MARATHONITOIDEA

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Superfamily MARATHONITOIDEA Ruzhentsev, 1938

[*nom. transl.* Ruzhentsev, 1957, p. 58, *ex* Marathonitinae Ruzhentsev, 1938, p. 258]

Conch usually thickly discoidal (rarely thinly lenticular as mature modification), with umbilicus ranging from narrow to closed. Shell surfaces lack conspicuous sculpture, but growth lines may be accentuated into subtle asymmetric ridges with shallow backward sag at midflank and shallowly rounded hyponomic sinus. Mature modifications commonly comprise slight to extreme geniculation of mature body chamber, accompanied by changes in whorl section and by constriction at terminal peristome. Basic suture comprises 20 lobes, 18 of which originated by tripartition and subsequent full isolation of subdivisions of primary external lateral, umbilical, and internal lateral lobes (L, U, and I [Russian]). Up to four additional lobes were produced by subsequent bifurcation of dorsal subdivision of L and of some elements in umbilical complex. External and internal lateral lobes initially tridentate or bidentate, but external laterals became complexly and irregularly digitate in course of evolution. *Pennsylvanian (Moscovian* [rare in *Atokan, Desmoinesian])–Lopingian (Wuchiapingian).*

Family MARATHONITIDAE Ruzhentsev, 1938

[*nom. transl.* Ruzhentsev, 1940e, p. 124, *ex* Marathonitinae Ruzhentsev, 1938, p. 258] [=Kargalitinae Ruzhentsev, 1960d, p. 226; ?=Jilingitinae Liang, 1982, p. 651]

Ancestral marathonitoids characterized by simple, bidentate, or tridentate external and internal lateral lobes. Conch involute, subquadrate in section. Mature modifications commonly comprise slight to extreme geniculation and terminal constriction, but lappets are unknown. Sutures maintain basic tripartition of external lateral lobe ($L > L_2L_1L_2$), umbilical lobe ($U > U_2U_1U_2$), and internal lateral lobe ($I > I_2I_1I_2$). Dorsal subdivision of primary umbilical lobe lies internally near umbilical seam, so that basic sutural formula is: $(V_1V_1)L_2L_1L_2U_2U_1{:}U_2I_2I_1I_2D$ [Russian]. [Intraspecific sutural variation is extreme, and third-order subdivisions of lobes may appear sporadically (e.g., Ruzhentsev, 1956b, fig. 88), especially in first external lateral lobe. In light of this variation, recognition of two subfamilies based primarily upon bidentate versus tridentate form of the first external lateral lobe (e.g., Bogoslovskaia, 1990) is untenable. Detailed biostratigraphic studies of Pennsylvanian ancestors (Boardman, Work, & Mapes, 1994) add support to the contention that subfamilies defined on details of lobe subdivision are polyphyletic. Dorsal lobe is trifid in ancestral forms but became only tridentate and eventually entire in some descendants (Ruzhentsev & Bogoslovskaia, 1978). Terminal progenesis resulted in sutural simplification (Glenister & Furnish, 1988a). Marathonitids are characteristic elements of Cisuralian ammonoid faunas (e.g., Ruzhentsev, 1956b) but appeared in the Middle Pennsylvanian (rare in Atokan, Desmoinesian; Chatelain, 1984) and ranged to rarity and extinction in the Guadalupian (Glenister & Furnish, 1988a).] *Pennsylvanian (Moscovian* [rare in *Atokan, Desmoinesian])–Guadalupian (Capitanian).*

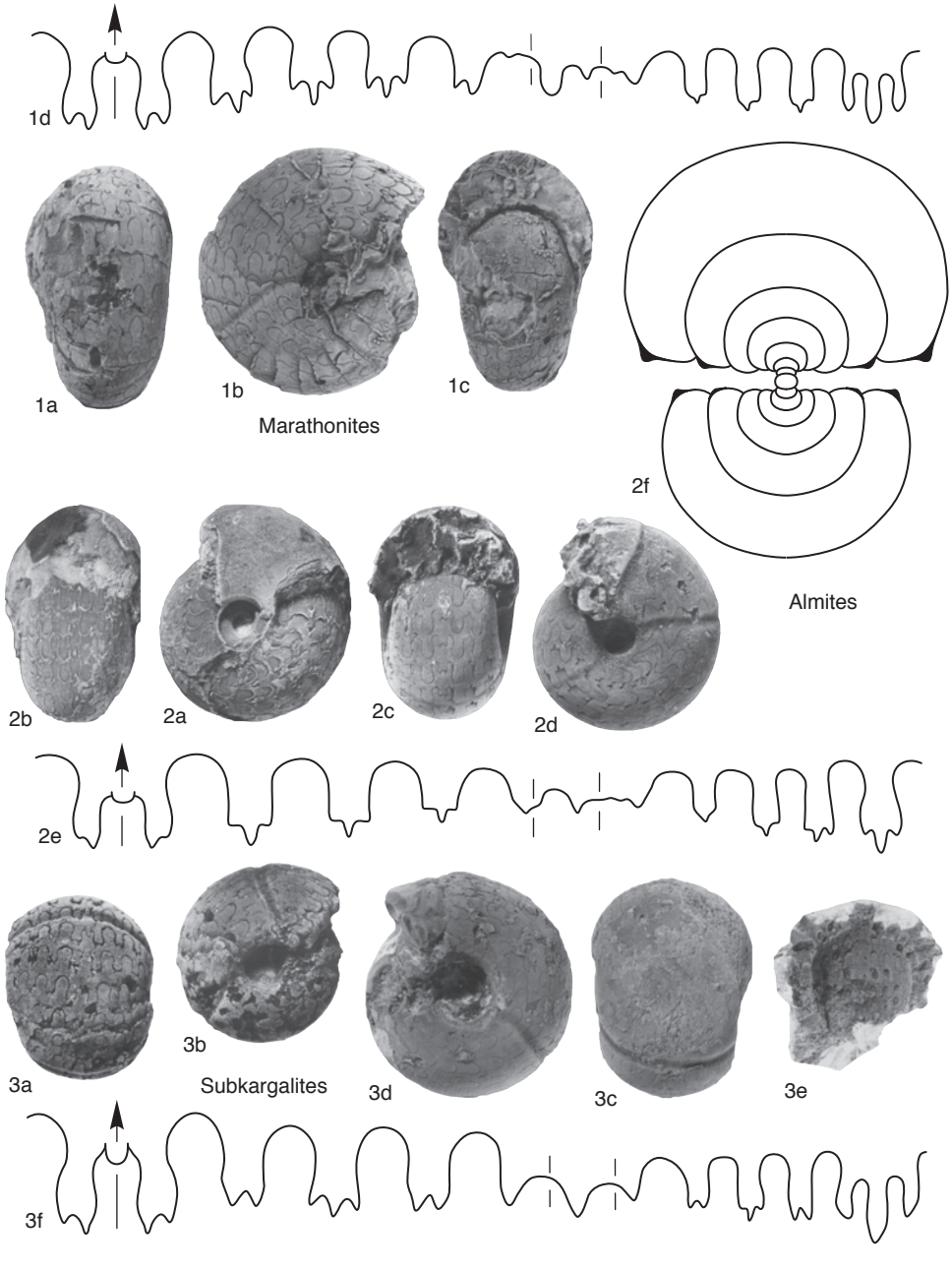

FIG. 98. Marathonitidae (p. 160–163).

Marathonites Böse, 1919, p. 133 [**M. J. P. Smithi;* OD] [=*Policeras* Tumanskaia, 1939, p. 18 (type, *Marathonites vidriensis* Böse, 1919, p. 141, OD); =*Martites* Tumanskaia, 1949, p. 68 (type, *Marathonites sulcatus* Böse, 1919, p. 139, OD)]. Marathonitids in which the first external lateral lobe resembles the other two external lateral elements in being symmetrically tridentate. Dorsal lobe broad and deeply tripartite ($D_2D_1D_2$) to conch diameters in excess of 2 cm. Mature specimens may exhibit weak geniculate coiling, but umbilicus remains open. Three named species. *Pennsylvanian (upper Moscovian–Gzhelian)*: USA (Texas, Oklahoma, Ohio), *Desmoinesian–Virgilian;* Russia and Kazakhstan (Southern Urals), *Gzhelian.*——Fig. 98,*1a–d*. **M. jpsmithi*, upper Gaptank Formation, Virgilian, Wolfcamp Hills, western Texas; *a–c*, lectotype (herein), TMM-B34364 (Böse, 1919, pl. 6,*78,81–83*), ×1.67 (new); *d*, topotype, diameter at 23 mm (Miller & Furnish, 1940a).

Almites Tumanskaia, 1941, p. 261 [**Marathonites sellardsi* Plummer & Scott, 1937, p. 146; OD] [?=*Paraperrinites* Tumanskaia, 1939, p. 17 (type, *Perrinites Brouweri* Smith, 1927a, p. 55, OD). The type of *P. brouweri* (MTHD 12791; Smith, 1927a, pl. 14,*1–2*) is a marathonitid, probably *Almites gracilis* (Smith, 1927a); it must be considered the holotype (ICZN *Code*, Article 73, a, i) despite the fact that a cotype (MTHD 12792; Smith, 1927a, pl. 14,*3–4*) is a well-preserved perrinitid, referable to *Perrinites subcumminsi* (Haniel, 1915); =*Neomarathonites* Ruzhentsev, 1950, p. 190 (type, *Marathonites invariabilis* Ruzhentsev, 1933, p. 173, OD)]. Similar to *Marathonites*, but dorsal lobe narrow and weakly tridentate. Twelve species. *Upper Pennsylvanian (Gzhelian)–Cisuralian (Artinskian):* USA (Texas), *Virgilian;* USA (Texas, New Mexico, California, Nevada), Guatemala, Ukraine (Crimea), Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), Austria (Karawanken Mountains), southern China (Guangxi, Guizhou), Indonesia (Timor), *Asselian–Artinskian [Baigendzhinian].*——Fig. 98,*2a–e*. **A. sellardsi* (Plummer & Scott), Admiral Formation, Sakmarian, Coleman County, central Texas; *a–b*, lectotype (herein), TMM-P849 (Plummer & Scott, 1937, pl. 32,*6*), ×2; *c–d*, paralectotype, TMM-P848 (Plummer & Scott, 1937, pl. 32,*3–5*), ×2.67 (new); *e*, diameter at 16 mm (Miller & Furnish, 1940a).——Fig. 98,*2f. A. invariabilis* (Ruzhentsev), Artinskian, Southern Urals, diameter at 9.5 mm (Ruzhentsev, 1940e).

Cardiella Pavlov, 1967, p.76 [**C. gracia*; OD] [=*Aksuites* Pavlov, 1967, p. 77 (type, *A. permicus,* OD)]. Small to medium size marathonitids (1.5–4.0 cm mature diameter), similar to *Almites* in suture and juvenile conch but characterized by moderate to extreme geniculate coiling and modification of cross section in ultimate volution. Terminal restriction reduced apertural area to one-half, accompanied by shell thickening that closed umbilicus and produced deep furrow on internal mold. Ten named species. [*Cardiella* is gradational with *Almites*, representatives of which (e.g., *A. ganti* Smith, 1903) may display umbilical closure and slight geniculation.] *Upper Pennsylvanian (Kasimovian)–Cisuralian (Artinskian):* USA (Texas, Oklahoma, Kansas), *Missourian–Virgilian*; Tajikistan (Pamir), Ukraine (Crimea), Russia and Kazakhstan (Southern Urals), southern China (Guangxi), Indonesia (Timor), USA (Nevada), *Asselian–Artinskian [Baigendzhinian].*——Fig. 99,*1a–e*. **C. gracia*, Kochusu Formation, Bolorian-Kungurian, Pamir; *a–c*, ×1; *d*, diameter at 23 mm; *e*, diameter approximately 15 mm (Leonova, 1981).——Fig. 99,*1f–g*. *C. martodjojoi* Glenister & Furnish, Bitauni beds, Baigendzhinian, Bitauni, Timor, ×1 (Glenister & Furnish, 1987).——Fig. 99,*1h*. *C. shyndensis* Leonova, Bolorian, Pamir, diameter approximately 15 mm (Leonova, 1981).

Jilingites Liang, 1982, p. 651 [**J. bidentus*; OD]. Incompletely understood taxon, resembling *Kargalites*, but differing in bidentate form of external lateral lobes. Two species. *Guadalupian (?Wordian, Capitanian):* China (Jilin), Japan (Kitakami).

Kargalites Ruzhentsev, 1938, p. 259 [**Marathonites timorensis typica* Ruzhentsev, 1933, p. 175; OD]. Marathonitids in which dorsal lobe is narrow and undivided to weakly tridentate. Eleven named species. [Intraspecific variation is extreme in this genus, even for marathonitids. Populations of the type species display ventral prongs that range from undivided to bidentate; irregularly bidentate first external lateral lobes that may possess third-order subdivision of the denticles; and a dorsal lobe that ranges from undivided through asymmetrically bidentate to narrowly tridentate (Ruzhentsev, 1956b).] *Upper Pennsylvanian (Gzhelian)–Cisuralian (Kungurian):* USA (Texas, Ohio), *Virgilian;* Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), China (Guangxi), Indonesia (Timor), Mexico (Chiapas), Canada (Ellesmere Island), Japan (Kitakami), *Asselian–Kungurian.*——Fig. 100,*1a–f*. **K. typicus* (Ruzhentsev), Aktastinian, Artinskian, Southern Urals; *a–d,* ×1; *e*, diameter at 20 mm; *f,* diameter at 10 mm (Ruzhentsev, 1956b).

Promarathonites A. Popov, 1992, p. 58 [**P. maclai* = *P. maklayi* (sic); OD]. Inadequately known group, apparently intermediates morphologically and stratigraphically between *Subkargalites* and *Marathonites*. Characterized by combination of bidentate first external lateral lobe with tridentate second and third external laterals. Three species. *Upper Pennsylvanian:* Uzbekistan (Fergana: Karachatyr Ridge), *Gzhelian;* USA (Texas, Kansas), *Missourian–Virgilian*.

Pseudovidrioceras Ruzhentsev, 1936b, p. 1087 [**Vidrioceras girtyi* Miller & Cline, 1934b, p. 290; OD]. Terminal paedomorphs (smallest, youngest, and rarest genus of Marathonitidae) characterized by small conch (diameter 1.5 cm or less at maturity), compressed whorls (W/D, approximately 0.5), undivided prongs of ventral lobe, three tridentate external lateral lobes, and primary umbilical lobe that is undivided or incipiently trifid. Mature modifications comprise complete

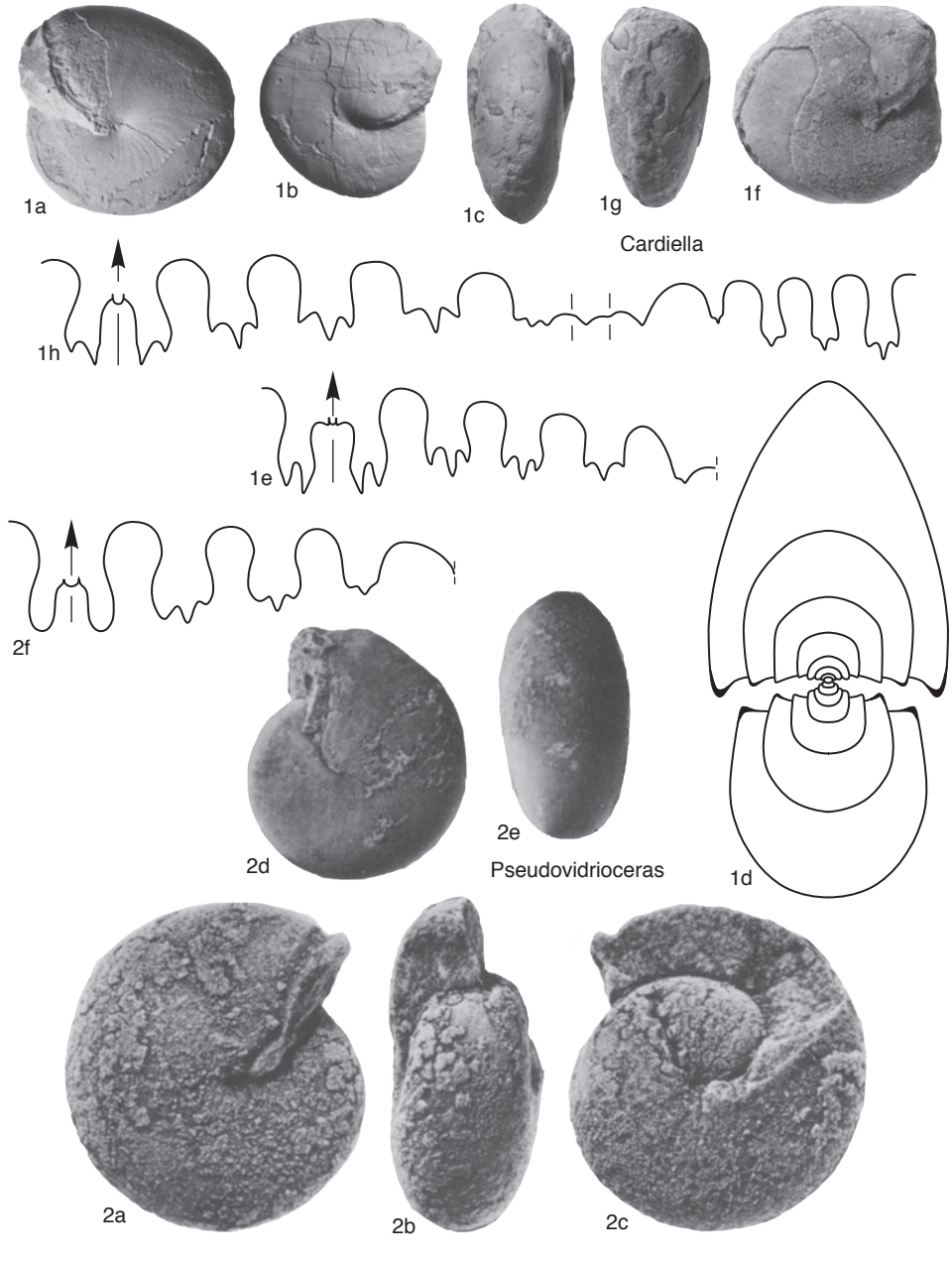

FIG. 99. Marathonitidae (p. 160–161).

closure of umbilicus, subterminal constriction, and formation of narrow U-shaped hyponomic sinus. Four species. *Guadalupian (Roadian–Wordian):* USA (Wyoming, Texas, New Mexico), Italy (Sicily), Ukraine (Crimea), Tajikistan (Pamir).——FIG. 99,*2a–c.* **P. girtyi* (MILLER & CLINE), ×3 (Glenister & Furnish, 1988a).——FIG. 99,*2d–f. P. pygmaeum* (GEMMELLARO); *d–e*, ×3; *f*, diameter at 6.5 mm (Glenister & Furnish, 1988a).

Suakites LEONOVA, 1982, p. 31 [**S. compositus*; OD]. Relatively poorly known but similar generally to other marathonitids and perhaps differing in advanced form of external lateral lobes, all three of which are deeply and asymmetrically tridentate

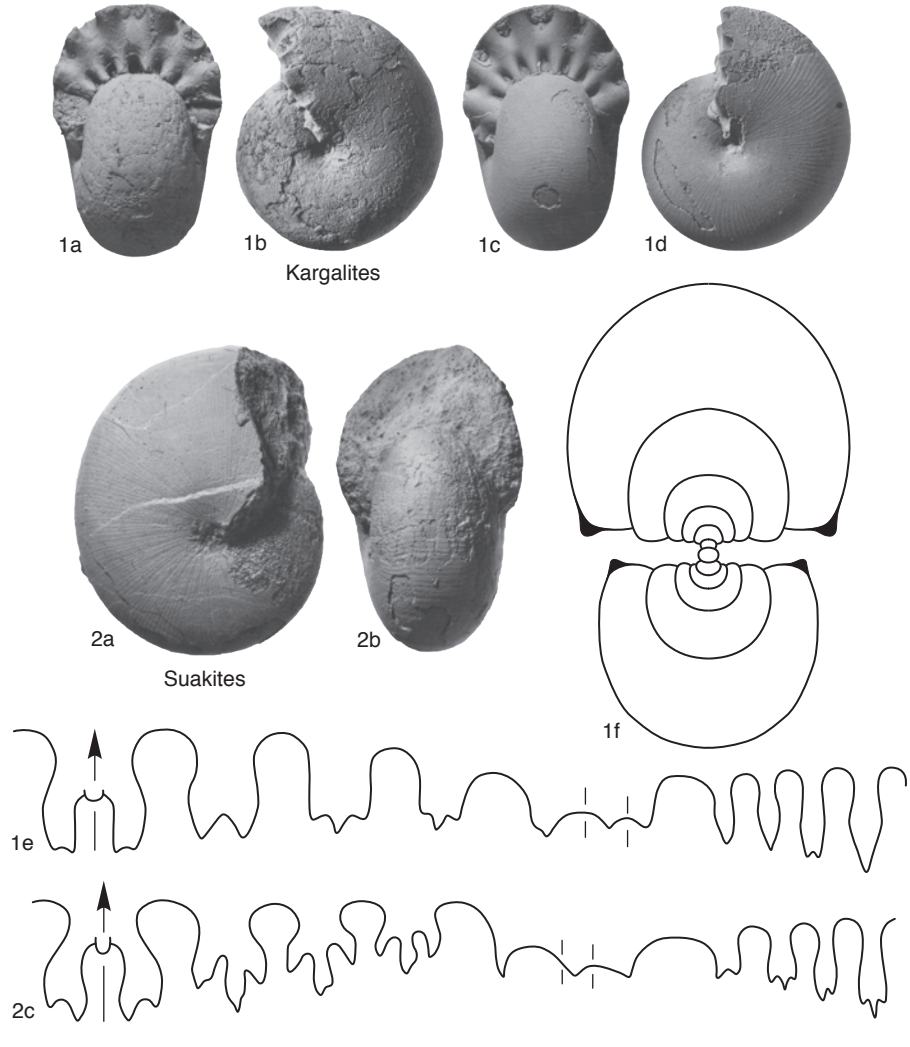

FIG. 100. Marathonitidae (p. 160–162).

and may display secondary crenulation of denticles. One species. [As the marathonitid with the most advanced suture, *Sua kites* resembles *Eohyattoceras*, the ancestral representative of the descendant marathonitoid Hyattoceratidae. *Eohyattoceras* differs primarily (GLENISTER & FURNISH, 1987) in the incipient isolation of a fourth external lateral lobe $L_2 > (L_{2.1}L_{2.2})$]. *Cisuralian (Artinskian):* Pamir.——FIG. 100,*2a–c. *S. compositus*, Kochusu Formation, Bolorian-Kungurian; *a–b*, ×2; *c*, diameter approximately 35 mm (Leonova & Dmitriev, 1989).

