

Revision of the Early Cretaceous genera *Heminautilus* SPATH, 1927,
and *Josanautilus* MARTÍNEZ & GRAUGES, 2006
(Nautilida, Cenoceratidae)

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Abstract: In spite of recent interest, the various species belonging to the genera *Heminautilus* SPATH, 1927, and *Josanautilus* MARTÍNEZ & GRAUGES, 2006, have never been the object of a general revision. More than 160 specimens belonging to various species of these two genera were studied, with the aim of identifying the specific characteristics and the stratigraphical and paleogeographical distribution of the various species which compose them, as well as to propose a phylogeny for the group. This study confirms the non-synonymy of *H. saxbii* (MORRIS, 1848) and *H. lallierianus* (ORBIGNY, 1841), establishes that *H. tejeriensis* MARTÍNEZ & GRAUGES, 2006, and *H. verneuilli* (VILANOVA, 1870) represent junior synonyms of *H. saxbii* (MORRIS) and suggests the creation of the species *H. ? japonicus* sp. nov. The origin of the genus *Heminautilus* SPATH from *Pseudocenoceras* SPATH, 1927, proposed by TINTANT and the origin of *Josanautilus* MARTÍNEZ & GRAUGES from *Heminautilus* SPATH are both confirmed.

Key Words: Nautiloidea; Cenoceratidae; *Heminautilus*; *Josanautilus*; Early Cretaceous; Barremian; Aptian.

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Résumé : *Révision des genres Heminautilus SPATH, 1927, et Josanautilus MARTÍNEZ & GRAUGES, 2006 (Nautilida, Cenoceratidae), du Crétacé inférieur.*- Malgré des travaux récents, les différentes espèces appartenant aux genres *Heminautilus* SPATH, 1927, et *Josanautilus* MARTÍNEZ & GRAUGES, 2006, n'ont jamais fait l'objet d'une révision d'ensemble. Plus de 160 spécimens appartenant à différentes espèces de ces deux genres ont été étudiés dans le but de cerner les caractères spécifiques et la répartition stratigraphique et paléogéographique des différentes espèces qui les composent, ainsi que de proposer un schéma phylogénétique de ce groupe. Cette étude a permis en particulier de confirmer la

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non-synonymie d'*Heminautilus saxbii* (MORRIS, 1848) et d'*H. lallierianus* (ORBIGNY, 1841), d'établir qu'*H. tejeriensis* MARTÍNEZ & GRAUGES, 2006, et *H. verneuilli* (VILANOVA, 1870) représentent des synonymes juniors d'*H. saxbii* (MORRIS), et de créer l'espèce *H. ? japonicus* sp. nov. L'origine du genre *Heminautilus* SPATH chez *Pseudocenoceras* SPATH, 1927, proposée par TINTANT, a pu être confortée et l'origine de *Josanautilus* MARTÍNEZ & GRAUGES chez *Heminautilus* SPATH a également pu être confirmée.

Mots-clefs : Nautiloidea ; Cenoceratidae ; *Heminautilus* ; *Josanautilus* ; Crétacé inférieur ; Barrémien ; Aptien.

I. Introduction

The genus *Heminautilus* SPATH, 1927, includes forms present in the Early Cretaceous (Early Barremian to Early Aptian), with very distinctive and easily recognizable morphology within the Nautiloidea BLAINVILLE, 1825. Its various representatives share a relatively compressed section, a strongly differentiated ventral region and a sinuous suture line, with a particularly well developed ventral lobe. For a long time the genus was poorly known and, in numerous works (F.-J. PICTET & CAMPICHE, 1858; DOUVILLÉ, 1916; DIMITROVA, 1967; OBATA & OGAWA, 1976; OBATA *et al.*, 1984; NIKOLOV & PARASHKEVANOV, 1995; ALY, 2006; ABU-ZIED, 2008), its European and North African representatives were attributed without distinction to the species *H. lallierianus* (ORBIGNY, 1841) and *H. saxbii* (MORRIS, 1848), sometimes in spite of characteristics that clearly separate them from the type specimens. The recent works of CONTE (1980, 1985, 1989, 2007, 2010), MARTÍNEZ & GRAUGES (2006) and DELANOY *et al.* (2012) contributed to a better knowledge of the genus, in particular with the creation of the species *H. sanctaecrucis* CONTE, 1980, *H. tejeriensis* MARTÍNEZ & GRAUGES, 2006, and *H. boselliorum* DELANOY *et al.*, 2012. Furthermore, MARTÍNEZ & GRAUGES recently erected the monospecific genus *Josanautilus* MARTÍNEZ & GRAUGES, 2006, for the species *Nautilus lacerdae* VILANOVA, 1870, phylogenetically very close to the genus *Heminautilus* SPATH. However, no global revision of these two genera has been undertaken until now. The object of the present work is to clarify the diagnostic characteristics of the various species and to summarise their geographical and stratigraphical distribution as well as the phyletic links between them.

We also look at the possible synonymy between the species *H. lallierianus* (ORBIGNY, 1841) and *H. saxbii* (MORRIS, 1848), that has been suggested by numerous authors (ORBIGNY, 1850; F.-J. PICTET & CAMPICHE, 1858; DOUVILLÉ, 1916; SCOTT, 1943).

II. Phylogeny

1. The systematic position and origin of the genus *Heminautilus* SPATH, 1927

The classification of SPATH

SPATH (1927) is the first author to propose a classification of Nautiloidea, based purely on morphological criteria. Thus he classifies the genus *Heminautilus* SPATH, 1927, in the Family Paracenoceratidae SPATH, 1927, which gathers all the forms with a differentiated ventral region and a suture line containing a well developed ventral lobe. However, SPATH (1927, p. 25) himself recognizes the polyphyletic character of this family. The works of TINTANT (TINTANT & KABAMBA, 1983; TINTANT, 1993) will later show that this classification does not actually take into account phyletic data and that numerous identical morphological characteristics appear in an iterative way in various lineages. The classification of SPATH was used, however, by DZIK (1984, p. 181) who presented a phylogenetic outline of the Family Paracenoceratidae SPATH.

The classification of KUMMEL

In 1956, KUMMEL briefly returns to the classification proposed by SPATH (1927). He keeps most of the families proposed by the latter but reducing them to the rank of subfamily. However, he moves the genus *Heminautilus* SPATH, 1927, into the Subfamily Cymatoceratinae SPATH, 1927. Indeed, he notes (p. 435) that the suture line of the genus *Heminautilus* SPATH is more sinuous than that of the other representatives of the Paracenoceratidae SPATH, 1927, and that some specimens of *Heminautilus* SPATH [specimens attributed to *Nautilus lallieri* ORBIGNY, 1841, by DOUVILLÉ, 1916, Pl. 17, figs. 2-4, 6; *Heminautilus rangei* (HOPPE, 1922)] possess sinuous ribbing close to that observed on the genus *Cymatoceras* HYATT, 1884, while other representatives of the Paracenoceratidae SPATH show no ribbing.

However, in a recent work, CHIRAT & BUCHER (2006, p. 62) showed that the structure of the shell as well as the ribbing observed on the specimens of *Heminautilus* SPATH illustrated by DOUVILLÉ (1916, Pl. 17, figs. 2-4, 6) are very different from that observed on *Cymatoceras* HYATT, and that consequently there is no direct phyletic link between these two genera.

The works of TINTANT

In various papers (TINTANT & KABAMBA, 1983, 1985; TINTANT, 1980, 1989, 1993), TINTANT established a new classification based on phyletic data rather than strictly morphological. Thus, he established (1993) that characteristics such as the presence of ribbing, a flat or concave ventral region, or even a sinuous suture line, appear in an iterative way in very different lineages. These features are interpreted as an adaptive answer to a particular environment and are not systematically considered as the consequence of a phyletic link. To establish his new classification, TINTANT used the usual specific characters (ornamentation, suture line, section and ventral region shape, position of the siphon) by interpreting them either as the indication of a phyletic link or as an iterative homeomorphy, in particular for stratigraphically distant species. For TINTANT & KABAMBA (1983), the genus *Heminautilus* SPATH, 1927, derives from the genus *Pseudococeras* SPATH, 1927, by the appearance of a sinuous suture line and a concave ventral region. However, this last genus, in the conception of KUMMEL (1956), seems polyphyletic: it contains various species distributed from the Berriasian to the Maastrichtian. In the Early Cretaceous, the only known species are *Pseudococeras berriasensis* (F.-J. PICTET, 1867) from the Berriasian of southeast France, *Pseudococeras campichei* (KARAKASCH, 1907) from the Hauterivian? of Crimea and *Pseudococeras picteti* (KARAKASCH, 1907) from the Early Barremian? of Crimea. No representative of the genus *Pseudococeras* SPATH seems to be known in the Valanginian, Aptian and Albian; in the Cenomanian the genus is again present, particularly in the form of its type species *P. largilliertianus* (ORBIGNY, 1841). It seems clear that for TINTANT the genus *Heminautilus* SPATH derives from the group formed by the Early Cretaceous taxa *P. berriasensis* (F.-J. PICTET), *P. campichei* (KARAKASCH) and *P. picteti* (KARAKASCH), even if the phyletic links amongst these three species remain to be specified.

The systematic position adopted in this work

By considering the morphological characteristics and the stratigraphical position of the various representatives of the genus *Heminautilus* SPATH, 1927, another hypothesis on the phyletic position of this genus can be envisaged. Indeed, the genus *Xenocheilus* SHIMANSKY & ERLANGER, 1955, present from the Berriasian to the Hauterivian, even to the Early Barremian, shows morphological characteristics close to *Heminautilus* SPATH. According to SHIMANSKY (1975), followed by TINTANT & KABAMBA (1983), this genus belongs to the Family Pseudonautilidae SHIMANSKY & ERLANGER, 1955, close to the genera *Pseudonautilus* MEEK, 1876, and *Aulaconautilus* SPATH, 1927, which would indicate that all three derive from the Jurassic genus *Pseudaganides* SPATH, 1927.

The genus *Xenocheilus* SHIMANSKY & ERLANGER, and in particular the taxon *Xenocheilus ulixis* SHIMANSKY & ERLANGER, 1955, from the Hauterivian of Crimea (see Pl. I, fig. 1), have a very involute coiling with a flat or slightly concave ventral region, and a suture line with a deep lateral lobe and a well indented ventral lobe. As observed by DZIK (1984, p. 180-181), it would be possible to postulate here the origin of the first representatives of the genus *Heminautilus* SPATH, which could derive from *Xenocheilus ulixis* SHIMANSKY & ERLANGER by a slight modification of the sutural line (lateral lobe shallower, wider and round in *Heminautilus* SPATH) and a reduction of the width of the ventral region. However, the position of the siphuncle is a major obstacle to the hypothesis of a direct ancestor-descendant relationship between *Xenocheilus* and *Heminautilus*, because in *Heminautilus* SPATH the siphuncle is always situated in the lower half of the section while it is close to the ventral region in *Xenocheilus* SHIMANSKY & ERLANGER and in all the Pseudonautilidae SHIMANSKY & ERLANGER. These ornamental and sutural similarities were previously noted by SHIMANSKY (1975) who considered them due to morphological convergence.

The systematic position adopted by TINTANT (TINTANT & KABAMBA, 1983; TINTANT, 1993), who considers that the genus *Heminautilus* SPATH, 1927, comes from *Pseudococeras* SPATH, 1927, corresponds best with the current data, and consequently the genus *Heminautilus* SPATH is here placed within the Family Cenoceratidae TINTANT & KABAMBA, 1983. The main characteristics of the genus *Pseudococeras* SPATH, 1927, are a wide and flattened ventral region, a subrectangular section, a slightly sinuous suture line and the siphuncle in a subcentral position, closer to the dorsal face than to the ventral region. In the hypothesis of TINTANT, the genus *Heminautilus* SPATH would thus derive from *Pseudococeras* SPATH by the appearance of a sinuous suture line developing a strong lateral lobe, and of a ventral region with angular edges, as well as by a slight lower position of the siphuncle on the section. From this perspective, the taxon *Pseudococeras campichei* (KARAKASCH, 1907), from the Hauterivian? of Crimea (Pl. I, fig. 2), seems to be the best candidate for the origin of the genus *Heminautilus* SPATH, both morphologically and stratigraphically. However, the current data on these two genera and, in particular, on possible specimens from the Late Hauterivian - Early Barremian remain too fragmentary to provide confirmation, and the hypothesis of TINTANT needs to be supported by a more plentiful material.

2. The systematic position and origin of the genus *Josanautilus* MARTÍNEZ & GRAUGES, 2006

The monospecific genus *Josanautilus* MARTÍNEZ & GRAUGES, 2006, based on its type species *Nautilus lacerdae* VILANOVA, 1870, is a taxon known only from the Early Aptian of Spain and southeast France. Its ornamental and sutural characteristics, as well as its stratigraphical position, show that this species is very close to the genus *Heminautilus* SPATH, 1927, as noted by SHIMANSKY (1975, p. 124) and MARTÍNEZ & GRAUGES (2006, p. 17). Furthermore, both genera seem to have similar environmental requirements and are generally present only in the outer platform domain; the genus *Heminautilus* SPATH is generally associated with *Josanautilus* MARTÍNEZ & GRAUGES in deposits where the latter is present. They have in common a similar sutural line, a siphuncle placed in the lower half of the section, a flat ventral region, a trapezoidal section and very involute coiling. The ribbing on the flanks of the body chamber in *Josanautilus* MARTÍNEZ & GRAUGES is also similar to that observable on some ornamented forms of the genus *Heminautilus* SPATH. The essential difference between the genera is the presence in *Josanautilus* MARTÍNEZ & GRAUGES of a wider and slightly convex ventral region, with a strong central keel surrounded by one or two longitudinal ribs. These characteristics show clearly that *Josanautilus* MARTÍNEZ & GRAUGES comes from the genus *Heminautilus* SPATH, probably by way of the taxon *Heminautilus sanctae-crucis* CONTE, 1980, whose ventral region shows a median keel.

On the other hand, *Josanautilus lacerdae* (VILANOVA, 1870) shows morphological similarities with the Berriasian species *Aulaconautilus sexcarinatus* (F.-J. PICTET, 1867), the cast of whose holotype is shown here (Pl. II, fig. 1). Indeed, this last taxon is characterized by a sinuous suture line, as well as by the presence of six or eight longitudinal ribs on a wide and flattened ventral region. However *Aulaconautilus sexcarinatus* (F.-J. PICTET) differs from *Josanautilus lacerdae* (VILANOVA) by clear differences in the suture line which shows a far less developed lateral saddle and a narrower and less round lateral lobe. The ornamentation of the ventral region of *J. lacerdae* (VILANOVA) also presents only superficial similarities to that of *A. sexcarinatus* (F.-J. PICTET) and can be distinguished easily by the presence of a median keel and the absence of longitudinal ribs on the phragmocone. Furthermore, no ribbing is visible on the flanks in *A. sexcarinatus* (F.-J. PICTET); the section of the latter is clearly narrower, and subrectangular instead of trapezoidal as in *J. lacerdae* (VILANOVA); and the whorls' height increases more slowly than in *J. lacerdae* (VILANOVA). All of these characteristics,

associated with a very different stratigraphical position [Berriasian for *A. sexcarinatus* (F.-J. PICTET) and Early Aptian for *J. lacerdae* (VILANOVA)], show that the similarities between these taxa represent only homeomorphic characteristics and not the consequence of a phyletic link, as noted by MARTÍNEZ & GRAUGES (2006, p. 17).

III. Systematic paleontology

Methodology and conventions: the measurements of height (H), thickness of the whorls (E) and width of the ventral region (M) were made at various diameters (D) (Fig. 1). The measurements of the variation of the lateral lobe of the suture line were made according to the method of MARCHAND & TINTANT (1971): L indicates the width of the lateral lobe and P indicates its depth (Fig. 1). The measurements indicated in bold and italic type were made from photos and are thus subject to some uncertainty (Tables 2-14). To simplify the text, repositories of the studied or quoted specimens are abbreviated (Table 1). The biozonation of the Early Cretaceous used here (Fig. 2) is the one developed by the IUGS Lower Cretaceous Ammonite Working Group (REBOULET *et al.*, 2011, 2014), for the North-Tethyan Domain, with the exception of the *Imerites giraudi* Zone which is split into three subzones at the top of the Barremian (BERT *et al.*, 2008, and REBOULET *et al.*, 2011). It is correlated for the end of the Early Aptian with the biozonation developed by MORENO-BEDMAR *et al.* (2015) for Mexico and southern North America and the one developed by ETAYO-SERNA (1979) for Colombia.

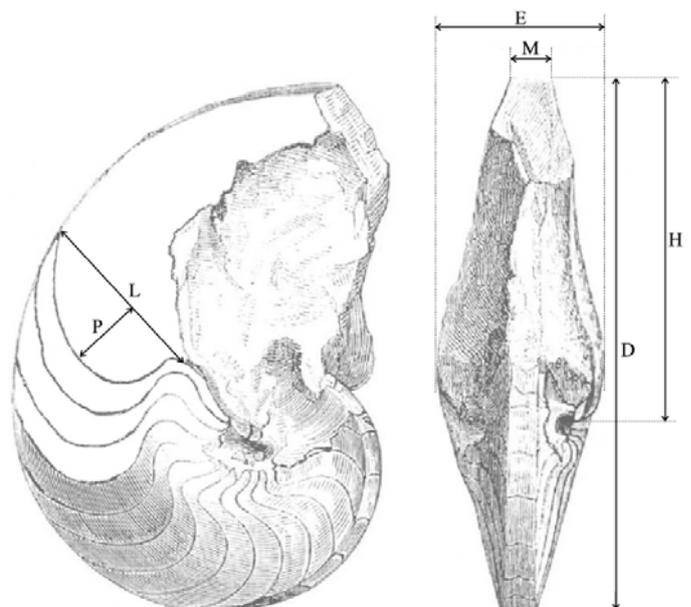


Figure 1: Explanatory scheme for the measurements made on the studied specimens.

	I.C.S.	North-Tethyan Domain (REBOULET <i>et al.</i> , 2011, 2014; BERT <i>et al.</i> ; 2008)		North America and Mexico (MORENO-BEDMAR <i>et al.</i> , 2015)	Colombia (ETAYO-SERNA, 1979)	
		Zones		Subzones	Zones	Zones
Aptian	Late	Late	<i>Hypacanthoplites jacobi</i>		?	-----?
			<i>Acanthoplites nolani</i>	<i>Diadochoceras nodosocostatum</i>		
			<i>Parahoplites melchioris</i>			
			<i>Epicheloniceras martini</i>	<i>Epicheloniceras buxtorfi</i>		
				<i>Epicheloniceras gracile</i>		
			<i>Epicheloniceras debile</i>		<i>Caseyella</i> sp.	<i>Dufrenoyia sanctorum-Stoyanowiceras treffryanus</i> Assemblage zone
		<i>Dufrenoyia furcata</i>	<i>Dufrenoyia dufrenoyi</i>	<i>Dufrenoyia justinae</i>		
			<i>Dufrenoyia furcata</i>			
	Early	Early	<i>Deshayesites deshayesi</i>	<i>Deshayesites grandis</i>		
			<i>Deshayesites forbesi</i>	<i>Roloboceras hambrovi</i>		
<i>Deshayesites ogranlensis</i>			<i>Deshayesites luppovi</i>			
Barremian	Late	Late	<i>Imerites giraudi</i>	<i>Pseudocrioceras waagenoides</i>		
				<i>Martelites sarasini</i>		
				<i>Imerites giraudi</i>		
			<i>Gerhardtia sartousiana</i>	<i>Hemihoplites feraudianus</i>		
				<i>Gerhardtia provincialis</i>		
		<i>Gerhardtia sartousiana</i>				
		<i>Toxancyloceras vandenheckii</i>	<i>Barrancyloceras barremense</i>			
			<i>Toxancyloceras vandenheckii</i>			
	Early	Early	<i>Moutoniceras moutonianum</i>			
			<i>Kotetishvilia compressissima</i>			
<i>Nicklelesia pulchella</i>						
<i>Kotetishvilia nicklesi</i>						
<i>Taveraidiscus hugii auctororum</i>			<i>Psilotissotia colombiana</i>			
		<i>Taveraidiscus hugii auctororum</i>				

Figure 2: Biozonation of the Barremian and Aptian (Early Cretaceous) used in this work.

Order Nautilida AGASSIZ, 1847

Superfamily Nautiloidea BLAINVILLE, 1825

Family Cenoceratidae TINTANT & KABAMBA, 1983

Genus *Heminautilus* SPATH, 1927

(= *Vorticoceras* SCOTT, 1940; ? *Platynautilus*

YABE & OZAKI, 1953)

Type species: *Nautilus saxbii* MORRIS, 1848 [by original designation of SPATH (1927, p. 22)].

Discussion: the genus *Vorticoceras* SCOTT, 1940, is a synonym of *Heminautilus* SPATH, 1927, as established previously SCOTT (1943) and KUMMEL (1956). The genus *Platynautilus* YABE & OZAKI, 1953, is probably also a synonym of *Heminautilus* SPATH (see discussion in section V). The genus *Heminautilus* SPATH includes the species *H. boselliorum* DELANOY *et al.*, 2012, *H. rangei* (HOPPE, 1922), *H. sanctaerucis* CONTE, 1980, *H. saxbii* (MORRIS, 1848) [= *H. verneuilli* (VILANOVA, 1870); *H. tejeriensis* MARTÍNEZ & GRAUGES, 2006], *H. lallierianus* (ORBIGNY, 1841),

H. etheringtoni DURHAM, 1946, *H. stantoni* (SCOTT, 1940), *H. ? japonicus* sp. nov. and *H. ? tyosiensis* (YABE & OZAKI, 1953); its known stratigraphical distribution extends from the Early Barremian, *Kotetishvilia nicklesi* Zone, to the top of the Early Aptian, *Dufrenoyia furcata* Zone. It is present in Europe (Bulgaria, England, France, Hungary, Spain and Switzerland), North Africa (Egypt and Tunisia), Ethiopia, Japan, North America (USA [Arkansas], Mexico [Puebla and Durango states]), and northern South America (Colombia and Venezuela).

The taxon *Heminautilus akatsui* MATSUMOTO, 1980 (*in* MATSUMOTO *et al.*, 1980), from the Early Albian of Japan, shows an unusual stratigraphical position and ornamental and sutural characteristics very different from those classically present in the genus *Heminautilus* SPATH and in particular in its type species; it certainly belongs to a different genus. Its holotype is featured in this work (Pl. II, fig. 2).

Table 1: List of abbreviations used in the text.

AMNH	American Museum of Natural History, New York, United States
BEG	Bureau of Economic Geology, Austin, Texas, United States
BMNH	British Museum of Natural History, England
EM	École des Mines, Claude BERNARD University, Lyon, France
FSM	Faculté des Sciences of Marseille, France
GK	Kyushu University, Japan
GMMU	Geological Museum of Mansoura University, Egypt
GSUB	Geosciences Collection of the University of Bremen, Germany
HNHM	Hungarian Natural history Museum
IGM	Instituto de Geología, Universidad Nacional Autónoma de México
MB	Natural History Museum of Bâle, Switzerland
MCGL	Muséum Géologique Cantonal of Lausanne, Switzerland
MGB	Museu de Geologia de Barcelona, Spain
MGNR	Museo Geológico Nacional J. Royo y Gómez, Bogotá, Colombia
MHNA	Natural History Museum of Auxerre, France
MHNG	Natural History Museum of Geneva, Switzerland
MHNN	Natural History Museum of Neuchâtel, Switzerland
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum National d'Histoire Naturelle of Paris, France
MPL	Museo Paleontológico Laguna, Torreón, Coahuila State, Mexico
MPUC	Museum of Paleontology, California University, United States
MPUS	Museum of Paleontology, Sofia University, Bulgaria
MV	Museum of Valltorta, Spain
NMNS	National Science Museum, Tokyo, Japan
PNRL	Parc Naturel Régional du Lubéron, France
PUAB	Universitat Autònoma de Barcelona, Spain
UNCB	Colecciones Paleontológicas, Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá
UPMC	Pierre et Marie CURIE University, Paris, France
USNM	United States National Museum, Washington, United States

***Heminautilus boselliorum* DELANOY *et al.*, 2012**

Pl. II, fig. 3; Pl. III, figs. 1-3; Pl. IV, figs. 1-3;
 Pl. V, figs. 1-2; Pl. VI, figs. 1-2;
 Pl. VII, figs. 1-2, 4; Pl. VIII, figs. 1-3;
 Pl. IX, figs. 1-3

- ? 1975 *Heminautilus* sp. - SHIMANSKY, Pl. 27, fig. 4.
- pars 1995 *Heminautilus saxbii* (MORRIS, 1848) – NIKOLOV & PARASHKEVANOV, p. 65: no. K1 1693, K1 1694, non no. K1 6005, Pl. 5, fig. 1, 1a (= ? *H. sanctaecrucis* CONTE, 1980).
- 2002 *Heminautilus* aff. *saxbii* (MORRIS, 1848) - VERMEULEN, p. 37.
- 2012 *Heminautilus boselliorum* sp. nov. – DELANOY *et al.*, p. 157, Pl. 1, fig. 1; Pl. 2, figs. 1-2; Pl. 3, figs. 1-2; Pl. 4, fig. 2; Pl. 8, fig. 2; Pl. 9, fig. 2; Pl. 11, fig. 2; Pl. 12, fig. 1.
- 2013 *Heminautilus* sp. - FŐZY & SZENTE, p. 183.

Material studied (N = 13): specimens no. Mej01a, Mej02, Mej03, Mej11, coll. BAUDOUIN, no. RG2000, RG2001, RG2002a, b, coll. GONNET, no. LUS01, LUS02, coll. BOSELLI, no. MNHN.F.A52065, Early Barremian, *Nicklesia pulchella* Zone, La Lèque, Lussan (Gard, France); specimen no. MHNG GEPI 15935, *Nicklesia pulchella* Zone?, Escragnolles (Alpes-Maritimes, France); specimen no. 415950, coll. VERMEULEN, upper part of the *Kotetishvilia nicklesi* Zone, section no. 833, Comps-sur-Artuby (Var).

Type: the holotype (by original designation) is the specimen no. Mej01a, coll. BAUDOUIN, presented by DELANOY *et al.* (2012, Pl. 1, fig. 1a-c); a cast is deposited in the paleontology collections of the Muséum National d'Histoire Naturelle of Paris with the no. MNHN.F.A52064.

Geographical distribution: the species is known from France (departments of the Gard, the Var and the Alpes-Maritimes), Bulgaria and Hungary.

Table 2: Measurements of *Heminautilus boselliorum* DELANOY *et al.*, 2012.

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. Mej01a	156	89.4	56.3	0.57	0.36	0.63	15	0.1	0.17	-	-	-	-
	141.9	85.5	48.7	0.6	0.34	0.57	14	0.1	0.16	-	-	-	-
	122.2	73.3	36.5	0.6	0.3	0.5	12.3	0.1	0.17	16	56	0.29	0.76
	113.1	67	33.2	0.59	0.29	0.5	10.7	0.09	0.16	16	51	0.31	0.76
	-	50	26.1	-	-	0.52	8.6	-	0.17	14	35	0.4	0.7
	-	43.5	24.1	-	-	0.55	8.5	-	0.2	9.4	33	0.28	0.76
no. Mej02	139.3	74.4	44.5	0.53	0.32	0.6	12.4	0.09	0.17	-	-	-	-
	-	54	-	-	-	-	8	-	0.15	12	41	0.29	0.76
no. Mej03	133.5	c80	34	0.6	0.25	0.43	12.5	0.09	0.16	-	-	-	-
	102.8	c58	29.5	0.56	0.29	0.51	8.7	0.08	0.15	16.3	47	0.35	0.81
	95.2	53.8	29.3	0.57	0.31	0.54	8.2	0.09	0.15	15.5	45	0.34	0.84
no. Mej11	-	89.7	-	-	-	-	16.3	-	0.18	-	-	-	-
	-	70.1	37.9	-	-	0.54	13.1	-	0.19	11.1	58.3	0.19	0.83
no. RG2000	131.3	78.2	-	0.6	-	-	12.4	0.09	0.16	-	-	-	-
	112.3	71.2	-	0.63	-	-	11.3	0.1	0.16	14.9	52.2	0.29	0.73
	98.2	61.9	-	0.63	-	-	8.7	0.09	0.14	16.6	48.2	0.34	0.78
no. RG2001	148.8	87.4	46.6	0.59	0.31	0.53	-	-	-	-	-	-	-
	134.3	82.1	c32.6	0.61	0.24	0.4	c10.2	0.08	0.12	18.8	59.6	0.32	0.73
	-	52.4	c22.8	-	-	0.44	c4.5	-	0.09	9.4	40.4	0.23	0.77
no. RG2002a	155.8	92.8	55.5	0.6	0.36	0.6	14.2	0.09	0.15	-	-	-	-
	-	71	40.9	-	-	0.58	12.3	-	0.17	19.2	59.7	0.32	0.84
	-	63.3	33.2	-	-	0.52	11	-	0.17	18.2	51.4	0.35	0.81
no. RG2002b	153	82.2	c54.7	0.54	0.36	0.67	21.1	0.14	0.26	-	-	-	-
	132	82.1	c41.2	0.62	0.31	0.5	14.2	0.11	0.17	15.8	60.7	0.26	0.74
no. MNHN.F.A52065	65.7	c41	24.5	0.62	0.37	0.6	5	0.08	0.12	-	-	-	-
no. LUS01	148.7	83.8	45.9	0.56	0.31	0.55	18.5	0.12	0.22	-	-	-	-
	108.9	69	30.4	0.63	0.28	0.44	9.7	0.09	0.14	11.7	52.8	0.22	0.77
	92	58.9	-	0.64	-	-	7.6	0.08	0.13	11.8	44.7	0.26	0.76
no. LUS02	68.3	41.2	21.7	0.6	0.32	0.53	7.6	0.11	0.18	9.1	30.1	0.3	0.73
	-	26.5	16	-	-	0.6	4.4	-	0.17	5.1	20.5	0.25	0.77
no. MHNG GEPI 15935	128	81	-	0.63	-	-	15	0.12	0.19	-	-	-	-
	-	78	-	-	-	-	13.5	-	0.17	15	54	0.28	0.69
	-	65	-	-	-	-	9	-	0.14	14	46.5	0.3	0.72
no. 415950	83.5	47.3	26.1	0.57	0.31	0.55	7.4	0.09	0.16	-	-	-	-
	74.5	43.5	22.1	0.58	0.3	0.51	6.5	0.09	0.15	11.3	34.1	0.33	0.78
	-	28.6	19.6	-	-	0.69	5.3	-	0.19	8.8	22.6	0.39	0.79
no. K1 1693	-	85.6	43.4	-	-	0.51	13.5	-	0.16	-	-	-	-
	-	74.4	-	-	-	-	11.5	-	0.15	14.9	54.9	0.27	0.74
	-	54.1	-	-	-	-	-	-	-	13.3	43.3	0.31	0.8
no. K1 1694	-	30.4	17.9	-	-	0.59	6.3	-	0.21	5.9	22.7	0.26	0.75
	-	27.9	-	-	-	-	5.2	-	0.19	6	20.8	0.29	0.75
	-	23.3	-	-	-	-	-	-	-	5.5	18.7	0.29	0.8
no. M 2002.554	104.1	60.9	-	0.59	-	-	-	-	-	14.9	44.5	0.33	0.73
	79.1	45.4	-	0.57	-	-	-	-	-	10.5	32.6	0.32	0.72

Stratigraphical distribution: *Heminautilus boselliorum* DELANOY *et al.*, 2012, is present in the Early Barremian, upper part of the *Kotetishvilia nicklesi* Zone and *Nicklesia pulchella* Zone of southeast France, and in the lower part of the *Kotetishvilia compressissima* Zone in Hungary (specimen no. M 2002.554, coll. HNHM, Pl. IX, fig. 2, bed 126 of the Bersek quarry, Gerecse Mountains; FÖZY & JANSSEN, 2009). The Bulgarian specimens (coll. MPUS) no. K1 1693 (Pl. VIII, fig. 1; Pl. IX, fig. 1) and K1 1694 (Pl. VIII, fig. 2) (studied by NIKOLOV & PARASHKEVANOV, 1995, p. 65) come from the Early Barremian without more precision. The specimen no. MHNG GEPI 15935 (Pl. VII, fig. 1; Pl. IX, fig. 3) from Escragnolles (Alpes-Maritimes, France) is assumed to come from the *Nicklesia pulchella* Zone based upon the character of its matrix.

