

FIRST MEETING OF THE RESEARCH GROUP FOR PALEOBIOLOGY AND BIOSTRATIGRAPHY OF THE AMMONITES - COMMUNICATIONS -

Didier BERT (editor), Stéphane BERSAC (associate editor)



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Foreword

The Laboratory of the “Research Group for Paleobiology and biostratigraphy of the Ammonites” (G.P.A; homepage: <http://laboratoire.gpa.pagesperso-orange.fr>) is localised in Southeastern France, in the Alpes de Haute-Provence near Digne-les-Bains. This area is famous since the 19th century for its abundant ammonite localities and because of the Geological Reserve of Haute-Provence, which protect them. The G.P.A. is organized around a working group of scientific colleagues from diverse countries and different research laboratories or universities, and of some amateur collaborators, all interested in ammonites and research on related issues.

The “1st Meeting” of the “Research Group for Paleobiology and biostratigraphy of the Ammonites” (G.P.A), organized by Didier Bert, was held in La Mure-Argens (France) from September 15 to 16, 2012. Eight communications were presented on various subjects about ammonites and nautiloids, their evolution, phylogeny, taxonomy and their use in biostratigraphy, especially with examples of the Upper Jurassic (Kimmeridgian) and the Lower Cretaceous (Barremian and Aptian).

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Communications

- The genera *Heminautilus* Spath, 1927 and *Eucymatoceras* Spath, 1927 (Nautilida, Nautiloidea) in the Lower Barremian of Gard department (South-east of France). *G. Delanoy, C. Baudouin, R. Gonnet, G. Conte & C. Frau* 2
- The Upper Barremian *pro parte* of the Angles stratotype (SE France). *D. Bert* 3
- Variability and evolution of the Deshayesitidae (Ammonoidea, Lower Aptian, Lower Cretaceous) from Southern England. *S. Bersac & D. Bert* 7
- Revision of *Deshayesites deshayesi*: taxonomic and biostratigraphic consequences. *S. Bersac, D. Bert & B. Matrimon* 11
- Evolution of the Cheloniceratinae: an alternative to Deshayesitidae for the Lower Aptian biozonation? Preliminary observations. *A. Pictet* 14
- Phylogenetic relationships among the Hemihoplitidae Spath, 1924 (Ammonoidea, Upper Barremian). *D. Bert* 17
- Preview on the ontogeny, variability and dimorphism of the genera *Taramelliceras* and *Streblites* (Ammonoidea) of the Acanthicum Zone (Upper Kimmeridgian) from Mount Crussol (Ardèche, France). *C. Baudouin, D. Bert & P. Boselli* 19
- Rediscovery of the type specimen and status of *Ezeiceras heberti* Fallot, 1884 (Ammonoidea, Hemihoplitidae, Barremian). *D. Bert & S. Bersac* 22

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The genera *Heminautilus* Spath, 1927 and *Eucymatoceras* Spath, 1927 (Nautilida, Nautiloidea) in the Lower Barremian of Gard Department (South-east of France).

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During the Lower Cretaceous carbonate platforms (known as Urgonian) developed in south-east France in the periphery of the Vocontian Basin. These platforms are present in the north (Jura platform), west (Ard che platform) and south (Provence platform) of the basin. These platforms are characterized by the accumulation of great thicknesses of bioclastic limestones and rest on Valanginian to Barremian deposits.

In the north of the Gard Department and in the southern part of the Ard che platform, Urgonian facies settled during the Lower Barremian. In the northwest of Bagnols-sur-C ze, the plateau of M jannes-le-Clap consists almost entirely of Urgonian limestone, with rudists, whose thickness is about 300 m. In the west and south-west of the plateau, outcrops of marly limestones and white limestones from the Lower Barremian are exposed along the border of the mighty Urgonian formation. They contain a rich ammonite fauna of the *Nicklesia pulchella* Zone: *Emericiceras emerici* (L veill , 1835), *Acrioceras terveri* (Astier, 1851), *Nicklesia pulchella* (d'Orbigny, 1841), *Davidiceras potieri* (Matheron, 1879), *Abrytusites neumayri* (Haug, 1889), *Phylloceras* (*Hypophylloceras*) *ponticuli* (Rousseau, 1842), and some species belonging to the genera *Torcapella* Busnardo, 1870 [including *T. fabrei* (Torcapel, 1884)], *Valdedorsella* Breistroffer, 1947, *Barremites* Kilian, 1913, *Lytoceras* Suess, 1865, *Paraspiticeras* Kilian, 1910, *Dissimilites* Sarkar, 1954 and *Toxoceras* d'Orbigny, 1842. There also occur nautiloids of the genera *Heminautilus* Spath, 1927, *Cymatoceras* Hyatt, 1884 and *Eucymatoceras* Spath, 1927, large gastropods and some belemnites, fish teeth and remains of crustaceans. This fauna associated with abundant traces of bioturbation indicates a platform deposited in a relatively shallow water. This facies with cephalopods will be replaced during the upper Barremian by the Urgonian facies, with rudist bioherms and other organisms, indicating a gradual decrease of the water column. The most notable feature of this fauna is the presence of representatives of the genera *Heminautilus* Spath, 1927 and *Eucymatoceras* Spath, 1927 (Nautilida, Nautiloidea), two genera hitherto known with certainty only in the uppermost Barremian and lower Aptian.

The study of the collected *Heminautilus* leads to the description of a new species to be presented formally elsewhere. This is the oldest known species of the genus. This new taxon is characterized by a compressed shell almost completely smooth, with convex flanks, a nearly flat to slightly ventral area on the phragmocone beginning concave on the body chamber. Ornamentation appears at the end of the body chamber and it consists of marginal and short rursiradiate ribs.

The suture line shows a large lateral lobe and a ventral lobe indented by a saddle strap.

The new species differs from other *Heminautilus* species from the Upper Barremian and lower Aptian [*H. sanctaecrucis* Conte, 1980, *H. lallierianus* (d'Orbigny, 1841), *H. saxbii* (Morris, 1848), *H. tejeriensis* Martinez & Grauges, 2006] by a set of morphological, ornamental and suture line features, namely the *P/L* ratio, the ventral lobe, the ventral region and, on the other hand, by its stratigraphic position.

The small population of *Eucymatoceras* of the *plicatum/requienianum* complex studied in this work do not confirm or refute the synonymy of the species *Eucymatoceras plicatum* (Fitton, 1836) and *E. requienianum* (d'Orbigny, 1840) generally accepted by authors who have studied these taxa. Discrimination from ornamental or morphological features now seems possible for separation these two species, regardless of stratigraphic position.

The study of the specimens of M jannes-le-Clap, the specimens of the d'Orbigny and Requien collections, and the descriptions and representations in the literature show fairly large variations, particularly with regard to the density of ribbing, the angle of the ventral chevron, the point of reflection on the sides and in the shape of the whorl section more or less wide with a ventral region more or less flattened. None of these characters seem to represent an evolutionary change from the Lower Barremian to the summit of the Lower Aptian.

Nevertheless, it should be pointed out that in all the specimens studied a number of them have a rather poor state of preservation or require clarification of their true geographic or stratigraphic position (case of specimens from the d'Orbigny's collection). A specimen suitable for typification of this latter species is one of the Requien collection stored in Avignon, the specimen MR2.001.195.

The biostratigraphic distribution of *Eucymatoceras plicatum* (Fitton, 1836) therefore extends from the Lower Barremian (*Nicklesia pulchella* Zone) to the upper part of the Lower Aptian.

The third species of nautilid studied is *Cymatoceras neocomiense* (d'Orbigny, 1840), a relatively common species in the Lower Barremian deposits. The small population studied confirms the synonymy of *C. varusensis* (d'Orbigny, 1850), already recognized by Boule in his review of the types of Prodrome de Pal ontologie of d'Orbigny. In accord with Boule we consider that the differences between these two nominal species are only due to the difference in the preservation of specimens studied by d'Orbigny.

Key words: Nautiloidea, Lower Cretaceous, Barremian, Aptian, South-East France.

The Upper Barremian *pro parte* of the Angles stratotype (SE France)

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The section of the Barremian stratotype (herein noted *A* - Lower Cretaceous) has been depicted in detail by Busnardo (1965), by Delanoy (1994, 1997) in its upper part and fully by Vermeulen (2005). It extends on about 660 m (500 m for the Barremian alone) along the Angles road (Alpes de Haute-Provence, France) on two East-West oriented hills. Unfortunately the basal part of the Upper Barremian is very poorly exposed (East Hill). First, because of the difficult access of the outcrop that occurs along a slope road cliff. Secondly, because of the existence of disturbances with growth faults affecting the succession of local beds and does not allow their study (Fig. 1). And finally, by the existence of certain anomalies of deposition (of reducing sedimentation type) that have been previously reported in the literature (Bert et al. 2008). Correlations between the two sides of this faulted set have been proposed by Busnardo (1965; by omission between beds 155 and 156 in Fig. 1) and Vermeulen (2005, fig. 82; by addition of a certain number of beds between 155-2 to 162 in Fig. 1), but they do not correspond to the beds observed *in situ* and do not correlate with the other sections of the same area that have yet a fairly good lateral continuity bed by bed.

Given the difficulties encountered in the reference section *A*, a new survey (denoted *A**, see Fig. 2) was therefore carried out in the vertical continuity of the series of the first hill of the stratotype (West). For this work, the log of section *A** contains the first two zones of the Upper Barremian (*Toxancyloceras vandenhekei* and *Gerhardtia Sartousiana* zones), those that concentrate the more anomalies in the historical survey *A*. Whenever possible the beds numbering follows that of the stratotype *A*, but the differences or additions were numbered with an asterisk. This sequence includes the *Camereiceras breistrofferi* and *C. marchandi* horizons (beds *A*/156-12** to *156-15**) ever reported so far along the road (East hill). Other differences can be found between sections *A* and *A**. In particular the section *A** seems a bit more expanded in the *G. sartousiana* Zone. Thus the *Hemihoplites feraudianus* Zone is more complete than along the road without visible abnormalities deposit.

The contribution of the section *A** (West hill of the stratotype) now allows a new approach to the correlation of both sides of the set faulted of the edge road (section *A*, East hill). For this purpose a High definition wide-field panoramic photography was performed for a total length of about 65 m along the road (Fig. 1). These new observations complement the historical section *A* to resume the section-numbering of Busnardo (1965) supplemented by Vermeulen (2005). Supplementary beds (denoted with an asterisk) were numbered according to the near section *A**. Thus, there is at all no less than six compartments between the faults, denoted I to VI from West to East. Compartments I and II are slightly shifted with respect to each other (strike slip of approximately 1 m), but they are separated from the other compartments by a fault (b)

shifting the succession of almost 4 m and continuing to at least 60 m length in the slope. In compartment II, beyond beds 156-3 and 156-5 especially, it becomes very difficult to observe the beds *in situ* because of their inaccessibility. Panoramic photographs and comparison with the section *A** can complete the log until at least the bed 156-12*. On the other hand, continuity of the sets III, IV and V (low strike slip faults c and d), allows to number the succession downward from bed 160-1 to 156-12*. This latter is observed only over a short distance to the lowest part of the compartments IV and V. Note that due to the bevel disappearance of compartment IV, the bed 156-13* dramatically increases in thickness in compartment V. Across the entire faulted in the compartment VI, the normal succession occurs again from the bed 156-6 (156-16* here), albeit from the bed 157-2 to 162 (9 beds in total) the observed the succession is not consistent with the historical survey. Finally, from these new observations it appears that the historical survey section *A* is incomplete between beds 156-5 and 156-6 (= 156-16*), where it lacks a dozen beds (approximately 3 m thick), and it is defective between the beds 157-2 and 162. A new reference survey is necessary (Fig. 3; see Busnardo 1965, Delanoy 1994, 1997, Vermeulen 2005 and Bert et al. accepted, for the distribution of the ammonite faunas).