Subkargalites RUZHENTSEV, 1950, p. 191 [*?*Marathonites Hargisi sic* BÖSE, 1919, p. 144; OD]. Ancestral marathonitids, similar to *Kargalites*, but dorsal lobe broad and deeply tripartite ($D_2D_1D_2$) to conch diameters exceeding 2 cm. Four named

species. *Middle Pennsylvanian–Cisuralian (Asselian):* USA (Texas, Oklahoma, Kansas), rare in *Atokan, Desmoinesian–Missourian;* Canada (Ellesmere Island), probably *Asselian*; Russia (Southern Urals), Uzbekistan (Fergana: Karachatyr Range), *Kasimovian.*——Fig. 98,*3a–f. *S. hargisi* (Böse), lower Gaptank Formation, Missourian, western Texas; *a–b*, holotype, TMM-B36183 (Böse, 1919, pl. 7,*33–39*), ×2; *c–e*, hypotype, YPM 12938B (external) and YPM 12938C (internal) (Miller, 1930, pl. 39,*1–5*), ×1; *f,* diameter approximately 20 mm (new, suture courtesy of D. M. Work).

Family HYATTOCERATIDAE Miller, Furnish, & Schindewolf, 1957

[*nom. transl.* Glenister & Furnish, 1987, p. 987, *ex* Hyattoceratinae Miller, Furnish, & Schindewolf, 1957, p. 53]

Distinctive advanced marathonitoids characterized by 20–24 sutural elements and complex irregular phylloid serration of external lateral lobes. Conch discoidal, with small to closed umbilicus. Mature modifications occur in advanced forms and include geniculate coiling, modification in whorl section, and penultimate constriction followed by terminal flare of ventral peristome. Spectacular dimorphism is suggested (Davis, Furnish, & Glenister, 1969). [Derivation from the Marathonitidae occurred in the early Permian, plausibly from the marathonitid *Almites*, through the rare ancestral hyattoceratid *Eohyattoceras.* However, abundance is limited to the Guadalupian and Lopingian, where representatives are sporadically common from the Wordian through the Wuchiapingian (Glenister & Furnish, 1987).] *Cisuralian (*probably *upper Sakmarian or lower Artinskian)–Lopingian (Wuchiapingian).*

Hyattoceras Gemmellaro, 1887, p. 14 [**H. Geinitzi* Gemmellaro, 1887, p. 16; SD Diener, 1921, p. 25] [=*Abichia* Gemmellaro, 1887, p. 18 (type, *Hyattoceras (Abichia) Abichi*, M]. Advanced hyattoceratids with fourth external lateral lobe ($L_{2.2}$) fully isolated by 2.5 cm conch diameter. Sutural formula: $(V_1V_1)L_2L_1L_{2.1}L_{2.2}U_2U_{1.1}$:$U_{1.1}U_2I_2I_1I_2D$ [Russian]. Mature modifications are characteristic. Spectacular dimorphism is probable, but has not been confirmed fully. Eight named species, several of which may be dimorphs. *Cisuralian (?upper Artinskian [?Baigendzhinian]), Guadalupian (Wordian)–Lopingian (Wuchiapingian):* Italy (Sicily), Indonesia (Timor), China (Jiangxi, Gansu, Xizang), Canada (British Columbia).——Fig. 101*a–e. *H. geinitzi*, Sosio limestone, Wordian, Sicily; *a–d,* ×1.33 (Davis, Furnish, & Glenister, 1969); *e*, diameter at 22 mm (Glenister & Furnish, 1987).——Fig. 101*f–g. H. abichi* (Gemmellaro), Sosio limestone, plausible dimorph of associated *H. geinitzi*, ×2 (Davis, Furnish, & Glenister, 1969).——Fig. 101*h. H. guembeli* (Gemmellaro), Sosio limestone, diameter at 20 mm (Glenister & Furnish, 1987).——Fig. 101*i–j. H. subgeinitzi* (Haniel), Amarassi beds, Wuchiapingian, Amarassi, Timor, terminal paedomorph of Hyattoceratidae (youngest, smallest, rarest, lobe digitation reduced), diameter ranging 12–14 mm (Glenister & Furnish, 1987).

Eohyattoceras Glenister & Furnish, 1987, p. 988 [**E. gerthi*; OD] [=*Prohyattoceras* Oyens, 1938, p. 1123, *nom. nud.*; =*Demarezites* Ruzhentsev, 1955a, p. 703, *partim* (type, *Waagenoceras oyensi* Gerth, 1950, p. 250, OD); =*Leeites* Bogoslovskaia, 1990, p. 72 (type, *Eohyattoceras leei* Glenister & Furnish, 1987, OD)]. Ancestral hyattoceratids with fourth external lateral lobe ($L_{2.2}$) incompletely isolated, and denticulation relatively simple and confined to bottom one-half of lobes. Sutural formula for type species (U_1 is undivided in ancestors): $(V_1V_1)L_2L_1(L_{2.1}L_{2.2})U_2U_{1.1}$:$U_{1.2}U_2I_2I_1I_2D$ [Russian]. Two species. *Cisuralian (upper Sakmarian or lower Artinskian)–Guadalupian (Roadian):* Indonesia (Timor), USA (Nevada).——Fig. 102*a–g. *E. gerthi*, Tae Wei beds, ?Roadian, Timor; *a–f*, ×2; *g*, diameter approximately 26 mm (Glenister & Furnish, 1987).——Fig. 102*h. E. leei* (Glenister & Furnish), Riepetown Formation, ?Sakmarian, Nevada , diameter at 30 mm (Glenister & Furnish, 1987).

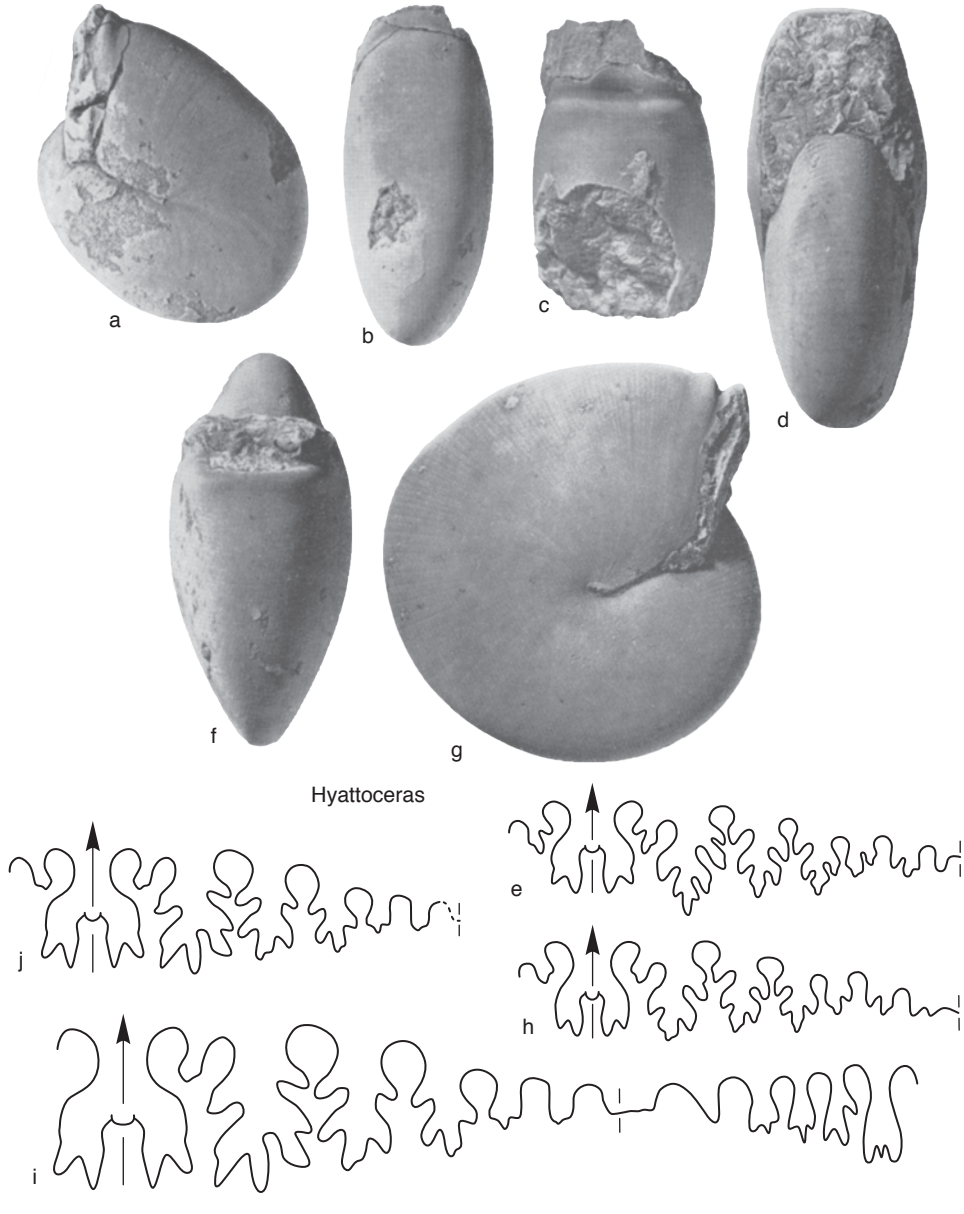

FIG. 101. Hyattoceratidae (p. 163).

FIG. 102. Hyattoceratidae (p. 163).

NEOICOCERATOIDEA

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Superfamily NEOICOCERATOIDEA Hyatt, 1900

[*nom. transl.* RUZHENTSEV & BOGOSLOVSKAIA, 1978, p. 68, *ex* Neoicoceratidae HYATT, 1900, p. 550]

Conch form, sculpture, and apertural outline highly variable. Large specimens of ancestral stock (Neoicoceratidae, mainly *Eoasianites*) are commonly globular, lacking in conspicuous ornament, and characterized by a ventral salient and simple 8-lobed suture. Basic sutural formula: (V_1V_1)LU:ID [Russian], $(E_1E_mE_1)$ALUI [German]. [Major early Permian radiation comprises Paragastrioceratidae, which retained the basic suture but transformed the ventral salient into a deep hyponomic sinus, and Metalegoceratidae, which transformed the suture from a total of 8 to 16 lobes by repeated tripartition of the primary umbilical lobe (U).] *Pennsylvanian (Bashkirian)–Lopingian (Changhsingian).*

Family NEOICOCERATIDAE Hyatt, 1900

[Neoicoceratidae HYATT, 1900, p. 550]

[Materials for this family prepared by Jürgen Kullmann]

Conch form discoidal to subdiscoidal, evolute. Umbilical nodes or lateral ribs may be present on immature or adult stages. Sutural formula: $(E_1E_mE_1)$ALUI [German], (V_1V_1)LU:ID [Russian]; no additional elements. [For discussion, see RUZHENTSEV & BOGOSLOVSKAIA, 1978, p. 68.] *Pennsylvanian (Bashkirian)–Cisuralian (Asselian).*

Neoicoceras HYATT, 1900, p. 550 [**Goniatites elkhornensis* MILLER & GURLEY, 1896, p. 37; OD]. Conch cross section low trapezoidal, umbilicus extremely wide. Suture similar to *Eoasianites*, but median saddle about half as high as entire ventral lobe. Three or four species. [The holotype of the type species (the only specimen) is fragmental and does not show shell ornamentation. Genus may be related to *Somoholites* or early schistoceratids. For discussion, see FURNISH & KNAPP, 1966, p. 300.] *Pennsylvanian (Bashkirian–Moscovian):* Russia (Novaia Zemlia), Canada (Northwest Territories), USA (Kentucky, Texas).——FIG. 103,*3. *N. elkhornense* (MILLER & GURLEY), suture of holotype, fragment, Big Sandy River, Elkhorn Creek, Kendrick Shale, Breathitt Formation, eastern Kentucky, USA, upper Morrowan, WMUC 6210, ×1.7 (Furnish & Knapp, 1966).

?Akiyoshiceras KYUMA & NISHIDA, 1987, p. 26 [**A. subridens* KYUMA & NISHIDA, 1987, p. 28; OD]. No conspicuous ornamentation at early and later whorls. Depressions and transverse swellings of adult conch developed regularly. Median saddle of suture considerably higher than half height of entire ventral lobe. Two species. [The generic assignment is questionable for this genus. The conch form and suture suggest a close relationship to *Eoasianites.*] *Pennsylvanian (lower Moscovian):* Japan.——FIG. 103,*1a–c. *A. subridens,* holotype, Mine City, Quarry Isa machi, Akiyoshi, Yamaguchi prefecture, lower part of Akiyoshi Limestone, ASM50439; *a–b,* ×0.75; *c,* suture, diameter at 37 mm, ×1.9 (Kyuma & Nishida, 1987).

Eoasianites RUZHENTSEV, 1933, p. 165 [**E. subhanieli* RUZHENTSEV, 1933, p. 166; OD] [=*Prometalegoceras* RUZHENTSEV, 1936a, p. 505, obj.; =*Trochilioceras* PLUMMER & SCOTT, 1937, p. 181 (type, *T. tenuosum* PLUMMER & SCOTT, 1937, p. 183, OD); =*Pronoceras* PLUMMER, 1950, pl. 19 (type, *Gastrioceras prone* MILLER & OWEN, 1937, p. 415, M, *nom. nud.*]. Conch form subdiscoidal, evolute, with low height of aperture. Transverse striae usually with orad salient. Umbilical tubercles confined to immature stages; constrictions may be present. Ventral lobe with slightly pouched prongs, median saddle exceeding two-thirds height of entire ventral lobe. First lateral saddle subacute. More than ten species. [The type species of *Trochilioceras* and *Pronoceras* are regarded as congeneric with *Eoasianites.* For discussion, see RUZHENTSEV, 1950, p. 129.] *Pennsylvanian (Kasimovian)–Cisuralian (Asselian):* Russia and Kazakhstan (South Urals), China (Guangxi, Xinjiang), Tajikistan (Pamirs), Canada (Yukon), USA (Alaska, Kansas, Oklahoma, Texas).——FIG. 103,*2a–b. *E. subhanieli,* holotype, Sholak-sai river, South Urals, uppermost Asselian, PIN 318/1207,

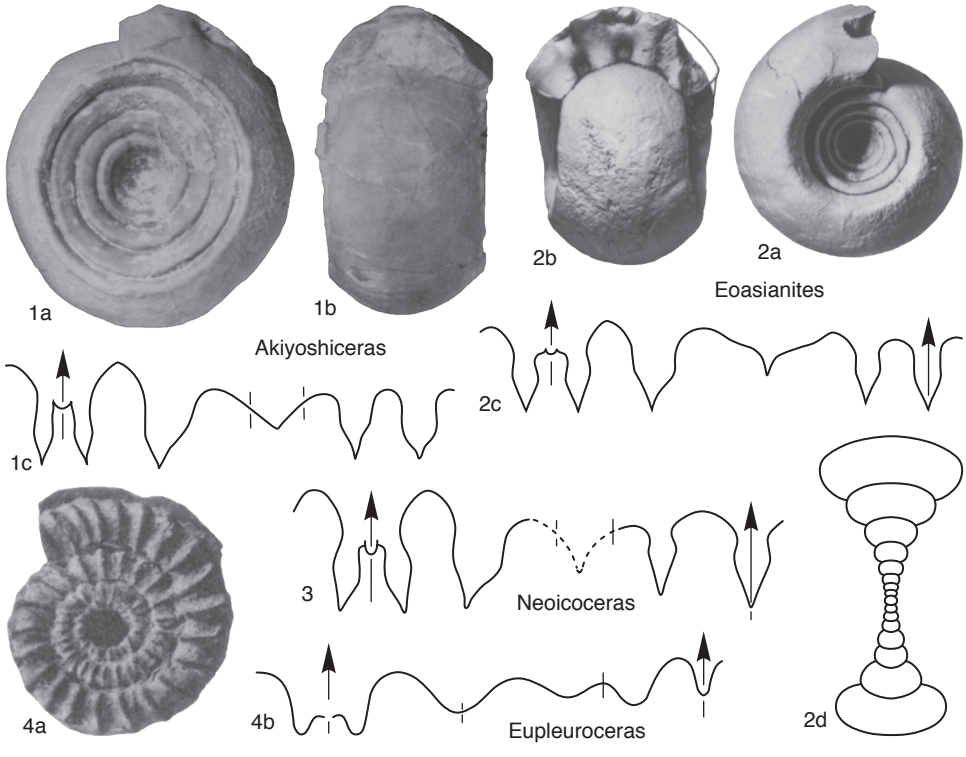

FIG. 103. Neoicoceratidae and Eupleuroceratidae (p. 166–167).

×1 (Ruzhentsev, 1951).——FIG. 103,*2c. E. hartmannae* RUZHENTSEV, suture, Zhaksy-Kargala river, South Urals, uppermost Asselian, PIN 318/312, whorl height at 9.8 mm, whorl width 19.6 mm, ×1.8 (Ruzhentsev, 1951).——FIG. 103,*2d. E. concinnus* RUZHENTSEV, cross section, west of Nikolskii, right bank of Ural river, Chkalovskaia Oblast', South Urals, lower part of Orenburg formation, Gzhelian, PIN 320/1740, ×4 (Ruzhentsev, 1950).

Family EUPLEUROCERATIDAE Ruzhentsev, 1957

[Eupleuroceratidae RUZHENTSEV, 1957, p. 59]

[Materials for this family prepared by Jürgen Kullmann]

Conch form snakelike, with keel. Sculpture with lateral ribs. [The relationship of this family to Neoicoceratidae is uncertain.] *Pennsylvanian (Kasimovian).*

Eupleuroceras MILLER & CLINE, 1934a, p. 179 [**E. bellulum* MILLER & CLINE, 1934a, p. 180; OD]. Conch snakelike, coiled, evolute, with a small and sharp ventral keel. Sculpture with conspicuous prorsiradiate ribs on flanks, reaching ventrolateral margin. Lobes of adults acute at their base, median saddle relatively low. One species (holotype, immature). [Conch form, ornamentation, and suture configuration suggests a relationship to Neoicoceratidae.] *Pennsylvanian (Kasimovian):* USA (Kansas, Oklahoma, Texas).——FIG. 103,*4a–b. *E. bellulum,* 4.8 km west and 1 km north of Cherryvale, Montgomery County, Kansas, Drum limestone, Nelly Bly Formation, Missourian, probably immature cotype, SUI; *a,* ×4; *b,* suture, approximately ×25 (Miller & Cline, 1934a).

