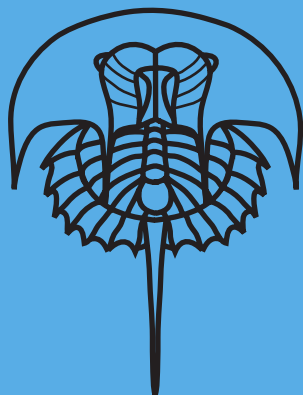




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JURASSIC AMMONITES: SYSTEMATIC DESCRIPTIONS OF THE JURASSIC STRIGOCERATOIDEA AND HAPLOCERATOIDEA

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INTRODUCTION: TAXONOMIC AND EVOLUTIONARY CRITERIA

Ammonites traditionally included in Haploceratoidea (here Haploceratoidea and Strigoceratoidea) usually present taxonomic complications, especially in establishing the phylogenetic relationships between their different taxa (both at the species, genus, subfamily, or family level). As they often have little ornamentation, other apparently less significant criteria sometimes become necessary in order to separate certain taxa from others.

To establish the taxonomy, the following criteria of the shells have been taken into account: a) size both of macroconchs and microconchs; b) types of coiling (involute, semi-evolute, evolute, platyconic, oxyconic, sphaeroconic, eccentric or ellipticone, and scaphitoid); c) whorl section, with special attention to the umbilical edge and ventral region; d) absence or presence and type of keel; e) ornamentation, including absence or presence and type of ribs or striae, spiral striation, lateral grooves or depressions and lateral spiral raises, umbilical thickening, presence and position of tubercles, nodes, spiniform thickenings, clavi, and bullae; f) type of aperture and apertural modifications (lappets, ventral rostrum); g) presence

and type of dimorphism; h) suture and its changes or modifications. Neither Haploceratoidea nor Strigoceratoidea have constrictions commonly found in other ammonite groups.

The phylogeny of the Strigoceratoidea and *Middle-Upper Jurassic* Haploceratoidea (FIG. 1) and the *upper Toarcian* to *Tithonian* biostratigraphic ammonite zones used herein were derived from a variety of sources (ELMI, 1967; STURANI, 1971; OLÓRIZ, 1978; COPE & others, 1980; CALLOMON, 1981, 1984, 2003; OLÓRIZ & SCHAIRER, 1983; SANDOVAL, 1983, 1985, 1986; FERNÁNDEZ-LÓPEZ, 1985, 2012; CARIOU & HANTZPERGUE, 1997; SCHWEIGERT & DIETZE, 1998; SCHWEIGERT & others, 1999, 2000, 2003, 2007, 2011; ROGOV, 2000, 2002; SCHWEIGERT & KAPITZKE, 2018; PAVIA & FERNÁNDEZ-LÓPEZ, 2019; ÉNAY & MANGOLD, 2021; etc.). Notwithstanding, the same ammonite zones used in other chapters of this *Treatise* (HOWARTH, 2013, 2017, 2020; HOFFMANN, 2015; ÉNAY & HOWARTH, 2019) are here utilized where appropriate.

For determining phylogenetic relationships, besides the bibliographic data and changes of morphology observed between related taxa, the stratigraphic or temporal continuity between successive forms were analysed.

Superfamily
STRIGOCERATOIDEA
Buckman, 1924

[*nom. transl.* SANDOVAL herein,
ex Strigoceratidae BUCKMAN, 1924, p. 7]
[=Phlycticeratinae SPATH, 1928, p. 89]

Ever since it was established by BUCKMAN (1924), the family Strigoceratidae (Strigoceratinae and Phlycticeratinae) has usually been included in the superfamily Haploceratoidea; however, such an interpretation may not be appropriate, as this group of ammonoids appeared long before Lissoceratidae, the oldest typical Haploceratoidea, and appears to have no direct phylogenetic relationships with this latter group. In such a case, Strigoceratidae BUCKMAN, 1924, should be elevated to the rank of superfamily, instead of being considered a family within Haploceratoidea. The dimorphic couple *Onychoceras* (microconch)–*Csernyeiceras* (macroconch) would then be the oldest genus of the superfamily Strigoceratoidea (FIG. 1), which presumably derived from Grammoceratinae BUCKMAN, 1905, with the late Toarcian genera *Esericeras*

or *Phlyseogrammoceras* (see below) as probable ancestors. The superfamily Strigoceratoidea includes a single family, Strigoceratidae BUCKMAN, 1924, which, following to SCHWEIGERT & DIETZE (1998), SCHWEIGERT & others (1999, 2000, 2003, 2007), and BARDHAN & others (2010), is here divided into two subfamilies: Strigoceratinae BUCKMAN, 1924, and Phlycticeratinae SPATH, 1928.

Family STRIGOCERATIDAE
Buckman, 1924

[Strigoceratidae BUCKMAN, 1924, p. 7]
[=Phlycticeratinae SPATH, 1928,
Oecoptychiinae WESTERMANN, 1956
(*partim*), p. 273, and Oecoptychiidae
ARKELL, 1957 (*partim*), p. 296]

The shells are compressed to oxyconic, involute with more-or-less marked eccentric coiling and with narrow or minute umbilicus. The innermost whorls are smooth or scarcely ornamented early on and later develop ribbing, in many cases almost confined to outer half of whorl sides, single or irregularly branched, not parallel to growth lines.

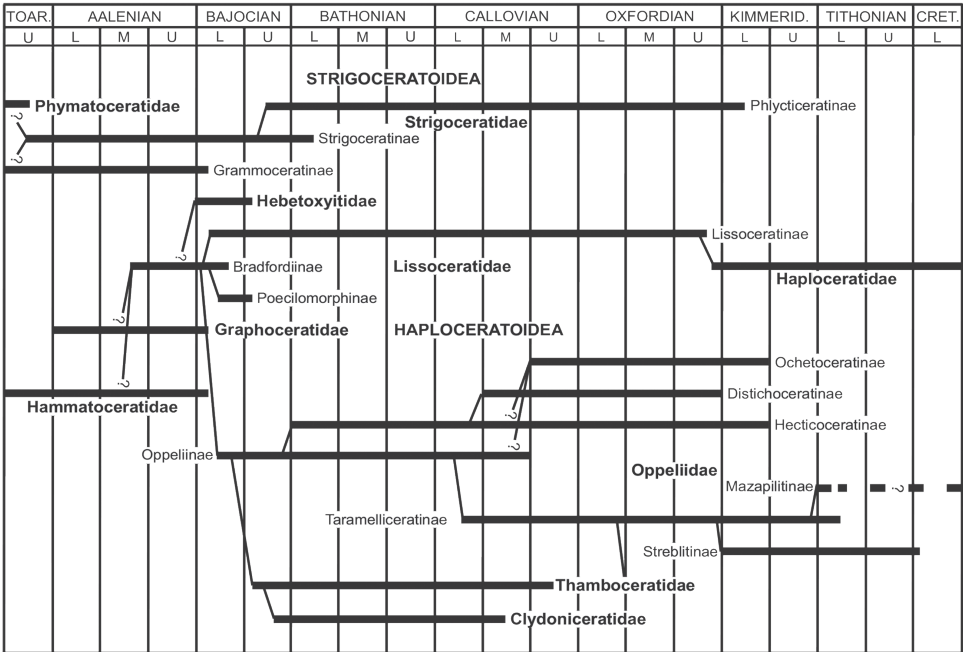


FIG. 1. Phylogeny of the superfamilies Strigoceratoidea and Haploceratoidea.

Lateral tubercles appear in some genera. Whorl sides with longitudinal spiral striation and with lateral depressions or furrows are poorly marked in primitive forms.

Dimorphism is generally well differentiated in all the Strigoceratidae; the macroconchs are generally much longer than microconchs, which have a more eccentric coiling, well-developed lateral lappets, and ventral rostrum in the aperture. Sutures are usually complex in macroconchs, with E deeper than L; the umbilical lobe is not retracted, and with a graded series of auxiliary lobes; sutures are much simpler in microconchs.

According to SCHWEIGERT & others (2007, p. 6) and PARENT & WESTERMANN (2016, p. 105), there seems to be not a single record of aptychi associated with strigoceratoid ammonites, although these structures could have been very thin and thus not preserved.

The Strigoceratidae are generally scarce, in no case being the dominant elements in the *Middle-Upper Jurassic* ammonite assemblages, which makes it difficult to establish the phylogenetic relationships between the various taxa and reduces their biostratigraphic significance. *Uppermost Lower Jurassic (uppermost Toarcian)–Upper Jurassic (lower Kimmeridgian)*: worldwide.

Strigoceratidae have traditionally been included in the Haploceratoidea (ARKELL, 1957, p. 271; STURANI, 1971; GALÁ CZ, 1980; PAVIA, 1983; FERNÁNDEZ-LÓPEZ, 1985; SANDOVAL, 1985; SCHWEIGERT & others, 2007; etc.), but the presence of spiral striation and unsculptured septicarinate keel separates Strigoceratidae from this superfamily.

According to recent observations (SCHWEIGERT & others, 2007, p. 60 and references therein), the dimorphous pair *Onychoceras* WUNSTORF, 1905–*Csernyeiceras* GÉ CZY, 1966, the oldest typical Strigoceratidae, is directly linked phylogenetically to the Grammocerotinae (*Phlyseogrammoceras* BUCKMAN, 1901) or Phymatoceratidae (*Esericeras* BUCKMAN, 1920) of the late Toarcian (FIG. 1). Consequently, all the Strigoceratidae (Strigoceratinae and Phlycticerotinae) would successively descend from this common ancestor.

However, the origin of the oldest typical Haploceratoidea (*Bradfordia* BUCKMAN, 1910) is currently unclear. Many authors (ARKELL, 1957, p. 274; ELMI, 1967, p. 779; GÉ CZY, 1967, p. 224; WESTERMANN, 1969, p. 49–52; SAPUNOV, 1971, p. 74; GALÁ CZ, 1980, p. 55; CALLOMON, 1981, p. 143; FERNÁNDEZ-LÓPEZ, 1985, p. 173; SADKI, 1988, p. 239; PAVIA & FERNÁNDEZ-LÓPEZ, 2019, p. 32) considered *Bradfordia* to be derived from late Aalenian hammatoceratids, while other authors (STURANI, 1971, p. 89; SANDOVAL, 1986, p. 451) have argued that haploceratoids were derived from Aalenian graphoceratids. This latter view is supported by the fact that the graphoceratids, *Leioceras* and mainly *Brasilia*, as well as the haploceratoid *Bradfordia*, have many common characters, such as the vertical umbilical wall, periumbilical depression, and similar types of ribbing. Sutures are also very similar in Graphoceratidae and Lissoceratidae. The phyletic relationship between *Bradfordia* and the earlier species of Lissoceratinae (*Semilissoceras ellipticum* PAVIA & FERNÁNDEZ-LÓPEZ, *S. turgidum* PAVIA & FERNÁNDEZ-LÓPEZ) seems clear, once the affinities in ornamentation and suture are recognized.

In conclusion, if *Bradfordia* represents the oldest Lissoceratidae (Haploceratoidea) and this in turn has no phylogenetic relationship with the Strigoceratidae, which appear far earlier in time (late Toarcian vs. latest middle Aalenian or late Aalenian), Strigoceratidae and Haploceratoidea could not have a direct phylogenetic relationship and, therefore, Strigoceratidae should be considered as belonging to a superfamily other than Lissoceratidae.

Subfamily STRIGOCERATINAE Buckman, 1924

[=Strigoceratidae BUCKMAN, 1924, p. 7]

Shells are of variable size, with a high-oval to oxyconic cross section, and are involute with very narrow umbilicus and rounded umbilical wall. Coiling more-

or-less eccentric, with eccentricity being more pronounced in the microconchs than the macroconchs. Whorl section ogival or subtriangular, compressed, with maximum thickness on the inner half of the flanks, and a hollow (septicarinate) and smooth keel. Ribs falcoid, sinuous, poorly marked, and invariably more developed on the upper part of the flanks, with more-or-less developed spiral striation mainly in microconchs, and with one to four lateral depressions or furrows. Suture usually complex, and incised in macroconchs, with E deeper than L. *Uppermost Toarcian* (Levesquei Zone)–*lower Bathonian* (Zigzag Zone, *Macrescens Subzone*).

SCHWEIGERT & others (2007) and SCHWEIGERT & KAPITZKE (2018) included the genera *Strigoceras* QUENSTEDT, 1886, *Cadomoceras* MUNIER-CHAMAS, 1892, *Granulochetoceras* GEYER, 1960, *Cymaceras* QUENSTEDT, 1887, and *Trochiskiocras* SCHAIRER & SCHLAMPP, 1991, in the subfamily Strigoceratinae. The macroconch *Granulochetoceras*, and the dimorphous partner *Cymaceras-Trochiskiocras*, have been transferred to the subfamily Phlycticeratinae because their morphological characters are closer to the Phlycticeratinae than Strigoceratinae, and because they appeared in the late Callovian, long after the last typical Strigoceratidae became extinct (early Bathonian). However, *Csernyeiceras* GÉCZY, 1966, and *Onychoceras* WUNSTORF, 1905, which were classified as Phlycticeratinae by SCHWEIGERT & others (2000, 2003), are here included in Strigoceratinae, and the genus *Praestrigites* BUCKMAN, 1924, is also accepted.

Pandemic distribution: Europe, North Africa, Caucasus, Turkmenistan, North America (Mexico, Alaska, Oregon, Canada), South America (Andean Cordillera), Thailand, and Japan.

Onychoceras WUNSTORF, 1905, p. 508 [**O. differens* WUNSTORF, 1905; SD HOWARTH, 2013, p. 103] [= *Csernyeiceras* GÉCZY, 1966, p. 83 (type *Hammatoceras verpillierense* ROMAN & BOYER, 1923, p.

34; OD)]. Macroconch (*Csernyeiceras*) have large, planulate, relatively involute oxyconic shells, subtriangular to ogival compressed whorl section reaching its maximum thickness at mid-flank height, and narrow, sharp ventral area extending into a well-marked hollow keel. Ribs fine, gently sigmoid, bifurcating at the half of whorl side, quickly becoming smooth on outer whorls. Suture strigoceratoid with long E, slightly asymmetrical L, and branched (incised), slightly oblique auxiliary lobes. Microconchs (*Onychoceras*) are dwarf, *Cymbites*-like, and become adult at 15–20 mm in diameter, with lateral lappets along the mouth border; whorls globular, depressed, with rounded venter and no keel; ribs rursiradiate on the side of the whorl, and disappear, leaving venter smooth, or divided into faint striate secondaries on venter. The macroconch (*Csernyeiceras*) has been included in Hammatoceratidae, as a synonym for *Euaptetoceras*, by HOWARTH (2013, p. 105). However, in agreement with SCHWEIGERT & DIETZE (1998), SCHWEIGERT & others (2000, 2007), KOVÁCS (2009), and SANDOVAL & others (2020), this is not a hammatoceratid but a typical strigoceratid. *Onychoceras* WUNSTORF, 1905, was also included in Hammatoceratidae by GUÉX (1967), HOWARTH (2013), and SANDOVAL & others (2020), but typical hammatoceratid microconchs have sharply different morphologies compared to *Onychoceras*. SCHWEIGERT & DIETZE (1998), SCHWEIGERT & others (2000, 2003, 2007), and SCHWEIGERT & KAPITZKE (2018) considered to the microconch *Onychoceras* and the macroconch *Csernyeiceras* to be a dimorphous couple and was assigned to the subfamily Phlycticeratinae. However, this couple is transferred here to Strigoceratinae, because the first records of typical Phlycticeratinae are in the *upper Bajocian* (Garantiana Zone), whereas *Onychoceras-Csernyeiceras*, the oldest Strigoceratoidea, are restricted to the *upper Toarcian*–*middle Aalenian*. *Uppermost Toarcian* (Levesquei Zone)–*middle Aalenian* (Bradfordensis Zone): Bulgaria, England,

France, Germany, Hungary, Italy (including Sicily), Portugal, Spain (Betic Cordillera), Iran, Morocco, Thailand, Argentina, Chile (the Andean Cordillera).—FIG. 2, *a–d*. **O. differens* WUNSTORF; *a–c*, lectotype (designated by HOWARTH, 2013), microconch, lateral view, cross section and suture; *upper Toarcian*, Gallberg, Salzgitten, Germany; *a–b*, $\times 1$, *c*, $\times 2$ (WUNSTORF, 1905, pl. 20, 12–13, 16); *d*, paralectotype, $\times 1$ (WUNSTORF, 1905, pl. 20, 14).—FIG. 2, *e–f*. **O. verpillierense* (ROMAN & BOYER), holotype, macroconch, *upper Toarcian*, Aalensis Zone, Saint Quentin-Fallavier, Isère, France, $\times 0.7$ (RULLEAU, 2009, pl. 55, 1*a–b*; also figured by SCHWEIGERT & others, 2007, text-fig. 2, 3; Lyon University Collection, FSL 1096).

Strigoceras QUENSTEDT, 1886 in 1882–1888, p. 395 [**Ammonites truellei* D'ORBIGNY, 1845 in 1842–1851, p. 361] [= *Cadomoceras*

MUNIER-CHALMAS, 1892, p. 171 (type, *Ammonites cadomensis* DEFRANCE, 1840 in DE BLAINVILLE, 1840, p. 153; OD); = *Stringoceras* DOUVILLÉ, 1916, p. 41, obj.; = *Varistrigites* BUCKMAN, 1924, pl. 468 (type, *Ammonites truellei* var. *compressus* ETHERIDGE in WRIGHT, 1860; OD); = *Strigites* BUCKMAN, 1924, pl. 469A (type, *S. strigifer*; OD); = *Plectostrigites* BUCKMAN, 1924, pl. 471A (type, *P. symplectus*, OD); = *Lepostrigites* BUCKMAN, 1924, pl. 477A (type, *L. languidus*; OD)]. Dimorphism strongly accentuated. Macroconchs (*Strigoceras* and all the synonyms, excluding *Cadomoceras*) of medium size, discoidal oxyconic; involute with very small umbilicus and only slightly eccentric coiling; the whorl section, subtriangular to oval, high and compressed, ending in a hollow, unsculptured septicarinat keel; sinuous to falcoid or irregular ribs, normally divided to the height of the inflexion points, more

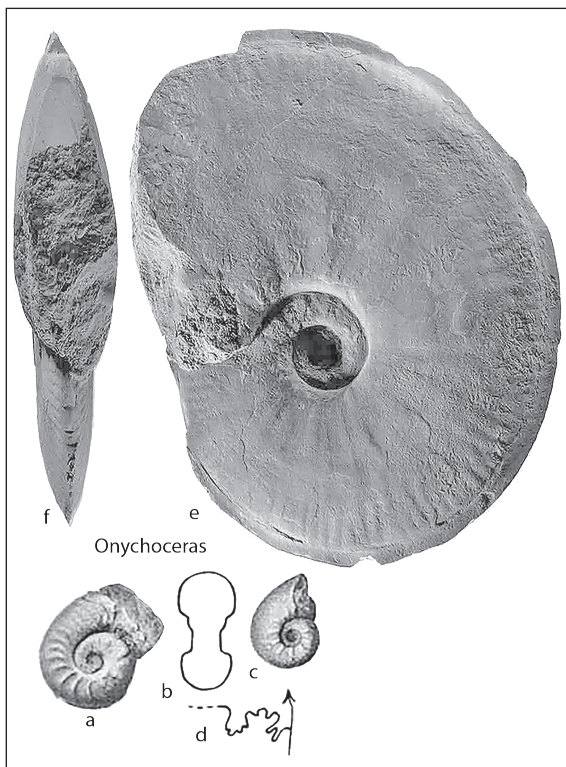


FIG. 2. Strigoceratidae, Strigoceratinae 1.

developed on the upper part of the flanks; more-or-less developed spiral striation, clearly visible in specimens with preserved shells; one to four lateral depressions or furrows; complex suture with E deeper than L and with incised elements. Microconchs (*Cadomoceras*) of small size (15–25 mm in diameter), eccentric coiling with involute inner whorls and accentuated uncoiling on the body chamber; shells smooth on inner whorls or occasionally with falcoid secondary ribs on outer whorls, venter carinate, mainly on inner whorls, or rounded. Aperture with large spatulate lateral apophyses and ventral rostrum. *Middle Jurassic*: *lower Bajocian* (Ovale Zone)—*lower Bathonian* (Zigzag Zone, Macrescens Subzone): Austria, Belgium, France (extra-Alpine and Alps), England, Germany, Hungary, Italy (Apennines and Sicily), Poland, Portugal, Slovakia, Spain (including Balearic Islands), Switzerland, North Africa,

Egypt (Sinai), Caucasus, Turkmenistan, Iran, ?India, Japan, ?Madagascar, Mexico, USA (Oregon and Alaska) and Canada.—FIG. 3, 1*a–d*. **S. truellei* (D'ORBIGNY); 1*a–c*, holotype, macroconch, *upper Bajocian*, Parkinsoni Zone, Densicostata Subzone, Bayeux, Calvados, France, $\times 0.48$ (new; also figured by RIOULT & others in FISCHER & others, 1994, pl. 50, 2, MNHN.FR04117, Muséum National d'Histoire Naturelle, Paris); 1*d*, suture (original of D'ORBIGNY, 1845 in 1842–1851, pl. 117, 2).—FIG. 3, 1*e–j*. *S. cadomense* (DEFrance); 1*e*, holotype, microconch; $\times 1$ (D'ORBIGNY, 1846 in 1842–1851, pl. 129, 4); 1*f–h*, microconch, *upper Bajocian*, Sully, Calvados, France, $\times 1.5$ (new; collection Rioult, MNHN.FB46072).—FIG. 3, 1*i–j*. *S. nepos* (PARONA), lectotype, microconch, *upper Bajocian*, Subfurcatum Zone, Schroederi Subzone, Monte Melleta, Gallio, Vicenza, Italy, $\times 1.5$ (new, original in PARONA, 1896, pl. 1, 13; also figured in STURANI, 1971, pl. 5, 7; Museo Regionale di Scienze Naturali di Torino).

Praestrigites BUCKMAN, 1924, pl. 466 [**P. praenuntius*; OD] [= *Deltostrigites* BUCKMAN, 1924, pl. 467 (type, *D. deltatus*; OD)]. Medium-sized macroconchs, discoidal, involute oxycones, with well-developed hollow keel, ribs irregularly branched but sometimes smooth and featureless, without spiral fluting or furrows; suture quite similar to that of *Strigoceras*. Microconchs unknown. For SCHWEIGERT & others (2007, p. 6) this is synonymous with *Strigoceras* but has less marked ribbing, has no spiral furrows, and precedes it in the stratigraphic record. *Middle Aalenian* (Bradfordensis Zone)–*lower Bajocian* (Discites Zone): England, France, Germany, Hungary, Italy, Portugal, Spain (Betic Cordillera and Iberian Range), Morocco (Atlas), and USA (Oregon, ?Alaska).—FIG. 3, 2*a–c*. **P. praenuntius* (BUCKMAN), holotype, macroconch, *middle Aalenian*, Bradfordensis Zone, *Brasilia gigantea* horizon, Horn Park, Inferior Oolite, bed 5a, Dorset, England, $\times 0.8$ (2*a*, SCHWEIGERT & others, 2007, text-fig. 2;

2*b–c*, new from BG3D Type Fossils; British Geological Society, inventory no. BGS GSM 37314).

Subfamily PHLYCTICERATINAE Spath, 1928

[Phlycticeratinae SPATH, 1928, p. 89]

[=Phlycticeratidae ARKELL, 1950, p. 365;
=Oecoptychiinae (*partim*) WESTERMANN,
1956, p. 273 =Oecoptychiidae ARKELL,
1957 (*partim*), p. 296]

Shells involute, of variable size, with macroconchs much larger than microconchs, and eccentric coiling especially well-marked in microconchs. Ribs not very strong, usually with tubercles, and with spiral striation; venter with strong, sometimes serrated hollow keel. Nuclei of macroconchs and microconchs very similar but differ sharply in adults. Sutures in macroconchs complex, with ramified elements, but are simple in microconchs, with highly developed lappets.

The family Oecoptychiidae ARKELL, 1957, is synonymous with Phlycticeratinae because, as shown by SCHWEIGERT & DIETZE (1998) and SCHWEIGERT & others (2003, 2007), the microconch *Oecoptychius* and the macroconch *Phlycticeras* are dimorphs.

According to SCHWEIGERT & others (2007, p. 62), modified by SCHWEIGERT & KAPITZKE (2018, p. 119), the following genera should be included in Phlycticeratinae: *Esericeras* BUCKMAN, 1920, *Csernyeiceras* GÉCZY, 1966, *Onychoceras* WUNSTORF, 1905, *Phlycticeras* HYATT, 1900, *Oecoptychius* NEUMAYR, 1878, *Strungia* ARKELL, 1952a, *Petitclercia* ROLLIER, 1909, *Oxydiscites* DACQUÉ, 1934, *Sphaerodomites* ROLLIER, 1909, and *Neopetitclercia* SCHWEIGERT & KAPITZKE, 2018, but some inconsistencies appear in this classification. The genus *Esericeras* belongs to the Phymatoceratinae, as proposed by HOWARTH (2013, p. 100). The dimorphous couple *Onychoceras*–*Csernyeiceras*, included in Hammatoceratidae by HOWARTH (2013, p. 103, 105), are actually the oldest genuine Strigoceratidae. Here, these are excluded from Phlycticeratinae and

transferred to Strigoceratinae because they originate (late Toarcian) and becomes

extinct (early Aalenian) long before of the first appearance (late Bajocian) of the

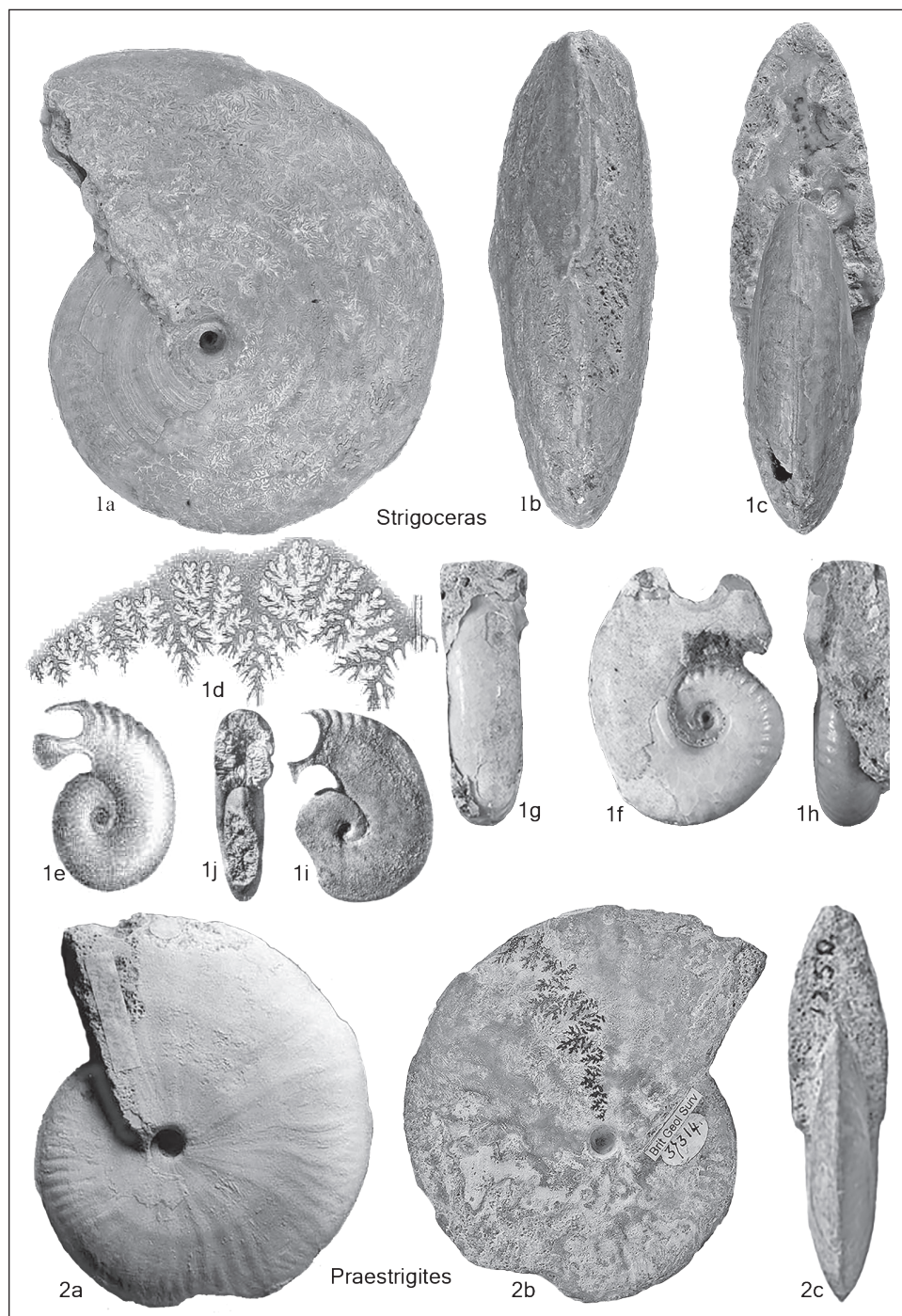


FIG. 3. Strigoceratidae, Strigoceratinae 2.

genuine Phlycticeratinae. As noted above, *Granulochetoceras* and *Cymaceras*, included in Strigoceratinae by SCHWEIGERT & others (2007, 2011), are here transferred to Phlycticeratinae. The microconch *Oecoptychoceras* BUCKMAN, 1920, and its probable dimorphous *Melendezia* FERNÁNDEZ-LÓPEZ, 1985, are here also included in this subfamily, being the oldest Phlycticeratinae, which possibly descend from Strigoceratinae in the late Bajocian (Garantiana Zone). *Diplesioceras* BUCKMAN, 1920, an *incertae sedis* form that was considered a dimorphic microconch of *Melendezia* by FERNÁNDEZ-LÓPEZ (1985), has been included as a possible Hildoceratoidea by HOWARTH (2013, p. 121). Meanwhile, *Protophites* EBRAY, 1858, included in Oecoptychiidae by ARKELL (1957, p. 296), is a microconch currently placed in the family Pachyceratidae by ÉNAY & HOWARTH (2019), and should be excluded from Phlycticeratinae.

SCHWEIGERT & DIETZE (1998) and SCHWEIGERT & others (2003, 2007) noted that *Csernyeiceras*, which has usually been included in Hammatoceratidae, is a typical Strigoceratidae and could represent the direct ancestor of *Phlycticeratidae* and therefore of all the Phlycticeratinae, whereas *Strigoceras* belongs to a convergent lineage which split off in the Aalenian from the “*Phlycticeratidae*” lineage of the Strigoceratidae. However, as shown above, the couple *Onychoceras*-*Csernyeiceras* is not a Phlycticeratinae, and represents the direct ancestor of the Strigoceratinae (*Praestrigitidae* and *Strigoceras*). The large interval between the last records of *Csernyeiceras* (lower Aalenian) and the first records of the genuine Phlycticeratinae (upper Bajocian, Garantiana Zone) support this proposal. The origin of the Phlycticeratinae occurred in late Bajocian, with the dimorphic pair *Oecoptychoceras*-*Melendezia* possibly being a transitional genus between the subfamilies Strigoceratinae and Phlycticeratinae (see DONOVAN & others, 1981, p. 144; FERNÁNDEZ-LÓPEZ, 1985, p. 140). *Middle Jurassic* (upper Bajocian,

Garantiana Zone)–*Upper Jurassic* (lower Kimmeridgian, Hypselocyclum Zone): Europe, Indo-Madagascan Province (India and Madagascar) and East Pacific (Oregon, Mexico, and Andes).

Oecoptychoceras BUCKMAN, 1920, T.A. III, p. 24 [**O. subrefractum*, pl. 176; OD] [= *Melendezia* FERNÁNDEZ LÓPEZ, 1985, p. 205 (type, *M. aenigmatica* FERNÁNDEZ LÓPEZ, 1985, OD)]. Microconchs are transitional between those of *Strigoceras*, *Cadomoceras*, and *Oecoptychius*, have small, highly involute inner whorls, which uncoil strongly the body chamber; fine, dense ribs on inner whorls, interrupted on the venter, become falcid, stronger, and are frequently grouped or divided in the lower third of the flanks in the adult stage; the adult aperture has well-developed lateral lappets and a ventral rostrum preceded by pronounced narrowing. Macroconchs (*Melendezia*) have medium-sized shells with a simple aperture; moderately involute coiling, ogival compressed whorl section; acute umbilical edge, and a fine, slightly undulating keel on the venter; simple, falcid, or sinuous ribs on early whorls become frequently grouped or divided on the lower part of the flanks in adults; suture unknown in both dimorphs. FERNÁNDEZ-LÓPEZ (1985, p. 204) considered *Diplesioceras* BUCKMAN, 1920, the possible microconch of *Melendezia*, but this cannot be confirmed. On the other hand, *Oecoptychoceras* was included in Sphaeroceratidae by ARKELL (1957, p. 292), and more recently its type species has been included in the genus *Oecoptychius* (SCHWEIGERT & DIETZE, 1998; SCHWEIGERT & others, 2003; BARDHAN & others, 2010; etc.). Nevertheless, it is more likely that it represents the dimorphic microconch of *Melendezia* FERNÁNDEZ-LÓPEZ, because the partner *Oecoptychoceras*-*Melendezia* corresponds better to the morphology of the Phlycticeratinae and because the two possible dimorphs occupy the same stratigraphic range. According to SCHWEIGERT & DIETZE (1998, p. 5, 22) and JAIN (2017,

p. 138), *Melendezia* FERNÁNDEZ-LÓPEZ and *Oecoptychoceras* BUCKMAN are junior synonyms of *Phlycticeras* and *Oecoptychius*. The dimorphic pair *Oecoptychoceras-Melendezia* are assumed to be a transitional genus between the subfamilies Strigoceratinae and Phlycticeratinae (see DONOVAN & others, 1981, p. 144; FERNÁNDEZ-LÓPEZ, 1985, p. 140). *Upper Bajocian* (Subfurcatum–Parkinsoni Zones): England, France, Germany, Italy (Sicily), and Spain (Iberian Cordillera).—FIG. 4, 1a–b. *O. aenigmaticum* (FERNÁNDEZ LÓPEZ), holotype, macroconch, *upper Bajocian*, Garantiana Zone, Cella, Teruel, Spain, $\times 1$ (FERNÁNDEZ-LÓPEZ, 1985, pl. 17, 11a–b; ICE2/12, Museo de Paleontología, Universidad Complutense, Madrid).—FIG. 4, 1c–e. **O. subrefractum* BUCKMAN, holotype, microconch, *upper Bajocian*, ?Parkinsoni Zone, Inferior Oolite Group, Broadwindsor, England, $\times 2$ (new; original in BUCKMAN, 1920, pl. 176; British Geological Survey, BGS GSM 32023).—FIG. 4, 1f–g. *O. grossouvrei* (BRASIL), microconch, *upper Bajocian*, Parkinsoni Zone, Oolithe ferrugineuse de Bayeux, Port-en-Bessin, France, $\times 1.5$ (new; also figured by SCHWEIGERT & DIETZE, 1998, pl. 1, 3; Staatliches Museum für Naturkunde Stuttgart, inventory no. 69291, cast of a specimen from a private collection).

Oecoptychius NEUMAYR, 1878, p. 78 [**Nautilus refractus* REINECKE, 1818, p. 66; SD MUNIER-CHALMAS, 1892, p. 171] [= *Phlycticeras* HYATT, 1900, p. 569 (type *Nautilus pustulatus* REINECKE, 1818, p. 84; OD), *pro Lophoceras* PARONA & BONARELLI, 1897, p. 44 (*non* HYATT, 1893, p. 466) (Nautilida; type, *Nautilus pentagonus* J. SOWERBY, 1819, p. 89)]. *Oecoptychius* was included in Sphaeroceratidae by ARKELL (1957, p. 296), but the dimorphism between *Phlycticeras* and *Oecoptychius* is well established (CALLOMON, 1981; SCHWEIGERT & DIETZE, 1998, 1999; SCHWEIGERT & others, 2000, 2003, 2007), although BARDHAN & others (2010) disagree with this view.

The size ratio between macroconchs and microconchs is enormous, as much as 10–15 mm. Macroconchs (*Phlycticeras*) of medium size with involute to semi-evolute coiling, subpentagonal to oval compressed whorl section, ending in thin and elevated (sometimes dentate) hollow keel; ribs radial to slightly falcoid, sometimes divided; up to three rows of tubercles and more-or-less developed spiral striation; suture complex with E as deep as L and an elevated and branched E–L saddle. Microconchs (*Oecoptychius*) very small in size with smooth, almost spherical inner whorls and uncoiling strongly with elliptical (scaphitoid) last whorl; fine biplicate ribs in the adult stage that are interrupted on the venter but lacking a keel; aperture complex with large lateral lappets and a highly elevated frontal rostrum. Early whorls and suture of the nuclei similar, but with accentuated differences between macro- and microconchs; for example, *Oecoptychius* with no tubercles at all and, most importantly, lacking the ventral keel of *Phlycticeras*. ?*Uppermost Bajocian* (Parkinsoni Zone)–*upper Callovian* (Athleta Zone, Trezeense Subzone): Austria, England, France, Germany, Hungary, Italy (Sicily), Poland, South America (Andes), Spain (Betic Cordillera and Iberian Range), Switzerland, India (Kutch), Madagascar, Mexico, USA (Oregon).—FIG. 4, 2a–d. **O. pustulatus* (REINECKE); 2a–b, lectotype, juvenile macroconch, *middle Callovian*, Coronatum Zone, Ützing, Eastern Franconian Jura, Germany, $\times 2$ (new; also figured SCHWEIGERT & DIETZE, 1998, pl. 9, 2a–b; Coburg Natural History Museum Collection, no. 1349/1, coll. Reinecke); 2c–d, macroconch, *middle Callovian*, Coronatum Zone, Arçay at Loudun, Poitou, West France, $\times 0.8$ (SCHWEIGERT & DIETZE, 1998, pl. 9, 2a–b; Staatliches Museum für Naturkunde Stuttgart, inventory no. 63455/1, leg. F. Bemmerer).—FIG. 4, 2e–g. **O. mexicanus* (SANDOVAL & WESTERMANN); 2e–g, holotype, macroconch, *lower Callovian*, Bodenbenderi Zone, Frickites Association, Unit 13 of section Ct, Couailote, Guerrero State,

México, $\times 0.5$ (SANDOVAL & WESTERMANN in SANDOVAL & others, 1990, pl. 4, 2a–b; IGM-4219, UNAM, México); 2g, suture of the specimen GM 4030 at H = 40 mm, from the same locality and association as the previous specimen (SANDOVAL & WESTERMANN in SANDOVAL & others, 1990, text-fig. 9, d).—FIG. 4, 2b–k. **O. refractus* (REINECKE); 2b–i, lectotype, microconch, middle Callovian, Coronatum Zone, Eastern Franconian Jura, Germany, $\times 2$ (new; also figured SCHWEIGERT & DIETZE, 1998, pl. 10, 10a–c; Coburg Natural History Museum Collection (no. 52/1, coll. Reinecke); j–k, complete adult microconch with well-developed apertural apophysis, middle Callovian, Jason Zone, Saint-Laon near Loudun, France, $\times 2$ (SCHWEIGERT & DIETZE, 1998, pl. 9, 4; Staatliches Museum für Naturkunde Stuttgart, inventory no. 63459/1).

Strungia ARKELL, 1952a, p. 287 [**Oppelia redlichi* POPOVICI-HATZEG, 1905, p. 18; OD]. Macroconchs medium-sized; involute with subrectangular-ovate whorl section, tectiform venter becoming rounded in the adult stage; ribs faint, fasciculate ending in ventrolateral tubercles; surface with spiral striation; suture unknown. Microconchs not identified. According to SCHWEIGERT & others (2003, 2007), *Oppelia redlichi* POPOVICI-HATZEG represents an early offshoot of *Phlycticeras* in the middle Bathonian and clearly belongs to Phlycticeratinae. Likewise, according to SCHWEIGERT & others (2007, p. 45), another unique “*Strungia*” *arabica* ARKELL, from Central Arabia (ARKELL, 1952a, p. 287, pl. 28, fig. 2) displays a relatively wide umbilicus and hardly resembles a strigoceratid. It might be better interpreted as a microconch of the co-occurring genus *Micromphalites*. The Callovian species “*Strungia*” *voultensis* LISSAJOUS morphologically differs significantly from *S. redlichi* and may represent a hectioceratin (ELMI, 1967; SCHWEIGERT & others, 2003, 2007). Middle Bathonian–?lower Callovian

(Gracilis Zone): Bulgaria, France, Germany, Spain, Romania, Saudi Arabia, South America (Andes).—FIG. 5, 1a–b. **S. redlichi* (POPOVICI-HATZEG), lectotype, macroconch, upper Bathonian, Mount Strunga, Bucegi Massif, Romania, $\times 0.7$ (POPOVICI-HATZEG, 1905, pl. 5, 1a–b).

Petitclercia ROLLIER, 1909, p. 621 [**Ammonites mirabilis* DE GROSSOUVRE, 1891, p. 258; SD ROLLIER, 1909, p. 621]. Small macroconch; moderately involute, whorl section tightly compressed, vertical umbilical wall, sharp umbilical angle, and sharp fastigate venter; inner whorls smooth; ribs prorsiradiate and weak or absent on lower part of flank, becoming rectiradiate on upper part of flank; three rows of lateral thickenings. Dimorphism unknown. BRASIL (1895) included *Ammonites mirabilis* DE GROSSOUVRE, 1891, the type species of *Petitclercia*, in *Strigoceras*, but according to SCHWEIGERT & others (2007), *Petitclercia* represents an offshoot of Phlycticeratinae, in view of its three longitudinal rows of nodules on the flanks, reflecting homologous sculptural characters of the early Callovian *Phlycticeras*. The loss of the septicarinate keel is a noteworthy development distinguishing *Petitclercia* and *Neopetitclercia* from all other Phlycticeratinae. Middle Jurassic (lower-middle Callovian): France.—FIG. 5, 2a–c. **P. mirabilis* (DE GROSSOUVRE); 2a–b, lectotype, ?macroconch, middle Callovian, Anceps or Coronatum Zones, Luçon, Vendée, France, $\times 1$ (DE GROSSOUVRE, 1891, pl. 9, 4a–b); 2c, macroconch, upper Callovian, Athleta Zone, Trezeense Subzone, Montreuil-Bellay, Maine-et-Loire, France, $\times 1$ (SCHWEIGERT & KAPITZKE, 2018, fig. 3H; private collection of P.-Y. Boursicot, no. Mb9331).

Granulochetoceras GEYER, 1960, p. 423 [**Ammonites (Ochetoceras) uracensis* DIETLEN, 1911, p. 332; OD]. Small- to medium-sized oxyconic ammonite; narrow umbilicus; steep umbilical wall; rounded umbilical edge; one or two lateral furrows; shell with

spiral striation; falcoid ribbing, primaries starting from nodules at the umbilical edge;

secondaries starting from strong bases or nodules; ribs not reaching keel; serrate,

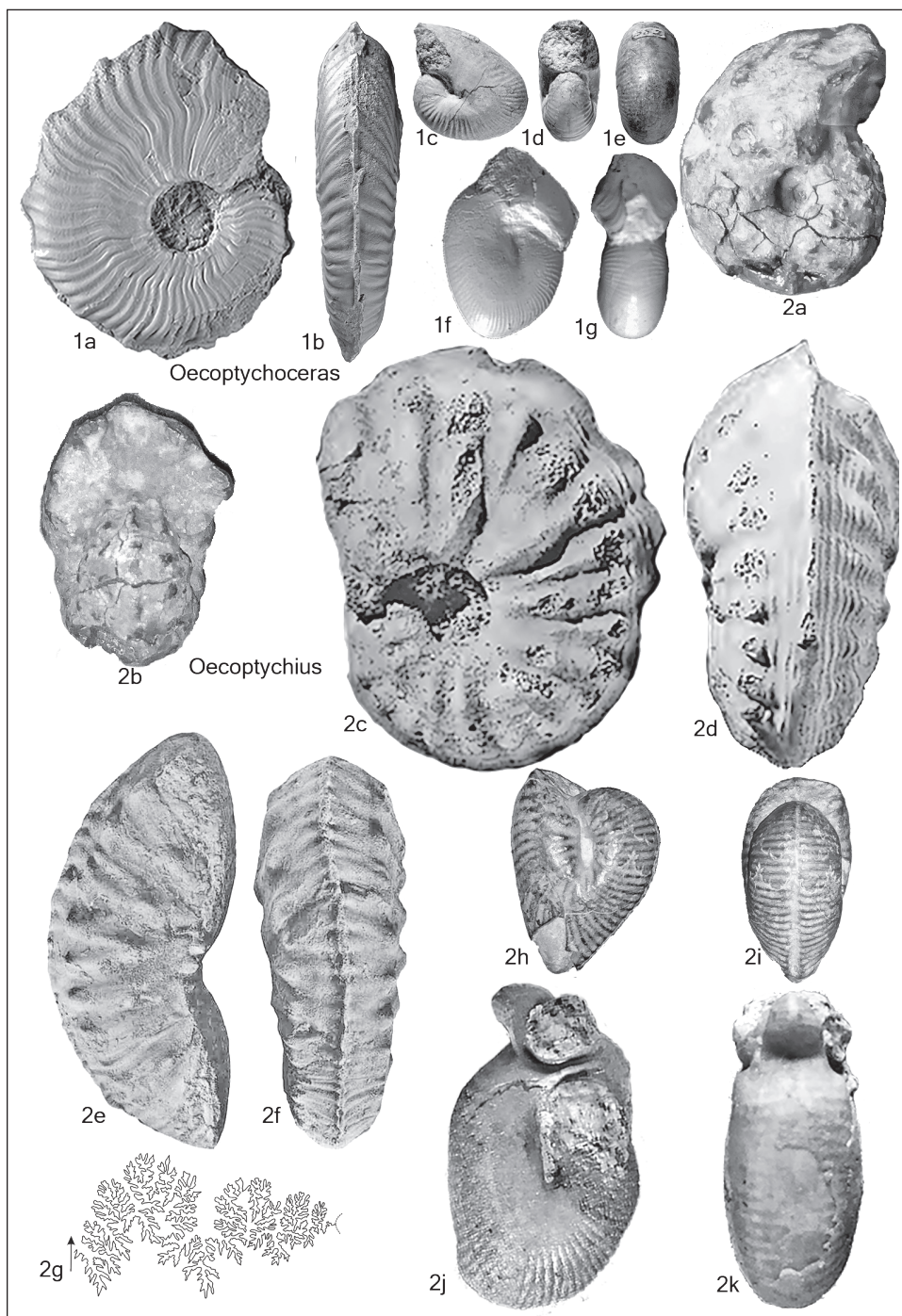


FIG. 4. Strigoceratidae, Phlycticeratinae 1.

partly undulating septicarinate keel. Suture is not well known. GEYER, 1960, defined the genus *Granulochetoceras* as based on the specimen described and figured as *Ammonites* (*Ochetoceras*) *uracensis* by DIETLEN (1911). Much later, SCHWEIGERT & others (2011, p. 283) showed that the specimen described by Dietlen is very similar to the specimen of *Ammonites argonautoides* MAYER var. *sulculifera* FONTANNES, 1876, in DUMORTIER & FONTANNES (1876, p. 50, pl. 5, fig. 5) and therefore is a subjective synonym of *G. sulculiferum* (FONTANNES, 1876). *Upper Callovian–upper Kimmeridgian* (excluding “*Granulochetoceras*” *oppeliisculptum* SCHWEIGERT & others, 2007, from *upper Bajocian*, Garantiana Zone of northeast Spain, which clearly should not be included in this genus and should be transferred to the genera *Oppelia* or *Strigoceras*): France, Germany, Hungary, Iran, Switzerland, and Spain.—FIG. 5, 3a–b. **G. uracense* (DIETLEN); 3a, lectotype, macroconch, *lower-Kimmeridgian*, Bad Urach, Baden-Württemberg, southern Germany, $\times 1$ (DIETLEN, 1911, fig. 1); 3b, photograph of the same specimen classified by SCHWEIGERT & others (2011) as *G. sulculiferum* (FONTANNES) (= holotype of *Ammonites uracensis* DIETLEN, $\times 1$ (SCHWEIGERT & others, 2011, fig. 1; Staatliches Museum für Naturkunde Stuttgart, inventory no. 12822)).—FIG. 5, 3c. *G. argonautoides* (MAYER), macroconch, *lower Kimmeridgian*, Hypselocyclum Zone, Schwarzbach-Formation, Almenbüel, Randen/Kt. Schaffhausen, Germany, $\times 1$ (MOOR, 2009, pl. 10; also figured by SCHWEIGERT & others, 2011, fig. 1; Moor Collection, MO.2009/11).—FIG. 5, 3d. *G. cristatum* (DIETERICH), *lower Kimmeridgian*, Planula Zone, Wohlgeschichteten Kalke Formation, Sausserbrunnen near Laufen, Bavaria, east Germany, $\times 1$ (SCHWEIGERT & others, 2011, fig. 2; Staatliches Museum für Naturkunde Stuttgart, inventory no. 67763).

Vastites ARKELL, 1951a, p. 27 [**V. vastus*; OD]. Large, almost smooth, compressed, involute; inner whorls with strong, hollow

keel (septicarinate), and outer whorls with rounded venter; whorl sides with little or no ornament except for vague, wide, sigmoid ribs near the aperture. Sutures with long, thick-stemmed L and U₂, and wide, blunt auxiliaries; the first bifid and possibly formed by twinning of the first two auxiliaries. *Vastites* remains rare and poorly understood. ARKELL (1957, p. 270) included it in Sonniniidae; however, according to CALLOMON (1981, p. 118) and PAGE (1996, p. 47), it may be a complete adult macroconch of a late species of *Strigoceras*. SCHWEIGERT & others (2007, p. 45) debated the taxonomic status of *Vastites* and concluded that for the moment, the systematic position of *Vastites* within strigoceratids remains doubtful, but nonetheless agree that *Vastites* should be included in the Strigoceratidae due to its falcoid or falcate ribbing and lateral spiral ridge. More material is needed for further discussion. *Lower Bathonian*: England. — FIG. 5, 4a–b. **V. vastus* ARKELL, holotype, macroconch, *lower Bathonian*, Zigzag Zone, Brambleditch quarry, South of Doultling, Somerset, England, $\times 0.25$ (new; also figured by ARKELL, 1951a, pl. 1, 1a–c and ARKELL, 1957, fig. 313, 1a–b; Sedgwick Museum of Earth Sciences, University of Cambridge, England, J.21368).

