# SYSTEMATIC DESCRIPTIONS

## Order AMMONOIDEA Zittel, 1884

Cretaceous ammonites belong to the four suborders Phylloceratina, Lytoceratina, Ammonitina, and Ancyloceratina. The longranging Phylloceratina extend from low in the Triassic to the top of the Cretaceous, and those that occur in the Cretaceous belong to genera that originated in the Jurassic or are closely related to them. None of them form a suprageneric group that is characteristic of the Cretaceous. Consequently, Phylloceratina that occur in the Cretaceous are included in this volume as a genus list only. Abbreviated details of their type species, synonyms, and biostratigraphical ranges within the Cretaceous are given here, but a full description of each genus will be found in the Jurassic volume of the ammonoid Treatise.

Lytoceratina range from the base of the Jurassic to the top of the Cretaceous, and two superfamilies are recognized, Lytocerataceae and Tetragonitaceae. Cretaceous Lytocerataceae range to the Cenomanian and belong to genera that originated in the Jurassic or are closely related to them, so they are also included here as a generic list only. These genera will be described fully in the Jurassic *Treatise* volume. Tetragonitaceae, on the other hand, are confined to the Cretaceous, where they form a characteristic superfamily ranging from the Barremian to the Maastrichtian. They are described in full in this volume.

Ammonitina likewise range from the base of the Jurassic to the top of the Cretaceous. A few survivors of the largely Jurassic Haplocerataceae, Haploceratidae and Oppeliidae (Streblitinae), range into the Cretaceous and are described in this volume with the wholly Cretaceous Oppeliidae (Aconeceratinae) and Binneyitidae. The Perisphinctaceae are predominately Jurassic, but three important families—Polyptychitidae, Olcostephanidae, and Neocomitidae—are mainly Lower Cretaceous and, with minor derivative families, are fully described here. Desmocerataceae, Pulchelliaceae, Hoplitaceae, and Acanthocerataceae are wholly Cretaceous and are dealt with in this volume.

Ancyloceratina had a few late Jurassic members but flourished in the Cretaceous and are all described in this volume.

# Suborder PHYLLOCERATINA Arkell, 1950

# Superfamily PHYLLOCERATACEAE Zittel, 1884

## Family PHYLLOCERATIDAE Zittel, 1884

#### Subfamily PHYLLOCERATINAE Zittel, 1884

- Phylloceras (Phylloceras) SUESS, 1865 [\*Ammonites heterophyllus J. SOWERBY, 1820] [=Rhacoceras HYATT, 1867; Xeinophylloceras BUCKMAN, 1921 in 1909–1930; Heterophylloceras KOVACS, 1939; Pseudophylloceras BEZNOSOV, 1957]. Lower Cretaceous (Berriasian–Barremian).
- P. (Partschiceras) FUCINI, 1923 in 1923–1935 [\*Ammonites partschi HAUER, 1854, non KLIPSTEIN, 1843] [=Procliviceras FUCINI, 1923 in 1923–1935; Macrophylloceras SPATH, 1927a; Procliviceras Ro-MAN, 1938; Partschiphylloceras ROMAN, 1938; Adobofoloceras JOLY, 1977]. Lower Cretaceous (Berriasian)–Upper Cretaceous (Maastrichtian).
- P. (Zetoceras) KOVACS, 1939 [\*Ammonites zetes OR-BIGNY, 1850a] [=Lavizzaroceras KOVACS, 1939]. Lower Cretaceous (Berriasian–Valanginian).
- Phyllopachyceras SPATH, 1925e [\*Ammonites infundibulum OrBIGNY, 1841]. Lower Cretaceous (Barremian)–Upper Cretaceous (Maastrichtian).
- Hypophylloceras (Hypophylloceras) SALFELD, 1924 [\*Phylloceras onoense STANTON, 1895] [=Goretophylloceras Collignon, 1948; Euphylloceras DRUSHCHITS, 1953b; Aphroditiceras MAHMOUD, 1955]. Lower Cretaceous (Valanginian)–Upper Cretaceous (Cenomanian).
- H. (Neophylloceras) SHIMIZU, 1934 [\*Ammonites (Scaphites?) ramosus MEEK, 1857] [=Paraphylloceras SHIMIZU, 1935a, non SALFELD, 1919; Hyporbulites BREISTROFFER, 1947a; Epiphylloceras COLLIGNON, 1956]. Lower Cretaceous (Aptian)–Upper Cretaceous (Maastrichtian).
- Carinophylloceras KLINGER, WIEDMANN, & KENNEDY, 1975 [\*C. collignoni KLINGER, WIEDMANN, & KEN-NEDY]. Lower Cretaceous (Lower Albian).

## Subfamily CALLIPHYLLOCERATINAE Spath, 1927

- Calliphylloceras SPATH, 1927a [\**Phylloceras disputabile* ZITTEL, 1869] [=*Neocalliphylloceras* BESAIRIE, 1936; *Capitanioceras* KOVACS, 1939]. Lower Cretaceous (Berriasian–Albian).
- Holcophylloceras SPATH, 1927a [\*Phylloceras mediterraneum NEUMAYR, 1871] [=Salfeldiella SPATH, 1927a; Telegdiceras KOVACS, 1942]. Lower Cretaceous (Berriasian–Aptian).
- Ptychophylloceras SPATH, 1927a [\*Phylloceras feddeni WAAGEN, 1875 in 1873–1875] [=Tatroceras KOVACS, 1939; Neumayriceras SORRENTINO, 1942, non ROLLIER, 1909; Tatrophylloceras BEZNOSOV, 1957]. Lower Cretaceous (Berriasian–Aptian).
- Sowerbyceras PARONA & BONARELLI, 1895 [\*Ammonites tortisulcatus Orbigny, 1841] [=Martelliceras SORRENTINO, 1942, non Schindewolf, 1925; Gyrophyllites Wiedmann, 1963]. Lower Cretaceous (Berriasian-Albian).

## Suborder LYTOCERATINA Hyatt, 1889

## Superfamily LYTOCERATACEAE Neumayr, 1875b

#### Family LYTOCERATIDAE Neumayr, 1875b

#### Subfamily LYTOCERATINAE Neumayr, 1875b

- Lytoceras SUESS, 1865 [\*Ammonites fimbriatus J. SOWERBY, 1817a] [=Ophiceras SUESS, 1865; Thysanoceras HYATT, 1867; Thysanolytoceras BUCKMAN, 1905; Trachylytoceras BUCKMAN, 1913 in 1909– 1930; Fimbrilytoceras BUCKMAN, 1918 in 1909– 1930; Kallilytoceras BUCKMAN, 1921 in 1909–1930; Lobolytoceras BUCKMAN, 1923 in 1909–1930; Cosmolytoceras SPATH, 1924; Crenilytoceras BUCKMAN, 1926 in 1909–1930; Orcholytoceras BUCKMAN, 1926 in 1909–1930; Saturnoceras ANDERSON, 1938; Biasaloceras DRUSHCHITS, 1953a; Dinolytoceras BEZNOSOV, 1956; Valentolytoceras BEZNOSOV, 1956]. Lower Cretaceous (Cerniasian)–Upper Cretaceous (Cenomanian).
- Pterolytoceras SPATH, 1927a [\*Ammonites exoticus OPPEL, 1863 in 1862–1863]. Lower Cretaceous (Berriasian–Valanginian).
- Eulytoceras SPATH, 1927a [\*Ammonites inaequalicostatus ORBIGNY, 1840]. Lower Cretaceous (Hauterivian– Lower Aptian).
- Hemilytoceras SPATH, 1927a [\*Ammonites immanis OPPEL, 1865]. ?Lower Cretaceous.
- Metalytoceras SPATH, 1927a [\*Lytoceras triboleti UHLIG, 1902]. Lower Cretaceous (Valanginian).
- Ammonoceratites BOWDITCH, 1822 [\*Ammonites lamarcki BOWDITCH, 1822] [=Ammonoceras La-MARCK, 1822]. Lower Cretaceous (Albian).

- Argonauticeras ANDERSON, 1938 [\*Lytoceras argonautarum ANDERSON, 1902] [=Pseudotetragonites DRUSHCHITS, 1956]. Lower Cretaceous (Upper Aptian-Middle Albian).
- Pictetia UHLIG, 1883 [\**Crioceras astierianum* ORBIGNY, 1842]. *Lower Cretaceous (Upper Aptian–Middle Albian).*
- Protetragonites HYATT, 1900 [\*Ammonites quadrisculcatus ORBIGNY, 1841] [=Hemitetragonites SPATH, 1927a; Leptotetragonites SPATH, 1927a]. Lower Cretaceous (Berriasian–Upper Albian).
- Carinolytoceras WIEDMANN, 1962c [\*C. carinatum WIEDMANN, 1962c]. Lower Cretaceous (Upper Aptian).

## Superfamily TETRAGONITACEAE Hyatt, 1900

[nom. transl. WIEDMANN, 1962a, p. 147, ex Tetragonitidae HYATT, 1900, p. 568]

More involute than Lytocerataceae, with whorl section less circular and becoming angled in some forms; several auxiliary saddles developing in suture line; shell lirate, striate, smooth, or occasionally strongly ribbed, and constrictions usually present. *Lower Cretaceous (Barremian)–Upper Cretaceous (Maastrichtian).* 

Derived from *Protetragonites* (Lytoceratidae) in the Barremian. The two families, Gaudryceratidae and Tetragonitidae, are closely related in the Lower Cretaceous but more distinct in the Upper Cretaceous. Gaudryceratidae retain the quinquelobate primary suture of the Lytocerataceae, but some Tetragonitidae develop a sexlobate primary suture. HENDERSON, 1970; KENNEDY & HENDERSON, 1992a; KULLMANN & WIED-MANN, 1970; MURPHY, 1967c; WIEDMANN, 1962a, 1962b; WRIGHT & KENNEDY, 1984; WRIGHT & MATSUMOTO, 1954.

## Family GAUDRYCERATIDAE Spath, 1927

[Gaudryceratidae SPATH, 1927a, p. 66] [=Gaudryceratinae WRIGHT, 1957b, p. 200; Hypogaudryceratinae SHIMIZU, 1934, p. 67; Kossmatellinae BREISTROFFER, 1953b, p. 71; Vertebritinae WIEDMANN, 1962a, p. 150]

Whorl section typically rounded or elliptical, sometimes depressed; shell ornamented with lirae or fine riblets, occasionally smooth, and with constrictions; suture with symmetrically bifid saddles and a single main saddle in internal suture, but with additional small saddles in some forms. KENNEDY & KLINGER, 1979b; KENNEDY & SUMMES-BERGER, 1986. Lower Cretaceous (Barremian)–Upper Cretaceous (Maastrichtian).

- Eogaudryceras SPATH, 1927a, p. 66 [\*Ammonites numidus COQUAND, 1880, p. 22; OD]. Moderately evolute; whorl section rounded to rectangular; smooth or ornamented with fine radial lirae; constrictions present in some and may become strong. KENNEDY & KLINGER, 1979b. Lower Cretaceous (Barremian–Upper Albian): France, Spain, England, Bulgaria, Caucasus, Italy, Switzerland, Algeria, South Africa (Zululand), Madagascar, Egypt (Sinai), California, Antarctica (Alexander Island).
  - E. (Eogaudryceras). Whorl section initially trapezoidal, becoming rounded and sometimes compressed in adults; fine, sinuous lirae projected strongly forwards over venter, but mold is smooth; constrictions weak or absent, typically on inner whorls only; suture with symmetrically bifd saddles and large suspensive lobe. MURPHY, 1967c. Occurrence and distribution as for genus.——FIG. 1,3a-d. \*E. (E.) numidum (Co-QUAND), Barremian; a,b, lectotype (designated HOWARTH, herein), Algeria (Djebel-Ouach, Constantine), ×1 (Sayn, 1890, pl. 1, fig. 3a,b); c,d, France (Hyèges, Alpes-de-Haute Provence), ×1 (Murphy, 1967c, pl. 5, fig. 1–2).
  - E. (Eotetragonites) BREISTROFFER, 1947b, p. 72 [\*E. raspaili; OD]. Whorl section initially rather depressed and more angular or rectangular than in E. (Eogaudryceras) at all growth stages; outer surface of shell smooth or finely striate; constrictions moderate to strong at all growth stages and projected gently forwards over venter; suture line with asymmetrically bifid saddles and incipient second lateral saddle in internal suture. Derived from E. (Eogaudryceras) in the Upper Aptian. Lower Cretaceous (Upper Aptian-Middle Albian): France, Spain, Switzerland, Bulgaria, Caucasus, South Africa (Zululand), Madagascar, Egypt (Sinai), California, Antarctica (Alexander Island).—FIG. 1, 1a, b. \*E. (Eotetragonites) raspaili BREISTROFFER, Upper Aptian, France (Hyèges, Alpes-de-Haute Provence); ×1 (Kilian, 1913, pl. 11, fig. 3).——FIG. 1, 1c, d. E. (E.) wintunium (ANDERSON), Upper Aptian, northern California; ×1 (Murphy, 1967c, pl. 3, fig. 5-6).
- Anagaudryceras SHIMIZU, 1934, p. 67 [\*Ammonites sacya FORBES, 1846, p. 113; OD] [=Paragaudryceras SHIMIZU, 1934, p. 67 (type, Gaudryceras limatum YABE, 1903, p. 34; OD); Murphyella MATSUMOTO in MATSUMOTO, MURAMOTO, & TAKAHASHI, 1972, p. 208 (type, Kossmatella (Murphyella) enigma; OD)]. Whorl section always rounded; early whorls circular or depressed; later whorls compressed and higher; mold smooth, but shell with very fine, prorsiradiate or sinuous lirae; periodic, collared constrictions on inner whorls becoming more numerous on outer whorls, where they form broad,

flattened, foldlike ribs. Derived from *E. (Eogaudryceras)* in the early Albian. KENNEDY & KLINGER, 1979b; WRIGHT & KENNEDY, 1984; HENDERSON & MCNAMARA, 1985. *Lower Cretaceous (Middle Albian)–Upper Cretaceous (Mastrichtian):* England, France, Germany, Austria, Romania, Algeria, Angola, South Africa (Zululand), Madagascar, southeastern India, Japan, Sakhalin, Kamchatka, Alaska, British Columbia, California, New Zealand, Antarctica (Seymour Island).——FIG. 1,4*a*–*d.* \**A. sacya* (FORBES), Upper Albian or Cenomanian, southeastern India (Verdachellum); *a,b*, holotype, BMNH C.51067, ×1 (new); *c,d*, holotype of *Ammonites buddha* FORBES, BMNH C.22673, ×0.7 (new).

- Gaudryceras GROSSOUVRE, 1894, p. 225 [\*Ammonites mitis HAUER, 1866, p. 305; SD BOULE, LEMOINE, & THEVENIN, 1906, p. 11(31)] [=Epigaudryceras SHIMIZU, 1934, p. 67 (type, Lytoceras striatum JIMBO, 1894, p. 35(181); OD); Hemigaudryceras SHIMIZU, 1934, p. 67 (type, Lytoceras (Gaudryceras) denmanense WHITEAVES, 1901, p. 31; OD); Neogaudryceras SHIMIZU, 1934, p. 67 (type, Gaudryceras tenuiliratum YABE, 1903, p. 19; OD); Pseudogaudryceras SHIMIZU, 1934, p. 67 (type, Gaudryceras tenuiliratum var. infrequens YABE, 1903, p. 28; OD)]. Inner whorls evolute, serpenticone, rounded or depressed; later whorls expanding more rapidly and becoming compressed; ornamented with lirae or wirelike, flexuous ribs, single or branched, which may coarsen and bunch on the outer whorls; variable, foldlike ribs may also develop on the outer whorls; periodic constrictions on inner mold marked by depressions and collars on the shell surface. Suture with wide, bifid saddles and lobes and a retracted suspensive lobe. Lirae and ribs coarser than in Anagaudryceras. KENNEDY & KLINGER, 1979b. Lower Cretaceous (Upper Albian)-Upper Cretaceous (Maastrichtian): worldwide.
  - G. (Gaudryceras). Large, with constrictions; developing foldlike ribs on body chamber. KENNEDY & SUMMESBERGER, 1979. Occurrence and distribution as for genus.——FIG. 2,4*a,b.* \**G.* (*G.*) *mite* (HAUER), Coniacian, Gosau Beds, Austria (Strobl, Wolfgangsee); holotype, ×0.7 (Kennedy & Summesberger, 1979, pl. 1).
  - G. (Mesogaudryceras) SPATH, 1927a, p. 66 [\*Ammonites leptonema SHARPE, 1855, p. 32; OD]. Smaller, more involute and expanding more quickly than G. (Gaudryceras); whorls more compressed from an early stage, sometimes developing trigonal whorl section, widest near umbilicus, and with narrowly arched venter; lirae distant at first, then fine, dense, and strongly projected on the venter; no constrictions. WRIGHT & KENNEDY, 1984. Upper Cretaceous (Lower Cenomanian-Middle Cenomanian): England, France, Germany, Romania, Ukraine (Crimea), Turkmenistan (Kopet-Dag), Greenland.—FIG. 2,3a,b. \*G. (M.) leptonema (SHARPE), Lower or Middle Cenomanian, Lower Chalk, England (Ventnor, Isle of Wight); holotype, GSM 7762, ×1.

# Cephalopoda—Cretaceous Ammonoidea



FIG. 1. Gaudryceratidae (p. 3-5)

Vertebrites MARSHALL, 1926, p. 138 [\*V. murdachi; M]. Very evolute, slowly expanding serpenticones retaining depressed, subrectangular whorl section throughout growth; fine, prorsiradiate lirae dividing into many finer lirae over venter; internal suture containing several saddles. HENDERSON, 1970; KEN- NEDY & KLINGER, 1979b. Upper Cretaceous (Santonian–Maastrichtian): Belgium, Algeria, South Africa (Zululand, Pondoland), Madagascar, southeastern India, Japan, New Caledonia, New Zealand, California, Texas, Mexico, Chile.——FIG. 1,2a-c. \*V. murdochi MARSHALL, Upper Campanian, New

Zealand (west shore of Waitapu Bay, Whangaroa Harbour); *a*, lectotype, ×1; *b*, lectotype, ×1.7; *c*, lectotype, ×4 (all Marshall, 1926, pl. 20, fig. 9, pl. 30, fig. 1–2).

Zelandites MARSHALL, 1926, p. 147 [\*Z. kaiparaensis;
 M] [=Varunaites SHIMIZU, 1926, p. 548 (type, Ammonites varuna FORBES, 1846, p. 107; OD);
 Hypogaudryceras SHIMIZU, 1934, p. 67 (type, Desmoceras kawanoi JIMBO, 1894, p. 28(174); M);
 Anazelandites MATSUMOTO, 1938c, p. 146 (type, Lytoceras (Gaudryceras) flicki PERVINQUIERE, 1907, p. 65; OD)]. Earliest whorls round but quickly be-

coming more compressed, high-whorled, and more involute, typically with long, sloping umbilical walls and whorl sides convergent towards a rounded venter; smooth or with very fine lirae and frequent, moderate to strong, radial or prorsiradiate and gently sinuous constrictions on internal mold; suture with asymmetrical first lateral lobe and many recurved auxiliary saddles. *Lower Cretaceous (Lower Albian)–Upper Cretaceous (Upper Maastrichtian):* England, France, Sardinia, Spain, Tunisia, South Africa (Zululand), Madagascar, southeastern India, Japan, Sakhalin, New Zealand, Alaska, British Co-



Fig. 2. Gaudryceratidae (p. 3–6) © 2009 University of Kansas Paleontological Institute lumbia, California, Chile, Antarctica (Seymour Island).——FIG. 2, *Ia,b. \*Z. kaiparaensis* MARSHALL, Upper Campanian, New Zealand (Bull's Point, Kaipara Harbour); paralectotype, ×1.5 (Marshall, 1926, pl. 31, fig. 1–2).——FIG. 2, *Ic,d. Z. varuna* (FORBES), Maastrichtian, Seymour Island; ×1.4 (Macellari, 1986, fig. 11.11–12).

Kossmatella JACOB, 1907, p. 285 [\*Ammonites agassizianus Pictet, 1847, p. 303; SD Roman, 1938, p. 43] [=Guderianites WIEDMANN, 1962b, p. 63 (type, Kossmatella costata H. DOUVILLÉ, 1916, p. 96; OD)]. Whorl section rounded and depressed in early whorls and becoming higher, compressed, and more involute in later whorls; deep constrictions occurring on inner mold, with large lateral bulge between constrictions; bulges in some forming swollen lateral tubercles, in others forming a row of nodes near umbilical edge which bifurcate or trifurcate into smaller bulges that are continuous over venter; shell surface with fine, single or bifurcating lirae; suture containing several recurved auxiliary saddles. WIEDMANN, 1962b; WIEDMANN & DIENI, 1968; KENNEDY & KLINGER, 1979b. Lower Cretaceous (Upper Aptian)-Upper Cretaceous (Middle Cenomanian): France, Spain, Sardinia, Italy, Poland, South Africa (Zululand), Madagascar, Egypt (Sinai), southeastern India, Alaska, California, Mexico.—FIG. 2,2a-c. \*K. agassizianus (PICTET), Upper Albian, Switzerland (Saxonet, Savoyen); a, b, lectotype, Muséum d'Histoire Naturelle de Genève, Pi"GV"/4,3a,b,d, ×1 (new); c, ×5 (Wiedmann, 1962a, p. 166, fig. 25).

#### Family TETRAGONITIDAE Hyatt, 1900

#### [Tetragonitidae HYATT, 1900, p. 568]

Whorl section rectangular or trapezoidal in early whorls, sometimes depressed; usually smooth, but some genera lirate or striate; constrictions on internal mold strongly prorsiradiate but usually recurved across venter, corresponding with collars on outer shell surface; major saddles of suture are irregularly trifid, several auxiliary saddles present, and there are two or more saddles in internal suture; dorsal lobe may form a septal lobe on preceding septum. Derived from *Eogaudryceras*. MURPHY, 1967c; KENNEDY & KLINGER, 1977a. *Lower Cretaceous (Upper Aptian)– Upper Cretaceous (Maastrichtian).* 

#### Subfamily TETRAGONITINAE Hyatt, 1900

[nom. transl. WRIGHT, 1957b, p. 203, ex Tetragonitidae Hyatt, 1900, p. 568]

Whorl section angled in early whorls, but may become rounded and inflated in later

whorls. MURPHY, 1967a. Lower Cretaceous (Upper Aptian)–Upper Cretaceous (Maastrichtian).

