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Upper Tithonian ammonites (Himalayitidae Spath, 1925 and Neocomitidae Salfeld, 1921) from Charens (Drôme, France)

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Abstract: This contribution focuses on the Perisphinctoidea ammonite taxa from the Upper Tithonian at Charens (Drôme, south-east France). Emphasis is laid on five genera that belong to the families Himalayitidae and Neocomitidae. We document the precise vertical range of the index-species *Micracanthoceras microcanthum*, and a comparative ontogenetic-biometric analysis sheds new light on its range of variation and dimorphism as compared to the best-known Spanish populations. As herein understood, the lower boundary of the *M. microcanthum* Zone (base of the Upper Tithonian) is fixed at the FAD of its index species. The faunal assemblages and species distribution of the *P. andreaei* Zone are rather similar to those described at the key-section of Le Chouet as confirmed by the co-occurrence of the genera *Protacanthodiscus*, *Boughdiriella* and *Pratumidiscus*. New palaeontological evidence supports the view that the basal Neocomitidae *Busnardoiceras busnardoi* was derived from *Protacanthodiscus andreaei* in the upper part of the *P. andreaei* Zone.

Key words: Ammonoidea, Tithonian, Jurassic, biostratigraphy, Drôme, France.

Introduction

Within the activity of the Berriasian Working Group (BWG) of the International Subcommission for Cretaceous Stratigraphy (ISCS/IUGS), Bulot et al. (2014) and Frau et al. (2015) focused on the systematics of the late Tithonian Perisphinctoidea (Ammonitina, Ammonoidea) from Le Chouet (Drôme); a section that stands as a reference for the definition of the Jurassic/Cretaceous boundary in south-east France (Wimbledon et al. 2013). However, we failed to characterize the exact range and intraspecific variation of the late Tithonian index species *Micracanthoceras microcanthum* (Oppel, 1865) due to its sporadic occurrence and the poor preservation of the specimens collected (Bulot et al. 2014). A new survey of the sections of the Drôme river valley already documented by Remane (1970) led us to sample in detail the Charens section where the lower part of the Upper Tithonian is better exposed than at Le Chouet and it has yielded rich ammonite faunas. The aim of the present contribution is to discuss the taxonomy and illustrate the Himalayitidae and Neocomitidae in this new collection.

Geological setting

The Charens section is located about three kilometres to the west of Le Chouet (Drôme, France, Fig. 1). This section is part of the late Kimmeridgian to early Berriasian "turbiditic" system of the Subalpine Basin deposited along the northern Tethys margin (Ferry & Grosheny 2013). The locality lies in the upper valley of the Drôme River (Long 5°31'08"E, Lat 44°32'42"N) off the local road (D93) from Die to Beaurières. It comprises a low mural section, 250 m-long, along a single-track road (D145) on the east side of the Charens gorge. The section extends around the slope from an altitude of 756 m to 768 m and dips 10 degrees to the North.

The studied part of the succession consists of 41 metres of well-bedded limestone autochthonous intervals intercalated between conglomeratic, clast or matrix-supported breccias (Fig. 1). The bottom part of the section corresponds to thin-bedded biocalcarenites (beds 5 to 12) above a thick conglomeratic breccia (bed 1 to 5), that pass into a 12m-long, ammonite-bearing, biomicrite succession (beds 13 to 67). The first occurrence of ammonites is reported in bed 17 and contains *Burckhardticeras ponti* (Fallot & Termier, 1923) and *Lemencia* sp. This assemblage is indicative of the *Burckhardticeras ponti* Zone *sensu* Enay & Geyssant (1975) that marks the uppermost Lower Tithonian. The First Appearance Datum of *M. microcanthum* is herein reported at the base of the bed 25 in association with *Lemencia* sp. and poorly-preserved fragments of *Cordubiceras* cf. *cordubae* (Olóriz & Tavera, 1979) (Fig. 1). As herein understood, the FAD of *M. microcanthum* marks the lower boundary of the Upper Tithonian (see discussion in the Conclusion). Above, thick massive, clast- and matrix supported breccias affect the succession. The biomicrite interval (beds 79 to 98) that crops out above the

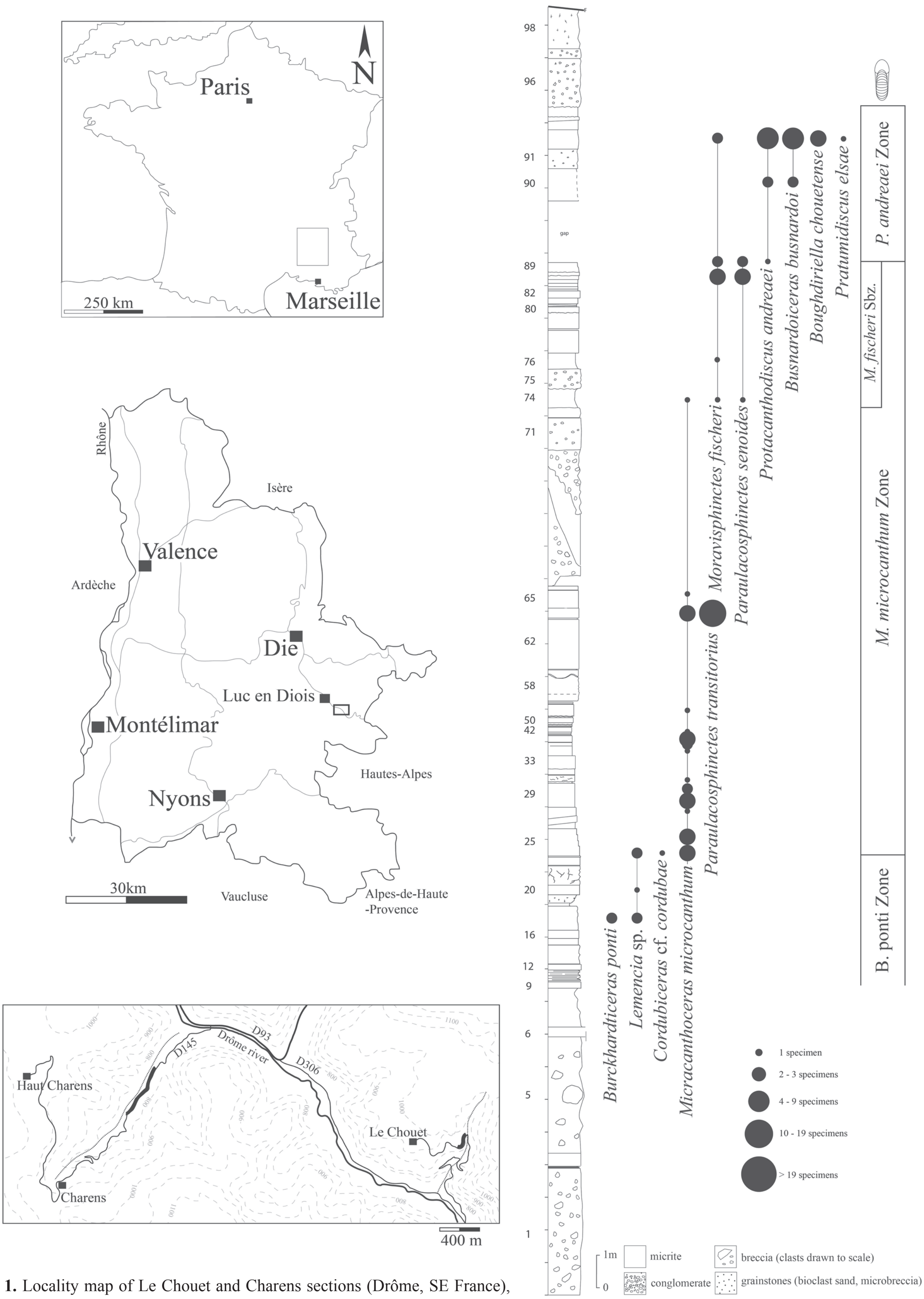

Fig. 1. Locality map of Le Chouet and Charens sections (Drôme, SE France), biostratigraphy and vertical range of the late Tithonian Himalayitidae and Neocomitidae studied in this paper.

brecciated interval can be correlated with certainty to beds 72 to 89 at Le Chouet section. This is supported by ammonite occurrences [*Moravisphinctes fischeri* (Kilian, 1889), *Paraulacosphinctes senoides* Tavera, 1985, *Protacanthodiscus andreaei* (Kilian, 1889) etc.] and useful lithological markers such as the intraclastic/microbreccia bed 88 (= bed 80 of Le Chouet section) and the clast-supported breccia bed 95–97 that correspond to the grainstone-conglomerate-grainstone triplet of Le Chouet (= beds 86 to 88).

The calpionellid assemblages of the Charens section were previously described by Remane (1970, fig. 6) but the resolution of the drawing prevents us from a bed-by-bed correlation. A detailed study of the calpionellids and calcareous nannofossils, is currently in progress in the BWG.

Systematic palaeontology

Preservation of our specimens as crushed internal moulds prevents us from giving other measurements than Dmax = larger measurable diameter, U = adult width of the umbilicus and Wh = adult whorl height. The ratios U/D, Wh/D and Wb/D (umbilical dimension, whorl height and whorl breath as a percentage of the adult diameter), are discussed in systematic descriptions. In synonymies, we distinguished the macroconch [M] and microconch [m] specimens.

All studied specimens are deposited in the Frau/Bulot collection at the *Musée Paléontologique de Provence* (MPP) of the Aix-Marseille Université, France. All specimens from Charens were coated with ammonium chloride prior to photography. The following abbreviations indicate the repository of specimens mentioned in the text:

FSL and EM: University of Claude Bernard — Lyon-I.

UJF-ID: University of Grenoble.

BSPM: Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

Order **Ammonoidea** Zittel, 1884
Suborder **Ammonitina** Hyatt, 1889
Superfamily **Perisphinctoidea** Steinmann, 1890
Family **Himalayitidae** Spath, 1925
Subfamily **Himalayitinae** Spath, 1925
Genus *Micracanthoceras* Spath, 1925

Type species. *Ammonites microcanthus* Oppel *in* Zittel, 1868, by original designation of Spath (1925, p. 144).

Remarks. Bulot et al. (2014) recently shed new light on the content of *Micracanthoceras* to which the reader is referred. However, this revision was not supported by palaeontological evidence due to the poorly-preserved specimens collected at Le Chouet. New collections from Charens allow the study of intraspecific variation in *Micracanthoceras microcanthum* (Oppel *in* Zittel, 1868) throughout its range. A biometric comparison with the many species introduced by Tavera (1985) from the Betic Cordillera (Spain) is provided) (see Table 1 in Supplementary data).

Micracanthoceras microcanthum (Oppel *in* Zittel, 1868)
Figs. 2A–C, 3A,B and 4A,U

Macroconchs [M]

1865 *Ammonites Symbolus* – Oppel, p. 555
1865 *Ammonites Köllikeri* – Oppel, p. 555
1868 *Ammonites microcanthus* – Oppel *in* Zittel, p. 93, pl. 17, figs. 1a-b,2
1868 *Ammonites Symbolus* – Oppel *in* Zittel, p. 96, pl. 16, figs. 6a,c, 7a,c
1868 *Ammonites Köllikeri* – Oppel *in* Zittel, p. 95, pl. 18, fig. 1a,c
non 1868 *Ammonites Köllikeri* – Oppel *in* Zittel, p. 95, pl. 18, fig. 2a,c [= *Ardesciella rhodanica* (Mazenot)]
non 1886 *Perisphinctes Köllikeri* (Oppel) – Nicolis & Parona, p. 77, pl. 4, fig. 6 (= ?Simoceratidae gen. et sp. indet.)
non 1890 *Hoplites Koellikeri* (Oppel) – Toucas, p. 607, pl. 18, fig. 11A,B [= *Ardesciella rhodanica* (Mazenot)]
1897 *Hoplites microcanthus* (Oppel) – Roman, p. 284, pl. 1, fig. 10a,b
non 1897 *Reineckeia Koellikeri* (Oppel) – Steuer, p. 31, pl. 32(8), fig. 5 [= *Corongoceras mendozanum* (Behrendsen)], 6
non 1900 *Reineckeia Koellikeri* (Oppel) – Burckhardt, p. 16, pl. 20, figs. 14, 15, pl. 21, fig. 1 [= *Steueria alternans* (Gerth)]
non 1922 *Reineckeia Koellikeri* (Oppel) – Steuer, p. 57 pl. 8, figs. 5, 6 (= Steuer, 1897, pl. 32(8), figs. 5, 6)
1928 *Ammonites Köellikeri* (Oppel) – Krantz, pl. 28, pl. 3, fig. 1a,b
non 1931 *Berriasella Köellikeri* (Oppel) – Windhausen, pl. 29, figs. 4a,b, 7
1931 *Micracanthoceras* aff. *microcanthum* (Oppel) – Yin, p. 33, pl. 2, fig. 1,1a (= Roman, 1897, pl. 1, fig. 10a,b)
1936 *Himalayites* (*Corongoceras*) *lamberti* – Roman, p. 21, pl. 3, fig. 5,5a
non 1936 *Himalayites* (*Corongoceras*) *Kollikeri* (Oppel) – Roman, p. 27, pl. 4, figs. 19,19a, 20 (= ?*Protacanthodiscus* sp. juv.)
1939 *Himalayites (Micracanthoceras) microcanthum* (Oppel *in* Zittel) – Mazenot, p. 233, pl. 37, fig. 12a,b (= Zittel, 1868, pl. 17, fig. 1a, 2)
non 1960 *Corongoceras Lamberti* Roman – Collignon, pl. 167, fig. 756 [= ?*Micracanthoceras brightoni* (Spath)]
non 1960 *Micracanthoceras cf. symbolus* (Oppel) – Collignon, pl. 175, fig. 753 [= ?*Micracanthoceras brightoni* (Spath)]
1966 *Micracanthoceras (Corongoceras*) *lamberti* Roman – Linares & Vera, pl. 6, fig. 4, pl. 7, figs. 2, 4
non 1976 *Himalayites* cf. *kollikeri* (Oppel) – Khimchiashvili, p. 118, pl. 11, fig. 3 (= Neocomitidae gen. et sp. indet.)
1985 *Djurjuriceras mutari* – Tavera, p. 150, pl. 19, fig. 2, pl. 20, fig. 1, text-fig. 11B
1985 *Djurjuriceras mediterraneum* – Tavera, p. 152, pl. 19, fig. 1, text-fig. 11A
1985 *Djurjuriceras sinuosum* – Tavera, p. 154, pl. 20, fig. 2, text-fig. 11C
1985 *Micracanthoceras* (*Corongoceras*) *symbolum* (Oppel) – Tavera, p. 189, pl. 24, fig. 1a,b, text-fig. 14A
1985 *Micracanthoceras (Corongoceras*) *ornatum* –Tavera, p. 191, pl. 25, fig. 8, text-fig. 14E
non 1985 "*Corongoceras*" *köllikeri* (Oppel) – Tavera, p. 194, pl. 28, fig. 2a,b, text-fig. 17G [= *Protacanthodiscus hexagonum* (Tavera)]
non 1986 *Corongoceras symbolum* (Oppel) – De Wever et al., p. 166, pl. 3, fig. 4 (= Himalayitidae gen. et sp. indet.)
1990 *Micracanthoceras microcanthum* (Oppel) – Főzy, p. 329, pl. 3, fig. 4
1990 *Corongoceras symbolum* (Oppel) – Főzy, p. 328, pl. 5, fig. 2
non 1997 "*Corongoceras*" *kollikeri* (Oppel) – Benzaggagh & Atrops, p. 158, pl. 7, fig. 3 [= *Dalmasiceras spiticeroides* (Djanélidzé)]