Family PARAGASTRIOCERATIDAE Ruzhentsev, 1951

[Paragastrioceratidae RUZHENTSEV, 1951, p. 138]
[=Aulacogastrioceratidae ZHAO & ZHENG, 1977, p. 240]

[Materials for this family prepared by Brian F. Glenister, William M. Furnish, and Zhou Zuren]

Eight-lobed neoicoceratoideans characterized initially by widely evolute narrow conch, strongly depressed whorls, and by transverse

ribs that form a high ventral salient. Sutural formula: (V_1V_1)LU:ID [Russian], ($E_1E_mE_1$) ALUI [German]. Primary evolutionary trends comprised reduction in relative umbilical diameter, restriction of strong transverse ornament to inner volutions, and development of a deep hyponomic sinus. Accompanying modifications involved compressed whorls, angular venter, dorsolateral ribs and nodes, and coarse strigae. *Cisuralian (Asselian)–Lopingian (Changhsingian).*

Subfamily PARAGASTRIOCERATINAE Ruzhentsev, 1951

[*nom. transl.* Furnish, 1966, p. 278, *ex* Paragastrioceratidae Ruzhentsev, 1951, p. 138]

Paragastrioceratids in which growth lines form a ventral salient. *Cisuralian (Asselian–Kungurian).*

Paragastrioceras Chernov, 1907, p. 288 [**Goniatites Jossae* de Verneuil, 1845, p. 371; SD Ruzhentsev, 1936b, p. 1079] [=*Girtyites* Wedekind, 1918, p. 160, obj.; ?=*Eotumaroceras* Andrianov, 1985, p. 143 (type, *E. endybalense,* OD); ?=*Baraioceras* Andrianov, 1985, p. 155 (type, *A. stepanovi,* OD)]. Conch large, thickly subdiscoidal (W/D, commonly 0.4–0.6) with wide umbilicus (U/D, greater than one-third) and depressed whorls (H/W, commonly two-thirds). Pronounced nodes or laterally attenuate ribs generally retained on umbilical shoulders to maturity. Strong longitudinal strigae and weaker convex growth lines produce reticulate sculpture. Prongs of ventral lobe characteristically much narrower than lateral lobe; both prongs and lateral lobe (V_1 and L) are attenuated adapically and constricted adorally. Thirty named species. [A fully mature aperture has been observed in this genus, rarely, to comprise long paired ventral salients bisected by a deep hyponomic sinus.] *Cisuralian (Asselian–Kungurian):* Kazakhstan (Southern Urals), Russia (Urals, Verkhoian, Ochtsko-Kolymskiy Massif), Tajikistan (?Darvas), Italy (Carnic Alps), Slovenia, Canada (Arctic Archipelago, Yukon), Western Australia, China (Nei Mongol).——Fig. 104,*1a–c.* **P. jossae jossae* (de Verneuil), Baigendzhinian, Southern Urals; *a–b*, ×0.67; *c*, diameter at 70 mm (Ruzhentsev, 1956b).

Epijuresanites Y. Popov, 1970, p. 134 [**E. musalitini;* OD]. Poorly understood group of species, possibly distinguishable by combination of broadly expanded prongs of ventral lobe, medially expanded lateral lobe (L), and incipiently trifid umbilical lobe. Conch discoidal (W/D, 0.3–0.6), umbilicus narrow (Umin/D, 0.2–0.4). Longitudinal and transverse ornament usually fine; growth lines form low ventral salient or shallow sinus. Seven species. *Cisuralian (Kungurian):* Russia (Verkhoian), China (Gansu, ?Nei Mongol), Australia (New South Wales, Queensland).——Fig. 105*a–b.* **E. musalitini*, holotype, Tumara Suite, western Verkhoian, NIIGA 48/8717, plastoholotype, SUI 35144; *a*, ×0.67; *b*, diameter at approximately 55 mm (new).

Svetlanoceras Ruzhentsev, 1974a, p. 23 [**Uraloceras serpentinum* Maksimova, 1948, p. 7; OD]. Small (commonly less than 2.5 cm mature diameter), thinly discoidal paragastrioceratins (W/D, less than 0.4) with depressed whorls (H/W, less than 0.8) and wide umbilicus (Umin/D, 0.4–0.7). Numerous ribs across umbilical wall and shoulder multiply by intercalation and bifurcation to produce finer ornament across flanks and venter; ribs and constrictions form high ventral salient; longitudinal lirae less pronounced than transverse ornament. Suture primitive: prongs of ventral lobe narrower and deeper than lateral lobe; lateral lobe approximately symmetrical, with flanks diverging adorally. Seven species. [Primitive features of this ancestral paragastrioceratid are consistent with its small mature size. *Svetlanoceras* is the rootstock of both the Paragastrioceratinae and the Pseudogastrioceratinae. It is the dominant paragastrioceratid in the Asselian, but transitions to descendant *Uraloceras* extend as high as the upper Sakmarian (Sterlitamakian).] *Cisuralian (Asselian–Sakmarian [Tastubian]):* Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), India (?Eastern Himalaya), southern China (Guangxi), Western Australia, USA (western Texas), Canada (Yukon).——Fig. 104,*3a–c.* **S. serpentinum* (Maksimova), Asselian, Southern Urals; *a–b*, ×1.5; *c*, diameter at 15 mm (Ruzhentsev, 1951).

Synuraloceras Ruzhentsev, 1952b. p. 73 [**S. carinatum*; OD]. Similar to *Svetlanoceras*, from which it was probably derived, but with smaller umbilicus (Umin/D, 0.3–0.4) and angular mature venter. One species. [*Synuraloceras* resembles the pseudogastrioceratin genus *Strigogoniatites* in both suture and whorl section. However, *Strigogoniatites* differs fundamentally in possession of the deep hyponomic sinus that characterizes all Lopingian Paragastrioceratidae.] *Cisuralian (lower Sakmarian [Tastubian]):* Kazakhstan (Southern Urals).——Fig. 104,*5a–d.* **S. carinatum*; *a–c*, ×1; *d*, diameter at 25 mm (Ruzhentsev, 1952b).

Tumaroceras Ruzhentsev, 1961, p. 57 [**T. yakutorum*; OD] [?=*Strigotumaroceras* Y. Popov, 1970, p. 133 (type, *S. zavodowskii,* OD), genus is reputed to be distinguishable by its angular venter, but types are crushed and unsatisfactory for reference; ?=*Bulunites* Andrianov, 1985, p. 131 (type, *B. mezhvilki,* OD), the suture drawings are suspect for taxonomic assignment and may be *Epijuresanites*]. Similar to *Paragastrioceras*, but with wider whorls (W/D, 0.7), smaller umbilicus (Umin/D, 0.3), and lacking ventrolateral nodes or other conspicuous

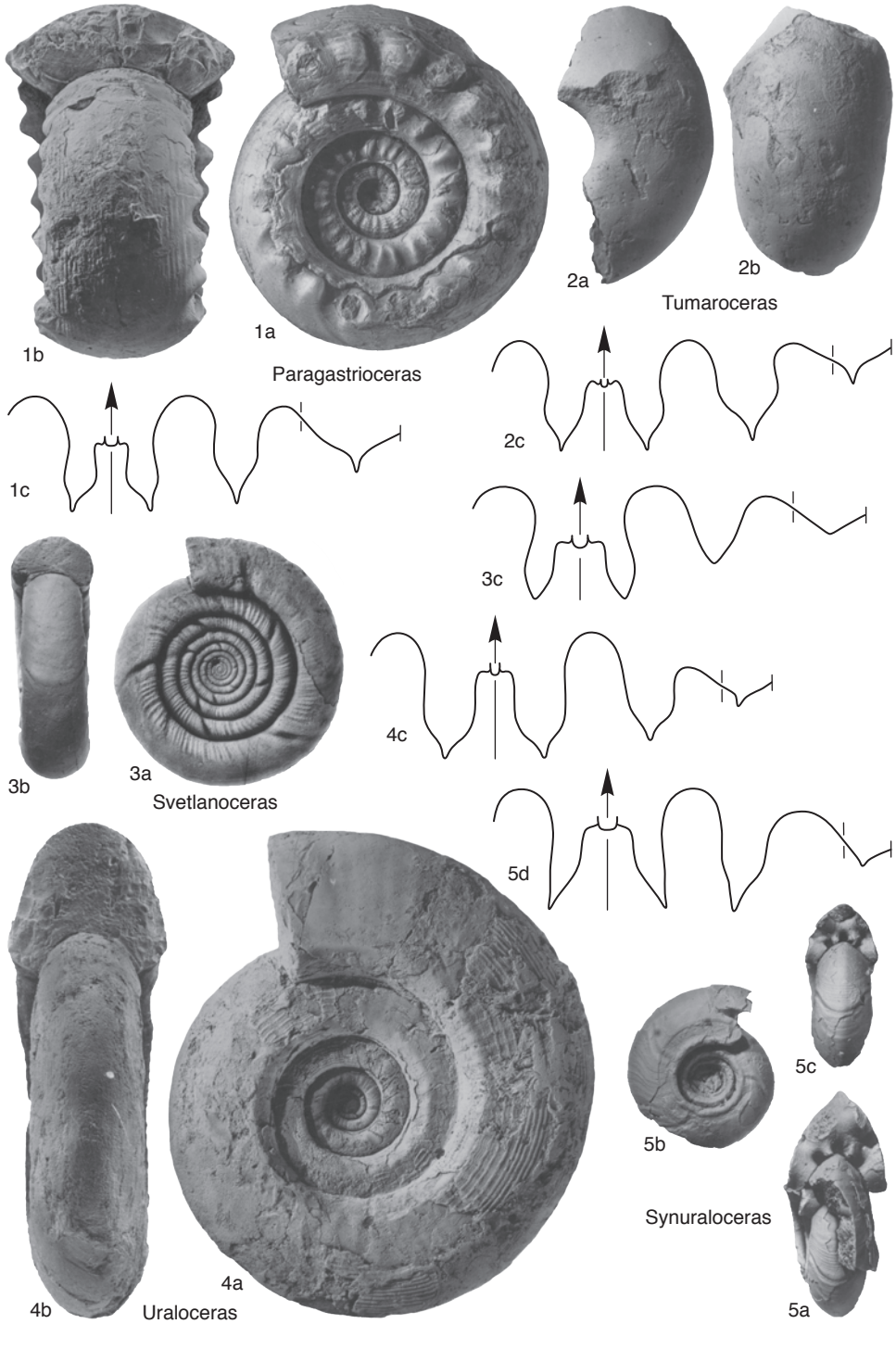

FIG. 104. Paragastrioceratidae (p. 168–170).

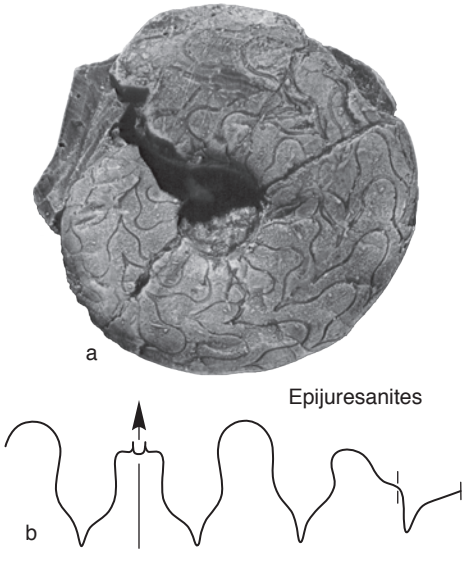

FIG. 105. Paragastrioceratidae (p. 168).

ornament. Six named species. *Cisuralian (Kunguri-an):* Russia (North Urals: Pay-Khoy and Vaigach, Verkhoian, Omolon Massif).——FIG. 104,*2a–c*. **T. yakutorum*, Member B, Endybal' Formation, Siberia, western Verkhoian; *a–b*, ×0.9; *c*, whorl height 25 mm (Ruzhentsev, 1961).

Uraloceras RUZHENTSEV, 1936b, p. 1080 [**Gastrioceras Suessi* KARPINSKII, 1889, p. 52; OD]. Similar to *Paragastrioceras*, but thinner (W/D, generally less than 0.4), usually more involute (Umin/D, 0.3–0.5), and with equidimensional whorl section (H/W, 0.8–1.1). Umbilical ribs characterize juveniles but are not retained in larger whorls. Prongs of ventral lobe equal to or wider than lateral lobe. Twenty-four named species. [Fully mature aperture comprises constriction and terminal flare (expansion), both forming a ventral salient without a hyponomic sinus.] *Cisuralian (Sakmarian–Artinskian)*: Kazakhstan (Southern Urals), Russia (Southern and Central Urals, Verkhoian, Omolon Massif, North Urals: Pechora Basin, Pai-Khoi, Vaigach Island), Canada (Arctic, Yukon, British Columbia), USA (Nevada, Alaska), Australia (New South Wales, Queensland), China (Xizang, Nei Mongol, Gansu, Guangxi).——FIG. 104,*4a–c*. **U. suessi* (KARPINSKII), Baigendzhinian, Southern Urals; *a–b*, ×0.5; *c*, diameter at 100 mm (Ruzhentsev, 1956b).

Subfamily PSEUDOGASTRIOCERATINAE Furnish, 1966

[Pseudogastrioceratinae FURNISH, 1966, p. 278]

Paragastrioceratids in which growth lines form shallow to deep hyponomic sinus. *Cisuralian (lower Sakmarian [Tastubian])–Lopingian (Changhsingian).*

Pseudogastrioceras SPATH, 1930, p. 8 [**Goniatites Abichianus* MÖLLER, 1879, p. 230; M] [=*Grabauites* SUN, 1939, p. 41 (type, *Gastrioceras (Girtyites) liui* GRABAU, 1924, p. 478, OD)]. Conch large, involute (Umin/D, 0.1–0.2) with strongly compressed whorls and narrowly rounded, mature venter. Coarse longitudinal strigae are confined to venter and ventrolateral flanks; conspicuous dorsolateral ornament absent in all growth stages. Sutures characterized by strongly divergent flanks of ventral lobe, wide asymmetric ventral prongs (width V_1/L approximates 1.0), and relatively unconstricted flaring flanks of lateral lobe. Six species. [*Pseudogastrioceras* resembles and intergrades with the weakly ornamented involute species of both *Roadoceras* and *Altudoceras*, e.g., *R. roadense* (BÖSE, 1919) and *A. altudense* (BÖSE, 1919); but it is separable primarily on conch form and sutural contours.] *Lopingian:* Armenia, Azerbaijan (Nakhichevan), Iran (north, central), southern China (widespread), Japan (Kitakami).——FIG. 106,*5a–c*. **P. abichianum* (MÖLLER), Wuchiapingian, vicinity of Dzhulfa, Nakhichevan; *a–b,* ×0.67; *c,* diameter at 60 mm (Ruzhentsev, 1974a).

Altudoceras RUZHENTSEV, 1940c, p. 286 [**Gastrioceras altudense* BÖSE, 1919, p. 88; OD] [=*Hengshanites* ZHOU, 1985, p. 196 (type, *Altudoceras hunanense* XU in XU & WEI, 1977, p. 568, OD)]. Similar to *Pseudogastrioceras* in general conch form, but with wider umbilicus (Umin/D, 0.25–0.5) and conspicuous dorsolateral ribs or nodes in at least juvenile stages. Hyponomic sinus deep and rounded. Ventral lobe characterized by subparallel flanks and narrow asymmetric prongs (width V_1/L 0.6–1.0). Fourteen named species. *Guadalupian (Wordian–Capitanian):* USA (western Texas, Alaska), Mexico (Coahuila), Italy (Sicily), Tunisia, Oman, Iraq (Kurdistan), Pakistan, China (widespread), Russia (Novaia Zemlia), Indonesia (Timor).——FIG. 106,*4a–d*. **A. altudense* (BÖSE), Wordian, western Texas; *a–c*, ×1.33; *d*, diameter at 20 mm (Miller & Furnish, 1940a).

Aulacogastrioceras ZHAO & ZHENG, 1977, p. 240 [**A. spinosum*; OD]. Conch evolute (U/D, 0.5),

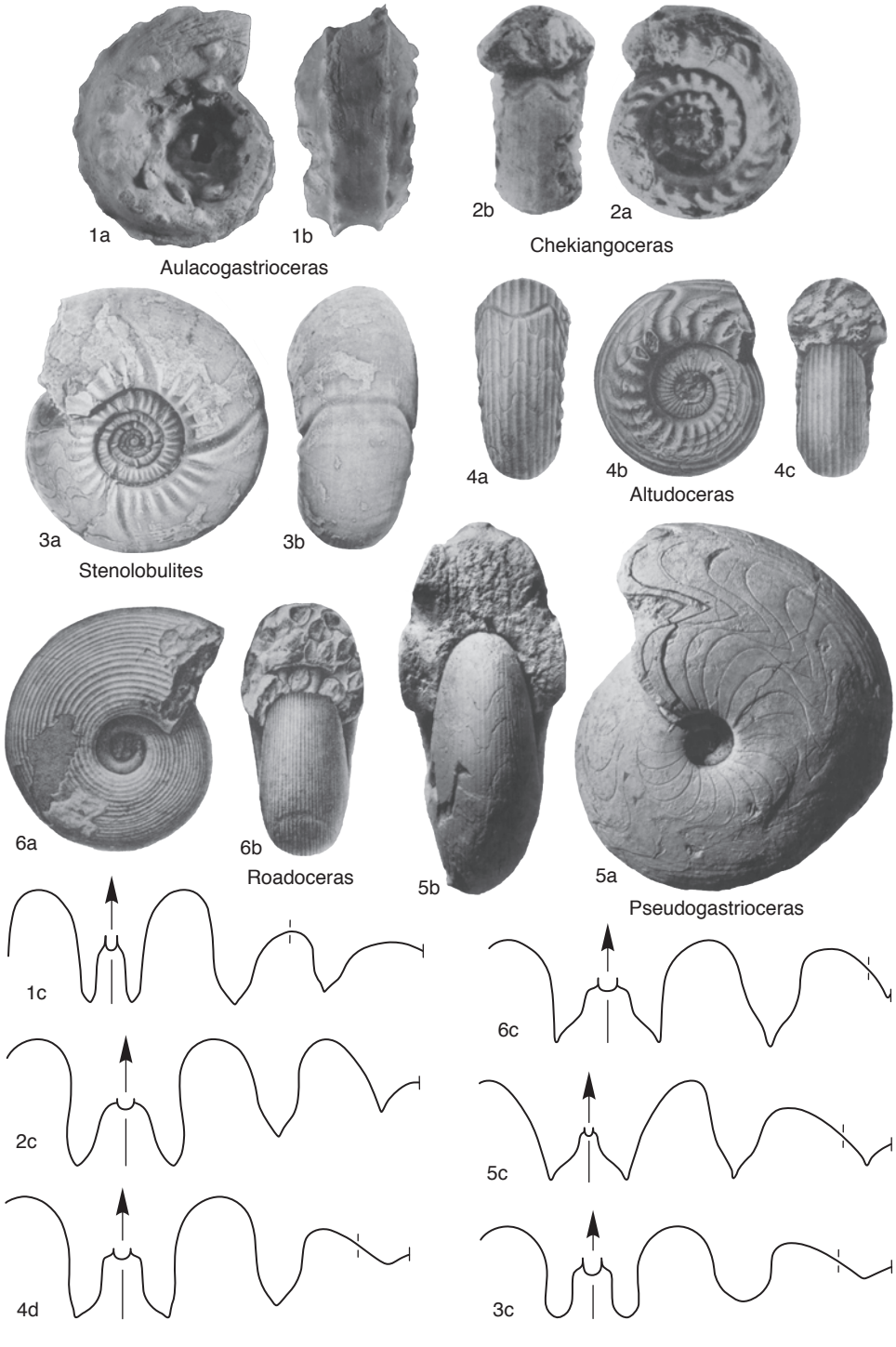

FIG. 106. Paragastrioceratidae (p. 170–172).

characterized by subtrapezoidal whorl section and conspicuous ornament. Venter shallowly concave with width one-half that of corresponding maximum whorl width, bounded by pair of narrow ventrolateral keels comprising longitudinally elongate bladelike nodes. Each whorl flank displays a row of coarse equidimensional nodes that are progressively more prominent apically. Suture has narrow ventral prongs (width V_1/L less than 0.5) and primary umbilical lobe similar in shape to corresponding lateral lobe (unlike flaring, divergent, V-shaped flanks of U in other pseudogastrioceratins). One species, rare and aberrant in South China. *Guadalupian (?Roadian–?Wordian)*: southern China (Jiangxi), Hutang Formation.——Fig. 106,*1a–c. *A. spinosum*; *a–b*, ×1; *c*, diameter at 28 mm (Zhao & Zheng, 1977).

Chekiangoceras Ruzhentsev, 1974a, p. 24 [**C. carinatum;* OD; *nom. nov. pro Paragastrioceras carinatum* Chao, 1965, p. 1817, *nom. nud.*, Zhao & Zheng, 1977, p. 236]. Similar to *Altudoceras*, but mature whorls depressed, trapezoidal in section, and bluntly angular ventrally. One species. [Although accompanied by adequate illustrations, the original attempt to name the type species (Chao, 1965) did not fulfill the requirements of ICZN *Code* Article 13(a). Ruzhentsev (1974a) validated the specific name; he must be considered to be the author, as he alone meets the requirements of Article 50.] *Guadalupian (?Roadian–?Wordian):* southern China (Zhejiang), Shimei Member, Dingjiashan Formation.——Fig. 106,*2a–c. *C. carinatum*; *a–b*, ×0.67; *c*, diameter at 45 mm (Chao, 1965).