The new stratotype reference sections *A* (Fig. 3) and *A** (Fig. 2) are complementary and allow to optimize future studies on the Upper Barremian.

Key words: Upper Barremian, Stratotype section, Angles road, SE France, New reference survey.

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Figure 1. Wide field panoramic photograph of the Upper Barremian (*pro parte*) stratotype of the Angles road (section A, East hill - Alpes de Haute-Provence, France) with their faults and strike slips, the crushed zones and the bed numbers (this work).

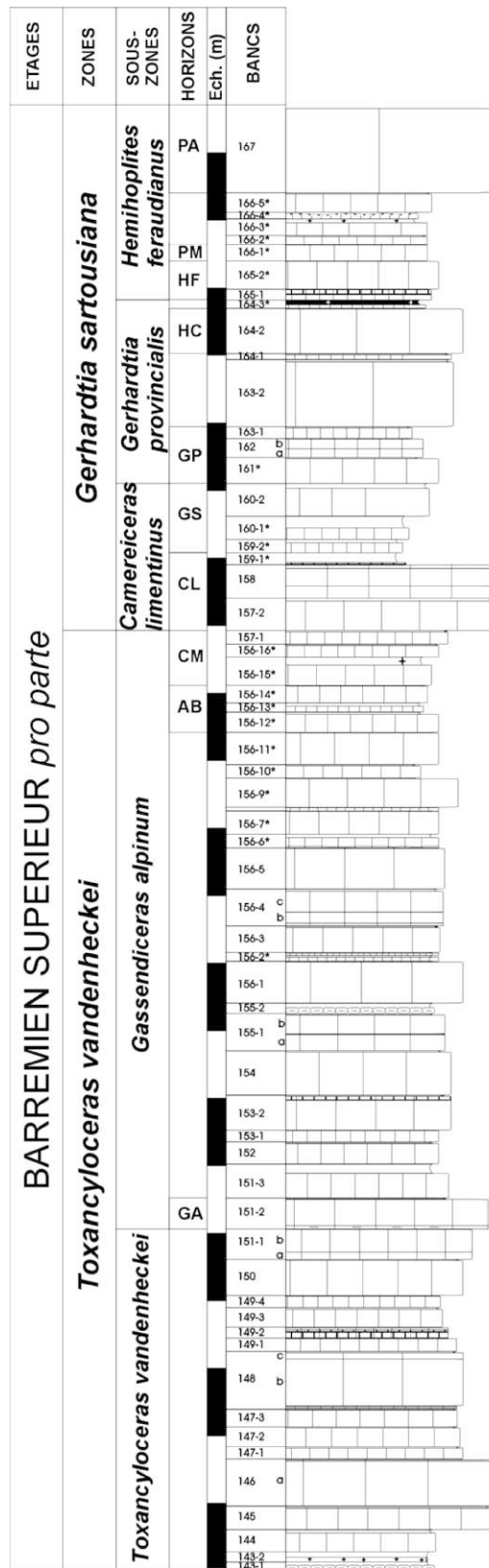


Figure 2. Upper Barremian (*pro parte*) log-section A* (West hill) of the Angles stratotype (Alpes de Haute-Provence). Stratigraphic framework after Reboulet et al. (2007, 2009), modified by Bert et al. (2008, 2010, 2011) and Bert & Delanoy (2009). Biostratigraphic horizons: GA = *Gassendicerias alpinum*; AB = *Camereiceras breistrofferi*; CM = *C. marchandi*; CL = *C. limentinus*; GS = *Gerhardtia sartousiana*; GP = *G. provincialis*; HC = *Hemihoplites casanovai*; HF = *H. feraudianus*; PM = *Pseudoshasticerias magnini*; PA = *P. autrani*. Note that GS is an acme horizon. Faunal distributions are given in Bert et al. (accepted).

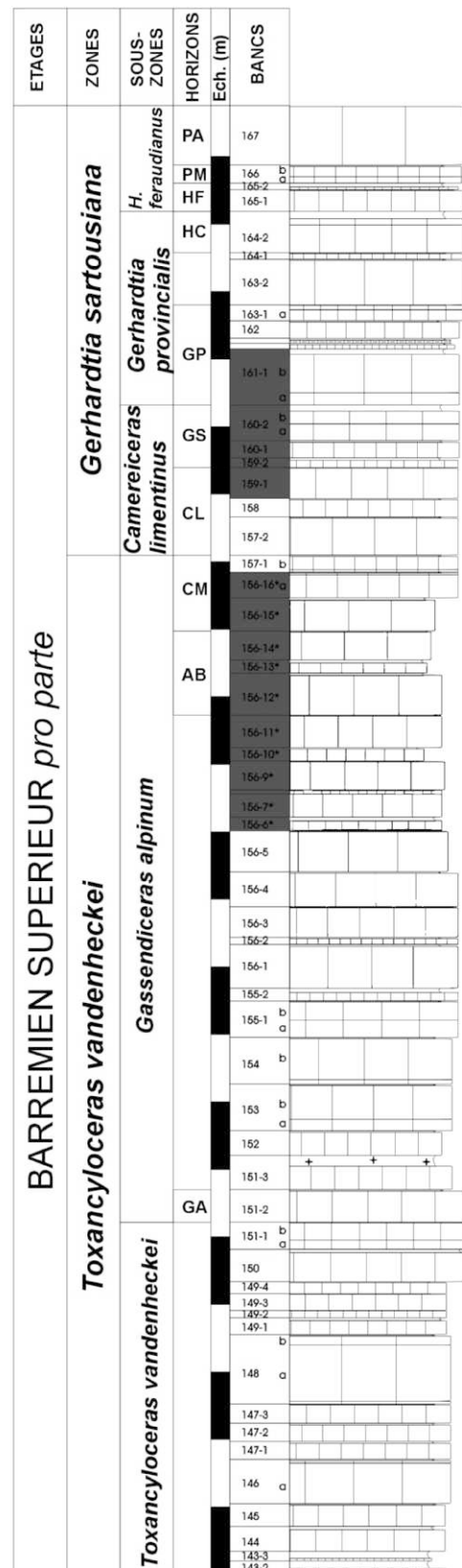


Figure 3. New Upper Barremian (*pro parte*) log-section A (East hill) of the Angles stratotype (Alpes de Haute-Provence, France). Beds bracketed by the right-hand bar are those influenced by growth faults. Beds shaded (grey) are missing on the historical surveys and/or are renumbered herein (see explanation in text). See Fig. 2 for notation of the biostratigraphic horizons.

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Variability and evolution of the Deshayesitidae (Ammonoidea, Lower Aptian, Lower Cretaceous) from Southern England.

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The Deshayesitidae of the Southern England Lower Greensand Formation (Ammonoidea, Lower Aptian, Lower Cretaceous) were revised in the light of a paleobiological approach on the basis of Casey (1963, 1980) and Casey et al. (1998). The biostratigraphic scale used (Fig. 1) is that of Casey et al. (1998). Specimens from the same biostratigraphic subzone were grouped within a single sample. Then the Casey (1963, 1980) and Casey et al. (1998) taxonomic descriptions were reinterpreted in order to highlight characters that change through time (evolutionary characters) and those which fall within intraspecific/intragroup variability. A morphometric analysis of the specimens figured or described by Casey (1963,

1980) was performed to complete the descriptions and reinterpretation. The results are as follows.

Ontogeny

Ontogeny of the post-embryonic whorls and of the flanks:

- Stage A “with trace of lateral sculpture” (in Casey 1963), appears just after the ammonitella and is restricted to the first whorls of the shell.
- Stage B with a “*Kossmatella* like” morphology.
- Stage C “with thin ribbing”: thin, dense and flexuous inclined forward ribs, with sometimes a peri-umbilical thickening. Fast

Lithostratigraphy of the Isle of Wight after Fitton (1847), amended by Simpson (1985)				Casey & al., 1998		Present paper		Reboulet et al., 2011	
St.	Gr.	Form.	Members	Zones	Subzones	Zones	Subzones	Zones	Subzones
Lower Aptian	Lower Greensand (pars.)	Ferruginous Sands (pars.)	Walpen Clay and Sands	<i>Tropaeum howarthi</i>	<i>Chelonicerias meyendorffi</i>	<i>Dufrenoyia furcata</i>	<i>Dufrenoyia dufrenoyi</i>	Furcata	Dufrenoyi
			Lower Crioceris Beds		<i>Dufrenoyia transitoria</i>		<i>Dufrenoyia furcata</i>		Furcata
			Scaphites Beds	<i>Desh. deshayesi</i>	<i>Desh. grandis</i>	<i>Desh. deshayesi</i>	<i>Desh. grandis</i>	<i>Deshayesites deshayesi</i>	Grandis
			Lower Gryphaea Beds		<i>Chelonicerias parinodum</i>		<i>Deshayesites deshayesi</i>		
		Atherfield Clay	Upper Lobster Beds	<i>Deshayesites forbesi</i>	<i>Deshayesites annelidus</i>	<i>Deshayesites forbesi</i>	<i>Deshayesites annelidus</i>	<i>Deshayesites forbesi</i>	Hambrovi
			Crackers		<i>Deshayesites callidiscus</i>		<i>Deshayesites forbesi</i>		
			Lower Lobster Beds		<i>Deshayesites kiliani</i>		<i>Deshayesites fittoni</i>		
			Chale Clay		<i>Deshayesites fittoni</i>		<i>Deshayesites fittoni</i>		
		X	Perna Beds	<i>Prodeshayesites fissicostatus</i>	<i>Prodeshayesites obsoletus</i>	<i>Deshayesites fissicostatus</i>	<i>D. fissicostatus obsoletus</i>	<i>D. fissicostatus fissicostatus</i>	Luppovi
			X		<i>Prodeshayesites bodei</i>		<i>D. fissicostatus fissicostatus</i>		
Barremian (pars.)	Wealdian (pars.)								
	Wessex (pars.)		Vectis						

Figure 1. Lithostratigraphy and biostratigraphy of the Lower Aptian in the Isle of Wight (Southern England), with a tentative correlation with the “standard” scale (Reboulet et al. 2011). Form. = formation, Gr. = group, St. = stage, X = formation absent in the Isle of Wight.

