

SPIRIFERIDA

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Order SPIRIFERIDA

Waagen, 1883

[*nom. correct.* MOORE, LALICKER, & FISCHER, 1952, p. 221, *pro* order Spiriferacea KUHN, 1949, p. 104, *nom. transl. ex* suborder Spiriferacea WAAGEN, 1883a, p. 447; *emend.*, CARTER & others, 1994, p. 328]

Generally biconvex; generally transverse with moderately wide to extended straight

hinge line; ribbing very fine to coarse; small dorsal and larger ventral interareas always developed; spiralia directed laterally or posterolaterally with primary lamellae parallel and close to sagittal plane; jugum absent; shell substance impunctate. *upper Upper Ordovician–Lower Triassic, ?Middle Triassic–?Upper Triassic.*

INTRODUCTION

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Spiriferids *sensu lato* consist of two large but distinct groups, namely those that are impunctate and those that are punctate. In the first edition of the *Treatise* PITRAT (1965) freely intermixed the impunctate and punctate genera, assuming punctation to have appeared independently in several groups. In the intervening years new studies (IVANOVA, 1972, 1981; CARTER, 1985; ERLANGER & SOLOMINA, 1989) have shown that the punctate genera assigned to impunctate superfamilies such as the syringothyridids are in fact unrelated and conversely that the impunctate genera such as *Punctothyris*, *Odontospirifer*, and *Spiriferinaella*, which were assigned to punctate families, are not related to them and are readily assignable to well-established impunctate superfamilies. In the classification adopted here the two groups are treated as separate orders of unknown origin, appearing cryptogenically in the Late Ordovician and earliest Devonian respectively.

The recent discovery of the genus *Eospirifer* in the Upper Ordovician of China by RONG, ZHAN, and HAN (1994) and elucidation of its internal morphology by RONG and ZHAN (1996) may give light to the ori-

gin of the Spiriferida. These authors suggested that *Eospirifer* may have been derived from some unknown ancestor similar to the atrypid *Cyclospira*. The origin of the punctate Spiriferinida is unknown. The first representative of this group, *Cyrtina*, appears at the base of the Devonian as a very morphologically complex genus and is unlikely to be the ancestral spiriferinide.

The classification used here generally follows that of CARTER and others (1994). Since the publication of that paper a new family of cyrtospiriferoids has been proposed by MA and DAY (2000), and some of the martinioids have been subdivided further by WATERHOUSE (1998) and reassigned to the Delthyridina. The Delthyridina, however, are characterized by having complicated concentric microornament that is absent from WATERHOUSE's taxa, and we retain the WATERHOUSE taxa within the Martinioidea. Numerous new genera have been proposed since 1994 and will be included in *Treatise, Part H, revised*, volume 6.

Criticism of the CARTER and others classification (1994), although invited, has been minimal. DAGYS (1996) discounted the synapomorphous nature of the crenulate

hinge line (even and regular low amplitude folds of each interarea with posterior tooth-like projections that interlock, similar to interlacing the teeth of two combs) of the Spondylospiroidea and redistributed the genera into other superfamilies. Instead he placed great importance on the presence of a sessile jugum with a net in various cyrtiniform genera with a shallow dorsal valve claiming that they were unique to his superfamily Bittneruloidea, which is characterized by having a distinct spondylium, dental plates, and a sessile jugum with net. In fact the Bittnerulidae lack dental plates and a true spondylium. Furthermore, of sixty Triassic spiriferinide genera, the jugum is known for only nineteen. Finally, the sessile jugum with a net occurred early in the history of this group in the genus *Komiella* of Middle Devonian age. It is still contended here that the crenulate hinge line is a uniquely evolved character that is unlikely to have occurred in unrelated stocks. This character is not described in other brachiopod groups and manifestly does not occur in other spiriferide or spiriferinide taxa.

Several other challenges to this classification have recently been registered. BOUCOT, COCKS, and RACHEBOEUF (1999) disregarded the assignment of *Rhynchospirifer* to Rhynchospiriferinae (Ambocoeliidae) and *Prosserella* to Reticulariopsinae (Reticulariidae); we accept the justification for both assignments by PITRAT (1965) and FAGERSTROM (1971). BIZZARRO and LESPÉRANCE (1999) questioned our assignment of some genera to subfamilies and families within the Delthyridoidea and questioned the evidence supporting evolutionary relationships among those confamilial genera. The phylogenetic analysis that they presented, in which 9 characters were coded among 12 subfamilial taxa of ambiguous definition and scope, is insufficient to support their revision of the superfamily. MA and DAY (2000) rejected *Conispirifer* as a synonym of *Tenticospirifer* and removed it from the Cyrtospiriferidae to erect a new family Conispiriferidae. They

recommended a thorough revision of the Cyrtospiriferoidae, with which we concur. Discovery of new fossils and establishment of new taxa will continue to require revision of any classification proposed; we reassert that the classification presented here accommodates best the available fossil evidence. Future analyses of spiriferide genera and higher taxa will undoubtedly clarify further the phylogenetic relationships within this diverse and interesting group of spire-bearing brachiopods.

The term spirifer is used generally to denote medium to large, strophic, biconvex, ribbed shells that internally bear a calcified spiral brachidium. As noted above, the term usually refers to both impunctate and punctate forms; but, lacking certain indication of ancestry, the two groups are treated as separate orders here, the Spiriferida and Spiriferinida, respectively. Figure 1102 shows the abundance and stratigraphic distribution of both groups.

The exterior of a typical member of the impunctate Spiriferida is generally transversely biconvex with a wide hinge line, high flattened ventral interarea, acute incurved ventral beak, distinct dorsal fold and ventral sulcus, and ribbed lateral slopes. Maximum width is attained normally at or near the hinge line. Internally, the calcified brachidium has posterolaterally directed spiralia (Fig. 1103). All Spiriferida are extinct, being restricted to the Paleozoic or possibly the basal Triassic.

Insofar as is known all Spiriferida lived either attached to the substrate or each other by means of a muscular pedicle or freely on the seafloor, resting on the umbones of the longer, heavier ventral valves. They are found in most marine sedimentary rocks of shallow to moderately deep origin but are notably absent or rare in most deep-basinal sediments such as black shales, although they do sometimes occur in starved-basin carbonates. They were cosmopolitan in distribution throughout most of their stratigraphic range, occurring in most normal-marine biotas and often dominating them in terms of both

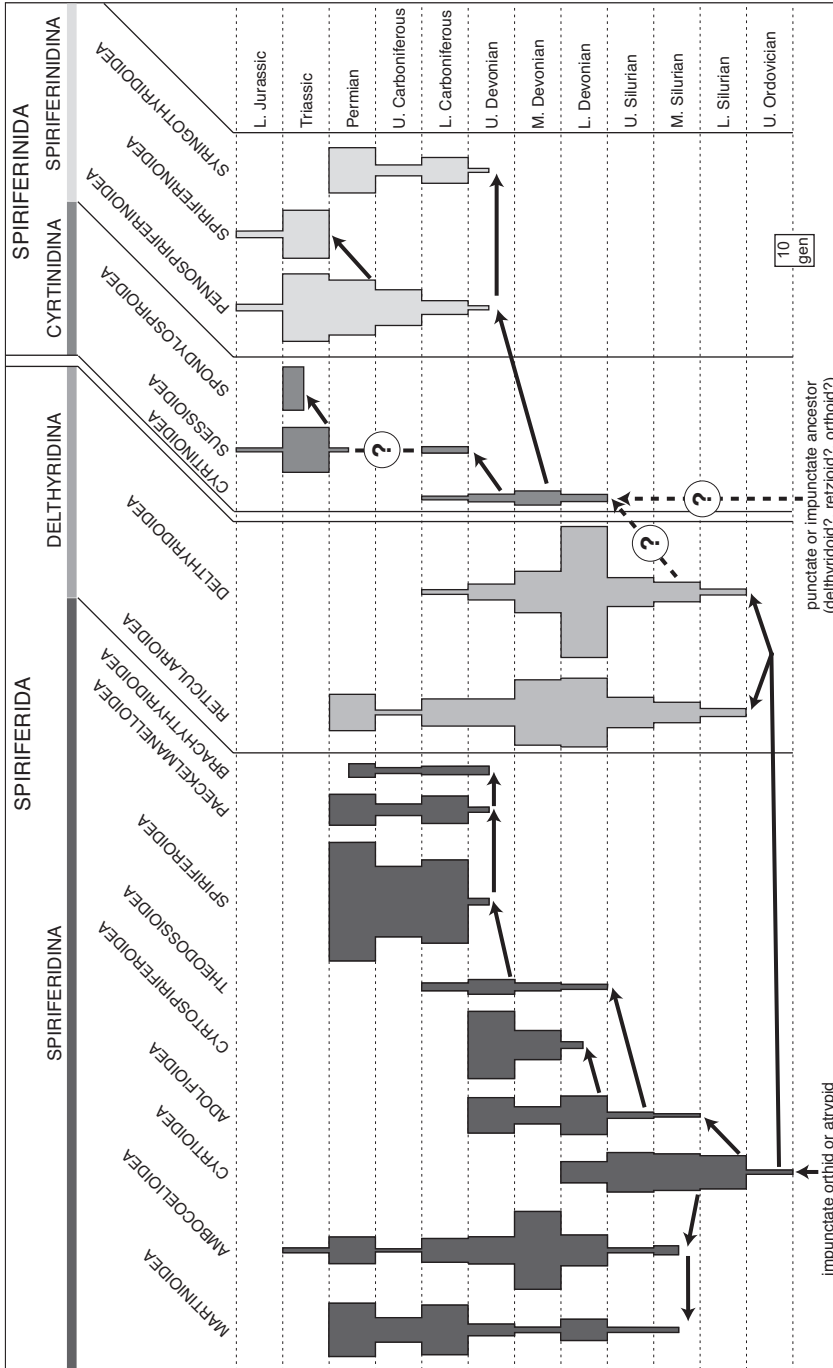


FIG. 1102. Stratigraphic distribution and relative generic abundance of the spiriferid brachiopods (new).

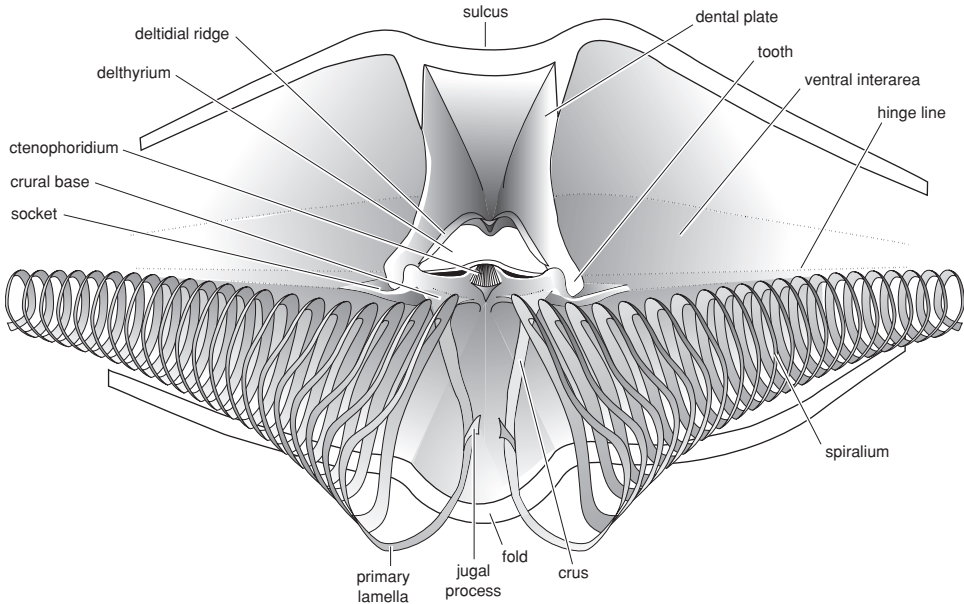


FIG. 1103. Diagrammatic representation of the internal morphology of the spiriferid shell: anterior view of the interior with ventral valve up, dorsal valve down (new).

numbers of individuals and taxonomic diversity, particularly in the Devonian and Carboniferous.

The order Spiriferida, as treated herein, consists of two suborders, the Spiriferidina and Delthyridina, with both suborders comprising over 400 distinct genera in 11 superfamilies. The Spiriferidina appeared first as the genus *Eospirifer* of the superfamily Cyrtioidea in the Upper Ordovician (middle Ashgill) of Asia and Australia. The suborder Delthyridina appeared later, in the lower Silurian (middle Llandovery), but its origin is uncertain. The delthyridines are characterized by having a fimbriate ornament, which does not occur in the Cyrtioidea, and may indicate derivation from a common ancestor with the eospiriferoids, rather than directly from them.

Our knowledge of the evolution of the Spiriferida is highly incomplete. For this reason the classification used in this edition of the *Treatise* must be viewed as a temporary

progress report on a highly subjective matter. It is probable that we will never have enough information to know with certainty the exact course of evolution. In the discussion that follows we hope to point out in this group the general course of morphologic changes that occurred in the spiriferide superfamilies throughout geologic time (Fig. 1104).

The cyrtioids are the earliest and most morphologically primitive spiriferidine superfamily. They are characterized by having a finely ribbed ornament but internally are highly variable, although the early genera lack a ctenophoridium (Fig. 1104), which is a characteristic cardinal structure in most spiriferids. They radiated fairly rapidly in the Silurian, producing another 20 genera by the Early Devonian, and gave rise to the superfamilies Adolfoidea, Theodossioidea, and Ambocoelioidea in the late Silurian. The Adolfoidea became differentiated from the cyrtioids by acquiring a more coarsely ribbed

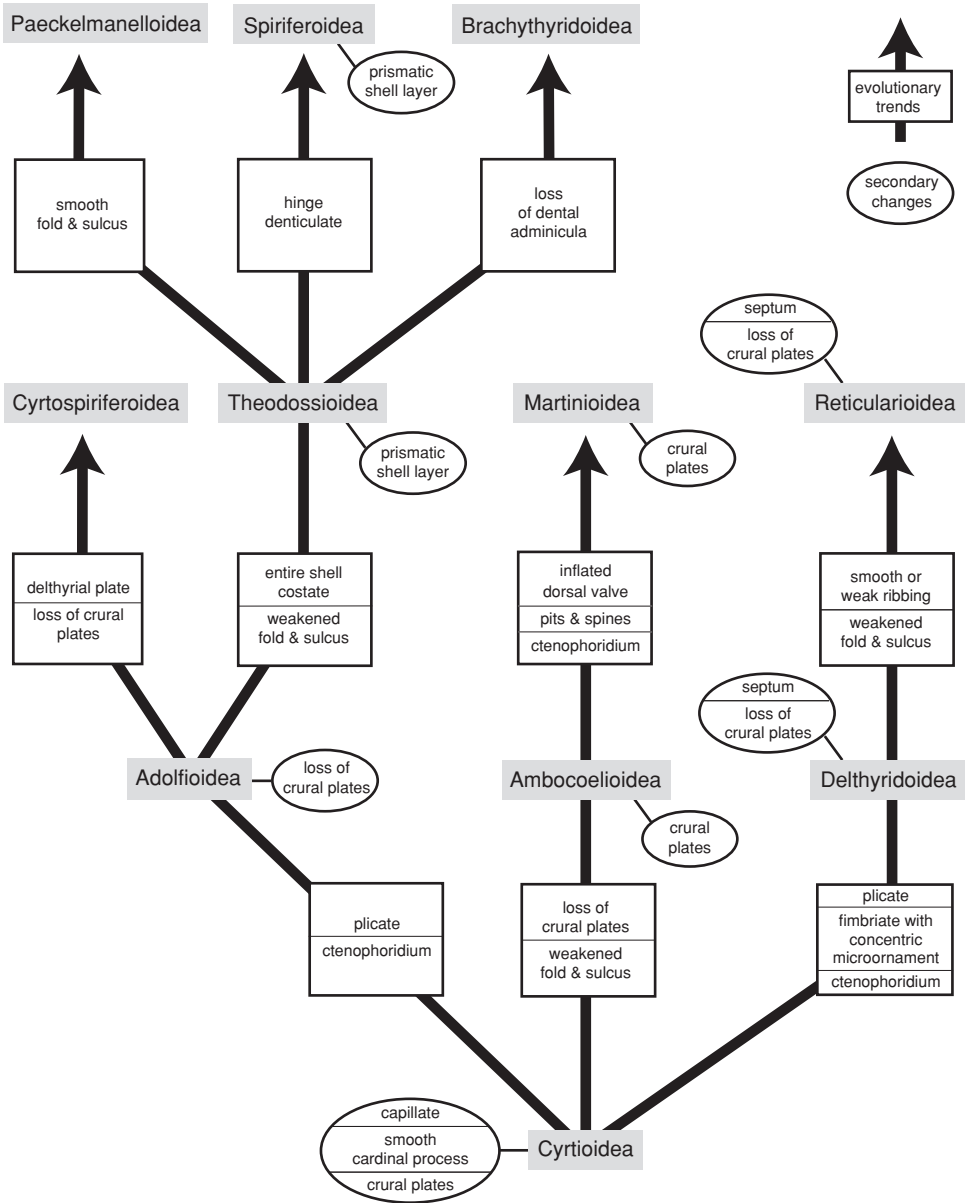


FIG. 1104. General evolutionary path within the Spiriferida with indication of primary and secondary innovations or changes (new).

ornament with capillate microornament and a consistent fold and sulcus. The theodossioidea, on the other hand, retained the weak or absent fold-sulcus and uniform ribbing of many cyrtioidea, but the ribbing is coarser than in most cyrtioidea. The tiny, small, smooth Ambocoelioidea also evolved directly from the cyrtioidea in the late Silurian by the paedomorphic loss of ribbing and fold-sulcus externally and crural and dental plates internally. These ambocoelioidea in turn gave rise before the end of the Silurian to the smooth but much larger Martinioidea, which flourished mainly in the late Paleozoic.

The Spiriferidina underwent a second evolutionary radiation in the Devonian, especially in the superfamilies Adolfoidea and Theodossioidea, which lack a delthyrial plate, and the Cyrtospiriferoidea, which generally have a well-developed delthyrial plate. Near the close of the Devonian most of the Devonian spiriferidine superfamilies became extinct, but the theodossioid family Ulbo-spiriferidae evolved the first spiriferide inner prismatic shell layer, also found in the late Paleozoic spiriferidine superfamilies Spiriferoidea, Paeckelmanelloidea, and Brachythyridoidea. The Spiriferoidea differ from all of the early Paleozoic superfamilies in having a denticulate hinge line formed from small calcite rods that occur just below the primary shell layer of the ventral interarea. In addition, almost all the early Carboniferous spiriferoid genera have a distinctive capillate microornament. The Paeckelmanelloidea appeared at about the same time as the Spiriferoidea and are also denticulate and capillate, which may indicate derivation from a common ancestor. They are invariably strongly transverse and, unlike the Spiriferoidea, generally lack ribs on the fold-sulcus. The Brachythyridoidea differ from the other Carboniferous superfamilies in consistently having an ovate outline with concomitant narrow hinge line. Denticulation and capillation are suppressed or absent, and the interiors of both valves are devoid of plates, presumably through paedomorphosis.

During the Carboniferous and Permian these three superfamilies plus the Martinioidea underwent a third and final radiation, which produced many additional families and genera before the suborder became extinct near the close of the era.

The Delthyridina evolved more or less parallel with the Spiriferidina but with less diversity and morphological innovation. There are only two superfamilies in this suborder, the Delthyridoidea and Reticularioidea, both generally with fimbriate microornament. The former, with plicate shells and well-developed fold and sulcus, appeared in the lower Silurian (middle Llandovery) of Kazakhstan with the genus *Howellella*, but the group evolved slowly until the Early Devonian when several families and numerous genera appeared. The group then flourished throughout the Devonian before becoming extinct in the early Carboniferous (Viséan). The superfamily Reticularioidea generally has smooth or weakly plicated shells and poorly developed fold and sulcus. They first appeared in the upper Llandovery, but their origin within the Delthyridoidea is uncertain. The two earliest reticularioid genera, *Spirinella* from Australia and *Eohowellella* from Siberia, appeared at about the same time in the upper Llandovery. They could have been derived either from a primitive delthyridoid or from the same spiriferidine ancestor as *Howellella*. Unlike the delthyridoids, the reticularioidea flourished in the late Paleozoic before becoming extinct at the end of the Permian.

Suborder SPIRIFERIDINA Waagen, 1883

[*nom. correct.* PITRAT, 1965, p. 668, *pro* suborder Spiriferacea WAAGEN, 1883a, p. 447; *emend.*, CARTER, JOHNSON, & GOURVENNEC in CARTER & others, 1994, p. 330]

Lateral slopes plicate or costate; fold and sulcus commonly well developed; fine ornament, if present, capillate, pustulose, or imbricate; spinose ornament absent; ctenophoridium absent in early forms. *upper Upper Ordovician, ?Middle Triassic–?Upper Triassic.*

CYRTIOIDEA

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Superfamily CYRTIOIDEA Frederiks, 1924

[*nom. correct.* JOHNSON, GOURVENNEC, & HOU in CARTER & others, 1994, p. 330, *pro* superfamily Cyrtiacea PITRAT, 1965, p. 668, *nom. transl. ex* Cyrtiinae FREDERIKS, 1924, p. 312]

Commonly with fold and sulcus; surface smooth or plicate; microornament of non-spinose capillae crossed by variably nodose growth lines; delthyrium occluded by deltidium, delthyrial plate, or stegidial plates; dental plates present; crural plates variably developed. *upper Upper Ordovician–Lower Devonian (Emsian)*.

Family CYRTIIDAE Frederiks, 1924

[*nom. transl.* IVANOVA, 1959, p. 55, *ex* Cyrtiinae FREDERIKS, 1924, p. 312] [=Eospiriferinae SCHUCHERT, 1929, p. 20]

Delthyrial plate and stegidial plates lacking; crural plates commonly well developed. *upper Upper Ordovician–Lower Devonian (Emsian)*.

Subfamily CYRTIINAE Frederiks, 1924

[Cyrtiinae FREDERIKS, 1924, p. 312]

Ventribiconvex; ventral valve hemipyramidal, with catacline or procline interarea and narrowly elongate delthyrium; deltidium with medial foramen; ctenophoridium absent. *Silurian (upper Llandovery–Ludlow)*.

Cyrtia DALMAN, 1828, p. 97 [**Anomites exporrectus* WAHLENBERG, 1821, p. 64; SD DAVIDSON, 1853, p. 83]. Nontransverse to transverse; lacking plications. *Silurian (upper Llandovery–lower Ludlow)*: cosmopolitan.—FIG. 1105, 1a–d. **C. exporrecta* (WAHLENBERG), upper Llandovery, Gotland; posterior, anterior, side, and ventral views, ×3 (Boucot, 1963a).

Dongbeispirifer LIU in LIU & HUANG, 1977, p. 58 [**D. typica*; OD]. Small, transverse, with prominent catacline ventral interarea; planoconvex, with ill-defined fold; dental plates very short; dorsal interior unknown. [No satisfactory illustrations are available for this genus.] *Silurian (Ludlow)*: northeastern China.

Plicocyrtia BOUCOT, 1963a, p. 704 [**Spirifer petasus* BARRANDE, 1848, p. 183; OD]. Transverse, with plicate flanks; sulcus-bounding dental plates. *Sil-*

urian (upper Wenlock): Czech Republic, USA (Nevada).—FIG. 1105, 2a–f. **P. petasus* (BARRANDE), Czech Republic; a–c, dorsal, lateral, and ventral views, ×1; d, microornament, ×3; e–f, dorsal and ventral internal molds, ×2 (Boucot, 1963a).

Subfamily EOSPIRIFERINAE Schuchert, 1929

[Eospiriferinae SCHUCHERT, 1929, p. 20]

Biconvex with curved, commonly apsacline ventral interarea; deltidium present; cardinal process or ctenophoridium commonly absent. *upper Upper Ordovician–Lower Devonian (Emsian)*.

Eospirifer SCHUCHERT, 1913, p. 411 [**Spirifer radiatus* J. de C. SOWERBY, 1835, p. 245; OD; =*Spirifer lineatus* J. de C. SOWERBY, 1825 in 1823–1825, p. 151, *non Conchyliolites anomites lineatus* MARTIN, 1809, =*Terebratula? lineata* SOWERBY, 1822 in 1821–1822, p. 39]. Smooth or with broad low plications that originate on flanks; extrasinal dental plates; cardinal process lacking; crural plates absent in some early species. *upper Upper Ordovician–Lower Devonian (upper Emsian)*: cosmopolitan.—FIG. 1106, 1a–f. **E. radiatus* (SOWERBY), Wenlock, Gotland; a–c, anterior, lateral, and posterior views; d–e, dorsal and ventral views; f, posterior view of internal mold, ×1 (Boucot, 1963a).

Badainjarania ZHANG Yan, 1981, p. 388 [392] [**B. striata*; OD]. Small, subcircular, ventral interarea narrow; sulcus lacking and fold low, flat, with median groove; plications on flanks low, rounded; surface capillate; dental plates thin and long; platelike crural bases. *Lower Devonian (Emsian)*: northwestern China (Inner Mongolia).—FIG. 1106, 2a–e. **B. striata*, upper Emsian; a–d, ventral, dorsal, anterior, and lateral views, ×2; e, exterior showing fine ornament, ×5 (Zhang, 1981).

Endospirifer TACHIBANA, 1981a, p. 36 [**E. nipponicus*; OD]. Small, with deltidium; few low plications near fold and sulcus; extrasinal dental plates; rudimentary ctenophoridium. *Silurian (upper Llandovery–Wenlock, ?Ludlow)*: eastern Australia, Japan, southwestern China.—FIG. 1106, 5a–g. **E. nipponicus*, ?Ludlow, Japan; a–d, holotype, ventral, dorsal, posterior, and anterior views, ×5; e, ventral valve ornament, ×6; f, ventral internal mold, ×5; g, posterior view of dorsal mold, ×4 (Tachibana, 1981a).

Espella NILOVA, 1965, p. 102 [**E. kazachstanica*; OD] [= *Laevispirifer* USHATINSKAIA, 1977, p. 137 (type, *L. zhamankonensis* USHATINSKAIA, 1977, p. 138, OD)].

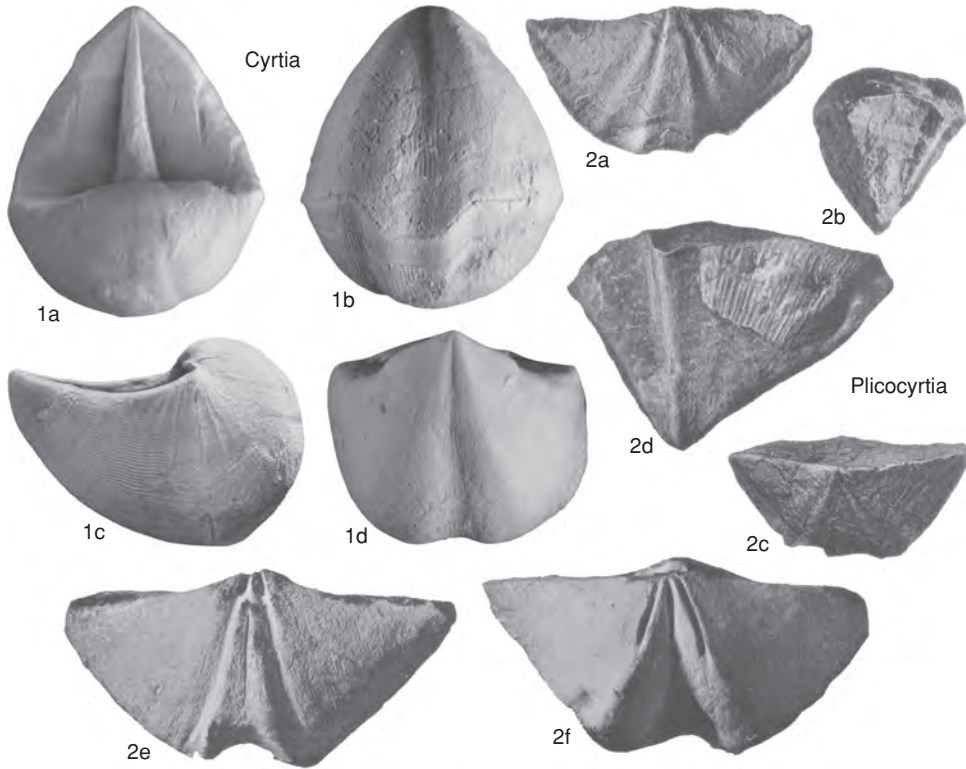


FIG. 1105. Cyrtiidae (p. 1695).

Biconvex, with obtuse cardinal angles; ventral interarea short, apsacline; fold and sulcus absent; flattened capillae; thin dental plates; long crural plates joining valve posteriorly, converging anteriorly with short median septum, forming cruralium. *Silurian (middle Llandovery–Wenlock)*: central Kazakhstan.—FIG. 1107, 2a–g. **E. kazachstanica*; a–c, holotype, ventral, dorsal, and lateral views, $\times 1$; d–g, serial sections, $\times 2$ (Nilova, 1965).

Havlicekia BOUCOT, 1963a, p. 693 [**Spirifer secans* BARRANDE, 1848, p. 168; OD]. Plicate in early growth stages, smooth in later growth stages, with narrow intercapillary grooves. *Silurian (Ludlow)–Lower Devonian (Emsian)*: Europe, Salair, Gorny Altai, Bithynia, northern Africa, New Zealand.—FIG. 1107, 1a–f. **H. secans* (BARRANDE), Pragian, Bohemia; a–b, dorsal and anterior views; c–f, ventral, dorsal, anterior, and side views, $\times 1$ (Havliček, 1980).

Hedeina BOUCOT, 1957b, p. 323 [**Anomia crispa* LINNAEUS, 1758, p. 702; OD]. With broad, low plications. *Silurian (upper Wenlock)–Lower Devonian (upper Emsian)*: Europe, Kazakhstan.—FIG. 1107, 3a–f. **H. crispa* (LINNAEUS), origin uncertain; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$; f, microornament, $\times 3.7$ (Brunton, Cocks, & Dance, 1967).

Janius HAVLIČEK, 1957a, p. 245 [**Spirifer nobilis* BARRANDE, 1848, p. 184; OD]. Strongly plicate with plications that bifurcate and intercalate; small plications may be present in sulcus. [No satisfactory illustration of the type (a damaged dorsal valve) is available.] *Silurian (upper Wenlock)–Lower Devonian (Emsian)*: cosmopolitan.—FIG. 1106, 4a–d. *J. exsul* (BARRANDE), upper Wenlock, Bohemia; ventral, dorsal, anterior, and side views, $\times 1$ (Havliček, 1980).—FIG. 1106, 4e. *J. bouskai* HAVLIČEK, Ludlow, Bohemia; ornament, $\times 6$ (Havliček, 1980).

Lobvia BREIVEL & BREIVEL, 1977, p. 97 [**Theodossia (L.) praesuperbus*; OD]. Smooth posteriorly, low, rounded plications anteriorly on flanks; ctenophoridium probable. *Lower Devonian (Emsian)*: Urals.—FIG. 1107, 4a–d. **L. praesuperbus* BREIVEL & BREIVEL; ventral, dorsal, lateral, and anterior views, $\times 1$ (Breivel & Breivel, 1977).

Macropleura BOUCOT, 1963a, p. 690 [**Delthyris macropleura* CONRAD, 1840, p. 207; OD] [= *Ejnespirifer* FU, 1982, p. 176 (type, *E. styphelus* FU, 1982, p. 177, OD)]. With few prominent plications and deep, U-shaped interspaces; dental plates extrasinal. *Silurian (upper Llandovery)–Lower Devonian (Emsian)*: North America, Europe, Kazakhstan, northeastern China, Australia.—FIG. 1108, 1a–g. **M. macropleura* (CONRAD),

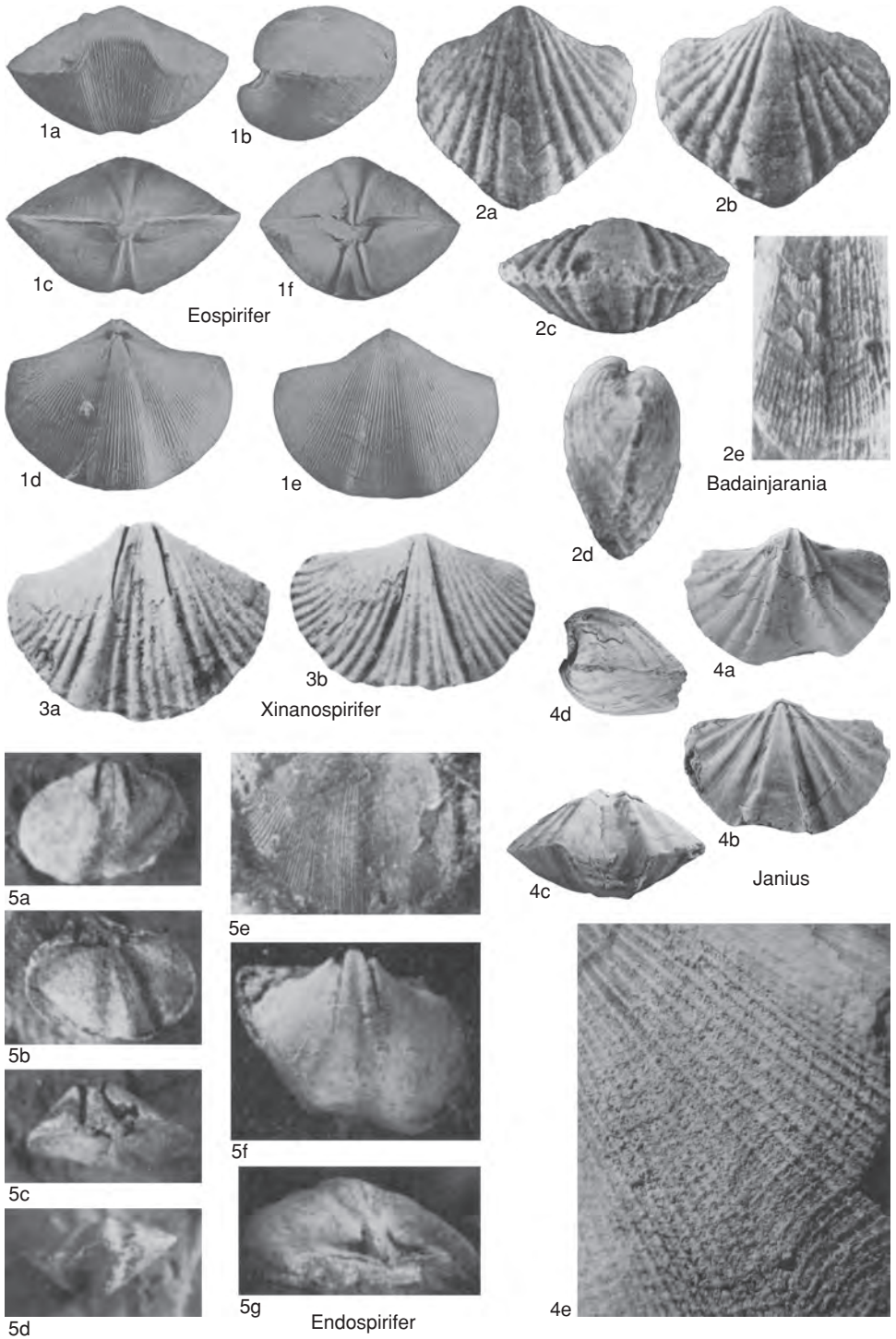


FIG. 1106. Cyrtoidea (p. 1695–1701).

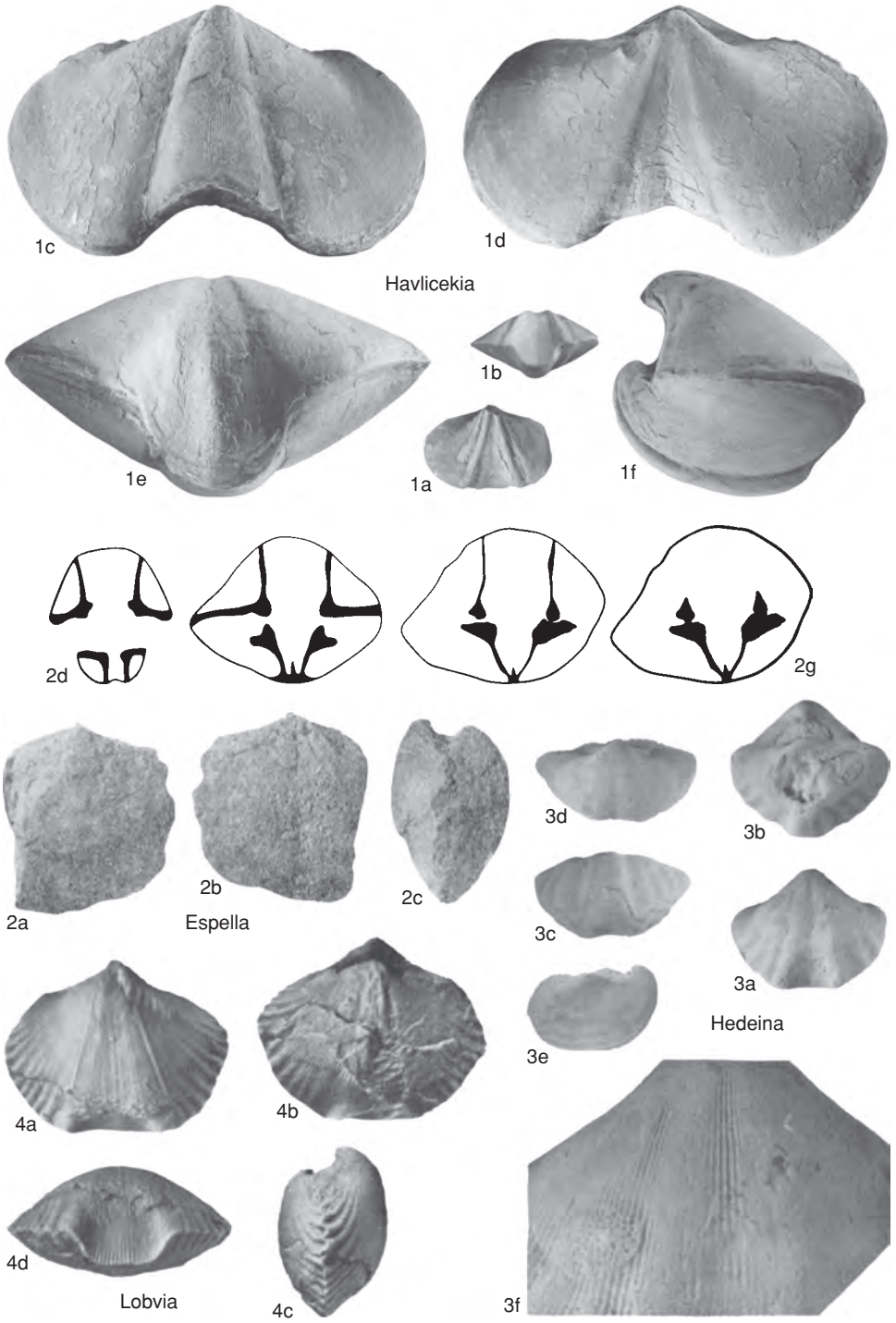


FIG. 1107. Cyrtiidae (p. 1695–1696).

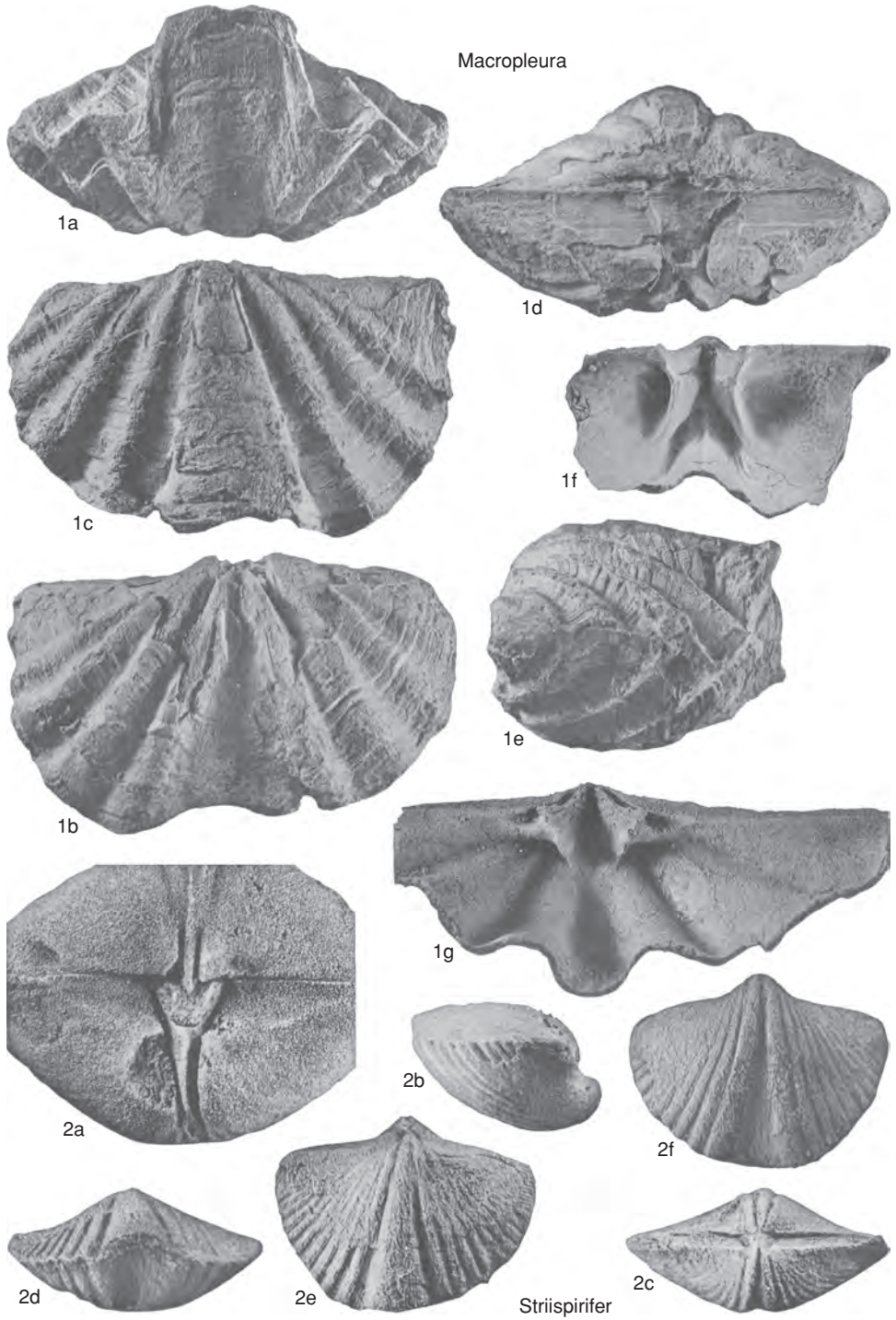


FIG. 1108. Cyrtiidae (p. 1696–1701).