- Tetragonites KOSSMAT, 1895, p. 131 [\*Ammonites timotheanus PICTET, 1847, p. 295; OD] [=Epigoniceras SPATH, 1925f, p. 29 (type, Lytoceras (Tetragonites) epigonus KOSSMAT, 1895, p. 135(39); OD); Eoepigoniceras SHIMIZU, 1935a, p. 165, nom. nud. (type, Tetragonites kingianus KOSSMAT, 1895, p. 137; OD); Neoepigoniceras SHIMIZU, 1935a, p. 165, nom nud. (type, N. schmidti; OD); Tingriceras Снао, 1976, р. 538 (type, T. chanaense; OD]. Moderately evolute; whorl section subrectangular, trapezoidal, or rounded; shell smooth or with growth lines only; usually with oblique, prorsiradiate constrictions on internal mold only, with corresponding collars on outside of shell; suture with deep external lobe, several auxiliary saddles, either straight or recurved, and two or more unequal internal saddles. KENNEDY & KLINGER, 1977a; WRIGHT & KENNEDY, 1984. Lower Cretaceous (Upper Aptian)-Upper Cretaceous (Maastrichtian): England, France, Spain, Switzerland, Ukraine (Crimea), Caucasus, Algeria, Tunisia, Angola, South Africa (Zululand), Mozambique, Madagascar, Egypt (Sinai), southeastern India, Tibet, Japan, Sakhalin, New Zealand, Alaska, British Columbia, California, Oregon, Texas, Mexico, Peru, Antarctic Peninsula.
  - T. (Tetragonites). No siphonal ridge on venter; constrictions prorsiradiate on side of whorl, then bending backwards at ventrolateral shoulder to form a sinus on venter. Occurrence and distribution as for genus.——FIG. 3,3a-c. \*T. (T.) timotheanus (PICTET), Upper Albian, Switzerland (Saxonet, Savoyen); a, b, lectotype, Muséum d'Histoire Naturelle de Genève, Pi<sup>°</sup>GV<sup>°</sup>/3,1, ×1 (new); c, ×3 (Wiedmann, 1962a, p. 172, fig. 31).——FIG. 3,3d,e. T. (T.) epigonus (KOSSMAT), Campanian, southeastern India (Varagur); lectotype, ×1 (Kossmat, 1895, pl. 17, fig. 4a,b).
  - T. (Carinites) WIEDMANN, 1973b, p. 609 [\*T. spathi FABRE, 1940, p. 214; OD]. Developing a feeble ventral ridge; constrictions projected forwards to form angle on venter. WRIGHT & KENNEDY, 1984. Upper Cretaceous (Middle Cenomanian): England, France, Ukraine (Crimea), Caucasus, Russia (Dagestan).—FIG. 3,4a,b. \*T. (C.) spathi FABRE, France (Cassis, Bouches-du-Rhône); holotype, ×1 (Wiedmann, 1973b, pl. 8, fig. 10b,c).
- Saghalinites WRIGHT & MATSUMOTO, 1954, p. 110 (ex SHIMIZU, 1935a, p. 181, nom. nud.) [\*Ammonites cala FORBES, 1846, p. 104; OD]. Similar to Tetragonites but more evolute, serpenticone, and with whorls enlarging very slowly; whorl section rounded, slightly depressed, becoming trapezoidal or octagonal; smooth or with growth striae only; constrictions weak to strong, usually highly oblique and curved. KENNEDY & KLINGER, 1977a; KENNEDY, 1986a; KENNEDY & HENDERSON, 1992a. Upper Cre-



FIG. 3. Tetragonitidae (p. 6-9)

taceous (Upper Santonian-Maastrichtian): France, Switzerland, The Netherlands, Denmark, Italy, Germany, Austria, Spain, Ukraine, Tunisia, South Africa (Zululand, Pondoland), Madagascar, Japan, southeastern India, Sakhalin, Greenland, Argentina (Patagonia), Antarctic Peninsula.—FIG. 3,1a-d.

\*S. cala (FORBES), Maastrichtian, southeastern India (Pondicherry); *a*,*b*, lectotype, BMNH C.51057, ×1 (new); c,d, paralectotype, BMNH C.51058, ×0.7 (new).

Pseudophyllites KOSSMAT, 1895, p. 137(41) [\*Ammonites indra Forbes, 1846, p. 105; M]. Largest

7

tetragonitid genus, with adults up to 300 mm in diameter; inner whorls as in Tetragonites but quickly becoming much more involute and inflated, with higher whorls, a rounded whorl section, and no constrictions; fine radial growth lines and spiral striae forming reticulate pattern on shell; suture highly incised, with several auxiliary saddles. KEN-NEDY, 1986d; KENNEDY & KLINGER, 1977a; KEN-NEDY & HENDERSON, 1992a. Upper Cretaceous (Upper Santonian-Upper Maastrichtian): Northern Ireland, France, Spain, Poland, Austria, South Africa (Zululand), Madagascar, southeastern India, Japan, Sakhalin, Western Australia, New Zealand, Greenland, Alaska, British Columbia, California, New Jersey, Mississippi, Chile, Argentina, ?Brazil, Antarctic Peninsula.—FIG. 4, 1a-c. \*P. indra (FORBES), Maastrichtian, southeastern India (Pondicherry); a, b, lectotype, BMNH C.51068, ×0.5 (new); c, ×0.8 (Kossmat, 1895, pl. 17, fig. 6). Parajaubertella MATSUMOTO, 1942c, p. 666 [\*P.

kawakitana; OD]. Outer whorls like Takahashia or large Anagaudryceras, enlarging rapidly, with back-

wardly curving, foldlike ribs; inner whorls of 10 to 40 mm diameter more depressed, with vertical umbilical walls and rounded umbilical edge; also resembling a large Gabbioceras, but inner whorls having neither the sloping umbilical walls (resulting in a funnel-shaped umbilicus) nor the angled umbilical edge of that genus; suture much incised, with several recurved auxiliary saddles. MATSUMOTO, 1959; MURPHY, 1967c. Lower Cretaceous (?Upper Albian)-Upper Cretaceous (Lower Cenomanian): Japan, Sakhalin, Alaska.-FIG. 4,2a-c. \*P. kawakitana, Lower Cenomanian, South Sakhalin (Yuno-sawa, Naibuchi valley); a, holotype, University of Tokyo, Geology Department I-371.b, ×0.5 (new); b,c, paratypes, b, ×2.5, c, ×2 (Matsumoto, 1942c, p. 668, fig. 2c,d).

Takahashia MATSUMOTO, 1984b, p. 33 [\*T. eureka; OD]. Very similar to *Pseudophyllites* in size, shell form, ornament, and suture, but of much older geological age and developing moderately strong radial ribs, which curve backwards on side of whorl and form a shallow sinus on the venter. *Upper Cre-*



FIG. 4. Tetragonitidae (p. 7-8)

*taceous (Lower Cenomanian):* Japan.——FIG. 3,2*a*,*b.* \**T. eureka* MATSUMOTO, Hokkaido (Katsurazawa quarry, Ikushumbets River); holo-type, ×0.4 (Matsumoto, 1984b, fig. 1).

#### Subfamily GABBIOCERATINAE Breistroffer, 1953

#### [Gabbioceratinae BREISTROFFER, 1953b, p. 71]

Highly depressed, cadicone forms, with a sharp ventrolateral angle, but may become compressed and round-whorled on two outermost whorls; shell lirate, with constrictions and collars; suture with one or two auxiliary saddles and two unequal internal saddles. Derived from *Eogaudryceras (E.) numidum* (CoQUAND) in the mid-Aptian. WIEDMANN, 1962c; MURPHY, 1967b; KENNEDY & KLINGER, 1977a. *Lower Cretaceous (Upper Aptian)–Upper Cretaceous (Lower Cenomanian).* 

- Gabbioceras HYATT, 1900, p. 570 [\*Ammonites batesi GABB, 1869, p. 132, non TRASK, 1855; OD; =Gabbioceras angulatum ANDERSON, 1902, p. 87]. Inner whorls evolute, highly depressed, cadicone, with flat, sloping umbilical walls, sharp ventrolateral angle, and highly arched venter; later whorls losing cadicone shape to become rounded, compressed, with no ventrolateral angle; shell with prorsiradiate lirae; constrictions on inner mold, with corresponding collars on shell surface, occurring occasionally on cadicone whorls and more frequently on outer whorls. MURPHY, 1967b. Lower Cretaceous (Upper Aptian)–Upper Cretaceous (Lower Cenomanian): France, Spain, Caucasus, northern Africa, Madagascar, California.——FIG. 5, 1a-c. \*G. angulatum ANDERSON, Upper Aptian, northern California; a, b, lectotype of Ammonites batesi GABB, ×0.7 (GABB, 1869, pl. 21, fig. 10); c, California (Ono), ×1 (Murphy, 1967b, pl. 64, fig. 1).
- Jauberticeras JACOB, 1907, p. 285 [\*Ammonites jaubertianus ORBIGNY, 1850b, p. 200; OD] [=Jaubertella JACOB, 1908, p. 12, 17 (type, Ammonites jaubertianus Orbigny, 1850b, p. 200; SD Spath, 1927a, p. 66)]. Known only up to posterior part of body chamber at a small size; whorls always cadicone; differing from Gabbioceras in having almost flat or only slightly arched venter; shell lirate, especially on umbilical wall, and occasional constrictions on internal mold corresponding with collars on the shell. KENNEDY & KLINGER, 1977b. Lower Cretaceous (Upper Aptian-Upper Albian): France, Spain, Caucasus, northern Africa, Madagascar, South Africa (Zululand).—FIG. 5,2a-f. \*J. jaubertianus (ORBIGNY), Upper Aptian, France (Hyèges, Alpes-de-Haute Provence); a-c, lectotype, MNHN 5591, ×1 (new); *d*-*f*, ×1 (Murphy, 1967b, pl. 64, fig. 20-22).

## Suborder AMMONITINA Hyatt, 1889

## Superfamily HAPLOCERATACEAE Zittel, 1884

[*nom. transl.* ARKELL, 1957, p. 271, *ex* Haploceratidae ZITTEL, 1884, p. 411]

Typically compressed to discoidal; whorl sections ranging from oval with narrowly rounded venter to uni- or tricarinate oxycones with sharp keel; ribbing falcoid or falcate to obsolescent. Dimorphism moderate to extreme; microconchs often with aberrantly coiled and ornamented adult body chambers, their peristomes with prominent lappets. Double-valved aptychi known in many groups, sometimes as the only evidence of the former presence of ammonites (Aptychus Limestone facies of the Alps). Distribution pandemic but concentrated in the lower paleolatitudes of the Tethyan Realm. Middle Jurassic (Aalenian)-Upper Cretaceous (Lower Santonian).

The origin of the superfamily remains uncertain. Three of the main stems appeared more or less simultaneously in the Upper Aalenian, but the roots must lie lower, in the Toarcian. The lappeted microconchs point to the Hildoceratinae, as do iterative homeomorphies in such characters as tricarinate venters and midlateral spiral grooves. Rates of evolution in some lineages were imperceptibly low (Lissoceratidae, Haploceratidae). Distribution patterns coupled with the almost total absence of ribbing at all stages in both dimorphs suggest a pelagic habitat for these, akin to that of most Lytoceratina and Phylloceratina.

#### Family HAPLOCERATIDAE Zittel, 1884

#### [Haploceratidae ZITTEL, 1884, p. 411]

Small to medium-sized, fairly involute, smooth, featureless shells. Strongly but inconspicuously dimorphic; macroconchs with sinuous adult peristomes, moderately complex septal sutures characterized by well-

## Cephalopoda—Cretaceous Ammonoidea



FIG. 5. Tetragonitidae (p. 9)

incised, somewhat asymmetric lobes; microconchs with short lappets. Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Upper Hauterivian, ?Lower Barremian).

10

This family is probably derived from Taramelliceratinae of the Oppeliidae via Metahaploceras and Glochiceras (partim) in the Kimmeridgian, persisting almost unchanged through the Tithonian to the Barremian. Haploceratidae are homeomorphs of Lissoceratidae, an equally featureless and unchanging lineage that ranged from early Middle Jurassic into the Upper Oxfordian, but probably not directly related, for Lissoceratidae and Oppeliinae, ancestors of the Taramelliceratinae, were already fully differentiated at their first joint appearance in the Lower Bajocian. The septal sutures of Lissoceratidae are also characteristically distinct.

Haploceras ZITTEL, 1870, p. 166 [\*Ammonites elimatus OPPEL, 1865, p. 549; SD SPATH, 1923d, p. 14]
[=Hypolissoceras BREISTROFFER, 1947a, 2nd unnumbered page (type, Ammonites carachtheis ZEUSCHNER, 1846, pl. 4, fig. 1; OD); Neoglochiceras PATRULIUS & AVRAM, 1976, p. 168 (non COLLIGNON, 1960, explanation of pl. 145, nom. nud.), obj.]. Whorl section high-ovate. Microconchs with ventral crenulation on adult body chamber. Upper Jurassic (Kimmeridgian, beckeri Zone)–Lower Cretaceous (Valanginian): Tethys.—FIG. 6,1*a*,b. \*H. elimatum (OPPEL); macroconch, Upper Tithonian, Czech Republic, X0.7 (Zittel, 1868).—FIG. 6,1*c*–e. H. carachtheis (ZEUSCHNER), Upper Tithonian, Czech Republic; microconch, X1 (Zittel, 1868).

Neolissoceras SPATH, 1923d, p. 33 [\*Ammonites grasianus ORBIGNY, 1841, p. 141; M]. Compressed, involute, smooth; differing from Haploceras in flat-sided whorl section, flatly rounded venter, and distinct umbilical margin; one species with blunt keel. Sutures as in Haploceras. Contains Aptychus beyrichi var. fractocostata TRAUTH. Upper Jurassic (?Upper Tithonian), Lower Cretaceous (Berriasian-Upper Hauterivian, ?Lower Barremian): southern Europe, Madagascar, Punjab.——FIG. 6,2a-c. \*N. grasianum (ORBIGNY); a,b, Upper Tithonian, France; ×0.5 (Orbigny, 1840–1842); c, Valanginian, France, ×10 (Wiedmann, 1966a).

#### Family OPPELIIDAE H. Douvillé, 1890

[nom. correct. ARKELL, 1951, p. 6 pro Oppelidae BONARELLI, 1894, p. 81, nom. correct. pro Oppeliidés H. DOUVILLÉ, 1890, p. 287]

Typically compressed to oxycone; involute; strongly dimorphic. Macroconchs with distant, falcoid to falcate primary ribbing becoming smooth, simple aperture, and dense, complex sutures with deeply incised lobes arranged regularly on a straight baseline in decreasing length from external to umbilical edges. Microconchs tending to genicular coiling on adult body chamber, with highly developed, often spatulate, lappets. Sutures generally regular but complex. *Middle Jurassic (Lower Bajocian)–Lower Cretaceous (Upper Albian).* 

This is a diverse clade with a common root in the Oppeliinae of the early Middle Jurassic (Bajocian), the precise origin of which is still uncertain. The earliest forms appear to be *Praeoppelia* from the uppermost Aalenian, which share some morphological features of coiling, ribbing, and dimorphism with contemporary *Bradfordia* and *Lissoceras* but differ strongly in other features, including the falcoid ribbing and complex sutures. A line of descent can then be followed via oxycone *Oxycerites* of the late Middle Jurassic into Ochetoceratinae of the Oxfordian and thence, as assumed here, into the Streblitinae from the Kimmeridgian into the Hauterivian. Subsequent branches became more evolute and strongly ribbed (Hecticoceratinae), acquired runcinate biclavellate venters (Distichoceratinae), or developed various styles of blunt tuberculation (Taramelliceratinae).

### Subfamily STREBLITINAE Spath, 1925

[nom. transl. SPATH, 1928b, p. 147, ex Streblitidae SPATH, 1925b, p. 115]

Discoidal oxycones with very narrow umbilici; macroconchs high-keeled or narrowly tabulate with sharp, crenulate keels, becoming inflated on the adult body chamber; venter on adult body chamber broadening and developing shallow sulcus; ribbing variable but frequently recapitulating distant, falcate primaries with midlateral spiral groove so characteristic of ancestral *Oxycerites*, with fine but dense secondaries or even tertiaries



FIG. 6. Haploceratidae (p. 10)



FIG. 7. Oppeliidae (p. 12)

strengthening outwards towards the external margin. Microconchs very variable, smooth to densely ribbed with finely crenulate keels; adult body chambers more or less strongly modified, excentrically coiled, sometimes bizarrely (*Cyrtosiceras*), with prominent lappets. *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Hauterivian)*.

Taken here to have evolved from Ochetoceratinae via forms such as *Strebliticeras* HÖLDER, 1955.

- Uhligites KILIAN, 1913, p. 338 [\*Streblites kraffii UHLIG, 1903, p. 44; SD ROMAN, 1938, p. 164]. Venter rounded; ribbing feeble. Suture with exceptionally large lobe L. Lower Cretaceous (Upper Valanginian): Madagascar.
- Substreblites SPATH, 1925b, p. 115 [\*Ammonites zonarius OPPEL, 1865, p. 548; OD]. Like Streblites (Upper Jurassic), but venter with narrow, raised, flat band; sutures similar to Streblites with dense, strongly incised, long lobes on straight baseline but even more and narrower. Upper Jurassic (Tithonian)-Lower Cretaceous (Upper Valanginian): France, central Europe, Ukraine (Crimea), Pakistan (Salt Range), Antarctica.——FIG. 7,3a-c. \*S. zonarius (OPPEL), Upper Tithonian, Czech Republic; ×1 (Zittel, 1868).
- Cyrtosiceras HYATT, 1900, p. 569 [\*Ammonites macrotelus OPPEL, 1865, p. 548; OD] [=Meunieria GREGORIO, 1922, p. 16 (non KIEFFER, 1904, p. 408(42)), obj.]. Compressed; umbilicus occluded; phragmocone with minutely crenulate venter; adult body chamber modifying strongly, with coiling becoming excentrically geniculate, ventral crenulae swelling briefly before fading altogether, final aperture contracting by umbilical uncoiling, and peristome marked by terminal constriction and subspatulate lappet. Sutures similar to those of Substreblites. These forms are almost certainly the microconchs of Substreblites, but sutures are somewhat less strongly incised. Upper Jurassic (Upper Tithonian)-Lower Cretaceous (Berriasian): Czech Republic (Moravia), Romania, Ukraine (Crimea). -FIG. 7,2a,b. \*C. macrotelus (OPPEL), Upper Tithonian, Carpathians; ×1 (Zittel, 1868).
- Bornhardticeras BÖHM & RIEDEL, 1933, p. 122 [\*Placenticeras discoidale MÜLLER, 1900, p. 558; M]. Whorl section squarish in early stages, heightening later; adult platycone with rounded keelless venter as in Uhligites; ribs falcoid, sporadically with 2 rows of lateral tubercles, fading in adult. Sutures with long, tapering lobes with short lateral branches; saddle E/L divided by large adventive lobe. Lower Cretaceous (Hauterivian): Tanzania.——FIG. 7,1.
  \*B. discoidale (MÜLLER); X0.3 (Böhm & Riedel, 1933).

## Subfamily ACONECERATINAE Spath, 1923

[nom. transl. WRIGHT, 1957b, p. 285 ex Aconeceratidae SPATH, 1923d, p. 35]

ls; Small to medium-sized; involute; comly pressed; sides flat or slightly convex; keel es sharp to slightly rounded, entire or crenu-© 2009 University of Kansas Paleontological Institute



FIG. 8. Oppeliidae (p. 13–14)

late. Aperture of microconchs with long rostrum and lappets. Shell smooth or with flexuous to falcate lirae or ribs. Suture with second lateral saddle projecting well in front of the first. CASEY, 1961d; KENNEDY & KLINGER, 1979a.

WIEDMANN (1966a, p. 70) derives the subfamily (as a family) from the bluntly keeled *Neolissoceras aberrans* (Upper Valanginian, France), but since the subfamily evolves into haploceratoid forms (CASEY, 1961d, p. 119), it is more likely that it was derived from Streblitinae, which survived at least to the Hauterivian. Lower Cretaceous (Upper Hauterivian–Upper Albian).

Protaconeceras CASEY, 1954b, p. 269 [\*Oppelia patagoniensis FAVRE, 1908, p. 634; OD]. Keel low, coarsely crenulate in early stages; sides rather convex; flexuous striae or feeble, typically flat, ribs on outer flank of body chamber continuous to keel. Suture with wider and shallower elements than in Aconeceras. Lower Cretaceous (Upper Hauterivian): England, France, Argentina (Patagonia).——FIG. 8, 1a-f. \*P. patagoniense (FAVRE), Upper Hauterivian, Patagonia; a, ×2 (Favre, 1908); b-d, macro-

conch,  $\times 1$  (Riccardi, Aguirre Urreta, & Medina, 1987); *e*, microconch,  $\times 1$ ; *f*, suture,  $\times 2$  (Riccardi, Aguirre Urreta, & Medina, 1987).——FIG. 8,*Ig*,*h*. *P*. sp., Upper Hauterivian, England; *g*,  $\times 2$ ; *h*,  $\times 3$ (Casey, 1954b).

- Aconeceras HYATT, 1903, p. 100 [\*Ammonites nisus ORBIGNY, 1841, p. 184; M] [=Adolphia STOLLEY, 1907, p. 269, obj. (type, Ammonites nisus; SD CASEY, 1961d, p. 123); Adolphites HENNIG, 1932, p. 348 (? error for Adolphia)]. Involute oxycones with finely to coarsely serrate, solid or hollow keel, flat or gently convex sides, and angular umbilical rim; smooth at first but sooner or later with prorsiradiate, falcate striae or feeble to strong, flat ribs. Suture variable with long and narrow to short and wide elements; saddles may be phylloid. [Attempts to divide the more or less oxycone aconeceratines on the basis of ribs or height and fineness of denticulation of keel seem unsuccessful; in Barremian to Albian populations there is no stratigraphical separation of the various features. Aconeceras is therefore here interpreted widely with the conventional genera retained provisionally as subgenera.] Lower Cretaceous (Upper Barremian-Lower Albian): Europe, Greenland, Algeria, South Africa, Madagascar, Australia (Queensland), Western Australia, Argentina, Nepal.
  - A. (Aconeceras). Compressed; sides more or less flat; keel low, finely denticulate; ribs feeble, appearing late in ontogeny. Occurrence and distribution as for genus.——FIG. 9,7*a*-*c*. \**A*. (*A*.) *nisus* (ORBIGNY), Upper Aptian, France; *a*, ×1.5; *b*, ×1; *c*, ×4 (all Sarasin, 1893).
  - A. (Sanmartinoceras) BONARELLI in BONARELLI & NÁGERA, 1921, p. 27 [\*S. patagonicum; M] [=Eofalciferella BRUNNSCHWEILER, 1959, p. 13 (type, E. condoni; OD)]. Whorl section stouter and sides more convex than in A. (Aconeceras); keel high and serrated to low; juvenile stage smooth, then falciform striae strengthening into rather strong ribs on outer part of side or throughout. Microconchs with long rostrum and lappets and spiral depression at midflank; presumed macroconchs with no depression. Lower Cretaceous (Upper Aptian-Lower Albian): Europe, South Africa (Zululand), Madagascar, Nepal, Western Australia, Argentina, Antarctica, Greenland.——FIG. 9,2. A. (S.) groenlandicum ROSENKRANTZ in BOGVAD & ROSENKRANTZ, Upper Aptian, Greenland; microconch, ×1 (Casey, 1961d).
  - A. (Sinzovia) SAZONOVA, 1958, p. 126 [\*Ammonites trautscholdi SINZOW, 1870, p. 118; OD; =S. (S.) sazonovae WRIGHT, herein, nom. nov. pro Ammonites trautscholdi SINZOW, non OPPEL, 1862 in 1862–1863, p. 143]. Keel very low; juvenile smooth stage shorter than in A. (Sanmartinoceras); inner part of side tending to be smooth. Lower Cretaceous (Lower Aptian–Lower Albian): Europe, Russia, Madagascar, Nepal, southern Australia, Argentina.—FIG. 9,3a–c. \*A. (S.) sazonovae (WRIGHT), Lower Aptian, Russia; a,b, ×1; c, approximately ×2 (all Casey, 1961d).