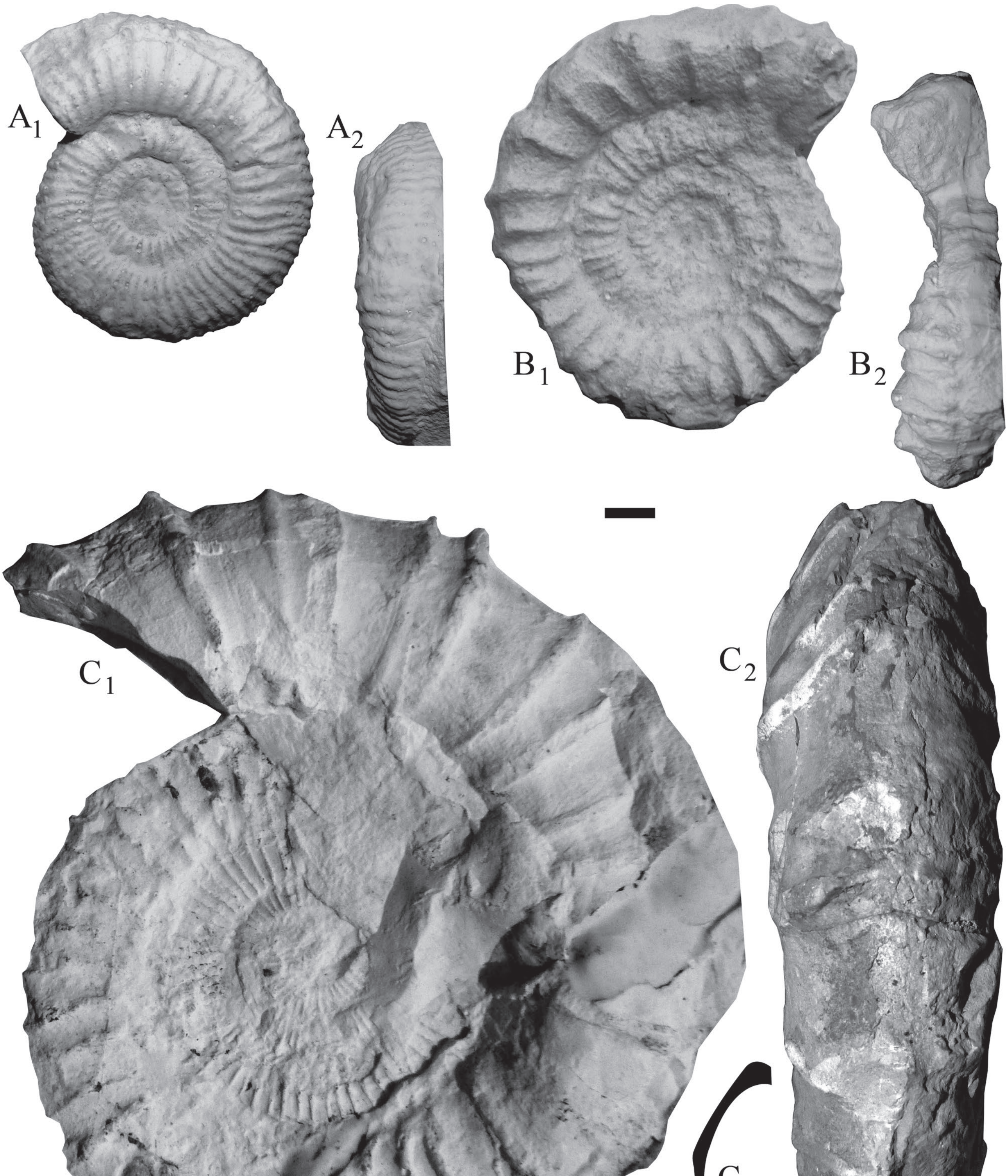

Fig. 2. *Micracanthoceras microcanthum* (Oppel in Zittel, 1868): **A1–2** — plaster cast FSL.136039 of the lectotype of *Ammonites microcanthus* Oppel in Zittel, 1868 [m]; **B1–2** — plaster cast FSL.13049 of *Ammonites symbolus* Oppel in Zittel, 1868 [M]; **C1–3** — MPP–CHR.37/3 [M] bed 37. Scale bar is 10 mm.

Fig. 3. *Micracanthoceras microcanthum* (Oppel in Zittel, 1868): **A1–4** — plaster cast FSL. FSL. 13086 of the paratype of *Ammonites microcanthus* Oppel in Zittel, 1868 [M]; **B1–2** — re-illustration of the holotype of Ammonites koellikeri Oppel in Zittel, 1868 (BSPG–AS/III/468) from Parent et al. (2011, fig. 32) [M]. Scale bar is 10 mm.

1997 *Micracanthoceras* (*Corongoceras*) *rhodanicum* (Mazenot) – Benzaggagh & Atrops, p. pl. 6, fig. 2
2000 *Micracanthoceras* (*Corongoceras*) *rhodanicum* (Mazenot) – Benzaggagh, pl. 4, fig. 3 (= Benzaggagh & Atrops 1997, pl. 6, fig. 2)
non 2010 *Corongoceras* cf. *symbolum* (Oppel) – Benzaggagh et al., figs. 5j,k, l,m [= [m] *Protacanthodiscus andreaei* (Kilian)]
2013 ?*Djurjuriceras* sp. – Bujtor et al., Fig. 4F
non 2013 *Micracanthoceras* (*Corongoceras*) *koellikeri* (Oppel) – Szives & Főzy, p. 300, pl. 4, fig. 1 [= [m] *Protacanthodiscus andreaei* (Kilian)], pl. 6, fig. 7 (= *Protacanthodiscus* juv.), pl. 8, figs. 3 [= [m] *Protacanthodiscus andreaei* (Kilian)], 4a,b (= Perisphinctoidea indet. juv.), 9 (= Perisphinctoidea indet.)
2016 *Micracanthoceras* (*Corongoceras*) sp. – Bahrouni et al., figs. 5.7, 5.12

Microconchs [m]

1865 *Ammonites microcanthus* – Oppel, p. 155
1868 *Ammonites microcanthus* – Oppel *in* Zittel, p. 93, pl. 17, figs. 3a,b, 4, 5a,c
1868 *Ammonites fraudator* – Zittel, p. 110, pl. 21, figs. 1a,b, 2a,b, 3
1890 *Hoplites microcanthus* (Oppel) – Toucas, p. 608, pl. 18, fig. 12
non 1897 *Reineckeia microcantha* (Oppel) – Steuer, p. 156(30), pl. 31(7), fig. 3,5 [= ?*Corongoceras steinmanni* (Krantz)]
non 1900 *Reineckeia microcantha* (Oppel) – Burckhardt, p. 16, pl. 20, fig. 16,17 (Perisphinctoidea indet.)
non 1903 *Hoplites microcanthus* Péron sp. non Oppel– Burckhardt, p. 58, pl. 10, fig. 12,16 [= ?*Corongoceras mendozanum* (Behrendsen)]
non 1921 *Hoplites* aff. *microcanthus* (Oppel) – Burckhardt, pl. 18, fig. 5,9 (= Perisphinctoidea gen et sp. nov.)
non 1922 *Reineckeia microcantha* (Oppel) – Steuer, p. 56, pl. 7, fig. 3,5 (= Steuer, 1897, pl. 31(7), fig. 3-5)
non 1931 *Micracanthoceras* aff. *microcanthum* (Oppel) – Spath, p. 543, pl. 92, fig. 3a,b [= *Micracanthoceras brightoni* (Spath)]
non 1931 *Micracanthoceras* sp. nov. aff. *fraudator* (Zittel) – Spath, p. 545, pl. 109, fig. 15 [= *Micracanthoceras brightoni* (Spath)]
1934 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) – Dacqué, pl. 46, fig. 6, 6a (= Zittel, 1868, pl. 17, fig. 3a,b)
1936 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) – Roman, p. 22, pl. 4, fig. 6,6a
1936 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) var. *marocana* nov. var. – Roman, p. 24, pl. 4, fig. 8,8a
non 1936 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) var. *marocana* nov. var. – Roman, p. 24, pl. 4, fig. 9,9a (= *Burckhardticeras* sp.)
1938 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) – Roman, p. 321, pl. 31, fig. 302,302a (= Zittel, 1868, pl. 17, fig. 3a,b), text-fig. 302 (= Zittel, 1868, pl. 17, fig. 1b)
non 1939 *Micracanthoceras* n. sp. aff. *koellikeri* (Oppel) – Imlay, p. 44, pl. 17, figs. 2, 3, 4 [= *Parrasiella astillerense* (Imlay) nom. correct.]
1939 *Himalayites (Micracanthoceras) microcanthum* (Oppel *in* Zittel) – Mazenot, p. 233, pl. 37, fig. 2 a,b (= Toucas, 1890, pl. 18, fig. 12), 3
non 1956 *Himalayites* (*Micracanthoceras*) cf. *microcanthus*? (Oppel) – Ksiazkiewicz, p. 214, pl. 25, fig. 3 (= Perisphinctoidea indet.)
1957 *Micracanthoceras microcanthus* (Oppel) – Arkell *et al.* , p. L356, fig. 468.1a,b (= Zittel, 1868, pl. 17, fig. 3a,b)
non 1960 *Micracanthoceras microcanthus* (Oppel) – Collignon, pl. 65, figs. 754, 755 [= *Micracanthoceras* aff. *brightoni* (Spath)]
1966 *Himalayites (Micracanthoceras) microcanthus* (Oppel) – Linares & Vera, pl. 5, fig. 2a,b, pl. 6, fig. 5, pl. 7, fig. 3
1977 *Himalayites (Micracanthoceras) microcanthus* (Oppel) – Sapunov, pl. 5, fig. 3
1977 *Himalayites (Micracanthoceras) fraudator* (Oppel) – Sapunov, pl. 5, fig. 5
1977 *Aulacosphinctes linoptychus* (Uhlig) – Sapunov, pl. 6, fig. 1
1979 *Himalayites (Micracanthoceras) microcanthus* (Oppel) – Sapunov, p. 193, pl. 58, fig. 4 (= Sapunov, 1977, pl. 5, fig. 3)
1979 *Himalayites (Micracanthoceras) fraudator* (Zittel) – Sapunov, p. 194, pl. 58, fig. 5
1979 *Aulacosphinctes linoptychus* (Uhlig) – Sapunov, p. 195, pl. 59, fig. 1 (= Sapunov, 1977, pl. 6, fig. 1)
1979 *Aulacosphinctes venustus* Collignon – Sapunov, p. 195, pl. 59, fig. 2a,b
1982 *Himalayites (Micracanthoceras) microcanthus* (Oppel) – Nikolov, p. 213, pl. 77, fig. 1 (= Sapunov, 1977, pl. 5, fig. 3)
1982 *Himalayites (Micracanthoceras) fraudator* (Zittel) – Nikolov, p. 213, pl. 77, fig. 2 (= Zittel, 1868, pl. 21, fig. 2a)
1982 *Berriasella* (*Picteticeras*) *subeudichotoma* – Nikolov, p. 64, pl. 13, fig. 8
1982 *Aulacosphinctes linoptychus* (Uhlig) – Nikolov, p. 218, pl. 78, fig. 5
non 1982 *Aulacosphinctes linoptychus* (Uhlig) – Nikolov, p. 218, pl. 78, fig. 4a, b, c [= *Aulacosphinctes linoptychus* (Uhlig)]
1985 *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel) – Haas et al., pl. 20, fig. 7
1984 *Micracanthoceras (Micracanthoceras) microcanthus* (Oppel) *densecostatus* nov. ssp. – Vigh, p. 76, pl. 3, fig. 3a,b
1985 *Micracanthoceras (Micracanthoceras) microcanthum* (Oppel) – Tavera, p. 169, pl. 21, figs. 1a,b, 2, 3, 4, text-figs. 13A, E, G
1985 *Micracanthoceras (Micracanthoceras)* cf. *brightoni* (Spath) – Tavera, p. 175, pl. 21, fig. 5, text-fig. 13F
1985 *Micracanthoceras (Corongoceras) rhodanicum* Mazenot – Tavera, p. 180, pl. 22, figs. 7, 8a,b, 9a,b, text-fig. 14D
1985 *Micracanthoceras (Corongoceras) flexuosum* – Tavera, p. 187, pl. 23, figs. 5a,b, 6, 7, text-fig. 14C
1985 *Micracanthoceras (Corongoceras) radians* – Tavera, p. 178, pl. 23, figs. 1, 2, 3a,b, 4a,b, text-fig. 14I
1985 *Micracanthoceras (Corongoceras) lotenoense* (Spath) – Tavera, p. 176, pl. 23, figs. 11, 12, 13a,b, text-figs. 14J, K
1985 *Micracanthoceras (Corongoceras) minor* – Tavera, p. 182, pl. 23, figs. 8a,b, 9, 10, text-fig. 14H
1985 *Micracanthoceras (Corongoceras) mendozanum* (Behrendsen) – Tavera, p. 186, pl. 25, fig. 3a,b, text-fig. 14G
1985 *Micracanthoceras (Corongoceras) leanzai* – Tavera, p. 192, pl. 25, figs. 4, 5, text-fig. 14F
1985 Himalayitidae gen. y sp. indeterminados – Tavera, p. 233, pl. 28, figs. 5, 6, text-fig. 17F
1985 *Aulacosphinctes parvulus* (Uhlig) – Tavera, p. 144, pl. 17, fig. 4, text-fig. 10G
1985 *Aulacosphinctes macer* (Collignon) – Tavera, p. 146, pl. 17, fig. 3
1985 *Aulacosphinctes sulcatus* – Tavera, p. 146, pl. 17, figs. 1a,b, 2a,b, text-figs. 10E, H
1985 *Aulacosphinctes venustus* Collignon – Tavera, p. 147, pl. 17, fig. 5, text-fig. 10F
1985 *Micracanthoceras* (*Corongoceras*) *symbolum* (Oppel) – Tavera, p. 189, pl. 24, figs. 2, 3, pl. 25, figs. 1a,b, 2, 3, text-fig. 14B
1985 *Corongoceras symbolum* (Oppel) – Cecca, p. 143, pl. 1, fig. 3
1989 *Micracanthoceras microcanthum* (Oppel) – Cecca et al., p. 65, pl. 1, figs. 3, 4a,b
1989 *Micracanthoceras* aff. *microcanthum* (Oppel) – Kaiser-Weidich & Schaier, p. 363, pl. 4, fig. 3a,b
1995 *Micracanthoceras microcanthum* (Oppel) – Főzy, p. 138, pl. 21, fig. 7
1995 *Micracanthoceras microcanthum* (Oppel) – Eliáš & Vašíček, pl. 1, fig. 4

