359; *d,* hypotype, ventral valve interior, BMNH BD9360, ×8.5 (new).——FIG. 1304,*1e. D. longirostris* (BOSQUET), middle Danian, Geulheim, The Netherlands; dorsal valve interior, ×7.5 (Backhaus, 1959).

Eolacazella ELLIOTT, 1953a, p. 694 [**Thecidium affine* BOSQUET, 1860, p. 25; OD]. Small; irregular to trigonal; ventral valve with high, narrow pseudodeltidium; internal ventral median ridge spinose; dorsal valve laterally subrectangular, border ornamented by fine ribbing, median septum with few short ramuli, and sinus obscured by development of pair of lateral septa originating anteriorly; fibrous secondary shell completely suppressed, whole shell granular. *Upper Cretaceous (upper Maastrichtian):* The Netherlands, Belgium.——Fig. 1304,*2a–b.* **E. affine* (BOSQUET), Saint-Pierre de Maastricht, The Netherlands; *a,* dorsal valve interior, ×10 (Backhaus, 1959); *b,* ventral valve interior, ×12 (Elliott, 1965c).

Neothecidella PAJAUD, 1970, p. 108 [**Thecidea antiqua* GOLDFUSS, 1840, p. 290; OD]. Small, with large cicatrix, ventral interarea indistinct with convex pseudodeltidium, hinge line relatively short; ventral valve interior ornamented by longitudinal ridges; dorsal valve with flattened area behind umbo, which may represent interarea, border with ribbed ornament, cardinal process small, median septum with well-developed sinus not fully open posteriorly, termination united with jugal pillar, brachial lobes small, reniform; occurrence of fibrous secondary shell restricted to teeth and tooth ridges of ventral valve in at least one species. [Preservation of detail in the type material is poor. Generic characters are more clearly illustrated in *N. parviserrata.*] *Upper Jurassic (middle Oxfordian)–Lower Cretaceous (upper Aptian):* France, Germany, Switzerland, *middle Oxfordian;* southern England, *upper Aptian.*——FIG. 1305,*2a–e. N. parviserrata* BAKER & LAURIE, upper Aptian, Faringdon, southern England; *a,* dorsal valve interior; *b,* dorsal valve, oblique anterior view; *c,* dorsal valve lateral view; *d,* dorsal valve posterior view; *e,* ventral valve, oblique posterior view, ×20 (Baker & Laurie, 1978).

Pajaudina LOGAN, 1988, p. 546 [**P. atlantica* LOGAN, 1988, p. 550; OD]. Relatively large, elongate with convex pseudodeltidium; hemispondylium with supporting septum; dorsal interarea hypercline, cardinal process incipiently trilobed, bridge with marsupial notch, brachial apparatus consisting of 2 crescentic, lateral ramuli, and posterior, upraised, median ridge divided into short septules, troughs of ramuli perforate, brachial lobes interdigitating with ramuli and septules; shell granular except for superficial, fibrous secondary layer on teeth; mantle spiculate. *Holocene:* southeastern North Atlantic (Canary Islands, Salvage Islands).——FIG. 1305, *1a–d.* **P. atlantica,* off Palma, Canary Islands; *a,* dorsal view; *b,* dorsal valve interior; *c,* dorsal valve interior, lateral oblique view; *d,* ventral valve interior, ×4 (Logan, 1988).

Parabifolium PAJAUD, 1966c, p. 70 [**P. priscum;* OD]. Small, externally similar to *Neothecidella;* dorsal valve interior with median septum divided over entire length with thin, lateral septum on either side converging posteriorly, brachial lobes well developed. *Upper Jurassic (lower Kimmeridgian):* Germany.——FIG. 1304,*3a–b.* **P. priscum,* Nattheim; *a,* dorsal valve interior; *b,* ventral valve interior, ×10 (Pajaud, 1970).

Praelacazella SMIRNOVA, 1969a, p. 81 [**Thecidium valangiense* DE LORIOL, 1868, p. 59; OD]. Small to medium size, elongately to rounded subtriangular with greatest width close to anterior margin, large cicatrix, ventral interarea obscure with convex pseudodeltidium; dorsal valve circular-tetragonal, dorsal interarea hypocline, cardinal process with pronounced dorsal deflection, median septum with wide sinus divided posteriorly to form pair of ramuli and central, jugal pillar, brachial lobes reniform with lanceolate interdigitation with ramuli; fibrous secondary shell partially supressed in ventral valve, heavily suppressed in dorsal valve, acicular crystallite tracts in dorsal valve. *Lower Cretaceous (upper Valanginian)–Upper Cretaceous (Maastrichtian):* Switzerland, *upper Valanginian;* Crimea, western Germany, *Hauterivian;* France, Czech Republic, Slovakia, *Cenomanian–Santonian;* southern

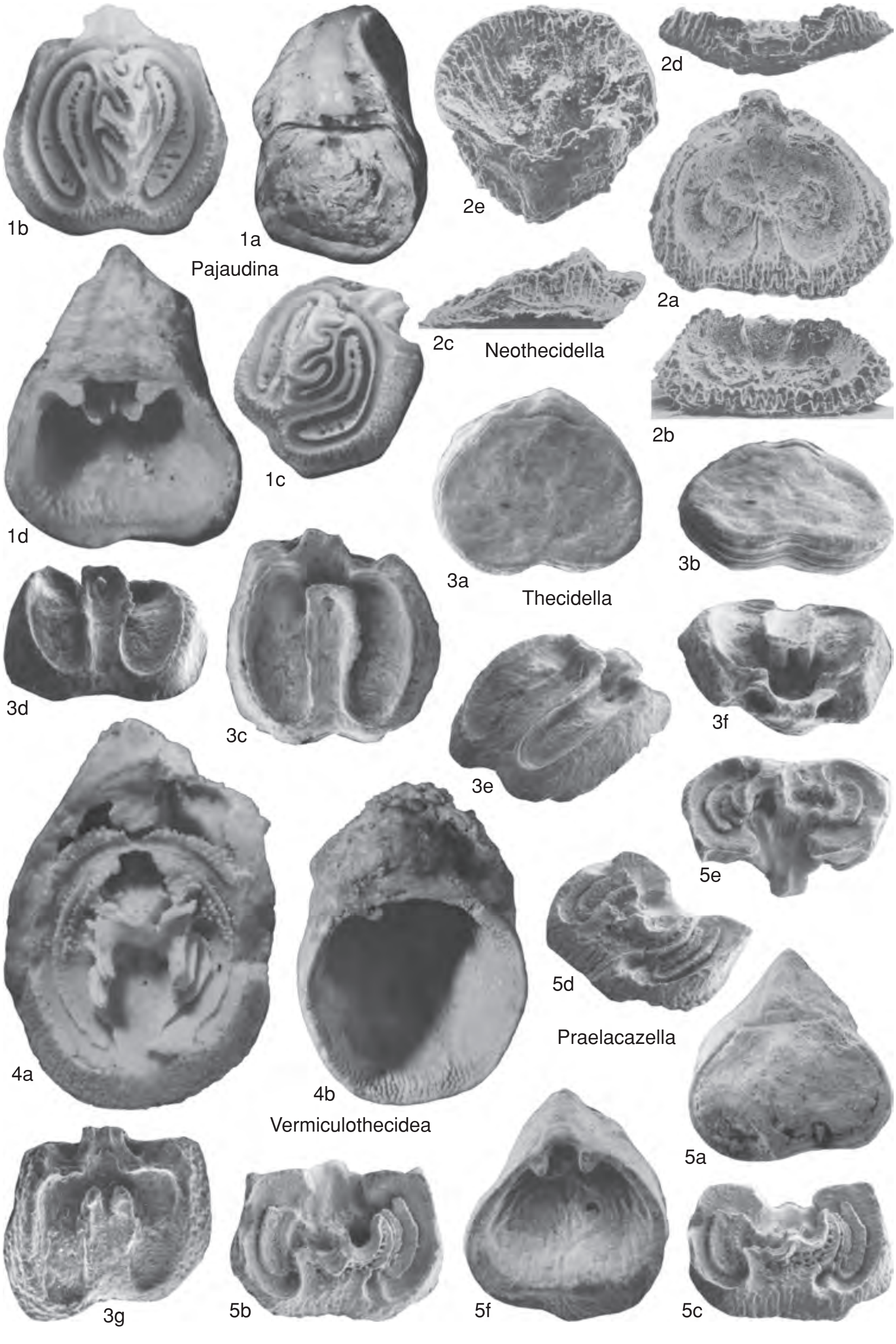

FIG. 1305. Thecideidae (p. 1962–1964).

England, Germany, *Maastrichtian;* Denmark, *Coniacian.*——FIG. 1305,*5a–f. P. lacazelliformis* (ELLIOTT), upper Cenomanian, Zbyslav, Bohemia, Czech Republic; *a,* hypotype, dorsal view, BMNH BD9136; *b,* dorsal valve interior; *c,* dorsal valve, oblique anterior view; *d,* dorsal valve, interior oblique lateral view; *e,* hypotype, dorsal valve, interior oblique posterior view, BMNH BD9137; *f,* hypotype, ventral valve interior, BMNH BD9138, ×12 (new).

Thecidella MUNIER-CHALMAS, 1887, p. 40 [**Thecidea rustica* DAVIDSON, 1851, p. 15; OD; =*Thecidea (Thecidella) normaniana* MUNIER-CHALMAS in OEHLERT, 1887b, p. 1,331]. Small, with large cicatrix, ventral interarea obscure, broad, with strongly convex pseudodeltidium; dorsal valve quadrangular to transversely rectangular, anterior margin with shallow sulcus, dorsal interarea vestigial, cardinal process prostrate and relatively small, median septum wide, divided by sinus over its entire length, variable in outline with denticulate margins, walls commonly uniting to form posterior, centrally perforate termination, brachial cavities without brachial lobes or lophophore grooves; fibrous secondary shell forming continuous lining in both valves. *Lower Jurassic (Toarcian)–Middle Jurassic (middle Bajocian):* southern England, France, *Toarcian;* Germany, *middle Bajocian.*——FIG. 1305,*3a–g.* **T. rustica* (DAVIDSON), lower Toarcian, May-sur-Orne, France; *a,* dorsal view; *b,* hypotype, oblique anterior view, BMNH BD9362, ×7; *c,* dorsal valve interior; *d,* dorsal valve, oblique anterior view; *e,* dorsal valve, oblique lateral view; *f,* hypotype, dorsal valve, oblique posterior view, BMNH BD9363, ×10; *g,* hypotype, dorsal valve interior showing typical state of preservation of median septum, BMNH B36895, ×10 (new).

Vermiculothecidea ELLIOTT, 1953a, p. 694 [**Terebratulites vermicularis* SCHLOTHEIM, 1813, p. 113; OD]. Large, irregularly elongate, ventral interarea and pseudodeltidium poorly differentiated; ventral valve deep with interior ornamented by small tubercles; dorsal valve subcircular to longitudinally oval, brachial apparatus elaborate, sinus very wide with septum free from valve floor posteriorly, folded into up to 12 ramuli with spinose edges, brachial lobes well developed with large reticulum and rodlike interdigitation with ramuli. *Upper Cretaceous (Cenomanian–upper Maastrichtian):* The Netherlands, Belgium, Germany, Denmark, Switzerland, France, Romania, *upper Maastrichtian;* southern England, *Cenomanian.*——FIG. 1305,*4a–b.* **V. vermicularis* (SCHLOTHEIM), upper Maastrichtian, Maastricht, The Netherlands; *a,* dorsal valve interior; *b,* ventral valve interior, ×6 (Elliott, 1965c).

TEREBRATULIDA

D. E. Lee,[1] D. I. MacKinnon,[2] T. N. Smirnova,[3] P. G. Baker,[4]
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Order TERLBRATULIDA Waagen, 1883

[*nom. correct.* Moore, 1952, p. 220, *pro* order Terebratulacea Kuhn, 1949, p. 105, *nom. transl. ex* suborder Terebratulacea Waagen, 1883a, p. 447; *emend.,* Lee & MacKinnon, herein]

Small to large, endopunctate articulated brachiopods with functional pedicle, shell commonly biconvex, smooth, but may be costate or costellate; with astrophic hinge line, hinge teeth cyrtomatodont; delthyrium partially or completely closed by deltidial plates or symphytium; dental plates present or absent; lophophore supported by morphologically variable calcareous loop arising from crura alone, or in conjuction with septal pillar; lophophore commonly plectolophous but may be trocholophous, schizolophous, zygolophous, or ptycholophous; calcareous spicules may be present in mantle and lophophore in some families. *Lower Devonian–Holocene.*

INTRODUCTION

D. E. Lee and D. I. MacKinnon

[University of Otago; and University of Canterbury]

Terebratulides are a very large, distinctive, and important group of middle Paleozoic to Holocene articulated brachiopods that includes more than 600 genera. Terebratulides could be considered the most successful of all brachiopods since they have persisted from their origins in the Early Devonian through the end-Devonian and end-Permian extinctions to become the dominant group of brachiopods in the Mesozoic, and they remain so to the present day. Figure 1306 provides a generalized histogram of terebratulide generic diversity through time. In modern oceans, terebratulides make up about three-quarters of all living brachiopod genera (20 percent of the rest are rhynchonellides) and most brachiopod individuals living in the ocean today. Living terebratulides occur in most parts of the world's oceans down to depths of more than 5,000 m but are most abundant in shelf environments. Most of the information on the biology and ecology of fossil brachiopods comes from study of the living members of this long-ranging order.

Members of the morphologically diverse order Terebratulida can be distinguished from all other brachiopods by the possession of endopunctae, a loop, and a generally functional pedicle. Terebratulides range in size from very small to very large, have a narrow astrophic hinge line, and possess a moderately large functional pedicle opening in a partly or completely closed delthyrium. The exterior of a typical terebratulide is biconvex, elongate oval in outline, generally smooth or occasionally ribbed, and commonly with a rectimarginate, sulcate, or plicate anterior commissure. The lophophore in terebratulides is supported by a morphologically variable, short or long calcareous loop that may arise either from the crura alone (Terebratulidina) or from crura and septal pillar combined (Terebratellidina).

HIGHER-LEVEL CLASSIFICATION

A brief history of the classification of Brachiopoda was given by MUIR-WOOD (1955), and a revised classification for genera placed in the order Terebratulida was provided by MUIR-WOOD and STEHLI (1965). The classification presented herein has been revised substantially, and a single introduction is provided that encompasses all Paleozoic and Mesozoic to Holocene genera in order to emphasize the unifying features of the order Terebratulida.

We now recognize two suborders, the Terebratulidina and the Terebratellidina, and have discarded the third suborder, Centronellidina, which was erected by STEHLI (1965). In preparing our revision of the Paleozoic terebratulides, we realized that only one superfamily, the Devonian Stringocephaloidea, could be assigned to the Centronellidina and that the distinction made by STEHLI was invalid. We thus follow DAGYS (1972b) and COOPER and GRANT (1976b) in assigning all Paleozoic terebratulides to the suborder Terebratulidina, which ranges in age from Early Devonian to Holocene. The second suborder, Terebratellidina, ranges from the Early Triassic to Holocene and includes the largest number of living genera in any brachiopod order. Sixteen superfamilies are now recognized; seven are included in suborder Terebratulidina; and the remaining nine are placed in suborder Terebratellidina (Fig. 1307).

SUBORDER TEREBRATULIDINA

Differentiation of superfamilies within the suborder Terebratulidina is based on presence or absence of dental plates, presence or absence of a perforate cardinal plate, loop size and shape, loop ontogenetic stages, and final loop form in adult brachiopods. As redefined herein, this suborder now includes all short-looped and some long-looped terebratulides in which the loop develops by extension of the crura without the involvement of either a septal pillar or a median septum. Suborder Terebratulidina includes seven superfamilies, three of which, Stringocephaloidea, Cryptonelloidea, and Dielasmatoidea, appear first in the Lower Devonian (Fig. 1307). The Stringocephaloidea, in which the adult loop is commonly acuminate, were widespread during the Devonian but became extinct in the Frasnian. The Cryptonelloidea, which are characterized by an undivided and commonly perforate hinge plate, include forms with short loops (Cranaenidae) and less commonly long loops (Cryptonellidae). This superfamily, while never dominant in the upper Paleozoic, ranges into the Lower Triassic.

The Dielasmatoidea, in which the loop developed commonly from the acuminate to deltiform condition, are the only terebratulides to cross the Permian-Triassic boundary with little loss of diversity, and the superfamily ranges up into the Lower Jurassic. The diverse families included within the Dielasmatoidea may be the precursors of all other short-looped terebratulides. Thus, the Heterelasminidae, in which the deltiform loop is formed by fusion of the descending branches, may lead to the Terebratuloidea, the Cancellothyridoidea, and the Dyscolioidea. The family Pseudodielasmatidae, in which the short deltiform loop undergoes a complex development, may be the precursor of the most diverse superfamily of all, the Mesozoic Loboidothyridoidea, which is characterized by short to moderately long loops that are commonly long flanged.

One of the most substantive changes in systematic placing has involved transfer to the Loboidothyridoidea of many Jurassic short-looped taxa, which were previously included in superfamily Terebratulacea (now Terebratuloidea) in the 1965 *Treatise* (MOORE, 1965). Most were placed in family Terebratulidae along with such living and Cenozoic short-looped genera as *Liothyrella, Gryphus,* and *Terebratula s.s.* DAGYS (1968, 1974) and SMIRNOVA (1990a), among others,

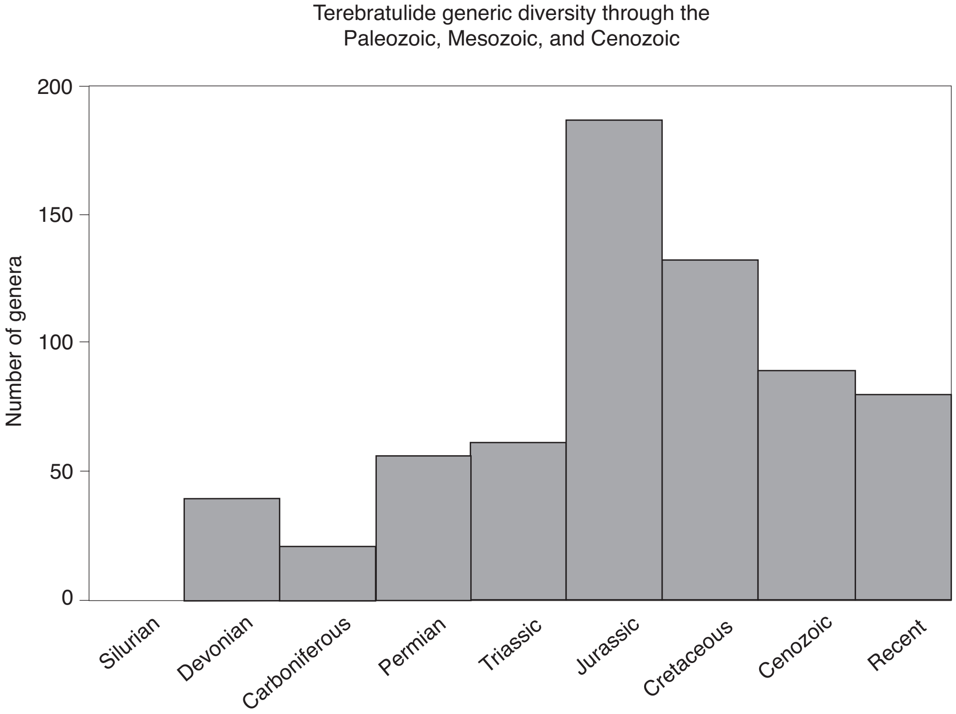

FIG. 1306. Generalized histogram of terebratulide generic diversity through time; all genera present during each time period are included; thus, where a genus, e.g, *Dielasma,* spans more than one period (Carboniferous and Permian), it is counted in both; not to scale; all periods or epochs shown as equal in length (new).

however, demonstrated that some of these long-flanged genera pass through a complex loop development during early ontogeny. Unfortunately, loop development is known for only a few genera (*Viligothyris, Lobothyris*), and until the early stages are studied further, the true affinities of many genera placed in superfamily Loboidothyridoidea remain unknown. Thus, superfamily Loboidothyridoidea, which ranges from Lower Triassic to Lower Cretaceous, is most likely polyphyletic and with further study may prove to incorporate a number of different groups.

SUBORDER TEREBRATELLIDINA

The second suborder, Terebratellidina, may have arisen from the family Angustothyrididae, now included in superfamily Dielasmatoidea, during the late Permian to Early Triassic. In this suborder, loop ontogeny is complex and always involves the median septum or septal pillar. Differentiation of superfamilies within the suborder Terebratellidina is based on such features as presence or absence of dental plates, presence or absence of a septal pillar and its part in loop development, loop ontogenetic stages, and final loop form in adult brachiopods.

All nine superfamilies included in suborder Terebratellidina have living representatives, including the Zeillerioidea, Kingenoidea, and Laqueoidea that first appeared in the Late Triassic. Although laqueoids are still relatively common in modern seas, zeillerioids and kingenoids are each now represented by a single living genus. *Macandrevia,* which is widespread in modern oceans, is the only post-Cretaceous survivor of the diverse Mesozoic zeillerioids, and the enigmatic

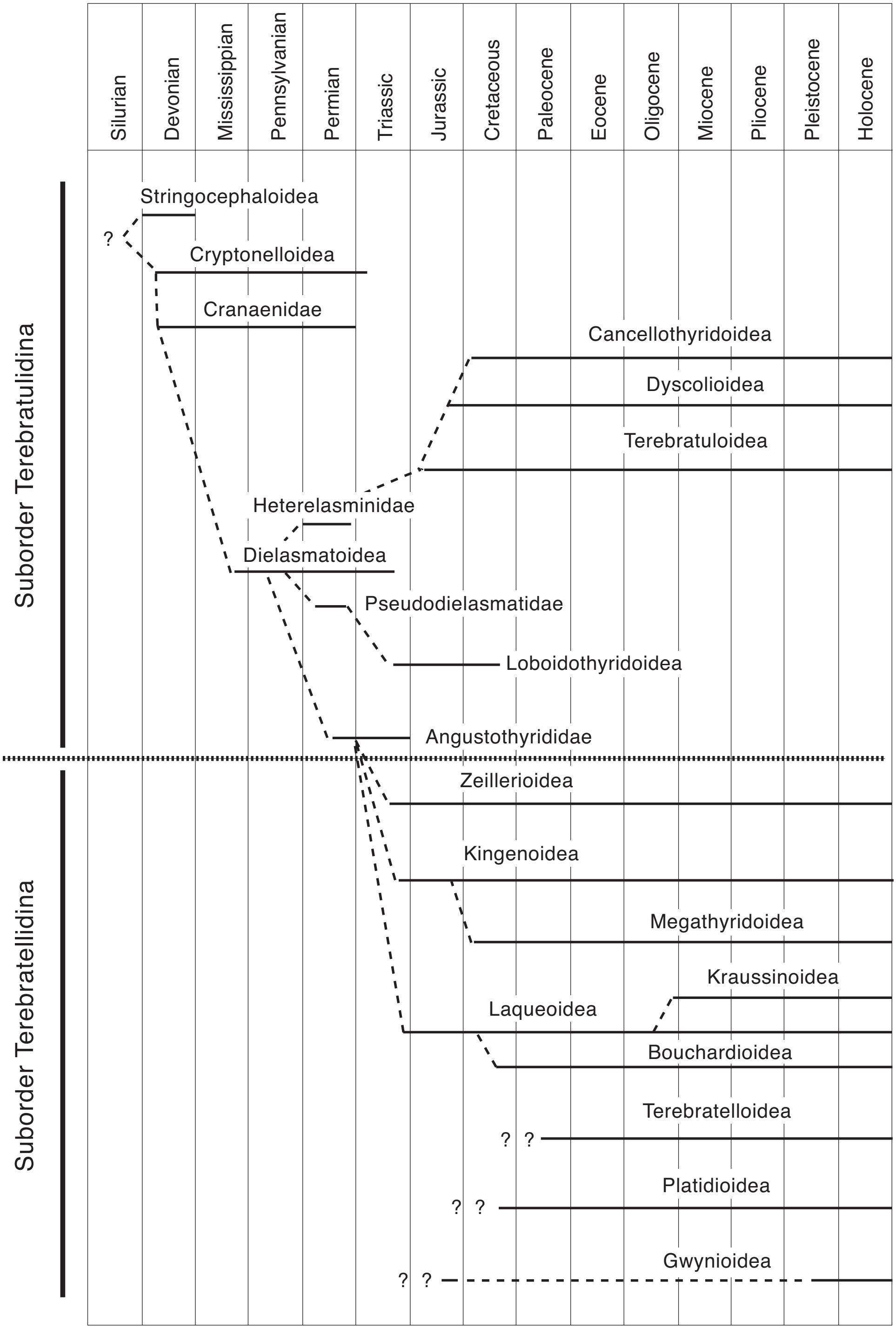

FIG. 1307. Stratigraphic ranges and phylogeny for terebratulide superfamilies and selected families; not to scale; all periods or epochs shown as equal in length (new).

genus *Ecnomiosa* appears to be the only remaining taxon of the superfamily Kingenoidea. Megathyridoids may have been derived from kingenoids in the Late Jurassic–Early Cretaceous (MacKinnon, 2001). Both bouchardioids, which first appeared in the Early Cretaceous, and kraussinoids, which are known from the Miocene to the Holocene, may have evolved independently from Laqueoidea. The ancestral stocks from which the platidioids (Late Cretaceous onward) and terebratelloids (Paleocene onward) arose have not yet been established. The origin and affinities of the Gwynioidea are not clear.

Note that superfamily Dallinoidea as used by Smirnova (1990a) and many others has been discarded. MacKinnon (1996) confirmed the earlier observations of Atkins (1960b) that *Dallina septigera,* the type species of *Dallina,* lacks dental plates throughout ontogeny and is not closely related phylogenetically to the many other genera and families previously assigned to the former superfamily Dallinoidea.

ORIGINS

The oldest representatives of order Terebratulida occur in rocks of earliest Devonian age, although their origins must extend back into the latest Silurian. Boucot (in Boucot & Wilson, 1994) suggested that the primitive earliest terebratulides have morphological features consistent with an origin from the Atrypoidea and in particular *Nalivkinia,* a late Silurian impunctate atrypoid with discrete hinge plates, short dental plates, and spiralia and jugum. *Mutationella* and *Podolella,* among the earliest known terebratulides placed into superfamily Stringocephaloidea, are morphologically similar to *Nalivkinia,* but possess endopunctae and lack spiralia.

The discovery by Jin and Chatterton (1996) of a late Wenlockian silicified brachiopod, *Microbilobata avalanchensis,* which may possess a centronelliform (acuminate) loop and is possibly endopunctate, raises the possibility that the terebratulides are polyphyletic. Doubts about the presence of endopunctae and very different external morphology, however, suggest that *Microbilobata* should be considered at present as an independent taxon that did not give rise to the terebratulides.

TEREBRATULIDE MORPHOLOGY

The classification of order Terebratulida is based on both external and internal morphological features. As emphasized by Stehli (1965, p. 732), external variation in terebratulide shells "is limited, and both parallelism and convergence are common. Thus, it is absolutely mandatory that the internal structures of all shells be studied if inordinate taxonomic confusion is to be avoided."

We illustrate the dorsal, lateral, and anterior views of most genera, together with the dorsal interior. Where a loop illustration is not available, we provide serial transverse sections. Stehli (1965) illustrated most Paleozoic terebratulides by means of stylized or composite line drawings. Here we have provided photographs showing external and internal features for all taxa for which these are available. Note that the loop is unknown for about a third of Paleozoic terebratulide genera, and most Paleozoic terebratulide workers have not made use of serial sections. We have included photographs of the actual loop in preference to serial sections or loop reconstructions. Cooper (1983, p. 1–3) commented in some detail on the lack of correspondence between some loop reconstructions and the actual dissected loop.

EXTERNAL FEATURES

Most terebratulides are ovate, biconvex, and smooth or less commonly ribbed, with a conspicuous open foramen with the delthyrium partly or wholly closed by deltidial plates or a symphytium. "Notwithstanding the risks involved in making taxonomic assignments on the basis of external features alone, there is considerable variation in the shape, size, and ornamentation of terebratulide shells which is useful in their study. Differences in size can be important, but are notoriously subject to error of interpretation, since environmental factors during life and after death may have influenced size distributions. Before size may be used as a taxonomic criterion, ontogenetic sequences and the range of variation within and between populations must be known with some certainty" (STEHLI, 1965, p. 732). This statement can be applied also to the study of internal variation in terebratulides, and it is unfortunate that more students of terebratulide brachiopods did not heed STEHLI's caution before describing a number of genera that are undoubtedly synonyms of existing taxa.