Daubichites Y. Popov, 1963, p. 149 [**D. orientalis;* OD]. Similar to paragastrioceratin *Tumaroceras* in general conch form, but narrower (W/D, commonly 0.5) and with smaller umbilicus (Umin/D, 0.2–0.3). Ribs invariably present on umbilical shoulders of juveniles and may persist to maturity; growth lines and constrictions form shallow to deep hyponomic sinus. Prongs of ventral lobe and lateral lobe both approximately bilaterally symmetrical, subequal in size (width V_1/L 0.7–1.0). Eleven species. *Guadalupian (Roadian, ?Wordian):* Russia (Maritime Territory, Verkhoian, Novaia Zemlia), China (Zhejiang, Nei Mongol, ?Xizang), Canada (Arctic, ?British Columbia), USA (Wyoming, Idaho, Texas, ?Arizona), Western Australia, Indonesia (Timor).——Fig. 107,*2a–c. *D. orientalis*, holotype, ?Wordian, Maritime Territory, TsGM 1/8236, plastoholotype, SUI 32740; *a–b*, ×1; *c*, diameter at 55 mm (new).

Roadoceras Zhou, 1985, p. 195 [**Gastrioceras roadense* Böse, 1919, p. 85; OD]. Suture and general conch form similar to *Altudoceras*, including asymmetry of ventral prongs, but differing in generally smaller umbilicus (Umin/D, approximately one-quarter) and early suppression of coarse dorsolateral ribs so that longitudinal strigae are the only conspicuous ornament at diameters greater than 25 mm. Six species. *Guadalupian (Wordian)–Lopingian (Wuchiapingian):* USA (western Texas), Mexico (Coahuila), Russia (Amur), southern China (Hunan).——Fig. 106,*6a–c. *R. roadense* (Böse), Wordian, western Texas; *a–b*, ×1 (Miller & Furnish, 1940a); *c*, topotype, SUI 13589, diameter at 22 mm (new).

Stenolobulites Mikesh, Glenister, & Furnish, 1988, p. 2 [**S. stenolobulus*; OD]. Similar to *Altudoceras*, but with prongs of the ventral lobe that are symmetrical and less than 0.6 the width of lateral lobe. Seven species. [Ancestral pseudogastrioceratin, derived from paragastrioceratin genus *Svetlanoceras* and gradational with it and with diverse pseudogastrioceratins of the Roadian and Guadalupian. As with *Svetlanoceras*, many features of the conch and suture are largely a function of its small mature size.] *Cisuralian (lower Sakmarian [Tastubian])–Guadalupian (Roadian):* USA (Texas, New Mexico, Utah, Idaho), Guatemala.——Fig. 106,*3a–c. *S. stenolobulus*, Roadian, western Texas; *a–b*, ×3; *c*, diameter at 12 mm (Mikesh, Glenister, & Furnish, 1988).

Strigogoniatites Spath, 1934, p. 15 [**Glyphioceras angulatum* Haniel, 1915, p. 51; OD] [=*Retiogastrioceras* Zhao, Liang, & Zheng, 1978, p. 76 (type, *R. pulchrium,* OD); ?=*Metagastrioceras* Zhao, Liang, & Zheng, 1978, p. 75 (type, *M. fengchengense,* OD); ?=*Sabaliceras* Yang & Yang, 1992, p. 597 (type, *S. wangrenense,* OD)]. Similar to *Altudoceras*, from which it evolved, but with smaller umbilicus (Umin/D, commonly 0.2–0.25). Ornament comprises strong strigae that are restricted progressively to ventrolateral flanks as maturity is approached. Transverse section of mature whorls characterized by shallowly concave dorsolateral flanks separated by broad ridge from flat ventrolateral flanks that converge to an angular to narrowly rounded venter. Ventral lobe constricted medially in advanced forms, with wedge-shaped anteriorly divergent prongs. Fourteen species. [Both *Retiogastrioceras* and *Metagastrioceras* were proposed for specimens from the Laoshan Shale of Jiangxi; the precise zonation is uncertain, but the age is probably Wuchiapingian. All features of shell and suture of *Retiogastrioceras* are consistent with reference to *Strigogoniatites*, but the rare juvenile types of *Metagastrioceras* cannot be assigned confidently.] *Guadalupian (Wordian)–Lopingian (Wuchiapingian, ?Changhsingian):* Indonesia (Timor), USA (western Texas), Mexico (Coahuila), southern China (widespread), Tunisia, Iran (northern).——Fig. 107,*1a–c. *S. angulatum* (Haniel), holotype, Amarassi beds, Wuchiapingian, Amarassi, Timor, MTHD 12703; *a–b*, ×0.67; *c*, diameter at 72 mm (new).

Subfamily ATSABITINAE Furnish, 1966

[Atsabitinae Furnish, 1966, p. 278]

Thinly discoidal paragastrioceratids with wide umbilicus and prosiradiate ribs on the flanks. Suture characterized by exceptionally broad ventral lobe. [Affinities between the two included genera are dubious, as is the

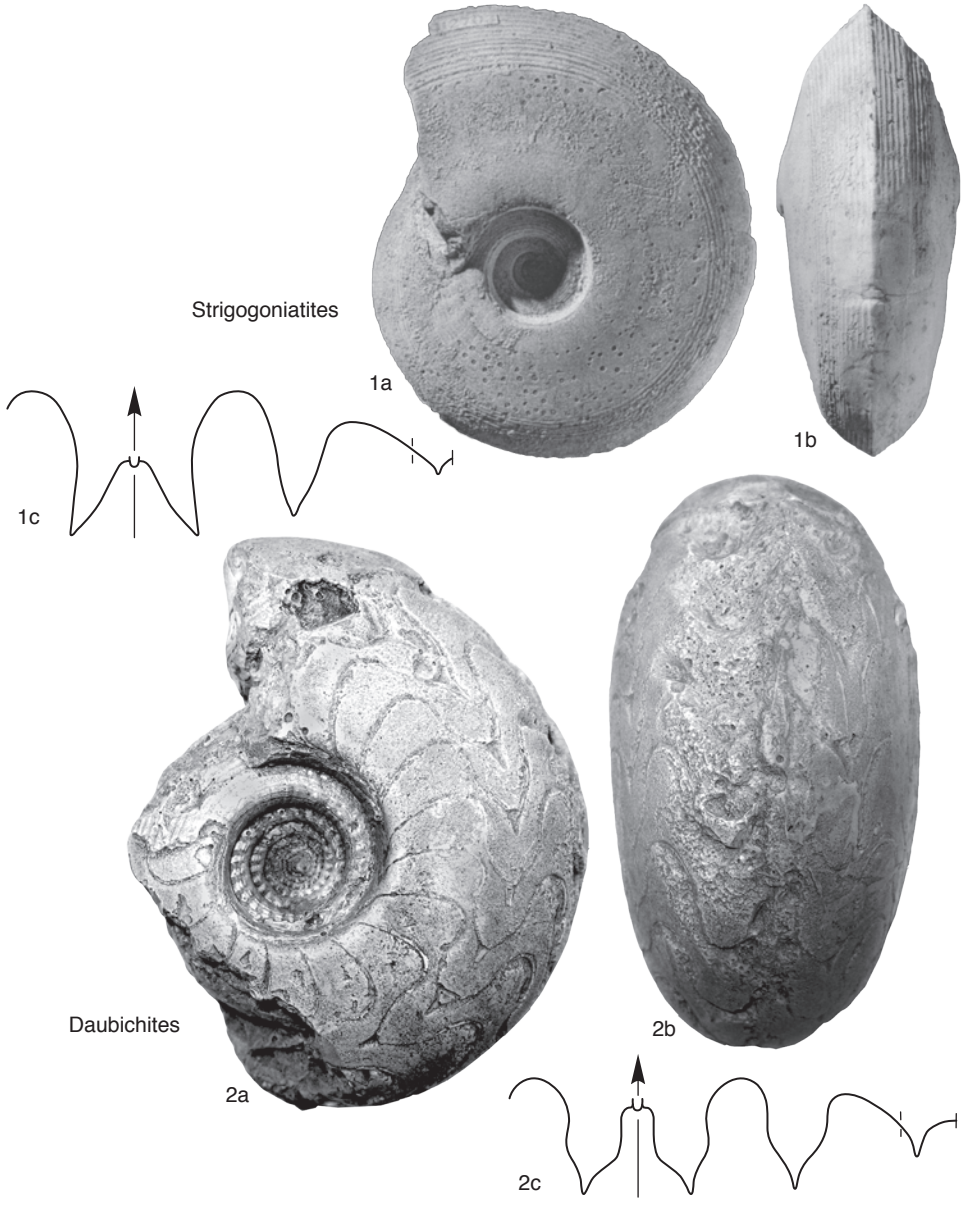

FIG. 107. Paragastrioceratidae (p. 172).

relationship to the apparent homeomorph *Eupleuroceras* MILLER & CLINE, 1934b, a genus referred herein with question to the neoicoceratoidean family Neoicoceratidae.] *Cisuralian (Artinskian)–Guadalupian (Wordian).*

Atsabites HANIEL, 1915, p. 50 [**A. Weberi*; M]. Atsabitin characterized by ventral lobe with parallel sides and width four times that of deep lateral lobe. One species. *Cisuralian (Artinskian)*: Indonesia (Timor).——FIG. 108,*2a–c*. **A. weberi*; *a*, hypotype of WANNER (1932, pl. 10,*3*), between Nilulet and Namaban, Bitauni, Timor, ×1; *b*, lectotype (herein), PIUB 11 of HANIEL (1915, pl. 4,*1a–c*), Hatu Dame, Timor, ×1 (Haniel, 1915); *c*, lectotype, diameter at 75 mm (new).

Anatsabites RUZHENTSEV, 1957, p. 59 [**Paraceltites multiliratus* PLUMMER & SCOTT, 1937, p. 369;

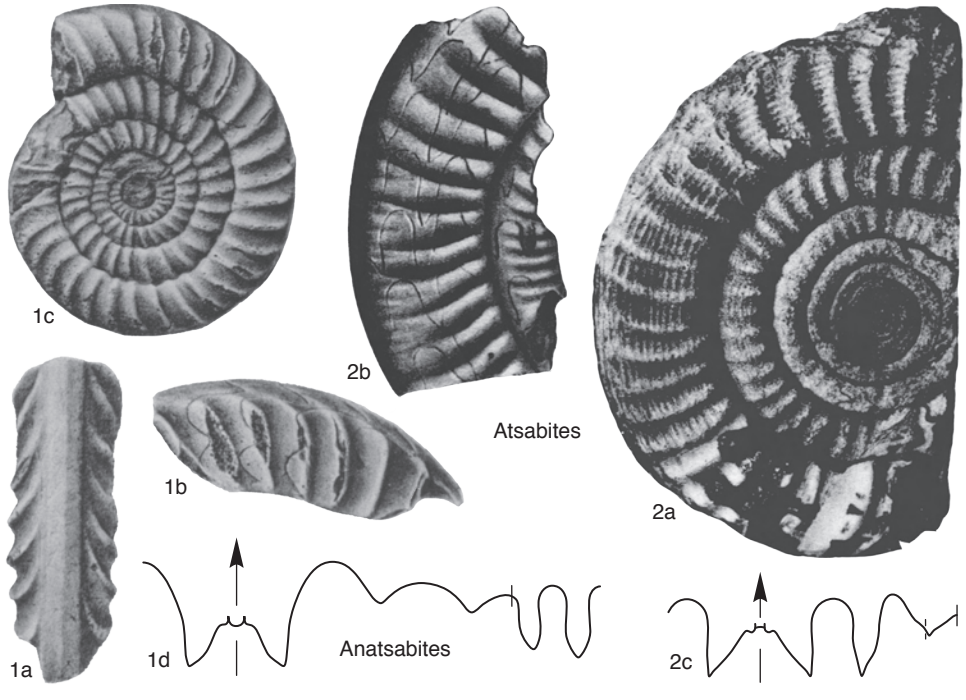

FIG. 108. Paragastrioceratidae (p. 173–174).

OD]. Similar to *Atsabites* in conch form, but with coarser ventral strigae; distinguished by divergent flanks of ventral lobe and by anomalously shallow lateral lobe. Two species. *Guadalupian (Wordian):* USA (western Texas).——FIG. 108,*1a–d. *A. multiradiatus* (PLUMMER & SCOTT); *a–b*, ×2; *c*, ×1.5; *d*, diameter at 34 mm (Miller & Furnish, 1940a).

Family METALEGOCERATIDAE Plummer & Scott, 1937

[Metalegoceratidae PLUMMER & SCOTT, 1937, p. 258] [=Pericycloceratidae ZHAO & ZHENG, 1977, p. 243; LEONOVA in LEONOVA & DMITRIEV, 1989, p. 123]

[Materials for this family prepared by Brian F. Glenister, William M. Furnish, and Zhou Zuren]

Neoicoceratoideans exhibiting a wide range in conch form, from subglobular and narrowly umbilicate to thinly lenticular and evolute. Evolution proceeded from smooth shelled to strongly ribbed, with progressive development of a deep hyponomic sinus. Family is characterized by tripartition of primary umbilical lobe ($U > U_2U_1U_3$), then repeated to transform total number of lobes from 12 to 16 ($U_1 > U_{1.2}U_{1.1}U_{1.2}$). [Subfamilies are distinguishable on conch form and relative width of prongs in the ventral lobe (V_1).] *Cisuralian (Asselian)–Guadalupian (Wordian).*

Subfamily METALEGOCERATINAE Plummer & Scott, 1937

[*nom. transl.* NASSICHUK, 1970, p. 86, *ex* Metalegoceratidae PLUMMER & SCOTT, 1937, p. 258] [=Pericyclolobidae ZHAO & ZHENG, 1977, p. 243; LEONOVA in LEONOVA & DMITRIEV, 1989, p. 123]

Conch large (up to 60 cm diameter), subdiscoidal to globular, and narrowly umbilicate to openly evolute. Growth lines and constrictions are transverse (rectiradiate) or with shallow ventral sinus; generally smooth at maturity. Characterized by 12 or 16 lobes, with prongs of ventral lobe no more than two-thirds as wide as corresponding lateral lobe. *Cisuralian (Asselian–Artinskian), Guadalupian (?Roadian–?Wordian).*

Metalegoceras SCHINDEWOLF, 1931, p. 199 [**Paralegoceras sundaicum* form. *evoluta* HANIEL, 1915, p. 60; OD] [=*Epilegoceras* CHERNOV, 1907, p. 292, *nom. nud.; =Asianites* RUZHENTSEV, 1933, p. 166 (type, *A. sogurensis,* OD); =*Dodecalegoceras* VOINOVA,

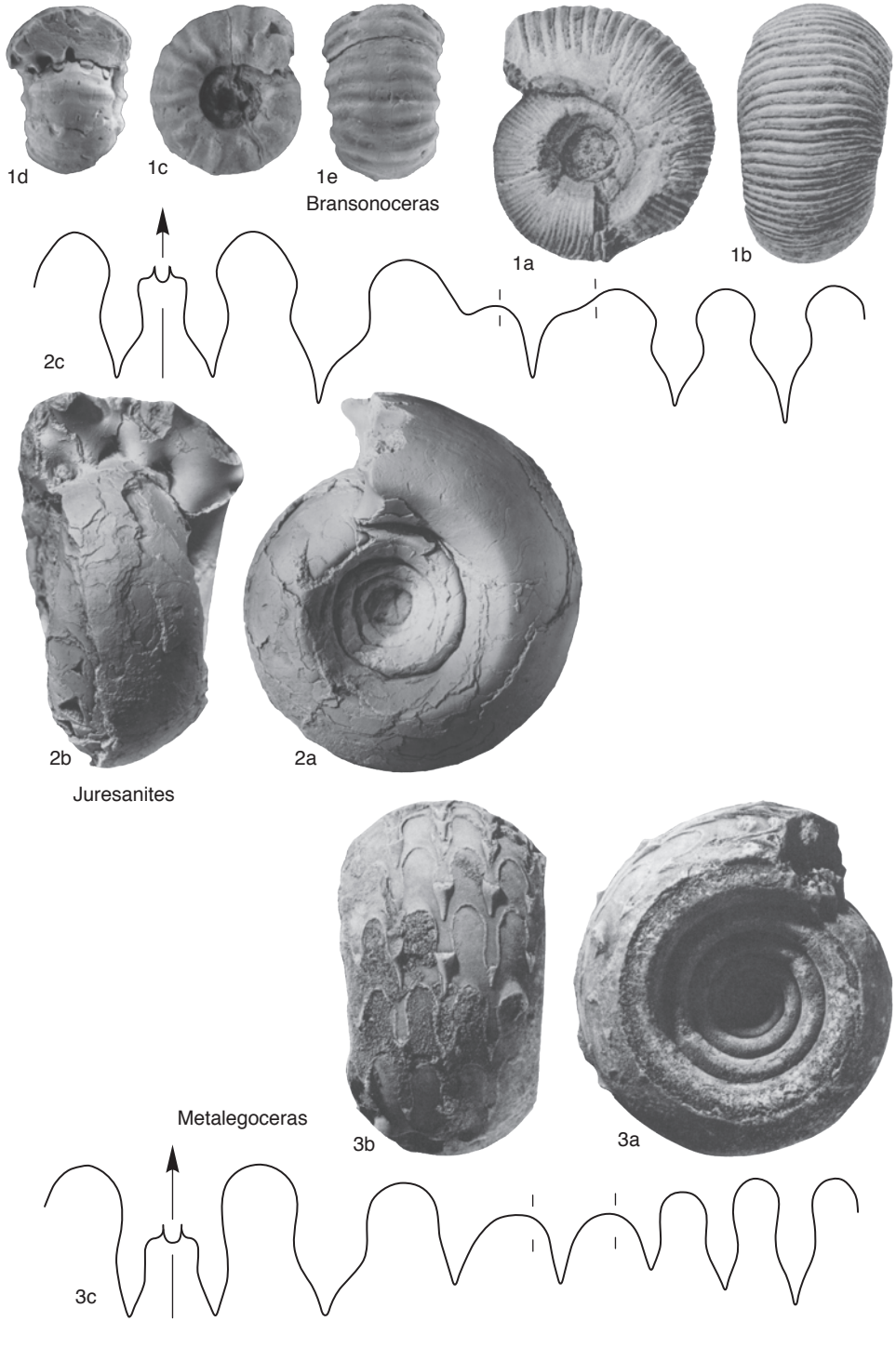

FIG. 109. Metalegoceratidae (p. 174–177).

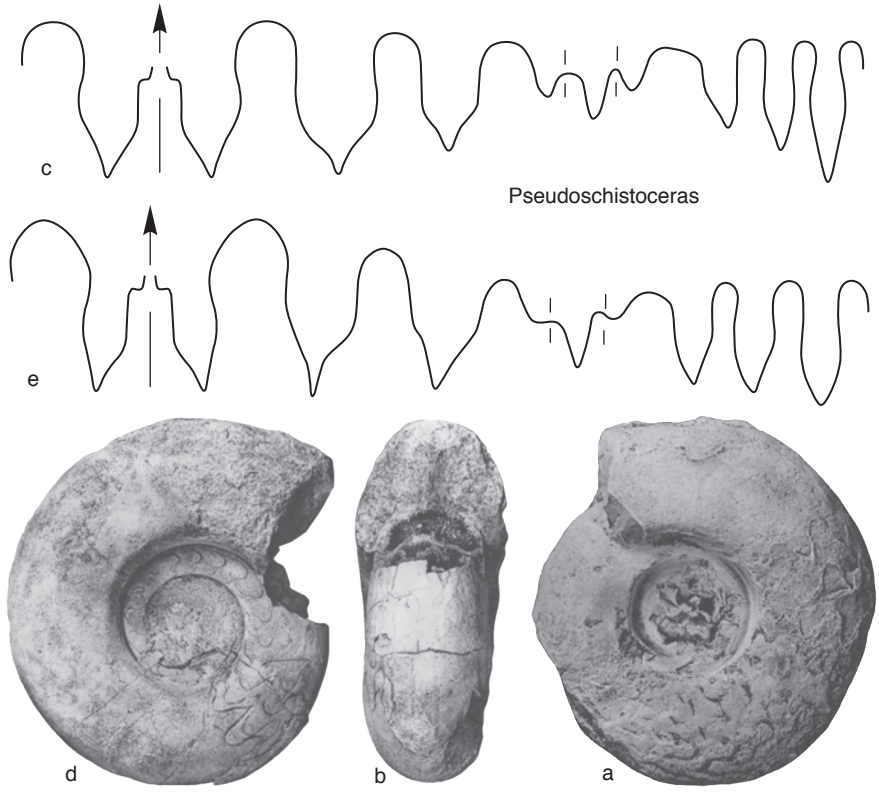

FIG. 110. Metalegoceratidae (p. 177).