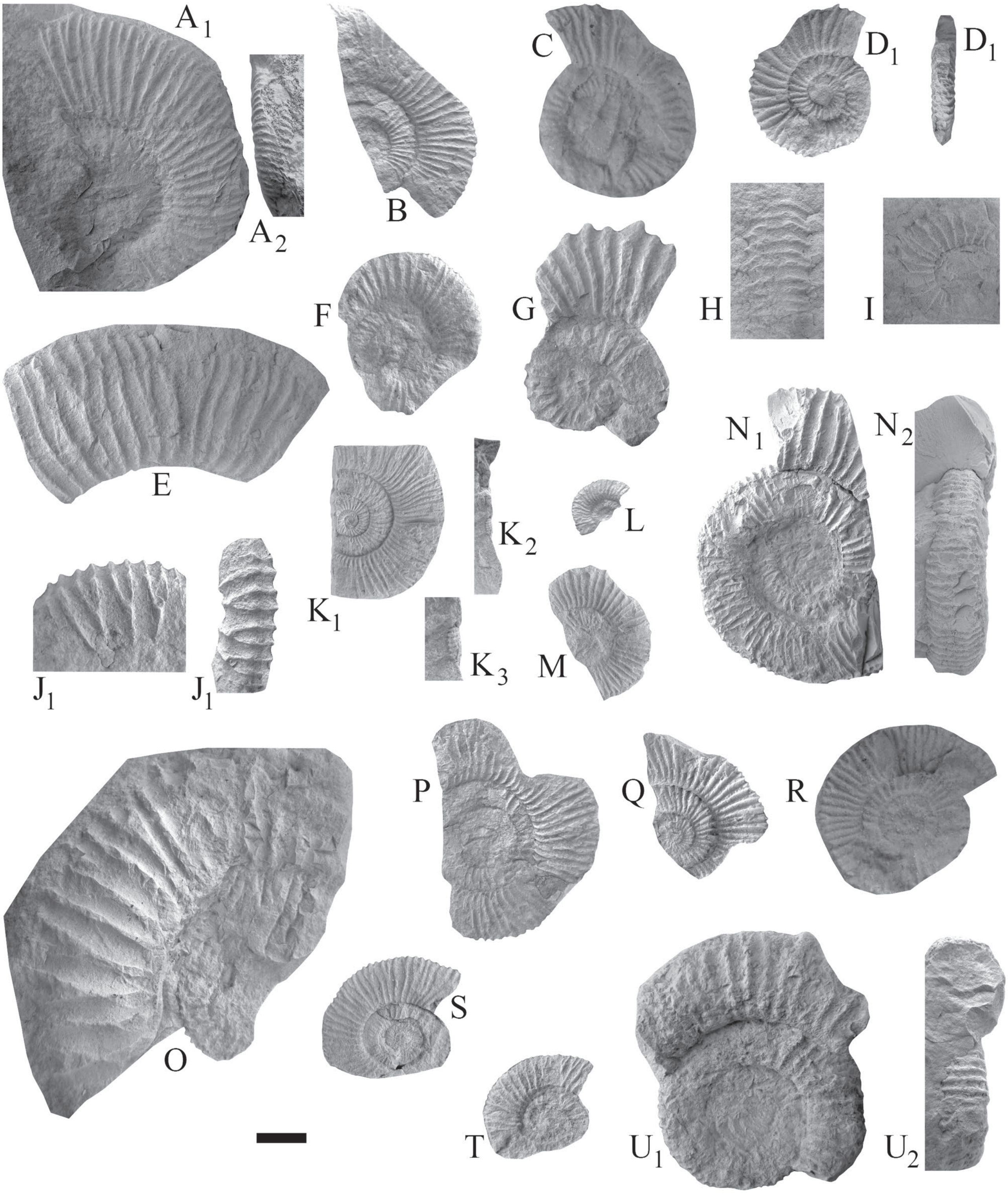

Fig. 4. *Micracanthoceras microcanthum* (Oppel in Zittel, 1868): **A1–2** — MPP–CHR.54/1a [?m] bed 25 (top); **B** — MPP–CHR.34/2 [m] bed 25 (top); **C1–2** — plaster cast of MPP–CHR.29/1 [m] bed 29; **D1–2** — MPP–CHR.50/3 [m] bed 25 (base); **E** — MPP–CHR.34/1 [?M] bed 25 (top); **F** — MPP–CHR.60/6 [m] bed 28 (base); **G** — MPP–CHR.54/1b [m] bed 25 (top); **H** — MPP–CHR.50/1 [m] bed 25 (base); **I** — MPP–CHR.53/2 [m] bed 31; **J1–2** — MPP–CHR.60/7 [m] bed 25 (base); **K1–3** — MPP–CHR.67/4 [m] bed 35 (base); **L** — MPP–CHR.51/2 [m] bed 29 (top); **M** — MPP–CHR.67/9 [m] bed 35; **N1–2** — MPP–CHR.82/1 [m] bed 53; **O** — MPP–CHR.45/1 [M] bed 45; **P** — MPP–CHR.92/11 [m] bed 64; **Q** — MPP–CHR.92/28 [m] bed 64; **R** — plaster cast of MPP–CHR.87/1 [m] bed 66; **S** — MPP–CHR.92/13 [m] bed 64; **T** — MPP–CHR.92/10 [m] bed 64; **U1–2** — MPP–CHR.98/1 [m] bed 76. Scale bar is 10 mm.

1997 *Micracanthoceras microcanthum* (Oppel) – Benzaggagh & Atrops, pl. 5, fig. 4
1997 *Micracanthoceras microcanthum* (Oppel) – Geyssant *in* Cariou & Hantzpergue, pl. 26, fig. 1 (= Zittel, 1868, pl. 17, fig. 3a,b)
non 1998 *Micracanthoceras fraudator* (Zittel) – Howarth, p. 79, pl. 15, fig. 2a,b (= Perisphinctoidea indet.)
non 1999 *Micracanthoceras fraudator* (Zittel) – Fatmi & Zeiss, p. 97, pl. 45, fig. 3a,b, pl. 55, fig. 5a,b [= *Micracanthoceras brightoni* (Spath)]
2000 *Micracanthoceras microcanthum* (Oppel) – Benzaggagh, pl. 4, fig. 4 (= Benzaggagh & Atrops, 1997, pl. 5, fig. 4)
non 2009 *Micracanthoceras* cf. *microcanthum* (Oppel) – Shome & Bardhan, p. 199, pl. 4, figs. a,g [= *Micracanthoceras brightoni* (Spath)]
2004 *Micracanthoceras microcanthum* (Oppel) – Marino et al., pl. 2, fig. 7
2005 *Micracanthoceras* sp. gr. *microcanthum* (Oppel) – Boughdiri et al., pl. 2, fig. 9, 10
2005 *Aulacosphinctes* sp. gr. *sulcatus* Tavera – Boughdiri et al., pl. 2, fig. 7
non 2012 *Micracanthoceras microcanthum* (Oppel) – Salazar, p. 90, figs. 4.13a,m (= *Steueria* sp.)
2010 *Aulacosphinctes* sp. – Benzaggagh et al., fig. 5d,e
non 2015 *Micracanthoceras microcanthum* (Oppel) – Salazar & Stinnesbeck, p. 19, figs. 15a,m (= Salazar, 2012, figs. 13a,m)

Types: The lectotype is the specimen drawn by Zittel (1868, pl. 17, fig. 3a,b). A plaster cast of the lectotype (FSL.136039) and the large (FSL. 13086) Zittel's paratype (see Zittel, pl. 17, fig. 1a,2) are herein illustrated in Fig. 2A and Fig. 3A. For comparison, we re-illustrate the lectotype BSPM-AS/III/468 of *Ammonites köllikeri* Zittel, 1868 in Fig. 3B, that was designated and illustrated by Parent et al. (2011, fig. 32A1). A plaster cast (FSL.13049) of the lectotype of *Ammonites symbolus* illustrated by Zittel (1868, pl. 16, fig. 6a,c) is herein illustrated for the first time on Fig. 2B.

Emended diagnosis: Small to large, widely umbilicate, dimorphic Himalayitidae. Small, lappeted microconchs with two ornamental stages composed of (*i*) a perisphinctid stage in juvenile whorls with rigid, straight to prorsiradiate, bifurcate ribs — subrounded whorl section with convex flanks — ribs cross the venter but a ventral groove progressively appears and form a shallow or deep sulcus — (*ii*) a *microcanthum* stage in intermediate and adult whorls characterized by regular and/or irregular, rigid or dense, alternation of variable number of single, bifurcate and sporadically trifurcate, ribs — greater or lesser thickenings, punctiform tubercles at the furcation point — narrow venter with a ventral groove or deep sulcus bordered by more or less thickenings on latero-ventral ends of ribs — subrectangular to laterally compressed subhexagonal whorl section. Macroconchs are large and develop (*iii*) an adult ornamental stage. Two extreme morphotypes are recognized (*i*) *koellikeri* morphotype characterized by compressed, subrectangular, higher than wide, whorl section — flat venter covered by a more or less attenuated ventral band — *microcanthum* stage with enlarged ribs on the umbilical shoulder combined with more or less numerous trifurcate primary ribs — (*ii*) *symbolum* morphotype characterized by a depressed subhexagonal whorl section — rigid *microcanthum* stage with strong lateral tubercles and thickenings on the ventral shoulder delimiting a narrow sulcus. Himalayitid suture line marked by large trifid lateral lobe.