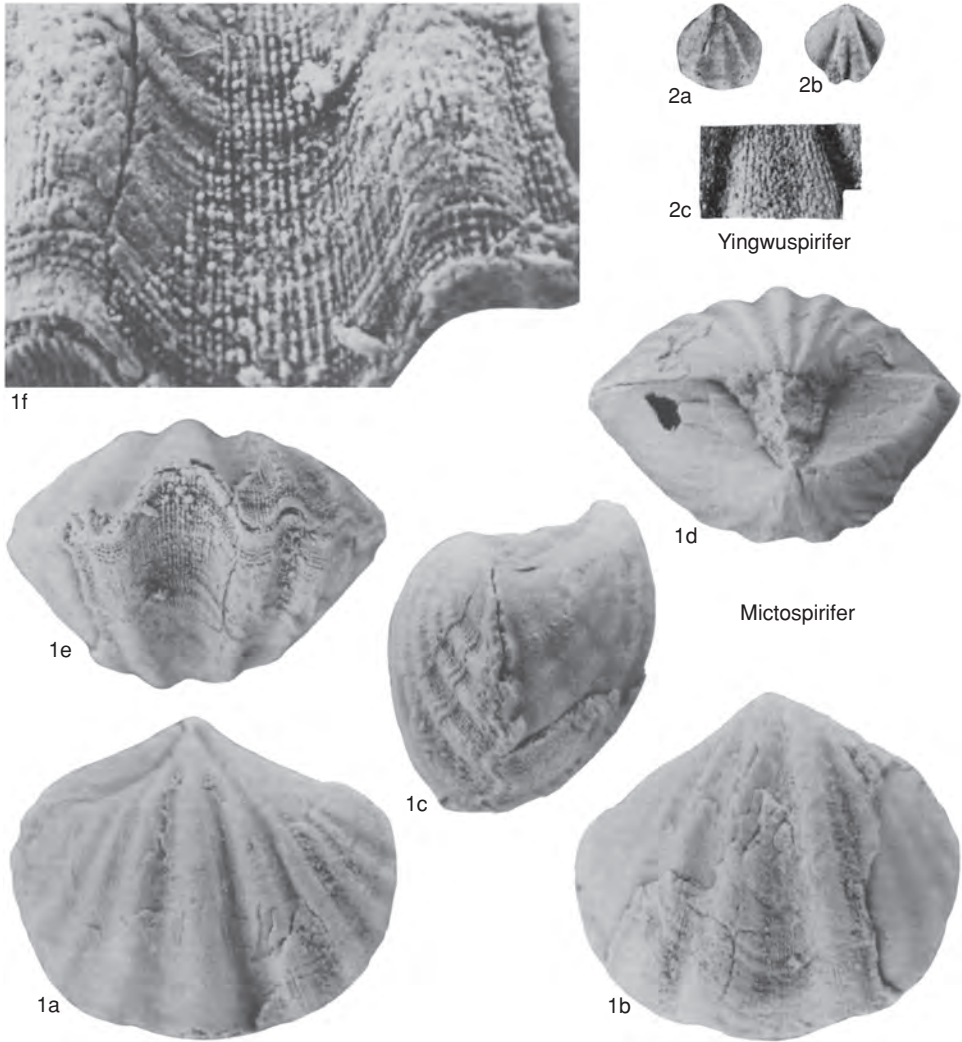


FIG. 1109. Cyrtiidae (p. 1700–1701).

Lochkovian, New York, USA; *a–e*, anterior, ventral, dorsal, posterior, and lateral views, $\times 1$; *f*, ventral interior; *g*, dorsal interior, $\times 2$ (Boucot, 1963a).

Mictospirifer JOHNSON, 1995b, p. 607 [**M. jini*; OD; =*Howellella elegans* JIN, CALDWELL, & NORFORD, 1993, p. 106, non MUIR-WOOD, 1925]. With few prominent plications and deep, U-shaped interspaces; dental plates short, extrasinal; crural plates and ttenophoridium rudimentary or evanescent. *Silurian* (upper Llandovery): Canada.—FIG. 1109, 1*a–f*. **M. jini*; *a–e*, dorsal, ventral, lateral, posterior, and anterior views of hypotype, $\times 4$; *f*, microornament, $\times 12$ (Jin, Caldwell, & Norford, 1993).

Myriospirifer HAVLÍČEK, 1978, p. 105 [**M. myriofila* HAVLÍČEK, 1978, p. 106; OD] [=*Acutilineolus* AMSDEN, 1978, p. 31 (type, *Eospirifer acutolineatus* AMSDEN, 1968, p. 64, OD)]. Nonplicate, with narrow intercapillar interspaces. *Silurian* (upper Llandovery)–Lower Devonian (Emsian): cosmopolitan.—FIG. 1110, 1*a–e*. **M. myriofila*, Pragian, Bohemia; *a–d*, ventral, dorsal, anterior, and side views, $\times 1$; *e*, ornament, $\times 6$ (Havlíček, 1980).

Nurataella LARIN, 1973, p. 135 [**N. miranda* LARIN, 1973, p. 137; OD] [=*Baterospirifer* RONG, SU, & LI, 1984, p. 64 [67] (type, *B. rectimarginatus* RONG, SU, & LI, 1984, p. 65, OD)]. Dorsal valve nearly flat but with faint posterior fold; sulcus lacking;

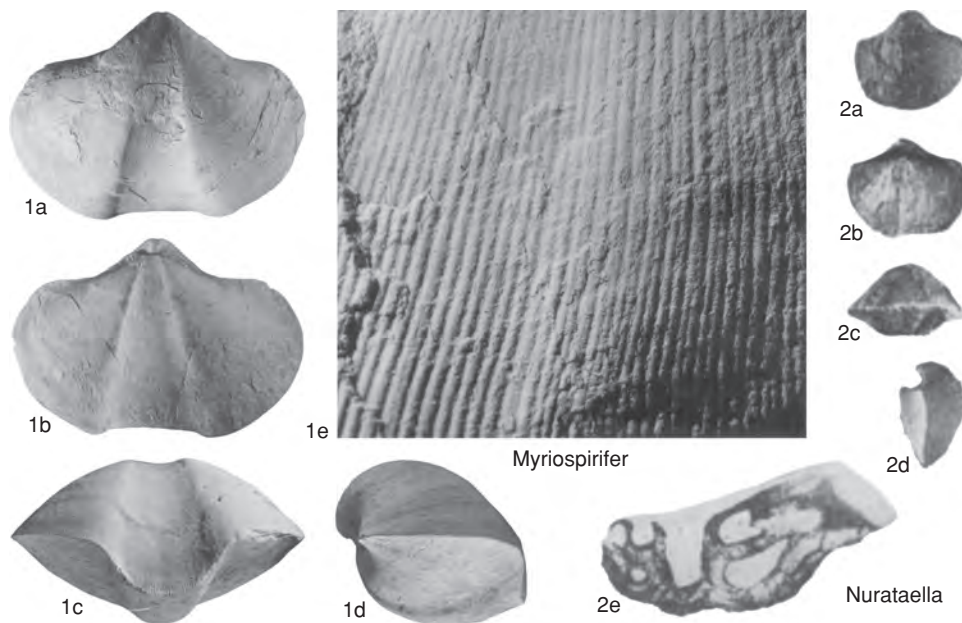


FIG. 1110. Cyrtiidae (p. 1700–1701).

rudimentary delthyrial plate present. *Silurian* (upper *Wenlock–Pridoli*): central Asia, China (Inner Mongolia).—FIG. 1110, 2a–e. **N. miranda*, upper *Wenlock*, Russia; a–d, holotype, ventral, dorsal, anterior, and lateral views, $\times 4$; e, transverse section of dorsal valve, $\times 11$ (Larin, 1973).

Striispirifer COOPER & MUIR-WOOD, 1951, p. 195, *nom. nov. pro Schuchertia* FREDERIKS, 1926, p. 406, *non* GREGORY, 1899, p. 351 [**Delthyris niagarensis* CONRAD, 1842, p. 261; OD]. With numerous low, rounded, simple plications on flanks. *Silurian* (upper *Llandovery–lower Ludlow*): Europe, North America.—FIG. 1108, 2a–f. **S. niagarensis* (CONRAD), New York, USA; a, posterior view of dorsal mold; b–f, lateral, posterior, anterior, dorsal, and ventral views, $\times 2$ (Boucot, 1963a).

Yingwuspirifer RONG, XU, & YANG, 1974, p. 201 [**Y. orientalis*; OD]. Small, with single prominent plication in sulcus and median groove on fold; flanks nonplicate. *Silurian* (*Rhuddanian*): southern China.—FIG. 1109, 2a–c. **Y. orientalis*; a–b, ventral and dorsal views, $\times 1$; c, microornament, $\times 4$ (Rong, Xu, & Yang, 1974).

Xinanospirifer RONG, XU, & YANG, 1974, p. 206 [**X. flabellum*; OD]. With numerous low, rounded, simple plications on flanks and same size plications, increasing by insertion, in sulcus; dental plates thin, bounding sulcus; short crural plates present. *Silurian* (*Telychian*): southwestern China.—FIG. 1106, 3a–b. **X. flabellum*; ventral and dorsal valves, $\times 1.5$ (Rong, Xu, & Yang, 1974).

Family HEDEINOPSIDAE Gourvennec, 1990

[*nom. transl.* JOHNSON in CARTER & others, 1994, p. 331, *ex* *Hedeinopsinae* GOURVENNEC, 1990, p. 142]

Plicate, ventribiconvex, with stegidial plates and delthyrial plate; crural plates rudimentary or absent; ctenophoridium present. *Silurian* (*Wenlock–Pridoli*).

Subfamily HEDEINOPSINAE Gourvennec, 1990

[*Hedeinopsinae* GOURVENNEC, 1990, p. 142]

Characters as for family. *Silurian* (*Wenlock–Pridoli*).

Hedeinopsis GOURVENNEC, 1990, p. 142 [**H. hispanica* GOURVENNEC, 1990, p. 143; OD]. Transverse, with low, apsacline ventral interarea; strong simple plications, with fine capillae; small apical delthyrial plate present; dental plates partly obscured by umbonal callus; short crural plates may be obscured by thick shell; narrow ctenophoridium present. *Silurian* (*Wenlock–Ludlow*): Spain, Morocco, Algeria.—FIG. 1111, 1a–b. **H. hispanica hispanica*, Spain; a, mold of dorsal valve; b, holotype, mold of ventral valve, $\times 2$ (Gourvennec, 1990).—FIG. 1111, 1c–d. *H. hispanica*

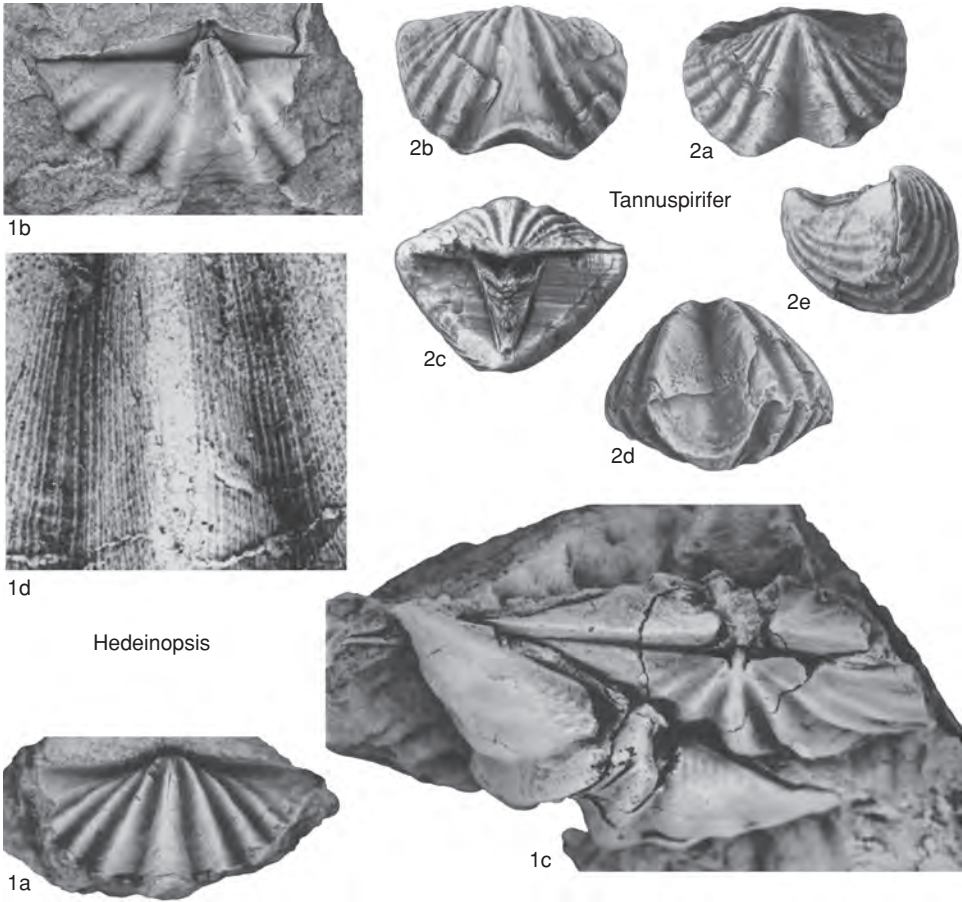


FIG. 1111. Hedeinopsidae (p. 1701–1702).

disparisulcata GOURVENNEC, Wenlock, Spain; *c*, steinkern of complete specimen, $\times 2$; *d*, microornament, $\times 10$ (Gourvennec, 1990).

Tannuspirifer IVANOVA, 1960, p. 267 [**Spirifer pedaschenkoi* CHERNYSHEV, 1937, p. 51; OD]. Ventral valve hemipyramidal, with high interarea; dorsal valve flat or weakly convex; fold and sulcus prominent, smooth; flanks with strong, rounded, simple plications; microornament of fine capillae

and fila of reticulate pattern; thin dental plates with well-developed delthyrial plate present; ctenophoridium present; crural plates absent. [No satisfactory illustration of the type is available.] *Silurian (Ludlow–Pridoli)*: Altai, Sayan, Tuva basin, Canadian Arctic Islands.—FIG. 1111, 2*a–e*. *T. dixonii* JONES, Pridoli, Arctic Canada; ventral, dorsal, posterior, anterior, and lateral views, $\times 2$ (new).

ADOLFIOIDEA

J. G. JOHNSON

[deceased, formerly of Oregon State University]

Superfamily ADOLFIOIDEA Sartenaer, 1966

[*nom. transl.* JOHNSON, herein, *pro* Adolfinae SARTENAER, 1966, p. 386]
[=Spinelloidea JOHNSON, 1970, p. 205]

Fold and sulcus present; surface plicate, capillate or smooth, nonfrilly; dental plates present, delthyrial plate and median septum lacking; ctenophoridium present. *Silurian* (*Wenlock*)–*Upper Devonian* (*upper Famennian*).

Family ADOLFIIDAE Sartenaer, 1966

[*nom. transl.* JOHNSON, herein, *pro* Adolfinae SARTENAER, 1966, p. 386]
[=Spinellidae JOHNSON, 1970, p. 205]

Multiplicate, with smooth or medially grooved fold and smooth or medially plicate sulcus. *Silurian* (*Wenlock*)–*Upper Devonian* (*upper Famennian*).

Subfamily ADOLFIINAE Sartenaer, 1966

[Adolfinae SARTENAER, 1966, p. 386, *nom. nov. pro* Guerichellinae PAECKELMANN, 1931, p. 24, based on invalid junior synonym]
[=Spinellinae JOHNSON, 1970, p. 205]

Capillate, with height of ventral area medium to high; crural plates short or lacking. [JOHNSON (1970) erected the subfamily Spinellinae as a *nom. nov. pro* Guerichellinae PAECKELMANN, 1931, based on the invalid genus *Guerichella*. SARTENAER (1966), in a clarification of the status of the genera *Adolfia* and *Guerichella*, had already established a new subfamily named Adolfinae. The latter has priority and is restored here. As a consequence, the family and superfamily names are modified in order to conform with the principle of coordination.] *Lower Devonian* (*Pragian*)–*Upper Devonian* (*upper Famennian*).

Adolfia GÜRICH, 1909, p. 136 [**Spirifer deflexus* ROEMER, 1843, p. 13; SD SCHUCHERT, 1929, p. 27]
[=*Guerichella* PAECKELMANN, 1913, p. 299, obj.;
Changshaispirifer ZHAO in YANG De-Li & others,

1977, p. 428 (type, *C. lianhuagiaensis*, OD)]. Medium size, transverse, with obtuse cardinal angles; ventral interarea curved, apsacline; fold and sulcus prominent, smooth, or with a few incipient plications; flanks with numerous, bifurcating, rounded plications and narrow, U-shaped interspaces; microornament of subradial capillae; dental plates free of umbonal callus; ctenophoridium without crural plates. *Lower Devonian* (*upper Pragian*)–*Upper Devonian* (*Frasnian*): Europe, North America, southern China.—FIG. 1112, 2a–d. **A. deflexa* (ROEMER), lower Frasnian, Germany; holotype, ventral, dorsal, posterior, and lateral views, $\times 1$ (Vandercammen, 1967).

Acutatheca STAINBROOK, 1945, p. 55 [**A. proparia*; OD]. Small, ventribiconvex, equidimensional; cardinal angles obtuse; ventral interarea high, flat to slightly curved, steeply apsacline to catacline; delthyrium partially closed by apical plate; fold and sulcus smooth; flanks strongly pauciplicate, with fine capillae; slightly divergent dental plates present; hinge plates supported by median ridge. *Upper Devonian* (*Frasnian*): midcontinent and western North America.—FIG. 1113, 2a–b. **A. proparia*, Iowa, USA; a, ventral valve, $\times 1.5$; b, posterior view, $\times 3$ (Stainbrook, 1945).

Allanella CRICKMAY, 1953b, p. 5 [**Spirifer allani* WARREN, 1944, p. 123; OD] [=Allanaria CRICKMAY, 1953b, p. 5, obj.; *Minutilla* CRICKMAY, 1967, p. 10 (type, *Acutatheca* (*M.*) *layeri*, OD)]. Small, ventribiconvex, equidimensional; cardinal angles obtuse to slightly acute; ventral interarea of moderate height, slightly curved, apsacline; fold and sulcus broad, fold not elevated; flanks with simple, low rounded plications; surface capillate, with fila; dental plates extrasinal; ctenophoridium and short crural plates present. [CRICKMAY erroneously considered *Allanella* as invalid and replaced this name by *Allanaria* in a section entitled Errata & Addenda. As first reviser, PITRAT (1965, p. 691) invalidated the name *Allanaria*.] *Middle Devonian* (*upper Givetian*)–*Upper Devonian* (*Frasnian*): North America.—FIG. 1113, 1a–e. **A. allani* (WARREN), upper Givetian, Alberta, Canada; lectotype, ventral, dorsal, posterior, anterior, and lateral views, $\times 1.5$ (Crickmay, 1953b).

Chimaerothyris PAULUS, STRUVE, & WOLFART, 1963, p. 463 [**C. hotzi* PAULUS, STRUVE, & WOLFART, 1963, p. 465; OD]. Ventribiconvex, transverse with acute cardinal angles; ventral interarea long, low, apsacline to orthocline; fold and sulcus prominent, unplicated; flanks with numerous, simple, rounded

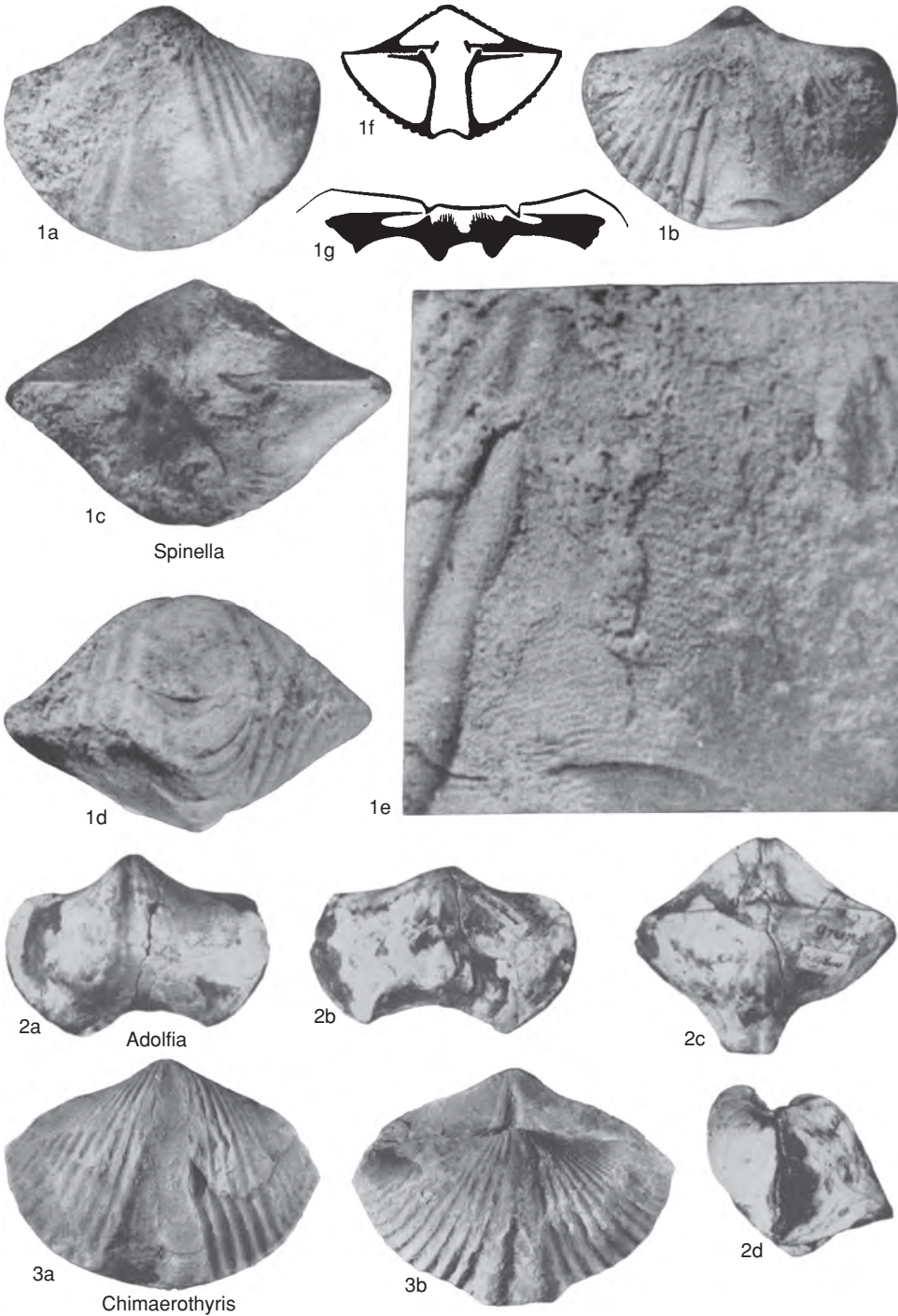


FIG. 1112. Adolfidae (p. 1703–1707).

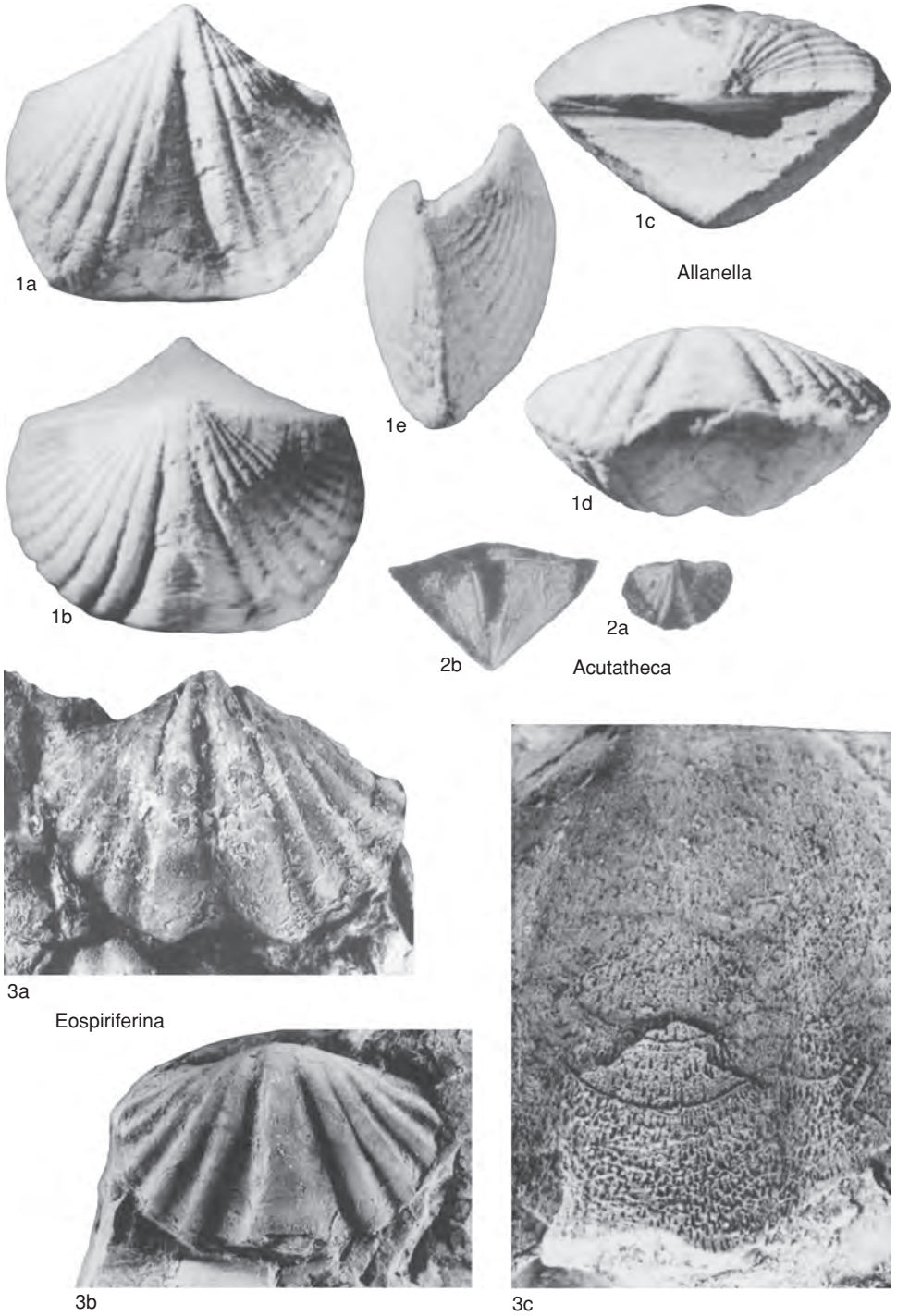


FIG. 1113. Adolfoidea (p. 1703–1706).

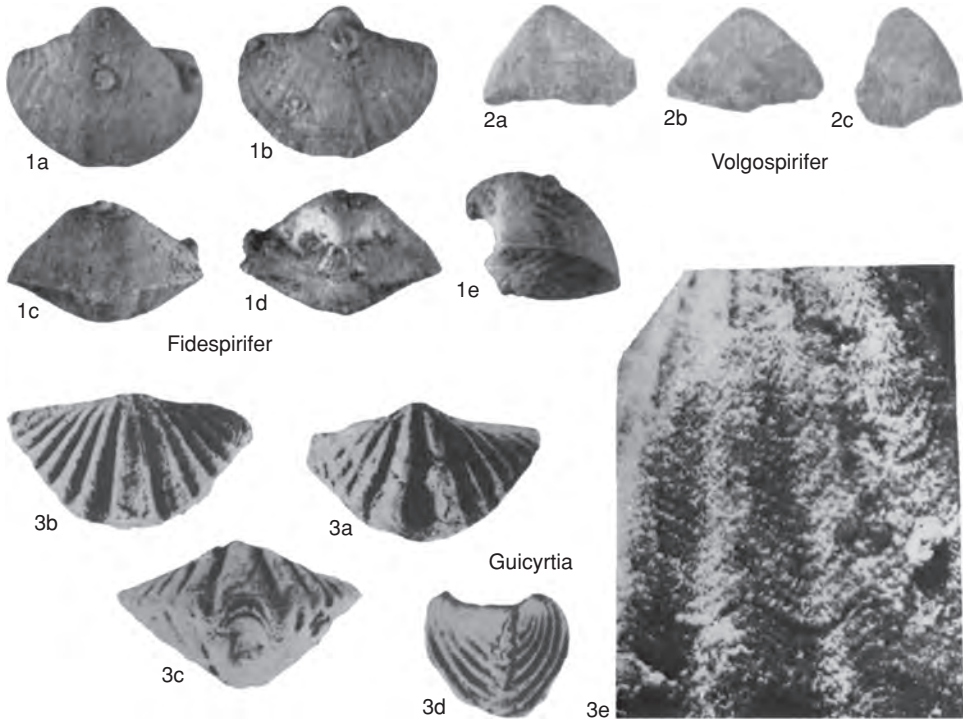


FIG. 1114. Adolphiidae (p. 1706–1707).

plications; microornament of subradial capillae crossed by irregularly spaced growth lines; dental plates straight, strong, partly obscured by umbonal callus; ctenophoridium elongate, situated on inner hinge plates. *Middle Devonian (Eifelian)*: Europe. —FIG. 1112, 3a–b. **C. hotzi*, Germany; holotype, ventral and dorsal views, $\times 1$ (Paulus, Struve, & Wolfart, 1963).

Eospiriferina GRABAU, 1931b, p. 494 [**Spiriferina* (*E. lachrymosa*); OD]. Medium size, biconvex, slightly transverse, with obtuse cardinal angles; ventral interarea curved, apsacline; fold and sulcus smooth; flanks with a few strong, rounded plications separated by U-shaped interspaces; microornament of oval to elongate-oval pustules arranged quincuncially or subradially; strong, thin, intrasinal dental plates present; anteriorly convergent crural plates present. *Lower Devonian (upper Emsian)–Middle Devonian (Eifelian)*: southern China (Guangxi). —FIG. 1113, 3a–c. **E. lachrymosa* GRABAU, Eifelian; a–b, ventral and dorsal internal molds, $\times 2$; c, exterior showing fine ornament, $\times 5$ (new).

Fidespirifer LIASHENKO, 1973, p. 129 [**F. striatus*; OD]. Small, ventribiconvex, slightly transverse, with obtuse cardinal angles; ventral interarea curved, apsacline; fold and sulcus smooth; flanks with few, very low, rounded plications; surface capillate; divergent dental plates present; short crural plates. *Upper Devonian (lower Frasnian)*: southern Timan. —FIG. 1114, 1a–e. **F. striatus*; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 2$ (Liashenko, 1973).

Guicyrtia WANG & ZHU, 1979, p. 59 [93] [**G. triangulata*; OD]. Small, transverse, with acute cardinal angles; ventral interarea high, apsacline to catacline, with deltidium; fold and sulcus narrow, rounded, with few strong, rounded plications on flanks; microornament of teardrop-shaped pustules and weak growth lines; interior unknown. *Middle Devonian*: China. —FIG. 1114, 3a–e. **G. triangulata*, Eifelian; a–d, ventral, dorsal, anterior, and side views, $\times 2.5$; e, exterior showing fine ornament, $\times 14$ (new).

Spinella TALENT, 1956, p. 21 [**S. buchanensis* TALENT, 1956, p. 22; OD]. Equidimensional, with curved,

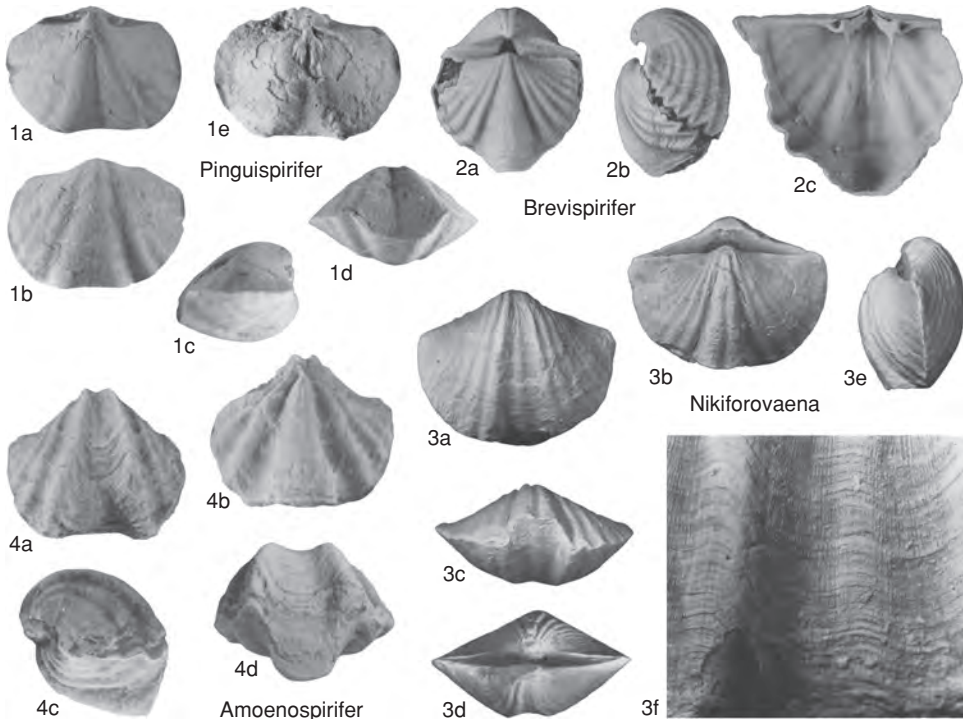


FIG. 1115. Adolfoidea (p. 1707–1709).

apsaline ventral interarea; fold and sulcus well defined, smooth; flanks with numerous, simple, rounded plications and narrow, U-shaped interspaces; microornament of very fine oval to elongate-oval spine bases arranged quincuncially or subradially; long dental plates present; bilobed ctenophoridium present; crural plates lacking. *Lower Devonian (Pragian–lower Emsian)*: Australia.—FIG. 1112, 1a–g. **S. buchanensis*; a–d, ventral, dorsal, posterior, and anterior views, $\times 1.5$; e, microornament, $\times 10.5$; f, transverse section, $\times 1$; g, transverse section of cardinalia, enlarged (Talent, 1956).

Volgospirifer SHEVCHENKO, 1970, p. 111 [**V. volgensis* SHEVCHENKO, 1970, p. 113; OD]. Small to medium size, ventribiconvex, hemipyramidal; cardinal angles slightly acute; ventral interarea high, flat, catacline; fold and sulcus smooth, faintly developed or absent; fold with median furrow; flanks smooth or pauciplicate; surface with bifurcating capillae; dental plates and low, distally grooved median septum present. *Upper Devonian (upper Famennian)*: Russian Platform.—FIG. 1114, 2a–c. **V. volgensis*;

holotype, ventral, posterior, and lateral views, $\times 1$ (Shevchenko, 1970).

Subfamily PINGUISPIRIFERINAE Havlíček, 1971

[Pinguispiriferinae HAVLÍČEK, 1971, p. 27]

Plicate, with weak to obscure capillae, crossed by fila; crural plates short or lacking. *Silurian (Wenlock)–Middle Devonian (Eifelian)*.

Pinguispirifer HAVLÍČEK, 1957a, p. 246 [**Spirifer infirmus* BARRANDE, 1879, p. 47; OD]. Fold and sulcus nonplicate; flanks with a few low, rounded plications; dental plates partly concealed by secondary shell material. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: Czech Republic.—FIG. 1115, 1a–e. **P. infirmus* (BARRANDE), upper Emsian, Bohemia; ventral, dorsal, side, and anterior views, and ventral view of exfoliated specimen, $\times 1$ (Havlíček, 1959).

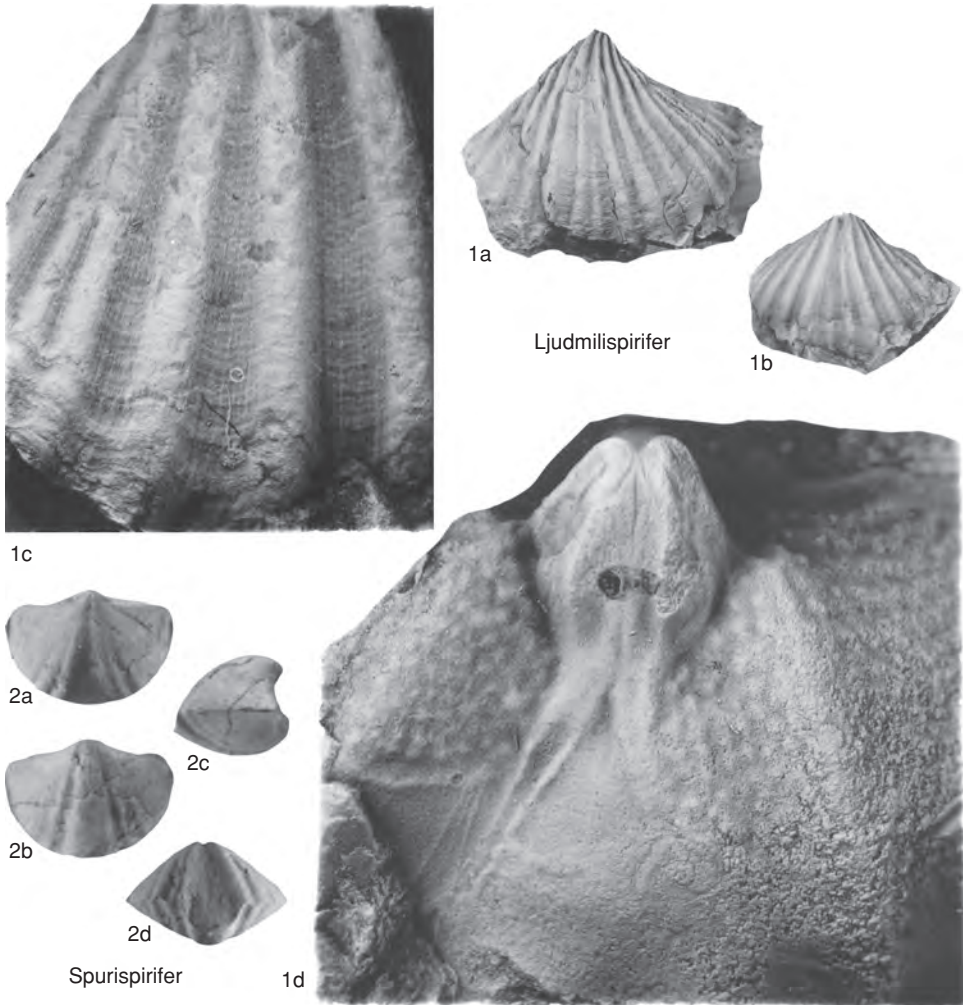


FIG. 1116. Adolphiidae (p. 1708–1709).

Amoenospirifer HAVLÍČEK, 1957b, p. 436 [**Spirifer thetidis* BARRANDE, 1848, p. 176; OD]. Fold and sulcus nonplicate; flanks with few prominent, rounded plications; dental plates lacking; ventral umbonal area with thick secondary shell material; vascular impressions strong. [No satisfactory illustration of the type is available.] *Lower Devonian (Emsian)*: Czech Republic.—FIG. 1115,4a–d. *A. amoenoides* HAVLÍČEK, upper Emsian, Bohemia; ventral, dorsal, side, and anterior views, $\times 1.5$ (Havlíček, 1959).

Brevispirifer COOPER, 1942, p. 231 [**Spirifer gregaria* CLAPP in HALL, 1857, p. 127; OD]. Equidimensional or elongate; fold and sulcus prominent, smooth, or with medial plication in sulcus; flanks

with a few rounded plications; dental plates thick, partly buried in umbonal callus; crural plates short or lacking. *Middle Devonian (lower Eifelian)*: eastern and midcontinent North America.—FIG. 1115,2a–c. **B. gregarius* (CLAPP), New York, USA; a–b, dorsal and lateral views, $\times 1$; c, dorsal interior, enlarged (Cooper, 1944).

Ljudmilspirifer CHERKESOVA, 1976, p. 90 [**Delthyris irregularis* NALIVKIN in MARKOVSKI, 1960, p. 396; OD]. One or more plications in sulcus; flanks with few prominent, rounded plications; dental plates absent; ventral umbonal region with secondary prismatic shell; vascular impressions strong. *Lower Devonian (upper Emsian)*: Russia (Novaya Zemlya). —FIG. 1116,1a–d. **L. irregularis* (NALIVKIN);

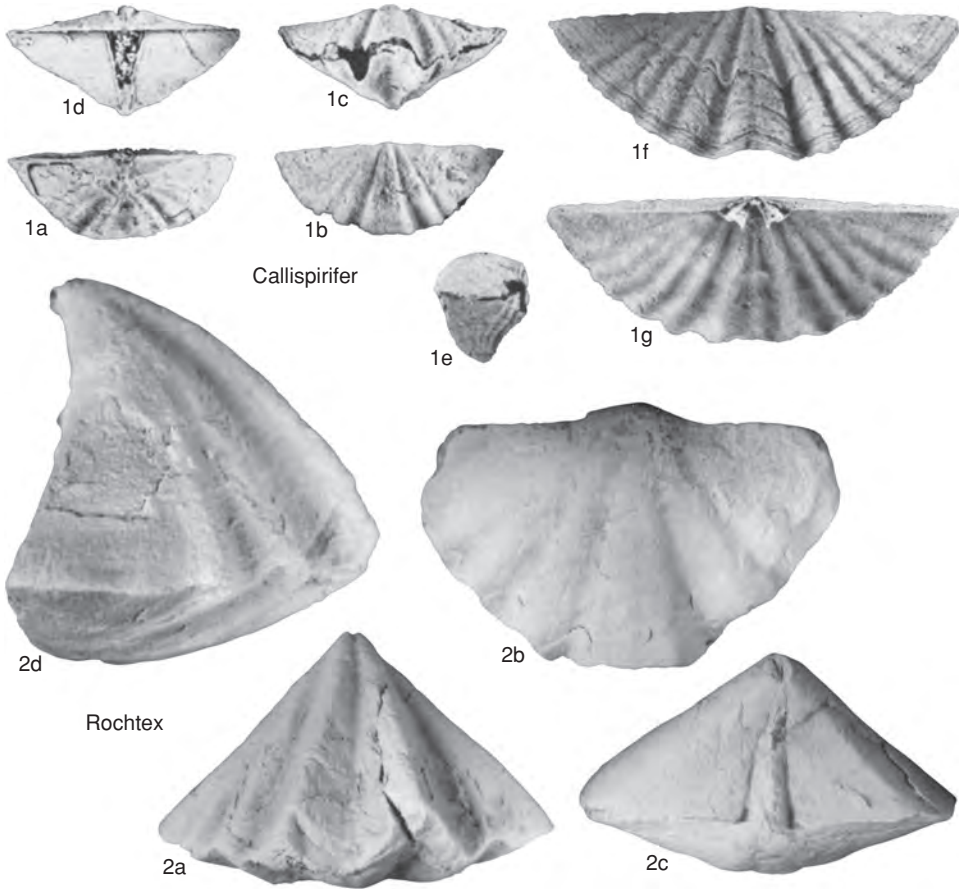


FIG. 1117. Adolfoidea (p. 1709–1710).

a–b, ventral, exterior views, $\times 1$; *c–d*, ventral exterior showing ornament and ventral internal mold, $\times 5$ (Cherkesova, 1976).

Nikiforovaena BOUCOT, 1963a, p. 697 [*Spirifer* (*Eospirifer*) *ferganensis* NIKIFOROVA, 1937, p. 48; OD]. One or more plications in sulcus; flanks with numerous low, rounded plications; dental plates present; ctenophoridium and short divergent crural plates present. *Silurian* (*Pridoli*)–*Lower Devonian* (*Emsian*): Turkestan, Salair, Altai, Yunnan, Japan, Australia.—FIG. 1115, 3a–f. **N. ferganensis* (NIKIFOROVA), Ludlow, Ferghana; *a–e*, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$; *f*, microornament, $\times 5$ (new).

Spurispirifer HAVLÍČEK, 1971, p. 27 [*Spirifer spurius* BARRANDE, 1848, p. 174; OD]. Deltidium apical; fold and sulcus nonplicate, or fold with median groove; flanks with few low, rounded plications. *Silurian* (*Wenlock*)–*Lower Devonian* (*Lochkovian*): Czech Republic, Canadian Arctic Islands.—FIG.

1116, 2a–d. **S. spurius* (BARRANDE), Ludlow, Bohemia; ventral, dorsal, side, and anterior views, $\times 1.5$ (Havlíček, 1959).

Subfamily CALLISPIRIFERINAE Johnson, 1994

[Callispiriferinae JOHNSON in CARTER & others, 1994, p. 332]

Noncapillate, with high, flat ventral interarea. *Lower Devonian* (*Emsian*).

Callispirifer PERRY, 1984, p. 115 [*C. teniostrakon*; OD]. Medium size, transverse; ventral interarea high, flat, procline or catacline, with apical deltidium; cardinal angles acute; flanks with few rounded plications; fold and sulcus smooth with fold flattened or medially grooved; growth lines may be prominent anteriorly; dental plates short, thin, closely spaced; ctenophoridium without crural plates. *Lower Devonian* (*lower Emsian*): Canadian



FIG. 1118. Adolfidae (p. 1711).

Arctic Islands, USA (Alaska).—FIG. 1117, 1a–g. **C. teniostrakon*, Yukon Territory; a–e, ventral, dorsal, anterior, posterior, and lateral views, $\times 1.3$; f–g, holotype, exterior and interior views of dorsal valve, $\times 2.5$ (Perry, 1984).

