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Labyrinthoceras and Frogdenites (Sphaeroceratidae, Ammonitina) from Western Tethys: The origin of the Sphaeroceratidae^{\star}

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ARTICLE INFO

Article history: Received 22 July 2014 Accepted 21 November 2014 Available online 27 November 2014

Keywords: Sphaeroceratidae Systematics Middle Jurassic Southern Spain Southern England Western Tethys

ABSTRACT

A biostratigraphical and systematic revision of the genera Labyrinthoceras and Frogdenites is presented, based mostly on new specimens from the Lower Bajocian of the Betic Cordillera (Southern Spain). Types and other supporting specimens are described, including some from southwestern England with precise biostratigraphy. Frogdenites is shown to span the Lower Bajocian (Ovale Zone to lowermost part of the Propinquans Zone), whereas Labyrinthoceras ranges from the Laeviuscula Zone (Trigonalis Subzone) to the Propinguans Zone. Both genera show well-marked dimorphism; the microconchs may have reduced lateral lappets. Labyrinthoceras meniscum (Waagen) [M] & [m] = Manselites mansellii (J. Buckman) is described along with specimens that are placed in the new species Labyrinthoceras dietzei nov. sp. [M]. Frogdenites is grouped into three morphospecies: Frogdenites fernandezlopezi nov. sp. [M] & [m?], an evolute morph with poorly developed tubercles; F. spiniger Buckman [M] & [m], which is more involute with strongly forward curving projecting ribs; and F. extensus (Buckman) [M] & [m] with a more eccentric coiling. Docidoceras tolleyi nov. sp., which possesses a morphology intermediate between Docidoceras and Frogdenites, is described. Phylogenetic analysis shows that the Sphaeroceratidae originated in the Earliest Bajocian (Ovale Zone) and that Frogdenites is the oldest genus of this lineage. Docidoceras rather than Emileia may be the ancestor of the Sphaeroceratidae. The evolutionary path from Frogdenites to Labyrinthoceras, with "Chondroceras obornensis" Parsons, 1980 (unpubl. manuscript), as an intermediate step, involves size increase and disappearance of tubercles.

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1. Introduction

Labyrinthoceras Buckman, 1919 and Frogdenites Buckman, 1921 are ammonite genera of great systematic significance. They may represent transitional forms between the Otoitidae and Sphaeroceratidae (Galácz, 1990), two ammonite families of great biostratigraphical and palaeobiogeographical interest for the uppermost Aalenian–Bajocian interval in the Tethyan and Eastern Pacific realms. References to biostratigraphy and taxonomy of the genera *Labyrinthoceras* and *Frogdenites* from the Western Tethys are relatively common in the literature (e.g., d'Orbigny, 1842–49; Waagen, 1867; Buckman, 1881, 1882, 1909–1930; Maubeuge, 1951; Westermann, 1964; Parsons, 1974, 1976, 1977, 1979, 1980; Galácz, 1982, 1990, 2001; Pavia, 1983, 1994; Sandoval, 1983, 1990, 2013; Fernández-López, 1985; Fernández-López et al., 1988; Sadki,

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http://dx.doi.org/10.1016/j.geobios.2014.11.005 0016-6995/© 2014 Elsevier Masson SAS. All rights reserved. 1994, 1996; Sandoval et al., 2001; Galácz and Kovács, 2013). Outside the Western Tethyan palaeogeographical domain, *Labyr-inthoceras* occurs in Alaska (Imlay, 1964; Westermann, 1993) and possibly also in New Guinea (Westermann, 1995; Westermann and Getty, 1970). *Frogdenites* has not hitherto been cited outside Western Tethys where records are scarce (Galácz, 2001). In the references cited above, several specimens of *Labyrinthoceras* and *Frogdenites* were figured, including the types (holotype or lectotype) of all the species so far erected.