During preparation of this work, it has become apparent that in spite of the advances made since the 1965 *Treatise* (MOORE, 1965), a large number of terebratulide genera are incompletely known.

Because of the substantial amount of variability of external features and probably of most internal features, we stress here that a large number of individuals, including representatives of different ontogenetic stages, must be studied before adequate understanding of true taxonomic placing can be made. Thus, study of the loop by means of serial sections or dissected loops in the case of fossil species is required to describe adequately a new genus. A substantial number of genera listed in this volume are imperfectly understood; loop structure may be entirely unknown (e.g., *Magharithyris, Moisseevia, Moraviatura, Phymatothyris*) or imperfectly known (*Eogryphus, Miogryphus, Waisiuthyrina*); serial sections may be incomplete (e.g., *Naradanithyris, Weldonithyris*). In some cases, only a single specimen was available for study (e.g., *Mayothyris*), and this is an inadequate basis for naming a new genus. Of the Paleozoic terebratulides included herein, the loops of 85 genera are known with some certainty, while 50 other genera are classified on the basis of external morphology or features of the cardinalia alone. Many older genera, such as those described by BITTNER (1888, 1890, 1892) and BUCKMAN (1918), need to be reexamined as some newly described genera are undoubtedly synonyms of older but poorly known taxa. Similarly, comparisons between genera must be detailed, and full justification of the proposed new genus must be provided, taking into account the known variation in other related species or, better still, in living terebratulides.

Overall size and shape

Shells of adult terebratulides range in length from 1 mm to >100 mm, although most are in the 20 to 50 mm class. To standardize size terminology, adult shells <3 mm in length are described as very small, between 3 to 10 mm as small, 10 to 25 mm as medium, 25 to 50 mm as large, and >50 mm as very large. Although arbitrary, these size ranges correlate in part to superfamily groupings: thus, most species of Platidioidea are very small; most members of Cancellothyridoidea are of small to medium size; whereas most members of Terebratuloidea are medium to large. Some terebratulides are among the largest of all brachiopods: some Devonian genera including *Stringocephalus* and *Scaphiocoelia* reached 120 mm in length, and late Cenozoic species of *Terebratula s.s.* were up to 95 mm long. The maximum size that can be achieved by terebratulides with particular types of lophophores may be set by scaling factors (PECK, 1992). As PECK and HOLMES (1989, p. 141) pointed out, "Large brachiopods may suffer space constraints because of the volume needed to house the lophophore." Thus, in some species, more than 75 percent of total body volume may be occupied by the lophophore and mantle cavity. Terebratulides are commonly ventribiconvex, although most platidioids are planoconvex (*Platidia, Amphithyris*), as are occasional members of other superfamilies (*Centronella, Antiptychina*).

Many terebratulides are subcircular in outline as juveniles, becoming subpentagonal, subcircular, elongate oval, or rarely transverse as adults. A few have distinctive outlines (e.g., *Agulhasia, Bouchardia, Pygope, Trigonellina, Trigonosemus*), but in most the shell shape alone is not a reliable diagnostic feature. "Variations in shell shape are quite likely to express a true genotypic variation and are, thus, more likely to be taxonomically significant than size alone. Because of the nature of growth in most brachiopod shells (Rudwick, 1959; Williams, 1956), most changes in shape are simply changes in growth rate or in proportion. These changes generally affect the relations between length, width, and thickness of the shell but also commonly affect the length or attitude of the beak, changes in shell curvature, and the development of major folding" (Stehli, 1965, p. 732).

Folding

The type of folding has been widely used to discriminate terebratulide genera. As pointed out by Stehli (1965, p. 732), "Since folding is apparently related to nature and disposition of the lophophore within the shell and the efficient control of incurrent and excurrent water streams, it may reflect important changes in soft parts and be of considerable taxonomic significance."

There have been few studies of the variation in folding within and between species and genera. From the limited studies available (e.g., Gaspard, 1988), it seems that the degree of folding may be variable even within a single species of living terebratulide, and care is needed in using folding alone as a diagnostic character.

Most brachiopods are rectimarginate as juveniles, and folding may develop in tandem with sexual maturity. Most Paleozoic terebratulides are rectimarginate to uniplicate. Mesozoic terebratulides are more commonly unisulcate or sulciplicate; only a few are characterized by uniplicate folding. Living terebratulides are commonly unisulcate, and gerontic adults may have accentuated sulciplication of the commissure. The main types of commissure folding are illustrated in Williams, 2000 (see fig. 289, p. xxx).

Ornament

Most terebratulides are externally smooth; the spacing of comarginal growth bands or growth halts on brachiopod shells reflects the ecological conditions under which the animals were living and possibly their longevity. It is unlikely to be of taxonomic value, though it is mentioned sometimes in older descriptions. Some of the earliest Devonian terebratulides (e.g., *Podolella, Rensselaerina*) have smooth umbones but develop peripheral costae, while others (e.g., *Cloudella, Rhipodothyris*) are entirely costellate. All members of the Cancellothyridoidea are finely capillate (e.g., *Terebratulina, Eucalathis*); some kraussinoids are costellate (e.g., *Kraussina, Megerlia*); and most megathyridoids (e.g., *Argyrotheca, Megathiris*) carry broad costae. A small number of Mesozoic zeillerioids (e.g., *Eudesia, Flabellothyris*) and a few genera placed in superfamily Loboidothyridoidea (e.g., *Striithyris, Plectoidothyris*) are costate, costellate, or semicostate. *Kingena* has an unusual ornament of spinose pustules or granules.

Some laqueoids are costate (e.g., *Gemmarcula, Trigonosemus, Dereta*), as are a few terebratelloids, although closely related genera within the same family may be costate or smooth (e.g., *Terebratella* and *Calloria*).

Shell Structure

All members of the order Terebratulida are endopunctate, with primary and secondary shell layers largely of low-magnesium calcite. A few terebratulides (e.g., *Gryphus* and *Liothyrella*) possess a tertiary shell layer modified from the secondary layer. Although some workers (e.g., Katz & Popov, 1974a, 1974b) have used the presence of a tertiary layer in generic discrimination, the taxonomic value of this feature has not been demonstrated. The highly thickened modified secondary shell (perhaps the tertiary layer) of the Devonian stringocephalids is a consistent feature of the family.

Beak and Foramen

Beak characters of terebratulides are generally conservative. In juvenile terebratulides the pedicle emerges from a triangular delthyrium that may become restricted by disjunct or conjunct deltidial plates or by a symphytium. As growth proceeds, attrition in the apical region of the umbo where the shell is in direct contact with the substrate commonly leads to breaching of the posteromedian apex of the delthyrium by the pedicle in varying degrees. The foramen is submesothyrid, mesothyrid, or permesothyrid in most Mesozoic and Cenozoic terebratulides but may be amphithyrid (*Amphithyris, Platidia*) or rarely hypothyrid (*Malleia*) (see WILLIAMS, BRUNTON, & MACKINNON, 1997, p. 356, fig. 318). Rarely, the beak is elongated to produce a distinctive rostrum as in the Cretaceous *Terebrirostra* and Miocene to Holocene *Agulhasia.*

The foramen varies in size from a pinhole, as in the Upper Cretaceous terebratuloid genus *Gibbithyris,* to a large, circular to subcircular or oval opening, which accommodated an always functional pedicle. Deltidial plates are commonly conjunct, although in cancellothyridoids these are characteristically disjunct. Members of such Paleozoic families as Notothyrididae and Cranaenidae possess a labiate foramen that is also present in a few Cenozoic genera such as *Liothyrella.*

Color

Shell coloration is a characteristic feature of many living terebratulides, and color patterns are not uncommonly preserved in some Paleozoic and Mesozoic brachiopods (e.g., *Cranaena, Beachia, Coenothyris*) (CLOUD, 1942; BLODGETT, BOUCOT, & KOCH, 1988; HAGDORN & SANDY, 1998). The most distinctive colors are shades of pink, red, pale orange, or red-brown; the entire shell exterior may be colored (e.g., *Argyrotheca, Bouchardia, Kraussina, Neothyris*), or there may be a radiating pattern characteristic of a particular species (e.g., *Frenulina sanguinolenta, Calloria variegata*). Bright colors are characteristic of species living in shallow water (usually less than 50 m). The pigments are derived from the algae ingested by the living brachiopod (CUSACK & others, 1992), and thus it is probable that fossil species exhibiting shell coloration were also inhabitants of shallow water. Deep-water terebratulides are commonly white, cream, or pale gray. Color may have some deterrent effect on predators.

INTERNAL STRUCTURES

Spiculation

Spicules are variably developed in a number of terebratulide families. Typical spicule morphology is shown in WILLIAMS, BRUNTON, and MACKINNON (1997, fig. 339 and 340). Well-developed spiculation in the lophophore and mantle is characteristic of most living members of superfamilies Cancellothyridoidea, Dyscolioidea, Terebratuloidea, Platidioidea, and Kraussinoidea. Some genera of Kingenoidea and Laqueoidea may be weakly spiculate. Spicules are preserved occasionally in fossil shells (e.g., STEINICH, 1963) and are assumed to have been present in other fossil examples of the strongly spiculate groups. Spicules appear to be most abundant in families with small, short loops and may have provided additional support for the lophophore.

Ventral Valve Interior

The ventral valve of most terebratulides is relatively simple. Apart from the presence or absence of a pedicle collar, hinge teeth, and differences in definition of muscle scars (which may produce a myophragm), the feature of major importance at a higher taxonomic level is the presence or absence of dental plates. In a few superfamilies, the teeth are supported by well-defined dental plates of secondary shell that extend to the floor of the ventral valve. The presence of well-developed dental plates is a diagnostic character of Zeillerioidea, Laqueoidea, and Kingenoidea. Short dental plates, although quite common in Paleozoic genera, are not used usually in taxonomic discrimination. The significance of presence or absence of dental plates as a possible family-level character in Dielasmatoidea needs to be reassessed.

A ventral median septum is present in some stringocephalid genera but absent from most other Devonian taxa. Occasionally, a very distinctive ventral muscle field allows separation of genera with similar cardinalia (e.g., *Rhenorensselaeria* and *Globithyris*). Within the Terebratellidina, only members of the Megathyridoidea possess a median septum in the ventral valve. Pedicle collars are absent or indistinct in most Paleozoic forms but are commonly present in Mesozoic and Cenozoic genera.

Hinge Teeth

All terebratulides bear well-defined cyrtomatodont hinge teeth on an astrophic hinge line. Some Cenozoic and living terebratellids are characterized by extremely swollen hinge teeth bases (e.g., *Neothyris, Stethothyris*) that may be related to strong posterior shell thickening. Such swollen bases may be grooved to accommodate the socket ridges as in *Bouchardia.* A few genera (e.g., *Dyscolia*) have seemingly disproportionately small hinge teeth for large adult shells.

DORSAL VALVE INTERIOR

Cardinalia

Almost all adult terebratulide brachiopods, with the exception of the Zeillerioidea, possess a small, often thin, flattened, ridgelike or bosslike cardinal process to which the diductor muscles were attached (BRUNTON, ALVAREZ, & MACKINNON, 1996). In most terebratulides the cardinal process is a transverse, semielliptical structure that is sometimes bilobed and occasionally becomes heavily thickened to form a protuberant myophore. The cardinal process of Paleozoic terebratulides is highly variable and in some Devonian brachiopods (e.g., *Stringocephalus*) may be very large, rodlike, and terminally bifid (BOUCOT, JOHNSON, & STRUVE, 1966). Heavily thickened cardinal processes occur in terebratulides of Cretaceous age (e.g., the short-looped *Carneithyris* and long-looped *Terebrirostra* and *Trigonosemus*), and in some Cenozoic and extant terebratellids (e.g., *Rhizothyris, Neothyris*).

A cardinal plate perforated by a dorsal foramen is characteristic of many Paleozoic stringocephaloids and cryptonelloids, and features of the cardinalia are important diagnostic characters in cryptonelloids and dielasmatoids. The presence of outer or less commonly inner hinge plates is an important diagnostic feature in short-looped terebratulidines.

Socket Ridges

"Socket ridges are seldom of importance in generic definition" (COOPER, 1983, p. 23). Sockets are related to the size and shape of the hinge teeth and are of diagnostic value for cancellothyridoid brachiopods (e.g., *Terebratulina*) in which crural bases are directly attached to the well-developed socket ridges.

LOOP MORPHOLOGY AND TERMINOLOGY IN TEREBRATULIDA

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Studies of living brachiopods of the order Terebratulida have shown that most adult taxa possess a plectolophous lophophore that is supported internally by a brachidium that may vary markedly in size, shape, and preservability. Depending on whether support for both the side arms and central coil of the plectolophe is provided by a twisted ribbon composed of secondary layer fibers and brachiotest (Mackay, MacKinnon, & Williams, 1993) or a spicular meshwork (Schumann, 1973), the brachidium of terebratulide brachiopods may be broadly categorized as either long looped or short looped. (Note, however, that although the terms short loop and long loop provide a quick and ready means of discriminating between adult brachiopods of the suborders Terebratulidina and Terebratellidina, they indicate nothing of the phylogenetically significant complexities of loop ontogenetic development that may occur within both suborders.)

Just as the terebratulide lophophore may undergo ontogenetic change from trocholophe to schizolophe, zygolophe, and ultimately plectolophe (Williams, Brunton, & MacKinnon, 1997, p. 115, fig. 114), so also may the supporting brachidium; and for more than a century brachiopod workers have grappled with the complexities of brachidial development, particularly in long-looped Terebratellidina. Following the lead of Friele (1877), succeeding workers chose to avoid long and detailed morphological descriptions by indicating the sequential forms of loop displayed in different species by means of adjectival names derived from typical genera. Each term was defined initially on the final, adult stage of loop development in the genus chosen, but the term was then applied in other taxa to any morphologically comparable stage of loop development, not necessarily the final stage. In particular Fischer and Oehlert (1892), Beecher (1893), and Thomson (1915a) were influential in both the development of a genus-name–based terminology and in establishing patterns of loop development as the principal basis for recognizing and differentiating groups of genera at both family and subfamily levels.

As the ontogenies of an increasing number of fossil and living brachiopods were investigated and as new taxonomic groupings were established, many new and different patterns of loop development were reported in the literature. Often, reports of loop development were accompanied by additional, new loop terminology (Cooper, 1957a; Elliott, 1965a; Elliott & Hatai, 1965; Hatai, 1965b; Dagys, 1968, 1972b, 1974; Baker, 1972; Smirnova, 1984; Smirnova & Dagys, 1986; Zezina, 1985). Elliott (1965a, p. 835), for example, considered that members of the subfamily Dallininae were characterized by loops that passed through some or all growth stages described as “precampagiform, campagiform, frenuliniform, terebrataliiform and dalliniform” (alluding to adult loop configurations in the genera *Campages, Frenulina, Terebratalia,* and *Dallina*). Similarly Elliott and Hatai (1965, p. 847) diagnosed members of the family Terebratellidae as passing through all or part of a loop development sequence termed “premagadiniform, magadiniform, magelliform, terebratelliform and magellaniform” (alluding to adult loop configurations in the genera *Magadina, Magella, Terebratella,* and *Magellania*). In terms of basic loop morphology, however, the adult loops of *Terebratalia* and *Terebratella* (and for that matter *Dallina* and *Magellania*) are virtually indistinguishable. Thus the loop terminology applied to any particular taxon was

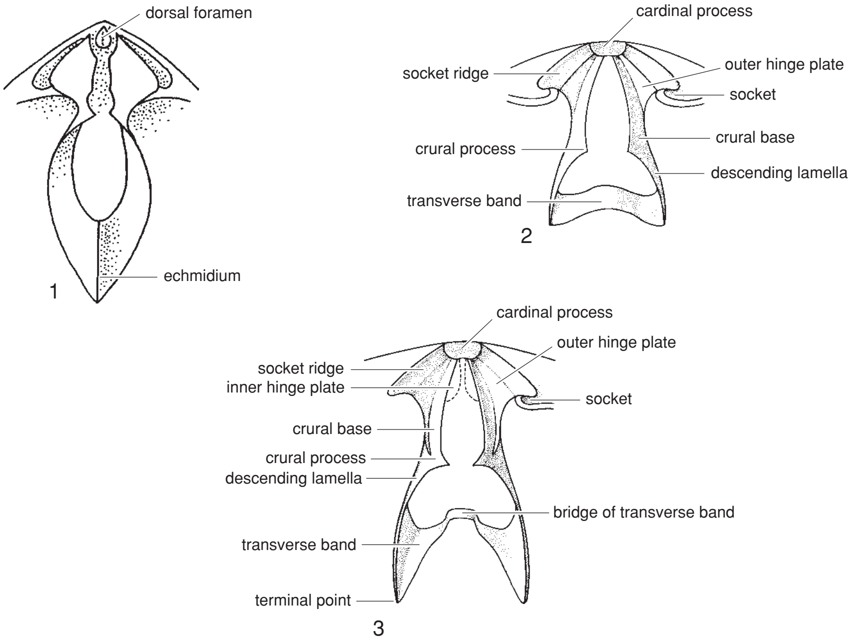

FIG. 1308. Internal morphology of representative short-looped terebratulidine brachiopods: *1,* acuminate loop typical of many Paleozoic terebratulides (adapted from Stehli, 1965); *2,* deltiform loop typical of many Mesozoic-Holocene short-looped terebratulides; *3,* long-flanged deltiform loop typical of Mesozoic Loboidothyridoidea (adapted from Cooper, 1983).

largely dependent on preconceived taxonomic affinities.

At the time of the publication of the 1965 *Treatise* (MOORE, 1965), few full sequences of loop development were known. In most, the limitations on resolution imposed by light microscopy precluded the recognition of a number of important distinctions in both early and late stages of loop development revealed by subsequent investigations using scanning electron microscopy. These latest studies (MACKINNON, 1993, 1996; MACKAY, MACKINNON, & WILLIAMS, 1993; MACKINNON & GASPARD, 1996; SAITO, 1996; MACKINNON, SAITO, & ENDO, 1997; SAITO & ENDO, 2001) have led to major taxonomic revisions that render many of the genus-name-based terms redundant.

For example, loop development studies of a variety of taxa that were previously assigned to the family Dallinidae, as constituted in the 1965 *Treatise* (MOORE, 1965), have identified at least three quite distinct and unrelated patterns of loop development in the genera *Dallina, Macandrevia,* and *Terebratalia.* Indeed, the type species of the genus *Dallina* [*D. septigera* (LOVÉN)] is characterized by an array of morphological characters, including loop development, that suggests closer affinities to Terebratellidae than to most other taxa hitherto assigned to the family Dallinidae (MACKINNON, 1996). *Macandrevia,* on the other hand, has a loop ontogeny comparable to that of Mesozoic zeillerioids (MACKINNON & GASPARD, 1996), and *Terebratalia* has a loop ontogeny suggesting closer affinities with laqueoids (SAITO, 1996; SAITO & ENDO, 2001).

TERMINOLOGY

The long-standing and up to now still widely used scheme based on names of

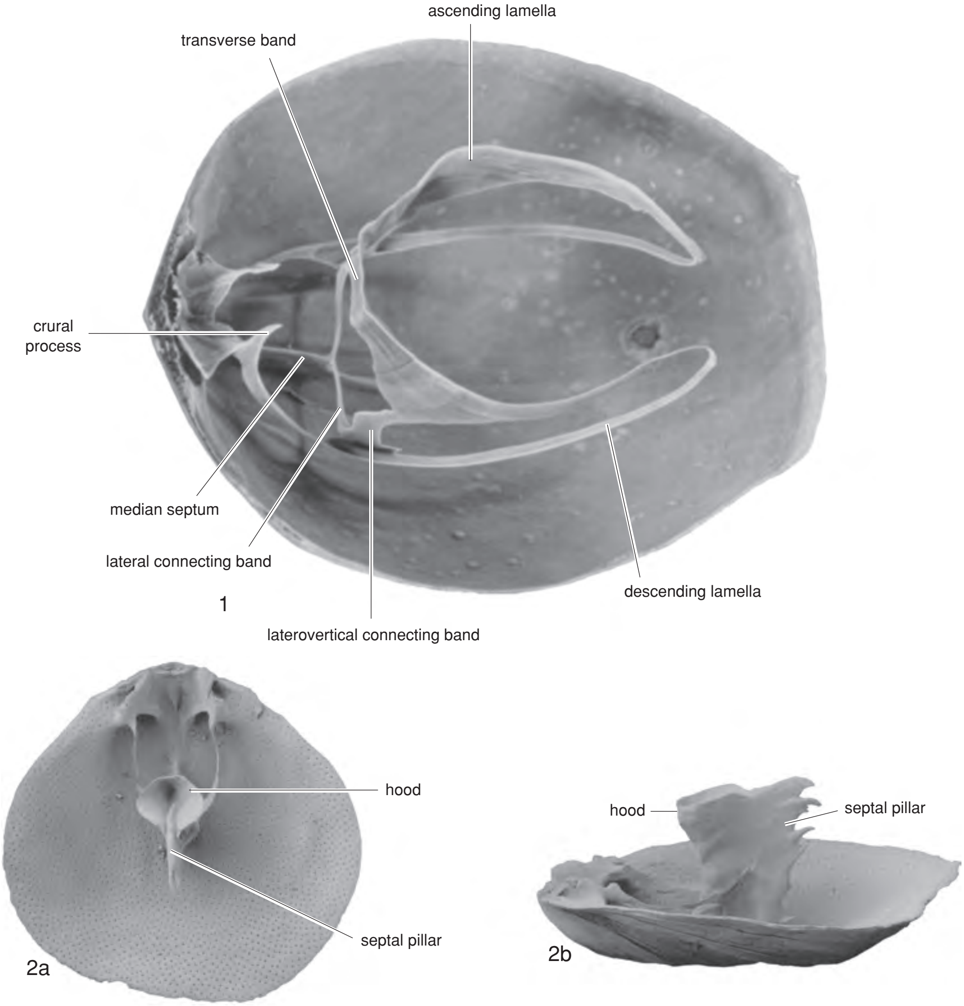

FIG. 1309. Terminology of the loop: *1, Laqueus erythraeus* DALL, oblique lateral view of adult dorsal interior showing bilateral loop phase, ×2 (new); *2a–b, Calloria inconspicua* (SOWERBY), *a–b*, dorsal and lateral views of very small juvenile showing cucullate loop phase, ×8 (new).

genera has become increasingly unworkable, and we here advocate the adoption of an alternative simpler terminology that may be applied to morphologically comparable stages of loop growth in unrelated stocks. A key advantage of a scheme eschewing a taxon-based etymology is that of being unaffected by subsequent taxonomic revision.

The terminology first applied by RICHARDSON (1975a) to post-Paleozoic long-looped terebratulides is now modified to correct some ambiguities and expanded to apply to all members of the order (see Fig. 1310–1311). The term axial is now restricted to a stage before development of a hood, and the new term cucullate is introduced for the phase coinciding with development of a hood. It should be noted that two sets of terminology are used in discussions of terebratulide brachidia. One set of terms (see Fig. 1309–1311; e.g., septal pillar) is used to describe particular loop components or supporting structures that may persist through several phases of loop development. The second set of terms (see Fig. 1310–1312; e.g., acuminate) applies to the transient (juvenile) or terminal (adult) phases of loop development themselves. Apart from the teloform loop phase, which is always a terminal phase, loop phases may be either transient or terminal.

SHORT-LOOPED TEREBRATULIDA

In short-looped terebratulidines, diagnostic features are based in part on external characters and, more importantly, on morphological features of the loop and cardinalia (Fig. 1308). In short-looped terebratulides, support for the loop is provided only by the crura. Thus, directly or indirectly, descending (as well as any ascending) loop elements are derived entirely from extensions of the cardinalia. The simplest form of support that occurs in Paleozoic terebratuloids is formed by a pair of gently curved descending lamellae that extend anteriorly from the crura and fuse anteromedially; the site of fusion of the descending branches may become enlarged to form a broad, pointed blade, the echmidium (COOPER, 1957a). This loop form has been variously referred to in the literature as centronellid, centronelloid, or centronelliform; the nongeneric term acuminate is introduced herein for this form of loop (Fig. 1308.1 and Fig. 1311.1). In various Paleozoic taxa, an acuminate loop persisted in adult shells with little modification other than a general increase in size. Indeed, an acuminate loop developed to such large size in some Stringocephalidae, for example, that, technically, such loops could be regarded as long rather than short. Furthermore, in some Paleozoic and Mesozoic terebratulides, a ventrally projecting, medially aligned, vertical plate developed normal to the echmidium. In most short-looped brachiopods, such as dielasmatoids and terebratuloids, a juvenile acuminate phase (with or without a vertical plate) gave rise to an adult, deltiform phase consisting of a variably disposed transverse band extending between the distal ends of two relatively short, divergent, descending lamellae (Fig. 1308.2, 1313.3a–e, and 1314.1a–f).

Some Jurassic and Early Cretaceous genera have a long-flanged deltiform loop that differs from a typical deltiform loop in the anterior extension of the terminal points beyond the transverse band as two long flanges (Fig. 1308.3 and 1311.3). In some Mesozoic Loboidothyridoidea with an adult long-flanged deltiform loop, more complicated intermediate phases of loop metamorphosis occur (DAGYS, 1968, 1972b) that involve the development of a vertical plate bisecting the echmidium. In several genera (e.g., *Viligothyris*) the intermediate phases of loop development involving the vertical plate paralleled to a remarkable degree the intermediate phases of loop development involving a septal pillar in many long-looped taxa (see Fig. 1314.2). Thus, even though the vertical plate and septal pillar are not truly homologous structures, due to strong similarities in their metamorphoses much of the descriptive terminology may be readily applied to taxa with both kinds of loop development.

Although there are some published studies (BEECHER & SCHUCHERT, 1893; WATSON, 1909; STEHLI, 1956; DAGYS, 1958, 1968, 1972b, 1974; STEINICH, 1965; CARTER, 1967b; COOPER & GRANT, 1976b), general patterns of loop development in many short-looped brachiopods are unknown. In particular, general patterns of loop development in the 140 or so long-flanged genera (mainly of Jurassic age) placed presently into superfamily Loboidothyridoidea are yet to be established.