Dimensions (in mm): see Table 2.

Description: the studied specimens show a compressed section (E/H between 0.40 and 0.69) and a very involute conch, with convex flanks, with maximum thickness situated approximately at the bottom third. Until $D = 35$ mm the ventral region is slightly convex, becoming then clearly flat, with two angular edges. On the body chamber, the angular edges heighten as weak keels and give a clearly concave shape to the ventral region. In well preserved specimens, we also observe the presence of a very slight keel, wide and rounded, especially visible at the end of the phragmocone and the beginning of the body chamber.

Virtually none of the shells displays ornamentation. However, in the adult specimens, some weak rursiradiate ribs appear at the end of the body chamber, in the upper third of the flanks. Specimen no. MHNG GEPI 15935, from the *Nicklesia pulchella* Zone? of Escragnolles (Alpes-Maritimes), shows similar ornamentation which appears earlier on the body chamber. Its characteristics and stratigraphical position permits its assignment to *H. boselliorum* DELANOY *et al.*

The suture line (Fig. 3) contains a very wide, relatively shallow lateral lobe (P/L ranges between 0.19 and 0.40), a reduced umbilical saddle and an indented ventral lobe. The siphuncle, highly visible on specimens no. Mej11 (Pl. III, fig. 3c) and no. LUS02 (Pl. IV, fig. 3b) is located very low, near the dorsal edge of the section.

Variability: the sample ($N = 13$) studied here consists of sufficient well stratigraphically located specimens to allow a statistical analysis. The sample constitutes a quite homogeneous group, permitting us to estimate the intraspecific variability. The variability is minor and involves only the wideness of the conch and the morphology of the ventral region. The thickness of the shell varies from thin, in which the ratio E/H is between 0.40 and 0.50, to clearly

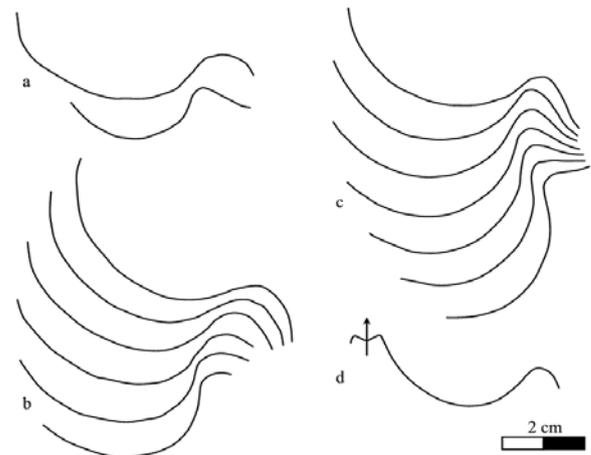


Figure 3: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Suture line of specimens no. Mej01, left side (a), MHNG GEPI 15935, right side (b), RG2001, left side (c) and Mej02, right side (d).

thicker in which E/H can exceed 0.60. The width of the ventral region is directly correlated to the thickness of the shell: in the thin forms M/H is between 0.10 and 0.15, while in thick morphs this ratio can exceed 0.25. Independently, the shape of the ventral region varies on the phragmocone from flat to slightly concave, with the presence or absence of a very slight central keel, generally towards the end of the phragmocone or the beginning of the body chamber. To a lesser extent, we also observe a certain variability in the the suture line, with a more or less deep lateral lobe, whose ratio P/L can vary from 0.19 to 0.40. Rather significant variations in its depth are sometimes observed in the same specimen at various diameters, without an obvious link to an ontogenic stage.

Discussion and comparisons: *Heminautilus boselliorum* DELANOY *et al.*, 2012, is a species very close to *H. saxbii* (MORRIS, 1848). However, it can be distinguished from *H. saxbii* (MORRIS) by a slightly less developed lateral lobe, with the average ratio P/L of 0.30 in *H. boselliorum* DELANOY *et al.*, and of 0.35 in *H. saxbii* (MORRIS). In reference to the ornamentation and form of the shell, it can be distinguished by the presence of a very slight keel on the ventral region of the best preserved specimens of *H. boselliorum* DELANOY *et al.* and a slightly differing section, as well as by ribbing which appears earlier on the body chamber of *H. saxbii* (MORRIS). *H. boselliorum* DELANOY *et al.* also occupies a stratigraphical position very different from that of *H. saxbii* (MORRIS, 1848); this last taxon is known only in the Early Aptian, *Deshayesites forbesi* Zone.

H. boselliorum DELANOY *et al.* is also similar to *H. sanctaerucis* CONTE, 1980, from the latest Barremian - Early Aptian, *Deshayesites forbesi* Zone. *H. sanctaerucis* CONTE can be easily distinguished by the presence of a strong median keel on the ventral region, as well as by

shoulders lining the ventral region which are clearly stronger on the body chamber of adult specimens.

Finally, *H. boselliorum* DELANOY *et al.* can be distinguished readily from *H. lallierianus* (ORBIGNY, 1841) from the Early Aptian by its far less developed lateral lobe [P/L between 0.35 and 0.50 in *H. lallierianus* (ORBIGNY)], its far less concave ventral region and its ontogenetically much later ribbing on the body chamber.

Heminautilus rangei (HOPPE, 1922)

Pl. VII, fig. 3; Pl. IX, figs. 4-5;
Pl. X, figs. 1-3; Pl. XI, figs. 1-2

pars 1916 *Nautilus lallieri* ORBIGNY, 1841 – DOUVILLÉ, p. 129, Pl. 17, figs. 2-4, 6, non fig. 5 [= *H. saxbii* (MORRIS, 1848)].

1922 *Nautilus rangei* nov. sp. - HOPPE, p. 144, Pl. 4, figs. 2-3.

2008 *Heminautilus lallierianus* (ORBIGNY, 1841) - ABU-ZIED, fig. 3, A-C.

Material studied (N = 4): specimens no. EM696, EM697, EM698, EM699, Late Barremian?, Bir Lagama (north Sinai, Egypt).

Type: HOPPE (1922) figured two specimens (Pl. 4, figs. 2-3) from "Ledschime" (north Sinai, Egypt; Fig. 4), without nomination of a holotype; the illustration of HOPPE (1922) is reproduced here on Pl. XI, figs. 1-2. These two specimens belonged to the RANGE collection, stored in the Geologisch-paläontologischen Institut der Universität Leipzig (Germany), but could not be found and can be considered as lost. The original figures of HOPPE (1922, reproduced here Pl. XI, figs. 1-2) prevent the development of a complete picture of the species. In particular, the shape of the ventral region is difficult to construe and gives the impression of being strongly concave. The specimens no. EM696, EM697, EM698 and EM699, as well as specimen no. TK25/15 (Pl. X, fig. 3) illustrated by ABU-ZIED (2008), show that the ventral region of this species is not strongly concave. Furthermore, in the original depictions the specimen in lateral view is fragmentary, so that only the ornamentation of the upper part of the flanks is visible. In the absence of specimens attributable to this species in the RANGE collection, we erect as a neotype the specimen no. EM699 (Pl. X, fig. 1), illustrated by DOUVILLÉ (1916, Pl. 17, fig. 6a-b) and stored in the collection of the École des Mines (Université Claude BERNARD, Lyon, France). It comes from Bir Lagama, a locality very close to that of the type specimens displayed in HOPPE (1922) (Fig. 4), and is probably from the Late Barremian, *Gerhardtia sartousiana* or *Imerites giraudi* zones (cf. section "stratigraphical distribution").

By means of this neotype, completed by the paratypes no. EM696, EM697 and EM698 showing the various ontogenetic stages of the species, we can define the specific characteristics of *H. rangei* HOPPE, 1922, more accurately than using the original depiction of HOPPE, 1922.

Geographical distribution: the species is known only in the north of the Sinai (Egypt). All the known specimens come from a very restricted area (Fig. 4): those presented by HOPPE (1922) come from "Ledschime", a location corresponding approximately (RANGE, 1920, Pl. 8) to the section of El Tourkumanyia described by ABU-ZIED (2008), the source of the specimen no. TK25/15 (coll. GMMU); the neotype no. EM699 and the three paratypes no. EM696, EM697 and EM698 come from Bir Lagama, situated slightly further west in the same massif.

Stratigraphical distribution: both specimens shown in HOPPE (1922) were dated, according to him, from the Vraconian (= latest Albanian). However, the presence in the same formation ("Ledschime-Horizont") of representatives of the genus *Pseudohaploceras* HYATT, 1900, close to *P. douvillei* (FALLOT, 1920) (= *Puzosia kossmati* sp. nov. in HOPPE, 1922, p. 140, Pl. 3, fig. 10) indicates a very likely Late Barremian age. The specimen no. TK25/15 (Pl. X, fig. 3) illustrated by ABU-ZIED (2008) comes from the Late Barremian, *Subpulchellia oehlerti* Zone [= *Mogharaceras priscum* (DOUVILLÉ, 1916)]. According to BULOT *et al.* (2011), *Mogharaceras priscum* (DOUVILLÉ) is a Late Barremian species, probably present in an interval included in *Gerhardtia sartousiana* to *Imerites giraudi* zones. ABU-ZIED (2008) also indicates, without figures, the presence of *Heminautilus lallierianus* (ORBIGNY, 1841) [= *Heminautilus rangei* (HOPPE, 1922) or *Heminautilus saxbii* (MORRIS, 1848) ?] in the Early Aptian. Specimens depicted by DOUVILLÉ are attributed by him to the Aptian without more precision. However, compared with the specimens shown by ABU-ZIED (2008), which presents exactly the same ornamental and morphological characteristics, such a stratigraphical position seems doubtful and these specimens are more likely from the Late Barremian. These specimens were also reallocated to the Barremian by MAHMOUD (1955, p. 12). Thus *Heminautilus rangei* (HOPPE, 1922) is clearly present in the Late Barremian, in the *Gerhardtia sartousiana* Zone or *Imerites giraudi* Zone; its supposed presence in the Early Aptian is unproven and might stem from the confusion with another species collected in higher levels as attested by the presence of *Heminautilus saxbii* (MORRIS, 1848) among the material collected by DOUVILLÉ (1916).

Dimensions (in mm): see Table 3.

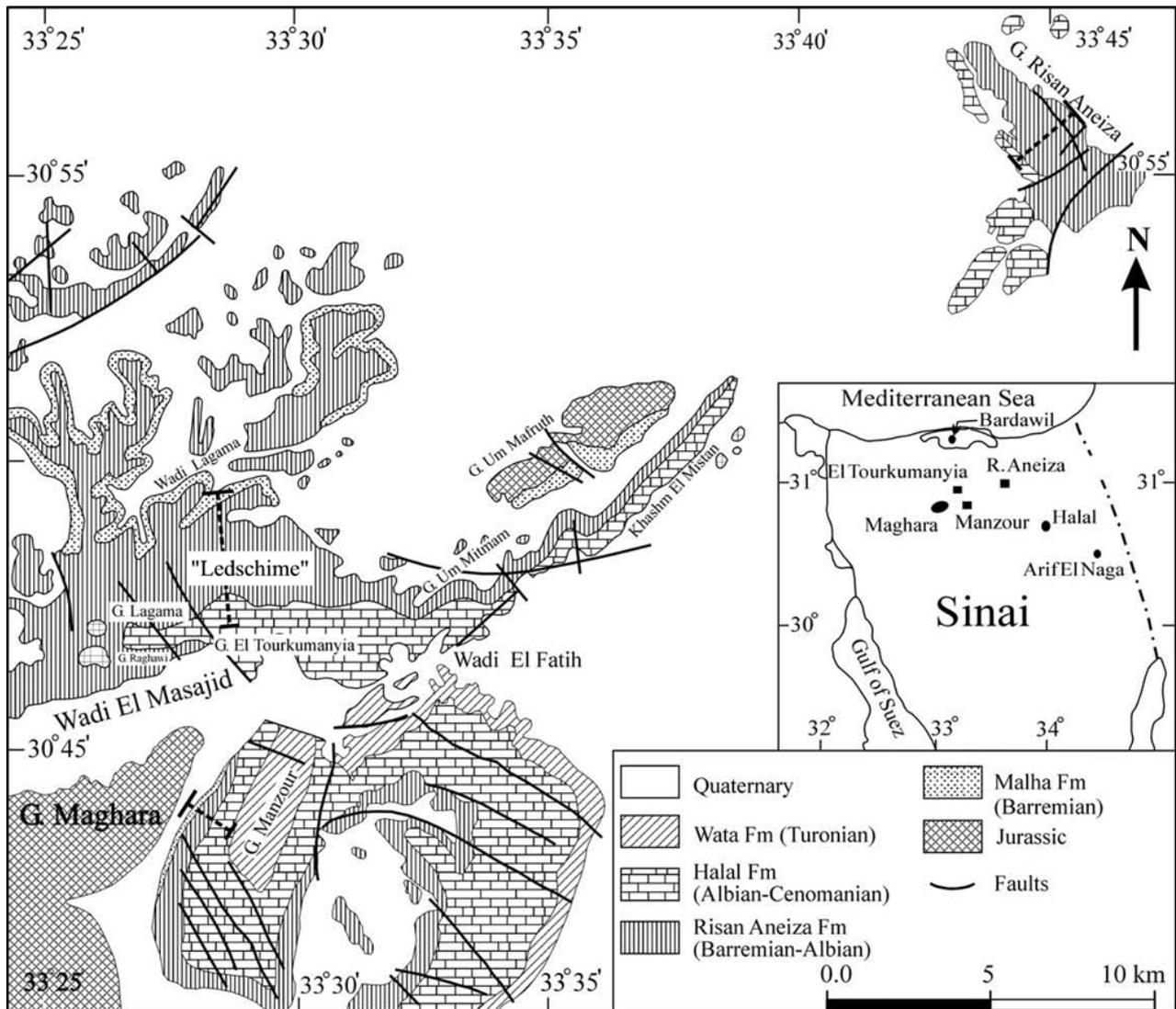


Figure 4: Geological map of the north Sinai (Egypt). Modified from ABU-ZIED (2008).

Table 3: Measurements of *Heminautilus rangei* (HOPPE, 1922).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Type specimen (HOPPE, 1922)	125	80	50	0.64	0.4	0.63	-	-	-	-	-	-	-
Neotype no. EM699	135.8	87.8	-	0.65	-	-	16.1	0.12	0.18	-	-	-	-
	94.1	55.5	38.4	0.59	0.41	0.69	10.4	0.11	0.19	-	-	-	-
no. EM698	72.5	43.6	28.7	0.6	0.4	0.66	6.3	0.09	0.14	9.6	35	0.27	0.8
	52.8	34.8	22.5	0.66	0.43	0.65	5.3	0.1	0.15	7.5	28	0.27	0.8
no. EM697	59	38	24.6	0.64	0.42	0.65	5.6	0.09	0.15	-	-	-	-
	46.3	28.8	18.5	0.62	0.4	0.64	4.7	0.1	0.16	6.1	23.5	0.26	0.82
	32.3	19.8	13.9	0.61	0.43	0.7	3.5	0.11	0.18	4.1	16.4	0.25	0.83
no. EM696	35	24.7	15.6	0.71	0.45	0.63	3.8	0.11	0.15	-	-	-	-
no. TK25/15 (ABU-ZIED, 2008)	125	74	41	0.59	0.33	0.55	12	0.1	0.16	-	-	-	-

Description: the four specimens of the collection of the École des Mines, all illustrated by DOUVILLÉ (1916, Pl. 17) as *Nautilus lallierianus* ORBIGNY, 1841, provide precise knowledge about the ontogeny and the characteristics of this species. The neotype no. EM699, preserved with at least a part of its body chamber, probably represents the adult stage of the species.

With a diameter of up to about 20 mm, no ornamentation is visible with the exception of fine longitudinal striae on the flanks and the ventral region, visible on the shell of the paratype no. EM696 (Pl. IX, fig. 4). The section is oval, with rounded flanks and ventral region. Beyond this diameter, the section changes and becomes trapezoidal; flanks flatten and converge on the ventral region which very gradually becomes flat, with the appearance of a slight ventro-lateral shoulder. At the same time, the ribbing appears, consisting of broad ribs arising near the umbilical border and whose aboral edge follows a flat slope while the adoral edge is clearly more abrupt. Ribs are radial or slightly rursiradiate in the lower half of the flanks, becoming strongly rursiradiate beyond, and then fading approaching the ventral region. With growth, these ribs become broader and their point of appearance moves higher on the flanks. From approximately $D = 70$ mm, the ventral region is clearly flat (specimen no. EM698, Pl. IX, fig. 5; Pl. X, fig. 2). Finally, in the adult specimens (no. EM699, Pl. X, fig. 1; no. TK25/15, Pl. X, fig. 3), ribs appear slightly before the middle of flanks; they are very broad, flat, and barely separated by a narrow groove. They become irregular in their spacing, delineation and point of appearance on the flanks. The ventral region is lined by strong shoulders, giving to the ventral region a slightly to clearly concave shape (for example in the specimen illustrated by HOPPE (1922) Pl. 4, fig. 3; reproduced here Pl. XI, fig. 2). We also observe fine growth lines there forming a rounded chevron (specimen no. EM699, Pl. X, fig. 1b). Finally, at the end of the preserved part of the neotype no. EM699, a wide and slightly raised keel appears on the ventral region.

The suture line (Fig. 5), easily observable on specimens no. EM697 and no. EM698, shows a relatively undeveloped, rather narrow lateral saddle and a wide and shallow lateral lobe (P/L between 0.25 and 0.27). It crosses the ventral region straight, without forming a ventral lobe. The siphuncle, visible on specimens no. EM696 and no. EM697, is situated near the dorsal edge of the section.

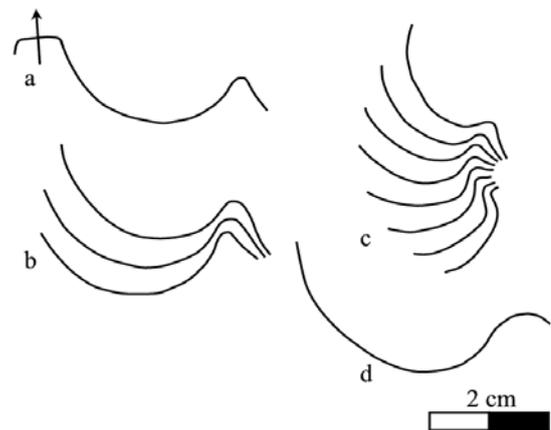


Figure 5: *Heminutilus rangei* (HOPPE, 1922). Suture line of specimens no. EM698, right side (a-b), EM697, left side (c) and of the unregistered specimen, right side (d) figured by HOPPE (1922; Pl. 4, fig. 2).

Discussion and comparisons: the very characteristic ornamentation of *Heminutilus rangei* (HOPPE, 1922) differentiates it immediately from most of the other species of the genus *Heminutilus* SPATH, 1927, where the ornamentation is absent or only present on the adoral part of the body chamber, with much narrower rounded ribs.

However, some characteristics of the shell of *H. rangei* (HOPPE), in particular the pattern of its suture line and the shape of its ventral region, indicate that this species is close to *H. boselliorum* DELANOY *et al.*, 2012, and *H. sanctaecrucis* CONTE, 1980. In *H. sanctaecrucis* CONTE the median keel is consistently well developed in all specimens, whereas in *H. rangei* (HOPPE) it is observable in one specimen, the neotype no. EM699, but less developed than *H. sanctaecrucis* CONTE.

H. rangei (HOPPE) is also similar to *H. ? japonicus* sp. nov., in particular its slightly concave ventral region, ornamented with fine growth lines, as well as its very similar stratigraphical position in the Late Barremian. However the suture line and the ribbing of *H. ? japonicus* sp. nov. are very different, which distinguishes it easily from *H. rangei* (HOPPE).

H. rangei (HOPPE) also shows some affinities with the Japanese species *H. ? tyosiensis* (YABE & OSAKI, 1953), because of its slightly concave ventral region lined with two strong shoulders, and the presence of comparable ribbing on a part of the phragmocone. However, *H. ? tyosiensis* (YABE & OSAKI) can be easily distinguished from *H. rangei* (HOPPE) by its much wider ventral region, its quickly fading ribbing and a different suture line, with a clearly deeper lateral lobe. *H. ? tyosiensis* (YABE & OSAKI) also occupies a very different stratigraphical and geographical position (= *Dufrenoyia furcata* Zone, Japan).

***Heminautilus sanctaecrucis* CONTE, 1980**

- Pl. XI, figs. 3-5; Pl. XII, figs. 1-3;
 Pl. XIII, figs. 1-3; Pl. XIV, figs. 1-2;
 Pl. XV, fig. 1; Pl. XVI, fig. 1
- 1858** *Nautilus lallierianus* ORBIGNY, 1841 - F.-J. PICTET & CAMPICHE, p. 148, Pl. 19, fig. 6a-c.
- 1967** *Xenocheilus lallierianus* (ORBIGNY, 1841) - DIMITROVA, p. 18, Pl. 4, fig. 1.
- 1980** *Heminautilus sanctaecrucis* sp. nov. - CONTE, p. 137, Pl. 1, figs. 1-2, 4a.
- 1985** *Heminautilus* cf. *sanctaecrucis* CONTE, 1980 - CONTE, p. 30, Pl. 1, fig. 6.
- 1989** *Heminautilus sanctaecrucis* CONTE, 1980 - CONTE, p. 30, Figs. 5-7.
- pars **1995** *Heminautilus sanctaecrucis* CONTE, 1980 - NIKOLOV & PARASHKEVANOV, p. 63, Pl. 1, fig. 1?; Pl. 2, fig. 1?; Pl. 3, figs. 1?, 2, 2a; Pl. 4, figs. 1, 1a, 2, 2a.
- ? **1995** *Heminautilus saxbii* (MORRIS, 1848) - NIKOLOV & PARASHKEVANOV, p. 65, Pl. 5, fig. 1, 1a.
- 2009** *Heminautilus sanctaecrucis* CONTE, 1980 - LEHMANN *et al.*, p. 904, Pl. 1, figs. 6.
- 2010** *Heminautilus sanctaecrucis* CONTE, 1980 - CONTE, p. 118, Figs. 6-7.

Material studied (N = 4): specimen no. MCGL 20747, Early Aptian, *Deshayesites forbesi* Zone, Sainte-Croix (Switzerland); specimens no. MHNG GEPI 15936, MHNN 26904, Early Aptian, *Deshayesites forbesi* Zone, La Presta, Val-de-Travers (Switzerland); specimen no. Bw599, coll. FSM, Late Barremian, *Imerites giraudi* Zone, *Pseudocrioceras waagenoides* Subzone, bed 78, Les Caniers, La Bédoule (Bouches du Rhône, France).

Type: the holotype (by original designation of CONTE, 1980, p. 138) is the specimen no. MCGL 20747 illustrated by F.-J. PICTET & CAMPICHE (1858) Pl. 19, fig. 6, as *Nautilus lallierianus* ORBIGNY, 1841. Stored in the Muséum Géologique Cantonal of Lausanne (Switzerland), it is depicted anew in this work Pl. XI, fig. 3.

Geographical distribution: the species is known in Switzerland, Bulgaria, southeast France and Tunisia.

Stratigraphical distribution: the holotype comes from the base of the "Marnes jaunes de la Vraconne" (F.-J. PICTET & CAMPICHE, 1858) at Sainte-Croix (Switzerland), immediately above the Urgonian Limestone. The bottom third of these Jura marls corresponds to the Grunten Member defined in the Helvetic Domain, whose base is attributed to the *Deshayesites forbesi* Zone (A. PICTET *et al.*, 2009, p. 492-493). The Bulgarian specimens (coll. MPUS) studied by DIMITROVA (1967) and NIKOLOV & PARASHKEVANOV (1995) are attributed to the Late Barremian

(specimens no. K1 6001, K1 6002, K1 6003, K1 6004) and to the Early Aptian (specimen no. K1 1692) without more precision. In Tunisia the species is present in the Early Aptian, *Deshayesites oglanlensis* Zone (specimen no. GSUB C4035, LEHMANN *et al.*, 2009). In southeast France, the range of *Heminautilus sanctaecrucis* CONTE, 1980, seems to be latest Barremian/earliest Aptian. The unregistered specimen of the FRASALI collection (Pl. XV, fig. 1) comes from the Coustellet quarry (Vaucluse, France), situated in the units 3 and 4 of the series of the southwest region of the Vaucluse mountains and attributed to the Early Bedoulian by MASSE (1976, p. 38-42). The specimen no. 131H (coll. GESBERT, Pl. XI, fig. 5; Pl. XII, fig. 1) comes from the col des Abeilles, Monieux (Vaucluse, France), and corresponds to the unit of the "Calcaires fins des Colombières" of the Nesque series, attributed to the latest Barremian/earliest Aptian by MASSE (1976, p. 34-38). At La Bédoule (Bouches du Rhône, France) the species was collected at the top of the Late Barremian, *Imerites giraudi* Zone, *Pseudocrioceras waagenoides* Subzone (specimen no. Bw599, Pl. XII, fig. 2; Pl. XIII, fig. 1). *Heminautilus sanctaecrucis* CONTE, 1980, is thus present from the Late Barremian, top of the *Imerites giraudi* Zone, to the Early Aptian, *Deshayesites forbesi* Zone.

Dimensions (in mm): see Table 4.

Description: the studied specimens show a relatively compressed section, with slightly rounded flanks, where maximum thickness is in the lower third. The ventral region is rather narrow and flat or slightly concave. It is lined by two more or less strongly angular ventrolateral shoulders and shows a clear median keel, especially visible in the last whorl. On the specimen no. Bw599, this median keel seems to appear where the diameter is about 85 mm, later than on the holotype where it is visible from approximately $D = 60$ mm. The ornamentation is absent on almost all the shell; we observe however some sinuous ribs present only at the adoral part of the body chamber of adult specimens (specimen no. 131H, Pl. XII, fig. 1). The body chamber is only partially preserved on the holotype and probably for this reason there are no ribs present.

The suture line is slightly sinuous, with a shallow lateral lobe (P/L most of the time between 0.20 and 0.35). It crosses the ventral region without forming a ventral lobe, except when the ventral region shows strong shoulders, where it forms a shallow ventral lobe (Fig. 6). The siphuncle, visible on specimen no. MHNN 26904 (Pl. XIII, fig. 3), is situated in the dorsal half of the section.

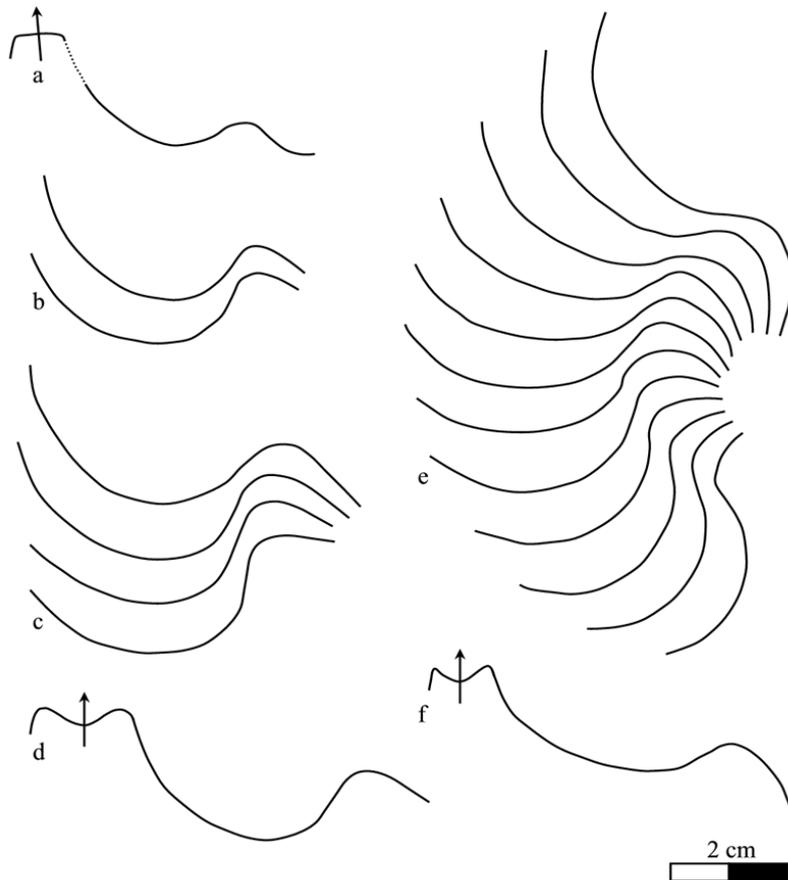
Table 4: Measurements of *Heminautilus sanctaecrucis* CONTE, 1980.

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H	
Holotype no. MCGL 20747	96.3	55.4	34	0.58	0.35	0.61	9.8	0.1	0.18	-	-	-	-	
	86.3	51	26.8	0.59	0.31	0.53	8.7	0.10	0.17	-	-	-	-	
	69.2	41.3	21.9	0.6	0.32	0.53	7.2	0.10	0.17	-	-	-	-	
	-	-	-	-	-	-	-	-	-	-	7	34	0.21	-
	-	-	-	-	-	-	-	-	-	-	9.5	34	0.28	-
no. BW599	126.1	72.4	-	0.57	-	-	9.5	0.08	0.13	-	-	-	-	
	104.3	60.1	-	0.58	-	-	8.2	0.08	0.14	11	48.2	0.23	0.8	
	-	48.2	-	-	-	-	6.8	-	0.14	7.3	37.7	0.19	0.78	
Unregistered specimen (coll. FRASALI)	154.1	92.9	45.4	0.6	0.29	0.49	17.9	0.12	0.19	-	-	-	-	
	-	-	-	-	-	-	-	-	-	7.2	49.9	0.14	-	
no. 131H	170	90	-	0.53	-	-	-	-	-	-	-	-	-	
	-	78	-	-	-	-	-	-	-	20	52	0.38	0.67	
	-	60	-	-	-	-	-	-	-	20	42	0.48	0.7	
no. K1 1692 (NIKOLOV & PARASHKEVANOV, 1995)	133	80	53	0.6	0.4	0.66	12	0.09	0.15	16	47	0.34	0.59	
	-	58	-	-	-	-	-	-	-	14	39	0.36	0.67	
no. K1 6001 (NIKOLOV & PARASHKEVANOV, 1995)	147	97	59	0.66	0.4	0.61	13	0.09	0.13	-	-	-	-	
no. K1 6003 (NIKOLOV & PARASHKEVANOV, 1995)	109	67	-	0.61	-	-	-	-	-	-	-	-	-	
	-	55	-	-	-	-	-	-	-	13	37	0.35	0.67	
no. K1 6005 (NIKOLOV & PARASHKEVANOV, 1995)	53	35	24	0.66	0.45	0.69	4	0.08	0.11	-	-	-	-	

Description: the studied specimens show a relatively compressed section, with slightly rounded flanks, where maximum thickness is in the lower third. The ventral region is rather narrow and flat or slightly concave. It is lined by two more or less strongly angular ventro-lateral shoulders and shows a clear median keel, especially visible in the last whorl. On the specimen no. Bw599, this median keel seems to appear where the diameter is about 85 mm, later than on the holotype where it is visible from approximately D = 60 mm. The ornamentation is absent on almost all the shell; we observe however some sinuous ribs present only at the adoral part of the body chamber of adult specimens (specimen no. 131H, Pl. XII, fig. 1). The body chamber is only partially preserved on the holotype and probably for this reason there are no ribs present.

