Acta Geologica Polonica, Vol. 66 (2016), No. 2, pp. 175–204
DOI: 10.1515/agp-2016-0008

Systematic palaeontology of the Perisphinctoidea in the Jurassic/Cretaceous boundary interval at Le Chouet (Drôme, France), and its implications for biostratigraphy

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ABSTRACT:

Frau, C., Bulot, L.G., Wimbledon, W.A.P. and Ifrim, C. 2016. Systematic palaeontology of the Perisphinctoidea in the Jurassic/Cretaceous boundary interval at Le Chouet (Drôme, France), and its implications for biostratigraphy *Acta Geologica Polonica*, **66** (2), 175–204. Warszawa.

This study describes ammonite taxa of the Perisphinctoidea in the Jurassic/Cretaceous boundary interval at Le Chouet (Drôme, France). Emphasis is placed on new and poorly known Himalayitidae, Neocomitidae and Olcostephanidae from the lower part of the Jacobi Zone *auctorum*. Significant results relate the introduction of *Lopeziceras* gen. nov., grouping himalayitid-like forms with two rows of tubercles, and *Praedalmasiceras* gen. nov., grouping the early Berriasian *Dalmasiceras* taxa. Study of the ontogenetic sequences of both genera show that they were derived from late Tithonian Himalayitidae. This supports the distinction between the subfamilies Himalayitinae and Dalmasiceratidae subfam. nov. Content, variation, dimorphism and vertical range of the Neocomitidae *Berriasella*, *Pseudoneocomites*, *Elenaella* and *Delphinella* are discussed. A conservative use of the Olcostephanidae *Proniceras* is followed herein.

Keywords: Ammonites; Berriasian; Cretaceous; Biostratigraphy; Le Chouet; France.

INTRODUCTION

This contribution completes the systematic description of the ammonite faunas collected across the Jurassic/Cretaceous boundary at Le Chouet (Les Près, Drôme, southeast France) as part of the work of the Berriasian Working Group of the International Subcommission on Cretaceous Stratigraphy (I.S.C.S, I.U.G.S.). Previous articles (Bulot *et al*. 2014; Frau *et al*. 2015) concentrated on the families Ataxioceratidae Buckman, 1921, Himalayitidae Spath, 1925 and the first representatives of the Neocomitidae Salfeld, 1921 from the upper Tithonian. Herein we focus on the Perisphinctoidea taxa that were originally reported by Wimbledon *et al*. (2013) from the Jacobi Zone *auctorum*.

GEOLOGICAL SETTING

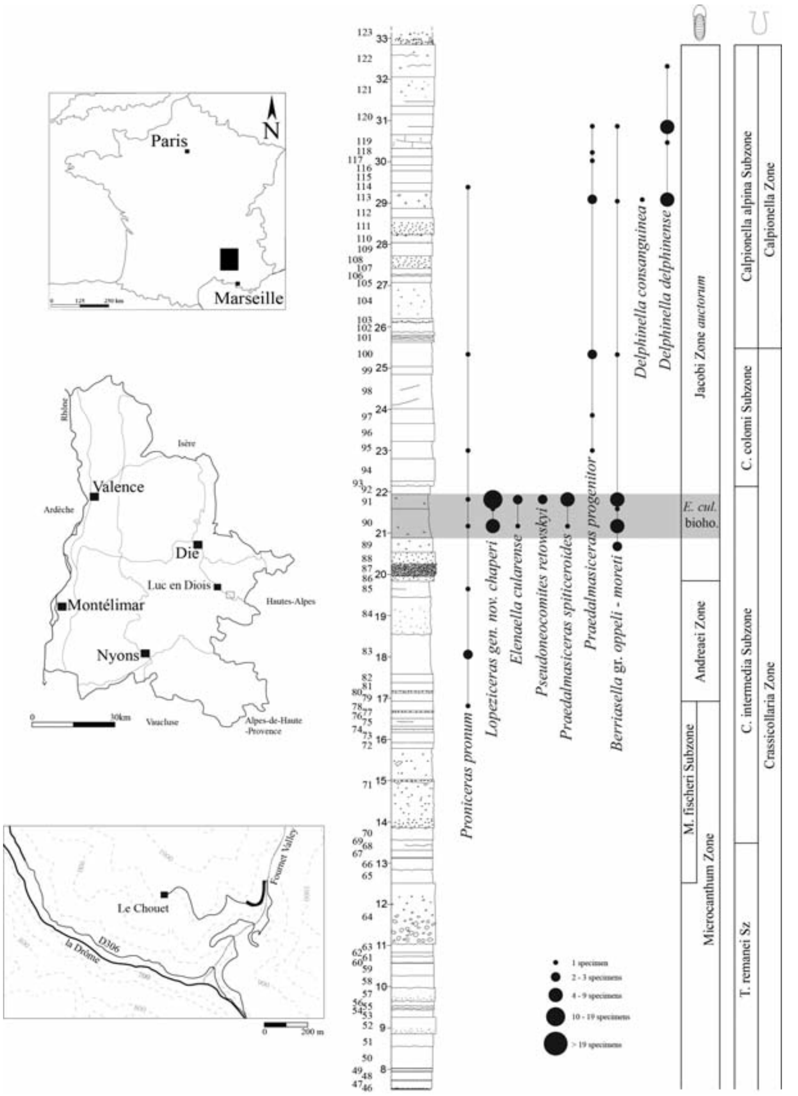
The reader is referred to the work of Wimbledon *et al*. (2013) for further details about the lithology, biostratigraphy (ammonites, calpionellids and calcareous nannofossils) and magnetostratigraphy documented at Le Chouet. To avoid redundancy, we chose to synthesize the data discussed herein on Text-fig. 1. The bed numbers used herein follow those in Wimbledon *et al*. (2013).

By comparison with the original ammonite distribution published by Wimbledon *et al*. (2013, fig. 12), several changes have been made by Bulot *et al*. (2014) and Frau *et al*. (2015), to which the reader is referred. It should be noted that the previous report of *Dalmasiceras* cf. *crassicostatum* Djanélidzé, 1922a in bed 97 was based on a poorly preserved specimen, that is herein referred to *Praedalmasiceras* gen. nov. *progenitor* (Oppel in Zittel, 1868). A re-investigation in the upper part of the section allowed the first representatives of the genus *Delphinella* Le Hégarat, 1971 to be found, in beds 113 to 120, and of *Berriasella* of the *oppeli* (Kilian, 1889) – *moreti* Mazenot, 1939 group in bed 120.

REPOSITORIES OF SPECIMENS

All specimens studied are deposited in the Frau/Bulot collection at the Musée Paléontologique de Provence (MPP) of Aix-Marseille Université. The following abbreviations indicate the repository of specimens mentioned in the text:

FSL: University of Claude Bernard; Lyon-I.
UJF-ID: University of Grenoble.
MNHN.F: Muséum National d'Histoire Naturelles de Paris.
BSPM: Bayerische Staatssammlung für Paläontologie und Geologie, Münich.
CNIGR: F.N. Chernyshev Central Research Geological Museum, St. Petersburg.



Text-fig. 1. Locality map of Le Chouet (Les Près, Drôme, SE France) and integrated stratigraphy and vertical range of the Perisphinctoidea taxa studied in this work. Grey line indicates the *E. cularense* biohorizon sensu Tavera *et al*. (1994)

SYSTEMATIC PALAEONTOLOGY

All dimensions of specimens are given in millimetres: Dmax = larger measurable diameter, D = adult diameter, U = umbilical diameter; Wh = whorl height, Wb = Whorl breath. Ratios such as U/D, Wh/D and Wb/D are dimensions as a percentage of the adult diameter. In synonymy, we distinguished the macroconch and microconch specimens.

All specimens are coated with ammonium chloride.

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Family Himalayitidae Spath, 1925
Family Himalayitinae Spath, 1925
Genus *Lopeziceras* gen. nov.
(= *Chapericeras* Hoedemaeker, 1981 *nomen nudum*)

DERIVATION OF THE NAME: Named in honour of Jean-Pierre, Martine and Emmanuel Lopez, the owner of the Le Chouet hameau, for their hospitality and friendship during our fieldwork seasons.

TYPES SPECIES: *Ammonites chaperi* Pictet, 1868. It should be noted that *Chapericeras* was introduced by Hoedemaeker (1981) with *A. chaperi* as the type species. As pointed out by Klein (2005), *Chapericeras* is a *nomen nudum* since it does not fulfil article 13.1.1 of the I.C.Z.N. Code.

DIAGNOSIS: Small to medium size, dimorphic Himalayitidae with compressed planulate shell. Whorl section subrectangular with flat or flattened venter at all stages of ontogeny. Deep ventral groove on phragmocone evolving towards a ventral band in adult. Ornamentation composed of up to four stages: (*i*) *himalayitid* stage (with prorsiradiate, simple, rigid ribs which sometimes bear minute lateral tubercles on the innermost whorls) (D < 20 mm); (*ii*) *intermediate* stage (with rigid to dense, straight to prorsiradiate, bifurcate ribs at diameters between 20 mm and 50 mm. Branches of ribs projected forward on upper flank and ending as pinched tubercles on ventral shoulder, sometimes denser with sporadic single and fasciculate ribs); (*iii*) *subadult* stage (with alternating bi- and trifurcate primary ribs connected, more or less, to variable number of intercalatories. Primary ribs thicken on umbilical shoulder and at the furcation point, forming progressively lateral tubercles) (D < 70 mm); (*iv*) *macroconch* stage (with ribbing stronger on body chamber, ribs spaced with attenuation at mid flank. Ribs thickening on ventral shoulder, with some development of prominent tubercles. Umbilical tubercles radially elongated. Microconchs smaller than macroconchs and never developing a *macroconch stage*. Suture line markedly dissected with dissymmetric lateral lobe.

DISCUSSION: Mazenot (1939, p. 33) referred *Ammonites chaperi* Pictet, 1868 to the genus *Berriasella* Uhlig, 1905, and more specifically to his group of "*Berriaselles à deux rangs de tubercules*". Recent literature is highly confusing regarding the generic treatment of *A. chaperi*. Following Le Hégarat (1973), most authors included *A. chaperi* in *Malbosiceras* Grigorieva, 1928 (type species: *A. malbosi* Pictet, 1867); a view that is consistent with Mazenot's original opinion. Besides, it should be noted that some authors regarded *A. chaperi* as a *Protacanthodiscus* Spath, 1925 (Patrulius 1969; Lefeld 1974; Boughdiri 1994).

Hoedemaeker (1981, p. 245) introduced a new genus *Chapericeras* for early Berriasian berriasellids with two rows of tubercles (*A. chaperi*, *Hoplites tarini* Kilian, 1889, *Berriasella aizyensis* Mazenot, 1939 and *Berriasella aspera* Mazenot, 1939) that were placed in *Malbosiceras* and *Mazenoticeras* Nikolov, 1966, by Le Hégarat (1973, table 5). *Ammonites chaperi* was designated as the type species, but the genus lacks a formal description and therefore is a *nomen nudum* (I.C.Z.N. Code article 13.1.1). Nevertheless, it is obvious that the ontogenetic sequence of the early Berriasian forms with lateral and umbilical tubercles, generally included in *Malbosiceras* and *Mazenoticeras,* do not match that of the type species of these genera, e.g. *Malbosiceras malbosi* (Pictet, 1867) and *Mazenoticeras broussei* (Mazenot, 1939). The same is true for *Protacanthodiscus* and its type species *Protacanthodiscus andreaei* (Kilian, 1889), recently revised by Frau *et al*. (2015).

The re-examination of the type material supplemented by the detailed analysis of the material collected at Le Chouet (see discussion below) showed us that *Hoplites tarini*, *Hoplites macphersoni* Kilian, 1889, *Hoplites vasseuri* Kilian, 1889, *Hoplites castroi* Kilian, 1889, *Berriasella aspera* and *Berriasella aizyensis* are junior subjective synonyms of *Ammonites chaperi*. and this motivates us to introduce *Lopeziceras* gen. nov.

Dalmasiceras aristidis Mazenot, 1939 should also be included in *Lopeziceras* gen. nov., since it shares great affinities with *L. chaperi,* from which it can only be distinguished by the occurrence of minute lateral tubercles on the juvenile whorls (e.g. *himalayitid* stage). This feature has never been observed on the material from Le Chouet nor on the type specimens of *L. chaperi* and its synonyms. We believe that this ornamental feature supports a link with *Protacanthodiscus*, confirming hypothesis already made by Boughdiri (1994).

CONTENT: *Lopeziceras* gen. nov. includes *C. chaperi* (and its junior subjective synonyms *L. tarini*, *L. macphersoni*, *L. vasseuri*, L. *castroi*, *L. aspera* and *L. aizyensis*) and *L. aristidis.* In southern Spain and southeast France, the genus is restricted to the *E. cularense* biohorizon, at the base of the Jacobi Zone *auctorum* (upper part of the *C. intermedia* Subzone, Crassicollaria Zone). The genus also occurs in Hungary, Poland and Bulgaria.

Lopeziceras chaperi (Pictet, 1868)
(Text-fig. 2A–K)

Microconchs

1889. *Hoplites vasseuri* Kilian, p. 663, pl. 30, fig. 2a, b.
1889. *Hoplites castroi* Kilian, p. 665, pl. 32, fig. 2.
1889. *Hoplites chaperi* (Pictet); Kilian, p. 666, pl. 30, fig. 5.
1889. *Hoplites macphersoni* Kilian, p. 668, pl. 31, fig. 2a, b.
1939. *Berriasella vasseuri* (Kilian); Mazenot, p. 76, pl. 7, fig. 5a, b (= Kilian, 1889, pl. 30, fig. 2b).
1939. *Berriasella* sp. ind. gr. de *B. chaperi* (Pictet); Mazenot, pl. 11, fig. 5a, b.
1939. *Berriasella aspera* Mazenot, p. 84, pl. 9, fig. 2a–c.
1939. *Berriasella aizyensis* Mazenot, p. 86, pl. 9, fig. 4a–q, 5a, b, 6a, b; pl. 10, fig. 1a–c.
1939. *Berriasella macphersoni* (Kilian); Mazenot, p. 102, pl. 10, fig. 2a–c (= Kilian, 1889, pl. 31, fig. 2a, b).
1960. *Dalmasiceras aristidis* Mazenot; Nikolov, p. 171, pl. 14, fig. 2.
1973. *Malbosiceras asper* (Mazenot); Le Hégarat, p. 84, pl. 9, figs 1, 2 (= Mazenot, 1939, pl. 9, fig. 2b).
1973. *Subalpinites aristides* (Mazenot); Le Hégarat, p. 221, pl. 34, figs 1, 2; pl. 53, fig. 10.
1976. *Subalpinites aristides* (Mazenot); Fülöp, pl. 35, fig. 6.
1977. *Malbosiceras chaperi* (Pictet); Sapunov, pl. 6, fig. 2.
1979. *Malbosiceras asper* (Mazenot); Sapunov, p. 183, pl. 57, fig. 1a, b (= Sapunov, 1977, pl. 6, fig. 3).
1979. *Malbosiceras chaperi* (Pictet); Sapunov, p. 184, pl. 57, figs 2, 4, 5 (= Sapunov, 1977, pl. 6, fig. 2).
1979. *Subalpinites aristides* (Mazenot); Sapunov, p. 186, pl. 59, fig. 5 (= Nikolov, 1960, pl. 14, fig. 2).
1982. *Dalmasiceras* (*Elenaella*) *vasseuri* (Kilian); Nikolov, p. 106, pl. 26, fig. 3a, b (= Kilian, 1889, pl. 30, fig. 2a, b).
1982. *Malbosiceras asper* (Mazenot); Nikolov, p. 126, pl. 42, fig. 3 (= Mazenot, 1939, pl. 9, fig. 2b), 4a, b (= Sapunov 1979, pl. 57, fig. 1a).
1982. *Malbosiceras chaperi* (Pictet); Nikolov, p. 128, pl. 42, fig. 5 (= Sapunov 1979, pl. 57, fig. 2), 6 (= Sapunov 1979, pl. 57, fig. 4).
1982. *Subalpinites aristides* (Mazenot); Nikolov, p. 200, pl. 70, fig. 2 (= Le Hégarat 1973, pl. 53, fig. 10), 3 (= Nikolov 1960, pl. 14, fig. 2).
1985. *Malbosiceras chaperi* (Pictet); Tavera, p. 271, pl. 39, fig. 3a, b, text-fig. 20D.
1985. *Malbosiceras tarini* (Kilian); Tavera, p. 273, pl. 39, fig. 4, 5a, b, text-fig. 20E.