LONG-LOOPED TEREBRATULIDA

In long-looped terebratellidines, the loop structures and associated terminology are commonly more complex because of the major developmental changes that take place during ontogeny (Fig. 1310–1312). Post-Paleozoic long-looped brachiopods

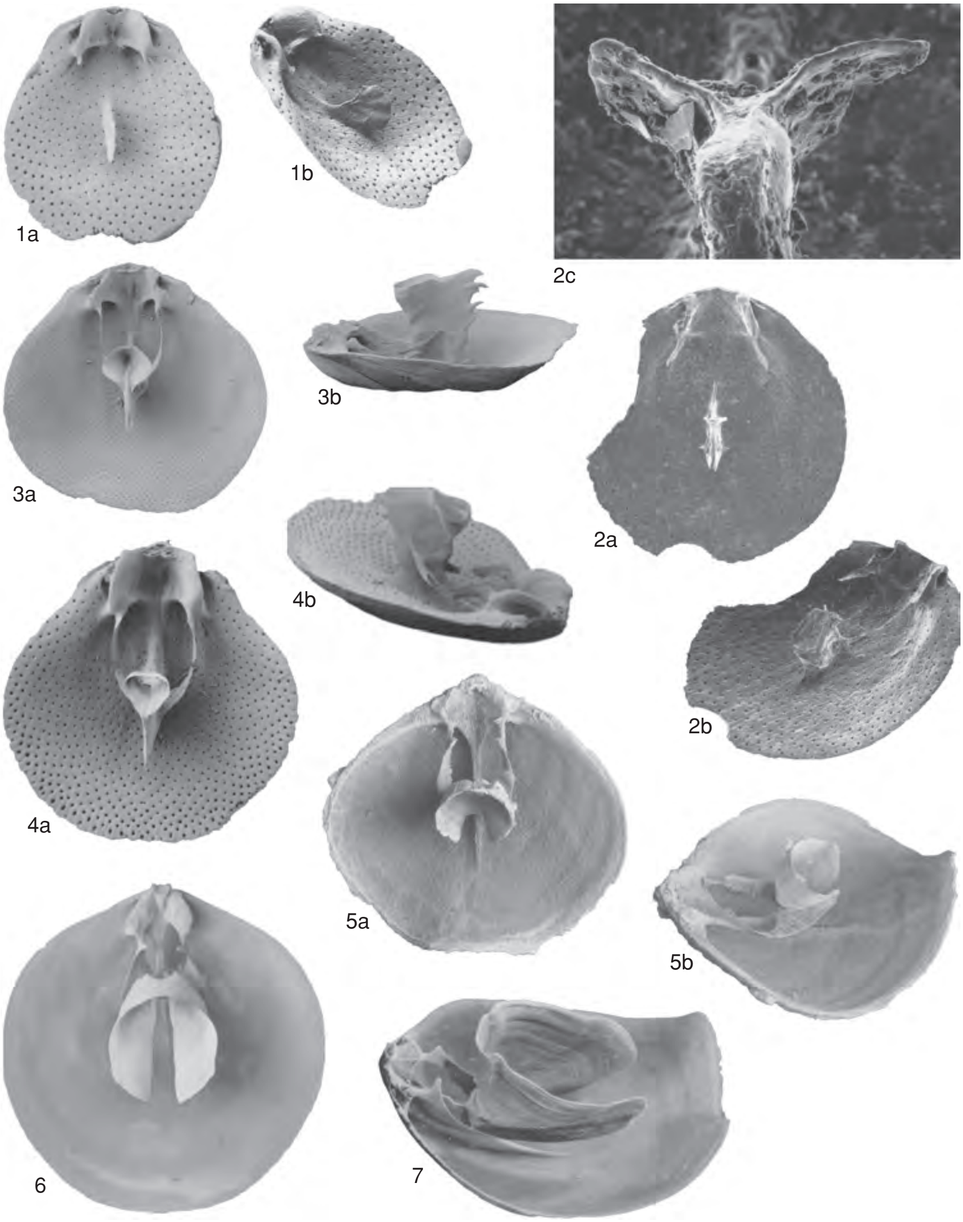

FIG. 1310. *For explanation, see facing page.*

(Terebratellidina) are characterized early in ontogeny by the development of a median septal pillar that grows from the floor of the dorsal valve (Fig. 1310.1a–b). Characteristic of Laqueoidea is the development of a pair of laterally directed septal flanges (Fig. 1310.2a–c) on the posterior edge of the septal pillar. The septal pillar is generally involved intimately in the early ontogenetic development of the ascending loop elements, which develop first as a hood (Fig. 1310.3a–b) and second as a ring (Fig. 1310.4a–b), before uniting with the descending elements (incipient descending lamellae), which also develop in part from the septal pillar. Later in ontogeny, the septal pillar may grow into a full median septum from which the loop may become detached.

In *Laqueus* (Fig. 1309), the adult loop consists of a pair of gently curved and partially twisted descending lamellae that terminate posteriorly as a pair of pointed crural processes close to the point of union of the descending lamellae with the crura. At their anterior extremities the descending lamellae bend tightly through approximately 180° and extend posteriorly as rather more strongly curved and twisted ascending lamellae that are united posteriorly by a transverse band. A pair of lateral connecting bands joins the descending lamellae to the median septum, and the ascending and descending lamellae are braced by a pair of laterovertical connecting bands. In *Ecnomiosa,* a pair of mediovertical connecting bands extend between the transverse band and median septum (see Fig. 1311.11a–b).

In the post-Paleozoic Terebratellidina for which full developmental sequences are known (but excluding, most notably, the

FIG. 1310. New terminology and illustrations of terebratulide developmental phases, with synonyms.

Annular phase: with a ring formed by resorption of the posterior apex of the hood. The ring and descending lamellae are attached separately to the septal pillar, but are not yet united (see haptoid phase); syn: cryptacanthiform (early), magadiniform, premagadiniform; syncampagiform; *4a–b, Magellania flavescens* (LAMARCK), ventral and oblique lateral views of dorsal valve interior, ×18 (new).

Axial phase: with a vertical plate (Paleozoic forms) or septal pillar (post-Paleozoic forms); descending lamellae complete in Paleozoic forms, rudimentary in most post-Paleozoic forms; syn: centronelliform, platidiiform, preparamagadiniform; *1a–b, Calloria inconspicua* (SOWERBY), ventral and oblique lateral views of dorsal valve interior, ×10 (new).

Cucullate phase: with a hood on either vertical plate or septal pillar. Descending lamellae complete in Paleozoic forms, commonly incomplete in post-Paleozoic forms; syn: early cryptacanthiform, paramagadiniform, precampagiform, premagadiniform, quasipremagadiniform; *3a–b, Calloria inconspicua* (SOWERBY), ventral and oblique lateral views of dorsal valve interior, ×8 (new).

Diploform phase: with adjacent ascending and descending elements fused and free of the septum except at their posterior extremities. At this stage (early diploform) the transverse band and posterior sections of the ascending lamellae are defined. The descending branches are defined (late diploform) with resorption of the anterior segments of the ascending branches; syn: campagiform, cryptacanthiform, ismeniform, magadiform, pre-ismeniform; *6, Jaffaia jaffaensis* BLOCHMANN, ventral view of dorsal valve interior, ×3; *7, Campages furcifera* HEDLEY, lateral oblique of dorsal valve interior, ×2 (new).

Haptoid phase: with anterior fusion of ascending and descending elements and their accompanying separation from the vertical plate or septal pillar. Posterior sections of the ascending and descending elements are still separately attached to vertical plate or septal pillar; syn: cryptacanthiform (in part), dictyothyridiform, magelliform, magaselliform; *5a–b, Magella carinata* THOMSON, ventral and oblique lateral views of dorsal valve interior, ×4 (new).

Septal flange: 2*a–b*, ventral and oblique views, ×20, *2c,* closeup of septal flanges in *Laqueus erythraeus* DALL, ×40 (new).

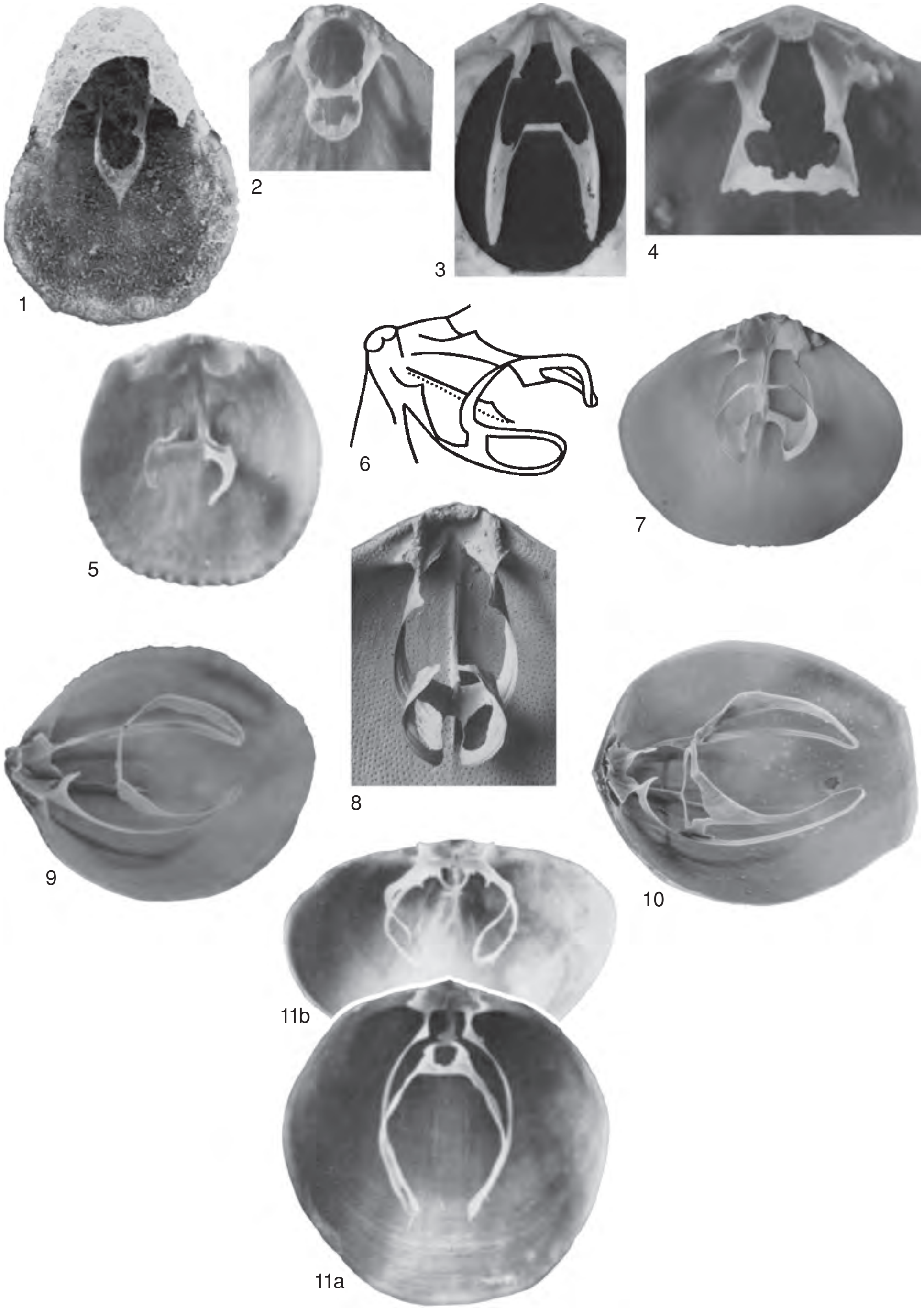

FIG. 1311. *For explanation, see facing page.*

genera *Macandrevia* and *Ecnomiosa* and the Megathyridoidea), only the posterior sections of the descending lamellae arise from the cardinalia but all other parts of the loop, including anterior segments of the descending lamellae, derive from a septal pillar (Baker, 1972, 1989b; Richardson, 1975b; MacKinnon, 1993; MacKinnon & Gaspard, 1996).

In the Terebratelloidea, Laqueoidea, Zeillerioidea, and Kingenoidea, the following sequential phases of loop development occur.

1. Formation of a septal pillar on the dorsal valve floor (axial phase) (Fig. 1310.1a–b).

2. Formation of a hood on the ventral or posteroventral crest of the septal pillar (cucullate phase) (Fig. 1310.3a–b).

3. Enlargement of the hood and resorption of its apex to form a ring, segments of which ultimately form the ascending lamellae and transverse band (annular phase) (Fig. 1310.4a–b).

4. Fusion of the growing (anterior) edges of the descending lamellae and ring, followed by the progressive detachment in an anterior direction of the fused elements from the septal pillar or septum (haptoid phase) (e.g., *Magella,* Fig. 1310.5a–b). In several genera the haptoid phase may be succeeded by a phase in which the hood becomes enormously expanded anteriorly, while the descending lamellae retain points of attachment to a median septum (diploform phase) (e.g., *Campages, Jaffaia,* Fig. 1310.7 and 1310.6).

Up to the haptoid or diploform phases, development of the loop is comparable in all four of the above superfamilies, but thereafter the development proceeds along different routes that are determined primarily by subsequent resorptive and accretionary processes.

In Terebratelloidea, the ascending loop elements continue to expand through accretion along the anterior (outward-facing)

Fig. 1311. New terminology and illustrations of terebratulide developmental phases, with synonyms.

Acuminate phase: with laterally bowed, descending lamellae extending from crura but otherwise unsupported and uniting anteromedially to form an echmidium; syn: centronelliform; *1, Dielasma zebratum* Cooper & Grant, ventral view of dorsal valve interior, ×10 (new).

Bifurcate phase: with Y-shaped median septum (characteristic of Kraussinidae); syn: kraussinid; *5, Kraussina rubra* (Pallas), ventral view of dorsal valve interior, ×1.5 (Cooper, 1973b).

Bilacunar phase: with two lacunae in the dorsal segments of the band forming the ring; syn: frenuliform, frenuliniform, ismeniform, kingeniform; *8, Frenulina sanguinolenta* (Gmelin), ventral view of dorsal valve interior of slightly damaged loop, ×5 (new).

Bilateral phase: with two pairs of connecting bands, lateral and laterovertical; syn: laqueiform; *10, Laqueus erythraeus* Dall, lateral oblique view of dorsal valve interior, ×1 (new).

Deltiform phase: with a variably disposed transverse band extending between the distal ends of two relatively short, divergent, descending lamellae; syn: chilidonophorid, cranaeniform, dielasmoid, pygopid, terebratuloid, terebratuliform, terebratuliniform, sulcatinelliform; *2, Terebratulina latifrons* Dall, ventral view of loop, ×4 (Cooper, 1983); *4, Liothyrella neozelanica* Thomson, ventral view of loop, ×2 (Cooper, 1983).

Laterovertical phase: with laterovertical connecting bands only; syn: pictothyridiform; *6, Pictothyris picta* (Dillwyn), lateral view of loop, ×3 (after Saito & Endo, 2001).

Long-flanged deltiform: deltiform loop in which descending branches are extended as flanges beyond the transverse band; syn: loboidothyrid; *3, Monsardithyris ventricosa* (Zieten), ventral view of dorsal valve interior, ×1.5 (new).

Mediovertical phase: with a pair of mediovertical connecting bands extending from the median septum to the transverse band; syn: belothyridiform, megerliiform, muehlfeldtiform; *11a–b, Ecnomiosa gerda* Cooper, ventral and anterior views of loop showing mediovertical connecting bands, ×1.6 (Cooper, 1977).

Teloform phase: with loop free of septum; syn: aulacothyroidiform, cryptonelliform, dalliniform, glossothyropsiform, glossothyropsidiform, magellaniform, zeilleriform, zeilleriid; *9, Magellania flavescens* (Lamarck), oblique lateral view of dorsal valve interior, ×2 (new).

Trabecular phase: with lateral connecting bands only; syn: terebratelliform, terebrataliiform; *7, Calloria inconspicua* (Sowerby), ventral view of dorsal valve interior, ×4 (new).

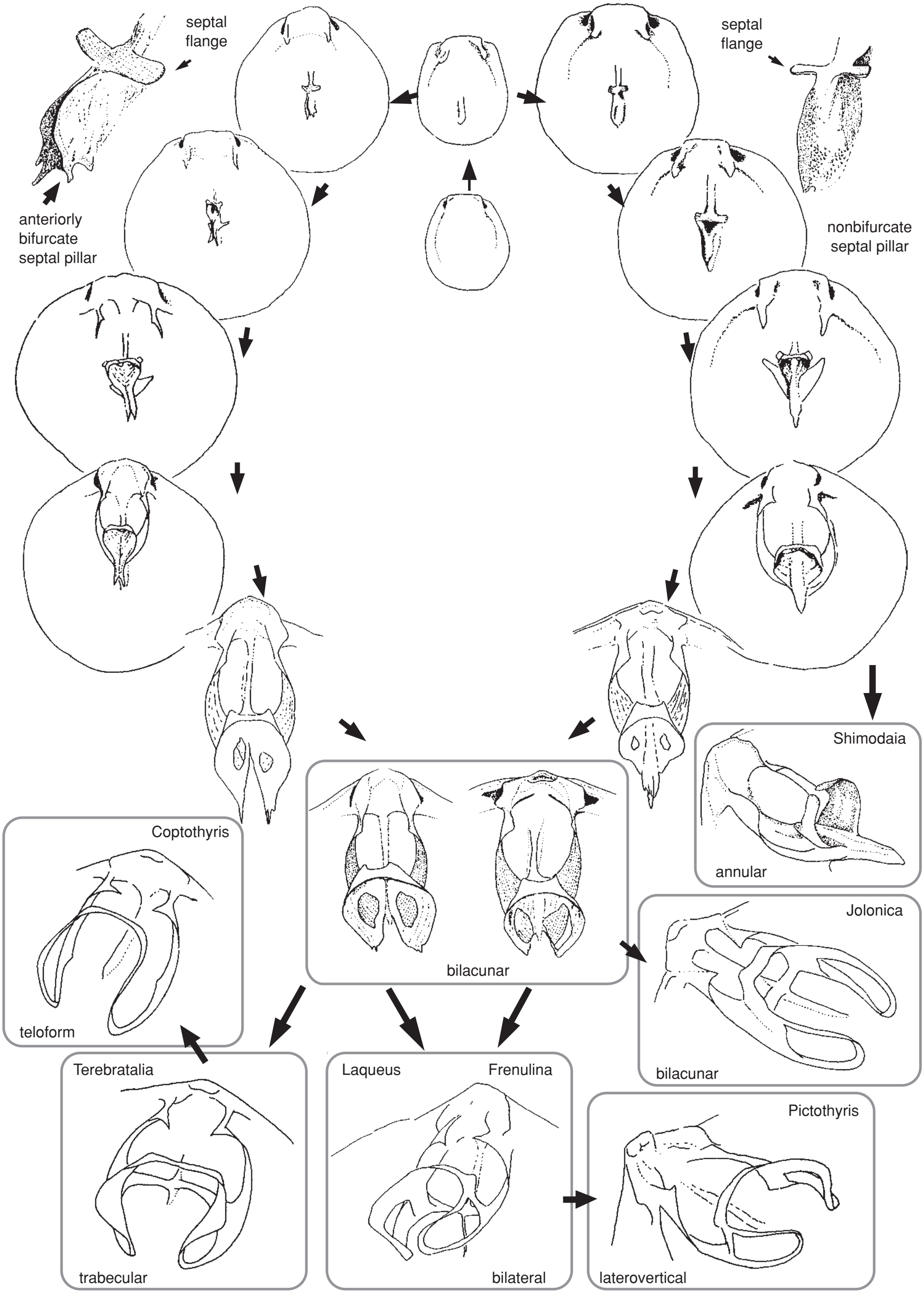

FIG. 1312. Loop ontogeny of selected recent Laqeoidea; drawings not to scale; Laqueoidea are characterized by presence of a pair of flanges on septal pillar at axial phase. The route to transient bilacunar phase may follow one of two paths: one with, and one without, anterior bifurcation of the median septum. Various terminal adult loop phases, following on from the transient bilacunar phase, are shown (adapted from Saito & Endo, 2001).

edge and resorption along the posterior (inward-facing) edge. Detachment of the descending lamellae from the median septum by resorption of the junction gives rise to a long, reflected loop free of attachments (teloform phase; e.g., *Magellania,* Fig. 1311.9). In certain Terebratelloidea (e.g., *Calloria*), the descending lamellae, although well separated from the median septum, are braced by a pair of narrow, lateral connecting bands formed from lateral extensions of the median septum (trabecular phase) (Fig. 1311.7).

Following the haptoid phase of some Laqueoidea, Zeillerioidea, and Kingenoidea, a pair of lacunae may form within the ascending lamellae as a result of localized resorption (bilacunar phase) (e.g., *Frenulina,* Fig. 1311.8). The pair of steeply inclined loop segments immediately posterior of the resorption lacunae are conveniently referred to as vertical connecting bands that feature in various later loop phases. The adult loop of the genus *Laqueus* (Laqueoidea) is characterized by the development of two pairs of connecting bands, lateral and laterovertical (bilateral phase) (Fig. 1311.10). The adult loop of the genus *Pictothyris* (Laqueoidea) is characterized by only laterovertical connecting bands (laterovertical phase) (Fig. 1311.6). The adult loop of *Ecnomiosa* (Kingenoidea) is characterized by only mediovertical connecting bands (mediovertical phase) (Fig. 1311.11a–b).

UNUSUAL OR ABERRANT POST-PALEOZOIC LONG-LOOPED BRACHIOPODS

Several Cenozoic terebratulide superfamilies contain unusual and commonly micromorphic species in which a loop is either absent, rudimentary, or in a form that is not readily comparable with the growth stages common to other loop-bearing superfamilies.

KRAUSSINOIDEA

A distinctive Y-shaped median septum is characteristic of all Kraussinoidea. In the past, the two ventrally divergent branches of the septum have been termed ascending lamellae (THOMSON, 1927; ELLIOTT, 1949; RICHARDSON, 1975a), but scanning electron microscopy has revealed that these projections have an origin and shell ultrastructure quite different from the ascending lamellae of typical long-looped terebratulides.

Consequently the standard kraussinoid brachidium is recognized as a unique loop form, herein termed bifurcate (Fig. 1311.5). In *Megerlia truncata,* however, further loop development is apparent. First, in juvenile *M. truncata,* the distal extremities of the Y-shaped median septum become united by a narrow transverse band to form a ring, i.e., an annular phase (but of very different origin from the annular phase of most other long-looped brachiopods). Thereafter, rudiments of descending branches grow from both the ring and crura, eventually uniting and giving rise to a hybrid diploform loop phase resembling that of the terebratellid *Campages* but formed by a very different growth process (see Fig. 1317.4).

PLATIDIOIDEA

Various genera of Platidioidea are characterized by a high septal pillar from which narrow lamellae may extend posterolaterally to connect with crura, and thus their adult loop phase might nominally be termed axial (see Fig. 1317.2). The variably coiled lophophores occurring in these taxa, however, are supported principally by dense spicular meshworks more comparable to that found in, for example, Cancellothyrididae, rather than ribbonlike lamellae composed of secondary layer fibers and brachiotest (MACKAY, MACKINNON, & WILLIAMS, 1993); thus Platidiidae currently defy easy categorization.

MEGATHYRIDOIDEA

Megathyridoidea are commonly characterized by a pair of arcuate descending branches that, after descending to fuse with the dorsal valve floor, rise again to unite anteromedially on a high septal pillar (see Fig. 1316.3). Compared with other long-looped forms, the axial stage of megathyroids is unusual in that the descending elements are commonly fully developed at this stage. The megathyroid brachidium is comparable to the earliest loop phase in both *Macandrevia* and *Ecnomiosa* (MacKinnon & Gaspard, 1996).

PALEOZOIC LONG-LOOPED CRYPTONELLOIDEA

An initial acuminate phase characterizes the loop development of the upper Paleozoic–lower Mesozoic long-looped Cryptonelloidea described by Cooper (1957) and Cooper and Grant (1976b). No vertical plate is developed, and the ascending loop elements arise directly from the echmidium (Fig. 1313.2). A median septum, if present, is never involved in the loop development of Cryptonelloidea (Cooper & Grant, 1976b).

These differences in the origins of parts of the cryptonelloid loop result in distinctly different developmental sequences from those found in post-Paleozoic long-looped forms. In Cryptonelloidea, as in the long-flanged Loboidothyridoidea, the initial development of the descending lamellae is complete before the ascending elements appear. In most post-Paleozoic long-looped terebratulides both ascending and descending elements develop concurrently. In most other respects, however, the patterns and processes of loop formation in both Paleozoic and post-Paleozoic taxa are remarkably similar. Similarities include those listed below.

1. Formation of a vertical plate on either an echmidium or a septal pillar on the dorsal valve floor.
2. Formation of a hood on either the ventral surface of an echmidium or on the ventral crest of either a vertical plate or septal pillar.
3. Enlargement of the hood and resorption of its apex to form a ring, segments of which ultimately form the ascending lamellae and transverse band.
4. Combining of anterior growing edges of ascending and descending loop elements, followed by progressive anterior growth and divergence of the leading edges away from the septal pillar.
5. Retention of a posterior connection between the descending lamellae either directly (in Paleozoic forms) or as a pair of lateral connecting bands fused to a septum.
6. Resorption of the direct connection (in Paleozoic forms) or lateral connecting bands (in post-Paleozoic forms) to give a long, reflected loop free of attachments.

METHODS OF STUDYING LOOPS

Understanding loop morphology and ontogenetic development is essential in terebratulide classification. Several methods of obtaining information on loops are used.

Manual preparation of loops of living brachiopods, after dissolution of the tissue, is straightforward except for highly spiculate genera where attempts to remove the spicules may damage or destroy delicate loop structures. Acid treatment and etching of silicified Paleozoic specimens facilitated study of growth series of entire loops (Cloud, 1942; Cooper & Grant, 1976b). For many sediment-infilled Mesozoic and Cenozoic terebratuloids, Cooper (1983) demonstrated that it is possible with patience and care to dissect the loops of many brachiopods preserved in weakly lithified sediments. Because of the time-consuming effort required, however, only one or a few examples of a species (where possible the type species) are usually prepared.

For most Mesozoic terebratulides, the principal method of establishing loop morphology has been by the preparation of transverse serial sections of oriented shells (Sandy, 1986b) and reconstructions of loops using distances between sections. [Note that in the 1965 *Treatise* (Moore, 1965), sections were oriented with the ventral valve uppermost, and distances between successive sections were not supplied.] Previous attempts to reconstruct loops from serial sections have exhibited varying degrees of accuracy (Cooper, 1983b, p. 1); computer-drawn three-dimensional reconstructions based on serial sections should eventually provide more accurate information on the disposition of loops.

It is emphasized that understanding of loop ontogeny may be critical for correct taxonomic placing of terebratulides, and juveniles as well as adults need to be studied. And, although variability in external morphology is adequately known for a few terebratulides (even if rarely taken into account when new putative genera are described), it must be recognized that the degree of variability in internal structures of terebratulides is almost completely unknown. Where a large number of loops of well-preserved specimens from a single species and locality have been figured [e.g., *Colosia* in COOPER (1983, pl. 35); *Liothyrella* in LEE, CARLSON, & others (2001)], the variability is considerable.

Because the information on loops derived from serial sectioning and from dissection differs in terminology, it is difficult to make comparisons between loop morphological information obtained by these different methods. Some workers have preferred to use only information from serial sections (e.g., MIDDLEMISS, 1959, 1980; ALMÉRAS, 1971; AGER, 1990); others, notably COOPER (1983), have used serial sections only when dissection failed. In this work, we have used illustrations of actual exposed loops wherever possible. Where genera, particularly Mesozoic taxa, are studied principally using serial sections, at least the name bearer of each family or subfamily is illustrated by means of sections. Loop reconstructions from serial sections are provided where no actual loop is available, but these should be used with caution.

HOMOPLASY

As MUIR-WOOD (1965a, p. 767) stressed, homoplasy (or homeomorphy) occurs repeatedly among Paleozoic, Mesozoic, and Cenozoic terebratulides and constitutes one of the major problems in their identification and classification. Without careful examination of internal structures, it may be impossible to distinguish between some representatives of the Terebratuloidea, Zeillerioidea, and Terebratelloidea. As examples of such external morphological similarity (convergence), MUIR-WOOD (1965a) listed four Late Jurassic genera: *Cheirothyris* (Zeillerioidea), *Trigonellina* and *Ismenia* (Laqueoidea), and the short-looped *Cheirothyropsis* (Loboidothyridoidea). Similarly, unless internal structures and punctation are examined, it may be difficult to distinguish between Late Triassic terebratuloids, zeillerioids, spiriferoids, and rhynchonelloids that have smooth shells and unisulcate dorsal valves. Homeomorphy poses particular problems in the many Paleozoic forms where the loop is unknown. At least one Devonian terebratulide, *Scaphiocoelia,* was thought to be a rhynchonellide until endopunctae were observed. A similar type of homoplasy occurs in some Holocene brachiopods, including the short-looped *Dallithyris* and the long-looped *Dallina.* And, as described above, identical adult loops in many terebratulide superfamilies may be arrived at from very different ontogenetic pathways.

SUBORDER TEREBRATULIDINA

Differentiation of superfamilies within suborder Terebratulidina is based upon presence or absence of dental plates, presence or absence of a perforate cardinal plate, loop size and shape, loop ontogenetic stages, and final loop form in adult brachiopods.