Material: Forty-one specimens MPP-CHR.29/1, MPP-CHR.34/1, MPP-CHR.34/2, MPP-CHR.37/1, MPP-CHR.37/2, MPP-CHR.37/3, MPP-CHR.45/1, MPP-CHR.50/1, MPP-CHR.50/2, MPP-CHR.50/3, MPP-CHR.51/1, MPP-CHR.51/2, MPP-CHR.53/2, MPP-CHR.53/4a and b, MPP-CHR.54/1a and b, MPP-CHR.60/3, MPP-CHR.60/4, MPP-CHR.60/6, MPP-CHR.60/7, MPP-CHR.60/1, MPP-CHR.60/2, MPP-CHR.62/1, MPP-CHR.63/1, MPP-CHR.67/4, MPP-CHR.67/7, MPP-CHR.67/9, MPP-CHR.68/1, MPP-CHR.68/2, MPP-CHR.82/1, MPP-CHR.92/2, MPP-CHR.92/4, MPP-CHR.92/5, MPP-CHR.92/10, MPP-CHR.92/11, MPP-CHR.92/13, MPP-CHR.92/28, MPP-CHR.87/1, MPP-CHR.98/1, MPP-CHR.R100/6.

Measurements (mm): See Table 2 in Supplementary data.

Description: Specimens MPP-CHR.67/4 (Fig. 4K), MPP-CHR.82/1 (Fig. 4N), MPP-CHR.87/1 (Fig. 4R), MPP-CHR.92/11, MPP-CHR.92/28 (Fig. 4Q), MPP-CHR.98/1 (Fig. 4U) and MPP-CHR.R100/6 perfectly match the morphological and ornamental features of the lectotype of *M. microcanthum*.

MPP-CHR.29/1 (Fig. 4C) and MPP-CHR.50/3 (Fig. 4D) differ from the lectotype by their smaller size and less evolute coiling. These specimens show a long perisphinctid stage that extends over the phragmocone with a ventral groove or sulcus. The *microcanthum* stage is attenuated and limited to the end of the body chamber.

Specimens MPP-CHR.34/1 and MPP-CHR.45/1 are fragments of medium size body chambers characterized by a rigid *microcanthum* stage.

Specimen MPP-CHR.37/3 is a large size, subcomplete specimen characterized by a suboval whorl section. The ornamentation of the inner whorls matches the morphological and ornamental features of the lectotype. The ornamentation of the body chamber is composed of spaced, sharp, single, sometimes bifurcate ribs with smooth interspaces. Lateral tubercles occur at the furcation point.

Bivariate diagrams of the dimensional growth parameters of the shell (U, Wh in function of D) of the well-preserved specimens show homogeneous scatters around the mean curve with R^2 still high >0.9 in every case (see Figs. S1–S4 in Supplementary data). The growth of those parameters is isometric and harmonic, and corresponds to the relationship $Y=bD$. Preservation of our specimens as crushed internal moulds prevent us from studying Wb/D and Wb/Wh ratios.

Dimorphism (Fig. 5)**:** Bulot et al. (2014) outlined that the understanding of *M. microcanthum* was limited to the morphology of the lectotype and its accepted variability illustrated by Spanish material. In this regard, *M. fraudator* (Zittel) as well as *Berriasella* (*Picteticeras*) *subeudichotoma* Nikolov perfectly match the lectotype of *M. microcanthum*. Bulot et al. (2014) also assumed that the great majority of specimens referred to *Corongoceras* from the Betic Cordillera by Tavera (1985) belongs to *Micracanthoceras*. The biometric analysis investigated on Tavera's measurements strengthen the contention that the many typological *Corongoceras* species from the Betic Cordillera fit into a homogeneous sample similar to that of *M. microcanthum* (see Supplementary data). Bivariate diagrams of the dimensional growth parameters of the shell (D, U, Wh and Wb in function of D) show homogeneous scatters around the mean curve and the growth of those parameters is isometric and harmonic. We therefore consider that *M. microcanthum* is the senior subjective synonym of *M. (C.) flexuosum* Tavera, *M. (C.) radians* Tavera, *M. (C.) minor* Tavera and *M. (C.) leanzai* Tavera. Since several specimens illustrated by Tavera (1985), such as the one on pl. 22, fig. 2,

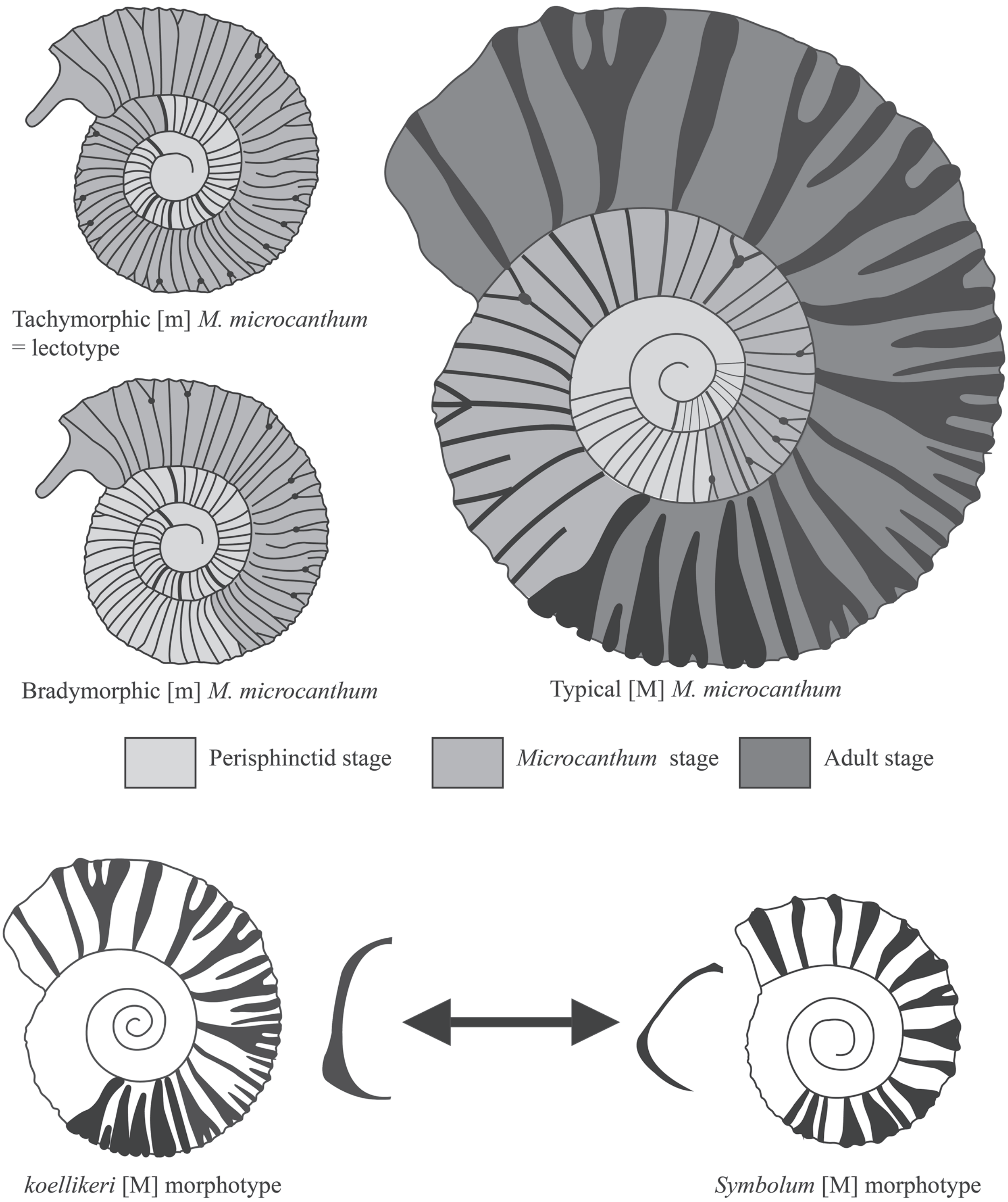

Fig. 5. Supposed dimorphism and intraspecific variations observed in *Micracanthoceras microcanthum* (Oppel, 1865). Note that microconchs show different rates of shell morphogenesis (tachymorphic versus bradymorphic variants), while macroconchs range between two extreme (robust versus slender) morphologies related to the Buckman's first law of covariation.

bear short lateral lappets, it seems obvious that the morphology of the lectotype of *M. microcanthum* corresponds to a microconch form.

From a re-examination of the literature and the material collected at Charens (see for example MPP-CHR.37/3 on Fig. 2C), we consider that the macroconchs of *M. microcanthum* match the morphology of Zittel's paratype of *M. microcanthum* and the lectotype of *M. koellikeri*. Both forms show similar inner whorls to that of microconchs of *M. microcanthum*, but differ by their large size and the addition of an adult ornamental stage. We support the supposition that both morphotypes range between two extreme morphologies, namely robust and slender poles, related to the Buckman's first law of covariation between shell shape and ornamentation. The macroconch *koellikeri* morphotype is characterized by large size, moderately evolute coiling, compressed, subrectangular, higher than wide, whorl section — with a flat venter covered by a more or less attenuated ventral band — and develops a robust *microcanthum* stage in the adult. The other macroconch morphotype corresponds to the typological species *Micracanthoceras symbolum* and *M. lamberti*. This morphotype is characterized by a smaller size than the other one, evolute coiling, robust ornamentation, depressed subhexagonal whorl section and spaced, rigid *microcanthum* stage in the adult. As herein understood, the species *Djurjuriceras mutari* Tavera, *Djurjuriceras mediterraneum* Tavera and *Djurjuriceras sinuosum* Tavera link the two macroconch poles of *M. microcanthum* by their elevated, sub-hexagonal adult whorl section with simplified *microcanthum* stage (see for example specimen MPP-CHR.37/3 on Fig. 2C).

The co-occurrence of the two micro- and macroconch morphologies on the northern (Czech Republic, Hungary, Austria, south-east France) and southern (Morocco, Algeria, Sicily) margins of the Mediterranean-Caucasian Subrealm support the dimorphism observed in *M. microcanthum*.

Remarks: A close examination of the literature convinced us that great confusions exist between *M. microcanthum* and the many Mediterranean-Caucasian forms referred to *Aulacosphinctes* Uhlig, 1910 by Sapunov (1979), Nikolov (1982), Tavera (1985), Boughdiri et al. (2005) and Benzaggagh et al. (2010). In these works, the specimens referred to *Aulacosphinctes* either belong to:

• juveniles of *M. microcanthum* (compare Tavera 1985, pl. 17, fig. 3, 4a,b and Benzaggagh et al. 2010, fig. 5d,e with MPP-CHR.50/3 on Fig. 4D) or;

• gracile microconchs of *M. microcanthum* (compare Nikolov 1982, pl. 78, fig. 5 and Sapunov 1979, pl. 59, fig. 1, 2a,b with MPP-CHT.92/13 and MPP-CHR.92/10 on Fig. 4S and 4T).

The type specimens of *Aulacosphinctes sulcatus* from the Betic Cordillera differs from the lectotype of *M. microcanthum* by its long perisphinctid stage with deep ventral sulcus, and a limited *Microcanthum* stage at the end of the adult whorl. The general features of *A. sulcatus* therefore coincide with a delayed shift of the ontogenetic sequence of *M. microcanthum*. This form co-occurs with the typical *M. microcanthum* at the base of the Microcanthum Zone in southern Spain as well as at Charens where similar specimens were collected (see for example MPP-CHT.29/1 on Fig. 4C). We therefore assume that *A. sulcatus* is a bradymorphic variant of *M. microcanthum* in the sense of Beznosov & Mitta (1995) (see also fig. 5). In this regard, the morphological and ornamental features of the Spanish *Aulacosphinctes* specimens described by Tavera (1985) fall well into the range of variation of the Spanish *M. microcanthum* (see Supplementary data).

Olóriz (1978) previously introduced new *Aulacosphinctes* species from the Betic Cordillera that are *A. trifidus*, *A. quadri* and *A. berriaselliformis*. As pointed out by that author, these species co-occur in the uppermost Lower Tithonian, and closely resemble *Burckhardticeras peroni* (Roman, 1936), but they could be distinguished by the presence of a ventral groove at the sub-adult and adult stages. Olóriz (1978) pointed out that *B. peroni* is a microconch form that develops a thin ventral groove at the end of the adult whorl. Olóriz noticed that the species shows a wide range of intraspecific variation, but that it had, unfortunately, never been evaluated. One may wonder if the presence of a ventral groove might not result from extreme intraspecific variation of *B. peroni* or reflect a phyletic link with *M. microcanthum*. In any case, it is clear that the genus *Aulacosphinctes* should be limited to its type species *Ammonites mörikeanus* Oppel, 1863 and those closely allied Indian and Malagasy taxa described by Oppel (1863), Uhlig (1910), Besairie (1936), Collignon (1960) and Fatmi (1973).

Occurrence: *M. microcanthum* occurs between beds 25 and 76, *M. microcanthum* Zone, Upper Tithonian. The species has been reported from the Czech Republic, Austria, Hungary, Germany, Bulgaria, Italy (Umbria, Sicily), South East France, southern Spain, Morocco, Tunisia and Algeria.

Genus *Protacanthodiscus* Spath, 1923

Type species: *Hoplites andreaei* Kilian, 1889, by original designation.

Remarks: A detailed revision of the ontogeny, variability, dimorphism and age of the type species *Protacanthodiscus andreaei* was recently given by the authors of the present paper and the reader is referred to it (see Frau et al. 2015).