Rochtex HAVLIČEK in HAVLIČEK & KUKAL, 1990, p. 175 [**R. lissopleura* HAVLIČEK in HAVLIČEK & KUKAL, 1990, p. 176; OD]. Small, with hemipyramidal ventral valve; ventral interarea catacline to procline, flat or slightly curved, with large imperforate deltidium; dorsal valve flat or weakly convex; flanks with few low, rounded plications; fold and sulcus smooth; dental plates short, slightly divergent; cru-

ral plates absent. *Lower Devonian (upper Emsian):* Czech Republic.—FIG. 1117, 2a–d. **R. lissopleura*, Bohemia; anterior, dorsal, posterior, and side views, $\times 2$ (Havlíček & Kukul, 1990).

Subfamily EUREKASPIRIFERINAE Johnson, 1994

[Eurekaspiriferinae JOHNSON in CARTER & others, 1994, p. 332]

Capillate, with dorsal adminicula. *Lower Devonian (lower Emsian).*

Eurekaspirifer JOHNSON, 1966b, p. 1,045 [**Spirifer (Trigonotreta) pinyonensis* MEEK, 1870, p. 60; OD]. Ventribiconvex, transverse to equidimensional, with curved, apsacline ventral interarea; fold and sulcus well defined, smooth, or with median groove on fold anteriorly; flanks with numerous, simple, rounded plications and U-shaped interspaces; growth lamellae absent or irregularly spaced, crossed by subradial capillae; dental plates long, recurring anteriorly toward midline; ctenophoridium bilobed, anterior to notothyrial chamber; dorsal adminicula long; crural plates lacking. *Lower Devonian (lower Emsian)*: USA (Nevada).—FIG. 1118a–e. **E. pinyonensis* (MEEK); a, ventral view, $\times 1$; b, ventral interior, $\times 2$; c, dorsal interior, $\times 3$; d, cardinalia showing bilobed ctenophoridium; e, ventral view showing capillae, $\times 5$ (Johnson, 1966b).

Family ECHINOSPIRIFERIDAE

Liashenko, 1973

[Echinospiriferidae LIASHENKO, 1973, p. 109] [=Rigauxidae BRICE, 1988, p. 371]

Multiplicate, including fold and sulcus. *Lower Devonian (Pragian)–Upper Devonian (upper Famennian)*.

Echinospirifer LIASHENKO, 1973, p. 109 [**E. distinctus*; OD]. Medium to large, ventribiconvex, transverse with rounded acute cardinal angles; ventral interarea moderately high, curved, apsacline; prominent fold and sulcus with small plications tending to obsolescence anteriorly; flanks with simple, rounded plications; tuberculate surface with fila; dental plates thickened medially in apex; crural plates present. *Upper Devonian (lower Frasnian)*: Russian Platform, Urals, Timan, Siberian Platform, Russian Arctic.—FIG. 1119,2a–f. **E. distinctus*, Timan; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$; f, microornament, $\times 10$ (Liashenko, 1973).

Adolfspirifer KRYLOVA, 1962, p. 75 [**Spirifer Jeremejewi* CHERNYSHEV, 1887, p. 61; OD]. Medium size, ventribiconvex, transverse with rounded cardinal angles; ventral interarea moderately high, curved, apsacline; fold and sulcus plicate; flanks with simple, rarely bifurcating plications; surface with subradial capillae; dental plates thickened. *Upper Devonian (Frasnian)*: Urals, Siberian Platform.—FIG. 1119,4a–d. **A. jeremejewi* (CHERNYSHEV), Siberian Platform; ventral, dorsal, lateral, and anterior views, $\times 1$ (Krylova, 1962).

Arctospirifer STAINBROOK, 1950, p. 382 [**A. constrictus*; OD]. Small, biconvex, equidimensional, rarely auriculate; low, apsacline ventral interarea with apical pseudodeltidium; fold and sulcus weak, plicate; flanks with simple or bifurcating plications; microornament of intrasinal capillae and numerous tubercles mostly on crests of ribs; short dental plates present; crural plates lacking. *Upper Devonian (Famennian)*: midcontinent North America.—

FIG. 1119,1a–f. **A. constrictus*, Iowa, USA; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1.5$; f, holotype, microornament, $\times 4$ (new).

Enchondrospirifer BRICE, 1971, p. 175 [**E. ghorensis*; OD]. Medium size, biconvex, slightly transverse with obtuse cardinal angles; ventral interarea moderately high, incurved, apsacline; fold, sulcus, and flanks with numerous low, rounded plications; surface capillate, becoming tuberculate; dental plates intrasinal; ctenophoridium and crural plates present. *Upper Devonian (upper Famennian)*: Afghanistan.—FIG. 1120,1a–e. **E. ghorensis*; ventral, dorsal, posterior, anterior, and side views, $\times 1$ (Brice, 1971).

Hispidaria COOPER & DUTRO, 1982, p. 110 [**H. posterogranulosa*; OD]. Small, ventribiconvex, transverse with acute cardinal angles; ventral interarea moderately high, slightly curved, steeply apsacline; fold and sulcus plicate, with strong plications bounding sulcus; flanks with narrow, rounded simple plications and U-shaped interspaces; surface, including interarea, tuberculate; interior unknown. *Upper Devonian (Famennian)*: western North America.—FIG. 1119,3a–e. **H. posterogranulosa*, upper Famennian, New Mexico, USA; a–d, holotype, anterior, ventral, lateral, and dorsal views, $\times 2$; e, posterior view, $\times 4$ (Cooper & Dutro, 1982).

Howittia TALENT, 1956, p. 34 [**Spirifer howitti* CHAPMAN, 1905, p. 18; OD] [= *Glyptospirifer* HOU & XIAN, 1975, p. 72 (type, *Spirifer chui* GRABAU, 1931b, p. 376, OD)]. Medium size, biconvex, transverse, with curved, apsacline ventral interarea; fold and sulcus prominent, sulcus with one or more plications; flanks with numerous, simple, rounded or subangular plications and narrow, U-shaped interspaces; growth lamellae may be prominent anteriorly; fila crossed by subradial capillae; dental plates extrasinal; ctenophoridium may be bilobed; without crural plates. *Lower Devonian (Pragian–Emsian)*: Australia, Mongolia, southern China, northern Vietnam.—FIG. 1121a–e. **H. howitti* (CHAPMAN), Australia; a–c, dorsal, anterior, and posterior views, $\times 1.5$; d, transverse section of ventral valve, $\times 3$; e, transverse section of dorsal valve, $\times 10$ (Talent, 1956).

Indospirifer GRABAU, 1931b, p. 359 [**Spirifer padaukpinensis* REED, 1908, p. 101; OD] [= *Schizospirifer* GRABAU, 1931b, p. 353, *nom. nud.* (type, *Spirifer aperturatus* var. *latistriatus* FRECH, 1911, p. 53, OD)]. Medium size, ventribiconvex, transverse, with obtuse or acute cardinal angles; ventral interarea curved, apsacline to nearly orthocline; fold and sulcus prominent, with small, nonradial plications; flanks with rounded, elevated plications, commonly simple, less commonly branching; microornament of prominent growth lines anteriorly and subradial capillae; delthyrial cavity with some callus; dental plates extrasinal; short crural plates converging anterodorsally that may be obscured by callus and elevated ctenophoridium. *Lower Devonian (Emsian)–Middle*

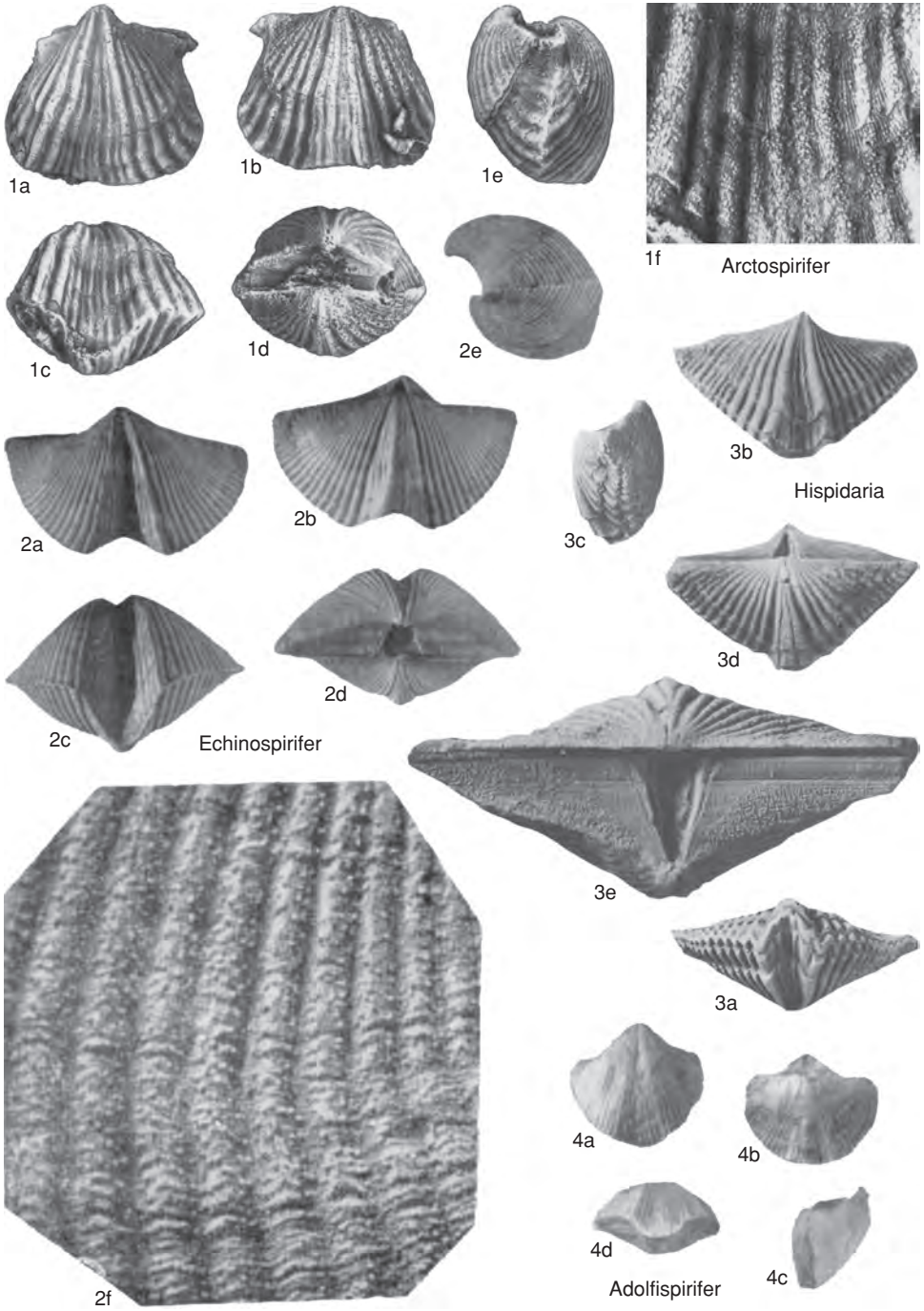


FIG. 1119. Echinospiriferidae (p. 1711).

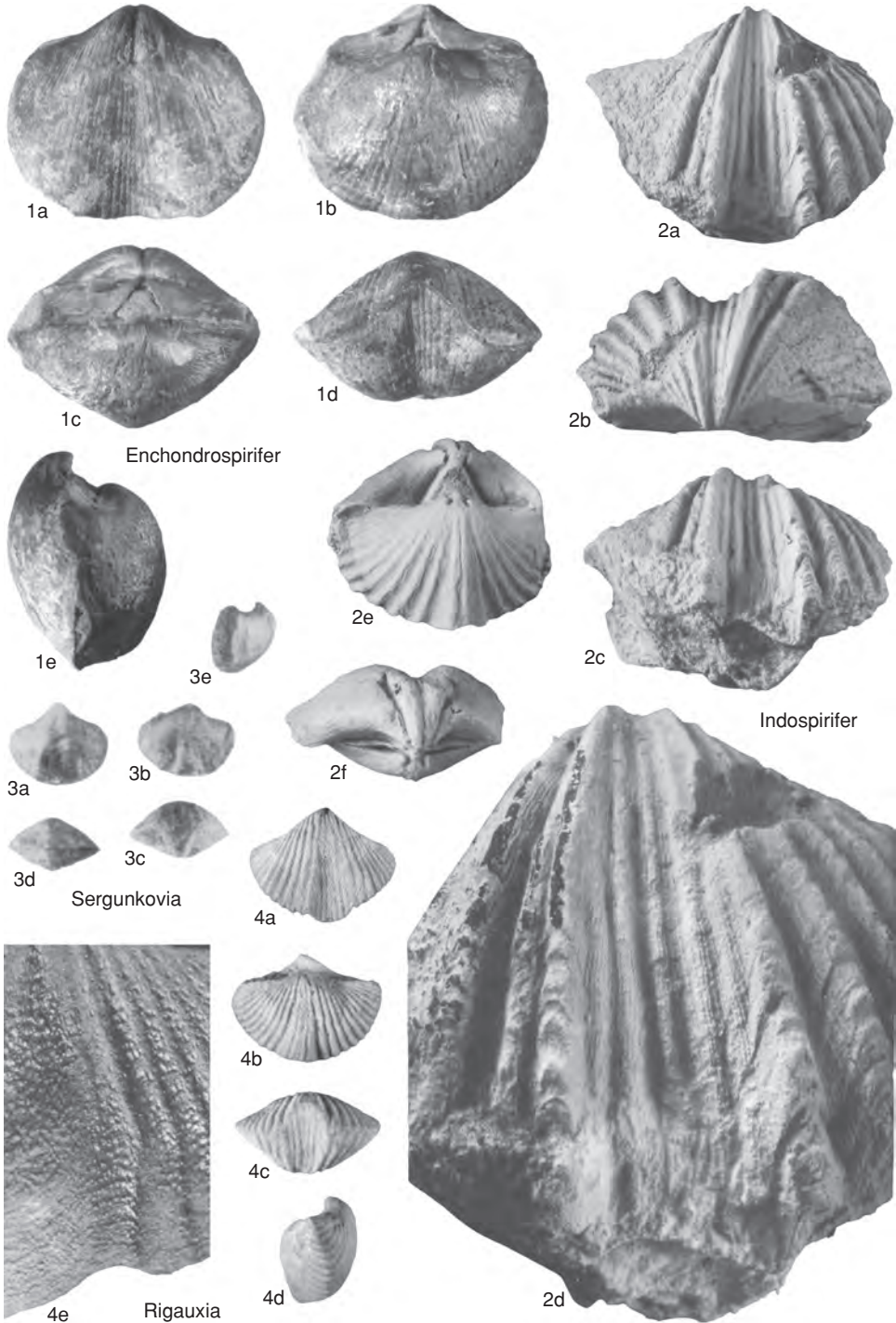


FIG. 1120. Echinospiriferidae (p. 1711–1714).

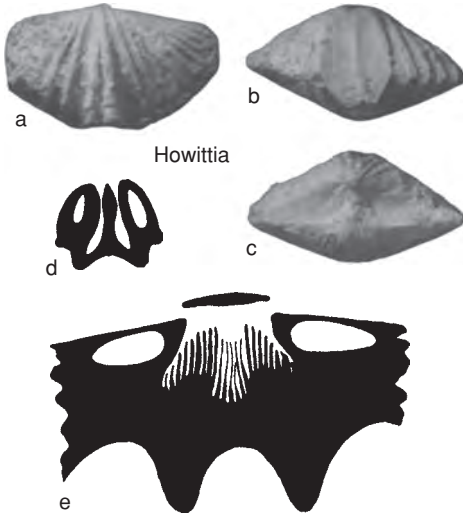


FIG. 1121. Echinospiriferidae (p. 1711).

Devonian (lower Givetian): Salair, Guangxi, northern Vietnam, Burma.—FIG. 1120,2*a–f*. **I. padaukpinensis* (REED), Eifelian, Burma; *a–c*, ventral, posterior, and anterior views, $\times 2$; *d*, ventral sulcus showing capillae, $\times 5$; *e–f*, dorsal and poste-

rior views of internal mold, $\times 2$ (Anderson, Boucot, & Johnson, 1969).

Rigauxia BRICE, 1988, p. 371 [**Spirifer acutosinu* RIGAUX, 1908, p. 15; OD]. Small to medium size, ventribiconvex, transverse, with obtuse or acute cardinal angles, commonly rounded; ventral interarea curved, apsacline; fold and sulcus with small plications; flanks with simple, rounded plications; surface with subradial capillae, becoming tuberculate; delthyrial cavity with apical callus; dental plates strong, extrasinal, weakly divergent; short crural plates may be obscured by callus and elevated ctenophoridium. *Upper Devonian (Frasnian)*: cosmopolitan.—FIG. 1120,4*a–e*. **R. acutosinu* (RIGAUX), lower Frasnian, France; *a–d*, ventral, dorsal, anterior, and side views, $\times 2$; *e*, exterior showing fine ornament, $\times 10$ (Brice, 1988).

Sergunkovia NALIVKIN, 1979, p. 129 [**Paulonia talassica* VASILEVA in VASILEVA & POIARKOV, 1957, p. 58; OD]. Medium size, biconvex, slightly transverse; cardinal angles obtuse; ventral interarea short, curved, apsacline; fold and sulcus prominent, plicate or with plications becoming obsolescent; flanks with numerous, rounded plications; surface capillate; short dental plates present; hinge plates discrete. *Upper Devonian (upper Famennian)*: Urals, Kazakhstan, northern Tian Shan, Karatau and Talassk Alatau ranges.—FIG. 1120,3*a–e*. **S. talassica* (VASILEVA), northern Tian Shan; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$ (Vasileva & Poiarkov, 1957).

THEODOSSIOIDEA

J. G. JOHNSON,¹ J. L. CARTER,² and HOU HONG-FEI³

[¹deceased, formerly of Oregon State University; ²retired from Carnegie Museum of Natural History; and ³China University of Geosciences]

Superfamily THEODOSSIOIDEA Ivanova, 1959

[*nom. transl.* JOHNSON, CARTER, & HOU in CARTER & others, 1994, p. 333, ex Theodossinae IVANOVA, 1959, p. 61]

Uniformly plicate or costate; fold and sulcus indistinct or lacking; delthyrial plate lacking. *Lower Devonian (Pragian)–Carboniferous (Tournaisian)*.

Family THEODOSSIIDAE Ivanova, 1959

[*nom. transl.* JOHNSON, CARTER, & HOU in CARTER & others, 1994, p. 333, ex Theodossinae IVANOVA, 1959, p. 61]

[Materials for this family prepared by J. G. Johnson & Hou Hong-fei]

Without inner prismatic shell layer. *Lower Devonian (Pragian)–Upper Devonian (Frasnian)*.

Subfamily THEODOSSIINAE

Ivanova, 1959

[Theodossiiinae IVANOVA, 1959, p. 61]

Capillate. *Middle Devonian (Eifelian)–Upper Devonian (Frasnian)*.

Theodossia NALIVKIN, 1925, p. 267 [**Spirifer Anosofi* DE VERNEUIL, 1845, p. 153; OD] [= *Vandergrachtella* CRICKMAY, 1953b, p. 7 (type, *V. arcuum* CRICKMAY, 1953b, p. 8, OD)]. Medium size, ventribiconvex, equidimensional to moderately transverse; cardinal angles obtusely rounded; ventral interarea strongly curved, apsacline to orthocline; fold and sulcus not prominent, blending with flanks; costae simple on fold, sulcus, and flanks, rarely bifurcating anteriorly on fold and sulcus; capillate; dental plates thin, straight, extrasinal; short crural plates obscured by callus; ctenophoridium elevated. *Upper Devonian (Frasnian)*: cosmopolitan.—FIG. 1122a–b. **T. anosofi* (DE VERNEUIL), Russia; lectotype, dorsal and anterior views, $\times 1$ (Vandercammen, 1959).—FIG. 1123a–b. **T. anosofi* (DE VERNEUIL), Russia; lectotype, lateral and ventral views, $\times 1$ (Vandercammen, 1959).

Paralazutkinia JIANG in XIAN & JIANG, 1978, p. 314 [**P. pinghuangshanensis*; OD] [= *Pinghuangella* JIANG in XIAN & JIANG, 1978, p. 315 (type, *P. bisulcata* JIANG in XIAN & JIANG, 1978, p. 316, OD)]. Ventribiconvex, moderately transverse; ventral interarea long, curved, apsacline; surface with low, rounded plications, strongest medially, with fold and sulcus indistinct or lacking; microornament of fine capillae; shell thick with short dental plates; ctenophoridium located on cruralium and low median septum. *Middle Devonian (Eifelian)*: southern China.—FIG. 1124, 2a–c. **P. pinghuangshanensis*; ventral, dorsal, and side views, $\times 2$ (Xian & Jiang, 1978).

Urella RZHONSNITSKAIA in MARKOVSKI, 1960, p. 402 [**U. asiatica*; OD] [= *Retzspirifer* KULKOV, 1960, p. 929 (type, *R. uriensis* KULKOV, 1960, p. 930, OD)]. Biconvex with obtuse cardinal angles; interarea curved, narrow, poorly defined; surface with numerous low, rounded, simple or bifurcating plications; fold and sulcus lacking; microornament capillate; shell thin; dental plates short; ctenophoridium with outer hinge plates attached to median ridge posteriorly, free anteriorly; crural plates absent. *Middle Devonian (Eifelian–Givetian)*: Urals, Kuznets basin, Salair.—FIG. 1124, 1a–c. **U. asiatica*, Kuznets basin; holotype, ventral, dorsal, and lateral views, $\times 1$ (Markovski, 1960).

Subfamily BRANIKIINAE

Johnson & Hou, 1994

[Branikiinae JOHNSON & HOU in CARTER & others, 1994, p. 333]

Noncapillate. *Lower Devonian (Pragian)–Middle Devonian (Eifelian)*.

Branikia HAVLÍČEK, 1957b, p. 437 [**Spirifer Ascanius* BARRANDE, 1879, pl. 74, case V; OD] [= *Bidentatus* KHODALEVICH & BREIVEL, 1972, p. 202 (type, *B. strabo*, OD)]. Biconvex with obtuse cardinal angles; ventral interarea curved, nearly orthocline; surface with numerous low, rounded plications; fold and sulcus indistinct or lacking; microornament of concentric lamellae; shell thick; dental plates short; hinge plates with elevated, knoblike cardinal process, lacking crural plates. *Lower Devonian (Pragian)*: Czech Republic, central Urals.—FIG. 1125, 2a–d. **B. ascania* (BARRANDE), Czech Republic; lectotype, ventral, dorsal, anterior, and lateral views, $\times 1.5$ (Havlíček, 1959).

Jilinspirifer SU, 1980, p. 317 [**J. yungjiensis* SU, 1980, p. 318; OD]. Small, ventribiconvex, transverse; ventral interarea high, apsacline; plications on flanks numerous, simple, but smooth posterolaterally; fold and sulcus lacking; dental plates lacking; microornament and dorsal interior unknown. *Middle Devonian (Eifelian)*: China (Jilin).—FIG. 1125, 1a–e. **J. yungjiensis*; holotype, ventral, dorsal, lateral, posterior, and anterior views, $\times 1$ (Su, 1980).

Lenzia PERRY, BOUCOT, & GABRIELSE, 1981, p. 35 [**L. pachystrakon*; OD]. Medium size, biconvex, equidimensional, with obtuse cardinal angles; ventral interarea slightly curved, apsacline; fold and sulcus indistinct, flaring, with 2 or 3 plications, tending to obsolescence in sulcus; flanks with few simple, strong, rounded or subangular plications; dental plates short, obsolescent in umbonal callus; cardinal process low, moundlike, without crural plates. *Lower Devonian (lower Emsian)*: western North America.—FIG. 1125, 3a–d. **L. pachystrakon*, British Columbia; a–b, ventral valve exterior and interior; c–d, dorsal valve exterior and interior, $\times 1.5$ (new).

Family ULBOSPIRIFERIDAE

Johnson & Carter, 1994

[Ulbospiriferidae JOHNSON & CARTER in CARTER & others, 1994, p. 334]

With inner prismatic shell layer. *Upper Devonian (upper Famennian)*.

Subfamily ULBOSPIRIFERINAE

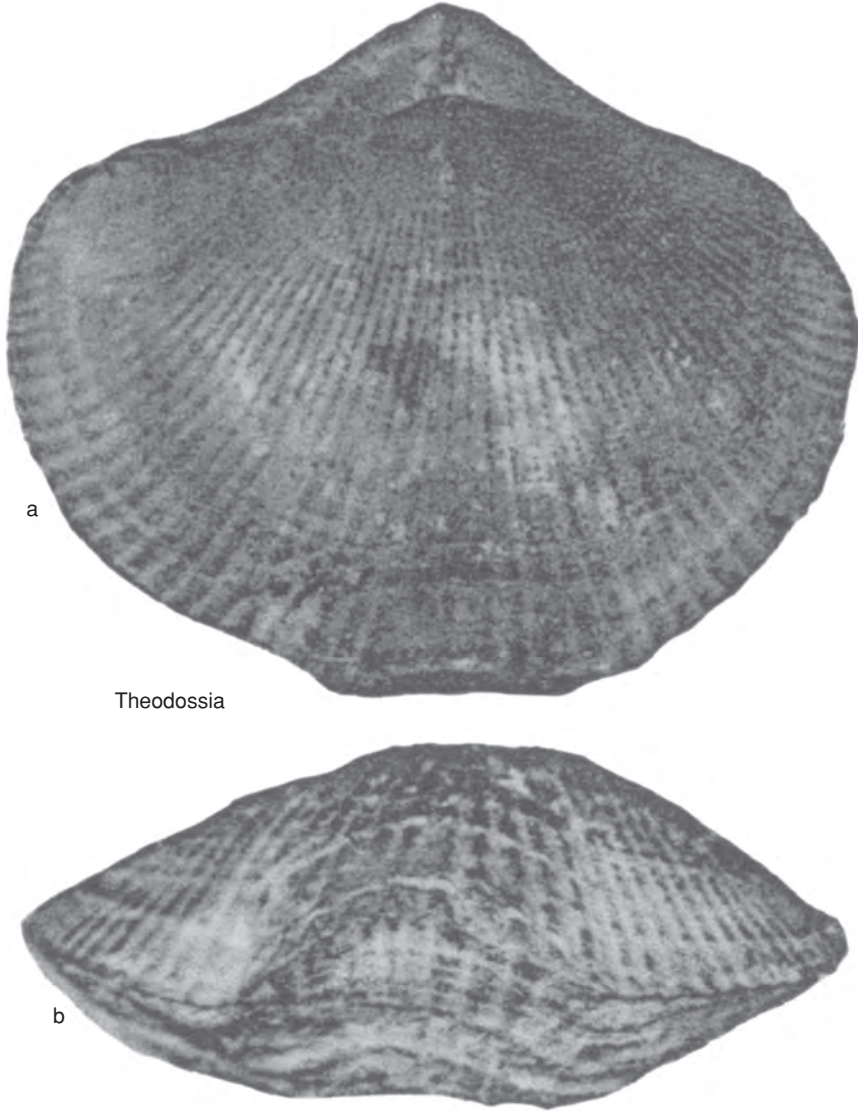
Johnson & Carter, 1994

[Ulbospiriferinae JOHNSON & CARTER in CARTER & others, 1994, p. 334]

[Materials for this subfamily prepared by J. G. Johnson & Hou Hong-fei]

Uniformly costate. *Upper Devonian (upper Famennian)*.

Ulbospirifer GRECHISHNIKOVA, 1965, p. 33 [**U. altaicus* GRECHISHNIKOVA, 1965, p. 35; OD]. Medium to large, ventribiconvex, equidimensional or



Theodosia

FIG. 1122. Theodosiidae (p. 1715).

slightly transverse, cardinal angles obtuse; ventral interarea of moderate height, curved, apsacline; fold and sulcus costate as on flanks, with numerous rounded costae; surface tuberculate; ventral umbones thick, with short median septum; dental plates thick and slightly recurved; hinge plates unsupported. *Upper Devonian (upper Famennian):*

Rudny Altai.—FIG. 1126, 1a–g. **U. altaicus*; a, holotype, ventral valve, $\times 1$; b, microornament, $\times 8$; c–g, transverse sections of ventral valve, $\times 1.7$ (Grechishnikova, 1965).

Cyrtiorina COOPER & DUTRO, 1982, p. 111 [**Cyrtospirifer kindlei* STAINBROOK, 1947, p. 318; OD]. Medium to large, ventribiconvex,

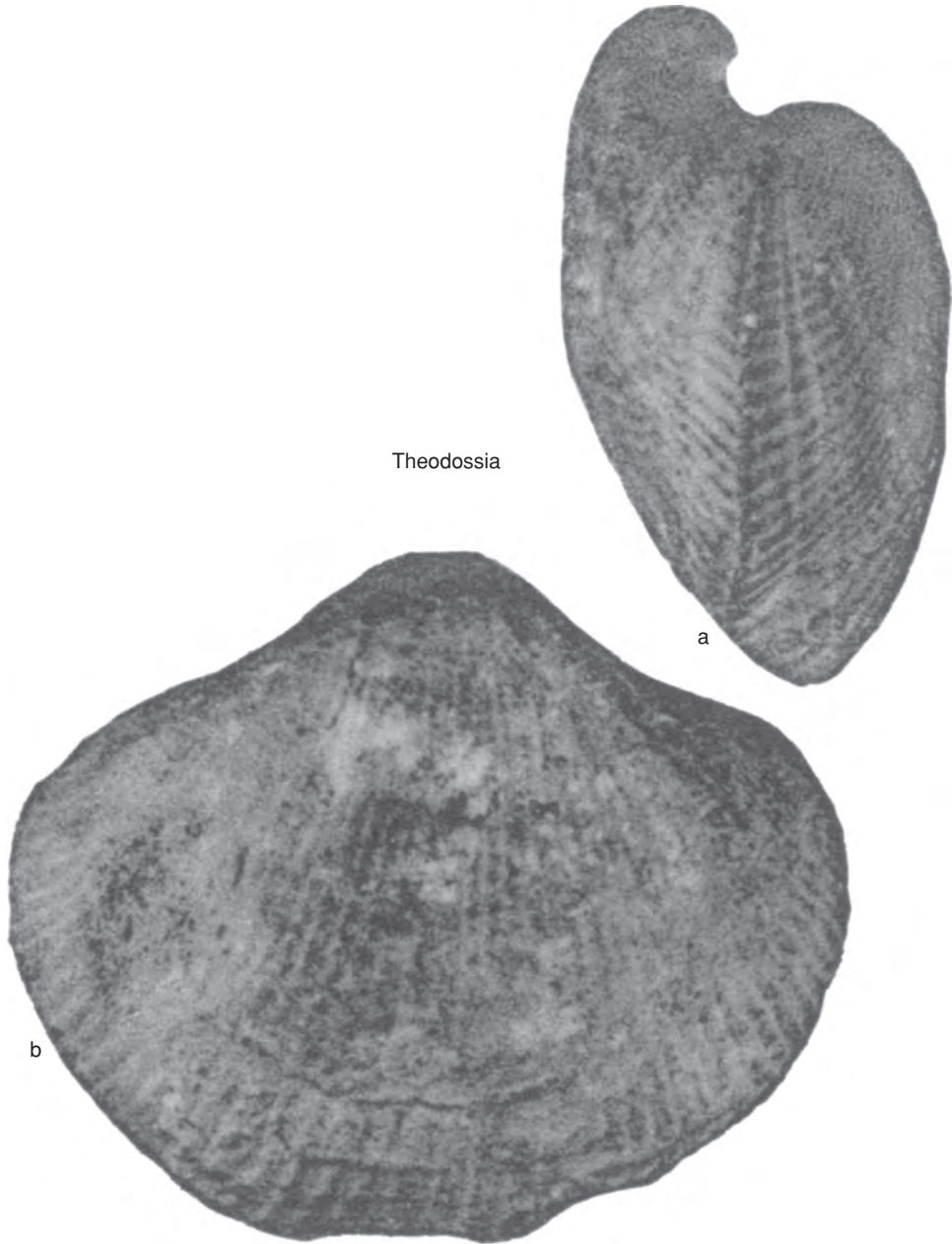


FIG. 1123. Theodossiidae (p. 1715).

equidimensional or slightly transverse, cardinal angles obtuse or slightly auriculate; ventral interarea with moderate height, curved, apsacline; fold and sulcus costate as on flanks, with numerous rounded costae, becoming flattened anteriorly; surface

capillate, becoming tuberculate; dental plates long, subparallel, slightly recurving; ctenophoridium concave. *Upper Devonian (upper Famennian)*: western North America.—FIG. 1126, 2a–e. **C. kindlei* (STAINBROOK), New Mexico, USA; posterior, lateral,

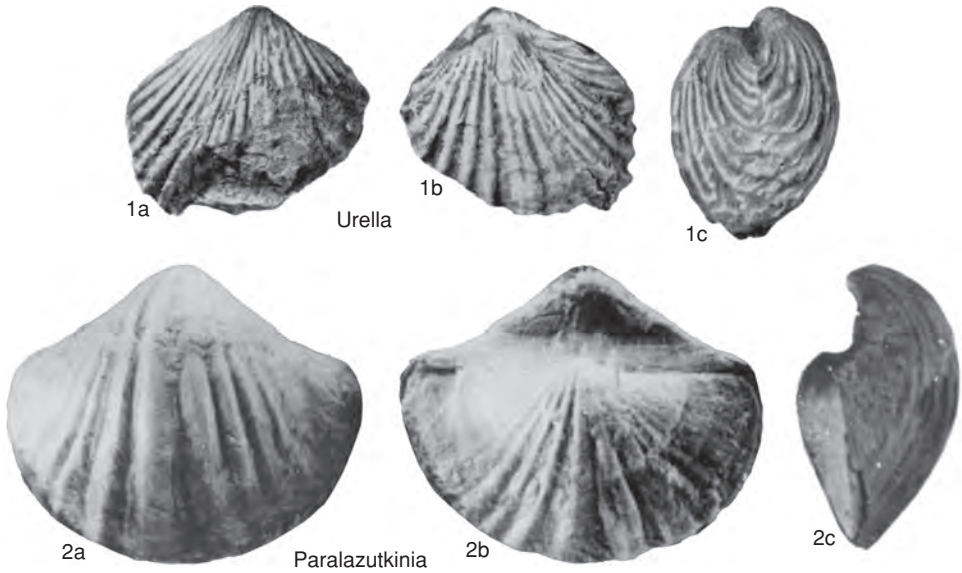


FIG. 1124. Theodossiidae (p. 1715).

anterior, ventral, and dorsal views, $\times 1$ (Cooper & Dutro, 1982).

Tenia MARTYNOVA, 1970, p. 68 [**Spirifer* (*Cyrtospirifer*) *dada* NALIVKIN, 1937, p. 97; OD] [= *Omolonospirifer* SIMAKOV in AFANAS'eva & SIMAKOV, 1970, p. 86, obj.]. Medium to large, biconvex, equidimensional, cardinal angles obtuse; ventral interarea low, strongly curved; fold and

sulcus absent or poorly developed, costate as on flanks, with numerous rounded costae; surface capillate; umbones thick, dental plates thick and slightly recurved; hinge plates supported by median ridge. *Upper Devonian (upper Famennian):* Kazakhstan.—FIG. 1126, 3a–b. **T. dada* (NALIVKIN); holotype, ventral and dorsal views, $\times 1$ (Nalivkin, 1937).

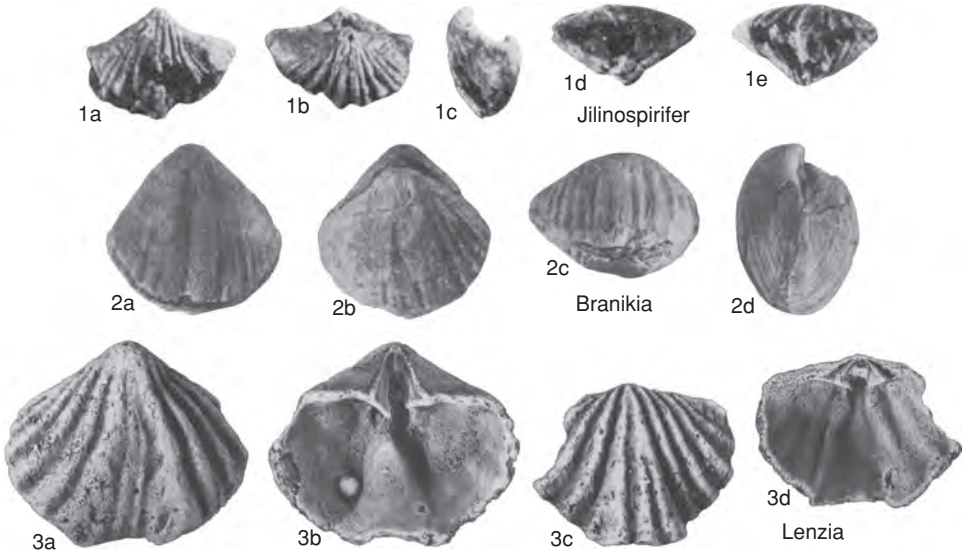


FIG. 1125. Theodossiidae (p. 1715).

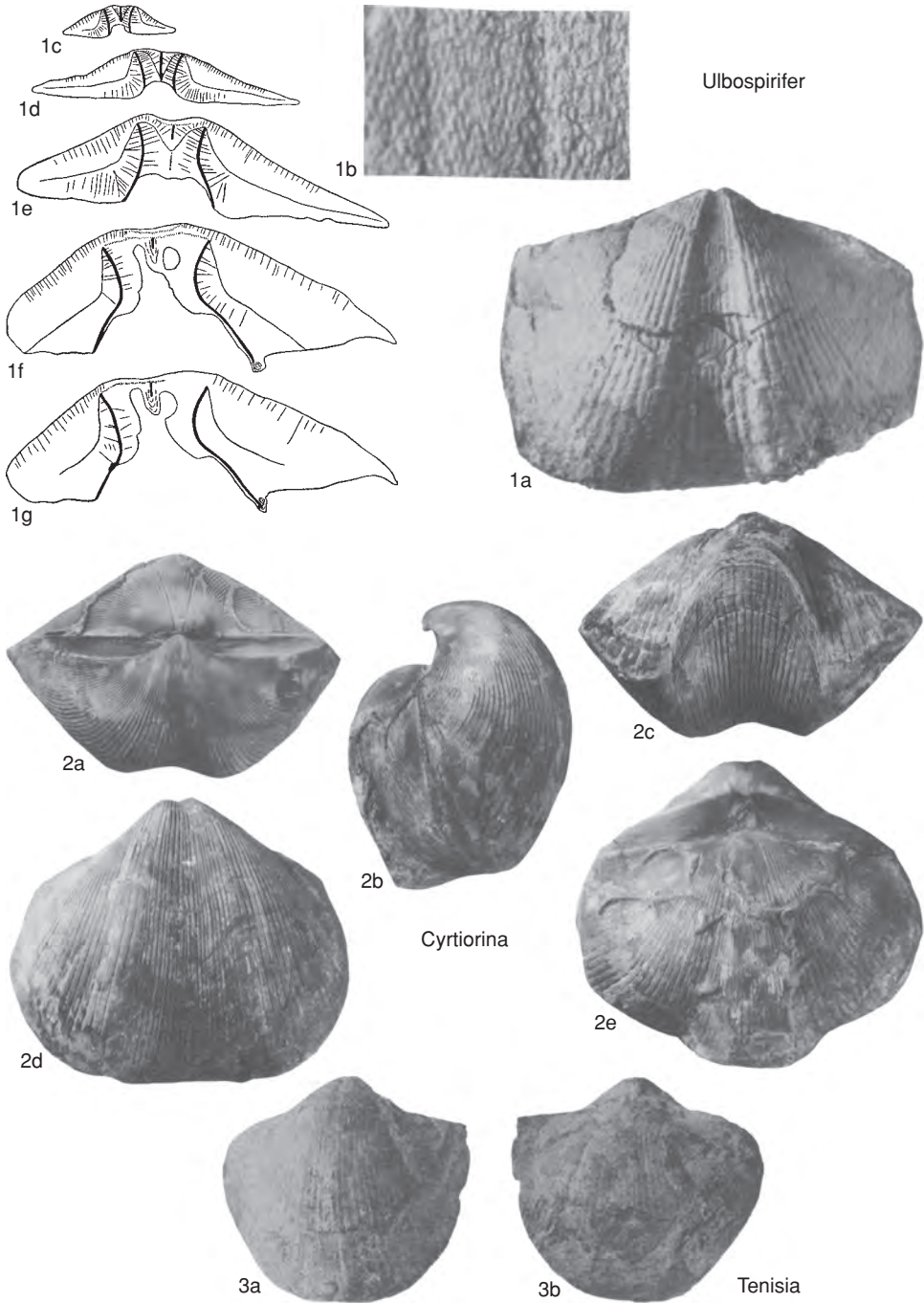


FIG. 1126. Ulbospiriferidae (p. 1715–1718).

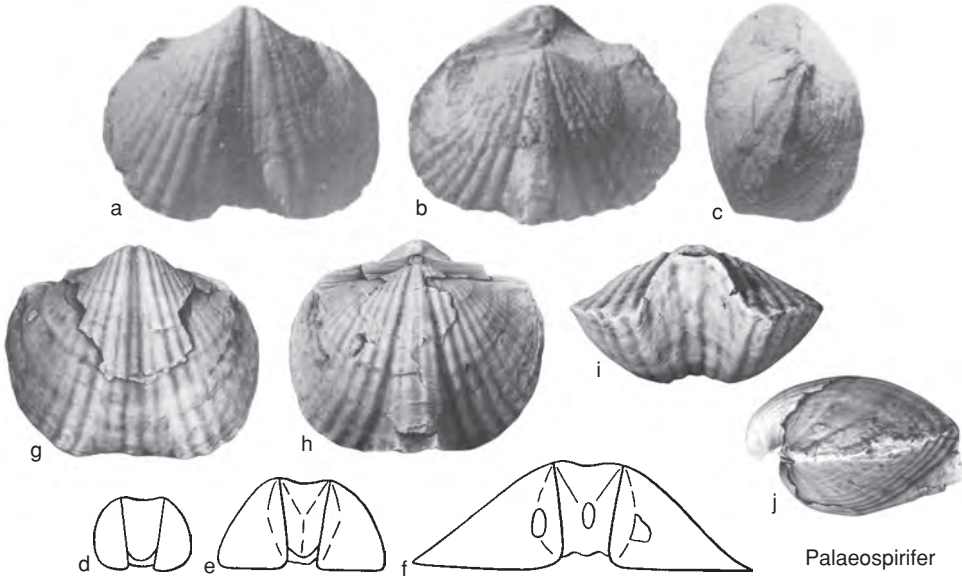


FIG. 1127. Ulbospiriferidae (p. 1720).

Subfamily PALAEOSPIRIFERINAE Carter, Johnson, and Hou, 1994

[Palaeospiriferinae CARTER, JOHNSON, & HOU in CARTER & others, 1994, p. 334]

[Materials for this subfamily prepared by J. G. Johnson, J. L. Carter, & Hou Hong-fei]

With low, rounded plications. *Upper Devonian (upper Famennian)*.

Palaeospirifer MARTYNOVA & SVERBILOVA, 1968, p. 26 [**Cyrtospirifer? karagatshicus* SVERBILOVA in LITVINOVICH & SVERBILOVA, 1963, p. 286; OD] [= *Goungjunsipirifer* ZHANG F. M. in ZHANG Chuan & others, 1983, p. 346 (type, *G. sinicus*, OD)]. Medium size; transversely subovate; cardinal angles well rounded; interarea low; fold and sulcus moderately developed, moderately wide; flanks with few broad rounded plications, one or more of which may bifurcate; sulcus with distinct simple median plication and 1 or 2 pairs of lateral sulcal plications; surface strongly capillate; dental plates very short, divergent. *Upper Devonian (upper Famennian)*: Kazakhstan, China. —FIG. 1127a–f. **P. karagatshicus* (SVERBILOVA); a–c, ventral, dorsal, and side views, $\times 1$; d–f, transverse sections, $\times 3$ (Martynova & Sverbilova, 1968). —FIG. 1127g–j. *P. sinicus* (ZHANG), China; ventral, dorsal, anterior, and side views, $\times 1$ (Zhang Chuan & others, 1983).

Family PALAEOCHORISTITIDAE Carter, 1994

[Palaeochoristitidae CARTER in CARTER & others, 1994, p. 334]

[Materials for this family prepared by J. L. Carter]

Cardinal extremities rounded in juveniles, outline variable in adults; with well-developed dental plates and dorsal adminicula; delthyrial plate absent; microornament absent. *Upper Devonian (upper Famennian)–Carboniferous (Tournaisian)*.