1934, p. 14 (type, *D. razumowskajae* VOINOVA, 1934, p. 18); =*Parametalegoceras* BOGOSLOVSKAIA in BOGOSLOVSKAIA, USTRITSKII, & CHERNIAK, 1982, p. 62 (type, *P. arcticum,* OD); =*Pseudometalegoceras* BOGOSLOVSKAIA, 1985, p. 62 (type, *Metalegoceras liratum* ZHAO & ZHENG, 1977, p. 242, OD); ?=*Lingzhouceras* SHENG, 1988a, p. 131 (type, *L. ornatum,* OD)]. Conch variable in relative width (W/D, 0.5–0.9) and umbilical diameter (Umax/D, 0.3–0.8). Suture has 12 lobes, 7 external; 3 umbilical elements ($U_2U_1U_3$) are fully isolated; U_2 subequal to or larger in area than U_1, both external; U_3 internal and subequal to U_1. Sutural formula: $(V_1V_1)LU_2U_1$:U_3ID [Russian], $(E_1E_mE_1)AL_vL_mL_dUI$ [German]. Thirty-seven named species. [Several new species of metalegoceratid have been described (ZHAO & ZHENG, 1977) from the Hutang Formation (Roadian–Wordian) of southern China (Jiangxi) and referred to *Metalegoceras*. They represent the basis for extending the range of the subfamily above the Baigendzhinian, although some aspects of both morphology and occurrence remain unclear.] *Cisuralian (Sakmarian–Artinskian), Guadalupian (?Roadian–?Wordian):* Kazakhstan (Southern Urals), Russia (Urals, Novaia Zemlia, Okhotskii Massif, Kulu-Tasskiy region), Tajikistan (Pamir), Indonesia (Timor), Australia (Canning Basin), China (Jilin, Xizang, Guizhou, Jiangxi), USA (Texas, New Mexico), Canada (Yukon, Northwest Territories), Oman.——FIG. 109,*3a–c*. **M. evolutum* (HANIEL); *a–b*, Bitauni beds, Baigendzhinian, Timor, Indonesia, ×0.67 (Glenister, Windle, & Furnish, 1973); *c*, Baigendzhinian, Southern Urals, diameter at 30 mm (Ruzhentsev, 1956b).

Bransonoceras MILLER & PARIZEK, 1948, p. 354 [**B. bakeri;* OD] [=*Pericycloceras* ZHAO & ZHENG, 1977, p. 243 (type, *P. costatum,* OD); =*Eolegoceras* LEONOVA in LEONOVA & DMITRIEV, 1989, p. 123 (type, *E. murgabense,* OD)]. Similar to *Metalegoceras*, but with strong transverse ribs retained to maturity. Three or four species. [The single specimen referred to *Pericycloceras costatum* exhibits a shallow crenulation on the fourth external saddle, close to the umbilical seam. Such features are developed sporadically in other metalegoceratids and are regarded as pathologic or capricious (GLENISTER, WINDLE, & FURNISH, 1973).] *Cisuralian (Artinskian), Guadalupian (?Roadian–?Wordian):* USA (New Mexico, Nevada, California), China (Guizhou, Zhejiang), Tajikistan (Pamir).——FIG. 109,*1a–b*. **B. bakeri*, holotype, USNM 112961, middle Hueco Formation, Artinskian, New Mexico, ×1.5 (Miller & Parizek, 1948).——FIG. 109,*1c–e*. *B. costatum*, type species of *Pericycloceras,* Dingji-

ashan Formation, ?Roadian, Zhejiang, ×1.5 (Zhao & Zheng, 1977).

Juresanites MAKSIMOVA, 1940b, p. 862 [**J. primitivus*; OD] [?=*Mennneroceras* ANDRIANOV, 1985, p. 127 (type, *M. menneri*, OD); described from a single specimen, on which subdivision details of the umbilical lobe are unclear]. Conch variable in relative width (W/D, 0.6–0.9) and umbilical diameter (Umin/D, 0.25–0.6). Characterized by incomplete isolation of three subdivisions of umbilical lobe: outer subdivision (U_2) is close to umbilical shoulder, with an area less than one half that of U_1; dorsal subdivision (U_3) is a shallow crenulation centered on umbilical seam or wall. Sutural formula: (V_1V_1) $L(U_2U_1U_3)$:ID [Russian]. Ten named species. *Cisuralian (Asselian–lower Sakmarian [Tastubian]):* Kazakhstan (Southern Urals), Russia (Southern Urals, Verkhoian), Western Australia (Perth Basin), Indonesia (Timor).——FIG. 109,*2a–c. *J. primitivus*, Asselian, Southern Urals; *a–b*, ×0.67; *c*, diameter at 45 mm (Ruzhentsev, 1952b).

Pseudoschistoceras TEICHERT, 1944, p. 87 [**P. simile*; OD] [?=*Gaoyaonites* XU, 1979, p. 42 (type, *G. guangdongensis,* OD]. Conch relatively narrow (W/D, 0.45–0.6) with small umbilicus (Umin/D, 0.25–0.35). Suture characterized by second tripartition of umbilical lobe to form a total of 16 lobes, 9 external. Sutural formula: (V_1V_1)$LU_2(U_{1.2}U_{1.1}$:$U_{1.2}$) U_3ID [Russian]. Three or four species. *Cisuralian (Artinskian [Baigendzhinian,* and possibly *Aktastinian]):* Western Australia (Carnarvon Basin), Indonesia (Timor, Western Irian Jaya), ?southern China (Guizhou, Guangdong).——FIG. 110*a–c. *P. simile*, Cordalia Sandstone, Carnarvon Basin, Western Australia; *a–b*, ×0.67; *c*, diameter at 80 mm (Glenister & Furnish, 1961).——FIG. 110*d–e. *P. gigas* (SMITH), Bitauni beds, Baigendzhinian, Timor; *d*, ×0.33; *e*, diameter at 115 mm (Glenister & Furnish, 1961).

Subfamily SPIROLEGOCERATINAE Nassichuk, 1970

[Spirolegoceratinae NASSICHUK, 1970, p. 86; RUZHENTSEV, 1974a, p. 28; BOGOSLOVSKAIA & PAVLOVA, 1988, p. 112, *partim*] [=Anuitidae ANDRIANOV, 1985, p. 154, *partim*]

Conch intermediate in size (up to 20 cm diameter), subdiscoidal and narrowly umbilicate (U/D, less than 0.4). Growth lines and constrictions prosiradiate; ornament reticulate, with prominent longitudinal lirae retained to maturity. Sutures twelve lobed, characterized by broad ventral prongs. Sutural formula: (V_1V_1)LU_2U_1:U_3ID [Russian]. [A rare unnamed metalegoceratid species from the Cisuralian (Sakmarian) of Western Australia (GLENISTER, WINDLE, & FURNISH, 1973, p. 1040) has sutural and conch characteristics of ancestral *Sverdrupites* and perhaps also of *Spirolegoceras.*] *Cisuralian (?upper Sakmarian [?Sterlitamakian]), Guadalupian (Roadian).*

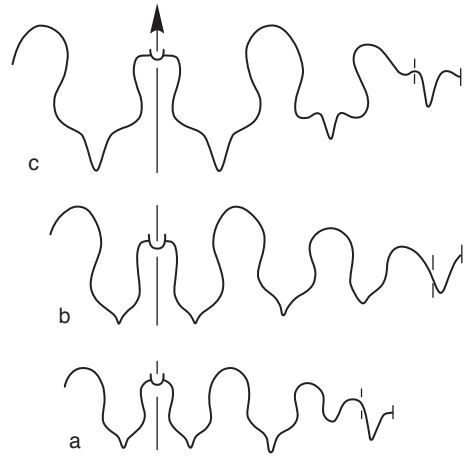

FIG. 111. Variations in width of ventral lobe prongs and in shape of lobes in Spirolegoceratinae (p. 177–178).

Spirolegoceras MILLER, FURNISH, & CLARK, 1957, p. 1064 [**S. fischeri;* OD][=*Gobioceras* BOGOSLOVSKAIA in BOGOSLOVSKAIA & PAVLOVA, 1988, p. 112 (type, *G. elenae*, OD)]. Suture characterized by prongs of ventral lobe that are wider than lateral lobe; ventral prongs and lateral lobe are strongly expanded medially, incipiently trifid at maturity; ventral subdivision of umbilical lobe (U_2) retains curved divergent flanks through ontogeny. Two species. [*Gobioceras* was named for a Roadian species from the Kirgizian Tien-Shan. It may serve as a primitive subgenus of *Spirolegoceras*, in which the ventral trifurcation (U_2) of the primary umbilical lobe remained smaller than the original element (U_1).] *Guadalupian (Roadian):* USA (Idaho), Mongolia (Gobi Tien-Shan).——FIG. 112,*1a–c. *S. fischeri*, Meade Peak Member, Phosphoria Formation; *a–b,* topotype, SUI 33053, ×1.33; *c*, diameter at 21 mm (Nassichuk, 1970).——FIG. 112,*1d–e. *S. elenae*, Roadian, Gobi Tien-Shan, ×0.67 (Bogoslovskaia & Pavlova, 1988).——FIG. 111*c. *S. elenae*, Roadian, Gobi Tien-Shan; diameter approximately 60 mm (Bogoslovskaia & Pavlova, 1988).

Sverdrupites NASSICHUK, 1970, p. 89 [**Spirolegoceras harkeri* RUZHENTSEV, 1961, p. 61; OD] [=*Anuites* ANDRIANOV, 1985, p. 156 (type, *A. Kosynskyi*, OD); =*Pseudosverdrupites* KUTYGIN, 1996, p. 18 (type, *P. Bidnikovi*, OD)]. Similar to *Spirolegoceras*, but lateral lobe and prongs of ventral lobe did not become incipiently trifid; width of ventral prongs 0.85–1.2 mm (V_1/L) that of corresponding lateral lobe. Ventral subdivision of umbilical lobe (U_2) is expanded medially in all but the questionable Australian representative. Three or four species. [Figures 112,*1d,* 112,*2d,* and 112,*2e* herein portray stages in development of the two external subdivisions

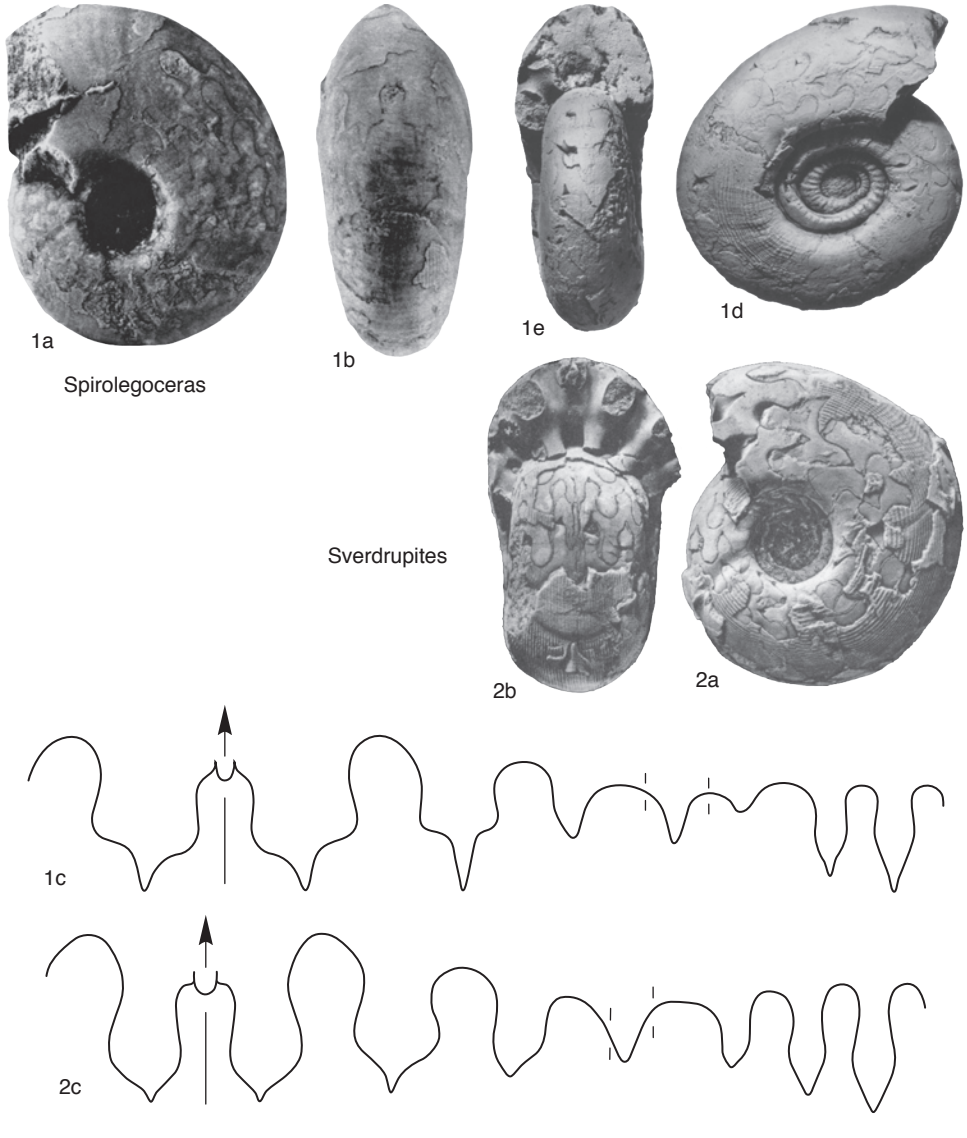

FIG. 112. Metalegoceratidae (p. 177–178).

of the primary umbilical lobe, confirming metalegoceratid affinities.] *Cisuralian (?upper Sakmarian [?Sterlitamakian]), Guadalupian (Roadian):* Canada (Arctic Archipelago: Devon Island, Melville), Russia (Novaia Zemlia,Volga-Urals, Omolon Massif, Okhotskii Massif, Verkhoian), Western Australia (?Carnarvon Basin).——FIG. 112,*2a–c.* **S. harkeri* (RUZHENTSEV), Assistance Formation, Roadian, Devon Island, Canada; *a–b*, ×1.3 (Nassichuk, Furnish, & Glenister, 1966); *c*, diameter at 60 mm (Nassichuk, 1970).——FIG. 111*b.* **S. harkeri* (RUZHENTSEV), Assistance Formation, Roadian, Devon Island, Canada; external part of Figure 112,*2c* (Nassichuk, 1970).——FIG. 111*a. S.* sp., Assistance Formation, Devon Island, diameter at 30.5 mm (Nassichuk, 1970).

Subfamily EOTHINITINAE Ruzhentsev, 1956

[*nom. transl.* FURNISH, 1973, p. 526, *ex* Eothinitidae RUZHENTSEV, 1956b, p. 193] [=Epiglyphioceratinae ZAKHAROV, 1984, p. 152]

Discoidal metalegoceratids with wide umbilicus; strong ribs form deep ventral sinus. Twelve lobes, seven external. Sutural

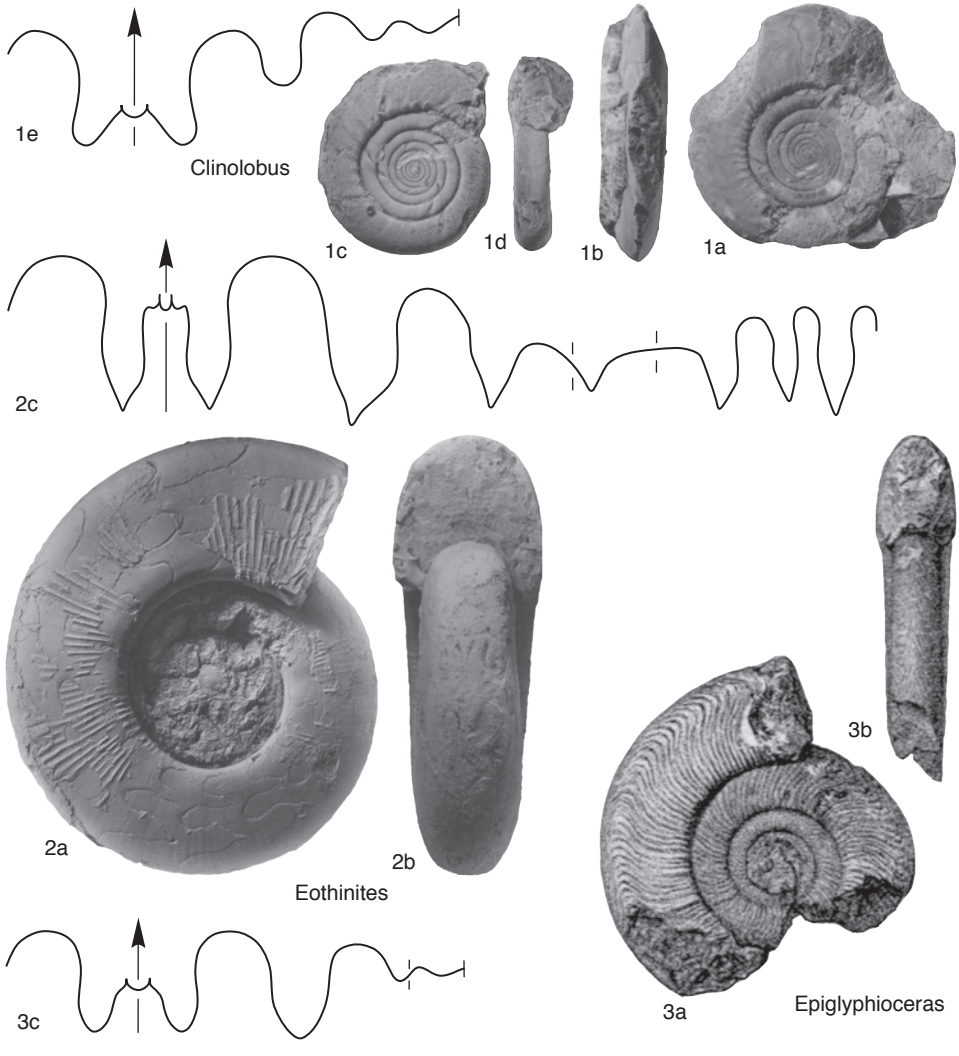

FIG. 113. Metalegoceratidae (p. 179–180).

formula: $(V_1V_1)LU_2U_1{:}U_3ID$ [Russian]. [Full familial status may be justifiable, but is not recognized herein due to uncertainty of some aspects of phylogenesis. Wordian eothinitins represent the terminal paedomorphs of the Metalegoceratidae.] *Cisuralian (lower Artinskian)–Guadalupian (Wordian).*

Eothinites RUZHENTSEV, 1933, p. 169 [**E. kargalensis*; OD] [=*Uralites* CHERNOV, 1907, p. 292, *nom. nud.*, *non* VOINOVA, 1934, p. 3, *nom. nud.*; =*Rhiphaeites* RUZHENTSEV, 1933, p. 171 (type, *Paralegoceras pseudo-meneghinii* HANIEL, 1915, p. 64, OD)]. Conch subdiscoidal (W/D, 0.2–0.4) with moderately wide umbilicus (Umin/D, 0.35–0.7). Ribs commonly bifurcate on umbilical shoulder and may be associated with weaker longitudinal lirae; shallow sinus across flanks is separated from deeper ventral sinus by prominent ventrolateral salient. Prongs of ventral lobe are generally much narrower than corresponding lateral lobe, but may be up to 1.5 times that width. Thirteen species. [Extreme variation in the relative width of prongs of the ventral lobe may indicate polyphyletic derivation; narrow prongs resemble those of *Paragastrioceras*, wider ones *Uraloceras*, and each may warrant full generic status.] *Cisuralian (lower Artinskian [Aktastinian]–Kungurian):* Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), Ukraine (Crimea), Indonesia (Timor), USA (Texas), China (Guizhou, Guangxi, Xinjiang).——FIG. 113,*2a–c.*

Epiglyphioceras* Spath, 1930, p. 13 [Glyphioceras meneghinii* Gemmellaro, 1887, p. 92; OD]. Similar to *Eothinites* in general conch form, but smaller and with ribs outlining deeper sinus across venter (depth of sinus one-half corresponding whorl width). Prongs of ventral lobe less than two-thirds width of lateral lobe. Two species. [Tripartition of primary umbilical lobe, at about 10 mm phragmocone diameter, has not been reported previously. As the diminutive terminal paedomorph of the Eothinitinae, *Epiglyphioceras* closely resembles similar-sized juvenile stages of the large Cisuralian ancestor *Eothinites*.] *Guadalupian (?Roadian, Wordian):* Italy (Sicily), Tajikistan (Pamir), Afghanistan. ——Fig. 113,*3a–c*. **E. meneghinii* (Gemmellaro), lectotype (herein), MGUP 134 (Gemmellaro, 1887, pl. 10,*39–40*), Sosio limestone, Sicily; *a–b*, ×2 (Gemmellaro, 1887); *c*, diameter at 15 mm (new).