The suture line is slightly sinuous, with a shallow lateral lobe (*P/L* most of the time between 0.20 and 0.35). It crosses the ventral region without forming a ventral lobe, except when the ventral region shows strong shoulders, where it forms a shallow ventral lobe (Fig. 6). The siphuncle, visible on specimen no. MHNN 26904 (Pl. XIII, fig. 3), is situated in the dorsal half of the section.

The specimen no. K1 6001, shown by NIKOLOV & PARASHKEVANOV (1995) and depicted anew (Pl. XIV, fig. 1; Pl. XVI, fig. 1), is tentatively attributed to *Heminautilus sanctaecrucis* CONTE, 1980. It differs from other representatives of the species by the presence of clear rursiradiate ribbing on the top of the flanks of the body chamber and by the shape of its ventral region, lined by two very strong ventro-lateral ridges. This last characteristic may be a consequence of the different mode of preservation of this specimen, where the shell is very well preserved on the ventral region because it is recrystallized, while the other specimens are preserved as internal molds.



◀ **Figure 6:** *Heminutilus sanctaerucis* CONTE, 1980. Suture line of specimens no. MCGL 20747, right side (a), 131H, right side (b), K1 1692, left side (c, d) and Bw599, left side (e, f).

Discussion and comparisons: *Heminutilus sanctaerucis* CONTE, 1980, is a species close to *H. lallierianus* (ORBIGNY, 1841) and *H. saxbii* (MORRIS, 1848). It can be distinguished from both taxa by its suture line, since the lateral lobe is clearly shallower [P/L is mostly between 0.20 and 0.35 while it is generally between 0.30 and 0.40 for *H. saxbii* (MORRIS) and between 0.35 and 0.50 for *H. lallierianus* (ORBIGNY)], as well as by the appearance of a keel on the ventral region proximal to the body chamber. *H. sanctaerucis* CONTE can also be distinguished from *H. lallierianus* (ORBIGNY) by a less concave ventral region and by the almost total absence of ornamentation. *H. sanctaerucis* CONTE also shows numerous affinities with *H. boselliorum* DELANOY *et al.*, 2012, with a similar suture line, an identical section and the same type of ornamentation visible at the adoral part of the body chamber. The two can be distinguished by the ventral keel, well defined on the main part of the shell in *H. sanctaerucis* CONTE while it is very discreet or absent in *H. boselliorum* DELANOY *et al.*

The shape of the ventral region of *H. sanctaerucis* CONTE is also similar to *H. rangei* (HOPPE, 1922), but can readily be distinguished from it by the absence of ornamentation on the flanks of the main part of the shell.

***Heminutilus* aff. *sanctaerucis* CONTE, 1980**

Pl. XII, fig. 4

Material studied (N = 1): specimen no. 415951, coll. BAUDOUIN (donated by VERMEULEN), Late Barremian, *Gerhardtia sartousiana* Zone, base of the *Hemihoplites feraudianus* Subzone, bed 165/041, Angles (Alpes-de-Haute-Provence, France).

Dimensions (in mm): see Table 5.

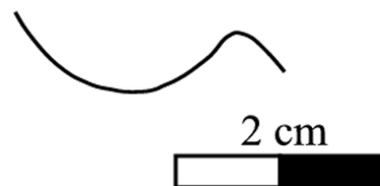


Figure 7: *Heminutilus* aff. *sanctaerucis* CONTE, 1980. Suture line of specimen no. 415951, right side.

Table 5: Measurements of *Heminautilus* aff. *sanctaecrucis* CONTE, 1980.

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
no. 415951	58.1	35	-	0.6	-	-	4.3	0.07	0.12	-	-	-	-
	-	28.6	14.7	-	-	0.51	4.5	-	0.16	6.2	21.1	0.29	0.74

Description: small incomplete specimen, consisting of part of the phragmocone and the beginning of the body chamber. The section is narrow, with maximum thickness in the lower third of the flanks, with a flat ventral region with angular edges, and slightly rounded flanks where no ornamentation is visible. On the ventral region, there is a visible yet relatively undeveloped median keel.

The suture line is sinuous, with a wide, round and relatively shallow lateral lobe (Fig. 7). The ventral lobe, difficult to observe, seems shallow or absent. The position of the siphuncle is not visible.

Discussion and comparisons: this specimen has a stratigraphical position intermediate between *Heminautilus boselliorum* DELANOY *et al.*, 2012, and *H. sanctaecrucis* CONTE, 1980. The suture line and the section of *H. aff. sanctaecrucis* CONTE are identical to those observed in *H. boselliorum* DELANOY *et al.* and *H. sanctaecrucis* CONTE; *H. aff. sanctaecrucis* CONTE can be distinguished from *H. boselliorum* DELANOY *et al.* by its clearly visible ventral keel, but it is weaker than the one observed in *H. sanctaecrucis* CONTE. Its fragmentary state does not allow us to be more precise on its taxonomic identification.

Heminautilus saxbii (MORRIS, 1848)

Pl. XV, fig. 2; Pl. XVI, figs. 2-3;
Pl. XVII, figs. 1-3; Pl. XVIII, figs. 1-3;
Pl. XIX, figs. 1-3; Pl. XX, figs. 1-3;
Pl. XXI, figs. 1-4; Pl. XXII, figs. 1-3;
Pl. XXIII, figs. 1-4; Pl. XXIV, figs. 1-3;
Pl. XXV, figs. 1-4; Pl. XXVI, figs. 1-3;
Pl. XXXI, fig. 3

- 1848** *Nautilus saxbii* nov. sp. - MORRIS, p. 106, unnumbered fig.
1870 *Nautilus verneuilli* nov. sp. - VILANOVA, Pl. 3, fig. 4.
pars **1916** *Nautilus lallieri* ORBIGNY, 1841 - DOUVILLÉ, p. 129, Pl. 17, fig. 5, non figs. 2-4, 6 [= *H. rangei* (HOPPE, 1922)].
1956 *Heminautilus saxbii* (MORRIS, 1848) - KUMMEL, p. 434, Pl. 10, figs. 1-2.
1964 *Heminautilus saxbii* (MORRIS, 1848) - KUMMEL, p. K454, Fig. 335, 2a-b.
1980 *Heminautilus saxbii* (MORRIS, 1848) - CONTE, p. 139, Pl. 1, fig. 4b.
1985 *Heminautilus saxbii* (MORRIS, 1848) - CONTE, p. 30, Fig. 4.

1988 *Heminautilus lallierianus* (ORBIGNY, 1841) - GOMEZ-ALBA, p. 356, Pl. 175, fig. 3.

non **1995** *Heminautilus saxbii* (MORRIS, 1848) - NIKOLOV & PARASHKEVANOV, p. 65, Pl. 5, fig. 1, 1a (= ? *H. sanctaecrucis* CONTE, 1980).

non **2002** *Heminautilus* aff. *saxbii* (MORRIS, 1848) - VERMEULEN, p. 37 (= *H. boselliorum* DELANOY *et al.*, 2012).

2003 *Heminautilus saxbii* (MORRIS, 1848) - DONOVAN & BAKER, Fig. 3b, f.

? **2006** *Heminautilus lallierianus* (ORBIGNY, 1841) - ALY, p. 101, Pl. 1, figs. 1-3.

2006 *Heminautilus saxbii* (MORRIS, 1848) - MARTÍNEZ & GRAUGES, p. 22, Figs. 3b, 5a-d.

2006 *Heminautilus tejeriensis* nov. sp. - MARTÍNEZ & GRAUGES, p. 24, Figs. 3c, 4a, 6a, 7a-b.

pars **2007** *Heminautilus saxbii* (MORRIS, 1848) - CONTE, p. 11, photos 1-2, 11, 12?.

2007 *Heminautilus saxbii* (MORRIS, 1848) - MORENO *et al.*, Figs. 16-17.

2010 *Heminautilus saxbii* (MORRIS, 1848) - CONTE, p. 117, Figs. 1-2, 4-5.

2011 *Heminautilus saxbii* (MORRIS, 1848) - PEROPADRE MEDINA, Fig. 3.12A, B.

Material studied (N = 101): specimens no. EM700, Early Aptian?, Bir Lagama, Gabal Maghara (Egypt); no. PNRL 1189, Early Aptian, *Deshayesites forbesi* Zone, Murs (Vaucluse, France); no. PM1, PM2, PM3, PM4, PM5, PM6, PM13, PM3N1, PM3N2, PM3N11, PMBb2, coll. MNHN, no. A-114, A-117, A-119, A-122, A-127, A-131, A-140, A-144, A-145, A-146, AG-3, AG-13, JM-26, JM-34, JM-36, JM-37, JM-38, M-8, PUAB 5905, PUAB 48011, PUAB 48013, PUAB 48018, PUAB 48027, PUAB 48035, PUAB 48037, PUAB 48040, PUAB 48042, PUAB 48043, PUAB 48044, PUAB 48046, PUAB 48064, PUAB 48074, PUAB 48080, PUAB 48092, PUAB 48098, PUAB 48106, PUAB 48125, PUAB 48127, PUAB 48128, PUAB 48133, PUAB 48143, PUAB 48158, PUAB 48163, PUAB 48164, PUAB 48165, PUAB 48169, PUAB 48202, PUAB 48205, PUAB 48215, PUAB 48223, PUAB 48232, PUAB 48242, PUAB 48246, PUAB 48254, PUAB 48255, PUAB 48256, PUAB 48261, PUAB 48275, PUAB 48277, PUAB 48278, PUAB 48282, PUAB 48288, PUAB 48292, PUAB 48295, PUAB 48304, PUAB 48314, PUAB 48316, PUAB 48318, PUAB 48321, PUAB 48322, PUAB 48328, PUAB 48366, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain); no. PUAB

48177, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Alacón, Province of Teruel (Spain); no. PUAB 89786, PUAB 89787, PUAB 89788, PUAB 89790, PUAB 89791, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Galve, Province of Teruel (Spain); no. PUAB 88767, PUAB 88770, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Tolodella, Maestrat Basin (Spain); no. MV 423.1, MV 428.2, MV 428.3, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mola Murada, Maestrat Basin (Spain); no. PUAB 88762, PUAB 88763, Early Aptian, Cabo Marls Formation, *Deshayesites forbesi* Zone, Lo Pui, Organyà Basin (Spain); no. PUAB 88372, PUAB 88373, Early Aptian, Patrocínio Formation, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Cuchía, Basque Cantabrian Basin (Spain); no. MB RE1962A, Early Aptian, Tibú Formation, Seboruco section (east of Mérida, Venezuela).

Type: the holotype (by monotypy) is the specimen illustrated by MORRIS (1848) p. 106, stored in the SAXBY collection at the British Museum of Natural History with the no. BMNH 47019. It comes from the Early Aptian of the Isle of Wight (England) and is depicted anew here Pl. XVI, fig. 2.

Geographical distribution: the species is known from England, France, Spain and Egypt. It may be present in Venezuela (specimen no. MB RE1962A, Pl. XXIV, fig. 3).

Stratigraphical distribution: the type of MORRIS comes from the Lower Greensand, "Crackers' group" of Atherfield, Isle of Wight and is dated as the *Deshayesites forbesi* Zone; it most certainly comes from the Lower Lobster Beds Formation (SIMPSON, written communication, 2013), corresponding to the bottom of the *Roloboceras hambrovi* Subzone (SIMPSON, 1985; CASEY *et al.*, 1998). All the Spanish specimens studied here come from levels dated as the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone (MORENO *et al.*, 2007). The Egyptian specimen no. EM700 is assigned by DOUVILLE (1916) to the Early Aptian, as well as the specimens displayed in ALY (2006); however, a stratigraphical position in the top of the Late Barremian cannot be excluded. The specimens quoted by NIKOLOV & PARASHKEVANOV (1995; coll. MPUS) in the Early Barremian (no. K1 1693 and no. K1 1694, displayed anew Pl. VII, figs. 1-2; Pl. IX, fig. 1) and the Late Barremian (no. K1 6005) belong to taxa different from *Heminautilus saxbii* (MORRIS, 1848). The specimen no. K1 6005 probably belongs to *H. sanctaerucis* CONTE, 1980; however, without a visible suture line and with a very weak ventral keel

confirmation is not possible. The specimens no. K1 1693 and no. K1 1694 belong to *H. boseliorum* DELANOY *et al.*, 2012, as does the specimen of *H. aff. saxbii* (MORRIS) of VERMEULEN (2002, p. 37; figured here Pl. VI, fig. 2; Pl. VII, fig. 4) in the *Kotetishvilia nicklesi* Zone. The specimens of *H. saxbii* (MORRIS) of southeast France [specimens displayed by CONTE (2007, 2010) and specimen no. 12576, coll. FSM, shown Pl. XXIV, fig. 1; Pl. XXV, fig. 1] come from the Early Aptian without more precision. Finally, specimen no. MB RE1962A, tentatively attributed to *H. saxbii* (MORRIS), comes from the Seboruco section (Venezuela). This section also yielded ammonites attributed to the genus *Roloboceras* CASEY, 1954, by RENZ (1982, p. 19), but which more likely belong to the genus *Chelonoceras* HYATT, 1903; the stratigraphical position of this specimen can thus be situated approximately in the top of the Early Aptian.

Heminautilus saxbii (MORRIS, 1848) is thus a species present in the Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, in particular in the bottom of the subzone. The existence of older or more recent representatives of the species remains doubtful and remains to be confirmed.

Dimensions (in mm): see Table 6.

Description: the studied specimens show a relatively compressed section (*E/H* generally between 0.50 and 0.70), with slightly convex flanks, with maximum thickness located in the lower third of the flanks. The ventral region is relatively narrow; convex in the inner whorls (specimen no. PUAB 48158, Pl. XXIII, fig. 3), it quickly becomes slightly concave or flat, with angular edges, or very slightly convex on the body chamber of some specimens (holotype of *Heminautilus tejeriensis* MARTÍNEZ & GRAUGES, 2006, no. PUAB 48292; Pl. XXVI, fig. 1). In the most internal whorls, rursiradiate fine growth riblets are visible on the flanks and the ventral region where they form an angular chevron (no. PUAB specimen 48158, Pl. XXXI, fig. 3); no other ornamentation is visible on the phragmone. On the body chamber of adult specimens, strongly rursiradiate ribs appear in the upper half of the flanks, more or less broad and high (specimens no. A-127, Pl. XVII, fig. 2; no. MV 428.3, Pl. XIX, fig. 1; no. MV 428.2, Pl. XXI, fig. 1; no. PUAB 48042, Pl. XXIII, fig. 1).

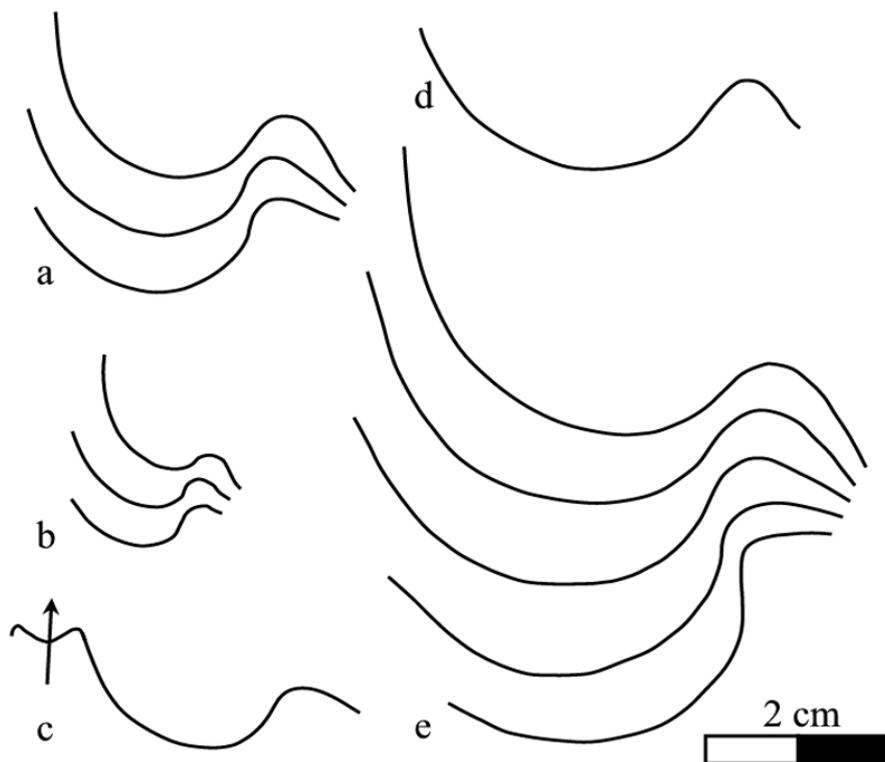
The suture line is sinuous (Fig. 8), with a wide and relatively deep lateral lobe (*P/L* generally between 0.30 and 0.40) and a fairly narrow and angular lateral saddle, becoming round with growth. The ventral lobe is shallow or absent.

Table 6: Measurements of *Heminautilus saxbii* (MORRIS, 1848).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. BMNH 47019	86	56	32	0.65	0.37	0.57	7	0.08	0.13	-	-	-	-
	69	42	-	0.61	-	-	8	0.12	0.19	13	31	0.42	0.74
	52	31	-	0.60	-	-	6	0.12	0.19	8	23	0.35	0.74
no. EM700	128.6	83.6	49.2	0.65	0.38	0.59	12.2	0.09	0.15	-	-	-	-
	90.6	57.8	35.1	0.64	0.39	0.61	9.8	0.11	0.17	14.5	42.4	0.34	0.73
no. PNRL 1189	-	87.2	43.3	-	-	0.50	13.7	-	0.16	-	-	-	-
	-	77.5	30.5	-	-	0.39	9.7	-	0.13	14.7	57.1	0.26	0.74
no. 12576	197	118	50	0.60	0.25	0.42	-	-	-	-	-	-	-
	145	100	-	0.69	-	-	-	-	-	32	70	0.46	0.70
	-	89	-	-	-	-	-	-	-	25	67	0.37	0.74
no. PM1	138	85	51	0.62	0.37	0.60	20	0.14	0.24	-	-	-	-
	-	63	36	-	-	0.57	9	-	0.14	17	49	0.35	0.78
	-	46	30	-	-	0.65	8	-	0.17	11	36	0.31	0.78
no. PM2	126	-	45	-	0.36	-	16	0.13	-	-	-	-	-
	98	-	33	-	0.34	-	7	0.07	-	14	45	0.31	-
no. PM3	129	81	54	0.63	0.42	0.67	19	0.15	0.23	-	-	-	-
no. PM4	81	53	29	0.65	0.36	0.55	9	0.11	0.17	13	38	0.34	0.72
	67	43	25	0.64	0.37	0.58	8	0.12	0.19	10	31	0.32	0.72
no. PM5	144	c87	55	0.60	0.38	0.63	20	0.14	0.23	-	-	-	-
	-	c58	35	-	-	0.60	8	-	0.14	15	40	0.38	0.69
no. PM6	125	80	-	0.64	-	-	11	0.09	0.14	-	-	-	-
	106	67	36	0.63	0.34	0.54	8	0.08	0.12	17	50	0.34	0.75
	81	50	31	0.62	0.38	0.62	7	0.09	0.14	14	40	0.35	0.80
no. PM13	146	87	-	0.60	-	-	18	0.12	0.21	-	-	-	-
	109	65	38	0.60	0.35	0.58	8	0.07	0.12	18	49	0.37	0.75
	-	52	32	-	-	0.62	7	-	0.13	12	37	0.32	0.71
no. PM3N1	-	74	39	-	-	0.53	11	-	0.15	20	54	0.37	0.73
	-	53	31	-	-	0.58	8	-	0.15	14	37	0.38	0.70
no. PM3N2	118	75	38	0.64	0.32	0.51	10	0.08	0.13	-	-	-	-
	114	72	38	0.63	0.33	0.53	9	0.08	0.13	20	54	0.37	0.75
	74	48	29	0.65	0.39	0.60	7	0.09	0.15	12	35	0.34	0.73
no. PM3N11	97	60	36	0.62	0.37	0.60	11	0.11	0.18	-	-	-	-
	72	44	29	0.61	0.40	0.66	8	0.11	0.18	9	34	0.26	0.77
no. PMBb2	-	51	29	-	-	0.57	7	-	0.14	11	41	0.27	0.80
	-	41	26	-	-	0.63	6	-	0.15	10	33	0.30	0.80
no. A-114	106.3	66.2	-	0.62	-	-	10.5	0.10	0.16	16.6	49.2	0.34	0.74
	-	43.7	33.3	-	-	0.76	9.5	-	0.22	9.4	29.9	0.31	0.68
no. A-145	116.7	70.0	43.5	0.6	0.37	0.62	11.6	0.10	0.17	14.6	49.9	0.29	0.71
	85.5	49.9	-	0.58	-	-	10.8	0.13	0.22	12.9	37.1	0.35	0.74
no. A-146	84.9	50.1	-	0.59	-	-	8.1	0.10	0.16	14.4	38.9	0.37	0.78
	72.5	41.8	-	0.58	-	-	-	-	-	11.8	33.3	0.35	0.8
	-	26.2	-	-	-	-	-	-	-	6.7	20.5	0.33	0.78
no. AG-3	99.8	61.9	-	0.62	-	-	8.0	0.08	0.13	17.2	45.7	0.38	0.74
no. AG-13	52.7	30.8	23.1	0.58	0.44	0.75	7.2	0.14	0.23	8.2	22.8	0.36	0.74
	-	21.2	-	-	-	-	5.7	-	0.27	5.0	15.8	0.32	0.74

no. JM-34	117.1	73.1	47.8	0.62	0.41	0.65	12.3	0.10	0.17	22.5	51.3	0.44	0.7
	-	32.9	-	-	-	-	7.5	-	0.23	9.1	25.4	0.36	0.77
no. JM-36	127	74	50	0.58	0.39	0.68	-	-	-	-	-	-	-
no. M-8	-	67.0	39.1	-	-	0.58	10.0	-	0.15	15.7	48.0	0.33	0.72
no. PUAB 5905	-	56.2	-	-	-	-	8.7	-	0.15	12.5	38.6	0.32	0.69
	-	33.6	-	-	-	-	5.4	-	0.16	6.6	25.0	0.26	0.74
no. PUAB 48011	99.8	59.3	-	0.59	-	-	9.4	0.09	0.16	16.2	43.8	0.37	0.74
no. PUAB 48013	113.0	73.0	-	0.65	-	-	-	-	-	16.5	51.4	0.32	0.7
	-	44.9	30.4	-	-	0.68	8.4	-	0.19	11.1	33.8	0.33	0.75
	-	36.9	-	-	-	-	7.7	-	0.21	8.5	28.0	0.3	0.76
no. PUAB 48027	94.1	59.8	-	0.64	-	-	8.2	0.09	0.14	15.1	44.1	0.34	0.74
no. PUAB 48040	-	48.9	32.3	-	-	0.66	8.5	-	0.17	13.9	36.5	0.38	0.75
	-	39.2	27.6	-	-	0.7	8.1	-	0.21	10.8	30.5	0.35	0.78
no. PUAB 48042	-	34.2	25.4	-	-	0.74	7.5	-	0.22	7.9	25.1	0.32	0.73
	126	69	49	0.55	0.39	0.71	17	0.13	0.25	-	-	-	-
	c99	59	-	0.60	-	-	12	0.12	0.20	17	45	0.38	0.76
no. PUAB 48044	-	44	-	0.44	-	-	-	-	-	13	33	0.39	0.75
	120	68	45	0.57	0.38	0.66	-	-	-	-	-	-	-
	99.2	61.7	35.1	0.62	0.35	0.57	8.3	0.08	0.13	18.7	44.6	0.42	0.72
	85.6	49.8	34.3	0.58	0.4	0.69	9.5	0.11	0.19	14.7	35.1	0.42	0.71
no. PUAB 48046	119.3	40.9	31.4	0.34	0.26	0.77	8.4	0.07	0.21	11.0	29.6	0.37	0.72
	136	80	60	0.59	0.44	0.75	-	-	-	-	-	-	-
no. PUAB 48098	-	47.4	31.3	-	-	0.66	9.4	-	0.20	13.5	39.3	0.34	0.83
no. PUAB 48128	153	90	49	0.59	0.32	0.54	-	-	-	-	-	-	-
no. PUAB 48143	-	27.6	17.5	-	-	0.63	4.7	-	0.17	8.4	19.6	0.43	0.71
no. PUAB 48163	60.8	35.1	-	0.58	-	-	7.6	0.13	0.22	8.0	25.5	0.31	0.73
no. PUAB 48164	81.5	52.9	34.3	0.65	0.42	0.65	7.7	0.09	0.15	14.0	36.1	0.39	0.68
	76.7	47.9	29.9	0.62	0.39	0.62	6.7	0.09	0.14	11.6	34.7	0.33	0.72
no. PUAB 48205	-	54.6	35.4	-	-	0.65	8.5	-	0.16	14.8	33.5	0.44	0.61
no. PUAB 48215	109.8	69.5	37.2	0.63	0.34	0.53	8.9	0.08	0.13	14.7	51.6	0.28	0.74
	-	51.0	-	-	-	-	8.9	-	0.17	11.3	37.2	0.3	0.73
	-	37.9	-	-	-	-	8.2	-	0.22	8.6	29.8	0.29	0.78
no. PUAB 48202	-	51.9	36.1	-	-	0.7	7.8	-	0.15	15.3	36.1	0.43	0.7
	-	36.1	27.3	-	-	0.76	-	-	-	11.7	30.1	0.39	0.83
no. PUAB 48246	-	49.4	34.4	-	-	0.7	-	-	-	14.0	36.5	0.38	0.74
no. PUAB 48254	-	63.9	-	-	-	-	9.6	-	0.15	12.4	46.1	0.27	0.72
no. PUAB 48255	-	63.5	37.8	-	-	0.59	9.0	-	0.14	18.2	43.5	0.42	0.68
	-	42.0	26.4	-	-	0.63	7.5	-	0.18	11.8	30.9	0.38	0.74
no. PUAB 48256	-	49.4	31.5	-	-	0.64	8.1	-	0.16	13.9	38.7	0.36	0.78
no. PUAB 48261	-	71.9	44.0	-	-	0.61	9.2	-	0.13	19.1	46.6	0.41	0.65
	-	65.3	40.6	-	-	0.62	8.8	-	0.13	17.6	42.2	0.42	0.65
	-	56.8	35.0	-	-	0.62	8.2	-	0.14	16.2	39.2	0.41	0.69
no. PUAB 48275	-	76.7	-	-	-	-	12.4	-	0.16	16.5	52.3	0.32	0.68
no. PUAB 48292	128	76	56	0.59	0.44	0.74	17	0.13	0.22	-	-	-	-
	111.8	68.6	38.5	0.61	0.34	0.56	10.5	0.09	0.15	14.6	49.6	0.29	0.72
	109.0	63.5	37.5	0.58	0.34	0.59	9.9	0.09	0.16	15.2	49.6	0.31	0.78
no. PUAB 48295	-	53.8	-	-	-	-	8.5	-	0.16	16	42	0.38	0.78

no. PUAB 48366	-	65.2	-	-	-	-	11.8	-	0.18	15.3	48.3	0.32	0.74
	-	61.4	-	-	-	-	9.4	-	0.15	14.2	47.1	0.3	0.77
no. PUAB 89788	-	66.0	-	-	-	-	10.3	-	0.16	16.1	45.5	0.35	0.69
	-	60.0	34.4	-	-	0.57	9.9	-	0.16	15.1	42.8	0.35	0.71
	-	46.5	29.3	-	-	0.63	19.1	-	0.41	13.0	35.9	0.36	0.77
no. PUAB 89791	-	62.2	31.6	-	-	0.51	9.7	-	0.16	16.7	47.0	0.35	0.76
no. PUAB 48009 (MARTINEZ & GRAUGES, 2006)	85	52	33	0.61	0.39	0.63	-	-	-	-	-	-	-
no. PUAB 48093 (MARTINEZ & GRAUGES, 2006)	147	80	56	0.54	0.38	0.70	-	-	-	-	-	-	-
no. PUAB 48095 (MARTINEZ & GRAUGES, 2006)	65	42	26	0.65	0.40	0.62	-	-	-	-	-	-	-
Specimen photo 11 (CONTE, 2007)	-	73	-	-	-	-	-	-	-	20	58	0.34	0.79
Specimen Fig. 3.12 (PEROPADRE MEDINA, 2011)	-	58	-	-	-	-	12	-	0.21	16	48	0.33	0.83
Holotype of <i>Nautilus verneuilli</i> VILANOVA, 1870	118	76	38	0.64	0.32	0.50	2	0.02	0.03	-	-	-	-
	112	71	-	0.63	-	-	4	0.04	0.06	18	54	0.33	0.76
	89	57	-	0.64	-	-	5	0.06	0.09	14	47	0.30	0.82
no. MB RE1962A	-	47	-	-	-	-	-	-	-	10	32	0.31	0.68
	-	45	-	-	-	-	7	-	0.16	12	32	0.38	0.71



◀ **Figure 8:** *Heminutilus saxbii* (MORRIS, 1848). Suture line of specimens no. BMNH 47019, right side (a-c), EM700, left side (d) and PM1, right side (e).

The siphuncle, particularly visible in the specimen no. PMBb2 (Pl. XVII, fig. 3), is located between the dorsum and the center of the section, near the dorsal region.