Palaeochoristites SOKOLSKAYA, 1941, p. 26 [**Spirifer cinctus* KEYSERLING, 1846, p. 229; OD]. Medium to large; transversely subovate in outline; moderately and subequally biconvex; ventral umbonal region broad, evenly rounded, poorly differentiated from lateral slopes; beak small, incurved; ventral interarea acutely triangular; cardinal extremities rounded to subangular, maximum width attained anterior to hinge line; fold and sulcus absent; hinge line nondenticulate; entire surface multicostate; costae numerous, flattened, freely bifurcating or trifurcating, with narrow interspaces; ventral interior with long, slender, slightly diverging dental adminicula; dorsal interior with long, slender, subparallel, vertical dorsal adminicula; vascular impressions unknown;

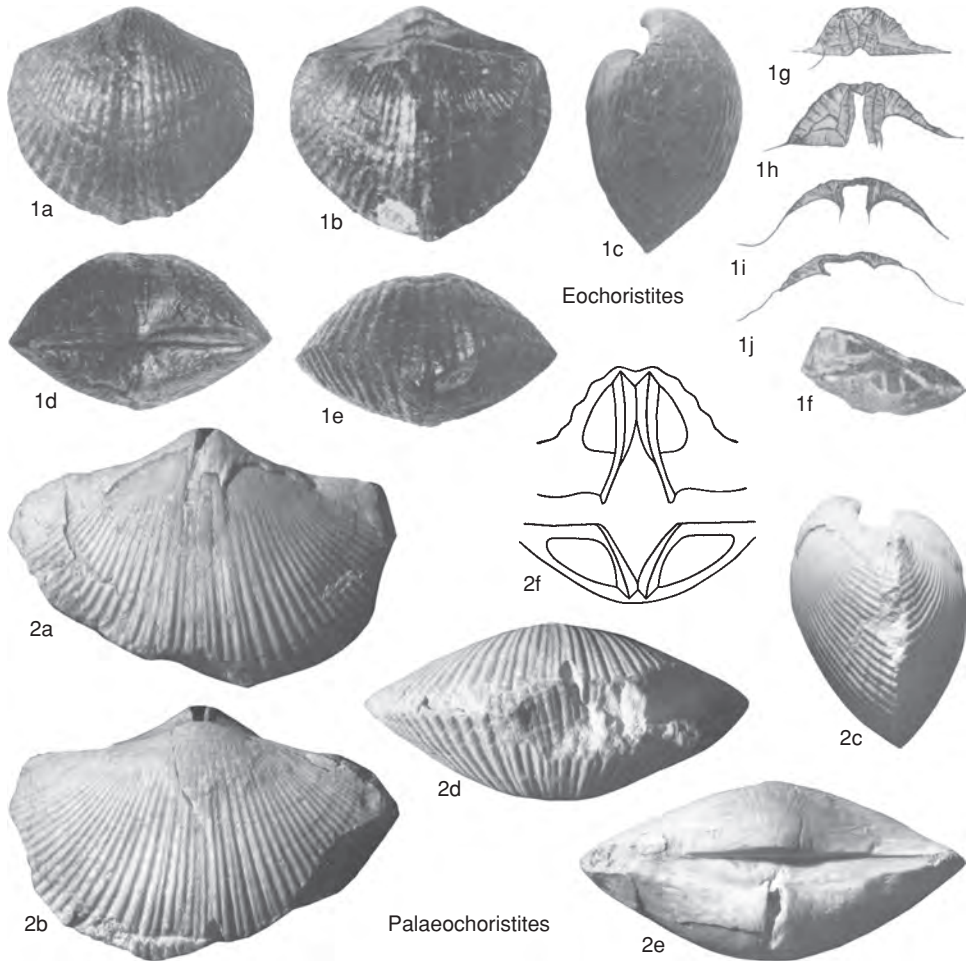


FIG. 1128. Palaeochoristitidae (p. 1720–1721).

umbonal region of ventral valve greatly thickened. *Carboniferous (Tournaisian)*: Russia.—FIG. 1128, 2a–f. **P. cinctus* (KEYSERLING), European Russia; a–e, holotype, ventral, dorsal, lateral, anterior, and posterior views, $\times 1$ (new); f, transverse section, $\times 3$ (Ivanova, 1960).

Eochoristites CHU, 1933, p. 28 [**E. neipentaiensis*; OD] [?= *Centrospirifer* TIEN, 1938, p. 110 (type, *Spirifer (Sinospirifer) chaoi* GRABAU, 1931b, p. 263, OD)]. Medium size; subequally and moderately biconvex; ventral umbo broad, weakly inflated; ventral beak small, moderately incurved; ventral interarea truncated; hinge line nondenticulate; fold and sulcus narrow to moderately wide, weakly developed; costae mostly simple on lateral slopes; sulcus with strong, simple, or bifurcating median costa

and several, mostly simple, lateral sulcal costae that bifurcate from bounding costae; dorsal adminicula moderately long; otherwise similar to *Palaeochoristites*. [According to HOU Hong-fei (personal communication, 1993), the types of *Centrospirifer chaoi* (GRABAU, 1931b) are from the Banxiang Formation of early Tournaisian age and are from nearly the same region and beds as the types of *Eochoristites neipentaiensis* CHU. The interior of *C. chaoi* is unknown.] *Upper Devonian (upper Famennian)–Carboniferous (Tournaisian)*: southeastern China.—FIG. 1128, 1a–j. **E. neipentaiensis*, Tournaisian; a–e, holotype, ventral, dorsal, lateral, posterior, and anterior views, $\times 1$; f, transverse section of dorsal valve; g–j, transverse sections of ventral valve, $\times 1$ (Chu, 1933).

CYRTOSPIRIFEROIDEA

J. G. JOHNSON

[deceased, formerly of Oregon State University]

Superfamily CYRTOSPIRIFEROIDEA Termier & Termier, 1949

[*nom. correct.* JOHNSON in CARTER & others, 1994, p. 334, *pro* Cyrtospiriferacea IVANOVA, 1972, p. 31, *nom. transl. ex* Cyrtospiriferinae TERMIER & TERMIER, 1949a, p. 99]

Capillate or pustulose, nonfrilly; with dental plates and ctenophoridium, generally with delthyrial plate; generally without crural plates. *Lower Devonian (Emsian)*–*Upper Devonian (upper Famennian)*.

Family SPINOCYRTIIDAE Ivanova, 1959

[*nom. transl.* PITRAT, 1965, p. 688, *ex* Spinocyrtiidae STRUVE in PAULUS, STRUVE, & WOLFART, 1963, p. 462, *nom. correct. pro* Spinocyrtinae IVANOVA, 1959, p. 59]

With numerous simple plicae on flanks; fold and sulcus smooth or with single medial ventral rib and dorsal groove. *Lower Devonian (Emsian)*–*Upper Devonian (Frasnian)*.

Spinocyrtia FREDERIKS, 1916, p. 18 [**Delthyris granulosa* CONRAD, 1839, p. 65; SD FREDERIKS, 1926, p. 411]. Medium to large, biconvex, transverse; ventral interarea flat or slightly curved, apsacline; stegidial plates present; cardinal angles acute, auriculate; fold and sulcus prominent, smooth, with plications tending to form on parietal slopes anteriorly; fold may have median groove; flanks with numerous low, rounded plications separated by narrow interspaces; surface tuberculate, with radially arranged, tear-shaped granules on microfla; dental plates straight, divergent, mostly buried in umbonal callus with impressed muscle field; broad ctenophoridium impressed in thick shell. *Middle Devonian*: cosmopolitan.—FIG. 1129,1a–d. **S. granulosa* (CONRAD), Givetian, New York, USA; dorsal, ventral, anterior, and lateral views, $\times 1$ (Ehlers & Wright, 1955).

Acutoria COOPER & DUTRO, 1982, p. 100 [**A. angulata*; OD]. Medium to large, dorsibiconvex, transverse; cardinal angles acute to rounded; ventral interarea curved, apsacline; fold and sulcus smooth, angular, becoming carinate with flanks; flanks with numerous, simple, flat plications; surface capillate; dental plates long, divergent; ctenophoridium supported by median septum. *Middle Devonian (Givetian)*: western North America.—FIG. 1130,4a–b. **A. angulata*, New Mexico, USA; dorsal and ventral valves, $\times 1$ (Cooper & Dutro, 1982).

Alatiformia STRUVE, 1963, p. 499 [**Spirifer alatiformis* DREVERMANN, 1907, p. 126; OD; =*Spirifer subcuspidatus* var. *alata* KAYSER, 1871, p. 573]. Medium to large, ventribiconvex, strongly transverse; ventral interarea flat, steeply apsacline to catacline; fold and sulcus prominent, smooth; flanks with numerous simple plications crossed by closely spaced, nodose growth lines; dental plates widely divergent. [DREVERMANN (1907) erected the new species (in fact gave a new name to) *alatiformis* from the “var” *subcuspidatus* var. *alata* KAYSER, 1871 that does not belong to the species *subcuspidatus*.] *Lower Devonian (Emsian)*–*Middle Devonian (Eifelian)*: Europe, USA (Nevada).—FIG. 1129,2a–c. **A. alatiformis* (DREVERMANN), Emsian, Germany; posterior, ventral, and dorsal views of natural internal mold, $\times 1.5$ (Struve, 1964).

Carpinaria STRUVE, 1982, p. 213 [**Spinocyrtia (Carpinaria) carpinensis* STRUVE, 1982, p. 213; OD]. Microornament as in *Spinocyrtia*; ventral interarea very high, nearly catacline; otherwise similar to *Orthospirifer. Middle Devonian (Givetian)*: Germany, Russia.—FIG. 1130,1a–e. **C. carpinensis*, upper Givetian, Germany; holotype, ventral, dorsal, lateral, posterior, and anterior views, $\times 1$ (Struve, 1982).

Duryeella BOUCOT, 1975, p. 370 [**Spirifer macra* HALL, 1857, p. 134; OD]. Medium size, strongly transverse; ventral interarea apsacline, slightly curved; cardinal angles acute; fold and sulcus smooth; flanks with numerous rounded plications; growth lines closely spaced; dental plates largely buried in umbonal callus. *Lower Devonian (upper Emsian)*–*Middle Devonian (lower Eifelian)*: eastern North America.—FIG. 1129,4a–c. **D. macra* (HALL), lower Eifelian, New York, USA; a, ventral valve, $\times 1$ (Hall, 1867b); b–c, dorsal and posterior views of dorsal internal mold, $\times 2$ (Boucot, 1975).

Eosyringothyris STAINBROOK, 1943, p. 431 [**Spirifer aspera* HALL, 1858, p. 508; OD]. Medium size, ventribiconvex, transverse; ventral interarea high, flat, steeply apsacline to procline; stegidial plates present; cardinal angles acute; fold and sulcus broad, low, smooth; surface papillose; delthyrial plate with median anterior spine; dental plates straight or slightly curved. *Middle Devonian (upper Givetian)*–*Upper Devonian (lower Frasnian)*: midcontinent North America.—FIG. 1129,3a–c. **E. aspera* (HALL), upper Givetian, Iowa, USA; ventral, dorsal, and posterior views, $\times 1$ (Stainbrook, 1943).

Mediospirifer BUBLICHENKO, 1956, p. 102 [**Delthyris medialis* HALL, 1843, p. 208; OD; =*Delthyris audacula* CONRAD, 1842, p. 262]. Medium to large, ventribiconvex, transverse, with acute cardinal angles; ventral interarea of moderate height, slightly

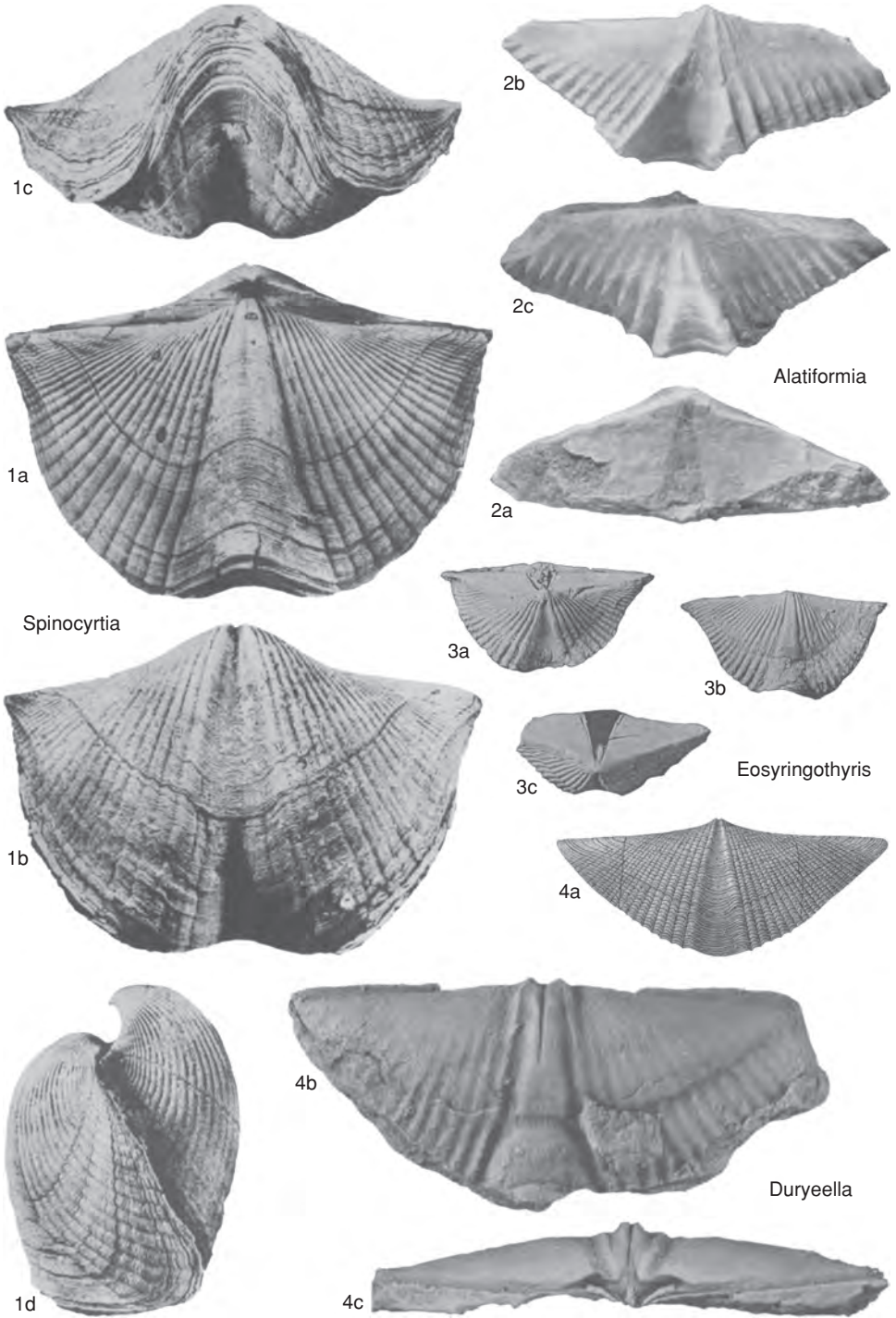


FIG. 1129. Spinocyrtiidae (p. 1722).

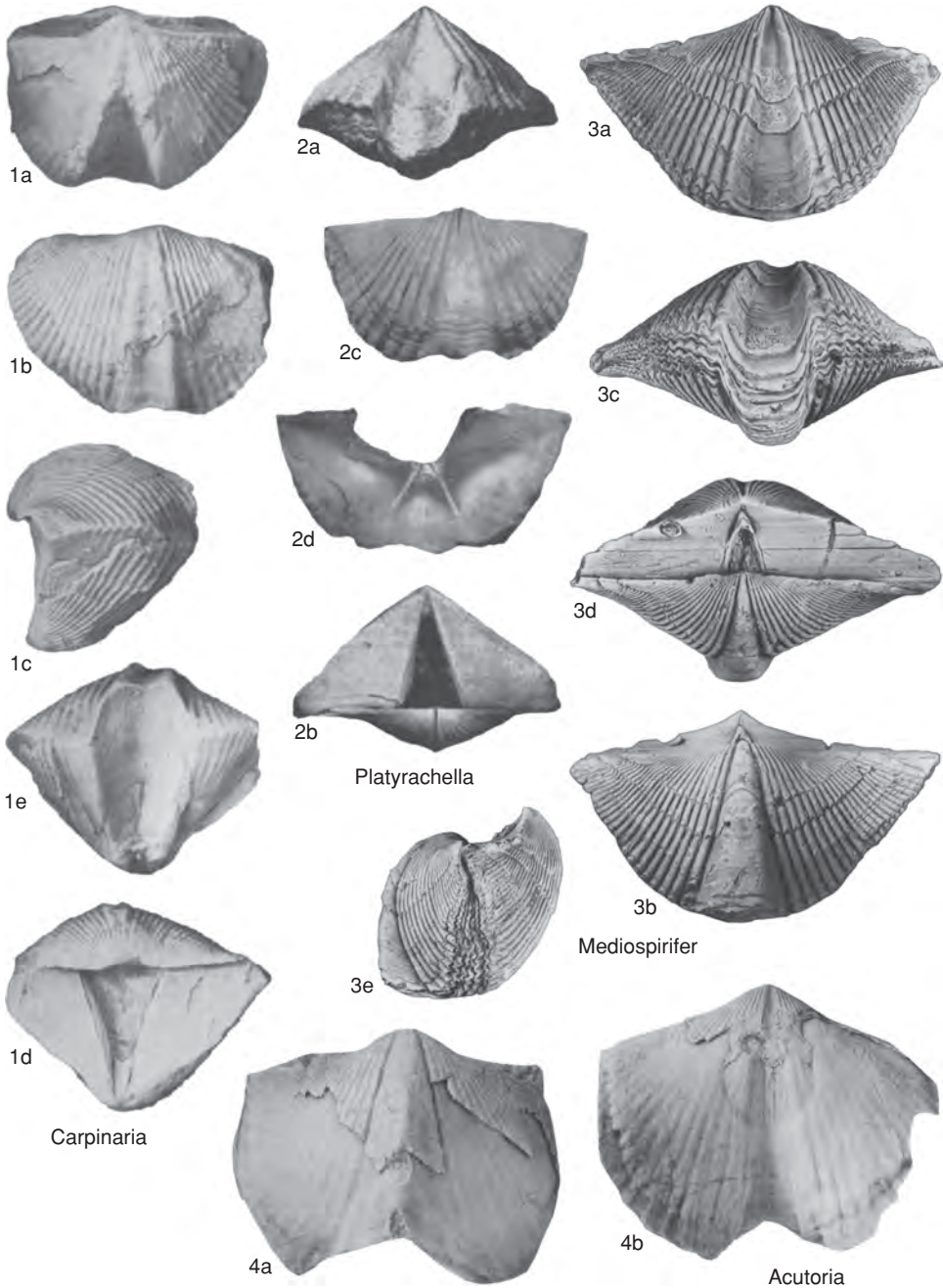


FIG. 1130. Spinocyrtiidae (p. 1722–1725).

curved, steeply apsacline; stegidial plates present; fold and sulcus prominent, smooth; flanks with numerous simple plications crossed by closely spaced growth lines. *Middle Devonian (Givetian)*: North America, Germany.—FIG. 1130,3a–e. *M.

audaculus (CONRAD), New York, USA; ventral, dorsal, anterior, posterior, and lateral views, x1 (new). *Orthospirifer* PITRAT, 1975, p. 387 [**O. missouriensis* PITRAT, 1975, p. 389; OD]. Medium to large,

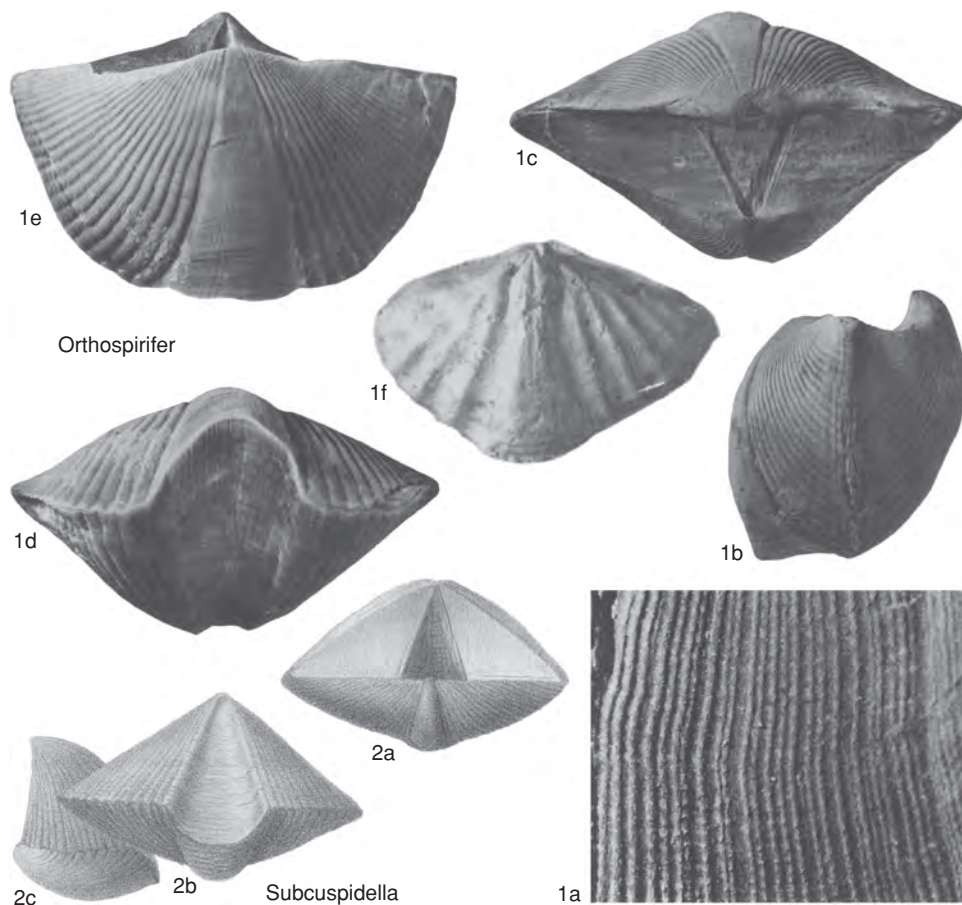


FIG. 1131. Spinocyrtiidae (p. 1724–1726).

biconvex, transverse; ventral interarea of medium height, slightly curved, apsacline; cardinal angles acute; fold and sulcus broad, low, smooth; flanks with numerous, simple, low, rounded to flat plications; surface with prominent nodose capillae; ctenophoridium supported by myophragm. *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian)*: eastern and midcontinent North America and western Canada.—FIG. 1131, 1a–f. **O. missouriensis*, Frasnian, Missouri, USA; a, microornament, $\times 5$; b–f, holotype, lateral, posterior, anterior, dorsal, and ventral views, $\times 1$ (Pitrat, 1975).

Platyrachella FENTON & FENTON, 1924, p. 158 [**Spirifera macbridei* CALVIN, 1883, p. 433; OD]. Medium size, ventribiconvex, transverse; ventral interarea high, flat, steeply apsacline or catacline; cardinal angles acute; fold and sulcus broad, low, smooth, or with low anterior plication in sulcus; flanks with numerous, simple plications; surface with fine capillae; dental plates short, straight,

divergent. *Upper Devonian (Frasnian)*: midcontinent North America.—FIG. 1130, 2a–d. **P. macbridei* (CALVIN), Iowa, USA; a–c, anterior, posterior, and dorsal views, $\times 1$; d, ventral interior, enlarged (Fenton & Fenton, 1924).

Subcuspidella MITTMAYER, 1965, p. 80 [**Spirifer subcuspidatus* SCHNUR, 1851, p. 10; OD] [=? *Tenuicostella* MITTMAYER & GEIB, 1967, p. 40 (type, *Spirifer subcuspidatus tenuicosta* SCUPIN, 1900, p. 223, pl. 1(24), 15a–c, OD)]. Medium size, transverse; ventral interarea high, flat, apsacline or catacline; cardinal angles acute; flanks with numerous rounded plications; fold and sulcus smooth, crossed by closely spaced, nodose growth lines; dental plates straight, divergent; ctenophoridium and short crural plates present. [Well-preserved specimens of *Subcuspidella subcuspidatus* and *Tenuicostella tenuicosta* are apparently rare. Revisionary work is required to ascertain the validity of *Tenuicostella*.] *Middle Devonian (Eifelian)*: western Europe.—FIG. 1131, 2a–c. **S. subcuspidatus*

(SCHNUR). Germany; posterior, anterior, and lateral views, $\times 1$ (Schnur, 1853 in 1853–1854).

Family CYRTOSPIRIFERIDAE

Termier & Termier, 1949

[*nom. transl.* BEZNOVA, 1958, p. 17, ex *Cyrtospiriferinae* TERMIER & TERMIER, 1949a, p. 99]

Flanks costate, nonfrilly; fold and sulcus finely costate. *Middle Devonian (upper Givetian)–Upper Devonian (upper Famennian)*.

Subfamily CYRTOSPIRIFERINAE

Termier & Termier, 1949

[*Cyrtospiriferinae* TERMIER & TERMIER, 1949a, p. 99] [= *Hunanospiriferinae* BEZNOVA, 1958, p. 17]

Wide interarea with acute cardinal angles. *Upper Devonian (Frasnian–upper Famennian)*.

Cyrtospirifer NALIVKIN in FREDERIKS, 1924, p. 312 [**Spirifer Verneuili* MURCHISON, 1840, p. 252; OD] [= *Hunanospirifer* TIEN, 1938, p. 113 [139] (type, *Spirifer (H.) wangi*, OD); *Grabauspirifer* GATINAUD, 1949, p. 413 (type, *Spirifer (Sinospirifer) archiaciformis* GRABAU, 1931b, p. 257, OD); *Eurytatospirifer* GATINAUD, 1949, p. 487 (type, *Spirifer disjunctus* SOWERBY in SEDGWICK & MURCHISON, 1840, p. 704, OD); *Deothossia* GATINAUD, 1949, p. 488 (type, *Spirifer (Sinospirifer) anossofioides* GRABAU, 1931b, p. 273, OD); *Lamarckispirifer* GATINAUD, 1949, p. 489 (type, *Spirifer (Sinospirifer) hayasakai* GRABAU, 1931b, p. 305, OD); *Subquadriangulispirifer* SARTENAER, 1982, p. 153 (type, *Spirifer Malaisi* GOSSELET, 1894, p. 47, OD)]. Medium to large, ventribiconvex, moderately transverse; cardinal angles acute, commonly auriculate; ventral interarea high, strongly curved, apsacline; fold and sulcus broad, well defined, not prominent; costae of fold and sulcus increasing by implantation; flanks with numerous simple, rounded costae; surface with capillae and fila; dental plates extrasinal to sulcus bounding; ctenophoridium on median ridge. *Upper Devonian (Frasnian–lower Famennian)*: cosmopolitan.—FIG. 1132, 1a–f. **C. verneuili* (MURCHISON), Frasnian, France; a–e, ventral, dorsal, anterior, posterior, and lateral views; f, ventral valve internal mold, $\times 1$ (new).

Austrospirifer GLENISTER, 1956, p. 58 [**A. variabilis* GLENISTER, 1956, p. 59; OD]. Small to medium size, biconvex, strongly transverse, with acute cardinal angles; ventral interarea low, orthocline to apsacline, with apical pseudodeltidium; fold and sulcus well defined, narrow, plicate; flanks with numerous simple, rounded plications and U-shaped interspaces; surface with inconspicuous growth

lines; dental plates short. *Upper Devonian (Famennian)*: Western Australia.—FIG. 1132, 4a–d. **A. variabilis*: holotype, dorsal, ventral, posterior, and anterior views, $\times 2$ (Glenister, 1956).

Geminisulcispirifer SARTENAER, 1982, p. 149 [**Spirifer bisinus* LE HON, 1870, p. 497; OD]. Medium to large size, biconvex; transverse, with acute cardinal angles; ventral interarea low, curved, apsacline, with pseudodeltidium; fold and sulcus well defined, costate; sulcus triangular, fold with anteriorly widening median furrow; flanks with numerous simple and bifurcating costae; surface with capillae interrupted by microfila, giving rise to small granules; dental plates intrasinal in type species. *Upper Devonian (Frasnian–Famennian)*: Europe, western North America.—FIG. 1132, 2a–e. **G. bisinus* (LE HON), Frasnian, France; lectotype, dorsal, ventral, anterior, posterior, and lateral views, $\times 1$ (Sartenaer, 1982).

Liraspirifer STAINBROOK, 1950, p. 380 [**L. tricostatus* STAINBROOK, 1950, p. 381; OD]. Small to medium size, biconvex, transverse, with acute cardinal angles; ventral interarea slightly curved, apsacline; fold and sulcus plicate, well defined, with fold low; flanks with numerous low, rounded costate plications and wide interspaces (or plications flattened and longitudinally grooved); dental plates straight, divergent, extrasinal, with short delthyrial plate; broad ctenophoridium on notothyrial platform. *Upper Devonian (Famennian)*: midcontinent North America.—FIG. 1133, 1a–e. **L. tricostatus*, Iowa, USA; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1.5$ (new).

Petshorospirifer FOTIEVA, 1985, p. 56 [**P. petshorensis*; OD]. Small to medium size, ventribiconvex, hemipyramidal; cardinal angles slightly acute; ventral interarea high, flat, catacline; flanks smooth or with faint plications; surface capillate to tuberculate; delthyrial plate short. [No satisfactory photographs are available.] *Upper Devonian (upper Famennian)*: northwestern Russia (Petshora region).

Regelia CRICKMAY, 1952b, p. 2 [**Cyrtospirifer glaucus* CRICKMAY, 1952a, p. 600; OD]. Medium size, ventribiconvex, strongly transverse and mucronate; ventral interarea low, curved, apsacline; fold and sulcus costate, with prominent plications bounding sulcus; flanks with numerous, simple costae; surface with fine capillae; long, extrasinal dental plates and umbonal thickening present. *Upper Devonian (Frasnian)*: western Canada.—FIG. 1132, 5a–c. **R. glaucus* (CRICKMAY), Alberta; two ventral valves and one dorsal valve, $\times 1$ (Crickmay, 1952a).

Sinospirifer GATINAUD, 1949, p. 413 (GRABAU, 1931b, p. 231) [**Spirifer (Sinospirifer) chinensis* GRABAU, 1923 in 1923–1924, p. 169; OD; *nom. imperf.*; = *Spirifer (Sinospirifer) sinensis* GRABAU, 1931b, p. 241]. Medium to large, biconvex; transverse, with acute or auriculate cardinal angles; ventral interarea curved, apsacline, with open delthyrium; fold and sulcus well defined, costate, costae increasing by

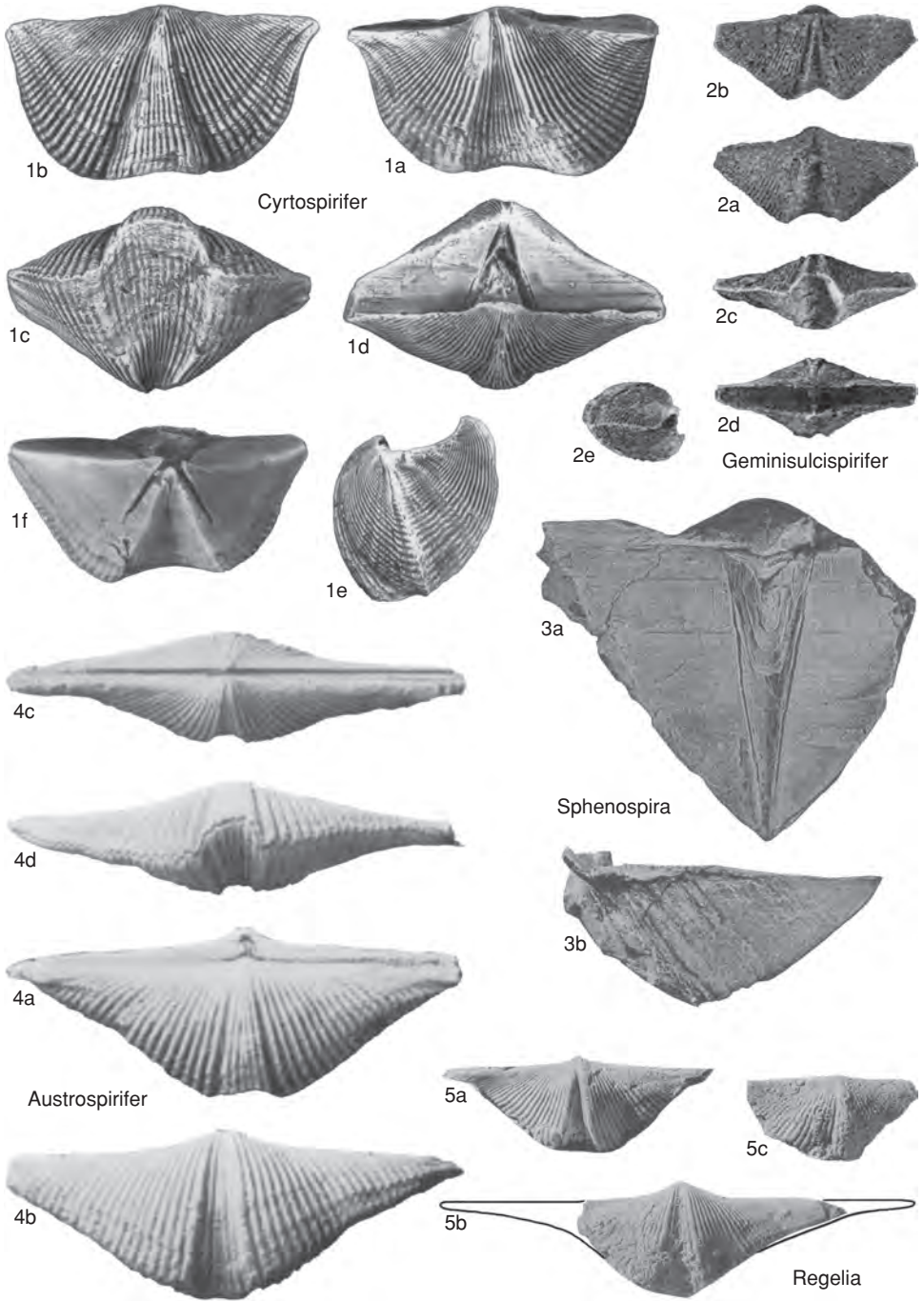


FIG. 1132. Cyrtospiriferidae (p. 1726–1729).

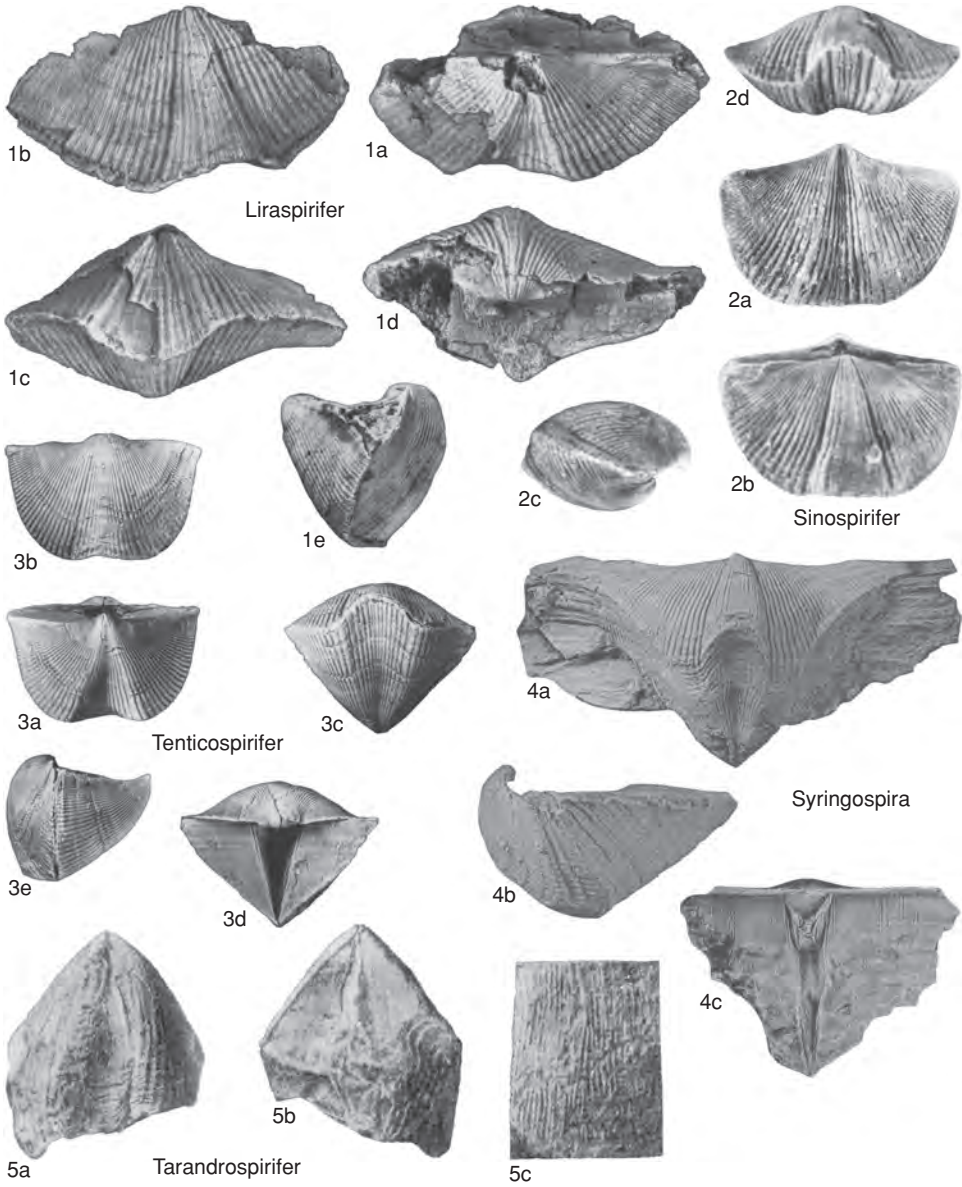


FIG. 1133. Cyrtospiriferidae (p. 1726–1729).

implantation; flanks with simple rounded costae; surface capillate; ventral interior with thickened umbonal region and myophragm; dorsal interior with strong, platelike crural bases but without crural plates. *Upper Devonian (Frasnian–Famennian):* China.—FIG. 1133,2a–d. **S. sinensis* (GRABAU); ventral, dorsal, side, and anterior views, ×1 (new).

Sphenospira COOPER, 1954b, p. 330 [**Spirifera alta* HALL, 1867b, p. 248; OD]. Medium size, strongly ventribiconvex, transverse, with semiconical ventral valve; ventral interarea high, flat, catacline, sometimes with frills; delthyrium occluded by long delthyrial plate and stegidium; cardinal angles acute; fold and sulcus rounded, relatively narrow;

- surface tuberculate; dental plates long, divergent; ctenophoridium bilobed. *Upper Devonian (Famennian)*: eastern North America.—FIG. 1132,3a–b. **S. alta* (HALL), Ohio; posterior and lateral views, $\times 1$ (Cooper, 1954b).
- Syringospira** KINDLE, 1909, p. 28 [**S. prima* KINDLE, 1909, p. 29; OD]. Medium size, strongly ventribiconvex, transverse, with semiconical ventral valve; ventral interarea high, flat, catacline; delthyrium occluded by long delthyrial plate and stegidium; cardinal angles acute; fold and sulcus rounded, relatively narrow; surface tuberculate; dental plates short; umbonal chambers with blisterlike plates; ctenophoridium bilobed. *Upper Devonian (Famennian)*: western North America.—FIG. 1133,4a–c. **S. prima*, upper Famennian, New Mexico, USA; anterior, lateral, and posterior views, $\times 1$ (Cooper, 1954b).
- Tarandrospirifer** SIMAKOV in AFANAS'eva & SIMAKOV, 1970, p. 88 [**Cyrtospirifer tarandrus* NALIVKIN in MARKOVSKI, 1960, p. 384; OD]. Small to medium size, ventribiconvex, hemipyramidal; cardinal angles slightly acute; ventral interarea high, flat, catacline; fold and sulcus smooth or with 1 or 2 pairs of costae in sulcus; flanks with simple, rounded plications; surface capillate; delthyrial plate short. *Upper Devonian (upper Famennian)*: Omolonsk massif, Kolyma region, Pai Khoi, Arctic.—FIG. 1133,5a–c. **T. tarandrus* (NALIVKIN), Arctic Siberia; a–b, holotype, ventral valve, ventral and posterior views, $\times 1$; c, microornament, $\times 6$ (Markovski, 1960).
- Tenticospirifer** TIEN, 1938, p. 113 [139] [**Spirifer tenticulum* DE VERNEUIL, 1845, p. 159; OD] [= *Conispirifer* LIASHENKO, 1985, p. 16 (type, *C. rotundus*, OD)]. Small to medium size, ventribiconvex, hemipyramidal; cardinal angles slightly acute; ventral interarea high, flat, catacline; fold, sulcus, and flanks with simple, rounded plications; surface capillate; ctenophoridium elevated on median ridge. *Upper Devonian (Frasnian)*: cosmopolitan.—FIG. 1133,3a–e. *T. tenticulum* (DE VERNEUIL), Russian Platform; ventral, dorsal, anterior, posterior, and lateral views, $\times 1$ (new).
- Subfamily CYRTIOPSINAE**
Ivanova, 1972
- [Cyrtiopsinae IVANOVA, 1972, p. 33] [=?Uchtospiriferidae LIASHENKO, 1973, p. 87]
- Interarea narrow, with rounded cardinal angles. *Middle Devonian (upper Givetian)–Upper Devonian (Famennian)*.
- Cyrtiopsis** GRABAU, 1923 in 1923–1924, p. 194 [**C. davidsoni* GRABAU, 1923 in 1923–1924, p. 195; SD GRABAU, 1931b, p. 435] [= *Grabauicyrtiopsis* GATINAUD, 1949, p. 490 (type, *Cyrtiopsis graciosa* GRABAU, 1923 in 1923–1924, p. 195, OD); *Sino-cyrtiopsis* GATINAUD, 1949, p. 491 (type, *Cyrtiopsis transversa* GRABAU, 1924 in 1923–1924, p. 466, OD)]. Small to large, biconvex to ventribiconvex, equidimensional or elongate, with obtuse cardinal angles; deltidium present; ventral interarea high, slightly curved, apsacline; fold and sulcus prominent, costate; flanks with numerous small, simple plications; surface with radial or subradial capillae, becoming tuberculate; dental plates intrasinal, subparallel, with rudimentary delthyrial plate; ctenophoridium elevated. *Upper Devonian (lower Famennian)*: southern China.—FIG. 1134,3a–e. **C. davidsoni*; holotype, dorsal, ventral, lateral, posterior, and anterior views, $\times 1.5$ (Ma & Day, 1999).
- Acutella** LIASHENKO, 1973, p. 119 [**Uchtospirifer angulosus* LIASHENKO, 1959, p. 128; OD]. Medium to large, biconvex, equidimensional to transverse, with obtuse cardinal angles; ventral interarea curved, apsacline; ventral beak prominent; fold and sulcus prominent, fold strongly arched or acuminate, costate posteriorly, costae becoming obsolescent anteriorly; flanks with numerous, low, rounded costae and narrow interspaces; surface with radial or subradial capillae and fila; dental plates extrasinal or bordering. *Upper Devonian (Frasnian)*: Russian Platform, Urals.—FIG. 1135,1a–e. **A. angulosa* (LIASHENKO), Timan; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$ (Liashenko, 1973).
- Dichospirifer** BRICE, 1971, p. 192 [**D. thylakistoides* BRICE, 1971, p. 194; OD]. Medium size, biconvex, equidimensional; cardinal angles obtuse, less than maximum width; ventral interarea low, strongly curved, apsacline; fold and sulcus indistinct; fold, sulcus, and flanks with bifurcating costae; microornament of growth fila and faint capillae; dental plates extrasinal, with rudimentary delthyrial plate; dorsal interior with short crural plates. *Upper Devonian (Famennian)*: Afghanistan, western North America.—FIG. 1136,3a–f. **D. thylakistoides*, upper Famennian, Afghanistan; a–e, ventral, dorsal, posterior, anterior, and side views, $\times 1$; f, exterior showing fine ornament, $\times 12$ (Brice, 1971).
- Dmitria** SIDIACHENKO, 1961, p. 80 [**Spirifer (Cyrtospirifer) Romanowskii* NALIVKIN, 1930, p. 127; OD]. Medium to large, strongly biconvex; equidimensional or elongate, with obtuse cardinal angles; ventral interarea short, strongly incurved; fold and sulcus poorly differentiated; entire surface with numerous fine costellae and capillae; dental plates long, thin, intrasinal; ctenophoridium elevated on median ridge. *Upper Devonian (Famennian)*: Tian Shan, Kazakhstan, western Canada.—FIG. 1134,2a–d. **D. romanowskii* (NALIVKIN), Tian Shan; dorsal, ventral, anterior, and lateral views, $\times 0.7$ (Nalivkin, 1930).
- Eodmitria** BRICE, 1982a, p. 575 [**E. supradisjuncta boloniensis* BRICE, 1982a, p. 578; OD]. Medium to large, ventribiconvex to lenticular, transverse with obtuse to acute cardinal angles; ventral interarea low, narrow, apsacline; fold low, sulcus poorly defined, costae of fold-sulcus increasing by implantation; flanks with simple rounded costae;

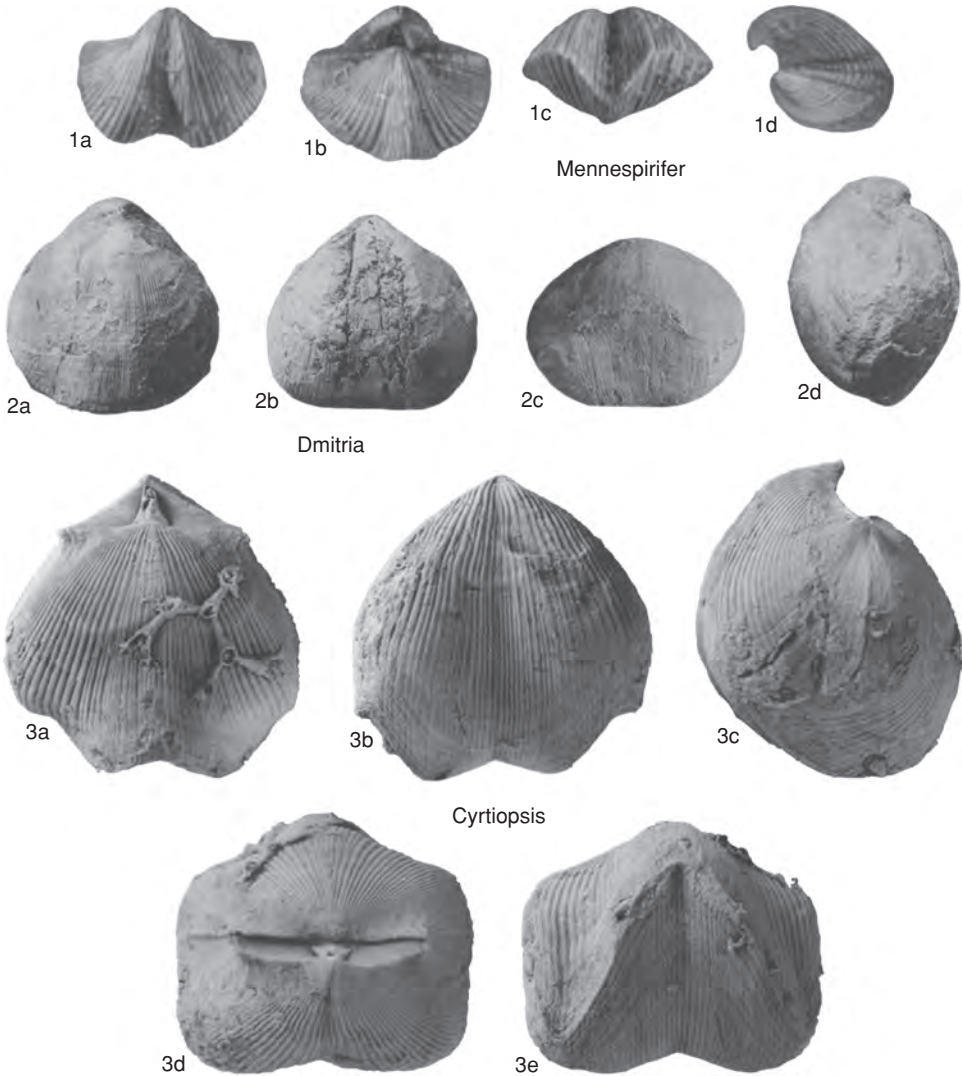


FIG. 1134. Cyrtospiriferidae (p. 1729–1731).

surface papillose; dental plates extrasinal; ctenophoridium elevated. *Upper Devonian (lower Frasnian–middle Frasnian)*: western Europe.—FIG. 1135, 2a–d. **E. supradijuncta boloniensis*, lower Frasnian, France; holotype, ventral, dorsal, posterior, and anterior views, $\times 1$ (Brice, 1982a).