Galácz (1990) carried out a detailed analysis of the genus *Labyrinthoceras* (taxonomy, stratigraphical and geographical distribution, dimorphism, phylogeny, etc.) based on the relatively abundant and well sampled Hungarian material alongside data from the literature, but unfortunately, no specimens were figured. In a detailed study based mainly on Hungarian specimens, Galácz (2001) considered *Frogdenites* to include the earliest Sphaeroceratidae and demonstrated the existence of a subtle dimorphism. Galácz and Kovács (2013) figured the dimorphic pair *L. meniscum* [M] and *L. manselii* [m] from the Bakony Mountains (Hungary). The present paper aims to improve the state of knowledge regarding

the systematics and phylogeny of the genera *Labyrinthoceras* and *Frogdenites* within the family Sphaeroceratidae. In addition to previously published accounts, we describe new material recently collected in the Subbetic domain (Betic Cordillera, Southern Spain) and in southern England (Dorset and Somerset).

2. Localities and abbreviations

With the exception of one specimen of *Labyrinthoceras meniscum* (CM9.1) from Majorca Island, all the Spanish ammonites studied here come from the Subbetic basin of the southern part of the External Zones of the Betic Cordillera (Southern Spain). Localities and stratigraphic sections have been abbreviated to a letter-number code (from west to east):

- Ga9, Arroyo de la Losilla, Sierra de Gaena, Rute, province of Córdoba;
- C4 and BaGa7, Cañada del Hornillo and Puerto Escaño, Sierra de Gaena, Carcabuey, province of Córdoba;
- JVM, La Morenica, Valdepeñas de Jaén, province of Jaén;
- JAC3, JAC3', JAC6, JAC11, JAC20, JAC21 and JAC22, sections of sierra de Alta Coloma area, Campillo de Arenas and Noalejo, province of Jaén;
- JAQ1 (Barranco de Agua Larga), Noalejo, province of Jaén;
- FA and LGb, Rio Fardes, Gorafe, province of Granada;
- SHN, Sierra Hondón de las Nieves, Province of Alicante.

Most of these sections consist of well-bedded, regular alternations of hemipelagic grey-cream marly limestones and marls. Others sections at some intervals have horizons consisting of nodular limestone, or limestones with chert nodules. Ammonites (Sonninidae, Stephanoceratidae, Strigoceratidae, Haploceratidae, etc.) are abundant. The detailed bed-by-bed collecting from many of these sections has facilitated the construction of a very detailed biostratigraphical scheme (Sandoval, 1983, 1990; Hernández-Molina et al., 1991; Jiménez et al., 1999; Sandoval et al., 1999, etc.).

The British specimens have their locations given in full along with abbreviated faunal horizon codes (Callomon and Chandler, 1990; updated Chandler et al., 2013). The ammonite faunal horizons are for the Inferior Oolite (part of the Bajocian Stage only) of Dorset and Somerset, UK. The labelling of some horizons with additional letters (a, b, c) reflects the insertion of further horizons after Callomon and Chandler (1990) but does not denote any reduction of rank or importance. Institution codes for the deposition of specimens are as follows: NHMUK, Natural History Museum; BGS, British Geological Survey; WC, Wessex Cephalopod Club. The British Geological Survey (Keyworth, UK) was previously resident at the Geological Survey Museum, London; early specimens in the collection therefore have the prefix GSM.

Regarding measurements the following parameters are used: *D*, diameter of the shell (mm); *H*, whorl-section height of the shell (mm); *U*, umbilical diameter of the shell (mm); *W*, whorl-section width of the shell (mm); h = H/D, u = U/D, and w = W/D. Ph and BC refers to phragmocone and body-chamber respectively; [M] and [m] refer to macroconchs and microconchs respectively. The Propinquans Zone replaces the Sauzei Zone of earlier authors (Rioult et al., 1997: p. 47).

3. Systematic palaeontology

Order AMMONOIDEA Zittel, 1884 Suborder AMMONITINA Hyatt, 1889 Superfamily STEPHANOCERATOIDEA Neumayr, 1875 Family SPHAEROCERATIDAE Buckman, 1920 Genus *Labyrinthoceras* Buckman, 1919 1990. *Manselites* – Galácz, p. 345.

Type species: by original designation, *Labyrinthoceras perexpansum* (Buckman, 1919: T.A. III, pl. 134) for *Sphaeroceras perexpansum* Buckman, 1882 = subjective *syn. Labyrinthoceras meniscum* (Waagen, 1867); lectotype designed by Gauthier and Rioult in Fischer (1994: p. 128, pl. 40, figs. 3a–c, pl. 41, fig. 1).