Subfamily CLINOLOBINAE Miller, Furnish, & Schindewolf, 1957

[Clinolobinae Miller, Furnish, & Schindewolf, 1957, p. 67]

Similar to Eothinitinae in sutural ontogeny and general conch form, but narrowly lenticular with acutely angular venter at maturity. *Cisuralian (upper Artinskian [Baigendzhinian])–Guadalupian (Wordian).*

Clinolobus* Gemmellaro, 1887, p. 84 [C. Telleri;* OD]. Small metalegoceratids (2 cm maximum diameter), with umbilical ratio (Umin/D) approximating 0.5. Conch narrowly discoidal with rounded venter to 10 mm diameter, thereafter lenticular with acutely angular venter. Low nodes closely spaced on dorsolateral shoulder; fine ribs became strongly biconvex coincident with development of angular venter. All lobe bases rounded to maximum observed conch diameter; primary umbilical lobe strongly tripartite by 8 mm phragmocone diameter. Two species. [Juveniles closely resemble *Epiglyphioceras* in conch form, ornament, and suture. Distinguishing generic characters developed coincident with formation of angular venter.] *Cisuralian (upper Artinskian [Baigendzhinian])–Guadalupian (Wordian):* Italy (Sicily), USA (western Texas).——Fig. 113,*1a–e*. **C. telleri*, Sosio limestone, Wordian, Sicily; *a–b*, lectotype (herein), MGUP 127A of Gemmellaro (1887, pl. 10,*29–30*), ×2; *c–d*, paralectotype, MGUP 127B of Gemmellaro (1887, pl. 10,*31–33*), mature and juvenile conchs, respectively, ×2; *e*, diameter at 8 mm (all new).

POPANOCERATOIDEA

Brian F. Glenister,[1] William M. Furnish,[2] and Zhou Zuren[3]

[1]retired, formerly of the University of Iowa; [2]deceased, formerly of the University of Iowa; [3]Nanjing Institute of Geology and Palaeontology]

Superfamily POPANOCERATOIDEA Hyatt, 1900

[*nom. transl.* Ruzhentsev, 1957, p. 59, *ex* Popanoceratidae Hyatt, 1900, p. 564]

Conch small (diameter less than 10 cm), narrowly discoidal (W/D, 0.1–0.35), and usually involute beyond third or fourth volution. Ribs and constrictions form high dorsolateral salient and slope backward through shallow ventrolateral sinus to narrow U- or V-shaped sinus across rounded to flat venter. Distinctive hemispherical pits occur on shell surface and internal mold and across midflanks in many juveniles. Mature modifications comprise subterminal constriction, terminal flare, and formation of pair of narrow ventrolateral keels bounding accentuated hyponomic sinus. Basic sutural formula: $(V_1V_1)L_2L_1(L_{2.1}L_{2.1})U^1U_1{:}U^2U_2(I_{2.1}I_{2.1})I_{1.1}I_{1.2}(D_2D_1D_2)$ [Russian], $(E_1E_mE_1)A_{1v}A_{1m}A_{1dv}A_{1d2v}A_{1d3}A_2LU_2U_3U_{1v2}U_{1vd}U_{1m}U_{1d}(I_1I_mI_1)$ [German].

All saddles rounded, dorsal lobe (D) incipiently trifid, most lateral lobes strongly denticulate at base, especially in advanced forms. Total number of lobes 22 to 38. Umbilical complex stabilized at 4 lobes, 2 of them derived from saddles ($U > U^1U_1{:}U^2U_2$). External lateral lobes added by repeated bifurcation and subsequent isolation of lateral lobe nearest umbilicus: $L_2 > L_{2.1}L_{2.1} > L_{2.1}(L_{2.1.1}L_{2.1.1})$. Mode of addition of internal lateral lobes distinctive, according to formula: $I > I_2I_1 > (I_{2.1}I_{2.1})I_{1.1}I_{1.2} > (I_{2.1.1}I_{2.1.1})$

$I_{2.1}I_{1.1}I_{1.2}$. *Cisuralian (Asselian)–Lopingian (Wuchiapingian).*

Family POPANOCERATIDAE Hyatt, 1900

[Popanoceratidae Hyatt, 1900, p. 564] [=Tauroceratinae Tumanskaia, 1939, p. 18; =Pamiropopanoceratinae Leonova, 2002, p. 96]

Involute popanoceratoideans (U/D, 0.1–0.2) that during phylembryogenesis developed prongs of ventral lobe that are substantially broader than adjacent lateral lobes, and strong denticulation of most external lateral lobes. Sutural trace straight and directly transverse. [This ancestral family originated in the earliest Permian Asselian age with one rare, diminutive species. Size, abundance, and specific diversity increased to maxima in the Guadalupian (Artinskian through Wordian). Thereafter, the group declined to eventual extinction, ending with a rare paedomorphic relic in the basal Wuchiapingian Stage, substantially before the end of the Permian (Glenister & Furnish, 1988b).] *Cisuralian (Asselian)–Lopingian (Wuchiapingian).*

Popanoceras Hyatt, 1884 in 1883–1884, p. 337 [**Goniatites sobolewskyanus* de Verneuil, 1845, p. 372; SD Gemmellaro, 1887, p. 19, as *Popanoceras Sobolewskianum* (*sic*)] [=*Pamiropopanoceras* Leonova in Leonova & Dmitriev, 1989, p. 174 (type, *P. meridionale,* OD)]. Prongs of ventral lobe (V_1) equal to or wider than adjacent lateral lobe, bidentate to quadridentate; four or five external lateral lobes moderately dentate. Twelve named species. *Cisuralian (lower Artinskian [Aktastinian])–Guadalupian (Roadian):* Kazakhstan (Southern Urals), Russia (Southern Urals), China (Xizang, Jilin, Guizhou), Japan (Fukushima), Madagascar, Tajikistan (Pamir), Ukraine (Crimea), Indonesia (Timor), Western Australia (Carnarvon Basin), USA (Texas).——Fig. 114,*1a–e.* **P. sobolewskyanum* (de Verneuil), upper Artinskian, Baigendzhinian, Southern Urals; *a–c,* ×0.67; *d,* diameter approximately 25 mm (Ruzhentsev, 1956b); *e*, diameter at 35 mm (Miller & Furnish, 1940a).

Epitauroceras Glenister & Furnish, 1988b, p. 57 [**E. soewarnoi*; OD]. Terminal relics of Popanoceratidae, characterized by small size (diameter less than 25 mm), and first lateral lobe with denticulation extending more than one-half distance to crest of first lateral saddle. One species. [*Epitauroceras* conforms to pattern now recognized for a significant number of Late Paleozoic ammonoid family-group taxa (Glenister & Furnish, 1988b) in which the last survivors for each group are rare, diminutive paedomorphs.] *Lopingian (Wuchiapingian):* Indonesia (Timor).——Fig. 114,*2a–e.* **E. soewarnoi*, Amarassi beds; *a–c*, ×0.67; *d–e*, diameter about 10–12 mm (Glenister & Furnish, 1988b).

Neopopanoceras Schindewolf, 1939a, p. 447, *nom. nov.* Zhou & Glenister, herein, p. 218, *pro Tauroceras* Tumanskaia, 1938b, p. 145 (type, *Tauroceras scrobiculatum* Tumanskaia, 1938b, p. 145, OD), *non* Hope, 1840, modern insect, Coleoptera, *fide* ICZN *Code* Articles 23.3.5, 52.2 [**Popanoceras scrobiculatum* Gemmellaro, 1887, p. 25; OD; *fide* ICZN *Code* 67.8–67.8.1] [=*Gemmellaroceras* Tumanskaia, 1937d, p. 470, *nom. nud.*, *non* Hyatt, 1900, p. 574, Jurassic ammonoid]. Prongs of ventral lobe much wider than adjacent lateral lobe. Six or seven external lateral lobes at maturity, most strongly denticulate like ventral prongs. Eleven named species. *Guadalupian (Wordian):* Italy (Sicily), Tunisia, Oman, Iraq (Kurdistan), Afghanistan, Ukraine (Crimea), Tajikistan (Pamir), Malaya, China (Jilin, Xizang, Xinjiang), USA (western Texas), Mexico (Coahuila).——Fig. 115,*1a–f.* **N. scrobiculatum* (Gemmellaro), Sosio limestone, Sicily; *a–c,* topotype, MGUP 45 of Gemmellaro (1888, pl. B,*2–4*), ×0.67; *d–f,* ×1.33 (Glenister & Furnish, 1988b).——Fig. 115,*1g. N. bowmani* (Böse), Word Limestone, western Texas, diameter at 40 mm (Miller & Furnish, 1940a).

Propopanoceras Tumanskaia, 1938a, p. 108 [**Popanoceras Lahuseni* Karpinskii, 1889, p. 67; OD)]. Prongs of ventral lobe bidentate and narrower than corresponding first lateral lobe. Four or five external lateral lobes, at least one of which is tridentate or quadridentate, fourth or fifth incipiently bifid. Seven named species. [There are no suitable illustrations of the holotype available.] *Cisuralian (Sakmarian):* Russia and Kazakhstan (Southern Urals), Indonesia (Timor), Western Australia (Canning Basin), USA (western Texas).——Fig. 115,*2a–c. P. simense*, Tastubian, Urals; *a–b*, ×1.5; *c*, diameter at 23 mm (Ruzhentsev, 1951).

Protopopanoceras Ruzhentsev, 1938, p. 260 [**Popanoceras sublahuseni* Gerasimov, 1937, p. 18; OD]. Rare ancestral popanoceratids characterized by combination of ventral prongs narrower than adjacent lateral lobe, bidentate first and second lateral lobes, and bifid third lateral ($L_{2.1}L_{2.1}$). One species. *Cisuralian (Asselian):* Russia (Southern Urals).——Fig. 115,*3a–c.* **P. sublahuseni* (Gerassimov); *a–b,* ×1; *c,* diameter at 25 mm (Ruzhentsev, 1951).

Family MONGOLOCERATIDAE Ruzhentsev & Bogoslovskaia, 1978

[*nom. transl.* Glenister & Furnish, 1981, p. 64, *ex* Mongoloceratinae Ruzhentsev & Bogoslovskaia, 1978, p. 87]

Involute to comparatively evolute popanoceratoideans (U/D, 0.01–0.35) that maintained narrow prongs of ventral lobe during phylogenesis but developed numerous strongly denticulate lobes and also an arched

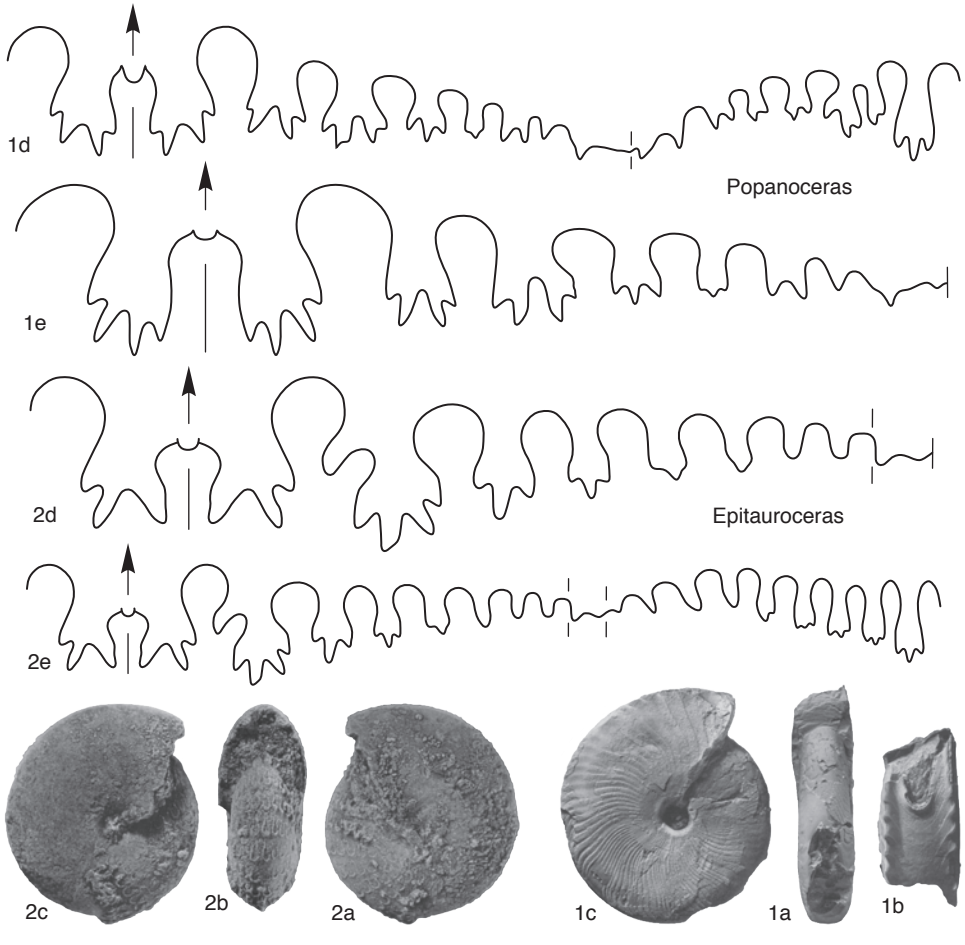

FIG. 114. Popanoceratidae (p. 181).

trace of external suture across dorsolateral flanks. [The early Permian history of the family, after presumed divergence from primitive popanoceratids, is unknown.] *Cisuralian (Kungurian)–Guadalupian (*probably *Capitanian).*

Mongoloceras RUZHENTSEV, 1960a, p. 110 [**M. gobiense;* OD]. Prongs of ventral lobe and most of six or seven external lateral lobes strongly denticulate. Mature sutures resemble popanoceratid *Tauroceras*, but juveniles have ventral prongs narrower than adjacent first lateral lobe, and arched trace of external suture dorsad of third lateral saddle. Two named species. *Guadalupian:* Mongolia (Usu-Hongor), Oman, China (?Jilin).——FIG. 116, *1a–c.* **M. gobiense*, Honguer-Ula Limestone, probable Capitanian, southern Mongolia; *a–b,* ×1.33; *c*, diameter at 22 mm (Ruzhentsev, 1960a).——FIG. 116,*1d–i. M. omanicum* GLENISTER & FURNISH, Wordian, near Ba'id, Oman; *d–h,* ×1; *i*, diameter at 40 mm (Glenister & Furnish, 1988b).

Angrenoceras SHENG, 1988b, p. 153 [**A. langcuoense*; OD]. Poorly known mongoloceratids, probably distinguishable generically by exceptionally broad secondary ventral saddle (width one-half that of entire ventral lobe). Two named species. *Guadalupian (*probably *Capitanian):* China (Xizang).

Biarmiceras LEONOVA, KUTYGIN, & SHILOVSKY, 2005, p. 479 [**Popanoceras tumarense* RUZHENTSEV, 1961, p. 60; OD]. Resembles *Mongoloceras* in narrow

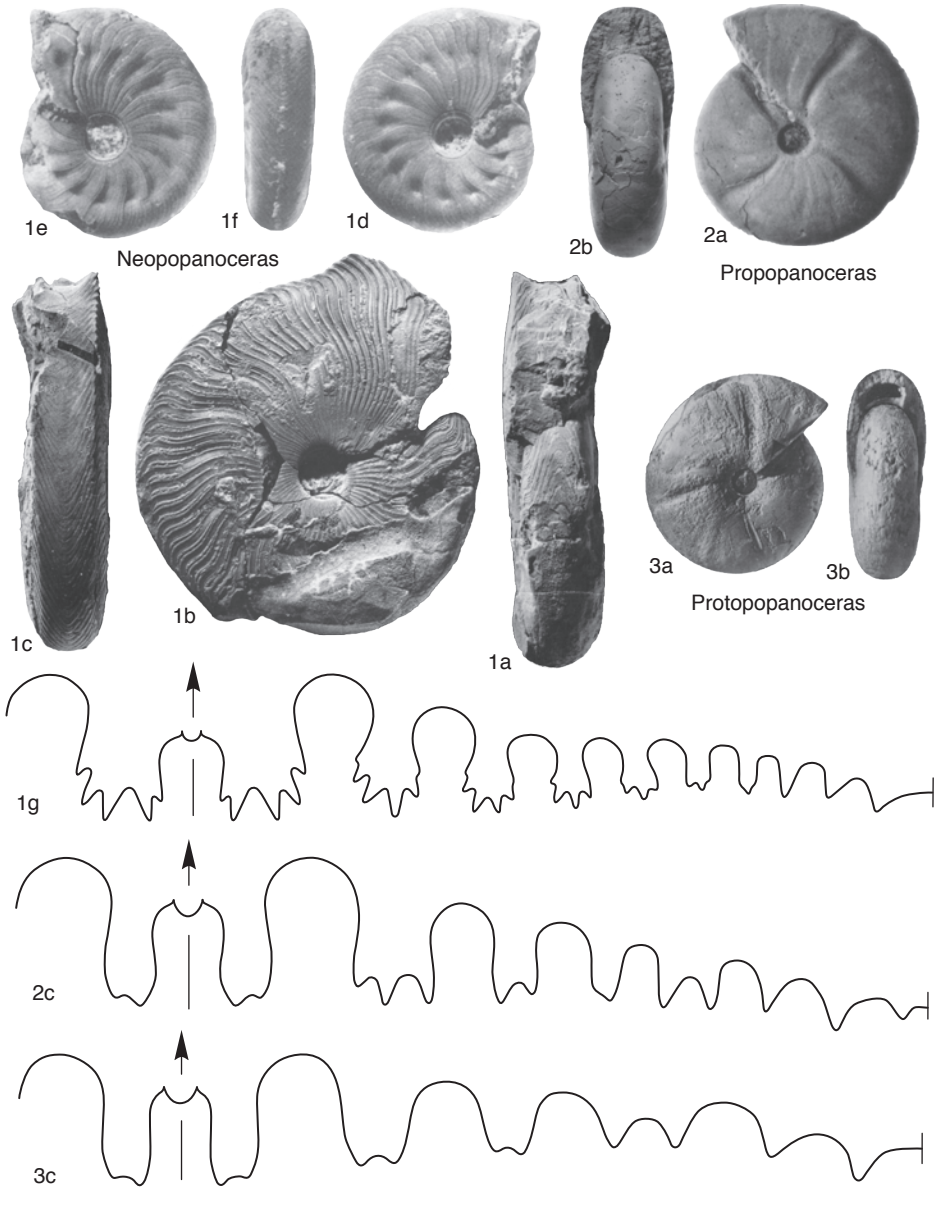

FIG. 115. Popanoceratidae (p. 181).

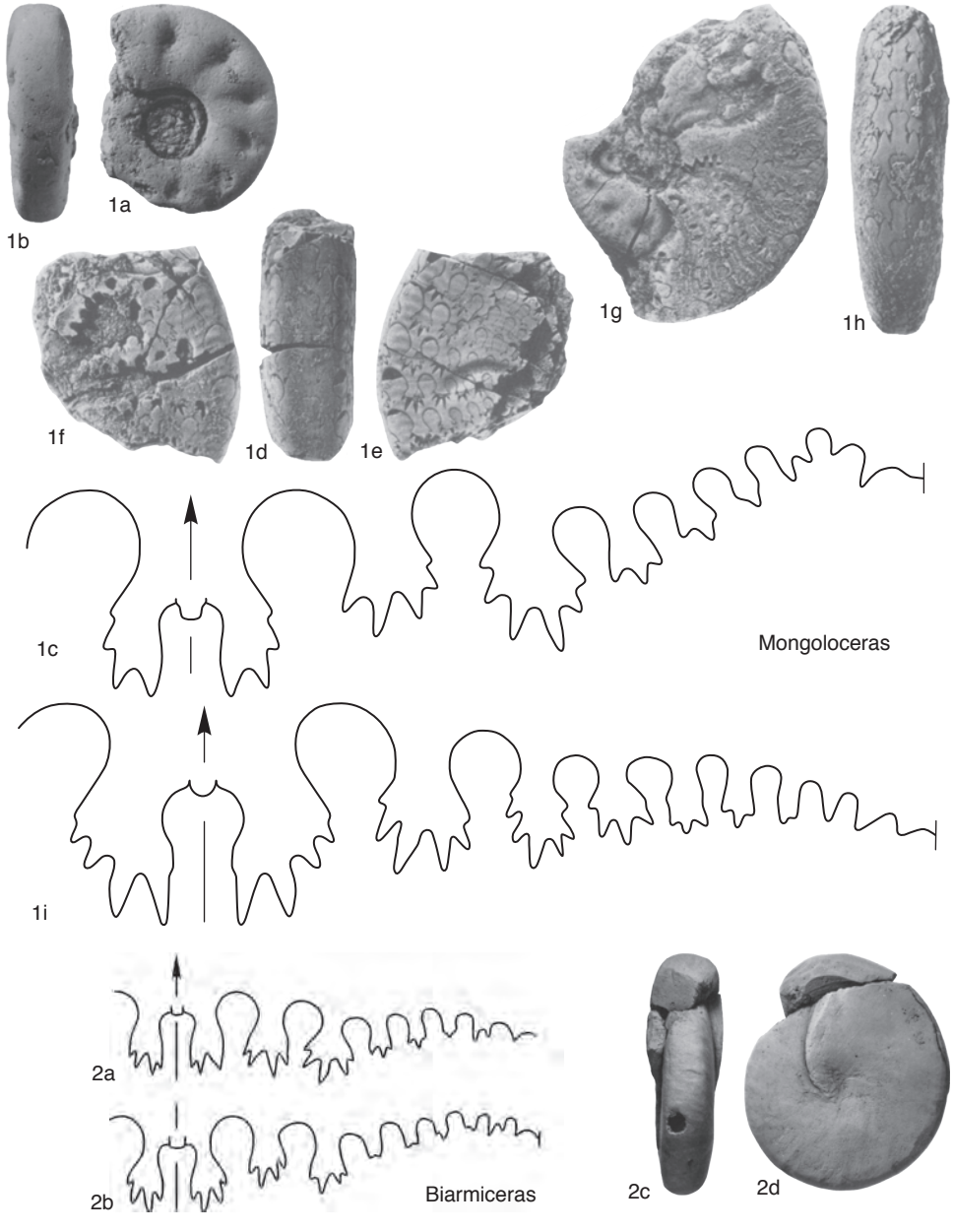

FIG. 116. Mongoloceratidae (p. 182–184).

ventral prongs, arched trace of external suture, and dorsad subdivision of third lateral saddle, but distinguishable by nearly closed or very small umbilicus (U/D 0.01–0.13). Five species. *Cisuralian (Kungurian)–Guadalupian (Roadian):* Russia (western Verkhoian, Volga-Urals), Canada (Northwest Territories).——FIG. 116,*2a. *B. tumarense* (RUZHENTSEV), holotype, Kungurian, Tumara basin, western Verkhoian, PIN 1802/31, diameter at 21.5 mm (new, courtesy of T. B. Leonova).——FIG. 116,*2b–d. B. kremeshkense* LEONOVA, KUTYGIN, & SHILOVSKY, Kazanian Stage, Volga-Urals; *b*, diameter at 31 mm; *c–d*, ×1.5 (Leonova, Kutygin, & Shilovsky, 2005).