Macroconchs

1868. *Ammonites chaperi* Pictet, p. 242, pl. 37, figs 1a–c, 2, 3.
1889. *Hoplites chaperi* (Pictet); Kilian, p. 666, pl. 31, fig. 1.
1889. *Hoplites tarini* Kilian, p. 667, pl. 30, fig. 4a, b.
1890. *Hoplites chaperi* (Pictet); Toucas, p. 606, pl. 18, fig. 8.
1939. *Berriasella chaperi* (Pictet); Mazenot, p. 80, pl. 8, fig. 5a, b, 6a–c, 7a–c, (= Pictet 1868, pl. 37, fig. 1a–c), 8, 9; pl. 9, fig. 1a, b.
1939. *Berriasella aspera* n. sp. Mazenot, p. 84, pl. 9, fig. 3a, b.
1939. *Berriasella tarini* (Kilian); Mazenot, p. 89, pl. 10, fig. 3a–c (= Kilian 1889, pl. 30, fig. 4a, b).
1969. *Protacanthodiscus chaperi* (Pictet); Patrulius, pl. 3, fig. 2.
1973. *Malbosiceras aizyensis* (Mazenot); Le Hégarat, p. 82, pl. 9, fig. 3 (= Mazenot 1939, pl. 10, fig. 1b).
1973. *Malbosiceras chaperi* (Pictet); Le Hégarat, p. 86, pl. 9, fig. 6 (= Mazenot 1939, pl. 8, fig. 8), 7.
1974. *Protacanthodiscus chaperi* (Pictet); Lefeld, p. 347, pl. 9, fig. 4.
1977. *Malbosiceras asper* (Mazenot); Sapunov, pl. 6, fig. 3.
1982. *Malbosiceras chaperi* (Pictet); Nikolov, p. 128, pl. 43, fig. 1a–c (= Pictet 1868, pl. 37, fig. 1a–c).
1982. *Pomeliceras* (*Mazenoticeras*) *tarini* (Kilian); Nikolov, p. 154, pl. 53, fig. 1 (= Kilian 1889, pl. 30, fig. 4a).
1994. *Durangites* (*Protacanthodiscus*) sp. aff. *macphersoni* (Kilian); Boughdiri, p. 161, pl. 4, fig. 3; pl. 5, fig. 4.
1995. *Durangites* (*Protacanthodiscus*) *chaperi* (Pictet); Boughdiri, p. 154, pl. 5, figs 1, 2a, b, 3, 5, 6a, b, 7.

TYPE: The lectotype, from the Brèche d'Aizy (Isère, France), designated and re-illustrated by Mazenot (1939, p. 81, pl. 8, 7a–c,), is specimen FSL. 35807 in the Kilian collection.

MATERIAL: Seventeen specimens MPP-CHT.26/12, MPP-CHT.26/4, MPP-CHT.26/14, MPP-CHT.26/9, MPP-CHT.26/27/0, MPP-CHT.27/10, MPP-CHT.27/14, MPP-CHT.27/19, MPP-CHT.27/22, MPP-CHT.27/24, MPP-CHT.27/26, MPP-CHT.27/27, MPP-CHT.27/31, MPP-CHT.27/32, MPP-CHT.27/35, MPP-CHT.27/37 and MPP-CHT.27/38.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.26/12	–	–	31.4	17.2
MPP-CHT.26/4	18.6	5.9	7.5	6.2
MPP-CHT.26/14	–	–	22.7	–
MPP-CHT.26/27/0	–	–	c 27.3	–
MPP-CHT.27/10	–	–	21.9	–
MPP-CHT.27/14	–	16.5	4.9	–
MPP-CHT.27/24	65.9	21.7	23.7	
MPP-CHT.27/31	–	–	11.1	–
MPP-CHT.27/32	–	–	14.4	9.5
MPP-CHT.27/35	c 20.4	6.2	c 9.6	–
MPP-CHT.27/38	–	–	c 24.3	11.3

DESCRIPTION: This is a small to medium size, compressed planulate ammonite. The whorl section is subrounded on the innermost whorl, becoming subrectangular on the rest of the shell. The umbilicus is open and moderately deep. The flanks and the venter are flattened at all ontogenetic stages. A deep ventral groove occurs on the phragmocone and evolves into a ventral band in the adult. The body chamber occupies half of the last whorl.

MPP-CHT.26/4 and MPP-CHT.27/35 are small, juvenile specimens characterized by an involute coiling, subrounded whorl section with absent *himalayitid* stage. The *intermediate* stage is well expressed by dense, prorsiradiate, bifurcate and sporadic single ribs.

MPP-CHT.26/14 and MPP-CHT.27/31 are small, incomplete specimens that exhibit typical *intermediate* and *subadult* stages. The ribs are markedly denser in MPP-CHT.26/14 compared to MPP-CHT.27/31, and sporadic fasciculate ribs occur. The venter could not be studied.

MPP-CHT.26-27/0, MPP-CHT.27/10 MPP-CHT.27/19 are fragments of body chamber. They show the transition between the *subadult* stage and the *adult* stage. Umbilical and lateral tubercles are irregularly disposed on primary ribs.

MPP-CHT.27/24 is a large, almost complete specimen, but the inner whorls are not preserved. It shows a rigid *intermediate* stage followed by a long *subadult* stage.

MPP-CHT.26/12 is a large fragment of body chamber with a well-expressed *adult* stage.

DISCUSSION: The material at our disposal encompasses the morphological and ornamental features of several typological species originally included in *Chapericeras* in the sense of Hoedemaeker (1981). The most diagnostic specimen, MPP-CHT.26/14, matches well the holotype of *L. aizyensis*. These forms are medium size, are moderately evolute and have not developed the adult stage. They are almost identical to *L. vasseuri*, *L. castroi* and *L. macphersoni*, that only differ in their robust shell shape and rigid *intermediate* and *subadult* stages. From the type material illustrated by Mazenot (1939), we believe that these features fall within the scope of intraspecific variation. The specimen MPP-CHT.27/24 closely resembles *L. aspera*, which is herein considered as a juvenile macroconch form. The specimens MPP-CHT.26/12, MPP-CHT.26-27/0 and MPP-CHT.27/10 perfectly match the type series of *L. chaperi* and *L. tarini* – characterized by medium to large size and the addition of the *adult* stage on the body chamber.

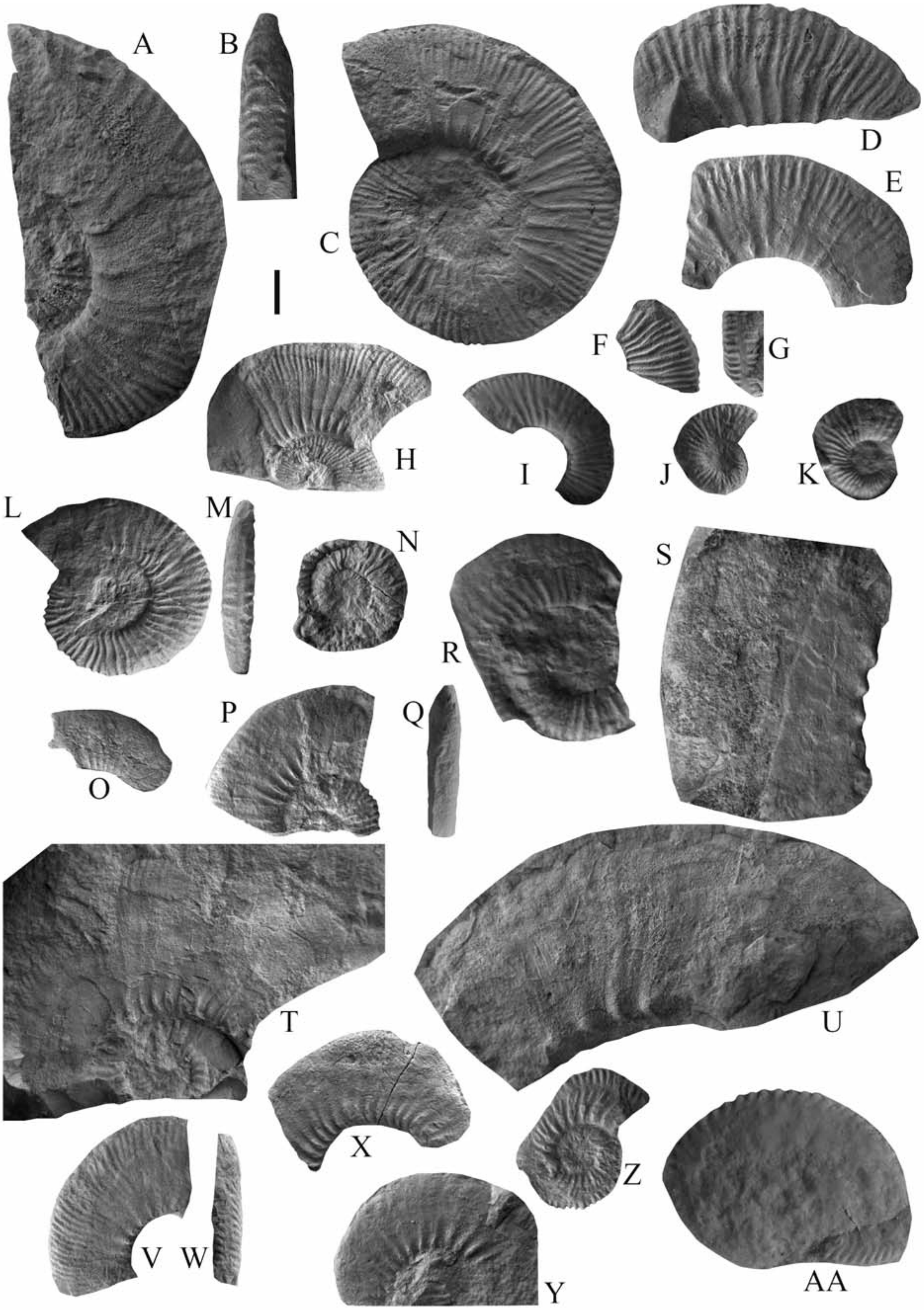
The distinction of two morphological groups, based on the ontogenetic sequence, strongly suggests intraspecific dimorphism, as already documented in *Protacanthodiscus andreaei* by Frau *et al*. (2015). However, none of the specimens at our disposal, or illustrated in the literature, show the structure of the peristome. Since our new collection originates from only two successive beds, we believe that the adult size and ontogenetic sequence support the interpretation that the taxa discussed above represent typological morphotypes of a single dimorphic species.

OCCURRENCE: *Lopeziceras chaperi* gen. nov. occurs in beds 90 and 91, in the *E. cularense* biohorizon, at the base of the Jacobi Zone *auctorum* (upper part of the *C. intermedia* Subzone, of the Crassicollaria Zone).

Subfamily Dalmasiceratinae subfam. nov.

TYPE GENUS: *Dalmasiceras* Djanélidzé, 1922a.

DIAGNOSIS: Small to large size, dimorphic, discoidal, compressed Himalayitidae with at least two of the four following ornamental stages: (i) *juvenile* stage (with spaced, prorsiradiate, single ribs; (ii) *himalayitid* stage (*Protacanthodiscus*-like stage composed of straight, rigid, prorsiradiate ribs with small punctiform tubercles at the furcation point; adoral branch of bifurcated ribs ending in pinched tubercles on the ventral shoulder; depressed whorl section with marked ventral groove; (iii) *fasciculate* stage (with flexuous, spaced primary ribs that fasciculate at mid-flank; umbilical tubercles becoming stronger, with more or less marked retrocurvature; *(iv) adult* stage: fading of ribs at mid-flank or their complete loss. Tubercles become stronger on the umbilical shoulder, forming slight retrocurvature. Microconch smaller than macroconch, with small lateral lappets possessing a small ventral extension. Suture line composed of long, more or less dissymmetric lateral lobe.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REMARKS: Hypotheses on the origin of *Dalmasiceras* are diverse. Originally, Mazenot (1939, p. 144, fig. 6) considered *Dalmasiceras* as a derivative of *Berriasella* and therefore placed it in the Neocomitidae Salfeld, 1921. It has been established since then, that his opinion was based on an inaccurate understanding of the ammonite distribution across the Tithonian/Berriasian boundary (Le Hégarat 1973). Subsequently, Le Hégarat (1973, p. 206) outlined the morphological similarities between *Dalmasiceras* and *Ammonites moravicus* Oppel, 1865. This latter species was diversely interpreted by authors until the introduction of *Moravisphinctes* by Tavera (1985) and its placement in the Ataxioceratidae by Cecca *et al*. (1989). The paraphyletic origin of *Dalmasiceras* from *Moravisphinctes* and *Paraulacosphinctes* Schindewolf, 1925 was assumed by Tavera (1985, p. 330, table 1a). In our opinion *Dalmasiceras*, *Moravisphinctes* and *Paraulacosphinctes* only have in common the convergent attenuation of the ornamentation and thickened ribs on the umbilical shoulder in the adult. Moreover, *Moravisphinctes* is now considered a morphological genus that groups the microconch forms of *Paraulacosphinctes* of the *senex* (Oppel *in* Zittel, 1868) group (Parent 2003).

In our opinion, the origin of *Dalmasiceras* lies in the Himalayitidae. This view was already suggested by Boughdiri *et al*. (1999), who outlined the similarities and potential phyletic links between the late Tithonian himalayitid *Hegaratites* Boughdiri, Enay, Le Hégarat, Memmi, 1999 and *Dalmasiceras.* Whether there is a link between *Dalmasiceras* and *Hegaratites* or not, those authors overlooked the fact that the early ontogenetic stage of the *Dalmasiceras* of the *spiticeroides* (Djanélidzé, 1922a) group is almost identical to that of *Protacanthodiscus.* As already pointed out by Le Hégarat (1973, p. 219), this is the case with both the topotype specimen of *D. spiticeroides* of Mazenot (1939, pl. 24, fig. 21) and the juvenile paratype of *D. toucasi* Mazenot, 1939, illustrated by the same author on pl. 24, fig. 10. Our new data show that those morphologies occur only at the base of the Jacobi Zone *auctorum* (*E. cularense* biohorizon) and are similar to those described in *Protacanthodiscus hexagonum* (Tavera, 1985). The occurrence of *P. hexagonum* at the top of the Andreaei Zone (Frau *et al*. 2015) strongly supports the idea that *Dalmasiceras spiticeroides*, for which *Praedalmasiceras* gen nov. is introduced below, evolved from *Protacanthodiscus* by a peramorphic developmental shift combined with a deep modification (i.e. long, more or less dissymmetric lateral lobe) of the suture line (see discussion in Mazenot, 1939, p. 145). In our view, *Praedalmasiceras* gen. nov. and its descendant *Dalmasiceras* should be excluded from the Neocomitidae, and referred to a new subfamily, Dalmasiceratinae subfam nov. of the family Himalayitidae.

CONTENT: The new subfamily Dalmasiceratinae subfam. nov. includes *Praedalmasiceras* gen. nov. and its descendant genus *Dalmasiceras* Djanélidzé, 1922a.

Praedalmasiceras gen. nov.

DERIVATION OF THE NAME: *Prae* (latin): before; *Dalmasiceras*: ammonite genus named by Djanélidzé (1922a) in honour of the French geologist J.B. Dalmas (1811–1881).

TYPE SPECIES: *Dalmasiceras spiticeroides* Djanélidzé, 1922a.

DIAGNOSIS: Small to large size, discoidal, compressed Himalayitidae, with moderately involute coiling and a narrow umbilicus. Whorl section suboval, higher than wide, with flat to slightly convex flanks. Ventral band of the phragmocone disappearing progressively. Four ornamental stages: *(i) juvenile* stage (with spaced, prorsiradiate, single ribs); *(ii) himalayitid* stage (*Protacanthodiscus*-like stage with straight, rigid, prorsiradiate ribs with small punctiform tubercles at furcation point; adoral branch of bifurcated ribs ended by pinched tubercles on ventral shoulder; depressed whorl section with marked ventral groove); *(iii) fasciculate* stage (with flexuous, spaced primary ribs branching on the mid-flank; umbilical tubercles becoming stronger, with more or less marked retrocurvature; *(iv) adult* stage (with fading of ribs on the mid-flank, or completely lost). Tubercles on umbilical shoulder becoming stronger, forming slight retrocurvature. Suture line composed of long, more or less dissymmetric lateral lobe.

