geodiversitas

2022 • 44 • 27

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art. 44 (27) — Published on 15 September 2022
www.geodiversitas.com

PUBLICATIONS SCIENTIFIQUES
MUSÉUM NATIONAL D'HISTOIRE NATURELLE

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Geodiversitas *is a fast track journal published by the Museum Science Press, Paris*

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 1280-9659/ ISSN (électronique / *electronic*) : 1638-9395

Sonniniidae (Ammonitina, Middle Jurassic) from Southern Spain: taxonomic, biostratigraphical and palaeobiogeographical analysis

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Submitted on 7 November 2021 | accepted on 11 January 2022 | published on 15 September 2022

urn:lsid:zoobank.org:pub:E4896081-9312-4EA6-AE33-AAC44201748E

Sandoval J. 2022. — Sonniniidae (Ammonitina, Middle Jurassic) from Southern Spain: taxonomic, biostratigraphical and palaeobiogeographical analysis. *Geodiversitas* 44 (27): 801-851. https://doi.org/10.5252/geodiversitas2022v44a27. http://geodiversitas.com/44/27

ABSTRACT
A taxonomic and biostratigraphical revision of the sonniniids is presented using bibliographic data and mainly the material collected in the Subbetic domain (Betic Cordillera, southern Spain). The Sonniniidae are shown to range from the uppermost Aalenian (Concavum Zone, Limitatum Subzone) to the Lower Bajocian (Humphriesianum Zone, Romani Subzone). Subbetic Sonniniidae are represented by the subfamilies: Sonniniinae, with the genera *Sonninia* and the subgenera *S.* (*Sonninia*), *S.* (*Euhoploceras*), *S.* (*Papilliceras*), and *Sonninites*; and Witchelliinae, with the genera *Witchellia* and *Dorsetensia*. The taxa *Sonninia* (*Alaskinia*), *Shirbuirnia,* and *Pseudoshirbuirnia* have not been recorded so far in the Subbetic domain. Taxonomical analyses indicate that the genus *Dorsetensia*, classically included in the Sonniniinae (Howarth 2013: *Treatise*), should be transferred to Witchelliinae, whereas the genera *Asthenoceras*, *Fontannesia,* and *Newmarracarroceras* (Witchelliinae in *Treatise*) appear to represent the latest Grammoceratinae instead of primitive Witchelliinae. Dimorphism and possible polymorphism are present in the Subbetic Sonniniidae. Of the 31 sonniniid morphospecies described, 22 are macroconchs and nine are microconchs. Two new species of *Witchellia* are nominated and described: *W. companyi* n. sp., evolute with wide and shallow umbilicus, rectangular compressed section and fine keel; and *W. striata* n. sp., relatively involute, shallow umbilicus, compressed rectangular section with a very shallow depression in the lower part of the flanks, fine falcate ribbing that fades, being replaced by bundles of striae in the body-chamber.

KEY WORDS
Ammonites,
Jurassic,
Bajocian,
Southern Spain,
biostratigraphy,
lectotypification,
new synonym,
new combinations,
new species.

RÉSUMÉ

Sonniniidae (Ammonitina, Jurassique moyen) du sud de l'Espagne: analyse taxonomique, biostratigraphique et paléobiogéographique.

L'objet de cette étude est la révision taxonomique et biostratigraphique des sonniniidés basée essentiellement sur le matériel collecté dans le Domaine Subbétique (Cordillère Bétique, sud de l'Espagne), et complétée par l'analyse des données bibliographiques. Il apparait que les Sonniniidae s'étendent de la partie supérieure de l'Aalénien supérieur (Zone à Concavum, Sous-zone à Limitatum) au Bajocien inférieur (Zone Humphriesianum, sous-zone Romani). Les Sonniniidae subbétiques sont représentés par les sous-familles: Sonniniinae, avec les genres *Sonninia,* sous-genres *S.* (*Sonninia*), *S.* (*Euhoploceras*), *S.* (*Papilliceras*) et *Sonninites* ; et Witchelliinae, avec les genres *Witchellia* et *Dorsetensia*. Jusqu'à présent *Sonninia* (*Alaskinia*), *Shirbuirnia* et *Pseudoshirbuirnia* n'ont pas été reconnus dans le Domaine Subbétique. L'analyse taxonomique suggère que le genre *Dorsetensia*, clasiquemment inclus dans les Sonniniinae (Howarth 2013: *Treatise*), devrait être transféré au sein des Witchelliinae, tandis que les genres *Asthenoceras*, *Fontannesia* et *Newmarracarroceras* ne sont pas des Witchelliinae primitifs (Howarth 2013: *Treatise*), mais représentent les derniers Grammoceratinae. Un dimorphisme et un polymorphisme potentiel sont reconnus chez les Sonniniidae subbétiques. Sur les 31 morphospèces de sonniniidés décrites, 22 sont des macroconches et neuf sont des microconques. Deux nouvelles espèces de *Witchellia* sont proposées et décrites : *W. companyi* n. sp. (forme évolute avec ombilic large et peu profond, section rectangulaire comprimée et carène fine) ; et *W. striata* n. sp. (espèce relativement involute avec ombilic peu profond, section rectangulaire comprimée, dont dépression très peu marquée sur partie inférieure des flancs. Sur loge d'habitation, côtes falciformes fines s'estompant et remplacées par faisceaux de stries).

MOTS CLÉS
Ammonites,
Jurassique,
Bajocien,
sud de l'Espagne,
biostratigraphie,
lectotypification,
synonyme nouveau,
combinaisons nouvelles,
espèces nouvelles.

INTRODUCTION

The study of Sonniniidae (Hildoceratoidea, Ammonitida) has been fundamental for biostratigraphic analyses of the uppermost Aalenian and Lower Bajocian. In this biostratigraphic interval, sonniniids constitute the prime fossil group for biostratigraphic (chronostratigraphic) dating and correlation purposes. Sonniniidae are common in many west Tethyan areas, including United Kingdom, Belgium, Luxembourg, France, Germany, Hungary, Poland, Bulgaria, the Caucasus, Italy, Spain (Betic Cordillera, Iberian ranges and Balearic Islands), Portugal, and Morocco, these being the origins of most of the species described so far (e.g. Sowerby 1824; Roemer 1836; d'Orbigny 1842-1851; Quenstedt 1856-1858, 1882-1888; Oppel 1862; Waagen 1867; Bayle 1878; Branco 1879; Douvillé 1879, 1885; Buckman 1887-1907, 1893, 1909-1930; Haug 1887, 1893; Brasil 1893, 1895; Borissjak 1908; Dorn 1935; Gillet 1937; Hiltermann 1939; Maubeuge 1948-1949, 1951, 1955; Oechsle 1958; Kopik 1967; Huf 1968; Morton 1972, 1973, 1975; Dietl & Haag 1980; Pavia 1983; Dietl *et al.* 1984; Fernández-López 1985; Schlegelmilch 1985; Ohmert 1988, 2004; Callomon & Chandler 1990, 1994; Cresta & Galácz 1990; Dietl 1990; Galácz 1991a, b; Fernández-López & Mouterde 1994; Contini 1994; Sadki 1994, 1996, 2015; Cresta *et al.* 1995; Ohmert *et al.* 1995; Dietze *et al.* 2003, 2005, 2006, 2007, 2008, 2009, 2010a, 2011a, b, 2012a, 2019, 2020; Myczynski 2004; Chandler *et al.* 2006, 2014; De Baets *et al.* 2008; Topchishvili & Lominadze 2012; Howarth 2013; Pavia *et al.* 2013; Metodiev & Tsvetkova 2014; Galácz *et al.* 2015; Sadki *et al.* 2015; Chandler 2019; Metodiev 2019). In some areas outside the Tethyan, especially in the western Pacific (western interior United States and Alaska, Canada, Argentina, Chile, Peru, etc.) sonniniids are also common (Gottsche 1878; Tornquist 1898; Jaworki 1926; Imlay 1964, 1973, 1984, 1986; Westermann 1964, 1969; Westermann & Riccardi 1972; Hall 1989; Taylor 1988, 2014; Poulton *et al.* 1992; Hillebrandt 2001; Dietze *et al.* 2010b, 2012b). Sonniniids have also been recorded in Iran (Seyed-Emami 1988; Seyed-Emami *et al.* 2000, 2004, 2005), Tibet (Arkell 1953; Westermann & Wang 1988; Énay & Mangold 1994), the Arabian Peninsula (Arkell 1952; Énay & Mangold 1994, 2021), Madagascar (Collignon 1958), Kenya (Spath 1933), New Guinea (Westermann & Getty 1970), Eastern Indonesia (Hasibuan 2012), and Western Australia (Arkell & Playford 1954; Hall 1989).

In the Subbetic domain (Betic Cordillera, S Spain), a typical Mediterranean domain, Sonniniidae are abundant and often relatively well preserved, making them apt for use as a basis for the biozonation of this stratigraphic interval (Sandoval 1979, 1983, 1990; Linares & Sandoval 1990; Hernández-Molina *et al.* 1991; Jiménez *et al.* 1999; Sandoval *et al.* 1999; Sandoval & Chandler 2000; Sandoval & O'Dogherty 2018; Aurell *et al.* 2002). Although the diverse genera and species of sonniniids have been essential for establishing of the Lower Bajocian biostratigraphy of this Western Mediterranean domain, most Subbetic sonniniids have not yet been studied from a palaeobiological approach, apart from Sandoval & Chandler (2000), who performed a palaeontological analysis of the genus *Euhoploceras* from south-western England and the Betic Cordillera.

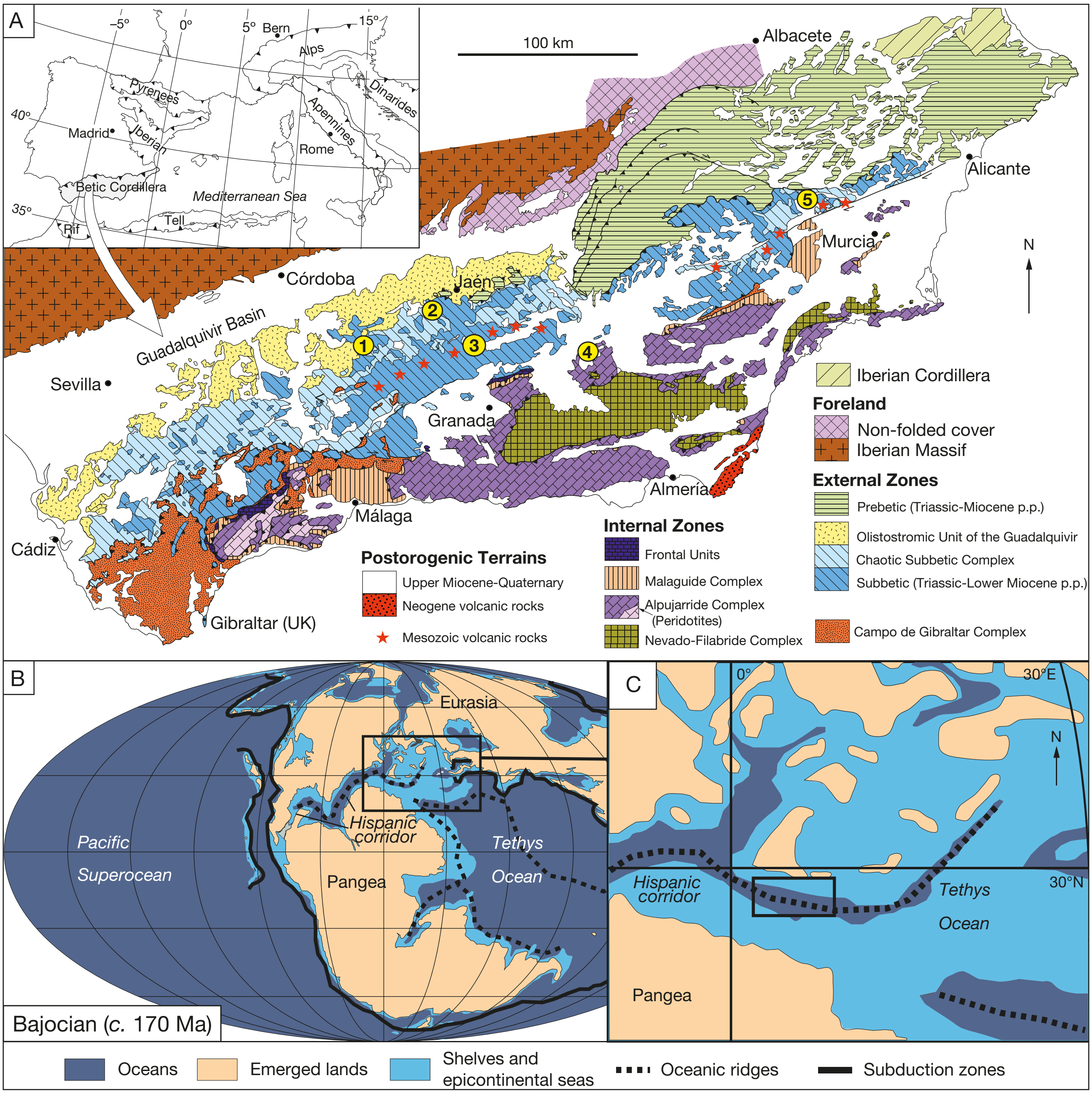


FIG. 1. — **A**, General sketch of the Betic Cordillera with approximate location of the study areas with the more significant sections containing sonniniids: **1**, Sierra de Gaena (sections JGa2 and JGa7), Córdoba Province; **2**, Alto de la Morenica (section JVM), Jaén Province; **3**, Sierra del Trigo-Sierra de Alta Coloma-Barranco de Agua Larga (JST, MOC, JAC3, JAC3', JAC4, JAC6, JAC11, JAC13; JAC20, JAC21, JAC22 and JAQ1 sections), Jaén Province; **4**, Rio Fardes (JFA and LGb sections), Granada Province; **5**, Sierra de Ricote (section JRi3), Murcia Province; **B**, global palaeogeographic map (Mollweide projection) showing the distribution of oceans and lands in the Early Bajocian (*c.* 170 Ma); **C**, focus on the Western Tethys-Central Atlantic showing the approximate location of the Subbetic basin (rectangle) in relation to the trans-Pangaean seaway. Modified after Aguado *et al.* 2017.

The present study aims to complete the taxonomical, biostratigraphic and biogeographical analysis of the uppermost Aalenian-Bajocian Sonniniidae (Ammonitida) of the Subbetic domain (Betic Cordillera, S Spain). This proposal encompasses over than 600 sonniniid ammonites, which were collected primarily in bed-by-bed samplings from various stratigraphic sections of the Subbetic domain.

GEOGRAPHICAL AND GEOLOGICAL SETTING

All sampled sections containing sonniniids (Fig. 1A) were part of the southern margin of the Iberian Plate, which, during the Bajocian (Middle Jurassic) was located near the eastern end of the Hispanic Corridor (Fig. 1B). This corridor was a relatively narrow sea channel that during certain time intervals (i.e. Early

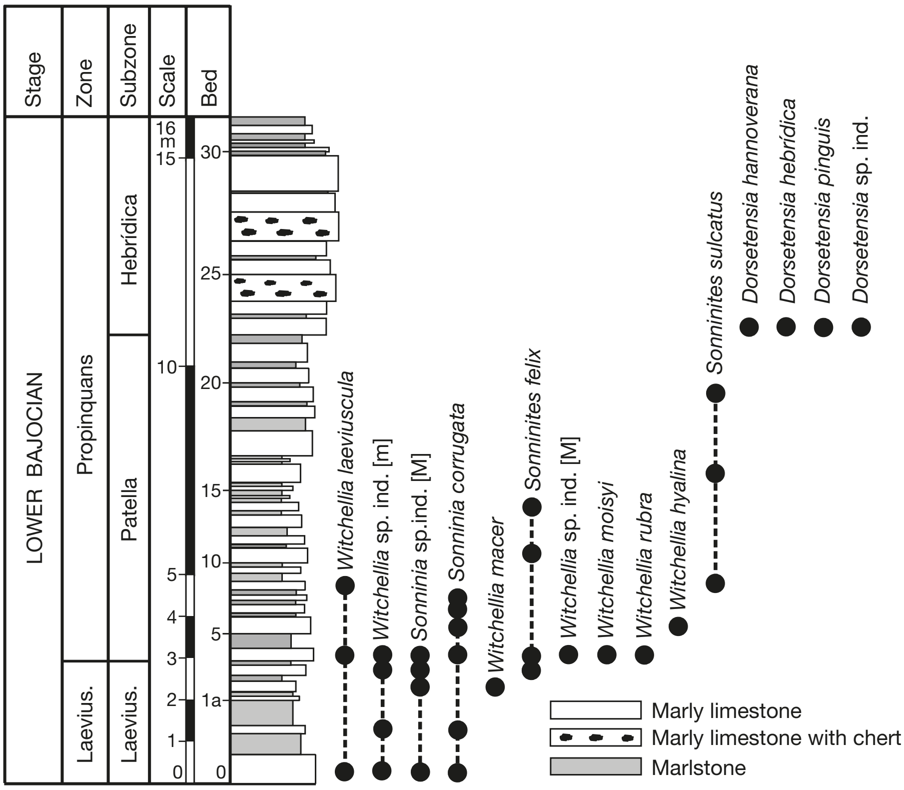


Fig. 2. — Lithology and stratigraphic range of sonniniids in JAC11 section, Sierra de Alta Coloma area, Campillo de Arenas, Jaén Province, Andalucía.

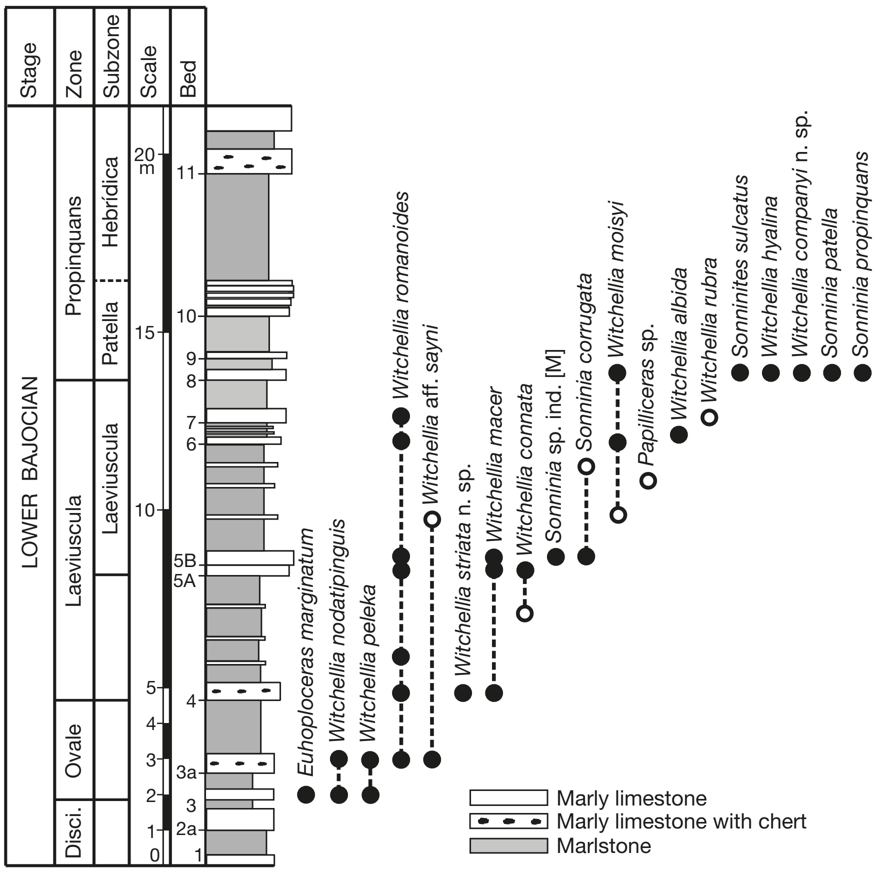


Fig. 3. — Lithology and stratigraphic range of sonniniids in JAC22 section, Sierra de Alta Coloma area, Campillo de Arenas, Jaén Province, Andalucía. Circles indicate that the stratigraphic position is only approximate.

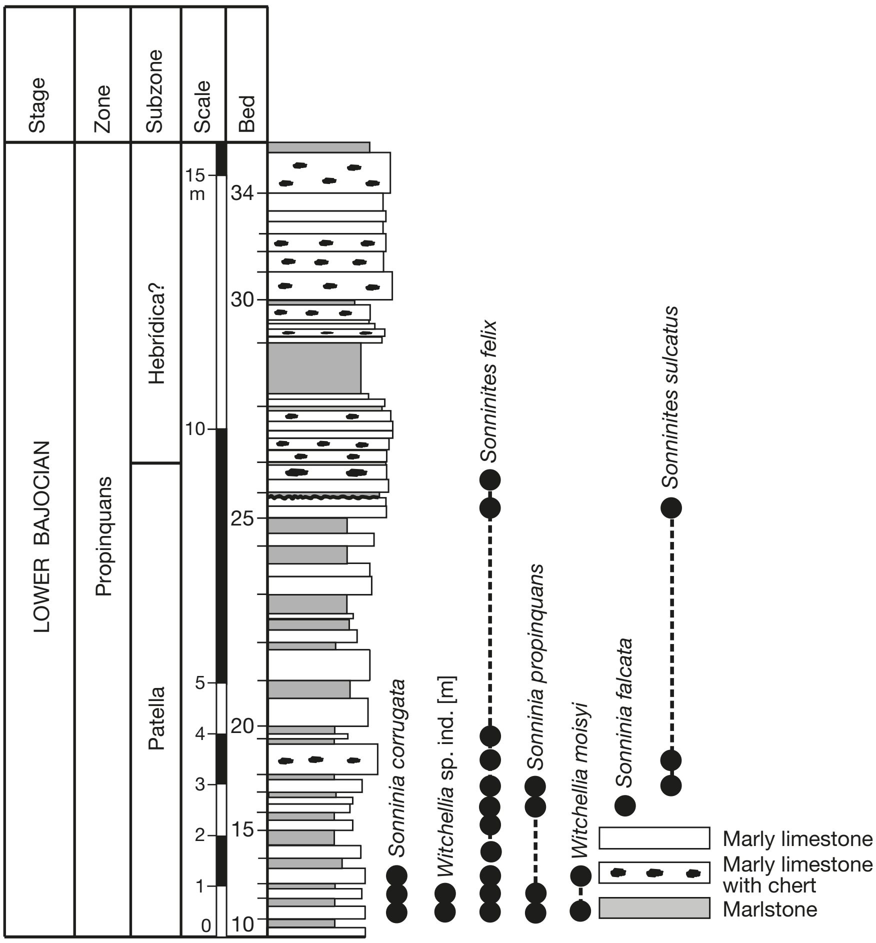


Fig. 4. — Lithology and stratigraphic range of sonniniids in JAC3' section, Sierra de Alta Coloma area, Campillo de Arenas, Jaén Province, Andalucía.

Bajocian-earliest Late Bajocian and Late Bathonian-Early Callovian) connected the Western Tethys with the Eastern Pacific (Aguado *et al.* 2017 and references therein). The area containing sections studied here was located at a palaeolatitude of about 26°N (Fig. 1C) within the southern Iberian continental margin by the Early Bajocian (*c.* 170 Ma). These sites are currently located in southern Spain (Fig. 1A), being part of the External Zones of the Betic Cordillera.

Most of the sections sampled (Figs 2-5) consist mainly of regular alternations of hemipelagic grey-cream marly limestones and marlstones. In some of these sections and at some stratigraphic intervals, beds consist of marly limestones with chert nodules. Microfacies are largely mudstones to wackestones with radiolarians and finely shelled bivalves (*Bositra*). Trace fossils, especially *Chondrites* and *Zoophycos,* are locally abundant. In the External Subbetic subdomain (Sierra de Gaena, La Morenica, Río Frío, Sierra de Lúgar) and Internal Subbetic (Sierra Harana and Río Fardes) the beds locally containing ammonites are heavily condensed nodular red limestones.

MATERIAL AND METHODS

Localities

As indicated above, all the ammonites studied come from selected stratigraphic sections of the Subbetic domain (Betic Cordillera, S Spain). Whenever possible, all these sections were numbered, measured, and sampled in detail, bed by bed. Localities and stratigraphic sections were abbreviated to a letter-number code following the customary rules of the Department of Stratigraphy and Palaeontology (University of Granada, Spain). The most noteworthy sampled stratigraphic sections were: JGa2 and JGa7, Arroyo de la Losilla, Sierra de Gaena in Rute (Córdoba Province); JVM, La Morenica and JST, Sierra del Trigo, Valdepeñas de Jaén (Jaén Province); MOD, JAC3, JAC3', JAC4, JAC6, JAC11, JAC13, JAC20, JAC21 and JAC22, Sierra de Alta Coloma area, Campillo de Arenas and Noalejo (Jaén Province) and Montillana (Granada Province); JAQ1, Barranco de Agua Larga, Noalejo (Jaén Province); JFA and JFB, Rio Fardes, Gorafe (Granada Province); and JRi3, Sierra de Ricote (Murcia region). From the total number of

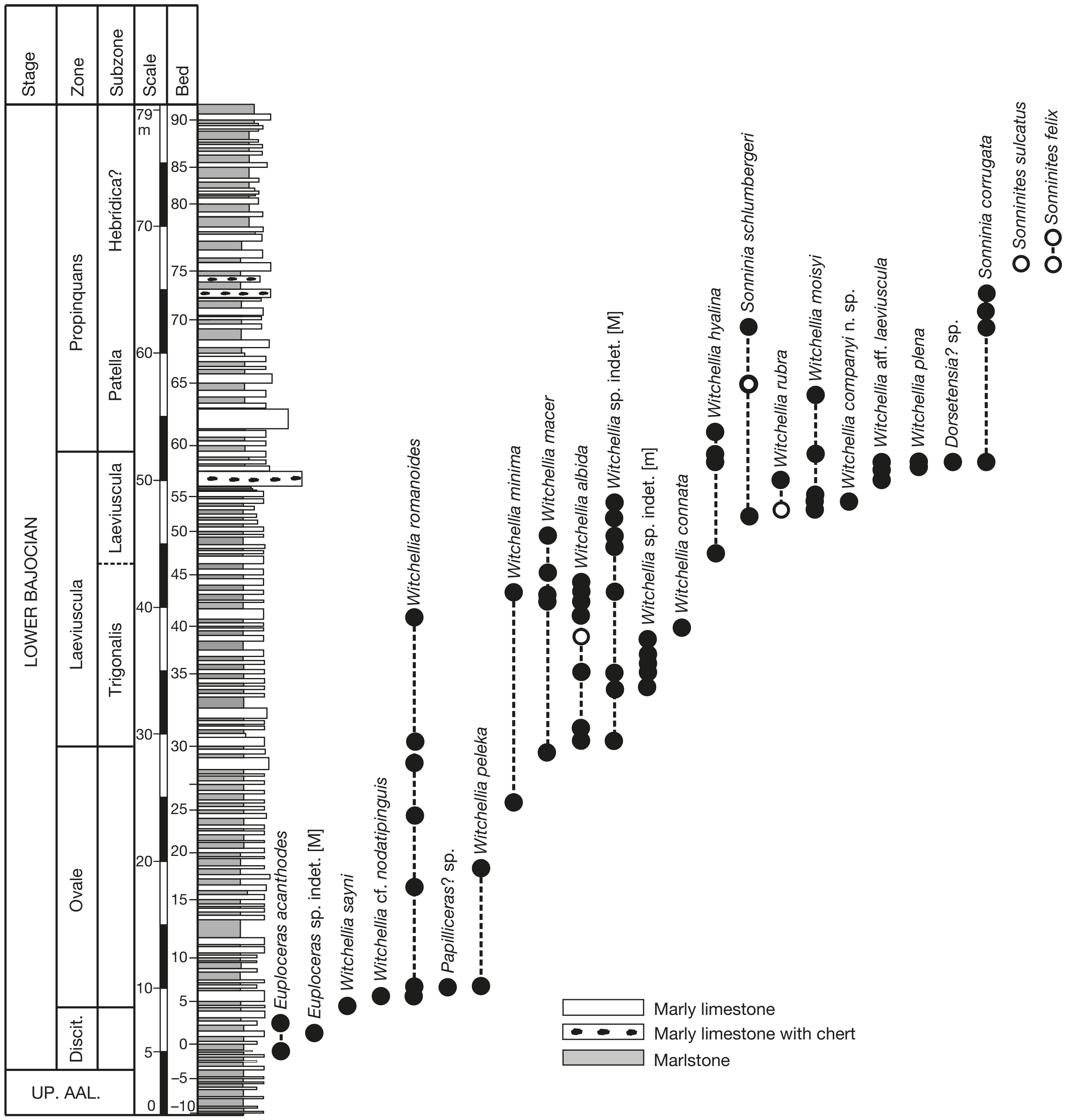


Fig. 5. — Lithology and stratigraphic range of sonniniids in JAC21 section, Sierra de Alta Coloma area, Campillo de Arenas, Jaén Province, Andalucía. Circles indicate that the stratigraphic position is only approximate.

sonniniids collected, only those preserved well enough for adequate taxonomic classification were used in this study.