Variability: the number of specimens of *Heminutilus saxbii* (MORRIS, 1848) studied here, with a particularly important sample from Josa, Province of Teruel (Spain), allows estimation of the variability of the species. The

variability essentially concerns the width of the conch (Fig. 9), the shape of the ventral region, the ornamentation and the plan of the suture line. The thickness of the shell varies from compressed forms where E/H is about 0.50 (specimen no. PUAB 89791) to wide forms where E/H reaches 0.76 (specimen no. PUAB 48044, Pl. XXVI, fig. 2). The shape of the ventral region varies from slightly concave to flat, even very slightly convex. The ornamentation of the body

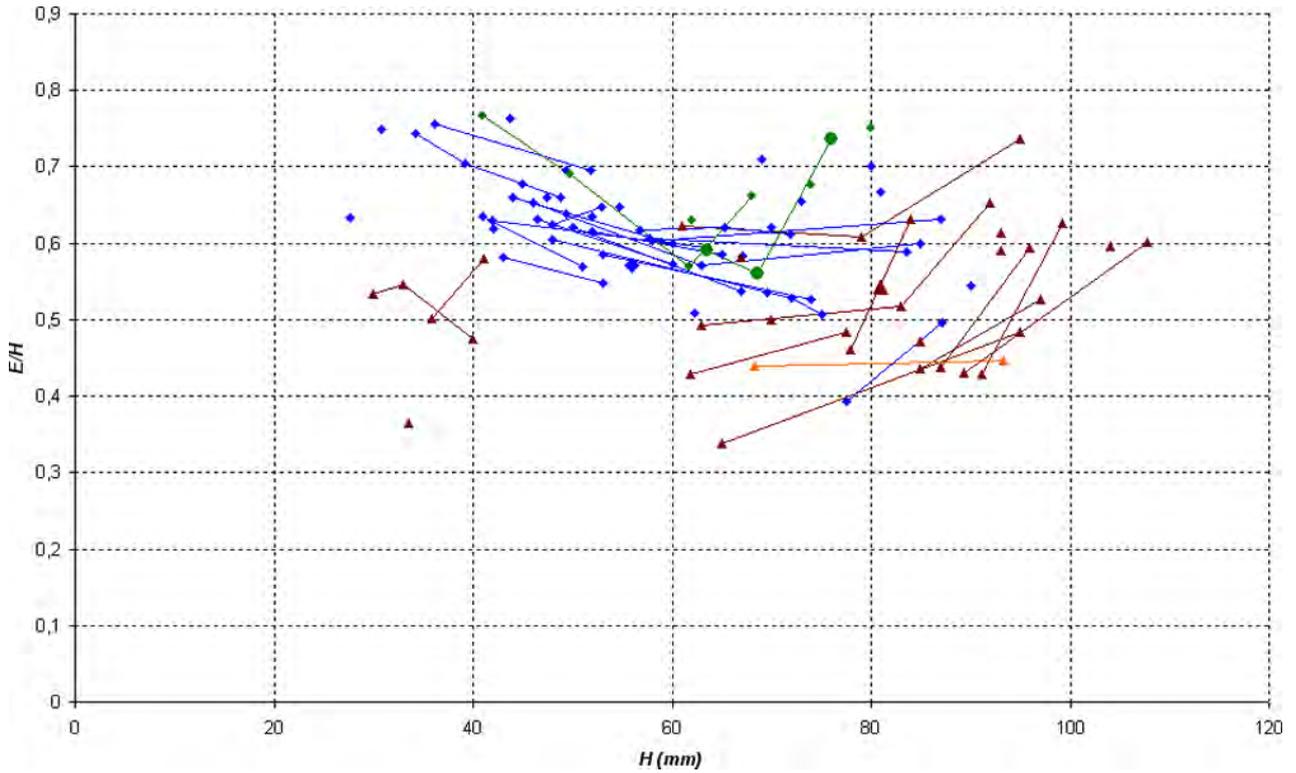


Figure 9: E/H in function of H . In red, *Heminutilus lallierianus* (ORBIGNY, 1841); in orange, *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841); in blue, *Heminutilus saxbii* (MORRIS, 1848); in green, specimens attributed to *Heminutilus tejeriensis* MARTÍNEZ & GRAUGES, 2006 [= *H. saxbii* (MORRIS)] by MARTÍNEZ & GRAUGES (2006). When taken at various diameters, measurements of the same specimen are connected by a line. The enlarged symbols represent the respective type specimens.

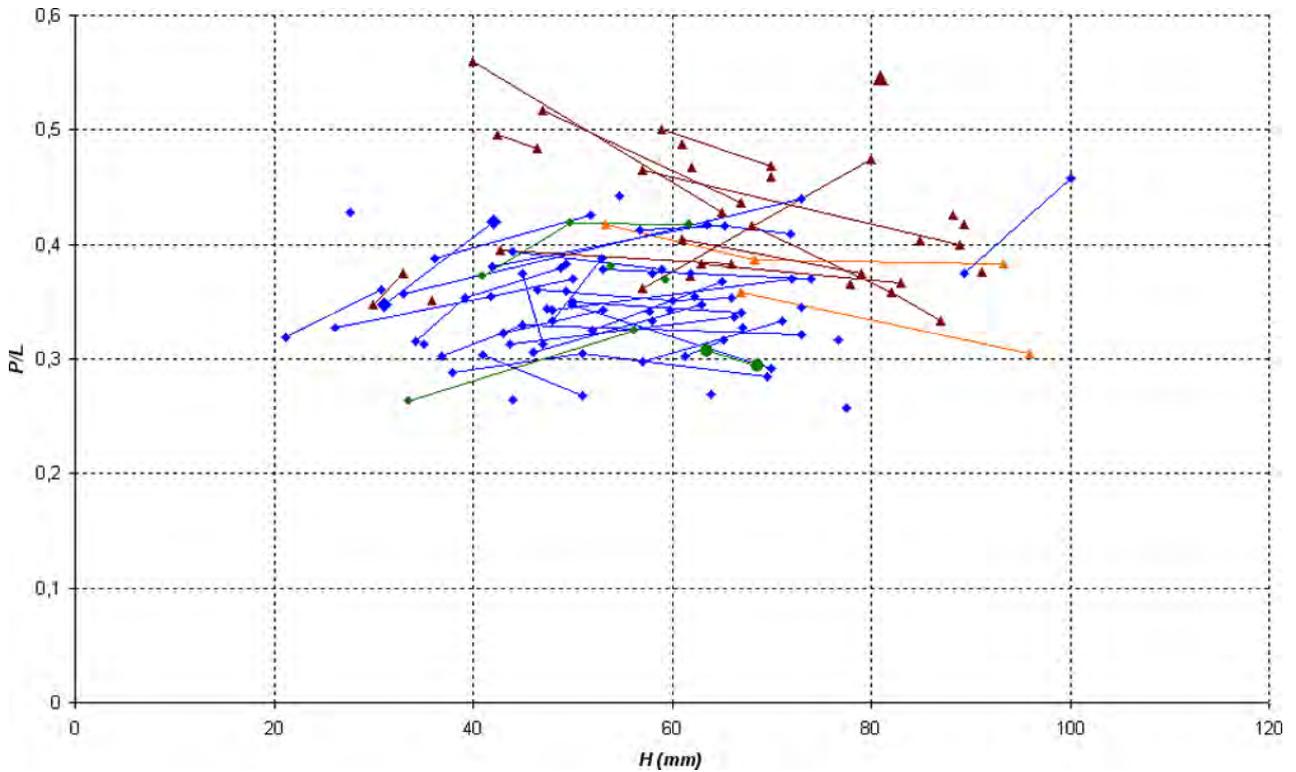


Figure 10: P/L in function of H . In red, *Heminutilus lallierianus* (ORBIGNY, 1841); in orange, *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841); in blue, *Heminutilus saxbii* (MORRIS, 1848); in green, specimens attributed to *Heminutilus tejeriensis* MARTÍNEZ & GRAUGES, 2006 [= *H. saxbii* (MORRIS)] by MARTÍNEZ & GRAUGES (2006). When taken at various diameters, measurements of the same specimen are connected by a line. The enlarged symbols represent the respective type specimens.

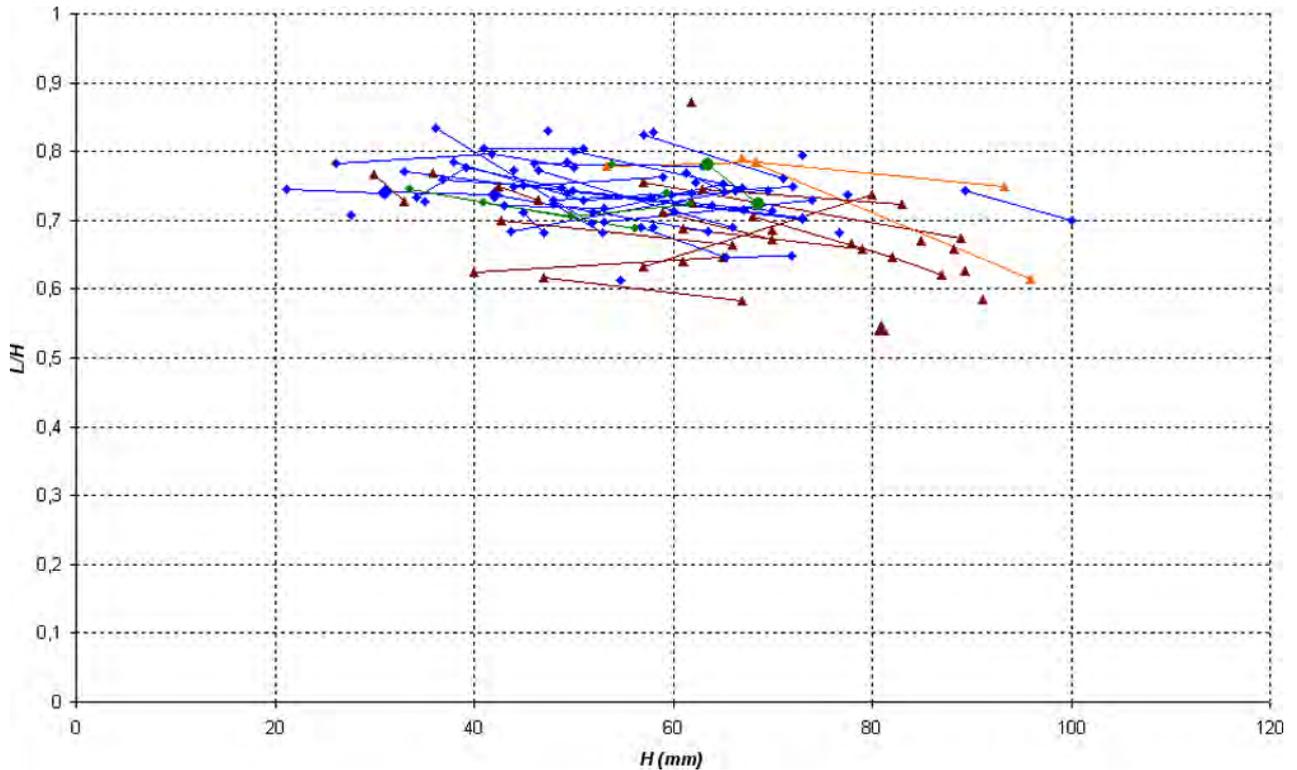


Figure 11: L/H in function of H . In red, *Heminutilus lallierianus* (ORBIGNY, 1841); in orange, *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841); in blue, *Heminutilus saxbii* (MORRIS, 1848); in green, specimens attributed to *Heminutilus tejeriensis* MARTÍNEZ & GRAUGES, 2006 [= *H. saxbii* (MORRIS)] by MARTÍNEZ & GRAUGES (2006). When taken at various diameters, measurements of the same specimen are connected by a line. The enlarged symbols represent the respective type specimens.

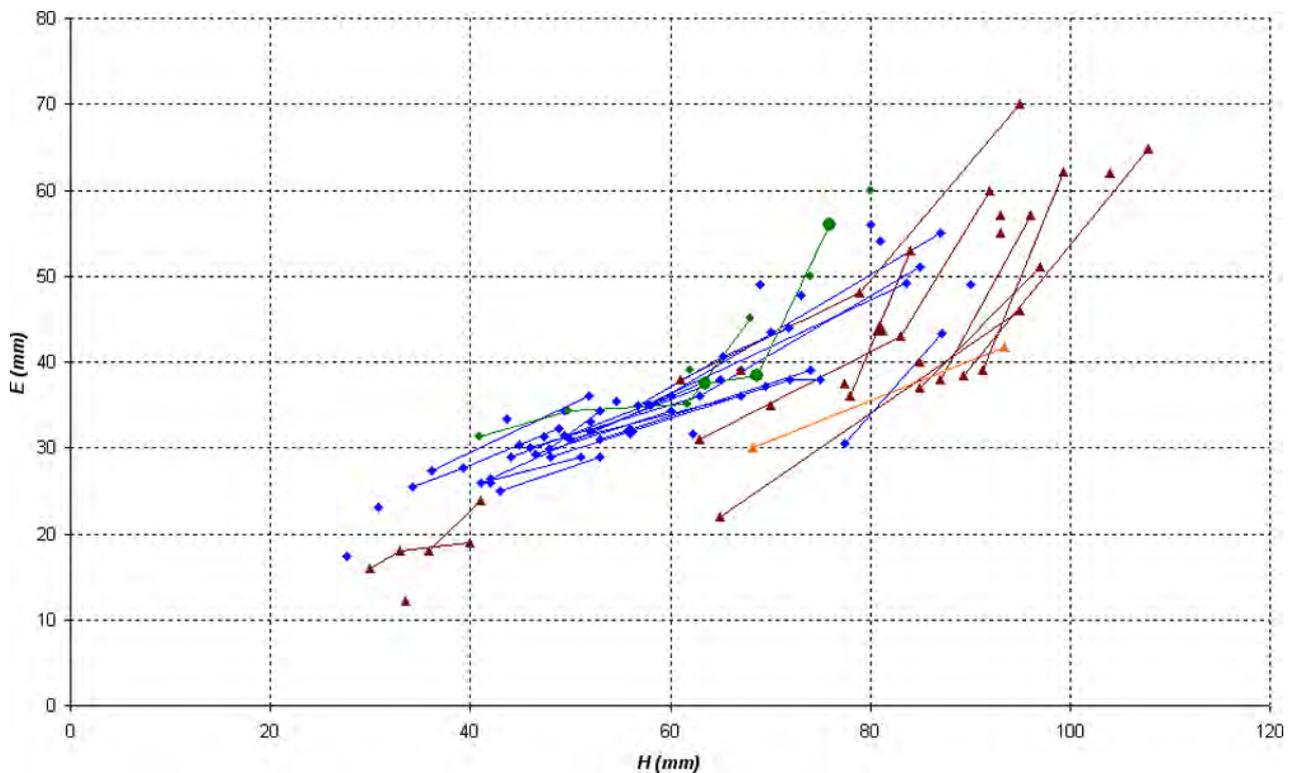


Figure 12: E in function of H . In red, *Heminutilus lallierianus* (ORBIGNY, 1841); in orange, *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841); in blue, *Heminutilus saxbii* (MORRIS, 1848); in green, specimens attributed to *Heminutilus tejeriensis* MARTÍNEZ & GRAUGES, 2006 [= *H. saxbii* (MORRIS)] by MARTÍNEZ & GRAUGES (2006). When taken at various diameters, measurements of the same specimen are connected by a line. The enlarged symbols represent the respective type specimens.

chamber of the adult specimens is also rather variable, being almost smooth (specimen no. PM13, Pl. XXII, fig. 1), or with broad and well defined ribs (specimens no. MV 428.3, Pl. XIX, fig. 1; no. MV 428.2, Pl. XXI, fig. 1), with intermediate forms with very visible but narrower and weaker ribs (specimen no. PUAB 48042, Pl. XXIII, fig. 1). Finally, the suture line shows a lateral lobe of variable depth, with P/L between 0.26 (specimen no. PM3N11, Pl. XXI, fig. 2) and 0.44 (specimen no. JM-34, Pl. XIX, fig. 3), and a shallow to absent ventral lobe.

Discussion and comparisons: *Heminautilus saxbii* (MORRIS, 1848) is particularly close to *Heminautilus lallierianus* (ORBIGNY, 1841). The latter can be distinguished from *H. saxbii* (MORRIS) by its clearly more sinuous suture line, showing a deeper and narrower lateral lobe (P/L generally near 0.35 - 0.50; Fig. 10; L/H generally between 0.70 and 0.80 in *H. saxbii* (MORRIS), between 0.60 and 0.75 in *H. lallierianus* (ORBIGNY); Fig. 11) and a wider and rounded lateral saddle, as well as by the shape of the strongly concave ventral region which contains a deep ventral lobe. The shell of *H. lallierianus* (ORBIGNY) is also more compressed (Fig. 12) than that of *H. saxbii* (MORRIS), with E/H generally between 0.40 and 0.60 in *H. lallierianus* (ORBIGNY) and between 0.50 and 0.70 in *H. saxbii* (MORRIS). According to numerous authors these species are synonyms (ORBIGNY, 1850; F.-J. PICTET & CAMPICHE, 1858; DOUVILLE, 1916; SCOTT, 1943) while other later authors consider them distinct (CONTE, 1980, 1985, 2007; MARTÍNEZ & GRAUGES, 2006). In Europe both taxa occupy very close stratigraphical positions within the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone. This leads us to two possible hypotheses: either the taxa represent two morphological poles of the same relatively variable species, or they represent two distinct species.

The study of numerous specimens coming from the section of Josa (Province of Teruel, Spain) establishes that, of these specimens, almost all are unambiguously morphologically attributable to *H. saxbii* (MORRIS) and that the morphologies of *lallierianus* (ORBIGNY) type are almost absent. These taxa do not appear to coexist and occupy slightly different stratigraphic positions in Europe within the *Roloboceras hambrovi* Subzone. On the Isle of Wight, the holotype and an important population of *H. saxbii* (MORRIS) were collected in the Lower Lobster Beds Formation (SIMPSON, written communication, 2013) and are thus situated in the bottom of the *Roloboceras hambrovi* Subzone (SIMPSON, 1985; CASEY *et al.*, 1998). The population of *H. saxbii* (MORRIS) from the section of Josa comes from a slightly condensed level attributed to the *Roloboceras hambrovi* Subzone (MORENO *et al.*, 2007); however, the

dominance of the genus *Roloboceras* CASEY, 1954, and the scarcity of the genus *Megatyloceras* HUMPHREY, 1949, among Roloboceratinae of this level indicate a stratigraphical position in the bottom of the *Roloboceras hambrovi* Subzone (equivalent to the Lower Lobster Beds Formation of the Isle of Wight). On the other hand, the small population of *H. lallierianus* (ORBIGNY) of Le Teil and Viviers (Ardèche, France), where no typical specimen of *H. saxbii* (MORRIS) is known, is associated with numerous *Megatyloceras* HUMPHREY and is probably situated at the top of the *Roloboceras hambrovi* Subzone (equivalent of the Upper Lobster Beds Formation of the Isle of Wight; CASEY *et al.*, 1998).

So, although the two taxa are undoubtedly phylogenetically very close, they never coexist in the localities studied here. Consequently, *H. lallierianus* (ORBIGNY) represents a species separate from *H. saxbii* (MORRIS), which it probably replaces within the *Roloboceras hambrovi* Subzone in Europe.

On the other hand, the important sample from Josa allows us to consider *Heminautilus tejeriensis* MARTÍNEZ & GRAUGES, 2006, as a junior synonym of *H. saxbii* (MORRIS, 1848). In the original description, *H. tejeriensis* MARTÍNEZ & GRAUGES was characterized essentially by the shape of its ventral region, flat or very slightly convex, as well as by the absence of a ventral lobe, while *H. saxbii* (MORRIS) shows a slightly concave to flat ventral region, with a shallow ventral lobe. Other than the ventral region, the suture lines of both taxa are identical. However, these slight differences appear to represent only minor intraspecific variability within the one species. Indeed, we frequently observe, on the same specimen [in particular in the holotype of *H. saxbii* (MORRIS)], some suture lines forming a lobe at the passage of the ventral region while others cross it straight, or even form a slight convexity (specimen no. PUAB 48044, Pl. XXV, fig. 4; Pl. XXVI, fig. 2). Most of the specimens attributed to *H. tejeriensis* MARTÍNEZ & GRAUGES show a flat ventral region identical to that of the holotype of *H. saxbii* (MORRIS). Only the holotype of *H. tejeriensis* MARTÍNEZ & GRAUGES shows a very slight convexity that solely affects the ventral region of the body chamber; this singular characteristic does not appear to justify a differentiation at the species level. Furthermore, all specimens attributed to *H. tejeriensis* MARTÍNEZ & GRAUGES come from the Province of Teruel (Spain) where they are associated with numerous clearly coeval specimens of *H. saxbii* (MORRIS). The contemporaneity of these two taxa and minimal morphological differences lead us to consider them as the expression of a slight intraspecific variability within the species *H. saxbii* (MORRIS).

Also, *Heminautilus verneuilli* (VILANOVA, 1870), whose holotype also comes from Josa, Province of Teruel (Spain), shows characteristics identical to those of *H. saxbii* (MORRIS). Following MARTÍNEZ & GRAUGES (2006), we consider this taxon as a junior synonym of *H. saxbii* (MORRIS). The original illustration of VILANOVA (1870) is reproduced here (Pl. XXVI, fig. 3).

Heminautilus saxbii (MORRIS) is also close to *H. boselliorum* DELANOY *et al.*, 2012, and *H. sanctaegrucis* CONTE, 1980. The differences with these two species were highlighted in the pertinent sections.

Remarks: the specimen no. MB RE1962A (Seboruco section, Venezuela; Pl. XXIV, fig. 3) shows morphological and sutural characteristics that lead us to attribute it to *H. saxbii* (MORRIS). However, the presence of *Heminautilus etheringtoni* DURHAM, 1946 (specimen no. MB RE1962a, Pl. XXXII, fig. 2), in the same section makes this attribution tentative; this specimen may also represent a slender variant of *H. etheringtoni* DURHAM. Only the study of a more representative population of this last taxon would provide more certainty about its variability.

Heminautilus lallierianus (ORBIGNY, 1841)

- Pl. XXVII, figs. 1-2; Pl. XXVIII, figs. 1-3;
Pl. XXIX, figs. 1-3; Pl. XXX, figs. 1-2;
Pl. XXXI, figs. 1-2; Pl. XXXII, fig. 1;
Pl. XXXIII, fig. 1; Pl. XXXIV, fig. 1;
Pl. XXXV, figs. 1-2; Pl. XXXVI, fig. 1;
Pl. XXXVII, fig. 1; Pl. XXXVIII, fig. 1;
Pl. XL, fig. 2; Pl. XLI, fig. 1
- 1841 *Nautilus lallierianus* nov. sp. - ORBIGNY, p. 318
- non 1858 *Nautilus lallierianus* ORBIGNY, 1841 - F.-J. PICTET & CAMPICHE, p. 148, Pl. 19, fig. 6 (= *H. sanctaegrucis* CONTE, 1980).
- non 1916 *Nautilus lallieri* ORBIGNY, 1841 - DOUVILLÉ, p. 129, Pl. 17, figs. 2-6 [figs. 2-4, 6 = *H. rangei* (HOPPE, 1922); fig. 5 = *H. saxbii* (MORRIS, 1848)].
- 1943 *Heminautilus lallieri* (ORBIGNY, 1841) - SCOTT, p. 90, Pl. 25, fig. 2.
- non 1967 *Xenocheilus lallierianus* (ORBIGNY, 1841) - DIMITROVA, p. 18, Pl. 4, fig. 1 (= *H. sanctaegrucis* CONTE, 1980).
- non 1976 *Heminautilus lallierianus* (ORBIGNY, 1841) - OBATA & OGAWA, p. 103, Fig. 7a-c; Pl. 2, fig. 3 (= *H. ? japonicus* sp. nov.).
- 1980 *Heminautilus lallierianus* (ORBIGNY, 1841) - CONTE, Pl. 1, Figs. 3, 4c.
- non 1984 *Heminautilus* cf. *H. lallierianus* (ORBIGNY, 1841) - OBATA *et al.*, p. 30, Fig. 3; Pl. 5, fig. 1a-b; Pl. 6, fig. 1 (= *H. ? japonicus* sp. nov.).

- 1985 *Heminautilus lallierianus* (ORBIGNY, 1841) - CONTE, p. 30, Pl. 1, figs. 1-5.
- non 2006 *Heminautilus lallierianus* (ORBIGNY, 1841) - ALY, p. 101, Pl. 1, figs. 1-3 [= ? *H. saxbii* (MORRIS, 1848)].
- 2007 *Heminautilus lallierianus* (ORBIGNY, 1841) - CONTE, p. 10, photos 1-7, 9, 10.
- non 2008 *Heminautilus lallierianus* (ORBIGNY, 1841) - ABU-ZIED, Fig. 3, A-C [= *H. rangei* (HOPPE, 1922)].
- 2008 *Heminautilus lallierianus* (ORBIGNY, 1841) - MORENO *et al.*, Fig. 4.
- 2012 *Heminautilus lallierianus* (ORBIGNY, 1841) - DELANOY *et al.*, Pl. 1, fig. 2.

Material studied (N = 17): lectotype no. MNHN.F.A32800, Early Aptian, top of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France); specimen no. UPMC-250, Early Aptian, top of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France); specimens no. tI028, tI029, tI056, tI069, tI078, tI079, tI080, coll. BAUDOUIN, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France); no. BRG098, BRG103, coll. BAUDOUIN, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, bed no. 12, Pierrelatte section (Drôme, France; cf. A. PICTET *et al.*, 2009, Fig. 2); no. VI009, VI012, coll. BOSELLI, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France); no. MPP.B-EM.69, coll. FSM, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, bed no. 148, La Bédoule (Bouches du Rhône, France); no. PM95, coll. MNHN, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain); no. PUAB 89780, Early Aptian, probably *Deshayesites forbesi* Zone, El Vendrell, Garraf (Spain); no. MGB 22607, Early Aptian, Garraf (Spain).

Type: the species was created by ORBIGNY (1841) with no illustration and without designation of holotype; a specimen was shown by CONTE (1980, 2007) with the description "type"; the same specimen was depicted anew by DELANOY *et al.* (2012) with the description "holotype". It is the syntype no. MNHN.F.A32800, coll. ORBIGNY (no. 5573) stored in the Muséum d'Histoire Naturelle of Paris, which we therefore designate as the lectotype. It is shown in this work as Pl. XXIX, fig. 1 and comes from the Early Aptian of Gurgy (Yonne, France).

Geographical distribution: the species seems to be known with certainty only from France, Spain and Ethiopia.

Table 7: Measurements of *Heminautilus lallierianus* (ORBIGNY, 1841).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Lectotype no. MNHN.F.A32800	124	81	44	0.55	0.30	0.54	9	0.06	0.11	24	44	0.55	0.54
	-	68	-	-	-	-	-	-	-	20	40	0.50	0.59
	-	48	-	-	-	-	-	-	-	15	30	0.50	0.63
no. 77-543	176	104	62	0.59	0.35	0.60	-	-	-	-	-	-	-
	112	70	-	0.63	-	-	10	0.09	0.14	22	48	0.46	0.69
no. 85-3	-	67	39	-	-	0.58	9	-	0.13	17	39	0.44	0.58
	-	47	-	-	-	-	8	-	0.17	15	29	0.52	0.62
no. UPMC-250	-	42.7	-	-	-	-	6.8	-	0.16	11.8	29.9	0.39	0.70
	-	66	-	-	-	-	9.6	-	0.15	16.8	43.8	0.38	0.66
no. tl028	67	40	19	0.60	0.28	0.48	12	0.18	0.30	-	-	-	-
	55	33	18	0.60	0.33	0.55	6	0.11	0.18	9	24	0.38	0.73
	49	30	16	0.61	0.33	0.53	6	0.12	0.20	8	23	0.35	0.77
no. tl029	154	96	57	0.62	0.37	0.59	13	0.08	0.14	-	-	-	-
	122	87	38	0.71	0.31	0.44	8	0.07	0.09	18	54	0.33	0.62
	119	82	-	0.69	-	-	6	0.05	0.07	19	53	0.36	0.65
	-	68	-	-	-	-	-	-	-	20	48	0.42	0.71
no. tl056	153	93	55	0.61	0.36	0.59	13	0.08	0.14	-	-	-	-
	135	89	-	0.66	-	-	10	0.07	0.11	24	60	0.40	0.67
	-	57	-	-	-	-	c6	-	0.11	20	43	0.47	0.75
no. tl069	159	97	c51	0.61	0.32	0.53	11	0.07	0.11	-	-	-	-
	c132	85	c37	0.64	0.28	0.44	6	0.05	0.07	23	57	0.40	0.67
no. tl078	173.9	108	64.9	0.62	0.37	0.60	11.3	0.06	0.10	-	-	-	-
	128.9	89.3	38.4	0.69	0.30	0.43	7.4	0.06	0.08	23.4	56	0.42	0.63
no. tl079	-	88.3	-	-	-	-	7.4	-	0.08	24.7	58.1	0.43	0.66
no. tl080	-	99.3	62.1	-	-	0.63	15.3	-	0.15	-	-	-	-
	139.1	91.2	39.1	0.66	0.28	0.43	11.6	0.08	0.13	20.1	53.4	0.38	0.59
no. BRG098	-	41.1	23.8	-	-	0.58	6.6	-	0.16	-	-	-	-
	-	35.9	18	-	-	0.50	4.8	-	0.13	9.7	27.6	0.35	0.77
no. BRG103	134.3	77.5	37.5	0.58	0.28	0.48	7.5	0.06	0.10	-	-	-	-
	-	61.8	26.5	-	-	0.43	6.2	-	0.10	20.1	53.9	0.37	0.87
no. VI009	148	84	53	0.57	0.36	0.63	15	0.10	0.18	-	-	-	-
	122	78	c36	0.64	0.30	0.46	8	0.07	0.10	19	52	0.37	0.67
no. VI012	153	92	60	0.60	0.39	0.65	9	0.06	0.10	-	-	-	-
	128	83	43	0.65	0.34	0.52	5	0.04	0.06	22	60	0.37	0.72
	-	63	31	-	-	0.49	-	-	-	18	47	0.38	0.75
no. MPP.B-EM.69	58	33.5	12.2	0.58	0.21	0.36	4.9	0.08	0.15	-	-	-	-
no. PM95	159	95	70	0.60	0.44	0.74	17	0.11	0.18	-	-	-	-
	128	79	48	0.62	0.38	0.61	13	0.10	0.16	19.5	52	0.38	0.66
no. PUAB 89780	-	61	38	-	-	0.62	10	-	0.16	17	42	0.40	0.69
	-	46.5	-	-	-	-	-	-	-	16.4	33.9	0.48	0.73
no. AMNH 25455 (SCOTT, 1943)	-	42.5	-	-	-	-	-	-	-	15.8	31.8	0.5	0.75
	146	93	57	0.64	0.39	0.61	-	-	-	-	-	-	-
	116	80	-	0.69	-	-	-	-	-	28	59	0.47	0.74
	-	57	-	-	-	-	-	-	-	13	36	0.36	0.63

no. 12572	145	85	40	0.59	0.28	0.47	-	-	-	-	-	-	-
	90	61	-	0.68	-	-	-	-	-	19	39	0.49	0.64
	-	35	-	-	-	-	4	-	0.11	-	-	-	-
no. 12573	160	95	46	0.59	0.29	0.48	-	-	-	-	-	-	-
	c95	65	22	0.68	0.23	0.34	-	-	-	18	42	0.43	0.65
	-	40	-	-	-	-	6.5	-	0.16	14	25	0.56	0.63
Specimen photo 7 (CONTE, 2007)	c121	69	-	0.57	-	-	-	-	-	-	-	-	-
	-	62	-	-	-	-	-	-	-	21	45	0.47	0.73
no. MGB 22607 (MORENO <i>et al.</i> , 2008)	c113	70	35	0.62	0.31	0.50	6	0.05	0.09	22	47	0.47	0.67
	-	59	-	-	-	-	-	-	-	21	42	0.50	0.71

Stratigraphical distribution: the lectotype and the topotypes no. 77-543, no. 85-3 (coll. MHNA) and no. UPMC-250 come from the Argiles à Plicatules Formation of Gurgy (Yonne), where the accompanying ammonite fauna indicates a stratigraphical position between the top of the *Deshayesites forbesi* Zone and the *Deshayesites deshayesi* Zone (CORROY, 1925; AMÉDRO & MATRION, 2004). However, the preservation of these four specimens, as calcareous moulds of relatively large size, differs from that typically encountered in the form of pyritic nucleus and could be characteristic of a particular level within the Argiles à Plicatules. The holotype of *Roloboceras transiens* CASEY, 1961, with the same preservation and from the same locality, suggests a stratigraphical position of this level in the top of the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone. Specimens no. tI028, tI029, tI056, tI069, tI078, tI079 and VI009, collected in association with numerous representatives of the genus *Megatylloceras* HUMPHREY, 1949, come from the top of the *Roloboceras hambrovi* Subzone (CASEY *et al.*, 1998). Specimens no. BRG098 and BRG103, from bed no. 12 of the Pierrelatte section, would come from the lower part of the *Roloboceras hambrovi* Subzone (A. PICTET *et al.*, 2009, 2015). Specimen no. AMNH 25455 depicted by SCOTT (1943) comes from the Harrar region (Ethiopia). The local geology was studied by BOSELLINI *et al.* (1999), who show that in this region there is only a very short Aptian marine incursion, with sandy fluvial deposition before and after; the presence of *Palorbitolina lenticularis* (BLUMENBACH, 1805) and *Praeorbitolina cormyi* SCHROEDER, 1964, allows us to determine a middle Early Aptian age for this formation (SCHROEDER *et al.*, 2010). *Heminautilus lallierianus* (ORBIGNY, 1841) is thus present in Europe in the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, in particular at the top of the subzone.

