



Part L, Revised, Volume 3B, Chapter 2: Systematic Descriptions of the Jurassic and Cretaceous Phylloceratoidea, Boreophylloceratoidea, and Aequiloboidea

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# PART L, REVISED, VOLUME 3B, CHAPTER 2: SYSTEMATIC DESCRIPTIONS OF THE JURASSIC AND CRETACEOUS PHYLLOCERATOIDEA, BOREOPHYLLOCERATOIDEA, AND AEQUILOBOIDEA

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#### Superfamily PHYLLOCERATOIDEA Zittel, 1884

[nom. correct. MEISTER & others, 2002, p. 391, pro Phylloceratida HYATT, 1900, p. 566, nom. transl. ex Phylloceratidae ZITTEL, 1884, p. 434]

Phylloceratoidea were a persistent, conservative stock that gave rise to the Psiloceratoidea near the base of the Jurassic and thus to the Lytoceratina and all post-Triassic ammonoids (Fig. 1). Some Phylloceratoidea remained relatively little changed into the Upper Cretaceous. They inhabited open oceans such as Tethys and others in the Jurassic and Cretaceous, except for the more boreal areas, and were less common in the shelf seas of the continents.

Involute to evolute; with rounded to oval whorls, rarely with ventral keel, and thin shell in most forms; smooth or ornamented with fine lirae, riblets, sometimes bundled in groups from umbilicus between occasional stronger ribs, and with broad fold-like ribs or flares in some; occasionally with tubercles and falciform to sigmoidal constrictions in some forms; suture complex, with several auxiliaries; lobes basically trifid, saddles much divided, with diphyllic, triphyllic, tetraphyllic or occasionally polyphylic ending; phylloid saddle endings (Fig. 2c) and a lituid internal mid-dorsal lobe (Fig. 3c; Fig. 20,2d; Fig. 23,1f; Fig. 24d) are characterisitic of many forms, except in the higher Cretaceous in which the phylloid character of the saddles may be lost; features of sutures assume a more important diagnostic character than in many other Jurassic and Cretaceous ammonites. Dimorphism probably widespread, but rarely identified probably because expressed only as size differences in many forms. The lowest Jurassic forms were derived from Upper Triassic members of the superfamily, probably from Discophyllitidae. There are two families in the Jurassic and Cretaceous, the Phylloceratidae and Juraphyllitidae. *Triassic– Upper Cretaceous:* worldwide, but scarce in the Boreal Realm.

## Family PHYLLOCERATIDAE Zittel, 1884

# [Phylloceratidae ZITTEL, 1884, p. 434] [=Neophylloceratidae JOLY, 1993, p. 14, 58]

Involute; whorl section oval with small to minute umbilicus, rarely with ventral keel; smooth with thin shell, many covered with fine growth lines or lirae, occasionally ribbed, and sometimes bunched from umbilicus with periodic stronger ribs; with or without sigmoidal to falciform constrictions; no tubercles. Sutures complex; saddles diphyllic, triphyllic or tetraphyllic, or rarely multiphyllic; saddle endings spatulate phylloid. Includes the final phylloceratids before their extinction at the top of the upper Maastrichtian. Lower Jurassic (Hettangian)-Upper Cretaceous (Maastrichtian): worldwide, abundant in Tethyan and Pacific realms, rare in Boreal realm.

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#### Subfamily PHYLLOCERATINAE Zittel, 1884

[Phylloceratinae ZIITEL, 1884, p. 434] [= Hypophylloceratinae SPATH, 1927 in 1927–1933, p. 38; =Pseudophylloceratinae BENNOSOV 1957, p. 166; =Hyporbulitinae JOLY, 1993, p. 14, 58; =Neophylloceratinae JOLY, 1993, p. 15, 72].

Involute; compressed oval whorls with rounded venter, but a ventral keel developed in *Carinophylloceras;* with striae or fine to moderate ribs, and occasionally with radial undulations; weak constrictions only on inner whorls of some; suture with diphyllic saddles in early forms, triphyllic and tetraphyllic in later forms. *Lower Jurassic (Hettangian)–Upper Cretaceous (Maastrichtian):* worldwide.

- Phylloceras SUESS, 1865, p. 76 [\*Ammonites hetero*phyllus* J. SOWERBY, 1820, p. 119; OD] [*=Rhacoceras* HYATT, 1867, p. 86–87, 97, obj., SD BUCKMAN, 1912, p. vii; =Xeinophylloceras BUCKMAN, 1921, pl. 266 (type, X. xeinus, OD); =Hantkeniceras Kovács, 1939, p. 304 (type, Ammonites hantkeni SCHLOENBACH, 1867, p. 359, by virtual tautonomy); =Heterophylloceras Kovács, 1939, p. 310, obj., T); =Pseudophylloceras BESNOSOV, 1957, p. 166 (type, Ammonites kudernatschi HAUER, 1854a, p. 902, OD)]. Involute; umbilicus almost or completely closed, compressed elliptical whorl section, rounded umbilical slope; smooth or with fine, curved, or sickle-shaped striae on outer surface of shell; internal mold usually smooth; low, wide folds radiate from umbilicus in some forms; suture with diphyllic or triphyllic saddles and large terminal foliols. Lower Jurassic (Hettangian)-Upper Cretaceous (Cenomanian): worldwide. FIG. 2a-c. \*P. heterophylum (J. SOWERBY), holotype, Toarcian, Bifrons Zone, Whitby, Yorkshire, England; a-b, ×0.4; c, suture, ×0.7 (Howarth, new, The Natural History Museum, London, England, NHMUK 43879).—FIG. 2d-e. P. hantkeni (SCHLOENBACH), lower Pliensbachian, 5 km south of Bakonycsernye, Hungary; *d*, holotype, ×0.4 (Géczy, 1967, pl. 1, *I*); e, suture, ×0.7 (Prinz, 1904, pl. 11,c).
- Euphylloceras DRUSHCHITZ, 1953, p. 141 [\*Ammonites ponticuli ROUSSEAU, 1842, p. 783; OD]. Derived from and similar to Phylloceras, differing in its medium-sized riblets and constrictions on the immature whorls; suture with diphyllic or triphyllic saddles, becoming more complex than in Phylloceras. Lower Cretaceous (Berriasian-lower Albian): worldwide.-FIG. 3a-c. \*E. ponticuli (ROUS-SEAU); a-b, holotype, Barremian, Verkhorichchya (formerly Bia-Sala), Crimea, Russia, ×1 (Rousseau, 1842, pl. 1,3, 3a); c, complete suture showing lituid dorsal lobe, Barremian, Bakhchysarais'kyi district, southwestern Crimean Peninsula, ×7 (Drushchitz, 1956, p. 112, fig. 48u).-Fig. 3 d-f. E. californicum (ANDERSON), lower Albian, Cottonwood Creek, Shasta County, California, USA; d-e, ×0.55 (Murphy & Rodda, 2006, pl. 3,1,3); f, suture, ×3 (Murphy & Rodda, 2006, p. 29, fig. 12f).

- Neophylloceras SHIMIZU, 1934, p. 61 [\*Ammonites (Scaphites?) ramosus MEEK, 1858, p. 45; OD] [=Hyporbulites BREISTROFFER, 1947, p. 98 (type, Phylloceras velledae var. seresitense PERVINQUIÈRE, 1907, p. 52, OD); = Epiphylloceras COLLIGNON, 1956, p. 12, nom. nov. pro Paraphylloceras SHIMIZU, 1935, p. 173, 180, non Paraphylloceras SALFELD, 1919, p. 459 (Hettangian, Psiloceratinae) (type, Ammonites surya FORBES, 1846, p. 106, OD)]. Involute; very small or closed umbilicus, whorl section subquadrate with flattened sides and arched venter; riblets fine to medium, bundled from larger ribs near the umbilicus; suture complex, triphyllic, tetraphyllic, or multiphyllic with highly dissected lobes and saddles; saddle terminations tend to lose their spatulate terminations, and 1st lateral lobes and saddles are asymmetric in some species. Lower Cretaceous (Hauterivian)–Upper Cretaceous (Maastrichtian): worldwide.—FIG. 4,1a-c. \*N. ramosum (MEEK), Campanian, Comax (originally Komax or Komooks), Vancouver Island, British Columbia, Canada; a-b, holotype, ×1 (Matsumoto, 1959a, pl. 1,1); c, suture, ×6 (Matsumoto, 1959b, fig. 4).-FIG. 4,1d-f. N. surya (FORBES), upper Maastrichtian, Pondicherry, India; d-e, lectotype, ×0.6 (Kennedy & Henderson, 1992, pl. 1,13-14); f, suture, Lower Maastrichtian, Giralia Range, 30 km southwest of Giralia, Western Australia, ×2.5 (Henderson & McNamara, 1985, p. 39, fig. 2g).—FIG. 4, 1g-i. H. seresitensis (PERVINQUIÈRE), lectotype (designated by Howarth, herein), Cenomanian, Berrouaghia, Algeria; g-h, ×2; i, suture, ×6 (Pervinquière, 1910, p. 9, fig. 2, pl. 1,3a-b).
- Goretophylloceras COLLIGNON, 1948, p. 68 [\*Phylloceras goreti KILIAN, 1888, p. 31; by virtual tautonomy; see also KILIAN, 1889, p. 357]. Whorl section triangular, with greatest thickness near the umbilicus; ribs fine to moderate, falciform, and weaker on the inner part of the whorl; suture diphyllic with large saddle terminations. Lower Cretaceous (Valanginian–Albian): France, Madagascar, USA (California).——FIG. 4,2a-c. \*G. goreti (KILIAN), upper Aptian, Hyèges, Basses-Alpes, France; a-b, lectotype (designated by HowARTH, herein), ×1; c, paralectotype, ×1 (Sayn & Kilian, 1892, pl. 1,3a-c).——FIG. 4,2d. Goretophylloceras sp., suture, Albian, France, ×3 (Joly, 2000, p. 181, fig. 415I).
- Lepeniceras RABRENOVIĆ, 1989, p. 371 [\*L. lepensis; OD]. Similar to Goretophylloceras, but characterized by numerous sigmoidal constrictions projected forwards on the venter. Suture poorly known; dimorphism unknown. Lower Cretaceous (upper Barremian): Serbia. ——FIG. 5, 1a-b. \*L. lepensis, holotype, 1 km east of Boljetin, Serbia, ×1.5 (Vasicek & others, 2014, p. 144, fig. 2C–D).
- Geyeroceras HYATT, 1900, p. 568 [\*Ammonites cylindricus J. de C. SOWERBY, 1831, p. 318; OD] [=Calaiceras KOVACS, 1939, p. 312 (type, Ammonites calais MENEGHINI, 1881 in 1867–1881, appendix p. 24, by virtual tautonomy)]. Involute, compressed, whorls tend to be quadrate with flattened sides; smooth; may have weak constrictions on inner whorls; suture simpler than *Phylloceras*, with diphyllic saddles and