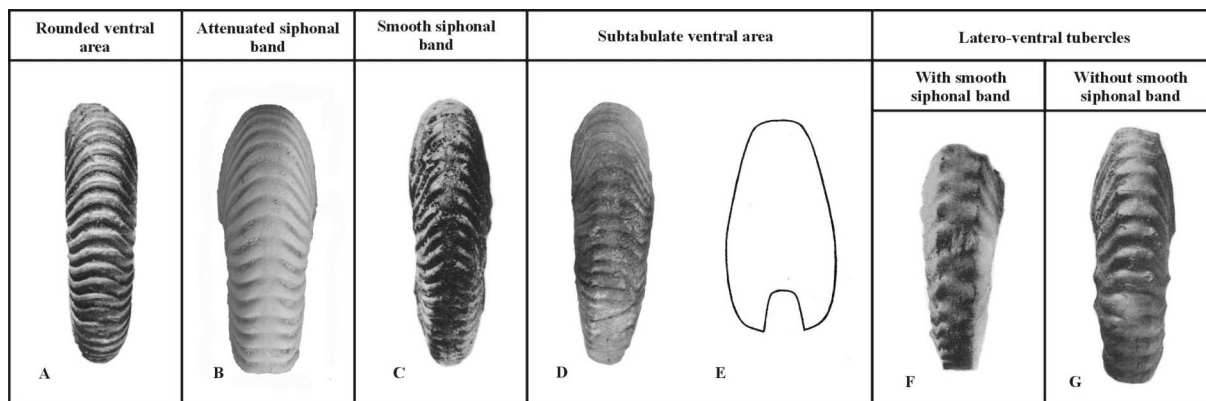


Figure 2. Various shapes of the Deshayesitidae ventral area from the Lower Greensand. All figures are from Casey (1963), except figure B from The Natural History Museum, London. Identification of the figured specimens: A) GSM 30918 (*Deshayesites forbesi*, holotype, in Casey 1963: pl. 47: 1b) [x 0,53], B) BM 30667 (*Deshayesites forbesi* identified as *Deshayesites euglyphus* in Casey 1963: pl. 52: 4) [x 2,06], C) GSM 108185 (*Deshayesites grandis* in Casey 1963: pl. 44: 3c) [x 1,77], D) GSM Geol. Soc. Col. 2300 (*Deshayesites grandis*, holotype, in Casey 1963: pl. 44: b) [x 0,36]), E) GSM Zm1917 (*Deshayesites grandis* in Casey 1963: text.-fig. 110c) [x 0,42], F) GSM 108186 (*Dufrenoyia furcata* identified as *Dufrenoyia cf. mackesoni* in Casey 1963: pl. 62: 4b) [x 1,17], G) GSM 108195 (*Dufrenoyia dufrenoyi* identified as *Dufrenoyia scalata* in Casey 1963: 66: 1b) [x 0,71].

whorl height growth and narrower whorl section.

- Stage D “with strong ribbing”: thicker and less dense ribs. Less inclined forward and less flexuous ribs without peri-umbilical thickening. Whorl height grows slower and the whorl section is thicker.

- “Adult” stage E: strong, simple and straight ribs only visible on the macroconch adult body chamber (see below).

Ontogeny of the ventral area (Fig. 2): this ontogenic sequence varies over time (evolutionary features) and is treated below.

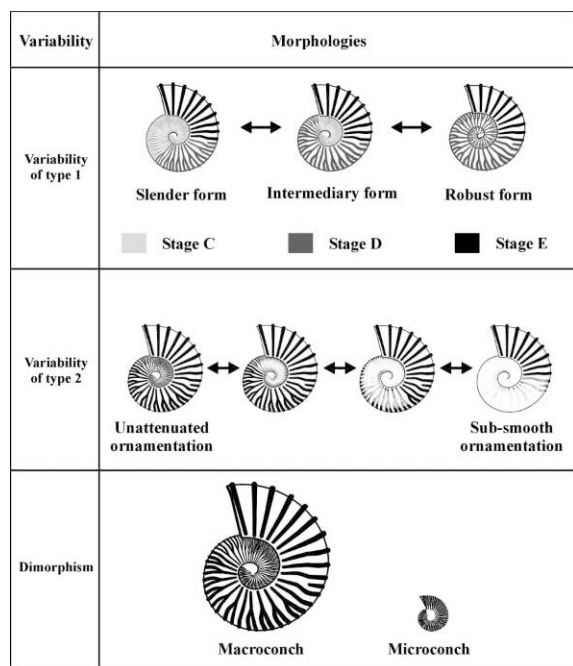


Figure 3. Intraspecific variability and dimorphism among the Deshayesitidae of the Lower Greensand (see text for details).

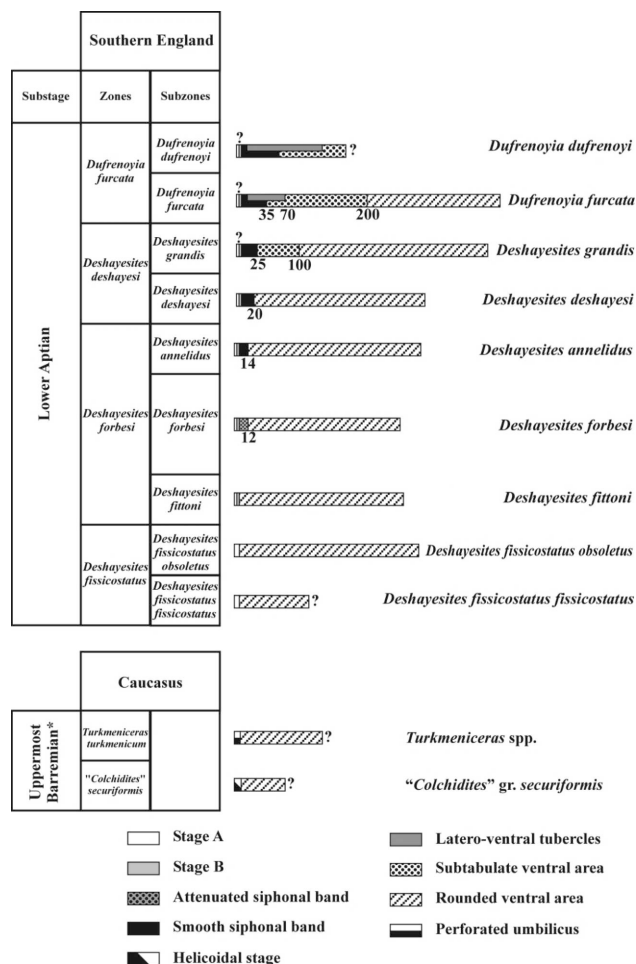


Figure 4. Evolutionary scheme of the Deshayesitidae of the Lower Greensand, with revised biostratigraphic scale (this paper). Numbers attached to the cartouches represent shell mean diameter of appearance of the various stages. Supposed ontogenic stages are pointed out by a question mark above them. Question mark at the right end of cartouche indicates that adult stage is unknown. Supposed ancestral forms “*Colchidites*” gr. *securiformis* and *Turkmeniceras* gr. *turkmenicum*, absent in Southern England, were added for comparison (Bogdanova & Mikhailova 2004; Kakabadze 1971). See Bogdanova & Mikhailova (2004: 191) for a discussion on the stratigraphical position of the *T. turkmenicum* Zone.

Species / Subspecies	Nepionic whorls	Septal suture	Ventral area	Predominant morphology
<i>Dufrenoyia dufrenoyi</i>	Unknown	More incised	Smooth siphonal band up to D = 35 mm, latero-ventral tubercles remain beyond D = 70 mm	None?
<i>Dufrenoyia furcata</i>			Smooth siphonal band at 25 mm < D ≤ 35 mm, latero-ventral tubercles until D = 70 mm	
<i>Deshayesites grandis</i>			Smooth siphonal band at 20 mm < D ≤ 25 mm, subtabulate ventral area until D about 100 mm	
<i>Deshayesites deshayesi</i>	Stage A short Stage B present		Smooth siphonal band at 15 mm ≤ D ≤ 20 mm	Robust (variability of type 1)
<i>Deshayesites annelidus</i>			Smooth siphonal band until D = 14 mm	
<i>Deshayesites forbesi</i>			Attenuated siphonal band until D = 12 mm	None?
<i>Deshayesites fittoni</i>				
<i>Deshayesites fissicostatus obsoletus</i>	Stage A long Stage B absent	Less incised	Rounded without attenuation of ribbing on siphonal area	Sub-smooth (variability of type 2)
<i>Deshayesites fissicostatus fissicostatus</i>				None?

Figure 5. Specific features of the eight paleospecies and two subspecies of Deshayesitidae recognized for the Lower Greensand.

Dimorphism (Fig. 3)

The qualitative study highlighted the presence of large-size (macroconchs, $D > 250$ mm with expression of stage E) and small-size (microconchs, $D < 70$ mm, with no stage E) adult specimens in almost all isochronous samples. This is interpreted as the expression of a probably sexual dimorphism. The morphometric analysis failed to highlight such a dimorphism.

Intraspecific variability

It follows the same patterns in each sample and can be divided into two types:

Intraspecific variability of "Type 1" (Fig. 3): occurs between slender (high whorl height grow, narrow whorl section and mainly slender ornamentation) and robust (slow whorl height grow, thick whorl section and mainly robust ornamentation) forms. Slender specimens seem to have a more incised septal suture. This polymorphic variability is controlled by several parameters:

(1) the rib density, whorl height growth and whorl section of ontogenic stages C (with thin ribbing) and D (with strong ribbing) can present a certain variability.

(2) the duration of the ontogenic stage C with thin ribbing can vary significantly from one specimen to other and determines the general aspect of the shell: the longer this stage is, the more the stage D delays, and the more the shell retains a slender overall appearance. The duration of the stage D with strong ribbing also varies and determines the diameter at which appears the adult stage E in macroconchs.

(3) the transitional duration between every ontogenic stage can be brief or progressive.

Variability of type 1 and the variation of the shell shape correspond to the "First Law of Covariation" (Westermann 1966). The variation of septal suture corresponds to the Second Law of Covariation (see Westermann 1966). These changes in the ontogenetic sequence determining the variability of the shell shape can be interpreted in the light of the heterochronies of development (*sensu* Gould 1977). The robust morphological pole is rather peramorphic with a very short or absent stage C and thus an early stage D. Conversely, the slender morphological pole with a longer stage C is rather paedomorphic.

Intraspecific variability of "Type 2" (Fig. 3): concerns only the ribbing relief and it is organized between a pole with unattenuated ornamentation and a pole with sub-smooth ornamentation. When present, this attenuation of the ornamentation can concern the entire phragmocone or only a small part of it. It may concern either the entire ventral area, or the flanks, or both. The variability of type 2 can concern as well slender individuals as robust ones. It never concerns the adult stage E of which the ornamentation is never attenuated, even in sub-smooth specimens. In individuals with high ornamental attenuation, the phragmocone ventral area can also lose all its ornamentation, which makes undetectable the possible evolutionary changes of this area (see below).

