Dissertation

Submitted to the
Combined Faculty of Natural Sciences and for Mathematics
Heidelberg University, Germany
for the degree of
Doctor of Natural Sciences (Dr. rer. nat.)

presented by

MSc Camille Frau

Oral examination: 17th July 2018

Systematics and biostratigraphy of the Perisphinctoidea (Ammonoidea) across the Tithonian/Berriasian boundary in South East France

Camille Frau

Referees:
PD Dr. Christina Ifrim (Ruprecht-Karls-Universität)
Prof. em. Dr. Peter Bengtson (Ruprecht-Karls-Universität)
Prof. Dr. Mario Trieloff (Ruprecht-Karls-Universität)
Prof. Dr. Oliver Friedrich (Ruprecht-Karls-Universität)

Declaration

This thesis is submitted to the Combined Faculty of Natural Sciences and for Mathematics of the Heidelberg University for the degree of Doctorate of Natural Sciences.
I, the undersigned, declare that this thesis is my own work and has not been submitted in any form from another degree, diploma or study at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

Camille Frau
On March 9 2018

Abstract

The present thesis documents and revises the systematics and biostratigraphy of the Perisphinctoidea (Ammonoidea) faunas across the Tithonian/Berriasian boundary from three basinal sections (i.e. Charens, Le Chouet and Les Combes) of eastern Drôme (South East France). Emphasis is laid on the specific diagnosis, ontogeny and dimorphism of new and little-studied Himalayitidae *Micracanthoceras*, *Protacanthodiscus*, *Boughdiriella*, *Pratumidiscus*, *Ardesciella*, *Chapericeras* and *Praedalmasiceras*, Neocomitidae *Pseudargentiniceras*, *Busnardoiceras*, *Berriasella*, *Elenaella*, *Delphinella*, *Pseudoneocomites* and *Strambergella* as well as the Olcostephanidae *Proniceras*. New data is provided on the systematic and age of the Neocomitidae *Pseudosubplanites*, *Hegaratella* and *Retowskiceras*. The distribution of these key biochronological genera is plotted next to accurate litho-logs and compared to the calpionellid zonation documented in the three sections. This provides the sound basis for a refined zonal scheme. The base of the upper Tithonian is fixed at the First Appearance Datum (FAD) of *M. microcanthum* that falls within the upper part of the tintinnid Chitinoidella Zone. The revision of the "Mediterranean *Durangites*" supports the rejection of a *Durangites* spp. Zone as part of the standard zonation for the upper Tithonian, and its replacement by the *P. andreaei* Zone. The lower boundary of the zone is fixed at the FAD of *Protacanthodiscus andreaei* that falls within the lower part of the calpionellid *C. intermedia* Subzone of the Crassicollaria Zone. Both zones are workable at the scale of the Mediterran-Caucasian Subrealm. The *Elenaella cularense* biohorizon that typifies the base of the *Berriasella jacobi* Zone *auctorum* is documented for the first time in South East France and occurs in the uppermost part of the calpionellid *C. intermedia* Subzone of the Crassicollaria Zone. This occurrence confirms the diachronism between the base of the *B. jacobi* Zone *auctorum* and those of the Calpionella Zone previously documented in southern Spain. This diachronism strongly alters the current definition of the Tithonian/Berriasian boundary. Re-examination of the type specimens of *Berriasella jacobi* supplemented by newly collected material show that this taxon should be transferred to the genus *Strambergella*. Preliminary integrated data on the stratigraphic distribution of *Strambergella jacobi* questions its value as an index species for the base of the Berriasian. No major faunal turnover is documented across the Tithonian/Berriasian boundary and the provincialism of Mediterran-Caucasian Perisphinctoidea is much higher than it was previously assumed in the literature. As a result, no ammonite species can be considered as consistent candidate for a primary boundary marker for the base of the Berriasian.

Kurzfassung

Die vorliegende Arbeit dokumentiert und revidiert die Systematik und Biostratigraphie der Perisphinctoidea (Ammonoidea) über die Tithon/Berrias-Grenze in drei Profilen (d. h. Charens, Le Chouet und Les Combes) in Ost-Drôme (Südostfrankreich). Der Schwerpunkt liegt auf der Artbestimmung, der Ontogenese, Variation und dem Dimorphismus der neuen, wenig bekannten Himalayitidae *Micracanthoceras*, *Protacanthodiscus*, *Boughdiriella*, *Pratumidiscus*, *Ardesciella*, *Chapericeras* und *Praedalmasiceras*, sowie der Neocomitidae *Pseudargentiniceras*, *Busnardoiceras*, *Berriasella*, *Elenaella*, *Delphinella*, *Pseudoneocomites* und *Strambergella*. Die vertikalen Reichweiten der Vertreter dieser Gattungen werden genau gegen akkurate lithostratigraphische Profile aufgetragen, sowie die der Neocomitidae *Pseudosubplanites*, *Hegaratella* und *Retowskiceras*. Die jeweilige Verteilung dieser biostratigraphischen Schlüsselgattungen wird mit der Calpionellidenzonierung verglichen, die in den drei Profilen dokumentiert wird und die eine solide Basis für eine verfeinerte Zonierung bietet. Die Basis des Obertithon ist festgelegt durch das Erstauftreten von *M. microcanthum*, das in den oberen Teil der Chitinoidella-Tintinniden-Zone fällt. Die Revision der "mediterranen *Durangites*" unterstreicht die Aufgabe der *Durangites*-spp.-Zone als Teil der Standardzonierung im Obertithon und ihren Ersatz durch die Andreaei-Zone. Die Untergrenze dieser Zone ist durch das Erstauftreten von *Protacanthodiscus andreaei* festgelegt, das im Unterteil der *C.-intermedia*-Calpionelliden-Subzone der Crassicollaria-Zone liegt. Beide Zonen sind im Bereich des Mediterran-kaukasischen Unterreiches praktikabel. Der *Elenaella-cularense*-Biohorizont, der die Basis der *Berriasella jacobi*-Zone *auctorum* repräsentiert, wird zum ersten Mal in Südfrankreich dokumentiert und tritt im obersten Teil der *C.-intermedia*-Calpionelliden-Subzone der Crassicollaria-Zone auf. Dieses Auftreten bestätigt den Diachronismus zwischen der Basis der *B. jacobi*-Zone *auctorum* und der Calpionella-Zone, die zuvor in Südspanien dokumentiert wurde. Dieser Diachronismus verändert deutlich die aktuelle Definition der Tithon-Berrias-Grenze. Die Neuuntersuchung der Typusexemplare von *Berriasella jacobi*, die von neugesammeltem Material ergänzt wird, zeigt, dass dieses Taxon in die Gattung *Strambergella* gestellt werden sollte. Vorläufige ganzheitliche Daten zur stratigraphischen Verbreitung von *Strambergella jacobi* stellen ihren Wert als Indexart für die Basis des Tithon in Frage. Über die Tithon/Berrias-Grenze hinweg ist kein größerer Faunenumschwung dokumentiert, und der Provinzialismus der mediterran-kaukasischen Perisphinctoidea ist viel ausgeprägter als zuvor in der Literatur angenommen.

Als Ergebnis kann keine Ammonitenart als passender Kandidat als primärer Grenzmarker für die Basis des Berrias betrachtet werden.

Table of contents

Appendix 1: Wimbledon W.A.P., Reháková D., Pszczółkowski A., Cassellato C.E., Halásová E., Frau C., Bulot L.G., Grabowski J., Sobień K., Pruner P., Schnabl P., Čížková K.,Tchoumatchenco P., 2013 - A preliminary account of the bio- and magnetostratigraphy of the upper Tithonian- lower Berriasian interval at Le Chouet, Drôme (SE France). Geologica Carpathica 64(6): 437-460.

Appendix 2: Bulot L.G., Frau C., Wimbledon W.A.P., 2014 - New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Drôme, SE France). Volumina Jurassica, XII (1): 113-128.

Appendix 3: Frau C., Bulot L.G., Wimbledon W.A.P., 2015 - The late Tithonian Himalayitidae (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): systematic implications. Geologica Carpathica 66(2): 117-132.

Appendix 4: Frau C., Bulot L.G., Wimbledon W.A.P., 2016 - Systematic palaeontology of the Perisphinctoidea across the Jurassic-Cretaceous boundary at Le Chouet (Drôme, France) and its biostratigraphic implications. Acta Geologica Polonica 66(2): 157-177.

Appendix 5: Frau C., Bulot L.G., Reháková D., Wimbledon W.A.P., 2016 - Upper Tithonian ammonites (Himalayitidae Spath, 1925 and Neocomitidae Salfeld, 1921) from Charens (Drôme, France). Geologica Carpathica 67(6): 543-559.

Appendix 6: Frau C., Bulot L.G., Reháková D., Wimbledon W.A.P., 2016 - Revision of the ammonite index species *Berriasella jacobi* Mazenot, 1939 and its consequence for the biostratigraphy of the Berriasian Stage. Cretaceous Research 66: 94-114.

Appendix 7: Lehmann J., Ifrim C., Bulot L.G., Frau C., 2015 - Chapter II, Part 9. Paleobiogeography of early Cretaceous ammonites In**:** Klug**,** C., Korn**,** D., De Baets**,** K., Kruta**,** I., Mapes**,** R.H. (Eds.) Ammonoid Paleobiology: From macroevolution to paleobiogeography. Topics in Geobiology 44, Springer Netherlands, 598 pp.

Chapter 1 - Introduction

The ammonite faunas across the Jurassic/Cretaceous (J/K) boundary undoubtedly exhibit one of the most pronounced cases of provincialism in the Mesozoic (Cecca, 1999; Cecca et al., 2005). At that time, faunal endemism reached its maximum due to the complete seperation of the Boreal and Tethyan realms, as well as inside the Tethyan Realm where a Mediterranean-Caucasian and an Indo-Pacific subrealms have been recognized by Westermann (2000a-b). This provincialism has for generations prevented substantial progress with long-range correlation (Wimbledon, 2008), and strongly influenced the nationalistic use of regional stage names (e.g. Danubian, Ardescian, Bolonian for the Tethyan Realm; Portlandian, Volgian, Ryazanian for the Boreal Realm) even after the ratification of the Tithonian and Berriasian as Primary Standard Stages of the Upper Jurassic and Lower Cretaceous, respectively (Cope, 2008, 2013; Wimbledon, 2008; Wimbledon et al., 2011). This explains why the base of the Cretaceous is the last system boundary which is not yet defined formally in a Global Boundary Stratotype Section and Point (Wimbledon et al., 2011).

It should be kept in mind that the base of the Cretaceous is inextricably linked to the Tithonian/Berriasian (T/B) boundary (Wiedmann, 1973; Remane et al., 1986; Zakharov et al., 1996; Wimbledon et al., 2011), but it has been an intractable problem, despite some 40 years of debate within successive working groups dedicated to this issue (Zakharov et al., 1996). Nevertheless, the original conception of the Berriasian by Coquand (1869, 1875) at the locality of Berrias-et-Casteljau (Ardèche, South East France) was entirely ammonite-based, and the ammonite biostratigraphy of Mediterrean-Caucasian settings still has much to contribute to the definition of the J/K boundary.

1.1. The Mediterranean-Caucasian ammonite record across the T/B boundary

The knowledge of the Mediterran-Caucasian ammonites across the T/B boundary is substantial, and mostly concerns the super-family Perisphinctoidea Steinmann *in* Steinmann & Döderlein, 1890 that is represented by six families, e.g. Aspidoceratidae Zittel, 1895, Ataxioceratidae Buckman, 1921, Simoceratidae Spath, 1924, Himalayitidae Spath, 1925, Neocomitidae Salfeld, 1921 and Olcostephanidae Haug, 1910 reported from, at least, fifteen major regions (Tab.1).

Mediterran-Caucasian settings	References
South East France	Pictet, 1867, 1868; Toucas, 1890; Djanélidzé, 1921, 1922; Mazenot, 1939; Le Hégarat, 1973; Cecca et al., 1989a; Enay & Cecca, 1986; Enay et al., 1998a-c
Crimea	Retowski, 1893; Kvantaliani 1989; 1999; Bogdanova & Arkadiev, 1999, 2005; Bogdanova et al., 1984, 1999; Arkadiev, 2004, 2007a-b, 2008, 2011a-b, 2014; Arkadiev & Bogdanova, 2005; Arkadiev et al., 2005, 2007, 2008, 2011, 2012
Austria	Zeiss, 2001
Bulgaria	Nikolov, 1960, 1966, 1967a, b, 1982 ; Nikolov & Mandov, 1967; Sapunov, 1977a-b, 1979; Ivanov et al., 2009, 2010
Hungary	Fözy & Scherzinger, 2013; Szives & Fözy, 2013
Poland	Marek, 1967
Romania	Patrulius & Avram, 1976
Czech Republic	Oppel, 1865, Zittel, 1868, 1870; Vašíček & Skupien, 2013, 2014; Vašíček et al., 2013
Italy	Canavari, 1899; Cecca, 1985, Cecca et al., 2001
southern Spain	Enay & Geyssant, 1975; Hoedemaeker, 1979, 1981, 1982; Olóriz, 1978; Olóriz & Tavera, 1979a-b, 1981, 1989; Tavera, 1985; Tavera et al. 1986, 1994; Enay et al., 1998a-c
Morocco	Benzaggagh & Atrops, 1997; Benzaggagh, 2000; Benzaggagh et al., 2010
Tunisia	Arnould-Saget, 1953; Memmi, 1967; Memmi & Salaj, 1975; Donze et al., 1975; Busnardo et al., 1976, 1985; Boughdiri et al., 1999, 2005; Olóriz et al., 2006; Maalaoui & Zargouni, 2016
Algeria	Pomel, 1889; Roman, 1936; Benest et al., 1977; Tchoumatchenco et al., 1995
Turkey	Enay et al., 1971
northern Iran	Cecca et al., 2011

Table 1. Main references of T/B boundary ammonites from the Mediterran-Caucasian Subrealm.

Despite the tremendous quantity of fossil material illustrated and/or listed by those authors, a critical review of the dataset shows that the picture one can discerned of the evolution of the Perisphinctoidea from the base of the upper Tithonian to the upper Berriasian is far from complete clarity. Even if most publications have concentrated on the Himalayitidae and Neocomitidae their systematic are still full of varying interpretations. This is linked to diverging concepts between authors, but also to preservation problems (e.g. pyritic nuclei from Tunisia; crushed moulds from Bulgaria) which clearly affects attempts to identify and compare taxa (Wimbledon et al., 2011). Moreover, detailed bed-by-bed ammonite distributions plotted against accurate lithologic logs are not available for reference sections of Spain, Algeria and Bulgaria. In some other cases, stratigraphic columns lack sufficiently illustrated fossils, such as in Crimea where only stylised, and sometimes composite, sections have been published

(Bakhmutov et al 2017). As a consequence, only a limited number of sections have been documented accurately; most of which are located in South East France, southern Spain, Morocco and Tunisia. Among those sections, a discontinuous palaeontological record is the rule. It can either be linked to reworking of sediments (a common feature in South East Spain and France - Tavera, 1985; Le Hégarat, 1973), scarcity of fossils (barren intervals in the Tunisian sections - Busnardo et al., 1976, 1985; Boughdiri et al., 1999), poor exposure of key intervals (Rio Argos, Spain - Hoedemaeker, 1982), and non-deposition and major hiatuses (Rif of Morocco - Benzaggagh & Atrops, 1997).

The upper Tithonian standard ammonite zonation of Mediterran-Caucasian settings is largely inherited from the works of Enay & Geyssant (1975), Olóriz & Tavera (1979a-b), Tavera (1985) and Tavera et al. (1994) based on the Rosso Ammonitico successions of the Betic Cordillera, southern Spain. Enay & Geyssant (1975) never gave a formal definition of the biostratigraphic units they proposed (e.g. *Micracanthoceras microcanthum* Zone and *Durangites* Zone) contrary to the Spanish authors who clearly indicated the status of their zones (Taxon range zones for the *Simplisphinctes* and *Paraulacosphinctes transitorius* zones; Acme Zone for the *Durangites* Zone) (Fig. 1.1).

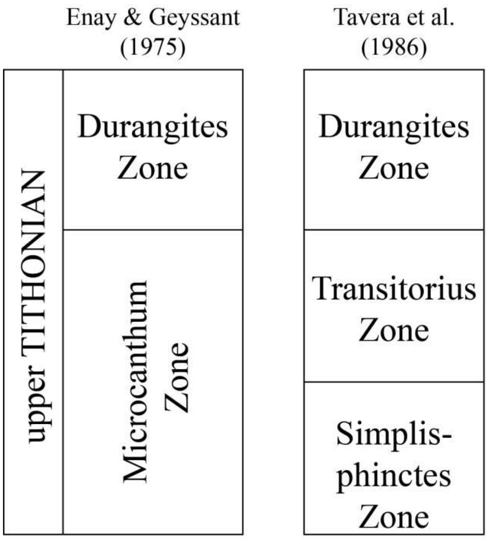


Figure 1.1. Comparison between the original ammonite zonation of the upper Tithonian of the Rosso Ammonitico succession of southern Spain of Enay & Geyssant (1975) and Tavera et al. (1986).

Nevertheless, French and Spanish authors have agreed that the Himalayitidae *Durangites* Burckhardt, 1912 marks the uppermost Tithonian. This taxon is based on material from Mexico and its content was supplemented by Verma & Westermann (1973). Until recently, there was general agreement that the *Durangites* assemblage described by Verma & Westermann (1973) from the El Verde member of the La Caja Formation (Sierra Catorce, Mexico) were of late

Tithonian age (Adatte et al., 1994, 1996). However, most localities from which *Durangites* were collected are hill slopes, and therefore most of the material was collected loose (Verma & Westermann, 1973). A complete reappraisal on the age of *Durangites* in Mexico was presented by Olóriz et al. (1999), who found the genus to be restricted to the middle Berriasian. The occurrence of *Durangites* in Turkey, southern Spain and South East France were not reported until the early 1970's to early 1980's by Enay et al. (1971), Enay & Geyssant (1975) and Olóriz & Tavera (1979a-b, 1981) and its understanding was based on a limited number of specimens illustrated by Tavera (1985), Boughdiri (1994) and Enay et al. (1998a). Most of specimens come from the uppermost Tithonian of South East Spain (Carabuey and La Coronilla sections mainly) and France (Le Chouet section). Boughdiri (1994) and Enay et al. (1998a) considered *Durangites* and *Protacanthodiscus* Spath, 1923 as a sexual dimorphic pair; a view that was not supported by Tavera (1985), since no *Protacanthodiscus* occurs in the Mexican assemblage. As a consequence, the understanding of both genera, as well as their vertical range, remain unclear in the Mexican, Spanish and French assemblages.

The Berriasian standard ammonite zonation of Mediterran-Caucasian settings is largely inherited from the works of Le Hégarat & Remane (1968) and Le Hégarat (1973) who published idealized ammonite distributions from numerous sections of South East France. Following the recommendation of the Colloquium at Lyon in 1973 (Flandrin et al., 1975), the first ammonite zone of the Berriasian corresponds to the combined *Berriasella jacobi* - *Pseudosubplanites grandis* Zone, herein referred as the *B. jacobi* Zone *auctorum*. The understanding of this zone is based on reworked ammonite assemblages from breccia deposits in Ardèche ('*Brèche de Chomérac*') and Isère ('*Brèche d'Aizy*'), including *Berriasella jacobi* Mazenot, 1939, *Delphinella delphinense* (Kilian, 1889), *Elenaella cularense* (Mazenot, 1939) and *Proniceras pronum* (Oppel *in* Zittel, 1868) with typical late Tithonian forms such as *Micracanthoceras microcanthum* (Oppel *in* Zittel, 1868). Most recent literature subsequently fails to document a continuous ammonite distribution in South East France since the T/B boundary interval is affected by a thick and complex carbonate breccia system (Le Hégarat, 1973; Cecca et al., 1989a-b).

According to Mazenot (1939), this stratigraphic gap, called '*lacune des connaissances*', would correspond to the ammonite assemblage - including *Paraulacosphinctes transitorius* (Oppel *in* Zittel, 1868) - from the Štramberk limestone *pro parte* (Outer Western Carpathians of Moravia, Czech Republic), listed by Oppel (1865) as a reference locality for the Tithonian. However, the precise age of this assemblage also remains unclear, since the Štramberk limestone is complex, and has been interpreted as including base-of-slope conglomerates and slump bodies of Cretaceous age, and part of the Hradiště Formation (Picha et al., 2006). The ammonite zonation of the Berriasian thus evolved very little between the first meeting of Lower Cretaceous Cephalopod Working Group of IGCP Project 262, held in July 1990 at Digne, France (Hoedemaeker & Bulot, 1990; Hoedemaeker et al., 1993) and the last one that took place on August 2013 at Ankara, Turkey (Reboulet et al., 2014) (Fig. 1.2). Hoedemaeker & Bulot (1990) previously outlined that the great majority of the Le Hégarat's zones and subzones have been maintained, notwithstanding the fact that they are not defined by the first appearance of their index species – a necessity to preserve stability in stratigraphic nomenclature.

		Hoedemaeker & Bulot (1990)		Zakharov et al. (1996)		Reboulet et al. (2014)	
Berriasian	upper	F. boissieri	un-named	F. boissieri	T. alpillensis	S. boissieri	T. otopeta
			B. picteti		P. picteti		T. alpillensis
			M. paramimouna		M. paramimounum		P. picteti
							paramimounum
	middle	T. occitanica	D. dalmasi	T. occitanica	D. dalmasi	S. occitanica	D. dalmasi
			B. privasensis		B. privasensis		B. privasensis
			T. subalpina		T. subalpina		S. subalpina
	lower	B. jacobi	P. grandis	B. jacobi	P. grandis	B. jacobi	
			B. jacobi		B. jacobi		

Figure 1.2. Comparison of the ammonite standard zonation of the Berriasian between three Cephalopod Working Group meetings (Hoedemaeker & Bulot, 1990; Zakharov et al., 1996 and Reboulet et al., 2014).

Finally, Le Hégarat & Remane (1968) and Le Hégarat (1973) revised the ammonite distribution of the historical stratotype of the Berriasian at Berrias-et-Casteljau, a 25m-thick succession of blue-grey micritic hemipelagic limestones that crop out as overgrown structural surfaces. A large number of works devoted to the microfaunas and floras, carbon/oxygen isotopes, sequence- and magnetostratigraphy were subsequently published on Berrias-et-Casteljau (Naud & Reboulet, 2008 with references), but these works used different lithological logs and three generations of bed-numbering were followed. Therefore, it is impossible to correlate the detailed log of Le Hégarat & Remane (1973) with the ones published by Le Hégarat & Remane (1968), Galbrun (1985), Galbrun et al. (1986) and Jan Du Chêne et al. (1993) (Fig. 1.3). In any case, these works showed that the historical fossiliferous section does not extend low enough to reach the putative base of the Berriasian (Le Hégarat, 1973; Wimbledon et al., 2011). Thus, the unit-stratotypical section is not suitable for the study of the T/B boundary.

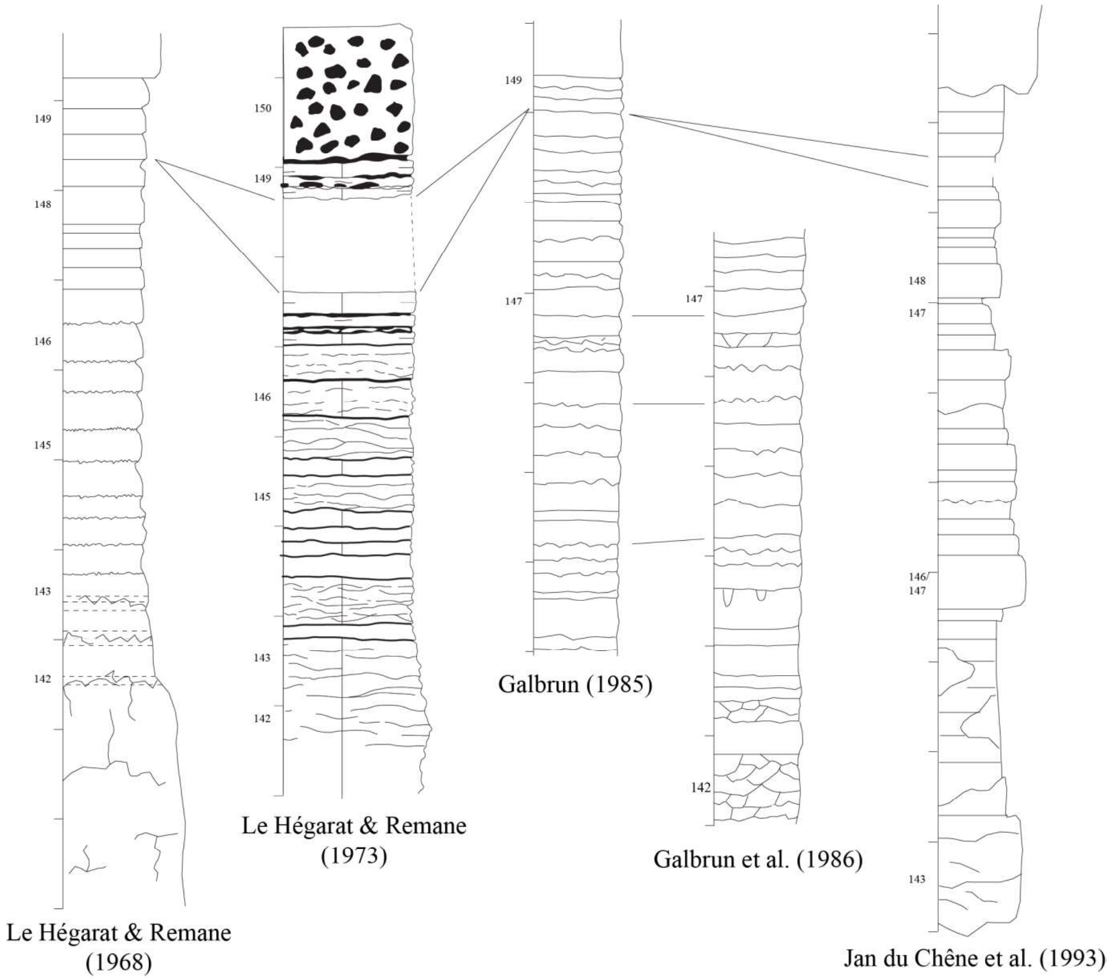


Figure 1.3. Comparison of published litho-logs of the Berrias-et-Casteljau section between Le Hégarat & Remane (1968, 1973), Le Hégarat (1972), Galbrun (1985), Galbrun et al. (1986) and Jan du Chêne et al. (1993) (modified from Wimbledon, unpublished data).

In summary, the use of ammonites to define precisely the base of the Berriasian is handicapped by:

1 - Lack of a modern discussion of the systematics of age-diagnostic taxa;

2 - Scarcity of data in expanded key stratigraphic intervals, such as the base of the *B. jacobi* Zone *auctorum*;

3 – Poor definition of biostratigraphic units, which prevents high-resolution correlation.

1.2. The calpionellid solution?

The widespread identification of calpionellids, *incertæ sedis* planktonic microfossils (Remane *in* Bolli et al., 1989), has afforded a parallel framework to the ammonite biostratigraphy, and became the dominant biostratigraphic tool where no ammonite were to be found (Wimbledon et al., 2011). Above early hyaline forms that characterize the Chitinoidella Zone, five successive calpionellid assemblages (firstly labelled A to E) were originally documented from the reference sections of South East France by Remane and Le Hégarat (Remane (1963), Le Hégarat & Remane (1968), Le Hégarat (1973) and then documented in the Tethyan Realm, from Mexico to the Caucasus. Following the international meetings at Rome (Allemann et al., 1975) and Sümeg (Remane et al., 1986), the zonation was based on four calpionellids (*Crassicollaria, Calpionella, Calpionellopsis* and *Calpionellites*) standard zones supplemented by several sub-zones (Fig. 1.4).

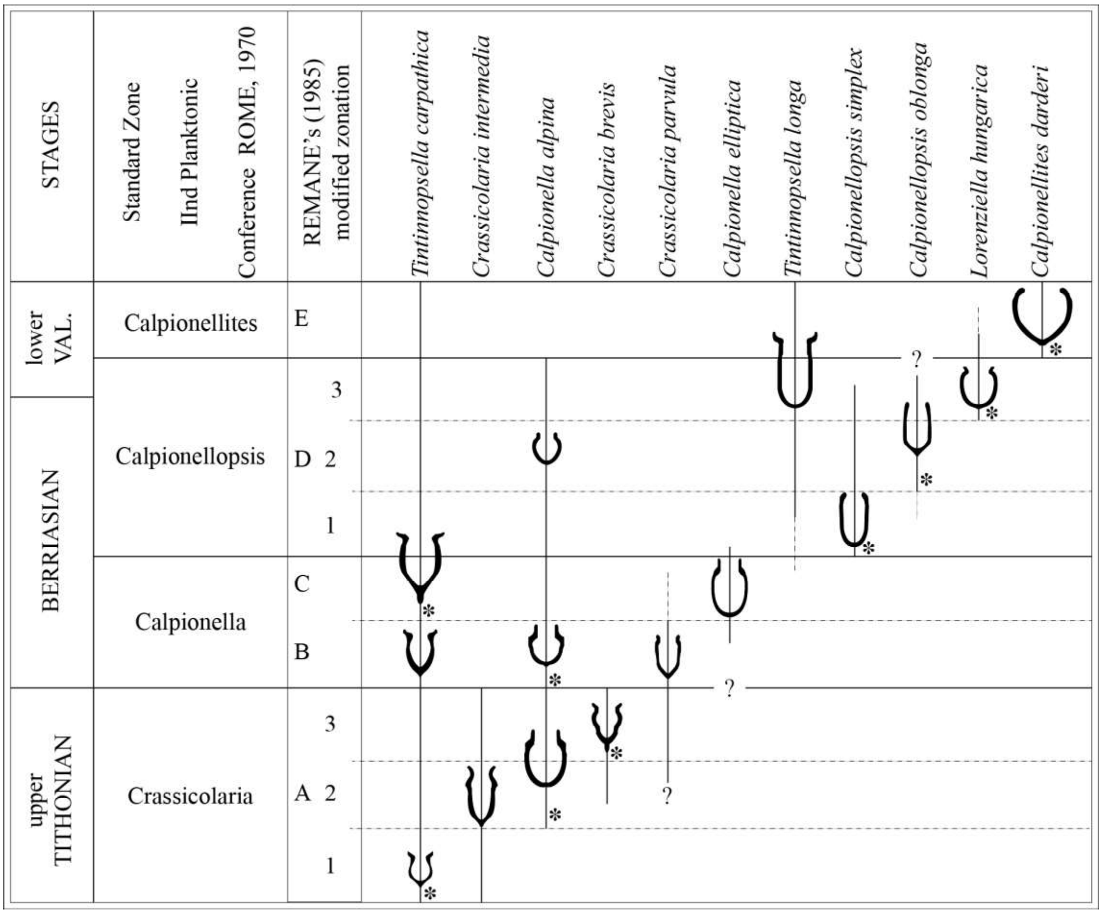


Figure 1.4. Synthetic stratigraphic distribution of the most significant calpionellids species (after Remane *in* Cariou & Hantzpergue, 1997). The asterisk indicates the calpionellid bio-events on which the lower boundary of the zones and subzones are based.

The base of the Calpionella Zone (i.e. *C. alpina* Subzone) is defined by the 'explosion' of small, globular *Calpionella alpina* Lorenz, 1902 and stands among the most widespread and consistent candidate for a primary boundary marker (Wimbledon, 2014; Wimbledon et al., 2011). Enay & Geyssant (1975) stressed that the base of the Calpionella Zone matches the boundary between the ammonite *Durangites* Zone and the *B. jacobi* Zone *auctorum* in the Rosso Ammonitico succession of the Betic Cordillera. Even though, this view was not been supported by integrated sedimentological-biostratigraphical data from detailed litho-log, it was retained as the definition of the T/B boundary in the 1975 J/K boundary colloquium (Flandrin et al., 1975) and subsequently followed by Zeiss (1983), Cecca et al. (1989a-b), Boughdiri (1994), Blau & Grün (1997), Geyssant *in* Cariou & Hantzpergue (1997), Boughdiri et al. (2006), Benzaggagh & Atrops (1997) and Benzaggagh et al. (2010) (Fig. 1.5). The recent examination of a Rosso Ammonitico section (i.e. Puerto Escaño) from the Betic Cordillera by Tavera et al. (1994) showed that the base of the *B. jacobi* Zone *auctorum* is characterized by a distinctive ammonite assemblage, i.e. the *Elenaella cularense* biohorizon, that falls in the upper part of the Crassicolaria Zone (Fig. 1.5). Therefore, the definition of the T/B boundary was strongly altered and the parallel use of ammonites and calpionellids should be considered with caution.

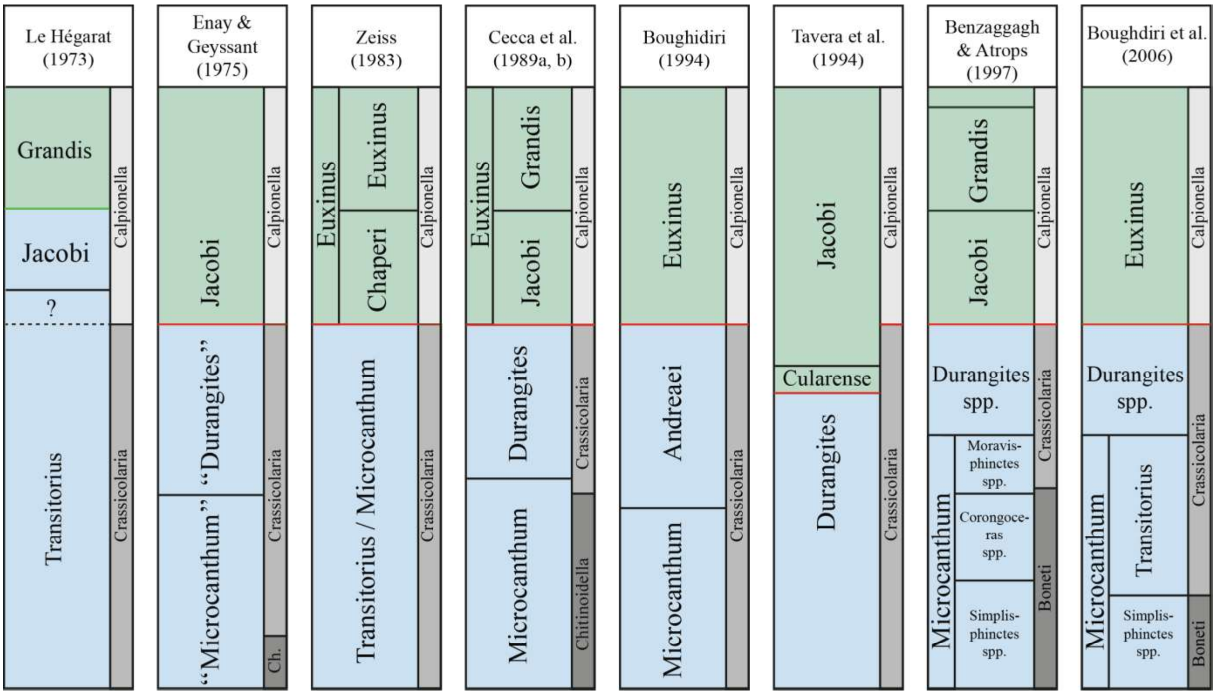


Figure 1.5. Comparison between integrated zonation from the works discussed in the text from different Mediterran-Caucasian settings. Red line indicates the T/B boundary in the sense of the 1975 colloquium (Flandrin et al., 1975).

1.3. Recent directions and objectives

The Berriasian Working Group (BWG) of the International Union of Geological Sciences (IUGS) recently stated that one of its most challenging direction is to re-visit the ammonite faunas, re-examine the validity of taxa and their ranges and question the definition of previously proposed biostratigraphic units of the Tethyan Realm (Wimbledon et al., 2011). The BWG then also gave a compilation of primary and secondary markers under examination as potentially useful T/B boundary indicators in the Tethyan Realm. These include biological markers, e.g. macro- [ammonites] and micro- [calpionellids, nannoconnids] fossils, and their proxies, i.e. magnetostratigraphy (Fig. 1.6).

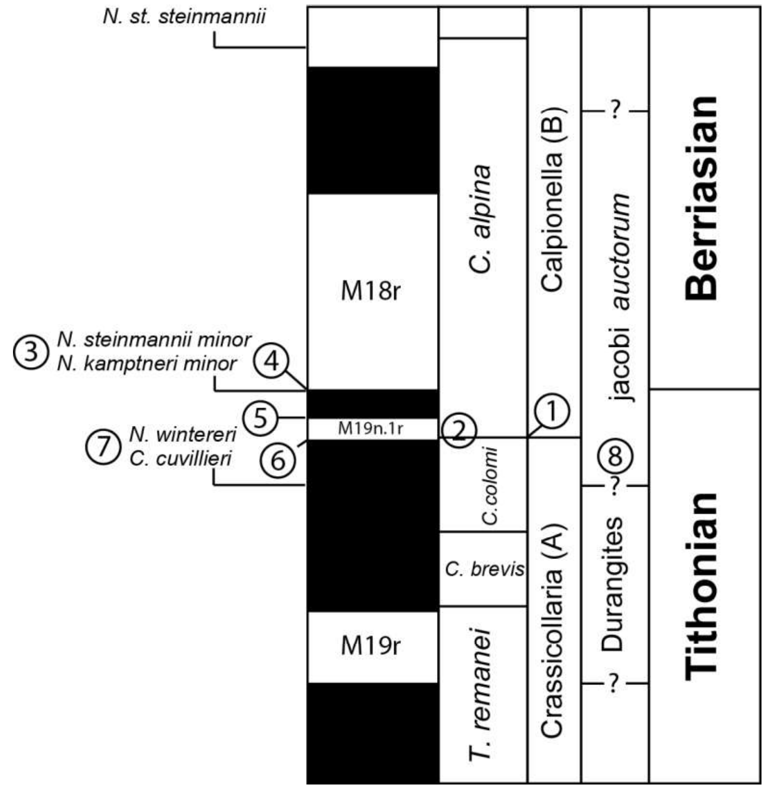


Figure 1.6. Primary and secondary markers under examination as potentially useful in defining the J/K boundary interval in the Tethyan Realm: (1) Base of Calpionella Standard Zone (B Zone); (2) 'explosion' of small, globular *C. alpina*; (3) FAD of *Nannoconus steinmanii minor* and *N. kamptneri minor*: (4) Base of magnetozone M18r; (5) Base of magnetozone M19n.1n; (6) Base of magnetozone M19n.1r; (7) FAD of *Nannoconus winteri* and *Cruciellipsis cuvillieri*; (8) Base of Jacobi *auctorum* Zone (modified after Wimbledon et al., 2011).

To achieve this, the revision of the reference sections of South East France should be undertaken since it is a critical area for the definition of the Tithonian and Berriasian stages by means of ammonites (Wimbledon, 2008). First recognition at Berrias-et-Casteljau (Ardèche, South East France) in 2009-2011 by members of the BWG (W.A.P. Wimbledon, L.G. Bulot) confirmed that the unit-stratotypical section of the Berriasian does not extend low enough to reach the putative base for the Berriasian. Therefore, a start has been made on examining other localities in southern France – seeking 'templates' for the topmost Tithonian ("*Durangites* Zone") to the lower Berriasian (*B. jacobi* Zone *auctorum*). These include the little-studied sections of Le Chouet, Charens and Les Combes located in eastern Drôme that were previously listed as crucial for the understanding of the T/B boundary (Remane, 1970; Le Hégarat, 1973; Boughdiri, 1994; Enay et al., 1998a). These sections were sampled bed-by-bed, including macro- (ammonites) and microfossils (calpionellids, nannofossils) between 2012 and 2015; Le Chouet and Les Combes sections were sampled for magnetostratigraphy in 2011-2012. The integration of the results documented at Le Chouet led to the publication of a work of major interest that forms the litho-, bio and magnetostratigraphic core of this thesis (Appendix 1):

Appendix 1 - Wimbledon W.A.P., Reháková D., Pszczółkowski A., Cassellato C.E., Halásová E., Frau C., Bulot L.G., Grabowski J., Sobień K., Pruner P., Schnabl P., Čížková K.,Tchoumatchenco P., 2013 - A preliminary account of the bio- and magnetostratigraphy of the upper Tithonian- lower Berriasian interval at Le Chouet, Drôme (SE France). Geologica Carpathica 64(6): 437-460.

From the ammonites collected, five papers on the systematic and biostratigraphy of the age-diagnostic ammonite taxa were subsequently published in peer-reviewed journals (Appendix 2, 3, 4, 5, 6).

Appendix 2: Bulot L.G., Frau C., Wimbledon W.A.P., 2014 - New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Drôme, SE France). Volumina Jurassica, XII (1): 113-128.

Appendix 3: Frau C., Bulot L.G., Wimbledon W.A.P., 2015 - The late Tithonian Himalayitidae (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): systematic implications. Geologica Carpathica 66(2): 117-132.

Appendix 4: Frau C., Bulot L.G., Wimbledon W.A.P., 2016 - Systematic palaeontology of the Perisphinctoidea across the Jurassic-Cretaceous boundary at Le Chouet (Drôme, France) and its biostratigraphic implications. Acta Geologica Polonica 66(2): 157-177.

Appendix 5: Frau C., Bulot L.G., Reháková D., Wimbledon W.A.P., 2016 - Late Tithonian Himalayitidae Spath, 1925 and Neocomitidae Salfeld, 1921 from the Tithonian of Charens (Drôme, France). Geologica Carpathica 67(6): 543-559.

Appendix 6: Frau C., Bulot L.G., Reháková D., Wimbledon W.A.P., 2016 - Revision of the ammonite index species *Berriasella jacobi* Mazenot, 1939 and its consequence on the ammonite biostratigraphy of the Berriasian Stage. Cretaceous Research 66: 94-114.

The revised systematics allowed us to discuss the palaeobiogeographic distribution of early Berriasian ammonites in a chapter of the book Ammonoid Paleobiology (Appendix 7).

Appendix 7 - Lehmann J., Ifrim C., Bulot L.G., Frau C., (2015) - Chapter II, Part 9. Paleobiogeography of early Cretaceous ammonites In: Klug**, C.,** Korn**,** D.**,** De Baets**,** K.**,** Kruta**,** I.**,** Mapes**,** R.H. (Eds.) Ammonoid Paleobiology: From macroevolution to paleobiogeography. Topics in Geobiology 44, Springer Netherlands, 598 pp.

The principal objectives of the present thesis are:

- To document the vertical ranges of Perisphinctoidea in the best-developed successions of South East France;
- To provide systematic revision of the taxa that have high-stratigraphic value;
- To propose a revised biostratigraphic scheme;
- To integrate the ammonite zonation with that of the calpionellids;

Additional aspects involve the palaeobiogeographic distribution of Perisphinctoidea among the Tethyan Realm, and their potential use as primary markers for the T/B boundary.

Chapter 2 - Geological setting

2.1. Generalities on the Subalpine Basin (South East France)

According to Baudrimont & Dubois (1977) and Debrand-Passard et al. (1984), the Subalpine Basin (here labelled SB) of South East France appeared as a result of post-Triassic Alpine extension, and it deepened through the Lower Cretaceous. During the J/K boundary time interval, the basinal area of the SB occupied an approximately triangular area, its base extending across northern Provence to the Bas-Vivarais, 250 km west to east, with a prolongation northwards to a narrow apex that covers the subalpine ranges (Fig. 2.1).

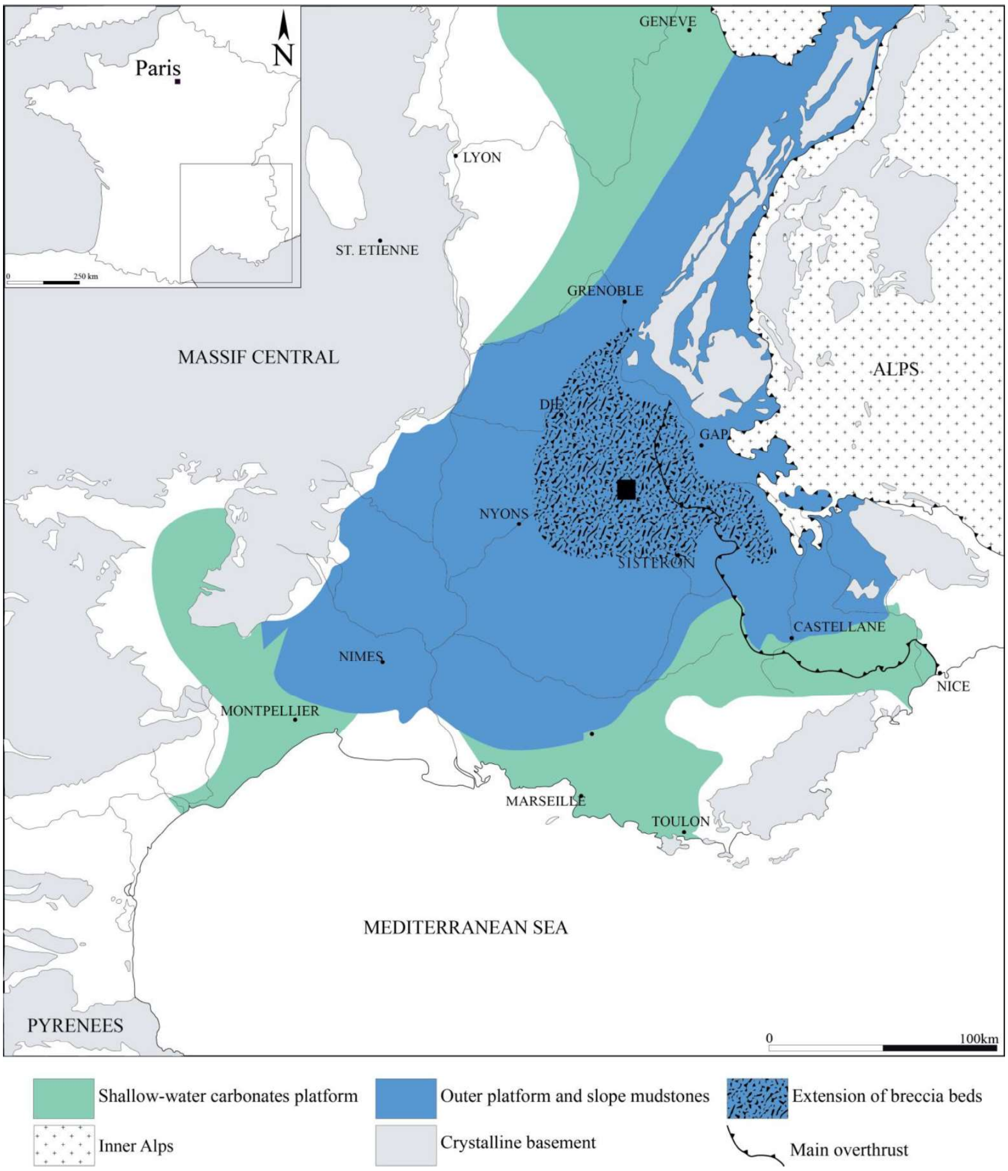


Figure 2.1. Location and palaeogeography of the Subalpine Basin at the Tithonian/Berriasian boundary (modified after Courjault, 2011). The black square corresponds to the studied area.

The upper Kimmeridgian to lowermost Berriasian interval of the deep area corresponds to deep-water hemipelagic deposits affected by submarine gravity reworkings (slumps, breccias) that leave only few autochthonous, ammonite-bearing intervals (Courjault, 2011). According to Le Hégarat (1973), the area between Die (Drôme) and Veynes (Hautes-Alpes) contains the best-developed successions of the SB with attenuated reworked deposits. Extensive fieldwork on this area led to the re-examination of several little-studied sections: these are Le Chouet, and its nearby equivalent section of Charens, and Les Combes (eastern Drôme) that have yielded the Perisphinctoidea studied in this thesis.

2.2. Description of the sections

2.2.1. Le Chouet

Localisation: The locality lies in the cliffed upper valley of the River Drôme, in pine forest (Long 5°33'33"E, Lat 44°32'32"N) off the local road (D306) from Die to Valdrôme (Fig. 2.2). The section comprises a low mural section, 200 m-long, along a single-track road on the north-west side of a precipitous gorge, the Ravin de Fournet. The section extends around the slope from an altitude of 928 m to a little above 1000 m and dips 10 degree to the North northeast.

Background: A detailed historical background on this section is given in Appendix 1 (p. 438), to which the reader is referred. The microfossils (i.e. calpionellids, nannofossils) and magnetozones were documented by scientists of the BWG (see Appendix 1), and this provides a solid litho-, bio- and magnetostratigraphic scheme.

Lithology: The succession exposed totals 43 metres and consists of well-bedded micrite and biomicrite – mudstone, wackestone and packstone- limestones beds. Only the lower beds (beds 1 to 51) show any appreciable argillaceous partings or thin beds (Fig. 2.3a-b). Massive conglomerates and breccias (both clast and matrix supported) and thin intraclastic/microbreccia beds (beds 77 and 80, Fig. 2.4a) punctuate the sequence. These are variable in their grain sizes and textures: units with graded bedding (beds 52, 57, 64, Fig. 2.3b), coarse bases (beds 64, 71a-b, Fig. 2.4b), 'floating' larger clasts in micrite (beds 84, 104, Fig; 2.5a) and clast-supported beds (bed 87, 94, 96). Topping the section, a 10 m-thick, massive or poorly bedded micrite occurs with 'floating' pebbles and derived, abraded body fossils (bed 123, Fig. 2.5b).

Fossils and taphonomy: Ammonites, and aptychi, are numerous in micritic limestone beds, excepting in the lowest ten metres (bed 1 to 64). Occasional isolated bivalves and pygopid brachiopods have been noticed in beds 82 and 90, and belemnites are common in bed 103. The great majority of ammonite specimens are characterized by internal calcareous molds that rarely exceed 100 mm in diameter, with innermost whorls generally crushed by compaction. The ammonite assemblages show a high proportion of complete specimens, but peristomes are generally lacking.

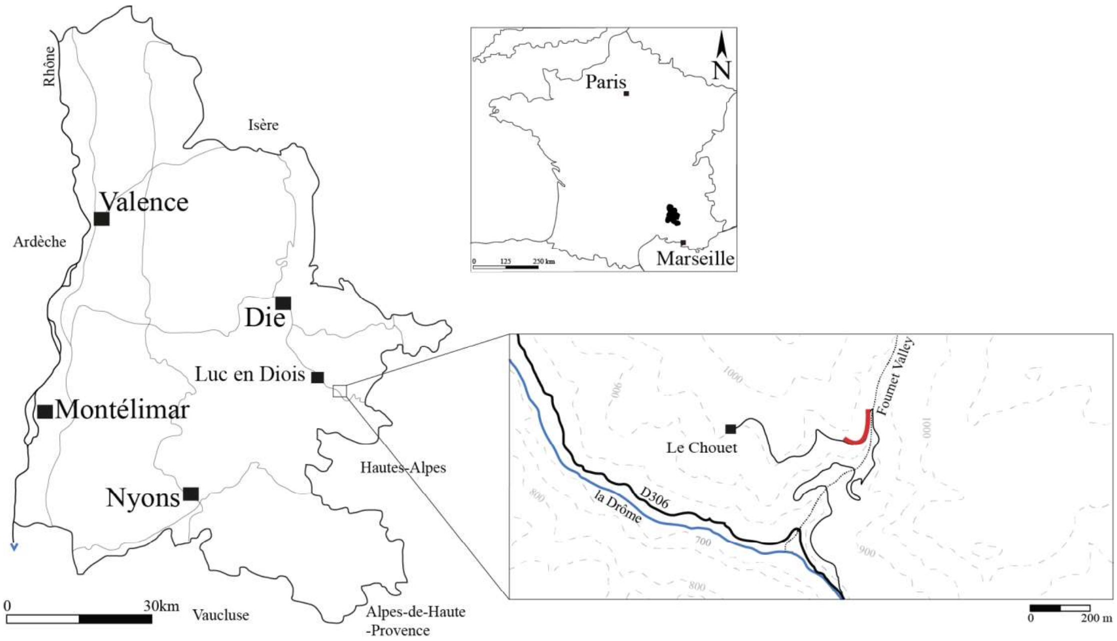
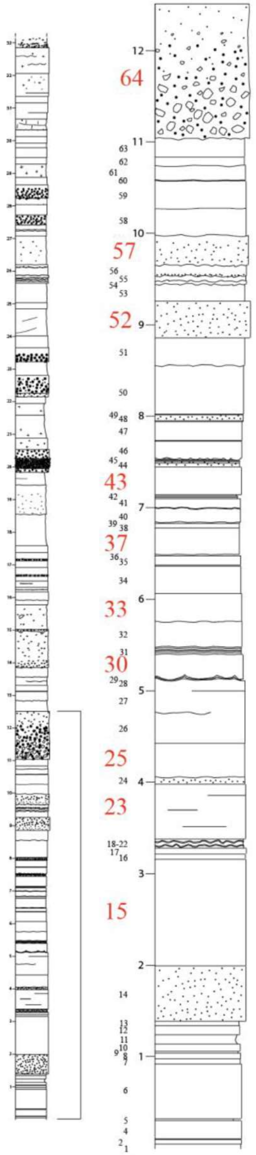


Figure 2.2. Location of Le Chouet section, eastern Drôme, South East France.



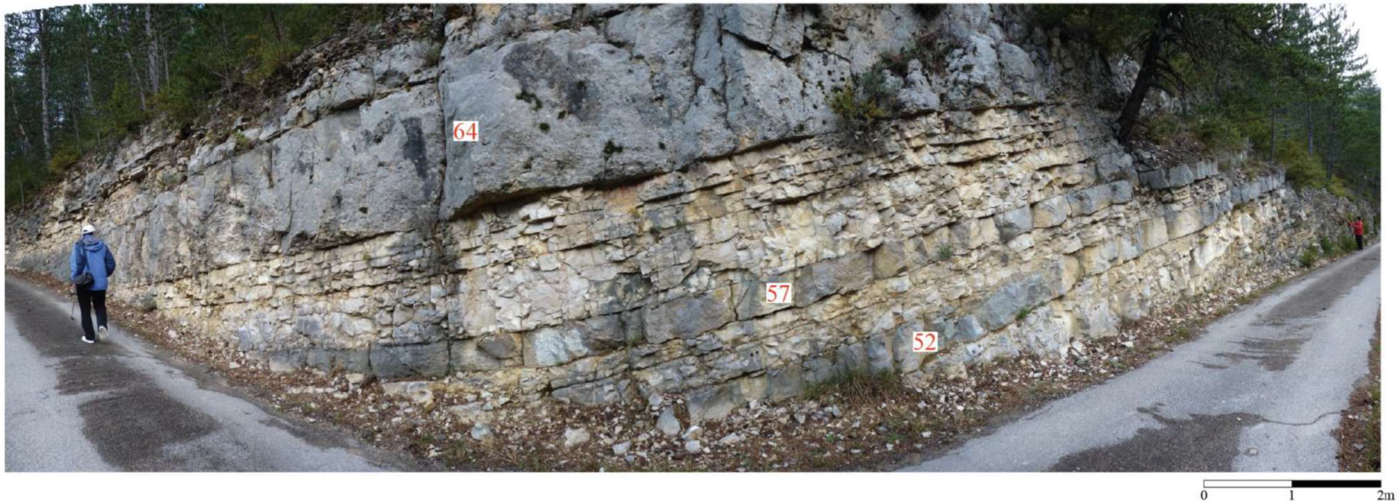


Figure 2.3b. Wide field panoramic photography of the lower part (beds 52 to 64) of Le Chouet section (Drôme) with marker beds.

Figure 2.3a. Wide field panoramic photography of the bottom part (beds 15 to 52) of Le Chouet section (Drôme) with marker beds.

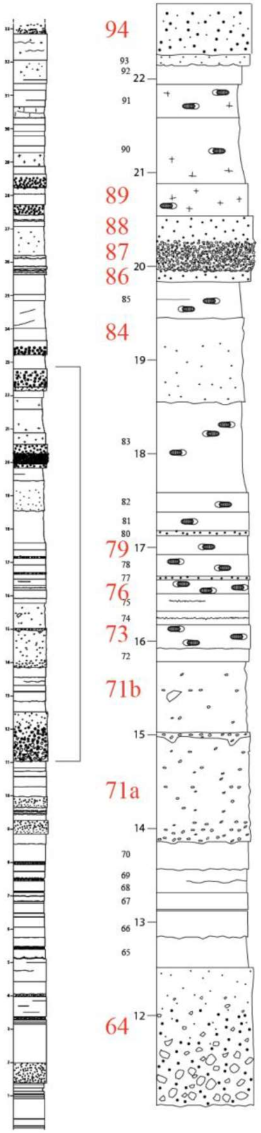


Figure 2.4b. Wide field panoramic photography of the grainstone—conglomerate—grainstone triplet (beds 86-88) of the upper Le Chouet section (Drôme).

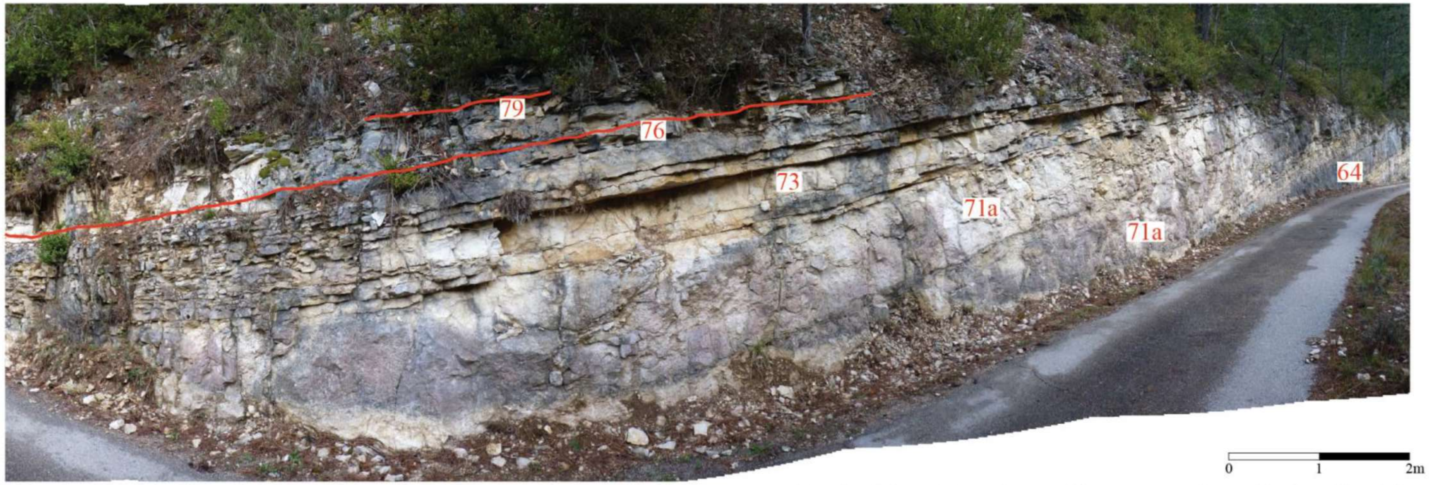


Figure 2.4a. Wide field panoramic photography of the lower part (beds 64 to 79) of Le Chouet section (Drôme) with marker beds. The red lines indicate the microbreccia beds 77 and 80.

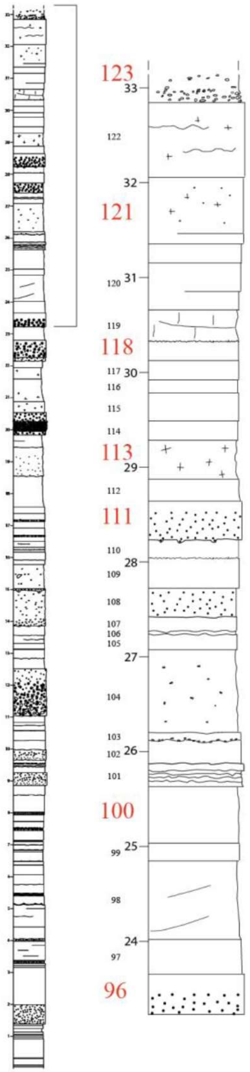


Figure 2.5b. Wide field panoramic photography of the uppermost part (beds 100 to 123) of Le Chouet section (Drôme) with marker beds.

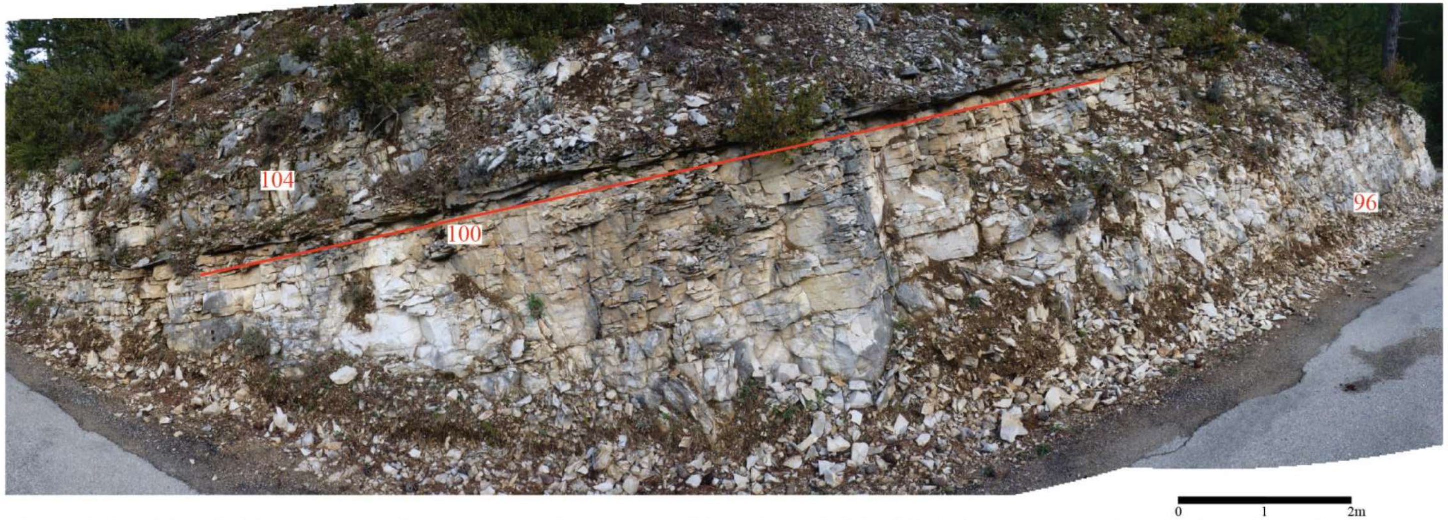


Figure 2.5a. Wide field panoramic photography of upper part (beds 96 to 104) of Le Chouet section (Drôme) with marker beds. The red line indicates the boundary between the calpionellids Crassicolaria and Calpionella zones.

2.2.2. Charens

Localisation: The locality is situated almost three kilometres to the west of the key-section of Le Chouet (Drôme, France, Fig. 2.6). It lies in the cliffed upper valley of the River Drôme (Long 5°31’08”E, Lat 44°32’42”N), off the local road (D93) from Die to Beaurières. It comprises a low mural section, 250 m-long, along a single-track road (D145) on the east side of the Charens gorge. The section extends around the slope from an altitude of 758 m to a little above 766 m and dips 10 degrees to the North.

Background: The Charens section was originally studied for its gravity flows by Remane (1970) and subsequently by Bouchette et al. (2001), Seguret et al. (2001), Courjault (2011) and Courjault et al. (2011). The latter authors clearly demonstrated that the sequence forms part of a large-scale, deep-water carbonate breccia lobe.

A first reconnaissance of the Charens section in 2012 showed that the lower upper Tithonian interval is better exposed than Le Chouet and yields rich ammonite faunas. Detailed investigations, including study of calpionellids and calcareous nannofossils, are still ongoing within the framework of the BWG, and that will later be submitted to publication. For the time being, only the boundary between the Chitinoidella and the Crassicollaria zones is documented.

Lithology: The studied succession consists of 41 metres of well-bedded biomicrite - mudstone, wackestone and packstone - autochthonous intervals intercalated between thick, conglomeratic, clast- or matrix-supported breccias. The lower beds correspond to thin-bedded biocalcarenites (beds 5 to 17, Fig. 2.7a) that overlies conformably a thick conglomeratic breccia (bed 1 to 5). The succession is then characterized by a well-bedded micrite and biomicrite autochthonous interval (Fig. 2.7a). This interval is topped by a thick massive, clast and matrix supported breccia and a number of metre-scale calcarenitic beds at its base (beds 58 and 62, Fig. 2.7b). The biomicrite interval (beds 79 to 98, Fig. 2.8a) above the thin conglomeratic breccia (bed 75) can be correlated with certainty to beds 72 to 89 at Le Chouet. This is supported by similar ammonites occurrences and useful lithological markers such as the intraclastic/microbreccia bed 88 (e.g. = bed 80 of Le Chouet section) and the clast-supported bed 96 (= bed 87 of Le Chouet section) (Figure 2.8a-b). The studied section is ended by a normal fault.

Fossils and taphonomy: Assemblages of body fossils and taphonomic features are rather similar to those found at Le Chouet. A mass-occurrence of buchiid bivalves occurs in a thin horizon (base of bed 64).

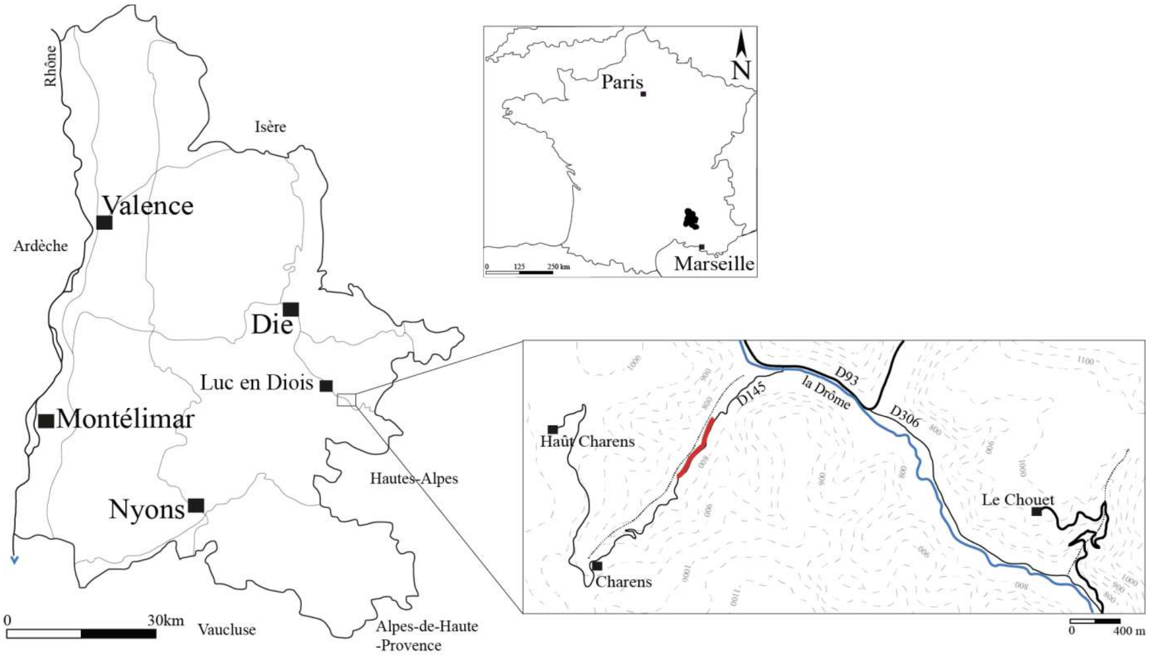
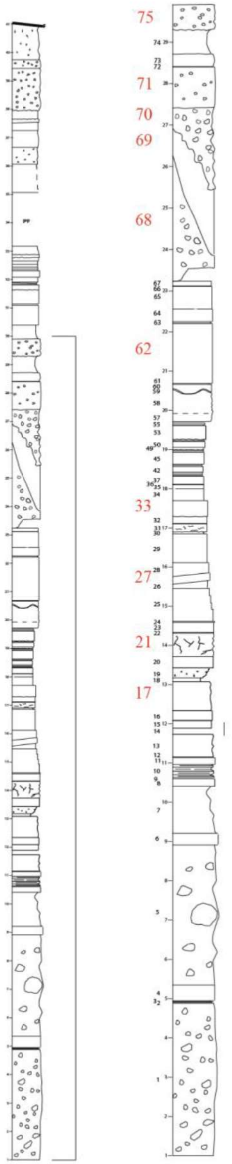


Figure 2.6. Location of the Charens section, eastern Drôme, South East France.



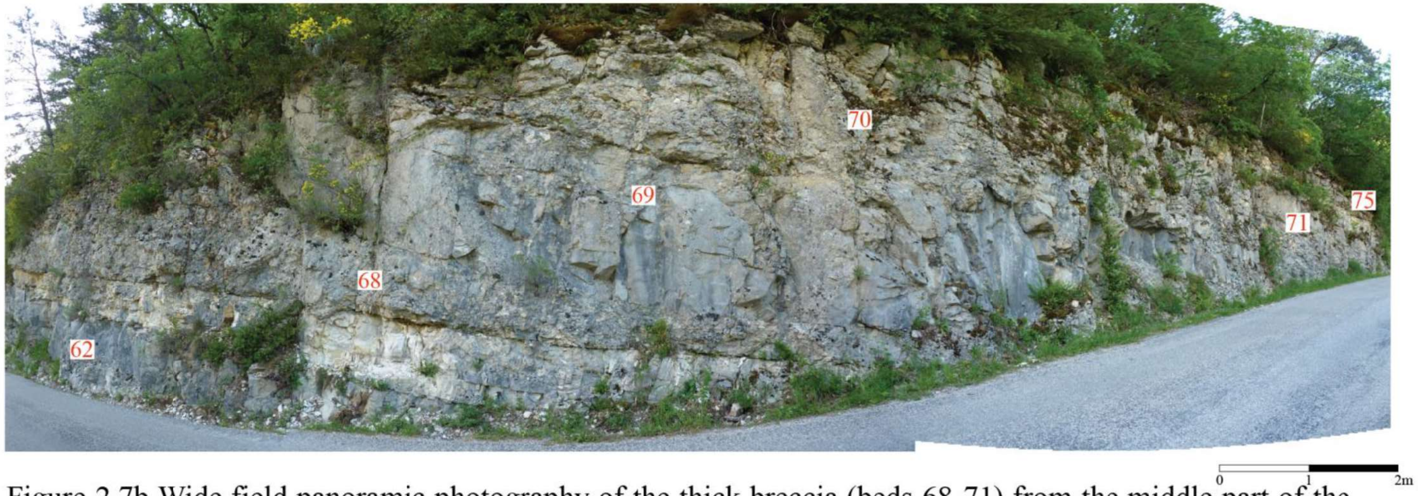
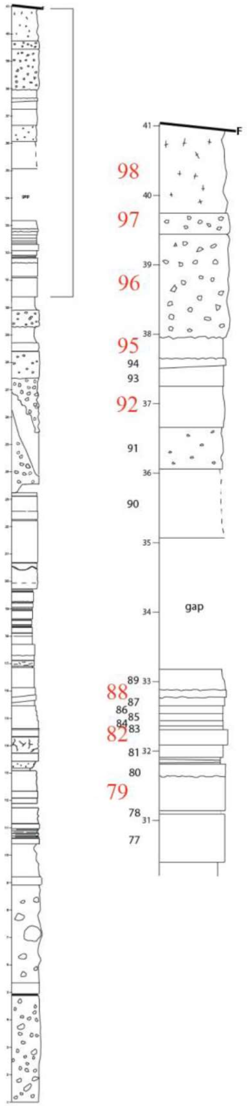


Figure 2.7b Wide field panoramic photography of the thick breccia (beds 68-71) from the middle part of the Charens section (Drôme) with marker beds.

Figure 2.7a. Wide field panoramic photography of the lower part (beds 17 to 62) of the Charens section (Drôme) with marker beds. The red line indicates the base of the Microcanthum Zone.



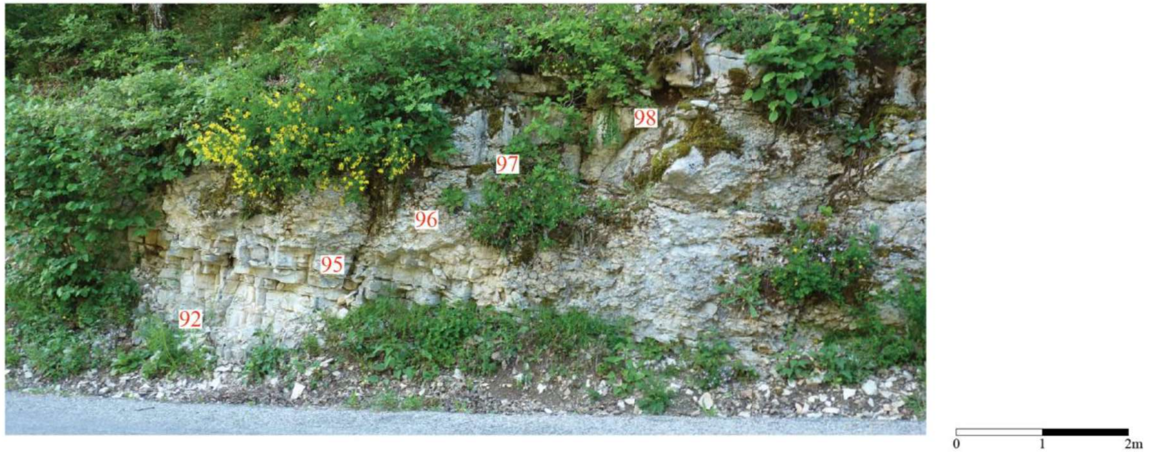


Figure 2.8b. Wide field panoramic photography of the grainstone—conglomerate—grainstone triplet (beds 94 to 97) of the Charens section (Drôme) with marker beds.

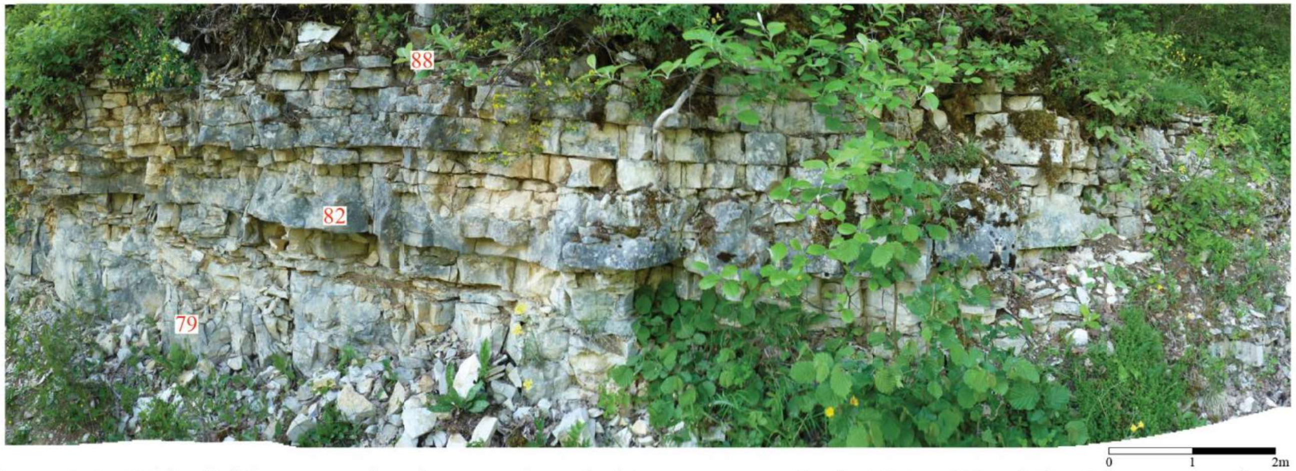


Figure 2.8a.Wide field panoramic photography of the upper part (beds 79 to 89) of the Charens section (Drôme) with marker beds.

3.2.3. Les Combes

Localisation: The locality (Fig. 2.9) lies in the cliffed upper valley of the Grimone stream, in pine forest (Long 5°37'00"E, Lat 44°42'09"N) off the local road (D539) from Glandage to Lus-la-Croix-Haute. The locality comprises a partially overgrown section, 60 m-long, along a single-track road on the north side of the Ravin de Font Bertrand. The section extends around the slope from an altitude of 1040 m to almost 1070 m and dips 10° W.

Background: The Les Combes section was only mentioned by Le Hégarat (1973, p. 267, tabl. 4) for its ammonite-rich levels from the lowermost Berriasian. He gave a stylized section with an underestimated thickness.

Several campaigns on this section by members of the BWG have documented the calpionellids (and nannofossil) content and magnetozones. For the time being, only the preliminary results on the calpionellid zonation are used in the present contribution.

Lithology: The studied section comprises three different parts. The lower (beds -52 to -29) is composed of stacked - mud- to wackestone - limestone beds characterized by the occurrence of small chert nodules. This interval overlies a thick clast-supported breccia (beds -56 and -55). The middle part (beds -28 to 30) contains thin marly interbeds and well-bedded limestone beds ranging in thickness from 5 to 100 cm (beds -25, 22, 22, Fig. 2.10a). This interval displays an obvious thin breccia (bed -10). A part of this interval is overgrown to a depth of about 4 metres (Fig. 2.10b). The third part (beds 32 to 111) is more argillaceous; it is composed of a thick marl-limestone alternations. The upper part of this interval includes recessed poorly exposed outcrops (beds 83 to 92) that is more argillaceous than the rest of the sequence. The base of the limestone beds are sharp or burrowed, and they grade into the overlying marly interbeds. Structures of bioturbation of centimetric size are abundant within limestone beds.

Fossils and taphonomy: At Les Combes, ammonite are abundant and diverse except for the cherty-rich part in the lowest part of the sequence. Dissolution and fragmentation of shells are the norm and specimens are preserved as internal, calcareous moulds with discontinuous compaction. This results in hollow ammonites in which the sedimentary infill is restricted to the body chamber. Resedimented ammonite with complete peristome are only found locally.

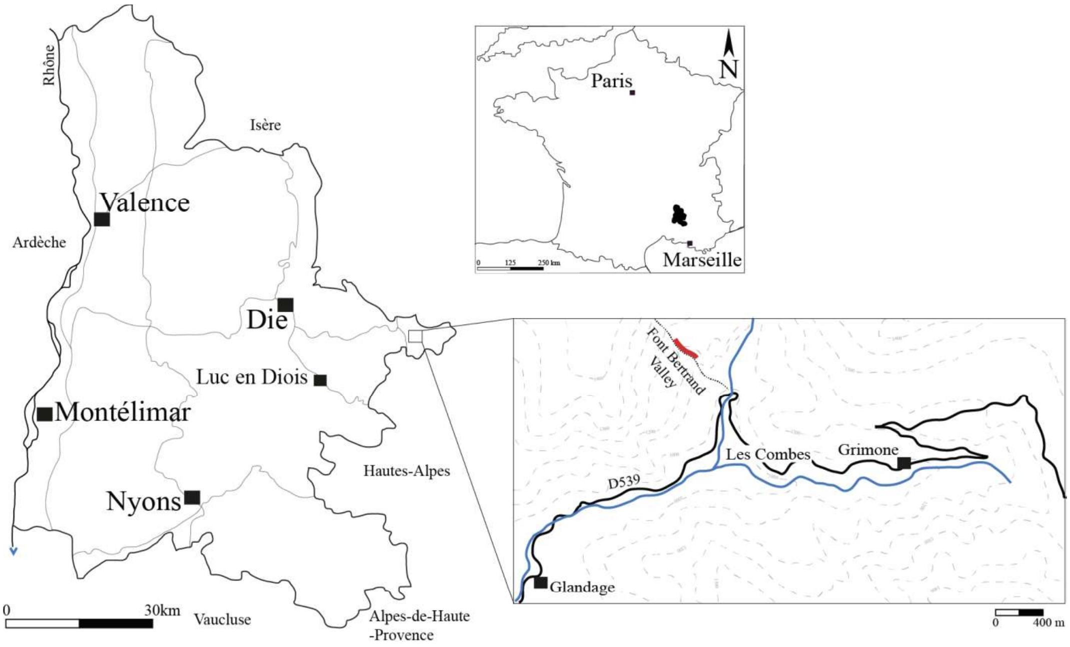


Figure 2.9. Location of Les Combes section, eastern Drôme, South East France.

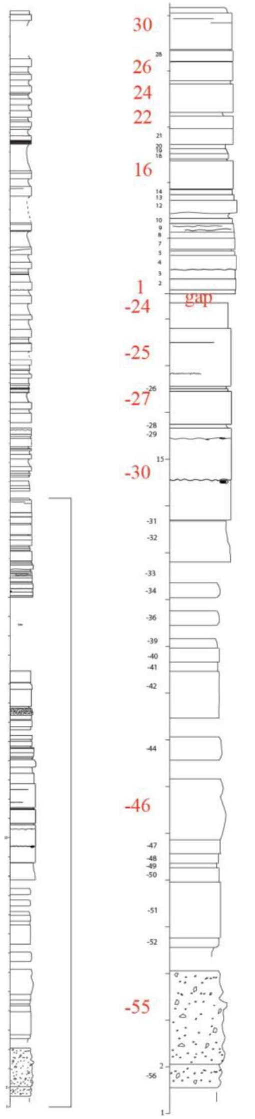


Figure 2.10b. Wide field panoramic photography of the base of the middle part (beds 1 to 30) of Les Combes section (Drôme) with marker beds.

Figure 2.10a. Wide field panoramic photography of the lower part (beds -30 to -24) of Les Combes section (Drôme) with marker beds.

Chapter 3 - Results for each section

3.1. Le Chouet section

3.1.1. Distribution and systematics

A preliminary ammonite distribution based on the recognition of 22 genera from Le Chouet was published in Wimbledon et al. (2013) (Appendix 1). The taxa belonging of to the families Ataxioceratidae, Himalayitidae, Neocomitidae and Olcostephanidae were subsequently described and the first distribution was supplemented and corrected (Appendix 2, 3 and 4). The bottom part of the section is poorly fossiliferous, with only fragments of the index-species *Micracanthoceras microcanthum* (Oppel *in* Zittel, 1868) found (Appendices 1 and 2). Above, Perisphinctoidea are diverse and five successive faunal assemblages were recognized (Appendix 4); these are from oldest to youngest (Fig. 3.1):

- an assemblage dominated by the Ataxioceratidae *Paraulacosphinctes senoides* Tavera, 1985 and *Moravisphinctes fischeri* Kilian, 1889, and which is also marked by the lowest occurrence of the Himalayitidae *Protacanthodiscus andreaei* (Kilian, 1889). A limited number of specimens of *Toucasiella gerardi* Enay, Boughdiri & Le Hégarat, 1998b occur, as well as the doubtful Neocomitidae *Pseudargentiniceras* sp.;
- an assemblage dominated by *P. andreaei* together with new Himalayitidae and the Neocomitidae *Busnardoiceras busnardoi* (Le Hégarat, 1973);
- an assemblage dominated by the Himalayitidae *Chapericeras chaperi* (Pictet, 1867) and *Praedalmasiceras spiticeroides* (Djanélidzé, 1921) together with the Neocomitidae *Elenaella cularense* (Mazenot, 1939), *Berriasella* gr. *oppeli* (Kilian, 1889) - *moreti* Mazenot, 1939;
- an assemblage dominated by *Praedalmasiceras progenitor* (Oppel *in* Zittel, 1868);
- an assemblage dominated by *Delphinella delphinense* (Kilian, 1889) and *Delphinella consanguinea* (Retowski, 1893).

Sporadic occurrences of the Olcostephanidae *Proniceras pronum* (Oppel *in* Zittel, 1868) are reported at different levels.

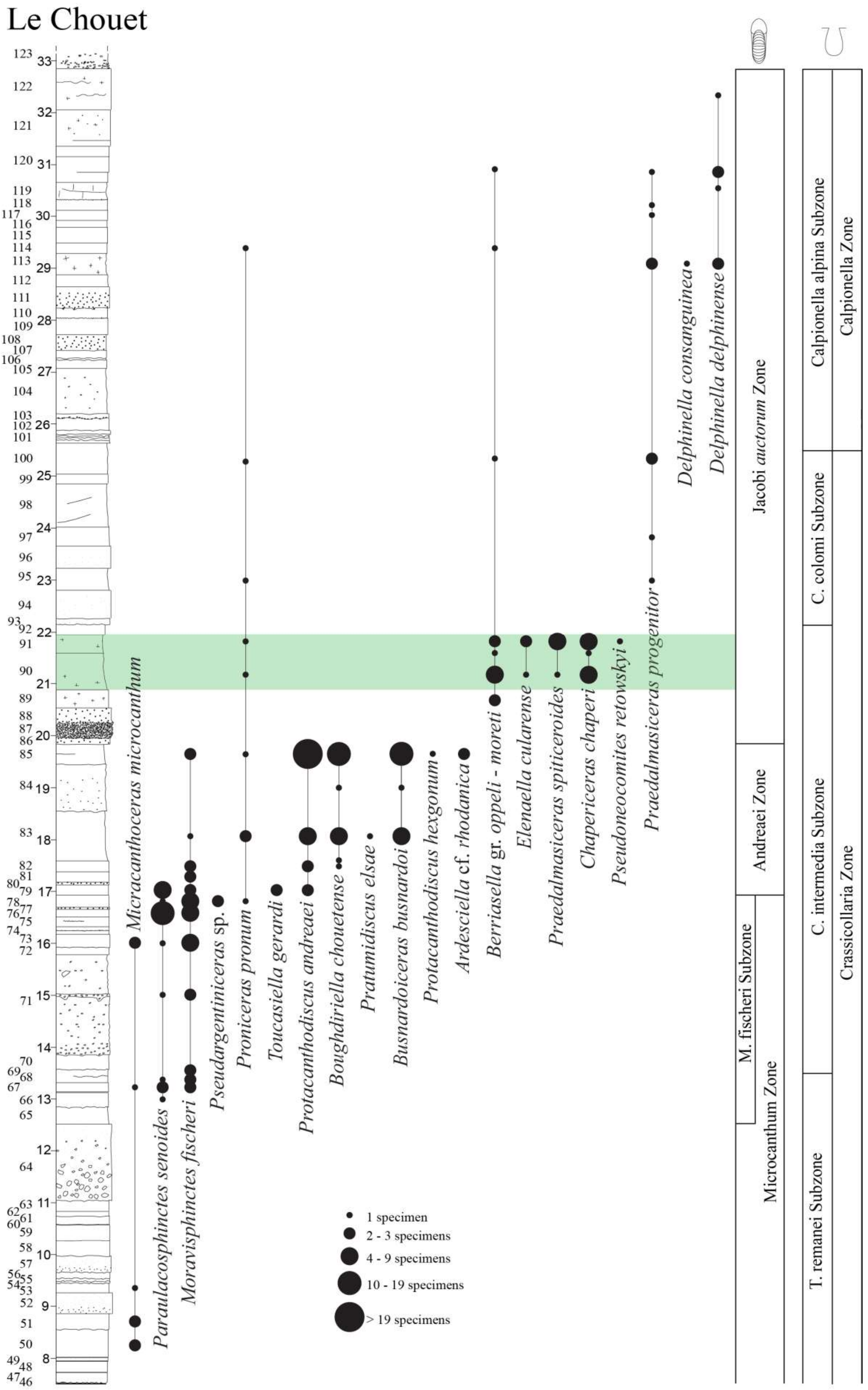


Figure 3.1. Vertical ranges of Perisphinctoidea from Le Chouet and integrated biostratigraphy. Green bar indicates the *E. cularense* biohorizon (modified after Appendices 1, 2, 3, 4).

Major systematic results concern the revision of the Himalayitidae. Based on a numerically large sample, the ontogeny, variation and dimorphism of *Protacanthodiscus andreaei* have been studied (Appendix 3): and it has been demonstrated that the type species of the genus *P. andreaei* is dimorphic, with medium- to large-size macroconchs that develop a robust adult stage, as compared to the microconchs (Appendix 3, fig. 5, 6, 7). Macroconchs range between two extreme morphologies, with slender and robust poles, related to the first Buckman's law of covariation. Based on a re-examination of the type material of *Durangites* from Mexico (Appendix 3), the great majority of specimens from Mediterran-Caucasian settings that have been previously referred to *Durangites* are now interpreted as juveniles and/or microconchs of *P. andreaei*. Moreover, comparisons between specimens from France, Spain and Bulgaria formerly assigned to *Durangites astillerensis* Imlay, 1942 and the type material of this species, supported the introduction of *Boughdiriella chouetense* Frau, Bulot & Wimbledon, 2015 (Appendix 3, fig. 4). Therefore, the occurrence of the genus *Durangites* in the Mediterran-Caucasian Subrealm has to be ruled out.

Four new himalayitid genera are introduced:

Ardesciella Bulot, Frau & Wimbledon, 2014 - for a group of Mediterranean ammonites that is homeomorphic with the Andean genus *Corongoceras* Spath (Appendix 2, fig. 5);

Pratumidiscus Bulot, Frau & Wimbledon, 2014 - for an endemic form that shows morphological similarities with the Boreal genus *Riasanites* Spath, 1925 (Appendix 2, fig. 6);

Chapericeras Frau, Bulot, Wimbledon, submitted (Appendix 4), based on *C. chaperi* (Pictet, 1867) - for dimorphic himalayitid-like forms with two rows of lateral tubercles (Appendix 4, text-fig. 2).

Praedalmasiceras Frau, Bulot, Wimbledon, submitted for the taxa *P. spiticeroides* and *P. progenitor* (Appendix 4, text-fig. 2). Study of the early ontogeny and deep modification of the suture line supports the contention that *Praedalmasiceras* and its middle Berriasian descendant *Dalmasiceras* should be excluded from the Neocomitidae, and distinguished as a new subfamily Dalmasiceratinae within the Himalayitidae (Appendix 4, p. 12).

Regarding the Neocomitidae, their occurrence in the uppermost Tithonian is documented by the presence of the (reputedly Berriasian) taxa *Pseudargentiniceras* sp. and *Busnardoiceras busnardoi* (Le Hégarat, 1973) (Appendix 2). A new account on the content, variation and dimorphism of the genera *Berriasella* Uhlig, 1905, *Elenaella* Nikolov, 1966, *Pseudoneocomites* Hoedemaeker, 1981 and *Delphinella* Le Hégarat, 1971 is to be found in Appendix 4. It has been suggested that the genus *Busnardoiceras* is the basal form from which the other Neocomitidae were derived.

Finally, a conservative use of the Olcostephanidae binomen *Proniceras pronum* (Oppel *in* Zittel, 1868) is here followed, since no modern revision of the Spiticeratinae Spath, 1924, based on well-provenanced collections (with regard to horizon), has been yet undertaken (Appendix 4, p.49).

3.1.2. Biostratigraphy

Three zones were distinguished (Appendix 1): the *M. microcanthum*, *P. andreaei* and *B. jacobi* zones.

The *M. microcanthum* Zone (*pro parte*): The first results suggested a partition of the zone, with the establishment of a *M. fischeri* Subzone at its top, with its base at bed 66. This was used as a replacement for the *P. transitorius* Zone *sensu* Olóriz & Tavera (1979a) as already suggested by Cecca et al. (1989a-b) in South East France, and by Benzaggagh & Atrops (1997) in Morocco. The last occurrence of the genus *Moravisphinctes* is located below the top of the calpionellid *C. intermedia* Subzone. These results are in disagreement with findings from Morocco (Benzaggagh & Atrops, 1997), where *Moravisphinctes* spp. last occur in the *T. remanei* Subzone. Recognition of a fauna indicating the base of *M. microcanthum* Zone (i.e. the *Simplisphinctes* Subzone *sensu* Tavera, 1985) has not been possible. The upper boundary of the *M. microcanthum* Zone is fixed at the FAD of *P. andreaei* (bed 79) that characterizes the next ammonite zone.

The *P. andreaei* Zone: The *P. andreaei* Zone was introduced as a replacement for the much-quoted "*Durangites* Zone" of the topmost Tithonian, because 'Mediterranean *Durangites'* either belong to *P. andreaei* or to *B. chouetense*. In its first appearances within the *C. intermedia* Subzone, specimens of *P. andreaei* are few in number, and its acme is seen in beds 83 to 85; a similar pattern of distribution to that which has been observed in Spain (Olóriz & Tavera, 1989).

The *B. jacobi* Zone *auctorum* (*pro parte*): The first "Berriasian" ammonite assemblage appears one third of the way up the calpionellid *C. colomi* Subzone and corresponds to the *E. cularense* biohorizon *sensu* Tavera et al. (1994). This biohorizon matches beds 90 and 91 at Le Chouet. Though the index species had not been recognized, Wimbledon et al. (2013) (Appendix 1) maintained the use of a *Berriasella jacobi* Subzone for stability of stratigraphic nomenclature. Following Hoedemaeker & Bulot (1990), Bulot et al. (2014) (Appendix 2) and Frau et al. (2015, submitted) (Appendices 3, 4) subsequently retained a *B. jacobi* Zone *auctorum*. In any case, the base of the *B. jacobi* Zone *auctorum* at Le Chouet (bed 90) does not correspond to the base of the calpionellid Calpionella Zone (bed 100), becasue it falls within the lower part of the *C. colomi* Subzone of the Crassicollaria Zone.

3.2. Charens section

3.2.1. Distribution and systematics

For the time being, only the late Tithonian Himalayitidae and Neocomitidae from Charens have been studied in detail (Appendix 5). Two ammonite assemblages have been recognized; these are from oldest to youngest (Fig. 3.2):

- an assemblage dominated by *M. microcanthum*;
- an assemblage dominated by *P. andreaei* and *B. busnardoi*.

From a comparative ontogenetic and biometric study, *M. microcanthum* exhibits a wide range of variation that lies sexual dimorphism and non-sexual polymorphism (Appendix 5, fig. 2, 3, 4). Heterochronic shifts in development occurred in microconchs, whereas macroconchs range between two extreme morphological poles, related to Buckman's law of covariation. As was discussed in Appendix 5, *P. andreaei* was derived from *M. microcanthum* at the top of the *M. microcanthum* Zone, by changes in shell shape and the strength of the ornamentation.

Regarding the Neocomitidae, only *B. busnardoi* is reported at Charens, but its vertical range is identical to that documented at Le Chouet (Appendix 5). New palaeontological evidence suggests that *B. busnardoi* was derived from *P. andreaei,* by peramorphic change and modifications of the whorl shape and ornamentation.

3.2.2. Biostratigraphy

Two zones were recognized (Appendix 5):

The *M. microcanthum* Zone: The lower boundary of this zone was fixed at the FAD of its index species (bed 25), falling within the upper part of the Chitinoidella Zone: thus confirming similar results achieved in Spain (Pruner et al., 2010) and Morocco (Benzaggagh et al., 2010).

The *P. andreaei* Zone: The vertical ranges of the age-diagnostic species *P. andreaei*, as well as the associated faunal assemblage (*Protacanthodiscus*, *Boughdiriella* and *Pratumidiscus*), are rather similar to those described at Le Chouet.

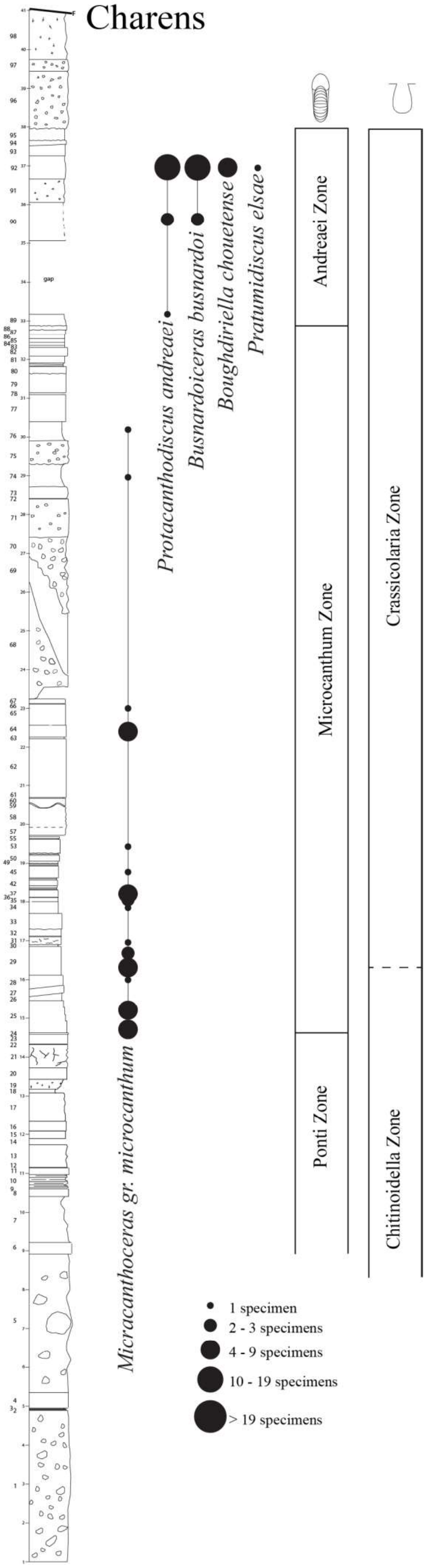


Figure 3.2. Vertical range of Perisphinctoidea taxa from Charens (Drôme, France) and preliminary integrated biostratigraphy. Dashed line indicates the approximate lower boundary of the calpionellid Crassicollaria Zone (modified after Appendix 5).

3.3. Les Combes section

3.3.1. Distribution and systematics

A comprehensive work on the Perisphinctoidea from Les Combes is still to be published, and only the ammonite distribution is provided in the systematic revision of the genus *Strambergella* (Appendix 6). Three ammonite assemblages are recognized (Appendix 6), from oldest to youngest (Fig. 3.4):

- an assemblage dominated by the group of *D. delphinense*;
- an assemblage dominated by the group of *P. lorioli* together with *Retowskiceras andrussowi* (Retowksi, 1893) and *Hegaratella paramacilenta* (Mazenot, 1939);
- an assemblage dominated by *Strambergella carpathica* (Oppel *in* Zittel, 1868) and *Strambergella jacobi* (Mazenot, 1939).

Above, the succession is poorly fossiliferous and it only contains a limited number of specimens referable to *Tirnovella subalpina* (Pictet, 1867) and *D. ellenica* (Nikolov, 1960).

Based on historical material and newly collected specimens from Les Combes, the revision of the index-species *Berriasella jacobi* shows that this taxon is dimorphic and its features (umbilicus height, umbilical wall, ribbing style and aspect of the ventral area) do not compare well with those of the genus *Berriasella*, but match closely the morphological features of the genus *Strambergella* (see discussion in Appendix 6). The co-occurrence of the type species *Strambergella carpathica* and *S. jacobi* documented for the first time in the uppermost part of the *B. jacobi* Zone *auctorum* supports this view (Appendix 6, Fig. 4 and 5). Most records of *S. jacobi* from the Mediterran-Caucasian Subrealm are based on the misinterpretation of specimens that either belong to *Pseudosubplanites*, *Pseudoneocomites*, *Berriasella* or *Delphinella*, but true sporadic occurrences are documented in southern Spain, Italy, Bulgaria, Central Tunisia and Crimea (Appendix 6). The records from Tibet, Madagascar and Chile are based on specimens that belong to *Blandfordiceras* or endemic Andean ammonites, which remain of uncertain taxonomic assignment.

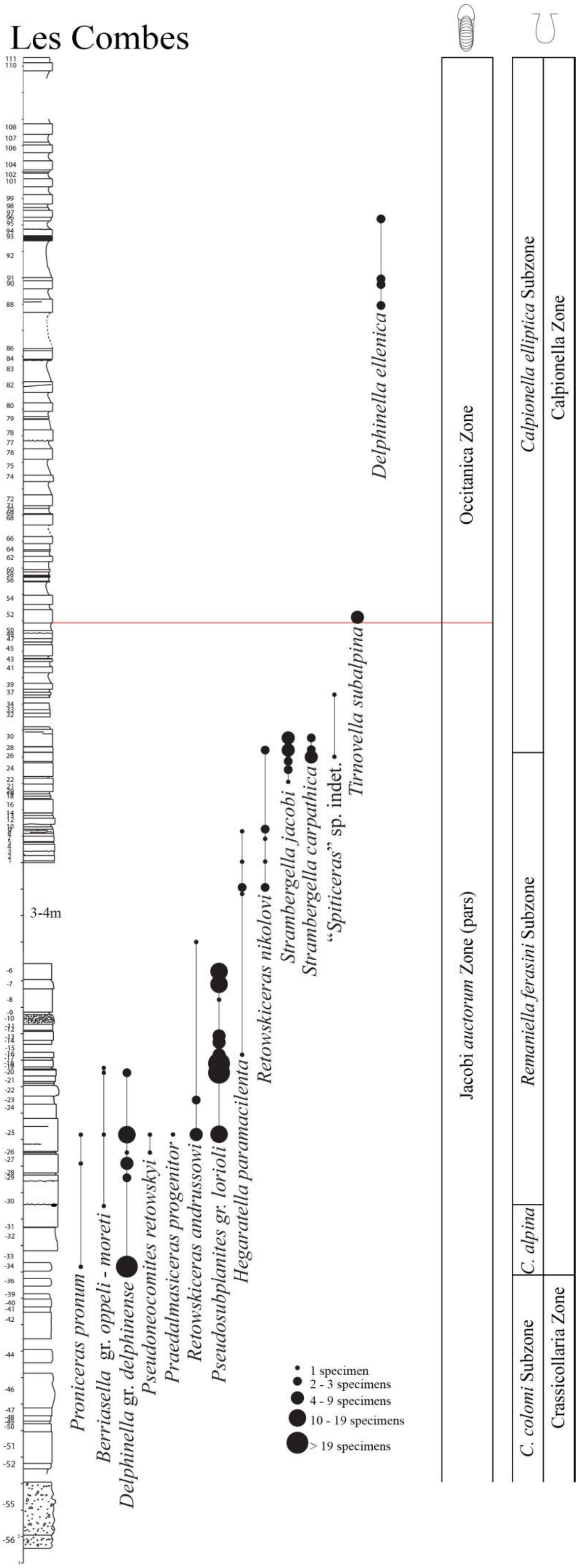


Figure 3.4. Vertical range of Perisphinctoidea taxa from Les Combes (Drôme, France) and integrated biostratigraphy. Red line indicates the boundary between the lower and middle Berriasian in the sense of Le Hégarat (1973) (modified after Appendix 6).

Pending the forthcoming paper on the systematics of the other taxa, significant results are given below:

- The latest occurrence of the Himalayitidae *P. progenitor* is reported at the base of the *Remaniella ferasini* Subzone (Fig. 3.5A);
- Analysis of large *Pseudosubplanites* and *Delphinella* specimens shows that the species of these genera most likely represent a limited number of dimorphic taxa, which, respectively, are herein referred to the group of *P. lorioli* (e.g. including *P. grandis*) and the group of *D. delphinense* (Fig. 3.5G, H).
- Examination of the type specimens and our collection of *H. paramacilenta* shows that their shells had no ventral groove. By its stratigraphic occurrence, it is clear that *H. paramacilenta* was derived from *P.* gr. *lorioli* by minor changes in the width of the umbilicus, and the density and pattern of the ribs (Fig. 3.5I, J).
- Typical specimens of the little-studied *R. andrussowi* are documented for the first time in South East France (Fig. 3.5K, L). The species originates from the lower part of the *R. ferasini* Subzone.
- Examination of the type specimens of *Malbosiceras nikolovi* Le Hégarat, 1973 from Les Combes, supplemented by a new collection of topotypes, leaves no doubt that the species is dimorphic and belongs to *Retowskiceras* by its ontogenetic succession and the aspect of the ventral area (Fig. 3.5K-N). Palaeontological evidence (e.g. similar inner whorls, successive stratigraphic occurrence) support a lineage between *R. andrussowi* and *R. nikolovi*.