Protacanthodiscus andreaei (Kilian, 1889)
Fig. 6A,C

Macroconchs [M]

1889 *Hoplites Andreaei* – Kilian, p. 670, pl. 32, fig. la,b
1907 *Hoplites* (*Acanthodiscus*) *Andreaei* var. *punica* – Pervinquière, p. 38, pl. 2, fig. l2a,b
1939 *Berriasella Andreaei* (Kilian) – Mazenot, p. 96, pl. 12, fig. la,b (= Kilian, 1889, pl. 32, fig. la,b)
non 1939 *Berriasella Andreaei* (Kilian) – Mazenot, p. 96, pl. 13, fig. 4a,b [=*Jabronella* (*Erdenella*) *isare* (Pomel) nom. correct.]
non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* (Kilian) – Collignon, pl. 165, fig. 665 (=Himalayitidae gen. et sp. indet. juv.)

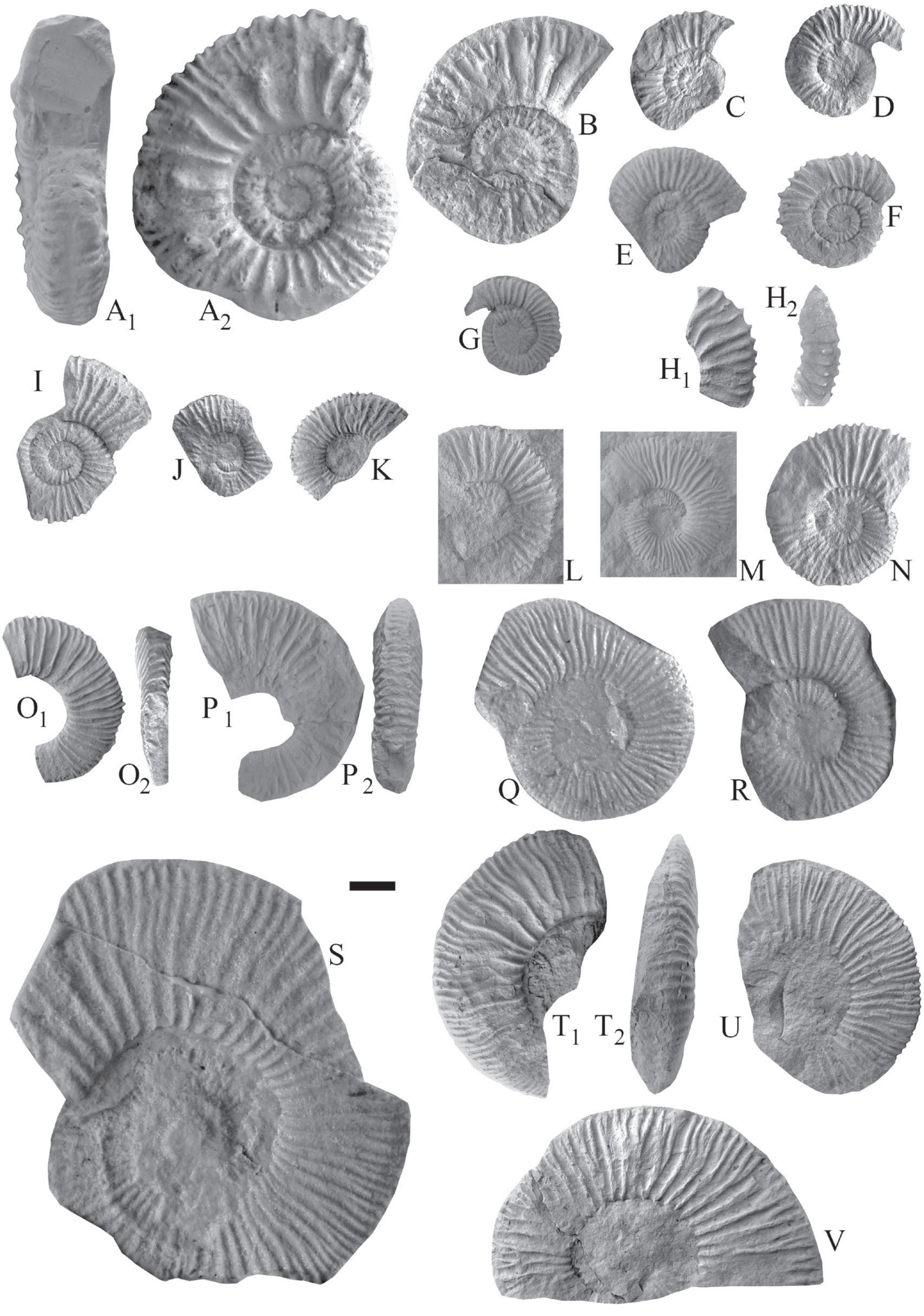

Fig. 6. *Protacanthodiscus andreaei* (Kilian, 1889): **A1–2** — Plaster cast of the holotype (FSL.13056); **B** — MPP–CHR.79/4 [M] bed 89; **C** — MPP–CHR.21/25 [m] bed 92. *Boughdiriella chouetense* Frau, Bulot & Wimbledon, 2015 nom. correct.: **D** — MPP–CHR.21/24 [m] bed 92; **E** — plaster cast of MPP–CHR.21/33 [?M] bed 92; **F** — MPP–CHR.19/1 [m] bed 90; **G** — MPP–CHR.21/35 [m] bed 92. *Pratumidiscus elsae* Bulot, Frau & Wimbledon, 2014: **H1–2** — MPP–CHR.21/43 [?m] bed 92. Busnardoiceras busnardoi (Le Hégarat, 1973): **I** — MPP–CHR.19/1 [m] bed 90; **J** — MPP–CHR.21/2 [m] bed 92; **K** — MPP–CHR.21/16 [m] bed 92; **L** — MPP–CHR.21/14 [m]; **M** — MPP–CHR.19/3 [m] bed 90; **N** — MPP–CHR.21/15 [m] bed 92; **O1–2** — MPP–CHR.21/42 [m] bed 92; **P1–2** — MPP–CHR.19/4 [M] bed 90; **Q** — plaster cast of MPP–CHR.21/38 [M] bed 92; **R** — plaster cast of MPP–CHR.21/12 [M] bed 92; **S** — MPP–CHR.21/36 [M] bed 92; **T1–2** — MPP–CHR.21/26 [M] bed 92; **U** — MPP–CHR.21/18 [M] bed 92; **V** — MPP–CHR.21/7 [M] bed 92. Scale bar is 10 mm.

non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* var. *variabilis* – Collignon, pl. 165, figs. 666, 667 (=Himalayitidae gen. et sp. indet. juv.)
? 1960 *Protacanthodiscus andreaei* (Kilian) – Christ, p. 125, pl. 9, fig. 5
1979 *Protacanthodiscus andreaei* (Kilian) – Sapunov, pl. 57, fig. 6
1982 *Protacanthodiscus andreaei* (Kilian) – Nikolov, p. 211, pl. 73, fig. 2a,b (= Kilian, 1889, pl. 32, fig. 1a,b), pl. 74, fig. 2 (= Sapunov, 1973, pl. 57, fig. 6)
1985 *Neoperisphinctes falloti* (Kilian) – Tavera, p. 132, pl. 16, fig. 10a,b
1985 *Durangites gigantis* – Tavera, p. 162, pl. 18, figs. 8, 9, text-fig. 12A, B
1985 *Protacanthodiscus andreaei* (Kilian) – Tavera, p. 198, pl. 26, figs. 5a,b, 6, text-fig. 15H
1985 *Protacanthodiscus* sp. 1 gr. *andreaei* (Kilian) – Tavera, p. 199, pl. 26, figs. 1a,b, 2, text-figs. 12H, 15E, I
1985 *Protacanthodiscus berriasensis* – Tavera, p. 206, pl. 28, fig. 1a,b, text-fig. 15D
1985 *Protacanthodiscus coronatus* – Tavera, p. 200, pl. 27, fig. 1a,b, text-fig. 15A
1985 *Protacanthodiscus darwini* – Tavera, p. 203, pl. 26, figs. 3, 4, text-fig. 15B
1985 *Protacanthodiscus nodusus* – Tavera, p. 202, pl. 27, fig. 2, text-fig. 15C
1994 *Protacanthodiscus* (*Protacanthodiscus*) *andreaei* (Kilian) – Boughdiri, p. 147, pl. 3, figs. 1a,c (= Kilian, 1889, pl. 32, fig. la,b), 3a,b, pl. 4, fig. 2
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. A – Boughdiri, p. 208, pl. 3, fig. 5
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 7 – Boughdiri, p. 176, pl. 3, fig. 2
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 11 – Boughdiri, p. 186, pl. 3, fig. 6
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 12 – Boughdiri, p. 188, pl. 4, fig. 1
1994 *Protacanthodiscus* (*Protacanthodiscus*) *coronatus* (Tavera) – Boughdiri, p. 151, pl. 4, figs. 6, 7
1998 *Durangites* (*Protacanthodiscus*) *andreaei* (Kilian) – Enay et al., figs. 2.16a,b (= Kilian, 1889, pl. 32, fig. la,b)
1998 *Durangites* (*Protacanthodiscus*) *apertus* (Tavera) – Enay et al., figs. 2.13, 14
2010 *Protacanthodiscus apertus* (Tavera) – Benzaggagh et al., fig. 5i
2010 *Durangites humboldti* Burckhardt – Benzaggagh et al., fig. 5n
non 2013 *Protacanthodiscus coronatus* (Tavera) – Szives & Főzy, p. 301, pl. 1, figs. 2, 4 (= Himalayitidae gen. nov. et sp. nov.)
non 2013 *Protacanthodiscus andreaei* (Kilian) – Szives & Főzy, p. 300, pl. 5, fig. 4a,b, pl. 6, fig. 5a,b, pl. 8, fig. 10a,b (=Himalayitidae gen. nov. et sp. nov.)
2015 *Protacanthodiscus andreaei* (Kilian, 1889) – Frau et al., p. 125, figs. 7A,C

Microconchs [m]

1983 *Durangites acanthicus* Burckhardt – Cecca et al., p. 128, pl. 5, fig. 1a,b
1985 *Durangites singularis* – Tavera, p. 168, pl. 17, figs. 6, 7, 8a,b, 9a,b, text-fig. 12E
1985 *Durangites sutneroides* – Tavera, p. 168, pl. 18, figs. 1, 2, 3, 5
non 1985 *Durangites sutneroides* – Tavera, p. 168, pl. 18, figs. 4 (= Spiticeratinae indet. juv.)
1985 *Durangites heilprini* (Aguilera) – Tavera, p. 164, pl. 18, figs. 6, 7, text-fig. 12G
1985 *Durangites acanthicus* Burckhardt – Tavera, p. 156, pl. 18, figs. 10a,b, 11, text-fig. 12C
1985 *Durangites vulgaris* Burckhardt – Tavera, p. 157, pl. 18, figs. 12, 13a,b, text-fig. 12I
1985 *Durangites apertus* –Tavera, p. 161, pl. 18, figs. 14, 15a,b, text-fig. 12F
1985 *Durangites* cf. *astillerensis* Imlay – Tavera, p. 166, pl. 18, fig. 16, text-fig. 12D
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 3 – Boughdiri, p. 168, pl. 3, fig. 7
1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 4 – Boughdiri, p. 170, pl. 2, fig. 17
1994 *Durangites* (*Durangites*) *humboldti* (Burckhardt) – Boughdiri, p. 99, pl. 1, figs. 33a,b, 34
1994 *Durangites* (*Durangites*) *juanense* (Cantú-Chapa) – Boughdiri, p. 106, pl. 1, fig. 35
1998 *Durangites* (*Durangites*) *juanensis* Cantú-Chapa – Enay et al., figs. 2-6, 7 (= Boughdiri, 1994, pl. 1, fig. 35)
1998 *Durangites* (*Durangites*) *humboldti* Burckhardt – Enay et al., figs. 2.8, 9, 10a,b
1998 *Durangites* (*Protacanthodiscus*) sp. – Enay et al., figs. 2.11
2010 *Protacanthodiscus* cf. *andreaei* (Kilian) – Ivanov et al., pl. 3, fig. 3
2010 *Durangites* aff. *fusicostatus* Burckhardt – Ivanov et al., pl. 3, fig. 1a,b
2010 *Durangites* cf. *vulgaris* Burckhardt – Ivanov et al., pl. 3, fig. 2a,b
2010 *Durangites singularis* Tavera – Ivanov et al., pl. 3, fig. 4
2010 *Corongoceras* cf. *symbolum* (Oppel) – Benzaggagh et al., Figs. 5j,m
2013 *Micracanthoceras* (*Corongoceras*) *koellikeri* (Oppel) – Szives & Főzy, p. 300, pl. 4, fig. 1, ? pl. 6, fig. 7, pl. 8, fig. 3
2015 *Protacanthodiscus andreaei* (Kilian, 1889) – Frau et al., p. 125, figs. 5A,L, 6A,E

Type: The holotype is specimen no. EM.1930 from the De Verneuil collection, originally drawned by Kilian (1889, pl. 32, fig. la,b). A plaster cast (FSL.13056) is herein illustrated in Fig. 6A.

Material: Eleven specimens MPP-CHR.79/4, MPP-CHR.19/1, MPP-CHR.19/5, MPP-CHR.21/2, MPP-CHR.21/3, MPP-CHR.21/6, MPP-CHR.21/19, MPP-CHR.21/29, MPP-CHR.21/32, MPP-CHR.21/33, MPP-CHR.21/39.