Sphaerodomites ROLLIER, 1909, p. 619 [**Ammonites calcaratus* COQUAND, 1853, p. 441; OD] [= *Oxydiscites* DACQUÉ, 1934, p. 330 (ex. ROLLIER, 1909 (*nom. nud.*)) (type, *Ammonites laffoni* MOESCH, 1867, p. 293; OD) = *Barthelia* OLÓRIZ & SCHAIRER, 1983, p. 577 (type, *B. subbetica*, OD); = *Securisites* CARIOU, ELMI, & MANGOLD, 1992, p. 1267 (type, *S. securicristatus*; OD)]. The dimorphism between the macroconch *Oxydiscites* and the microconch *Sphaerodomites* is well established (SCHWEIGERT & others, 1999, p. 59). Macroconchs (*Oxydiscites*, *Securisites*) small to medium size, involute with minute umbilicus and scaphitoid last whorl; inner whorls sphaeroconic, later having an ogival whorl section and sharp venter with a finely

serrate, high-septicarinat keel. Ribs falcoid, similar to those of *Cymaceras* and divided at

the inflection points; spiral striation visible in well-preserved specimens; small ventrolateral

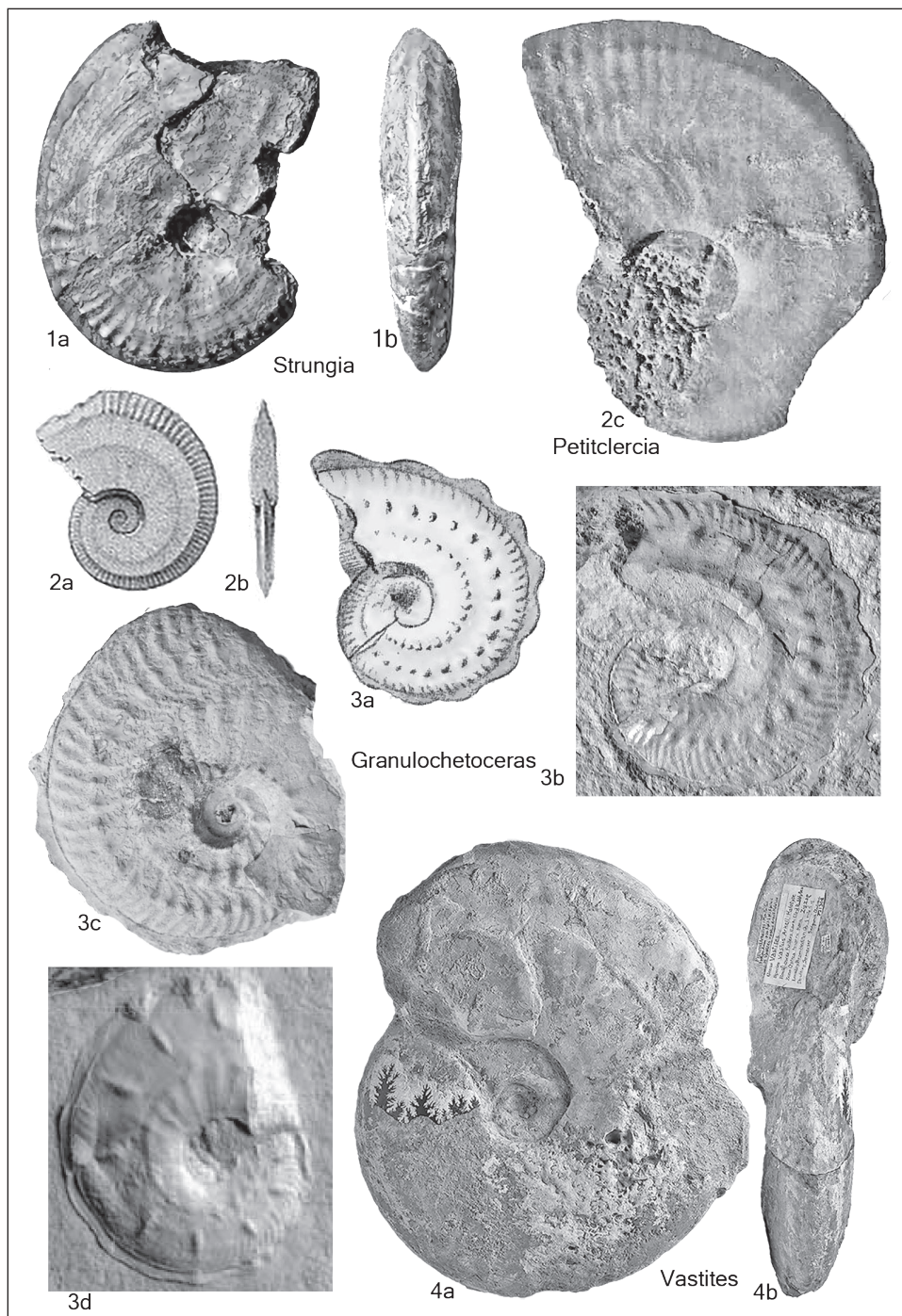


FIG. 5. Strigoceratidae, Phlycticeratinae 2.

tubercles present in some species. Suture similar to those of *Cymaceras* and *Ochetoceras*, simple with several elements, but hardly ramified. Microconchs (*Sphaerodomites*, *Barthelia*) are small size sphaerocones, with scaphitoid last whorl, minute umbilicus, a finely serrate keel bordered by smooth bands or shallow grooves; aperture with lateral lappets and a hook-like umbilical thickening; ribs falcoid to polyschizotome, and spiral striation present in well-preserved specimens; suture rather simple. The macroconchs have been included in Ochetoceratinae (ARKELL, 1957, p. 279; GEYER, 1960, p. 418; ZIEGLER, 1974, p. 33), in Streblitinae (OLÓRIZ, 1978, p. 55) or in Taramelliceratinae (CARIOU & SEQUEIROS, 1987, p. 500). The microconchs were included in Taramelliceratinae by ARKELL (1957, p. 282; OLÓRIZ & SCHAIRER, 1983, p. 577; MARCHAND & others, 2002, p. 470); however, according to SCHWEIGERT & others (1999, 2007) and SCHWEIGERT & KAPITZKE (2018), these forms are presumably junior synonyms of *Sphaerodomites*, representing the dimorphic partner *Oxydiscites*/*Sphaerodomites* and should be included in Phlycticeratinae. *Middle Jurassic–Upper Jurassic, upper Callovian* (Athleta Zone)–*lower Kimmeridgian* (Hypsolocyclum Zone): Algeria, England, France, Germany, Italy (Sicily), Morocco, Spain, Switzerland, Syria.—FIG. 6, 1*a–d*. **S. calcaratus* (COQUAND); 1*a–b*, microconch, *lower Oxfordian*, Renggeri Zone, Liesberg, Basel, Switzerland, ×1 (DE LORIO, 1898, pl. 5, 2*a–b*; Naturhistorische Museum Basel collection); 1*c–d*, microconch, *lower Oxfordian*, Mariae Zone, Praecordatum Subzone, Pont du Diable (Doubs), east France, ×1.5 (MARCHAND & others, 2002, pl. 1, 6; coll. P. Courville).—FIG. 6, 1*e–h*. *S. laffoni* (MOESCH); 1*e–f*, holotype, macroconch, Malm gamma, Randen bei Blamberg/Baden, Schaffhausen, Switzerland, ×1 (1*e*, SCHLEGELMILCH, 1994, pl. 15, 12; 1*f*, MOESCH, 1867, pl. 1, 4*b*; also figured by DE LORIO, 1876 in 1876–1878, pl. 2, 2, ARKELL, 1957, fig. 325, 6, GEYER,

1960, text-fig. 5, and HÖROLDT, 1964, pl. 6, 8; Geol. Inst. E.T.H. Zürich collection, inventory no. Po. 8103); 1*g*, macroconch, *lower Kimmeridgian*, Platynota Zone, Saufang Quarry, near Geisingen, Germany, ×1 (SCHWEIGERT & KAPITZKE, 2018, Fig. 3*G*; Staatliches Museum für Naturkunde Stuttgart, inventory no. 704225, leg H. Schick); 1*h*, suture of a specimen from Weisser Jura Epsilon, Tuttlingen, Württemberg, Germany; inventory no. 19786, Staatliches Museum für Naturkunde Stuttgart, Germany, ×3 (GEYER, 1960, text-fig. 4).—FIG. 6, 1*i*. *S. securicristatus* (CARIOU & others), holotype, macroconch, *upper Callovian*, Montreuil-Bellay (Maine-et-Loire), France, ×0.8 (CARIOU & others, 1992, pl. 1, 1; also figured by SCHWEIGERT & others, 1999, text-fig. 1; Charreau coll., Université de Poitiers, MBe8323).

Neopetitlercia SCHWEIGERT & KAPITZKE, 2018, p. 123 [**N. jantschkei*; OD]. Macroconchs, small, oxyconic, body chamber with eccentric coiling; umbilicus very narrow, umbilical wall steep to overhanging, venter narrow, rounded, without a keel; ribs rursiradial, weak in preadult whorls, stronger, with nodules at the inflection point, and weak lateral sulcus in the adult whorl; suture extremely complex. Microconchs very small; sphaerocones, smooth without keel or ribs with very narrow umbilicus, body chamber with eccentric coiling, and aperture with lateral lappets; *lowermost Kimmeridgian* (Bimammatum Zone): France, Germany. —FIG. 6, 2*a–c*. **N. jantschkei* SCHWEIGERT & KAPITZKE; 2*a*, holotype, macroconch, *lower Kimmeridgian*, Bimammatum Zone, Hauffianum Subzone, Plattenberg quarry, near Schömberg, SW Germany, ×1 (SCHWEIGERT & KAPITZKE, 2018, text-fig. 3*a*; Staatliches Museum für Naturkunde Stuttgart, inventory no. 70417); 2*b–c*, allotype, microconch, same stratigraphic position and locality as above, ×2 (SCHWEIGERT & KAPITZKE, 2018, text-fig. 3*b–c*; Staatliches Museum für Naturkunde Stuttgart, inventory no. 70418).

Cymaceras QUENSTEDT, 1887 in 1882–1888, p. 842 [**Ammonites guembeli*

OPPEL, 1862 in 1862–1863, p. 159; OD] [= *Trochiskioceras* SCHAIRER & SCHLAMPP,

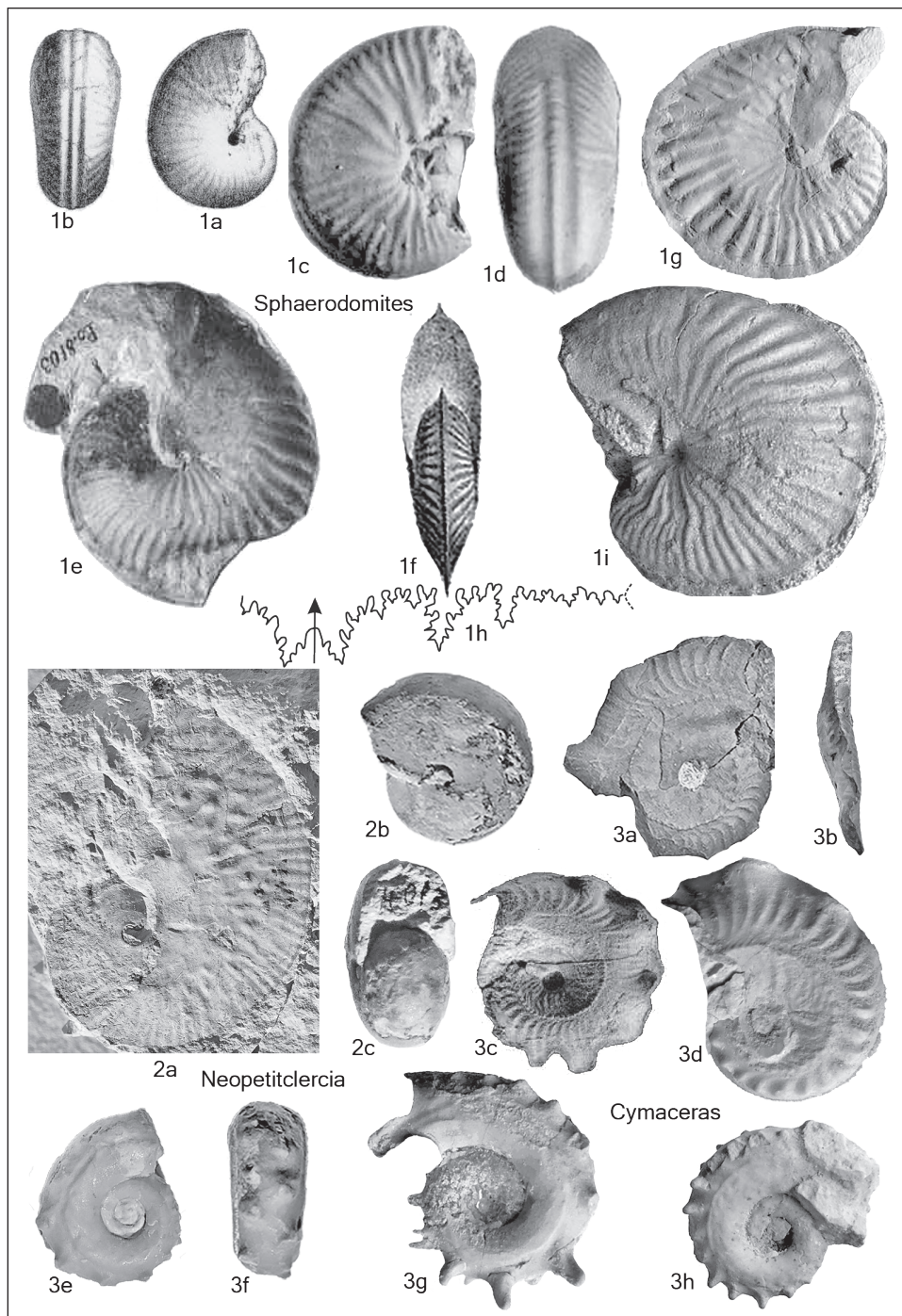


FIG. 6. Strigoceratidae, Phlycticeratinae 3.

1991, p. 108 (type, *Ammonites bidentosus* QUENSTEDT, 1857 in 1856–1858, p. 616, ICZN 2005, Opinion 2123, p. 159; OD)]. Macroconchs (*Cymaceras*), medium to small size, involute, with an ogival-subtriangular whorl section much higher than wide, with small midlateral crest or spiral groove; ribs falcoid with faintly marked prorsiradiate primaries and rursiradiate secondaries, sometimes very strong, arising from a median row of minute tubercles; inner whorls with small ventrolateral tubercles; venter becomes sharpened and coarsely crenulated on middle and outer whorls with crenulation or tubercles bent towards the opposite side; suture unknown. Some specimens exhibit both spiral striation and lateral spiral grooves, indicating affiliation with Strigoceratidae (SCHWEIGERT & others, 2007). Microconchs (*Trochiskioceras*) of very small size, moderately evolute to involute; aperture with two large lateral lappets and pronounced frontal rostrum; on the outer half of the flank a spiral crest or a spiral lateral groove, which may be externally accompanied by a filamentary spiral keel; a row of large spines alternating on the outer side of each flank in adult stage and rounded nodes in the inner whorls; the final part of the body chamber again having ventrolateral nodes or tubercles; suture simple. *Cymaceras* was included in Ochetoceratinae by ARKELL (1957, p. 278) and subsequent authors (GEYER, 1960; SCHAIRER & SCHLAMPP 1991; SCHICK, 2003; HORNING, 2004) and in Strigoceratinae by SCHWEIGERT & others (1999, 2007). However, given its general morphology and stratigraphic range, it may be more accurate to include it as a final branch of Phlycticeratinae. *Lower Kimmeridgian* (Platynota and Hypselocyclum Zones): Germany, Switzerland (MOOR, 2009), Sicily (WENDT, 2017), and Iran (SEYED-EMAMI & SCHAIRER, 2011). — FIG. 6, 3a–d. **C. guembeli* (OPPEL); 3a–b, lectotype, macroconch, *lower Kimmeridgian*, Hypselocyclum Zone, Thalmäding, Franconia, Germany, ×1 (new; also figured by WEGELE, 1930, pl. 1, 1, HÖROLDT, 1964,

pl. 6, 5–6, and SCHLEGELMILCH, 1994, pl. 15, 8; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS I 630); *c*, macroconch, *lower Kimmeridgian*, Hypselocyclum Zone, Esselberg, Bavaria, Germany, ×1 (SCHAIRER & SCHLAMPP, 1991, pl. 1, 1; specimen 1986 II 71); 3d, macroconch, *lower Kimmeridgian*, Platynota Zone, Randen, Schaffhausen, Switzerland, ×1 (MOOR, 2009, pl. 3, 3; specimen no. MO.1990/12). — FIG. 6, 3e–h. *C. bidentosum* (QUENSTEDT); 3e–f, hypotype, microconch, *lower Kimmeridgian*, Germany, ×2.5 (new; Geologische Institut, Universität Tübingen, Germany; inventory no. GPIT-PV-62077); 3g, microconch, *lower Kimmeridgian*, Hypselocyclum Zone, Schaffhausen, Switzerland, ×2 (MOOR, 2009, pl. 3, 6; specimen no. MO.1991/12); 3h, microconch, *lower Kimmeridgian*, Hypselocyclum Zone, Schaffhausen, Switzerland, ×2 (MOOR, 2009, pl. 3, 7; specimen no. MO.1989/08).

Superfamily HAPLOCERATOIDEA Zittel, 1884

[*nom. transl.* ARKELL, 1957, p. 271
(*ex* Haploceratidae ZITTEL, 1884,
p. 411)] [=Oppeliaceae BUCKMAN, 1919,
p. xvi (superfamily); Oppeliaceae ARKELL
1950, p. 63 (superfamily); Oppeliaceae
ELMI, 1967, p. 530 (superfamily);
=Haploceratina BESNOV & MICHAILOVA,
1983, p. 733 (suborder)]

Haploceratoidea includes ammonites of variable size, small or medium being dominant, only exceptionally large. Morphology highly diverse: involute to moderately evolute oxycones, platycones, or even sphaerocones, variable whorl sections; from smooth or slightly ornamented (Lissoceratidae and Haploceratidae) to relatively well ornamented, but all having smooth innermost whorls, with different types of ribs, tubercles, and ventrolateral clavi (Hecticoceratinae, Taramelliceratinae, Distichoceratinae);

usually with ventral keels, unicarinate (many Oppeliinae or Hecticoceratinae), bicarinate (Thamboceratidae), apparently tricarinate (Ochetoceratinae) or with discontinuous keel (Taramelliceratinae), and occasionally with a non-keeled venter (Lissoceratinae, Haploceratoidea) or a flat venter bordered by keels. In Haploceratoidea, dimorphism is widespread and usually pronounced. Macroconchs, though larger than microconchs, rarely surpass 250 mm in diameter, and have slight eccentric coiling, with simple apertures. Microconchs, usually well differentiated from their corresponding macroconchs, can be dwarf (maximum diameter 70 mm), coiled eccentrically with frequent scaphitoid forms, with highly developed lappets and a ventral rostrum, and, at times, with diverse ornamentation (ribs and tubercles) that often makes it difficult to associate microconchs with their respective macroconchs. In some taxa (e.g., *Lissoceras-Microlissoceras*, *Poecilomorphus-Micropoecilomorphus*, *Oppelia-Oecotraustes*), dimorphism is clear and the dimorphic partners are firmly established. In other taxa, such as several Hecticoceratinae, and mainly in Clydoniceratidae (*Clydoniceras-Delecticeras*) and Thamboceratidae, dimorphism is less apparent, often making macroconchs and microconchs difficult to distinguish. Lastly, in some taxa (Hecticoceratinae, Ochetoceratinae, Taramelliceratinae, and Streblitinae), despite the appreciable differences in size and morphology between microconchs and macroconchs, the generic differences are less noticeable in microconchs, leading some microconchs to be assigned to more than one macroconch. Sutures are very variable, from relatively complex (Oppeliinae) to degenerated and simple (Thamboceratidae and Clydoniceratidae), but all are characterized by having a relatively high, wide, and asymmetric saddle L-U₂.

The origin of the Haploceratoidea and its phylogenetic relationships with other taxa has not been fully clarified. Several authors (ARKELL, 1957, p. 274; ELMI, 1967, p. 779; GÉCZY, 1967, p. 224; WESTERMANN,

1969, p. 49–52; SAPUNOV, 1971, p. 74; GALÁČZ, 1980, p. 55; CALLOMON, 1981, p. 143; FERNÁNDEZ-LÓPEZ, 1985, p. 173; SADKI, 1988, p. 239) have proposed that the *Bradfordia* group, the earliest Lissoceratidae, descended from late Aalenian hammatoceratids, whereas others (STURANI, 1971, p. 89; SANDOVAL, 1986, p. 451) contend that the haploceratoids are linked to the middle Aalenian graphoceratids. In fact, graphoceratids and the oldest lissoceratids (*Bradfordia*) have many common characters, such as the umbilical wall, periumbilical depression, and ribbing type. The suture is also very similar in Graphoceratidae and primitive Haploceratoidea.

Aptychi are calcitic bivalved plates commonly found singly or in pairs, are commonly isolated or associated with ammonites, but rarely are found *in situ*, and differ according to family. Aptychi with well-developed ribs (lamellaptychi and punctaptychi) have been associated with Haploceratoidea (Oppeliidae and Haploceratidae). These aptychi are abundant in the late-Jurassic and early Cretaceous forms (mainly *Neolissoceras*) but scarce or even absent in the mid-Jurassic ones. Lamellaptychi occur *in situ* in some oppeliids and haploceratids, such as *Taramelliceras* (QUEREILHAC, 2009), *Neochetoceras* (SCHERZINGER & others, 2015), *Fontannesella*, “*Lingulaticeras*,” and *Metahaploceras* (SCHWEIGERT, 2009), and lamellaptychi and punctaptychi appear *in situ* in the Oppeliidae (MĚCHOVÁ & others, 2010). Currently, it is accepted that the aptychi were part of the buccal apparatus and that its main function was to act as the lower jaw of the ammonoids, but other possible functions have been proposed. In the specific case of lamellaptychi, it has also been shown that, in addition to serving as a jaw, this structure can perform as an operculum, as ballast, or as a stabilizer, and possibly also for flushing and filtering (PARENT & others, 2014; PARENT & WESTERMANN, 2016).

Haploceratoidea includes the families Hebertoxyitidae, Lissoceratidae, Haplocera-

tidae, Oppeliidae, Thamboceratidae, and Clydoniceratidae. *Middle Jurassic (middle Aalenian, Bradfordensis Zone) – Lower Cretaceous*: worldwide.

Family HEBETOXYITIDAE Buckman, 1924

[Hebetoxyitidae BUCKMAN, 1924, p. 8)]

BUCKMAN, 1924 (T.A. V, p. 8) established the family Hebetoxyitidae to include *Hebetoxyites* BUCKMAN, 1924, *Kleistoxyites* BUCKMAN, 1922, and *Amblyoxyites* BUCKMAN, 1922 (the latter being synonymous with *Bradfordia*). These forms have discoidal shells that lack a keel and have a rounded venter, falcoid ribs, and moderately complex sutures. The rounded venter and suture are of the lissoceratid type, whereas the falcate or falcoid ribbing and lateral spiral ridge resemble the morphology of Strigoceratidae. Hebetoxyitidae was included in Strigoceratidae by ARKELL (1957, p. 271), but members of Hebetoxyitidae, particularly *Hebetoxyites*, differ from Strigoceratidae in lacking the hollow-floored keel and well-marked striation. In *Hebetoxyites*, the suture is less complex than in *Lissoceras*, whereas in *Amblyoxyites* this structure attains almost the complexity of an oppeliid, and therefore in agreement with ARKELL (1957, p. 275) and SCHWEIGERT & others (2003), this genus is here included in Bradfordiinae (Oppeliidae) as a junior synonym of *Bradfordia*. In Hebetoxyitidae, the ribs continue across the whorl, whereas in oppeliids the ribbing is irregular, with primary ribs splitting into secondaries, which are often confined to the outer part of the flanks. BUCKMAN (1924, in BUCKMAN 1909–1930) considered the phyletic position of the Hebetoxyitidae to be after Lissoceratidae, with an origin similar to oppeliids. *Kleistoxyites* was included in Strigoceratidae (synonymous with *Strigoceras*) by ARKELL (1957, p. 272) yet excluded from this family by SCHWEIGERT & others (2007, p. 49), who considered it likely to be an early representative of the Oppeliidae.

According to FERNÁNDEZ-LÓPEZ (2012), who accepted the family Hebetoxyitidae, “the phyletic position of the monospecific genus *Kleistoxyites*, from the Discites Zone of England, which appears to be older and has more complex sutures than *Hebetoxyites*, needs further investigation.” However, here it is shown that the differences in sutures are minimal and that *Kleistoxyites* (Discites Zone) immediately precedes *Hebetoxyites* (Ovale–Sauzei zones). The origin of Hebetoxyitidae remains unresolved, but Hebetoxyitidae evolved in addition to the parallel phyletic groups of Haploceratoidea (Lissoceratidae and Oppeliidae) during the late Aalenian and early Bajocian (FERNÁNDEZ-LÓPEZ, 2012, p. 72). This justifies including Hebetoxyitidae in Haploceratoidea rather than in Strigoceratoidea. *Middle Jurassic (uppermost Aalenian – lowermost upper Bajocian)*: Europe, Morocco, Tibet, USA (Oregon, Alaska), western Canada, Mexico, and Chile.

Hebetoxyites BUCKMAN, 1924, pl. 475 [*H. hebes*; OD]. Discoidal shells from small to medium size; compressed to oxycones, with a slight rise of the flanks around two-fifths of the whorl height. Umbilicus narrow in post-juvenile stages, with distinct or raised margin. Whorl section broadest at the lateral ridge, from which ventrally the flanks converge gently towards a narrow-rounded venter. Inner whorls smooth, with a rounded venter; mid and outer whorls with a blunt fastigate venter, but without a keel. Aperture simple in macroconchs, bearing lappets in microconchs. Ribbing falcoid or falcate, with blunt costae, simple or irregularly branched, sometimes becoming stronger on the outer half of the flank. Primaries bundled at the lower part of the flanks. The ribbing abutting the venter but not projected forward at the periphery and weakening on the outer flank through ontogeny. On the adult body chamber, ribbing faint or fading completely. Suture moderately complex with wide E, moderately broad L extending beyond the E and U₂ lobes. The second

lateral saddle higher than the first. *Lower Bajocian* (Ovale *Zone*—lower part of the Sauzei

Zone): England, France, Italy, Spain (Iberian and Betic ranges), Morocco, Tibet, USA

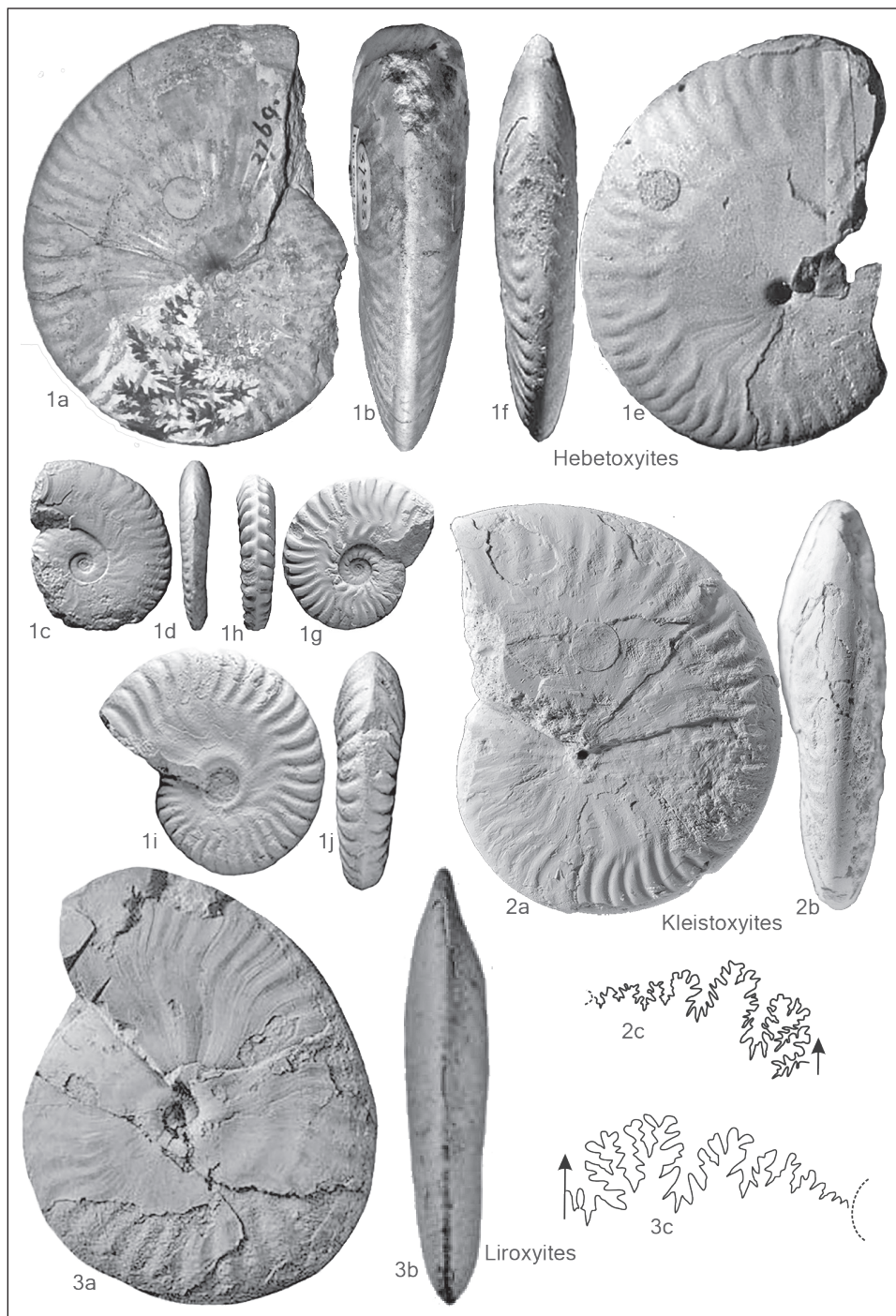


FIG. 7. Hebetoxyitidae.

(Alaska, Oregon), western Canada.—FIG. 7, 1*a–d*. **H. hebes* BUCKMAN; 1*a–b*, holotype, macroconch, *lower Bajocian*, Laeviuscula Zone and Subzone, Inferior Oolite Group, Dundry, Somerset, S England, $\times 1$ (new; also figured by BUCKMAN, 1924, pl. 475; British Geological Survey, BGS GSM37323); 1*c–d*, microconch, *lower Bajocian*, Laeviuscula Zone, Masada Toyuela, Teruel, Spain, $\times 2$ (FERNÁNDEZ-LÓPEZ, 2012, fig. 5, *N*; MT2/370, Universidad Complutense Madrid).—FIG. 7, 1*e–f*. **H. incongruens* BUCKMAN, holotype, macroconch, *lower Bajocian*, Laeviuscula Zone, Inferior Oolite Group, Fossil Bed, Brocchii Bed of BUCKMAN, 1893, Sandford Lane near Sherborne, S England, $\times 1$ (SCHWEIGERT & others, 2007, text-fig. 27; also figured by BUCKMAN, 1924, pl. 597; British Geological Survey, BGS GSM 47539).—FIG. 7, 1*g–j*. *H. mouterdei*, FERNÁNDEZ-LÓPEZ; 1*g–h*, holotype, microconch, *lower Bajocian*, Ovale Zone, Obon, Teruel, Spain, $\times 2$ (FERNÁNDEZ-LÓPEZ, 2012, fig. 7*L*; Universidad Complutense, Madrid, ON17/1); 1*i–j*, macroconch, *lower Bajocian*, Ovale or Laeviuscula Zone, Masada Toyuela, Teruel, Spain, $\times 1$ (FERNÁNDEZ-LÓPEZ, 2012, fig. 7, *F*; Universidad Complutense, Madrid, 1MT2/1211).

Kleistoxyites BUCKMAN, 1922, pl. 317 (**K. protrusus*; OD). Similar to *Hebetoxyites* but older and with more complex suture. Macroconchs of medium size, strongly involute, high oxyconic whorl section with maximum whorl thickness above the mid-flank. The irregular broad falcoid ribs divided above half flank. The lack of striation and of a septicarinate keel distinguish it from *Strigoceratidae* and make it closer to *Hebetoxyitidae*. Suture moderately complex, showing poorly incised elements and E deeper than L. *Lower Bajocian* (Discites Zone): England.—FIG. 7, 2*a–c*, **K. protrusus* BUCKMAN, holotype, macroconch, *lower Bajocian*, Discites Zone, Inferior Oolite Group, Bradford Abbas, Dorset, S England, lateral and ventral views (2*a–b*), $\times 0.8$ and suture (*c*) (new; also figured by BUCKMAN,

1922, pl. 317; British Geological Survey, inventory no. BGS GSM47132).

Liroxyites IMLAY, 1961, p. 470 [**Oppelia* (*L. kellumi*; OD)]. Discoid shells with a shallow furrow on lower part of the flank and sharp venter; highly involute with eccentric coiling on the adult body chamber; falcoid ribs, broad and closely spaced, with conspicuous falcoid striae on the outer surface of preserved shell; ribs and striae persist well onto the adult body chamber; weak crenulation on the keel formed by the continuations of the ribs and striae, some specimens with two raised spiral lateral bands; suture bears numerous auxiliary lobes. Dimorphism unknown. Similar to *Hebetoxyites* but larger, slightly more evolute with eccentric coiling, and with a furrow on lower part of the flank. Lacking the septicarinate keel and longitudinal striation that are typical of *Strigoceratidae*. According to SCHWEIGERT & others (2007, p. 25), the specimen cited by SANDOVAL & WESTERMANN (1986) from Oaxaca (Mexico) as *Strigoceras* (*Liroxyites*) cf. *kellumi* belongs to *Strigoceras symplectum* (BUCKMAN, 1924). *Uppermost lower Bajocian–lowermost upper Bajocian*: Alaska, Siberia, Mexico, Chile (FERNÁNDEZ-LÓPEZ & others, 1994).—FIG. 7, 3*a–c*. **L. kellumi* IMLAY, macroconch, lateral and ventral views (*a–b*) and suture (*c*), *lowermost upper Bajocian*, lower part of the Bowser member of the Tuxedni Formation, Iniskin Peninsula, Alaska, USA; 3*a*, holotype, USNM 130886, $\times 0.7$ (IMLAY, 1961, pl. 63, 8); 3*b*, USNM 130883, $\times 0.8$ (IMLAY, 1961, pl. 63, 7); 3*c*, USNM 130889*a*, $\times 2$ (IMLAY, 1961, pl. 63, 5).

Family LISSOCERATIDAE Douvillé, 1885

[*Lissoceratidae* DOUVILLÉ, 1885, p. 32]
[*nom. transl.* CALLOMON in DONOVAN & others, 1981, p. 144]

With a wide range of morphologies, *Lissoceratidae* includes ammonites of variable size, platycones to oxycones,

involute to moderately evolute, ovate or ogival, compressed to subrectangular, sometimes with a depressed whorl section; the venter is rounded to keeled and bisulcate; inner whorls smooth, adult whorls are sometimes with striation and ribs that can be well-developed on the upper part of the flanks. Sutures are rather simple and typically haploceratoid. Dimorphism is widespread, with lappets terminating most adult microconchs, which do not exceed 50 mm in diameter, whereas macroconchs are larger, usually up to 200 mm in diameter. Morphological and phylogenetic characters differentiate three subfamilies (Lissoceratinae DOUVILLÉ, 1885, Poecilomorphinae HYATT, 1900, and Bradfordiinae CALLOMON, 1981). *Middle Jurassic (middle Aalenian, Bradfordensis Zone)–Upper Jurassic (middle Oxfordian)*: worldwide.

Subfamily BRADFORDIINAE Callomon, 1981

[Bradfordiinae CALLOMON, 1981, p. 143]

Shells, small to medium size, oxycones, rarely platycones; involute to semi-evolute, compressed whorl section with elevated umbilical edge, and a lateral depression on the inner third of the flanks; venter rounded to tabulate, sometimes with an incipient keel, and inner whorls are smooth; ribs, usually weak, on middle and outer whorls are broad and blunt, and only on the outer half of the flanks. Dimorphism is well marked in *Bradfordia*: Macroconchs are more involute, with a simple aperture that has small ventral projection. Microconchs are more evolute, with small lateral lappets in the adult. CALLOMON (1981, p. 118–120) proposed the subfamily Bradfordiinae (originally referred to Oppeliidae), making two distinct phyletic strands of the Oppeliidae. PAVIA (1983) and PAVIA & FERNÁNDEZ-LÓPEZ (2019, p. 32) placed Bradfordiinae CALLOMON, 1981, in Lissoceratidae DOUVILLÉ, 1885. SANDOVAL (1986) considered Bradfordiinae, Lissoceratinae, and Haploceratinae to

rank as subfamilies within the family Haploceratidae ZITTEL, 1884. *Middle Jurassic (middle Aalenian, Bradfordensis Zone–lower Bajocian, Sauzei Zone)*: Bulgaria, England, France, Germany, Italy, Portugal, Romania, Spain (including the Balearic Islands), Switzerland, Morocco, Iran, ?New Zealand, South America (Argentina, Chile) and USA (Oregon, Alaska).

Bradfordia BUCKMAN, 1910, p. 94 [**B. liomphala*; OD] [= *Amblyoxyites* BUCKMAN, 1922, pl. 303 (type, *A. amblys*, OD); = *Iokastelia* RENZ, 1925, p. 30 (type, *Oppelia* (*I.*) *helenae* RENZ, 1925, p. 28, pl. 2, fig. 3; SD SAPUNOV, 1971, p. 79); = *Protoecotraustes* SPATH, 1928, p. 78 (type, *P. dundriensis*, OD); = *Etropolia* SAPUNOV, 1971, p. 82 (type, *Harpoceras blumius* GREGORIO, 1886, p. 12, pl. 4, fig. 5; SD SAPUNOV, 1971, p. 82)]. Macroconchs (*Bradfordia*, *Amblyoxyites*, *Iokastelia*, *Etropolia*) small- to medium-sized (20–100 mm in diameter), are involute to moderately evolute; compressed ovate whorl section, vertical umbilical wall, inner third of the flanks more-or-less depressed and elevated umbilical edge; venter rounded, without a keel; ribs falcoid or sigmoidal, weak on inner half of the whorl, moderate to strong and radial on outer half, and end at mid-ventral smooth band; suture with short E, deep L, and a high and strongly asymmetrical E-L saddle. Microconch (*Protoecotraustes*) small, semi-evolute with smooth inner whorls and rounded venter; outer whorls more compressed, subrectangular, with single or furcate sigmoid ribs, that may end in ventrolateral clavi and a tabulate venter, and an incipient keel; aperture with small lateral lappets and a barely expanded ventral rostrum; suture relatively simple as in the typical Haploceratoidea, with short E, long L, and asymmetrical E-L saddle. *Middle Jurassic (middle Aalenian, Bradfordensis Zone–lower Bajocian, Sauzei Zone)*: Bulgaria, England, France, Germany, Italy (including Sicily), Portugal, Romania, Russia, Spain (including Balearic Islands), Switzerland, Morocco, Iran, New Zealand, Argentina,

and USA (Oregon and Alaska). — FIG. 8, 1*a*. **B. liomphala* BUCKMAN, holotype, macroconch, *lower Bajocian*, Discites Zone, Inferior Oolite Group, Bradford Abbas, Fossil Bed, Dorset, S England, $\times 1$ (new; also figured by BUCKMAN, 1910, pl. 10, 4–5; Manchester Museum MANUM). — FIG. 8, 1*b*. *B. amblys* (BUCKMAN), holotype, macroconch, *lower Bajocian*, Sauzei Zone, Inferior Oolite Group, Stopford, Somerset, S England, $\times 1$ (new; also figured by BUCKMAN, 1922, pl. 303; British Geological Survey, inventory no. BGS GSM47121). — FIG. 8, 1*c*. *B. dundriensis* (SPATH), holotype, microconch, *lower Bajocian*, Sauzei Zone, Inferior Oolite Group, Dundry, Somerset, S England, $\times 1$ (new; also figured by SPATH, 1928, pl. 9, 7; Oxford University Museum of Natural History no. 67855). — FIG. 8, 1*d–f*. *B. etheridgii* (BUCKMAN), holotype, macroconch, *lower Bajocian*, “Sowerbyi Zone,” Inferior Oolite Group, Bradford Abbas, Sherborne, Dorset, England, $\times 1$ (new; also figured by BUCKMAN, 1883, pl. 3, 3; Manchester Museum, MANUM L1293).

Pracoppelia WESTERMANN, 1969, p. 48 [**Bradfordia?* (*P.*) *oppeliiformis*; OD]. Similar to *Bradfordia*, but larger, slightly more involute, and with more distinct ribbing. Macroconch large, involute, section ovate, strongly compressed, with a shallow depression on lower flanks; falcoid ribs short, dividing into dense rursiradiate secondaries that end in blunt chevrons; moderately complex suture with E larger than in *Bradfordia*, typical trifold L, slightly deeper than E, elevated bifid E-L saddle, and several auxiliary lobes. Presumably microconchs, the specimens described and figured by WESTERMANN (1969, p. 44, pl. 9, 1*a–2b*) as *Hebetoxyites* sp. aff. *H. hebes* BUCKMAN appear to be associated with macroconchs of *Pracoppelia* (WESTERMANN, 1969, p. 48). The only complete specimen (45 mm in diameter) has coiling similar to that of the macroconchs of *Bradfordia?* (*P.*) *oppeliiformis*, although with pronounced uncoiling in the body chamber, and similar whorl section,

ribbing, and suture; the complex aperture has a slightly projected ventral rostrum and prominent midlateral lappets. *Middle Jurassic* (*upper Aalenian–lower Bajocian*, Sauzei Zone): Bulgaria, England, Germany, Hungary, Italy, Spain, Morocco, USA (Oregon, Alaska). — FIG. 8, 2*a–g*. **P. oppeliiformis* WESTERMANN; 2*a–c*, holotype, macroconch, *lower Bajocian*, “Sowerbyi Zone,” locality USGS 19863, Kialagvik Formation, Wide Bay, Alaska Peninsula, Alaska (USA), $\times 0.5$ (WESTERMANN, 1969, pl. 11, fig. 1, 2*a–c*; U.S. National Museum no. USNM 160922); 2*d*, cross section of a specimen from locality USGS 21252, $\times 1$ (WESTERMANN, 1969, text-fig. 16*a*; U.S. National Museum no. USNM 160923); 2*e*, suture of a specimen from locality UW WA-11, $\times 1.5$ (WESTERMANN, 1969, text-fig. 16*b*); 2*f–g*, microconch of the specimen described as *Hebetoxyites* sp. aff. *H. hebes* by WESTERMANN (1969, p. 44), *lower Bajocian*, “Sowerbyi Zone,” locality WA-5, Kialagvik Formation, Wide Bay, Alaska Peninsula, Alaska (USA), $\times 1$ (WESTERMANN, 1969, pl. 10, fig. 1*a–b*; McMaster University, Hamilton, Ontario, Canada, McM J 1043).

Subfamily LISSOCERATINAE Douvillé, 1885

[Lissoceratinae DOUVILLÉ, 1885 (p. 32)]

Shells of variable size from discocones to platycones, moderately evolute to mid-involute; whorl section varies from typically ovate compressed to subcircular or almost trapezoidal. The ornamentation, usually reduced to sigmoid and falcoid growth lines, is absent mainly on the internal mould; only outer whorls of some forms develop sigmoid or falcoid and fasciculate ribs, especially on the outer half of the flanks of the body chamber. Dimorphism is well developed within lissoceratids: macroconchs up to 200 mm in diameter, microconchs up to 50 mm in diameter. Macroconchs have simple or sinuous apertures and sometimes ventral expansion while microconchs bear apertures with marked lateral lappets and

small ventral rostrum. The suture varies from simple to relatively complex. *Lower Bajocian* (Ovale Zone)–*upper Oxfordian*: England,

Scotland, France, Germany, Switzerland, Spain (including Balearic Islands), Portugal, Austria, Italy (including Sicily) Slovakia,

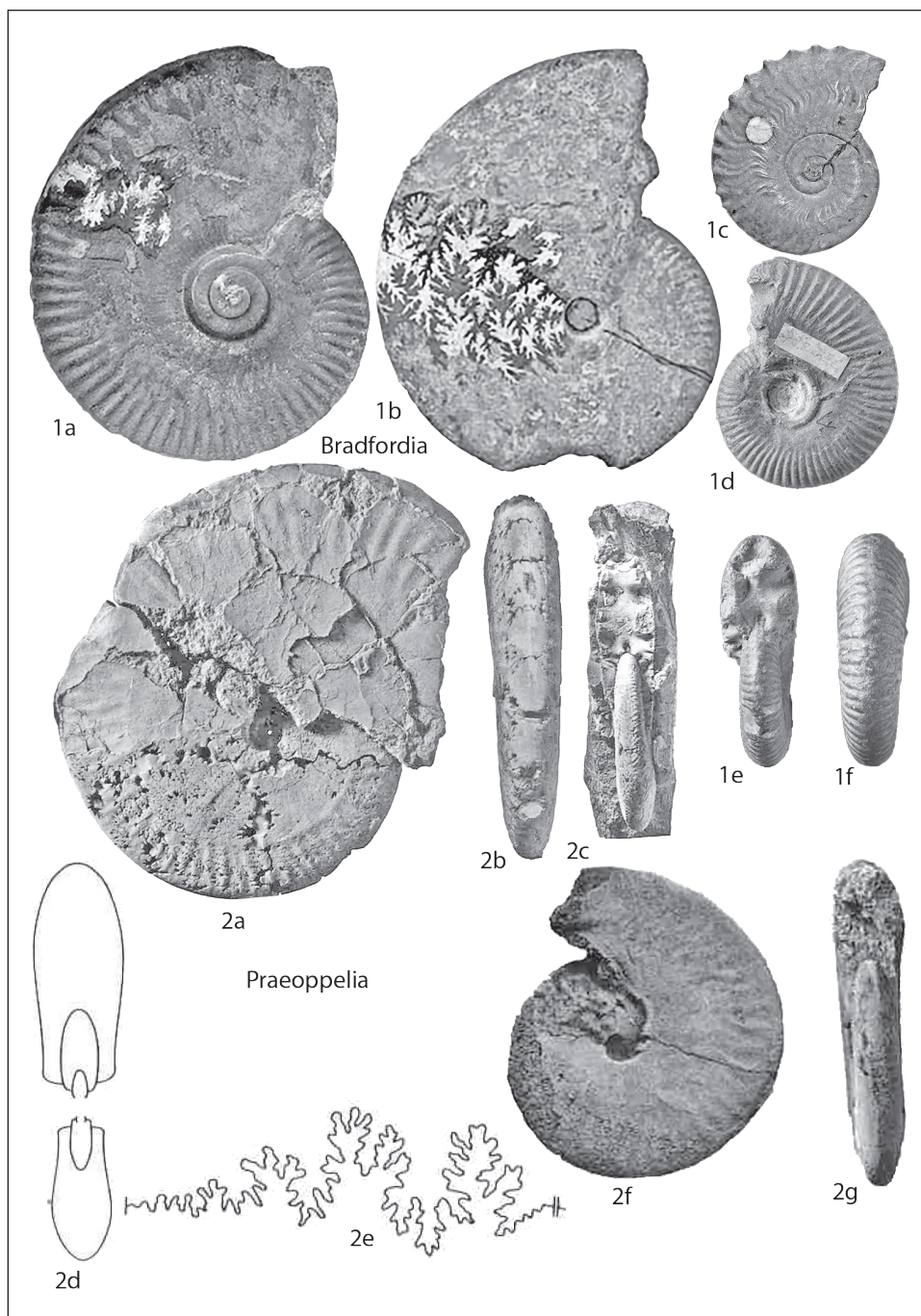


FIG. 8. Lissoceratidae, Bradfordiinae.

Poland, Romania, Bulgaria, Russia, Turkmenistan, Iran, India, Indonesia, Algeria, Morocco, Egypt (Sinai), Kenya, Madagascar, ?New Zealand, Argentina, Chile, Mexico, USA (Oregon, Alaska).

Lissoceras BAYLE, 1879, p. 34 [**Ammonites psilodiscus* SCHLOENBACH, 1865, p. 177; OD] [= *Lissoceratoides* SPATH, 1923, p. 14 (type, *Ammonites erato* D'ORBIGNY, 1850 in 1842–1851, p. 531; OD); = *Microlissoceras* STURANI, 1971, p. 93 (type, *M. pusillum*; OD)]. Dimorphic, small- to medium-size with macroconchs up to 200 mm and microconchs up to 50 mm; macroconchs have simple or sinuous apertures and microconchs develop lateral lappets. Macroconchs (*Lissoceras*, *Lissoceratoides*) evolute to mid-involute, discocones to platycones, with compressed, ovate to subcircular or subtriangular whorl section, becoming less compressed in the adult stage; umbilicus narrow or medium (U/D = 15–45%), relatively deep, with steep umbilical wall and rounded edge; flanks gently convex to rounded, converging to a convex venter, sometimes with flat venter and angular ventrolateral margin; sigmoid or falcoid growth lines with peripheral projection usually visible on shell only. Microconchs (*Microlissoceras*, including “*Lingulaticeras cornutum*” ZIEGLER, which represents the dimorphic microconch of *Lissoceras erato*; see MAKOWSKI, 1963, p. 24) evolute platycones with shallow umbilicus; whorl section compressed, oval, or elliptical with short umbilical wall and convex venter; sigmoid growth lines are usually scant but occasionally show more relief at mid-flank; adult aperture with pointed to stout lateral lappets and small ventral rostrum. Suture simple to relatively complex, with short E, very deep L, asymmetrical saddle L-U₂ significantly higher than E/L, and wide suspensive lobe with 3–4 auxiliary saddles. *Middle Jurassic* (lower *Bajocian*, *Humphriesianum Zone*)–*Upper Jurassic* (*Tithonian*, including all the forms traditionally classified as *Lissoceratoides*): Austria, Bulgaria, England, France, Germany, Italy, Poland, Portugal,

Romania, Slovakia, Spain (including Balearic Islands), Switzerland, Russia, Turkmenistan, Iran, India, Indonesia, Algeria, Morocco, Egypt (Sinai), Kenya, Madagascar, ?New Zealand, Argentina, Chile, Mexico, Cuba, USA (Oregon, Alaska).—FIG. 9, *a–e*. **L. psilodiscus* (SCHLOENBACH); *a–c*, holotype, macroconch, lower *Bathonian*, Germany, ×1 (SCHLOENBACH, 1865, pl. 28, 6), *c*, septal suture; *d–e*, macroconch, lower *Bathonian*, lower *Zigzag Zone*, Bas Auran, France, ×1 (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, pl. 1, 16; Museo di Geologia e Paleontologia at the University of Torino, Italy, MGPUPU 111445).—FIG. 9, *f*. *L. vultense* (OPPEL), macroconch, lower *Callovian*, *Gracilis Zone*, Sierra del Corque, Murcia Region, Spain, ×1 (SANDOVAL, 2016, fig. 10c; Dpto. Estratigrafía y Paleontología, Universidad de Granada, JSCo.43.85). —FIG. 9, *g–h*. *L. pusillum* STURANI, 1971, holotype, microconch, *Humphriesianum Zone*, *Romani Subzone*, Troch 1, Italy, ×2 (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, pl. 4, 9; Museo di Geologia e Paleontologia at the University of Torino, Italy, MGPUPU 36068). —FIG. 9, *i–j*. *L. inflatum* WETZEL, microconch, upper *Bajocian*, *Parkinsoni Zone*, Sainte-Honorine-des-Pertes, France, ×2 (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, pl. 1, 6; MGUPU-PU 112722).