Dimensions (in mm): see Table 7.

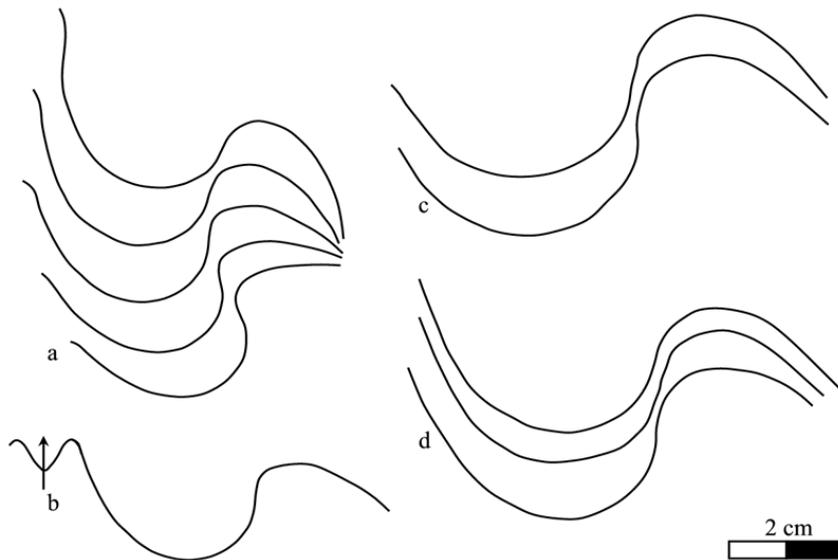
Description: *Heminautilus lallierianus* (ORBIGNY, 1841) has a large shell (D = 176 mm, specimen no. 77-543, Pl. XXX, fig. 1), compressed (E/H generally between 0.40 and 0.60;

Fig. 9), with slightly rounded flanks, of maximum thickness in the lower third of the flanks. The initial whorls are unknown; from a small diameter, the ventral region is narrow, strongly concave (specimen no. MPP.B-EM.69, Pl. XXXVIII, fig. 3), lined with angular ventrolateral edges. On the body chamber of adult specimens, the concavity of the ventral region frequently becomes less pronounced (no. 77-543, Pl. XXIX, fig. 2; no. tI078, Pl. XXXV, fig. 2; no. tI029, Pl. XXXVI, fig. 1). No ornamentation is present on the phragmocone. On the body chamber, the ornamentation shows some variability. Some complete adult specimens are completely smooth (no. BRG103, Pl. XXXI, fig. 2; no. tI029, Pl. XXXV, fig. 1; no. tI056, Pl. XXXI, fig. 1; no. VI009, Pl. XXXII, fig. 1; no. tI069, Pl. XXXIII, fig. 1), while others show at the end of the body chamber broad and strongly rursiradiate ribs, restricted to the upper part of the flanks (no. PUAB 89780, Pl. XXVII, fig. 1; no. PM95, Pl. XXXVIII, fig. 1; no. 77-543, Pl. XXX, fig. 1; no. tI078, Pl. XXXIV, fig. 1).

The suture line is strongly sinuous (Fig. 13), with a fairly wide and deep lateral lobe (Fig. 11; P/L generally between 0.35 and 0.50, Fig. 10), a wide and rounded lateral saddle and a well defined, angular ventral lobe. In some specimens, we observe the space between the last suture lines narrowing, characteristic of the adult stage (no. PM95, Pl. XXXVIII, fig. 1; no. tI056, Pl. XXXI, fig. 1). The siphuncle, very visible in the lectotype no. MNHN.F.A32800 (Pl. XXIX, fig. 1) and the specimen no. 85-3 (Pl. XXVII, fig. 2), is placed very low on the section, near the dorsal edge.

Discussion and comparisons: *Heminautilus lallierianus* (ORBIGNY, 1841) is very similar to *H. saxbii* (MORRIS, 1848). Relationships between these two taxa were discussed in the section on *H. saxbii* (MORRIS, 1848).

The specific characteristics of *H. lallierianus* (ORBIGNY), in particular its strongly concave and narrow ventral region, as well as its very sinuous suture line with a deep lateral lobe, readily distinguish it from other species of the genus *Heminautilus* SPATH, 1927.



◀ **Figure 13:** *Heminutilus lallierianus* (ORBIGNY, 1841). Suture line of specimens no. MNHN.F.A32800, left side (a-b), PM95, right side (c) and t1056, left side (d).

***Heminutilus* aff. *lallierianus* (ORBIGNY, 1841)**

Pl. XXXIX, fig. 1; Pl. XL, fig. 1

2015 *Heminutilus* cf. *lallierianus* (ORBIGNY, 1841) - MORENO-BEDMAR *et al.*, p. 209.

Material studied (N = 2): specimen no. IGM 10050, Early Aptian, *Dufrenoyia justinae* Zone, bed no. 15, Mina Texali, Santa Isabel Atenayuca, Puebla State (Mexico); specimen no. MPL1, Early Aptian, *Dufrenoyia justinae* Zone, Sierra del Rosario, Durango State (Mexico).

Geographical distribution: *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841) is known only in Mexico.

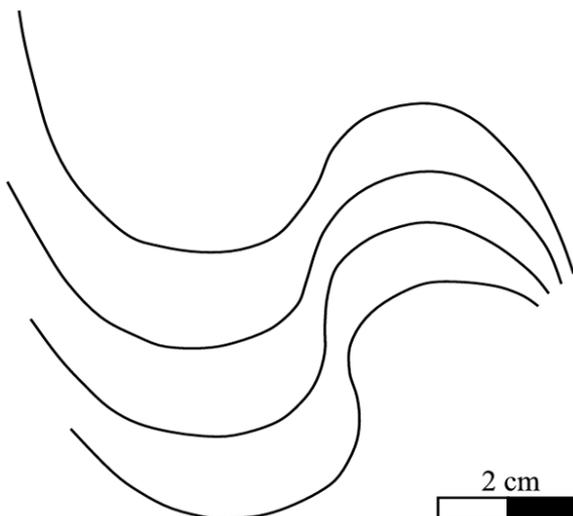


Figure 14: *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841). Suture line of specimen no. IGM 10050, left side.

Stratigraphical distribution: the specimen no. IGM 10050 comes from the *Dufrenoyia justinae* Zone (= top of the *Dufrenoyia furcata* Zone, MORENO-BEDMAR *et al.*, 2012, 2015). The specimen no. MPL1 comes from the La Peña Formation, corresponding to a stratigraphical interval ranging from the *Dufrenoyia justinae* Zone to the lowermost part of the *Caseyella aguilerae* Zone [personal observations of one of us (J.A. MORENO-BEDMAR); cf. CANTÚ-CHAPA, 1989; MORENO-BEDMAR *et al.*, 2013]. It was found ex-situ in a section that can be attributed to the *Dufrenoyia justinae* Zone.

Dimensions (in mm): see Table 8.

Description: *Heminutilus* aff. *lallierianus* (ORBIGNY, 1841) has a relatively compressed section, with rounded flanks, of maximum thickness close to the umbilical edge. The ventral region is narrow, clearly concave and lined with two angular ventro-lateral edges. No ornamentation is visible in the specimen no. IGM 10050; in the specimen no. MPL1 some broad and strongly rursiradiate ribs are observable on the top of the flanks at the end of the body chamber. *Heminutilus* aff. *lallierianus* (ORBIGNY) can reach a large size (D = 180 mm in specimen no. MPL1, Pl. XL, fig. 1).

The suture line is very sinuous (Fig. 14), with a rounded and well developed lateral saddle and a deep lateral lobe (*P/L* between 0.31 and 0.44). The ventral lobe is well defined and angular in shape. The position of the siphuncle is not visible.

Table 8: Measurements of *Heminautilus* aff. *lallierianus* (ORBIGNY, 1841).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
no. IGM 10050	146.8	93.9	47.6	0.64	0.32	0.51	c7.8	0.05	0.08	27.1	61.8	0.44	0.66
	-	68.3	30	-	-	0.44	7.4	-	0.11	20.9	49.5	0.42	0.72
	-	53.3	-	-	-	-	-	-	-	16.7	39.9	0.42	0.75
no. MPL1	180.0	95.0	-	-	-	-	-	-	-	-	-	-	-
	-	96.0	-	-	-	-	-	-	-	18.0	59.0	0.31	0.61
	-	67.0	-	-	-	-	-	-	-	19.0	53.0	0.36	0.79

Discussion and comparisons: *Heminautilus* aff. *lallierianus* (ORBIGNY, 1841) is very close to *H. lallierianus* (ORBIGNY) and can be distinguished from it only by a slightly wider lateral saddle and a ventral region which is less concave. However, its stratigraphical position is clearly higher, in the *Dufrenoyia justinae* Zone (= top of the *Dufrenoyia furcata* Zone, MORENO-BEDMAR *et al.*, 2012, 2015), while *H. lallierianus* (ORBIGNY) is known only in the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone. This unusual stratigraphical position, as well as its very distant geographical distribution, makes its incorporation into ORBIGNY's species uncertain, with additional data on specimens of intermediate stratigraphical position needed.

H. aff. lallierianus (ORBIGNY) can be easily distinguished from the other American species of the genus, *H. etheringtoni* DURHAM, 1946, and *H. stantoni* (SCOTT, 1940). It differs from *H. etheringtoni* DURHAM by its narrower section and ventral region, from *H. stantoni* (SCOTT, 1940) by the absence of ribbing on the phragmocone, and from both taxa by its clearly more concave ventral region and its different suture line, with a deep lateral lobe and a well developed lateral saddle.

Heminautilus etheringtoni DURHAM, 1946

Pl. XXX, fig. 3; Pl. XXXII, fig. 2;
Pl. XLII, fig. 1; Pl. XLIII, fig. 1;
Pl. XLIV, figs. 1-2; Pl. XLV, figs. 1-2

1946 *Heminautilus etheringtoni* nov. sp. - DURHAM, p. 432, Pl. 62, fig. 4; Pl. 63, figs. 3, 5-7; Pl. 64, figs. 1-3.

1947 *Heminautilus etheringtoni* DURHAM, 1946 - DURHAM, p. 576, Figs. 1-3.

1979 *Heminautilus etheringtoni* DURHAM, 1946 - ETAYO-SERNA, p. 104, Pl. 4, fig. 8; Pl. 5, fig. 9.

? **2008** *Heminautilus etheringtoni* DURHAM, 1946 - VEGA *et al.*, Fig. 3c.

Material studied (N = 4): specimens no. M3, 124, coll. UNCB, Early Aptian, Quebrada el Cobre, Payandé, Tolima department (Colombia); no. UN-DG-NT-001, coll. UNCB, Early Aptian, Firavitoba, Boyacá department (Colombia); no. MB RE1962a, Early Aptian, Tibú Formation, Seboruco section, east of Mérida (Venezuela).

Type: the holotype (by original designation) is specimen no. 35731 (coll. MPUC) shown in DURHAM (1946: Pl. 62, fig. 4; Pl. 63, fig. 6; Pl. 64, fig. 3), stored in the collections of the Museum of Paleontology, University of California. It comes from locality A of DURHAM (1946), situated between El Valle and Payandé in Tolima department (Colombia) and is depicted anew in this work Pl. XLII, fig. 1; Pl. XLIII, fig. 1.

Geographical distribution: the species is known in Colombia and Venezuela.

Stratigraphical distribution: according to DURHAM, 1946, the holotype comes from locality A, associated with representatives of the genus *Chelonicerias* HYATT, 1903. It is consequently possible to attribute it a stratigraphical position near the top of the Early Aptian. Also, specimen no. MB RE1962a comes from the Seboruco section (Venezuela) which, according to RENZ (1982, p. 19), yielded ammonites of the genus *Roloboceras* CASEY, 1954, but which more likely belong to the genus *Chelonicerias* HYATT, 1903; its stratigraphical position is also near the top of the Early Aptian. Specimen no. F-15 (coll. MGNR) illustrated by ETAYO-SERNA (1979) comes from the uppermost part of the Early Aptian, *Dufrenoyia sanctorum-Stoyanowiceras treffryanus* Assemblage zone. The stratigraphical position of the specimens no. M3, 124 and UN-DG-NT-001 is not known.

Heminautilus etheringtoni DURHAM, 1946, is thus a species present at the top of the Early Aptian (= *Dufrenoyia furcata* Zone); its presence at a lower stratigraphical level in the Early Aptian is possible but remains hypothetical with the data in our possession.

Dimensions (in mm): see Table 9.

Description: specimens illustrated by DURHAM (1946) show a fairly compressed section in the internal whorls, which widens through its ontogeny, particularly on the adult body chamber (holotype no. 35731, Pl. XLIII, fig. 1; specimen no. MB RE1962a, Pl. XXXII, fig. 2). The flanks, rounded in the internal whorls, quickly become flat and convergent towards the ventral region, with maximum thickness situated near the umbilical edge. The ventral region is fairly wide and rounded in the internal whorls; it widens and becomes gradually flat with a relatively angular ventro-lateral edge on the body chamber.

Table 9: Measurements of *Heminautilus etheringtoni* DURHAM, 1946.

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. 35731	153	86	77	0.56	0.5	0.9	32	0.21	0.37	-	-	-	-
	116	65	-	0.56	-	-	-	-	-	17	45	0.38	0.69
	-	53	59	-	-	1.11	-	-	-	12	38	0.32	0.72
no. 124	105	-	-	-	-	-	-	-	-	-	-	-	-
	-	50.2	-	-	-	-	-	-	-	9.2	33.2	0.28	0.66
	-	32	-	-	-	-	-	-	-	5.8	23.2	0.25	0.73
no. M3	80	-	-	-	-	-	-	-	-	-	-	-	-
	-	48.9	-	-	-	-	-	-	-	6.6	33.1	0.2	0.68
	-	42.2	-	-	-	-	-	-	-	8.3	32.3	0.26	0.77
no. UN-DG-NT-001	154	-	-	-	-	-	-	-	-	-	-	-	-
	-	72.3	-	-	-	-	-	-	-	15.3	53.8	0.28	0.74
	-	65.1	-	-	-	-	-	-	-	13.6	49.5	0.27	0.76
no. 35733 (DURHAM, 1946)	53	31	25	0.58	0.47	0.81	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	3.5	12	0.29	-
no. F-15 (ETAYO-SERNA, 1979)	115	75	52	0.65	0.45	0.69	14	0.12	0.19	-	-	-	-
	-	-	-	-	-	-	-	-	-	6	20	0.30	-
no. MB RE1962a	-	78	49	-	-	0.63	18	-	0.23	-	-	-	-
	-	60	-	-	-	-	14	-	0.23	12	53	0.23	0.88

The ornamentation is formed by ribs and growth lines. Ribs, rounded, wide and weak, are present on the top of the flanks of the holotype's body chamber, where the shell is preserved. They are convex and become gradually strongly rursiradiate near the ventral region. Growth lines are visible on the ventral region; they are weak and form an angular sinus.

The suture line is fairly sinuous (Fig. 15), with a very wide and relatively deep lateral lobe (P/L between 0.32 and 0.38 in the holotype). The ventral lobe is shallow. The siphuncle is placed near the dorsal edge of the section [specimen no. M3 (coll. UNCB), Pl. XLIV, fig. 2; no. 124 (coll. UNCB), Pl. XLV, fig. 2].

Discussion and comparisons: *Heminautilus etheringtoni* DURHAM, 1946, presents affinities with *H. ? tyosiensis* (YABE & OSAKI, 1953), a species with a comparable shape of the body chamber section, associated with a wide ventral region, ornamented by growth lines forming an angular sinus. However, *H. ? tyosiensis* (YABE & OSAKI) can be distinguished by its clearly more concave ventral region and its different ribbing, well defined on the phragmocone and absent on the body chamber. Its suture line is also different, with a more developed lateral saddle and a clearly deeper lateral lobe [P/L between 0.40 and 0.50 in *H. ? tyosiensis* (YABE & OSAKI)].

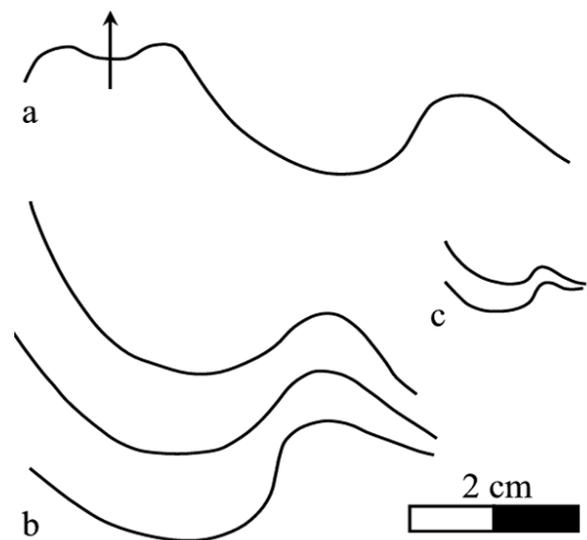


Figure 15: *Heminautilus etheringtoni* DURHAM, 1946. Suture line of specimens no. 35731, right side (a-b) and 35733, left side (c).

H. etheringtoni DURHAM is also rather close to *H. saxbii* (MORRIS, 1848), particularly in its similar ornamentation and suture line, but can be distinguished by its section and its much wider ventral region, as well as by a much more rounded ventro-lateral shoulder, especially on the phragmocone.

Table 10: Measurements of *Heminautilus stantoni* (SCOTT, 1940).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. 1162	114	69	40	0.61	0.35	0.58	-	-	-	16	51	0.31	0.74
	98	60	-	0.61	-	-	-	-	-	13	43	0.3	0.72

H. etheringtoni DURHAM can also be compared to *Josanautilus lacerdae* (VILANOVA, 1870) by its section and the form of its ventral region, but it can readily be distinguished from it by the absence of a median keel and of longitudinal ornamentation on the ventral region.

Heminautilus stantoni (SCOTT, 1940)

Pl. XXXVI, figs. 2-3

1940 *Vorticoceras stantoni* nov. sp. - SCOTT, p. 1076, Pl. 68, figs. 4-5.

Type: the holotype (by original designation) is specimen no. USNM103260, shown in SCOTT (1940) Pl. 68, figs. 4-5, stored in the collections of the United States National Museum, Washington, and coming from the locality M15 (SCOTT, 1940, p. 988), near Murfreesboro, Arkansas (USA). It is depicted anew in this work in Pl. XXXVI, fig. 3. A plaster cast of it (no. 35688, coll. BEG) is also shown in Pl. XXXVI, fig. 2.

Geographical distribution: the species is known only by its holotype, coming from Arkansas (USA).

Stratigraphical distribution: the holotype comes from the Dierks Limestone, Trinity Group of Arkansas. SCOTT (1940) indicates in this formation the presence of representatives of the genus *Pseudosaynella* SPATH, 1923. In Mexico and in the south of the USA, the genus *Pseudosaynella* SPATH appears to occupy a restricted stratigraphical position, limited to the uppermost part of the Early Aptian (SCOTT, 1940, p. 976; MORENO-BEDMAR *et al.*, 2015). Furthermore, IMLAY (1945) reported the presence of the genus *Pseudosaynella* SPATH, associated with *Dufrenoyia* KILIAN & REBOUL, 1915, at the top of the Pine Island Shale (lateral equivalent in Louisiana of the Dierks Limestone). These observations allow us to attribute to *Heminautilus stantoni* (SCOTT, 1940) a stratigraphical position at the top of the Early Aptian, confidently placed in the *Dufrenoyia justinae* Zone (= top of the *Dufrenoyia furcata* Zone, MORENO-BEDMAR *et al.*, 2012, 2013, 2015).

Dimensions (in mm): see Table 10.

Description: the holotype no. USNM103260 consists of an incomplete phragmocone. It shows a fairly compressed section, with flanks clearly convex and bulging in their lower half and otherwise flat, converging to the ventral region. The ventral region is fairly wide and seems slightly concave, lined with two well defined shoulders.

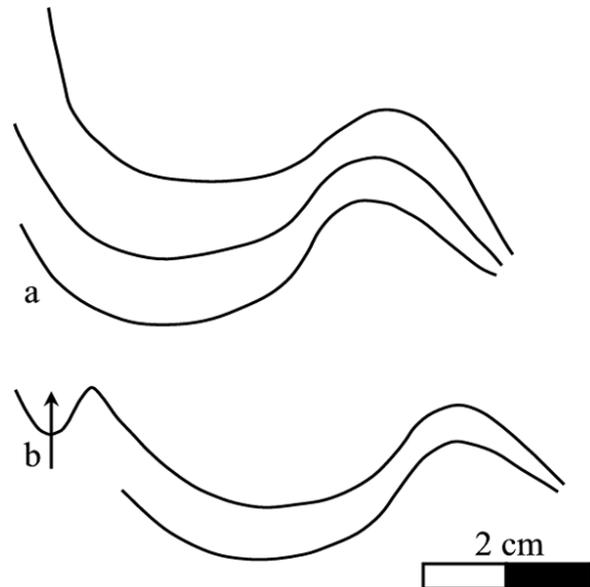


Figure 16: *Heminautilus stantoni* (SCOTT, 1940). Suture line of specimen no. USNM103260, left side.

The ornamentation is formed of spaced, wide, rursiradiate and rounded ribs, becoming higher and thus more visible in the upper half of the flanks.

The suture line (Fig. 16) is sinuous, with a wide and rounded lateral saddle, a well developed, fairly deep lateral lobe (P/L close to 0.30) and a narrow and well defined ventral lobe. The position of the siphuncle is not known.

Discussion and comparisons: *Heminautilus stantoni* (SCOTT, 1940) is relatively close to *H. saxbii* (MORRIS, 1848) in its section, the shape of its ventral region and its suture line. *H. stantoni* (SCOTT) can be distinguished from *H. saxbii* (MORRIS) by its ribbing, consisting of very wide ribs and present on the phragmocone, which is only visible on the body chamber in *H. saxbii* (MORRIS). Its suture line also contains a lateral saddle more developed than the one of *H. saxbii* (MORRIS).

Heminautilus stantoni (SCOTT) also shows some affinities with *H. lallierianus* (ORBIGNY, 1841), in particular in the presence of a well developed lateral saddle. It differs, however, from *H. lallierianus* (ORBIGNY) in the presence of well defined ribbing on the phragmocone, a clearly shallower lateral lobe and a less concave ventral region.

Heminautilus stantoni (SCOTT) can be distinguished immediately from other species of the genus *Heminautilus* SPATH, 1927, by its section, the shape of the ribbing and the presence of ribbing on the phragmocone.

Table 11: Measurements of *Heminautilus ? japonicus* sp. nov.

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. SH-1	74.4	42.3	32	0.57	0.43	0.76	7	0.09	0.17	-	-	-	-
	-	46	-	-	-	-	-	-	-	14	39	0.36	0.85
Unregistered specimen (OBATA & OGAWA, 1976)	106	69	45	0.65	0.42	0.65	17	0.16	0.25	-	-	-	-
	77	55	-	0.71	-	-	14	0.18	0.25	20	45	0.44	0.82

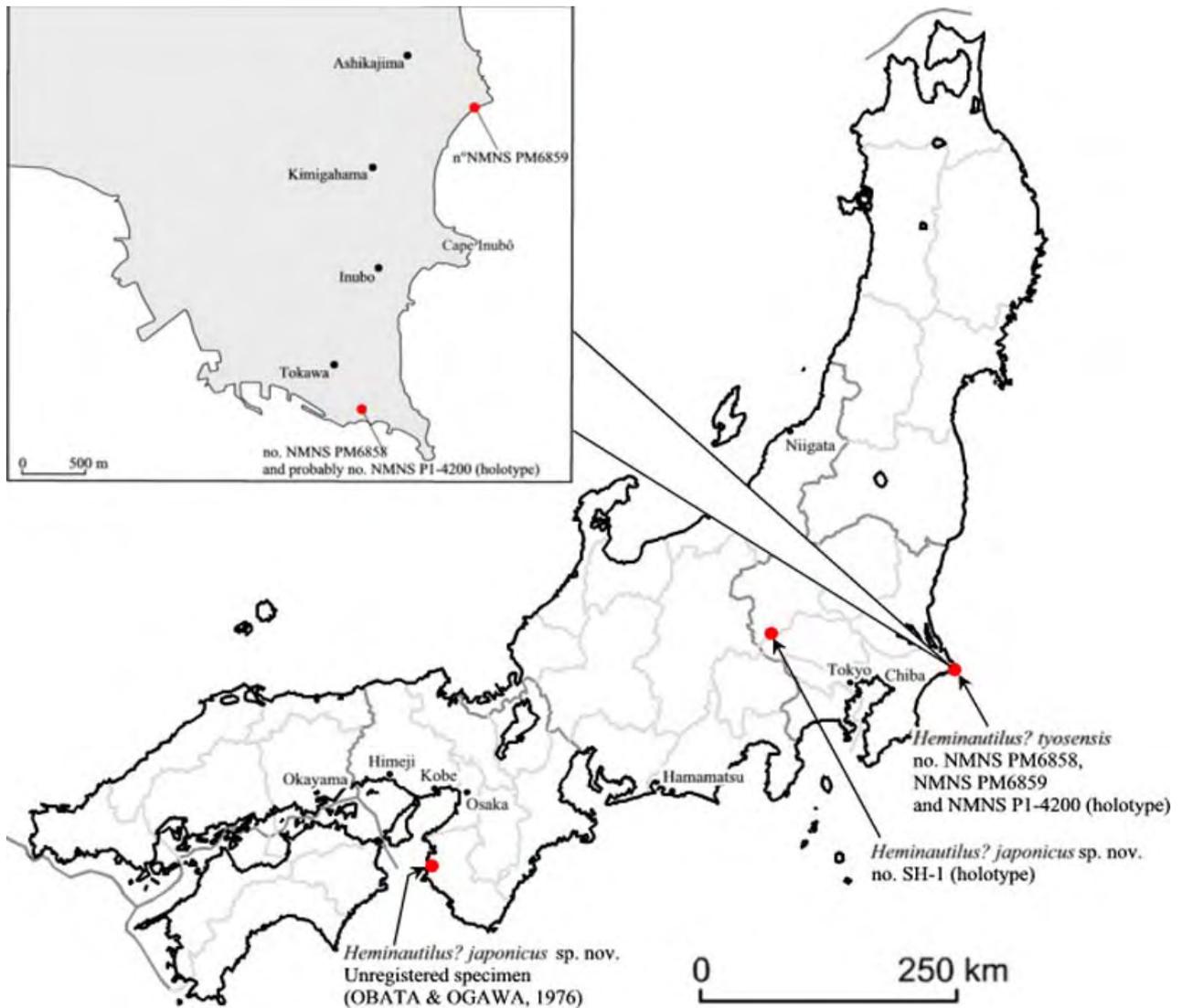


Figure 17: Geographical position of specimens of *Heminautilus ? japonicus* sp. nov. and *Heminautilus ? tyosensis* (YABE & OSAKI, 1953) referred to in the text.

***Heminautilus ? japonicus* sp. nov.**

Pl. XXXVIII, fig. 2; Pl. XLIX, fig. 2;
Pl. L, fig. 3

1976 *Heminautilus lallierianus* (ORBIGNY, 1841) - OBATA & OGAWA, p. 103, Fig. 7a-c; Pl. 2, fig. 3.

1984 *Heminautilus* cf. *H. lallierianus* (ORBIGNY, 1841) - OBATA *et al.*, p. 30, Fig. 3; Pl. 5, fig. 1a-b; Pl. 6, fig. 1.

Holotype: specimen no. SH-1 (coll. E. Shimizu), illustrated by OBATA *et al.* (1984) and depicted anew here in Pl. XLIX, fig. 2 and Pl. L, fig. 3. A cast is deposited in the National Science Museum in Tokyo, Japan under the no. NSM-PM 9381.

Origin of the name: the name comes from Japan, the origin of the holotype.

Type locality: according to OBATA *et al.* (1984), the holotype comes from locality 203 of the sector of Sanchu, Kwanto Mountains (Gunma Prefecture, Japan).

Type strata: the presence, in the horizon where the holotype comes from, of *Phylloceras* sp., *Barremites* aff. *strettostoma* (UHLIG, 1883), *Pseudohaploceras japonicum* OBATA *et al.*, 1984, and *Heteroceras* aff. *astierianum* ORBIGNY, 1851, allows us to attribute *Heminautilus ? japonicus* sp. nov. to the latest Barremian (= *Imerites giraudi* Zone).

Geographical distribution: this taxon is known only in Japan. The holotype no. SH-1 comes from the Kwanto Mountains (Gunma Prefecture) and the specimen studied by OBATA & OGAWA (1976) comes from the north of Yuasamachi (Wakayama Prefecture) (Fig. 17).

Stratigraphical distribution: the holotype is dated from the latest Barremian (= *Imerites giraudi* Zone). The specimen illustrated by OBATA & OGAWA (1976) as *Heminautilus lallierianus* (ORBIGNY, 1841) comes from the Arida Formation, whose uppermost part delivered *Heteroceras* aff. *astieri* ORBIGNY, 1851. It is contemporary with specimens attributed to *Anahamulina* cf. *subcylindrica* (ORBIGNY, 1850) (OBATA & OGAWA, 1976, Pl. 4, figs. 9a-b, 10) but which are probably fragmentary representatives of *Heteroceras* ORBIGNY, 1849. Consequently this specimen comes certainly from the uppermost part of the Late Barremian (= *Imerites giraudi* Zone?). The species is only known with certainty in the latest Barremian (= *Imerites giraudi* Zone).

Dimensions (in mm): see Table 11.

Diagnosis: species of small size, relatively compressed, with rounded flanks, concave ventral region, ornamented with fine growth lines in chevron. Ornamentation absent or formed by fine rursiradiate ribs, only present on the top of the flanks of the body chamber. Suture line very sinuous, with a wide, deep and asymmetrical lateral lobe and a clear ventral lobe.

Description: *Heminautilus ? japonicus* sp. nov. is small-sized, with a fairly wide section and rounded flanks, of maximum thickness near the umbilical edge. The ventral region is narrow to fairly wide, clearly concave, with an angular ventro-lateral edge. It is ornamented with fine growth lines, which form an angular sinus. On the phragmocone, no ornamentation is visible on the flanks. On the body chamber, the holotype no. SH-1 shows an ornamentation formed by fine rursiradiate ribs, tight and only visible on the top of the flanks (Pl. L, fig. 3). No ornamentation seems to be present on the flanks of the specimen shown by OBATA & OGAWA (1976).

The suture line is strongly sinuous (Fig. 18), with a very wide, deep and asymmetrical lateral lobe (P/L close to 0.40), and a very narrow and rounded lateral saddle. The ventral lobe is well defined and angular.