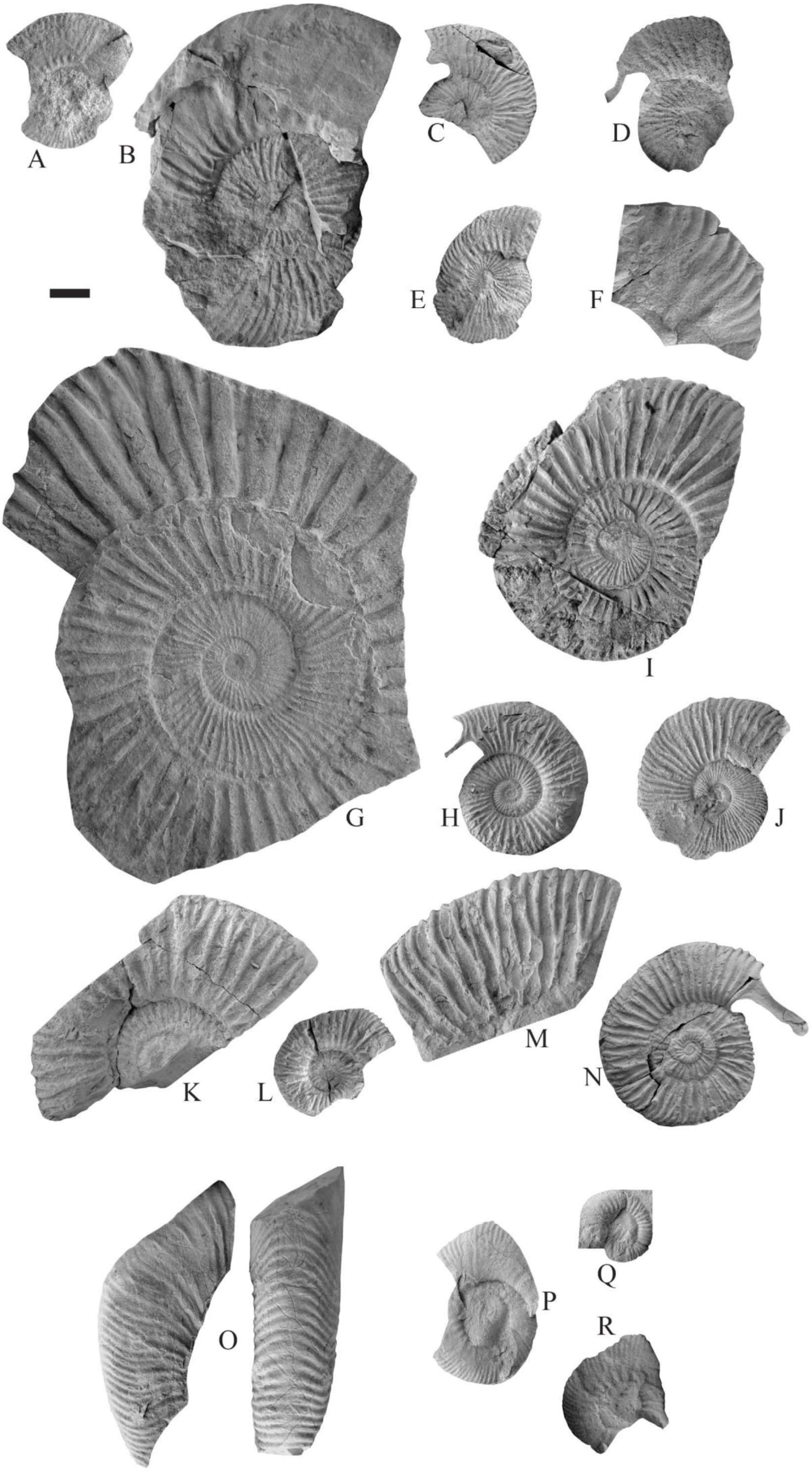
3.3.2. Biostratigraphy

From the ammonite distribution given above, two zones were recognized: the *B. jacobi* and *T. occitanica* zones.

The *B. jacobi* Zone *auctorum* (*pro parte*): By comparison with Le Chouet, the lowermost part of the *B. jacobi* Zone *auctorum* at Les Combes cannot be characterized, since it corresponds to a barren interval linked to the lithology. The first ammonite fauna, including *D.* gr. *delphinense,* is reported at the base of the calpionellid *C. alpina* Subzone that seems to be less thick than it is documented at Le Chouet. Interestingly, the age-diagnostic taxa *P.* gr. *lorioli* and *S. jacobi* show a limited stratigraphical range within the *B. jacobi* Zone *auctorum*. Their precise vertical range is for the first time compared to the calpionellid zonation, and this leads one to question their use as index-species, becasue they occur in the middle and upper parts of the *R. ferasini* Subzone.

The *T. occitanica* Zone (*pro parte*): The index species *T. subalpina* marks the base of the middle Berriasian (e.g. *T. subalpina* Subzone *sensu* Le Hégarat 1973) in the current zonation. However, precise characterization of the *T. subalpina* Subzone cannot be undertaken since the succession is characterized by a quasi-barren interval.

Figure 3.5 (next page). Selected undescribed Himalayitidae, Neocomitidae and Olcostephanidae from Les Combes (Drôme, France): *Praedalmasiceras progenitor* (Oppel *in* Zittel, 1868): (A) plaster cast of MPP-LCB.158 [m] (bed -25); *Delphinella ellenica* (Nikolov, 1960): (B) MPP-LCB.290 [m] (bed 90) and (C) MPP-LCB.247 [m] (bed 96); *Delphinella* gr. *delphinense* (Kilian, 1889): (D) plaster cast of MPP-LCB.156 [m] (bed -25), (E) plaster cast of MPP-LCB.185 [m] (bed -25) and (F) MPP-LCB.188 [M] (bed -25); *Pseudosubplanites* gr. *lorioli* (Oppel *in* Zittel, 1868): (G) MPP-LCB.285 [M] (bed -6) and (H) MPP-LCB.220 [m] (bed -16); *Hegaratella paramacilenta* (Mazenot, 1939): (I) MPP-LCB.257 [M] (bed -7) and (J) MPP-LCB.233 [m] (bed -7); *Retowskiceras andrussowi* (Retowski, 1893): (K) MPP-LCB.143 [M] (bed -25) and (L) MPP-LCB.274 [m] (bed -25); *Retowskiceras nikolovi* (Le Hégarat, 1973): (M) MPP-LCB.54 [M] (bed 7) and (N) MPP-LCB.297 [m] (bed 10); *Tirnovella subalpina* (Mazenot, 1939): (O) MPP-LCB.253 (bed 52); *Proniceras pronum* (Oppel *in* Zittel, 1868): (P) MPP-LCB.164 [?m] (bed -25), (Q) MPP-LCB.174 [?m] (bed -27) and (R) plaster cast of MPP-LCB.287 [?m] (bed -33). Scale bar is 10 mm. Scale bar is 10 mm. All specimens are coated with ammonium chloride.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R

Chapter 4 - Discussion

4.1. A refined integrated bio- and magnetostratigraphic scheme

The sections of Charens, Le Chouet and Les Combes embody a continuous composite succession from the base of the upper Tithonian to the base of the middle Berriasian. Eight successive ammonite assemblages are documented. These are, from bottom to top (Fig. 4.1):

- An assemblage dominated by *Micracanthoceras microcanthum*;
- An assemblage dominated by *Moravisphinctes fischeri*;
- An assemblage dominated by *Protacanthodiscus andreaei*;
- An assemblage dominated by *Elenaella cularense*;
- An assemblage dominated by *Praedalmasiceras progenitor*;
- An assemblage dominated by *Delphinella* spp.;
- An assemblage dominated by *Pseudosubplanites* spp.;
- An assemblage dominated by *Strambergella* spp.;
- An assemblage dominated by the basal *Tirnovella*.

The detailed analysis of the ammonite successions from the Charens, Le Chouet and Les Combes sections provides a sound basis for a refined interpretation for T/B boundary interval biostratigraphy (Fig. 4.1). The base of the upper Tithonian is fixed at the FAD of the index-species *Micracanthoceras microcanthum*, which falls in the upper part of the Chitinoidella Zone. The revision of "Mediterranean *Durangites*" supports the rejection of a *Durangites* spp. Zone as part of the standard zonation for the upper Tithonian, and its replacement by the *P. andreaei* Zone that encompasses the middle part of the *C. intermedia* Subzone of the Crassicollaria Zone. The *M. microcanthum* and *P. andreaei* zones are defined as biochronozones and could be retained as workable units at the scale of the Mediterran-Caucasian Subrealm. The *E. cularense* biohorizon that typifies the base of the *B. jacobi* Zone *auctorum* is documented for the first time in a basinal section, and it is confirmed that it is not synchronous with the *Crassicollaria/Calpionella* turnover. It is clear that *Strambergella jacobi* cannot be used as a primary marker for the T/B boundary, since the species has a limited range in the uppermost part of the *B. jacobi* Zone *auctorum*. Its range is restricted, for it occurs across the calpionellids *C. ferasini* and *C. elliptica* subzonal boundary. The systematic study of the ammonites from Les Combes is needed in order to clarify the ammonite biostratigraphy at the base of the Berriasian, and to provide an alternative to the *B. jacobi* Zone *auctorum*.

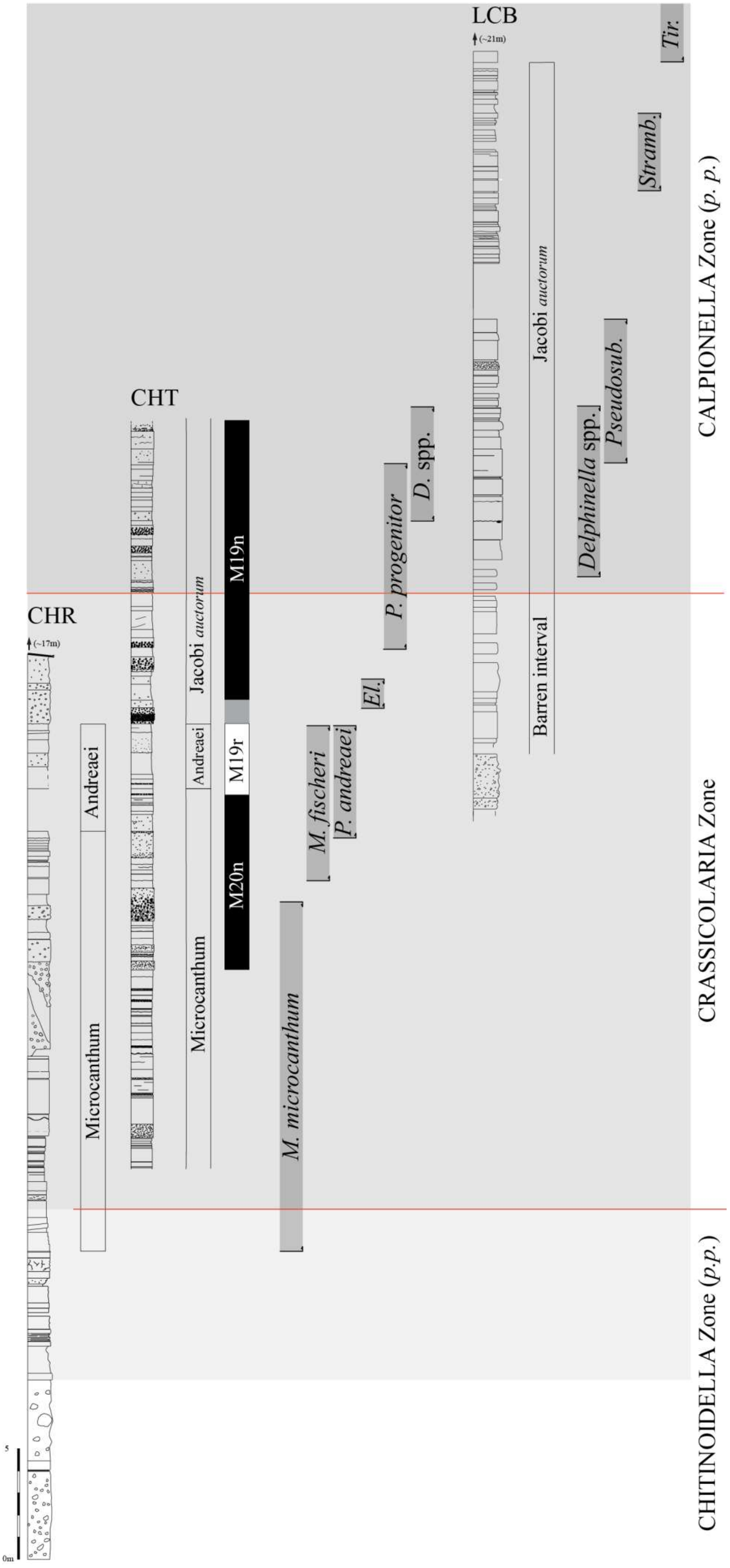
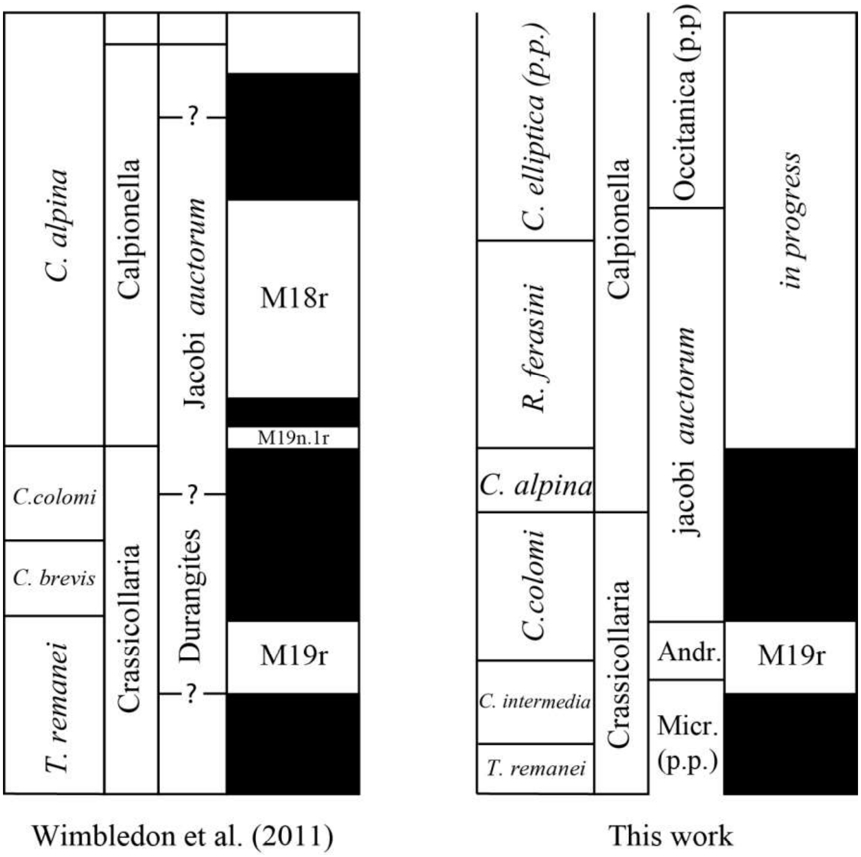


Figure 4.1. Comparison of the litho-, bio- and magnetostratigraphic scheme of the Charens, Le Chouet and Les Combes section.
Red lines indicate the boundaries of the calpionellid zones. Vertical range of the eight ammonite assemblage discussed in the text are reported.

The first occurrence of the index-species *T. subalpina*, marking the base of the middle Berriasian, is reported in the lower part of the *C. elliptica* Subzone of the Calpionella Zone. The *T. subalpina* Subzone is marked by a barren interval.

For the time being, the comparison between ammonite and calpionellid zonations plotted against magnetozones has be only achieved at Le Chouet (Fig. 4.1). The boundary between the *M. microcanthum* Zone and *P. andreaei* zones falls in the lower part of the M19r. The lower boundary of the *B. jacobi* Zone *auctorum* matches the base of the M19n.2n. However, the grainstone-conglomerate-grainstone triplet (i.e. beds 86 to 88) that coincides with the base of the *B. jacobi* Zone *auctorum* perhaps indicates some hiatus (see discussion in Appendix 1).
A comparison between the synthetic integrated biostratigraphic scheme of the Berriasian Working Group (Wimbledon et al., 2011) and the refined one proposed in this thesis is given below (Fig. 4.2).



4.2. Comparison between the original integrated bio- and magnetostratigraphic scheme of the Berriasian Working Group and the refined one proposed in this thesis for South East France. Abbreviations indicate: Micr. = *M. microcanthum* Zone, Andr. = *P. andreaei* Zone, p.p. = pro parte. Calibration is based on the reversed magnetozone M19r.

4.2. Ammonite faunal turnover at T/B boundary, if any?

The age-old controversial debate of the J/K boundary has been traditionally explained as the result of stratigraphic difficulties caused by the lack of faunal turnover across the T/B boundary interval. The question of ammonite faunal turnovers at that time was first addressed by Tavera (1985) and Tavera et al. (1986) based on a large dataset from the Betic Cordillera. Those authors pointed out that the ammonite faunas experienced four main phases of 'renovation' between the base of the upper Tithonian and the base of the Valanginian:

- The first ammonite 'renovation' occurs in the uppermost lower Tithonian, marked by the first occurrence of Simoceratidae and basal Himalayitidae together with the last Lithacoceratinae (*sensu* Tavera 1985). They are progressively replaced by the first ornamented Himalayitidae in the lowermost upper Tithonian.
- The second 'renovation' comes in the *P. andreaei* Zone (e.g. *Durangites* Zone *sensu* Tavera, 1985) where the ammonite assemblage is dominated by *Protacanthodiscus* together with the last Paraulacosphinctinae (*sensu* Tavera 1985) (*Moravisphinctes*, *Paraulacosphinctes*), Aspidoceratidae and Physodoceratinae. The Olcostephanidae become a common element, while the first Neocomitidae appeared.
- The third phase of 'renovation' occurs at the base of the *B jacobi* Zone *auctorum* where Ataxioceratidae disappear, the Himalayitidae are only represented by *Praedalmasiceras,* and Neocomitidae and Olcostephanidae flourished as the more significant components.
- A gradual renewal is detected from the middle to upper Berriasian and the Berriasian/Valanginian boundary record the last 'renovation' marked by a significant faunal turnover at the generic level within the Neocomitidae and Olcostephanidae.

A compilation of the systematic and biostratigraphic data obtained from South East France, plotted next to the ammonite and calpionellid zonations support the chart of total ranges established for each genus (Fig. 4.3). Four phases of faunal change and two pinpoint events are identifiable in the ammonite compositions. Their significance is discussed below, with respect particularly to the 'renovations' recognized in southern Spain:

- The first phase of faunal change (R1 in Fig. 4.3) is characterized by the emergence of the Himalayitidae *Micracanthoceras* that dominates the lower part of the upper Tithonian. At that time, the ammonite assemblage was poorly-diversified. This fauna matches the first 'renovation' in the sense of Tavera et al. (1986). The genus *Micracanthoceras* is largely distributed across the Mediterran-Caucasian Subrealm (Appendix 5) and its phyletic origin still remains unclear in the literature.

- The second phase of faunal change (R2 in Fig. 4.3) occurs at the base of the *P. andreaei* Zone and corresponds to the second phase of 'renovation' *sensu* Tavera et al. (1986). At the genus level, it is characterized by the FAD of *Protacanthodiscus* - evolved from *Micracanthoceras*. This is a widespread bio-event across the Mediterran-Caucasian Subrealm and it provides an obvious biostratigraphic datum. This phase is also marked by the emergence of the Olcostephanidae *Proniceras* that will persist successfully up into the *B. jacobi* Zone *auctorum*. This interval also records the sporadic occurrence of the Himalayitidae *Toucasiella* and the Neocomitidae *Pseudargentiniceras*.

- Two successive steps characterize the third renovation. The first step (R3a in Fig. 4.3) corresponds to an adaptative radiation of the Himalayitidae, marked by *in situ* appearance of *Boughdiriella*, *Ardesciella* and *Pratumidiscus* evolving from *Protacanthodiscus*. This step is also marked by the massive appearance of *Busnardoiceras*, the first true Neocomitidae, which also evolved from *Protacanthodiscus* at the top of the *P. andreaei* Zone. This phyletic link strongly questions the validity of the Neocomitidae from a cladistic point of view.

The second step (*E. cularense* biohorizon; R3b in Fig. 4.3) was marked by the complete extinction affecting the Ataxioceratidae and Himalayitinae, but the Dalmasiceratinae appeared and dominated the assemblage in the lowermost part of the *B. jacobi* Zone *auctorum*. This phase also records an episode of speciation of the Neocomitidae, reflected the co-occurrence of *Elenaella*, *Berriasella* and *Pseudoneocomites* that probably evolved from *Busnardoiceras*. The second step thus corresponds to a fairly complex turnover that affected almost all taxonomic categories - subfamilies, genera and species. This event corresponds to the third phase of 'renovation' *sensu* Tavera et al. (1986).

- The fourth renovation (R4 in Fig. 4.3) also corresponds to a complex turnover, this time linked to the establishment of a rhythmic marlstone-limestone sedimentation. At the local scale, the extinction of two genera (*Praedalmasiceras* and *Pseudoneocomites*) is balanced by the appearance of three Neocomitidae (*Pseudosubplanites*, *Hegaratella* and *Retowskiceras*). This phase is also marked by the collapse of *Delphinella*. As it was suggested above, this renovation is not documented at Puerto Escaño because this interval probably corresponds to a hiatus.

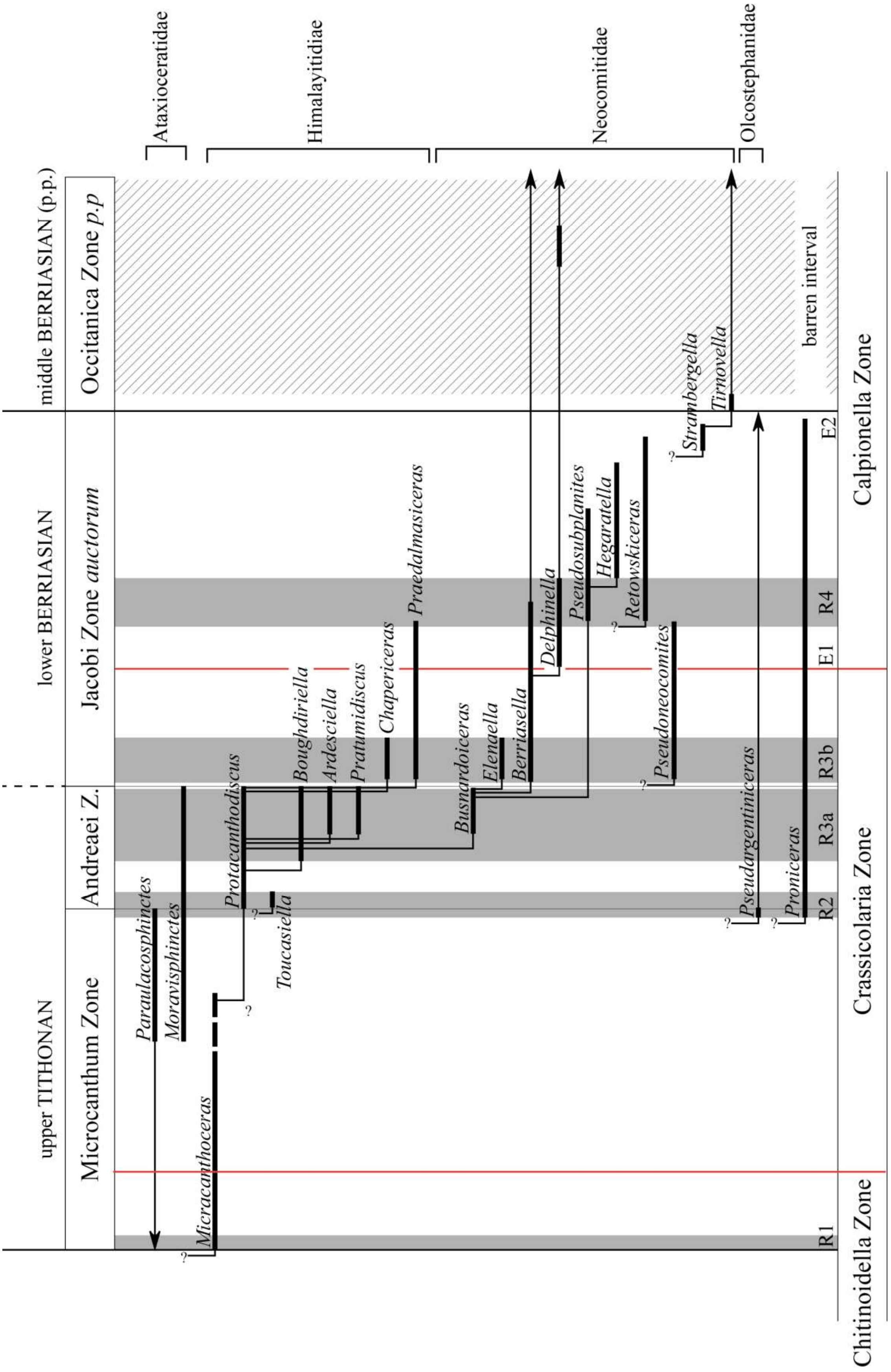


Figure 4.3. Stratophenetic analysis of the Perisphinctoidea from the Tithonian/Berriasian boundary interval in South East France with integrated biostratigraphy.

- The base of the middle Berriasian is marked by a period of collapse in the diversity and abundance of ammonites even though no sharp lithological contrasts affect the lithological succession (Barren interval in Fig. 4.3). Three Neocomitidae (*Berriasella*, *Delphinella* and *Tirnovella*) as well as two subfamilies (Dalmasiceratinae and Spiticeratinae) are known to re-appear above this barren interval (Le Hégarat, 1973). This gap in the ammonite record exemplifies well the concept of "ghost lineage", but the taxonomy of the corresponding lineages needs urgent revision. A critical review of the published Mediterran-Caucasian sections clearly points to the fact that none shows a continuous palaeontological record for that time interval. In this regard, this apparent faunal turnover was repeatedly proposed as an alternative for the base of the Berriasian by Hoedemaeker (1979, 1982, 1987) based on Spanish successions. However, this must be regarded with much caution since the ammonite low that apparently characterizes this interval in South East France and Spain may be due to a combination of collection failure, systematic misinterpretation and/or diagenetic problems that only affect ammonite shells.

Beyond the main features of the evolution of the ammonite faunas described, two pinpoint events whose significance could be important for inter-regional correlations can be reported:

- The first one (E1 in Fig. 4.3) is observed between Phases 3 and 4, at the base of the Calpionella Zone. It is characterized by the emergence of the Neocomitidae *Delphinella* whose stratigraphical range is restricted. The genus probably evolved from *Berriasella* and it has been recorded from numerous settings of the Mediterran-Caucasian Subrealm, from Tunisia to Crimea. However, the content, variability and dimorphism of *Delphinella* remain unclear as no taxonomic revision has yet been undertaken, and the genus has often been confused with other Neocomitidae. Its revision would strengthen its use as an age-diagnostic taxon (see discussion in Reboulet et al., 2014) even more, as its FAD is almost co-eval with the bloom of *Calpionella alpina*.

- The second event (E2 in Fig. 4.3) is situated at the boundary between the *C. ferasini* and *C. elliptica* subzones. It is characterized by a diversification of the Neocomitidae *Strambergella*, whose vertical range is also restricted and ends with the ammonite barren interval in the lowermost middle Berriasian. The origin of the lineage *S. carpathica* and *S. jacobi* remains unclear. At a larger scale, data in the literature hardly allows one to document with certainty the second pinpoint event in other Mediterran-Caucasian settings, where we are lacking sufficiently detailed successions that allow recognition of this adaptative radiation.

Nevertheless, available data support its occurrence in the uppermost part of the *B. jacobi* Zone *auctorum* in, for instance, southern Spain, Italy, Bulgaria, Central Tunisia and Crimea.

In summary, the phases of faunal changes recognized in South East France are synchronous with those documented in southern Spain. These faunal changes probably also occurred in other Mediterran-Caucasian regions, but there is a lack of integrated biostratigraphic-sedimentological data for many reference areas. In any case, it is clear that none of these faunal renovations is abrupt, and they can be compared with the major turnovers that characterize other stages of the Mesozoic. Moreover, the evolution of Perisphinctoidea from the base of the upper Tithonian to the base of the middle Berriasian was a gradual, small-scale process that mostly affected specific and generic levels.

4.3. New insights into ammonite palaeobiogeography at the T/B boundary

As was mentioned at the opening of this thesis, T/B boundary ammonites demonstrate the highest provincialism of the Mesozoic, due to the complete separation of Boreal and Tethyan regions. Provincialism is also marked within the Tethyan Realm where Mediterran-Caucasian and Indo-Pacific subrealms are distinguished by Westermann (2000a-b). But several authors have repeatedly assumed that diverse Himalayitidae (*Micracanthoceras*, *Protacanthodiscus*, *Durangites*, *Himalayites*, *Tithopeltoceras*), Neocomitidae (*Berriasella*, *Delphinella*, *Subthurmannia*, *Hegaratella*) and Olcostephanidae (*Proniceras*, *Spiticeras*) genera were more widely distributed, and that this allows long-distance correlation (e.g. Boughdiri, 1994; Bardhan et al., 2007; Cantu-Chapa, 2012). From the taxonomic revision of certain of the taxa listed above (Appendices 2, 3, 4, 5, 6), I assume that the provincialism of the Tethyan ammonites is much higher than has been previously assumed in the literature, and that homeomorphy has led to erroneous taxonomic interpretations (Appendix 7). New, challenging results are synthesized below.

4.3.1. Faunal pattern of the Mediterran-Caucasian Province

Cecca (1999) and Cecca et al. (2005) made a distinction in the lower Tithonian between mediterranean *sensu stricto* and sub-mediterranean assemblages in the Mediterran-Caucasian Subrealm, since more diverse and homogenous faunas are to be found at its southern margin. Those authors stated that this faunal divergence is not relevant in the T/B boundary interval, but thus far no quantitative work on this has been undertaken. From the revised synonymies, the precise distribution of the studied Perisphinctoidea can be drawn across the Mediterran-Caucasian Subrealm. I can thus present a quantitative analysis based on the abundance of species (Fig. 4.4) and specimens (Fig. 4.5) for five intervals between the base of the upper Tithonian and the base of the middle Berriasian from the three Drômois sections.

Diagrams of abundance of specimens and species show that widespread Mediterran-Caucasian taxa (e.g. *Micracanthoceras microcanthum*, *Protacanthodiscus andreaei*, *Praedalmasiceras progenitor*, *Berriasella* gr. *oppeli-moreti*) dominate the assemblages throughout the corresponding interval. A limited increase of mediterranean taxa (e.g. *Protacanthodiscus hexagonum*, *Elenaella cularense*, *Toucasiella gerardi*, *Ardesciella rhodanica*), as well as endemic taxa (e.g. *Pratumidiscus elsae*, *Retowskiceras nikolovi*) occur during a short time interval encompassing the top of the *P. andreaei* Zone and the lower part of the *B. jacobi* Zone *auctorum*. The increase of the mediterranean and endemic taxa is recorded in the most diversified and abundant assemblages that typify the *P. andreaei* Zone and the middle part of the *B. jacobi* Zone *auctorum*. Thus, only one short time interval records a limited faunal divergence. These results emphasize that assemblages from the *M. microcanthum* Zone to the base of the *T. occitanica* Zone are rather homogenous between the northern and southern margins of the Mediterranean, as well as the northern margin of Central Tethys (Crimea, northern Iran), that form the Mediterran-Caucasian Province in the sense of Cecca (1999) (see Fig. 4.6). Interestingly, ammonite assemblages from the eastern part (Caucasian and Transcaspian areas) of the Mediterran-Caucasian Subrealm show a marked faunal divergence during the mid and late Berriasian (Appendix 7 with references). Endemic forms such as *Riasanites*, *Transcaspiites*, *Tauricoceras* and *Gechiceras* flourished in the Trans-Caucasian areas and spread into the Polish Lowland and Russian Platform (i.e. southern part of the Boreal-Atlantic Subrealm of the Boreal Realm *sensu* Westermann, 2000a-b). As a result, the T/B boundary interval could be regarded as a period of homogenization of Mediterran-Caucasian Perisphinctoidea between two intervals (i.e. lower Tithonian, and middle Berriasian) of marked faunal divergence.

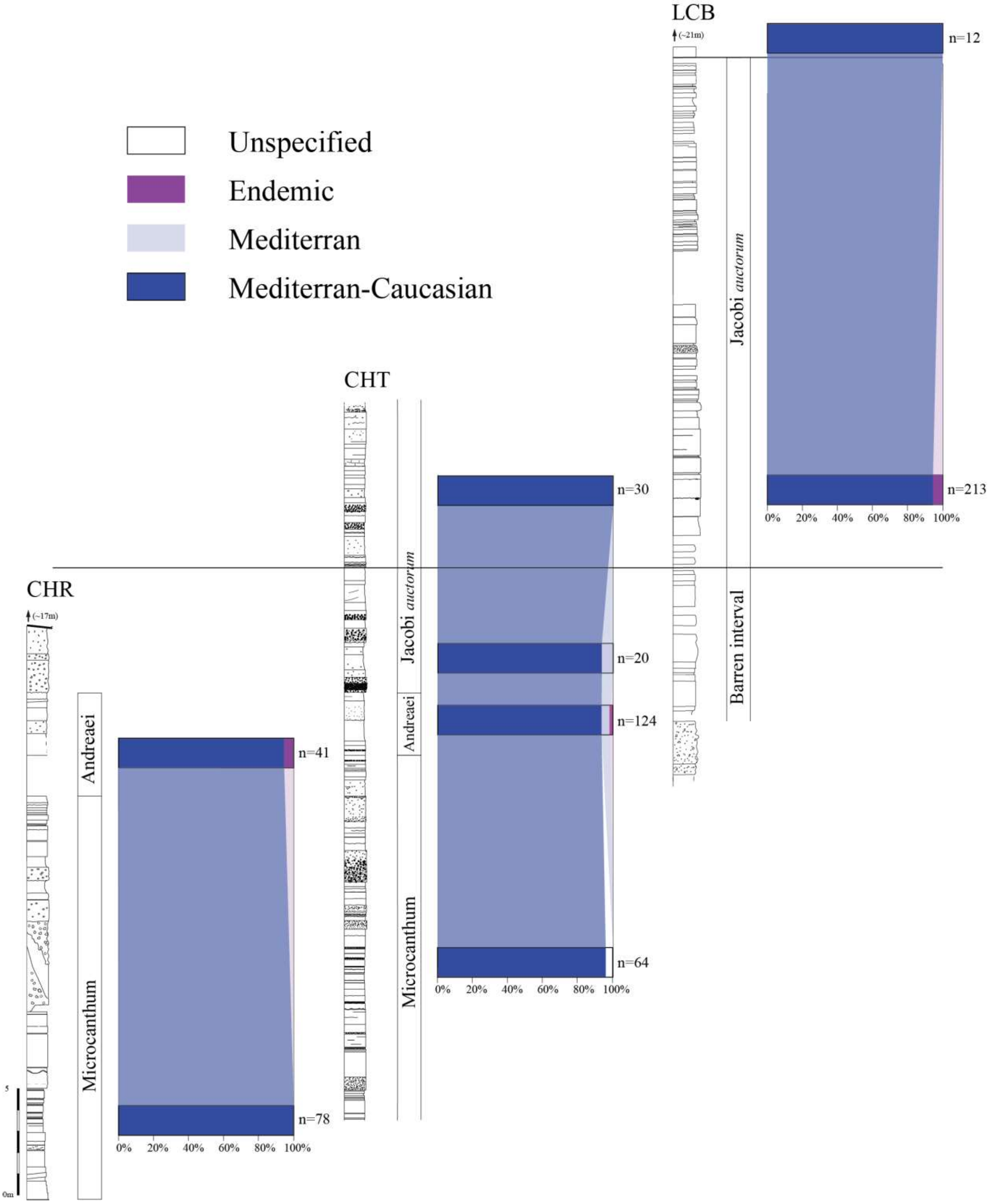


Figure 4.4. Diagram of abundance of specimens from five interval across the T/B boundary interval from the studied Drômois sections. Black line indicates the *Crassicollaria*/*Calpionella* turnover.

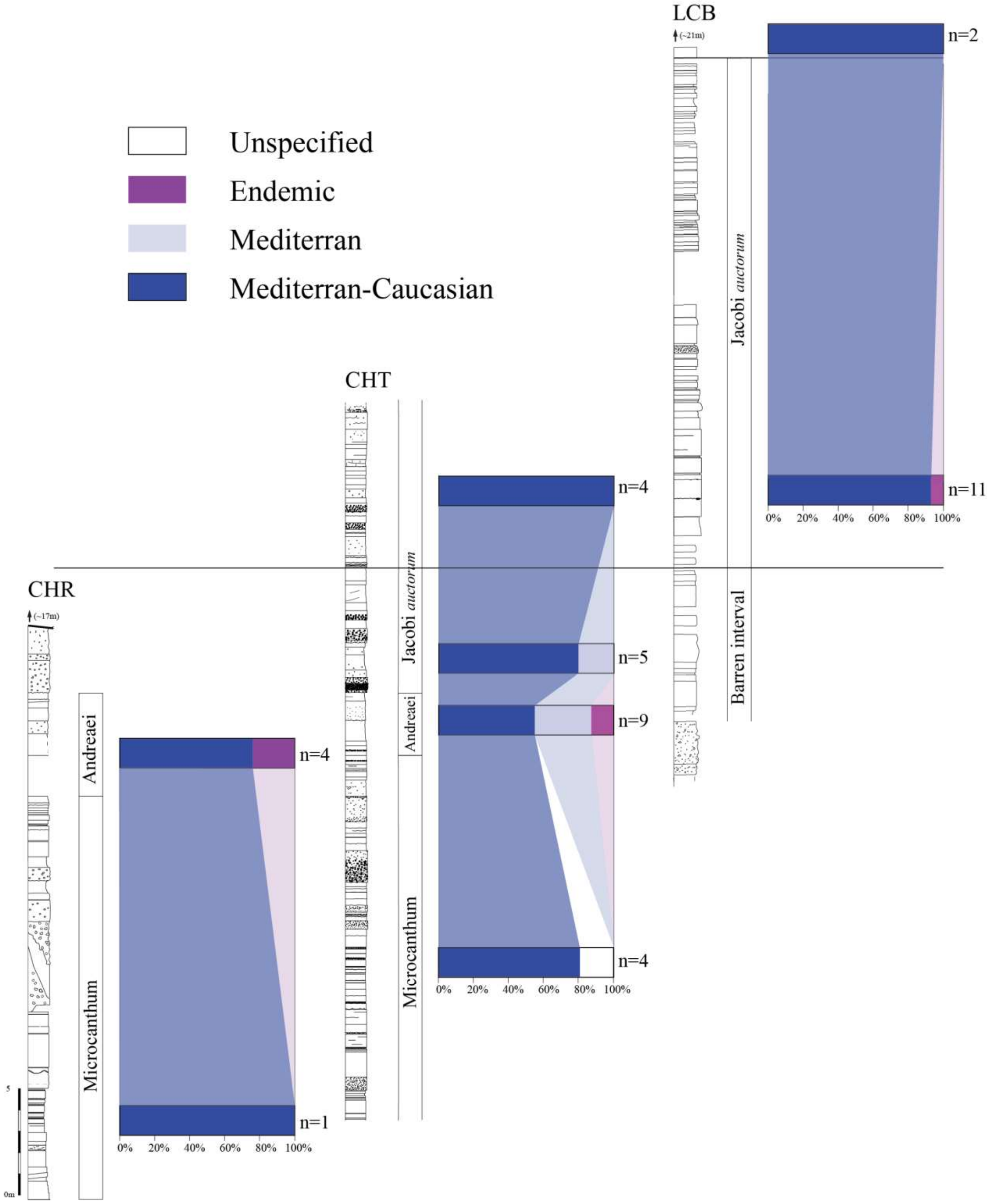


Figure 4.5. Diagram of abundance of species from five interval across the T/B boundary interval from the studied Drômois sections. Black line indicates the *Crassicollaria*/*Calpionella* turnover.

4.3.2. Palaeobiogeographic boundaries of the Mediterran-Caucasian Province

According to Cecca (1999) and Cecca et al. (2005), the ammonite assemblages were markedly impoverished in the east, from the centre of the Mediterran-Caucasian Subrealm to Central

Tethys. However, these authors assumed that the ammonites from South Primoriye (Russian Far East) illustrated by Sey & Kalacheva (1999) are still of Mediterran-Caucasian affinities (Fig. 4.6). A re-examination of this fauna leaves no doubt that the specific and generic assignment should be re-considered because this fauna does not belong to Mediterran-Caucasian Neocomitidae. According to Cecca (1999), wide areas of the northern margin of Central and Eastern Tethys have been destroyed during the Alpino-Himalayian orogenesis and no fauna has yet been reported from these regions. Therefore, the northeastern boundary of the Mediterran-Caucasian Province cannot be drawn accurately with the current state of knowledge, even if the boundary will be found in Trans-Caucasian areas.

On the other hand, T/B boundary ammonites from the southeastern margin of the Central Tethys are known from southeastern Turkey and Kurdistan (Fig. 4.6). In southeastern Turkey, Enay et al. (1971) reported Perisphinctoidea of Mediterran-Caucasian affinities but, for the time being, no specimen has been yet illustrated and their age remains unclear. On the contrary, ammonites (e.g. *Chigaroceras*, *Groebericeras*) from Kurdistan illustrated by Spath (1950) and Howarth (1992) show strong affinities with those from the Indo-Pacific Province. As a result, the study of the ammonites from southwest Turkey is urgent, so as to fix the southeastern boundary of the Mediterran-Caucasian Province.

Numerous authors have previously assumed that Mediterran-Caucasian Himalayitidae (*Micracanthoceras*, *Protacanthodiscus*), Neocomitidae (*Berriasella*, *Delphinella*, *Hegaratella*), and Olcostephanidae (*Proniceras*) spread toward the Caribbean regions via the Hispanic corridor (*sensu* Westermann, 1984), and vice versa (e.g. *Corongoceras*, *Durangites*, *Substeueroceras*), during T/B boundary times (e.g. Imlay, 1942; Verma & Westermann, 1972; Cantu-Chapa, 1963, 1967, 1976; Myczyński, 1989, 1994, 1999; Myczyński & Pszczółkowski, 1990; Adatte et al., 1994; Pszczółkowski & Myczyński, 2010). These authors have thus regarded the Caribbean, and its adjacent areas, as a subprovince of the Mediterran-Caucasian Province. Given the erroneous taxonomic interpretation documented in the present thesis (i.e. Appendices 2, 3, 5 and 6), the occurrence of Caribbean genera in the Mediterran-Caucasian Subrealm has to be ruled out. In this connection, Myczyński (1989) previously stated that the proto-Atlantic connection was less of a migratory route during T/B boundary times. This is supported by the observations of Olóriz et al. (1999) who documented an increasing endemism of ammonites through the Tithonian and lowermost Berriasian in the Caribbean (e.g. *Dickersonia*; "*Lytohoplites*"), Gulf of Mexico (e.g. *Durangites*, *Suarites*, *Acevedites*, *Wichmanniceras*, "*Kossmatia*") and southern United States (e.g. "*Blanfordiceras*" gr. *californicum*) that form the Caribbean Province in the sense of Myczyński (1989) (Fig. 4.6).

In our current stage of understanding, early Olcostephanidae (i.e. Spiticeratinae) are the only taxa which spread throughout the Tethyan Realm. They link the Mediterran-Caucasian and Indo-Pacific provinces, with populations reported from the Pacific coast of the USA, Madagascar and the shelf basins of South America and Antarctica (Appendix 7 with references). However, the subfamily Spiticeratinae has suffered from extreme taxonomic splitting, and a brief re-examination of the literature shows that homeomorphy has been overlooked (Appendix 4). Following Enay (2009), I consider that the relationships between the Spiticeratinae from the Mediterran-Caucasian Province and those from the Indo-Pacific are considerably more complex than previously thought, and that they are in need a careful revision.

4.2.3. Conclusions on the palaeobiogeography

As herein understood, the Mediterran-Caucasian and Caribbean provinces extend latitudinally from 30°N to a little above the equator, and they are sandwiched by the Boreal and the Indo-Pacific provinces, respectively of high-latitudes (60°N to 30°N) and low-latitudes (60°S to 15°S) (Fig. 4.6). Following Ross et al. (1992), albeit for different reasons, Central Tethys probably acted as a physical barrier, for ammonites of Mediterran-Caucasian affinities are restricted by a longitude 60°E. It could be argued that the Caribbean seaway to the West and the Hispanic corridor to the East also acted as physical barriers that enhanced endemicity of Caribbean Perisphinctoidea, following the late Tithonian lowering sea level (see Haq, 2014). Interestingly, calpionellids are now well-documented among the Caribbean regions (e.g. Olóriz et al., 2003; Cobiella-Reguera & Olóriz, 2009; López-Martínez et al., 2013, 2015) and Pacific margin of South America (e.g. Kietzmann et al., 2011, 2015; Vennari et al., 2013). As a matter of fact, the recognition of the Chitinoidella and Crassicollaria zones is still imprecise because of the scarcity and poor preservation of the microfaunas (e.g. Cantú-Chapa, 1989; Adatte et al., 1994; López-Martínez et al., 2013, 2015), whereas the Calpionella Zone often records the first massive occurrence of richer microfacies (Adatte et al., 1996; Pszczółkowski & Myczyński, 2010). These results thus confirm that the influence of western Tethys on the Caribbean Province during the Crassicollaria Zone was sporadic, without a permanent connection and probably became effective after Calpionella Zone times (see discussion in Zell et al., 2015). On the contrary, the homogeneous faunal assemblages of the Indo-Pacific Province support an effective connection through the Indo-Austral seaway. This is still not reflected by the taxonomy and it corresponds to a "*geographic bias*" in the sense of Ifrim et al. (2015). Besides the lack of a revised taxonomy for the Caribbean and Indo-Pacific assemblages, which prevents a clear distinction between the two provinces, these preliminary results mainly indicate that the global distribution of Perisphinctoidea is marked by a progressive change from cosmopolitan to latitudinally-restricted distribution across the T/B boundary. The driving factors of such a distribution still remain poorly understood given the limited knowledge, whatever the province, of palaeoceanographic conditions and global sea temperatures in T/B boundary times.

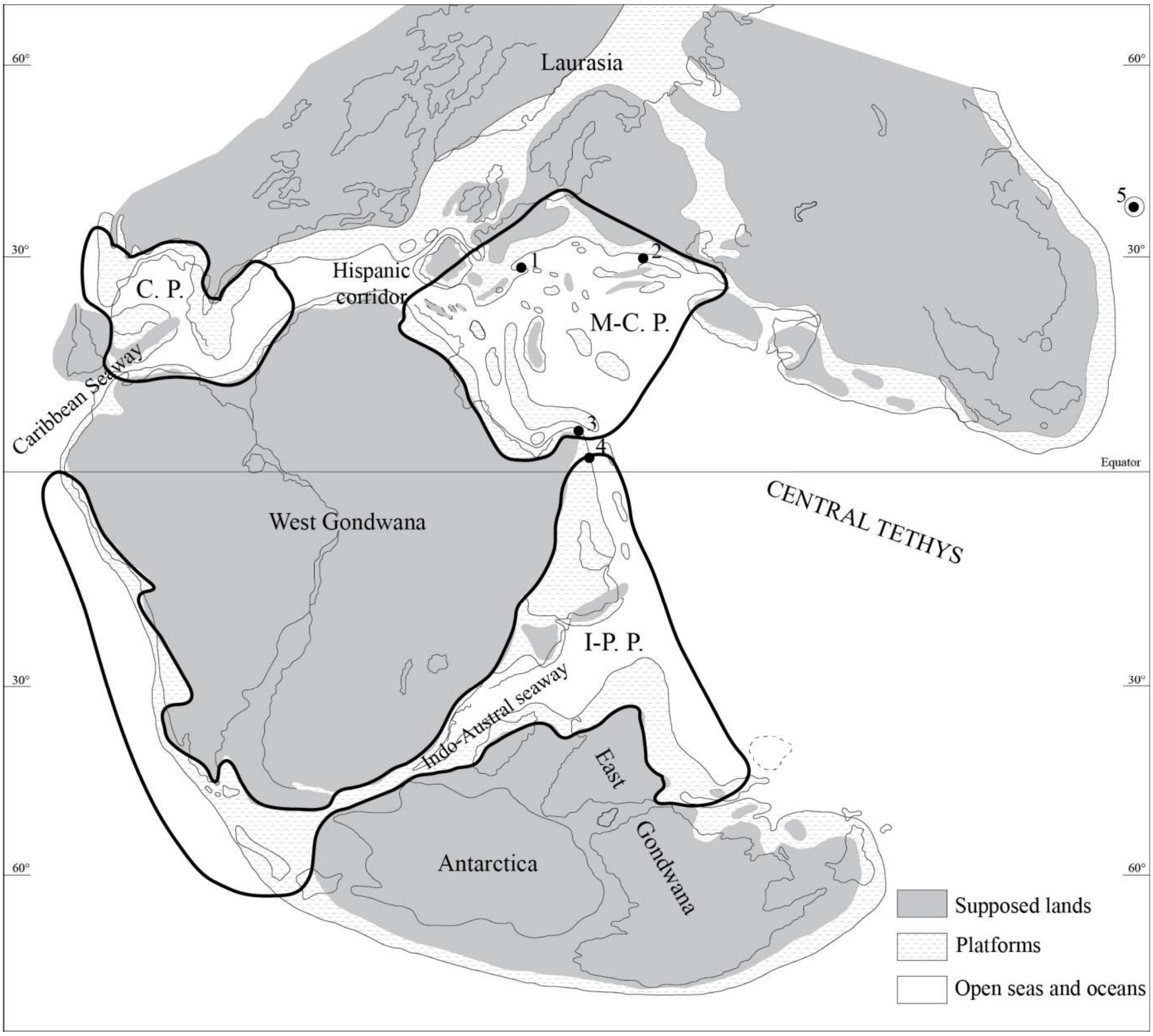


Figure 4.6. Palaeogeographic map of the T/B boundary interval (modified after Cecca, 1999). Acronyms indicate the Caribbean (C.P.), Mediterran-Caucasian (M-C.P.) and Indo-Pacific (I-P.P.) provinces. Number indicate localities discussed in the text: 1= South East France (Study area), 2= Trans-Caucasian areas, 3= souwestern Turkey, 4= Kurdistan, 5= South Primorie.

Chapter 5 - Conclusion

The present thesis focusses on the systematics and biostratigraphy of the Perisphinctoidea across the Tithonian/Berriasian boundary in three key, basinal sections of the Subalpine Basin (South East France). The palaeontological contributions fulfil the main aims of this thesis, these being the revision of the ammonite systematics and of the vertical ranges of taxa with high-stratigraphic value, supporting the refinement of the ammonite zonation. All this is compared and allied to calpionellid bio-events and, partly, to the magnetozones. The revised integrated ammonite zonation is workable at the scale of the Mediterran-Caucasian Subrealm of the Tethyan Realm, and it provides a solid working base for the Berriasian Working Group.

The provincialism of Tethyan Perisphinctoidea across the T/B boundary, at all systematic levels, is much higher than has been previously assumed in the literature and no major faunal turnover was documented in the Mediterran-Caucasian Subrealm. As a result, no ammonite species can be considered as a consistent candidate as a primary marker for the base of the Berriasian. Nevertheless, precise calibration of the ammonite scale with special respect to the 'explosive' appearance of the calpionellid *Calpionella alpina* should be continued, as it corresponds to the most widespread bio-event in the Tethys. Preliminary results on the stratophenetic and palaeobiogeography of T/B boundary ammonites show that they can serve as a challenging model in many areas of macroevolutionary investigation. However, a global revision of the taxonomy is required, and this could only be part of a long-term process.

At the scale of the Subalpine Basin:

The revision of the Neocomitidae from Les Combes is still to be published. New investigations on the microfossil content and magnetostratigraphy are ongoing, and these will constrain the FAD of age-diagnostic taxa from the *B. jacobi* Zone *auctorum*;

Much attention must be paid to the break in the Neocomitidae assemblages that occurs from the base of the middle Berriasian. The sampling of new, continuous, ammonite-rich sections that span the lower/middle Berriasian boundary is essential.

At the scale of the Tethyan Realm:

- A lack of integrated sedimentological-biostratigraphical analysis in many Mediterran-Caucasian reference sections hampers high-resolution correlations. A revision based on abundant and well-localised ammonite faunas from Ukraine and Turkey is necessary;

- A systematic revision of the Caribbean Perisphinctoidea is urgently needed to question the faunal affinities the area has with the Mediterran-Caucasian and Indo-Pacific assemblages.

Acknowledgements

It is a great pleasure for me, after these years of fieldwork and research, to address my warmest thanks to PD Dr. Christina Ifrim who offered me the opportunity to defend this thesis at the Combined Faculty of Natural Sciences and for Mathematics of the Heidelberg University. I am very grateful for the time and support she gave me through the process. Prof. em. Dr. Peter Bengston, Prof. Dr. Mario Trieloff and Prof. Dr. Oliver Friedrich (Heidelberg University) are gratefully acknowledge to be part of my jury.

I am greatly indebted to Luc G. Bulot (University of Aix-Marseille) and William A.P. Wimbledon (University of Bristol) for much help, momentum and encouragement since we first met. I am indebted to both of you for the opportunity to undertake this project and to continue after the end of my master degree at the University of Burgundy. This thesis benefited from the limitless knowledge on Cretaceous ammonites of Luc who solved many scientific (and practical) problems over the years.

Within the framework of the Berriasian Working Group, I have been fortunate enough to meet and collaborate with remarkable geologists. Thanks to the "*two Petrs*", Petr Pruner and Petr Schnabl (Academy of Sciences of Czech Republic), and Jacek Grabowski (Polish Geological Institute) who provided stunning magnetostratigraphic results. Special thanks are also due to Daniela Reháková (University of Comenius, Slovak Republic) for the invaluable help that you have been in providing the calpionellid content of the studied sections. I wish to acknowledge Gang Li and Jianguo Li from (Academy of Science of China) for the memorable fieldwork campaign in their company.

For providing missing references, photographs/casts of various types specimens or just for fruitful discussions, I am indebted to Raymond Enay and Stéphane Reboulet (University Claude Bernard - Lyon I, France), Jean-Pierre Masse and Mukerrem Fenerci-Masse (University of Aix-Marseille), Jaap Klein (University of Amsterdam), Jens Lehmann (University of Bremen), Vasily Mitta (University of Moscow), Andrzej Pszczółkowski (Polish Academy of Sciences, Poland) Istvan Fözy (Hungarian Natural History Museum), Mikheil Kakabadzé (Academy of Sciences of Georgia), Miguel Company and Federico Olóriz (University of Granada), Mabrouk Boughdiri (University of Bizerte), Horacio Parent (University of Rosario) and the PhD students of the Heidelberg University Patrick Zell and Fabio Hering. In addition I would like to acknowledge Emmanuel Robert (University of Lyon-I) to let me access to the collections in his care and Josep A. Moreno Bedmar (Universidad Nacional Autónoma de Mexico) who provided photographs of the type material of *Durangites* collected by Burckhardt in Mexico.

I am deeply grateful to Jean-Pierre Lopez and Martine Broin families who welcomed me with open arms during numerous fieldwork seasons. I will never forget your hospitality and I hope that you will keep alive your valleys for long time.

I do not know how to thank Emile Hourqueig (University of Bordeaux), Cyprien Lanteaume and Anthony J.B. Tendil (University of Aix-Marseille) for their continuous friendship during all over the years. All together you have provided much help during fieldwork and have contributed to this PhD project via fruitful discussions and comments. I hope that you will keep your incredible sense of duty to collect ammonites bed-by-bed.

I acknowledge all the "*Fracas de la Plaine*" and especially Thomas, Audrey, Nicolas, Thibault, Eloise, Quentin, Hadrien, Tony, Bonnie and Dora for the wild nights during my extended weekends at Marseille...

Last, but definitively not least, thanks to Mom, Dad and my family, for their continuous support and confidence in my choices. This work is dedicated to your long-suffering patience...

References

Adatte, T., Stinnesbeck, W. & Remane, J., 1994. The Jurassic-Cretaceous boundary in Northeastern Mexico. Confrontation and correlations by microfacies, clay mineral mineralogy, calpionellids and ammonites. Géobios 17, 37-56.

Adatte, T., Stinnesbeck, W., Remane, J. & Hubberten, H. 1996. Paleooceanographic change at the Jurassic-Cretaceous boundary in the western Tethys, northeastern Mexico. Cretaceous Research 17, 671-689.

Allemann, F., Grün, W. & Wiedmann, J., 1975. The Berriasian of Caravaca (Prov. of Murcia) in the subbetic zone of Spain and its importance for defining this stage and the Jurassic-Cretaceous boundary. In: Colloque sur la limite Jurassique-Crétacé, Lyon Neuchâtel September 1973. Mémoires du Bureau de Recherches Géologiques et Minières 86, 14-22.

Arkadiev, V.V., 2004. The first record of a late Tithonian ammonite in the Feodosiya section of eastern Crimea. Paleontological Journal 38(3), 265-267.

Arkadiev, V.V., 2007a. Ammonite *Fauriella boissieri* (Pictet), the index species of the Berriasian upper zone from the Crimean Mountains. Stratigraphy and Geological Correlation 15(2), 185-192.

Arkadiev, V.V., 2007b. Some Upper Berriasian ammonites of the Crimean Mountains. Questions of stratigraphy, paleontology and paleogeography (in memoir of 100 anniversary of G.Ya.Krimholz), 103-117.

Arkadiev, V.V., 2008. Representatives of the Family Bochianitidae (Ammonoidea) from the Lower Cretaceous of the Crimean Mountains. Paleontological Journal 42(5), 458-478.

Arkadiev, V.V., 2011a. Representatives of genera *Fauriella*, *Tirnovella* and *Jabronella* (Neocomitidae, Ammonoidea) from the Berriasian of the Mountainous Crimea and their stratigraphic significance. Bulletin of the Saint-Petersburg State University, Series 7 Geology, Geography 2, 3-20.

Arkadiev, V.V., 2011b. New data on ammonoids of the genus *Paraulacosphinctes* from the upper Tithonian of the Moutainous Crimea. Stratigraphy and Geological correlation 19(2), 238-242.

Arkadiev, V.V., 2014. Representatives of the *Substeuroceras* genus (Neocomitidae, Ammonoidea) from the Berriasian of the Mountainous Crimea. Bulletin of the Saint-Petersburg State University, Series 7 Geology, Geography 4, 79-87.

Arkadiev, V.V. & Bogdanova, T.N., 2005. Genus *Delphinella* (Ammonoidea) from the Berriasian of the Crimean Mountains. Paleontological Journal 39(5), 487-497.

Arkadiev, V.V., Bogdanova, T.N. & Lobacheva, S.V., 2005. The new data on biostratigraphy of the Berriasian deposits of the Tonas River Basin (Moutain Crimea). in: Arkadiev, V.V. & Prozorovski, V.A. (Eds.). The Cretaceous System of Russia: problems of stratigraphy and paleogeography. Saint-Petersburg, 111-135.

Arkadiev, V.V., Bogdanova, T.N. & Lysenko, N.Y., 2007. Representatives of Genera *Malbosiceras* and *Pomeliceras* (Neocomitidae, Ammonoidea) from the Berriasian of the Crimean Mountains. Stratigraphy and Geological Correlation 15(3), 277-296.

Arkadiev, V.V., Bogdanova, T.N., Lobacheva, S.V., Kalacheva, E.D. & Sey, I.I., 2008. Berriasian Stage of the Crimean Moutains: Zonal subdivisions and correlation. Stratigraphy and Geological Correlation 16(4), 400-422.

Arkadiev V.V., Rogov, M.A. & Perminov, V.A., 2011. New occurrences of heteromorph ammonites in the Berriasian-Valanginian of the Crimean Mountains. Paleontological Journal 4, 35-40.

Arkadiev, V.V., Bogdanova, T.N., Guzhikov, A.Y., Lobacheva, S.V., Myshkina, N.V., Platonov, E.S., Savelyeva, Y.N., Shurekova, O.V. & Yanin, B.T., 2012. In: Arkadiev, V.V. & Bogdanova, T. N., (Eds). Berrias gornogo Kryma, 1-472.

Arnould-Saget, S., 1953. Les Ammonites pyriteuses du Tithonique Supérieur et du Berriasien de Tunisie Centrale. Annales des Mines et de la Geologie 10, 1-133.

Bardhan, S., Shome, S. & Roy, P., 2001. Chapter 17 Biogeography of Kutch ammonites during the latest Jurassic (Tithonian) and a global Paleobiogeographic overview. In: Landman N. H. (Ed.). Cephalopods Present and Past: New Insights and Fresh Perspectives, 375-395.

Bakhmutov, V.G., Halasova, E., Ivanova, D.K., Jozsa, Š., Rehakova, D. & Wimbledon, W.A.P., 2018. Biostratigraphy and magnetostratigraphy of the Uppermost Tithonian – Lower Berriasian in the Theodosia area of southern Ukraine. Geological Quarterly 62, 197-236.

Baudrimont, A.F. & Dubois, P., 1977. Un bassin mésogéen du domaine péri-alpin: le Sud-Est de la France. Bulletin des Centres de Recherche Exploration-Production Elf-Aquitaine 1, 261-308.

Benest, M., Donze, P. & Le Hegarat, G., 1977. Nouvelles données paléontologiques, paléoécologiques et sédimentologiques sur le Berriasien de la région Lamoricière (Ouled Mimoun et El Rhoraf, Monts de Tlemcen, Algerie). Géobios 10, 195-249.

Benzaggagh, M., 2000. Le Malm supérieur et le Berriasien dans le Prérif interne et le Mésorif (Rif, Maroc). Biostratigraphie, lithostratigraphie, paléogéographie et évolution tectono-sédimentaire. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 152, 1-347.

Benzaggagh, M. & Atrops, F., 1997. Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). Newsletters on Stratigraphy 3, 127-163.

Benzaggagh, M., Cecca, F. & Rouget, I. 2010. Biostratigraphy distribution of ammonites and calpionellids in the Tithonian of the internal Prerif (Msila area, Morocco). Paläontologische Zeitschrift 84, 301–315.

Blau, J. & Grün, B., 1997. Late Jurassic/Early Cretaceous revised calpionellid zonal and subzonal division and correlation with ammonite and absolute time scales. Mineralia Slovaca 29, 297-300.

Bogdanova, T.N. & Arkadiev, V.V., 1999. The genus *Dalmasiceras* (Ammonoidea) from the Berriasian of the Mountainous Crimea. Paleontological Journal 4, 20-28.

Bogdanova, T.N. & Arkadiev, V.V., 2005. Revision of species of the ammonite genus *Pseudosubplanites* from the Berriassian of the Crimean Mountains. Cretaceous Research 26, 488-506.

Bogdanova, T. N., Lobacheva, S.V., Prozorovsky, V.A. & Favorskaya, T.A., 1984. The Berriasian of eastern Crimea and the Jurassic-Cretaceous boundary. In: Boundary Stages of the Jurassic-Cretaceous Systems. Trudy Instituta Geologii i Geofiziki Akademii Nauk, Sibirskoe Otdelinie 644, 28-35.

Bogdanova, T.N., Kalacheva, E.D. & Sey, I.L., 1999. On the occurrence of the Tirnovella occitanica Zone (Lower Cretaceous, Berriasian) in the Feodosian section of eastern Crimea. Regional Geology and Metallogeny 9, 27-32.

Bouchette, F., Séguret, M. & Moussine-Pouchkine, A., 2001. Coarse carbonate breccias as a result of water-wave cyclic loading (uppermost Jurassic—South-East Basin, France). Sedimentology 48, 767-789.

Boughdiri, M., 1994. Les genres d'ammonites *Durangites* et *Protacanthodiscus* (Tithonien supérieur) dans la Téthys occidentale (SE Espagne, SE France, Algérie et Tunisie). Stratigraphie, Paléontologie et Biogéographie. Thèse Doctorat, Université Claude Bernard Lyon-I, 1-268.

Boughdiri, M., Enay, R., Le Hégarat, G. & Memmi, L., 1999. *Hegaratites* nov. gen. (Ammonitina): Himalayitidae nouveau du Tithonien supérieur da la coupe du Jebel Rhéouis (Axe nord-sud, Tunisie centrale). Précisions stratigraphiques, approche phylétique et signification biogéographique. Revue de Paléobiologie 18, 105-121.

Boughdiri, M., Olóriz, F., Lopez Marques B., Layeb, M., De Matos, J. & Sallouhi, H., 2005. Upper Kimmeridgian and Tithonian ammonites from the Tunisian «Dorsale» (NE Tunisia): updated biostratigraphy from the Jebel Oust. Rivista Italiana di Paleontologia e Stratigrafia 111(2), 305-316.

Boughdiri, M., Sallouhi, H., Maalaoui, K., Soussi, M. & Cordey, F., 2006. Calpionellid zonation of the Jurassic–Cretaceous transition in North-Atlasic Tunisia. Updated Upper Jurassic stratigraphy of the "Tunisian trough" and regional correlations. Comptes Rendus Geoscience 338, 1250-1259.

Buckmann, S.S., 1909-1930. Yorkshire Type Ammonites, vol.1-2; Type ammonites, vol. 3-7. Wesley & Son, London, 790 pp.

Burckhardt, C., 1912. Faunes jurassiques et crétaciques de San Pedro del Gallo. Boletin del Instituto de Geologia de México 29, 1-137.

Busnardo, R., Donze, P., Le Hegarat, G., Memmi, L. & M'rabet, A., 1976. Précisions biostratigraphiques nouvelles sur le Berriasien des Jebels Nara et Sidi Kralif (Tunisie centrale). Géobios 9, 231-250.

Busnardo, R., Donze, P., Khessibi, M., Le Hegarat, G., Memmi, L. & M'rabet, A., 1985. La formation Sidi Kralif (Tithonique-Berriasien) en Tunisie centrale: Synthèse stratigraphique et sédimentologique. In: Actes du 1er Congrès National des Sciences de la Terre de Tunisie, 115-126.

Callomon, J.H., 1985. Biostratigraphy, chronostratigraphy and all that - again! Proceedings of the International Symposium on Jurassic Stratigraphy (1984) 3, 611-624.

Canavari, M., 1899. Hopliti Totoniani dell Appennino centrale. Atti della Societa Toscana di Scienze Naturali 17, 95-103.

Cantú-Chapa, A., 1963. Etude biostratigraphique des ammonites du Centre et de l'Est du Mexique (Jurassique supérieur et Crétacé). Mémoires de la Société Géologique de France, Nouvelle Série, Mémoire 99, 102 pp.

Cantú-Chapa, A., 1967. El límite Jurásico-Cretácico en Mazatepec, Puebla. Instituto Mexicano del Petróleo, Sección Geología, Monografía 1, 3-24.

Cantú-Chapa, A., 1976. El contacto Jurásico-Cretácico, la Estratigrafía del Neocomiano, el Hiato Hauteriviano Superior-Eoceno Inferior y las amonitas del pozo Bejuco (Centro-Este de México). Boletín de la Sociedad Geológica Mexicana 37, 60-83.

Cantú-Chapa, A., 1989. Precisiones sobre el límite Jurásico–Cretácico en el subsuelo del Este de México: Revista de la Sociedad Mexicana de Paleontología, 2, 26-65.

Cantú-Chapa, A., 2012. Présence d' *Hegaratella* Nikolov & Sapunov, 1977, ammonite du Berriasien (Crétacé inférieur) à Victoria, au nord-est du Mexique. Revue de Paléobiologie 11, 53-61.

Cecca, F., 1985. Alcune ammoniti provenienti dalla "Maiolica" dell'Appennino Centrale (Umbria, Marche e Sabina). Bolletin dell Servicio de Geologia Italiana 103,133-162.

Cecca, F., 1999. Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 147, 1-37

Cecca, F., Enay, R. & Le Hegarat, G., 1989a. L'Ardescien (Tithonique supérieur) de la région stratotypique: série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. Documents du Laboratoire de Géologie de la Faculté des Sciences de Lyon 107, 1-115.

Cecca, F., Enay, R. & Le Hegarat, G., 1989b. The Tithonian of Ardèche (South-East France): new stratigraphical data and revision of the type-section of the "Ardescian" (Toucas 1890). Newsletters on Stratigraphy 20-3), 115-129.

Cecca, F., Savary, B., Bartolini, A., Remane, J. & Cordey, F., 2001. The Middle Jurassic - Lower Cretaceous Rosso Ammonitico successioon of Monte Inici (Trapanese domain, western Sicily): sedimentology, biostratigraphy and isotope stratigraphy. Bulletin de la Société Géologique de France 172(5), 647-660.

Cecca, F., Vrielynck, B., Lavoyer, T., Gaget, H., 2005. Changes in the ammonite taxonomical diversity gradient during the Late Jurassic–Early Cretaceous. Journal of Biogeography 32, 535-547.

Cecca, F., Seyed-Emami, F., Schnyder, J., Benzagaggh, M., Majidifard, M. R. & Mohammadi Monfared, M., 2011. Early Berriasian ammonites from Shal, Talesh region (NW Alborz Mountains, Iran). Cretaceous Research 33, 106-115.

Cobiella-Reguera, J.L. & Olóriz, F., 2009. Oxfordian-Berriasian stratigraphy of the North American paleomargin in western Cuba: Constraints for the geological history of the proto-Caribbean and the early Gulf of Mexico. In: Bartolini, C. & Roman Ramos, J.R. (Eds.). Petroleum systems in the southern Gulf of Mexico. AAPG Memoir 90, 421-451.

Contini, D., Marchand, D. & Thierry, J., 1984. Réflexions sur la notion de genre et de sous-genre chez les ammonites : exemples pris essentiellement dans le Jurassique moyen, Bulletin de la Société Géologique de France 7(4), 653-661.

Cope, J.C.W., 2008. Drawing the line: the history of the Jurassic-Cretaceous boundary. Proceedings of the Geologists' Association 119, 105-117.

Cope, J.C.W., 2013. Stage nomenclature in the uppermost Jurassic rocks of Britain. Geoscience in South-West England 13, 216-221.

Coquand, H., 1869. Note sur les assises qui, dans les Bouches-du-Rhône, sont placées entre l'Oxfordien supérieur et l'étage Valanginien (base du terrain crétacé). Bulletin de la Société Géologique de France 2, 100-131.

Coquand, H., 1875. Note sur les Calcaires coralliens à *Terebratula repelliniana* de la Basse Provence et du Languedoc. Bulletin de la Société Géologique de France 3, 1-670.

Courjault, T., 2011. Brèches gravitaires sous-marines du Tithonien subalpin (S–E France). Thèse Doctorat, Université de Strasbourg, 339 pp.

Courjault, T., Grosheny, D., Ferry, S. & Sausse, J., 2011. Detailed anatomy of a deep-water carbonate breccia lobe (Upper Jurassic, French subalpine basin). Sedimentary Geology 238, 156-171.

De Baets, K., Bert, D., Hoffmann, R., Monnet, C., Yacobucci, M.Y. & Klug, C., 2015. Ammonoid Intraspecific Variability. In: Mapes, R.H., (Ed.). Ammonoid paleobiology: From anatomy to ecology: 503 Topics in geobiology. Springer. Netherlands, 935 pp.

Debrand-Passard, S., Courbouleix, S. & Lienhardt, M.J., 1984. Synthèse géologique du Sud-Est de la France. Mémoires Bureau de Recherches Géologiques et Minières 125 (Stratigraphie Paleogéographie) and 126 (Atlas).

Djanélidzé, A., 1921. *Dalmasiceras*, un sous-genre nouveau du genre *Hoplites*. Bulletin de la Société Géologique de France 4(21), 256-274.

Djanélidzé, A., 1922. Les *Spiticeras* du sud-est de la France. Mémoires pour servir à l´explication de la Carte Géologique détaillée de la France, Masson, Paris, 255 pp.

Donze, P., Le Hegarat, G. & Memmi, L., 1975. Les formations de la limite Jurassique-Crétacé en Tunisie septentrionale (Djebel Oust). Série lithologique; résultats biostratigraphiques et paléogéographiques d'après les ammonites, les calpionelles et les ostracodes. Géobios 8, 147-151.

Enay, R. 2009. Les faunes d’ammonites de l’Oxfordien au Tithonien et la biostratigraphie des Spiti-Shales (Callovien supérieur-Thitonien) de Thakkhola, Népal Central. Documents des Laboratoires de Géologie Lyon 166, 1–351.

Enay, R. & Geyssant, J. R., 1975. Faunes tithoniques des chaînes bétiques (Espagne méridionale. In: Colloque sur la limite Jurassique/Crétacé, Lyon-Neuchâtel. Mémoires du Bureau de Recherches Géologiques et Minières, 39-55.

Enay, R. & Cecca, F., 1986. Structure et évolution des populations tithoniques du genre d'ammonites téthysien Haploceras Zittel, 1868. In: Fossili Evoluzione Ambiente, Atti I Convegno Pergola 1984 (commemorazione di Raffaele Piccinin), 37-61.

Enay R., Martin, C., Monod, O. & Thieuloy, J.-P., 1971. Jurassique supérieur à Ammonites (Kimméridgien—Tithonique) dans l’autochtone du Taurus de Beysehir, Turquie meridionale. Annales Instituti Geologici Publublici Hungari 54, 397-422.

Enay, R., Boughdiri, M. & Le Hégarat, G., 1998a. *Durangites*, *Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien supérieur – Berriasien dans la Téthys méditerranéenne (SE France, Espagne, Algérie et Tunisie). Comptes Rendus de l’Académie des Sciences 327, 425-430.

Enay, R., Boughdiri, M. & Le Hégarat, G., 1998b. *Toucasiella* gen. nov., Himalayitidae (Ammonitina) nouveau du Tithonien supérieur: origine de Durangites. Comptes Rendus de l’Académie des Sciences 327, 471-477.

Enay, R., Boughdiri, M. & Le Hégarat, G., 1998c. *Kilianites* gen. nov., Himalayitidae (Ammonitina) nouveau du Berriasien de la région de Cabra (province de Cordoba, SE Espagne). Comptes Rendus de l'Académie des Sciences, Paris, Sciences de la terre et des planètes 327, 549-554.

Flandrin, J., Schaer, J.P., Enay, R., Remane, J. (coord.), (1975). Colloque sur la limite Jurassique-Crétacé (Lyon-Neuchâtel, 1973). Mémoires du Bureau de Recherches Géologiques et Minières 86, 1-393.

Föz y, I. & Scherzinger, A., 2013. Systematic descriptions of Tithonian ammonites of the Gerecse Mountains. In: Föz y, I., (Ed.). Late Jurassic–Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis Mountains (Transdanubian Range, Hungary). Institute of Geosciences, University of Szeged, GeoLitera Publishing House, 207-292.

Galbrun, B., 1985. Magnetostratigraphy of the Berriasian stratotype section (Berrias, France). Earth Planetary Sciences Letters 74, 130-136.

Galbrun, B., Rasplus, L., Le Hégarat, G., 1986. Données nouvelles sur le stratotype du Berriasien: corrélations entre magnétostratigraphie et biostratigraphie. Bulletin de la Société Géologique de France 8 (2), 575-584.

Geyssant, J.R., 1997. Tithonien. In: Cariou, E. & Hantzpergue, P., (Eds.). Biostratigraphie du Jurassique ouest-européen et méditerranéen : zonations parallèles et distribution des invertébrés et microfossiles, Elf Aquitaine édition 79, 97-102.

Haq, B.U., 2014. Cretaceous eustasy revisited. Global and Planetary Change 113, 44–58.

Haug, E., 1910. Période Crétacée. In: Haug, E. (Ed.). Traité de géologie, vol. 2. Les Périodes géologiques, fascicule 2, Colin, 1153-1396.

Hoedemaeker, P.J., 1979. The Jurassic-Cretaceous boundary near Miravetes (Caravaca, SE Spain); arguments for a position at the base of the Occitanica Zone. Cuadernos Geologicos 10, 235-247 (1981).

Hoedemaeker, P.J., 1981. The Jurassic-Cretaceous boundary near Miravetes (Caravaca, SE Spain): arguments for its position at the base of the Occitanica Zone. Cuadernos de Geolgia Iberica 10, 235-247.

Hoedemaeker, P.J., 1982. Ammonite biostratigraphy of the uppermost Tithonian, Berriasian, and Lower Valanginian along the Rıo Argos (Caravaca, SE Spain). Scripta Geologica 65, 1-81.

Hoedemaeker, P.J., 1987. Correlation possibilities around the Jurassic/Cretaceous boundary. Scripta Geologica 84, 1-64.

Hoedemaeker, P.J. & Bulot, L.G., 1990. Preliminary ammonite zonation for the Lower Cretaceous of the Mediterranean region. Géologie alpine 66, 123-127.

Hoedemaeker, P. J. & Company, M., Aguirre-Urreta, M.B., Avram, E., Bogdanova, T.N., Bujtor, L., Bulot, L.G., Cecca, F., Delanoy, G., Ettachfini, M., Memmi, L., Owen, H.G., Rawson, P.F., Sandoval, J., Tavera, J.-M., Thieuloy, J.P., Tovbina, S.Z. & Vašíček, Z., 1993. Ammonite zonation for the Lower Cretaceous of the Mediterranean Region; basis for the stratigraphic correlation within IGCP-Project 262. Revista Española de Paleontología 8(1), 117-120.

Howarth, M.K., 1992. Tithonian and Berriasian ammonites from the Chia Gara Formation in Northern Iraq. Palaeontology 35, 597-655.

Ifrim, C., Lehmann, J. and Ward, P. D., 2015. Paleobiogeography of the Late Cretaceous Ammonoids. 259-274. In: Klug, C., Korn, D., De Baets, K., Kurta, I. & Mapes, R. H. (Eds.). Ammonoid Paleobiology: From anatomy to ecology, and from macroevolution to paleogeography. Topics in Geobiology, Springer, Netherlands, 598 pp.

Imlay, R.W., 1942. Late Jurassic fossils from Cuba and their economic significance. Bulletin of the Geological Society of America 53, 1417-1478.

Ivanov, M., Stoykova, K. & Idakieva, V., 2009. Revision of the ammonite criteria for the Jurassic-Cretaceous boundary in Bulgaria. Geosciences 2009, 57-58.

Ivanov, M., Stoykova, K. & Idakieva, V., 2010. New biostratigraphic data on the Upper Tithonian and Lower Berriasian in the Krayshte area (Southwestern Bulgaria). Annuaire de l'*Université* de *Sofia* “St. Kliment Ohridski”, Livre 1-Géologie 102, 21-42.

Jan Du Chêne, R., Busnardo, R., Charollais, J., Clavel, B., Deconinck, J.-F., Emmanuel, L., Gardin, S., Gorin, G., Manivit, H., Monteil, E., Raynaud, J.-F., Renard, M., Steffen,D., Steinhauser, N., Strasser, A., Strohmenger, C. & Vail, P.R., 1993. Sequence-stratigraphic interpretation of upper Tithonian-Berriasian reference sections in south-east France: a multidisciplinary approach. In: Bulletin des Centres de recherches exploration-production Elf-Aquitaine 17, 151-181.

Kietzmann, D.A., Blau, J., Riccardi, A.C., Palma, R.M., 2011b. An interesting finding of chitinoidellids (Calpionellidea Bonet) in the Jurassic-Cretaceous boundary of the Neuquén Basin. 18 Congreso Geológico Argentino, Actas CD, Neuquén, 1480–1481.

Kietzmann, D.A., Palma, R.M. & Iglesia Llanos, M.P., 2015. Cyclostratigraphy of and orbitally-driven Tithonian-Valanginian carbonate ramp succession, Southern Mendoza, Argentina: Implications for the Jurassic-Cretaceous boundary in the Neuquen Basin. Sedimentary Geology 315, 29-46.

Kilian, W., 1889. Études paléontologiques sur les terraines secondaires et tertiaires de l'Andalousie. In: Bertrand, M. & Kilian, W., (Eds). Mission d'Andalousie. Mémoires de l'Académie des Sciences de l'Institute National de France 30(2), 601-739.

Klug, C., Zatoń, M., Parent, H., Hostettler, B. & Takija, A., 2015. Chapitre 7 Mature Modifications and Sexual Dimrophism. In: Mapes, R.H., (Ed.). Ammonoid paleobiology: From anatomy to ecology: 503 Topics in geobiology. Springer. Netherlands, 935 pp.

Kvantaliani, I.V., 1989. Early Cretaceous ammonitids of the Crimea and Caucasus and their biostratigraphic significance. Trudy Geologicheskogo Instituta AN *Gruzii*, Moscow, 229 pp.

Kvantaliani, I.V., 1999. Berriasian Cephalopoda of the Crimea and Caucasus. Proceedings of the Geological Institute of the Georgian Academy of Sciences 112, 1-284.

Le Hégarat, G., 1971. Perisphinctidae et Berriasellidae de la limite Jurassique-Crétacé. Genres nouveaux et révision critique de quelques définitions taxinomiques antérieures. Comptes Rendus de l'Académie des Sciences, Paris 273, 850-853.

Le Hégarat, G., 1973. Le Berriasien du Sud Est de la France. Document du Laboratoire de Géologie de la Faculté des Sciences de Lyon 43, 1-576.

Le Hégarat, G. & Remane, J. 1968. Tithonique supérieur et Berriasien de l'Ardèche et de l'Hérault. Corrélation des Ammonites et des Calpionelles. Géobios 1, 7-70.

Le Hégarat, G. & Remane, J., 1973. Excursion A, coupes A. I-2: Berrias (stratotype). In: Colloque sur la limite Jurassique-Crétacé (Lyon-Neuchâtel, 7-16 septembre 1973) : livret-guide des excursions : bordure cévenole, chaînes subalpines, Jura. Documents des Laboratoires de géologie de la Faculté des sciences de Lyon, Hors Série 1, 71-78.

López-Martínez, R., Barragán, R. & Reháková, D., 2013, The Jurassic/Cretaceous boundary in the Apulco area by means of calpionellids and calcareous dinoflagellates: An alternative to the classical Mazatepec section in eastern Mexico: Journal of South American Earth Sciences 47, 142-151.

López-Martínez, R., Barragán, R., Reháková, D., Martini, M. & Eguiluz de Antuñano, S., 2015. Calpionellid biostratigraphy, U-Pb geochronology and microfacies of the Upper Jurassic-Lower Cretaceous Pimienta Formation (Tamazunchale, San Luis Potosi, central-eastern Mexico). Boletin de la Sociedad Geologica Mexicana 61, 75-86.

Lorenz, T., 1902. Geologische Studien im Grenzgebiete zwischen helvetischer und ostalpiner Facies. II Des südlichen Rhaetikons. Eclogae Geologicae Helvetiae 6(2), 155-156.

Maalaoui, K. & Zargouni, F., 2016. The Lower and Middle Berriasian in Central Tunisia: Integrated ammonite and calpionellid biostratigraphy of the Sidi Kralif Formation. Acta Geologica Polonica 66(1), 43-58.

Marek, S., 1967. The Infravalanginian of Kujawy. Bulletin de l'Institut de Géologie 200, 133-236.

Mazenot, G., 1939. Les Palaeophoplitidae tithoniques et berriasiens du sud est de la France. Mémoire de la Société Géologique de France, 41, 1-303.

Memmi, L., 1967. Succession des faunes dans le Tithonique supérieur et le Berriasien du Jebel Nara (Tunisie centrale). Bulletin de la Société Géologique de France 7, 267-272.

Memmi, L. & Salaj, J., 1975. Le Berriasien de Tunisie. Succession de faunes d'ammonites, de foraminifères et de tintinnoïdiens. In: Colloque sur la limite Jurassique Crétacé, Lyon, Neuchâtel. Mémoire du Bureau de Recherche Géologique et Minière, 58-67.

Myczyński, R., 1989. Ammonite biostratigraphy of the Tithonian of western Cuba. Annales Societatis Geologorum Poloniae 59, 43-125.

Myczyński, R., 1994. Caribbean ammonite assemblages from Upper Jurassic– Lower Cretaceous sequences of Cuba. Studia Geologica Polonica 105, 91-108.

Myczyński, R., 1999. Some ammonite genera from the Tithonian of western Cuba and their palaeobiogeographic importance. Studia Geologica Polonica 114, 93-112.

Myczyński R. & Pszczółkowski A. 1990. Tithonian stratigraphy in the Sierra de los Organos, Western Cuba: correlation of the ammonite and microfossil zones. In: Pallini G., Cecca F., Cresta S. & Sanantonio M. (Eds.). Fossili, Evoluzione, Ambiente. Atti del secondo convegno internazionale, Pergola 25-30 ottobre 1987, 405-415.

Naud, G. & Reboulet, S., 2008. Le stratotype de Berrias (Ardèche, France): référence géologique international de l'étage Berriasien. Les cahiers de Paiolive 1, 71-88

Nikolov, T.G., 1960. La faune d'ammonites dans le Valanginien du Prébalkan oriental. Travaux sur la géologie de Bulgarie 2, 143-264.

Nikolov, T.G., 1966. New genera and subgenera of ammonites of family Berriasellidae. Comptes Rendus de l'Académie bulgare des Sciences 19(7), 639-642.

Nikolov, T., 1967a. Sur la présence de *Berriasella grandis* Mazenot dans le Berriasien du Prébalkan oriental. Comptes Rendus de l'Académie bulgare des Sciences 20(6), 607-608.

Nikolov, T., 1967b. Les ammonites berriasiennes du genre *Protoleptoceras* Nikolov. Bulletin of the Geological Institute, serie paleontology 16, 35-45.

Nikolov, T.G., 1982. Les Ammonites de la famille Berriasellidae Spath, 1922. Tithonique supérieur-Berriasien. Académie bulgare des Sciences 10, 1-251.

Nikolov, T.G. & Mandov, M., 1967. Sur quelques nouvelles espèces d'ammonites berriasiennes du Prébalkan (Bulgarie du Nord). Bulletin de Géologie de l'Institut de Bulgarie de l'Académie des Sciences, Paléontologie 16, 41-46.

Olóriz, F., 1978. Kimmeridgiense-Tithonico inferior en el Sector central de las Cordilleras Béticas (Zona Sub-bética). Paleontologia, Bioestratigrafia. Tesis Doctorales, Universidad de Granada, 758 pp.

Olóriz, F. & Tavera, J.-M., 1979a. Nuevo Simoceratinae - *Simoceras* (*Cordubiceras*) - en la base del Tithonico superior de las Cordilleras Béticas (Zona Sub-betica). Tecniterrae "S-200" 29, 1-5.

Olóriz, F. & Tavera, J.-M., 1979b. Consideraciones sobre el género *Tithopeltoceras*, Arkell (1953) en las Cordilleras béticas (zone subbética, sector central). Estudios geologicos 35, 137-147.

Olóriz, F. & Tavera, J.-M., 1981. El Jurasico superior en el Sector Central de la Zona Subbetica. Introduccion al conocimiento de las facies. Indices y correlaciones. Real Academia de Ciencias Exactas, Fisicas y naturales 2, 207-239.

Olóriz, F. & Tavera, J.-M., 1989. The significance of Mediterranean ammonites with regard to the traditional Jurassic-Cretaceous boundary. Cretaceous Research 10, 221-237.

Olóriz, F., Villaseñor, A.B., Gonzalez-Arreola, C. & Westermann, G.E.G., 1999. Ammonite biostratigraphy and correlations in the Upper Jurassic lowermost and correlations in the Upper Jurassic lowermost Mexico (Sierra de Catorce, San Luis Potosí). In: Olóriz, F. & Rodriguez-Tovar, F.J. (Eds.): Advancing research on living and fossil Cephalopods. Kluwer Academic/Plenum Publishers, New York, 463-492.

Olóriz, F., Villaseñor, A.B. & Gonzalez-Arreola, C., 2003. Major lithostratigraphic units in land-outcrops of north-central Mexico and the subsurface along the northern rim of Gulf of Mexico Basin (Upper Jurassic–lowermost Cretaceous): a proposal for correlation of tectono-eustatic sequences. Journal of South American Earth Sciences 16, 119-142.

Olóriz, F., Boughdiri, M. & Marques, B., 2006. Remarks on relative phenotype stability in two Tithonian ammonite species first described from the Tunisian Dorsale - apreliminary approach to interpreting metapopulation dynamics in ammonites. Neues Jahrbuch für Geologie und Paläontologie, Abteilung 241(2), 287-302.

Oppel, A., 1865. Die tithonische Etage. Zeitschrift der Deutschen Geologischen Gesellschaft 17, 535-558.

Parent, H., Scherzinger, A. & Schweigert, G., 2011. The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina. Boletín del Instituto de Fisiografía y Geología 79-81, 21-94.

Parent, H., Garrido, A.C., Scherzinger, A., Schweigert, G & Fözy, I., 2015. The Tithonian-Lower Valanginian stratigraphy and ammonite fauna of Pampa Tril, Neuquén Basin, Argentina. Boletín del Instituto de Fisiografía y Geología 86, 1-96.

Patrulius, D. & Avram, E., 1976. Les céphalopodes des Couches de Carhaga (Tithonique supérieur Barrémien inférieur). In: Contributions à la paléontologie du Jurassique terminal et Crétacé des Carpates. Mémoire de l'institut de Géologie et Géophysique, 153-201.

Picha, E.J., Stráník, Z. & Krejèí, O., 2006. Geology and hydrocarbon resources of the Outer Western Carpathians and their foreland, Czech Republic. In: Golonka, J. & Picha, F. J., (Eds.). The Carpathians and Their Foreland: Geology and Hydrocarbon Resources. AAPG Memoir 84, 49-175.

Pictet, F.J., 1867. Etudes paléontologiques sur la faune à *Terebratula diphyoides* de Berrias (Ardèche). Mémoire de la Société de Physique et d'Histoire Naturelle de Genève 7, 43-130.

Pictet, F.J., 1868. Étude provisoire des fossiles de la Porte-de- France, d’Aizy et de Lémenc. Mémoire de la Société de Physique et d'Histoire Naturelle de Genève 4, 207-312.

Pomel, A., 1889. Les Céphalopodes néocomiens. Matériaux pour la Carte Géologique de L’Algérie, Paléontologie 2, 1-123.

Pruner, P., Houša, V.F., Olóriz, F., Košák, M.M., Krs, M., Man, O., Schnabl, P., Venhodová, D., Tavera, J.M., Mazuch, M., 2010. High-resolution magnetostratigraphy and biostratigraphic zonation of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain). Cretaceous Research 31(2), 192-206.

Pszczółkowski, A. & Myczyński, R., 2010. Tithonian–Early Valanginian evolution of deposition along the proto-Caribbean margin of North America recorded in Guaniguanico successions (western Cuba). Journal of South American Earth Sciences 29, 225-253.

Reboulet, S., Szives, O., Aguirre-Urreta, B., Barragán, R., Company, M., Idakieva, V., Ivanov, M., Kakabadzé, M.V., Moreno-Bedmar, J.A., Sandoval, J., Baraboshkin, E.J., Çağlar, M.K., Fözy, I., González-Arreola, C., Kenjo, S., Lukeneder, A., Raisossadat, S.N., Rawson, P.F., Tavera, J.-M., 2014. Report on the 5th International Meeting of the IUGS Lower Cretaceous Ammonite Working Group, the Kilian Group (Ankara, Turkey, 31st August 2013). Cretaceous Research 50, 126-137.

Remane, J., 1963. Les Calpionelles dans les couches de passage Jurassique-Crétacé de la fosse vocontienne. Travaux du Laboratoire de Géologie de Grenoble 39, 25-82.

Remane, J., 1970. Die Entstehung der resedimentären Breccien im Obertithon der subalpinen Ketten Frankreichs. Eclogae geologica Helvetiae 63-3), 685-740.

Remane, J., 1989. Calpionellids. In: Bolli, H.M., Saunders, J.B. & Perch-Nielsen, K., (Eds.) Plkanton Stratigraphy. Cambridge University Press, Cambridge, 555-572.

Remane, J., 1997. Les zones de calpionelles du passage Jurassique-Crétacé. In: Cariou, E. & Hantzpergue, P., (Eds.). Biostratigraphie du Jurassique ouest-européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. Elf Aquitaine édition, 243-247.

Remane J., Borza, K., Nagy, I., Bakalova-Ivanova, D., Knauer, J., Pop, G. & Tardi-Filácz, E., 1986. Agreement on the subdivision of the standard calpionellid zones defined at the 2nd Planktonic Conference Roma, 1970. Acta Geologica Hungarica 29, 5-14.

Retowski, O., 1893. Die tithonischen Ablagerungen von Theodosia. Bulletin de la Société des Naturalistes de Moscou 7, 206-301.

Roman, F., 1936. Le Tithonique du massif du Djurdjura (province d'Alger). Matériaux pour la Carte géologique de l'Algérie 7, 1-43.

Ross, C.A., Moore, G.T. & Hayashida, D.N., 1992. Late Jurassic paleoclimate simulation - Paleoecological implications for Ammonoid provinciality. Palaios 7, 487-507.

Salfeld, H., 1921. Kiel- und Furchenbildung auf der Schalenaussenseite der Ammonoideen in ihrer Bedeutung für die Systematik und Festlegung von Biozonen. Zentralblatt für Mineralogie, Geologie und Paläontologie 1921, 343-347.

Sapunov, I.G., 1977a. Richterellinae subfam. n. (Perisphictidae, Ammonoidea; Tithonian). Comptes Rendus de l'Académie bulgare de Science 30, 103-107.

Sapunov, I.G., 1977b. Ammonite biostratigraphy of the Upper Jurassic in Bulgaria. IV Tithonian: Substages, Zones and Subzones. Geologica Balcanica 7, 43-64.

Sapunov, I.G., 1979. Les fossiles de Bulgarie. III. 3. Jurassique supérieur, Ammonoidea. Académie Bulgare des Sciences, 263 pp.

Sarasin, C. and Schöndelmayer, C., 1901. Etude monographique des Ammonites du Crétacique inférieur de Châtel-Saint-Denis. Mémoire de la Société Paléontologique Suisse 24, 95-187.

Sarti, C., 1988. Biostratigraphic subdivision for the Upper Jurassic of Venetian Alps (Northern Italy) on the base of ammonites. 2nd International Symposium on Jurassic Stratigraphy, Lisboa, 459-476.

Seguret, M., Moussine-Pouchkine, A., Raja-Gabaglia, G. & Bouchette, F., 2001. Storm deposits and storm-generated coarse carbonate breccias on a pelagic outer shelf (South-East Basin, France). Sedimentology 48, 231-254.

Sey, I.I. & Kalacheva, E.D., 1999. Lower Berriasian of Southern Primorye (Far East Russia) and the problem of Boreal–Tethyan correlation. Palaeogeography, Palaeoclimatology, Palaeoecology 150, 49-63.

Spath, L.F., 1923. Appendix: On ammonites from New Zealand. In: Trechmann, C.T. The Jurassic rocks of New Zealand. The Quarterly Journal of the Geological Society of London 79, 286-308.

Spath, L.F., 1924. On the ammonites of the Speeton Clay and the subdivisions of the Neocomian. Geological Magazine 61, 73-89.

Spath, L.F., 1925. Ammonites and Aptychi. The Collection of Fossils and Rocks from Somaliland. Monographs Geological Department of the Hunterian Museum 1, 111-164.

Spath, L.F., 1950. A new Tithonian ammonite fauna from Kurdistan, northern Iraq. Bulletin of the British Museum of Natural History 1, 95-137.

Steinmann, G. 1890. Abtheitung II. Ammonitidae. In: Steinmann, G. & Döderlein, L. (Eds.). Elemente der Paläontologie., Leipzig 848, 400-447.

Szives, O. & Fözy, I., 2013. Systematic descriptions of Early Cretaceous ammonites of the carbonate formations of the Gerecse Moutains, Hungary. In: Főzy, I., (Ed.). Late Jurassic–Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis Mountains (Transdanubian Range, Hungary). Institute of Geosciences, University of Szeged, GeoLitera Publishing House, 293-342.

Tavera, J.-M., 1985. Les ammonites del Tithonico superior-Berriasense de la Zona Subbetica (Cordilleras Béticas). Unpublished Ph.D. dissertation, University of Granada, 381 pp.

Tavera J.-M., Checa, A., Olóriz, F. & Company, M., 1986. Mediterranean ammonites and the Jurassic-Cretaceous boundary in southern Spain (Subbetic Zone). Acta Geologica Hungarica 29(1-2), 151-159.

Tavera, J. -M., Aguado, R., Company, M. & Olóriz, F., 1994. Integrated biostratigraphy of the Durangites and Jacobi Zones (J/K boundary) at the Puerto Escaño section in southern Spain (Province of Cordoba). Géobios 17, 469-476.

Tchoumatchenco, P., Nikolov, T. & Kozhukharov, D., 1995. Le Crétacé inférieur dans le Massif de l'Ouarsenis (Atlas tellien) et les Monts de Tiaret (Hauts Plateaux oranais) (Algérie du Nord). Geologica balcanica 25, 27-59.

Toucas, A., 1890. Etude de la Faune des Couches tithoniques de l'Ardèche. Bulletin de la Société Géologique de France 18, 560-629.

Uhlig, V. 1905. Einige Bemerkungen uber die Ammonitengattung Hoplites Neumayr. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, mathematisch–naturwissenschaftliche Klasse 114, 591-636.

Vašíček, Z. & Skupien, P., 2013. Early Berriasian ammonites from the Štramberk Limestone in the Kotouč Quarry (Outer Western Carpathians, Czech Republic). Annales Societatis Geologorum Poloniae 83, 329-342.

Vašíček, Z. & Skupien, P., 2014. Recent discoveries of Tithonian ammonites in the Štramberk Limestone (Kotouč Quarry, Outer Western Carpathians). Annales Societatis Geologorum Poloniae 84, 131-141.

Vašíček, Z., Skupien, P. & Jirásek, J., 2013. The northernmost occurrence of the Lower Berriasian ammonite Pseudosubplanites grandis (Štramberk Limestone, Outer Western Carpathian, Czech Republic). Geologica Carpathica 64(6), 461-466.

Vennari, V.V., Lescano, M., Naipauer, M., Aguirre-Urreta, B., Concheyro, A., Schaltegger, U., Armstrong, R., Pimentel, M. & Ramos, V.A., 2014. New constraints in the Jurassic-Cretaceous boundary in the High Andes using high-precision U-Pb data. Gondwana Research 26, 374-385.

Verma, H.M. & Westermann, G.E.G., 1973. The Tithonian (Jurassic) ammonite fauna and stratigraphy of Sierra Catorce, San Luis Potosí, México. Bulletins of American Paleontology 63, 108-137.

Villaseñor, A.B., Olóriz, F., López Palomino, I., López-Caballero, I., 2012. Updated ammonite biostratigraphy from Upper Jurassic deposits in Mexico. Revue de Paléobiologie 11, 249-267.

Westermann, G.E.G., 2000a. Biochore classification and nomenclature in paleobiogeography: an attempt at order. Palaeogeography, Palaeoclimatology, Palaeoecology 158, 1-13.

Westermann, G.E.G., 2000b. Marine faunal realms of the Mesozoic: review and revision under the new guidelines for biogeographic classification and nomenclature. Palaeogeography, Palaeoclimatology, Palaeoecology 163, 49–68.

Wiedmann, J., 1973. Evolution or revolution of ammonoids at Mesozoic system boundary. Biological Reviews 48, 159-194.

Wimbledon, W.A.P., 2008. The Jurassic-Cretaceous boundary: an age-old correlative enigma. Episodes 31, 1-6.

Wimbledon, W.A.P., 2014. Warsaw Remarks–Berriasian Progress. Volumina Jurassica 12, 107-112.

Wimbledon, W.A.P., Casellato, C.E., Reháková, D., Bulot, L.G., Erba, E., Gardin, S., Verreusel, R.M.C.H., Munstermann, D.K. & Hunt, C.O., 2011. Fixing a basal Berriasian and Jurassic/Cretaceous (J/K) boundary – is there perhaps some light at the end of the tunnel?. Rivista Italiana di Paleontologia e Stratigrafia, 117, 295-307.

Wimbledon, W. A. P., Reháková, D., Pszczółkowski, A., Cassellato, C. E., Halásová, E., Frau, C., Bulot, L. G., Grabowski, J., Sobień, K., Pruner:, Schnabl, P. and Čížková, K., 2013. A preliminary account of the bio– and magnetostratigraphy of the upper Tithonian–lower Berriasian interval at Le Chouet, Drôme (SE France). Geologica Carpathica 64, 437-460.

Zakharov, V., Bown, P. & Rawson, P. F., 1996. The Berriasian Stage and the Jurassic-Cretaceous boundary. In: Rawson, P.F., (Ed.). Proceedings of the Second International Symposium on Cretaceous Stage Boundaries. Bulletin de l'Institut Royal des Sciences Naturelle de Belgique, 7-10.

Zeiss, A., 1983. Zur Frage der Aquivalenz der Stufen Tithon/Berrias/Wolga/Portland in Eurdsien und Amerika. Ein Beitrag zur Klarung der weltweiten korrelation der Jura-Kreide-Grenzschichten im marinen Bereich. Zitteliana 10, 427-438.

Zeiss, A., 2001. Die Ammonitenfauna der Tithonklippen von Ernstbrunn, Niederösterreich, Neue Denkschriften des naturhistorischen Museum in Wien 6, 1-115.

Zell, P., Stinnesbeck, W., Beckmann, S., Adatte, T., Hering, F., 2015. The Berriasian-Valanginian (Early Cretaceous) boundary transition at Santa Catarina Ticuá, Oaxaca State, southern Mexico: Ammonites, bivalves, calpionellids and their paleobiogeographic significance. Journal of South American Earth Sciences 62, 33-57.

Zittel, von K.A., 1868. Die Cephalopoden der Stramberger Schichten. Paläontologische Mittheilungen aus dem Museum des königlich Bayerischen Staates 2, 33-118.

Zittel, von K.A., 1870. Die Fauna der älteren cephalopodenführenden Tithonbildungen. Palaeontographica 2 (Supplement 1), 1-192.

Zittel, von K.A., 1895. Grundzüge der Palaeontologie (Palaeozoologie). Munich & Leipzig: R. Oldenbourg, vii+972 pp.