Diagnosis: The genus includes relatively large Sphaeroceratidae, with ovate-broad and depressed whorls, a contracted bodychamber and a narrow and deep umbilicus. The ribs are very fine and dense, they divide at two-thirds flank height and there are no spines or tubercles at the point of division. Dimorphism is wellmarked by size difference. Microconchs have modified apertures with a depressed, broad rim and mid-lateral projections at the peristome; some specimens possess small lateral lappets that narrow orally. The mouth borders of macroconchs have a deep constriction followed by an expanded smooth lip.

Remarks: Since Buckman (1919) erected the genus *Labyr-inthoceras*, different authors have included in the genus the following species:

- *L. meniscum* (Waagen, 1867, pp. 602–603) = *Ammonites gervillii* (d'Orbigny non Sow. 1842–51: pl. 140, figs. 1, 2, non 3–8);
- *L. manselii* (J. Buckman, 1881), holotype in Buckman (1882: pl. II, fig. 3), refigured by Parsons (1980: text-fig. 6) and Galácz (1990: text-fig. 4);
- "Sphaeroceras" perexpansum Buckman (1882: p. 142, pl. 2, fig. 4a,b), holotype refigured in Buckman (1919: T.A. III, pls. 134A, 134B);
- *L. intricatum* Buckman (1919: T. A. III, pl. 135, holotype, and pl. 135A, paratype);
- L. extensum Buckman (1921: T. A. III, Pl. 214, figs. 1, 2, holotype);
- L. gibberulum Buckman (1922: T. A. IV, Pl. 278, holotype);
- L. amphilaphes Buckman (1922: T. A. IV, pl. 279, holotype);
- *L. glabrum* Imlay (1964: p. 41, pl. 9, figs. 1–3, pl. 10, figs. 1–7, 4, 5, holotype).

Besides these species, *Labyrinthoceras* sp. 1 in Sandoval (1983: p. 205, pl. 4, fig. 2), *Labyrinthoceras* (n. subg.) n. sp. in Sandoval (1983: p. 206, pl. 3., fig. 4), and *Labyrinthoceras* nov. sp. 1 in Fernández-López (1985: p. 371, pl. 40., fig. 2) were also described in open nomenclature. "*Sphaeroceras gervillii*" in Maubeuge (1951: pl. 12, fig. 5a–c) and "*Otoites" filicostatus* Imlay (holotype in Imlay, 1964: pl. 10, figs. 9, 10) also add to the record. According to Galácz (1990), the former is a *Labyrinthoceras* and "*O." filicostatus* may be the microconch of *L. glabrum* Imlay (Sandoval, 1983) and should also be included in the genus *Labyrinthoceras*. According to Westermann (1995), *Bullatimorphites? (Trectoceras?) costidensus* Westermann and Getty (1970: p. 262, pl. 55, figs. 1–4) and *Bullatimorphites?* (*Trectoceras?*) n. sp. A (Westermann and Getty, 1970: p. 26, pl. 55, figs. 1–4) from New Guinea are dimorphic partners typical of *Labyrinthoceras*.

Some of these "species" have subsequently been excluded from *Labyrinthoceras* (Westermann, 1964; Parsons, 1977, 1979, 1980; Fernández-López, 1985; Galácz, 1990, 2001; Galácz and Kovács, 2013). In agreement with Parsons (1979) and Galácz (2001), "*L*." *extensum* Buckman is a *Frogdenites*. "*L*." *gibberulum* Buckman has also been included in the genus *Frogdenites* (Parsons, 1977, 1979, 1980; Fernández-López, 1985; Galácz, 1990, 2001). Parsons (1980) considers the type of "*L*." *manselii* (J. Buckman) as a *Sphaeroceras*; however Galácz (1990) and Galácz and Kovács (2013) consider this microconch to represent the dimorphic partner of *L. meniscum*. According to Parsons (1980), *L. meniscum* (Waagen) and *L. amphilaphes* Buckman, 1922 are the only valid Tethyan species. He considers *L. perexpansum* (Buckman) and *L. intricatum* Buckman to be synonyms of *L. meniscum* (Waagen). For Sandoval (1983), Fernández-López (1985) and Galácz (1990), *L. meniscum*

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