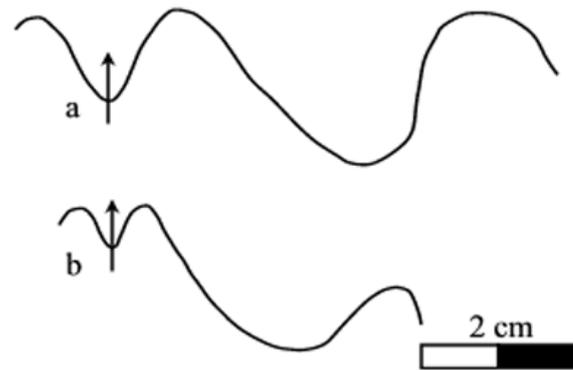


Figure 18: *Heminautilus ? japonicus* sp. nov. Suture line of the unregistered specimen, right side (a) illustrated by OBATA & OGAWA (1976) and of specimen no. SH-1, left side (b).

The position of the siphuncle is not known.

Discussion and comparisons: *Heminautilus ? japonicus* sp. nov. is close to *H. ? tyosiensis* (YABE & OSAKI, 1953), possessing a similar suture line and a ventral region ornamented with fine growth lines. *H. ? tyosiensis* (YABE & OSAKI) can however be distinguished by its much wider ventral region, as well as the presence of a well defined ribbing on the flanks of the phragmocone. The stratigraphical position of *H. ? tyosiensis* (YABE & OSAKI) is also different, at the top of the Early Aptian (= *Dufrenoyia furcata* Zone).

Heminautilus ? japonicus sp. nov. is also relatively close to *H. rangei* (HOPPE, 1922), having a similar shape and ornamentation of its ventral region. Relationships between both species were analyzed in the section concerning *H. rangei* (HOPPE); the similarities observed could indicate a phyletic link between these taxa.

Heminautilus ? japonicus sp. nov. also presents some affinities with *H. lallierianus* (ORBIGNY, 1841), with in particular its concave ventral area, but can be distinguished from it easily by its small size, the ornamentation of its ventral area, its rounded flanks, its distinct suture line and its clearly older stratigraphical position.

As in *H. ? tyosiensis* (YABE & OSAKI), the plan of the suture line of *H. ? japonicus* sp. nov., relatively different from that of the other representatives of the genus *Heminautilus* SPATH, 1927, could be compared to the one of the genus *Xenocheilus* SHIMANSKY & ERLANGER, 1955. The important stratigraphical gap as well as the misunderstanding of the position of the siphuncle in *H. ? japonicus* sp. nov. do not allow us to retain this hypothesis. For these reasons the attribution to the genus *Heminautilus* SPATH, 1927, remains conditional.

Table 12: Measurements of *Heminautilus ? tyosiensis* (YABE & OSAKI, 1953).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. NMNS P1-4200	70	43	20	0.61	0.29	0.47	18	0.26	0.42	-	-	-	-
	-	36	-	-	-	-	-	-	-	11	28	0.39	0.78
	-	26	-	-	-	-	-	-	-	11	22	0.5	0.85

***Heminautilus ? tyosiensis* (YABE & OSAKI, 1953)**

Pl. XXXIII, fig. 2; Pl. XXXIV, figs. 2-3;
Pl. XXXV, fig. 3

1953 *Platynautilus tyosiensis* nov. sp. - YABE & OSAKI, p. 57, Pl. 1, figs. 1-4.

1975 *Heminautilus tyosiensis* (YABE & OSAKI, 1953) - OBATA *et al.*, p. 28, Pl. 2, fig. 2; Pl. 4, fig. 4.

1975 *Heminautilus* aff. *tyosiensis* (YABE & OSAKI, 1953) - OBATA *et al.*, p. 28, Pl. 4, fig. 2.

Type: the holotype (by original designation) is the specimen no. NMNS P1-4200 illustrated by YABE & OSAKI (1953), Pl. 1, figs. 1-4. It comes from the Tokawa quarry (Tyōsi Peninsula, Tiba Prefecture) and is stored in the National Science Museum in Tokyo, Japan. It is depicted anew in this work in Pl. XXXIII, fig. 2.

Geographical distribution: the species is known only in Japan, in the Choshi Peninsula (Chiba Prefecture) (Fig. 17).

Stratigraphical distribution: the holotype comes from the Inubouzaki Formation, dated doubtfully by YABE & OSAKI (1953) as Aptian. However, OBATA & MATSUKAWA (2009) indicate for this formation the presence of the genera *Australiceras* WHITEHOUSE, 1926, *Tropaeum* J. de C. SOWERBY, 1837, *Chelonicerias* HYATT, 1903, *Dufrenoyia* KILIAN & REBOUL, 1915, and *Colombiceras* SPATH, 1923, which allows us to attribute it without ambiguity to the top of the Early Aptian (= *Dufrenoyia furcata* Zone). According to these authors, specimens illustrated by OBATA *et al.* (1975) come from the Kimihagama Formation [likely equivalent to the major part of the Kimihagama, Inubouzaki and Toriakeura formations in the sense of OBATA & MATSUKAWA (2009)], above the Ashikajima Formation [with *Dufrenoyia* aff. *dufrenoyi* (ORBIGNY, 1841)] and below the Nagasakihana Formation [with *Chelonicerias meyndorffi* (ORBIGNY, 1845)]; these specimens can thus be attributed also to the top of the Early Aptian (= *Dufrenoyia furcata* Zone).

In the absence of figures and of bibliographical reference, the presence of *Heminautilus ? tyosiensis* (YABE & OSAKI, 1953) indicated by OBATA *et al.* (1982, p. 148) and by OBATA & MATSUKAWA (2009, p. 254) in the Ashi-

kajima Formation (in the sense of OBATA & MATSUKAWA (2009), not OBATA *et al.* (1975); Early Barremian) cannot be confirmed.

Heminautilus ? tyosiensis (YABE & OSAKI) is thus known with certainty only from the top of the Early Aptian.

Dimensions (in mm): see Table 12.

Description: the holotype (Pl. XXXIII, fig. 2) is a specimen of rather small size, preserved as a partially complete phragmocone with the major part of the body chamber. It shows a rather wide section, of maximum thickness near the umbilical edge, with a very involute coiling. Flanks are almost flat and converge on the ventral region. The ventral region is wide, slightly concave, surrounded by two angular edges; it shows in its median part a clear furrow.

On the adapical part of the phragmocone, four wide, weak and flexuous ribs are visible only on the outside part of the flanks. This ribbing quickly fades and then no ornamentation is visible on the flanks of the adoral part of the phragmocone and the body chamber. On the ventral region, the only discernible ornamentation consists of weak growth lines strongly retroverse and forming an angular chevron at the level of the median furrow.

The suture line, very sinuous (Fig. 19), shows a well developed lateral saddle and an asymmetrical, wide and deep lateral lobe, with a ratio *P/L* between 0.40 and 0.50. The depth of the lateral lobe decreases through ontogeny. The delineation of the suture line on the ventral region is not visible. The position of the siphuncle is unknown.

The specimens no. NMNS PM6858 and no. NMNS PM6859 are very fragmentary, and show characteristics identical to those observable in the holotype. The specimen no. NMNS PM6858 (Pl. XXXIV, fig. 2; Pl. XXXV, fig. 3) corresponds to a body chamber; we observe in particular, on the ventral region, the characteristic ornamentation visible in the holotype, constituted by fine growth lines forming an angular chevron. The specimen no. NMNS PM6859 (Pl. XXXV, fig. 3) is constituted by a fragment of a small-sized whorl (young specimen or fragment of inner whorls of an adult specimen). Flanks show an ornamentation formed by wide and radial ribs, flexuous, similar to the ones visible on the phragmocone of the holotype.

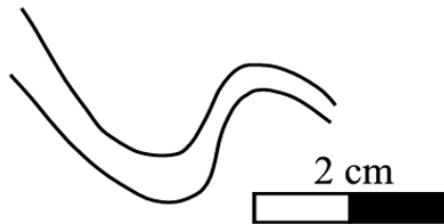


Figure 19: *Heminutilus ? tyosiensis* (YABE & OSAKI, 1953). Suture line of specimen no. NMNS P1-4200, right side.

Discussion and comparisons: *Heminutilus ? tyosiensis* (YABE & OSAKI, 1953) is close to *Heminutilus ? japonicus* sp. nov. The differences between both taxa were previously commented in the section of discussion and comparisons of *H. ? japonicus* sp. nov.

The very particular characteristics of *Heminutilus ? tyosiensis* (YABE & OSAKI) (the width of the ventral region and the presence of growth lines in the same part of the nautiloid) distinguish it from most of the other taxa of the genus *Heminutilus* SPATH, 1927. Furthermore, the general shape of the shell and the plan of its suture line, with an asymmetrical lateral lobe and a wide and rounded lateral saddle, could also move this taxon closer to the genus *Xenocheilus* SHIMANSKY & ERLANGER, 1955, in particular to the species *Xenocheilus ulixis* SHIMANSKY & ERLANGER, 1955, from the Hauterivian of Crimea. The stratigraphical gap as well as the unknown position of the siphuncle in *Heminutilus ? tyosiensis* (YABE & OSAKI) make it difficult to attribute this species with certainty to the genus *Heminutilus* SPATH.

Heminutilus etheringtoni DURHAM, 1946, shows, however, a comparable ventral region, but can be distinguished by a clearly more rounded ventro-lateral edge, as well as the absence of a median furrow and lateral ornamentation on the phragmocone. The plan of the suture line is also different, with a more reduced lateral saddle and a clearly shallower lateral lobe in *H. etheringtoni* DURHAM.

Heminutilus rangei (HOPPE, 1922) also presents some affinities with *Heminutilus ? tyosiensis* (YABE & OSAKI), in particular the presence of a rather similar ribbing on the phragmocone and of the ventro-lateral edges well defined on the body chamber. *H. ? tyosiensis* (YABE & OSAKI) can be distinguished from it easily by a greater thickness and by the absence of ribbing on the body chamber.

Genus *Josanautilus* MARTÍNEZ & GRAUGES, 2006

Type species: *Nautilus lacerdae* VILANOVA, 1870 (by original designation of MARTÍNEZ & GRAUGES, 2006, p. 17).

Discussion: the genus is monospecific. Its stratigraphic distribution is very restricted, limited to the Early Aptian, upper part of the *Deshayesites forbesi* Zone (*Roloboceras hambrovi* Subzone). It is known only from France and Spain.

Josanautilus lacerdae (VILANOVA, 1870)

Pl. XXXIX, figs. 2-3; Pl. XLI, figs. 2-3;
Pl. XLII, fig. 2; Pl. XLIII, fig. 2;
Pl. XLVI, figs. 1-3; Pl. XLVII, figs. 1-2;
Pl. XLVIII, figs. 1-3; Pl. XLIX, fig. 1;
Pl. L, fig. 1; Pl. LI, fig. 1

1870 *Nautilus lacerdae* sp. nov. - VILANOVA, Pl. 3, fig. 3.

1950 *Nautilus lacerdae* VILANOVA, 1870 - BATALLER, p. 64, Fig. 653.

1960 *Carinonautilus ? lacerdae* (VILANOVA, 1870) - WIEDMANN, p. 194, Fig. 24.

2006 *Josanautilus lacerdae* (VILANOVA, 1870) - MARTÍNEZ & GRAUGES, p. 18, Figs. 3a, 4b-e, 6b-c, 7c.

? **2007** *Nautilus* cf. *lacerdae* VILANOVA, 1870 - CONTE, p. 10, photos 8- 9.

Material studied (N = 15): specimens no. t1074, coll. BAUDOUIN, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France); no. VI011, coll. BOSELLI, no. CH01, coll. BAUDOUIN, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France); no. MHNG GEPI 83570, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Groumaud section, Bourg-Saint-Andéol (Ardèche, France); no. A-148, JM-35, PUAB 48003, PUAB 48057, PUAB 48082, PUAB 48086, PUAB 48178, PUAB 48222, PUAB 48276, PUAB 48302, coll. PUAB, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain); no. Se-11.1, coll. MV, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mas Segura, Province of Castellon (Spain).

Type: the holotype (by monotypy) is the specimen no. MNCN I-14855, coll. of the Museo Nacional de Ciencias Naturales (Madrid), drawn by VILANOVA (1870) and photographed by MARTÍNEZ & GRAUGES (2006). It comes from the Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone of Josa (Province of Teruel, Spain). The figure of MARTÍNEZ & GRAUGES (2006) is reproduced here Pl. XLII, fig. 2.

Geographical distribution: *Josanautilus lacerdae* (VILANOVA, 1870) is known only from France and Spain.

Table 13: Measurements of *Josanautilus lacerdae* (VILANOVA, 1870).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
Holotype no. MNCN I-14855	126	75	56	0.6	0.44	0.75	-	-	-	-	-	-	-
	109	71	-	0.65	-	-	-	-	-	22	49	0.45	0.69
	93	57	-	0.61	-	-	-	-	-	20	42	0.48	0.74
no. tl074	c167	106	72	0.63	0.43	0.68	c28	0.17	0.26	-	-	-	-
	-	80	46	-	-	-	19	-	0.24	-	-	-	-
no. MHNG GEPI 83570	c167	99	c65	0.59	0.39	0.66	-	-	-	-	-	-	-
	-	91	-	-	-	-	26	-	0.29	-	-	-	-
	-	75	-	-	-	-	23	-	0.31	16	61	0.26	0.81
no. VI011	148	95	72	0.64	0.49	0.76	31	0.21	0.33	-	-	-	-
	98	62	43	0.63	0.44	0.69	c13	0.13	0.21	-	-	-	-
no. CH01	156	110	92	0.71	0.59	0.84	-	-	-	-	-	-	-
no. A-148	87	57	41	0.66	0.47	0.72							
	58.8	31.5	35.6	0.53	0.61	1.13	12.6	0.21	0.40	8.6	22.5	0.38	0.72
	47.4	26.5	28.3	0.56	0.6	1.07	11.1	0.23	0.42	8.1	20.5	0.4	0.77
no. JM-35	-	-	-	-	-	-	-	-	-	-	-	-	-
no. PUAB 48003	c155	c96	c70	0.62	0.45	0.73							
	-	59.3	40.2	-	-	0.68	22.0	-	0.37	16.6	37.7	0.44	0.64
no. PUAB 48057	-	-	-	-	-	-	-	-	-	-	-	-	-
no. PUAB 48082	c165	98	c84	0.59	0.51	0.86	-	-	-	-	-	-	-
no. PUAB 48086	-	c57	53	-	-	0.93							
	-	45.2	47.1	-	-	1.04	18.7	-	0.41	11.6	31.2	0.37	0.69
no. PUAB 48178	c165	c100	-	0.61	-	-							
	135	88	57.3	0.65	0.42	0.65							
	-	80.8	58.3	-	-	0.72	27.4	-	0.34	16.9	50.5	0.33	0.63
	-	67.9	54.2	-	-	0.8	18.2	-	0.27	17.6	43.9	0.4	0.65
no. PUAB 48222	103	72.0	c48	0.7	0.47	0.67	-	-	-	-	-	-	-
	-	57.3	47.7	-	-	0.83	-	-	-	14.4	36.0	0.4	0.63
no. PUAB 48276	88	56	c46	0.64	0.52	0.82							
	-	35.3	42.3	-	-	1.2	14.3	-	0.41	7.4	23.9	0.31	0.68
no. PUAB 48302	78	53	c38	0.68	0.49	0.72							
	74.7	42.8	40.3	0.57	0.54	0.94	15.0	0.20	0.35	11.8	30.0	0.39	0.7
	52.5	30.0	27.7	0.57	0.53	0.92	10.1	0.19	0.34	8.0	22.1	0.36	0.74

Stratigraphical distribution: according to MORENO *et al.* (2007), the species *Josanautilus lacerdae* (VILANOVA, 1870) is present in the sector of Oliete and Josa, in the Margas del Forcall Formation, dated from the *Roloboceras hambrovi* Subzone by its plentiful fauna. It is likely that the holotype as well as paratypes studied by MARTÍNEZ & GRAUGES (2006) come from this formation. Specimens no. tl074, VI011, CH01 and MHNG GEPI 83570 also come from the *Roloboceras hambrovi* Subzone. Thus, *Josanautilus lacerdae* (VILANOVA) seems restricted to the upper part of the *Deshayesites forbesi* Zone (*Roloboceras hambrovi* Subzone).

Dimensions (in mm): see Table 13.

Description: the various studied specimens show a very involute coiling, with a wide trapezoidal section, whose maximum thickness is located near the umbilical edge. Flanks are flat, convergent towards a relatively wide ventral region.

In the internal whorls the ventral region is rounded, with a weak median keel, and becomes gradually flat through ontogeny, with rounded ventro-lateral edge. On the adoral part of the phragmocone and on the body chamber, the ventral region widens and the ventral ornamentation strengthens: the median keel becomes strong, with round relief, lined with longitudinal ribs which appear gradually, but

always remain weaker than the median keel. One or two longitudinal ribs are observable on each side of the keel at the beginning of the body chamber, up to three on each side at the end of the body chamber (specimen no. Se-11.1, Pl. XLVI, fig. 2).

Lateral ornamentation is almost absent: we observe only, as in some species of the genus *Heminautilus* SPATH, 1927, the appearance of convex and rursiradiate ribs at the end of the body chamber, especially visible in the upper half of the flanks (specimen no. Se-11.1, Pl. XLVIII fig. 3).

The suture line (Fig. 20) shows a well developed, rounded lateral saddle, and a wide lateral lobe of rather variable depth, with P/L between 0.26 and 0.48. It crosses the ventral region almost straight, without forming a ventral lobe. The siphuncle, whose position was unknown until now, is visible on the specimen no. CH01 (Pl. XLVII fig. 2): it is placed near the dorsal region, at approximately $1/3$ of the height of the section.

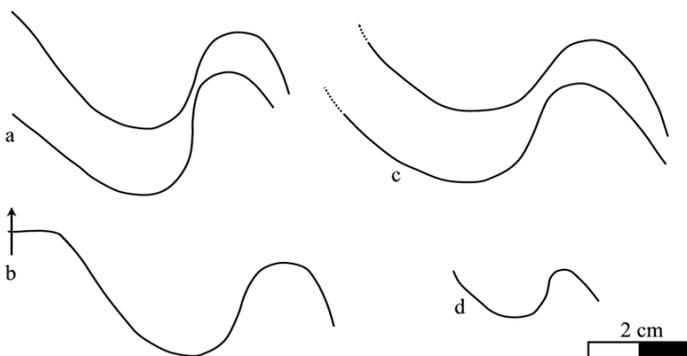


Figure 20: *Josanautilus lacerdae* (VILANOVA, 1870). Suture line of specimen no. MNCN I-14855, left side (a-b), PUAB 48222, right side (c) and A-148, left side (d).

Discussion and comparisons: the particular characteristics of *Josanautilus lacerdae* (VILANOVA, 1870) distinguish it immediately from most of the representatives of the genus *Heminautilus* SPATH, 1927.

J. lacerdae (VILANOVA) can, however, be compared to the slightly older (Late Barremian, *Imerites giraudi* Zone, to Early Aptian, *Deshayesites forbesi* Zone) species *Heminautilus sanctaecrucis* CONTE, 1980, which also shows a ventral keel, the same type of ribbing only present at the end of the body chamber, and a suture line which shows a comparable delineation. *J. lacerdae* (VILANOVA) can be distinguished from *H. sanctaecrucis* CONTE by its section and its much wider ventral region, its stronger and rounded ventral keel, and by the presence of longitudinal ribs on the ventral region of the body chamber.

The wide section of *J. lacerdae* (VILANOVA) is also comparable to that observed in the species *H. ? tyosiensis* (YABE & OSAKI, 1953) and *H. etheringtoni* DURHAM, 1946, but can be distinguished from them easily by the absence of longitudinal ornamentation in the latter two.

Josanautilus aff. *lacerdae* (VILANOVA, 1870)

Pl. L, fig. 2; Pl. LI, fig. 2

Material studied (N = 1): specimen no. VI010, coll. BOSELLI, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France).

Dimensions (in mm): see Table 14.

Description: adult specimen, badly preserved. The section is trapezoidal, relatively wide in the phragmocone, then widens very strongly in the body chamber. Flanks are flat or slightly convex, convergent towards the ventral region.

On the visible part of the phragmocone, the ventral region is fairly wide, flat, with a poorly defined median keel. On the body chamber, it strongly widens, where two longitudinal ribs gradually appear on each side of the median keel. On the last part of the body chamber, the longitudinal ribs and the median keel have the same strength.

No ornamentation can be seen on the major part of the flanks. On the second half of the body chamber, rursiradiate ribs appear, only visible near the ventral region.

The suture line (Fig. 21) shows a wide and rounded lateral saddle and a well developed and relatively deep lateral lobe (P/L between 0.33 and 0.37). There is no ventral lobe.



Figure 21: *Josanautilus* aff. *lacerdae* (VILANOVA, 1870). Suture line of specimen no. VI010, left side.

Discussion and comparisons: *Josanautilus* aff. *lacerdae* (VILANOVA, 1870) is very close to *J. lacerdae* (VILANOVA), but differs from it by its weaker median keel, of the same strength as the longitudinal ribs which frame it, as well as by its particularly wide section. It is not however excluded that these characteristics could represent only one slightly atypical morph of *J. lacerdae* (VILANOVA).

Table 14: Measurements of *Josanautilus* aff. *lacerdae* (VILANOVA, 1870).

	D	H	E	H/D	E/D	E/H	M	M/D	M/H	P	L	P/L	L/H
	146	95	83	0.65	0.57	0.87	27	0.18	0.28	-	-	-	-
no. VI010	90	62	50	0.69	0.56	0.81	23	0.26	0.37	17	46	0.37	0.74
	81	54	43	0.67	0.53	0.8	15	0.19	0.28	13	39	0.33	0.72

J. aff. lacerdae (VILANOVA) also shows some superficial resemblance with the Berrisian species *Aulaconautilus sexcarinatus* (F.-J. PICTET, 1867), but can be distinguished from it by the characteristics explained in the section II. 2.: a very different section, a higher expansion rate of whorls, the presence of a median keel on the ventral region, the presence of ribbing at the end of the body chamber and a suture line with a different plan.

IV. Phylogenetic relationships within the genera *Heminautilus* SPATH, 1927, and *Josanautilus* MARTÍNEZ & GRAUGES, 2006

1. *Heminautilus boselliorum* DELANOY et al., 2012

At present, *H. boselliorum* DELANOY et al. is the oldest known species of the genus *Heminautilus* SPATH, 1927, and is present in the Early Barremian, upper part of *Kotetishvilia nicklesi* Zone to lower part of *Kotetishvilia compressissima* Zone. As explained in the section II. 1., its origin must probably be related to the genus *Pseudocnoceras* SPATH, 1927, and in particular to the taxon *Pseudocnoceras campichei* (KARAKASCH, 1907), from the Hauterivian? However, the evolutionary relationship between these genera requires more data and for this reason remains to be developed.

2. *Heminautilus rangei* (HOPPE, 1922)

The characteristics observed in *H. rangei* (HOPPE) allow us to envisage an origin from the taxon *H. boselliorum* DELANOY et al., 2012 (Fig. 22): a comparable section; a similar ventral region, flat or slightly concave with the possible presence of a weak median keel; an identical suture line, with a lateral lobe of comparable depth (P/L most of the time between 0.25 and 0.30). Only a slightly wider section and especially the early appearance of characteristic ribbing clearly differentiate the species *H. rangei* (HOPPE) from *H. boselliorum* DELANOY et al. The very early appearance of the ribbing could be interpreted in this case as the result of a peramorphic process of acceleration. However, the stratigraphical gap between both taxa is large [Early Barremian, *Kotetishvilia nicklesi*, *Nicklesia pulchella* and *Kotetishvilia compres-*

sissima zones for *H. boselliorum* DELANOY et al., Late Barremian, *Gerhardtia sartousiana* or *Imerites giraudi* zones for *H. rangei* (HOPPE)]; with the absence of stratigraphically intermediate specimens, this hypothesis needs to be confirmed.

3. *Heminautilus sanctaerucis* CONTE, 1980

As *H. rangei* (HOPPE, 1922), *H. sanctaerucis* CONTE presents very numerous similarities with *H. boselliorum* DELANOY et al., 2012, in particular a similar suture line, an identical section with a ventral region of the same profile and the same type of ribbing present only at the adoral end of the body chamber of the adult specimens. All these characteristics lead us to envisage a direct filiation (Fig. 22) between *H. boselliorum* DELANOY et al. and *H. sanctaerucis* CONTE, the major evolutionary trend being the development of a well defined ventral keel. Here too, the stratigraphical gap between both species is important [Early Barremian, *Kotetishvilia nicklesi* Zone to *Kotetishvilia compressissima* Zone for *H. boselliorum* DELANOY et al.; Late Barremian, *Imerites giraudi* Zone to Early Aptian, *Deshayesites forbesi* Zone for *H. sanctaerucis* CONTE]. The presence of *H. aff. sanctaerucis* CONTE in the *Gerhardtia sartousiana* Zone (specimen no. 415951, Pl. XII, fig. 4), whose characteristics seem intermediate between *H. boselliorum* DELANOY et al. and *H. sanctaerucis* CONTE, confirms this hypothesis.

4. *Heminautilus saxbii* (MORRIS, 1848)

H. saxbii (MORRIS) replaces *H. sanctaerucis* CONTE, 1980, in the Early Aptian, *Deshayesites forbesi* Zone and seems to descend directly from it (Fig. 22), essentially by disappearance of the typical ventral keel of *H. sanctaerucis* CONTE, development of a suture line with a slightly deeper lateral lobe [P/L generally between 0.20 and 0.35 for *H. sanctaerucis* CONTE and between 0.30 and 0.40 for *H. saxbii* (MORRIS)] and a more premature appearance of the ribbing on the adult body chamber.

H. saxbii (MORRIS) has also affinities with *H. boselliorum* DELANOY et al., 2012, but the very large stratigraphical gap between these species does not allow us to retain the hypothesis of a direct phyletic relation.

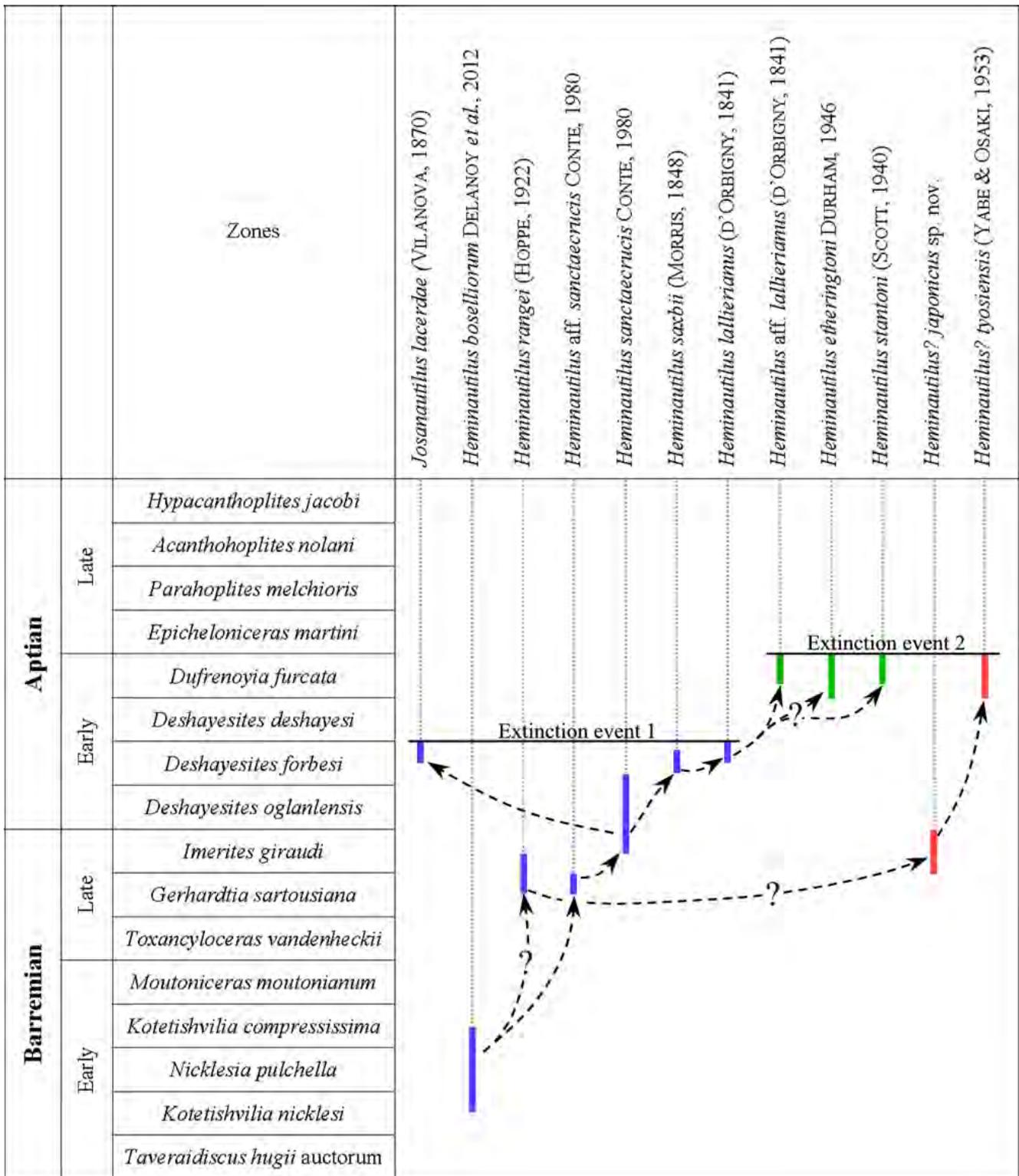


Figure 22: Phylogenetic relationships between the various species of the genera *Heminautilus* SPATH, 1927, and *Josanautilus* MARTÍNEZ & GRAUGES, 2006. In blue, species present only in the Tethyan Domain; in green, species present only in the North-Atlantic Domain; in red, species present only in Japan. Extinction event 1 represents the extinction of the genera *Heminautilus* SPATH and *Josanautilus* MARTÍNEZ & GRAUGES in the Tethyan Domain whereas extinction event 2 represents the global extinction of the genus *Heminautilus* SPATH. Explanations in text.

5. *Heminautilus lallierianus* (ORBIGNY, 1841)

As explained in part II, *H. lallierianus* (ORBIGNY) is a species very close to *H. saxbii* (MORRIS, 1848), and both taxa were considered as synonyms in numerous works. In reality, it seems that both species never coexisted; we think that *H. lallierianus* (ORBIGNY) represents a species different from *H. saxbii* (MORRIS) that in Europe, seems to have a slightly upper stratigraphical position in the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone. These data support that *H. lallierianus* (ORBIGNY) descends directly from *H. saxbii* (MORRIS) (Fig. 22), with the appearance of a more concave ventral region and the development of a more sinuous suture line (wider and rounded lateral saddle, clearly deeper lateral and ventral lobes).

6. *Heminautilus etheringtoni* DURHAM, 1946, and *Heminautilus stantoni* (SCOTT, 1940)

The presence of *H. aff. lallierianus* (ORBIGNY, 1841) in Mexico (specimen no. IGM 10050, Pl. XXXIX, fig. 1 and specimen no. MPL1, Pl. XL, fig. 1), in the *Dufrenoyia justinae* Zone (= top of the *Dufrenoyia furcata* Zone), shows that the genus *Heminautilus* SPATH, 1927, was present in Europe from the Early Barremian to the Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, but later during the latest Early Aptian the species *H. lallierianus* (ORBIGNY) probably migrated to America (cf. section V). *H. lallierianus* (ORBIGNY) is thus probably the ancestor (Fig. 22) of the species *H. etheringtoni* DURHAM and *H. stantoni* (SCOTT), known in Colombia, Venezuela and Arkansas (USA) in the uppermost part of the Early Aptian. The morphological differences with *H. lallierianus* (ORBIGNY) are relatively important: the appearance of a convex ventral region and a wider section in *H. etheringtoni* DURHAM, the development of a strong ribbing on the phragmocone in *H. stantoni* (SCOTT), and less sinuous suture lines in these two species. Furthermore, *H. etheringtoni* DURHAM and *H. stantoni* (SCOTT) also presents numerous similarities with *H. saxbii* (MORRIS, 1848) and an origin from this last species cannot be ruled out. In South America, Central America and southern North America, the genus *Heminautilus* SPATH, 1927, is only represented by some isolated specimens of often poorly known stratigraphical position; the evolution of the group in this paleogeographic domain remains uncertain.