Semilissoceras PAVIA & FERNÁNDEZ-LÓPEZ, 2019, p. 55 [**S. ellipticum*; OD]. Macroconchs of medium size bearing simple or sinuous aperture and small microconchs with lateral lappets. Mid-evolute with compressed, subelliptical to subtriangular whorl section, less compressed in the adult stage; moderately steep umbilical wall, rounded umbilical edge, flanks slightly convex, and convex venter, sometimes with incipient ventrolateral edges. Sigmoid or falcoid ribs, commonly fine and dense, single or bifurcate on the outer one-third of the flank, blunt and with low relief, very weak or absent on the inner half of the flanks, becoming stronger towards the ventrolateral area. The external ribs,

bifurcation of primaries or intercalations, are uniformly developed and are subradial, rursiradiate or slightly turned forwards, ending abruptly on the ventral edge or meeting roughly in the center of the venter in the phragmocone, becoming continuous in adult stage. Sigmoid radial growth lines with peripheral projection. Suture relatively complex with short E, deep L; saddle $L-U_2$ asymmetrical and higher than E–L, suspensive lobe with U_2 and U_3 developed,

and much smaller umbilical elements. *Middle Jurassic* (*Bajocian*, *Ovale–Garantiana Zones*): England, France, Germany, Italy, Portugal, European Russia, Spain (including Balearic Islands), Algeria, Morocco, Iran, ?India, ?Indonesia, and North America (Mexico, Oregon, and Alaska).—FIG. 10, *a–c*. **S. ellipticum* PAVIA & FERNÁNDEZ-LÓPEZ; *a–b*, holotype, macroconch, *lower Bajocian*, upper *Laeviuscula Zone*, Masada, Toyuela, Albarracín, Spain, $\times 1$

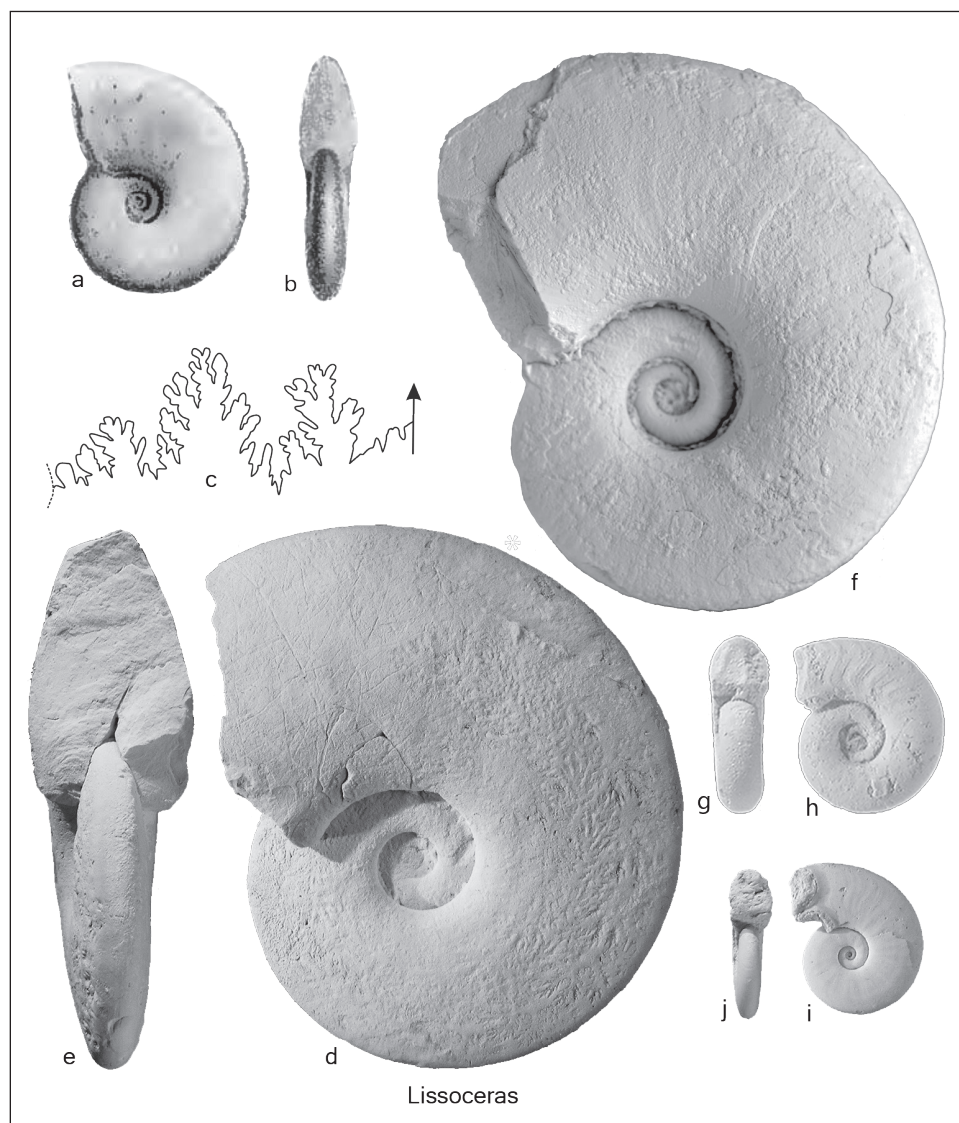


FIG. 9. Lissoceratidae, Lissoceratinae 1.

(PAVIA & FERNÁNDEZ-LÓPEZ, 2019, pl. 4, 26); *c*, suture, M10U50/5, paratype, macroconch, *lower Bajocian*, Laeviuscula Zone, Moscardón, Teruel, Spain (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, fig. 22A; Museo Aragonés de Paleontología, Teruel, Spain, MAP-MT2d/273).—FIG. 10, *d–e*. *S. semicostulatum* (BUCKMAN), macroconch, *lower Bajocian*, Laeviuscula Zone, Sandford Lane, Dorset, England, ×1 (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, fig. 23B; Wessex Cephalopod Club collection, Sh-SL X40390).—FIG. 10, *f*. *S. depereti* (FLAMAND), macroconch, *lower Bajocian*, Laeviuscula Zone, La Torquilla, Campillo de Arenas area, Jaén province, Spain, ×1 (SANDOVAL, 1986, pl. 1, 3; Depto. Estratigrafía y Paleontología, Universidad de Granada, JAC11.R.3).—FIG. 10, *g–h*. *S. ellipticum* PAVIA & FERNÁNDEZ-LÓPEZ, allotype, microconch, *lower Bajocian*, Laeviuscula Zone, Moscardón, Teruel, Spain ×1 (PAVIA & FERNÁNDEZ-LÓPEZ, 2019, pl. 4.21; Museo Aragonés de Paleontología, Teruel, Spain, MAP-MT2c/279).

Subfamily POECILOMORPHINAE Hyatt, 1900

[*nom. correct.* OHMERT in OHMERT & others, 1995, p. 63, *ex*. Poecilomorphidae HYATT, 1900, p. 576]

Poecilomorphinae includes small forms, with variable coiling from evolute to involute whorls, slightly compressed to depressed whorl sections, venter with incipient keel to low in the primitive forms, but well-developed keel, which can be accompanied by more-or-less marked sulci in the more evolved forms. The innermost whorls are smooth, but falcate ribs of variable thickness occur in the middle and outer whorls. Simple sutures have small, deep E and L and wide and asymmetric L-U₂ saddle. Dimorphism is well marked, with the macroconchs being more involute and having a simple aperture with a small ventral projection; microconchs

are more evolute, with very small lateral lappets and a ventral rostrum.

The family Poecilomorphidae was proposed by HYATT (1900); however, much later, OHMERT in OHMERT & others (1995, p. 63), perhaps unaware of Hyatt's proposal, introduced the new subfamily Poecilomorphinae only for the genus *Poecilomorphus*, which OHMERT included in the family Sonniniidae. This was possibly based on the great external morphologic similarity between some microconchs of sonniniids [(*Sonninites sulcatus* (BUCKMAN) and *Sonninia schlumbergeri* (HAUG)] with *Poecilomorphus cycloides* (D'ORBIGNY). However, as shown by several authors (STURANI, 1971; CALLOMON, 1981; PAVIA, 1983; FERNÁNDEZ-LÓPEZ, 1985; SANDOVAL, 1986; FISCHER & others, 1994; PAVIA & FERNÁNDEZ-LÓPEZ, 2019), the genus *Poecilomorphus* should be included in Lissoceratidae instead of Sonniniidae. STURANI (1971, p. 90) suggested the possibility that *Toxamblyites*, from which *Poecilomorphus* descended, arose in the earliest Bajocian more likely from "*Lissoceras*" *semicostulatum* than from some *Bradfordia*. Nonetheless, as suggested by SANDOVAL (1986, p. 454), the phylogenetic relationships *Bradfordia*-*Toxamblyites*-*Stegoxyites*-*Poecilomorphus*, in which a ventral keel develops progressively, are more feasible. *Middle Jurassic* (*lower Bajocian*, Sauzei Zone–Humphriesianum Zone): England, France, Germany, Italy, Spain (including the Balearic Islands), Switzerland, Morocco, Iran, ?New Zealand, and North America.

Poecilomorphus BUCKMAN, 1889, p. 115 [**Ammonites cycloides* D'ORBIGNY, 1846 in 1842–1851, p. 370; SD BUCKMAN, 1927, p. 10] [= *Micropoecilomorphus* STURANI, 1971, p. 111 (type, *Haploceras? vicentinum* PARONA, 1880, p. 262; OD)]. Small shells with variable coiling from evolute to almost involute; whorl section varying from strongly depressed to slightly compressed subrectangular; venter generally with low keel, which can be bordered by more-or-less developed sulci;

inner whorls, especially in microconchs, sometimes smooth, subsequently falcate ribs, highly variable in thickness and especially developed on outer half of flanks of last whorl. Macroconchs (*Poecilomorphus*) with a simple aperture. Microconchs (*Micropoecilomorphus*) usually more evolute than macroconchs with small lateral lappets. Suture of haploceratoid type with wide and strongly asymmetric saddle L-U₂. *Lower Bajocian* (Humphriesianum Zone): France, England, Germany, Switzerland, Italy, Spain (including the Balearic Islands), Morocco, USA (Oregon).—FIG. 11, 1a–h. *P. cycloides* (D'ORBIGNY); 1a–c, paratype, macroconch, *lower Bajocian*, Humphriesianum Zone, Saint-Vigor, Calvados, France, ×1 (new; Muséum d'Histoire Naturelle, Paris, D'ORBIGNY Collection, IPM-B.46063; also figured by Rioult in FISCHER & others, 1994, pl. 42, 5a,b; MNHN.F.B46063); 1d–e, macroconch, morphotype, involute

and strongly ribbed, Humphriesianum Zone, Romani Subzone, *Posidonia alpina* beds, Venetian Alps, Italy, ×2 (STURANI, 1971, pl. 11, 16); f–h, macroconch, morphotype, evolute and weakly ribbed, *lower Bajocian*, Humphriesianum Zone, Romani Subzone, *Posidonia alpina* beds, Venetian Alps, Italy, ×2 (STURANI, 1971, pl. 9, 16).—FIG. 11, 1i–m. *P. vicetinus* (PARONA); 1i–k, microconch, *lower Bajocian*, Humphriesianum Zone, Romani Subzone, *Posidonia alpina* beds, Venetian Alps, Italy, ×3 (STURANI, 1971, pl. 9, 9); 1l–m, lectotype, microconch, upper *lower Bajocian*, Humphriesianum Zone, Romani Subzone, Camporovere, Veneto, Italy, ×3.5 (STURANI, 1971, pl. 9, 10).

Toxamblyites BUCKMAN, 1924, p. 8, pl. 473 [**T. arcifer*; OD] [= *Microtoxamblyites* STURANI, 1971, p. 96 (type, *M. parvus*; OD)]. Medium-sized macroconchs

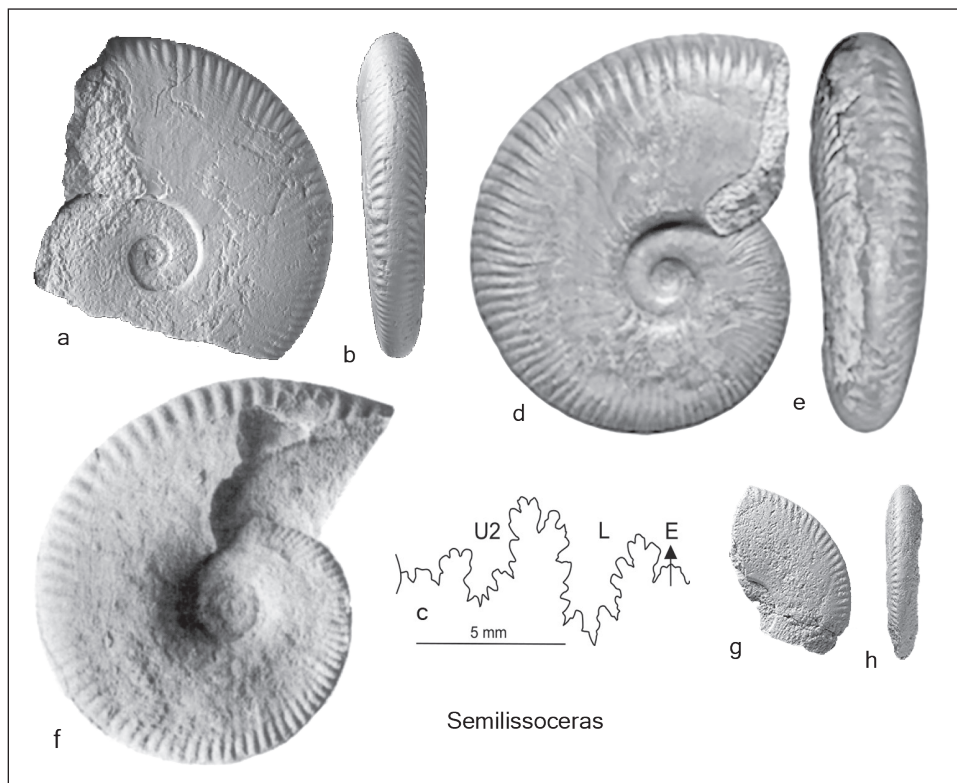


FIG. 10. Lissoceratidae, Lissoceratinae 2.

(*Toxamblyites*), with medium coiling and a whorl section varying from depressed to slightly compressed elliptical; flanks more-or-less convex, with venter subrounded, sometimes bearing an incipient keel. Ornamentation consisting of falcate, usually dense and thin ribs, which form as blunt chevrons on the venter; aperture simple. Microconchs (*Microtoxamblyites*) very similar to macroconchs, but smaller, slightly more evolute, with less developed ribbing and with small lateral lappets. Suture typical of haploceratoids, with high and strongly asymmetric saddle L-U₂. *Lower Bajocian* (Laeviuscula to Humphriesianum Zones): England, France, Italy, Spain (including the Balearic Islands), Morocco, Iran (SEYED-EMAMI, 1988), ?New Zealand (WESTERMANN & others, 2000).—FIG. 11, 2a–b. **T. arcifer* BUCKMAN, holotype, macroconch, *lower Bajocian*, Sauzei Zone, Inferior Oolite Group, Dundry, Somerset, England, ×1 (new; figured by BUCKMAN, 1924, pl. 473; British Geological Society, inventory no. BGS GSM37321).—FIG. 11, 2c–e. *T. parvus* STURANI, holotype, microconch, Humphriesianum Zone, Romani Subzone, *Posidonia alpina* beds, Venetian Alps, Italy, ×3 (STURANI, 1971, pl. 7, 8).

Stegoxyites BUCKMAN, 1924, p. 8, pl. 474 [**S. parvicarinatus*; OD]. Close to *Toxamblyites* but more involute; ovate-elliptical compressed whorl section with two faint sulci on whorl sides separated by a blunt spiral ridge, raised umbilical edge, and incipient ventral keel. Fine, dense falcate ribs divided into bundles below mid-flank; secondaries passing over the venter as small chevrons. Simple suture, typically haploceratoid. *Stegoxyites* was included in Oppeliidae by ARKELL (1957, p. 276), in Haploceratidae by STURANI (1971) and SANDOVAL (1986), and in Bradfordiinae, within Haploceratidae, by FERNÁNDEZ-LÓPEZ (1985). The keel and the ribbing bring it close to Poecilomorphinae. *Lower Bajocian* (Humphriesianum Zone): England, France, Germany, Italy, Spain, Morocco

(BENSHILI, 1989, SADKI, 1996) and ?New Zealand.—FIG. 11, 3. **S. parvicarinatus* BUCKMAN, holotype, macroconch, *lower Bajocian*, Sauzei Zone, Inferior Oolite Group, Frogden Quarry, Osborne, Somerset, England, ×1 (new; also figured by BUCKMAN, 1924, pl. 474; British Geological Society, inventory no. BGS GSM37322).

Family HAPLOCERATIDAE Zittel, 1884

[Haploceratidae ZITTEL, 1884, p. 569]

Haploceratidae includes ammonites of small to medium size, platycone or at times slightly ellipticone, rather involute; ovate, ogival to subrectangular compressed whorl section with typically rounded and usually unkeeled venter (only exceptionally somewhat keeled); inner whorls smooth, the adult whorls sometimes with striation and ribs sometimes well-developed on the upper part of the flanks. Dimorphism widespread; the macroconchs with peristomes having sinuous edges, and microconchs having ventral transversal ridges with apertures terminating in short lappets rather than narrow and pedunculated ones. Sutures from relatively simple to moderately complex with well incised and somewhat asymmetric lobes, unretracted or barely retracted umbilical lobe. Double-valved aptychi, usually with strong and sometimes tightly curved ornamentation. *Upper Jurassic* (*middle Oxfordian–Lower Cretaceous* (*Barremian*)): worldwide.

According to WRIGHT & others (1996, p. 10), the family derived from Taramelliceratinae (Oppeliidae) via *Metahaploceras* and “*Glochiceras*” (*partim*) in the Kimmeridgian. However, it is more likely that the Haploceratidae are direct descendants of the Lissoceratidae, with which they are homeomorphous, although the septal sutures may be somewhat different. The possible ancestor could be the Lissoceratidae *Lissoceras erato* (D’ORBIGNY), which ranged from the early Callovian

(SANDOVAL, 2016) into the early Tithonian (BUJTOR & ALBRECHT, 2021, p. 71),

whereas the first records of Haploceratidae are late Kimmeridgian. Even the Tithonian

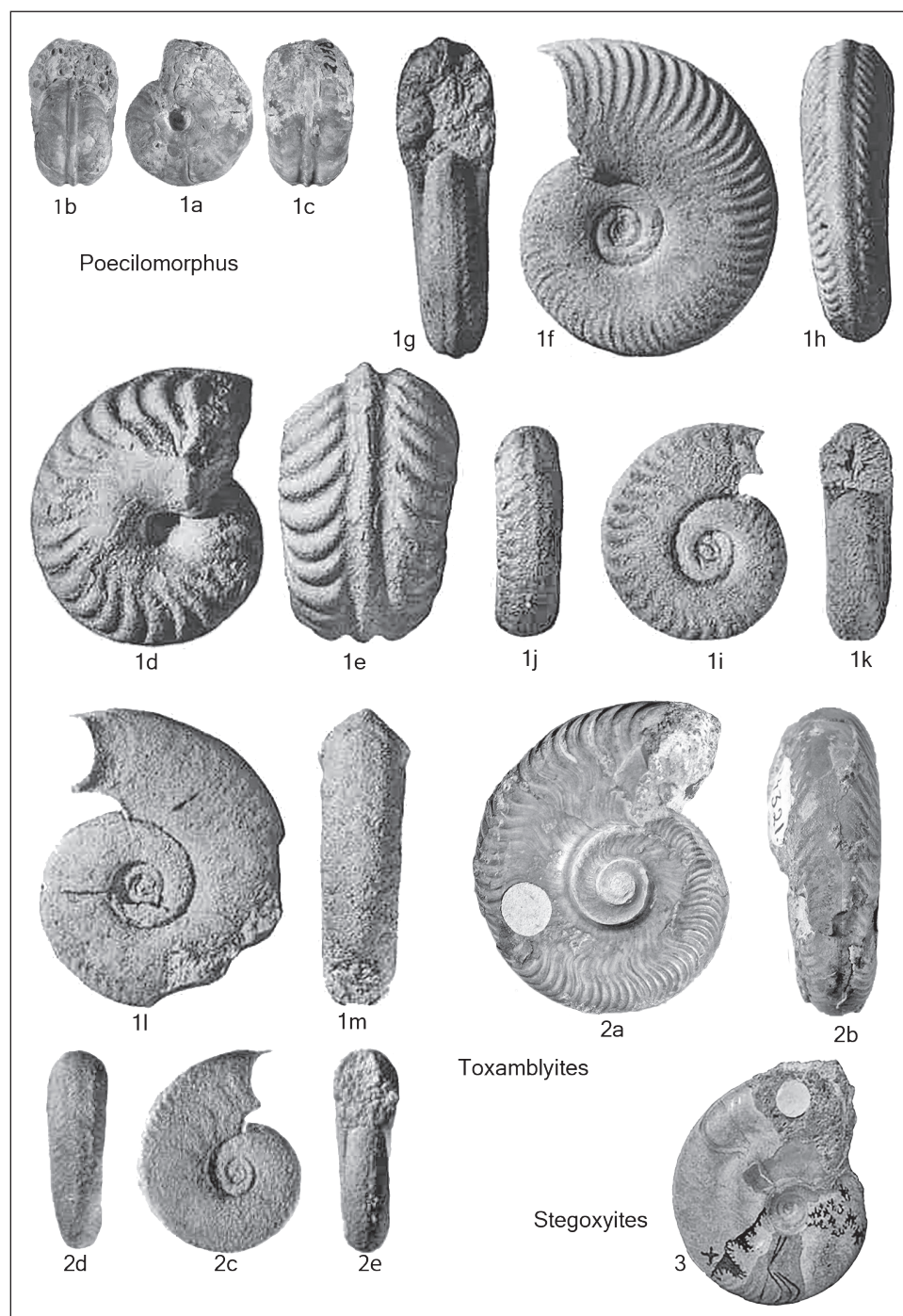


FIG. 11. Lissoceratidae, Poecilomorphinae.

genus *Pseudolissoceras*, here included in Haploceratidae, has been previously included by some authors (PARENT & others, 2015, p. 80) in Lissoceratidae. According to ZIEGLER (1974, p. 33), Haploceratidae includes only two Jurassic genera: *Haploceras* and *Pseudolissoceras*. However, subsequent research has shown that some genera that had formerly been included in the Glochiceratinae (invalid subfamily, as will be indicated below) or Taramelliceratinae should be transferred to Haploceratidae. The family includes the Jurassic genera *Haploceras* ZITTEL, 1870; *Hildoglochiceras* SPATH, 1924; *Pseudolissoceras* SPATH, 1925b; *Paraglochiceras* COLLIGNON, 1959; and *Salinites* CANTÚ-CHAPA, 1968. Likewise, some of the forms habitually classified as “*Glochiceras*” HYATT, 1900, or “*Coryceras*” ZIEGLER, 1958, may also represent microconchs of lissoceratids or haploceratids (MAKOWSKI, 1963, p. 24; QUEREILHAC, 2009, p. 14; QUEREILHAC & GUINOT, 2011, p. 32; PAVIA & FERNÁNDEZ-LÓPEZ, 2019, p. 34).

Haploceras ZITTEL, 1870, p. 48 [*Ammonites elimatus* OPPEL, 1865 in 1863–1865, p. 549 in ZITTEL, 1870; SD SPATH, 1923, p. 14] [= *Hypolissoceras* BREISTROFFER, 1947, p. 2 (type, *Ammonites carachtheis* ZEJSZNER, 1846, pl. 4, fig. 1); = *Rapidoceras* HOUŠA & DE LA NUEZ, 1973, p. 19, *nom. nud.* and invalid under ICZN Code, 1999, Article 13.1.1); = *Neoglochiceras* PATRULIUS & AVRAN, 1976, p. 166 (*non* COLLIGNON, 1960, pl. 145, *nom. nud.*) obj.; = *Volanites* ÉNAY & CECCA, 1986, p. 49, *nom. nud.* and invalid under ICZN Code, 1999, Article 13.1.1 (no description or differentiating characters given)]. Macroconchs of small to medium size, platycone semi-evolute with moderate spiral growth, high oval whorl section reaching maximum width near the rounded umbilical edge, gently convex flanks and rounded ventral region. Smooth, but if the original shell is preserved, growth striae can appear. Microconchs with ventral crenulation, or a small wart (*verruca*) on the venter on adult body chamber, and

aperture with small frontal rostrum in the mouth border and wide and rather short lateral lappets. Although *Haploceras* was previously included by WRIGHT & others (1996, p. 10) in the review of the Cretaceous ammonites, it is also included here because some of its species occur in the Upper Jurassic. *Upper Jurassic (Kimmeridgian)–Lower Cretaceous (Valanginian)*: Austria, Bulgaria, Czech Republic, England, France, Germany, Hungary, Italy, Poland, Romania, Spain (including Mallorca Island), Morocco, Tunisia, Algeria, Crimea, Russia, Iraq, Iran, Pakistan, India (Kutch), Japan, Madagascar, Yemen, Tanzania, New Zealand, Antarctica, Argentina, Peru, Mexico, USA, Cuba.—FIG. 12, 1a–b. *H. elimatum* (OPPEL), macroconch, *upper Tithonian*, Stramberg, Koniakaw, Villamowitz, Czech Republic, ×1 (new; original in ZITTEL, 1868, pl. 13, 2; Bayerische Staatssammlung für Paläontologie und Historische Geologie, Munich, AS III 801).—FIG. 12, 1c. *H. verruciferum* (ZITTEL), microconch, *lower Tithonian*, Semiforme Zone, Lókút Hill, Hungary, ×1 (Fözy & others, 2022, pl. 8, 8; Hungarian Natural History Museum, Budapest, no. INV.2014.76).—FIG. 12, 1d–e. *H. carachtheis* (ZEUSCHNER), microconch, *lower Tithonian*, Fallauxi Zone, Hárskút, Hungary, ×1 (Fözy & others, 2022, pl. 8, 1a–b; Hungarian Natural History Museum, Budapest, Hungary, no. J.10908).

Pseudolissoceras SPATH, 1925b, p. 113 [*Neumayria zitteli* BURCKHARDT, 1903, p. 55, pl. 10, fig. 6–7; SD ROMAN, 1938, p. 176] [= *Primoryites* JUDOLEY, 1960, p. 163, (type *P. primoryensis*; OD)]. Macroconchs similar to *Haploceras* but slightly more evolute, elliptical to oval whorl section with gently convex flanks and rounded venter; almost smooth throughout the entire ontogeny, although if the original shell is preserved, growth striations appear; septal suture simple with distant and short lobes and saddles. Microconchs of very small size and evolute; inner whorls with subcircular whorl section, almost smooth with only

gently marked growth striations; towards the outer whorls becoming slightly more evolute,

more compressed, with a rounded venter, and the sinuous growth lines projecting on

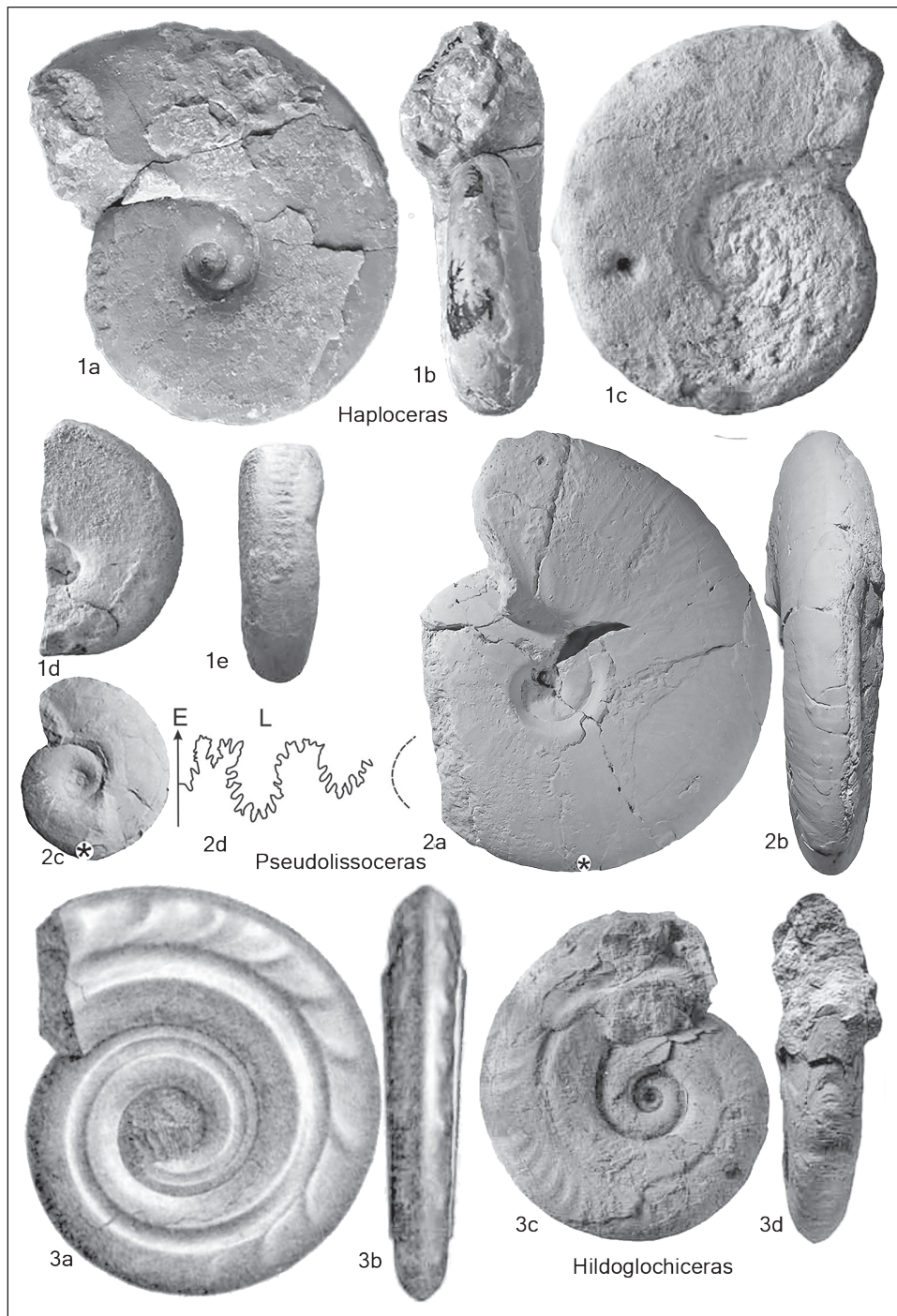


FIG. 12. Haploceratidae 1.

the small lateral lappets. Long and weakly ribbed aptychi. *Upper Jurassic (lower Tithonian, Hybonotum–Fallauxi Zone)*: France, Germany, Hungary, Italy, Spain, Algeria, Tunisia, Russia (Volga Region), Iraq, Iran, India, Antarctica, Argentina, Chile, Peru, Cuba, Mexico, USA (California).—FIG. 12, 2a–c. *P. zitteli* (BURCKHARDT); 2a–b, macroconch, upper-lower *Tithonian*, Zitteli Zone, Cerro Lotena, Argentina, $\times 1$ (PARENT, 2022, fig. 20, E; Museo Olsacher, Zapala, Neuquén, Argentina, no. MOZ-PI-7452); 2c, microconch, upper-lower *Tithonian*, Zitteli Zone, Portada Covunco, Argentina, $\times 2$ (PARENT, 2022, fig. 20, F; also figured by PARENT & others, 2013, fig. 26D; Museo Olsacher, Zapala, Neuquén, Argentina, no. MOZ-PI X7); 2e, suture at D 41 mm, upper-lower *Tithonian*, Zitteli Zone, Arroyo Cieneguita, Neuquén, Argentina (PARENT & others, 2011, fig. 39, B₃; Museo A. Moyano, Mendoza, no. MCNAM 24375).

Hildoglochiceras SPATH, 1924, p. 6 [**Hecticoceras latistrigatum* UHLIG, 1903, p. 27; OD]. Small to medium size, commonly evolute, with a subtriangular to oval whorl section, characterized by a lateral groove of variable width and located above the lower one-third to mid-height of the flank, narrow and rounded venter; a variable size for the beginning of ribbing, with more-or-less ornamented outer whorls. Dimorphism is probably present, which is marked on the basis of shell size and the diameter of the umbilicus. The microconch, small and with larger umbilical diameter and peristome, with small lappets with bases just below the end of the lateral groove. The macroconch, larger in size and with a proportionally wider subrectangular to oval whorl section and simple aperture. The taxonomic status of *Hildoglochiceras* is still uncertain; this genus has been included in Oppeliidae, (“Glochiceratinae”) or Haploceratidae depending on the authors; e.g., “Glochiceratinae” (ZIEGLER, 1974, p. 33; ÉNAY, 2009, p. 83; JAIN, 2025, p. 5) and Haploceratidae (PANDEY & others,

2016, p. 146; 2022, p. 23). *Upper Jurassic, uppermost Kimmeridgian–lowermost upper Tithonian*: ?Iraq, ?Pakistan, India, Nepal, Ethiopia, Kenya, Madagascar, Tanzania, Argentina, ?Peru, Mexico, USA, Cuba.—FIG. 12, 3a–b. **H. latistrigatum* (UHLIG), holotype by monotypy, ?macroconch, lower *Tithonian*, middle horizon of the Spiti Shales of Chidamu, Nepal, $\times 1$ (UHLIG, 1903, pl. 2, 4a, c).—FIG. 12, 3c–d. *H. kobelli* (OPPEL), microconch, lower *Tithonian*, Malagasites Beds, Chhokor, valley on the reverse side of villagers’ shale quarry (92 CH-E), Nepal, $\times 1$ (ÉNAY, 2009, pl. 1, 6a–b; Lyon University Collection, France, FSL 143 741).

Paraglochiceras COLLIGNON, 1959b, pl. 115, fig. 438 [**P. lauteli*; OD] [= *Neoglochiceras* COLLIGNON, 1960, pl. 145, fig. 572, *nom. nud.* and invalid under ICZN Code, 1999, Article 13.1.1]. Medium-sized shell, moderately involute with very slightly marked uncoiling towards the outer whorls, oval-wide to subtriangular whorl section, rounded umbilical edge, more-or-less convex flanks that converge to rounded unkeeled venter; thick external ribs, developed only in middle and outer whorls of some species, concave and projected forward on the outer part of flanks. Septal suture simple but not well preserved in the holotype. *Upper Jurassic, upper Kimmeridgian (Acanthicum Zone)–lower Tithonian (Semiforme Zone)*: Madagascar, India, Nepal.—FIG. 13, 1a–c. **P. lauteli* COLLIGNON, holotype, macroconch, lower *Tithonian*, Hybonotum Zone, outcrop 555, bed 3, West of the Ambohimaranitra ridge, East of Ampanihy sur Bevoay, Manera, Madagascar, $\times 1$ (a, new; original of COLLIGNON, 1959b, pl. 115, 438; Université de Bourgogne, Dijon, France, UBGD.010438).—FIG. 13, 1d–e. *Paraglochiceras tuberosum* COLLIGNON, holotype, macroconch, lower *Tithonian*, Kobelli Zone, outcrop 549, Springs of the Mandarana, Manera, Madagascar, $\times 1$ (new; original of COLLIGNON, 1960, pl. 145, 572; Université de Bourgogne, Dijon, France, UBGD.010572).

Salinites CANTÚ-CHAPA, 1968, p. 20 [**Hildoglochiceras grossicostatum* IMLAY, 1939, p. 27; OD]. Small- to medium-sized shells, moderately involute, oval to subrectangular compressed whorl section, rounded umbilical edge, flat or gently convex flanks, ventral area rounded and without keel on the inner and middle whorls, progressively flattening and developing a slightly marked keel in the adult stage. Inner whorls (diameter less than 10–12 mm) smooth, with ribs then emerging, initially confined to the ventro-

lateral area, markedly proverse and concave forwards; lastly, towards the body chamber end, ribs becoming progressively thicker, falcate, very thin in the inner half of the flank and thick and concave in the outer half; in the ventrolateral area, ribs strongly projected forward, ending just in the keel. The septal suture quite simple, with high and narrow saddles and deep lobes. Dimorphism present with smoothing of the ornamentation near the peristome in macroconchs and the presence of small lateral apophysis

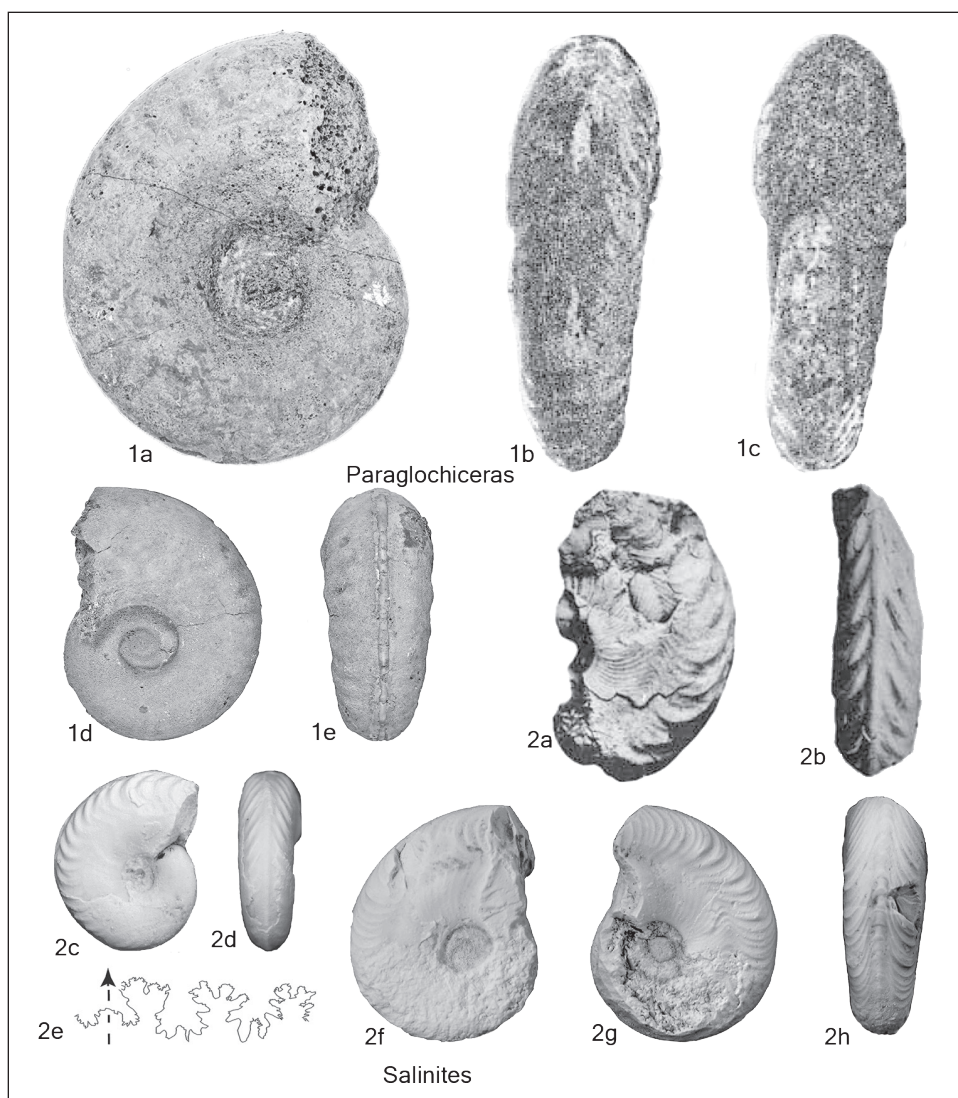


FIG. 13. Haploceratidae 2.

in microconchs. The phylogenetic origin of this Caribbean genus is unclear, but its morphological characters and type of suture are close to Haploceratidae, where it has traditionally been included (IMLAY, 1939; CANTÚ-CHAPA, 1963; ZELL & STINNESBECK, 2016a). *Upper Jurassic, Tithonian* (Durangites Zone)–*Lower Cretaceous (lower Berriasian)*: Mexico, Cuba, USA (Louisiana).—FIG. 13, 2a–d. **S. grossicostatum* (IMLAY); 2a–b, holotype, macroconch, *Tithonian*, Sierra de Parras, Coahuila State, Mexico, $\times 1$ (IMLAY, 1939, pl. 3, 3–4; Museum University of Michigan in Chicago, USA, no. UM 20020); 2c–d, microconch, *uppermost Tithonian*, Puerto Piñones, Coahuila state, Mexico, $\times 1$ (ZELL & STINNESBECK, 2016a, fig. 1, b_1 – b_2 ; Colección de Paleontología de Coahuila of the Museo del Desierto, Saltillo, Mexico, CPC 1404).—FIG. 13, 2e. suture at D 20, 9 mm (ZELL & STINNESBECK, 2016b, fig. 9; Colección de Paleontología de Coahuila of the Museo del Desierto, Saltillo, Mexico, CPC 1218)—FIG. 13, 2f–h. *S. finicostatum* ZELL & STINNESBECK, holotype, ?macroconch, *uppermost Tithonian*, La Caja Formation, Cañón de Huizachal, Tamaulipas state, Mexico, $\times 1$ (ZELL & STINNESBECK, 2016a, fig. 3a–c; Colección de Paleontología de Coahuila of the Museo del Desierto, Saltillo, Mexico, CPC 1408).

Family OPPELIIDAE Douvillé, 1890

[*Nom. correct.* ARKELL, 1951b, p. 50,
pro Oppeliidae BONARELLI, 1894, p. 77
(see also ÉNAY, 2009, p. 81)]

The name Oppeliidae, proposed by BONARELLI (1894, p. 77), which came after the proposition (Oppéliidés) of DOUVILLÉ (1890, p. 283), was corrected (Oppeliidae) by ARKELL (1951b or a).

Oppeliidae includes ammonites of variable size (small or medium are dominant), oxycones to platycones, involute to moderately evolute, subtriangular to oval compressed whorl section, usually with a

keel; and may have a median lateral spiral groove, a smooth band or fillet. Ribbing is usually falcoid or falcate, simple or bifurcate, and become smooth on outer whorls; ribs are usually more developed in the upper part of the flanks. The sutures are relatively complex, with E shallower than L, saddle E-L smaller than L-U₂ and a long series of evenly graded lobes and saddles with finely branched endings. Dimorphism is usually strong and well developed, with highly developed lappets in the microconchs, which are more evolute than the corresponding macroconchs, and usually do not exceed 70 mm in diameter; macroconchs are usually much larger, yet rarely surpass 250 mm in diameter. *Middle Jurassic (lower Bajocian, Sauzei Zone)*–*Lower Cretaceous*: worldwide, except Boreal.

ARKELL (1957) subdivided Oppeliidae into various subfamilies: Oppeliinae, Hecticoceratinae, Ochetoceratinae, Distichoceratinae, Taramelliceratinae, Phlycticeratinae, Streblitinae, Mazapilitinae, and Aconeceratinae; all, except Phlycticeratinae, which were transferred to Strigoceratidae (with which it is closely related phylogenetically), are here also accepted with the same taxonomical range, although there are some doubts about the taxonomic status of Mazapilitinae. The origin of Oppeliidae is probably linked to the morphologically similar genera, which preceded them in the time as the Lissoceratidae *Bradfordia* and *Praeoppelia*. These two genera are very similar to *Oppelia* (the oldest Oppeliidae), although they lack a keel on outer whorls (some Oppeliidae can also lose the keel in adult stages) and have a simpler suture.

Subfamily OPPELIINAE Douvillé, 1890

[*Nom. correct.* ARKELL, 1951b, p. 2,
pro Oppelinae BONARELLI, 1894, p. 77
(see also ÉNAY, 2009, p. 81)].

Shells of small or medium size, oxycones or platycones involute or moderately involute, subtriangular to ovate compressed

whorl section with maximum thickness in the inner half of the flanks. Venter

rounded, tectiform or acute, without a keel or with a slightly differentiated keel and a

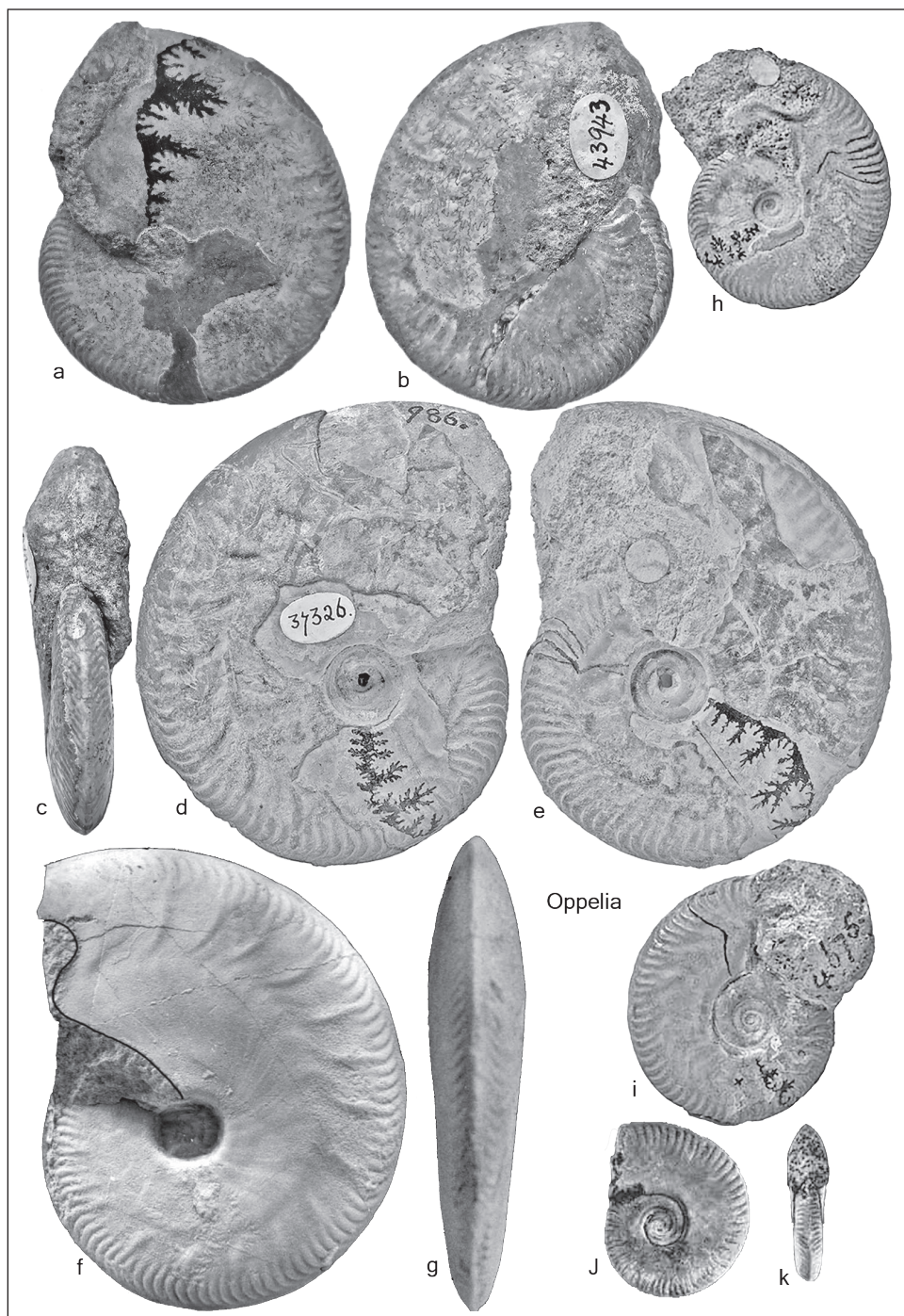


FIG. 14. Oppeliidae, Oppeliinae 1.

midlateral smooth band or fillet. Ribbing, more developed in the upper part of the flanks, is usually falcoid or falcate, simple or bifurcate, smoothly fading on outer whorls. Dimorphism is well marked, microconchs being more evolute, with slightly more eccentric coiling than the corresponding macroconchs and with prolonged lateral lappets. The suture, relatively complex, has L slightly deeper than E, the saddle E-L smaller than L-U₂, and un-retracted umbilical lobe. *Middle Jurassic (lower Bajocian, Sauzei Zone–middle Callovian)*: worldwide distribution, except Boreal.

Oppelia WAAGEN, 1869, p. 250 [**Ammonites subradiatus* J. DE C. SOWERBY, 1823, p. 23; SD DOUVILLÉ, 1885, p. 32] [= *Oecotraustes* WAAGEN, 1869, p. 251 (type, *O. genicularis* WAAGEN, 1869, p. 227; SD MUNIER-CHALMAS, 1892, p. 171, ICZN Opinion 324); = *Oekotraustes* WAAGEN, 1869, p. 251 (obj.); = *Pleuroxyites* BUCKMAN, 1924, pl. 478 (type, *P. pleurifer*; OD); = *Flexoxyites* BUCKMAN, 1924, pl. 525A (type, *F. flexus*; OD); = *Harpoxyites* BUCKMAN, 1924, pl. 480 (type, *H. harpophorus*; OD); = *Gonoxyites* BUCKMAN, 1924, pl. 481 (type, *G. goniophorus*; OD); = *Oppelina* BUCKMAN, 1926, pl. 670 (type, *O. pulchra*; OD). Macroconchs (*Oppelia*, *Pleuroxyites*, *Flexoxyites*, *Harpoxyites*, *Gonoxyites*) from medium to large size, involute to semi-involute with narrow umbilicus and rounded umbilical edge; ogival to subtriangular whorl section, more compressed on outer than inner whorls; venter rounded or tectiform (on inner whorls) with slightly differentiated keel; sometimes median lateral spiral groove, smooth band or fillet; simple aperture. Distant falcoid or falcate primary ribbing and fine, dense concave secondaries restricted to the outer third of the flanks. Microconchs (*Oecotraustes*, *Oppelina*) of small or medium size (20–75 mm in diameter), involute to moderately evolute and with slightly eccentric (elliptic) coiling; compressed whorl section with flat or slightly convex flanks without spiral groove, smooth fastigate

to rounded and non-keeled venter; aperture with well-developed spatulate lateral lappets. Ribs falcate to sigmoidal with outer part markedly rursiradiate and generally well developed, often with small ventrolateral nodules; suture less incised than in macroconchs. *Lower Bajocian* (upper part of *Sauzei Zone*)–*upper Bajocian* (*Parkinsoni Zone*): Austria, Bulgaria, England, France, Germany, Hungary, Italy, Poland, Portugal, Romania, Slovakia, Spain, Switzerland, Greenland, Caucasus, Turkmenistan, Turkey, Russia, Iran, Azerbaijan, Pamir, India, Japan, Egypt (Sinai), Morocco, Algeria, Kenya, Madagascar, Argentina, Chile, Peru, Mexico, USA (Oregon, Alaska).—FIG. 14, *a–c*. **O. subradiata* (J. DE C. SOWERBY), holotype, macroconch, *lower Bajocian*, *Sauzei Zone*, Dundry Hill, Somerset, England, ×1 (new; original in J. DE C. SOWERBY, 1823, pl. 421, 2; also figured by BUCKMAN, 1908, pl. 6, 3*a–b*, ARKELL, 1952b, fig. 11, *a, b* and ARKELL, 1957, fig. 319, 1*a, b*; BMNH Palaeont. Dept. 43943).—FIG. 14, *d–e*. *O. pleurifer* (BUCKMAN), macroconch, *upper Bajocian*, *Parkinsoni Zone*, Inferior Oolite Group, Burton Bradstock, Dorset, England, ×1 (new; figured by BUCKMAN, 1924, pl. 478; British Geological Society, inventory no. BGS GSM37326).—FIG. 14, *f–g*. *O. subcostata* (J. BUCKMAN), macroconch, *upper Bajocian*, *Garantiana Zone*, Tenuicostatus Subzone, Embalse del Arquillo de San Blás, Iberian Cordillera, Spain, ×1 (FERNÁNDEZ-LÓPEZ, 1985, pl. 19, 4; Universidad Complutense, Madrid, EB6/1).—FIG. 14, *h*. *O. pulchra* (BUCKMAN), holotype, microconch, *upper Bajocian*, *Subfurcatum Zone*, Inferior Oolite Group, Lower Clatcombe, Sherborne, Dorset, England, ×1 (new; figured by BUCKMAN, 1926, pl. 670; British Geological Society, inventory no. BGS GSM49271).—FIG. 14, *i*. *O. umbilicata* (BUCKMAN), holotype, microconch, *upper Bajocian*, *Subfurcatum Zone*, Inferior Oolite Group, Frogden Quarry, Dorset, England, ×1 (new; figured by BUCKMAN, 1926, pl. 671; British Geological Society, inventory no. BGS GSM49272). —

FIG. 14, j–k. *O. genicularis* (WAAGEN), holotype, microconch, *lower Bajocian* or *upper Bajocian*, Humphriesianum or Subfurcatum Zone, Sully, Calvados, France, $\times 1$ (original in WAAGEN, 1869, pl. 20, 4; also

figured by WESTERMANN, 1958, pl. 1, 1a–b, reproduced here, and by STEPANOV, 1966, pl. 1, 1; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS I 521).