REMARK: *Dalmasiceras* was introduced as a subgenus of *Hoplites* by Djanélidzé (1922a), but no type species was designated by this author. Subsequently,

Text-fig. 2. **A-K** – *Lopeziceras chaperi* (Pictet, 1868) gen. nov.; A-B – MPP-CHT.26/12 [M]; C – MPP-CHT.27/24 [M]; D – plaster cast of MPP-CHT.26-27/0 [M]; E – MPP-CHT.27/10 [M]; F-G – MPP-CHT.27/32 [?m]; H – MPP-CHT.26/14 [m]; I – plaster cast of MPP-CHT.27/31 [m]; J – MPP-CHT.26/4 [juvenile]; K – MPP-CHT.27/35 [juvenile]. **L-S** – *Praedalmasiceras spiticeroides* (Djanélidzé, 1922a) gen. nov.; L-M – MPP-CHT.27/41 [m]; N: MPP-CHT.26/5 [m]; O – MPP-CHT.276/18 [m]; P-Q – MPP-CHT.276/40 [m]; R – plaster cast of MPP-CHT.27/13 [m]; S – MPP-CHT.27-29/0 [?M]. T-AA – *Praedalmasiceras progenitor* (Oppel *in* Zittel, 1868) gen. nov.; T – MPP-CHT.47/3 [M]; U: MPP-CHT.31/1 [M]; V-W – MPP-CHT.35/4 [m]; X – MPP-CHT.52/1 [m]; Y – MPP-CHT.54/1 [m]; Z: MPP-CHT.47/2 [m]; AA – plaster cast of MPP-CHT.33/1 [m]. Scale bar is 10 mm

Roman (1938, p. 337) designated *Ammonites dalmasi* Pictet, 1867 as the type species of *Dalmasiceras*. Beacause most of the Djanélidzé's taxa were introduced as subspecies of *A. dalmasi,* Mazenot (1939) stated that this was an unfortunate choice and that the diagnosis of *Dalmasiceras* was based on numerous typological species from the Brèche de Chomérac and Brèche d'Aizy. Le Hégarat and Remane (1968) and Le Hégarat (1973) showed that *D. dalmasi* and its supposed macroconch, *D. punctatum* Djanélidzé, 1922a, characterize the upper part of the *Tirnovella occitanica* Zone (middle Berriasian). These forms are characterized by a peramorphic developmental shift of the *adult* stage that extends through most ontogenetic stages, compared to *D. spiticeroides* and *D. progenitor*.

Le Hégarat (1973, table 14) noticed, that there exists a significant stratigraphic gap between *Dalmasiceras* of the *dalmasi* group and the taxa from the Jacobi Zone *auctorum*, included herein in *Praedalmasiceras* gen. nov. This gap encompasses the top of the Jacobi Zone *auctorum* and the *T. subalpina* Subzone of the lower part of the Occitanica Zone. Only a limited number of specimens referred to *D. djanelidzei* and *D. gigas* were reported by Le Hégarat (1973, pl. 52, fig. 1, table 14) from the *B. privasensis* Subzone (e.g. middle part of the Occitanica Zone). Re-examination of these specimens leaves no doubt that they are closely allied to *Dalmasiceras* of the *dalmasi* group and link *Praedalmasiceras* gen. nov. to the middle Berriasian group of *D. dalmasi*. In any case, the peramorphic morphology of *D. dalmasi* and its allied species is distinctive.

CONTENT: As discussed by Cecca *et al*. (1989), many of the typological taxa from the Brèche de Chomérac and Brèche d'Aizy may fit into a limited number of palaeobiological species. Examination of the type material, based on literature, reveals that three groups of morphological species can be distinguished:

Praedalmasiceras spiticeroides; characterized by small and medium forms with a marked *himalayitid* stage in the inner whorls. This species includes the typological taxa: *Hoplites* (*Dalmasiceras*) *spiticeroides* Djanélidzé, 1922a, *Hoplites* (*Dalmasiceras*) *subspiticeroides* Djanélidzé, 1922a and *Hoplites* (*Dalmasiceras*) *dalmasi* var. *nana* Djanélidzé, 1922a.

Praedalmasiceras progenitor; characterized by small to large forms with a reduced or absent *himalyitid* stage that includes: *Ammonites progenitor* Oppel, 1865, *Hoplites* (*Dalmasiceras*) *subprogenitor* Jacob (in coll.) *in* Djanélidzé, 1922a, *Hoplites* (*Dalmasiceras*) *dalmasi* var. *gigas* Djanélidzé, 1922a, *Dalmasiceras toucasi* Mazenot, 1939, *Dalmasiceras subloevis* Mazenot, 1939, *Dalmasiceras subloevis* var. *praecox* Jacob (in coll.) *in* Mazenot, 1939, *Dalmasiceras djanelidzei* Mazenot, 1939, *Dalmasiceras djanelidzei* var. *gigas* Mazenot, 1939, *Dalmasiceras biplanum* Mazenot, 1939, and *Dalmasiceras pseudoprogenitor* Nikolov, 1982.

Praedalmasiceras botellae; characterized by medium to large forms, with a long *fasciculate* stage combined with a row of lateral tubercles, that include: *Hoplites botellae* Kilian, 1889, *Hoplites* (*Dalmasiceras*) *kiliani* Djanélidzé, 1922a, *Dalmasiceras gevreyi* Mazenot, 1939 and *Dalmasiceras sayniforme* Tavera, 1985.

The material collected at Le Chouet clearly shows that *P. spiticeroides* occurs only in the *E. cularense* biohorizon, at the base of the Jacobi Zone *auctorum*, whereas *P. progenitor* occurs at a slightly younger level of the same zone. No specimens from Le Chouet can be referred to *P. botellae*. Cecca *et al*. (1989, pp. 67, 68) mentioned that the addition of lateral tubercles in the *fasciculate* stage could have resulted from a covariation between whorl section and density of ribs. However, our material does not confirm this hypothesis. The group of *P. botellae* is thus kept separate, until new material is available.

Praedalmasiceras spiticeroides (Djanélidzé, 1922a)
(Text-fig. 2L–S)

Microconchs

1922a. *Hoplites* (*Dalmasiceras*) *dalmasi* (Pictet) var. *nana* Djanélidzé, p. 268, pl. 13, fig. 2a–c.
1939. *Dalmasiceras nanum* (Djanélidzé); Mazenot, p. 151, pl. 24, fig. 20a–c (= Djanélidzé, 1922a, pl. 13, fig. 2a–c.
1939. *Dalmasiceras toucasi* Mazenot, p. 152, pl. 24, fig. 9a, b, 10a, b, 11a, b, 12a, b.
1953. *Dalmasiceras toucasi* Mazenot; Arnould-Saget, p. 68, pl. 7, fig. 1a, b, 2a–c; text-fig. 25.
1973. *Dalmasiceras spiticeroides* (Djanélidzé); Le Hégarat, p. 219, pl. 53, fig. 6.
1985. *Dalmasiceras nanum* (Djanélidzé); Tavera, p. 320, pl. 49, fig. 9.
1985. *Dalmasiceras toucasi* Mazenot; Tavera, p. 321, pl. 49, fig. 10, 11, 12.
1989. *Dalmasiceras spiticeroides* (Djanélidzé); Cecca *et al*., p. 69, pl. 3, fig. 6, 7, 8, 9; pl. 4, fig. 5.

1989. *Dalmasiceras sublaevis* Mazenot; Cecca *et al*., p. 72, pl. 4, fig. 3 (*sol.*).
? 1997. "*Corongoceras*" *kollikeri* (Oppel *in* Zittel); Benzaggagh and Atrops, p. 158, pl. 7, fig. 3.

Macroconchs
1922a. *Hoplites* (*Dalmasiceras*) *spiticeroides* Djanélidzé, p. 262, pl. 12, fig. 1, text-fig. 1.
1922a. *Hoplites* (*Dalmasiceras*) *subspiticeroides* Djanélidzé, p. 264, pl. 12, fig. 2.
1939. *Dalmasiceras spiticeroides* (Djanélidzé); Mazenot, p. 154, pl. 24, fig. 21a–d, 22a–c (= Djanélidzé 1922a, pl. 12, fig. 1).
1939. *Dalmasiceras subspiticeroides* (Djanélidzé); Mazenot, p. 155, pl. 24, fig. 23a–c (= Djanélidzé 1922a, pl. 12, fig. 2).
1979. *Dalmasiceras djanelidzei* Mazenot; Sapunov, p. 180, pl. 58, fig. 1.
? 1979. *Malbosiceras chaperi* (Pictet); Sapunov, p. 184, pl. 57, fig. 3a, b (*sol.*).
1982. *Dalmasiceras djanelidzei* Mazenot; Nikolov, p. 95, pl. 24, fig. 1 (= Sapunov 1979, pl. 58, fig. 1).
1982. *Dalmasiceras* (*Dalmasiceras*) *toucasi* Mazenot; Nikolov, p. 99, pl. 24, fig. 11.
1985. *Jabronella companyi* Tavera, p. 302, pl. 46, fig. 2, 3; text-fig. 23D.

TYPE: The holotype, from the Brèche de Chomérac (Ardèche, France), illustrated by Djanélidzé (1922a, pl. 12, figs 2, 3), is specimen UJF-ID.679 in the collections of the Dolomieu Institute.

MATERIAL: Nine specimens: MPP-CHT.26/5, MPP-CHT.27/11, MPP.CHT.27/13, MPP.CHT.27/16, MPP.CHT.27/18, MPP.CHT.27/20, MPP-CHT.27/40, MPP.CHT.27/41, and MPP.CHT.27-29/0.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.26/5	–	c 22.7	15.0	8.3
MPP-CHT.27/11	c 22.5	8.5	9.9	c 7.0
MPP.CHT.27/13	40.4	18.0	15.8	–
MPP.CHT.27/16	–	–	14.3	–
MPP.CHT.27/18	–	13.7	–	–
MPP-CHT.27/40	c 40.0	16.1	7.3	–
MPP.CHT.27/41	42.0	15.6	14.9	c 6.4
MPP.CHT.27-29/0	–	–	48.5	c 22.0

DESCRIPTION: MPP-CHT.27/40 is a small specimen with a moderately evolute coiling. Its whorl section is subrounded in innermost whorls and becomes subrectangular, with slightly convex flank, on the phragmocone. The innermost whorls show the dense, fine, single ribs of the *juvenile* stage. The *himalayitid* stage is poorly-preserved, but shows straight, rigid, bifurcate and single ribs. Small punctiform tubercles occur at the furcation point. Some adoral branches of bifurcate ribs are ended by pinched tubercles on the ventral shoulder. The venter could not be studied. The transition to the *fasciculate* stage is not preserved. The body chamber develops a compressed, subrectangular, higher-than-wide whorl section, with flat flanks and rounded venter. The *adult* stage is composed of smooth ribs that are attenuated in mid-flank. The ribs originate in small, spaced bullae on the umbilical shoulder.

MPP.CHT.27/13 is a fragment of the phragmocone and of the body chamber. The phragmocone shows the end of the *himalyitid* stage, with rigid simple and bifurcate ribs. No tubercles occur at the furcation points, but the branches of the ribs are ended by pinched tubercles on the ventral shoulder. The whorl section is subrectangular, with convex flanks. The body chamber exhibits well the *adult* stage, with numerous umbilical bullae marked by a slight retrovurcature. The ribs are strongly attenuated above the mid-flank.

MPP-CHT.26/5 and MPP-CHT./11 are juvenile specimens that match well the ornamental and morphological features of the *juvenile* and *himalayitid* stages. Both specimens indicate a fast growth rate and have a depressed, subrounded whorl section.

MPP-CHT.27/41 is an incomplete phragmocone with the innermost whorls not preserved. Its gracile *himalayitid* stage is ornamented with spaced, single and bifurcate ribs. The ends of branches are slightly enlarged on the upper flank and delimit a ventral groove. The transition to the *fasciculate* stage is poorly-preserved.

MPP-CHT.27/16, MPP-CHT.27/18 and MPP-CHT.27/20 are three fragments of body chamber. Their whorl sections are subrectangular, higher than wide, with rounded venter. The peristome of MPP-CHT.27/18 is preserved and shows a small lappet combined with a small ventral extension.

MPP-CHT.27-29/0 is a large fragment of body chamber with a subrectangular, higher- than-wide whorl section, with flat flanks and a markedly rounded venter. The *adult* stage is characterised by strong tubercles on the umbilical shoulder and a complete fading of the ribs. The umbilical wall is steep.

In summary, the specimens collected at Le Chouet match well the morphological and ornamental features of *P. spiticeroides* as defined above. The *himalayitid* stage, that typifies the species, extends through most of the phragmocone. The *fasciculate* stage is strongly reduced and occurs at the transition between the phragmocone and the body chamber. A ventral groove occurs in the inner whorls and gradually changes to a flat ventral band at the end of the phragmocone. The *adult* stage is limited to the body chamber.

DISCUSSION: Based on the re-examination of the type material and our own material, we believe that *P. spiticeroides* is a dimorphic species. The microconchs match the morphology of *P. nanum*, that is characterized by its small size, depressed whorl section, and strong *juvenile* and *himalyitid* stages. The *fasciculate* and *adult* stages are limited to the end of the last whorl. Ornamentation is characterized by radially elongated tubercles, with a more or less marked retrocurvature on the umbilical shoulder, and the complete fading of ribs. The peristome bears short lateral lappets with a small ventral extension.

The morphology of the holotypes of *P. spiticeroides* and of *P. subspiticeroides* corresponds to that of macroconchs. They are characterized by a larger size than those of microconchs, less involute coiling, short *juvenile* stage, moderately long *himalyitid* stage and *fasciculate* stage on the phragmocone. The *adult* stage is also limited to the body chamber, but it develops stronger tubercles on the umbilical shoulder. The peristome is unknown.

As herein understood, the type material of *Jabronella companyi* Tavera, 1985, from the Jacobi Zone *auctorum* of the Betic Cordillera, corresponds to juvenile macroconchs of *P. spiticeroides*. *Praedalmasiceras spiticeroides* differs from *P. pseudoprogenitor* in having evolute coiling, depressed juvenile morphology with a strong *himalayitid* stage and a markedly reduced *fasciculate* stage.

OCCURRENCE: *Praedalmasiceras spiticeroides* occurs in beds 90 and 91 of the *E. cularense* biohorizon, at the base of the *B. jacobi* Zone *auctorum* (upper part of the *C. intermedia* Subzone, of the Crassicollaria Zone).