FIG. 1. Biostratigraphical distribution and probable phylogeny of Phylloceratoidea in the Jurassic and Cretaceous (Howarth, new).

fewer auxiliaries. Lower Jurassic (Hettangian–lower Pliensbachian): southern and eastern Europe.——FIG. 5,2*a–c.* \*G. cylindricum (J. de C. SOWERBY), neotype (designated by FANTINI SESTINI, 1969, p. 89), upper Hettangian–lower Sinemurian, Campiglia, La Spezia, Italy: *a–b*, ×1.5; *c*, suture, ×3 (Howarth, new, Museo di Paleontologia dell'Università di Pisa). Partschiceras FUCINI, 1923, p. 95 [\*Ammonites tenuistriatus MENEGHINI, 1868, p. 321; SD by HOWARTH, herein] [=Procliviceras FUCINI, 1923, p. 93 (type, Phylloceras proclive ROSENBERG, 1909, p. 216, M); =Macrophylloceras SPATH, 1927 in 1927–1933, p. 38 (type, Phylloceras ptychostoma ZITTEL, 1868, p. 68, OD); =Procliviaceras ROMAN, 1938, p. 11, nom.



FIG. 2. Phylloceratidae, Phylloceratinae (p. 2).

null., misspelling of Procliviceras; =Partschiphylloceras ROMAN, 1938, p. 16, nom. null., misspelling of Procliviceras]. Similar to Phylloceras, but whorl section compressed with flat sides, and with moderate prorsiradiate ribs on outer half of whorl and venter; inner whorls with slight constrictions in some; suture has diphyllic saddles. [All subsequent designations made previously of the type species of Partschiceras are not valid. FUCINI (1923, p. 95) referred three species to Partschiceras in his original proposal: Ammonites partschi STUR 1851, p. 26 (non Ammonites partschi KLIPSTEIN, 1843, p. 109, Joannitidae, Triassic); Ammonites tenuistriatus MENEGHINI, 1868, p. 321; and Ammonites sturi REYNES, 1868, p. 95. Ŝpath's (1927 in 1927-1933, p. 38) designation of Ammonites partschi, which was followed by ARKELL (1957, p. 187) and other authors, is not valid because STUR's species is a nomen nudumthere being no description, figure, or indication in the original publication; it is an unavailable specific name, and, therefore, not eligible for designation as type species (ICZN Code, 1999, Article 12). Ammonites partschi HAUER, 1854a, p. 881 (non STUR, 1851, a nomen nudum) is a valid and available specific name, but it is not available for designation as type species because it was not a species included in FUCINI's original description of the genus (ICZN Code, 1999, Article 67.2 and 67.2.1). FANTINI SESTINI'S (1971, p. 377) designation of Ammonites striatocostatus MENEGHINI (1854, p. 68) as the type species is invalid because

it was not a species included in FUCINI's original description. Consequently, *Ammonites tenuistriatus* MENEGHINI, 1868, is now designated by HOWARTH, herein, as type species of *Partschiceras.*] *Lower Jurassic (Hettangian)–Middle Jurassic (Aalemain):* worldwide.—FIG. 5, *3a–c.* \**P. tenuistriatum* (MENEGHINI), Sinemurian, Monte Calvi, Toscana, Italy; a, lectotype, ×1; *b–c*, paralectotype, ×1 (Fantini Sestini, 1971, pl. 33, *1–2*).—FIG. 5, *3d–e.* P. striatocostatum (MENEGHINI), Simemurian, lectotype, Monte Calvi, Toscana, Italy, ×0.7 (Fantini Sestini, 1971, pl. 31, 2).—FIG. 5, *3f. Partschiceras* sp., suture, upper Pliensbachian, France, ×0.8 (Joly, 2000, p. 181, fig. 415F).

Adabofoloceras JOLY, 1976, p. 118 [\*Partschiceras adabofolense COLLIGNON, 1958, pl. 12,63; OD]. Involute, whorl section broad, oval with slightly flattened sides; fine striae on outer surface of shell; moderately strong prorsiradiate ribs on outer half of whorl and venter of middle and outer whorls or on body chamber only in some; suture with tetraphyllic first and second lateral saddles. Similar to Partschiceras, but with thicker whorls, stronger ribs, and tetraphyllic saddles in suture. Middle Jurassic (Bajocian)-Upper Jurassic (Oxfordian): France, Madagascar, USA (Alaska), ?northern Canada.-FIG. 6, 1a-c. \*A. adabofolense (COLLIGNON); a-b, holotype, lower Callovian, Adabofolo, 23°07'S, 44°25'E, Sakaraha, Toliara, southwestern Madagascar, ×1 (Joly, 1976, pl. 1,1, pl. 38,1b); c, suture, Bajocian, France, ×1 (Joly, 2000, p. 181, fig. 415J).



FIG. 3. Phylloceratidae, Phylloceratinae (p. 2).

- Zetoceras Kovács, 1939, p. 307 [\*Ammonites zetes D'ORBIGNY, 1850, p. 247; by virtual tautonomy] [=Lavizzaroceras KOVACS, 1939, p. 310 (type, Ammonites lavizzarii HAUER, 1854a, p. 875, by virtual tautonomy); = Pseudozetoceras VENTURI & SASSAROLI in VENTURI & others, 2010, p. 131 (type, P. pseudozetes, OD)]. Highly involute, compressed, oval whorl section; smooth or with fine radial striae and indistinct backwardly curving constrictions; suture complex with some tetraphyllic saddles. Lower Jurassic (Sinemurian-Oxfordian): Europe, Morocco, Tunisia, Madagascar, USA (Alaska), ?northern Canada.—\_FIG. 6,2a-c. \*Z. zetes (D'ORBIGNY), holotype, lower Pliensbachian, Breitenbach, Germany; a-b, ×0.5 (a, Quenstedt, 1885 in 1882-1888, pl. 40,1; b,Quenstedt, 1845 in 1845–1849, pl. 6,1); c, suture, upper Pleinsbachian, France, ×1.5 (Joly, 2000, p. 182, fig. 415K). FIG. 6,2d-e. Z. pseudozetes (Venturi & Sassaroli), holotype, lower Toarcian, Monte Serrone, Umbria, Italy; d, ×1; e, suture, ×1.5 (Venturi & Sassaroli in Venturi & others, 2010, p. 131).
- Carinophylloceras KLINGER, WIEDMANN, & KENNEDY, 1975, p. 657 [\**C. collignoni;* OD]. Involute, with narrow umbilicus; whorl section ovoid, maximum width at umbilical margin; venter fastigate or with

keel; biconcave striae; suture with tetraphyllic first and second lateral saddles. The keeled or angled venter is characteristic. *Lower Cretaceous* (*lower Albian*): South Africa.——FIG. 7*a-c.* \**C. collignoni; a-b*, holotype, Mzinene River, 27°58'S, 32°18.5'E, 7 km northeast of Hluhluwe, KwaZulu Natal (Zululand), South Africa, ×0.5 (Klinger, Wiedmann, & Kennedy, 1975, pl. 76, *la-b*); *c*, paratype, suture, Mlambangwenya Spruit, 27°11'S, 32°11.3'E, northern KwaZulu Natal (Zululand), South Africa, ×1 (Klinger, Wiedmann, & Kennedy, 1975, p. 660, fig. 1*a*).

