

New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Drôme, SE France)

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Key words: Ammonoidea, Ataxioceratidae, Himalayitidae, Neocomitidae, Upper Tithonian, Le Chouet, South-East France.

Abstract. The aim of this paper is to document the ammonite fauna of the upper part of the Late Tithonian collected at the key section of Le Chouet (Drôme, SE France). Emphasis is laid on new and poorly known Ataxioceratidae, Himalayitidae and Neocomitidae from the upper part of the Tithonian. Among the Ataxioceratidae, a new account on the taxonomy and relationship between *Paraulacosphinctes* Schindewolf and *Moravisphinctes* Tavera is presented. Regarding the Himalayitidae, the range and content of *Micracanthoceras* Spath is discussed and two new genera are introduced: *Ardesciella* gen. nov., for a group of Mediterranean ammonites that is homoeomorphic with the Andean genus *Corongoceras* Spath, and *Pratumidiscus* gen. nov. for a specimen that shows morphological similarities with the Boreal genera *Riasanites* Spath and *Riasanella* Mitta. Finally, the occurrence of Neocomitidae in the uppermost Tithonian is documented by the presence of the reputedly Berriasian genera *Busnardoiceras* Tavera and *Pseudargentinoceras* Spath.

INTRODUCTION

The unique character of the ammonite fauna of Le Chouet (near Les Près, Drôme, France) (Fig. 1) has already been outlined by Le Hégarat (1973), but, so far, only a handful of specimens have been illustrated by Enay *et al.* (1998a, fig. 2). In recent years, new fieldwork has allowed us to sample the Chouet section bed by bed and to collect over 400 new specimens. A preliminary account on the ammonite distribution across the Tithonian-Berriasian boundary was published by Wimbledon *et al.* (2013), but in that paper we did not illustrate the fauna. The aim of the present contribution is to document the taxonomy and illustrate new and poorly

known Perisphinctoidea from the Upper Tithonian of this reference section. Additional data on the Himalayitidae including the description and discussion of *Boughdiriella chouetensis* gen. nov. sp. nov. are to be published elsewhere (Frau *et al.*, 2014).

GEOLOGICAL SETTING

A detailed geological description of the Le Chouet section, including lithostratigraphy, sedimentology, biostratigraphy (calpionellids, calcareous nannofossils and ammonites) and magnetostratigraphy has been published by

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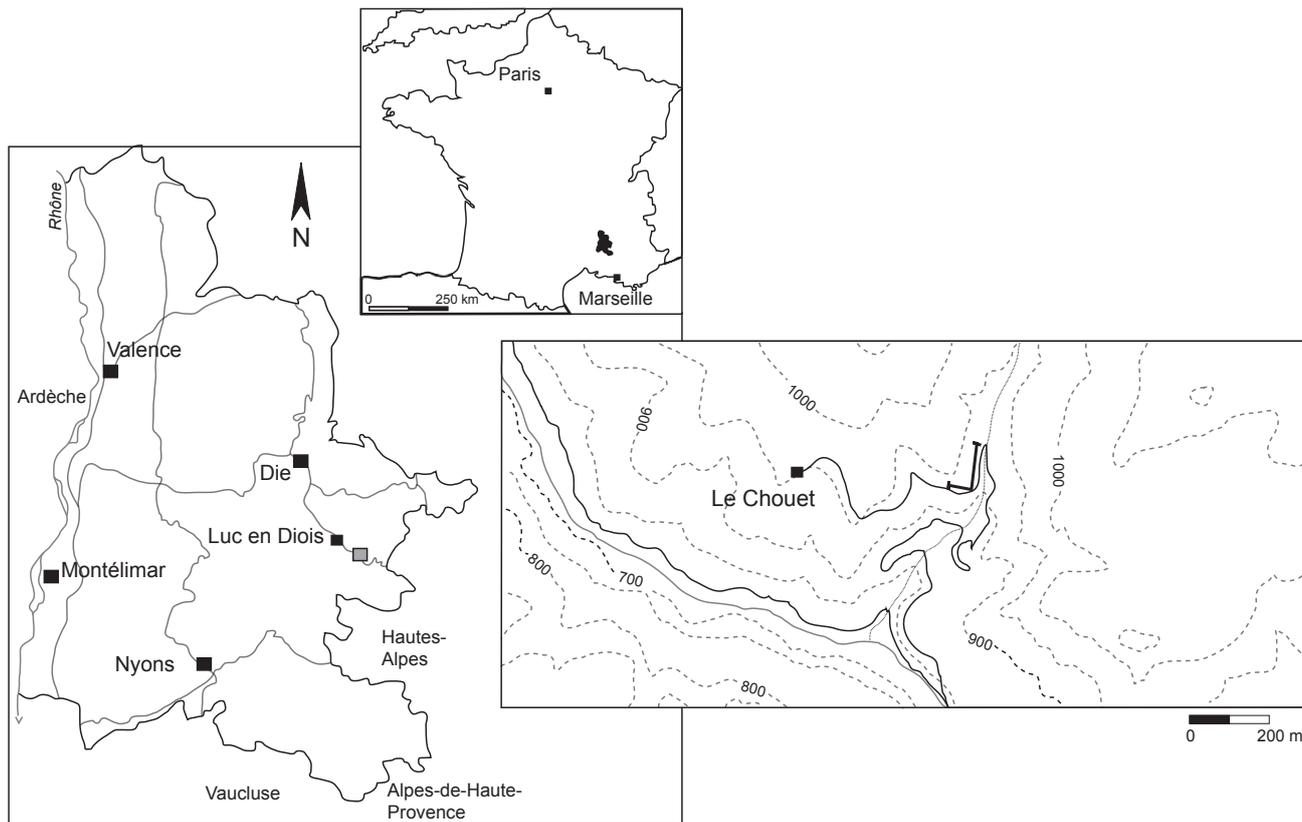


Fig. 1. Locality map of Le Chouet (Les Près, Drôme, SE France)

The studied section is marked by a black line

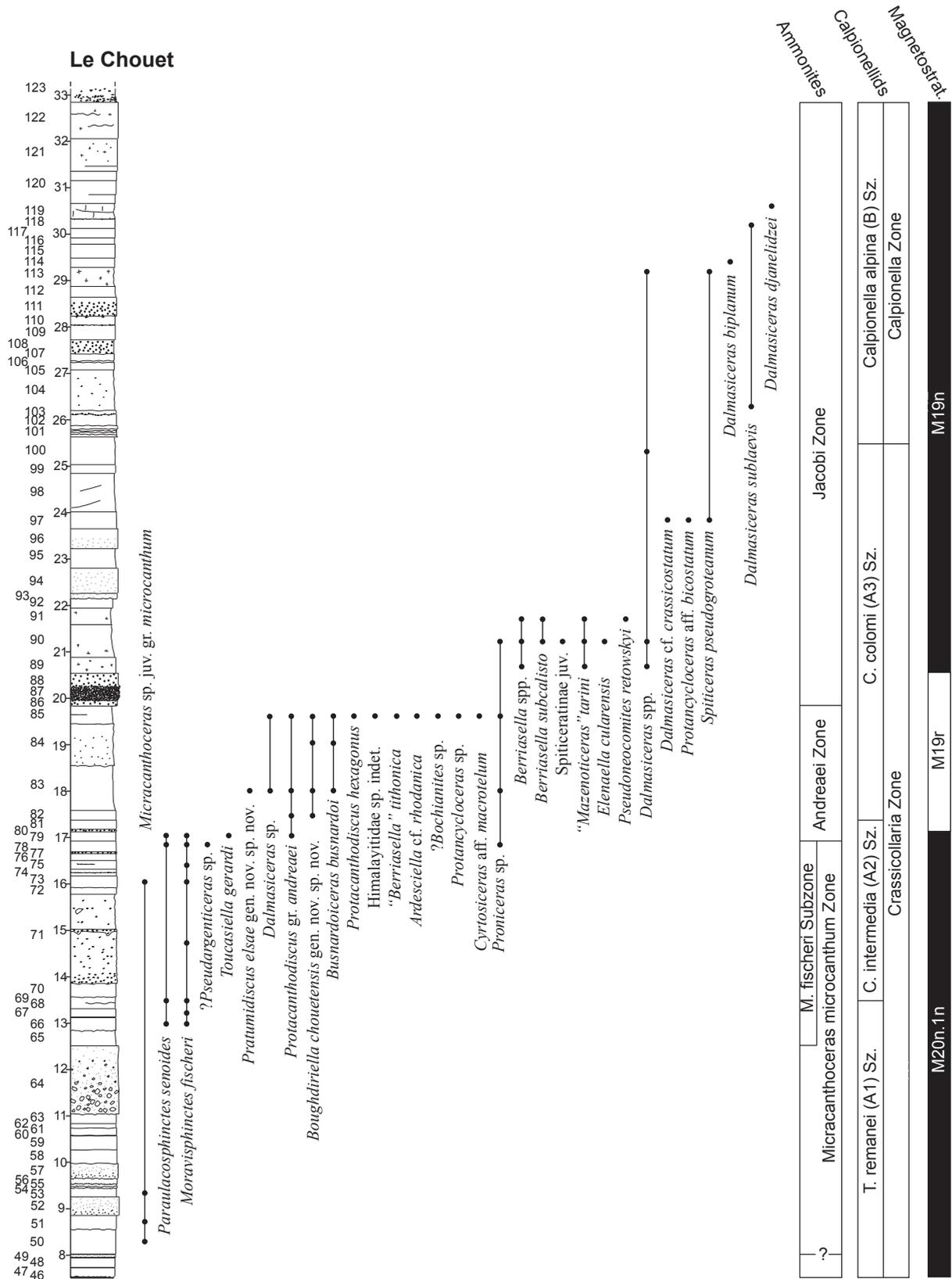
Wimbledon *et al.* (2013). A revised version of the ammonite distribution is presented herein (Fig. 2), as a contribution toward the integrated stratigraphic scheme of Wimbledon *et al.* (2013). From bottom to top, three biostratigraphic units can be recognized: the upper part of the *Micracanthoceras microcanthum* (= *Microcanthum*) Zone [*Moravisphinctes fischeri* (= *Fischeri*) Subzone], the *Protacanthodiscus andreaei* (= *Andreaei*) Zone (as a replacement for the *Durangites* spp. Zone of the literature) and the lower part of the *Berriasella jacobi* (= *Jacobi*) Zone (*sensu* Hoedemaeker, Bulot, 1990).