- A. (Theganoceras) WHITEHOUSE, 1926, p. 202 [\*Oppelia scalata KOENEN, 1902, p. 54; OD]. Keel low; juvenile smooth stage short; ribs acutely falcate, fine, and more or less continuous from umbilical rim; ribs may form small umbilical bullae and incipient ventrolateral clavi. Suture with short, wide saddles. Lower Cretaceous (Lower Aptian–Upper Aptian): England, Germany, South Africa (Zululand), Antarctica (Alexander Island).—FiG. 9,6. \*A. (T.) scalatum (KOENEN), Upper Aptian, Germany; ×1 (Koenen, 1902).
- A. (Gyaloceras) WHITEHOUSE, 1927, p. 114 [\*G. smithi; OD]. Inflated; body chamber with rounded venter. Possibly macroconch of some Aconeceras. Lower Cretaceous (Upper Aptian): Queensland. Lower Cretaceous (Upper Albian): Nigeria.——FIG. 9, I. \*A. (G.) smithi, Upper Aptian, Queensland; ×0.75 (adapted from Whitehouse, 1927).
- Doridiscus CASEY, 1961d, p. 137 [\*D. rotulus; OD]. Evolute and inflated with subrectangular section, flat sides, and rounded shoulders; keel very low, minutely beaded; weak, falcoid lirae on sides. Suture simpler than Aconeceras and with fewer auxiliaries. Lower Cretaceous (Lower Aptian): England.——FIG. 9,5a-c. \*D. rotulus, Isle of Wight; ×1 (all Casey, 1961d).
- Nothodiscus CASEY in COLLIGNON, 1962b, p. 32 [\*N. planus; OD]. Very evolute with flat sides and narrow, flat venter; ventrolateral shoulders sharply rounded but not angular; feeble keel persisting to diameter of 35 mm; test with falcoid growth lines. Suture with same number of elements as Aconeceras but simpler. Lower Cretaceous (Upper Aptian): Madagascar.
- Falciferella CASEY, 1954b, p. 273 [\*F. milbournei; OD]. Flat-sided with venter rounded, then feebly keeled, and then flat; with irregular, fine, dense, falcate striae or riblets. Suture simplifying but still with moderately incised elements; lobe L trifid; U2 bifid. Falciferella is transitional to and resembles the Binneyitidae in shape, but it retains the aconeceratine keel at some stage, and lobe L at least is more or less trifid. Lower Cretaceous (Middle Albian–Upper Albian): England, France.——FIG. 9,4a–c. \*F. milbournei, Middle Albian, England; a,b, X2; c, X4 (all Casey, 1954b).
- Naramoceras MCNAMARA, 1985, p. 263 [\*Falciferella breadeni BRUNNSCHWEILER, 1959, p. 15; OD]. Venter rounded on phragmocone, feebly keeled on body chamber; with falcate ribs. More evolute and suture simpler than in Falciferella. Probably a progenetic dwarf offshoot of Falciferella. Lower Cretaceous (Middle Albian–Upper Albian): South Australia.—FIG. 8,2a,b. \*N. breadeni (BRUNN-SCHWEILER); a, X3; b, X7 (both McNamara, 1985).
- Koloceras RICCARDI, AGUIRRE URRETA, & MEDINA, 1987, p. 167 [\**K. talenkanum*; OD]. Venter rounded to tabulate with intermittent, feeble keel; with falcate striae to weak ribs. Suture with lobes L and U2 trifid to subbifid. *Lower Cretaceous (Upper Albian)*: Argentina (Patagonia), Angola.



FIG. 9. Oppeliidae (p. 14)

## Family BINNEYITIDAE Reeside, 1927

[Binneyitidae REESIDE, 1927a, p. 4]

Small, compressed, flat-sided, with flat or sulcate venter and weak ornament of sinuous to falcate striae or riblets; ornament may be strengthened or visible only on shoulders. Sutures simplifying with one or more lobes bifid, tending to have long, narrow, simple or entire elements with parallel sides; second lateral saddle projecting beyond first. Nacreous shell with metallic luster as in

15



FIG. 10. Oppeliidae & Family Uncertain (p. 16-17)

Aconeceratinae. Binneyitidae are derived from the Aconeceratinae by way of *Falciferella. Lower Cretaceous (Upper Albian)– Upper Cretaceous (Lower Santonian).* 

Borissjakoceras ARKHANGELSKY, 1916, p. 55 [\*B. mirabilis; OD]. Moderately evolute to rather involute; flat-sided; venter bluntly trapezoidal to rounded; surface smooth except for traces of prorsiradiate ribs on shoulders. Suture simple with deep, narrow, parallel-sided L and broad saddles; saddle E/L bifid or entire, L/U trifid. Lower Cretaceous (Upper Albian)–Upper Cretaceous (Lower Turonian): France, Angola, South Africa (Zululand), northern Siberia, Turkestan, Bathurst Island, New Zealand, Alaska, British Columbia, USA (Western Interior), Colombia, Argentina, Greenland.——FIG. 10,3a– *c.* \**B. mirabilis*, Lower Turonian, Turkestan; *a,b*, ×1; *c*, ×3 (all Arkhangelsky, 1916).

- Johnsonites COBBAN, 1961, p. 743 [\**J. sulcatus;* OD]. Flat-sided, with flat to feebly sulcate venter; smooth or with weak, falcoid ribs. Suture with deep, narrow external lobe divided by long, narrow foliole. *Upper Cretaceous (Upper Cenomanian):* Wyoming, Colorado.——FIG. 10,2*a*-*d.* \**J. sulcatus*, Wyoming; *a,b*, ×1; *c,d*, ×4 (all Cobban, 1961).
- Binneyites REESIDE, 1927a, p. 4 [\*B. parkensis; M]. Very involute; venter flat; shoulders sharper and ventrolateral ornament stronger than in Borissjakoceras. Suture with long, narrow, parallelsided, bifd or entire first lateral saddle, simple and broadening L, and very simple other elements; auxiliaries tending to increase in number with time. Upper Cretaceous (Lower Turonian-Lower Santonian): USA (Western Interior).——FIG. 10, 1a-c.

16

\**B. parkensis*, Coniacian, Wyoming; *a,b*, ×2; *c*, ×4 (Reeside, 1927a).

#### Family Uncertain

Tropitoides SPATH, 1925e, p. 102 [\*Ammonites obesus STOLICZKA, 1865, p. 55; OD]. Involute, highwhorled, with slightly convex sides sloping towards rather narrow venter bearing prominent, slightly rounded keel; close, rather flat, falcoid ribs ending in feeble ventrolateral clavi. [Suture with second lateral saddle projecting beyond other elements and the minute umbilicus recall Aconeceratinae but other features and stratigraphical horizon render connection unlikely.] Upper Cretaceous (?Middle Turonian, Upper Turonian): France, Israel, southern India.——FIG. 10,4a-c. \*T. obesus (STOLICZKA), ?Middle Turonian, southern India; a,b, ×0.75; c, ×1 (all Kossmat, 1895–1898).

## Superfamily PERISPHINCTACEAE Steinmann, 1890

#### Family POLYPTYCHITIDAE Wedekind, 1918

# [nom. correct. SPATH, 1924a, p. 87, pro Polyptichitidae WEDEKIND, 1918, p. 103]

With the widespread retreat of the seas from many marginal areas of the northern hemisphere at the end of the Jurassic, the descendents of the boreal Dorsoplanitinae diversified in separate faunal provinces or subprovinces covering a rapidly changing pattern of partially isolated, shallow epicontinental seas. Their remains are now found in scattered outcrops of highly incomplete, often condensed successions with phosphatic concretions. Difficulty in correlation is such that each faunal province retains its own scheme of zonation. Six such provinces may be distinguished: (1) Spilsby (eastern England-eastern Greenland); (2) Lower Saxony; (3) Russian Platform; (4) Siberian Arctic (including the Barents shelf and Spitsbergen); (5) Canadian Arctic (Sverdrup basin, Yukon); (6) northern Pacific cordillera (northern California, Oregon, Washington, British Columbia). It is often difficult to decide to what extent faunal differences reflect differences in age or provincialism, and condensation can make it hard to establish the variability of contemporaneous assemblages or biospecies. Classification has therefore led to phylogenetic schemes of improbable complexity.

Morphologically, the range of forms found in the family is unusually wide and untypical of perisphinctids in general. It includes involute, compressed homeomorphs of some Macrocephalitinae or Aulacostephanidae (Tollia); sphaerocones or cadicones that may be hard to distinguish from Cadoceratinae or Pachyceratidae (*Polyptychites*); serpenticones, homeomorphs of Stephanoceratinae (Simbirskites); and even oxycones, homeomorphic with Oxynoticeratinae (*Platylenticeras*). Sometimes the whole range from platy- to sphaerocones is found within the variability of what is almost certainly but a single biospecies (e.g., Thorsteinssonoceras ellesmerense JELETZKY, 1965). Interruption of ribbing on the venter to give a smooth band evolved several times in the family and has therefore as little systematic value here as elsewhere in the Perisphinctaceae. Constrictions similarly came and went.

The transition from the typical perisphinctid, ancestral Jurassic Dorsoplanitinae to the Craspeditinae was accompanied by an extensive modification of the external septal suture to a characteristic and persistent craspeditid plan. The external and lateral lobes shortened, thickened at their bases, and became less incised. The retracted umbilical or suspensive lobe was replaced as a major element by a series of 4 to 7 auxiliary lobes arranged in order of steadily decreasing size away from the first lateral lobe towards the umbilical seam, sometimes so simplified as to be almost vestigial. The baseline is straight or only gently curved, and its sweep towards the umbilicus can be slightly adapical (retracted) or even adoral, sometimes called reversed. In the Polyptychitinae there was a partial return to the more usual perisphinctid plan. The family carries on consistently the style of dimorphism established earlier. The microconchs are isocostate with no adult peristomal modifications of any kind, as in Dorsoplanites, making them often inconspicuous. The macroconchs are usually

variocostate, many becoming smooth, but there are isocostate exceptions (early Polypty*chites*). The dimorphic size ratio lies between 2:1 and 4:1. Relative abundances can be highly polarized, some known assemblages consisting almost completely of either macro- or microconchs. Ribbing is variable, but broad, short, subdued primary ribs or bullae are prominent up to the Valanginian. Most notable, however, is the frequent occurrence of polyschizotomous secondary ribbing in all combinations from dichotomous and bidichotomous to truly virgatotome, repeating the whole range found in what are thus seen to have been the ultimate ancestors, the Ataxioceratidae of the middle Upper Jurassic. This and the form of dimorphism distinguish Polyptychitidae from Olcostephanidae, with which they have at times been confused. Upper Jurassic (Upper Volgian)–Lower Cretaceous (Upper Hauterivian).

#### Subfamily CRASPEDITINAE Spath, 1924

[nom. transl. SPATH, 1931b, p. 547, ex Craspeditidae SPATH, 1924c, p. 17] [=Garniericeratinae SPATH, 1952, p. 9]

Inner whorls compressed and involute; ribbing light and dense, soon fading; macroconchs tending to become inflated with residual, widely spaced, bullate primary ribs. Adults small to medium sized. Sutures highly simplified. Includes two separate series of faunas, one in the Spilsby Province, the other in the Russian Platform, Siberian Arctic, and Canadian Arctic provinces. GERASIMOV, 1969; JELETZKY, 1966; CASEY, 1973; SHUL'GINA, 1969a. Upper Jurassic (Upper Volgian)–Lower Cretaceous (Lower Ryazanian).

- Subcraspedites SPATH, 1923c, p. 308 [\*Ammonites plicomphalus J. de C. SOWERBY, 1823, p. 145, non J. SOWERBY, 1822, p. 82; SD SPATH, 1924c, p. 17; =S. sowerbyi SPATH, 1952, p. 18]. Inner whorls finely ribbed, with secondary ribs in dense sheaves projected on venter; outer whorls developing coarse, blunt, short primary ribs. Sharpness of secondary ribbing external, not impressed on internal molds. Intermediate between Laugeites and Craspedites. CASEY, 1973. Upper Jurassic (Upper Volgian)–Lower Cretaceous (Lower Ryazanian): England.
  - S. (Swinnertonia) SHUL'GINA, 1972b, p. 138 [\*Subcraspedites cristatus SWINNERTON, 1935, p.

33; OD]. The earliest forms of Subcraspedites; evolute, densely ribbed like ancestral Laugeites (Upper Jurassic); ribbing suddenly and strongly modified in small adult macroconchs, giving widely spaced, sharp, primary ribs and dense sheaves of secondary ribs persisting to the end. CASEY, 1973; SWINNERTON, 1935. Upper Jurassic (Upper Volgian, primitivus Zone): England.— FIG. 11,3a. S. (Swinnertonia) subundulatus; topotype, macroconch, ×1 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).——FIG. 11,3b,c. \*S. (Swinnertonia) cristatus; holotype, ×1 (Swinnerton, 1935).

- S. (Subcraspedites) [=Volgidiscus CASEY, 1973, p. 239 (type, Subcraspedites lamplughi SPATH, 1936, p. 81; OD)]. Outer whorls moderately involute, primary ribs subdued, secondary ribs fine and dense, persisting to the end; adult body chamber beginning to resemble Craspedites. Upper Jurassic (Upper Volgian, preplicomphalus-lamplughi Zones): England.—FIG. 11, 1a-d. \*S. (S.) sowerbyi SPATH; a,b, holotype, macroconch, X1; c, X1, d, X1.5, topotypes (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).
- S. (Runctonia) CASEY, 1973, p. 240 [\*R. runctoni; OD]. Involute, compressed microconchs with semifastigiate venter; secondary ribs chevronlike, fading on venter; suture simplified on ascending baseline. Macroconchs apparently smooth except for ornament on umbilical and ventrolateral shoulders. Morphologically transitional to *Hectoroceras. Lower Cretaceous (Lower Ryazanian,* runctoni Zone): England.—FIG. 11,2a-d. \*S. (R.) runctoni CASEY, holotype; a, b, shell, ×1; c,d, section, ×1; e, suture, ×1.5 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).
- Craspedites PAVLOW, 1892, p. 474 [non "Craspedites (pro -donites HAECKEL, 1865) ALLMAN, 1872, p. 174," cited by NEAVE, 1939, p. 860, but no trace of *Craspedites* in ALLMAN (hydroids), hence presumably an incorrect subsequent spelling of *Craspedonites* without status] [\**Ammonites okensis* ORBIGNY, 1845b, p. 436; SD R. DOUVILLÉ, 1911, fiche no. 213]. Inner whorls compressed, involute, finely and densely ribbed; macroconchs becoming inflated, umbilicus narrow and craterlike, ribbing becoming rounded and subdued or fading altogether. Some species with constrictions. *Upper Jurassic (Upper Volgian):* England, Russian Platform, Arctic.
  - C. (Craspedites) [=Mosquites SAZONOVA, 1971, p. 30 (type, Craspedites mosquensis GERASIMOV, 1960, p. 171; OD); Trautscholdiceras SAZONOVA, 1977, p. 90 (type, Ammonites kaschpurensis TRAUTSCHOLD, 1866, p. 16; OD); Vitaliites SHUL'GINA, 1985, p. 116 (type, Ammonites subditus TRAUTSCHOLD, 1877, p. 392; OD)]. Highly variable, usually involute and inflated, with smooth outer whorls; simple sutures typical of subfamily. [Mosquites (for small cadicones retaining subdued secondary ribbing to the end but losing primary ribs) and Trautscholdiceras (for small cadicones with constrictions and with



FIG. 11. Polyptychitidae (p. 18)

smooth body chambers except for well-spaced circumumbilical bullae) seem unnecessary.] GERASIMOV, 1969; SHUL'GINA, 1969a. Upper Jurassic (Upper Volgian): England, Russian Platform (Moscow and Volga basins, Pechora), northern Urals, northern Siberia, Novaya Zemlya, Spitsbergen.——FIG. 12,2*a*–*c*. \**C. (C.) okensis* (ORBIGNY), Russia; lectotype, macroconch, ×1 (R. Douvillé, 1911).

C. (Taimyroceras) BODYLEVSKII, 1956, p. 82 [\* T. taimyrense; OD]. Has most of the characters of C. (Craspedites), but venter flatter with smooth band. [A large collection from a single concretion gives a good idea of intraspecific variability (JELETZKY, 1966).] ERSHOVA, 1969. Upper Jurassic (Upper Volgian, taimyrensis Zone): northern Siberia, Spitsbergen, Arctic Canada (Ellesmere Island).——FIG. 12, Ia-c. \*C. (T.) taimyrensis BODYLEVSKII, Kheta basin, northern Siberia; topotype?, macroconch, X1 (Shul'gina, 1969a).

C. (Kachpurites) SPATH, 1923c, p. 307 [\*Ammonites fulgens TRAUTSCHOLD, 1861, p. 270; SD SPATH, 1924c, p. 17]. Small, smooth; probably microconchs of C. (Craspedites) whose inner whorls they resemble; adult body chambers compressed and evolute; ribbing variable, some forms wholly smooth, some regaining short, distant primary ribs, others retaining secondary ribs only. GERASIMOV, 1969; SHUL'GINA, 1969. Occurrence and distribution much as for genus.——FIG. 12,3*a*-*c*. \**C*. (*K*.) fulgens (TRAUTSCHOLD), Moscow basin; *a*,*b*, lectotype designated herein, *non* NIKITIN, 1881, pl. 4, fig. 48, designated by SPATH (1947, p. 12), but not a syntype, ×1 (Trautschold, 1861); *c*, ribbed variant, ×1 (Gerasimov, 1969).——FIG. 12,3*d*-*f*. *C*. (*K*.) *nekrassovi* (PRIGORIEVSKY), Moscow basin; showing peristome, ×1 (Gerasimov, 1969).

Garniericeras SPATH, 1923c, p. 307, nom. nov. pro Garnieria BOURGUIGNAT, 1877, p. 2, non SAYN, 1901, p. 14 (which is an objective synonym of Platylenticeras HYATT, 1900, p. 590) [\*Ammonites catenulatus FISCHER VON WALDHEIM, 1837 in 1830– 1837, p. 169; SD SPATH, 1924c, p. 17 (incorrectly



Fig. 12. Polyptychitidae (p. 18–20) © 2009 University of Kansas Paleontological Institute



FIG. 13. Polyptychitidae (p. 20-22)

2009

given as "Oxynoticeras" catenulatum TRAUTSCHOLD, but later (SPATH, 1947, p. 12) rectified)]. Involute oxycones with sharp to keeled venters; radial primary ribs faint or obsolete; sutures of craspeditid plan but even more simplified. Dimorphic; sizes similar to those of *Craspedites* and *Kachpurites*; tests of microconchs becoming markedly striated near the adult aperture as in some *Kachpurites*. SPATH, 1947; GERASIMOV, 1969; SHUL'GINA, 1969a. Upper Jurassic (Upper Volgian)–Lower Cretaceous (Lower Ryazanian, fulgens-rjazanensis Zones): Russian Platform, northern Urals, northern Siberia.——FIG. 13,2a-c. \*G. catenulatum (FISCHER VON WALD-HEIM); a,b, macroconch, X0.7 (Nikitin, 1884); c, X1.5 (Spath, 1947).——FIG. 13,2d,e. G. interjectum (NIKITIN), Moscow basin; microconch, X0.7 (Gerasimov, 1969).

Praetollia SPATH, 1952, p. 12 [\**P. maynci;* OD]. Involute, compressed; ribbing fine, slightly flexed, dividing low on side as in *Hectoroceras*, but sharper and 09 University of Kansas Paleontological Institute

stronger, mostly bifurcate in young, later trifurcate or with intercalatories, uninterrupted on venter, resembling *Pectinatites* (Upper Jurassic). Suture craspeditid. [Slightly older than *Hectoroceras* but overlapping in range; phyletic relations somewhat uncertain.] CASEY, 1973. *Lower Cretaceous (Lower Ryazanian*, kochi *Zone):* eastern Greenland (main occurrence), North Sea, northern Siberia, Moscow basin (rare).—FIG. 13,3a,b, \*P. maynci, eastern Greenland; a, holotype, ×0.7; b, ×1 (Spath, 1952).

- Hectoroceras SPATH, 1947, p. 20 [\*H. kochi; OD]. Compressed, flat-sided, with small to minute umbilicus. Ribbing flexuous and subdued, branching low on sides. Sutures with many auxiliaries. [A widespread, specialized offshoot from main craspeditid lineage.] Upper Jurassic (?Upper Volgian)–Lower Cretaceous (Lower Ryazanian): England, Russian Platform, northern Siberia, eastern Greenland.
  - H. (Hectoroceras). Venter narrowly arched and sharpened; ribbing dense; regular, rounded, straight, and prorsiradiate primary ribs branching at midside or higher into 2 or 3 falcoid secondary ribs; secondary ribs disappearing on venter; towards end of adult body chamber, ribs becoming single, equal, and continuous across venter and fading. SHUL'GINA, 1972a; KLIMOVA, 1972; CASEY, 1973; SURLYK & others, 1973; CASEY, MESEZHNIKO, & SHUL'GINA, 1977. Lower Cretaceous (Lower Ryazanian, kochi Zone): eastern Greenland, eastern England, Denmark, Moscow basin (rare), northern Urals, northern Siberia. ——FIG. 13, 1a-c. \*H. kochi, eastern Greenland, topotype; a,b, ×0.7 (Surlyk & others, 1973); c, ×1.4 (Spath, 1947).
  - H. (Shulginites) CASEY, 1973, p. 239 [\*Oxynoticeras tolijense NIKITIN, 1884, p. 65; OD] [=Toljaiceras SHUL'GINA in SAKS & SHUL'GINA, 1974, p. 545, obj.]. Venter subacute on early whorls, becoming rounded; ribbing as in *H. (Hectoroceras)* but fading, leaving adult body chamber smooth. Suture ascending. Upper Jurassic (?Upper Volgian)– Lower Cretaceous (?Lower Ryazanian): northern Urals, northern Siberia.—FIG. 13,4a-c. \*H. (S.) tolijense (NIKITIN), probably Lower Ryazanian, western Siberia; a, lectotype, ×1 (Nikitin, 1884); b,c, topotype, ×1 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).