In addition to Sonniniidae, other Ammonitida (Graphoceratidae, Erycitidae, Hammatoceratidae, Stephanoceratidae, Otoitidae, Sphaeroceratidae, Strigoceratidae, Lissoceratidae and Hebetoxyitidae) together with Phylloceratida and Lytoceratida are abundant or common in the Lower Bajocian of the above-mentioned stratigraphic sections.

Biostratigraphic scheme

The detailed biostratigraphic scheme used here is based on several previous studies performed in the Subbetic since the 1980s (Sandoval 1979, 1983, 1985, 1986, 1990; Linares & Sandoval 1988, 1990, 1993, 1996; Hernández-Molina *et al.* 1991; Sandoval *et al.* 1999, 2012, 2015, 2020; Jiménez *et al.* 1999; Sandoval & Chandler 2000, 2015; Linares 2002; Martínez *et al.* 2015).

The present work follows the standard ammonite zonation for the Mediterranean Province (Rioult *et al.* 1997), but raising the Ovale Subzone to zonal rank. The Propinquans Zone is equivalent to the old Sauzei Zone still used by some British and by German researchers. The Hebridica Subzone (upper part of the Propinquans Zone) is equivalent to the Pinguis Subzone of German researchers, who place it at the base of the Humphriesianum Zone. References are frequently made to the faunal horizons (Bj-1 to Bj-12) used by Chandler *et al.* (2006).

Abbreviations

Measurements

Regarding measurements, the following abbreviations are used:

D	diameter of the shell (mm);
U	umbilical diameter of the shell (mm);
H	whorl-section height of the shell (mm);
W	whorl-section width of the shell (mm);

h = H/D; u = U/D; w = W/D: Some of these parameters are approximate, because most of the specimens, mainly from marly-limestone facies, were laterally flattened (crushed) by compression. Only the most significant specimens were measured.

Other abbreviations

PH	phragmocone;
BC	body chamber;
E	external lobe;
L	lateral lobe;
U_2-U_5	umbilical lobes;
HT	holotype;
LT	lectotype;
OD	original designation;
T.A.	Type Ammonites of Buckman (1909-1930);
[M]	macroconchs;
[m]	microconchs.

Housing institution

All specimens studied are on deposit in the "Departamento de Estratigrafía y Paleontología", University of Granada, Spain (UGR). Only representative specimens are figured.

SYSTEMATIC PALAEONTOLOGY

Order AMMONOIDEA Zittel, 1884
Suborder AMMONITINA Hyatt, 1889
Superfamily HILDOCERATOIDEA Hyatt, 1867

Family Soninniidae
Buckman, 1892 *in* Buckman (1887-1907)

Description

Howarth (2013, in *Treatise*), describes Sonniniidae as follows: "Typical forms are stout planulates with strong hollow keel, ribs, and midlateral tubercles at least early in growth. Other forms show great variety, from evolute planulates to sphaerocones and oxycones, but almost all have Sonninia like innermost whorls, and ribs, tubercles or spines at some stage. Several genera are dimorphic".

Remarks

In the latest version of the *Treatise* (Howarth 2013), the family Sonniniidae is divided into two subfamilies: Sonniniinae Buckman, 1892 and Witchelliinae Callomon & Chandler, 2006 in Chandler *et al.* (2006). In Sonniniinae, Howarth included the following genera: *Sonninia* [with the subgenera *S.* (*Sonninia*) Douvillé, 1879; *S.* (*Euhoploceras*) Buckman, 1913; *S.* (*Papilliceras*) Buckman, 1920; and *S.* (*Alaskinia*) Westermann, 1978]; *Sonninites* Buckman, 1923; *Shirbuirnia* Buckman, 1910; *Pseudoshirbuirnia* Dietze *et al.*, 2005; and *Dorsetensia* Buckman, 1892. In Witchelliinae, Howarth (2013) included the genera: *Witchellia* Buckman, 1889; *Asthenoceras* Buckman, 1899; *Fontannesia* Buckman, 1902; *Newmarracarroceras* Hall, 1989; and *Guhsania* McLearn, 1926.

Almost simultaneously to the publication of the *Treatise* by Howarth, a study by Sandoval *et al.* (2012) concerning the latest Grammoceratinae, and later a follow-up study by Sandoval & O'Dogherty (2018) characterized *Asthenoceras* as typical of Grammoceratinae with close phylogenetic relationships with the Late Toarcian-Middle Aalenian genus *Vacekia*. Thus, the latest forms of *Vacekia* and earliest forms of *Asthenoceras* are morphologically very similar, with a simple septal suture and a hollow, notably high keel. The genus *Fontannesia,* which has been classified as possibly belonging to Grammoceratinae (Linares & Sandoval 1988) or Witchelliinae (Chandler *et al.* 2006), has a simple septal suture, but not as simplified as among contemporaneous Grammoceratinae, and keel is not as high. The genus *Newmarracarroceras* (type, *Dorsetensia clarkei* Crick, 1894 [Crick 1894: 388]; OD), from Western Australia, New Guinea, and eastern Indonesia, is remarkably similar to *Fontannesia* in the type of coiling, cross-section, ribbing, keel, and septal suture. It has only minor differences with respect to *Fontannesia*, i.e. a more compressed whorl section and weaker ribbing, which disappears before the end of the PH. In view of these small dissimilarities in addition to the remote geographical areas they occupied, *Fontannesia* and *Newmarracarroceras* could be classified as two separate genera but certainly with close phylogenetic relationships.

The genus *Latiwitchellia* Imlay, 1973 (type species *Witchellia* (*Latiwitchellia*) *evoluta* Imlay, 1973 [Imlay 1973: 70, pls 31-33; HT, OD, the specimen of the pl. 31: figs 1, 2, 5, 6]), from Oregon (United States), which was originally included by Imlay (1973: 70) as a subgenus of *Witchellia*, occurs in some sections of the Subbetic (Betic Cordillera, Spain). This genus, which is not mentioned by Howarth (2013, in the *Treatise*), shows similarities with *Asthenoceras* and, particularly, with *Linaresites* Sandoval, 2012 (type species, *Fontannesia montillanensis* Linares & Sandoval, 1988 [Linares & Sandoval 1988: 8, HT in pl. 1: figs 12, 13]), which is not mentioned either in the new *Treatise*. According to Sandoval *et al.* (2012), *Latiwitchellia,* which occurs in the Discites and Ovale zones of the Subbetic, appears to be the latest representative of the subfamily Grammoceratinae, rather than a primitive Witchelliinae.

The genus *Guhsania* McLearn, 1926 (McLearn 1926: 98) from Middle Jurassic (Lower Bajocian, Laeviuscula Zone) of British Columbia (Canada) shows similarities with *Witchellia* but is less involute and the ribs become large and widely spaced on the outer whorl.

Lastly, the genus *Dorsetensia*, with a relatively simple septal suture, and closely similar to *Witchellia* in general morphology, ornamentation, size, and type of dimorphism, should be included in Witchelliinae rather than in Sonniniinae.

In short, the genus *Asthenoceras* is excluded from Sonniniidae; *Dorsetensia* is transferred from Sonniniinae to Witchelliinae, while certain doubts remain concerning the taxonomic status of *Fontannesia*, *Newmarracarroceras*, and *Latiwitchellia*, which appear to be the last representatives of Grammoceratinae.

Dimorphism

Dimorphism is remarkably common and usually quite pronounced in the sonniniids. Macroconchs [M] are relatively large in size and have a simple peristome. Although several Subbetic shells are incomplete and lack an intact peristome, making it difficult to discriminate from the inner whorls of larger forms, some genera have two distinct types of dimorphism: Type 1) Several specimens, well preserved, complete with mouth borders and signs of maturity such as crowding of sutures, eccentric coiling of the last whorl, modification of the ribbing on the last third of the BC, and constriction of the peristome, have plain mouth borders and have no lappets. Westermann (1966: 309) proposed that such specimens likely represented dimorphous of *Euhoploceras*. This idea was supported by Sandoval & Chandler (2000: see pl. 9, figs 1-5), after analyzing the genus *Euhoploceras* of southwest England and southern Spain. According to the *Treatise* (Howarth 2013), this type of dimorphism is common in the subfamily Sonniniinae. Chandler (2019: 782) supposed that these forms are small adult macroconchs, which he named as mesoconchs. Type 2) More common are small specimens (< 40 mm in diameter) that have lateral lappets, which are long and spatulate in some forms. In certain cases, these microconchs have modified coiling of the last whorl. These '*Pelekodites*-style' ammonites vary from rare spinose forms to more common ribbed-only shells and are slightly more evolute than their corresponding macroconchs. According to Howarth (2013, in the *Treatise*) this type of dimorphism with clearly differentiated [M] and [m] is common in the subfamily Witchelliinae. Here, it is assumed that this latter dimorphism, more characteristic than the former type, occurs in both Sonniniinae and Witchelliinae.

Although dimorphism is common and readily apparent in sonniniids, it is almost always difficult to assign macroconchs and microconchs to the same taxon, particularly at species level. Therefore, in species descriptions, [M] is used for the "macro" forms and [m] for "micro", but macro- and microconchs are often not assigned to the same species and sometimes not even to the same genus.

Distribution

Sonniniids extend from the Upper Aalenian (Concavum Zone) to the Lower Bajocian (Humphriesianum Zone) worldwide, except in the Boreal Realm. This stratigraphic range is occupied in the Subbetic domain. The sampled sections in this domain have provided specimens belonging to the genera *Sonninia* (subgenera *Euhoploceras*, *Sonninia*, and *Papilliceras*), *Sonninites*, *Witchellia* and *Dorsetensia.* Sandoval & Chandler (2000) made a detailed study of the upper Aalenian-lowermost Bajocian *S.* (*Euhoploceras*), and therefore, this subgenus will be analysed only briefly here. The Figure 6 shows the approximate stratigraphic range of the sonniniid "species" recorded in the Subbetic domain.

Subfamily Soninniinae Buckman, 1892

Description

Serpenticone, platycone to oxycone macroconchs, sometimes reaching large sizes, microconchs being much smaller. Whorl sections vary from subrectangular, subtriangular, oval to ogival, and the venter has a more or less developed hollow keel persisting to the BC. Ornamentation varies widely from smooth forms, to others with strongly ribbed or ribbed and tuberculate. The innermost whorls can be smooth, whereas later inner whorls have ribs. Many forms have well-developed tubercles or spines. The degree to which the spinose/tuberculate stage persists is highly variable and specimens rarely retain strong ribbing beyond the end of the PH, whereas in others the ornamentation is reduced to the inner whorls and from an early stage are striated or smooth. Complete macroconchs [M] have simple peristomes with plain mouth borders. In microconchs [m], the aperture morphology is variable, but usually they have expanded lateral lappets. Like the corresponding macroconchs, microconchs can have non-tuberculate, tuberculate, and even spiny internal whorls. The septal suture is relatively complex, with a ramified deep L, and slightly retracted U_2-U_5 lobes.

Remarks

As mentioned above, *Asthenoceras, Fontannesia, Newmarracarroceras*, and *Dorsetensia,* all included within Sonniniinae in the new version of the *Treatise* (Howarth 2013), should be separated from this subfamily and transferred to Grammoceratinae (the first three) and Witchelliinae (the last). The more common dimorphism of Sonniniinae appears to belong to the aforementioned type 1, i.e. large, "classical" macroconchs associated with relatively small macroconchs (mesoconchs according to Chandler 2019) with plain mouth borders and without lateral lappets. Coexisting with *Sonninia* [M] and *Sonninites* [M], microconchiate forms also occur with well-developed lateral lappets (aforementioned dimorphism type 2, possibly representing their dimorphic partners. In this case, the two types of dimorphism would be clearly represented in this subfamily.

Distribution

Sonniniinae range throughout the Upper Aalenian (Concavum Zone)-Lower Bajocian (Humphriesianum Zone) interval, with a worldwide distribution, except in the Boreal Realm. In the Subbetic domain, they have this stratigraphic range, and occur in the External, Median, and Internal subdomains, being most abundant in the central sector of the Median Subbetic, the origin of most of the specimens studied here.

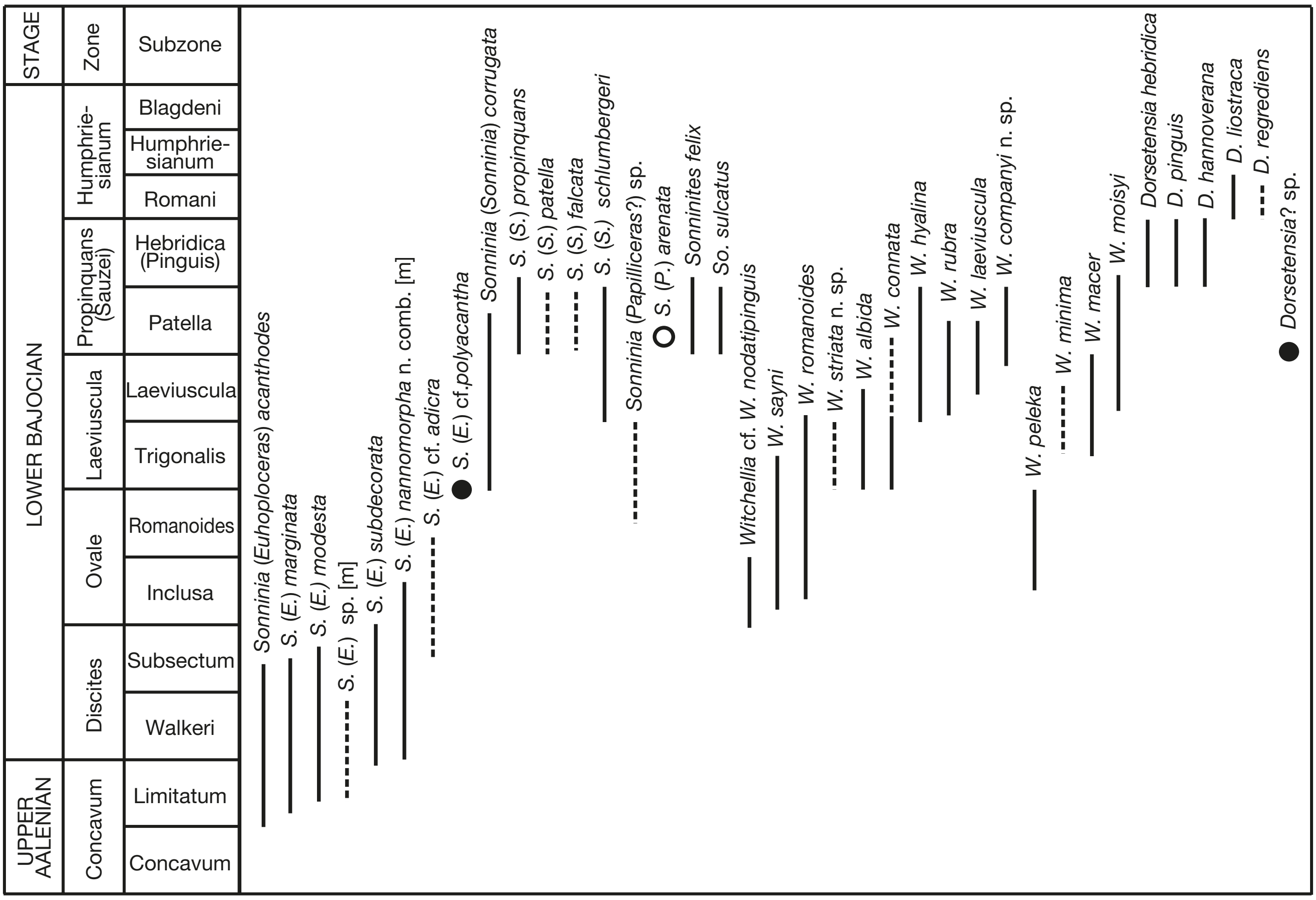


Fig. 6. — Approximate stratigraphic range of sonniniids species in the Subbetic domain (southern Spain). Circles indicate that the stratigraphic position is only approximate.

Genus *Sonninia* Douvillé, 1879

Sonninia Douvillé, 1879: 92.

Waagenia Bayle, 1878: pl. 84, *non* Kriechbaumer, 1874 (insect).

Type species. — *Waagenia propinquans* Bayle, 1878 (Bayle 1878: pl. 84, fig. 1 [OD]).

Description

The following description is modified from the *Treatise* (Howarth 2013). Evolute planulate shells, becoming more involute and compressed on larger whorls. The whorl section is rounded initially, becoming more or less compressed on outer whorls, with a strong keel on rounded or arched venter. The ribs and tubercles are highly variable. The ribs are often strong, mainly on inner whorls, but may be irregular. Large, well-spaced midlateral tubercles or spines occur at least on early and middle whorls. This genus is dimorphic, but some small forms (mesoconchs), which have plain mouth borders, are undefined. Others have lateral lappets and, like the corresponding macroconchs, can have non-tuberculate, tuberculate, and even spiny internal whorls.

Remarks

Howarth (2013: 115) states that the author of *Sonninia* is Douvillé, not Bayle, as assumed previously, because Douvillé (1879: 92) was the author of the note in which S*onninia* was proposed as a replacement for Bayle's preoccupied genus *Waagenia*.

Subgenus *Sonninia* (*Sonninia*) Douvillé, 1879 [M] & [m]?

Type species. — *Waagenia propinquans* Bayle, 1878 (Bayle 1878: pl. 84, fig. 1 [OD]) (LT designated by Gillet 1937: 29).

Description

Macroconchs of medium to large size, planulate slightly involute to evolute. The whorl section varies from subquadrangular to compressed ogival throughout its ontogenetic development and the ventral area has a hollow, moderately high to high keel. The innermost whorls are usually smooth. Subsequently, more or less irregular ribs appear below the umbilical edge, some dividing the lower part of the flank, near the umbilical rim, as well as irregularly developed tubercles, which are usually located in the division of the ribs. Tubercles fade on middle whorls, and ribs fade on outer whorls, which become smooth, more involute,

Table 1. — Measurements of *Sonninia* (*Sonninia*) *propinquans* (Bayle, 1878) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC11.8.8	72.0	30.0	0.42	25.0	0.33	18.0	0.25	Complete?	
	62.0	27.5	0.44	22.5	0.36				
JAC11.8.9	45.0	17.4	0.39	18.0	0.40	–	–	Complete?	
	30.0	12.0	0.40	11.5	0.38				
JAC11.R.55	40.0	15.0	0.375	17.0	0.425	–	–	–	
	29.0	11.4	0.39	11.0	0.38				
JAC11.R.60	31.0	13.5	0.40	11.0	0.355	10.5	0.34	PH	Propinquans Zone, Patella Subzone?
	22.0	9.0	0.41	8.0	0.36	8.5	0.9		
JAC6.40.1	55.0	20.0	0.36	19.5	0.35	–	–	–	
JAC13.R.1	52.0	17.1	0.33	22.0	0.42	15.0	0.29		
	38.0	13.0	0.34	15.0	0.39	11.0	0.29		
JAC21.16.4	56.0	17.5	0.31	23.0	0.41	–	–		
	43.0	13.5	0.31	19.0	0.44	–	–		

and compressed. The septal suture is relatively complex, with a ramified deep L, and slightly retracted U2-U5 lobes.

The *S.* (*Sonninia*) microconchs [m] have not yet been clearly identified, and thus are difficult to distinguish from those of *Witchellia*. Some of the "*Pelekodites*" forms as "*P.*" *schlumbergeri* (Haug, 1893) and "*Maceratites*" forms, which occur frequently in the upper part of the Laeviuscula Zone and in the Propinquans Zone in the Subbetic domain, most likely represent the dimorphic microconchs of *S.* (*Sonninia*).

Remarks

Some species of *S.* (*Sonninia*) can strongly resemble *S.* (*Euhoploceras*), but the latter is more evolute and has a massive subquadrate or subrectangular whorl section and rursiradiate ribbing. *S.* (*Papilliceras*) is similar in almost all the characters, but has a row of well-aligned midlateral tubercles, which differentiates it from *S.* (*Sonninia*). Some *S.* (*Sonninia*) species may have similarities with *Sonninites* Buckman, but this genus is generally more involute, has less marked ribbing, and the tubercles, if present, are restricted to the innermost whorls. *Witchellia*, another related genus, has a more planulate whorl section, lacks tubercles, or these are reduced to innermost whorls, and has a simpler septal suture.

Distribution

In agreement with Howarth (2013, in *Treatise*: 15), the stratigraphic range of *S.* (*Sonninia*) is limited to the Propinquans Zone. However, some species traditionally included in *Sonninia*, such as *S.* (*S.*) *corrugata* (J. de C. Sowerby, 1824) or *S.* (*S.*) *micracanthica* (Buckman, 1925), are frequently cited in the Laeviuscula Zone (see also Dietze *et al.* 2019). Other species [*S.* (*S.*) *patella* (Waagen, 1867), *S.* (*S.*) *carinodisca* (Quenstedt, 1886), *S.* (*S.*) *furticarinata* (Quenstedt, 1858), "*S.* (*S.*)" *disciformis* Dorn, 1935] have been cited in the lowermost part of the Humphriesianum Zone (Fernández-López 1985; De Baets *et al.* 2008; Dietze *et al.* 2008, 2013). The genus is found in Europe, North Africa (Atlas Mountains), Madagascar, the Caucasus, Azerbaijan, Iran, China (Tibet), Japan, western Australia, United States (Alaska, Oregon), Chile, and Argentina. Subbetic specimens occur in the upper part of the Laeviuscula Zone and Propinquans Zone from various localities.

Sonninia* (*Sonninia*) *propinquans (Bayle, 1878) [M] (Fig. 7A-D)

Waagenia propinquans Bayle, 1878: pl. 84, fig. 1 (LT designated by Gillet 1937: 29) to fig. 6.

Sonninia sowerbyi – Douvillé 1885: 20, pl. 1, fig. 1.

Sonninia propinquans – Douvillé 1885: 20, pl. 1, fig. 2. — Riche & Roman 1921: 136, pl. 6, fig. 1. — Buckman 1922: T.A. 4, pl. 298. — Pavia 1983: pl. 5, fig. 1. — Contini 1994: 104, pl. 39, figs 1a-c, 2. — Sandoval 1994: 206, pl. 1, fig. 3. — Sadki 1996: 176, pl. 4, fig. 11. — Rioult *et al.* 1997: 104, pl. 14, fig. 4. — Seyed-Emami *et al.* 2000: 257, fig. 3/5. — Dietze *et al.* 2009: 30, pl. 9, fig. 2, pl. 10, fig. 7. — Metodiev & Tsvetkova 2014: 31, figs 3.1-5. — Chandler & Whicher 2015: pl. 14, fig. 1. — Dietze *et al.* 2020: 64, pl. 6, fig. 5, pl. 12, fig. 2, pl. 13, fig. 1.

Sonninia cf. *propinquans* – Fernández-López 1985: 45, text-fig. 4f, pl. 8, fig. 2. — Henriques *et al.* 1985: 104, pl. 1, figs 1, 2.

Sonninia ex gr. *propinquans* – Metodiev 2019: 19, figs e, f.

Material examined. — JAC6.40.1, JAC11.8.8, JAC11.R.56, JAC11.R.57, JAC11.R.58, JAC11.R.59, JAC11.R.60, JAC13.R.1, JAC21.16.4 and JAC21.16.5.

Measurements. — See Table 1.

Description

Medium-sized macroconchs, relatively evolute, but with quite variable coiling (U/D varying from 0.31 to 0.42 in Subbetic specimens), being somewhat more evolute in the

Fig. 7. — **A**-**D**, *Sonninia* (*Sonninia*) *propinquans* (Bayle, 1878) [M]: **A**, JAC13.R.1, Propinquans Zone, Sierra de Alta Coloma (JAC13 section); **B**, **D**, JAC11.8.8, JAC11.8.9, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC11 section); **C**, JAC21.16.4, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC21 section); **E**, *Sonninia* (*Sonninia*) *patella* (Waagen, 1867) [M], JAC20.(7-6).5, Propinquans Zone, Patella Subzone, Caminno de Casa Blanca section; **F**, **G**, *Sonninia* (*Sonninia*) *falcata* Haug, 1893 [M?], *non* Quenstedt, 1886: **F**, JAC21.17.5, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC21 section); **G**, JCH.2.2, Propinquans Zone, Charilla, Jaén province (JCH section); **H**-**K**, *Sonninia* (*Sonninia*) *corrugata* (J. de C. Sowerby, 1824) [M]: **H**, **I**, JAC21.12.5,

JAC21.12.14, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC21 section); **J**, JAC22.62.9, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC22 section); **K**, JAC3.59.1, Laeviuscula Zone, Sierra de Alta Coloma (JAC3 section); **L**, **M**, *Sonninia* (*Sonninia*) *schlumbergeri* Haug, 1893 [m]: **L**, JAC22.69.2, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC22 section); **M**, JAC22.52.11, Laeviuscula Subzone, Sierra de Alta Coloma (JAC22 section); **N**, *Sonninia* (*Euhoploceras*) cf. *polyacantha* (Waagen, 1867) [M], JAQ1.3.1, Laeviuscula Zone, Barranco de Agua Larga (JAQ1 section). Scale bar: 1 cm.

TABLE 2. — Measurements of *Sonninia* (*Sonninia*) *patella* (Waagen, 1867) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC20.(6-7).5	88.0	18.0	0.20	44.0	0.50	18.0	0.20	Incomplete	Propinquans Zone
	60.0	15.0	0.25	27.0	0.45	–	–		
JAC13.R.2	82.0	22.3	0.27	37.0	0.45	19.0	0.23	Complete	
	57.0	17.0	0.30	25.0	0.44	–	–		

inner whorls than in the outer ones. The whorl section varies throughout ontogeny, as subcircular to subrectangular or ovate shape in the inner whorls becoming compressed ogival in the outer ones. The oblique to rounded umbilical wall merges with the rounded umbilical edge, and the flanks, gently convex, converge to the venter, which supports a moderately high hollow keel. Ornamentation varies throughout ontogeny and among specimens. Usually, inner whorls have subradial ribs that during ontogenetic development become uneven in relief and, from a variable diameter on the more prominent ribs, rounded tubercles are differentiated, which are located near the line of involution. In the intermediate whorls, the tubercles are thicker and more prominent than in the internal ones, and are located in the middle of flanks, where two or, more frequently, three secondary ribs generally arise. Between the tuberculate ribs, one to four less prominent simple ribs can usually be found. From the ventrolateral edge, ribs are strongly curved forward and, although quickly fading, extend nearly to the keel. The septal suture is not preserved in the specimens analysed.

Remarks

Like other species of *S.* (*Sonninia*) and *S.* (*Euhoploceras*) (see Sandoval & Chandler 2000; Dietze *et al.* 2005), *S.* (*S.*) *propinquans* has wide intraspecific variability, which is noticeable in the degree of coiling, changes in the type of section throughout ontogeny, and changes in ornamentation such as the type of ribbing and, especially, length of the tuberculate stage. The most similar species is *S.* (*S.*) *patella* (Waagen, 1867), which is more involute, has a more compressed whorl section, mainly in the BC of the adult stages, and has a shorter tuberculate stage, with less developed tubercles.

Distribution

The type horizon of the type species of *S.* (*S.*) *propinquans* [*Waagenia propinquans* Bayle, 1878] lies in the Sauzei Zone in les Moutiers, near Caen, France (Bayle 1878: pl. 84; Gillet 1937: 29; Contini 1994: 104; Dietze *et al.* 2005: 23, 2009: 30). The species has been mentioned in numerous localities among the characteristic fossils of the Propinquans Zone in Western Europe. With the same stratigraphic range, it occurs in Morocco (Sadki 1994, 1996) and Iran (Seyed-Emami 1988; Seyed-Emami *et al.* 2000). In the Subbetic, the species appears in the Propinquans Zone (Patella Subzone) from several Median and External Subbetic localities.

Sonninia* (*Sonninia*) *patella (Waagen, 1867) [M] (Fig. 7E)

Ammonites patellum Waagen, 1867: 597, pl. 25, figs 2, 3 (LT designed by Oechsle 1958).

Sonninia patella – Dorn 1935: 51, text-fig. pl. 5, figs 1, 2; pl. 14, figs 1, 6. — Pavia 1983: pl. 4, fig. 4. — Schlegelmilch 1985: 61, pl. 18, fig. 2 (LT refigured). — Rioult *et al.* 1997: 48, pl. 14, figs 3a, b. — De Baets *et al.* 2008: 571, fig. 6b. — Chandler & Whicher 2015: pl. 13, fig. 4 (reproduction of the original figure of Waagen 1867). — Dietze *et al.* 2020: 66, pl. 6, fig. 8, pl. 12, figs 4-5, pl. 14, fig. 18. — Sadki & Dietze 2021: 7, text-fig.10 (LT refigured) (*cum syn.*).