The minor discrepancies between figure 12 in Wimbledon *et al.* (2013) and Figure 2 of this paper concern the distribution of *Micracanthoceras* Spath, 1925 and the occurrence of supposed Boreal ammonites reported by Wimbledon *et al.* (2013, p. 451). The range of *Micracanthoceras* will be discussed below. The reported occurrence of Boreal ammonites was based on the identification of *?Praetollia* sp. (a single specimen of complex interpretation whose identity with true *Praetollia* Spath from Greenland is highly doubtful) and *?Riasanites* sp. (herein reinterpreted as *Pratumidiscus elsae* gen. nov. sp. nov.).

SYSTEMATIC PALAEOLOGY

At the suprageneric level, the taxonomy adopted herein is conservative and follows the classification proposed by Cecca *et al.* (1989) for the Ataxioceratidae; Tavera (1985) for the Himalayitidae and Wright *et al.* (1996) for the Neocomitidae. As already pointed out by Donovan *et al.* (1981), Company (1987) and Cecca *et al.* (1989), the systematics of these families are in a state of chaos and the understanding of their phylogenetic relationships is still at a very preliminary stage. Unfortunately, the material at our disposal is not yet sufficient for further considerations of these wider issues.

Fig. 2. Integrated stratigraphy and distribution of the Ancyloceratina and Ammonitina around the Tithonian-Berriasian boundary at Le Chouet modified after Wimbledon *et al.* (2013)



Conventions: Preservation of our specimens as crushed internal moulds prevents us from giving other measurements than D_{max} = larger measurable diameter and U/D ratio (umbilical dimension as a percentage of the diameter at the point of measurement).

Unless otherwise mentioned, all specimens are deposited in the Frau/Bulot collection at the Musée Paléontologique de Provence (MPP) of Aix-Marseille University (Saint-Charles), France.

Order **Ammonoidea** Zittel, 1884

Suborder **Ammonitina** Hyatt, 1889

Superfamily **Perisphinctoidea** Steinmann, 1890

Family **Ataxioceratidae** Buckman, 1921

Subfamily **Lithacoceratinae** Zeiss, 1968

Genus *Paraulacosphinctes* Schindewolf, 1925

Type species: *Ammonites senex* Oppel in Zittel, 1868; by subsequent designation of Sapunov (1979, p. 126).

Remarks. – In its original conception, the genus *Paraulacosphinctes* was based on perisphinctids with a ventral groove from the classical Tithonian localities around Stramberg (= Štramberk, Czech Republic). Tavera (1985) considerably expanded the definition of the genus by the introduction of twelve new typological species and of four allied genera (*Zittelia* Tavera, 1985, *Neoperisphinctes* Tavera, 1985, *Moravispinctes* Tavera, 1985 and *Andaluspinctes* Tavera, 1985) that were grouped in the new subfamily Paraulacosphinctinae Oloriz and Tavera in Tavera, 1985. Lacking an exhaustive view of the content of this subfamily, we subscribe to the opinion of Cecca *et al.* (1989) that the relationships between Lithacoceratinae and Paraulacosphinctinae remains unclear and the use of the name Paraulacosphinctinae is unnecessary. On the other hand, our fairly abundant and well-preserved new material allows us to comment on some of the views expressed by Cecca *et al.* (1989) and Parent (2003) about the taxonomy of the Paraulacosphinctinae.

Paraulacosphinctes senoides Tavera, 1985

Fig. 3A–E

- pars 1868. *Ammonites senex* Oppel in Zittel, p. 113, pl. 23: 1, 2; non fig. 3 (= *P. senex*).
1985. *Paraulacosphinctes senoides* Tavera, p. 79, pl. 13: 1–5, text-fig. 7E.
- non 2011. *Paraulacosphinctes* cf. *senoides* Tavera: Arkadiev, p. 242, pl. 1: 5 (= *P. transitorius* Oppel, 1865).
- non 2012. *Paraulacosphinctes* cf. *senoides* Tavera: Arkadiev, p. 141, pl. 1: 5 (= Arkadiev, 2011, pl. 1: 5).

Material. – MPP-CHT.2/1, MPP-CHT.4/2, MPP-CHT.9/7, MPP-CHT.12/6, MPP-CHT.12/9, MPP-CHT.12/19, MPP-CHT.12/25, MPP-CHT.12/26, MPP-CHT.12/29, MPP-CHT.12/30, MPP-CHT.12/32, MPP-CHT.14/10, MPP-CHT.15/13, MPP-CHT.15/15, MPP-CHT.15/17.

Description. – Middle-sized planulate ammonites ($D_{max} < 50$ mm) that show rapid growth of the whorl height throughout ontogeny. The whorl section is suboval with convex flanks. Moderately open ($0.30 < U/D < 0.33$) and relatively deep umbilicus with poorly marked umbilical wall. The ornamentation is mainly composed of fine and dense bifurcate ribs. The bifurcation occurs at, or just above, the middle of the flank. On the inner whorls, the ribs are interrupted on the venter by a smooth ventral band. On the body chamber, the ribs cross the venter, and several specimens exhibit a more complicated rib pattern with low bifurcations and irregular intercalatories (Fig. 3A).

Remarks. – Our material matches well the type series illustrated by Tavera (1985), with special reference to the specimens of pl. 13: 2, 5.

P. senex differs from *P. senoides* in its larger adult size, wider umbilicus and complete loss of ornamentation on the later ontogenic stages. According to Cecca *et al.* (1989, p. 59), there is no difference between the two species and the loss of the ornamentation in *P. senex* would be an adult character not seen in *P. senoides* because that taxon is based on incomplete specimens. This view is not supported by our material, which does not show any fading of the ornamentation on the adult body chamber. It should be noted also that the early whorls of the holotype of *P. senex* are not preserved and do not allow comparison with those of *P. senoides*.

P. transitorius (Oppel, 1865) can easily be distinguished by its wider umbilicus, steep umbilical wall, less compressed whorl section and distinctive spaced ribs. The twelve morphological taxa introduced by Tavera (1985) are in need of revision in the light of the law of covariation of characters. At first sight, the range of variability of the group of species characterized by a suboval section suggests covariation – in U/D ratio, rigidity of ribbing and the position of the furcation point. A biometric study would be necessary for a better understanding of the spectrum of intra- and interspecific variabilities within *Paraulacosphinctes*.

Stratigraphical and geographical distribution. – Upper Tithonian, Le Chouet beds 66, 67, 68, 73, 76, 78 and 79, Microcanthum Zone, Fischeri Subzone, and base of the Andraeae Zone (Crassicollaria calpionellid Zone, uppermost part of the Remanei Subzone and Intermedia Subzone). Even so, all illustrated specimens of *P. senoides* originate from SE France and Spain, and the species is reported from Morocco. Our observations confirm the range of the species given by Tavera (1985) and Benzaggagh, Atrops (1997).