#### Subfamily CALLIPHYLLOCERATINAE Spath, 1927

[Calliphylloceratinae SPATH, 1927 in 1927–1933, p. 37, 38; Calliphylloceratinae is retained as the name of this subfamily under the provisions of ICZN Code, 1999, Article 40.1, despite *Calliphylloceras*]
 [=Hypophylloceratinae SPATH, 1927 in 1927–1933, p. 38; =Holcophylloceratinae DRUSHCHITZ, 1956, p. 131; =Neocalliphylloceratinae JOLY, 2000, p. 10, 147].

Moderately to highly involute; whorl section compressed oval with rounded venter; shell smooth or with sigmoidal striae



FIG. 4. Phylloceratidae, Phylloceratinae (p. 2).



FIG. 5. Phylloceratidae, Phylloceratinae (p. 2-4).

or ribs, and some with strong radial ribs or folds; deep, curved, falcoid, or markedly falcate constrictions present at all growth stages on internal mold, but not usually on outer surface of shell; constrictions preceded by raised rib on venter in some forms; suture diphyllic or triphyllic. Differs from Phylloceratinae by the presence of prominent constrictions. *Lower Jurassic (Hettangian)– Upper Cretaceous (Cenomanian):* worldwide.

Hypophylloceras SALFELD, 1924, p. 6 [\*Phylloceras onoense STANTON, 1896, p. 74; M] [=Calliphylloceras SPATH, 1927 in 1927–1933, p. 38 (type, Phylloceras disputabile ZITTEL, 1869, p. 63, OD); =Salfeldiella



FIG. 6. Phylloceratidae, Phylloceratinae (p. 4-5).

SPATH, 1927 in 1927–1933, p. 38 (type, Ammonites guettardi RASPAIL, 1831, p. 115, OD); = Capitanioceras KOVACS, 1939, p. 313 (type, Ammonites capitanii CATULLO, 1847, p. 5, by virtual tautonomy); =Aphroditiceras MAHMOUD, 1955, p. 75 (Aphroditiceras MAHMOUD in BREISTROFFER, 1952, p. 2635, nom. nud.) (type, Phylloceras aphrodite FALLOT & TERMIER, 1923, p. 25, M); ?=Fergusonites GUEX, 1980, p. 132 (type, F. striatus, OD); =Johyceras VERMEULEN, 2005, p. 164 (type, Pylloceras paquieri SAYN, 1920, p. 198, OD). Highly involute; compressed, elliptical whorl section, rounded umbilical slope; fine ribs curving forwards on outer surface of shell; forwardly curving constrictions on internal mold, usually with corresponding flares on ventral half of whorl; constrictions falcate in some small specimens; suture with diphyllic saddles, but first lateral saddle triphyllic in some. *Calliphylloceras* is transferred here from Phylloceratinae as a junior synonym of *Hypophylloceras*, because of the presence of more prominent constrictions and flares. JOLY & DELAMETTE, 2008. *Upper Jurassic (Tithonian)–Upper Cretaceous (Cenomanian):* worldwide, except Boreal.——FIG. 8*a–e.* \**H. onoense* (STANTON); *a–c*, Aptian, Ono, Shasta



FIG. 7. Phylloceratidae, Phylloceratinae (p. 5).

County, California, USA; a-b, lectotype (designated by PACKARD, 1960, p. 421); a, ×0.5; b, suture, ×7 (Packard, 1960, p. 423, fig. 1; pl. 55,1); c, ×0.6 (Anderson, 1938, pl. 11,1); d-e, Aptian, Alderson Creek, 22 km southwest of Redding, Shasta County, California, USA, ×0.7 (Khiama & Murphy, 1988, p. 591, fig. 6,1, 4).—FIG. 8f. Hypophylloceras sp., suture, Aptian, France, ×0.7 (Joly, 2000, p. 181, fig. 415H).—FIG. 8g-i. H. disputabile (ZITTEL), lectotype, type species of Calliphylloceras, Bathonian-Callovian, Swinitza, Romania; g-h, × 0.7; i, sutures, ×1 (Kudernatsch, 1852, pl. 1, *I*-2, 4).— —FIG. 8*j—n.* H. guettardi (RASPAIL); j-k, neotype (designated by JOLY in FISCHER & GAUTHIER, 2006, p. 61), type species of Salfeldiella, upper Aptian, Barrême, Alpesdes-Haute Provence, France, ×1.5 (*j*, Joly, 2000, pl. 37,6; k, Joly in Fischer & Gauthier, 2006, pl. 31,7b); l, suture, ×1.5 (Joly in Fischer & Gauthier, 2006, p. 62, fig. 38); m-n, upper Aptian, Nyons St-Ferréol-Trente-Pas, Drôme, France, ×0.9 (Joly, 2000, pl. 37,7*a*-*d*).

Gyrophylloceras HOWARTH in ÉNAY & HOWARTH, 2018, p. 1, nom. nou. pro Gyrophyllites WIEDMANN, 1963, p. 260, non Gyrophyllites GLOCHER, 1841, p. 322 (ichnotaxon [trace fossil]) [\*Phylloceras lateumbilicatum PERVINQUIÈRE, 1907, p. 60; OD]. Moderately wide umbilicus, subcircular whorl section; smooth with many radial constrictions, especially on small inner whorls; suture simple with diphyllic saddles. Known only from inner whorls; similar to *Hypophylloceras*, but more evolute and with wider umbilicus. *Lower Cretaceous (Aptian–Albian):* Tunisa, Spain.——FIG. 9, 1a-c. \**G. lateumbilicatum* (PERVINQUIÈRE), holotype, Béjà-gare, Tunisia; a-b, x2, c, x6 (Pervinquière, 1907, p. 61, fig. 9; pl. 3, 13a, c).

- Neocalliphylloceras BESAIRIE, 1936, p. 165 [\*N. collignoni; OD]. Involute, compressed oval whorl section, narrow umbilicus; smooth or with numerous fine striae; 5 to 9 prominent, gently sinuous constrictions per whorl on internal mold; suture simple with diphyllic or triphyllic saddles. Known only from poorly preserved internal molds that have the features of Hypophylloceras, of which it might be a junior synonym. Lower Cretaceous (Upper Barremian-Albian): Madagascar, France, ?Russia (Crimea).—FIG. 9,2a-c. \*N. collignoni; a-b, holotype, phragmocone, Androlavy (Androiavy), 14°43'S, 47°45'E, Mahajanga Province, northwest Madagascar, ×1 (Besairie, 1936, pl. 16,7-8); c, suture, Madagascar, ×3 (Joly, 1993, p. 12, fig. 1E).
- Summersites MURPHY & RODDA, 2006, p. 53 [\*S. summersi; OD]. Differs from Hypophylloceras by its coarser, biconcave ribs on side of the whorl, dividing into fine riblets on the venter, and absence



FIG. 8. Phylloceratidae, Calliphylloceratinae (p. 7–9).



FIG. 9. Phylloceratidae, Calliphylloceratinae (p. 9-12).

of flares; constrictions sickle-shaped or biconcave; suture with diphyllic saddles. *Lower Cretaceous (upper Aptian):* USA (California).——FIG. 9,3*a–e.* \**S. summersi; a–c,* holotype, Alderson Gulch, Ono Quadrangle, California, USA; *a–b*, opposite side views, ×0.5 (Murphy & Rodda, 2006, pl. 6, *I*, pl. 7, *I*); *c*, 1st lateral lobe, ×2 (Murphy & Rodda, 2006, p. 54, fig. 17*d*); *3d–e*, paratype, North Fork



FIG. 10. Phylloceratidae, Calliphylloceratinae (p. 12).

of Cottonwood Creek, Mono County, California, USA; d, venter, ×0.5 (Murphy & Rodda, 2006, pl. 6,2); e, part of internal suture showing lituid dorsal lobe, ×2 (Murphy & Rodda, 2006, p. 54, fig. 17e). Costiphylloceras JOLY, 2000, p. 11, 90 [\*Ammonites argelliezi REYNÈS, 1868, p. 105; OD]. Involute with small umbilicus and compressed, elliptical whorl section; strong, gently curving ribs on the phragmocone, becoming large, broad folds on the adult body chamber, which attains sizes up to at least 380 mm in diameter; occasional constrictions occur on the earlier whorls; suture has diphyllic or triphyllic saddles. Differs from Holcophylloceras in having moderate to strong ribs throughout. Lower Jurassic (Toarcian)–Middle Jurassic (upper Bajocian–?lower Bathonian): France, Hungary.-FIG. 10a-d. \*C. argelliezi (REYNES); a-b, holotype, Toarcian, Bifrons Zone, Le Clapier, Aveyron, France, ×1.5 (Reynès, 1868, pl. 6,3a-b); c-d, Toarcian, Barjac, Lozère, France, ×1.5 (Joly, 2000, pl. 20,6).--FIG. 10e. C. madouxi JOLY, holotype, large adult 380 mm in diameter with large folds on last half whorl, upper Bajocian, Parkinsoni Zone, Esparron St-Martindes-Pallières, Var, France, ×0.2 (Joly, 2000, pl. 23,3).—FIG. 10f. C. lexouiense JOLY, holotype, suture, Toarcian, Fresney-le-Puceau, Calvados, France, ×0.5 (Joly, 2000, p. 93, fig. 196a).