Evolutionary patterns (Fig. 4)

The Deshayesitidae from Southern England evolve over time according to modalities summarized in the Figs. 4-5: they concern the septal suture, the post-embryonic stages (A and B) and the shape/ornamentation of the ventral area.

Evolution of the ontogenetic sequence can be interpreted in the light of the heterochronies of development as a neotenic

evolution of three successive early novelties (*sensu* Gould 1977, smooth siphonal band, then subtabulate ventral area, then latero-ventral tubercles) that invade younger stages of the shell, i.e. a proterogenesis.

The majoritary representation of certain morphologies depending on the variability of type 1 and/or type 2 during some periods of the Deshayesitidae evolutionary history in Southern England could be explained by sea level variations (eustatism): hydrodynamic sub-smooth forms were predominant during a transgressive episode (Perna Beds, *P. obsoletus* Subzone), and robust forms during a major regressive phase (*D. forbesi* Zone) (Ruffel & Wach 1991).

Taxonomic revision (Fig. 5)

Each one of the Deshayesitidae samples is considered as monospecific and their evolution occurs in an anagenetic way. Eight paleospecies with two subspecies divided into two genera (*Deshayesites* Kasansky, 1914 and *Dufrenoyia* Kilian & Reboul, 1915) were recognized. *Prodeshayesites* Casey, 1961, *Paradeshayesites* Kemper, 1967 and *Obsoleticeras* Bogdanova & Mikhailova, 1999 are considered here as junior synonyms of *Deshayesites*. The paleospecies recognized in this work have been designed on the basis of the abundant literature and following the principle of priority (ICZN, Art. 23), with a few exceptions (particularly if the type-specimens are uninterpretable because of unobservability of the evolutionary discriminating criteria). The proposed taxonomic succession is the following: (1) *Deshayesites fissicostatus fissicostatus* (Phillips, 1829) for the *P. fissicostatus* Zone, *P. bodei* Subzone; (2) *Deshayesites fissicostatus obsoletus* (Casey, 1961) for the *P. fissicostatus* Zone, *P. obsoletus* Subzone; (3) *Deshayesites fittoni* Casey, 1961 for the *D. forbesi* Zone, *D. fittoni* Subzone; (4) *Deshayesites forbesi* Casey, 1961 for the *D. forbesi* Zone, *D. kiliani* and *D. callidiscus* subzones; (5) *Deshayesites annelidus* Casey, 1963 for the *D. forbesi* Zone, *D. annelidus* Subzone; (6) *Deshayesites deshayesi* (d'Orbigny, 1841) for the *D. deshayesi* Zone, *C. parinodum* Subzone; (7) *Deshayesites grandis* Spath, 1930 for the *D. deshayesi* Zone, *D. grandis* Subzone; (8) *Dufrenoyia furcata* (Sowerby, 1836) for the *T. bowerbanki* Zone, *D. transitoria* Subzone; and (9) *Dufrenoyia dufrenoyi* (d'Orbigny, 1841) for the *T. bowerbanki* Zone, *C. meyerendorffi* Subzone.

Compared to the English *D. deshayesi*, the evolutionary characters of the lectotype of this species (Casey 1963), from Southern Paris Basin, are similar to those of the sample of the *D. annelidus* Subzone. This could be due to a possible slight intraspecific variation of evolutionary characters, but it has to be confirmed by a revision of *D. deshayesi*.

Each of the recognised taxa of the Lower Greensand Deshayesitidae is proposed to be used as a biostratigraphic index. This implies to rename or to modify some of the boundaries of the units of the biostratigraphic scale of Casey et al. (1998) as shown in Fig. 1. Uncertain correlations with the "standard" scale (Reboulet et al. 2011) are due to divergences in taxonomic interpretations with some index-taxa of Deshayesitidae and to a different acceptance in the

stratigraphic position of the Roloboceratinae. Indeed, according to the "standard" scale, the Roloboceratinae (*Roloboceras* Casey, 1954 and *Megatyloceras* Humphrey, 1949) and in particular the index-species *Roloboceras hambrovi* (Forbes, 1845) occur simultaneously at the top of the Forbesi Zone. But in Southern England (Casey et al. 1998) *Roloboceras* is present alone from the top of the *Deshayesites fittoni* Subzone up to the base of the *Deshayesites annelidus* Subzone, and then is immediately followed by the genus *Megatyloceras* that disappears at the top of the *Deshayesites annelidus* Subzone. A revision of this group could clarify this astonishing difference.

Key words: Ammonoidea, Deshayesitidae, Lower Aptian, Southern England, evolution, variability, biostratigraphy.

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Revision of the index species *Deshayesites deshayesi* (Ammonoidea, Lower Aptian, Lower Cretaceous): taxonomic and biostratigraphic consequences

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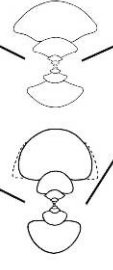







The Lower Aptian (Lower Cretaceous) ammonite biostratigraphy is mainly based on the Deshayesitidae family (Reboullet et al. 2011; see Table 1). The specific identification within this family was hitherto unclear, due to the usually typological approach for this group and the use of disparate criteria. A recent revision of the Southern England Deshayesitidae –the sole paleogeographic area allowing a revision based on published data– was performed by Bersac & Bert (accepted). These authors have reinterpreted the Deshayesitidae of this area as a group evolving in an anagenetic way on a proterogenetic mode, with the successive appearance of three early novelties (*sensu* Gould 1977) during their history: the smooth siphonal band, followed by the subtabulate ventral area then the latero-ventral tubercles. There is also a trend of increasing septal suture complexity, and an additional post-embryonic ontogenetic stage that appears one time in their evolution. The intraspecific variability occurs according to the Laws of Covariation (*i.e.* Deshayesitidae variability of type 1 in Bersac & Bert, accepted) and by a more or less pronounced attenuation of the ornamentation (variability of type 2). A

sexual dimorphism could be present. The eight species and two subspecies recognized by Bersac & Bert (accepted) are, in chronological order: *Deshayesites fissicostatus fissicostatus*, *D. fissicostatus obsoletus*, *D. fittoni*, *D. forbesi*, *D. annelidus*, *D. deshayesi*, *D. grandis*, *Dufrenoyia furcata*, *Dufrenoyia dufrenoyi*. The identification criteria are based on evolutionary characters and were precised for each of them (Bersac & Bert accepted). Only *D. deshayesi* presents a discordance between the evolutionary characters of the English specimens attributed to this species by Bersac & Bert (accepted) and the lectotype of *D. deshayesi* from the Paris Basin (France, see Casey 1963): this latter has its evolutionary characters similar to those of the earlier species *D. annelidus*, interpreted by Bersac & Bert (accepted) as the mother species of *D. deshayesi*. Indeed, the “English *D. deshayesi*” has a smooth siphonal band up to 15 to 20 mm in diameter, and *D. annelidus* has it up to 14 mm in mean diameter. But the lectotype of *D. deshayesi* has a smooth siphonal band up to 12 mm in diameter. It is therefore necessary to determine the age and to characterize the identification criteria of the population from which comes the lectotype of *D.*

Table 1. Lower Aptian biostratigraphy of Southern England and Standard Zonal Scale (SZS).

St.	Southern England (Casey & al., 1998)		Southern England (present paper)			SZS (present paper)			SZS (Reboullet <i>et al.</i> 2011)	
	Zones	Subzones	Zones	Subzones		Zones	Subzones		Zones	Subzones
Lower Aptian	<i>Tropacum bowerbanki</i>	<i>Chelonicerias meyendorffi</i>	<i>Dufrenoyia furcata</i>	<i>Dufrenoyia dufrenoyi</i>	---	Furcata	Dufrenoyi	---	Furcata	Dufrenoyi
		<i>Dufrenoyia transitoria</i>		<i>Dufrenoyia furcata</i>	---		Furcata	---		Furcata
	<i>Desh. deshayesi</i>	<i>Desh. grandis</i>	<i>Deshayesites deshayesi</i>	<i>Desh. grandis</i>	---	<i>Deshayesi</i>	Grandis	---	<i>Deshayesi</i>	Grandis
		<i>Chelonicerias parinodum</i>		<i>Deshayesites multicostatus</i>	---			---		
	<i>Deshayesites forbesi</i>	<i>Deshayesites annelidus</i>	<i>Deshayesites forbesi</i>	<i>Deshayesites deshayesi</i>	---	<i>Forbesi</i>	Hambrovi	---	<i>Forbesi</i>	Hambrovi
		<i>Deshayesites callidiscus</i>		<i>Deshayesites forbesi</i>	---			---		
		<i>Deshayesites kiliani</i>		<i>Deshayesites fittoni</i>	---			---		
		<i>Deshayesites fittoni</i>		<i>Deshayesites fittoni</i>	---			---		
	<i>Prodesh. fissicostatus</i>	<i>Prodeshayesites obsoletus</i>	<i>Deshayesites fissicostatus</i>	<i>D. fissicostatus obsoletus</i>	---	<i>Oglanlensis</i>	Luppovi	---	<i>Oglanlensis</i>	Luppovi
		<i>Prodeshayesites bodei</i>		<i>D. fissicostatus fissicostatus</i>	---			---		
					---			---		

Table 2. Stratigraphic distribution of the Douvilleiceratidae *Roloboceras* (grey) and *Megatyloceras* (black), according to Casey et al. (1998) and Reboulet et al. (2011).

Zone	Subz.	Casey et al. 1998		Reboulet et al. 2011	Subz.
<i>Deshayesites forbesi</i>	<i>Desh. annelidus</i>				Hambrovi
	<i>Desh. callidisc.</i>				
	<i>Desh. kiliani</i>				
	<i>Desh. fittoni</i>				

deshayesi in order to estimate if this discordance is the result of intraspecific variability or of diachronism between the English and French *D. deshayesi*. It is important to note that the evolutionary patterns of the English and Paris Basin Deshayesitidae can be considered as similar and synchronous (see Bersac & Bert accepted). The lectotype of *D. deshayesi* comes from a clayey formation of the Eastern-Southeastern Paris Basin: the *Argiles à Plicatules* ("Plicatula Clays", Amédéo & Matrimon 2004). The majority of its ammonitofauna was collected during industrial exploitation, which ended in the early 20th Century (Corroy 1925). Since, only one outcrop is still accessible but the bad conditions of observation do not allow providing useful data about the *Argiles à Plicatules*. For this reason the population study of the Deshayesitidae of the *Argiles à Plicatules* was based on "historical" specimens deposited in public collections.