Mennespirifer LIASHENKO, 1973, p. 101 [**Uchtospirifer menneri* LIASHENKO, 1959, p. 129] [= *Komispirifer* LIASHENKO, 1973, p. 105 (type, *Uchtospirifer*

formosus LIASHENKO, 1960, p. 25, OD)]. Medium size, biconvex, transverse, with obtuse cardinal angles; ventral interarea curved, aplanaline; fold and sulcus costate; flanks with low rounded costae and narrow interspaces; surface with radial or subradial capillae, becoming tuberculate; dental plates extrasinal. *Middle Devonian (upper Givetian)–Upper Devonian (Frasnian)*: Russian Platform, Timan Range, Urals.—FIG. 1134, 1a–d. **M. menneri*

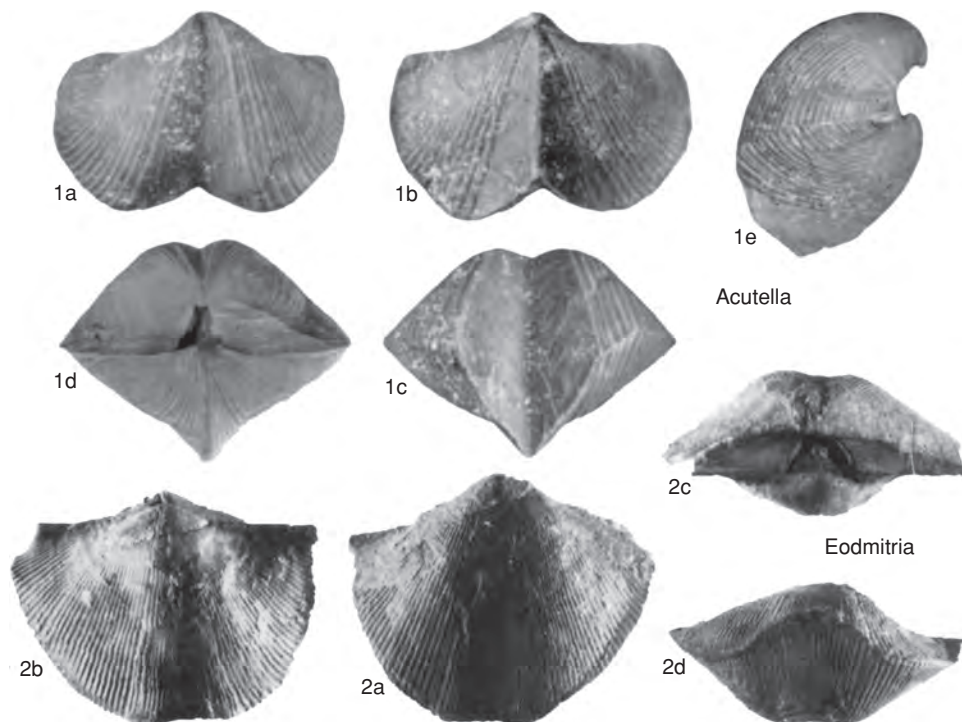


FIG. 1135. Cyrtospiriferidae (p. 1729–1730).

(LIASHENKO), lower Frasnian, Timan; holotype, ventral, dorsal, anterior, and lateral views, $\times 1$ (Liashenko, 1973).

Platyspirifer GRABAU, 1931b, p. 355 [**Schizophoria paronai* MARTELLI, 1902, p. 365; OD]. Small to medium size, biconvex, transversely oval or equidimensional, with rounded, obtuse cardinal angles; ventral interarea low, curved, apsacline; fold low, sulcus poorly defined, costae of fold-sulcus increasing by implantation; flanks with simple rounded costae; surface capillate; dental plates thickened; ctenophoridium elevated. *Upper Devonian (Famennian)*: Afghanistan, China.—FIG. 1136, 1a–e. **P. paronai* (MARTELLI), China; ventral, dorsal, side, posterior, and anterior views, $\times 1$ (new).

Uchtospirifer LIASHENKO, 1957, p. 885 [**U. naliivkini* LIASHENKO, 1957, p. 886; OD] [= *Timanospirifer* LIASHENKO, 1973, p. 92 (type, *Uchtospirifer*

timanicus LIASHENKO, 1958, p. 147, OD); *Nordispirifer* LIASHENKO, 1973, p. 104 (type, *N. celeber*, OD); *Clivospirifer* LIASHENKO, 1973, p. 108 (type, *Uchtospirifer clivosus* LIASHENKO, 1969b, p. 53, OD)]. Medium to large, biconvex, equidimensional to transverse, with obtuse cardinal angles; ventral interarea curved, apsacline; ventral beak commonly prominent; fold and sulcus prominent, costate; flanks with numerous, fine, low, rounded costae and narrow interspaces; surface with radial or subradial capillae, becoming tuberculate; dental plates intrasinal, delthyrial plate short. *Middle Devonian (upper Givetian)–Upper Devonian (Famennian)*: Russian Platform, Timan Range, Urals, western North America.—FIG. 1136, 2a–e. **U. naliivkini*, Frasnian, Timan; ventral, dorsal, anterior, posterior, and lateral views, $\times 1$ (Liashenko, 1973).

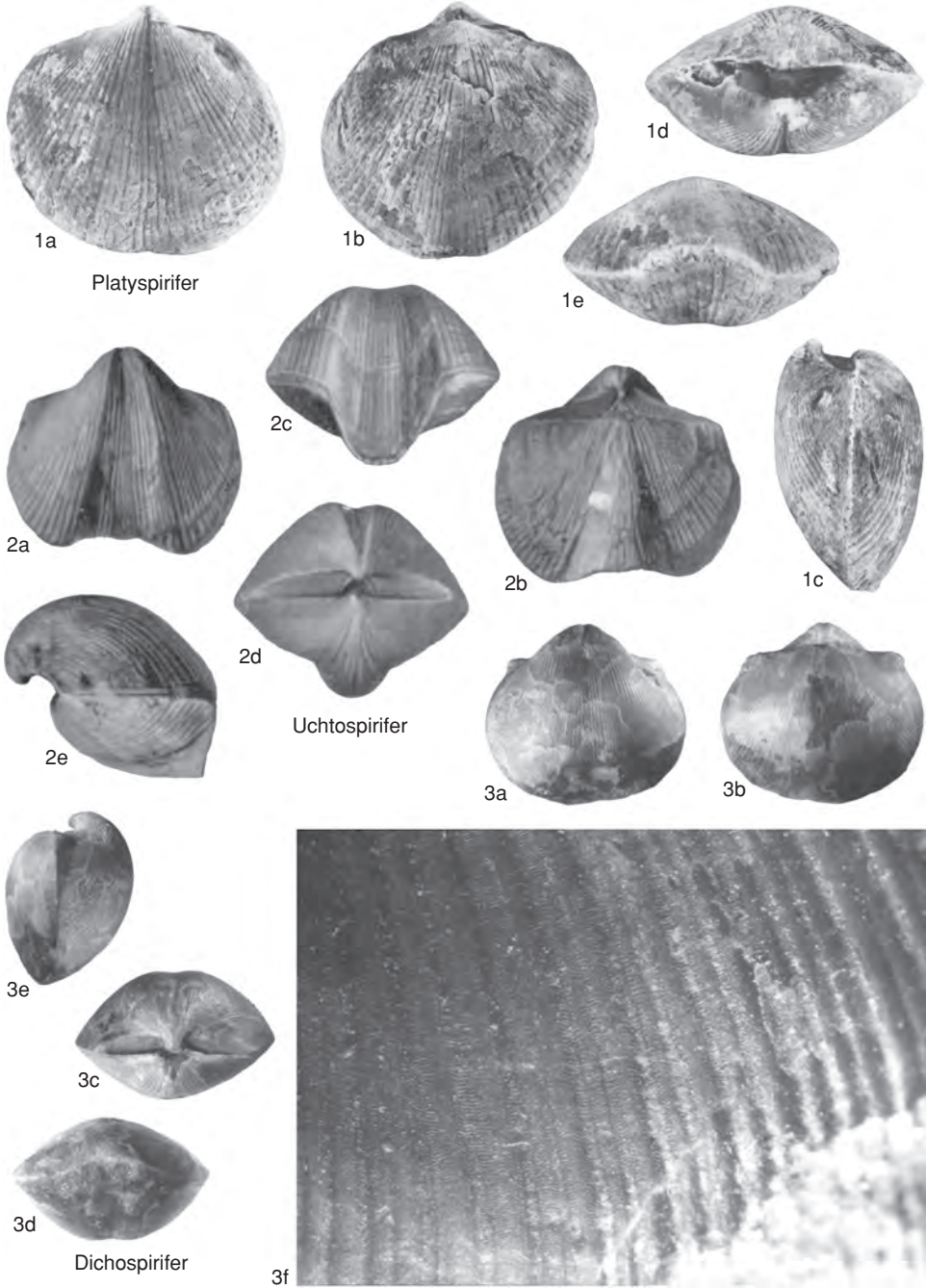


FIG. 1136. Cyrtospiriferidae (p. 1729–1731).

AMBOCOELIOIDEA

J. G. JOHNSON,¹ J. L. CARTER,² and HOU HONG-FEI³

[¹deceased, formerly of Oregon State University; ²retired from Carnegie Museum of Natural History; and ³China University of Geosciences]

Superfamily AMBOCOELIOIDEA George, 1931

[*nom. transl.* JOHNSON & CARTER in CARTER & others, 1994, p. 336, ex Ambocoeliinae GEORGE, 1931, p. 42]

Commonly small, lacking well-developed fold and sulcus; cardinal process commonly simple, knoblike; outer hinge plates broad, well developed; cruralium variably developed. *Silurian (Wenlock)–Lower Triassic, ?Middle Triassic–?Upper Triassic.*

Family AMBOCOELIIDAE George, 1931

[*nom. transl.* IVANOVA, 1959, p. 56, ex Ambocoeliinae GEORGE, 1931, p. 42]

Ventribiconvex smooth shells, rarely pauciplicate. *Silurian (Wenlock)–Lower Triassic, ?Middle Triassic–?Upper Triassic.*

Subfamily AMBOCOELIINAE George, 1931

[Ambocoeliinae GEORGE, 1931, p. 42]

[Materials for this subfamily prepared by J. G. Johnson, J. L. Carter, and Hou Hong-fei]

Crural plates vestigial or lacking; commonly with fine concentric growth lamellae; dental plates lacking. *Silurian (Wenlock)–Lower Triassic, ?Middle Triassic–?Upper Triassic.*

Ambocoelia HALL, 1860, p. 71 [**Orthis umbonata* CONRAD, 1842, p. 264; OD]. Planoconvex to concavoconvex; megathyrid; ventral interarea low, with beak incurved; commissure uniplicate or straight; with faint growth lines and weak to obscure capillae. *Devonian*: cosmopolitan.—FIG. 1137, 1a–c. **A. umbonata* (CONRAD); ventral, dorsal, lateral views, $\times 1.5$; d–e, dorsal and ventral interiors, $\times 3$ (Pitrat, 1965).

Attenuatella STEHLI, 1954, p. 343 [**A. texana*; OD]. Ventral valve strongly inflated, longitudinally elongated, with strongly incurved beak and shallow sulcus; dorsal valve nearly flat, nonsulcate; ventral interior with diductor scars raised on long, low narrow ridge with low lateral flanges; dorsal interior with diverging crural bases nearly touching poste-

rior of valve; crura very long, rodlike; spiralia absent; microornament as in *Crurithyris*. *Permian (Artinskian–Lopingian)*: USA (Texas), Russia, Mexico, Australia, New Zealand.—FIG. 1137, 4a–d. **A. texana*, Artinskian, Texas; ventral, posterior, lateral, and interior views of ventral valve, $\times 2$ (Cooper & Grant, 1976a).—FIG. 1137, 4e–f: *A. attenuata* (CLOUD), Wordian, Mexico; internal molds of both valves, $\times 3$ (Cooper & Grant, 1976a).

Aviformia XIAN, 1988, p. 227 [**A. grandia* XIAN, 1988, p. 228; OD]. Large, ventribiconvex, transversely triangular, megathyrid; fold and sulcus distinct, narrow; growth lines with capillae; umbonal callus present; hinge plates widely discrete; cardinal process not observed. *Lower Devonian (Emsian)–Middle Devonian (Eifelian)*: southern China.—FIG. 1137, 3a–b. **A. grandia*, Eifelian; ventral, dorsal views, $\times 1$ (Xian, 1988).

Biconvexiella WATERHOUSE, 1983b, p. 154 [**Attenuatella convexa* ARMSTRONG, 1968, p. 788; OD]. Ventral valve moderately inflated; dorsal valve evenly convex; ventral umbo moderately incurved, not obscuring delthyrium; ventral adductor ridge moderately developed, anterior median ridge short; crura long, rodlike, terminating in posteriorly reflexed S-shaped extensions; otherwise similar to *Attenuatella*. *Permian*: Australia.—FIG. 1138, 1a–e. **B. convexa* (ARMSTRONG); a, holotype, dorsal valve; b–c, ventral and lateral views of ventral valve; d–e, internal molds of both valves, $\times 4$ (Armstrong, 1968).

Bisinocoelia HAVLIČEK, 1953, p. 7 [**B. bisinuata* HAVLIČEK, 1953, p. 8; OD]. Ventribiconvex with prominent ventral umbo; megathyrid; valves bisulcate; notothyrial cavity with pair of ridges that join low median septum; exterior ornament weak. *Lower Devonian–Middle Devonian*: central Bohemia.—FIG. 1137, 5a–b. **B. bisinuata*, Pragian; ventral and anterior views of dorsal interior, $\times 7.8$ (new).

Cruricella GRANT, 1976, p. 187 [**C. couria*; OD]. Sulci lacking in either valve; cardinal extremities subangular; cardinal process knoblike, finely striate; microornament absent or of fine pustules, not spinose; otherwise similar to *Crurithyris*. *Carboniferous (Pennsylvanian)–Permian (Lopingian)*, ?*Triassic*: cosmopolitan.—FIG. 1137, 2a–g. **C. couria*, Lopingian, Thailand; a–e, holotype, ventral, dorsal, lateral, posterior, and anterior views; f–g, dorsal and ventral interiors, $\times 6$ (Grant, 1976).

Crurithyris GEORGE, 1931, p. 42 [**Spirifer urei* FLEMING, 1828, p. 376]. Ventribiconvex; both valves with weak sulci; anterior commissure emarginate; microornament of fine spinules of 2 distinct sizes, roughly concentrically arranged; cardinal process knoblike; dorsal interior with adductor scars in

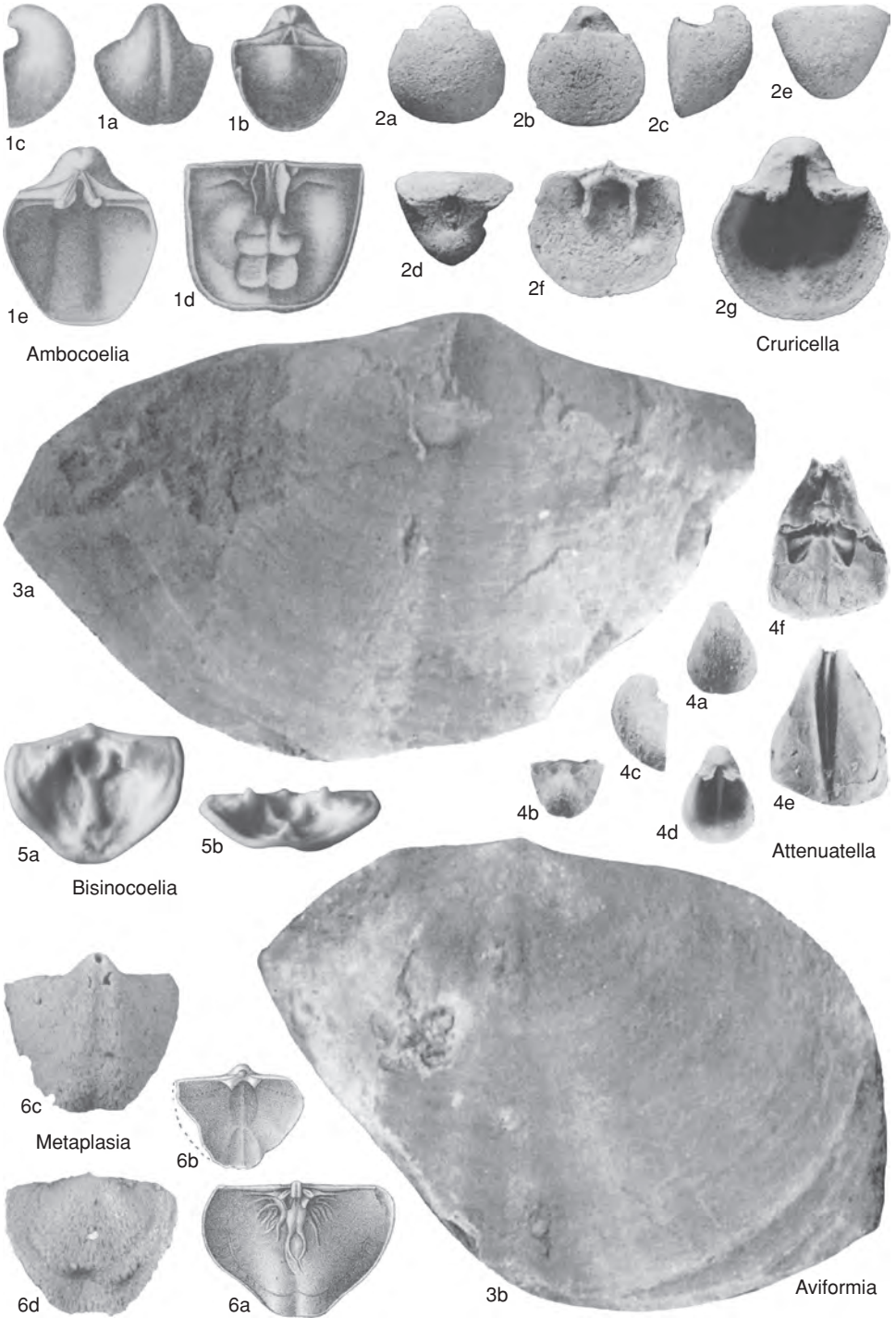


FIG. 1137. Ambocoeliidae (p. 1733–1736).

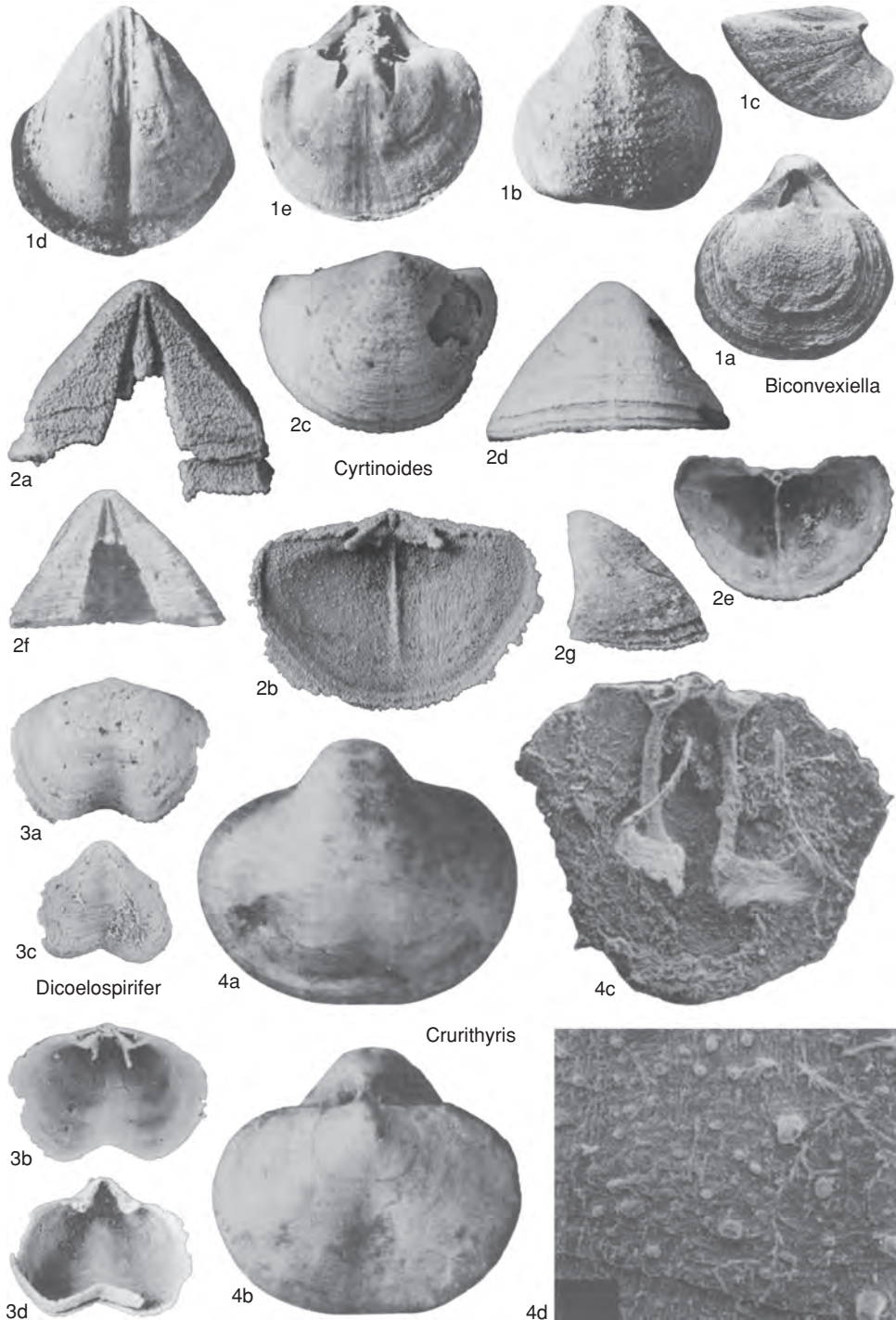


FIG. 1138. Ambocoeliidae (p. 1733–1736).

- normal position; otherwise similar to *Ambocoelia*. *Upper Devonian–Permian*: cosmopolitan.—FIG. 1138, 4a–d. **C. urei* (FLEMING), Mississippian, Carboniferous, Great Britain; a–b, lectotype, ventral and dorsal views, $\times 9$ (George, 1931); c, dorsal interior, $\times 20$; d, microornament, $\times 75$ (Brunton, 1984).
- Cyrtinoides** IUDINA & RZHONSNIITSKAIA, 1985, p. 82 [**C. ajica*; OD] [= *Mucroclipeus* GOLDMAN & MITCHELL, 1990, p. 85 (type, *M. eliei* GOLDMAN & MITCHELL, 1990, p. 88, OD)]. Ventral median septum and tichorhinum present; tichorhinum lacking dividing partition. [No satisfactory illustration of the type is available.] *Middle Devonian*: North America, Russian Platform, southern Urals.—FIG. 1138, 2a–g. *C. septata* (JOHNSON), Eifelian, Nevada, USA; a, ventral posterior view; b, dorsal interior view, $\times 6$ (Johnson, 1971); c–g, ventral, anterior, interior, posterior, and side views, $\times 4$ (Johnson, Klapper, & Trojan, 1980).
- Dicoelospirifer** ZHANG Ning, 1989, p. 18 [**D. dicoelospirifer*; OD]. Ventribiconvex, interareas lacking; submegathyrid; valves bisulcate; concentric growth lines. *Silurian* (*Wenlock*): Arctic Islands, Canada.—FIG. 1138, 3a–d. **D. dicoelospirifer*; a–b, holotype, external and interior views of dorsal valve, $\times 8$; c, external view of ventral valve, $\times 6$; d, interior view of ventral valve, $\times 8$ (Zhang, 1989).
- Echinocoelia** COOPER & WILLIAMS, 1935, p. 844 [**E. ambocoelioides*; OD] [= *Pyramina* LIASHENKO, 1969a, p. 23 (type, *P. oskolensis* LIASHENKO, 1969a, p. 24, OD)]. Ventribiconvex with high apsacline ventral interarea; delthyrium closed by apical plate; megathyrid; with concentric growth lines and spines. [No satisfactory illustration of the type is available.] *Middle Devonian*: North America, Russian Platform, China (Guangxi), northern Africa.—FIG. 1139, 1a–f. *E. denayensis* JOHNSON, Eifelian, Nevada, USA; a–d, anterior, posterior, ventral, and side views; e–f, exterior and interior of dorsal valve, $\times 3$ (Johnson, 1966a).
- Eoplicoplasia** JOHNSON & LENZ, 1992, p. 530 [**Plicoplasia acutiplicata* LENZ, 1972, p. 102; OD]. Ventribiconvex; megathyrid; cardinal extremities slightly mucronate; ventral interarea high, apsacline to catacline, curved to flat; fold and sulcus moderately expressed; valves strongly plicate, with concentric growth lines and weak to obscure capillae; commissure uniplicate to parasulcate; short rudimentary dental plates. [*Eoplicoplasia* is the oldest ambocoeliid genus and presents analogies with the eospiriferines from which it is probably derived, but it lacks crural plates, hence its assignment to the Ambocoeliinae.] *Silurian* (*upper Wenlock*)–*Lower Devonian* (*Pragian*): North America, Australia.—FIG. 1139, 2a–f. **E. acutiplicata* (LENZ), upper Lochkovian, Yukon Territory; a–c, ventral, dorsal, and dorsal interior views, $\times 3$; d–f, posterior, anterior, and side views, $\times 2.8$ (Lenz, 1977).
- Guangxiispirifer** XIAN Si-yuan, 1983a, p. 12 [**G. subaequatus* XIAN Si-yuan, 1983a, p. 13; OD]. Large, ventribiconvex, submegathyrid; ventral interarea high, curved, apsacline, with deltidial plates; dorsal interarea low, flat, anacline; fold and sulcus lacking; surface with concentric growth lines and capillae; strong dental flanges; inner hinge plates united into triangular platform, with prominent cardinal process. *Middle Devonian* (*Eifelian–Givetian*): western Europe, southern China.—FIG. 1139, 3a–d. **G. subaequatus*, Givetian, southern China; a–c, ventral, dorsal, and side views, $\times 1$ (new); d, interior of dorsal valve, $\times 1$ (Xian, 1983a).
- Metaplasia** HALL & CLARKE, 1893, p. 56 [**Spirifer pyxidatus* HALL, 1859 in 1859–1861, p. 428; OD]. Ventribiconvex; submegathyrid; ventral interarea low, with beak incurved; valves smooth, lacking spines; commissure intraplicate. *Lower Devonian*: North America.—FIG. 1137, 6a–b. **M. pyxidata* (HALL), Pragian, Ontario, Canada; dorsal and ventral interiors, $\times 1$ (Hall & Clarke, 1893).—FIG. 1137, 6c–d. *M. paucicostata* (SCHUCHERT), Emsian, Nevada, USA; ventral and dorsal exteriors, $\times 5$ (Johnson, 1970).
- Orbicoelia** WATERHOUSE & PIYASIN, 1970, p. 144 [**O. fraturculus*; OD]. Unequally biconvex; cardinal extremities well rounded; fold and sulcus absent; ventral interior lacking plates or ridges; cardinal process composed of 2 low lobes in juveniles, becoming low platform in adults; microornament of long, very fine spinules; otherwise similar to *Crurithyris*. *Permian* (*Roadian*): Thailand.—FIG. 1140, 5a–e. **O. fraturculus*; a–c, holotype, ventral, dorsal, and lateral views; d–e, exterior and internal views of ventral valve, $\times 3$ (Waterhouse & Piyasin, 1970).
- Paracrurithyris** LIAO, 1981, p. 54 [85] [**Crurithyris pygmaea* LIAO, 1980, p. 264; OD]. Dorsal valve moderately to deeply concave; dorsal interior with small, wedge-shaped cardinal process, thick socket ridges and crural bases; microornament poorly known; otherwise similar to *Ambocoelia*. *Permian* (*Lopingian*)–*Lower Triassic*: China.—FIG. 1140, 3a–d. **P. pygmaea* (LIAO); a–b, dorsal exterior and mold of dorsal interior, $\times 4$; c–d, two molds of ventral interiors, $\times 4$ (new).
- Plicoplasia** BOUCOT, 1959a, p. 19 [**P. cooperi* BOUCOT, 1959a, p. 20; OD]. Ventribiconvex; megathyrid; ventral interarea low, with beak incurved; valves plicate, with weak to obscure capillae; commissure parasulcate. *Lower Devonian* (*Pragian*): North America, South America, South Africa.—FIG. 1140, 4a–f. **P. cooperi*, New York, USA; a–d, holotype, ventral, dorsal, anterior, and lateral views; e–f, dorsal and ventral interiors, $\times 3$ (Boucot, 1959a).
- Spinoplasia** BOUCOT, 1959a, p. 18 [**S. gaspensis*; OD]. Ventribiconvex; submegathyrid; ventral interarea low, with beak incurved; valves smooth, bearing fine spines; commissure intraplicate. *Lower Devonian*: North America.—FIG. 1140, 1a–c. **S. gaspensis*, Lochkovian, Quebec; a–b, dorsal and ventral internal molds; c, microornament, $\times 10$ (Boucot, 1959a).
- Swaicoelia** HAMADA, 1968a, p. 6 [**S. rotunda*; OD]. Ventribiconvex; submegathyrid; ventral interarea low, with beak incurved; valves smooth, bearing

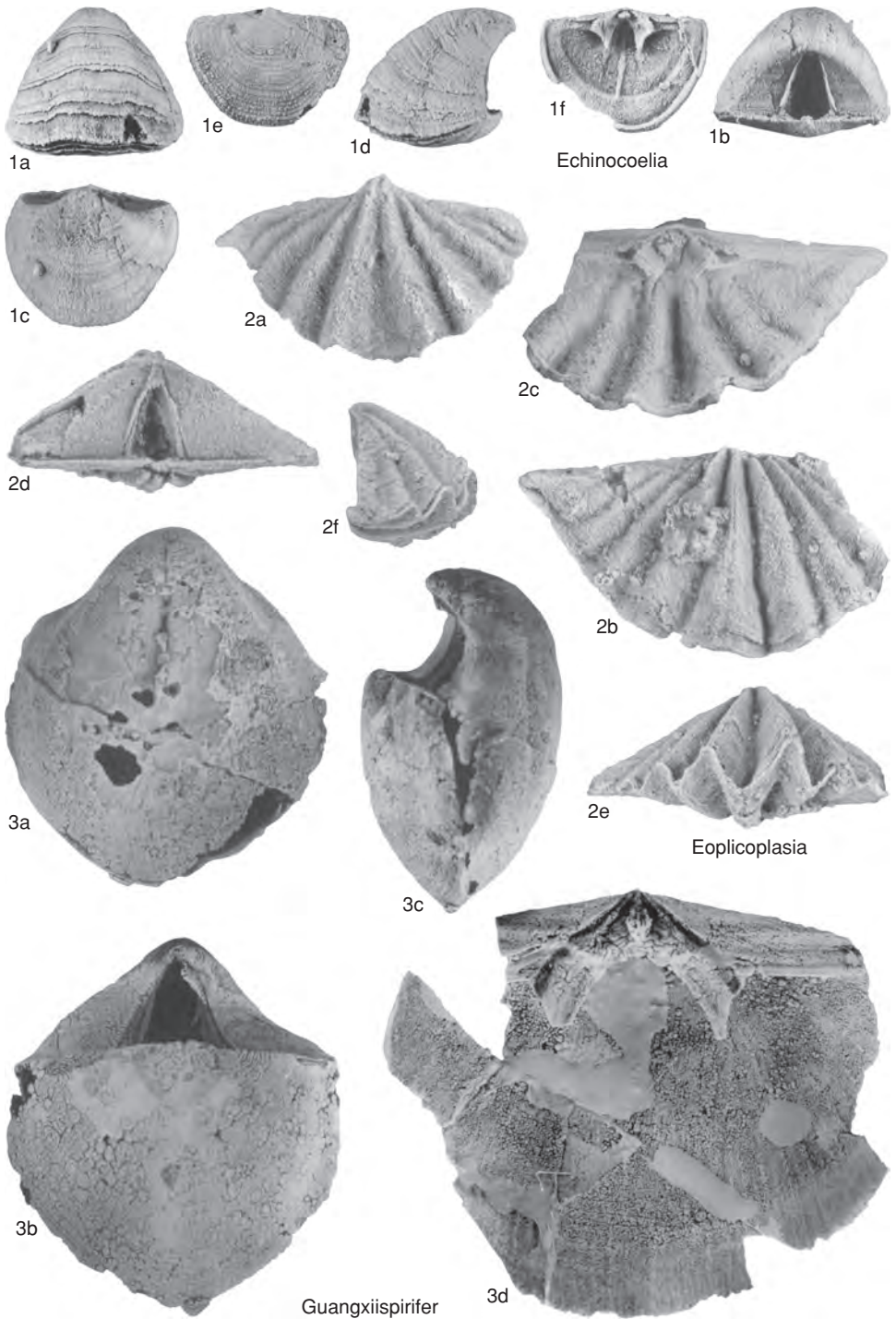


FIG. 1139. Ambocoeliidae (p. 1736).

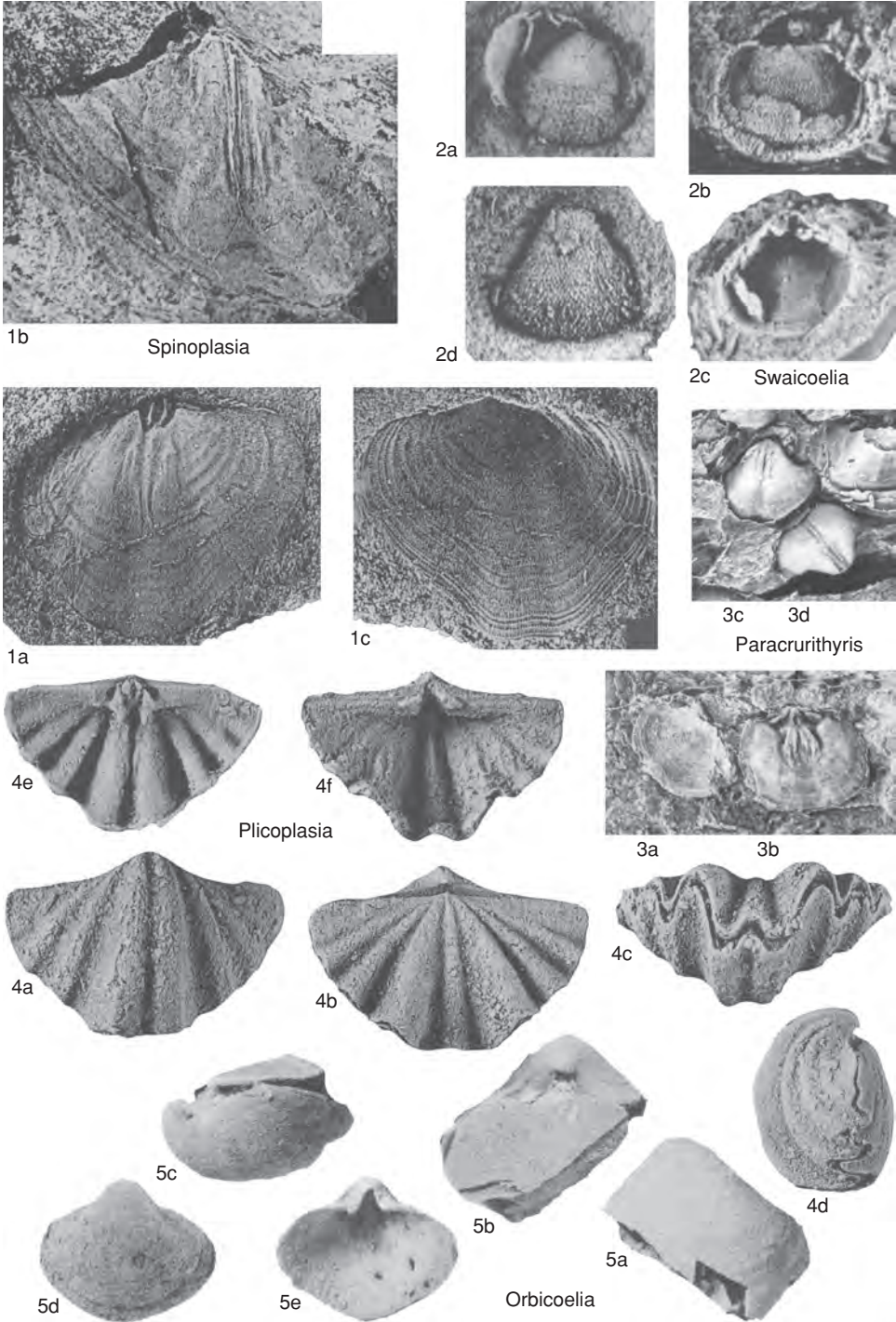


FIG. 1140. Ambocoeliidae (p. 1736–1739).

fine, erect, uniform, randomly distributed spines. ?*Upper Devonian, Carboniferous* (?*Mississippian*): northern Thailand.—FIG. 1140,2a–d. **S. rotunda*; a, holotype, dorsal interior; b–d, dorsal exterior, ventral interior, ventral exterior, $\times 5$ (Hamada, 1968a).

Subfamily RHYNCHOSPIRIFERINAE

Paulus, 1957

[Rhynchospiriferinae PAULUS, 1957, p. 51] [=Imeniinae DÜRKOOP, 1970, p. 195]

[Materials for this subfamily prepared by
J. G. Johnson & Hou Hong-fei]

Crural plates well developed, either discrete or joined to form a cruralium; commonly with fine capillae; dental plates variably present. *Lower Devonian* (*Emsian*)–*Upper Devonian* (*Frasnian*).

Rhynchospirifer PAULUS, 1957, p. 51 [**R. halleri* PAULUS, 1957, p. 52; OD] [=*Biarella* MARKOVSKI, 1988, p. 82 (type, *Orthis hians* VON BUCH, 1837, p. 64, OD)]. Strongly ventribiconvex; submegathyrid, rarely megathyrid; ventral interarea high, strongly incurved; commissure straight; capillate; dental plates thin, subparallel, closely spaced; cruralium triangular to subquadrate in outline, not anteriorly emarginate, supported by median septum. *Middle Devonian*: Europe, Asia.—FIG. 1141,5a–f. **R. halleri*, Eifelian, Germany; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 2$; f, dorsal interior, $\times 3.3$ (Paulus, 1957).

Amboglossa WANG & ZHU, 1979, p. 59 [94] [**Ambothyris transversa* WANG & others, 1974, p. 242; OD]. Strongly ventribiconvex; submegathyrid, rarely megathyrid; ventral interarea high, flat to incurved; valves bisulcate; dental plates lacking; outer hinge plates form cruralium supported by median septum. *Lower Devonian* (*Emsian*)–*Middle Devonian* (*Eifelian*): Russian Platform, Urals, Timan, China.—FIG. 1141,1a–c. **A. transversa* (WANG & others), Eifelian, China; a–b, exterior and interior of ventral valve, $\times 2.5$; c, interior of dorsal valve, $\times 6$ (new).

Ambothyris GEORGE, 1931, p. 42 [**Spirifera infima* WHIDBORNE, 1893, p. 108; OD]. Ventribiconvex; submegathyrid; ventral interarea high, moderately incurved; commissure straight or slightly sulcate; surface capillate; dental plates lacking; crural plates short, discrete, anteriorly convergent. *Middle Devonian* (*Givetian*)–*Upper Devonian* (*Frasnian*): western Europe.—FIG. 1141,2a–c. **A. infima* (WHIDBORNE), Givetian, Belgium; dorsal, ventral, and lateral views, $\times 4$ (Vandercammen, 1956).

Changtangella XIAN Si-yuan, 1983a, p. 9 [**C. bisepta* XIAN, 1983a, p. 11; OD]. Strongly ventribiconvex; submegathyrid, rarely megathyrid; ventral interarea high, strongly incurved; commissure straight; valves smooth, with variably developed capillae; dental

plates converge with median septum to form spondylium; cruralium supported by median septum. *Middle Devonian* (*Givetian*): southern China.—FIG. 1141,4a–d. **C. bisepta*; ventral, dorsal, lateral, and posterior views, $\times 1$ (new).