Sonninia cf. *patella* [M] – Dietze *et al.* 2009: 25, pl. 7, fig. 1, pl. 9, fig. 5.

MATERIAL EXAMINED. — JAC11. R.62, JAC11. R.63, JAC13. R.2, JAC20.(7-2).1, JAC20.(7-6).5 and JAC20.R.1.

MEASUREMENTS. — See Table 2.

Description

Medium-sized planulate shell, relatively involute with outer whorls being more involute than the inner ones. The whorl section is ovate, from subrectangular to compressed subtriangular. The umbilical wall, oblique in the inner whorls, becomes vertical in the last whorls. The convex flanks converge to a somewhat narrow venter, which bears a relatively prominent floored keel. The inner whorls, visible in a specimen, are ornamented with rather strong irregular, often bundled, radial sigmoid ribs, some of which split at a node located near the umbilical edge. Ribs erase gradually on the external whorls, and the BC end can be almost smooth.

Remarks

S. (*S.*) *patella* is a frequently cited species, but, except for the HT, few specimens have been figured, and these show noteworthy intraspecific variations. The most similar species may be *S.* (*S.*) *propinquans* (Bayle, 1878), but the latter is slightly more evolute, has an ovate-ogival whorl section, no vertical umbilical wall, and more persistent ribbed and tuberculate stages.

Distribution

The LT comes from an unknown level of the Sowerbyi oolith of Gingen/Fils of the eastern Swabian Alb (Dietze *et al.* 2005; Sadki & Dietze 2021). The species usually occurs in the lower half of the Propinquans Zone of diverse Western European localities, but it has also been cited in the Laeviuscula Zone. Subbetic specimens are from the Propinquans Zone (Patella Subzone), from Sierra de Alta Coloma area (JAC11, JAC13, JAC20 sections, Jaén Province).

Table 3. — Measurements of *Sonninia* (*Sonninia*) *falcata* Haug, 1893 [M?].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JCH.2.2	*c.* 67.0	*c.* 24.5	*c.* 0.37	*c.* 25.0	*c.* 0.37	23.0	0.34	Complete	Propinquans Zone
	49.0	18.0	0.37	19.0	0.39	16.0	0.33		
JAC21.17.5	45.0	14.5	0.32	18.0	0.40	15.0	0.33		
	37.0	12.0	0.32	15.0	0.40	–	–		

Sonninia* (*Sonninia*) *falcata
(Quenstedt, 1886) [M?],
(Fig. 7F, G)

Ammonites tessonianus var. *falcatus* Quenstedt, 1886: 507, pl. 63, fig. 10, ?11, *non* fig. 9.

Ammonites tessonianus – Quenstedt 1858: 394, pl. 53, fig. 9.

Harpoceras alsaticum Haug, 1885: 677 (for above).

Sonninia falcata – Haug 1893: 288 (LT designated by Dietze *et al.* 2020: 68).

Sonnites alsaticus – Buckman 1924: T.A. 6, pl. 528A.

Sonninia (*Sonninia*?) *alsatica* – Westermann & Riccardi 1972: 49, text-figs 9-11 ([LT refigured], incorrectly nominated as HT for *S. alsatica* Haug, 1885), pl. 10, figs 1-7.

Material examined. — JCH.2.2 and JAC21.17.5.

Measurements. — See Table 3.

Description

Small planulate macroconchs, with moderately evolute whorls, which vary in section from rounded subquadrate to moderately subrectangular compressed with almost vertical umbilical walls, slightly rounded umbilical edges and gently convex flanks. The broad venter bears a highly prominent floored keel. On the inner whorls, observable in the specimen JCH.2.2, the keel is limited by shallow sulci. The ornament consists of prominent rectiradiate to weakly rursiradiate, slightly concave ribs, which project onto the shoulders and are most prominent at mid-flank. The ribs vary from rather dense and mostly single, to more separate, extremely prominent, often fasciculating in pairs. The inner or intermediate whorls may bear irregular lateral tubercles. The septal suture is not preserved in the Subbetic specimens.

Remarks

Haug (1885: 677) described *Harpoceras Alsaticum* for *Ammonites Tessonianus non* d'Orbigny, 1845 (Quenstedt [1858: 294, pl. 53, fig. 9]). Later, Haug (1893: 288) indicated that this figure is incorrect, judging from the new figure of the same specimen (Quenstedt 1886: pl. 63, fig. 10). Then, the same author (Haug 1893: 288) designated as the type (LT) of *S.* (*S.*) *alsatica* the specimen that he figured on pl. 10, fig. 1. Westermann & Riccardi (1972: 49, text-fig. 9), erroneously stating that the HT of *S. alsatica* (Haug 1885: 677) is the specimen figured by Quenstedt (1858: pl. 53, fig. 9) and Quenstedt 1886: pl. 63, fig. 10). However, as indicated by Dietze *et al.* (2020: 68), this specimen is the type (LT) of *S.* (*S.*) *falcata* Haug, 1893. This specimen (type of *S. falcata*) is not the same as the one figured by Haug (1893: pl. 10, fig. 1) because Haug's specimen has less dense and more radial ribbing, and a somewhat more rectangular whorl section. *S.* (*S.*) *propinquans*, which occurs in the same stratigraphic levels, is quite similar to *S.* (*S.*) *falcata*, but is larger, is usually slightly more evolute, has a more ovate-compressed whorl section, and has less prominent ribbing.

Distribution

The type of *S.* (*S.*) *falcata* reportedly comes from the "Brauner Jura (Sowerbyi or Sauzei zones) of Spaichingen, Württemberg (Westermann & Riccardi 1972; Dietze *et al.* 2020). In the Inferior Oolite at South Main Road Quarry, Dundry, Avon (England) *S.* (*S.*) *alsatica* (maybe *S. falcata*) occurs in a bed which corresponds closely to the lower or middle part of the Propinquans (Sauzei) Zone (horizons Bj-10b, B-11a and Bj-11b) (Dietze *et al.* 2009). In SW Germany *S.* (*S.*) *falcata* occurs in the upper part of the Pinguis Subzone = Hebridica Subzone (Dietze *et al.* 2008, 2011b). In Argentina, it occurs in the Sauzei Zone of Neuquén (Westermann & Riccardi 1972). In Spain, specimens are from the Subbetic Propinquans Zone (Patella Subzone?) of Charilla (JCH) and Sierra de Alta Coloma (JAC21) sections.

Sonninia* (*Sonninia*) *corrugata (J. de C. Sowerby, 1824) [M]
(Fig. 7H-K)

Ammonites corrugatus J. de C. Sowerby, 1824: 74, pl. 451, fig. 3 (HT). — Buckman & Woodward 1908: pl. 6, figs 4a, b (HT refigured).

Sonninia corrugata – Buckman 1923: T.A. 4, pl. 412. — Hiltermann 1939: 163, pl. 11, fig. 7. — Morton 1975: 70, pl. 11, figs 4-9. — Fernández-López 1985:45, text-figs 4C, 5, pl. 8, figs 4-8. — Chandler *et al.* 2006: 369, fig. 4.6. — De Baets *et al.* 2008: 570, fig. 6a. — Metodiev 2019: 18, figs 7A-D. — Dietze *et al.* 2020: 66, pl. 6, figs 7, 9, pl. 12, fig. 6.

Sonninites felix – Buckman 1923: T.A. 5, pl. 428B.

Witchellia corrugata – Dorn 1935: 107, pl. 5, fig. 4. — Gillet 1937: 34, fig. 24.

Material examined. — JAC3.35.1, JAC3.59.1, JAC3.68.4, JAC3.69.1, JAC3.69.2. JAC3.70.1, JAC3.70.4, JAC3.70.5, JAC3.71.5, JAC3.71.6 , JAC3'.0.7, JAC3'.4.4, JAC3'.4.6, JAC3'.4.9, JAC3'.4.15, JAC3'.4.20, JAC3'.4.24, JAC3'.4.36, JAC3'.5.6, JAC3'.5.7, JAC3'.5.10, JAC3'.5.11, JAC3'.5.12, JAC3'.6.13, JAC3'.6.14, JAC3'.6.16, JAC3'.6.18, JAC3'.6.19, JAC3'.6.21,

Table 4. — Measurements of *Sonninia* (*Sonninia*) *corrugata* (J. de C. Sowerby, 1824) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.59.1	41.0	13.2	0.32	17.0	0.415	11.5	0.28	Mostly incomplete and crushed specimens	Laeviuscula Zone
	31.0	10.0	0.32	11.5	0.37	8.6	0.28		
JAC3.69.2	29.0	8.2	0.28	13.0	0.44	8.2	0.28		
JAC3'.0.7	35.0	10.5	0.30	14.0	0.40	–	–		
	27.0	7.5	0.28	10.5	0.39	6.5	0.24		
JAC21.12.5	27.0	7.5	0.30	12.0	0.44				Propinquans Zone
	19.0	5.3	0.28	9.5	0.50	7.0	0.37		
JAC21.12.17	33.0	8.5	0.26	14.0	0.42	–	–		
	27.0	7.0	0.28	11.5	0.46	–	–		
JAC22.58.2	35.0	9.5	0.27	16.5	0.47	8.3	0.24		Laeviuscula Zone
	30.0	8.0	0.27	13.7	0.46	7.1	0.24		
JAC22.62.9	58.0	17.0	0.29	24.5	0.42	–	–		Propinquans Zone
	45.0	13.5	0.30	20.0	0.44	–	–		

JAC3'.6.23, JAC3'.7.4, JAC4.64.2, JAC11.5.2, JAC11.5.24, JAC11.5.25, JAC11.5.27, JAC11.R.10, JAC11.R.64, JAC20.6.2, JAC20.6.11, JAC21.11.2, JAC21.12.5, JAC21.12.17, JAC22.58.2, JAC22.62.9, JAC22.69.3, JAC22.71.1 and JTT.F.A.

Measurements. — See Table 4.

Description

Discoidal, small to medium-sized shells with moderately involute coiling. The whorl section varies throughout ontogeny. The inner whorls are subcircular to subquadrangular and slightly depressed with a broad ventral region, which has a small keel bordered by faint furrows. In the intermediate and outer whorls, the section becomes progressively ogival and compressed whereas the flanks become subparallel in the lower half, and convex and converging towards the ventral area in the outer half. The maximum whorl width is reached near the umbilical edge, which is rounded, and the umbilical wall is vertical. From the intermediate whorls, the external region and the ventrolateral edges are no longer differentiated and the keel is high and narrow, with no lateral grooves. The innermost whorls are smooth, and small tubercles can be differentiated only in the end part of the second whorl of some specimens. The intermediate whorls, from 10 to 15 mm in diameter, have ribs, which emerge from the coiling suture. These are flexuous, subradial or only slightly proverse, with irregular relief, and fasciculate in 2 or 3 from a small thickening located near the umbilical edge, and they curve forward in the external region. In the outer whorls, the ribbing progressively fades and the end of the BC of adult specimens can be completely smooth. The septal suture, only partially preserved in Subbetic specimens, is complex with long and highly branched L and slightly retracted umbilical lobe.

Remarks

As indicated by Fernández-López (1985: 49), the interpretation of *S.* (*S.*) *corrugata* sharply contrasts among various authors. Regarding the uncertainty surrounding the nature of the HT, such as it degree of maturity, of whether it is a macro- or microconch, Chandler *et al.* (2006: 369) proposed that it might be best to set the species aside as a *taxon dubium* within the framework of precision of current ammonite taxonomy. However, the species is accepted here for small specimens that have a high and narrow keel, well-marked ribs on inner and middle whorls, and a notably reduced tuberculate stage. The specimen figured as *Sonninites felix* Buckman, 1923 (Buckman 1923: T.A. 5, pl. 428B) is so similar to HT of *S.* (*S.*) *corrugata* for both coiling, whorl section, and ornamentation that it is included here in this species.

Distribution

According to Chandler *et al.* (2006: 369), the type of *S.* (*S.*) *corrugata* was confidently assigned to the undivided 'Brown Ironshot' by Buckman (Buckman & Wilson 1896; Buckman 1923: T.A. 4, pl. 412 only, 'topotype'; Parsons 1979). However, re-examination by Chandler of the specimen in the Natural History Museum (London) suggests that it may have come from somewhat lower down, from a part of the White Ironshot, Trigonalis Subzone. The species has been frequently cited from the Laeviuscula and Propinquans (Sauzei) zones of many Tethyan localities (Dorn 1935; Gillet 1937; Hiltermann 1939; Oechsle 1958; Morton 1975; Fernández-López 1985; Seyed-Emami 1988; Sadki 1996; Chandler *et al.* 2006; De Baets *et al.* 2008; Metodiev 2019, etc.). The Subbetic specimens extend from Laeviuscula Zone (Trigonalis Subzone) to lower part of the Propinquans Zone, being abundant mainly in Sierra de Alta Coloma area, (sections JAC3, JAC3', JAC4, JAC11, JAC20, JAC21 & JAC22), Campillo de Arenas, and Noalejo (Jaén Province).

Sonninia* (*Sonninia*) *schlumbergeri Haug, 1893 [m] (Figs 7L-M; 9A)

Sonninia (?*Poecilomorphus*) *schlumbergeri* Haug, 1893: 296, fig. 7, pl. 8, figs 6a, b (HT).

Poecilomorphus schlumbergeri – Brasil 1895: 36, pl. 3, figs 4, 5.

Sonninia schlumbergeri var. *erycina* Renz, 1925: 19, pl. 2, figs 9, 9a.

? *Witchellia sayni* – Dorn 1935: 117, pl. 10, fig. 3.

Sonninia (*Poecilomorphus*) *schlumbergeri* – Huf 1968: 31, pl. 1, figs 4a-d (HT refigured), 5a-d.

TABLE 5. — Measurements of *Sonninia* (*Sonninia*) *schlumbergeri* Haug, 1893 [m].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC4.39.10	33.5	15.0	0.45	12.0	0.36	12.0	0.36	Complete adult Microconchs	Laeviuscula Zone
JAC22.52.11	25.0	11.0	0.44	8.3	0.33	7.0	0.28		
JAC22.69.2	33.0	13.4	0.42	10.5	0.32	8.0	0.24		Propinqu. Zone
TT.76.2	37.0	15.0	0.40	13.3	0.36	–	–		Laeviuscula Zone?
	25.5	10.0	0.37	9.5	0.37	–	–		

Pelekodites schlumbergeri – Schlegelmilch 1985: 64, pl. 19, fig. 6 (HT refigured). — Ohmert 2004: 65, text-figs 17, 18, pl. 16, figs 5-7. — Dietze *et al.* 2019: 60, figs 5(7a, b; 9a, b), 7(4a, b), 8(8a, b).

Pelekodites cf. *schlumbergeri* – Ohmert 2004: 67, pl. 16, fig. 8. — Dietze *et al.* 2019: 60, figs 5(2-3b, 8a, b).

Pelekodites cf. *schlumbergeri* [m] – Dietze *et al.* 2008: 144, pl. 4, fig. 6; 2009: 21, figs 15a, b, 20a, b.

Dorsetensia cf. *schlumbergeri* [m] — Énay & Mangold 2021: p. 56, pl. 8, fig. 4.

MATERIAL EXAMINED. — JAC3.R.11, JAC4.38.49, JAC4.38.50, JAC4.39.10, JAC11.R.66, JAC13.R.25, JAC22.52.11, JAC22.69.2, JAC22.≥60.2, CB.75 and TT.76.2.

MEASUREMENTS. — See Table 5.

DESCRIPTION
Small microconchs with maximum diameters varying from 25 to 33 mm and strongly evolute coiling (U/D from 0. 42 to 0.45) for the complete Subbetic specimens. The whorl section is subsquare to slightly compressed rectangular, with faintly convex flanks and a ventral area with a keel that is bordered by two more or less developed furrows. The innermost whorls are smooth or only slightly ornamented. Later, usually simple ribs appear, which arise at the base of the umbilical wall; somewhat sigmoid, these become stronger in upper part of the flanks, and some support mid-lateral nodes on intermediate whorls. At the BC end, the ribs weaken but do not vanish completely. The aperture is complex with lateral lappets. The septal suture of the HT is simpler but not preserved in the Subbetic specimens.

REMARKS
"*Pelekodites*" *schlumbergeri*, which has tubercles or nodes, could correspond as microconch of *S.* (*S.*) *propinquans*, which occurs in equivalent stratigraphic interval "*P.*" *macer* (Buckman, 1889) may be the most similar "species" but has a more compressed whorl section, no tuberculate stage, and a venter without ventral sulci. *Fontannesia curvata* Buckman, 1902 is also similar but is more evolute and has denser and more curvate ribs, which persist up to the BC end and lack tubercles. The tuberculate stage of *S.* (*S.*) *schlumbergeri* and its stratigraphic distribution indicate that this species may in reality be a dimorphic microconch of *Sonninia* and not of *Witchellia*.

DISTRIBUTION
The type of "*Sonninia Schlumbergeri*", the only Haug specimen of this species, comes from the *Otoites Sauzei* zone (Propinquans Zone), from the Haye forest, near Nancy (France). In the Atlas Mountains (Morocco), this species occurs in the upper part of the Laeviuscula and lower part of the Propinquans zones (Sadki 1996). In the western part of the Swabian Alb (Germany), *P.* cf. *schlumbergeri* occurs in the Pinguis Subzone (which is equivalent to the Hebridica Subzone of British researchers [Dietze *et al.* 2008]) and in Kahlenberg, near Ringsheim (Upper Rhine Valley), in the Laeviuscula Zone, Trigonalis Subzone (Dietze *et al.* 2009). This stratigraphic range is occupied by *P. schlumbergeri* in the Wedelsandstein-Formation in the "Zollernalb" of south-western Germany (Dietze *et al.* 2019). In the Subbetic, *S.* (*S.*) *schlumbergeri* occurs in the Laeviuscula Zone (Laeviuscula Subzone) and in the Propinquans Zone (Patella Subzone) of Sierra de Alta Coloma area (sections JAC3, JAC4, JAC11, JAC13, JAC22 and JAQ1; Jaén Province).

Subgenus *Sonninia* (*Euhoploceras*) Buckman, 1913 [M] & [m]

Sonninia (*Euhoploceras*) Buckman, 1913: 4.

?*Stiphromorphites* Buckman, 1923 [M]: pl. 398. — Type species: *S. nodatipinguis* Buckman, 1923 (OD).

Sherbonites Buckman, 1923 [M]: pl. 411. — Type species: *S. projectifer* Buckman, 1923 (OD).

Nannoceras Buckman, 1923 [m]: pl. 445, **n. syn.** — Type species: *N. nannomorphum* Buckman, 1923 (OD).

TYPE SPECIES. — *Sonninia acanthodes* Buckman, 1889 (Buckman 1889: 658 [OD]); HT figured in Buckman (1892: pl. 60, pl. 63, fig. 1).

DESCRIPTION
Macroconchs evolute to moderately involute with rectangular (sometimes almost square) to ovate, slightly compressed whorl sections. The venter is subtabulate, often slightly bisulcate and possesses a low hollow keel persisting to end of the BC. The inner whorls have weak primary ribs and many shells have well-developed tubercles or spines. The length of the spinose/tuberculate stage varies widely and it is not uncommon to find specimens that retain strong ribbing beyond the end of the PH. The BC commonly has single or, more rarely, some bifurcate ribs, which extend as far as the peristome. In others, tubercles give way to ribs, which progressively fade, the BC becoming striated or completely smooth. Conversely, many lack strong ornamentation throughout ontogeny occasionally with tiny spines present only on the earliest inner whorls.

Table 6. — Measurements of *Sonninia* (*Euhoploceras*) cf. *polyacantha* (Waagen, 1867) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAQ1.3.1	88.0 65.0	38.0 26.2	0.43 0.40	28.5 23.0	0.32 0.35	19.7 16.5	0.24 0.25	PH	Laeviuscula Zone

Secondary ribs range from strong to weak. The septal suture is relatively complex, with a ramified deep L, and slightly retracted U2-U5 lobes. Complete macroconchs have simple, only very slightly constricted peristomes, which appear to be rather weak and are consequently rarely preserved. The microconchs (*Nannoceras*) are much smaller, with more persistent ribbing and spatulate lateral lappets.

Remarks
According to some authors (Buckman 1928, T.A. 7: 13; Fernández-López 1985: 94), *Nannoceras* probably represents the dimorphous microconch of *S.* (*Euhoploceras*). Actually, other authors (Dietze *et al.* 2005: 59; Dietze *et al.* 2007: 16, 2011a: 217; Chandler *et al.* 2006: 370; Howarth 2013 in the *Treatise*) have suggested that *Fontannesia* Buckman [M] and the lappeted *Nannoceras* Buckman [m] constitute a dimorphous pair, which in turn are the most plausible ancestors of *Witchellia* [M] – *Pelekodites* [m]. Chandler (2019: 181, fig. 8e-g) figured three specimens of *S.* (*Euhoploceras*) [m], which are lappeted and have strong ribbing, and two have tuberculate inner whorls, which undoubtedly correspond to "*Nannoceras*". Dr. R.B. Chandler confirmed to me (personal communication, March 2021) that, as Fernández-López (1985) had indicated, *Nannoceras* [m] is the dimorphic pair of *S.* (*Euploceras*) [M] and he generously sent me some plaster casts and photographs of typical *Nannoceras* from the upper Aalenian (Concavum Zone, Limitatum Subzone) and Lower Bajocian (Discites Zone) of Dorset (S England), which stratigraphically coexist with *S.* (*Euhoploceras*).

Distribution
In agreement with the *Treatise* by Howarth (2013: 116), the present study concludes that the stratigraphic range of *S.* (*Euhoploceras*) extends throughout the upper Aalenian (Concavum Zone) to the lower Bajocian (Laeviuscula Zone) of Europe, North Africa (Atlas Ranges), Arabian Peninsula, China (Tibet), western Australia, Canada (British Columbia, Alberta), United States (Alaska, Oregon, California), Chile, and Argentina.

Sonninia* (*Euhoploceras*) cf. *polyacantha
(Waagen, 1867) [M]
(Figs 7N; 8A)

Material examined. — JAQ1.3.1.

Measurements. — See Table 6.

Description
The only available specimen is an incomplete, somewhat eroded PH. The internal mould of the PH measures 88 mm in diameter with the inner whorls, which are not preserved. The shell is a relatively evolute discoidal platycone. The whorl section is compressed subrectangular with a subvertical umbilical wall, rounded umbilical edge, and slightly convex, almost flat flanks. The venter is rounded, while the keel is hollow and partially preserved only in the first quarter of the last preserved whorl. The ribs, first slightly uneven, and then uniform, arise near the umbilical edge, radial and not strong, and fade on the upper part of the flank, where they lean slightly forward. Some of the stronger ribs appear to support small lateral tubercles. The septal suture (Fig. 8A) is typical of *S.* (*Euhoploceras*), being sharply divided with a deep L and slightly retracted umbilical lobes.

Remarks
In this subbetic specimen the intermediate whorls closely resemble those of the HT of *S.* (*E.*) *polyacantha* (Waagen, 1867), (refigured in Dorn 1935: pl. 9, fig. 1; Schlegelmilch 1985: pl. 17, fig. 2; Sadki & Dietze 2021: 4, text-fig. 7), the two specimens coinciding in the type of coiling, section, and radial ribbing, but the ribs are much weaker in the former.

Distribution
The HT of *S.* (*E.*) *polyacantha* comes from the Laeviuscula Zone (Trigonalis Subzone) of Gingen/Fils, southern Germany (Dietze *et al.* 2005; Sadki & Dietze 2021). The Subbetic specimen comes from the Laeviuscula Zone of the Barranco de Agua Larga section, Noalejo (Jaén Province).

Sonninia* (*Euhoploceras*) *nannomorpha
(Buckman, 1923), n. comb. [m]
(Fig. 9B)

Nannoceras nannomorphum Buckman, 1923: T.A. 5, pl. 445. — Dietze *et al.* 2011a: 226, pl. 7, figs 18-20 (HT refigured).

Nannoceras sp. cf. *N. nannomorphum* – Sadki *et al.* 2015: 61, pl. 14, fig. C.

Material examined. — JAC3.R.27, JAC22.5.1, MOD.X.319, MOD.X.320, MOD.X.321, MOD.X.322, MOD.X.323, MOD.X.330, MOD.X.332 and MOD.X.337.

Measurements. — See Table 7.

Description
Small microconchs with moderately evolute coiling. The whorl section, being depressed suboval in the innermost whorls, gradu-

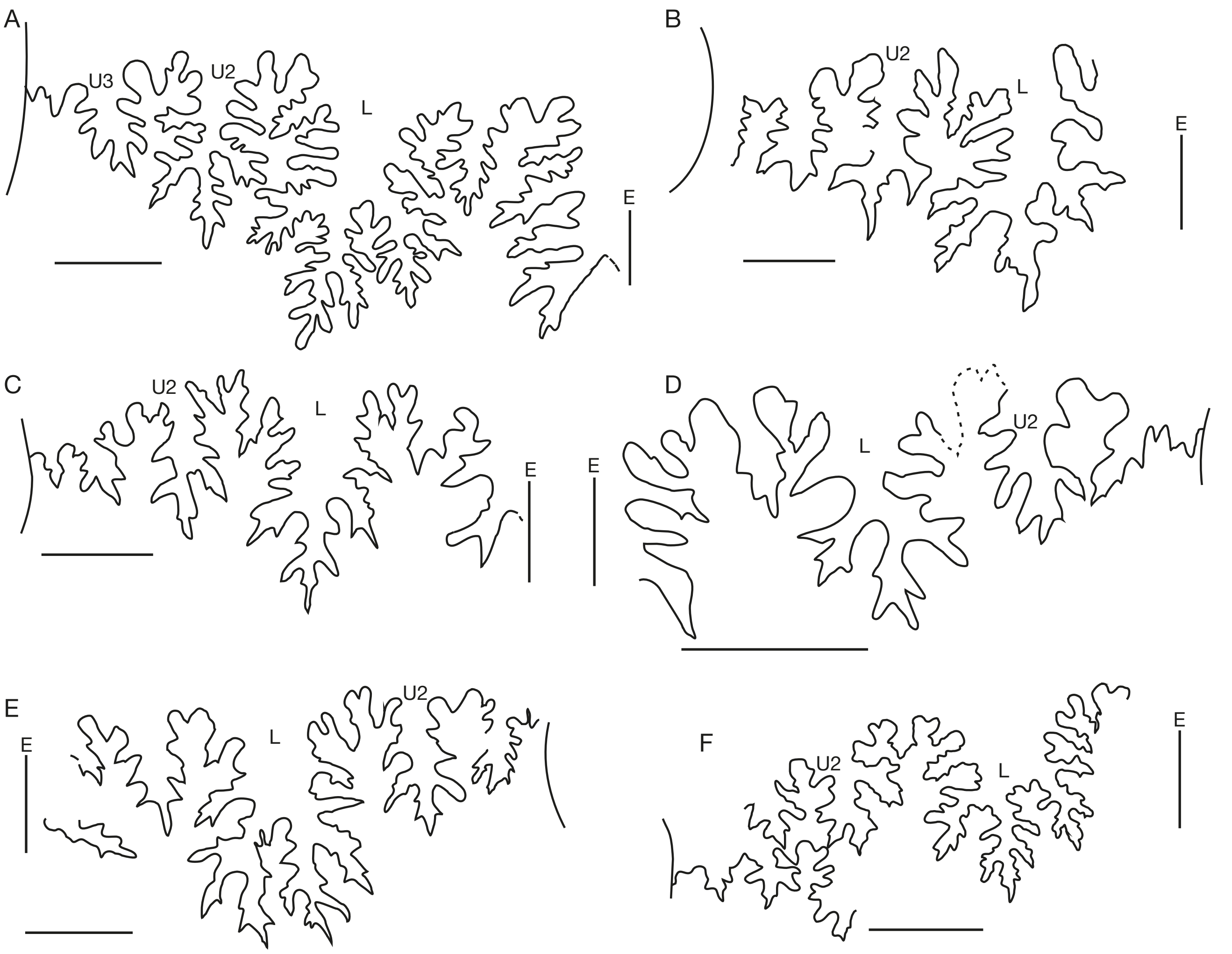


Fig. 8. — Septal suture of some Subbetic sonniniids: **A**, *Sonninia* (*Euhoploceras*) cf. *polyacantha* (Waagen, 1867) [M], specimen JAQ1.3.1; **B**, *Witchellia albida* (Buckman, 1926) [M], specimen JAC13.R.3; **C**, *Witchellia hyalina* (Buckman, 1924) [M], specimen JAC11.8.21; **D**, **E**, *Witchellia companyi* n. sp. [M], specimens JAC11.8.22 and JAC11.8.16 (HT); **F**, *Dorsetensia liostraca* Buckman, 1892 [M], specimen JGa8.32.4. Scale bars: 5 mm.