Praedalmasiceras progenitor (Oppel *in* Zittel, 1868)
(Text-fig. 2T–AA)

Microconch

1865. *Ammonites progenitor* Oppel, p. 554.
1868. *Ammonites progenitor* Oppel *in* Zittel, p. 99, pl. 18, fig. 3a–d.
1889. *Hoplites*? *dalmasi* (Pictet); Kilian, p. 420(184), figs 57, 58.
1890. *Hoplites botellae* Kilian; Toucas, p. 606, pl. 18, fig. 10A, B (*sol.*).
1890. *Hoplites boissieri* (Pictet); Toucas, p. 6023, pl. 18, fig. 1A, B.
1890. *Hoplites progenitor* (Oppel *in* Zittel); Toucas, p. 603, pl. 18, figs 3A, B, 4.
1890. *Hoplites occitanicus* (Pictet); Toucas, p. 603, pl. 18, fig. 5A, B.
1890. *Hoplites dalmasi* (Pictet); Toucas, p. 604, pl. 18, fig. 6A, B.
1922a. *Hoplites* (*Dalmasiceras*) *subspiticeroides* n. sp. Djanélidzé, p. 264, pl. 12, fig. 3a, b (*sol.*).
1922a. *Hoplites* (*Dalmasiceras*) *dalmasi* (Pictet); Djanélidzé, p. 266, pl. 12, fig. 4a–c; pl. 13, fig. 1a, b.
1922a. *Hoplites* (*Dalmasiceras*) n. sp. aff. *dalmasi* (Pictet); Djanélidzé, p. 269, pl. 12, fig. 5.
1939. *Dalmasiceras toucasi* n. sp. Mazenot, p. 152, pl. 24, fig. 6a, b, 7a, b, 8a–c (*sol.*).
1939. *Dalmasiceras subprogenitor* (Jacob *in* Djanélidzé); Mazenot, p. 157, pl. 24, fig. 19a-b (= Toucas 1890, pl. 18, fig. 1A, B).
1939. *Dalmasiceras progenitor* (Oppel *in* Zittel); Mazenot, p. 158, pl. 24, fig. 13a, b, 14a–c (= Zittel 1868, pl. 18, fig. 3a), 15a–c, 16a–b (= Toucas, 1890, pl. 28, fig. 3A, B), 17a, b, 18a, b.
1939. *Dalmasiceras djanelidzei* n. sp. Mazenot, p. 161, pl. 25, fig. 1a–d, 2a, b, 3a–c, 4.
1939. *Dalmasiceras* n. sp. aff. *dalmasi* (Pictet); Mazenot, p. 163, pl. 25, fig. 5a–c (= Djanélidzé, 1922a, pl. 12, fig. 5).
1939. *Dalmasiceras sublaevis* n. sp. Mazenot, p. 169, pl. 26, figs 5a, b, 7a–c; pl. 27, fig. 2a, b, 3a, b.
1939. *Dalmasiceras sublaevis* var. *praecox* Jacob in coll. Mazenot, p. 170, pl. 26, fig. 6a, b.
1953. *Dalmasiceras progenitor* (Oppel *in* Zittel); Arnould-Saget, p. 70, pl. 7, fig. 3a–c.
1953. *Dalmasiceras sublaevis* Mazenot; Arnould-Saget, p. 71, pl. 7, fig. 4a–c, 5a–c.
1967. *Dalmasiceras sublaevis* Mazenot; Dimitrova, p. 103, pl. 50, fig. 1 (*sol.*).
1973. *Dalmasiceras djanelidzei* Mazenot; Le Hégarat, p. 209, pl. 53, fig. 2 (= Mazenot 1939, pl. 25, fig. 1a).
1973. *Dalmasiceras progenitor* (Oppel *in* Zittel); Le Hégarat, p. 217, pl. 33, fig. 3 (= Zittel 1868, pl. 18, fig. 3a).
1979. *Dalmasiceras subprogenitor* (Jacob *in* Djanélidzé); Sapunov, p. 182, pl. 58, fig. 3.
1979. *Dalmasiceras subloevis* Mazenot; Sapunov, p. 182, pl. 58, fig. 2 (= Dimitrova 1967, pl. 50, fig. 1).
1979. *Dalmasiceras subprogenitor* (Jacob *in* Djanélidzé); Nikolov, p. 98, pl. 24, figs 5, 6, 7 (= Sapunov 1979, pl. 58, fig. 3), 8.
1982. *Dalmasiceras subloevis* Mazenot; Nikolov, p. 98, pl. 24, fig. 3 (= Dimitrova 1967, pl. 50, fig. 1), 4.

1982. *Dalmasiceras* (*Dalmasiceras*) *gevreyi* (Djanélidzé); Nikolov, p. 96, pl. 24, fig. 2.
1982. *Dalmasiceras* (*Dalmasiceras*) *pseudoprogenitor* sp. n. Nikolov, p. 99, pl. 24, figs 9, 10.
1985. *Dalmasiceras djanelidzei* Mazenot; Tavera, p. 312, pl. 47, figs 1, 2; text-fig. 24A, B.
1985. *Dalmasiceras gigas* (Djanélidzé); Tavera, p. 314, pl. 47, fig. 3; text-fig. 23I.
1985. *Dalmasiceras progenitor* (Oppel *in* Zittel); Tavera, p. 315, pl. 49, figs 2, 3; text-fig. 23G.
1985. *Dalmasiceras subloevis* Mazenot; Tavera, p. 317, pl. 49, figs 4, 5, 6; text-fig. 23H.
1985. *Dalmasiceras praecox* Jacob *in* Mazenot, 1939; Tavera, p. 318, pl. 49, figs 7, 8; text-fig. 23F.
1989. *Dalmasiceras djanelidzei* Mazenot; Cecca *et al*., p. 70, pl. 3, fig. 1 (= Mazenot 1939, pl. 25, fig. 1a), 2a, b, 3, 4, 5.
1989. *Dalmasiceras sublaevis* Mazenot; Cecca *et al*., p. 72, pl. 4, figs 1, 2, 4.
1989. *Dalmasiceras* (?*Elenaella*) aff. *cularense*? (Mazenot); Cecca *et al*., p. 75, pl. 4, figs 6, 7a, b.
1989. *Dalmasiceras sublaevis* Mazenot; Föz y, p. 144, pl. 4, fig. 4; pl. 5, fig. 1.
1989. *Dalmasiceras* cf. *sublaevis* Mazenot; Fözy, p. 329, pl. 4, fig. 4 (= Fözy 1989, pl. 5, fig. 1), 5.

Macroconchs

1922a. *Hoplites* (*Dalmasiceras*) *dalmasi* (Pictet) var. *gigas* Djanélidzé, p. 268, pl. 13, fig. 1a,b; text-fig. 3.
1939. *Dalmasiceras djanelidzei* var. *gigas* (Djanélidzé); Mazenot, p. 161, pl. 25, figs 2a, b, 3a, c (= Djanélidzé 1922, text-fig. 3).
1939. *Dalmasiceras biplanum* Mazenot, p. 170, pl. 26, fig. 8a, b.
1989. *Dalmasiceras djanelidzei* morph *gigas* (Djanélidzé); Cecca *et al*., p. 71, pl. 3, fig. 5.
1989. *Dalmasiceras* cf. *biplanum* Mazenot; Cecca *et al*., p. 73, pl. 5, figs 1, 2.
1997. *Dalmasiceras* cf. *djanelidzei* Mazenot; Benzaggagh and Atrops, p. 157, pl. 6, fig. 4.

TYPE: The specimen drawned by Zittel (1868, pl. 18, fig. 3a–d) from Stramberg (Štramberk, Czech Republic) was designated as the holotype and properly illustrated by Mazenot (1939, pl. 24, fig. 14a–c). A cast of the holotype, FSL.13224, is deposited in the collection of the Université Claude-Bernard–Lyon-I.

MATERIAL: Nine specimens: MPP-CHT.31/1, MPP-CHT.33/1, MPP-CHT.35/3, MPP-CHT.35/4, MPP-CHT.47/2, MPP-CHT.47/3, MPP-CHT.47/5, MPP-CHT.52/1, MPP-CHT.54/1.
DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.31/1	–	c 36	–	–
MPP-CHT.35/3	–	–	18.3	c 6.3
MPP-CHT.35/4	–	–	23.4	–
MPP-CHT.47/2	c 32.6	12.6	12.6	–
MPP-CHT.47/3	–	c 21.7	c 37.7	–
MPP-CHT.47/5	–	–	14.3	–
MPP-CHT.52/1	–	–	19.6	c 9.2
MPP-CHT.54/1	–	–	15.9	–

DESCRIPTION: MPP-CHT.47/2 is a small, almost complete, specimen characterized by moderately involute coiling, subrectangular, higher-than-wide whorl, with flat flanks. Its *juvenile* stage is poorly-preserved and limited to the innermost whorls. A gracile *himalayitid* stage occurs at the beginning of the last whorl. No lateral tubercles occur on the bifurcate ribs, but ribs branches end with small pinched tubercles on the ventral shoulder. A *fasciculate* stage extends over the adult whorl. The ribs are rursiradiate, and branch from strong tubercles on the umbilical shoulder. The umbilical wall is moderately steep. The venter could not be studied.

MPP-CHT.35/3 and MPP-CHT.47/5 are two small phragmocone fragments that exhibit a dense *fasciculate* stage. The ribs are joined to umbilical bullae characterised by a marked retrocurvature. The ribs branches end on the ventral shoulder in small thickenings that delimit a thin groove. The venter is flat.

MPP-CHT.52/1 and MPP-CHT.54/1 are two medium-sized fragments of the body chamber, and have a subrectangular, higher-than-wide whorl section, with flat flanks and rounded venter. The ornamentation is marked by numerous bullae on the umbilical shoulder and the complete fading of ribs.

MPP-CHT.35/4 is a medium-size phragmocone fragment, with a whorl section that is subrectangular, higher than wide, with slightly convex flanks and subrounded venter. A thin ventral groove occurs. The ornamentation is that of the *fasciculate* stage, with three to four ribs that branch on spaced umbilical bullae. The ribs are slightly attenuated at the mid-flank. The umbilical wall is steep.

MPP-CHT.33/1 is a poorly-preserved fragment of body chamber, with regular thickenings on the ventral shoulder. The venter seems to be markedly flattened.

MPP-CHT.31/1 is a large fragment of body chamber with a whorl section that is subrectangular, higher than wide, and with slightly convex flanks. The flexuous, flattened fasciculate ribs branch at strong umbilical tubercles, characterised by marked retrocurvature. The ribs fade on the upper flanks. The umbilical wall is steep. The venter seems to be markedly rounded.

MPP-CHT.47/3 is a large, almost complete specimen with a compressed, subrectangular, higher-than-wide, whorl section, shallow umbilicus, and a typical *adult* stage.

DISCUSSION: The material at our disposal matches the morphological and ornamental features of several typological species included in the synonymy of *P. progenitor*.

MPP-CHT.35/3, MPP-CHT.47/2 and MPP-CHT.47/5 match well the size, shell shape and ornamentation of *P. toucasi*, *P. progenitor*, *P. subprogenitor* and *P. pseudoprogenitor*. MPP-CHT.35/4 is a medium-sized form that matches the inner whorl of *P. djanelidzei*, whereas MPP-CHT.52/1 and MPP-CHT.54/1 are identical to the adult features of its closely allied species *P. gigas*.

The taxa included herein in *D. progenitor* form ahomogenous group marked by shells with a small adult size, exhibiting fast growth rate, and a subrectangular, higher-than-wide whorl section with markedly flat flank and tabulate venter at almost all ontogenetic stages. The succession of ornamental stages is rather similar to reduced *juvenile* and *himalayitid* stages. The ventral groove is deep on the innermost whorls and progressively forms a flat ventral band in the adult. The umbilicus is deep and the umbilical wall is steep. As already outlined by Cecca *et al*. (1989), the *fasciculate* and *adult* stages are variable in length, but in certain specimens the *adult* stage appears to extend through ontogeny in its entirety. It should be noted, that numerous specimens referred to these species bear short lateral lappets with strong ventral extension (see for example Mazenot 1939, pl. 25, fig. 3a). These forms have repeatedly been considered as microconchs.

MPP-CHT.31/1, MPP-CHT.33/1 and specifically MPP-CHT.47/3 perfectly match *P. biplanum*, *P. sublaevis* and large specimens of *P. djanelidzei* (such as those illustrated by Tavera 1985, pl. 47, fig. 2), that were interpreted as macroconchs by Cecca *et al*. (1989). These authors also suggested that there exists variation of the umbilicus width and rib density between these forms, that could support their distinction at the species level.

Based on close examination of the type material and of our own collection, we believe that all these taxa fall within the intraspecific variation of a single, dimorphic species.

As herein understood, the microconchs are small to medium size and share strongly reduced *juvenile* and *himalayitid* stages, whereas the *fasciculate* and *adult* stages are variable in length. The macroconchs are markedly larger, with a more or less involute coiling and their *adult* stage may extend throughout ontogeny.

OCCURRENCE: *Praedalmasiceras progenitor* occurs in beds 95, 97, 100, 113, 118 and 120, in the lower part of the Jacobi Zone *auctorum* (upper part of the Crassicollaria Zone and lower part of the *C. alpina* Subzone of the Calpionella Zone).

Family Neocomitidae Salfeld, 1921 emend. Company (1987)

Genus *Berriasella* Uhlig, 1905

(= *pars Picteticeras* Le Hégarat, 1971)

TYPE SPECIES: *Berriasella privasensis* (Pictet, 1867); by subsequent designation of Roman (1938).

REMARKS: Our understanding of *Berriasella* is far more conservative than that of Wright *et al*. (1996, p. 50), since we consider *Picteticeras* Le Hégarat, 1971, *Parodontoceras* Spath, 1923 and *Hegaratella* Nikolov and Sapunov, 1977, to be distinct genera. It should be noted that *Picteticeras* is not a *nomen nudum*, as assumed by Wright *et al*. (1996) and Klein (2005), since it was published with the designation of a formal type species and diagnosis by Le Hégarat (1971, p. 851-852). Moreover, we share the opinion of Tavera (1985), who gave full generic status to *Elenaella* Nikolov, 1966, and did not regard it as a subgenus of *Berriasella*, as Wright *et al*. (1996, p. 50) did. This is also the case with *Delphinella* Le Hégarat, 1971, which was suspected of being a subjective synonym of *Elenaella* by Wright *et al*. (1996).

The genus *Berriasella* was introduced by Uhlig (1905, p. 601) without formal designation of a type species. The original list of taxa included by Uhlig (1905) in the taxonomic content of *Berriasella* includes species that have since been transferred to other taxa, such as *Strambergella* Nikolov, *Pseudargentiniceras* Spath, *Delphinella* Le Hégarat, *Pseudosubplanites* Nikolov, and *Riasanites* Spath. Only four species originally listed by Uhlig are still included in *Berriasella*: *B. privasensis* (Pictet, 1867), *B. calisto* (d'Orbigny, 1847), *B. subcalisto* (Toucas, 1890) and *B. oppeli* (Kilian, 1889). The type species of the genus (*B. privasensis*) was designated subsequently by Roman (1938).

The original description of *Berriasella privasensis* by Pictet (1867) was based on two specimens from the Calcaire à *Terebratula diphyoides* at Berrias

(Ardèche, France). Following Jacob's unpublished opinion, Mazenot (1939, pp. 45, 46) showed that the two specimens were not conspecific, and the lectotype is the specimen illustrated by Pictet (1867, pl. 18, fig. 1a, b), and already designated by Roman (1938, p. 324) as the type specimen of *B. privasensis*. The lectotype was re-illustrated by Mazenot (1939, pl. 2, fig. 3a, b).

Following the views of Mazenot (1939), recent views (Le Hégarat 1973; Nikolov 1982; Tavera 1985; Arkadiev *et al*. 2012) restrict *Berriasella sensu stricto* to a limited number of species of topmost Tithonian to upper Berriasian age in a Western Tethyan ammonite realm. It is now established that *B. privasensis* is a typical middle Berriasian ammonite (Le Hégarat and Remane 1968; Le Hégarat 1973). The general features of *B. privasensis* are unique among the species currently regarded as *Berriasella sensu stricto*. *Berriasella* can easily be characterized, by its: (1) ogival whorl section that is slightly convex on the body-chamber; (2) flexuous ribs throughout ontogeny; (3) low point of bifurcation of the primary ribs. The only other species that share these characters is the late Berriasian *B. calisto*, but it is characterised by its smaller umbilicus and higher whorl section, flat venter and even lower point of bifurcation of the primary ribs. Early Berriasian *Berriasella*, that includes *B. moreti* Mazenot, 1939, *B. oppeli* (Kilian, 1889), *B. subcalisto* (Toucas, 1890) and *B. sabatasi* Le Hégarat, 1973, are characterized by medium to large forms whose inner whorls match well those of several species of *Picteticeras* Le Hégarat, 1973, including *P. aurousei* Le Hégarat, 1973, *P. elmii* Le Hégarat, 1973, and *P. enayi* Le Hégarat, 1973. Due to the presence of lappets, these *Picteticeras* species were considered as the potential microconchs of *Berriasella* of the same age (Le Hégarat 1973). This view is accepted herein and the *Picteticeras* species listed above are transferred to *Berriasella*. All these species are characterized by: (1) suboval whorl section in the inner whorls, (2) an abrupt umbilical wall, and (3) rigid, straight to prorsiradiate ribs. These morphological features allow the distinction at the specific level between the *Berriasella privasensis–calisto* and the *B. oppeli–moreti* groups.

CONTENT: A detailed discussion on the specific content of *Beriasella* will be given in a forthcoming paper devoted to the revision of the type species of *B. privasensis*. That notwithstanding, the following species are here included in *Berriasella*: *B. privasensis*, *B. calisto*, *B.* of the *oppeli-moreti* group (including *B. sabatasi*, *B. subcalisto*, *B. elmii*, *B. aurousei* and *B. enayi*, and, possibly, *B. oxycostata* Mazenot, 1939, *B. moesica* Nikolov and Mandov, 1967 and *B. nastaseanui* Avram, 1990.