Stringocephaloids (Fig. 1313.1) are small to very large, commonly ventribiconvex or rarely planoconvex, subcircular to elongate oval in outline, and smooth, although some are finely striate, costellate, or peripherally costate. The anterior commissure is usually rectimarginate but may be uniplicate, plicosulcate, or unisulcate. The foramen may be submesothyrid or hypothyrid, with conjunct or disjunct deltidial plates. Dental plates vary from well developed to obsolete. A cardinal process may be well developed or absent. Hinge plates are commonly discrete

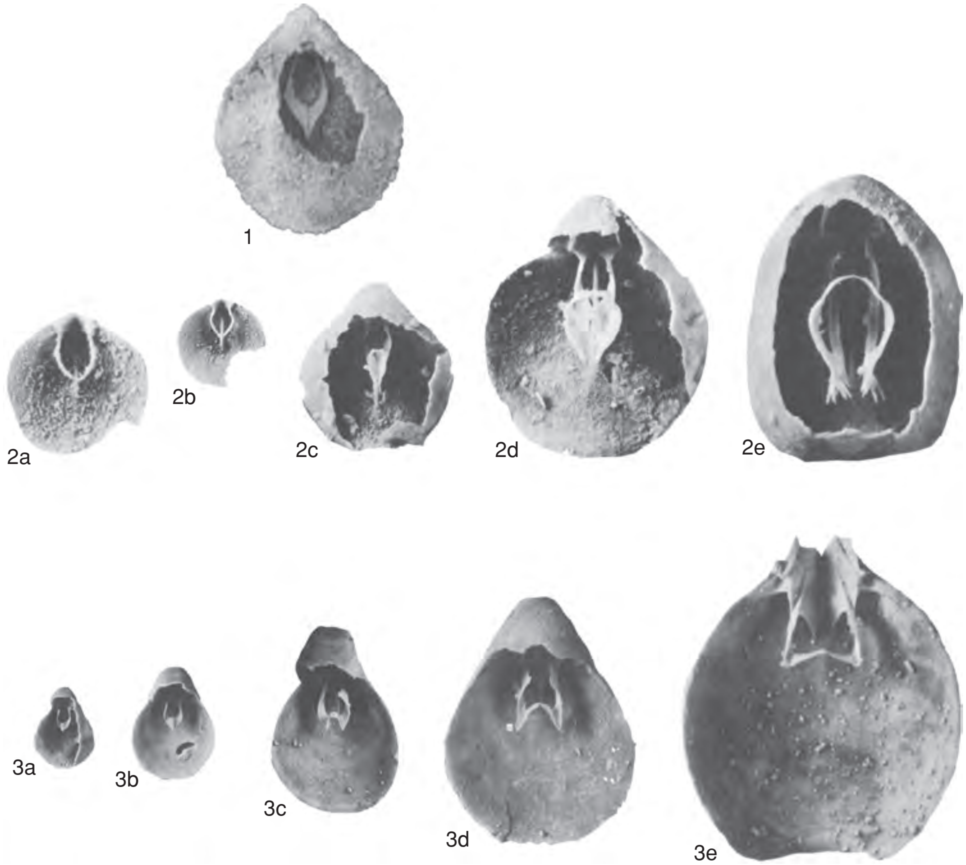

FIG. 1313. Loop ontogeny or adult loop morphology for terebratulide superfamilies; *1*, Stringocephaloidea, Centronellidae; adult loop morphology in *Nanothyris mutabilis,* ×4 (Boucot & Wilson, 1994); *2a–e,* Cryptonelloidea, Cryptonellidae; loop ontogeny in *Glossothyropsis rectangulata; a–d*, ×5, *e,* ×3 (Cooper & Grant, 1976b); *3a–e*, Dielasmatoidea, Dielasmatidae; loop ontogeny in *Dielasma zebratum*, ×2 (Cooper & Grant, 1976b).

but may be united to form a septalium. A perforate or imperforate cardinal plate may be present, and it may be supported by crural plates. A median septum may be absent, present in the dorsal valve, in the ventral valve, or in both valves. The adult loop is usually acuminate and may be marginal, with or without spines; rarely the loop is teloform.

Cryptonelloids (Fig. 1313.2) are small to medium, ventribiconvex, elongate oval to subpentagonal in outline, and smooth or sometimes plicate anteriorly. The anterior commissure may be rectimarginate, unisulcate, or sulciplicate. The foramen is typically permesothyrid or submesothyrid and is often labiate. Deltidial plates are usually conjunct, and a pedicle collar and dental plates may be present or absent. The hinge plate is commonly undivided and perforate, and a median septum and crural plates are rarely developed. The adult loop is highly variable and may be short and acuminate, deltiform or diploform, or long and teloform.

The Dielasmatoidea (Fig. 1313.3) are a large and complex, probably polyphyletic group of terebratulides. Adult shells are small to medium in size, biconvex, elongate oval to subcircular or subpentagonal in outline, and usually smooth or sometimes anteriorly plicate. The highly variable anterior commissure may be rectimarginate to uniplicate, unisulcate, bisulcate, or sulciplicate. The foramen is usually medium in size, permesothyrid or mesothyrid, and often labiate. A pedicle collar is commonly present, and dental plates are present in some families. The cardinal process is small, and a dorsal median septum may be present or absent. Outer hinge plates are weakly developed, and inner hinge plates may be absent, present and discrete, joined near the valve floor, or joined to median septum to form a septalium. The loop is usually short, acuminate in juveniles, and becoming deltiform in adults by fission and resorption of echmidium and insertion of transverse lamellae. Some families have more complex developmental stages, and in some taxa the loop is moderately long with descending and ascending lamellae.

Terebratuloids (Fig. 1314.1) are small to very large, commonly smooth or rarely capillate, subpentagonal to elongate oval in outline, and usually biconvex or ventribiconvex. The anterior commissure is rectimarginate in juveniles, but adults may be uniplicate, paraplicate, bisulcate, or sulciplicate. The foramen is usually medium to large and mesothyrid or permesothyrid. Deltidial plates may be conjunct, disjunct, or form a symphytium that may be visible or concealed. There are no dental plates nor a dorsal median septum. A variable cardinal process is commonly present. The loop is short and deltiform, with simple development of the loop as an extension of the crura. Other hinge plates are generally present, but inner hinge plates are rare. Crural processes may be short or very long, and the transverse band of the loop is commonly arched. The lophophore is plectolophous, and spicules are present in living species.

The Loboidothyridoidea (Fig. 1314.2) are a very large and complex, probably polyphyletic group of brachiopods that are difficult to classify because the ontogenetic development of most genera is unknown. They vary in size from small to very large and are commonly smooth, although a few are capillate or anteriorly costate. Most are ventribiconvex and subpentagonal to elongate oval in outline. The anterior commissure varies from rectimarginate to biplicate or sulciplicate. The foramen is commonly large and permesothyrid. There are no dental plates nor median septum. A cardinal process and outer hinge plates are commonly well developed, but inner hinge plates are rare. The adult loop is deltiform, extending for 0.4 to 0.6 of the dorsal valve length, and is commonly long flanged with a strongly arched transverse band. The loop ontogeny may be complex, but developmental stages of most genera are not known.

Dyscolioids (Fig. 1314.3) are small to very large, commonly biconvex, and subtriangular to subcircular or elongate oval in outline. They are smooth or very finely capillate with a large, mesothyrid to permesothyrid foramen. The anterior commissure may be rectimarginate or deeply unisulcate and may develop as two lateral lobes in juveniles, which fuse in adults to enclose a median perforation. There is no median septum nor dental plates; the cardinal process is commonly small; and hinge plates are poorly defined. The deltiform loop is very short, commonly wide, and anteriorly rounded with inconspicuous crural processes. The lophophore may be plectolophous or trocholophous (in living *Dyscolia*), and living species are strongly spiculate.

Cancellothyridoids (Fig. 1314.4) share a number of features that differentiate them from other terebratulides, particularly their capillate, costate, or costellate ornament; short loop; and crural processes that may be disjunct or unite to form a short, ringlike loop or tube. They are typically small to medium in size, elongate oval, subcircular or subtrigonal in outline, and commonly rectimarginate. There are no dental plates nor median septum, and outer and inner hinge plates are rarely developed. Crural bases are attached to strong, elevated socket ridges; and dorsal pedicle muscles are attached to the floor of the dorsal valve between the

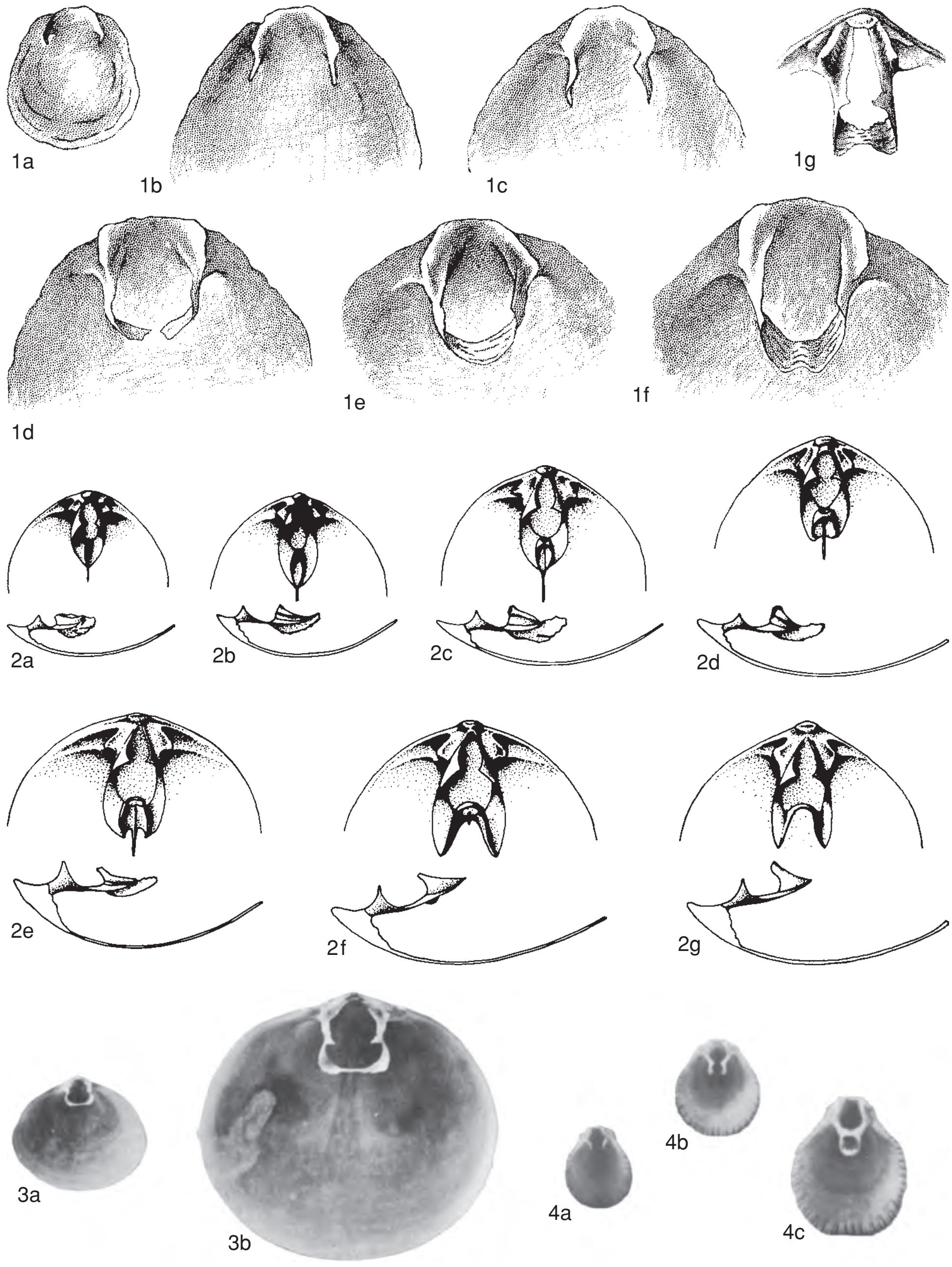

FIG. 1314. Loop ontogeny or adult loop morphology for terebratulide superfamilies: *1*, Terebratuloidea, Terebratulidae; loop ontogeny in *Liothyrella blochmanni, 1a–f*, ×14; *1g*, ×4; *2a–g*, Loboidothyridoidea, Triadithyrididae; loop ontogeny in *Viligothyris viligaensis*, ×3 (Dagys, 1968); *3a–b*, Dyscolioidea, Dyscoliidae; loop ontogeny in *Dyscolia ewingi*, ×1 (Cooper, 1973a); *4a–c*, Cancellothyridoidea, Cancellothyrididae; loop ontogeny in *Terebratulina retusa*, ×2 (Logan, 1979).

adductor muscles. The lophophore may be spirolophous or plectolophous, and mantle and body wall are usually strongly spiculate.

SUBORDER TEREBRATELLIDINA

Differentiation of superfamilies within suborder Terebratellidina is based on such features as presence or absence of dental plates, presence or absence of a septal pillar and its part in loop development, loop ontogenetic stages, and final loop form in adult brachiopods.

Zeillerioids (Fig. 1315) are small to large, subpentagonal, oval to elongate oval in outline, biconvex or ventribiconvex, and smooth, although costae or rugae may be developed rarely. The anterior commissure may be rectimarginate, unisulcate, or uniplicate. Deltidial plates are commonly conjunct or may be disjunct or form a symphytium. The foramen may be small to large and mesothyrid to permesothyrid, and beak ridges are commonly well developed. A pedicle collar may be present, but a cardinal process is rarely developed. Dental plates are invariably present and may be partly or wholly enveloped in callus. The adult loop is teloform, commonly long and slender, with or without spines. Development of the loop may be associated with a septal pillar very early in ontogeny, but there is no adult connection of the loop with the median septum.

Kingenoids (Fig. 1316.1) are small to medium, smooth or granular, generally subcircular to subpentagonal in outline, and rectimarginate, unisulcate, or intraplicate. Deltidial plates may be conjunct or disjunct. They have a broad, sessile pedicle collar and well-developed dental plates. Outer hinge plates are commonly well developed, and inner hinge plates are united to form a septalium. The septal pillar is retained throughout ontogeny, commonly developing as a long, thin median septum. The lophophore is plectolophous, and the mantle may be spiculate.

Laqueoids (Fig. 1316.2) are small to large, subcircular to transverse or elongate oval in outline, and rectimarginate to unisulcate. Most are smooth, but a few are multicostate. Deltidial plates may be conjunct, disjunct, or form a symphytium. As with kingenoids, they have a broad sessile pedicle collar and well-developed dental plates. A dorsal septal pillar or median septum is present. Outer hinge plates are well developed, but inner hinge plates may be disjunct, united to form a septalium, or absent. The adult loop stage is highly variable and may be axial, annular, haptoid, trabecular, bilacunar, bilateral, or laterovertical (Fig. 1312). Septal flanges are present on the septal pillar during axial, cucullate, and annular phases of loop ontogeny. The lophophore is plectolophous, and the mantle may be spiculate.

Megathyridoids (Fig. 1316.3) are commonly small, subquadrate in outline, and commonly multiplicate with a wide hinge line and well-developed interareas. The beak is attrite and the foramen large. The pedicle collar is long, wide, and elevated; and a short low ventral median septum is commonly present. Dental plates are absent in living species and obscured by later thickening in Early Cretaceous taxa. A narrow, dorsal median septum is commonly present. There are no outer hinge plates, but conjunct inner hinge plates may form a low septalium. The loop is axial, consisting only of laterally arcuate, ribbonlike descending branches derived from short crura and commonly fused to valve floor. The distal end of the loop converges on a high, triangular median septum, but there are no ascending loop elements. The lophophore is schizolophous or ptycholophous, and spicules are rarely present.

Bouchardioids (Fig. 1317.1) are small to medium, smooth, oval to elongate oval in outline, and unisulcate with a pronounced ventral carina. The beak is straight with a small, commonly permesothyrid apical foramen. The strong hinge teeth have swollen

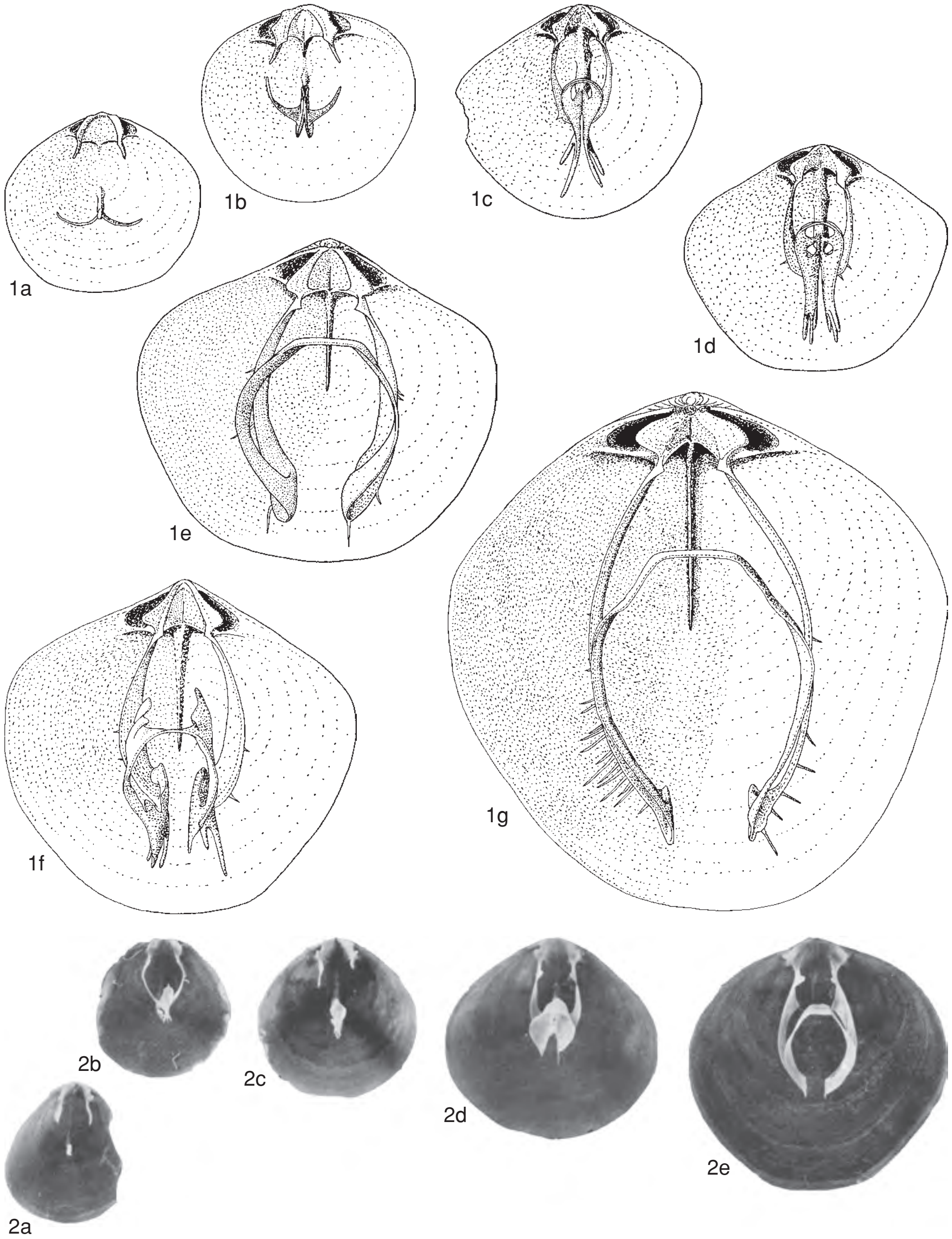

FIG. 1315. Loop ontogeny or adult loop morphology for terebratulide superfamilies; *1a–g*, Zeilleroidea, Zeilleriidae; loop ontogeny in *Zeilleria leckenbyi; a*, L = 1.5 mm; *b*, L = 2.1 mm; *c*, L = 3.0 mm; *d,* L = 3.9 mm; *e*, L = 5.9 mm; *f,* L = 12.2 mm; *g*, L = 23.5 mm (Baker, 1972); *2a–e*, loop ontogeny in *Macandrevia africana*, ×5 (Cooper, 1975).

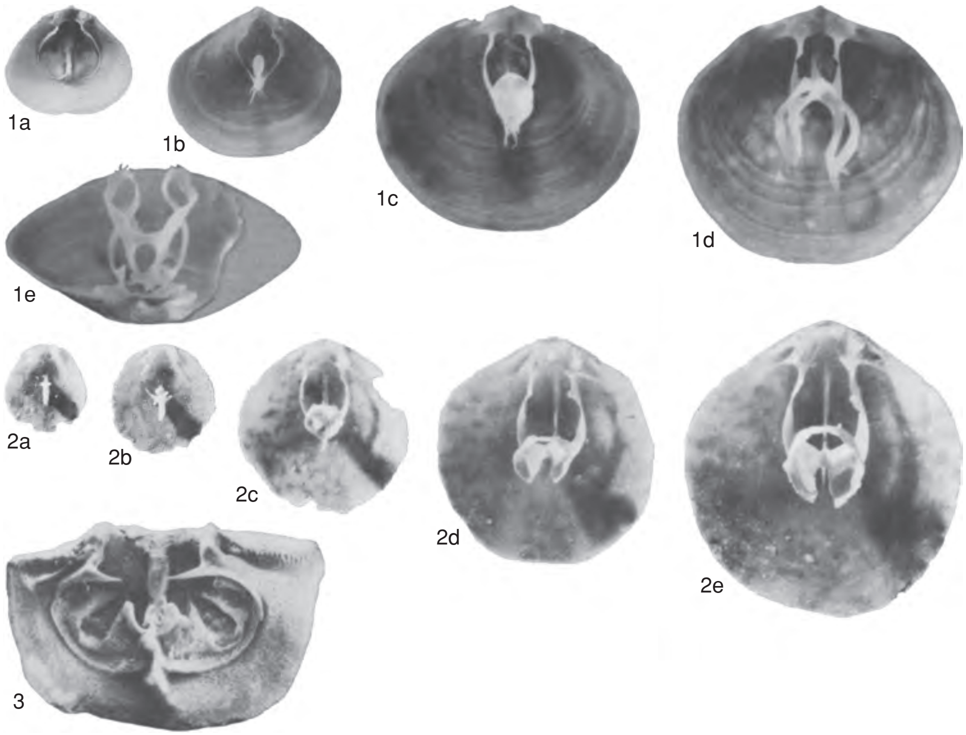

FIG. 1316. Loop ontogeny or adult loop morphology for terebratulide superfamilies; *1a–e*, Kingenoidea, Kingenidae; loop ontogeny in *Ecnomiosa inexpectata, a–c*, ×4, *d–e*, ×2 (Cooper, 1981); *2a–e*, Laqueoidea, Frenulinidae; loop ontogeny in *Frenulina sanguinolenta*, ×9 (Cooper, 1973a); *3,* Megathyridoidea, Megathyrididae; adult loop morphology in *Argyrotheca cuneata*, ×20 (Logan, 1979).

bases with a groove to accommodate socket ridges. Crura are vestigial to absent with no descending branches. The cardinal process and inner socket ridges are fused commonly to form a solid hinge platform bearing a deep diductor muscle scar impression. The septal pillar is high, and brachidial supports are incomplete. The lophophore is plectolophous, and spicules are absent.

Platidioids (Fig. 1317.2) are small or very small, planoconvex, convexoplane or slightly biconvex, subcircular or ovate in outline, and rectimarginate. Most examples are smooth, but faint capillae or small spines may be present. The foramen is large and amphithyrid or hypothyrid, and most living species are closely pressed to the substrate. The pedicle collar is short and sessile, and dental plates are weak or absent. Hinge plates are not developed. Crura, when present, are long and slender, extending from inner socket ridges. Descending branches, or a high triangular septal pillar that may have posterolateral septal flanges, may be developed. The lophophore is schizolophous or zygolophous, and the lophophore and mantle are strongly spiculate.

Terebratelloids (Fig. 1317.3) are the most abundant, diverse, and best-known group of brachiopods in modern oceans. They are generally medium to large, biconvex, subcircular to elongate oval in outline, and rectimarginate to unisulcate. Most are smooth, although a few genera are

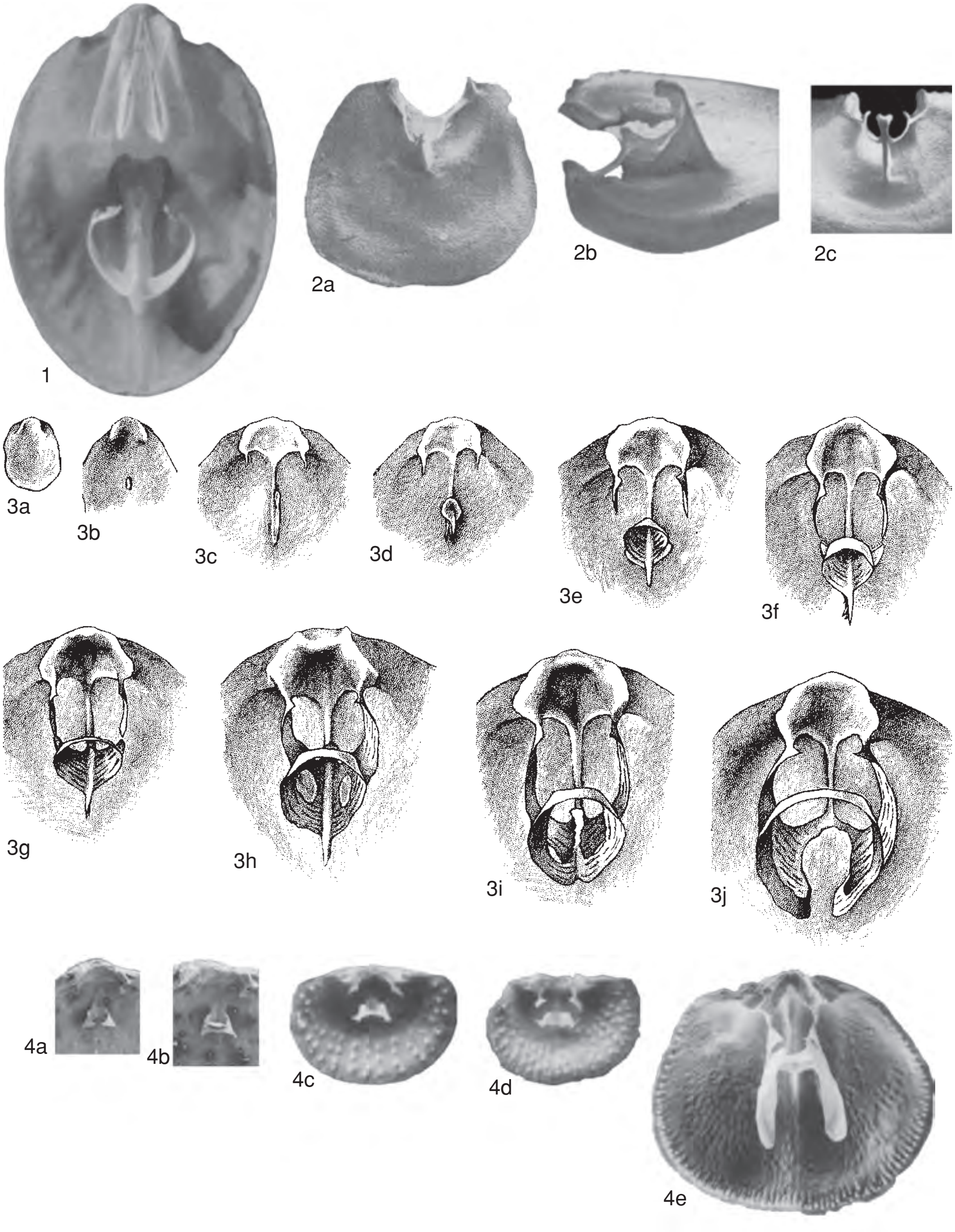

FIG. 1317. Loop ontogeny or adult loop morphology for terebratulide superfamilies; *1*, Bouchardioidea, Bouchardiidae; adult loop morphology in *Bouchardia rosea*, ×5 (Brunton, 1996); *2a–c,* Platidioidea, Platiidae; adult loop morphology in *Platidia anomioides, a–b,* ×9, *c*, ×10 (Logan, 1979)*; 3a–j*, Terebratelloidea, Terebratellidae; preadult loop ontogeny in *Magellania macquariensis, a–i*, ×10, *j,* ×5 (Foster, 1974); *4a–e*, Kraussinoidea, Kraussinidae, loop ontogeny in *Megerlia truncata; a–b,* ×9; *c–d,* ×6, *e,* ×1.5 (Logan, 1979).

multicostate. The foramen is small to large, mesothyrid to permesothyrid, and deltidial plates may be conjunct, disjunct, or form a symphytium. Dental plates are absent, and the pedicle collar is short and sessile. The septal pillar is retained throughout ontogeny and commonly develops as a median septum, with hinge plates uniting to form a septalium. The adult loop is commonly teloform but may be annular, haptoid, diploform, or trabecular. The lophophore is plectolophous, and spicules are absent.