Table 7. — Measurements of *Sonninia* (*Euhoploceras*) *nannomorpha* (Buckman, 1923), n. comb. [m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.R.27	22.0	8.5	0.37	8.0	0.36	–	–	Adult microconchs	Discites Zone?
	17.0	6.0	0.35	6.2	0.36	–	–		
JAC22.5.1	18.0	7.2	0.40	6.0	0.33	–	–		Ovale Zone
	13.0	5.1	0.39	4.8	0.37	–	–		
MOD.X.319	31.0	12.0	0.39	11.1	0.36	–	–		Discites Zone

ally becomes compressed subrectangular in the adult BC. The umbilicus is wide and shallow with a rounded umbilical edge. The ventral region is weakly tabulated with a broad, low keel bordered by small sulci, which persist up to the vicinity of the adult peristome bearing spatulate lateral lappets. The ribs are usually simple, very rarely grouped near the umbilical edge or divided on the flanks, subradial or retroverse but slightly sinuous, gradually thickening from the umbilical edge to the ventrolateral margin. At the BC end, the ribs weaken but do not disappear completely. The inner whorls can be tuberculate. The septal suture is not well preserved in the available specimens.

Remarks

As indicated above regarding the genus, *Nannoceras* is the dimorphic partner of *S.* (*Euploceras*) and consequently "*N.*" *nannomorphum* should included in this genus.

Distribution

The HT of "*N.*" *nannomorphum* comes from the Discites Zone of Bradford Abbas Fossil Bed, near Yeovil, England (Buckman 1923; Dietze *et al.* 2011a), but according to Callomon & Chandler (1990) it is common at the base of Ovale Zone (Bj-4 horizon) of southern England. The species occurs

TABLE 8. — Measurements of *Sonninia* (*Papilliceras*?) sp. [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC22.6.13	64.0	24.5	0.38	24.0	0.375	–	–		Ovale Zone

in the Discites-lower part of the Ovale zones of the Atlas, Morocco (Sadki 1996), in the Discites Zone of the Iberian Range, Spain (Fernández-López 1985), and in the Discites Zone? of Luxembourg (Sadki *et al.* 2015). Subbetic specimens are from the Discites Zone of the MOD section, Montillana (Granada Province) and from the base of the Ovale zone of JAC22 section, Campillo de Arenas (Jaén Province).

Subgenus *Sonninia* (*Papilliceras*) Buckman, 1913 [M]

Sonninia (*Papilliceras*) Buckman, 1920: pl. 150.

Prepapillites Buckman, 1927: pl. 709. — Type species: *Ammonites arenatus* Quenstedt, 1886, *in* Quenstedt 1882-1888: 482, pl. 60, fig. 10 (OD).

TYPE SPECIES. — *Papilliceras papillatum* Buckman, 1923 (Buckman 1923: T.A. 3, pl. 150 [OD]).

DESCRIPTION
Sonninia (*Papilliceras*) is strongly similar to *S.* (*Sonninia*). The only appreciable generic difference is the presence of a row of lateral tubercles, one on each rib, persisting on the evolute compressed BC, even after the ribs have faded, or tubercles occur only on the BC. Some specimens have strigate ornament.

DISTRIBUTION
Lower Bajocian, Laeviuscula and Propinquans zones: Europe, Thailand, United States (Alaska, Oregon), Chile, Argentina and Peru. In the Subbetic domain, it is rare, occurring in the upper part of the Laeviuscula Zone of Sierra de Alta Coloma area (Jaén Province).

Sonninia* (*Papilliceras*) *arenata (Quenstedt, 1886) [M] (Fig. 9C)

Ammonites arenatus Quenstedt, 1886: 482-484, pl. 60, fig. 10 (HT).

Prepapillites arenatus – Buckman 1927: pl. 709.

Sonninia arenata – Dorn 1935: 38, pl. 7, fig. 1 (HT refigured), text-fig. pl. 3, figs 3, 4. — Schlegelmilch 1985: 60, pl. 16, fig. 4 (HT refigured).

Papilliceras arenatum – Maubeuge 1951: 49, pl. 3, fig. 2. — Sadki 1996: 175, pl. 5, fig. 1.

Sonninia patella arenata – Oechsle 1958: 102, pl. 12, fig. 10.

?*Sonninia* (*Papilliceras*) cf. *S.* (*P.*) *arenata* – Imlay 1964: B34, pl. 6, figs 1-3. — Imlay 1973: 68, pl. 26, fig. 11.

Sonninia (*Papilliceras*) *arenata* – Morton 1973: pl. 18, fig. 3; 1975: 73, pl. 11, figs 1, 2, pl. 12, figs 1, 2.

MATERIAL EXAMINED. — A.9.9.2.2-1.

REMARKS
The only available specimen is a BC fragment of a medium-sized specimen in which the coiling and the subrectangular whorl section, with gently convex flanks and ventral area with a high hollow keel, coincide with the HT of *Papilliceras arenatum*. The ornamentation consists of concave faint ridge-shaped ribs that end in the mid-lateral-tubercles.

DISTRIBUTION
According to Dietze *et al.* (2005: 23), the type horizon of *Ammonites arenatus* Quenstedt, 1886 lies in the Sauzei Zone. In Scotland, *S.* (*P.*) *arenata* is common in the Sauzei Zone (Morton 1973, 1975), while in Morocco it occurs near the Laeviuscula-Propinquans boundary (Sadki 1996). In Somerset-Dorset (England), the *S. micracanthica-arenata* assemblage is from the Laeviuscula Zone (Chandler *et al.* 2006: 366; Dietze *et al.* (2007: 12). In south-western Germany *S.* (*P.*) *arenata* appears from upper Laeviuscula and lower Sauzei (Propinquans) Zone (Dietze *et al.* (2008, 2009, 2011b). The exact beds of the sole Subbetic specimen (collected by J.M. Tavera), from La Torquilla (Sierra Alta Coloma area), are not known, but the lithology is characteristic of the uppermost Laeviuscula Zone or lowermost Propinquans Zone.

Sonninia (*Papilliceras*?) sp. [M] (Fig. 9D)

MATERIAL EXAMINED. — JAC11.R.61 and JAC22.6.13.

MEASUREMENTS. — See Table 8.

DESCRIPTION
The best-preserved specimen consists of a little more than three-quarters of whorl, including the end of the PH and the BC. The second specimen preserves just over a third of a whorl. These rather small macroconchs are relatively evolute and have moderate whorl expansion. The section is compressed subrectangular with a subvertical umbilical wall, rounded umbilical edge, faintly convex flanks, and a rounded ventral area with a

FIG. 9. — **A**, *Sonninia* (*Sonninia*) *schlumbergeri* Haug, 1893 [m], JAC4.39.10, Laeviuscula Zone, Sierra de Alta Coloma (JAC4 section); **B**, *Sonninia* (*Euhoploceras*) *nannomorpha* (Buckman, 1923), n. comb. ([m], JAC22.5.9, Ovale Zone, Sierra de Alta Coloma (JAC22 section); **C**, *Sonninia* (*Papilliceras*) *arenata* (Quenstedt, 1886) [M], A.9.9.2.2-1, Propinquans Zone?, Sierra de Alta Coloma; **D**, *Sonninia* (*Papilliceras*?) sp. [M], JAC22.6.13, Ovale Zone, Sierra de Alta Coloma (JAC22

section); **E**-**G**, *Sonninites felix* Buckman, 1923 [M]: **E**, **F**, JAC21.13.1, JAC21.16.1, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC21 section); **G**, JAC3'.10.1, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC3' section); **H**-**J**, *Sonninites sulcatus* (Buckman, 1889), n. comb. [m]: **H**, JAC11.8.32, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC11 section); **I**, JAC3'.8.1, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC3' section); **J**, JAQ1.8.1, Propinquans Zone, Barranco de Agua Larga (JAQ1 section); **K**, *Witchellia* cf. *W. nodatipinguis* (Buckman, 1923) [M], JAC11.R.50, Ovale Zone?, Sierra de Alta Coloma (JAC11 section). Scale bars: 1 cm (note that B element has a different scale bar).

high hollow keel. The ribs, well marked throughout ontogeny, are radial and bend forward near the venter. In the PH, between every 3 to 5 non-tuberculate ribs, a stronger one appears with a well-developed mid-lateral tubercle; subsequently the ribs become progressively uniform, all bearing less developed mid-lateral tubercles. Septal sutures are not preserved.

Remarks
The described specimens show intermediate characters between *S.* (*Euhoploceras*) and *S.* (*Papilliceras*), but the presence of typical mid-lateral tubercles has led to their being included, although with doubts, in *Papilliceras*. The most similar form may be "*Sonninia*" *mayeri* (Waagen, 1867), which has been considered synonymous to *S.* (*Euhoploceras*) *polyacantha* (Waagen, 1867) by Schlegelmilch (1985) and as a *nomen dubium* by Dietze *et al.* (2005: 35). However, German specimens are much larger and somewhat more evolute.

Distribution
The HT of the most similar species, *S.* (*E.*) *polyacantha*, comes from the Laeviuscula Zone, Trigonalis Subzone (*adicra* α or *adicra* β horizon) of Gingen/Fils, Germany (Sadki & Dietze 2021). The only Subbetic specimen sampled *in situ* is slightly older and comes from the Ovale Zone of the Barranco del Almendro Gordo section (JAC22), Sierra de Alta Coloma area, Campillo de Arenas (Jaén Province).

Genus *Sonninites* Buckman, 1923 [M] & [m]?

Sonninites Buckman, 1923: pl. 428A.

Sonnites – Buckman 1925: T.A. 5, pl. 528A, *nom. null.* (misspelling).

Type species. — *Sonninites felix* Buckman, 1923 (Buckman 1923: T.A. 5, pl. 428A [OD]).

Description
Inner whorls planulate, then involute and again uncoiling in the last half whorl. In the middle and outer whorls, the whorl section is oxycone compressed with steep, sharp-edged umbilical walls, flat or slightly convex sides, and rounded to fastigiate and keeled ventral region. Subdued ribbing on the inner whorls show single or divided ribs that are hardly if ever tuberculate and become completely smooth quite early while retaining a characteristic radial striation. The suture is complex and highly indented. Specimens, which clearly represent *Sonninites* microconchs, have not been described, although according to Chandler *et al.* (2006: 369), the paratype of *Sonninites felix* Buckman, 1923 (Buckman 1923: T.A. 5, pl. 423B) is almost certainly the microconch of this species, nevertheless this form is more probably *S.* (*Sonninia*) *corrugata* (Sowerby, 1824). In the Subbetic domain, in beds containing abundant *Sonninites* [M], microconchiate forms ("*Pelekodites*" *sulcatus*) appear showing attenuated ribs in the middle part of the flanks on the adult BC, which is keeled and occasionally bisulcate well-developed lateral lappets; they, represent their dimorphic partner of *Sonninites*.

Remarks
Sonninites macroconchs can be similar to certain involute species of *Witchellia*, but are smoother, have a more complex suture, and lack the subquadratic whorl section and the tabulate or bisulcate ventral area of that genus. *S.* (*Sonninia*) is more evolute and has more marked and persistent ribbing and tubercles. The presumable microconchiate *Sonninites* ("*Pelekodites*" *sulcatus* group) are practically indistinguishable from the microconchs of *Witchellia*.

Distribution
The HT of the type species, *So. felix* (Buckman, 1923) comes from the Sauzei (Propinquans) Zone, Bj-11a horizon, (Chandler *et al.* 2006: 369). The genus spans the Laeviuscula? – Propinquans zones: England (Buckman 1892, 1923, 1926; Chandler *et al.* 2006), Scotland (Morton 1975), France (Gillet 1937, Roché 1943, Pavia 1983, De Baets *et al.* 2008), Germany (Dorn 1935, Dietze *et al.* 2009, 2011a, b, 2020), Morocco (Sadki 1996), and the Iberian Cordillera and Majorca in Spain (Fernández-López 1985; Sandoval 1983, 1994). In the Subbetic domain, the subgenus is common in the Propinquans Zone of Sierra de Alta Coloma area (Jaén Province).

Sonninites felix Buckman, 1923 [M]
(Fig. 9E-G)

Sonninites felix (*in pars*) Buckman, 1923: T.A. 5, pl. 428A (HT), *non* pl. 428B (corresponds to *Sonninia corrugata* (Sowerby, 1824)).

Sonninia aff. *felix* – Gillet 1937: 35, pl. 4, fig. 4.

Sonninia felix – Fernández-López 1985: 54, pl. 8, figs 2, 3.

Sonninia ["*Sonninites*"] aff. *felix* – Dietze *et al.* 2009: 25, pl. 8, figs 1-3, *non* fig. 4, pl. 11, fig. 3.

Sonninia ["*Sonninites*"] *felix* – Dietze *et al.* 2011a: 213, pl. 6, fig. 6.

Sonninia (*Sonninites*) *felix* [M] – Chandler 2019: 777, fig. 16, b1-b2.

?*Sonninia carinodisca* – Dietze *et al.* 2020: 68, pl. 15, fig. 1.

Material examined. — JAC3.83.1, JAC3.91.2, JAC3'.4.30, JAC3'.10.1, JAC3'.13.1, JAC4.68.3, JAC4.R.21, JAC20.R.1, JAC21.12.8, JAC21.12.9, JAC21.13.1, JAC21.13.2, JAC21.13.4, JAC21.14.1, JAC21.15.3, JAC21.16.1, JAC21.17.2, JAC21.17.3, JAC21.17.4, JAC21.18.1, JAC21.18.2 and JAC22.(70-80).3.

Measurements. — See Table 9.

Description
Large discoidal shells of moderately involute coiling, with intermediate whorls more involute than the internal or external ones. Inner whorls have a subrectangular whorl section. The intermediate ones have a compressed ogival (oval) section, with the maximum width located near the middle part of the flanks, which are weakly convex. The umbilical wall is low, subvertical or strongly sloping and

TABLE 9. — Measurements of *Sonninites felix* Buckman, 1923 [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.91.2	46.0	11.0	0.24	20.0	0.43	–	–	Incomplete	Propinquans Zone
	38.0	8.5	0.22	17.0	0.45	–	–		
JAC3'.10.1	64.0	13.5	0.21	31.0	0.48	–	–		
	44.0	10.0	0.23	22.0	0.50	–	–		
JAC21.13.1	140.0	40.0	0.29	60.0	0.43	26.0	0.19	Complete adut	
	105.0	27.0	0.26	44.5	0.42	19.0	0.18		
JAC21.16.1	67.0	14.5	0.22	31.5	0.47	–	–	Incomplete specimens?	
	59.0	12.0	0.20	28.5	0.48	–	–		
JAC21.17.3	58.0	11.5	0.20	30.0	0.52	–	–		
	41.0	9.0	0.22	20.0	0.49	–	–		

the ventral region is ogival, with a narrow, high and hollow keel. Ornamentation varies throughout ontogeny. In the internal whorls with furcate ribs, the splitting point of the ribs coincides with a thickening near the umbilical edge, and subsequently the division point gradually becomes more external. In the intermediate whorls, the ribbing is subradial or slightly sigmoid, bending forward on the outer side of the flanks, irregular in relief, fasciculate in two or three at variable height in the lower half of the flanks. Simple ribs (*c.* 40-50 mm in diameter) are common, slightly flexuous, rectiradiate, and prominent in the inner half of the flanks, but weaker and curved forward in the outer half. In addition, some weaker intercalatory ribs appear, and finally, on the end portion of the PH and in the BC of adult specimens, the ribbing is extremely attenuated, or even absent, and the ornamentation diminishes to weak undulations and growth lines or striae. The septal suture is relatively complex, with highly branched L and U_2 that are wide and not deep, whereas the E-L and L-U_2 saddles are rather narrow, and the umbilical lobes are weakly retracted.

REMARKS

Sonninites celans Buckman, 1924 (Buckman 1924: T.A. 5, pl. 461) is more involute, mainly in intermediate whorls, and has more radial ribbing. "*Dundryites*" *albidus* Buckman and "*Sonninites*" *simulans* Buckman (here considered synonymous and ascribed to the genus *Witchellia*) have similar ribbing on median and external whorls, but have no tuberculate inner whorls and a rectangular whorl section, with a tabulate venter. *Sonninia* (*S.*) *corrugata* (Sowerby, 1824) has similar inner whorls, but is smaller, has more persistent ribbing, and is slightly more evolute. *Dorsetensia subtecta* Buckman, 1892 (in Buckman 1887-1907: 309, pl. 55, only pl. 54, figs 3-5, here included as synonymous of *Dorsetensia liostraca*) has quite similar coiling and ornamentation on the outer whorls, but its ribbing sharply differs on inner whorls, it lacks tubercles, and its umbilical wall is not subvertical.

DISTRIBUTION

According to Chandler *et al.* (2006: 369) the HT of *Sonninites felix* (Buckman, 1923) comes from the Sauzei (Propinquans) Zone, Patella Subzone, Bj-11a horizon, Inferior Oolite at South Main Road Quarry, Dundry, Avon (England). Recently, Dr R. B. Chandler (pers. communication) indicated the exact stratigraphic horizon from which the HT of *So. felix* came (i.e. the *Stephanoceras rhytum* horizon, Bj-12, top of the Sauzei = Propinquans Zone). In England, this species is present also in the horizon Bj-11b (Dietze *et al.* 2011a). In Germany, *So. felix* and *So.* aff. *felix* occur in the Macrum horizon, in the upper part of the Propinquans (Sauzei) Zone (Dietze *et al.* 2009, 2011a, b). In La Baume (Castellane area, SE France), *So.* cf. *felix* occurs in the Propinquans Zone (De Baets *et al.* 2008). In the Iberian Cordillera (Spain), the species is common in the lower and middle parts of the Sauzei (Propinquans) Zone (Fernández-López 1985). In the Subbetic, it occurs in the Propinquans Zone, being especially abundant in Sierra de Alta Coloma area (sections, JAC3, JAC3', JAC4, JAC11, JAC21 and JAC.22; Jaén Province).

Sonninites sulcatus (Buckman, 1889), n. comb. [m]
(Fig. 9H-J)

Lillia sulcata Buckman, 1889: 109, pl. 22, figs 32, 33, pl. 33, fig. 1 (LT here designated).

Sonninia sulcata – Haug 1893: 290, text-fig. 5, pl. 9, figs 1-3, pl. 10, fig. 9.

Sonninia deltafalcata – Haug 1893: 293, pl. 9, fig. 8 (non figs 5, 9).

Pelekodites sulcatus – Pavia 1983: 60, pl. 5, figs 4, 5. — Sandoval 1990: 147, pl. 2, fig. 2.

Pelekodites sp. – Pavia 1983: 60, pl. 5, figs 6, 7.

Maceratites sulcatus "sensu" Haug 1893 – Fernández-López 1985: 107, pl. 10, fig. 12.

Pelekodites sulcatus [m] – Dietze *et al.* 2009: 27, pl. 4, fig. 4.

MATERIAL EXAMINED. — JAC3.60.1, JAC3.60.2, JAC3.83.2, JAC3.89.1, JAC3'.8.1, JAC3'.15.1, JAC11.8.30, JAC11.8.32, JAC4.54.1, JAC21.(14-8).1, JAC21.17.6, JAC21.18.6 JAC21.25.1, JAC21.R.1, JAQ1.8.1 and APM.71.

MEASUREMENTS. — See Table 10.

TABLE 10. — Measurements of *Sonninites sulcatus* (Buckman, 1889), n. comb. [m].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC3.83.2	20.0	7.4	0.37	7.0	0.35	–	–	Adult complete microconchs	Propinquans Zone
JAC3.89.1	28.5	10.5	0.37	10.5	0.37	7.0	0.25		
JAC3'.8.1	36.0	12.0	0.33	12.0	0.33	–	–		
JAC11.8.32	31.0	11.0	0.35	11.0	0.35	8.0	0.26		
JAQ1.8.1	31.0	10.3	0.33	11.0	0.35	8.0	0.26		

DESCRIPTION

Small shells, moderately evolute coiling (U/D varying from 0.33 to 0.37 in the Subbetic specimens and is 0.39 in the specimen figured by Buckman [1888: pl. 22, figs 32, 33]; LT here designated). The whorl section is suboval with convex flanks in the inner and intermediate whorls, becoming compressed subrectangular with almost flat flanks and a wide, rounded ventral area in the adult BC. The wide venter has a low keel bordered by wide grooves throughout the PH that fade progressively in the BC and disappear near the adult peristome, which bears well-developed lateral apophyses and a small ventral rostrum. In the inner whorls, flexuous, subradial, simple or paired ribs end in a small tubercle near the umbilical seam. In the middle whorls, the ribs become more proverse and generally become paired in a thickening near the umbilical edge. In the adult BC, the ribs attenuate, mainly in the middle part of the flanks, where they can almost disappear. The septal suture is not well preserved in the Subbetic specimens.

REMARKS

The Subbetic specimens differ from the HT in being slightly smaller, having a more compressed whorl section, and being somewhat more involute. However, they coincide well with the specimens figured by Haug (1893), Pavia (1983, especially with the specimens nominated as *Pelekodites* sp.), Fernández-López (1985), and by Dietze *et al.* (2009). *Sonninites sulcatus* n. comb. [m] occurs frequently in the same beds as *Sonninites felix* [M], suggesting that the two taxa may be a dimorphic pair.

DISTRIBUTION

According to Buckman (1889: 109) the type of "*Lillia sulcata*" comes from the Humphriesianum Zone of Bradford Abbas (Dorset, England). The specimens figured by Haug (1893) are from the Sauzei Zone (Bayeux and Nancy, France). In the Digne area of south-eastern France, "*P.*" *sulcatus* occurs in the Propinquans Zone (Pavia 1983). In the Iberian Range (Spain), this species appears in the Humphriesianum Zone, in a presumably reworked material (Fernández-López 1985). In Kahlenberg, near Ringsheim, Upper Rhine Valley (SW Germany), "*P.*" *sulcatus* occurs in the upper part of the Sauzei Zone (Propinquans Zone, Hebridica Subzone; Dietze *et al.* 2009, 2011b). In the Subbetic, *Sonninites sulcatus* n. comb. is relatively common in the Propinquans Zone but rarer in the Laeviuscula Subzone, from some Median Subbetic sections of Sierra de Alta Coloma area (Granada and Jaén Provinces).

Subfamily WITCHELLIINAE Callomon & Chandler, 2006

Witchelliinae Callomon & Chandler *in* Chandler, Callomon, King, Jeffreys, Varah & Bentley, 2006: 370.

DESCRIPTION

Medium to relatively large macroconchs [M], but smaller than those of Sonniniinae. Coiling is involute to moderately evolute, with a compressed whorl section, varying from typically rectangular or subtriangular, to even ovate or oxycone, with a more or less developed keel. The ribs, radial or slightly proverse and simple or divided near the umbilical edge, have irregular thickness and usually fade towards the outer whorls, which in some forms become completely smooth or the ornamentation is reduced to striae. The innermost whorls of some forms have small lateral tubercles. The aperture has plain mouth borders. Dimorphic microconchs [m], (until now usually nominated *Pelekodites*), small adult at 20-60 mm in diameter, are usually ribbed to the end of the BC and have final adult mouth borders with long, spatulate lappets in some forms. The dimorphic size ratio is modest, between 2:1 and 3:1. The septal suture is simple, with L wide and short; scarcely retracted umbilical lobe, and barely trimmed saddles.

REMARKS

As indicated above, Howarth (2013) included the genera *Asthenoceras* Buckman, 1899, *Fontannesia* Buckman, 1902, *Newmarracarroceras* Hall, 1989, *Witchellia* Buckman, 1889, and *Guhsania* McLearn, 1926 in the subfamily Witchelliinae but placed *Dorsetensia* in Sonniniinae. However, as also shown above, *Asthenoceras* and presumably also *Fontannesia, Newmarracarroceras,* and *Latiwitchellia* should be transferred to Grammoceratinae, as they coincide in coiling, ribbing, and type of keel as well as presenting an extremely simple septal suture (see Sandoval *et al.* 2012). Nevertheless, the genus *Dorsetensia*, which succeeds *Witchellia* in time, and from which it possibly descended, is included here in Witchelliinae. *Witchellia* and *Dorsetensia* have a similar section, similar coiling and ornamentation, and also a comparable dimorphism. The slightly more complex septal suture of *Dorsetensia* is the only remarkable difference.

DISTRIBUTION

Middle Jurassic (Lower Bajocian, Ovale Zone-Humphriesianum Zone): Europe (England, Belgium, Bulgaria, France, Germany, Italy, Luxembourg, Poland, Portugal, Romania, Spain, and Switzerland), North Africa (Atlas Ranges), Madagascar, Caucasus, Iran, China (Tibet), Japan, western Australia, Canada (British Columbia), United States (Alaska, Oregon), and Argentina. In the Subbetic domain, Witchelliinae spans the Lower Bajocian (Ovale, Laeviuscula Propinquans and Humphriesianum zones), being especially abundant in the Laeviuscula Zone of the central sector of the Median Subbetic, Sierra de Alta Coloma area (Jaén Province).

Genus *Witchellia* Buckman, 1889 [M] & [m]

Witchellia Buckman, 1889: 82.

Zugophorites Buckman, 1922 [M]: pl. 341. — Type species: *Z. zugophorus* Buckman, 1922 (OD).

?*Stiphromorphites* Buckman, 1923 [M]: pl. 398. — Type species: *S. nodatipinguis* Buckman, 1923 (OD).

Pelekodites Buckman, 1923 [m]: pl. 399. — Type species: *P. pelekus* Buckman, 1923 (OD).

Hyalinites Buckman, 1924 [M]: pl. 519. — Type species: *H. hyalinus* Buckman, 1924 OD.

Gelasinites Buckman, 1925 [M]: pl. 593A. — Type species: *G. gelasinus* Buckman, 1925 (OD).

Rubrileiites Buckman, 1926 [M]: pl. 642. — Type species: *R. ruber* Buckman, 1926 (OD).

Anolkoleiites Buckman, 1926 [M]: pl. 659. — Type species: *A. plenus* Buckman, 1926 (OD).

Dundryites Buckman, 1926 [M]: pl. 687. — Type species: *D. albidus* Buckman, 1926 (OD).

Zugella Buckman, 1927 [M]: pl. 750. — Type species: *Z. connata* Buckman, 1927 (OD).

Spatulites Buckman, 1928 [m]: pl. 765. — Type species: *S. spatians* Buckman, 1928 (OD).

Maceratites Buckman, 1928 [m]: pl. 766. — Type species: *M. aurifer* Buckman, 1928 (OD).

Type species. — *Ammonites laeviusculus* J. de C. Sowerby, 1824 (Sowerby 1824: 73, pl. 451, figs 1, 2 [OD]).

Description

The dimorphism in Witchelliinae is consistent and clear. Macroconchs [M], discoidal of medium to relatively large size, are involute to semi-evolute with innermost whorls more evolute than the middle and outer ones, with a subrectangular whorl section, an almost vertical umbilical wall, rounded umbilical margin, and flanks that are flat or very slightly convex. The venter is tabulate, sometimes bisulcate, mainly on inner whorls, rarely tricarinate bisulcate, and the more or less developed keel persists throughout ontogeny. The ribbing has irregular thickness, sinuous, radial or slightly proverse. The ribs, simple or more usually grouped in pairs near the umbilical edge, progressively fade throughout ontogeny, sometimes completely disappearing at the adult stages, when they become smooth or finely striated. Some species can have very small tubercles on inner whorls. The peristome is simple. The septal suture is also simple, with wide and short L, and a few incised saddles. The microconchs [m] (formely *Pelekodites*, *Maceratites* and *Spatulites*), much smaller and slightly more evolute than macroconchs, are usually ribbed to the BC end (although some forms are striate throughout ontogeny) and have spatulate lateral lappets.

Remarks

Fernández-López (1985) maintained that the non-tuberculate microconchs, which he included in *Maceratites*, constitute the dimorphous partner [m] of *Witchellia,* whereas the tuberculate forms, which he included in *Pelekodites*, are dimorphic of *Sonninia*. However, this assertion can not be confirmed because the type species of *Pelekodites* (see Howarth 2013: fig. 82, 4c-d) is not tuberculate.