As already pointed out by Enay *et al*. (1998, p. 476), *Hoplites calisto* (d'Orbigny) var. *chomeracensis* Toucas, 1890 and *Berriasella subvetusta* (Steuer) var. *mazenoti* Breistroffer, 1937, are problematic species that are provisionally maintained in *Berriasella* because of their superficial similarities to *B. aurousei*.

We recently assumed (Frau *et al*. 2016) that *Berriasella jacobi* Mazenot, 1939 is a microconch that belongs to *Strambergella* Nikolov, 1966. Re-examination of the type material of *Berriasella tithonica* Tavera, 1985 showed us, however, that it is a junior subjective synonym of *Busnardoiceras busnardoi* (Le Hégarat, 1973).

As herein understood, *Berriasella* is restricted to the Berriasian of the Mediterran-Caucasian Subrealm of the Tethyan Realm. It has also been reported from northern Iran, the Caucasus, Crimea, southern and central Europe, and northern Africa. The records of the genus from Arabia, Madagascar and the Pacific coast of the North and South America are based on endemic neocomitids that do not compare with the Mediterranean-Caucasian species, and should better be referred to as "*Berriasella*".

Berriasella gr. *oppeli* (Kilian, 1889) – *moreti* (Le Hégarat, 1973)
(Text-fig. 3A–E)

Microconchs

1868. *Ammonites Calisto* Zittel, p. 100, pl. 20, fig. 1a–c, 2, 3a–c, 4 (*sol.*).
1889. *Perisphinctes oppeli* Kilian, p. 662.
1890. *Hoplites Calisto* var. *subcalisto* Toucas, p. 601, pl. 17, fig. 4A, B, 5A, B .
1939. *Berriasella praecox* Schneid; Mazenot, p. 41, pl. 1, fig. 11a–c, 12a, b.
1939. *Berriasella oppeli* (Kilian); Mazenot, p. 49, pl. 3, fig. 1a–c (= Zittel 1868, pl. 20, fig. 1a–c), 2a–c, 3a, b, 4a, b, 6a, b, 8a–c (*sol.*).
1939 *Berriasella subcallisto* (Toucas); Mazenot, p. 53, pl. 3, fig. 11a, b, 14a, b (*sol.*).
non 1939. *Berriaselllla* aff. *subcallisto* (Toucas); Mazenot, p. 53, pl. 3, fig. 12a–c (= Toucas 1890, pl. 17, fig. 5A, B).
1968. *Berriasella subcallisto* (Toucas); Le Hégarat and Remane, p. 24, pl. 5, fig. 4.
1973. *Berriasella* (*Berriasella*) *oppeli* (Kilian); Le Hégarat, p. 58, pl. 5, figs 1, 2 (= Zittel 1868, pl. 20, fig. 1); pl. 38, figs 4, 5.

1973. *Berriasella (Berriasella) jacobi* Mazenot; Le Hégarat, pl. 6, fig. 12; pl. 38, fig. 3 (= Toucas 1890, pl. 17, fig. 3a, b) .

1973. *Berriasella (Berriasella) subcallisto* (Toucas); Le Hégarat, p. 66, pl. 6, figs 3, 4 (= Mazenot 1939, pl. 3, fig. 14a), 5, 6; pl. 39, fig. 2.

1973. *Berriasella* (*Picteticeras*) *aurousei* Le Hégarat, p. 67, pl. 7, figs 1, 2; pl. 39, figs 3, 6.

pars 1973. *Berriasella* (*Picteticeras*) *elmii* Le Hégarat, p. 71, pl. 39, fig. 4 (*sol.*).

1973. *Berriasella* (*Picteticeras*) *enayi* Le Hégarat, p. 72, pl. 7, fig. 10, fig. 11 (= Mazenot, 1939, pl. 1, fig. 12a-b), 12 (= Mazenot, 1939, pl. 1, fig. 11a–c).

1988. *Berriasella oppeli* (Kilian); Klein, pl. 1, fig. 11.

1989. *Berriasella* sp. ind. cf. *oppeli* (Kilian); Cecca *et al*., p. 66, pl. 1, figs 5, 6, 7.

Macroconchs

1939. *Berriasella moreti* Mazenot, p. 61, pl. 5, fig. 1a, b, 2a, b, 3a–c.

1973. *Berriasella* (*Berriasella*) *moreti* Mazenot; Le Hégarat, p. 57, pl. 4, figs 4, 5 (= Mazenot 1939, pl. 5, fig. 3a), 6.

1973. *Berriasella* (*Berriasella*) *sabatasi* Le Hégarat, p. 63, pl. 6, fig. 7; pl. 38, fig. 10 (= Mazenot 1939, pl. 5, fig. 1a).

TYPES: The holotype of *B. oppeli* is the specimen drawned by Zittel (1868, pl. 20, fig. 1b) from Koniaków (Czech Republic). A plaster cast of the holotype (FSL.131118) was illustrated by Mazenot (1939, pl. 3, fig. 1a–c). The holotype of *B. moreti* is specimen MNHN.F/R03215 from Fuente de los Frailes (Cabra, Spain), illustrated by Mazenot (1939, pl. 5, fig. a–c).

MATERIAL: Sixteen specimens MPP-CHT.25/1, MPP-CHT.25/2, MPP-CHT.26/3, MPP-CHT.26/6, MPP-CHT.26/7, MPP-CHT.26/11, MPP-CHT.26/13a and b, MPP-CHT.26/15, MPP-CHT.26/10, MPP-CHT.26/27.1, MPP-CHT.27/30, MPP-CHT.27/33, MPP-CHT.27/36, MPP-CHT.35/2 and MPP-CHT.54/2.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.25/2	–	34.9	14	14.2
MPP-CHT.26/6	–	–	–	13.6
MPP-CHT.26/7	–	35.1	12.5	13.8
MPP-CHT.26/13b	c 40	13.7	c 15	5.9
MPP-CHT.26/15	c 32.6	c 12.9	12	–
MPP-CHT.26/27.1	c 44	19.9	c 14.4	–
MPP-CHT.27/33	–	–	13.4	–
MPP-CHT.35/2	–	c 32	–	10.8
MPP-CHT.54/2	–	c 36.4	16.3	10.9

DESCRIPTION: The material at our disposal comprises small (D < 50 mm), planulate, moderately, evolute (U/D ~ 0.40) neocomitids with shallow umbilicus. The whorl section is subrectangular, higher-than-wide, with a low umbilical wall, slightly convex to flat flanks and a flattened venter. A more-or-less, deep ventral groove at all stages of ontogeny that could be attenuated in the adult. The ornamentation is composed of uniform, straight to prorsiradiate, mostly bifurcate ribs, and sporadic single ribs. The furcation point occurs on the upper part of the flank. Two morphotypes are recognized, based on adult size and ribs density: The first comprise small forms with spaced (30 to 40 ribs on the last whorl) and rigid ribs. Ends of rib branches are slightly projected forward on the upper flanks, and they rarely thicken on the ventral shoulder. This morphotype matches the typological species *B. aurousei* and *B. enayi*.

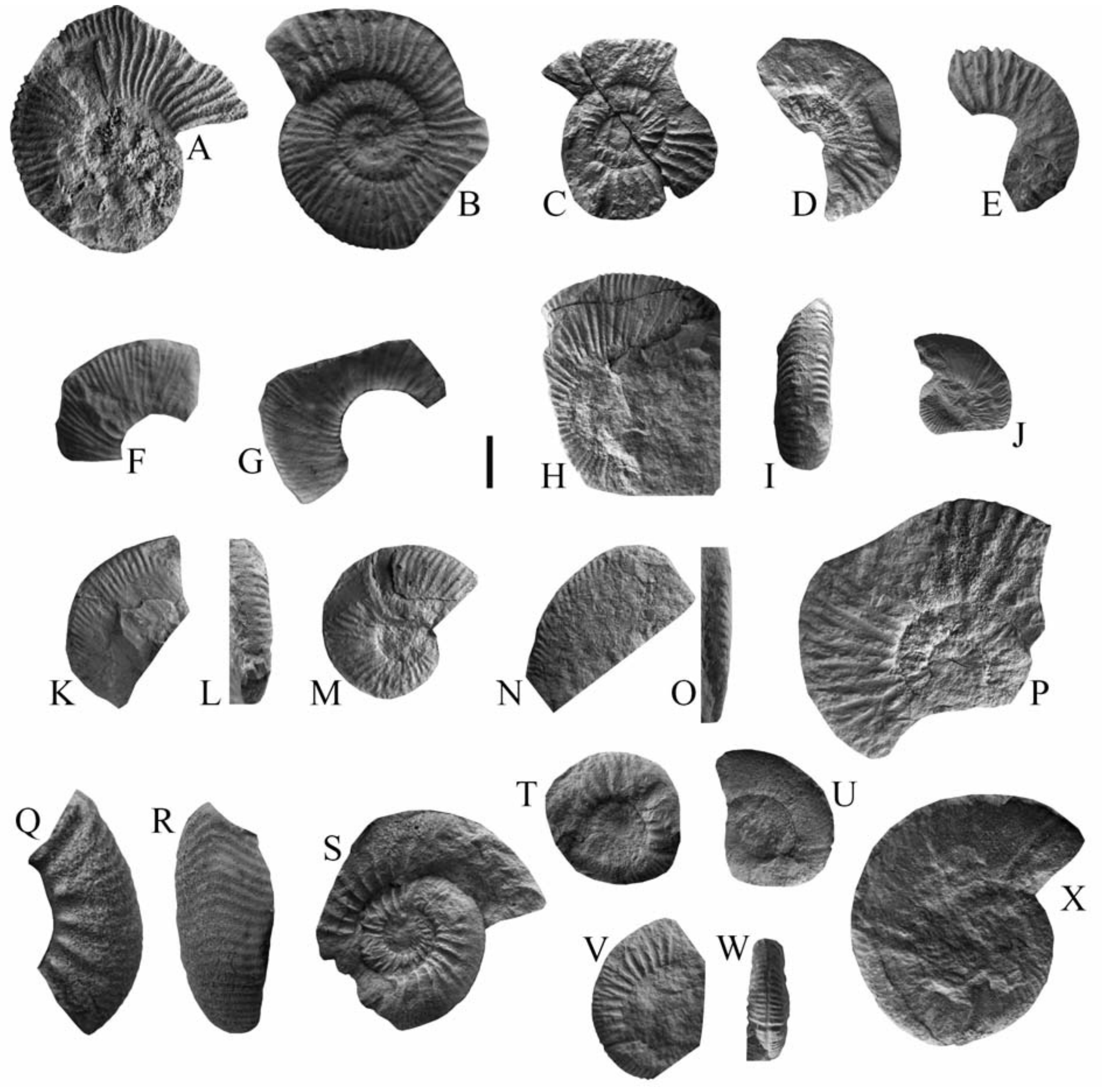
The second comprise small to middle-sized forms with dense (more than 40 ribs on the last whorl), prorsiradiate to slightly flexuous ribs. Ends of branches project slightly forward on the upper flanks, and are rare thickened on the ventral shoulder. This morphotype matches the species *B. oppeli* and *B. subcalisto*.

DISCUSSION: The re-examination of the type specimens of early Berriasian *Berriasella* shows that the morphological and ornamental features noted by Le Hégarat (1973) are not relevant in differentiating between the species known from the literature. We recommend here the use of the *Berriasella oppeli – moreti* group for those forms. The type material and our new collection shows that the *B. aurousei – oxycostata* morphotype on the one hand, and the *B. oppeli – subcalisto* morphotype on the other, respectively, correspond to the robust and a slender morphologies of a single species, resulting from Buckman's first law of covariation. *B. elmii* links these two morphologies.

Among these taxa, several specimens bear short lateral lappets and have been previously considered to be microconchs by Le Hégarat (1973). In this context, Le Hégarat suggested that *B. moreti* and *B. sabatasi* might correspond to the macroconchs of *B. oppeli* and *B. subcalisto*.

No specimen from Le Chouet can yet be referred with certainty to *B. moreti* and *B. sabatasi*, but we strongly support the interpretation that both species are macroconchs. They can be distinguished by their larger adult size (90 mm < D < 180 mm vs. 20 mm < D < 80 mm in microconchs), smaller umbilicus (U/D ~ 0.35 vs. U/D ~ 0.43 in microconchs), more compressed whorl section (Wb/Wh ~ 0.68 vs. Wh/Wh ~ 0.72 in microconchs) and steep umbilical wall. The ornamentation of macroconchs matches well that of the slender microconchs as discussed above.

Finally, it should be noted that specimen MPP-CHT.26-27/1 from the base of the Jacobi Zone *auctorum* shows sporadic polygyrate ribs on the inner whorls like those observed throughout the ontogeny of *B. busnardoi,* but its morphological and ornamental features perfectly match those of *B. subcalisto*. Bulot *et al*. (2014) showed that *B. busnardoi* is one of the oldest Neocomitidae, since it occurs in the topmost Andreaei Zone. In our view, there is little doubt that *B. busnardoi* and *B. oppeli* – *moreti* are phyletically linked. *B. busnardoi* can easily be distinguished by the discrete tubercles on the ventral shoulder of its phragmocone, the absence of a ventral groove in macroconchs and the complex ribbing at all ontogenetic stages in both micro- and macroconchs.



Text-fig. 3. **A-E** – *Berriasella* gr. *oppeli* (Kilian, 1889) – *moreti* (Mazenot, 1939); A – MPP-CHT.26/13b [m]; B – plaster cast of MPP-CHT.26-27/1 [m]; C – MPP-CHT.54/2 [m]; D – MPP-CHT.26/15 [m]; E – MPP-CHT.35/2 [m]. **F-G** – *Pseudoneocomites retowskyi* (Sarasin and Schöndelmayer, 1901); F – plaster cast of MPP-CHT.27/12 [m]; G – plaster cast of MPP-CHT.27/17 [m]; **H-J** – *Elenaella cularense* (Mazenot, 1939); H-I – MPP-CHT.26/9x; J – MPP-CHT.27/34. **K-O** – *Delphinella delphinense* (Kilian, 1889); K-L – MPP-CHT.47/8; M – MPP-CHT.120/2 (bed 120); N-O – MPP-CHT.47/4. **P** – *Delphinella consanguinea* (Retowski, 1893); MPP-CHT.47/6. **Q-W** – *Proniceras pronum* (Oppel *in* Zittel, 1868); Q-R – MPP-CHT.33/4; R – MPP-CHT.21/67; T – MPP-CHT.48/1; U – MPP-CHT.19/2; V-W – MPP-CHT.19/9; W – MPP-CHT.26/8. Scale bar is 10 mm

OCCURRENCE: *Berriasella* of the *oppeli – moreti* group is found between bed 89 and bed 120, in the lower part of the Jacobi *auctorum* Zone (upper part of the Crassicollaria Zone and the lower part of the *C. alpina* Subzone of the Calpionella Zone). Check C A

Genus *Pseudoneocomites* Hoedemaeker, 1982

TYPE SPECIES: *Hoplites retowskyi* Sarasin and Schöndelmayer, 1901 [= *Hoplites occitanicus* Retowski, 1893 non Pictet (1867)]; by subsequent designation of Mazenot (1939).

REMARKS: As already outlined by Vašíček and Skupien (2013, p. 338), there is great confusion in recent literature regarding the taxonomic value of *Pseudoneocomites* and its relationship to *Tirnovella* Nikolov, 1966 (type species: *Berriasella alpillensis* Mazenot, 1939). This issue is crucial because it has direct implications for the biostratigraphy of the middle Berriasian and the identification of the index species, *T. occitanica* (Pictet, 1867).

In recent years, Bogdanova *et al*. (1999) and Arkadiev *et al*. (2008) have assumed that *T. occitanica* occurs in Crimea, based on the re-description of all the historical specimens described as *Hoplites occitanicus* by Retowski (1893, pl. 12, figs 7–9). In their discussion of the specimens, they noticed that *Hoplites occitanicus* Retowski *non* (Pictet) were selected by Sarasin and Schöndelmayer (1901) to define their new species *Neocomites retowskyi*. Confusion arose over the definition of the species, since Sarasin and Schöndelmayer (1901) did not designated a holotype for their new taxon and illustrated a Swiss specimen from Crêt Mory, a specimen that is not conspecific with Retowski's original material. This background misled Busnardo *et al.* (2003), who designated the Swiss specimen (Sarasin and Schöndelmayer, 1901, pl. 9, fig. 4) as the lectotype of *Neocomites retowskyi* and included it in the genus *Teschenites* Thieuloy, 1971. Busnardo et al. failed to take into account the comments of Bulot *et al*. (1993, p. 26) who showed that the original description of Sarasin and Schöndelmayer (1901, p. 72) unambiguously state that they created a separate species for the described and figured specimen by Retowski, under the name *Hoplites occitanicus*; and that Mazenot (1939, p. 218) designated the specimen illustrated by Retowski (1893, pl. 11, fig. 8) as the lectotype. In our view, the lectotype designation by Mazenot fulfils the rules of the I.C.Z.N. It was with this historical backdrop that Hoedemaeker (1982) introduced the genus *Pseudoneocomites* based on *Hoplites retowskyi*.