GEOLOGICA CARPATHICA, DECEMBER 2013, 64, 6, 437–460 doi: 10.2478/geoca-2013-0030

An account of the bio- and magnetostratigraphy of the Upper Tithonian–Lower Berriasian interval at Le Chouet, Drôme (SE France)

WILLIAM A.P. WIMBLEDON[1], DANIELA REHÁKOVÁ[2], ANDRZEJ PSZCZÓŁKOWSKI[3], CRISTINA E. CASELLATO[4], EVA HALÁSOVÁ[2], CAMILLE FRAU[5], LUC G. BULOT[6], JACEK GRABOWSKI[7], KATARZYNA SOBIEŃ[7], PETR PRUNER[8], PETR SCHNABL[8] and KRISTÝNA ČÍŽKOVÁ[8]

[1]Department of Earth Sciences, University of Bristol, Queens Road, Bristol BS8 1RJ, United Kingdom;
mishenka1@yahoo.co.uk; glwapw@bristol.ac.uk
[2]Department of Geology and Paleontology, Faculty of Natural Sciences, Comenius University, Mlynská dolina G-1, 842 15 Bratislava,
Slovak Republic; rehakova@fns.uniba.sk; halasova@fns.uniba.sk
[3]Institute of Geological Sciences, Polish Academy of Sciences, ul. Twarda 51/55, PL-00-818 Warsaw, Poland; pszczolkowski@yahoo.com
[4]Dipartimento di Scienze della Terra "A. Desio", Università degli Studi di Milano, via Mangiagalli 34, 20133 Milano, Italia;
cristina.casellato@unimi.it
[5]Biogéosciences, UMR-CNRS 5561, Université de Bourgogne, 6 Bd Gabriel, 21000 Dijon, France; camille_frau@hotmail.fr
[6]Géologie de Système Carbonatés, Université de Provence Aix-Marseille, Case 57, 3 place Victor Hugo, F 13331 Marseille, France;
lucgbulot@aol.com
[7]Polish Geological Institute–National Research Institute, Rakowiecka 4, 00-975 Warsaw, Poland;
jacek.grabowski@pgi.gov.pl; katarzyna.sobien@pgi.gov.pl
[8]Institute of Geology AS CR, v.v.i., Rozvojová 269, 165 00 Praha 6, Czech Republic;
pruner@gli.cas.cz; schnabl@gli.cas.cz; cizkovak@gli.cas.cz

(Manuscript received January 7, 2013; accepted in revised form October 16, 2013)

Abstract: This paper discusses the results of a study of the Le Chouet section, its lithologies, facies, magnetic properties and fossil record (ammonites, calcareous nannofossils, calpionellids and calcareous dinoflagellates). Data obtained have been applied to give a precise biostratigraphy for this carbonate sequence as well as a paleoenvironmental reconstruction. Its relationship to magnetostratigraphy, based on a modern study of a French site, is important. Investigation of the micro- and macrofossils shows that the site comprises a sedimentary sequence in the Microcanthum to Jacobi ammonite Zones, and the *Chitinoidella*, *Crassicollaria* and *Calpionella* Zones. Several calpionellid and nannofossil bioevents have been recorded on the basis of the distribution of stratigraphically important planktonic organisms. The site allows us to calibrate the levels of various biomarkers and biozonal boundaries, and correlate them with the magnetozones M20n, M19r and M19n.

Key words: Tithonian, Berriasian, integrated biostratigraphy, magnetostratigraphy, microfacies, ammonites, calcareous nannofossils, calcareous dinoflagellates, calpionellids.

Introduction

This study results from the decision of the Berriasian Working Group (International Subcommission on Cretaceous Stratigraphy) to better document sequences at and close to the Jurassic/Cretaceous (J/K) boundary, and it is our intention to publish comparative accounts of the best-developed sections, in line with the multidisciplinary standards exemplified by the studies made by Michalík et al. and Houša et al. Simultaneously, working-group members are re-examining classical localities and new sites to better assess and calibrate useful topmost Tithonian to lowest Berriasian markers and their proxies (Wimbledon et al. 2011). Significantly, though we commence work on the classical European sites, we are extending detailed study out from this core area to new sites in Africa, Asia and the Americas to better constrain the J/K boundary.

As at the historical stratotype of Berrias fossiliferous units do not extend low enough to reach the putative base for the Cretaceous, it is unsuitable for our purposes of stage and biozonal definition. Therefore, a start has been made on examining other localities in southern France — seeking 'templates' for the top Tithonian ("*Durangites* Zone"), and the *Berriasella jacobi* and *Pseudosubplanites grandis* zonal intervals. These included the only locality that had been noted with a relatively common latest Tithonian ammonite assemblage (Boughdiri 1994), and that is the section described in this work. A first reconnaissance in 2008 located the site, but also revealed the existence of common ammonite faunas overlying the supposed *Durangites*-bearing levels, and therefore the section was chosen for closer study; and it was then additionally sampled for calpionellids, calcareous nannofossils and, subsequently, magnetostratigraphy. Further work at this productive site on geochemistry, magnetic susceptibility, refinement of results on magnetostratigraphy, calpionellids and ammonites is still in progress and this will form a basis for further publications.

This paper is the first description of the locality, in the Fournet Ravine, 10 km SE of Luc-en-Diois, Drôme; a site straddling the top Tithonian and lowest Berriasian stages. Locally, well-bedded and massively bedded (averaging 0.20–1.00 m) Berriasian limestones form the upper slopes of the steep valley sides. Massive breccias (Remane 1970) in the Tithonian and Berriasian, sometimes tens of metres in thickness, are a dominating element of the landscape, forming inaccessible cliffs in local valleys.

Regionally, the Le Chouet and nearby Drôme sections (see Fig. 1) are part of the succession of the Domain vocontien or Basin vocontien (the Fosse Vocontienne or Vocontian trough of many earlier publications). This depositional basin occupies an approximately triangular area, its base extending across Languedoc and Provence, 250 km west to east, with a prolongation northwards to a narrow apex which reaches as far as Lake Geneva. Sedimentation was confined by older basement massifs: in the west by the Cévennes (Massif Central) and Les Maures in the south, with an opening eastwards to the oceanic Tethys. In the Upper Jurassic to lowest Cretaceous transition, it contains a sequence of deeper-water pelagic and hemipelagic sediments, whereas in some areas there were marginal marine or even terrestrial Purbeck facies, including evaporites, notably in the north (Maillard 1884; Détraz & Mojon 1989, etc.).

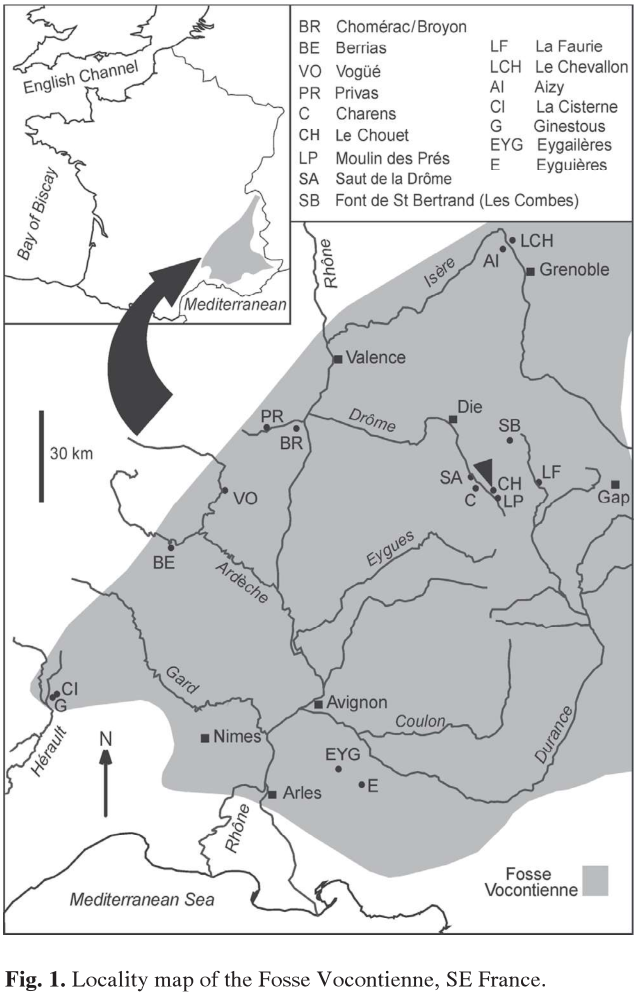


Fig. 1. Locality map of the Fosse Vocontienne, SE France.

The 'trough' thus includes classical areas and sites that have figured in studies of the Late Tithonian–Berriasian (Mazenot 1939; Le Hégarat 1971; Fig. 1 herein) — sites in the SW in the valley of the Hérault, along the River Ardèche (with the nominal type locality of Berrias), near Privas, including Chomérac, and across the catchments of the Durance, the Drôme and ultimately the River Isère, near to Grenoble. Putatively, the junction between the Tithonian and Berriasian in the western Tethys has been placed in ammonite schemes at the junction of the "*Durangites* Zone" and the *Berriasella jacobi* Subzone, despite the absence of any "*Durangites*" fauna. This has been the case among the classical French localities, many of which show abundant *Berriasella jacobi* assemblages, albeit often from breccia/conglomerate horizons, though very few have yielded any "*Durangites*".

Three previous authors have made significant mention of the Le Chouet site and its environs. Le Hégarat (1971) in his seminal work figured a somewhat stylized section for "Le Chouet" (as he did for other local sites). In that work he showed higher stratigraphic levels than are seen in the roadside section described here, and this seems to indicate another or a composite profile; perhaps involving outcrops further north, in the upper wooded reaches of the Fournet Valley (an area currently being studied). Remane (1970) gave an account of breccia developments in the Tithonian-Berriasian carbonates of the Drôme region, including both Le Chouet and the nearby Charens gorge section (3 km to the SSW). Remane's column for Le Chouet relates well to the section presented here: notably to eight useful marker beds up to his unit 1, breccias and conglomerates, which provide obvious comparable datums. Boughdiri (unpublished 1994) paid particular attention to the middle part of the sequence at Le Chouet, where he identified the *Durangites* Zone, illustrating several key ammonites, and noting a numbers of species of *Durangites* between our bed 78 and bed 85 (Fig. 11). Some of these ammonites were subsequently figured by Enay et al. (1998). Boughdiri also sampled seventeen levels for calpionellids, fixing the top of subzone A1 at the base of our bed 71 and the base of the *Calpionella* Zone at the base of bed 100.

Setting and geological description

In Late Jurassic to Late Cretaceous times, alternating periods of marl and limestone deposition characterized the region: however, in most areas during the Tithonian and the Berriasian, limestones were more common than marls: some few nearby Lower Berriasian sites have well-developed marl intervals (e.g. the sites of Saut de la Drôme and Les Combes (Fig. 1; Le Hégarat 1971)), but Le Chouet is more typical in comprising limestones.

The locality lies in the cliffed upper valley of the River Drôme, in pine forest (Long 5°33′33″ E, Lat 44°32′32″ N) off the local road (D306) from Die to Valdrôme. It comprises a low mural section, 200 m-long, along a single-track road on the north-west side of a precipitous gorge, the Ravin de Fournet. The section extends around the slope from an altitude of 928 m to a little above 1000 m. The sequence dips 10 degrees

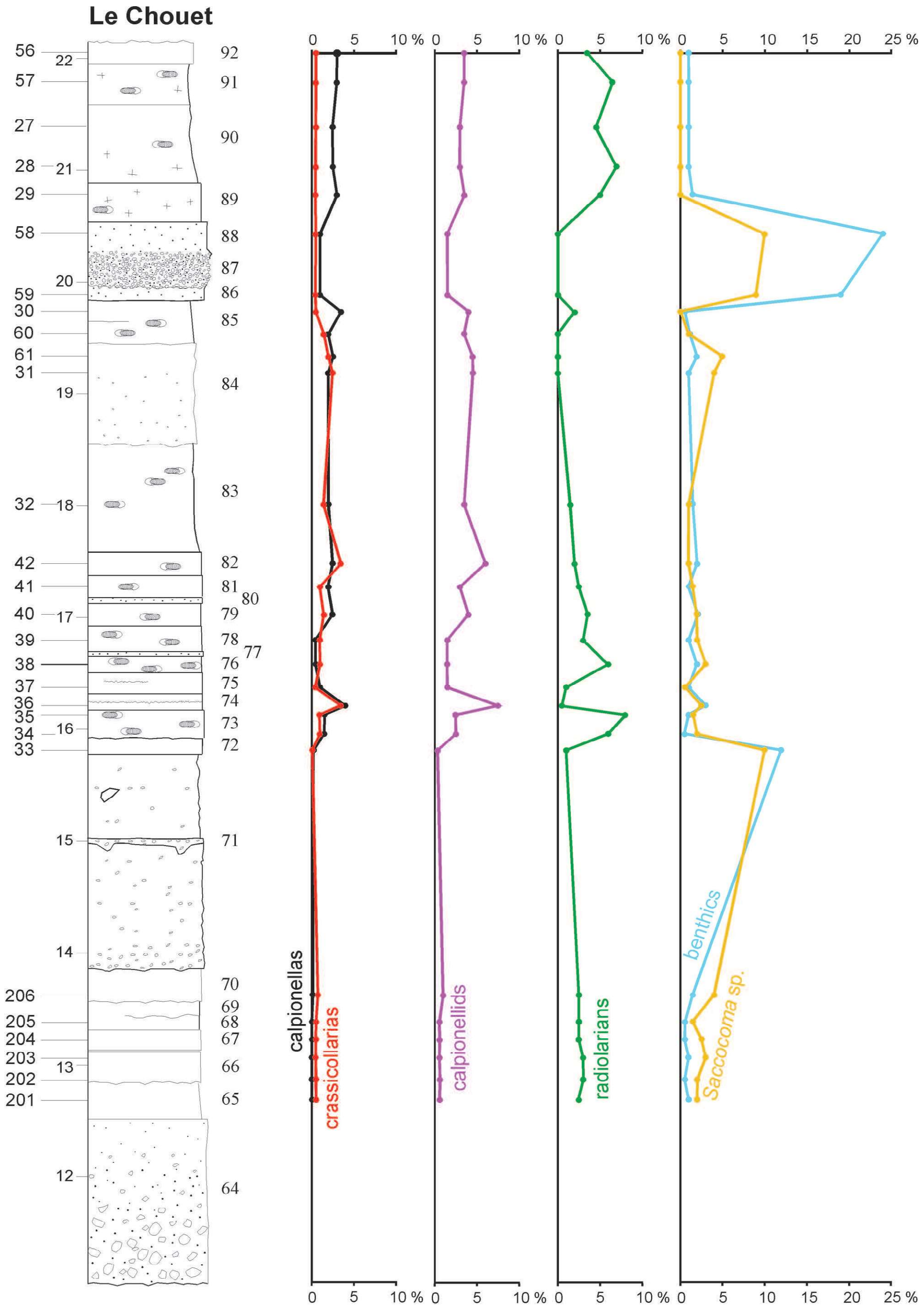


Fig. 2. Micropaleontological analysis — quantification of calpionellids and accompanying microfossils *sensu* Bacelle & Bossellini (1965).

at 155. The name for this trackside section previously used in the geological literature is that of the hamlet of Le Chouet (Le Chuot on older maps), which lies about 400 metres to the west of the section. Outcrops at supposed higher stratigraphic levels along the road to Le Chouet are not in stratigraphic continuity with the sequence here described, and tectonic dislocations are apparent between the broken exposures.

The succession exposed totals 43 metres, which includes, topping the section, a 10 m-thick, partly obscured, massive or poorly bedded micrite (bed 123) with 'floating' pebbles (Fig. 11). The majority of it consists of well-bedded micrite and biomicrite — mudstone, wackestone and packstone. Massive conglomerates and breccias (both clast and matrix supported) punctuate the sequence, and a number of intraclastic/microbreccia beds (grainstones) (e.g. beds 80, 108, 111; Fig. 11), grey in colour, alternate with the monotonous micrites. Pebble, boulder and grainstone levels make useful marker beds. These are variable in their grain sizes and textures, as noted in this region by Remane: units with coarse bases (e.g. beds 64, 71), 'floating' larger clasts in micrite (e.g. beds 71, 84, 104, 131), clast-supported beds (bed 87), and graded bedding (e.g. beds 52, 57, 64). Some of the thicker coarse-grained units mentioned above may be relatable to NW-SE submarine paleo-canyons that have been mapped in this region by Beaudoin and others (e.g. Joseph et al. 1988). Both Le Chouet and Charens lie inside one of the major canyons thus described, the Canyon de Ceuse. A range of slope and basinal settings have been postulated for Lower Berriasian sediments in the region, and origins as slumps, fans and channel fills have been suggested (e.g. Jan du Chęne et al. 1993). Only the lower beds (7–8 m) (not discussed in detail in this account) here show any appreciable argillaceous partings or thin beds, and therefore detectable indications of sedimentary rhythmicity.

Body fossils, apart from ammonites and aptychi, are rare; occasional isolated bivalves occur (common in a few beds), pygopid brachiopods have been noted, and common belemnites are found at one level (bed 103). Ammonites are numerous, excepting in the lowest ten metres, and most common in the central part of the sequence. Derived, abraded ammonites have been recorded in beds 64, 71, 87 and 123.

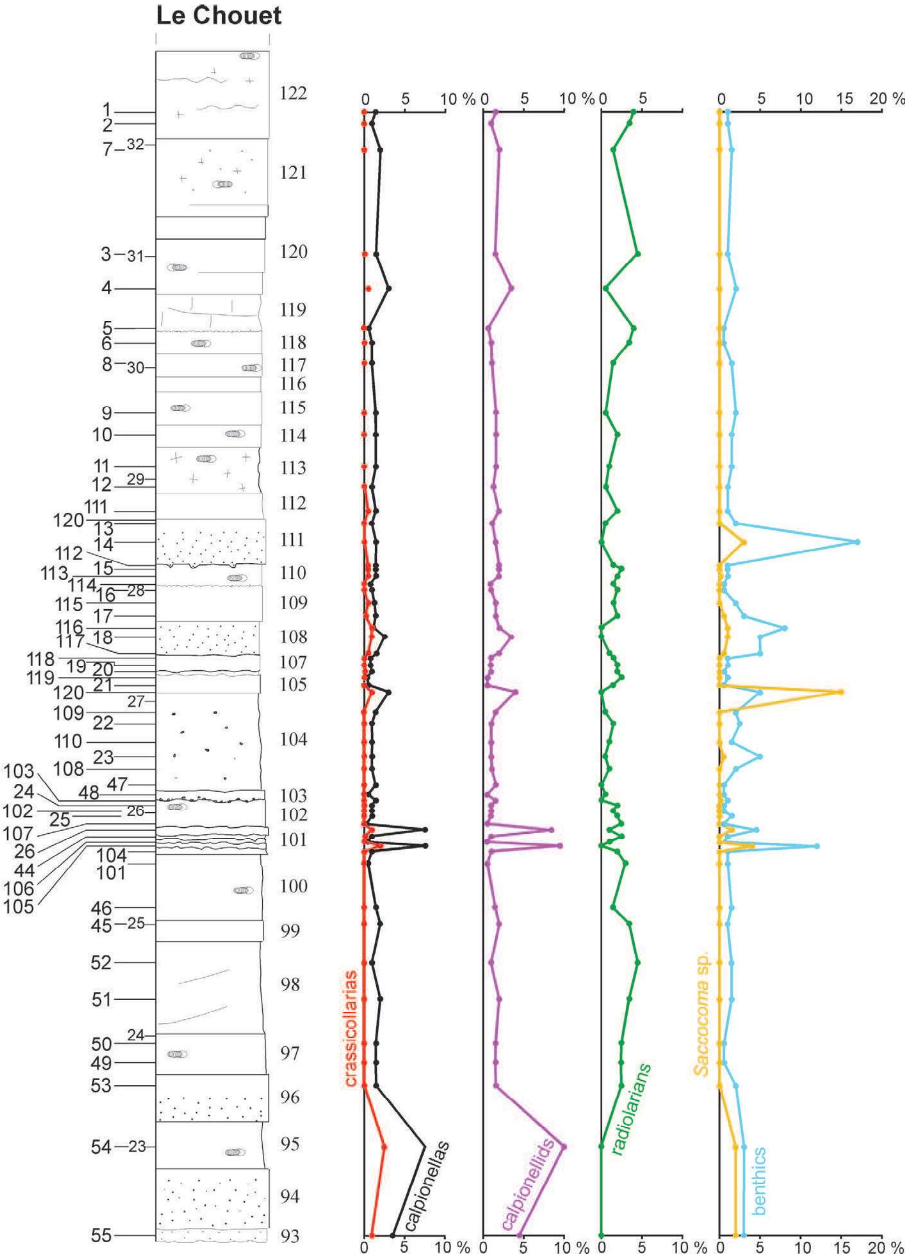


Fig. 3. Micropaleontological analysis — quantification of calpionellids and accompanying microfossils *sensu* Bacelle & Bossellini (1965).

Calpionellids and calcareous dinoflagellates — microfacies analysis

Samples used for microfacies analysis were collected in several steps; an initial 60 samples were later augmented at critical levels, to a total of 85 samples from an interval of 20 metres, between bed 65 and bed 122. (Higher and lower stratigraphic levels have since been sampled and these are currently being evaluated.) Allochems and micrite have been studied under an optical microscope (LEICA DM 2500) and the percentage rations of organic detrital grains, bioclasts etc. calculated. The data obtained are shown in graphic form, a representation of their relative changes (Figs. 2 and 3). Microfossil markers and microfacies were documented using a LEICA DFC 290 HD camera. The thin sections are stored in the collections of the Department of Geology and Paleontology (Faculty of Natural Sciences) in Bratislava.

The sequence studied is composed of biomicrite limestones (mudstones to wackestones) intercalated with pelbiomicrite, pelbiomicrosparite (packstones) and biomicrobrecciated limestones (grainstones). Calpionellids, radiolarians, saccocomids and residual biodetrital fragments have been quantitatively evaluated using the optical charts of Bacelle & Bosellini (1965). Intraclast fragments and saccocomids, crinoids, pellets and ooids were transported and resedimented, influenced probably by extensional pulses, synsedimentary erosion and/or eustatic fluctuations. Some intercalations bear the marks of storm sedimentation. Calpionellid and radiolarian curves are plotted on graphs (Figs. 2, 3), and they show a decrease in the abundance of calcareous plankton correlated with an increase of silica-producing organisms, as previously documented (Reháková & Michalík 1994; Michalík et al. 2009).

Calpionellids in the studied samples are generally well-preserved. Hyaline forms dominate. The calpionellid biostratigraphical scale (standard calpionellid zones and subzones) as proposed by Remane et al. (1986) and Reháková & Michalík (1997) and the calcareous dinoflagellate succession *sensu* Reháková (2000) have been adopted. Two calpionellid zones are well recognized, the *Crassicollaria* Zone (with Remanei, Intermedia and Colomi Subzones) and the *Calpionella* Zone (Alpina Subzone) (Fig. 4), with a less defined *Chitinoidella* Zone (Boneti Subzone) below.

Chitinoidella Zone, Boneti Subzone (*sensu* Borza 1984 and Grandesso 1977)

This zone has been identified on the basis of a few, spaced, samples. In beds below the thick mass-flow unit of bed 64, calpionellids are less common. The lowest 5 m of the

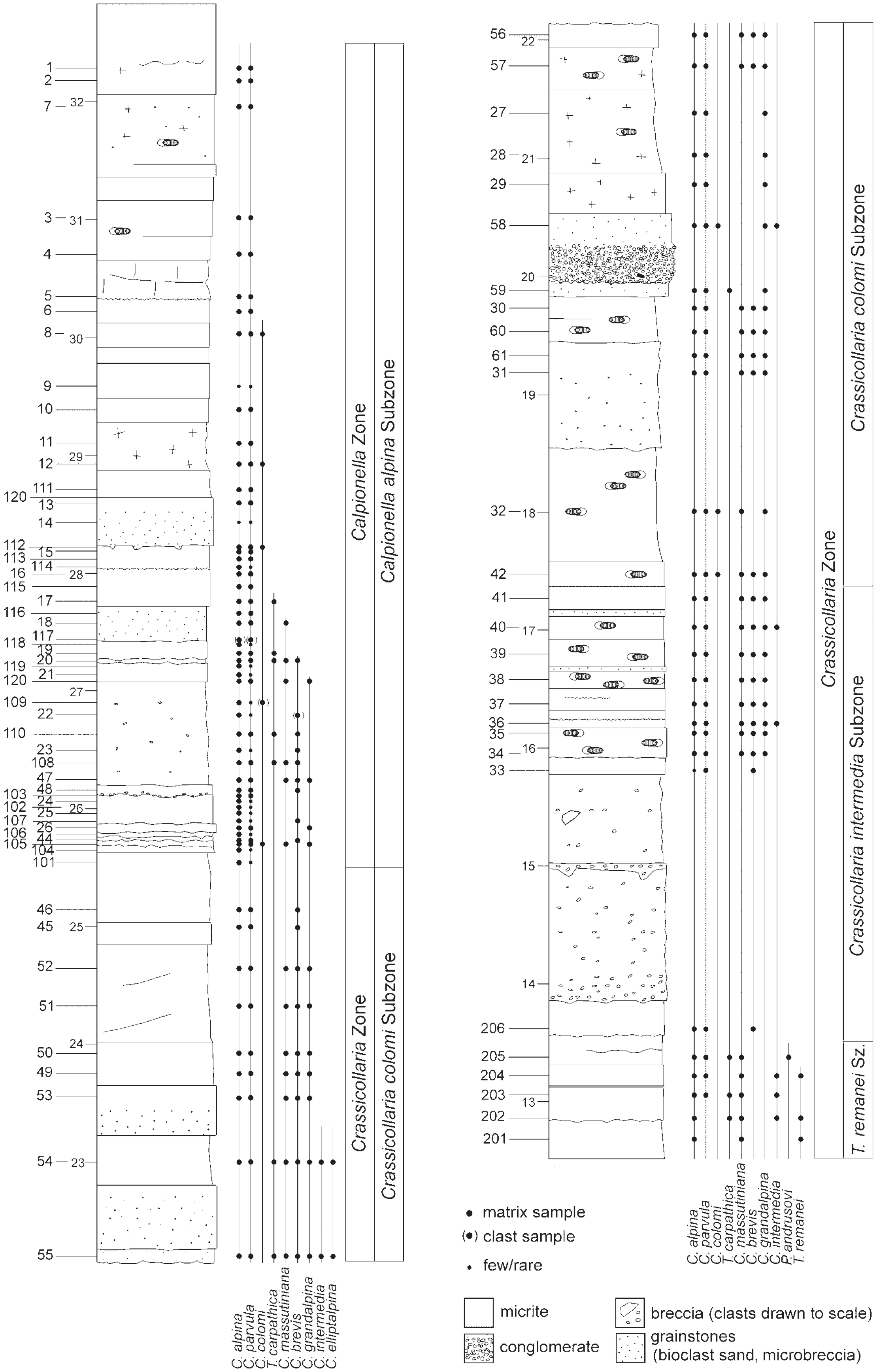


Fig. 4. Vertical ranges of calpionellid species. (Lithologies shown apply to all figures.)

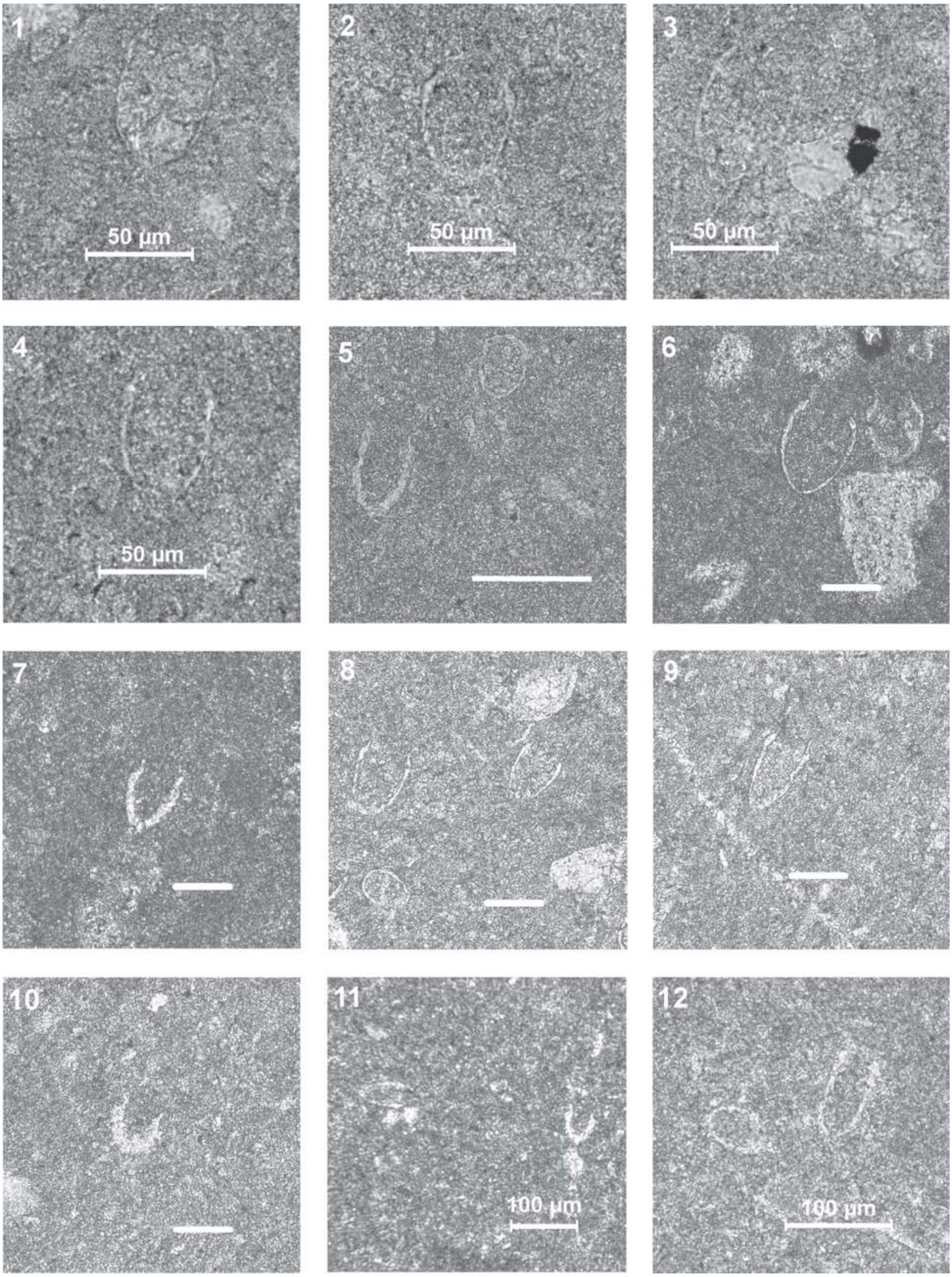


Fig. 5. 1 — *Praetintinnopsella andrusovi* Borza; Sample CH205. **2** — *Tintinnopsella remanei* Borza; Sample CH204. **3** — *Tintinnopsella carpathica* (Murgeanu & Filipescu); Sample CH203. **4** — *Crassicollaria massutiniana* (Colom); Sample CH206. **5** — *Crassicollaria* aff. *intermedia* (Durand Delga); Sample CH61. **6** — *Calpionella elliptalpina* Nagy; Sample CH55. **7** — *Crassicollaria brevis* Remane; Sample CH55. **8** — *Crassicollaria massutiniana* (Colom), *Crassicollaria parvula* Remane; Sample CH47. **9** — *Crassicollaria parvula* Remane; Sample CH47. **10** — *Calpionella alpina* Lorenz; Sample CH47. **11** — *Crassicollaria brevis* Remane; Sample CH110. **12** — *Crassicollaria colomi* Doben; Sample CH109. Scale bars in Figs. 5–10 are 100 µm.

Le Chouet section have yet to be sampled for microfossils, but the next 5.5 m (beds 33 to 63), mostly consisting of biomicrites, yield rare benthic forams (*Spirillina*, beds 50 and 56), poorly preserved calcified radiolaria (mostly noticeably possible *Spumellaria*), *Saccocoma* ossicles, and a few levels with chitinoidellids. Calcareous dinoflagellates are practically absent from the interval. The majority of samples demonstrate radiolarian-*Saccocoma* microfacies and lesser radiolarian microfacies (13 of 19 samples), with a few occurrences of *Saccocoma* microfacies and one of radiolarian-*Saccocoma-Globochaete* microfacies.

Chitinoidellids are scarce below bed 64, but they have been identified in beds 33, 34 and 61, albeit with poor preservation. Bed 33 yields *Chitinoidella* cf. *boneti* Doben and *Carpathella rumanica*, bed 34 has *Longicollaria* cf. *dobeni*, and bed 59 *Chitinoidella* ex gr. *boneti-elongata* and indeterminate Chitinoidellidae. Their presence makes it possible to assign at least beds 33 to 59 to the *Chitinoidella* Zone.

***Crassicollaria* Zone, Remanei Subzone** (*sensu* Remane et al. 1986) — samples CH201–CH205

Biomicrite limestones of globochaete-radiolarian microfacies (wackestones): they contain calcified radiolarians, sponges, globochaetes, ?*Praetintinnopsella andrusovi* Borza (Fig. 5.1), *Tintinnopsella remanei* Borza (Fig. 5.2), *Tintinnopsella carpathica* (Murgeanu & Filipescu), *Crassicollaria intermedia* (Durand Delga), *Crassicollaria massutiniana* (Colom), *Crassicollaria parvula* Remane, *Calpionella alpina* Lorenz, cysts of *Stomiosphaera moluccana* Wanner (Fig. 6.1), *Stomiosphaerina proxima* Řehánek, *Colomisphaera nagyi* (Borza) (Fig. 6.2), *Colomisphaera carpathica* (Borza), *Colomisphaera pieniniensis* (Borza) (Fig. 5.3), *Schizosphaerella minutissima* (Colom), filaments, ostracods, crinoids, aptychi, *Involutina* sp., and rare *Saccocoma* sp. It is noteworthy that some of the calpionellids and dinocysts mentioned above (*Colomisphaera pieniniensis* and *Stomiosphaera moluccana*) have never previously been observed in Upper Tithonian units (Reháková 2000), and *Praetintinnopsella andrusovi* has only been seen rarely (in the lower *Crassicollaria* Zone, with *T. remanei* and uncommon *C. alpina*). We surmise that they were re-sedimented.

***Crassicollaria* Zone, Intermedia Subzone** (*sensu* Remane et al. 1986) — samples CH206–CH41

Biomicrite limestones have calpionellid-globochaete-radiolarian, calpionellid-radiolarian, radiolarian-calpionellid-globochaete, globochaete-calpionellid, calpionellid-globochaete and radiolarian-calpionellid microfacies (wackestones) make-ups. It contains calcified radiolarians, sponges, globochaetes and diverse calpionellid associations including *Calpionella*

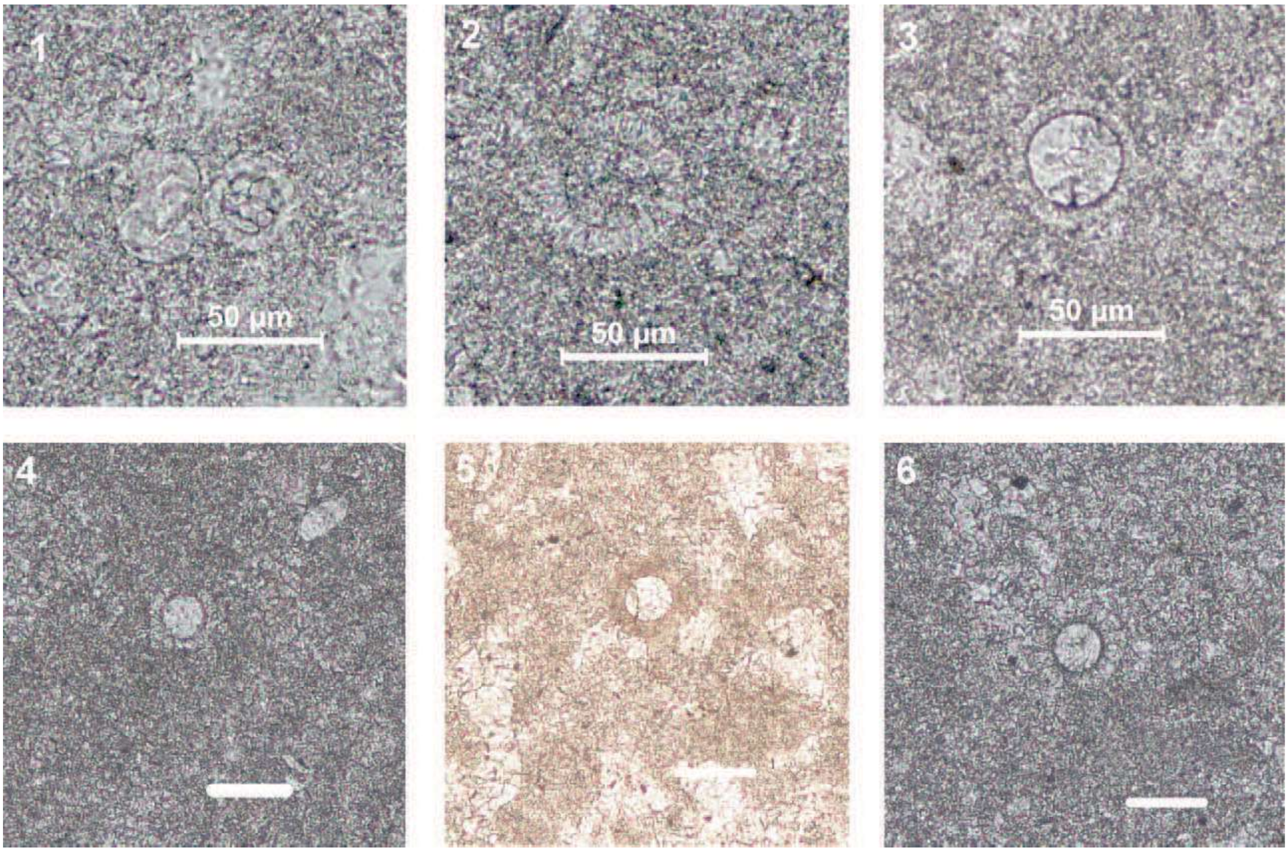


Fig. 6. 1 — *Stomiosphaera moluccana* Wanner; Sample CH202. **2** — *Colomisphaera nagyi* (Borza); Sample CH203. **3** — *Colomisphaera pieniniensis* (Borza); Sample CH205. **4** — *Schizosphaerella minutissima* (Vogler); Sample CH50. **5** — *Cadosina semiradiata fusca* Wanner; Sample CH47. **6** — *Colomisphaera carpathica* (Borza); Sample CH20. Scale bars in Figs. 4–6 are 50 µm.

alpina Lorenz, *Calpionella grandalpina* Nagy, *Calpionella elliptalpina* Nagy, *Crassicollaria massutiniana* (Colom), *Crassicollaria parvula* Remane, *Crassicollaria brevis* Remane, *Tintinnopsella carpathica* (Murgeanu & Filipescu), cysts of *Stomiosphaerina proxima* Řehánek, *Schizosphaerella minutissima* (Colom), *Cadosina semiradiata fusca* Wanner, bivalve fragments, filaments, miliolid foraminifers, crinoids, aptychi and rare planktonic crinoids — *Saccocoma* sp. Some crassicollarian loricas are very thin and deformed.

Two limestone layers (samples CH33 and CH36) show pelbiomicrite to pelbiomicrosparite/pelbiosparite structure (packestones and grainstones, Fig. 8.6). They contain small pellets, frequent globochaetes, fragments of planktonic crinoids (*Sacccoma* sp.), crinoid columnals, less frequent agglutinated and hyaline foraminifers, bivalves, ostracods, calcified radiolarians and rare calpionellids and cysts mentioned above: *Calpionella alpina* Lorenz, *Calpionella grandalpina* Nagy, *Crassicollaria intermedia* (Durand Delga), *Crassicollaria parvula* Remane, *Crassicollaria massutiniana* (Colom), *Crassicollaria brevis* Remane, cysts of *Cadosina semiradiata fusca* Wanner and *Schizosphaerella minutissima* (Colom).

***Crassicollaria* Zone, Colomi Subzone** (*sensu* Reháková & Michalík 1997) — samples CH42–CH46

Biomicrite limestones consist of calpionellid-globochaete, globochaete-calpionellid, calpionellid-radiolarian, radiolaria-calpionellid, and calpionellid-radiolarian-globochaete microfacies (wackestones to packstones). In some layers, crassicollarians increase in abundance, and some of them have thin and aberrant loricas (Fig. 8.5). Generally they contain frequent *Crassicollaria parvula* Remane, less common *Crassicollaria massutiniana* (Colom), rare *Crassicollaria brevis* Remane, *Crassicollaria colomi* Doben, *Calpionella alpina* Lorenz, *Calpionella grandalpina* Nagy, globochaetes, calcified radiolarians, fragments of planktonic *Saccocoma* sp., bivalves, ostracods, aptychi and infrequent cysts — *Cadosina semiradiata fusca* Wanner and *Schizosphaerella minutissima* (Colom) (Fig. 6.4).

This interval also contains layers with marks of re-sedimentation. Several of them (samples CH31, -59, -58, -56, -55 and -54) were investigated under the microscope. Some have fragments of *Saccocoma* sp., and crinoids dominate over foraminifers, ophiuroids, globochaetes, calpionellids and dinoflagellate cysts. On the other hand, pelbioclastic limestones (grainstones, Fig. 8.2) contain abundant pellets, globochaetes and the "acme" of the calpionellids *Calpionella alpina* Lorenz, *Calpionella grandalpina* Nagy, *Calpionella elliptalpina* Nagy (Fig. 5.6), *Tintinnopsella carpathica* (Murgeanu & Filipescu) (Fig. 8.3), *Crassicollaria intermedia* (Durand Delga) (Fig. 8.4), *Crassicollaria massutiniana* (Colom), *Crassicollaria parvula* Remane and *Crassicollaria brevis* Remane (Fig. 5.7). Many of the crassicollarian loricas are thin and deformed. *Cadosina semiradiata fusca* (Wanner), *Schizosphaerella minutissima* (Colom), calcified radiolarians, ostracods, crinoids, ophiuroids, bivalves, aptychi, agglutinated foraminifers and *Saccocoma* sp. are rare.

***Calpionella* Zone, Alpina Subzone** (*sensu* Remane et al. 1986; Reháková & Michalík 1997; Lakova et al. 1999; Boughdiri et al. 2006 and Andreini et al. 2007) — samples CH101–CH1

Biomicrites (predominantly wackestones) in which the ratio of calpionellids, radiolarians and globochaetes determines the type of microfacies (calpionellid-globochaete-radiolarian, calpionellid-radiolarian (Fig. 7.1), radiolarian-calpionellid, calpionellid-globochaete and globochaete-calpionellid (Fig. 7.2)). The *Crassicollaria-Calpionella* zonal boundary may be placed between 101 and the next sample below. Sample CH101 contains predominantly spherical forms of *Calpionella alpina* Lorenz (Fig. 8.1), two loricas of *Crassicollaria parvula* Remane, calcified radiolarians and sponges, globochaetes and very infrequent fragments of echinoids and ostracods. Higher up, in the samples of biomicrite wackestone, there are infrequent *Crassicollaria brevis* Remane, *Calpionella grandalpina* Nagy, cysts of *Cadosina semiradiata fusca* Wanner (Fig. 6.5), *Schizosphaerella minutissima* (Colom), *Colomisphaera carpathica* (Borza) (Fig. 6.6), rare ostracods, bivalves, aptychi and filaments were observed. The stratigraphical range of the above mentioned calpionellids has thus far been seen as being limited to the Upper Tithonian (Reháková 2000).

Crassicollaria parvula Remane increases in abundance in samples CH113, -15, and -112. Here rare fragments of planktonic crinoids, *Saccocoma* sp., were also identified. Borza (1984), in a chart showing microfossil stratigraphic ranges, indicated that saccocomids never cross the J/K boundary. We confirm the same experience. Events of increased abundance of crassicollarians visible in some sections (Houša et al. 2004; Pruner et al. 2010) were interpreted as a *Crassicollaria parvula* "acme" zone ("CPAZ") or a potential "epibole". We suppose that this assemblage represented the Alpina Subzone of the standard *Calpionella* Zone of the Lower Berriasian (*cf.* Reháková & Michalík 1997), but it occasionally contains some older *Crassicollaria*, from Upper Tithonian limestones, incorporated into the micrite matrix of the Alpina Subzone. A more dynamic, more agitated, water-body regime in the Jurassic/Cretaceous boundary interval was documented by Olóriz et al. (1995), and recently also by Grabowski et al. (2010a), Michalík & Reháková (2011) and Reháková et al. (2011).

Frequent intercalations composed of pelbiomicrites passing to pelbiomicrosparites/pelbiosparites and breccia layers (packstones to grainstones) were observed also in this part of the sequence (Fig. 7.3). They usually contain abundant pellets, bioclasts and intraclasts, which contain spectra of typical Late Tithonian calpionellids (Fig. 6.6). The abundance of calpionellids and globochaetes in some of these intercalations is greater than the abundances visible in the biomicrite layers described above. *Calpionella alpina* Lorenz, *Calpionella grandalpina* Nagy, *Tintinnopsella carpathica* (Murgeanu & Filipescu), *Crassicollaria massutiniana* (Colom), *Crassicollaria parvula* Remane, *Crassicollaria colomi* Doben, and cysts of *Cadosina semiradiata fusca* Wanner, *Schizosphaerella minutissima* (Colom) and *Colomisphaera* sp. were recognized. Deformed crassicollarian

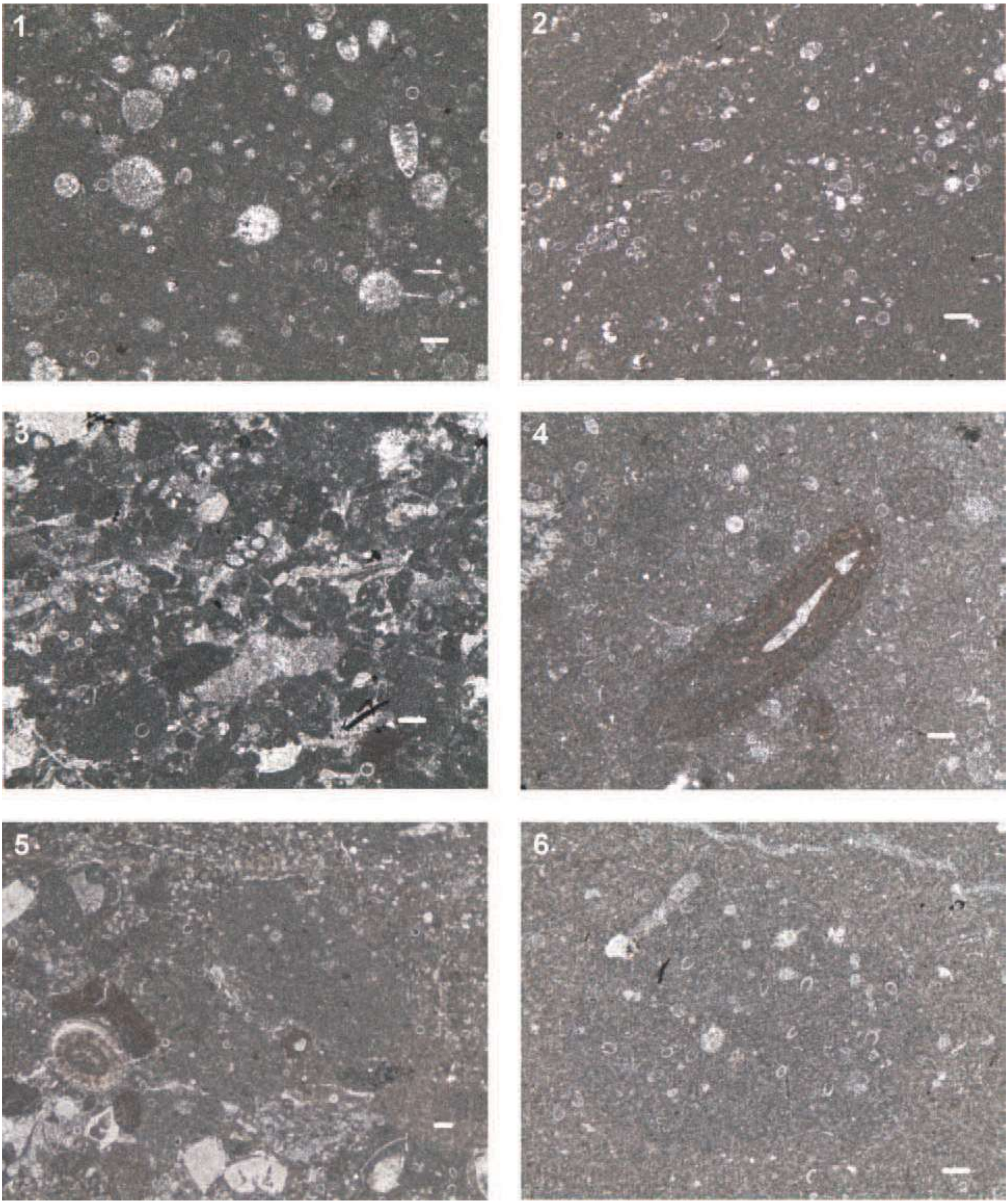


Fig. 7. 1 — *Calpionella*-radiolarian microfacies with calcified radiolarians and *Calpionella alpina* Lorenz; Sample CH6. **2** — Globochaete-*Calpionella* microfacies with *Calpionella alpina* and *Crassicollaria parvula*; Sample CH9. **3** — Microclastic limestone (grainstone) with *Calpionella alpina*, *Crassicollaria parvula*, agglutinated foraminifers, crinoids and bivalves; Sample CH14. **4** — *Crescentiella morronensis* (Crescenti) in biomicrite limestone (wackestone); Sample CH17. **5** — Microclastic limestone (grainstone) with the extraclasts of calpionellid limestones, and biogenic fragments coming from shallow-water environments (ooids and bryozoans). **6** — Clast of biomicrite wackestones with more abundant crassicollarians (*Crassicollaria brevis*, *Crassicollaria parvula*) in microbrecciated limestone; Sample CH23. Scale bars in all figures are 100 μm.

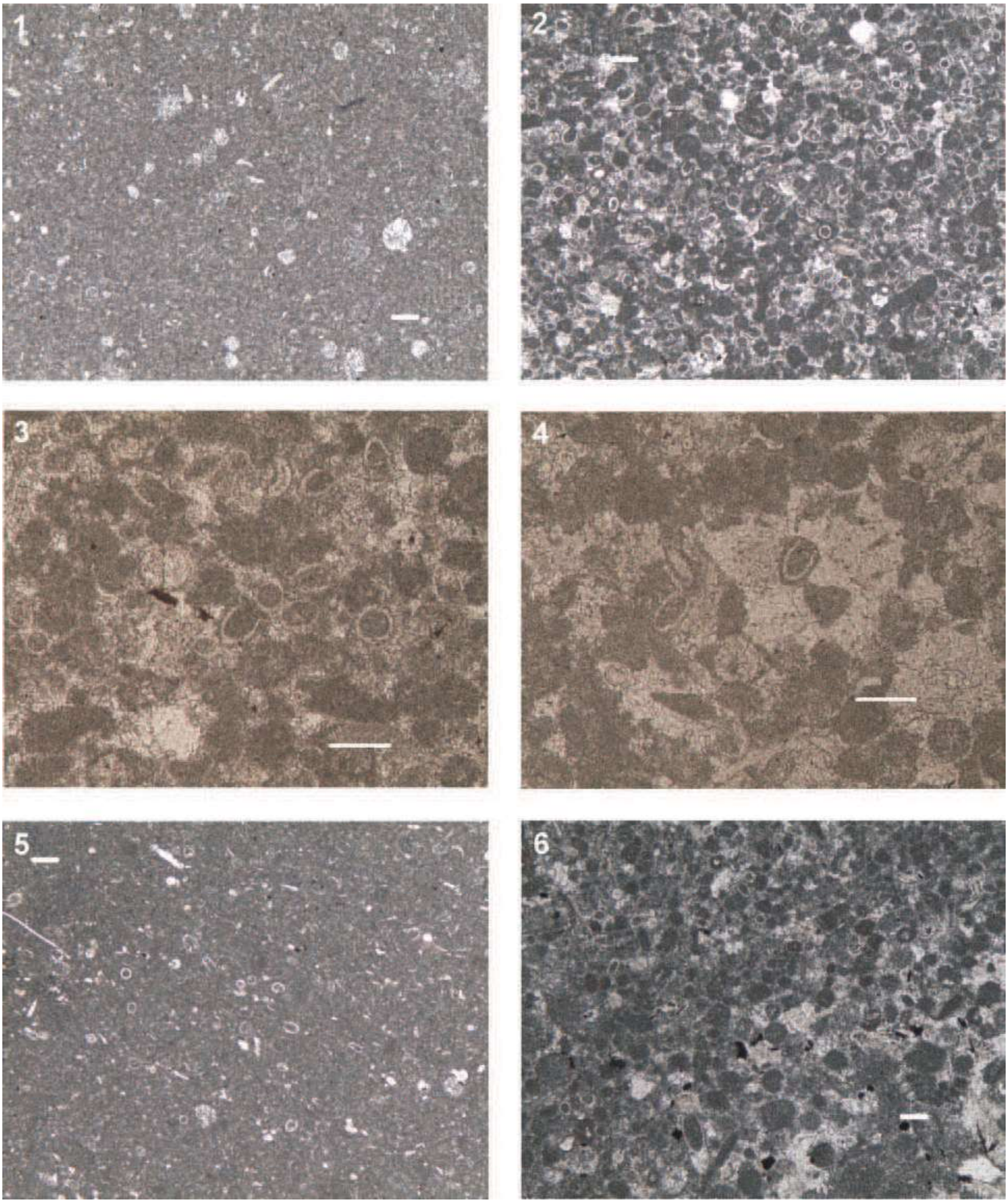


Fig. 8. 1 — Biomicrite limestone (wackestone) dominated by spherical forms of *Calpionella alpina*; Sample CH101. **2** — Pelbioclastic limestone (grainstone) with pellets, frequent calpionellids and rare benthic fragments (crinoids, bivalves, ophiuroids); Sample CH54. **3** — *Tintinnopsella carpathica* and common crassicollarians in pelbiomicrosparite limestone; Sample CH56. **4** — *Crassicollaria intermedia* in pelbiosparitic limestone in which *Saccocoma* sp., and benthic fragments dominated over rare calpionellids and globochaetes; Sample CH58. **5** — Biomicrite limestone of *Calpionella*-globochaete microfacies with common calpionellids. Some of the crassicollarian loricas are thin and aberrant; Sample CH61. **6** — Pelbiomicrosparite limestone with common *Saccocoma* sp., fragments of foraminifers, bivalves, ostracods and also rare calpionellids, cysts, radiolarians and globochaetes; Sample CH33. Scale bars in all figures are 100 μm.

loricas are still present. Benthos is represented by crinoids, ophiuroids, echinoid spines, agglutinated foraminifers, *Textularia* sp., *Lenticulina* sp. and ostracods; there are also uncommon *Saccocoma* sp. (Fig. 7.3). Bioclasts coming from more shallow-water environments, such as *Crescentiella morronensis* (Crescenti) (Fig. 7.4), *Bacinella irregularis* Radoičić, ooids (Fig. 7.5), and fragments of bryozoans and algae, have also been identified.

The sequence studied is composed of Upper Tithonian-Lower Berriasian limestones (peloidal wackestone/packstone, graded bioclastic grainstones, wackestones/packstones with ramp-derived intraclasts and bioclasts, marly limestones with intraclasts and limestone pebbles), sedimented in an outer ramp environment periodically influenced by storms/ or small-scale sea-level fluctuations, reflected in inputs of coarser materials.

Comments on calpionellid stratigraphy

Three calpionellid zones have been recognized: the *Chitinoidella* Zone, *Crassicollaria* Zone and *Calpionella* Zone. The middle part of that interval contains Late Tithonian taxa: *Tintinnopsella remanei*, *Tintinnopsella carpathica*, *Crassicollaria intermedia*, *Crassicollaria massutiniana*, *Crassicollaria brevis*, *Crassicollaria parvula*, *Crassicollaria colomi*, *Calpionella alpina*, and *Calpionella grandalpina*. The pelbiomicrites and microbreccia layers recognized there are composed of abundant taxa typical of the Intermedia Subzone (*Crassicollaria* Zone). The lowermost intercalations, with abundant *Saccocoma* sp., show indications of storm sedimentation, during which there were sudden inputs of saccocomids — identifiable in the rock by their chaotic orientation and intimate mixing with peloids.

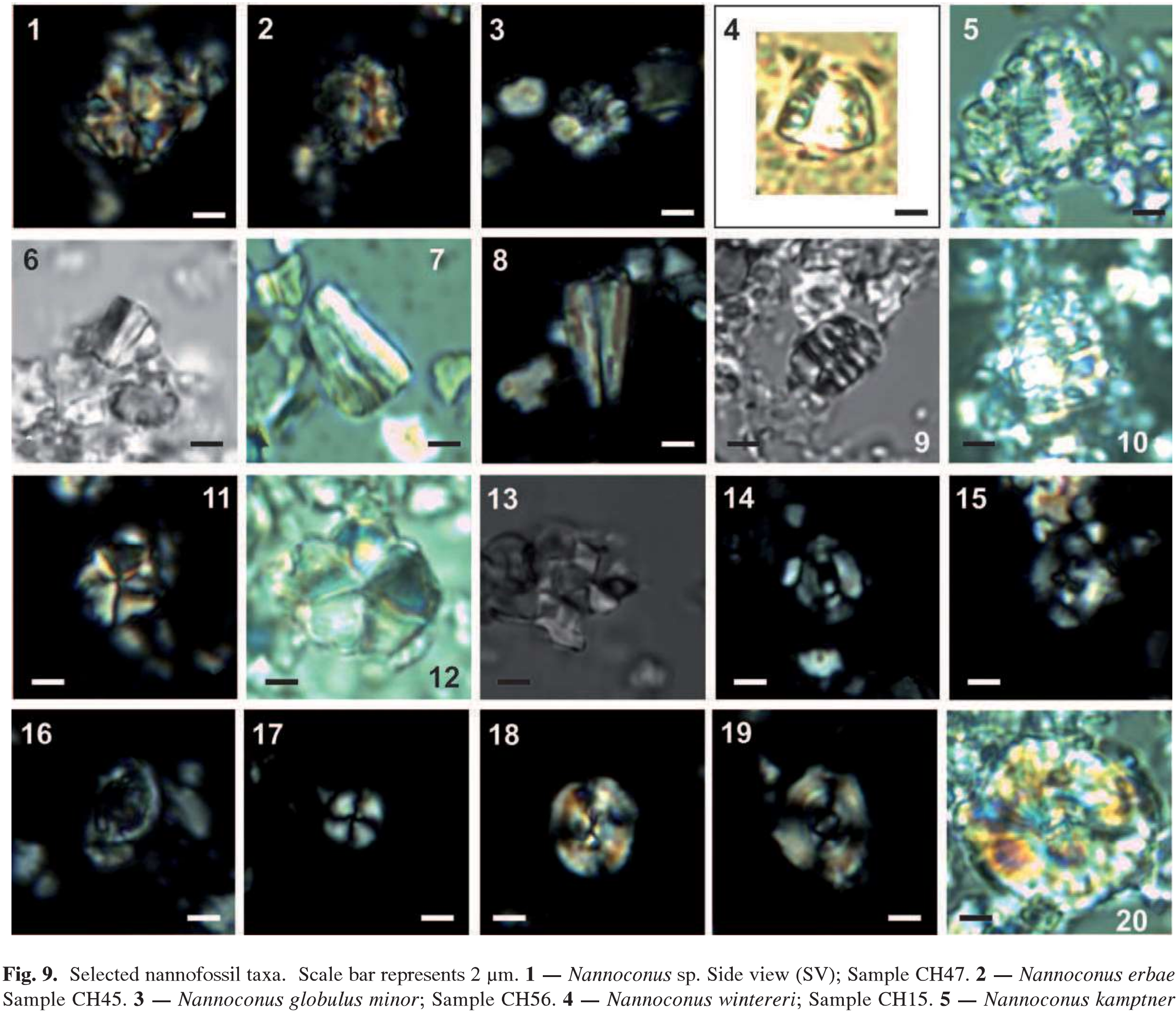


Fig. 9. Selected nannofossil taxa. Scale bar represents 2 μm. **1** — *Nannoconus* sp. Side view (SV); Sample CH47. **2** — *Nannoconus erbae*; Sample CH45. **3** — *Nannoconus globulus minor*; Sample CH56. **4** — *Nannoconus wintereri*; Sample CH15. **5** — *Nannoconus kamptneri minor*; Sample CH15. **6** — *Conusphaera mexicana minor*; Sample CH203. **7** — *Conusphaera mexicana mexicana*; Sample CH101. **8** — *Conusphaera mexicana mexicana*; Sample CH37. **9** — *Faviconus multicolumnatus*; Sample CH204. **10** — *Nannoconus steinmannii minor*; Sample CH15. **11** — Pentalith; Sample CH45. **12** — Pentalith; Sample CH47. **13** — *Hexalithus noeliae*; Sample CH17. **14** — *Microstaurus chiastius*; Sample CH37. **15** — *Cruciellipsis cuvillieri*; Sample CH45. **16** — *Rhagodiscus asper*; Sample CH25. **17** — *Cyclagelosphaera margerelii*; Sample CH37. **18** — *Watznaueria barnesiae*; Sample CH37. **19** — *Watznaueria britannica*; Sample CH56. **20** — *Watznaueria manivitiae*; Sample CH204.

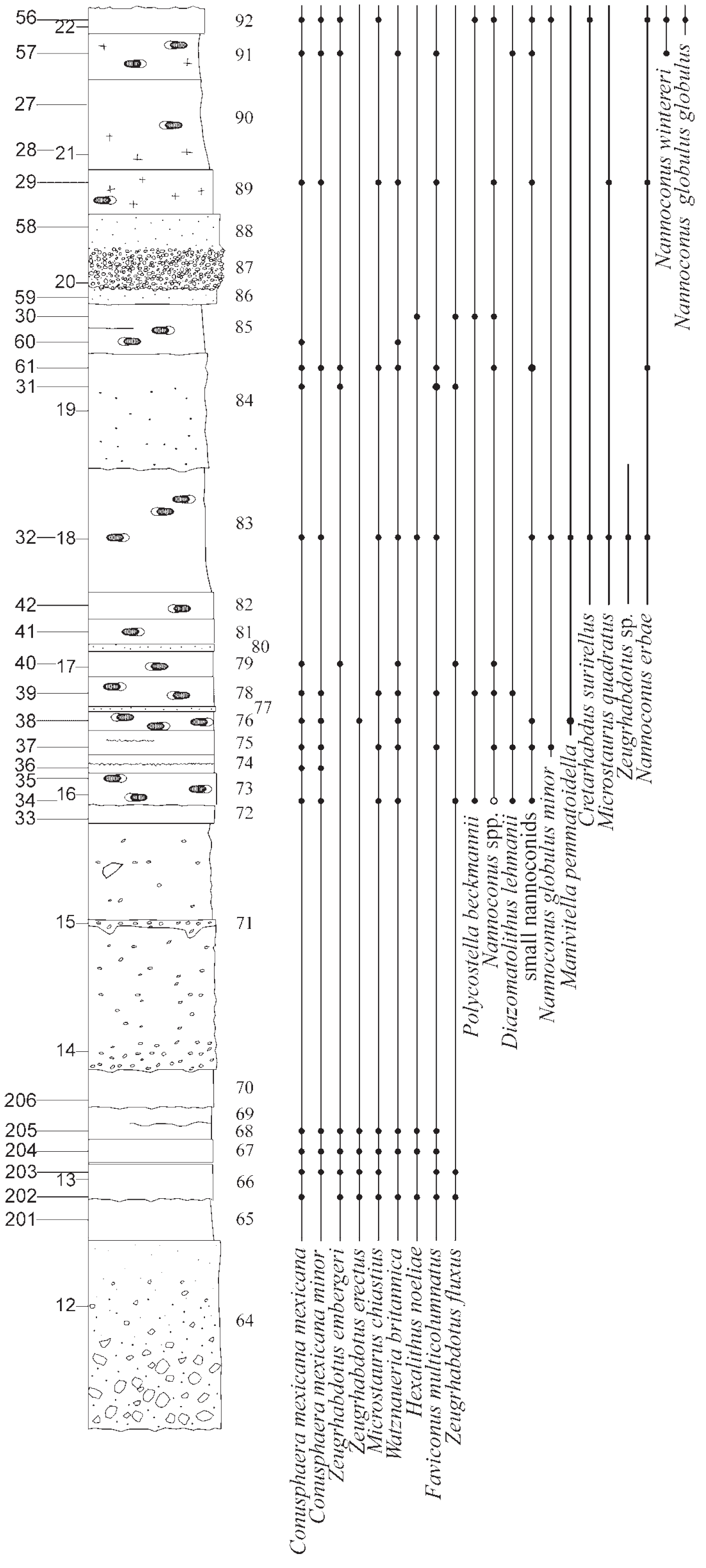


Fig. 10. Vertical ranges of selected calcareous nannofossils in beds 66–92. Open circles denote an uncertain specific identification.

The approximate Jurassic/Cretaceous boundary, the onset of the Alpina Subzone of the standard *Calpionella* Zone, is located in sample CH101 (bed 100). There, globochaetes and calcified radiolarians dominate over medium-sized spherical forms of *Calpionella alpina* (accompanied by infrequent *Crassicollaria parvula*) in biomicrites of the calpionellid-radiolaria-globochaete microfacies. Thus, the base of the Alpina Subzone corresponds to that described by Remane et al. (1986). Those authors noticed (but did not explain) the sudden rapid decrease in calpionellid abundance. A quantitative analysis of bio-elements shows that their decrease coincided with an increase of radiolarians. The upper part of the sequence, composed of wackestones, has yielded Early Berriasian taxa (*Calpionella alpina*, *Crassicollaria parvula* and *Tintinnopsella carpathica*). Pelbiomicrite/pelbiosparite and bioclastic intercalations show different spectra of redeposited bio-fragments. If compared with autochthonous deposits, their calpionellid associations (with double or triple abundances) are composed predominantly of spherical *Calpionella alpina*, with less frequent to common *Crassicollaria parvula*. Thus, the "acme" of calpionellids in this section represents a rather enriched taphocenosis, one linked with depositional dynamics resulting in the reworking and transport of sediments. This is also supported by the presence of ooids, agglutinated foraminifers, *Bacinella irregularis* Radoičić, *Crescentiella morronensis* (Crescenti) — elements typical of the shoals of inner ramp environments.

Microfacies, calpionellid associations and their distribution at the J/K boundary allow some comparisons between key sites. For instance, the interval at Le Chouet resembles those known from the Puerto Escaño section (Pruner et al. 2010) and the Caravaca, Rio Argos section (Michalík & Reháková 2011). The calpionellids of the Bosso Valley section (Houša et al. 2004) show similarities with those at Brodno (Houša et al. 1999; Michalík et al. 2009). On the other hand, microfacies as well as calpionellid distribution at Torre de'Busi (Casellato et al. 2008) are very similar to those known from the Nutzhof section (Lukeneder et al. 2010).

Calcareous nannofossils

A total of 64 samples for calcareous nannofossil biostratigraphic investigation have been examined. Biostratigraphic analyses were performed on simple smear slides, prepared as follows: a small amount of rock material was powdered adding a few drops of bi-distillated water; the obtained suspension was mounted onto a microscope slide, covered with a slide cover and fixed with Norland Optical Adhesive, without centrifuging, ultrasonic cleaning or settling of the sediment — in order to retain the original composition. The smear slides were then inspected using a light-polarizing microscope, at 1250× magnification. Calcareous nannofossils were documented using a MicroPublisher 5.0 RTV camera (Dept. Earth Sciences "A. Desio", Università degli Studi di Milano, Milan) and a LEICA DFC 290 HD camera (Dept. of Geology and Paleontology, Comenius University, Bratislava).

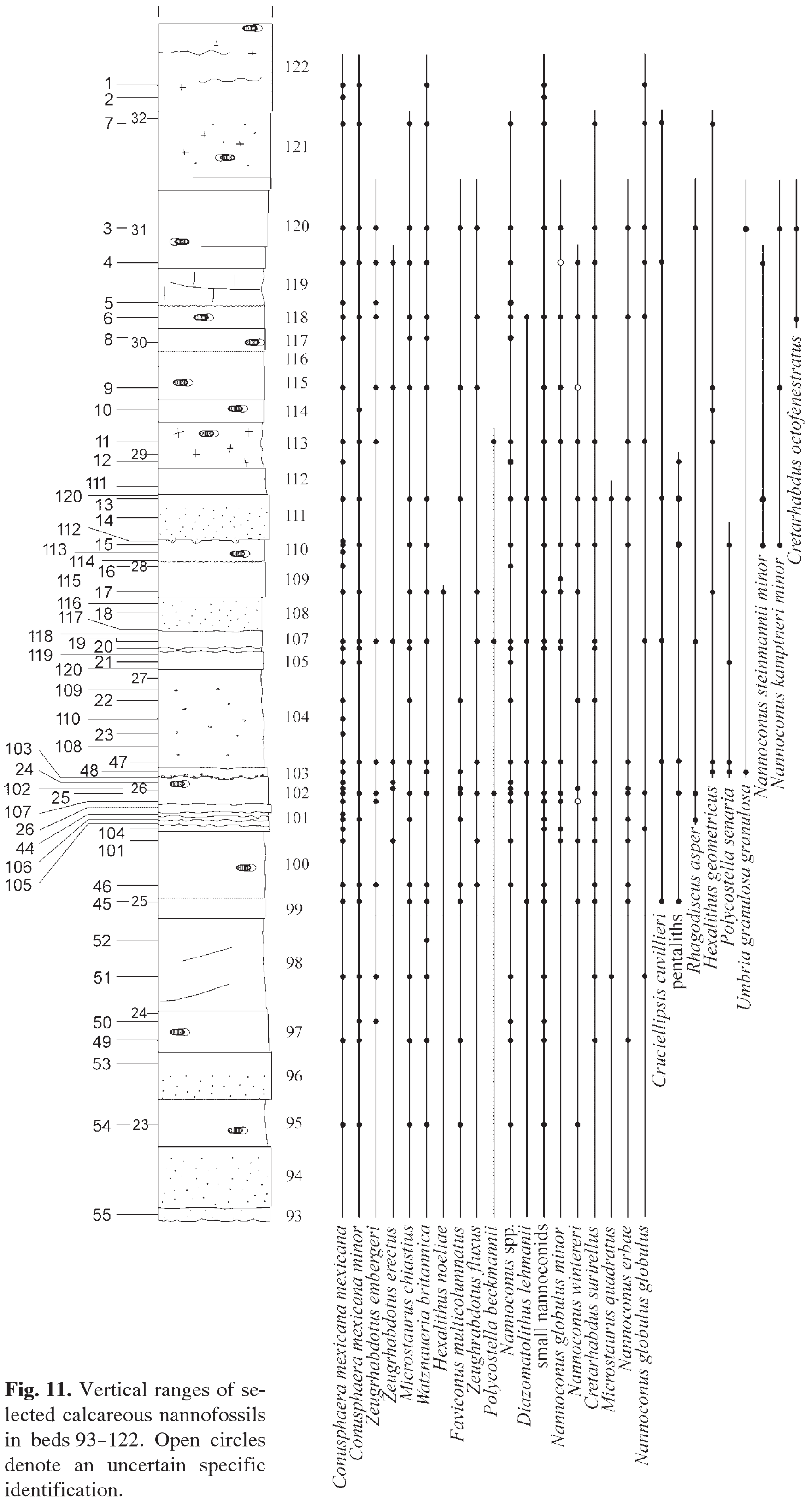


Fig. 11. Vertical ranges of selected calcareous nannofossils in beds 93–122. Open circles denote an uncertain specific identification.

In the samples studied, calcareous nannofossils are rare to common and very poorly to poorly preserved. They are affected by overgrowth and etching phenomena, and observed associations are often dominated by dissolution-resistant species (principally the genera *Watznaueria*, *Cyclagelosphaera* and *Conusphaera*) (Roth 1986). Nevertheless, the events suggested as useful in constraining the Jurassic/Cretaceous boundary (Wimbledon et al. 2011) have been detected, namely the first occurrences of: *N. wintereri* (in bed 91; Fig. 9.4), *C. cuvillieri* (bed 99; Fig. 9.15) and *N. steinmannii minor* along with *N. kamptneri minor* (bed 110; Fig. 9.10 and Fig. 9.5, respectively). A full list of the calcareous nannofossil taxa found in this study (genera, species and subspecies) is given below in an Appendix, in alphabetical order. The distribution of stratigraphically useful nannofossil taxa is shown in Figures 10 and 11.

Comments on calcareous nannofossil biostratigraphy

Calcareous nannofossil associations and their distribution in the J/K boundary interval at Le Chouet are consistent with calcareous nannofossil data reported from other key sites, such as Torre de'Busi, Brodno and Lokut. In particular, even though calcareous nannofossils are badly preserved, a few events present here have positions, relative to magnetozones and calpionellid zones, that are comparable to those at other localities. The first appearances of *N. wintereri* and *C. cuvilleri* are in the lower and lower-middle part of M19n, and the *Crassicollaria* Zone, respectively, as in the Torre de'Busi and Brodno sections. The first occurrences of *N. steinmannii minor* and *N. kamptneri minor* occur in the topmost part of the section, the uppermost part of M19n and *Calpionella* Zone, again consistent with data from Torre de'Busi and Lokut. Thus these events represent reliable data useful for long-range correlations, at least in low-latitude regions. The integrated results indicate that the first occurrences of *N. wintereri*, *C. cuvillieri*, *N. steinmannii minor* and *N. kamptneri minor* all occur in the *Berriasella jacobi* Subzone, a situation different to that previously reported by Bralower et al. (1989), who showed *N. wintereri* and *C. cuvillieri* as first appearing in the uppermost part of the *Durangites* Zone. The nannofossil zonation of Casellato (2010) is applied in Fig. 18.

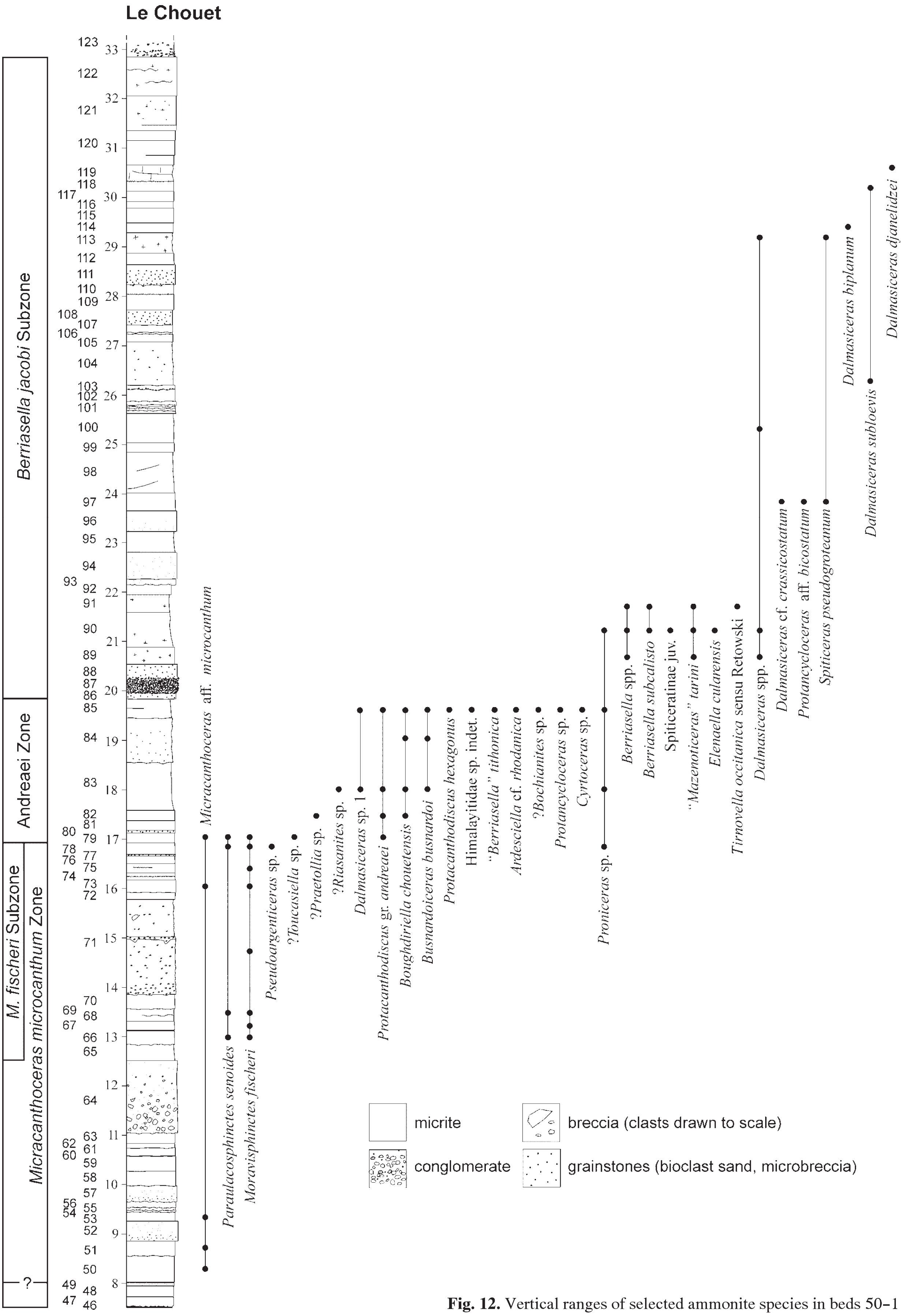


Fig. 12. Vertical ranges of selected ammonite species in beds 50–119.

Ammonites

The ammonite occurrences at Le Chouet are diverse. We have collected abundant material bed by bed, with 22 genera recognized, and our preliminary ammonite results provide a new biostratigraphical record for the Tithonian-Berriasian interval.

Figure 12 shows the vertical ranges of ammonite taxa, with the exception of common haploceratid, lytoceratid and phylloceratid species. A more detailed account of the ammonite fauna (with new taxa) will be published later, but as a synthesis of first results, the following may be related. In summary, four successive faunal assemblages can be recognized.

Micracanthoceras microcanthum Zone

At Le Chouet, the *Micracanthoceras microcanthum* Zone (Upper Tithonian) may be clearly recognized, though its base cannot be fixed precisely due to the lack of specimens below bed 50. Alongside the ammonite index, *M. microcanthum*, Phylloceratina and Lytoceratina predominate below, but just above a thick breccia (bed 64), the assemblage is composed essentially of *Paraulacosphinctes senoides* Tavera and *Moravisphinctes fischeri* Kilian, whereas *Micracanthoceras* becomes scarce.

Our first results thus suggest a partition of the *Microcanthum* Zone, with the establishment of a *Moravisphinctes fischeri* Subzone at the top, with its base at bed 66. This is used as a replacement for the Transitorius Zone, as already suggested (Cecca et al. 1989) in the type area for the Ardescian, and by authors in other Mediterranean marginal areas (Benzaggagh & Atrops 1997).

The last occurrence of the genus *Moravisphinctes* is located below the top of the *Crassicollaria intermedia* calpionellid Subzone. These results are in disagreement with findings from Morocco (Benzaggagh & Atrops 1997), where *Moravisphinctes* spp. last occurs in the Remanei Subzone.

Recognition of a fauna indicating the *Simplisphinctes* Subzone at the base of *M. microcanthum* Zone has not been possible and this requires further study. Thus, the current understanding of the *Microcanthum* Zone is an interval between the first occurrence of the index species (*sensu* Benzaggagh & Atrops 1997) and the first appearance of the genus *Protacanthodiscus* (in bed 79), which marks the next ammonite biostratigraphic unit, a zonal boundary, in calpionellid terms, still within the Intermedia Subzone.

Protacanthodiscus andreaei Zone

In its first appearances, specimens of *Protacanthodiscus* gr. *andreaei* (Kilian) are few in number, and its acme is seen in beds 83 to 85: a similar pattern of distribution to that which has been observed in Spain (Olóriz & Tavera 1989). The *Protacanthodiscus* gr. *andreaei* interval is a short one, whose top is affected by small-scale sedimentary reworking, though all within the lower part of the *C. colomi* Subzone.

The much-quoted "*Durangites* Zone" of the topmost Tithonian should be re-examined and perhaps abandoned because of the possibility that this genus may be endemic to the Mexican-Cuban region. Here we use a local index for the zone, *Protacanthodiscus andreaei.* The peak for *P. andreaei* coincides with the acme of *Busnardoiceras,* a common Lower Berriasian genus (first occurrence in bed 83), previously restricted by Le Hégarat to the *B. jacobi* and *P. grandis* Subzones. A new genus, *Bougdiriella* (type species *B. chouetensis* gen. and sp. nov., which we intend to describe separately) also appears in bed 82. This species has in the past usually been indentified as a Mediterranean "*Durangites*". We also intend to create a new genus, *Ardesciella*, for a group of Mediterranean species formerly assigned to *Corongoceras*, as suggested by Parent et al. (2011). The richness of the ammonite fauna of the Andreaei Zone at the genus level is a good faunal marker for this interval on all the margins of the Mediterranean Tethys.

?*Riasanites* sp. and ?*Praetollia* in the Andreaei Zone are reported for the first time in southern France. Both have traditionally been seen as typical boreal genera (Mitta 2007). The first, however, has been recorded in Tethyan Crimea (apparently in an equivalent of the *Berriasella picteti* Subzone: Kvantaliani & Lysenko 1979), in Yemen (*M. microcanthum* Zone: Howarth 1998) and in Argentina (Koeneni Zone: Zeiss & Leanza 2011) — thus, levels that stratigraphically bracket the Le Chouet occurrence. But the levels in Argentina, Yemen and at Le Chouet are all much older than the mid to Late Berriasian age of the type *Riasanites* zones in the Russian Platform embayment (?=*D. dalmasi* Subzone–*B. picteti* Subzone).

Berriasella jacobi Subzone

The first "Berriasian" ammonite assemblage appears here one third of the way up the *C. colomi* calpionellid Subzone. Though the index species has not been recognized yet, we maintain a *Berriasella jacobi* Subzone, for stability of stratigraphic nomenclature. The base of the *B. jacobi* Subzone at Le Chouet is marked by an increase in the numbers of morphospecies of *Dalmasiceras* (see Fig. 12), as observed by Le Hégarat (1971). This work provides the first recognition of the *Eleanella cularensis* horizon (Tavera et al. 1994) near the base of the *B. jacobi* Subzone. It is established that the base of the *B. jacobi* Subzone here does not correspond to the base of the calpionellid Alpina Subzone. In fact, none of the ammonite zonal boundaries correspond to any calpionellid boundaries. The grainstone–conglomerate–grainstone triplet that apparently coincides with the base of the Jacobi Subzone (Fig. 12) perhaps indicates some hiatus. However, the two massive breccias at lower levels, both with large angular clasts and irregular bases, may indicate more significant phases of erosion.

The boundary interval of the Tithonian–Berriasian generally shows clear losses at the family level, with the progressive decline of Himalayitidae in the highest Tithonian, replaced by berriasellids at the base of the Berriasian: what Wiedmann (1973) called the "the Tethysian boundary". As stated, this turnover is not synchronous with the *Crassicollaria/Calpionella* turnover used to define the base of the Alpina Subzone. The gap in phylogenetic knowledge and the conglomerate bed (bed 87) complicate a perception of the magnitude of the ammonite turnover at Le Chouet. It is worth noting that other fossil groups pass this level with no change: no taxon of calpionellid or calcareous nannofossil appears or disappears in beds 86–88.

Magnetostratigraphy

The section at Le Chouet complies with our aims in three fundamental criteria, it has: (a) essentially continuous sedimentation, uninterrupted by marked diastems, (b) rich fossil associations (calpionellids, ammonites) allowing its detailed biostratigraphic division, and (c) rocks with magnetic properties that are favourable for reliable determination of paleomagnetic polarity.

Paleomagnetic properties of pilot samples

Our study has thus far concentrated on the pilot investigation of a 30 m-thick portion of the section of the limestone strata near the J/K boundary (beds 1–121). The average sampling density for the whole section is about three samples per metre of true stratal thickness.

Paleomagnetic measurements were performed in the Paleomagnetic Laboratory of the Institute of Geology, Prague. Remanent magnetization (RM) of the rocks was measured using a Liquid helium-free Superconducting Rock Magnetometer, type 755 4K SRM, and the magnetic susceptibility of the samples was measured using a KLY-4 Kappabridge (Jelínek 1966, 1973). The samples were demagnetized by alternate field (AF) in an Automatic Sample Degaussing System 2G600, reaching 100 mT. Thermal demagnetization (TD)

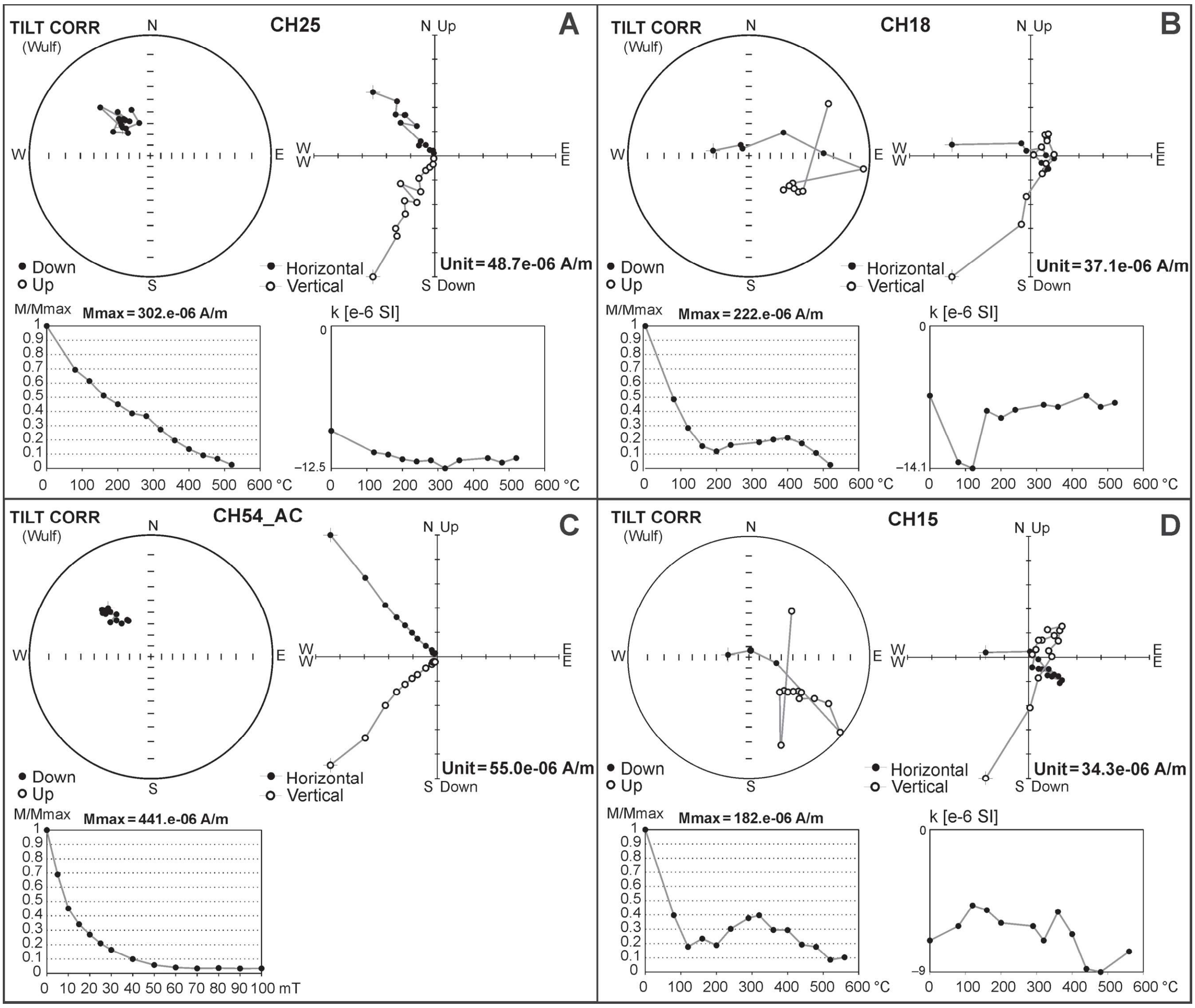


Fig. 13. Thermal (**A, B** and **D**) and AF demagnetization (**C**) of typical specimens. Top left diagrams: stereographic projection of demagnetization paths; full (open) symbols — lower (upper) hemisphere projection; top right diagrams: orthogonal projections of demagnetization paths (Zijderveld diagrams) on horizontal and vertical planes; bottom left diagrams: NRM intensity decay during demagnetization (M/Mmax); bottom right diagrams: susceptibility (k) changes during thermal treatment (A, B and D). Stereographic and orthogonal projections after tilt correction.

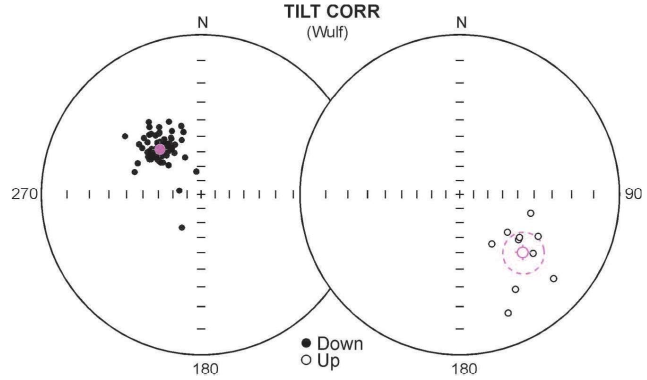


Fig. 14. Stereographic projection of the component C (after tectonic correction). **Left** — normal polarity directions, **right** — reversed polarity directions.

was performed in a non-magnetic oven placed in a Magnetic Vacuum System (MAVACS). The ambient magnetic field in the cooling chamber of the MAVACS demagnetizer did not exceed 1 nT, owing to a built-in rotating-coil magnetometer controlling the currents in its Helmholtz coil system (Příhoda et al. 1989). Processing of the output data, including, for instance, multicomponent analysis of the demagnetization path, was carried out using Remasoft 3.0 software (Chadima & Hrouda 2006).

Each of the 91 samples studied was subjected to TD or AF demagnetization in 12–13 temperatures or fields. Of the 91 samples, 83 yielded reliable paleomagnetic directions. As a result, the individual components could be precisely established in the majority of samples using a multicomponent analysis of remanence (Kirschvink 1980). Zijderveld diagrams and diagrams of normalized remanent values vs. labo-

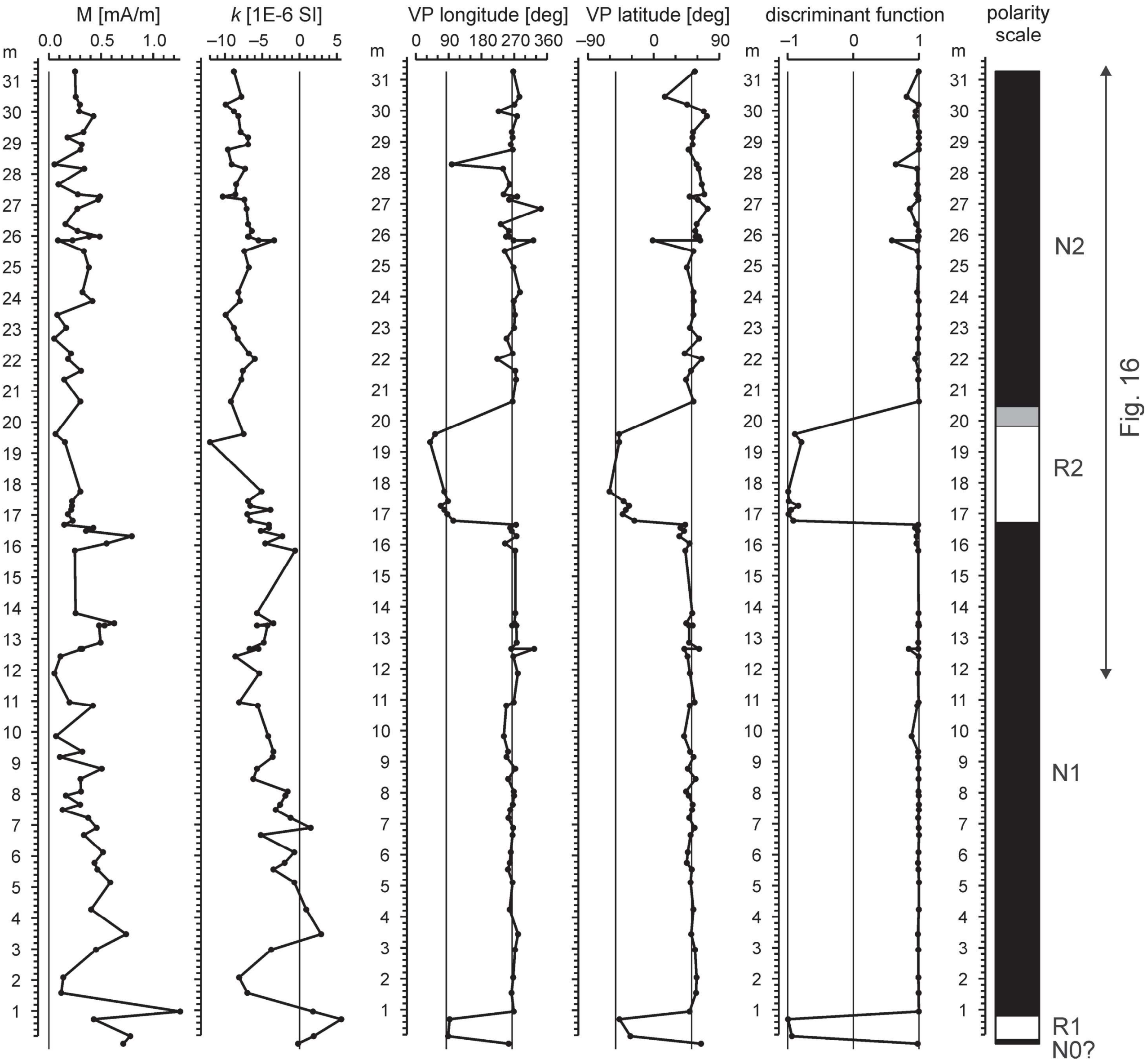


Fig. 15. Magnetostratigraphic profile through the Le Chouet section. **M** — remanent magnetization in natural state, **k** — volume magnetic susceptibility in natural state, **VP** — virtual pole. Magnetic polarity: **black** — normal, **white** — reversed. Grey indicates uncertain or mixed polarity.

ratory thermal demagnetizing field t (°C) were constructed for all samples.

The results of thermal (TD) and alternating field (AF) demagnetization procedures are displayed in Figure 13. They refer to two limestone samples with normal paleomagnetic directions (samples CH25 and CH54, from level 20.71 m in bed 89, and 31.18 m in bed 120, respectively) and two limestone samples with reverse paleomagnetic directions (samples CH15 and CH18, 17.07 m (bed 79) and 17.49 m (bed 82)). Analogous results were obtained for most samples through the Le Chouet section. The RM directions shown in the projections are corrected for the dip of the strata. The results of the multi-component analysis of remanence show that the rock samples display a two or three-component remanent magnetization. The A-component is undoubtedly of viscous origin and is demagnetizable in the temperature range of 20–120 °C (or AF 0–10 mT); the B-component is also of secondary origin, but shows 'harder' magnetic properties, being demagnetizable in a temperature range of 120–240 °C (or AF 10–15 mT); the C-component is the most stable, being demagnetizable in an unblocking temperature-range of ca. 400–520 °C (or AF unblocking fields 20–60 mT).

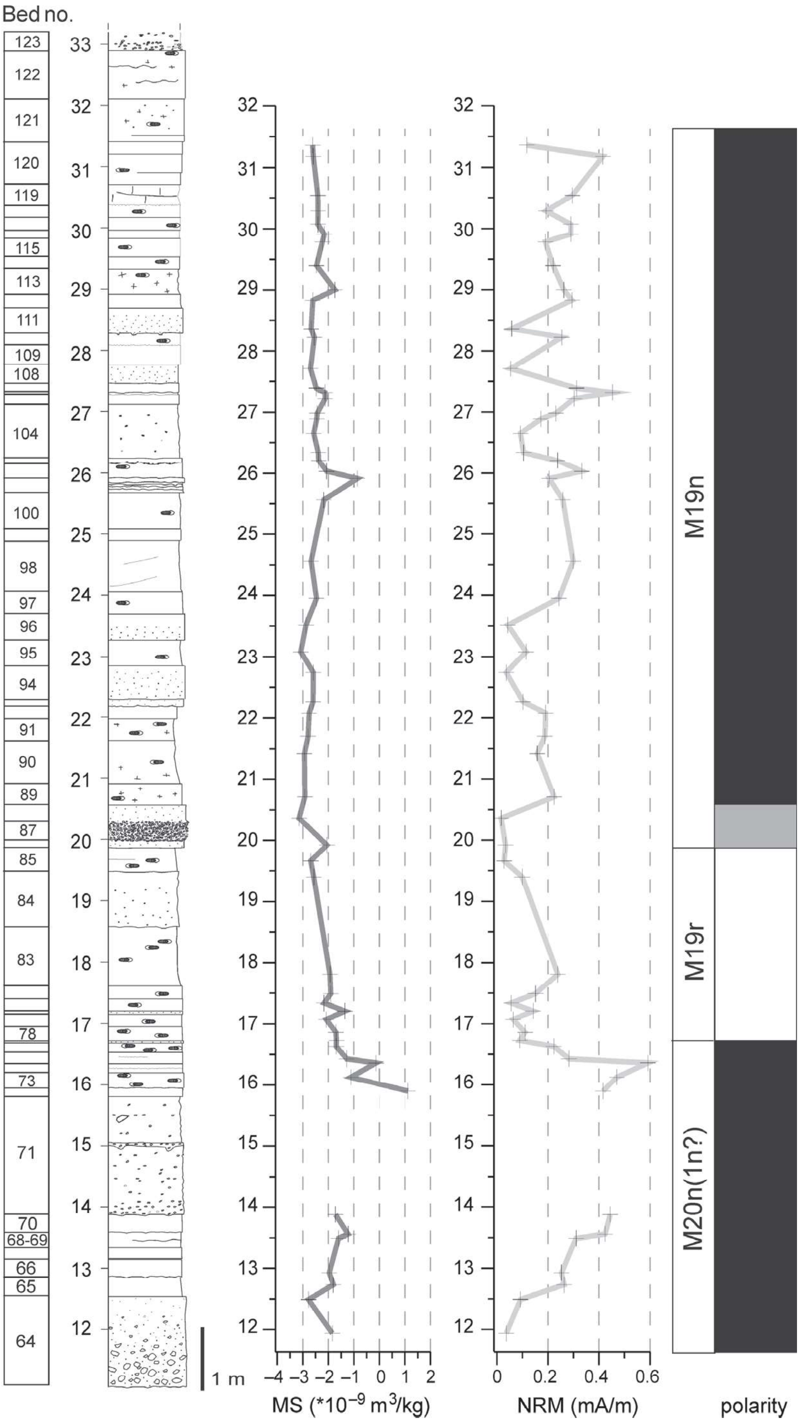


Fig. 16. Magnetostratigraphy and rock magnetic parameters: mass normalized magnetic susceptibility (MS) and natural remanent magnetization (NRM) intensity, from bed 64 upwards.

The mean directions and dispersions of components were calculated using Fisher's statistics (Fisher 1953) and were displayed on a Wulf stereographic projection. They are marked either by infilled or empty crossed circles, with a confidence circle circumscribed around the mean direction at the 95% probability level. Both magnetic polarities are present in the C-component directions. Consequently, after tectonic correction, the mean direction for samples with 'normal' polarity is D = 317.7°, I = 48.1°, α_{95} = 2.5°, and for those with reverse polarity it is D = 132.6°, I = –33.7°, α_{95} = 10.2° (Fig. 14). The paleolatitude (ca. 27°N) is in agreement with that obtained from the Berriasian type section (Galbrun 1985). Paleodeclination at Le Chouet implies a counterclockwise rotation of ca. 20–30°, which must be attributed to a local tectonic effect. The resulting magnetostratigraphic profile is shown in Fig. 15, displaying the following quantities: the modulus of natural remanent magnetization (*M*), volume magnetic susceptibility of samples in natural state (*k*), co-ordinates of the virtual pole position (VP longitude and VP latitude), and a discriminant function defining the polarity. Both the virtual pole position and the discriminant function are functions of the direction of the remanence C-component, and have been inferred by means of a multi-component analysis. As indicated in Fig. 15, normal (N) and reverse (R) polarity intervals, magnetozones and submagnetozones, are clearly manifested in the interpreted values of VP longitude and VP latitude and a discriminant function defining the polarity (Man 2008).

Low-field magnetic susceptibility (k) ranges from –12.0 to 5.6 × 10^{-6} SI and the intensity of the natural remanent magnetization (NRM) varies between 0.018 and 1.145 × 10^{-3} A/m.

These data given in the magnetostratigraphic profile indicate a gradual decrease in magnetization, from the older to the younger rocks (Fig. 15). An obvious decrease in these values up sequence in the vicinity of the J/K boundary has also been observed at Brodno, in the Bosso Valley and at Puerto Escaño (Houša et al. 1999, 2004; Pruner et al. 2010) as well as in sections from the Tatra (Central Carpathians — Grabowski & Pszczółkowski 2006) and the Transdanubian mountains (Lókút section — Grabowski et al. 2010b).

Discussion of the main magnetostratigraphic results

The preliminary magnetostratigraphic investigation of the basal 30 m of the profile, the measurement of basic magnetic properties and the results of multi-component analysis of remanence of the J/K boundary limestones have yielded new information on the correlation of paleomagnetic events with biozones, and with events elsewhere in Tethys. Magnetozones N0–N2 and R1–R2 (Fig. 15) might be roughly correlated to the Global Polarity Time Scale (GPTS). The correlation between magnetostratigraphy and calpionellid zonation in the J/K boundary interval is reliably tested in more than 20 land sections (see Ogg & Lowrie 1986; Channell et al. 1987; Ogg et al. 1991; Houša et al. 1999; Pruner et al. 2010; Grabowski 2011). Magnetozone N2, where the *Crassicollaria*/*Calpionella* zonal boundary is situated (see Fig. 16), must be correlated with magnetozone M19n (magnetosubzone M19n.2n). Reversed magnetozone R2 falls within the *Crassicollaria* Zone and should be interpreted as M19r. The sedimentation rate amounted to 10–15 m/Myr in the M19n–M19r interval. Magnetostratigraphic interpretation of the lower part of the section poses some problems. Bed 33 and approximately bed 60 belong to the *Chitinoidella* Zone. Magnetozone N1 might correspond to M20.1n, while N0 might be taken to be the topmost part of M20n.2n. However, interpretation of R1 as magnetosubzone M20n.1r is not straightforward. Its biostratigraphic position below the documented *Chitinoidella* Zone would deviate substantially from that in the Brodno and Puerto Escaño sections (there in the lowermost part of the *Crassicollaria* Zone — see Houša et al. 1999; Pruner et al. 2010). It might be compared with the Bosso valley section, where M20n.1r does occur in the middle part of the *Chitinoidella* Zone (Houša et al. 2004). However, interpretation of the R1 polarity interval as M20n.1r would imply a very high sedimentation rate in the *Chitinoidella* Zone and lower *Crassicollaria* Zone, at almost 50 m/Myr: a great contrast with sedimentation rates calculated for the upper *Crassicollaria* and Alpina Zones. Alternatively, the interval N1 might be interpreted as the whole of magnetozone M20n, and R1 as M20r. However, R1 is apparently too thin to be M20r (ca. 1 m) and this would imply a dramatic decrease in the sedimentation rate — no more than 1.5 m/Myr.