Certain problems arise concerning with the taxonomic status of the "genera" *Stiphromorphites* Buckman, 1923 (Buckman 1923: T.A. 4, pl. 398 (type *S. nodatipinguis,* OD) (in the *Treatise*, synonymous with *Euhoploceras*) and *Dundryites* Buckman, 1926 (Buckman 1926: T.A. 6, pl. 687 [type *D. albidus*, OD]) (in the *Treatise* synonymous with *Sonninites*), as these forms closely resemble *Witchellia* [M]. *Stiphromorphites nodatipinguis*, showing intermediate characters between *S.* (*Euhoploceras*) and *Witchellia,* was included in *Witchellia* by Parsons (1974: 168) and Fernández-López (1985: 67). However, Dietze *et al.* (2005: 25) considered it to be synonymous with *S.* (*Euhoploceras*) *adicra* (Waagen, 1867) whereas Chandler *et al.* (2006: 363) and Chandler & Whicher (2015: pl. 9, fig. 1) indicated that *S.* (*Euhoploceras*) *nodatipinguis* typifies the horizon Bj8-a, in the Laeviuscula Zone, Trigonalis Subzone in Dorset (England). *Dundryites albidus* was included as synonymous with *Witchellia* by Fernández-López (1985: 81), by Chandler & Whicher (2015) and, with some doubt, by Dietze *et al.* (2003: 11). However, Dietze *et al.* (2007: 13) excluded it from the Witchelliinae and revived Buckman's genus *Dundryites*. *D. albidus* is thus possibly the ancestor of *Sonninites,* displaying intermediate characters between *Witchellia* and *Sonninites.*

Witchellia bears considerable affinities with *S.* (*Sonninia*), *S.* (*Euhoploceras*), *Dorsetensia*, and *Sonninites*. *S.* (*Sonninia*) is usually larger, has an ovate or ogival whorl section without a ventral tabulate region, a higher keel, more persistent tubercles, and a more complex septal suture. As indicated above, some "*Pelekodites*" and/or "*Maceratites*", which are here included as synonymous of *Witchellia*, may represent *S.* (*Sonninia*) microconchs [m]. *S.* (*Euhoploceras*), which precedes it in time, is larger, generally more evolute, has no grouped ribs, more developed tubercles, and a more complex septal suture. *Dorsetensia* is similar to *Witchellia* in size, coiling, whorl section, keel, and dimorphism, but its ribs are single (only exceptionally are grouped), it has no tubercles, and its venter is not tabulate. Meanwhile, *Sonninites* is larger than *Witchellia* and generally more involute; also, it has an oxyconic whorl section, roughly rectangular in the middle and outer whorls, which are always striate or smooth, and it has a more complex septal suture.

Table 11. — Measurements of *Witchellia* cf. *W. nodatipinguis* (Buckman, 1923) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC11.3.3	85.0	27.0	0.32	34.0	0.40	18.0	0.21	Mostly incomplete specimens	Ovale Zone?
	59.0	19.0	0.32	25.1	0.43	14.0	0.24		
JAC11.3.5	45.0	12.5	0.28	19.0	0.42	10.0	0.22		
	35.0	9.5	0.27	15.0	0.43	8.3	0.24		
JAC11.R.43	35.0	8.9	0.25	15.0	0.43	–	–		
	24.0	6.3	0.26	10.2	0.43	–	–		
JAC11.R.49	37.0	11.0	0.30	16.0	0.43	–	–		
JAC11.R.50	38.5	13.0	0.34	14.5	0.38	10.0	0.26		
	27.0	8.7	0.32	10.0	0.37	6.0	0.22		

Distribution

Middle Jurassic (Lower Bajocian, Ovale Zone-Propinquans Zone): Europe (England, Belgium, Luxembourg, France, Germany, Switzerland, Poland, Romania, Bulgaria, Italy, Portugal, Spain), North Africa (Atlas Mountains), Arabian Peninsula, Madagascar, the Caucasus, Iran, Tibet (China), Japan, western Australia, Canada (British Columbia), United States (Alaska, Oregon), and Argentina. In the Subbetic, *Witchellia* ranges throughout the Ovale, Laeviuscula, and Propinquans zones, being especially abundant in the Laeviuscula Zone of the central sector of the Median Subbetic, Sierra de Alta Coloma area (Jaén Province).

Witchellia cf. *W. nodatipinguis* (Buckman, 1923) [M] (Figs 9K; 10A)

cf. *Stiphromorphites nodatipinguis* Buckman, 1923: T.A. 4, pl. 398 (HT).

Sonninia cf. *S. nodatipinguis* – Imlay 1973: 62, pl. 13, figs 1-4.

cf. *S.* (*Euhoploceras*) *nodatipinguis* – Chandler & Whicher 2015: pl. 9, fig. 1.

Material examined. — JAC11.3.3 to JAC11.3.8, JAC11.R.9, JAC11.R.43, JAC11.R.44, JAC11.R.45 and JAC11.R.48 to JAC11.R.53.

Measurements. — See Table 11.

Description

Small to medium-sized shells, platycone with relatively involute coiling (U/D varying between 0.25 and 0.34). The whorl section is ovate (inner whorls) to almost rectangular, with a vertical umbilical wall, slightly convex flanks, and a tabulate venter with a low keel. The peristome is not present in the available specimens. The innermost whorls appear to have small tubercles, later periumbilical tuberculiform thickenings or primary ribs appear, from which two secondary ribs emerge, one more prominent than the other and, in addition, some weak intercalate ribs appear. On the outer whorls the thickenings progressively disappear, and distinct and less distinct radial ribs alternate, all weakening at the upper half of the flanks, where they gently bend forward and progressively erase, leaving a smooth ventrolateral shoulder near the keel. In some of the smaller specimens (maybe microconchs) the ribs are replaced by striae in the BC. The septal suture is not well preserved but appears to be quite simple.

Remarks

The specimens described resemble "*Stiphromorphites*" *nodatipinguis* Buckman, 1923 (Buckman 1923, T.A. 4: pl. 398), but the Subbetic specimens are more involute than the HT of "*St.*" *nodatipinguis* and have different ornamentation on the inner whorls, and the two species occupy different stratigraphic ranges. Thus while "*St.*" *nodatipinguis*" constitutes a characteristic horizon (Bj-8a) in the Trigonalis Subzone of the Laeviuscula Zone (Chandler *et al.* 2006; Dietze *et al.* 2008, 2009, 2010a), the Subbetic forms are from the Ovale Zone or even the uppermost Discites Zone.

According to Dietze *et al.* (2005: 25), this "species" is a small adult form synonymous with *S.* (*Euhoploceras*) *adicra* (Waagen, 1867), but this could not be corroborated because actually *S.* (*Euhoploceras*) *adicra* has an ovate rather than rectangular whorl section on outer whorls and a well developed tuberculate stage that is not present on *W. nodatipinguis.* Some strongly ribbed *Witchellia* species such as *W. sutneri* (Branco, 1879) (HT refigured in Schlegelmilch 1985: pl. 19, fig. 4), *W. glauca* Buckman, 1925 (Buckman 1925, T.A. 6: pl. 594), *W. platymorpha* Buckman, 1926 (Buckman 1926, T.A. 6: pl. 580A), *W. falcata* Buckman, 1926 (Buckman 1926, T.A. 6: pl. 688), and *W. actinophora* Buckman, 1926 (Buckman 1926, T.A. 6: pl. 689) also bear similarities with the Subbetic specimens in whorl section, coiling, and septal suture, but the four Buckman' species have sigmoid rather than radial ribbing as well as a different stratigraphic position. The type of *W. sutneri* has well differentiated ventral sulci and a clear separation between the primary and secondary ribs. The relatively simple septal suture, the tabulate venter, and the absence of well-marked tubercles of the Subbetic specimens makes it closer to *Witchellia* than to *S.* (*Euhoploceras*).

Distribution

In the section at Redhole Lane, described by Buckman (1893), Parsons (1974), and Huxtable (2000), the critical interval lies in the so-called Blue Bed, bed 3. There, the upper part, 3b in the section as described by Huxtable, constitutes the type horizon of '*Stiphromorphites*' (*Euhoploceras*) *nodatipinguis* Buckman, Horizon Bj-8a, Laeviuscula Zone, Trigonalis Subzone (see Dietze *et al.* 2005: 76). The specimen figured

Fig. 10. — **A**, *Witchellia* cf. *W. nodatipinguis* (Buckman, 1923) [M], JAC11.3.3, Ovale Zone, Sierra de Alta Coloma (JAC11 section); **B**-**E**, *Witchellia connata* (Buckman, 1927) [M]: **B**, **C**, JAC3.33.1, JAC3.33.2, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC3 section); **D**, **E**, JAC11.5.32, JAC11.R.19, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC11 section); **F**-**K**, *Witchellia romanoides* (Douvillé, 1885) [M]: **F**, **J**, JAC22.5.22, JAC22.5.8, Ovale Zone, Sierra de Alta Coloma (JAC22 section); **G**, JAC3.21.2, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC3 section); **H**, JFB.R.1, Laeviuscula Zone, Río Fardes area (JFB section); **I**, **K**, JAC11.R.20, JAC11.4.14, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC11 section). Scale bar: 1 cm.

Table 12. — Measurements of *Witchellia connata* (Buckman, 1927) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.33.1	45.0	16.0	0.36	18.0	0.40	10.0	0.22	Mostly incomplete and crushed specimens	Laeviuscula Zone, Trigonalis Subzone
	35.0	12.5	0.36	13.3	0.38	7.5	0.21		
JAC3.33.2	55.0	21.0	0.38	20.0	0.36	11.0	0.20		
	41.0	16.0	0.39	16.0	0.39	–	–		
JAC11.5.32	41.0	16.0	0.39	14.0	0.34	–	–		
	32.0	12.1	0.38	11.5	0.36	–	–		
JAC11.R.19	54.0	21.0	0.39	20.0	0.37	*c.* 13.0	*c.* 0.24		Laeviuscula Zone?
	39.0	14.5	0.37	14.3	0.37	8.2	0.21		
JAC11.R.26	46.5	16.3	0.35	18.2	0.39	9.0	0.19		
	32.0	10.2	0.32	13.5	0.42	7.0	0.22		

by Chandler & Whicher (2015) comes from the same faunal horizon. The highly similar specimens, from Oregon (United States), described and figured by Imlay (1973) are also from the Trigonalis Subzone. All the Subbetic specimens appear to be stratigraphically older (lowermost part of the Trigonalis Subzone?, Ovale Zone or even the upper part of the Discites Zone) than any of the strongly ribbed species of *Witchellia*.

Witchellia connata (Buckman, 1927) [M] (Fig. 10B-E)

Zugella connata Buckman, 1927: T.A. 7, pl. 750, figs 1-3 (HT).

Witchellia connata – Imlay 1973: 69, pl. 20, fig. 4, pl. 21, figs 1-7, 10, 11. — Fernández-López 1985: 82, pl. 6, fig. 2. — Sadki 1996: 173, pl. 4, fig. 7. — Seyed-Emami *et al.* 2000: 258, figs 3/2-3. — Ohmert 2004: 49, text-figs 8, 9, pl. 12, figs 1-9.

Witchellia aff. *connata* [M] – Dietze *et al.* 2003: 9, pl. 1, fig. 2.

Witchellia connata [M] – Dietze *et al.* 2007: 6, figs 3a-d. — Dietze *et al.* 2019: 58, figs 4(4, 6).

Material examined. — JAC3.19.3, JAC3.20.10, JAC3.33.1, JAC3.33.2, JAC11.5.6, JAC11.5.32, JAC11.R.19, JAC11.R.26, JAC22.40.1, JAC22.40.2, JVM.26, JVM.31, JVM.32, JVM.33 and JVM.34.

Measurements. — See Table 12.

Description

Medium-sized discoidal shells, compressed with moderately evolute coiling. The whorl section is subrectangular, with a flat and sloping umbilical wall, rounded umbilical edge, weakly convex flanks converging towards the ventral region, which is rounded to tabulate with a keel, but without ventral sulci, at least on the outer whorls. The innermost whorls appear to be smooth, but later ribs emerge, barely sinuous, proverse or subradial, irregular in relief, and prominent, especially towards the outer region of the flank. Ribs are usually grouped two by two near the umbilical edge, or can be simple whereas a few others may bifurcate into the lower third of the flank and all project forward in the ventral region. Some specimens present occasional thickenings near the umbilical edge coinciding with grouping of the ribs, but without a tuberculate stage. The septal suture is relatively simple, with L being wide and short.

Remarks

W. connata is distinguished from most of the congeneric species for having more prominent ribs grouped in pairs next to the umbilical edge. The most similar species is *Witchellia zugophora* Buckman, 1923 (Buckman 1923: T.A. 4, pl. 341) which has comparable coiling and ribbing, but is much larger and has prominent sulci bordering the keel. Other *Witchellia* strongly ribbed are: *W. glauca* Buckman, 1926 (Buckman 1926: T.A. 6, pl. 688); *W. falcata* Buckman, 1925 (Buckman 1925: T.A. 6, pl. 594) and *W. actinophora* Buckman, 1926 (Buckman 1926: T.A. 6, pl. 689). The three forms, possibly synonymous with each other, are more involute and have markedly sigmoid ribbing.

Distribution

The HT of *W. connata* comes from Sherborne (England) and was referred, with doubts, to the "Hemera Fissilobata" by Buckman (1927). In southern England, *W. connata* constitutes a typical horizon in the Trigonalis Subzone of the Laeviuscula Zone, but it is cited also from the Ovale and Laeviuscula zones (Chandler & Dietze 2004; Dietze *et al.* 2007). In Germany, this species is recorded in the Laeviuscula Zone, Trigonalis Subzone (Dietze *et al.* 2003, 2005, 2010a, 2019). In the Iberian range (Spain), this species occurs in the Ovale and lower part of the Laeviuscula zones (Fernández-López 1985). In the Atlas Mountains (Morocco), it has been cited in the upper part of the Laeviuscula Zone (Sadki 1996). Subbetic specimens are from the Laeviuscula Zone (Trigonalis Subzone) of Sierra de Alta Coloma area (sections JAC3, JAC11 and JAC22) and from a condensate bed of La Morenica (section JVM), with ammonites of the Laeviuscula Zone and the base of the Propinquans Zone, Valdepeñas de Jaén, both in Jaén Province.

Witchellia romanoides (Douvillé, 1885) [M] (Fig. 10F-K)

Ludwigia romanoides Douvillé, 1885: 28, fig. 9, pl. 3, figs 3, 4 (LT designed by Dietze *et al.* 2007).

Witchellia (*W.*) *romanoides* – Parsons 1979: pl. 1, figs 3, 5.

Witchellia sp. – Pavia 1983: pl. 4, fig. 3.

TABLE 13. — Measurements of *Witchellia connata* (Buckman, 1927) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.21.2	78.0	30.0	0.38	27.0	0.35	–	–	Complete or nearly complete specimens	Laeviuscula Zone, Trigonalis Subzone
	56.0	21.0	0.375	21.5	0.38	–	–		
JAC3.31.5	43.0	13.5	0.31	18.0	0.42	–	–		
	34.0	10.0	0.29	13.5	0.40	–	–		
JAC3.R.5	57.0	20.0	0.35	20.5	0.36	11.0	0.19		Trigonalis Subzone?
	41.0	14.0	0.34	16.0	0.39	8.5	0.21		
JAC4.15.3	50.0	17.5	0.35	19.0	0.38	–	–		Laeviuscula Zone, Trigonalis Subzone
	38.0	12.0	0.32	15.0	0.40	–	–		
JAC4.33.2	52.0	15.5	0.30	21.0	0.40	–	–		
	34.0	10.0	0.29	15.0	0.44	–	–		
JAC11.4.11	64.0	21.0	0.33	26.5	0.41	–	–		
	50.0	16.5	0.33	21.5	0.43	–	–		
JAC11.4.14	63.0	21.5	0.33	22.0	0.35	–	–		
	52.0	16.0	0.31	21.0	0.40	–	–		
JAC11.4.24	51.0	17.5	0.34	20.0	0.39	*c.* 9.5	*c.* 0.19		
	40.0	13.5	0.34	16.0	0.40				
JAC11.R.20	66.0	23.3	0.35	25.0	0.38	–	–		Laeviuscula Zone?
	48.0	16.0	0.33	19.7	0.41	–	–		
JAC11.R.13	58.0	17.0	0.29	23.5	0.41	*c.* 13.0	*c.* 0.22		
	41.0	10.5	0.26	17.5	0.43	9.5	0.23		
JFB.R.1	66.0	21.5	0.33	24.5	0.37	12.0	0.18		
	50.0	16.0	0.32	19.0	0.38	*c.* 9.5	*c.* 0.19		
JAC22.5.8	62.0	18.1	0.29	27.5	0.44	13.0	0.21		Ovale Zone
	47.0	12.5	0.27	21.0	0.45	9.5	0.20		
JAC22.5.22	51.0	16.0	0.31	20.0	0.39	10.0	0.20		
	41.0	12.5	0.30	17.5	0.43	8.6	0.17		
JAC22.28.5	41.0	13.0	0.32	16.0	0.39	9.0	0.22		Trigonalis Subzone
	30.0	9.3	0.31	13.0	0.43	–	–		

Witchellia romanoides – Fernández-López 1985: 72, text-figs 8F, 8G, pl. 6, figs 5, 6. — Sadki 1996: 172, pl. 4, fig. 3. — Ohmert 2004: 56, pl. 15, figs 5, 6.

Witchellia romanoides [M] – Dietze *et al.* 2007: 10, pl. 4, figs 1-5.

Witchellia pseudoromanoides – Metodiev 2019: 15, figs 5c-e.

Witchellia patefactor – Metodiev 2019: 15, figs 5g, h.

MATERIAL EXAMINED. — JST.87.1, JST.93.1, JST.93.2, JST.93.3, JST.93.4, JST.93.5, JST.95.1, JAC3.R.5, JAC3.20.1 to JAC3.20.9, JAC3.21.1, JAC3.21.2, JAC3.23.1 JAC3.31.5, JAC3.R.5, JAC4.15.2, JAC4.15.3, JAC4.17.2, JAC4.30.1, JAC4.32.3, JAC4.32.4, JAC4.33.1, JAC4.33.2, JAC11.4.11 to JAC11.4.14, JAC11.4.16 to JAC11.4.26, JAC11.R.8, JAC11.R.11, JAC11.R.13, JAC11.R.14, JAC11.R.20, JAC11.R.21, JAC11.R.25, JAC11.R.53, JAC13.34.10, JAC13.34.11, JAC13.R.26, JAC13.R.27, JAC22.5.8, JAC22.5.22, JAC22.16.1, JAC22.16.2, JAC22.16.3, JAC22.16.4, JAC22.16.8, JAC22.24.2, JAC22.28.4, JAC22.28.5, JAC22.30.4, JAC22.33.1, JAC22.41.1, JVM.61, JVM.62, JVM.63, JVM.64, JVM.65, JFA.12.1, JFA.14.2, JFA.14.3, B.10.1, JFB.R.1 and TT.7.

MEASUREMENTS. — See Table 13.

DESCRIPTION

Medium-sized planulate macroconchs, compressed, with medium to moderately involute coiling (O/D of the Subbetic adult specimens varying between 0.29 and 0.38). The whorl section is almost rectangular, with a sloping umbilical wall and rounded umbilical edge, flattened flanks, narrow ventral region, tabulated, with a thin and prominent keel, without lateral grooves on the middle and outer whorls. The innermost whorls are smooth and have no tuberculate stage. The inner and intermediate whorls present weak flexuous, subradial ribs, strongly projecting forward in the ventral region, which during ontogenetic development are usually successively divided, fasciculate, grouped at the umbilical border and simple, but this varies according to the specimen. The outer whorls may become almost smooth, with flexuous growth striae arranged in bundles. The septal suture is relatively simple, with L wide and short.

REMARKS

The rectangular whorl section with a tabulate venter lacking sulci, relatively evolute coiling, and weak ribbing, which can almost disappear at the adult stages, distinguishes *W. romanoides* from other *Witchellia* species. The morphologically most similar species is "*Hyalinites*" *hyalinus* Buckman, 1924 (Buckman 1924: T.A. 5: pl. 519, HT), for which only the HT is known with a septate PH (92 mm in diameter), which is much larger than any known specimen of *W. romanoides*. According to Buckman (1924), this form comes from the Sauzei Zone of Clatcombe, Sandford Lane, Sherborne (England), and is therefore stratigraphically substantially later that *W. romanoides*. *W. pseudoromanoides* Dietze, Chandler & Schweigert, 2003, probably a descendent of the *W. romanoides* group (Dietze *et al.* 2003: 13), is another similar species but is more involute and has more coarsely ribbed ornamentation.

DISTRIBUTION

The stratigraphic position of the type of *W. romanoides* is not clear, but it is possibly from the Ovale Zone of the Vallée de Valaury, southern France (Dietze *et al.* 2007). The specimen

Table 14. — Measurements of *Witchellia albida* (Buckman, 1926) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC11.7.5	64.0	19.0	0.30	26.5	0.41	12.0	0.19		Laeviuscula Subzone
	47.0	13.5	0.29	20.5	0.44	10.0	0.21		
JAC13.R.3	65.0	17.0	0.27	29.0	0.45	14.7	0.23		Trigonalis Subzone?
	51.0	11..5	0.27	23.0	0.45	12.0	0.24		
JAC22.30.1	62.0	17.0	0.27	25.5	0.41	–	–		Trigonalis Subzone
	43.0	11.5	0.26	19.0	0.44	–	–		
JAC22.35.3	70.0	20.0	0.28	28.0	0.40	15.0	0.21		
	54.0	13.6	0.25	25.0	0.46	11.5	0.21		
JAC22.R.3	96.0	22.0	0.23	45.0	0.47	22.5	0.23		Laeviuscula Zone?
	67.0	14.5	0.22	32.0	0.48	17.0	0.25		
JFA.R.1	78.0	19.5	0.24	35.5	0.46	17.0	0.22		
	54.0	13.5	0.25	25.0	0.46	13.0	0.24		

figured by Pavia (1983) confirms this stratigraphical range. The species has been frequently cited in the Ovale and Laeviuscula zones. In England it extends from the Ovale Zone to the Laeviuscula Zone, Trigonalis Subzone (Parsons 1974, 1977, 1979; Callomon & Chandler 1990; Dietze *et al.* 2003, 2007; Chandler *et al.* 2006). A comparable stratigraphic range is occupied in Germany (Ohmert 2004), Morocco (Sadki 1994, 1996), Bulgaria (Metodiev 2019), and Spain (the Iberian range; Fernández-López 1985). In the Subbetic domain, *W. romanoides* appears in diverse localities, being especially abundant in the Ovale Zone and Laeviuscula Zone (Trigonalis Subzone) of Sierra de Alta Coloma area (Granada and Jaén Provinces).

Witchellia albida (Buckman, 1926) [M]
(Figs 8B; 11A; 12A-D)

Dundryites albidus Buckman, 1926: T.A. 6, pl. 687 (HT); 1926: T.A. 7, p. 12.

Witchellia albida – Fernández-López 1985: 81, text-figs 8D, 8E, pl. 5, fig. 6, pl. 6, fig. 3. — Chandler & Whicher 2015: pl. 19, figs 2, 3.

Dundryites aff. *albidus* [M] – Dietze *et al.* 2007: 6, pl. 3, fig. 1.

Dundryites albidus [M] – Dietze *et al.* 2007: 6, pl. 3, fig. 2.

Material examined. — JAC11.7.5, JAC13.R.3, JAC13.R.34, JAC22.30.1, JAC22.32.5, JAC22.35.3, JAC22.35.5, JAC22.42.7, JAC22.42.8, JAC22.43.14, JAC22.43.15, JAC22.43.16, JAC22.43.17, JAC22.43.18, JAC22.44.9, JAC22.44.10, JAC22.44.11, JAC22.R.3, JAC22.R.6 and JFA.R.1.

Measurements. — See Table 14.

Description
Medium-sized relatively involute macroconchs with medium (U/D varying between 0.23 and 0.30) and shallow umbilicus. The whorl section (Fig. 11A) is subrectangular with a subvertical umbilical wall, rounded umbilical edge, almost flat flanks and tabulate ventral area with a high keel. The innermost whorls are not preserved. In the inner whorls, the ribs, some of which arise divided from a small thickening near the umbilical edge, are moderately falcate. Later the ribbing is irregular with a thick rib, which can bifurcate at mid-flank height and is followed by secondary ribbing that is well marked only in the upper part of the flanks where the ribs bend strongly forward. Finally, the ribbing becomes wide and spaced and tends to fade at the BC end. The septal suture, preserved in the specimen JAC22.R.3 (Fig. 8B), is complex; L is tripartite, strongly asymmetrical and incised, and the L-U_2 saddle is narrow at the base and incised above.

Remarks
The Subbetic forms described above are quite similar to the HT of *W. albida* (Buckman, 1926), but some are slightly more evolute and have more persistent ribbing. Considering the morphology of the septal suture, Dietze *et al.* (2007: 13) excluded *W. albida* from the Witchelliinae, restoring the genus *Dundryites* Buckman. According to these authors, "*D.*" *albidus* Buckman shows intermediate characters between *Witchellia* and *Sonninites*.

Distribution
According to Buckman (1926), the HT of *W. albida* is from the Mollis horizon. Callomon & Chandler (1990: 97) cited it from the Trigonalis Subzone (Bj-8). According to Chandler *et al.* (2006: fig. 2), the type is from the Bj-5 horizon (Ovale Zone), but in the type locality the species is also present in the Laeviuscula Zone and Subzone (Bj-10a horizon). At Little Down Wood (Dundry Hill, Somerset, England), this species occurs in the Ovale Zone associated with *W. romanoides* (Douvillé, 1885), *W. patefactor* (Buckman, 1923), *W. pavimentaria* (Buckman, 1927), *W. connata* (Buckman, 1927), *W.* cf. *jugifera* (Waagen, 1867), *W.* cf. *zugophora* (Buckman, 1922), and *Fissilobiceras fissilobatum* (Waagen, 1867), among others, but specimens resembling '*Dundryites*' *albidus* range upwards into the Laeviuscula Zone (Dietze *et al.* 2007: 5-7). Chandler *et al.* (2014) cited *W. albida* in the Laeviuscula Zone (Trigonalis Subzone, Bj-8b horizon) from Frogden Quarry, Oborne, Dorset (England). The specimen figured by Chandler & Whicher (2015) is from the base of the Laeviuscula Zone (Sayni Subzone). In the Iberian range (Spain), the species is common in the Ovale Zone, but it is probably present also in the lower part of the Laeviuscula Zone (Fernández-López 1985: 82). The Subbetic specimens are found in the Laeviuscula Zone (Trigonalis and probably Laeviuscula subzones) of Sierra de Alta Coloma area (Jaén Province) and Rio Fardes area (Granada Province).

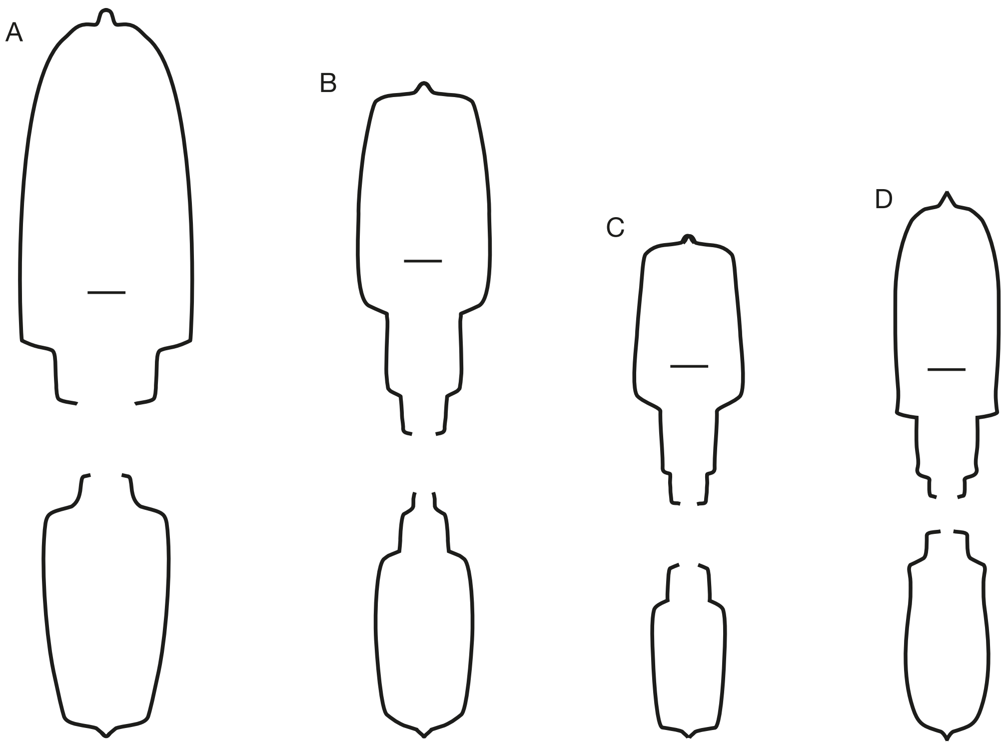


Fig. 11. — Cross-sections of some species of *Witchellia*: **A**, *Witchellia albida* (Buckman) [M], specimen JAC22.R.3; **B**, *Witchellia hyalina* (Buckman) [M], specimen JAC11.8.21; **C**, *Witchellia companyi* n. sp. [M], specimen JAC11.8.16 (HT); **D**, *Witchellia striata* n. sp. [M], specimen JAC11.4.27 (HT). Scale bars: 5 mm.

Table 15. — Measurements of *Witchellia rubra* (Buckman, 1926) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.71.4	76.0	23.0	0.30	31.1	0.40	16.0	0.21	Crushed specimens	Laeviuscula Subzone
	60.0	17.0	0.28	26.0	0.43	–	–		
JAC3'.4.11	93.0	23.0	0.25	41.0	0.44	–	–		Patella Subzone
	68.0	15.8	0.23	31.5	0.46	–	–		
JAC22.R.8	102.0	19.5	0.19	51.5	0.50	24.0	0.24	–	Laeviuscula Subzone?
	74.0	13.5	0.18	37.5	0.51	18.0	0.24		
JFA.16.2	91.0	22.0	0.24	42.0	0.46	24.0	0.26		
	72.0	17.0	0.24	33.0	0.46	20.0	0.28		

Witchellia rubra (Buckman, 1926) [M]
(Fig. 12E-G)

Rubrileiites ruber Buckman, 1926: T. A. 6, pl. 642 (HT).