Choperella LIASHENKO, 1969a, p. 22 [**C. ilmenica* LIASHENKO, 1969a, p. 23; OD]. Strongly ventribiconvex; megathyrid, variably alate; ventral interarea flat, catacline; valves bisulcate; with concentric growth lines and variably developed fine capillae; dental plates lacking; crural plates short, discrete. *Middle Devonian* (*Eifelian*)–*Upper Devonian* (*Frasnian*): western North America, Russian platform.—FIG. 1142,3a–e. **C. ilmenica*, Eifelian, Russian Platform; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 3$ (Liashenko, 1969a).

Crurispina GOLDMAN & MITCHELL, 1990, p. 95 [**Ambocoelia spinosa* CLARKE, 1894, p. 177; OD]. Planoconvex to strongly ventribiconvex; submegathyrid; ventral interarea low, incurved; commissure uniplicate; spines randomly distributed; dental plates lacking; crural plates short, discrete. *Middle Devonian*: eastern North America.—FIG. 1142,1a–e. **C. spinosa* (CLARKE), Givetian, New York, USA; dorsal, ventral, lateral, posterior, and anterior views, $\times 5$ (Goldman & Mitchell, 1990).

Diazoma DÜRKOOP, 1970, p. 195 [**Emanuella volhynica* KELUS, 1939, p. 3; OD] [=*Kelusia* MAMEDOV, 1978, p. 200, obj.]. Strongly ventribiconvex; submegathyrid; ventral interarea low, strongly incurved; commissure slightly uniplicate; secondary shell thick; concentric growth lamellae with fine, radially arranged spines; dental plates lacking; cruralium supported by median septum. *Middle Devonian* (*Eifelian*)–*Upper Devonian* (*Frasnian*): Europe, Asia.—FIG. 1142,5a–f. **D. volhynica* (KELUS), Middle Devonian, Afghanistan; a–e, neotype, dorsal, ventral, posterior, lateral, and anterior views, $\times 1$; f, posterior view of internal mold, $\times 1.5$ (Dürkoop, 1970).

Emanuella GRABAU, 1923 in 1923–1924, p. 192 [**Nucleospira takwanensis* KAYSER, 1883, p. 84; OD] [=*Paraemanuella* YANG, 1977, p. 415 (type, *P. orbicularia* YANG, 1977, p. 416, OD)]. Ventribiconvex; submegathyrid; ventral interarea low, strongly incurved; commissure slightly uniplicate; with concentric rows of small spines; dental plates lacking; crural plates short, discrete. *Middle Devonian*: cosmopolitan.—FIG. 1143,2a–d. **E. takwanensis* (KAYSER), Givetian, China; a–c, dorsal, side, and anterior views, $\times 2$ (Grabau, 1931b); d, exterior showing fine ornament, $\times 25$ (Veevers, 1959b).

Imenia NALIVKIN, 1941, p. 186 [**I. altovae* NALIVKIN, 1941, p. 187; OD]. Ventribiconvex; submegathyrid; ventral interarea low, incurved; commissure slightly uniplicate; capillate; dental plates short, divergent; crural plates short, discrete. *Middle Devonian*: cosmopolitan.—FIG. 1142,4a–d. **I. altovae*, Russia; ventral, dorsal, anterior, and lateral views, $\times 1$ (Nalivkin, 1941).

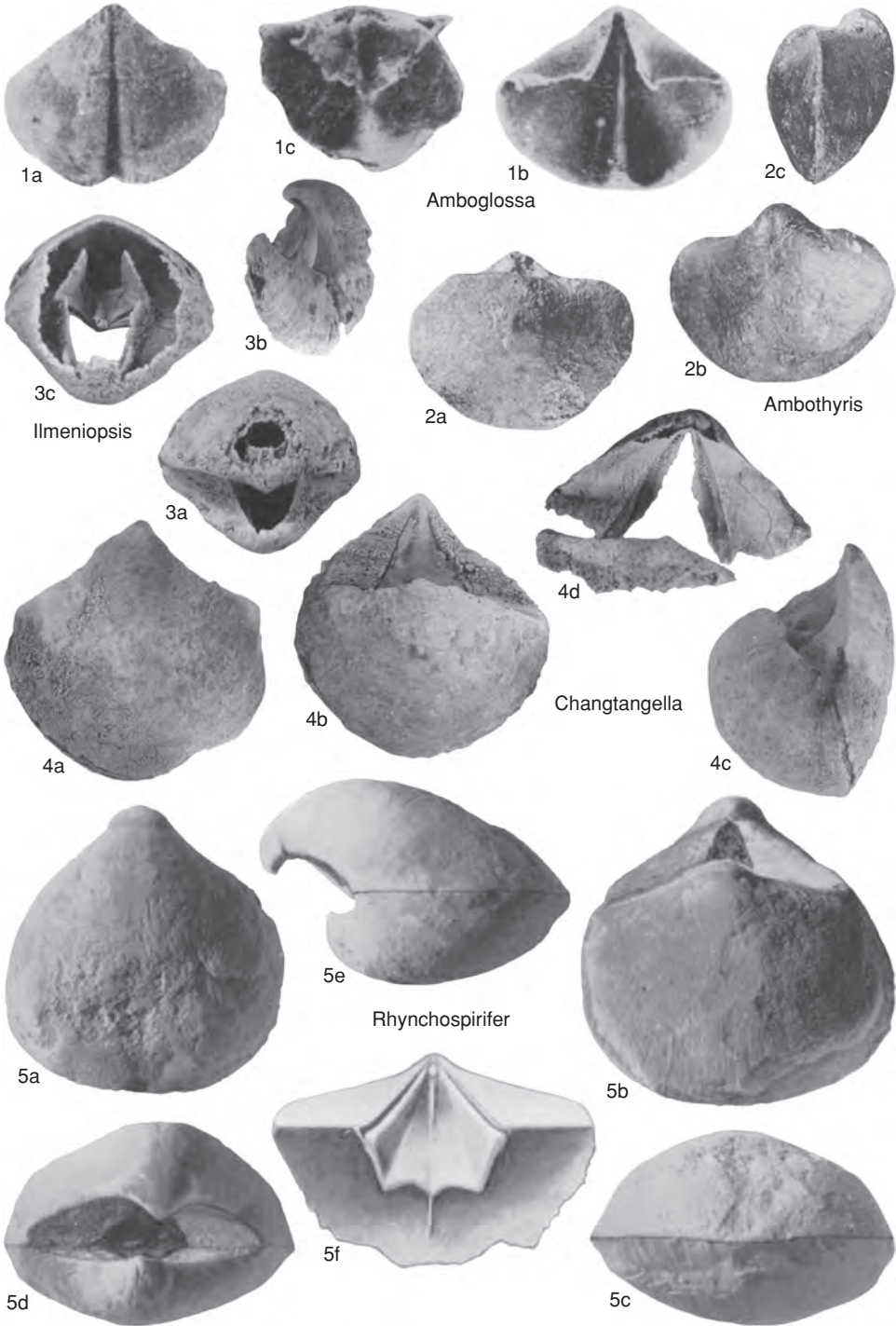


FIG. 1141. Ambocoeliidae (p. 1739–1743).

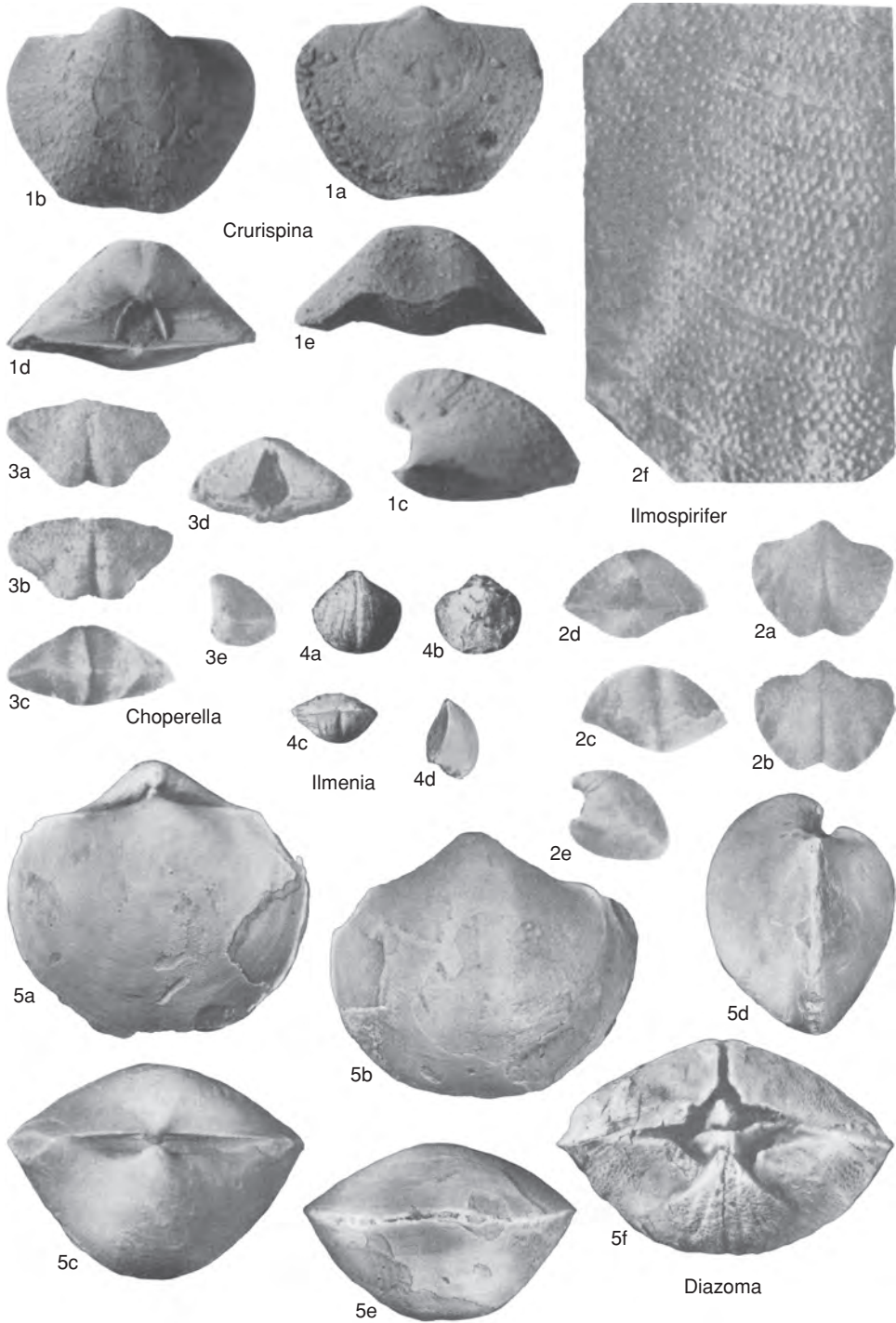


FIG. 1142. Ambocoeliidae (p. 1739–1743).

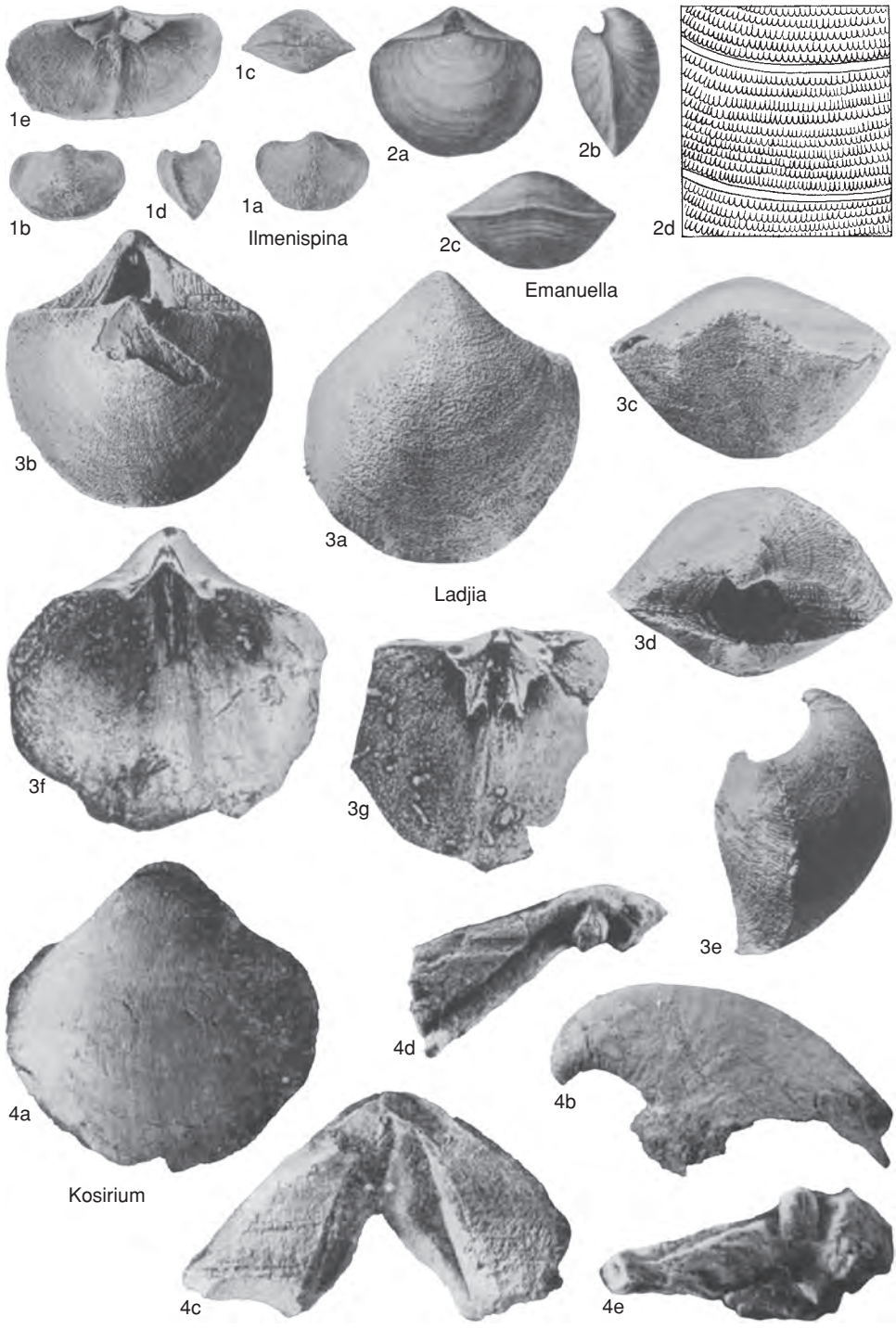


FIG. 1143. Ambocoeliidae (p. 1739–1743).

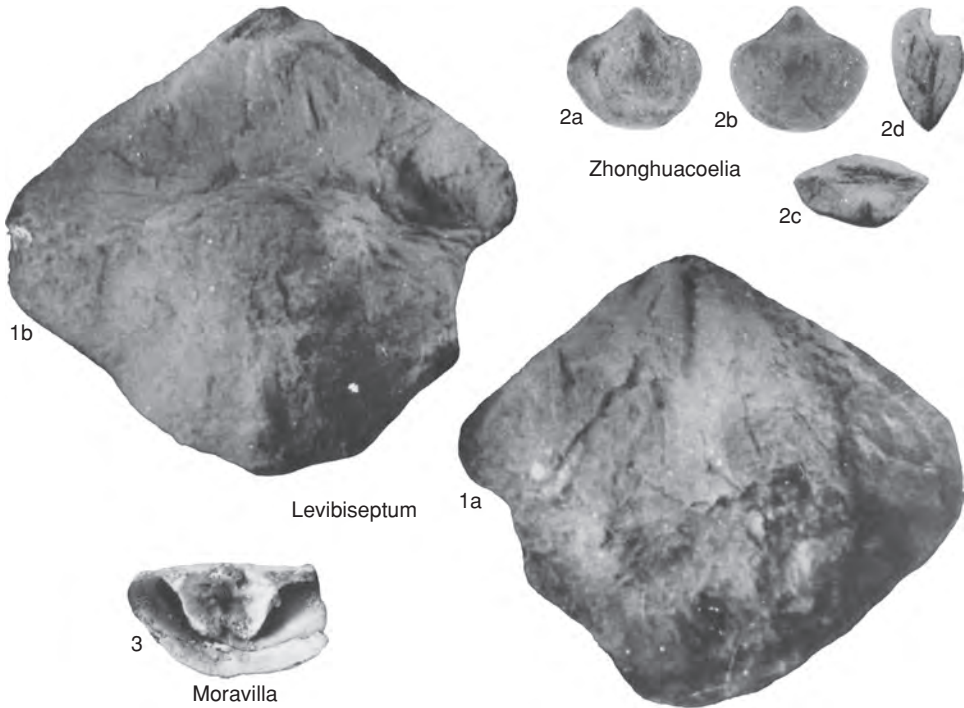


FIG. 1144. Ambocoeliidae (p. 1743–1744).

Ilmeniopsis XIAN, 1983a, p. 15 [**I. changtangensis*; OD]. Ventribiconvex; submegathyrid; ventral interarea low, incurved; commissure straight; faint concentric growth lines; dental plates short; crural plates short, discrete, connected posteriorly by suspended inner hinge plates. *Middle Devonian (Givetian)*: southern China.—FIG. 1141,3a–c. **I. changtangensis*; posterior, lateral, and anterior views, $\times 1$ (new).

Ilmenispina HAVLÍČEK, 1959, p. 180 [**I. hanaica* HAVLÍČEK, 1959, p. 181; OD]. Ventribiconvex; submegathyrid; ventral interarea low, incurved; commissure straight; faint capillae and spines; dental plates short, strong; crural plates broad, short, discrete or attached to low median ridge. *Middle Devonian (Givetian)*: Moravia.—FIG. 1143,1a–e. **I. hanaica*; a–d, holotype, ventral, dorsal, anterior, and lateral views, $\times 2$; e, dorsal interior, $\times 2.3$ (Havlíček, 1959).

Imospirifer LIASHENKO, 1969a, p. 18 [**I. graciosus* LIASHENKO, 1969a, p. 19; OD]. Ventribiconvex; megathyrid; ventral interarea low, with beak incurved; valves plicate, commissure episulcate; microornament of concentric rows of small spines; dental plates lacking; crural plates discrete or joined to form cruralium. *Middle Devonian (Eifelian)*: Russian Platform.—FIG. 1142,2a–f. **I. graciosus*; a–e, holotype, ventral, dorsal, anterior, posterior,

and lateral views, $\times 3$; f, microornament, $\times 20$ (Liashenko, 1969a).

Kosirium FICNER & HAVLÍČEK, 1975, p. 362 [**K. turbulentum*; OD]. Dental plates very thick, moderately divergent; cruralium short, deeply emarginate anteriorly; otherwise similar to *Rhynchospirifer*. *Middle Devonian*: Europe.—FIG. 1143,4a–e. **K. turbulentum*, upper Eifelian or lower Givetian, Czech Republic; a–b, ventral and lateral views of ventral valve, $\times 1$; c, ventral interarea, $\times 1.3$; d–e, dorsal and anterior views of dorsal interior, $\times 1.6$ (Ficner & Havlíček, 1975).

Ladjia VEEVERS, 1959a, p. 125 [**L. saltica* VEEVERS, 1959a, p. 126; OD]. Ventribiconvex; submegathyrid; ventral interarea medium height, incurved; commissure straight; capillae; dental plates lacking; crural plates discrete or joined to form a cruralium. *Middle Devonian (Givetian)–Upper Devonian (Frasnian)*: western North America, Australia.—FIG. 1143,3a–g. **L. saltica*, Australia; a–e, holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 3$; f–g, ventral and dorsal interiors, $\times 4.5$ (Veevers, 1959a).

Levibiseptum XIAN in HOU & XIAN, 1975, p. 31 [**L. dushanense*; OD]. Large, transversely oval, subequally biconvex; submegathyrid; ventral interarea of medium height; sulcus narrow, fold lacking; growth lines irregular; dental plates short; cruralium

supported by median septum. *Middle Devonian (Eifelian–lower Givetian)*: southern China.—FIG. 1144, 1a–b. **L. dushanense*, lower Givetian; ventral and dorsal views, $\times 1$ (new).

Moravilla HAVLIČEK, 1953, p. 4 [**M. ficneri* HAVLIČEK, 1953, p. 5; OD]. Strongly ventribiconvex, transverse, megathyrud; ventral interarea catacline; commissure straight; capillate; dental plates short, high; crural plates discrete. *Middle Devonian (Givetian)*: Moravia.—FIG. 1144, 3. *M. ficneri*, lower Givetian; interior of dorsal valve, $\times 3.4$ (Havlíček, 1959).

Zhonghuacoelia CHEN, 1978, p. 361 [**Z. bispina*; OD]. Ventribiconvex; submegathyrud; ventral interarea low, strongly incurved; commissure straight; concentric rows of small spines; short dental plates present; crural plates short, discrete. *Devonian (Givetian, ?Frasnian)*: southern China.—FIG. 1144, 2a–d. **Z. bispina*, ?Frasnian; ventral, dorsal, posterior, and side views, $\times 2.1$ (new).

Family LAZUTKINIIDAE Johnson & Hou, 1994

[Lazutkiniidae] JOHNSON & HOU in CARTER & others, 1994, p. 337]

[Materials for this family prepared by
J. G. Johnson & Hou Hong-fei]

Entirely plicate; capillae lacking; dental plates present. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*.

Lazutkinia RZHONSNIITSKAIA, 1952, p. 151 [**L. mamontovensis* RZHONSNIITSKAIA, 1952, p. 152; OD; =*Spirifer (Yavorskiella) mamontoviensis* LAZUTKIN in IAVORSKII, 1940, p. 44, *nom. nud.*] [=*Yavorskiella* LAZUTKIN in IAVORSKII, 1940, p. 44, *nom. nud.*]. Ventribiconvex with obtuse cardinal angles; ventral interarea long, curved, apsacline; plications numerous, low, rounded; fold and sulcus indistinct or lacking; microornament of numerous concentric lamellae; dental plates short and thick or lacking; knoblike cardinal process and cruralium sited on low median septum. *Middle Devonian (Eifelian–Givetian)*: Kuznetzk basin, Salair.—FIG. 1145, 1a–d. **L. mamontovensis*, Siberia; ventral, dorsal, anterior, and lateral views, $\times 1$ (Rzhonsniitkaia, 1955).

Prolazutkinia HOU & XIAN in XIAN Si-yuan, 1983a, p. 7 [**Lazutkinia lata* HOU & XIAN, 1975, p. 73; OD]. Ventribiconvex, transverse, with flat, steeply apsacline interarea; fold and sulcus lacking; simple and bifurcating plications numerous, rounded, with U-shaped interspaces; ventral umbonal thickening and long divergent dental plates present; crural plates dorsally converging. *Lower Devonian (Emsian)*: southern China.—FIG. 1145, 2a–d. **P. lata* (HOU & XIAN), upper Emsian; ventral, dorsal, posterior, and side views, $\times 2.6$ (new).

Family EUDOXINIDAE Nalivkin, 1979

[*nom. correct. et transl.* CARTER in CARTER & others, 1994, p. 337, *ex Eudoxiniinae* NALIVKIN, 1979, p. 145]

[Materials for this family prepared by J. L. Carter]

Small to very large; biconvex; costate or costellate; microornament papillose in some, absent or unknown in most genera; dental adminicula and protuberent ctenophoridium absent. [Due to the great difference in size between early Carboniferous and Permian representatives of this family and the absence of intermediate forms, the homogeneity for this group cannot be easily tested.] *Upper Devonian (Famennian)–Permian (Lopingian)*.

Eudoxina FREDERIKS & KRUGLOV, 1928, p. 801 [**Spirifer medius* LEBEDEV, 1912, p. 242; SD FREDERIKS, 1929, p. 382]. Medium to large; ventribiconvex, with rounded outline; fold and sulcus rounded, weakly to moderately developed; lateral extremities well rounded; entire surfaces of both valves finely costate or coarsely costellate, ribs bifurcating freely; microornament seemingly absent; inner shell layers pitted in some species; ventral interior with strong dental flanges; ventral muscle field deeply impressed; dorsal interior with concave apical area of diductor attachment, finely striate in some species, and high, divergent, inner socket ridges; brachidium unknown. *Carboniferous (Tournaisian)*: Russia, Ukraine, USA (Iowa, Illinois).—FIG. 1145, 3a–e. **E. media* (LEBEDEV), Russia; a, syntype, large ventral valve; b–d, syntype, ventral, anterior, and lateral views of smaller ventral valve; e, syntype, dorsal valve, $\times 1$ (new).

Costicrura HOOVER, 1981, p. 96 [**C. minuta*; OD]. Very small, ventribiconvex, usually transverse; ventral valve hemipyramidal with high catacline to apsacline interarea; dorsal valve weakly convex; fold and sulcus absent; cardinal extremities acute to obtuse; both valves weakly costellate; ventral interior lacking plates or recognizable muscle scars; dorsal interior with bilobed cardinal process divided by coarse median ridge; crural bases arising from posterior valve floor; microornament unknown. [See note under family description.] *Permian (Lopingian)*: Venezuela.—FIG. 1145, 6a–c. **C. minuta*; holotype, dorsal, posterior, and anterior views, $\times 10$ (Hoover, 1981).

Paulonia NALIVKIN, 1925, p. 267 [**Spirifer ranovensis* PEETZ, 1893, p. 53; OD]. Small to medium size, unequally biconvex, moderately transverse to equidimensional, outline rounded subpentagonal; fold and sulcus poorly to moderately developed; lateral extremities well rounded, hinge line much shorter than maximum width; entire surface with

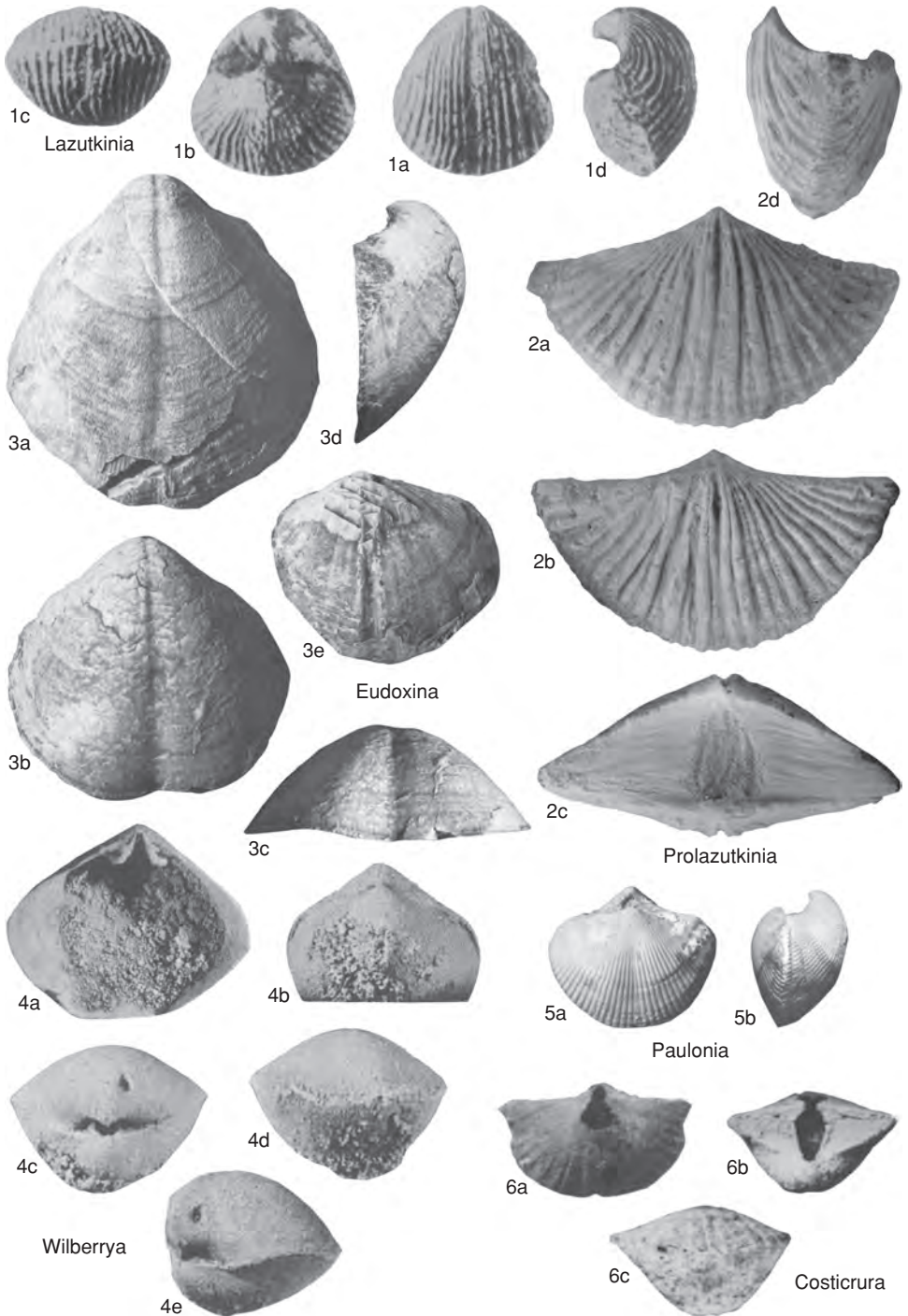


FIG. 1145. Lazutkiniidae and Eudoxinidae (p. 1744–1746).

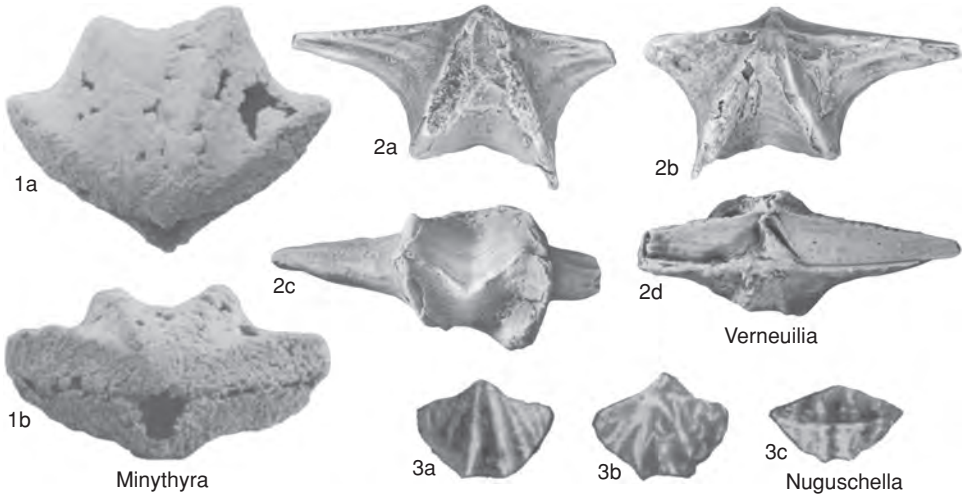


FIG. 1146. Verneuliidae (p. 1746).

numerous fine simple costellae; microornament consisting of fine oval papillae; inner fibrous shell layer pitted; ventral interior with delthyrial plate; dorsal interior unknown. *Upper Devonian (Famennian)–Carboniferous (Tournaisian)*: Russia, Ukraine.—FIG. 1145, 5a–b. **P. ranovensis* (PEETZ); dorsal and lateral views, $\times 2$ (new).

Wilberrya YANCEY, 1978, p. 301 [**W. fragilis*; OD]. Small, strongly biconvex, dorsal valve slightly less inflated than ventral valve; outline subpentagonal; hinge line narrow, indistinct; fold and sulcus weakly developed, anterior commissure slightly uniplicate; ornament of weakly developed irregular costellae; microornament unknown; dorsal interior with strong, high, inner socket ridges; cardinal process absent; crural bases projecting anteriorly from dorsomedial edges of inner socket ridges with long, slender crura set well above valve floor. [See note under family description.] *Permian (Cisuralian)*: USA (Nevada).—FIG. 1145, 4a–e. **W. fragilis*; a, holotype, ventral interior, $\times 5$; b–e, dorsal, posterior, anterior, and lateral views, $\times 4$ (Yancey, 1978).

Family VERNEULIIDAE Schuchert, 1929

[*nom. transl.* BRUNTON, 1984, p. 101, ex Verneuliinae SCHUCHERT, 1929, p. 21]

[Materials for this family prepared by J. G. Johnson]

Transverse to subcircular; biconvex, with opposite folding, forming ligate to metacariniate anterior margin; ventral interarea narrow to full width of valves; delthyrium open or restricted by apical deltidium. *Middle Devonian (Eifelian)–Carboniferous (Visean)*.

Verneulia HALL & CLARKE, 1893, p. 58 [**Spirifer cheiropteryx* D'ARCHIAC & DE VERNEUIL, 1842, p. 370; SD HALL & CLARKE, 1894, p. 762]. Small to medium size; very transverse with pointed cardinal extremities; flanks markedly concave; dental plates lacking; dorsal interior with small, knoblike cardinal process and short crural plates that merge with prominent, medially convergent hinge plates. [The Visean species from Belgium, *V. oceani* (D'ORBIGNY) is not congeneric with the type species, bearing strong dental flanges, a finely striated cardinal process, lacking crural plates, in having a clearly denticulate ventral interarea with wide perideltidial areas, and possibly a weakly capillate microornament. It belongs in the Spiriferoidea.] *Middle Devonian (Eifelian)–Carboniferous (Visean)*: USA (Alaska), Europe, Asia.—FIG. 1146, 2a–d. **V. cheiropteryx* (D'ARCHIAC & DE VERNEUIL), Middle Devonian, Germany; ventral, dorsal, anterior, and posterior views, $\times 2$ (Gourvenec, 1994a).

Minythyra BRUNTON, 1984, p. 102 [**M. lophi*; OD]. Minute, subcircular; hinge line less than maximum width; interarea low, apsacline with open delthyrium; flanks with 1 or 2 plications; no median septum. *Carboniferous (Visean)*: Great Britain.—FIG. 1146, 1a–b. **M. lophi*, Ireland; a, posterodorsal view; b, posterior view, $\times 20$ (Brunton, 1984).

Nuguschella TIAZHEVA, 1960, p. 408 [**N. polita*; OD]. Ventribiconvex; megathyrid; ventral interarea low, with beak incurved; valves bisulcate with rounded, opposed plications; capillate; dental plates lacking; crural plates closely discrete, or joined with prominent, medially convergent hinge plates to form cruralium. *Middle Devonian (Eifelian)*: Ural Mountains.—FIG. 1146, 3a–c. **N. polita*; holotype, ventral, dorsal, and anterior views, $\times 3$ (Tiazheva, 1960).

MARTINIOIDEA

J. L. CARTER and RÉMY GOURVENNEC

[retired from Carnegie Museum of Natural History; and Université de Bretagne Occidentale]

Superfamily MARTINIOIDEA Waagen, 1883

[*nom. correct.* CARTER, JOHNSON, & GOURVENNEC in CARTER & others, 1994, p. 338, *pro* Martiniacea IVANOVA, 1972, p. 41, *nom. transl. ex* Martiniinae WAAGEN, 1883a, p. 524]

Biconvex, with broadly rounded lateral extremities and short hinge line; lateral slopes smooth or with subdued ribbing; microornament often capillate, smooth, or very finely spinulose, but not strongly lamellose or concentrically disposed; ventral median septum absent; dorsal interior with ctenophoridium in all but the earliest genera; fibrous layer commonly pitted. *Silurian (upper Wenlock)–Permian (Lopingian)*.

Family TENELLODERMIDAE Carter, Johnson, & Gourvennec, 1994

[Tenellodermidae CARTER, JOHNSON, & GOURVENNEC in CARTER & others, 1994, p. 338]

[Materials for this family prepared by
Rémy Gourvennec]

Ctenophoridium absent; surface pitted or simple; dental plates present. *Silurian (upper Wenlock)–Middle Devonian (Eifelian)*.

Tenellodermis HAVLÍČEK, 1971, p. 11 [**T. microdermis*; OD]. Small to medium size, slightly transverse with high, catacline to procline ventral interarea; cardinal extremities rounded; sulcus and corresponding fold well delimited, shallow; commissure uniplicate; flanks smooth or bearing few (1 to 4) wide, low, rounded anterior plications; microornament of fine growth lines and minute pits either aligned between radial capillae or randomly arranged; dental plates long, thin; crural plates lacking; cardinal process consisting of simple tubercle. *Silurian (upper Wenlock)–Lower Devonian (Lochkovian)*: Czech Republic, USA (Nevada).—FIG. 1147, 2a–b. **T. microdermis*, Lochkovian, Czech Republic; dorsal and ventral views, $\times 2$ (Havlíček, 1971).—FIG. 1147, 2c–e. *T. tenellus* (BARRANDE), Ludlow, Czech Republic; c–d, anterior and lateral views, $\times 1.5$ (Havlíček, 1959); e, ornament, $\times 50$ (Havlíček, 1971).

Cingulodermis HAVLÍČEK, 1971, p. 15 [**C. cinctus*; OD]. Small to medium size, equidimensional to slightly transverse, with high, curved ventral interarea; fold and sulcus well defined anteriorly

resulting in uniplicate commissure; flanks smooth; microornament of growth lamellae only; dental plates short; muscle field deeply impressed; crural plates short; ctenophoridium lacking; cardinal process occasionally bifid. *Lower Devonian (Lochkovian)–Middle Devonian (Eifelian)*: Czech Republic, Germany, Morocco.—FIG. 1147, 1a–f. **C. cinctus*, Pragian, Czech Republic; a–d, dorsal, ventral, anterior, lateral views, $\times 2$; e, interior of ventral valve, $\times 2.6$ (Havlíček, 1959); f, ornament, $\times 4.4$ (Havlíček, 1971).

Family ELYTHYNIDAE Gourvennec, 1994

[Elythyinae GOURVENNEC in CARTER & others, 1994, p. 338]

[Materials for this family prepared by
Rémy Gourvennec]

Flanks plicate; ornament of fine pits or spines and pits; ctenophoridium, dental plates, and crural plates or dorsal adminicula present. *Lower Devonian (Pragian)–Middle Devonian (Givetian)*.

Elythyna RZHONSNITSKAIA, 1952, p. 61 [**E. salairica*; OD]. Medium to large, transverse, with rounded cardinal extremities; apsacline, rather low, curved ventral interarea; fold and sulcus distinct, some species with incipient costation on fold; flanks with 4 to 6 low, rounded, lateral plications, in some faintly expressed; microornament of concentric growth lines and randomly arranged pits; dental plates long, thick; muscle field deeply impressed; crural plates (or possible dorsal adminicula) and ctenophoridium well developed; strong apical thickening in both valves. *Lower Devonian (Emsian)–Middle Devonian (Givetian)*: Turkestan, Gansu Mongol, Arctic Canada.—FIG. 1148, 1a–i. **E. salairica*, Eifelian, Salair; a–e, dorsal, ventral, anterior, posterior, lateral views, $\times 0.7$; f, ornament, $\times 6$; g–h, dorsal, ventral views of internal mold, $\times 1$ (Rzhonsnitskaia, 1952); i, transverse section, $\times 2$ (new).

Najadospirifer HAVLÍČEK, 1957a, p. 246 [**Spirifer najadum* BARRANDE, 1848, p. 171; OD] [= *Naiadospirifer* HAVLÍČEK, 1957a, p. 246, *lapsus calami*, obj.]. Medium to large; transverse or equidimensional with rounded cardinal extremities; ventral interarea high, gently curved, apsacline to catacline; fold and sulcus absent posteriorly, more or less distinct anteriorly; anterior commissure strongly uniplicate, producing very high tongue; plicae lacking posteriorly, present only on anterior

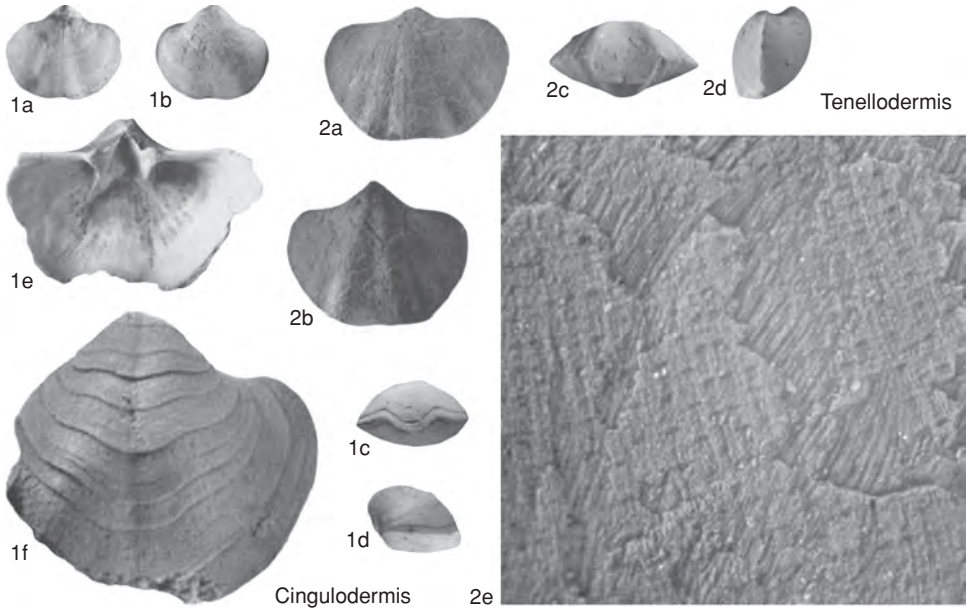


FIG. 1147. Tenellodermidae (p. 1747).

part of shell; microornament of radial rows of variably elongate minute pits and tubercles; dental plates long, divergent; crural plates short; ctenophoridium present. [In the original publication by HAVLÍČEK (1957a), the new genus is spelled *Naiadospirifer* nov. gen., but in the remaining parts of the text and in the English summary it is spelled *Najadospirifer* (and it is based on the species *najadum* BARRANDE).] *Lower Devonian (Pragian–Emsian)*: Czech Republic, Germany, Carnic Alps, ?Morocco.—FIG. 1148, 3a–f. **N. najadum* (BARRANDE), Pragian, Czech Republic; a–d, dorsal, ventral, anterior, lateral views, $\times 1$; e, transverse section, $\times 1.5$ (Havlíček, 1959); f, ornament, $\times 12$ (Havlíček, 1971).

Tatjanaspirifer CHERKESOVA, 1991, p. 91 [**T. variabilis*; OD]. Medium size; usually elongate with apsacline curved interarea and rounded cardinal extremities; ventral valve strongly swollen; sulcus and fold distinct; flanks with 1 to 3 wide, uncommonly bifurcating plications; microornament of concentric growth lines with marginal spines and somewhat coarser, randomly distributed spines; dental plates thick; muscle field and genital markings well impressed; crural plates short; ctenophoridium bilobed. *Lower Devonian (Pragian)*: Siberian Platform.—FIG. 1148, 2a–g. **T. variabilis*, Taymyr; a–d, dorsal, ventral, anterior, lateral views of partially decorticated specimen, $\times 1$; e–f, spinose ornament and pits, $\times 10$; g, interior of ventral valve, $\times 2$ (Cherkesova, 1991).

Family MARTINIIDAE

Waagen, 1883

[*nom. transl.* IVANOVA, 1959, p. 56, ex subfamily Martiniinae WAAGEN, 1883a, p. 524]

[Materials for this family prepared by J. L. Carter]

Subequally biconvex; lateral slopes smooth or weakly plicate; dorsal adminicula or crural plates absent; microornament of scattered surficial pits, or capillae, or absent. *Upper Devonian (?lower Famennian–?middle Famennian, upper Famennian)–Permian (Lopingian)*.

Subfamily MARTINIINAE

Waagen, 1883

[Martiniinae WAAGEN, 1883a, p. 524]

Without plates or septa in either valve; microornament of fine pits only. *Carboniferous (Tournaisian)–Permian (Lopingian)*.