The next step in the paleomagnetic investigation will be a more refined determination of the magnetostratigraphic boundaries, with special emphasis on documentation of the short reversed magnetosubzones M20n.1r and M19n.1r. The average sampling density for the whole section should be

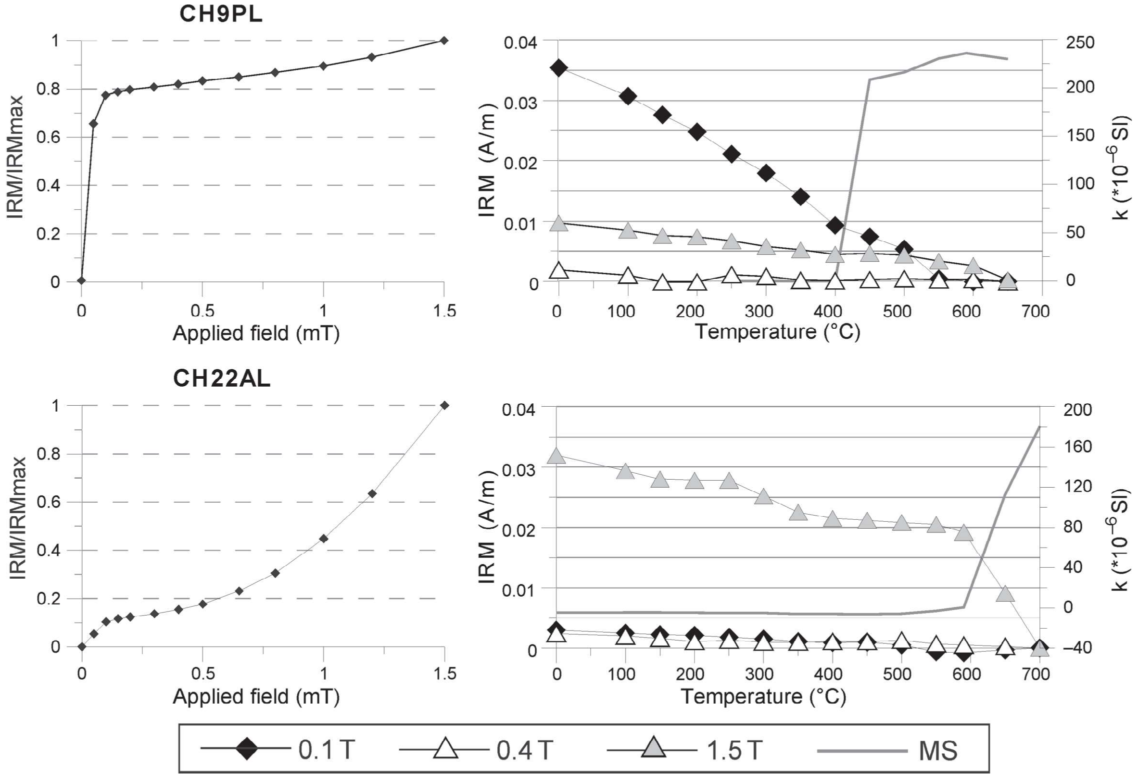


Fig. 17. Isothermal remanent magnetization (IRM) acquisition curves, thermal demagnetization of the 3 axes IRM acquired in the fields of 0.1 T, 0.4 T and 1.5 T and volume magnetic susceptibility (k) changes during thermal treatment for selected samples. Upper row: sample CH9PL (bed 73, 16.13 m). Lower row: sample CH22AL (bed 86, 19.92 m).

about 5–8 per metre, with 20 or more samples per metre at critical levels such as zonal boundaries.

Rock magnetism

Basic rock magnetic investigations were performed for all the horizons sampled for magnetostratigraphy. They were carried out in the Paleomagnetic Laboratory of the Polish Geological Institute–National Research Institute and included measurements of mass normalized magnetic susceptibility (MS) and isothermal remanent magnetization (IRM) acquired in the field of 1 T along the Z-axis of the cylindrical specimen and then anti-parallel in the field of 100 mT. The S-ratio calculated as a ratio of IRM intensities acquired in both fields was an indicator of proportions of low and high coercivity minerals. Selected samples with contrasting S-ratios were subjected to stepwise IRM acquisition and thermal demagnetization of 3 axes IRM (acquired in the fields of 0.1 T, 0.4 T and 1.5 T in three perpendicular directions) in order to identify magnetic minerals by recognition of their unblocking temperature spectra (Lowrie 1990). The detailed results of a rock magnetic study will be presented in a future paper, thus they are summarized here only briefly.

Both low- and high-coercivity minerals are present throughout the section (Fig. 17). The low-coercivity mineral is interpreted as magnetite, as its maximum unblocking temperature is between 550° and 600 °C. A high-coercivity mineral with maximum unblocking temperatures between 600° and 700 °C (hematite) is also present. Magnetite-dominated samples (like CH9PL in Fig. 17) contain the primary component C. Hematite-dominated samples (like CH22AL in Fig. 17) typically occur in brecciated and detrital horizons. Hematite does not carry any natural remanence, therefore it is most probably a product of secondary (diagenetic) oxidation.

Conclusion

We here calibrate calpionellid, nannofossil, ammonite and magnetostratigraphic data in this interval (Fig. 18).

The base of the *Calpionella* Zone (Alpina Subzone) is located within M19n.2n, which is consistent with its position relative to magnetostratigraphy at, for instance, Puerto Escaño and Lókút, though not at Brodno (*sensu* Michalík et al. 2009). At Le Chouet, the base and top of the Andreaei Zone are within M19r, whereas at Puerto Escaño the "*Durangites* Zone" is reported as straddling M20n, M19r and the lowest part of M19n.2n.

A series of nannofossil first-appearance datums has been recognized (Fig. 18), as follows: *Nannoconus globulus minor* (16.38 m), *Cretarhabdus surirellus* and *Nannoconus erbae* (18.00 m), *N. wintereri* (21.80 m), *N. globulus globulus* (22.05 m), *Cruciellipsis cuvillieri* (25.00 m), *N. steinmanni minor* and *N. kamptneri minor* (28.15 m). The base of the *Calpionella alpina* Zone, with its predominance of small globular *C. alpina*, is bracketed between the FADs of *Nannoconus wintereri* and *N. globulus globulus* and that of *N. steinmanni minor* and *N. kamptneri minor*, and the FAD of *Cruciellipsis cuvillieri* lies about half a metre below the zonal boundary. The Upper Jurassic to Lower Cretaceous sequence at Le Chouet may be compared to other well-documented sites with intervals that cross the J/K boundary (Fig. 19).

Acknowledgments: Many colleagues helped us in this work, with both moral and practical support. We thank three reviewers for their stimulating suggestions. Thanks are due to Mgr Stanislav Šlechta and Ing. Tadeusz Sztyrak for field

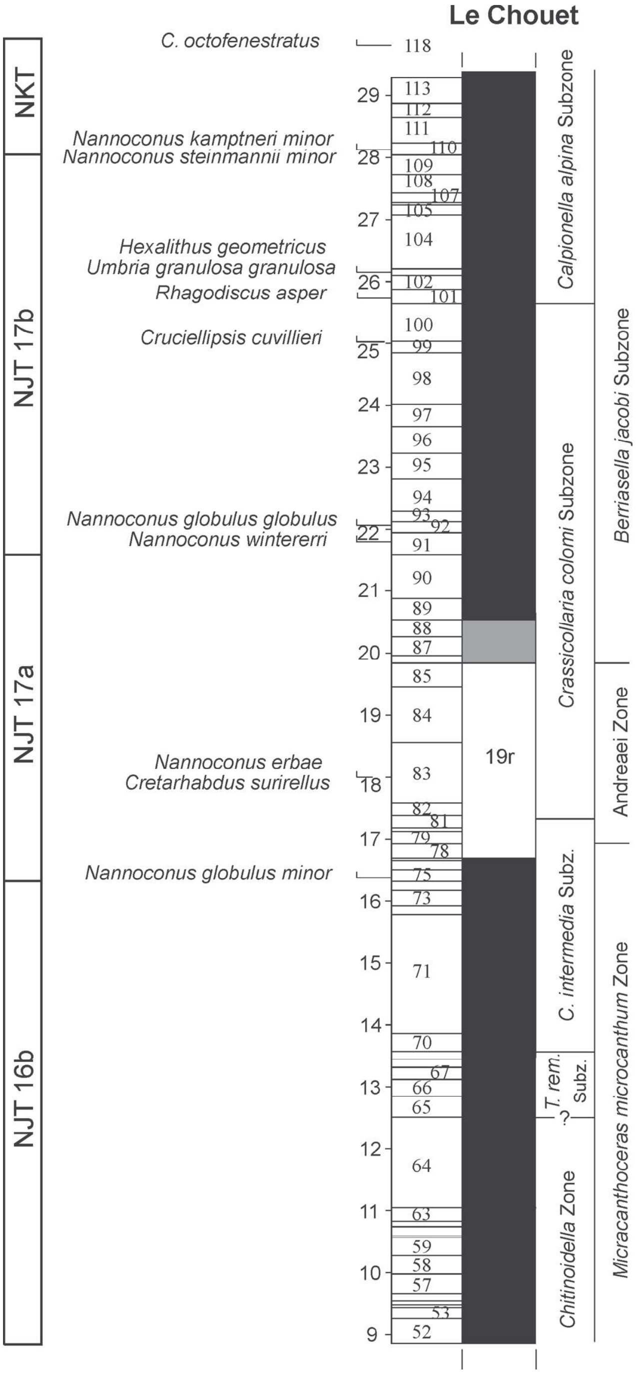


Fig. 18. Calibration of magnetozonal and biozonal (ammonite, calpionellid) boundaries and selected FADS for calcareous nannofossils at Le Chouet. Nannofossil zones follow Casellato (2010). Grey in the magnetozone column indicates uncertain or mixed polarity.

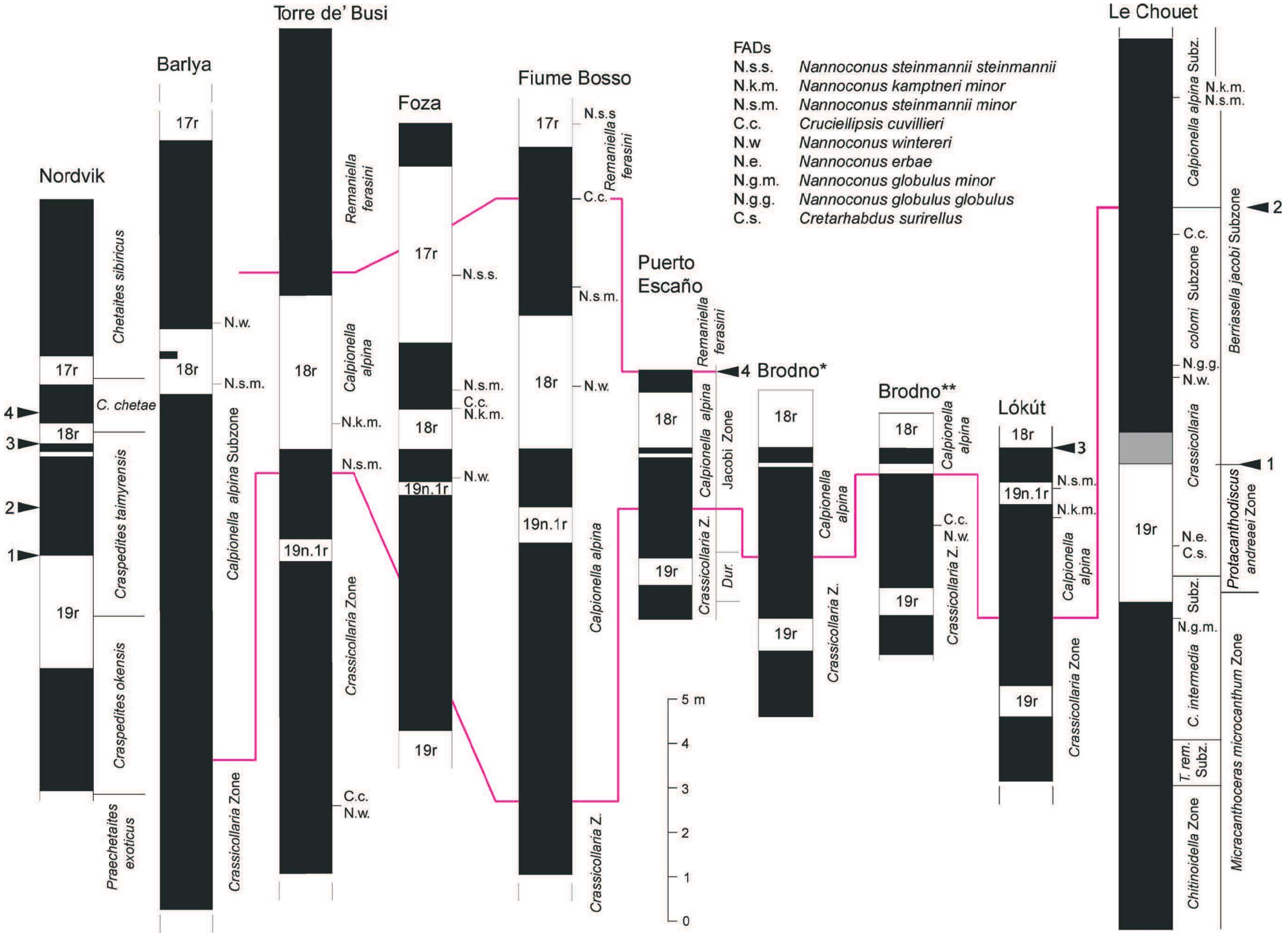


Fig. 19. Correlation of selected sequences showing the M20–M17 interval. Revised from Wimbledon et al. (2011). Brodno columns based on data in ** Michalík et al. (2009) and *Houša et al. (2009). Data 1–4 in Tethys (base of *B. jacobi* Subzone, base of Alpina Subzone, top of M19n.2n, and base of Ferasini Subzone) and their approximate positions at Nordvik (column after Houša et al. 2007). The Barlya column is based on data provided by Platon Tchoumatchenco (unpublished magnetozones by B. Galbrun). Lókút after Grabowski et al. (2010b).

assistance. Paleomagnetic analyses were performed by Dr Daniela Venhodová, Mrs Jana Drahotová and Mr Jiří Petráček. Software for evaluation of paleomagnetic measurements was prepared by Dr Ota Man. We thank Dr Platon Tchoumatchenco, Institute of Geology BAS, Sofia, for his contribution of unpublished data on Barlya. PP and PS gratefully acknowledge the Research Plan of the IG AS CR No. CEZ AV0Z30130516 for financial support. They also acknowledge support from the Institute of Geology ASCR, v.v.i. through its internal Project 9342 "Magnetostratigraphy and magnetomineralogy of the J/K boundary interval on the Le Chouet, St. Bernard's Spring and Barlya sites". JG and KS were financially supported by the Polish-French bilateral cooperation Project No. 683/N-POLONIUM/2010/0. This is also a contribution to projects of the Slovak Grant Agency: APVV-0280-07, APVV-0644-10, LPP 0120-09 and VEGA grant 2/0042/12 and VEGA 2/0068/11. We thank Gloria Andreini and colleagues in the University of Perugia for their essential help processing calpionellid samples from the lower part of the section. CEC warmly thanks the Micropaleontology Research Group, Università degli Studi di Milano, and specifically Prof. E. Erba, for continuous support.

References

Andreini G., Caracuel J.E. & Parisi G. 2007: Calpionellid biostratigraphy of the Upper Tithonian–Upper Valanginian interval in Western Sicily (Italy). *Swiss J. Geosci.* 100, 179–198.

Bacelle L. & Bosellini A. 1965: Diagrammi per la stima visiva della composizione perventualle nelle rocce sedimentarie. *Ann. Univ. Ferrara, N.S., Sez. IX., Sci. Geol. Paleont.* 1, 59–62.

Benzaggagh M. & Atrops F. 1997: Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). *Newslett. Stratigr.* 35, 127–163.

Borza K. 1984: The upper Jurassic–Lower Cretaceous parabiostratigraphic scale on the basis of Tintinninae, Cadosinidae, Stomiosphaeridae, Calcisphaerulidae and other microfossils from the West Carpathians. *Geol. Zborn. Geol. Carpath.* 35, 539–550.

Boughdiri M. 1994: Les genres d'ammonites *Durangites* et *Protacanthodiscus* (Tithonien superieur) dans la Tethys occidentale (SE Espagne, SE France, Algerie et Tunisie). *Stratigraphie, Paleontologie, Biogeographie, These, Univ. Claude-Bernard-Lyon I*, 351–94.

Boughdiri M., Sallouhi H., Maâlaoui K., Soussi M. & Cordey F. 2006: Calpionellid zonation of the Jurassic-Cretaceous transition in north Atlasic Tunisia. Updated Upper Jurassic stratigraphy of the "Tunisian Trough" and regional correlations. *Compt. Rendus Geosci.* 338, 1250–1259.

Bown P.R. & Cooper M.K.E. 1998: Jurassic. In: Bown P.R. (Ed.): Calcareous nannofossil biostratigraphy. *Kluwer Academic Publishers*, Cambridge, 34–85.

Bralower T.J., Monechi S. & Thierstein H.R. 1989: Calcareous nannofossils Zonation of the Jurassic-Cretaceous Boundary interval and correlations with the Geomagnetic Polarity Timescale. *Mar. Micropal.* 14, 153–235.

Casellato C.E. 2010: Calcareous nannofossil biostratigraphy of Upper Callovian-Lower Berriasian successions from Southern Alps, North Italy. *Riv. Ital. Paleont. Stratigr.*116, 357–404.

Casellato C.E., Andreini G., Erba E. & Parisi G. 2008: Calcareous Nannofossil and Calpionellid calcification events across the Tithonian-Berriasian time interval and low latitudes paleoceanographic implications. Proceedings of 12th INA, Lyon, France, 7–11 September 2008. *J. Nannoplankton Res., Spec. Publ.*, 33–33.

Cecca F., Enay R. & Le Hégarat G. 1989: L'Ardescien (Tithonique supérieur) de la région stratotypique: série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. *Doc. Lab. Géol. Lyon* 107, 1–115.

Chadima M. & Hrouda F. 2006: Remasoft 3.0 — A user-friendly palaeomagnetic data browser and analyzer. *Travaux Géophysiques* XXXVIII, 20–21.

Channell J.E.T., Casellato C.E., Muttoni G. & Erba E. 2010: Magnetostratigraphy, nannofossil stratigraphy and apparent polar wander for Adria-Africa in the Jurassic-Cretaceous boundary interval. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 293, 51–75.

Détraz H. & Mojon P.O. 1989: Evolution paléogeographique de la marge jurassiene de la Tethys du Tithonique-Portlandien au Valanginien: correlations biostratigraphique et sequentielle des facies marins a continentaux. *Eclogae Geol. Helv.* 82, 37–112.

Enay R., Boughdiri M. & Le Hégarat G. 1998: *Durangites, Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien superieur — Berriasian dans la Tethys mediterreenne (SE France, Espagne, Algerie et Tunisie). *C.R. Acad. Sci. Paris* 327, 425–430.

Fisher R. 1953: Dispersion on a sphere. *Proc. Roy. Soc.* A 217, 295–305.

Galbrun B. 1985: Magnetostratigraphy of the Berriasian stratotype section (Berrias, France). *Earth Planet. Sci. Lett.* 74, 130–136.

Grabowski J. 2011: Magnetostratigraphy of the Jurassic/Cretaceous boundary interval in the Western Tethys and its correlations with other regions: a review. *Volumina Jurassica* 9, 105–128

Grabowski J. & Pszczółkowski A. 2006: Magneto- and biostratigraphy of the Tithonian-Berriasian pelagic sediments in the Tatra Mountains (central Western Carpathians, Poland): sedimentary and rock magnetic changes at the Jurassic/Cretaceous boundary. *Cretaceous Research* 27, 398–417.

Grabowski J., Michalík J., Pszczółkowski A. & Lintnerová O. 2010a: Magneto- and isotope stratigraphy around the Jurassic/Cretaceous boundary in the Vysoká Unit (Malé Karpaty Mts, Slovakia): correlations and tectonic implications. *Geol. Carpathica* 61, 309–326.

Grabowski J., Haas J., Márton E. & Pszczółkowski A. 2010b: Magneto- and biostratigraphy of the Jurassic/Cretaceous boundary in the Lókút section (Transdanubian Range, Hungary). *Stud. Geophys. Geodet.* 54, 1–26.

Grandesso P. 1977: Gli strati a Precalpionellidi del Titoniano e I loro raporti conil Rosso Ammonitico Veneto. *Mem. Sci. Geol.* 32, 1–15.

Houša V., Krs M., Krsová M., Man O., Pruner P. & Venhodová D. 1999: High-resolution magnetostratigraphy and micropaleontology across the J/K boundary strata at Brodno near Žilina, western Slovakia: summary results. *Cretaceous Research* 20, 699–717.

Houša V., Krs M., Man O., Pruner P.,Venhodová D., Cecca F., Nard G. & Piscitello M. 2004: Combined magnetostratigraphic, paleomagnetic and calpionellid investigations across Jurassic/Cretaceous boundary strata in the Bosso Valley, Umbria, central Italy. *Cretaceous Research* 25, 771–785.

Houša V., Pruner P., Zakharov V.A., Košťák M., Chadima M., Rogov M.A., Slechta S. & Mazuch M. 2007: Boreal-Tethyan Correlation of the Jurassic-Cretaceous boundary interval by magneto- and biostratigraphy. *Stratigr. Geol. Correlation* 15, 297–309.

Howarth M.K. 1998: Tithonian and Berriasian ammonites from the Chia Gara Formation of northern Iraq. *Palaeontology* 35, 597–655.

Jan du Chęne R. , Busnardo R., Charollais J., Clavel B., Deconinck J.-F., Emmanuel L., Gardin S., Gorin G., Manivit H., Monteil E., Raynaud J.-F., Renard M., Steffen D., Steinhauser N., Strasser A., Strohmenger C. & Vail P.R. 1993: Sequence-stratigraphic interpretation of Upper Tithonian-Berriasian reference sections in South-East France: a multidisciplinary approach. *Bull. Cent. Rech. Expl.-Prod. Elf Aquitain* 17, 1, 151–181.

Jelínek V. 1966: A high-sensitivity spinner magnetometer. *Stud. Geophys. Geodaet.* 10, 58–78.

Jelínek V. 1973: Precision A.C. bridge set for measuring magnetic susceptibility and its anisotropy. *Stud. Geophys. Geodaet.* 17, 36–48.

Joseph P., Beaudoin B., Sempéré T. & Maillart J. 1988: Vallées sous-marines et systemes d'épandage carbonatés du Berraisien vocontien (Alpes méridionales francaises). *Bull. Soc. Géol. France* 4, 363–374.

Joseph P., Beaudoin B., Fries G. & Parize O. 1989: Les vallées sous-marines enregistrent au Crétacé inférieur le fonctionnement en blocs basculés du domain vocontien. *C.R. Acad. Sci. Paris* 309, 1031–1038.

Kirschvink J.L. 1980: The least-squares line and plane and the analysis of palaeomagnetic data. *Geophys. J. Roy. Astron. Soc.* 62, 699–718.

Kvantaliani I.V. & Lysenko N.I. 1979: On the problem of a Berriasian zonation in Crimea. *Soobsch. Akad. Nauk. Gruz. SSR* 94, 629–632.

Lakova I., Stoykova K. & Ivanova D. 1999: Calpionellid, nannofossils and calcareous dinocyst bioevents and integrated biochronology of the Tithonian to Valanginian in the West Balkan Mountains, Bulgaria. *Geol. Carpathica* 50, 151–168.

Le Hégarat G. 1971: Le Berriasian du sud-est de France. *Doc. Lab. Geol. Fac. Sci. Lyon* 43, 1, 1–308.

Lowrie W. 1990: Identification of ferromagnetic minerals in a rock by coercivity and unblocking temperature properties. *Geophys. Res. Lett.* 17, 159–162.

Lukeneder A., Halásová E., Kroh A., Mayrhofer S., Pruner P., Reháková D., Schnabl P., Sprovieri M. & Wagreich M. 2010: Multistratigraphic investigations of the Jurassic-Cretaceous boundary interval in the Gresten Klippenbelt (Austria) — evidence for depositional and evolutionary events. *Geol. Carpathica* 61, 365–381.

Maillard G. 1884: Invertébrés du Purbeckien du Jura. *Mém. Soc. Paléont. Suisse* 11, 1–156.

Man O. 2008: On the identification of magnetistratigraphic polarity zones. *Stud. Geophys. Geodaet.* 52, 173–186.

Mazenot G. 1939: Le Paléohoplitidae tithoniques et Berriasiens du Sud-est de la France. *Mém. Soc. Géol. France* 41, 1–303.

Michalík J. & Reháková D. 2011: Possible markers of the Jurassic/Cretaceous boundary in the Mediterranean Tethys — A review and state of art. *Geosci. Frontiers* 2, 475–490.

Michalík J., Reháková D., Halásová E. & Lintnerová O. 2009: The Brodno section — potential regional stratotype of the Jurassic/Cretaceous boundary (Western Carpathians). *Geol. Carpathica* 60, 213–232.

Mitta V.V. 2007: Ammonite assemblages from basal layers of the Ryazanian Stage (Lower Cretaceous) of Central Russia. *Stratigr. Geol. Correlation* 15, 193–205.

Ogg J.G. & Lowrie W. 1986: Magnetostratigraphy of the Jurassic/Cretaceous boundary. *Geology* 14, 547–550.

Ogg J.G., Hasenyager R.W., Wimbledon W.A., Channell J.E.T. & Bralower T.J. 1991: Magnetostratigraphy of the Jurassic-Cretaceous boundary interval-Tethyan and English faunal realms. *Cretaceous Research* 1, 455–482.

Olóriz F. & Tavera J.M. 1989: The significance of Mediterranean ammonites with regard to the traditional Jurassic-Cretaceous boundary. *Cretaceous Research* 10, 221–237.

Olóriz F., Caracuel J.E., Marques B. & Rodríguez-Tovar F.J. 1995: Asociaciones de Tintinnoides en facies ammonitico rosso de la Sierra Norte (Mallorca). *Rev. Esp. Paleont.*, 77–93.

Parent H., Scherzinger A. & Schweigert G. 2011: The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina. *Bol. Inst. Fisiografía Geol.* 79–81, 21–94.

Perch-Nielsen K. 1985: Mesozoic calcareous nannofossils. In: Bolli H.M., Saunders J.B. & Perch-Nielsen K. (Eds.): Plankton stratigraphy. *Cambridge University Press*, Cambridge, 329–426.

Pruner P., Houša V., Olóriz F., Košťák M., Krs M., Man O., Schnabl P., Venhodová D., Tavera J.M. & Mazuch M. 2009: High-resolution magnetostratigraphy and biostratigraphic zonation of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain). *Cretaceous Research* 31, 192–206.

Příhoda K., Krs M., Pešina B. & Bláha J. 1989: MAVACS — a new system creating a nonmagnetic environment for palaeomagnetic studies. In: Banda E. (Ed.): Paleomagnetismo-palaeomagnetism, CSIC, Madrid, 1988–1989. *Cuadernos de Geologia Iberica*, 223–250.

Reháková D. 2000: Evolution and distribution of the Late Jurassic and Early Cretaceous calcareous dinoflagellates recorded in the Western Carpathians pelagic carbonate facies. *Miner. Slovaca* 32, 79–88.

Reháková D. & Michalík J. 1994: Abundance and distribution of late Jurassic-Early Cretaceous microplankton in Western Carpathians. *Geobios* 27, 135–156.

Reháková D. & Michalík J. 1997: Evolution and distribution of calpionellids — the most characteristic constituents of Lower Cretaceous Tethyan microplankton. *Cretaceous Research* 18, 493–504.

Reháková D., Matyja B.A., Wierzbowski A., Schlögl J., Krobicki M. & Barski M. 2011: Stratigraphy and microfacies of the Jurassic and Lowermost Cretaceous of the Veliky Kamenets section (Pieniny Klippen belt, Carpathians, Western Ukraine). *Volumina Jurassica* 9, 61–104.

Remane J. 1970: Die Entstehung der resedimentarun Breccien in Obertithon der subalpen Ketten Frankreiches. *Eclogae Geol. Helv.* 63, 685–740.

Remane J., Borza K., Nagy I., Bakalova-Ivanova D., Knauer J., Pop G. & Tardi-Filácz E. 1986: Agreement on the subdivision of the standard calpionellid zones defined at the IInd Planktonic Conference Roma 1970. *Acta Geol. Hung.* 29, 5–14.

Roth P.H. 1983: Jurassic and Lower Cretaceous calcareous nannofossil in the Western North Atlantic (Site 534): biostratigraphy, preservation and some observation on biogeography and paleoceanography. *Initial Reports of the Deep Sea Drilling Project*, Washington D.C. 76, 587–621.

Roth P.H. 1986: Mesozoic palaeoceanography of the North Atlantic and Tethys Oceans. In: Summerhays C.P. & Shackleton N.J. (Eds.): North Atlantic Paleoceanography. *Geol. Soc., Spec. Publ.* 26, 299–320.

Tavera J.M. 1985: Los ammonites del Tithonico superior-Berriasense de la zona Subbetica (Cordilleros beticas). *Thesis Doctoral Univerisdad Granada*, 1–379.

Tavera J.M., Aguado R., Company M. & Olóriz F. 1994: Integrated biostratigraphy of the Durangites and Jacobi zones (J/K boundary) at the Puerto Escaño section in southern Spain (province of Cordoba). *Geobios Mem. Spec.* 17, 469–476.

Wiedmann J. 1973: Evolution or revolution of ammonoids at Mesozoic system boundaries. *Biological Rev.* 48,159–194.

Wimbledon W.A.P., Casellato C.E., Reháková D., Bulot L.G., Erba E., Gardin S., Verreussel R.M.C.H., Munsterman D.K. & Hunt C. 2011: Fixing a basal Berriasian and Jurassic-Cretaceous (J-K) boundary — perhaps there is some light at the end of the tunnel? *Riv. Ital. Paleont. Stratigr.* 117, 295–307.

Zeiss A. & Leanza H. 2011: Upper Jurassic (Tithonian) ammonites from the lithographic limestones of the Zapala region, Neuquén Basin, Argentina. *Beringeria* 41, 1–52.

Appendix: Calcareous nannofossils

Authors and date of the original description and, where appropriate, emendations are provided. See Perch-Nielsen (1985), Bralower et al. (1989), Bown & Cooper (1998), Casellato (2010) and references therein for full information on taxonomy and authorships.

Conusphaera mexicana (Trejo, 1969) subsp. *mexicana* Bralower *in* Bralower et al., 1989
Conusphaera mexicana (Trejo, 1969) subsp. *minor* (Bown & Cooper, 1989) Bralower *in* Bralower et al., 1989
Cretarhabdus octofenestratus Bralower *in* Bralower et al., 1989
Cretarhabdus surirellus (Deflandre *in* Deflandre & Fert, 1954) Reinhardt, 1970
Cruciellipsis cuvillieri (Manivit, 1956) Thierstein, 1971
Cyclagelosphaera argoensis Bown, 1992
Cyclagelosphaera deflandrei (Manivit, 1966) Roth, 1973
Cyclagelosphaera margerelii Noël, 1965
Cyclagelosphaera riyadhensis Varol, 2006
Cyclagelosphaera tubulata (Grün & Zweili, 1980) Cooper, 1987
Diazomatolithus lehmanii Noël, 1965
Faviconus multicolumnatus Bralower *in* Bralower et al., 1989
Hexalithus geometricus Casellato, 2010
Hexalithus noeliae (Noël, 1956) Loeblich & Tappan, 1966
Manivitella pemmatoidea (Deflandre *ex* Manivit, 1965) Thierstein, 1971
Microstaurus chiastius (Worsley, 1971) Bralower et al., 1989
Microstaurus quadratus Black, 1971
Nannoconus erbae Casellato, 2010
Nannoconus globulus (Brönnimann, 1955) subsp. *globulus* Bralower *in* Bralower et al., 1989
Nannoconus globulus (Brönnimann, 1955) subsp. *minor* Bralower *in* Bralower et al., 1989
Nannoconus infans Bralower *in* Bralower et al., 1989
Nannoconus kamptneri (Brönnimann, 1955) subsp. *minor* Bralower *in* Bralower et al., 1989
Nannoconus puer Casellato, 2010
Nannoconus steinmannii (Kamptner, 1931) subsp. *minor* Deres & Achéritéguy, 1980
Nannoconus wintereri Bralower & Thierstein *in* Bralower et al., 1989
Polycostella beckmannii Thierstein, 1971
Polycostella senaria Thierstein, 1971
Rhagodiscus asper (Stradner, 1963) Reinhardt, 1967
Umbria granulosa subsp. *granulosa* Bralower & Thierstein *in* Bralower et al., 1989
Watznaueria barnesiae (Black *in* Black & Barnes, 1959) Perch-Nielsen, 1968
Watznaueria britannica (Stradner, 1963) Reinhardt, 1964
Watznaueria communis Reinhardt, 1964
Watznaueria fossacincta (Black, 1971a) Bown *in* Bown & Cooper, 1989
Watznaueria manivitiae (Bukry, 1973) Moshkovitz & Ehrlich, 1987
Zeugrhabdotus cooperi Bown, 1992b
Zeugrhabdotus embergeri (Noël, 1958) Perch-Nielsen, 1984
Zeugrhabdotus erectus (Deflandre *in* Deflandre & Fert, 1954) Reinhardt, 1965
Zeugrhabdotus fluxus Casellato, 2010

VOLUMINA JURASSICA, 2014, XII (1): 113–128

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

Luc G. BULOT[1], Camille FRAU[2], William A.P. WIMBLEDON[3]

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

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

INTRODUCTION

The unique character of the ammonite fauna of Le Chouet (near Les Près, Drôme, France) (Fig. 1) has already been outlined by Le Hégarat (1973), but, so far, only a handful of specimens have been illustrated by Enay *et al.* (1998a, fig. 2). In recent years, new fieldwork has allowed us to sample the Chouet section bed by bed and to collect over 400 new specimens. A preliminary account on the ammonite distribution across the Tithonian-Berriasian boundary was published by Wimbledon *et al.* (2013), but in that paper we did not illustrate the fauna. The aim of the present contribution is to document the taxonomy and illustrate new and poorly known Perisphinctoidea from the Upper Tithonian of this reference section. Additional data on the Himalayitidae including the description and discussion of *Boughdiriella chouetensis* gen. nov. sp. nov. are to be published elsewhere (Frau *et al.*, 2014).

GEOLOGICAL SETTING

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

---

[1] Aix-Marseille Université, UMR-CNRS 7330 CEREGE, Centre Saint-Charles, case 67, 3 place Victor Hugo, 13331 Marseille cedex 03, France; e-mail: bulot@cerege.fr

[2] 9bis, Chemin des Poissonniers, 13600 La Ciotat, France

[3] School of Earth Sciences, University of Bristol, Queens Road, Bristol BS8 1RJ, United Kingdom

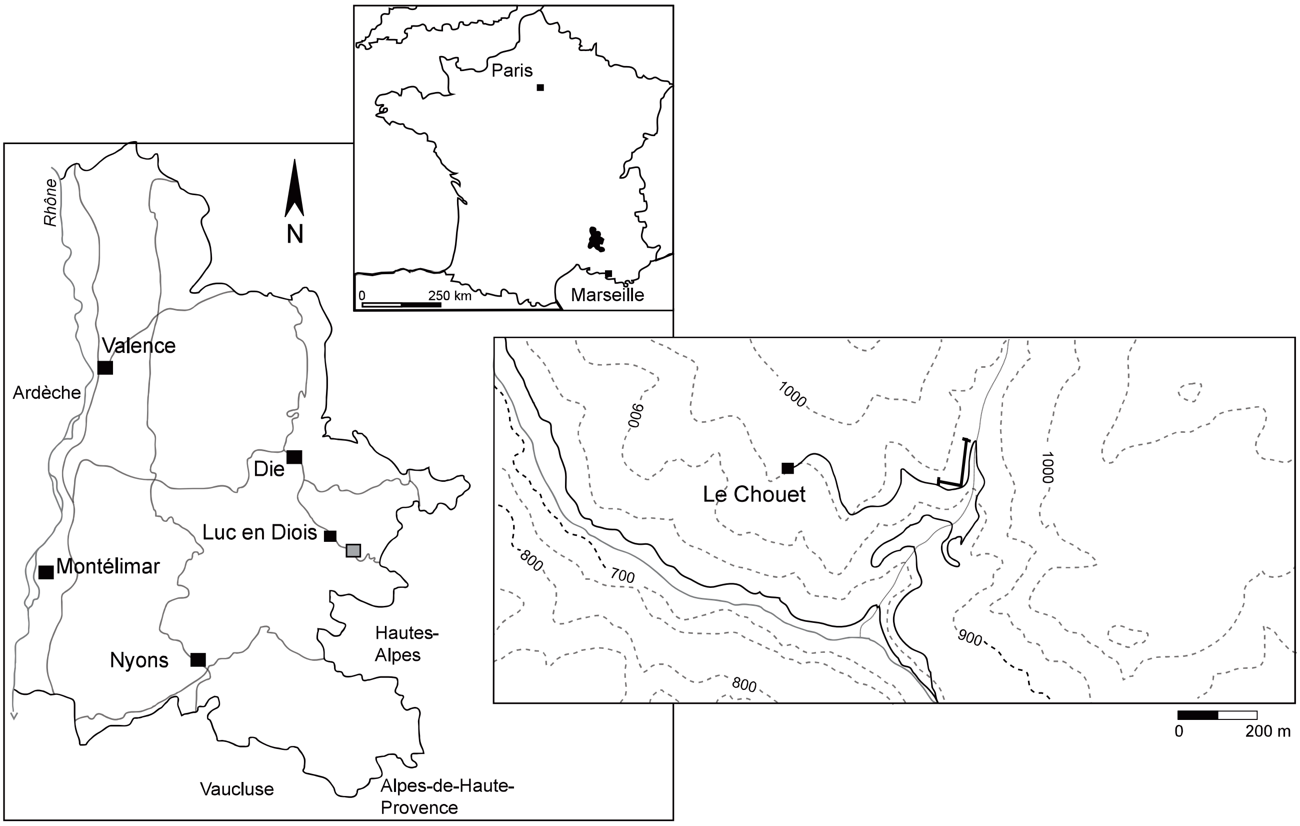


Fig. 1. Locality map of Le Chouet (Les Près, Drôme, SE France)

The studied section is marked by a black line

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

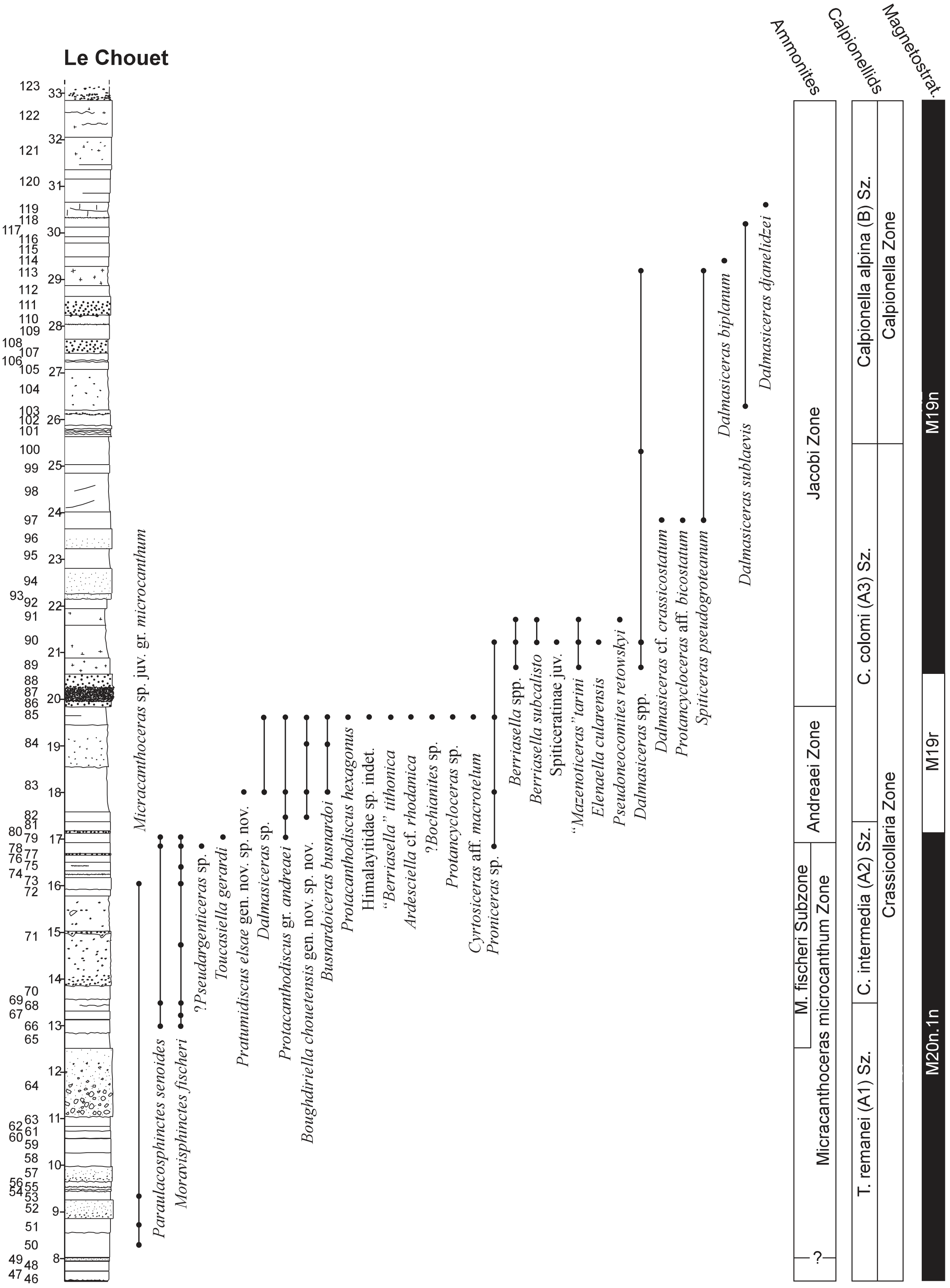
The minor discrepancies between figure 12 *in* Wimbledon *et al.* (2013) and Figure 2 of this paper concern the distribution of *Micracanthoceras* Spath, 1925 and the occurrence of supposed Boreal ammonites reported by Wimbledon *et al.* (2013, p. 451). The range of *Micracanthoceras* will be discussed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

SYSTEMATIC PALAEONTOLOGY

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

→

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


Le Chouet
123
122
121
120
119
118
117
116
115
114
113
112
111
110
109
108
107
106
105
104
103
102
101
100
99
98
97
96
95
94
93
92
91
90
89
88
87
86
85
84
83
82
81
80
79
78
77
76
75
74
73
72
71
70
69
68
67
66
65
64
63
62
61
60
59
58
57
56
55
54
53
52
51
50
49
48
47
46
33
32
31
30
29
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
Micracanthoceras sp. juv. gr. *microcanthum*
Paraulacosphinctes senoides
Moravisphinctes fischeri
?Pseudargenticeras sp.
Toucasiella gerardi
Pratumidiscus elsae gen. nov. sp. nov.
Dalmasiceras sp.
Protacanthodiscus gr. *andreaei*
Boughdiriella chouetensis gen. nov. sp. nov.
Busnardoiceras busnardoi
Protacanthodiscus hexagonus
Himalayitidae sp. indet.
"Berriasella" tithonica
Ardesciella cf. *rhodanica*
?Bochianites sp.
Protancycloceras sp.
Cyrtosiceras aff. *macrotelum*
Proniceras sp.
Berriasella spp.
Berriasella subcalisto
Spiticeratinae juv.
"Mazenoticeras" tarini
Elenaella cularensis
Pseudoneocomites retowskyi
Dalmasiceras spp.
Dalmasiceras cf. *crassicostatum*
Protancycloceras aff. *bicostatum*
Spiticeras pseudogroteanum
Dalmasiceras sublaevis
Dalmasiceras biplanum
Dalmasiceras djanelidzei
Ammonites
Calpionellids
Magnetostrat.
Jacobi Zone
Andreaei Zone
M. fischeri Subzone
Micracanthoceras microcanthum Zone
?
Calpionella alpina (B) Sz.
C. colomi (A3) Sz.
C. intermedia (A2) Sz.
T. remanei (A1) Sz.
Calpionella Zone
Crassicollaria Zone
M19n
M19r
M20n.1n

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

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

Order **Ammonoidea** Zittel, 1884

Suborder **Ammonitina** Hyatt, 1889

Superfamily **Perisphinctoidea** Steinmann, 1890

Family **Ataxioceratidae** Buckman, 1921

Subfamily **Lithacoceratinae** Zeiss, 1968

Genus *Paraulacosphinctes* Schindewolf, 1925

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

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

Paraulacosphinctes senoides Tavera, 1985

Fig. 3A–E

pars 1868. *Ammonites senex* Oppel *in* Zittel, p. 113, pl. 23: 1, 2; non fig. 3 (= *P. senex*).

1985. *Paraulacosphinctes senoides* Tavera, p. 79, pl. 13: 1–5, text-fig. 7E.

non 2011. *Paraulacosphinctes* cf. *senoides* Tavera: Arkadiev, p. 242, pl. 1: 5 (= *P. transitorius* Oppel, 1865).

non 2012. *Paraulacosphinctes* cf. *senoides* Tavera: Arkadiev, p. 141, pl. 1: 5 (= Arkadiev, 2011, pl. 1: 5).

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

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

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

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

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

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

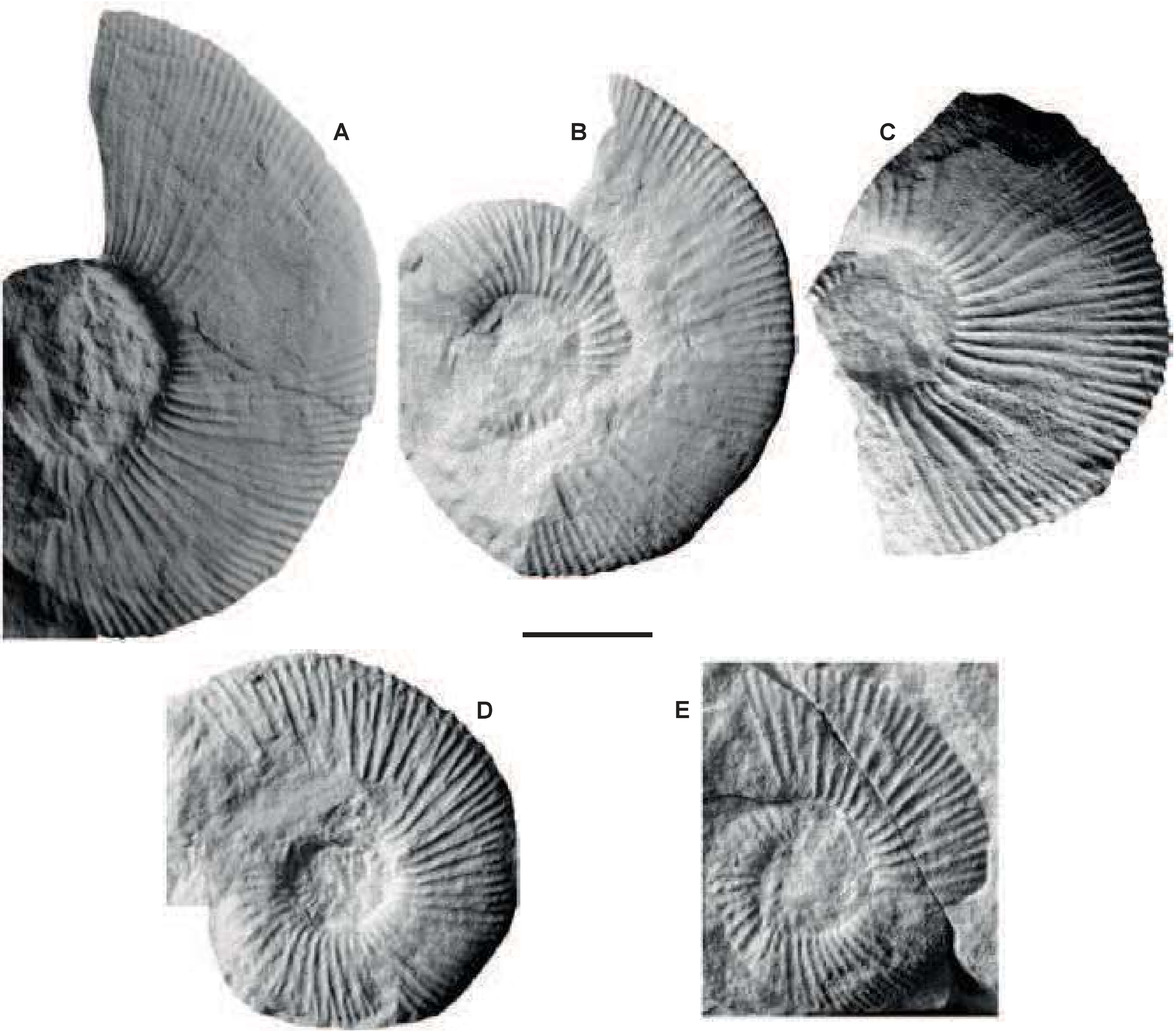


Fig. 3. ***Paraulacosphinctes senoides*** **Tavera**

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

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

Genus *Moravisphinctes* Tavera, 1985

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

Moravisphinctes fischeri (Kilian, 1889)

Fig. 4A–E

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

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

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

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

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

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

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

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

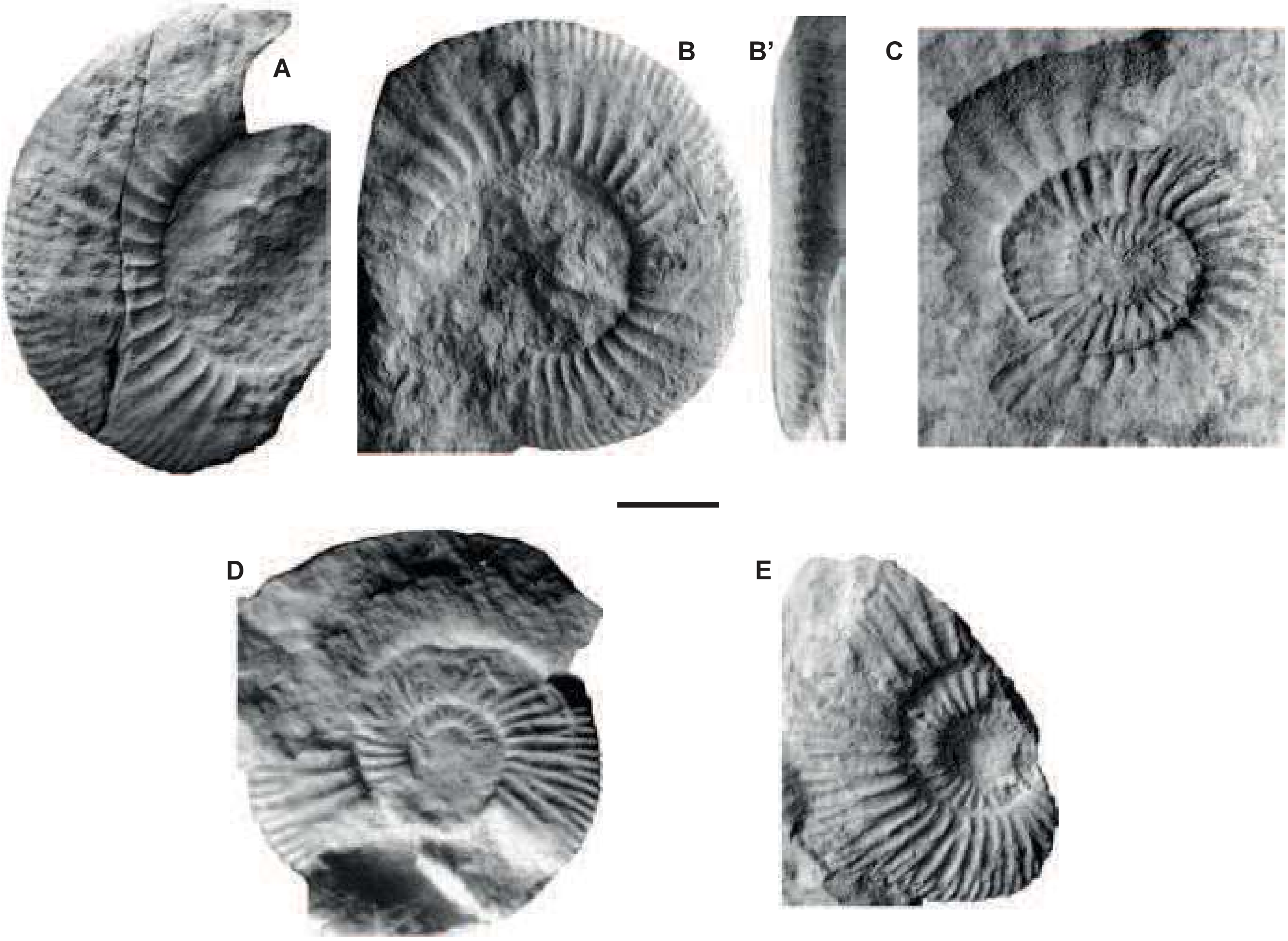


Fig. 4. *Moravisphinctes fischeri* (Kilian)

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

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

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

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

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

Family **Himalayitidae** Spath, 1925

Genus *Micracanthoceras* Spath, 1925

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

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

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

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

Most recently, the designation of the lectotype of *Ammonites koellikeri* Oppel, 1865 by Parent *et al.* (2011, p. 72: 32A) sheds new light on the content of *Micracanthoceras* and its relationships with the European taxa most often referred to *Corongoceras* Spath, 1925. We agree with those authors that the juvenile ontogenetic stages of *Ammonites koellikeri* are very close to those of *M. microcanthum* and that the two species should be placed in the same genus. Moreover, as far as one can tell from Mazenot's illustration (1939, pl. 37: 12a, b), the ontogenetic development of Oppel's larger specimen of *M. microcanthum* is very similar to that of the lectotype of *M. koellikeri.* Another closely allied species is *Ammonites fraudator* Zittel, 1868, attributed to *Micracanthoceras* by Spath (1931, p. 545). We accept this view, also held by Sapunov (1979), who selected as lectotype the specimen illustrated by Zittel (1868, pl. 21: 2a, b).

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

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

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

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

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

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

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

Genus *Ardesciella* gen. nov.

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

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

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

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

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

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

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

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

Ardesciella cf. *rhodanica* (Mazenot, 1939)

Fig. 5A–B

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

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

Description. – Specimen MPP-CHT.21/68 is an incomplete juvenile phragmocone that shows the typical characters seen in the type specimen of *Ardesciella*. It matches well Mazenot's holotype (1939) in its small size and irregular ornament. The second specimen (MPP-CHT.21/12) is a complete juvenile that shows perfectly two successive ontogenetic stages. Compared to the first specimen, its rib density is higher, with rare single intercalatory ribs. Ornamentation is coarser and it rises sharply towards the venter, with 'pinched' ventro-lateral tubercles.

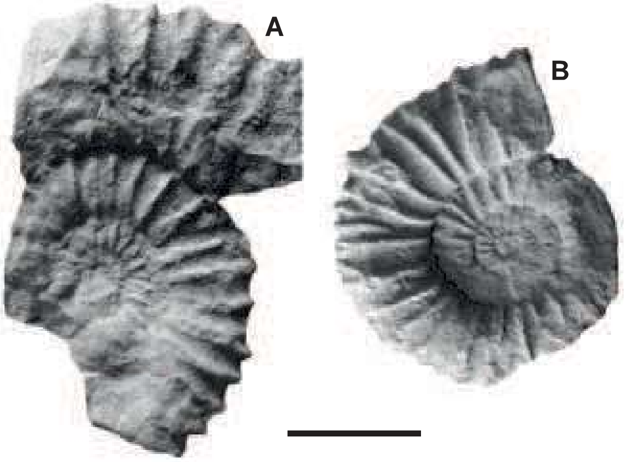


Fig. 5. *Ardesciella* cf. *rhodanica* (Mazenot)

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

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

Genus *Pratumidiscus* nov. gen.

Derivation of name: From *pratum,* latin for Les Près, near where the Le Chouet section is located.
Type species: *Pratumidiscus elsae* gen. nov., sp. nov.
Locus typicus: Le Chouet, Les Près, Drôme.
Diagnosis: Shell small, compressed with a wide and low umbilicus. Whorl section subquadrate to subrectangulate, with

weakly convex flanks and tabulate venter. Complex and irregular ornamentation composed of single, bifurcate, intercalatory and simplified virgatotome ribs. All ribs thicken on the ventral shoulder in radially elongated bullae that delimit the ventral groove. Suture line is unknown.
Stratigraphical and geographical distribution: Andreaei Zone (Crassicollaria calpionellid Zone, top of the Intermedia Subzone). For the time being, the genus is monotypic and known by a single specimen from the type locality.

Pratumidiscus elsae gen. nov. sp. nov.

Fig. 6

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

Derivation of name: Dedicated to Elsa Schnebelen-David for her participation to our latest field trip at Le Chouet and continuous support to one of us (LGB) during the preparation of this work.
Holotype: MPP-CHT.19/5.
Type locality: Le Chouet, commune de Les Près, Drôme.
Stratigraphical distribution: Bed 83, Andreaei Zone (Crassicollaria calpionellid Zone, top of the Intermedia Subzone), Upper Tithonian.
Diagnosis: As for the genus.

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

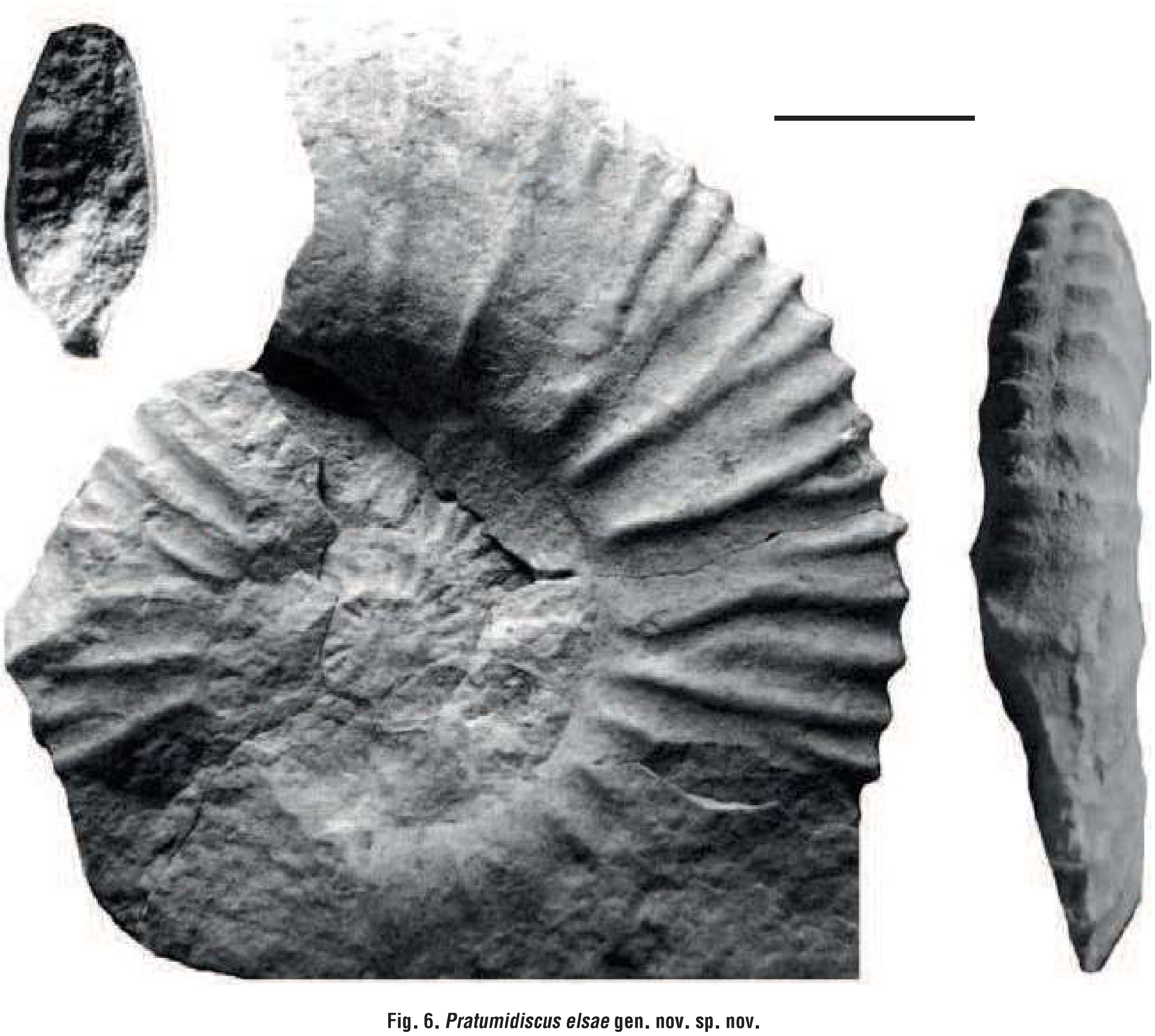


Fig. 6. *Pratumidiscus elsae* gen. nov. sp. nov.

Lateral, ventral and whorl section of MPP-CHT.19/5. Bar scale is 1 cm that recall juvenile Himalayitidae morphology. At later shell growth stages, the whorl section is almost subrectangular with weakly convex flanks and a tabulate venter. The umbilical wall gets slightly steeper. The ornamentation is marked by the complex and irregular alternation of simple, bifurcate, intercalated and simplified virgatotome ribs. Bifurcations occur at different heights, but most often just above the middle of the flank. The intercostal space varies greatly. On the last whorl, the primary ribs are more prominently developed above the umbilical shoulder. The venter is marked by a ventral groove delimited by the interruption and strengthening of the ribs.

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

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

Family **Neocomitidae** Salfeld, 1921

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

Genus *Pseudargentiniceras* Spath, 1925

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

Remarks. – It should be noted that Spath (1925, p. 145) is not fully explicit regarding the designation of the specimen illustrated by Zittel (1868, pl. 19: 4a–c) as the lectotype of *Ammonites abscissus*. As a consequence, Mazenot (1939, see footnote 1, p. 35 and p. 105–106) formally designated as lectotype the specimen figured by Zittel (1868, pl. 19: 1a–b) on which the original diagnosis was based. Both specimens were re-illustrated by Mazenot (1939, pl. 15: 1, 3) and seem to be conspecific (Le Hégarat, 1973; Nikolov, 1982; Tavera, 1985).

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

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

?*Pseudargentiniceras* sp.

Fig. 7

1985. *Substeueroceras* sp. Tavera, p. 327, pl. 33: 1, 2.
1989. *Substeueroceras* sp. Olóriz et Tavera, p. 232, fig. 2: 1a, b.

Material. – MPP-CHT.14/17

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

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

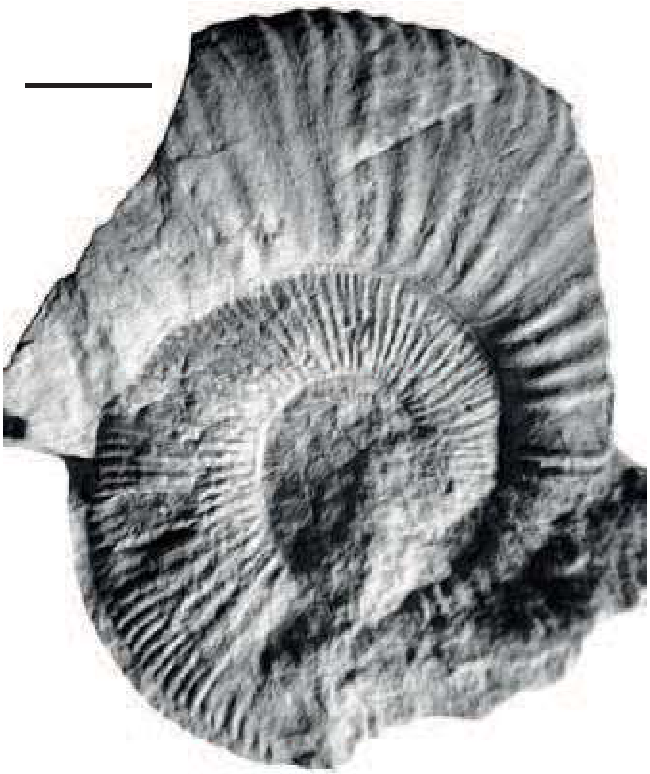


Fig. 7. ?*Pseudargentiniceras* sp.

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

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

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

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

This problem also addresses the origin of the Neocomitidae. According to Tavera (1985, p. 78), the origin of the Neocomitidae is to be found in *Paraulacosphinctes* and its closely allied taxa. This is based on the fact that in its original conception, *Paraulacosphinctes* is based on perisphinctids with a smooth ventral band. However, the last *Paraulacosphintes* of the *P. senoides* group found at Le Chouet may represent the direct ancestor of ?*Pseudargentiniceras* sp., since both forms are characterized by the absence of a ventral band at late ontogenetic stages. This is also the case of several specimens of the *Paraulacosphinctes – Oloriziceras* plexus figured by Tavera (1985). As a consequence, the suprageneric attribution of *Pseudargentiniceras abscissum, P. flandrini* and ?*Pseudargentiniceras* sp. remains unclear.

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

Genus *Busnardoiceras* Tavera, 1985

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

Busnardoiceras busnardoi (Le Hégarat, 1973)
Fig. 8A–F

1939. *Berriasella ciliata* Schneid: Mazenot, p. 37, pl. 1: 1a, b (sol.).
1973. *Parapallasiceras busnardoi* Le Hégarat, p. 47, pl. 3: 4, 5 (= Mazenot, 1939, pl. 1: 1a, b), ? pl. 38: 2.
2001. *Parapallasiceras busnardoi* Le Hégarat: Wippich, p. 78, pl. 20: 2.

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

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

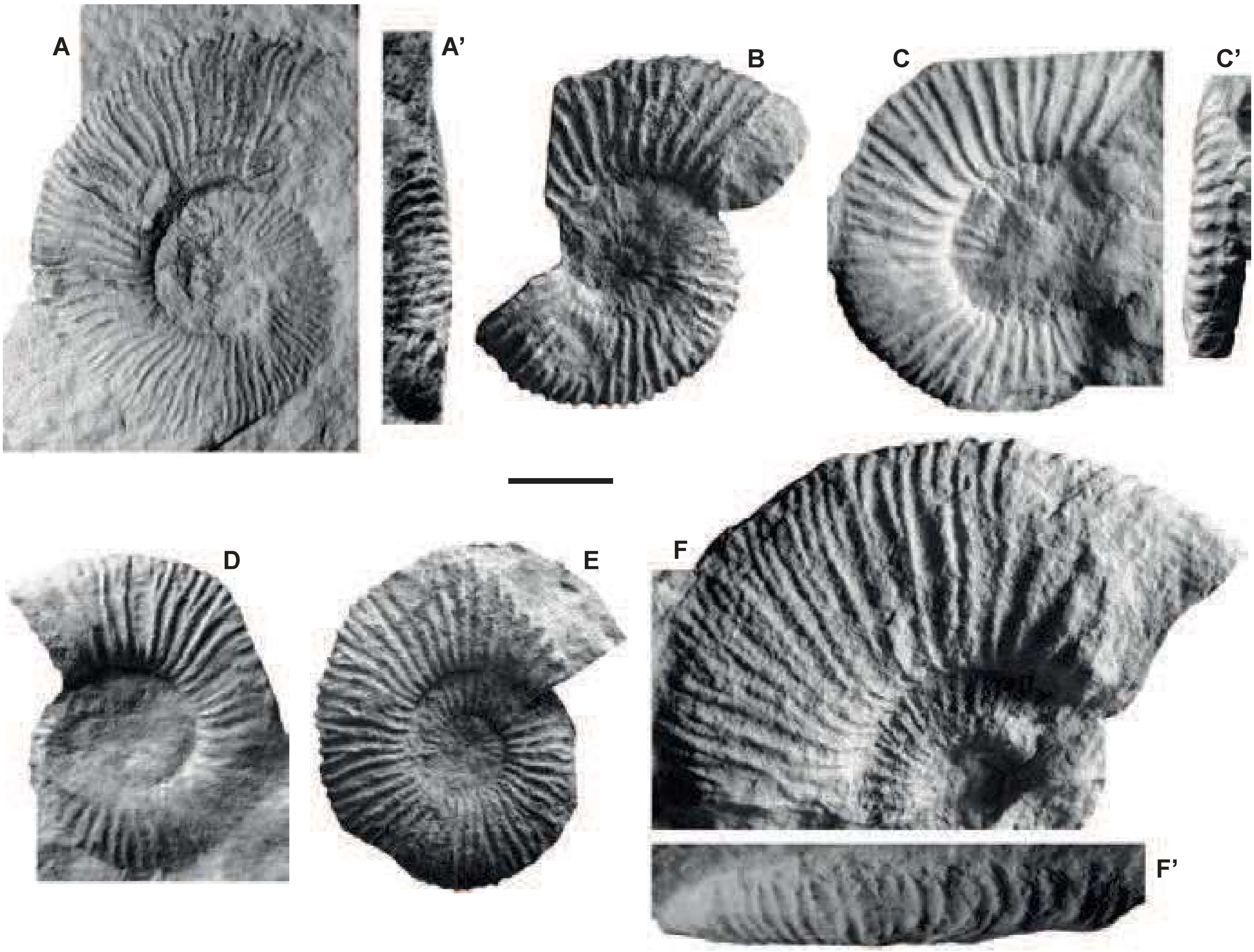


Fig. 8. *Busnardoiceras busnardoi* (Le Hégarat)

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

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

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

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

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

CONCLUSIONS

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

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

Acknowledgements. This work is a contribution of the Berriasian Working Group (BWG) of the International Subcommission on Cretaceous Stratigraphy (ISCS). Jens Lehmann (University of Bremen), Miguel Company (University of Granada) and Josep Moreno Bedmar (University Nacional Autónoma de Mexico) are gratefully acknowledged for providing missing references. Valuable discussions with Vasily Mitta (University of Moscow) and Mabrouk Boughdiri (University of Bizerte) greatly improved this paper. 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.

REFERENCES

ARKADIEV V.V., 2011 — New data on ammonoids of the genus *Paraulacosphinctes* from the Upper Tithonian of the Mountainous Crimea. *Stratigraphy and Geological Correlation*, **19**: 238–242.

ARKADIEV V.V., BOGDANOVA T.N., GUZHIKOV A.Y., LOBACHEVA S.V., MYSHKINA N.V., PLATANOV E.S., SAVELYEVA Y.N., SHUREKOVA O.V., YANIN B.T., 2012 — Berriasian Stage of the Mountainous Crimea. Saint-Petersburg: LEMA [in Russian with English summary].

ARNOULD-SAGET S., 1953 — Les Ammonites pyriteuses du Tithonique Supérieur et du Berriasien de Tunisie Centrale. *Annales des Mines et de la Géologie*, **10**: 1–133.

BEHRENDSEN O., 1891 — Zur Geologie des Ostabhangs der argentinischen Cordillere. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **44**: 369–420.

BENZAGGAGH M., 2000 — Le Malm supérieur et le Berriasien dans le Prérif interne et le Mésorif (Rif, Maroc). Biostratigraphie, lithostratigraphie, paléogéographie et évolution tectono-sédimentaire. *Documents des Laboratoires de Géologie, Lyon*, **152**: 1–347.

BENZAGGAGH M., ATROPS F., 1997 — Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). *Newsletters on Stratigraphy*, **35**: 127–163.

BOUGHDIRI M., OLÓRIZ F., LOPEZ MARQUES B., LAYEB M., De MATOS J., SALLOUH H., 2005 — Upper Kimmeridgian and Tithonian ammonites from the Tunisian «Dorsale» (NE Tunisia): updated biostratigraphie from the Jebel Oust. *Rivista Italiana di Paleontologia e Stratigrafia*, **111**: 305–316.

CECCA F., 1985 —Alcune ammoniti provenienti dalla "Maiolica" dell'Appennino Centrale (Umbria, Marche e Sabina). *Bollettino del Servizio Geologico d'Italia*, **103**: 133–162.

CECCA F., 1999 — Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **147**: 1–37.

CECCA F., ENAY R., 1991— Les ammonites des zones à Semiforme et à Fallauxi du Tithonique de l'Ardèche (Sud-Est de la France): stratigraphie, paléontologie, paléobiogéographie. *Palaeontographica,* A, **219**: 1–87.

CECCA F., ENAY R., LE HEGARAT, G., 1989 — L'Ardescien (Tithonique supérieur) de la région stratotypique: série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. *Documents des Laboratoire de Géologie, Lyon*, **107**: 1–115.

COLLIGNON M., 1960 — Atlas des fossiles caractéristiques de Madagascar. Fascicule VI (Tithonique): 134–175. Service Géologique de Madagascar, Tananarive.

COMPANY M., 1987 — Los Ammonites del Valanginiense del sector de las Cordieras Béticas (SE de Espana) [PhD Thesis]. University of Granada.

DONOVAN D.T., CALLOMON J.H., HOWARTH M.K., 1981— Classification of the Jurassic Ammonitina. *In*: The Ammonoidea, Systematics Association Special Volume (eds M.R. House, J.R. Senior): 101–155.

ELIÁŠ, M., VAŠÍČEK, V., 1995— Early Berriasian ammonites from the Štramberk Limestone of Kotouč quarry (Outer Carpathians, Silesian Unit, Štramberk, Czech Republic). *Véstník Českého Geologického Ústavu*, **70**: 1–32.

ENAY R., BOUGHDIRI M., Le HÉGARAT G., 1998a — *Durangites*, *Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien supérieur – Berriasien dans la Téthys méditerranéenne (SE France, Espagne, Algérie et Tunisie). *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes*, **327**: 425–430.

ENAY R., BOUGHDIRI M., Le HÉGARAT G., 1998b — *Toucasiella gen. nov.,* Himalayitidae (Ammonitina) nouveau du Tithonien supérieur: origine des *Durangites*. *Comptes Rendus de l'Académie des Sciences de Paris, Sciences de la Terre et des Planètes*, **327**: 471–477.

FRAU C., BULOT L.G., WIMBLEDON W.A.P., 2014 — Late Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) From Le Chouet (Drôme, France). *Geologica Carpathica* [submitted].

GEYSSANT J., 1997 — Tithonien. *In*: Biostratigraphie du Jurassique ouest européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles (eds. E. Cariou, P. Hantzpergue): 97–102. Elf Aquitaine édition, Pau.

HOEDEMAEKER P.J., BULOT L.G., 1990 — Preliminary ammonite zonation for the Lower Cretaceous of the Mediterranean region. *Géologie Alpine*, **66**: 123–127.

HYATT A., 1889 — Genesis of the Arietidae. *Memoirs of the Museum of Comparative Zoology*, **16**: 1–238.

IMLAY R.W., 1939 — Upper Jurassic ammonites from Mexico. *Geological Society of America, Bulletin*, **50**: 1–78.

KILIAN W., 1889 — Etudes paléontologiques sur les terrains secondaires et tertiaires de l'Andalousie. *In*: Mission d'Andalousie. — *Mémoire de l'Académie des Sciences de l'Institut de France*, **30**: 580–733.

Le HEGARAT G., 1973 — Le Berriasien du Sud Est de la France. *Document des Laboratoires de Géologie de la Faculté des Sciences de Lyon*, **43**: 1–576.

LINARES A., VERA J.A., 1966 — Precisiones estratigráficas sobre la serie mesozoica de Sierra Gorda, Cordilleras Béticas (provincia de Granada). *Estudios Geologicos*, **22**: 65–99.

MAZENOT G., 1939 — Les Palaeophoplitidae tithoniques et berriasiens du sud est de la France. *Mémoires de la Société Géologique de France*, **41**: 5–303.

MITTA V., 2007 — The Berriasian (= Ryazanian) Stage of the Russian Platform: The first Cretaceous Invasion of Tethyan Ammonites. *In*: 1st International Meeting on Correlation of Cretaceous Micro- and Macrofossils, Vienna (Berichte der Geologischen Bundesanstalt): 76–77.

MITTA V.V., 2008 — Ammonites of Tethyan Origin from the Ryazanian of the Russian Platform: Genus *Riasanites* Spath. *Paleontological Journal*, **42**: 251–259.

MITTA V.V., 2011— Ammonites of Tethyan origin in the Ryazanian Stage of the Russian Platform: Genus *Riasanella* gen. nov. *Paleontological Journal*, **45**: 13–22.

NIKITIN S.N., 1888 — Traces of the Cretaceous period in Central Russia. *Mémoires du Comité Géologique*, **5**: 1–205 (in Russion).

NIKOLOV T.G., 1982 — Les Ammonites de la famille Berriasellidae Spath, 1922. Tithonique supérieur-Berriasien. Académie Bulgare des Sciences.

OLÓRIZ F., TAVERA J.M., 1989 — The significance of Mediterranean ammonites with regard to the traditional Jurassic-Cretaceous boundary. *Cretaceous Research*, **10**: 221–237.

OPPEL A., 1865 — Die tithonische Etage. *Zeitschrift der Deutschen Geologischen Geselshaft*, **17**: 535–558.

PARENT, H., 2003 — The ataxioceratid ammonite fauna of the Tithonian (Upper Jurassic) of Casa Pincheira, Mendoza (Argentina). *Journal of South American Earth Sciences*, **16**: 143–165.

PARENT H., SCHERZINGER A., SCHWEIGERT G., 2011 — The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina. *Boletín del Instituto de Fisiografía y Geología*, **79–81**: 21–94.

ROMAN F., 1936 — Le Tithonique du massif du Djurdjura (province d'Alger). *Matériaux pour la Carte géologique de l'Algérie, Paléontologie*, 7: 1–43.

SAPUNOV I.G., 1977 — Ammonite stratigraphy of the Upper Jurassic in Bulgaria. IV. Tithonian: Substages, Zones and Subzones. *Geologica Balcanica*, **7**: 43–64.

SAPUNOV I.G., 1979 — Les fossiles de Bulgarie. III.3. Jurassique supérieur, Ammonoidea. Académie Bulgare des Sciences.

SHOME S., BARDHAN S., 2009 — A new Late Tithonian ammonite assemblage from Kutch, Western India. *Journal of the Palaeontological Society of India*, **54**: 1–18.

SPATH L.F., 1923 — Appendix: On ammonites from New Zealand. *In*: The Jurassic rocks of New Zealand (Ed. C.T. Trechmann). *Quarterly Journal of the Geological Society of London*, **79**: 286–308.

SPATH L.F., 1925 — Ammonites and Aptychi. The Collection of Fossils and Rocks from Somaliland.– *Monographs Geological Department of the Hunterian Museum*, **1**: 111–164.

SPATH L.F., 1931 — Revision of the Jurassic cephalopod fauna of Kachh (Cutch), Part IV. *Palaeontologia Indica*, **9**: 1–945.

STEINMANN G., 1890 — Cephalopoda. *In*: Elemente der Paläontologie, (eds G. Steinmann, L. Döderlein): 344–475, Engelmann, Leipzig.

TAVERA J.M., 1985 — Les ammonites del Tithonico superior-Berriasense de la Zona Subbetica (Cordilleras Beticas) [PhD Thesis]. University of Granada.

TOUCAS A., 1890 — Etude de la faune des couches tithoniques de l'Ardèche. *Bulletin de la Société Géologique de France*, **18**: 560–629.

WIMBLEDON W.A.P., REHÁKOVÁ D., PSZCZÓŁKOWSKI A., CASSELLATO C.E., HALÁSOVÁ E., FRAU C., BULOT L.G., GRABOWSKI J., SOBIEŃ K., PRUNER P., SCHNABL P., ČÍŽKOVÁ K., TCHOUMATCHENCO P., 2013 — A preliminary account of the bio- and magnetostratigraphy of the Upper Tithonian – Lower Berriasian interval at Le Chouet, Drôme (SE France). *Geologica Carpathica*, **64**: 437–460.

WIPPICH M.G.E., 2001 — Die tiefe Unter-Kreide (Berrias bis Unter-Hauterive) im Südwestmarokkanischen Becken: Ammonitenfauna, Bio- und Sequenzstratigraphie. PhD Thesis, University of Ruhr, Bochum, 474pp.

WRIGHT C.W., CALLOMON J.H., HOWARTH M.K., 1996 — Cretaceous Ammonoidea. *In*: Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Revised, Volume 4 (Ed. R.L. Kaesler): 1–362, The Geological Society of America and the University of Kansas Press, Boulder, CO, and Lawrence, KS.

ZEISS A., 1968 — Untersuchungen zur Paläontologie der Cephalopoden des Unter-Tithon der südlichen Frankenalb. *Bayerische Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse*, Abhandlungen, **132**: 1–191.

ZITTEL K.A., 1865 — Die Cephalopoden der Stramberger Schichten. *Paläontologische Mittheilungen aus dem Museum des königlich Bayerischen Staates*, **2**: 33–118.

ZITTEL K.A., 1884 — Cephalopoda. *In*: Handbuch der Palaeontologie, 329–522, Band 1, Abteilung 2, Lieferung 3. Oldenbourg, Munich/Leipzig.

GEOLOGICA CARPATHICA, APRIL 2015, 66, 2, 117–132 doi: 10.1515/geoca-2015-0014

Upper Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): implications for the systematics

CAMILLE FRAU[1], LUC G. BULOT[2] and WILLIAM A.P. WIMBLEDON[3]

[1]9bis Chemin des Poissonniers, 13600 La Ciotat, France; camille_frau@hotmail.fr
[2]Aix-Marseille Université, UMR-CNRS 7330 CEREGE, Centre Saint-Charles, case 67, place Victor Hugo 3, 13331 Marseille cedex 03, France; bulot@cerege.fr
[3]School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, United Kingdom; mishenka1@yahoo.co.uk

(Manuscript received November 4, 2014; accepted in revised form March 12, 2015)

Abstract: This contribution focuses on the late Tithonian ammonite faunas belonging to the Family Himalayitidae Spath in the key-section of Le Chouet (Drôme, France). The great majority of specimens from the Mediterranean Tethys, previously referred to *Durangites* Burckhardt, are now interpreted as juveniles and/or microconchs of the highly variable species *Protacanthodiscus andreaei* (Kilian). Moreover, comparison between specimens from France, Spain and Bulgaria formerly assigned to *Durangites astillerensis* Imlay and the type material of this species, supports the introduction of *Boughdiriella chouetensis* gen. nov. et sp. nov. Further, the revision of the type specimens of *D. astillerensis* and *Durangites* of the *D. vulgaris* group shows that the former species deserves a new generic status, for which *Parrasiella* gen. nov. is erected. *Toucasiella,* previously only known from Spain and Tunisia, is also reported for the first time from south east France. The revision of the "Mediterranean *Durangites*" supports the rejection of a *Durangites* spp. Zone as part of the standard zonation for the upper Tithonian, and its replacement by the *P. andreaei* Zone (= *D. vulgaris* Zone *sensu* Sarti, 1988).

Key words: Himalayitidae, late Tithonian, Mexico, ammonite faunas, taxonomy, Mediterranean Tethys.

Introduction

Within the activity of the Berriasian Working Group (International Subcommission on Cretaceous Stratigraphy — I.S.C.S.), macrofossil sampling in the upper Tithonian to lower Berriasian interval has promoted the collection of new ammonite faunas from southeast France. A first account of the most significant late Tithonian Perisphinctoidea (Ammonitina) from Le Chouet (Drôme, France) highlighted several taxonomic and biostratigraphic problems (Bulot et al. 2014). Regarding the family Himalayitidae Spath, 1925, the genus *Micracanthoceras* Spath, 1925 was discussed and the new genera *Ardesciella* and *Pratumidiscus* were introduced for Mediterranean himalayitids that had previously been attributed to *Corongoceras* Spath, 1925 or *Riasanites* Spath, 1923.

A new biostratigraphic scheme was proposed for the upper Tithonian of Le Chouet (Wimbledon et al. 2013; Bulot et al. 2014). A *Moravisphinctes fischeri* Subzone was introduced for the upper part of the *Micracanthoceras microcanthum* Zone that correlates with the uppermost part of the calpionellid *Tintinopsella remanei* and *Crassicolaria intermedia* Subzones (*Crassicollaria* Zone). In the uppermost upper Tithonian, a *Protacanthodiscus andreaei* Zone (= *D. vulgaris* Zone *sensu* Sarti, 1988) was defined on the first occurrence of the genus *Protacanthodiscus* Spath, 1923. This zone coincides in calpionellid terms with the uppermost part of the *C. intermedia* Subzone and lower part of the *C. colomi* Subzone.

However, both papers lack description of the fauna that supports rejection of the use of a *Durangites* spp. Zone in the standard zonation of the upper Tithonian (Geyssant 1997). Thus, in the present paper, special attention is given to "Mediterranean *Durangites*", that are either reinterpreted as juvenile and microconch forms of *Protacanthodiscus* and/or *Boughdiriella* gen. nov. Detailed examination of *Durangites* Burckhardt, 1912 supports the introduction of *Parrasiella* gen. nov. for the peculiar *Durangites* of the *D. astillerensis* group Imlay, 1939. Finally, the first report of *Toucasiella* Enay, Boughdiri & Le Hégarat, 1998a in southeastern France sheds light on the phylogeny of late Tithonian himalayitids.

Geological setting

The reader is referred to the work of Wimbledon et al. (2013) and Bulot et al. (2014) for further details about the lithology, biostratigraphy (ammonites, calpionellids and calcareous nannofossils) and magnetostratigraphy of the Le Chouet section. To avoid redundancy, we chose to synthesize the data discussed herein on Fig. 1. A map of the Mexican localities is presented on Fig. 2 and their geological descriptions are to be found in Burckhart (1912), Imlay (1939), Verma & Westermann (1973) and Olóriz et al. (1999).

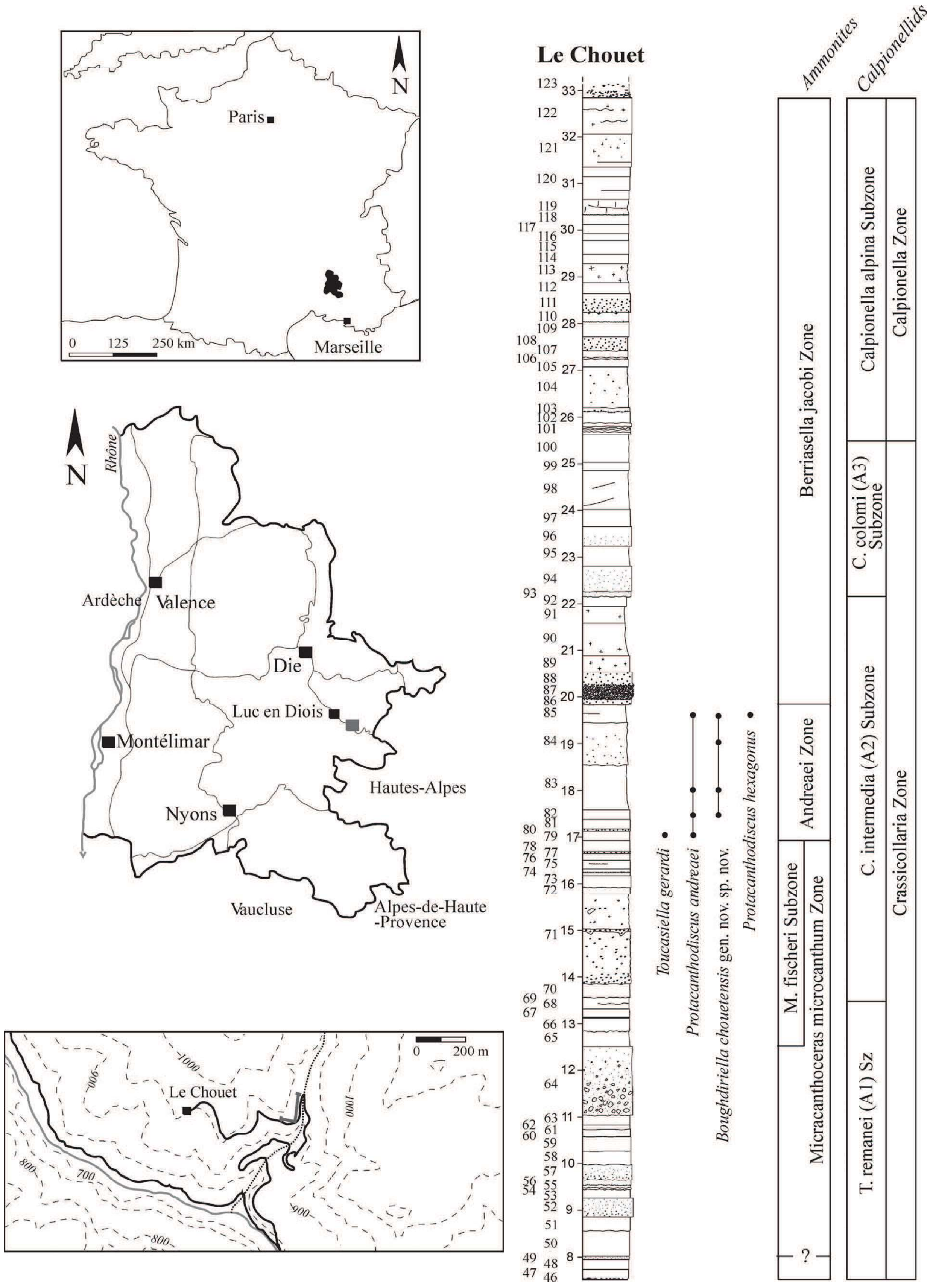


Fig. 1. Locality map of Le Chouet (Les Près, Drôme, SE France), integrated stratigraphy and distribution of the late Tithonian Himalayitidae studied in this paper (modified after Wimbledon et al. (2013)).

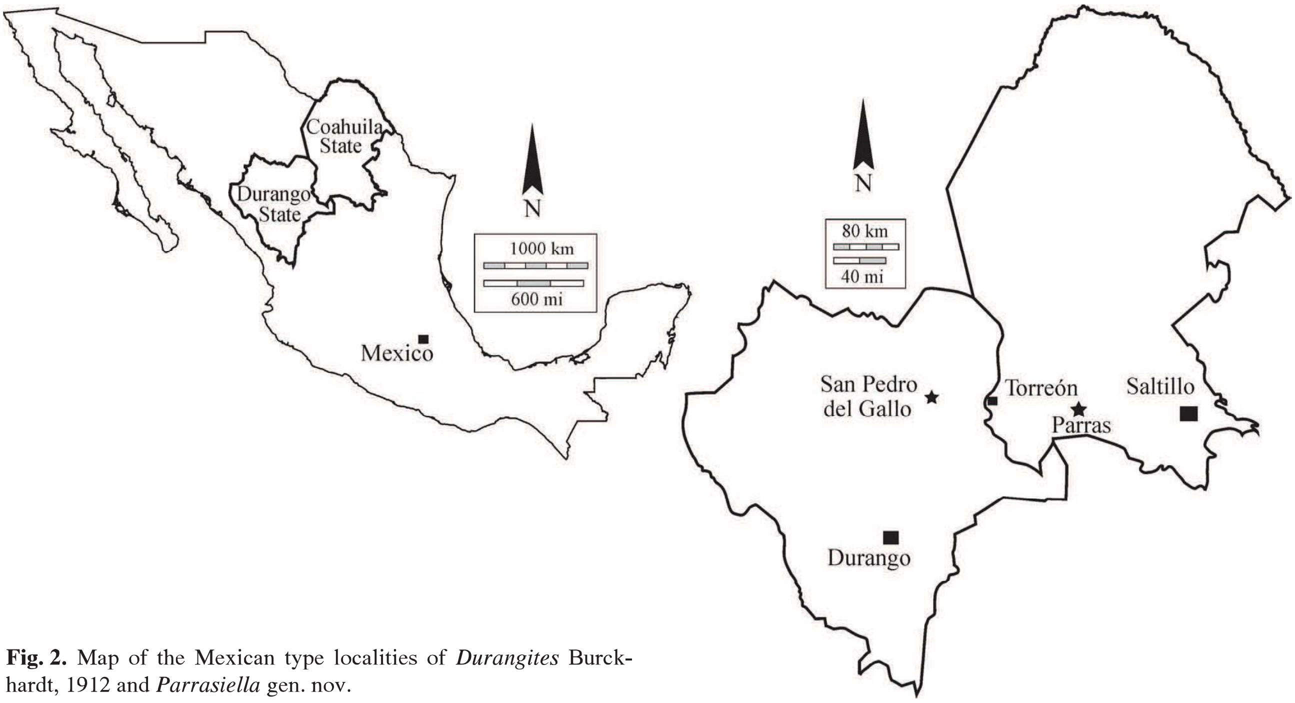


Fig. 2. Map of the Mexican type localities of *Durangites* Burckhardt, 1912 and *Parrasiella* gen. nov.

Systematic paleontology

All dimensions of specimens are given in millimetres: Dmax = larger measurable diameter, D = diameter, Wh = whorl height, U = umbilical diameter. Ratios such as Wh/D and U/D are dimensions as a percentage of the diameter at the point of measurement. The suture terminology is that of Korn et al. (2003). The bed numbers for the Le Chouet section follow that of Wimbledon et al. (2013) and Bulot et al. (2014) as shown on Fig. 1.

Acronyms. Unless otherwise mentioned, all specimens are deposited in the Frau/Bulot collection at the *Musée Paléontologique de Provence* (MPP) of Aix-Marseille University. Other specimens studied herein are deposited in the paleontological collections of the Universidad Nacional Autonoma de Mexico (UNAM), University of Michigan (U.M.) and University of Lyon-1 (FSL).

Order: **Ammonitida** Fisher, 1882
Suborder: **Ammonitina** Fisher, 1882
Superfamily: **Perisphinctoidea** Steinmann, 1890
Family: **Himalayitidae** Spath, 1925
Genus: *Durangites* Burckhardt, 1912

Type species: *Durangites vulgaris* Burckhardt, 1912, by subsequent designation of Cantú-Chapa (1968, p. 22).

When introducing his new genus, Burckhardt (1912) did not designate a type species. The subsequent designation as type species of *Durangites acanthicus* Burckhardt, 1912 by Roman (1938, p. 323) is invalid under article 67.5 of the I.C.Z.N. As already pointed out by Cantú-Chapa (1968, p. 22) and Verma & Westermann (1973, p. 253–254), *Durangites acanthicus* is a problematic species based on a single, incomplete and poorly preserved specimen that only shows two of the four ornamental stages that characterize the genus *Durangites* as it was originally defined by Burckhardt (1912, p. 144).

On the contrary, re-examination of the well-preserved type series of *Durangites vulgaris* shows that this species exhibits the four ornamental stages that were given in the original definition. As a consequence, the designation of *D. vulgaris* as type species of *Durangites* by Cantú-Chapa (1968, p. 22) should be considered as valid, albeit for the wrong reasons.

The lectotype (UNAM IGM 504) of *D. vulgaris* Burckhardt (1912, pl. 37, figs. 1, 2, 5, 18, refigured herein Fig. 3B) by subsequent designation of Tavera (1985, p. 158) is unfortunately lost (Moreno-Bedmar, personal communication, 2014). According to article 72.4 of the I.C.Z.N., the type series is composed by all the specimens figured by Burckhardt (1912) on pl. 37, figs. 1–35 and pl. 38, figs. 1–4, as well as any other specimen mentioned in the text. For the reasons given above, we designate as neotype the specimen UNAM IGM 504a of Burckhardt (1912, pl. 37, figs. 3, 4, 6, 9), re-illustrated herein (Fig. 3B). This designation is in agreement with article 75.3 of the I.C.Z.N.

Emended diagnosis: Small-sized planulate ammonites with a compressed shell and a deep evolute umbilicus ($0.34 < U/D < 0.45$). Rounded to sub-quadrate whorl section with well-defined umbilical wall. When preserved, body chamber generally occupies almost half of the last whorl. Ornamentation varies through ontogeny and three different stages can be recognized.

Primary stage ($D < 10$ mm) characterized by straight and fine ribs, simple or bifurcate on the upper third of the flank; feeble lateral and small ventro-lateral tubercles; deep smooth ventral sulcus ("*stade microcanthus*" and "*stade Köllikeri*" of Burckhardt).

Secondary stage marked by straight simple and intercalatory ribs mostly divided on upper part of the flank; dis-

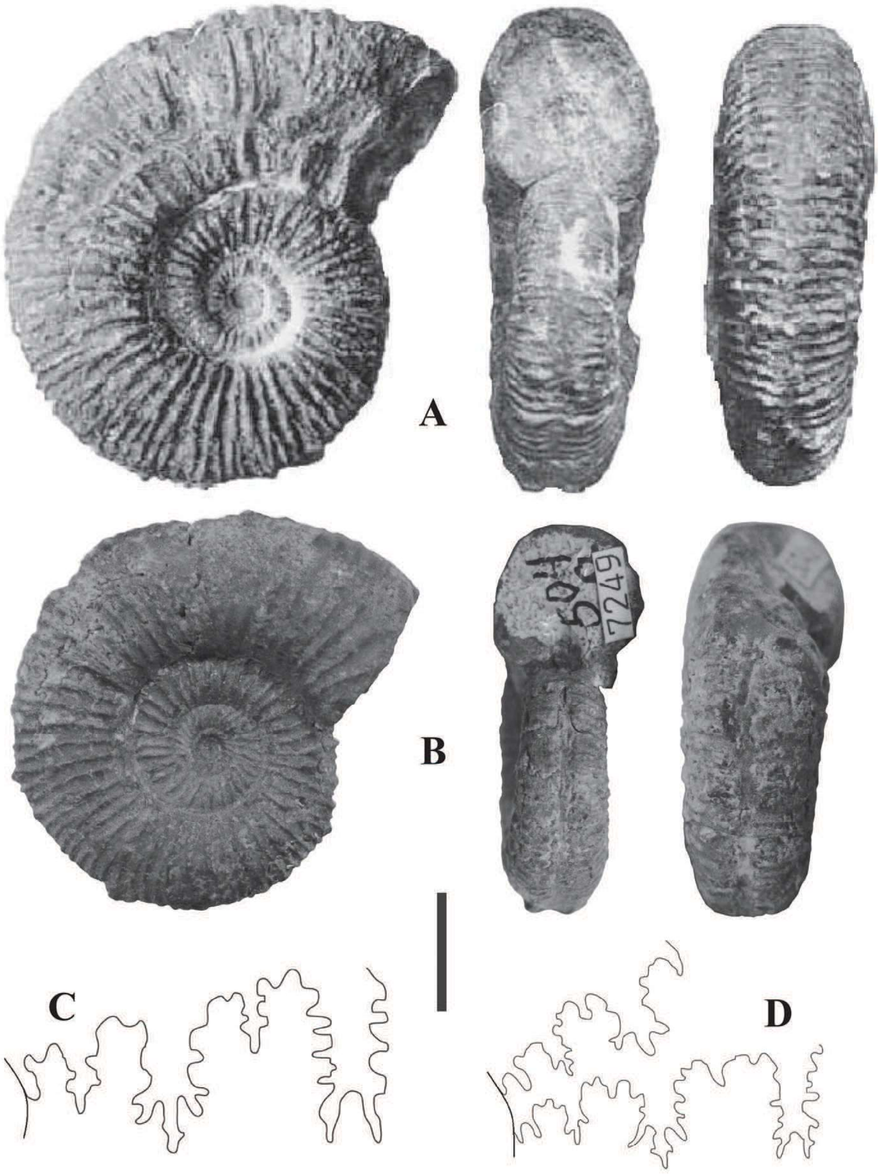


Fig. 3. *Durangites vulgaris* Burckhardt, 1912. **A** — the lost lectotype of *D. vulgaris* reproduced after Burckhardt (1912, pl. 37, figs. 1, 2, 5); **B** — the neotype IGM 504a, MPIG; **C** — suture line (×2) of the lost lectotype reproduced after Burckhardt (1912, pl. 37, fig. 18); **D** — suture line (×2) of the neotype reproduced after Burckhardt (1912, pl. 37, fig. 6). Bar scale is 10 mm.

appearance of lateral tubercles; development of prominent radially elongated ventro-lateral tubercles; smooth ventral furrow ("*stade typique*" of Burckhardt).

Final stage characterized by mostly divided radiate to rursiradiate ribs; progressive disappearance of the ventro-lateral tubercles and replacement of smooth ventral furrow by a flattened ventral band with weakened ribs that may curve adorally ("*stade adulte*" of Burckhardt).

Suture line simple with bifid external lobe and trifid adventive lobe; large asymmetrical external saddle with higher external branch (Fig. 3C and D).

Dimorphism: The existence of dimorphic pairs in Mexican *Durangites* was suggested by Verma & Westermann (1973, p. 254). A re-examination of the material illustrated by Burckhardt (1912) allows us to distinguish two morphotypes.

A first group of small-sized forms (Dmax <40 mm) match perfectly the diagnosis of the genus given above. This group includes: *D. vulgaris* pro parte, *D. acanthicus*, *D. latesellatus* Burckhardt, 1912, *D. incertus* Burckhardt, 1912 and *D. nodulatus* Burckhardt, 1912.

The other morphotype encompasses larger forms (Dmax >40 mm); it is characterized by distinctive secondary and final growth stages marked by higher rib(s) densities, attenuated tubercles, an individualized ventral band throughout ontogeny, and by the scaphitoid shape to the outer whorls due to the fast growth rate of the last whorl. This group includes: *D. vulgaris* pro parte, *D. humboldti* Burckhardt, 1912, *D. densestriatus* Burckardt, 1912 and *D. fusicostatus* Burckhardt, 1912. Additionally, *D. coghlani* (Aguilera in Castillo & Aguilera, 1895) and *D. alencasteri* Verma & Westermann, 1973 also belongs to this group. *D. heilprini* (Aguilera in Castillo & Aguilera, 1895) merely corresponds to a juvenile of this group.

Even if the features that suggest the distinction of the two morphological variants strongly suggest intrageneric sexual dimorphism, the preservation of Mexican specimens allows no sign of a differentiated peristome that could support such an interpretation. Moreover, even though the great majority of the specimens were collected at Cerro de Las Liebres, Burckhardt (1912, p. 220–221) clearly stated that the thickness of the "*couches à Durangites*" of the San Pedro del Gallo area (Durango State) exceeds 100 metres. It is therefore not possible to assume that the taxa are synchronous, even though Imlay (1939, p. 15 and 18) suggested that the specimens collected by Burckhardt originated from a limited number of phosphatic limestone concretions. If so, the Mexican taxa listed above may only represent typological morphotypes of a single paleobiological species.

It should be noted that Enay et al. (1998b) proposed sexual dimorphism between the genera *Durangites* and *Protacanthodiscus*. This view is not retained herein and will be discussed below.

Specific content: In our opinion, *Durangites* should be strictly restricted in its scope to the species listed above, as illustrated by Aguilera in Castillo & Aguilera (1895), Burckhardt (1912), Verma & Westermann (1973) and Olóriz et al. (1999).

Durangites zigzagcostatus Cantú-Chapa, 2006 is based on juvenile specimens with dense ribbing that forms a chevron across the venter. These specimens most likely belong to the group of "*Kossmatia*" *victoris* (Burckhardt, 1906).

Durangites astillerensis Imlay, 1939, and the species *D. juanensis*, *D. latiumbilicatum* and *D. galeanense* described by Cantú-Chapa (1968) should be excluded from *Durangites* because they do not show the succession of ontogenetic stages which we describe above and which will be further discussed in the description of *Parrasiella* gen. nov. section of this paper. *D. vulgaris* and *D.* cf. *D. acanthicus* from Cuba illustrated by Imlay (1942, pl. 3, figs. 1, 5–7) belong to the same group. Moreover, they belong to a very specific assemblage dominated by *Salinites* Cantú-Chapa, 1968, a genus that never occurs in the classical "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of San Pedro del Gallo and Sierra de Catorce. *Durangites rarifurcatus* Imlay, 1939 also seems to be related to *Parrasiella* gen. nov.

Other records from Cuba (Myczynski, 1989) and California (Anderson, 1945) are based on material too poorly preserved for identification.

Outside the New World, *Durangites* has been reported from the Mediterranean (Enay et al. 1971; Enay & Geyssant 1975; Cecca et al. 1983; Tavera 1985), Bulgaria (Ivanov et al. 2010), India (Shome & Bardhan 2009), and the Russian Pacific coast (Sey & Kalacheva 1983). In our opinion none of these records truly belong to *Durangites*. The Mediterranean occurrences will be addressed in detail in the *Protacanthodiscus* and *Boughdiriella* gen. nov. sections of this paper. *Durangites* cf. *heilprini*, *Durangites*. sp. A and *Durangites* sp. from Kutch (India, Shome & Bardham 2009) falls into the range of variation of *Micracanthoceras brightoni* Spath, 1931. Finally, preservation of the *Durangites* sp. ind. from Primorye (Sey & Kalacheva 1983, pl. 2, fig. 5) does not allow identification at the genus level.