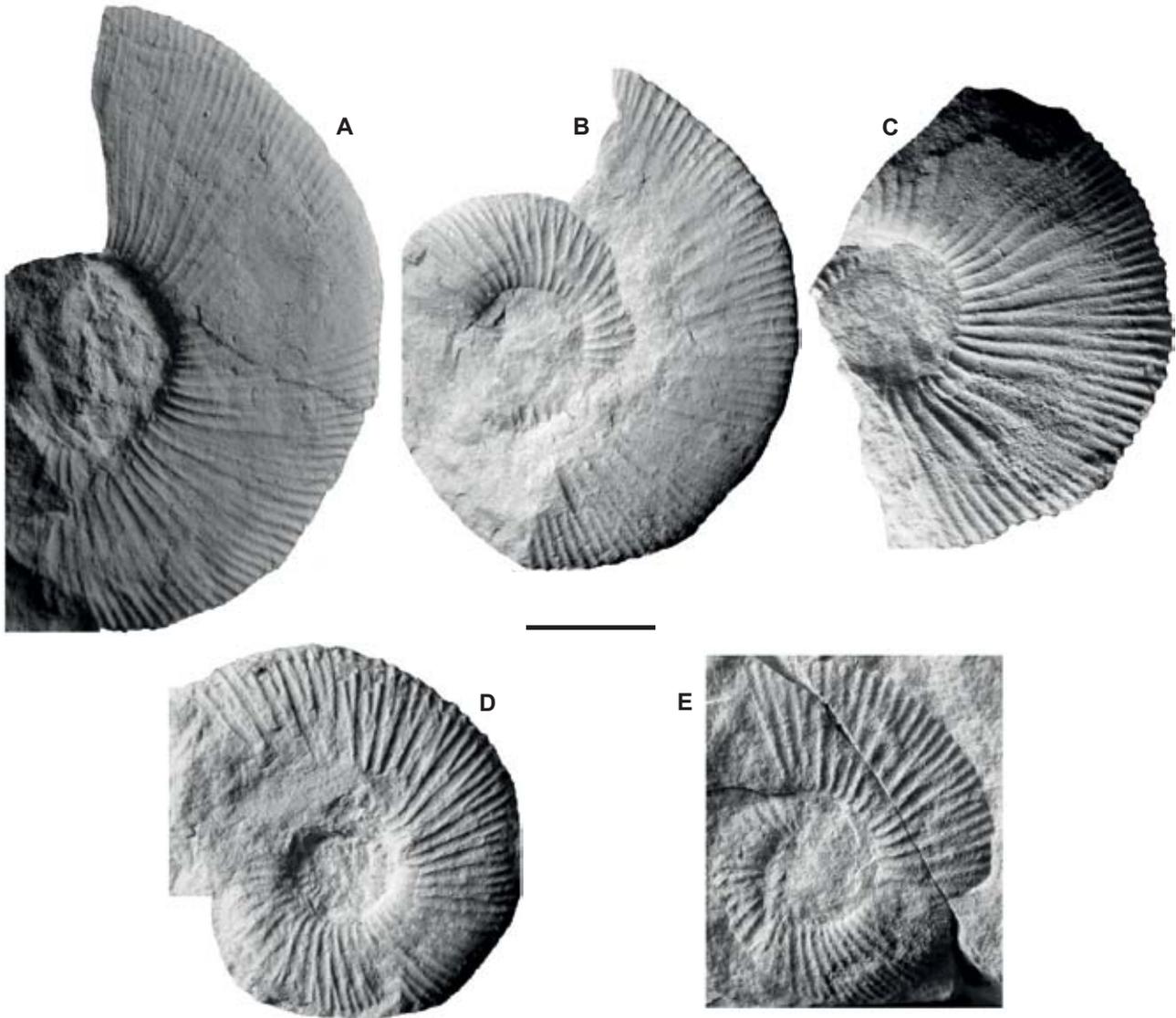


Fig. 3. *Paraulacosphinctes senoides* Tavera

A. MPP-CHT.12/26. **B.** MPP-CHT.12/23. **C.** MPP-CHT.15/15. **D.** MPP-CHT.12/6. **E.** MPP-CHT.4/2. Bar scale is 1 cm

The occurrence in Ukraine (Crimea) is based on the mis-identification of *P. transitorius* (Arkadiev, 2011, 2012).

Genus *Moravisphinctes* Tavera, 1985

Type species: *Ammonites moravicus* Oppel in Zittel, 1868, by original designation.

Moravisphinctes fischeri (Kilian, 1889)

Fig. 4A–E

1889. *Perisphinctes fischeri* n. sp. Kilian, p. 655, pl. 28: 2a, b.

1985. *Moravisphinctes fischeri* (Kilian): Tavera, p. 108, pl. 13: 6–8, text-fig. 8D.

1985. *Moravisphinctes moravicus* (Oppel): Tavera, p. 104, pl. 14: 1–5, text-fig. 8E.

1985. *Moravisphinctes flexuosus* Tavera, p. 107, pl. 14: 6, 7, text-fig. 8B.

1985. *Moravisphinctes* sp. 1, Tavera, p. 113, pl. 14: 10, text-fig. 8C.

1989. *Moravisphinctes fischeri* (Kilian): Cecca *et al.*, p. 61, pl. 2: 2–13; text-fig. 21a, c–f.

2000. *Moravisphinctes fischeri* (Kilian): Benzaggagh, pl. 3: 6.

2005. *Moravisphinctes* sp. gr. *fischeri* (Kilian) – *moravicus* (Oppel), Boughdiri *et al.*, pl. 2: 8.

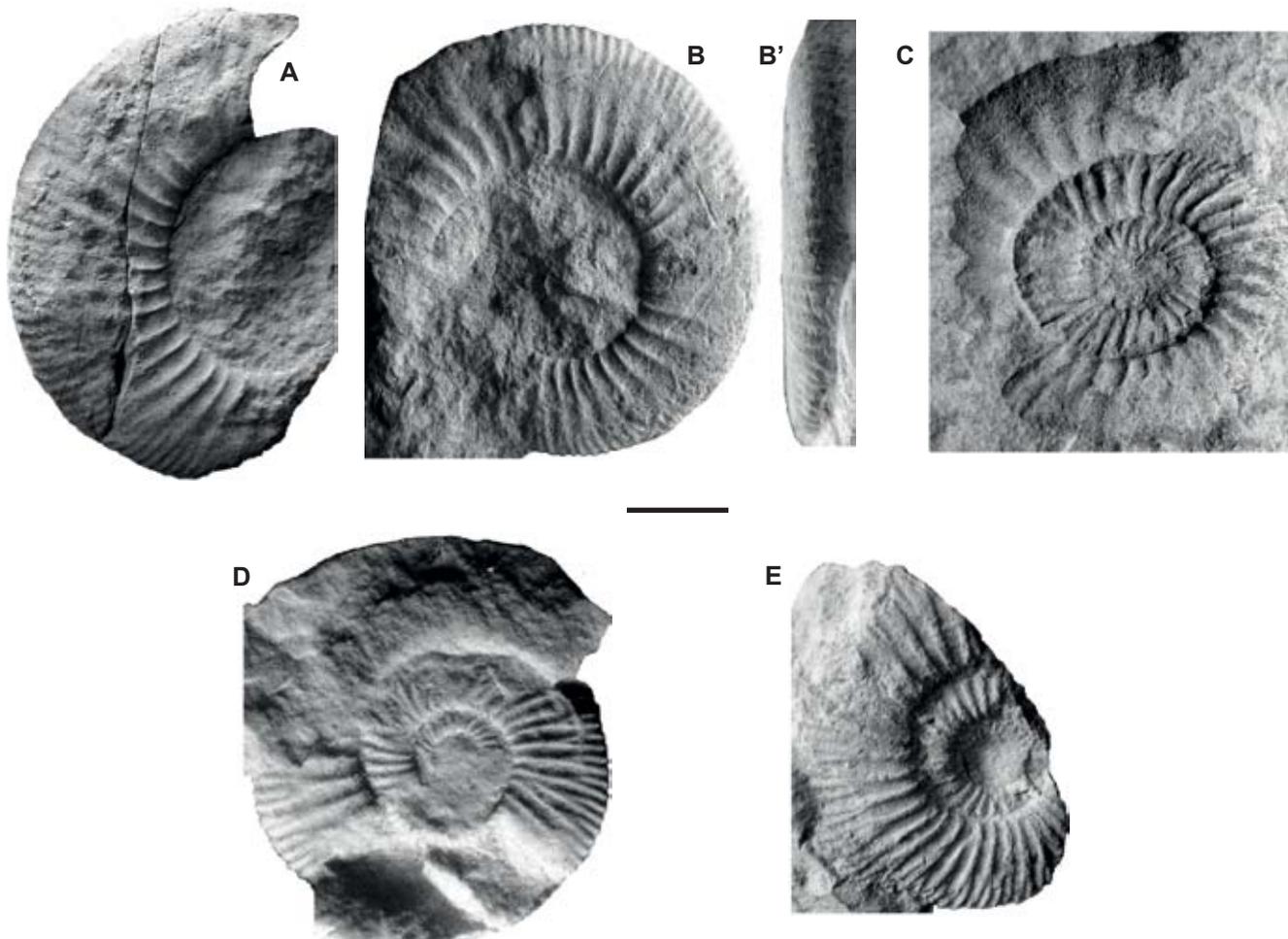


Fig. 4. *Moravisphinctes fischeri* (Kilian)

A. MPP-CHT.14/22. B-B': MPP-CHT.14/8. C. MPP-CHT.14/14. D: MPP-CHT.17/9. E. MPP-CHT.14/25. Bar scale is 1 cm

Material. – MPP-CHT.3/2, MPP-CHT.9/6, MPP-CHT.12/1, MPP-CHT.12/5, MPP-CHT.12/10, MPP-CHT.12/12, MPP-CHT.14/14, MPP-CHT.14/7, MPP-CHT.14/23, MPP-CHT.14/29, MPP-CHT.15/11, MPP-CHT.17/7, MPP-CHT.17/9.