#### Subfamily TOLLIINAE Spath, 1952

[nom. correct. ARKELL, 1957, p. 344, ex Tollinae SPATH, 1952, p. 9] [=Suritidae SAZONOVA, 1971, p. 24; Menjaitinae SAZONOVA, 1971, p. 73; Peregrinoceratinae SAZONOVA & SAZONOVA, 1984, p. 97 (where cited as "Peregrinoceratinae SAZONOVA, 1979," reference not traced)]

Predominantly compressed and rather involute; strong primary ribs typically dividing at midside, either indistinctly (early forms) or clearly di- to polyschizotomously (later forms), into numerous secondary ribs; secondary ribs projecting on venter; macroconchs tending to become smooth. Sutures still craspeditid in plan. Descendants of Craspeditinae (*Subcraspedites*), the dividing line being arbitrary. Most genera widespread throughout the Boreal Realm, but some local faunas developed (e.g., *Menjaites*). *Lower Cretaceous (Lower Ryazanian–Valanginian)*.

- Borealites KLIMOVA, 1969, p. 129 [\*B. fedorovi; OD]. Inner whorls with oval section and strong ribbing bifurcating at or above midside, as in later Surites; middle whorls in macroconchs more inflated, with thickened primary ribs trifurcating; later still intercalatories appearing and ribs disappearing be low branching point, as in ancestral Subcraspedites. [The subgenera are doubtfully distinct.] CASEY, 1973; KLIMOVA, 1972. Lower Cretaceous (Lower Ryazanian–Upper Ryazanian): England, Russia, Spitsbergen, northern Canada, northern and eastern Greenland.
  - B. (Borealites) [=?Pronjaites SAZONOVA, 1971, p. 54 (type, Olcostephanus bidevexus BOGOSLOVSKII, 1897, p. 55; OD)]. Similar to genus, but ribbing persisting on venter. Holotype of type species is macroconch. [Type material of Pronjaites is too fragmentary for distinct generic diagnosis and probably comprises only a compressed species of *B. (Borealites).*] Lower Cretaceous (Lower Ryazanian): distribution as for genus.—FIG. 14,1a-c. \*B. (B.) fedorovi, kochi Zone, Siberia (northern Urals); holotype, macroconch, ×11 (Klimova, 1969).—FIG. 14,1d,e. ?B. (B.) bidevexus, (BOGOSLOVSKII), sibiricus Zone, Siberia; ×1 (Bogoslovskii, 1897).
  - B. (Pseudocraspedites) CASEY, MESEZHNIKOV, & SHUL'GINA, 1977, p. 30 [\*Subcraspedites anglicus SHUL'GINA, 1972b, p. 139; OD]. Large, more finely ribbed than B. (Borealites); outer whorls becoming evolute and almost smooth, retaining distant primary bullae; homeomorphs of some Subcraspedites and even Dorsoplanites (Upper Jurassic), although suture remaining craspeditid. Lower Cretaceous (Lower Ryazanian, kochi Zone): northern Siberia, northern Canada.——FiG. 14,2a,b. \*B. (P) anglicus, northern Siberia; holotype, ×0.75 (Shul'gina, 1972b).
  - B. (Ronkinites) SHUL'GINA, 1972b, p. 147 (non BASOV & others, 1970, p. 21, nom. nud.) [\*Subcraspedites (Ronkinites) rossicus; OD]. Whorl section round to squarish; constrictions weak. ?Microconch of B. (Pseudocraspedites). Lower Cretaceous (Upper Ryazanian): Siberia, northern Canada.——FIG. 14,3a,b. \*B. (R.) rossicus (SHUL'GINA), Siberia; ×0.75 (Shul'gina, 1972b).
- Surites SAZONOV, 1951, p. 59 [\*S. pechorensis; OD]. Compressed to inflated, evolute to involute, but all forms slowly uncoiling, with many whorls exposed in the umbilicus; inner and middle whorls with strong, sharp ribbing; primary ribs bifurcating at or above midside into sharp, strong secondary ribs; secondary ribs moderately to strongly projected on venter. Macroconchs variocostate, some retaining



FIG. 14. Polyptychitidae (p. 22)

only traces of circumumbilical, bullate primary ribs or faint secondary ribs on flattened venter. Many genera doubtfully distinct, even at specific level. SAZONOVA, 1971, 1972, 1977; CASEY, 1973. Lower Cretaceous (Lower Ryazanian–Upper Ryazanian) Russian Platform, northern Urals, northern Siberia, eastern Greenland, England, northern Canada.

- S. (Praesurites) MEGEZHNIKOV & ALEKSEEV in MESEZHNIKOV & others, 1983, p. 122 [\*S. (P) elegans; OD]. Involute, compressed; transitional between Craspedites and S. (Surites), retaining coiling of Craspedites but having coarse, projected, biplicate secondary ribbing of Surites on inner whorls. Lower Cretaceous (Lower Ryazanian): subpolar Urals.——FIG. 15, Ia, b. \*S. (P) elegans; holotype, ×1 (Mesezhnikov & others, 1983).
- S. (Surites) [=? Chandomirovia SAZONOV, 1951, p. 61 (type, C. ilekensis; OD); Bogoslovskia SAZO-NOVA, 1965, p. 103 (1961, p. 12, nom. nud.) (type, Olcostephanus stenomphalus PAVLOW, 1890, p. 117, partim, pl. 3, fig. 10 only; OD; =B. pseudostenomphala SAZONOVA, 1971, p. 53); Stchirowskiceras SAZONOVA, 1971, p. 57 (type, S. principale; OD); Subpolyptychites SAZONOVA, 1971, p. 88 (type, S. distinctus; OD); Suridiscus SAZONOVA, 1977, p. 63 (type, Stchirowskiceras (Suridiscus) subprincipale; OD)]. Macroconchs large, coarsely ribbed, moderately involute, and inflated. Occurrence and distribution as for genus. ——FIG. 15,2a-c. \*S. (S.) pechorensis SAZO-NOV, Upper Ryazanian, Russia (River Sura); holotype, macroconch, X1 (Sazonova, 1965). -FIG. 15,2d,e. S. (S.) simplex (BOGOSLOVSKII),



FIG. 15. Polyptychitidae (p. 23-25)



FIG. 16. Polyptychitidae (p. 25-26)

Russia (River Sura); lectotype, microconch, ×1 (Sazonova, 1971).——FIG. 15,2*f*,*g*. *S.* (*S.*) *pseudostenomphalus* (SAZONOVA), Upper Ryazanian, Moscow basin; neotype, ×1 (Sazonova, 1972).

- S. (Caseyiceras) SAZONOVA, 1971, p. 44 [\*C. caseyi; OD]. Evolute with depressed whorls; ribs coarse, dominantly biplicate, and only moderately projected on venter. Lower Cretaceous (Ryazanian): Russia.——FIG. 16, Ia, b. \*S. (C.) caseyi (SAZO-NOVA); holotype, probably microconch, ×1 (Sazonova, 1972).
- S. (Externiceras) SAZONOVA, 1971, p. 49 [\*Perisphinctes solowaticus BOGOSLOVSKII, 1897, p. 78; OD]. Evolute; densely and finely ribbed; Perisphinctes-like, long, thin primary ribs branching two-thirds up side. Lower Cretaceous (Upper Ryazanian): Russia.——FIG. 15,4a,b. \*S. (E.) solowaticus (BOGOSLOVSKII); microconch, ×1 (Sazonova, 1971).
- S. (Lynnia) CASEY, 1973, p. 254 [\*S. (L.) icenii; OD]. Whorl section subquadrate; microconchs with ribs fine at first, later coarse and trifurcating high on side. Lower Cretaceous (Upper Ryazanian, icenii Zone): England.——FIG. 15,3a-c. \*S. (L.) icenii, holotype; a,b, ×1; c, ×3 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).
- S. (Bojarkia) SHUL'GINA, 1969b, p. 46 [\*B. mesezhnikowi; OD]. Whorl sides flat, subparallel; venter broadly rounded; ribs rather fine and close; biplicate secondary ribbing disappearing early. Not well distinguished from S. (Surites); late forms transitional to Tollia, particularly the inner whorls. Lower Cretaceous (Upper Ryazanian): England, Russia, Siberia.— FIG. 16,2a,b. \*S. (B.) mesezhnikowi (SHUL'GINA), mesezhnikowi Zone, northern Siberia; holotype, macroconch, X0.7 (Shul'gina, 1969b).——FIG. 16,2c,d. S. (B.) stenomphalus (PAVLOW),

stenomphalus Zone, England; lectotype, microconch, X1 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).

- Peregrinoceras SAZONOVA, 1971, p. 63 [\*Olcostephanus pressulus BOGOSLOVSKII, 1897, p. 68; OD]. Inner whorls polygyrate as in Surites but with welldifferentiated ribbing as in Tollia; primary ribs well spaced, short, dividing indistinctly at midside into sheaves of dense, fine secondary ribs projected on venter; outer whorls of macroconchs involute and tending to smoothness. SAZONOVA, 1971, 1972; CASEY, 1973. Lower Cretaceous (Upper Ryazanian, tzikwinianus and albidum Zones): England, northern Greenland, Russian Platform, Transcaspia.-FIG. 17,3a. \*P. pressulum (BOGOSLOVSKII), Moscow basin; topotype, macroconch, X1 (Sazonova, 1972).—FIG. 17,3b,c. P. cf. albidum CASEY, England; microconch, X0.7 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).
- Tollia PAVLOW, 1914, p. 39 [\* T. tolli; SD ARKELL, 1957, p. 344]. More or less involute and high-whorled; compressed; primary ribs distinct, rising with sharp curve on umbilical shoulder and running straight and prorsiradiate on inner part of side; secondary ribs projected strongly ventrolaterally. On early whorls each primary rib with 2 or 3 fine secondary ribs; on middle whorls primary ribs normally trifurcate with 1 or 2 intercalatories but occasionally bidichotomous. Macroconchs with ribs tending to weaken at midside and outer whorls smooth or having secondary ribs only on ventrolateral shoulders; constrictions present. Suture craspeditid, with graded auxiliaries. [Forms found in the Upper Valanginian resemble Tollia in coiling but have bi- and polyschizotomous secondary ribbing in the style of Dichotomites (subfamily Polyptychitinae). They have therefore usually been regarded as homeomorphs and assigned to the separate genus Homolsomites.] SHUL'GINA, 1972; KLIMOVA, 1972a. Lower Cretaceous (Lower Valanginian–Upper Valanginian): England, northern Germany, Russia (Pechora region, northern Urals, northern Siberia, Novaya Zemlya), northern and eastern Greenland, northern Canada, British Columbia, Oregon, northern California.
  - T. (Tollia) [=Neotollia SHUL'GINA, 1969b, p. 48 (type, Tollia klimovskiensis KRIMGOL'TS in KRIMGOL'TS, PETROVA, & PCHELINTSEV, 1953, p. 76; OD); Bodylevskites KLIMOVA, 1978b, p. 50 (type, B. harabylensis; OD)]. Compressed at all stages, with not much variability; ribs bi- or trifurcating on inner whorls. [Neotollia, with ribbing regularly bifurcating on the inner whorls and primary ribs less differentiated, and Bodylevskites, based on poor type material of late forms from the syzranicus Zone of northern Siberia with secondary ribs already in part polyptychitid, seem unnecessary.] Occurrence as for genus: distribution more restricted than Surites or Polyptychites, largely displaced on the central Russian Platform and in lower Saxony by other groups.-FIG. 17,1a,b. \*T. (T.) tolli PAV-

LOW, northern Siberia; a,b, paralectotype, macroconch, ×0.5 (Pavlow, 1914).-FIG. 17,1c,d. T. sp. aff. tolli, England; microconch, ×1 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).

- T. (Neocraspedites) SPATH, 1924c, p. 17 [\*Craspedites semilaevis KOENEN, 1902, p. 80; OD]. Rather involute and compressed with weak umbilical bullae, smooth sides, and fine, even secondary ribs on venter. [KEMPER's claim (1978, p. 194) that the craspeditid (i.e., tolliine) Lower Valanginian type species is unrelated to Upper Valanginian species of the group of T. undulatus and complanatus (KOENEN), said to be derived from Dichotomites, is questionable.] Lower Cretaceous (Lower Valanginian–Upper Valanginian): England, northern Germany, Greenland.-FIG. 17,4a,b. \*T. (N.) semilaevis (KOENEN), Lower Valanginian, Germany; ×1 (Koenen, 1902).
- Virgatoptychites VORONETS, 1958, p. 68 [\* V. changalassensis; OD]. Similar to Tollia in coiling and style of ribbing but with macroconchs smaller, strongly ribbed to the end; middle and outer whorls slightly variocostate, with strong polyschizotomous secondary ribbing of varying degree up to and including true virgatotome. A widespread group coeval with and derived from Tollia. At some levels, possibly only one extreme of range of the variability of Tollia; at others, distinct with no intergrading. Microconchs probably inseparable from those of Tollia. VORONETS, 1962. Lower Cretaceous (Lower Valanginian): England, northern Germany, northern Siberia, northern Canada.
  - V. (Virgatoptychites). More inflated than Tollia, with whorl section broadly oval; outer whorls with regularly virgatotome ribs. Occurrence as for genus: northern Siberia, northern Canada. -FIG. 18, 3a, b. \*V. (V.) pachsaensis VORONETS, northern Siberia; ×0.7 (Voronets, 1962).
  - V. (Propolyptychites) KEMPER, 1964, p. 23 [\*Polyptychites quadrifidus KOENEN, 1902, p. 109; OD] [=Paratollia CASEY, 1973, p. 257 (type, P. kemperi; OD)]. Ribbing relatively delicate, with or without weak umbilical nodes; compressed, Tollia-like stage of early whorls prolonged; secondary ribs irregularly polyschizotomous as in Polyptychites, but not virgatotome. [Paratollia merely covers the more densely and finely ribbed forms.] Occurrence as for genus: England, northern Germany.-FIG. 18,2a,b. \*V. (P.) quadrifidus (KOENEN), northern Germany; ×1 (Kemper, 1964).—FIG. 18,2c,d. V. (P.) pumilio (VOGEL), northern Germany; paratype, microconch, ×1 (Vogel, 1959).
- Nikitinoceras D. N. SOKOLOV, 1913, p. 80 [\*Olcostephanus hoplitoides NIKITIN, 1888, p. 96; SD SAZO-NOVA, 1961, p. 12, 1977, p. 76, non Jeletzky, 1979, p. 11] [= Temnoptychites PAVLOW, 1914, p. 44, obj. (for dates of publication of SOKOLOV and PAVLOW, see BODYLEVSKII, 1967, p. 103; SAZONOVA & SAZONOV, 1991, p. 61; and synonymy already indicated by SPATH, 1924c, p. 17)]. Highly variable, re-



FIG. 17. Polyptychitidae (p. 26-29)



FIG. 18. Polyptychitidae (p. 26-29)

peating the whole range of forms found in the earlier *Surites* and later *Polyptychites*, from compressed to cadicone, involute to evolute, finely to extremely

ared biplicate ribs to the end; macroconchs small, with strong biplicate ribs to the end; macroconchs variocostate, ely ribbing modifying to indistinct polyptychitid before © 2009 University of Kansas Paleontological Institute fading altogether; all forms united by a common but variably persistent feature, the fading or complete interruption of the secondary ribbing on the venter. Sutures typically craspeditid. [The subgenera may reflect largely the extremes of coiling but in part also small differences in ages.] BODYLEVSKII, 1967; JELETZKY, 1979. Lower Cretaceous (Lower Valanginian): Russian Platform (hoplitoides Zone), western and northern Siberia (syrzanicum Zone), Novaya Zemlya, Greenland, northern Canada (troelseni and kemperi Zones).

- N. (Bodylevskiceras) SAZONOVA, 1977, p. 75 (non 1971, p. 74, nom. nud.) [\*Temnoptychites elegans BODYLEVSKII in LUPPOV, BODYLEVSKII, & GLAZU-NOVA, 1949, p. 200; OD]. Compressed, Tollialike forms, some species having quite narrow ranges of variability. Lower Cretaceous (Lower Valanginian): northern Siberia, Novaya Zemlya, northern Canada.——FIG. 19,3a-d. \*N. (B.) elegans (BODYLEVSKII), Novaya Zemlya; a-c, holotype, X0.7; d, topotype, X1 (Bodylevskii, 1967).
- N. (Nikitinoceras). Macroconchs of intermediate inflation and coarseness of ribbing; polyschizotomy setting in fairly early. Occurrence and distribution as for genus.——FIG. 19, *Ia*, *b*. \**N*. (*N.*) hoplitoides (NIKITIN), Moscow basin, lectotype; ×1 (Nikitin, 1888).
- N. (Russanovia) BODYLEVSKII, 1967, p. 109 [\*Am*monites diptychus* KEYSERLING, 1846, p. 32; OD] [=Subtemnoptychites KLIMOVA, 1978a, p. 101 (type, Temnoptychites (S.) prodigialis; OD); Keyserlingyceras SAZONOVA, 1961, p. 12, nom. nud.]. Cadicones with depressed whorl section; microconchs and early whorls of macroconchs with coarse, strong, distant bifurcating ribs weakening sometimes only barely perceptibly on the venter; outer whorls of macroconchs like typical Polyptychites. Occurrence and distribution as for genus.—\_FIG. 19,2a,b. \*N. (R.) *diptychum* (KEYSERLING), Pechora; lectotype, ×1 (Bodylevskii, 1967).—FIG. 19,2c,d. N. (R.) rudis BODYLEVSKII, 1967, Novaya Zemlya; holotype, microconch, ×1 (Bodylevskii, 1967).
- Thorsteinssonoceras JELETZKY, 1965, p. 1 (1964, p. 40, nom. nud.) [\* T. ellesmerense; OD]. Involute; whorl section somewhat wider than high to depressed-coronate; ribbing very variable; middle whorls with umbilical bullae and virgatotome, simple or bidichotomous bundles of 3 to 5 secondary ribs; last 2 whorls smoth except for umbilical bullae. Constrictions normally present. Early whorls indistinguishable from *Polyptychites*, but suture with 4 or 5 ascending auxiliaries. *Lower Cretaceous (Lower Valanginian):* Siberia, Spitsbergen, Ellesmere Island, *a-c*, ×0.5; *d*, ×1 (Jeletzky, 1965; courtesy of the Geological Survey of Canada).
- Menjaites SAZONOVA, 1971, p. 74 [\*M. imperceptus; OD] [=Costamenjaites SAZONOVA, 1971, p. 83 (type, C. jucundus; OD); Luppoviceras SAZONOVA, 1977, p. 52 (type, L. validum; OD); Sabydites BOGOMOLOV & BURDYKINA, 1989, p. 18 (type, S. menjaiteformis; OD)]. Moderately involute; whorl

section high-oval; umbilical wall shallow and rounded. Ribbing on inner whorls variable but always subdued and soon fading; in some species weak primary ribs branching into bundles of threadlike secondary ribs but fading early, with or without strong constrictions; in others more pronounced, bullate primary ribs dividing into sheaves as in Tollia, persisting to the middle whorls, and sometimes interrupted on the venter (Costamenjaites); macroconchs becoming large, with middle and outer whorls wholly smooth. Craspeditid suture much simplified on a rectiradiate baseline. [A well-defined local group confined largely to the central Russian Platform where it takes the place of the closely related Tollia.] Lower Cretaceous (Lower Valanginian, undulatoplicatilis Zone): Russia, ?England. ----FIG. 18,1a-d. \*M. imperceptus, central Russia (River Menya);  $a, b, \times 0.75$ ;  $c, d, \times 1$  (Sazonova, 1971).-FIG. 18,1e,f. M. certus (SAZO-NOVA), central Russia; ×1 (Sazonova, 1971).

#### Subfamily POLYPTYCHITINAE Wedekind, 1918

#### [Polyptychitinae WEDEKIND, 1918, p. 103]

Very variable. In earlier groups rather evolute forms dominant, ranging from moderately inflated to very depressed, cadicone, or sphaerocone; macroconchs medium-sized, mildly to strongly variocostate. Later forms involute to evolute but on the whole only moderately inflated and large to very large, so that microconchs may be homeomorphic with earlier macroconchs. Ribbing variable; inner whorls may be smooth and constricted up to 15 mm diameter; middle and outer whorls generally with elevated or bullate primary ribs branching in simple bundles, irregularly polyschizotomously or virgatotomously (*Polyptychites*) or bidichotomously (Dichotomites). Lower Cretaceous (Lower Valanginian–Lower Hauterivian).

Most of these characters appear already in various Tolliinae, from which the Polyptychitinae as a whole were undoubtedly derived; but the precise phyletic pathway remains unclear. Alternatives include *Nikitinoceras* or *Virgatoptychites* (*Propolyptychites*). There is no clear morphological demarcation except possibly in the sutures, which continue broadly craspeditid in plan but with longer, more slender lateral lobes and a reduced number of auxiliaries in the earlier forms. Most genera are widespread in the Boreal Realm, but some are local (e.g., *Wellsia*). IMLAY, 1960; KEMPER, 1978.



FIG. 19. Polyptychitidae (p. 29)

Polyptychites PAVLOW, 1892, p. 476 [\*Ammonites polyptychus KEYSERLING, 1846, p. 327; SD ROMAN, 1938, p. 391]. Moderately involute to very evolute; whorl section rather compressed to depressed, coronate or sphaerocone; more or less prominent, normally oblique umbilical bullae or round tubercles giving rise to 2 or more ribs; some ribs branching once or twice again; ribbing may be virgatotome; inner whorls of some species may have sharp, high, biplicate or triplicate ribs. Suture with 2 or 3 auxiliary lobes. Lower Cretaceous (Lower Va*langinian–Upper Valanginian):* northern Eurasia, France, ?Mexico, ?California, northern Canada, Greenland.

P. (Siberiptychites) KEMPER & JELETZKY in KEMPER, 1977, p. 3 [\*Ammonites stubendorffi SCHMIDT, 1872, p. 133; OD]. Cadicones with steep umbilical walls, dense and fine ribbing; homeomorphs of Macrocephalites but with constrictions, sometimes to a late stage; suture with 3 auxiliary lobes. Lower Cretaceous (Lower Valanginian, stubendorffi Zone): northern Siberia, Greenland, northern Canada.——FIG. 20,*1a–c.* \**P. (S.) stubendorffi* (SCHMIDT), northern Siberia; lectotype, herein designated, ×0.7 (Pavlow, 1914, pl. 6, fig. 1a–c).