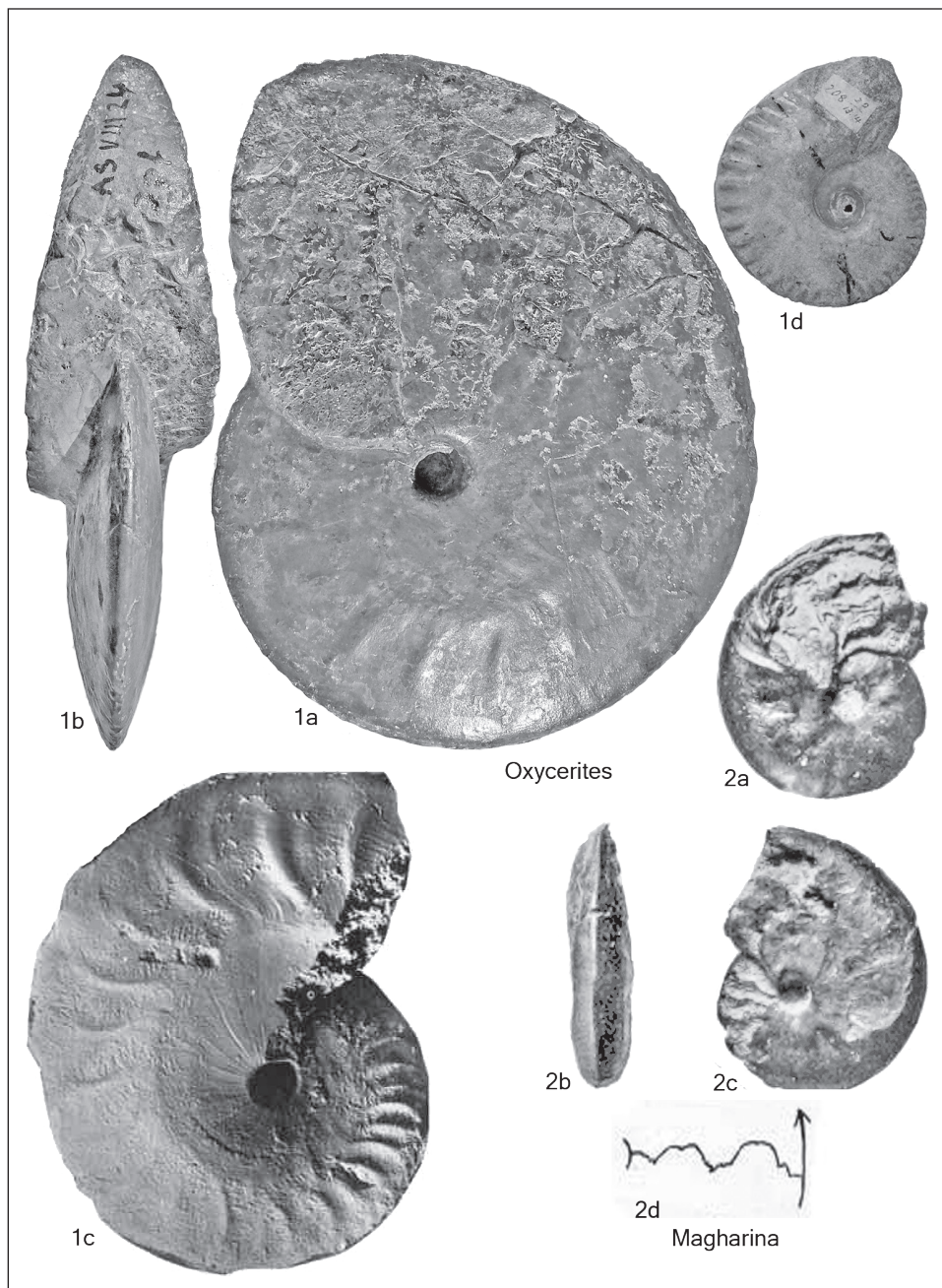


FIG. 15. Oppeliidae, Oppeliinae 2.

Oxycerites ROLLIER, 1909, p. 621 [**Ammonites aspidoides* OPPEL, 1857 in 1856–1858, p. 474; OD] [= *Nodiferites* WESTERMANN, 1958, p. 36 (type, *Oecotraustes nodifer* BUCKMAN, 1905, p. 195, for *O. conjugens* BUCKMAN, 1889, pl. 20, figs 13, 14; OD); = *Limoxites* WESTERMANN, 1958, p. 45 (type, *Oppelia nivernensis* DE GROSSOUVRE, 1919, p. 407; OD)]. Descending from *Oppelia*. Macroconchs (*Oxycerites*) similar to *Oppelia* [M], but differing in being slightly more involute, having sharper venter, and lacking secondary ribbing except in juvenile stages of some species. The microconchs (*Paroecotraustes* (*partim*), *Nodiferites*, *Limoxites*) likewise similar to *Oppelia* [m], but usually with midlateral groove, with more elliptical coiling in some species, but not all. More spaced, wider, and stronger secondary ribs, at times with small ventrolateral nodes; complex aperture with ventral rostrum and lateral lappets. Although *Ammonites serrigerus* WAAGEN, 1869 (type species of *Paroecotraustes* SPATH, 1928), should be considered a dimorphic microconch of *Prohecticoceras* SPATH, 1928, several species traditionally included in “*Paroecotraustes*” are dimorphic microconchs of *Oxycerites*. *Uppermost Bajocian* (Parkinsoni Zone)—*lower* or ?*middle Callovian*: Austria, Bulgaria, England, France, Germany, Hungary, Italy, Poland, Portugal, Slovakia, Spain, Switzerland, Greenland, North Africa (Algeria), Caucasus, Turkey, Russia, Iran, Azerbaijan, Pamir, Turkmenistan, Tibet, Nepal, India, Indonesia (Sula Islands and New Guinea), Japan, Saudi Arabia, Kenya, Madagascar, South America (Argentina, Peru), Mexico, USA (Oregon, Alaska).—FIG. 15, 1*a–b*. **O. aspidoides* (OPPEL), holotype, macroconch, *upper Bajocian*, upper Parkinsoni Zone, Bopfingen Ostalb, Germany, $\times 0.7$ (new, original in OPPEL, 1862 in 1862–1863, pl. 47, 4, also figured by WESTERMANN, 1958, pl. 6, *a–b*, and by SCHLEGELMILCH, 1985, pl. 4, 5; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS VIII 24).—FIG. 15, 1*c*. *O. yeovilensis* ROLLIER,

holotype, macroconch, *lower Bathonian*, Zigzag Zone, Yeovil, Somerset, England, $\times 1$ (HAHN, 1968, pl. 2, 2; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS I 515).—FIG. 15, 1*d*. *O. nodifer* (BUCKMAN), holotype, microconch, *upper Bathonian*, Zigzag Zone, Crackment Limestone, Bradford Abbas, Dorset, England, $\times 1$ (new; original of *O. conjugens* BUCKMAN, 1889, pl. 20, 13–14; also figured by ARKELL, 1951b, pl. 7, 8*a–b*; Sedgwick Museum of Earth Sciences, University of Cambridge, England, J.6417).

Magharina ARKELL, 1952a, p. 307 [**M. magharensis*; OD]. Small keeled oxycones, involute with regular coiling, faint ribbing, prominent growth lines, and simple sutures. *Magharina* could represent the dimorphic partner microconch of *Trimarginia*, in which case the name *Magharina* would have priority over *Trimarginia*, because ARKELL (1952a) nominated *Magharina* on p. 307 and *Trimarginia* on p. 308. Only the poorly preserved specimens of ARKELL (1952a) are known, and thus it is not possible to confirm this hypothesis. *Middle Jurassic* (*upper Bajocian*; ?*Subfurcatum Zone*–Parkinsoni Zone): Saudi Arabia.—FIG. 15, 2*a–d*. **M. magharensis* ARKELL, holotype, *upper Bajocian*, *Subfurcatum Zone*, Jebel Tuwaiq, Central Saudi Arabia, $\times 2$ (ARKELL, 1952a, pl. 30, 7*a–d*).

Alcidia ROLLIER, 1913, p. 277 [**Ammonites subdiscus* D’ORBIGNY, 1846 in 1842–1851, p. 421; SD WESTERMANN & CALLOMON, 1988, p. 28), *non* WESTWOOD, 1879, p. 524 (Lepidoptera), *non* BOURGUIGNAT, 1889, p. 46 (Mollusca, Gastropoda), *non* MONTEROSATO, 1890, p. 147 (Mollusca, Gastropoda), [= *Paralcidia* SPATH, 1928, (type, *P. khengari* SPATH, 1928, p. 88, for *Oppelia* cf. *glabella* LECKENBY in WAAGEN, 1875, p. 49, pl. 10, fig. 7, 7*a*; OD), *non* WARREN, 1906, p. 145 (Insecta, Lepidoptera); = *Pseudoppelia* LEANZA, 1946, p. 66 (type, *Streblites* (*Pseudoppelia*) *oxynota*, pl. 1, fig. 1–2; SD, PARENT, 2006, p. 18); = *Paroxycerites* BREISTROFFER,

1947, p. 3, (*non. nov.* for *Alcidia* ROLLIER, 1913; syn. obj.); = *Alcidellus* WESTERMANN, 1958, p. 40 (type, *Ammonites tenuistriatus* DE GROSSOUVRE, 1888, p. 374; OD; syn. obj.); = *Mesoxytes* WESTERMANN, 1958, p. 52 (type, *Ammonites waterhousei* MORRIS

& LYCETT, 1850, p. 13; OD)]. According to ARKELL (1957, p. 275), the valid genus name for *Ammonites subdiscus* D'ORBIGNY is *Paralcidia* SPATH, 1928, because the name *Alcidia* ROLLIER, 1913, was previously applied and both genera were considered



FIG. 16. Oppeliidae, Oppeliinae 3.

synonymous. Later, ÖZDIKMEŖ (2013, p. 239) showed that the valid generic name for *Ammonites subdiscus* is *Alcidia* ROLLIER, 1913, because the taxa that were nominated *Alcidia* prior to 1913 are synonymous with other genera previously named. Macroconchs (*Alcidia*, *Paralcidia*, *Paroxycerites*, *Alcidellus*, *Mesoxites*) are oxycones similar to those of *Oxycerites*; relatively large, involute to moderately involute; whorl section subtriangular, becoming subovate and slightly inflated in the body chamber; venter fastigate, sometimes apparently tricarinate in the phragmocone, becoming rounded towards the body chamber end, with the central keel containing the siphuncle; ribs falcate or sigmoidal in some, blunt to obsolete, wide and spaced; in others smooth or with fine striation. Suture relatively simple with several auxiliary (U_n) lobes, but without incised endings. BONNOT & others (1999, p. 245) cited a microconch [m] of *Paralcidia couffoni* (possibly *Alcidia*), but no genus was nominated, which can be considered the dimorphic microconch [m] of *Alcidia*. However, among others, the specimens classified as *Oxycerites* (*Paroecotraustes*) cf. *bronni* by SANDOVAL & WESTERMANN in SANDOVAL & others (1990, p. 118, pl. 2, fig. 3, pl. 3, fig. 9) and as *Oxycerites* (*Paroecotraustes*) ex. gr. *waageni* (1990, p. 119, pl. 3, fig. 7, 10, 16) have inner whorls similar to those of some species of *Alcidia* [*A. cualacensis* (SANDOVAL & WESTERMANN, 1990), *A. obsoleteoides* (RICCARDI & others, 1989) and *A. gr. tenuistriata* (DE GROSSOUVRE, 1888)], and appear in the same beds. These microconchs (20–40 mm in diameter maximum) are involute to relatively evolute, with slightly convex flanks, midlateral groove on the body chamber, and ventral area that is carinate in inner and middle whorls and becomes rounded in the body chamber end. The aperture has lateral lappets and small ventral rostrum. Some specimens are entirely smooth, while others develop very blunt falcoid secondaries between the midlateral groove and the ventrolateral margin, which can become

prominent towards the venter in the body chamber. The suture is very simple. *Middle Jurassic* (middle Bathonian–?upper Callovian): Austria, Bulgaria, England, France, Germany, Hungary, Portugal, ?Romania, ?Serbia, Spain, Switzerland, Russia, Egypt (Sinai), Iran, Pakistan, India, Madagascar, Indonesia (Sula Islands and New Guinea), Mexico, Argentina, Chile.—FIG. 16, *a–c*. **A. subdisca* (D'ORBIGNY), lectotype, macroconch, upper Bathonian, Retrocostatum Zone, Niort (Deux-Sèvres), France, $\times 0.7$ (new; figured by ELMŖ & GAUTHIER in FISCHER & others, 1994, pl. 54, 2*a–b*; coll. D'ORBIGNY IPM-R.4122).—FIG. 16, *d–g*. *A. cualacensis* (SANDOVAL & WESTERMANN); *d–e*, holotype, macroconch, lower Callovian, Bodenbenderi Zone (=Herveyi or Gracilis standard zones), Section Cl-Arroyo del Rincón, near the village of Cuahulote, Cualac Area, Guerrero State, Mexico, $\times 0.5$ (SANDOVAL & WESTERMANN in SANDOVAL & others, 1990, pl. 2, 1*a–b*; Instituto de Geología, UNAM, Mexico, IGM-4010); *f*, suture at D = 88 mm; *g*, microconch, lower Callovian, lower Bodenbenderi Zone, Caracoles, Chile, $\times 1$ [(figured as *Oxycerites* (*Paroecotraustes*) gr. *waageni* (STEPHANOV) by SANDOVAL & WESTERMANN in SANDOVAL & others, 1990, pl. 3, 16; McMaster University, Hamilton, Ontario, Canada, McM-J1141)].

Trimarginia ARKELL, 1952a, p. 308 [**T. sinaitica*; OD]. Medium size (macroconchs 70–90 mm in diameter; microconchs 20–40 mm); whorls oxyconic, involute, with tricarinate venter; ribs similar to those of *Oppelia*, fasciculate, falcoid or flexuous, but strongly attenuated, crossing the venter, as blunt chevrons; adult microconchs have small lateral lappets, macroconchs with a simple aperture; suture of oppeliid type with L deeper than E, and U_n with several auxiliary lobes. *Upper Bajocian* (Subfurcatum–Garantiana zones)–?upper Bathonian: France, ?Germany, ?Italy (Sicily), Spain (Iberian Range and Balearic Islands), ?Switzerland, Egypt (Sinai), Kenya. The upper Bathonian specimens from Sicily (WENDT, 1963, p.

123) and from Switzerland (MANGOLD & GYGI, 1997, p. 502, fig. 3.2a, 2b) that were classified as *Trimarginia* are probably inner whorls of *Alcidia tenuistriata* (DE GROSSOUVRE). In this case, the stratigraphic range of *Trimarginia* would be restricted to the upper Bajocian.—FIG. 17, a–c. **T. sinaitica* ARKELL, holotype, macroconch, Sinai, Egypt, $\times 1$ (DOUVILLÉ, 1916, pl. 3, 7; also figured by FERNÁNDEZ-LÓPEZ, 2000, fig. 1a–c; Geological Survey Museum, Cairo, no. 16685)—FIG. 17, d–g. *T. iberica*, FERNÁNDEZ-LÓPEZ; d–e, macroconch, upper Bajocian, Garantiana Zone, Tenuicostatus Subzone, Embalse del Arquillo de San Blás, Iberian Cordillera, Spain, $\times 1$ (FERNÁNDEZ-LÓPEZ, 1985, pl. 17, 2a–b; Universidad Complutense, Madrid, EG6/11); f, microconch, upper Bajocian, Garantiana Zone, Tenuicostatus Subzone, Embalse del Arquillo de San Blás, Iberian Cordillera, Spain, $\times 1$ (FERNÁNDEZ-LÓPEZ, 1985, pl. 17, 13; Universidad Complutense, Madrid, 9EB137U80/11); g, macroconch, suture, upper Bajocian, Garantiana Zone, Domeño, Iberian Cordillera, Spain, FERNÁNDEZ-LÓPEZ, 1985, fig. 26; Universidad Complutense, Madrid, 3DM90U25/1).

Subfamily HECTICOCERATINAE Spath, 1925a

[*nom. correct.* ARKELL, 1950, p. 363
(*pro* Hecticoceratidae SPATH, 1925a, p. 8)].

Shells of varied size, macroconchs reach 150 mm in diameter whereas microconchs are quite small. The shells are involute to semi-evolute or even evolute, with a compressed or moderately thick section and subparallel slightly convex flanks. The venter is usually keeled and may be fastigate (tricarinate) and rounded only in the body chamber. Ribs falcoid or falcate (except nuclei, which can be smooth), usually strong and covering inner as well as outer parts of the flanks; some genera can be tuberculate at the division points of the ribs and/or on ventrolateral shoulder. Sutures are relatively simple. Dimorphism occurs, but less apparent than in other haploceratoids. Microconchs have lateral lappets. The suture is typically haploceratoid, with E slightly less deep than the tripartite L, asymmetrical L-U₂ saddle; auxiliary lobes are not retracted. Hecticoceratinae originated in

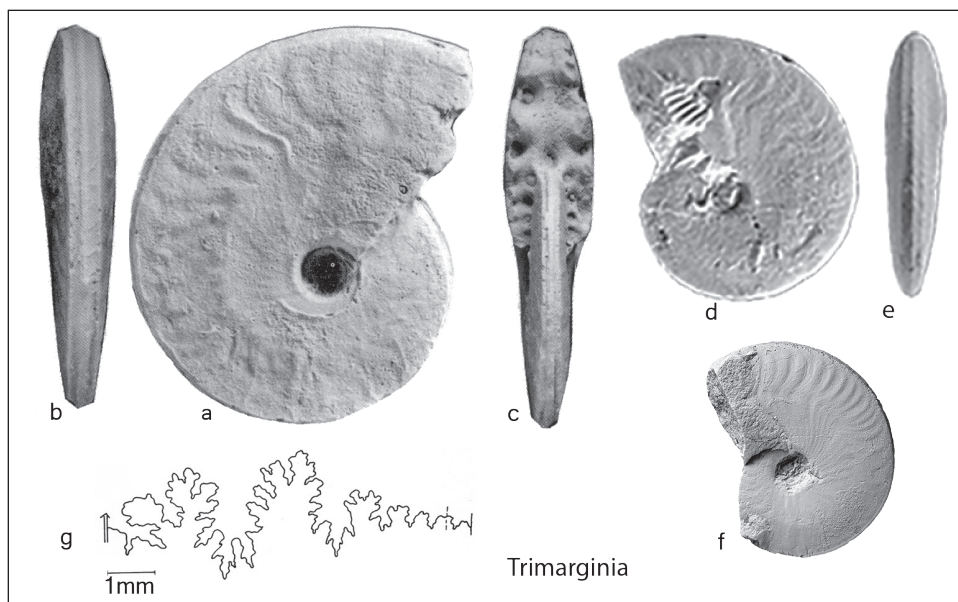


FIG. 17. Oppeliidae, Oppeliinae 4.

the latest Bajocian or early Bathonian, being possibly a direct paedomorphic descendant of Oppeliinae (*Oxycerites*). *Middle Jurassic (lower Bathonian)–Upper Jurassic (lower Kimmeridgian)*: worldwide.

Prohecticoceras SPATH, 1928, p. 100 [**Ammonites retrocostatus* DE GROSSOUVRE, 1888, p. 374; OD] [= *Paroecotraustes* SPATH, 1928, p. 80 (type, *Ammonites serrigerus* WAAGEN, 1869, p. 230; SD, LISSAJOUS, 1923, p. 120); = *Pseudoecotraustes* KHMISHASHVILI & STEPANOV in STEPANOV, 1966, p. 59 (type, *Oecotraustes* (*P.*) *bifurcus* KHMISHASHVILI & STEPANOV, 1966, p. 59; OD); = *Thraxites* STEPANOV, 1966, p. 60 (type, *Oecotraustes* (*T.*) *thrax* STEPANOV, 1966, p. 64; OD)]. Macroconchs of medium size, involute or semi-evolute, ogival to subrectangular whorl section with unicarinate flat venter; falcoid regular more-or-less defined ribs with strongly prorsiradiate primaries and slightly curved retroverse secondaries ending in small ventrolateral tubercles; ribs sometimes fade on the body chamber; aperture simple. The presumable microconchs (*Paroecotraustes*, *Pseudoecotraustes*, *Thraxites*) of small size (30–50 mm in diameter), moderately evolute with fastigiated venter and with a keel fading on the body chamber; falcate ribs, well developed in the phragmocone, end with small to well-marked ventrolateral clavi; aperture with lateral lappets. *Middle Jurassic (upper-middle Bathonian–lower Callovian)*: Austria, Azerbaijan, Bulgaria, England, France, Germany, Hungary, Italy, Poland, Portugal, Romania, Slovakia, Spain, Switzerland, Algeria, Morocco, Somalia, India, Nepal, Indonesia, (Sula Islands and New Guinea), Argentina, Chile, Mexico. — Fig. 18, a–b. *P. ochraceum* ELMI, holotype, macroconch, (coll. Dumortier), *middle Bathonian*, Subcontractus Zone, Ruisseau de Beulet, Crussol, Guilherand (Ardèche), France, ×1 (ELMI, 1967, pl. 5, 1a–b; Lyon University Collection, MHNL 11549) — Fig. 18, c–d. *P. retrocostatum* (DE GROSSOUVRE), macroconch (coll. Dumortier), *upper Batho-*

nian, Blanaz, St-Rambert-en-Bugey (Ain), France, ×1 (ELMI, 1967, pl. 5, 7a–b; Lyon University Collection, MHNL 1156). — Fig. 18, e–f. *P. pseudolunula* ELMI, macroconch, *lower Callovian*, La Grimaudière (Deux-Sèvres), France, ×1 (ELMI, 1967, pl. 6, 1; coll. Roman, Lyon University Collection, FSL 61032). — Fig. 18, g–j. *P. serrigerus* WAAGEN; g–h, microconch, lectotype of *Oecotraustes* (*Paroecotraustes*) *serrigerus* (WAAGEN), designated by LISSAJOUS (1923, p. 120) (lost), *upper Bathonian*, Orbis zone, Balin, Kraków, Poland, ×1 (reproduction of the original figure of WAAGEN, 1869, pl. 20, 7a–b); i–j, (neotype designated by STEPANOV, 1961, p. 829), microconch, *Bathonian*, Retrocostatum Zone, Serrigerus Bed, Polaten Limestones, near the village of Glojane (Teteven), Bulgaria, ×1 (STEPANOV, 1966, pl. 3, 12; Coll. BAN, no. J601). — Fig. 18, k–l. *P. waageni* (STEPANOV), neotype (designated by STEPANOV (1961, p. 829), microconch, *upper Bathonian*, Retrocostatum Zone or Orbis Zone, Lechstedt near Hildesheim, Lower Saxony, Germany, ×1 (STEPANOV, 1966, pl. 3, 9; also figured by WESTERMANN, 1958, pl. 1, 6a–d; Mus. Geol. Bundesanstalt für Bodenforschung, Hannover, Coll. Hann. n°. b302; J 6417).

Otoxyites WESTERMANN, 1958, p. 51 [**Ammonites canaliculatus fuscus* QUENSTEDT, 1849 in 1845–1849, p. 118; SD ROLLIER, 1911, p. 305] [= *Eohecticoceras* ZEISS, 1959, p. 103 (type, *Oppelia costata* ROEMER, 1911, p. 39; SD ARKELL, 1952b, p. 72); = *Zeissoceras* ELMI, 1967, p. 569 (type, *Hecticoceras primaevum* DE GROSSOUVRE, 1919, p. 410; OD)]. Macroconchs (*Eohecticoceras*, *Zeissoceras*) with discoidal shells of medium size, relatively involute, ogival compressed to rarely subrectangular section, ventral area fairly acute except near the aperture, and with low keel. Barely ornamented inner whorls; later, falcate ribs with division points on the inner third of the flanks, diffuse primaries and stronger secondaries with ventrolateral thickening,

but without developing true nodules. The ?microconchs (*Otoxyites*) are small and more evolute than the macroconchs; falcate ribs on the end of phragmocone and body chamber,

and with midlateral groove coinciding with the divisions of the ribs; the secondaries, thicker than primaries and strongly rursiradial, protruding from the keel-like ends.

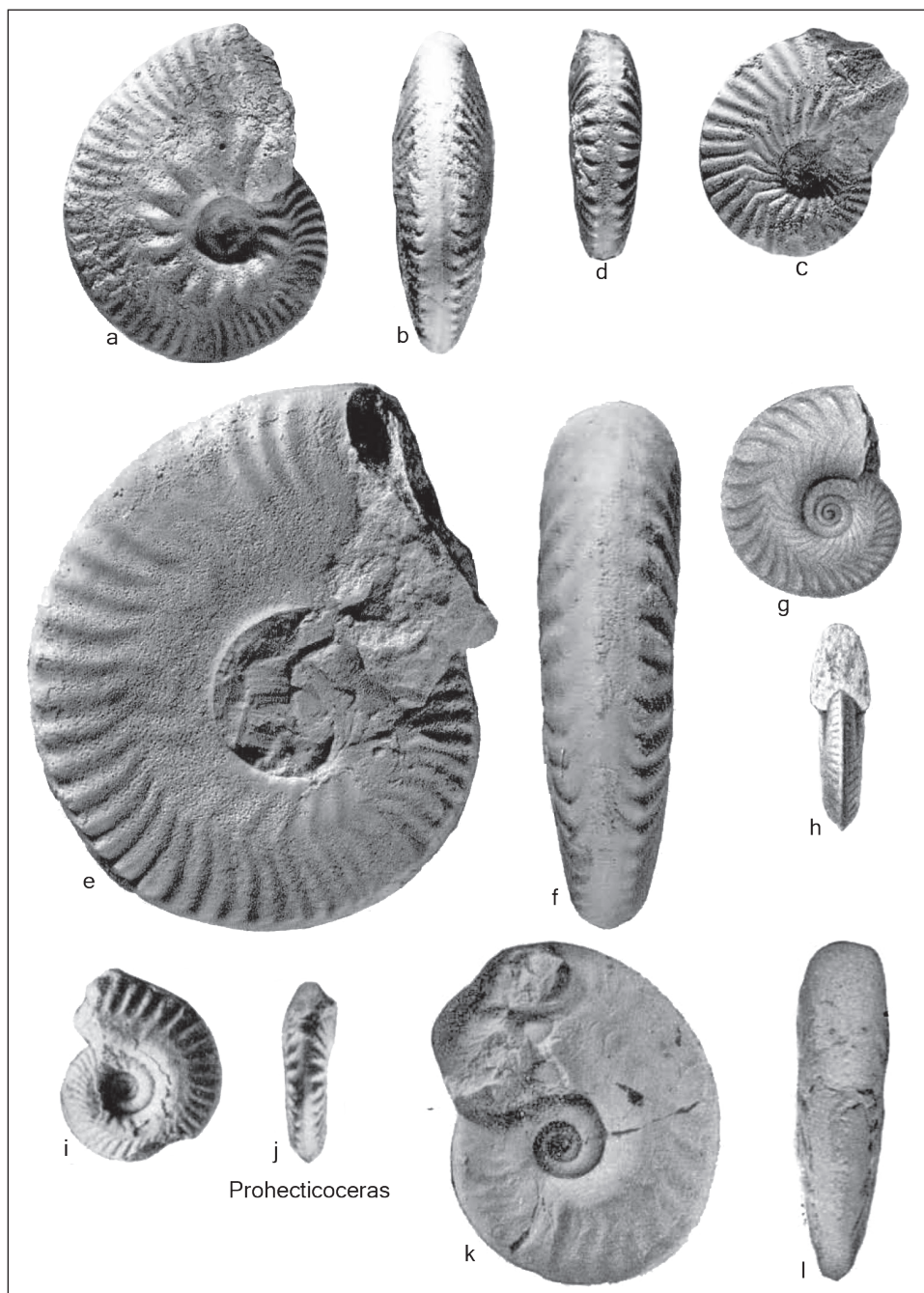


FIG. 18. Oppeliidae, Hecticoceratinae 1.

Suture simple, with lobe L slightly deeper than E. *Middle Jurassic (lower Bathonian–lowermost Callovian)*: England, France, Spain, Portugal, Germany, Switzerland, Italy, Serbia, Poland, Romania, Bulgaria, Algeria, Morocco, India, Indonesia. —FIG. 19, 1a–c. **O. fuscus* (QUENSTEDT), holotype, ?microconch, *middle Bathonian*, Öschingen, Germany, $\times 1.5$; 1a, original of QUENSTEDT, 1849 in 1845–1849, pl. 8, 7; 1b–c, refigured by WESTERMANN, 1958, pl. 10, 8d–e; Geologische Institut, Universität Tübingen, Germany. —FIG. 19, 1d–e. *O. costatus* (ROEMER), holotype, macroconch, *upper Bathonian*, Lechstedt, Hildesheim, Germany, $\times 1$ (1d, from ROEMER, 1911, pl. 8, 7; 1e, from WESTERMANN 1958, pl. 2, 6b; Institut für Geologie und Paläontologie, Universität Göttingen Collection). —FIG. 19, 1f. *O. primaevum* (DE GROSSOUVRE), lectotype of *Hecticoceras primaevum* (designated by ELMI, 1967, p. 571), macroconch, *lower Bathonian*, Sainte-Pezenne, Nièvre, France, $\times 1$ (new; Lyon University Collection, FSL EM 178).

Hecticoceras BONARELLI, 1894, p. 77 [**Nautilus hecticus* REINECKE, 1818, p. 70; OD] [= *Lunuloceras* BONARELLI, 1894, p. 77 (type, *Nautilus lunula* REINECKE, 1818, p. 69; OD); = *Concavites* JEANNET, 1951, p. 34 (type, *Nautilus Parallelus* REINECKE, 1818, p. 67; OD); = *Eulunulites* ELMI, 1967, p. 551 (type, *Lunuloceras pompeckyi* PARONA & BONARELLI, 1897, p. 106; OD); = *Lemoineiceras* ELMI, 1967, p. 560 (type, *Hecticoceras margaritae* LEMOINE, 1932, p. 133; OD)]. Medium-sized macroconchs (*Hecticoceras*, *Lunuloceras*, *Concavites*), evolute to semi-evolute, subrectangular to ovate whorl section with flat unicarinate venter. Ribbing paired, usually strong, arising at the umbilical edge, sometimes from small tubercles, and ending in ventrolateral tubercles. Microconch (*Eulunulites*, *Lemoineiceras*), small, with semi-evolute to evolute coiling, ovate-slightly compressed whorl section with small keel; almost non-existent inner ribs, and short and concave

outer ribs. Suture simple with deep auxiliary lobes. The holotypes of the type species of *Hecticoceras*, *Lunuloceras*, and *Concavites* come from the same locality (Bad Staffelstein-Uetzing, Upper Franconia, Germany) and from the same faunal horizon (*Parallelum horizon*, *Enodotum Subzone*, *Calloviense Zone*, *lower Callovian*; see DIETL & MÖNNIG, 2016). At this horizon, a large number of intermediate forms from the three so-called genera coexist and therefore could belong not only to the same genus, but to the same biological species. *Middle Jurassic (lower Callovian–?middle Callovian, Coronatum Zone) –?lowermost Oxfordian*: Bulgaria, England, France, Germany, Italy, Poland, Portugal, Romania, Slovakia, Spain, Switzerland, Russia, (Russian Platform, Caucasus, Crimea), Iran, Israel, Pamirs, Nepal, India (Kutch), Japan, Indonesia, Somaliland, Madagascar, South America, Argentina, Chile, Peru, Mexico, USA (?California). —FIG. 19, 2a–c. **H. hecticum* (REINCKE); 2a–b, holotype, macroconch, *lower Callovian*, *Calloviense Zone*, ?*Enodatum Subzone*, Langheim, Germany, $\times 1$ (Original illustration of REINECKE, 1818, pl. 4, 37–38); 2c, topotype, *lower Callovian*, *Calloviense Zone*, ?*Enodatum Subzone*, Langheim, Germany, $\times 1$ (new; photograph kindly provided by Dr. E. Mönnig from Coburg). —FIG. 19, 2d. *H. margaritae* LEMOINE, (type species of *Lemoineiceras* ELMI, 1967), holotype, microconch, *middle Callovian*, Chanaz (Savoy), France, $\times 1$ (new; original in LEMOINE, 1932, pl. 7, 4; Lyon University Collection, FSL EM 178). —FIG. 19, 2e–f. *H. boginense* PETITCLERC, macroconch, *lower Callovian*, Prahecq (Deux-Sèvres), France, $\times 1$ (ELMI, 1967, pl. 11, 5a–b, original figure in P. PETITCLERC, 1921, pl. 21, 9d; FSP, coll. Petitclerc). —FIG. 19, 2g–h. *H. pompeckyi* (PARONA & BONARELLI), microconch, holotype of *Eulunulites pompeckyi assionense* ELMI, *lower Callovian*, *Koenigi Zone*, Sainte-Appolonie, Les Assions (Ardèche), France, $\times 1$ (ELMI, 1967, pl. 3, a–b; M 184, coll. Maillard).

Chanasia ROLLIER, 1922, p. 359 [*Hecticoceras chansiense* PARONA & BONARELLI, 1897, p. 134; OD] [= *Jeanneticeras* ZEISS,

1956, p. 19 (type, *Ammonites hecticus perlatus* QUENSTEDT, 1887 in 1882–1888, p. 700; OD); = *Jeannetites* COLLIGNON, 1960, p. 2,

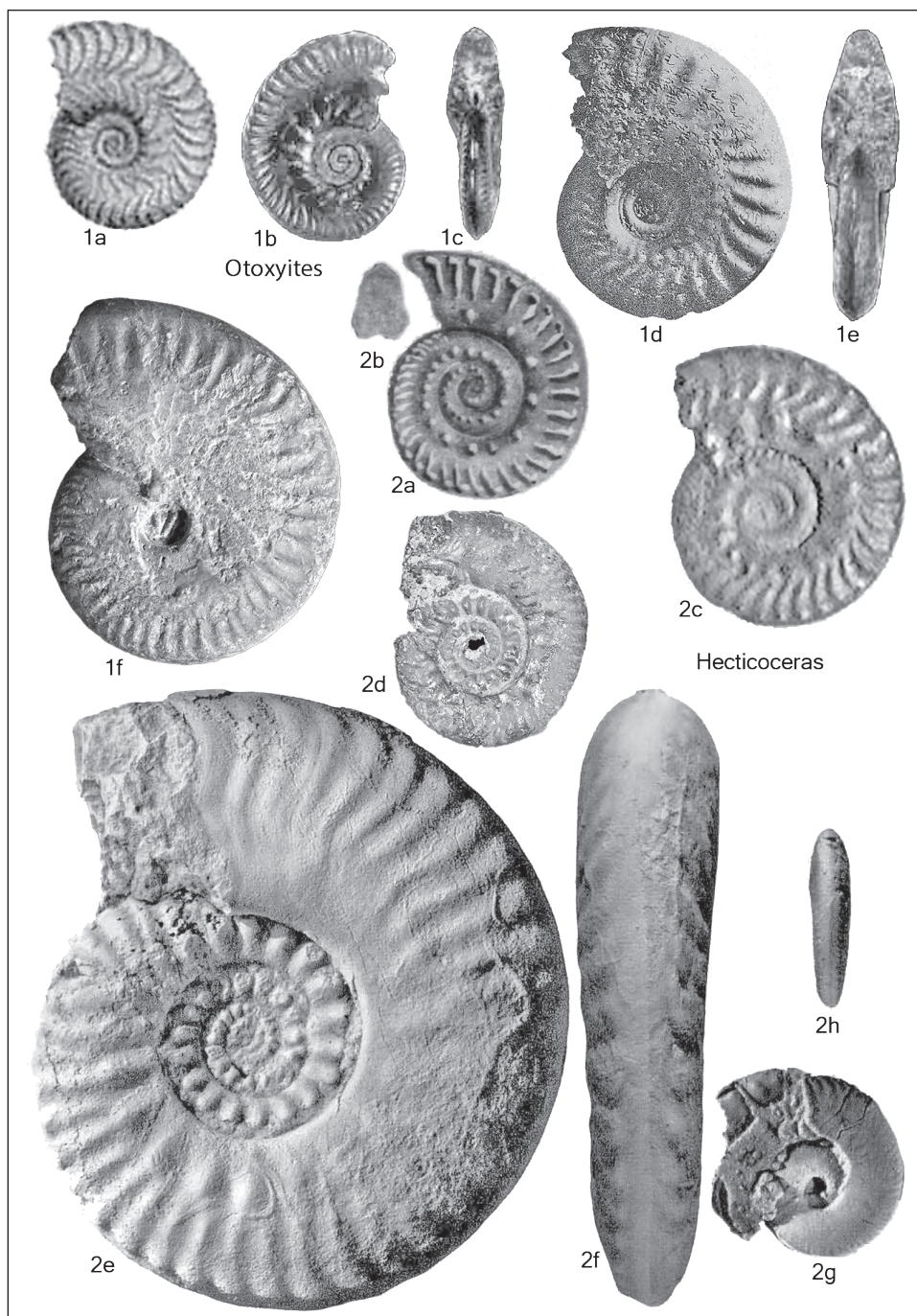


FIG. 19. Oppeliidae, Hecticoceratinae 2.

nom. nov. pro Jeannetia COLLIGNON, 1958, pl. 13, fig. 69, *non* MERCIER, 1936, p. 421 (Echinoidea); *nom. nov. pro Jeanneticeras* COLLIGNON, 1959a, p. 2 (errata); *non* ZEISS, 1956, p. 19 (preoccupied for other ammonites) (type, *Jeannetia hourcqii* COLLIGNON, 1958, pl. 13, fig. 69; OD)]. Macroconchs (*Chanasia*) medium size with well-marked lateral groove on the phragmocone; some with midlateral and ventrolateral tubercles, strong external ribs and variable internal ribbing; some with fine longitudinal clavi between the well-developed ventrolateral tubercles and the keel, which may be crenulated; the lateral furrow and the internal ribbing disappears progressively on the body chamber; the keel and the marginal tubercles become erased near the aperture. Relatively complex suture with wide L and with narrow saddles. Microconch (*Jeanneticeras*, ?*Eulunulites* (*partim*)) small to medium size, rather evolute, ovate to subrectangular section, with tectiform unicarinate prominent venter; irregular primary ribs and secondaries, prominent on the upper flank, terminating in the ventrolateral shoulder, usually at pronounced nodes; complex aperture with small ventral rostrum and lateral lappets with peristome grooves. *Middle Jurassic; lower Callovian* (Koenigi Zone)—*middle Callovian* (Anceps Zone): France, Germany, Poland, Portugal, Bulgaria, Romania, Spain, Switzerland, Crimea, India, Pamir, Madagascar, Argentina, ?Chile.—FIG. 20, 1a–b. *C. chanasienne* (PARONA & BONARELLI), macroconch, lectotype (designated by ELMI, 1967, p. 621), *lower Callovian*, Chanaz, Savoy, France, ×1 (new; original in PARONA & BONARELLI, 1897, pl. 4, 1; Museo Regionale di Scienze Naturali di Torino, no. 34157.1) —FIG. 19, 1c–d. **C. perlata* (QUENSTEDT), lectotype, ?microconch, (type species of *Jeanneticeras* ZEISS, 1956), *lower Callovian*, Macrocephalus Zone, Geisingen, Gutmadingen/Baden, Germany, ×1 (new; also figured by SCHLEGELMILCH, 1985, pl. 6, 13; Geologische Institut, Universität Tübingen, GPIF-PV.61665). —FIG. 20, 1e–f. *C. turgida* (LÓCZY) = *Hecticoceras* (*C.*)

hartmanni ZEISS, holotype, macroconch, *lower-middle Callovian* transition, near Niort (Deux-Sèvres), France, ×1 (ELMI, 1967, pl. 9, 1a–b, original of D'ORBIGNY, 1847 in 1842–1851, pl. 152, fig. 1–2; MNHN.F.B11343, Muséum National d'Histoire Naturelle, Paris).

Brightia ROLLIER, 1922, p. 360 [**Hecticoceras* (*Lunuloceras*) *nodosum* BONARELLI, 1894, p. 94; OD] [= *Ammonites hecticus nodosus* QUENSTEDT, 1849 in 1845–1849, p. 118; pl. 8, fig. 4] [= *Glyptia* ROGOV, 2000, p. 172 (type, *Ammonites hecticus canaliculatus* QUENSTEDT, 1849 in 1845–1849, p. 118; OD)]. Macroconchs, medium-sized, evolute to semi-involute with ovate to subrectangular compressed whorl section; venter rounded with variously developed keel; inner half of the flanks with growth lines, ribs, or distant bullate nodes; outer half have fine, sickle-shaped rursiradiate ribs without tubercles on the ventrolateral edge; midlateral furrow is a thin spiral line or a wide spiral gap; suture simple, haploceratoid. Microconchs are smaller, more evolute, with more attenuated ornamentation, and have lateral lappets at the adult aperture (BONNOT & others, 1999, p. 252, pl. 1, fig. 8–11; ROGOV, 2000, pl. 5, fig. 10–11). The specimens included by ROGOV (2000, p. 172, pl. 5, fig. 4, 5, 9, 13) in the subgenus *Brightia* (*Glyptia*) show characters typical of microconchs. *Middle-upper Callovian* (Coronatum Zone)—*lowermost Oxfordian* (Mariae Zone): England, France, Germany, Italy, Poland, Portugal, Bulgaria, Romania, Spain, Switzerland, Slovakia, Russia (central), Crimea, Iran, Turkmenistan, Egypt (Sinai), Pamir, India (Kutch), Algeria, Madagascar, USA (?Alaska). —FIG. 20, 2a. **B. nodosa* (QUENSTEDT), holotype, ?macroconch, *Callovian*, ×1.5 (new; original of *Ammonites hecticus nodosus* QUENSTEDT, 1849 in 1845–1849, pl. 8, 4; Staatliches Museum für Naturkunde Stuttgart, inventory no. 28339). —FIG. 20, 2b. **B. nodosiformis* ROGOV, holotype, macroconch, *upper Callovian*, Athleta Zone, Ryazan Region, quarry Mikhailovtsement, ×1 (ROGOV, 2000, pl. 5, 6; PIN no. 4771/14).

Putealicer BUCKMAN, 1922, pl. 297 11; OD] [= *Sublunuloceras* SPATH, 1928, p. 102 (type, *Harpoceras lairense* WAAGEN, [**Ammonites putealis* LECKENBY, 1859, p.

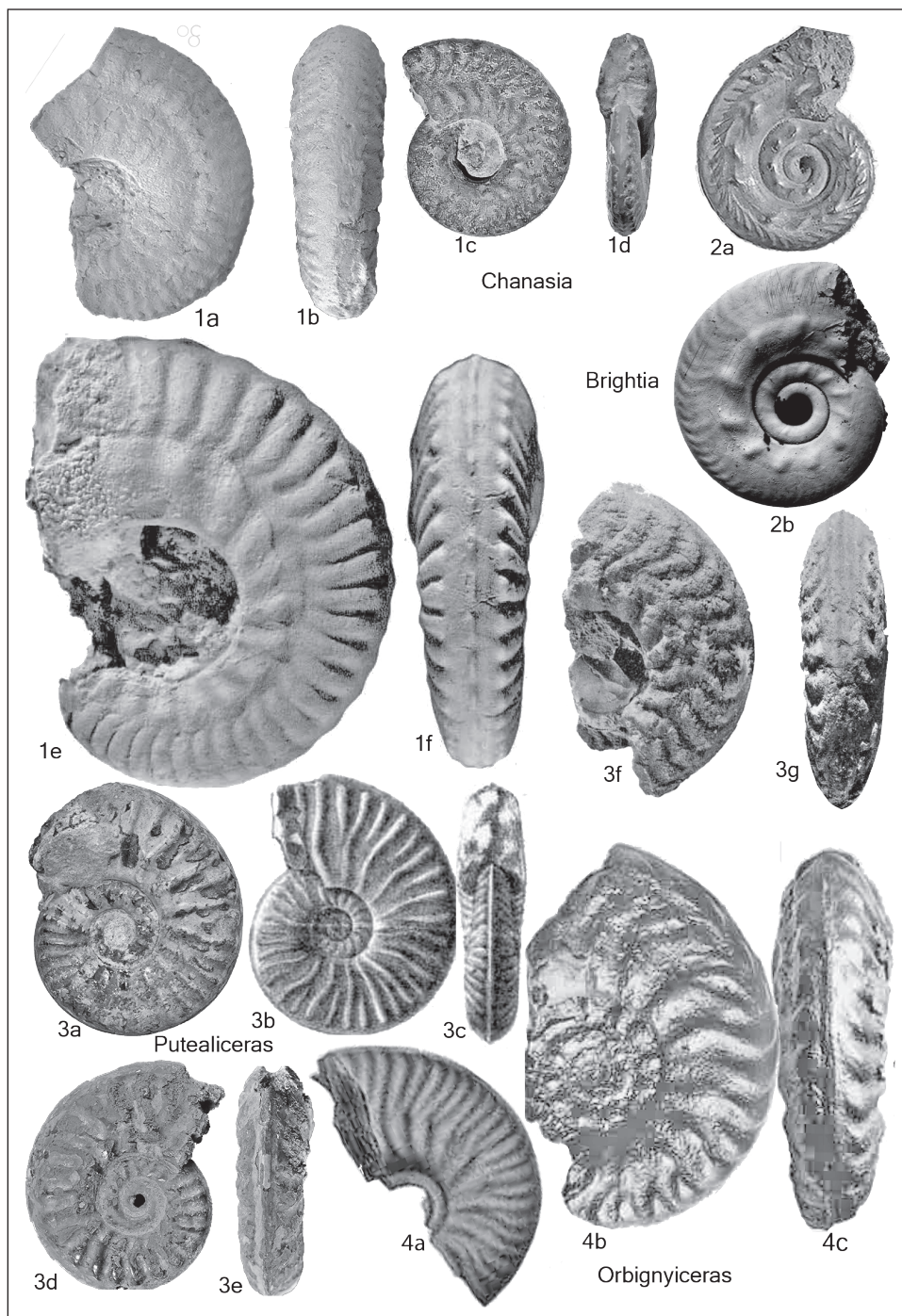


FIG. 20. Oppliidae, Hecticoceratinae 3.

1875, p. 65; OD); =*Pseudobrightia* SPATH, 1928, p. 116 (type, *P. dhosaensis*; OD); =*Eocheioceras* SPATH, 1928, p. 128 (type, *Ammonites hersilia* D'ORBIGNY, 1850, p. 351; SD ROMAN, 1938, p. 162)]. Small to medium-sized, semi-evolute to evolute, with ovate to subrectangular whorl section; innermost whorls smooth; later, strong irregularly divided ribs with short proverse primaries and longer rursiradiate secondaries ending in small tubercles, with division points sometimes reduced to nodes. Similar to *Brightia*, but with spiral lateral groove absent in *Putealicer*, and with thinner and more numerous secondary ribs in the external part of the flanks. Possible microconchs approximately 40–50% in diameter relative to the macroconchs, but without a modified aperture. Suture haploceratoid, simple with three or four umbilical lobes. *Pseudobrightia* SPATH, 1928, is also considered to be synonymous with *Putealicer*, given that ROY (2014, p.175) has shown that the type species *Pseudobrightia dhosaensis* SPATH should be included in this genus. *Middle Callovian* (Anceps Zone)–?lowermost *Oxfordian*: England, Germany, France, Portugal, Switzerland, Italy, Hungary, Serbia, Poland, Bulgaria, Romania, Russia (Russian Platform), Caucasus, Crimea, Algeria, Madagascar, Syria, Israel, Iran, Pamir, India, Japan, Indonesia, Argentina.—FIG. 20, 3a. **P. puteale* (LECKENBY), holotype, macroconch, *Callovian*, The Castle Rock, Scarborough, Yorkshire, England, $\times 1$ (new; also figured by BUCKMAN, 1922, pl. 297, 1–3; Sedgwick Museum, University of Cambridge, England, J. 3309). —FIG. 20, 3b–c. **P. lairens* (WAAGEN), lectotype (designated by SANDOVAL, herein), macroconch, *upper Callovian*, Kutch, western India, $\times 1$ (WAAGEN, 1875, pl.13, 3a–b). —FIG. 20, 3d–e. *P. hersilia* (D'ORBIGNY), type species of *Eocheioceras* SPATH, 1928, holotype, ?macroconch, Salins-les-Bain, Jura, France, $\times 1$ (new; also figured by COTTREAU, 1927, pl. 14, 14–15; coll. D'ORBIGNY, MNHN.F.R02048, Muséum National d'Histoire Naturelle, Paris). —FIG. 20,

3f–g. *P. dhosaensis* (SPATH), holotype, type species of *Pseudobrightia* SPATH, macroconch, *upper Callovian*, Athleta Zone, Dhosa Oolite, Fakirwadi, India, $\times 0.5$ (SPATH, 1928, pl. 13, 10a–b).

Orbignyceras GÉRARD & CONTAUT, 1936, p. 34 [**Harpoceras pseudopunctatum* LAHUSEN, 1883, p. 89; SD ZEISS, 1956, p. 38] [= *Rossienceras* GÉRARD & CONTAUT, 1936, p. 38 (type, *Harpoceras rossiense* TEISSEYRE, 1884, p. 544; SD ZEISS, 1956, p. 50)]. Thick forms of medium size, semi-evolute with relatively deep umbilicus and with subparallel and slightly convex flanks; in juveniles the umbilical wall gently slopes, then gradually lifts to become strongly inclined, to almost vertical in adults; umbilical edge rounded. The venter is broad, rounded, with a keel, and is often accompanied at the end of the last whorl by two barely visible lateral elevations. Proverse primary ribs appear very early and bifurcate at nodules at mid-whorl height, becoming tubercles with growth; in parallel with the divisions into two slightly rursiradiate secondary ribs becoming less clear and intercalate secondary ribs appearing; secondaries bending forward on the ventral edge, where they reach maximum thickness. Smallest, evolute forms resemble microconchs, but dimorphism is not very apparent. Suture with a divergent E, a wide and not very high E-L saddle, L tripartite and asymmetric, the saddle L-U₂ very high and quite strongly pinched at its asymmetrical base; narrow, high auxiliary saddles with narrow and deep lobes. The presence of midlateral nodules differentiates this genus, with subboreal affinities, from *Putealicer* with Tethyan characters. *Middle Callovian*–lowermost *Oxfordian*: France, Germany, Portugal, Spain, Switzerland, Italy, Poland, Bulgaria, Romania, Russia (Dagestan, Ryazan), Syria, Iran, Pakistan (Karakorum), India.—FIG. 20, 4a. **O. pseudopunctatum* (LAHUSEN), lectotype, macroconch, ?*Callovian*, Kirchdorf Podnowolok, Russia, $\times 1$ (LAHUSEN, 1883,

pl.11, 11).—FIG. 20, 4*b*–*c*. *O. rossiense* (TEISSEYRE), holotype of the type species of

Rossienceras GÉRARD & CONTAUT, 1936, macroconch, *Callovian*, Pronsk, Rjasan,

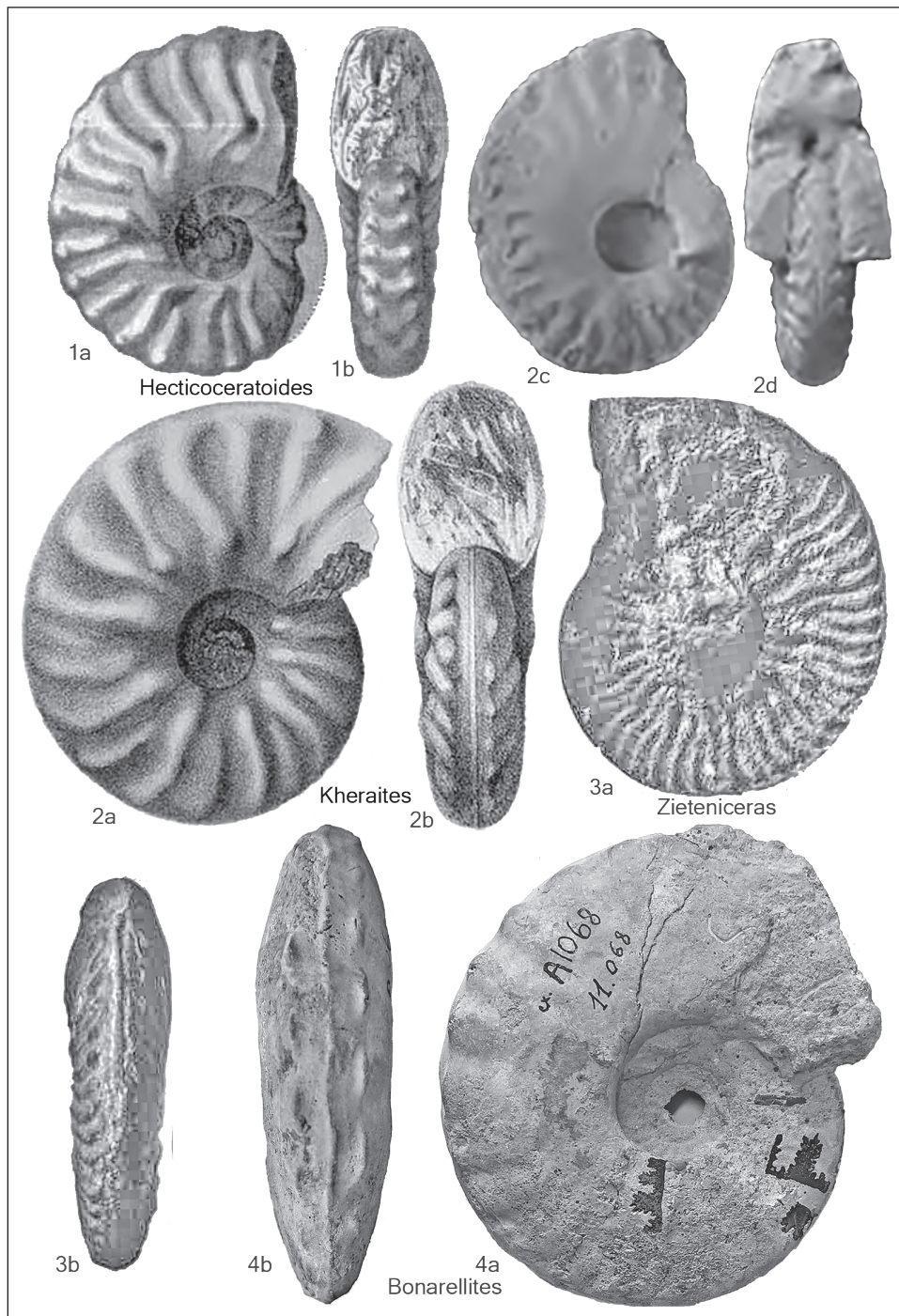


FIG. 21. Oppliidae, Hecticoceratinae 4.