Martinia M'COY, 1844, p. 128 [**Spirifer glaber* SOWERBY, 1820 in 1818–1821, p. 123; SD ICZN Opinion 421, 1956b, p. 171] [= *Pseudomartinia* LEIDHOLD, 1928, p. 82, obj.; *Paramartinia* REED, 1949, p. 471 (type, *Martinia (Paramartinia)*)]

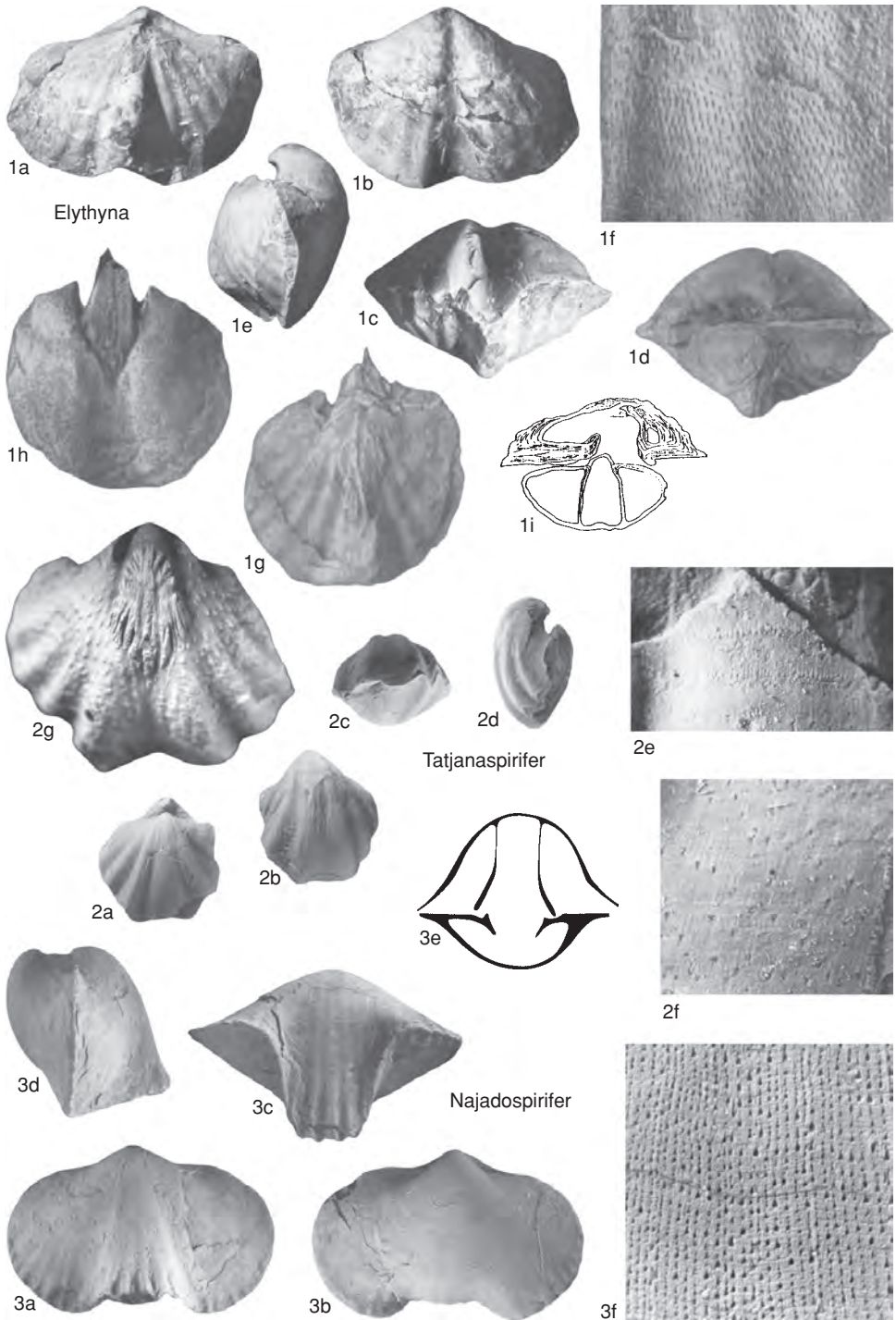


FIG. 1148. Elythynidae (p. 1747–1748).

- lingulata* REED, 1949, p. 471, OD]. Unequally biconvex; outline subovate to subpentagonal; fold and sulcus weakly to moderately developed, well rounded, often poorly delimited; ventral interarea well developed, apsacline; macroornament absent; microornament often absent, rarely with shagreen (finely pitted) surface; inner shell layers more commonly pitted; ventral interior simple, with dental flanges and impressed lanceolate muscle scar bisected by weak, narrow medial groove that extends from beak region to or near anterior margin; dorsal interior simple, with small ctenophoridium and narrow medial groove similar to that of opposite valve; vascular impressions of both valves pinnate. *Carboniferous* (Mississippian)–*Permian* (Lopingian): cosmopolitan.—FIG. 1149, 2a–b. **M. glabra* (SOWERBY), Viséan, England; lectotype, anterior and dorsal views, $\times 1$ (Muir-Wood, 1951).
- Beschevella** POLETAEV, 1975, p. 51 [**Martinia* (*Ella*) *snjatkovi* ROTAI, 1931, p. 86; OD]. Medium to large, strongly and subequally biconvex; outline transversely subrhomboidal to subpentagonal; surface smooth or vaguely ribbed; thin shelled; well-developed fold and sulcus; dorsal fold flattened or with shallow medial furrow; delthyrium partly closed by convex pseudodeltidium; microornament of numerous small pits, densely and crudely arranged in quincunx; umbonal region of ventral valve with 2 short, broad, weakly diverging ridges; vascular impressions not observed, possibly absent; otherwise similar to *Martinia*. *Carboniferous* (*Bashkirian*): Ukraine (Donets basin).—FIG. 1149, 1a–f. **B. snjatkovi* (ROTAI); a–e, ventral, posterior, dorsal, lateral, and anterior views, $\times 1$; f, microornament, $\times 8$ (Poletaev, 1975).
- Implexina** POLETAEV, 1971, p. 79 [**Spirifer* (*Martiniopsis*?) *implex* ROTAI, 1931, p. 90; OD]. Medium to large; unequally biconvex; moderately to strongly inflated, relatively thin shelled; outline subovate; fold and sulcus absent; ventral valve with broad, posteriorly extended umbonal region; posterolateral slopes of ventral valve bent strongly inward, forming large palintrope lateral to ventral interarea; ventral interarea high, narrow, clearly defined, strongly apsacline; radial ornament absent; microornament of small, elongate pits; ventral interior with strong dental flanges; muscle field moderately impressed with pair of long narrow furrows medially separated by low median ridge and bounded laterally by low ridges; dorsal interior with analogous muscle impressions and low ridges and thick, arcuate, bilobed ctenophoridium. *Carboniferous* (*Tournaisian*): Ukraine.—FIG. 1150, 2a–d. **I. implex* (ROTAI); a–c, ventral, posterior, and lateral views of ventral valve; d, dorsal valve, $\times 1$ (new).
- Jilimartinia** LI & GU, 1980, p. 488 [491] [**Brachythyris shansiensis* CHAO, 1929, p. 55] [= *Kalitvella* LAZAREV & POLETAEV, 1982, p. 92 (type, *Spirifer* (*Brachythyris*) *sokolovi* var. *laevis* LIKHAREV, 1938, p. 83, OD)]. Large; lateral plicae absent or very faint; interior with 2 vascula media and reticulate vascular pattern; otherwise similar to *Martinia*. *Carboniferous* (?*Moscovian*, *Kasimovian*): Ukraine (Donets basin), China.—FIG. 1151, 1a. **J. shansiensis* (CHAO), ?*Kasimovian*, China; syntype, ventral valve, $\times 1$ (Chao, 1929).—FIG. 1151, 1b–f. *J. laevis* (LIKHAREV), *Kasimovian*, Donets basin; holotype, ventral, dorsal, lateral, anterior, and posterior views, $\times 1$ (new).
- Postamartinia** WANG & YANG, 1993, p. 7 [**P. grandiplica*; OD]. Medium size; outline transversely subpentagonal; ventral interarea low; lateral slopes with 3 to 4 smooth, low, broad plicae; internally similar to *Martinia*; microornament, if any, unknown. *Permian* (*Sakmarian*): China (Xinjiang).—FIG. 1151, 2a–d. **P. grandiplica*; holotype, ventral, dorsal, lateral, and anterior views, $\times 1$ (Wang & Yang, 1993).
- Spinomartinia** WATERHOUSE, 1968, p. 53 [**S. spinosa*; OD]. Microornament of fine erect spines; otherwise similar to *Martinia*. *Permian* (*Cisuralian*–*Lopingian*): Thailand, Australia, *Cisuralian*; New Zealand, *Lopingian*.—FIG. 1152, 2a–c. **S. spinosa*, *Cisuralian*, Thailand; holotype, dorsal, posterior, and ventral views, $\times 2$ (Waterhouse, 1968).
- Tiramnia** GRUNT, 1977b, p. 64 [**Martinia uralica* CHERNYSHEV, 1902, p. 183; OD]. With ramiform vascular impressions; otherwise similar to *Martinia*. *Carboniferous* (*Moscovian*)–*Permian* (*Cisuralian*): Arctic Russia, Greenland, Arctic Canada.—FIG. 1152, 1a–f. **T. uralica* (CHERNYSHEV), *Cisuralian*, Arctic Russia; a–b, large syntype, ventral and dorsal views; c–f, small syntype, ventral, dorsal, anterior, and lateral views, $\times 1$ (new).
- Weiningia** JIN & LIAO, 1974, p. 282 [**W. transversa*; OD] [= *Elenchus* ALEKSANDROV in ALEKSANDROV & SOLOMINA, 1973, p. 118 (type, *E. areatus*, OD), *non* CURTIS, 1840]. Medium size; subequally biconvex; outline subovate, subtrigonal, or guttate with acuminate ventral beak; hinge line much shorter than maximum width; fold absent; valves evenly convex or with weak sulci in one or both valves; ventral interarea moderately high, triangular, concave, poorly defined; low dorsal interarea variably present; ornament absent except for growth varices and indistinct plications; microornament absent or with weak indistinct capillae; ventral interior with obscure dental flanges; ventral muscle scars deeply incised, in 2 distinct pairs, separated by low median ridge; dorsal interior with large cardinal process, thick crural bases, and median ridge; both valves greatly thickened by callus; vascular impressions pinnate. *Carboniferous* (*Serpukhovian*–*Bashkirian*): China (Guizhou), Russia (southern Urals), Japan (Akiyoshi Province).—FIG. 1150, 1a–c. **W. transversa*, Weiningian, Guizhou, China; holotype, ventral, dorsal, and lateral views, $\times 1$ (new).—FIG. 1150, 1d–f. *W. areatus* ALEKSANDROV; holotype, ventral, dorsal, and lateral views, $\times 1$ (Aleksandrov & Solomina, 1973).

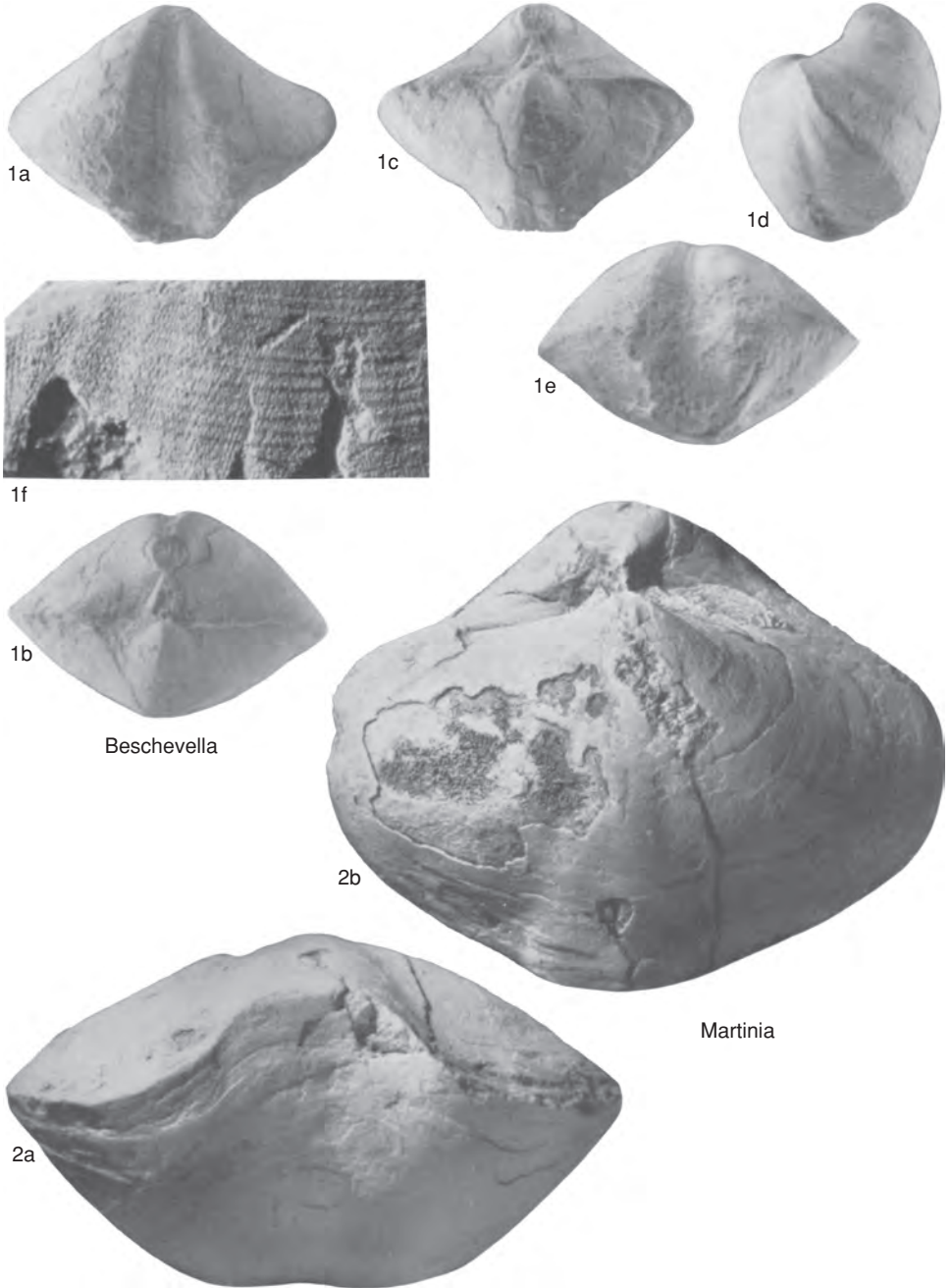


FIG. 1149. Martiniidae (p. 1748–1750).

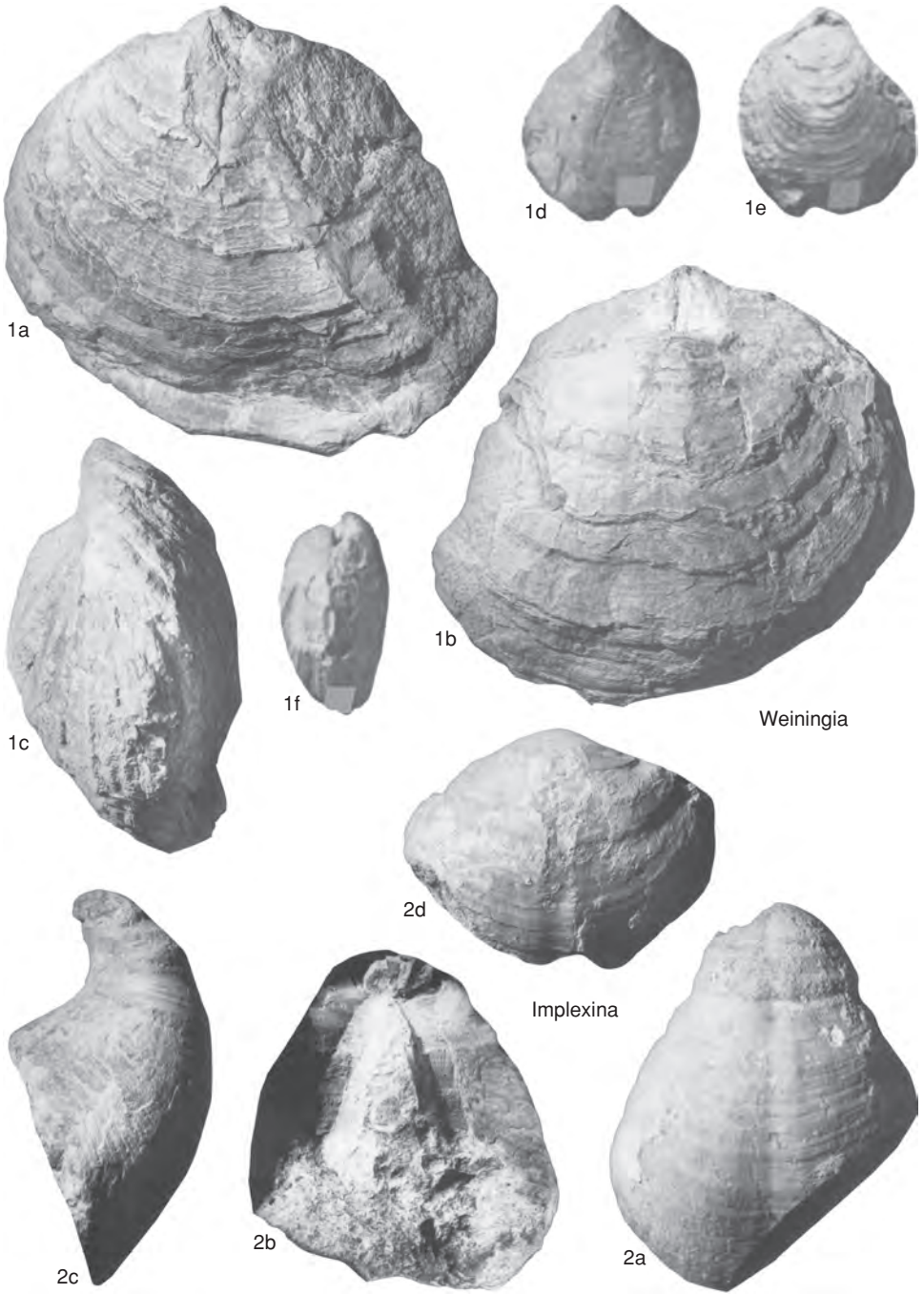


FIG. 1150. Martiniidae (p. 1750).

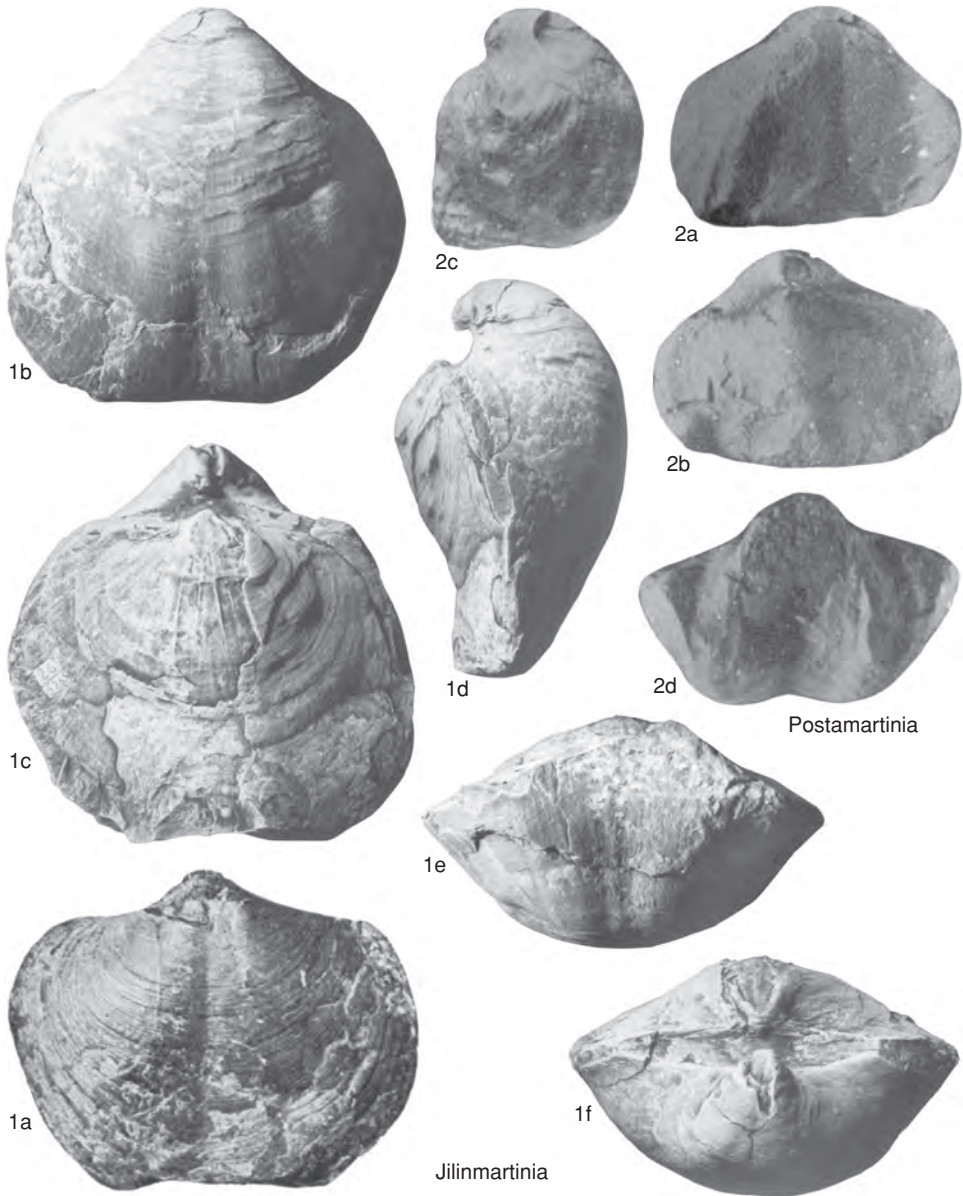


FIG. 1151. Martiniidae (p. 1750).

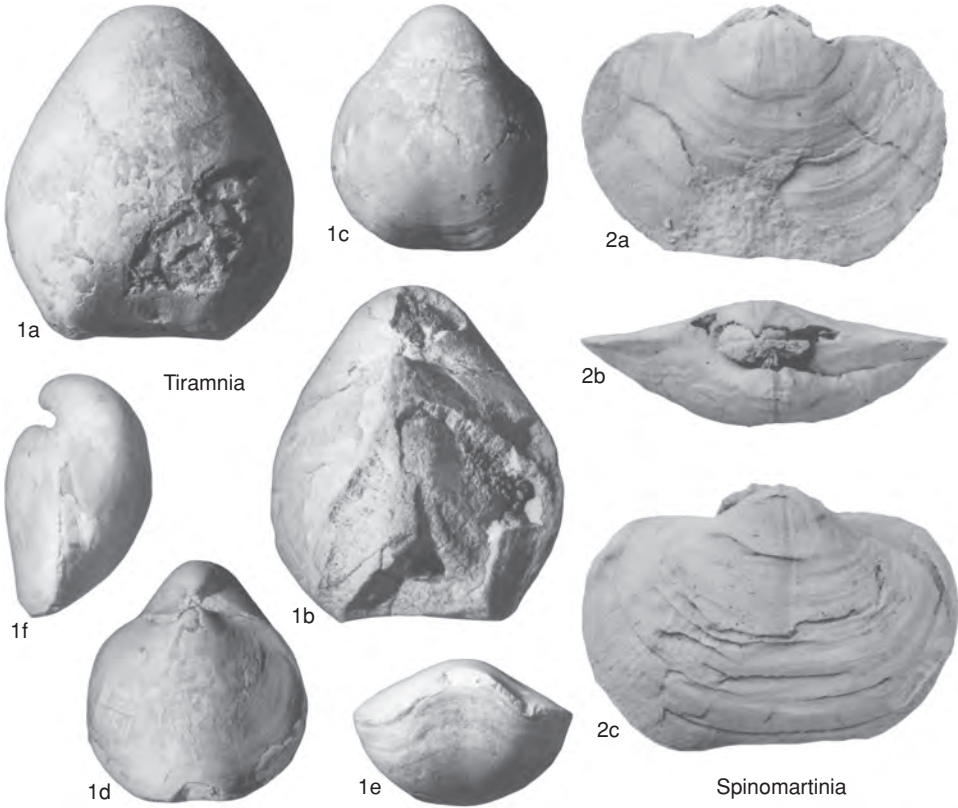


FIG. 1152. Martiniidae (p. 1750).

Subfamily EOMARTINIOPSINAE Carter, 1994

[Eomartiniopsinae CARTER in CARTER & others, 1994, p. 339]

Dental adminicula present; lateral slopes commonly weakly ribbed. *Upper Devonian* (?Famennian), *Carboniferous* (Tournaisian)–*Permian* (Guadalupian).

Eomartiniopsis SOKOLSKAYA, 1941, p. 78 [*E. elongata*; OD]. Medium size, subequally biconvex; subovate to subpentagonal in outline; fold and sulcus rounded, moderately to well developed; ornament absent or of few, very weak sinuous plications on flanks; microornament of surficial pits in some species, absent in others; inner shell layers pitted; ventral interior with well-developed dental adminicula; crural plates or dorsal adminicula probably lacking. [SOKOLSKAYA (1941) attributed very short (1 mm long) so-called septal plates to the type species. Her

diagram (fig. 31) and photograph (pl. 12, 1b) of a transversely cut thin section of the posterior dorsal interior of *E. elongata* fail to support this assertion. None of the North American or Australian species assigned to this genus possess apparent dorsal adminicula or crural plates.] *Devonian* (?Famennian), *Carboniferous* (Tournaisian): Europe, North America, Australia.—FIG. 1153, 1a–d. **E. elongata*, Russia; holotype, ventral, dorsal, anterior, and lateral views, $\times 1$ (new).

Globispirifer TACHIBANA, 1964, p. 37 [41] [*Spirifer* (*Martiniopsis*?) *nagasakiensis* TACHIBANA, 1956, p. 13; OD]. Medium size; biconvex; subovate in outline, possibly slightly elongate; ventral beak acute, incurved; ventral interarea poorly delimited; delthyrium open; venter rounded, sulcus absent; lateral slopes of ventral valve smooth; dorsal fold moderately developed; lateral slopes of dorsal valve weakly plicate; microornament not observable; ventral interior with well-developed, slightly divergent dental adminicula and deeply impressed

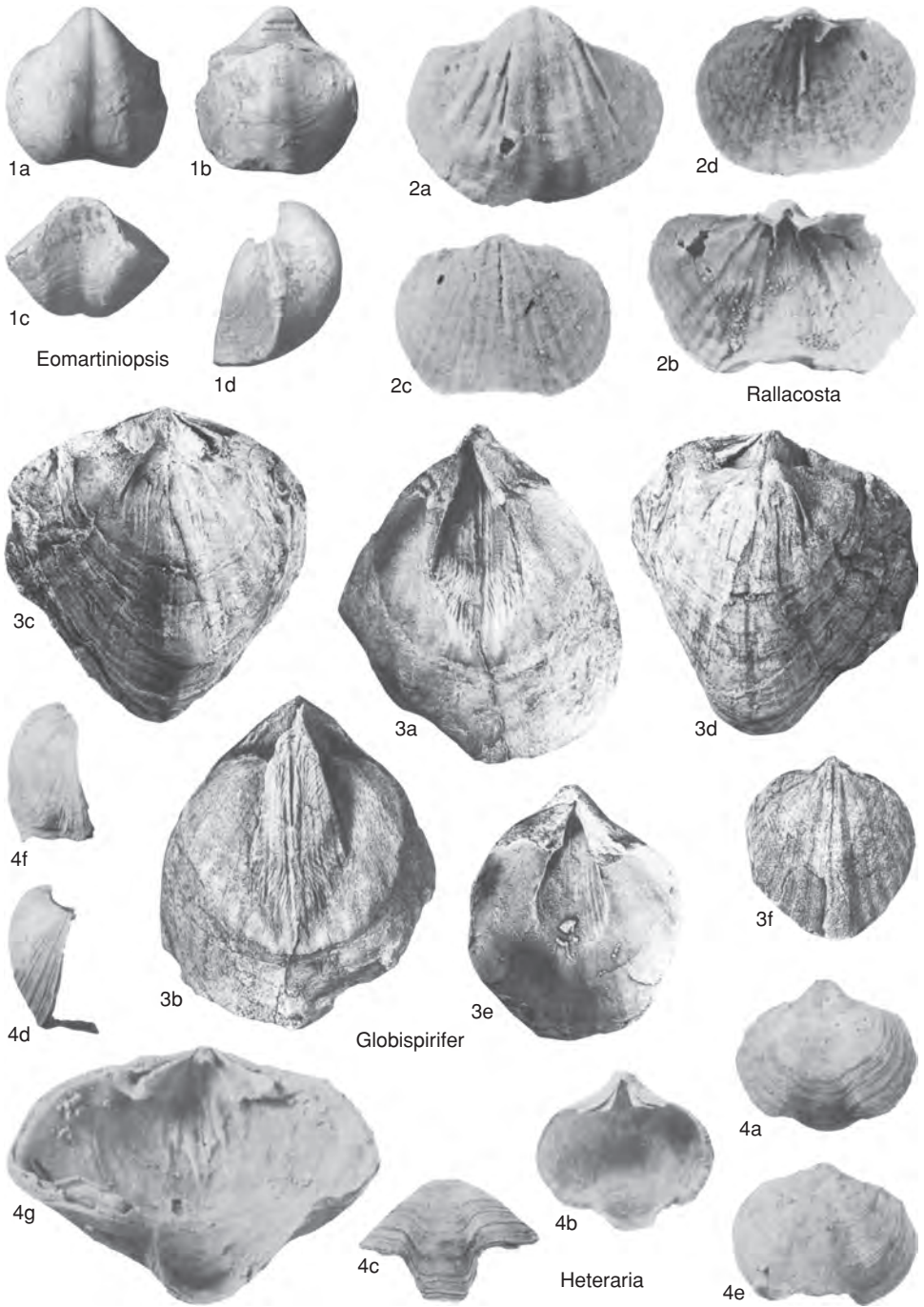


FIG. 1153. Martiniidae (p. 1754–1756).

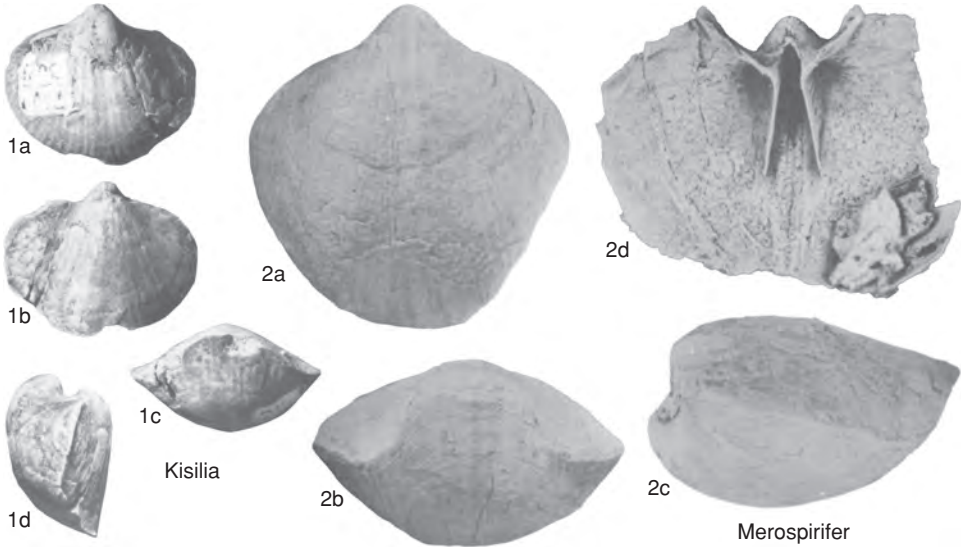


FIG. 1154. Martiniidae (p. 1756).

rhomboidal muscle field; dorsal interior with large ctenophoridium and short broad myophragm; crural bases broad, long, and bladelike; dorsal adductor field large, subovate, moderately impressed, longitudinally striated; vascular impressions finely pinnate. *Carboniferous* (lower Tournaisian): Japan. —FIG. 1153,3a–f. **G. nagasakaensis* (TACHIBANA), syntype; a–b, mold and cast of large ventral valve; c–d, mold and cast of large dorsal valve; e, cast of small ventral valve; f, cast of small dorsal valve, $\times 1$ (new).

Heteraria COOPER & GRANT, 1976a, p. 2,275 [**H. blakemorei*; OD]. Ventral valve with short, receding dental adminicula and very wide dental ridges; microornament seemingly absent but poorly known; otherwise similar to *Eomartiniopsis*. *Permian* (Cisuralian): USA (Texas). —FIG. 1153,4a–g. **H. blakemorei*; a–d, holotype, ventral, ventral interior, anterior, and lateral views of ventral valve; e–f, dorsal and anterior views of dorsal valve, $\times 1$; g, oblique enlargement of dorsal interior, $\times 2$ (Cooper & Grant, 1976a).

Kisilia NALIVKIN, 1979, p. 146 [**K. linguata*; OD]. Small to medium size; outline rounded, nearly equidimensional; fold moderately developed, rounded; sulcus very weakly developed, indistinct; faint, thin plicae on both valves; microornament unknown; ventral interior with short, thin dental adminicula and short, thick median ridge; dorsal interior unknown. *Carboniferous* (Tournaisian): Ural Mountains, Russia. —FIG. 1154,1a–d. **K.*

linguata; holotype, ventral, dorsal, anterior, and lateral views, $\times 2$ (new).

Merospirifer REED, 1949, p. 467 [**Martinia* (*M. insolita*) REED, 1949, p. 467; OD]. Outline broadly subovate; lateral profile rounded, transversely rhombic; lateral slopes with indistinct plicae in late ontogeny; ventral interior with subparallel dental adminicula; microornament of fine pits. *Carboniferous* (Visean): Scotland, England, and Ireland. —FIG. 1154,2a–d. **M. insolita* (REED); a–c, lectotype, ventral, anterior, and lateral views, $\times 1$; d, ventral interior, $\times 2$ (Brunton, 1984).

Rallacosta COOPER & GRANT, 1976a, p. 2,277 [**R. imporcata*; OD]. Ventral interarea absent or much reduced; ventral interior with short dental adminicula; dorsal interior with very small ctenophoridium composed of few plates; ornament of few low plications over entire surfaces of valves, with or without weak fasciculate costae or costellae; microornament seemingly absent but preservation poor; otherwise similar to *Eomartiniopsis*. *Permian* (Guadalupian): Texas. —FIG. 1153,2a–d. **R. imporcata*; a, holotype, ventral valve; b, ventral interior; c–d, dorsal valve exterior and interior, $\times 2$ (Cooper & Grant, 1976a).

Subfamily ELIVELLINAE Carter, 1994

[Elivellinae CARTER in CARTER & others, 1994, p. 340]

Microornament of capillae and fine pits; dental plates becoming progressively shorter

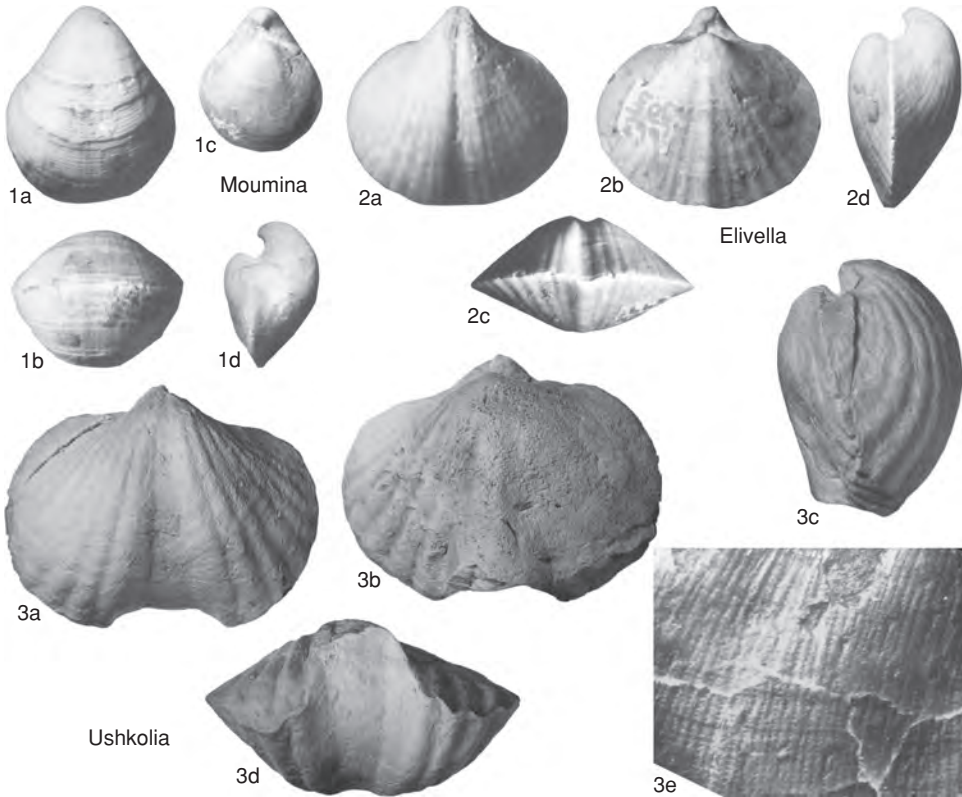


FIG. 1155. Martiniidae (p. 1757).

or absent in younger genera. *Upper Devonian (upper Famennian)–Permian (Cisuralian)*.

Elivella FREDERIKS, 1924, p. 316 [**Martiniopsis bashkirica* CHERNYSHEV, 1902, p. 558; SD FREDERIKS, 1926, p. 403]. Medium size, unequally biconvex, outline subovate; ventral umbonal region short; ventral beak incurved; fold and sulcus weakly developed, narrow; entire surfaces of both valves with numerous simple, low, rounded costae; ventral interior with short dental adminicula. *Permian (Cisuralian)*: Russia.—FIG. 1155, 2a–d. **E. bashkirica* (CHERNYSHEV); holotype, ventral, dorsal, anterior, and lateral views, $\times 2$ (new).

?**Martiniella** GRABAU & TIEN in GRABAU, 1931a, p. 420 [**M. nasuta, nom. nud.*; OD]. Microornament capillate; otherwise similar to *Merospirifer*. [*M. nasuta* GRABAU & TIEN is a *nomen nudum* and thus is not available, according to Code Article 13 (ICZN, 1999).] *Carboniferous (Mississippian)*: China.

Moumina FREDERIKS, 1924, p. 321 [**Martinia incerta* CHERNYSHEV, 1902, p. 569; OD]. Small, guttate in outline; ventral umbonal region elongated; hinge line narrow; ventral sulcus absent; weak, dorsal median sulcus or groove present; anterior commissure rectimarginate; internally similar to *Martinia*. *Permian (Cisuralian)*: Russia.—FIG. 1155, 1a–d. **M. incerta* (CHERNYSHEV); a–b, large syntype, ventral and anterior views; c–d, small syntype, dorsal and lateral views, $\times 2$ (new).

Ushkolia MARTYNOVA & SVERBILOVA, 1969, p. 96 [**U. litvinovitchae*; OD]. Medium to large size; biconvex, equidimensional; cardinal extremities well rounded; hinge line much narrower than maximum width; ventral interarea low, strongly curved, apsacline; fold and sulcus smooth or with faint parietal plications; flanks with broad, low, rounded, simple plications; dental adminicula straight, subparallel. *Upper Devonian (upper Famennian)*: Kazakhstan.—FIG. 1155, 3a–e. **U. litvinovitchae*; a–d, holotype, ventral, dorsal, lateral, and anterior views, $\times 1$; e, microornament, $\times 15$ (new).

Family CRASSUMBIDAE new family

[Crassumbidae CARTER, herein] [type genus, *Crassumbo* CARTER, 1967b, p. 408]

[Materials for this family prepared by J. L. Carter]

Dental and dorsal adminicula (or possibly crural plates) present; lateral slopes commonly with weak plications; microornament usually weakly to strongly capillate, rarely papillose. *Carboniferous (Tournaisian)–Permian (Guadalupian)*.

Crassumbo CARTER, 1967b, p. 408 [**C. inornatus*; OD]. Small to medium size, subequally biconvex, wider than long; lateral slopes smooth or with very weak, narrow ribs; fold and sulcus poorly to well defined; ventral interarea small, acutely triangular; shell substance thick in umbonal regions of both valves; ventral interior with thin, subparallel dental adminicula, partially buried in callus; ventral muscle field deeply incised posteriorly; ventral median ridge present in juveniles; dorsal interior with strong, high crural bases (possibly adminicula) obscured by callus deposits and reaching floor of valve as crural plates in juveniles; microornament of capillae separated by very narrow interspaces, with scattered nodes or papillae. *Carboniferous (Tournaisian)*: USA (Texas), Australia.—FIG. 1156,3a–h. **C. inornatus*, middle Tournaisian, Texas; a–e, holotype, ventral, dorsal, lateral, anterior, and posterior views, $\times 1$; f–g, transverse sections, $\times 1.5$; h, microornament, $\times 10$ (Carter, 1967b).

Arktikina GRUNT, 1977b, p. 69 [**A. longa*; OD]. Shell large, massive, with subrhomboidal to subpentagonal outline and wide delthyrium; ventral interior with thick callus deposits and massive dental adminicula that converge to simulate delthyrial plate; broad, thick myophragm present apically; ventral muscle field deeply impressed, lanceolate; ovarian pits numerous; dorsal interior with long, diverging adminicula that delimit dorsal adductor field; microornament unknown. *Carboniferous (Pennsylvanian)*: Arctic Siberia.—FIG. 1156,2a–e. **A. longa*; holotype, ventral, dorsal, anterior, posterior, and lateral views, $\times 1$ (new).

Nodaea TACHIBANA, 1981b, p. 67 [**N. okubo*; OD]. Medium size; cardinal extremities rounded; delthyrium with apical deltidium; fold and sulcus well developed, nonplicate; lateral slopes with 5 or 6 low, broad, rounded simple plicae; microornament of fine capillae; ventral interior with thin, subparallel dental adminicula, lacking median ridge or septum; dorsal interior with short, divergent adminicula; shell material thin; otherwise similar to *Crassumbo*. *Carboniferous (Tournaisian)*: Japan.—FIG. 1156,1a–c. **N. okubo*; a, holotype, ventral valve, $\times 0.7$; b, dorsal valve, $\times 1.2$; c, microornament, $\times 3.5$ (Tachibana, 1981b).

Roespirifer WATERHOUSE & PIYASIN, 1970, p. 156 [**R. ruinosus*; OD]. Small to medium, transversely subovate; fold and sulcus lacking; flanks smooth; microornament of numerous fine papillae only; dorsal adminicula long. *Permian (Guadalupian)*: Thailand.—FIG. 1156,4a–d. **R. ruinosus*; a–c, ventral valve, dorsal interior, ventral interior, $\times 2$; d, microornament, $\times 10$ (Waterhouse & Piyasin, 1970).

Family INGELARELLIDAE Campbell, 1959

[*nom. transl.* ARCHBOLD & THOMAS, 1986, p. 582, ex Ingelarellinae CAMPBELL, 1959a, p. 333]

[Materials for this family prepared by J. L. Carter]

Microornament of quincuncially arranged elongate grooves and ridges; dental adminicula present. [The genera in this family are differentiated and assigned to subfamilies on the basis of microornament, the nature of which is poorly known for several genera.] *Carboniferous (Visean)–Permian (Lopingian)*.

Subfamily INGELARELLINAE Campbell, 1959

[Ingelarellinae CAMPBELL, 1959a, p. 333]

Spinules absent; dorsal adminicula well developed. *Carboniferous (Visean)–Permian (Lopingian)*.

Ingelarella CAMPBELL, 1959a, p. 340 [**I. angulata*; OD]. Medium to very large, biconvex, usually transverse; fold and sulcus generally present, variably developed; sulcus with or without median groove, sometimes with pair of weak plicae; lateral slopes smooth or with several broad, low plicae; microornament of elongate grooves arranged in quincunx; interior with well-developed ventral and dorsal adminicula; dorsal median septum absent, weak myophragm commonly present well anterior to cardinalia. *Permian*: Australia, New Zealand.—FIG. 1157,3a–e. **I. angulata*; a–c, holotype, ventral, dorsal, and anterior views, $\times 1$; d–e, transverse sections, $\times 1$ (Campbell, 1959a).—FIG. 1157,3f. *I. profunda* (CAMPBELL); microornament, $\times 10$ (Armstrong, 1970b).

?**Ambikella** SAHNI & SRIVASTAVA, 1956, p. 207 [**A. fructiformis*; OD]. Morphology inadequately known. Seemingly similar to *Ingelarella* but based on a single poorly preserved specimen. *Carboniferous (?Pennsylvanian)*: India.—FIG. 1157,2a–d. **A. fructiformis*; a–c, ventral, dorsal, posterior views, $\times 1$; d, oblique-posterior view, enlarged (Sahni & Srivastava, 1956).