Kraussinoids (Fig. 1317.4) are small to medium, biconvex or sometimes planoconvex, costate, and rectimarginate or unisulcate. The beak is attrite and the foramen usually large, with disjunct deltidial plates. The pedicle collar is short and sessile, and dental plates are absent. The interiors of both dorsal and ventral valves are commonly tuberculate. Inner socket ridges are prominent and divergent, and hinge plates may not be differentiated. Crura and descending lamellae may be present or absent. Septal flanges expand during ontogeny to form a strongly bifurcate septal pillar, which may have slender distal extensions that may unite to form a ring. The lophophore is zygolophous or plectolophous, and the mantle is moderately to strongly spiculate.

Gwynioids (see Fig. 1494,*1f* herein)are minute, smooth, subcircular to subquadrate, slightly strophic, planoconvex or biconvex, rectimarginate shells whose affinities are uncertain. The dorsal umbo is larger than that of the ventral valve, and the foramen is large and amphithyrid. The pedicle collar is weakly developed, and dental plates are absent. Inner and outer socket ridges are well developed. The trocholophous or schizolophous lophophore is supported by bladelike, arcuate submarginal ridges that are fused to the valve floor.

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The authors of order Terebratulida wish to acknowledge assistance from many colleagues without whose help this research could not have been completed. In particular, we acknowledge the contribution of A. J. Boucot, who provided diagnoses for the majority of Devonian terebratulides. In addition, we would like to thank Y. Alméras, F. Alvarez, M. A. Bitner, C. H. C. Brunton, S. Calzada Badia, S. J. Carlson, the late J. D. Campbell, R. A. Doescher, K. Endo, M. Florence, M. W. Foster, D. Gaspard, R. Gourvennec, E. Gradinaru, the late R. E. Grant, N. Hiller, Jisuo Jin, J. Kerns, A. Logan, C. Lueter, S. J. Long, M. O. Manceñido, D. A. B. Macfarlan, F. A. Middlemiss, E. F. Owen, S. Read, E. Ruggiero, J. H. Robinson, M. Saito, M. Siblík, E. Simon, G. Steinich, A. Vörös, O. N. Zezina, and the Science Librarians at the University of Otago, for providing access to collections, arranging the loan of type and other material, providing books and reprints, reading and commenting on drafts of parts of the manuscript, lending and/or scanning illustrations, and checking numerous references in often obscure publications. P. K. Tubbs and J. D. D. Smith provided help with nomenclatorial problems. Finally, we are indebted to the late Sir Alwyn Williams for guidance and support during the course of preparation of this volume and to Jill Hardesty for her exemplary editorial assistance and encouragement.

TEREBRATULIDINA

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Suborder TEREBRATULIDINA Waagen, 1883

[*nom. correct.* MUIR-WOOD & STEHLI, 1965, p. 730, *pro* suborder Terebratulacea WAAGEN, 1883a, p. 447]

All short-looped, and some long-looped terebratulides, in which the loop develops by extension of the crura without the involvement of either a septal pillar or median septum. *Lower Devonian–Holocene.*

STRINGOCEPHALOIDEA

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Superfamily STRINGOCEPHALOIDEA King, 1850

[*nom. transl.* STEHLI, 1965, p. 740, *ex* Stringocephalidae DAVIDSON, 1853, p. 51, *nom. correct. pro* Strigocephalidae KING, 1850, p. 141]

Adult shells small to very large; commonly ventribiconvex, rarely planoconvex; subcircular to elongate oval; commonly smooth, but may be finely striate, costate, costellate, or peripherally costate; anterior commissure commonly rectimarginate, but may be uniplicate, intraplicate, or unisulcate; ventral foramen may be submesothyrid to hypothyrid; deltidial plates may be conjunct or disjunct. Dental plates may be well developed, obsolescent, or obsolete. Cardinal process may be well developed or absent; hinge plates commonly discrete, but may be united to form a septalium; perforate or imperforate cardinal plate may be present, and may be supported by crural plates; median septae may be absent, present in both valves, or in one valve only. Adult loop commonly acuminate (centronelliform), and may be marginal, with or without spines; rarely teloform (cryptonelliform). *Silurian (?Pridoli), Lower Devonian (Lochkovian)–Upper Devonian (Frasnian).*

Family CENTRONELLIDAE Waagen, 1882

[*nom. transl.* HALL & CLARKE, 1895, p. 356, *ex* Centronellinae WAAGEN, 1882, p. 331]

Cardinal plate supported by long crural plates in large specimens, no crural plates in minute specimens; crural plates commonly not apparent in specimens with sessile cardinal plate; loop acuminate (centronelliform). *Lower Devonian (Lochkovian)–Middle Devonian (Givetian).*

Subfamily CENTRONELLINAE Waagen, 1882

[Centronellinae WAAGEN, 1882, p. 331]

Small to medium, smooth, planoconvex to unequally biconvex, naviculate; gently unisulcate dorsal valve; obsolete cardinal plates and dental plates; ponderous hinge teeth; sessile cardinal plate, concave; loop acuminate (centronelliform). *Lower Devonian (Pragian)–Middle Devonian (Givetian).*

Centronella BILLINGS, 1859, p. 131 [**Rhynchonella glans-fagea* HALL, 1857, p. 125; SD HALL, 1863, p. 45]. Small; concavoconvex, naviculate; sessile, swollen hinge plates medially divided by cleft, but forming part of a basally sessile cardinal plate; small cardinal process apically situated; dental plates obsolete, swollen hinge teeth; loop acuminate (0.5–

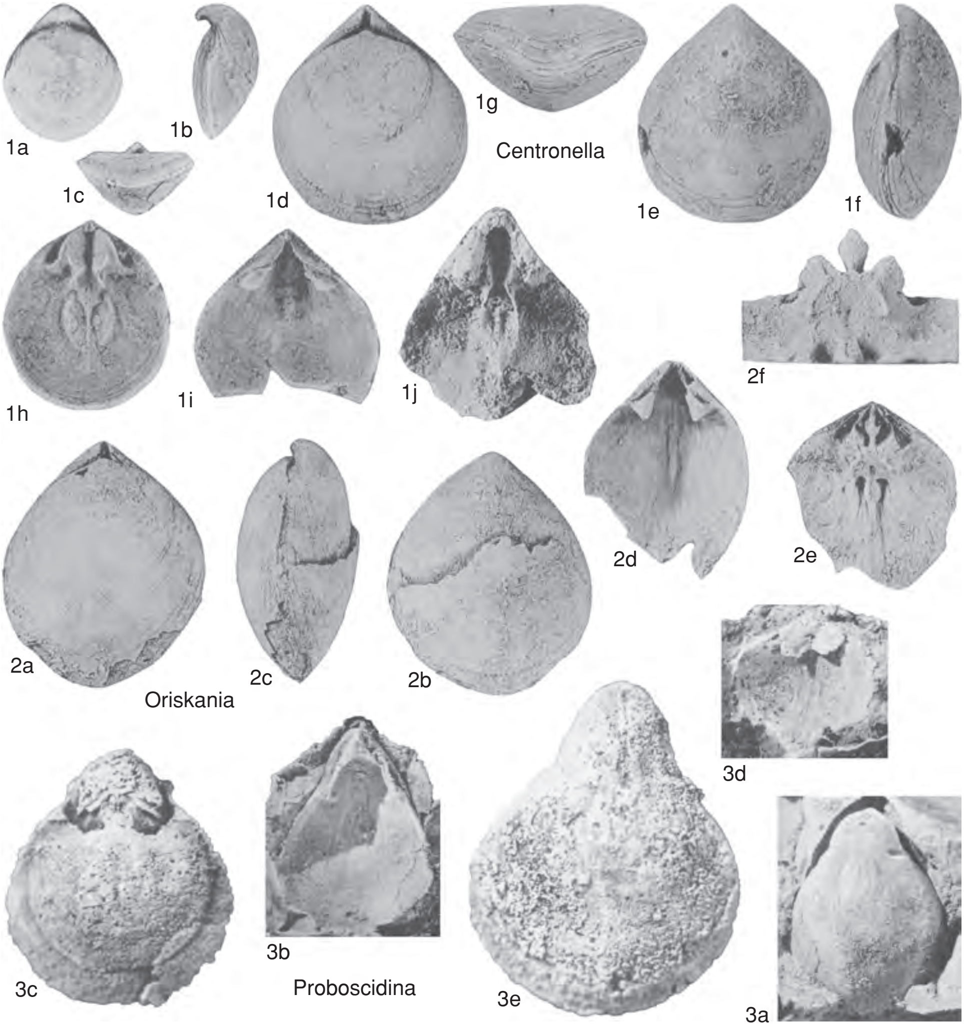

FIG. 1318. Centronellidae (p. 1994–1995).

0.6 dorsal valve length). *Lower Devonian (Emsian)–Middle Devonian (Givetian):* North America.——FIG. 1318,*1a–c.* **C. glansfagea* (HALL), New York, USA; dorsal, lateral, and ventral views, ×2 (Cloud, 1942).——FIG. 1318,*1d–j. C. campbelli* CLOUD, Indiana, USA; *d–g,* holotype, dorsal, ventral, lateral, and anterior views, USNM 109028A; *h–i,* interior of dorsal and ventral valves, ×2; *j,* ventral view of loop, ×4 (Cloud, 1942).

Oriskania HALL & CLARKE, 1893, p. 269 [**O. navicella;* OD]. Medium; ventribiconvex, naviculate; subcircular to elongate; dorsal valve gently unisulcate; thickened, sessile cardinal plate; cardinal process linear. *Lower Devonian (Pragian):* eastern North America, USA (Nevada).——FIG. 1318,*2a–f.* **O. navicella,* New York, USA; *a–c,* dorsal, ventral, and lateral views; *d,* interior of ventral valve; *e,* ventral view of dorsal valve interior, ×1; *f,* cardinalia, ×2 (Cloud, 1942).

Proboscidina ISAACSON, 1977, p. 192 [**Centronella arcei* ULRICH, 1892, p. 53; OD]. Small; elongate, dorsibiconvex, rectimarginate; hinge teeth massive; large ventral valve muscle field; cardinal plate nonsessile, medially grooved; loop unknown. *Lower Devonian (Emsian):* Bolivia, South Africa.——FIG. 1318,*3a–e.* **P. arcei* (ULRICH), Bolivia; *a–b,* impression of ventral valve interior, and latex replica of ventral valve interior, ×1.7; *c,* dorsal view of steinkern; *d,* latex replica of dorsal valve; *e,* ventral view of steinkern, ×2 (Isaacson, 1977).

Subfamily RENSSELAERIINAE Raymond, 1923

[Rensselaeriinae RAYMOND, 1923, p. 467]

Small to large, smooth to costellate; umbones may be radially ornamented; moderately to strongly biconvex; dental plates discrete, obsolescent; cardinal plate perforate in large specimens, discrete plates in small ones; long crural plates in large specimens. *Lower Devonian (Lochkovian–Emsian).*

Rensselaeria HALL, 1859, p. 39 [**Terebratula ovoides* EATON, 1832, p. 45, *non* SOWERBY, 1812, p. 227; SD HALL & CLARKE, 1893, p. 257; =*Atrypa elongata* CONRAD, 1839, p. 65]. Large; shell entirely costellate, costellae moderately strong; shell elongate, subovate to subcircular; ventribiconvex; commissure rectimarginate. Long dental plates obsolescent, largely submerged in secondary material laterally; thick, foramenate cardinal plate sessile posteriorly; thick crural plates; loop long, transverse plate long. *middle Lower Devonian:* North America.——FIG. 1319,*3a–c*. **R. elongata* (CONRAD), New York, USA; *a–b,* dorsal and lateral views, dorsal valve slightly crushed, ×1; *c,* rubber replica of dorsal interior, ×1 (Cloud, 1942).——FIG. 1319,*3d–h*. *R. marylandica* HALL, Maryland, USA; *d–f,* dorsal, lateral, and posterior views; *g,* interior of posterior part of ventral valve; *h,* reconstructed loop, ×1 (Cloud, 1942).

Etymothyris CLOUD, 1942, p. 59 [**Rensselaeria ovoides gaspensis* CLARKE, 1909, p. 238; OD]. Large; exterior and dorsal interior as in *Rensselaeria;* dental plates not obsolete, subparallel. *Lower Devonian (Emsian):* eastern North America.——FIG. 1319,*1a–g*. **E. gaspensis* (CLARKE), Quebec, Canada; *a–b,* dorsal and lateral views, ×1; *c–d,* interior of dorsal and ventral valves, ×1; *e–g,* lateral, anterior, and posterior views of steinkern of immature specimen, ×1 (Cloud, 1942).

Nanothyris CLOUD, 1942, p. 45 [**Meganteris mutabilis* HALL, 1857, p. 97; OD]. Small to medium; ventribiconvex; smooth umbones, costellate peripherally, commissure rectimarginate. Dental plates discrete; cardinal plate posteriorly foramenate; crural plates long in large specimens, commonly absent in minute specimens. *Lower Devonian (Lochkovian–Pragian):* eastern North America.——FIG. 1319,*2a–g*. **N. mutabilis* (HALL), New York, USA; *a–c,* dorsal, lateral, and anterior views, ×2; *d–e,* posterior and dorsal views of steinkern showing dental and crural plates, ×2 (Cloud, 1942); *f,* oblique view of loop; *g,* interior of dorsal valve, ×3.5 (Boucot & Wilson, 1994).

Rensselaerina DUNBAR, 1917, p. 466 [**R. medioplicata;* OD]. Small to medium; smooth umbones, ventribiconvex, anteromedial radial ornamentation, strong costae, rectimarginate and crenulate commissure; dental plates obsolescent in larger specimens, partially to completely sessile, posteriorly foramenate, massive cardinal plate; crural plates secondarily thickened to submerged; loop variable. *Lower Devonian (Lochkovian):* eastern North America.——FIG. 1320*a–e*. **R. medioplicata,* Tennessee, USA; *a,* interior of ventral valve, ×2; *b–c,* ventral and anterior views of cardinal plates, ×2 (Cloud, 1942); *d–e,* ventral and lateral views of reconstructed loop, ×0.5 (Dunbar, 1917).——FIG. 1320*f–h*. *R. haraganana* CLOUD, Oklahoma, USA; *f–g,* dorsal and anterior views; *h,* ventral view of loop, ×1 (Cloud, 1942).

Subfamily AMPHIGENIINAE Cloud, 1942

[Amphigeniinae CLOUD, 1942, p. 77]

Centronellidae with ventral valve spondylium duplex supported by median septum formed from continuation of conjunct dental plates. Spondylium supported posterolaterally by pair of mystrochial plates. *Lower Devonian (Emsian)–Middle Devonian (Eifelian).*

Amphigenia HALL, 1867b, p. 374 [**Pentamerus elongata* VANUXEM, 1842, p. 132; OD]. Medium to large; subcircular to elongate; ventribiconvex; umbonal region smooth, anterolateral regions may be faintly costellate; anterior commissure rectimarginate, may be weakly crenulate; cardinal plate posteriorly sessile, foramenate posteriorly in smaller specimens; crural plates; ventral valve spondylium supported by median septum and mystrochial plates, both formed from convergent dental plates, except in oldest form where plates barely unite anteriorly. *Lower Devonian (Emsian)–Middle Devonian (Eifelian):* central and eastern North America, northwestern Africa, France, Brazil (Amazon Basin), Venezuela.——FIG. 1321*a–f*. **A. elongata* (VANUXEM), New York, USA; *a–b,* dorsal and lateral views; *c,* posterior view of interior of conjoined valves; *d–e,* interior views of dorsal valves, ×1 (Cloud, 1942); *f,* interior of silicified ventral valve, ×1 (Boucot, 1959b).

Subfamily EURYTHYRIDINAE Cloud, 1942

[*nom. correct.* STEHLI, 1965, p. 743, *pro* Eurythyrinae CLOUD, 1942, p. 60]

Small to medium sized; ventribiconvex; smooth to finely costellate peripherally; introverted lateral margins; outline circular to moderately elongate; rectimarginate; conjunct deltidial plates; obsolete dental plates; cardinal plate perforate in small specimens and sessile in larger specimens; crural plates

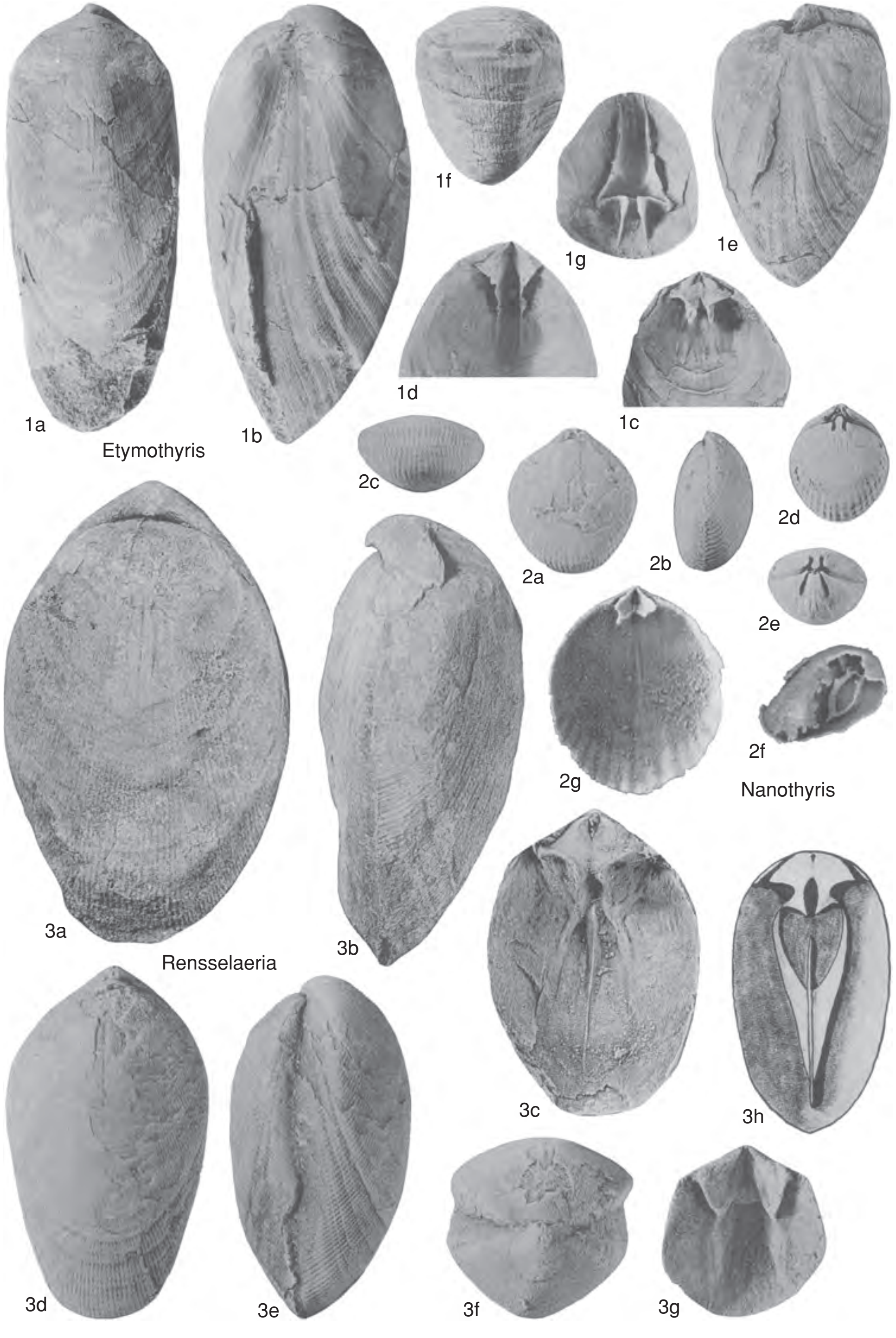

FIG. 1319. Centronellidae (p. 1996).

FIG. 1320. Centronellidae (p. 1996).

commonly submerged in secondary material. *Lower Devonian (Pragian–Emsian).*

Eurythyris CLOUD, 1942, p. 63 [**Oriskania lucerna* SCHUCHERT in SCHUCHERT & MAYNARD, 1913, p. 390; OD]. Smooth to peripherally finely costellate; naviculate; dental plates obsolete; cardinal plate sessile, swollen; linear cardinal process. *Lower Devonian (Pragian):* east-central North America.——FIG. 1322,*1a–b.* **E. lucerna* (SCHUCHERT), Maryland; *a,* interior of ventral valve posterior, ×1; *b,* ventral view of loop, ×1 (Cloud, 1942).——FIG. 1322,*1c–f. E. dunbari* CLOUD, Maryland, USA; holotype, dorsal, ventral, lateral, and anterior views, YPM S3369, ×1 (Cloud, 1942).

Beachia HALL & CLARKE, 1893, p. 260 [**Meganteris suessana* HALL, 1857, p. 100; OD]. Umbones smooth, peripherally finely costellate; subcircular to moderately elongate; dental plates free in small specimens, obsolescent to obsolete in large specimens; cardinal plate perforate in small specimens, imperforate in large specimens; cardinal plate free in small to medium specimens, moundlike to swollen in large; crural plates free in small specimens, submerged in large specimens. *Lower Devonian (Pragian):* eastern North America.——FIG. 1322,*4a–h.* **B. suessana* (HALL), Maryland, USA; *a–d,* dorsal, ventral, lateral, and anterior views, ×1; *e,* posterior of dorsal valve, ×1; *f,* cardinal plate, ×2; *g–h,* ventral views of loops, ×1 (Cloud, 1942).

Cloudothyris BOUCOT & JOHNSON, 1968, p. 19 [**C. postovalis;* OD]. Smooth; subcircular; dental plates obsolescent to obsolete; cardinal plate supporting a massive, medially clefted, elongate cardinal process; crural plates visible in small specimens, submerged in sessile, larger cardinal plate; loop unknown. *Lower Devonian (Emsian):* North America (Maine, New York, ?New Hampshire, ?Gaspé).——FIG.

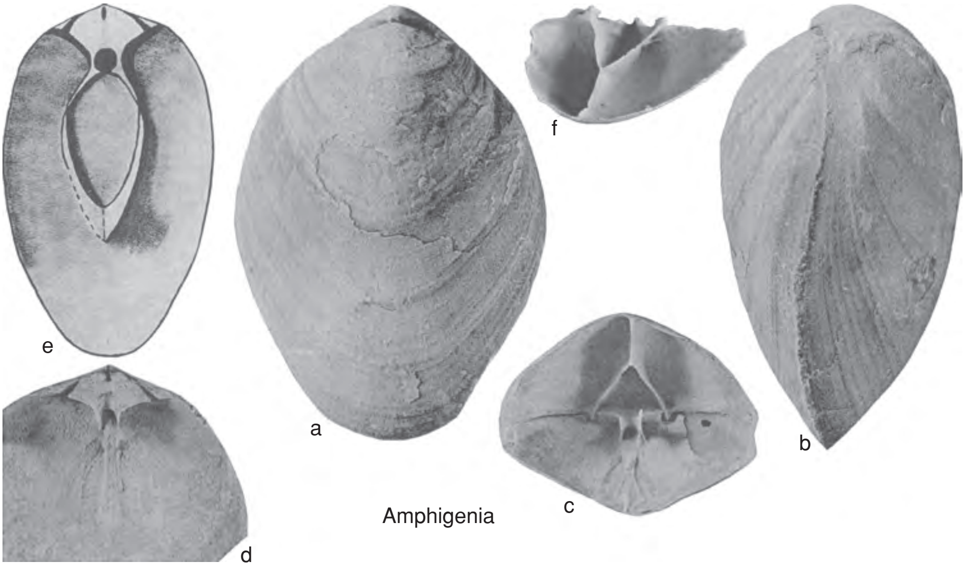

FIG. 1321. Centronellidae (p. 1996).

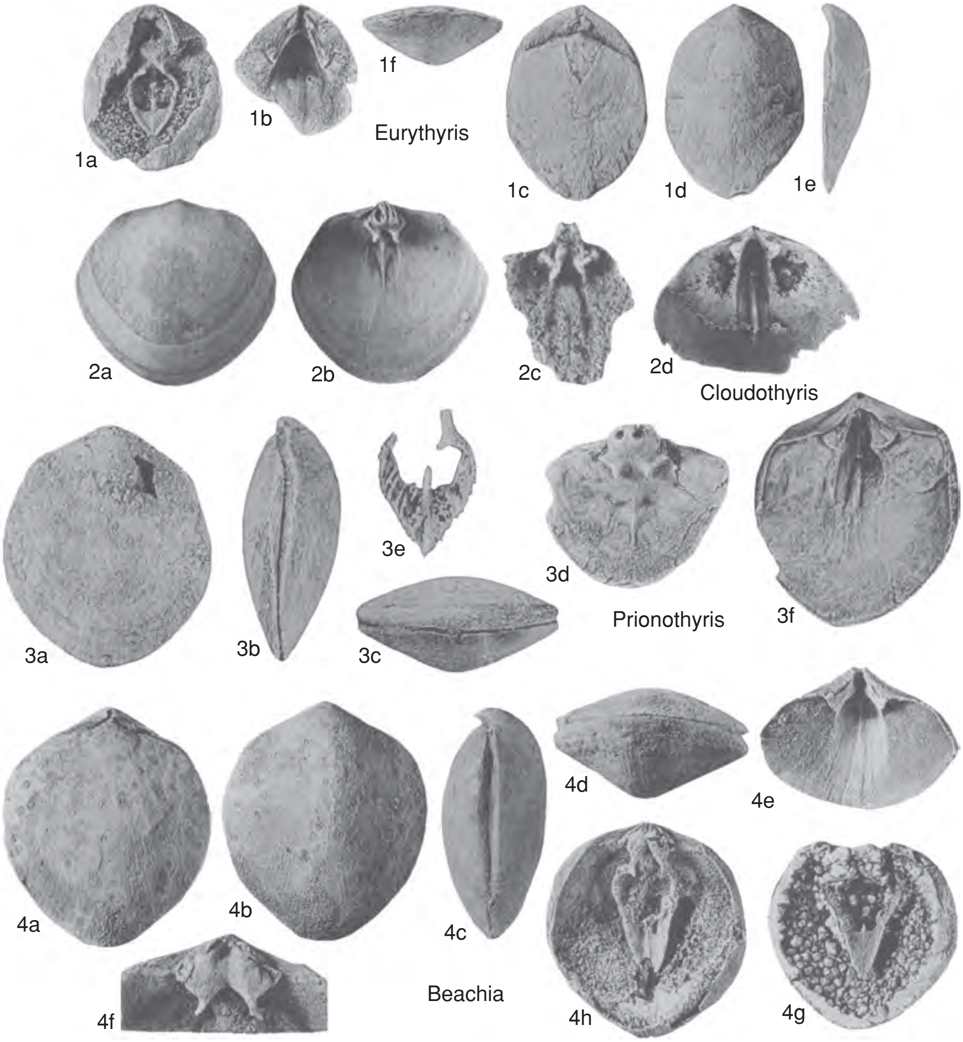

FIG. 1322. Centronellidae (p. 1998–1999).

1322,*2a–d.* **C. postovalis,* New York, USA; *a,* dorsal valve exterior, ×1; *b,* interior of dorsal valve, ×1; *c,* interior of dorsal valve, ×3; *d,* interior of ventral valve, ×1 (Boucot & Johnson, 1968).

Prionothyris CLOUD, 1942, p. 66 [**P. perovalis;* OD]. Umbones smooth, peripherally finely costellate; subcircular to moderately elongate; dental plates obsolescent to obsolete; massive, sessile, imperforate cardinal plate; posteriorly trifid, striate. *Lower Devonian (Pragian–Emsian):* eastern North America, Colombia.——FIG. 1322,*3a–f.* **P. perovalis,* New York, USA; *a–c,* holotype, ventral, lateral, and anterior views, USNM 108481, ×1; *d,* posterior of dorsal valve, ×1; *e,* ventral view of free loop, ×2; *f,* interior of ventral valve, ×1 (Cloud, 1942).