7. *Heminautilus ? japonicus* sp. nov.

This new species is known only by two specimens, coming from the Late Barremian of Japan (= *Imerites giraudi* Zone). Its origin is difficult to specify:

- *Heminautilus ? japonicus* sp. nov. shows clear morphological affinities with *H. rangei* (HOPPE, 1922), from the Late Barremian of Egypt, explained in the paleontological study of the Japanese taxon. It could have descended from it (Fig. 22), by the disappearance of the characteristic ribbing of *H. rangei* (HOPPE) and the development of a clearly wider and deeper lateral lobe. However, the important geographical gap between these taxa suppose a migration which cannot be confirmed by the current available data.
- As explained previously, the characteristics of *Heminautilus ? japonicus* sp. nov. could indicate a relationship with some representatives of the genus *Xenocheilus* SHIMANSKY & ERLANGER, 1955, but the stratigraphical gap and the uncertain position of the siphuncle in *Heminautilus ? japonicus* sp. nov. prevent confirmation.

8. *Heminautilus ? tyosiensis* (YABE & OSAKI, 1953)

H. ? tyosiensis (YABE & OSAKI) is only represented by the four specimens illustrated by YABE & OSAKI, 1953, and OBATA *et al.*, 1975 (three of them shown here: Pl. XXXIII, fig. 2; Pl. XXXIV, figs. 2-3; Pl. XXXV, fig. 3), all coming from the uppermost part of the Early Aptian (= *Dufrenoyia furcata* Zone) from the Choshi Peninsula (Chiba Prefecture, Japan). This species is very close to *Heminautilus ? japonicus* sp. nov. from the Late Barremian of Japan and shows a similar sutural plan and the same ornamentation on the ventral region, formed by growth lines arranged in a chevron. *H. ? tyosiensis* (YABE & OSAKI) probably descended from *Heminautilus ? japonicus* sp. nov. (Fig. 22), with the appearance of a much wider ventral region and a ribbing well defined on the phragmocone.

9. *Josanautilus lacerdae* (VILANOVA, 1870)

The characteristics of *J. lacerdae* (VILANOVA), from the *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone of Spain and France, are very close to those of the genus *Heminautilus* SPATH, 1927, and were discussed in the section II. 2. *Josanautilus* MARTÍNEZ & GRAUGES, 2006, probably had its origin from *Heminautilus sanctaerucis* CONTE, 1980 (Fig. 22). These species follow one another in the *Deshayesites forbesi* Zone and have numerous common characteristics, in particular the presence of a ventral median keel; the main morphological change is the appearance in *J. lacerdae* (VILANOVA) of a wider section and a clearly different ventral region (wider and on which longitudinal ribs are added to the median keel on the body chamber).

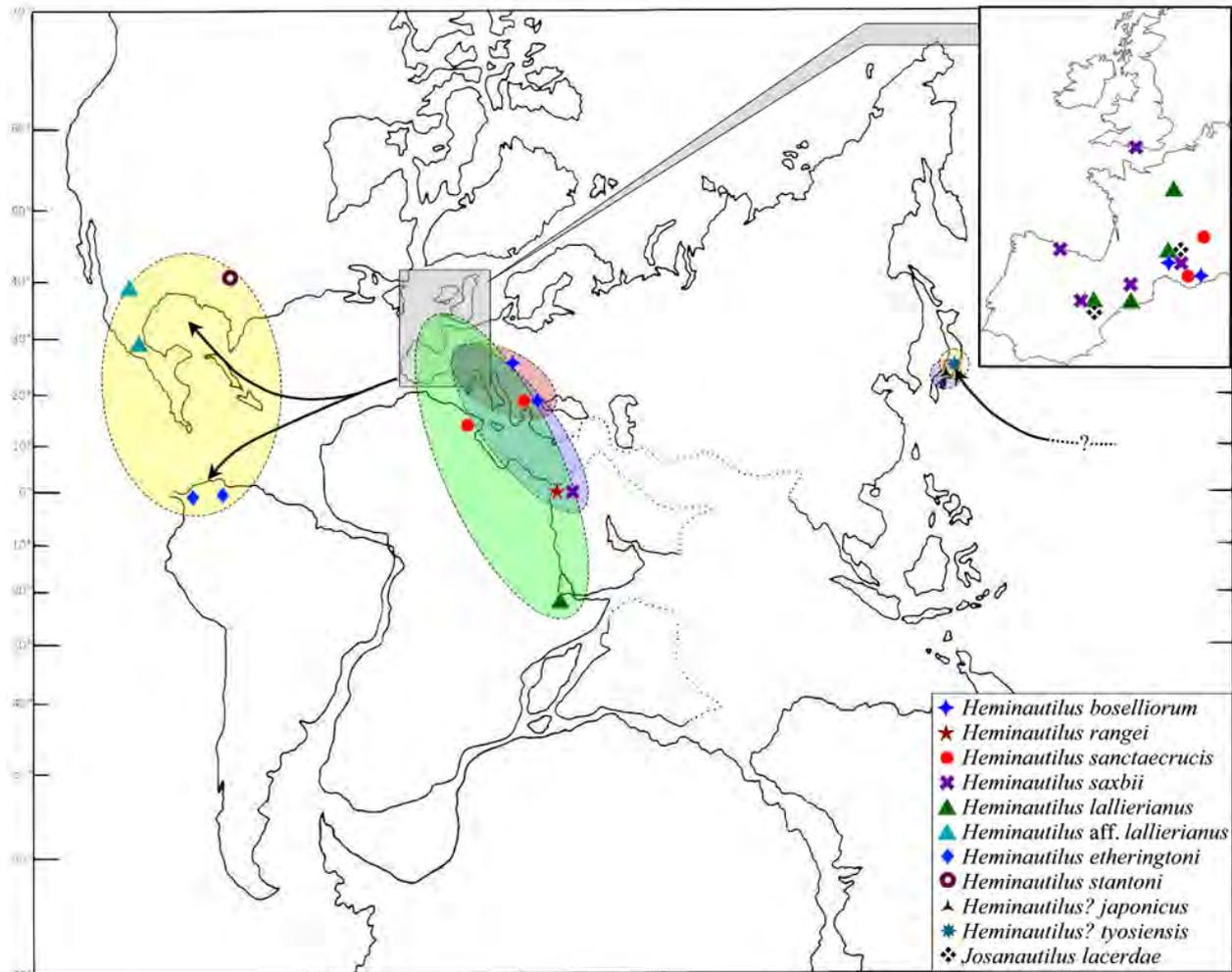


Figure 23: Geographical distribution of the various species of the genus *Heminautilus* SPATH, 1927 (paleogeographical map of the Aptian from KLINGER & KENNEDY, 1977, modified). In red, distribution of the genus *Heminautilus* SPATH during the Early Barremian; in blue, distribution of the genus *Heminautilus* SPATH during the Late Barremian; in green, distribution of the genera *Heminautilus* SPATH and *Josanautilus* MARTÍNEZ & GRAUGES, 2006, during the early Early Aptian (*Deshayesites oganlensis* and *Deshayesites forbesi* zones); in yellow, distribution of the genus *Heminautilus* SPATH during the late Early Aptian (*Dufrenoyia furcata* Zone).

V. Stratigraphical and paleogeographical distribution

As mentioned above, the oldest representatives of the genus *Heminautilus* SPATH, 1927, whose stratigraphical positions are exactly known belong to the species *H. boselliorum* DELANOY *et al.*, 2012, from the Early Barremian, *Kotetishvilia nicklesi*, *Nicklesia pulchella* and *Kotetishvilia compressissima* zones. In Europe, North Africa and Japan, the genus is known at intervals up to the Early Aptian. In particular, no specimens are known with certainty from the uppermost part of the Early Barremian or the lowermost part of the Late Barremian, in the *Moutoniceras moutonianum* and *Toxancyloceras vandenheckii* zones. The genus presents its acme in the Early Aptian, *Deshayesites forbesi* Zone, with the species *H. sanctaerucis* CONTE, 1980, *H. saxbii* (MORRIS, 1848) and *H. lallierianus* (ORBIGNY, 1841), particularly frequent in Spain, France and England (Isle of

Wight; SIMPSON, written communication, 2013). No younger specimens are known with certainty from Europe and North Africa. In the uppermost part of the Early Aptian, the genus seems to have migrated outside the Tethyan Domain (Fig. 23). Indeed, the taxa *H. aff. lallierianus* (ORBIGNY, 1841), *H. etheringtoni* DURHAM, 1946, *H. stantoni* (SCOTT, 1940) and *H. ? tyosiensis* (YABE & OSAKI, 1953) are known only from the uppermost part of the Early Aptian of Mexico, Colombia, Venezuela, USA (Arkansas) and Japan, respectively.

With the exception of the Japanese specimens, the stratigraphical and paleogeographical distribution of the genus *Heminautilus* SPATH (Fig. 23) can be split into two clearly different phases:

- A first phase, beginning in the Early Barremian, *Kotetishvilia nicklesi* Zone and continuing to the Early Aptian, uppermost part of the *Deshayesites forbesi* Zone, where the

genus is only present in the Tethyan Domain (Europe, North Africa and certainly Ethiopia; OGG *et al.*, 2012, p. 793). This phase is marked by the progressive extension of the paleogeographic domain of distribution of the genus *Heminautilus* SPATH (Fig. 23) and by the appearance of numerous species, differing in their ornamentation, the plan of their suture line and the shape of their ventral region, as well as by the appearance of the genus *Josanautilus* MARTÍNEZ & GRAUGES, 2006. Such a progressive extension of their distribution seems to be linked to the progressive expansion of the Early Barremian platforms (SKELTON *et al.*, 2003; MASSE & FENERCI-MASSE, 2011), which were their main habitat. This phase ends at the top of the *Deshayesites forbesi* Zone with the disappearance of the genus *Josanautilus* MARTÍNEZ & GRAUGES and the migration of the genus *Heminautilus* SPATH outside the Tethyan Domain (Extinction event 1, Fig. 22), which coincides with the end of the Oceanic Anoxic Event 1a (MORENO-BEDMAR *et al.*, 2009).

- A second phase, situated at the upper part of the Early Aptian, in the *Dufrenoyia furcata* Zone, where the genus *Heminautilus* SPATH is absent in the Tethyan Domain and present in the North-Atlantic Domain [Mexico, USA (Arkansas), Colombia and Venezuela; OGG *et al.*, 2012, p. 793], with forms of clearly less diversified morphology. The genus *Heminautilus* SPATH is here very frequently associated with diverse species of the genera *Dufrenoyia* KILIAN & REBOUL, 1915, and *Pseudosaynella* SPATH, 1923, and it is likely that it followed the same migratory routes as these latter (Fig. 23), thanks to the marine transgression recorded in the uppermost part of the Early Aptian (Ap4 tethyan sequence; MORENO *et al.*, 2012). This phase ends at the top of the Early Aptian by the disappearance of the genus *Heminautilus* SPATH (Extinction event 2, Fig. 22). It should be noted that with the current knowledge, no specimen is known with certainty from an interval corresponding in Europe to the *Deshayesites deshayesi* Zone and the lower part of the *Dufrenoyia furcata* Zone, between the top of the *Deshayesites forbesi* Zone of Europe and the uppermost part of the Early Aptian (*Dufrenoyia justinae* Zone of North America and Mexico (= top of the *Dufrenoyia furcata* Zone); *Dufrenoyia sanctorum-Stoyanowiceras treffryanus* Assemblage zone in Colombia).

The Japanese specimens studied here, belonging to the species *Heminautilus* ? *japonicus* sp. nov. and *H.* ? *tyosiensis* (YABE & OSAKI, 1953) are present in the Late Barremian (=

Imerites giraudi Zone) and the Early Aptian (= *Dufrenoyia furcata* Zone), perhaps even in the Early Barremian (OBATA *et al.*, 1982, p. 148; OBATA & MATSUKAWA, 2009, p. 254). The Japanese species seem to correspond to a local radiation of the group in a different domain (Pacific Domain; OGG *et al.*, 2012, p. 793) with a particular migration pattern and an endemic species evolution that remains poorly known. However, the particular morphology of this group does not allow excluding an origin in *Xenocheilus* SHIMANSKY & ERLANGER, 1955 (cf. section IV. 7.), which, if it were proved true by new data, could involve the restoration of the genus *Platynautilus* YABE & OSAKI, 1953 (type species *Platynautilus tyosiensis* YABE & OSAKI, 1953), for these species.

The genera *Heminautilus* SPATH and *Josanautilus* MARTÍNEZ & GRAUGES seem to have particular ecological requirements and to be generally present only in the outer platform domain. They are nearly absent in deeper marine environments, for example in the Vcontian Basin (southeast France) or the Subbetic Domain (Spain), where other genera like *Cymatoceras* HYATT, 1884, are nevertheless present. *Heminautilus* SPATH and *Josanautilus* MARTÍNEZ & GRAUGES are also frequently associated with ammonoids that are also characteristic of an outer platform environment:

- *Heminautilus boselliorum* DELANOY *et al.*, 2012, mainly known in the Lussan area (Gard, France), is associated there with numerous ammonites and nautilids characteristic of an external platform environment, belonging in particular to the genera *Davidiceras* VERMEULEN, 2003, *Torcapella* BUSNARDO, 1970, and *Eucymatoceras* SPATH, 1927. This species is also present at Escagnolles (Alpes-Maritimes) and Comps-sur-Artuby (Var), where the Early Barremian contains similar ammonite fauna and is represented by strongly condensed and glauconitic deposits, characteristic of a drowned platform deposit under a relatively shallow water depth (ARNAUD, 2005).
- Apparently, *Heminautilus sanctaecrucis* CONTE, 1980, is also only present in an external platform environment. Indeed the holotype no. MCGL 20747 comes from the "Marnes jaunes de la Vraconne" immediately above the Urgonian Limestone. The specimen no. Bw599 comes from the *Pseudocrioceras waagenoides* Subzone of La Bédoule (Bouches du Rhône, France), where it is associated with representatives of the genus *Pseudocrioceras* SPATH, 1924, typical of such an environment. Both the specimen of the FRASALI collection (Pl. XV, fig. 1a-b) and the specimen no. 131H (Pl. XI, fig. 5; Pl. XII, fig. 1) come from the Urgonian Limestone of the Vaucluse, which

represents deposits of carbonate platform associated with a reef environment. Finally, the specimens from Bulgaria no. K1 6001, K1 6002, K1 6003, K1 6004, K1 1692 studied by NIKOLOV & PARASHKEVANOV (1995) also come from platform deposits. However, the presence of *Heminautilus* aff. *sanctae-crucis* CONTE, 1980 (Pl. XII, fig. 4), in the stratotypic section of Angles (Alpes de Haute-Provence, Vocontian Basin, France) shows that an episodic presence in basinal settings is possible.

- In Spain, France and England, the species *Heminautilus saxbii* (MORRIS, 1848), *H. lallierianus* (ORBIGNY, 1841) and *Josanautilus lacerdae* (VILANOVA, 1870) are frequently associated with ammonites belonging to the genera *Roloboceras* CASEY, 1954, and *Megatyloceras* HUMPHREY, 1949, also characteristic of an external platform environment (MORENO-BEDMAR *et al.*, 2009, p. 70). Furthermore, the specimen of *Heminautilus* aff. *lallierianus* (ORBIGNY) no. IGM 10050, from the *Dufrenoyia justinae* Zone of Mexico, is associated in the same deposit with the genus *Pseudosaynella* SPATH, 1923, also characteristic of a platform environment. The specimen no. AMNH 25455 (illustrated by SCOTT, 1943) comes from the Harrar region (Ethiopia) where, during the Aptian, only a very short marine incursion is recorded within sandstone formations of fluvial origin (BOSELLINI *et al.*, 1999), very certainly representing a marine deposit under a very shallow water depth.

As previously explained about the genus *Angulithes* MONTFORT, 1808 (FRANK, 2010), the frequent appearance of ribbing on the body chamber or near the peristome can be interpreted as a strengthening of the shell, representing an adaptation to an environment of relatively high energy.

VI. Conclusions

The study of more than 160 specimens of the genera *Heminautilus* SPATH, 1927, and *Josanautilus* MARTÍNEZ & GRAUGES, 2006, allows us to identify more exactly the specific and stratigraphical characteristics of the various taxa of these two genera. In particular, this study demonstrates accurately the validity of the species *H. saxbii* (MORRIS, 1848) and *H. lallierianus* (ORBIGNY, 1841), and shows that *H. tejeriensis* MARTÍNEZ & GRAUGES, 2006, is a junior synonym of *H. saxbii* (MORRIS), of which it represents a slightly atypical morph. As well, some specimens filled, at least partially, important gaps in the knowledge of the genus *Heminautilus* SPATH, whose stratigraphical distribution is very intermittent between the Early Barremian and the upper part of the Early Aptian, as well as showing that the genus

Heminautilus SPATH was present from the Early Barremian, *Kotetishvilia nicklesi* Zone.

This work also highlights the existence of an important migration of the genus *Heminautilus* SPATH, 1927, during the Early Aptian. Indeed, with the exception of the Japanese specimens (belonging to a group with particular morphology and attributed with doubt to the genus *Heminautilus* SPATH), the genus seems to be only present in the Tethyan Domain (Europe and Africa) up to the uppermost part of the *Deshayesites forbesi* Zone, and later, it is absent in this domain, but it is present in the North-Atlantic Domain (Colombia, Venezuela, Mexico and the USA). Due to this paleogeographic migration and successive disappearances and appearances, we define two successive extinction events (Fig. 22).

It was also possible to formulate hypotheses about the origin and the phylogenetic and paleogeographic evolution of these two genera. In particular, the proposal of TINTANT (TINTANT & KABAMBA, 1983; TINTANT, 1993), who suggested the origin of *Heminautilus* SPATH from *Pseudocerceras* SPATH, 1927, seems the most likely with the current data. However, the incomplete knowledge of the genus *Heminautilus* SPATH, in particular during the Barremian, does not allow confirmation of this hypothesis. New specimens will be necessary for confirmation, in particular in the stratigraphical levels where the genus is unknown, in the middle part of the Barremian (*Moutoniceras moutonianum* and *Toxancyloceras vandenheckii* zones in particular), but also in the Early Aptian, between the uppermost part of the *Deshayesites forbesi* Zone and the uppermost part of the Early Aptian (= *Dufrenoyia furcata* Zone).

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Plates

Plate I

Fig. 1a-b: *Xenocheilus ulixis* SHIMANSKY & ERLANGER, 1955. Holotype no. 103/101, Early Hauterivian, Biassala (Crimea, Ukraine). Reproduction of the original illustration of KARAKASCH (1907; *Nautilus malbosii* F.-J. PICTET, Pl. I, fig. 12a-b).

Fig. 2a-b: *Pseudocenoceras campichei* (KARAKASCH, 1907). Holotype, Hauterivian?, Biassala (Crimea, Ukraine). Reproduction of the original illustration of KARAKASCH (1907; Pl. VIII, fig. 13a-b).

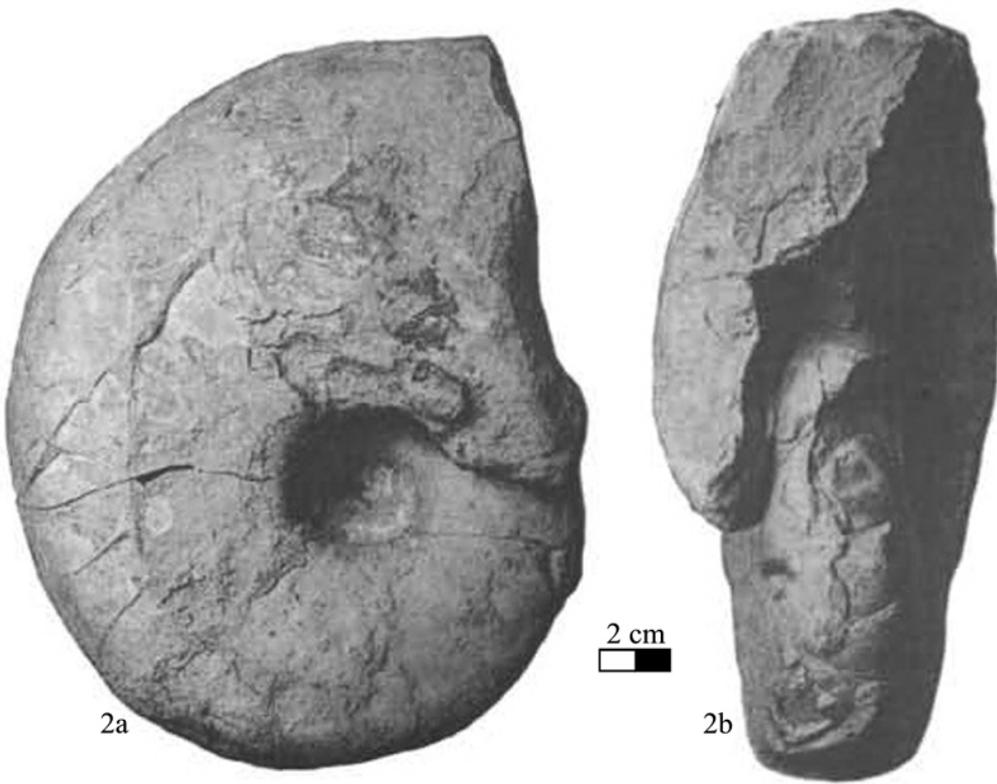
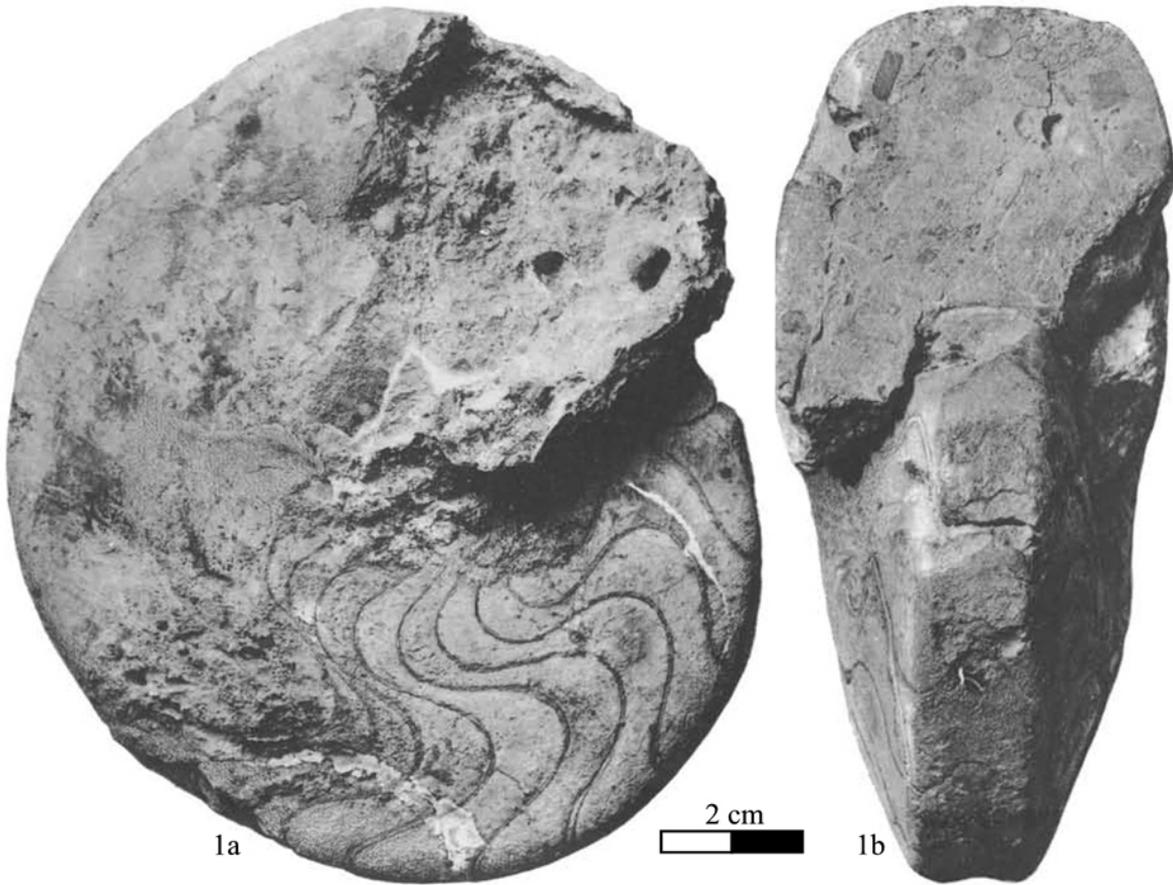


Plate II

Fig. 1a-b: *Aulaconutilus sexcarinatus* (F.-J. PICTET, 1867). Cast of the holotype no. MHNG GEPI 15856, Berriasian, Berrias (Ardèche, France). Coll. F.-J. PICTET.

Fig. 2a-b: "*Heminautilus*" *akatsui* MATSUMOTO, 1980. Holotype no. GK. H6909, Early Albian, Bishô (Kumamoto Prefecture, Japan).

Fig. 3a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Holotype no. Mej01a, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BAUDOUIN.

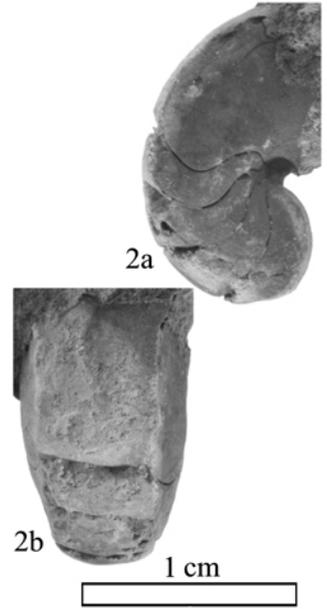


Plate III

Fig. 1: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Holotype no. Mej01a, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BAUDOUIN.

Fig. 2a-c: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. MNHN.F.A52065, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. FRAU.

Fig. 3a-c: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. Mej11, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BAUDOUIN.



Plate IV

Fig. 1a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. Mej03, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BAUDOUIN.

Fig. 2: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. Mej02, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BAUDOUIN.

Fig. 3a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. LUS02, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BOSELLI.



Plate V

Fig. 1a-c: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. RG2001, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. GONNET.

Fig. 2: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. LUS02, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BOSELLI.

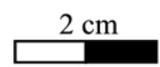
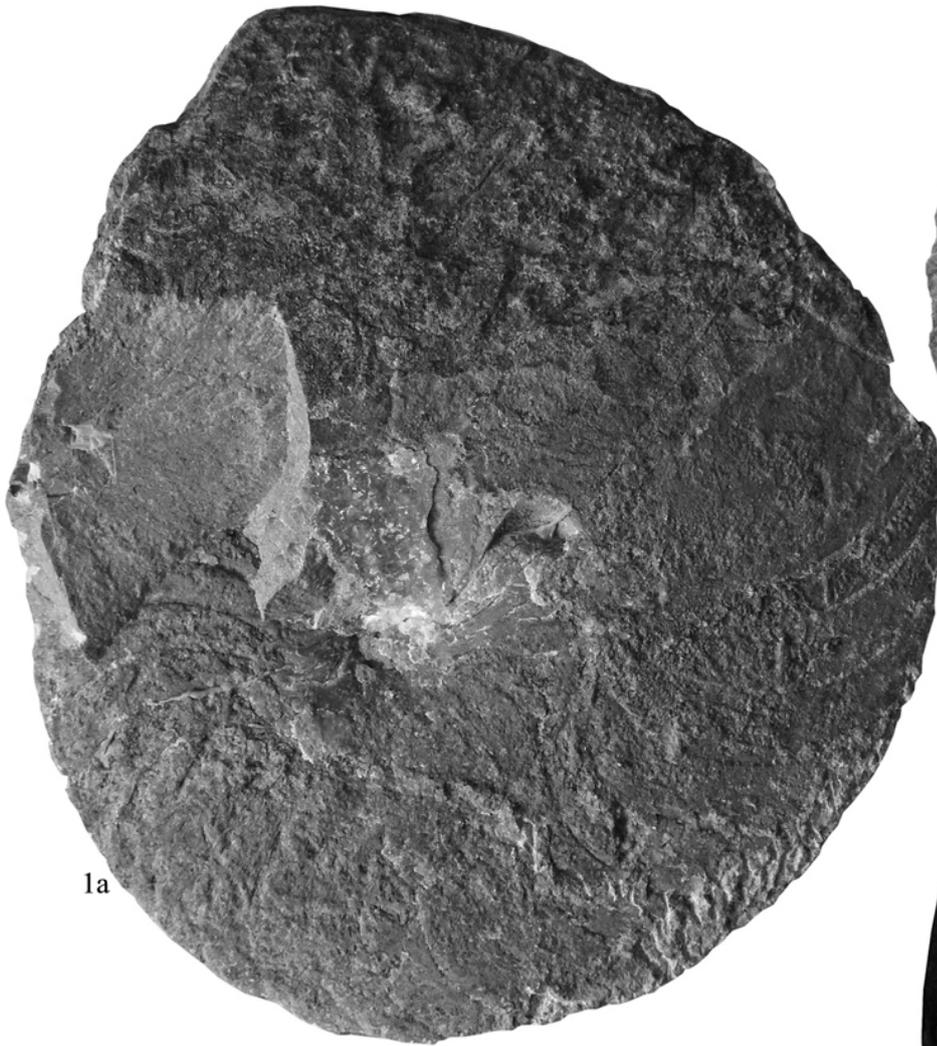


Plate VI

Fig. 1a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. RG2002b, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. GONNET.

Fig. 2: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. 415950, upper part of the *Kotetishvilia nicklesi* Zone, section no. 833, Comps-sur-Artuby (Var). Coll. VERMEULEN.