- P. (Astieriptychites) BODYLEVSKII, 1960, p. 172 (non 1950 MS, nec in VORONETS, 1958a, p. 24, nom. nud.) [\*Astieriptychites astieriptychus BODYLEVSKII, 1960, p. 172 (Polyptychites astieriptychus BODY LEVSKII, 1957, p. 98, nom. nud.); OD] [=Neopolyptychites SHUI'GINA, 1983, p. 85 (type, N. arcticus; OD)]. Cadicones with well-spaced, strong primary nodes on umbilical edge dividing immediately into sheaves of dense, fine secondary ribs as in Olcostephanus. Lower Cretaceous (Lower Valanginian, below P. (Polyptychites)): northern Siberia, northern Canada.——FIG. 21,1a,b. \*P. (A.) astieriptychus (BODYLEVSKII); holotype, X0.7 (Bodylevskii, 1960).
- P. (Euryptychites) PAVLOW, 1914, p. 18 [\*Olcostephanus latissimus NEUMAYR & UHLIG, 1881, p. 159(30); SD WRIGHT, 1957b, p. 348] [=Pseudoeuryptychites JELETZKY, 1986, p. 352 (type, Euryptychites pavlovi VORONETS, 1962, p. 78; OD); Hollwediceras JELETZKY & KEMPER, 1988, p. 86 (type, Polyptychites sphaericus KOENEN, 1902, p. 122; OD); Palaeodichotomites BOGOMO-LOV, 1989, p. 59 (type, Olcostephanus (Polyptychites) triplodiptychus PAVLOW, 1892, p. 480; OD)]. Cadicones with closer umbilical nodes and fewer ribs than in P. (Astieriptychites). Lower Cretaceous (Lower Valanginian): distribution as for genus.-FIG. 20,3a,c. \*P. (E.) latissimus (NEUMAYR & UHLIG), Germany; *a*, *b*, ×0.5; *c*, ×1 (Neumayr & Uhlig, 1881).
- P. (Primitiviptychites) KLIMOVA, 1983, p. 117 [\*Olcostephanus rectangulatum BOGOSLOVSKII, 1902, p. 136; OD]. Small, cadicone, strongly and sharply ribbed microconchs, probably of several subgenera of Polyptychites. Lower Cretaceous (Lower Valanginian): northern Russia, Siberia.——FIG. 20,2a,b. P. (P.) rectangulatum (BOGOSLOVSKII); lectotype, ×1 (Bogoslovskii, 1902).
- P. (Siberites) KLIMOVA in GOL'BERT & KLIMOVA, 1983, p. 149 [\*S. savitzkii; OD]. Compressed, involute, with dense, virgatotome ribbing as in other groups of *Polyptychites*, of which it may be merely a compressed end-member in range of variability. *Lower Cretaceous (Lower Valanginian,* syrzanicus Zone): northern Siberia.——FIG. 21,2. \*P. (S.) savitzkii; holotype, ×1 (Gol'bert & Klimova, 1983).
- P. (Polyptychites) [=Amundiptychites KEMPER & JELETZKY, 1979, p. 3 (type, A. sverdrupi; OD)]. Typically fairly evolute; whorl section moderately compressed to moderately depressed; ribs dense and rather high to sparse, low, and rounded. Early forms medium-sized; later ones becoming large. Occurrence and distribution as for genus.—FIG. 21,3a-c. P. (P.) keyserlingi (NEUMAYR & UHLIG), Lower Valanginian (keyserlingi Zone), northern Germany; a,b, lectotype, ×0.7; c, ×0.5 (Koenen, 1902).—FIG.

21,3*d. P. euomphalus* KOENEN, Lower Valanginian (*keyserlingi* Zone), northern Germany; microconch, X0.7 (Koenen, 1902).

- Dichotomites KOENEN, 1909, p. 9 [\*Ammonites bidichotomus Orbigny, 1841, p. 190; M] [=Bidichotomites SAZONOV, 1951, p. 57, obj., ?lapsus, nom. nud.]. Inner and middle whorls moderately involute, flat-sided, and compressed, with high-arched and narrow venter; outer whorls may become more evolute and round-whorled, but no cadicones or sphaerocones; ribbing dense, with primary ribs short, accentuated on steep umbilical margins; ribbing on inner whorls and microconchs frequently to regularly bidichotomous with 2 distinct levels of bifurcation low and high on whorl side, becoming irregularly polyschizotomous on outer whorls as in ancestral Polyptychites. Macroconchs large to very large (up to 450 mm), only mildly variocostate, retaining at least vestigial dense ribbing to end. Sutures generally with 3 auxiliary lobes, on a rectiradiate (craspeditid) baseline in microconchs, but becoming florid and retracted into an umbilical lobe on outer whorls of macroconchs as these reapproach the more usual perisphinctid mode of coiling. [Boreal, but with considerable southerly spread into sub-Mediterranean province; some local faunas.] NEUMAYR & UHLIG, 1881; THIEULOY, 1977a; KEMPER, 1978. Lower Cretaceous (Upper Valanginian): southern and eastern Paris basin, southern Jura mountains, northern Germany, Pechora region, northern Siberia, northern Canada, British Columbia.
  - D. (Prodichotomites) KEMPER, 1971, p. 52 [\*Polyptychites polytomus KOENEN, 1902, p. 88; OD] [=Ringnesiceras KEMPER & JELETZKY, 1979, p. 5 (type, R. amundense; OD); Elleficeras KEMPER & JELETZKY, 1979, p. 11 (type, Ringnesiceras (E.) ellefense; OD)]. Rather inflated, with convex sides; microconchs becoming evolute; ribbing strong, dense, sharp, with irregular branching. Early forms transitional from Polyptychites, from compressed forms of which they may be barely distinguishable. KEMPER, 1978. Lower Cretaceous (Upper Valanginian, hollwedensis-triptychoides Zones): northern Germany, France, northern Canada.—FIG. 22,2a,b. \*D. (P.) polytomus (KOENEN), *polytomus* Zone, northern Germany; holotype, ×0.5 (Koenen, 1902).
  - D. (Dichotomites). Sides more or less flat, subparallel or convergent; ribbing coarse to fine. Occurrence and distribution as for genus.—
    FIG. 22,1*a-c.* \**D.* (*D.*) bidichotomus (ORBIGNY); *a*, nucleus of macroconch, callidiscus Zone, France, ×0.5 (Thieuloy, 1977a); *b,c*, complete microconch, bidichotomoides Zone, northern Germany, ×0.7 (Kemper, 1978).—FIG. 22,1*d-f. D. (D.) grotriani* NEUMAYR & UHLIG, northern Germany; macroconch (closely resembling syntype of *D. bidichotomus* in ORBIGNY, 1841), *d,e*, ×0.25; *f*, ×0.5 (Neumayr & Uhlig, 1881).
- Homolsomites CRICKMAY, 1930, p. 63 [\**H. poecilotomus;* OD; =*Holcodiscus? stantoni* McLELLAN, 1927,



FIG. 20. Polyptychitidae (p. 30-31)



FIG. 21. Polyptychitidae (p. 31)



FIG. 22. Polyptychitidae (p. 31)

p. 115] [=Wellsia IMLAY, 1957, p. 275 (type, Dichotomites oregonensis ANDERSON, 1938, p. 1; OD)]. Similar to Tollia in its coiling, whorl section, size, and dimorphism, but ribbing and suture like those of Dichotomites; primary ribs dense, rectiradiate, dividing bidichotomously; secondary ribs projected on venter. Suture with long, narrow, and florid lobes. [Either late descendants of Tollia that have independently evolved the bidichotomous ribbing of Dichotomites or, more probably, yet another independent development of a Tollia-like morphology as found previously in such genera as Craspedites (Taimyroceras) and subsequently in Simbirskites (Craspedodiscus). Distribution limited, predominantly in the North Pacific Cordilleran Province.] Lower Cretaceous (Upper Valanginian– Lower Hauterivian): northern Siberia, British Columbia, northern Canada, California, Oregon, Washington.——FIG. 23a–e. \*H. stantoni (MCLEL-LAN), Upper Valanginian, Washington; a–c, holotype, microconch, ×1; d,e, inner whorls and suture of a macroconch, ×1 (Imlay, 1960).——FIG. 23fg. H. oregonensis (ANDERSON), Lower Hauterivian, Oregon; macroconch, ×0.7 (Imlay, 1960).

#### Subfamily PLATYLENTICERATINAE Casey, 1973

[Platylenticeratinae CASEY, 1973, p. 258]

Compressed, involute; venter narrowly tabulate to oxyconic; ribbing subdued or absent; craspeditid sutures highly simplified on straight or only gently curved baseline, with principal lobes little differentiated, squat, and often asymmetrical and broad saddles bearing many auxiliaries. *Lower Cretaceous* (Lower Valanginian–Upper Valanginian).

*Platylenticeras* of the Lower Valanginian is widely distributed but mostly boreal, dominant in northern Germany. Its origins lie in Polyptychitinae (KEMPER, 1961) rather than in Berriasellinae (CASEY, 1973) or in Olcostephanidae (KEMPER, RAWSON, & THIEULOY, 1981). Some small forms of uncertain affinities (*Paquiericeras*) are found in the Valanginian of the northern margins of the Tethys.

- Platylenticeras HYATT, 1900, p. 590 [\*Amaltheus (Oxynoticeras) heteropleurus NEUMAYR & UHLIG, 1881, p. 135; OD] [=Garnieria SANN, 1901, p. 14, non BOURGUIGNAT, 1877, p. 2 (type, A. (O.) heteropleurus NEUMAYR & UHLIG, 1881, p. 135; SD CALLOMON & WRIGHT, herein)]. Rather evolute to very involute, more or less compressed oxycones; early whorls ribbed; later ones smooth; one stock with, the other without umbilical tubercles. Suture asymmetrical, with short element bluntly subdivided. KEMPER, 1961; THIEULOY, 1977a. Lower Cretaceous (Lower Valanginian): England, France, Germany, Switzerland, Czechoslovakia, Poland, ?Spitsbergen, ?Russia (northern Urals).
  - P. (Platylenticeras). Without umbilical tubercles. Occurrence and distribution as for genus.— FIG. 24,2*a*-*c*. \**P*. (*P*) heteropleurum (NEUMAYR & UHLIG), Germany; *a*,*b*, ×0.7 (Neumayr & Uhlig, 1881); *c*, ×1.5 (Kemper, 1961).



FIG. 23. Polyptychitidae (p. 31-34)

- P. (Tolypeceras) HYATT, 1903, p. 103 [\*Ammonites marcousianus PICTET & CAMPICHE, 1859, p. 168 (ORBIGNY, 1850a, p. 65, nom nud.); OD]. Umbilical tubercles present, generally large and rounded. Lower Cretaceous (Lower Valanginian): France, Germany, Switzerland.——FIG. 24, Ia, b. \*P. (T.) marcousianum (PICTET & CAMPICHE), France; ×0.5 (Pictet & Campiche, 1858–1864).
- Delphinites SAYN, 1901, p. 23 [\*D. ritteri; M] [=Pseudogarnieria SPATH, 1923c, p. 307 (type, Oxynoticeras undulatoplicatile STCHIROWSKY, 1894, p. 372; OD); Proleopoldia SPATH, 1923c, p. 307 (type, Hoplites kurmyschensis STCHIROWSKY, 1894, p. 378; OD)]. Early whorls to varying stage with more or less convex sides and tabulate to slightly concave venter bordered by small, opposite clavi; later whorls with lanceolate section and slightly flexed, well-spaced ribs, with or without strong umbilical bullae. THIEULOY, 1977a. Lower Cretaceous (Lower Valanginian): England, France, Russia.----FIG. 24,5a,b. \*D. ritteri, France; ×1 (Sayn, 1901).-FIG. 24,5c,d. D. cf. kurmyschensis (STCHIROWSKY), England; ×1 (Casey, 1973; reprinted by permission of John Wiley & Sons, Ltd., © 1973).-FIG. 24,5e-g. D. kurmyschensis (STCHIROWSKY), Russia; ×0.5 (Stchirowsky, 1894).-FIG. 24,5h-j. D. undulatoplicatile (STCHIROWSKY), Russia; ×0.5 (Stchirowsky, 1894).
- Paquiericeras SAYN, 1901, p. 26 [\*? paradoxum; M]. Small, evolute, with narrowly rounded, fastigiate or sharp venter; smooth or with weak or strong ribs, with or without minute umbilical tubercles. Suture with narrow-necked, ovoid lobes, simple or complex. THIEULOY, 1977a. Lower Cretaceous (upper Lower Valanginian-lower Upper Valanginian): France.
  - P. (Paquiericeras). Flat-sided with narrowly rounded to fastigiate venter; smooth or with very weak lirae and flexuous riblets. Lobes of suture simple. Occurrence and distribution as for genus.——FiG. 24,4*a*,*b*. \**P*. (*P*) paradoxum; ×1.——Fig. 24,4*c*,*d*, *P*. (*P*) paradoxum tuberculatum VERMEULEN, Upper Valanginian, France; ×1 (Vermeulen, 1972).
  - P. (Julianites) THIEULOY, 1977a, p. 407 [\*P. (J.) undulatum; OD]. Oxycones with keel undulating, at least in mature stages; ribs strong and straight, close or distant. Suture more incised than in P. (Paquiericeras) with wider E. Lower Cretaceous (upper Lower Valanginian): France. —FIG. 24,3a,b. \*P. (J.) undulatum (THIEU-LOY); a, X1; b, X3 (Thieuloy, 1977a).

#### Subfamily SIMBIRSKITINAE Spath, 1924

[nom. transl. SPATH, 1931b, p. 546, ex Simbirskitidae SPATH, 1924a, p. 87]

Repeats most characters of various Polyptychitinae but with difference of aspect. Macroconchs large, involute to evolute, compressed to coronate but not cadicone; primary ribs generally with spinate or bullate tubercles on umbilical shoulder or at midside (as in some Stephanoceras or Reineckeia of the Jurassic) giving rise to 2 to 6 secondary ribs, more or less projected on the venter; ribs may weaken or disappear on outer whorls of compressed forms. Microconchs isocostate, ranging from perisphinctoid homeomorphs of Pavlovia (of the Jurassic) to discoidal imitations of Subcraspedites or Tollia. Sutures normally with 3 auxiliary lobes; baseline in macroconchs ascending to second lateral, then retracted to incipient umbilical lobe in evolute forms. Derived from Polyptychitinae, from which separation is arbitrary and depends largely on stratigraphical breaks. Boreal with considerable extensions into sub-Mediterranean provinces. CHERNOVA, 1951, 1952; RAWSON, 1971; IMLAY, 1960. Lower Cretaceous (Lower Hauterivian–Upper Hauterivian).

- Simbirskites PAVLOW, 1892, p. 499 [\*Ammonites decheni F. A. ROEMER, 1841, p. 85; SD ROMAN, 1938, p. 393]. Degree of involution variable between species and with growth; compressed; whorl section rounded or coronate; umbilical bullae more or less prominent, tending in later species to move up sides, and each giving rise to 2 to 4 secondary ribs; secondary ribs fine on inner whorls but coarse, low, and rounded on outer; ribbing variable, in simple bundles or polyptychitine. Suture with broad or narrow saddles. [Subgenera largely intergrade.] Lower Cretaceous (Lower Hauterivian–Upper Hauterivian): northern Eurasia, France, Japan, California, Oregon, northwestern Canada.
  - S. (Hollisites) IMLAY, 1957, p. 276 [\*H. lucasi; OD] [=Hertleinites IMLAY, 1958, p. 1032, nom. nov. pro Hertleinia IMLAY, 1957, p. 275, non MARKS, 1949, p. 457 (type, Neocraspedites aguila ANDER-SON, 1938, p. 156; OD)]. Macroconchs large; inner whorls moderately involute and whorl section subquadrate, compressed; becoming more evolute, perisphinctoid, on outer whorls; ribbing dense; primaries gently curved, untuberculate, branching into polyptychitoid sheaves of secondaries. Microconchs with predominately dichotomous ribs. Suture florid. Early forms probably transitional from *Dichotomites*. IMLAY, 1960. Lower Cretaceous (Lower Hauterivian): California, Oregon.—FIG. 25a-c. \*S. (H.) lucasi (IMLAY), Oregon; holotype, ×0.5 (Imlay, 1960). -FIG. 25d, e. S. (H.) dichotomus (IMLAY), Oregon; holotype, microconch, X1 (Imlay, 1960).——FIG. 26a-c. S. (H.) aguila (ANDERson), California; *a*,*b*, ×0.6, *c*, ×1 (Imlay, 1960).



Fig. 24. Polyptychitidae (p. 35-36)



Fig. 25. Polyptychitidae (p. 36)

S. (Speetoniceras) SPATH, 1924a, p. 76, 87 [\*S. subbipliciforme; OD] [=Subspeetoniceras IVANOV & ARISTOV, 1969, p. 90 (ARISTOV, 1968, p. 174, nom. nud.) (type, Speetoniceras inversioides ARISTOV, 1967, p. 21; OD)]. Up to 60 cm in diameter; moderately to very evolute, with sharp, bullate primary ribs giving rise to 2 or 3 sharp, high, well-spaced secondary ribs; secondary ribs crossing venter with marked forward bend; innermost whorls may be more finely ribbed, foreshadowing S. (Milanowskia), but thereafter whorl section and ribbing remains uniform. Suture with relatively broad saddles. Lower Cretaceous (Lower Hauterivian): England, Heligoland, Spitsbergen, Russia, Oregon.——FIG. 27,2*a,b.* \*S. (S.) subbipliciformis (SPATH), England; holotype, ×1 (Rawson, 1971).——FIG. 27,2*c,d. S.* (S.) inverselobatus (NEUMAYR & UHLIG), Germany; macroconch, ×0.25 (Neumayr & Uhlig, 1881).——FIG. 27,2*e,f. S (S.) inversum* (PAV-LOW), Russia; microconch, ×0.7 (Rawson, 1971).

S. (Simbirskites) [= Thysanotoceras WHITEHOUSE, 1927, p. 109 (type, Ammonites picteti WEERTH, 1884, p. 12; OD); ?Californiceras SHIMIZU, 1931, p. 15 (type, Ammonites traski GABB, 1864, p. 63; OD; type material destroyed, see IMLAY, 1960a, p. 210); Gorodzovia Ivanov & Aristov, 1969, p. 91 (type, G. mosquitini; OD)]. Inflated; whorl section rounded to coronate, at least on middle whorls; short primary ribs branching at prominent spinate or bullate tubercles into 2 to 4 secondary ribs as in Reineckeia. Microconchs reverting to simple or biplicate ribbing on adult body chamber. Occurrence and distribution as for genus.—FIG. 28a-c. \*S. (S.) decheni (ROEMER), Upper Hauterivian, Siberia; ×1 (Pavlow, 1901).—FIG. 28d,e. S. (S.) nodocinctus (WEERTH), Upper Hauterivian, Germany; microconch, ×1 (Weerth, 1884).——FIG. 28f,g. S. (S.) arminius (WEERTH), Upper Hauterivian, Germany; microconch, X1 (Pavlow, 1901).-FIG. 28h. S. (S.) picteti (WEERTH), Upper Hauterivian, Germany; macroconch, ×1 (Weerth, 1884).

S. (Milanowskia) CHERNOVA, 1952, p. 50 [\*Ammonites spetonensis G. M. YOUNG & BIRD, 1828, p. 265; OD (original spelling)] [=Pavlovites IVANOV & ARISTOV, 1969, p. 88 (type, Speetoniceras polyptychoides ARISTOV, 1967, p. 18; OD)]. More or less compressed; short primary ribs branching at subdued tubercles into 2 to 5 generally close and low secondary or intercalated ribs. Occurrence and distribution as for genus.—FIG. 27, 1a, b. \*S. (M.) spetonensis (YOUNG & BIRD),

Upper Hauterivian, England;  $\times 1$  (Howarth, 1962).

S. (Craspedodiscus) SPATH, 1924a, p. 77 [\*Ammonites clypeiformis JUDD, 1867, p. 246, non OR-BIGNY, 1841, p. 137; OD; a deliberate misapplication under Article 70(c), and type thereby becomes \* Craspedodiscus clypeiformis SPATH, 1924a, p. 77 [Article 70(c)(i)], of which S. (C.) juddi Rawson, 1971, p. 62 is a junior synonym; S. (C.) juddi RAWSON is available to replace it. However, S. (C.) clypeiforme SPATH is probably a subjective synonym of Ammonites discofalcatus LAHUSEN, 1874, p. 67] [=Hannoverites KEMPER, 1968, p. 148, nom. nud.]. Inner whorls involute, compressed, flat-sided, with narrowly arched, densely ribbed venter; primary ribs dividing indistinctly into sheaves of many fine secondary ribs; lateral tubercles very fine or absent. Outer whorls of macroconchs becoming evolute in early forms but remaining involute and becoming acute in later forms; in some later forms venter almost carinate, the whole shell discoidal; ribbing becoming subdued or disappearing. RAWSON, 1971. Lower Cretaceous (Upper Hauterivian): England, northern Germany, Russia.——FIG. 27, 3a, b. \*S. (C.) clypeiformis SPATH, England; holotype, ×0.5 (Rawson, 1971).-FIG. 27, 3c-e. S. (C.) discofalcatus (LAHUSEN), Russia; ×0.5 (Pavlow, 1901).



Fig. 26. Polyptychitidae (p. 36)



Fig. 27. Polyptychitidae (p. 38-39)



Fig. 28. Polyptychitidae (p. 38-39)

#### Family OOSTERELLIDAE Breistroffer, 1940

[nom. transl. WRIGHT, 1957b, p. 362, ex Oosterellinae BREISTROFFER, 1940, p. 143(73)]

Keeled, strongly ribbed, more or less compressed derivatives of Platylenticeratinae. VERMEULEN, 1972; COMPANY, 1987. Lower Cretaceous (Upper Valanginian–Lower Hauterivian).

- Oosterella KILIAN, 1911, p. 117, nom. nov. pro Nicklesia KILIAN, 1910c, p. 226, non HYATT, 1903, p. 138 [\*Ammonites cultratus ORBIGNY, 1841, p. 145; SD ROMAN, 1938, p. 345]. Involute, compressed, with high keel that may undulate; ribs strong, blunt, irregularly simple and branching; point of furcation may rise with growth and may form prominent midlateral tubercles. Lower Cretaceous (Upper Valanginian-Lower Hauterivian): France, Spain, Germany, Switzerland, Austria, Morocco, Algeria, Mexico, Columbia.—FIG. 29, Ia, b. \*O. cultrata (ORBIGNY), Lower Hauterivian, France; ×0.5 (Orbigny, 1840–1842).
- Pseudosterella SPATH, 1924a, p. 88 [\*Mortoniceras fischeri NICKLES, 1892, p. 191; SD ROMAN, 1938, p. 346]. Compressed, evolute, with stout, serrated keel; ribs strong, simple, rectiradiate, and sharply projected on shoulders. Homeomorph of Amoebites (Lower Kimmeridgian). Lower Cretaceous (Upper Valanginian): Spain, France, Columbia.—FIG. 29,2a,b. \*P. fischeri (NICKLES); X3 (Nicklès, 1892).

## Family OLCOSTEPHANIDAE Haug, 1910

[Holcostephanidae HAUG, 1910, p. 1167 (incorrect original spelling); ICZN Opinion 575, 1959, Family-Group Name No. 281]

Round-whorled to moderately compressed, normally with strong constrictions. Ribs typically bundled at umbilical tubercles, but some genera with single ribs. Inner whorls and dwarf genera may have lateral or ventrolateral tubercles. Strongly dimorphic; microconchs with long, spatulate lappets. Primitive subfamily Spiticeratinae includes members that overlap Olcostephaninae morphologically, and the latter are presumably derived from the former. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Lower Hauterivian).