Fredericksia PAECKELMANN, 1931, p. 48, *nom. nov. pro Munia* FREDERIKS, 1918a, p. 88, *non* HODGE, 1836

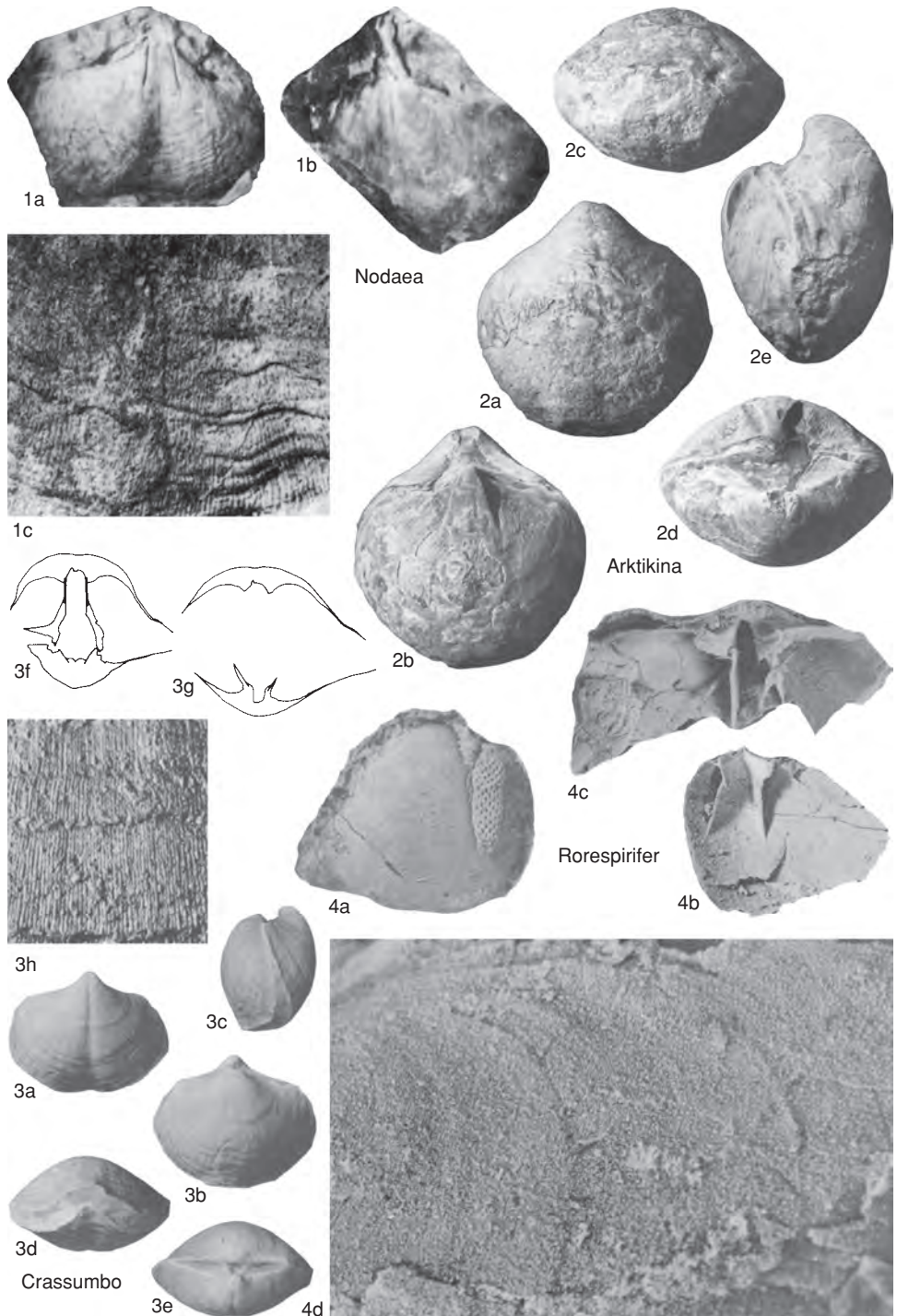


FIG. 1156. Crassumbidae (p. 1758).

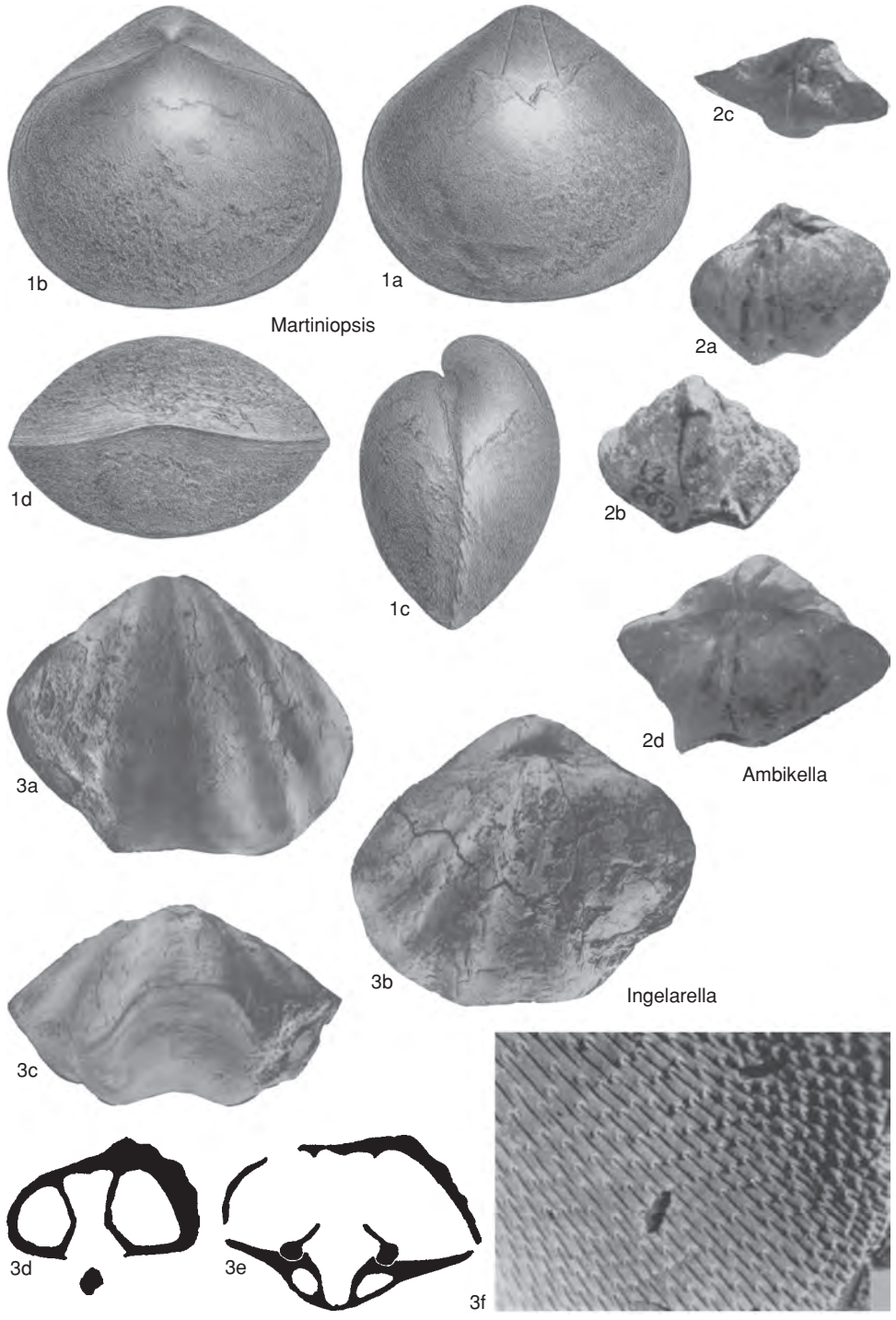


FIG. 1157. Ingelarellidae (p. 1758–1762).

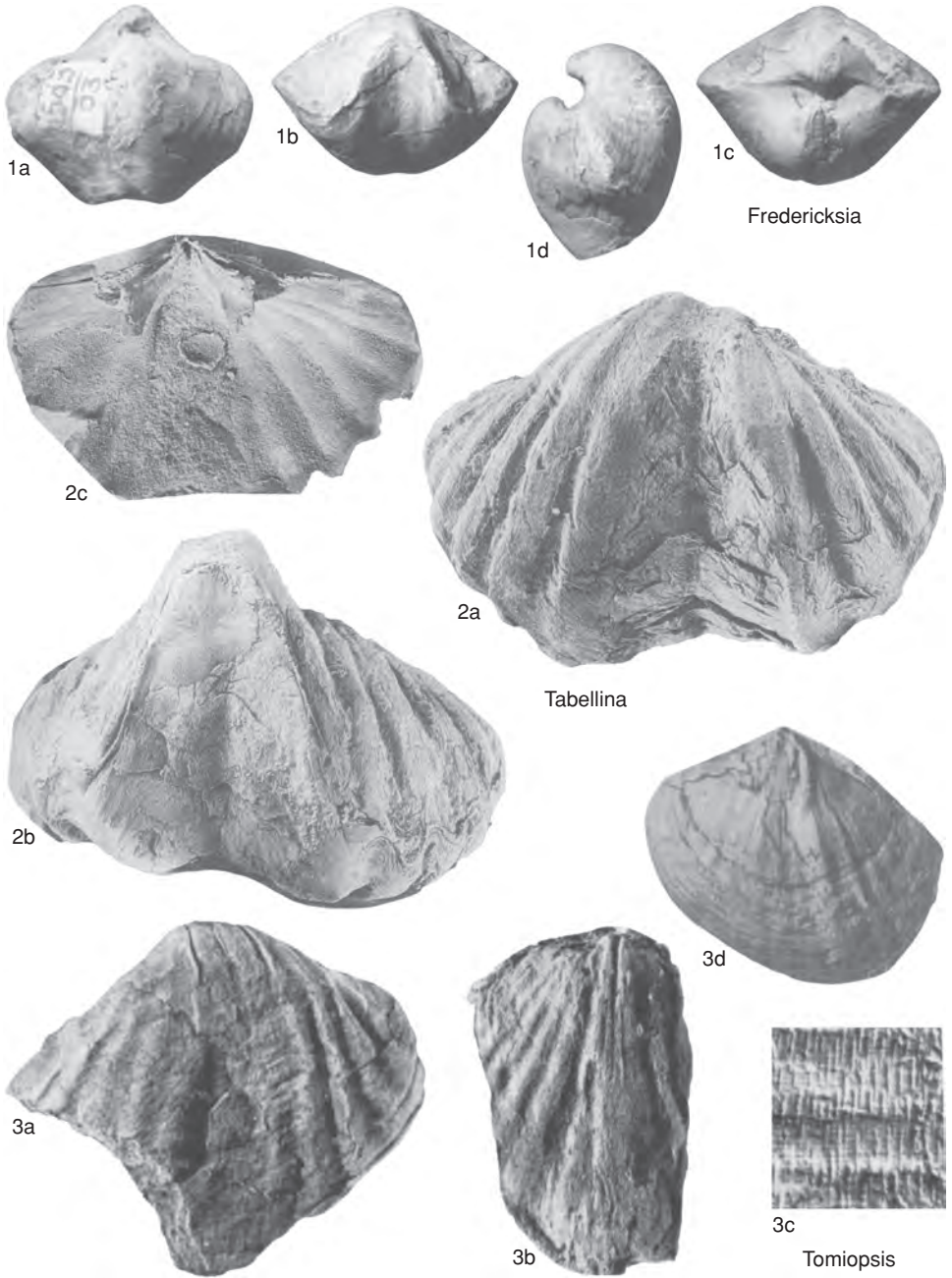


FIG. 1158. Ingelarellidae (p. 1758–1762).

[**Spiriferina* (*Mentzelia*) *simensis* CHERNYSHEV, 1902, p. 514; OD]. Small, moderately biconvex, outline subovate to subpentagonal; fold and sulcus moderately to well developed; lateral slopes with several indistinct plications; ventral interior with thin dental adminicula, septum absent; dorsal interior with moderately long dorsal adminicula; microornament of fine, discontinuous radial grooves; otherwise similar to *Tomioopsis*. *Carboniferous* (*Pennsylvanian*)—*Permian* (*Cisuralian*): Urals, Russia.—FIG. 1158, 1a–d. **F. simensis* (CHERNYSHEV); holotype, dorsal, anterior, posterior, and lateral views, $\times 2$ (new).

Martiniopsis WAAGEN, 1883a, p. 524 [**M. inflata*; SD ETHERIDGE in JACK & ETHERIDGE, 1892, p. 238]. Small to medium size; outline subovate; ventral interarea very small, narrow; delthyrium open; fold and sulcus weakly to moderately developed or absent; macroornament absent; microornament of fine, elongate pits or grooves and fine, regular growth lines; ventral interior with long, slender, closely set, subparallel dental adminicula; dorsal interior with short to long adminicula. *Carboniferous* (*Pennsylvanian*)—*Permian* (*Lopingian*): Europe, Asia.—FIG. 1157, 1a–d. **M. inflata*, Lopingian, Pakistan; ventral, dorsal, lateral, and anterior views, $\times 1$ (Waagen, 1883a).

Tabellina WATERHOUSE, 1986b, p. 4 [**Ingelarella denmeadi* CAMPBELL, 1961b, p. 171; OD]. Lateral slopes strongly plicate; dorsal interior lacking plates or with very short dorsal adminicula; otherwise similar to *Tomioopsis*. *Carboniferous* (*Pennsylvanian*): Australia.—FIG. 1158, 2a–c. **T. denmeadi* (CAMPBELL); a–b, holotype, ventral and anterior views; c, dorsal interior, $\times 1$ (Campbell, 1961b).

Tomioopsis BENEDIKTOVA, 1956, p. 169, *nom. conserv.* ICZN Opinion 1395, 1986, p. 146, *non Tomioopsis* COPE, 1893, p. 317 [**Brachythyris kumpani* YANISHEVSKY, 1935, p. 68; OD] [= *Danzania* PAVLOVA in AFANAS'eva & others, 1988, p. 55 (type, *D. khalginica*, OD)]. Small to medium size; outline transversely to longitudinally rounded; fold and sulcus usually developed; sulcus, when present, rounded or sometimes with 1 or 2 weak plicae; lateral slopes smooth or more commonly with several low, wide, simple plications; anterior commissure rectimarginate to uniplicate, rarely parasulcate; ventral interior with subparallel dental adminicula enclosing moderately impressed muscle field; dorsal interior with short to long subparallel dorsal adminicula and short to moderately long, stout median septum; microornament consisting of fine, simple, elongate, narrow grooves crudely to symmetrically arranged in quincunx. *Carboniferous* (*Visean*)—*Permian* (*Lopingian*): Russia, Asia.—FIG. 1158, 3a–c. **T. kumpani* (YANISHEVSKY), upper Visean or Namurian, Kuznets basin; a–b, spalled ventral exterior and dorsal internal mold showing median septum, $\times 1$; c, microornament of external mold, $\times 10$

(Sokolskaya, 1959).—FIG. 1158, 3d. *T. khalginica* PAVLOVA, Visean, Mongolia; holotype, ventral valve, $\times 1$ (Afanas'eva & others, 1988).

Subfamily NOTOSPIRIFERINAE Archbold & Thomas, 1986

[Notospiriferinae ARCHBOLD & THOMAS, 1986, p. 584]

Fold and sulcus well developed; microornament of quincuncially arranged grooves and ridges, with anteriorly directed spinules at posterior ends of short grooves, and with deep, elongate globose pits extending into secondary layer under spinules; dorsal adminicula short or absent. *Permian*.

Notospirifer HARRINGTON, 1955, p. 115 [**Spirifer darwini* MORRIS, 1845, p. 279; OD]. Transversely subovate; fold and sulcus well developed, smooth; lateral slopes with moderately strong plicae; dorsal adminicula short or absent; pits penetrating fibrous layer under spinules. *Permian*: Australia.—FIG. 1159, 1a–e. **N. darwini* (MORRIS); a–d, holotype, lateral, dorsal, ventral, and anterior views, $\times 1$ (Harrington, 1955); e, microornament, $\times 10$ (Armstrong, 1970b).

Farmerella CLARKE, 1992, p. 73 [**F. exoporosa*; OD]. Externally and internally homeomorphic with *Glendonina* but with microornament as in *Notospirifer*. *Permian* (*Sakmarian*–*Artinskian*): Tasmania.—FIG. 1159, 2a–c. **F. exoporosa*; a–b, holotype, dorsal and ventral views of internal mold, $\times 1$; c, external mold of microornament, $\times 20$ (Clarke, 1992).

Subfamily GLENDONIINAE Clarke, 1992

[Glendoninae CLARKE, 1992, p. 75]

Microornament of quincuncially arranged, shallow, elongate grooves terminated anteriorly by low, elongate spinules and shallow, elongate pits. *Upper Carboniferous* (?*Pennsylvanian*), *Permian* (*Lopingian*).

Glendonina McCLUNG & ARMSTRONG, 1978, p. 2 [**G. ulladullensis*; OD]. Small to medium size, subequally biconvex; transversely subovate to subrhomboidal in outline; fold and sulcus narrow; lateral slopes with several high, subangular plicae; sulcus with single, narrow, median plica; fold usually with distinct median groove; dorsal interior usually with variably long adminicula. *Permian* (*Lopingian*): eastern Australia, Tasmania.—FIG. 1160, 1a–d. **G. ulladullensis*; a–c, holotype, anterior, ventral, and dorsal views of internal mold, $\times 1$;

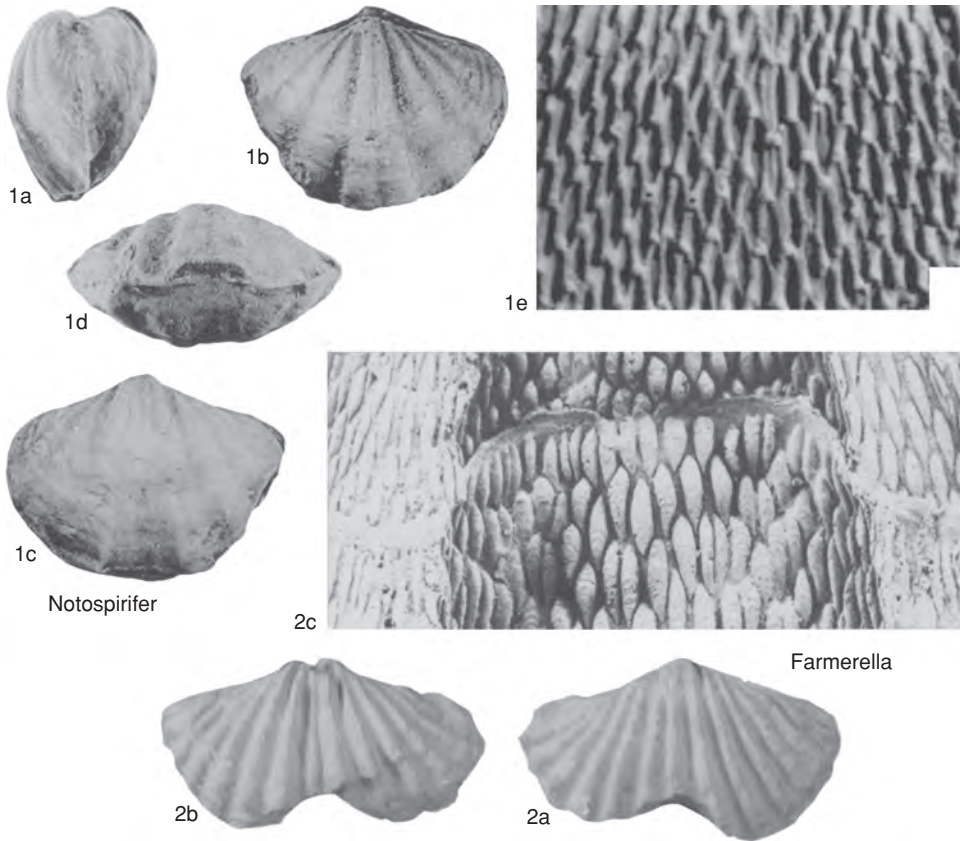


FIG. 1159. Ingelarellidae (p. 1762).

d, microornament, $\times 15$ (McClung & Armstrong, 1978).

Birchsella CLARKE, 1987, p. 282 [**B. spinosa*; OD]. Fold and sulcus smooth, lateral slopes with few low, rounded plications; ventral valve interior with dental adminicula buried in thick callus; dorsal valve interior lacking adminicula; otherwise similar to *Glendonina*. *Permian (Lopingian)*: Tasmania.—FIG. 1161, 2*a-d*. **B. spinosa*; *a*, dorsal exterior; *b-c*, ventral and dorsal views of internal mold, $\times 1$; *d*, microornament, $\times 10$ (Clarke, 1987).

Homevalaria WATERHOUSE, 1986a, p. 110 [**Ingelarella ovata* CAMPBELL, 1961b, p. 177; OD]. Microornament of quincuncially arranged, elongate grooves posteriorly terminated by low C-spines; otherwise closely similar to *Ingelarella*. *Permian (Sakmarian)*: Queensland.—FIG. 1160, 2*a-e*. **H. ovata* (CAMP-

BELL); *a-c*, holotype, ventral, dorsal, and anterior views of internal mold; *d*, dorsal interior, $\times 1$; *e*, microornament, $\times 8$ (Campbell, 1961b).

Kelsovia CLARKE, 1990, p. 70 [**K. superba*; OD]. Small to medium size; fold and sulcus well developed, smooth or very weakly grooved, flaring anteriorly; lateral slopes with well-developed, rounded plications; ventral interior with dental adminicula and minor posterolateral thickening; dorsal interior with short, flexed dorsal adminicula and long, low myophragm; microornament as in *Glendonina*. *Carboniferous (?Pennsylvanian), ?lower Permian*: Tasmania.—FIG. 1161, 1*a-e*. **K. superba*; *a-b*, holotype, dorsal exterior and dorsal internal mold counterpart, $\times 1$; *c-e*, paratype, ventral, dorsal, and posterior views of internal mold, $\times 1$ (Clarke, 1990).

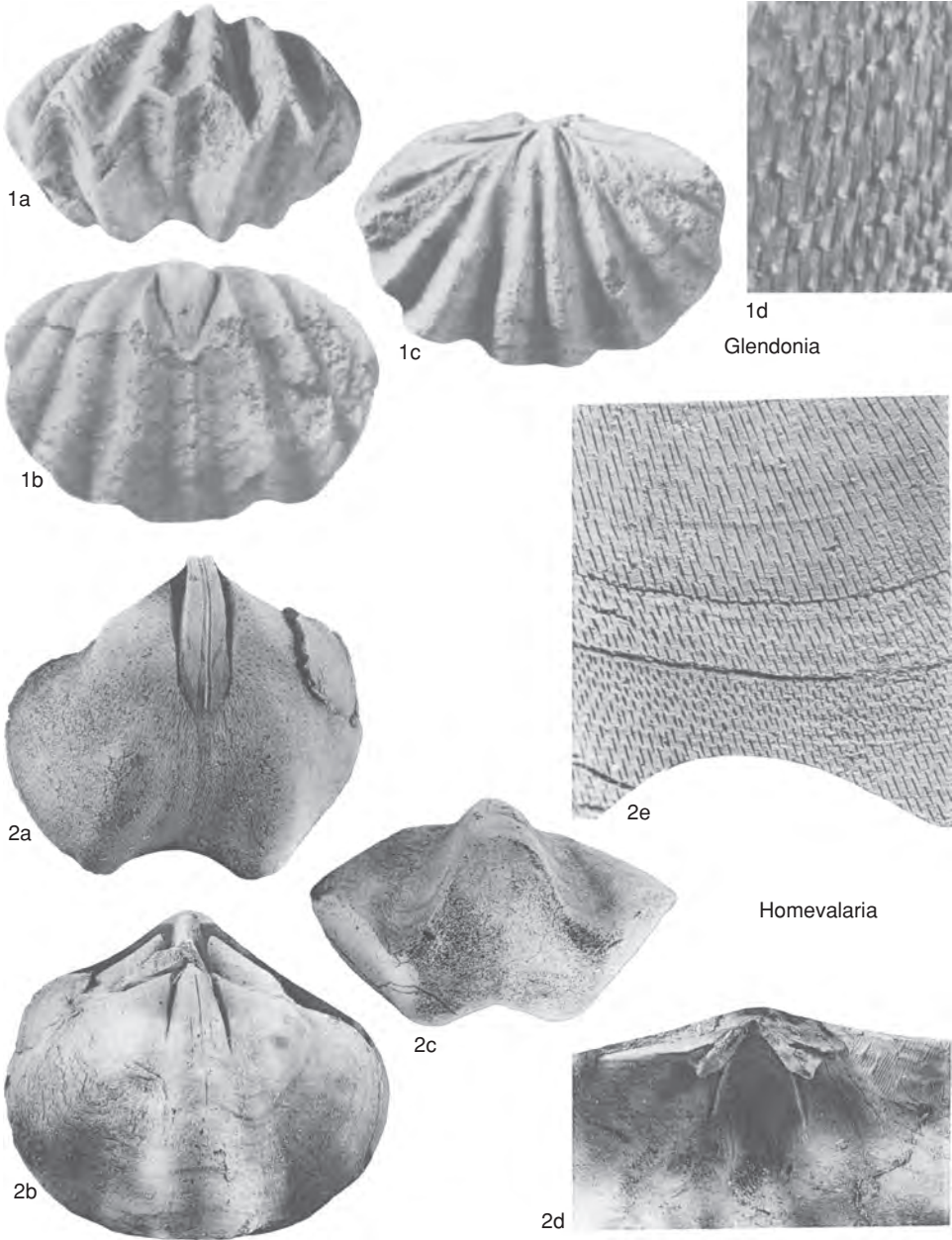


FIG. 1160. Ingelarellidae (p. 1762–1763).

Family GERKISPIRIDAE Carter, 1985

[Gerkispiridae CARTER, 1985, p. 376]

[Materials for this family prepared by J. L. Carter]

Ovate to transverse; lateral slopes costate; hinge line short; fold-sulcus moderately to

well developed; delthyrium with low, thin, flaring, stegidial plates; short, thin, dental adminicula commonly with low apical myophragm; short converging crural plates and small ctenophoridium present; microornament of quincuncially arranged, very

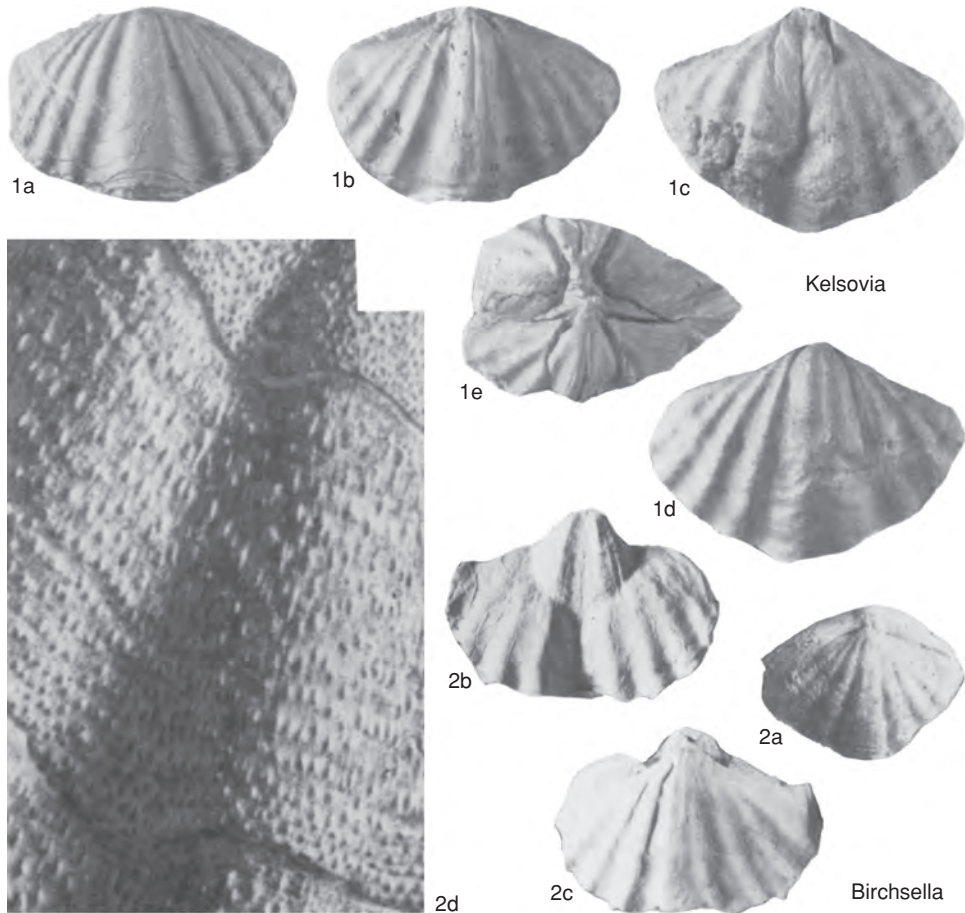


FIG. 1161. Ingelarellidae (p. 1763).

fine, uniramous, hollow spinules or papillae that originate in fibrous layer. *Upper Devonian (lower Famennian)–Carboniferous (upper Tournaisian)*.

Gerkispira CARTER, 1983, p. 72 [**G. spinosa*; OD]. Small, subequally biconvex; strongly transverse with rounded lateral extremities; ventral interarea acutely triangular, moderately low, apsacline; delthyrium with narrow, laterally flaring stegidial plates; fold and sulcus moderately well developed but poorly delimited from flanks; numerous simple or rarely bifurcating costae on flanks and fold-sulcus; numerous fine, hollow, erect spinules on crests of costae. *Carboniferous (upper Tournaisian)*: USA (Iowa). —FIG. 1162, 2a–f. **G. spinosa*; a–e, ventral, dorsal, anterior, posterior, and lateral views, $\times 2$; f, microornament, $\times 5$ (new).

Acanthospirina SCHUCHERT & LEVENE, 1929, p. 119, *nom. nov. pro Acanthospira* WELLER, 1914, p. 418,

non REINSCH, 1877 [**Spirifer aciculifera* ROWLEY, 1893, p. 307; OD]. Very small; ventribiconvex; moderately transverse, with slightly rounded cardinal extremities; ventral interarea moderately high, flattened or weakly concave, procline; stegidium short, convex; lateral slopes with few simple, rounded costellae; fold and sulcus narrow, smooth; sulcus well developed; fold low, flattened, well delimited by deep interspaces; numerous fine, hollow spinules crudely arranged in quincunx; spinule bases extending anteriorly as longitudinally elongate tubules within primary layer; dental adminicula short, slender, subparallel; ventral septum absent; very short crural plates and median callus present. *Upper Devonian (upper Famennian)*: North America. —FIG. 1162, 3a–b. **A. aciculifera* (ROWLEY), Missouri, USA; ventral, dorsal valve, $\times 6$ (new).

Oiosia COOPER & DUTRO, 1982, p. 117 [**Brachythyris putilla* STAINBROOK, 1947, p. 322; OD]. Small, ventribiconvex; outline subovate to subquadrate;

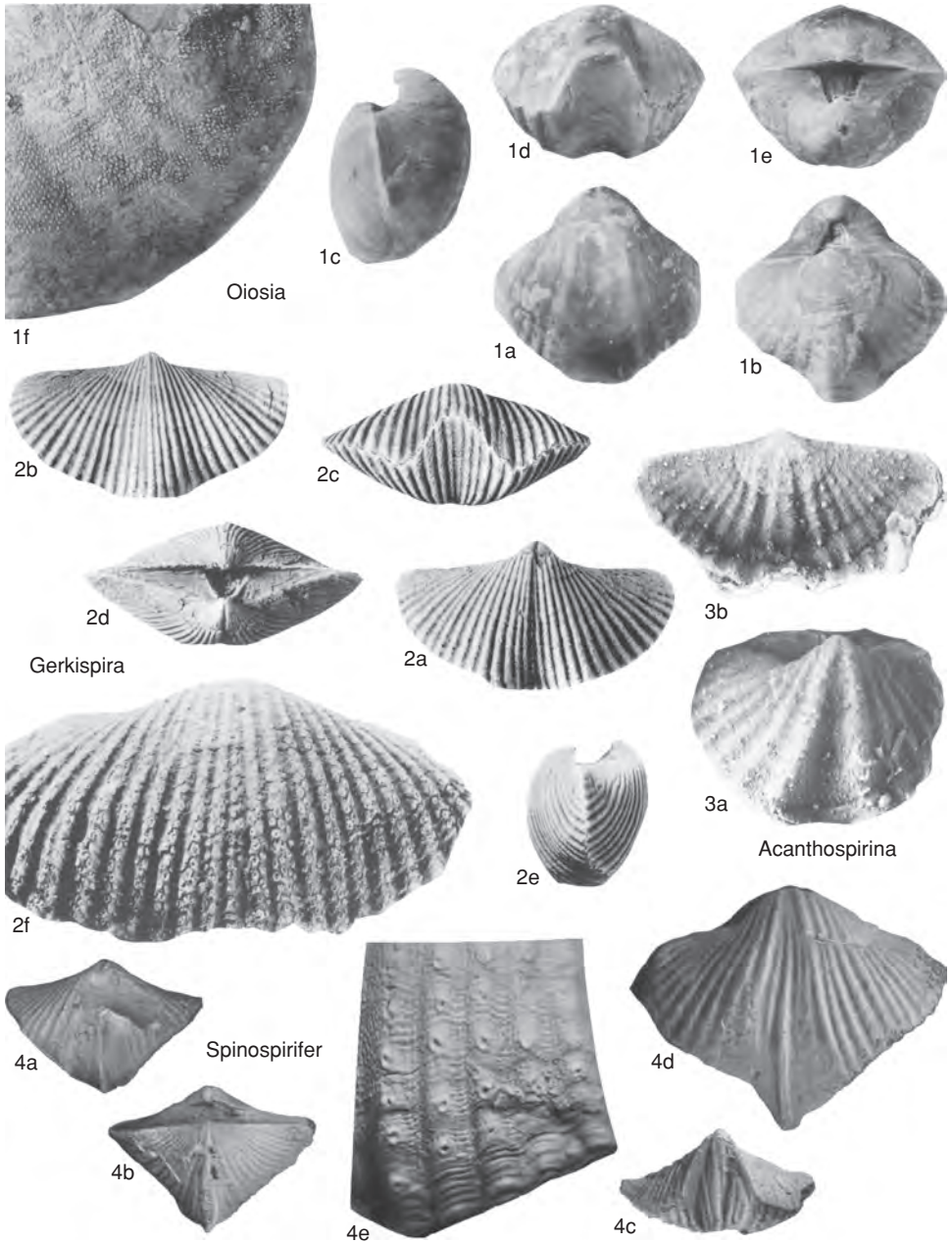


FIG. 1162. Gerkispiridae (p. 1765–1767).

cardinal extremities well rounded, ventral interarea narrow; delthyrium partially closed by stegidial plates; fold and sulcus well developed, smooth, rounded, flaring slightly anteriorly; lateral slopes with several weak, low, simple plicae; very fine

hollow microspines or papillae arranged in quincunx; otherwise similar to *Punctothyris*. *Upper Devonian (upper Famennian)*: USA (New Mexico).—FIG. 1162, 1a–f. **O. putilla* (STAINBROOK); a–e, ventral, dorsal, lateral, anterior, and posterior views,

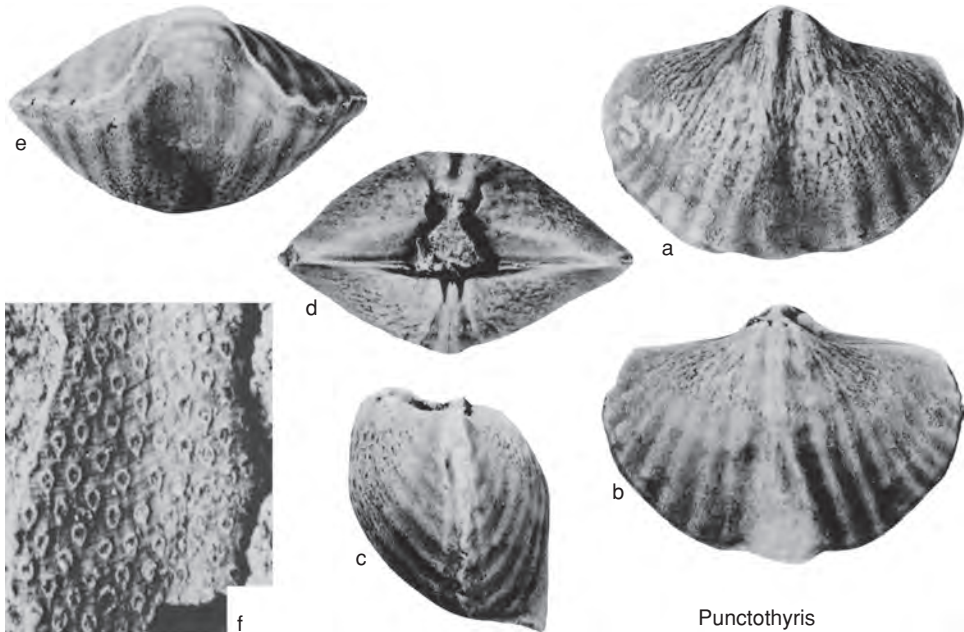


FIG. 1163. Gerkispiridae (p. 1767).

×2; *f*, microornament, ×5 (Cooper & Dutro, 1982).

Punctothyris HYDE, 1953, p. 287 [**P. argus*; OD].

Small to medium size; ovate to slightly transverse; fold and sulcus well delimited; both valves with moderate number of simple costae on lateral slopes; sulcus with one to several simple costae; sulcus-bounding costae prominent and giving rise to lateral sulcal costae, when present, and occasionally to nearest costae on flanks; numerous fine, hollow, erect or semierect spinules or papillae over entire surface, including interspaces. *Carboniferous (middle Tournaisian–upper Tournaisian)*: USA (Ohio, Missouri, Oklahoma, Virginia).—FIG. 1163*a–f*. **P. argus*; *a–e*, holotype, ventral, dorsal, lateral, posterior, and anterior views, ×3; *f*, microornament, ×22 (Carter, 1985).

Spinospirifer MARTYNOVA, 1961, p. 106, *non Spinospirifer* BIERNAT, 1966 [**Spirifer* (?*Lamellispirifer*) *nuraensis* SIMORIN, 1956, p. 163; OD]. Small to medium size, biconvex to ventribiconvex, transverse; cardinal angles acute; ventral interarea low to medium height, curved, apsacline; fold and sulcus costate, with strong, rounded, median rib in sulcus and 1 or 2 lateral pairs added anteriorly; flanks with numerous rounded costae that may bifurcate near maximum length; crests of costae with open pustules; microornament of well-defined growth lines and weak capillae; dental plates short, thin. *Upper Devonian (lower Famennian)*: Kazakh-

stan.—FIG. 1162, *4a–e*. **S. nuraensis* (SIMORIN); *a–c*, ventral, dorsal, and anterior views, ×1; *d*, ventral valve enlarged, ×1.5; *e*, microornament, ×12 (new).

Family PERISSOTHYRIDIDAE
Carter, 1994

[Perissothyrididae CARTER in CARTER & others, 1994, p. 342]

[Materials for this family prepared by J. L. Carter]

Subequally biconvex; transversely sub-ovate; low concave interareas present in both valves; fold moderately well developed; sulcus weak, shallow, poorly delimited; lateral slopes with weak simple ribbing; microornament absent; delthyrium very wide, partially occluded apically by so-called pseudo-delthyrial plate (possibly fused dental flanges); ventral valve much thickened with callus; dental adminicula absent; large, wide, clublike teeth attached to posterolateral valve wall; wide, dorsally reflexed dental flanges directed medially from bases of teeth; dorsal interior with large ctenophoridium supported by short median ridge; inner socket

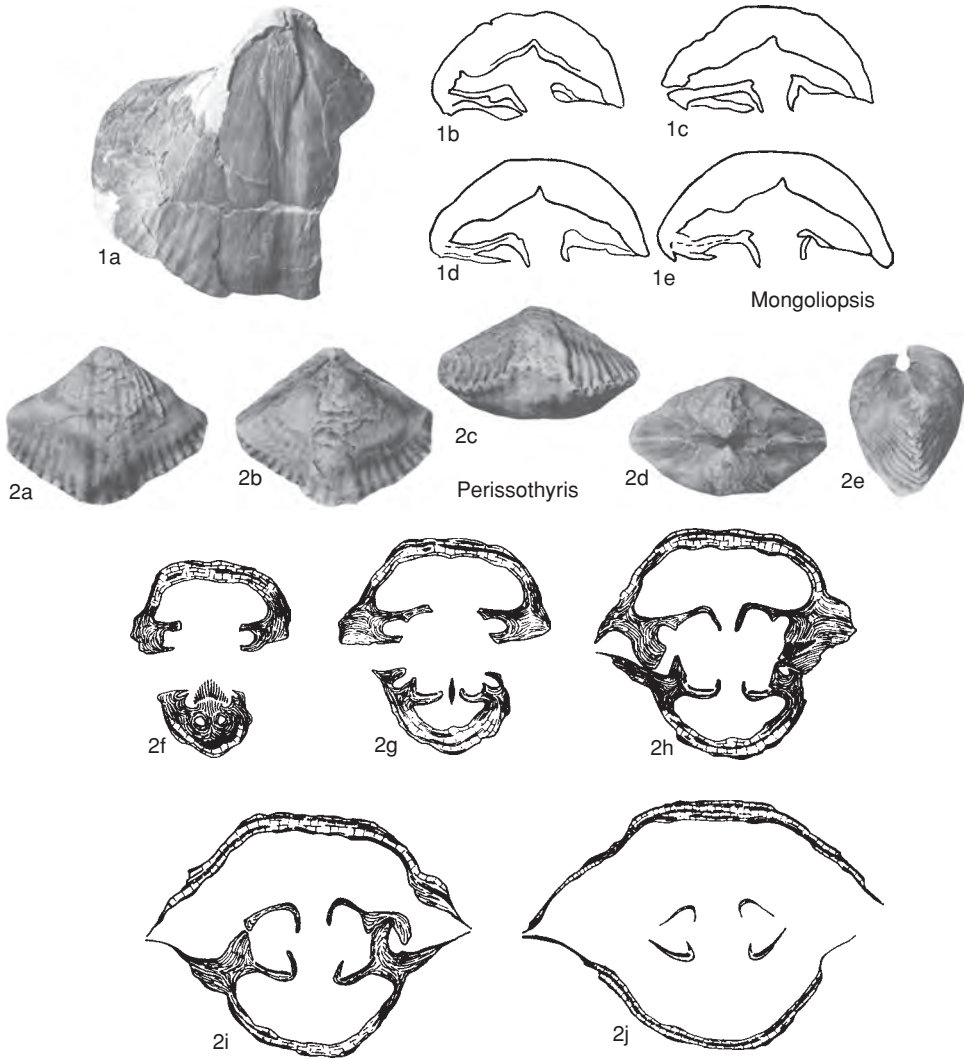


FIG. 1164. Perissothyrididae (p. 1768).

ridges thick, high; crural bases medially directed, with ventrally reflexed medial flanges. *Carboniferous (Mississippian)*.

Perissothyris CARTER, 1967a, p. 587 [**P. masonensis*; OD]. Medium sized; outline asymmetrical; dorsibiconvex; both valves entirely ribbed, with numerous weak, simple costae; dorsal umbo much more inflated than ventral; both valves with large, chordate muscle fields. *Carboniferous (Visean)*: USA (Texas).—FIG. 1164, 2a–j. **P. masonensis*; a–e, holotype, ventral, dorsal, anterior, posterior, and

lateral views, x1; f–j, transverse sections, x2.5 (Carter, 1967a).

Mongoliopsis GRUNT, 1977a, p. 79 [**M. orkheinensis*; OD]. Medium to large; outline subovate; lateral slopes smooth or with weak, simple plications; ventral interarea low, strongly incurved; short, very thick median ridge in ventral umbonal region; dorsal interior with short, thick median ridge and pair of subparallel longitudinal ridges; otherwise similar to *Perissothyris*. *Carboniferous (Mississippian)*: western Mongolia.—FIG. 1164, 1a–e. **M. orkheinensis*; a, holotype, spalled ventral valve, x1; b–e, transverse sections, x2.6 (Grunt, 1977a).