Holcophylloceras SPATH, 1927 in 1927–1933, p. 38 [\*Phylloceras mediterraneum NEUMAYR, 1871, p. 340; OD; =Ammonites zignodianum D'ORBIGNY, 1848 in 1842–1851, p. 493] [=Telegdiceras KOVÁCS, 1942, p. 25 (KOVÁCS, 1939, p. 315, nom. nud., type species not fixed) (type, Phylloceras ultramontanum ZITTEL, 1869, p. 66, OD)]. Similar to Hypophylloceras, but less involute with wider umbilicus, sigmoidal ribs on outer half of whorl, and prominent, deep, strongly curved, falcoid, falcate or angled constrictions on both outer and inner surfaces of shell. Suture with mainly diphyllic saddles, but 1st lateral saddle triphyllic in some. Lower Jurassic (Pliensbachian)-Lower Cretaceous (Valanginian): worldwide .--—FIG. 11*a-c.* \*H. mediterraneum (NEUMAYR), holotype, lower Callovian, Macrocephalus Zone, Brielthal, Gosau, Austria; *a–b*, ×0.5; *c*, suture, ×1.5 (Neumayr, 1871, pl. 17,2-3).——FIG. 11d-f. H. indicum (LEMOINE); *d-e*, phragmocone, Amboromihanto, 45°37′E, 16°40'S, 11 km southeast of Andranomavo, Mahajanga Region, northwestern Madagascar, ×0.6 (Joly, 1976, pl. 26,2, pl. 53,3); f, phragmocone and twothirds of a whorl of (?adult) body chamber, west of Lagniro, Betioky, Toliara, southwest Madagascar, ×0.4 (Joly, 1976, pl. 37).

Sowerbyceras Parona & Bonarelli, 1895, p. 686 [\*Ammonites tortisulcatus D'ORBIGNY, 1841 in 1840-1842, p. 162; OD] [=Martelliceras SORRENTINO, 1942, p. 14 (non SCHINDEWOLF, 1925, p. 326), obj., OD); =Leiophylloceras Arkadiev, 2002, p. 609 (type, Ammonites calypso D'ORBIGNY, 1841 in 1840-1842, p. 167, OD)]. Planulate, umbilicus moderately wide; whorl section rounded or quadrate with flat venter and vertical umbilical wall; smooth, rarely with occasional ribs or folds; three to five sigmoidal or angled constrictions on both shell and internal mold; inner whorls may be evolute and rounded with nearly straight radial constrictions; suture with large diphyllic or triphyllic saddles. Middle Jurassic (Bathonian)–Lower Cretaceous (Valanginian): Europe, Turkey, Russia (Crimea), Caucasus, Iran, India, northern Africa, India.——FIG. 12, 1a-d. \*S.



FIG. 11. Phylloceratidae, Calliphylloceratinae (p. 12).

tortisulcatum (D'ORBIGNY), Oxfordian; *a*–*b*, lectotype (designated by ATROPS in FISCHER & others, 1994, p. 167), Gigondas, Vaucluse, France, ×1 (Fischer & others, 1994, pl. 73,3*a*–*b*); *c*–*d*, l'Ile d'Elle, Vendée, France, ×0.7 (d'Orbigny, 1849 in 1842–1851, pl. 189,*I*–2).——FIG. 12,*Ie. S. delettrei* (MUNIER-CHALMAS in COLLOT, 1880), suture, Oxfordian, La Voulte, Ardèche, France, ×0.5 (Joly, 2000, p. 109, fig. 229*a*).

?Holcolissoceras SPATH, 1928 in 1927–1933, p. 154 [\*Lissoceras pintacudae STEFANO, 1884, p. 30; OD]. Moderately evolute, with rounded-oval whorl section; smooth, except for gently sinuous constrictions bordered adorally by raised collars; suture of holotype unknown. The holotype is the only specimen known from the Kimmeridgian of Italy, but two specimens from the Callovian of France and Germany, figured by JOIY (2000, p. 109, pl. 27,6–7), might also belong to this genus. Middle Jurassic (Callovian)–Upper Jurassic (*Kimmeridgian*): Italy (Sicily), ?France, ?Germany.— FIG. 12,2*a*–*b*. \**H. pintacudae* (STEFANO), holotype, between Chiusa-Sclafani and Palazzo Adriano, Palermo Province, Sicily, Italy, ×1 (Stefano, 1884, pl. 2,11).

## Subfamily PTYCHOPHYLLOCERATINAE Collignon, 1956

[Ptychophylloceratinae COLLIGNON, 1956, p. 10]

Characterized by riblike flares (labial ridges) across the venter, and occasional groups of deep, prorsiradiate folds on the venter in some; occasional curved constrictions on outer part of whorl and venter. *Lower Jurassic (Toarcian)–Upper Cretaceous (lower Cenomanian):* worldwide.



FIG. 12. Phylloceratidae, Calliphylloceratinae (p. 12-13).

- Ptychophylloceras SPATH, 1927 in 1927–1933, p. 38 [\**Phylloceras feddeni* WAAGEN, 1875, p. 27; OD]. Involute, rounded whorl section with broad, arched venter and gentle umbilical slope; five to ten curved constrictions per whorl emanate from the umbilicus, then quickly fade at midwhorl; in some forms periodic groups of two to six coarse ribs or ridges are angled forwards across the venter and are present on both shell and internal mold; widely spaced radial or rursiradiate ribs on venter of probable macroconchs; suture with diphyllic, triphyllic, or with tetraphyllic first and second lateral saddles. Dimorphic (ÉNAY, 1977; CECCA & ÉNAY, 1991). *Lower Jurassic (Toarcian)–Upper Cretaceous (lower Cenomanian):* worldwide.
- P. (Tatroceras) KOVACS, 1939, p. 315 [\*Ammonites tatricus PUSCH, 1837, p. 158; by virtual tautonomy]

[=Neumayriceras SORRENTINO, 1942, p. 14, non Neumayriceras ROLLIER, 1909, p. 623, synonym of Upper Jurassic, Haploceratoidea Taramelliceras (type, Ammonites tatricus PUSCH, 1837, p. 158, OD); = Tatrophylloceras BESNOSOV, 1957, p. 166 (type, Ammonites tatricus PUSCH, 1837, p. 158, OD)]. Early forms with diphyllic saddles. Lower Jurassic (Toarcian)-Middle Jurassic (lower Bajocian): worldwide.——FIG. 13, Ia-c. \*P. (T.) tatricum (PUSCH), holotype, Zaskale, Szaflary, Tara, Poland; a-b, ×1; c, suture, ×1.5 (Zittel, 1869, pl. 1,1a-b,3).

P. (Ptychophylloceras). Later forms, with diphyllic or triphyllic first and second lateral saddles and constrictions confined to venter; ribs radial in some forms, prosiradiate and confined to venter in others. *Middle Jurassic (upper Aalenian)–Upper* 



FIG. 13. Phylloceratidae, Ptychophylloceratinae (p. 14-15).

*Cretaceous (?lower Cenomanian):* worldwide.— FIG. 13,2*a–c.* \**P. (P.) feddeni* (WAAGEN), holotype, phragmocone, middle Callovian, *Anceps* Zone, northeast of Dhosa (Waagen, 1875, p. 27: "road from Jooria to Dhosa"), Kutch, India; *a–b*, ×0.5; *c*, suture, ×0.66 (Waagen, 1875, pl. 7, *1a–c*).——FIG. 13,2*d–f. P. (P.) haloricum* (HAUER, 1854a, p. 903), lower Bathonian, Cava Magnavacca, Monti Lessini Veronesi, Venetian Alps, Italy; *d–e*, ×0.75; *f*, suture, ×2 (Pavia, 1983, p. 12, fig. 2; pl. 3,6).

P. (Semisulcatoceras) JOLY, 2000, p. 11, 126 [\*Ammonites semisulcatus D'ORBIGNY, 1841 in 1840–1842, p. 172; OD]. First and second lateral saddles become triphyllic or tetraphyllic; several prominent groups of coarse, prorsiradiate ribs or folds on the venter, and some widely spaced ribs or folds on the venter of questionable macroconchs. Dimorphic; both dimorphs with constriction before final mouth border, which is more strongly curved in microconchs. *Middle Jurassic (Oxfordian)–Upper Cretaceous (lower Cenomanian):* worldwide.——FIG. 14*a–c.* \*P. (S.) semisulcatum (D'ORBIGNY), lectotype (designated by Joly in Fischer & Gauthier, 2006, p. 63), phragmocone, Valanginian, Sisteron,



FIG. 14. Phylloceratidae, Ptychophylloceratinae (p. 15-17).