PAVLOW (1892, p. 470) used the term Olcostephanini to cover a wide range of species referred by some authors to several genera. He in fact referred them all to *Olcostephanus*, distributing them in several subgenera. Olcostephanini must be treated



Fig. 29. Oosterellidae (p. 42)

as a plural noun referring to members of a genus under Article 11(f)(i)(2) of the *International Code of Zoological Nomenclature* (3rd Edition). Since it was not accepted generally as a family name, as required by Article 11(f)(iii), it does not take priority over Olcostephanidae HAUG, 1910.

## Subfamily SPITICERATINAE Spath, 1924

[*nom. transl.* ARKELL & WRIGHT, 1957 in ARKELL, KUMMEL, & WRIGHT, p. 345, *ex* Spiticeratidae SPATH, 1924a, p. 89]

Whorls rounded or higher than wide, moderately evolute, with strong, normally curved constrictions; early whorls commonly with primary ribs bearing lateral tubercles (at which ribs branch) and with ventral groove bordered, in some, by ventrolateral tubercles; later whorls having umbilical bullae with 2 to 4 bundled, prorsiradiate ribs branching again irregularly and crossing venter in obtuse chevrons or transversely; in some ornament weakening or disappearing at varying stages. Suture in some with strongly retracted suspensive lobe. UHLIG, 1903, 1910c; DJANÉLIDZÉ, 1922b. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Upper Berriasian).

- Proniceras BURCKHARDT, 1919, p. 40 [\*Ammonites pronus OPPEL, 1865, p. 554; SD ROMAN, 1938, p. 381]. Rather small; inner whorls with ribs simple or bifurcating high up side, strongly curved, and without tubercles; later whorls with curved umbilical bullae and simple, biplicate or triplicate ribs; ornament may weaken on body chamber. Upper Jurassic (Upper Tithonian): southern and central Europe, northern Africa, Madagascar, Iraq, Iran, Pakistan, California, Mexico.—FIG. 30,2a,b. \*P. pronus OPPEL, Poland; lectotype designated herein, ×1 (Zittel, 1868, pl. 15, fig. 8a,b).
- Simospiticeras OLORIZ & TAVERA, 1979, p. 183 [\*S. lojense; OD]. Evolute; whorl section subquadrate to trigonal, almost keeled at middle growth stages; ornament poorly known because of bad preservation, but blunt umbilical nodes and ventral ribs in forwardly pointing chevrons are visible; lateral ornament not preserved; 3 or 4 curved constrictions to a whorl. [Genus is one of the earliest Spiticeratinae and may be a link with Simoceratidae.] Upper Jurassic (basal Upper Tithonian): Spain.—Fig. 30, 1a, b. \*S. lojense; holotype, ×0.75 (Oloriz & Tavera, 1979).
- Umiaites SPATH, 1931b, p. 546 [\*U. rajnathi; OD]. Poorly known from specimens still septate at 100 mm diameter. Close to Proniceras but largest known specimen septate, with whorl compressed and nearly smooth. Upper Jurassic (Upper Tithonian): India (Kachchh).——FIG. 30,3a,b. \*U. rajnathi SPATH; holotype, X0.7 (Spath, 1931b).
- Spiticeras UHLIG, 1903, p. 83 [\*Ammonites spitiensis BLANFORD, 1863, p. 131; SD ROMAN, 1938, p. 380] [=Somaliceras SPATH, 1925b, p. 145 (type, S. isariforme; OD)]. Inner whorls inflated, with ribs branching from midlateral tubercles; later whorls inflated to compressed or subquadrate, with fine ribs branching from umbilical tubercles, but some species tending to become smooth; curved constrictions generally present. Suture with more or less strongly developed suspensive lobe. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Berriasian): southern and central Europe, northern Africa, Somalia, Madagascar, Iraq, Yemen, Pakistan, India, California, Mexico, Cuba, Argentina, Chile.
  - S. (Spiticeras) [=Bihenduloceras SPATH, 1925b, p. 152 (type, B. gregoryi; M)]. Inner whorls coronate with lateral tubercles, followed from diameter of 10 to 30 mm by bituberculate stage with umbilical and lateral tubercles, then lateral tubercles fading; ribs bifurcate from the lateral tubercles, then later issuing in bundles from the umbilical tubercles; some species tending to become smooth. Outer whorls with high, narrowly rounded venter or subquadrate. Occurrence and distribution as for genus.—FIG. 31, *1a–d. \*S. (S.) spitiense* (BLANFORD), Berriasian, India (Spiti Valley); *a,b*, holotype, ×0.5; *c,d*, paratype, ×0.5

(Uhlig, 1903).——FIG. 31,*Ie*,*f. S. (S.) gregoryi* (SPATH), Berriasian, Somalia; ×0.5 (Spath, 1925b).

- S. (Kilianiceras) DJANELIDZE, 1922b, p. 49 [\*Stephanoceras damesi STEUER, 1897, p. 193(67); SD ROMAN, 1938, p. 382]. Evolute up to large size; whorl section rounded; ornament coarse; bituberculate stage much more persistent than in S. (Spiticeras). Occurrence as for genus: France, Madagascar, Argentina, ?California.— FIG. 31,2a,b. \*S. (K.) damesi (STEUER), Berriasian, Argentina; holotype, ×0.5 (Steuer, 1897).
- Negreliceras DJANÉLIDZÉ, 1922b, p. 49 [\*Ammonites negreli MATHERON, 1880 in 1878–1880, pl. B-27; SD ROMAN, 1938, p. 382] [=Praenegreliceras COL-LIGNON, 1960, explanation of pl. 164, fig. 663, nom. nud. because no differentia was given and no type species designated]. Compressed from early stage and without lateral tubercles; fine ribs branching from umbilical bullae, but later whorls tending to become smooth. Suture with strongly retracted suspensive lobe. Upper Jurassic (Upper Tithonian)– Lower Cretaceous (Lower Berriasian): southern and central Europe, Tunisia, Pakistan, Madagascar, California, Mexico, Argentina.——FIG. 31,3a,b. \*N. negreli (MATHERON), Lower Berriasian, France; ×0.75 (Djanélidzé, 1922b).
- Groebericeras A. F. LEANZA, 1945, p. 82 [\*G. bifrons; OD; =Ammonites rocardi POMEL, 1889, p. 65]. Moderately involute, becoming more evolute with age; whorl section compressed to rounded, widest at umbilical margin, tapering to narrowly rounded venter; ribs curved, prorsiradiate, and single with intercalated secondaries, ribs tending to weaken and in some to disappear on outer whorls; constrictions following course of ribs; umbilical, lateral, and ventrolateral tubercles may be present up to small diameters. Suspensive lobe of suture not markedly retracted. Lower Cretaceous (?Lower Berriasian, Upper Berriasian): Spain, Algeria, Iraq, Nepal, Argentina. ——FIG. 31, 4a, b. \*G. rocardi (POMEL), ?Lower Berriasian, Argentina; lectotype of G. bifrons LEANZA, X0.75 (A. F. Leanza, 1945).
- ?Aspidostephanus SPATH, 1925b, p. 144 [\*Holcostephanus depressus STEUER, 1897, p. 192(66); OD]. Inflated and depressed to coronate, with broad, smooth venter; early whorls with strong, distant ribs bearing umbilical and lateral tubercles, but later whorls smooth except for umbilical tubercles and whorl height increasing. Upper Jurassic (?Tithonian)-Lower Cretaceous (Berriasian): France, Balearic Islands, northern Africa, Argentina.— FIG. 30,4a-c. \*A. depressus (STEUER), Berriasian, Argentina; ×0.7 (Steuer, 1897).

#### Subfamily OLCOSTEPHANINAE Haug, 1910

[Olcostephaninae HAUG, 1910, p. 1167] [=Taraisitinae A. CANTU-CHAPA, 1966, p. 16; ?Provalanginitinae FATMI, 1972, p. 351]

Moderately involute to moderately evolute, compressed to globular or cadicone; generally primary ribs splitting on umbilical © 2009 University of Kansas Paleontological Institute



FIG. 30. Olcostephanidae (p. 43)

shoulder at spine or bulla into sheaf of secondary ribs that cross venter without interruption; strong constrictions normally present at some stage of growth. Typical forms include large macroconchs with simple apertures and smaller, lappeted microconchs. Subfamily also includes succession of dwarf genera with specialized ribbing and tuberculation on outer whorls, derived from different species of *Olcostephanus* or other genera. *Upper Jurassic* 



Fig. 31. Olcostephanidae (p. 43) © 2009 University of Kansas Paleontological Institute

# (?Tithonian)–Lower Cretaceous (Lower Valanginian–Lower Hauterivian).

- Olcostephanus NEUMAYR, 1875b, p. 922, ICZN Opinion 575 [\*Ammonites astierianus ORBIGNY, 1840, p. 115; OD] [=Holcostephanus SAYN, 1889, p. 679, illegit. emend., ICZN Rejected Name no. 1301; Astieria PAVLOW, 1892, p. 471, obj. (type, Ammonites astierianus ORBIGNY, 1840, p. 115; SD WRIGHT, herein)]. Rather evolute to rather involute, compressed to globose or cadicone, with wellrounded venter; short primary ribs on umbilical wall, with or without umbilical bullae or spines, giving rise to 2 or more straight or slightly curved, radial, rursi- or prorsiradiate secondary ribs; additional secondary ribs may be intercalated; secondary ribs may, rarely, branch but are never virgatotome; marked constrictions with collared ribs, oblique to other ribs, present in early stages of macroconchs or throughout. Macroconchs with simple, collared apertures; microconchs with short to long, spatulate lappets. Lower Cretaceous (Lower Valanginian-Lower Hauterivian): Europe, southern Africa, eastern Africa, Madagascar, Pakistan, Mexico, Colombia, Peru.
  - O. (Olcostephanus) [=Subastieria SPATH, 1923d, p. 32 (type, Olcostephanus (Astieria) sulcosus PAV-LOW, 1892, p. 499; OD); Rogersites SPATH, 1924a, p. 75; (type, Holcostephanus modderensis KITCHIN, 1908, p. 202; OD; =H. rogersi KITCHIN, 1908, p. 201); Taraisites A. CANTU-CHAPA, 1966, p. 16 (type, T. boesi; OD); Satoites A. CANTU-CHAPA, 1966, p. 16, nom. nud. (type, S. oshimense, nom. nud.; OD); Lemurostephanus THIEULOY, 1977a, p. 432 (type, O. madagascariensis LEMOINE, 1906, p. 182; OD); Jeanthieuloyites COOPER, 1981, p. 260 (type, Rogersites quinquestriatus BESAIRIE, 1936, p. 142; OD)]. Ribbing sharp and dense to coarse and distant; umbilical tubercles present. Occurrence and distribution as for genus.——FIG. 32a,b. \*O. (O.) astierianus (ORBIGNY), Upper Valanginian, France; lectotype, macroconch, X0.75 (Cooper, 1981).--FIG. 32c,d. O. (O.) atherstoni (SHARPE), Upper Valanginian, Germany; microconch, ×0.75 (Neumayr & Uhlig, 1881).-FIG. 32e, f. O. (O.) sulcosus PAVLOW, Lower Hauterivian, England; holotype, X1 (Pavlow, -FIG. 32g,h. O. (O.) rogersi (KITCHIN), 1892).---Upper Valanginian, southern Africa; holotype, macroconch, ×0.5 (Kitchin, 1908). -—Fig. 32i. O. (O.) madagascariensis LEMOINE, Upper Valanginian, Madagascar; holotype, ×0.75 (Collignon, 1962a).
  - O. (Mexicanoceras) IMLAY, 1938, p. 562 [\*M. kanei; OD] [=Maderia IMLAY, 1938, p. 557 (type, M. coronata; OD)]. Tending to have smooth siphonal band, typically forming distinct groove, but significance uncertain as probably all figured specimens are nuclei. [Maderia comprises coronate forms with less distinct smooth band.] Lower Cretaceous (Lower Hauterivian): Mexico.——FIG. 33,1a-c. \*O. (M.) kanei; X1 (Imlay, 1938).

- O. (Jeannoticeras) THIEULOY, 1965, p. 212 [\*Ammonites jeannotii ORBIGNY, 1841, p. 188; OD]. Compressed; pairs of secondary ribs branching from barely bullate primary ribs and separated by single intercalatory. Lower Cretaceous (Upper Valanginian–Lower Hauterivian): Europe, Tanzania, Oregon, Mexico.——FIG. 33,2a-d. \*O. (J.) jeannotii (ORBIGNY), Lower Hauterivian, France; a, b, X1 (Orbigny, 1840); c, macroconch and d, microconch, X1 (courtesy of L. Bulot).
- Baronnites BULOT, COMPANY, & THIEULOY, 1990, p. 403 [\*Saynoceras hirsutum FALLOT & TERMIER, 1923, p. 41; OD]. Dwarf; inner whorls as in Olcostephanus; ribs gradually fading on venter and strong umbilical and ventral tubercles appearing. Lower Cretaceous (Lower Valanginian): Spain, France.
- Saynoceras MUNIER-CHALMAS in MUNIER-CHALMAS & DE LAPPARENT, 1894, p. 464 [\*Ammonites vertucosus ORBIGNY, 1841, p. 191; OD]. Dwarf, involute; inner whorls inflated, smooth or with weak ribs; outer whorls trapezoidal in section, with variable, sharp lateral and ventrolateral tubercles, opposite or alternate on venter, appearing suddenly by thickening of ribs. Aperture of microconchs with long lappets. Suture with wide, short elements. THIEULOY, 1965. Lower Cretaceous (Lower Valanginian–Upper Valanginian): France, Spain, Balearic Islands, Germany, Mexico.——FIG. 34,4a,b. \*S. vertucosum (OR-BIGNY), France; ×1 (Fallot & Termier, 1923).
- Parastieria SPATH, 1923b, p. 144 [\*Acantoceras? peltoceroides PAVLOW, 1892, p. 510; OD]. Dwarf; inner whorls as in O. (Olcostephanus), with 2 or 3 secondary ribs arising from slight umbilical bullae; outer whorl high and compressed, with straight or slightly sinuous, distant, high, flat-topped ribs and no tubercles. Aperture of microconchs with long, spatulate lappets. Lower Cretaceous (Lower Hauterivian): England.——FIG. 34,3a,b. \*P. peltoceroides (PAVLOW); ×1 (Pavlow, 1892).
- Capeloites LISSON, 1937, p. 3 [\*C. larozai; OD; =Ammonites perelegans MATHERON, 1878, pl. C-21, fig. 3]. Dwarf; outer whorl compressed with narrow, rounded venter, in early whorls umbilical bullae pinched, with coarse and fine ribs branching irregularly; in later whorls umbilical bullae weakening and all ribs fine; aperture of microconch collared with broad, spatulate lappets. Lower Cretaceous (?Lower Hauterivian): France, Peru. FIG. 34,2a,b. \*C. perelegans (MATHERON), Peru; X1 (Thieuloy, 1969).
- Ceratotuberculus IMLAY, 1938, p. 568 [\**C. casitensis;* OD]. Dwarf; inner whorls as in *Olcostephanus;* outer whorls high, compressed, with prominent umbilical and ventrolateral bullae joined by bundled, looped, or zigzagged ribs; venter more oo less grooved. *Lower Cretaceous (Lower Hauterivian):* Mexico.——FIG. 34,5*c, d. \*C. casitensis;* ×1 (Imlay, 1938).——FIG. 34,5*c, d. C. linguituberculatus* IMLAY; ×1 (Imlay, 1938).
- Valanginites KILIAN, 1910c, p. 196 [\*Ammonites nucleus F. A. ROEMER, 1841, p. 87 (non PHILLIPS, 1829, p. 174; see ICZN Opinion 1610, 1990); SD ROMAN, 1938, p. 386] [=Rotundites Stolley, 1937,



FIG. 32. Olcostephanidae (p. 46)

p. 450, nom. nud.; Dobrodgeiceras NIKOLOV, 1963, p. 94, nom. nov. pro Dobrodgeites NIKOLOV, 1962, p. 69, non KITTL, 1908, p. 522 (type, Dobrodgeites ventrotuberculatus NIKOLOV, 1962, p. 70; OD; =Holcostephanus wilfridi KARAKASCH, 1902, p. 14)]. Small, very involute sphaerocones with elliptical umbilicus and oblique, constricted, and collared aperture; ornament ranging from very weak, straight, bundled or bidichotomous ribs with or without slight umbilical bullae to coarse, blunt, concave primary ribs branching at midside, with or without a large tubercle, into 3 to 6 strong secondary ribs; variably with (Dobrodgeiceras) or without large siphonal tubercles on some ribs on later part of body chamber. THIEULOY & GAZAY, 1967; RICCARDI & WESTERMANN, 1970. Lower Cretaceous (Lower

Valanginian–Upper Valanginian): France, Germany, Switzerland, Bulgaria, Ukraine (Crimea), Peru, Argentina.—FIG. 34, *1a,b.* \* V. nucleus (ROEMER), Upper Valanginian, Germany; ×1 (Koenen, 1902).—FIG. 34, *1c,d. V. wilfridi* (KARAKASCH), Upper Valanginian, Bulgaria; ×1 (Nikolov, 1962).

Provalanginites FATMI, 1972, p. 351 [\*P. rhodesi; OD]. Excentrumbilicate sphaerocones agreeing in all respects with Valanginites KILIAN. [But recorded from more than one locality in the lowest of three members of the Chichale Formation of Pakistan. Provalanginites is found at least 15 meters below the top, in beds said to be Kimmeridgian to Upper Tithonian, and apparently associated with Proniceras and lying below Himalayites, and is succeeded, however, by the middle member, most of which is



Upper Valanginian with abundant *Olcostephanus* but not, apparently, *Valanginites*. The genus has not been recorded from the Tithonian anywhere else, and there are no known plausible Tithonian relatives. The stratigraphic position needs reconfirmation]. *Upper Jurassic (?Tithonian):* Pakistan.

#### Family HOLCODISCIDAE Spath, 1923

[Holcodiscidae SPATH, 1923d, p. 35] [=Astieridiscidae TZANKOV & BRESKOVSKI, 1982, p. 492; Metahoplitidae TZANKOV & BRESKOVSKI, 1982, p. 492]

Moderately involute with rounded, rectangular, or depressed whorl section; straight or sinuous, fine, dense ribs typically continuing over venter and may be periodically truncated by oblique, enlarged ribs, with or without umbilical, lateral, and ventrolateral tubercles. Suture rather simple. *Lower Cretaceous (?Middle Hauterivian, Barremian).* 

Probably derived from Olcostephaninae from which distinction is doubtful; separation into subfamilies, on the lines of the families of TZANKOV & BRESKOVSKI (1982), may be found to be useful.

- ?Holcoptychites GERTH, 1921, p. 143 [\*Polyptychites neuquensis R. DOUVILLÉ, 1910, p. 10; SD WRIGHT, 1957b, p. 371]. Whorl section with convergent, convex sides; constrictions rather numerous and straight, bordered by prominent, rounded ribs; primary ribs single or branching from umbilical bullae; most ribs branching again at midflank; ribs may disappear on outer whorls. H. A. LEANZA & WIED-MANN, 1980. Lower Cretaceous (Middle Hauterivian): Argentina.——FiG. 35,2a,b. \*H. neuquensis (DOUVILLÉ), X0.7 (R. Douvillé, 1910).
- Astieridiscus KILIAN, 1910c, p. 265 [\*Holcodiscus morleti KILIAN, 1889a, p. 676; SD ROMAN, 1938, p. 389]. Sides slightly flattened; venter rounded; with dense, sharp, slightly flexuous, simple or branching ribs but no umbilical or other tubercles except on innermost whorls. Superficially resembles Olcostephanus. Lower Cretaceous (Barremian): France, Spain, Balearic Islands.—FIG. 35,3a,b. \*A. morleti (KILIAN), France; X1 (Kilian, 1889a).
- Holcodiscus UHLIG, 1882a, p. 86, 93 [\*Ammonites caillaudianus ORBIGNY, 1850a, p. 99; OD]. Circular to rectangular whorl section; fine, low, straight or flexuous, simple or branched ribs, periodically truncated by thin, high, enlarged ribs bearing lateral and ventrolateral tubercles; inner whorls tending to have depressed whorl section and to resemble Olcostephanus. Lower Cretaceous (Barremian): central and southern Europe, California, Mexico.——FIG. 35,4a,b. \*H. caillaudianus (ORBIGNY), France; X1 (Kilian, 1889a).
- Almohadites WIEDMANN, 1966b, p. 66 [\*A. subcamelinus; OD]. Similar to Holcodiscus but with simplifying suture and ventral furrow between rib



FIG. 34. Olcostephanidae (p. 46-47)

endings. Lower Cretaceous (Lower Barremian): central and southern Europe.——FIG. 35, 5a-c. \*A. subcamelinus, Spain;  $a, b, \times 2$ ; c, enlarged (Wiedmann, 1966b).

- Parasaynoceras BREISTROFFER, 1947b, p. 92(76) [\*Ammonites horridus ORBIGNY, 1850a, p. 100; OD]
  [=?Neoastieria OBATA & MATSUKAWA, 1984, p. 172 (type, Astieria cadoceroides KARAKASCH, 1907, p. 127; OD)]. Depressed offshoot of Holcodiscus with very large lateral and ventrolateral spines, each covering several fine, sharp ribs. [Neoastieria is probably transitional from Holcodiscus.] Lower Cretaceous (Barremian): France, ?]apan, Mexico, Colombia.
  ——FIG. 35,6a,b. \*P. horridum (ORBIGNY); a, France; X1 (Cottreau, 1937); b, Colombia, X1 (Etayo-Serna, 1968).
- Metahoplites SPATH, 1924a, p. 84 [\*Ammonites henoni COQUAND, 1880, p. 369; M]. Involute (evolute forms are probably distinct generically), compressed, rather high-whorled, with venter flattened sooner or later; dense, fine ribs branching near umbilicus. Lower Cretaceous (Barremian): France, Balearic Islands, northern Africa.
  - M. (Metahoplites). Venter flat from early stage; at first with ribs uniting in twos and threes at small ventrolateral clavi; later whorls with no clavi and ribs crossing venter transversely; no constrictions

on later whorls. Occurrence and distribution as for genus.——FIG. 35,7*a*–*d*. \**M*. (*M*.) henoni (COQUAND), Tunisia; ×1 (Sayn, 1891).

- M. (Medjeziceras) BUSNARDO & DAVID, 1957, p. 110 [\*Spitidiscus (Medjeziceras) collignoni; OD]. Retaining rounded venter later than M. (Metahoplites); later whorls with concave venter having smooth, sharp edges; constrictions throughout. Lower Cretaceous (Lower Barremian): Algeria.—FIG. 35, 1a-c. \*M. (M.) collignoni (BUSNARDO & DAVID); X2 (BUSNARDO & David, 1957).
- ?Gymnoplites SPATH, 1933a, p. 828 [\*G. simplex; OD]. Poorly known. Outer whorl smooth. Possibly related to Astieridiscus. Lower Cretaceous (?Barremian): western India.