Description. – Small-sized planulate ammonites ($D_{max} < 56$ mm) with a compressed and evolute shell ($0.4 < U/D < 0.46$). The whorl section is subelliptical with slightly convex flanks and rounded venter. On the inner whorls, the ornamentation is mainly composed of prominent, prorsiradial ribs that bifurcate on the upper third of the flanks. At a later stage, the ornamentation is marked by a high number of virgatotome ribs. On our most complete specimens, the ornamentation fades on the mid flank of the body chamber. All ribs cross the venter.

Remarks. – Cecca *et al.* (1989, p. 61–62) provide a revised diagnosis of *M. fischeri* based on a large population from the historical area of the Ardésien (Ardèche, SE France). Our material shows a similar morphological variability and the specimen MPP-CHT.14/14, characterized by numerous virgatotome ribs, is close to the extreme morphology of *M. fischeri* figured by Cecca *et al.* (1989, pl. 2: 12–13) and Tavera (1985, pl. 14: 10). When well preserved, *M. fischeri* shows a distinct lappeted peristome, and at Le Chouet, the stratigraphical distributions of *Moravisphinctes* and *Paraulacosphinctes* are identical. This would support the view of Cecca *et al.* (1989) and Parent (2003) who proposed sexual dimorphism between the two genera. However, as already outlined by Cecca *et al.* (1989), the boundary between *Paraulacosphinctes* and its allied microconch

genera, such as *Moravispinctes* and *Andaluspinctes* Tavera, 1985, remains largely unclear. Unfortunately, the material from Le Chouet is too fragmentary to allow us to further discuss this problem.

Stratigraphical distribution. – Upper Tithonian, beds 66, 67, 68, 71, 73, 74, 76, 78 and 79, Microcanthum Zone, Fischeri Subzone, and base of the Andreaei Zone (Crassicollaria calpionellid Zone, uppermost part of the Remanei Subzone and Intermedia Subzone). Besides SE France, there is no doubt that *M. fisheri* also occurs in Spain, Tunisia and Morocco, and the species has also been reported from Italy (see synonymy in Cecca *et al.*, 1989).

Family **Himalayitidae** Spath, 1925

Genus *Micracanthoceras* Spath, 1925

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

Remarks. – According to Nikolov (1982, p. 213), the specimen illustrated by Zittel (1868, pl. 17: 3a, b) was designated as the type specimen of *Micracanthoceras microcanthus* by Spath (1925). Even if the footnote in Spath (1925, p. 144) is not fully explicit regarding the designation of a type specimen, the same author (Spath, 1931, p. 544) clearly refers to this specimen as the lectotype of *M. microcanthus*. As a consequence the designation of a different type specimen by Mazenot (1939, p. 233–234) is invalid according to Art. 61 of the ICZN.

It should be noted that the original diagnosis and description of *M. microcanthus* is composite and based on a juvenile (the lectotype), a large adult and a third specimen only known by its suture line. According to Spath (1931, p. 544), Mazenot (1939, p. 233) and Cecca *et al.* (1989, p. 65), all three specimens are conspecific, whereas Tavera (1985, p. 169) considers that the larger specimen (Zittel, 1868, pl. 17: 1a, 2) is a *Himalayites* sp.

In recent years, Tavera's opinion has prevailed (see Cecca *et al.*, 1989; Benzaggagh, Atrops, 1997; Benzaggagh, 2000; Boughdiri *et al.*, 2005) and the understanding of *M. microcanthus* has been based on the juvenile morphology of the lectotype and its accepted variability illustrated by additional Spanish material. As a consequence, the genus *Micracanthoceras* has been defined as follows: “widely umbilicate forms, with fine and dense ornamentation of single, bifurcate and sometimes trifurcate ribs, marked by a tubercle at the furcation point, and there can be a second row of tubercles on the outer flanks” (according to Tavera, 1985).

Most recently, the designation of the lectotype of *Ammonites koellikeri* Oppel, 1865 by Parent *et al.* (2011, p. 72:

32A) sheds new light on the content of *Micracanthoceras* and its relationships with the European taxa most often referred to *Corongoceras* Spath, 1925. We agree with those authors that the juvenile ontogenetic stages of *Ammonites koellikeri* are very close to those of *M. microcanthus* and that the two species should be placed in the same genus. Moreover, as far as one can tell from Mazenot's illustration (1939, pl. 37: 12a, b), the ontogenetic development of Oppel's larger specimen of *M. microcanthus* is very similar to that of the lectotype of *M. koellikeri*. Another closely allied species is *Ammonites fraudator* Zittel, 1868, attributed to *Micracanthoceras* by Spath (1931, p. 545). We accept this view, also held by Sapunov (1979), who selected as lectotype the specimen illustrated by Zittel (1868, pl. 21: 2a, b).

According to Tavera (1985, p. 176), *Corongoceras* is a subgenus of *Micracanthoceras*, both taxa being linked by intermediate forms, and the two morphological extremes within this group are represented by *M. microcanthus* and *C. symbolum* (Oppel, 1865). Most recently, Parent *et al.* (2011) showed that *Corongoceras* should be restricted to a limited number of Andean species (see also discussion below in the *Ardesciella* paragraph). As a consequence, the taxonomy of the European species of *Corongoceras* is open again to discussion. Re-examination of the material illustrated by Tavera (1985) shows that the great majority of the specimens that this author includes in *Corongoceras* are characterized by typical *Micracanthoceras* juvenile ornamentation. Moreover, there is no significant difference between the adult ornamentation of the larger specimens (such as *C. symbolum* in Tavera, 1985, pl. 24: 1a, b) and that of *M. koellikeri*, or the larger specimens in the type series of *M. microcanthus*. In our opinion, with the exception of *C. hispanicum* Tavera, 1985 (that we include in *Ardesciella*), all *Corongoceras* illustrated by Tavera should be transferred to *Micracanthoceras*. This is reflected by the synonymy of *M. microcanthus* given below.

It is most often assumed that *Micracanthoceras* is a cosmopolitan genus (Cecca, 1999). We regard this view as requiring reconsideration, since the South American reports were reassigned by Parent *et al.* (2011) to *Blanfordiceras* Cossmann, 1907, and *Steueria* Parent, Scherzinger and Schweigert, 2011. Similarly, the taxonomy of *Micracanthoceras* from Mexico described by Imlay (1939) remains unclear. In our opinion, only a limited number of specimens from outside Europe truly belong to *Micracanthoceras*, and we provisionally retain only *Micracanthoceras brightoni* Spath, 1931 (see also Shome, Bardhan, 2009) and the closely related forms described from Madagascar by Collignon (1960, pl. 175: 754–757) as members of the genus.