Russia, $\times 1$ (TEISSEYRE, 1884, pl. 1, 6; also figured by SCHLEGELMILCH, 1985, pl. 8, 1; Palaeont. Inst. Universität Wien).

Hecticoceratoides SPATH, 1924, p. 5 [**H. suborientalis* SPATH, for *Oppelia orientalis* WAAGEN, 1875, non D'ORBIGNY, p. 58, pl. 11, fig. 5; OD]. Possibly macroconchs, medium size, with coiling, and whorl section similar to that of *Kheraites*; ribs falcate ending at ventro-lateral nodes which are connected across venter by prorsiradiate chevrons. ?Lower-middle Callovian: ?Spain, India, Madagascar. —FIG. 21, 1a–b. **H. suborientalis* SPATH, lectotype, macroconch (?), lower Callovian, India (western part, Kutch), $\times 1$ (WAAGEN, 1875, pl. 11, 5; No. 117).

Kheraites SPATH, 1925a, p. 8 [**Harpoceras crassefalcatum* WAAGEN, 1875, p. 70; OD]. Similar to *Putealicerias* and perhaps closely related, but more involute and more strongly ribbed. Medium to small size, and rather involute; whorls elliptical to compressed ovate, venter rounded with a keel; ribs weakly prorsiradiate from umbilicus, dividing at bullae on the lower third of the flank; secondaries flattened, coarse, and concave towards the aperture, ending in clavi or projected bullae at ventrolateral margin. Dimorphism is not clear, but according to ROY (2014, p. 178), microconchs, *K. gr. crassefalcatum* (WAAGEN), are smaller, approximately 50% of the diameter of macroconchs, *K. gr. ignobilis* (J. DE C. SOWERBY), and have proportionally stronger ribbing. The suture is simple, with L only slightly deeper than E and high and asymmetric saddle L-U₂. Middle Callovian: France, Germany, Hungary, Switzerland, India, Israel, Egypt (Sinai). —FIG. 21, 2a–b. **K. crassefalcatum* (WAAGEN), lectotype, macroconch, phragmocone, lower Callovian, Rehmanni Subzone, Khera Hill Kutch, western India, $\times 1$ (WAAGEN, 1875, pl. 12, 6–6a). —FIG. 21, 2c–d. *K. ignobile* (J. de C. SOWERBY), macroconch, middle Callovian, Anceps Zone, K17, Jara bed 2, India (Kutch, western part), $\times 1$ (ROY, 2014, fig. 3, a–b).

Zieteniceras ZEISS, 1956, p. 24 [**Hecticoceras zietenii* DE TSYTOVITCH, 1911, p. 25; OD]. Possibly descendents of *Hecticoceras*. Macroconchs medium-sized, relatively evolute with a subtrapezoidal whorl section; proverse primary ribs very short and sometimes reduced to pointed nodes, and long secondaries concave forward, ending in ventrolateral tubercles elongated forwards onto the venter up to a thick keel; suture simple with moderately incised elements. According to ELMi (1967, p. 580), *Zieteniceras* ZEISS, 1956, is synonymous with *Prohecticoceras* SPATH, 1928; SCHLEGELMILCH (1985, p. 35) indicated that differentiation between the two is problematic. Here, the two genera are accepted because the morphology and stratigraphic range of their type species are quite distinct. Perhaps the uppermost-lower Callovian–middle Callovian species of hecticoceratins that ELMi (1967) included in *Prohecticoceras* should be transferred to *Zieteniceras*. Middle Jurassic (uppermost-lower Callovian–middle Callovian): England, France, Germany, Spain, Hungary, Poland, Bulgaria, Russia. —FIG. 21, 3a–b. **Z. zietenii* (DE TSYTOVITCH), holotype, macroconch, ?middle Callovian, Crêt de Châlame, Chézery, France, $\times 1$ (DE TSYTOVITCH, 1911, pl. 1, 2; also figured by SCHLEGELMILCH, 1985, pl. 6, 5. Muséum d'histoire naturelle de Genève).

Bonarellites ELMi, 1967, p. 686 [**Hecticoceras* (B.) *alternans*; OD]. Macroconchs are middle sized and similar to *Chanasia*, but slightly more evolute, with a subrectangular whorl section and a poorly developed lateral groove; ribs on internal surface of shell blunt with widely spaced secondaries; keel weakly crenulated with ventrolateral clavi-shaped tubercles or lateral pseudocarina. Suture typically haploceratoid, with E slightly less deep than L, and saddle L-U₂ wide and asymmetrical. Some small middle Callovian forms, with wide and spaced secondary ribs ending in ventrolateral clavi, and a peristome with lateral lappets that were classified as “*Jeanneticeras*” by ELMi (1967), could be

the microconch of *Bonarellites*. *Uppermost-lower Callovian—middle Callovian* (Anceps and Coronatum Zones): France.—FIG. 21, 4a–b. **B. alternans* (ELMI), holotype, macroconch, *lower ?Callovian*, Banc “pain de noix” de Doux (Deux-Sèvres), France, $\times 0.7$ (new; also figured by ELMI, 1967, pl.

12, 1a–b; coll. Roman, Lyon University Collection, FSL 11068).

Ankobites COLLIGNON, 1958, fig. 120 [**A. saintoursi*; OD]. Medium-sized and rather involute with subrectangular whorl section and deep midlateral groove; ribs very strong,

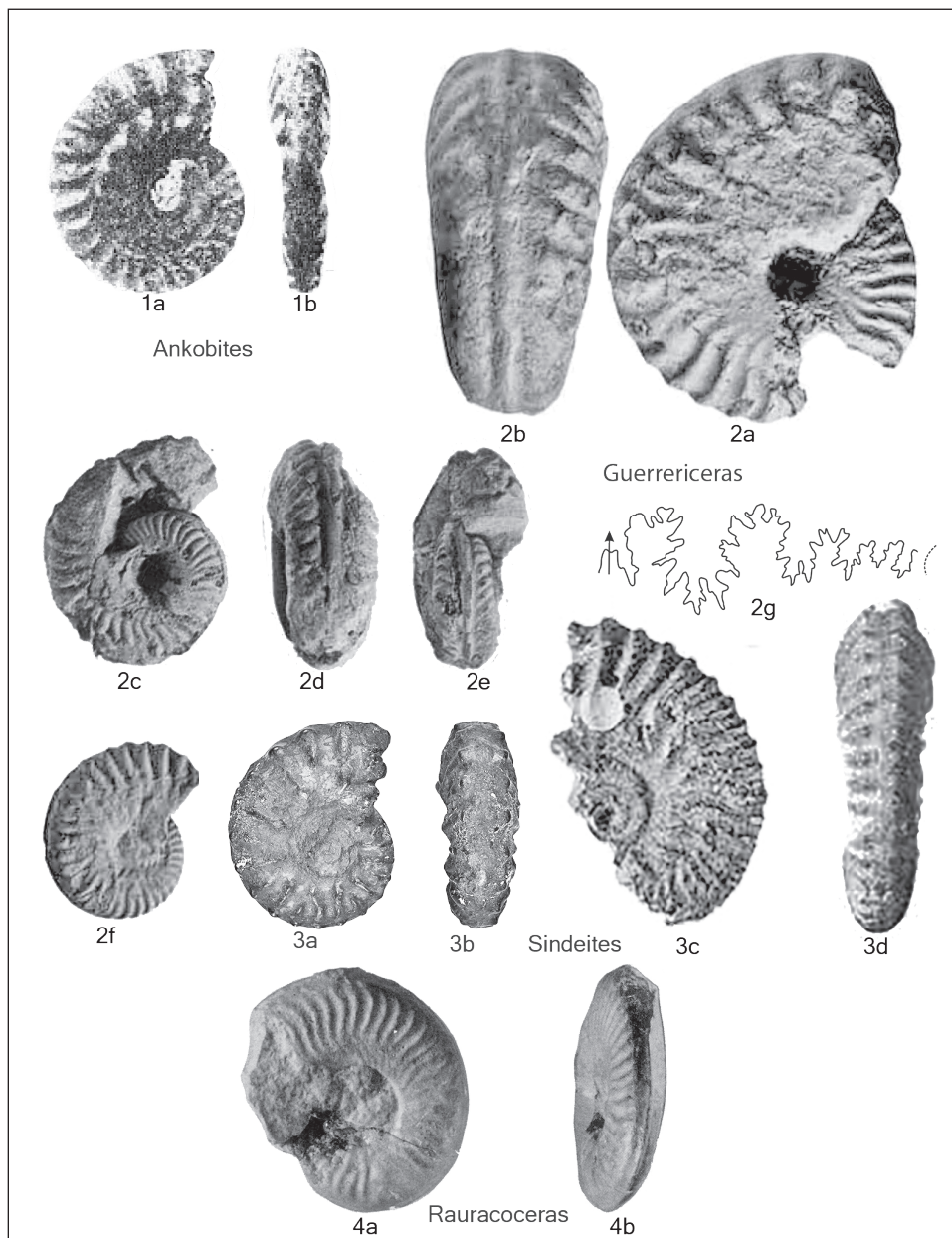


FIG. 22. Oppeliidae, Hecticeratinae 5.

thick, and spaced, terminating at the ventrolateral margin in strong tubercles elongated forwards; keel low and wide. Dimorphism unknown. Similar to *Chanasia*, with well-developed midlateral groove, but more strongly ornamented. *Middle Callovian*: ?France, Madagascar.—FIG. 22, 1*a–b*. **A. saintoursi* COLLIGNON, holotype, ?macroconch, *middle Callovian*, Ancaps Zone, Saint Ours, Ankoba (Mitsinjo), Madagascar, $\times 1$ (COLLIGNON, 1958, pl. 28, 120).

Guerrericeras SANDOVAL & WESTERMANN, 1990, p. 120 [**Clydoniceras inflatum* WESTERMANN, 1984 (in WESTERMANN & others, 1984, p. 103; OD)]. Relatively small macro- and microconchs, involute with narrow and deep umbilicus, subquadratic or subrectangular whorl section, strongly carinate and bisulcate venter, prominent falcate ribbing, stronger on the outer half of the flanks. Suture typical of Hecticoceratidae; E is less deep than the wide and trifold L, saddle L-U₂ is wide, with umbilical elements not retracted. Similar to strigoceratid *Sphaerodomites calcaratus* [m], but slightly more evolute and with better marked ornamentation (ribs and keel). *Middle Jurassic (lower Callovian, Gracilis Zone)*: Mexico (Guerrero), Chile.—FIG. 22, 2*a–g*. *G. inflatum* (WESTERMANN), *lower Callovian*, Bodenbenderi Zone (=Gracilis Zone), *inflatum* Association, unit 15 of section Cl-Arroyo del Rincón, near the village of Cuahulote, Cualac Area, Guerrero State, Mexico; 2*a–b*, topotype, macroconch, $\times 1$ (SANDOVAL & WESTERMANN, in SANDOVAL & others, 1990, pl. 2, 5*a–b*; Instituto de Geología, UNAM, Mexico, IGM-4205); *2*c–e*, holotype, microconch, $\times 1$ (WESTERMANN & others, 1984, pl. 1, 2*a–c*, McMaster University, Hamilton, Ontario, J 2110a); 2*f*, topotype, microconch, $\times 1$ (SANDOVAL & WESTERMANN, in SANDOVAL & others, 1990, pl. 3, 14; Instituto de Geología, UNAM, Mexico); 2*g*, suture at D = 38 mm (SANDOVAL & WESTERMANN, in SANDOVAL & others, 1990, text-fig. 9*b*; Instituto de Geología, UNAM, México, IGM-4026).

Sindeites SPATH, 1925a, p. 12 [**S. mada-gascariensis* SPATH; OD]. The holotype of the type species (small fragment) relatively evolute with carinate subtrapezoidal section, smooth inner whorls, and later sharp ribbing ending in small ventrolateral tubercles; typical hecticoceratin suture. *Sindeites* was included in the Distichoceratinae HYATT, 1900, by ARKELL (1957, p. 279), but all morphological characters and the suture line are closer to those of Hecticoceratinae more than to those of Distichoceratinae. *Lower–?middle Callovian*: India, Madagascar, Kenya, and Tanzania.—FIG. 22, 3*a–b*. **S. mada-gascariensis* SPATH, ?macroconch, *middle Callovian*, 1 km. east of Mont Ambohidroa (Antsalova), Madagascar, $\times 1$ (new; figured by COLLIGNON, 1958, pl. 28, 117; Université de Bourgogne, Dijon, UBGD.010117).—FIG. 22, 3*c–d*. *S. sindensis* SPATH, holotype, *Callovian*, Jesmlmir, Sinde, Kutch, western India, $\times 2$ (SPATH, 1928, pl. 9, 10*a–b*; B. M. No. C. 23545).

Rauracoceras MAUBEUGE, 1962, p. 413 [**R. rauracum*; OD]. Macroconch of small size, moderately evolute, subrectangular in section that throughout ontogeny becomes more compressed towards the base; keel well developed with flat bands on both sides. Ribs heavily falcoid, not fasciculate, although some visibly joined at the base, thicker in the outer half of the flanks; suture unknown. Microconchs are not known. This strange and rare form is possibly a descendant of *Zieteniceras*, which it resembles, but lacks ventrolateral tubercles and is stratigraphically much higher. ?*Oxfordian* (?Transversarium Zone): Germany and Switzerland.—FIG. 22, 4*a–b*. **R. rauracum*. MAUBEUGE, holotype, ?macroconch, ?*middle Oxfordian*, ?Transversarium Zone, Weisser Jura, Switzerland, $\times 1$ (MAUBEUGE, 1962, fig. 1*a, c*; Muséum de Liestal, Bâle-Campagne, Switzerland, n^o. 2062).

Pseudosonninia PARENT, GARRIDO, SCHWEIGERT, & BRAMBILLA, 2019, p. 4 [**P. chacaymelehuensis*; OD]. Medium-sized,

inner whorls evolute, with sub-oval whorl section, becoming compressed platyconic; smooth to weakly ribbed. Macroconch with subadult and adult whorls moderately involute; inflated-oxyconic whorl section, and strong keel; lower half of flanks sometimes smooth or tuberculate, ribs curve strongly forwards on upper part of whorl, ending beside a sharp prominent, unfloored keel. Microconch small, platyconic with short rursiradiate ribs on the upper flank on the body chamber; long lateral lappets. Suture finely incised. *Middle Jurassic (Callovian)*: Argentina.—FIG. 23, *a–f*.

**P. chacaymelehuensis* PARENT, GARRIDO, SCHWEIGERT, & BRAMBILLA, *middle Callovian*, “Jason” Zone, Los Molles Fm., faunal-level C, Chacay Melehué, Neuquén Basin, Argentina; *a–c*, holotype, macroconch with body chamber, lateral and ventral views, and cross section, $\times 1$ (PARENT & others, 2019, fig. 2, *A1*, *A3–A4*; also figured by PARENT, 2022, fig. 12*Q₁–Q₃*; MOZ-PI-3553/1); *d–f*, paratype, a complete adult microconch, same locality and faunal level, $\times 2$ (PARENT & others, 2019, fig. 2, *C4–C6*; also figured by PARENT, 2022, fig. 12*R₁–R₂*; MOZ-PI-3553/2).

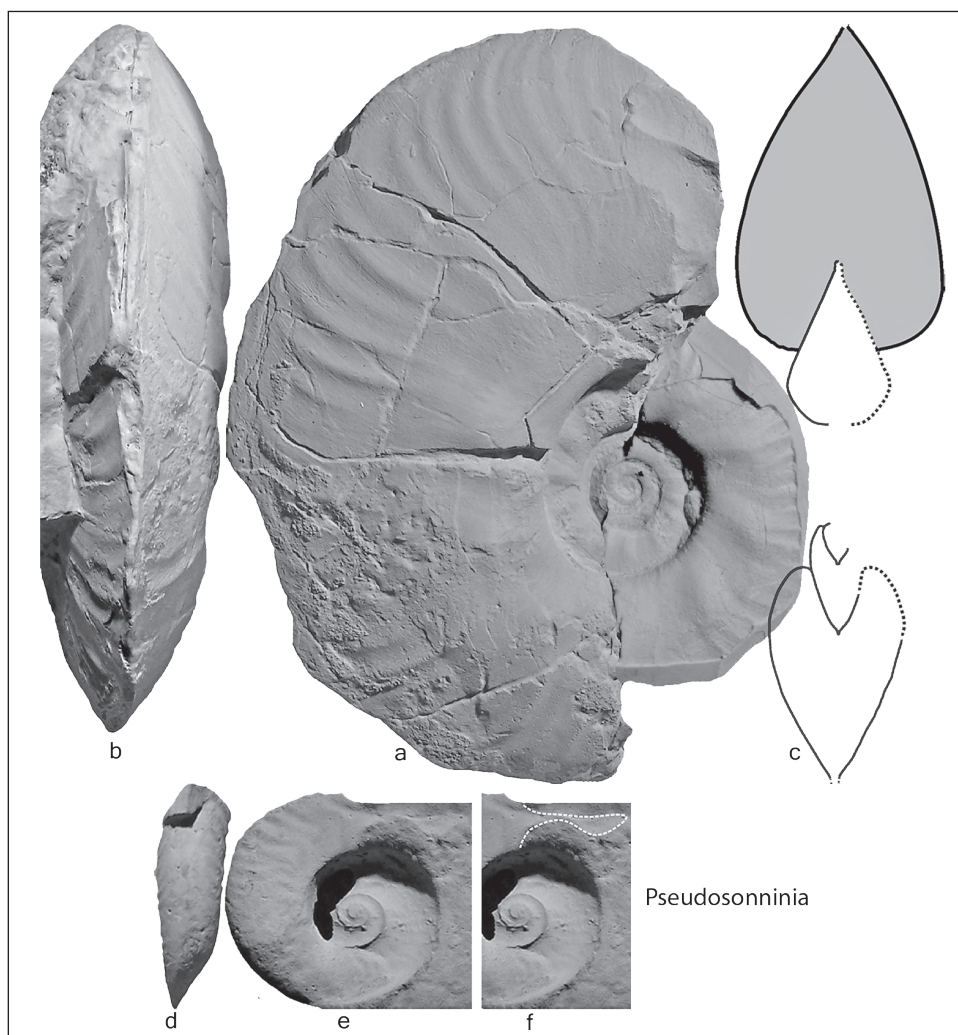


FIG. 23. Oppliidae, Hecticoceratinae 6.

Subfamily OCHETOCERATINAE Spath, 1928

[Ochetoceratinae SPATH, 1928 (p. 127)]

The macroconchs include medium-sized oxycones with typical ogival to ovate whorl section, falcoid ribs divided at a midlateral groove or fillet, with the secondary ribs wider and stronger than the primaries and curving forwards; the venter is unicarinate, fastigate, or tricarinate, with median keel tallest and somewhat minutely serrated. The microconchs usually included in “Glochiceratinae” are small, almost smooth and lappeted. Dimorphism is not clear at the genus level; however, some genera, as *Neocampylites* CALLOMON, 1973, have specimens that are clearly microconchs, and others, including the type species of “*Glochiceras*” (*Ammonites nimbatus* OPPEL, 1863, p. 191), are clearly dimorphic microconchs of *Ochetoceras* (ZIEGLER, 1974, p. 28; WIERZBOWSKI & MATYJA, 2014, p. 64). According to ARKELL (1957, p. 278), Ochetoceratinae are probably polyphyletic derivatives of Hecticoceratinae and Oppeliinae, but a relationship with Hecticoceratinae alone is more likely (CHRIST, 1961, p. 315). *Neocampylites* could represent the link between Hecticoceratinae and Ochetoceratinae: the coiling whorl section, ribbing with well-marked primaries and secondaries, and ventrolateral tubercles make it closer to Hecticoceratinae, while the tricarinate venter and suture recall Ochetoceratinae. On the other hand, the type of ventral region and style of ribbing of some Ochetoceratinae move them closer to the oppeliin *Aldidia*. CALLOMON (1981, p. 143), GYGI (2013, p. 69) and JANTSCHKE & SCHWEIGERT (2020, p. 99) included *Ochetoceras* in the subfamily “Glochiceratinae” HYATT, 1900; PARENT & others (2014) included it in Hecticoceratinae SPATH, 1925a, whereas according to SCHWEIGERT (pers. com. 08-10-2019) the attribution should be with Streblitinae SPATH, 1925b. Either option would nullify the subfamily Ochetoceratinae, which is based

on the genus *Ochetoceras*. *Uppermost Middle Jurassic (upper Callovian)–Upper Jurassic (lower Kimmeridgian)*: England, France, Germany, Spain, Portugal, Switzerland, Italy, Poland, Russia (European part and northern Siberia), Iran, Pakistan, India, Japan, Argentina, Chile, Cuba, Mexico, USA (California), Canada, Greenland, and Norway (Spitsbergen Island).

Taxonomic status of the “glochiceratids.”

The different authors have generally included in the family Glochiceratidae or subfamily Glochiceratinae microconchiate forms of various affinities. Since the family Glochiceratidae was first established by HYATT (1900, in ZITTEL, p. 569), it has been given different meanings or taxonomic ranks. **a**, Synonym with Haploceratidae (ARKELL, 1957, in the former *Treatise*, p. 272). **b**, Family rank: ZIEGLER (1974), who revised the Upper Jurassic Haploceratoidea, including in Glochiceratidae the subfamilies Hecticoceratinae, Distichoceratinae, Ochetoceratinae, and Glochiceratinae, the latter containing only the microconchs with lateral lappets (“*Glochiceras*” HYATT, 1900; “*Coryceras*” ZIEGLER, 1958; “*Lingulaticeras*” ZIEGLER, 1958, and “*Paralingulaticeras*” ZIEGLER, 1958; ? “*Bukowskites*” JEANNET, 1951, and *Hildoglochiceras* SPATH, 1924); MATYJA (1986), GYGI (1991), RODRÍGUEZ-TOVAR (1993), SCHWEIGERT (1995, who considered Streblitinae, including *Oxydiscites* and *Barthelia*, as a subfamily of Glochiceratidae), SCHAIRER & SCHLAMPP (1991, 2003), QUEREILHAC & GUINOT (2011), SEYED-EMAMI & SCHAIRER (2011), QUEREILHAC (2013), and SEYED-EMAMI & others (2020). **c**, Subfamily of Oppeliidae: OLÓRIZ (1978), CALLOMON (1981, who considered Ochetoceratinae as synonymous with Glochiceratinae), SCHAIRER (1984a), VILLASEÑOR & GONZÁLEZ-ARREOLA (1988), PAGE (1991), OLÓRIZ & others (1993), ÉNAY & GYGI (2001), PARENT (2006), ÉNAY (2009), GYGI (2013), FÖZY & SCHERZINGER (2013), LÓPEZ-PALOMINO (2013, who included the macroconchs *Ochetoceras*

and *Cubaochetoceras* in this subfamily), PARENT & GARRIDO (2015, who included *Neoprionoceras* in Glochiceratinae), GRIGORE (2018, 2019), JANTSCHKE & SCHWEIGERT (2020, who included in the subfamily the genera *Trimarginites* and *Ochetoceras*), BUJTOR & ALBRECHT (2021), JANTSCHKE & others (2025), JAIN (2025). **d**, Subfamily of Haploceratidae (ROGOV, 2002, 2004).

Ever since ZIEGLER (1974) revised the systematics of the Upper Jurassic Haploceratoidea, the Glochiceratidae or Glochiceratinae have been frequently used in the literature, but almost always limited to the small microconchs with lateral lappets: “*Glochiceras*,” “*Coryceras*,” “*Lingulaticeras*,” “*Paralingulaticeras*,” and “*Rogoviceras*” SCHERZINGER & MITTA, 2006, which was originally considered a subgenus of “*Lingulaticeras*.” However, several authors (ÉNAY, 2009, p. 81, 82; BAUDOUIN & others, 2011, p. 656; QUEREILHAC & GUINOT, 2011, p. 37; QUEREILHAC, 2013, p. 219; FÖZY & others, 2022, p. 254; etc.) have shown that the term Glochiceratidae or Glochiceratinae is currently only used for indiscriminately aggregating microconchs that are dimorphic pairs of macroconchs and are attributed to different families (Lissoceratidae, Haploceratidae, and Oppeliidae), mainly belonging to the subfamilies Streblitinae SPATH, 1925b, Ochetoceratinae SPATH, 1928, and Taramelliceratinae SPATH, 1928.

The analysis of the type species of each of these microconchiate “genera” shows these to be a dimorphic microconch of a macroconchiate “genus.” The type species of “*Glochiceras*” HYATT, 1900, p. 569 (*Ammonites nimbatius* OPPEL, 1863, p. 191) and “*Glochiceras subclausum*” (OPPEL, 1863 in 1862–1863, p. 190) are dimorphic microconchs of *Ochetoceras* (see MATYJA, 1986, p. 52; QUEREILHAC, 2013, p. 213; WIERZBOWSKI & MATYJA, 2014, p. 64). This would indicate that Glochiceratidae HYATT, 1900, and Ochetoceratinae SPATH, 1928, are synonyms, and that Glochiceratidae would have nomenclature priority due to its older age. However, as we will show

below, the names Glochiceratidae or Glochiceratinae should not be used with the current meaning. The taxonomic status of “*Coryceras*” is quite problematic. According to QUEREILHAC (2009, p. 34), the type species of “*Coryceras*,” *Ammonites microdomus* OPPEL, 1863 in OPPEL (1862–1863, p. 204), is the dimorphous microconch of *Richeiceras lochense* (OPPEL); for WIERZBOWSKI & MATYJA (2014, p. 65) the type species of “*Coryceras*” is the dimorphous microconch of *Richeiceras*; JANTSCHKE & SCHWEIGERT (2020, p. 98) regarded this type species as the dimorphous partner of *Taramelliceras externodosum* (DORN, 1931). “*Lingulaticeras nudatum* (OPPEL, 1863), type species of “*Lingulaticeras*,” is a dimorphous microconch of *Taramelliceras* (SCHWEIGERT, 2009, p. 324; BAUDOUIN & others, 2011, p. 626; WIERZBOWSKI & MATYJA, 2014, p. 65; FÖZY & others, 2022, p. 254) and therefore synonymous with *Taramelliceras*, whereas “*Langulaticeras*” gr. *solenoides* (QUENSTEDT) is a dimorphous partner of *Neochetoceras* (PARENT & others, 2010, p. 453; FÖZY & SCHERZINGER, 2013, p. 221; SCHERZINGER & others, 2015, p. 3; FÖZY & others, 2022, p. 255). The type species of “*Paralingulaticeras*” (*Ammonites lithographicus* OPPEL, 1863 in 1862–1863, p. 248) and “*Rogoviceras*” (*Glochiceras lithographicum efimovi* ROGOV, 2002, p. 360) are dimorphous microconchs of *Fontannesella* (ROGOV, 2004, p. 41; FÖZY & SCHERZINGER, 2013, p. 219; FÖZY & others, 2022, p. 254).

In conclusion, the glochiceratids are polyphyletic and, as indicated by QUEREILHAC (2013, p. 219), “the terms defining the family Glochiceratidae, the subfamily Glochiceratinae HYATT, 1900 (1913), the genus “*Glochiceras*” HYATT, 1900 (1913), and the subgenera “*Glochiceras*” HYATT, 1900, “*Coryceras*” ZIEGLER, 1958, “*Lingulaticeras*” ZIEGLER, 1958, “*Paralingulaticeras*” ZIEGLER, 1958, and “*Rogoviceras*” SCHERZINGER & MITTA, 2006, should be enclosed in quotation marks because do not represent (by grouping only microconch forms of Haploceratidae,

Lissocerotidae, Ochetoceratinae, Streblitinae and Taramelliceratinae) in the strict sense the family/subfamily and its subdivisions" [sic].

Ochetoceras HAUG, 1885, p. 696 [**Ammonites canaliculatus* VON BUCH, 1831, pl. 1, fig. 6–8 in OPPEL 1862 in 1862–1863, p. 157; SD MUNIER-CHALMAS, 1892, p. 151] [= *Glochiceras* HYATT, 1900, p. 569, (type *Ammonites nimbatum* OPPEL, 1863 in 1862–1863, p. 191; OD); = *Fehlmannites* JEANNET, 1951, p. 89 (type, *F. jurensis*; OD) = *Canaliculites* JEANNET, 1951, p. 90 (type, *C. argoviensis*; OD)]. Macroconch (*Ochetoceras*, *Fehlmannites*, and *Canaliculites*) medium-sized, flat, discoidal, and involute; semi-ogival compressed whorl section, with convergent flanks, varying through ontogeny; ventral area ranging from carinate with small keel bordered by weak smooth part to rounded with only median keel, which can be minutely serrated on the body chamber; midlateral groove or, rarely, a raised area; crescent-shaped ribs on the outer half of the flanks, and with a very fine dividing line. Microconchs, some forms traditionally classified as "*Glochiceras nimbatum*" (OPPEL) and "*G. subclausum*" (OPPEL), small in size, moderately evolute with slightly eccentric coiling with marked uncoiling in body chamber end; compressed whorl section with gently curved flanks, but frequently with a mid-lateral groove and rounded venter which can also become keeled with serrations; smooth or rarely weakly ribbed on the body chamber; aperture with long lateral lappets and small ventral rostrum. Suture, relatively simple with E almost as deep as L, this being asymmetrically trifid; the saddle L-U₂ high and narrow. *Fehlmannites* JEANNET, 1951, was considered a subgenus of *Ochetoceras* by ARKELL (1957, p. 278), but the two subgenera are morphologically very similar and coincide in the stratigraphic record (*lower Oxfordian*) of various localities and therefore are considered here to be synonymous. *Upper Jurassic (lower Oxfordian–lowermost Kimmeridgian)*: England, France, Germany, Italy, Poland,

Portugal, Spain, Switzerland, Bulgaria, Russia (central part), Iran, ?Pakistan, Egypt, India (Kutch), Nepal, Japan, Yemen, Somalia, Tanzania, Madagascar, Antarctic Peninsula, Argentina, Chile, Cuba, Mexico, and USA (California).—FIG. 24, 1a–d, **O. canaliculatum* (VON BUCH); 1a–c, cast of the holotype, macroconch, *Oxfordian*, Transversarium Zone, ×1 (new; original in OPPEL, 1863 in 1862–1863, pl. 51, 3; also figured by QUEREILHAC, 2013, pl. 1, 1a–b; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS I 627); 1d. microconch, holotype of "*Glochiceras* (*G.*) *subclausum*" (OPPEL), *middle Oxfordian*, Transversarium Zone, Birnenstorf, Switzerland, ×1 (ZIEGLER, 1958, pl. 10, 3; also figured by QUEREILHAC, 2013, pl. 1, 3a–b; Geol. Inst. E.T.H. Zürich, Ve. S. 35). —FIG. 24, 1e. *O. jurensis* (JEANNET), lectotype (designated by SANDOVAL, herein) of *Fehlmannites jurensis* JEANNET, macroconch, *lower Oxfordian*, Cordatum Zone, Herznach mine, Herznach, Aargau, Switzerland, ×1 (JEANNET, 1951, pl. 20, 9; Bw. N°. F. 306, Frei coll.). —FIG. 24, 1f. *O. nimbatum* (OPPEL), holotype, microconch, *middle Oxfordian* (Plicatilis Zone, Tenuicostatum Subzone), Badener Schichten, Rieden, Bavaria, Germany, ×1.5 (ZIEGLER, 1958, pl. 10, 7; Geolog. Inst. der E.T.H. Zürich, Ve. S. 210).—FIG. 24, 1g. *O. argoviensis* (JEANNET), lectotype (designated by SANDOVAL, herein), macroconch, *lower Oxfordian*, Cordatum Zone, ×1 (JEANNET, 1951, pl. 27, 5; No. F. 301, Frei collection).

Neocampylites CALLOMON, 1973, p. 1003 [**Ammonites delmontanus* OPPEL, 1863 in 1862–1863, p. 194; OD] [= *Campylites* ROLLIER, 1922, p. 360, *non* EICHWALD, 1856 (Polychaeta; type, *Serpulites longissimus* MURCHISON & J. DE C. SOWERBY, 1839); = *Pseudocampylites* JEANNET, 1951, p. 76 (type, *P. jolleri*; OD); = *Neocampylites* CALLOMON, 1973]. *Campylites* ROLLIER, 1922 (= *Neocampylites* CALLOMON, 1973) was included by ARKELL (1957, p. 278),

CHRIST (1961, p. 278) and PAGE & others (2015, p. 181) in the subfamily Ochetoc-

eratinae (Oppeliidae), whereas other authors (JEANNET, 1951, p. 42; ZEISS, 1956, p. 19)

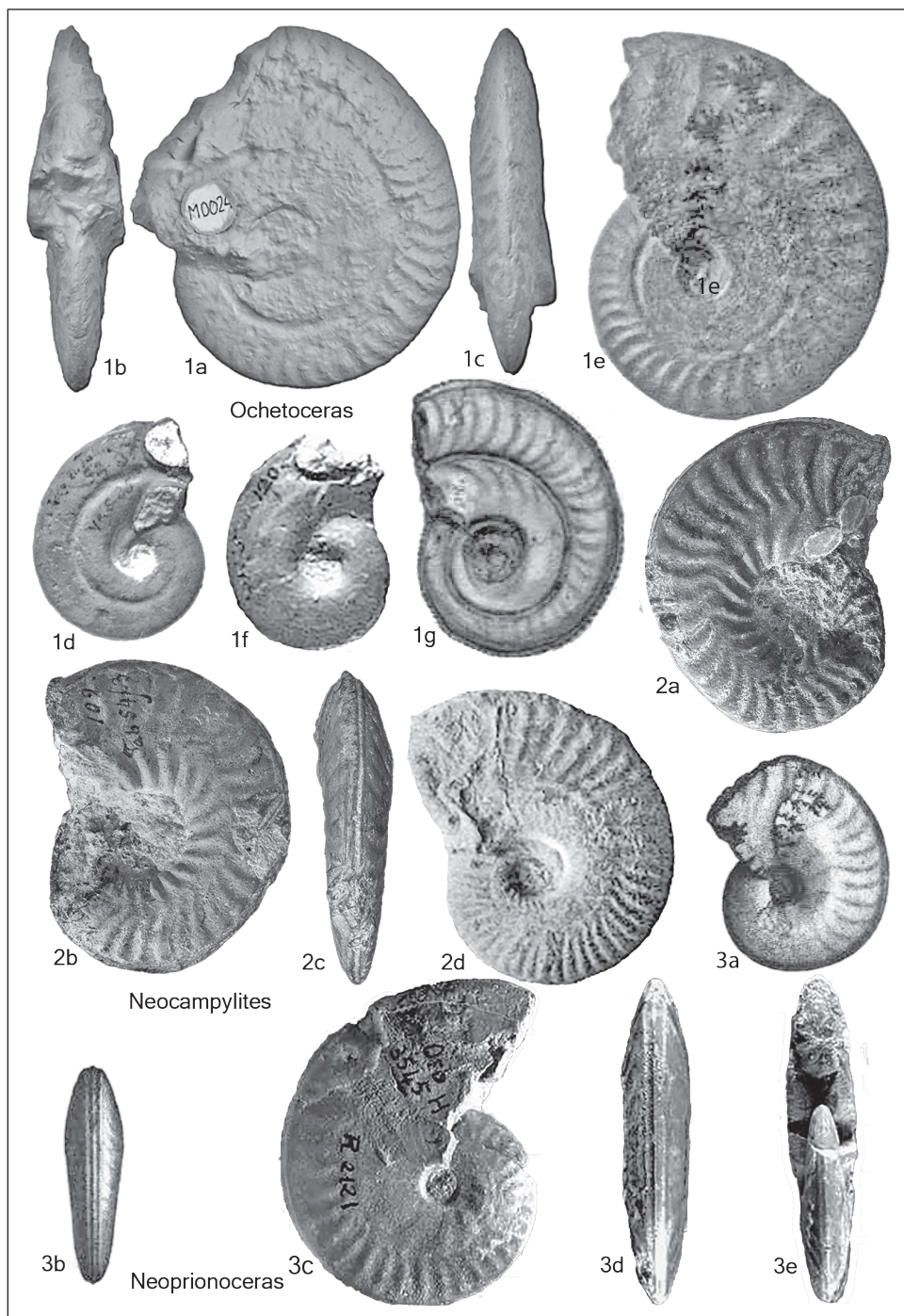


FIG. 24. Oppeliidae, Ochetoceratinae 1.

included it in Hecticoceratinae. *Neocampylites* are small- to medium-sized in both dimorphs, and have some characters with hecticoceratin tendencies, such as the ovate whorl section, strong falcoid ribs, with the primaries strongly marked at the base (similar to those of *Prohecticoceras*); however, the tricarinate venter confers it a special character that recalls some Oppeliinae, such as *Trimarginia* and *Alcidia*, or Ochetoceratinae. The suture is typically haploceratoid, relatively simple with lobe L deeper than E and U_2 , high and asymmetrical saddle E- U_2 , and few auxiliary lobes. *Neocampylites* could represent the connecting link between Hecticoceratinae and Ochetoceratinae or between Oppeliinae and Ochetoceratinae, but affinities with Hecticoceratinae seem to be stronger. *Uppermost Callovian-lower Oxfordian*: England, France, Germany, Spain (Iberian Range, Betic Cordillera and Balearic Islands), Switzerland, Italy (Sicily), Slovakia, Poland, Bulgaria, Turkey, Syria, Russia (central part), India, Japan, Madagascar, Argentina, Chile, Caribbean, Mexico.—FIG. 24, 2a-c. **N. delmontanum* (OPPEL), holotype, macroconch, *lower Oxfordian*, Mariae or Cordatum Zone, Paturatte bei Delemont, Canton of Bern, Switzerland, $\times 1$ (new; original in OPPEL, 1863 in 1862–1863, pl. 114, 3).—FIG. 24, 2d. *N. jolleri* (JEANNET), holotype of *Pseudocampylites jolleri* JEANNET, macroconch, ?*upper Oxfordian*, Herznach mine, bed F.2, Herznach, Aargau, Switzerland, $\times 0.8$ (JEANNET, 1951, pl. 18, 4).

Neoprionoceras SPATH, 1928, p. 128 [**Oppelia girardoti* DE LORIO, 1902, p. 40; OD]. *Neoprionoceras* was considered synonymous with *Campylites* ROLLIER, 1922 (= *Neocampylites* CALLOMON, 1973) by ARKELL (1957, p. 279), but it is more involute, and the keel, ribs, and suture differ from that of *Neocampylites*. Macroconchs medium-sized, involute, platycone to suboxycone compressed, with a well-developed ventral keel and two weak carinas or small elevations at the ventrolateral edge;

inner whorls smooth, later whorls have very weak sigmoidal primaries which bifurcate at mid-flank; secondary ribs prominent on upper half of the flanks and raised on the ventrolateral shoulder. Suture relatively complex, with L deeper than E, the L- U_2 saddle quite high, and several auxiliary lobes. Presumed microconch are smaller, more evolute, with incipient uncoiling, and smooth on lower part of flanks. *Upper Jurassic (lower-middle Oxfordian)*: France, Switzerland; Spain, Russia (central part), Argentina, Chile, Caribbean (Cuba), Mexico.—FIG. 24, 3a-b. **N. girardoti* (DE LORIO), holotype, macroconch, ?*middle Oxfordian*, La Boissière (Mont Pelé), Switzerland, $\times 1$ (DE LORIO, 1902, pl. 3, 8–8a).—FIG. 24, 3c-e. *N. henrizi* (D'ORBIGNY), lectotype, macroconch, *middle Oxfordian*, Plicatilis Zone, Antecedens Subzone, Précý, Yonne, France, $\times 1$ (new; original of D'ORBIGNY, 1850 in 1842–1851, pl. 198, 1–3; also figured by ÉNAY & GAUTHIER in FISCHER & others, 1994, pl. 73, 5a-c; Muséum National d'Histoire Naturelle, Paris, no. MNHN.F.R02121, Collection D'ORBIGNY, no. 3545 H-1).

Trimarginites ROLLIER, 1909, p. 622 [**Ammonites trimarginatus* OPPEL, 1862 in 1862–1863, p. 159; SD ARKELL, 1943, p. lxxxiv; see CHRIST, 1961, p. 282–283]. Macroconch similar to the oppeliid *Oxycerites*, involute, disc-shaped, heavily flattened shells with ogival-subtriangular whorl section, strongly tricarinate in inner whorls; ribs very wide, slightly retroverse and widely spaced, reduced to the outer half of the flanks on middle whorls; lateral groove absent or faint. Suture relatively complex with E almost as deep as L, and various auxiliary lobes and incised elements. Microconchs (gr. of *T. stenorynchus* (OPPEL)) small, flattened, with slightly eccentric coiling, smooth or with outer ribs and midlateral groove only on the body chamber; aperture with long lateral lappets and small ventral rostrum. *Upper Jurassic, uppermostlower Oxfordian* (Plicatilis

Zone)—upper Oxfordian (Bimammatum Zone): England, France, Spain, Switzerland,

Slovakia, Italy (Sicily), Poland, India, Egypt, Madagascar, Argentina.—FIG. 25, 1a–b.

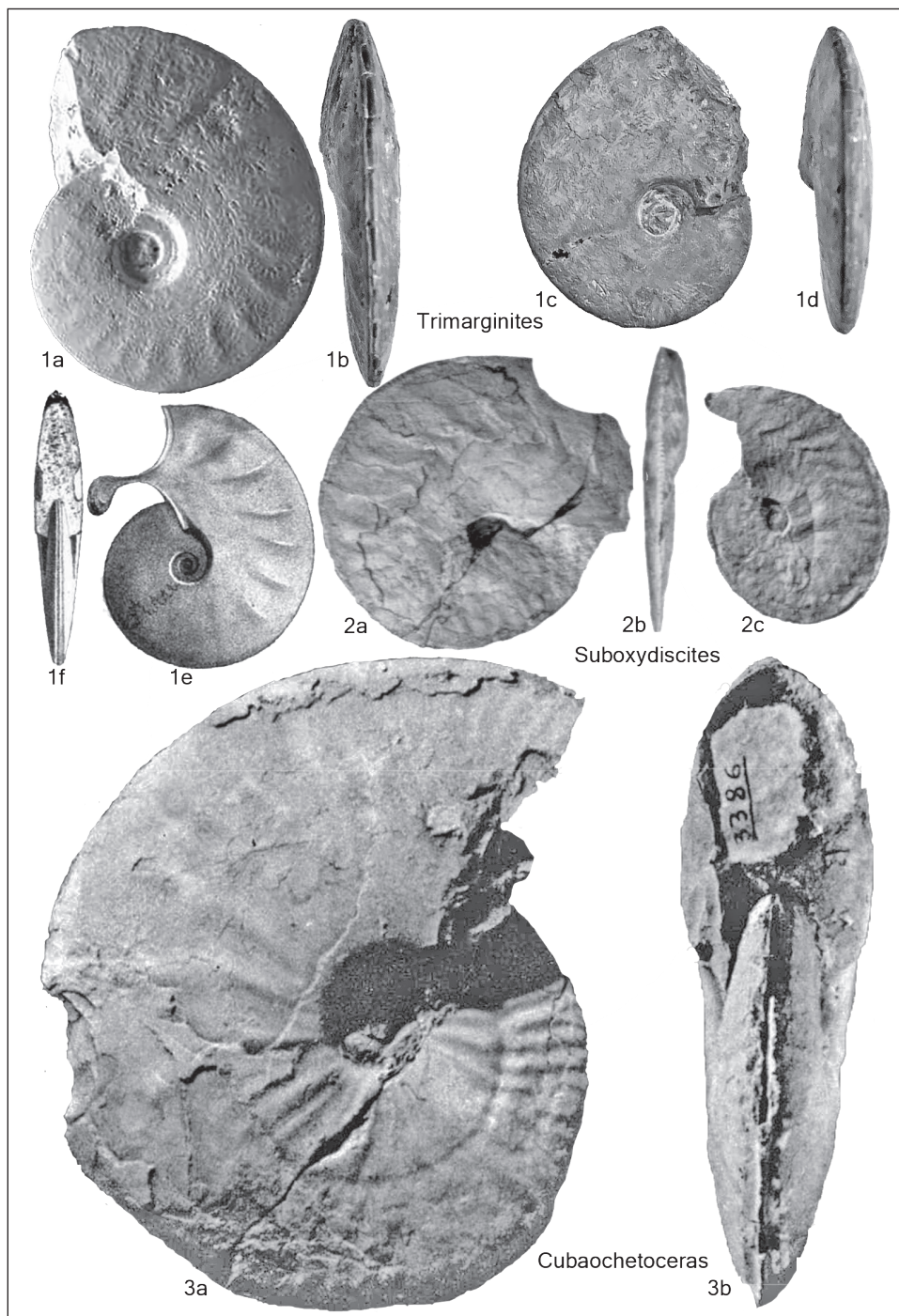


FIG. 25. Oppeliidae, Ochetoceratinae 2.

**T. trimarginatus* (OPPEL), holotype, macroconch, *Oxfordian*, Gegend von Balingen, Baden-Württemberg, Germany, $\times 1$ (new; original of OPPEL, 1862 in 1862–1863, pl. 50, 2–b; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS VIII 38). —FIG. 25, 1c–d. *T. arolicus* (OPPEL), macroconch, *Oxfordian*, Transversarium Zone, Birmensdorf bei Baden, Aargau, Switzerland, $\times 1$ (new; original of OPPEL, 1863 in 1862–1863, pl. 51, 2a–b; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS VIII 40). —FIG. 25, 1e–f. *T. stenorhynchus* (OPPEL), holotype, microconch, *Oxfordian*, Transversarium Zone, Birmensdorf bei Baden, Aargau, Switzerland, $\times 1$ (OPPEL, 1863 in 1862–1863, pl. 52, 1a–b, refigured by SCHLEGELMILCH, 1994, pl. 14, 4).

Suboxydiscites POULTON, ZEISS, & JELETZKY, 1988, p. 104 [**Ochetoceras* (*Suboxydiscites*) *manningsensis*; OD]. Macro- and microconchs medium to small size, oxycones strongly compressed, involute with a very narrow umbilicus, a serrated, non-undulating keel, very weak internal ribs, and retrocostate, single, strong outer ribs. Microconchs, with a lateral groove sometimes present on the lower quarter of the flank, and a short protrusion of the aperture border at the end of the groove, perhaps marking the beginning of lateral lappets, with the ribs somewhat denser near aperture. *Suboxydiscites* is the only Boreal late Jurassic *Ochetoceratinae*, directly connected with *Ochetoceras* s. str. *Upper Jurassic (lower to middle Kimmeridgian)*: Cuba, Mexico, Canada, Greenland, Norway (Spitsbergen Island), Russia (European part and northern Siberia), Germany. —FIG. 25, 2a–c. **S. manningensis* (POULTON, ZEISS, & JELETZKY), GSC locality C-128986, *Kimmeridgian*, southwestern British Columbia, Canada; 2a–b, holotype, macroconch, $\times 1$ (POULTON & others, 1988, pl. 5.1, 1–2; GSC 83491); 2c, microconch, $\times 1$ (POULTON & others, 1988, pl. 5.1, 12; GSC 83499).

Cubaochetoceras SÁNCHEZ-ROIG, 1951, p. 66 [**Ochetoceras imlayi* SÁNCHEZ-ROIG, p. 66; SD ARKELL, 1957, p. 278]. Medium to large, involute, with ovate compressed to subtriangular whorl section; venter with a small keel and thin crenulations; ribs varied, irregular, and stronger on the outer half of the flanks; spiral midlateral groove usually poorly marked; suture complex, with E as deep as L, and several deep auxiliary lobes. *Upper Jurassic (upper Oxfordian)*: Cuba, Mexico. —FIG. 25, 3a–b. **C. imlayi* (SÁNCHEZ ROIG), holotype, macroconch, *upper Oxfordian*, Laguna de Piedra, Viñales, Provincia Pinar del Río, Cuba, $\times 0.8$ (JUDOLEY & FURRAZOLA-BERMÚDEZ, 1968, pl. 8, a–b; no. J-F-22, Col. Acad. de Ciencias de Cuba).

Subfamily

DISTICHOCERATINAE Hyatt, 1900

[*nom. trans. et correct.* ARKELL, 1957, p. 279, *ex* Distichioceratidae HYATT, 1900, p. 570] [=Bonarellidae SPATH, 1925b, p. 114]

Derived of Hecticoceratinae, the most primitive Distichoceratinae (*Geminites* BALOGÉ & CARIU, 1997) thus rather resembles the hecticoceratins *Chanasia*, which may have looped ribs and ventrolateral clavi. Dimorphism is readily apparent in some genera. Macroconchs are compressed and medium-sized, with a carinate, fastigate, or tabulate venter. Ornamentation is variable but characterized by external ribs that are frequently fibulate and hack-arched, and looped in the distal part to a clavus. On the ventral side, clavi are often crested and remarkably lengthened. Microconchs are small with variable ornament and are smooth or slightly ribbed with prominent ventral clavi. In the former *Treatise* (ARKELL, 1957, p. 279), the subfamily Distichoceratinae included the genera *Distichoceras* MUNIER-CHALMAS, 1892, *Horioceras* MUNIER-CHALMAS, 1892, *Petitclercia* ROLLIER, 1909, *Chanasia* ROLLIER, 1922, *Sindeites*

SPATH, 1925a, *Subbonarellia* SPATH, 1928, ?*Styracoceras* HYATT, 1903, and ?*Concavites* JEANNET, 1951. Later, BALOG & CARIOU (1997) described *Geminites*, which also was included in this subfamily. *Styracoceras* is a Cenomanian Schloenbachiidae (WRIGHT & others, 1996), *Petitclercia* is currently included in Phlycticeratinae (SCHWEIGERT & others, 2007; SCHWEIGERT & KAPITZKE, 2018), *Chanasia* and *Sindeites* (treated above) have been shown to be hectioceratin, and *Concavites* is (as previously seen) synonymous with *Hectioceras*. Therefore, here, only *Distichoceras*, *Horioceras*, *Subbonarellia*, and *Geminites* are included in the subfamily Distichoceratinae. According to BALOG & CARIOU (1997, p. 942), Distichoceratinae are phylogenetically linked to Hectioceratinae through *Chanasia*, from which they derived in the uppermost early Callovian–late Callovian. *Upper Middle Jurassic (uppermost lower Callovian–upper Callovian)*: worldwide.