PROLECANITIDA

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Order PROLECANITIDA Miller & Furnish, 1954

[*nom. transl.* Teichert, 1967, p. 206, *ex* Prolecanitina Miller & Furnish, 1954, p. 687] [=Medlicottiida Zakharov, 1983, p. 29]

Conch thinly discoidal to lenticular, initially widely evolute. Umbilicus narrow or closed at maturity in most representatives in the Pennsylvanian, Permian, and Triassic. Shell generally smooth or with fine growth lines that form low lateral and ventral salients; ventrolateral ribs and nodes on ventrolateral shoulder appear rarely in Carboniferous but are common in Permian. Full body chamber preserved rarely, approximately one-half volution in length, generally lacking conspicuous mature modifications. Siphuncle simple, retrochoanitic, and ventral-marginal in position. Basic formula: EALUI [German], VLU:ID [Russian]. Ventral lobe initially narrow and undivided, later tridentate to trifid, rarely broad; dorsal lobe narrow, undivided, or bidentate. Sutures characteristically comprise series of subequal lobes, lateral in position, most successively derived from saddles of umbilical lobe complex; number ranges from 8 to more than 30. Ventrolateral saddle generally lower than adjacent second lateral saddle in ancestral forms, characteristically highest element in Permian and Triassic. First lateral lobe almost invariably widest sutural element, subdivided (usually bifid) in all but ancestral representatives; in later forms ventral prong commonly transformed into complexly subdivided first lateral saddle. *Mississippian (lower Tournaisian)–Lower Triassic (Induan).*

Some uncertainty remains concerning derivation and affinities of the Prolecanitida. Several Paleozoic ammonoid specialists (Karpinskii, 1896; Schindewolf, 1933, 1951c, 1954, 1959; Ruzhentsev, 1949b, 1951, 1960d) maintained that the first lateral lobe represents the primary umbilical element, and that the basic formula therefore is: ELU_2U_1I [German], VUU[1]:ID [Russian]. However, conclusions of more recent studies (Hodgkinson, 1965; Knapp, 1965; for discussion, see Nassichuk, 1975) have confirmed the assumption that, with the possible exception of *Protocanites* and perhaps rare other relatives of ancestral forms (Knapp, 1965), all other genera usually referred to the Prolecanitida have a first so-called lateral lobe that was derived adventitiously. Consequently, the formula is EALUI [German], VLU:ID [Russian]. Affinities with the Goniatitida are therefore closer than visualized previously.

Despite recognition of basic similarity between the sutural ontogeny of Prolecanitida and Goniatitida, the former represents an evolutionary complex that can be distinguished consistently on other features of the suture as well as conch form. It may be interpreted to be ancestral to the Permian representatives of the ceratitid suborder Paraceltitina and their descendant Mesozoic lineages (Spinosa, Furnish, & Glenister, 1975). However, ontogenetic acceleration of earliest sutural development precludes unambiguous determination of the ontogenetic origin of the first so-called lateral lobe in Mesozoic ammonoids. Such determination may be afforded only by Paleozoic ancestors.

Superfamily PROLECANITOIDEA Hyatt, 1884

[*nom. transl.* Miller & Furnish, 1954, p. 687, *ex* Prolecanitidae Hyatt, 1884 in 1883–1884, p. 331]

Conch widely evolute to moderately involute, discoidal, with wide or moderately narrow umbilicus. Shell surface in general smooth except for rare ribbed species. Ventral lobe simple or trifid. Lateral and umbilical lobes simple, acute, or rounded, in some forms denticulate. Total number of lobes 10 to 22. Basic sutural formula: $EALUU_nI$ [German], $VLUU^n$:ID [Russian]. Primary lateral and umbilical lobes (L and U) maintain their identity throughout ontogeny; new elements (U_{1+n}, U^{1+n}) were added by successive derivation in saddles of umbilical lobe complex. Succession of subequal umbilical lobes decreases in size toward umbilicus. *Mississippian (lower Tournaisian)–Guadalupian (Wordian).*

Family PROLECANITIDAE Hyatt, 1884

[Prolecanitidae Hyatt, 1884 in 1883–1884, p. 331] [=Ibergiceratidae Haug, 1898, table 1]

[Materials for this family prepared by Jürgen Kullmann]

Ventral lobe simple, undivided; suture line on flanks with at least two pointed or bifid lobes. Conch shape widely umbilicate. Shell surface smooth, except for rare ribbed species; growth lines linear or sinuous. *Mississippian (lower Tournaisian–lower Serpukhovian), Pennsylvanian (?lower Bashkirian).*

Subfamily PROLECANITINAE Hyatt, 1884

[*nom. transl.* Schindewolf, 1922, p. 14, *ex* Prolecanitidae Hyatt, 1884 in 1883–1884, p. 331] [=Eocanitinae Weyer, 1972a, p. 322]

Ventral lobe pouched, orad wide or slightly narrowed, at its base pointed or pipelike elongated; suture line on flanks with at least three or more simple pointed lobes. Phylogenetic lineage: *Eocanites–Becanites–Michiganites–Prolecanites–Metacanites-Dombarocanites. Mississippian (lower Tournaisian–lower Serpukhovian), Pennsylvanian (?lower Bashkirian).*

Prolecanites Mojsisovics, 1882, p. 199 [**Goniatites mixolobus* G. Sandberger & F. Sandberger, 1850, p. 67, *pars, non* Phillips, 1836, p. 236; SD Hyatt, 1884 in 1883–1884, p. 335; =*Prolecanites mojsisovicsi* Miller, 1938, p. 181, obj.; =?*Goniatites serpentinus* Phillips, 1836, p. 237, subj.] [=*Rhipaeocanites* Ruzhentsev, 1949c, p. 737 (type, *R. librovitchi,* OD)]. Suture line with twelve lobes. Ventral lobe parallel sided or pouched, four lobes on flanks. Sutural formula: $EALU_2U_1U_3I$ [German], $VLUU^1U^2$:ID [Russian]. Many species. [The ontogenetic development of the suture is insufficiently known, and the type species is insufficiently known.] *Mississippian (upper Visean–lower Serpukhovian), Pennsylvanian (?lower Bashkirian):* Belgium, Great Britain, Germany, Bosnia-Herzegovina, Spain, Algeria, Morocco, Poland, Russia and Kazakhstan (South Urals), China (Xinjiang, Xizang), USA (Illinois, Indiana, California); China (Xinjiang), *?lower Bashkirian.*——Fig. 117,*1a–c. P. discoides* Foord & Crick, holotype, Carboniferous Limestone, Yorkshire, England, upper Visean, BMNH C.231; *a–b,* ×1; *c,* suture, diameter at 45 mm, enlarged (Foord & Crick, 1897).

Becanites Korn, 1997, p. 34 [**Prolecanites algarbiensis* Pruvost, 1914, p. 17; OD]. Similar to eight lobes of *Protocanites.* Two lobes on flanks, first lateral lobe slightly pouched, second lateral lobe next to umbilicus lanceolate and long. Six species. [The ontogenetic development of the suture for this genus is insufficiently known.] *Mississippian (middle Tournaisian, ?lower upper Tournaisian):* Germany, Portugal, Morocco, Russia and Kazakhstan (South Urals), USA (Kentucky, Missouri).——Fig. 117,*3a–b. *B. algarbiensis* (Pruvost), neotype, 0.6 km southwest of Bordeira, Portugal, from Bordalete Formation, middle Tournaisian, IGML 253; *a,* ×2; *b,* incomplete suture, diameter at 16 mm, ×5.5 (Korn, 1997).

Dombarocanites Ruzhentsev, 1949c, p. 738 [**D. chancharensis* Ruzhentsev, 1949c, p. 739; OD]. Conch cross section oval. Suture line in general similar to *Prolecanites* and *Metacanites.* Upper part of ventral lobe wide, parallel sided or divergent; basic part very narrow, pipelike. Dorsal lobe bifid. Four species. [This genus is transitional to *Prolecanites* and *Metacanites* and may be a junior synonym of either one; for discussion, see Weyer, 1972a, p. 329.] *Mississippian (upper Visean–lower Serpukhovian):* Serbia, Russia and Kazakhstan (South Urals), Uzbekistan (Fergana), USA (Utah, California).——Fig. 118,*2a–c. *D. chancharensis*, Dombar Hills, South Urals, Kazakhstan; *a–b,* uppermost Visean, PIN 455/1109, ×1; *c,* suture of holotype, lower Serpukhovian, PIN 455/12, whorl height at 8.5 mm, whorl width 5 mm, ×4.8 (Ruzhentsev & Bogoslovskaia, 1971).

Eocanites Librovich, 1957, p. 263 [**Protocanites supradevonicus* Schindewolf, 1926a, p. 104; OD]. Only eight lobes; two lobes on flanks, first lateral lobe considerately longer than second. Sutural formula: EALUI [German], VLU:ID [Russian] Many species. [The ontogenetic development

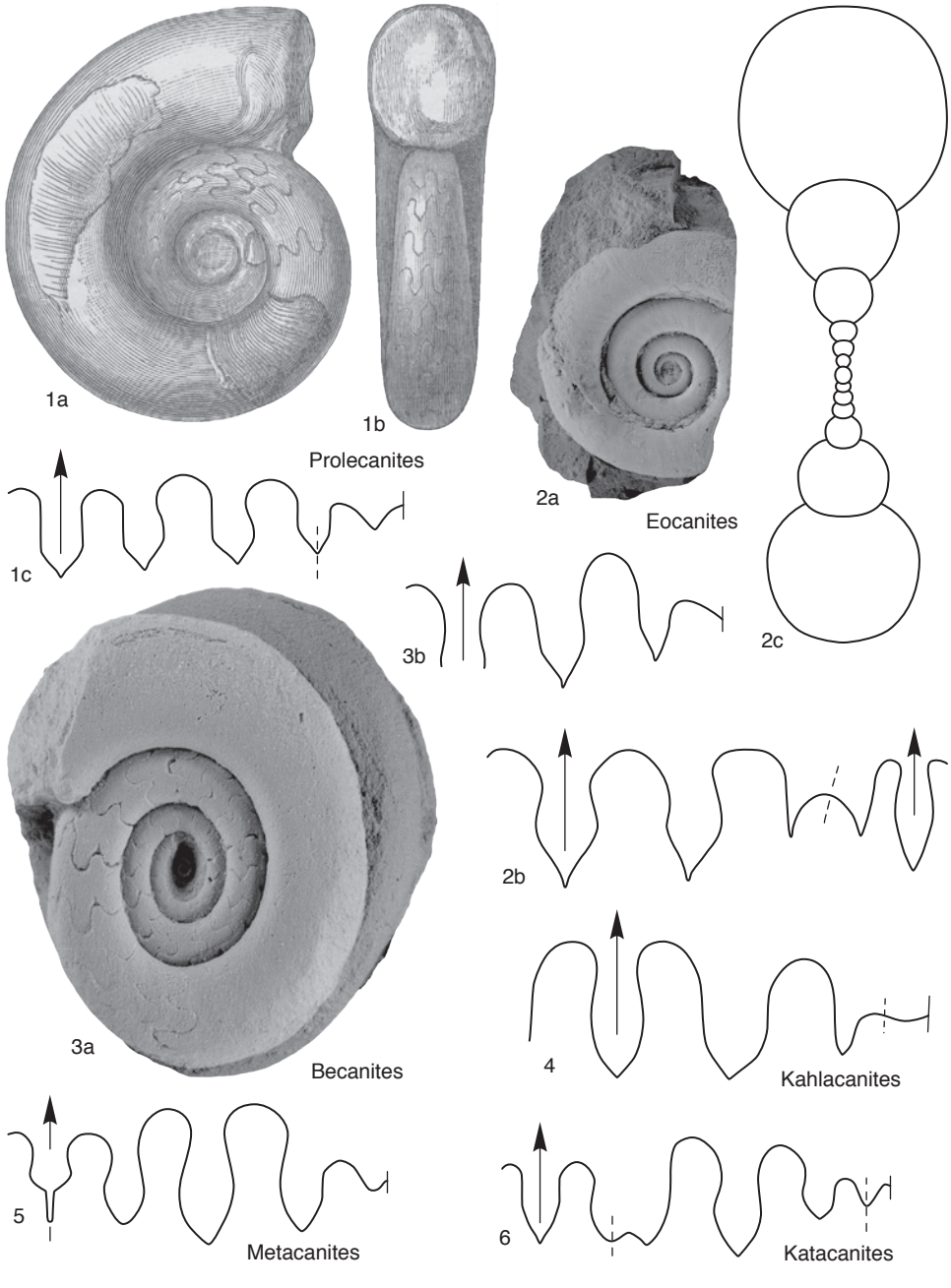

FIG. 117. Prolecanitidae (p. 186–188).

of the suture is insufficiently known.] *Mississippian (lower Tournaisian, ?middle Tournaisian):* Germany, Austria, France, Portugal, ?Morocco, Poland, ?Kazakhstan, China (Guizhou), ?Canada (Alberta).——FIG. 117,*2a–c. *E. supradevonicus* (SCHINDEWOLF); *a,* Ober-Rödinghausen, railway cut, Sauerland, Rhenish Massif, Germany, lowermost layer of Hangenberg limestone, lowermost Tournaisian, GPIT 1130/161, ×1.25; *b,* suture, whorl height at 6.5 mm, whorl width 6.8 mm, GPIT

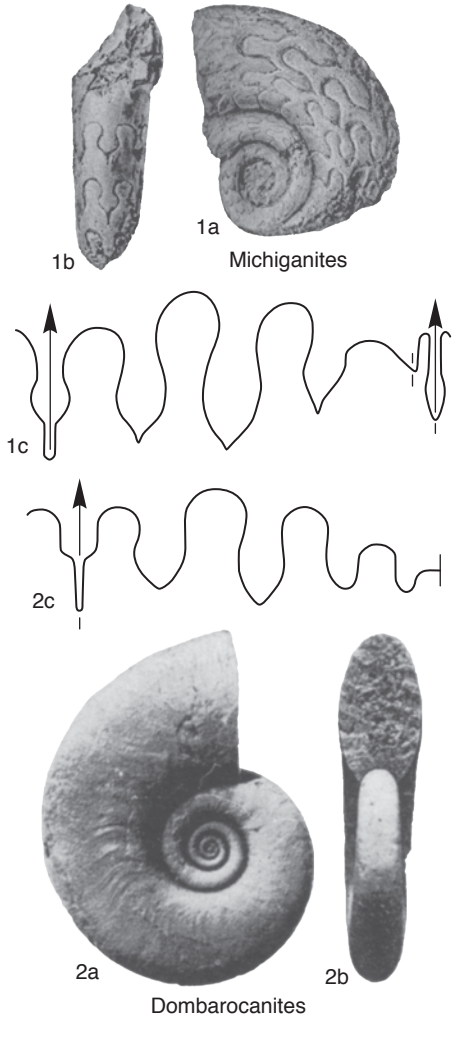

FIG. 118. Prolecanitidae (p. 186–188).

1130/181, ×4.8 (Korn, 1994); *c,* cross section, GPIT 1130/133-134, ×2.5 (Vöhringer, 1960).

Kahlacanites EBBIGHAUSEN & others, 2004, p. 144 [**K. mariae* EBBIGHAUSEN & others, 2004, p. 147; OD]. Ten lobes, three lobes on flanks; second lateral lobe small and hooklike, third rounded and shallow. Sutural formula: EAL_1L_2UI [German], VLU^1U^2:ID [Russian]. Three species. [The ontogenetic development of the suture for this genus is insufficiently known.] *Mississippian (lower Tournaisian):* Algeria.——FIG. 117,*4. *K. mariae,* Gara el Kahla, 35 km southwest of Timimoun, Gourara, Algeria, Grès Supérieur de Kahla, MB.C.5471.1, diameter at 13.9 mm, whorl height 5.0 mm, whorl width 5 mm, ×6.6 (Ebbighausen & others, 2004).

?Katacanites KULLMANN, 1963, p. 283 [**K. quadratoides* KULLMANN, 1963, p. 284; OD]. First lateral lobe bifid, three simple umbilical lobes on flank. One species. [The relationship of the genus is questionable, because the ontogenetic development of the suture is unknown.] *Mississippian (upper Visean):* Spain.——FIG. 117,*6. *K. quadratoides,* holotype, suture, Peña Roscas, Crémenes, León Province, red limestones, Alba Formation, GPIT 1237/363, whorl height at 13.5 mm, whorl width 9.5 mm, ×2.7 (Kullmann, 1963).

?Metacanites SCHINDEWOLF, 1922, p. 15 [**M. serpentinus;* OD; =*Prolecanites serpentinus* DOLLÉ, 1912, p. 251, *non Goniatites serpentinus* PHILLIPS, 1836, p. 237; in accordance with ICZN *Code* Art. 7b]. Conch cross section oval. Suture line in general similar to *Prolecanites.* Upper part of ventral lobe wide, pouched, and orad narrowed; basic part very narrow, pipelike. Two or three species. [This genus is transitional to *Prolecanites* and may be its junior synonym; it is also transitional to *Dombarocanites* and may be its senior synonym; for discussion, see WEYER, 1972a, p. 330. The type species is insufficiently known.] *Mississippian (upper Visean):* Spain, Algeria.——FIG. 117,*5. M. primitivus* KULLMANN, holotype, suture, Peña Roscas, Crémenes, León Province, Spain, red limestones, Alba Formation, GPI T 1237/518, whorl height at approximately 9 mm, whorl width 5 mm, ×4.4 (Kullmann, 1963).

Michiganites RUZHENTSEV in BOGOSLOVSKII, LIBROVICH, & RUZHENTSEV, 1962, p. 348 [**Goniatites marshallensis* WINCHELL, 1862, p. 362; OD]. Suture line with ten lobes. Ventral lobe pouched, three lobes on flanks. Sutural formula: $EALU_2U_1I$ [German], $VLUU^1$: ID [Russian]. Eight or nine species. [The ontogenetic development of the suture is insufficiently known.] *Mississippian (upper Tournaisian–lower Visean):* Great Britain, Ireland, Germany, Russia (North Urals), Spain, Algeria, China (Xizang, Yunnan), Kazakhstan, Kyrgyzstan (Tian Shan), Mongolia, Argentina, USA (Indiana, Michigan, Ohio).——FIG. 118,*1a–c. *M. marshallensis* (WINCHELL), Marshall, Calhoun County, Michigan, Marshall Sandstone, Osagean; *a,* adoral half of specimen, UM 30713b, ×1; *b,* syntype, side view, UM 26685a, ×1; *c,* suture, whorl height at 13 mm, ×2.6 (Miller & Garner, 1955).