Micracanthoceras sp. juv. gr. *microcanthum*
(Oppel, 1865)

1865. *Ammonites microcanthus* n. sp. Oppel, p. 155.
 1868. *Ammonites microcanthus* Oppel in Zittel, p. 93, pl. 17: 1–5.
 1890. *Hoplites microcanthus* (Oppel in Zittel): Toucas, p. 608, pl. 18: 12.
 1939. *Himalayites* (*Micracanthoceras*) *microcanthum* (Oppel in Zittel): Mazenot, p. 233, pl. 37: 2 a, b (= Toucas, 1890, pl. 18: 12), 3, 12a, b (= Zittel, 1868, pl. 17: 1a, 2).
 1966. *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel in Zittel): Linares et Vera, pl. 5: 2a, b (sol.).
 1977. *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel in Zittel): Sapunov, pl. 5: 3.
 1979. *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel in Zittel): Sapunov, p. 193, pl. 58: 4 (= Sapunov, 1977, pl. 5: 3).
 1982. *Himalayites* (*Micracanthoceras*) *microcanthus* (Oppel in Zittel): Nikolov, p. 213, pl. 77: 1 (= Sapunov, 1977, pl. 5: 3).
 1985. *Micracanthoceras* (*Micracanthoceras*) *microcanthum* (Oppel in Zittel): Tavera, p. 169–174, pl. 21: 1–4; pl. 22: 1–6, text-fig. 13A–E, G.
 1985. *Micracanthoceras* (*Micracanthoceras*) cf. *brightoni* (Spath): Tavera, p. 175, pl. 21: 5, text-fig. 13F.
 1985. *Micracanthoceras* (*Corongoceras*) *rhodanicum* Mazenot: Tavera, p. 180, pl. 22: 7, 8a, b, 9a, b, text-fig. 14D.
 1985. *Micracanthoceras* (*Corongoceras*) *flexuosum* n. sp. Tavera, p. 187, pl. 23: 6 (sol.).
 1985. *Micracanthoceras* (*Corongoceras*) *leanzai* n. sp. Tavera, p. 192, pl. 25: 5 (sol.).
 1989. *Micracanthoceras microcanthum* (Oppel in Zittel): Cecca *et al.*, p. 65, pl. 1: 3; 4a, b.
 1995. *Micracanthoceras microcanthum* (Oppel in Zittel): Eliáš et Vašíček, pl. 1: 4.
 1997. *Micracanthoceras microcanthum* (Oppel in Zittel): Benzagagh et Atrops, pl. 5: 3.
 1997. *Micracanthoceras microcanthum* (Oppel in Zittel): Geyssant in Cariou et Hantzpergue, pl. 26: 1 (= Zittel, 1868, pl. 17: 3a, b).
 2000. *Micracanthoceras microcanthum* (Oppel in Zittel): Benzagagh, pl. 4: 4.
 2005. *Micracanthoceras* sp. gr. *microcanthum* (Oppel in Zittel): Boughdiri *et al.*, pl. 2: 9, 10.

Material. – MPP-CHT.-12b/1, MPP-CHT.-12b/2, MPP-CHT.-12b/3; MPP-CHT.-13/2, MPP-CHT.-13/3, MPP-CHT.-13/4, and a loose specimen MPP-CHT-?10/1.

Description. – The poor quality of our material does not allow the definite attribution of these specimens to *M. microcanthum*, even considering that the evolute coiling and low umbilicus of our specimens matches the Spanish specimens well. The whorl section is circular, with straight and rigid ribs, bifurcate or sometimes simple. Tubercles at the furcation point are sporadic from one specimen to another. They are more regular on specimen MPP-CHT.-13/2 and occur at a smaller diameter. Specimen MPP-CHT.-12/1 shows

a weakly differentiated ventral band bordered by thin ribs on the shoulders.

Stratigraphical distribution. – Upper Tithonian, spot occurrences from beds 50 to 73, Microcanthum Zone (Crassicollaria calpionellid Zone, Remanei Subzone to top of Intermedia Subzone). The report from the Andreaei Zone by Wimbledon *et al.* (2013, fig. 12) is based on the misidentification of *Toucasiaella gerardi* Enay *et al.*, 1998b. The specimen will be illustrated in a forthcoming paper (Frau *et al.*, submitted)

Genus *Ardesciella* gen. nov.

Derivation of name: from *Ardèche*, a French department, where the historical Tithonian substage called the Ardeskien was defined by Toucas (1890), and since revised by Cecca *et al.* (1989).

Type species: *Himalayites* (?*Corongoceras*) *rhodanicum* Mazenot, 1939.

Diagnosis. – Small to middle-sized serpenticone ammonite, with regular and slow increase of the Wh/D ratio. Wide and low umbilicus. Rounded whorl section at juvenile stages, becoming subrectangulate to subquadrate at adult stages. Strongly convex flanks, rounded umbilical shoulder with a vertical and low umbilical wall. Ventral region characterized by a clear ventral furrow that is weakly attenuated in the adult ontogenic stage. Ornamentation composite with straight, rigid, slightly prorsiradiate, single or bifurcate ribs. Bifurcations develop from punctiform tubercles situated on the upper third of the whorl. On the adult stage, ornamentation tends to lose rigidity and to become slightly flexuose and rursiradiate toward the umbilical margin. The angle of bifurcation of the ribs is marked. On the ventral shoulder, most ribs thicken radially into elongated bullae that delimit the ventral furrow. Rarely ribs weaken where they cross the ventral area. Suture line unknown.

Remarks. – Parent *et al.* (2011, p. 70) pointed out that *Corongoceras* had been used to accommodate innumerable ammonites from the Tethyan Realm. Considering the limitations imposed by the type species, we accept a concept of the genus that restricts *Corongoceras* to Andean, Mexican and Caribbean forms such as *C. lotenoense* (Spath, 1925, type species), *C. mendozanum* (Behrendsen), and, doubtfully, *C. steinmanni* (Krantz) and *C. filicostatum* Imlay. We also agree that, for the time being, the multitude of typological names introduced by Collignon (1960) for the Madagascar forms, some of which are considered as synonyms of *C. mendozanum* by Parent *et al.* (2011, p. 70), should be retained in *Corongoceras*. As already discussed above, the great majority of specimens referred to *Corongoceras* in Europe belongs to *Micracanthoceras*.

The juvenile growth stages of *Corongoceras sensu* Parent *et al.* (2011) is similar to those observed in *Ardesciella*, but it can be easily distinguished by its lower number of whorls, lower whorl height and more numerous rigid ribs at the adult stage. Regularity of bifurcation and intercostal spaces are more marked in *Corongoceras* than in *Ardesciella*.

Micracanthoceras and *Ardesciella* show strong affinities. Nevertheless, *Micracanthoceras* is a homogeneous group with well-expressed serpenticone coiling, a wide umbilicus and very dense ribbing – characters that never occur in *Ardesciella*. The sub-circular and depressed whorl section, the irregularity of tuberculation, and the lower point of bifurcation on the flanks allow easy distinction from *Ardesciella*. The ventral band is also always less marked in *Micracanthoceras*.

Generic content. – *Ardesciella rhodanica* (Mazenot, 1939) (type species) and *Ardesciella hispanica* (Tavera, 1985).

Stratigraphical and geographical distribution. – When reliably dated the genus is restricted to the Late Tithonian (Microcanthum and Andreaei Zones) of the Mediterranean Tethys (SE Spain, SE France, Algeria, and Morocco).

Ardesciella cf. rhodanica (Mazenot, 1939)

Fig. 5A–B

1890. *Hoplites Koellikeri* Oppel: Toucas, p. 607, pl. 18: 11a, b.
 1936. *Himalayites (Corongoceras) Kollikeri* (Oppel): Roman, p. 27, pl. 4: 19, 19a, 20.
 1939. *Himalayites (Corongoceras) rhodanicus* n. sp. Mazenot, p. 230, pl. 37: 1a, b, 5a, b (= Toucas, p. 607, pl. 18: 11a, b), 7a–c, 8a–b, 9a–b.
 1953. *Himalayites (Corongoceras) rhodanicus* Mazenot: Arnould-Saget, p. 16, pl. 2: 1a–c, 2a–c.
 ? 1953. *Himalayites (Corongoceras) cf. rhodanicus* Mazenot: Arnould-Saget, p. 16, pl. 2: 5a–c.
 non 1966. *Himalayites (Corongoceras) rhodanicus* Mazenot: Linares et Vera, pl. 6: 3.
 1982. *Corongoceras (Corongoceras) rhodanicum* (Mazenot): Nikolov, p. 214, pl. 78: 1a–c (=Mazenot, 1939, p. 230, pl. 37: 7a–c), ?2.
 non 1985. *Corongoceras rhodanicus* Mazenot: Cecca, p. 144, pl. 1: 2. (= *Protacanthodiscus* sp.).
 non 1985 *Micracanthoceras (Corongoceras) rhodanicum* Mazenot: Tavera, p. 180, pl. 22: 7, 8a, b, 9a, b; text-fig. 14D. (= *Micracanthoceras microcanthum*).
 1997. *Micracanthoceras (Corongoceras) rhodanicum* (Mazenot): Benzaggagh et Atrops, p. 153, pl. 6: 2, ?5.
 2000. *Micracanthoceras (Corongoceras) rhodanicum* (Mazenot): Benzaggagh, pl. 4: 3. (= Benzaggagh et Atrops, 1997, pl. 6: 2).

Material. – MPP-CHT.21/12 and MPP-CHT.21/68.