Distichoceras MUNIER-CHALMAS, 1892, p. 171 [**Ammonites bicostatus* STAHL, 1824, p. 49; OD] [= *Bonarellia* COSSMANN, 1898, p. 77 (obj.); = *Horioceras* MUNIER-CHALMAS, 1892, p. 171 (type, *Ammonites Baugieri* D'ORBIGNY, 1847 in 1842–1851, p. 445; OD)]. *Horioceras* MUNIER-CHALMAS, 1892, is the microconch of *Distichoceras* MUNIER-CHALMAS, 1892 (see BONNOT & others, 1999). Macroconchs (*Distichoceras*) of medium size, relatively involute, whorl section becoming ovate in the body chamber; unicarinate with concave or flat venter; weak primary (inner) ribs are reduced to striae in some forms, outer ribs are more marked, irregular in thickness and irregularly looped, often united in ventrolateral clavi; on the body chamber, outer ribs become very wide and spaced with midlateral spiral ridge or small groove; suture extremely simple. Microconchs (*Horioceras*) very small, without ribbing, and with only large

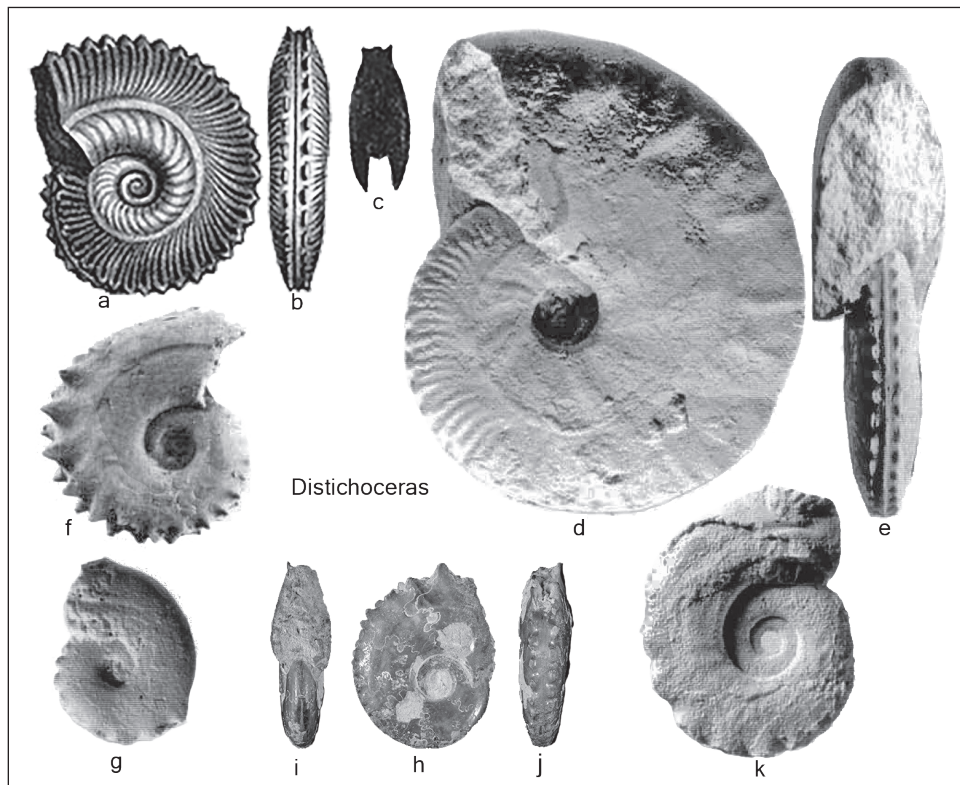


FIG. 26. Oppliidae, Distichoceratinae 1.

clavi that alternate on both sides of the venter and occupy only a small part of the phragmocone and most of the body chamber; peristome has long lateral lappets and small ventral rostrum. *Horioceras baugieri* probably represents the microconch of *Distichoceras bipartitum* (PALFRAMAN, 1967, p. 67). The types of *Ammonites bicostatum* and *Ammonites baugieri* are lost and neotypes are required for both. Uppermost *Middle Jurassic* (upper *Callovian*)—Upper *Jurassic* (?lowermost *Oxfordian*): Bulgaria, England, France, Germany, Hungary, Italy (Sicily), Poland, Portugal, Slovakia, Spain, Switzerland, Algeria, ?Israel, Egypt (Sinai), India, Tibet, Japan, Chile, and Peru.—FIG. 26, *a–e*. **D. bicostatum* (STAHL); *a–c*, macroconch (lost), lateral and ventral views, and cross section, ?*Callovian*, Inferior Oolite, Guttenberg, Germany, $\times 1$ (ZIETEN, 1830 in 1830–1833, pl. 13, 6*a–c*); *d–e*, neotype (designated by SANDOVAL, herein), macroconch, upper *Callovian*, Athleta Zone, Collotiformis Subzone, Momreuil-Bellay, Maine-et-Loire, France, $\times 0.8$ (BALOGÉ & CARIOU, 2001, pl. 5, 19–20; specimen MN/712).—FIG. 26, *f–j*. *D. baugieri* (D'ORBIGNY); *f*, microconch, Oxford Clay, near Chippenham, Wiltshire, England, $\times 1$ (PALFRAMAN, 1967, pl. 11, 6; BM 37755); *g*, microconch, upper *Callovian*, Athleta Zone, Trezeense Subzone, Montreuil-Bellay, Maine-et-Loire, collection Balogé, $\times 1$ (BALOGÉ, 1999, pl. 4, 16; specimen MNJ261); *h–j*, microconch, upper *Callovian*, Lamberti Zone, Villers-sur-Mer, Calvados, France, $\times 2$ (new; also figured by ELMI & GAUTHIER in FISCHER & others, 1994, pl. 65, 4*a–c*; Muséum National d'Histoire Naturelle, Paris, Collection Gauthier, MNHN.F.B46065).)—FIG. 26, *k*. *D. semseyi* (LÓCZY), microconch, complete adult, with lateral lappets, middle *Callovian*, Coronatum Zone, Le Grand Breuil, near Rouillé, France, $\times 1$ (BALOGÉ, 1999, pl. 4, 5; collection Balogé, specimen SA/LGB/20A).

Geminites BALOGÉ & CARIOU, 1997, p. 941 [**Hecticoceras* (*Zieteniceras*) *janus* ZEISS,

1959, p. 96; *nom. nov. pro Hecticoceras bipartitum* (QUENSTEDT) in DE TSYTOVITCH, 1911, p. 34, pl. 2, fig. 1; OD]. Platycone, relatively evolute ammonite with lanceolate whorl section; fastigate, tricarinate venter with a crenulate median keel; lateral spiral groove irregularly marked. Primary ribs prorsiradiate, dense and coarse; back arched external (secondary) ribs flattened, spatulate, and often regularly looped (fibulate) on a great part of the shell; ventrolateral clavi remarkably lengthened and prominent; similar to *Distichoceras* but more evolute, the ornamentation of the inner whorls well-marked with longer outer ribs in the adult stage. So far, macroconchs and microconchs have not been differentiated, but some evolute microconchs (*Horioceras* sp., in BALOGÉ & CARIOU, 2001, pl. 1, 13–14), which have similar biostratigraphic range, could be dimorphs of *Geminites*. The suture closely resembles that of *Chanasia*. Uppermost-lower *Callovian*—upper *Callovian* (Lamberti Zone): France, Germany. —FIG. 27, 1*a–d*. *G. janus* (ZEISS); *1*a–b*; holotype, macroconch, middle *Callovian*, Crêt de Châlame, Chézery, France, $\times 1$ (DE TSYTOVITCH, 1911, pl. 2, 1); 1*c–d*, macroconch, middle *Callovian*, Coronatum Zone, Leuthardt Subzone, Saint-Laon (Vienne), France, $\times 0.8$ (BALOGÉ & CARIOU, 2001, pl. 1, 8–9; specimen LM/15).

Subbonarellia SPATH, 1928, p. 98 [**S. decipiens* SPATH; OD]. Medium-sized, semi-involute, compressed with subovate to subrectangular whorl section; venter from planulate on inner or median whorls to rounded at end of body chamber, with central keel; on middle whorls, the ribbing falcate, single or bifurcate, with only some looped, coarse, and distant, some with small midlateral tubercles, ending in ventrolateral clavi. In adults, ribbing and tubercles fade progressively, but outer ribs remain very wide and widely spaced; wide and low midlateral ridge. The specimen figured by SPATH (1928, pl. 9, 14) is possibly a microconch, being slightly

more evolute and having inner ribs less strongly marked than in the macroconchs. The suture is rather simple with elements widely and sparsely ramified. Uppermost *Middle Jurassic (upper Callovian)*: ?France, ?Switzerland, India. —FIG. 27, 2*a–c*. **S. decipiens* SPATH, holotype, ?macroconch, lateral and ventral views (*a–b*) and suture (*c*), *middle Callovian*, Anceps Zone, Fakirwadi, India (western part, Kutch), $\times 1$ (SPATH, 1928, pl. 9, 5*a–c*).

Subfamily
TARAMELLICERATINAE Spath,
1928

[*nom. correct.* SPATH, 1928, p. 130 (*pro* Neumayriceratidae SPATH, 1925b, p. 114)]

Dimorphism, while evident in some genera, has not been shown in others. Macroconchs discoidal, of markedly variable size from small to relatively large (see ZIEGLER, 1974, fig. 6), involute to relatively

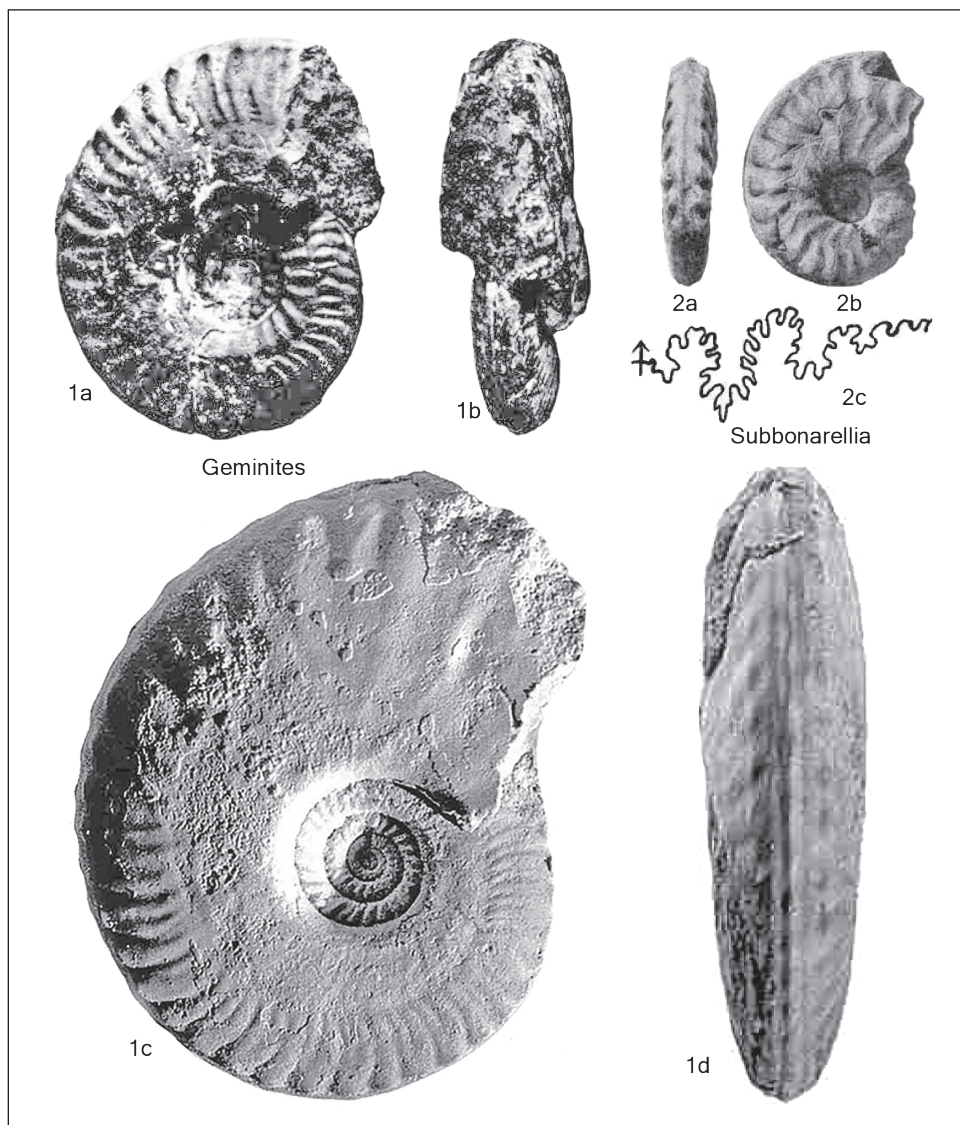


FIG. 27. Oppeliidae, Distichoceratinae 2.

evolute, thick subrectangular to oval whorl section, thick without median lateral groove or fillet. Innermost whorls smooth, and then the ornamentation variable, with ribbing, frequently with primary and secondary ribs that cross whole whorl sides; some with lateral tubercles and various others developing ventral serrations or continuous keels and/or ventrolateral clavi, often crested and remarkably lengthened, bordering the venter; complex septal suture. Microconch of small size, moderately involute with marked uncoiling in body chamber end; oval compressed whorl section with gently curved flanks, sometimes with a midlateral groove at the body chamber, and rounded venter which can also become keeled with a serrate keel; variable ornament, from smooth or weakly ribbed on the body chamber, sometimes with prominent ventral clavi. Aperture with big lateral lappets and small ventral rostrum. Relatively simple septal suture with lobes and saddles small and barely incised.

In the former *Treatise* (ARKELL, 1957, p. 279–282), the subfamily Taramelliceratinae included the genera *Taramelliceras* DEL CAMPANA, 1904, *Proscaphites* ROLLIER, 1909, *Fontannesiella* SPATH, 1925, *Metahaploceras* SPATH, 1925, *Hemihaploceras* SPATH, 1925, *Lorioloceras* SPATH, 1928, *Berniceras* JEANNET, 1951, *Strebliticeras* HÖLDER, 1955, *Acanthaecites* ROLLIER, 1909, *Creniceras* MUNIER-CHALMAS, 1892, *Scaphitodites* BUCKMAN, 1924, *Popanites* ROLLIER, 1909, and *Sphaerodomites* ROLLIER, 1909. The genus *Richeiceras* JEANNET, 1951, considered by ARKELL (1957) as synonymous of *Proscaphites*, was included by CARIOU & SEQUEIROS (1987) as a synonym for *Taramelliceras*, whereas other authors (ZIEGLER, 1974; SCHAIRER & SCHLAMPP, 2003; QUEREILHAC, 2009; WIERZBOWSKI & others, 2016; JANTSCHKE & SCHWEIGERT, 2020) have considered it a subgenus of *Taramelliceras* or even given it a generic rank. *Oxyoppelia* BERCKHEMER, 1926, and *Eymarites* JEANNET, 1951, which were not cited by ARKELL (1957, in the former *Treatise*), show morphological characteristics

of Taramelliceratinae and are considered genera with systemic value. The genera *Barthelia* OLÓRIZ & SCHAIRER, 1983, *Zittelliceras* SANTANTONIO, 1983, *Flexispinites* SCHAIRER, 1984b, *Rogoviceras* SCHERZINGER & MITTA, 2006 (indet. Subfamily, but whose type species was originally included in “*Paralingulaticeras*”), *Pasottia* PARENT, SCHWEIGERT, SCHERZINGER, & ÉNAY, 2008, *Metauhligites* ÉNAY, 2009, and *Cieneguiticeras* PARENT, MYCZINSKI, SCHERZINGER, & SCHWEIGERT, 2010, were also originally included in Taramelliceratinae. *Strebliticeras* HÖLDER, 1955, is synonymous with *Streblites* (ZIEGLER, 1974, p. 34, 35; SCHWEIGERT & CALLOMON, 1997, p. 13; SEYED-EMAMI & SCHAIRER, 2011, p. 5; WIERZBOWSKI & MATYJA, 2014, p. 65; PANDEY & others, 2022, p. 101) or synonymous with *Taramelliceras* (QUEREILHAC, 2009, p. 29, 30). The genera *Eurynoticerias* CANAVARI, 1897, and *Mazapilites* BURCKHARDT, 1919, which in the old *Treatise* (ARKELL, 1957, p. 284) appear as the only member of the subfamily Mazapilitinae SPATH, 1928, were included in the subfamily Taramelliceratinae by some authors (ZIEGLER, 1974, p. 32; CALLOMON, 1981, p. 144; VILLASEÑOR & others, 2005, p. 71). Others continue to differentiate Mazapilitinae, either as a subfamily of Oppeliidae (MYCZYŃSKI, 1989, p. 92) or as a subfamily of Berriasellidae (CANTÚ-CHAPA, 2009, p. A205). As indicated above (see superfamily Strigoceratoidea nov.), *Sphaerodomites* and *Barthelia* (synonymous with *Sphaerodomites*) belong to the family Strigoceratidae.

The origin of the Taramelliceratinae is not clear; the subfamily shows common characteristics with Hecticoceratinae and Distichoceratinae, from either of which it may have descended. It is more feasible that the oldest Taramelliceratinae are phylogenetically linked to the early Callovian Hecticoceratinae, from which they derived through *Chanasia*, which can bear looped ribs and ventrolateral clavi, as in the Taramelliceratinae. However, according to CARIOU & SEQUEIROS (1987, p. 507), the

Taramelliceratinae probably differentiated from *Paralcidia* by a progenetic process as early as the Callovian. Upper *Middle Jurassic* (lower Callovian, Gracilis Zone) –Upper *Jurassic* (lower Tithonian): worldwide.

Taramelliceras DEL CAMPANA, 1904, p. 251; *nom. nov. pro Taramellia* DEL CAMPANA, 1903, p. 383; *non* SEGUENZA, 1903 (Gastropoda) [**Ammonites trachinotus* OPPEL, 1863 in 1862–1863, p. 214; SD DOUVILLÉ, 1879, p. 91 for *Neumayria* BAYLE, 1878, pl. 92 (*non* DE STEFANI, 1877 (Gasteropoda), *nec* NIKITIN, 1881, p. 61 (Craspeditidae, Perisphinctoidea), type, *Ammonites catenulatum* FISCHER DE WALDHEIM, 1830–1837, p.169); =*Neumayriceras* ROLLIER, 1909, p. 623, obj.; =*Lingulaticeras* ZIEGLER, 1958, p. 127 (type *Ammonites nudatus* OPPEL, 1958 in 1856–1858, p. 687, for *Ammonites lingulatus expansus* QUENSTEDT, 1848 in 1845–1849, p. 130, pl. 9, fig. 8; OD)]. Macroconchs of variable size, with a narrow to median umbilicus, vertical umbilical wall, and angular umbilical edge; almost rectangular and relatively high and wide whorl section, with convex flanks and blunt to broad (rounded) external region. Sinuous aperture without lateral lappets. Inner whorls may be smooth, but middle and outer ones are usually well ornamented with ribs of variable thickness and more-or-less flexuous, at times looped (by two or three) on elongated ventrolateral clavi, whereas others remain free; ventral area have serrations or a row of elongate siphonal tubercles. The microconchs (“*Lingulaticeras*” (*partim*), “*Coryceras*” (*partim*), and “*Creniceras*” (*partim*)) are small, one-third to one-fifth of the size of the macroconchs; evolve with marked uncoiling in the body chamber, gently oval compressed whorl section with rounded umbilical edge, gently convex flanks (sides) and curved venter; aperture with small ventral rostrum and developed lateral lappets; a few marked midlateral grooves can appear in the body chamber end, which extend through the central part

of the lappets. Inner whorls are smooth or almost so, while outer ones are more-or-less ribbed with weak, falcate primary ribs that divide only approximately at mid-flank; the secondary ones, usually weak, radially cross the venter, where they can become thick; no ventrolateral tubercles. The type species of “*Lingulaticeras*” is a dimorphous partner of *Taramelliceras* (SCHWEIGERT, 2009, p. 324; BAUDOUIN & others, 2011, p. 626; WIERZBOWSKI & MATYJA, 2014, p. 65; FÖZY & others, 2022, p. 254), but other species usually included in “*Lingulaticeras*” (“*L. gr. solenoides*”) are dimorphic partners of *Neochetoceras* (PARENT & others, 2010, p. 455; FÖZY & SCHERZINGER, 2013, p. 221; SCHERZINGER & others, 2015, p. 5; FÖZY & others, 2022, p. 255). *Lower Callovian* (Gracilis Zone)–*lower Tithonian*: England, Germany, France, Hungary, Italy, Czech Republic, Poland, Spain, Portugal, Croatia, Bulgaria, Romania, Switzerland, Morocco, Algeria, Tunisia, Ukraine, Russia, Turkey, Iran, Pakistan, Yemen, India, Nepal, Japan, Madagascar, Kenia, Tanzania, Somalia, Antarctica, Argentina, ?Cuba, USA (California, Texas, Louisiana).—FIG. 28, *a–c*. **T. trachinotum* (OPPEL); *a–b*, neotype (designated by HÖLDER, 1955, p. 102), macroconch, Mittlerer Weisser Jura, Fuchseck bei Göppingen, Baden-Württemberg, Germany, $\times 0.5$ (new; original of *Ammonites flexuosus auritus* QUENSTEDT, 1887 in 1882–1888, pl. 97, 15; also figured by SCHLEGELMILCH, 1994, pl. 9, 4; Geologische Institut, Universität Tübingen, Germany, GPIT-PV-61909); *c*, macroconch, complete adult specimen, Weisser Jura, Steinenkirch, Baden-Württemberg, Germany, $\times 0.5$ (plaster cast, new; figured in HÖLDER 1955, pl. 18, 21; Coll. Geologische Institut, Universität Tübingen, Germany, Ce 1023/29).—FIG. 28, *d–f*. *T. compsum* (OPPEL); *d–e*, cast of the lectotype, Malm Formation, Weissjura Delta, Swaewische Alp, Germany, $\times 0.6$ (BAUDOUIN & others, 2011, pl. 2, 2*a–b*; original of *Ammonites compsum* OPPEL, 1863, pl. 57, 1; Bayerische Staatsammlung für Paläontologie und

Historische Geologie, Munich, Germany; 1f, suture of macroconch (HÖLDER, 1955, fig. 16, b); g–h, microconch, holotype of *Ammonites lingulatus crenosus* QUENSTEDT, 1887, *Upper Jurassic*, Weissjura Garnma, Germany, x1 (ZIEGLER, 1958, pl. 13, 10–11; Geologische Institut, Universität Tübingen, Germany, Ce 5/92/32).——FIG. 28 i–l, *T. limgulaum*, lectotype (designated by ZIEGLER, 1958, p. 133), microconch; i–k, *upper middle Oxfordian*, Mössingen-Thalheim, Germany, x1 (new; original of *Ammonites lingulatus expansus* QUENSTEDT, 1887 in 1882–1888, pl. 92, 28; also figured by ZIEGLER, 1958, pl. 12, 9, and by SCHLEGELMILCH, 1994, pl. 16, 8; Geologische Institut, Universität Tübingen, Germany, GPIT-PV-61805); l, suture, Weissjura Beta, Eybach, Germany, x5 (ZIEGLER, 1958, fig. 43a; Geologische Institut, Universität Tübingen, Germany, Ce 1113/28).

Flexispinites SCHAIRER, 1984b, p. 39 [**Ammonites flexispinatum* OPPEL, 1857 in 1856–1859, p. 561; OD, for *Ammonites flexuosus globulus* in QUENSTEDT, 1849 in 1845–1849, pl. 9, fig. 6]. Small, involute, more-or-less inflated shell with a wide and low whorl section tapering towards the apertural margin, which is upturned and has external and lateral projections and an umbilical hook. The ribbing, variable in strength, consisting of rectiradiate to rursiradiate, biconcave to falcoid, bifurcate, or simple with free intercalated ribs; ventrolateral and medioventral nodes or serrations appearing where the median node row may be replaced by a weak, thread-like keel. The septal suture comparable to that of other small Taramelliceratinae, appearing simplified compared to that of the large ones. No dimorphism is known (DIETL, 2011, p. 39). *Sphaerodomites* ROLLIER, 1909 (a Strigoceratidae), is somewhat similar to *Flexispinites* in the ribbing, but larger, bearing a keel limited by shallow furrows, and lacking tubercles or clavi. *Upper Callovian* (Lamberti Zone)–*lower Oxfordian* (Cordatum Zone): France, Germany,

Switzerland, ?Spain, Russia.——FIG. 29, 1a–c. **F. flexispinatus* (OPPEL); a–b, neotype (designated by SCHAIRER, 1984b, p. 40), ?macroconch, *upper Callovian*, Lochen, Baden-Württemberg, Germany, x2 (new; original in SCHAIRER, 1984b, pl. 9, 1; also figured by SCHWEIGERT, 2023, fig. 6a–c; Paleontological Museum, Munich, Germany, BSPG no. 1971XVII-12); c, suture at Dm 8 mm and Wh 5.5 mm (SCHAIRER, 1984b, fig. 1a; BSPG no. 1952 XV 592).

Acanthaecites ROLLIER, 1909, p. 620 [**Ammonites velox* OPPEL, 1862 in 1862–1863, p. 156; OD]. Very small, globose, spherically swollen shell with wide whorl section and rounded venter; aperture preceded by a small constriction followed by an elevated smooth lip and a small ventral rostrum, but without lateral lappets; smooth except for a median ventral row of sharp distant tubercles or serrations which vanish on the body chamber. Very similar to *Flexispinites*, with which it is phylogenetically linked, and could even be synonyms, but has neither ribs nor ventrolateral tubercles, and the ventral ones disappear on the body chamber. The suture shows only two auxiliary lobes on the flank and extends over the median tubercles. *Middle Jurassic* (*upper Callovian*)–*Upper Jurassic* (*lower Oxfordian*, Mariae Zone): Germany. —— FIG. 29, 2a–b. **A. velox* (OPPEL), (holotype by monotype), microconch, *upper Callovian*, Athleta Zone, Ursulaberg bei Pfullingen, Baden-Württemberg, Germany, x2 (new; original in OPPEL, 1862 in 1862–1863, pl. 49, 5a–d; also figured by SCHWEIGERT, 2023, fig. 2a–c; Paleontological Museum, Munich, Germany, BSPG no. AS VIII 167).

Lorioloceras SPATH, 1928, p. 90 [**Oppelia* (*Neumayriceras*) *kormosi* LÓCZY, 1915, p. 310; SD ROMAN, 1938, p. 166] [= *Taramelliceras* ROLLIER, 1909, p. 623, *non* DEL CAMPANA, 1904, p. 251]; = *Rollieria* JEANNET, 1951, p. 98, *non* COSSMANN, 1920, p. 82 (Mollusca, Bivalvia); = *Rollioceras* HAAS, 1958, p. 625, *nom. nud. pro*

Rollieria JEANNET, 1951 (type *Ammonites flexuosus canaliculatus* QUENSTEDT, 1858 in 1852–1858, p. 532; OD)]. Medium-sized,

involute with rapid expansion of the spiral, whorls ovate, compressed in cross section, flanks convex and the venter rounded; blunt,

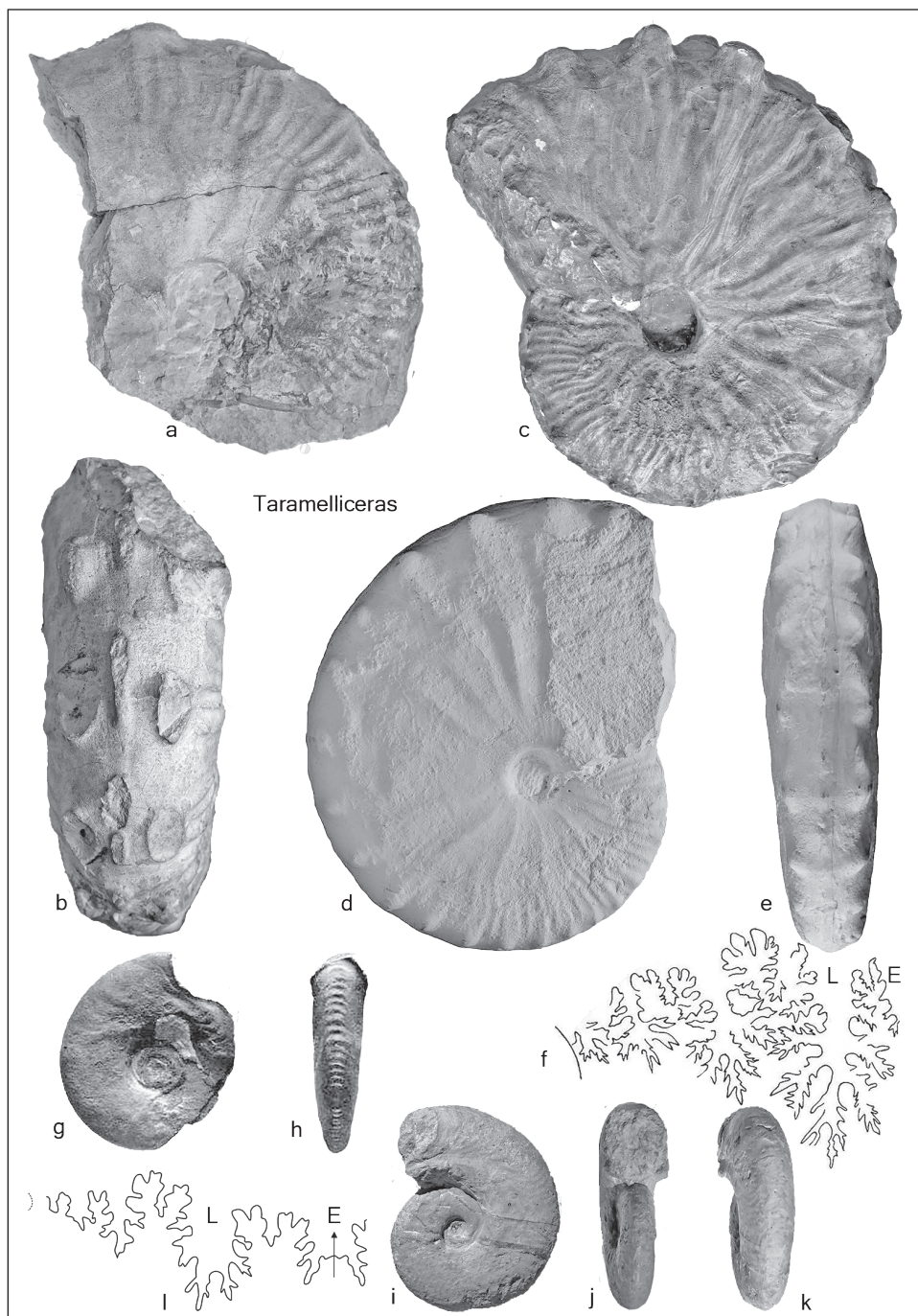


FIG. 28. Oppeliidae, Taramelliceratinae 1.

pearled or at least interrupted keel, thick nodular, widely spaced, radial or slightly proverse and irregular primary ribs ending slightly above the mid-flank, sometimes coinciding with a spiral furrow; the secondaries, denser and finer than the primaries, slightly concave, occupying the outer third of the flank, sometimes with node-bearing on both sides of the siphonal region, which, however, do not appear in the juvenile stage; the secondary ribs, then the primaries, weakening and sometimes become erased on the body chamber. Complex septal suture of the *taramelliceratin* type with strongly incised elements, mainly lobes. PAGE (1991, p. 95) indicated that *Lorioloceras* SPATH, 1928, and *Proscaphites* ROLLIER, 1909, are dimorphic macroconchs of *Creniceras* MUNIER-CHALMAS, 1892, but only some forms usually included in "*Creniceras*" could represent the dimorphous partner microconch of *Lorioloceras*. *Uppermost-middle Callovian* (Coronatum Zone)–*lowermost Oxfordian*: France, England, Germany, Switzerland, Hungary, Italy (Sicily), Spain, ?Russia, India (Kutch). —FIG. 29, 3a–b. **L. kormosi* (LÓCZY), holotype, macroconch, lateral view and cross section sketch, ?*upper Callovian*, Templom Hill, Villány, Hungary, ×1 (LÓCZY, 1915, pl. 3, 16 and text-fig. 77; Hungarian Natural History Museum, Budapest, Hungary, inventory no. J824) —FIG. 29, 3c–d. *L. rollieri* (JEANNET), holotype, macroconch, *lowermost Oxfordian*, Herznach, canton of Aargau, Switzerland, ×1 (new; original in JEANNET, 1951, pl. 27, 11; Geolog. Inst. der E.T.H. Zürich, Switzerland, ETH. 000015056).

Creniceras MUNIER-CHALMAS, 1892, p. 171 [**Ammonites renggeri* OPPEL, 1863 in 1862–1863, p. 203; OD] [=*Bukowskites* JEANNET, 1951, p. 101 (*nom. nud.*, ICZN Code, 1999, Art. 52.3; type, *Oppelia distorta* BUKOWSKI, 1887, p. 119, pl. 25, fig. 4; OD; *non Bukowskites* DIENER, 1905, (Ceratitida)]. Small-sized microconchs (*Creniceras*, *Bukowskites*, and "*Coryceras*" (*partim*)), eccentric coiling with involute inner whorls

and uncoiling in the body chamber; ovate whorl section with sides slightly convex, smooth on inner and middle whorls, which only on the body chamber are adorned with barely perceptible ribs; ventral region with a row of median blunt coxcomb serration on the body chamber, mouth border with well-developed lappets. Complex septal suture for a microconch with quite incised lobes and saddles. Macroconchs ("*Taramelliceras*" gr. *richei*) of small to medium size, involute with narrow umbilicus, laterally compressed with slightly convex flanks and a denticulated or pearly keel venter. Inner whorls smooth; latter more-or-less regular ribs occurring without tubercles, and presence of intercalary ribs; on the latero-ventral edge, all ribs similar in strength. PALFRAMAN (1966), MATYJA (1986, p. 53), PAGE (1991, p. 95), MARCHAND & others, 2002 p. 476, and ÉNAY (2009, p. 82) have considered "*Taramelliceras richi*" (DE LORIO, 1898) as a dimorphous partner to *Creniceras renggeri* (OPPEL, 1863), type species of *Creniceras*. *Upper-lower Callovian–Oxfordian*: England, France, Germany, Italy, Spain, Switzerland, Portugal, Poland, Bulgaria, Romania, ?Hungary, Russia, Algeria, Syria, Sinai, Iran, ?Nepal, Mexico. —FIG. 29, 4a–e. *C. renggeri* (OPPEL); 4a–c, microconch, *lower Oxfordian*, Renggeri Zone, Les Vauches Noires, Calvados, France, ×2 (new; Muséum National d'Histoire Naturelle, Paris, France, Collection Reynaud, no. MNHN.FA52341); 4d, microconch, *lower Oxfordian*, Mariae Zone, Praecordatum Subzone, clay marl, Crouzet-Migette, France, ×2 (JÄGGI, 2008, pl. 1, 9; CJ JMO 82); 4e, suture of microconch ×12 at D 10.61 mm (PALFRAMAN, 1966, text-fig. 12A). OUM J25244. —FIG. 29, 4f–i. *C. richi* (DE LORIO), holotype, macroconch, *lower Oxfordian*, Mariae or Renggeri Zone, clay marl, La Racine, near Glovelier, canton of Jura, Switzerland, ×1 (DE LORIO, 1898, pl. 4, 13a–b; also figured by JÄGGI, 2008, pl. 1, 14); 4i, suture ×9 at D 15 mm (PALFRAMAN, 1966, text-fig. 8A, OUM J25013).

Richeiceras JEANNET, 1951, p. 95 [*Ammonites pichleri* OPPEL, 1863 in 1862–1863, p. 212; OD] [= *Coryceras* (type *Ammonites*

microdomus OPPEL, 1863 in 1862–1863, p. 204; OD)]. Macroconchs (*Richeiceras*) of small to medium size, involute with narrow

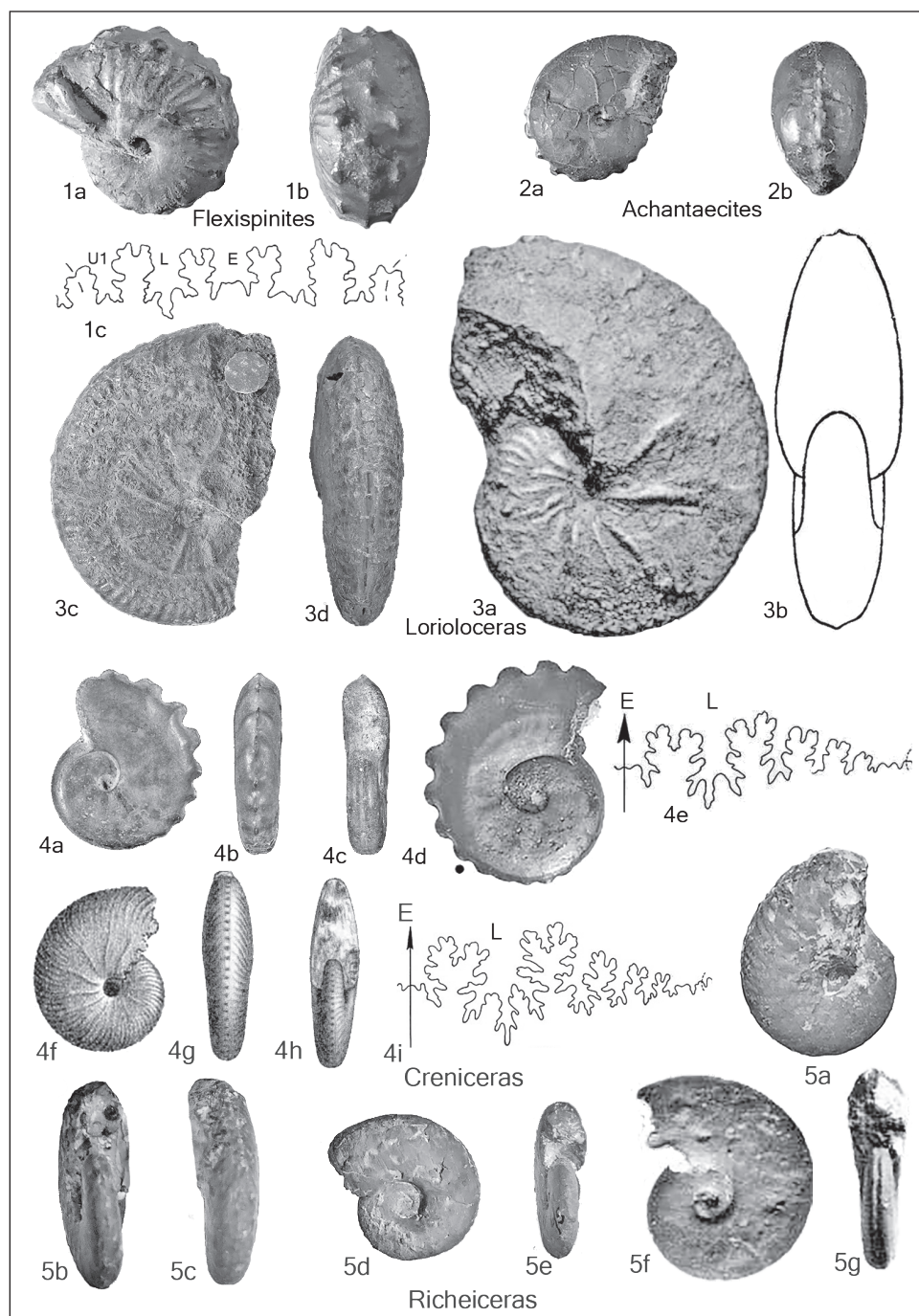


FIG. 29. Oppliidae, Taramelliceratinae 2.

umbilicus, laterally compressed with slightly convex flanks and a denticulated or pearly keel venter. Inner whorls smooth; later more-or-less regular ribs appearing without tubercles, and presence of intercalary ribs; all ribs similar in strength on the latero-ventral edge. The microconchs (“*Coryceras*”) of small size, more evolute than macroconchs, with subrectangular slightly compressed to subovate whorl section, rounded umbilical edge, flat to gently convex flanks sometimes presenting a well-marked mid-lateral groove on adult stages, and almost flat to arched venter frequently bearing tubercles or being crenulate and sometimes joining to form a keel; usually with very poorly developed ribbing; mouth border with weakly developed lateral lappets into which the lateral groove opens, and ventral rostrum. Simple septal suture of Haploceratidae or Lissoceratidae type with very broad E-L saddle. CARIOU & SEQUEIROS (1987, p. 497) and JÄGGI (2008, p. 117) considered *Richeiceras* as synonymous of *Taramelliceras* while ZIGLER (1973, p. 30), QUEREILHAC (2009, p. 33), WIERZBOWSKI & others (2010, 2016, p. 27), WIERZBOWSKI & MATYJA (2014), and JANTSCHKE & SCHWEIGERT (2020, p. 96) consider this to be a subgenus of *Taramelliceras*, with which it has a great similarity; or to have generic value, but it is smaller, with thinner ribs and less-developed ventrolateral clavi. According to QUEREILHAC (2009, p. 34, pl. 23–24), “*Coryceras*” *microdomum* is the microconch partner of *Richeiceras lochense* (OPPEL), while according to JANTSCHKE & SCHWEIGERT (2020, p. 97), the microconchiolate partner of *Richeiceras lochense* is “*Coryceras*” *canale* (QUENSTEDT). *Upper lower Callovian–lowermost Kimmeridgian*: Germany, France, Italy, Spain, Switzerland, Poland, Slovakia, Romania, Russia, Iran, India, Nepal, Mexico, USA. —FIG. 29, 5a–c. **R. pichleri* (OPPEL), holotype, macroconch, *upper Oxfordian*, Bimammatum Zone, Streitberg, Bavaria, Germany, $\times 1.5$ (new; original in OPPEL, 1863 in 1862–1863, pl. 51, 4; also figured by JANTSCHKE & SCHWEIGERT, 2020, pl. 1,

14a–c; ISNSB Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. ASI 1126). —FIG. 29, 5d–e. *R. microdomum* (OPPEL), holotype, microconch, *upper Oxfordian*, Bimammatum Zone, Lochen near Balingen, Germany, $\times 1$ (new; original of *Ammonites microdomus* OPPEL, 1863 in 1862–1863, pl. 53, 5; also figured by ZIEGLER, 1958, pl. 11, 12, and by JANTSCHKE & SCHWEIGERT, 2020, pl. 2, 14a–c; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, AS-VIII-6/5). —FIG. 29, 5f–g. *R. canale* (QUENSTEDT), holotype, *upper Oxfordian*, Lochen Member, Lochen near Balingen, Germany, $\times 1.5$ (ZIEGLER, 1958, pl. 11, 16–17; original of *Ammonites lingulatus canalus* QUENSTEDT, 1887, pl. 92, 41; also figured by JANTSCHKE & SCHWEIGERT, 2020, pl. 2, 8a–c; Geologische Institut, Universität Tübingen, Germany, GPIT CP17618).

Proscaphites ROLLIER, 1909, p. 614 [**Ammonites anar* OPPEL, 1863 in 1862–1863, p. 207; OD] [= *Popanites* ROLLIER, 1909, p. 614 (type *Ammonites paturattensis* GREPPIN, 1870, p. 341; OD); = *Scaphitodites* BUCKMAN, 1924, pl. 459 (type *Scaphitodites navicula*; OD)]. Macroconch (*Proscaphites*, *Popanites*) of small to medium size, involute with minute umbilicus on inner and middle whorls, followed by a small straight part, but not separated from the spiral; before the opening, a more-or-less pronounced geniculation appears, which returns the whorl to the primary coiling; subrectangular compressed whorl section with rounded venter except at the end of the body chamber; ribs fine, some divided in the lower part of the sides, others simple and some intercalated; ribbing radially crossing the venter; beaded keel or median row of serrations, strongly separated ventrolateral serrations or clavi on outer whorls. Complex septal suture with deep E and L, and narrow and high L-U₂ saddle. Microconch (*Scaphitodites*) very small, involute inner whorls and strong uncoiling in the body chamber,

similar to the *Strigoceras* microconchs; compressed to globose whorl section with rounded venter, but with a small ventral

groove sometimes appearing at the phragmocone end; completely smooth. According to MAKOWSKI (1963, p. 24) and QUEREILHAC

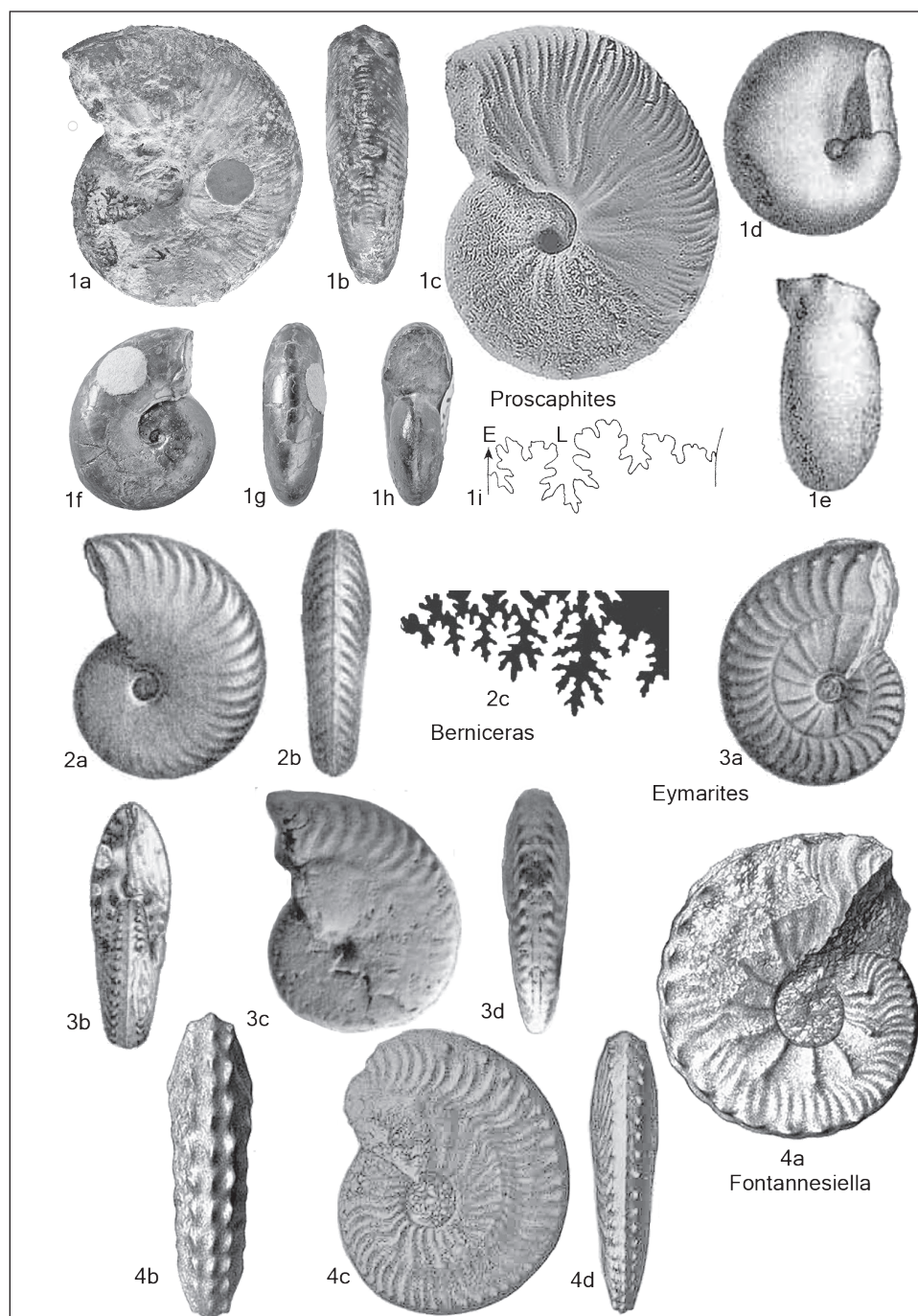


FIG. 30. Oppeliidae, Taramelliceratinae 3.

(2009, p. 29), *Scaphitodites* represents the microconch dimorphous partner of *Proscaphites*, but new data are necessary to confirm this hypothesis. *Upper Callovian–middle Oxfordian*: England, France, Germany, Italy (Sicily), Switzerland, Spain, Poland, Slovakia, Russia, Tunisia, Syria, Caucasus, Iran, India (Kutch), Madagascar. —FIG. 30, 1a–c. **P. anar* (OPPEL); 1a–b, holotype, macroconch, *middle Oxfordian*, Plicatilis Zone, Birmensdorf, Thalheim and Fricktal, Canton of Aargau, northern Switzerland, $\times 1$ (new; original of OPPEL, 1863 in 1962–1963, pl. 55, 1a–d; Geolog. Inst. der E.T.H. Zürich, Switzerland, no. ETHZ-0000000001668); 1c, macroconch, *lower Oxfordian*, Transversarium Zone, Antecedents Subzone, upper Mumienkalk bed, section RG Sib. bed 14b, excavation below Räckosterenbuck Gachlingen, $\times 1.5$ (GYGI, 2013, pl. 7, 2; SH. J 25960, leg. R. & S. Gyi). —FIG. 30, 1d–e. *P. paturattensis* (GREPPIN), microconch, *lower Oxfordian*, La Paturatte, Bernese Jura, Switzerland, $\times 1.5$ (DE LORIO, 1901, pl. 1, 8–8a). —FIG. 30, 1f–h. *S. navicula* (BUCKMAN), holotype, microconch, nearly complete specimen, *lower Oxfordian*, Mariae Zone, Oxford clay formation, St. Ives, Hunts, England, $\times 2$ (new; original of BUCKMAN 1924, pl. 459; British Geological Survey, BGS P 1033919). —FIG. 30i. suture of *S. scaphitoides* (COQUAND), *lower Oxfordian*, France (NEIGE & others, 1997, fig. 2A).

Berniceras JEANNET, 1951, p. 35 [**Oppelia inconspicua* DE LORIO, 1898, p. 58; OD]. Small size, involute with narrow umbilicus, ovate compressed whorl section, slightly convex flanks and rounded venter with a weak keel. Inner whorls smooth, then primary ribs slightly marked, and uniform marginal outer ribs bent forward on the ventrolateral shoulder. Complex, very incised septal suture with a high E–L saddle and very deep lateral lobe. Possibly microconch, but no dimorphism has been recognized. *Upper Callovian* (Lamberti Zone)–*lower Oxfordian* (Mariae Zone): ?England, France,

Germany, Switzerland, ?Russia. —FIG. 30, 2a–c. **B. inconspicuum* (DE LORIO), lectotype (designated by SANDOVAL, herein), macroconch, lateral and ventral views, and suture, *lower Oxfordian*, Châtillon, canton of Jura, Switzerland, $\times 1.3$ (DE LORIO, 1898, pl. 4, 27a–b and text-fig. 22; Geolog. Inst. der E.T.H. Zürich, Switzerland).

Eymarites JEANNET, 1951, p. 86 [**Oppelia mayeri* DE LORIO, 1898, p. 62; OD]. Similar to *Berniceras* in terms of coiling, whorl section and keel, but with a midlateral furrow and with strong ventrolateral tubercles; smooth inner whorls and then thick, widely spaced, radial primary ribs terminating without tubercle ahead of the radial sulcus midway up the flank; arched secondary ribs ending with a prominent rounded tubercle. Suture lines with deeply indented lobes and saddles. No dimorphism known for this genus. *Eymarites* has been included as synonymous of *Taramelliceras* by QUEREILHAC (2009, p. 10), in *Berniceras* by JARDAT (2010, p. 6) or even in “*Hecticoceras*” by ZEISS (1959, p. 123) and by MARCHAND & others (2002, p. 474), but it differs from them by its style of ribbing and by the mediolateral groove of the adult stage. *Lower Oxfordian*: Switzerland, France. —FIG. 30, 3a–d. *E. mayeri* (DE LORIO); 3a–b, lectotype (designated by SANDOVAL, herein), macroconch, *lower Oxfordian*, Châtillon, canton of Jura, Switzerland, $\times 1$ (DE LORIO, 1898, pl. 4, 21–21a and text-fig. 22; Geolog. Inst. der E.T.H. Zürich, maybe not preserved); 3c–d, *lower Oxfordian*, Mariae Zone, Scarburgense Subzone, Montlouis, Cher, France, $\times 1$ (MARCHAND & others, 2002, pl. 1, 16).