Witchellia aff. *rubra* – Morton 1975: 56, pl. 9, figs 1-34.

Witchellia cfr. *rubra* – Pavia 1983: pl. 5, fig. 9.

Witchellia rubra – Fernández-López 1985: 78, text-fig. 8B, pl. 7, fig. 1. — Hernández-Molina *et al.* 1991: fig. 15.3.

Witchellia albida – Sandoval 1990: pl. 2, fig. 1.

non *Witchellia rubra* – Sandoval 1990: 146, pl. 1, fig. 7 (corresponds to *Witchellia striata* n. sp.).

Witchellia sp. – Dietze *et al.* 2005: 61, fig. 34c, f.

Witchellia cf. *rubra* – Chandler *et al.* 2006: fig. 8(3). — Dietze *et al.* 2007: 15, pl. 5, fig. 1.

Witchellia cf. *sayni/pseudoromanoides* – De Baets *et al.* 2008: 574, figs 5d, e.

Material examined. — JAC3.71.4, JAC3'.4.2, JAC3'.4.11, JAC4.64.3, JAC4.64.5, JAC22.56.14, JAC22.56.15, JAC22.56.16, JAC22.R.8, JFA.15.1 and JFA.16.2.

Measurements. — See Table 15.

Description
Medium to relatively large macroconchs with rather involute coiling (U/D varying from 0.22 to 0.30), broad whorl expansion, narrow and relatively deep umbilicus. The section, subrectangular compressed on inner and intermediate whorls, becomes subtriangular in the adult BC, where the ventral region is narrow with a relatively high keel. The umbilical wall is almost vertical, the umbilical edge rounded and the flanks gently convex. Inner and intermediate whorls have weak irregular ribs, generally simple, flexuous, and subradial, with the ventral termination frequently projecting forward. The PH end, at times the intermediate whorls, and the BC are almost smooth and have no tubercles or thickening of the ribs near the umbilical border. The septal suture is simple with L wide and short.

Fig. 12. — **A**-**D**, *Witchellia albida* (Buckman, 1926) [M]: **A**, JAC11.7.5, Laeviuscula Zone, Sierra de Alta Coloma (JAC11 section); **B**, JAC22.35.5, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC22 section); **C**, JAC13.R.3, Laeviuscula Zone?, Sierra de Alta Coloma (JAC13 section); **D**, JAC22.R.3, Laeviuscula Zone?, Sierra de Alta Coloma (JAC22 section). **E**-**G**, *Witchellia rubra* (Buckman, 1926) [M]: **E**, JAC3.71.4, Laeviuscula Subzone, Sierra de Alta Coloma (JAC3 section); **F**, JAC22.R.8, Laeviuscula Zone?, Sierra de Alta Coloma (JAC11 section); **G**, JAC3'.4.11, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC3' section). Scale bar: 1 cm.

Table 16. — Measurements of *Witchellia hyalina* (Buckman, 1924) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3'.5.8	78.0	23.5	0.30	31.5	0.40	–	–	Adult complete specimens	Propinquans Zone, Patella Subzone
JAC11.8.21	86.0	32.0	0.37	31.0	0.36	18.0	0.21		
	64.0	22.0	0.34	24.5	0.38	13.0	0.20		
JAC11.8.22	73.0	27.3	0.37	27.0	0.37	13.0	0.18		
	59.0	19.5	0.33	22.5	0.38	13.0	0.22		

Remarks

The HTs of *W. albida* and *W. rubra* are remarkably alike in size, coiling, whorl section, keel, and ornamentation. Judged by these external morphological characters, the two species could be synonymous. In this case, *W. rubra* would have nomenclature priority because it was nominated by Buckman (1926: T.A. 6, pl. 642) and *W. albida* was nominated by Buckman in the same year, but in pl. 687. The only appreciable distinction is the septal suture, which is more complex in *W. albida* than in *W. rubra*. Also, the types of each species come from different faunal horizons, since *W. albida* is from the Ovale Zone, Bj-5 horizon (Chandler *et al.* 2006), whereas the type of *W. rubra* is from the Laeviuscula Zone and Subzone, Bj-9 horizon (Dietze *et al.* 2007).

Distribution

The type horizon of "*Rubrileiites*" *ruber* is in the upper part of the Laeviuscula Zone, Laeviuscula Subzone, Bj-9 horizon (Dietze *et al.* 2007). In the Iberian range (Spain), most of the specimens are from the Laeviuscula Zone, but some specimens are reworked together with fossils from the base of the (Sauzei) Propinquans Zone (Fernández-López 1985: 79). Subbetic specimens are from the upper part of the Laeviuscula Zone (Laeviuscula Subzone) and of the lower part of the Propinquans Zone from Sierra Alta Coloma area (section JAC3, JAC3', JAC4, JAC22; Jaén Province), and from Rio Fardes (section JFA; Gorafe, Granada Province).

Witchellia hyalina (Buckman, 1924) [M]
(Figs 8C; 11B; 13A)

Hyalinites hyalinus Buckman, 1924: T.A. 5, pl. 519 (HT).

Sonninites simulans – Buckman 1926: T.A. 6, pl. 631. — Chandler & Whicher 2015: pl. 11, fig. 3.

Sonninites aff. *simulans* – Sandoval 1994: 205, pl. 1, fig. 1.

Material examined. — JAC3'.5.8, JAC3'.5.9, JAC11.8.21, JAC11.8.22, JAC22.47.7, JAC22.47.8, JAC22.58.3, AC22.58.4, JAC22.59.7 and JAC22.61.3.

Measurements. — See Table 16.

Description

Planulate evolute shells, with scarcely appreciable uncoiling throughout ontogeny. The umbilicus is relatively wide and shallow. A rectangular compressed whorl section (Fig. 11B) has an almost vertically sloping umbilical wall, rounded umbilical edge, almost flat flanks and rounded venter with a well-developed keel. The aperture has sinuous edges and a long ventral prolongation that adjusts to the path of the growth striae. The inner whorls vary depending on the specimen, but generally thickenings are present near the umbilical edge, from which one or two sinuous ribs emerge that weaken in the outer part of the flanks. This ornamentation progressively fades, so that throughout almost the entire last whorl of the PH and in the BC, the ribbing is replaced by growth striae. The septal suture (Fig. 8C) is more complex than in other *Witchellia* species; L, tripartite, is deeper than E, the E-L saddle is wide and high, L-U_2 is narrow, incised and asymmetric, and the umbilical lobes are gently retracted.

Remarks

The HT of "*Hyalinites*" *hyalinus* Buckman, from Sherborne, Dorset (England) is a septate PH of 92 mm in diameter. Subbetic specimens are smaller and slightly more evolute, but coincide in all other characters. Differences in size may be the consequence of the habitat where they lived. For example, a British specimen is from marine offshore with a large amount of aliments, whereas Subbetic forms are from a typical marine basin where, generally, food is scarcer. The differences in the degree of coiling may come from the fact that the Subbetic forms are complete or nearly complete adult specimens, whereas the English forms are PHs, and, as indicated above, little uncoiling of the shells occurs throughout ontogeny. The type of "*Sonninites*" *simulans* Buckman closely resembles the type of "*H.*" *hyalinus*, as both forms coincide in coiling, whorl-section, keel, ornamentation in the last preserved whorls, and septal suture. Only minor differences are detected on the innermost whorls, but these are not considered sufficient to separate two species. Furthermore, both HTs are from the same locality and from the same stratigraphic level. Therefore, here, the two forms are considered synonymous.

Distribution

The only known specimen figured and nominated as "*Hyalinites*" *hyalinus* Buckman is the HT that, according to Buckman (1924) comes from the Sauzei of Clatcombe, Sandford Lane, Sherborne, Dorset (England). The HT of "*Sonninites*" *simulans* Buckman is also from the Sauzei Zone of Sandford Lane, Sherborne. The specimen figured by Chandler & Whicher (2015), from the Inferior Oolite of Dorset, is from Bj-11 horizon, Propinquans Zone (Patella Subzone). In Morocco, this species occurs in the lower part of the Propinquans Zone (Sadki 1996). Subbetic specimens are from the Laeviuscula

Table 17. — Measurements of *Witchellia sayni* Haug, 1893 [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.R.6	70.0	25.0	0.37	25.0	0.37	–	–		Laeviuscula Zone
	54.0	19.0	0.35	22.0	0.41	–	–		
JAC11.(4-7).1	78.0	27.5	0.35	30.0	0.38	–	–		
	60.0	21.0	0.35	23.5	0.40	–	–		
JAC22.4.1	55.0	19.3	0.35	21.0	0.38	–	–		Ovale Zone
	44.0	15.5	0.35	18.0	0.41	–	–		
JAC11.R.24	63.0	22.0	0.35	24.5	0.39	11.5	0.18		Laeviuscula Zone?
	46.0	15.0	0.32	18.0	0.39	9.4	0.20		
JFA.(14-16).1	76.0	28.4	0.37	29.5	0.39	18.0	0.24		Laeviuscula Zone
	58.0	20.5	0.35	23.0	0.39	15.0	0.26		

Zone (Laeviuscula Subzone) and the Propinquans Zone (Patella Subzone?) of the Sierra of Alta Coloma (JAC3', JAC11 and JAC22 sections; Jaén Province).

Witchellia sayni Haug, 1893 [M]
(Fig. 13B)

Witchellia sayni Haug, 1893: 308.

Ludwigia corrugata – Douvillé 1885: 26, pl. 2, figs 1 (LT designed by Dietze *et al.* 2007) to fig. 5, pl. 3, figs 1, 2, text-figs 6, 7.

Witchellia cf. *sayni* – Pavia 1983: pl. 4, fig. 2.

Witchellia sayni – Fernández-López 1985: 74, text-fig. 8J, pl. 5, fig. 3. — Fernández-López *et al.* 1988: 312, pl. 1, fig. 5. — Hernández-Molina *et al.* 1991: fig. 13.5. — Sadki 1996: 172, pl. 4, fig. 3. — Dietze *et al.* 2007: 13, pl. 6, figs 1a, b (LT refigured). — Galácz *et al.* 2015: 10, pl. 3, fig. 3. — Chandler & Whicher 2015: pl. 19, fig. 1.

non *Witchellia sayni* – Sandoval 1990: 146, pl. 1, fig. 5.

Material examined. — JAC3.R.6, JAC4.37.1, JAC11.(4-7).1, JAC11.3a'.3, JAC11.R.24, JAC22.4.1, JFA.14.16 and JFA.(14-16).1.

Measurements. — See Table 17.

Description
Medium to large macroconchs, relatively evolute (U/D varying between 0.35 and 0.37 in the available specimens). The ovate to subrectangular compressed whorl section has an almost vertical umbilical wall and a rounded umbilical edge, flat to gently convex flanks, and has a venter with a high keel. The innermost whorls are not preserved and the dense intermediate whorl ribs arise near the umbilical edge, where some may be grouped. Subsequently, the ribs, mainly simple, are radial or slightly proverse in the lower two thirds of the flank and bend forward in the upper third, being erased near the keel. In the BC, the ribs fade somewhat, but are not erased. The aperture and septal suture is not preserved in the Subbetic specimens.

Remarks
The Subbetic specimens strongly resemble the LT of the species, mainly in the coiling, whorl section, and ribbing, but are smaller and lack or barely have a tabulated ventral area.

Distribution
The exact stratigraphic situation of the type of *W. sayni*, which is from 'couche ocreuse, Ovale Zone? of the Vallée de Valaury' (S. France) remains uncertain (see Dietze *et al.* 2007: 34). The species has been cited from the Ovale and Laeviuscula zones in France (Douvillé 1885; Haug 1893; Gillet 1937; Pavia 1983; De Baets *et al.* 2008); England (Chandler *et al.* 2006, 2014; Chandler & Whicher 2015); Germany (Dietze *et al.* 2007); Hungary (Galácz *et al.* 2015); Spain, both in the Iberian Cordillera (Fernández-López 1985; Fernández-López *et al.* 1988) and in the Subbetic basin (Sandoval 1983, 1990; Hernández-Molina *et al.* 1991); and Morocco (Sadki 1994, 1996). The stratigraphic range of the species is probably restricted to the interval compressed between the Ovale Zone and Laeviuscula Zone (Trigonalis Subzone).

Witchellia laeviuscula (J. de C. Sowerby, 1824) [M]
(Fig. 13C)

Ammonites laeviusculus J. de C. Sowerby, 1824: 73, pl. 451, figs 1, 2. — Buckman & Woodward 1908: pl. 6, fig. 1 (LT refigured).

Harpoceras laeviusculum – Haug 1885: 682, pl. 12, fig. 6.

Witchellia laeviuscula – Buckman 1927: T.A. 7, pl. 745. — Dorn 1935: 106, pl. 6, fig. 3, pl. 14, fig. 2, pl. 15, fig. 3, text-fig. pl. 9 (4, 5). — Gillet 1937: 61, pl. 1, fig. 8, pl. 2, fig. 6, pl. 3, fig. 1.). — Westermann 1969: 111, fig. 35 (LT refigured). — Schlegelmilch 1985: 63, pl. 19, fig. 3 (LT refigured). — Fernández-López 1985: 70, text-fig. 8A, pl. 7, fig. 2. — Chandler *et al.* 2006: 351, figs 4.1-4.3 (LT refigured), 5.1-5.2. — Metodiev 2019: 15, fig. 5a, b.

cf. *Witchellia* aff. *laeviuscula* – Morton 1975:18, pl. 10, figs 1, 2.

Witchellia aff. *laeviuscula* – Chandler *et al.* 2006: 351, fig. 4 (4).

Witchellia laeviuscula [M] – Dietze *et al.* 2009: 21, figs 21, 22, 26.

Material examined. — JAC3.71.2, JAC3.72.1, JAC3.77.1, Jpe1, JAC3'.0.5, JAC3'.4.37, JAC3'.8.2, JAC22.56.23, JAC22.57.4.

Measurements. — See Table 18.

Description
Disc-shaped shells with relatively involute coiling. The compressed whorl section is subtriangular with flanks slightly convex and convergent towards the outer region;

Fig. 13. — **A**, *Witchellia hyalina* (Buckman, 1924) [M], JAC11.8.21, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC11 section); **B**, *Witchellia sayni* Haug, 1893 [M], JAC11.(4-7).1, Laeviuscula Zone?, Sierra de Alta Coloma (JAC11 section); **C**, *Witchellia laeviuscula* (J. de C. Sowerby, 1824) [M], JAC3.71.2, Laeviuscula Subzone, Sierra de Alta Coloma (JAC3 section); **D**-**F**, *Witchellia companyi* n. sp. [M], JAC11.8.16 (HT), JAC11.8.22, JAC11.8.14, Propinquans Zone, Patella Subzone, Sierra de Alta Coloma (JAC11 section); **G**, **H**, *Witchellia striata* n. sp. [M]; **G**, JAC11.4.27 (HT), Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC11 section); **H**, JAC4.36.1, Laeviuscula Zone, Sierra de Alta Coloma (JAC4 section). Scale bar: 1 cm.

Table 18. — Measurements of *Witchellia laeviuscula* (J. de C. Sowerby, 1824) [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3.71.2	51.0	13.0	0.25	23.0	0.45	*c.* 11.0	*c.* 0.22		Laeviuscula Subzone
	36.0	8.5	0.24	17.5	0.47	–	–		
JAC3.77.1	68.0	16.5	0.24	31.0	0.46	–	–		
	52.0	13.5	0.26	24.0	0.46	15.0	0.29		
JAC3'.4.37	47.0	11.0	0.23	22.5	0.48	–	–		Propinquans Zone
	32.0	7.9	0.25	15.5	0.49	–	–		

the maximum width of the whorl is located near the lower third of the height of the flanks. The umbilicus is moderately narrow and deep. The umbilical wall is flat and nearly vertical, with a slightly rounded umbilical edge and a barely differentiated ventrolateral shoulder; the narrow ventral region which is tabulated in the inner and median whorls. The keel is thin and prominent, without lateral grooves at least in the middle and outer whorls. The ribbing is irregular, with a thick rib followed by two weak, blunt, and widely spaced ribs in the middle whorls, becoming increasingly attenuated and disappearing almost completely throughout ontogeny. The ribs are flexuous and generally bifurcate near the umbilical edge; the primaries are hardly marked, proverse and short whereas the secondaries, divided from the primaries near the umbilical edge, project strongly forward in the ventral region. In the HT, the internal whorls, somewhat more evolute than the intermediate ones, have dilated primary ribs next to the umbilical edge. The septal suture, relatively simple, with a wide and short L in the HT, is poorly preserved in the Subbetic specimens.

Remarks

Subbetic specimens are slightly more evolute than the HT, but they coincide with it in the other characters. Callomon & Chandler in Chandler *et al.* (2006: 370) point out that several relatively involute forms of *Witchellia* as *W. laeviuscula* (Sowerby, 1824), *W. actinophora* Buckman, 1926, *W. falcata* Buckman, 1926, *W. glauca* Buckman, 1925, *W. plena* (Buckman, 1926), *W. patefactor* (Buckman, 1923), and *W. spinifera* Buckman, 1920, whose types come from the same bed, are almost undoubtedly only variants of a single biospecies. However, more material from the type area would be necessary to confirm such conjecture.

Distribution

Chandler *et al.* (2006) showed that, in the type locality (Inferior Oolite at South Main Road Quarry, Dundry, Avon, England), *W. laeviuscula* occurs in the last horizon (BJ-10b) of the Laeviuscula Zone and Subzone. The species has been frequently cited, although few typical specimens were figured except for the LT. The species appears to be restricted to the Laeviuscula Subzone and the base of the Propinquans Zone of Europe and Morocco. Subbetic specimens are from the Laeviuscula Zone and Subzone and the base of the Propinquans Zone (Patella Subzone) of the Sierra of Alta Coloma (JAC3, JAC3' and JAC22 sections; Jaén Province).

Witchellia companyi n. sp. [M]
(Figs 8D-E; 11C; 13D-F)

urn:lsid:zoobank.org:act:A30DAB70-2DED-4484-8755-90D94C4825A5

Diagnosis. — Macroconch planulate and evolute with wide and shallow umbilicus, rectangular compressed section, fine keel, ribbing varying throughout ontogeny with the BC end becoming smooth or finely striate, very simple septal suture.

Type material. — **Holotype**: Specimen JAC11.8.16 (HT), Department of Stratigraphy and Palaeontology, Faculty of Sciences, University of Granada (Spain). — **Paratypes**: specimens JAC11.8.14, JAC11.8.15, JAC11.8.17, JAC11.8.18, and JAC11.8.19 (PT).

Type locality and occurrence. — Sierra Alta Coloma (JAC11 section, Jaén Province, central sector of the Median Subbetic, Betic Cordillera, Spain), Lower Bajocian (Propinquans Zone, Patella Subzone).

Derivation of name. — In honour of my colleague Miguel Company, professor of Palaeontology at the University of Granada, Spain.

Material examined. — JAC11.8.14, JAC11.8.15, JAC11.8.16, JAC11.8.17, JAC11.8.18, JAC11.8.19, JAC11.8.23, JAC11.8.31, JAC22.54.6 and JAC22.54.7.

Measurements. — See Table 19.

Description

Medium-sized planulate macroconchs, evolute (U/D varying between 0.39 and 0.42 in complete adult specimens) with moderate whorl expansion and a relatively wide and shallow umbilicus. The whorl section (Fig. 11C) is almost rectangular, with flat and inclined (at times almost vertical) umbilical wall, a rounded umbilical edge, flattened flanks, and a narrow, tabulated ventral region, with a thin and relatively high keel lacking lateral grooves. It has a simple opening with little ventral expansion. The ornamentation is reminiscent of that of *W. romanoides*. The innermost whorls are not detectable in any of the available specimens and have no tuberculate stage. The inner and intermediate whorls present weak flexuous, subradial ribs, strongly projecting forward in the ventral region, which during ontogenetic development are usually successively simple, divided, fasciculate, grouped at the umbilical border, and again simple. The outer whorls may become almost smooth, with flexuous growth striae arranged in bundles. The septal suture (Fig. 8D-E) is relatively simple; E is as deep as L, the saddle E-L is wide and strongly asymmetrical, L is tripartite, L-U_2 is narrow and high, and the umbilical lobes are slightly retracted.

Table 19. — Measurements of *Witchellia companyi* n. sp. [M].

Specimen	D	U	U	H	H	W	w	Remarks	Biostratigraphy
JAC11.8.14 (PT)	72.0	30.0	0.42	23.7	0.33	–	–		
	64.0	27.2	0.42	21.5	0.34	–	–		
	49.0	20.0	0.41	16.7	0.34	–	–		
JAC11.8.15 (PT)	71.0	27.5	0.39	24.0	0.34	–	–		
	58.0	23.0	0.40	21.0	0.36	–	–		
JAC11.8.16 (HT)	64.0	25.0	0.39	23.0	0.36	12.0	0.19	Complete or almost complete adult specimens	
	48.0	18.1	0.38	17.5	0.36	9.0	0.19		Propinquans Zone, Patella Subzone
JAC11.8.17 (PT)	49.0	19.0	0.39	18.0	0.37	10.0	0.20		
	37.5	14.3	0.38	13.6	0.36	–	–		
JAC11.8.19 (PT)	70.0	27.0	0.39	25.4	0.36	16.0	0.23		
	55.0	21.5	0.39	21.0	0.38	12.0	0.22		
JAC11.8?.23	100.0	39.5	0.395	34.0	0.34	–	–		
	76.0	28.0	0.37	27.2	0.36	–	–		
JAC11.8.31	40.0	14.3	0.36	15.5	0.39	9.5	0.24	Juvenile?	
	30.0	10.5	0.35	12.0	0.40	7.8	0.26		

Table 20. — Measurements of *Witchellia striata* n. sp. [M].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC4.36.1	51.0	12.5	0.245	24.0	0.47	*c.* 12.0	0.24		
	37.0	8.9	0.24	18.0	0.49	–	–	Nearly complete specimens	Laeviuscula Zone, Trigonalis Subzone
JAC11.4.27 (HT)	72.0	18.0	0.25	29.0	0.40	13.8	0.19		
	56.0	12.0	0.21	25.0	0.45	11.0	0.20		

Remarks

The most similar species are *W. romanoides* (Douvillé, 1885) and *W. pseudoromanoides* Dietze, Chandler & Schweigert 2003, but both are more involute and the former is also usually less ornamented whereas the latter is more strongly ribbed and has a broader whorl expansion. *W. companyi* n. sp. could possibly be a direct descendant of latest *W. romanoides*.

Distribution

Lower Bajocian, Laeviuscula Zone (Laeviuscula Subzone)–Propinquans Zone (Patella Subzone). The species has been recorded only in the Sierra de Alta Coloma area (Granada and Jaén Provinces).

Witchellia striata n. sp. [M]
(Figs 11D; 13G-H)

urn:lsid:zoobank.org:act:565D9D7B-5E38-4DA9-82A3-74C76491E98B

Witchellia rubra – Sandoval 1990: 146, pl. 1, fig. 7, *non* Buckman, 1926.

Diagnosis. — Macroconch, planulate, relatively involute with shallow umbilicus, compressed rectangular section with a very shallow depression in the lower part of the flanks, tabulate venter with a relatively high hollow keel. Weak falcate ribbing that progressively fades, being replaced by bundles of striae. The septal suture is simple.

Type material. — **Holotype**: specimen JAC11.4.27, held in the Department of Stratigraphy and Palaeontology, Faculty of Sciences, University of Granada (Spain).

Type locality and occurrence. — Sierra Alta Coloma (JAC11 section; Jaén Province), central sector of the Median Subbetic, Betic Cordillera, S Spain, Lower Bajocian (Laeviuscula Zone, Trigonalis Subzone).

Derivation of name. — Ornamentation composed mainly of striae.

Material examined. — Two specimens: JAC4.36.1, JAC11.4.27 (HT).

Measurements. — See Table 20.

Description

Planulate semi-involute, medium-sized shells, with appreciable uncoiling throughout ontogeny and with medium-wide, shallow umbilicus. An almost rectangular compressed whorl section (Fig. 11D), which has a vertical umbilical wall, an abrupt umbilical edge at right angles, and almost flat flanks with a very shallow depression (barely noticeable) in its lower part. The venter is clearly tabulate with a high hollow keel. The aperture is not well preserved, although the holotype is almost complete and appears to be adult. The inner and middle whorls support fine falcate ribs, which are single or divided into the inner third of the flanks. The weak and poorly marked secondaries strongly project forward along the ventrolateral edge. From the last part of the PH, ribbing progressively weakens, being replaced by bundles of striae or by very faint ribs in the BC. The septal suture, typical of *Witchellia*, has short lobes and low saddles.

Remarks

These Subbetic forms are quite similar to the HT of *W. hyalina* but are slightly more involute, have less marked ribs on inner whorls, falcate rather than sinuous ornamentation, and bear striae that form bundles in the BC. Moreover, the new species appears to be chronostratigraphically earlier. *W. romanoides* is more evolute, has any depression in the lower part of the flank and has more pronounced and less striate ornamentation.

Table 21. — Measurements of *Witchellia peleka* (Buckman, 1923) [m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
MOD.R.1	27.0	9.5	0.35	10.0	0.37	–	–		
JAC11.(3-7).1	32.0	12.2	0.38	11.5	0.36	7.5	0.23		
	22.0	8.4	0.38	8.7	0.40	–	–		
JAC11.R.54	35.0	12.5	0.36	12.0	0.34	–	–		
	25.0	8.0	0.32	10.6	0.42	–	–	Adult microconchs	Ovale Zone
TT.76.1	35.0	13.0	0.37	12.5	0.36	–	–		
	26.0	9.0	0.35	11.0	0.42	–	–		
JSP.1	29.0	10.5	0.36	10.2	0.35	–	–		
	23.0	7.8	0.34	8.5	0.37	–	–		

Distribution

Laeviuscula Zone, Trigonalis Subzone; Sierra de Alta Coloma (sections JAC4 and JAC11; Jaén Province).

Witchellia peleka (Buckman, 1923) [m]
(Fig. 14A-E)

Pelekodites pelekus Buckman, 1923: T.A. 4, pl. 399, figs 1-2 (HT). — Chandler *et al.* 2006: 370, fig. 4.5. — Dietze *et al.* 2007: figs 4a, b, d-g.

Maceratites spatians – Sandoval 1990: pl. 1, fig. 8.

Witchellia pelekus – Howarth 2013 (in *Treatise*): 121, fig. 82 4c-d (HT refigured).

Material examined. — MOD.R.1, JAC3.(7-14).1, JAC3.(7-14).2, JAC3.(7-14).3, JAC3.19.1, JAC4.11.5, JAC4.15.1, JAC6.R.6, JAC11.3.1, JAC11.3a.2, JAC11.(3-7).1 JAC11.4.8, JAC11.R.54, JAC11.R.65, JAC13.34.1, JAC13.34.2, JAC13.34.3, JAC13.34.5, JAC13.34.5, JAC13.34.5b, JAC13.34.6, JAC13.34.8, JAC13.34.9, JAC13.34.1, JAC22.5.24, JAC22.18.3, JAQ1.(-16), 1JAQ1.(-15).1, JAQ1.(-15).2, TT.76.1 and JSP.1.

Measurements. — See Table 21.

Description

Small microconchs, relatively evolute with apparent uncoiling in BC. The whorl section is subovate with a subrounded umbilical wall, almost as wide as high in the HT. The keel, well developed, is limited in some specimens by small sulci. The aperture is complex with well-developed spatulate lappets. The inner whorls are smooth or have faint ornamentation, without apparent tubercles. Later, ribs surging near the rounded umbilical edge are sigmoid, first strongly proverse and afterwards strongly retroverse with a faint forward projection on the ventrolateral edge. The ribbing weakens progressively on the BC, whose final part can be smooth. The septal suture is not preserved in the Subbetic specimens.

Remarks

The specimen figured as "*Poecilomorphus Macer*" by Buckman (1889: 116, pl. 22, figs 27-28), for which Buckman (1928: 11) proposed the subtitute name "*Maceratites*" *aurifer*, and which was included in the present species by Fernández-López (1985: 96), closely resembles the HT of *W. peleka,* but has slightly more evolute coiling and a slightly more compressed whorl section in addition to an almost oblique to sub-vertical umbilical wall. According to Callomon & Chandler (1990: 98), "*P.*" *pelekus* includes *Maceratites macer* Buckman, 1889 (Buckman 1889: only figs 23, 24) and *Spatulites spatians* Buckman, 1928. Later, Chandler *et al.* (2006) and Dietze *et al.* (2007) showed that the type species of "*P.*" *pelekus*, from the Ovale Zone (Bj-5 horizon), has a chronostratigraphy that sharply differs from that of the types of "*M.*" *macer* (Bj-10a horizon) and "*Sp.*" *spatians* (Bj-10a or Bj-10b horizons), which are from the upper part of the Laeviuscula Zone. Thus, "*Sp.*" *spatians* and "*M.*" *macer* could be synonymous with each other, but not with *W. peleka*.