Measurements (mm): See Table 3 in Supplementary data.

Description: The material collected at Charens is identical to specimens described at Le Chouet (Frau et al. 2015). *P. andreaei* corresponds to medium to large size Himalayitidae with a moderately open and deep umbilicus. The whorl section is subcircular with convex flanks on juveniles that become progressively subrectangular to subhexagonal on the adults. Ornamentation is composed of bifurcate and trifurcate ribs with a tubercle at the furcation point. Some ribs can be looped on the ventral shoulder. On the body chamber, bifurcate ribs end on the ventral shoulder with a latero-ventral tubercle on the first, or occasionally the second, branch. The venter is marked by a flattened band or a shallow sulcus depending on the shape of the whorl section.

Remarks: The *koellikeri* macroconch morphotype of *M. microcanthum* share great affinities with macroconchs of *Protacanthodiscus andreaei* (Kilian, 1889) (see for example Frau et al. 2015, fig. 7a,c). *P. andreaei* can be distinguished by its more involute coiling and the occurrence of strong tubercles at the furcation point and on the end of the posterior branches of the bifurcate ribs. Following the revision of

P. andreaei by Frau et al. (2015), it seems obvious that *P. andreaei* was derived from *M. microcanthum* in the upper part of the *M. microcanthum* Zone (=*M. fischeri* Subzone *sensu* Wimbledon et al. 2013).

Occurrence: The first occurrence of *P. andreaei* is found in bed 89 at Charens. This occurrence is identical to that documented at Le Chouet (Wimbledon et al. 2013; Frau et al. 2015). *P. andreaei* has been reported from south-east Spain and France, Italy, Bulgaria, Tunisia and Morocco.

Genus *Boughdiriella* Frau, Bulot & Wimbledon, 2015

Type species: *Boughdiriella chouetensis* Frau, Bulot & Wimbledon, 2015, by original designation

Remarks: The genus was recently introduced by the authors of the present contribution to distinguish small Himalayitidae forms which had previously been referred to the "Mediterranean *Durangites*" (see discussion in Frau et al. 2015).

Boughdiriella chouetense Frau, Bulot & Wimbledon, 2015
nom. correct.
Figs. 6D–G

2015 *Boughdiriella chouetensis* – Frau, Bulot & Wimbledon, p. 123, figs. 4A,I [*cum. syn.*].

Type: The holotype is specimen no. MPP-CHT.21/65 from the Frau/Bulot collection. It was illustrated by Frau et al. (2015, fig. 4A).

Material: Seven specimens MPP-CHR.21/4, MPP-CHR.21/8, MPP-CHR.21/11, MPP-CHR.21/24, MPP-CHR.21/27, MPP-CHR.21/35, MPP-CHR.21/40.

Measurements (mm): See Table 4 in Supplementary data.

Description: The material collected at Charens is identical to that described from Le Chouet (Frau et al. 2015). *B. chouetense* is composed of small-sized Himalayitidae with a discoidal and moderately evolute shell. The whorl section is sub-circular in inner whorls and compressed, sub-oval whorl section in adult. The umbilical wall is low. The ornamentation is composed of rigid, straight, simple ribs in the inner whorls. From D~15 mm to the end of the body chamber, ribs are flexuous, prominent and bifurcated on the upper third of the flanks. Sporadic trifurcate and intercalated ribs occur. Ribs delimit a shallow furrow on the venter that is progressively attenuated at the end of the adult whorl.

Remarks: As discussed by Frau et al. (2015), *Boughdiriella* and *Protacanthodiscus* share strong affinities but the latter genus can be distinguished by its subrectangular to subhexagonal whorl section combined with tuberculation at almost all ontogenetic stages in both micro- and macroconch forms. R. Enay (comm. pers. 2015) expressed doubt about the interpretation of the peristome in *Boughdiriella*. He suggested that the genus may group only microconchs. Therefore, one may wonder if *B. chouetense* might not correspond to an extreme microconch morphology of *P. andreaei*. A detailed biometric analysis is currently in progress to decipher the range of variability of both species.

Occurrence: *B. chouetense* only occurs in bed 92 at Charens, topmost Andreaei Zone, Upper Tithonian. The vertical range of the species is shorter than at Le Chouet. *B. chouetense* is reported from south-east France and Bulgaria but its occurrence in Tunisia, Turkey, Italy and Morocco cannot be excluded (see discussion in Frau et al. 2015).

Genus *Pratumidiscus* Bulot, Frau & Wimbledon, 2014

Type species: *Pratumidiscus elsae* Bulot, Frau & Wimbledon, 2014, by original designation.

Remarks: The genus *Pratumidiscus* was introduced by Bulot et al. (2014) based on a single specimen from the uppermost Tithonian of Le Chouet. The genus was considered to be endemic in South East France but its general features closely resemble those of the Boreal lineage *Riasanella* Mitta, 2011—*Riasanites* Spath, 1923 and therefore it was considered as the probable Tethyan rootstock.

On the other hand, *P. elsae* shares strong affinities with the gracile morphotype of *P. andreaei* that was recently described by Frau et al. (2015). *P. elsae* can be distinguished by its more evolute coiling, irregular ribbing and loss of the lateral tubercles on the body chamber. In this regard, we assume that *P. elsae* was derived from the gracile morphotype of *P. andreaei* such as those illustrated by Frau et al. (2015, Fig. 6C and D).

Pratumidiscus elsae Bulot, Frau & Wimbledon, 2014
Fig. 6H

2014 *Pratumidiscus elsae* – Bulot, Frau & Wimbledon, p. 122, fig. 6

Type: The holotype is specimen no. MPP-CHT.19/5 from the Frau/Bulot collection. It was illustrated by Bulot et al. (2014, fig. 6).

Material: A single specimen MPP-CHR.21/43.

Measurements (mm): See Table 5 in Supplementary data.

Description: Small fragment of a body chamber with a subrectangular whorl section and tabulate venter. Ribbing composed of irregular single, bifurcate and intercalate ribs. All ribs thicken on the ventral shoulder into radially elongated bullae that delimit a ventral groove.

Remarks: The specimen at our disposal matches well the adult features of *P. elsae*. It differs in its smaller size and slightly rursiradiate ribs. These features suggest that this specimen corresponds to a microconch form. New specimens are urgently needed to document the range of variation and dimorphism of *P. elsae*.

Occurrence: *P. elsae* is found in bed 92 at Charens, topmost *P. andreaei* Zone, Upper Tithonian. This matches the occurrence of the holotype found at Le Chouet (Bulot et al. 2014). *P. elsae* is endemic to south-east France.

Family **Neocomitidae** Salfeld, 1921
Genus *Busnardoiceras* Tavera, 1985

Type species: *Parapallasiceras busnardoi* Le Hégarat, 1973, by original designation.

Remarks: A revised account of the genus *Busnardoiceras* and its type species was recently provided by the authors of the present contribution to which the reader is referred (Bulot et al. 2014).

Busnardoiceras busnardoi (Le Hégarat, 1973)
Figs. 6I–V

Macroconchs [M]

1939 *Berriasella ciliata* Schneid – Mazenot, p. 37, pl. 1, fig. 1a,b
1973 *Parapallasiceras busnardoi* – Le Hégarat, p. 47, pl. 3, figs. 4, 5 (= Mazenot, 1939, pl. 1, fig. 1a,b), ? pl. 38, fig. 2
2014 *Busnardoiceras busnardoi* (Le Hégarat) – Bulot et al., p. 124, fig. 8F,F'

Microconchs [m]

1982 *Fauriella shipkovensis* (Nikolov & Mandov) – Nikolov, p. 109, pl. 31, fig. 1
1985 *Berriasella* (*Berriasella*) *tithonica* – Tavera, p. 237, pl. 33, figs. 4a,b, 5, 6
? 2001 *Parapallasiceras busnardoi* Le Hégarat – Wippich, p. 78, pl. 20, fig. 2
2014 *Busnardoiceras busnardoi* (Le Hégarat) – Bulot et al., p. 124, figs. 8A,E

Type: The holotype is specimen no. UJF-ID.563 from the Mazenot collection. It was illustrated by Mazenot (1939, pl. 1, fig. 1a,b).

Material: Nineteen specimens MPP-CHR.19/1, MPP-CHR.19/3, MPP-CHR.19/4, MPP-CHR.21/2, MPP-CHR.21/7, MPP-CHR.21/10, MPP-CHR.21/12, MPP-CHR.21/13, MPP-CHR.21/14, MPP-CHR.21/15, MPP-CHR.21/16, MPP-CHR.21/17, MPP-CHR.21/18, MPP-CHR.21/26, MPP-CHR.21/28, MPP-CHR.21/36, MPP-CHR.21/37, MPP-CHR.21/38, MPP-CHR.21/42.

Measurements (mm): See Table 6 in Supplementary data.

Description: The material collected at Charens is similar to that from Le Chouet recently described by Bulot et al. (2014). *B. busnardoi* comprises small to medium size, planulate neocomitid forms with high and compressed, subrectangular whorl section and moderately evolute shallow umbilicus. The ornamentation is composed of straight to slightly prorsiradiate, bifurcate ribs on the phragmocone. Ribs bifurcate on the upper third of the flanks. The ornamentation of the body chamber is composed of dense slightly sinuous, irregular, bifurcate and intercalate rib. Sporadic virgatotome and simple ribs occur. Ribs are interrupted on the ventral shoulder by small punctiform tubercles delimiting a shallow groove on the inner whorls. In macroconchs, ribs cross the venter.

Remarks: The newly collected material from Charens shows that the innermost whorls of *B. busnardoi* match well the juvenile and intermediate ornamental stages of microconchs of *P. andreaei* as described by Frau et al. (2015). *B. busnardoi* can easily be distinguished since the species never develops lateral tubercle at the furcation point. *B. busnardoi* is further characterized by its adult neocomitid morphology. We therefore believe that *B. busnardoi* was derived from *P. andreaei* since both species co-occur in the topmost *P. andreaei* Zone in the Le Chouet and Charens sections.

Occurrence: *B. busnardoi* occurs between beds 90 and 92, topmost *P. andreaei* Zone, Upper Tithonian. This occurrence matches well the vertical range documented at Le Chouet by Wimbledon et al. (2013) and Bulot et al. (2014). The revised synonymy list of *B. busnardoi* shows that representatives of the species are more widespread than it was previously thought. Examination of the type specimen of *Berriasella tithonica* Tavera, 1985 shows that it is a junior subjective synonym of *B. busnardoi*. Therefore, the species occurs in Bulgaria, SE France, southern Spain and probably in Morocco.

Conclusion

Based on bed-by-bed sampling, we document the precise distribution of *Micracanthoceras microcanthum* at Charens. This confirms its high stratigraphic value for defining the base of the Upper Tithonian. As herein understood, the lower boundary of the *M. microcanthum* Zone is fixed at the FAD of the index species at Charens (i.e. bed 25). According to the preliminary calpionellid zonation from Charens (Wimbledon & Reháková unpublished data), the FAD of *M. microcanthum* falls within the upper part of the Chitinoidella Standard Zone, thus confirming similar result achieved in Spain (Pruner et al. 2010) and Morocco (Benzaggagh et al. 2010). A comparative analysis of the ammonite and calpionellid zonation is still ongoing and will shed new light on this problem. In this regard, the occurrence of ammonites below the FAD of *M. microcanthum* is confirmed at Charens which indicates the *B. ponti* Zone *sensu* Enay & Geyssant (1975). This fauna will be described elsewhere (Frau et al. in prep.).

From our detailed ontogenetic and biometric studies, we assume that *M. microcanthum* shows a wide range of variation that represents sexual and non-sexual polymorphism. Heterochronic shifts in development are documented in microconchs while macroconchs range between two extreme morphological poles related to the Buckman's first law of covariation (Fig. 5).

The vertical range of the age-diagnostic species *Protacanthodiscus andreaei* is rather similar to that described at Le Chouet (Frau et al. 2015). The FAD of this species typifies the lower boundary of the *P. andreaei* Zone *sensu* Wimbledon et al. (2013). The radiation of the Himalayitidae in the *P. andreaei* Zone is confirmed by the co-occurrence of the genera *Protacanthodiscus*, *Boughdiriella* and *Pratumidiscus*. As a result, the *M. microcanthum* Zone and the *P. andreaei* Zone are two biochronozones in the sense of Callomon (1985) since they are defined by the FAD of their index-species and characterized by their faunal assemblages. The two zones could be retained as workable on a larger geographical scale since both index species are widespread across the

Mediterranean-Caucasian Subrealm of the Tethyan Realm *sensu* Westermann (2000) (Fig. 7).

A close examination of a new collection of the basal Neocomitidae *Busnardoiceras busnardoi* shows that its inner whorls closely resemble those described by Frau et al. (2015) in *P. andreaei*. An ongoing revision of the early Berriasian Perisphinctoidea taxa originally reported at Le Chouet by Wimbledon et al. (2013) will shed new light on the relationships between *B. busnardoi* and other basal Neocomitidae. Nevertheless, there is no doubt that *B. busnardoi* represents an important element that links the radiation of the Neocomitidae from the Himalayitidae at the base of the *B. jacobi* Zone *auctorum*.