#### Family NEOCOMITIDAE Salfeld, 1921

[nom. transl. SPATH, 1923d, p. 31, ex Neocomitinae SALFELD, 1921, p. 347] [=Palaeohoplitidae ROMAN, 1938, p. 319, nom. nud. because not named after an included genus]

A very varied family characterized by tendency to become compressed and flat-sided with tabulate or grooved venter. Primitive forms differing little from many earlier Perisphinctaceae, but different genera developing umbilical, lateral, or ventrolateral tubercles in various combinations. Initially ribs simple at umbilical margin and bifurcating on outer part of sides (Berriasellinae), but in Neocomitinae ribs branching both at umbilical margin and again on outer part of sides. Slight changes in the suture at the umbilical seam mark a third subfamily (Endemoceratinae), which may well not be monophyletic. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Upper Hauterivian, ?Lower Barremian).

#### Subfamily BERRIASELLINAE Spath, 1922

[nom. transl. ROMAN, 1938, p. 324, ex Berriasellidae SPATH, 1922a, p. 111]

The primitive subfamily, more or less compressed, with ribs single at umbilical margin, branching halfway or more up sides; venter tabulate or grooved at least at some stage of growth; with no tubercles or with some combination of umbilical, midlateral, and ventrolateral tubercles. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Upper Berriasian, ?Lower Valanginian).

- Berriasella UHLIG, 1905, p. 601 [\*Ammonites privasensis PICTET, 1867, p. 84; SD ROMAN, 1938, p. 324] [=Stenoceras UHLIG, 1911, p. 354, non OR-BIGNY, 1849, p. 287 (type, Hoplites storrsi STANTON, 1895, p. 79; M); Parodontoceras SPATH, 1923c, p. 305 (type, Hoplites callistoides BEHRENDSEN, 1891, p. 402; OD); Picteticeras LE HÉGARAT, 1973, p. 67, nom. nud. because no type species designated; Hegaratella NIKOLOV & SAPUNOV, 1977, p. 102 (type, Berriasella paramacilenta MAZENOT, 1939, p. 127; OD)]. More or less compressed but generally with convex sides; ribbing distinct and sharp, biplicate or simple, not modifying until close to aperture; venter with narrow, smooth band or groove at least on early whorls. GRIGORIEVA, 1938; LE HÉGARAT, 1973; MAZENOT, 1939; NIKOLOV, 1966a; UHLIG, 1903–1910. Upper Jurassic (Upper Tithonian)-Lower Cretaceous (Berriasian): southern and central Europe, northern Africa, Madagascar, Turkey, Ukraine (Crimea), Iran, Himalayas, New Caledonia, New Zealand, California, Mexico, Cuba, Argentina.
  - B. (Berriasella). No tubercles. Occurrence and distribution as for genus.—FIG. 36, *Ia,b.* \*B. (B.) privasensis (PICTET), Upper Tithonian, France; lectotype, ×0.75 (Mazenot, 1939).—FIG. 36, *Ic,d. B. (B.) callistoides* (BEHRENDSEN), Upper Tithonian, Argentina; holotype, ×0.7 (Mazenot, 1939).

- B. (Elenaella) NIKOLOV, 1966, p. 640 [\*B. cularensis MAZENOT, 1939, p. 75; OD] [=?Delphinella LE HÉGARAT, 1971, p. 852 (type, Hoplites delphinensis KILIAN, 1889c, p. 662; OD)]. Inner whorls as in B. (Berriasella) but slightly more evolute; outer whorls, at least of macroconchs, with umbilical tubercles developing and ribs disappearing. Occurrence as for genus: France. —FIG. 36,2a,b. \*B. (E.) cularensis, Upper Tithonian, France; holotype, ×1 (Mazenot, 1939).
- Substeueroceras SPATH, 1923c, p. 305 [\*Odontoceras koeneni STEUER, 1897, p. 171(45); OD]. Ribbing fine and dense, with secondaries branching at midside, transverse and not interrupted on tabulate venter. Upper Jurassic (Upper Tithonian): ?Somalia, Iraq, Iran, California, Mexico, Peru, Argentina.
   —FIG. 36,4a-c. \*S. koeneni (STEUER), Argentina; X0.4 (Steuer, 1897).
- Andiceras KRANTZ, 1928, p. 37 [\*A. trigonostomum; SD ARKELL in ARKELL, KUMMEL, & WRIGHT, 1957, p. 352]. Very evolute, with wiry, simple, and widely biplicate ribs, not projected; venter narrow, deeply grooved. Upper Jurassic (Upper Tithonian): Paraguay.——FIG. 36,5a,b. \*A. trigonostomum; X0.7 (Krantz, 1928).
- Parandiceras SPATH, 1939a, p. 76 [\**P. rota;* OD]. Very evolute, compressed; ribs fine, simple or bifurcating at midside, ending in small ventrolateral tubercles bordering narrow venter with narrow groove; with shallow constrictions. *Lower Cretaceous (Berriasian or Lower Valanginian):* Pakistan, Argentina.— FIG. 36, *3a, b.* \**P. rota,* Pakistan; ×0.5 (Spath, 1939a).
- Riasanites SPATH, 1923c, p. 306 [\*Ammonites rjasanensis LAHUSEN, 1883, p. 69; OD] [=Tauricoceras KVANTALIANI & LYSENKO, 1979, p. 629 (type, T. crassicostatum; OD]. Compressed; ribs strong, coarsely biplicate; venter with smooth band or grooved. Lower Cretaceous (Lower Ryazanian, Berriasian): Russia, Ukraine (Crimea), ?Turkey, ?Mexico, ?Argentina.—FIG. 37,3a,b. \*R. rjasanensis (LAHUSEN), Lower Ryazanian, Russia; ×0.7 (Nikitin, 1888).
- Blanfordiceras COSSMANN, 1907, p. 64, nom. nov. pro Blanfordia UHLIG, 1905, p. 602, non ADAMS, 1863, p. 424 [\*Ammonites wallichi GRAY, 1832, pl. 100, fig. 3] [=Blanfordiceras SPATH, 1923e, p. 16, obj. syn. and hom.; Pseudoblanfordia SPATH, 1925b, p. 145 (type, Hoplites australis BURCKHARDT, 1903, p. 64; OD)]. Like Berriasella but inflation greater, ribs more projected on shoulders and minutely tuberculate on either side of stronger and more persistent ventral groove; ribs becoming stronger and more widely spaced on body chamber. Upper Junssic (Upper Tithonian): Pakistan, Himalayas, Indonesia, New Guinea, California, Argentina.——FIG. 38, I.a, b. \* B. wallichi (GRAY), India (Spiti Valley); holotype, BMNH C.5041, ×0.7 (new).
- Malbosiceras GRIGORIEVA, 1938, p. 102 [\*Ammonites malbosi PICTET, 1867, p. 77; OD] [=Pomeliceras GRIGORIEVA, 1938, p. 103, non HOEDEMAKER, 1981, p. 246 (type, Ammonites breveti POMEL, 1889, p. 74; OD); Mazenoticeras NIKOLOV, 1966a, p. 641 (type,



FIG. 35. Holcodiscidae (p. 48-49)

Berriasella broussi MAZENOT, 1939, p. 91; OD); Retowskiceras NIKOLOV, 1966a, p. 641 (type, Perisphinctes andrussovi RETOWSKI, 1893, p. 257(52); OD); Chapericeras HOEDEMAKER, 1981, p. 245 (type, Ammonites chaperi PICTET, 1868, p. 242; OD)]. Inner whorls much as in Berriasella with venter variably rounded, truncated, or feebly grooved; at varying stage in midgrowth midlateral tubercles appearing later; intercalated ribs without tubercles are confined or not to outer third of side. [Some synonyms may be useful as subgenera, but variation between type species seems to be continuous.] Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Upper Berriasian): southern Europe, northern Africa, Madagascar.—FIG. 37,2a–c. \*M. malbosi (PICTET), Berriasian, France; holotype, ×0.5 (Mazenot, 1939).

Protacanthodiscus SPATH, 1923c, p. 305 [\*Hoplites andreae KILIAN, 1889c, p. 670; OD]. Inner whorls as in Berriasella, but lateral tubercles may appear on some ribs; middle and outer whorls with some distant, bituberculate primary ribs irregularly branching at later tubercles, with many intercalatories and

51



FIG. 36. Neocomitidae (p. 50)

untuberculate primaries; venter with smooth band, in some bordered by incipient small bullae, in others by parabolic nodes. *Upper Jurassic (Upper Tithonian)*: southern Europe, northern Africa, Ukraine (Crimea), Pakistan, California, Mexico, Peru, Argentina.——FIG. 37, *Ia, b. \* P. andreae* (KILIAN), Spain; holotype, ×0.7 (Mazenot, 1939). Chigaroceras HOWARTH, 1992, p. 641 [\*C. banikense; OD]. Involute, compressed, with rounded venter; umbilical wall undercut, umbilical edge well defined; primary ribs arising mostly from small umbilical tubercles, rectiradiate or slightly prorsiradiate, branching into 2 or 3 secondaries at midflank, mostly at distinct midlateral tubercles. Upper Jurassic (Upper Tithonian): Iraq.——FIG. 37,4a,b. \*C. banikense; holotype, X0.75 (Howarth, 1992).

Neocosmoceras BLANCHET, 1922, p. 158 [\**Hoplites sayni* SIMIONESCU, 1899, p. 6; SD ROMAN, 1938, p.

332] [=Octagoniceras SPATH, 1924a, p. 88 (type, Ammonites octagonus BLANFORD in SALTER & BLANFORD, 1865, p. 83; M); Euthymiceras GRIGORIEVA, 1938, p. 102 (type, Ammonites euthymi PICTET, 1867, p. 76; OD); Transcaspiites LUPPOV in



FIG. 37. Neocomitidae (p. 50-54)



FIG. 38. Neocomitidae (p. 50-55)

BOGDANOVA, LUPPOV, & MIKHAILOVA, 1985, p. 146 (type, *Protacanthodiscus transcaspius* LUPPOV, BODY-LEVSKII, & GLAZUNOVA, 1949, p. 222; OD)]. Whorl section polygonal; from early stage very coarse, distant, trituberculate ribs branching obscurely at lateral tubercle; umbilical tubercles bullate, tending to weaken with growth; large ventrolateral tubercles bordering smooth, concave venter, in some produced into large, recurved spines on body chamber. [*Euthymiceras*, distinguished only by bullate rather than clavate ventrolateral tubercles, should be included. Distinction from *Protacanthodiscus* is uncertain.] *Lower Cretaceous (Berriasian):* southern Europe, northern Africa, Madagascar, Ukraine (Crimea), Pakistan, Himalayas, California, Peru, Argentina.——FIG. 37, *5a, b.* \*N. sayni (SIMIO-NESCU), France; lectotype, X0.5 (Mazenot, 1939). Banikoceras HOWARTH, 1992, p. 648 [\**B. involutum;* 

OD]. Inner whorls much as in *Neocosmoceras;* outer whorls smooth, very involute, high-whorled with converging sides, and with deeply undercut umbilical wall. *Lower Cretaceous (Upper Berriasian):* Iraq.——FIG. 38,3*a*–*c.* \**B. involutum,* holotype; *a*,  $\times$ 2; *b*,*c*,  $\times$ 0.7 (Howarth, 1992).

Lytohoplites SPATH, 1925b, p. 144 [\*Hoplites burckhardti MAYER-EYMAR in BURCKHARDT, 1900, p. 17; OD]. Very evolute; whorl section subquadrate to polygonal; main ribs distant, high, thin, twinned, and simple or obscurely biplicate; intermediate ribs feeble to strong, some looped; main ribs ending in transverse or oblique ventrolateral bullae bordering ventral furrow. Upper Jurassic (Upper Tithonian)-Lower Cretaceous (Berriasian): Algeria, Madagascar, Cuba, Argentina.—FIG. 38,2ad. \*L. burckhardti (MAYER-EYMAR), ?Upper Tithonian, Argentina; ×1 (Burckhardt, 1903).— FIG. 38,2e,f. L. besairei COLLIGNON, Upper Tithonian, Madagascar; ×1 (Collignon, 1960).

#### Subfamily NEOCOMITINAE Salfeld, 1921

#### [Neocomitinae SALFELD, 1921, p. 347]

Derivatives of, perhaps various, Berriasellinae, normally with flat or grooved venter and angular shoulders, typically with some or all ribs branching at umbilical shoulder. The compressed high-whorled forms with tabular venter are presumably the central stock that gave rise to a succession of branches that were either more evolute with subquadrate or polygonal whorl section and distant, tuberculate ribs or were involute, high-whorled, and smooth. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Lower Hauterivian).

- Pseudargentiniceras SPATH, 1925b, p. 145 [\*Ammonites abscissus OPPEL in ZITTEL, 1868, p. 97; OD]. Evolute, compressed; venter with persistent, smooth band or groove; ribbing fine, dense at first, bifurcating on outer part of side, gradually becoming more distant with varying proportion of ribs branching in pairs at umbilical margin and umbilical tubercles developing. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Berriasian): southern and central Europe, northern Africa, ?Himalayas.—FIG. 39, 1a, b. \*P. abscissum (OPPEL), Upper Tithonian, Austria; lectotype, ×1 (Zittel, 1868).
- Protothurmannia CRICKMAY, 1932, p. 1 [\*P. rezanoffiana; OD]. Differing from Pseudoargentiniceras only in loss of ventral smooth band in maturity and perhaps in having more complex suture. Upper Jurassic (Upper Tithonian): California.
- Dalmasiceras DJANÉLIDZÉ, 1922a, p. 256 [\*Ammonites dalmasi PICTET, 1867, p. 73; SD ROMAN, 1938, p.

337]. Compressed; early whorls with ribs branching from small but distinct umbilical tubercles, interrupted on venter and tending to form ventrolateral tubercles; later whorls with persistent umbilical tubercles but ribs tending to disappear and venter becoming rounded without groove. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Upper Berriasian): southern Europe, Tunisia.——FIG. 39,4a–c. \*D. dalmasi (PICTET), Upper Tithonian, France; neotype, X1 (Mazenot, 1939).

- Subalpinites MAZENOT, 1939, p. 224 [\*S. fauriensis; OD] [= Jabronella NIKOLOV, 1966a, p. 640 (type, Berriasella jabronensis MAZENOT, 1939, p. 120; OD); Erdenella NIKOLOV, 1979, p. 337 (type, Hoplites paquieri SIMIONESCU, 1899, p. 7; OD); Pomeliceras HOEDEMAKER, 1981, p. 246, non GRIGORIEVA, 1938, p. 103, obj.]. Compressed, with convex flanks and slightly flattened, indistinctly grooved venter; early whorls with ribs mainly branching in twos and threes from umbilical margin and again at midflank; later whorls with strong umbilical and weaker lateral tubercles on main ribs, branching at midflank, with variable intercalatories. Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Lower Valanginian): France, Spain, Bulgaria, Madagascar.—FIG. 39,2a,b. \*S. fauriensis MAZENOT, Upper Berriasian, France; ×0.8 (Le Hegarat, 1973).
- Argentiniceras SPATH, 1924a, p. 89 [\*Odontoceras malarguense STEUER, 1897, p. 181(55); OD] [=Andesites GERTH, 1925, p. 74 (type, Perisphinctes loncochensis STEUER, 1897, p. 187(61); OD); ?Boncheviceras NIKOLOV, 1966a, p. 641 (type, Berriasella ardescensis MAZENOT, 1939, p. 136; OD)]. Whorl section subquadrate; coarse ribs not interrupted on venter, branching irregularly, their umbilical ends tending to form incipient tubercles. Lower Cretaceous (Berriasian): ?France, Argentina. ——FIG. 39,3a-c. \*A. malarguense (STEUER), Argentina; ×0.5 (Steuer, 1897).
- Frenguelliceras A. F. LEANZA, 1945, p. 4 [\**F. magister*; OD]. Very evolute; with coarse, simple or widely splayed ribs branching at umbilical margin; venter with gradually weakening groove bordered by incipiently tuberculate rib endings. *Lower Cretaceous* (*Lower Berriasian*): Argentina.—FIG. 39,5a,b. \**F. magister*; X0.5 (A. F. Leanza, 1945).
- Subthurmannia SPATH, 1939a, p. 48 [\*S. fermori; OD] [=Subthurmanniceras NIKOLOV, 1960, p. 171, obj. (illegitimate emendation); Tirnovella NIKOLOV, 1966a, p. 639 (type, Berriasella alpillensis MAZENOT, 1939, p. 73; OD); Fauriella NIKOLOV, 1966a, p. 640 (type, Berriasella gallica MAZENOT, 1939, p. 140; OD); Strambergella NIKOLOV, 1966a, p. 640 (type, Ammonites carpathicus ZITTEL, 1868, p. 107; OD); Pseudoneocomites HOEDEMAKER, 1982, p. 68 (type, Hoplites retouskyi SARASIN & SCHÖNDELMAYER, 1901, p. 72; OD)]. Rather evolute, compressed, with gently convex sides; early whorls with flat venter and with ribs single or in pairs at umbilical margin, the branching point raised in a slight bulla, and with most ribs branching again at outer third of



FIG. 39. Neocomitidae (p. 55-58)

side; later whorls with rounded venter, with or without smooth band or shallow groove, in some with primary ribs becoming coarse and distant. [Separation as *Tirnovella* of slightly more involute, higher-whorled species with tendency of ornament to weaken on body chamber seems unnecessary.] Upper Jurassic (Upper Tithonian)–Lower Cretaceous (Lower Valanginian): southern Europe, Pakistan, Peru.—FIG. 40,3*a*,*b*. \*S. fermori, ?Berriasian, Pakistan; ×0.3 (Spath, 1939a).—FIG. 40,3*c*,*d*. S. gallica (MAZENOT), Lower Berriasian, France; ×1 (Mazenot, 1939).

Raimondiceras SPATH, 1924a, p. 87 [\*Hoplites raimondii LISSON, 1907, p. 41; OD] [=Pfluckeria LISSON in LISSON & BOIT, 1924, p. 57, obj.]. With every third or fourth rib flared and bituberculate, branching at lateral tubercles; secondaries acutely projected on narrowly rounded venter. Venter is not grooved as stated in SPATH's diagnosis (see *Acantholissonia*). ["Hoplites juv. raimondii (GABB)" in LISSON, 1907 bears no resemblance to "Ammonites Remondii" GABB, 1864, p. 66, and little to "Ammonites Raimondianus" GABB, 1877, p. 268, and is here treated as a new species Hoplites



FIG. 40. Neocomitidae (p. 55-58)

*raimondii* LISSON.] *Upper Jurassic (Upper Tithonian):* ?Pakistan, Peru.——FIG. 39,6*a,b.* \**R. raimondii* (LISSON); ×0.5 (Lisson, 1907).

- Acantholissonia H. A. LEANZA, 1972, p. 67 [\*Spiticeras gerthi WEAVER, 1931, p. 428; OD]. Like Raimondiceras but with stronger tuberculation and persistent, deep ventral groove. Lower Cretaceous (Lower Valanginian): Colombia, Argentina.—\_\_\_\_\_\_\_FIG. 40,4a,b. \*A. gerthi (WEAVER), Argentina; ×1 (H. A. Leanza, 1972).
- Cuyaniceras A. F. LEANZA, 1945, p. 52 [\*Odontoceras transgrediens STEUER, 1897, p. 186(40); SD ARKELL, 1952, p. 860]. Moderately compressed; inner whorls involute, with fine ribs branching near umbilical margin and most again on outer part of side; outer whorl more evolute with most ribs single and ending in a small, rounded or clavate tubercle; venter distinctly but shallowly grooved. Lower Cretaceous (Berriasian): Mexico, Argentina.— FIG. 40,2a-c. \*C. transgrediens (STEUER), Argentina; ×0.5 (Steuer, 1897).
- Calliptychoceras SPATH, 1924a, p. 88 [\*Neocomites calliptychus UHLIG, 1910a, p. 251; M]. More evolute and inflated than N. (Neocomites), with sinuous ribs, fine at first, coarse later, branching from distinct umbilical tubercles, most branching again at midflank, with slight, sharp, oblique ventrolateral bullae bordering smooth venter. Lower Cretaceous (Berriasian–Valanginian): Madagascar, India.—
   FIG. 40, 1a, b. \*C. calliptychum (UHLIG), Valanginian, India (Spiti Valley); ×0.7 (Uhlig, 1910a).
- Odontodiscoceras SPATH, 1924a, p. 88 [\*Neocomites odontodiscus UHLIG, 1910a, p. 250; M]. Rather compressed, with convex sides; ribs mainly single from umbilicus, branching more or less regularly at midflank, ending in small ventrolateral clavi beside smooth venter. Lower Cretaceous (Berriasian-Valanginian): Madagascar, India.—FiG. 40,5a,b. \*O. odontodiscum (UHLIG), Valanginian, India (Spiti Valley); ×0.5 (Uhlig, 1910a).
- Thurmanniceras COSSMANN, 1901, p. 58, nom. nov. pro Thurmannia HYATT, 1900, p. 585, non HEER, 1852, p. 11 [\*Ammonites thurmanni PICTET & CAMPICHE, 1860, p. 250; OD] [=Thurmannites KILIAN & REBOUL, 1914, p. 2, obj.]. Compressed, rather evolute; venter flat on early and rounded on later whorls; ribs arising singly or in twos from slight umbilical bullae; ribs feeble to strong, gently flexuous to falcoid, irregularly branched near midside or simple with intercalatories, with small, transverse ventrolateral bullae, interrupted or not on venter; commonly with strong constrictions; ornament tending to weaken at midflank near aperture. Most described forms are microconchs with long lappets. Lower Cretaceous (Upper Berriasian-Upper Valanginian): southern and central Europe, Morocco, Madagascar, Pakistan, Himalayas, Sumatra, California, Mexico, Peru, Argentina.
  - T. (Thurmanniceras). Body chamber more or less unmodified. Occurrence as for genus.——FIG. 41,1*a-c.* \**T.* (*T.*) thurmanni (PICTET &

CAMPICHE), Lower Valanginian, France; ×1 (Sayn, 1907a).