CONTENT: The type species and its synonyms (*Neocomites suprajurensis* Mazenot, 1939; *N. allobrogensis* Mazenot, 1939, *Neocomites beneckei* Roman and Mazenot, 1937 and *Delphinella tresannensis* Le Hégarat, 1973; see discussion below).

Tirnovella davidi Le Hégarat, 1973 was originally included in *Pseudoneocomites* by Hoedemaeker (1982). The species is poorly known, since it is based on a single specimen. In our opinion, and despite its narrow umbilicus and high whorl section, it should be provisionally retained in *Tirnovella,* since it shows the well-developed umbilical bullae that characterize *Tirnovella* of the *subalpina – occitanica* group.

Despite superficial similarities to *Pseudoneocomites retowskyi*, *Neocomites neocomiensis* (d'Orbigny) in Sayn (1907, pl. 3, fig. 14), from the early late Valanginian of Beaumugne (Hautes-Alpes, France), falls in the range of variation of *N. neocomiensis* as has been understood in recent literature (Reboulet 1996, pl. 4 and 5).

Pseudoneocomites retowskyi (Sarasin and Schöndelmayer, 1901)
(Text-fig. 3F–G)

Microconch

1868. *Ammonites transitorius* Oppel *in* Zittel; Pictet, p. 246, pl. 38, fig. 5a, b.
1890. *Hoplites carpathicus* (Zittel); Toucas, p. 602, pl. 17, fig. 11.
1939. *Neocomites beneckei* Mazenot, p. 208, pl. 32, fig. 9a, b, 10a, b, 11a, b, 12a, c, 13, 14.
1953. *Neocomites beneckei* Mazenot; Arnould-Saget, p. 73, pl. 7, fig. 6a–c, 7a–c, 9a–c; text-fig. 27.
1953. *Neocomites occitanicus* (Pictet); Arnould-Saget, p. 78, pl. 7, fig. 8a–c.
1953. *Neocomites suprajurensis* Mazenot; Arnould-Saget, p. 76, pl. 7, figs 10a–c, 11a–c.
1953. *Neocomites* cf. *suprajurensis* Mazenot; Arnould-Saget, p. 76, pl. 7, fig. 12a–c.
1960. *Neocomites beneckei* Mazenot; Drushchits, p. 282, pl. 26, fig. 1.
1968. *Neocomites* (?) *beneckei* Mazenot; Le Hégarat and Remane, p. 23, pl. 5, fig. 3.
1973. *Pseudargentiniceras beneckei* (Mazenot); Le Hégarat, p. 172, pl. 26, figs 2, 3, 4 (= Mazenot 1939, pl. 32, fig. 10a, 11a, 12a), 5, 6.
1973. *Delphinella tresannensis* Le Hégarat, p. 113, pl. 13, fig. 15; pl. 42, fig. 1, 2
1974. *Neocomites beneckei* Mazenot; Lefeld, p. 348, pl. 9, figs 2, ?3.

1978. *Tirnovella retowskyi* (Sarasin and Schöndelmayer); Kvantaliani and Kvernadze, p. 34, pl. 1, fig. 1.
1979. *Tirnovella allobrogensis* (Mazenot); Sapunov, p. 196, pl. 59, fig. 3.
1979. *Tirnovella beneckei* (Mazenot); Sapunov, p. 197, pl. 59, fig. 4.
1982. *Substeueroceras beneckei* (Mazenot); Nikolov, p. 208, pl. 72, fig. 3a, b (= Mazenot 1939, pl. 32, fig. 12a, b), 4, 5, 6, 7, 8, 9.
1982. *Tirnovella allobrogensis* (Mazenot); Nikolov, p. 228, pl. 82, figs 3a, b (= Mazenot 1939, pl. 33, fig. 4a, b), 4, 5, 6.
? 1982. *Berriasella* (*Delphinella*) *tresannensis* (Le Hégarat); Hoedemaeker, pl. 1, fig. 4.
non 1982. *Pseudoneocomites retowskyi* (Sarasin and Schöndelmayer); Hoedemaeker, p. 68, pl. 2, fig. 7 (= *Tirnovella* sp.).
1984. *Delphinella crimense* (Burckhardt); Bogdanova *et al*., pl. 2, fig. 6.
1984. *Delphinella tresannensis* Le Hégarat; Bogdanova *et al*., pl. 2, fig. 8.
1984. *Fauriella shipkovensis* (Nikolov and Mandov); Bogdanova *et al*., pl. 4, fig. 3.
? 1988. *Neocomites retowskyi* (Sarasin and Schöndelmayer); Khalilov, p. 350, pl. 10, fig. 2.
1999. *Berriasella (Tirnovella) retowskyi* (Sarasin and Schöndelmayer); Kvantaliani, p. 94, pl. 11, figs 6a, b (= Kvantaliani and Kvernadze, 1978, pl. 1, fig. 1), 7.
1999. *Berriasella* (*Tirnovella*) cf. *allobrogensis* (Mazenot); Kvantaliani, p. 95, pl. 12, fig. 1a, b.
2001. *Substeueroceras beneckei* (Mazenot); Wippich, p. 79, pl. 6, figs 4, 6.
2005. *Delphinella tresannensis* Le Hégarat; Arkadiev and Bogdanova, p. 493, pl. 5, figs 6, 7 (= Bogdanova *et al*. 1984, pl. 2, fig. 8) .
2011. *Fauriella* aff . *carpathica* (Zittel); Arkadiev, p. 9, pl. 3, fig. 6a, b .
2011. *Fauriella shipkovensis* (Nikolov and Mandov); Arkadiev, p. 8, pl. 3, figs 2, 3.
2011. *Tirnovella allobrogensis* (Mazenot); Arkadiev, p. 11, pl. 3, figs 3, 4, 5 (= Bogdanova *et al*. 1984, pl. 4, fig. 3).
2011. *Fauriella* aff. *shipkovensis* (Nikolov and Mandov); Arkadiev, p. 9, pl. 3, figs 6, 7.
non 2011. *Fauriella* aff. *shipkovensis* (Nikolov and Mandov); Arkadiev, p. 9, pl. 3, fig. 7 (= *Strambergella jacobi*).
2012. *Fauriella shipkovensis* (Nikolov and Mandov); Arkadiev *et al*., p. 154, pl. 7, figs 3, 4 (= Arkadiev 2011, pl. 3, fig. 2, 3).
2012. *Fauriella* aff. *carpathica* (Zittel); Arkadiev *et al*., p. 155, pl. 7, fig. 5 (= Arkadiev 2011, pl. 3, fig. 6).
2012. *Tirnovella allobrogensis* (Mazenot); Arkadiev *et al*., p. 159, pl. 7, figs 7, 8 (= Arkadiev 2011, pl. 3, fig. 3, 4), 9 (= Bogdanova *et al*., 1984, pl. 4, fig. 3).
2012. *Delphinella crimensis* (Burckhardt); Arkadiev *et al*., p. 161, pl. 10, fig. 7 (*sol*.).
2012. *Delphinella tresannensis* Le Hégarat; Arkadiev *et al*., p. 163, pl. 11, fig. 4, (= Arkadiev and Bogdanova 2005, pl. 5, fig. 4), 5 (= Bogdanova *et al*., 1984, pl. 2, fig. 8).
2012. *Delphinella* cf. *tresannensis* Le Hégarat; Guzhikov *et al*., p. 278, pl. 2, fig. 7 .
2013. *Berriasella jacobi* Mazenot; Vašíček and Skupien, p. 335, fig. 5D–I (*sol*.).

Macroconchs

1893. *Hoplites occitanicus* Retowski, p. 265, pl. 11, figs 7, 8, 9.
non 1901. *Hoplites Retowskyi* Sarasin and Schöndelmayer, p. 72, pl. 9, fig. 4 (= *Teschenites rebouleti*).
1939. *Neocomites allobrogensis* Mazenot, p. 210, pl. 33, fig. 4a, b.
1939. *Neocomites suprajurensis* Mazenot, p. 211, pl. 33, fig. 5a–c.
1960. *Neocomites retowskyi* (Sarasin and Schöndelmayer); Drushchits, p. 282, pl. 25, fig. 5 (= Retowski 1893, pl. 11, fig. 9).
1973. *Tirnovella suprajurensis* (Mazenot); Le Hégarat, p. 88, pl. 28, fig. 3 (= Mazenot, 1939, pl. 33, fig. 5a–c).
1973. *Tirnovella allobrogensis* (Mazenot); Le Hégarat, p. 177, pl. 27, fig. 6 (= Mazenot 1939, pl. 32, fig. 9a, b).
1982. *Tirnovella allobrogensis* (Mazenot); Hoedemaeker, pl. 1, fig. 2.
non 1985. *Tirnovella allobrogensis* (Mazenot); Tavera, p. 296, pl. 45, fig. 22C (= *Strambergella jacobi*).
non 1986. *Tirnovella* sp. cf. *suprajurensis* (Mazenot); De Wever *et al*., p. 182, pl. 1, fig. 5 (= *Strambergella jacobi*).
? 1986. *Tirnovella* gr. *allobrogensis*-*suprajurensis* (Mazenot); Clavel *et al*., p. 326, pl. 1, fig. 6.
1989. *Tirnovella allobrogensis* (Mazenot); Khimchiashvili, p. 16, pl. 1, fig. 2; pl. 6, fig. 1.
1989. *Tirnovella suprajurensis* (Mazenot); Khimchiashvili, p. 16, pl. 6, fig. 2.
1990. *Tirnovella allobrogensis* (Mazenot); Khimchiashvili, p. 375, pl. 1, fig. 7 (= Khimchiashvili, 1989, pl. 1, fig. 2).
1999. *Tirnovella occitanica* (Pictet); Bogdanova *et al*., p. 31, pl. 1, fig. 1a, b, 2a, b (= Retowski, 1893, pl. 11, fig. 9); pl. 2, fig. 1, 2a, b, 3a, b (= Retowski 1893, pl. 11, fig. 8).

non 2003. *Teschenites retowskyi* (Sarasin and Schöndelmayer); Busnardo *et al*., p. 45, pl. 2, fig. 2, 3, 4 (= Sarasin and Schöndelmayer 1901, pl. 9, fig. 4).
2004. *Tirnovella allobrogensis* (Mazenot); Ettachfini, p. 103, pl. 1, fig. 4a, b.
2012. *Tirnovella occitanicus* (Pictet); Arkadiev *et al*., p. 157, pl. 9, fig. 1a, b (= Retowski 1893, pl. 11, fig. 9), 2a, b (= Bogdanova *et al*., 1999, pl. 1, fig. 1a, b).

TYPE: As designated by Mazenot (1939), the lectotype is the Retowski's specimen CNIGR.39/10916 from Theodosia (Feodosiya, Crimea, Ukraine), first illustrated by Retowski (1897, pl. 11, fig. 8).

MATERIAL: MPP.CHT.27/12 and MPP.CHT.27/17.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP.CHT.27/12	–	–	14.4	–
MPP.CHT.27/17	–	c 14.6	–	–

DESCRIPTION: The material at our disposal consists of two involute fragments of body chamber. The flanks are slightly rounded. The umbilical wall is low in inner whorls and becomes markedly recurved and overhanging in the adult. The ornamentation is composed of dense, thin, bifurcate and single ribs. Ribs sometimes branch from the umbilical shoulder and they are attenuated near the aperture.

REMARKS: Bulot *et al*. (2014, p. 123) and Vašíček and Skupien (2013, p. 337) suggested that the taxa *Neocomites beneckei* Mazenot, 1939, *Neocomites allobrogensis* Mazenot, 1939, *Neocomites suprajurensis* Mazenot, 1939 form a homogenous group, to which should be added the crushed holotype of *Delphinella tresannensis* Le Hégarat, 1973 from the Jacobi Zone *auctorum* of Trésanne (Isère, France). Excepting their adult size, none of their ornamental or morphological features allows us to distinguish these taxa from the type series of *P. retowskyi*.

Even though the material collected at Le Chouet is too limited to allow a definitive conclusion, a thorough re-examination of the literature convinces us that the difference between the adult size of *P. retowskyi* and its allied species reflects intraspecific dimorphism. Therefore, we support the view that *P. retowskyi* is merely the macroconch, and therefore the senior subjective synonym, of the typological species listed above.

As shown by the synonymy list, *P. retowskyi* has been repeatedly confused with the middle Berriasian index species *Tirnovella occitanica*. As herein defined, *P. retowskyi* can be easily distinguished from *T. occitanica* by its inflated, involute shell, deep umbilicus, its adult recurved umbilical wall, dense and fine ribs that are progressively attenuated on the body-chamber, and the lack of umbilical tubercles at all stages of ontogeny.

OCCURRENCE: *P. retowskyi* was found in bed 91, *E. cularense* Biohorizon, base of the Jacobi *auctorum* Zone (upper part of the C. intermedia Subzone of the Crassicollaria Zone).

Genus *Elenaella* Nikolov, 1966

TYPE SPECIES: *Berriasella cularensis* Mazenot, 1939; by original designation.

REMARKS: Mazenot (1939, p. 76) originally noticed a convergence between the adult stage of *Berriasella cularense* and those of the genus *Dalmasiceras*. However, Nikolov (1966) designated *B. cularense* as the type species of *Elenaella* (referred to as subgenus of *Berriasella*). The same author (Nikolov 1982) subsequently rectified this, since *Elenaella* was considered a subgenus of *Dalmasiceras*, because of its ontogenetic succession and the strong relationships of the suture line, despite „*some specific details*“ (English translation). According to Cecca *et al*. (1989), this is not supportable because the type material of *E. cularense* does not show the strong dissymmetric lateral lobe that typifies *Dalmasiceras*. Tavera (1985) used *Elenaella* as a distinct neocomitid genus because its inner whorls showed great ornamental affinities with those of the earliest *Berriasella sensu lato*. *Elenaella* is used herein in the sense of Tavera.

CONTENT: As here understood, *Elenaella* is monospecific. In our view, other species formerly referred to *Elenaella* in the literature should be transferred to other genera.

Dalmasiceras (*Elenaella*) *collignoni* Nikolov, 1982 is a junior objective synonym of *Delphinella sevenieri* Le Hégarat, 1973. Confusion with *Elenaella* was due to the fading of ornamentation on it body chamber, which is a convergent adult character among the Neocomitidae.

Dalmasiceras (*Elenaella*) *subcularense* Nikolov, 1982, is a late Berriasian species that is closely allied to *Jabronella subisaris* (Mazenot, 1939). A revision of the genus *Jabronella* is needed before there can further discussion of this matter.

Dalmasiceras (*Elenaella*) *prorsiradiatum* Howarth, 1992, from northern Iraq, is an endemic species of poorly constrained age. General coiling and ribbing style on the venter area suggest that it should rather be placed in *Groebericeras* Leanza, 1945, as interpreted by Howarth (1992).

The generic status of the poorly-understood *Delphinella auzonensis* Le Hégarat, 1973, that was included (with no discussion) in *Elenaella* by Klein (2005), remains unclear, even if its type specimen shows some affinities with *D. sevenieri*.

Elenaella cularense (Mazenot, 1939)
(Text-fig. 3H–J)

1939. *Berriasella cularensis* Mazenot, 1939, p. 75, pl. 8, fig. 1a–c, 2.
1939. *Berriasella* sp. ind. aff. *B. cularensis* aff. *B. vasseuri* Mazenot, p. 77, pl. 7, fig. 3Ab.
1985. *Elenaella cularensis* (Mazenot); Tavera, p. 262, pl. 38, fig. 1; text-fig. 20F.
non 1989. *Dalmasiceras* (?*Elenaella*) aff. *cularense*? (Mazenot); Cecca *et al*., p. 75, pl. 4, fig. 6, 7a, b (= *Praedalmasiceras progenitor*).

TYPE: As designated by Mazenot (1939, p. 75, pl. 8, fig. 1a–c), the holotype is specimen ID.632 from the Brèche d'Aizy (Isère, France), in the Gevrey collection.