The studied material is composed of 38 "historical" specimens coming from 8 different nowadays-inaccessible outcrops and it is supposed to be representative of the *Deshayesites* population of the *Argiles à Plicatules*. Their maximal diameter reaches only 57 mm, due to local fossilisation conditions. None of these fossils was precisely located within the *Argiles à Plicatules*. The goal of the present work is to test the null hypothesis of monospecificity of the studied group, and to determine its specific characteristics. The studied parameters are *D* (maximum diameter), *H* (whorl height), *W* (whorl width), *U* (umbilical diameter), *R1* (total rib density per whorl), *R2* (primary rib density per whorl), *SSB* (end diameter of the smooth siphonal band), *ASB* (end diameter of the attenuated siphonal band). Statistical analysis was performed using PAST software version 2.08b (Hammer et al. 2001). The hypothesis of monospecificity was tested (1) by testing the absence of difference between samples for the whole parameters using ANOSIM, and for the sole quantified evolutionary character (*SSB*) with a Kruskal-Wallis Test; (2) by studying the plot dispersion for the whole parameters on bivariate diagrams and the frequency histograms of the values of the plot projections on the first two components of a principal component analysis (PCA) and for the sole evolutionary character (*SSB*), by a frequency histogram of its value. In case of significant probability of monospecificity of the studied group, its characteristics were determined as follows: (1) search for covariant parameters in analysing bivariate diagrams with regression curve for *H/D*, *W/H*, *R1*, *R2*; (2) search for sexual dimorphism in analysing the plot

dispersion of $D = f(U/H)$; and (3) calculation of the mean value of *SSB* within the studied group.

The analysis highlights the absence of significant difference between samples and strongly supports the monospecificity of the studied group, especially by the close dispersion of the values of *SSB* around their mean ($p < 0.05$).

The characteristics of the studied group are as follows: (1) the shell parameters variability is similar to the variability of type 1 of the Southern England Deshayesitidae (= First Law of Covariation, see Bersac & Bert accepted); (2) An eventual sexual dimorphism could not be detected due to the small size of the specimens; and (3) the mean value of *SSB* is 11.9 mm. This latter value implies *de facto* the synchronicity of the studied group (and *in extenso* the *Argiles à Plicatules'* Deshayesitidae) with the species *D. annelidus* from Southern England. This synchronism is strengthened by the presence of the Douvilleiceratidae *Megatyloceras* within the *Argiles à Plicatules*, because this genus is a "relatively good" co-index of the *D. annelidus* Subzone of Southern England (Casey 1961, Casey et al. 1998, Amédéo & Matrimon 2004, Bersac & Bert accepted; see Table 2).

According to the principle of priority (ICZN: art. 23), the *Argiles à Plicatules* Deshayesitidae belong to the species *D. deshayesi*. *D. annelidus* is therefore a junior synonym of *D. deshayesi* and the "English *D. deshayesi*" has to be renamed in *D. multicostatus*, still according to the principle of priority, and because the holotype of this latter species comes from the *D. deshayesi* Subzone of Southern England. Thus, the *D. annelidus* Subzone of Southern England has to be renamed in *D. deshayesi* Subzone, and the current *D. deshayesi* Subzone in *D. multicostatus* Subzone. We propose to move down the lower limit of the *D. deshayesi* Zone in consequence (Table 1).

Key words: Deshayesitidae, *Deshayesites deshayesi*, Lower Aptian, revision, biostratigraphy.

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Evolution of the Cheloniceratinae: an alternative to Deshayesitidae for the Lower Aptian biozonation? Preliminary observations

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The Mediterranean biozonation of the Lower Aptian is based on the Deshayesitidae, with four zones, defined by the first appearance (FAD) of the index fossil. Unfortunately, this biozonation is subject to numerous controversies. This biozonation has many problems as it is based on bad-defined indexes. The Weissi zone, now replaced by the Forbesi zone, was set to a German specimen which type was lost and the original figure difficult to interpret (Bogdanova & Mikhailova 2004, Ropolo et al. 2006, Reboulet et al. 2009). The Deshayesi zone was based on a pyritic nucleus with no clear stratigraphic position. It is almost impossible to make comparisons of adult specimens with the holotype (Moreno-Bedmar 2010).

The index species are generally rare in SE France and there are only adult specimens of average conservation. It turned out that the adult morphs are indeterminable. It was therefore preferable to locate through Cheloniceratinae, well developed and diversified, allowing to support the Deshayesitidae biozonation as potential substitute, or at least a complementary group.

The Cheloniceratinae show an evolutionary line between the different genera *Procheloniceras*-*Cheloniceras*-*Epicheloniceras* (Ropolo et al. 2008) already recognized by ammonitologists. It becomes more interesting to focus on the morphological changes within close species, but also the differences between them. It allows to recognize evolutionary lines on a smaller scale than mentioned above, which is between species (Fig.1). The characters playing important roles are: (1) the section; (2) the strength of the spines; (3) the number of intercalary ribs; (4) bifurcations; and (5) regularity of ornamentation. These characters can be regarded as intraspecific ornamental variability in what would be only a few species, which is highly possible. However, some criteria such as the flattening of the section, increasing of the frequency of bifurcations, then trifurcations and changes in the spines, clearly show evolutionary trends across temporal and geographical scales. It is also noted that the ecological environment, such as bathymetric variations, appears to play an important role in species turnover among Aptian Douvilleiceratidae, including limits of sequences related to the complete replacement of one kind from another. The sequence boundary SB Ai3 delimits roughly the replacing of *Procheloniceras* by *Cheloniceras* (Fig.1). The latter is replaced by *Epicheloniceras* at the SB Ai4 as this limit is currently located to the top of the Furcata Zone

The biostratigraphic distribution of Cheloniceratinae can be summarized as follow (Fig. 1):

The Oglanlensis Zone: The basis of this zone begins with the appearance of *Deshayesites*. It cannot yet be defined solely on the basis of Cheloniceratinae since *Procheloniceras* begins with *P. sporadicum* and *P. pachystepahus* in the late Barremian (Sarasini Subzone) to the lower part of the Forbesi Zone

(Delanoy 1995, 1997, Ropolo et al. 2008). In conclusion, it is characterized by a combination of the genus *Deshayesites* and *P. pachystephanum*.

The Forbesi Zone: Ropolo et al. (2008) show that the basis of this zone appears to coincide with the FAD of *P. albrechtiaustriae* followed by *P. stobieskii* and *P. dechauxi*. These are quickly replaced by small indeterminate *Cheloniceras* close to *C. cornuelianum*. This latter becomes quickly very abundant in the upper part of the Forbesi Zone. *C. parinodum* and *C. seminodosum* appear shortly after *C. cornuelianum*, from which those are probably derived. Hambrovi Subzone begins with the appearance of *Roloboceras hambrovi* and ends with its latest occurrence (Casey 1961, Moreno-Bedmar 2010). The genus *Megatyloceras*, although not representing the entire Hambrovi Subzone, is also a good marker of the latter (Moreno-Bedmar 2010).

The Deshayesi Zone: This zone is initiated by the disappearance of *R. hambrovi*. It can be seen the appearance of *Cheloniceras crassum*, *C. minimum*, *C. disparile*, *C. kirkaldyi* and *C. quadrarium* marking the basis of the Grandis Subzone (Casey 1961, 1962, Ropolo et al. 2008). The top of the Deshayesi Zone is characterized by the disappearance of *C. quadrarium*, *C. mackesoni* and *C. seminodosum*. The two species *C. minimum* and *C. parinodum* disappear just a little later, at the base of the Furcata Zone (Ropolo et al. 2008).

The Furcata Zone: The Furcata Zone starts with the LAD of the species named above. *C. meyendorffi*, probably resulting from *C. minimum*, marks the Menyendorffi / Dufrenoyi Subzone. The top of the zone is limited by the disappearance of all the *Cheloniceras s.str.*, and the emergence of the genus *Epicheloniceras* with *Epicheloniceras martini*, *E. martinoides*, and *E. debile*. (Casey 1961, 1962; Ropolo et al. 2008).

In conclusion, the Cheloniceratinae show an evolutionary lineage *Procheloniceras*-*Cheloniceras*-*Epicheloniceras* marked by several morphological changes enough characteristic to allow the individualization of clear biostratigraphic intervals. However, there will be many crops and analysis on relatively distant sections to correct, improve, and make evolve this frame still relatively fragile and uncertain of the Cheloniceratinae evolution.

Key words: Lower Aptian, Cheloniceratinae, biozonation, evolution.

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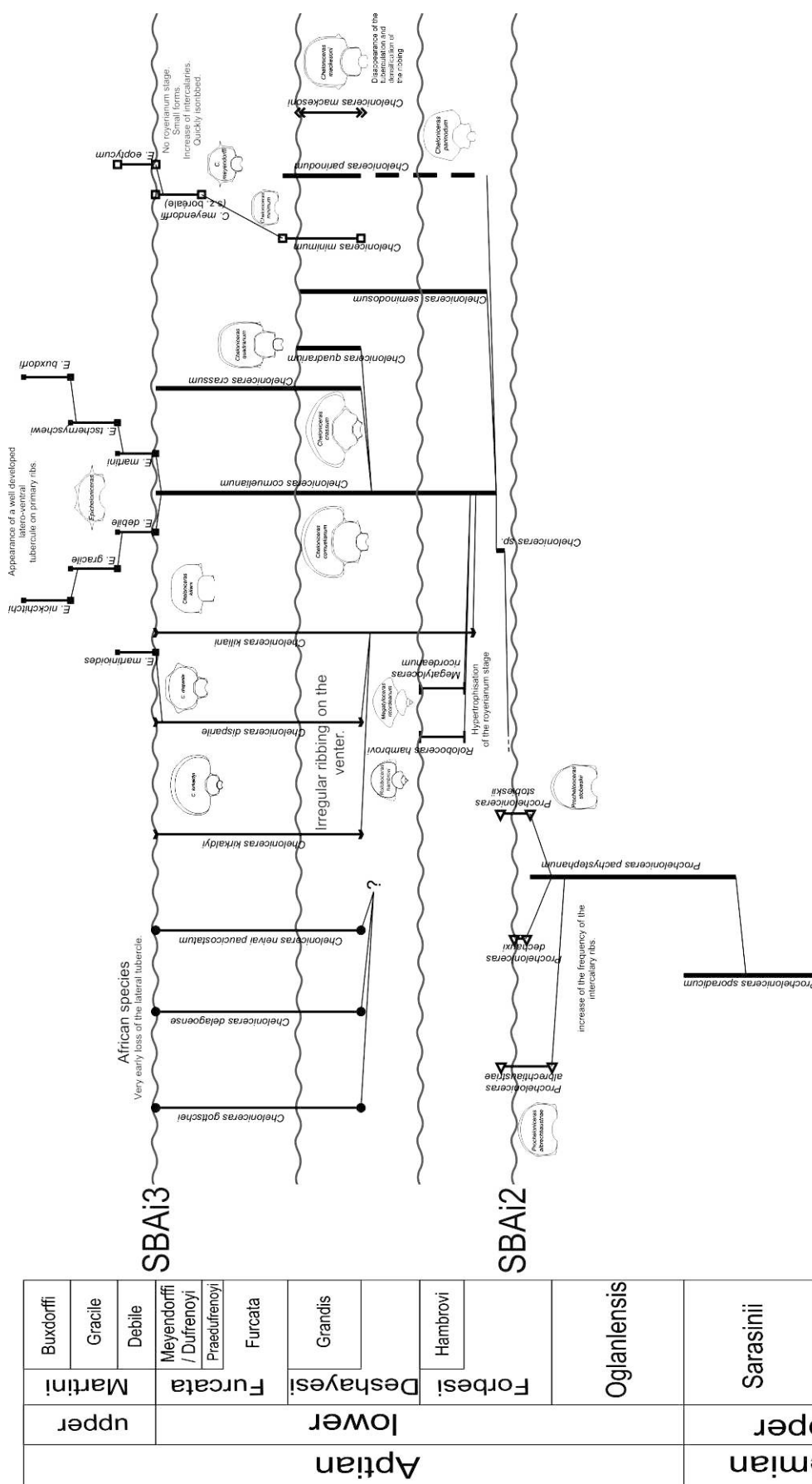


Figure 1: Evolution of the Douvilleiceratidae and keypoints. Ondulate lines indicate major discontinuities. Similarities between species are represented by same marks.