Family STRINGOCEPHALIDAE
King, 1850

[*nom. correct.* DAVIDSON, 1853, p. 51, *pro* Strigocephalidae KING, 1850, p. 141]

Very large; thick shelled; commonly smooth; rectimarginate; dental plates obsolescent to obsolete; median septae may be absent, present in both valves, or present in one valve only; hinge plates discrete; crural plates present in some forms; loop long, marginal, acuminate (centronelliform). *Middle Devonian (upper Eifelian–Givetian).*

Subfamily STRINGOCEPHALINAE King, 1850

[*nom. transl. et correct.* CLOUD, 1942, p. 104, *ex* Strigocephalidae KING, 1850, p. 141]

Subglobular; outline subcircular; smooth; may have prominent beak; prominent median septae in both valves; long, stalklike, terminally bifid, cardinal process; no crural plates. *Middle Devonian (upper Eifelian–Givetian).*

Stringocephalus DEFRANCE in DE BLAINVILLE, 1827 in 1825–1827, p. 511, *nom. nov.* SANDBERGER, 1842, p. 386, *pro Strygocephale* DEFRANCE in DE BLAINVILLE, 1825 in 1825–1827, p. 511, ICZN Opinion 807, 1967, p. 81; see STEHLI, 1965, p. 748 for discussion about name history [**Terebratula Burtini* DEFRANCE in DE BLAINVILLE, 1825 in 1825–1827, p. 511; OD] [=*Strygocephalus* DEFRANCE in DE BLAINVILLE, 1827 in 1825–1827, pl. 53,*1,* obj.; *Strigocephalus* J. DE C. SOWERBY, 1840b, pl. 56,*10,* obj.]. Very large; subglobular; ventribiconvex; ventral valve beak large, pointed, slightly asymmetrical; dental plates obsolescent; henidium in gerontic adults; median septae in both valves; cardinal process stout, stalklike, distally bifid; long, marginal loop with or without posteriorly directed spines. *Middle Devonian (upper Eifelian–Givetian):* Asia, northwestern Africa, Europe, extra-Appalachian North America, Australia.——FIG. 1323*a–g.* **S. burtini* (DEFRANCE), Germany; *a–b,* dorsal and posterior views, ×1; *c,* posterior interior of ventral valve, ×1; *d,* ventral view, ×0.5 (Cloud, 1942); *e,* anterior view, ×0.5; *f,* anterior oblique view of latex impression of ventral median septum, dorsal cardinal process, and crura, ×1 (Boucot, Johnson, & Struve, 1966); *g,* drawing of partly restored loop, ×0.5 (Cloud, 1942).

Parastringocephalus STRUVE, 1965, p. 467 [**Strygocephalus dorsalis* D'ARCHIAC & DE VERNEUIL, 1842, p. 369; OD]. Similar to *Stringocephalus,* but bisulcate and finely striate; loop unknown. *Middle Devonian (Givetian):* Eurasia, USA (Nevada).——FIG. 1324,*1a–b.* **P. dorsalis* (D'ARCHIAC & DE VERNEUIL), Germany; dorsal and ventral views, ×0.5 (Torley, 1934).

Stringodiscus STRUVE, 1982, p. 221 [**Strigocephalus giganteus* J. de C. SOWERBY, 1840b, pl. 56,*10–11;* OD]. Large, moderately ventribiconvex (so-called disclike); interior undescribed; otherwise similar to *Stringocephalus. Middle Devonian (Givetian):* Europe, North America, Asia.——FIG. 1324,*2a–b.* **S. giganteus* (J. de C. SOWERBY), Germany; dorsal and lateral views, ×0.5 (Torley, 1934).

Subfamily KAPLEXINAE Sun & Boucot, 1999

[Kaplexinae SUN & BOUCOT, 1999, p. 866]

Moderately large, smooth, rectimarginate, may have prominent beak, no cardinal process or crural plates; dental plates obsolete; median septum in ventral valve only. *Middle Devonian (upper Eifelian–Givetian).*

Kaplex FICNER & HAVLÍČEK, 1975, p. 362 [**K. obesissimus;* OD]. Moderately ventribiconvex; hinge plates anteriorly discrete; loop unknown. *Middle Devonian (upper Eifelian–lower Givetian):* Moravia.——FIG. 1325,*1a–d.***K. obesissimus; a–b,* exterior and interior views of incomplete dorsal valve, ×1.3; *c–d,* exterior and lateral views of ventral valve, ×1 (Ficner & Havlíček, 1978).

Erectocephalus XIAN in XIAN & JIANG, 1978, p. 333 [**E. trigonus;* OD]. Circular to elongate; ventral valve median septum low; massive hinge plates; loop unknown. *Middle Devonian (Givetian):* China (Guizhou).——FIG. 1325,*3a–b.* **E. trigonus; a,* dorsal view; *b,* sectioned specimen, ×1 (Xian & Jiang, 1978).

Subfamily OMOLONINAE Sun & Boucot, 1999

[Omoloninae SUN & BOUCOT, 1999, p. 866]

Smooth or finely striate; large; no dorsal median septum, ventral median septum present, cardinal process present, commonly discrete hinge plates, may have spondylium. *Middle Devonian (Givetian).*

Omolonia ALEKSEEVA in ALEKSEEVA & NUZHDINA, 1967, p. 138 [**O. antiqua;* OD]. Smooth; strongly biconvex; terminally biconvex cardinal process; conjunct hinge plates; large dental plates; loop unknown. *Middle Devonian (Givetian):* Asia, western North America.——FIG. 1326*a–c.* **O. antiqua,* Yukagir Plateau, northeastern Russia; holotype, dorsal, lateral, and ventral views, IGiG 280, ×1 (Alekseeva & Nuzhdina, 1967).

Hemistringocephalus SMIRNOV, 1985, p. 31 [**H. mirabilis;* OD] Smooth; planoconvex; posterior portion of ventral valve unknown; prominent ventral median septum; terminally bifid cardinal process; hinge plates unite medially with cardinal process; no dorsal valve median septum; loop unknown. *Middle Devonian (Givetian):* central Asia (Tian Shan).——FIG. 1327,*1a–f.* **H. mirabilis; a–d,* dorsal, ventral, posterior, and anterior views, ×1; *e–f,* sectioned specimen, ×1 (Smirnov, 1985).

Kumbella KHODALEVICH, 1975, p. 137 [**K. kumbensis;* OD]. Smooth to finely striate, ventribiconvex, subcircular, spondylium duplex supported by median septum, bulbous cardinal process, septal and crural plates, loop unknown. *Middle Devonian*

FIG. 1323. Stringocephalidae (p. 2000).

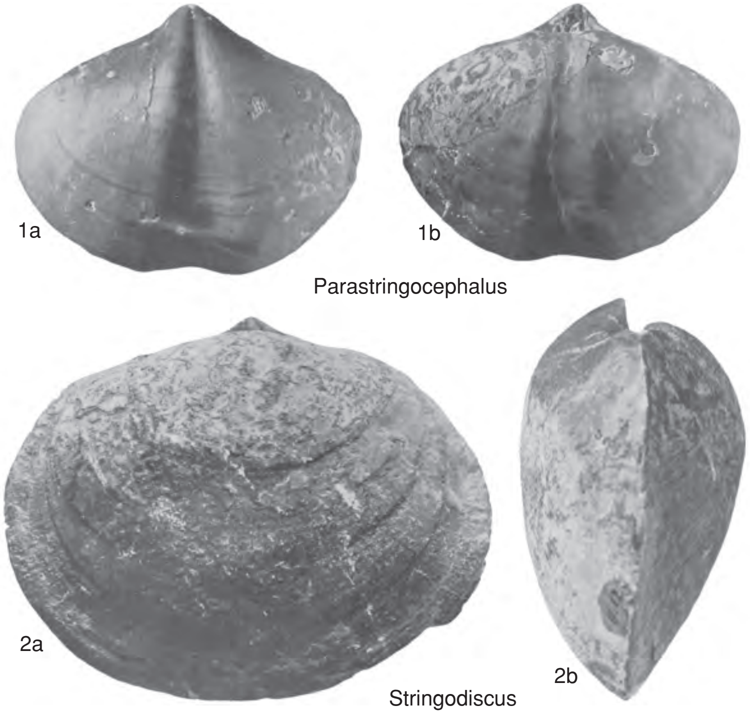

FIG. 1324. Stringocephalidae (p. 2000).

(Givetian): east-central Urals.——FIG. 1327,*2a–d.* **K. kumbensis; a–b,* holotype, ventral and lateral views; *c,* dorsal view, ×1; *d,* transverse section of posterior of dorsal valve, ×3 (Khodalevich, 1975).

Subfamily GERANOCEPHALINAE Johnson, 1975

[Geranocephalinae JOHNSON, 1975, p. 981]

Medium size; ventral valve beak straight; moderately ventribiconvex; crural plates may be present; moderate-sized cardinal process; no median septae. *Middle Devonian (Givetian).*

Geranocephalus CRICKMAY, 1954, p. 157 [**G. inopinus;* OD] [=*Acrothyris* HOU, 1963, p. 419 (type, *A. kwangsiensis* HOU, 1963, p. 432, OD); *Catacephalus* YANG in ZHANG, FU, & DING, 1983, p. 381 (type, *C. tianshanensis,* OD); *Conomimus* JOHNSON, BOUCOT, & GRONBERG, 1968, p. 406 (type, *C. truncatus,* OD)]. Medium, smooth, ventribiconvex; dental plates short; median septae absent in both valves; crural plates absent; cardinal plate formed from conjunct hinge plates; large, terminally bifid cardinal process; loop unknown. *Middle Devonian (Givetian):* North America, Europe, Asia, Australia.——FIG. 1328,*1a–f.* **G. inopinus,* Nevada, USA; *a,* dorsal view, ×3; *b–c,* ventral and lateral views, ×2; *d,* interior of ventral valve, ×4; *e,* anterodorsal view of dorsal valve; *f,* interior of dorsal valve, ×3 (Johnson, Boucot, & Gronberg, 1968).

Paracrothyris WU in WANG, YU, & WU, 1974, p. 42 [**P. distorta;* OD]. Similar to *Geranocephalus* except for the presence of crural plates. *Middle Devonian (Givetian):* China, North America.——FIG. 1328,*4a–b.* **P. distorta,* China; dorsal and lateral views, ×1 (Wang, Yu, & Wu, 1974).——FIG. 1328,*4c. P.* sp., Nevada, USA; interior of dorsal valve, ×3 (Johnson, 1975).

Stringomimus STRUVE, 1965, p. 461, *nom. transl.* JIN & LEE, herein, *ex Geranocephalus (Stringomimus)* STRUVE, 1965, p. 463 [**Geranocephalus (Stringomimus) pseudopaedicus* STRUVE, 1965, p. 463; OD]. Similar to *Geranocephalus* except that ventral valve beak is less attenuated, and cardinal process more slender; remainder of interior unknown. *Middle Devonian (Givetian):* Europe.——FIG. 1328,*3a–d.* **S. pseudopaedicus,* Germany; dorsal, ventral, lateral, and posterior views, ×1 (Struve, 1965).

Xiangzhounia NI & YANG, 1977, p. 464 [**X. typica;* OD]. Similar to *Geranocephalus* except for presence of short dental plates. *Middle Devonian (Givetian):* Asia.——FIG. 1328,*2a–b.* **X. typica,* China; dorsal and lateral views, ×1 (Ni & Yang, 1977).

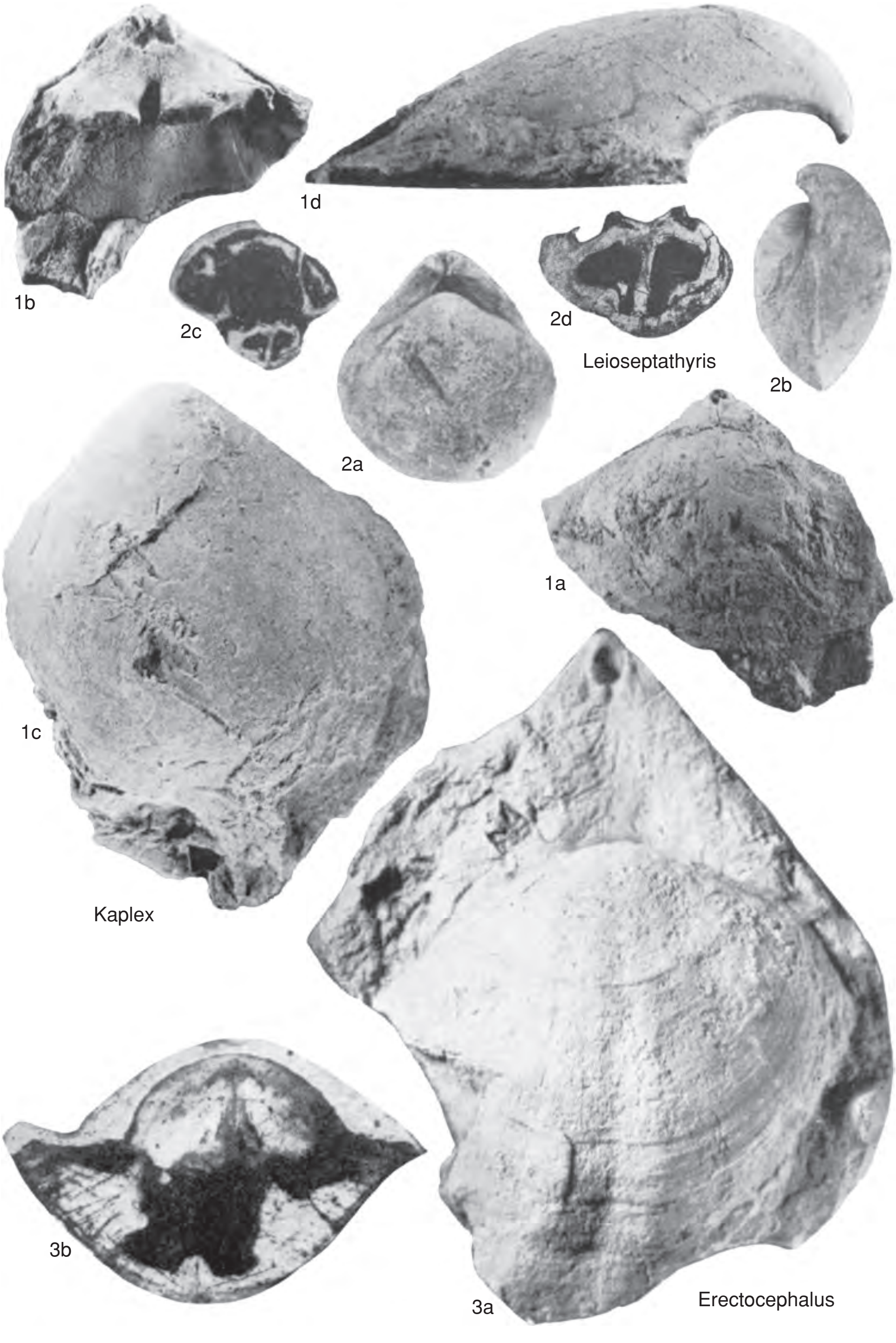

FIG. 1325. Stringocephalidae (p. 2000–2004).

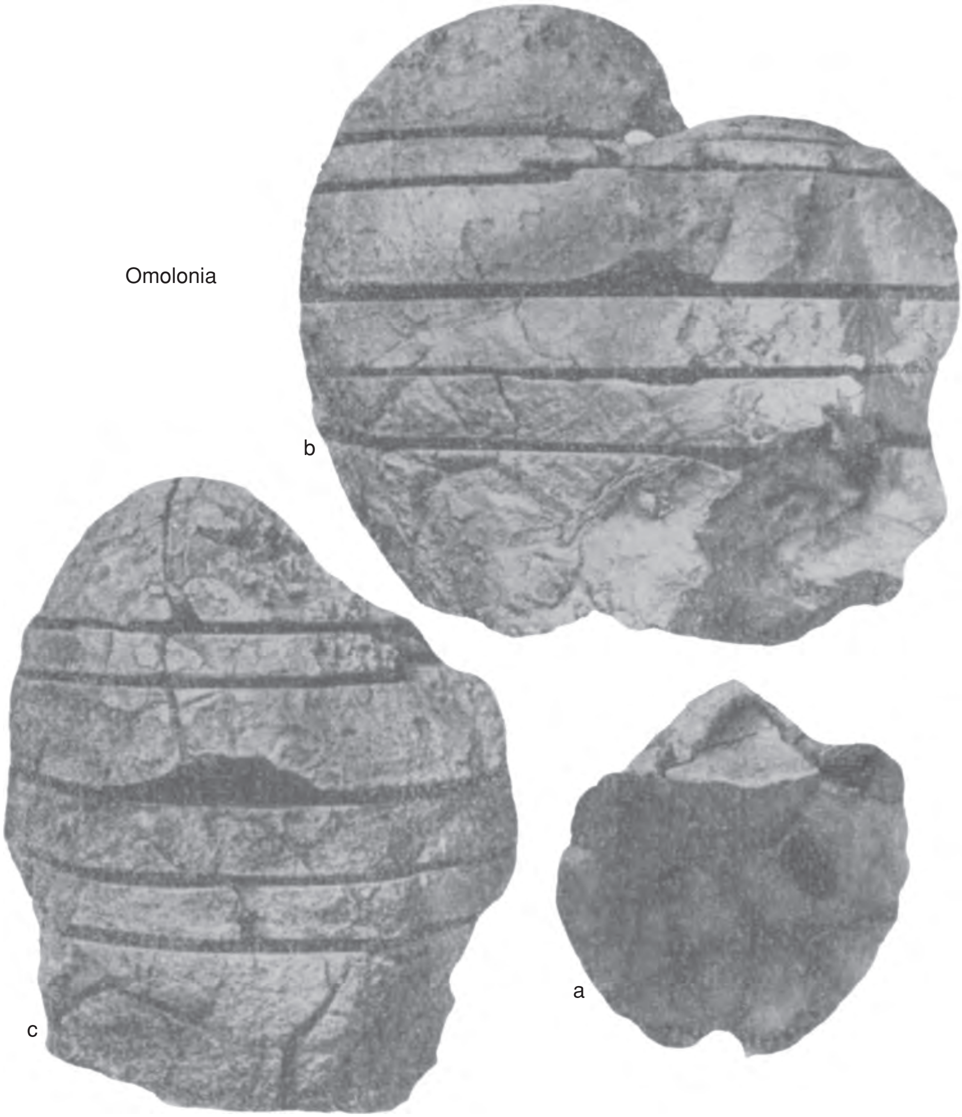

FIG. 1326. Stringocephalidae (p. 2000).

Subfamily LEIOSEPTATHYRIDINAE
Sun & Boucot, 1999

[*nom. correct.* JIN & LEE, herein, *pro* Leioseptathyrinae SUN & BOUCOT, 1999, p. 866]

Medium, smooth, dorsal median septum present. *Middle Devonian (Givetian).*

Leioseptathyris WU in WANG, YU, & WU, 1974, p. 42 [**L. modica;* OD]. Subcircular, ventribiconvex; dental plates present; conjunct hinge plates forming cardinal plate; low cardinal process formed from laterally directed processes; loop unknown. *Middle Devonian (Givetian):* Asia.——FIG. 1325,*2a–d.* **L. modica,* China; *a–b,* dorsal and lateral views, ×1; *c,* sectioned specimen, ×2; *d,* sectioned specimen, ×5 (Wang, Yu, & Wu, 1974).

Subfamily RENSSELANDIINAE
Cloud, 1942

[Rensselandiinae CLOUD, 1942, p. 92]

Medium to large; subcircular to elongate; ventribiconvex; rectimarginate or uniplicate;

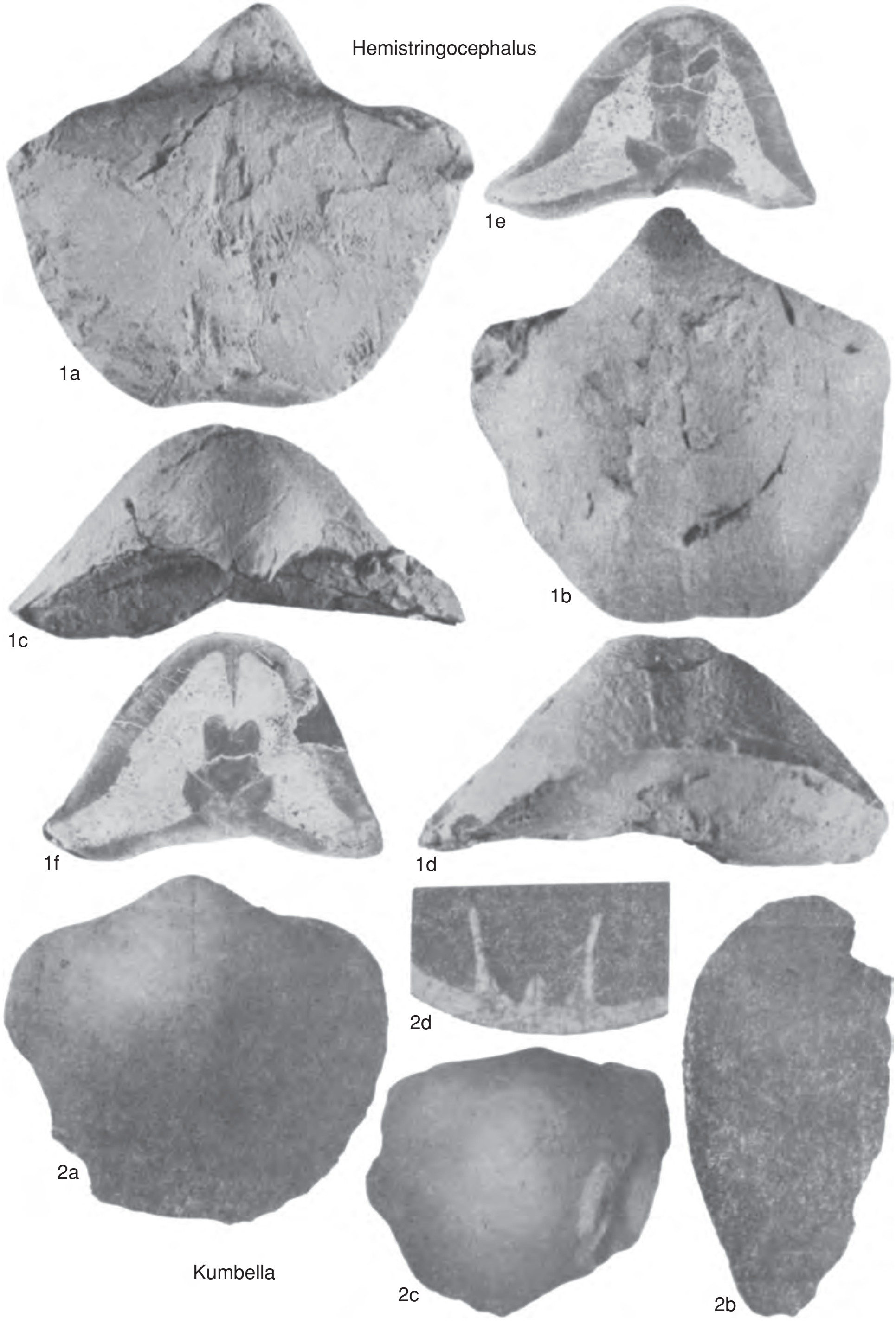

FIG. 1327. Stringocephalidae (p. 2000–2002).

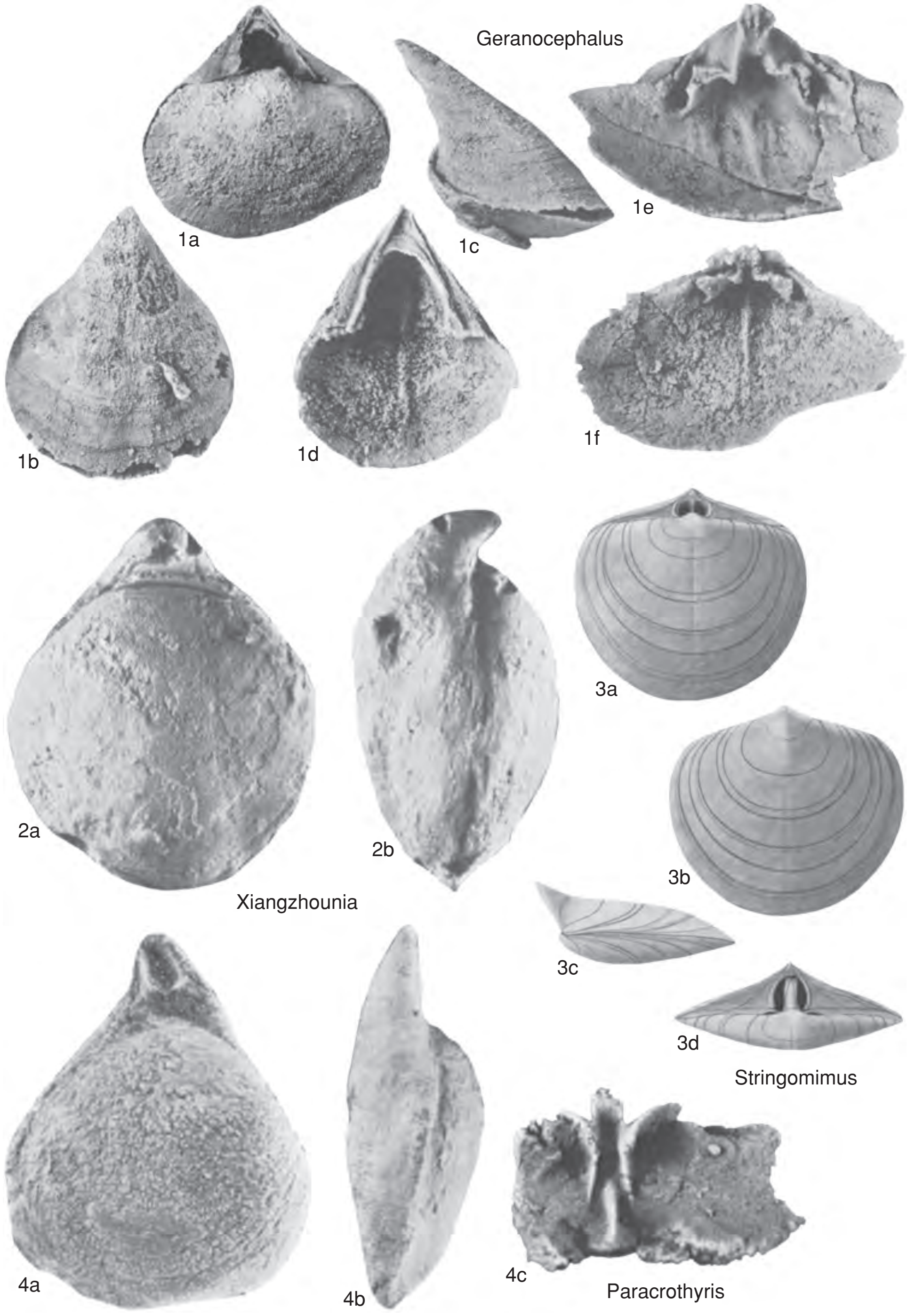

FIG. 1328. Stringocephalidae (p. 2002).

beak small and strongly incurved; no median septae, with the exception of *Rensselandioidea,* which has a dorsal median septum; cardinal process commonly absent; hinge plates may be supported by crural plates; long, marginal, acuminate (centronelliform) loop. *Middle Devonian (upper Eifelian–Givetian).*

Newberria HALL in WHITEAVES, 1891, p. 236 [**Rensselaeria? johanni* HALL, 1867b, p. 385; SD SCHUCHERT, 1897, p. 271] [=*Rensselandia* HALL, 1867b, p. 385, obj., *nom. cond.; Macroplectane* COSSMANN, 1909, p. 215 (type, *Denckmannia circularis* HOLZAPFEL, 1912, p. 119, SD SCHUCHERT & LEVENE, 1929a, p. 51), *nom. nov. pro Denckmannia* HOLZAPFEL, 1912, p. 115, *non* BUCKMAN, 1898; *Denckmannella* SCHUCHERT & LEVENE, 1929b, p. 120 (type, *Denckmannia circularis* HOLZAPFEL, 1912, p. 119, SD SCHUCHERT & LEVENE, 1929a, p. 51), *nom. nov. pro Denckmannia* HOLZAPFEL, 1912, p. 115, *non* BUCKMAN, 1898]. Medium to large; smooth; rectimarginate; dental plates obsolete or obsolescent; well impressed muscle field; no cardinal process; discrete hinge plates; crural plates absent except in some small specimens; loop long, marginal; may have median plate. *Middle Devonian (Givetian):* North America, Europe, Asia.——FIG. 1329,*1a–e.* **N. johanni* (HALL), Iowa, USA; *a–d,* dorsal, lateral, posterior, and anterior views; *e,* ventral view of loop, ×1 (Cloud, 1942).