MATERIAL: MPP-CHT.26/9x and MPP.CHT.27-34.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.26/9x	c 44.1	–	16.1	9.1
MPP.CHT.27-34	c 20.4	5.7	7.8	–

DESCRIPTION: This is a small neocomitid ammonite with moderately involute coiling. The sub-rounded whorl section of the inner whorl passes towards a sub-oval whorl section, higher than wide, with flattened flanks. The umbilical wall is low and obliquely inclined. The ornamentation of the phragmocone consists of fine, prorsiradiate, bifurcate ribs, and scarce single ribs. On the body-chamber, the ornamentation is progressively attenuated at the mid-flank. Some ribs remain on the external shoulder as well as regular bullae on the umbilical shoulder. The change between these two types of ornamentation is abrupt.

REMARKS: The understanding of *E. cularense* is based on a limited number of specimens, but the material at our disposal matches the holotype well. It should be noted that the holotype originates from the Brèche d'Aizy and its age remains unclear at its type locality, since this level contains reworked ammonites from the Andreaei Zone and most of the Jacobi Zone *auctorum*. The specimen illustrated by Cecca *et al.* (1989) from Le Pouzin (Ardèche, France) clearly belongs to *Praedalmasiceras* gen. nov. on the basis of its fasciculate ribs on its inner whorls and its dissymmetric lateral lobe. Tavera (1985) illustrated a single specimen of *E. cularense* from the Betic Cordillera (southern Spain) that perfectly matches the *E. cularense* holotype.

OCCURRENCE: *E. cularense* was found in beds 89 and 90, *E. cularense* Biohorizon, from the base of the Jacobi Zone *auctorum* (upper part of the *C. intermedia* Subzone of the Crassicollaria Zone).

Genus *Delphinella* Le Hégarat, 1971

TYPE SPECIES: *Hoplites delphinensis* Kilian, 1889; by original designation.

REMARKS: Le Hégarat (1973) showed that two morphological groups co-occur throughout the stratigraphic range of the genus. The first group is distinguished by its small adult size and attenuation of the ornament on the body chamber. The second group is characterized by larger forms with more or less marked tubercles at the rib furcation points on the body chamber.

In the Jacobi Zone *auctorum*, *D. delphinense* (Kilian, 1889), *D. berthei* (Toucas, 1890), *D. garnieri* (Mazenot, 1939), *D. janus* (Retowski, 1893), *D. obtusenodosa* (Retowski, 1893) and *D. pectinata* Arkadiev and Bogdanova, 2005 belong to the first group. *D. subchaperi* (Retowski, 1893) and *D. consanguinea* (Retowski, 1893) belong to the second group. Both groups are recognized in our collection from Le Chouet, but the material is too scarce and fragmentary to determine sexual dimorphs. Pending the description of a large collection of well-preserved specimens made by us at Les Combes (Glandage, Drôme, France), we here follow a [fairly] conservative taxonomic treatment of *Delphinella*.

As already discussed above, the holotype and single specimen of *Delphinella tresannensis* Le Hégarat, 1973 is a crushed *Pseudoneocomites retowskyi*.

Delphinella delphinense (Kilian, 1889) nom. correct
(Text-fig. 3K–O)

1889. *Hoplites delphinensis* Kilian, p. 662, text-fig. 1.
1893. *Hoplites calisto* d'Orbigny; Retowski, p. 55, pl. 12, fig. 1.
1939. *Berriasella delphinensis* (Kilian); Mazenot, p. 67, pl. 6, fig. 14a, b, 15a–c (= Kilian 1889, text-fig. 1).
1939. *Berriasella garnieri* Mazenot, p. 69, pl. 6, fig. 13a–c.
1939. *Berriasella Garnieri* Mazenot, p. 69, pl. 6, fig. 13a–c.
1939. *Berriasella moravica* (Oppel); Mazenot, p. 71, pl. 6, fig. 18a, b (*sol.*).
1953. *Berriasella delphinensis* (Kilian); Arnould-Saget, p. 67, pl. 4, fig. 10a–c, 11a, b.
1956. *Berriasella delphinensis* (Kilian); Arkell, pl. 44, fig. 3a, b (= Mazenot 1939, pl. 6, fig. 15a, b).
non 1957. *Berriasella* aff. *delphinensis* (Kilian); Bürgl, pl. 2, fig. 4 (= Perisphinctoidea indet.).
1961. *Berriasella delphinensis* (Kilian); Eristavi, p. 91, pl. 3, fig. 3.
1973. *Delphinella delphinensis* (Kilian); Le Hégarat, p. 104, pl. 13, fig. 7 (= Mazenot 1939, pl. 6, fig. 15), fig. 8; pl. 42, figs 3, 9.
1973. *Delphinella garnieri* (Mazenot); Le Hégarat, p. 107, pl. 13, fig. 9 (= Mazenot, 1939, pl. 6, fig. 13a–c); pl. 42, fig. 5 (= Mazenot 1939, pl. 6, fig. 13).
non 1977. *Berriasella* (*Delphinella*) cf. *delphinensis* (Kilian); Sapunov, pl. 6, fig. 5 (=*Moravisphinctes mollovi*).
non 1979. *Berriasella* (*Delphinella*) cf. *delphinensis* (Kilian); Sapunov, p. 177, pl. 56, fig. 7 (= Sapunov 1977, pl. 6, fig. 5).
1982. *Delphinella delphinensis* (Kilian); Nikolov, p. 86, pl. 20, fig. 2a, b (= Kilian, 1889, text-fig. 1), 3, 4 (= Le Hégarat 1973, pl. 42, fig. 9).
1984. *Berriasella delphinensis* (Kilian); Bogdanova *et al.*, p. 32, pl. 2, fig. 3a, b; pl. 3, fig. 5.
1992. *Berriasella* (*Delphinella*) cf. *delphinensis* (Kilian); Wierzbowski and Remane, p. 874, pl. 2, figs 3, 4 .
1999. *Delphinella* cf. *delphinensis* (Kilian); Kvantaliani, p. 96, pl. 12, fig. 2a, b.
1999. *Delphinella garnieri* (Mazenot); Kvantaliani, p. 97, pl. 12, fig. 3a, b.
2005. *Delphinella delphinensis* (Kilian); Arkadiev and Bogdanova, p. 494, pl. 6, fig. 5.
2012 *Delphinella delphinensis* (Kilian); Arkadiev *et al.*, p. 164, pl. 10, fig. 4 (= Arkadiev and Bogdanova 2005, pl. 6, fig. 5).

TYPE: Mazenot (1939, p. 67, pl. 6, fig. 15a–c) designated specimen FSL.127337 from Claps-de-Luc (Drôme, France), Sorbonne collection, as the holotype of *D. delphinense*. Kilian (1889), however, did not designate a type and consequently, specimen FSL.127337 is the lectotype.

MATERIAL: Eight specimens: MPP-CHT.47/4, MPP-CHT.47/7, MPP-CHT.47/8, MPP-CHT.53/1, MPP-CHT.120/1, MPP-CHT.120/2, MPP-CHT.120/3, MPP-CHT.120/4 and MPP-CHT.123/1.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.47/4	–	–	–	c 6.0
MPP-CHT.120/2	28.9	9.4	14.7	–

DESCRIPTION: The species is represented in our collections by several poorly-preserved fragments of small, discoidal Neocomitidae with a moderately involute coiling, shallow umbilicus and subrectangular, higher-than-wide, whorl section. All specimens show a tabulate venter. The early ontogeny of our specimens is poorly preserved, but they show a ventral groove that changes to a flat ventral band in the adult. The flanks are flattened or slightly convex. The umbilical wall is low. The ornamentation is composed of rigid to dense, straight to prorsiradiate bifurcating ribs on the inner whorls. On the body chamber, bifurcate ribs are flattened on the upper flank and they are attenuated at mid-flank at the end of the adult whorl.

REMARKS: The material at our disposal is poorly-preserved, but can be referred to *D. delphinense* based on its small size, its subrectangular, higher-than-wide whorl section with a tabulate venter, rigid to dense bifurcate ribs that flatten on the upper flank and are interrupted on the venter. The type series of *D. garnieri* (Mazenot, 1939) cannot be distinguished from *D. delphinense*, and we thus assume that the latter species is a senior subjective synonym.

D. obtusenodosa (Retowski, 1893) differs from *D. delphinense* by its larger adult size, denser ribbing and the occurrence on the body chamber of thickenings at the furcation points. It is clear that *D. crimense* (Retowski, 1893) and *D. janus* (Retowski, 1893) correspond to juveniles or smaller forms of *D. obtusenodosa*.

D. berthei differs from *D. delphinense* by its rigid bifurcate ribs on the inner whorls and the absence of the fading of ribs on the body chamber.

A re-examination of *Delphinella mollovi* Nikolov, 1982 leaves no doubt that the species belongs to *Moravisphinctes* Tavera, 1985, based on its evolute coiling and trifurcate ribs on the body chamber.

OCCURRENCE: *D. delphinense* occurs in beds 113, 119, 120 and 123, lower part of the Jacobi Zone *auctorum* (lower part of the C. alpina Subzone, Calpionella Zone).

Delphinella consanguinea (Retowski, 1893)
(Text-fig. 3P)

1893. *Hoplites consanguineus* Retowski, p. 268, pl. 12, fig. 1a, b, 2.
1939. *Berriasella consanguinea* (Retowski); Mazenot, p. 79, pl. 7, fig. 4a–c.
1960. *Berriasella consanguinea* (Retowski); Drushchits, p. 276, pl. 20, fig. 5a, b (= Retowski 1893, pl. 12, fig. 1a, b).
non 1962. *Berriasella* sp. cf. *consanguinea* (Retowski); Collignon, p. 6, pl. 178, figs 774, 775, 776 (= Neocomitidae gen. et sp. indet.).

TYPE: As designated by Mazenot (1939, p. 79), the lectotype is the (?) unnumbered Retowski's specimen from Feodosiya (Crimea). It was first illustrated by Retowski (1893, pl. 12, fig. 1a, b).

MATERIAL: A single specimen MPP-CHT.47/6.

DIMENSIONS (mm):

Specimen	D	U	Wh	Wb
MPP-CHT.47/6	54.6	21.8	20.5	–

DESCRIPTION: MPP-CHT.47/6 is a medium size, discoidal member of the Neocomitidae with moderately involute coiling, shallow umbilicus and subrectangular, higher-than-wide whorl section with a tabulate venter. The flanks are flat. The umbilical wall is low. The early ontogenic stage is poorly preserved, but its ornament is composed of rigid, straight, single ribs on the innermost whorls. On the body chamber, the ribs are spaced, prorsiradiate and bifurcate on the midflank. They are thickened on the umbilical shoulder. At the end of the whorl, tubercles appear on the umbilical shoulder and at the furcation point. The rib branches are flattened on the upper flanks and they delimit a flat ventral band.

DISCUSSION: *D. consanguinea* and *D. subchaperi* belong to the group of *Delphinella* with two rows of tubercles on the adult whorl. *D. subchaperi* can easily be distinguished from *D. consanguinea* by its more involute coiling and denser ribbing at all stages of ontogeny. It is possible that *D. subchaperi* could represent an extreme morphology of *D. consanguinea* resulting from a covariation of the shell shape and density of ribs.

It should be noted that *D. consanguinea* and *D. subchaperi* are markedly larger than *D. delphinense*, *D. berthei* and *D.* gr. *obtusenodosa,* which were considered microconch forms since they had lateral lappets (Le Hégarat 1973). Therefore, it seems obvious that the tuberculate *Delphinella* probably corresponds to the macroconch form. A biometric study based on sufficient material is necessary for a better understanding of the intra- and interspecific variation within *Delphinella*.

OCCURRENCE: *D. consanguinea* occurs in bed 113, lower part of the Jacobi Zone *auctorum* (lower part of the *C. alpina* Subzone, Calpionella Zone).

Family Olcostephanidae Haug, 1910
Subfamily Spiticeratinae Spath, 1924

REMARKS: The subfamily Spiticeratinae has suffered from extreme taxonomic splitting and Spiticeratinae actually encompasses more than one hundred species and subspecies referred to eleven genera (see Klein 2005). Among this subfamily, *Proniceras* Burckhardt, 1919, *Spiticeras* Uhlig, 1903, *Negreliceras* Djanélidzé, 1922b and *Kilianiceras* Djanélidzé, 1922b include the great majority of the species and are considered to be distributed worldwide (except in boreal regions) across the Tithonian/Berriasian boundary interval, despite strong provincialism among Tethyan ammonite faunas at that time (Lehmann *et al*. 2015).

With the excpetion of the recently re-illustrated type of *Ammonites pronus* by Parent *et al*. (2011), the type species of *Spiticeras*, *Kilianiceras* and *Negreliceras* are still poorly documented and no other illustrations apart from the original hand-drawings are available. Since the monographic work of Djanélidzé (1922b), no modern revision of the subfamily based on new and stratigraphically well-located collecting has been undertaken. As a consequence, no precise description of the morphological and ornamental features that could help define the boundary using these genera and species is available. Even if most authors agree that there is a marked sexual dimorphism among the Spiticeratinae, the recognition of the dimorphic pairs remains unclear.

It should be noted that Parent *et al*. (2011, p. 62, 63) considered *Spiticeras* as a major synonym of the other genera listed above. This view is based on the re-examination of the holotype of *P. pronus* which shows that the hand-drawn illustration by Zittel (1868, pl. 15, fig. 8a, b) overlooked morphological characters that show affinities with the original illustration of *Spiticeras spitiensis* (Blanford, 1864).

Our efforts to locate the type specimen of *S. spitiense* have been unsuccessful and direct comparison with the holotype of *P. pronus* remains impossible. Examination of the available literature suggests that *S. spitiense* and the many typological species from the Spiti Shales (Oppel 1863; Blanford 1864; Uhlig 1903, 1910; Djanélidzé 1922b; Spath 1939; Liu 1988) and Malagasy faunas (Collignon 1960, 1962) are characterised by a larger adult size, subtriangular adult whorl section and strong tubercles on the umbilical shoulder. Following Enay (2009), we agree that the relationships between the Spiticeratinae taxa of the eastern and western areas of the Tethys are considerably more complex than has been thought. As a consequence, we follow the conservative views of Wright *et al.* (1996) regarding the systematics of the Spiticeratinae.

Genus *Proniceras* Burckhardt, 1919

TYPE SPECIES: *Ammonites pronus* Oppel *in* Zittel, 1868; by subsequent designation of Roman (1938).

REMARK: The type specimen of *Ammonites pronus* originates from the Štramberk limestone (Outer Western Carpathians of Moravia, Czech Republic) that constitutes base-of-slope conglomerates and slump bodies within the Cretaceous part of the Hradiště Formation (Eliáš and Eliášová 1986; Picha *et al.* 2006). Therefore, the precise age of *A. pronus* in its type locality remains unclear, even if a late Tithonian age has long been assigned. Toucas (1890) and Djanélidzé (1922b) reported *Ammonites pronus* in the reworked ammonite assemblage of the Brèche de Chomérac and the Brèche d'Aizy. Additional works reported and introduced new *Proniceras* species from the Tithonian/Berriasian boundary interval in Crimea (Retowski 1893; Kilian 1910) and Tunisia (Arnould-Saget 1953). The many typological *Proniceras* species could be distributed between a limited number of morphological groups that merely reflect intraspecific variation and sexual dimorphism. Unfortunately the material at our disposal is not sufficient to allow a proper revision of the content of *Proniceras*. Pending new detailed investigation we refer our specimens to *P. pronum*.