Distribution

According to Chandler *et al.* (2006: 370), the type of *W. peleka* (Buckman 1923) comes from lower part of Ovale Zone (horizon Bj-5) of Dundry, Somerset (England). In the same locality and same stratigraphic position, the species has been cited by Dietze *et al.* (2007). In south-western Germany, it has been cited from the Laeviuscula Zone, Trigonalis Subzone (Dietze *et al.* 2011b). In the Iberian Range, "*P.*" *pelekus* has been cited in the Ovale Zone (Fernández-López 1985), but the specimens figured there are quite different from the HT. The Subbetic specimens classified as *W. peleka* are mainly from the Ovale Zone of Sierra de Alta Coloma and Barranco de Agua Larga (Jaén Province).

Witchellia macer (Buckman, 1889) [m]
(Fig. 14F-I)

Poecilomorphus macer S. Buckman, 1889: 116, pl. 22, only figs 23-28. (HT).

Maceratites aurifer Buckman, 1928: T.A. 7, p. 11, pl. 766, figs 1-3. — Fernández-López 1985: 95, pl. 11, figs 11, 12, 14. — Ohmert 2004: 62, pl. 16, figs 1, 2. — Metodiev 2019: 17, fig. 6.

Maceratites costulatus Buckman, 1928: T.A. 7, p. 11.

Pelekodites macer – Morton 1975: 65, pl.10, figs 5, 6, 11, 12, 17-22, 25-30. — Ohmert 2004: 64, pl. 16, figs 3, 4. — Dietze *et al.* 2019: 58, figs 4(3), 8(2a-10b).

non *Maceratites macer* – Fernández-López 1985: 97, text-fig. 9, pl. 11, figs 17, 18.

Maceratites costulatus – Fernández-López 1985: 98, pl. 11, fig. 13.

Table 22. — Measurements of *Witchellia macer* (Buckman, 1889) [m].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC11.3?.1	28.0	10.5	0.375	10.5	0.375	–	–	Complete adult microconchs	Laeviuscula Zone
	21.0	7.5	0.36	8.5	0.40	–	–		
JAC11.5.8	22.0	8.0	0.36	8.0	0.36	–	–		
JAC11.5.16	22.0	8.3	0.38	8.4	0.38	–	–		
	16.0	5.8	0.36	6.2	0.39	–	–		
JAC22.39.3	22.5	8.0	0.36	8.2	0.36	–	–		
JAC22.44.9	27.0	9.5	0.35	10.2	0.38	–	–		
	18.0	6.5	0.36	7.0	0.39	–	–		
JAC22.49.1	27.5	11.0	0.40	10.0	0.36	–	–		
	22.5	8.5	0.38	8.0	0.36	–	–		
FAa.4.1	23.0	9.0	0.39	8.0	0.35	–	–		Laeviuscula Zone?
	19.0	7.0	0.37	7.5	0.39	–	–		
JST.93.6	19.0	7.1	0.37	7.2	0.38	–	–		Laeviuscula Subzone
	16.0	5.1	0.32	6.1	0.38	–	–		
JVM.42	28.0	9.2	0.33	10.0	0.36	7.0	0.25		Laeviuscula or Propinquans zones
JVM.43	27.0	9.7	0.36	10.5	0.39	7.0	0.26		
	21.0	7.6	0.36	8.7	0.41	6.0	0.29		

Pelekodites cf. *aurifer* – Dietze *et al.* 2007: 16, figs 4h-k.

Pelekodites cf. *macer* – Dietze *et al.* 2019: 58, figs 8(11a, b).

?*Pelekodites boweri* – Dietze *et al.* 2019: 60, figs 8(1a, b).

Material examined. — JST.93.6, FAa.4.1, JAC3.R.1, JAC3'.2.5, JAC4.39.58, JAC11.4.3, JAC11.5.8, JAC11.5.16, JAC22.39.3, JAC22.42.9, JAC22.42.10, JAC22.42.11, JAC22.42.12, JAC22.42.13, JAC22.43.20, JAC22.43.21, JAC22.43.22, JAC22.43.23, JAC22.43.24, JAC22.43.25, JAC22.44.9, JAC22.45.12, JAC22.45.13, JAC22. 49.1, JAC22.R.7. JVM.36, JVM.37, JVM.38, JVM.41, JVM.42 and JVM.43.

Measurements. — See Table 22.

Description

Small and evolute shells (O/D varying from 0.35 to 0.40) with ovate-subrectangular compressed whorl section, convex umbilical wall, rounded umbilical edge, slightly convex flanks, venter with fine and well-marked keel, but not high and at times bordered by small sulci. The aperture is complex with lateral lappets and a small ventral rostrum. The inner whorls are smooth or almost smooth, without apparent ribs or tubercles, and later develop sigmoid ribs, well-differentiated at least up to the first half of the adult BC. These ribs, usually simple and sometimes grouped in pairs just at the umbilical border, are decidedly proverse in the inner third of the flanks, where they are weak; then they become prominent and sharp extending to the outer region, strongly projecting forward as they again become thinner and weaker. The septal suture is not visible in the Subbetic specimens.

Remarks

The types of "*Maceratites*" *macer* and "*M.*" *aurifer* are strikingly similar and have equivalent stratigraphic positions in the type localities. The only observable differences are less strongly falcate and slightly stronger ribbing in "*M.*" *aurifer* and the presence of small grooves (sulci) limiting the keel in "*M.*" *macer*, which are absent in "*M.*" *aurifer*. The two Buckman species are considered synonymous here, with "*M.*" *macer* having nomenclatorial priority. Also, "*Maceratites*" *costulatus* (Buckman, 1928: 11; HT, *Poecilomorphus macer* Buckman in S. Buckman 1889, pl. 22, only figs 25, 26) may be synonymous with "*M.*" *macer.* This morphotype was originally distinguished from "*M.*" *macer* by having more regular, prominent, and dense ribbing in the adult stage. It shows intermediate characters between typical "*M.*" *macer* and the primitive *Witchellia moisyi* (Brasil, 1893).

Distribution

The LT of "*Witchellia macer* comes from the marl with green grains of Frogden Quarry, Dorset, England (Buckman 1928: 12), Lower Bajocian (Laeviuscula Zone and Subzone). The species has also been cited from the Laeviuscula Zone in England (Parsons 1974, 1979) and Scotland (Morton 1975). According to Dietze *et al.* (2009, 2010a, 2011b, 2019), *W. macer* marks a typical horizon in the Trigonalis Subzone of the Upper Rhine Valley (SW Germany). In the Iberian Range (Spain), it is abundant in the upper part of the Ovale Zone and in the lower part of the Laeviuscula Zone (Fernández-López 1985: 97, fig. 113), but the specimens figured there diverge markedly from of the LT, with ornamentation reduced to striae, and it is not clear that they belong to this species. The HT of "*Maceratites aurifer*" (Buckman, 1928) comes from Bj-10a (Laeviuscula Zone and Subzone) from Dundry (Dorset, England) (Chandler *et al.* 2006: 348, fig. 2). In the Iberian range, the specimens classified as "*Maceratites aurifer*" are from the Ovale, Laeviuscula, and the base of the Propinquans zones (Fernández-López 1985: fig. 13). The Subbetic specimens are from the Laeviuscula Zone of JVM section (Cerro de la Martinica), Valdepeñas de Jaén, JST (Sierra del Trigo), JAC3, JAC3', JAC4, JAC11 and JAC22 (Sierra de Alta Coloma area) sections (Jaén Province).

TABLE 23. — Measurements of *Witchellia minima* (Hiltermann, 1939) [m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC22.26.2	13.0	4.0	0.31	5.0	0.38	–	–	Complete adult microconchs	Trigonalis Subzone
	11.0	3.3	0.30	4.3	0.39	–	–		
JAC22.43.26	9.5	3.5	0.37	3.0	0.32	–	–		Laeviuscula Subzone
	6.2	2.1	0.34	2.3	0.37	–	–		

Witchellia minima (Hiltermann, 1939) [m] (Fig. 14J)

Sonninia deltafalcata minima Hiltermann, 1939: 174, pl. 12, figs 4, 6.

Sonninia (*Poecilomorphus*) *boweri minima* – Huf 1968: 50, pl. 4, figs 4(LT refigured)-6.

Pelekodites minimus – Morton 1975: 66, pl. 10, figs 23, 24, 31-34.

Maceratites minimus – Fernández-López 1985: 104, pl. 11, fig. 16.

?*Pelekodites* aff. *minimus* [m] – Dietze *et al.* 2007: 6, fig. 4c.

MATERIAL EXAMINED. — JAC22.26.2 and JAC22.43.26.

MEASUREMENTS. — See Table 23.

DESCRIPTION

Small evolute microconch with slightly compressed ovate whorl section, rounded umbilical edge and barely convex flanks, as well as a rounded venter with a faint keel. It is scarcely ornamented with smooth inner whorls; intermediate whorls have barely visible irregular sigmoid ribs, some bifurcating near the umbilical edge. The outer whorls are smooth or almost so. The peristome has spatulate lappets and a small ventral rostrum. The septal suture is not preserved in the Subbetic specimen.

REMARKS

W. macer is the most similar species to *W. minima*, but it is somewhat larger and has a more marked ribbing. In the Subbetic, both taxa appear at equivalent stratigraphic levels. *W. minima* may represent an extreme morphotype of *W. macer.*

DISTRIBUTION

In Scotland, *W. minima* occurs in the Laeviuscula and Propinquans? zones (Morton 1975). Dietze *et al.* (2007) cited "*P.*" aff. *minimus* in the Ovale Zone of Dundry Hill, Somerset (SW England). In the Iberian range (Spain), the species is present in the Ovale and Laeviuscula zones (Fernández-López 1985) and in the Atlas (Morocco) it occurs in the Laeviuscula Zone (Sadki 1996). The Subbetic specimens are from the Laeviuscula Zone of JAC22 section, Sierra de Alta Coloma area (Jaén Province).

Witchellia moisyi (Brasil, 1893) [m] (Fig. 14K-O)

Poecilomorphus moisyi Brasil, 1893: 36, pl. 3, figs 6, 7 (HT).

Pelekodites zurcheri – Morton 1975: 64, pl. 10, figs 7-10, 13-16.

Maceratites moisyi – Fernández-López 1985: 99, text-fig. 9, pl. 11, figs 9, 10.

Pelekodites moisyi [m] – Dietze *et al.* 2009: 25, pl. 4, fig. 3, pl. 10, figs 1-3, 5, 6 [*non* fig. 4, corresponds to *Sonninites sulcatus* (Buckman, 1889), n. comb.]. — Metodiev & Tsvetkova 2014: 34, figs 3.9, 3.10. — Metodiev 2019: 17, figs 6a-d.

MATERIAL EXAMINED. — JAC3'.4.16, JAC3'.4.19, JAC6.R.7, JAC6.R.8, JAC6.R.9, JAC6.R.14, JAC6.R.15, JAC6.R.16, JAC11.6?.7, JAC11.5.26, JAC11.8.27, JAC11.8.29, JAC21.13.3, JAC21.13.10, JAC22.53.6, JAC22.53.8, JAC22.53.9, JAC22.53.10, JAC22.53.13, JAC22.54.8, JAC22.54.9, JAC22.54.13, JAC22.55.8, JAC22.55.9, JAC22.55.10, JAC22.55.11, JAC22.55.12, JAC22.59.6, JAC22.64.2, JAQ1.25.1, JAQ1.67.1, JAQ1.67.2, JAQ1.67.4 and JAQ1.71.2.

MEASUREMENTS. — See Table 24.

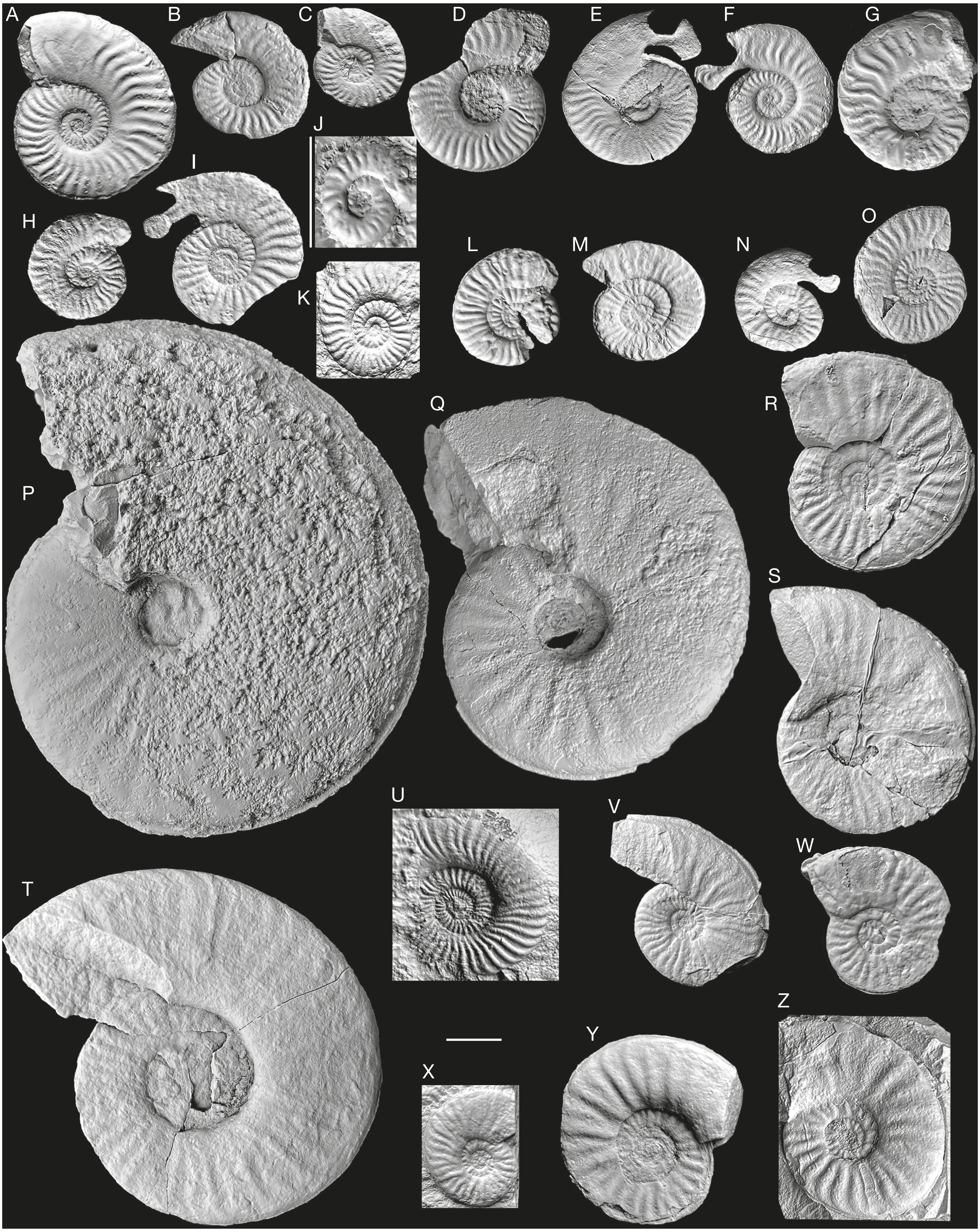
DESCRIPTION

Small microconchs, strongly evolute (U/D varying between 0.41 and 0.45 in complete adult specimens), with an oval to rectangular slightly compressed whorl section, venter keeled with two little marked sulci. The ribs, relatively dense, are mainly simple, with only scant bifurcation near the umbilical edge, sinuous, marked, and especially thick at the ventrolateral edge. The inner whorls are not tuberculate. The aperture is complex with developed spatulate lateral lappets. The septal suture is not visible in the Subbetic specimens.

REMARKS

According to Morton (1975: 64), "*Pelekodites*" *moisyi* (Brasil, 1893) is synonymous with "*Pelekodites*" *zurcheri* (Douvillé, 1885), but Fernández-López (1985: 99) contended that the specimens described and figured by Morton (1975) as "*P.*" *zurcheri* (Douvillé, 1885), are really "*P.*" *moisyi* (Brasil, 1893). The most similar species is probably *Sonninites sulcatus*

FIG. 14. — **A**-**E**, *Witchellia peleka* (Buckman, 1923) [m]: **A**, TT.76.1, Ovale? Zone, Sierra de Alta Coloma; **B**, JA13.34.2, Ovale Zone, Sierra de Alta Coloma (JAC13 section); **C**, JAQ1.(-15).1, Ovale Zone, Barranco de Agua Larga (JAQ1 section); **D**, JSP1, Ovale Zone, Sierra de San Pedro, Jaén province; **E**, MOD.R.1, Ovale Zone?, Montillana, (MOD section); **F**-**I**, *Witchellia macer* (Buckman, 1889) [m]; **F**, FAa.4.1, Laeviuscula Zone?, Sierra de Alta Coloma área; **G**, JVM.42, bed with ammonite of the Laeviuscula and Propinquans zones, La Martinica section; **H**, JST.93.6, Laeviuscula Zone, Sierra del Trigo, Jaén province; **I**, JAC22.49.1, Laeviuscula Subzone, Sierra de Alta Coloma (JAC22 section); **J**, *Witchellia minima* (Hiltermann, 1939) [m], JAC22.43.26, Laeviuscula Zone, Trigonalis Subzone, Sierra de Alta Coloma (JAC22 section); **K**-**O**, *Witchellia moisyi* (Brasil, 1893) [m]; **K**, JAC11.6?.7, Laeviuscula Zone?, Sierra de Alta Coloma, (JAC11 section); **L**, **M**, JAC6.R.14, JAC6.R.7, Propinquans Zone, Sierra de Alta Coloma área, (JAC6 section); **N**, **O**, JAQ1.67.2, JAQ1.67.1, Propinquans Zone, Barranco de Agua Larga (JAQ1 section); **P**, **Q**, *Dorsetensia liostraca* Buckman, 1892 [M], JGa8.32.4, JGa8.32.2, Humphriesianum Zone, Romani Subzone, Sierra de Gaena (sections, JGa2); **R**, **S**, *Dorsetensia hebridica* Morton, 1972 [M]; **R**, JAC3.118.4, Propinquans Zone, Hebridica Subzone, Sierra de Alta Coloma (JAC3 section); **S**, JAC3'.22.44,



Propinquans Zone, Hebridica Subzone, Sierra de Alta Coloma (JAC3' section); **T**, *Dorsetensia?* sp. [M], AC22.57.2, upper part of the Laeviuscula Zone, Sierra de Alta Coloma (JAC22 section); **U**, *Dorsetensia regrediens* (Haug, 1893) [m], JRi3.28.1, Humphriesianum Zone, Romani Subzone, Sierra de Ricote (sections, JRi3); **V**, **W**, **X**, *Dorsetensia pinguis* (Roemer, 1836) [m], JAC3'.22.28, JAC3'.22.36, JAC3'.22.18, Propinquans Zone, Hebridica Subzone, Sierra de Alta Coloma (JAC3' section); **Y**, **Z**, *Dorsetensia hannoverana* (Hiltermann, 1939) [M?]; **Y**, JAC3'.22.3, JAC3'.22.18, Propinquans Zone, Hebridica Subzone, Sierra de Alta Coloma (JAC3' section); **Z**, JAQ1.67.3, Propinquans Zone, Barranco de Agua Larga (JAQ1 section). Scale bars: 1 cm (note that J element has a different scale bar).

Table 24. — Measurements of *Witchellia moisyi* (Brasil, 1893) [m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC6.R.7	22.0	10.0	0.45	6.5	0.26	–	–	Adult complete microconchs	Propinquans Zone
JAC6.R.9	23.0	10.3	0.45	7.0	0.30	–	–		
JAC6.R.14	20.0	9.0	0.45	7.0	0.35	–	–		
JAC11.6?.7	20.0	9.0	0.45	6.6	0.33	–	–		
JAC11.8.27	31.0	13.0	0.42	10.0	0.32	–	–		
	24.0	9.1	0.38	8.5	0.35	–	–		
JAC11.8.29	22.0	9.0	0.41	8.0	0.36	6.0	0.27		
	17.0	7.0	0.41	6.2	0.36	5.0	0.29		
JAC22.55.9	30.0	13.5	0.45	9.0	0.30	6.0	0.20		Laeviuscula Zone
JAC22.59.6	32.0	14.0	0.44	10.0	0.31	–	–		
	27.0	11.0	0.41	8.5	0.31	–	–		
JAC22.64.2	27.0	11.0	O.41	8.8	0.33	–	–		Propinquans. Zone
	21.0	8.5	0.40	7.5	0.36	6.0	0.29		
JAQ1.67.1	25.0	10.5	0.42	7.2	0.29	–	–		

(Buckman, 1889), n. comb., which is more involute, has a somewhat less compressed whorl section, and has less sigmoid ribbing with several ribs dividing from very small thickenings located near the umbilical edge. *W. macer*, (including *P. aurifer* and *P. costulatus*) resembles *W. moisyi* but is slightly more involute and has less pronounced ribbing, less convex flanks, and less apparent ventral grooves. In addition, *W. moisyi* is stratigraphically higher. The types of "*Nannina*" *evoluta* Buckman, 1927 (Buckman 1927: T.A. 7, pl. 752) and "*N.*" *undifera* Buckman, 1927 (Buckman 1927: T.A. 7, pl. 753) are notably similar to *W. moisyi* and have comparable stratigraphic ranges, but the former two taxa may be Sonniniinae, having a small tuberculate inner stage that is absent in *W. moisyi*.

Distribution

According to Brasil (1895: 37), in the type locality (Feuguerolles-sur-Orne, France), *W. moisyi* occurs in the middle Bajocian ("couches a *Witchellia*"). Also, the species appears in the Ovale and Laeviuscula zones of the Iberian Cordillera, Spain (Fernández-López 1985), near Ringsheim (Upper Rhine Valley, SW Germany), and in the Propinquans (Sauzei) Zone (Dietze *et al.* 2009). In the Subbetic, *W. moisyi* is common in the uppermost part of the Laeviuscula Zone and lower part of the Propinquans Zone.

Genus *Dorsetensia* Buckman, 1892 [M] & [m]

Type species. — *Ammonites edouardianus* d'Orbigny, 1846 in d'Orbigny (1842-1851: 393, pl. 130, figs 3-5) (OD).

Description

Macroconch [M] of medium-sized to large shells. The inner whorls are evolute with simple or, rarely, bifurcate (only in the earliest forms), radial or slightly flexuous ribs and no tubercles. The middle and outer whorls are more involute and compressed, with a sharp, sometimes undercut, umbilical edge, more or less flattened flanks, and a narrow venter with a full keel at all the stages. The ribbing usually weakens throughout ontogeny becoming smooth on the outer whorls. The mouth has plain borders. In some species, ribs are replaced by striation in the BC. The dimorphic microconch [m], traditionally classified with the name *Nannina* (gr. of *Witchellia regrediens* Haug, 1893) are small and evolute, have ribs to the end of the BC and have lateral lappets on the mouth border. The septal suture, though relatively simple, is slightly more complex than in *Witchellia* with wide and a rather shallow L, and the umbilical lobe is barely retracted.

Remarks

Dorsetensia, included in the subfamily Sonniniinae in the *Treatise* (Howarth 2013), is here formally transferred to Witchelliinae, because it shares many characters with *Witchellia*, such as: coiling; whorl section; ribbing; keel; and type of dimorphism with medium-sized macroconchs that have a simple aperture, and much smaller microconchs that have a complex aperture and well-developed lateral lappets. The primary differences are that *Dorsetensia* never has tubercles and the venter is not tabulate, whereas *Witchellia* has a relatively simpler septal suture. Some forms of *Sonninites* can also be quite similar to *Dorsetensia*, but *Sonninites*, usually more involute, has different ribbing with several furcate ribs in the inner whorls, may have tubercles in inner whorls, and has a more complex suture line.

Some authors (e.g. Buckman 1927; Huf 1968: 78, Pavia 1983: 62; Fernández-López 1985: 21; Fernández-López & Mouterde 1994: 124; Sadki 1996: 170; Myczynski 2004: 111) have considered *Nannina* to be the dimorphous partner [m] of *Dorsetensia* [M]. However, Howarth (2013, in *Treatise*: 119) deemed *Nannina* Buckman, 1927 as a junior synonym of *Fontannesia* Buckman, 1902. Clearly, *Nannina* is not the dimorphic microconch of *Dorsetensia* because the inner whorls of the type species of the two genera are different. Furthermore, *Nannina* has a small coronate stage, a character that makes it closer to Sonniniinae and farther from *Dorsetensia*. Nor is *Nannina* synonymous with *Fontannesia*, as Howarth (2013) postulated, because the type species of the two taxa are quite distinct: *Fontannesia* has inner whorls with well-defined simple ribs that are in no case tuberculate, differentiating this species from *Nannina* (type species *N. evoluta* Buckman,

Table 25. — Measurements of *Dorsetensia liostraca* Buckman, 1892 [M].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JGa7.32.2	74.0	15.0	0.20	38.0	0.51	19.0	0.26	PH	Humphriesianum Zone, Romani Subzone
	51.0	11.5	0.22	24.4	0.44	14.0	0.27		
JGa7.32.3	128.0	16.0	0.125	69.0	0.54	30.0	0.23	PH & BC	
	85.0	12.0	0.14	45.0	0.53	23.0	0.27		
JGa7.32.4	95.0	13.0	0.14	49.0	0.52	24.0	0.25	PHs	
	66.0	10.0	0.15	33.5	0.51	17.5	0.25		
JGa7.32.5	70.0	14.0	0.20	35.0	0.50	24.0	0.34		
	52.0	12.0	0.23	25.5	0.49	18.3	0.35		
JGa7.32.10	43.0	9.0	0.21	20.0	0.48	12.0	0.28		

1927 [Buckman 1927: T.A. 7, pl. 752]). Furthermore, the stratigraphic ranges also substantially differ, as *Fontannesia* is restricted to the interval between the Concavum (Upper Aalenian) and Ovale zones, whereas the first stratigraphic records for *Nannina* do not appear until the upper part of the Propinquans Zone (see Pavia 1983: 62; Fernández-López 1985: 115). The above mentioned shows that the taxonomic status of the HT of *Nannina evoluta* is not clear, but given its coiling, the coronate stage on the inner whorls and its stratigraphic distribution (Propinquans Zone), it could represent a dimorphic microconch of *S.* (*Sonninia*).

Distribution

Lower Bajocian (uppermost Propinquans Zone-Humphriesianum Zone): Europe, North Africa (Atlas Ranges), Kenya, Madagascar, Saudi Arabia, Russia (south-eastern Pamirs), the Caucasus, China (Tibet), United States (Alaska, California, Oregon), Chile, and Argentina. In the Subbetic domain, *Dorsetensia* shares this stratigraphic distribution, appearing in the three Subbetic subdomains (External, Median, and Internal), but the genus is scarce except in the Pinguis horizon of the central sector of the Median Subbetic (Sierra de Alta Coloma area).

Dorsetensia liostraca Buckman, 1892 [M] (Figs 8F; 14P-Q)

Dorsetensia liostraca Buckman, 1892: 310, pl. 53, figs 11-16, pl. 55, fig. 3 (LT designed by Huf 1968: 98) to fig. 5, pl. 56, fig. 1. — Dorn 1935: 101, pl. 9, fig. 5, pl. 22, fig. 3, pl. 27, fig. 1. — Kopik 1967: 25, pl. 6, fig. 4, pl. 7, figs 1-4. — Morton 1972: 506, pl. 102, pl. 103, figs 1, 2, pl. 104, figs 1, 2. — Sandoval 1990: pl. 2, fig. 10. — Fernández-López & Mouterde 1994: 133, pl. 1, figs 8-11. — Dietze *et al.* 2013: 38, pl. 3, figs 5, 8. — Chandler & Whicher 2015: pl. 20, fig. 2. — Énay & Mangold 2021: 54, pl. 7, figs 2, 3, pl. 8, figs 1-3.

Dorsetensia liostraca liostraca – Huf 1968: 97, pls 30-40 (*cum syn.*). — Fernández-López 1985: 61, text-fig. 6C. — Ohmert *et al.* 1995: 60, text-figs 9, 10, pl. 2, fig. 3. — Dietze *et al.* 2011a: 222, pl. 4, figs 1-7, pl. 5, figs 1-4, pl. 6, figs 1-3, 5, 7 (*cum syn.*).

Dorsetensia liostraca subtecta – Huf 1968: 103, pls 41-46, pl. 47, fig. 1 (*cum syn.*). — Dietl *et al.* 1984: 310, fig. 2/1. — Schlegelmilch 1985: 66, pl. 20, fig. 3 (HT refigured). — Ohmert *et al.* 1995: 59, pl. 1, fig. 6, pl. 3, fig. 1.