Occurrence: Since the work of Enay et al. (1971) and Enay & Geyssant (1975), *Durangites* has been considered as a widespread key genus defining the top of the Tithonian Stage. This view needs to be completely reconsidered in the light of the taxonomic opinions presented herein.

As herein understood, *Durangites* is a strictly Mexican genus and is a major element of the "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of Verma & Westermann (1973): an assemblage that was originally considered to be a late Tithonian fauna, based on the study of the Caja Formation (Sierra de Catorce). According to the preliminary revision of Olóriz et al. (1999), *Durangites* is restricted and dominant in the upper part of the Caja Formation where it co-occurs with less frequent *Substeueroceras* and rare "*Kossmatia*". Calibration with calpionellids at this locality indicates a late early to middle Berriasian age for this fauna (Olóriz et al. 1999). A *Substeueroceras-Durangites* assemblage was also reported by Adatte et al. (1994a,b, 1996) just below the *Crassicollaria/Calpionella* zones boundary *sensu* Remane et al. (1986). Therefore, the first occurrence of *Durangites* in the late late Tithonian cannot be ruled out. Nevertheless, it should be noted that the base of the *Calpionella* Zone is ill defined in the sections studied (Adatte et al., 1996, p. 679) and that with the exception of a single doubtful specimen (*Durangites* sp. in Adatte et al. 1994b, pl. 2, fig. 5) the fauna is still to be formally documented.

Genus **Parrasiella** gen. nov.

Type species: *Durangites astillerensis* Imlay, 1939.

Derivation of name: From Sierra de Parras, a north-central region of Mexico.

Diagnosis: Small-sized discoidal ammonite with a shallow and wide open umbilicus ($0.40<U/D<0.47$). Sub-rounded to ovate whorl section, with convex flank. Body chamber generally occupies almost half of the last whorl. Highly distinctive ornamentation of bifurcated and parabolic ribs at the end of the phragmocone. Posterior branches of bifurcate ribs marked by radially elongated ventro-lateral tubercles that delimit a shallow ventral band. Body chamber ornamentation composed of bifurcate and simple rursiradiate ribs that cross the venter with a slightly weakening.

Specific content: Beside the type species, *Parrasiella* gen. nov. comprises *Durangites rarifurcatus* Imlay, 1939; *Durangites galeanense* Cantú-Chapa, 1968; *Durangites latiumbilicatum* Cantú-Chapa, 1968 and *Durangites juanensis* Cantú-Chapa, 1968.

Remarks: The type species of *Parrasiella* gen. nov. has previously been included in the genus *Durangites* following the work of Imlay (1939, 1942) and Cantú-Chapa (1968). As herein understood, the genus *Parrasiella* differs by its evolute coiling, shallow umbilicus, rounded whorl section throughout ontogeny and the regular disposition of ventro-lateral tubercles on the phragmocone. In the literature, the type species of *Parrasiella* gen. nov. has been reported from the western Tethys (Boughdiri 1994; Enay et al. 1998b;

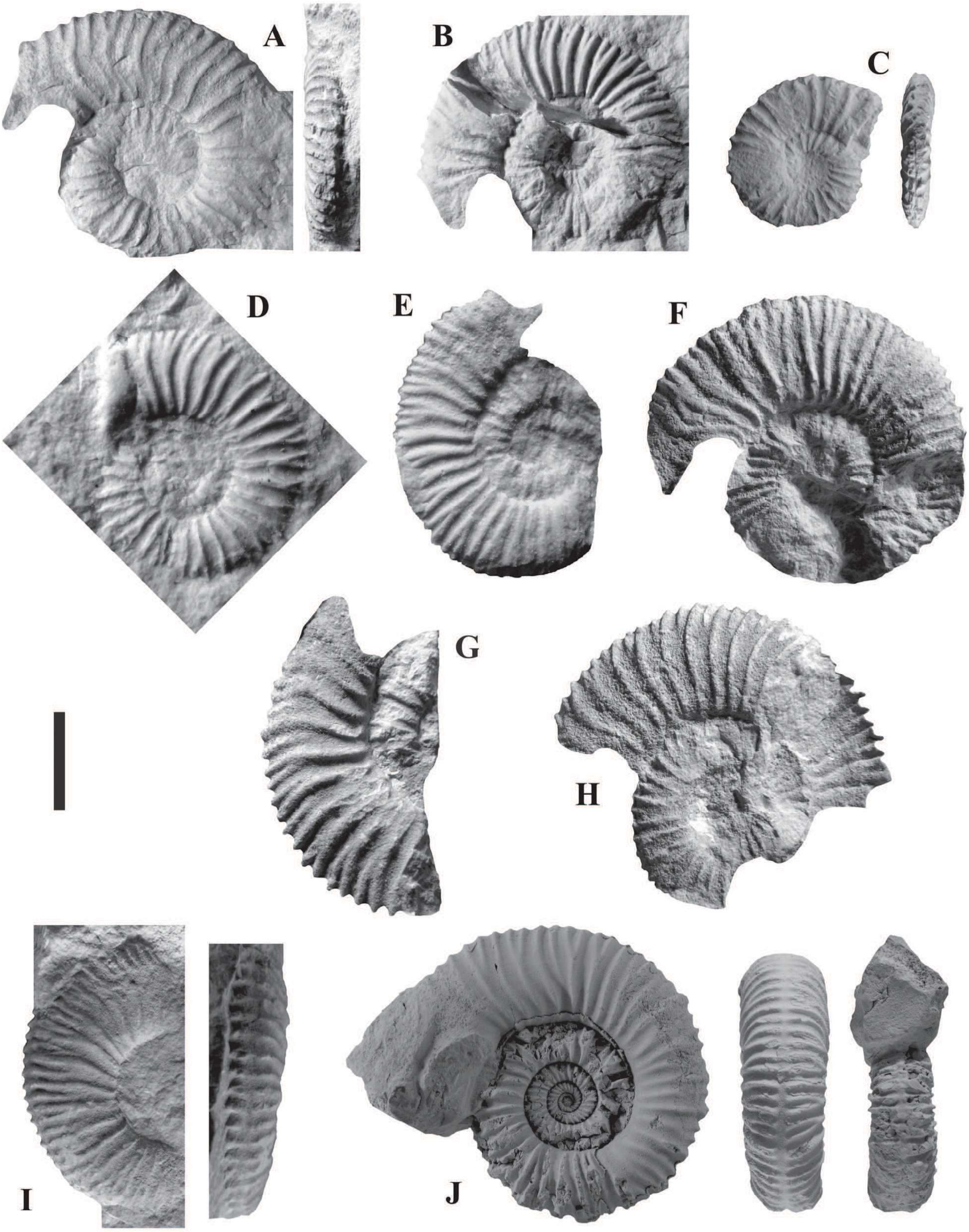


Fig. 4. *Boughdiriella chouetensis* gen. and sp. nov. from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A —** Holotype MPP-CHT.19/26 [m] (bed 83); **B —** MPP-CHT.18/12 [m] (bed 82); **C —** MPP-CHT.21/94 [m] (bed 85); **D —** MPP-CHT.21/93 [m] (bed 85); E — MPP-CHT.21/33 [m] (bed 85); **F —** MPP-CHT.19/29 [m] (bed 83); **G —** MPP-CHT.21/64 [m] (bed 85); **H —** MPP-CHT.21/23 [m] (bed 85); **I —** MPP-CHT.19/16 [?m] (bed 83); **J —** Lateral and ventral views of the holotype (U.M. 17707) of *Parrasiella astillerensis* (Imlay 1939, pl. 10, figs. 10–12) from Mexico (Sierra de Parras, Coahuila). Bar scale is 10 mm.

Ivanov et al. 2010). In our view, none of the specimens illustrated are actually of the Mexican species: these will be discussed in the *Boughdiriella* gen. nov. section of this paper.

Occurrence: According to Imlay (1939, p. 5), *Parrasiella astillerensis* co-occurs with *Salinites grossicostatum* (Imlay, 1939), *Salinites ecarinatum* (Imlay, 1939), and misidentified *Durangites* cf. *acanthicus*. At locality K2, Imlay (1939) reported *Durangites rarifurcatus* in association with *Salinites*. In Mexico, *D. galeanense*, *D. latiumbilicatum* and *D. juanensis* were also described in association with *S. grossicostatum* by Cantú-Chapa (1968).

The age of the *Salinites* Cantú-Chapa, 1968 and *Parrasiella* gen. nov. assemblage is unclear and the two genera are not members of the classical "*Kossmatia*"–*Durangites*–"*Corongoceras*" assemblage of San Pedro del Gallo and Sierra de Catorce (Mexico).

In Cuba, Myczynski (1999) reports *Salinites* at the base of the upper part of the La Zarza member above the "*Vinalesites*–*Protancyloceras*" assemblage, and from the El Americano member. According to Myczynski & Pszczółkowski (1994) and Myczynski (1999), both units are of late Tithonian age based on the presence of tintinnoids. However, this age has been much debated (see Cobiella-Reguera & Olóriz 2009, with references). According to the last-cited authors, the upper part of the El Americano member belongs to the upper *Crassicollaria* and/or *Calpionella* zones, and that indicates a late late Tithonian to early middle Berriasian age.

Parrasiella astillerensis (Imlay, 1939)
Fig. 4J

1939 *Durangites astillerensis* n. sp. — Imlay, p. 46, pl. 10, figs. 10–12

Types: by original designation, According to Imlay (1939, p. 46), the holotype is the specimen U.M. 17707. It is herein re-illustrated (Fig. 4J). Imlay (1939) designated as paratype another specimen (U.M. 20008).

Type locality: Both specimens originate from locality 34 of Imlay (1939) in the Sierra de Parras (Coahuila, north-central Mexico) from the La Casita formation.

Remarks: The type specimen of *Parrasiella astillerensis* bears long lateral necked lappets. It should be noted that the other species are only known from a few specimens with no aperture visible. In our view, *P. latiumbilicatum* and *P. juanensis* described by Cantú-Chapa (1968) are closely related to, if not synonyms of, *Parrasiella astillerensis.* It should be noted that the ornamentation of the early whorls of *P. astillerensis* matches well that seen in *P. rarifurcatus* and *P. galeanense.* Both taxa are characterized by a larger adult size, but their apertures are unknown. Pending new studies on the Mexican faunas, these species could represent the macroconch of *P. astillerensis.*

Occurrence: *Parrasiella astillerensis* occurs in north-central Mexico and western Cuba. As discussed above the precise age of *P. astillerensis* is disputed.

Genus *Boughdiriella* gen. nov.

Type species: *Boughdiriella chouetensis* gen. et sp. nov.

Derivation of name: Dedicated to Mabrouk Boughdiri, Head of the Geological Sciences Department of Bizerte University (Tunisia), for his contribution to the systematics of late Tithonian ammonites.

Diagnosis: Small-sized dimorphic ammonites with a discoidal and evolute shell. Sub-circular whorl section in inner whorls; compressed sub-oval whorl section in adult. Shallow and moderately open umbilicus. Umbilical wall slightly convex. Ornamentation of inner whorls (up to D ~ 10 mm) composed by rigid, straight, simple ribs. From D ~ 15 mm to the end of the body chamber, ribs flexuous, prominent and bifurcated on the upper third of the flanks. Scarce trifurcate, and intercalated ribs. Venter marked by a shallow furrow. The suture line is unknown.

Remarks: Understanding of the "Mediterranean *Durangites*" has been based on a limited number of specimens illustrated by Cecca et al. (1983), Tavera (1985), Boughdiri (1994), Enay et al. (1998b), and Ivanov et al. (2010), specimens that were referred to *D. vulgaris* and/or *Parrasiella astillerensis*. Detailed examination of the important material collected at Le Chouet shows that the similarities to *Durangites* and *Parrasiella* gen. nov. are only superficial. Both genera differ in their marked tuberculated stage on the ventral area, distinctive whorl sections and steep umbilical margin.

Occurrence: *P. andreaei* Zone (base of the calpionellid *C. colomi* Subzone), late Tithonian. *Boughdiriella* gen. nov. is known from Spain (Tavera, 1985), South East France (Boughdiri 1994; Enay et al. 1998b — this paper) and Bulgaria (Ivanov et al. 2010). Potential occurrence in Tunisia (Boughdiri et al. 1999), Turkey (Enay et al. 1971), Italy (Sarti, 1995) and Morocco (Benzaggagh & Atrops 1997, p. 158) needs to be illustrated.

Boughdiriella chouetensis nov. sp.
Fig. 4A–I

1985 *Durangites acanthicus* Burckhardt — Tavera, p. 156, pl. 18, fig. 11
1994 *Durangites* (*Durangites*) n. sp. 5 — Boughdiri, p. 123–128, pl. 1, figs. 24, 28–32
1994 *Durangites* (*Durangites*) *astillerensis* Imlay — Boughdiri, pl. 1, figs. 20–23
1998b *Durangites* (*Durangites*) gr. *astillerensis* Imlay — Enay et al., fig. 2, n° 17
1998b *Durangites* (*Durangites*) *astillerensis* Imlay — Enay et al., fig. 2, n° 12
1998b *Durangites* (*Durangites*) aff. *astillerensis* Imlay — Enay et al., fig. 2, n° 1–3
1998b *Durangites* (*Durangites*) *vulgaris* Burckhardt — Enay et al., fig. 2, n° 4
1998 *Durangites* (*Durangites*) sp. — Enay et al., fig. 2, n° 5
2010 *Durangites* (*Durangites*) aff. *astillerensis* Imlay — Ivanov et al., pl. 3, fig. 5

Type: The holotype is the specimen MPP-CHT.21/65 herein illustrated on Fig. 2A.

Paratypes: MPP-CHT.18/12, MPP-CHT.21/17, MPP-CHT.21/18, MPP-CHT.21/23, MPP-CHT.19/29, MPP-CHT.21/28, MPP-CHT.21/29, MPP-CHT.21/33.

Derivation of name: After Le Chouet.

Type locality: Le Chouet, near Les Près (Drôme, France).

Diagnosis: Small-sized dimorphic ammonites with a discoidal and evolute shell. Sub-circular whorl section in inner whorls; compressed sub-oval whorl section in adult. Shallow and moderately open umbilicus. Umbilical wall slightly convex. Ornamentation of inner whorls (up to D ~10 mm) composed by rigid, straight, simple ribs. From D ~15 mm to the end of the body chamber, ribs flexuous, prominent and bifurcated on the upper third of the flanks. Scarce trifurcate, and intercalated ribs. Venter marked by a shallow furrow. The suture line is unknown.

Measurements: See Table 1.

Remarks: Although there is no significant ornamental and/or size difference between micro- and macroconchs, sexual dimorphism is recognizable. Microconchs are characterized by short lateral lappets (Fig. 4A,B,D and E) while macroconchs show a collared aperture (Fig. 4F,G and H).

Compared to *Durangites vulgaris*, *Boughdiriella chouetensis* gen. et sp. nov. is easily distinguished by its compressed sub-rectangular whorl section and the absence of a short stage with tubercles on the venter.

Specimens of *B. chouetensis* illustrated in the literature have generally been assigned to *Parrasiella astillerensis*. That species differs in its open umbilicus, sub-oval whorl section, and a phragmocone end that has a prominent and long tuberculated section on its venter. The phragmocone — body chamber transition is marked by 'pinched' ventro-lateral tubercles.

Hegaratia busnardoi Patrulius & Avram, 1976 shows some superficial similarities to *B. chouetensis*, but it can be easily distinguished by its higher U/D ratio, coarse bifurcate ribs and lateral constrictions.

Berriasella (*Picteticeras*) *jauberti* (Mazenot, 1939) shows morphological similarities with *B. chouetensis,* but differs in its larger adult size (60 to 85 mm), evolute coiling, sub-rectangular whorl section throughout ontogeny and higher rib density.

Occurrence: As for the genus. At Le Chouet, *B. chouetensis* occurs at the top (e.g. beds 82 to 85) of the *P. andreaei* Zone (base of the calpionellid *C. colomi* Subzone), late Tithonian.

Genus *Protacanthodiscus* Spath, 1923

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

Emended diagnosis: Middle to large-sized (Dmax < 165 mm) dimorphic ammonites with an open ($0.40 < U/D < 0.50$) and relatively deep umbilicus in the adult stage. Subcircular whorl section, with convex flanks on juveniles, which become progressively sub-rectangular to sub-hexagonal on adults. Ornamentation mainly composed of bifurcate, and trifurcate ribs with a tubercle at the furcation point. Some ribs can be looped. On the body chamber, bifurcate ribs are ended on the ventral shoulder by a latero-ventral tubercle on the first, or occasionally the second, branch. Ventral area marked by a more or less flattened ventral band, depending on the shape of the whorl section. Suture line is simple with large trifid lateral lobe, which is as deep as the external lobe.

Dimorphism: Roman (1936, p. 22) gave the first diagnosis of *Protacanthodiscus*, subsequently emended by Tavera (1985, p. 197). In the opinion of the latter author, *Protacanthodiscus* is a dimorphic genus. In his unpublished thesis, Boughdiri (1994) reconsidered the systematic content of *Protacanthodiscus* and included it as a subgenus of *Durangites* accommodating macroconch forms. Subsequently, Boughdiri (personal communication, 2011) suggested that the "Mediterranean *Durangites*" figured by Tavera (1985) could be: "*inner whorls and/or juveniles of other species that would belong to other closely allied genera*" (english translation). The present study supports this opinion (see synonymy list of *Protacanthodiscus andreaei*). Moreover, the comparatively expanded succession at Le Chouet shows that the first occurrence of *Protacanthodiscus* occurs at a lower level than that of *Boughdiriella* gen. nov., that was until now regarded as a "Mediterranean *Durangites*".

Table 1: Measurements of *Boughdiriella chouetensis* gen. and sp. nov. U/D and Wh/D ratios are dimensions as a percentage of the diameter at the point of measurement.

Specimen	D	Wh	U	U/D	Wh/D
CHT 19–26	28	9	11	0.39	0.32
CHT 19–16	29	11	12	0.41	0.38
CHT 19–19	/	12	18	/	/
CHT 19–26	28	9	11	0.39	0.32
CHT 19–29	36	11	15	0.42	0.31
CHT 18–12	26	8.5	9.5	0.37	0.33
CHT 21–22	30	10	13	0.43	0.33
CHT 21–23	/	12	18	/	/
CHT 21–24	38	12	17	0.45	0.32
CHT 21–64	/	11	/	/	/
CHT 21–83	20	7	8	0.40	0.35
CHT 21–93	29	11	13	0.45	0.38
CHT 21–94	18.5	6	8	0.43	0.32

The hypothesis of sexual dimorphism between true *Durangites* and *Protacanthodiscus* is also to be ruled out in Mexico, where no *Protacanthodiscus stricto sensu* have been collected in association with *Durangites* (see Verma & Westermann 1973). Contrary to the opinion of Boughdiri (1994) and Enay et al. (1998b), we consider that *Acanthodiscus euthymiformis* Burckhardt, 1912 and *Acanthodiscus transatlanticus* Burckhardt, 1912 cannot be included in *Protacanthodiscus.*

Remarks: Spath (1923, p. 305) introduced the genus *Protacanthodiscus* (based on *Hoplites andreaei* Kilian, 1889) without diagnosis and specific content. When creating the family Himalayitidae (Spath, 1925, p. 144), Spath included *Hoplites incompositus* Retowski, 1893 in *Protacanthodiscus.* This species has since been transferred to the Neocomitidae (Bogdanova et al. 1984; Khimchiashvili 1989); and the description and the original figure leave no doubt that the *H. incompositus* is a neocomitid species.

Tavera (1985), considered that *Hoplites heterocosmus* Canavari, 1899 and *Hoplites bonarellii* Canavari, 1899 belong to *Protacanthodiscus*, and he described four news species from the Betic Cordilleras: *Protacanthodiscus coronatus* Tavera, 1985; *P. darwini* Tavera, 1985; *P. nodosus* Tavera, 1985; and *P. berriasensis* Tavera, 1985.

The expanded conception of *Protacanthodiscus* of Boughdiri (1994) was only partly accepted by Enay et al. (1998a,b) and Boughdiri et al. (1999). Despite the introduction of *Kilianites* by Enay et al. (1998c) (type species: *P. canavarii* Enay, Boughdiri & Le Hégarat, 1998c) and *Hegaratites* Boughdiri, Enay & Le Hégarat, 1999 (type species: *Hegara-*

tites rheouisensis Boughdiri, Enay & Le Hégarat, 1999); the exact content of *Protacanthodiscus* remained unclear for those authors.

Based on the material at our disposal, we consider that *P. andreaei* shows a large morphological intraspecific variability that encompass the typological species *P. coronatus*, *P. darwini* and *P. nodosus*. Further, examination of *Neoperisphinctes falloti* Tavera (non Kilian, 1889); *Durangites singularis* Tavera, 1985; *Durangites sutneroides* Tavera, 1985; *D. gigantis* Tavera, 1985 and *Durangites apertus* Tavera, 1985, suggest that these species also fall in the range of variation of *Protacanthodiscus andreaei*.

Contrary to the opinions of Boughdiri (1994) and Enay et al. (1998b), we consider that *Hoplites macphersoni* Kilian, 1889 and *H. malladae* Kilian, 1889 are in need of a proper revision and cannot be included in *Protacanthodiscus*. This is also the case for *Hoplites heterocosmus* and *H. bonarellii,* originally described by Canavari (1899).

Occurrence of *Protacanthodiscus* in the New World is based on material described by Steuer (1897), Anderson (1945), Leanza (1945, 1968), Rivera (1951), Cantú-Chapa (1967) and Imlay & Jones (1970). As already suggested by Klein (2005), the taxonomy of those forms is doubtful. Examination of the type material of *Hoplites quadripartitus* Steuer, 1897, *Protacanthodiscus pacificum* Rivera, 1951 and *P. puenteingaensis* Rivera, 1951 has convinced us that these species are homeomorphic with true *Protacanthodiscus* and that they deserve a generic status in their own right. This systematic problem will be addressed elsewhere, as part of the revision of the fauna from the Puente Inga formation (Lima Coast, Peru).

Specific content: *Protacanthodiscus andreaei* (and its synonyms: *Hoplites* (*Acanthodiscus*) *andreaei* Kilian *var. punica* Pervinquière, 1907; *Protacanthodiscus coronatus*, *P. darwini*, *P. nodosus*, *Durangites singularis*, *D. sutneroides*, *D. gigantis*, and *D. apertus*), *P. savornini* (Roman, 1936), *Protacanthodiscus berriasensis* and "*Corongoceras*" *hexagonus* Tavera, 1985.

Occurrence: At Le Chouet, *Protacanthodiscus* is restricted to the uppermost Tithonian (top of the calpionellid *C. intermedia* Subzone and lower part of the *C. colomi* Subzone). In Spain, occurrence of *P. berriasensis* in the *E. cularensis* horizon (base of the *B. jacobi* Zone) suggests that the genus occurs as a rarity in the middle part of the *C. colomi* Subzone. To our knowledge, the genus is reported from SE France, Italy, Spain, Bulgaria, Morocco, Tunisia and Algeria.

Protacanthodiscus andreaei (Kilian, 1889)
Figs. 5A–L, 6A–E and 7A–C

1889 *Hoplites Andreaei* — Kilian, p. 670, pl. 32, fig. la,b

1889 *Hoplites* (*Acanthodiscus*) *Andreaei* Kilian var. *Punica* — Pervinquière, p. 38, pl. 2, fig. l2a,b

pars 1939 *Berriasella Andreaei* (Kilian) — Mazenot, p. 96, pl. 12, fig. la,b, non fig. 4a,b

non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* (Kilian) — Collignon, pl. CLXV, fig. 665

non 1960 *Berriasella* (*Protacanthodiscus*) aff. *andreaei* var. *variabilis* Collignon, pl. CLXV, figs. 666, 667

?1960 *Protacanthodiscus andreaei* (Kilian) — Christ, p. 125, pl. 9, fig. 5

1979 *Protacanthodiscus andreaei* (Kilian) — Sapunov, p. 1985, pl. LVII, fig. 6

1983 *Durangites acanthicus* Burckhardt — Cecca et al., p. 128, pl. 5, fig. 1a,b

1985 *Protacanthodiscus andreaei* (Kilian) — Tavera, p. 198, pl. 26, figs. 5a,b, 6, text-fig. 15H

1985 *Protacanthodiscus* sp. 1 gr. *andreaei* (Kilian) — Tavera, p. 199, pl. 26, figs. 1a,b, 2, text-fig. 15E,I, text-fig. 12H

1985 *Protacanthodiscus berriasensis* n. sp. — Tavera, p. 206, pl. 26, fig. 1a,b, pl. 28, fig. 1a,b, text-fig. 15D

1985 *Protacanthodiscus coronatus* n. sp. — Tavera, p. 200, pl. 27, fig. 1a,b, text-fig. 15A

1985 *Protacanthodiscus darwini* n. sp. — Tavera, p. 203, pl. 26, figs. 3, 4, text-fig. 15B

1985 *Protacanthodiscus nodusus* n. sp. — Tavera, p. 202, pl. 27, fig. 2, text-fig. 15C

1985 *Durangites singularis* n. sp. — Tavera, p. 168, pl. 17, figs. 6–9, text-fig. 12E

pars 1985 *Durangites sutneroides* n. sp. —Tavera, p. 168, pl. 18, figs. 1, 2, 3, 5, non fig. 4a,b

1985 *Durangites heilprini* (Aguilera) — Tavera, p. 164, pl. 18, figs. 6, 7, text-fig. 12G

1985 *Durangites gigantis* n. sp. — Tavera, p. 162, pl. 18, figs. 8, 9, text-fig. 12A,B

1985 *Durangites acanthicus* Burckhardt — Tavera, p. 156, pl. 18, figs. 10a,b, 11, text-fig. 12C

1985 *Durangites vulgaris* Burckhardt — Tavera, p. 157, pl. 18, figs. 12, 13a,b, text-fig. 12I

1985 *Durangites apertus* n. sp. — Tavera, p. 161, pl. 18, figs. 14, 15a,b, text-fig. 12F

1985 *Durangites* cf. *astillerensis* Imlay — Tavera, p. 166, pl. 18, fig. 16, text-fig. 12D

1985 *Neoperisphinctes falloti* (Kilian) — Tavera, p. 132, pl. 16, fig. 10a,b

1994 *Protacanthodiscus* (*Protacanthodiscus*) *andreaei* (Kilian) — Boughdiri, p. 147, pl. 3, figs. 1a,c, 3a,b, pl. 4, fig. 2

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. A — Boughdiri, p. 208, pl. 3, fig. 5

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 3 — Boughdiri, p. 168, pl. 3, fig. 7

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 4 — Boughdiri, p. 170, pl. 2, fig. 17

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 7 — Boughdiri, p. 176, pl. 3, fig. 2

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 11 — Boughdiri, p. 186, pl. 3, fig. 6

1994 *Protacanthodiscus* (*Protacanthodiscus*) n. sp. 12 — Boughdiri, p. 188, pl. 4, fig. 1

1994 *Protacanthodiscus* (*Protacanthodiscus*) *coronatus* (Tavera) — Boughdiri, p. 151, pl. 4, figs. 6, 7

1994 *Durangites* (*Durangites*) *humboldti* (Burckhardt) — Boughdiri, p. 99, pl. 1, figs. 33a,b, 34

1994 *Durangites* (*Durangites*) *juanense* (Cantú-Chapa) — Boughdiri, p. 106, pl. 1, fig. 34

1998b *Durangites* (*Protacanthodiscus*) *andreaei* (Kilian) — Enay et al., figs. 2, n° 16a,b (= Kilian, 1889, pl. 32, fig. la,b)

1998b *Durangites* (*Durangites*) *juanensis* Cantú-Chapa — Enay et al., figs. 2, n° 6, 7 (= Boughdiri, 1994, pl. 1, fig. 35)

1998b *Durangites* (*Durangites*) *humboldti* Burckhardt — Enay et al., figs. 2, n° 8–10a,b

1998b *Durangites* (*Protacanthodiscus*) sp. — Enay et al., figs. 2, n° 11

1998b *Durangites* (*Protacanthodiscus*) *apertus* (Tavera) — Enay et al., figs. 2, n° 13–14

2010 *Protacanthodiscus* cf. *andreaei* (Kilian) — Ivanov et al., pl. 3, fig. 3

2010 *Durangites* aff. *fusicostatus* Burckhardt — Ivanov et al., pl. 3, fig. 1a,b

2010 *Durangites* cf. *vulgaris* Burckhardt — Ivanov et al., pl. 3, fig. 2a,b

2010 *Durangites singularis* Tavera — Ivanov et al., pl. 3, fig. 4

2010 *Protacanthodiscus apertus* (Tavera) — Benzaggagh et al., fig. 5i

2010 *Durangites humboldti* Burckhardt — Benzaggagh et al., fig. 5n

non 2013 *Protacanthodiscus coronatus* (Tavera) — Szives & Főzy, p. 301, pl. 1, figs. 2, 4 (= Himalayitidae gen. nov. et sp. nov.)

non 2013 *Protacanthodiscus andreaei* (Kilian) — Szives & Főzy, p. 300, pl. 5, fig. 4a,b, pl. 6, fig. 5a,b, pl. 8, fig. 10a,b (= Himalayitidae gen. nov. et sp. nov.)

non 2013 *Protacanthodiscus andreaei* (Kilian) — Főzy & Scherzinger, p. 257 (= Himalayitidae gen. nov. et sp. nov.)

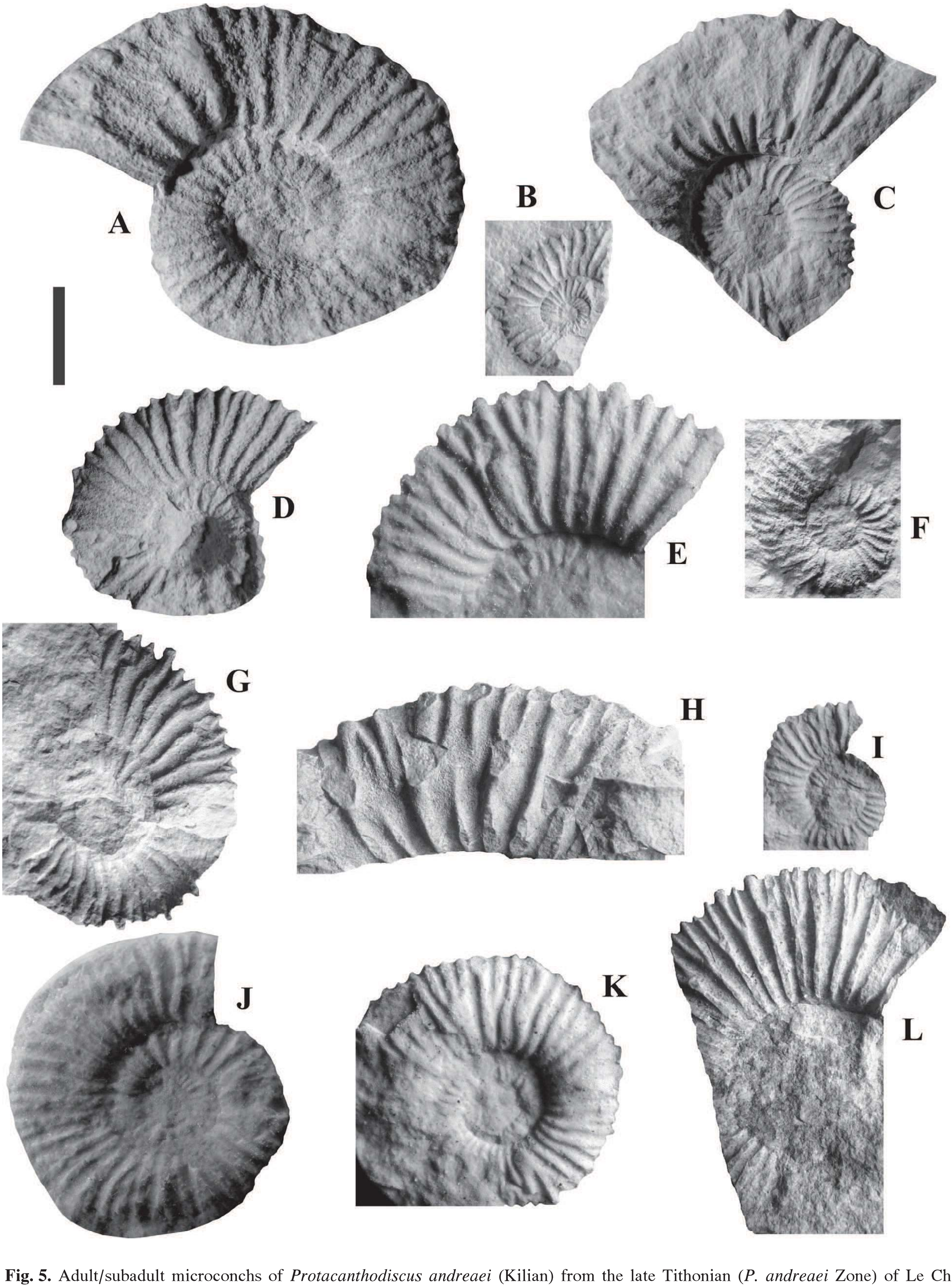


Fig. 5. Adult/subadult microconchs of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A** — MPP-CHT.21/57 (bed 85), **B** — MPP-CHT.21/87 (bed 85), **C** — MPP-CHT.19/13 (bed 83), **D** — MPP-CHT.21/25 (bed 85), **E** — MPP-CHT.18/20 (bed 82), **F** — MPP-CHT.21/31 (bed 85), **G** — MPP-CHT.19/24 (bed 83), **H** — MPP-CHT.15/06 (bed 79), **I** — MPP-CHT.21/19 (bed 85), **J** — MPP-CHT.21/96 (bed 85), **K** — MPP-CHT.19/34 (bed 83), **L** — MPP-CHT.15/21 (bed 79). Bar scale is 10 mm.

Holotype: The specimen illustrated by Kilian (1889, p. 670, pl. 32, fig. la,b) from the De Verneuil collection (FSL.13056). It was re-illustrated by Enay et al. (1998b, figs. 2–16a,b).

Material: MPP-CHT.15/4, MPP-CHT.15/6, MPP-CHT.15/21, MPP-CHT.18/1, MPP-CHT.18/20, MPP-CHT.19/7, MPP-CHT.19/12, MPP-CHT.19/13, MPP-CHT.19/14, MPP-CHT.19/15, MPP-CHT.19/24, MPP-CHT.19/25, MPP-CHT.19/31, MPP-CHT.19/34, MPP-CHT.19/35, MPP-CHT.21/5, MPP-CHT.21/7, MPP-CHT.21/16, MPP-CHT.21/19, MPP-CHT.21/20, MPP-CHT.21/25, MPP-CHT.21/26, MPP-CHT.21/27, MPP-CHT.21/32, MPP-CHT.21/35, MPP-CHT.21/37, MPP-CHT.21/38, MPP-CHT.21/39, MPP-CHT.21/40, MPP-CHT.21/41, MPP-CHT.21/57, MPP-CHT.21/62.

Measurements: See Table 2.

Description: A detailed examination of the material at our disposal reveals marked sexual dimorphism. Microconchs (Dmax < 50 mm) exhibit three ontogenetic stages:

- On inner whorls (D<15 mm), the ornamentation is composed of straight, rigid, prosiradiate ribs marked by small punctiform shoulders at the furcation point;
- To D ~ 30 mm, ornamentation is irregular, composed of rigid bifurcate ribs. The furcation point is higher on the flank. The umbilical wall and margin are more abrupt. The whorls section is sub-circular;
- On the adult stage (D > 30 mm), ornamentation is characterized by marked irregular ribbing. Most of the ribs bifurcate on the mid flank with more or less strong lateral tubercles at the furcation point. Generally, on bifurcate ribs, the adoral branch is ended by a pinched ventro-lateral tubercle on the axis of the coiling. At that stage, ribs can also be simple, trifurcate, intercalated or looped. Several specimens possess regular prosiradiate and flexuous bifurcate ribs on the body chamber. At the mouth of the shell, the whorl section is more or less sub-oval to sub-rectangular.

Table 2: Measurements of *Protacanthodiscus andreaei* (Kilian). U = umbilical diameter, Wh = whorl height, D = diameter. U/D and Wh/D ratios are dimensions as a percentage of the diameter at the point of measurement.

Specimen	D	Wh	U	U/D	Wh/D
CHT 15–04	/	17.5	/	/	/
CHT 15–06	40	17	15	0.38	0.43
CHT 15–21	40	15	16	0.40	0.38
CHT 18–01	/	/	/	/	/
CHT 18–20	/	15	/	/	/
CHT 19–07	17	6	8.5	/	0.35
CHT 19–12	19	6	7	0.37	0.32
CHT 19–13	36	14.5	15	0.42	0.40
CHT 19–14	31	12	/	/	0.39
CHT 19–15	37	13	18	0.49	0.35
CHT 19–24	38	12.5	13	0.34	0.33
CHT 19–25	55	21	24	0.44	0.38
CHT 19–31	22	7	10	0.45	0.32
CHT 19–34	28.5	10.5	10	0.35	0.37
CHT 19–35	62	22	26	0.42	0.35
CHT 21–05	/	20	/	/	/
CHT 21–07	32	11	12	0.38	0.34
CHT 21–16	/	/	/	/	/
CHT 21–19	16	6	7	0.44	0.38
CHT 21–20	22	8.5	8	0.36	0.39
CHT 21–25	24	8	8.5	0.35	0.33
CHT 21–26	21	8	8	0.38	0.38
CHT 21–27	36	12	15	0.42	0.33
CHT 21–32	/	14	15.5	/	/
CHT 21–35	29.5	10.5	10	0.34	0.36
CHT 21–37	/	/	/	/	/
CHT 21–38	37	23	22	0.59	0.62
CHT 21–39	/	/	/	/	/
CHT 21–40	/	/	/	/	/
CHT 21–41	70	28	28	0.40	0.40
CHT 21–57	34	13	12.5	0.37	0.38
CHT 21–62	41	14	17	0.41	0.34

Macroconchs (Dmax up to 165 mm) also show three ontogenetic stages:

- The juvenile stage is similar to that of the microconchs;
- The intermediate stage can reach D ~ 50 mm. Compared to the microconchs, this stage is marked by dense and flexuous ribs. The furcation point is lower on the flank;
- At the adult stage, two marked morphotypes can be distinguished. (1) A slender group characterized by a dense ribbing and a sub-rectangular whorl section, higher than wide. The ribs are mainly bifurcated and the tubercles are feeble or absent. The ventral band is attenuated and the ribs can cross the venter with a shallow weakening. (2) A robust group characterized by larger size, an irregular and coarse ribbing pattern and a marked sub-hexagonal whorl section with a flattened ventral area. Trifurcate ribs are common, with massive tubercles at the furcation point.

Occurrence: Beds 79 to 85, *P. andreaei* Zone (top of calpionellid *C. intermedia* Subzone and lower part of the *C. colomi* Subzone), upper Tithonian. As outlined by Tavera (1985), the appearance and increase in abundance of the species is gradual. *P. andreaei* is reported from South East Spain and France, Italy, Bulgaria, Tunisia and Morocco. Since *D. vulgaris* Tavera *non* Burckhardt is herein considered as a microconch of *P. andreaei*, the *D. vulgaris* Zone of Sarti (1988) is a junior subjective synonym of the *P. andreaei* Zone introduced by Wimbledon et al. (2013).

Protacanthodiscus hexagonus (Tavera, 1985)
Fig. 7D

1985 "*Corongoceras*" *hexagonus* Tavera, p. 195, pl. 28, figs. 3a,b, 4a,b, text-fig. 17H

2010 *Protacanthodiscus hexagonus* Tavera — Benzaggagh et al., p. 309, figs. 5, l-m

Type: The holotype is specimen T.Co.3.1. from the Tavera collection, deposited in the collections of the University of Granada.

Material: MPP-CHT.21/7.

Description: The single specimen shows the first ontogenetic stage of the type-species of *Protacanthodiscus*. By comparison to *P. andreaei*, the intermediate stage is very reduced and the morphology that characterizes the adult stage of the robust macroconch occurs at a diameter similar to that seen in small adult microconchs. Trifurcations and lateral and ventral tubercles are prominent. The whorl section is almost sub-hexagonal.

Remarks: Tavera (1985) separated a group of "*Corongoceras*", based on "*C.*" *hexagonus*, seen as the phyletic link between *Corongoceras sensu lato* (= *Ardesciella* Bulot et al. 2014) and *Protacanthodiscus*. This view is not supported by

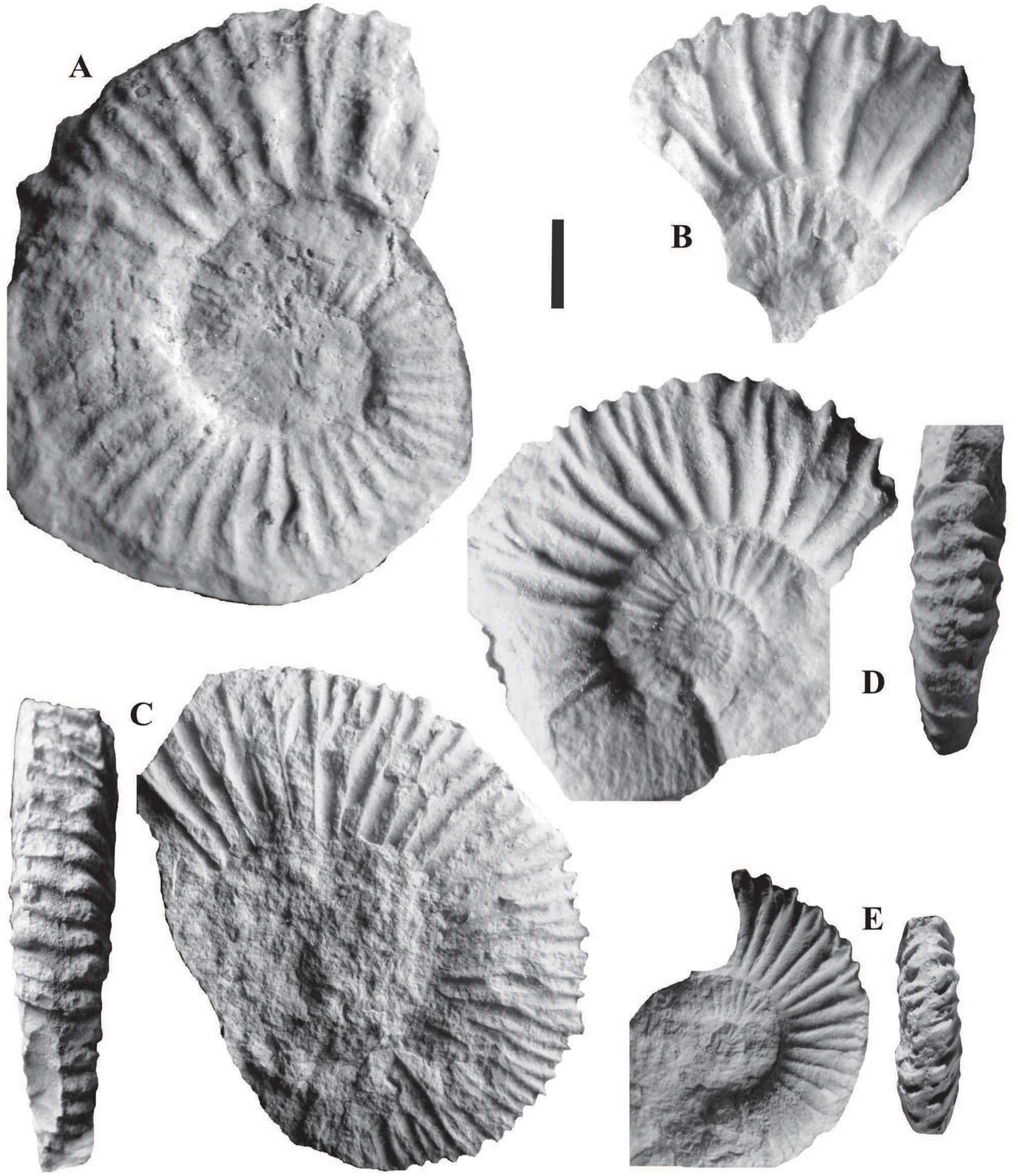


Fig. 6. Adult macroconchs of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet. **A** — MPP-CHT.21/41 (bed 85), **B** — MPP-CHT.21/5 (bed 85), **C** — MPP-CHT.21/54 (bed 85), **D** — MPP-CHT.21/5 (bed 85), **E** — MPP-CHT.21/27 (bed 85). Bar scale is 10 mm.

the observed stratigraphical fossil distribution at Le Chouet, where *P. hexagonus* co-occurs with the last *P. andreaei* at the top of the upper Tithonian. In our opinion, *P. hexagonus* present a peramorphic change combined with miniaturization. Such forms have already been documented in several perisphinctid lineages and have been called miniconchs (see discussion in Davis et al. 1996).

Occurrence: Bed 85, top of *P. andreaei* Zone (middle part of the calpionellid *C. colomi* Subzone), upper Tithonian. *P. hexagonus* is only known in southeast France, Spain and Morocco.

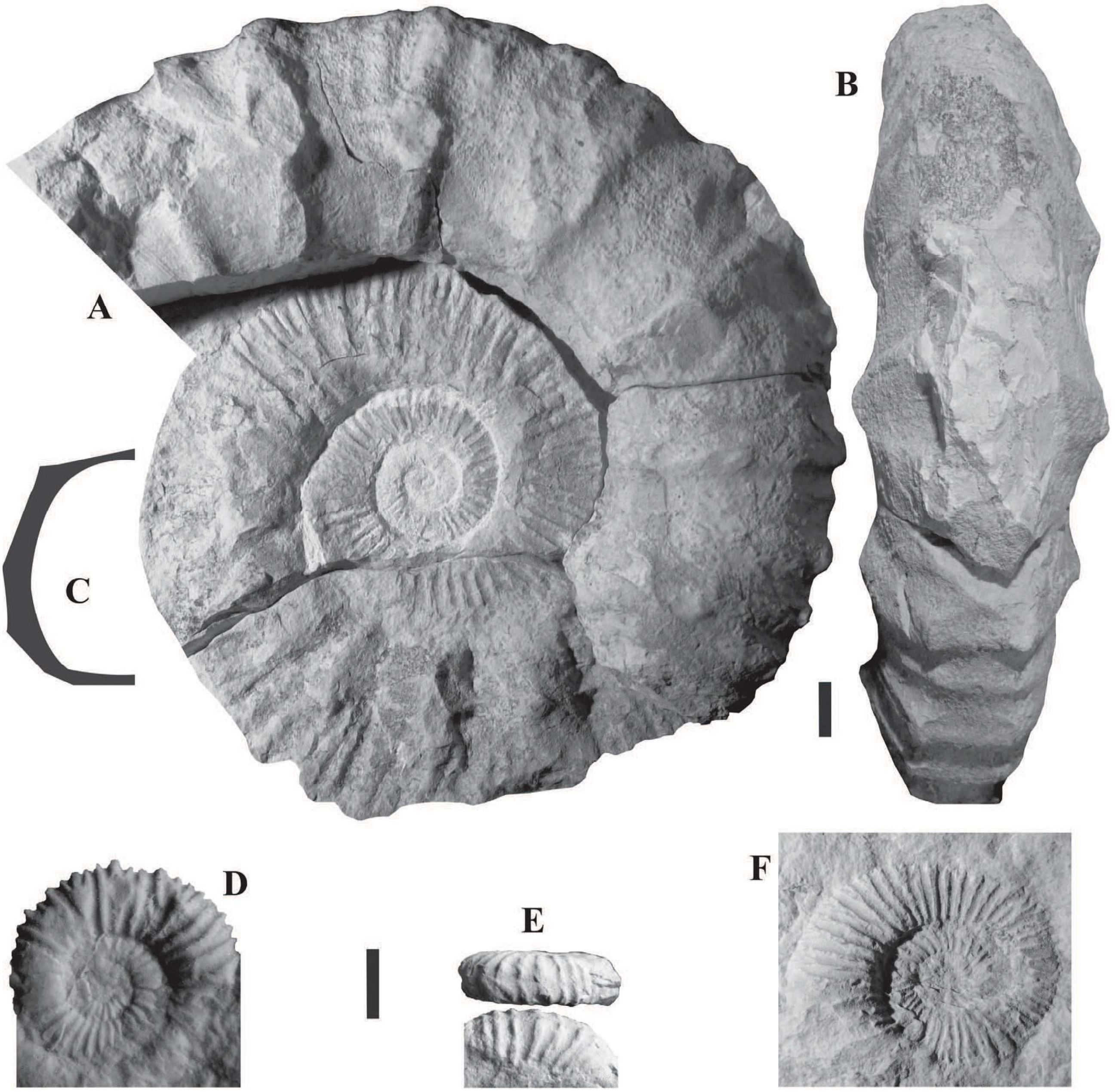


Fig. 7. Lateral (**A**), ventral (**B**) views, and whorl section at about D = 131 mm (**C**) of complete macroconch of *Protacanthodiscus andreaei* (Kilian) from the late Tithonian (*P. andreaei* Zone) of Le Chouet: MPP-CHT.21/95 (bed 85). **D** — *Protacanthodiscus hexagonus* (Tavera) from the *P. andreaei* Zone (bed 85) of Le Chouet: MPP-CHT.21/7. *Toucasiella gerardi* Enay et al., from the *P. andreaei* Zone of Le Chouet: **E** — MPP-CHT.15/9 [m] (bed 79), **F** — MPP-CHT.15t/14 [m] (bed 79). Bar scale is 10 mm.

Genus *Toucasiella* Enay, Boughdiri & Le Hégarat, 1998a

Type species: *Toucasiella gerardi* Enay, Boughdiri, Le Hégarat, 1998b; by original designation.

Toucasiella gerardi Enay, Boughdiri & Le Hégarat, 1998a
Fig. 7E–F

1994 *Durangites* (*Durangites*) *mazenoti* (Mazenot, 1939) non (Breistroffer, 1937) — Boughdiri, pl. 1, figs. 7, 8a,b, 11, 12

1998a *Toucasiella gerardi* n. sp. Enay et al., p. 471, figs. 1–21

Holotype: the unnumbered specimen illustrated by Enay et al. (1998a, fig. 4) from Cabra (Spain).

Material: MPP-CHT.15t/14 and MPP-CHT.15/9.

Description: The specimen MPP-CHT.15/9 is an incomplete body-chamber of a typical microconch form. It shows the extreme adult ornamental pattern of *T. gerardi*, with strong and spaced simple ribs, ended by externo-lateral and ventro-lateral tubercles (compare with fig. 18a–b in Enay et al. 1998a). At the end of the body chamber, the whorl section is sub-rectangular, the ventral furrow is weak and it is crossed by the ribs.

The specimen MPP-CHT.15t/14 perfectly matches the morphological and ornamental pattern of the adult macroconch of *T. gerardi*, in its middling size, compressed section, single and bifurcate ribs with lateral tubercles at the furcation points (compare with fig. 8 in Enay et al. 1998a).

Remarks: According to Enay et al. (1998a), *Toucasiella gerardi* is based on small-sized himalayitids from the *M. microcanthum* Zone (*Chitinoidella* Zone) of south east Spain and central Tunisia. Our specimens originate from a higher level at the base of the *P. andreaei* Zone (*Crassicollaria* Zone, top of the *C. intermedia* Subzone).

However, it should be noted that Boughdiri et al. (1999, p. 107) reported *Toucasiella gerardi* from bed RHS-4 in the Sidi Khalif Formation (Tunisia). Due to the dolomitization of the lower part of that formation, there is no consensus on the calpionellid biostratigraphic scheme at the base of the upper Tithonian (see Boughdiri et al. 1999, fig. 2). Thus, there is no counter-argument to consider an expansion of the *C. intermedia* Subzone in the Sidi Khalif Formation. This hypothesis is more consistent with the calpionellids data at Le Chouet (Wimbledon et al. 2013; Bulot et al. 2014).

Occurrence: Bed 79, *P. andreaei* Zone (top of the *C. intermedia* Subzone), upper Tithonian. Beside the well-documented occurrences in SE Spain and Tunisia, this is the first report of the species in SE France.

Conclusion

Due to morphological convergence and misdated stratigraphic occurrences, the taxonomy of himalayitid genera is still at a very preliminary stage. The overlooked late Tithonian endemism of the family at the genus level is much higher than was previously assumed in the literature. This is reflected by our introduction of *Parrasiella* gen. nov. for Mexican and Cuban species hitherto considered to be true *Durangites*. Evidence suggests that the latter genus only occurs in the lower to lower middle Berriasian of Mexico. As a consequence, the use of *Durangites* as a marker for the late Tithonian should be abandoned.

Also, none of the records of the genus in the Mediterranean Tethys belong to *Durangites*: the great majority of these reports refer to inner whorls and/or juveniles of *Protacanthodiscus* or to *Boughdiriella chouetensis* gen. et sp. nov. The record of the himalayitids is very homogenous across the regions of the Mediterranean and it is dominated by the highly variable species *Protacanthodiscus andreaei*. As a result, the geographical and stratigraphical pattern of the species is very useful in defining a zone at the top of the upper Tithonian.

Acknowledgments: This work is a contribution of the Berriasian Working Group (BWG) of the International Subcommission on Cretaceous Stratigraphy (I.S.C.S.). Emmanuel Robert (University of Lyon I), Istvan Főzy (Hungarian Natural History Museum), Josep Anton Moreno Bedmar (Universidad Nacional Autónoma de Mexico), Manuel Aldana (INGEMMET, Lima, Peru) and Joachim Reitner (University of Göttingen) are gratefully acknowledged for providing missing references and access to type material. Valuable discussions with Mabrouk Boughdiri (University of Bizerte) greatly improved this paper. 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, to Cyprien Lanteaume (Aix-Marseille Université) and Emile Hourqueig (Toulouse) for continuous support to one of us (C.F.). Comments by two anonymous reviewers contributed to improvement of the original manuscript.

References

Adatte T., Stinnesbeck W. & Remane J. 1994a: The Jurassic-Cretaceous boundary in Northeastern Mexico. Confrontation and correlations by microfacies, clay mineral mineralogy, calpionellids and ammonites. *Géobios* 17, 37–56.

Adatte T., Stinnesbeck W., Hubberten H. & Remane J. 1994b: Correlaciones multiestratigráficas en el límite Jurásico–Cretácico en el Noreste de México. *Bol. Soc. Geol. México* 51, 23–51.

Adatte T., Stinnesbeck W., Remane J. & Hubberten H. 1996: Paleoceanographic change at the Jurassic–Cretaceous boundary in the western Tethys, northeastern Mexico. *Cretaceous Research* 17, 671–689.

Anderson F.M. 1945: Knoxville Series in the California Mesozoic. *Geol. Soc. Amer. Bull.* 56, 910–1014.

Benzaggagh M. & Atrops F. 1997: Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). *Newslett. Stratigr.* 35, 127–163.

Benzaggagh M., Cecca F. & Rouget I. 2010: Biostratigraphy distribution of ammonites and calpionellids in the Tithonian of the internal Prerif (Msila area, Morocco). *Paläont. Z.* 84, 301–315.

Bogdanova T.N., Lobacheva S.V., Prozorovskii V.A. & Favorskaya T.A. 1984: The Berriasian stage in the Eastern Crimea and the Jurassic–Cretaceous Boundary. In: Menner V.V. (Ed.): The Jurassic and Cretaceous boundary stages. *Trans. Geol. Geophys., Siberian Branch of the Academy of Sciences of USSR* 644, 28–36.

Boughdiri M. 1994: Les genres d'ammonites *Durangites* et *Protacanthodiscus* (Tithonien supérieur) dans la Téthys occidentale (SE Espagne, SE France, Algérie et Tunisie). Stratigraphie, Paléontologie et Biogéographie. *Thèse*, *Univ. Claude Bernard Lyon I*, 1–268.

Boughdiri M., Enay R., Le Hégarat G. & Memmi L. 1999: *Hegaratites* nov. gen. (Ammonitina): Himalayitidae nouveau du Tithonien supérieur da la coupe du Jebel Rhéouis (Axe nord–sud, Tunisie centrale). Précisions stratigraphiques, approche phylétique et signification biogéographique. *Rev. Paléobiologie* 18, 105–121.

Breistroffer M. 1937: Sur un remarquable gisement à fossiles pyriteux du Tithonique supérieur de Tunisie. *C.R. Soc. Géol. France,* 18–20.

Bulot L.G., Frau C. & Wimbledon W.A.P. 2014: New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Les Près, Drôme, SE France). *Volumina Jurassica* 12, 113–128.

Burckhardt C. 1912: Faunes jurassiques et crétaciques de San Pedro del Gallo. *Bol. Inst. Geol. México* 29, 1–137.

Canavari M. 1899: Hopliti Titoniani dell Appennino centrale. *Atti Soc. Toscana Sci. Natur.* 17, 95–103.

Cantú-Chapa A. 1967: El límite Jurásico–Cretácico en Mazatepec, Puebla. *Inst. Mex. Petrol., Technologia Explor., Sec. Geol., Monogr.* 1, 3–24.

Cantú-Chapa A. 1968: Sobre una asociacion *Proniceras–Durangites–"Hildoglochiceras"* del Noreste de Mexico. *Inst. Mex. Petrol.* 2, 19–26.

Cantú-Chapa A. 2006: New Upper Tithonian (Jurassic) Ammonites of the Chinameca Formation in Southern Veracruz, Eastern Mexico. *J. Paleontology* 80, 294–308.

Castillo A. del & Aguilera J.G. 1895: Fauna fósil de la Sierra de Catorce, San Luis Potosi. *Bol. Inst. Geol. México* 1, 1–55.

Cecca F., Cresta S. & Santantonio M. 1983: Alcune ammoniti provenienti dalla "Maiolica" dell'Appennino Centrale (Umbria, Marche e Sabina). *Boll. Serv. Geol. Ital.* 103, 133–162.

Christ H.A. 1960: Beiträge zur Stratigraphie and Paläontologie des Malm von Westsizilien. *Schweiz. Paläeont. Abh.* 77, 1–44.

Cobiella-Reguera J.L. & Olóriz F. 2009: Oxfordian–Berriasian stratigraphy of the North American paleomargin in western Cuba: Constraints for the geological history of the proto-Caribbean and the early Gulf of Mexico. In: Bartolini C. & Roman Ramos J.R. (Eds.): Petroleum systems in the southern Gulf of Mexico. *AAPG Memoir* 90, 421–451.

Collignon M. 1960: Atlas des fossiles caractéristiques de Madagascar. Fascicule VI (Tithonique). *Serv. Géol. Madagascar*, Tananarive, 134–175.

Davis R.A., Landman N.H., Dommergues J.-L., Marchand D. & Bucher H. 1996: Mature modifications and sexual dimorphism in ammonoids. In: Landman N.H., Tanabe K. & Davis R.A. (Eds.): Ammonoid Paleobiology. *Topics in Geobiology* 13, 463–539.

Enay R. & Geyssant J.R. 1975: Faunes tithoniques des chaînes bétiques (Espagne méridionale). *Mém. Bur. Rech. Géol. Min.* 86, 39–55.

Enay R., Boughdiri M. & Le Hégarat G. 1998a: *Toucasiella* gen. nov., Himalayitidae (Ammonitina) nouveau du Tithonien supérieur: origine des *Durangites*. *C.R. Acad. Sci. Paris*, *Sér. 2a, Sciences de la Terre et des Planètes* 327, 471–477.

Enay R., Boughdiri M. & Le Hégarat G. 1998b: *Durangites*, *Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien supérieur–Berriasien dans la Téthys méditerranéenne (SE France, Espagne, Algérie et Tunisie). *C.R. Acad. Sci. Paris*, *Sér. 2a, Sciences de la Terre et des Planètes* 327, 425–430.

Enay R., Boughdiri M. & Le Hégarat G. 1998c: *Kilianites* gen. nov., Himalayitidae (Ammonitina) nouveau du Berriasian de la région de Cabra (province de Cordoba, SE Espagne): descendance de *Protacanthodiscus*. *C.R. Acad. Sci. Paris*, *Sér. 2a, Sciences de la terre et des planètes* 327, 549–554.

Enay R., Martin C., Monod O. & Thieuloy J.-P. 1971: Jurassique supérieur à Ammonites (Kimméridgien–Tithonique) dans l'autochtone du Taurus de Beysehir, Turquie meridionale. *Ann. Inst. Geol. Publ. Hung.* 54, 397–422.

Fischer P. 1882: Manuel de Conchyliologie et de Paléontologique conchyliologique ou Histoire naturelle des Mollusques vivants et fossiles: Fascicule IV. *Masson*, Paris, 305–416.

Főzy I. & Scherzinger A. 2013: Systematic descriptions of Tithonian ammonites of the Gerecse Mountains. In: Főzy I. (Ed.): Late Jurassic–Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis mountains (Transdanubian Range, Hungary). *GeoLitera*, Szeged, 207–292.

Geyssant J.R. 1997: Tithonien. In: Cariou E. & Hantzpergue P. (Eds): Biostratigraphie du Jurassique ouest européen et méditerranéen: zonations parallèles et distribution des invertébrés et microfossiles. *Elf Aquitaine édition*, Pau, 97–102.

Hoedemaeker P.J. & Bulot L.G. 1990: Preliminary ammonite zonation for the Lower Cretaceous of the Mediterranean region. *Géol. Alp.* 66, 123–127.

Imlay R.W. 1939: Upper Jurassic ammonites from Mexico. *Geol. Soc. Amer. Bull.* 50, 1–78.

Imlay R.W. 1942: Late Jurassic fossils from Cuba and their economic significance. *Geol. Soc. Amer. Bull.* 53, 1417–1478.

Imlay R.W. & Jones D.L. 1970: Ammonites from the *Buchia* zones in northwestern California and southwestern Oregon. *Geol. Surv. Profess. Pap.* 647-B, B1–B59.

Ivanov M., Stoykova K. & Idakieva V. 2010: New biostratigraphic data on the Upper Tithonian and Lower Berriasian in the Krayshte area (Southwestern Bulgaria). *Ann. Univ. Sofia "St. Kliment Ohridski", Livre 1, Géol.* 102, 21–42.

Khimshiashvili N.G. 1989: The Berriasellidae of Abkhazia. The Tithonian fauna of mount Lakorizi-Tau (basin of Bzibi river). *Metsniereba*, Tbilisi, 1–87 (in Russian).

Kilian W. 1889: Etudes paléontologiques sur les terrains secondaires et tertiaires de l'Andalousie. *Mém. Acad. Sci. Inst. France* 30, 580–733.

Klein J. 2005: Lower Cretaceous Ammonites I. Perisphinctaceae 1. Himalayitidae, Olcostephanidae, Holcodiscidae, Neocomitidae, Oosterellidae. In: Riegraf W. (Ed.): Fossilium catalogus I: Animalia, pars 139. *Backhuys Publishers,* Leiden, 1–484.

Korn D., Ebbighausen V., Bockwinkel J. & Klug C. 2003: The A-mode sutural ontogeny in prolecanitid Ammonoids. *Palaeontology* 46, 1123–1132.

Le Hégarat G. 1973: Le Berriasien du sud–est de la France. *Doc. Lab. Géol. Fac. Sci. Lyon* 43, 1–576.

Leanza A.F. 1945: Amonites del Jurásico superior y del Cretácico inferior de la Sierra Azul, en la parte meridional de la provincia de Mendoza. *Anal. Mus. La Plata, NS Paleont.* 1, 1–99.

Leanza A.F. 1968: *Anotaciones* sobre los fósiles Jurásico–Cretácicos de *Patagonia austral* (colección Feruglio) conservados en la Universidad de Bologna. *Acta Geol. Lilloana* 9, 121–179.

Mazenot G. 1939: Les Palaeophoplitidae tithoniques et berriasiens du sud est de la France. *Mém. Soc. Géol. France (Nouvelle Sér.)* 18, *Mémoire* 41, 1–303.

Myczynski R. 1989: Ammonite biostratigraphy of the Tithonian of western Cuba. *Ann. Soc. Geol. Pol.* 5, 43–125.

Myczynski R. 1999: Some ammonite genera from the Tithonian of western Cuba and their palaeobiogeographic importance. *Stud. Geol. Pol.* 114, 91–112.

Myczynski R. & Pszczółkowski A. 1994: Tithonian stratigraphy and microfacies in the Sierra del Rosario, western Cuba. *Stud. Geol. Pol.* 105, 7–38.

Olóriz F., Villaseñor A.B., Gonzalez-Arreola C. & Westermann G.E.G. 1999: Ammonite biostratigraphy and correlations in the Upper Jurassic lowermost and correlations in the Upper Jurassic lowermost Mexico (Sierra de Catorce, San Luis Potosí). In: Olóriz F. & Rodriguez-Tovar F.J. (Eds.): Advancing research on living and fossil Cephalopods. *Kluwer Academic/Plenum Publishers*, New York, 463–492.

Patrulius D. & Avram E. 1976: Les céphalopodes des Couches de Carhaga (Tithonique supérieur–Barrémien inférieur). *Mém. Inst. Géol. Géophys.* 24, 153–201.

Pervinquière L. 1907: Étude de paléontologie tunisienne. I. Céphalopodes des terrains secondaires. Direction générale des Travaux publics. Carte géologique de la Tunisie. *De Rudeval*, Paris, 1–438.

Retowski O. 1893: Die tithonischen Ablagerungen von Theodosia. *Bull. Soc. Natur. Moscou* 7, 206–301.

Rivera R. 1951: La fauna de los estratos de Puente Inga, Lima. *Bol. Soc. Geol. Peru* 22, 5–53.

Roman F. 1936: Le Tithonique du massif du Djurdjura (province d'Alger). *Matériaux pour la Carte Géologique de l'Algérie, Paléontologie* 7, 1–43.

Roman F. 1938: Les ammonites jurassiques et crétacées. Essai de genera. *Masson*, Paris, 1–554.

Sapunov I.G. 1979: Les fossiles de Bulgarie. III. 3. Jurassique supérieur, Ammonoidea. *Ed. Acad. Bulgar. Sci.*, 1–263.

Sarti C. 1988: Biostratigraphic subdivision for the Upper Jurassic of

Venetian Alps (Northern Italy) on the base of ammonites. *2nd International Symposium on Jurassic Stratigraphy*, Lisboa, 459–476.

Sarti C. 1995: *Ptychophylloceras bisulcatum* (*Ammonoidea*): nuova specie di *Phylloceratidae* nel Titoniano del “Trento Plateau” (Alpi meridionali, Italia). *Mem. Sci. Geol. Univ. Padova* 47, 245–251.

Sey I.I. & Kalacheva E.D. 1983: On invasions of Tethyan ammonites in Boreal Late Jurassic basins of the East of USSR. In: Zakharov V.A. & Nalnyaeva T.I. (Eds.): Mesozoic of the Soviet Arctic. *Trudy Inst. Geol. Geofiz.* 555, 61–72.

Shome S. & Bardhan S. 2009: A new Late Tithonian ammonite assemblage from Kutch, Western India. *J. Palaeont. Soc. India* 54, 1–18.

Spath L.F. 1923: Appendix: On ammonites from New Zealand. In: Trechmann C.T. (Ed.): The Jurassic rocks of New Zealand. *Quart. J. Geol. Soc. London* 79, 286–308.

Spath L.F. 1925: Ammonites and aptychi. The collection of fossils and rocks from Somaliland. *Monographs Geological Department of the Hunterian Museum* 1, 111–164.

Spath L.F. 1931: Revision of the Jurassic cephalopod fauna of Kachh (Cutch). Part IV. *Palaeontologia Indica* 9, 1–945.

Steinmann G. 1890: Cephalopoda. In: Steinmann G. & Döderlein L. (Eds.): Elemente der Paläontologie. *Engelmann*, Leipzig, 344–475.

Steuer A. 1897: Argentinische Jura-Ablagerungen. Ein Beitrag zur Kenntnis der Geologie und Paläontologie der argentinischen Anden. *Palaeont. Abh.* 7 (N.F. 3), 129–222.

Szives O. & Fözy I. 2013: Systematic descriptions of Early Cretaceous ammonites of the carbonate formations of the Gerecse Mountains, Hungary. In: Fözy I. (Ed.): Late Jurassic–Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis mountains (Transdanubian Range, Hungary). *GeoLitera*, Szeged, 293–342.

Tavera Benitez J.M. 1985: Les ammonites del Tithonico superior–Berriasense de la Zona Subbetica (Cordilleras Beticas). *Tesis Doctoral. Universidad de Granada*, 1–381.

Verma H.M. & Westermann G.E.G. 1973: The Tithonian (Jurassic) ammonite fauna and stratigraphy of Sierra Catorce, San Luis Potosí, México. *Bull. Amer. Paleont.* 63, 108–137.

Wimbledon W.A.P., Reháková D., Pszczółkowski A., Cassellato C.E., Halásová E., Frau C., Bulot L.G., Grabowski J., Sobieñ K., Pruner P., Schnabl P., Čížková K. & Tchoumatchenco P. 2013: A preliminary account of the bio- and magnetostratigraphy of the upper Tithonian–lower Berriasian interval at Le Chouet, Drôme (SE France). *Geol. Carpathica* 64, 437–460.

Acta Geologica Polonica, Vol. 66 (2016), No. 2, pp. 157–177
DOI: 10.1515/agp-2016-0007

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

CAMILLE FRAU[1], LUC G. BULOT[2], WILLIAM A.P. WIMBLEDON[3] and CHRISTINA IFRIM[4]

[1]*Groupement d'Intérêt Paléontologique, Science et Exposition, 60 bd Georges Richard, 83000 Toulon, France. E-mail: camille_frau@hotmail.fr*
[2]*UM 34 Aix-Marseille Université ; CNRS (UMR 7330) ; IRD (UMR 161), Centre Saint-Charles, Case 67, 3 Place Victor Hugo, 13331 Marseille Cedex 03, France. E-mail: bulot@cerege.fr*
[3]*School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, United Kingdom. E-mail: mishenka1@yahoo.uk*
[4]*Institut für Geowissenschaften, Ruprecht-Karls-Universität, Im Neuenheimer Feld 234, 69120 Heidelberg, Germany. E-mail: christina.ifrim@geow.uni-heidelberg.de*

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), 157–177. 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*.

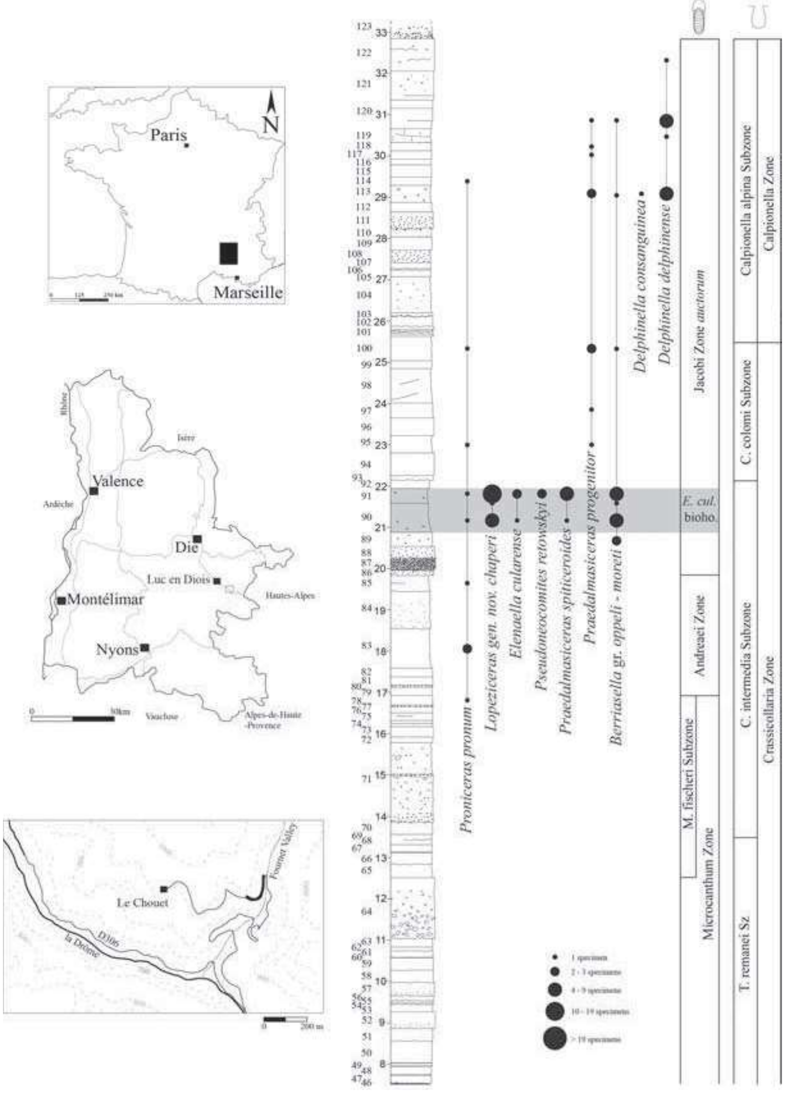
GEOLOGICAL SETTING

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.

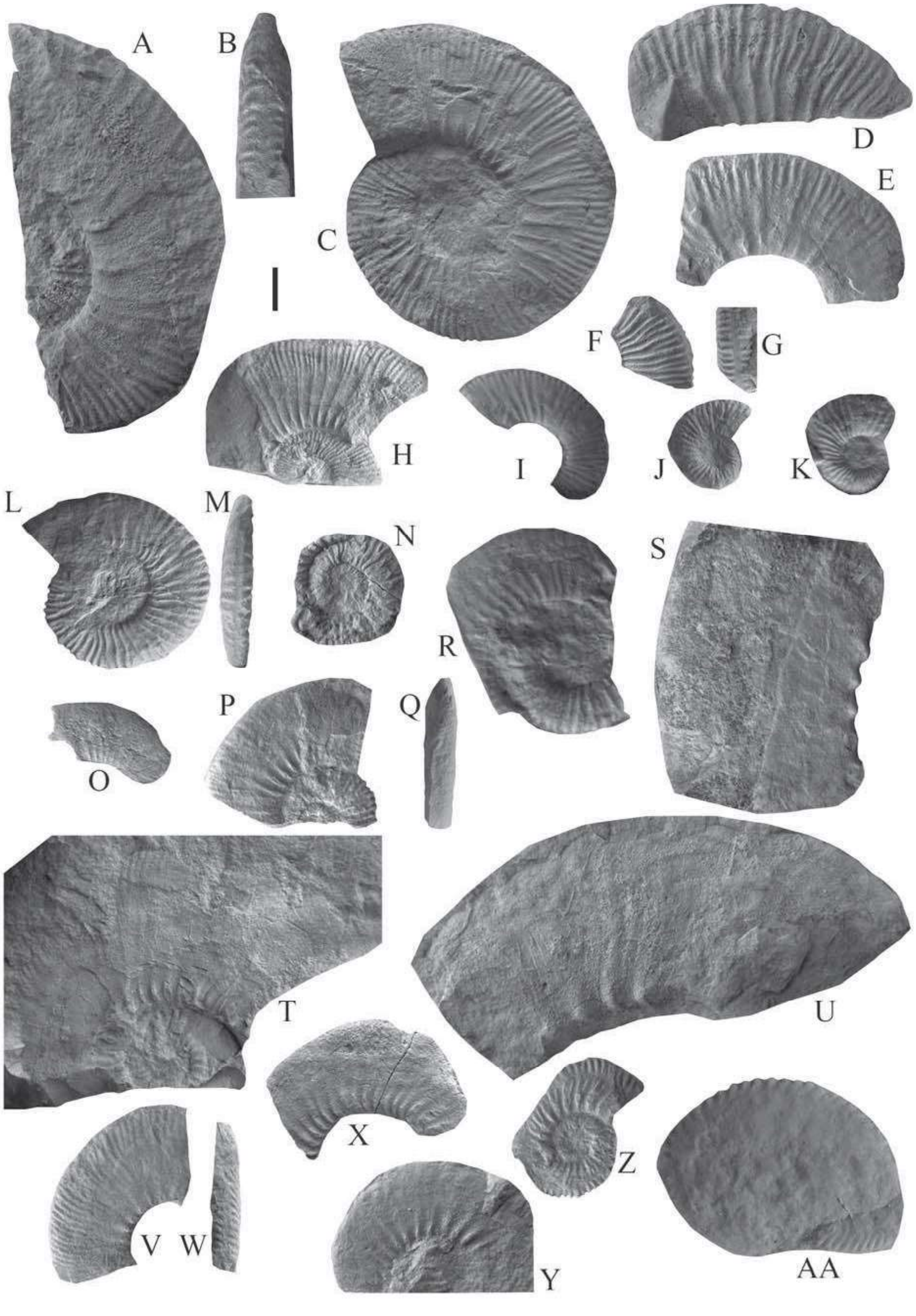
The distinction of two morphological groups, based on the ontogenetic sequence, strongly suggests intraspecific dimorphism, as already documented in *Protacanthodiscus andreaei* by Frau *et al.* (2015). However, none of the specimens at our disposal, or illustrated in the literature, show the structure 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.


A
B
C
D
E
F
G
H
I
J
K
L
M
N
O
P
Q
R
S
T
U
V
W
X
Y
Z
AA

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; Fözy, 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. *Berriasellla* 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

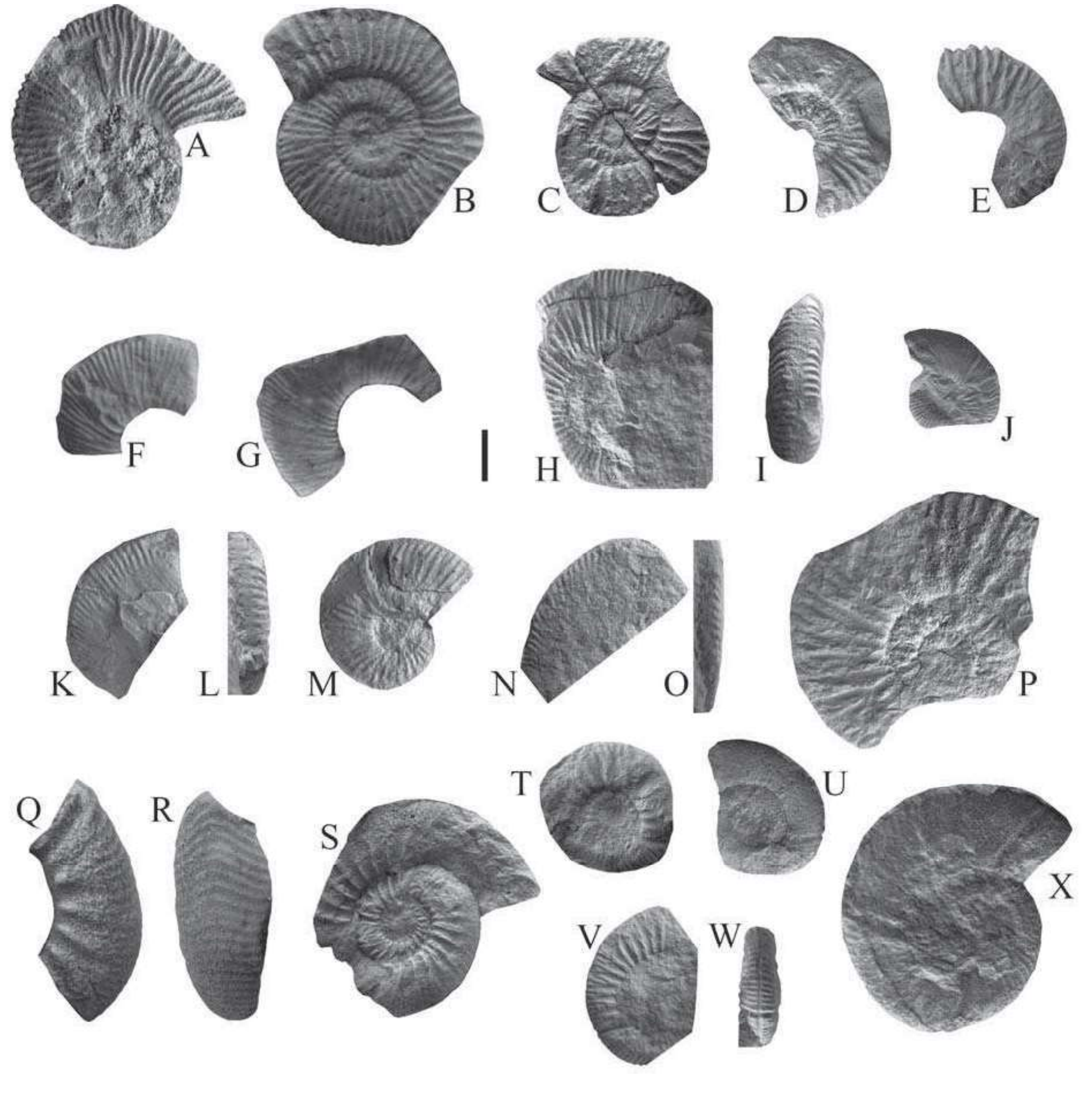
DESCRIPTION: The material at our disposal comprises small (D < 50 mm), planulate, moderately, evolute (U/D ~ 0.40) neocomitids with shallow umbilicus. The whorl section is subrectangular, higher-than-wide, with a low umbilical wall, slightly convex to flat flanks and a flattened venter. A more-or-less, 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).

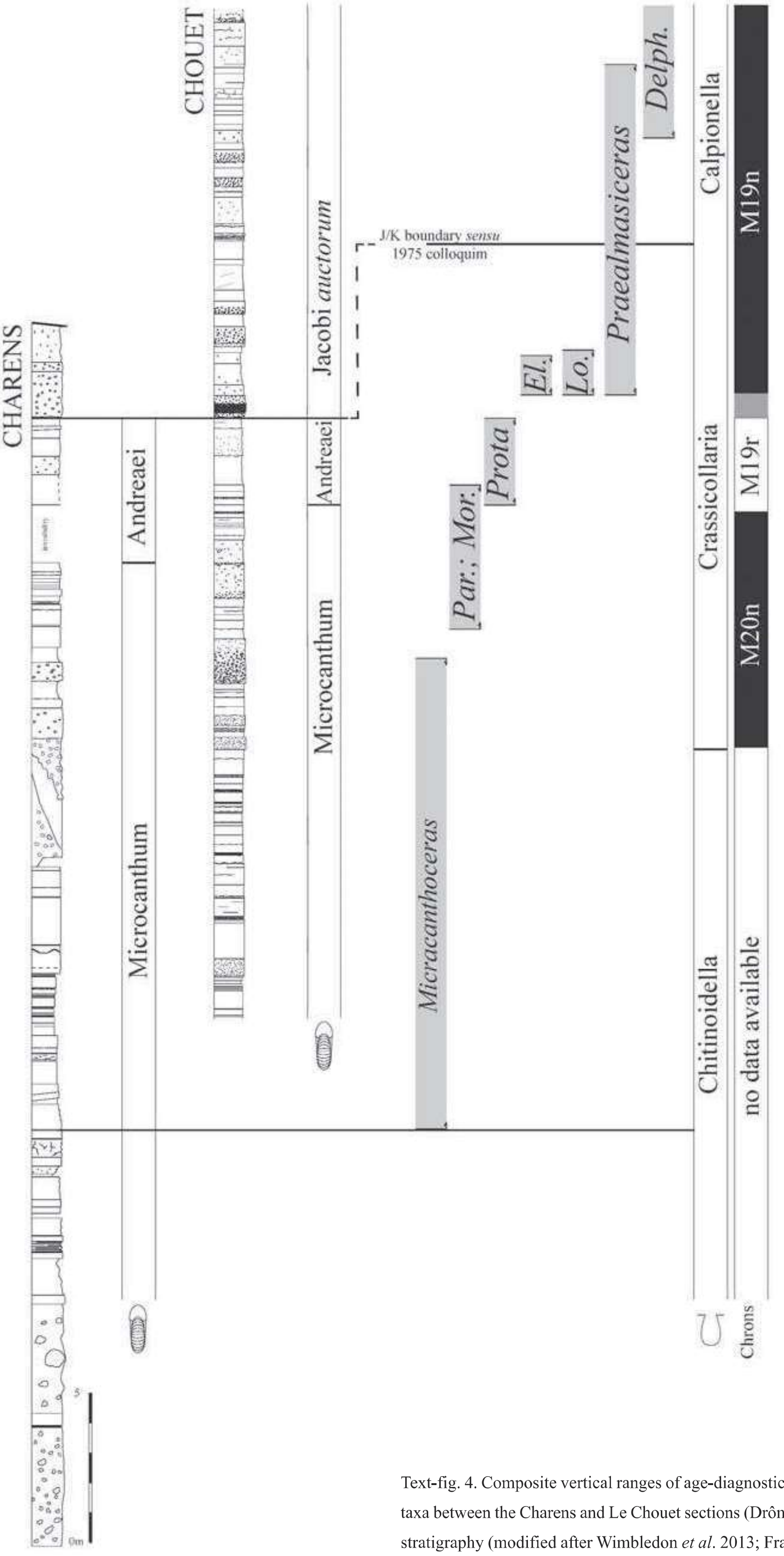
Our new collection shows that the ontogenetic sequence between *Proniceras* specimens is rather similar, but the length of ornamental stages and pattern of fasciculate ribs are strongly related to the adult shell shape. Two distinct morphologies co-occur: with small, compressed, evolute forms and larger, 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.

REFERENCES

Arkadiev, V.V. 2011. Representatives of genera *Fauriella*, *Tirnovella* and *Jabronella* (Neocomitidae, Ammonoidea) from the Berriasian of the Mountainous Crimea and their stratigraphic significance. *Bulletin of Saint-Petersburg University*, series 7 Geology, Geography, **2**, 3–20. [In Russian]

Arkadiev, V.V. and Bogdanova, T.N. 2005. Genus *Delphinella* (Ammonoidea) from the Berriasian of the Crimean Mountains. *Paleontological Journal*, **39**, 487–497

Arkadiev, V.V., Bogdanova, T.N., Lobacheva, S.V., Kalacheva, E.D. and Sey, I.I. 2008. Berriasian Stage of the Crimean Mountains: Zonal Subdivisions and Correlation. *Stratigraphy and Geological Correlation*, **16**, 400–422.

Arkadiev, V.V., Bogdanova, T.N., Guzhikov, A. Y., Lobacheva, S.V., Myshkina, N.V., Platonov, E.S., Savelyeva, Y.N., Shurekova, O.V. and Yanin, B.T. 2012. In: Arkadiev, V.V. and Bogdanova, T.N. (Eds), The Berriasian Stage of mountainous Crimea, 1– 472. [In Russian]

Arkell, W.J. 1956. Jurassic geology of the world. xv + 804 pp. Oliver and Boyd; Edinburgh and London.

Arnould-Saget, S. 1953. Les ammonites pyriteuses du Tithonique supérieur et du Berriasien de Tunisie centrale. *Annales des Mines et de la Géologie*, **10**, 1–132.

Avram, E.1990. Considérations sur l'âge des Marnes de Crivina (Zone Resita-SO de la Roumanie). *Dări de seamă ale sedintelor Institutul de Geologie si Geofizică*, **74**, 33–68.

Basse, E. 1952. Ammonoidea. In: Piveteau, J. (Ed.), Traité de Paléontologie, 2, pp. 581–688. Masson; Paris.

Benzaggagh, M. and Atrops, F. 1997. Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). *Newsletters on Stratigraphy*, **35**, 127–163.

Blanford, H.F. 1864. On Dr. Gerard's collection of fossils from the Spiti valley, in the Asiatic Society's Museum. *Journal of the Asiatic Society of Bengal*, **32**, 124–138.

Bulot, L.G., Thieuloy, J.P., Blanc, E. and Klein, J. 1993. Le cadre stratigraphique du Valanginien supérieur et de l'Hauterivien du Sud-Est de la France: définition des biochronozones et caractérisation de nouveaux biohorizons. *Géologie alpine*, **68**, 13–56.

Burckhardt, C. 1912. Faunes jurassiques et crétaciques de San Pedro del Gallo. *Boletín del Instituto* de *Geología* de México, **29**, 1–137.

Busnardo, R., Charollais, J., Weidmann, M. and Clavel, B. 2003. Le Crétacé inférieur de la Veveyse de Châtel (Ultrahelvétique des Préalpes externes; canton de Fribourg, Suisse). *Revue de Paléobiologie*, **22**,1–174

Bogdanova, T.N., Lobacheva, S.V., Prozorovsky, V.A. and Favorskaya, T.A. 1984. The Berriasian of eastern Crimea and the Jurassic–Cretaceous boundary. In: Boundary Stages of the Jurassic–Cretaceous Systems. *Trudy Instituta Geologii i Geofiziki Akademii Nauk, Sibirskoe Otdelinie*, **644**, 28–35. [In Russian]

Bogdanova, T.N., Kalacheva, E.D. and Sey, I.I. 1999. On presence of the Tirnovella occitanica Zone (Lower Cretaceous, Berriasian) in the Feodosia section, Eastern Crimea. *Regional Geology and Metallogeny*, **9**, 27–32. [In Russian]

Bogoslovsky, N.A. 1897. Der Rjasan–Horizont, seine Fauna, seine stratigraphischen Beziehungen und sein watacheinliclies Alter. *Materials for the geology of Russia*, **28**, 1–136.

Boughdiri, M. 1994. Les genres d'ammonites *Durangites* et *Protacanthodiscus* (Tithonien supérieur) dans la Téthys occidentale (SE Espagne, SE France, Algérie et Tunisie). Stratigraphie, Paléontologie et Biogéographie. Thèse de l'Université Claude Bernard Lyon I, 268 pp.

Boughdiri, M., Enay, R., Le Hégarat, G. and Memmi, L. 1999. *Hegaratites* nov. gen. (Ammonitina): Himalayitidae nouveau du Tithonien supérieur da la coupe du Jebel Rhéouis (Axe nord-sud, Tunisie centrale). Précisions stratigraphiques, approche phylétique et signification biogéographique. *Revue de Paléobiologie*, **18**, 105–121.

Breistroffer, M. 1937. Sur une remarquable gisement à fossiles pyriteux du Tithonique supérieur de Tunisie. *Compte Rendu Sommaire des Séances de la Société Géologique de France*, 18–20.

Buckman, S. 1909-1930. Yorkshire Type Ammonite, 1, 2, and Type Ammonite, 3, 7, I-XVI + 121 p. Welsey and Son; Londres.

Bulot, L.G., Frau, C. and Wimbledon, W.A.P. 2014. New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Les Près, Drôme, SE France). *Volumina Jurassica*, **12**, 113–128.

Burckhardt, C. 1919. Faunas Jurasicas de Symon (Zacatecas) y faunas Cretacicas de Zumpango del Río (Guerrero). Instituto Geologico de Mexico, Boletin 33, (1919) Tomo I, texto: 1–135; (1921) Tomo II: Atlas, pls 1–32.

Bürgl , H. 1957. Biostratigrafia de la Sabana de Bogota y sus alrededores. *Boletin Geologica*, **5**, 113–185.

Cecca, F., Enay, R. and Le Hégarat, G. 1989. L'Ardescien (Tithonique supérieur) de la région stratotypique: série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. *Documents du Laboratoire de Géologie de Lyon*, **107**, 1–115.

Clavel, B., Charollais, J., Busnardo, R. and Le Hégarat, G. 1986. Précisions stratigraphiques sur le Crétacé inférieur basal du Jura méridional. *Eclogae geologica Helvetiae*, **79**, 319–341.

Collignon, M. 1960. Atlas des fossiles caractéristiques de Madagascar. Fascicule VI (Tithonique). Service Géologique de Madagascar, 175 p.

Collignon, M. 1962. Atlas des fossiles caractéristiques de Madagascar(Ammonites) (Berriasien, Valanginien, Hauterivien, Barremien). *Service Geologique de Tananarive*, **8**, 176–214.

Company, M. 1987. Los Ammonites del Valanginiense del sector de las Cordieras Béticas (SE de Espana). Ph.D. Thesis of the University of Granada, 294 p.

Coquand, H. 1869. Note sur les assises qui, dans les Bouches–du–Rhône, sont placées entre l'Oxfordien supérieur et l'étage Valanginien (base du terrain crétacé). *Bulletin de la Société Géologique de France*, **2**, 100–131.

Coquand, H. 1875. Note sur les Calcaires coralliens à *Terebratula repelliniana* de la Basse Provence et du Languedoc. *Bulletin de la Société Géologique de France*, **3**, 1–670.

Courjault, T. 2011. Brèches gravitaires sous–marines du Tithonien subalpin (S–E France). Thèse Doctorat, Université de Strasbourg, 339 p.

De Wever, P., Geyssant, J. R., Azéma, J., Devos, I., Duée, G., Manivit, H. and Vrielynck, B. 1986. La coupe de Santa Anna (Zone de Sciacca, Sicile): une synthèse biostratigraphique des apports des macro-, micro- et nannofossiles du Jurassique supérieur et Crétacé inférieur. *Revue de Micropaléontologie*, **29**, 141–186.

Dimitrova, N. 1967. Fosilite na Bulgariya. IV. Dolna Kreda–Glavonogi (Fossils of Bulgaria. IV. Lower Cretaceous Cephalopoda (Nautiloidea and Ammonoidea). Bulgarian Academy of Sciences, 424 p.

Djanélidzé, A. 1922a. *Dalmasiceras*, un sous–genre nouveau du genre *Hoplites*. *Bulletin de la Société Géologique de France*, *Série 4*, **21**, 256–274.

Djanélidzé, A. 1922b. Les *Spiticeras* du sud–est de la France. *Mémoires pour server à* l'explication de Carte Géologique Détaillée de la France, 1922, pp. 1–255.

Drushchits, V. 1960. Ammonitii. In: Drushchits, V. and Kudrjavtsev, M.P. (Eds), Atlas Nizhnemelovoi fauny severnogo Kavkaza i Kryma (Atlas of the Lower Cretaceous faunas of the Northern Caucasus and the Crimea).Vsesoiuznyi Nauchno Issledovatel'skii Institut Prirodnykh Gasov, pp. 249–355.

Eliáš, M. and Eliášová, H. 1986. Elevation facies of the Malm in Moravia. Geologický Zborník. *Geologica Carpathica*, **37**, 532–550.

Enay, R. 2009. Les faunes d'ammonites de l'Oxfordien au Tithonien et la biostratigraphie des Spiti-Shales (Callovien supérieur-Thitonien) de Thakkhola, Népal Central. *Documents des Laboratoires de Géologie Lyon*, **166**, 1–351.

Enay, R. and Geyssant, J. R. 1975. Faunes tithoniques des chaînes bétiques (Espagne méridionale). In: Colloque limite Jurassique–Crétacé, Lyon – Neuchâtel, Septembre 1973. *Mémoires du Bureau de Recherches Géologique et Minières*, **86**, 39–55.

Enay, R., Boughdiri, M. and Le Hégarat, G. 1998. *Durangites*, *Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien supérieur–Berriasien dans la Téthys méditerranéenne (SE France, Espagne, Algérie et Tunisie). *Comptes Rendus de l'Académie des Sciences de Paris, Série 2a, Sciences de la Terre et des Planètes*, **327**, 425–430.

Eristavi, M.C. 1961. Einige Cephalopodenarten aus der unteren Kreide der Zentralkarpaten. *Geologické Práce. Zprávy*, **21**, 81–108.

Ettachfini, M. 2004. Les ammonites néocomiennes dans l'Atlas atlantique (Maroc). Biostratigraphie, paléontologie, paléobiogéographie et paléoécologie. *Strata, Série 2*, **43**, 223 pp.

Favre, E. 1880. Description des fossiles des couches tithoniques des alpes fribourgeoises. *Mémoires de la Société Paléontologique Suisse*, **6**, 1–75,

Főzy, I. 1989. Felsöjura ammonitesz biosztratigrafia a Balkony hegységben. *Földtani Közlöny*, **119**, 133–156.

Frau, C., Bulot, L.G. and Wimbledon, W.A.P. 2015. Upper Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): implications for the systematics. *Geologica Carpathica*, **66**, 117–132.

Frau, C., Bulot, L.G. and Wimbledon, W.A.P. [accepted]. Late Tithonian Himalayitidae Spath, 1925 and Neocomitidae Salfeld, 1921 (Perisphinctoidea, Ammonitina) from Charens (Drôme, France). *Geologica Carpathica*.

Frau, C., Bulot, L.G., Reháková, D. and Wimbledon, W.A.P. 2016. Revision of the ammonite index species *Berriasella jacobi* Mazenot, 1939 and its consequence on the biostratigraphy of the Berriasian Stage. *Cretaceous Research*, **66**, 94–114.

Fülöp, J. 1976. The mesozoic basement horst blocks of Tata. *Geologica Hungarica*, *Series Geologica*, **16**, 1–229.

Grigorieva, O.K. 1938. Fauna ammonitov nizhnego valanshina iz bassejna p. Beloj na severnom sklone Kavkaza (Maikopsikii raion). In: Azovo-Chernomorskii geologicheskii Tresi. Materialy po geologii i poleznym iskopaemiam, **1**, 83–122.

Guzhikov, A.Y., Arkadiev, V.V., Baraboshkin, E.Y., Bagaeva, M.I., Piskunov, V.K., Rud'ko, S.V., Perminov, V.A. and Mankin, A.G. 2012. Novye sedimentologicheckie, bio- i magnitostratigraficheskie dannye po pogranichnomuyurckomu–melovomu interval voctochnogo Kryma (g. Feodociya). *Stratigrafiya Geologicheskaya Korrelyatsiya*, **20**, 1–36.

Haug, E. 1910. Période Crétacée, In: Haug, E. Traité de géologie, vol. 2. Les Périodes géologiques, fascicule 2, pp. 1153–1396. Colin; Paris.

Hoedemaeker, P.J. 1981. The Jurassic-Cretaceous boundary near Miravetes (Caravaca, SE Spain); arguments for a position at the base of the Occitanica Zone. *Cuadernos Geologicos*, **10**, 235–247.

Hoedemaeker, P.J. 1982. Ammonite biostratigraphy of the uppermost Tithonian, Berriasian, and lower Valanginian along the Río Argos (Caravaca, SE Spain). *Scripta Geologica*, **65**, 1–81.

Howarth, M.K. 1992. Tithonian and Berriasian ammonites from the Chia Gara Formation in Northern Iraq. *Palaeontology*, **35**, 597–655.

Imlay, R.W. 1939. Upper Jurassic ammonites from Mexico. *Bulletin of the Geological Society of America*, **50**, 1–78.

Khalilov, A.G. 1988. Nautiloids and ammonites. In: Alizade, A.A. (Ed.), Cretaceous fauna of Azerbaydzhan, 330–389 p.

Khimchiashvili, N.G. 1989. The Berriasellidae of Abkhazia. Akademii Nauk Gruzhinskogo SSR., 24 p.

Khimshiashvili, N.G. 1990. The Tithonian–Berriasian ammonites of Georgia and their distribution. Atti del secondo convegno internazionale Fossili, Evolutione, Ambiente, Pergola, 1987, pp. 371–381.

Kilian, W. 1889. Etudes paléontologiques sur les terrains secondaires et tertiaires de l'Andalousie. *Mémoires de l'Académie des sciences de l'Institut de France*, **30**, 580–733.

Kilian, W. 1910. Valendis–Stufe; Hauterive–Stufe; Barrême Stufe; Apt–Stufe sowie 4 Ansichtstafeln und 8 Fossiltafeln. In: Frech F. Lethaea geognostica. Handbuch der Erdgeschichte, II. Teil: Das Mesozoicum. 3. Band. Kreide. Erste Abteilung: Unterkreide (Palaeocretacicum). Zweite Lieferung: Das bathyale Palaeocretacicum im Südöstlichen Frankreich, pp. 169–287.

Klein, J. 1988. Het Onder–Krijt van de Provence. *GEA*, **21**, 1–36.

Klein, J. 2005. Lower Cretaceous ammonites I. Fossilium Catalogus: Animalia, Pars 139: I-X, 484 p.

Kvantaliani, I.V. 1999. Berriasian cephalopodes of the Crimea and the Caucasus. *Proceedings of the Georgian Academy of Sciences Geological Institute, New Series*, **112**, 1–188.

Kvantaliani, I. and Kvernadze, A.V. 1978. On some Berriasellidae from the middle course of the River Psow. *Trudy Gruzhinskogo Politekhnicheskogo Instituta*, **4**, 34–38.

Leanza, A.F. 1945. Ammonites del Jurásico superiior y del Cretáceo inferior de la Sierra Azul, en la parte meridional de la provincial de Mendoza. *Anales del Museo de La Plata*, **1**, 1–99.

Lefeld, J. 1974. Middle–Upper Jurassic and Lower Cretaceous biostratigraphy and sedimentology of the sub-tatric succession in the Tatra Mts (Western Carpathians). *Acta Geologica Polonica*, **24**, 277–364.

Le Hégarat, G. 1971. Perisphinctidae et Berriasellidae de la limite Jurassique-Crétacé. Genres nouveaux et révision critique de quelques définitions taxinomiques antérieures. *Comptes Rendus des Séances de l'Académie des Sciences, Série D*, **10**, 850–853.

Le Hégarat, G. 1973. Le Berriasien du sud-est de la France. *Documents du Laboratoire de Géologie de Lyon*, **43**, 1–576.

Le Hégarat, G. and Remane, J. 1968. Tithonique supérieur et Berriasien de l'Ardèche et de l'Hérault. Corrélation des Ammonites et des Calpionelles. *Géobios*, **1**, 7–70.

Lehmann, J., Ifrim, C., Bulot, L.G. and Frau, C. 2015. Chapter II, Part 9. Paleobiogeography of early Cretaceous ammonites In: Klug, C., Korn, D., De Baets, K., Kruta, I. and Mapes, R.H. (Eds), Ammonoid Paleobiology: From macroevolution to paleobiogeography. Topics in Geobiology, 44, 598 p. Springer; Netherlands.

Liu, G. 1988. Upper Jurassic and Lower Cretaceous ammonites from Yamzho Yumco area Xizang (Tibet). In: Chinese Academy of geological sciences. Professional papers of Xizang (Tibet) Paleontology, pp. 66–122.

Mazenot, G. 1939. Les Palaeophoplitidae tithoniques et berriasiens du sud est de la France. *Mémoires de la Société Géologique de France, Nouvelle Série*, 18, **41**, 1–303.

Nikolov, T.G. 1960. La faune d'ammonites dans le Valanginien du Prébalkan oriental. *Travaux sur la Géologie de Bulgarie*, **2**, 143–264.

Nikolov, T.G. 1966. New genera and subgenera of ammonites of family Berriasellidae. *Comptes Rendus de l'Académie Bulgare des Sciences*, **19**, 7, 639–642.

Nikolov, T.G. 1982. Les Ammonites de la famille Berriasellidae Spath, 1922. Tithonique supérieur-Berriasien. *Académie Bulgare des Sciences*, **10**, 1–251.

Nikolov, T.G. and Mandov, G. 1967. Sur quelques nouvelles espèces d'ammonites berriasiennes du Pré-balkan (Bulgarie du Nord). *Bulletin de l'Institut Géologique, Série Paléontologie*, **16**, 41–46.

Nikolov, T.G. and Sapunov, I.G. 1977. Sur une sous-famille – Pseudosubplanitinae subfam. nov. (Berriasellidae). *Comptes Redus de l'Académie Bulgare des Sciences, Geologie, Paléontologie*, **30**, 101–103.

Oppel, A. 1863. Über jurassische Cephalopoden. *Palaeontologische Mittheilungen aus dem Museum des Koeniglich-Bayerischen Staates*, **3**, 127–266.

Oppel, A. 1865. Die tithonische Etage. *Zeitschrift der Deutschen Geologischen Gesellschaft*, **17**, 535–558.

Orbigny, A. d' 1842-1851. Paléontologie française. Description de tous les animaux mollusques et rayonnés, fossiles de France, comprenant leur application à la reconnaissance des couches. Terrains jurassiques. Tome premier, comprenant les céphalopodes.Masson, Paris, Texte, 642 pp.; Atlas, 234 pls.