Proniceras pronum (Oppel *in* Zittel, 1868)
(Text-fig. 3Q–X)

1865. *Ammonites pronus* Oppel, p. 554.
1868. *Ammonites pronus* Oppel in Zittel, p. 91, pl. 15, fig. 8a, b, 9a–c, 11a-b (*sol.*).
? 1880. *Ammonites* (*Olcostephanus*) *pronus* (Oppel *in* Zittel); Favre, p. 40, pl. 3, fig. 9a, b.
non 1890. *Holcostephanus pronus* (Oppel *in* Zittel); Toucas, p. 596, pl. 15, fig. 14a, b, 15a, b, 16a, b (= *Proniceras toucasi*).
non 1897. *Holcostephanus* cf. *pronus* (Oppel *in* Zittel); Bogoslovsky, p. 72, pl. 4, fig. 5a–d (= *Proniceras* sp.)
1922b. *Spiticeras* (*Proniceras*) *pronum* (Oppel *in* Zittel); Djanélidzé, p. 70, pl. 2, fig. 2a, b, 3a-b; pl. 4, fig. 7; text-fig. 10.
1938. *Spiticeras* (*Proniceras*) *pronum* (Oppel *in* Zittel); Roman, p. 381, pl. 38, figs 361, 361a (= Zittel 1868, pl. 15, fig. 8a, b); text-fig. 361 (= Djanélidzé 1922b, text-fig. 10).
non 1939. *Proniceras* aff. *pronum* (Oppel *in* Zittel); Imlay, p. 57, pl. 1, fig. 8, 9 (= Spiticeratinae gen. nov.).
1952. *Proniceras pronum* (Oppel *in* Zittel); Basse, p. 647, pl. 15, fig. 15, 15a (= Zittel, 1868, pl. 15, fig. 8a, b).
1953. *Proniceras pronum* (Oppel *in* Zittel); Arnould-Saget, p. 87, pl. 9, fig. 6a–c; text-fig. 37.
non 1960. *Proniceras pronum* (Oppel *in* Zittel); Collignon, pl. 162, fig. 655 (= *Spiticeras* sp. juv.).
1996. *Proniceras pronus* (Oppel *in* Zittel); Wright *et al.*, p. 43, fig. 30.2-2a (= Zittel, 1868, pl. 15, fig. 8a, b).

TYPE: As designated by Roman (1938, p. 381), the lectotype is specimen BSPG-AS/III/211 drawned by Zittel (1868, pl. 15, fig. 8) from Koniaków (Czech Republic). It was properly illustrated by Parent *et al.* (2011, fig. 28A1-3).

MATERIAL: Eight specimens MPP-CHT.14/19, MPP-CHT.19/2, MPP-CHT.19/9, MPP-CHT.21/67, MPP-CHT.26/8, MPP-CHT.27/28 , MPP-CHT.35/4 and MPP-CHT.48/1.

DIMENSIONS (mm):

Specimens	D	U	Wh	Wb
MPP-CHT.14/19	–	–	c 11.2	10.7
MPP-CHT.19/2	29.9	13.8	8.7	c 5.4
MPP-CHT.19/9	c 25.3	–	8.1	6.5
MPP-CHT.21/67	c 41.1	16.4	13.7	c 7.6
MPP-CHT.26/8	46.5	c 17.5	17	–
MPP-CHT.27/28	14.4	–	–	–
MPP-CHT.35/4	–	–	14.1	c 16.4
MPP-CHT.48/1	24.6	10	9.5	c 4.3

DESCRIPTION: MPP-CHT.19/9 is a small fragment of a juvenile whorl characterized by evolute coiling, compressed, sub-rounded whorl section. Umbilical wall is low. It exhibits well a thin, ventral groove. Two approximated constrictions occur.

MPP-CHT.21/67 is a almost complete specimen characterized by its small adult size, moderately evolute coiling and deep umbilicus. Whorl section is depressed, sub-rounded in the innermost whorls and becoming compressed and sub-oval in the adult. The venter is rounded at all stages of ontogeny. The ornamentation is composed of strong, prorsiradiate, single ribs that form primary fasciculate ribs deriving from umbilical bullae in the adult. The number of secondary branches increases progressively. The peristome is incomplete.

MPP-CHT.33/4 is a fragment of an adult body chamber. The whorl section is markedly depressed, quasi-trapezoidal. There are almost 22 ribs that fasciculate on four strong umbilical tubercles – that is, about five ribs per tubercle. Ribs cross the venter forming a marked chevron. Peristome seems to be preceded by a deep constriction.

MPP-CHT.48/1 is a small, adult specimen characterized by a subtrapezoidal whorl section, moderately involute coiling, and with a deep umbilicus. The umbilical wall is steep. The ornamentation is composed of strong, straight, single ribs that form primary fasciculate ribs from umbilical bullae in the adult. The number of secondary ribs seems to be lower than the other specimens. A deep constriction occurs on the adult whorl. The peristome could not be studied.

MPP-CHT.26/8 is small complete specimen, but the inner whorls are not preserved. It is characterized by moderately involute coiling, markedly compressed subrectangular, higher- than-wide whorl section, with a rounded venter. The ornamentation is strongly attenuated on the flank. Three constrictions occur on the adult whorl. The peristome could not be studied.

DISCUSSION: Among the material collected at Le Chouet, specimen MPP-CHT.21/67 matches well the juvenile morphological and ornamental features of the lectotype of *P. pronum,* as illustrated on Fig. 28.A_4 in Parent et al. (2011). Specimen MPP-CHT. 33/4 matches the adult whorl of *P. pronus* and its closely allied forms *P. orientale* (Kilian, 1910) and *P. pseudogroteanum* (Djanélidzé, 1922b), that only differ by their more evolute coiling. Specimen MPP-CHT.48/1 could be easily compared with *P. celsum* (Oppel, 1865) and *P. pseudogroteanum* var. *blancheti* (Djanélidzé, 1922b), since they share a small adult size, depressed whorl section and deep umbilicus. Specimen MPP-CHT.19/9 has great affinities with the microconch forms *P. mirum* (Retowski, 1893) and *P. proteus* (Retowski, 1893).
The morphological and ornamental features of MPP-CHT.26/8 encompass those of *P. gracile* (Djanélidzé, 1922b) and *P. simplex* (Djanélidzé, 1922b).

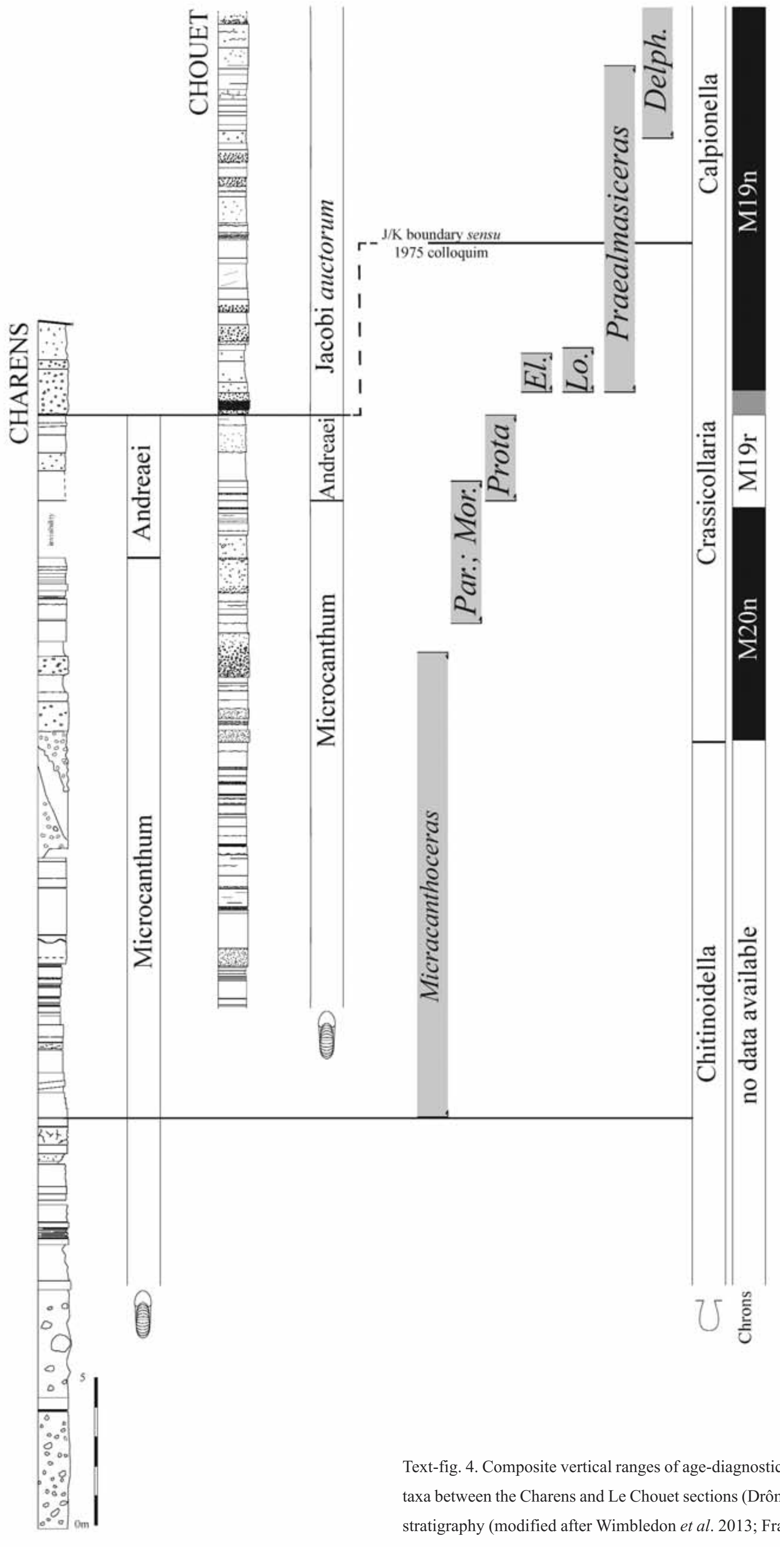
Our new collection shows that the ontogenetic sequence between *Proniceras* specimens is rather similar, but the length of ornamental stages and pattern of fasciculate ribs are strongly related to the adult shell shape. Two distinct morphologies co-occur: with small, compressed, evolute forms and larger, more or less depressed, involute forms – which may support a distinction between two antidimorphs. Unfortunately, as was discussed above, the material at our disposal is not sufficient to carry out a proper analysis of sexual dimorphism in *Proniceras*.

It should be noted that the occurrence of a thin ventral groove in the inner whorl of *P. pronum* distinguishes it from the Mexican taxa included in *Proniceras* by Burckhardt (1919). A re-examination of the illustrations of the taxa *P. aguilerae* Burckhardt, 1919, *P. idoceroides* Burckhardt, 1919, *P. victoris* Burckhardt, 1919, *P. torresense* Burckhardt, 1919, *P. subpronum* Burckhardt, 1919, *P. neohispanicum* Burckhardt, 1919 as well as *P. scorpionum* Imaly, 1939 and *P. jimulcense* Imaly, 1939 indicates that they do not compare with true *Proniceras* of the *pronum* group and deserve the introduction of a new generic name.

OCCURRENCE: *P. pronum* occurs between bed 78 and bed 114, topmost Microcanthum Zone to lower part of the Jacobi Zone *auctorum* (*C. intermedia* and *C. colomi* subzones of the Crassicollaria to the *C. alpina* Subzone of the Calpionella Zone). A similar range was reported from southern Spain by Enay and Geyssant (1975) and Tavera *et al*. (1986) but, thus far, this has not been documented.

BIOSTRATIGRAPHIC IMPLICATIONS

The original conception of the Berriasian, introduced by Coquand (1869, 1875) at the locality of Berrias-et-Casteljau (Ardèche, France) was entirely ammonite-based, and the ammonite biostratigraphy still has much to contribute to the definition of the J/K boundary (Wimbledon *et al*. 2011). However, it was previously assumed that the historical fossiliferous section did not extend low enough to reach the putative base of the Cretaceous (Le Hégarat 1973; Wimbledon *et al*. 2011, 2013). Also, thick and complex carbonate breccia systems strongly affected the ammonite-bearing, basinal succession of southeast France to such an extent that it is difficult to reconstruct a virtual complete succession across the Tithonian/Berriasian boundary (Courjault 2011).



Text-fig. 4. Composite vertical ranges of age-diagnostic Perisphinctoidea taxa between the Charens and Le Chouet sections (Drôme) and integrated stratigraphy (modified after Wimbledon *et al*. 2013; Frau *et al*. accepted)

In this connection, the section of Le Chouet, in eastern Drôme, is one of the best-developed successions, almost free of reworked facies, where it has proved possible to integrate, for the first time in southeast France, the macro- (ammonite) and microfossil (calpionellids, nannofossils) contents with magnetostratigraphy (Wimbledon *et al*. 2013). Investigation of the microfossils shows that the site comprises a sedimentary sequence in the Chitinoidella, Crassicollaria and Calpionella Zones that correlate with the magnetozones M20n, M19r and M19n. Wimbledon *et al*. (2013) confirmed that representatives of the Ataxioceratidae, Himalayitidae and Neocomitidae dominate the ammonite assemblage. The vertical range of age-diagnostic taxa allowed the recognition of the upper part of the Microcanthum Zone (= *M. fischeri* Subzone sensu Wimbledon *et al*. 2013) and the introduction of the Andreaei Zone to replace the Durangites Zone (sensu Enay and Geyssant, 1975), since that the genus Durangites Burckhardt, 1912 was considered to be endemic of Mexico (Frau *et al*. 2015).

At Le Chouet, the boundary between the Andreaei Zone and the Jacobi *auctorum* Zone falls within the calpionellid *Crassicollaria intermedia* Subzone, which confirms similar results achieved in the Rosso Ammonitico succession of Puerto Escaño, southern Spain (Tavera *et al.* 1994; Pruner *et al.* 2010). The diachronism between the base of the Jacobi Zone *auctorum* and those of the Calpionella Zone notably alters the definition of the base of the Berriasian in the sense of the 1975 colloquium on Jurassic/Cretaceous boundary based on the view of Enay and Geyssant (1975).

Bulot *et al*. (2014) and Frau *et al*. (2015) described and illustrated Perisphinctoidea taxa from the Microcanthum and Andreaei zones at Le Chouet. The present contribution ends the systematic description by the revision of the rest of the taxa of the Jacobi Zone *auctorum*. It should be noted that an additional account on the nearby Charens locality was undertaken (Frau *et al*. accepted); investigation of the macrofossils shows that that section comprises a complete Microcanthum Zone. Useful lithological and biological markers can be correlated between the Charens and Le Chouet sections and confirm that the former extends into the Andreaei Zone. A composite section may be drawn between the Charens and Le Chouet sections (Text-fig. 4). From the Microcanthum Zone to Jacobi Zone *auctorum*, four successive ammonites assemblages can be identified during this interval. From bottom to top:

An assemblage dominated by *Micracanthoceras microcanthum*;
An assemblage dominated by *Paraulacosphinctes* and *Moravisphinctes*;
An assemblage dominated by *Protacanthodiscus andreaei*;
An assemblage dominated by *Elenaella cularense, Lopeziceras chaperi* gen. nov. and *Praedalmasiceras spiticeroides* gen. nov.;
An assemblage dominated by *Praedalmasiceras progenitor* gen. nov.;
An assemblage dominated by *Delphinella*.

The preliminary results on the ammonite distribution in the nearby section of Les Combes (Glandage, Drôme) published by Frau *et al*. (2016) show that the assemblage dominated by *Delphinella* of the *delphinense* group appear at the lower boundary of the Calpionella Zone. This occurrence is slightly older than those herein documented at Le Chouet. Two distinct ammonite assemblages above the one dominated by *Delphinella* are documented at Les Combes; these are, from bottom to top:

An assemblage dominated by *Pseudosubplanites*;
An assemblage dominated by *Strambergella*

In this regard, our recent revision of the index species *Berriasella jacobi* Mazenot, 1939 convinced us that most of specimens illustrated as *B. jacobi* have been misidentified (Frau *et al*., 2016). New collection at Les Combes showed us that the type series corresponds to the microconch form of a dimorphic pair that belong to the genus *Strambergella* Nikolov, 1966. As a consequence, the vertical range of the species lead us to question its value as an index species for a lowest Berriasian biozone. Pending the description of the ammonite faunas from Les Combes, we herein follow a conservative use of the Jacobi Zone *auctorum*.

Acknowledgments

We are indebted to Emmanuel Robert (Université Claude Bernard - Lyon-I) and Fabienne Giraud (Université de Grenoble) who provided access to the palaeontological collections in their care. Valuable discussions with Raymond Enay (Université Claude Bernard - Lyon-I) and the reviewers Mikhail Rogov (Russian Academy of Science) and Horacio Parent (Universidad Nacional de Rosario) greatly improved this paper. Special thanks are due to Elsa Schebelen-David (Saint-Privat-de-Champclos) for her continuous support during this study. Warm thanks are due to the Jean-Pierre Lopez and Martine Broin families (Le Chouet and Les Près, France) for their hospitality and friendship during our fieldwork seasons.

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Manuscript submitted: 26th January 2016
Revised version accepted: 15th May 2016