Alpes-de-Haute-Provence, France; a-b, ×1 (Joly, 2000, pl. 39,4*a*-*b*); *c*, suture, ×2 (Joly, 2000, p. 162, fig. 382).—FIG. 14d-k. P. (S.) ptychoicum (QUENSTEDT, 1847 in 1845-1849, p. 219); d-f, lower Berriasian, Chromérac, Ardèche, France; *d*-*e*, inner whorl with three groups of two or three coarse ribs each on the venter, ×2 (Joly, 2000, pl. 31,4a-b; venter also figured by Toucas, 1890, pl. 15,6); f, inner whorl with a group of six coarse ribs on venter, ×2 (Joly, 2000, pl. 31,5); g, possible macroconch with widely spaced, rursiradiate ribs on venter, Tithonian or Berriasian, St-Laurent-sous-Coiron, Ardèche, France, ×1 (Joly, 2000, pl. 39,6); *h*-*k*, probable macroconch and microconch pair, both with body chambers, Tithonian, Stramberk (Stramberg), Czech Republic, ×1 (Zittel, 1868, pl. 4,5*a*-*b*, 6*a*-*b*).

#### Subfamily PHYLLOPACHYCERATINAE Collignon, 1937

[Phyllopachyceratinae COLLIGNON, 1937, p. 132]

Involute with small or minute umbilicus; broad, oval whorl section and rounded venter; strong radial or prorsiradiate ribs; no constrictions; suture with tetraphyllic saddles. Probably dimorphic, mainly in size difference. Differs from Phylloceratinae in having stronger ribs and lack of constrictions. *Middle Jurassic (Bajocian)–Upper Cretaceous (Maastrichtian):* worldwide.

- Phyllopachyceras SPATH, 1925, p. 101 [\*Ammonites infundibulum D'ORBIGNY, 1841 in 1840-1842, p. 131; OD]. Highly involute with minute umbilicus; oval whorl section with arched venter and gradual umbilical slope; inner whorls smooth or with fine striae only; middle and outer whorls with strong, straight ribs on midlateral to outer part of whorl and venter and intercalated ribs across the venter; suture with tetraphyllic 1st and 2nd lateral saddles. Middle Jurassic (Bajocian)-Upper Cretaceous (Maastrichtian): worldwide.-FIG. 15,1a-d, \*P. infundibulum (D'ORBIGNY), Barremian, Barrême, Basses-Alps, France; a-b, lectotype (designated by Joly in Fischer & Gauthier, 2006, p. 41), ×0.8 (Fischer & Gauthier, 2006, pl. 13,4); c-d, ×1 (d'Orbigny, 1841 in 1840-1842, pl. 39,4-5).-FIG. 15,1e. P. rouyanum (d'Orbigny), suture, upper Hauterivian, Castellane, Basses-Alpes, France, ×1 (d'Orbigny, 1841 in 1840-1842, pl. 110,5).
- Eidophylloceras JOLY, 1993, p. 10, 49 [\*E. wiedmanni; OD]. Involute with thick, oval whorls, arched venter and narrow umbilicus; smooth on inner mold, outer surface of shell unknown; suture highly complex, with broad, tetraphyllic 1st lateral saddle, the phyllites divided further into eight endings; 2nd and other lateral saddles less complex. Upper Cretaceous (upper Turonian-lower Santonian):

Madagascar.—FIG. 15,2*a*–*d.* \**E. wiedmanni; a–c,* holotype, upper Turonian, Masiaposa, 17°17'S, 45°58'E, Mahajanga, northwest Madagascar, ×1.5 (Collignon, 1956, pl. 1,*1*, pl. *1a–b*); *d*, suture, Madagascar, ×1.5 (Joly, 1993, pl. 32,2).

Haplophylloceras SPATH, 1925, p. 101 [\*Ammonites strigilis BLANFORD, 1863. p. 126; OD]. Involute, inner whorls smooth with circular cross section; outer whorls become quadrate with flat venter and develop large, foldlike ribs that curve strongly forwards on the side of the whorl and are projected forwards on the venter; suture saddle endings tend to lose the phylloid form and become multifid. Dimorphic in size difference; in the smaller microconch the ribs are projected strongly forwards on the venter forming coarse chevrons; ribs curved gently forwards on venter of macroconch. Upper Jurassic (lower Tithonian): India, Nepal, Indonesia, China (Tibet), New Guinea. FIG. 16a-c. \*H. strigile (Blanford), Chidamu Beds, Spiti Valley, Kashmir, India; a, holotype, microconch, ×1 (Uhlig, 1903, pl. 1,2a); b-c, venter, another microconch; b, ×1; c, suture, ×2 (Uhlig, 1903, pl. 1,1c; pl. 3,6).-FIG. 16d-e. \*H. pingue RyF, 1962, holotype, macroconch, Muktinath, Nepal, ×0.67 (Ryf, 1962, pl. 2, 1–2).

#### Family JURAPHYLLITIDAE Arkell, 1950

[Juraphyllitidae ARKELL, 1950, p. 359] [=Rhacophyllitinae SPATH, 1927 in 1927–1933, p. 38, based on *Rhacophyllites* auctorum, *non* ZITTEL, 1884, p. 439]

Generally more evolute than Phylloceratidae; whorls more compressed with flat sides and angled or keeled venter in some genera; most forms bear ribs, especially on the ventral part of the body chamber. Suture with diphyllic or triphyllic external saddles and monophyllic internal saddles. Dimorphism known in one genus. Derived from earliest Phylloceratinae or possibly independent descendents from Triassic Discophyllitidae. ARKELL, 1950; LEPORI, 1942; VADÁSZ, 1908. Lower Jurassic (Hettangian–lower Toarcian): worldwide.

Togaticeras RAKUS, 1993, p. 945 [\**Phylloceras togatum* NEUMAYR, 1879, p. 21; OD]. Moderately involute; whorl section oval to compressed with flat sides; smooth except for fine, sigmoidal growth striae; numerous prorsiradiate, slightly sigmoidal constrictions projected on venter; suture with diphyllic saddle endings. Probably dimorphic: most known specimens appear to be microconchs. The oldest juraphyllitid, appearing in the Lower Hettangian; differs from *D. (Dasyceras)* in its numerous constrictions and smooth shell and probable smaller size.



FIG. 15. Phylloceratidae, Phyllopachyceratinae (p. 17).

RAKÚS, 1999; LONGRIDGE, SMITH, & TIPPER, 2008. Lower Jurassic (Hettangian): Austria, Italy, Canada (British Columbia).——FiG. 17, *Ia–d.* \**T. togatum* (NEUMAYR), Zlambachgraben, Goisern, Salzkammergut, Austria; *a–b*, lectotype, possibly a microconch, with an almost complete body chamber; *a–b*, ×1; *c*, adult suture, ×3.5; *d*, paralectotype, ×1 (Rakús, 1993, p. 946, fig. 15; pl. 3,6–7).

Juraphyllites MÜLLER, 1939, p. 536 [\*Phylloceras diopsis GEMMELLARO, 1884, p. 172, OD] [=Rhacophyllites auctorum., non ZITTEL, 1884, p. 439 (Discophyllitidae, Upper Triassic)]. Evolute, with compressed, angled umbilical edge; inner whorls smooth, then develop prorsiradiate ribs or folds on ventral part of body chamber, which are projected strongly forwards on crossing the venter; widely spaced constrictions in some species (FUCINI, 1900, p. 152[8], pl. 19[1], *I*); suture with diphyllic saddles. The identity of the Jurassic species referred by many authors to *Rhacophyllites* ZITTEL 1884 (Discophyllitidae, Upper Triassic), which was discussed in detail by SPATH (1914, p. 354; 1923, p. 291; 1939, p. 77) and others, was finally settled by MULLER (1939) with the proposal



FIG. 16. Phylloceratidae, Phyllopachyceratinae (p. 17).

of his new genus Juraphyllites. Lower Jurassic (Sinemurian-lower Toarcian): southern and eastern Europe, Turkey, northern Africa, Japan, Indonesia.——FIG. 17,2*a*-*e*. \*J. diopsis (GEMMELLARO); *a*-*c*, lectotype (designated by HOWARTH, herein), lower Pliensbachian, Rocche Rosse, Galati, Sicily; *a*-*b*, ×0.6; *c*, suture, ×1.5 (Gemmellaro, 1884, pl. 2,6-8); *d*, microconch with lappet on lower part of mouth border, Gunoren, Pontide Mountains, Turkey, ×1.5 (Cope, 1992, p. 440, fig. 1); *e*, suture of larger specimen, France, ×2.5 (Joly, 2000, p. 181, fig 415D).