Description. – Specimen MPP-CHT.21/68 is an incomplete juvenile phragmocone that shows the typical charac-

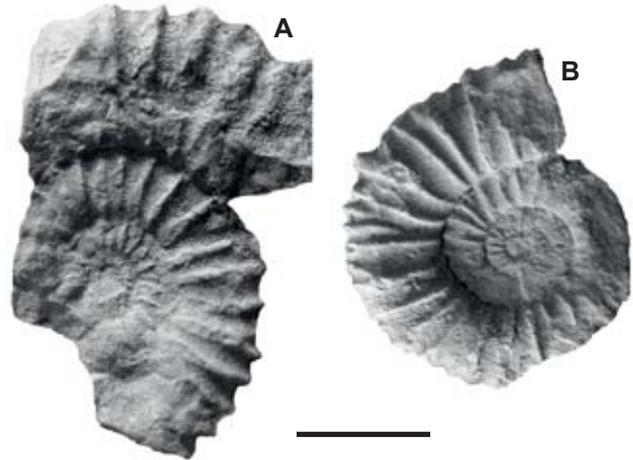


Fig. 5. *Ardesciella cf. rhodanica* (Mazenot)

A. MPP-CHT.21/12. B. MPP-CHT.21/68. Bar scale is 1 cm

ters seen in the type specimen of *Ardesciella*. It matches well Mazenot's holotype (1939) in its small size and irregular ornament. The second specimen (MPP-CHT.21/12) is a complete juvenile that shows perfectly two successive ontogenetic stages. Compared to the first specimen, its rib density is higher, with rare single intercalatory ribs. Ornamentation is coarser and it rises sharply towards the venter, with 'pinched' ventro-lateral tubercles.

Stratigraphical and geographical distribution. – Our specimens were collected from bed 85, Andreaei Zone (Crassicollaria Zone, lower part of the Colomi Subzone). The type series of *A. rhodanica* illustrated by Mazenot (1939) originated from the "Brèche d'Aizy" and the "Brèche de Chomérac". The ammonite assemblage of these lithostratigraphic units is dominated by Early Berriasian ammonites, but also contains reworked material from older strata (see discussion in Cecca *et al.*, 1989, p. 56). In Morocco, the species has been reported as ranging throughout the *M. microcanthum* Zone, where it co-occurs with *A. hispanica* (see fig. 8 in Benzaggagh, Atrops, 1997). As the species is understood herein, *A. rhodanica* is known to occur in SE France, Algeria, Morocco and, questionably, in Bulgaria.

Genus *Pratumidiscus* nov. gen.

Derivation of name: From *pratum*, latin for Les Près, near where the Le Chouet section is located.

Type species: *Pratumidiscus elsae* gen. nov., sp. nov.

Locus typicus: Le Chouet, Les Près, Drôme.

Diagnosis: Shell small, compressed with a wide and low umbilicus. Whorl section subquadrate to subrectangulate, with

weakly convex flanks and tabulate venter. Complex and irregular ornamentation composed of single, bifurcate, intercalatory and simplified virgatotome ribs. All ribs thicken on the ventral shoulder in radially elongated bullae that delimit the ventral groove. Suture line is unknown.

Stratigraphical and geographical distribution: Andreaei Zone (Crassicollaria calpionellid Zone, top of the Intermedia Subzone). For the time being, the genus is monotypic and known by a single specimen from the type locality.

Pratumidiscus elsae gen. nov. sp. nov.

Fig. 6

2013. ?*Riasanites* sp., Wimbledon *et al.*, p. 451, fig. 12.

Derivation of name: Dedicated to Elsa Schnebelen-David for her participation to our latest field trip at Le Chouet and continuous support to one of us (LGB) during the preparation of this work.

Holotype: MPP-CHT.19/5.

Type locality: Le Chouet, commune de Les Près, Drôme.

Stratigraphical distribution: Bed 83, Andreaei Zone (Crassicollaria calpionellid Zone, top of the Intermedia Subzone), Upper Tithonian.

Diagnosis: As for the genus.

Description. – The holotype is a small ($D_{max} < 45\text{mm}$), almost complete, specimen. The umbilicus is wide and open, with a U/D ratio of 0.31. The whorl section of the inner whorls is subquadrate with prominent, distant primary ribs

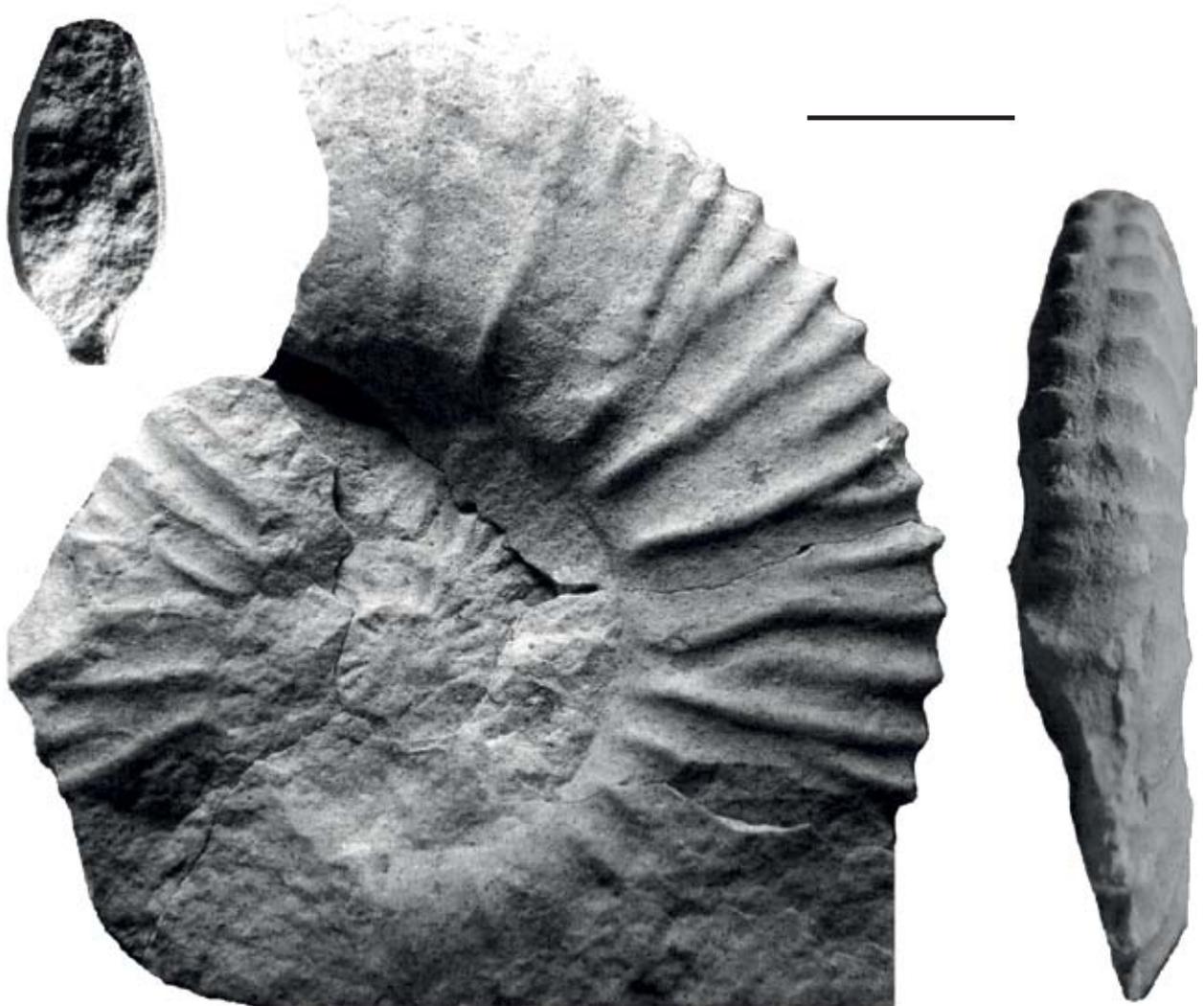


Fig. 6. *Pratumidiscus elsae* gen. nov. sp. nov.

Lateral, ventral and whorl section of MPP-CHT.19/5. Bar scale is 1 cm

that recall juvenile Himalayitidae morphology. At later shell growth stages, the whorl section is almost subrectangular with weakly convex flanks and a tabulate venter. The umbilical wall gets slightly steeper. The ornamentation is marked by the complex and irregular alternation of simple, bifurcate, intercalated and simplified virgatotome ribs. Bifurcations occur at different heights, but most often just above the middle of the flank. The intercostal space varies greatly. On the last whorl, the primary ribs are more prominently developed above the umbilical shoulder. The venter is marked by a ventral groove delimited by the interruption and strengthening of the ribs.

Remarks. – Originally, *Pratumidiscus elsae* gen. nov. sp. nov. was reported by Wimbledon *et al.* (2013) as a potential representative of the Boreal genus *Riasanites* Spath. The juvenile ornamentation of Russian *Riasanites*, e.g. *R. rjasanensis* (Nikitin) and *R. swistowianus* (Nikitin) (see Nikitin, 1888), is also complex and composed of irregular single, bifurcated, intercalatory, and tripartite ribs (see for example Mita, 2008, pl. 5: 5). However, *P. elsae* can easily be distinguished from the type species of *Riasanites* by its ventral groove and the smaller umbilicus on the body chamber.