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Phylogenetic relationships among the Hemihoplitidae Spath, 1924 (Ammonoidea, Upper Barremian)

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The family Hemihoplitidae Spath, 1924 (Ammonoidea) represents a separate entity from the Upper Barremian Tethyan Ancyloceratidae, and their rapid evolution and diversification make it one of the key groups for that period. The Hemihoplitidae are currently under revision by the author and several contributions have already been published (Bert & Delanoy 2000, 2009, Bert et al. 2006, 2008, 2009, 2010, 2011). These papers helped to recognize three major developments within this family. They are taxonomically materialized into three subfamilies: (1) the Gassendiceratinae Bert, Delanoy & Bersac, 2006, representing the stem of the whole group; they are present from the base (s.l.) of the Upper Barremian to the base of the Giraudi Zone. (2) The Hemihoplitinae Spath, 1924, ranging from the Alpinum Subzone up to the Feraudianus Subzone. And (3) the Peirescinae Bert, Delanoy & Bersac, 2006, which are present from the Alpinum Subzone up to the top of the Giraudi Subzone where they connect with the Douvilleiceratoidea Parona & Bonarelli, 1897. Although many taxa are not yet revised (works in progress), the extensive data already collected on the Hemihoplitidae allow to propose a phylogenetic organization of the genera on which they are composed (Fig. 1).

The Gassendiceratinae include the genera *Gassendiceras* Bert, Delanoy & Bersac, 2006, *Pseudoshastrioceras* Delanoy, 1998 and *Imerites* Rouchadze, 1933 that have close phylogenetic relationships. The genus *Gassendiceras* is characterized by a morphology particularly recognizable with an uncoiled shell, main ribs strongly marked and trituberculate alternating with intercalatory spineless ribs. The *Pseudoshastrioceras* are derived from the *Gassendiceras* near the base of the Feraudianus Subzone and show a tighter coiling, depletion of spineless ribs and proliferation of weakly tuberculate intermediate ribs (ribs less differentiated between them) (Bert & Delanoy 2009). The transition to *Imerites* (base of the Giraudi Zone) is through a major restructuration of the shell, which also determines the morphological appearance of dimorphism (Bert et al. 2009).

The first Hemihoplitinae appear rather suddenly in the middle of the Alpinum Subzone with the dimorphic genus *Camereiceras* Delanoy, 1990 ([m] = *Ancylezeiceras* Vermeulen, 2006) that seems to derive from *Gassendiceras*. The first representatives of *Camereiceras* retain certain characteristics of this later (ornamentation and shell morphology, sequence of ontogenetic stages, some of which are common to both genera, shell that may have non-contiguous whorls). In the Limentinus Subzone (Fig. 1), *Camereiceras* has always the whorls in contact, and they give rise to the genus *Pachyhemihoplites* Delanoy, 1992 ([m] = *Janusites* Bert & Delanoy, 2000) of which they retain some morphological characteristics and the expression of dimorphism. The dimorphic genus *Hemihoplites* ([M] =

Parahemihoplites Vermeulen et al., 2010, whose type species *P. ghertiformis* Vermeulen et al., 2009 is a junior synonym of *H. cornagoae* Bert et al., 2006; [m] = *Clementiceras* Vermeulen et al., 2010) is also derived from the *Camereiceras* by modification of the ontogenetic stages.

The Peirescinae arise from the genus *Gasendiceras* via the genus *Peirescites* Bert, Delanoy & Bersac, 2006 that appears quite early in the Alpinum Subzone. This later genus differs from the first only by the very characteristic inner whorls, including expression of a stage with very pronounced tubercles and many spineless inter-ribs (= "peirescites stage"). At the boundary between the Limentinus and Provincialis subzones, *Peirescites* evolves into the genus *Spinocrioceras* Kemper, 1973 by recoiling the shell whose whorls become joined, by the disappearance of the "peirescites stage" and the expression of a "polyspinosum stage" on the major part of the shell. This latter is so named because of its dominant presence in *S. polyspinosum* Kemper, 1973. The *Spinocrioceras* make the link with the *Procheloniceras* Spath, 1923 which appear from the base of the Sarasini Subzone, and which are the first Barremian Douvilleiceratoidea (see Bert et al. 2006: 223; Delanoy et al. 2008: 31). This evolution concerns in particular the appearance (by early novelty) of a new bituberculate ontogenetic stage with inter-ribs in the inner whorls, which will take greater importance during growth in the earlier *Procheloniceras* (neoteny).

Key words: Ammonoidea, Hemihoplitidae, Upper Barremian, Tethyan Realm, Phylogenetic relationships, Taxonomy.

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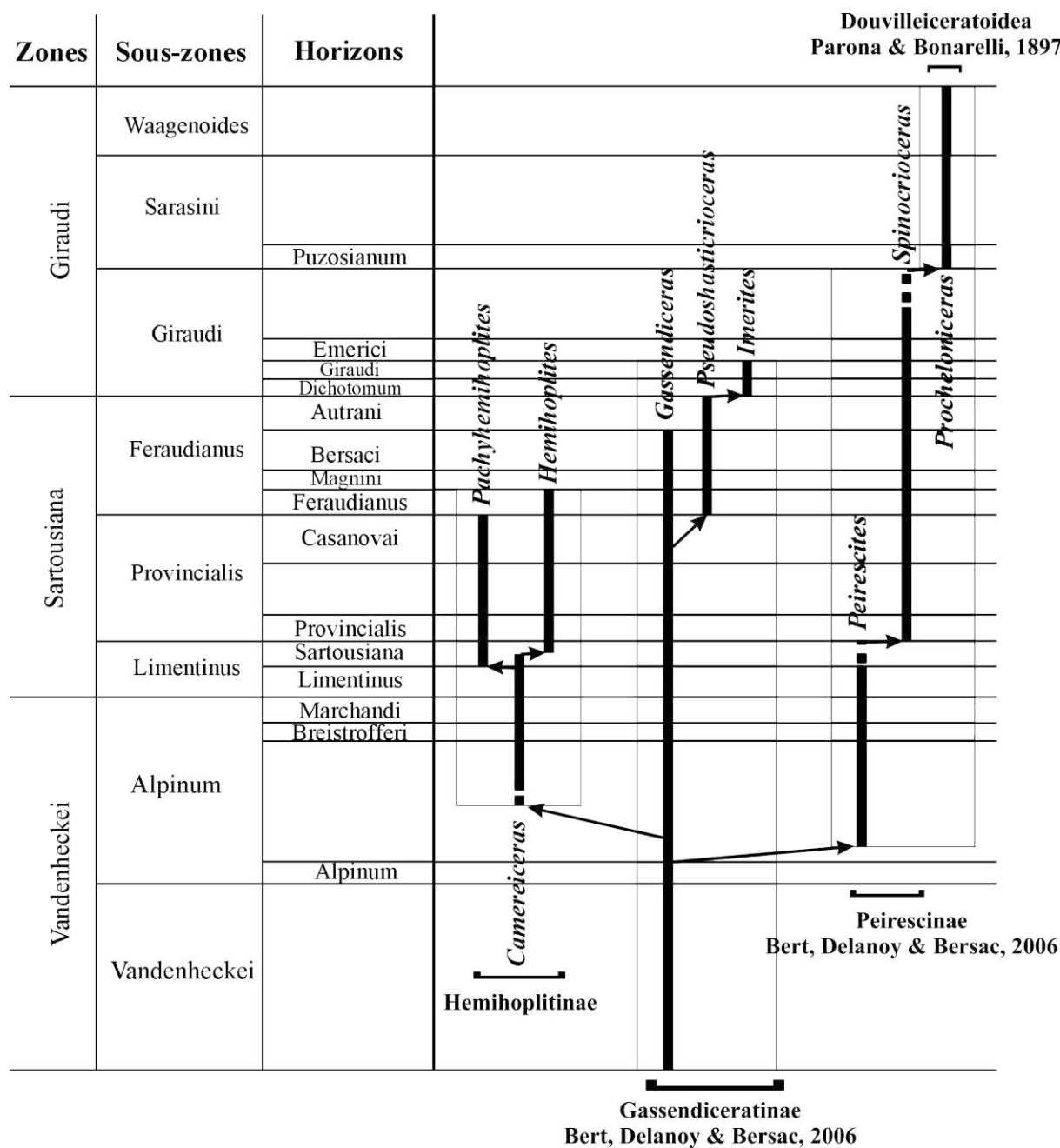


Figure 1. Phylogenetic relationships among the Hemihoplitidae Spath, 1924, according to studies cited in references and work in progress by the author. The Hemihoplitinae, Gassendiceratinae Bert, Delanoy & Bersac, 2006, Peirescinae Bert, Delanoy & Bersac, 2006 and Douvilleiceratoidea Parona & Bonarelli, 1897 are included (see explanation in text).

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Preview on the ontogeny, variability and dimorphism of the genera *Taramelliceras* and *Streblites* (Ammonoidea) of the Acanthicum Zone (Upper Kimmeridgian) from Mount Crussol (Ardèche, France).

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Mount Crussol is an historical area which has provided many Kimmeridgian ammonites studied especially by Dumortier & Fontannes (1876), Fontannes (1879), Atrops (1982), and more recently by Baudouin et al. (2011). A significant part of this fauna is constituted by representatives of the family Oppeliidae Douvillé, 1890. The orderly working on beds 193 and 195 provided numerous representatives of *Taramelliceras compsum* (Oppel, 1863) ([M] & [m]) and *Streblites weinlandi* (Oppel, 1863) ([M] & [m]). Biometric measurements, leading to the ontogenetic study of this Oppeliidae sample, enable a better understanding of their variability and sexual dimorphism.

***Taramelliceras compsum* (Oppel, 1863).**— It can be found in the Acanthicum Zone of the Mediterranean and Sub-Mediterranean realms. It even spreads at least in a part of the Pseudomutabilis Zone.

Macroconchs [M]: they show a relatively compressed involute shell with a subrectangular section of the whorls. The ornamentation consists of primary ribs, which regularly polyfurcate inwards the mid-flank at an inflection point, in peri-ventral clavis, and in small siphonal tubercles. Four ontogenetic stages can be described:

Stage 1 “smooth”: up to about $D = 15$ mm, no ornamentation is visible and the coiling is relatively evolute with an oval high and relatively compressed whorl section.