Subfamily PROTOCANITINAE Weyer, 1972

[Protocanitinae WEYER, 1972a, p. 325]

Ventral lobe funnel shaped; suture line on flanks with at least two or more simple pointed lobes. Phylogenetic lineage: *Protocanites–Merocanites–Cantabricanites. Mississippian (middle Tournaisian–upper Visean).*

Protocanites SCHMIDT in PAECKELMANN, 1922, p. 283 [**Goniatites lyoni* MEEK & WORTHEN, 1860, p. 471; SD LIBROVICH, 1940, p. 75]. Only eight lobes; two lobes on flanks. Sutural formula: EALUI [German], VLU:ID [Russian]. Seven species. [The ontogenetic development of the suture is insufficiently known]. *Mississippian (middle Tournaisian–upper*

Tournaisian): Belgium, Great Britain, Germany, France, Algeria, Morocco, China (Xinjiang), Japan, Australia (New South Wales, Queensland), USA (?Alaska, Arkansas, Idaho, Indiana, Michigan, Missouri, Kentucky, Nevada, Utah, Virginia).——Fig. 119,*1a–c.* **P. lyoni* (Meek & Worthen), Missouri, USA, Chouteau limestone, Kinderhookian; *a–b,* SUI 9545, ×1 (Miller, Furnish, & Schindewolf, 1957); *c,* suture, topotype, Rockford, Jackson County, Indiana, Rockford limestone, Osagean, ×2 (Miller & Garner, 1955).

Cantabricanites Weyer, 1965, p. 456 [**Prolecanites postapplanatus* Kullmann, 1963, p. 281; OD]. Conch form and suture in general similar to *Merocanites* but with twelve pointed lobes. Ventral lobe V-shaped, four lobes on flanks. Sutural formula: $EALU_2U_1U_3I$ [German], $VLUU^1U^2$:ID [Russian]. Three species. [The ontogenetic development of the suture is insufficiently known.] *Mississippian (upper Visean):* Spain, Canada (British Columbia), Australia (New South Wales).——Fig. 119,*2a–b.* **C. postapplanatus* (Kullmann), Crémenes, Pico Aguasalio, León, Spain, upper part of Alba Formation, BSM A IV/147; *a,* side view, ×0.7; *b,* suture, whorl height at approximately 40 mm, ×1.7 (Kullmann, 1963).

Merocanites Schindewolf, 1922, p. 15 [**Ellipsolites compressus* Sowerby, 1814, p. 84; OD] [=*Erdbachites* Weyer, 1965, p. 455 (type, *Prolecanites applanatus* Frech, 1899, pl. 46a,*9,* OD)]. Conch form oval or with flattened flanks. Ten pointed lobes; ventral lobe rather short lanceolate or V-shaped, three lobes on flanks. Sutural formula: $EALU_2U_1I$ [German], VLU^1:ID [Russian]. Conchs may be very large (diameter more than 25 cm). Many species. [The ontogenetic development of the suture is insufficiently known; Karpinskii, 1896, p. 184, fig. 2-14 described the suppression of A, indicating the formula ELU_2U_1I (German), VU^2U^1:ID (Russian). The type species is insufficiently known.] *Mississippian (upper Tournaisian [Pericyclus Zone]–lower Visean):* Great Britain, Ireland, Germany, France, Italy, Spain, Poland, Algeria, Morocco, Iran, Kazakhstan (Karaganda, South Urals), China (Xinjiang, Xizang), Kyrgyzstan (Tian Shan), Australia (New South Wales), Canada (British Columbia), USA (Kentucky, Michigan, Missouri).——Fig. 119,*3a–c. M. applanatus* (Frech), Crémenes, Pico Aguasalio, León, Spain, lower part of Alba Formation, upper part of lower Visean; *a–b,* side view, GPIT 1236/3, ×0.7; *c,* suture, GPIT 1236/2, whorl height at 31 mm, whorl width 17 mm, ×1 (Kullmann, 1963).

Family DARAELITIDAE Chernov, 1907

[*nom. transl.* Plummer & Scott, 1937, p. 98, *ex* Daraelitinae Chernov, 1907, p. 371] [=Epicanitinae Weyer, 1972a, p. 340]

[Materials for this family prepared by Brian F. Glenister, William M. Furnish, and Zhou Zuren]

Conch smooth, small (generally less than 5 cm), widely evolute, thinly discoidal, usually with elliptical whorl section. Suture characterized by broad trifid ventral lobe, prominent rounded lateral, and succession of subequal umbilically derived lobes that decrease in size toward umbilicus. Total number of lobes 10 to 22, may include as many as two pairs of umbilically derived internal laterals, in addition to internal lateral lobe I. Dorsal lobe bidentate. Prongs of ventral lobe and one to several adjacent external lateral lobes finely serrate at base, except in rare ancestral forms. Basic sutural formula: $(V_2V_1V_2)LUU^1.....U^n$:$I(D_1D_1)$ [Russian].

[Primary lateral and umbilical lobes (L and U) maintained their identity throughout phylembryogenesis, and new elements (U^{1+n}, where n ranges from 0–6) were added by successive derivation in saddles of umbilical lobe complex; up to two of these additions may occur in internal suture. During phylogeny, ventral lobe became progressively wider with corresponding decrease in width of adjacent lateral, serration increased in intensity and number of external lobes affected, and both external and internal umbilical lobes increased in number. Despite display of these several evolutionary trends, Daraelitidae constitute a long-ranging stable lineage that does not provide the basis for fine zonation. Genera are gradational, and definitions are arbitrary. After appearance in the Visean, daraelitids survived as ubiquitous but minor elements of open-marine faunas from Serpukhovian time to extinction in the Wordian.] *Mississippian (Visean)–Guadalupian (Wordian).*

Daraelites Gemmellaro, 1887, p. 65 [**D. Meeki;* OD] [=*Prodaraelites* Chernov, 1907, p. 390, *nom. nud.*]. Conch small (less than 5 cm diameter), discoidal (W/D, 0.35), evolute (Umin/D, 0.25 at 20 mm diameter). Suture characterized by ventral lobe twice width of lateral, serrate lobe bases from venter to midflank, up to nine pairs of umbilically derived lobes (two pairs of which may be internal) separated by asymmetrical saddles. Sutural formula: $(V_2V_1V_2)$ $LUU^1U^2U^3U^5U^7$:$U^6U^4I(D_1D_1)$ [Russian]. Five named species. *Cisuralian (Asselian)–Guadalupian (Wordian):* Italy (Sicily), Iraq (Kurdistan), Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), Afghanistan, southern China (Guizhou, Guangxi), Indonesia (Timor), USA (western Texas, Nevada), Canada (British Columbia).——Fig.

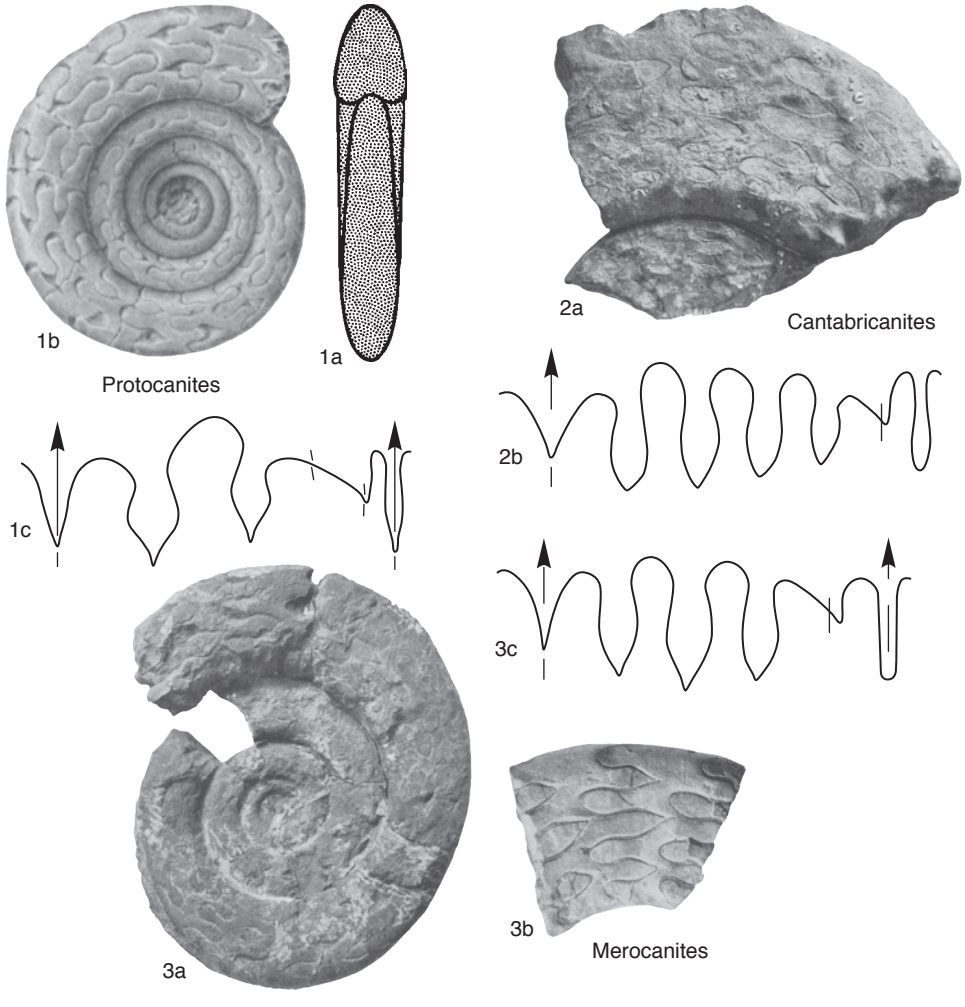

FIG. 119. Prolecanitidae (p. 188–189).

120,*1a–f.* **D. meeki,* Sosio limestone, Wordian, Sicily; *a–b,* lectotype (herein), MGUP 107 of GEMMELLARO (1887, pl. 10,*16–17*), ×1.5; *c–e,* ×1.33; *f,* diameter at 25 mm (Miller & Furnish, 1940a).——FIG. 120,*1g–h. D. elegans* CHERNOV; *g,* Leonard Group, Artinskian, western Texas, USA, diameter at 14 mm (Miller & Furnish, 1940a); *h,* hypotype, SUI 84897, Artinskian (?Aktastinian), Southern Urals, River Aktasty, diameter at 20 mm (new; courtesy of D. M. Work & W. B. Saunders).——FIG. 120,*1i. D. kingi* PLUMMER & SCOTT, Neal Ranch Formation, Asselian, western Texas, diameter at 30 mm (Hodgkinson, 1965).

Boesites MILLER & FURNISH, July 1, 1940b, p. 371 [**Daraelites texanus* BÖSE, 1919, p. 52; OD] [=*Metadaraelites* RUZHENTSEV in MAKSIMOVA & RUZHENTSEV, July 28, 1940, p. 161, obj.; =*Eoboesites* RUZHENTSEV & BOGOSLOVSKAIA, 1978, p. 125 (type, *Boesites (Eoboesites) asianus,* OD)]. Similar to *Daraelites,* but ventral and lateral lobes subequal, and with fewer umbilical lobes (5 or 6 pairs, one of which may be internal). Sutural formula: $(V_2V_1V_2)LUU^1U^2U^3U^5{:}U^4I(D_1D_1)$ [Russian]. Fourteen named species. *Pennsylvanian (Bashkirian)–Cisuralian (Sakmarian):* USA (Texas, Oklahoma, Arkansas), Canada (Arctic Archipelago: Ellesmere Island), Spain (Cantabrian Mountains), Russia and Kazakhstan (Southern Urals), Tajikistan (Pamir), Uzbekistan (Fergana, Kyzylkumy), Kyrgyzstan (southern Fergana, Tian Shan), southern China

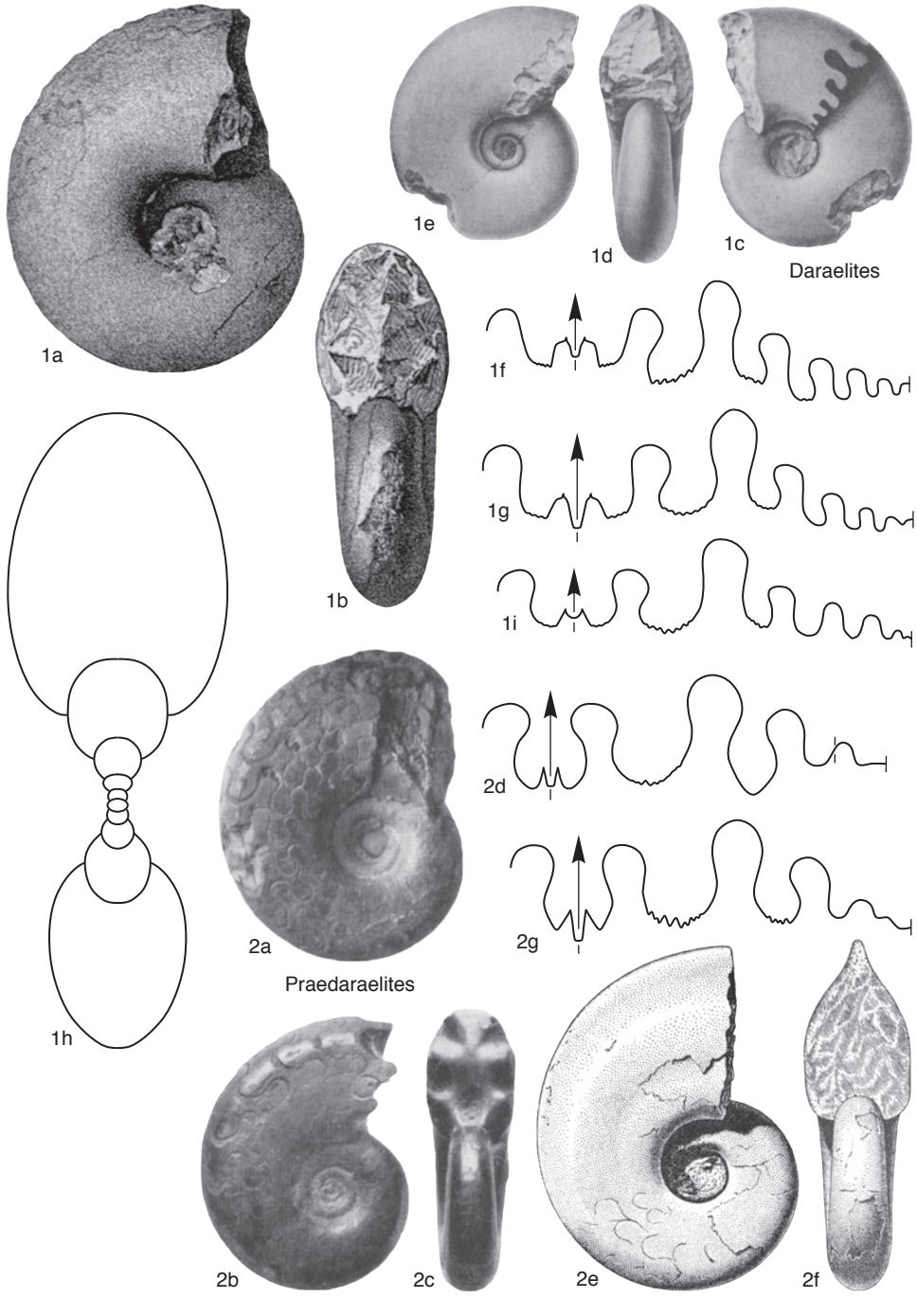

FIG. 120. Daraelitidae (p. 189–192).

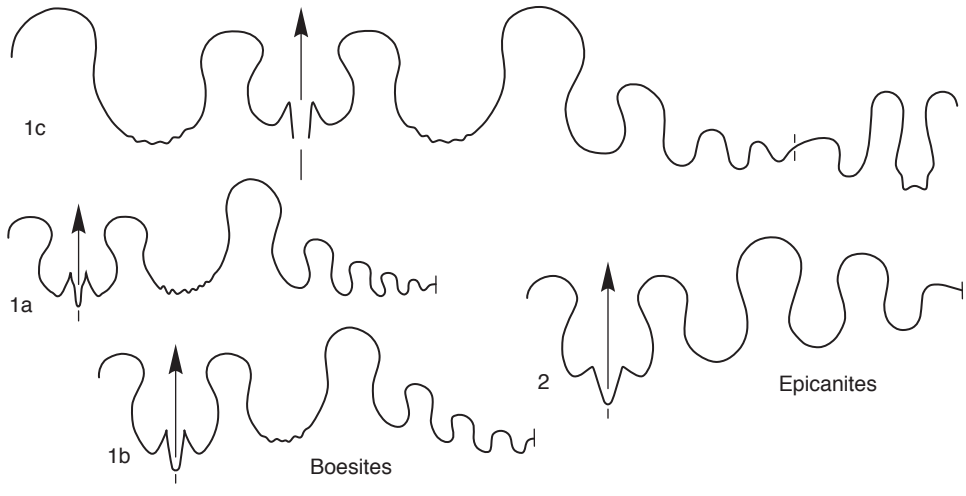

FIG. 121. Daraelitidae (p. 190–192).

(Guangxi), Japan (southwestern Honshu).——FIG. 121,*1a. *B. texanus* (BÖSE), Gaptank Formation, Virgilian–Stephanian, western Texas, diameter at 14 mm (Miller & Furnish, 1940a).——FIG. 121,*1b. B. scotti* (MILLER & FURNISH), Smithwick Shale, Atokan–Westphalian, central Texas, diameter at 16 mm (Miller & Furnish, 1940a).——FIG. 121,*1c. B. gracilis* NASSICHUK, Hare Fiord Formation, Atokan–Moscovian, Ellesmere Island, height of whorl at 13 mm, diameter at approximately 30 mm (Nassichuk, 1975).

Epicanites SCHINDEWOLF, 1926b, p. 75 [**Paraprolecanites Sandbergeri* SCHMIDT, 1925, p. 544; OD] [=*Paraprolecanites* KARPINSKII, 1889, p. 8, *partim* (type, *Prolecanites mojsisovicsi* MILLER, 1938, p. 181); =*Librovitchites* ANDRIANOV, 1985, p. 15 (type, *L. librovitchi,* OD)]. Incompletely known taxon, similar to *Boesites* but lateral lobe smaller than ventral and only slightly larger than two adjacent umbilical lobes (both external). Lobe serration absent or faint. Sutural formula: $(V_2V_1V_2)$ LUU^1U^2:$I(D_1D_1)$ [Russian]. Eight named species. [Primitive features, such as smooth to faintly serrate lobes and approximation to bilateral symmetry of umbilical saddles (latter, type species only) are at least partially a function of small size.] *Mississippian (upper Visean–Serpukhovian):* Ireland, England, France, Spain, Germany, Morocco, Algeria, Russia (Urals, Verkhoian), Kazakhstan (Southern Urals), Mongolia (Gobi Tian Shan), China (Xizang, Xinjiang, Ningxia, Guangxi), USA (Oklahoma).——FIG. 121,*2. *E. sandbergeri* (SCHMIDT), upper Visean, Algeria, diameter approximately 10 mm (Miller & Furnish, 1940b, adapted from Dollé, 1912).

Praedaraelites SCHINDEWOLF, 1934, p. 179 [**Daraelites culmiensis* KOBOLD, 1933, p. 506; OD] [=*Rotocanites* WEYER, 1972a, p. 341 (type, *Praedaraelites simulans* KULLMANN, 1962, p. 349, OD)]. Mature venter angular in one species. Suture as in *Boesites,* but lateral lobe conspicuously larger (in area) than ventral, and with three to five pairs of umbilical lobes (all external). Sutural formula: $(V_2V_1V_2)$ $LUU^1U^2U^3$:$I(D_1D_1)$ [Russian]. Nineteen named species. [The specimen portrayed by Fig. 120,*2e–f* displays a strongly modified whorl section in the ultimate one-third volution. Diameter of the specimen is close to 10 cm, whereas few other daraelitids exceed 5 cm. Subsequent collections from the same general locality show ventral angularity beginning at a diameter of 45 mm. Taxonomic assignment is certain, yet comparable modification is unknown elsewhere within the Prolecanitida.] *Mississippian (Visean–Serpukhovian):* Ireland, England, Germany, Portugal, Spain, France, Algeria, Tajikistan (Pamir), Uzbekistan (Fergana), Kazakhstan (Southern Urals), Russia (Urals, Novaia Zemlia, Verkhoian), China (Xizang, Guangxi), Malaysia.——FIG. 120,*2a–d. *P. culmiensis* (KOBOLD), upper Visean; *a–c*, Spain, ×2 (Kullmann, 1963); *d*, Ireland, diameter at 20 mm (Miller, Furnish, & Clark, 1957).——FIG. 120,*2e–g. P. aktubensis* RUZHENTSEV; *e–f*, ×0.9 (Ruzhentsev in Bogoslovskii, Librovich, & Ruzhentsev, 1962); *g*, diameter at 16 mm (Ruzhentsev, 1949c).