Parent, H. 2003. The Ataxioceratid ammonite fauna of the Tithonian (Upper Jurassic) of Casa Pincheira, Mendoza (Argentina). In: Parent, H., Olóriz, F. and Meléndez, G. (Eds), Jurassic of South America. *Journal of South American Earth Sciences* **16**, 143–165.

Parent, H., Scherzinger, A. and Schweigert, G. 2011. The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén–Mendoza Basin, Argentina. *Boletín del Instituto de Fisiografía y Geología*, 79–81.

Patrulius, D. 1969. Geologia Masivului Bucegi si a Culoarului Dambovicioara. Editura Academiei RSR, 321 p.

Picha, E. J., Stráník, Z. and Krejèí, O. 2006. Geology and hydrocarbon resources of the Outer Western Carpathians and their foreland, Czech Republic. In: Golonka, J. and Picha, F.J. (Eds), The Carpathians and their foreland: Geology and Hydrocarbon Resources. *American Association of Petroleum Geologists*, Memoir, **84**, 49–175.

Pictet F.-J. 1867. Études paléontologiques sur la faune à *Terebratula dipyoides* de Berrias (Ardèche). Mélanges Paléontologiques, deuxième livraison, pp. 43–150.

Pictet, F.-J. 1868. Étude provisoire des fossiles de la Porte-de-France, d'Aizy et de Lemenc. *Mémoire de la Société de Physique et d'Histoire Naturelle de Genève*, **4**, 207–312.

Pruner, P., Houša, V.F., Oloriz, F., Košak, M.M., Krs, M., Man, O., Schnabl, P., Venhodová, D., Tavera, J.M. and Mazuch, M. 2010. High-resolution magnetostratigraphy and biostratigraphic zonation of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain). *Cretaceous Research*, **31**, 192–206.

Reboulet, S. 1996. L'évolution des ammonites du Valanginien–Hauerivien inférieur du Bassin Vocontien et de la Plateforme provençale (Sud-Est de la France). *Documents des Laboratoires de Géologie Lyon*, **137**, 1–370.

Retowski, O. 1893. Die Tithonische Ablagerungen von Theodosia. Ein Beitrag zur Paläontologie der Krim. *Bulletin de la Société impériale des Naturalistes de Moscou*, *Nouvelle Série*, **7**, 206–301.

Roman, F. 1938. Les ammonites jurassiques et crétacées. Essai de genera, 554 p. Masson; Paris.

Roman, F. and Mazenot, G. 1937. Découverte d'une faune pyriteuse d'âge Tithonique supérieur aux environs de Chomérac (Ardèche). *Bulletin de la Société Géologique de France*, *Série* 5, **7**,179–186.

Salfeld, H. 1921. Kiel- und Furchenbildung auf der Schalenaussenseite der Ammonoideen in ihrer Bedeutung für die Systematik und Festlegung von Biozonen. *Zentralblatt für Mineralogie, Geologie und Paläontologie* (1921), 343–347.

Sapunov, I.G. 1977. Ammonite stratigraphy of the Upper Jurassic in Bulgaria. IV. Tithonian: substages, zones and subzones. *Geologica Balcanica*, **7**, 43–64.

Sapunov, I.G. 1979. Fosilite na B´lgarija. III. 3. Gorna Jurska Serija. Ammonoidea, 263 p. Izdatelstvo na B´lgarskata Akademia na naukite.

Sarasin, C. and Schöndelmayer, C. 1901. Étude monographique des Ammonites du Crétacique inférieur de Châtel-Saint-Denis. *Mémoire de la Société Paléontologique Suisse*, **24**, 95–187.

Sayn, G. 1901–1907. Les ammonites pyriteuses des marnes valanginiennes du sud-est de France. *Mémoires de la Société de France, Paléontologie, Memoire*, **23**, 1–66.

Schindewolf, O.H. 1925. Entwurfeiner Systematik der Perisphinctiden. *Neues Jahrbuch für Geologie und Paläeontologie*, **52**, 309–43.

Spath, L.F. 1923. Appendix: On ammonites from New Zealand. In: Trechmann, C.T. (Ed.), The Jurassic rocks of New Zealand. *The Quarterly Journal of the Geological Society of London*, **79**, 286–308.

Spath, L.F. 1925. Ammonites and aptychi. The collection of fossils and rocks from Somaliland. *Monographs Geological Department of the Hunterian Museum*, **1**, 111–164.

Spath, L.F. 1924. On the ammonites of the Speeton Clay and the subdivisions of the Neocomian. *Geological Magazine*, **61**, 73–89.

Spath, L.F. 1939. The Cephalopoda of the Neocomian Belemnite Beds of the Salt Range. Palaeontologia Indica. *Memoirs of the Geological Survey of India*, *New Series*, 25, Memoir, **1**, 1–154.

Tavera, J.-M. 1985. Les ammonites del Tithonico superior–Berriasense de la Zona Subbetica (Cordilleras Beticas). Ph.D. thesis Universidad de Granada, 381 p.

Tavera, J.-M., Checa, A., Olóriz, F. and Company, M. 1986. Mediterranean ammonites and the Jurassic-Cretaceous boundary in southern Spain (Subbetic Zone). *Acta Geologica Hungarica*, **29**, 151–159.

Tavera, J.-M., Aguado, R., Company, M. and Olóriz, F. 1994. Integrated biostratigraphy of the Durangites and Jacobi Zones (J/K boundary) at the Puerto Escaño section in southern Spain (Province of Cordoba). *Géobios*, **17**, 469–476.

Thieuloy, J.-P. 1971. Réflexions sur le genre *Lyticoceras*. *Comptes Rendus de l'Académie des Sciences*, **272**, 2297–2300.

Toucas, A. 1890. Étude sur la faune des couches tithoniques de l´Ardèche. *Bulletin de la Société Géologique de France*, **18**, 560–629.

Uhlig, V. 1903-1910. Himalayan fossils. The fossils of the Spiti Shales. *Memoirs of the Geological Survey of India*, Palaeontologica Indica, series 15, **4** (1903), 1–132; (1910), 133–306; (1910), 307–395.

Uhlig, V. 1905. Einige Bemerkungen uber die Ammonitengattung *Hoplites* Neumayr. *Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien, mathematisch-naturwissenschaftliche Klasse*, **114**, 591–636.

Vašíček, Z. and Skupien, P. 2013. Early Berriasian ammonites from the Štramberk Limestone in the Kotouč Quarry (Outer Western Carpathians, Czech Republic). *Annales Societatis Geologorum Poloniae*, **83**, 329–342.

Wierzbowski, A. and Remane, J. 1992. The ammonite and calpionellid stratigraphy of the Berriasian and lowermost Valanginian in the Pieniny Klippen (Carpathians, Poland). *Eclogae Geologica Helvetiae*, **85**, 871–891.

Wimbledon, W.A.P., Casellato, C.E., Rehakova, D., Bulot, L.G., Erba, E., Gardin, S., Verreusel, R.M.C.H., Munstermann, D.K. and Hunt, C.O. 2011. Fixing a basal Berriasian and Jurassic/Cretaceous (J/K) boundary – is there perhaps some light at the end of the tunnel? *Rivista Italiana di Paleontologia e Stratigrafia*, **117**, 295–307.

Wimbledon, W. A.P., Reháková, D., Pszczółkowski, A., Casellato, C.E., Halásová, E., Frau, C., Bulot, L.G., Grabowski, J., Sobień, K., Pruner:, Schnabl, P. and Čížková, K. 2013. A preliminary account of the bio- and magnetostratigraphy of the upper Tithonian–lower Berriasian interval at Le Chouet, Drôme (SE France). *Geologica Carpathica*, **64**, 437–460.

Wippich, M.G.E. 2001. Die tiefe Unter–Kreide (Berrias bis Unter-Hauterive) im Südwestmarokkanischen Becken: Ammonitenfauna, Bio- und Sequenzstratigraphie. Phd Thesis University of Ruhr, 474 p.

Wright, C.W., Callomon, J.H. and Howarth, M.K. 1996. Cretaceous Ammonoidea. In: Kaesler, R. Treatise on invertebrate Paleontology, Part L, Molluca 4 Revised, XX + 362 pp. The Geological Society of America, Inc. and University of Kansas.

Zittel, von K. 1868. Die Cephalopoden der Stramberger Schichten. *Paläontologische Mittheilungen aus dem Museum des Königlich–Bayerischen Staates*, **2**, 33–118.

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

GEOLOGICA CARPATHICA, DECEMBER 2016, 67, 6, 543–559 doi: 10.1515/geoca-2016-0034

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

CAMILLE FRAU[1], LUC G. BULOT[2], WILLIAM A.P. WIMBLEDON[3] and CHRISTINA IFRIM[4]

[1]Groupement d'Intérêt Paléontologique, Science et Exposition, 60 bd Georges Richard, 83000 Toulon, France; camille_frau@hotmail.fr
[2]UM 34 Aix-Marseille Université — CNRS (UMR 7330) — IRD (UMR 161), Centre Saint-Charles, Case 67, 3 Place Victor Hugo, 13331 Marseille Cedex 03, France
[3]School of Earth Sciences, University of Bristol, Queens Road, Bristol BS8 1RJ, United Kingdom
[4]Institut für Geowissenschaften, Ruprecht-Karls-Universität, Im Neuenheimer Feld 234, 69120 Heidelberg, Germany

(Manuscript received January 28, 2016; accepted in revised form September 22, 2016)

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

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

Introduction

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

Geological setting

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

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

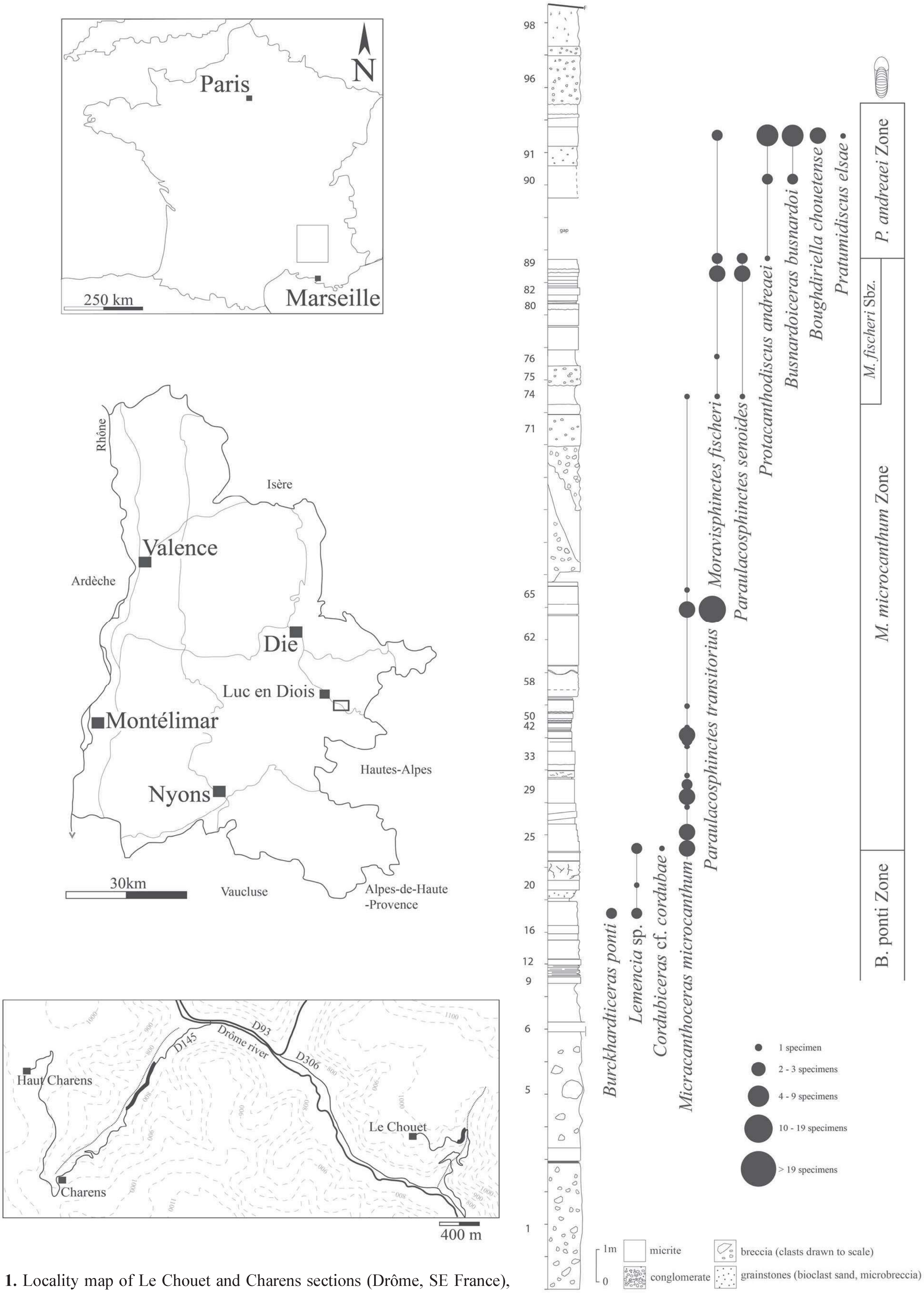


Fig. 1. Locality map of Le Chouet and Charens sections (Drôme, SE France), biostratigraphy and vertical range of the late Tithonian Himalayitidae and Neocomitidae studied in this paper.

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

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

Systematic palaeontology

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

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

FSL and EM: University of Claude Bernard — Lyon-I.
UJF-ID: University of Grenoble.
BSPM: Bayerische Staatssammlung für Paläontologie und Geologie, Munich.

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

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

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

Micracanthoceras microcanthum (Oppel *in* Zittel, 1868)

Figs. 2A–C, 3A,B and 4A,U

Macroconchs [M]

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

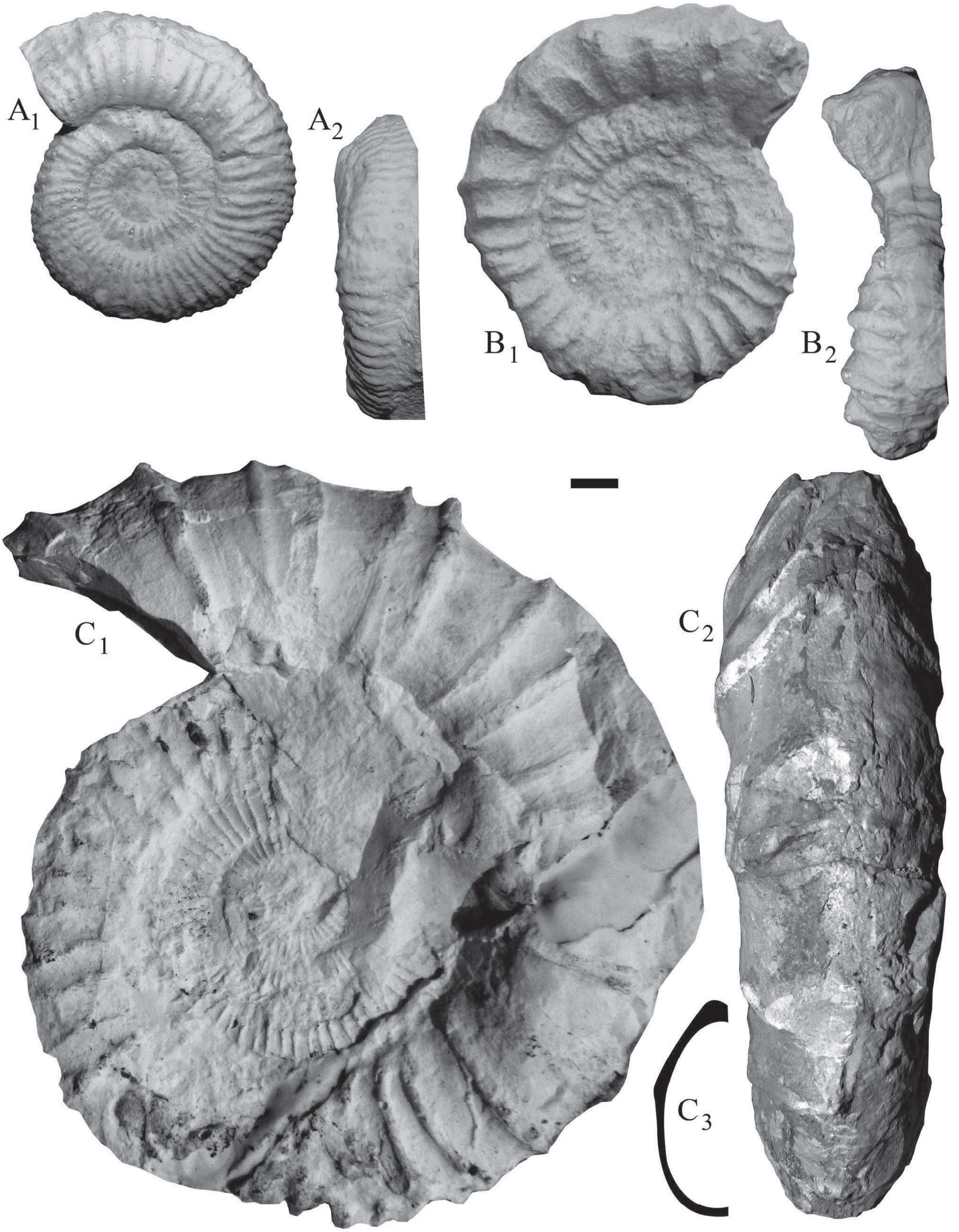


Fig. 2. *Micracanthoceras microcanthum* (Oppel in Zittel, 1868): **A1–2** — plaster cast FSL.136039 of the lectotype of *Ammonites microcanthus* Oppel in Zittel, 1868 [m]; **B1–2** — plaster cast FSL.13049 of *Ammonites symbolus* Oppel in Zittel, 1868 [M]; **C1–3** — MPP–CHR.37/3 [M] bed 37. Scale bar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

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

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

Microconchs [m]

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

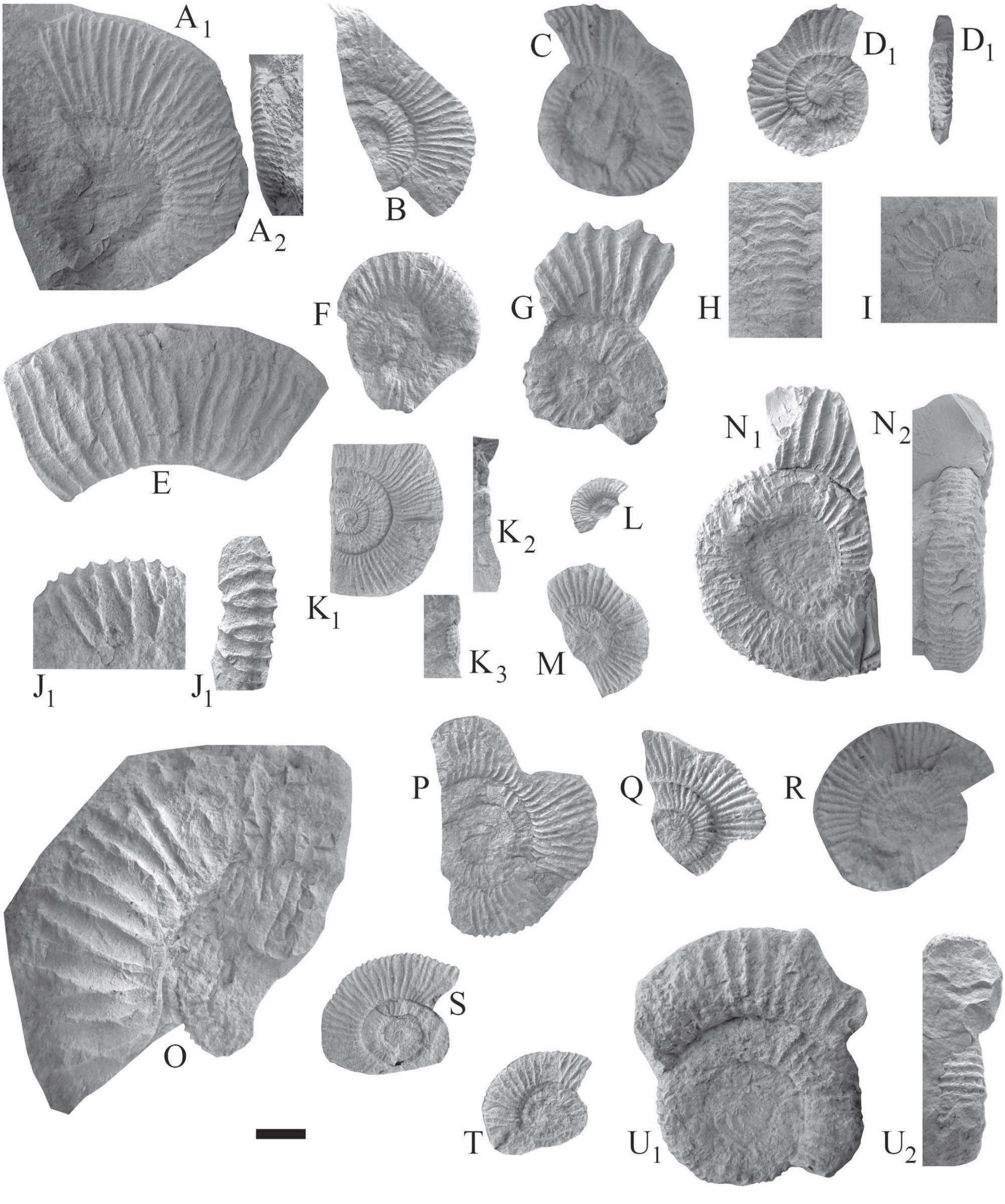


Fig. 4. *Micracanthoceras microcanthum* (Oppel in Zittel, 1868): **A1–2** — MPP–CHR.54/1a [?m] bed 25 (top); **B** — MPP–CHR.34/2 [m] bed 25 (top); **C1–2** — plaster cast of MPP–CHR.29/1 [m] bed 29; **D1–2** — MPP–CHR.50/3 [m] bed 25 (base); **E** — MPP–CHR.34/1 [?M] bed 25 (top); **F** — MPP–CHR.60/6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

1997 *Micracanthoceras microcanthum* (Oppel) – Benzaggagh & Atrops, pl. 5, fig. 4

1997 *Micracanthoceras microcanthum* (Oppel) – Geyssant *in* Cariou & Hantzpergue, pl. 26, fig. 1 (= Zittel, 1868, pl. 17, fig. 3a,b)

non 1998 *Micracanthoceras fraudator* (Zittel) – Howarth, p. 79, pl. 15, fig. 2a,b (= Perisphinctoidea indet.)

non 1999 *Micracanthoceras fraudator* (Zittel) – Fatmi & Zeiss, p. 97, pl. 45, fig. 3a,b, pl. 55, fig. 5a,b [= *Micracanthoceras brightoni* (Spath)]

2000 *Micracanthoceras microcanthum* (Oppel) – Benzaggagh, pl. 4, fig. 4 (= Benzaggagh & Atrops, 1997, pl. 5, fig. 4)

non 2009 *Micracanthoceras* cf. *microcanthum* (Oppel) – Shome & Bardhan, p. 199, pl. 4, figs. a,g [= *Micracanthoceras brightoni* (Spath)]

2004 *Micracanthoceras microcanthum* (Oppel) – Marino et al., pl. 2, fig. 7

2005 *Micracanthoceras* sp. gr. *microcanthum* (Oppel) – Boughdiri et al., pl. 2, fig. 9, 10

2005 *Aulacosphinctes* sp. gr. *sulcatus* Tavera – Boughdiri et al., pl. 2, fig. 7

non 2012 *Micracanthoceras microcanthum* (Oppel) – Salazar, p. 90, figs. 4.13a,m (= *Steueria* sp.)

2010 *Aulacosphinctes* sp. – Benzaggagh et al., fig. 5d,e

non 2015 *Micracanthoceras microcanthum* (Oppel) – Salazar & Stinnesbeck, p. 19, figs. 15a,m (= Salazar, 2012, figs. 13a,m)

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

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

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

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

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

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

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

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

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

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

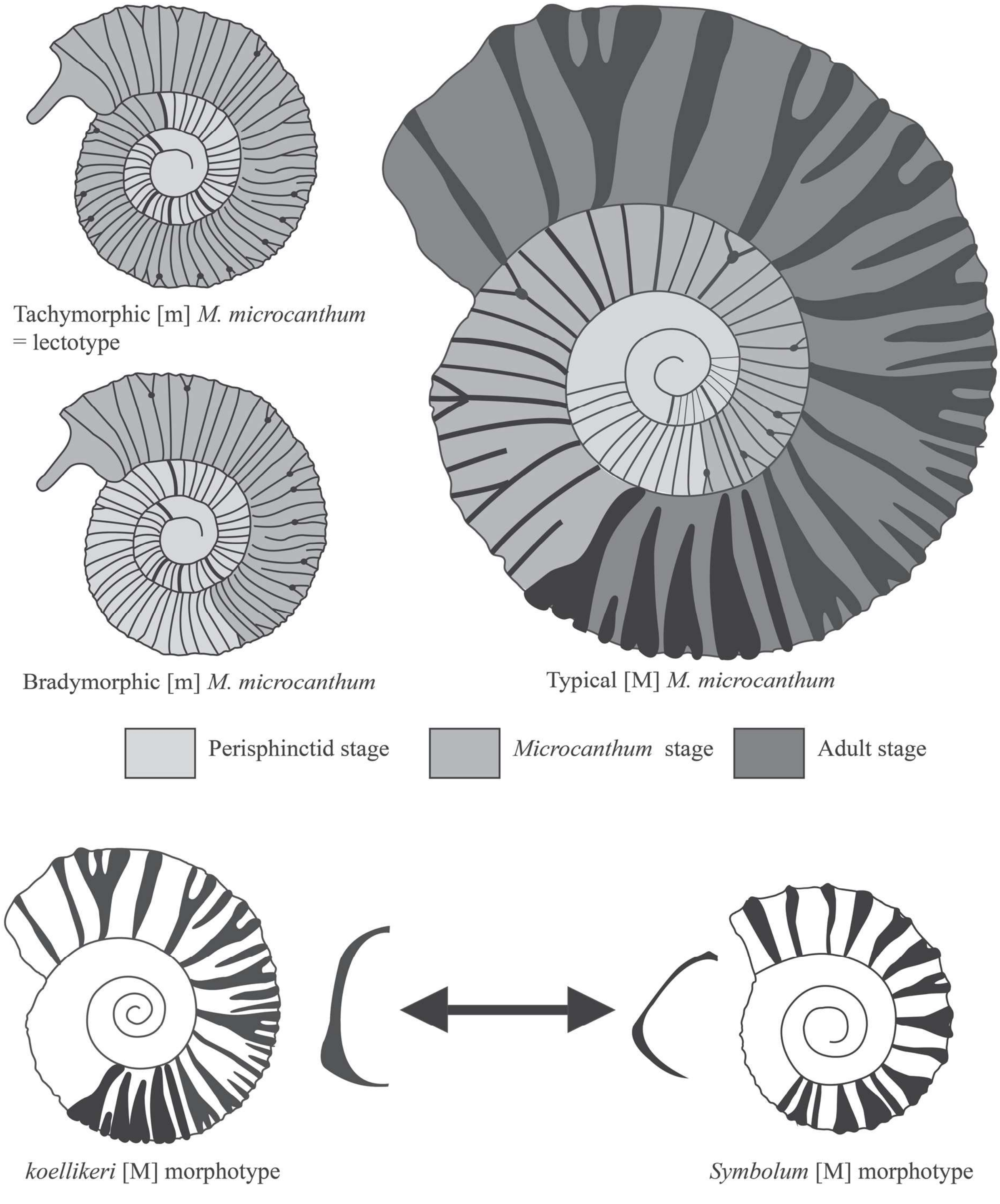


Fig. 5. Supposed dimorphism and intraspecific variations observed in *Micracanthoceras microcanthum* (Oppel, 1865). Note that microconchs show different rates of shell morphogenesis (tachymorphic versus bradymorphic variants), while macroconchs range between two extreme (robust versus slender) morphologies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

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

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

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

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

- juveniles of *M. microcanthum* (compare Tavera 1985, pl. 17, fig. 3, 4a,b and Benzaggagh et al. 2010, fig. 5d,e with MPP-CHR.50/3 on Fig. 4D) or;
- gracile microconchs of *M. microcanthum* (compare Nikolov 1982, pl. 78, fig. 5 and Sapunov 1979, pl. 59, fig. 1, 2a,b with MPP-CHT.92/13 and MPP-CHR.92/10 on Fig. 4S and 4T).

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

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

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

Genus *Protacanthodiscus* Spath, 1923

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

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

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

Macroconchs [M]

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

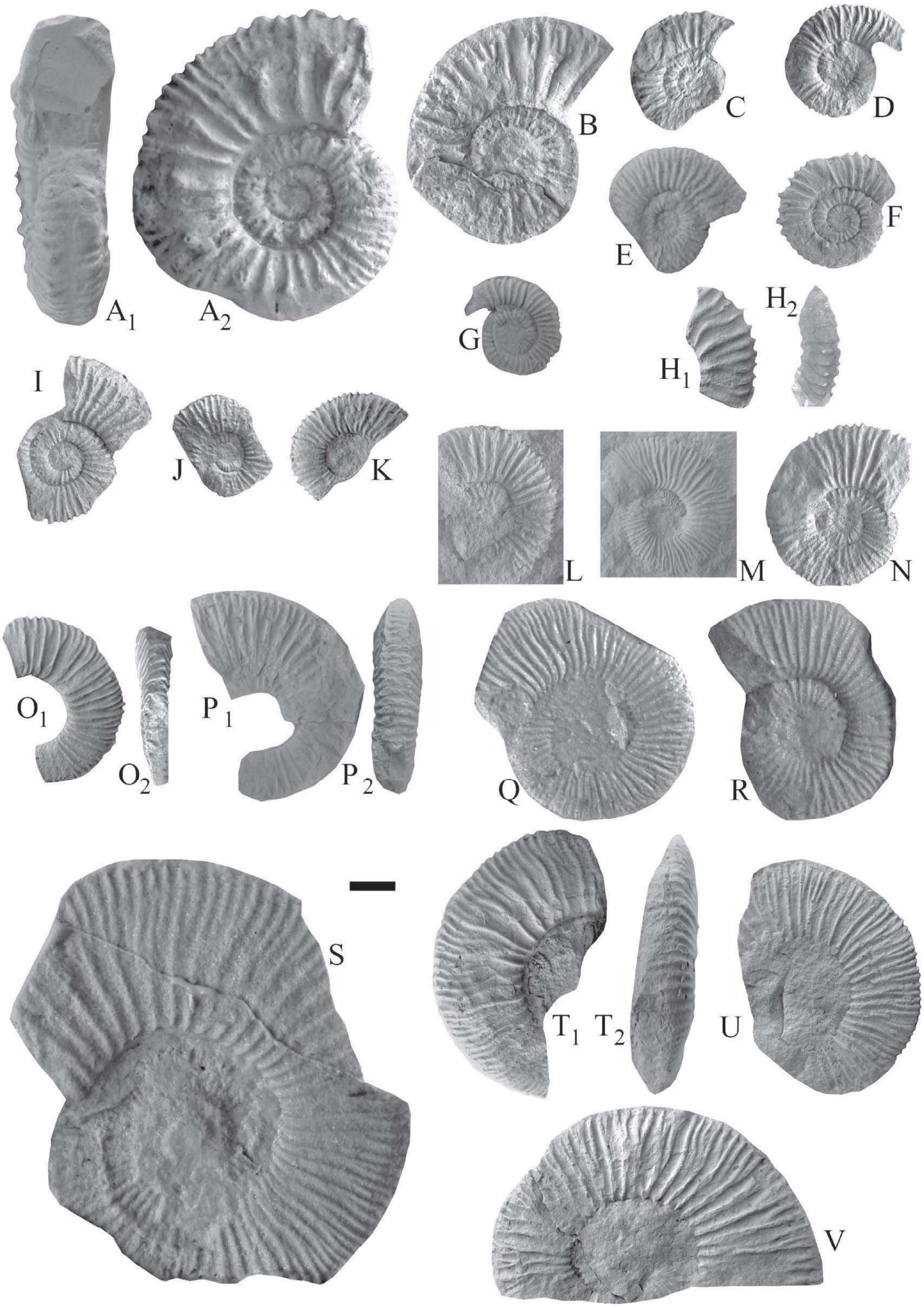


Fig. 6. *Protacanthodiscus andreaei* (Kilian, 1889): **A1–2** — Plaster cast of the holotype (FSL.13056); **B** — MPP–CHR.79/4 [M] bed 89; **C** — MPP–CHR.21/25 [m] bed 92. *Boughdiriella chouetense* Frau, Bulot & Wimbledon, 2015 nom. correct.: **D** — MPP–CHR.21/24 [m] bed 92; **E** — plaster cast of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

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

Microconchs [m]

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

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

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

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

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

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

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

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

Genus *Boughdiriella* Frau, Bulot & Wimbledon, 2015

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

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

Boughdiriella chouetense Frau, Bulot & Wimbledon, 2015 nom. correct.

Figs. 6D–G

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

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

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

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

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

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

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

Genus *Pratumidiscus* Bulot, Frau & Wimbledon, 2014

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

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

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

Pratumidiscus elsae Bulot, Frau & Wimbledon, 2014

Fig. 6H

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

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

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

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

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

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

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

Family **Neocomitidae** Salfeld, 1921

Genus *Busnardoiceras* Tavera, 1985

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

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

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

Macroconchs [M]

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

Microconchs [m]

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

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

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

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

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

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

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

Conclusion

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

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

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

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

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

Acknowledgements: This work is a contribution of the Berriasian Working Group (BWG) of the International Subcommission on Cretaceous Stratigraphy (I.S.C.S.). Jean-Marc Chabal, mayor of Charens, is gratefully acknowledged for providing access to the Charens section. Cyprien Lanteaume (Aix-Marseille Université) and Emile Hourqueig (Toulouse) are acknowledged for their help in collecting ammonites from the Charens section and for their continuous support during the fieldwork seasons of the first author (C.F.). The authors are indebted to Daniela Reháková (Comenius University) for providing the preliminary results on the calpionellid assemblages for the Charens section and Emmanuel Robert (University of Lyon I) for providing access to the collections under his care. Horacio Parent (Universidad Nacional de Rosario) is gratefully acknowledged for valuable discussion, photographs and measures of *Ammonites Koellikeri*. We thank the two anonymous reviewers for their useful comments. Warm thanks are due to the Jean-Pierre Lopez, Martine Broin and their families (Le Chouet and Les Près, France) for their hospitality and friendship during our fieldwork seasons, and to Elsa Schnebelen-Bulot (Saint-Privat-de-Champclos) for her continuous support during this study.

References

Arkell W.J., Kummel B. & Wright C.W. 1957: Mesozoic Ammonoidea. In: Moore R.C. (Ed.): Treatise of Invertebrate Paleontology, Part L, Mollusca 4, Cephalopoda, Ammonoidea. *The Geological Society of America & The University of Kansas Press*, New York & Lawrence, 80–437.

Bahrouni N., Houla Y., Soussi M., Boughdiri M., Ben Ali W., Nasri A. & Bouaziz S. 2016: Discovery of Jurassic ammonite bearing series in Jebel Bou Hedma (South-Central Tunisian Atlas). Implications for stratigraphic correlations and paleogeographic reconstruction. *J. Afr. Earth Sci.* 113, 101–113.

Benzaggagh M. 2000: Le Malm supérieur et le Berriasien dans le Prérif interne et le Mésorif (Rif, Maroc) — biostratigraphie, lithostratigraphie, paléogéographie et évolution tectono-sédimentaire. *Doc Lab. Géol. Fac. Sci. Lyon* 152, 1–347.

Benzaggagh M. & Atrops F. 1997: Stratigraphie et associations de faune d'ammonites des zones du Kimméridgien, Tithonien et Berriasien basal dans le Prérif interne (Rif, Maroc). *Newsl. Stratigr.* 35, 127–163.

Benzaggagh M., Cecca F. & Rouget I. 2010: Biostratigraphy distribution of ammonites and calpionellids in the Tithonian of the internal Prerif (Msila area, Morocco). *Pal. Zeitschrift* 84, 301–315.

Besairie H. 1936: Recherche géologiques à Madagascar. 1. La géologie du Nord-Ouest. *Mém. Acad. Malgache* 21, 1–259.

Beznosov N.V. & Mitta V.V. 1995: Polymorphism in the Jurassic ammonoids. *Paleontol. J.* 29, 46–57.

Boughdiri M. 1994: Les genres d'ammonites *Durangites* et *Protacanthodiscus* (Tithonien supérieur) dans la Téthys occidentale (SE Espagne, SE France, Algérie et Tunisie). Stratigraphie, Paléontologie et Biogéographie. *PhD thesis, Université Claude*

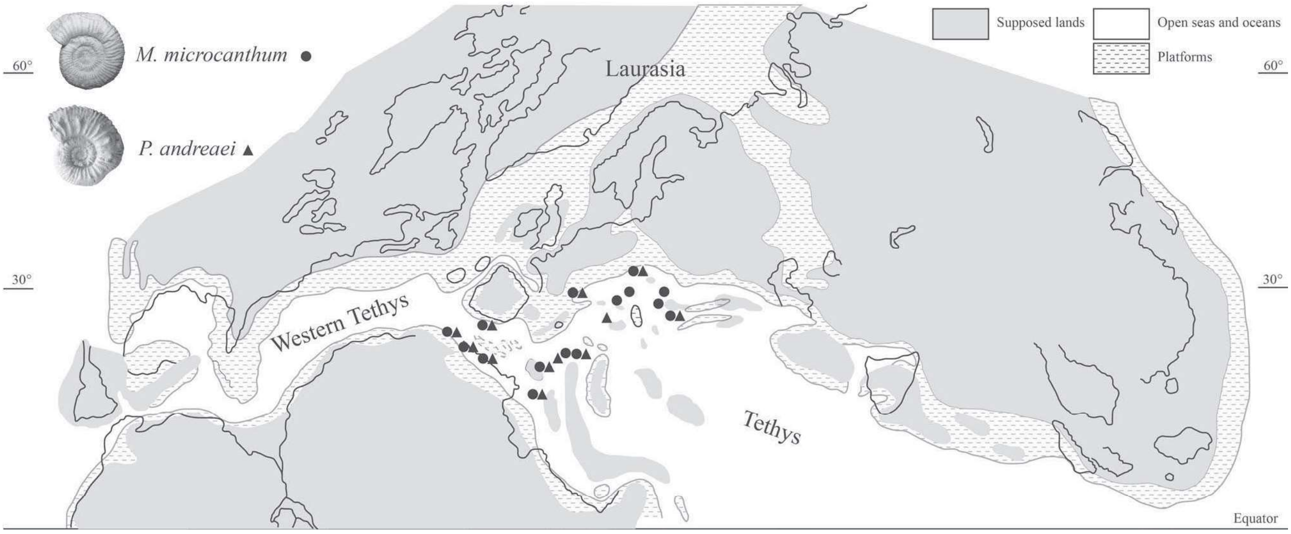


Fig. 7. Palaeo-biogeographical distribution of the two index species *Micracanthoceras microcanthum* (Oppel in Zittel, 1868) and *Protacanthodiscus andreaei* (Kilian, 1889) during the upper Tithonian (palaeogeographical map of the northern hemisphere modified after Cecca 1999).

Bernard Lyon I, 1–268.

Boughdiri M., Olóriz F., Lopez Marques B., Layeb M., De Matos E. & Sallouhi H. 2005: Upper Kimmeridgian and Tithonian Ammonites from the Tunisian "Dorsale" (NE Tunisia), updated biostratigraphy from J. Oust. *Riv. Ital. Paleontol. S.* 111, 305–316.

Bujtor L., Krische O. & Gawlick H.-J. 2013: Late Berriasian ammonite assemblage and biostratigraphy of the Leube quarry near Salzburg (Northern Calcareous Alps, Austria). *N. Jb. Geol. Palaont. Abh*. 267, 273–295.

Bulot L.G., Frau C. & Wimbledon W.A.P. 2014: New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Les Près, Drôme, SE France). *Volumina Jurassica* 12, 113–128.

Burckhardt C. 1900: Profils géologiques transversaux de la Cordillère Argentino-Chilienne. *Museo La Plata Sección Geológica y Mineralógica*, *Anales II*, La Plata, 1–136.

Burckhardt C. 1903: Beiträge zur Kenntnis der Jura, und Kreideformation der Cordillera. *Palaeontographica* 50, 1–144.

Burckhardt C. 1921: Faunas jurasicas de Symon (Zacatecas) (Atlas). *Bol. Inst. Geol. Mexico* 33, 32 pl.

Callomon J.H. 1985: Biostratigraphy, chronostratigraphy and all that — again! *Proceedings of the International Symposium on Jurassic Stratigraphy,* Erlangen 1984 3, 611–624.

Cecca F. 1985: On some ammonites from the "Maiolica" of Central Apennines (Umbria, Marche e Sabina). *Boll. Serv. Geol. Italia* 103, 133–162 (in Italian with English summary).

Cecca F. 1999: Palaeobiogeography of Tethyan ammonites during the Tithonian (latest Jurassic). *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 147, 1–37.

Cecca F., Cresta S. & Santantonio M. 1983: Ammonites from the Malm of the Marchigiana Apennines deposited in the Museum of the Geological Survey of Italy. *Boll. Serv. Geol. Italia*, 102 109–132 (in Italian with English summary).

Cecca F., Enay R. & Le Hégarat G. 1989: L'Ardescien (Tithonique supérieur) de la région stratotypique, p. série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. *Doc. Lab. Géol. Fac. Sci. Lyon* 107, 1–115.

Christ H.A. 1960: Beiträge zur Stratigraphie und Paläontologie des Malm von Westsizilien. *Schweiz. Paläontol. Abh*. 77, 1–44.

Collignon M. 1960: Atlas des fossiles caractéristiques de Madagascar. Fascicule VI (Tithonique). *Serv. Géol. Madagascar*, Tananarive, 1–175.

Dacqué E. 1934: Wirbellose des Jura. In: Gürich G. (Ed.): 7. Lieferung. Leitfossilien. *Borntraeger*, Berlin, 1–582.

De Wever P., Geyssant J.R., Azéma J., Devos I., Duée G., Manivit H. & Vrielynck B. 1986: La coupe de Santa Anna (Zone de Sciacca, Sicile): une synthèse biostratigraphique des apports macro-, micro- et nannofossiles du Jurassique supérieur et Crétacé inférieur. *Rev. Micropal.* 29, 141–186.

Eliáš M. & Vašíček V. 1995: Early Berriasian ammonites from the Štramberk Limestone of Kotouč quarry (Outer Carpathians, Silesian Unit, Štramberk, Czech Republic). *Bull. Czech Geol. Surv.* 70, 1–32.

Enay R. & Geyssant J.R. 1975: Faunes tithoniques des chaînes bétiques (Espagne méridionale). *Mém. Bur. Rech. Géol. Min.* 86, 39–55.

Enay R., Boughdiri M. & Le Hégarat G. 1998: *Durangites*, *Protacanthodiscus* (Ammonitina) et formes voisines du Tithonien supérieur-Berriasien dans la Téthys méditerranéenne (SE France, Espagne, Algérie et Tunisie). *C.R. Acad. Sci., Paris*, Série 2a, Sciences de la Terre et des Planètes 327, 425–430.

Fallot P. & Termier H. 1923: Ammonites nouvelles des îles Baléares. *Tra. Mus. Nac. Ci. Nat.*, Madrid, Série Geológica 32, 1–83.

Fatmi A.N. 1973: Late Jurassic and early Cretaceous (Berriasian) ammonites from Shaikh Budin Hills, D.I. Khan, N.W.F.P., Pakistan. *Rec. Geol. Surv. Pak.* 21, 2, ii+1–22.

Fatmi A.N. & Zeiss A. 1999: First Jurassic and Lower Cretaceous (Berriasian) ammonites from the Sembar Formation (Belemnite shales). Windar Nai. Lasbela — Balochistan, Pakistan. *Geol. Surv. Pak. Mem.* 19, 1–114.

Ferry S. & Grosheny D. 2013: Turbidites et brèches carbonatées (Jurassique et Crétacé du bassin subalpin). Livret-guide excursion ASF-GFC (20–23 novembre 2013). *http://hal.archives-ouvertes.fr/hal-00908177/fr/*, 1–101.

Frau C., Bulot L.G. & Wimbledon W.A.P. 2015: Upper Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): implications for the systematics. *Geol. Carpath.* 66, 117–132.

Főzy I. 1990: Ammonite succession from three Upper Jurassic sections in the Bakony Mts. (Hungary). In: Pallini G., Cecca F., Cresta S. & Santantonio M. (Eds): Atti II° Convegno Fossili, Evoluzione, Ambiente. Pergola, 323–339.

Főzy I. 1995: Upper Jurassic ammonites from Seno di Guidaloca (Western Sicily). *Hantk.Géczy Jub.* 1, 131–143.

Geyssant J.R. 1997: Tithonien. In: Cariou E. & Hantzpergue P. (Eds.): Biostratigraphie du Jurassique ouest européen et méditerranéen, p. zonations parallèles et distribution des invertébrés et microfossiles. *Elf Aquitaine édition*, 97–102

Haas J., Emoke J.E., Gidai L. Kaiser M., Kretzoi M. & Oravecz J. 1985: Geology of the Sümeg Area. *Geol. Hungarica* 20, 1–250.

Howarth M.K. 1998: Tithonian and Berriasian ammonites from the Chia Gara Formation of northern Iraq. *Palaeontology* 35, 597–655.

Imlay R.W. 1939: Upper Jurassic ammonites from Mexico. *Geol. Soc. Amer. Bull.* 50, 1–78.

Ivanov M., Stoykova K. & Idakieva V. 2010: New biostratigraphic data on the Upper Tithonian and Lower Berriasian in the Krayshte area (Southwestern Bulgaria). *Annuaire Univ. Sofia "St. Kliment Ohridski"* 102, 21–42.

Kaiser-Weidich B. & Schaier G. 1989: Stratigraphische Korrelation von Ammoniten, Calpionellen und Nannoconiden aus Oberjura und Unterkreider der Nördlichen Kalkalpen. *Ecl. Geol. Helv.* 83, 353–387.

Khimchiashvili N.G. 1976: Tithonian and Berriasian ammonites of the Caucasus. Tbilisi, 1–180.

Kilian W. 1889: Etudes paléontologiques sur les terrains secondaires et tertiaires de l'Andalousie. *Mém. Acad. Sci. Inst. France* 30, 580–733.

Krantz F. 1928: The fauna from the upper and middle Tithonian of the Argentina Cordillera in the southern part of the Mendoza province. *Act. Acad. Nac. Ciencas* 10, 5–57 (in Spanish).

Ksiazkiewicz M. 1956: Jurassic and Cretaceous of Bachowice. *Rocz. Pol. Tow. Geol.* 23, 119–405 (in Polish).

Le Hégarat G. 1973: Le Berriasien du sud-est de la France. *Doc. Lab. Géol. Fac. Sci. Lyon* 43, 1–576.

Linares A. & Vera J.A. 1966: Precisiones estratigráficas sobre la serie mesozoica de Sierra Gorda, Cordilleras Béticas (provincia de Granada). *Estud. Geol.* 22, 65–99.

Marino M. C. Andreini G., Baldanza A., D'Arpa C., Mariotti N., Pallini G., Parisi G. & Petti F. M. 2004: Middle Jurassic–early Cretaceous integrated biostratigraphy (ammonites, calcareous nannofossils and calpionellids) of the Contrada Diesi section (south-western Sicily, Italay). *Riv. Ital. Paleontol. S.* 110, 357–372.

Mazenot G. 1939: Les Palaeophoplitidae tithoniques et berriasiens du sud est de la France. *Mém. Soc. Géol. France*, Nouvelle Série 18 41, 1–303.

Mitta V.V. 2011: Ammonites of Tethyan origin in the Ryazanian Stage of the Russian Platform: Genus *Riasanella* gen. nov. *Paleontol J.* 45, 13–22.

Nicolis E. & Parona C.F. 1886: Stratigraphic and palaeontologic note on the Upper Jurassic from the Verona province. *B. Soc. Geol.*

Ital. 4 (1885), 1–96 (in Italian).

Nikolov T.G. 1982: Les Ammonites de la famille Berriasellidae Spath, 1922. Tithonique supérieur-Berriasien. *Acad. Bul. Sci.* 10, 1–251.

Olóriz F. 1978: Kimmeridgiense-Tithonico inferior en el Sector central de las Cordilleras Béticas (Zona Subbética). *PhD thesis, Universidad de Granada*, 1–758.

Olóriz F. & Tavera J.M. 1979: Nuevo Simoceratinae — *Simoceras* (*Cordubiceras*) — en la base del Tithónico Superior de las Cordilleras Béticas (Zona Sub-Bética). *Tecniterrae* 29, 1–5.

Oppel A. 1863: Über jurassische Cephalopoden. *Palaeont. Mitt. Mus. Koeniglich-Bayerischen Staates* 3, 127–266.

Oppel A. 1865: Die tithonische Etage. *Zeit. Deut. Geol. Ges.* 17, 535–558.

Parent H., Scherzinger A. & Schweigert G. 2011: The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina. *Bol. Inst. Fisio. y Geol.* 79–81, 21–94.

Pervinquière L. 1907: Étude de paléontologie tunisienne. I. Céphalopodes des terrains secondaires. Direction générale des Travaux publics. Carte géologique de la Tunisie. *De Rudeval,* Paris, 1–438.

Pruner P., Houša V. F., Oloriz F., Košak M. M., Krs M., Man O., Schnabl P., Venhodová D., Tavera J.-M. & Mazuch M. 2010: High-resolution magnetostratigraphy and biostratigraphic zonation of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain). *Cretaceous Res.* 31, 192–206.

Remane J. 1970: Die Entstehung der resedimentären Breccien im Obertithon der subalpinen Ketten Frankreichs. *Ecl. Geol. Hel.* 63, 685–740.

Roman F. 1897: Recherches stratigraphiques et paléontologiques dans le Bas-Languedoc. *Ann. Univ. Lyon* 34, 1–345.

Roman F. 1936: Le Tithonique du massif du Djurdjura (province d'Alger). *Mat. Carte Géol. Algérie*, Paléontologie 7, 1–43.

Roman F. 1938: Les ammonites jurassiques et crétacées. Essai de genera. *Masson,* Paris, 1–554.

Salazar C.A. 2012: The Jurassic–Cretaceous boundary (Tithonian–Hauterivian) in the Andean Basin of Central Chile:. ammonites, bio- and sequence stratigraphy and palaeobiogeography. *PhD. thesis, Rupecht-Karls-Universität Heidelberg*, 1–389.

Salazar C. & Stinnesbeck W. 2015: Tithonian–Berriasian ammonites from the Baños del Flaco Formation, central Chile. *J. Syst. Paleontol.* 0, 1–34.

Salfeld H. 1921: Kiel- und Furchenbildung auf der Schalenaussenseite der Ammonoideen in ihrer Bedeutung für die Systematik und Festlegung von Biozonen. *Zent. Min. Geol. Pal.* (1921), 343–347.

Sapunov I.G. 1977: Ammonite stratigraphy of the Upper Jurassic in Bulgaria. IV. Tithonian, substages, zones and subzones. *Geol. Balcanica* 7, 43–64.

Sapunov I.G. 1979: Fossils from Bulgaria. III. 3. Upper Jurassic series. Ammonoidea. *Izdat. B´lgarskata Akad. naukite*, Sofia, 1–263 (in Bulgarian with French summary).

Shome S. & Bardhan S. 2009: A new Late Tithonian ammonite assemblage from Kutch, Western India. *J. Pal. Soc. India* 54, 1–18.

Spath L.F. 1923: On ammonites from New Zealand. In: Trechmann C.T. (Ed.): The Jurassic rocks of New Zealand. *Quarterly J. Geol. Soc. London* 79, 286–308.

Spath L.F. 1925: Ammonites and aptychi. The collection of fossils and rocks from Somaliland. *Mono. Geol. Dep. Hunt. Museum* 1, 111–164.

Spath L.F. 1931: Revision of the Jurassic cephalopod fauna of Kachh (Cutch). Part IV. *Pal. Indica* 9, 1–945.

Steuer A. 1897: Argentinische Jura-Ablagerungen: Ein Beitrag zur Kenntniss der Geologie und Palaeontologie der argentinischen Anden. *Palaeontol. Abh., Jena new series* 7, 127–222.

Steuer A. 1922: Jurassic strata from Argentina. *Act. Acad. Nac. Cie. Córdoba* 7, 25–128 (in Spanish).

Szives O. & Főzy I. 2013: Systematic descriptions of Early Cretaceous ammonites of the carbonate formations of the Gerecse Mountains. In: Főzy I. (Ed.): Late Jurassic-Early Cretaceous fauna, biostratigraphy, facies and deformation history of the carbonate formations in the Gerecse and Pilis Mountains (Transdanubian Range, Hungary). *GeoLitera Publishing House,* Szeged, 293–342.

Tavera J.- M. 1985: The ammonites from the Upper Tithonian-Berriasian of the Subbetic zone (Betic Cordillera). *PhD. Thesis, Universidad de Granada*, 1–381 (in Spanish).

Toucas A. 1890: Étude sur la faune des couches tithoniques de l´Ardèche. *Bull. Soc. Géol. France* 18, 560–629.

Uhlig V. 1910: The Fauna of the Spiti Shales. *Memoirs of the Geological Survey of India*, *Pal. Indica* 15, 133–395.

Vigh G. 1984: Die biostratigraphische Auswertung einiger Ammoniten-Faunen aus dem Tithon des Bakonygebirges sowie aus dem Tithon-Berrias des Gerecsegebirges. *Ann. Inst. Geol. Hungarica* 67, 1–210.

Westermann G.E.G. 2000: Biochore classification and nomenclature in paleobiogeography: an attempt at order. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 158, 1–13.

Wimbledon W.A.P., Reháková D., Pszczółkowski A., Cassellato C.E., Halásová E., Frau C., Bulot L.G., Grabowski J., Sobień K., Pruner P., Schnabl P. & Čížková K. 2013: A preliminary account of the bio- and magnetostratigraphy of the upper Tithonian–lower Berriasian interval at Le Chouet, Drôme (SE France). *Geol. Carpath.* 64, 437–460.

Windhausen A. 1931: Geology of Argentina. Second Part, Historical and regional geology of the territory of Argentina. 1–645 (in Spanish).

Wippich M.G.E. 2001: Die tiefe Unter-Kreide (Berrias bis Unter-Hauterive) im Südwestmarokkanischen Becken: Ammonitenfauna, Bio- und Sequenzstratigraphie. *PhD Thesis, University of Ruhr,* Bochum, 1–474.

Yin T.H. 1931: Etude de la faune du Tithonique coralligène du Gard et de l'Hérault. *Trav. Lab. Géol. Fac. Sci. Lyon* 18, 1–193.

Zittel von K. 1868: Die Cephalopoden der Stramberger Schichten. *Pal. Mitt. Mus. Königlich-Bayerischen Staates* 2, 33–118.

SUPPLEMENTARY DATA

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

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

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

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

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

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

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

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

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

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

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

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

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

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

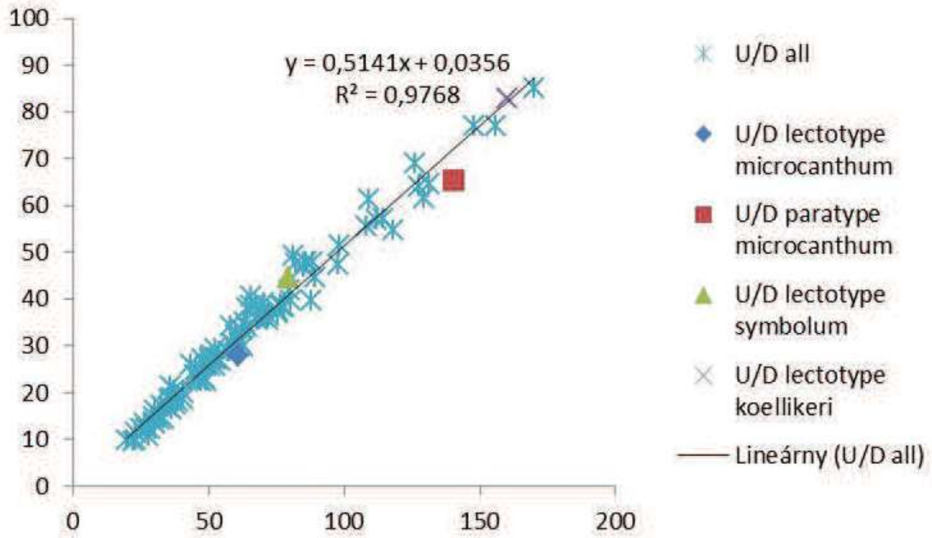


Fig. S1. *U=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

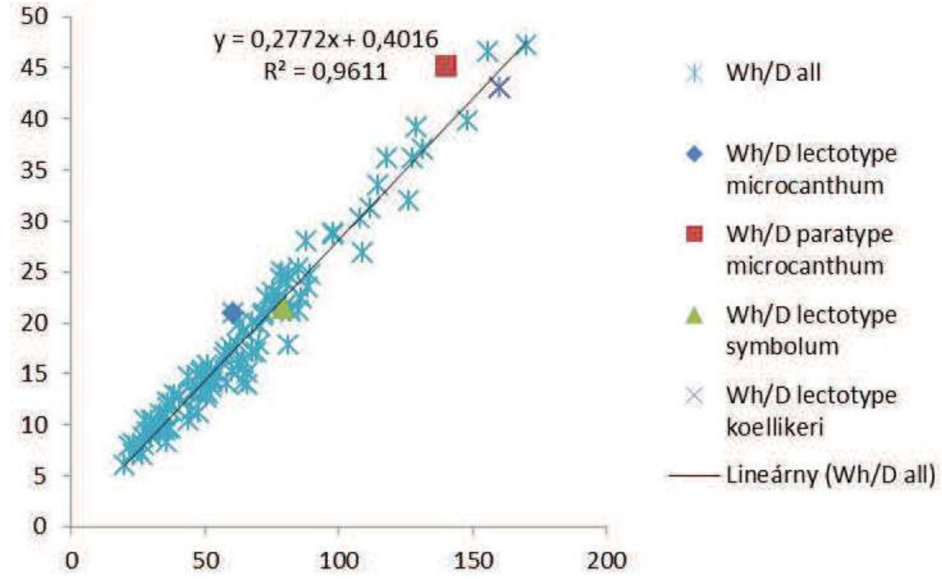


Fig. S2. *Wh=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

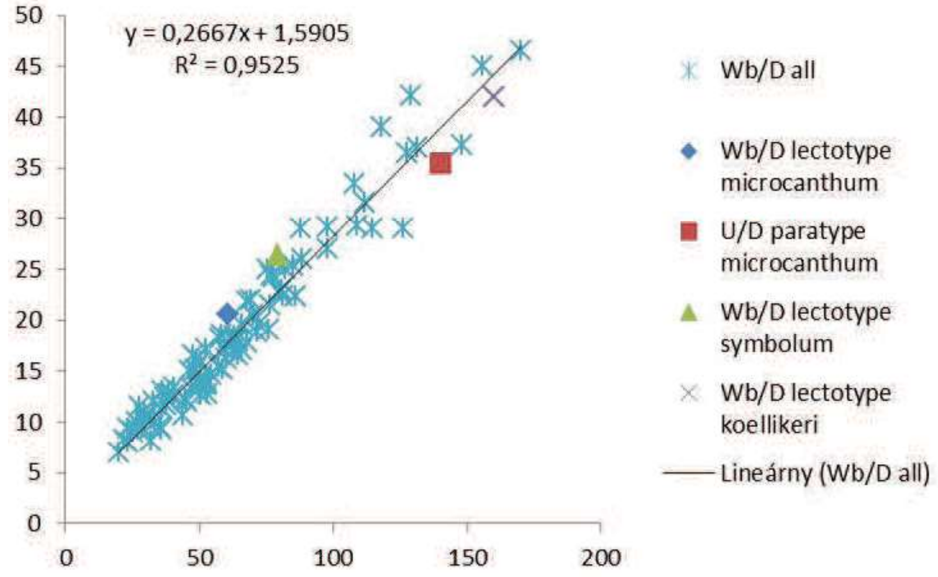


Fig. S3. *Wb=f(D)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

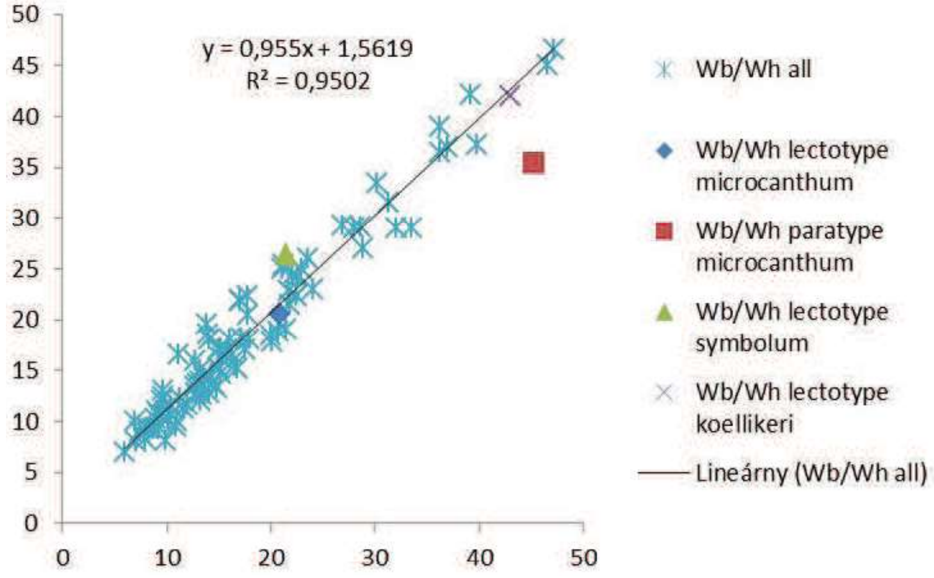


Fig. S4. *Wb=f(Wh)* for Spanish specimens referred to *M. microcanthum* and comparison with type specimens.

Cretaceous Research 66 (2016) 94–114

Contents lists available at ScienceDirect

Cretaceous Research

journal homepage: www.elsevier.com/locate/CretRes

Revision of the ammonite index species *Berriasella jacobi* Mazenot, 1939 and its consequences for the biostratigraphy of the Berriasian Stage

Camille Frau [a], [*], Luc G. Bulot [b], Daniela Reháková [c], William A.P. Wimbledon [d], Christina Ifrim [e]

[a] *Groupement d'Intérêt Paléontologique, Science et Exposition, 60 bd Georges Richard, 83000 Toulon, France*
[b] *UM 34 Aix–Marseille Université – CNRS (UMR 7330) – IRD (UMR 161), Centre Saint–Charles, Case 67, 3 Place Victor Hugo, 13331 Marseille Cedex 03, France*
[c] *Department of Geology and Palaeontology, Faculty of Natural Sciences, Comenius University, Mlynska dolina, Ilkovičova 6, SK–84215 Bratislava, Slovak Republic*
[d] *School of Earth Sciences, University of Bristol, Wills Memorial Building, Queens Road, Bristol BS8 1RJ, United Kingdom*
[e] *Institut für Geowissenschaften, Ruprecht–Karls–Universität, Im Neuenheimer Feld 234, 69120 Heidelberg, Germany*

ARTICLE INFO

Article history:
Received 26 January 2016
Received in revised form
25 May 2016
Accepted in revised form 29 May 2016
Available online 4 June 2016

Keywords:
Berriasella jacobi
Berriasian
Calpionellids
Ammonite biostratigraphy
Ardèche
France

ABSTRACT

Berriasella jacobi is a key ammonite taxon that has been widely used for the definition of the Tithonian/Berriasian boundary and has been widely quoted in the literature as the index species for the lowest zone of the Berriasian Stage. The taxonomic revision of *B. jacobi* shows that it should be excluded from the genus *Berriasella* and transferred to the genus *Strambergella*. Analysis of the literature has convinced us that most specimens illustrated as *B. jacobi* have been misidentified. New collection at Le Font de Saint Bertrand (Les Combes, Glandage, Drôme, France) shows us the type series corresponds to the microconch form of a dimorphic pair. New integrated data on its stratigraphic distribution causes us to question its value as an index species for the base of the Berriasian.

1. Introduction

The latest Jurassic to earliest Cretaceous time interval is a critical period for marine biota including ammonite faunas which were affected by a global sea–level lowstand and developments of episodic, or permanent, dys– to anaerobic conditions in seaways and marginal seas (Föllmi, 2012 with references). These conditions led to high provincialism in both species and genera due to the separation of the Tethyan and boreal regions (Lehmann et al., 2015). Despite these considerations, *Berriasella* Uhlig, 1905 is still considered as a cosmopolitan genus since its supposed recognition in southern and central Europe, North Africa, Madagascar, Turkey, Crimea, Iran, the Himalayas, New Caledonia, New Zealand, California, Mexico and Argentina (Wright et al., 1996).

Among the many species of the genus, *Berriasella jacobi* Mazenot, 1939 has been widely quoted throughout the Tethyan Realm and its first occurrence has been assumed to mark the base of the Berriasian (base of the Jacobi Zone *sensu* Le Hégarat, 1973 or base of the Euxinus Zone *sensu* Hoedemaeker, 1982 - see discussion in Wimbledon et al., 2011). This level was also assumed to correlate with the base of the calpionellid Calpionella Standard Zone (Enay and Geyssant, 1975; Remane et al., 1986; Cecca et al., 1989; Grün and Blau, 1997; Boughdiri et al., 2009; Benzaggagh et al., 2010). However, this view has been altered by recent investigations in southeast Spain (Tavera et al., 1994; Pruner et al., 2010) and France (Wimbledon et al., 2013) that showed that a distinctive ammonite assemblage that includes *Elenaella cularense* (Mazenot, 1939) and *Lopeziceras chaperi* (Pictet, 1868)

---

[*] Corresponding author.
E-mail addresses: camille_frau@hotmail.fr (C. Frau), bulot@cerege.fr (L.G. Bulot), rehakova@fns.uniba.sk (D. Reháková), mishenka1@yahoo.co.uk (W.A.P. Wimbledon), christina.ifrim@geow.uni-heidelberg.de (C. Ifrim).

http://dx.doi.org/10.1016/j.cretres.2016.05.007

characterizes the *E. cularense* biohorizon at the base of the Jacobi Zone *auctorum*. In both areas, this assemblage occurs in the upper part of the *Crassicollaria intermedia* Subzone of the Crassicollaria Standard Zone.

According to Tavera et al. (1994), *B. jacobi* does not occur at this level in Spain and this view is confirmed by our own observations in southeast France (Wimbledon et al., 2013; Bulot et al., 2014). As a consequence, the base of the *Jacobi* Zone *auctorum* is ill defined and the exact range of *B. jacobi* remains poorly understood.

Therefore *B. jacobi* is a critical taxon for the definition of the Tithonian/Berriasian boundary, and one that needs careful examination to settle taxonomic disputes and biostratigraphic uncertainties. This paper presents a revision of all available material of *B. jacobi* described in the French literature and new collection made at Les Combes. The re–evaluation of the systematics and stratigraphic position of *B. jacobi* leads us to question its value as an index species.

2. Origin of the material studied

2.1. Origin of the type material

Berriasella jacobi Mazenot, 1939 is based on four specimens from the Gevrey collection, whose source was Chomérac (Ardèche, France) (CHO in Fig. 1). The lithostratigraphic level from which these ammonites were collected is the *Brèche de Chomérac*. This unit was first described and named as the “*pseudo brèche de la Boissière, près Chomérac*” by Toucas (1890) who gave the first account of its palaeontological content. As already outlined by Roman and Mazenot (1937, p. 179), the great majority of the historical collections (late 19th and early 20th) centuries made at Chomérac (La Boissière and Sabatas) was collected ex situ, from dry stone walls and loose in cultivated fields. This is the case with the holotype and paratypes in the Gevrey collection.

Recent attempts to find a well exposed succession of the Jurassic/Cretaceous transition near La Boissière and Sabatas have failed due to faulting and poor exposure (Cecca et al., 1989, p. 41). In the course of the revision of the upper Tithonian (‘*Ardescien*’) of Ardèche, Cecca et al. (1989, p. 41) stated that when it crops out in good condition the *Brèche de Chomérac* is poorly fossiliferous and the ammonite faunas are ill preserved. This is the case at such localities as the Broyon Quarry (Le Pouzin, Ardèche) (BRO in Fig. 1) and the Fontasse section (Chomérac, Ardèche) (FON in Fig. 1).

It should be noted that beside typical taxa from the Jacobi Zone *auctorum* such as *Berriasella* of the *oppeli – moreti* Mazenot, 1939 group, *Dalmasiceras progenitor* (Oppel *in* Zittel, 1868), *Pseudoneocomites beneckei* (Mazenot, 1939) and *Pseudosubplanites lorioli* (Oppel, 1865), the fauna from the *Brèche de Chomérac* yielded late Tithonian ammonites such as *Micracanthoceras microcanthum* (Oppel, 1865) and *Ardesciella rhodanica* (Toucas, 1890) (Cecca et al., 1989; Bulot et al., 2014). By comparison with the expanded successions of the Vocontian Basin such as Le Chouet, it is now clear that the fauna from the *Brèche de Chomérac* includes reworked Tithonian elements from the Microcanthum and Andreaei zones in an assemblage dominated by ammonites from the lower and middle part of the Jacobi Zone *auctorum* (e.g. Cecca et al., 1989; Wimbledon et al., 2013; Bulot et al., 2014; Frau et al., 2015). As a consequence, at its type locality the precise age of *B. jacobi* cannot be established.

2.2. Additional specimens from the Le Hégarat collection

Following Mazenot's original description, Le Hégarat (1973) was the only author to present new data regarding the taxonomy and stratigraphic distribution of *B. jacobi* in southeast France. It should be noted that the taxonomic treatment of *B. jacobi* by that author was based on a limited number of specimens. Among them, a new collection from the *Brèche de Chomérac* made near Aurouse (Chomérac, Ardèche) (AUR in Fig. 1) included a single true *B. jacobi* (FSL.140452). The two other specimens of *B. jacobi* reported from this locality belong to *Berriasella oppeli* (Kilian, 1889) (FSL.127368) and *Delphinella* of the *D. delphinense* (Kilian, 1889) group (FSL.127371) (see discussion below). Cecca et al. (1989, p. 41) pointed out that those specimens were collected from cultivated fields.

Additional specimens from Champ Blanc (Saint–Laurent–sur–Coirons, Ardèche) (CB in Fig. 1), Les Combes (Glandage, Drôme) and Saut de la Drôme (Luc–en–Diois, Drôme) were used by Le Hégarat (1973) for his reappraisal of *B. jacobi*. Search in the Le Hégarat collection housed at Lyon–I University failed to find the specimens from Les Combes and showed that the specimens from Saut de la Drôme (FSL 127946, 127970 and 127972) are not relevant to an understanding of *B. jacobi* since they belong to *Delphinella* of the *D. delphinense* (Kilian, 1889) group (see below).

At Champ Blanc (Fig. 2), Le Hégarat (1973, p. 329) reported ammonites from the “*Calcaires et marnes du Berriasien*”, occurring above the hard ground surface at the top of the “*Calcaires Blancs*”. The poor quality of the exposures was indicated by Cecca et al. (1989, p. 54) and a recent visit to this locality by one of us (C.F.) failed to recognize the succession described by Cecca et al. (1989, fig. 18) since the outcrops are covered by vegetation and affected by faults. The matrix of the specimens collected by Le Hégarat at Champ Blanc (FSL 127389, 127398, 127401 and 141240) is a micritic limestone that does not show any trace of reworking. The microfacies is typical of the “*Calcaires et marnes du Berriasien*”. We made sediment thin sections in order to clarify the stratigraphic position of the ammonites by identifying the calpionellid assemblages present (see below).

2.3. New collection from Les Combes

After extensive collecting by the authors of the present contribution, new specimens that match perfectly the type series of *B. jacobi* were discovered near Les Combes. This locality lies in the cliffed upper valley of the Grimone stream, in pine forest (Long 5°37′00″E, Lat 44°42′09″N) off the local road (D539) from Glandage to Lus–la–Croix–Haute (Fig. 3). The section comprises a partially overgrown section, 60 m–long, along a single–track road on the north side of the Ravin de Font Bertrand.

The section contains three different lithological parts. The lower part (beds −52 to −29) is composed of stacked – mud– to wackestone – limestone beds characterized by the occurrence of small chert nodules that overly a thick clast–supported breccia (bed −56 and −55). The middle part (beds −28 to 30) contains well–bedded, ammonite–bearing, limestone beds and thin marly interbeds ranging in thickness from 0.05 m to 1 m. This interval displays a thin clast–supported breccia (bed −10). A part of this interval is overgrown to a depth of about 3–4 m. The third part (beds 31 to 111) is composed of a continuous marl–limestone alternations and it is marked by a recessive interval at its top that is more argillaceous than the rest of the section (beds 83 to 92).

Ammonite are abundant and diverse except for the chert–rich part of the section. A detailed ammonite distribution is given below together with the preliminary results on the calpionellids zonation (Fig. 3). The vertical range of *B. jacobi* extends between bed 22 and bed 30 in association with common *Strambergella carpathica* (Zittel, 1868) and rare *Retowskiceras nikolovi* (Le Hégarat, 1973), *Bochianites* sp. and *Proniceras* sp. that mark the upper part of the Jacobi Zone *auctorum*. The vertical

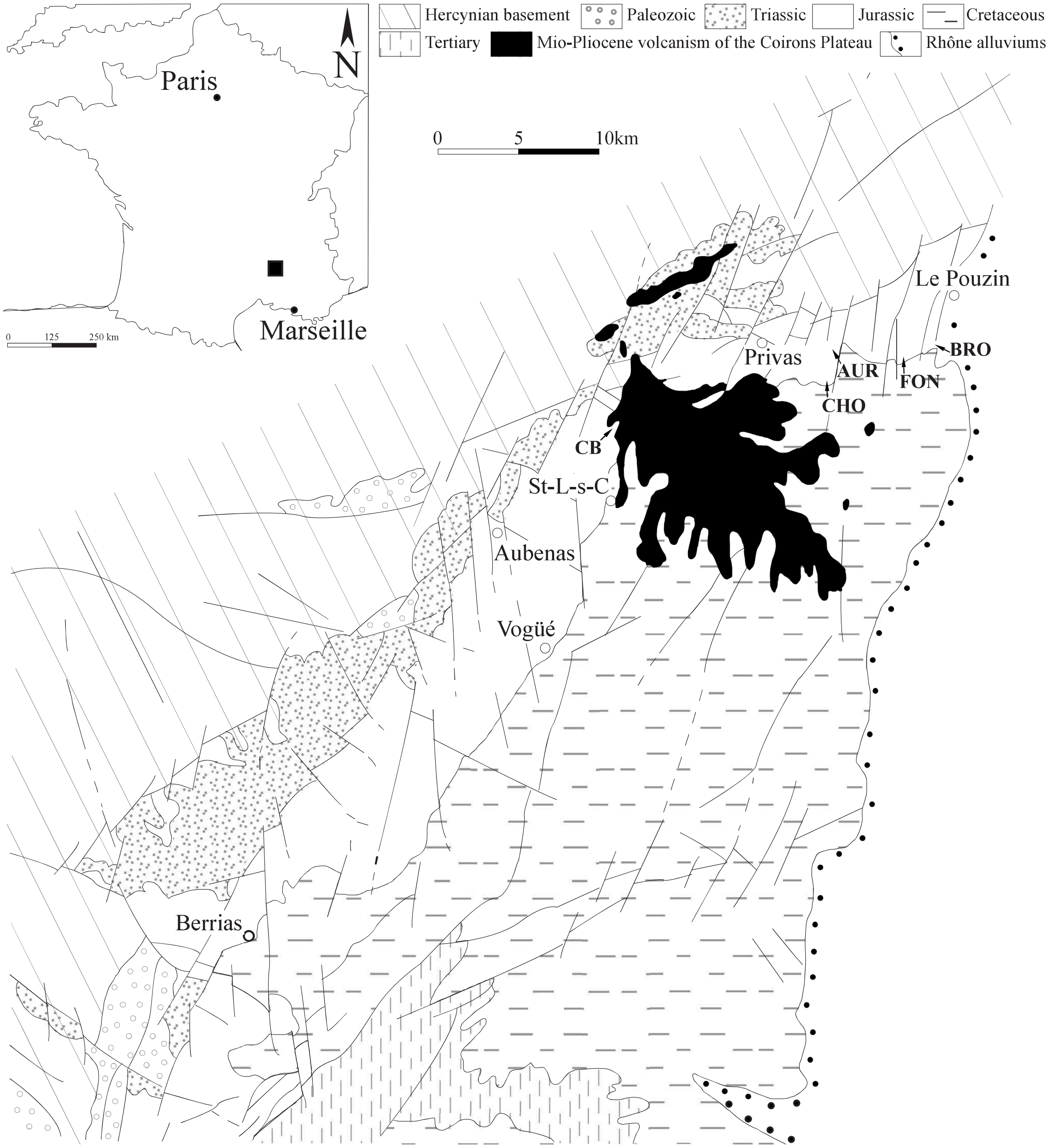


Fig. 1. Locality map of the historical sections of Gard and Ardèche (Southeast France) discussed in the text: BRO – Broyon, CHO – Chomérac, AUR – Aurouse, FON – Fontasse and CB – Champ Blanc.

range of *B. jacobi* encompasses the uppermost part of the *Remaniella ferasini* Subzone and the lowermost part of the *Calpionella elliptica* Zone of the Calpionella Zone. The occurrence of the age–diagnostic *Tirnovella subalpina* (Mazenot, 1939), index–species of the first subzone of the middle Berriasian (see Le Hégarat, 1973), is reported four metres above the last occurrence of *B. jacobi*.

The description of the ammonite and calpionellid assemblages from Les Combes will be addressed in full elsewhere, but the study of the new ammonite population shows that *B. jacobi* is closely related to *Strambergella carpathica* (Zittel, 1868). This new systematic treatment is discussed below.

3. Systematic palaeontology

Abbreviations: All dimensions of specimen are given in millimetres: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. Figures in parentheses are

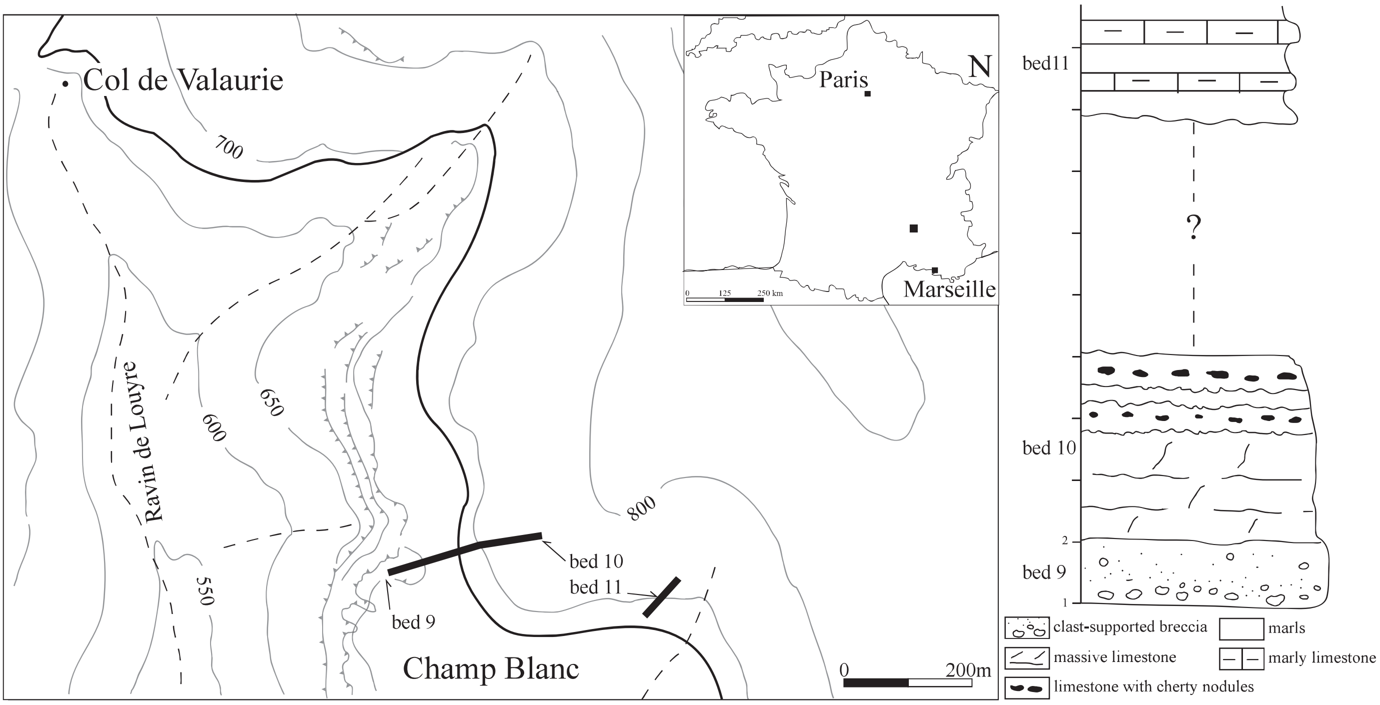


Fig. 2. Locality map and synthetic section (with original be numbers) of Champ Blanc (Ardèche, southeast France) modified from Cecca et al. (1989). The material collected by Le Hégarat (1973) originates from the "*Calcaires et marnes du Berriasien*" (= bed 11).

dimensions as a percentage of the diameter at the point of measurement.

The following abbreviation are used to indicate the repository of specimens mentioned in the text: BSPM — Bayerische Staatssammlung für Paläontologie und Geologie, Munich; FSL — Faculté des Sciences de Lyon, Université Claude Bernard — Lyon–I; MPP — Musée de Paléontologie de Provence, Aix–Marseille Université; UJF–ID —Université Joseph Fourier — Institut Dolomieu. All specimens from Les Combes (MPP–LCB) are deposited in the Frau/Bulot collection in Musée de Paléontologie de Provence.

Order Ammonitida Fisher, 1882
Suborder Ammonitina Fisher, 1882
Superfamily Perisphinctoidea Steinmann, 1890
Family Neocomitidae Salfeld, 1921

Genus *Strambergella* Nikolov, 1966
Type species: *Ammonites carpathicus* Zittel, 1868; by original designation.

Remarks. *Strambergella* was originally introduced as a subgenus of *Berriasella* by Nikolov (1966), a view that was subsequently maintained by this author (Nikolov, 1982). This view was dismissed by Le Hégarat (1973, p. 147) who clearly substantiated the relationship between *S. carpathica* and the type species of *Fauriella* Nikolov, 1966, e. g. *Fauriella gallica* (Mazenot, 1939), and considered *Strambergella* as a subgenus of *Fauriella*.

Hoedemaeker (1982) considered that *Fauriella* is a junior subjective synonym of *Subthurmannia* from which *Strambergella* is a distinct subgenus. Tavera (1985) and Wright et al. (1996, p. 50), respectively, considered this taxon as a junior subjective synonym of *Fauriella* Nikolov, 1966 and *Subthurmannia* Spath, 1939.

It is therefore admitted that whatever is the status of *Strambergella*, its type species cannot be maintained in *Berriasella* since it differs clearly from the typical *Berriasella* of the *B. privasensis* (Pictet, 1867) group in its development of fasciculate ribs from umbilical bullae on the body chamber. As already outlined by Le Hégarat (1973), this ornamental feature is also expressed in *Fauriella gallica* and its allied species such as *F. boissieri* (Pictet, 1867). We therefore support the view that *Strambergella* cannot be maintained as a subgenus of *Berriasella*.

On the other hand, we do not support the view that *Fauriella* is a junior synonym of *Subthurmannia*. This later genus was introduced by Spath (1939) to accommodate a group of Neocomitidae from the Belemnite Beds of the Salt Range (Pakistan) that includes *Suthurmannia fermori* Spath, 1939 (type species), *Subthurmannia filosa* Spath, 1939 and *Subthurmannia transitoria* Spath, 1939. Fatmi (1972) clearly established the Berriasian age of the *Subthurmannia* assemblage, including several species of *Spiticeras*. According to Fatmi (1977, p. 273), all *Subthurmannia* described by Spath (1939) originate from the same stratigraphic level, but its exact position in the Berriasian remains unknown. Even if *Fauriella* and *Subthurmannia* share superficial similarities, neither *F. gallica* nor any other *Fauriella* of the Mediterranean–Caucasian Subrealm show the subquadratic whorl section with marked flat venter and virgatotome ribbing that characterize *S. fermori* and allied species.

Strambergella can easily be distinguished from *Fauriella* by its typical *Berriasella*–like ornamentation that marks the early and middle ontogenetic stages. As a consequence and following Klein (2005), we consider *Strambergella* as a separate genus.

Emended diagnosis. Small to medium–sized dimorphic compressed neocomitids. Fairly open umbilicus. Subrectangular

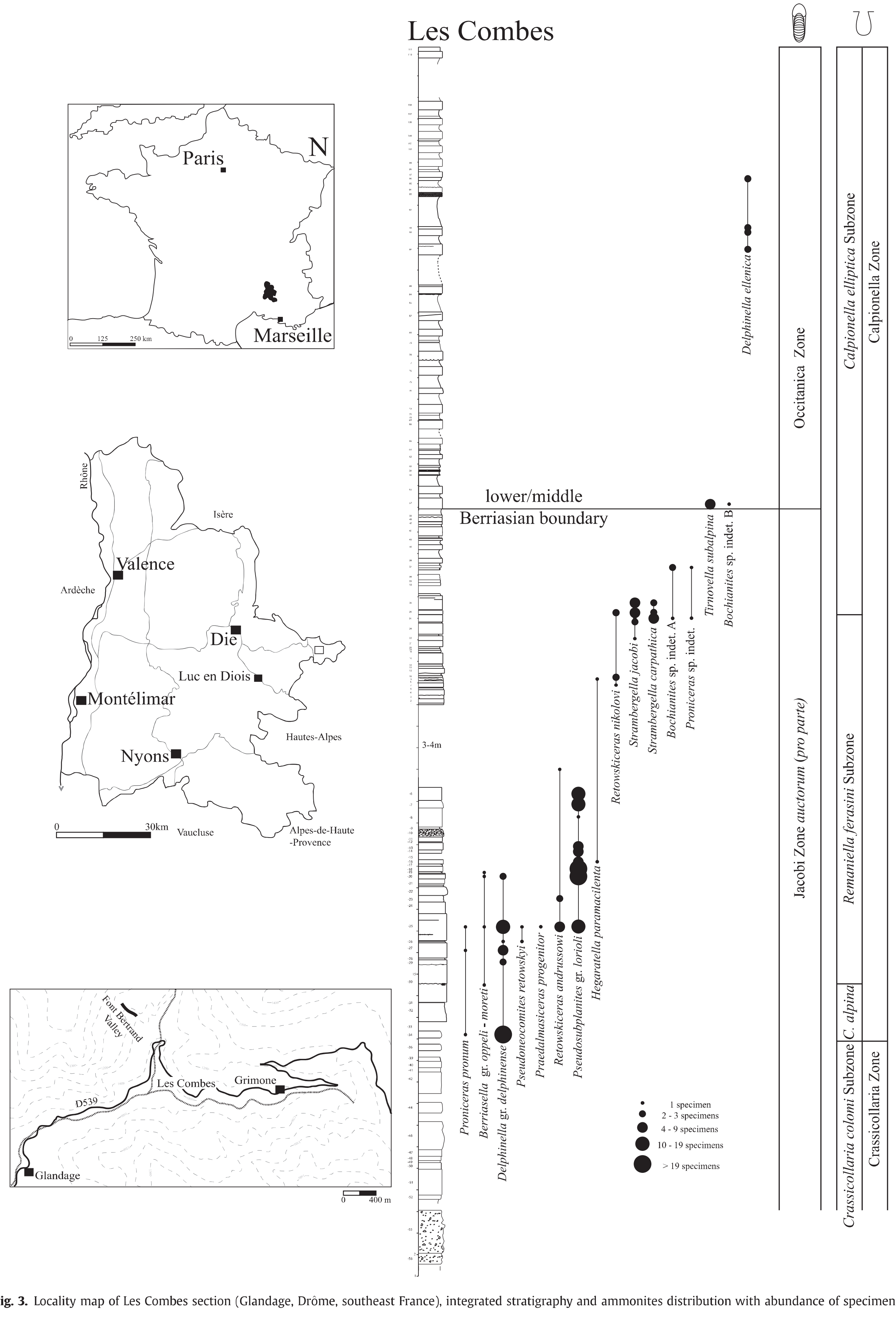


Fig. 3. Locality map of Les Combes section (Glandage, Drôme, southeast France), integrated stratigraphy and ammonites distribution with abundance of specimens.

whorl section throughout ontogeny with slightly rounded to flattened flanks. Flat ventral area with a smooth band in inner whorls that weakens in the adult. *Berriasella*–like ornamentation in inner whorls that progressively fasciculates on the umbilical margin from bullae or weak tubercles. Neocomitid suture line marked by narrow and bifid external lobe.

Specific content. As herein understood, *Strambergella* is strictly restricted to *Strambergella carpathica* (including its junior subjective synonym *Fauriella floquinensis* Le Hégarat, 1973), *Strambergella jacobi* (including its junior subjective synonym *Fauriella shipkovensis* Le Hégarat, 1973 *non* Nikolov & Mandov, 1967) and *Strambergella clareti* (Le Hégarat, 1973).

In our opinion, among the other species transferred to *Strambergella* by Hoedemaeker (1982), *Neocomites cabrensis* Fallot, 1922 and *Hoplites (Berriasella) carpathicus* var. *gracilis* Pervinquière, 1907 may correspond to inner whorls of *Lopeziceras chaperi* (Pictet, 1868); *Jabronella cisternensis* Le Hégarat, 1973 is a *Malbosiceras* of the *malbosi* (Pictet, 1867) group; and *Jabronella patruliusi* Le Hégarat, 1973 belongs to *Tirnovella* of the *alpillensis* (Mazenot, 1939) group. Contrary to the view of Hoedemaeker (1982) and in agreement with Le Hégarat (1973) and Tavera (1985), we maintain *Neocomites subalpinus* Mazenot, 1939 and *Ammonites occitanicus* Pictet, 1867 in the genus *Tirnovella* Nikolov, 1966. The late Berriasian *Berriasella tzankovi* Nikolov & Mandov, 1967, *Berriasella* (*Strambergella*) *catrafilovi* Nikolov, 1982 and *B.* (*S.*) *costelensis* Nikolov, 1982 are juvenile and/or microconchs of *Fauriella* of the *boissieri* (Pictet, 1867) group.

Occurrences. As herein understood, *Strambergella* ranges from the upper part of the Jacobi Zone *auctorum* to the middle part of the Occitanica Zone (*B. privasensis* Subzone *sensu* Le Hégarat, 1973). The genus is known to occur in the Mediterranean–Caucasian Subrealm of the Tethyan Realm *sensu* Westermann (2000) [France, Spain, Czech Republic (type locality – Koniakau), Hungary, Bulgaria, Crimea, Tunisia and ? Morocco].

Strambergella carpathica (Zittel, 1868)
Fig. 4A–G andE

v 1868 *Ammonites carpathicus* Zittel, p. 107, pl. 18, fig. 4A–d, ? 5.
non 1880 *Ammonites carpathicus* Zittel: Favre, p. 39, pl. 3, fig. 8 (= Neocomitidae gen. sp. indet.).
non 1889 *Hoplites carpathicus* (Zittel): Kilian, p. 660, pl. 30, fig. 1a–b (= ?*Lopeziceras* gr. *chaperi*).
non 1890 *Hoplites carpathicus* (Zittel): Toucas, p. 602, pl. 17, fig. 10a–b (= *Strambergella jacobi*).
non 1907 *Hoplites* (*Berriasella*) *carpathicus* var. *gracilis* Pervinquière, p. 37, pl. 2, fig. 13 (= ?*Lopeziceras* gr. *chaperi*).
1939 *Berriasella carpathicus* (Zittel): Mazenot, p. 103, pl. 13, fig. 4a–d (= Zittel, 1868, pl. 18, fig. 4c–d).
non 1939 *Berriasella carpathicus* (Zittel): Mazenot, p. 103, pl. 13, fig. 2a–b, 7a–b (= *Fauriella donzei*)
non 1939 *Berriasella carpathicus* (Zittel): Mazenot, p. 103, pl. 13, fig. 3a–b, ?6 (= *Fauriella berriasensis*)
non 1939 *Berriasella carpathicus* (Zittel): Mazenot, p. 103, pl. 13, fig. 5a–b (= *Erdenella subisaris*).
1939 *Berriasella* cf. *callistoides* (Behrendsen): Mazenot, p. 59, pl. 4, fig. 13a–b.
1953 *Berriasella* cf. *carpathica* (Zittel): Arnould–Saget, p. 54, pl. 5, fig. 5a–c, text–fig.18.
non 1957 *Berriasella carpathica* (Zittel): Sapunov, p. 155, pl. 2, fig. 1 (= Neocomitidae gen. sp. indet.).
non 1960 *Berriasella carpathica* (Zittel): Nikolov, p. 163, pl. 7, fig. 1, 2, 3, 4, 5 (= *Fauriella* sp.).
non 1967 *Subthurmannia carpathica* (Zittel): Dimitrova, p. 105, pl. 50, fig. 4 (= *Fauriella* sp.).
non 1968 *Berriasella* aff. *carpathica* (Zittel): Le Hégarat & Remane, p. 23, pl. 1, fig. 6 (= *Fauriella* sp.).
v 1973 *Fauriella* (*Strambergella*) aff. *carpathica* (Zittel): Le Hégarat, p. 152, pl. 21, fig. 4, 5, 6 (= Zittel, 1868, pl. 18, fig. 4b, 5), pl. 46, fig. 2.
v non 1973 *Fauriella* (*Strambergella*) aff. *carpathica* (Zittel): Le Hégarat, p. 152, pl. 46, fig. 3 (= *Strambergella jacobi*).
v 1973 *Fauriella floquinensis* n. sp. Le Hégarat, p. 156, pl. 23, fig. 1, 2, pl. 47, fig. 4, 5.
1979 *Berriasella* (*Strambergella*) *carpathica* (Zittel): Sapunov, p. 179, pl. 56, fig. 6.
1982 *Berriasella* (*Strambergella*) *carpathica* (Zittel): Nikolov, p. 82, pl. 19, fig. 1a–b (= Zittel, 1868, pl. 18, fig. 4b–c), fig. 2 (= Sapunov, 1979, pl. 56, fig. 6).
1982 *Fauriella floquinensis* Le Hégarat: Nikolov, p. 109, pl. 28, fig. 1a–b (= Le Hégarat, 1973, pl. 23, fig. 1, pl. 47, fig. 5), 2, pl. 29, fig. 1, 2.
non 1982 *Fauriella floquinensis* Le Hégarat: Nikolov, p. 109, pl. 29, fig. 2 (= *Strambergella clareti*).
1982 *Berriasella* (*Berriasella*) *privasensis* (Pictet): Hoedemaeker, pl. 2, fig. 2.
1985 *Fauriella* (*Strambergella*) aff. *carpathica* (Zittel): Cecca, p. 151, pl. 3, fig. 1.
non 1985 *Fauriella floquinensis* Le Hégarat: Tavera, p. 284, pl. 43, fig. 1, 2 (= *Strambergella clareti*).
non 1985 *Fauriella floquinensis* Le Hégarat: Tavera, p. 284, pl. 43, fig. 3, text–fig. 22E (= *Strambergella jacobi*).
non 1986 *Subthurmannia* (*Strambergella*) aff. *carpathica* (Zittel): Horváth & Knauer, p. 68, pl. 1, fig. 2 (= Neocomitidae gen. sp. indet.).
non 1987 *Subthurmannia* (*Strambergella*) aff. *carpathica* (Zittel): Horváth & Knauer, p. 410, pl. 1, fig. 2 (Horváth & Knauer, 1986, pl. 1, fig. 2).
non 1989 *Fauriella carpathica* (Zittel): Khimchiashvili, p. 11, pl. 2, fig. 1 (= Neocomitidae gen. sp. indet.).
non 1990 *Fauriella* (*Strambergella*) cf. *carpathica* (Zittel): Cecca et al., pl. 6, fig. 6 (= Neocomitidae gen. sp. indet.).
non 1999a *Fauriella* ex. gr. *floquinensis* Le Hégarat: Sey & Kalacheva, p. 85, pl. 1, fig. 3a–б (= Neocomitidae gen and sp. indet.).
non 2001 *Fauriella* ex. gr. *floquinensis* Le Hégarat: Sey & Kalacheva, p. 1096, pl. 1, fig. 3a–b (= Sey & Kalacheva, 1999a, pl. 1, fig. 3a–б).
non 2004 *Fauriella* ex. gr. *floquinensis* Le Hégarat: Sey & Kalacheva, p. 90, pl. 82, fig. 2 (= Sey & Kalacheva, 1999a, pl. 1, fig. 3a–б).
non 2011 *Fauriella* aff. *carpathica* (Zittel): Arkadiev, p. 9, pl. 3, fig. 6a–в (= *Pseudoneocomites beneckei*).
non 2011 *Fauriella* aff. *carpathica* (Zittel): Arkadiev, p. 9, pl. 3, fig. 7 (= *Strambergella jacobi*).
non 2012 *Fauriella* cf. *floquinensis* Le Hégarat: Arkadiev et al., p. 156, pl. 7, fig. 2 (= Neocomitidae gen. sp. indet.).
non 2012 *Fauriella* aff. *carpathica* (Zittel): Arkadiev et al., p. 155, pl. 7, fig. 5a–в, 6 (= Arkadiev, 2011, pl. 1, fig. 6a–в, 7).
non 2012 *Fauriella* cf. *floquinensis* Le Hégarat: Arkadiev et al., p. 156, pl. 7, fig. 2 (= Arkadiev, 2011, pl. 1, fig. 3).
? 2013 *Fauriella carpathica* (Zittel): Szives & Főzy, p. 308, pl. 3, fig. 1.

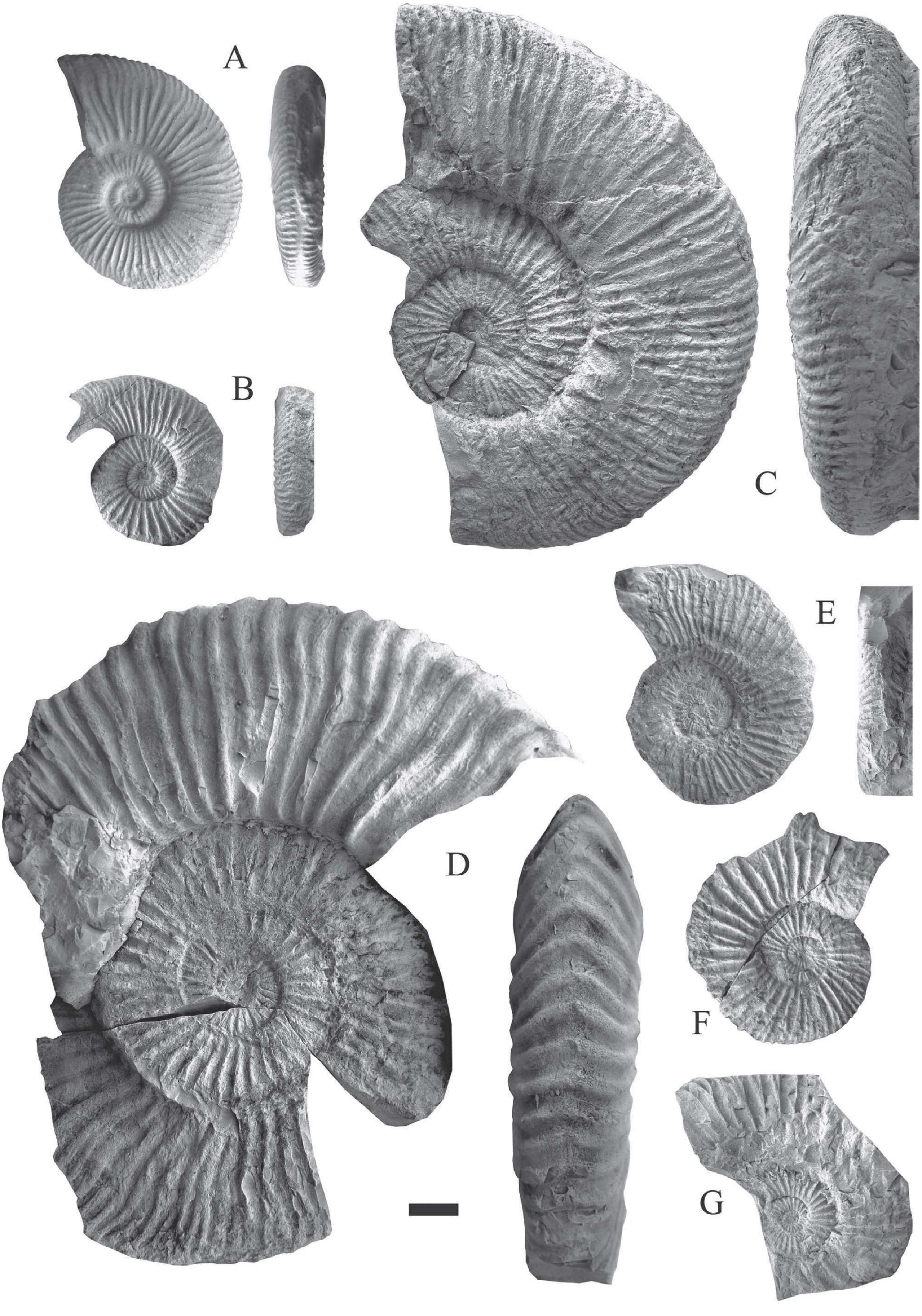
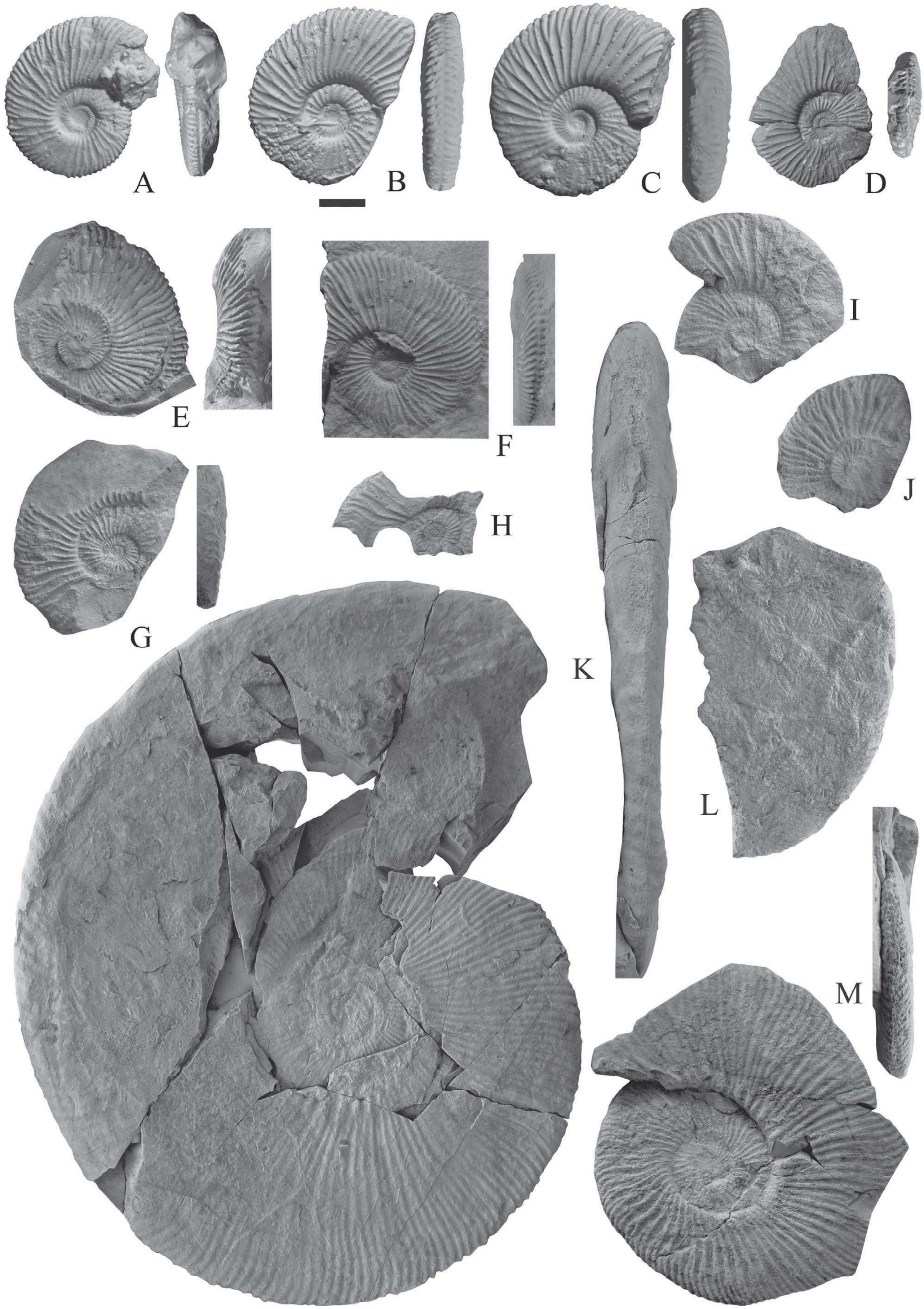


Fig. 4. *Strambergella carpathica* (Oppel *in* Zittel, 1868): (A) cast (FSL.13058) of the lectotype; (B) MPP–LCB.190 [m]; (C) MPP–LCB.191 [M]; (D) MPP–LCB.293 [M]; (E) MPP–LCB.237 [m]; (F) MPP–LCB.269 [juvenile M]; (G) MPP–LCB.264 [M]. Specimens MPP–LCB from les Combes (Glandage, Drôme) (Frau/Bulot collection) are coated with ammonium chloride. Scale bar is 10 mm.