Tragophylloceras HYATT, 1900, p. 568 [\*Ammonites heterophyllus numismalis QUENSTEDT, 1845 in 1845–1849, p. 100; OD] [=Phyllolobites VADASZ, 1907, p. 402 (type, Ammonites loscombi J. SOWERBY, 1817, p. 185, SD HOWARTH & DONOVAN, 1964, p. 291)]. More involute than Juraphyllites, with most species having more regular, sinuous or falcoid ribs covering the whole whorl side from earlier growth stages and forming strong plications or a keel on the venter; ventrolateral tubercles in some species; inner whorls may have constrictions. Dimorphic: macroconchs large (90-220 mm in diameter) with plain mouth border; microconchs small (30-50 mm in diameter) with more sinuous mouth border, usually preceded by a constriction, and a rudimentary lappet; suture phylloceratid with lituid dorsal lobe. HOWARTH & DONOVAN, 1964. Lower Jurassic (Pliensbachian, Jamesoni-Margaritatus Zones): Europe, northern Africa, USA (Oregon) .-FIG. 18a-d. \*T. numismale (QUENSTEDT); a-b, lectotype (designated by BUCKMAN, 1912, p. viii), Ofterdingen, Baden-Württemberg, Germany; a, ×0.65; b, dorsal part of suture showing lituid dorsal lobe, ×1.8 (Quenstedt, 1845 in 1845-1849, pl. 6,5a-b); c-d, macroconch, Jamesoni Zone, Radstock, England, ×0.65 (Buckman, 1921, pl. 233).—FIG. 18e-h. T. loscombi (J. SOWERBY), Margaritatus Zone, complete adult microconch with rudimentary lappet, Eype, Dorset, England; *e*–*g*, ×1(Howarth & Donovan, 1964, pl. 49, 4*a*–*c*); h, final three sutures showing approximation, ×5 (Howarth & Donovan, 1964, p. 288, fig.



FIG. 17. Juraphyllitidae (p. 17-19).

1f).——FIG. 18 *i–j. T. ibex* (QUENSTEDT), *Jamesoni* Zone, adult microconch with half a whorl of body chamber, Radstock, Somerset, England,  $\times 1$  (Howarth & Donovan, 1964, pl. 49, 2a-b).

Dasyceras HYATT, 1900, p. 567 [\**Phylloceras rakosense* HERBICH, 1878, p. 114; OD] [=*Paradadyceras* COSSMANN, 1901, p. 58, obj., unnecessary *nom. nov. pro Dasyceras* HYATT, 1900, which is not preoccupied by *Dasyceras* STEPHENS, 1829, part 2, p. 199 (Coleoptera)]. Moderately evolute to involute, with compressed round whorl section, rounder venter or ventral keel in some that may correspond to a groove on internal mold; smooth on early and middle whorls, then ribs or coarse folds on body chamber in some; suture line with shallow ventral lobe and asymmetrical 1st lateral saddle; saddle endings are not are phylloid in some. *Lower Jurassic* (*Hettangian–lower Sinemurian*): southern and eastern Europe, ?China (Tibet), New Caledonia.

D. (Dasyceras) [=Nevadaphyllites GUEX, 1980, p. 135 (type, N. compressus, OD)]. Moderately involute; smooth, but ribs or coarse folds on sides of body chamber in some; possibly dimorphic: macroconch body chamber with ribs or folds; microconchs with constriction at adult mouth border. Lower Jurasic (Hettangian-lower Sinemurian): occurrence as for genus.—FIG. 19,1a-c. \*D. (D.) rakosense (HERBICH), holotype, probable macroconch, lower



FIG. 18. Juraphyllitidae (p. 19-20).

Sinemurian, Rákos, 46°1.26'N, 25°26.2'E, Brasov District, Romania; a, ×1 (Vadász, 1908, pl. 6,3); b-c, ×1 (Herbich, 1878, pl. 20G,b-c).——FIG. 19, Id-e. D. (D.) compressus (GUEX), holotype, probable adult microconch, lower Hettangian, New York Canyon, Nevada, USA, ×1 (Guex, 1980, pl. 1,7).

- D. (Bouhamidoceras) DUBAR, 1962, p. 320 (DUBAR, 1961, p. 199, nom. nud.) [\*B. zizense; M]. Involute, with very small umbilicus, and bluntly angled or rounded venter; feeble, sinuous ribs on middle whorls, body chamber smooth. Lower Jurassic (lower Simemurian, Oxynotum Zone), Morocco.—FIG. 19,2a-b. \*D. (B) zizense (DUBAR), holotype, Bou-Hamid, High Atlas, Morocco, ×0.7 (Dubar, 1962, pl. 10,1).
- Schistophylloceras HYATT, 1900, p. 568 [\*Phylloceras aulonotum HERBICH, 1878, p. 115] [=Kochites PRINZ, 1905, p. 49, obj.]. Moderately evolute;

compressed oval whorl section, with rounded umbilical edge and ventral keel corresponding to a sulcus on the internal mold; smooth. *Lower Jurassic (Hettangian):* Europe, China (Tibet).— FIG. 19,3*a*-*e.* \**S. aulonotum* (HERBICH); *a*-*c*, original drawing of holotype, ×1 (Herbich, 1878, pl. 20G,2*a*-*c*); *d*-*e*, holotype, ×1 (Prinz, 1905, p. 51, fig. 1–2).

Paradasyceras SPATH, 1923, p. 291 [\*Phyllocenas uermoesense HERBICH, 1878, p. 173; OD]. Moderately evolute; whorl section compressed with flat sides on lower part of whorl and a rounded venter without a keel; at larger sizes umbilical edge becomes angled and umbilical wall is vertical; smooth. Lower Jurassic (Hettangian): Austria, northern Italy, Romania, New Caledonia.— FIG. 19,4a-d. \*P. uermoesense (HERBICH); a-b, holotype, Rákos, 46°1.26'N, 25°26.2'E, Brasov District, Romania, ×0.6 (Herbich, 1878, pl. 20K, 1a-b);



FIG. 19. Juraphyllitidae (p. 20–23).



FIG. 20. Juraphyllitidae (p. 23).

*c–d*, Schreinbach, Austria, ×0.4 (Wähner, 1898, pl. 24(66), *1a–b*).

- Meneghiniceras HYATT, 1900, p. 568 [\*Ammonites (Phylloceras) lariense MENEGHINI, 1874, p. 105; OD]. Evolute; round whorl section with angled venter; moderate, prorsiradiate ribs on outer half of whorl form a midventral row of clavi or serrated keel, especially on the body chamber; up to eight sinuous or prorsiradiate constrictions per whorl. Lower Jurassic (Sinemurian-lower Toarcian): Europe.——FIG. 20,1a-f. \*M. lariense (MENEGHINI); a-d, lectotype, lower Pliensbachian, Pian d'Erba, Como, Italy, ×1 (Meneghini, 1875 in 1867–1881, pl. 17,2); e-f, lower Toarcian, Tonuicostatum Zone, Hawsker Bottoms, Whitby, Yorkshire, England, ×0.7 (Howarth, 1976, p. 775, fig. 2).
- Harpophylloceras SPATH, 1927 in 1927–1933, p. 38 [\*Ammonites eximius HAUER, 1854a, p. 863; OD]. Moderately evolute; whorl section with flat sides, arched venter with a continuous keel; prorsiradite ribs on upper whorl side are projected forwards on the venter; weak radial constrictions on inner and middle whorls. Lower Jurassic (Pliensbachian): Europe.——FIG. 20,2a–d. \*H. eximium (HAUER); a–c, holotype, Austria, ×1 (Hauer, 1854a, pl. 2,1–3); d, complete suture showing lituid dorsal lobe, upper Pliensbachian, France, ×2 (Basse 1952, p. 601, fig. 48,1).
- Euphyllites WÄHNER, 1898, p. 168 [\*Aegoceras? struckmanni NEUMAYR, 1879, p. 35; SD SPATH, 1924, p. 193]. Evolute; whorls with flat sides, rounded umbilical edge, and arched venter; forwardcurving constrictions on inner whorls, middle



FIG. 21. Juraphyllitidae (p. 23-24).

whorls smooth, then outer whorls with low, broad ribs on whorl sides and numerous striae, both curving forwards across the venter. Similar to some Psiloceratidae, but the suture is phylloceratid with phylloid saddle endings. *Lower Jurassic (Hettangian):* Austria, India (Himalaya), ?New Zealand, USA (Nevada).——FIG. 21*a–g.* \*E. struckmanni (NEUMAYR), Pfonsjoche, Austria; *a–c*, lectotype (designated HOWARTH, herein), ×0.6 (Neumayr, 1879, pl. 6,5*a–c*); *d–f,* ×1(Wähner, 1898, pl. 22,4*a–c*), g. suture, ×1 (Wähner, 1898, pl. 22,1*d*).

## Superfamily BOREOPHYLLOCERATOIDEA Alexeev & Repin in Repin, Meledina, & Alexeev, 1998

# [nom. correct. HOWARTH, herein, pro Boreophyllocerataceae ALEXEEV & REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 464]

This superfamily was created for a small number of specimens, mostly less than 35 mm in diameter with the largest being 70 mm, from the far northeast of Siberia. Some are preserved well enough to be sectioned in the plane of coiling to reveal the protoconch and the earliest whorls up to at least the nepionic constriction, which is usually near the end of the first whorl. Their characteristic feature is the constant ventral position of the siphuncle from its emergence from the protoconch up to the nepionic constriction. The siphuncle is either attached to the ventral wall from the beginning, as in Boreophylloceratidae, or close to the ventral wall in the first whorl before becoming attached, as in Yukagiritidae. In this respect they differ from Phylloceratoidea in which the siphuncle may assume any position in the whorls up to the nepionic constriction. Other characteristics of Boreophylloceratoidea are the very large protoconch and caecum, the short ammonitella ending at the nepionic constriction, and the rapid development of the suture (the nepionic constriction is also known as the primary constriction, widely considered to be the point at which ammonites hatched from the egg; the ammonitella is the whorl(s) between the caecum and the nepionic constriction). Beyond the nepionic constriction, the siphuncle remains attached to the ventral wall and specimens quickly become homeomorphic with various genera of Phylloceratidae.