Mitta (2011) suggested that *Riasanites* originated from closely related forms that he included in his new genus *Riasanella*. The latter differs from *Riasanites* in its adult whorl section, which converges strongly towards the venter. The general morphology of *Riasanella* recalls that of *Pratumidiscus* in having elevated ventral shoulders and a narrow ventral groove, but differs in its subtrapezoidal whorl section, umbilical nodes and ventral chevron on the body chamber. It should be noted that Mita (2007, 2011) proposed a western Tethyan origin for the *Riasanites* – *Riasanella* plexus from an unknown Tithonian taxon. *Pratumidiscus* gen. nov. could be considered as such a potential ancestor.

Family **Neocomitidae** Salfeld, 1921

Remarks. – We fully agree with Company (1987, p. 103 and fig. 42), that the subdivision of the Neocomitidae into three subfamilies (e.g. Berriasellinae Spath, Neocomitinae Salfeld and Endemoceratinae Schindewolf) is artificial and not supported by any phylogenetic arguments. As a consequence, we consider that these subdivisions add to the state of chaos of the Neocomitidae taxonomy and should be abandoned.

Genus *Pseudargentinicer* Spath, 1925

Type species. – *Ammonites abscissus* Oppel in Zittel, 1868; by original designation of Spath (1925, p. 145).

Remarks. – It should be noted that Spath (1925, p. 145) is not fully explicit regarding the designation of the specimen illustrated by Zittel (1868, pl. 19: 4a–c) as the lectotype

of *Ammonites abscissus*. As a consequence, Mazenot (1939, see footnote 1, p. 35 and p. 105–106) formally designated as lectotype the specimen figured by Zittel (1868, pl. 19: 1a–b) on which the original diagnosis was based. Both specimens were re-illustrated by Mazenot (1939, pl. 15: 1, 3) and seem to be conspecific (Le Hégarat, 1973; Nikolov, 1982; Tavera, 1985).

Beside *P. abscissum*, the specific content of *Pseudargentinicer* is composed of *P. flandrini* Le Hégarat, 1973 and *P. benecke* (Mazenot, 1939). The general morphology of *P. flandrini* perfectly matches *Pseudargentinicer*. However, according to Le Hégarat (1973), it can be distinguished by its less angular section, finer and more sinuous ribbing, and early disappearance of the ventral groove. Unfortunately, this last feature has never been illustrated in the literature.

P. benecke is a species of difficult of interpretation (Nikolov, 1982, p. 208). According to Le Hégarat (1973), attribution of this taxon to *Pseudargentinicer* is based on its rounded section, moderately open umbilicus, fasciculate ribs and ventral band. The cast of the type specimen before us shows a narrow umbilicus (U/D = 0.20), a sub-rectangular section overhanging umbilical wall and a high rib density. These characters suggest that *P. benecke* does not belong to *Pseudargentinicer*, but is closely allied to the plexus of *Pseudoneocomites allobrogensis* (Mazenot, 1939) – *suprajurensis* (Mazenot, 1939), as already suggested by Sapunov (1979).

?*Pseudargentinicer* sp.

Fig. 7

1985. *Substeueroceras* sp. Tavera, p. 327, pl. 33: 1, 2.

1989. *Substeueroceras* sp. Olóriz et Tavera, p. 232, fig. 2: 1a, b.

Material. – MPP-CHT.14/17

Description. – ?*Pseudargentinicer* sp. is represented by an almost complete specimen. It is a middle-sized planulate ammonite (estimated Dmax = 70 mm) with a large and shallow umbilicus (U/D = 0.39). The innermost whorls are not preserved. The whorl section is elevated and suboval, but its exact shape is difficult to estimate due to the preservation. On the visible part of the phragmocone, the ornamentation is composed of fine, dense and radial bifurcate ribs which cross the venter. The bifurcation occurs on the upper third of the flank. On the body chamber, the pattern of the ornament changes to an irregular alternation of long bifurcate and short secondary ribs. All ribs are blunt, spaced and cross the venter, and they develop long bullae above the umbilical shoulder.

Remarks. – According to the literature (Le Hégarat, 1973; Tavera, 1985), *Pseudargentinicer* is known from the Upper Tithonian and Lower Berriasian (A and B calpionellid Zones). The type material and the Spanish speci-

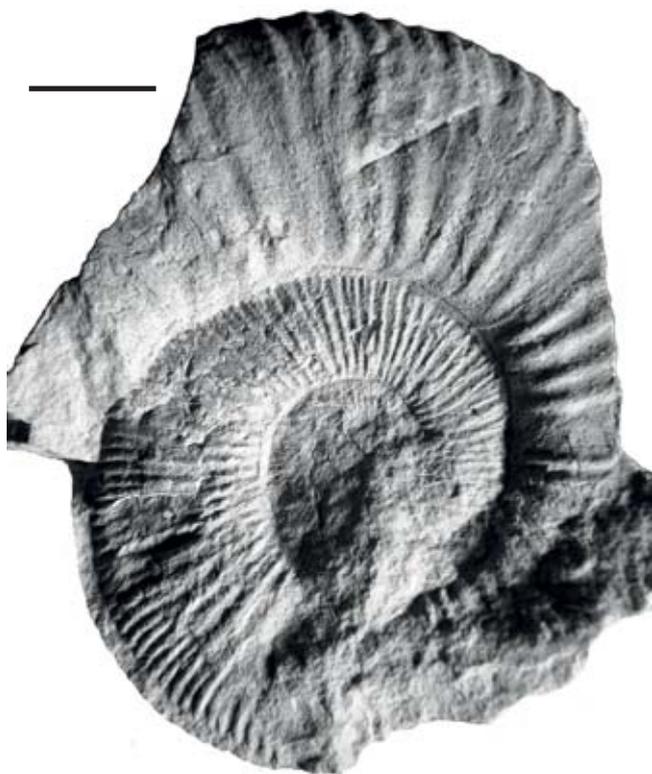


Fig. 7. *?Pseudargentinicerias* sp.

Lateral view of MPP-CHT.14/17. Bar scale is 1 cm

mens of *P. abscissum* illustrated by Tavera (1985, pl. 42: 1, 2) show the succession of ornamental stages observed on our specimen. The only difference is the presence of a smooth ventral band whose extension on the body chamber seems to vary from one specimen to the other.

Moreover, the two incomplete specimens attributed to *Substeuerocheras* sp. and illustrated by Tavera (1985, p. 232, fig. 2: 1a, b) and Olóriz, Tavera (1989, fig. 2: 1a) from the Late Tithonian of Spain perfectly match the phragmocone of the Le Chouet specimen in their ornamentation and in the absence of a ventral band.

Therefore, two groups of ammonites with *Pseudargentinicerias* ornament occur at the Tithonian-Berriasian transition in the Mediterranean region. They can only be distinguished by the presence or absence of a smooth ventral band, and its persistence on the phragmocone. Whether both groups should be included in the same genus or be kept in separate taxa depends on the taxonomic value one gives to the ventral morphology.

This problem also addresses the origin of the Neocomitidae. According to Tavera (1985, p. 78), the origin of the Neocomitidae is to be found in *Paraulacosphinctes* and its closely allied taxa. This is based on the fact that in its origi-

nal conception, *Paraulacosphinctes* is based on perisphinctids with a smooth ventral band. However, the last *Paraulacosphinctes* of the *P. senoides* group found at Le Chouet may represent the direct ancestor of *?Pseudargentinicerias* sp., since both forms are characterized by the absence of a ventral band at late ontogenetic stages. This is also the case of several specimens of the *Paraulacosphinctes* – *Olorizicerias* plexus figured by Tavera (1985). As a consequence, the suprageneric attribution of *Pseudargentinicerias abscissum*, *P. flandrini* and *?Pseudargentinicerias* sp. remains unclear.

Stratigraphical distribution. – Upper Tithonian, bed 79 of the Andreaei Zone (Crassicollaria calpionellid Zone, top of the Intermedia Subzone). This is consistent with the age of the Spanish specimens which we feel have been misidentified as *Substeuerocheras* sp. by Tavera (1985) and Olóriz, Tavera (1989).

Genus *Busnardoicerias* Tavera, 1985

Type species: *Parapallasicerias busnardoii* Le Hégarat, 1973, by original designation.

Remarks: Originally included in *Parapallasicerias* Spath, 1925 by Le Hégarat (1973), the species *P. busnardoii* Le Hégarat, 1973 and *P. bochianensis* (Mazenot, 1939) were transferred to the new subgenus *Berriasella* (*Busnardoicerias*) by Tavera (1985). In our opinion, *Busnardoicerias* is a member of the Neocomitidae that deserve the rank of a genus. It has no phylogenetic link with the Early Tithonian perisphinctid genus *Parapallasicerias sensu* Zeiss (1968) and Cecca, Enay (1991).