A
B
C
D
E
F
G
H
I
J
K
L
M

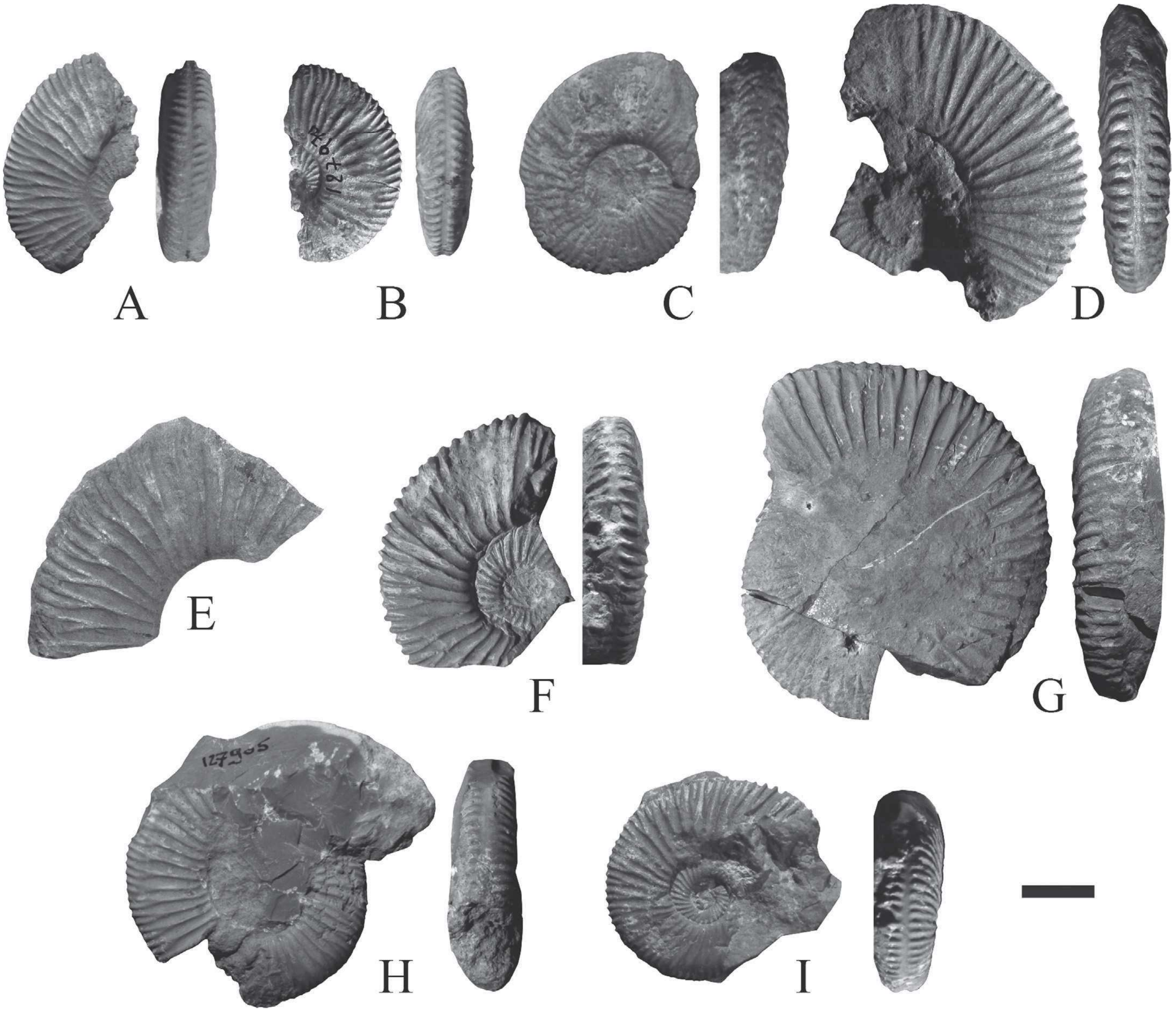


Fig. 6. The ammonite specimens originally reported to *Berriasella jacobi* Mazenot, 1939 by Le Hégarat (1973) that are herein referred to the *Delphinella* of the *delphinense* (Kilian, 1889) group [(A) FSL.127972, (B) FSL.127970, (C) FSL.127973 and (D) FSL.127946 from Saut de la Drôme; (E) FSL.127371 from Aurouse; (F) FSL.127589 from Peyrol]; *Pseudosubplanites* sp. indet. [(G) FSL.127368 from Aurouse]; and *Berriasella oppeli* (Kilian, 1889) [(H) FSL.127905 from Floquin and (I) FSL.127764 from Marignac en Diois]. Scale bar is 10 mm.

2013 *Fauriella floquinensis* Le Hégarat: Szives & Főzy, p. 308, pl. 9, fig. 1.
non 2013 *Fauriella floquinensis* Le Hégarat: Szives & Főzy, p. 308, pl. 9, fig. 4 (= *Jabronella* sp.).
non 2013 *Fauriella* cf. *floquinensis* Le Hégarat: Szives & Főzy, p. 309, pl. 7, fig. 8 (= *Lopeziceras* sp.).

Type. BSPM–AS.III.91, the lectotype, a subcomplete specimen (Oppel collection) (Zittel, 1868, pl. 18, fig. 4a–d). We illustrate a cast of the lectotype deposited in the collections of the Faculté des Sciences de Lyon–I (FSL.13058) (Fig. 4A).

Additional material. FSL.129357 and FSL.127854 (the holotype and paratype of *Fauriella floquinensis*); MPP–LCB.176, MPP–LCB.181, MPP–LCB.190, MPP–LCB.191, MPP–LCB.199, MPP–LCB.237, MPP–LCB.253, MPP–LCB.263, MPP–LCB.264, MPP–LCB.269, MPP–LCB.293. Most diagnostic specimens from Les Combes are illustrated on Fig. 4B–G.

Dimensions (mm).

Fig. 5. *Strambergella jacobi* (Mazenot, 1939): (A) cast of paratype UJF–ID.618 [m] (Gevrey coll.); (B) Cast of holotype UJF–ID.572 [m] (Gevrey coll.); (C) Cast of paratype UJF–ID.616 [m] (Gevrey coll.); (D) FSL.127161 [m] from Champ Blanc (Le Hégarat coll.); (E) cast of FSL.140542 from Aurouse [m] (Le Hégarat coll.); (F) FSL.140343 [m] from Champ Blanc (Le Hégarat coll.); (G) MPP–LCB.201 [m] (bed 26); (H) MPP–LCB.56 [m] (bed 28); (I) MPP–LCB.213 [m] (bed 30); (J) MPP–LCB.298 [m] (bed 25); (K) MPP–LCB.36 [M] (bed 22); (L) MPP–LCB.195 [M] (bed 28); (M) MPP–LCB.56 [M] (bed 30). Specimens MPP–LCB from les Combes (Glandage, Drôme) (Frau/Bulot collection) are coated with ammonium chloride. Scale bar is 10 mm.

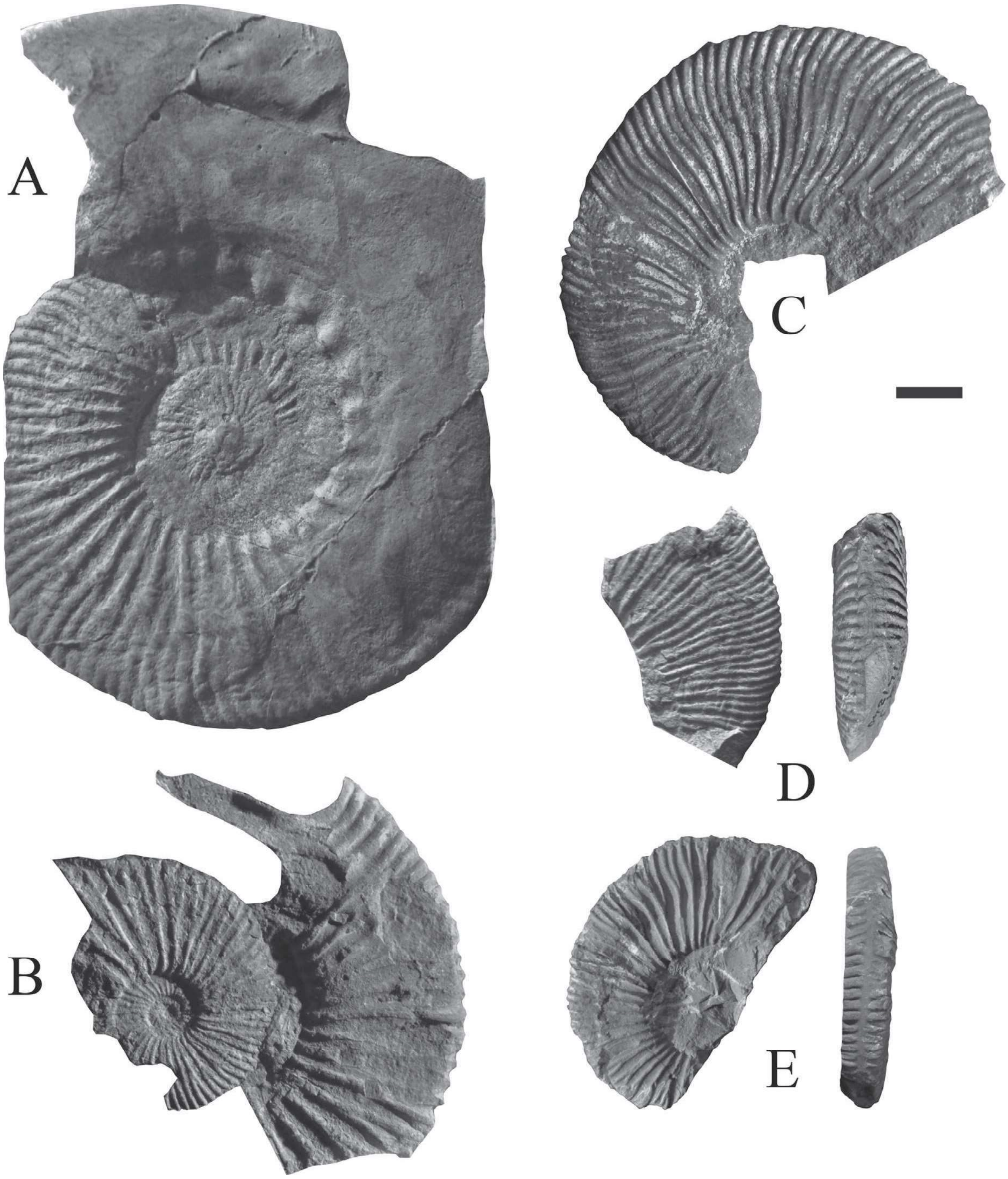


Fig. 7. Ammonites from Champ Blanc (Le Hégarat collection): (A) *Delphinella sevenieri* Le Hégarat, 1973, FSL.127401a [M]; (B) *Delphinella sevenieri* Le Hégarat, 1973, FSL.127398 [m] (= *Delphinella ellenica* (Nikolov, 1960) *in* Le Hégarat, 1973, p. 106); (C) *Pseudoneocomites* gr. *retowskyi* (Sarasin & Schöndelmayer, 1901), FSL.127389 [?M] (= *Fauriella shipkovensis* Nikolov & Mandov, 1967 *in* Le Hégarat, 1973, p. 166); (D) *Strambergella* sp., FSL.141240 [M] (= *Fauriella shipkovensis* Nikolov & Mandov, 1967 *in* Le Hégarat, 1973, p.166); (E) *Strambergella carpathica* (Zittel, 1868), FSL.127394 [m] (= *Parapallasiceras busnardoi* Le Hégarat, 1973 *in* Le Hégarat, 1973, p. 42).

Specimens	D	U	Wh	Wb	U/D	Wh/D	Wb/D	Wb/Wh
AS.III.91	53	17	22	14	0.32	0.41	0.26	0.63
FSL.129357	123	52	40	25	0.42	0.32	0.20	0.62
LCB.181	37.1	11.9	14.3		0.32	0.38		
LCB.190	33.9	12.7	11.7		0.37	0.34		
LCB.191	101.8	42.4	33.4		0.42	0.33		
LCB.264	52.0	18.8	21.7	10.0	0.36	0.41	0.19	0.46
LCB.237	47.3	15.5	18.2		0.33	0.38		
LCB.269	46.0	17.2	16.7		0.37	0.36		
LCB.293	139.3	59.2	49.9	25.7	0.42	0.36		

Emended diagnosis. Small to medium—sized (Dmax ~150 mm) neocomitid ammonite. Subrectangular whorl section throughout ontogeny with slightly rounded flanks. Flat ventral area with a smooth band in inner whorls that becomes rounded in the adult. Open umbilicus ($0.32 < U/D < 0.42$) with short umbilical wall with rounded margin. Microconchs characterized by rigid, straight to slightly prorsiradiate ribs. Ribs bifurcate regularly on the outer third of the flanks and delimit a marked siphonal band on the venter. On body chamber ribbing denser, crossing the venter forming a slight chevron. Aperture with short lateral lappets.

Inner whorls of macroconchs similar to that of microconchs. On body chamber, ribs are more or less regularly fasciculated on the umbilical margin. On the adult, composite ornamentation of single, intercalated and irregular bifurcate ribs that form a marked chevron on the venter. Aperture is simple.

Description. The lectotype is a medium—sized ammonite. The whorl section is subrectangular throughout ontogeny with markedly rounded flanks on the inner whorls that are slightly flattened on the body chamber. It shows the typical *Berriasella*—like ornamentation with rigid, regular, straight to prorsiradiate bifurcating ribs that span the whole phragmocone. Ribs bifurcate regularly on the outer third of the flanks. All ribs arise on the umbilical seam and cross the umbilical margin. The ribs end on the ventral margin where they delimit a narrow siphonal band. On the body chamber, ribs become denser and the ribs branch by two on the umbilical margin. In the last-preserved part of the adult, the ribs cross the venter.

Among the material at our disposal, the following specimens illustrate the ontogeny and variability of the species:

- MPP—LCB.190 is a small specimen that shows short lateral lappets at the aperture. The inner whorls of this specimen bear the rigid *Berriasella*—like ornamentation. At the transition between the phragmocone and body chamber, the ribs are markedly approximated. They cross the venter forming a slight chevron.
- MPP—LCB.191 is a sub—complete, medium—sized specimen that perfectly matches the morphology of *Fauriella floquinensis*. The umbilicus is markedly open compared to the lectotype. The whorl section is subrectangular throughout ontogeny with a rounded venter in the adult. The *Berriasella*—like ornamental stage is more rigid and longer than that of the lectotype. The beginning of the stage with fasciculate ornament is not visible due to preservation, but well expressed at the start of the body—chamber. The furcation point progressively strengthens in weak umbilical bullae. The ribbing becomes irregular with single or bifurcated ribs with intercalatories. The siphonal band is markedly weakened and ribs cross the venter forming a small chevron near the aperture.
- MPP—LCB.293 is the largest specimen at our disposal. Its inner whorls perfectly match the morphology and ornamental stages of the lectotype, and match the holotype of *F. floquinensis* on its adult whorls. Noteworthy is the compressed whorl section and the strong ornamentation of the body chamber aperture, marked by a well expressed ventral chevron.

Dimorphism. Examination of the material from Les Combes allows us to distinguish two morphotypes:

- A first group of small—sized forms (Dmax < 55 mm) is characterized by its *Berriasella*—like stage with spaced, rigid bifurcate ribs that can be strongly approximated and cross the venter on the body—chamber. This group includes the specimens MPP—LCB.176, MPP—LCB.190, MPP—LCB.199, MPP—LCB.237, MPP—LCB.253, MPP—LCB.263, MPP—LCB.264 and MPP—LCB.269. Among these, specimen MPP—LCB.190 shows short lateral lappets (Fig. 4B). The following specimens belong to this group, those illustrated by Mazenot (1939, pl. 4, fig. 13), Le Hégarat (1973, pl. 46, fig. 2), Sapunov (1979, pl. 56, fig. 6), Hoedemaeker (1982, pl. 2, fig. 2) and Cecca (1985, pl. 3, fig. 1) belong to this group.
- The other morphotype encompasses larger forms (Dmax < 140 mm) (such as specimens MPP—LCB.191 and MPP—LCB.293) characterized by a distinctive secondary ornamental stage with fasciculate ribs derived from irregular umbilical bullae, and a final growth stage marked by irregular ribs, attenuated tubercles and a ventral chevron. Coiling is more evolute and the umbilical wall is steeper. This group matches the morphology of the lectotype of *S. carpathica* as well as the typological species *Fauriella floquinensis* Le Hégarat, 1973. The peristome is simple and bears a short ventral extension (see MPP—LCB.293 on Fig. 4D).

Since both morphotypes co—occur in the uppermost Jacobi Zone *auctorum*, we deduce that they must correspond to the microconch and macroconch forms.

Discussion. Examination of the type specimens and comparison with the material collected at Les Combes leaves no doubt that *S. carpathica* corresponds to the juvenile and intermediate stage of *Fauriella floquinensis.* As a consequence, the latter species is herein considered as a junior subjective synonym of *S. carpathica. S. carpathica* and *S. jacobi* co—occur in the uppermost part of the Jacobi Zone *auctorum* at Les Combes, the former can be easily distinguished by its evolute coiling, less compressed whorl section, umbilical bullae at the fasciculate stage and marked ventral chevron on the body—chamber. The poorly—known species *S. clareti* differs from *S. carpathica* in having a short *Berriasella*—like stage, early disappearance of the ventral band, and dense ribbing at all ontogenetic stages.

Occurrences. Vašíček and Skupien (2013) noted that the age of the type specimen of *Strambergella carpathica* cannot be established at its type locality. At Les Combes, the species ranges from bed 24 to bed 30 (uppermost part of the *R. ferasini* Subzone and lowermost part of the *C. elliptica* Subzone, Calpionella Standard Zone). This represents a high level in the Jacobi Zone *auctorum.* The stratigraphic position of the type material of Le Hégarat (1973) is consistent with this age. The isolated specimens from other areas of the Mediterranean—Caucasian Subrealm lack detailed stratigraphic data. Outside France, the species is reported from Spain, ? Italy, Hungary, Bulgaria and Tunisia.

Strambergella jacobi (Mazenot, 1939)
Fig. 5A—M and 7C

1890 *Hoplites carpathicus* (Zittel): Toucas, p. 602, pl. 17, fig. 10a—b.

non 1890 *Hoplites carpathicus* (Zittel): Toucas, p. 602, pl. 17, fig. 11 (= ?*Pseudoneocomites* sp.).

v 1890 *Hoplites calisto* (d'Orbigny): Toucas, p. 600, pl. 17, fig. 3.

v 1939 *Berriasella jacobi* Mazenot, p. 54, pl. 4, fig. 1a—b (= holotype), 2a—b, 3a—b, 4.

non 1939 *Berriasella jacobi* Mazenot, p. 54, pl. 4, fig. 5a—b (= *Richterella richteri*).

1953 *Berriasella jacobi* Mazenot: Arnould—Saget, p. 33, pl. 3, fig. 11a—c; pl. 4, fig. 1a—c.

1953 *Neocomites allobrogensis* Mazenot: Arnould—Saget, p. 74, pl. 8, fig. 1

non 1960 *Berriasella jacobi* Mazenot: Collignon, pl. 165, fig. 668, 669 (= *Blanfordiceras* gr. *wallichi*).

1968 *Berriasella jacobi* Mazenot: Le Hégarat & Remane, p. 25, pl. 5, fig. 1—2 (= Toucas, 1890, pl. 17, fig. 10a—b).

v 1973 *Berriasella (Berriasella) jacobi* Mazenot: Le Hégarat, p. 56, pl. 6, fig. 9—10 (= Mazenot, 1939, pl. 4, fig. 1a), 11 (= Toucas, 1890, pl. 17, fig. 10a—b)

non 1973 *Berriasella (Berriasella) jacobi* Mazenot: Le Hégarat, pl. 6, fig. 12; pl. 38, fig. 3 (= Toucas, 1890, pl. 17, fig. 3a—b) (= *Berriasella* ex. gr. *oppeli* — *moreti*)

v ? 1973 *Berriasella (Berriasella) jacobi* Mazenot: Le Hégarat, pl. 38, fig. 6—7.

v 1973 *Fauriella (Strambergella)* aff. *carpathica* (Zittel): Le Hégarat, p. 152, pl. 46, fig. 3 (= *Strambergella jacobi*).

v 1973 *Fauriella shipkovensis* (Nikolov & Mandov): Le Hégarat, p. 164, pl. 23, fig. 3, 4, 5, 6, pl. 47, fig. 1, 2.

non 1979 *Berriasella (Berriasella) jacobi* Mazenot: Sapunov, p. 173, pl. 55, fig. 3a–b (= *Berriasella* sp. indet.).

1982 *Berriasella (Berriasella) jacobi* Mazenot: Nikolov, p. 51, pl. 8, fig. 4 (= Mazenot, 1939, pl. 4, fig. 1)

non 1982 *Berriasella (Berriasella) jacobi* Mazenot: Nikolov, p. 51, pl. 8, fig. 6 (= Sapunov, 1979, pl. 55, fig. 3a–b),

? 1982 *Berriasella (Berriasella) jacobi* Mazenot: Nikolov, p. 51, pl. 8, fig. 5, 7 (= Le Hégarat, 1973, pl. 38, fig. 6), 8.

1982 *Fauriella shipkovensis* (Nikolov & Mandov): Nikolov, p. 109, pl. 30, fig. 1a–b (= Le Hégarat, 1973, pl. 47, fig. 2), 4, pl. 31, fig. 1.

? 1982 *Berriasella (Hegaratella) jacobi* Mazenot: Hoedemaeker, pl. 1, fig. 7.

non 1983 *Berriasella (Berriasella)* cf. *jacobi* Mazenot: Geyer, p. 343, fig. 3g (= "*Berriasella*" *limensis*).

non 1985 *Berriasella (Berriasella) jacobi* Mazenot: Tavera, p. 238, pl. 33, fig. 7–11, text–fig. 19B (= *Berriasella* ex. gr. *oppeli – moreti*).

1985 *Fauriella floquinensis* Le Hégarat: Tavera, p. 284, pl. 43, fig. 3, text–fig. 22E.

? 1985 *Tirnovella allobrogensis* (Mazenot): Tavera, p. 296, pl. 45, fig. 22C.

? 1986 *Tirnovella* sp. cf. *suprajurensis* (Mazenot): De Wever et al., pl. 1, fig. 5.

non 1986 *Berriasella (Hegaratella) jacobi* Mazenot: Horváth & Knauer, p. 69, pl. 1, fig. 3 (? *Paraulacosphinctes* sp.).

non 1987 *Berriasella jacobi* Mazenot: Liu & Wang, pl. 1, fig. 6a–b, pl. 2, fig. 7a–b (= *Blanfordiceras* gr. *wallichi*).

non 1988 *Berriasella jacobi* Mazenot: Liu, p. 62, pl. 6, fig. 1a–b (= Liu & Wang, 1987, pl. 1, Fig. 6a–b), fig. 2a–b (= Liu & Wang, 1987, pl. 2, fig. 7a–b), fig. 4a–b, 5, pl. 7, fig. 7 (= *Blanfordiceras* gr. *wallichi*).

non 1988 *Berriasella* cf. *jacobi* Mazenot: Liu, p. 62, pl. 6, fig. 3a–b (= *Blanfordiceras* gr. *wallichi*).

? 1989 *Berriasella jacobi* Mazenot: Khimchiashvili, p. 9, pl. 4, fig. 3–4.

non 1990 *Berriasella jacobi* Mazenot: Sey & Kalacheva, pl. 1, fig. 1a–b, 2, 3a–b, 4, 5, 6a–b (= *Subplanitoides* ex. gr. *altegyratum sensu* Sey et al., 1992).

? 1990 *Berriasella jacobi* Mazenot: Khimchiashvili, p. 372, pl. 1, fig. 1, 6 (= Khimchiashvili, 1989, pl. 4, fig. 3–4).

non 1992 *Berriasella (Berriasella) jacobi* Mazenot: Howarth, p. 631, pl. 4, fig. 5 (= Neocomitidae gen. and sp. indet.).

v non 1992 *Berriasella (Berriasella) jacobi* Mazenot: Wierzbowski & Remane, p. 874, pl. 1, fig. 1 (= *Pseudosubplanites* sp. juv.), 2–3 (= Neocomitidae gen. and sp. indet.), 4 (= *Delphinella* sp.).

non 1994 *Berriasella (Berriasella) jacobi* Mazenot: Wierzbowski, p. 238, pl. 4, fig. 5 (= Neocomitidae gen. and sp. Indet.).

non 1996 Berriasella ex. gr. jacobi Mazenot: Sey & Kalacheva, p. 309, pl. 4, fig. 1a–b, 2–4, 6 (= Sey & Kalacheva, 1990, pl. 1, fig. 1a–b, 3a–b, 4–5, 6a–b).

non 1999b *Berriasella* ex. gr. *jacobi* Mazenot: Sey & Kalacheva, p. 55, pl. 1, fig. 2a–b, 6a–b, 7, 8 (= Sey & Kalacheva, 1990, pl. 1, fig. 2, 4, 3a–b, 6a–b), fig. 9–11 (= Sey & Kalacheva, 1990, pl. 1, fig.1a–b, 5), 12–13 (= *Subplanitoides* ex. gr. *altegyratum sensu* Sey et al., 1992).

non 1999 *Berriasella (Berriasella)* aff. *jacobi* Mazenot: Cantú-Chapa, fig. 3C (= "*Berriasella*" gr. *mazatepense*)

non 1999 *Berriasella (Berriasella) jacobi* Mazenot: Kvantaliani, p. 89, pl. 10, fig. 4–7 (= *Pseudosubplanites* ex. gr. *combesi*).

1999 *Fauriella shipkovensis* (Nikolov & Mandov): Kvantaliani, p. 100, pl. 12, fig. 7, pl. 13, fig. 1, 2.

non 2000 *Berriasella (Berriasella)* cf. *jacobi* Mazenot: Kvantaliani, p. 43, pl. 9, fig. 5 (= Kvantaliani, 1999, pl. 10, fig. 4).

non 2004 *Berriasella jacobi* Mazenot: Arkadiev & Bogdanova, p. 372, pl. 1, figs. 1a–b (= *Pseudosubplanites lorioli*), 2 (= ? *Pseudosubplanites* sp.).

non 2004 *Berriasella* ex. gr. *jacobi* Mazenot: Sey & Kalacheva, p. 55, pl. 180, fig. 1, 2–6, 13 (= Sey & Kalacheva, 1990, pl. 1, fig. 2, 4, 3a–b, 6a–b), fig. 9–11 (= Sey & Kalacheva, 1990, pl. 1, fig.1a–b, 5), 12–13 (= *Subplanitoides* ex. gr. *altegyratum sensu* Sey et al., 1992).

non 2005 *Berriasella jacobi* Mazenot: Arkadiev et al., pl. 1, fig. 2a–б (= *Delphinella* sp. indet.)

non 2006 *Berriasella jacobi* Mazenot: Arkadiev et al., pl. 2, fig. 5 (= Arkadiev et al., 2005, pl. 1, fig. 2a–б).

non 2008 *Berriasella jacobi* Mazenot: Arkadiev et al., pl. 1, fig. 3 (= Arkadiev & Bogdanova, 2004, pl. 1, fig. 1a–b).

non 2010 *Berriasella jacobi* Mazenot: Ivanov et al., pl. 4, fig. 2 (= Neocomitidae gen. sp. indet.).

2011 *Fauriella* aff. *carpathica* (Zittel): Arkadiev, p. 9, pl. 3, fig. 7.

2012 *Fauriella* aff. *carpathica* (Zittel): Arkadiev et al., p. 155, pl. 7, fig. 5a–в, 6 (= Arkadiev, 2011, pl. 1, fig. 6a–в, 7).

non 2012 *Berriasella jacobi* Mazenot: Arkadiev et al., p. 144, pl. 4, fig. 4 (= Arkadiev & Bogdanova, 2004, pl. 1, fig. 1a–b), 5–6.

non 2012 *Berriasella jacobi* Mazenot: Salazar, p. 172, fig. 4.52 a–q (= "*Berriasella*" *fraudans*).

non 2013 *Berriasella jacobi* Mazenot: Vašíček & Skupien, p. 335, pl. 5C, G–H (= *Delphinella* sp. juv.), D, I (= *Pseudoneocomites beneckei*).

non 2013 *Berriasella jacobi* Mazenot: Szives & Főzy, p. 306, pl. 9, fig. 2 (= ?*Pseudosubplanites* sp.).

Types. UJF–ID.572, the holotype, a subcomplete specimen (Gevrey collection) (Mazenot, 1939, pl. 4, fig. 1a–b); paratypes UJF–ID.616 (Mazenot, 1939, pl. 4, fig. 2a–b) and 618 (Mazenot, 1939, pl. 4, fig. 4), two subcomplete specimens. The third paratype UJF–ID.617 is lost. All specimens are re–illustrated herein (Fig. 5).

Additional material. FSL.127161 and FSL.140434 from Champ–Blanc (Saint–Laurent–sur–Coirons, Ardèche); FSL.140452 from Aurouse (Ardèche); all from Le Hégarat's collection; MPP–LCB.36, MPP–LCB.56, MPP–LCB.163, MPP–LCB.193, MPP–LCB.195, MPP–LCB.201, MPP–LCB.213 and MPP–LCB.298 from Les Combes (Fig. 5).

Specimens	D	U	Wh	Wb	U/D	Wh/D	Wb/D	Wb/Wh
UJF–ID.572	38.6	12.5	16.7	8.2	0.32	0.43	0.21	0.49
UJF–ID.616	42.2	13.6	17.8	12.7	0.32	0.42	0.30	0.71
UJF–ID.618	34.7	10.9	14.5		0.31	0.42		
FSL.127161	39.7	12.8	16.9		0.32	0.42		
FSL.140452		13.7	17.8					
LCB.36	155	48.5	57.2	18.1	0.31	0.37	0.11	0.31
LCB.56			16.4	7.1				0.43
LCB.163	75.9	25.3	31.7	9.8	0.33	0.33	0.13	0.31
LCB.194	30.4		13.3			0.43		
LCB.201		19.4	20.1					
LCB.213		17.8	20.6					
LCB.298		15.2	15.5					

Dimensions (mm).

Emended diagnosis. Small to medium–sized (Dmax ~ 160 mm) neocomitid ammonites. Subrectangular whorl section, higher than wide, throughout ontogeny with flattened flanks. Flat ventral area marked by a narrow band that weakens on the body chamber. Fairly open umbilicus with short and abrupt umbilical wall.

Inner whorls of the microconch characterised by spaced to dense and straight to slightly prorsiradiate, bifurcated ribs. Most ribs bifurcate on the outer third of the flanks; occasional single ribs are observed. Ribs arise on the umbilical seam and cross the umbilical wall with weak retrocurvature and project on the umbilical margin. Aperture with short lateral lappets.

Early ontogeny of macroconch is similar to that of the microconch. Ribs on body chamber become denser and flexuous and are regularly fasciculate on the umbilical margin. Furcation point at the umbilical margin strengthens in weak tubercles. Branches of bifurcate ribs are markedly prorsiradiate and near the aperture form a small chevron on the venter.

Description. The holotype and two other paratypes of *Strambergella jacobi* correspond to small, subcomplete forms with discoidal, compressed shell. They exhibit a subrectangular whorl section, higher than wide, throughout the ontogeny with flattened flanks and short, abrupt umbilical wall. The umbilicus is fairly open (0,31 < U/D < 0,33) and the venter is flat with a narrow smooth band. There is no significant morphological difference between the holotypes and paratypes with the exception of UJF–ID.616 which has a higher Wb/D ratio reflecting the increasing thickness of the whorl on the outer part of the body chamber. The innermost whorls are characterized by spaced to dense, straight to slightly prorsiradiate ribs on the inner whorls. Most of the ribs bifurcate on the outer third of the flanks; and occasional single ribs can be observed. The ribs arise at the umbilical seam and cross the umbilical wall with weak retrocurvature and they project on the umbilical margin on the last adult whorl.

Among the material collected at Les Combes, specimens MPP–LCB.56, MPP–LCB.201, MPP–LCB.2013 and MPP–LCB.298 (Fig. 5G, H, I and J) perfectly match the morphological and ornamental features of the type series (described above). The specimen MPP–LCB.56 bears short lateral lappets. These specimens co–occur with medium–sized forms that share identical inner whorls such as MPP–LCB.163 and MPP–LCB.36 (Fig. 5K and M, respectively). They are characterized by a larger diameter, fast growth of the adult whorl and development of a stage with fasciculate ornament on the body chamber. The ribs regularly branch from a weak tubercle on the umbilical margin. At this stage, the umbilical wall is markedly steeper. The fasciculate ribs are slightly flexuous and the branches are markedly prorsiradiate. The siphonal band weakens on the body chamber and gives way to a slight chevron. The lateral ribbing vanishes near the aperture.

Among the unfigured material listed by Le Hégarat (1973, p. 56–57) only three specimens perfectly match the diagnosis of *Strambergella jacobi* given above. They are illustrated herein (Fig. 5D, E, F). The other specimens (FSL 127371, 127970, 127972, 127946, 127973 and 127589 – Fig. 6A–F) from the Le Hégarat collection are juveniles of *Delphinella* of the D. *delphinense* group. They differ from *S. jacobi* in having a low umbilical wall, rigid ornamentation and thickening of the primary ribs at the furcation point. Specimens FSL 127368 and 127905 are typical *Berriasella oppeli* (Fig. 6H, I) whereas the poorly preserved specimen FSL.127764 (Fig. 6G) is referred to *Pseudosubplanites* sp. indet. because of the absence of a ventral groove.

Dimorphism. As reflected in description given above, two morphotypes can be distinguished among the material from Les Combes:

- One group of small forms (Dmax < 45 mm) that matches the type series. It includes the specimens MPP–LCB.56, MPP–LCB.193, MPP–LCB.201, MPP–LCB.213 and MPP–LCB.298. Among them, MPP–LCB.56 shows short lateral lappets.
- The other group encompasses larger forms (Dmax < 160 mm) (specimens MPP–LCB.36, MPP–LCB.163 and MPP–LCB.195). This group is characterized by a distinctive secondary ornamental stage with fasciculate ribs issuing from regular umbilical tubercles, and a final growth stage marked by the complete disappearance of the ribs on the venter. The larger forms show a scaphitoid outer-whorl shape due to the fast growth rate. The umbilical wall is steeper. This group matches the morphology of *Fauriella shipkovensis* Le Hégarat, 1973 *non* Nikolov & Mandov, 1967.

Both groups share similar inner whorls marked by a *Berriasella*–-like ornament, and they co–occur together in the uppermost part of the Jacobi Zone *auctorum*. We thus strongly support the contention that *Strambergella jacobi* is dimorphic, with a large macroconch that develops new ornamental stages compared to the lappeted microconchs.

Discussion. As recently outlined by Vašíček and Skupien (2013), the great majority of the specimens assigned to *S. jacobi* in the literature are poorly preserved and thus their identification is doubtful. This is reflected in the synonymy list above. It is impossible to place specimens that have been figured without a ventral view in *Strambergella* rather than in *Pseudosubplanites* or *Berriasella*. This is the case with many specimens illustrated by Le Hégarat (1973), Hoedemaeker (1982) and Khimchiashvili (1989, 1990).

Outside Europe, specimens reported from South America (Geyer, 1983; Salazar, 2012) fall within the range of variation of "*Berriasella*" *limensis* (Lisson, 1907) and "*Berriasella*" *fraudans* (Steuer, 1897). "*B.*" *limensis* differs from *S. jacobi* [m] in its wider umbilicus and the style of its ornament, composed of low branching and coarse ribs (see Lisson, 1907, pl. 10, fig. 1–2; Rivera, 1951, pl. 2, fig. 3–4; Rivera, 1979, fig. 1; Wiedmann, 1988, text–fig. 8A). "*B.*" *fraudans* can easily be distinguished by its larger umbilicus and subrounded whorl section (Steuer, 1897, pl. 9, fig. 4–6; Salazar, 2012, fig. 4.52 a–q). We therefore reject the synonymy between *S. jacobi* and "*B.*" *fraudans* proposed by Salazar (2012).

S. jacobi was also reported from Madagascar (Collignon, 1960) and Tibet (Liu and Wang, 1987; Liu, 1988). In our opinion all specimens illustrated by those authors are juveniles and/or microconchs that fall in the range of variation of the group of *Blanfordiceras wallichi* (Gray, 1832) as illustrated by Yin and Enay (2004) and Enay (2009). *B. wallichi* differs from the microconch of *S. jacobi* by its subquadratic whorl section, well marked ventral furrow on the inner whorls, coarser ribbing style and strong ventral chevron on the body chamber.

It should finally be noted that macroconchs of *S. jacobi* have great affinities to the middle Berriasian taxa *Tirnovella occitanica* (Pictet, 1867) and *T. subalpina* (Mazenot, 1939).

T. occitanica could be easily distinguished from a macroconch of *S. jacobi* by an inflated, involute morphology with a steep, recurved umbilical wall, less marked umbilical tubercles and dense ribbing. The holotype of *T. subalpina* are rather similar to macroconchs of *S. jacobi*, but it differs slightly in its steeper umbilical wall, denser ribbing and small umbilical bullae. The inner whorls of the type specimen are not preserved and this prevents further comparison with *S. jacobi*. Le Hégarat (1973) previously supported the idea that *T. subalpina* appeared before *T. occitanica* in southeast France. At Les Combes, *T. subalpina* is reported four metres above the last occurrence of *S. jacobi*. It could thus be suggested that there exists a phyletic lineage between *S. jacobi*, *T. subalpina* and *T. occitanica* across the lower/middle Berriasian boundary, but in the current state of knowledge, the precise vertical range, ontogeny, variability and dimorphism of *Tirnovella* taxa remain unclear. A systematic revision is urgently needed.

Occurrences. In our view, *Strambergella jacobi* is known from southeast France, southern Spain, Italy, Bulgaria, Central Tunisia and Crimea. Its occurrence in Georgia is suspected.

S. jacobi is precisely dated at Les Combes where the species is found in the uppermost part of the Jacobi Zone *auctorum*. By mean of calpionellids, this level correlates with the uppermost part of the *R. ferasini* Subzone and lowermost part of the *C. elliptica* Subzone of the Calpionella Standard Zone; an age similar to that documented using rock thin sections of *ex-situ* material from Champ Blanc (see below).

In Tunisia, the species was reported from an unknown level in the "*Argiles de Sidi Kralif*" at Jebel Nara (Arnould–Saget, 1953). According to Busnardo et al. (1976), the base of this formation is of lower Berriasian age (*Calpionella alpina* Zone) but no detailed published data is available regarding the distribution of *S. jacobi* in this section. The same is true for the isolated specimens from Spain, Italy, Bulgaria and Crimea.

4. Calpionellid and calcareous dinoflagellate assemblages of the Champ Blanc ammonite fauna

The microfacies analysis focused on the identification of calpionellid markers and accompanying microfossils that were studied under a light microscope in thin sections, a LEICA DM 2500. Calpionellids, dinoflagellates and residual bioclasts were quantitatively evaluated using the optical charts of Bacelle and Bosellini (1965). For microfacies and microfossil documentation a LEICA DFC 290 HD camera was used. The thin sections were made and are stored in the Department of Geology and Palaeontology (Faculty of Natural Sciences) of the University of Bratislava. Two of the standard calpionellid subzones were identified in the samples studied.

The *C. alpina* Subzone of the Calpionella Zone (*sensu* Remane et al., 1986, Reháková and Michalík 1997, Lakova et al., 1999, Boughdiri et al., 2006, Andreini et al., 2007, Wimbledon et al., 2013) was identified in thin section of sample FSL.127389 (*Pseudoneocomites gr. retowskyi* – Fig. 7C). The limestone is a biomicrite (predominantly wackestone) of *Calpionella*–globochaete microfacies (Fig. 8A). The sample contains spores of *Globochaete alpina* Lombard and predominant sphaerical forms of *Calpionella alpina* Lorenz (Fig. 9D) with rare loricas of *Crassicollaria parvula* Remane, *Calpionella grandalpina* Nagy, *Tintinnopsella carpathica* Murgeanu and Filipescu and *Tintinnopsella doliphormis* Colom (Fig. 10J). In addition, it rarely contains the calcareous dinocysts *Colomisphaera carpathica* (Borza) (Fig. 11C) and *Stomiosphaera proxima* Borza. The micritic matrix contains a small portion (2%) of very small bioclasts: bivalves, crinoids, ostracods and foraminifera (mainly *Spirilina* sp. was determined).

The *C. elliptica* Subzone of the *Calpionella* Zone (*sensu* Pop, 1974) was identified in thin sections of samples FSL.140434a & b (*Strambergella jacobi* – Fig. 5F), FSL.127401a & b and FSL.127398 (*Delphinella sevenieri* Le Hégarat, 1973 – Fig. 7A and B) and FSL.141240 (*Strambergella* sp. – Fig. 7D). The limestones are biomicrites

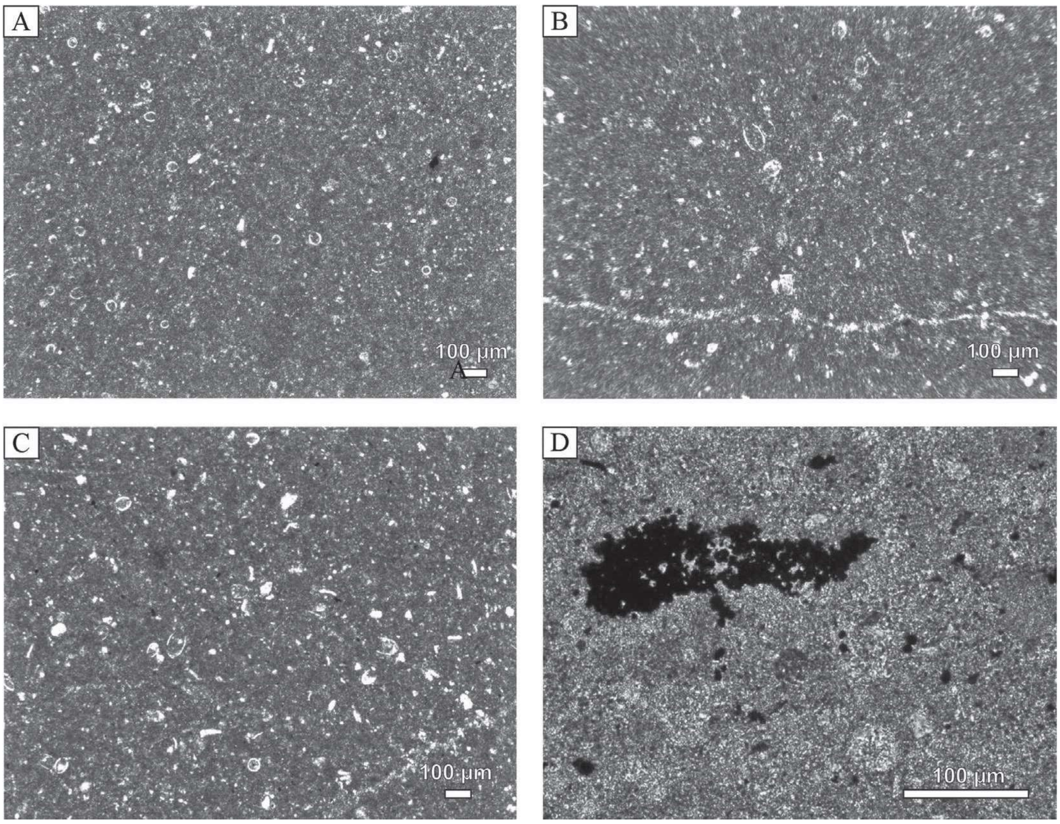


Fig. 8. Microfacies of the Alpina and Elliptica subzones of the Calpionella Zone of the matrix of the ammonites from Champ Blanc: (A) *Calpionella*–globochaete microfacies (wackestone) with predominance of sphaerical species of *Calpionella alpina* and seldom *Crassicollaria parvula*. Sample FSL.127 389; (B) *Calpionella elliptica* in biomicrite limestone (wackestone) with very small fragments of bioclasts. Sample FSL.127 398; (C) *Tintinnopsella carpathica*, *Calpionella elliptica* and *Calpionella alpina* in biomicritic limestone (wackestone) and higher portion of small fragments of bioclasts. FSL.127 401b; (D) Biomirite limestone (wackestone) with nest accumulations of framboidal pyrite. Pyrite is also scattered in matrix or impregnated bioclasts. Sample FSL.127 401a.

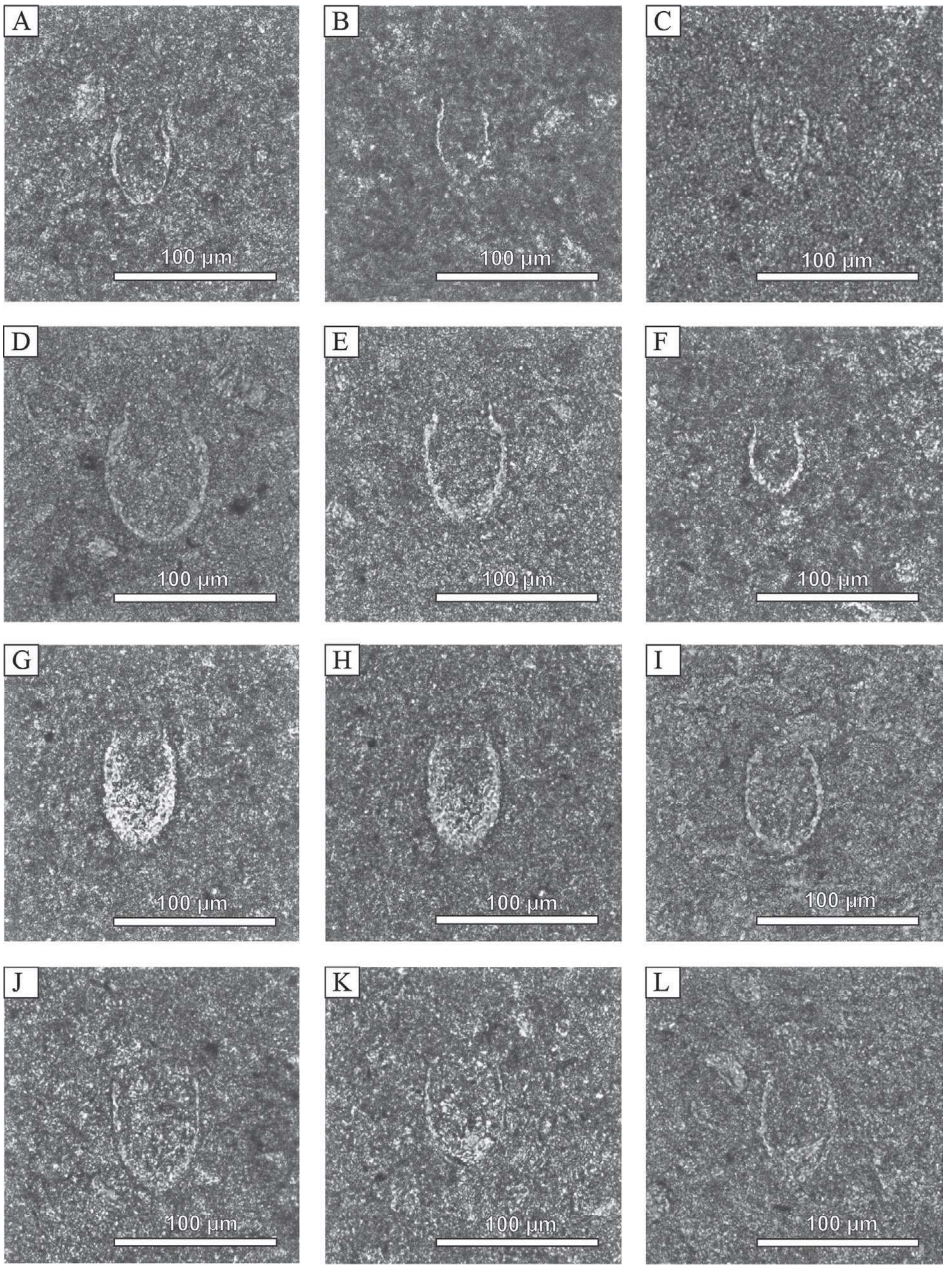


Fig. 9. Microfossils of the Alpina and Elliptica subzones of the Calpionella Zone of the matrix of the ammonites from Champ Blanc: (A) *Crassicollaria massutiniana* (Colom). Sample FSL.141 240; (C) and (B) *Crassicollaria parvula* Remane. Samples FSL.127 398, FSL.127 401b; (D) and (E) *Calpionella alpina* Lorenz. Samples FSL.127 389; FSL.140 434. F. *Calpionella minuta* Houša. Sample FSL.140 434; (G), (H) and (I) *Calpionella elliptica* Cadisch. Samples FSL.127 398; FSL.127 401b; FSL.140 434; (J) and (K) *Remaniella ferasini* (Catalano). Samples FSL.141 240; FSL.140 434; (L) *Remaniella catalanoi* Pop. Sample FSL.141 240.

(wackestones) of *Calpionella*–globochaete microfacies (Fig. 8B–D). Nannofossils constitute a substantial portion of the limestone's micrite matrix and allochems are represented by very small bioclasts (up to 5% of the total rock). The sample contain spores of *Globochaete alpina* (Fig. 11K) and the calpionellid associations are composed of *C. massutiniana* (Colom) (Fig. 9A), *Crassicollaria parvula* (Fig. 9B–C), *Calpionella alpina* (Fig. 9E), *C. minuta* Houša (Fig. 9F), *C. elliptica* Cadisch (Fig. 9G–I), large forms of *Tintinnopsella carpathica* (Fig. 10F–G), *T. subacuta* Colom (Fig. 10H–I), *Lorenziella hungarica* Knauer et Nagy (Fig. 10K), *L. plicata* Remane (Fig. 10L); and remaniellids such as *Remaniella catalanoi* Pop (Fig. 9L), *R. ferasini* Catalano (Fig. 9J–K), *R. duranddelgai* Pop (Fig. 10A–C), *R. borzai* (Fig. 10D) and *R. colomi* Pop (Fig. 10E). These samples in addition contain globochaetes, crinoids, bivalves, ostracods, small benthic foraminifera such as *Lenticulina* sp., *Spirilina* sp., *Dentalina* sp., *Patelina* sp. (Fig. 11L) and the microproblematicum *Gemeridella minuta* Borza et Mišík (Fig. 11J). Calcareous dinocysts are represented by *Colomisphaera lapidosa* Colom (Fig. 11A), *C. carpathica* (Fig. 11D), *Stomiosphaerina proxima* (Fig. 11B), *S. wanneri* Borza (Fig. 11G–H), *Cadosina semiradiata semiradiata* Wanner (Fig. 11F), *C. semiradiata fusca* Wanner (Fig. 11E) and *C. semiradiata olzae* Nowak (Fig. 11I). In sample FSL.127401, a few fragments of miliolid foraminifera and high portion of sponge spicules were observed. There, some of the bioclasts are slightly silicified. Silt–sized quartz grains are very rarely

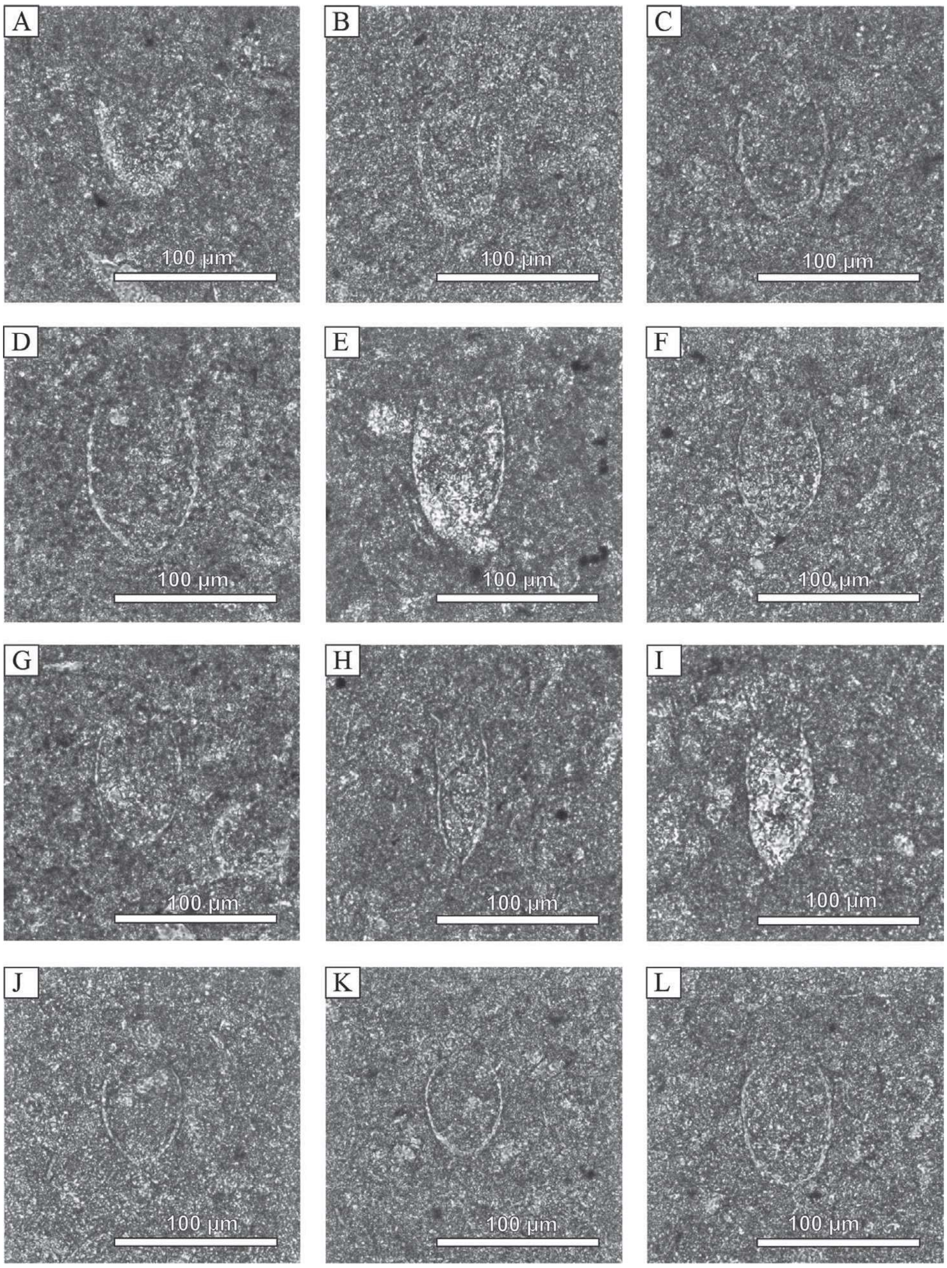


Fig. 10. Microfossils of the Alpina and Elliptica subzones of the Calpionella Zone of the matrix of the ammonites from Champ Blanc: (A), (B) and (C) *Remaniella durandelgai* Pop. Samples FSL.127 398; FSL.127 401a; FSL.140 434; (D) *Remaniella borzai* Pop. Sample FSL.127 401a; (E) *Remaniella colomi* Pop. Sample FSL.127 401b; (F) and (G) *Tintinnopsella carpathica* (Murgeanu et Filipescue). Samples FSL.127 401a; FSL.127 401b; (H) and (I) *Tintinnopsella subacuta* (Colom). Samples. FSL.127 401a; FSL.127 401b; (J) *Tintinnopsella doliphormis* (Colom). Sample FSL.127 389; (K) *Lorenziella hungarica* Knauer et Nagy. Sample FSL.127 398; (L) *Lorenziella plicata* Remane. Sample FSL.127 401b.

present (FSL.127401a and b). Scattered occurrences of pyrite (also framboidal) and Fe–hydroxides, locally accumulated in nests, were observed.

The calpionellid assemblages indicate the *C. alpina* and *C. elliptica* subzones of the Calpionella Standard Zone. As a result, the ammonite fauna collected by Le Hégarat originates from more than one level, but it cannot be older than the middle part of the Jacobi Zone *auctorum* by comparison with the ammonites distribution recognized at Les Combes. Moreover, the main bulk of the fauna, including *S. jacobi*, originates from the upper part of the Calpionella Standard Zone (*C. elliptica* Subzone), thus confirming similar result observed at Les Combes.

5. Discussion

On a pure taxonomic point of view, the revision of *Berriasella jacobi* shows that:

- This species is dimorphic and it shows peculiar morphological features (U/D ratio, umbilical wall, ribbing style and aspect of the ventral area) which do not compare with those of the genus *Berriasella*, but do match closely the morphological features of the genus *Strambergella*;
- A very limited number of specimens reported in the literature match the type material;

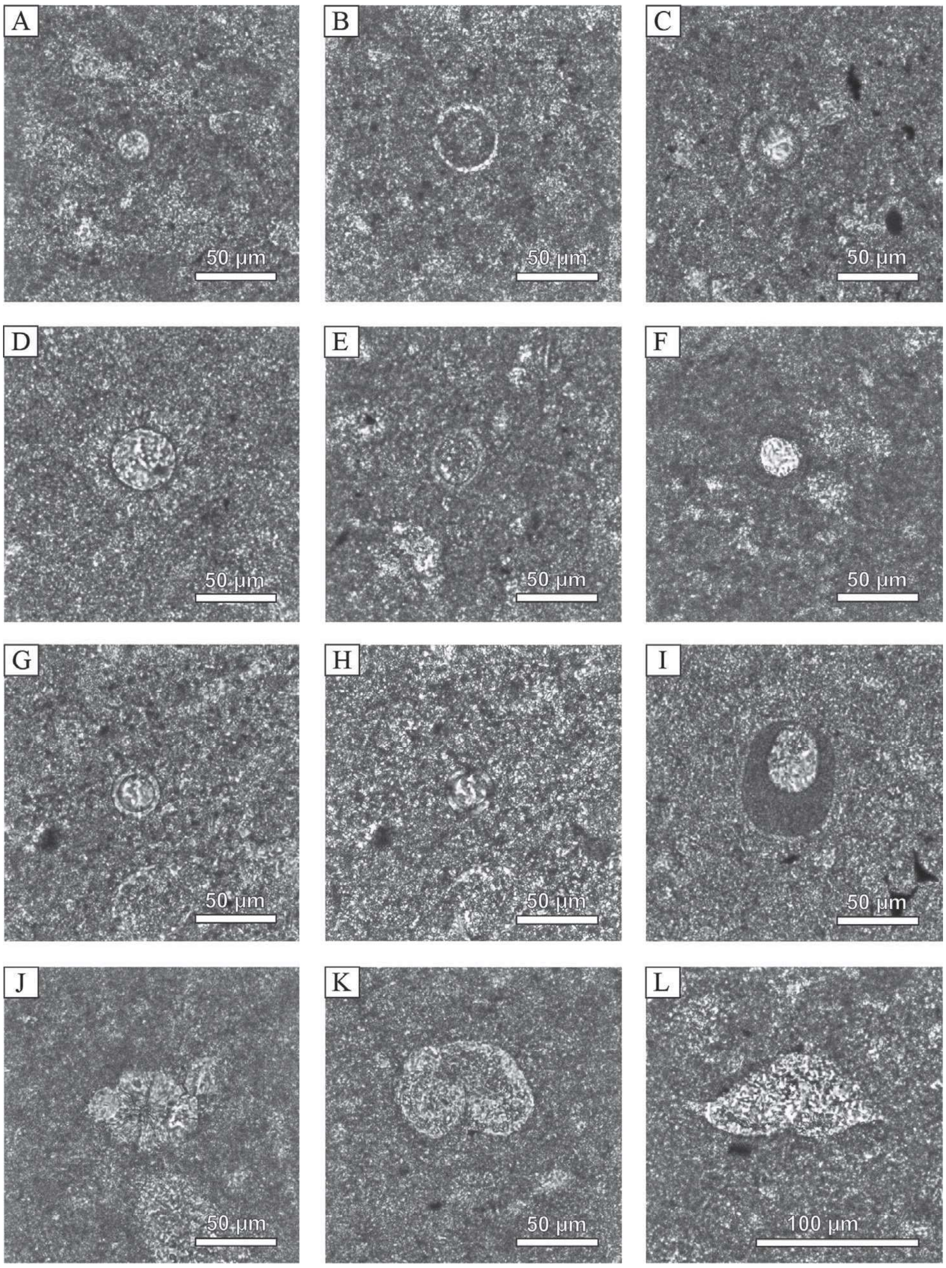


Fig. 11. Microfossils of the Alpina and Elliptica subzones of the Calpionella Zone of the matrix of the ammonites from Champ Blanc: (A) *Colomisphaera lapidosa* (Colom). Sample FSL.140 434; (B) *Stomiosphaerina proxima* Řehánek. Sample FSL.140 434; (C) and (D) *Colomisphaera carpathica* (Borza). Sample FSL.127 389; FSL.127 401b; (E) *Cadosina semiradiata fusca* Wanner. Sample FSL.127 401b; (F) *Cadosina semiradiata semiradiata* Wanner. Sample FSL.127 401b: (G) and (H) *Stomiosphaera wanneri* Borza. H. In polarized light. Sample FSL.127 401a; (I) *Cadosina semiradiata olzae* (Nowak). Sample FSL.127 398; (J) *Gemeridella minuta* Borza et Mišík. Sample FSL.127 398; (K) *Globochaeta alpina* Lombard. Sample FSL.141 240; (L) *Patelina* sp. Sample FSL.127 401b.

- Most records of the species from the Mediterranean–Caucasian Subrealm are based on the misinterpretation of specimens that either belong to *Pseudosubplanites*, *Pseudoneocomites*, *Berriasella* of the *B. oppeli* – *B. moreti* group or *Delphinella* of the *D. delphinense* group;
- Records from Tibet, Madagascar and Chile are based on specimens that belong to the genus *Blandfordiceras* and endemic Andean ammonites of uncertain taxonomic assignments.

New investigations at Les Combes and Champ Blanc indicate to us that the range of *S. jacobi* is limited to the uppermost part of the *R. ferasini* Subzone and lowermost part of the *C. elliptica* Subzone. As a consequence, the value of *S. jacobi* as an index species of the lowest Berriasian is highly questionable.

As a matter of fact, in recent literature (Cecca et al., 1989; Tavera et al., 1994; Benzaggagh et al., 2010; Vašíček and Skupien, 2013; Wimbledon et al., 2013; Bulot et al., 2014; Frau et al., in press), the recognition of the Jacobi Zone *auctorum* is most often based on taxa that were reported by Le Hégarat (1973, p. 277) as characteristic of the zone such as: *Berriasella* gr. *oppeli* – *moreti*, *Delphinella delphinense*, *Praedalmasiceras* of the *P. progenitor* (Oppel *in* Zittel, 1868) group and *Proniceras* of the *P. pronum* (Oppel *in* Zittel, 1868) group. Other species that were recently considered to mark the base of the Jacobi Zone *auctorum* include *Elenaella cularense* and

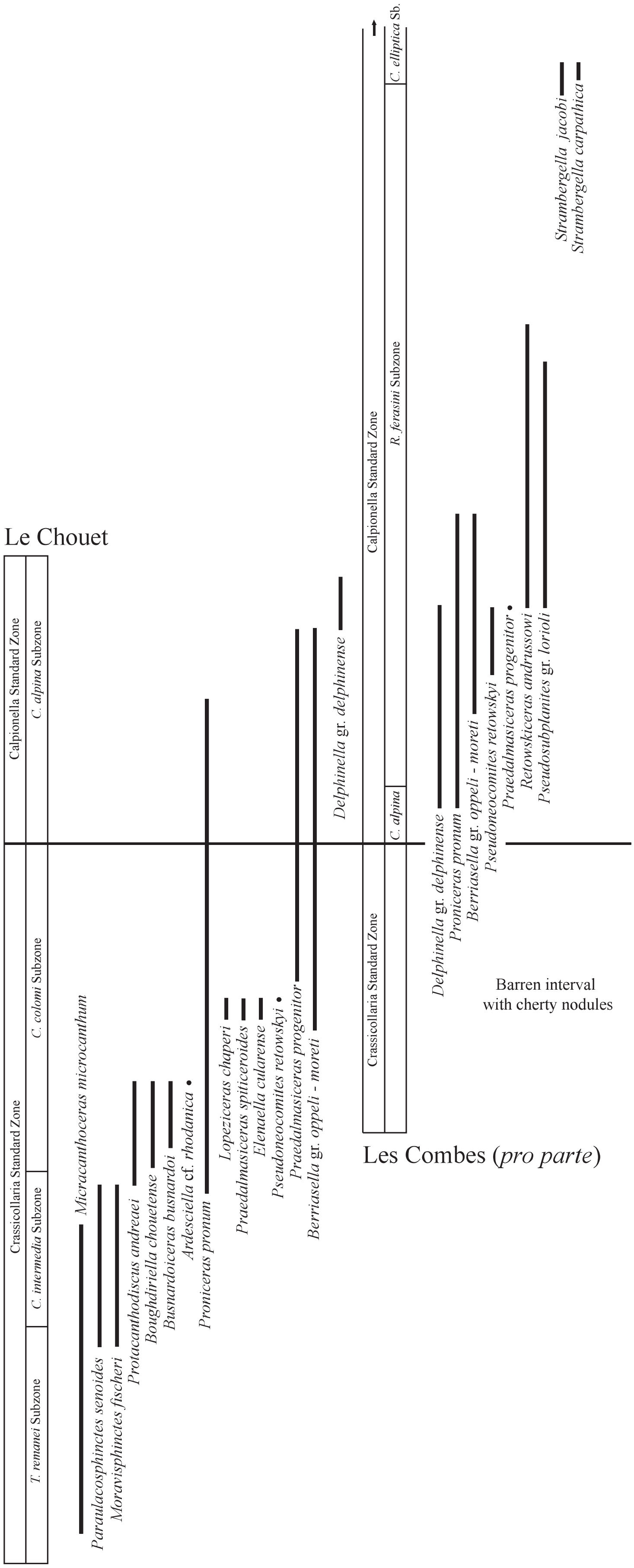


Fig. 12. Composite vertical range of selected age–diagnostic Perisphinctoidea from Le Chouet and Les Combes sections (Drôme) and integrated stratigraphy (modified after Wimbledon et al., 2013; Frau et al., 2015).

Lopeziceras chaperi that are known to have a restricted range (i.e. *E. cularense* biohorizon *sensu* Tavera et al., 1994) at the base of the zone (Frau et al., in press).

In order to clarify the ammonite biostratigraphy at the Tithonian/Berriasian transition and to provide an alternative to the Jacobi Zone *auctorum*, further investigations on the ammonite faunas that occurs in the Calpionella Standard Zone are urgently needed. The preliminary results from the expanded sections of the Vocontian Basin (Le Chouet and Les Combes) suggest that four successive assemblages can be identified within this time interval (Fig. 12). From oldest to youngest, these are:

- The *Elenaella cularense* assemblage;
- An assemblage dominated by *Praedalmasiceras* of the *P. progenitor* group;
- An assemblage dominated by *Delphinella* of the *D. delphinense* group that is also marked by the earliest occurrence of *Pseudosubplanites*;
- An assemblage dominated by *Pseudosubplanites*;
- An assemblage dominated by *Strambergella jacobi* and *S. carpathica.*

Ongoing research and systematic description of these faunas should allow us to propose a formal ammonite zonation calibrated with the standard calpionellid zones in the near future. We also hope that the results presented in this paper will stimulate new detailed investigations of the ammonite taxonomy in the late Tithonian to early Berriasian ammonite taxonomy of the Mediterranean—Caucasian Subrealm of the Tethyan Realm.

6. Conclusion

This work provides a revision of the Neocomitidae *Berriasella jacobi* Mazenot, 1939 (Perisphinctoidea, Ammonoidea), that has been widely used for the definition of the lower part of the Berriasian. The revision is based on the re-examination of the type material of *B. jacobi* from southeast France (Chomérac and Champ Blanc, Ardèche) and newly collected specimens from Les Combes (Drôme). The detailed description of the morphological and ornamental features supports that *B. jacobi* should be excluded from the genus *Berriasella* and transferred to the genus *Strambergella*. As herein understood, the type series of *Strambergella jacobi* corresponds to the microconch form of a dimorphic pair whose the macroconch form was previously referred as *Fauriella shipkovensis* Le Hégarat, 1973 *non* Nikolov & Mandov, 1967. Moreover, analysis of the literature has convinced us that most specimens illustrated as *B. jacobi* have been misidentified, and its presence in Tibet, Iraq, Madagascar and South America has to be ruled out. We only report *S. jacobi* in the Mediterranean—Caucasian Subrealm of the Tethyan Realm [France, Bulgaria, Crimea Spain, Tunisia, and doubtfully in Italy and Georgia].

Finally, new microfossil investigations at Font de Saint Bertrand and Champ Blanc indicate to us that the range of *S. jacobi* is limited to the uppermost part of the calpionellid *R. ferasini* Subzone and lowermost part of the *C. elliptica* Subzone (middle part of the *C. alpina* Zone). We thus believe that these facts render *S. jacobi* problematical as a marker for the lower boundary of the Berriasian, actually fixed at the base of the *C. alpina* Zone.

Acknowledgements

This work is a contribution of the Berriasian Working Group (BWG) of the International Subcommission on Cretaceous Stratigraphy (ISCS). We wish to express our warmest thanks to Emmanuel Robert (University Claude Bernard—Lyon I) who allowed us access to the collections in his care. This work would not have been possible without the help of Fabienne Giraud (Grenoble) who provided access to the type material of *Berriasella jacobi*. Special thanks are due to Elsa Schebelen—David and Jean—François Flandin (Saint—Privat—de—Champclos) for their continuous support during this study. The research of one of us (D.R) was supported by the AAPV – Grant Agency for Sciences in Slovakia (project APVV—14—0118, VEGA2/0034/16). I. Főzy (Hungarian Natural History Museum) and anonymous reviewer are gratefully acknowledge for their constructive remarks.

References

Andreini, G., Caracuel, J.E., Parisi, G., 2007. Calpionellid biostratigraphy of the Upper Tithonian –Upper Valanginian interval in Western Sicily (Italy). Swiss Journal of Geosciences 100, 179–198.

Arkadiev, V.V., 2011. Representatives of genera *Fauriella, Tirnovella* and *Jabronella* (Neocomitidae, Ammonoidea) from the Berriasian of the Mountainous Crimea and their stratigraphic significance. Bulletin of the Saint—Petersburg University 7 (2), 3–16 (in Russian).

Arkadiev, V.V., Bogdanova, T.N., 2004. The genus *Berriasella* (Ammonoidea) and zonal subdivision of the Berriasian of the Mountain Crimea. Stratigraphy and Geological correlation 12 (4), 54–67 (in Russian).

Arkadiev, V.V., Bogdanova, T.N., Lobacheva, S.V., 2005. The new data on biostratigraphy of the Berriasian deposits of the Tonas river basin (Mountain Crimea). In: Arkadiev, V.V., Prozorovsky, V.A. (Eds.), The Cretaceous System of Russia: Problems of Stratigraphy and Paleogeography, pp. 111–135. Saint—Petersburg. (in Russian).

Arkadiev, V.V., Fedorova, A.A., Savelieva, Y.N., Tesakova, E.M., 2006. Biostratigraphy of Jurassic—Cretaceous Boundary Sediments in the Eastern Crimea. Stratigraphy and Geological Correlation 14 (3), 302–330.

Arkadiev, V.V., Bogdanova, T.N., Guzhikov, A.Y., Lobacheva, S.V., Myshkina, N.V., Platonov, E.S., Savelyeva, Y.N., Shurekova, O.V., Yanin, B.T., 2012. Berriasian Stage of the Mountain Crimea, 472 pp. LEMA, Saint—Petersburg (in Russian with English abstract).

Arnould—Saget, S., 1953. Les ammonites pyriteuses du Tithonique supérieur et du Berriasien de Tunisie centrale. Annales des Mines et de la Géologie, Série A Mémoires 10, 1–132.

Bacelle, L., Bosellini, A., 1965. Diagrammi per la stima visiva della composizione perventualle nelle rocce sedimentarie. Annali dell'Università di Ferrara, Nuove Serie, Sezione IX, Scienze Geologiche e Paleontologiche 1, 59–62.

Benzaggagh, M., Cecca, F., Rouget, I., 2010. Biostratigraphy distribution of ammonites and calpionellids in the Tithonian of the internal Prerif (Msila area, Morocco). Paläontologische Zeitschrift 84, 301–315.

Boughdiri, M., Sallouhi, H., Maâlaoui, K., Soussi, M., Cordey, F., 2006. Calpionellid zonation of the Jurassic – Cretaceous transition in north Atlasic Tunisia. Updated Upper Jurassic stratigraphy of the "Tunisian Trough" and regional correlations. Comptes Rendus Geoscience 338, 1250–1259.

Boughdiri, M., Sallouhi, H., Haddad, S., Cordey, F., Soussi, M., 2009. Integrated biostratigraphy and regional correlations of Upper Jurassic—lowermost Cretaceous series in northern Tunisia. GFF 131, 71–81.

Bulot, L.G., Frau, C., Wimbledon, W.A.P., 2014. New and poorly known Perisphinctoidea (Ammonitina) from the Upper Tithonian of Le Chouet (Drôme, SE France). Volumina Jurassica 12 (1), 113–128.

Busnardo, R., Donze, P., Le Hegarat, G., Memmi, L., M'Rabet, A., 1976. Précisions biostratigraphiques nouvelles sur le Berriasien des Djebel Nara et Sidi Kralif (Tunisie Centrale). Geobios 9, 231–249.

Cantú-Chapa, A., 1999. El límite Jurásico-Cretácico en Mazatepec, Puebla (México). Instituto Mexicano del Petroleo, sección Geología, Monografía 1, 3–24.

Cecca, F., 1985. Alcune Ammoniti provenienti dalla Maiolica dell'Appennino Centrale (Umbria Marche e Sabina). Bolletino del Servizio Geologico d'Italia 1/13 (1982), 133–162.

Cecca, F., Enay, R., Le Hégarat, G., 1989. L'Ardescien (Tithonique supérieur) de la région stratotypique: série de référence et faunes (ammonites, calpionelles) de la bordure ardéchoise. Documents des Laboratoire Géologie de Lyon 107, 1–115.

Cecca, F., Cresta, S., Pallini, G., Santantonio, M., 1990. Il Giurassico di Monte Nerone (Appenino marchigiano, Italia Centrali): biostratigrafia, litostratigrafia ed evoluzione paleogeografia. In: Atti II° Convegno Internazionale Fossili, Evoluzione, Ambiente, Pergola, 1987, pp. 63–139.

Collignon, M., 1960. Atlas des fossiles caractéristiques de Madagascar. Fascicule VI (Tithonique), pp. 134–175. Service Géologique de Madagascar, Tananarive.

De Wever, P., Geyssant, J.R., Azéma, J., Devos, I., Duée, G., Manivit, H., Vrielynck, B., 1986. La coupe de Santa Anna (Zone de Sciacca. Sicile): une synthèse biostratigraphique des apports des macro—, micro— et nannofossiles du Jurassique supérieur et Crétacé inférieur. Revue de Micropaléontologie 29, 141–186.

Dimitrova, N.Y., 1967. Les fossiles de Bulgarie. IV. Crétacé Inférieur. Cephalopoda (Nautiloidea et Ammonoidea). 236 pp. Académie Bulgare des Sciences, Sofia.

Enay, R., 2009. Les faunes dámmonites de lÓxfordien au Tithonien et la biostratigraphie des Spiti–Shales (Callovien supérieur–Tithonien) de Thakkhola, Népal Central. Documents des Laboratoires de Géologie Lyon 166, 1–246.

Enay, R., Geyssant, J.R., 1975. Faunes tithoniques des chaînes bétiques (Espagne méridionale). Mémoires du Bureau de Recherches Géologiques et Minières 86, 39–55.

Fallot, P., 1922. Etude géologique de la Sierra de Majorque, 480 pp. Librairie polytechnique Ch. Béranger, Paris.

Fatmi, A.N., 1972. Stratigraphy of Jurassic and Lower Cretaceous rocks and Jurassic Ammonites from northern areas of West Pakistan. Bulletin of the British Museum of Natural History, Geology 20, 297–380.

Fatmi, A.N., 1977. Neocomian ammonites from northern areas of Pakistan. Bulletin of the British Museum of Natural History, Geology 28, 257–296.

Favre, E., 1880. Description des couches tithoniques des Alpes fribourgeoises. Mémoires Suisses de Paléontologie 3, 1–74.

Föllmi, K.B., 2012. Early Cretaceous life, climate and anoxia. Cretaceous Research 35, 230–257.

Frau, C., Bulot, L.G., Wimbledon, W.A.P., 2015. Upper Tithonian Himalayitidae Spath, 1925 (Perisphinctoidea, Ammonitina) from Le Chouet (Drôme, France): implications for the systematics. Geologica carpathica 66 (2), 117–132.

Frau, C., Bulot, L.G., Wimbledon, W.A.P., Ifrim, C., 2016. Systematic palaeontology of the Perisphinctoidea across the Jurassic/Cretaceous boundary at Le Chouet (Drôme, France) and its biostratigraphic implications. Acta Geologica Polonica (in press).

Geyer, O.F., 1983. Obertithonische Ammoniten–Faunen von Peru. Zentralblatt der Geologie und Paläontologie Teil I 3 (4), 335–350.

Gray, J.E., 1832. Illustrations of Indian Zoology, 1–2, 202 pl.

Grün, B., Blau, J., 1997. New aspects of calpionellid biochronology: proposal for a revised calpionellid zonal and subzonal division. Revue de Paléobiologie 16, 197–214.

Hoedemaeker, P.J., 1982. Ammonite biostratigraphy of the uppermost Tithonian, Berriasian, and lower Valanginian along the Río Argos (Caravaca, SE Spain). Scripta Geologica 65, 1–81.

Horváth, A., Knauer, J., 1986. Biostratigraphy of the Jurassic–Cretaceous boundary beds in the profile Közöskút Ravine II at Hárskút. Acta Geologica Hungarica 29 (1–2), 65–87.

Horváth, A., Knauer, J., 1987. Jura–Kréta határrétegek biosztratigráfiája a Hárskút, Közöskúti –Árok II. Szelvényben. A Mayar Allami Földtani intézet ëvi jelentése AZ 1985. Evrol, pp. 405–431.

Howarth, M.K., 1992. Tithonian and Berriasian ammonites from the Chia Gara Formation in northern Iraq. Palaeontology 35 (3), 597–654.

Ivanov, M., Stoykova, K., Idakieva, V., 2010. New biostratigraphic data on the Upper Tithonian and Lower Berriasian in the Krayshte area (Southwestern Bulgaria). Annuaire de l'Université de Sofia “St. Kliment Ohridski”, Livre 1 – Géologie 102, 21–42.

Khimchiashvili, N.G., 1989. The Berriasellidae of Abkhazia. The Tithonian fauna of mount Lakorizi–Tau (basin of Bzibi river). Metsniereba 1–87 (in Russian).

Khimchiashvili, N.G., 1990. The Tithonian–Berriasian ammonites of Georgia and their distribution. In: Atti II° Convegno Internazionale Fossili, Evoluzione, Ambiente, Pergola, 1987, pp. 371–381.

Kilian, W., 1889. Etudes paléontologiques sur les terrains secondaires et tertiaires de l'Andalousie. In: Mission d'Andalousie. Mémoire de l'Académie des Sciences de l'Institut de France, 30, pp. 580–733.

Klein, J., 2005. Lower Cretaceous Ammonites I. (Perisphinctaceae 1 – Himalayitidae, Olcostephanidae, Holcodiscidae, Neocomitidae, Oosterelliidae). In: Riegraf, W. (Ed.), Fossilium Catalogus I: Animalia, 139. Backhuys Publishers, Leiden, pp. 1–484.

Kvantaliani, I.V., 1999. Berriasian Cephalopods of the Crimea and Caucasus. Proceedings of the Geological Institute of the Georgian Academy of Sciences, New series 112, 1–188. “Metsniereba”,Tbilisi. (in Russian).

Kvantaliani, I.V., 2000. Middle Jurassic –Early Cretaceous Ammonites of Vedi Ophiolite Zone of Lesser Caucasus. Proceedings of the Geological Institute of the Georgian Academy of Sciences, New series 116, 1–70. “Metsniereba”, Tbilisi. (in Russian).

Lakova, I., Stoykova, K., Ivanova, D., 1999. Calpionellid, nannofossils and calcareous dinocyst bioevents and integrated biochronology of the Tithonian to Valanginian in the West Balkan Mountains, Bulgaria. Geologica Carpathica 50, 151–168.

Le Hégarat, G., 1973. Le Berriasien du Sud Est de la France. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 43, 1–576.

Le Hégarat, G., Remane, J., 1968. Tithonique supérieur et Berriasien de l'Ardèche et de l'Hérault. Corrélation des ammonites et des calpionelles. Géobios 1, 7–70.

Lehmann, J., Ifrim, C., Bulot, L.G., Frau, C., 2015. Paleobiogeography of Early Cretaceous ammonites. In: Klug, C., Korn, D., De Baets, K., Kruta, I., Mapes, R.H. (Eds.), Ammonoid Paleobiology: From Macroevolution to Paleogeography, Topics in Geobiology 44, volume II. Springer, pp. 229–257.

Lisson, C.I., 1907. Contribución a la Geología de Lima y sus alrededores. Gil, Lima, p. 123 p.

Liu, G.F., 1988. Late Jurassic and Early Cretaceous ammonites from Nyalam–Gucuo area, Xizang (Tibet). In: Professional Papers of Palaeontology in Xizang. Geological Publishing House, Beijing, pp. 1–65 (in Chinese, English abstract).

Liu, G.F., Wang, S.E., 1987. A new advance in study of the Upper Jurassic and Lower Cretaceous of the Himalayas, Xizang (Tibet). In: Editorial Committee of Professional Papers of Stratigraphy and Palaeontology, Chinese Academy of Geological Sciences (Ed.). Professional Papers of Stratigraphy and Palaeontology, 17. Geological Publishing House, Beijing, pp. 143–166 (in Chinese, English abstract).

Mazenot, G., 1939. Les Palaeophoplitidae tithoniques et berriasiens du sud–est de la France. Mémoires de la Société Géologique de France 41, 5–303.

Nikolov, T.G., 1960. La faune d'ammonites du Valanginien du Prebalkan oriental. Travaux sur la géologie de Bulgarie, série Paléontologie 2, 143–206.

Nikolov, T.G., 1966. New genera and subgenera of Ammonites of family Berriasellidae. Comptes Rendus de l'Académie bulgare des Sciences 19 (7), 639–642.

Nikolov, T.G., 1982. Les ammonites de la famille Berriasellidae Spath 1922 (Tithonique supérieur–Berriasien). Edition Académie bulgare des Sciences, Sofia, 245 pp.

Nikolov, T.G., Mandov, G., 1967. Sur quelques nouvelles espèces d'ammonites berriasiennes du Pré–balkan (Bulgarie du Nord). Bulletin de l'Institut Géologique, Série Paléontologie 16, 41–46.

Oppel, A., 1865. Die tithonische Etage. Zeitschrift der Deutschen Geologischen Geselshaft 17, 535–558.

Pervinquière, L., 1907. Étude de paléontologie tunisienne. 1 : Céphalopodes des terrains secondaires. Mémoires de la carte géologique de Tunisie, 438 pp.

Pictet, F.J., 1867. Étude provisoire des fossiles de la Porte–de–France, d'Aizy et de Lemenc. Mémoire de la Société de Physique et d'Histoire Naturelle de Genève 4, 207–312.

Pop, G., 1974. Les zones des calpionellides tithoniques–valanginiennes du sillon de Resita (Carpathes Méridionales). Revue Roumaine de Géologie 18, 109–125.

Pruner, P., Houša, V., Olóriz, F., Košťák, M., Krs, M., Man, O., Schnabl, P., Venhodová, D., Tavera, J.M., Mazuch, M., 2010. High–resolution magnetostratigraphy and biostratigraphic zonation of the Jurassic/Cretaceous boundary strata in the Puerto Escaño section (southern Spain). Cretaceous Research 31, 192–206.

Reháková, D., Michalík, J., 1997. Evolution and distribution of calpionellids – the most characteristic constituents of Lower Cretaceous Tethyan microplankton. Cretaceous Research 18, 493–504.

Remane, J., Borza, K., Nagy, I., Bakalova–Ivanova, D., Knauer, J., Pop, G., Tardi–Filácz, E., 1986. Agreement on the subdivision of the standard calpionellid zones defined at the IInd Planktonic Conference Roma 1970. Acta Geologica Hungarica 29, 5–14.

Rivera, R., 1951. La fauna de los estratos de Puente Inga, Lima. Boletin de la Sociedad Geologica del Peru 22, 5–53.

Rivera, R., 1979. Zonas faunisticas del Cretaceo de Lima. Boletin de la Sociedad Geologica del Peru 62, 19–24.

Roman, F., Mazenot, G., 1937. Découverte d'une faune pyriteuse d'âge Tithonique supérieur aux environs de Chomérac (Ardèche). Bulletin de la Société Géologique de France, cinquième série 7, 179–186.

Salazar, C.A., 2012. The Jurassic–Cretaceous Boundary (Tithonian – Hauterivian) in the Andean Basin of Central Chile: Ammonites, Bio– and Sequence Stratigraphy and Palaeobiogeography. Unpublished PhD Thesis, Heidelberg University, 409 pp.

Sapunov, I.G., 1957. Stratigraphie und Tektonik eines Teils des Vorbalkans zwischen dem Drjanovo und dem Veselinalluβ. Bulletin of the Geological Institute. Bulgarian Academy of Sciences 5, 139–214 (in Bulgarian).

Sapunov, I.G., 1979. Les fossiles de Bulgarie. III. 3. Jurassique supérieur. Ammonoidea. Académie Bulgare des Sciences Ed., 237 p. (in Bulgarian, French abstract).

Sarasin, C., Schöndelmayer, C., 1901. Étude monographique des Ammonites du Crétacique inférieur de Châtel-Saint-Denis. Mémoire de la Société Paléontologique Suisse 24, 95–187.

Sey, I.I., Kalacheva, E.D., 1990. Lower Berriasian deposits of South Primorye and the Jurassic–Cretaceous boundary in the Far East of the USSR. In: Menner, V.V. (Ed.), Boundary between the Jurassic and Cretaceous Systems, Transactions of Institute of Geology and Geophysics, 699. Siberian Branch Academy of Sciences USSR, pp. 118–187 (in Russian).

Sey, I.I., Kalacheva, E.D., 1996. Upper Jurassic–Lower Cretaceous biostratigraphy and fauna of South Primorie (Russian Far East). Geology of Pacific Ocean 12, 293–312.

Sey, I.I., Kalacheva, E.D., 1999a. Early Cretaceous ammonites of the Sikhote–Alin and their biostratigraphic and biogeographic implications. Tikhookeanskaia Geologiia 18, 83–92 (in Russian).

Sey, I.I., Kalacheva, E.D., 1999b. Lower Berriasian of Southern Primorye (Far East Russia) and the problem of Boreal–Tethyan correlation. Palaeogeography, Palaeoclimatology, Palaeoecology 150, 49–63.

Sey, I.I., Kalacheva, E.D., 2001. Early Cretaceous ammonites of the Sikhote–Alin and their biostratigraphic and biogeographic implications. Geology of Pacific Ocean 16, 1091–1106 (Russian version published in 1999).

Sey, I.I., Kalacheva, E.D., 2004. Ammonoidea. In: Sey, I.I., Okuneva, T.M., Zonova, T.D., Kalacheva, E.D., Yazykova, E.A. (Eds.), Atlas of the Mesozoic Marine Fauna of the Far East, Russia. Vserosyjskij Nauchno–Issledowatelskij Institut Press, Saint–Petersbourg, pp. 38–95.

Sey, I.I., Repin, E., Kalacheva, E.D., Okuneva, T.M., Parketsov, K.V., Polubotko, U.V., 1992. 11. Eastern Russia. In: Westermann, G.E.G. (Ed.), The Jurassic of the Circum–Pacific, pp. 225–245.

Spath, L.F., 1939. The Cephalopoda of the Neocomian Belemnite Beds of the Salt Range. Palaeontologia Indica. Memoirs of the Geological Survey of India, New Series 25, Memoir 1 1–154.

Steuer, A., 1897. Argentinische Jura–Ablagerungen. Beitäge zur Kenntnis der Geologie und Paläontologie der argentinischen Anden. Palaeontologische Abhandlungen 7 (3), 127–222.

Szives, O., Főzy, I., 2013. Systematic descriptions of Early Cretaceous ammonites of the carbonate formations of the Gerecse Mountains. In: Főzy, I. (Ed.), Late Jurassic–early Cretaceous Fauna, Biostratigraphy, Facies and Deformation

History of the Carbonate Formations in the Gerecse and Pilis Mountains (Transdanubian Range, Hungary), pp. 293–342. Institute of Geosciences, University of Szeged, GeoLitera Publishing House.

Tavera, J.–M., 1985. Los ammonites del Tithónico superior–Berriasense de la Zona Subbética (Cordilleras Béticas). Tesis Doctoral, Universidad de Granada, Granada, 381 pp.

Tavera, J.–M., Aguado, R., Company, M., Olóriz, F., 1994. Integrated biostratigraphy of the Durangites and Jacobi zones (J/K boundary) at the Puerto Escaño section in southern Spain (province of Cordoba). Géobios Mémoire Spécial 17, 469–476.

Toucas, A., 1890. Etude de la faune des couches tithoniques de l'Ardèche. Bulletin de la Société Géologique de France 18, 560–629.

Uhlig, V., 1905. Einige Bemerkungen über die Ammonitengattung Hoplites Neumayr. Sitzungsberichte der Kaiserlichen Akademie der Wissenschaften in Wien. Mathematischnaturwissenschaftliche Klasse 114, 591–636.

Vašíček, Z., Skupien, P., 2013. Early Berriasian ammonites from the Štramberk Limestone in the Kotouč Quarry (Outer Western Carpathians, Czech Republic). Annales Societatis Geologorum Poloniae 83, 329–342.

Westermann, G.E.G., 2000. Biochore classification and nomenclature in paleobiogeography: an attempt at order. Palaeogeography, Palaeoclimatology, Palaeoecology 158, 1–13.

Wiedmann, J., 1988. Plate tectonics, sea level changes, climate and the relationship to ammonite evolution, provincialism, and mode of life. In: Wiedmann, J., Kullman, J. (Eds.), Cephalopods–Present and Past. Schweizerbart, Stuttgart, pp. 737–765.

Wierzbowski, A., 1994. Late Middle Jurassic to earliest Cretaceous stratigraphy and microfacies of the Czorsztyn Succession in the Spisz area, Pieniny Klippen Belt, Poland. Acta Geologica Polonica 44 (3–4), 223–249.

Wierzbowski, A., Remane, J., 1992. The ammonite and calpionellid stratigraphy of the Berriasian and lowermost Valanginian in the Pieniny Klippen Belt (Carpathians, Poland). Eclogae Geologicae Helvetiae 85, 871–891.

Wimbledon, W.A.P., Casellato, C.E., Reháková, D., Bulot, L.G., Erba, E., Gardin, S., Verreussel, R.M.C.H., Munsterman, D.K., Hunt, C., 2011. Fixing a basal Berriasian and Jurassic–Cretaceous (J–K) boundary – perhaps there is some light at the end of the tunnel? Rivista Italiana di Stratigrafia e Paleontologia 117, 295–307.

Wimbledon, W.A.P., Reháková, D., Pszczółkowski, A., Casellato, C.E., Halásová, E., Frau, C., Bulot, L.G., Grabowski, J., Sobień, K., Pruner, P., Schnabl, P., Čížková, K., 2013. An account of the bio– and magnetostratigraphy of the upper Tithonian–lower Berriasian interval at Le Chouet, Drôme (SE France). Geologica Carpathica 64, 437–460.

Wright, C.W., Calomon, J.H., Howarth, M.K., 1996. Cretaceous Ammonoidea. In: Kaesler, R.L. (Ed.), Treatise on Invertebrate Paleontology, Part L, Mollusca 4, Revised, Volume 4, pp. 1–362. The Geological Society of America and the University of Kansas Press, Boulder, CO, and Lawrence, KS.

Yin, J., Enay, R., 2004. Tithonian ammonoid biostratigraphy in eastern Himalayan Tibet. Géobios 37, 667–686.

Zittel, von K.A., 1868. Die Cephalopoden der Stramberger Schichten. Palaeontologische Mittheilungen aus dem Museum des Koeniglich Bayerischen Staates 2 (1), 1–118.

Chapter 9

Paleobiogeography of Early Cretaceous Ammonoids

Jens Lehmann, Christina Ifrim, Luc Bulot and Camille Frau

9.1 Introduction

Ammonite dispersal is clearly related to paleogeographic patterns throughout the Mesozoic (Page 1996). Their distribution during life is thought to be controlled by physical barriers such as land masses and deep ocean basins, as well as by comprehensive environmental factors such as climate differences and oceanic circulation patterns (Kennedy and Cobban 1976; Cecca 2002; Cecca et al. 2005), while their biogeography is influenced by post-mortem transport along with other taphonomic and collection biases (Kennedy and Cobban 1976; De Baets et al. 2015; Naglik et al. 2015; Lukeneder 2015). Thus, a number of factors have an impact on their paleobiogeographic distribution.

The favored habitat of most ammonite families was the continental shelf (Westermann 1996), and these areas constantly changed as a result of fluctuating sea levels and plate tectonic movements on a large scale, particularly during the Early Cretaceous period (e.g. Föllmi 2012). Dynamic plate tectonic configurations that are strongly linked to sea-level changes trigger the migration of species

---

J. Lehmann (✉)
Geowissenschaftliche Sammlung, Universität Bremen, Klagenfurter Straße,
28359 Bremen, Germany
e-mail: jens.lehmann@uni-bremen.de

C. Ifrim
Institut für Geowissenschaften, Ruprecht-Karls-Universität,
Im Neuenheimer Feld 234, 69120 Heidelberg, Germany
e-mail: christina.ifrim@geow.uni-heidelberg.de

L. Bulot
Aix-Marseille Université, UMR CNRS 7330 CEREGE, Centre Saint-Charles,
Case 67, 3 Place Victor Hugo, Cedex 03, 13331 Marseille, France
e-mail: bulot@cerege.fr

C. Frau
9bis Chemin des Poissonniers, 13600 La Ciotat, France
e-mail: camille_frau@hotmail.fr

C. Klug et al. (eds.), *Ammonoid Paleobiology: From macroevolution to paleogeography,*
Topics in Geobiology 44, DOI 10.1007/978-94-017-9633-0_9

by opening new migration routes (e.g. Wiedmann 1988). A prominent Early Cretaceous example of this is the opening of the Atlantic Ocean. Ammonite faunas from Brazil suggest that the opening of the central Atlantic created new migration routes as early as the Aptian, and the deepening of the young ocean, accompanied by deep-water circulation, was not established until the late Albian (Bengtson et al. 2007). Besides the impact of these physical barriers, ammonite dispersal in the Early Cretaceous is also believed to be temperature-related (Scott 1940; Michael 1979; Mutterlose 1992; Reboulet 2001). In recent decades, it has been assumed that temperatures were cooler in the earliest Cretaceous and rather moderate and warm from the Albian onwards, with less pronounced climate belts (e.g. Frakes et al. 1992). However, in the Berriasian-Aptian, and even after the onset of a warmhouse world in the late Early Cretaceous, it is a matter of debate whether temperature differences were more pronounced than was believed near the end of last century (Mutterlose et al. 2009; Erbacher et al. 2011; Papp and Cociuba 2013; Zakharov et al. 2013). Ammonites apparently were able to cope with drastic sea-surface temperature changes. The magnitude and frequency of temperature change during the Cretaceous, however, are still poorly constrained (e.g. Schouten et al. 2003, Dumitrescu et al. 2006), and the challenging question arises whether restricted ammonite distribution patterns are caused by climatic conditions or other factors (e.g. Kemper and Schmitz 1981; Marcinowski and Wiedmann 1988; Owen 1988a). Besides the significance of overall temperature differences in their habitats, it is even more important to understand the ammonite lifestyle and reproduction strategies to correctly interpret paleobiogeographic affinities. The latter factor is very rarely addressed with regard to ammonites in general (Manger et al. 1999; Mapes and Nützel 2009; reviewed in De Baets et al. 2015), but there has been some progress made in reconstructing the ammonite lifestyle in recent years (Ritterbush et al. 2014; Lukeneder 2015; Moriya 2015). But there is still much to be learned. A few recent studies actually use an integrated approach to address paleoenvironmental change and ammonite occurrence in great detail for the Early Cretaceous (e.g. Reboulet et al. 2005). These could answer some crucial basic questions on the background of paleogeographic distributions of Early Cretaceous ammonites, but there are still many problems to solve as well.

Differing taxonomic concepts often obscure ammonite distributional patterns (Kennedy and Cobban 1976; compare De Baets et al. 2015) and here we address many of the currently debated problematic issues. We distinguish biogeographic areas based on the distribution of ammonite taxa, as was performed in the pioneer work byNeumayr (1883). However, paleobiogeographic terms are updated to comply with Westermann (2000) and Cecca (2002). In this nomenclature, superrealms are the largest biogeographic areas. In contrast to Page (1996), we recognize a number of realms: The Boreal Realm, the Tethyan Realm, and the Austral Realm (for late Barremian to Albian times only). Occassionally, the additional distinctions of an Arctic (= A Sr; Berriasian-Hauterivian and Albian), a Boreal-Atlantic- (= B-A Sr; Berriasian-Aptian) and a Boreal-Pacific (= B-P Sr;Valanginian-? early Barremian) Subrealm as parts of the Boreal Realm are found to be reasonable. Similarly, a Mediterran-Caucasian (= MC Sr; Berriasian-Aptian) and an Indo-Pacific (= I-P Sr, Berriasian—early Barremian) Subrealm are distinguished as part of the Tethyan Realm.

Despite abundant systematic descriptions, quantitative approaches to ammonite paleobiogeography are still lacking for the Early Cretaceous. The qualitative interpretations given here are therefore an interim state of the art and need quantification in the future.

9.2 Early Cretaceous Paleobiogeography

9.2.1 Berriasian

In the early Berriasian, no Tethyan immigrants are found in the Boreal Realm and, conversely, there are no boreal species recorded from the Tethyan Realm (Rawson 1995a; Bulot 1996). This is one of the reasons why the definition of the Jurassic/Cretaceous boundary has been highly debated for many years and correlations between the Boreal and Tethyan realms are still at a preliminary stage (Wimbledon et al. 2011). In recent years, integrated magneto- and biostratigraphy have allowed a better correlation between the two realms, and it is now generally accepted that the latest Volgian correlates with the earliest Berriasian (Zakharov and Rogov 2008; Wimbledon et al. 2011, 2013; Bragin et al. 2013; Rogov 2013). As a consequence, it is now clear that the Jurassic/Cretaceous boundary is not marked by a significant ammonite turnover above the suprageneric level, neither for the Boreal nor Tethyan realms (Tavera et al. 1986; Zakharov et al. 1996; Rogov 2013).

There is a clear difference between the Tethyan record and that of the Boreal Realm, underlining the distinction between these faunal realms (Fig. 9.1). In the Boreal Realm members of the family Polyptychitidae dominate the record, particularly *Craspedites, Praetollia* and *Chetaites* (Baraboshkin 2002; Zakharov and Rogov 2008).

In the earliest Berriasian, the Tethyan Realm ammonite faunas are more diverse than those of the Boreal Realm, and are dominated by ammonites of the family Neocomitidae. The distributions of *Berriasella, Pseudosubplanites, Malbosiceras, Delphinella, Dalmasiceras, Strambergella* and *Pseudoneocomites* are restricted to the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Kotetishvili 1988; Wimbledon et al. 2013). Earliest Berriasian *Berriasella s. str.* are only known from southern and central Europe, North Africa, Ukraine, the Caucasus and northern Iran (unpublished data), in contrast to a much wider geographic distribution often attributed in recent decades (Fig. 9.1) due to a more casual definition of this genus.