There are difficulties in assessing the systematic importance of these characters, which differ from those of most ammonites, especially in the position of the siphuncle in the earliest whorls. Further investigation is needed into their relationship with Phylloceratoidea, which also occur in northeast Siberia. The problem is that their separation from the Phylloceratoidea is based on features of the development of the siphuncle up to the nepionic constriction while the ammonite is still in the unhatched egg. Are features of development before hatching relevant? This has been investigated and commented on before in papers by SPATH (1933, 1950) and ARKELL (1957, p. 85), who found that the position of the siphuncle was unstable and wandered about in the ammonitella before finally settling against the ventral wall. Although SPATH (1933, p. 430) applied the phrase "the wandering siphuncle" to many ammonites that he investigated in thin sections, he expressed the opinion that authors should be careful not to attach too much significance to this variability. Work is required on phylloceratids elsewhere-e.g., in western Europe-to determine whether any with wholly ventral siphuncles throughout the ammonitella also occur in regions outside northeast Siberia. If Boreophylloceratoidea is accepted as a superfamily, any phylloceratids in which the ammonitella is not preserved, or cannot be sectioned to reveal features of the protoconch and ammonitella, are unlikely to be determinable. Lower Jurassic (Hettangian)–Lower Cretaceous (Valanginian): Russia (Krasnoyarsk Krai, Sakha Republic, Magadan Oblast).

### Family BOREOPHYLLOCERATIDAE Alexeev & Repin in Repin, Meledina, & Alexeev, 1998

[Boreophylloceratidae Alexeev & Repin in Repin, Meledina, & Alexeev, 1998, p. 464]

Characterized by a very large protoconch (up to 1.2 mm in diameter), caecum and short ammonitella (up to 2.9 mm in diameter and only approximately 290° long; see Fig. 22*d*), and a rapid increase in complexity of the suture; suture with chacteristic lituid dorsal lobe as in Phylloceratoidea. The siphuncle is ventral from its emergence from the caecum up to the nepionic constriction at the end of the ammonitella. *Boreophylloceras* is the only genus. *Upper Jurassic (Tithonian)–Lower*  *Cretaceous (Berriasian [Volgian–Ryazanian]):* Russia (northeastern Siberia, Sakha Republic, Krasnoyarsk Krai.

Boreophylloceras ALEXEEV & REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 464 [\*Phyllopachyceras praeinfundibulum Voronets, 1962, p. 26; OD]. Involute, whorl section oval; fine striae on inner whorls up to 25-30 mm in diameter; later whorls with moderate ribs on outer half of whorl and continuous across rounded venter; protoconch, caecum, and ammonitella very large; siphuncle attached to venter throughout ontogeny; third and subsequent sutures phylloid with eight lobes and prochoanitic septal necks. Characterized by the siphuncle attached to the venter on earliest whorls, otherwise similar to Partschiceras and Phyllopachyceras (Phylloceratidae). Upper Jurassic (Tithonian)-Lower Cretaceous (Berriasian [Volgian-Ryazanian]): Russia (northeastern Siberia, Sakha Republic, Krasnoyarsk Krai).-FIG. 22a-i. \*B. praeinfundibulum (VORONETS); a, holotype, Nordvik Peninsula, 42 km east of Nordvik, Sakha Republic, Russia, ×1 (Voronets, 1962, pl.1,2); b-h, Anabar River, Sakha Republic, Russia; b-c, ×1 (Repin, Meledina, & Alexeev, 1998, p. 467, fig. 4); d, protoconch and first whorl, showing the siphuncle attached to the inside of the venter (protoconch 1.2 mm in diameter; nepionic constriction at 2.4 mm in diameter; length of ammonitella 290°), ×25 (Repin, Meledina, & Alexeev, 1998, p. 462, fig. 1); e-i, sutures; e, prosuture with two lobes,  $\times 40$ ; f, primary suture with five lobes,  $\times 40$ ; *g*-*h*, third and fourth sutures with eight lobes,  $\times 25$ ; *i*, suture on second whorl, ×4.2 (Repin, Meledina, & Alexeev, 1998, p. 463, fig. 2a-c,j). FIG. 22j-l. B. densicostatum IGNOLIKOV, 2007, holotype, Boyarka River, basin of the Kheta River (Reka Kheta), Krasnoyarsk Krai, Russia; j-k, ×1; l, protoconch and first whorl up to nepionic constriction (marked with arrow), ×20 (Ignolikov, 2007, p. 129–130, fig. 1e-f, 2).

## Family YUKAGIRITIDAE Repin in Repin, Meledina, & Alexeev, 1998

[Yukagiritidae REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 464]

Small, involute, oval whorl section; protoconch moderately large; siphuncle close to the venter, but not actually attached to it until just before the nepionic constriction where the septal necks become prochoanitic; ribs thin or striate. Differs from Boreophylloceratidae in the smaller protoconch and ammonitella that may be more than one whorl long, the ventral position of the siphuncle becoming attached to the venter later in ontogeny, and the complexity of the suture increasing more gradually. *Lower* 



FIG. 22. Boreophylloceratidae (p. 25).

Jurassic (lower Hettangian)–Middle Jurassic (lower Callovian) and Lower Cretaceous (Valanginian): Russia (northeastern Siberia).

# Subfamily YUKAGIRITINAE Repin in Repin, Meledina, & Alexeev, 1998

[nom. transl. HOWARTH, herein, ex Yukagiritidae REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 464]

As for family. Lower Jurassic (lower Hettangian)–Middle Jurassic (lower Callovian) and Lower Cretaceous (Valanginian): Russia (northeastern Siberia).

- Yukagirites REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 465 [\*Y. molodoensis; OD]. Description as for family. Yukagirites is based only on three small holotypes of three species, all 20-22 mm in diameter: a phragmocone of the type species, and phragmocones and part of immature body chambers of Y. kinasovi REPIN and Y. bojarkensis REPIN. Lower Jurassic (upper Sinemurian-upper Pliensbachian) and Lower Cretaceous (Valanginian): Russia (northeast Siberia) .-FIG. 23, 1a-f. \*Y. molodoensis, holotype, upper Pliensbachian, Molodo River, Bulunsky District, Sakha Republic, Russia; a, ×1.5; b, protoconch and first whorl, showing ventral siphuncle, ×30 (Repin, Meledina, & Alexeev, 1998, pl. 4,4; pl. 5,8); c-f, suture; c-e, prosuture, primary suture, and sixth suture, ×30; f, suture on third whorl, ×5 (Repin, Meledina, & Alexeev, 1998, p. 469, fig. 6, a-b, i). FIG. 23, 1g. Y. kinasovi REPIN, holotype, Upper Sinemurian, Talaya River, 330 km N, 15°W of Magadan, Russia, ×1.5 (Repin, Meledina, & Alexeev, 1998, pl. 4,8).--Fig. 23,1h. Y. bojarkensis REPIN, holotype, lower Valanginian, Anabar River, Sakha Republic, Russia, ×1.5 (Repin, 2012, pl. 1,4).
- Kolymophylloceras REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 465 [\*K. turomchense; OD]. Small, oval whorl section; more involute than Yukagirites. Lower Jurassic (Hettangian): Russia (northeast Siberia).—FIG. 23,2a-b. \*K. turomchense, holotype, Malaya Turomcha River, Gizhiga River basin, Magadan Oblast, Russia; a, ×2; b, protoconch and first whorl, showing the ventral siphuncle, ×25 (Repin in Repin, Meledina, & Alexeev, 1998, pl. 4,3a-b).
- Platyphylloceras REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 469 [\*P. kedonicum; OD] [=Platypachyceras REPIN in REPIN, MELEDINA, & ALEXEEV, 1998, p. 469, spelling error corrected on same page.] Small to medium size, involute, whorl section with flattened sides and wide, rounded venter. Lower Jurassic (lower Hettangian)–Middle Jurassic (lower Callovian): Russia (northeast Siberia).——FIG. 23,3a. \*P. kedonicum, holotype, lower Toarcian, Golovnoi Creek, Kedon River basin, 64°17'N, 158°54'E, Magadan Oblast,

Russia, ×1 (Repin in Repin, Meledina, & Alexeev, 1998, pl. 4,2).——FIG. 23,3*b*–*d. P. lebedevi* REPIN (2005, p. 38), holotype, upper Aalenian, Shungyudz River, Lena River basin, Sakha Republic, Russia, ×1; *b*–*c*, ×1; *d*, protoconch and inner whorls, ×3 (Repin, 2005, pl. 1,2).

#### Subfamily ANABAROCERATINAE Repin, 2012

#### [Anabaroceratinae REPIN, 2012, p. 73]

This subfamily is separated from Yukagiritinae on account of its more advanced suture, with more finely divided saddles, probably due to its higher biostratigraphical position in the Valanginian; it retains the lituid dorsal lobe. *Lower Cretaceous* (Valanginian): Russia (Krasnoyarsk Krai).