Chascothyris HOLZAPFEL, 1895, p. 234 [**C. barroisi;* SD SCHUCHERT & LEVENE, 1929a, p. 40]. Medium to large; smooth; ventral sulcus and dorsal fold; uniplicate; subcircular; interior as in *Newberria. Middle Devonian (Givetian):* Europe, Asia.——FIG. 1329,*3a–b.* **C. barroisi,* Germany; dorsal and lateral views, ×1 (Cloud, 1942).

Ectorensselandia JOHNSON, 1973a, p. 1,105 [**Rensselaeria laevis* MEEK, 1868, p. 108; OD]. Large, smooth, elongate; rectimarginate, short, obsolete dental plates; hinge plates fuse posteriorly to form cardinal plate; no crural plates; bilobed cardinal process; loop peripheral (anterior half unknown). *Middle Devonian (Givetian):* Canada (District of Mackenzie).——FIG. 1329,*6a–c.* **E. laevis* (MEEK), Mackenzie River; dorsal, lateral, and anterior views, ×1 (McLaren, Norris, & McGregor, 1962).

Elmaria NALIVKIN, 1947, p. 133 [**E. glabra;* OD]. Small, rounded to elongate; smooth or peripherally costate; similar to *Newberria;* interior poorly known. *Middle Devonian (Givetian):* southern Urals.——FIG. 1329,*5a–b.* **E. glabra;* dorsal and lateral views, ×1 (Nalivkin, 1947).

Rensselandioidea YANG, 1983, p. 34 [**R. maanshanensis;* OD]. Similar to *Newberria* but with dorsal valve median septum. *Middle Devonian (Givetian):* Asia.——FIG. 1329,*4a–b.* **R. maanshanensis,* China; dorsal and lateral views, ×1 (Yang, 1973).

Subrensselandia CLOUD, 1942, p. 92 [**Newberria claypolii* HALL, 1891, p. 97; OD]. Medium to large; smooth; subcircular to elongate; rectimarginate; short dental plates; small teeth; broad, well-impressed muscle field; discrete hinge plates; crural plates; loop long, marginal. *Middle Devonian (upper Eifelian–lower Givetian):* North America, Europe.——FIG. 1329,*2a–e.* **S. claypolii* (HALL), lower Givetian, Pennsylvania; *a–c,* dorsal, lateral, and posterior views of steinkern, ×1; *d,* latex replica of *c,* ×1; *e,* latex replica of ventral valve interior, ×1 (Cloud, 1942).

Subfamily BORNHARDTININAE Cloud, 1942

[Bornhardtininae CLOUD, 1942, p. 100]

Large, rectimarginate, smooth; beak asymmetrical, incurved; with or without dental plates; stout hinge teeth; dental lamellae obsolete; discrete hinge plates; cardinal process and median septae absent; loop long, marginal, acuminate (centronelliform). *Middle Devonian (upper Eifelian–Givetian).*

Bornhardtina SCHULZ, 1914, p. 363 [**B. uncitoides;* SD CLOUD, 1942, p. 101] [=*Parabornhardtina* HOU & XIAN, 1964, p. 416 (type, *P. yunnanensis,* OD)]. Description as for subfamily, dental plates absent. *Middle Devonian (upper Eifelian–Givetian):* Europe, Asia.——FIG. 1330,*3a–d.* **B. uncitoides,* Germany; *a–c,* dorsal, lateral, and anterior views; *d,* latex replica of dorsal interior, ×1 (Cloud, 1942).

Hessenhausia STRUVE, 1982, p. 226 [**Rauffia pseudocaiqua* SCHULZ, 1914, p. 371; SD CLOUD, 1942, p. 102]. Similar to *Bornhardtina,* but with posterior sulcus on dorsal valve. *Middle Devonian (Givetian):* Germany.——FIG. 1330,*1a–c.* **H. pseudocaiqua* (SCHULZ); dorsal, lateral, and anterior views, ×0.5 (Schulz, 1914).

Pseudobornhardtina YANG, 1977, p. 460 [**P. xiangzhouensis;* OD]. Similar to *Bornhardtina* but with dental plates. *Middle Devonian (Givetian):* Asia.——FIG. 1330,*2a–d.* **P. xiangzhouensis; a–b,* dorsal and lateral views; *c–d,* serial transverse sections showing dental plates, ×1 (Yang, 1977).

Family MEGANTERIDIDAE Schuchert & LeVene, 1929

[*nom. correct.* JIN & LEE, herein, *pro* Meganteridae SCHUCHERT & LEVENE, 1929a, p. 23]

Small to large; crural plates commonly absent, except in entirely smooth forms; rarely present in some larger specimens, short, if present; loop acuminate or teloform (centronelliform or cryptonelliform). *Silurian (?Pridoli), Lower Devonian (Lochkovian)–Middle Devonian (Givetian).*

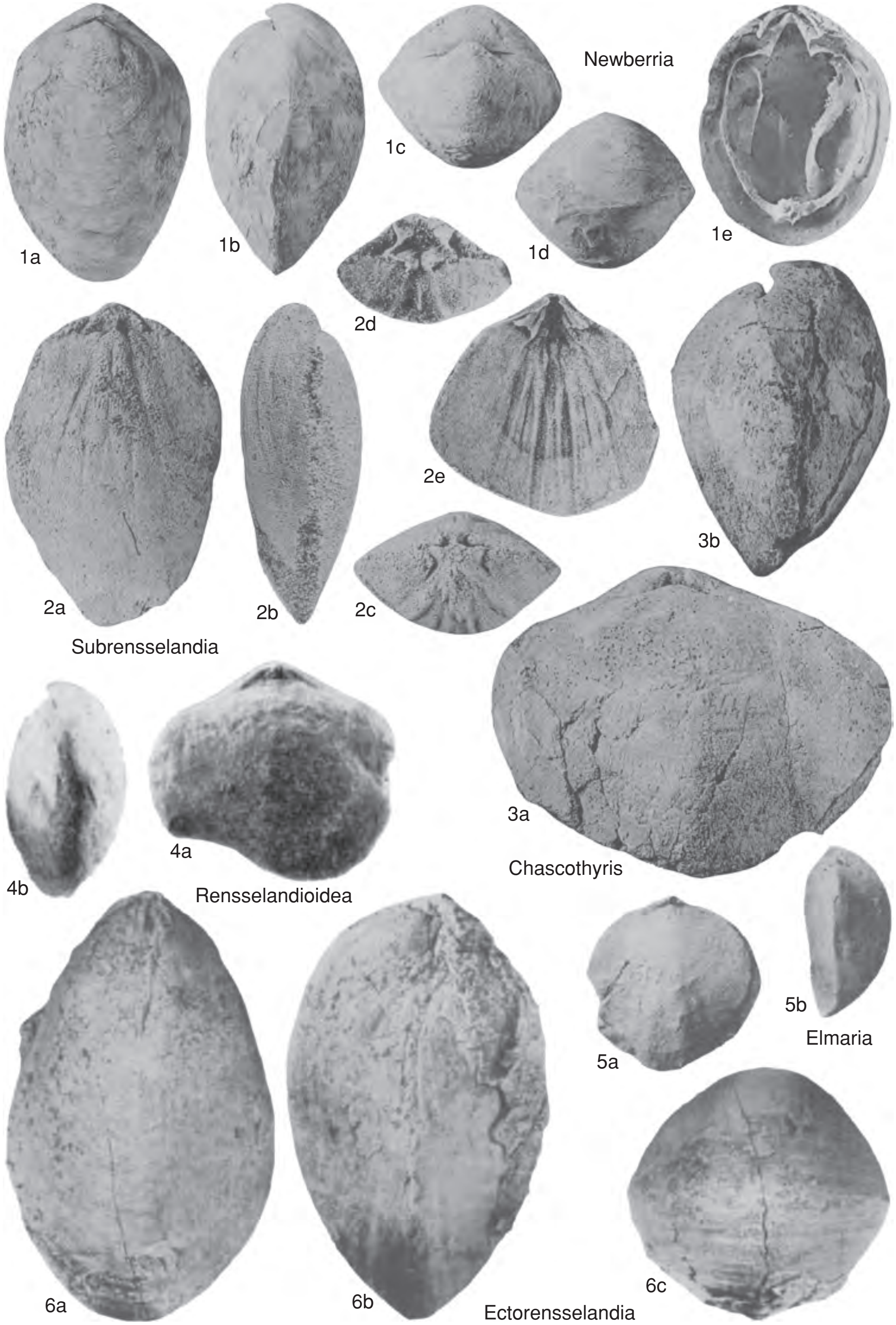

FIG. 1329. Stringocephalidae (p. 2007).

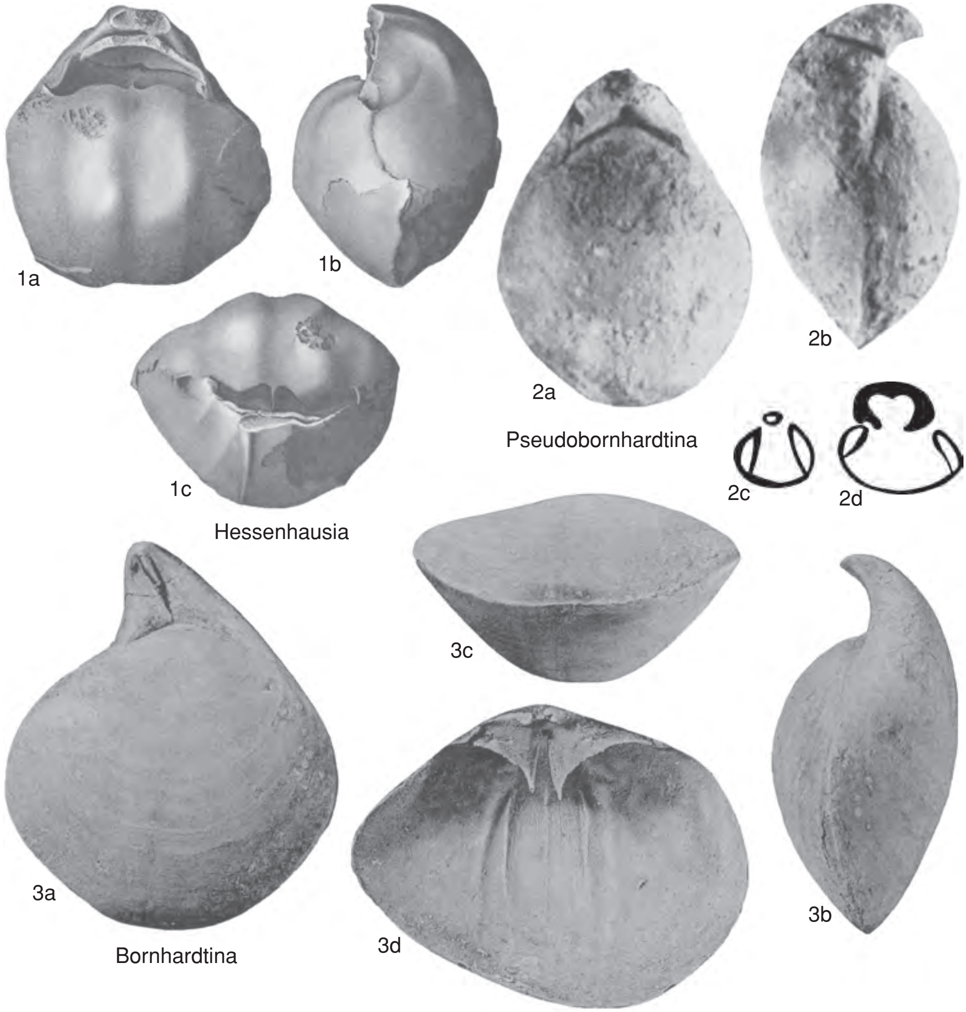

Fig. 1330. Stringocephalidae (p. 2007).

Subfamily MEGANTERIDINAE Schuchert & LeVene, 1929

[*nom. correct.* Stehli, 1965, p. 744, *pro* Meganterinae Boucot, 1959b, p. 766, *nom. transl. ex* Meganteridae Schuchert & LeVene, 1929a, p. 23]

Medium to large; smooth; subcircular; ventribiconvex; rectimarginate; hinge teeth large; cardinal plate; cardinal process and crural plates present. *Lower Devonian (Pragian–Emsian).*

Meganteris Suess, 1855a, p. 51 [**Terebratula archiaci* de Verneuil, 1850a, p. 175–176; SD Suess, 1856, p. 43] [=*Megalanteris* Oehlert, 1887b, p. 1,319, obj.; *Vltavothyris* Havlíček, 1956, p. 642 (type, *V. svobodai,* OD)]. Medium to large; subcircular; obsolete or obsolescent dental plates except in small specimens; crural plates in earlier growth stages; massive cardinal plate; bosslike cardinal process; hinge plates massive in large specimens; crural plates submerged in secondary material except in smaller specimens; loop teloform (cryptonelliform). *Lower Devonian (Pragian–Emsian):* Europe, Canada (Nova Scotia).——Fig. 1331,*1a.* **M. archiaci* (de Verneuil), France; incomplete dorsal interior of holotype, ×1 (Hall & Clarke, 1893).——Fig. 1331,*1b–g. M. suessi* Drevermann, Germany; *b–d,* latex replicas of dorsal and ventral interiors and lateral view of steinkern from which they were taken, ×0.5; *e–f,* anterior and ventral views of fragment of dorsal interior, ×1; *g,* reconstruction of loop, ×0.5 (Cloud, 1942).

Meganterella Boucot, 1959b, p. 767 [**M. finksi;* OD]. Medium; subcircular to elongate; short dental plates; cardinal plate sessile posteriorly; crural

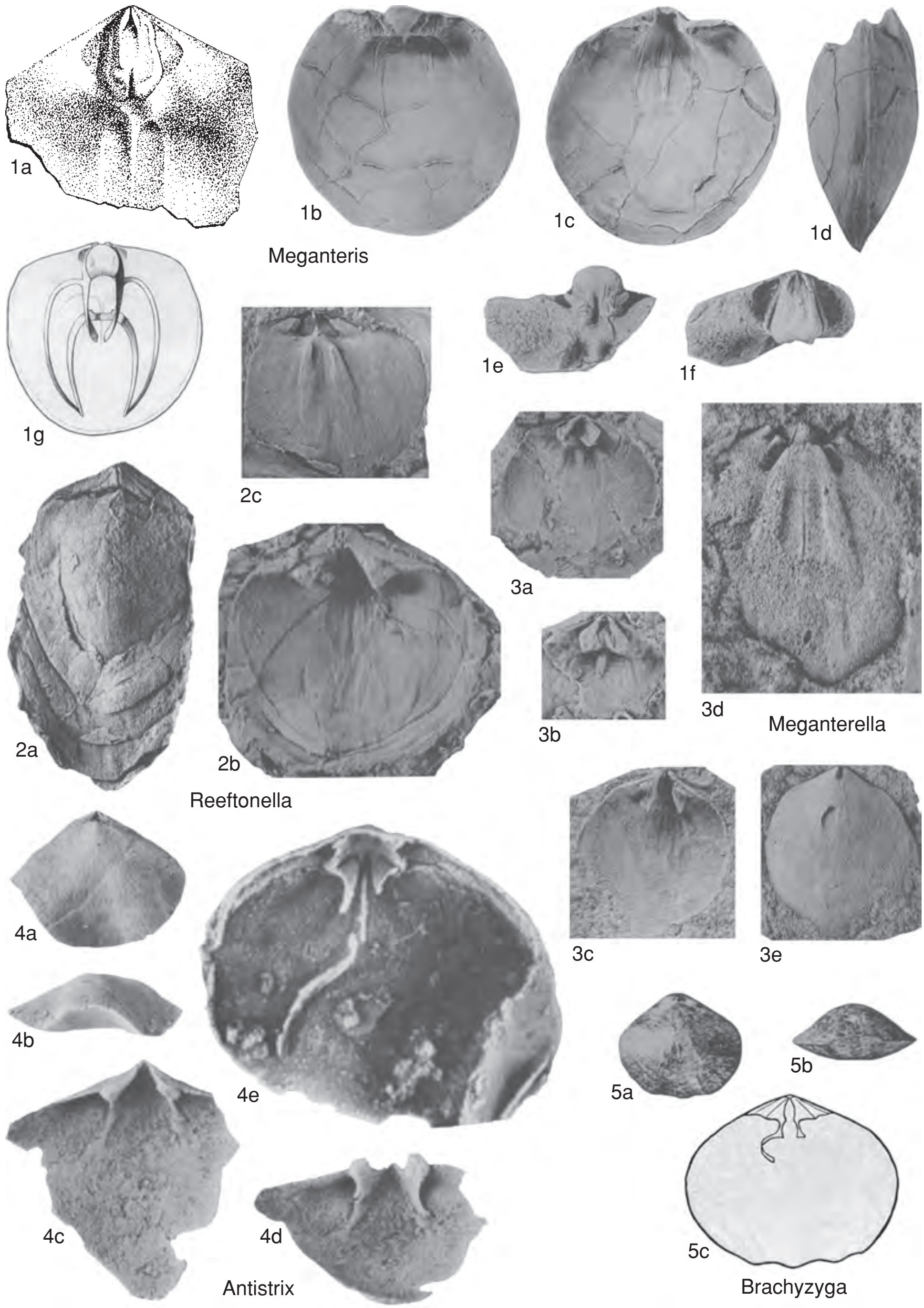

FIG. 1331. Meganterididae (p. 2009–2016).

plates; small cardinal process posteriorly; loop unknown. *Lower Devonian (Emsian):* USA (New York).——FIG. 1331,*3a–e*. **M. finksi,* Highland Mills; *a,* latex cast of dorsal valve interior, ×1; *b,* latex cast of dorsal valve interior, ×1; *c,* latex cast of ventral valve interior, ×1; *d,* impression of dorsal valve interior, ×3; *e,* latex cast of ventral valve exterior, ×1 (Boucot, 1959b).

Reeftonella BOUCOT, 1959b, p. 768 [**Meganteris neozelanica* ALLAN, 1935, p. 23; OD]. Subcircular to elongate oval; short dental plates in small shells to obsolete in large; stout hinge teeth; cordate muscle field; crural plates in smaller specimens to submerged in sessile cardinal plate in larger examples; no cardinal process; loop unknown. *Lower Devonian (Emsian):* New Zealand.——FIG. 1331,*2a–c*. **R. neozelanica* (ALLAN); *a,* latex replica of dorsal valve exterior, ×1 (Boucot & others, 1963); *b,* latex replica of interior of ventral valve, ×1 (Boucot, 1959b); *c,* impression of dorsal valve interior, ×1 (Boucot & others, 1963).

Subfamily MUTATIONELLINAE Cloud, 1942

[Mutationellinae CLOUD, 1942, p. 114]

Small to large; costate or costellate to peripherally costate; commonly rectimarginate; dental plates short; loop acuminate to deltiform (centronelliform to terebratuliform); hinge plates or cardinal plate; crural plates absent except in a few large specimens. *Lower Devonian (Lochkovian–Emsian).*

Mutationella KOZLOWSKI, 1929, p. 236 [**Waldheimia podolica* SIEMIRADZKI, 1906, p. 177; OD]. Small to medium; subcircular; ventribiconvex; costellate, short dental plates; weakly impressed muscle field; discrete hinge plates; short, anterior connecting band in large specimens; crural plates absent except for short examples in very rare, large specimens; loop acuminate to deltiform, but highly variable. *Lower Devonian (Lochkovian–Emsian):* Europe, eastern North America, South America, South Africa.——FIG. 1332,*1a–g*. **M. podolica* (SIEMIRADZKI), Poland; *a–c,* dorsal, lateral, and anterior views, ×2; *d–g,* drawings of 4 loops, ×4 (Cloud, 1942).——FIG. 1332,*1h–i*. *M. parlinensis* BOUCOT & others, Maine, USA; impressions of posterior and dorsal views, ×2 (Boucot, 1973).

Cloudella BOUCOT & JOHNSON, 1963, p. 123, *nom. nov. pro Pleurothyris* CLOUD, 1942, p. 123, *non* LOWE, 1843, *nec* SCHRAMMEN, 1912 [**Rensselaeria stewarti* CLARKE, 1907, p. 239; OD]. Medium; subcircular to elongate; costellate; costellae may increase partly by bifurcation; crenulate; ventribiconvex; short dental plates, obsolescent in larger individuals; muscle field deeply impressed in larger specimens; foramenate hinge plate or discrete hinge plates; muscle field deeply impressed in larger specimens; loop unknown. *Lower Devonian (Lochkovian–Pragian):* eastern North America.——FIG. 1332,*2a–e*. **C. stewarti* (CLARKE), Dalhousie, Canada; *a–c,* dorsal, lateral, and anterior views, ×1; *d,* posterior of ventral valve interior, ×1; *e,* posterior of dorsal valve interior, ×2 (Cloud, 1942).

Derbyina CLARKE, 1913b, p. 212, *non* GRABAU, 1931c [**Notothyris? smithi* DERBY, 1895, p. 81; SD CLARKE, 1913b, p. 212] [=*Paranaia* CLARKE, 1913a, pl. 21,*7–8* (type, *Centronella*? *margarida* DERBY, 1895, p. 84, OD); *Brasilica* GREGER, 1920, p. 70, *nom. null.; Chapadella* GREGER, 1920, p. 70 (type, *Centronella margarida* DERBY, 1895, p. 84, OD), *nom. nov. pro Brasilia* CLARKE, 1913b, p. 213, *non* BUCKMAN, 1898; *Brasilina* CLARKE, 1921, p. 138 (type, *Centronella margarida* DERBY, 1895, p. 84, OD), *nom. nov. pro Brasilia* CLARKE, 1913b, p. 213, *non* BUCKMAN, 1898; *Oliveirella* DE OLIVEIRA, 1934, p. 167 (type, *Centronella margarida* DERBY, 1895, p. 84, OD), *nom. nov. pro Brasilia* CLARKE, 1913b, p. 213, *non* BUCKMAN, 1898; *Chapadella* QUADROS, 1981, p. 88 (type, *C. mendesi* QUADROS, 1981, p. 89, OD)]. Small, umbones smooth; otherwise similar to coarsely costate *Mutationella.* [In 1920 GREGER named *Chapadella* as a substitute for *Brasilia* (see CLOUD, 1942, p. 122). In 1981 QUADROS named a new genus *Chapadella* in ignorance of GREGER's item. Adding to the confusion is the problem that the Malvinokaffric Realm costate mutationellinids are mostly represented by poor samples. Early growth stages of the genera (i.e., *Mendathyris, Cloudella, Scaphiocoelia,* and *Pleurothyrella*) look like *Mutationella* but develop their unique characters later in life as they become large. Therefore QUADROS's *Chapadella* could be the young of *Pleurothyrella* or just another synonym of the poorly known *Derbyina-Paranaia* confusion.] *Lower Devonian (Emsian):* central and southern South America.——FIG. 1332,*4a–c*. **D. smithi* (DERBY), Brazil; *a–b,* dorsal and lateral views, ×2; *c,* reconstruction of loop, approximately ×4 (Cloud, 1942).

Mendathyris CLOUD, 1942, p. 125 [**Rensselaeria mainensis* WILLIAMS, 1900, p. 80; OD]. Medium; subcircular to slightly elongate; subglobose, ventribiconvex; costellate; crenulate; short dental plates free in small specimens, obsolete in large specimens; muscle field deeply impressed in large specimens; discrete hinge plates in small specimens; swollen, perforate cardinal plate in large specimens; deeply impressed muscle field; loop unknown. *Lower Devonian (Lochkovian):* eastern North America.——FIG. 1332,*3a–e*. **M. mainensis* (WILLIAMS), Maine, USA; *a–b,* dorsal and lateral views; *c,* ventral view; *d,* latex replica of ventral valve interior; *e,* latex replica of dorsal valve interior, ×1 (Cloud, 1942).

Paulinella BOUCOT & RACHEBOEUF, 1987, p. 99 [**Terebratula guerangeri* DE VERNEUIL, 1850b, p. 780; OD]. Small; subcircular; costate to costellate; crenulate; gently ventribiconvex; short dental plates; discrete hinge plates or a foramenate cardinal plate; well-impressed muscle field. *Lower*

Devonian (Pragian–Emsian): Europe, Turkey.——FIG. 1333,*4a–d.* **P. guerangeri* (DE VERNEUIL), France; *a–b,* lectotype, dorsal and lateral views, ×2; *c,* interior of dorsal valve, ×2; *d,* reconstruction of loop, ×2 (Boucot & Racheboeuf, 1987).

Pleurothyrella BOUCOT & others, 1963, p. 89 [**Scaphiocoelia? africana* REED, 1906, p. 306; OD]. Large; subcircular to elongate; ventribiconvex; costate to costellate; costae may bifurcate; crenulate; short dental plates to obsolete; muscle field deeply impressed; discrete hinge plates in medium specimens to almost sessile, swollen cardinal plate in large specimens; posterior, small cardinal process may be present; muscle field deeply impressed; loop unknown. *Lower Devonian (Emsian):* Antarctica, New Zealand, South Africa, South America (Malvinokaffric Realm).——FIG. 1332,*6a–c.* **P. africana* (REED); *a,* latex replica of ventral valve; *b,* impression of dorsal valve interior; *c,* posterior view, ×1 (Boucot & others, 1963).——FIG. 1332,*6d–f. P. antarctica* BOUCOT & others, Antarctica; dorsal, lateral, anterior views, ×1 (Boucot & others, 1963).

Podolella KOZLOWSKI, 1929, p. 232 [**P. rensselaeroides;* OD]. Small, subcircular to elongate; umbonal region smooth; peripheral costae; short dental plates; perforate cardinal plate; no crural plates; loop acuminate. *Lower Devonian (Lochkovian):* Europe, Canada (Nova Scotia).——FIG. 1332,*5a–c.* **P. rensselaeroides,* Bohemia, Czech Republic; *a–b,* dorsal and anterior views, ×2; *c,* drawing of loop, ×3 (Cloud, 1942).

Prorensselaeria RAYMOND, 1923, p. 467 [**P. nylanderi;* OD]. Medium; subcircular; smooth umbo; costellate; crenulate; short dental plates; no crural plates in small specimens, to short crural plates in large specimens; discrete hinge plates; muscle field deeply impressed in large specimens; loop unknown. *Lower Devonian (Lochkovian):* eastern North America (Maine).——FIG. 1333,*1a–g.* **P. nylanderi,* New Brunswick; *a,* holotype, wax replica of exterior of ventral valve of steinkern (Cloud, 1942); *b,* impression of exterior; *c–f,* ventral, dorsal, posterior, and lateral views of internal mold; *g,* dorsal view of internal mold, ×1 (Boucot & Wilson, 1994).

Scaphiocoelia WHITFIELD in WENDT, 1891, p. 106 [**S. boliviensis;* OD]. Large; subcircular to elongate; naviculate, with ventral valve deep and dorsal valve gently sulcate; broadly unisulcate anterior commissure; costate; short dental plates in medium specimens to obsolete in large specimens; muscle field deeply impressed in large specimens; discrete hinge plates in medium specimens to posteriorly sessile, swollen cardinal plate in large individuals; bosslike cardinal process; loop present. *Lower Devonian (Emsian):* central and southern South America and southern Africa (Malvinokaffric Realm).——FIG. 1333,*3a–d.* **S. boliviensis,* Icla, Bolivia; *a,* impression of dorsal valve interior; *b,* impression of ventral interior; *c,* posterior view of impression of ventral interior; *d,* latex replica of ventral valve interior, ×1 (BOUCOT & others, 1963).

Xana GARCÍA-ALCALDE, 1972, p. 5 [**X. bubo;* OD]. Small; laterally elongate; naviculate; ventral valve gently convex; dorsal valve gently unisulcate, concave; coarsely costate; crenulate; short dental plates; discrete hinge plates united anteriorly by a median band; loop short, with recurved anteromedian vertical lamina. *Lower Devonian (Emsian):* northern Spain.——FIG. 1333,*2a–c.* **X. bubo; a–b,* holotype, dorsal and lateral views, DPO 284, ×1; *c,* reconstruction of loop, ×2 (García-Alcalde, 1972).

Subfamily BRACHYZYGINAE Cloud, 1942

[Brachyzyginae CLOUD, 1942, p. 113]

Small, smooth, broad, ventribiconvex, with dorsal sulcus and ventral fold; anterior commissure intraplicate; dental plates short; discrete, sessile hinge plates; no crural plates; loop short, acuminate. *Silurian (?Pridoli), Lower Devonian (Lochkovian).*

Brachyzyga KOZLOWSKI, 1929, p. 243 [**B. pentameroides;* OD]. Description as for subfamily. *Silurian (?Pridoli), Lower Devonian (Lochkovian):* Podolia, *Lochkovian;* central Asia, *?Pridoli.*——FIG. 1331,*5a–c.* **B. pentameroides,* Lochkovian, Podolia, Poland; *a–b,* holotype, dorsal and anterior views, ×1; *c,* drawing of loop, ×2 (Cloud, 1942).