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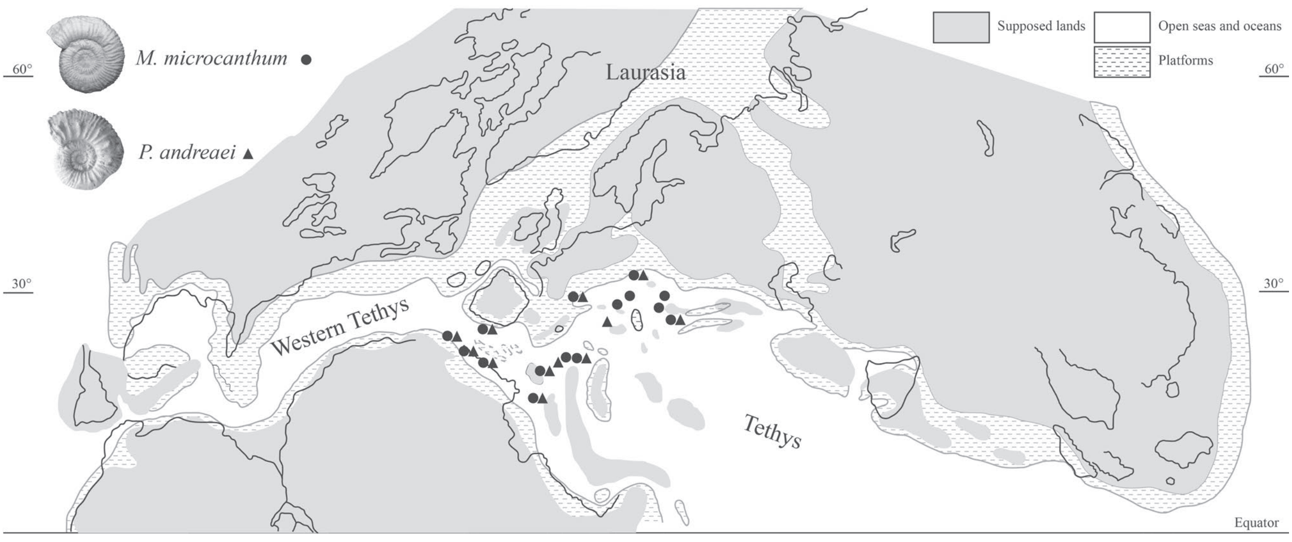

Fig. 7. Palaeo-biogeographical distribution of the two index species *Micracanthoceras microcanthum* (Oppel in Zittel, 1868) and *Protacanthodiscus andreaei* (Kilian, 1889) during the upper Tithonian (palaeogeographical map of the northern hemisphere modified after Cecca 1999).

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SUPPLEMENTARY DATA

Table 1: Dimensions of the type specimens and Spanish species referred to *M. microcanthum*. * indicates that the measurements of type specimens were performed on plaster cast.

species	no. Specimen	D	U	Wh	Wb	U/D	Wh/D	Wb/D	Wb/Wh
D. mutari	F.G1.12.1	170	85	47.2	46.6	0.5	0.28	0.27	0.99
		129.2	61.7	39.2	42.1	0.48	0.3	0.33	1.07
	T.G1.12.67	118.2	54.7	36.2	39	0.46	0.31	0.33	1.08
		87.6	39.7	28	29	0.45	0.32	0.33	1.04
	T.G1.12.70	127.5	64	36.2	36.5	0.5	0.28	0.29	1.01
		97.9	47.4	28.6	29.1	0.48	0.29	0.3	1.02
D. mediterraneum	T.GA1.1.1	148	77	39.8	37.2	0.52	0.27	0.25	0.93
		126	69	32	29	0.55	0.25	0.23	0.91
	F.G1.12.64	131.3	64.6	37	37	0.49	0.28	0.28	1
D. sinuosum	W.GA10.3.15	156	77	46.5	45	0.49	0.3	0.29	0.97
		114.4	57.3	33.5	29	0.5	0.29	0.25	0.87
H. gen. et sp. Indet	T.GA6b.1.45	98.1	51.4	28.8	27	0.52	0.29	0.28	0.94
	T.GA8.-3.5	112	56.9	31.3	31.6	0.51	0.28	0.28	1.01
M. (M.) microcanthum	AI-29	88.4	48	23.5	26	0.54	0.27	0.29	1.11
		70.3	39.2	17.8	20.4	0.56	0.25	0.29	1.15
	T.G23a.R.5.82	80.5	39.7	24	23	0.49	0.3	0.29	0.96
		61.9	30.6	17.9	18	0.49	0.29	0.29	1.01
	T.Gax	109	61.2	26.9	29.3	0.56	0.25	0.27	1.09
		85.8	48	22.5	22.4	0.56	0.26	0.26	1
	T.G23a.4.5	85.8	48	22.5	22.4	0.56	0.26	0.26	1
		52.5	29.3	13.7	14.2	0.56	0.26	0.27	1.04
	T.GA10.2.1.	44.7	23.8	11.3	12.3	0.53	0.25	0.28	1.09
		82.3	47.7	21.1	25	0.58	0.26	0.3	1.18
	T.G23a.4.120	64.3	38	14.1	18	0.59	0.22	0.28	1.28
		29.9	14.8	8.9	10.2	0.49	0.3	0.34	1.15
		25	12.4	7.5	9	0.5	0.3	0.36	1.2
	T.G23a.R.5.113	32.8	17.3	9.5	12	0.53	0.29	0.37	1.26
		26.6	13.4	7	10	0.5	0.26	0.38	1.43
	T.GA6.4.28	30	16.2	9.3	10.6	0.54	0.31	0.35	1.14
	T.GA6b.4.28	37.3	20.4	9.6	12.4	0.55	0.26	0.33	1.29
	T.A2c.10.1	45.2	25	13.2	12	0.55	0.29	0.27	0.91
		35.3	18.6	9.4		0.53	0.27	0	0
	T.G23a.R.5.97	65.8	38.7	15	17	0.59	0.23	0.26	1.13
	T.G23a.5.19	43.6	26	10.4	10.6	0.6	0.24	0.24	1.02
		35.7	21.4	8.3	9.2	0.6	0.23	0.26	1.11
M. (M.) cf. brightoni	W.G19b.5.1	69.3	37	17	22	0.53	0.25	0.32	1.29
		50.4	27.4	12.7	15.9	0.54	0.25	0.32	1.25
M. (C.) lotenoense	HOLOTYPE	27.7	10.6	10.4	11.5	0.38	0.38	0.42	1.11
	F.G1.12.3	31.9	14.3	10.1	10.2	0.45	0.32	0.32	1.01
	F.G1.12.64	26.9	12.3	8.7	9.2	0.46	0.32	0.34	1.06
		22	9.6	7.9	8.2	0.44	0.36	0.37	1.04
	F.G1.12.21	40.5	20	12.7	13.4	0.49	0.31	0.33	1.06
		29.6	13.8	9	11	0.47	0.3	0.37	1.22
M. (C.) radians	W.GA10.3.32	48.7	22.9	15.1	15.2	0.47	0.31	0.31	1.01
		37.7	17.4	12	11.6	0.46	0.32	0.31	0.97
	T.Co.R.3	40.4	18.5	12.8	12.6	0.46	0.32	0.31	0.98
		33.4	14.5	11	10	0.43	0.33	0.3	0.91
	W.PR.8.1	49.1	22.5	15.3	16.2	0.46	0.31	0.33	1.06
		38.7	18	12.9	12.7	0.47	0.33	0.33	0.98
	W.PR.8.4	36.3	16.5	11.6	11.2	0.45	0.32	0.31	0.97
		28.3	12.2	9.3	9.4	0.43	0.33	0.33	1.01
M. (C.) rhodanicum	NS-22	63.4	35	16	18	0.55	0.25	0.28	1.13
		50.9	28	13	13.7	0.55	0.26	0.27	1.05
	T.G23a.R.5.100	62.3	33.4	15.8	16.9	0.54	0.25	0.27	1.07
		50.3	25.7	14.2	14.4	0.51	0.28	0.29	1.01
	T.G1.11.49	49	25.6	13.2	13.9	0.52	0.27	0.28	1.05

Table 1 (continuation): Dimensions of the type specimens and Spanish species referred to *M. microcanthum*. * indicates that the measurements of type specimens were performed on plaster cast.

species	no. Specimen	D	U	Wh	Wb	U/D	Wh/D	Wb/D	Wb/Wh
M. (C.) minor	T.GA1.1.4	23	11.4	7.1	8	0.5	0.31	0.35	1.13
		20	9.8	6	7	0.49	0.3	0.35	1.17
	T.GA8.-3.7	30	13.5	10.4	10.6	0.45	0.35	0.35	1.02
		23.1	9.9	8.1	9.4	0.43	0.35	0.41	1.16
M. (C.) mendozanum	T.GA6b.1.52	35	17	10.9	9.5	0.49	0.31	0.27	0.87
		31.6	15.2	9.9	8.1	0.48	0.31	0.26	0.82
M. (C.) flexuosum	T.GA1.1.2	60	32.3	15.2	16.2	0.54	0.25	0.27	1.07
		50.5	27	13.3	12.6	0.53	0.26	0.25	0.95
	T.GA1.1.5	75.7	37.5	21.5	19	0.5	0.28	0.25	0.88
		64.4	33.9	16.3	16.6	0.53	0.25	0.26	1.02
	T.GA6b.1.40	72.2	36.5	20.9	19.6	0.51	0.29	0.27	0.94
		57.3	28.6	16.5	15.4	0.5	0.29	0.27	0.93
	W.GA10.3.21	76.4	38.8	21.8	21.5	0.51	0.29	0.28	0.99
		52.5	27	14.5	13.6	0.51	0.28	0.26	0.94
	W.GA10.3.22	58.5	30.3	16.8	15.2	0.52	0.29	0.26	0.9
		53	27.1	14.5	13.8	0.51	0.27	0.26	0.95
	W.GA10.3.25	59.5	30	17.5	17	0.5	0.29	0.29	0.97
		46.1	22.6	13.2	15	0.49	0.29	0.33	1.14
	W.GA10.3.36	71.6	35.5	20.7	18.8	0.5	0.29	0.26	0.91
		54.3	26.8	15.2	14.7	0.49	0.28	0.27	0.97
	T.G1.12.66	67.9	35.5	20.1	17.8	0.52	0.3	0.26	0.89
		52.8	27.3	14.1	12.8	0.52	0.27	0.24	0.91
M. (C.) koellikeri	T.GA7.26.30	63	29.8	20	18.4	0.47	0.32	0.29	0.92
		47	22.3	14.8	13.2	0.47	0.31	0.28	0.89
M. (C.) ornatum	T.GA8.-3.4	77	38.3	22.1	24.4	0.5	0.29	0.32	1.1
	W.GA10.3.18	75.6	37	23	25	0.49	0.3	0.33	1.09
		52.2	25.6	15.2	17.2	0.49	0.29	0.33	1.13
M. (C.) symbolum	T.G1.11.47	36.2	19	9.7	13	0.52	0.27	0.36	1.34
	T.G23a.R.5.77	58	34.1	14	18.6	0.59	0.24	0.32	1.33
		47.6	27	11.1	16.6	0.57	0.23	0.35	1.5
	T.Ce.R.6	81.3	49.2	17.8	22.4	0.61	0.22	0.28	1.26
		67.7	38.6	17	21.8	0.57	0.25	0.32	1.28
		65.8	40.4	13.9	19.6	0.61	0.21	0.3	1.41
	W.GA10.3.17	85	46.8	21.2	25.4	0.55	0.25	0.3	1.2
M. (C.) leanzai	T.GA6b.1.46	70.7	36	19.7		0.51	0.28	0	0
	T.GA6b.1.47	77.8	38.2	22.6	24.2	0.49	0.29	0.31	1.07
		57.7	28.6	17.1	18.2	0.5	0.3	0.32	1.06
	T.GA8.-3.2	108	55.5	30.2	33.4	0.51	0.28	0.31	1.11
		89.3	44.7	24.7		0.5	0.28	0	0
	T.GA8.-3.3	80	42	21.7	22.8	0.53	0.27	0.29	1.05
A. parvulus	T.G23a.R.5.90	33.6	17.6	9.5	9	0.52	0.28	0.27	0.95
		27.2	13.8	8	8.8	0.51	0.29	0.32	1.1
A. sulcatus	T.GA1.1.8	78.5	35.5	25	21	0.45	0.32	0.27	0.84
	T.GA6.1.8	78.1	37.4	24.3	20	0.48	0.31	0.26	0.82
	T.GA10.3.3	81.1	38.5	24.7	21.4	0.47	0.3	0.26	0.87
	T.G2.2.3	64.3	31.1	19.1	16	0.48	0.3	0.25	0.84
	T.G2.2.3	73	35.5	22.4	20	0.49	0.31	0.27	0.89
	T.G23a.R.13	64.5	30.5	19.2	18.5	0.47	0.3	0.29	0.96
		51.2	23.5	15.8	15.7	0.46	0.31	0.31	0.99
A. venustus	W.PR8.5	43.8	18.5	14.6	15.4	0.42	0.33	0.35	1.05
		36.3	15.8	12.2	13.4	0.44	0.34	0.37	1.1
		85	42.5	25.3	23.5	0.5	0.3	0.28	0.93
A. microcanthus	Lectototype*	60.7	27.85	20.9	20.6	0.46	0.34	0.34	0.99
A. microcanthus	Paratype*	140.1	65.3	45.15	35.5	0.47	0.32	0.25	0.79
A. symbolus	Lectotype*	79.25	44.5	21.45	26.4	0.56	0.27	0.33	1.23
A. koellikeri	Lectotype*	160	83	43	42	0.52	0.27	0.26	0.98