Dorsetensia liostraca tecta – Huf 1968: 107, pl. 47, figs 2-4, pls 48-51 (*cum syn.*). — Ohmert *in* Wittmann 1983: pl. 2, fig. 2. — Ohmert *et al.* 1995: 62 pl. 2, figs 1, 2.

Dorsetensia (*Dorsetensia*) *subtecta* – Pavia 1983: 62, pl. 5, figs 3, 8.

Dorsetensia subtecta – Galácz 1991b: 866, text-fig. 3b, pl. 2, fig. 4. — Fernández-López & Mouterde 1994: 134, pl. 2, figs 8-11, pl. 3, fig. 1.

Material examined. — JA2.40.1, JGa2.31.44, JGa2.31.45, JGa7.32.2, JGa7.32.3, JGa7.32.4, JGa7.32.5, JGa7.32.6, JGa7.32.10, JGa7.32.14.

Measurements. — See Table 25.

Description

All Subbetic specimens are incomplete, some preserving part of the BC. Shells are medium-sized, involute to moderately involute with narrow to moderately narrow umbilicus, more in outer whorls than inner ones. The whorl section, subrectangular in the inner whorls, becomes high compressed ogival to triangular in the outer ones. The umbilical wall is vertical, the umbilical edge is rounded, the flanks are more or less convex, and the venter has a well-separated floored keel. The inner whorls bear poorly developed ribs, some simple, some bifurcate, slightly sinuous and ventrally projecting, lacking nodes or spines. The middle and outer whorls become smooth. The suture line (Fig. 8F) is rather simple with a wide, shallow, and seldom branched L. The saddles are slightly indented with a broad base, and there are three well-differentiated umbilical lobes.

Remarks

According to Huf (1968: 97) and Dietze *et al.* (2011a: 222, 223), the separation of all the members of the "liostraca-group", *Dorsetensia tecta*, *D. subtecta*, and *D. liostraca*, is purely artificial as they are in reality synonymous. All other *Dorsetensia* species are more evolute, have a rectangular or subrectangular whorl section, a lower rate of whorl expansion, and the ribbed stage is usually more persistent.

Distribution

Specimens of *Dorsetensia*, belonging to the group of *D. liostraca*, has been mentioned in the lower part of the Humphriesianum Zone from numerous localities: England (Buckman 1892; Parsons 1977; Chandler *et al.* 2014; Chandler & Whicher 2015), Scotland (Morton 1972, 1976), France (Pavia & Sturani

Table 26. — Measurements of *Dorsetensia hebridica* Morton, 1972 [M].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC3.119.4	45.0	12.5	0.28	16.0	0.36	–	–	Almost complete	Propinquans Zone, Hebridica Subzone
	29.0	9.5	0.33	12.0	0.41	–	–		
JAC3'.22.19	35.0	10.0	0.29	15.0	0.43	–	–		
	30.0	8.8	0.29	14.0	0.47	–	–		
JAC3'.22.44	45.0	12.5	0.28	19.0	0.42	–	–	Almost complete	
	32.0	9.0	0.28	15.0	0.47	–	–		

1968; Rioult 1980, Pavia 1983; Pavia *et al.* 2013, Fernández-López & Mouterde 1994, De Baets *et al.* 2008), Germany (Buck *et al.* 1966; Huf 1968; Dietl & Rieber 1980; Ohmert *et al.* 1995; Dietze *et al.* 2008, 2011a, 2013), Poland (Kopik 1967), Spain (Iberian Mountain range and Betic Cordillera; Fernández-López 1985; Sandoval 1983, 1990), the Caucasus, the Transcaucasus (Azarjan 1982; Rostovtsev 1991), the Arabian Peninsula (Énay & Mangold 1994, 2021), and Tibet (Westermann & Wang 1988). In South America it occurs in Argentina and Chile (Westermann & Riccardi 1972; Hillebrandt 2001) and in North America it is found in Oregon, United States (Imlay 1973, 1986; Poulton *et al.* 1992). In the Subbetic domain, *D. liostraca* occurs in the Humphriesianum Zone, Romani Subzone from Sierra de Gaena (sections, JGa2 and JGa7), Lucena (Córdoba Province), and from Sierra Arana (section JA2; Granada Province).

Dorsetensia hebridica Morton, 1972 [M] (Fig. 14R-S)

Dorsetensia hebridica Morton, 1972: 516, pl. l05, figs 13, 14, 21, 22, 25-26 (HT). — Dietze *et al.* 2008: fig. 6d (HT refigured).

Dorsetensia gr. *hebridica* – Fernández-López 1985: 63, text-fig. 6A, pl. 10, figs 5-7.

Dorsetensia cf. *hebridica* – Sandoval 1990: 149, pl. 2, fig. 7.

Dorsetensia sp. aff. *D. hebridica* – Fernández-López & Mouterde 1994: 134, pl. 3, figs 2?, 3.

?*Dorsetensia* aff. *hebridica* – Dietze *et al.* 2011a: 51, pl. 8, fig. 6.

Material examined. — JAC3.119.4, JAC3'.22.4, JAC3'.22.15, JAC3'.22.19 and JAC3'.22.44.

Measurements. — See Table 26.

Description

Moderately involute to semievolute, whorl section compressed subrectangular with a steep to vertical umbilical wall, a rounded umbilical edge, barely convex flanks, and tabulate but non-bisulcate venter with a high keel. The ribs, which arise near the umbilical edge, are mainly simple, strong, and spaced on the inner and middle whorls, but fade on the outer whorls to become almost smooth in some specimens. The ribs are scarcely flexed on the whorl sides, but ventrally strongly project forward. The specimens available are incomplete but two preserve a half whorl of the BC; all are laterally flattened. The septal suture is not well preserved in the Subbetic specimens.

Remarks

According to Morton (1972), the species most closely related to *D. hebridica* are *D. pinguis*, and *D. hannoverana*, but the former is larger and slightly more involute. Also all specimens of *D. hebridica* show a decline of the ribbing on the BC, whereas this is sporadic in *D. pinguis* and in no case occurs in *D. hannoverana*. Morton (1972: 517) proposed a dimorphic relationship between *D. hannoverana* [M] and *D. hebridica* [M] on one hand and *D. pinguis* [m] on the other, assuming that the macroconchs *D. hannoverana* and *D. hebridica* are less variable than the microconch, including the microconchs in *D. pinguis*. The assumption here is that this is correct and consequently the three species are synonymous with each other. In this case, *D. pinguis* would be the valid species, but the material analysed here, not very abundant and quite deformed, does not provide conclusive results and therefore, it has been deemed preferable to use the three taxonomic names.

Distribution

According to Morton (1972: 517), the HT of *D. hebridica* comes from the lower part of the Humphriesianum Zone, basal bed of the Upper Sandstones, east of Torvaig, near Portree, Isle of Skye, Scotland. Later, Morton (1975, 1976) introduced a Hebridica Subzone for the upper part of the Sauzei (Propinquans) Zone. The species occurs in this stratigraphic interval in several localities of Western Europe and Morocco. The Subbetic specimens are from the uppermost part of the Propinquans Zone, Hebridica Subzone, of Sierra Alta Coloma (sections JAC3, JAC3'; Jaén Province).

Dorsetensia? sp. [M] (Fig. 14T)

Material examined. — JAC22.57.3.

Measurements. — See Table 27.

Description

Moderately evolute, whorl section compressed subrectangular with a low umbilical wall that almost matches the rounded umbilical edge. The flanks are gently convex and the ventral area is weakly tabulated with a moderately developed keel. The ribs, arising near the umbilical edge, somewhat irregular in thickness, are mainly simple but some tend to join in pairs near their base. Radial or only barely sinuous, they bend forward at the ventral edge. The ribbing weakens but does not disappear in the BC. The suture is not preserved.

Table 27. — Measurements of *Dorsetensia*? sp. [M].

Specimen	D	U	u	H	H	W	w	Remarks	Biostratigraphy
JAC22.57.3	65.0	22.0	0.34	23.0	0.35	–	–	Almost complete	Laeviuscula Subzone
	46.0	15.5	0.34	18.5	0.40	–	–		

Table 28. — Measurements of *Dorsetensia regrediens* (Haug, 1893) [m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JRi3.28.1	27.0	11.0	0.41	9.0	0.33	12.0	0.36		Romani Subz.

Remarks

The specimen described above displays common characters with *Witchellia* gr. *laeviuscula* (J. de C. Sowerby, 1824) and some primitive *Dorsetensia* such as *D. pinguis* (Roemer, 1836), D. *hannoverana* (Hiltermann, 1939), and *D. hebridica* Morton. *W. laeviuscula* has a similar ribbing style, but is more involute and has greater whorl expansion. Also, the section is subtriangular instead of subrectangular. *Dorsetensia* gr. *pinguis* specimens have similar coiling, but usually have more developed ribbing.

Distribution

This specimen is from the upper part of the Laeviuscula Zone, and is therefore older than *D.* gr. *pinguis*, from the JAC22 section, Campillo de Arenas (Jaén Province).

Dorsetensia regrediens (Haug, 1893) [m] (Fig. 14U)

Witchellia regrediens Haug, 1893: 318, pl. 10, fig. 7.

Dorsetensia edouardiana – Buckman 1892: 304, pl. 52, figs 8-13, 15-17.

Dorsetensia (*Nannina*) *regrediens* – Pavia 1983: 67, pl. 6, fig. 8.

Nannina regrediens – Fernández-López 1985: 119, pl. 10, fig. 2.

Dorsetensia regrediens – Dietze *et al.* 2011a: 215, pl. 1, figs 19-22.

Material examined. — JRi3.28.1.

Measurements. — See Table 28.

Description

The only available specimen is small with a discoidal shell, a wide umbilicus, almost vertical umbilical wall, rounded umbilical edge, and gently convex flanks. The ventral region cannot be seen, nor the shape of the aperture, although the specimen looks almost complete. The simple and relatively dense falcoid-sigmoid ribs persist to the end of the spiral.

Remarks

The most similar species is *Dorsetensia edouardiana* (d'Orbigny 1845: 392), but it is larger and more involute and has more sigmoid ribbing. According to Dietze *et al.* (2011a: 217), a LT of *D. regrediens* has never been selected. The same authors (Dietze *et al.* 2011a: 217) interpreted *D. edouardiana* (d'Orbigny, 1845), *D. pulchra* (Buckman, 1892), *D. regrediens* (Haug, 1893), and *D. lennieri* (Brasil, 1894) as microconchiate "species", which could be the dimorphic couple of *D. tessoniana* (d'Orbigny, 1845) [M]. However, several of the specimens figured as *D. edouardiana* by Huf (1968) and by Dietze *et al.* (2011a) seem rather to represent macroconchiate forms. If the idea proposed by Dietze *et al.* (2011a) were true, all four taxa would be synonymous.

Distribution

The type of *D. regrediens* is from the "Oolithe ferrugineuse" of Saint-Vigor, near Bayeux, France (Haug 1893; Dietze *et al.* 2011a). In Frogden Quarry (Dorset, England), *D. regrediens* occurs in the Inferior Oolite Formation, bed 4b, Lower Bajocian, the Humphriesianum Zone, Romani Subzone, Bj-14 horizon (Callomon & Chandler 1990; Dietze *et al.* 2011a: 218). In Chaudon, Digne area (SE France), in the Iberian ranges (Spain), and in the Atlas Mountains (Morocco), the species is present in the Romani Subzone, the lower part of the Humphriesianum Zone (Pavia 1983; Fernández-López 1985; Sadki 1996). The only Subbetic specimen is from the Humphriesianum Zone, Romani (= Cycloides) Subzone of Sierra de Ricote (Murcia Region).

Dorsetensia pinguis (Roemer, 1836) [m] & [M?] (Fig. 14V-X)

Ammonites pinguis Roemer, 1836: 186, pl. 12, fig. 3 (HT).

Sonninia (*Poecilomorphus*) *pinguis pinguis* – Huf 1968: 54, pl. 4, figs 7(HT refigured) to fig. 12, pl. 5, figs 1-8.

Dorsetensia pinguis – Morton 1972: 510, pl. 105, figs 1-10, 17-20. — Schlegelmilch 1985: 65, pl. 19, fig. 10 (HT refigured).

Nannina pinguis – Fernández-López 1985: 115, pl. 10, fig. 8.

Dorsetensia (*Nannia*) *pinguis* (m) – Metz 1990: 10, pl. 4, fig. 3.

Dorsetensia pinguis pinguis – Ohmert *et al.* 1995: 52, pl. 1, figs 1-3.

?*Sonninia* sp. [corresponds to *Dorsetensia pinguis* auct.] – Dietze *et al.* 2008: 148, figs 4e, g.

TABLE 29. — Measurements of *Dorsetensia pinguis* (Roemer, 1836) [m] & [M?].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3'.22.12	16.0	6.0	0.375	6.0	0.375	–	–	Microconch	Propinquans Zone, Hebridica Subzone
JAC3'.22.18	20.0	6.0	0.30	8.3	0.415	–	–	Microconchs?'	
	15.0	5.0	0.33	6.0	0.40	–	–		
JAC3'.22.26	31.0	7.5	0.31	15.0	0.48	–	–		
	23.0	6.8	0.30	11.0	0.48	–	–		
JAC3'.22.28	30.0	7.0	0.23	14.0	0.47	–	–		
	22.0	6.0	0.27	11.0	0.49	–	–		
JAC3'.22.31	21.0	6.3	0.30	8.9	0.42	–	–		
	15.0	4.5	0.30	6.9	0.46	–	–		
JAC3'.22.35	20.0	5.5	0.275	9.5	0.47	–	–		
	16.0	5.0	0.31	7.0	0.44	–	–		
JAC3'.22.36	25.0	8.5	0.34	11.2	0.45	–	–		
	18.5	6.5	0.36	7.2	0.39	–	–		
JAC3'.22.39	24.0	7.3	0.30	10.0	0.42	–	–		
	18.0	6.1	0.34	7.5	0.42	–	–		
JAC3'.22.45	27.0	8.2	0.30	11.0	0.41	–	–		
	20.0	6.0	0.30	9.0	0.45	–	–		
JAC3'.22.48	28.0	9.0	0.32	12.0	0.43	–	–		
	22.0	7.0	0.32	9.0	0.41	–	–		

MATERIAL EXAMINED. — JAC3.110.1, JAC3'.22.6, JAC3'.22.12, JAC3'.22.18, JAC3'.22.26, JAC3'.22.28, JAC3'.22.31, JAC3'.22.35, JAC3'.22.36, JAC3'.22.39, JAC3'.22.45, JAC3'.22.48, JAC11.R.68, JAQ1.70.4, JAQ1.71.4 and JAQ1.71.5.

MEASUREMENTS. — See Table 29.

DESCRIPTION

The HT (refigured by Huf 1968 and by Schlegelmilch 1985) is a small septate specimen showing only juvenile stages, with relatively evolute coiling and a barely compressed subquadrangular whorl section. The Subbetic specimens are relatively small, moderately evolute (O/D varying from 0.23 to 0.34 on last preserved whorl), with inner whorls somewhat more evolute than the outer ones. The whorl section is barely compressed, although this is difficult to verify due to the lateral crushing of the specimens. The umbilical wall is steep with a rounded umbilical edge and barely convex flanks while the venter is broad, tabulate with a prominent keel without grooves. The innermost whorls can be smooth, but later broad, simple or bifurcating ribs appear at the umbilical edge and fade on the top of the flanks before reaching the venter. The ribs are slightly flexed on the whorl sides and ventrally project forward. In some specimens, the ribs progressively erase on the outer whorls and the BC end becomes almost smooth. The crushing of the Subbetic specimens makes it difficult to differentiate all the taxonomic characters, but a specific diversity similar to those shown by Huf (1968) or Morton (1972) can be discerned, although most of the Subbetic specimens are smaller. The septal suture cannot be well observed in any of our specimens.

REMARKS

The differences with *D. hannoverana* (Hiltermann, 1939) are minimal, but the innermost whorls of *D. pinguis* can be almost smooth whereas they are strongly ornamented in *D. hannoverana* in all cases. Furthermore, *D. hannoverana* is more evolute whereas the whorl section of *D. pinguis* is more compressed and has no furrows limiting the keel. Both morphologies occur in equivalent or the same beds in many localities where they coexist with *D. hebridica*. As indicated above, Morton (1972: 517) proposed a dimorphic relationship of *D. hannoverana* [M] with *D. hebridica* [M] on the one hand with *D. pinguis* [m] on the other.

DISTRIBUTION

The type comes from Galgenberg near Hildesheim (Germany). In Germany, this species is characteristic of the Pinguis Subzone (Pinguis horizon), for which German authors (Dorn 1935; Buck *et al.* 1966; Huf 1968; Dietl 1977; Dietl *et al.* 1984, Metz 1990; Schweigert *et al.* 2007; Dietze *et al.* 2008, 2009, 2011a, 2013, 2015, 2017) place it at the base of the Humphriesianum Zone, which is equivalent to the Hebridica Subzone (the upper part of the Propinquans Zone), of current British authors (Morton 1975, 1976; Callomon & Chandler 1990; Chandler *et al.* 2006, 2017; Chandler & Whicher 2015). In this stratigraphic interval (Hebridica Subzone) is cited in France (Pavia 1983, Rioult *et al.* 1997; De Baets *et al.* 2008); Hungary (Galácz *et al.* 2015); Portugal (Fernández-López *et al.* 1988); Morocco (Sadki 1996); and Spain, in the Iberian Cordillera (Fernández-López 1985) and the Subbetic domain (Sandoval 1983, 1990). The Subbetic specimens come from the Propinquans Zone (Hebridica Subzone) of Sierra de Alta Coloma area (sections JAC3, JAC3'and JAC11) and Barranco de Agua Larga (section JAQ1; Jaén Province).

Dorsetensia hannoverana **(Hiltermann, 1939)**
[M] & [m] (Fig. 14Y, Z)

Sonninia pinguis hannoverana Hiltermann, 1939:167, text-figs 42-45, pl. 11, figs 8 (LT), 9. — Wendt 2017: fig. 6C.

Table 30. — Measurements of *Dorsetensia hannoverana* (Hiltermann, 1939) [M & m].

Specimen	D	U	u	H	h	W	w	Remarks	Biostratigraphy
JAC3'.22.3	32.0	13.0	0.40	12.0	0.375	–	–	Adult complete?	Propinquans Zone, Hebridica Subzone
	25.0	10.5	0.42	9.0	0.36	–	–		
JAC3'.22.25	28.0	9.0	0.32	12.0	0.43	–	–	Incomplete specimens	
	20.0	7.0	0.35	8.0	0.40	–	–		
JAQ1.67.3	33.0	11.0	0.33	13.0	0.39	–	–		
	23.0	7.6	0.33	10.0	0.43	–	–		

Sonninia pinguis westfalica Hiltermann, 1939: 168, pl. 11, fig. 10, text-figs 46-49.

Sonninia (*Poecilomorphus*) *pinguis hannoverana* – Huf 1968: 64, pl. 6, figs 5 (LT refigured) to fig. 12, pl. 7, figs 1-3, pl. 10, fig. 1.

Sonninia (*Poecilomorphus*) *pinguis westfalica* – Huf 1968: 69, pl. 7, figs 4, 5.

Dorsetensia hannoverana – Morton 1972: 513, pl. 105, figs 15, 16, 23, 24. — Pavia 1983: pl. 6, figs 9, 10. — Fernández-López 1985: 121, pl. 10, fig. 9. — Schlegelmilch 1985: 64, pl. 19, fig. 9 (LT refigured).

Nannina hannoverana – Fernández-López & Mouterde 1994: p. 131, pl. 3, fig. 4.

Dorsetensia pinguis hannoverana – Ohmert *et al.* 1995: 54, pl. 1, figs 4, 5.

?*Nannina* sp. [corresponds to *Dorsetensia hannoverana* auct.] – Dietze *et al.* 2008: 148, fig. 4C.

Material examined — JAC3'.22.3, JAC3'.22.25, JAC3'.22.32 and JAQ1.67.3.

Measurements. — See Table 30.

Description

The LT is small, evolute with a whorl section almost as wide as high (subquadrangular), broad ventral area with keel limited by small sulci. The ribs are mostly bifurcated from a small thickening on the umbilical edge. The Subbetic specimens, possibly macroconchs, are small sized, relatively evolute, although crushed (flattened and deformed by lateral pressure). The whorl section appears to be subrectangular with almost a vertical umbilical wall and rounded umbilical edge. The flanks are slightly convex and the ventral area is wide with a very high keel. None of the specimens analysed here preserve the peristome. The ribs, relatively strong on inner and intermediate whorls, are simple or grouped in pairs from a small thickening near the umbilical edge, and radial or only barely flexuous. Towards the outer whorls, the ribbing weakens, the simple ribs become more abundant and the ribs reach maximum relief near the middle of the flanks. The septal suture is not well preserved in the Subbetic specimens.

Remarks

Morton (1972: 517) suggested that *D. hannoverana* represents macroconch forms. Later, Pavia (1983, pl. 6, figs 9, 10a) figured two macroconch forms that he attributed to this species. Fernández-López (1985: 121) showed that the specimens from the Iberian Cordillera are microconchiate forms. Subbetic specimens do not preserve the peristome, but their size, ribbing, and coiling are more similar to those of the microconchs than to the macroconchs.

Distribution

The LT of *D. hannoverana* is from Hildesheim (Germany) and was placed in the "Pinguis Zone" by Huf (1968: 69). Representatives of this species from the uppermost part of Sauzei Zone have been reported in Skye, Scotland (Morton, 1976) and in the Iberian Cordillera (Fernández-López 1985). However, Pavia (1983) mentioned the species at the top of the Sauzei Zone and at the base of the Humphriesianum Zone (Subzone Romani) of Chaudon, near Digne (SE France). In Tendron (Cher, central France), the species is present in the Gervillii horizon of the Humphriesianum Zone (Fernández-López & Mouterde 1994). The Subbetic specimens are from the Propinquans Zone (Hebridica Subzone) of Sierra de Alta Coloma area (section JAC3') and Barranco de Agua Larga (section JAQ1), both from Jaén Province.

PALAEOBIOGEOGRAPHIC CONSIDERATIONS

As shown above (see Section 1), Sonniniidae have worldwide distribution, except in the Panboreal Realm. They are especially abundant in the western Tethys [Mediterranean-Caucasian Sub-realm (Mediterranean, Sub-Mediterranean, NW European, Caucasian and NE Tethyan provinces)] and in the East-Pacific Sub-realm (Andean, Shoshonean, and Athabascan provinces). In the Indo-Pacific Sub-realm, these sonniniids are scarce, but are found in the Ethiopian Province, Thailand, New Guinea, Indonesia, and Australia. Most of the taxa included here in Sonniniidae (mainly morphogenera) are relatively common in both regions.

The sonniniids in no case constitute the dominant taxa among the ammonite assemblages of the uppermost Aalenian (Concavum Zone, Limitatum Subzone) and lowermost Bajocian (Discites Zone) of the Subbetic, where they represent approximately 2-3% of all ammonites recorded, whereas Erycitidae (mainly *Haplopleuroceras*) constitute approximately 35% and the Graphoceratidae almost 40%. Sonniniids become much more abundant in the Ovale, Laeviuscula, and Propinquans zones, where they account for roughly 46% of all ammonoids, being predominant in many beds and more abundant than any other ammonoid group.

Several Sonniniidae taxa (genera and species) that are common in the Subbetic basin (located in the eastern end of the Hispanic Corridor) and in other Western Mediterranean areas are equally abundant in Submediterranean, NW European, and NE Tethyan provinces, and can also occur in the Andean, Shoshonean and Athabascan provinces. This indicates that during the latest Aalenian-Early Bajocian time interval, marine communications were good between these palaeogeographic domains, which was favoured because most of the Early Bajocian coincided with a transgressive marine interval and the corresponding sea-level rise (see O'Dogherty *et al.* 2006 and references therein). These transgressive events led to the opening of marine corridors that connected different palaeogeographic areas, allowing dispersion of diverse pelagic organisms. The most important event may have been the temporary opening of the Spanish Corridor, which connected the westernmost Tethys with the eastern Pacific (Aguado *et al.* 2017 and references therein).

Although several palaeogeographic domains contain the same or similar forms (genera or even species), size difference is a significant character differentiating the Subbetic sonniniids from other forms coming from platform areas (e.g. Iberian Range, SW England, SW Germany, etc.). Sonniniids from platforms are usually larger than specimens of the same species and morphotypes from the Subbetic (Betic Cordillera). Such contrast in size could be due to palaeoecological and/or palaeogeographic controls. Factors such as food availability are key parameters influencing the growth of individuals, and food is likely to have been more abundant on the shallow marine shelf (or in the epicontinental shelf seas) than in the Tethyan oceanic basin corresponding to the Subbetic domain (Betic Cordillera).

Taphonomic and palaeoecological analyses show that macroconchs and microconchs as well as the juvenile and adult forms coexisted both in Subbetic domain (Betic Cordillera) and in epicontinental shelf seas (Iberian Range, SW England, SW Germany, NE and central France, etc.). This implies that during the latest Aalenian and Early Bajocian, sonniniid populations lived and reproduced in both Tethyan oceanic basins and in epicontinental shelf seas. Certain differences appear in relative abundance, size, etc., at times fluctuating from level to level and depending on the different taxa.

During the latest Aalenian to Early Bajocian, the connection between the oceanic Subbetic basin, located in the Mediterranean province (westernmost Tethys) and the western part of the European epicontinental shelf seas basins (SW England, NE and central France, SW Germany, etc.), could have been continuous throughout the Iberian-Basque-Cantabrian basins, or through the Lusitanian Basin (Sandoval & Chandler 2000 and references therein). The nature of the Lusitanian and Iberian-Basque Cantabrian Aalenian and lower Bajocian ammonite assemblages, which display an intermediate character between NW European and typical Mediterranean taxa, supports the contention of a probable Subbetic-Lusitanian-NW European connection during this part of the Middle Jurassic. Such a connection may have allowed the migration of ammonites between these domains. The similarities, both in morphogenera and in morphospecies, among NW European, Submediterranean, and Subbetic sonniniids provide evidence that appears to support migrations between the two regions.

CONCLUSIONS

Sonniniids are abundant in the uppermost Aalenian-Lower Bajocian from several Median Subbetic areas (Betic Cordillera, Southern Spain), being the dominant ammonites in the Ovale, Laeviuscula, and Propinquans zones.

The hemipelagic-pelagic rhythmites of marly limestones and marls in continuous sequences, with ammonites, are the dominant facies in the Median Subbetic subdomain, enabling good biostratigraphic results and allowing the recognition of all the Lower Bajocian ammonite zones and subzones.

Sonninia (*Sonninia*) [M] & [m], *S.* (*Euhoploceras*) [M] & [m], *S.* (*Papilliceras*) [M] and *Sonninites* [M] & [m] are the Sonniniinae genera so far recorded in the Subbetic domain. *Witchellia* [M] & [m] and *Dorsetensia* [M] & [m] represent the Witchelliinae in the Subbetic.

Taxonomical aspects of *Fontannesia, Newmarracarroceras* and *Latiwitchellia* are debatable, so the taxonomic position of these taxa is not entirely clear. These three genera, traditionally classified as Sonniniidae, seem to have more affinities with the Grammoceratinae than with the sonniniids.

Dimorphism is common in sonniniids. The macroconchs [M] (♀) have a simple peristome. The majority of the microconchs [m] (♂) have a peristome with lateral lappets, but some small forms of *S.* (*Sonninia*) and *S.* (*Euhoploceras*) are probably microconchs without apertural modifications or small adult macroconchs (mesoconchs). It is not easy to differentiate the dimorphic pairs of the diverse taxa.

Comparisons of the Subbetic sonniniids (typical Mediterranean forms) with the types of different species from the Submediterranean, NW European, and NE Tethyan provinces reveal great similarities between the forms of these palaeogeographic provinces. However, two new forms have been described: *Witchellia companyi* n. sp. [M] and *W. striata* n. sp. [M] that until now have been recorded only in the Subbetic domain.

The widespread palaeogeographic distribution of the sonniniids is explained as the result of the early Bajocian time marking a transgressive marine interval and corresponding sea-level rise, which led to the opening of marine passageways between the various palaeogeographic realms and provinces, allowing communication between them.

Acknowledgements
This study forms part of the results of Research Project: P20_00783 (MINECO/FEDER) financed by the DGI (Dirección General de Investigación, Spain) and the EMMI Research Group (RNM 0178 Junta de Andalucia, Spain). I am very grateful to A. Galácz and G. Pavia whose constructive comments led to improvements in the final version of this paper, and to E. Côtez for his helpful editorial assistance. R. B. Chandler has sent me photographs and casts of various holotypes of English specimens. I am also grateful to my colleague L. O'Dogherty for photographic assistance and to Mr D. Nesbitt for reviewing the English text.

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Submitted on 7 November 2021;
accepted on 11 January 2022;
published on 15 September 2022.