Anabaroceras REPIN, 2012, p. 73 [\*A. anabarum; OD]. Based on a single phragmocone 60 mm in diameter. The suture becomes more complex and subdivided, with finely divided saddles and narrower lobes than in Kolymophylloceras and Platyphylloceras. The siphuncle is ventral in the innermost whorls up to the nepionic constriction; in other features Anabaroceras is homeomorphic with Phylloceras. Lower Cretaceous (Valanginian): Russia (Krasnoyarsk Krai).— FIG. 24a-d. \*A. anabarum, holotype, phragmocone, Popigay River, Krasnoyarsk Krai, Russia; a-b, ×1; c, protoconch and first whorl, ×35; d, suture, approximately ×2 (Repin, 2012, pl. 1,5, pl. 2,5; p. 76, fig. 1).

# **INCERTAE SEDIS**

#### Superfamily AEQUILOBOIDEA Bilotta in Venturi & others, 2010

[Aequiloboidea BILOTTA in VENTURI & others, 2010, p. 141]

As described below, the type genus of both this superfamily and the family Aequilobidae is based on inner whorls of ammonites that are too small to be identified. These specimens are figured herein at 100 or 200 percent in order to illustrate the small sizes of the largest known specimens. The taxonomic position of this superfamily and the other genera described below have been much discussed by VENTURI, NANNARONE, and BILOTTA (2005, 2007) and BILOTTA (2010), without them being able to reach a definite conclusion. *Lower Jurassic:* Italy, Austria, Hungary, Morocco, Tunisia.



FIG. 23. Yukagiritidae (p. 27).



FIG. 24. Yukagiritidae (p. 27).

## Family AEQUILOBIDAE Bilotta in Venturi & others, 2010

[Aequilobidae BILOTTA in VENTURI & others, 2010, p. 141]

Aequilobus BILOTTA in VENTURI & others, 2010, p. 143 [\*A. cuneostriatus; OD]. Small, the largest known specimen is 16 mm in diameter; very evolute inner whorls, moderately evolute later; whorl section rounded, compressed; initially smooth, then sinuous striae that curve forwards on the venter to form weak chevrons; suture pseudoceratitic at this small size. Specimens identified as Aequilobus could be inner whorls of several genera of Lytoceratidae or Psiloceratidae in the lower Sinemurian, but on the basis of the material described they are unidentifiable. Lower Jurassic (lower Sinemurian, Bucklandi Zone): Italy.—FIG. 25,1a-e. \*A. cuneostriatus, holotype, lower Sinemurian, Bucklandi Zone, Colle Paradiso, Monte Bove, Umbria-Marche Apennines, Italy; a-b,  $\times 2$ ; c-d,  $\times 1$ ; e, suture,  $\times 6$  (a, c, e, Bilotta in Venturi & others, 2010, p. 143; b, d, Bilotta, 2010, p. 583, fig. 3,1b,d).

#### Family UNCERTAIN

Xenoloboceras BILOTTA, 2010, p. 592 [\*X. micromorphum; OD]. The largest known specimen is 13.6 mm in diameter; evolute, rounded, compressed whorl section, with a rounded venter; poorly developed striae curve forwards on to the venter; gently sinuous shallow constrictions also curve forwards on to the venter; suture primative and undeveloped. Xenoloboceras is based on very small inner whorls of immature specimens that might belong to several genera of Psiloceratinae. The genus is not identifiable. Lower Jurassic (lower Hettangian): Italy.—FIG. 25, 2a-m. \*X. micromorphum, Capo la Serra, 2.5 km northeast of Castel del Monte, Abruzzo Apennines, Italy; *a–i*, holotype; *a–c*, ×2; d-f, ×1 (Bilotta, 2010, p. 584, fig. 5,11); g-h, ×2 (Bilotta, 2010, p. 594, fig. 15, 1); i, suture, ×4 (Bilotta, 2010, p. 594, fig. 15,2); j-m, paratype; j, ×2, k, ×1 (Bilotta, 2010, p. 584, fig. 5,11); l-m, ×2 (Bilotta, 2010, p. 594, fig. 15,3).

#### Family SINUICERATIDAE Venturi, Nannarone, & Bilotta, 2005

[Sinuiceratidae VENTURI, NANNARONE, & BILOTTA, 2005, p. 111]

*Sinuiceras* and *Sphenoacanthites* are closely related and the family Sinuiceratidae could be placed in the Psiloceratoidea, possibly derived from Oxynoticeratidae, or as an early family of the Eoderoceratoidea.



FIG. 25. Aequilobidae (p. 29).

- Sinuiceras Venturi & Ferri, 2001, p. 130 [\*S. planulatum; OD]. Small to medium size; evolute innermost whorls, then moderately involute; whorl section compressed oval with rounded venter; smooth, but weak striae on some specimens; up to six prominent biconcave constrictions per whorl on outer whorls; suture simple. *Lower Jurassic (lower Pliensbachian, Jamesoni–Ibex Zones):* Italy.——FiG. 26,1*a*–e. \*S. planulatum, holotype, Furlo Pass, Furlo, Pessaro and Urbino, Italy; *a–b*, ×2; *c–d*, ×1 (Venturi, Nannarone, & Bilotta, 2005, pl. 2,2); e, suture, ×3 (Venturi & Ferri, 2001, p. 130).
- Sphenoacanthites VENTURI, NANNARONE, & BILOTTA, 2007, p. 20 [\* Gorgheiceras costotuberculatum RAKÚS & GUEX, 2002, p. 50; OD]. Similar to Sinuiceras, but larger and develops biconcave striae or weak ribs on side of whorl, projected forwards on the venter, and prominent ventrolateral tubercles or spines. Lower Jurassic (lower Pliensbachian, Jamesoni-Ibex Zones): Tunisia, Italy, Hungary.-FIG. 26,2a-l. \*S. costotuberculatum (RAKÚS & GUEX); a-g, Djebel Staa, Massif du Zaghouan, Tunisia; a-f, holotype, ?adult with part of final body chamber; a-b, ×1.5; c-e, ×1(c-d, Rakús & Guex, 2002, pl. 25,2-3; e, Rakús & Guex, 2002, p. 51, fig. 40*b*); *f*, suture ×3 (Rakús & Guex, 2002, p. 51, fig. 40c); g-h, paratype; g, ×1.5; h, ×1 (Rakús & Guex, 2002, pl. 25,1); i-l, Furlo Pass, Furlo, Pessaro & Urbino, Italy; i-j, ×1.5; k-l, ×1 (Venturi, Nannarone, & Bilotta, 2007, p. 23, fig. 16j).

# Family POLYMORPHITIDAE Haug, 1887

[nom. correct. ARKELL, 1950, p. 361, pro Polymorphidae HAUG, 1887, p. 89, ICZN Opinion 575, 1959, p. 135]

As for genus. Lower Jurassic (upper Sinemurian): Austria, Italy, Hungary, Morocco, Tunisia.

#### Subfamily POLYMORPHITINAE Haug, 1887

[nom. correct. ARKELL, 1950, p. 361, pro Polymorphinae J. P. SMITH, 1913, p. 657, nom. transl. ex Polymorphidae HAUG, 1887, p. 89]

As for genus. *Lower Jurassic (upper Sinemurian):* Austria, Italy, Hungary, Morocco, Tunisia.

Dudresnayiceras RAKÚS, 1994, p. 303 [\*Ammonites suessi HAUER, 1854b, p. 401]. Small, evolute, whorls compressed oval with rounded venter; weak or striate ribs on innermost whorls develop into stronger, straight or sigmoidal ribs curving forwards on the venter; ribbing may be irregular with striate ribs between more widely space stronger ribs; suture asymmetrical in some specimens. Probably dimorphic. Similar to Polymorphites and Gemmellaroceras in many morphological features, including the asymmetric suture, but larger, and with stronger ribbing. Dudresnayiceras is probably a genus in the Polymorphitinae (superfamily Eoderoceratoidea). Lower Jurassic (upper Sinemurian): Austria, Italy, Hungary, Morocco, Tunisia.——FIG. 27a-g. \*D. suessi (HAUER), Oxynotum Zone; a-d, Hierlatz (Hirlatz), Hallstadt, Austria; a, lectotype, ×1.2 (Rakús, 1999, pl. 5,7); b-c, paralectotype, ×1.2 (Rakús, 1999, pl. 5,8); d, suture, asymmetrical, dashed line shows central line of venter, ×4 (Rakús, 1999, p. 362, fig. 39); e-g, probably complete adult (?microconch) with half a whorl of body chamber, Djebel Oust-Est, Tunisia; e-f, ×2 (Rakús & Guex, 2002, pl. 7,1); g, suture, slightly asymmetrical, dashed line shows central line of venter, ×4 (Rakús & Guex, 2002, p. 74, fig. 56a,d).



FIG. 26. Sinuiceratidae (p. 30).

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FIG. 27. Polymorphitidae (p. 30).

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