Table 2: Dimensions of *Micracanthoceras microcanthum* (Oppel *in* Zittel, 1868) from Charens. Yellow squares indicate approximated dimensions.

no. Specimens	D	U	Wh	U/D	Wh/D
MPP-CHT.29/1	41	18.9	14.25	0.46	0.35
MPP-CHR.34/1			28.6		
MPP-CHR.34/2			17.7		
MPP-CHR.37/1					
MPP-CHR.37/2					
MPP-CHR.37/3	190	88.2	55	0.46	0.29
MPP-CHR.45/1			26.3		
MPP-CHR.50/1					
MPP-CHR.50/2			12.9		
MPP-CHR.50/3	28.42	11.94	9.8	0.42	0.34
MPP-CHR.50/3x					
MPP-CHR.51/2	27	11.5	9.7	0.43	0.36
MPP-CHR.53/2					
MPP-CHR.53/4a-c		10.17	7.96		
MPP-CHR.54/1a	51		17.5		0.34
MPP-CHR.54/1b			14.2		
MPP-CHR.60/1			18.8		
MPP-CHR.60/2		25	16		
MPP-CHR.60/3			15.3		
MPP-CHR.60/4	50.6		15.5		0.31
MPP-CHR.60/6	39.3	18.3	12	0.47	0.31
MPP-CHR.60/7					
MPP-CHR.62/1			11.2		
MPP-CHR.63/1			9		
MPP-CHR.67/4	33.4	15.4	12.26	0.46	0.37
MPP-CHR.67/7					
MPP-CHR.67/9	38	17.2	11.5	0.45	0.3
MPP-CHR.68/1		16.25			
MPP-CHR.68/2	20.95	9.22	7.26	0.44	0.35
MPP-CHR.82/1	56.5	26.8	16.2		
MPP-CHR.87/1	41.3	20.7	10.7		
MPP-CHR.92/2	26.5				
MPP-CHR.92/4	51.4	24.8	14.5	0.48	0.28
MPP-CHR.92/5			28.7		
MPP-CHR.92/10	27.5	10.9	8.4	0.4	0.31
MPP-CHR.92/11	51.4	25.2	15.75	0.49	0.31
MPP-CHR.92/13	32.4	15.56	10.8	0.48	0.33
MPP-CHR.92/28		18.07	c14.5		
MPP-CHR.98/1	58	30.7	18.3	0.53	0.32
MPP-CHR.R100/6	57.4	26.7	18.3	0.47	0.32

Table 3: Dimensions of *Protacanthodiscus andreaei* (Kilian, 1889) from Charens. Yellow squares indicate approximated dimensions.

no. Specimens	D	U	Wh	U/D	Wh/D
MPP-CHR.79/4	52.46	19.03	19.2	0.4	0.4
MPP-CHR.19/5	12.8	4.6	4.5	0.4	0.4
MPP-CHR.21/3	41	18.2	13.6	0.4	0.3
MPP-CHR.21/6	27.48	11.7	11.11	0.4	0.4
MPP-CHR.21/19	43	20.5	15	0.5	0.3
MPP-CHR.21/20	17.4				
MPP-CHR.21/25	28.7	13.35	9.2	0.5	0.3
MPP-CHR.21/29	24.26	8.4	10	0.3	0.4
MPP-CHR.21/32	13.84	5.14	4.57	0.4	0.3
MPP-CHR.21/34			6		
MPP-CHR.21/42	25.5	12.9	6.4	0.5	0.3

Table 4: Dimensions of *Boughdiriella chouetense* Frau, Bulot & Wimbledon, 2015 from Charens. Yellow squares indicate approximated dimensions.

no. Specimens	D	U	Wh	U/D	Wh/D
MPP-CHR.19/1	23.3	7.2	11.7	0.3	0.5
MPP-CHR.21/4	35.2	14.5	11.5	0.4	0.3
MPP-CHR.21/8	31.64	12.8	11.03	0.4	0.3
MPP-CHR.21/11	26.07	9.7	9.9	0.4	0.4
MPP-CHR.21/24	27.96	11.36	9.2	0.4	0.3
MPP-CHR.21/27	29	14.9	9.5	0.5	0.3
MPP-CHR.21/33	31.7	15.57	13.61	0.5	0.4
MPP-CHR.21/35	12.5	12.1	8	1	0.6
MPP-CHR.21/40			8.7		

Table 5: Dimensions of *Pratumidiscus elsae* Bulot, Frau & Wimbledon, 2014 from Charens.

no. Specimens	D	U	Wh	U/D	Wh/D
MPP-CHR.21/43			9.8		

Table 6: Dimensions of *Busnardoiceras busnardoi* (Le Hégarat, 1973) from Charens. Yellow squares indicate approximated dimensions.

no. Specimens	D	U	Wh	U/D	Wh/D
MPP-CHR.19/1x	36.98	15.6	14.6	0.4	0.4
MPP-CHR.19/3	32.24	10.63	12.57	0.3	0.4
MPP-CHR.21/7	66.3	23.94	24.25	0.4	0.4
MPP-CHR.21/10	48	16.8	15.2	0.4	0.3
MPP-CHR.21/12	53.35	20.5	18.3	0.4	0.3
MPP-CHR.21/13	27.77	9.84	10.05	0.4	0.4
MPP-CHR.21/14	32.2	11.85	11.8	0.4	0.4
MPP-CHR.21/15	39.43	14.35	14.3	0.4	0.4
MPP-CHR.21/16	23.65	9.42	8.83	0.4	0.4
MPP-CHR.21/17	22.59	7.8	7.95	0.3	0.4
MPP-CHR.21/18					
MPP-CHR.21/26	60.37		20.97		0.3
MPP-CHR.21/28	25.61	11.1	9.6	0.4	0.4
MPP-CHR.21/36	94.7	37.87	34	0.4	0.4
MPP-CHR.21/37	28.4	11.7	11	0.4	0.4
MPP-CHR.21/38	53.6	20.7	19	0.4	0.4
MPP-CHR.21/42	40.5	15	14.8	0.4	0.4

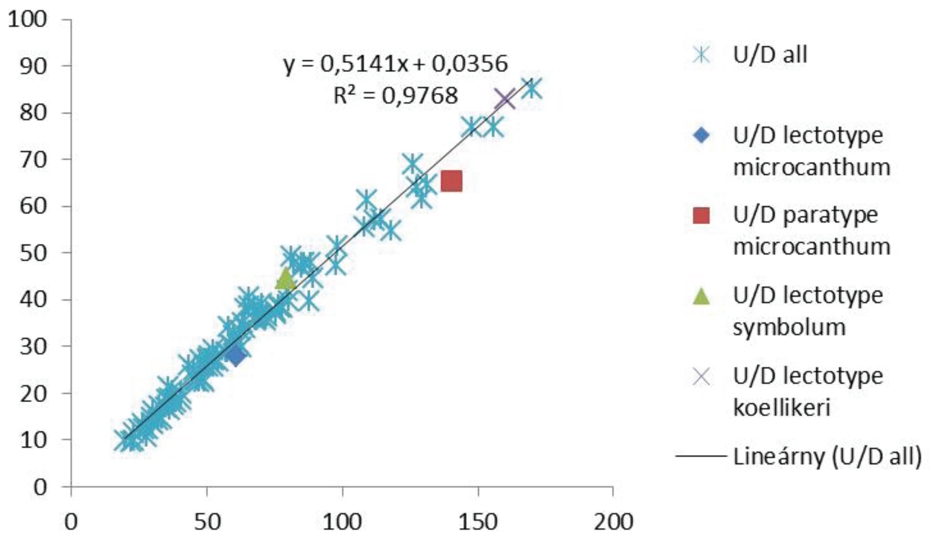

Fig. S1. *U=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

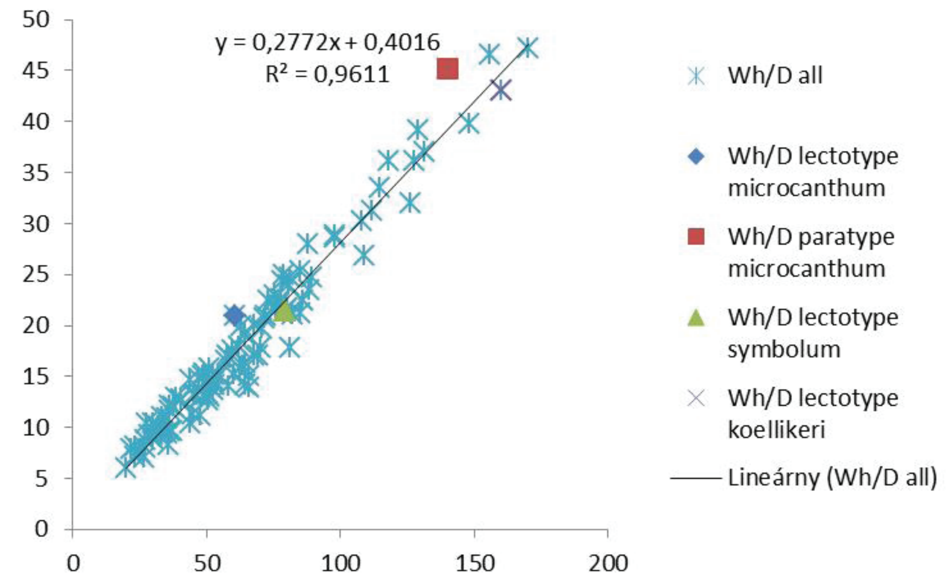

Fig. S2. *Wh=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

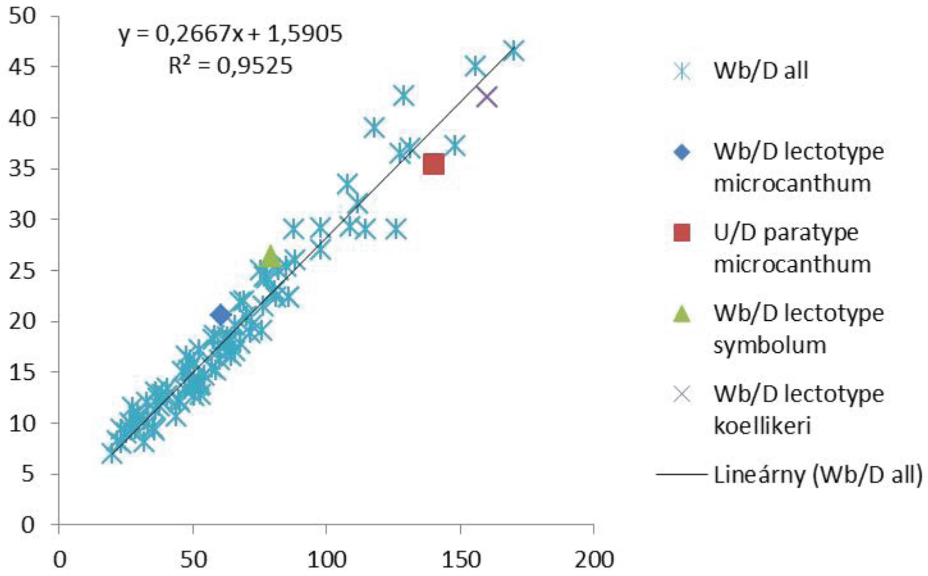

Fig. S3. *Wb=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

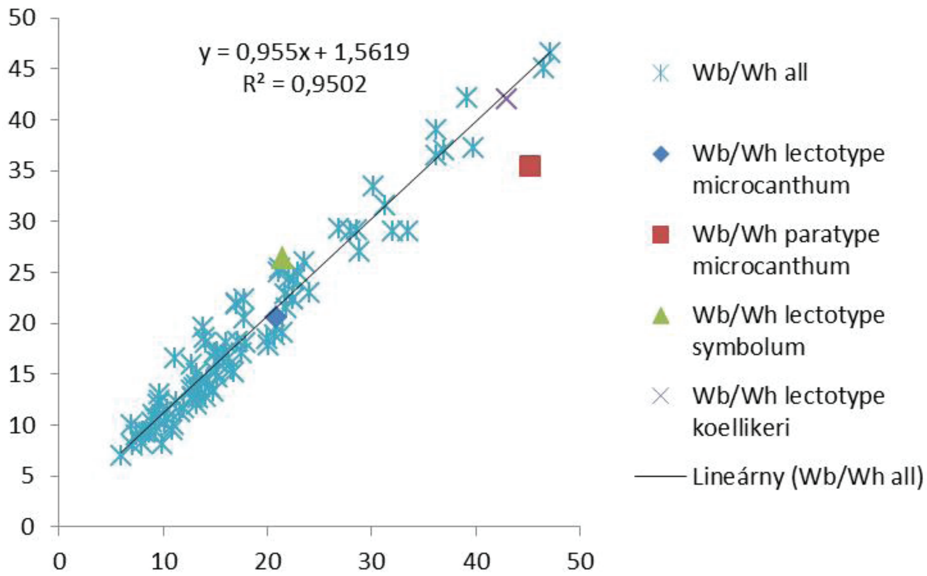

Fig. S4. *Wb=f(Wh)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.