Stage 2 “pichleri”: from about $D = 15$ mm the secondary ribs appear, all identical. There are no visible true latero-ventral tubercles. Small siphonal tubercles appear on the ventral rounded area. At $D = 20$ mm the primary ribs appear near the umbilical edge on the lower half of the flanks

Stage 3 “pseudoflexuosum”: from $D = 30$ to 40 mm, latero-ventral tubercles appear on some primary or secondary ribs, highly variable in number. They may either keep a small, round or slightly and radially elongated aspect (pseudoflexuosum morphology), or they may grow in strength, sometimes very strongly in other specimens and become claviform (compsum morphology).

Stage 4: it approximately corresponds to the body chamber of adult specimens. Secondary ribs get strongly attenuate and then disappear. Tubercles frequently (but not consistently) get attenuated as well.

Microconchs [m]: they show morphology of “*Glochiceras*” type with a small sized shell and a very attenuated ornamentation. Two ontogenetic stages can be described:

Stage 1 “smooth”: characteristics of the shell are identical to the macroconchs.

Stage 2 “crenatum”: beyond $D = 15$ mm, the coiling becomes much more evolute, while the whorl height and thickness growth is decreasing. The ornamentation is absent or hardly observable. There are crenulations on the ventral area, while on the flanks sometimes there are small falciform striations. The peristome shows well developed spatulate apophysis.

The variability in this sample is based on the onset diameter of the different stages, the adult size, as well the ribbing and tubercles (macroconchs). The most striking effect is focused on the macroconchs tubercles, which the onset is very variable, and a highly variable strength and persistence in stage 4.

***Streblites weinlandi* (Oppel, 1863).**— It can be found in the Divisum and Acanthicum zones in Germany, Switzerland, Southeastern France and probably in Spain.

Macroconchs [M]: they have a very involute discoidal shell, which is fairly compressed with high whorls. A tabular ventral area and a slight widening umbilicus characterize mature specimens.

We can recognize three successive stages during the ontogeny:

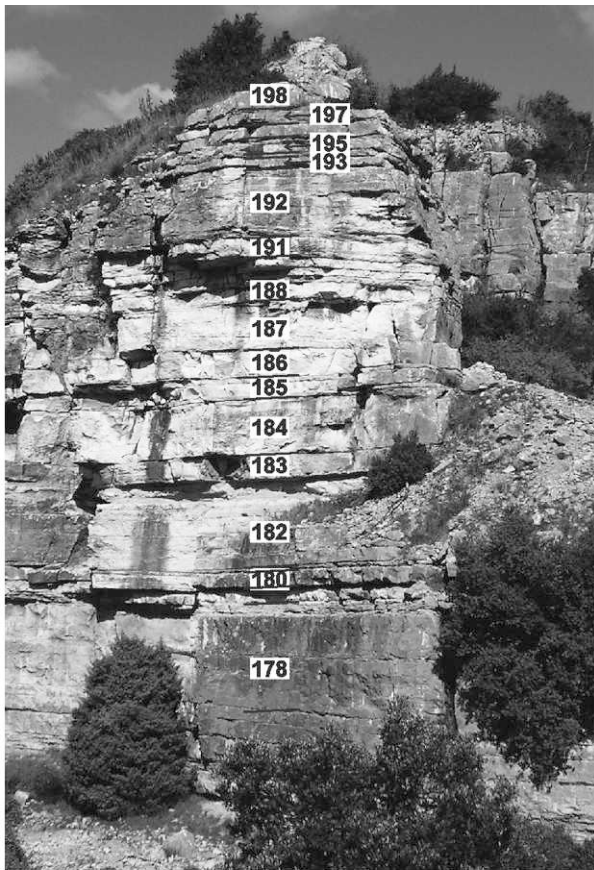
Stage 1: up to $D = 15$ -20 mm, the whorl section is compressed, oxycone, with an almost punctiform umbilicus, and a narrow and rounded venter that bears a conspicuous and finely indented keel. There is no visible ornamentation.

Stage 2 “levipictus”: from $D = 20$ mm a very discreet ornamentation is becoming visible with numerous secondary ribs in the upper third of the flanks; at about $D = 40$ mm a highly variable number of flexuous primary ribs appear often very feeble and slightly discernible.

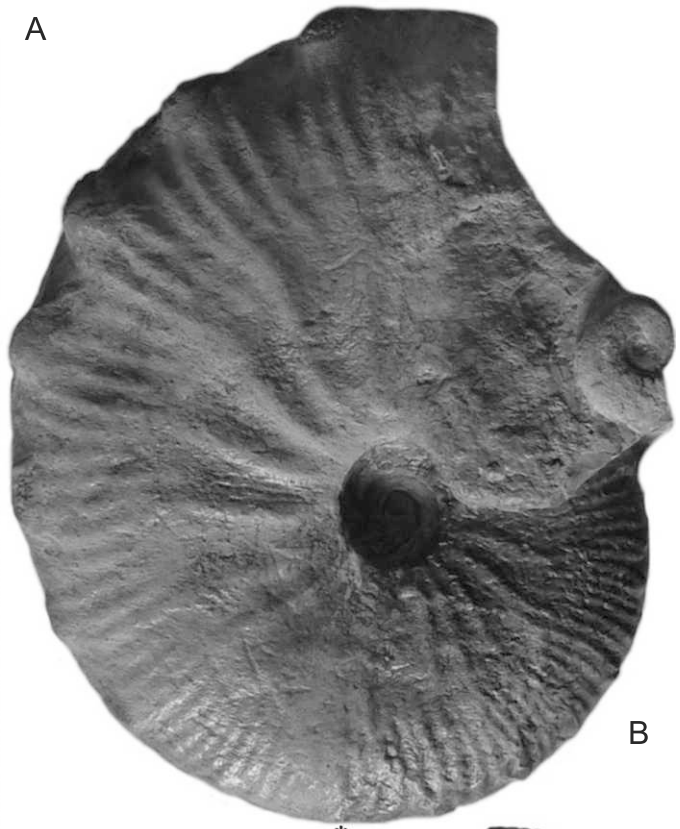
Stage 3 “weinlandi”: present in adults from 60 to 100 mm in diameter where the ventral aspect of the body chamber changes. It widens and becomes subtabulate. The keel can still be seen. The secondary ribs have disappeared and only the primary ribs persist as large bulges in the upper half of the flanks.

Microconchs [m]: they are small and discoidal. Adults are characterized by a distinctly different body chamber with a tabular venter, a significant reduction in the whorl height, and the presence of lateral apophysis. Two ontogenetic stages are expressed:

Stage 1: the shell characteristics are identical to the



A



B



C

D₁D₂

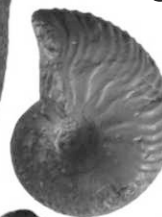
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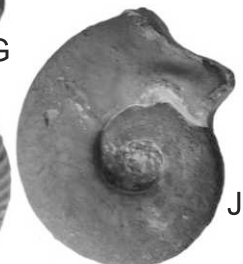
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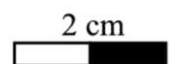
F



J

E₁E₂L₁L₂K₁K₂M₁M₂

N



macroconchs.

Stage 2 “dentatum”: the height growth of the adult body chamber reduces greatly while the coiling becomes much more evolute. The ventral area aspect changes abruptly, the keel gradually disappears, the venter stretches and becomes subtabulate or slightly concave. The peristome shows large spatulate lateral apophysis with a narrow base and a ventral rostrum.

The variability of *Streblites weinlandi* is based on the appearing stages diameter, on the strength of the ornamentation and on the whorl section thickness. These features seem to be correlated. Its most striking effect is focused on the stage 3 onset diameter: it is from $D = 60$ mm in the most robust specimens, which have also a larger section of the whorls and a relatively strong and persistent ornamentation, while it may appear after $D = 100$ mm in the most slender specimens.

Key words: Ammonoidea, Oppeliidae, *Taramelliceras*, *Streblites*, *Ochetoceras*, Upper Kimmeridgian, Upper Jurassic, Crussol, Ardèche, France.

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Figure 1. A: Outcrop section of the Acanthicum Zone of the Mount Crussol, showing the bed numbers cited herein. **B-J:** *Taramelliceras compsum*, Acanthicum Zone, Mount Crussol (Ardèche, France). **B:** [M], specimen cru056, bed 193 or 195. P. Boselli collection. **C:** [M], specimen crl028, bed 193. C. Baudouin collection. **D:** [M], specimen crl007, bed 193. C. Baudouin collection. **E:** [M], specimen cru085, bed 193. P. Boselli collection. **F:** [M], specimen cru086, bed 193. P. Boselli collection. **G:** [M], specimen cru002a, bed 195. P. Boselli collection. **H:** [M], specimen crl117c, bed 193. C. Baudouin collection. **I:** [m], specimen cru058, bed 193 or 195. P. Boselli collection. **J:** [m], specimen crl096, bed 193. C. Baudouin collection. **K-N:** *Streblites weinlandi*, Acanthicum Zone, Mount Crussol (Ardèche, France). **K:** [M], specimen crl055, bed 193. C. Baudouin collection. **L:** [M], specimen crl091, bed 193. C. Baudouin collection. **M:** [m], specimen crl099, bed 193. C. Baudouin collection. **N:** [m], specimen cru068, bed 193. P. Boselli collection. – All natural size (x1). The asterisks indicates the last septum.

Rediscovery of the type specimen and status of *Ezeiceras heberti* Fallot, 1884 (Ammonoidea, Hemihoplitidae, Barremian)

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Historical background

Crioceras heberti was introduced and described by Fallot (1884: 296, pl. 9: 2a and 2c-b) with a hand-drawing (Fig. 1A-C herein) of two small specimens ($D = 34.3$ and 51.4 mm) of “Gault” (= Upper Barremian) from the Nice region (Eze village railway station), but neither has been designated as the type in the original publication. On the original drawings, the species clearly uncoils with growth while the inner whorls are joined. This led Fallot to compare *C. heberti* with *Crioceras hoheneggeri* Uhlig, 1883, which is a tripartite very large form.

But since 1899, Simionescu (1899: 15) already noted the great similarity of “*C.*” *heberti* with the inner whorls of a specimen he identified as *C. barremense* [= *Gassendicerias alpinum* (d’Orbigny, 1850)]. On the basis of a small tripartite specimen in the Sisteron area, Kilian (1910) placed “*C.*” *heberti* in *Ancyloceras* (p. 247, 250), but he also admitted that this species is directly related to *Parahoplites soulieri* (p. 269, 272), which brings this taxon closer to the actual *Hemihoplites*.