- T. (Clavithurmannia) THIEULOY in BUSNARDO, THIEULOY, & MOULLADE, 1979, p. 43 [\*T. (C.) foraticostatum; OD]. Large; middle whorls as in T. (Thurmanniceras); last half of outer whorl as in Neocosmoceras, with trituberculate major ribs, ventrolateral clavi, and generally one intermediate rib. Questionably a macroconch of some Thurmanniceras. Lower Cretaceous (Lower Valanginian): France.—FIG. 41,2. \*T. (C.) foraticostatum; ×0.3 (Busnardo, Thieuloy, & Moullade, 1979).
- Limaites LISSON in LISSON & BOIT, 1924, p. 57 [\*Hoplites leopoldinus var. peruanum LISSON, 1907, p. 45; M]. Involute, very compressed, flat-sided, with narrow, tabulate venter; ribs fine, fasciculate, gradually fading on outer whorl except near venter; some weak midlateral tubercles. Lower Cretaceous (Berriasian or Lower Valanginian): Peru.—FIG. 41,4a-e. \*L. peruanus (LISSON); X1 (Lisson, 1907).
- Kilianella UHLIG, 1905, p. 614 [\*Hoplites pexiptychus Uhlig, 1882b, p. 389; SD Roman, 1938, p. 332] [=Parakilianella SATO, 1961, p. 537, nom. nud. (type, P. umazawensis; OD); Luppovella NIKOLOV, 1966a, p. 642 (type, Thurmannia (Killianella) superba SAYN, 1907a, p. 51; OD)]. Evolute; moderately compressed to moderately inflated; ribs strong, flexuous, simple or branching at midflank or in some at umbilical edge; ribs may be tuberculate at umbilical edge or midflank or ventrolaterally; constrictions generally present to a late stage. There seems to be a complete transition from untuberculate to trituberculate species. [Parakilianella is based on a probable microconch.] Lower Cretaceous (Upper Berriasian–Upper Valanginian, ?Lower Hauterivian): southern and central Europe, Madagascar, Pakistan, Himalayas, Sumatra, California, Mexico.—FIG. 41,3a. \*K. pexiptycha (UHLIG), Lower Valanginian, Austria; ×1 (Uhlig, 1882b).——FIG. 41,3b,c. K. roubaudiana (ORBIGNY), Valanginian, France; ×1 (Kilian, 1889a).—FIG. 41,3d,e. K. superba SAYN, Upper Valanginian, France; ×0.5 (Sayn, 1907a).
- Sarasinella UHLIG, 1905, p. 618 [\*Hoplites ambiguus Uhlig, 1902, p. 45; SD Lemoine, 1906, p. 180]. Moderately compressed to moderately inflated; inner whorls with some or all ribs bearing strong umbilical and midlateral tubercles at which ribs bifurcate and slight, sharp radial or oblique ventrolateral bullae; on outer whorls umbilical tubercles becoming dominant, with most ribs branching from them; midlateral tubercles dying out, although some second branching of ribs occurs; venter deeply grooved to flat. Lower Cretaceous (Valanginian): France, Austria, Ukraine (Crimea), Morocco, Madagascar, India (Spiti Valley), Pakistan (Salt Range), Alexander Land.—FIG. 42,2a,b. \*S. ambigua (UHLIG), Austria; ×0.75 (Uhlig, 1902). -FIG. 42,2c,d. S. varians UHLIG, Spiti; X0.5 (Uhlig, 1910a).



FIG. 41. Neocomitidae (p. 58)



- Neocomites UHLIG, 1905, p. 620 [\*Ammonites neocomiensis ORBIGNY, 1841, p. 202; SD SAYN, 1906, p. 122]. Rather involute, with flat sides; ribs flexuous, prorsiradiate, branching in small sheaves from slight umbilical tubercles and generally branching irregularly higher up the side or intercalated; all ribs ending in small, slightly oblique bullae on either side of smooth, flat venter; on later whorls ribs may cross venter more or less transversely. Sutures with large, subsymmetrical, trifid L with parallel sides. Lower Cretaceous (Lower Valanginian-Lower Hauterivian): southern and central Europe, northern Africa, Israel, Madagascar, Pakistan (Salt Range), Himalayas, Borneo, Sumatra, Texas, Mexico, Peru, Argentina.
  - N. (Neocomites) [=Busnardoites NIKOLOV, 1966a, p. 642 (type, Ammonites desori PICTET & CAMPICHE, 1860, p. 246; OD)]. Ribbing on body chamber unchanged; venter becoming only slightly rounded. Occurrence and distribution as for genus.——FIG. 43, 1a-c. \*N. (N.) neocomiensis (ORBIGNY), Lower Valanginian, France; a,b, X1 (Orbigny, 1840–1842); c, X10 (Wiedmann, 1966a).
  - N. (Varlheidites) RAWSON & KEMPER, 1978, p. 166 [\*V. peregrinus; OD]. Microconch and inner whorls of macroconch as in N. (Neocomites); outer whorl of macroconch with periodic, enlarged trituberculate ribs. Lower Cretaceous (lower Upper Valanginian): Germany.——FIG. 43,2a-d. \*N. (V.) peregrinus (RAWSON & KEMPER); a,b, holotype, inner whorls of macroconch, ×0.5; c,d, outer whorl of macroconch, ×0.5 (Rawson & Kemper, 1978).
  - N. (Teschenites) THIEULOY, 1971, p. 2298 [\*Hoplites neocomiensis var. (Ammonites neocomiensiformis HOHENEGGER in. litt.) UHLIG, 1902, p. 56; OD]. Body chamber with rounded venter; umbilical tubercles and primary ribs tending to strengthen and ribs to weaken on midflank, ventrolateral tubercles tending to be absent and ribs to cross venter in rounded arc. Lower Cretaceous (Upper Valanginian-Lower Hauterivian): France, Germany, Switzerland, Ukraine (Crimea), Israel.——FIG. 43,3. \*N. (T.) neocomiensiformis (UHLIG), Upper Valanginian, France; X0.75 (Thieuloy, 1977b).
  - N. (Eristavites) NIKOLOV, 1966a, p. 641 [\*Neocomites platycostatus SAYN, 1907a, p. 33; OD]. Venter becoming rather broad; ribs irregular, sparse, some thicker and tending to be trituberculate. Occurrence and distribution as for genus.——FIG. 43,5*a*,*b*. \*N. (E.) platycostatus SAYN, Upper Valanginian, France; ×1 (Sayn, 1907a).
- Criosarasinella THIEULOY, 1977b, p. 109 [\*C. furcillata; OD]. Early whorls crioconic, with simple, trituberculate, enlarged ribs and two to five simple minor ones; later whorls in contact and ornamented as in *Neocomites*, with secondary branching of ribs near ventrolateral shoulders. *Lower Cretaceous (Upper Valanginian):* France, Bulgaria.

——FIG. 43,*4.* \**C. furcillata*, France; ×0.7 (Thieuloy, 1977b).

Lissonia GERTH, 1925, p. 111 [\*Hoplites riveroi LISSON, 1907, p. 51; OD]. Compressed, involute, with deeply grooved venter; ribs fine, sharp, simple, bifurcating at midflank, strongly projected on rounded ventrolateral shoulder; no tubercles. Lower Cretaceous (Upper Valanginian): Peru.—FIG. 42, 1a,b. \*L. riveroi (LISSON); X1 (Lisson, 1907).

#### Subfamily ENDEMOCERATINAE Schindewolf, 1966

[nom. transl. WRIGHT, 1981, p. 173, ex Endemoceratidae SCHINDEWOLF, 1966, p. 375(551)] [=Leopoldiinae THIEULOY, 1971, p. 2298]

Differing from Neocomitinae only in having suture with lobe U1 not divided into ventral and dorsal elements and in tendency to greater asymmetry of L. Very doubtfully a single phylogenetic entity. *Lower Cretaceous* (Upper Valanginian–Upper Hauterivian, ?Lower Barremian).

- Karakaschiceras THIEULOY, 1971, p. 2299 [\*Hoplites biassalensis KARAKASCH, 1889, p. 435; OD]. Moderately to very involute; sides slightly convex, converging to more or less narrow venter, flat except on body chamber; ribs strong at least in young, springing in twos or threes from umbilical bullae and ending in distinct, small ventrolateral bullae, opposite or alternate, with smooth siphonal band. Lower Cretaceous (?Lower Valanginian, Upper Valanginian): England, France, Germany, Austria, Poland, Ukraine (Crimea), Argentina.—FIG. 44, *Ia*, *b*. \*K. biassalense (KARAKASCH); a, Crimea, ×0.75 (Karakasch, 1907); b, England, ×0.75 (Kemper, Rawson, & Thieuloy, 1981).
- Neohoploceras SPATH, 1939a, p. 105 [\*Ammonites submartini MALLADA, 1887, p. 17; OD] [=Arnoldia STOLLEY, 1937, p. 453, non MAYER-EYMAR, 1887, p. 27 (type, Ammonites arnoldi PICTET & CAMPICHE, 1860, p. 252; M)]. Inner whorls inflated, with ribs branching irregularly from umbilical and midlateral tubercles, some simple; deep constrictions with collars behind, commonly flared ventrolaterally; venter grooved, concave, or rounded; outer whorls becoming compressed, without constrictions. Lower Cretaceous (Upper Valanginian): England, France, Germany, Spain, Madagascar, Pakistan (Salt Range).
   ——FIG. 44,5a,b. \*N. submartini (MALLADA), Salt Range; X0.75 (Spath, 1939a).
- Stoicoceras WHITEHOUSE, 1927, p. 109 [\*Ammonites (Hoplites) teutobergensis WEERTH, 1884, p. 20; OD] [=Dicostella BUSNARDO, 1966b, p. 236 (type, D. pitrei; OD; =Hoplites (Neocomites) houdardi var. tuberculata ROMAN, 1933, p. 19)]. Large; moderately inflated and evolute to rather compressed and more involute; primary ribs strong, short, straight or flexed, with or without umbilical bullae at which they may branch, and branching at midflank into

two strongly curved secondaries, generally with slightly oblique ventrolateral bullae; venter flat, midline smooth. Approximate homeomorph of some Acanthodiscus. Lower Cretaceous (Upper Valanginian): France, Germany, Switzerland.——FiG. 45,5a,b. \*S. teutobergense (WEERTH), Germany; ×0.25 (Kemper, Rawson, & Thieuloy, 1981).— FiG. 45,3c. S. tuberculatum (ROMAN), France; ×0.5 (Busnardo, 1966b).

- Chamalocia THIEULOY, 1971, p. 2299 [\*Leopoldia subaenigmatica SAYN, 1907a, p. 55; OD]. Involute; whorls high, subrectangular; venter narrow and flat, separated from the sides by oblique bevels; ribs on sides and venter, with pointed ventrolateral tubercles, disappearing early. Suture rather simple, with short and very wide saddles. Lower Cretaceous (Upper Valanginian): France.—FIG. 45, 1a-c. \*C. subaenigmatica (SAYN), a,b, X1; c, X3 (Sayn, 1907).
- Lyticoceras HYATT, 1900, p. 586 [\*Ammonites cryptoceras ORBIGNY, 1840, p. 24; OD] [=Besairieceras COLLIGNON, 1962a, p. 58 (type, B. colcanapi; OD); Endemoceras THIERMANN, 1964, p. 369 (type, Hoplites amblygonius NEUMAYR & UHLIG, 1881, p. 168; OD); Eleniceras BRESKOVSKI, 1967, p. 47 (type, E. stevrecensis; OD)]. Rather evolute to rather involute; moderately to very compressed; venter gently rounded to tabulate; ribs more or less dense, sharp, slightly sinuous to falcoid, some branching near umbilical shoulder but most near middle or outer third of whorl side; primary ribs may be raised and sharpened at umbilical edge to form a slightly twisted bulla; all ribs generally bearing slight but distinct ventrolateral, spinate to clavate tubercles and crossing venter in gentle curve or distinct chevron but may be weak or absent on midline on internal molds; outer whorls may develop more or less regular, single or paired and looped, enlarged, trituberculate ribs, with or without associated constrictions. Suture with deeply incised saddles and very asymmetric L. Some forms are adult at diameters of 70 to 80 mm, others at over 300 mm; but boundaries between macroconchs and microconchs are not yet worked out. [Given the wide morphological variation within the northern group separated as Endemoceras, it seems unnecessary to separate the type species, cryptoceras, on the basis of its early and middle whorls not having ventral chevrons and ventrolateral tubercles being spinate rather than clavate, or Besairieceras on the basis of body chambers with large umbilical tubercles projecting into the umbilicus, or Eleniceras on the basis of enlarged trituberculate ribs appearing at an earlier stage.] Lower Cretaceous (Upper Valanginian–Lower Hauterivian): England, France, Germany, Poland, Czech Republic, Bulgaria, Madagascar.-FIG. 46a-d. \*L. cryptoceras (ORBIGNY), Lower Hauterivian, France; a,b, lectotype, ×0.5 (Wright, 1975); c,d, ×1 (Kemper, Rawson, & Thieuloy, 1981).---FIG. 46e. L. stevrecensis (BRESKOVSKI), Lower Hauterivian, Bulgaria; X0.75 (Breskovski, 1967).——FIG. 46f,g. L. colcanapi (COLLIGNON), Upper Valanginian, Madagascar; f, ×0.5; g, ×1 (Collignon,

# Cephalopoda—Cretaceous Ammonoidea



FIG. 43. Neocomitidae (p. 60-61)

1962a).——FIG. 47*a*, *b*. *L. amblygonium* (NEUMAYR & UHLIG), Lower Hauterivian, Germany; *a*, lecto-type,  $\times 0.5$ ; *b*,  $\times 0.5$  (Thiermann, 1963).——FIG. 47*c*, *d*. *L. regale* (PAVLOW), Lower Hauterivian, England; lectotype, BMNH C.34948,  $\times 0.75$  (new).

Favrella R. DOUVILLE, 1909a, p. 164 [\*Neocomites americanus FAVRE, 1908, p. 613; OD] [=Patagoniceras WETZEL, 1960, p. 249 (type, Neocomites steinmanni FAVRE, 1908, p. 620; OD)]. Very evolute, with dorsum barely impressed; ribs distant, narrow, and high, mostly simple but rarely branching at umbilical tubercles on early whorls, rectiradiate until outer third where they curve sharply forward to form acute ventral chevrons, interrupted



FIG. 44. Neocomitidae (p. 61-64)

siphonally on inner whorls, interrupted or not on outer. *Lower Cretaceous (?Lower Hauterivian):* Argentina.——FIG. 45,*6a,b.* \**F. americana* (FAVRE); lectotype, ×0.3 (Favre, 1908).

- Pseudofavrella A. F. LEANZA & H. A. LEANZA, 1973, p. 130 [\*Hoplites angulatiformis BEHRENDSEN, 1892, p. 16; OD]. Moderately evolute, with more or less trapezoidal whorl section. Sharp, high primary ribs springing from distant umbilical bullae and running radially for two-thirds of side, then bending forward at a subdued lateral tubercle and raised into fairly prominent ventrolateral tubercle, crossing the venter in a strong forward arc. Short secondary ribs with ventrolateral tubercles are irregularly intercalated. Suture with deep, rather wide lateral lobe and second and third lateral saddles projecting beyond the first. Distinguished from Lyticoceras by its rectiradiate primary and shorter secondary ribs. Lower Cretaceous (Lower Hauterivian): Colombia, Argentina.—FIG. 48,2a-c. \*P. angulatiformis (BEHRENDSON), Argentina; ×1 (A. F. Leanza & H. A. Leanza, 1973).
- ?Hatchericeras STANTON, 1901, p. 35 [\*H. patagonense; OD] [=Pseudohatchericeras A. F. LEANZA, 1970, p. 244 (type, Hatchericeras argentinense STANTON, 1901, p. 39; OD)]. Large, involute, compressed; early whorls with strong ribs, ranging from blunt and coarse to fine, branching from umbilical margin, with or without umbilical tubercles, slightly sinuous, prorsiradiate, widening on outer third of side or not, crossing venter transversely or interrupted; later whorls smooth with rounded venter. Suture with wide L divided by large folioles. Lower Cretaceous (Upper Hauterivian or Lower Barremian): South Africa (Zululand), Queensland, Argentina. —FIG. 44,6a-e. \*H. patagonense, Patagonia; a-c, ×0.2 (Stanton, 1901); d,e, ×1 (A. F. Leanza, 1970).
- Cruasiceras BUSNARDO, 1970b, p. 137 [\*Ammonites cruasensis TORCAPEL, 1884, p. 137(7); M]. Highwhorled, with rounded venter and regularly branching ribs. Perhaps descended from Lyticoceras. Lower Cretaceous (lower Upper Hauterivian): France.
- Distoloceras HYATT, 1900, p. 588 [\*Ammonites hystrix PHILLIPS, 1829, p. 123; OD] [=Rodighieroites COM-PANY, 1987, p. 158 (type, R. cardulus; OD)]. Very evolute to criocone; whorl section polygonal; ribs coarse and tuberculate from early stage, strongly projected ventrolaterally, differentiated on outer whorls; on inner whorls ribs with large ventrolateral, normally midlateral, and sometimes umbilical spines, with or without such spines on outer whorls. Suture as in Lyticoceras. Lower Cretaceous (Upper Valanginian-Lower Hauterivian): England, ?France, Spain, Germany.—FIG. 48, 1a, b. \*D. hystrix (PHILLIPS), Lower Hauterivian, England; ×1 (Howarth, 1962).—FIG. 48,1c,d. D. pavlowi SPATH, Lower Hauterivian, England; holotype, BMNH C.34976, X1 (new).
- Acanthodiscus UHLIG, 1905, p. 607 [\*Ammonites radiatus BRUGUIÈRE, 1789, p. 21; SD ROMAN, 1938, p. 338]. Whorls stout to compressed, with smooth, flat to concave venter; strong, straight primary ribs rising from moderate umbilical tubercles, simple,

bi-, or trifurcating at large midlateral tubercles and ending at smaller ventrolateral nodes; later whorls tending to be smooth. [SAYN's (1907b, p. 193) statement that it is convenient to restrict *Acanthodiscus* to the group of *A. radiatus* (BRUGUIERE) is not a valid lectotype designation of that species, nor is SPATH's similar statement (1924a, p. 87).] *Lower Cretaceous (Lower Hauterivian):* Europe, Morocco, Madagascar, California, Mexico.——FIG. 44,*3a,b.* \**A. radiatus* (BRUGUIERE), Germany; X0.4 (Neumayr & Uhlig, 1881).

- Leopoldia MAYER-EYMAR, 1887, p. 77 [\*Ammonites leopoldinus Orbigny, 1840, p. 104; SD Roman, 1938, p. 341] [=Hoplitides KOENEN, 1902, p. 170, obj.; Solgeria UHLIG, 1905, p. 624, obj.; Renevierites BUSNARDO & THIEULOY, 1989, p. 132 (type, Leopoldia renevieri BAUMBERGER, 1906, p. 38; OD]. Early whorls compressed, with parallel sides; primary ribs rather strong and flexuous; secondary ribs soon becoming confined to outer part of sides; all ribs ending in small ventrolateral clavi; middle and late whorls smooth, with high, oval section, generally with sides converging to narrowly rounded, rarely acute, venter. Probably derived from compressed Acanthodiscus. Lower Cretaceous (Lower Hauterivian): Europe, Morocco, Madagascar, Peru, Argentina.—FIG. 45,4a,b. \*L. leopoldina (OR-BIGNY), France; ×0.5 (Orbigny, 1840–1842).
- Suboosterella SPATH, 1924a, p. 88 [\*Ammonites heliacus ORBIGNY, 1840, p. 108; SD ROMAN, 1938, p. 346]. Compressed, discoidal, evolute, with smooth, narrowly rounded venter; ribs on early and middle whorls branching widely near midflank, on outer whorls simple with blunt ends. Lower Cretaceous (Lower Hauterivian): France, Austria.——FIG. 44,2a,b. \*S. heliaca (ORBIGNY), France; ×0.75 (Orbigny, 1840–1842).
- Breistrofferella THIEULOY, 1971, p. 2299 [\*Ammonites castellanensis ORBIGNY, 1840, p. 109; OD]. Rather involute, inflated microconchs with oval whorl section, smooth, rounded venter, and falcoid, alternately long and short ribs dying away on shoulders and with hardly any umbilical tuberculation. Lower Cretaceous (Lower Hauterivian): France, Switzerland.——FIG. 44,4a,b. \*B. castellanensis (ORBIGNY), France; X1 (Orbigny, 1840).
- Hannaites IMLAY, 1957, p. 275 [\*Neocomites riddlensis ANDERSON, 1938, p. 167; OD]. Like Leopoldia but with flat venter crossed by strong, transverse ribs, constrictions on outer whorls, and uncoiling body chamber. Lower Cretaceous (Lower Hauterivian): Oregon.—FIG. 45,3a,b. \*H. riddlensis (ANDER-SON); X1 (Anderson, 1938).
- Saynella KILIAN, 1910b, p. 150 [\*Ammonites clypeiformis ORBIGNY, 1841, p. 137; SD SPATH, 1924a, p. 88]. Smooth or feebly ribbed oxycones, after early ribbed stage. Probably derived from Leopoldia. Lower Cretaceous (Hauterivian): England, France, Switzerland.——FIG. 45, 2a, b. \*S. clypeiformis (ORBIGNY), France; ×0.125 (Orbigny, 1840–1842).
- Malgesaynella BUSNARDO, 1970a, p. 94 [\*Saynella besairiei COLLIGNON, 1949a, p. 73; OD]. Compressed, high-whorled; venter narrowly rounded;



FIG. 45. Neocomitidae (p. 61-64)



Fig. 46. Neocomitidae (p. 61–62) © 2009 University of Kansas Paleontological Institute inner whorls with fairly strong primary ribs around the umbilicus and fine secondaries on shoulders and periphery; outer whorls smooth. Suture with wide, rather short elements. *Lower Cretaceous (?Hauterivian):* Madagascar.——FIG. 48,*3a,b.* \**M. besairiei* (COLLIGNON); *a*, X1; *b*, X2 (Busnardo, 1970a).

# Superfamily DESMOCERATACEAE Zittel, 1895

[nom. transl. WRIGHT & WRIGHT, 1951, p. 18, ex Desmoceratidae ZITTEL, 1895, p. 426]

Generally round- or oval-whorled, but some lanceolate or keeled; commonly smooth or with weak ribs, but some genera and families strongly ribbed and tuberculate; constrictions commonly present. Suture simple or complex, with or without retracted suspensive lobe; L symmetrically or asymmetrically trifid in nearly all. Probably strongly dimorphic throughout; macroconchs with simple apertures; microconchs with lappets and rostrum in most families, but lappets appear to be lacking in Pachydiscidae. Lower Cretaceous (Upper Valanginian)–Upper Cretaceous (Upper Maastrichtian).

In recent years it has variously been suggested that the superfamily Desmocerataceae had a monophyletic origin in Phylloceratidae, diphyletic in Phylloceratidae and -Lytoceratidae, or monophyletic in Haplocerataceae. Some of the latter have sutures generally similar to those of early Desmocerataceae, but constrictions are not found in Haplocerataceae. Adult sutures of many Desmocerataceae repeatedly develop resemblances to those of some Lytocerataceae but only in particular features, and the basic pattern is quite different. It is probably equally significant that almost all characters of the ornament of Desmocerataceae and their derivatives Hoplitaceae and Acanthocerataceae repeat those of various Perisphinctaceae. The previously presumed most primitive desmoceratacean, Eodesmoceras, thought to be Valanginian, turns out to be based on probably Albian fragments of Puzosia and Desmoceras. Lower to Upper Hauterivian Spitidiscus include species with inner whorls closely resembling Barremites and Valdedor-



FIG. 47. Neocomitidae (p. 61-62)

*sella*; earliest species of *Spitidiscus* (Upper Valanginian) closely resemble *Olcostephanus*, and there is no significant sutural difference. Though a secure conclusion on the origin of the group cannot yet be reached, origin in Perisphinctaceae seems very natural.

The superfamily is here retained as distinct from its derivative Hoplitaceae,