Fontannesiella SPATH, 1925b, p. 113 [**Oppelia valentina* FONTANNES, 1879, p. 29; OD] [= *Paralingulaticeras* ZIEGLER, 1958, p. 149 (type *Ammonites lithographicus* OPPEL, 1863 in 1862–1863, p. 248; OD); = *Rogovicer* SCHERZINGER & MITTA, 2006, p. 243 (type *Glochiceras lithographicum efimovi* ROGOV, 2002, p.

360; OD]. Macroconch (*Fontannesella*) medium-sized, platycone, moderately involute with almost rectangular whorl section; quite similar to *Taramelliceras*, with well-marked ventrolateral clavi and a row of median ventral serrations, but differing by having distinctly differentiated thick and spaced primary ribs, which end in median-lateral tubercles; secondaries radial or slightly concave forward terminate in the ventrolateral clavi. Microconchs (*Paralingulaticeras*, “*Rogoviceras*”) small, relatively involute, almost rectangular whorl section with rounded umbilical edge, flat or gently convex flanks with a lateral groove variable in length on the last whorl, which extends in the lateral lappets. Inner whorls usually smooth, later there occur primary ribs proverse of variable thickness, which are divided below of the mid-flank into secondary ribs radial or concave, which usually end in more-or-less spaced ventrolateral clavi. For several authors this is a subgenus of *Taramelliceras*, from which it possibly descended. *Upper Kimmeridgian* (Beckeri Zone)–*lower Tithonian* (Albertinum Zone): France, Germany, Hungary, Italy including Sicily, Spain (including Mallorca Island), Bulgaria, Poland, Romania, Russia (Russian platform), Crimea, Algeria, Tunisia, ?Mexico.—FIG. 30, 4a–b. **F. valentina* (FONTANNES), holotype, macroconch, *lower Tithonian*, Mont Crussol, Ardèche, France, $\times 0.5$ (FONTANNES, 1879, pl. 4, 5a–b).—FIG. 30, 4c–d. *F. prolithographica* (FONTANNES), holotype, macroconch, *lower Tithonian*, Mont Crussol, Ardèche, France, $\times 1$ (FONTANNES, 1879, pl. 4, 2a–b; also figured by SCHLEGELMILCH, 1994, pl. 11, 6).—FIG. 31a. *F. lithographica* (OPPEL), lectotype (designated by ZIEGLER, 1958, p. 152), microconch, Malm Zeta, Lithographic Limestones, Solnhofen, Bavaria, Germany, $\times 1$ (OPPEL, 1863 in 1862–1863, pl. 68, 2; also figured by ZIEGLER, 1958, pl. 16, 1; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. AS VI 20.21).—FIG. 31, 1b–c. *P. parcevali* (FONTANNES), micro-

conch, Ulmensis-Schichten, Mörsnsheim, Bavaria, Germany, $\times 1$ (ZIEGLER, 1958, pl. 16, 7–8; Paläontolog. Inst. Univ., Munich, Germany, no. 1909 I 96).

Metahaploceras SPATH, 1925b, p. 113 [**M. affinis* SPATH, 1925b, p. 113, OD; =*Ammonites strombecki* OPPEL, 1857 in 1856–1958, p. 687, *nom. nov. pro Ammonites lingulatus nudus* QUENSTEDT, 1849 in 1845–1849, p. 130]. Medium-sized macroconch (*Metahaploceras*) moderately evolute, ovate-subrectangular whorl section with gently convex sides and rounded venter. Smooth inner whorls, finely ribbed outer whorls with elongated ventrolateral bullae in the direction of the ribs and smooth venter. Some forms traditionally included in “*Glochiceras* (*Coryceras*)” as “*G. (C.) modestiforme*” (OPPEL), represent the dimorphous microconch partner of *Metahaploceras* (SCHWEIGERT & CALLOMON, 1997; WIERZBOWSKI & others, 2010, p. 96; JANTSCHKE & SCHWEIGERT, 2023, p. 157). These forms are small-sized, evolute, and have subrectangular whorl section with slightly marked mediolateral groove in the body chamber, rounded venter and aperture with lateral lappets. *Upper Oxfordian*–*lower Kimmeridgian*–?*lower Tithonian*: France, Germany, Austria, Hungary, Italy, Poland, Portugal, Spain, Switzerland, Romania, Bulgaria, Tunisia, Russia, Pakistan, ?Nepal, Yemen, Madagascar, Tanzania, Argentina, ?Chile, Mexico, USA (Texas), Cuba.—FIG. 31, 2a–c. *M. affine* (SPATH), holotype, macroconch, *Upper Jurassic*, Beisser Jura gamma, Grubingen, Baden-Württemberg, southern Germany, $\times 1$ (new; original *Ammonites lingulatus nudus* QUENSTEDT, 1887 in 1882–1888, pl. 92, 55; also figured by SCHLEGELMILCH, 1994, pl. 11, 3; Geologische Institut, Universität Tübingen, Germany, GPIT-PV.618115).—FIG. 31, 2d–f. *M. modestiforme* (OPPEL, 1863 in 1862–1863); 2d–e, microconch, lectotype (designated by ZIEGLER, 1958, p. 125), *lower Kimmeridgian*, Planula Zone, Werkkalke Formation, Thalmässing, Franconian Alb,

Germany, x1.5 (JANTSCHKE & SCHWEIGERT, 2023, pl. 2, 12; original of *Ammonites modestiformis* OPPEL, 1863–1863, pl. 54, 5; also figured by ZIEGLER, 1958, pl. 11, 19; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. BPSG AS VIII 7); 2f, suture x10 (ZIEGLER, 1958, text-fig. 34a; Ce 1113/9).

Hemihaploceras SPATH, 1925b, p. 113 [**Oppelia nobilis* NEUMAYR, 1873, p. 167; OD]. Medium-sized shells, strongly evolute, subrectangular whorl section with vertical umbilical wall, angular umbilical edge, very slightly convex sides, venter smooth and flatly rounded. The inner whorls smooth, outer whorls normally developing sparsely placed simple ribs which end in large rounded ventrolateral tubercles; thinner ribs sometimes appearing, grouped together on the ventrolateral nodules. All the specimens figured so far appear to correspond to macroconchs. Septal suture is not known. *Upper Kimmeridgian*: Germany, Austria, Hungary, Italy, Spain, Romania, Bulgaria, Ukraine, Morocco.—FIG. 31, 3a–b. *H. nobile* (NEUMAYR), holotype, macroconch, *Upper Jurassic*, north-eastern Alps, Germany, x0.6 (NEUMAYR, 1873, pl. 32, 3a–b).

Oxyoppelia BERCKHEMER, 1926, p. 66 [**Oppelia fischeri* BERCKHEMER, 1922, p. 170; OD] [= *Sueviceras* ALDINGER & SEIBOLD, 1955, *nom. nud.* and invalid under ICZN Code, 1999, Article 13.1.1]. Medium size, involute, rapid whorl expansion; similar to *Taramelliceras*, from which it descends, with falcate ribs of variable thickness similar to those of *Taramelliceras*; primaries strongly proverse and concave forward secondaries that can end in radially elongate ventrolateral clavi but can also have wavy or smooth ventrolateral edges. Suture with broad, short-branched lobes. *Oxyoppelia* is distinguished from *Taramelliceras* by the sharpness of its medioventral cusps (tubercles), which tend to join to form a median wave crest or smooth keel. Septal suture with lobes

generally broader and less deeply divided than in *Taramelliceras*. Microconchs (“*Glochiceras*” s.l.) indistinguishable from those of *Taramelliceras*. *Upper Kimmeridgian*: Germany, ?Pakistan.—FIG. 31, 4a–b. *O. fischeri* (BERCKHEMER), neotype (designated by BERCKHEMER & HÖDER, 1959, p. 82), macroconch, *upper Kimmeridgian*, Subeumela Schichten, Blaubeuren-Gerhausen, Baden-Württemberg, Germany, x1 (original in BERCKHEMER & HÖLDER, 1959, fig. 62; also figured by SCHLEGELMILCH, 1994, pl. 12, 2; Staatliches Museum für Naturkunde Stuttgart, Germany, inventory no. 19508).

Zittelliceras SANTANTONIO, 1983, p. 149 [**Ammonites piccininii* ZITTEL, 1869, p. 146; OD]. Relatively large macroconch, evolute, similar to *Hemihaploceras* with subrectangular whorl section, flanks convex and smooth ventral area, but with internal whorls densely ornamented with primary ribs, secondary and intercalated ventrolateral ribs. Throughout ontogeny, only spaced sinuous ribs remaining, similar to those of *Hemihaploceras*, with a row of ventrolateral tubercles which progressively take on the appearance of stubby clubs. *Upper Kimmeridgian*, Beckeri Zone: Germany, Italy, Romania, Spain.—FIG. 32, 1. *Z. piccininii* (ZITTEL), holotype, macroconch, *upper Kimmeridgian*, Beckeri Zone, Monte Lacerone, Appennino Umbro-Marchigiano, Italy, x1 (new, original of SANTANTONIO, 1983, pl. 1, 5; Museo di Paleontologia, Istituto di Geologia e Paleontologia dell’Università di Roma, Italy, specimen no. NS3 Col 3).

Metauhligites ÉNAY, 2009, p. 86 [**Oppelia* (*Streblites*) *sphenodoma* UHLIG, 1903, p. 58; OD]. Small- to medium-sized shells with a rather narrow umbilicus, a compressed cross section, slightly convex flanks, and rather narrow ventral region that becomes rounded and wider on the body chamber end; simple, sinuous aperture. Barely visible flexuous striations or ribs on the umbilical part of the flanks, stronger on the outer part, some-

times with periodic reinforcement taking the form of radially stretched crescent-shaped ribs. Small punctiform tubercles sometimes

present on the median part of the ventral region, distinguishing them from *Metahaploceras*. Complex septal suture with broad

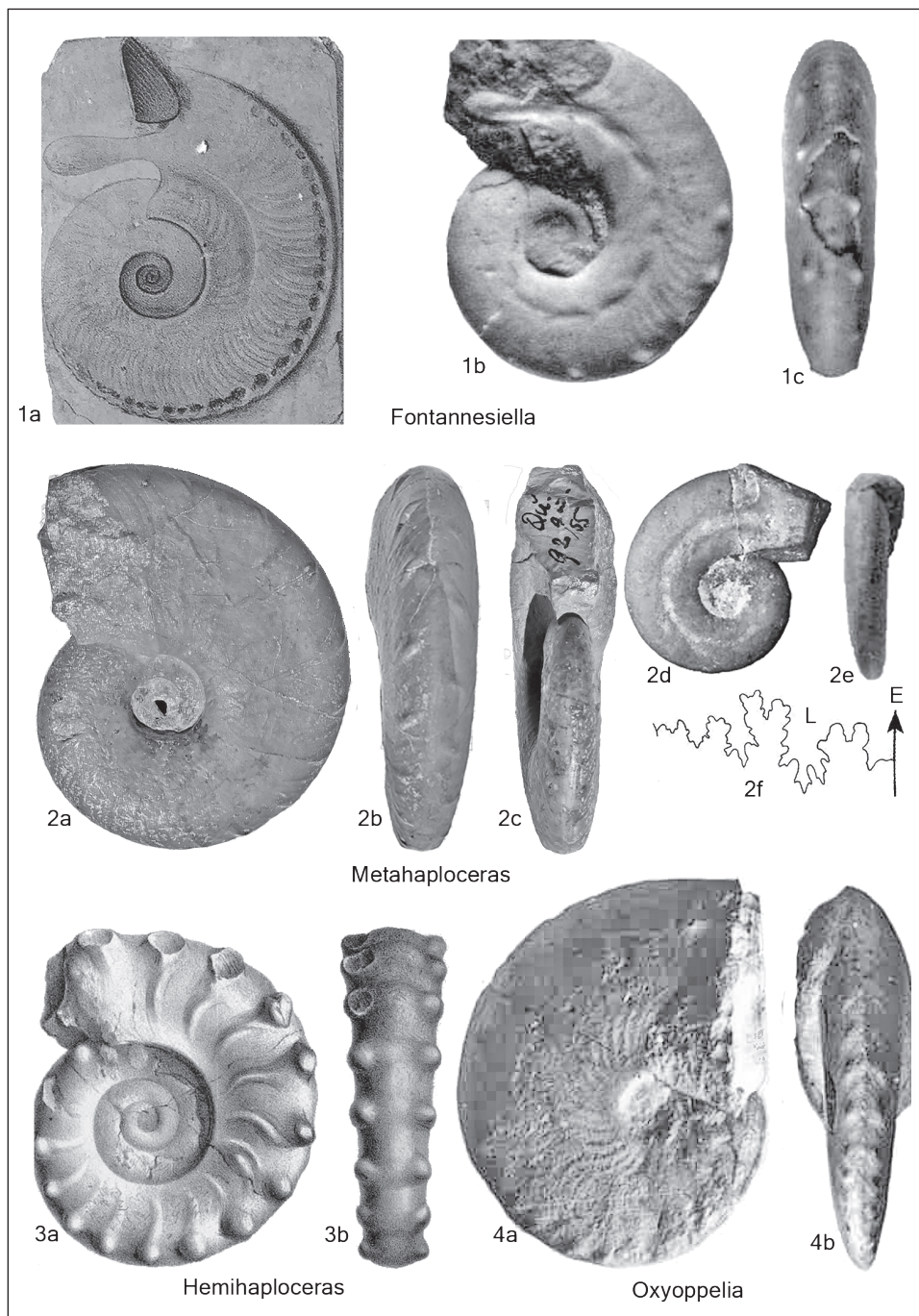


FIG. 31. Oppliidae, Taramelliceratinae 4.

and indented lobes. Possible macroconchs, no dimorphism known. *Uppermost Kimmeridgian–lower Tithonian*: Nepal, India, China.—FIG. 32, 2*a–e*. **M. sphenodoma* (UHLIG); 2*a–b*, holotype, macroconch; lateral and ventral views, $\times 1$ (UHLIG, 1903, pl. 6, 3*a–b*); 2*c*, suture of the same specimen (UHLIG, 1903, pl. 6, 3*e*); 2*d–e*, macroconch, *lower Tithonian*, Chhokor, villagers quarry of shales, Nepal, $\times 1$ (ÉNAY, 2009, pl. 2, 1*b*, 1*d*; Lyon University Collection, France, FSL 143 726).

Pasottia PARENT, SCHWEIGERT, SCHERZINGER, & ÉNAY, 2008, p. 26 [**P. andina*; OD]. Genus with well-developed dimorphism. Medium-sized smooth macroconch, compressed suboxycone with high ovate to subtriangular whorl section; phragmocone moderately involute with rounded umbilical shoulder becoming progressively uncoiled with sharp umbilical shoulder and flat, sloping wall. Body chamber becoming strongly contracted; the umbilical seam uncoiled. Microconch inner whorls like those in the macroconch; body chamber also strongly contracted, geniculate from a point at which the rounded umbilical shoulder of the phragmocone becomes sharp, and the umbilical wall flat and sloping. Last whorl of phragmocone and body chamber with a sulcus and a row of linguiform structures; lateral lappets not known. Relatively incised septal suture, but less complex than in most of the oppeliids. The E-L saddle high and quite digitized; L narrow, deep, and trifurcated; the L-U₂ saddle broad and low; and the suspensive lobe simplified. PARENT & others (2008) included the new genus *Pasottia* into the subfamily Taramelliceratinae, but its morphology, the absence of ornamentation, and the septal suture bring it closer to Haploceratidae; therefore, it could be included in this family. *Lower Tithonian*, Semiforme Zone: Argentina.—FIG. 32, 3*a–f*. **P. andina* PARENT & others; 3*a–d*, holotype, macroconch, lateral, ventral and apertural views, and suture, *lower Tithonian*,

Zitteli Zone (=Semiforme Zone), La Amarga, Neuquén-Mendoza Basin, Argentina, $\times 1$ (PARENT & others, 2008, fig. 2, *A*₁–*A*₄; also figured by PARENT, 2022, fig. 20, *I*₁–*I*₂; Laboratorio de Paleontología, Universidad Nacional de Rosario, Argentina, no. LPB 853); 3*e–f*, paratype, microconch, *lower Tithonian*, Zitteli Zone (=Semiforme Zone), Cerro Lotena, Neuquén-Mendoza Basin, Argentina, $\times 1$ (PARENT & others, 2008, fig. 3, *E*₁–*E*₂; also figured by PARENT, 2022, fig. 20, *J*₁–*J*₂; Museo Olsacher, Zapala, Neuquén, Argentina, no. MOZP 7535/1).

Cieneguiticeras PARENT, MYCZINSKI, SCHERZINGER, & SCHWEIGERT, 2010, p. 454 [**Haploceras falculatum* STEUER, 1897, p. 102; SD PARENT & others, 2010]. Macroconch of medium size, involute with moderate uncoiling in the body chamber; subplatycone in inner whorls to suboxycone on the outer whorls and body chamber, gently convex sides and rounded venter. Inner whorls smooth or faintly ribbed on the uppermost part of the flank; outer whorls of phragmocone with simple falcoid primary ribs, faint to very weak on lower half of flank, concave, thicker, and widely spaced on the upper third; adult body chamber smooth. Microconch: adult about one-third to one-fourth of the macroconch in size; inner whorls indistinguishable from those of the macroconch, body chamber more evolute, uncoiled in variable degree. End of phragmocone and body chamber covered by weak falcoid primary ribs reinforced on the mid-flank, forming a row of linguulate structures which reach the peristome. Lappets moderately long and narrow. The ornamentation and the septal suture bring *Cieneguiticeras* close to Haploceratidae. *Lower Tithonian*: Argentina, ?Cuba, ?Mexico, ?France.—FIG. 33, 1*a–e*. **C. falculatum* (STEUER); 3*a–c*, lectotype (designated by PARENT & others, 2010, p. 459), macroconch, *lower Tithonian*, Proximum Zone, Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina, $\times 1$ (PARENT & others, 2010, fig. 3, *A*₁–*A*₃; original of

STEUER, 1897, pl. 7, 11; Geoscience Center,
Georg-August-Universität Göttingen

Museum, Göttingen, Germany, no. GZG
499-23); 1d-e, topotype, microconch,

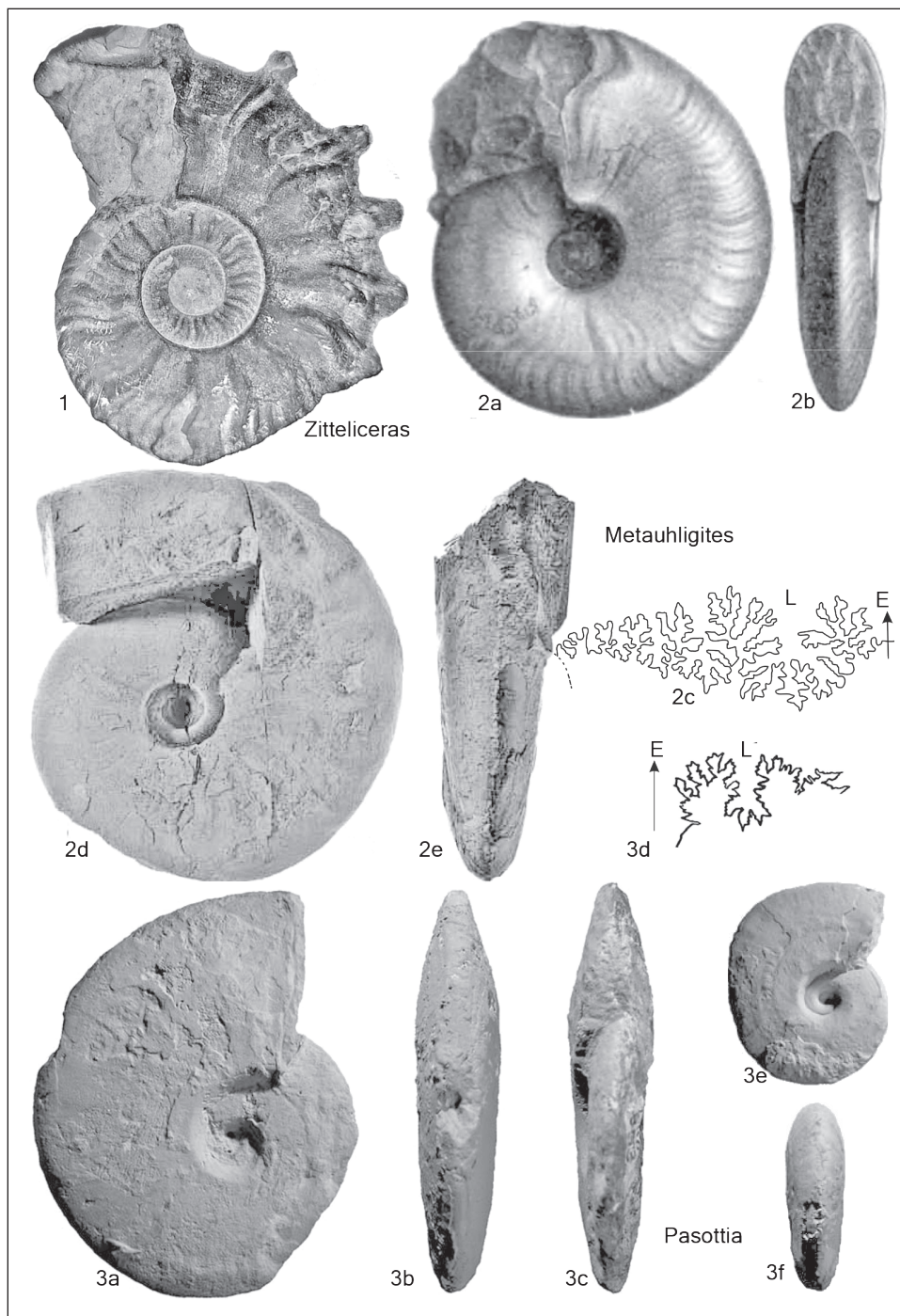


FIG. 32. Oppeliidae, Taramelliceratinae 5.

lower *Tithonian*, Proximum Zone, Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina, $\times 1$ (PARENT & others, 2010, fig. 5, C_1 – C_2 ; collections of the Museo de Ciencias Naturales, Mendoza, Argentina, no. MCNAMPI 24410/1).

Eurynoticeras CANAVARI, 1897, p. 46 [**E. paparellii*; SD ROMAN, 1938, p. 170]. Medium- or small-sized macro- and microconchs, semi-involute, with a compressed oval whorl section, gently convex flanks, and a wide and rounded ventral area. The peristome of the microconchs have small lateral auricles. The sigmoid ribs or folds cross the venter area, where they are thicker, and usually disappear on the body chamber. Throughout the ontogeny, growth striae and the ribs or folds of the outer region are visible. The sutural line with asymmetrical lobes, and the saddles and lobes slightly toothed and poorly developed in height and depth. Some authors have included *Eurynoticeras* in the Mazapilitinae, but it is more logical to include it in Taramelliceratinae where it was initially included by SPATH, 1928. *Upper Jurassic, Kimmeridgian*: Italy.—FIG. 33, 2a–b. **E. paparellii* CANAVARI, 1897; 2a, holotype by monotype, macroconch, *Kimmeridgian*; Monte Serra Presso, Camerino, Marche, Italy, $\times 0.7$ (CANAVARI, 1897, pl. 9, 1); 2b, microconch, *lower Kimmeridgian*, Planula or Eudoxus Zone, Sicily, Italy, $\times 1$ (WENT, 2017, box 16, K; Geological-Palaeontological Institute of the University of Tübingen, Germany, no. GPIT-CE-419638).

Parastreblites DONZE & ÉNAY, 1961, p. 48 [**Oppelia tenuilobata* OPPEL var. *circumnodosa* FONTANNES, 1879, p. 23, pl. 3, fig. 6; OD]. Medium-sized shells, involute, broad whorl section but higher than wide, with its maximum thickness at the mid-flank; the ventral region wide and rounded, with no keel or median tubercles; on the body chamber, the venter flattening and widening. The ornamentation reminiscent of *Streblites*; on the phragmocone, the primary ribs, wide,

spaced, and falcoid with a very pronounced angular cusp at the mid-flank; the outer portion swelling up into a crescent-shaped tubercle near the cusp, then diminishing in strength before ending in a small ventrolateral tubercle; five or six very faint secondary ribs between two primary ribs end on the outer part of the flank. On the body chamber, the ornamentation weakening, with only the primary ribs, reduced to the external part, and the peripheral tubercles remaining, but lastly sometimes disappearing completely. The suture line not complex. *Lower Tithonian*: France, Italy, Hungary, Spain, Poland, Romania, Tunisia, India, Madagascar, Argentina, Antarctica, Mexico, Cuba.—FIG. 33, 3a–c. **P. circumnodosa* (FONTANNES, 1879); 3a–b, holotype by monotypy, macroconch, *upper Kimmeridgian*–*lower Tithonian*, Calcaires du Château Formation, Crussol, Ardèche, France, $\times 1$ (original of *Oppelia tenuilobata* OPPEL var. *circumnodosa* of FONTANNES, 1879, pl. 3, 6a–6b; Lyon University Collection FSL A.1294); 3, suture of a topotype (DONZE & ÉNAY, 1961, text-fig. 5; Lyon University Collection FSL A.4639).—FIG. 33, 3d–e. *P. hoelderi* DONZE & ÉNAY, holotype, macroconch, adult with body chamber, *lower Tithonian*, “pseudobreccia” of St. Concors, Lémenc near Chambéry, France, $\times 0.6$; and whorl section on the body chamber (DONZE & ÉNAY, 1961, pl. 4, 1; text-fig. 8).

Subfamily STREBLITINAE Spath, 1925

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

Descendent of Taramelliceratinae. More or less oxycone shells, compressed, involute with very narrow umbilicus. Dimorphism well-differentiated in some genera and not observable in others. Macroconchs high-keeled, or with venter narrowly tabulate with sharp crenulated keels, becoming inflated on the adult body chambers, broadening and

developing shallow sulci; ribbing highly variable, but frequently recapitulating distant, falcate primaries with midlateral groove, with fine but dense secondaries or even tertiaries

strengthening towards the external margin. Microconchs extremely variable, smooth to densely ribbed with finely crenulated keels, adult body chambers more-or-less strongly

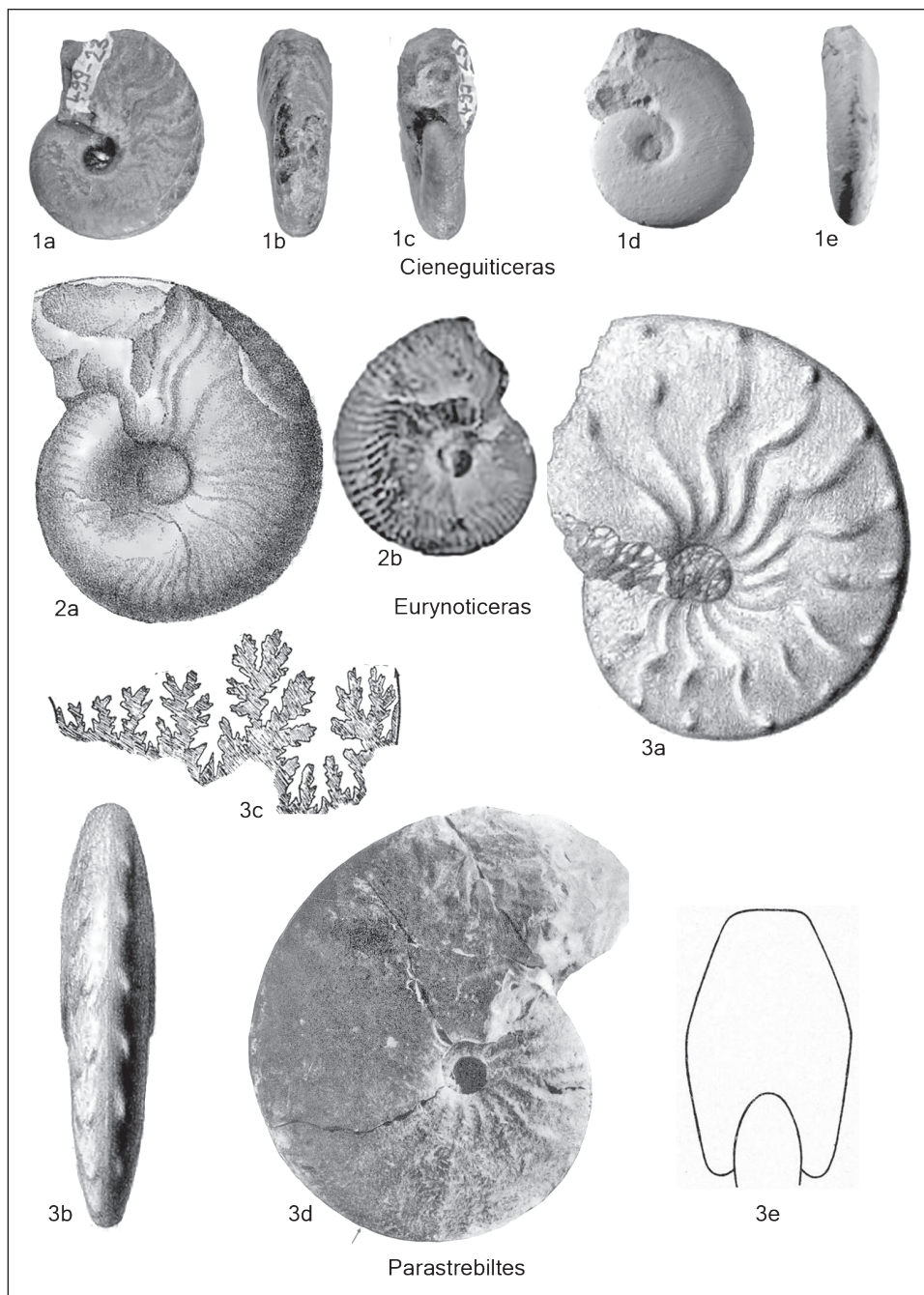


FIG. 33. Oppeliidae, Taramelliceratinae 6.

modified, eccentrically coiled, sometimes strangely (*Cyrtosiceras*) with prominent lappets. Very complex septal suture with generally highly incised elements, which separates them of the Haploceratidae and brings them closer to Taramelliceratinae.

ARKELL (1957, p. 283) included the subfamily Streblitinae into the family Oppeliidae and, since then, most researchers studying the Upper Jurassic or Lower Cretaceous Haploceratoidea have followed his taxonomy. However, some other researchers have used different taxonomic schemes; e.g., ZIEGLER (1974, p. 33), OLÓRIZ (1978, p. 44), SANTANTONIO (1983, p. 148), and RODRÍGUEZ-TOVAR (1993, p. 129) have classified them as a subfamily of Haploceratidae and, according to SCHWEIGERT (1995, p. 2), Streblitinae represent a subfamily within Glochiceratidae. According to ZIEGLER (1974, p. 33), the subfamily Streblitinae includes only four Jurassic genera: *Streblites* HYATT, 1900, *Substreblites* SPATH, 1925, *Neochetoceras* SPATH, 1925b, and *Semiformiceras* SPATH, 1925b. However, other Streblitinae genera such as *Cyrtosiceras* HYATT, 1900, *Uhligites* KILIAN, 1913, *Gymnodiscoceras* SPATH, 1925, *Oxynticeras* SPATH, 1950, *Rochites* COLLIGNON, 1960, *Parastreblites* DONZE & ÉNAY, 1961, and *Metastreblites* OLÓRIZ, 1978, come from the Upper Jurassic or, at least, some of their species occur in this stratigraphic interval. The genera *Uhligites*, *Substreblites*, and *Cyrtosiceras* were included in the new version of the *Treatise*: Cretaceous Ammonoidea (WRIGHT & others, 1996, p. 12) and are therefore not discussed here. Upper Jurassic (uppermost Oxfordian)–Lower Cretaceous (Hauterivian): worldwide.

Streblites HYATT, 1900, p. 569 [*Ammonites tenuilobatus* OPPEL, 1857 in 1856–1858, p. 686; OD] [= *Strebliticeras* HÖLDER, 1955, p. 90 (type *Ammonites pictus tegulatus* QUENSTEDT, 1887 in 1882–1888, pl. 120, fig. 3; ICZN 2005, Opinion 2123, p. 160), OD)]. Medium-sized macroconchs (*Streblites* & *Strebliticeras*), oxycone, involute with high oval to lanceolate whorl section, vertical

umbilical wall, flanks more-or-less convex, ventral region with fine to very fine clavate nodes resembling crenulations or even a keel. Distant, concave and relatively strong inner ribs ending at distinct nodes near where they divide; the main ribs, as a continuation of the inner ribs, are stronger and end at distinct ventrolateral nodes. Usually, several intercalate ribs occur between the main ribs, beginning above the mid-flank, while the outer ribs are finer and more densely spaced. The microconchs, "*Creniceras*" gr. *dentatus* (REINECKE), are small and discoid, characterized by a body chamber with a tabulate venter appearing with a significant reduction in the whorl height, and the presence of lateral apophysis. In the inner whorls, the whorl section is oxycone, compressed, with vertical and low umbilical walls, sharp or slightly rounded umbilical edge, slightly convex flanks, and a narrow and rounded venter that bears a conspicuous and finely indented keel; the narrow umbilicus is almost punctiform; no ribbing is visible. The increase of height in the adult body chamber reduces greatly while the coiling becomes much more evolute, determining a scaphitoid type shell; the ventral area changes, and the unbroken keel is replaced by fine denticulations in the first part of the adult body chamber; those denticulations then disappear when the venter stretches and becomes subtabulate or slightly concave with a more-or-less rounded ventrolateral edge except for the keel. In both macro- and microconchs the septal suture is very complex. *Kimmeridgian*–*lower Tithonian*, (Hybonotum Zone): France, Germany, Italy, Hungary, Portugal, Spain, Poland, Switzerland, Bulgaria, Romania, Ukraine, Morocco, Algeria, Tunisia, Russia, Iran, Pakistan, India (Kutch), Japan, Yemen, Somalia, Kenya, Tanzania, Madagascar, Philippines, Indonesia, Papua New Guinea, ?New Zealand, Antarctica, Argentina, Mexico, Cuba, USA (Texas), ?Greenland.——FIG. 34, 1a–b. **S. tenuilobatum* (OPPEL), holotype, macroconch, Jura gamma, Lauterstein-Weissenstein, Baden-Württemberg, Germany, ×1

(new; original of *Ammonites pictus costatus* 12; also figured by SCHLEGELMILCH, 1994, QUENSTEDT, 1887 in 1882–1888, pl. 119, pl. 12, 13; Geologische Institut, Univer-



FIG. 34. Oppeliidae, Streblitinae.

sität Tübingen, Germany, no. GPIT-PV-62175).—FIG. 34, 1c–g. *S. weinlandi* (OPPEL); 1c–d, macroconch, *upper Kimmeridgian*, *Acanthicum Zone*, Mount Crussol, Ardèche, France, x1 (BAUDOUIN & others, 2011, pl. 9, 1a–b; specimen no. cr1055, C. Baudouin's collection); 1e, microconch, *upper Kimmeridgian*, *Acanthicum Zone*, Mount Crussol, Ardèche, France, x1 (BAUDOUIN & others, 2011, pl. 10, 9; specimen no. cru068, P. Boselli's collection); 1f–g, microconch, *upper Kimmeridgian*, *Acanthicum Zone*, Mount Crussol, Ardèche, France, x1 (BAUDOUIN & others, 2011, pl. 10, 11a–b; specimen no. cru1099, C. Baudouin's collection).—FIG. 34, 1h–j. *S. tegulatum* (QUENSTEDT), lectotype, macroconch, *Upper Jurassic*, middle Weisser Jura delta, Melchingen, Baden-Württemberg, southern Germany, x1 (new; original of *Ammonites pictus tegulatus* QUENSTEDT, 1887 in 1882–1888, pl. 120, 3; also figured by SCHLEGELMILCH, 1994, pl. 12, 12; Geologische Institut, Universität Tübingen, Germany, no. GPIT-PV-62187).

Semiformiceras SPATH, 1925b, p. 115 [**Ammonites fallauxi* OPPEL, 1865 in 1863–1865, p. 547; OD]. Macroconch (*Semiformiceras*) of small to medium size, involute but with more-or-less uniform coiling and variable umbilicus, ovate to subrectangular whorl section; venter with minute median serrations which give place to a groove on last whorl; some lateral tubercles irregular and elongated, oblique lateral bullae on the body chamber. Aperture with simple peristome. Septal suture complex of the Streblitinae type. Microconch, some forms usually included in “*Cyrtosiceras gr. collegialis*” (OPPEL, 1865), not the type species (SCHWEIGERT, 1995, p. 8; SCHWEIGERT & others, 2002, p. 9; 2015, p. 8; FÖZY & SCHERZINGER, 2013, p. 221). Small, very involute in inner and middle whorls and strong uncoiling and spiral retraction in the adult body chamber; compressed whorl section with a shallow midlateral groove on the body chamber, venter minutely

crenulate in the phragmocone and ventral crenular swelling briefly before completely fading; aperture preceded by a small lip and with well-developed sub-spatulate lateral lappets; smooth, but the first half of the body chamber developing an elbow bend and having strong beaded ventral folds; complex septal suture with thin-stemmed lobes. *Lower Tithonian*: Germany, France, Hungary, Italy, Poland, Romania, Czech Republic, Spain, Crimea, Turkey, eastern Russia, Morocco, Tunisia, Iran, Nepal, Ethiopia, Argentina, Mexico.—FIG. 34, 2a–d. **S. fallauxi* (OPPEL); 2a–b, lectotype by monotypy, ?macroconch, *lower Tithonian*, *Fallauxi Zone*, Rogoźnik, Silesia, Poland, x1 (new; original in ZITTEL, 1870, pl. 28, 6; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. BSPG AS III 113); 2c–d, ?microconch, *lower Tithonian*, *Fallauxi Zone*, Rogoźnik, Silesia, Poland, x1 (new; original in ZITTEL, 1870, pl. 28, 5; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. BSPG AS III 112).—FIG. 34, 2e–f. *Semiformiceras collegialis* (OPPEL), lectotype, microconch, *lower Tithonian*, ?*Semiforme Zone*, Tardos, Szél Hill, Shaft, Gerecse Mountains, Hungary, x1.5 (FÖZY & others, 2022, pl. 7, 4a–b; also figured by FÖZY & others, 1994, pl. 1, 18, by FÖZY & SCHERZINGER, 2013, pl. 7, 4a–b, and by FÖZY, 2017, pl. 26, 4a–b; Hungarian Geological and Geophysical Institute, Budapest, no. 1962a).

Neochetoceras SPATH, 1925b, p. 116 [**Ammonites steraspis* OPPEL, 1863 in 1862–1863, p. 251; OD]. Macroconchs of medium size, involute, oxycone, whorl section lanceolate to oval compressed; the venter varying from wide to narrow, with or without marginal edges and a more-or-less developed keel, sometimes appearing somewhat depressed. More-or-less pronounced falcate primary ribs, with secondary and intercalatory ribs sometimes ending in a small node; ribbing tending to fade in the

macroconchs near the simple aperture. The microconchs, formerly mostly described as "*Lingulaticeras*" gr. *solenoides* (QUENSTEDT) (PARENT & others, 2010, p. 453; FÖZY & SCHERZINGER, 2013, p. 221; SCHERZINGER & others, 2015, p. 3; FÖZY & others, 2022, p. 255) are small in size, one-third to one-fifth the size of the macroconch; evolute with marked uncoiling in the body chamber,

gently oval, compressed whorl section with rounded umbilical edge, gently convex flanks (sides) and curved venter; aperture with small ventral rostrum and lateral lappets; a few marked midlateral grooves sometimes occurring in the body chamber end, extending through the central part of the lappets. Smooth or almost smooth on the inner whorls, and more-or-less ribbed in the

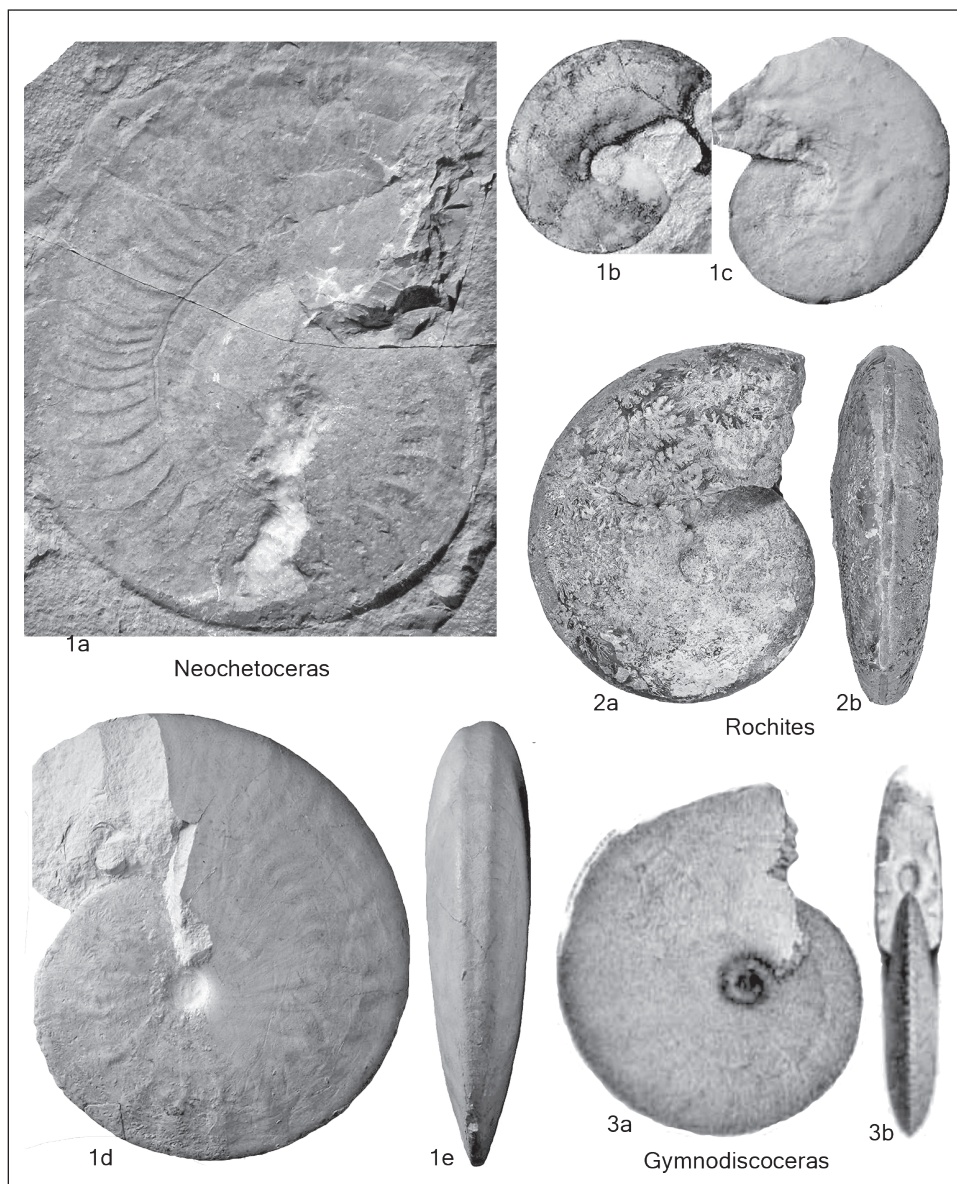


FIG. 35. Oppeliidae, Streblitinae 2.

outer ones with weak, falcate primary ribs, which divide approximately at midflank; the secondary ones, usually weak, radially crossing the venter and sometimes becoming thick; no ventrolateral tubercles. The taxonomic status of *Neochetoceras* is unclear; e.g., for SPATH (1925b, p. 118), OLÓRIZ (1978, p. 59), PARENT (2001, p. 27), and FÖZY & others (2022, p. 255), this is a Streblitinae, whereas for SCHERZINGER & others (2015, p. 3) it is a Taramelliceratinae. *Upper Kimmeridgian (Beckeri Zone)–lower Tithonian (Richteri Zone)*: Austria, France, Germany, Hungary, Italy, Poland, Czech Republic, Spain, Romania, Bulgaria, Russian platform, Morocco, Tunisia, Iran, India, ?Japan, ?Ethiopia, ?Antarctica, Argentina, Peru, Cuba.—FIG. 35, 1a–b. **N. steraspis* (OPPEL); 1a, lectotype, macroconch, Malm Zeta, Lithographic Limestones, Solnhofen, Bavaria, Germany, $\times 1$ (new; original of OPPEL, 1863 in 1862–1863, pl. 69, 1; also figured by SCHLEGELMILCH, 1994, pl. 13, 3; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, Germany, no. BSPG AS VI 5); 1b, microconch, *lower Tithonian*, Hybonotum Zone, Hummelberg Quarry, Solnhofen, Bavaria, Germany, $\times 1.4$ (SCHERZINGER & others, 2015, fig. 8, F_1 – F_2 ; Staatliches Museum für Naturkunde Stuttgart, Germany, no. 70291/2).—FIG. 35, 1c–e. *N. mohri* SCHERZINGER, PARENT, & SCHWEIGERT; c, microconch, *lower Tithonian*, Hybonotum Zone, Liptingen Quarry, southwest Swabia, Germany, $\times 1$ (SCHERZINGER & others, 2015, fig. 8, D; Staatliches Museum für Naturkunde Stuttgart, Germany, no. 70283/8); 1d–e, holotype, macroconch, *lower Tithonian*, Hybonotum Zone, Liptingen Quarry, southwest Swabia, Germany, $\times 0.51$ (SCHERZINGER & others, 2015, fig. 8, A_2 – A_3 ; Staatliches Museum für Naturkunde Stuttgart, Germany, no. 70283/1).

Rochites COLLIGNON, 1960, fig. 589, text in caption of pl. 147 [**R. rochi*; OD]. Similar to *Uhligites*, of which it could even be a synonym. Discoidal, involute with

narrow umbilicus, vertical umbilical wall and rounded umbilical edge; almost trapezoidal whorl section with maximum width near the umbilical edge, flat to very slightly convex flanks, sloping gently toward the rounded venter; ornamentation consisting of tightly packed periumbilical costules, slightly concave forward, bordered by a wide, very shallow spiral groove located in the mid-flank; the upper part of the flank smooth, but the ventrolateral region bearing very fine, tightly packed costules projecting forward and limited to the beginning of the last whorl; suture, essentially streblitiform, with extremely complex massive elements. *Lower Tithonian*: Madagascar.—FIG. 35, 2a–b. **R. rochi* COLLIGNON, paratype, macroconch, phragmocone, *lower Tithonian*, Kobelli Zone, Sources de la Mandarana, Madagascar, $\times 1$ (new; original in COLLIGNON, 1960, fig. 589; Université de Bourgogne, Dijon, France, UBGD.010589).

Gymnodiscoceras SPATH, 1925b, p. 116 [**Ammonites acucinctus* STRACHEY in BLANFORD, 1863, p. 126; OD]. Medium size, oxycone involute, compressed whorl section with almost flat flanks, rounded venter with finely serrated keel; smooth or almost smooth sides with only sigmoidal growth striae; septal suture simpler than for subfamily. No dimorphism known for this genus. According to HOWARTH (1998, p. 39) it is synonymous with *Uhligites*, but for ÉNAY (2009, p. 93), PANDEY & others (2022, p. 11), and JAIN (2025, p. 4) it is a valid genus. *Upper Jurassic (Tithonian)*: Spiti Shale (India), Nepal, Tibet, Yemen, ?Indonesia.—FIG. 35, 3a–b. **G. acucinctum* (STRACHEY in BLANFORD), holotype, macroconch, Spiti Valley, Nepal, $\times 1$ (UHLIG, 1903, pl. 4, 3a–b).

Metastreblites OLÓRIZ, 1978, p. 55 [**M. ellypticus*; OD]. Small-sized shells, involute elliptical, oval section with slightly convex flanks and wide and smooth ventral region; the beginning of the body chamber marked by a sudden narrowing of the whorl section

and development of lateral folds or thick ribs that occupy the external half of the flanks; subsequently, new widening of the whorl and flattening of ventral region, now with a weak median keel; in the second half of the body chamber, the ventral region sometimes smooth and convex or even with a groove. Simple and sinuous peristome. Relatively complex septal suture with a deep lateral lobe and four or five auxiliary lobes on the flank. According to SCHWEIGERT (1995, p. 1, 4) and SCHWEIGERT & others (1999, p. 59), *Metastrebrites* is a junior synonym of *Oxydiscites* and it was included (SCHWEIGERT & others, 1999) into the family Strigoceratidae. However, ÉNAY (2009, p. 92) placed *Metastrebrites* within the subfamily Streblitinae, as a genus very close to *Semiformiceras*. *Lower Kimmeridgian* (Strombecki–Divisum zones): Spain, Germany, Italy, Poland, Romania, Argentina.—FIG. 36, 1*a–b*. **M. ellypticus* OLÓRIZ, holotype, macroconch, *lower Kimmeridgian*, Strombecki Zone, Sierra Gorda, Granada, Spain, $\times 1$ (OLÓRIZ, 1978, pl. 2, 2*a–b*; also figured by SCHWEIGERT & others, 1999, fig. 17; collections of the Departamento de Estratigrafía

y Paleontología, Universidad de Granada, Spain, F.G15.7.13).

Oxylenticeras SPATH, 1950, p. 97 [**O. lepidum*, OD]. Medium size, involute with small umbilicus becoming closed at larger sizes; oxycones, whorl section compressed, flanks rounded, whorl breadth greatest on the inner half of the whorl; lanceolate, very sharp venter with well-marked keel; ornamentation consisting of sigmoidal growth-line striae grouped into very low undulations or ribs, especially on the outer half of the whorl; at larger sizes the striae curves strongly backwards on approaching the keel. Septal suture highly complex with strongly indented and undercut saddles. All the specimens figured so far are possibly macroconchs and no possible dimorphs are known in *Oxylenticeras*. *Upper Tithonian–lower Berriasian*: Iran, Iraq (Kurdistan), India, Nepal, Tibet, Indonesia, Ethiopia.—FIG. 36, 2*a–c*. *Oxylenticeras lepidum* SPATH; *a–b*, macroconch, wholly septate specimen, *upper Tithonian*, *Durangites* Zone, Chia Gara Formation, Banik, Kurdistan, Iraq, $\times 1$ (HOWARTH, 1992, pl. 2, 8–9; British

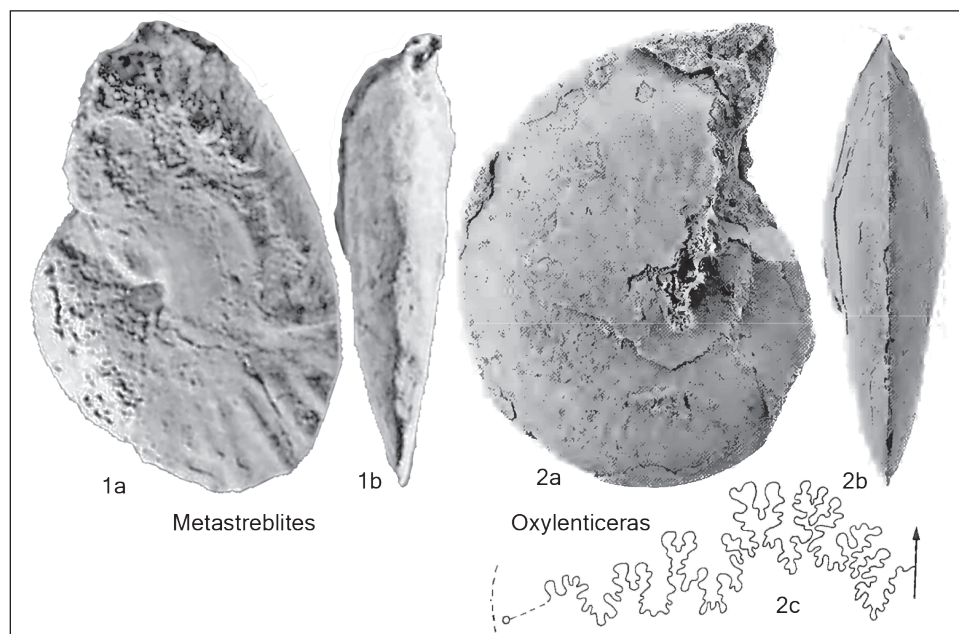


FIG. 36. Oppeliidae, Streblitinae 3.