A most interesting change in the ammonite distribution occurs during the (?) late early to early late Berriasian. The Boreal Realm is characterized by the decline of the Craspeditinae and Dorsoplanitinae and the diversification of the Tolliinae (Baraboshkin 1999). The Arctic and Boreal-Atlantic subrealms both exhibit

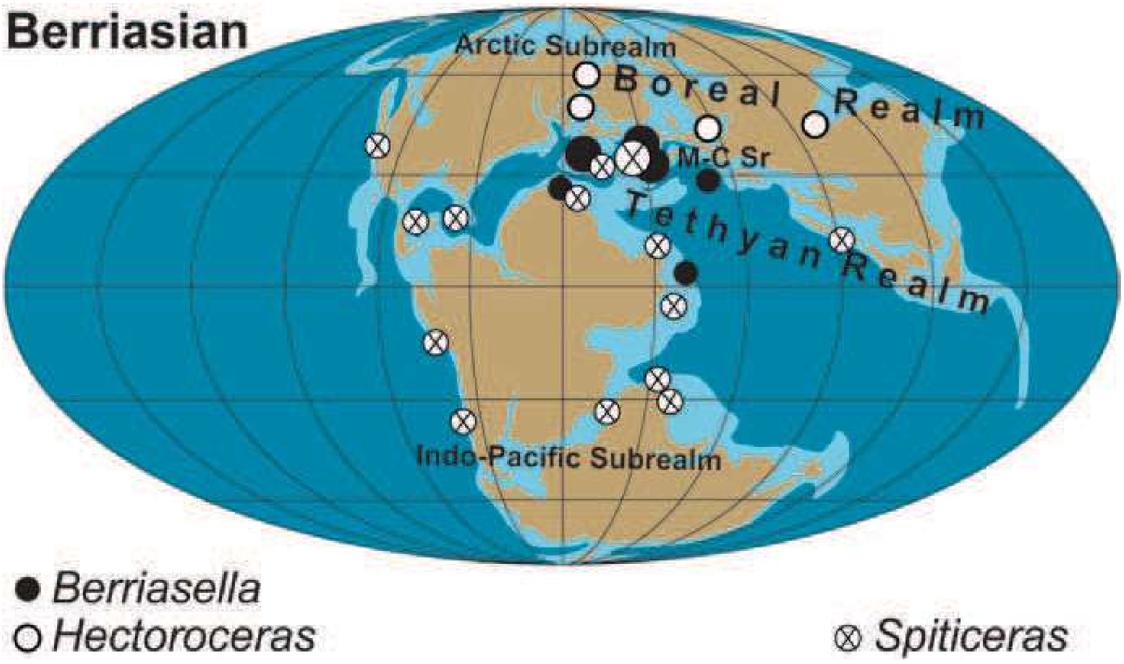


Fig. 9.1 Aspects of Berriasian ammonite paleobiogeography. Map based on 150 Ma reconstruction (paleomaps after Ronald Blakey, http://cpgeosystems.com/index.html, accessed 6th of June 2014). Larger dots indicate the home range and peak occurrence of a genus if it is more widely distributed. *M-C Sr* Mediterran-Caucasian Subrealm of the Tethyan Realm

the occurrence of *Hectoroceras* (Casey 1973; Birkelund et al. 1983; Baraboshkin 1999; Fig. 9.1). Among the Tolliinae, *Surites* is widely distributed in the late Berriasian of the Boreal Realm (Shul'gina 1985, 1989; Zakharov et al. 1996). According to Baraboshkin (1999), two areas of diversification of the Tolliinae can be distinguished that roughly correspond to the Arctic and Boreal-Atlantic subrealms. It should also be noted that the Eastern European part of the Boreal Atlantic Subprovince contains Tethyan genera that are also known from the eastern part of the Mediterran-Caucasian Subrealm, such as *Riasanites* and *Transcaspiites* (Mitta 2007, 2011).

Ongoing research (unpublished data) suggests that the affinities of the ammonites of Tethyan origin from the Polish Lowland and Russian Platform are even stronger with the fauna of Crimea, the Caucasus and Mangyshlak described by Luppov et al. (1988), Kvantaliani (1999) and Arkadiev et al. (2012). Assemblages of the eastern part of the Mediterran-Caucasian Subrealm (Caucasian and Transcaspian areas) are dominated by endemic Neocomitidae such as *Tauricoceras* and *Gechiceras*. Other important elements of the assemblage are *Euthymiceras* and *Hegaratia* (= *Balkites*), which are only known from a limited number of specimens in the western part of the Mediterran-Caucasian Subrealm (Le Hégarat 1973; Patrulius and Avram 1976). In contrast, the equivalent faunas from the western part of the Mediterran-Caucasian Subrealm are dominated by *Berriasella, Mazenoticeras, Tirnovella, Fauriella* and *Jabronella*.

Because of correlation problems (e.g. Zakharov et al. 1996), the limits of the Berriasian stage outside the areas discussed above are poorly understood. The marked endemism discussed above also affects the Indo-Pacific Subrealm. In Argentina and Chile, the faunas are dominated by *Andiceras*, *Argentiniceras*, *Frenguelliceras*, *Hemispiticeras*, *Cuyaniceras* and *Pseudoblanfordia* (Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011; Vennari et al. 2012). Similarly, the endemic *Kossmatia*, *Durangites* and *Substeueroceras* assemblage of Mexico is now considered as Berriasian (Olóriz et al. 1999).

The conspecificity of the Berriasian ammonites described by Collignon (1962) from Madagascar with Mediterran-Caucasian taxa is still unsolved, at least regarding *Berriasella* (unpublished data). In our opinion *Subthurmannia* from Pakistan (Spath 1939; Fatmi 1977) are fully distinct from *Fauriella* of the Mediterran-Caucasian Subrealm (Bulot 1995).

Our ongoing research suggests that the endemism of the Neocomitidae at the genus level during the Berriasian is much higher than it has been previously assumed in the literature, and that homeomorphy (see Monnet et al. 2015) has led to erroneous taxonomic interpretations.

In our current stage of understanding, *Spiticeras*, and early Olcostephanidae originally described from the Himalayas are the only taxa spread throughout the Tethyan Realm. This links the Mediterran-Caucasian and Indo-Pacific subrealms, with populations reported from the Pacific Coast of America (Jeletzky 1965; Imlay and Jones 1970), Madagascar (Collignon 1962) and the shelf basins of South America and Antartica (Thomson 1979; Riccardi 1988; Aguirre-Urreta et al. 2007a; Parent et al. 2011).

9.2.2 Valanginian

As already outlined by Rawson (1981), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006), the paleobiogeographic patterns of the early Valanginian are almost identical to the late Berriasian. The faunas of the Boreal Realm are dominated by the Tolliinae and their derivatives the Polyptychitinae, while the Tethyan are still characterized by the abundance of the Neocomitidae (Kotetishvili 1983). The distribution of ammonites in the Boreal Realm is complex, partly due to the individual flooding history of former mainlands, and was discussed in great details by Jeletzky and Kemper (1988), Shul'gina et al. (1994), Baraboshkin (1999) and Alsen (2006).

A striking feature is the emergence and radiation of the Platylenticeratinae in the Boreal-Atlantic Subrealm. *Platylenticeras* characterizes the earliest marine beds resting on the continental Early Cretaceous (Wealden facies) in North Germany (Kemper 1961; Kemper et al. 1981; Elstner and Mutterlose 1996). Although there are conflicting opinions in the literature today (Bulot 1996), the idea that *Platylenticeras* is a neocomitid with a Tethyan origin is now favoured (see discussions in Alsen and Rawson 2005). At any rate, in Germany, *Platylenticeras* developed a high diversity (Kemper 1961, 1992; Hoedemaeker 2012 refers to drift occurrences, probably originating from Germany). This is in contrast to other European countries, from which only a limited number of species are known and where it is rare (Baumberger 1908, 1928; Thieuloy 1977; Vašíček 1979, 1997). In Greenland, and simultaneously on the Russian plate, *Delphinites* (*Pseudogarnieria*) faunas developed, ammonites belonging to the same subfamily Platylenticeratinae (Alsen and Rawson 2005). *Delphinites* (*Pseudogarnieria*) emphasize the very endemic character of early Valanginian ammonite faunas in the Boreal Realm, as in *Platylenticeras* there is a number of regionally occuring species only.

A transgression in the middle part of the early Valanginian wiped out these strong differences of the earliest Valanginian, and Polyptychitinae replaced the platylenticeratid faunas in the Boreal-Atlantic Subrealm (Jeletzky and Kemper 1988; Rawson 1981, 1993, 1994; Alsen 2006).

In contrast, the earliest Valanginian assemblages of the Tethyan Realm are dominated by neocomitids; the most prominently recorded genera are *Neocomites*, *Kilianella*, *Sarasinella* and *Thurmanniceras* (Rawson 1981; Kotetishvili 1983; Company 1987). Except for *Sarasinella*, these genera were originally defined based on species originating from the western part of the Mediterran-Caucasian Subrealm. There is no consensus on the definitions and the paleogeographic distributions of *Thurmanniceras*, *Sarasinella* and *Neocomites*. This problem has been addressed often in the literature (Company 1987; Bulot 1995; Aguirre-Urreta and Rawson 1999; Ettachfini 2004; Rawson 2007; Aguirre-Urreta et al. 2008). According to our current stage of knowledge, *Kilianella* is the only neocomitid that had a widespread distribution over the Mediterran-Caucasian and Indo-Pacific Subrealms of the Tethyan Realm.

Most interesting is the development of a very peculiar earliest Valanginian assemblage dominated by *Lissonia* and its potential macroconch *Raimondiceras* in South American basins of the Indo-Pacific Subrealm (Lisson 1907; Haas 1960; Leanza 1972; Etayo-Serna 1985; Mourgues 2004; Aguirre-Urreta et al. 2007a). As already pointed out by Aguirre-Urreta and Rawson (1999) and Aguirre-Urreta et al. (2008), these forms most likely evolved from the earliest Valanginian endemic Neocomitidae. Poorly constrained early Valanginian faunas were also reported from the Pacific coast of North America, where a mixture of endemic Neocomitidae (*Paskentites*, alleged '*Kilianella*' and '*Thurmanniceras*' as well as '*Sarasinella*' *sensu lato*) and Tolliinae (*Tollia*, *Neocraspedites*) were described by Imlay (1960) and Imlay and Jones (1970).

The continuous significant sea level rise that marks the Lower/Upper Valanginian boundary interval (see discussion in Föllmi 2012) led to an enhanced exchange of genera in the wider transitional zone between the Tethyan and the Boreal Realms in Europe (Kemper et al. 1981; Rawson 1993; Bulot 1993, 1996; Föllmi 2012). At this time a group of six Tethyan immigrant genera appeared, even in the fairly isolated epicontinental basins of North Germany, northeastern England and Poland (Kemper et al. 1981; Kutek et al. 1989; Kemper 1992; Kutek and Marcinowski 1996).

Some of these taxa, including *Olcostephanus* (Fig. 9.2)*, Karakashiceras*, and *Neohoploceras,* originated in the central part of the Mediterran-Caucasian Subrealm, but were dispersed as a result of this event not only to the Boreal-Atlantic Subrealm, but also over most of the Indo-Pacific Subrealm. This assemblage is well documented in Pakistan, Madagascar and South Africa (Bulot, 1990), Central

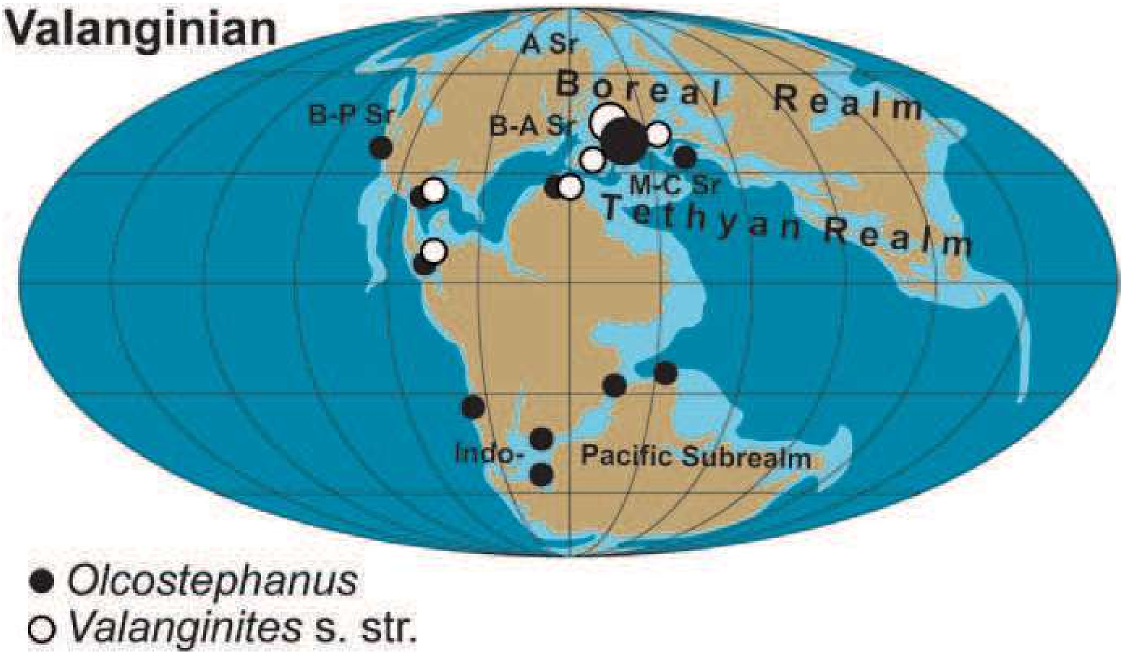


Fig. 9.2 Aspects of Valanginian ammonite paleobiogeography. Map based on 150 Ma reconstruction. *B-A Sr* Boreal-Atlantic Subrealm, *B-P Sr* Boreal-Pacific Subrealm, *A Sr* Arctic Subrealm, all of these are subrealms of the Boreal Realm. For further details see caption to Fig. 9.1

America (Etayo-Serna 1985; Young 1988; González-Arreola 2007) and the Andean Basins of South America (Rawson 2007; Aguirre-Urreta et al. 2007a, 2008). During that time *Olcostephanus* even reached the Pacific coast of North America (Imlay and Jones 1970) and Antartica (Howlett 1986).

In contrast, the worldwide distribution of the cadicone *Valanginites* appears doubtful. South American occurrences are clearly dated from the earliest Valanginian (see discussion in Aguirre-Urreta et al. 2008), whereas in the Mediterranean areas the stratigraphic distribution of *Valanginites* is well dated from the late early and early late Valanginian (Bulot et al. 1990). Aguirre-Urreta et al. (2008) claim that the South American *Valanginites* gave rise to the Mediterranean ones. In our opinion this view is open to discussion, and we favor the idea that *Valanginites* is paraphyletic and that two distinct lineages evolved from the *Olcostephanus* rootstocks at different times. We therefore indicate the distribution of *Valanginites* s. str. herein, contrasting a global distribution that is often attributed to this genus (Fig. 9.2). Dzik's (1990) interpretation of *Valanginites* as a macroconch of the small, spine-bearing *Saynoceras* refers to earliest Valanginian forms, but in addition to distinct shell features, the comparatively restricted paleobiogeographic distribution of *Saynoceras* compared to *Valanginites* argues against an interpretation as a dimorphic pair (see Ploch 2003, 2007 for an alternative interpretation).

In the Boreal Realm, the late early to early late Valanginian is marked by the rapid evolution of Polyptychitinae rising from the Polyptychitinae rootstock, and this radiation gave rise to new genera (*Hollwediceras*, *Prodichotomites*, *Dichotomites*, *Homolsomites*, *Ringnesiceras*, *Amundiptychites*) in the epicontinental basins of the Boreal-Atlantic, Boreal-Pacific and Arctic subrealms (Kemper 1978; Jeletzky and

Kemper 1988). The timing and phylogenetic relationships among those taxa remain largely unclear. Nevertheless, *Hollwediceras*, *Prodichotomites* and *Dichotomites* are known from scattered occurrences along the northern margin of the Mediterran-Caucasian Subrealm from Mangyshlak to southeastern France (Thieuloy 1977; Luppov et al. 1983; Thieuloy et al. 1990; Kuhn 1996; Reboulet 1996; Vašíček and Michalík 1999; Dziadzio et al. 2004; Lukeneder 2004).

Characterization of the latest Valanginian paleobiogeography in the Boreal Realm is difficult. It is generally accepted that *Homolsomites* and its junior subjective synonym *Wellsia,* dominate ammonite assemblages of the northern Boreal Realm, the Boreal-Pacific- and Arctic Subrealm of this time interval (Shul'gina et al. 1994; Wright et al. 1996; Baraboshkin 1999; Alsen 2006). Furthermore, successive pulses of Tethyan ammonite migrations from the Mediterran-Caucasian Subrealm characterize the latest Valanginian successions of the Boreal-Atlantic Subrealm, especially with regard to North Germany (Kemper et al. 1981; Kemper 1992; Rawson 1993). These progressive migrations peaked in the latest Valanginian with an ammonite assemblage almost entirely composed of Tethyan (*Olcostephanus*, '*Eleniceras*', *Teschenites*) or Tethyan derived (*Stoicoceras*) ammonites (Quensel 1988).

In the Tethyan Realm, the latest Valanginian is poorly documented outside the Mediterranean regions and Argentina. Recent investigations clearly show a strong endemism during this time interval in the Andean basins of the Indo-Pacific Subrealm with faunas dominated by endemic Neocomitidae (*Pseudofavrella*, *Chacantuceras*, *Decliveites*) (Aguirre Urreta and Rawson 2003, 2010). Outside Argentina, *Pseudofavrella* may be represented in Colombia (Etayo-Serna 1985), but the age of these Valanginian forms, which occur above the early Valanginian *Lissonia* fauna is very poorly constrained.

9.2.3 Hauterivian

The earliest Hauterivian is characterized by a radiation of the Neocomitidae (Ivanov and Aristov 1969; Baraboshkin 2002, with references; Baraboshkin et al. 2003; Alsen 2006). This excludes the Arctic Subrealm and the eastern part of the Boreal-Atlantic Subrealm, where impoverished polyptychitid faunas (*Homolsomites*, *Pavlovites*, *Subspeetoniceras* and *Gorodzovia*) occur. In the western part of the Boreal-Atlantic Subrealm, this faunal change is marked by the appearance of *Endemoceras*, a typical Tethyan-derived neocomitid (Kemper and Wiedenroth 1987; Rawson 1995a). The regularly coiled *Endemoceras*, a genus yielding important index species, progressed into the heteromorphic descendant *Distoloceras* (Kemper et al. 1981; Rawson 1993). *Distoloceras* is strictly restricted to the earliest Hauterivian of northern Europe, and the report of the genus from the late Valanginian is based on the misinterpretation of homeomorphic neocomitids that belong to *Rodighieroites* (Company 1987; Bulot 1995; Barragán and González-Arreola 2009). Interestingly, *Distoloceras* is a homeomorph (compare Monnet et al. 2015 for its definition) of crioceratids of Tethyan origin, with spines and a loosely coiled spiral (Kemper and Wiedenroth 1987).

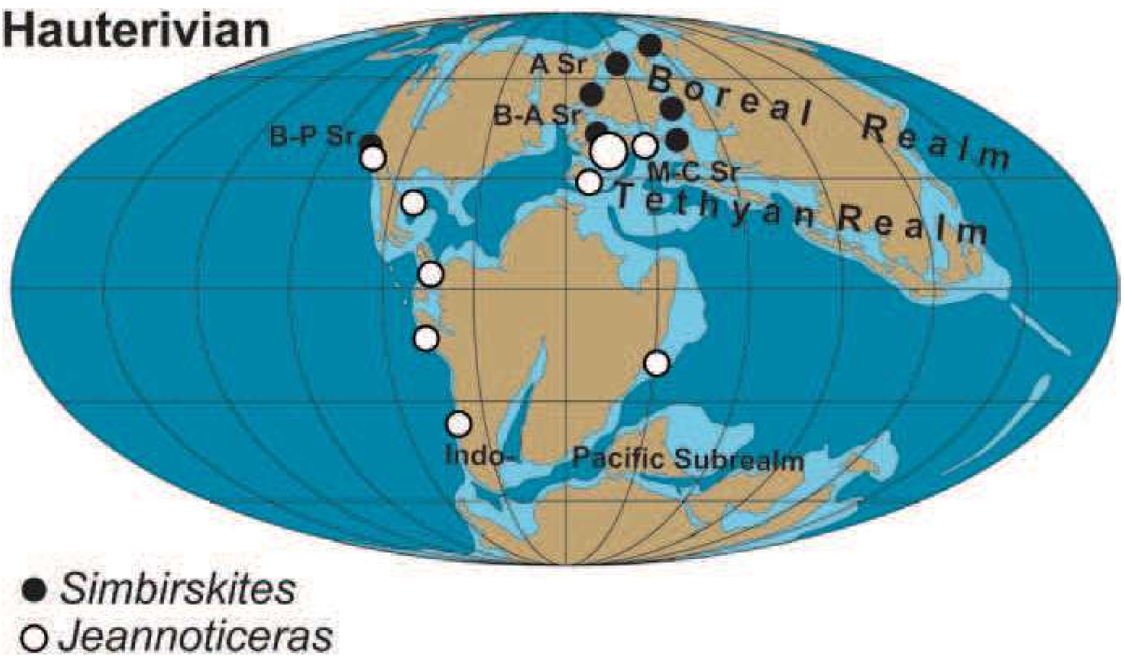


Fig. 9.3 Aspects of Hauterivian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Acanthodiscus, *Leopoldia* and *Breistrofferella* are rare elements of the western Boreal-Atlantic ammonite faunas (Kemper 1992; Bulot 1995; Rawson 1995a). These genera provide a very useful link between the Boreal and Tethyan realms during the early Hauterivian. The paleogeographic distribution of *Acanthodiscus* and *Leopoldia* is facies-controlled and centered on the shelves of the northern margin of the Mediterran-Caucasian Subrealm (France, Switzerland, Ukraine), although a single occurrence is known from Morocco (Wippich 2001; Ettachfini 2004). As in the case of *Distoloceras*, reported occurrences of *Acanthodiscus* and *Leopoldia* in the late Valanginian are based on misidentified homeomorphic genera, including *Neohoploceras, Karakashiceras, Chacantuceras* and *Pseudofavrella* (Company 1987; Bulot 1995; Reboulet 1996; Aguirre-Urreta and Rawson 1999, 2010). Nevertheless, earliest Hauterivian faunas are poorly documented in the Indo-Pacific Subrealm except for the Neuquén Basin of Argentina, where the fauna is almost exclusively composed of *Holcoptychites*, an endemic member of the Spiticeratinae (Aguirre-Urreta and Rawson 2003; Aguirre-Urreta et al. 2008). The *Favrella* fauna of Patagonia and Antarctica is also an endemic development, but its early Hauterivian age needs final proof (Aguirre-Urreta et al. 2007a).

A major Hauterivian ammonite event is seen in the widespread distribution of the short-lived olcostephanid *Jeannoticeras* and associated *Olcostephanus* species that is well documented from the Boreal-Atlantic, Mediterran-Caucasian and Indo-Pacific subrealms (Bulot 1990; Bulot et al. 1993; Aguirre-Urreta and Rawson 2001) in the middle part of the early Hauterivian (Fig. 9.3). This appearance marks the onset of the mid-Hauterivian episode according to Rawson (1993, 1994). In the western part of the Mediterran-Caucasian Subrealm the neocomitids vanished progressively in the early Hauterivian and were replaced by *Crioceratites, Spitidiscus* and late

Olcostephanus (Rawson 1993). The paleobiogeographic development of neocomitids is made even more complex by the disappearance of *Endemoceras* in England, which is followed by a substantial re-appearance of *Lyticoceras* in France, with the latter probably evolved from the latest *Endemoceras* species (Kemper et al. 1981; Rawson 1993). Another highly significant ammonite faunal turnover for this stratigraphic interval is marked by the replacement of *Endemoceras* in the western limits of the Boreal-Atlantic Subrealm by *Simbirskites* that evolved in the Arctic Subrealm during the earliest Hauterivian (Rawson 1994; Baraboshkin 2002; Baraboshkin et al. 2003; Fig. 9.3). The mid-Hauterivian faunal change also strongly triggered the development of heteromorphic ammonites, which spread into the Boreal-Atlantic-, Boreal-Pacific- and Indo-Pacific Subrealm (Immel 1978, 1979a, b; Rawson 1993, 2007; Baraboshkin 2002; Aguirre-Urreta et al. 2008).

Generally, in the late Hauterivian, heteromorphs become increasingly important and dominate the ammonite assemblages of the Tethyan Realm while the Boreal Realm faunas are dominated by *Simbirskites* (Rawson 1994; Baraboshkin 2002). Whereas *Simbirskites* is absent from the western part of the Meditterran-Caucasian Subrealm, this genus represents a significant element in the Transcaspian area (Kakabadzé 1983; Kemper and Wiedenroth 1987; Baraboshkin 2002). Following the decline and extinction of the Olcostephanidae, Neocomitidae and Leopoldidae, new families appeared or flourished in the Mediterran-Caucasian Subrealm, such as the Abrytusitidae (*Spitidiscus*), Pulchellidae (*Subsaynella, Discoidellia*) and Barremitidae (*Plesiospitidiscus*), which reached the Andean basins of the Indo-Pacific Subrealm in the early late Hauterivian (Vermeulen 2002, 2005, 2007; Vermeulen and Bulot 2007; Rawson 2007; Aguirre-Urreta et al. 2008). In the latest Hauterivian, the recoiling of crioceratids brings rise to *Pseudothurmannia* (Wiedmann 1969) and allied genera/subgenera as important index species in the Western Tethys (Cecca et al. 1998; Company et al. 2003; Vermeulen et al. 2009; Hoedemaeker 2013).

Late Hauterivian successions of the Indo-Pacific Subrealm are as poorly known as those of the early Hauterivian. Re-examination of *Menuthiocrioceras* and *Malgasaynella* has showed us that these genera are of late Barremian age (see below) and thus Collignon's (1948, 1962) record of late Hauterivian in Madagascar and Indonesia is incorrect. In contrast, late Hauterivian strata are well developed in the Andean basins of Argentina and Chile (Aguirre-Urreta et al. 2007a). Although relationsships of the Andean basins to the Mediterran-Caucasian Subrealm have been known for quite a long time, a strong endemism was assumed by Leanza and Wiedmann (1980). This is relativized today because diversity in this area is higher than previously believed (Aguirre-Urreta et al. 2007a, b). The most striking feature of the faunas is the presence of local heteromorphs that evolved from Tethyan-derived *Crioceratites.* Identification of *Hemihoplites* from the Hauterivian of Patagonia (Riccardi and Aguirre-Urreta 1989; Aguirre-Urreta 2002) is questionable, since the evolution of *Hemihoplites* in the late Barremian of southeastern France has now been well established (Bert et al. 2006, 2008) and the Patagonian species show only superficial morphological similarities with the Mediterranean taxa. An *Aegocrioceras* species reported from Chile (Aguirre-Urreta et al. 2007b) is most likely a local offshoot of the Tethyan-derived *Crioceratites* of the *schlagintweiti* group rather than indicating paleobiogeographic affinities to the European Boreal Realm.

9.2.4 Barremian

The sea-level lowstand initiated in the late Hauterivian, and marking the early Barremian, is believed to be responsible for an increasing diversity in ammonite faunas, as individual basins became isolated (Rawson 1993). The Barremian was marked by the prevalence of continental conditions over most of the Arctic Subrealm (Jeletzky 1970; Rawson 1981; Baraboshkin 2002 with references) while carbonate platforms developed on both margins of the Mediterran-Causasian Subrealm (Philip 2003 with references). The key feature of the Barremian ammonite faunas is the development of rich faunas with heteromorphic ammonites.

Boreal Barremian ammonite faunas are known from the United Kingdom and Germany only, thus representing a comparatively small area of this realm. In the earliest Barremian of the Boreal Realm, the last occurrence of *Craspedodiscus* is remarkable, since it represents the last subgenus of the major Boreal ammonoid clade of the family Polyptychitidae (Rawson 1971, 1981). It is worth noting that the reported occurrence of *Simbirskites* (*Milanowskia*) sp. from the early Barremian of Japan (Matsukawa 1988) is highly doubtful and based on poorly preserved specimens that superficially match Hauterivian simbirskitids. As a consequence, the migration of Boreal ammonites in the Tethyan-dominated assemblages of the Far-East terranes of Asia is not substantiated.

Boreal-Atlantic shelf deposits are characterized solely by Tethyan and/or Tethyan-derived heteromorphs after the extinction of simbirskitids. The systematic treatment of these heteromorphs varies from one author to another. The most frequently cited genus is *Paracrioceras*. It is considered to be a senior subjective synonym of *Emericiceras* by Rawson (1975) and Wright et al. (1996), a view that is rejected by Vermeulen (2004, 2006) and Kakabadzé and Hoedemaeker (2010), albeit for different reasons. By contrast, Wiedmann (1962) and Immel (1978) regarded *Paracrioceras* as a synonym of *Crioceratites*. Thus *Crioceratites*, *Paracrioceras* and *Emericiceras* are defined inconsistently and reflect the poor state of early Barremian heteromorph taxonomy, which is confusing. The problem was also addressed by Klinger & Kennedy (1992) and Kakabadzé & Hoedemaeker (2004) when discussing the systematic assignment of South African and South American faunas. In our opinion, *Crioceratites*, *Emericiceras* and *Paracrioceras* are unsuitable to define paleobiogeographic groupings in the Barremian. As a consequence they are of little help to define the limits of paleobiogeographic units.

Therefore, the limits of distribution of normally coiled ammonites occuring in the Tethyan Realm, excluding heteromorphs, is extremely important in drawing the southern boundary of the Boreal Realm (Hoedemaeker 1990), particularly since they do not occur in the Boreal Realm (Rawson (1993, (1994). Among others, the earliest to early late Barremian Holcodiscidae (*Holcodiscus*, *Parasaynoceras*), Pulchelliidae (*Pulchellia*, *Nicklesia, Heinzia*) and Barremitidae are widely distributed from Japan to northern South America (Mexico, Colombia). Along the Pacific coast, spot occurrences of Pulchellidae extend as far north as California (Murphy 1975) and as far south as northern Chile (Aguirre-Urreta et al. 2007a) where they are associated with a fairly diverse assemblage of heteromorphs including the

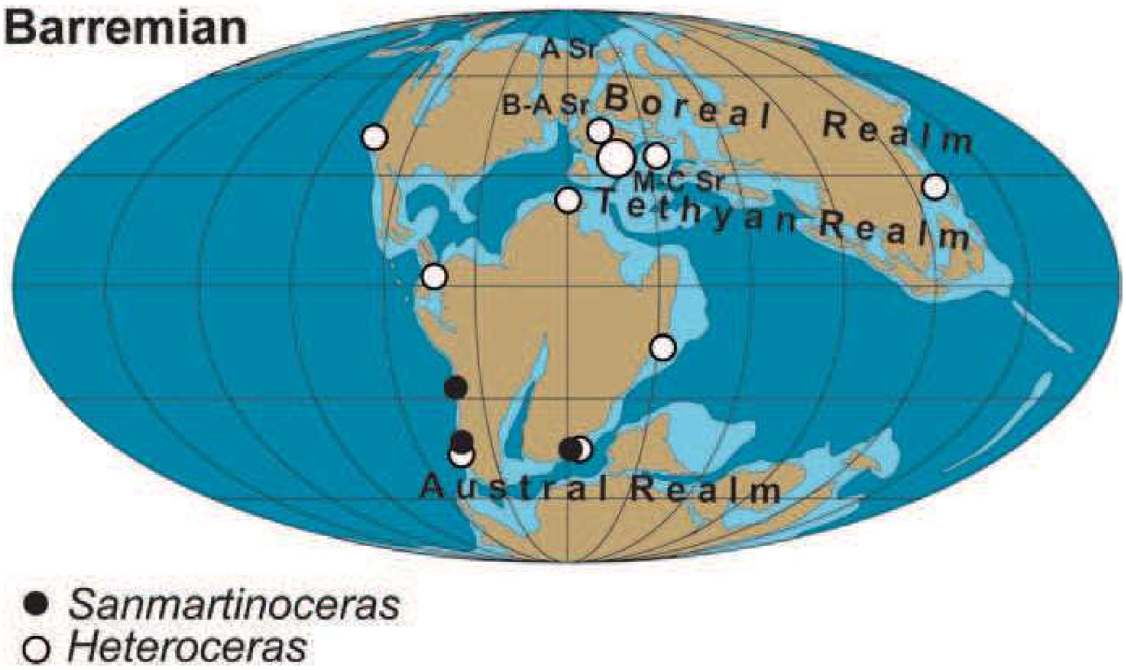


Fig. 9.4 Aspects of Barremian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Circum-Pacific genus *Shasticrioceras*, which is also known from Arctic Canada (Jeletzky 1970) and Japan (Matsukawa and Obata 1993).

In the Mediterran-Caucasian Subrealm, the late Barremian is marked by a drastic change in the evolution of the ammonite faunas. Holcodiscidae and Pulchellidae have dissappeared and heteromorphs are highly diverse (Vermeulen 2005; Bert et al. 2008). Among heteromorphs the Hemihoplitidae and Heteroceratidae show the most striking morphological changes; the former are characterized by a recoiling of the shell, and the latter by the development of a helicoidally coiled inner whorls (the global distribution of *Heteroceras* is shown in Fig. 9.4). Both families provide faunal links with the Boreal-Atlantic Subrealm, since *Spinocrioceras* has been reported from Germany (Kemper 1973, 1995) and *Heteroceras* from the United Kingdom (Rawson 1995b).

Although imperfectly dated, the onset of the Austral Realm, centered on Patagonia, Australia, Africa and Madagascar, most likely took place in the late early to early late Barremian. Non-heteromorphic ammonites endemic to this area includes *Hatchericeras*, which stands among the candidates for the last representative of the Perisphinctoidea, even though its last occurrence is not accurately dated with respect to the Simbirskitinae (Riccardi 1988; Kennedy and Klinger 1990). Associated fauna include *Malgasaynella* and *Menuthiocrioceras* (a peculiar group of endemic heteromorphs to which *Cryptocrioceras* is herein considered to be a junior subjective synonym; Collignon 1948, 1962; Skwarko and Thieuloy 1989; Aguirre-Urreta 1990; Klinger and Kennedy 1992). Characteristic for the latest Barremian is the spreading of the Heteroceratidae from the Tethyan Realm toward the Austral Realm. Simultaneously, the Aconeceratidae, including the significant genus *Sanmartinoceras* (Fig. 9.4), most likely evolved as a separate offshoot of Desmoceratidae.

9.2.5 Aptian

In terms of ammonite paleobiogeography the Aptian is generally considered to be a cosmopolitan time due to a major transgression that begins in the early Aptian (Owen 1996). This global event was linked to the northward propagation of the Atlantic rift system, which led to the opening of numerous gateways and established new faunal connections (Rawson 1994; Hallam 1981; Bengtson & Kakabadzé 1999). The faunal dispersals are also linked to a shift toward warmer conditions that equalized climate belts and ultimately led to a global warmhouse (Föllmi 2012, with references). As outlined by Rawson (1994) and Baraboshkin (2002), this reorganization broke down the "*old Boreal/Tethyan dichotomy*" that had led to the widespread distribution of the ancyloceratid-deshayesitid assemblage during the early Aptian. As outlined by Wright et al. (1996) and Kakabadzé et al. (2004), the ancyloceratids are known by their widespread distribution in the Tethyan- (Mediterran-Caucasian Subrealm including the Caribbean area), Boreal- (Boreal-Atlantic and Boreal-Pacific subrealms) and Austral realms. However, due to homeomorphy of the body-chamber ornamentation, most ancyloceratid genera, such as *Ancyloceras*, are ill-defined taxa that are in need of revision. In our opinion, the species from the Mediterran-Caucasian and Boreal-Atlantic subrealms on which the Ancyloceratidae genera introduced by Spath (1930), Casey (1960), Vermeulen and Lazarin (2007) and Delanoy et al. (2008) are based, cannot be compared with the large tripartite heteromorphs that occur in California (Anderson 1938; Murphy 1975), Colombia (Kakabadzé and Hoedemaker 2004), South Africa (Klinger and Kennedy 1977), Japan (Shimizu 1931) and Australia (Day 1967). A similar view was expressed by Pictet et al. (2009) for *Lithancylus* taxa that are now restricted to Spain, France, England and the Russian Platform. As a consequence, endemism in Ancyloceratidae has certainly been overlooked and needs further investigation, although it is partly reflected by the introduction of such genera as *Shastoceras* from California (Anderson 1938), *Laqueoceras* from Colombia (Kakabadzé et al. 2004) and *Helicancyloceras* from South Africa (Klinger and Kennedy 1977).

Deshayesitidae are recoiled heteromorphs that evolved from heteromorphic representatives of the Heteroceratidae by a recoiling of the shell at the end of the late Barremian (Delanoy 1997; Bogdanova and Mikhailova 2004; Delanoy and Bert 2006). The family shows a wide distribution in the Tethyan and Boreal realms during the early Aptian (Bersac and Bert 2012, with references). According to the latter authors, there are no significant morphological differences between the genus *Deshayesites* and the regional genera, *Turkmeniceras*, *Prodeshayesites*, *Paradeshayesites* and *Obsoleticeras* that occur in the northern and eastern parts of the Mediterran-Caucasian Subrealm and/or on the Russian Platform and adjacent areas of the Boreal Realm. Although widely distributed, *Deshayesites* is rare or even missing in some hemipelagic and pelagic settings in the Tethys, probably due to a bathymetric and/or facies control (Landra et al. 2000; Lehmann et al. 2009). *Deshayesites* evolved anagenetically toward *Dufrenoyia*, which marks the maximum geographic extension of the Deshayesitidae in the latest early Aptian (Fig. 9.5). *Juandurhamiceras* and

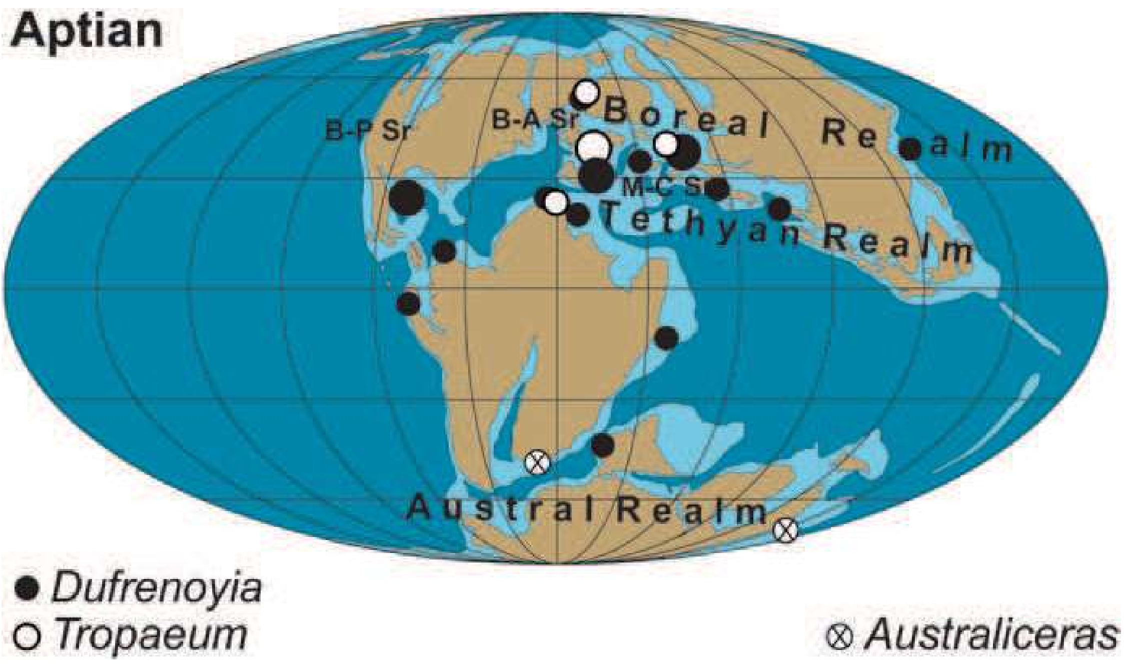


Fig. 9.5 Aspects of Aptian ammonite paleobiogeography. Map based on 120 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Burckhardtites (including *Burckhardites* reported from Turkmenistan (Bogdanova and Mikhailova 2004)) are Caribbean offshoots of *Dufrenoyia*. However, from our point of view the generic separation of these three genera also needs to be discussed carefully because of minor differences in shell shape only. The extinction of the family appears to be a sudden and almost synchronous event, marking the Lower/Upper Aptian boundary (Casey et al. 1998; Moreno-Bedmar et al. 2013).

During the continued Aptian trangression, faunas of isolated epicontinental basins show an increasing dispersal. Baraboshkin (2002), for example, recognized a Tethyan parahoplitid-douvilleiceratid and a Boreal ancyloceratid-aconeceratid assemblage around the Lower/Upper Aptian boundary on the Russian Platform. Simultaneously, large recoiled ancyloceratids occur almost worldwide, from the Austral to the Boreal Realm (Klinger and Kennedy 1977; Bengtson and Kakabadzé 1999). These forms have usually been referred to *Australiceras, Proaustraliceras* and *Tropaeum*, and are distinguished by the absence of a tuberculate stage on the inner whorls in the latter genus. Recently, McKenzie et al. (2014) argued that the two genera should be put in synonymy because the development of a tuberculate stage varies with intraspecific variability. Even if we agree that the Australian specimens attributed to *Tropaeum* in the literature (Whitehouse 1926; Day 1974) are macroconchs of *Australiceras*, comparison of the ornamental features of the early ontogeny of the European *Tropaeum* does not support the synonymy of the two genera. In our view, *Australiceras* is an endemic genus that characterizes the Austral Realm, since typical *Tropaeum* only occur on European shelves of the Mediterran-Caucasian Subrealm and the adjacent part of the Boreal Realm (Baraboshkin 2002; Fig. 9.5). *Proaustraliceras* shows a similar distribution, with no reliable records from the southern hemisphere (Kakabadzé et al. 2004). The relationships between these ancyloceratids are still obscure. Thus this group can not currently be used for defining paleobiogeographic boundaries. During the early Aptian, the Douvilleiceratidae are also a major component of the worldwide ammonite assemblage, although some genera possibly hint at a paraphyletic origin of this family. The *Procheloniceras*-*Cheloniceras*-*Epicheloniceras* lineage is characteristic of the Tethyan Realm and of the southern area of the Boreal Realm (Casey et al. 1998; Kakabadzé et al. 2004; Pictet 2012). In the late early Aptian, *Roloboceras* and *Megatyloceras,* closely-allied or possibly congeneric with *Cheloniceras*, are typically recorded during the early Aptian of the Mediterran-Caucasian Subrealm and southern area of the Boreal Realm (Casey 1961; Moreno-Bedmar et al. 2010; Ivanov and Idakieva 2013).

Dauphin (2002) documented a complex turnover in the earliest late Aptian that led to the appearance of the widespread family Parahoplitidae. This event was observed at the scale of the Tethyan Realm, from the Transcaspian to the Caribbean domains (Bogdanova and Tovbina 1995; Arnaud et al. 2002). The genus *Colombiceras* evolved from *Gargasiceras* in the late early Aptian and spread over the entire Tethyan Realm during late Aptian times, where it gave rise to the *Acanthohoplites*-*Hypacanthoplites* lineage (Bulot in Vincent et al. 2010, with references). *Colombiceras* may also be the rootstock of *Parahoplites* in the Mediterran-Caucasian Subrealm and adjacent Boreal areas, and of the closely allied genera *Sinzoviella* and *Kasanskiella* from the Caribbean. In the latest Aptian, the diversification of Acanthohoplitinae reached its peak. This is the case for *Diadochoceras* and the closely allied, if not synonymous, *Nodosohoplites,* which are considered to be an offshoot of *Acanthohoplites,* while *Neodeshayesites* is a New World derivative of *Hypacanthoplites s.l.* Other endemic genera of Acanthohoplitinae have been reported from North America (*Rhytidoplites* and *Immunitoceras*), eastern Mexico (*Penaceras*), Colombia (*Riedelites*), northwestern Caucasus (*Chaschupseceras*), Japan (*Oshimaceras*) and Tunisia (*Melleguieiceras*). The phylogenetic relationships of all these genera also remain largely unclear (Bulot in Vincent et al. 2010; Latil 2011; Bulot et al. 2014).

9.2.6 Albian

Albian paleobiogeography is generally distinguished from that of the Aptian by a more pronounced provincialism, although this trend tends to diminish in the upper part of the stage (Owen 1996; Baraboshkin 2002, with references). The peak of endemism is reached in the earliest Albian, where three faunal provinces have been recognized in the Boreal Realm (Owen 1979, 1988a; Alabushev and Wiedmann 1994; Baraboshkin 2002; Jagt-Yazykova and Zonova 2012): the Boreal-Atlantic Subrealm, characterised by *Leymeriella*, *Sonneratia* and hoplitinid ammonites (the latter e.g. with *Euhoplites*, Fig. 9.6); the Arctic Subrealm, where *Arcthoplites*, *Freboldiceras* and Gastroplitininae flourished; and the Boreal-Pacific Subrealm, which was dominated by cleoniceratids (*Leconteites, Brewericeras, Grycia*). In the earliest Albian, arcthoplitid ammonites from the Arctic entered northwestern Europe and

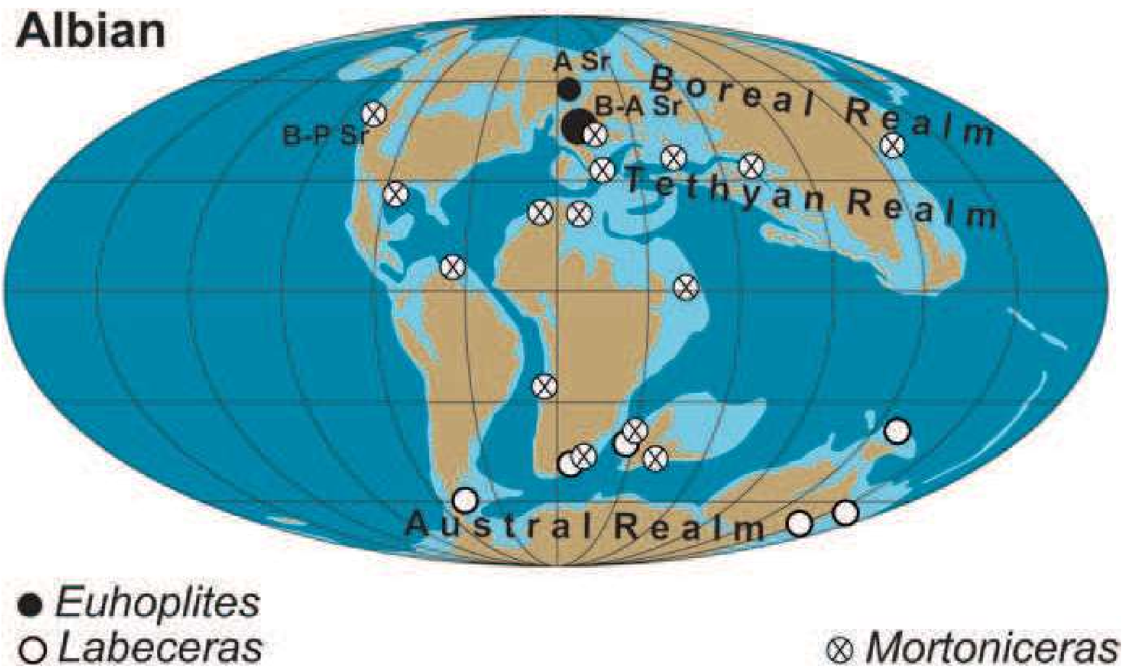


Fig. 9.6 Aspects of Albian ammonite paleobiogeography. Map based on 105 Ma reconstruction. For further details see captions to Figs. 9.1 and 9.2

Mangyshlak—thus these areas provide important information for the stratigraphic correlation on a global scale (Savel'ev 1973; Owen 11988a and b, 1996; Lehmann et al. 2013).

Compared to the limited area of the Boreal epicontinental shelf basins, the Tethyan Ocean had a vast expanse from northern South America and southern North America to Australia (Fluteau et al. 2007; Vrielynck 2010). In terms of ammonites, the assemblages of the Tethyan Realm mainly consist of brancoceratids (*Brancoceras*, *Prolyelliceras*, *Mirapelia*), lytoceratids (*Kossmatella*), desmoceratids (*Beudanticeras*), engonoceratids (*Parengonoceras*, *Knemiceras*, *Glotticeras*), and douvilleiceratids (*Douvilleiceras*) (Kennedy and Cobban 1976; Owen 1979, 1996; Marcinowski and Wiedmann 1990; Riccardi and Medina 2002; Robert and Bulot 2004; Bulot in Vincent et al. 2010; Latil 2011). In the earliest Albian new and distinguished families of heteromorphic ammonites (Anisoceratidae and Hamitidae) arose, spreading over most of the Tethyan Realm in the late early Albian (Monks 1999, 2002; Kennedy et al. 2000). During the early Albian the boundary between the Boreal and Tethyan realms was fairly sharp, despite scattered occurrences of *Leymeriella* on the Eurasian shelves of the northern margin of the Tethys (Kennedy et al. 2000, with references). Occasionally, in the late early and early middle Albian, *Douvilleiceras*, *Tegoceras, Lyelliceras* and *Oxytropidoceras* s.l. invaded the Boreal Realm of Europe and the northern Pacific coast of America (Owen 1971, 1988a; Amédro 1992; Amédro and Robaszynski 2005).

Different paleobiogeographic affinities between the early/middle and late Albian faunas are also recognized in the Austral Realm. However, in Australia itself these are influenced by a division into regional basins (Henderson and McKenzie 2002). In the middle Albian, fairly cosmopolitan anisoceratids and hamitids occur in the Great Artesian Basin in Australia (McNamara 1980; McKenzie 1999), but in the late Albian cosmopolitan genera occur only in the marginal areas of Australia, since, according to micro- and nannofossil data, the connection to the open ocean was restricted (Henderson and McKenzie 2002). Thus, a less diverse late Albian fauna evolved in the Great Artesian Basin, with dominant endemic heteromorph species of *Labeceras* and *Myloceras*, in contrast to the rich diversity of assemblages in Europe and elsewhere during this time interval, and only isolated records of Tethyan origin like *Goodhallites* (Henderson and Kennedy 2002). Although *Labeceras* (Fig. 9.6) and *Myloceras* characterize the ammonite province of the Austral Realm in the late Albian, endemic species developed also in the regional basins of Madagascar, southern Africa and South America (Förster 1975; Klinger 1976; Klinger and Kennedy 1989; Aguirre-Urreta and Riccardi 1988; Riccardi 1988).

During the late Albian a long-time trend toward more cosmopolitan faunas is established with the rapid rise and radiation of the Mortoniceratinae (e.g., *Mortoniceras*, Fig. 9.6) and Stolickaiellinae. However, the disappearance of the Early Cretaceous provincialism is a long-running process that did not end until the middle Cenomanian (Owen 1973; Wiedmann 1988; Ifrim et al. 2015).

Unusual insights to the paleobiogeographical affinities of Albian ammonite faunas in the Atlantic are given by a few drilling core sites of the DSDP/ODP programme (Wiedmann 1978; Wiedmann and Neugebauer 1978; Renz 1979a; Wiedmann 1988; Lehmann 2000; Owen and Mutterlose 2006). A fauna from the Biscay margin shows affinities to the Boreal realm for the early Albian, while middle to possibly late Albian ammonites indicate a Tethyan aspect (Renz 1979b). The other occurrences from the Atlantic are, as far as datable, late Albian faunas indicating strong Tethyan relations (with the Curacao debated, see Owen and Mutterlose 2006). Among these the relatively rich association from offshore Florida is remarkable, since it represents a hemipelagic or even pelagic assemblage with species with a preference for oceanic conditions and, despite the strong affinities to the Tethys, it generally reveals a cosmopolitan character (Lehmann 2000).

9.3 Conclusion and Future Perspectives

Many Early Cretaceous faunas are dominated by heteromorphic ammonites. While they play almost no role in the earliest Cretaceous, they dominate many faunal assemblages from the early late Hauterivian until the end of the Cretaceous period. However, reasons for this and most of the ecological constrains involved are still under debate, including trophic opportunities and sea-level changes (Wiedmann 1969; Nesis 1986; Cecca 1997; Keupp 2000). The global Cretaceous sea-level rise started in the Aptian, and despite an increased spreading of taxa, there is some strong provincialism in the Albian characterized by regularly coiled ammonites. This demonstrates that a complex pattern of sea-level changes and the opening and closure of seaways must be responsible for ammonite dispersal in the Early Cretaceous.

Ongoing research emphasizes that insufficient taxonomy is a factor masking paleobiogeographic affinities (Kennedy and Cobban 1976; Rawson 1993; Bengtson and Kakabadzé 1999), This is particularly true for the Berriasian, early Barremian and Aptian (present chapter). Furthermore, quantitative analyses of the spatial distribution of ammonoids—such as have been done for some other time intervals (Dera et al. 2011; Korn and Klug 2012; Korn and De Baets 2015)—are rare to absent for the Early Cretaceous Epoch. This hampers our ability to test the robustness of the paleogeographical affinities described in this chapter, and underlines the urgent need for quantitative studies earlier called for by Bengtson and Kakabadzé (1999). Therefore the interpretations presented here are thorough revisions and updates of earlier significant contributions in this field (Rawson 1981, 1993, 1994; Cecca 1998), but are likewise qualitative studies and thus still reflect a preliminary state.

Acknowledgments We thank Martin Krogmann (Bremen) for drawing the paleoglobes. JL acknowledges that this investigation was supported by the German Research Foundation (DFG) project "*Palaeobiology, morphology and diversity of macrofaunas: A case study on Early Cretaceous ammonites*" (project LE 1241/2–1). Antoine Pictet (Geneva), Dieter Korn (Berlin), Peter Ward (Adelaide) and an anonymous colleague are thanked for their helpful reviews. Walter Hale (Bremen) is thanked for linguistic improvements.

References

Aguirre-Urreta B (1990) Paleogeography and biostratigraphy of the Austral basin. An appeal for sound systematics. Episodes 13:247–255

Aguirre-Urreta MB (2002) Hemihoplitid ammonoids from the Austral Basin of Argentina and Chile. In: Summesberger H, Histon K, Daurer A (eds) Cephalopods—Present and past. Abhandlungen der Geologischen Bundesanstalt, Vienna

Aguirre-Urreta MB, Rawson PF (1999) Stratigraphic position of *Valanginites*, *Lissonia*, and *Acantholissonia* in the Lower Valanginian (Lower Cretaceous) ammonite sequence of Neuquén Basin, Argentina. In: Olóriz F, Rodríguez-Tovar FJ (eds) Advancing research on living and fossil Cephalopods. Kluwer/Plenum, New York, pp 521–529

Aguirre-Urreta MB, Rawson PF (2001) Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the Hauterivian neocomitid genus *Hoplitocrioceras* (Giovine, 1950). Cretac Res 22:201–218

Aguirre-Urreta MB, Rawson PF (2003) Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the Hauterivian genus *Holcoptychites*. Cretac Res 24:589–613

Aguirre-Urreta MB, Rawson PF (2010) Lower Cretaceous ammonites from the Neuquén Basin, Argentina: the neocomitids of the *Pseudofavrella angulatiformis* Zone (upper Valanginian). Cretac Res 31:321–343

Aguirre-Urreta MB, Riccardi AC (1988) Albian heteromorph ammonoids from southern Patagonia, Argentina. J Paleontol 62:598–614

Aguirre-Urreta MB, Mourgues FA, Rawson PF, Bulot LG, Jaillard E (2007a) The Lower Cretaceous Chañarcillo and Neuquén Andean basins: ammonoid biostratigraphy and correlations. Geol J 42:143–173

Aguirre-Urreta B, Suárez M, De La Cruz R, Ramos VA (2007b) Ammonoids (Crioceratitinae, Hauterivian) from the Austral Basin, Chile. Ameghiniana 44:387–397

Aguirre-Urreta MB, Casadío S, Cichowolski M, Lazo DG, Rodriguez DL (2008) Afinidades paleobiogeográficas de los invertebrados cretácicos de la Cuenca Neuquina. Ameghiniana 45:593–613

Alabushev AI, Wiedmann J (1994) Palaeogeographic significance of the distribution of Albian (Cretaceous) ammonite faunas in the Pacific coast of North-East Russia. N Jb Geol Paläontol Mh 4:193–204

Alsen P (2006) The Early cretaceous (late Ryazanian–early Hauterivian) ammonite fauna of North-East Greenland: taxonomy, biostratigraphy, and biogeography. Fossils and strata 53:1–229

Alsen P, Rawson PF (2005) The early Valanginian (Early Cretaceous) ammonite *Delphinites* (*Pseudogarnieria*) from North-East Greenland. Bull Geol Surv Denmark 52:201–212

Amédro F (1992) L'Albien du bassin Anglo-Parisien: Ammonites, zonation phylétique, séquences. Bull Centr Rech Explor-Prod Elf Aquitaine 16:187–223

Amédro F, Robaszynski F (2005) Corrélation des successions de l'Albien par les ammonites entre la Province Nord-Pacifique et les Provinces européenne et arctique du Domaine boréal: zonation, eustatisme et paléobiogéographie. Géobios 38:585–607

Anderson FM (1938) Lower Cretaceous deposits in California and Oregon. Waverly, Baltimore

Arkadiev V, Bogdanova TN, Guzhikov AY, Lobacheva SV, Myshkina NV, Platonov ES, Savelyeva YuN, Shurekova OV, Yanin BT (2012) Berriasian stage of the Crimean mountains. In: Arkadiev V, Bogdanova TN (eds) Lema, Saint-Petersburg

Arnaud H, Arnaud-Vanneau A, Bulot LG, Beck C, Mascotay O, Stephan J-F, Vivas V (2002) Le Crétacé Inférieur du Venezuela oriental: stratigraphie séquentielle des carbonates sur la transversale Casanay-Maturin (États de Anzoâtegui, Monagas et Sucre). Géol Alpine 76:3–81

Baraboshkin EJ (1999) Berriasian-Valanginian (Early Cretaceous) sea-ways of the Russian platform basin and the problem of Boreal/Tethyan correlation. Geol Carp 50:1–16

Baraboshkin EJ (2002) Early Cretaceous seaways of the Russian platform and the problem of Boreal/Tethyan correlation. In: Michalík J (ed) Tethyan/Boreal Cretaceous correlation. Mediterranean and Boreal Cretaceous paleobiogeographic areas in Central and Eastern Europe. Publishing House of the Slovak Academy of Sciences, Bratislava

Baraboshkin EY, Alekseev AS, Kopaevich LF (2003) Cretaceous palaeogeography of the North-Eastern Peri-Tethys. Palaeogeogr Palaeoclimatol Palaeoecol 196:177–208

Barragán R, González-Arreola C (2009) *Rodighieroites belimelensis* (Mandov) (Ammonoidea) from the Taraises Formation (upper Valanginian), Durango, Northeastern Mexico: biostratigraphic and paleobiogeographic implications. Cretac Res 30:300–306

Baumberger E (1908) Fauna der untern Kreide im westschweizerischen Jura. Fünfter Teil. Die Ammonitiden der untern Kreide im westschweizerischen Jura (Fortsetzung). Abh Schweiz Paläont Ges 35:1–40

Baumberger E (1928) Beitrag zur Kenntnis der Garnierien aus der schweizerischen und französischen Unterkreide. Ecl Geol Helv 21:218–227

Bengtson P, Kakabadzé MV (1999) Biogeography of Cretaceous ammonites—a review of procedures and problems. In: Kuhnt W, Erbacher J, Gräfe K-U (eds) Contributions to Cretaceous stratigraphy and palaeobiogeography in honor of Jost Wiedmann. Schweizerbart, Stuttgart. (N Jb Geol Pal, Abh.)

Bengtson P, Koutsoukos EaM, Kakabadzé MV, Zucon MH (2007) Ammonite and foraminiferal evidence for opening of the South Atlantic Ocean in the early/mid Aptian (Early Cretaceous). In: Budd GE, Streng M, Daley AC, Willman S (eds) The Palaeontological Association, 51st Annual Meeting, 16th–19th December 2007, Uppsala University, Upsala

Bersac S, Bert D (2012) Ontogenesis, variability and evolution of the Lower Greensand Deshayesitidae (Ammonoidea, Lower Cretaceous, Southern England): reinterpretation of literature data; taxonomic and biostratigraphic implications. Ann Mus d'Hist Nat Nice 27:197–270

Bert D, Delanoy G, Bersac S (2006) Descriptions de représentants nouveaux ou peu connus de la famille des Hemihoplitidae Spath, 1924 (Barrémien supérieur, Sud-est de la France): conséquences taxinomiques et phylétiques. Ann Mus d'Hist Nat Nice 21:179–253

Bert D, Delanoy G, Bersac S (2008) Nouveaux biohorizons et propositions pour le découpage biozonal ammonitique du Barrémien supérieur du Sud-Est de la France. Carn Géol/Noteb Geol 3:1–18

Birkelund T, Clausen CK, Hansen HN, Holm L (1983) The *Hectoroceras kochi* Zone (Ryazanian) in the North sea central Graben and remarks on the late Cimmerian unconformity. Dan Geol Unders 1982:53–72

Bogdanova TN, Mikhailova IA (2004) Origin, evolution and stratigraphic significance of the superfamily Deshayesitaceae Stoyanow, 1949. Bull l'Inst Royal Sci Nat Belgique Sci Terre 74:189–243

Bogdanova TN, Tovbina SZ (1995) On development of the Aptian ammonite zonal standard for the Mediterranean region. In: Bulot LG, Argot M, Arnaud HM (eds) Lower Cretaceous Cephalopod biostratigraphy of the Western Tethys: recent developments, regional synthesis and outstanding problems, Géol Alp, Mém Hors Ser, vol 20. Laboratoire de Géologie de l'Université Joseph Fourier, Grenoble

Bragin VY, Dzyuba OS, Kazansky AY, Shurygin BN (2013) New data on the magnetostratigraphy of the Jurassic-Cretaceous boundary interval, Nordvik Peninsula (northern East Siberia). Russ Geol Geophys 54:335–348

Bulot LG (1990) Évolution des Olcostephaninae (Ammonitina, Cephalopoda) dans le contexte paléo-biogéographique du Crétacé Inférieur (Valanginien-Hauterivien) du Sud-Est de la France. Université de Bourgogne, Dijon

Bulot LG (1993) Stratigraphical implications of the relationships between ammonites and facies: examples taken from the Lower Cretaceous (Valanginian-Hauterivian) of the Western Tethys. In: House MR (ed) The Ammonoidea: environment, ecology, and evolutionary change, The Systematics Association special volume. Clarendon, Oxford

Bulot LG (1995) Les formations à ammonites du Crétacé Inférieur dans le Sud-Est de la France (Berriasien à Hauterivien): biostratigraphie, paléontologie et cycles sédimentaires. Mus Nat d'Hist Nat, Paris, p 375

Bulot LG (1996) The Valanginian stage. In: Rawson PF, Dhondt AV, Hancock JM, Kennedy WJ (eds) Proceedings second international symposium on Cretaceous stage boundaries. Brussels 8–16 September 1995. (Bull l'Inst Roy Sc Nat Belgique, Sc Terre, Suppl, Brussels)

Bulot LG, Company M, Thieuloy J-P (1990) Origine, évolution et systématique du genre Valanginien *Saynoceras* (Ammonitina, Olcostephaninae). Géobios 23:399–413

Bulot LG, Thieuloy J-P, Blanc É, Klein J (1993) Le cadre stratigraphique du Valanginien supérieur et de l'Hauterivien du Sud-Est de la France: définition des biochronozones et caractérisation de nouveaux biohorizons. Géol Alpine 68:13–56

Bulot LG, Latil J-L, Hairabian A, Fournillon A (2014) New insight on the genus *Nolaniceras* Casey, 1961 (Ammonoidea, Cretaceous) and its consequences on the biostratigraphy of the aptian stage. Proc Geol Assoc 125:227–232

Casey R (1960) A monograph of the Ammonoidea of the Lower Greensand Part I, monograph of the Palaeontographical Society, 113.i-xxxvi+1–4

Casey R (1961) A monograph of the Ammonoidea of the Lower Greensand Part III, monograph of the Palaeontographical Society, 115. pp 119–216

Casey R (1973) The ammonite succession at the Jurassic-Cretaceous boundary in Eastern England. In: Casey R, Rawson PF (eds) The Boreal Lower Cretaceous, Geological Journal Special Issue. Seel House Press, Liverpool

Casey R, Bayliss HM, Simpson MI (1998) Observations on the lithostratigraphy and ammonite succession of the Aptian (Lower Cretaceous) Lower Greensand of Chale Bay, Isle of Wight, UK. Cretac Res 19:511–535

Cecca F (1997) Late Jurassic and Early Cretaceous uncoiled ammonites: trophism-related evolutionary processes. Com Rend l'Acad Sci, Ser IIA Earth Planet Sci 325:629–634

Cecca F (1998) Early Cretaceous (pre-Aptian) ammonites of the Mediterranean Tethys: palaeoecology and palaeobiogeography. Palaeogeogr, Palaeoclimat, Palaeoecol 138:305–323

Cecca F (2002) Palaeobiogeography of marine invertebrates. Concepts and methods. CRC, Taylor & Francis, London

Cecca F, Faraoni P, Marini A (1998) Latest Hauterivian (Early Cretaceous) ammonites from Umbria-Marche Apennines (Central Italy). Palaeontogr Ital 85:61–110

Cecca F, Vrielynck B, Lavoyer T, Gaget H (2005) Changes in the ammonite taxonomical diversity gradient during the Late Jurassic–Early Cretaceous. J Biogeogr 32:535–547

Collignon M (1948) Faune Néocomienne des Couches à Criocères de Belohasifaka, Cercle de Sitampiky, Madagascar. Ann Géol Serv Mines 15:54–85

Collignon M (1962) Atlas des fossiles caractéristiques de Madagascar (Ammonites). VIII (Berriasien, Valanginian, Hauterivian, Barremian). Serv Géol Tananar, Tananarive

Company M (1987) Los Ammonites del Valanginiense del Sector Oriental de las Cordilleras Béticas (SE de España). Universidad de Granada, Granada

Company M, Sandoval J, Tavera JM (2003) Ammonite biostratigraphy of the uppermost Hauterivian in the Betic Cordillera (SE Spain). Géobios 36:685–694

Dauphin L (2002) Litho-, bio-, et chronostratigraphie comparées dans le bassin Vocontien à l'Aptien. Université des sciences et technologies de Lille I, Lille

Day RW (1967) *Lithancylus australis* sp. nov., a new ammonite from the Aptian of Queensland. J Geol Soc Australia 14:19–22

Day RW (1974) Aptian ammonites from the Eromanga and Surat Basins, Queensland. Public Geol Surv Queensland. 360: 1–19

De Baets K, Bert D, Hofmann R, Monnet C, Yacobucci MM, Klug C (2015) Ammonoid intraspecific variability. In: Klug C, Korn D, De Baets K, Kruta I, Mapes R (eds) Ammonoid paleobiology: From anatomy to paleoecology

Delanoy G (1997) Biostratigraphie des faunes d'Ammonites à la limite Barrémien-Aptien dans la région d'Angles-Barrême-Castellane. Etude particulière de la famille des Heteroceratina Spath, 1922 (Ancyloceratina, Ammonoidea). Ann Mus d'Hist Nat Nice 12:1–270

Delanoy G, Bert D (2006) Nouvelles unités taxinomiques de la famille des Heteroceratidae Spath 1924. Ann Mus d'Hist Nat Nice 21:255–295

Delanoy G, Madou E, Penagé E, Baraterro X, Lhaumet G (2008) *Taxyites* nov. gen. un nouveau genre d'ammonite heteromorphe de l'Aptien inferieur du Sud-Est de la France (Ammonoidea, Ancyloceratina). Ann Mus d'Hist Nat Nice 23:1–9

Dera G, Neige P, Dommergues J-L et al (2011) Ammonite paleobiogeography during the Pliensbachian-Toarcian crisis (Early Jurassic) reflecting paleoclimate, eustasy, and extinctions. Glob Planet Change 78:92–105

Dumitrescu M, Brassell SC, Schouten S et al. (2006) Instability in tropical Pacific sea-surface temperatures during the early Aptian. Geology 34:833–836

Dziadzio PS, Gaździcka E, Ploch I, Smoleń J (2004) Biostratigraphy and sequence stratigraphy of the Lower Cretaceous in central and SE Poland. Ann Soc Geol Poloniae 74:125–196

Dzik J (1990) The concept of chronospecies in ammonites. In: Pallini G, Cecca F, Cresta S, Santantonio M (eds) Atti del secondo convegno internazionale Fossili, Evoluzione, Ambiente (Pergola 25-30 Ottobre 1987), Pergola

Elstner F, Mutterlose J (1996) The Lower Cretaceous (Berriasian and Valanginian) in NW Germany. Cretac Res 17:119–131

Erbacher J, Friedrich O, Wilson PA, Lehmann J, Weiss W (2011) Short-term warming events during the boreal Albian (mid-Cretaceous). Geology 39:223–226

Etayo-Serna F (1985) El limite Jurasico-Cretacico en Colombia. Public geol espec Ingeom 16:1–4

Ettachfini M (2004) Les ammonites Neocomiennes dans l'Atlas Atlantique (Maroc). Biostratigraphie, paléontologie, paléobiogéographie et paléoécologie. Strata 43:1–225

Fatmi AN (1977) Neocomian ammonites from northern areas of Pakistan. Bull Br Mus Nat Hist 28:255–296

Fluteau F, Ramstein G, Besse J, Guiraud R, Masse J-P (2007) Impacts of palaeogeography and sea level changes on Mid-Cretaceous climate. Palaeogeogr Palaeoclimatol Palaeoecol 247:357–381

Föllmi KB (2012) Early Cretaceous life, climate and anoxia. Cretac Res 35:230–257

Förster R (1975) Die geologische Entwicklung von Süd-Mozambique seit der Unterkreide und die Ammoniten-Fauna von Unterkreide und Cenoman. Geol Jb 12:3–324

Frakes LA, Francis JE, Syktus JI (1992) Climate modes of the Phanerozoic. Cambridge University, Cambridge

González-Arreola C (2007) *Oosterella* (Ammonoidea) from the Taraises Faraises Formation (Upper Valanginian), Durango, Northeast Mexico. Cretac Res 28:419–427

Haas O (1960) Lower Cretaceous ammonites from Colombia, South America. Amer Mus Novitates 2005: 1–62

Hallam A (1994) An outline of Phanerozoic biogeography. Oxford University, Oxford

Henderson RA, Kennedy WJ (2002) Occurrence of the ammonite *Goodhallites goodhalli* (J. Sowerby) in the Eromanga Basin, Queensland: an index species for the late Albian (Cretaceous). Alcheringa 26:233–247

Henderson RA, McKenzie DE (2002) *Idanoceras*, a new heteromorph ammonite genus from the Late Albian of Eastern Australia. J Paleontol 76:906–909

Hoedemaeker PJ (1990) The Neocomian boundaries of the Tethyan Realm based on the distribution of ammonites. Cretac Res 11:331–342

Hoedemaeker PJ (2012) Ammonieten uit het Vroeg-Krijt. In: Hoedemaeker PJ, Brouwers GLLM, Bont W, Akkerman H, Buijs J, Fraaije RHB, Jagt JWM, Janssen NMM, Klompmaker AA, Mulder EWA, Burger AW, Oosterink H (eds) Fossiele cephalopoden van Nederland. Staringia. Grondboor & Hamer, Enschede

Hoedemaeker PJ (2013) Genus *Pseudothurmannia* Spath, 1923 and related subgenera *Crioceratites* (*Balearites*) Sarkar, 1954 and *C.* (*Binelliceras*) Sarkar, 1977 (Lower Cretaceous Ammonoidea). Rev Paléob 32:1–209

Howlett PJ (1986) *Olcostephanus* (Ammonitina) from the Fossil Bluff Formation, Alexander Island, and its stratigraphical significance. Br Antarctic Surv Bull 70:71–77

Ifrim C, Lehmann J, Ward PD (2015) Paleobiogeography of Late Cretaceous Ammonoidea. This volume

Imlay RW (1960) Ammonites of Early Cretaceous age (Valanginian and Hauterivian) from the Pacific Coast states. U.S. Geological Survey Professional Paper 334F:iii. pp 167–228

Imlay RW, Jones DL (1970) Ammonites from the *Buchia* Zones in northwestern California and southwestern Oregon. Geological Survey Professional Paper 647B:iv. pp 1–55

Immel H (1978) Die Crioceratiten (Ancyloceratina, Ammonoidea) des mediterranen und borealen Hauterive-Barreme (Unterkreide). Palaeontogr 163:1–85

Immel H (1979a) Die Ammonitengliederung des mediterranen und borealen Hauterive und Barreme unter besonderer Berücksichtigung heteromorpher Ammoniten der Gattung *Crioceratites* Leveille. Newsl Stratigr 7:121–141

Immel H (1979b) Über den Ursprung der borealen Crioceratiten und zur Phylogenie der Gattung *Crioceratites* Léveillé (Ammonoidea, Kreide). In: Wiedmann J (ed) Aspekte der Kreide Europas. IUGS Series. Schweizerbart, Stuttgart

Ivanov AN, Aristov VN (1969) New ammonite genera from the Lower Cretaceous in the vicinity of Yaroslavl and the origin of simbirskitids. Bull Soc imp natur Moscou 44:84–97

Ivanov M, Idakieva V (2013) Lower Aptian ammonite biostratigraphy and potential for further studies of OAE 1a in Bulgaria. Cretac Res 39:47–69

Jagt-Yazykova EA, Zonova TD (2012) Paleogeography of Cretaceous ammonoids of the Pacific coast of Russia. Stratigr Geol Corr 20:295–315

Jeletzky JA (1965) Late Upper Jurassic and early Lower Cretaceous fossil zones of the Canadian Western Cordillera, British Columbia. Bull Geol Surv Can 103:1–70

Jeletzky JA (1970) Marine Cretaceous biotic provinces and paleogeography of Western and Arctic Canada: Illustrated by a detailed study of ammonites. Pap Geol Surv Canada, Dep Energy. Min Res 70–22:1–92

Jeletzky JA, Kemper E (1988) Comparative paleontology and stratigraphy of Valanginian Polyptychitinae and Simbirskitinae in Sverdrup Basin (Arctic Canada) and lower Saxony Basin (Northwestern Germany). Bull Geol Sur Can 377:1–355

Kakabadzé MV (1983) On the Hauterivian-Barremian correlation between the south of the USSR and certain southern and northern regions of Europe. In: Herm D (ed) 2. Symposium Kreide München 1982. (Zitteliana 10:501–508)

Kakabadzé MV, Hoedemaeker PJ (2004) Heteromorphic ammonites from the Barremian and Aptian strata of Colombia. Scripta Geol 128:39–182

Kakabadzé MV, Hoedemaeker PJ (2010) New data on Early Cretaceous (Hauterivian–Barremian) heteromorphic ammonites from Northern Germany. Scripta Geol 140:1–168

Kakabadzé MV, Hoedemaeker PJ, Bogdanova TN, Sharikadze MZ (2004) On the Barremian-Early Albian biogeography (by ammonites) of Colombia. Scripta Geol 128:515–558

Kemper E (1961) Die Ammonitengattung *Platylenticeras* (= *Garnieria*). Beih Geol Jb 47:1–195

Kemper E (1973) Die Unterkreide im Untergrund der Gehrdener Berge und in der Deister-Mulde. Ber Naturhist Ges Hannover 117:29–54

Kemper E (1978) Einige neue, biostratigraphisch bedeutsame Arten der Ammoniten-Gattung *Dichotomites* (NW-Deutschland, Obervalangin). Geol Jb 45:183–253

Kemper E (1992) Die tiefe Unterkreide im Vechte-Dinkel-Gebiet (westliches Niedersächsisches Becken). Stichting het Staringmonument te Losser. Dobler-Druck, Alfeld

Kemper E (1995) Die Entfaltung der Ammoniten und die Meeresverbindungen im borealen Unter- und Mittel-Apt. Geol Jb A141:171–199

Kemper E, Schmitz HH (1981) Glendonite-Indikatoren des polarmarinen Ablagerungsmilieus. Geol Rundschau 70:759–773

Kemper E, Wiedenroth K (1987) Klima und Tier-Migrationen am Beispiel der frühkretazischen Ammoniten Nordwestdeutschlands. Geol Jb A96:315–363

Kemper E, Rawson PF, Thieuloy J-P (1981) Ammonites of Tethyan ancestry in the early Lower Cretaceous of North-West Europe. Palaeontology 24:34–47

Kennedy WJ, Cobban WA (1976) Aspects of ammonite biology, biogeography, and biostratigraphy. Spec Pap Palaeont 17:1–94

Kennedy WJ, Klinger HC (1990) Cretaceous faunas from Zululand and Natal, South Africa. *Hatchericeras* Stanton, 1901 (Cephalopoda, Ammonoidea), from the Barremian of Zululand. Ann South Afr Mus 99:231–243

Kennedy WJ, Gale AS, Bown PR, Caron M, Davey RJ, Gröcke DR, Wray DS (2000) Integrated stratigraphy across the Aptian-Albian boundary in the Marnes Bleues at the Col de Pré-Guittard, Arnayon (Drôme), and at Tartonne (Alpes-de-Haute-Provence), France: a candidate global boundary stratotype section and boundary point for the base of the Albian stage. Cretac Res 21:591–720

Keupp H (2000) Ammoniten - Paläobiologische Erfolgsspiralen. Thorbecke, Stuttgart, 1–165

Klinger HC (1976) Cretaceous heteromorph ammonites from Zululand. Mem Geol Surv South Africa 69:ix + 1–142

Klinger HC, Kennedy WJ (1977) Cretaceous faunas from Zululand, South Africa and Southern Mozambique. The Aptian Ancyloceratidae (Ammonoidea). Ann South Afr Mus 73:215–359

Klinger HC, Kennedy WJ (1989) The ammonite subfamily Labeceratinae Spath, 1925: systematics, phylogeny, dimorphism and distribution (with a description of a new species). Ann South Afr Mus 98:189–219

Klinger HC, Kennedy WJ (1992) Cretaceous faunas from Zululand and Natal, South Africa. Barremian representatives of the ammonite family Ancyloceratidae Gill, 1871. Ann South Afr Mus 101:71–138

Korn D, De Baets K (2015) Biogeography of Paleozoic ammonoids. This volume

Korn D, Klug C (2012) Palaeozoic Ammonoids-diversity and development of conch morphology. In: Talent J (ed) Earth and life. Springer, The Netherlands

Kotetishvili EV (1983) Sur la paléozoogéographie des bassins eocrétacés du Caucase. In: Herm D (ed) 2. Symposium Kreide München 1982. (Zitteliana 10, Munich)

Kotetishvili EV (1988) Distribution globale des ammonites éocrétacés du Caucase. In: Wiedmann J, Kullmann J (eds) Cephalopods-Present and Past. Schweizerbart, Stuttgart

Kuhn O (1996) Der Einfluss von Verwitterung auf die Paläozeanographie zu Beginn des Kreide-Treibhausklimas (Valanginian und Hauterivian) in der West–Tethys. ETH Zürich, Zürich

Kutek J, Marcinowski R (1996) Faunal changes in the Valanginian of Poland: tectonic or eustatic control? In: Spaeth C (ed) New developments in Cretaceous research topics, Proceedings of the 4th international Cretaceous symposium, Hamburg, 1992. (Mitt Geol-Paläont Inst Univ Hamburg 77, Hamburg)

Kutek J, Marcinowski R, Wiedmann J (1989) The Wawal section, Central Poland-An important link between Boreal and Tethyan Valanginian. In: Wiedmann J (ed) Cretaceous of the Western Tethys. Proceedings of the 3rd international Cretaceous symposium, Tübingen, 1987. (Schweizerbart, Stuttgart)

Kvantaliani IV (1999) Berriasian cephalopods of the Crimea and Caucasus. Proc Geol Inst Georg Acad Sc 112:1–188.

Landra G, Cecca F, Vašíček Z (2000) Early Aptian ammonites from the top of the Maiolica and the anoxic "Selli level" (Lombardy, Southern Alps). Boll Soc Paleontol Ital 39:29–45

Latil J-L (2011) Early Albian ammonites from Central Tunisia and adjacent areas of Algeria. Rev Paléobiol 30:321–429

Leanza AF (1972) Prospección de rocas fosfáticas en la Argentina, para la fabricación de fertilizantes. IDIA 291:53–60

Leanza HA, Wiedmann J (1980) Ammoniten des Valangin und Hauterive (Unterkreide) von Neuquén und Mendoza, Argentinien. Ecl Geol Helv 73:941–981

Lehmann J (2000) Upper Albian ammonites from ODP Leg 171B off northern Florida. Palaeontology 43:41–61

Lehmann J, Heldt M, Bachmann M, Negra MEH (2009) Aptian (Lower Cretaceous) biostratigraphy and cephalopods from north central Tunisia. Cretac Res 30:895–910

Lehmann J, Owen HG, Beckert W (2013) A new ammonite fauna from NE-Germany-evidence for an Early Albian cooling and the initial transgression in the Danish-Polish Trough. N Jb Geol Paläontol Abh 268:199–235

Le Hégarat G (1973) Le Berriasien du Sud-Est de la France. Documents des Laboratoires de Géologie de la Faculté des Sciences de Lyon 43:1–576

Lisson CI (1907) Geología de Lima y sus alrededores. Librería é imprenta Gil, Lima

Lukeneder A (2004) Late Valanginian ammonoids: Mediterranean and Boreal elements–Implications on sea-level controlled migration (Ebenforst Syncline; Northern Calcareous Alps; Upper Austria). Austr J Earth Sci 95/96:46–59

Lukeneder A (2014) Ammonoid habitats and life history. This volume

Luppov NP, Alekseev AS, Bogdanova TN (1983) Valanginian of Mangyshlak. Nauka, Moscow

Luppov NP, Bogdanova TN, Lobacheva SV, Akopygan VT, Dzhalilov MR, Korotkov VA, Myatluyuk EV, Poretskaya ES (1988) Berriasian of Mangyshlak [in Russian]. Nauka, Leningrad

Manger WL, Stephen DA, Meeks LK (1999) Possible cephalopod reproductive mass mortality reflected by Middle Carboniferous assemblages, Arkansas, southern United States. In: Olóriz F, Rodríguez-Tovar FJ (eds) Advancing research on living and fossil Cephalopods. Kluwer/Plenum, New York

Mapes RH, Nützel A (2009) Late Palaeozoic mollusc reproduction: cephalopod egg-laying behavior and gastropod larval palaeobiology. Lethaia 42:341–356

Marcinowski R, Wiedmann J (1988) Paleogeographic implications of the Albian ammonite faunas of Poland. In: Wiedmann J, Kullmann J (eds) Cephalopods—present and past. Schweizerbart, Stuttgart

Marcinowski R, Wiedmann J (1990) The Albian ammonites of Poland. Palaeontol Pol 50:1–94

Matsukawa M (1988) Barremian ammonites from the Ishido Formation, Japan. Transact Proceed Palaeont Soc Japan 149:396–416

Matsukawa M, Obata I (1993) The ammonites *Crioceratites* (*Paracrioceras*) and *Shasticrioceras* from the Barremian of Southwest Japan. Palaeontology 36:249–266

McKenzie ED (1999) A new early to middle Albian (Cretaceous) ammonite fauna from the Great Artesian Basin, Australia. Proc Royal Soc Queensland 108:57–88

McKenzie ED, Rozefelds AC, Deacon P (2014) An ancyloceratid ammonite from the Aptian Maryborough Formation, Queensland, Australia, and synonymy of *Australiceras* Whitehouse with *Tropaeum* Sowerby. Alcheringa 38:1–10

McNamara KJ (1980) Heteromorph ammonites from the Albian of South Australia. Trans Royal Soc South Aust 104:145–159

Michael E (1979) Mediterrane Fauneneinflüsse in den borealen Unterkreide-Becken Europas, besonders in Nordwestdeutschland. In: Wiedmann J (ed) Aspekte der Kreide Europas. IUGS Series A. Schweizerbart, Stuttgart

Mitta VV (2007) Ammonite assemblages from basal layers of the Ryazanian stage (Lower Cretaceous) of Central Russia. Stratigr Geol Correl 15:193–205

Mitta VV (2011) Ammonites of Tethyan origin from the Ryazanian stage of the Russian platform: genus *Mazenoticeras* (Mazenot) and other Neocomitidae. Paleontol J 45:379–389

Monks N (1999) Cladistic analysis of Albian heteromorph ammonites. Palaeontology 42:907–925

Monks N (2002) Cladistic analysis of a problematic ammonite group: the Hamitidae (Cretaceous, Albian-Turonian) and proposals for new cladistic terms. Palaeontology 45:689–708

Monnet C, Klug C, De Baets K (2015) Evolutionary patterns of ammonoids: phenotypic trends, convergence, and parallel evolution. This volume

Moreno-Bedmar JA, Company M, Bover-Arnal T, Salas R, Delanoy G, Maurasse FJ-MR, Grauges A, Martinez R (2010) Lower Aptian ammonite biostratigraphy in the Maestrat Basin (Eastern Iberian Chain, Eastern Spain). A Tethyan transgressive record enhanced by synrift subsidence. Geol Acta 8:281–299

Moreno-Bedmar JA, Barragán Manzo R, Company Sempere M, Bulot, LG (2013) Aptian (Lower Cretaceous) ammonite biostratigraphy of the Francisco Zarco Dam stratigraphic section (Durango state, Northeast Mexico). J South Am Earth Sci 42:150–158

Moriya K (2015) Isotope signature of ammonoid shells. In: Klug C, Korn D, De Baets K, Kruta I, Mapes R (eds) Ammonoid paleobiology: From anatomy to paleoecology

Mourgues FA (2004) Advances in ammonite biostratigraphy of the marine Atacama basin (Lower Cretaceous), Northern Chile, and its relationship with the Neuquén basin, Argentina. J South Am Earth Sci 17:3–10

Murphy MA (1975) Paleontology and stratigraphy of the lower Chichabally mudstone (Barremian-Aptian) in the Ono quadrangle, Northern California. Univ Calif Public Geol Sc 113:1–52

Mutterlose J (1992) Migration and evolution patterns of floras and faunas in marine Early Cretaceous sediments of NW Europe. Palaeogeogr Palaeoclimatol Palaeoecol 94:261–282

Mutterlose J, Pauly S, Steuber T (2009) Temperature controlled deposition of early Cretaceous (Barremian-early Aptian) black shales in an epicontinental sea. Palaeogeogr Palaeoclimatol Palaeoecol 273:330–345

Naglik C, Tajika A, Chamberlain JA, Klug C (2015) Ammonoid locomotion. In: Klug C, Korn D, De Baets K, Kruta I, Mapes R (eds) Ammonoid paleobiology: From anatomy to paleoecology

Neumayr M (1883) Über klimatische Zonen während der Jura- und Kreidezeit, Denkschr Akad Wiss Wien 47:277–310

Nesis KN (1986) On the feeding and the causes of extinction of certain heteromorph ammonites. Paleontol J 1986:5–11

Olóriz F, Villaseñor AB, Gonzalez-Arreola C, Westermann GEG (1999) Ammonite biostratigraphy and correlations in the Upper Jurassic-lowermost Cretaceous la Caja Formation of North-Central Mexico (Sierra de Catorce, San Luis Potosí). In: Olóriz F, Rodríguez-Tovar FJ (eds) Advancing research on living and fossil Cephalopods. Kluwer/Plenum, New York

Owen HG (1971) Middle Albian stratigraphy in the Anglo-Paris Basin. Bull Br Mus Nat Hist 8:3–164

Owen HG (1973) Ammonite faunal provinces in the Middle and Upper Albian and their palaeogeographical significance. In: Casey R, Rawson PF (eds) The Boreal Lower Cretaceous. Geological Journal Special Issue 5. Seel House Press, Liverpool

Owen HG (1979) Ammonite zonal stratigraphy in the Albian of North Germany and its setting in the hoplitinid faunal province. In: Wiedmann J (ed) Aspekte der Kreide Europas. IUGS Series A. Schweizerbart, Stuttgart

Owen HG (1988a) Correlation of ammonite faunal provinces in the Lower Albian (mid-Cretaceous). In: Wiedmann J, Kullmann J (eds) Cephalopods-present and past. Schweizerbart, Stuttgart

Owen HG (1988b) The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* superzone (Lower Albian) in Europe. Bull Brit Mus Nat Hist 44:177–231

Owen HG (1996) Boreal and Tethys late Aptian to late Albian ammonite zonation and palaeobiogeography. In: Spaeth C (ed) New developments in Cretaceous research topics, Proceedings of the 4th international Cretaceous symposium, Hamburg, 1992. (Mitt Geol-Pal Inst Univ Hamburg, Hamburg)

Owen HG, Mutterlose J (2006) Late Albian ammonites from offshore Suriname: implications for biostratigraphy and palaeobiogeography. Cretac Res 27:717–727

Page KN (1996) Mesozoic ammonoids in space and time. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid paleobiology. Topics in Geobiology. Plenum, New York

Papp DC, Cociuba I (2013) Anoxic events in the Early Cretaceous succession of Pădurea Craiului. Correlation and comparison with other Carpathian areas. Geol Soc, Lond Spec Publ 382:49–62

Parent H, Scherzinger A, Schweigert G (2011) The Tithonian-Berriasian ammonite fauna and stratigraphy of Arroyo Cieneguita, Neuquén-Mendoza Basin, Argentina. Bol Instit Fisiogr Geol 79–81:21–94

Patrulius D, Avram E (1976) Stratigraphie et corrélation des terrains Néocomiens et Barrémo-Bédouliens du couloir de Dîmbovicioara (Carpates orientales). Dari seama sedintelor. Inst Geol Geof Bucuresti 62:135–160

Philip J (2003) Peri-Tethyan neritic carbonate areas: distribution through time and driving factors. Palaeogeogr Palaeoclimatol Palaeoecol 196:19–37

Pictet A (2012) Evolution of the Cheloniceratinae: an alternative to Deshayesitidae for the Lower Aptian biozonation? Preliminary observations. Bol Inst Fisiogr Geol 82:34–36

Pictet A, Delanoy G, Baudouin C, Boselli P (2009) Le genre *Lithancylus* Casey, 1960 (Ammonoidea, Ancyloceratina) dans l'Aptien inférieur du Couloir rhodanien (Drôme, Sud-Est de la France). Rev Paléobiol 28:491–509

Ploch I (2003) Taxonomic interpretation and sexual dimorphism in the Early Cretaceous (Valanginian) ammonite *Valanginites nucleus* (Roemer, 1841). Acta Geol Pol 53:201–208

Ploch I (2007) Intraspecific variability and problematic dimorphism in the Early Cretaceous (Valanginian) Ammonite *Saynoceras verrucosum* (d'Orbigny, 1841). Acta Geol Sinica 81:877–882

Quensel P (1988) Die Ammonitenfauna im Valangin-Hauterive-Grenzbereich vom Mittellandkanal bei Pollhagen. In: Keupp H, Janofske D (eds) Die Valangin-Hauterive-Grenze im zentralen Niedersächsischen Becken. (Berliner Geowiss Abh, A 94)

Rawson PF (1971) Lower Cretaceous ammonites from North-East England: The Hauterivian genus *Simbirskites*. Bull Br Mus Nat Hist 20:27–86

Rawson PF (1975) The interpretation of the Lower Cretaceous heteromorph ammonite genera *Paracrioceras* and *Hoplocrioceras* Spath. Palaeontology 18:275–283

Rawson PF (1981) Early Cretaceous ammonite biostratigraphy and biogeography. In: House MR, Senior JR (eds) The Ammonoidea, Systematics Association, special vol, 18. Academic, London

Rawson PF (1993) The influence of sea-level changes on the migration and evolution of Early Cretaceous (pre-Aptian) ammonites. In: House MR (ed) The Ammonoidea: environment, ecology and evolutionary change, Systematics Association, special vol, 47. Clarendon, Oxford

Rawson PF (1994) Sea level changes and their influence on ammonite biogeography in the European Early Cretaceous. In: Proceedings of the 3rd Pergola international symposium. Palaeopelagos special Publication, 1. pp 317–326

Rawson PF (1995a) The "Boreal" Early Cretaceous (pre-Aptian) ammonite sequences of NW Europe and their correlation with the western Mediterranean faunas. In: Cecca F (ed) Proceedings 3rd Workshop on Early Cretaceous Cephalopods, 5–8 July 1994, Piobbico. (Mem descritt Carta Geol d'Ital 51. Ist Poligr Zecca dello Stato, Rome)

Rawson PF (1995b) Biogeographical affinities of NW European Barremian ammonite faunas and their palaeogeographical implications. In: Cecca F (ed) Proceedings 3rd workshop on Early Cretaceous Cephalopods, 5–8 July 1994, Piobbico. (Mem descritt Carta Geol d'Ital 51. Ist Poligr Zecca dello Stato, Rome)

Rawson PF (2007) Global relationships of Argentine (Neuquén Basin) Early Cretaceous ammonite faunas. Geol J 42:175–183

Reboulet S (1996) L'évolution des ammonites du Valanginien-Hauterivien inférieur du bassin vocontien et de la plate-forme provençale (sud-est de la France): relations avec la stratigraphie séquentielle et implications biostratigraphiques. Docum Laborat Géol Lyon 137:1–371

Reboulet S (2001) Limiting factors on shell growth, mode of life and segregation of Valanginian ammonoid populations: Evidence from adult-size variations. Geobios 34:423–435

Reboulet S, Giraud F, Proux O (2005) Ammonoid abundance variations related to changes in trophic conditions across the Oceanic Anoxic Event 1d (Latest Albian, SE France). Palaios 20:121–141

Renz O (1979a) Lower Cretaceous Ammonoidea from the Northern Atlantic, leg 47 B, hole 398 D, DSDP. In: Sibuet JC, Ryan WBF et al (eds) Deep Sea Drilling Project report. Washington

Renz O (1979b) Ammonoidea from the Lower Cretaceous of hole 402 A in the Bay of Biscay, DSDP leg 48. In: Montadert L, Roberts DG (eds) Deep Sea Drill Project report. Washington

Riccardi AC (1988) The Cretaceous system of southern South America. Memoirs of Geological Society of America, 186. Geological Society of America, Boulder

Riccardi AC, Aguirre Urreta MB (1989) Hemihoplitid ammonoides from the Lower Cretaceous of southern Patagonia. Palaeontology 32:447–462

Riccardi AC, Medina FA (2002) The Beudanticeratinae and Cleoniceratinae (Ammonitida) from the lower Albian of Patagonia. Rev Paléobiol 21:291–351

Robert E, Bulot L G (2004) Origin, phylogeny, faunal composition, and stratigraphical significance of the Albian engonoceratidae (Pulchelliaceae, Ammonitina) of Peru. J South Amer Earth Sc 17:11–23

Ritterbush KA, Hoffmann R, Lukeneder A, De Baets K (2014) Pelagic palaeoecology: the importance of recent constraints on ammonoid palaeobiology and life history. J Zool 292:229–241

Rogov MA (2013) The end-Jurassic extinction. In: MacLeod N (ed) Grzimek's animal life encyclopedia. Extinction. Grzimek's animal life encyclopedia. Gale Cengage Learning

Savel'ev AA (1973) Stratigrafiya i Ammonity Nizhnego Al'ba Mangyshlaka (Zonae *Leymeriella tardefurcata* i *Leymeriella regularis*) (in Russian; Stratigraphy and ammonites of the Lower Albian of Mangyshlak (*Leymeriella tardefurcata* and *Leymeriella regularis* zones). Trudy Vses N-Issled Geolog Nefteg Inst 323:1–339

Schouten S, Hopmans EC, Forster A, van Breugel Y, Kuypers MMM, Damsté JSS (2003) Extremely high sea-surface temperatures at low latitudes during the middle Cretaceous as revealed by archaeal membrane lipids. Geology 31:1069–1072

Scott G (1940) Paleoecological factors controlling the distribution and mode of life of Cretaceous ammonoids in the Texas area. J Paleontol 14:299–323

Shimizu S (1931) The marine Lower Cretaceous deposits of Japan, with special reference to the ammonite-bearing zones. Sc Rep Tohoku Imp Univ 15:1–40

Shul'gina NI (1985) Boreal basins at the Jurassic-Cretaceous boundary. Nedra, Leningrad

Shul'gina NI (1989) Subdivisions of the marine "Neocomian" in Siberia and correlation with the type sections-a review. In: Wiedmann J (ed) Cretaceous of the Western Tethys. Proceedings of the 3rd international Cretaceous symposium, Tübingen, 1987. Schweizerbart, Stuttgart

Shul'gina NI, Burdykina MD, Basov VA, Århus N (1994) Distribution of ammonites, foraminifera and dinoflagellate cysts in the Lower Cretaceous reference sections of the Khatanga Basin, and Boreal Valanginian biogeography. Cretac Res 15:1–16

Skwarko SK, Thieuloy J-P (1989) Early Barremian (Early Cretaceous) mollusca from western Irian Jaya, Indonesia. Public Geol Res Developm, Centre Paleont, 6:26–43

Spath LF (1930) On some Ammonoidea from the Lower Greensand. Ann Mag Nat Hist 5:417–464

Spath LF (1939) The Cephalopoda of the Neocomian belemnite beds of the Salt Range. Palaeont Indica 25. Geological Survey of India, pp 1–15

Tavera Benitez JM, Checa OF, Company M (1986) Mediterranean ammonites and the Jurassic-Cretaceous boundary in southern Spain (Subbetic zone). Acta Geol Hung 29:151–159

Thieuloy J-P (1977) Les ammonites boréales des formations Néocomiennes du Sud-est français (province subméditerranéenne). Geobios 10:395–461

Thieuloy J-P, Fuhr M, Bulot LG (1990) Biostratigraphie du Crétacé Inférieur de l'Arc de Castellane (S.E. de la France). 1: Faunes d'ammonites du Valanginien supérieur et age de l'horizon dit de "La grande Lumachelle". Géol Méditerr 17:55–99

Thomson MRA (1979) Upper Jurassic and Lower Cretaceous ammonite faunas of the Ablation point area, Alexander Island. Scient Rep, Brit Antartic Surv 97:1–37

Vašíček Z (1979) Die Cephalopoden der schlesischen Unterkreide und ihre paläogeographische Bedeutung. In: Wiedmann J (ed) Aspekte der Kreide Europas. IUGS Series A. Schweizerbart, Stuttgart

Vašíček Z (1997) Ammonite stratigraphy of the pre-Albian Lower Cretaceous formations of the Western Carpathians (Czech and Slovak Republics). Geol Carpathica 48:231–242

Vašíček Z, Michalík J (1999) Early Cretaceous ammonoid paleobiogeography of the West Carpathian part of the Paleoeuropean shelf margin. N Jb Geol Paläontol Abh 212:241–262

Vennari VV, Álvarez PP, Aguirre-Urreta B (2012) A new species of *Andiceras* Krantz (Cephalopoda: Ammonoidea) from the Late Jurassic-Early Cretaceous of the Neuquén Basin, Mendoza, Argentina. Systematics and biostratigraphy. Andean Geol 39:92–105

Vermeulen J (2002) Etude stratigraphique et paléontologique de la famille des Pulchelliidae (Ammonoidea, Ammonitina, Endemocerataceae). Géol Alpine Mém 42:1–333

Vermeulen J (2004) Vers une nouvelle classification à fondement phylogénétique des ammonites hétéromorphes du Crétacé Inférieur méditerranéen. Le cas des Crioceratitidae Gill, 1871. nom. correct. Wright, 1952, des Emericiceratidae fam. nov. et des Acrioceratidae fam. nov. (Ancylocerataceae Gill, 1871). Riv Scient 88:69–92

Vermeulen J (2005) Boundaries, ammonite fauna and main subdivisions of the stratotype of the Barremian. Géol Alp sér spéc<<colloques et excursions>>7:147–173

Vermeulen J (2006) Nouvelle classification à fondement phylogénetique des ammonites hétéromorphes du Crétacé inférieur. Ann Mus d'Hist Nat Nice 21:137–178

Vermeulen J (2007) Nouvelles données sur l'évolution et la classification des Holcodiscidae Spath, 1923 (Ammonitida, Ammonitina, Silesitoidea). Ann Mus d'Hist Nat Nice 22:87–100

Vermeulen J, Bulot LG (2007) Données nouvelles sur la classification phylogénétique des ammonites du Crétacé Inférieur. Ann Mus d'Hist Nat Nice 22:101–112

Vermeulen J, Lazarin P (2007) Nouvelles données sur les Ancyloceratoidea Gill, 1871 (Ancyloceratina Wiedmann, 1966 emend. Vermeulen, 2005) du Barrémien supérieur et de l' Aptien inférieur. Ann Mu d'Hist Nat Nice 12:27–86

Vermeulen J, Duyé J-P, Lazarin P, Leroy L, Mascarelli E (2009) Nouvelles données taxonomiques sur la famille des Crioceratitidae Gill, 1871 (Ancyloceratina, Ancyloceratoidea). Riv Scient 92:65–76

Vincent B, Van Buchem FSP, Bulot LG, Immenhauser A, Caron M, Baghbani D, Huc AY (2010) Carbon-isotope stratigraphy, biostratigraphy and organic matter distribution in the Aptian-Lower Albian successions of southwest Iran (Dariyan and Kazhdumi formations). In: Van Buchem FSP Al-Husseini MI Maurer F Droste HJ (eds) Barremian-Aptian stratigraphy and hydrocarbon habitat of the eastern Arabian Plate, GeoArabia special publication. Gulf Petro-Link, Manama

Vrielynck B (2010) Reconstruction cinématique de la Terre à l'Albien. In: Colleté C (ed) Stratotype Albien. Mus nat d'Hist nat, Paris; Biotope, Mèze; BRGM. Orléans, Paris

Westermann GEG (1996) Ammonoid life and habit. In: Landman NH, Tanabe K, Davis RA (eds) Ammonoid paleobiology. Topics in Geobiology. Plenum, New York

Westermann GEG (2000) Biochore classification and nomenclature in paleobiogeography: an attempt at order. Palaeogeogr Palaeoclimatol Palaeoecol 158:1–13

Whitehouse FW (1926) The Cretaceous Ammonoidea of eastern Australia. Mem Queensland Mus 8:195–242

Wiedmann J (1962) Unterkreide-Ammoniten von Mallorca. 1. Lieferung: Lytoceratina, Aptychi. Akad Wiss Lit, Abh mathem-naturwiss Kl 1962:1–148

Wiedmann J (1969) The heteromorphs and ammonoid extinction. Biol Rev 44:563–602

Wiedmann J (1978) Ammonites from the Curaçao Lava Formation, Curaçao, Caribbean. Geol Mijnbouw 57:361–364

Wiedmann J (1988) Plate tectonics, sea level changes, climate-and the relationship to ammonite evolution, provincialism, and mode of life. In: Wiedmann J, Kullmann J (eds) Cephalopods-Present and Past. Schweizerbart, Stuttgart

Wiedmann J, Neugebauer J (1978) Lower Cretaceous ammonites from the South Atlantic leg 40 (DSDP), their stratigraphic value and sedimentologic properties. In: Bolli HM, Ryan WBF, (eds). Deep Sea Drill Project report, Washington

Wimbledon WAP, Casellato CE, Reháková D, Bulot LG, Erba E, Gardin S, Verreussel RMCH, Munsterman DK, Hunt CO (2011) Fixing a basal Berriasian and Jurassic/Cretaceous (J/K) boundary–is there perhaps some light at the end of the tunnel? Riv Ital Paleont Stratigr 117:295–307

Wimbledon WAP, Reháková D, Pszczólkowski A, Casellato CE, Halásová E, Frau C, Bulot LG, Grabowski J, Sobien K, Pruner P, Schnabl P, Cizková K (2013) An account of the bio- and magnetostratigraphy of the Upper Tithonian-Lower Berriasian interval at Le Chouet, Drôme (SE France). Geol Carpathica 64:437–460

Wippich MGE (2001) Die tiefe Unter-Kreide (Berrias bis Unter-Hauterive) im südwestmarokkanischen Becken: Ammonitenfauna, Bio- und Sequenzstratigraphie. PhD thesis, Ruhr-Universität, Bochum

Wright CW, Callomon JH, Howarth MK (1996) Treatise on invertebrate paleontology, Part L, Mollusca 4, vol 4. In: Kaesler RL (ed) Cretaceous Ammonoidea. GSA and The University of Kansas Press, Boulder

Young K (1988) *Karakaschiceras* and the late Valanginian of Northern Mexico and Texas. In: Wiedmann J, Kullmann J (eds) Cephalopods-present and past. Schweizerbart, Stuttgart

Zakharov VA, Rogov MA (2008) Let the Volgian stage stay in the Jurassic. Russian Geol Geoph 49:408–412

Zakharov VA, Bown PA, Rawson PF (1996) The Berriasian stage and the Jurassic-Cretaceous boundary. In: Rawson PF, Dhondt AV, Hancock JM, Kennedy WJ (eds) Proceedings second international symposium on Cretaceous stage boundaries, Brussels, 8–16 September, 1995. (Bull l'Inst Roy Sc Natur Belgique, Sc Terre, Suppl, Brussels)

Zakharov YD, Baraboshkin EY, Weissert H, Michailova IA, Smyshlyaeva OP, Safronov PP (2013) Late Barremian-early Aptian climate of the northern middle latitudes: stable isotope evidence from bivalve and cephalopod molluscs of the Russian platform. Cretac Res 44:183–201