Busnardoicerias busnardoii (Le Hégarat, 1973)

Fig. 8A–F

1939. *Berriasella ciliata* Schneid: Mazenot, p. 37, pl. 1: 1a, b (sol.).

1973. *Parapallasicerias busnardoii* Le Hégarat, p. 47, pl. 3: 4, 5 (= Mazenot, 1939, pl. 1: 1a, b), ? pl. 38: 2.

2001. *Parapallasicerias busnardoii* Le Hégarat: Wippich, p. 78, pl. 20: 2.

Material. – MPP-CHT.19/20, MPP-CHT.19/28, MPP-CHT.19/32, MPP-CHT.19/36, MPP-CHT.21/14, MPP-CHT.21/24, MPP-CHT.21/42, MPP-CHT.21/56, MPP-CHT.21/59, MPP-CHT.21/60, MPP-CHT.21/66.

Description. – Middle-sized planulate ammonites (Dmax < 76 mm) with high and compressed whorl section, and moderately evolute shallow umbilicus (0.37 < U/D < 0.40). On the phragmocone, the ornamentation is mainly composed of straight to slightly prorsiradiate, bifurcate ribs. The bifurcation occurs on the upper third of the flanks. On the body chamber, the ornamentation is composed of 55 to 60 slightly sinuous ribs and marked by the irregular intercalation of virgatotome and simple ribs. Ribbing is interrupted on the ventral shoulders, delimiting a shallow groove.

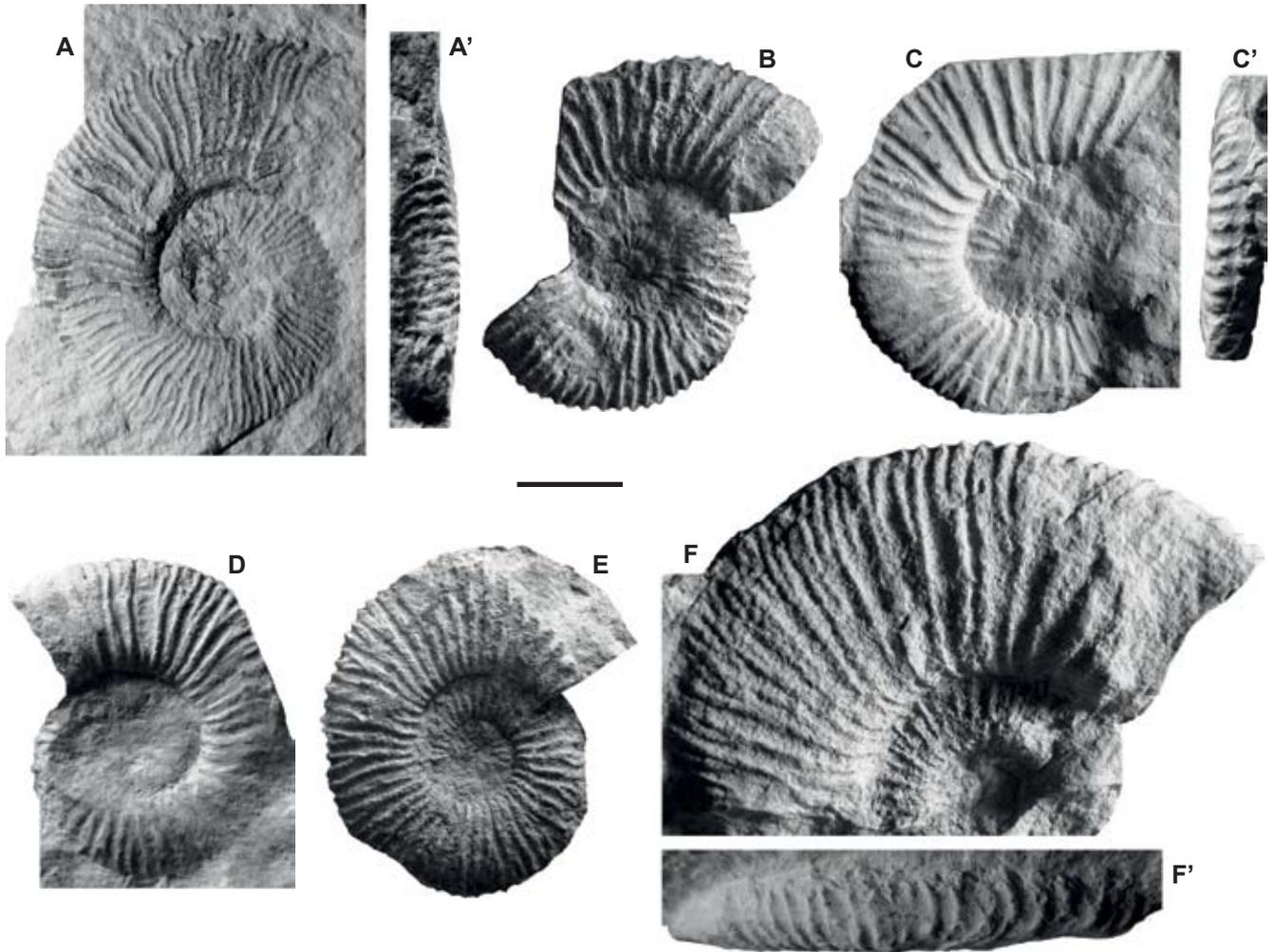


Fig. 8. *Busnardoiceras busnardoii* (Le Hégarat)

A–A'. MPP-CHT.21/44. B. MPP-CHT.21/59. C–C'. MPP-CHT.19/28. D. MPP-CHT.21/66. E. MPP-CHT.21/60. F–F'. MPP-CHT.21/56. Bar scale is 1 cm

Remarks and stratigraphic implications. – According to Le Hégarat (1973), *B. busnardoii* is strictly limited to the Lower Berriasian (Jacobi Zone *sensu* Hoedemaeker, Bulot, 1990). Nevertheless, the exact stratigraphic position of the four specimens used by Le Hégarat (1973, p. 47–48) is not documented. Among them, the holotype was collected from the “*Brèche d’Aizy*”, as stated, a lithostratigraphic unit that contains a mixture of reworked Tithonian elements in an assemblage dominated by ammonites from the Jacobi Zone. Outside SE France, the only specimen ever attributed to *B. busnardoii* is an isolated specimen from Morocco whose stratigraphic position is not well calibrated. Therefore the exact range of *Busnardoiceras* is not established.

At Le Chouet, *B. busnardoii* is represented by a large population that co-occurs with *P. andreaei*. Within the Le Chouet population, several larger complete specimens ex-

hibit body chambers with prominent ribs that cross the venter (see for example fig. 8C). These forms, herein considered as the adult macroconchs, are almost identical to true *Pseudosubplanites*, such as *P. berriasensis* Le Hégarat, 1973. In *Pseudosubplanites*, the ribs cross the venter throughout ontogeny, whereas this character is restricted to the body chamber on the macroconchs of *Busnardoiceras*. In our opinion, *Pseudosubplanites* may have derived from *Busnardoiceras* by a peramorphic change. New material from Le Chouet and Les Combes (Glandage, Drôme) strongly suggests that this anagenetic speciation occurred in the lower part of the Jacobi Zone (C. Frau, L. Bulot, W.A.P. Wimbledon, unpublished data).

Stratigraphical distribution. – Upper Tithonian, beds 83, 84 and 85, Andreaei Zone (Crassicollaria calpionellid Zone, Colomi Subzone). The Berriasian specimen figured by Le

Hégarat (1973, pl. 38: 2) does not show the ventral area and could either be a *B. busnardoï* or a *P. berriasensis*. Based on the description of the specimen, the occurrence in Morocco (Wippich, 2001) is accepted, even though the ventral area of the specimen was not illustrated.

CONCLUSIONS

Based on bed by bed collections from the upper part of the Late Tithonian at Le Chouet (Drôme, SE France), the high stratigraphic value and precise distribution of *Paraulacosphinctes senoides*, *Moravispinctes fisheri* and *Micracanthoceras microcanthum* already documented in Spain and Morocco are confirmed. In addition, the occurrence of the reputedly Berriasian neocomitid genera *Busnardoiceras* and *Pseudargentinoceras* in the Andreaei Zone (Late Tithonian) is established for the first time.

Two new genera are introduced: *Ardesciella* gen. nov., for Mediterranean himalayitids that are homoeomorphic with the Andean genus *Corongoceras*, and *Pratumidiscus* gen. nov. for a taxon that may represent the rootstock of the Boreal Berriasian genera *Riasanites*.

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