Subfamily ADRENINAE Boucot, 1994

[Adreninae BOUCOT in BOUCOT & WILSON, 1994, p. 1,018]

Small, commonly ventribiconvex, smooth to strongly costate; unisulcate dorsal valve and opposing, ventral valve fold; loop acuminate (centronelliform). *Lower Devonian (Lochkovian–Emsian).*

Adrenia CHATTERTON, 1973, p. 126 [**A. expansa;* OD]. Subcircular to elongate; very weak dorsal valve sulcus and low ventral valve fold; ventribiconvex to subglobular; costate; rectimarginate to unisulcate, crenulate anterior margin; deltidial plates forming deltidial sheath; short dental plates; median septum supporting conjunct hinge plates to form a septalium. *Lower Devonian (Emsian):* eastern Australia.——FIG. 1334,*5a–f.* **A. expansa; a–d,* holotype, dorsal, ventral, lateral, and anterior views, ANU 18986, ×3.8; *e,* close-up of beak, ×11; *f,* reconstruction of dorsal valve interior, ×8 (Chatterton, 1973).

Barbarothyris WANG Yü & RONG, 1986, p. 264 [**B. glabra;* OD]. Elongate; ventribiconvex; smooth umbos; periphery weakly to strongly costate; dorsal valve sulcus and ventral valve fold; ventral valve fold may be deeply plicate; anterior commissure unisulcate to uniplicate, crenulate; short dental plates; foramenate cardinal plate; loop with median plate. *Lower Devonian (Emsian):* China (Guangxi).——FIG. 1334,*6a–d.* **B. glabra; a–c,* holotype, dorsal, lateral, and anterior views, ×6; *d,* reconstruction of

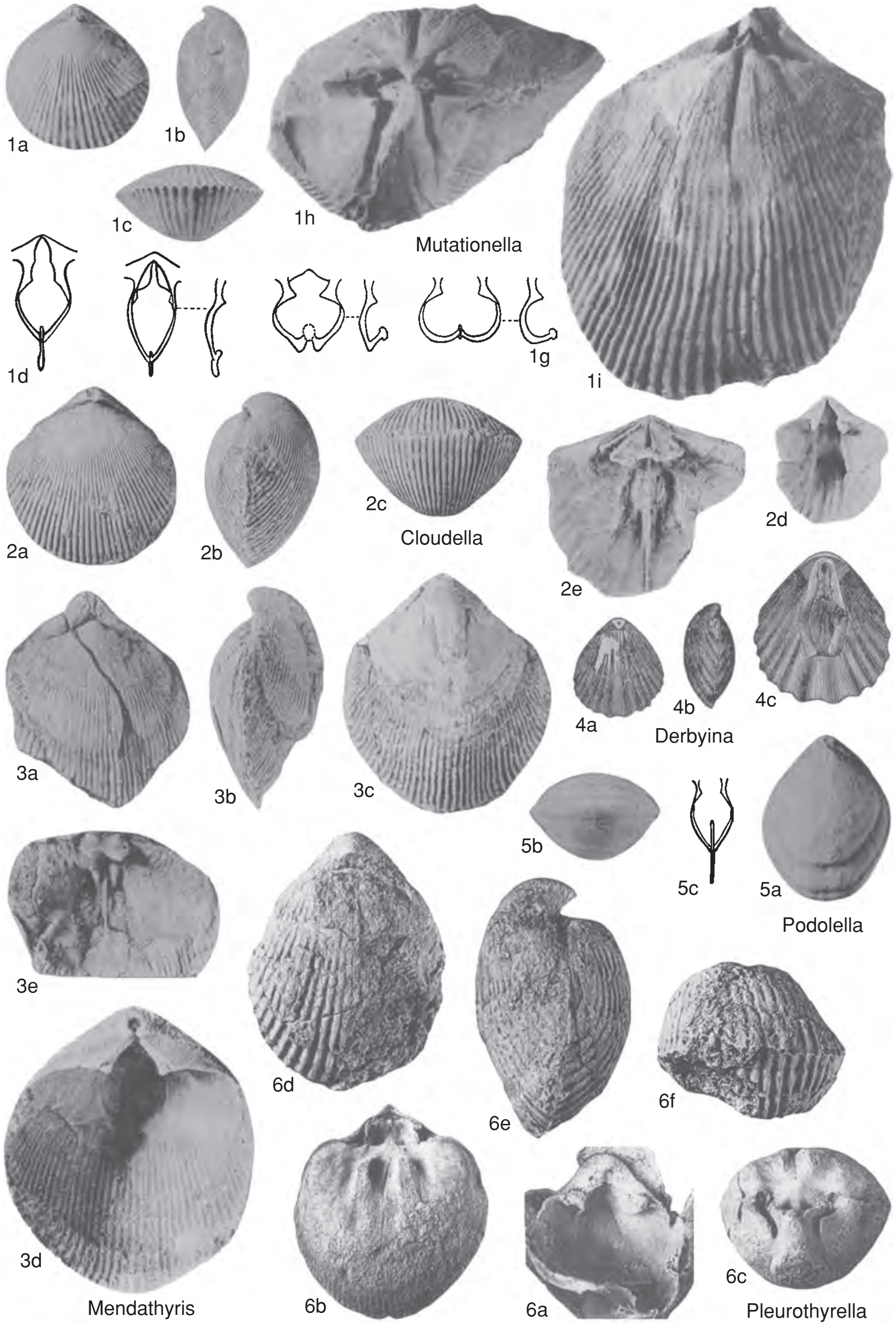

FIG. 1332. Meganterididae (p. 2011–2012).

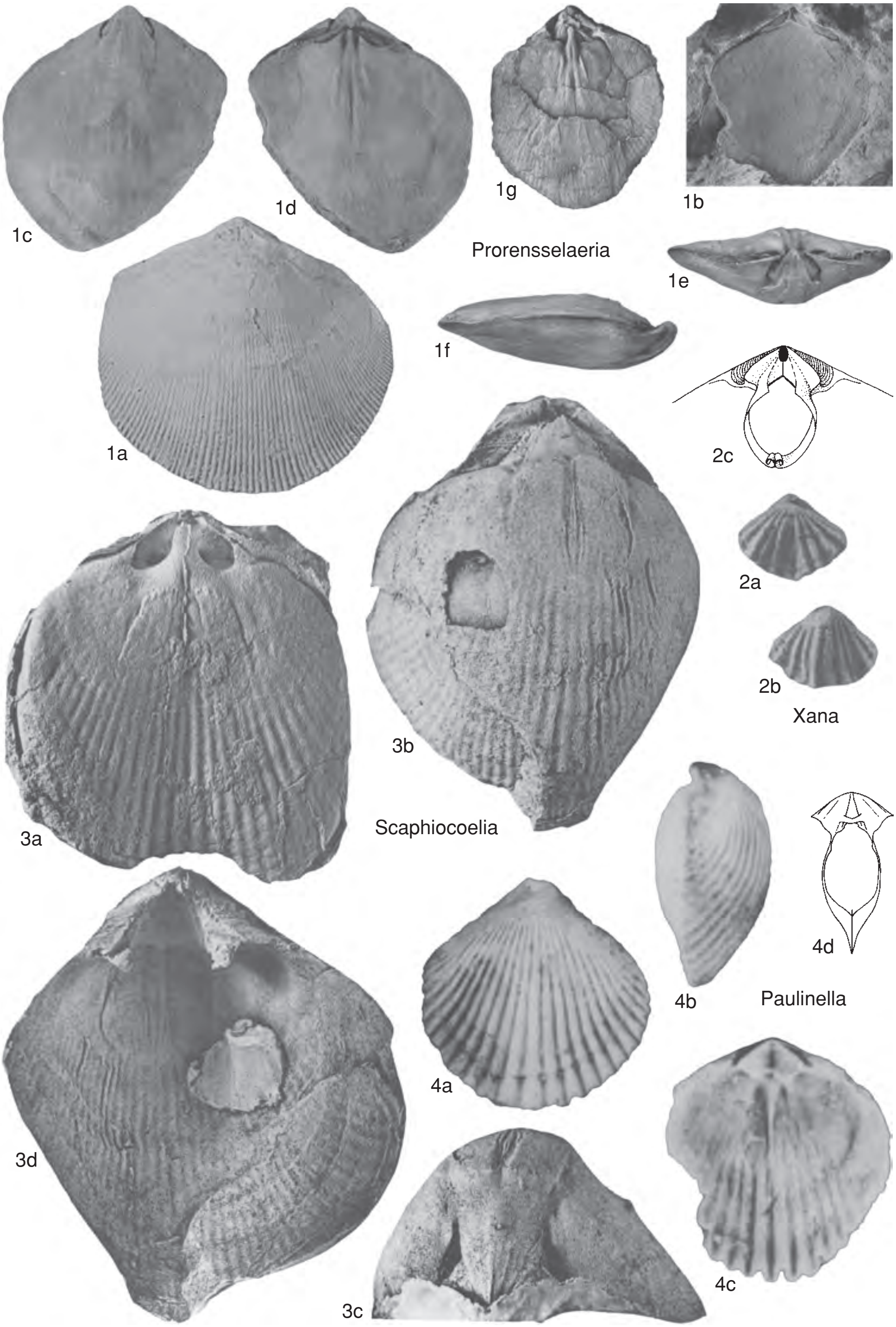

FIG. 1333. Meganterididae (p. 2011–2012).

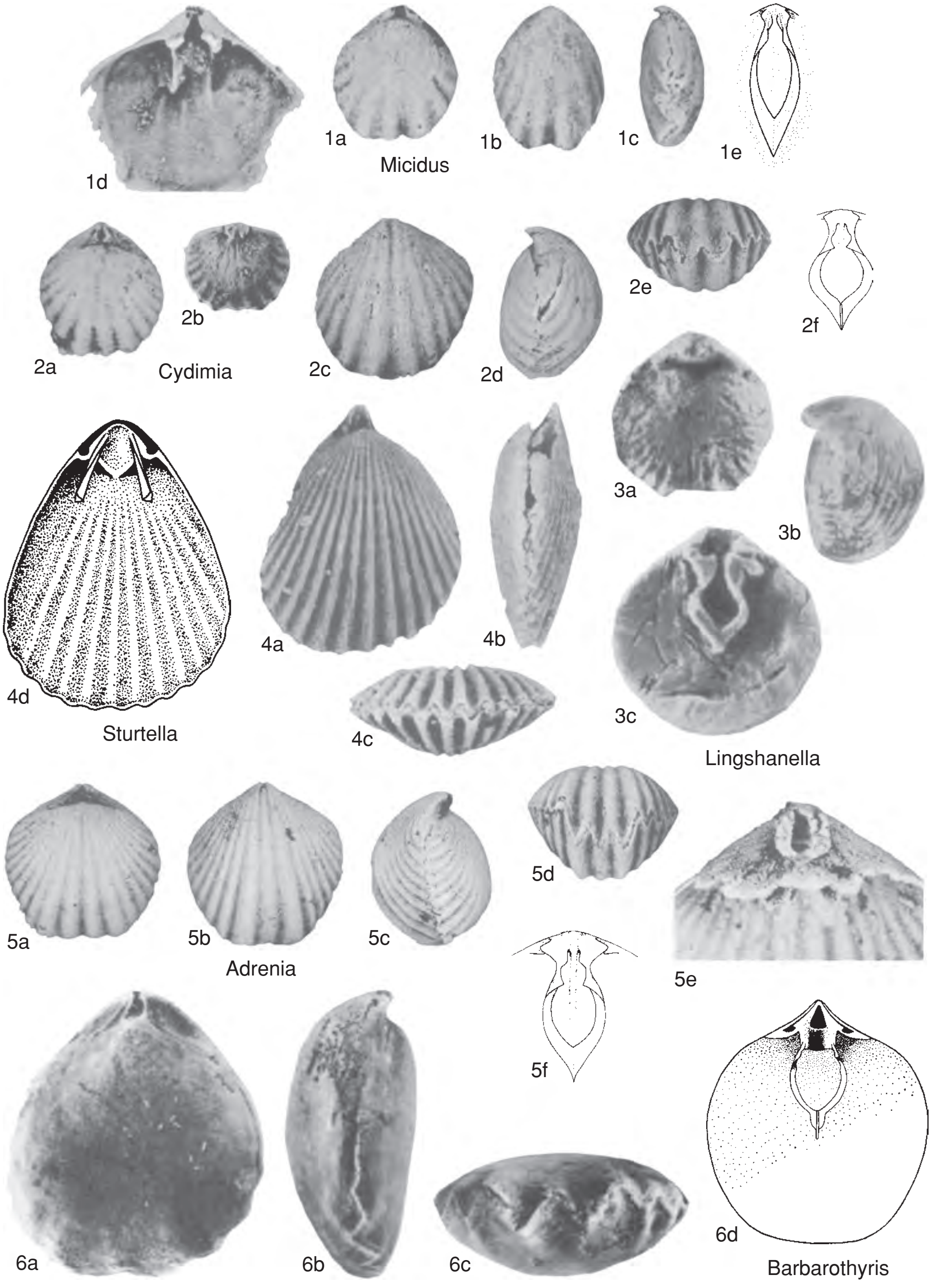

FIG. 1334. Meganteridiidae (p. 2012–2016).

interior of dorsal valve, ×5 (Wang Yü & Rong, 1986).

Cydimia Chatterton, 1973, p. 131 [**C. robertsi;* OD]. Subcircular to elongate; ventribiconvex; costate except for smooth umbonal region in some forms; broad, weak dorsal valve sulcus and corresponding ventral valve fold; unisulcate, crenulate anterior margin; deltidial plates forming deltidial sheath; short dental plates; hinge plates forming a septalium supported by a low median septum; loop with vertical median plate. *Lower Devonian (Emsian):* New South Wales, Australia, *Emsian;* China (Guangxi), *?Emsian.*——Fig. 1334,*2a–f.* **C. robertsi,* New South Wales; *a–b,* external and internal views of dorsal valves, ×3.5; *c–e,* holotype, ventral, lateral, and anterior views, ANU 18992, ×3.6; *f,* reconstruction of dorsal valve interior, ×8 (Chatterton, 1973).

Lingshanella Xu & Yao, 1986, p. 174 [**L. convexa;* OD]. Subcircular; naviculate with flat to concave dorsal valve and very convex ventral valve; costate with smooth umbos; dorsal sulcus and ventral valve fold; anterior margin unisulcate, crenulate; short dental plates; hinge plates fused posteriorly, discrete anteriorly. *Lower Devonian (Emsian):* China (Guangxi).——Fig. 1334,*3a–b.* **L. convexa;* dorsal and lateral views of holotype, ×2 (Xu & Yao, 1986).——Fig. 1334,*3c. L. changlingensis;* interior of dorsal valve, ×2 (Xu & Yao, 1986).

Micidus Chatterton, 1973, p. 134 [**M. shandkyddi;* OD]. Elongate; ventribiconvex; umbos smooth, periphery smooth or plicate; weak dorsal sulcus and corresponding ventral valve fold; weakly unisulcate, crenulate anterior margin; short dental plates; discrete hinge plates. *Lower Devonian (Emsian):* Australia (New South Wales), USA (southeastern Alaska).——Fig. 1334,*1a–e.* **M. shandkyddi,* New South Wales; *a,* holotype, dorsal view, ANU 18988, ×4.7; *b–c,* ventral and lateral views, ×4.7; *d,* interior of ventral valve, ×11.3; *e,* reconstruction of dorsal valve interior, ×8 (Chatterton, 1973).

Sturtella Savage, 1971, p. 417 [**S. mandageriensis;* OD]. Ventribiconvex; elongate; weak dorsal valve sulcus; rectimarginate, costellate; anterior commissure crenulate; dental plates well developed; medially conjunct hinge plates resting on valve floor as a septalium; long crura; loop unknown. *Lower Devonian (Lochkovian):* Australia (New South Wales).——Fig. 1334,*4a–d.* **S. mandageriensis; a–c,* dorsal, lateral, and anterior views, ×8; *d,* drawing of dorsal valve interior, ×10 (Savage, 1971).

Subfamily ANTISTRIXINAE
Johnson, 1972

[*nom. transl.* Jin & Lee, herein, *ex* Antistrixidae Johnson, 1972, p. 121]

Small, smooth, transverse, outline oval, strongly unisulcate dorsal valve and corresponding fold on ventral valve; unisulcate anterior commissure; short dental plates; discrete hinge plates; ventrally directed spine in valve posterior; acuminate (centronelliform) loop with median plate. *Middle Devonian (Givetian).*

Antistrix Johnson, 1972, p. 121 [**A. invicta;* OD]. Description as for subfamily. *Middle Devonian (Givetian):* USA (Nevada).——Fig. 1331,*4a–e.* **A. invicta; a–b,* dorsal and anterior views, ×3; *c–d,* interior views of ventral valve, ×5 (Johnson, 1972); *e,* dorsal valve interior showing incomplete loop, ×5 (Johnson, 1976).

Family RHIPIDOTHYRIDIDAE
Cloud, 1942

[*nom. correct.* Stehli, 1965, p. 748, *pro* Rhipidothyridae Cloud, 1942, p. 80]

Small to large; smooth or costate, rectimarginate; ventral foramen submesothyrid to hypothyrid; dental plates well developed to obsolescent; hinge plates discrete or united to form a septalium supported by a median septum duplex formed from crural plates; loop unknown. *Lower Devonian (Lochkovian)–Upper Devonian (Frasnian).*

Subfamily RHIPIDOTHYRIDINAE
Cloud, 1942

[*nom. correct.* Stehli, 1965, p. 749, *pro* Rhipidothyrinae Cloud, 1942, p. 87]

Small to medium, smooth or costate, moderately ventribiconvex; ventral foramen submesothyrid; septalium formed from conjunct hinge plates; supported by median septum formed from fused, long crural plates; dental plates free; loop probably acuminate (centronelliform). *Middle Devonian (Eifelian)–Upper Devonian (Frasnian).*

Rhipidothyris Cooper & Williams, 1935, p. 846 [**R. plicata;* OD]. Small to medium, costate, subcircular to subovate, ventribiconvex; dental plates short; imperforate cardinal plate forming septalium supported by median septum; loop unknown. *Middle Devonian (Eifelian–Givetian):* eastern North America, USA (Nevada), Bolivia, Libya, South Africa.——Fig. 1335,*3a.* **R. plicata,* New York, USA; holotype, internal impression of dorsal valve, USNM 89771c, ×2 (Cloud, 1942).——Fig. 1335,*3b–d. R. lepida* (Hall), New York; dorsal, lateral, and anterior views, ×2 (Cloud, 1942).

Neoglobithyris Havlíček, 1984, p. 59 [**N. tmisanensis;* OD]. Medium; smooth umbones, costellate anteriorly, costae and interspaces rounded in cross section, 30 to 40 costae, subcircular outline, weakly ventribiconvex, anterior margin rectimarginate, crenulate, rounded; small deltidial plates border open delthyrium, dental lamellae short, ventral

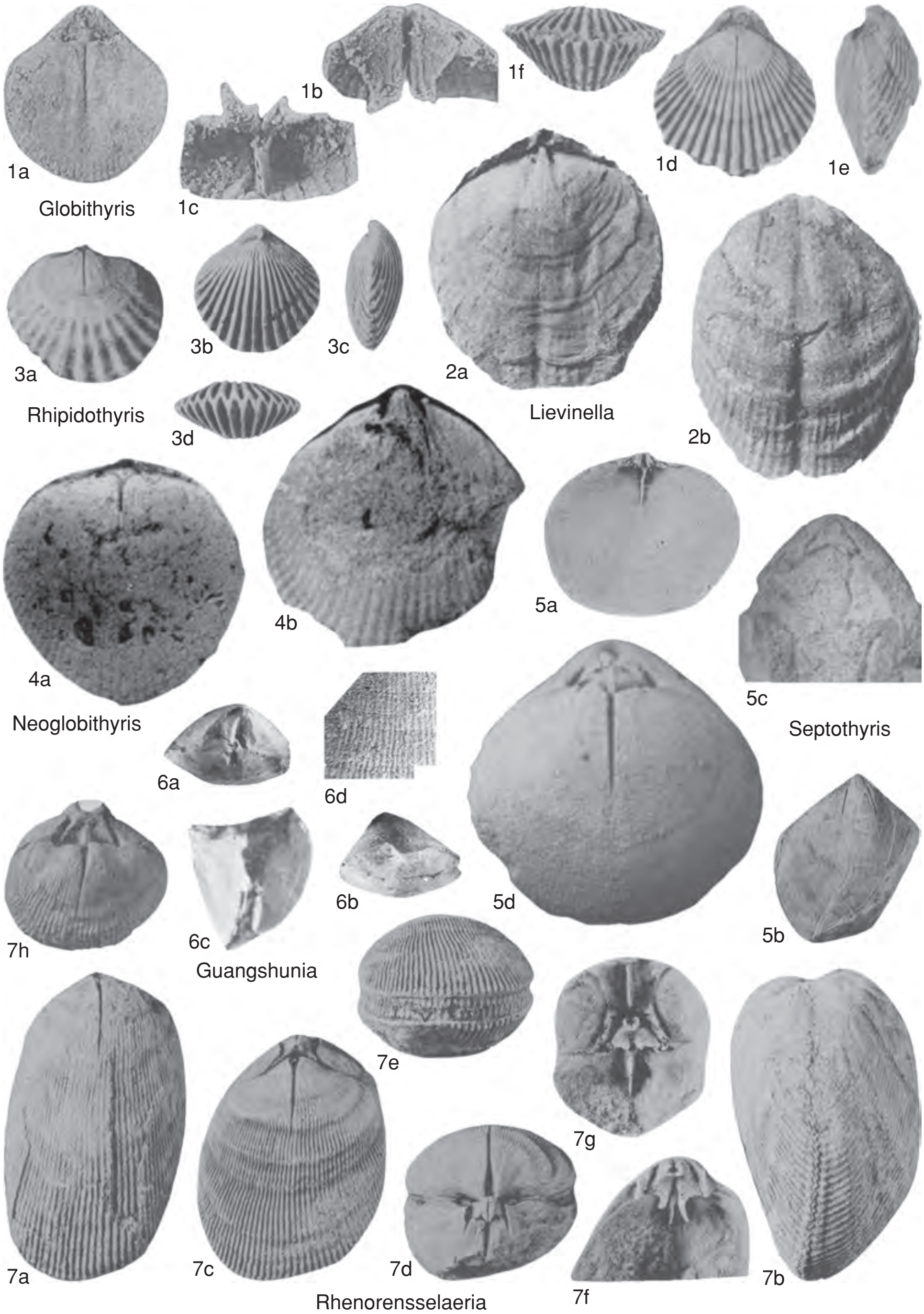

FIG. 1335. Rhipidothyrididae and Uncertain (p. 2016–2018).

muscle field variably impressed, dorsal median septum, short to moderately long, supporting small cruralium. *Middle Devonian (Givetian):* Libya.——FIG. 1335,*4a–b.* **N. tmisanensis; a,* internal mold of dorsal valve, ×1.8; *b,* holotype, internal mold of ventral valve, ×2.8 (Havlíček, 1984).

Septothyris COOPER & WILLIAMS, 1935, p. 848 [**S. septata;* OD]. Small to medium, smooth, subcircular to subovate, ventribiconvex; free dental plates; septalium formed from conjunct hinge plates supported by a median septum formed from fused crural plates; loop probably acuminate (centronelliform). *Middle Devonian (Givetian)–Upper Devonian (Frasnian):* eastern North America, Libya, Bolivia, South Africa.——FIG. 1335,*5a–b.* **S. septata,* New York, USA; *a,* holotype, latex replica of impression of dorsal valve, USNM 89775, ×2; *b,* impression of ventral interior, ×1 (Cloud, 1942).——FIG. 1335,*5c–d. S. boucoti* MERGL & MASSA, Frasnian, Libya; *c,* internal mold showing shape of loop, ×4; *d,* internal mold, ×5 (Mergl & Massa, 1992).

Subfamily GLOBITHYRIDINAE Cloud, 1942

[*nom. correct.* STEHLI, 1965, p. 750, *pro* Globithyrinae CLOUD, 1942, p. 81]

Small to large, moderately to strongly biconvex, subcircular to suboval; ventral foramen hypothyrid, hinge plates conjunct to form a septalium in larger specimens, supported by median septum formed from crural plates; no cardinal process; free dental plates; loop unknown. *Lower Devonian (Pragian)–Upper Devonian (Frasnian).*

Globithyris CLOUD, 1942, p. 82 [**Rensselaeria callida* CLARKE, 1907, p. 241; OD]. Costate, ventribiconvex; free dental plates; discrete crural plates in juveniles, medially conjunct to form median septum when larger; medially fused hinge plates forming septalium supported by median septum in larger specimens; loop unknown. *Lower Devonian (Pragian)–Upper Devonian (Frasnian):* eastern North America, northern Europe.——FIG. 1335,*1a–c.* **G. callida* (CLARKE), Emsian, Maine, USA; *a,* dorsal view of steinkern; *b–c,* ventral and anterior views of cardinal plate of young specimen, ×4 (Cloud, 1942).——FIG. 1335,*1d–f. G. diania* (CLARKE), Emsian, Maine, USA; dorsal, lateral, and anterior views, ×2 (Boucot, 1973).

Subfamily RHENORENSSELAERINAE Boucot, 1975

[*nom. transl.* JIN & LEE, herein, *pro* Rhenorensselaeridae BOUCOT, 1975, p. 372]

Small to large, subcircular to elongate, costellate, ventribiconvex, rectimarginate, crenulate, dental plates obsolescent to obsolete; ventral valve muscle field deeply impressed and subdivided, hinge plates either discrete or conjoined medially; discrete crural plates or median septum formed from conjunct crural plates; loop unknown. *Lower Devonian (Lochkovian–Emsian).*

Rhenorensselaeria KEGEL, 1913, p. 126 [**Terebratula strigiceps* ROEMER, 1844, p. 58; SD SCHUCHERT & LEVENE, 1929a, p. 107]. Medium to large; dental plates obsolete to obsolescent; ventral valve muscle field deeply impressed and subdivided; cardinal plate formed from conjunct hinge plates, supported by median septum formed from fused crural plates; small, bifid cardinal process; loop unknown. *Lower Devonian (Pragian–Emsian):* eastern North America (Gaspé), northern Europe.——FIG. 1335,*7a–g.* **R. strigiceps* (ROEMER), Pragian, Germany; *a–b,* dorsal and lateral views of steinkern; *c–e,* dorsal, posterior, and anterior views of steinkern; *f–g,* latex replicas of posterior of steinkern, ×1 (Cloud, 1942).——FIG. 1335,*7h. R. macgerriglei* BOUCOT, Gaspé, Canada; dorsal view of internal impression, ×1 (Boucot, Cumming, & Jaeger, 1967).

Lievinella BOUCOT, 1975, p. 372 [**Rensselaerina primaeva* BARROIS, PRUVOST, & DUBOIS, 1920, p. 102; OD]. Small to medium; bisulcate; obsolescent dental plates; ventral valve muscle field deeply impressed; discrete crural plates; discrete hinge plates; loop unknown. *Lower Devonian (Lochkovian):* northern France.——FIG. 1335,*2a–b.* **L. primaeva* (BARROIS, PRUVOST, & DUBOIS); *a,* internal mold of dorsal valve, ×1; *b,* internal mold of ventral valve, ×1 (Barrois, Pruvost, & Dubois, 1920).

Family UNCERTAIN

?Guangshunia XIAN & JIANG, 1978, p. 317 [**G. pagodiformis* XIAN & JIANG, 1978, p. 318; OD]. Small to medium, hemipyramidal; very fine radial costellae; hinge line straight, less than maximum width; long ventral interarea, triangular, catacline; open delthyrium; no fold or sulcus; stout dental plates; faint median ridge; stout, undivided hinge plate supported by high median septum; stout cardinal process, circular cross section, comblike process posteriorly, which is bosslike anteriorly. *Middle Devonian (Givetian):* southern China (southern Guizhou).——FIG. 1335,*6a–d.* **G. pagodiformis; a–c,* posterior, anterior, and lateral views of holotype, GB451, ×1; *d,* close-up view of shell ornament, ×3 (Xian & Jiang, 1978).