Museum of Natural History, no. BMNH C. 86866); *c*, suture at 22 mm whorl height (HOWARTH, 1992, text-fig. 6, *b*; British Museum of Natural History, no. BMNH C.87051.

INCERTAE SEDIS IN OPPELIIDAE OR BERRIASOLIDAE

Subfamily MAZAPILITINAE Spath, 1928

[Mazapitinae SPATH, 1925b, p. 154]

The Subfamily Mazapilitinae includes involute shells with subrounded or gently tabulate venter and coarse, fold-like, branched ribbing. In the old *Treatise* (ARKELL, 1957, p. 284), the Subfamily Mazapilitinae (genera *Eurynoticer* CANAVARI, 1897, and *Mazapilites* BURCKHARDT, 1919 in 1919–1921) was included in the Family Oppeliidae. As indicated by SPATH (1928, p. 13), the Mediterranean genus *Eurynoticer* must be situated among the Taramelliceratinae. The genus *Mazapilites* has been included in Mazapilitinae (MYCZYŃSKI, 1989; OLIVA-MARTÍN & others, 2017, Cuba) or in Taramelliceratinae (BERCKHEMER & HÖLDER, 1959, p. 73; ZIEGLER, 1974, p. 32; VILLASEÑOR & others, 2005, p. 71). For CANTÚ-CHAPA (2009, p. 205), Mazapilitinae should be included as a subfamily in the Family Berriasellidae SPATH, 1922 (Perisphinctoidea) and includes the genera *Mazapilites* BURCKHARDT, 1919, *Submazapilites* CANTÚ-CHAPA, 1963, and *Chigaroceras* HOWARTH, 1992. The genus *Chigaroceras* was originally placed in the subfamily Berriasellinae within Neocomitidae SALFELD, 1921, by HOWARTH (1992, p. 641), which was subsequently followed in the new version of the *Treatise*, Cretaceous Ammonoidea (WRIGHT & others, 1996, p. 52; PARENT & others, 2011, p. 62). However, COOPER (2025, p. 48) placed *Chigaroceras* in the subfamily Mazapilitinae, but within Taramelliceratidae. The rare and

scarce *Submazapilites* is known only from its holotype; its poor preservation prevents a complete understanding of its morphological characteristics, but it appears to be closely related to *Mazapilites*. So, excluding *Chigaroceras*, the subfamily Mazapilitinae, with uncertain affinities (*incertae sedis*), would be reduced to the genera *Mazapilites* and *Submazapilites*. *Upper Jurassic, uppermost Kimmeridgian* (Beckeri Zone)–? *Lower Cretaceous* (Berriasian): Endemic to the Caribbean area (Mexico, Cuba).

Mazapilites BURCKHARDT, 1919 in BURCKHARDT (1919–1921, p. 2). [**M. symonensis*; SD ROMAN, 1938, p. 169]. Medium-sized shells, involute with a narrow umbilicus and rapidly growing whorls. Whorl section changing from more-or-less oval (taller than wide) with gently convex flanks and rounded ventrolateral edges to acute during ontogeny and in some cases becoming acutely arrow-shaped in the outer whorls. Venter tricarination with tuberculous external keel and weak lateral keels, with variable development, occurring during an ephemeral ontogenetic phase in some forms and sometimes disappearing early or late in ontogeny. Ornamentation consisting of well-marked, flexuous, simple and intercalate ribs, which thicken considerably on the upper part of the flanks; intercalate ribs sometimes connected to umbilical or primary ribs at the mid-flank inflexion; on the body chamber of adult specimens, ribbing progressively weakening, sometimes reduced to growth striae. Septal suture relatively complex; the E lobe with a short, narrow trunk with two broad terminal branches, somewhat shallower than L, which is tripartite and asymmetric with well-defined branches; the E-L saddle notably asymmetrical, divided into two branches, the inner one being taller and larger; three or four slightly oblique auxiliary lobes. No dimorphism observed. *Upper Jurassic, uppermost Kimmeridgian* (Beckeri Zone)–lowermost *Tithonian* (Hybonotum Zone): Endemic to the Caribbean area

(Mexico, Cuba).—FIG. 37, 1a–c. **M. symonensis* BURCKHARDT; 1a–b, holotype, macroconch, *lower Tithonian*, Cañon del Taboos, Sierra de Symon, Durango State, Mexico, $\times 1$ (BURCKHARDT, 1919, pl. 1, 2–3; refigured by CANTÚ-CHAPA, 2009, fig. 7, i, j; figured again by OLÓRIZ & VILLASEÑOR, 2018, fig. 7, 9; Instituto de Geología, UNAM, Mexico, IGM-1562); 1c, macroconch, adult with body chamber, *lower Tithonian*, $\times 0.5$ (OLÓRIZ & VILLASEÑOR, 2018, fig. 7, 10; Instituto de Geología, UNAM, Mexico, IGM-1563).—FIG. 37, 1d. *M. crassicostratus* BURCKHARDT, lectotype (designated by SANDOVAL, herein), macro-

conch, *lower Tithonian*, Cañon del Taboos, Sierra de Symon, Durango State, Mexico, $\times 1$ (OLÓRIZ & VILLASEÑOR, 2018, fig. 7, 11, original of BURCKHARDT, 1919, pl. 2, 6; Instituto de Geología, UNAM, Mexico, IGM-2684).

Submazapilites CANTÚ-CHAPA, 1963, p. 33 [**S. mexicanus* CANTÚ-CHAPA, 1963, p. 33; OD]. Medium-sized shells, involute, compressed whorl section with maximum width below the middle of the flanks and the venter, not sharp, having two rows of small tubercles at the beginning of the last whorl. The primary ribs, radial, bifurcate

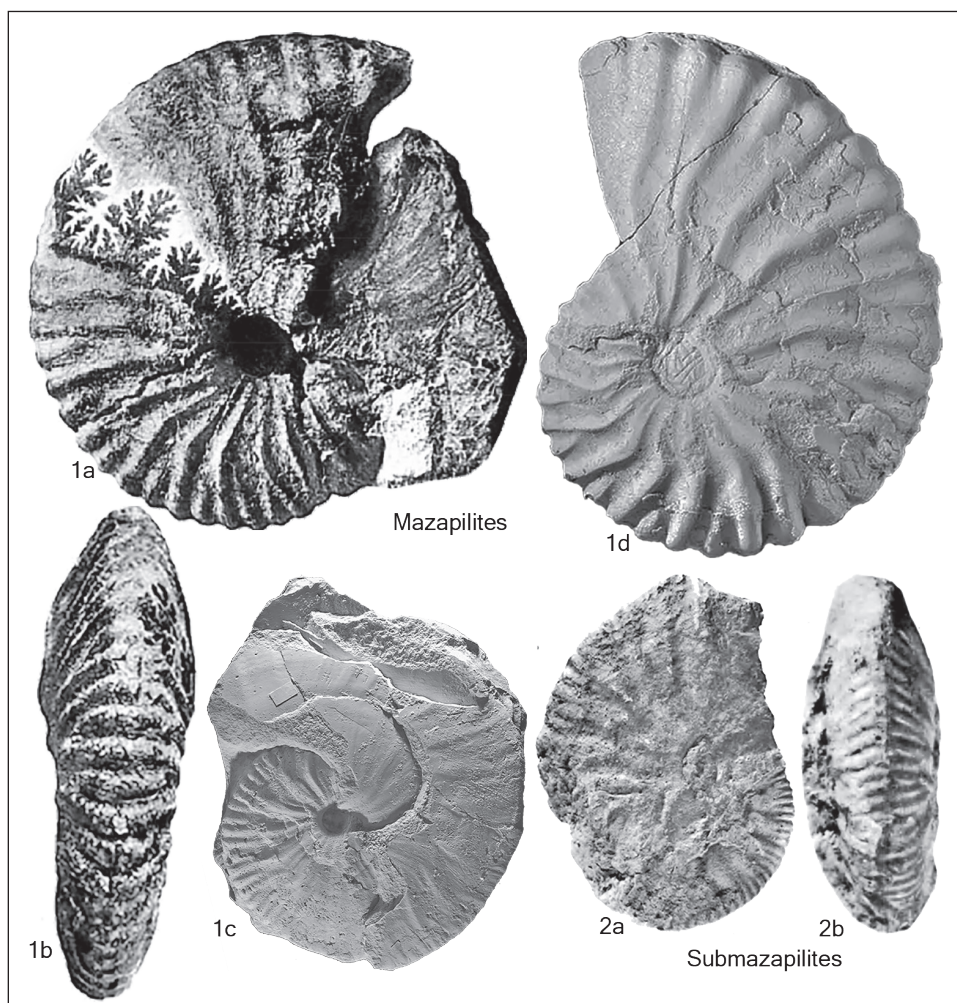


FIG. 37. Mazapilitinae.

or trifurcate from a lateral tubercle and alternating with free secondaries from the midlateral area. Septal suture not preserved, with no dimorphism known. *Upper Tithonian–?Berriasian*; Mexico, Cuba.—FIG. 37, 2a–b. **S. mexicanus* CANTÚ-CHAPA, holotype, macroconch, *upper Tithonian–Berriasian*, Arroyo San José, Veracruz State, Mexico, $\times 0.5$ (CANTÚ-CHAPA, 1963, pl. 2, 2–2a; specimen Ry 1225c).

Family THAMBOCERATIDAE

Arkell, 1952a

[ARKELL, 1952a, p. 278

This small ammonite group, *Thamboceratidae*, have oxyconic involute, bicarinate shells with single or furcate ribs of clydoniceratid type, but these can also be obsolete. The highly variable degenerated suture is simple to strongly digitated, with a relatively deep E, a large E-L saddle, and a narrow L followed by a bifid L-U₂ saddle; the following three saddles up to the umbilical seam are notably broad and low and are separated by narrow lobes. This suture pattern differs considerably from that of the *Clydoniceratidae*, which may have a very broad L (e.g., in *Clydoniceras* and *Dhru-maites*) and a very broad second lateral saddle (e.g., in *Clydoniceras*, *Clydomphalites*, and *Micromphalites*). To date, no typical dimorphs have been described or figured.

ARKELL (1952a, 1957, p. 290, 291) included the families *Clydoniceratidae* BUCKMAN, 1924, and *Thamboceratidae* ARKELL, 1952a, in the superfamily *Stephanoceratoidea*. Later, CALLOMON (1981, p. 143), combined these two families in *Clydoniceratinae*, a subfamily of the *Oppeliidae*, and thus in *Haploceratoidea*, and this classification was followed by several later authors (GILL & others, 1985; PARNES, 1988; CARIU & others, 1989; BESNOSOV & MICHAILOVA, 1991; PANDEY & CALLOMON, 1995; ÉNAY & others, 2001; THIERRY, 2003; ÉNAY & MANGOLD, 2021, etc.). However, other authors (LEWY, 1983; ÉNAY & others,

2012; PANDEY & PATHAK, 2015) continued to include *thamboceratids* and *clydoniceratids* in *Stephanoceratoidea*. The new version of the *Treatise* (HOWARTH, 2017) did not include these groups of ammonites in *Stephanoceratoidea*.

The origin of these characteristic Middle Eastern ammonites is not yet clear. ARKELL (1952a, p. 283) conjectured that *Clydoniceratidae* are probably derived from *Thambites* and the *Bajocian Thamboceras*, and the latter was perhaps in turn derived from *Ermoceras*. Thus, ARKELL (1952a, 1957, p. 290, 291) placed *Thamboceratidae* and *Clydoniceratidae* in *Stephanoceratoidea*. For CALLOMON (1981, p. 145, fig. 3), the origin of the first *thamboceratids* could be directly from *Bradfordiinae* rather than via *Oppelia*. Thereby, this ammonite group with a “simplified suture” was integrated into *Haploceratoidea*. The general morphology of the shells, the oxyconic section, ornamentation in the inner and intermediate whorls with falcate ribbing on the phragmocone, the type of suture, as well as the biostratigraphic data seem to strongly support this hypothesis, which nevertheless would need to be confirmed with new data. The *upper Bajocian* *tricarinate Trimarginia* ARKELL, 1952a, an *Oppeliidae* that is common in the Middle East and Spain (ARKELL, 1952a; PARNES, 1988; FERNÁNDEZ-LÓPEZ, 1985, 2000), where *Thamboceratidae* are more common, appears as another plausible ancestor for this family of ammonites. *Middle Jurassic (upper Bajocian–upper Callovian)*: France, Algeria, Morocco, Israel, Egypt, Saudi Arabia, Oman, Madagascar.

Thamboceras DOUVILLÉ, 1916, p. 21 [**T. mirum*; OD]. Medium size, from relatively involute to relatively evolute, being more evolute than other *Thamboceratidae*. Subrectangular to trapezoidal whorl section, vertical umbilical wall, slightly convex flanks converging towards the smooth, and bicarinate venter. Primary ribs arise from the umbilical edge, are mainly radial, and divided in the upper part of the flanks; secondaries, short, and some

longer and intercalate, bend forwards to the ventrolateral margin; the ribbing, primaries first and secondaries later, fade progressively

to become smooth. Typical thamboceratid suture with extremely wide saddles and shallow lobes. According to PARNES (1988),

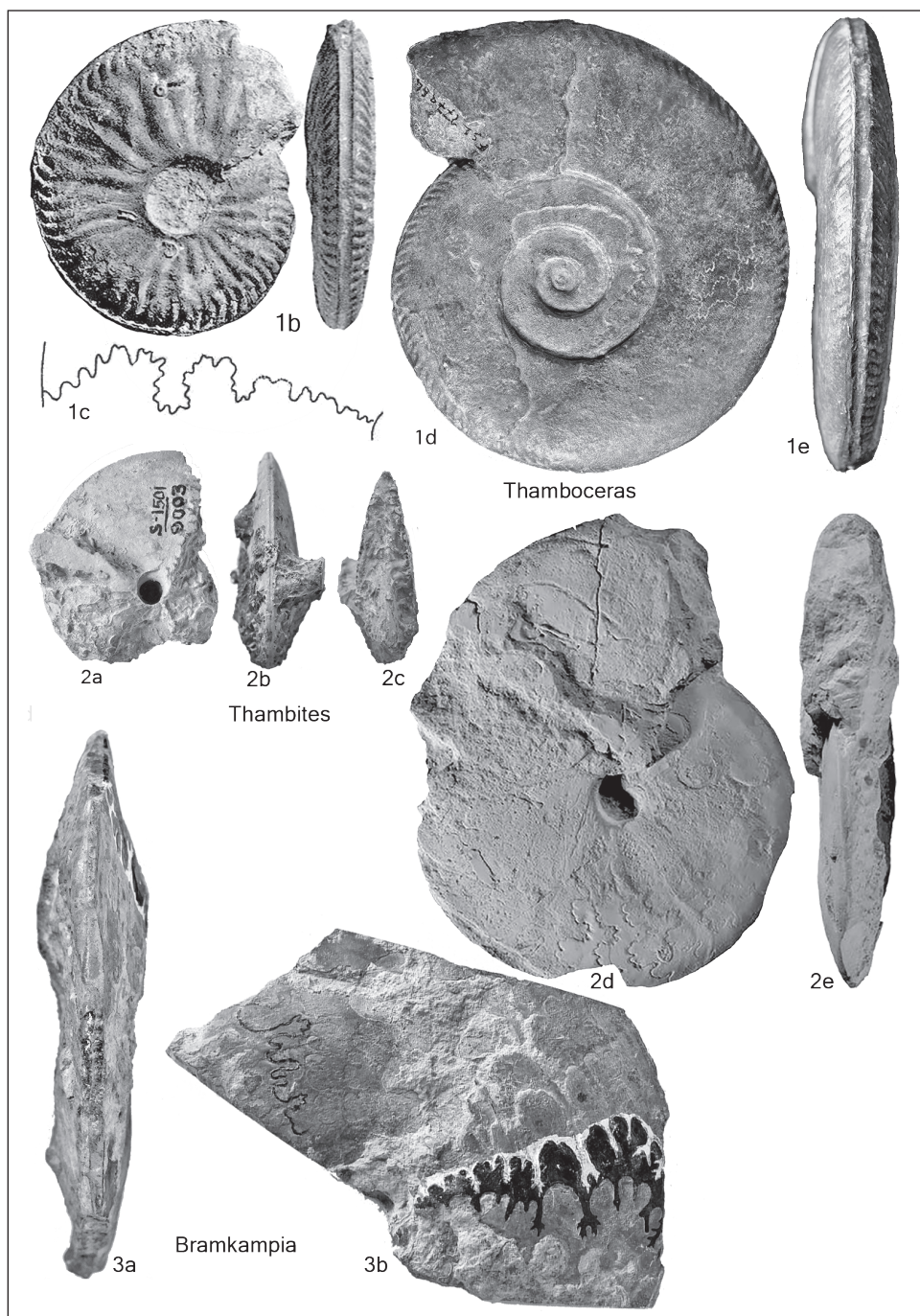


FIG. 38. Thamboceratidae.

Thamboceras mirabile ARKELL, smaller and less ribbed, may possibly be the microconch of *Thamboceras mirum* DOUVILLÉ, but this dimorphism has not been proved. Also, ÉNAY & others (2012) claimed that *Th. mirum* DOUVILLÉ was dimorphic. *Upper Bajocian*: France, Israel, Egypt, Saudi Arabia.—FIG. 38, 1a–c. **T. mirum* DOUVILLÉ, holotype, macroconch, *upper Bajocian*, Mogharensse Zone; 1a–b, lateral and ventral views; 1c, suture; Jebel Aroussieh, Moghara, Sinai, Egypt, $\times 1$ (DOUVILLÉ, 1916, pl. 2, 11, text-fig. 9, Lyon University Collection, UCBL EM 1808).—FIG. 38, 1d–e. **T. normannianum* ÉNAY & others, holotype, incomplete specimen of large size, *upper Bajocian*, Garantiana Zone, ferruginous Oolite of Bayeux, Verson, southwest of Caen, Calvados, France, $\times 0.5$ (ÉNAY & others, 2012, fig. 4, 1a–c; coll. Musitelli, cast in the Lyon University, FSL 177 964).

Thambites ARKELL, 1952a, p. 279 [**T. planus*; OD]. Large discoidal oxycones, involute shells with narrow umbilicus, compressed whorl section with concave, bicarinate venter; ribbing obsolete; sutures degenerate, with large prominent L, its side branch or branches sometimes being developed as an incipient adventitious lobe, the rest of the suture more-or-less reduced, as in *Thamboceras*. *Thambites* differs from *Thamboceras* in that the former has a larger, more prominent external lobe, lacks ribs, has a smaller umbilicus, and a narrower venter, on which two sharp keels are separated by a mere slit. Although the various specimens figured by ARKELL (1952a) differ substantially in size, dimorphism has not been demonstrated. *Uppermost Bajocian* (Parkinsoni Zone)—*middle Bathonian*: Egypt, Saudi Arabia, Oman (ÉNAY, 2011), Morocco, Algeria.—FIG. 38, 2a–e. **T. planus* ARKELL, *2a–c, holotype, ?macroconch, Juraifa area, locality 6, Saudi Arabia, $\times 1$ (new; also figured by ARKELL, 1952a, pl. 24, 6a–b; Sedgwick Museum, Cambridge, England, SM. F 10761); 2d–e, macroconch, nearly complete specimen

with a quarter whorl of body chamber, *Planus Zone* (equivalent to the Parkinsoni Zone), Mafrq Formation, north of the Haushi-Huqf Massif, Saudi Arabia, $\times 0.6$ (ÉNAY, 2011, fig. 7a1–a2; Lyon University Collection, FSL 162837).

Bramkampia ARKELL, 1952a, p. 282 [**B. steneikei*; OD]. Size unknown, but existing fragments indicate fairly large specimens; oxyconic, involute, periphery possibly acute and with bicarinate venter with a narrow central groove. The suture is the distinctive character, which is extremely degenerated with irregular lobes, digitate to candelabra shaped and extremely narrow relative to the wide and large saddles. Only three fragmentary specimens are currently known: the specimens figured by ARKELL, 1952a, including holotype of the type species, and the specimen described and figured by DOUVILLÉ (1916, p. 40, pl. 6, fig. 1) as “*Oxynoticeras*” *orientale*. According to GILL & others (1985), these three fragments could belong to the same species. *Upper Bajocian*: Saudi Arabia.—FIG. 38, 3a–b. **B. steneikei* ARKELL, holotype, macroconch, *uppermost-upper Bajocian*, base of the Middle Dhruma Formation near Juraifa, locality 8, Saudi Arabia, $\times 0.8$ (new; also figured by ARKELL, 1952a, pl. 23, 9–10; Sedgwick Museum of Earth Sciences, University of Cambridge, England, SM. F 10754).

Family CLYDONICERATIDAE Buckman, 1924

[BUCKMAN, 1924, p. 32
(see ARKELL, 1952a, p. 282)]

Specimens are of variable size, involute or semi-involute, oxycones, carinate on inner whorls, a rounded venter may appear in adult stages. Falcoid ribs are usually well-marked on inner and middle whorls, can fade on outer whorls, which become smooth. Sutures are highly variable, but are reduced, simplified, and degenerate with little, deep lobes and wide and low saddles resembling

those of the specialized bouleiceratins of the Toarcian. Dimorphism is confirmed in some genera, as in the dimorphic partners

Clydoniceras [M] and *Delecticeras* [m] (PAGE, 1996; FERNÁNDEZ-LÓPEZ, 2001; THIERRY, 2003). Microconchs are smaller in size, more

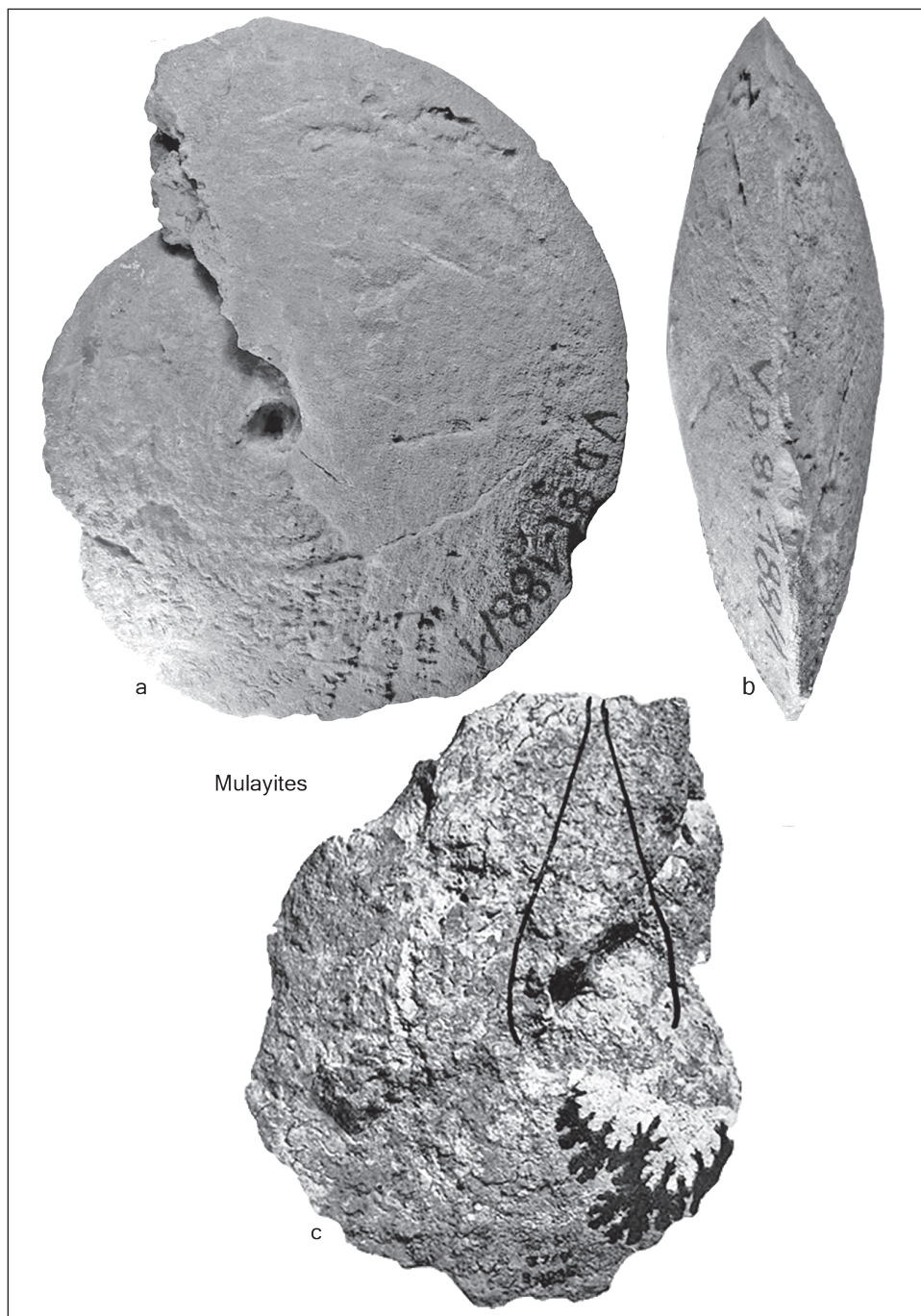


FIG. 39. *Clydoniceratidae* 1.

evolute, and more strongly ornamented, but apertural modifications, such as lateral lappets and ventral rostrums, are unknown. The origin of the Clydoniceratidae remains unclear. ARKELL (1957, p. 290) proposed that Clydoniceratidae are derived from *Thambites* in late Bajocian. The evolutionary process of Thamboceratidae to Clydoniceratidae involves the replacement of the flat ventral groove by a carinate venter through the fusion of the two “keels,” sometimes with incipient lateral sulci and minor modifications in the suture. *Middle Jurassic (upper Bajocian–lower Callovian–?middle Callovian)*: Bulgaria, England, France, Germany, Poland, Romania, Russia, Slovakia, Spain, Switzerland, Uzbekistan, Turkmenistan, Algeria, Morocco, Iran, Pakistan, India, Tibet, Israel, Jordan, Egypt, Saudi Arabia, Oman, Kenya, Somalia, Tanzania, Madagascar.

Mulayites ÉNAY & MANGOLD, 2021, p. 60 [**Thambites avus* ARKELL, 1952a, p. 281; OD] [= *Reboulliceras* BRANGER in VADET & others, 2011, p. 23], *nom. nud.* and invalid under ICZN Code, 1999, Article 16.4]. Similar to the thamboceratid *Thambites*, but whorl section less compressed and with a sharply acute keeled venter. Large oxycones, involute with an uncoiling body chamber, and narrow and deep umbilicus; high lanceolate or sub-triangular, compressed whorl section, with vertical umbilical wall and rounded umbilical rim; flanks slightly rounded, reaching their maximum thickness towards the inner quarter of the whorl sides; near the ventral area, the flanks joining to form a sharp and acute venter. Inner whorls with weak, distant, radial, simple ribs fading before the venter; middle and outer whorls smooth. Sutures simple, but with lobes and saddles well indented, E deep, E-L and L-U₂ saddles broad and divided by auxiliary lobes, L trifold and not very deep in the holotype. All specimens so far known appear to be macroconchs. *Middle Jurassic (upper Bajocian, Parkinsoni Zone)*: Morocco, Algeria, Saudi Arabia.—FIG. 39, *a–c*. *M.*

avus (ARKELL); *a–b*, nearly complete and fully-grown specimen, with half a whorl body of chamber, *uppermost Bajocian*, Planus Zone, Dhurma Formation, D3 Unit, south of Khashm Abu al Jiwar, Saudi Arabia, ×0.26 (ÉNAY & MANGOLD, 2021, pl. 20, *2a–b*; Lyon University Collection, UCBL-FSL 177 453); **c*, holotype, macroconch, lateral view and cross section, *uppermost Bajocian*, Planus Zone, Khashm adh Dhibi, Saudi Arabia, ×0.8 (ARKELL, 1952a, pl. 24, 7; Sedgwick Museum of Earth Sciences, University of Cambridge, England, SM F.10762).

Clydoniceras BLAKE, 1905, p. 58 [**Ammonites discus* J. SOWERBY, 1813, p. 37; OD] [= *Harpoceratidarum* POMPECKJ, 1906, p. 260 (type, *Ammonites discus* J. SOWERBY in OPPEL 1862 in 1862–1863, p. 146, pl. 47, fig. 1; SD ARKELL, 1951a, p. 32; = *Benedictites* BUCKMAN, 1924, pl. 523 (type, *Ammonites hochstetteri* OPPEL, 1857 in 1856–1858, p. 473; OD); = *Delecticeras* ARKELL, 1951a, p. 32 (type, *D. delectum* ARKELL; OD)]. Macroconchs (*Clydoniceras*) medium-sized, involute with small to minute or occluded umbilicus, except in the last whorl; whorl section varying from almost trapezoidal, carinate with two flat bands bordering the keel, on inner and middle whorls, to typically lanceolate on the body chamber. Inner whorls with dense, thin, gently falcoid ribbing divided at the umbilical edge; outer whorls may become smooth. Microconchs (*Delecticeras*) much smaller and more evolute, with trapezoidal or subrectangular whorl section through ontogeny, venter with keel bordered by small flat bands; fine, but well-marked falcoid ribs persist to end of body chamber. Suture degenerate with shallow lobes and saddles very wide and low. *Middle Jurassic (middle–upper Bathonian)*: England, France, Germany, Poland, Bulgaria, Romania, Spain, Switzerland, Uzbekistan, Turkmenistan, Iran, Pakistan, India, Morocco, Madagascar.—FIG. 40, *1a–d*. **C. discus* (J. SOWERBY); *1a–b*, holotype, macroconch, *upper Bathonian*, Discus Zone, Bedford, England, ×0.8

(ARKELL, 1951a, pl. 2, 2a–c; also figured in SCHLEGELMILCH, 1985, pl. 20, 4; BM 43942); 1c, macroconch, *upper Bathonian*, Discus Zone, Aargau, Switzerland, $\times 1$ (new;

original figure in OPPEL, 1862, pl. 47, 1a–b; Bayerische Staatsammlung für Paläontologie und Historische Geologie, Munich, AS VIII 23).—FIG. 40, 1d–e, **C. delectum*

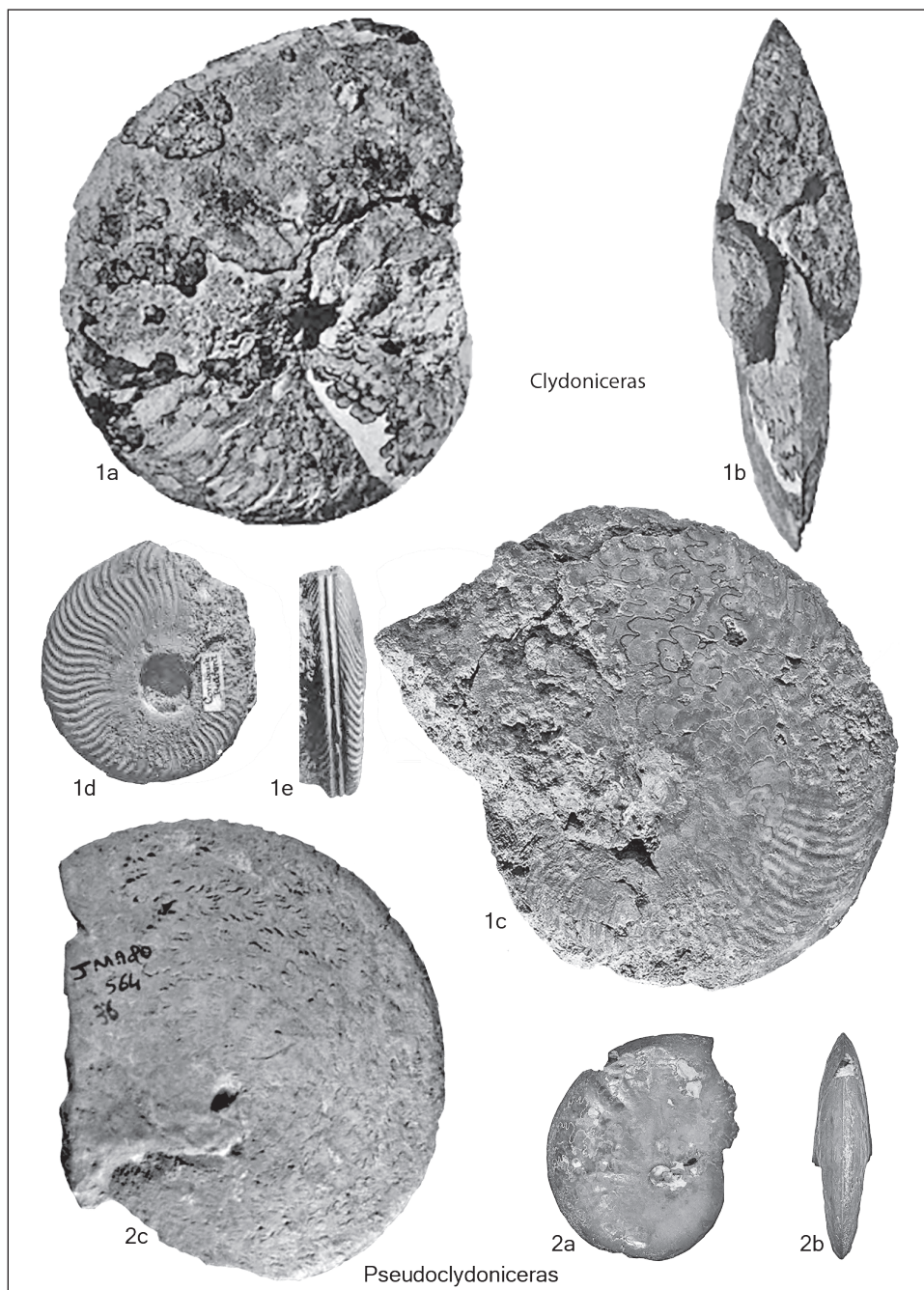


FIG. 40. Clydoniceratidae 2.

(ARKELL), holotype, microconch, *upper Bathonian*, Retrocostatum Zone, Cornbrash, Bedford, England, $\times 1$ (ARKELL 1951a, pl. 4, 12; British Geological Society, inventory no. BGS GSM 62626).

Pseudoclydoniceras COLLIGNON, 1958, pl. 25, fig. 102. [**P. besairiei*; OD] [=? *Nubidites* WIEDMANN & KULLMANN, 1979, p. 249 (type, *N. omarai*; OD); = *Levanticeras* LEWY, 1981, p. 42, *nom. nud.* and invalid under ICZN Code, 1999, Article 13.1.1); = *Levanticeras* LEWY, 1983, p. 21, preoccupied name (type, *L. levantinense* LEWY, 1983, p. 21, pl. 2, fig. 1, 3; OD)]. Medium-sized oxycones, very involute with almost punctiform umbilicus; whorl section subtriangular, compressed with acutely keeled venter; smooth, or with more-or-less obtuse ribs with irregular divisions, stronger on the upper part of the whorl and fading progressively towards the body chamber. Suture simplified with short and relatively narrow L, hardly ramified umbilical lobes, broad saddles, with the first two cut by a deep entry and the following one simple; U_1 not divided; all sutural elements radially arranged. Dimorphism unknown. WRIGHT & others (1996, p. 206) included *Nubidites* WIEDMANN & KULLMANN, 1979, in the Upper Cretaceous family Sphenodiscidae HYATT, 1900. However, according to LEWY (1983), *Nubidites* could be synonymous with *Levanticeras* LEWY, 1983, and CARIOU & others (1989, p. 684) showed that *Levanticeras* is synonymous with *Pseudoclydoniceras* COLLIGNON, 1958. Therefore, it can be concluded that *Nubidites* is a Middle Jurassic rather than an Upper Cretaceous ammonite and is synonymous with *Pseudoclydoniceras*. *Middle Jurassic*, *uppermost Bajocian* (Parkinsoni Zone)—? *upper Callovian* (Athleta Zone): France, Egypt, Saudi Arabia, Madagascar.—FIG. 40, 2a–b. **P. besairiei* (COLLIGNON), holotype, ?macroconch, *lower Callovian*, Gracilis Zone, Patina Subzone, Besavoa, Betioky, Madagascar, $\times 1$ (new; also

figured by COLLIGNON, 1958, pl. 25, 108; Université de Bourgogne, Dijon, France, UBGD 010102).—FIG. 40, 2c. *P. pseudodiscus* (ARKELL), macroconch, medium-sized specimen, *uppermost Bajocian*, Planus Zone, Dhurma Formation, Khashm Munayifiyah, Saudi Arabia, $\times 0.6$ (ÉNAY & MANGOLD, 2021, pl. 22, 4; Lyon University Collection, UCBL-FSL 177 629).

Micromphalites BUCKMAN, 1923, pl. 453 [**Ammonites micromphalum* PHILLIPS, 1871, p. 177; SD ARKELL, 1951a, p. 46] [= *Neactinoceras* SPATH, 1924, (obj.); = *Jordaniceras* BANDEL & ZEISS, 1987, p. 518 (type, *Micromphalites* (*J.*) *jordanicum*; OD)]. Medium-sized, involute with narrow umbilicus, vertical-walled cylindrical umbilicus surrounded by a bulge, which occupies approximately from the inner third to half of the whorl sides; venter square-shouldered, with persistent tall keel; wide, blunt ribs, bifurcating near the umbilical edge, tending in some species to tuberculation both on the umbilical edge as well as on the ventrolateral edge, where they bend forward near the keel. Suture with narrow L and broad U_2 on the earlier whorls, but the first laterals broadening on later whorls until the suture resembles that of *Clydoniceras*. Although specimens of varying sizes and morphologies have been described and figured, no clear dimorphism has been shown in this genus. According to ÉNAY & others (2001, p. 507) and ÉNAY & MANGOLD (2021, p. 68), the proposal of *Jordaniceras* by BANDEL & ZEISS (1987), based on a single specimen, is not justified. Considering the great similarity with *Micromphalites* and the stratigraphic position of both, *Jordaniceras* is here included in this genus. *Lower Bathonian*: France, England, Spain, Slovakia, ?Uzbekistan, ?Pakistan, India, Egypt (Sinai), Jordan, Saudi Arabia, Oman, Morocco, Madagascar.—FIG. 41, 1a–b. **M. micromphalus* (PHILLIPS), lectotype, macroconch, *Bathonian*, Stonesfield, Oxfordshire, England, $\times 1$ (new; also figured by ARKELL, 1951a, pl. 4, 4; J.01117).

Clydomphalites ARKELL, 1952a, p. 286 [**Micromphalites clydocromphalus*; OD]. Medium size, discoidal, compressed, similar to *Micromphalites*, but more involute with minute umbilicus, which suddenly opens outward on the last whorl and without circum-umbilical bulge or nodes. *Clydomphalites* is between *Clydoniceras* and

Micromphalites in form and resembles *Clydoniceras*, but the suture has a narrow L and a very wide saddle L-U₂, and ribs and keel are similar to those of *Micromphalites*. In agreement with ÉNAY & MANGOLD's (2021, p. 62) conclusion, *Clydomphalites* should be included in *Micromphalites*, but differences in ornamentation (ribbing and tubercles)

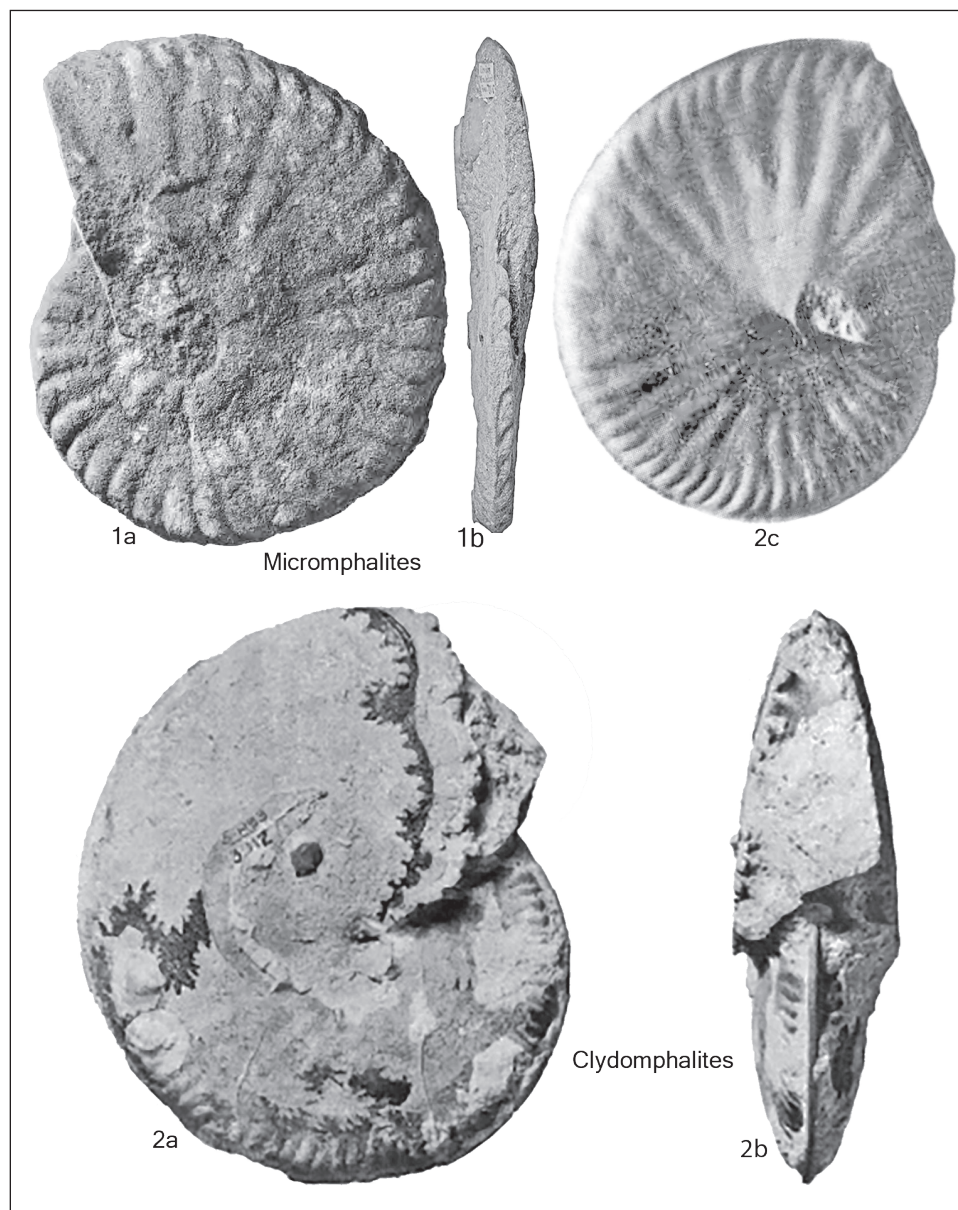


FIG. 41. Clydoniceratidae 3.

are significant, so it is preferable to keep this genus. *Middle Jurassic* (lower-middle *Bathonian*): England, France, Morocco, Algeria, Saudi Arabia, India (JAIN 2014).—FIG. 41, 2a–c. **C. clydocromphalus* (ARKELL);

2a–b, holotype, macroconch, lower *Bathonian*, Zigzag Zone (see ÉNAY & MANGOLD, 2021, p. 25), Dhurma Formation, the red clay near Juraifa, locality 16, Saudi Arabia, ×1 (new; also figured by ARKELL, 1952a,

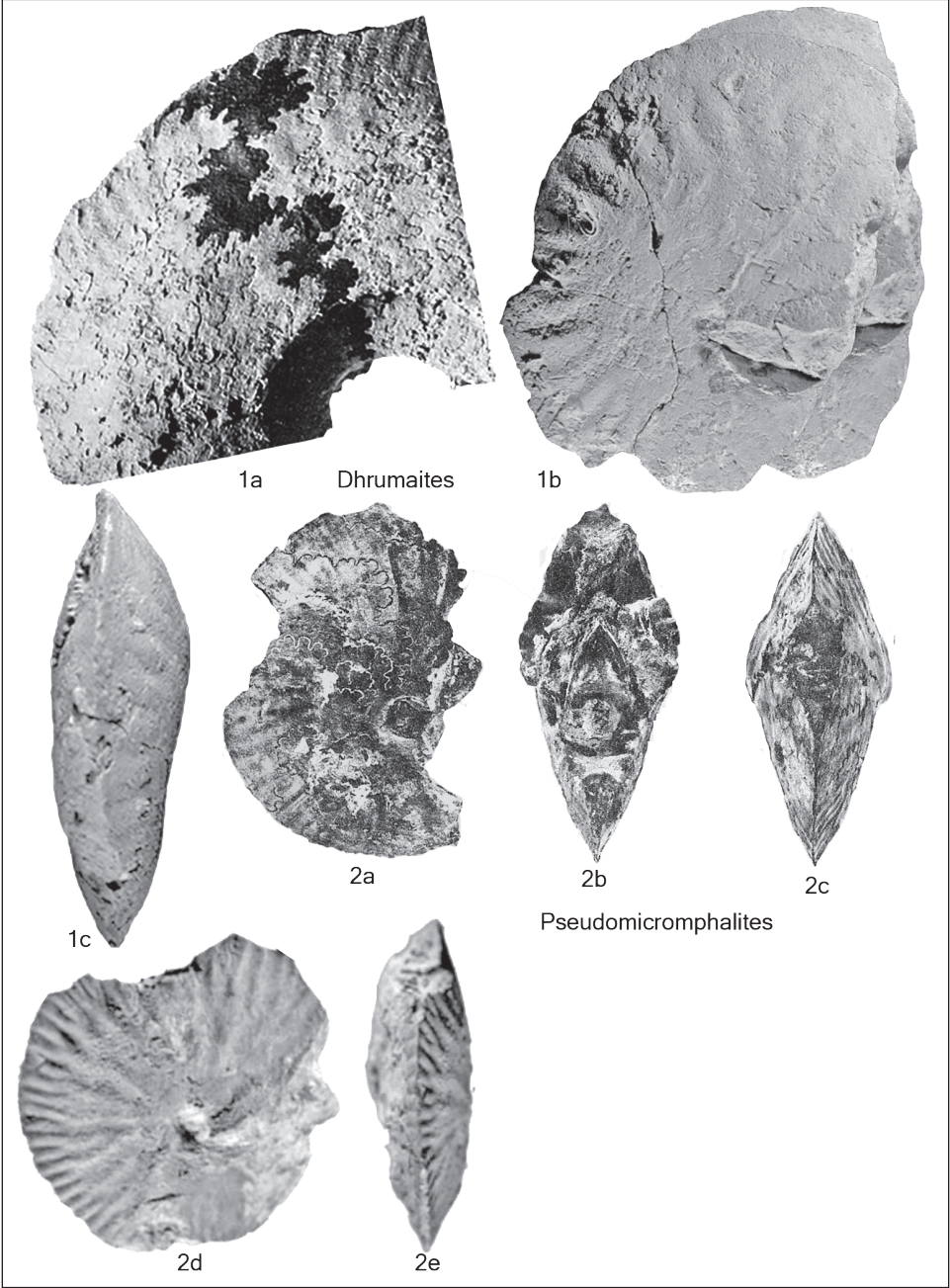


FIG. 42. Clydoniceratidae 4.

pl. 26, 2a–c; Sedgwick Museum of Earth Sciences, University of Cambridge, England, SM. F.10773); 2c, almost complete specimen, *lower Bathonian*, west of Limon (la Métairie), France, $\times 1$ (ÉNAY & others, 2001, pl. 1, 1b; Coll. Trevisan, cast in the Lyon University, FSL 175 861).

Dhrumaites ARKELL, 1952a, p. 288 [**D. cardioceratoides*; OD]. Very large-sized oxyconic shells, but with no full adult specimens being known; involute with narrow umbilicus, lanceolate whorl section with maximum thickness at mid-flank height, vertical umbilical wall that rounds rather abruptly into the flanks; these slightly convex, ending in a sharp venter with keel; inner part of the flanks smooth and the outer part with faint, broad, gently flexuous ribs. Suture with a broad E-L saddle, an irregular broad L, and a bifid U_2 ; the first and second lateral saddles becoming lower and broader during growth. All specimens hitherto recorded are large-sized, and therefore dimorphism is unknown. *Middle Jurassic* (?upper-middle Bathonian–upper Bathonian): Saudi Arabia, Madagascar.—FIG. 42, 1a–c. *D. cardioceratoides* ARKELL; *1a, holotype, macroconch, fragment of a wholly septate specimen, *middle* or, more probably, *upper Bathonian*, *Cardioceratoides Zone*, Dhruma area, locality 42, Saudi Arabia, $\times 0.3$ (ARKELL, 1952a, pl. 25, 8; Sedgwick Museum of Earth Sciences, University of Cambridge, England, SM. F.10771); 1b–c, macroconch, *middle* or, more probably, *upper Bathonian*, *Cardioceratoides Zone*; Dhruma Formation, D6 unit, *Darmā' Quadrangle*: JMA82.320, Wadi al Jufayr, Saudi Arabia, $\times 0.5$ (ÉNAY & MANGOLD, 2021, pl. 26, 1a–c; Lyon University Collection, UCBL-FSL 177 242).

Pseudomicromphalites COLLIGNON, 1966, p. 22 [**P. kuntzi*; OD]. Medium-sized; deep umbilicus with a rounded umbilical edge; whorl section semi-ogival or lanceolate, with flat flanks convergent to a sharp keel on the venter; ribs are weakly convex forwards,

arising in pairs from very weak tubercles at the umbilical edge and divide high on the side of the whorl into prorsiradial secondary ribs that end at the sharp venter; suture simple, resembling that of *Micromphalites*, but L situated near mid-flank. Although the Collignon collection is held in the museum of the University of Burgundy (France), the holotype of the type species has not been located. Dimorphism is not known. *Middle Jurassic* (lower-middle Callovian): Saudi Arabia, Madagascar.—FIG. 42, 2a–e. *P. kuntzi* (COLLIGNON); *2a–c, holotype, ?macroconch, *lower Callovian*, *Gracilis Zone*, level of *Pseudoclydoniceras besairiei*, Malakialiu, Marovoay, Madagascar, $\times 1.5$ (COLLIGNON, 1966, pl. 7, 2–2b); poor-quality photograph because the type specimen has not been located; 2d–e, well-preserved, wholly septate specimen, *middle Callovian*, *Ogivalis Zone*, Kuntzi horizon, Upper Dhruma Formation, unit D7, upper part (Hisyan Member), *Shaqra' Quadrangle*, Al Jurayfah, Central Saudi Arabia, $\times 1$ (ÉNAY & MANGOLD, 2021, pl. 25, 6a–b; Lyon University Collection, UCBL-FSL 177 187).

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Prof. José Sandoval obtained his BSc in Geological Sciences from Granada University (UGR), Spain. He was a recipient of a National Research Personnel Plan grant in Spain to investigate ammonites and Middle Jurassic biostratigraphy.

He received his PhD at the UGR on Middle Jurassic ammonite taxonomy and biostratigraphy from Southern Spain. Then, José completed a Postdoctoral Fellowship at McMaster University, Hamilton, Ontario (1984–1985), supported by an NSERC Postdoctoral Fellowship (Canada) and researching paleobiology and biostratigraphy of Middle Jurassic ammonites from Southern Mexico.

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Dr. Michael Kingsley Howarth was a British paleontologist born in the early 1930's and was a highly accomplished expert on ammonites. He did his undergraduate work at Manchester University and received his doctorate from the University of Cambridge in 1956. He collected and published on ammonites from around the globe and produced numerous important monographs as well as systematic and stratigraphic publications. He worked in the fossil cephalopod department at The Natural History Museum, London from 1980 to 1992. He further played a key role as coordinating author in producing the Revised Volume L3 on Jurassic ammonites which this paper is a part of. Dr. Howarth passed away suddenly in 2024. This publication stands as a testament to his dedicated research.