For Douvillé (1916), the ornamentation of *C. (Acanthodiscus) hammatoptychum* (= *Pseudoshasticrioceras* gr. *bersaci*) from Sinai, which he described in his article on the Barremian of the Moghara Mountain, is very similar to “*C.*” *heberti*. He also reported the discovery by Caméré of a series of similar specimens “*but where the whorls expand in the adult, while remaining in contact; the flanks ornamentation disappears and the external tubercles persist*”. The Caméré’s ammonites were studied by Delanoy (1990), and we also review them in the collections of the Ecole des Mines (stored in Lyon). These specimens are all assigned here to macroconchs of *Camereiceras limentinus* (Thieuloy, 1979). The observations made by Douvillé (1916) prompted him to propose some hypotheses rather innovative at that time: “*It seems that these ammonites with large whorls could represent the female form with Cr. heberti would be male. In sum, all these forms are extremely similar, regardless of their mode of coiling, with adjacent to or partially or completely disjoint whorls; their relationship is certainly very close*”.

For Sarkar (1955: 149-150) “*C.*” *heberti* should be classified in the genus *Matheronites* (= *Hemihoplites*) near *M. astarte* (whose affinities have been subsequently recognized by Delanoy 1992), and the tripartite specimen Kilian found in the Sisteron area is not belonging to the same species (Sarkar 1955 individualized this latter specimen under the name *Ancyloceras breistrofferi*). On the other hand, according to Sarkar who was able to examine the specimens of Fallot herein shown in Fig. 2a-b (he did not found the specimen shown in Fig. 2c, which was considered lost), the artist has exaggerated the importance of the uncoiling of the last whorl, and he also made some mistakes in the drawn of the ornamentation.

Thieuloy (1979: 307) cited *M. heberti* in the “Sartousiana Zone” fauna in the Vercors and Lure, and he

considered this species very close to the inner whorls of *M. limentinus*. Moreover, his description of the latter (p. 308) corresponds to the “*heberti* stage” we individualized later.

The first redescription of “*C.*” *heberti* since Sarkar, and especially its first representation from the paper by Fallot, is due to Vermeulen & Bert (1998) who assigned it to the genus *Ezeiceras* (then a *nomen nudum* for lack of diagnosis and comparisons, but reintroduced later by Vermeulen 2000).

However, since 2000, in the absence of the Fallot original specimens, *E. heberti* was recognized as a *nomen dubium* and serves more to the definition of the ontogenetic “*heberti* stage” present in the inner whorls of most Hemihoplitidae to the rank of family (Bert & Delanoy 2000, Bert et al. 2006). This stage is characterized by its sub-octagonal or oval whorl section and by its trituberculate simple ribs.

Clarifications on the type specimen of *Ezeiceras heberti* (Fallot, 1884)

Type locality: the section of the Eze village railway station. Researches in the area indicated by Fallot have been conducted, but they failed to find any Barremian outcrop because the area is highly urbanized. It seems that the section has been destroyed, or at least it is now inaccessible.

Type horizon: bed 2 is a “*crumbly limestone filled with glauconite, very fossiliferous*” according to Fallot (1884: 293). In the former collections of the *La Sorbonne*, only a few fossils from Eze have been preserved. They belong to the Bréon, Baron and Fallot collections. The other ammonites grouped with the type of *E. heberti* are all dated from the Late Barremian, specifically from the *Gassendicerias alpinum* Subzone (*Toxancyloceras vandenheckei* Zone) and the *Camereiceras limentinus* Subzone (*Gerhardtia sartousiana* Zone). These ammonites are: *Camereiceras* sp., *Camereiceras* gr. *limentinus*, *Gassendicerias* gr. *alpinum* (d’Orbigny, 1850) and *Barremites charrierianus* (d’Orbigny, 1842).

Type specimen: Vermeulen & Bert (1998) mentioned as holotype the specimen of the Bréon collection figured by Fallot (1884: pl. 9: 2). They were followed by Klein et al. (2007: 220) who even specified “holotype by monotypy”. But this designation is inappropriate because it refers to two different specimens on the same figure (Fallot 1884: Fig. 2a-b and 2c). In fact, the designation of a type specimen of *Ezeiceras heberti* has never been clearly established in the literature. The mention hypotype for a specimen in the Vermeulen collection from La Saurée (Alpes-Maritimes, France), not depicted and not described by Vermeulen & Bert (1998, p. 82), has no value. The specimens studied by Fallot were rediscovered in the collections of UPMC (Jussieu, ex *La Sorbonne* collection)

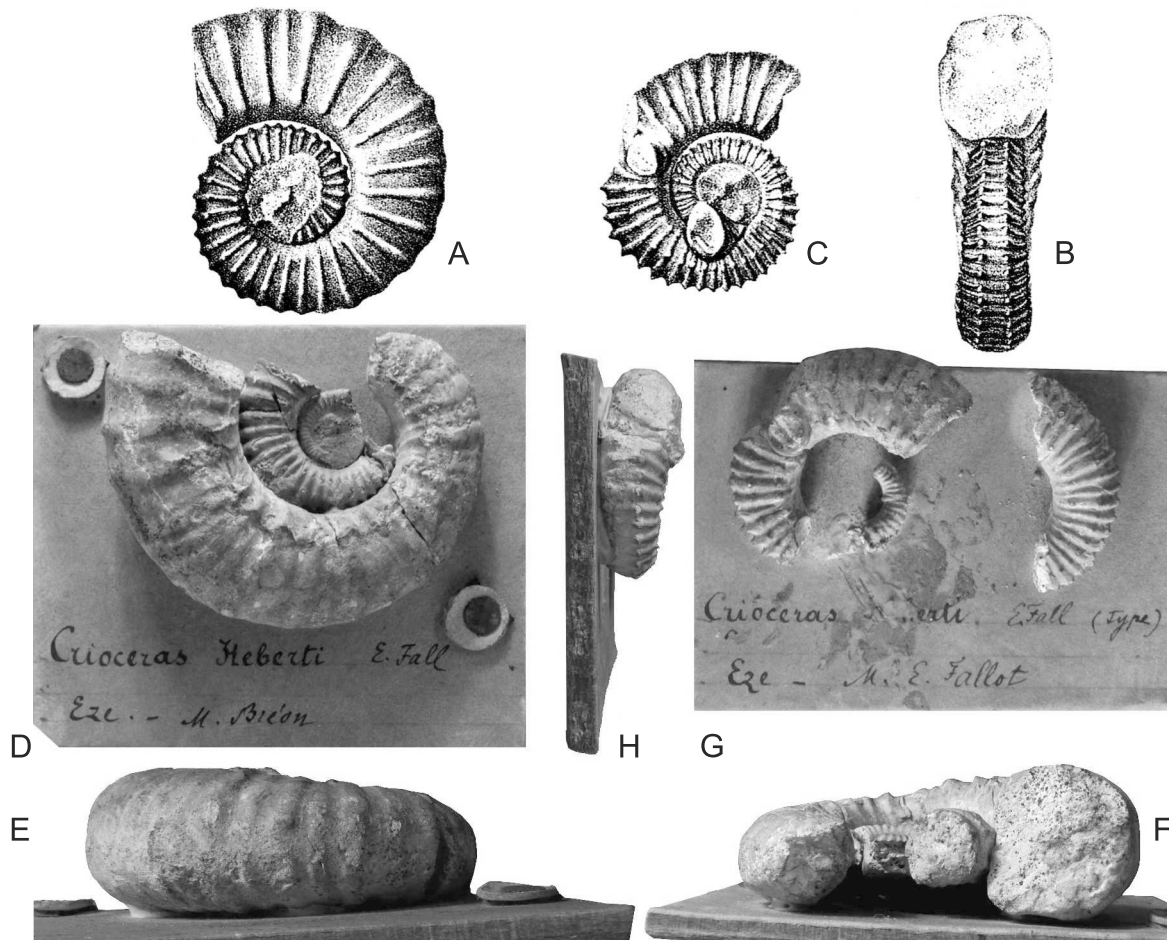


Figure 1. A-C: Reproduction of the original hand-drawings of *Ezeiceras heberti* in Fallot (1884: pl. 9: 2a-c, respectively). D-F: Photographic refiguration (lateral, ventral and apertural views) of the specimen in A-B. G-H: The original small plate having used for the hand-drawings shown in C. As can be seen the original hand-drawings are very idealized even they are composites.

and the specimen in Fallot (1884: fig. 2a-b; herein Fig. 1D-F) is the only that belongs to the Bréon collection, the other belonging to the Fallot collection. But the explanations made on the small plates on which the fossils are glued, indicate clearly and indisputably the specimen in the fig. 2c of Fallot (1884) as the type of *Ezeiceras heberti* (cf. Fig. 1G-H, herein). However, on this last small plate there are actually three fragments glued belonging to different individuals. They were clearly rearranged into a synthetic drawing by the designer of the plate of the paper by Fallot (1884). The only fragment that is perfectly distinguishable from the original drawings is the biggest one that has the “perforations” reported by Fallot. Given the traces of old collages, it is reasonable to believe that another fragment was present on the small plate, which was in connection with the “perforated” fragment, but it could not be found. So the remaining “perforated” fragment is herein designated lectotype of the species.

It is impossible to assess whether the smallest fragment belongs to the same specimen or not, but it is important to note that in the old collection of *La Sorbonne*, it is common to see several fragmentary individuals glued together on the same small plates in order to form a single composite. The last fragment present on the small plate of *E. heberti* is obviously in this case and belongs to another specimen.

The coiling shown in the drawing of Fallot (1884) is interpretive, and because of the actual preservation of the fossils it is impossible to say whether the fragments belonged to a specimen with uncoiled whorls or not. In all cases, given their very fragmentary state and their very small size, the adult morphology is unknown and it is impossible to determine precisely these specimens. This kind of morphology and ornamentation is also well known in the very inner whorls of *Camereiceras*, *Gassendiceras*, *Pseudoshasticioceras*, *Pachyhemihoplites* or in some tuberculated *Hemihoplites*. This is what led us (Bert & Delanoy 2000) to individualize the ontogenic “heberti” stage in Hemihoplitidae.

Although the section of the Eze railway station could not be found, a good knowledge of the Cretaceous deposits of the southern Alpes-Maritimes allows specifying that the preservation of the ammonites of these condensed levels is not homogeneous (authors pers. obs., and see Fernandez-Lopez 2000 for identification of patterns of inhomogeneous condensed deposits). Thus, the preservation of the type specimen of *Ezeiceras heberti* rather reminds the one usually known for the *Camereiceras* in this area, even of course if it is not a decisive determination argument. In the immature type specimen, the presence of salient ventral ribs and well marked (except on the last section of the largest fragment because of the

absence of the shell and of a little treadbare) argues in favour of this hypothesis.

The larger of the two specimens figured by Fallot (1884: fig. 2a-b) has lost its shell on the last whorl, which complicates its identification. In any case, as Sarkar (1955) pointed out, it is much less uncoiled than the original figure of Fallot, since the whorls are just sub-jointed (this is certainly due to the poor gluing of the inner whorls). Due to its characteristics, it is possible to compare this ammonite with robust microconch specimens of *Camereiceras* gr. *limentinus* [m].

Finally, these new observations confirm our previous interpretation of *E. heberti*, which is a *nomen dubium* (Bert & Delanoy 2000, Bert et al. 2006). *Ezeiceras* appears to be most likely a junior synonym of *Camereiceras*.

Key words: Hemihoplitidae, *Ezeiceras heberti*, Upper Barremian, Eze Station.

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