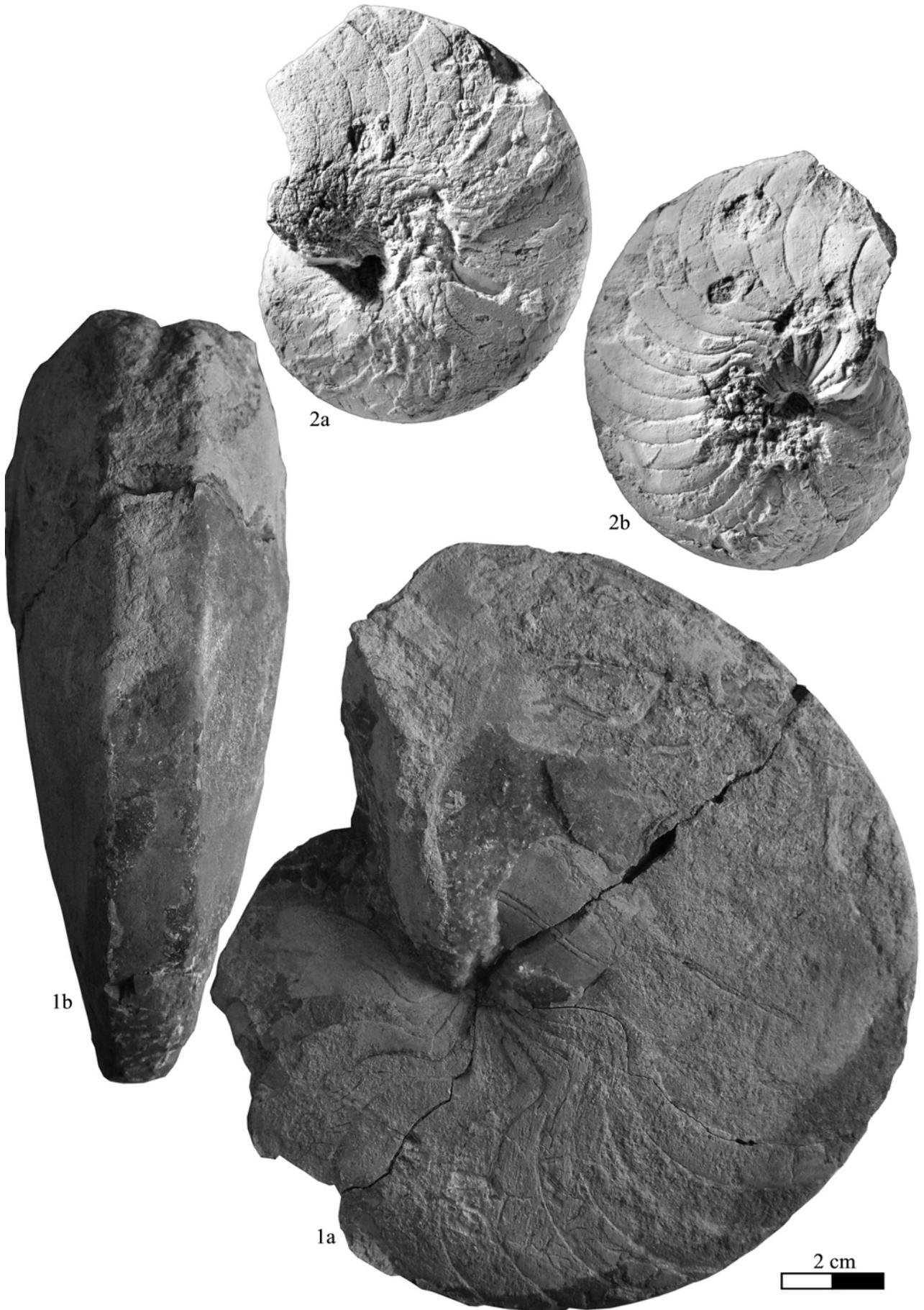


Plate VII

Fig. 1a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. LUS01, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. BOSELLI.

Fig. 2: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. MHNG GEPI 15935, Early Barremian, *Nicklesia pulchella* Zone?, Escragnolles (Alpes-Maritimes, France). Coll. F.-J. PICTET.

Fig. 3a-d: *Heminautilus rangei* (HOPPE, 1922). Specimen no. EM697, Late Barremian?, Bir Lagama, Gabal Maghara (north Sinai, Egypt).

Fig. 4a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. 415950, upper part of the *Kotetishvilia nicklesi* Zone, section no. 833, Comps-sur-Artuby (Var). Coll. VERMEULEN.

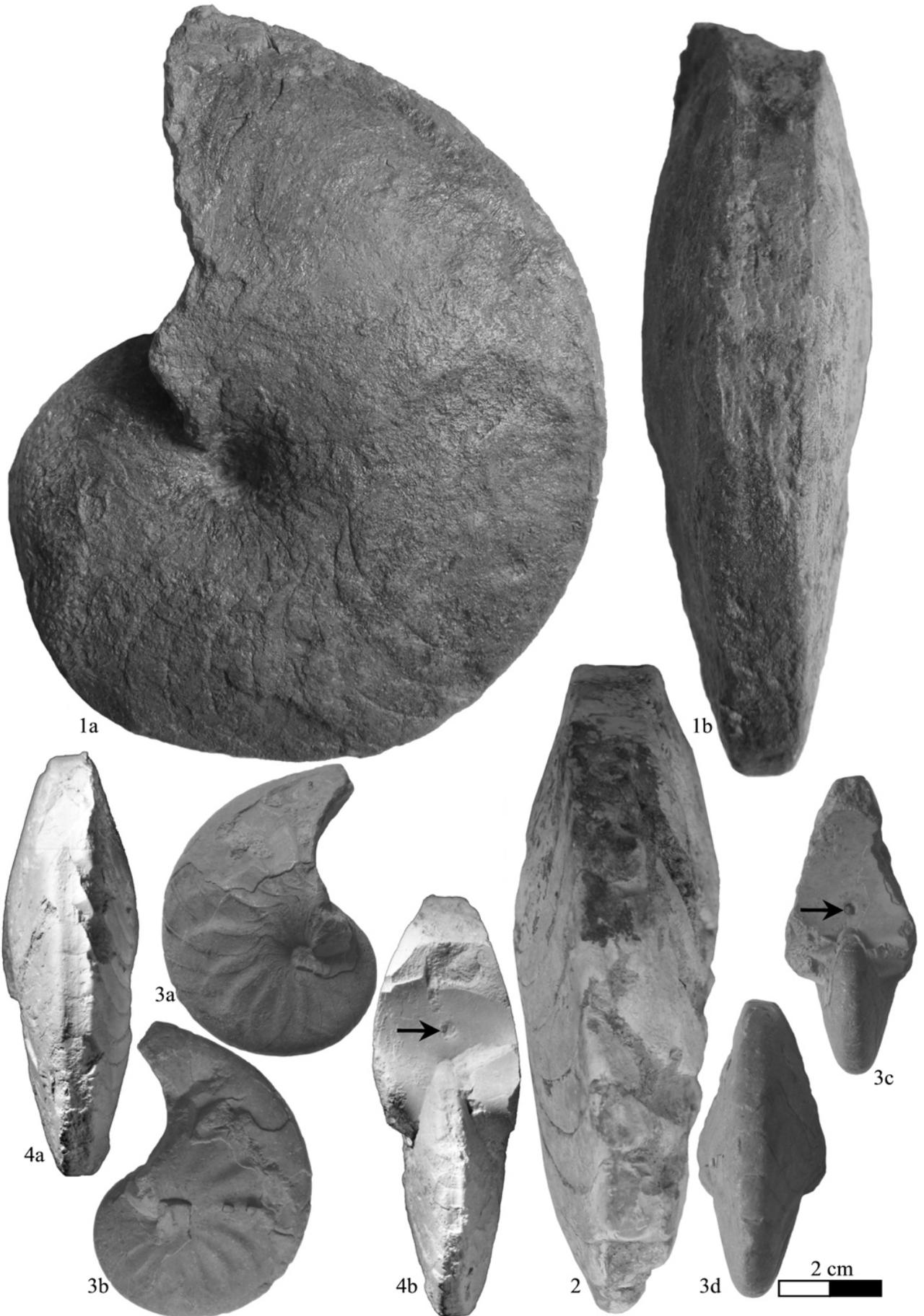


Plate VIII

Fig. 1: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. K1 1693, Early Barremian, Kara Mihal village (Šumen District, Bulgaria). Coll. MPUS.

Fig. 2a-c: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. K1 1694, Early Barremian, Kriva Reka village (Šumen District, Bulgaria). Coll. MPUS.

Fig. 3a-b: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. RG2002a, Early Barremian, *Nicklesia pulchella* Zone, la Lèque, Lussan (Gard, France). Coll. GONNET.

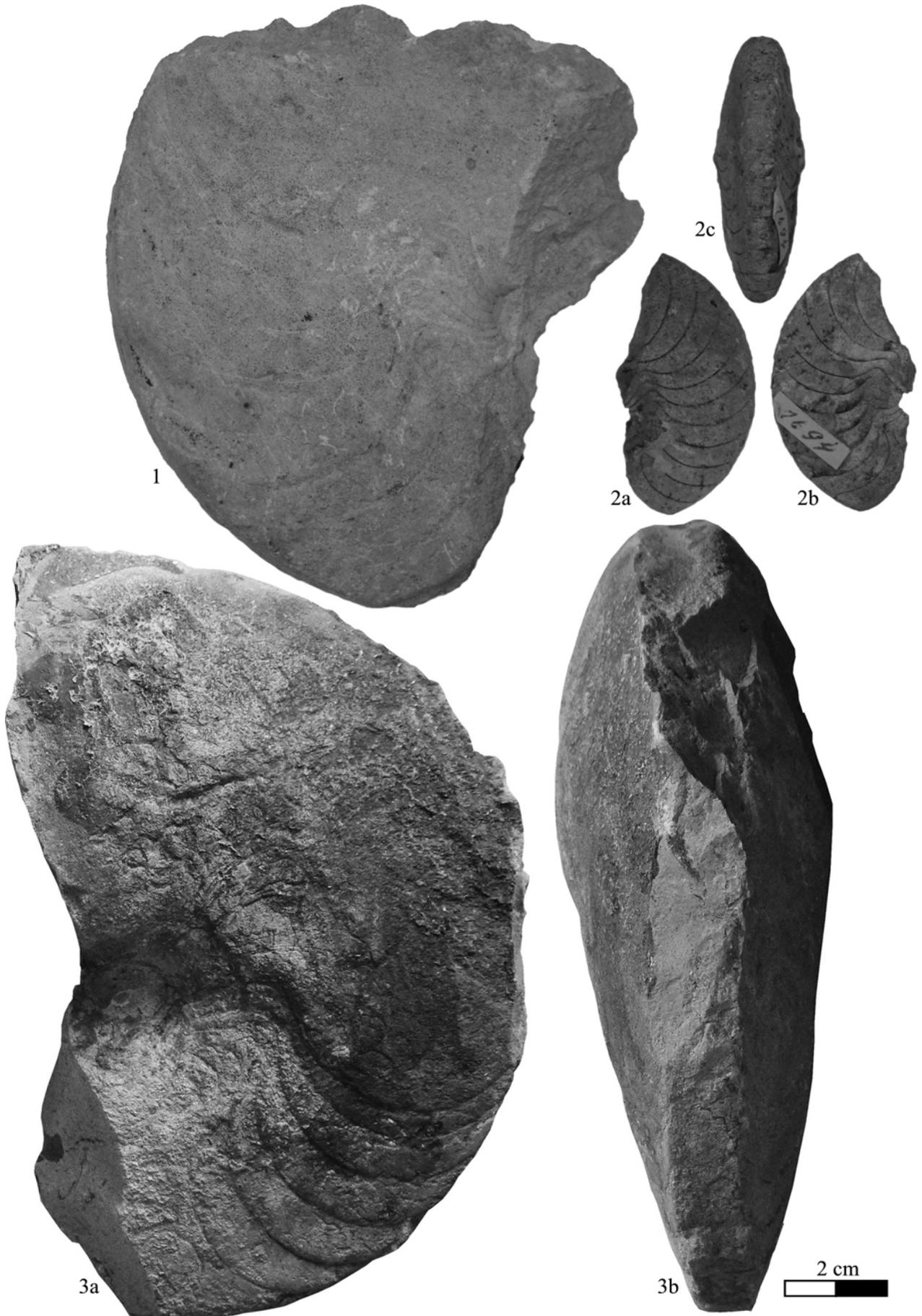


Plate IX

Fig. 1: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. K1 1693, Early Barremian, Kara Mihal village (Šumen District, Bulgaria). Coll. MPUS.

Fig. 2a-c: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. M 2002.554, Early Barremian, *Kotetishvilia compressissima* Zone, Bersek quarry (Gerecse Mountains, Hungary). Coll. HNHM.

Fig. 3: *Heminautilus boselliorum* DELANOY *et al.*, 2012. Specimen no. MHNG GEPI 15935, Early Barremian, *Nicklesia pulchella* Zone?, Escragnolles (Alpes-Maritimes, France). Coll. F.-J. PICTET.

Fig. 4a-c: *Heminautilus rangei* (HOPPE, 1922). Specimen no. EM696, Late Barremian?, Bir Lagama, Gabal Maghara (north Sinai, Egypt).

Fig. 5a-b: *Heminautilus rangei* (HOPPE, 1922). Specimen no. EM698, Late Barremian?, Bir Lagama, Gabal Maghara (north Sinai, Egypt).

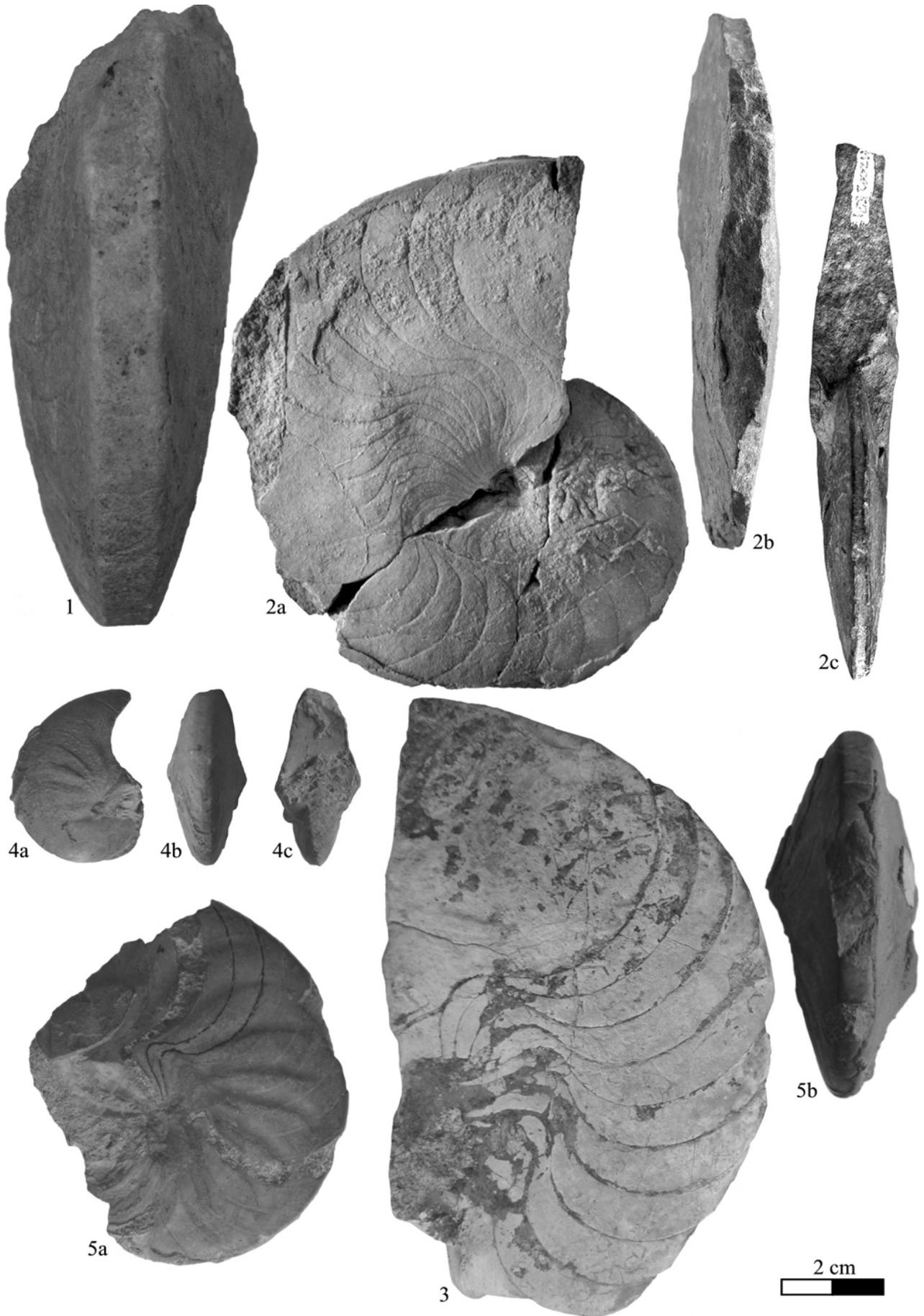


Plate X

Fig. 1a-b: *Heminautilus rangei* (HOPPE, 1922). Neotype no. EM699, Late Barremian?, Bir Lagama, Gabal Maghara (north Sinai, Egypt).

Fig. 2: *Heminautilus rangei* (HOPPE, 1922). Specimen no. EM698, Late Barremian?, Bir Lagama (north Sinai, Egypt).

Fig. 3a-c: *Heminautilus rangei* (HOPPE, 1922). Specimen no. TK25-15, Late Barremian, El Tourkumanyia (north Sinai, Egypt). Coll. GMMU.

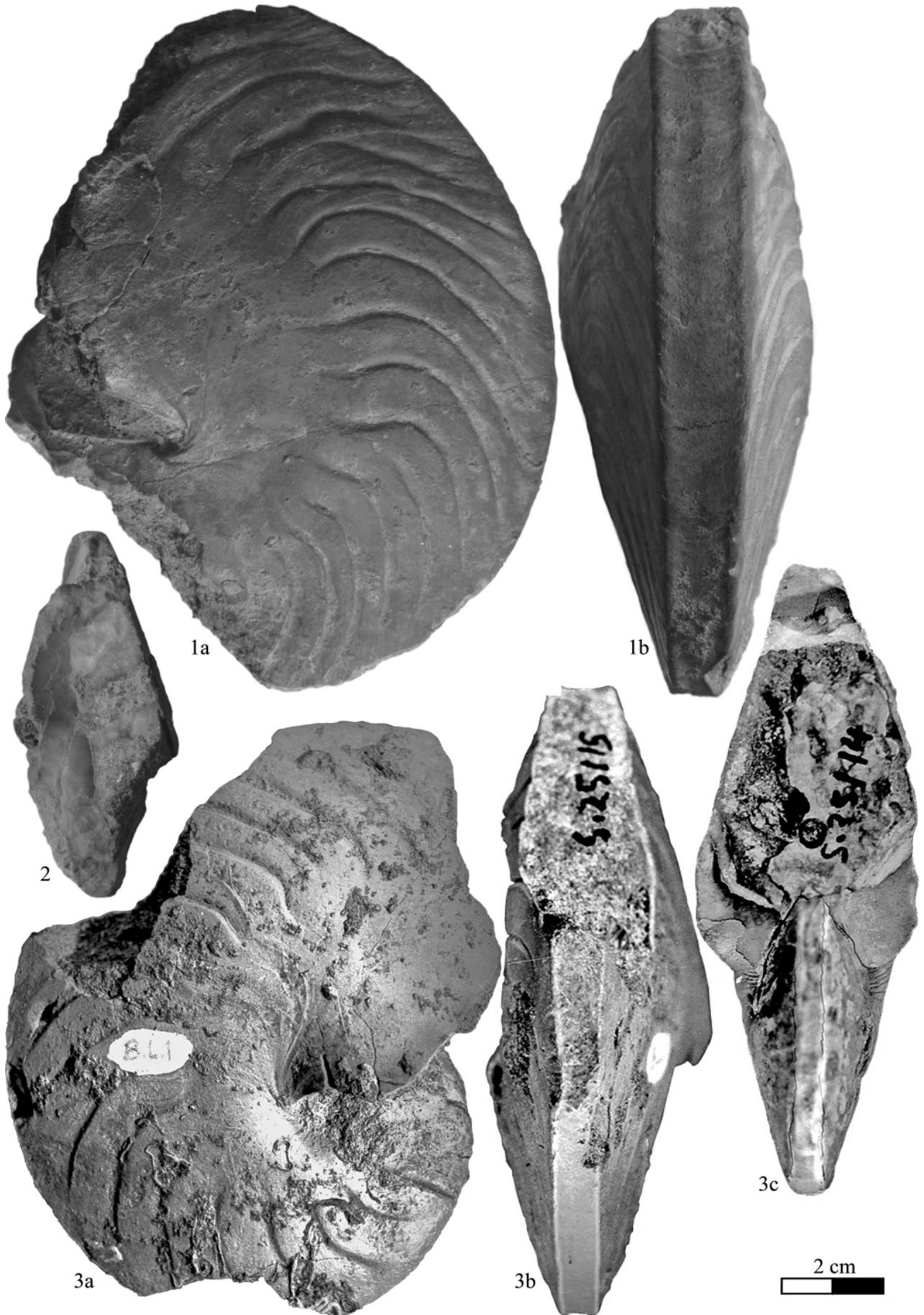


Plate XI

Fig. 1: *Heminautilus rangei* (HOPPE, 1922). Late Barremian?, "Ledschime", (north Sinai, Egypt). Reproduction of the original illustration of HOPPE (1922; Pl. 4, fig. 2).

Fig. 2: *Heminautilus rangei* (HOPPE, 1922). Late Barremian?, "Ledschime", (north Sinai, Egypt). Reproduction of the original illustration of HOPPE (1922; Pl. 4, fig. 3).

Fig. 3a-c: *Heminautilus sanctaerucis* CONTE, 1980. Holotype no. MCGL 20747, Early Aptian, *Deshayesites forbesi* Zone, Sainte-Croix (Switzerland). Coll. F.-J. PICTET.

Fig. 4: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. MHNG GEPI 15936, Early Aptian, *Deshayesites forbesi* Zone, La Presta, Val-de-Travers (Switzerland). Coll. F.-J. PICTET.

Fig. 5: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. 131H, latest Barremian/earliest Aptian, col des Abeilles, Monieux (Vaucluse, France). Coll. GESBERT.



Plate XII

Fig. 1: *Heminautilus sanctaecrucis* CONTE, 1980. Specimen no. 131H, latest Barremian/earliest Aptian, col des Abeilles, Monieux (Vaucluse, France). Coll. GESBERT.

Fig. 2: *Heminautilus sanctaecrucis* CONTE, 1980. Specimen no. Bw599, Late Barremian, *Imerites giraudi* Zone, *Pseudocrioceras waagenoides* Subzone, bed 78, Les Caniers, La Bédoule (Bouches du Rhône, France). Coll. GONNET, FSM.

Fig. 3a-b: *Heminautilus sanctaecrucis* CONTE, 1980. Specimen no. K1 6003, Late Barremian, nord of the Puševo village (Veliko Tŕrnovo District, Bulgaria). Coll. MPUS.

Fig. 4a-b: *Heminautilus* aff. *sanctaecrucis* CONTE, 1980. Specimen no. 415951, Late Barremian, *Gerhardtia sartousiana* Zone, base of the *Hemihoplites feraudianus* Subzone, bed 165/041, Angles (Alpes-de-Haute-Provence, France). Coll. BAUDOUIN (donated by VERMEULEN).

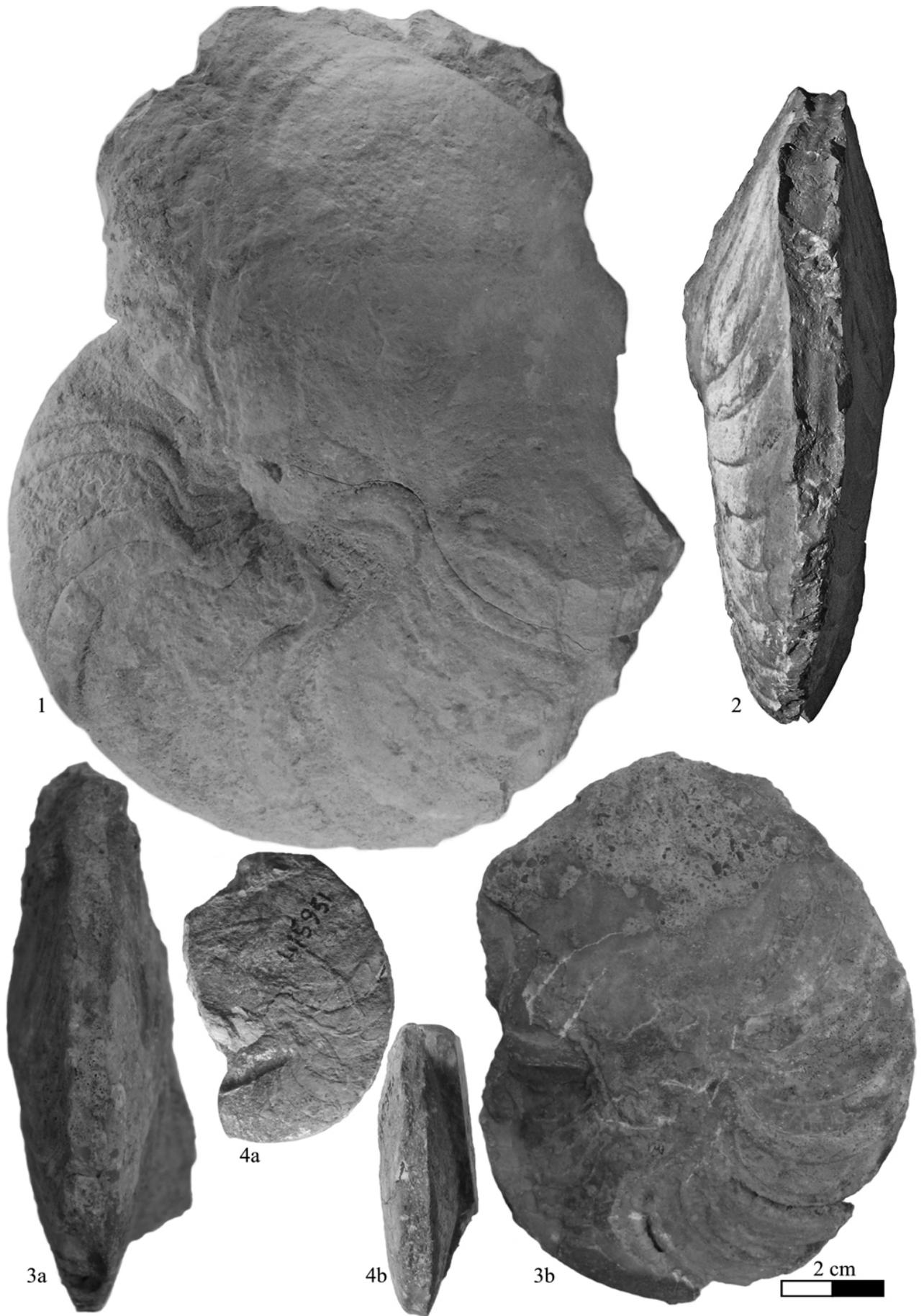


Plate XIII

Fig. 1a-b: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. Bw599, Late Barremian, *Imerites giraudi* Zone, *Pseudocrioceras waagenoides* Subzone, bed 78, Les Caniers, La Bédoule (Bouches du Rhône, France). Coll. GONNET, FSM.

Fig. 2a-b: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. K1 1692, Late Barremian, Lipnica village (Veliko Tárnovo District, Bulgaria). Coll. MPUS.

Fig. 3a-c: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. MHNN 26904, Early Aptian, *Deshayesites forbesi* Zone, La Presta, Val-de-Travers (Switzerland). Coll. JACQUART.



Plate XIV

Fig. 1a-b: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. K1 6001, Late Barremian, north of the Puševo village (Veliko Târnovo District, Bulgaria). Coll. MPUS.

Fig. 2a-b: *Heminautilus sanctaerucis* CONTE, 1980. Specimen no. K1 6002, Late Barremian, north of the Puševo village (Veliko Târnovo District, Bulgaria). Coll. MPUS.



1a



1b



2a



2b

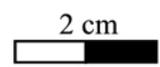


Plate XV

Fig. 1a-b: *Heminautilus sanctaecrucis* CONTE, 1980. Unregistered specimen, Early Aptian, Coustellet quarry (Vaucluse, France). Coll. FRASALI.

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 88770, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Tolodella, Maestrat Basin (Spain).

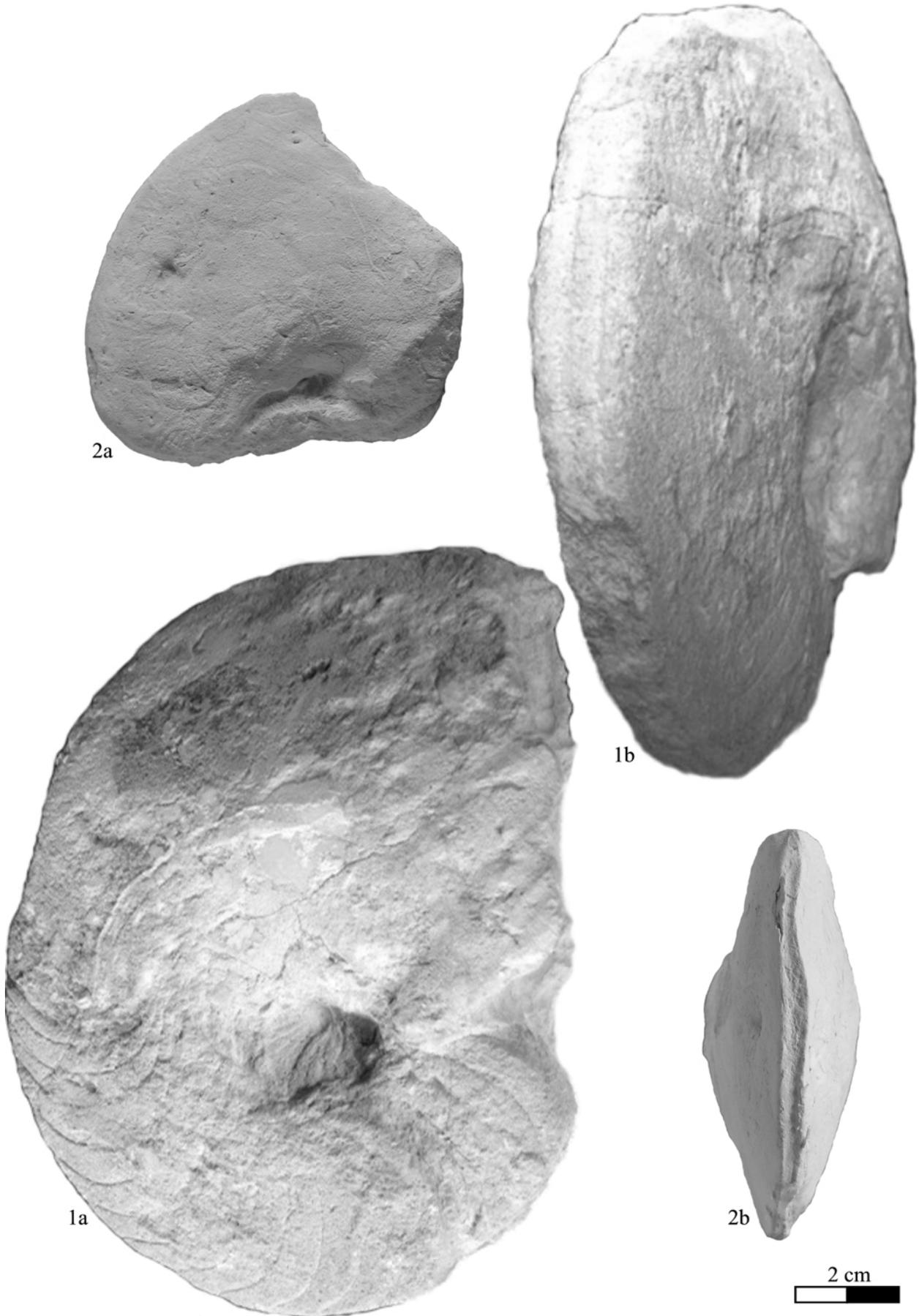


Plate XVI

Fig. 1: *Heminautilus sanctaecrucis* CONTE, 1980. Specimen no. K1 6001, Late Barremian, north of the Puševo village (Veliko Tarnovo District, Bulgaria). Coll. MPUS.

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Holotype no. BMNH 47019, Early Aptian, *Deshayesites forbesi* Zone, Isle of Wight (England). Coll. Saxby.

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. EM700, Early Aptian?, Bir Lagama, Gabal Maghara (Egypt).

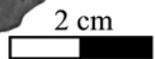
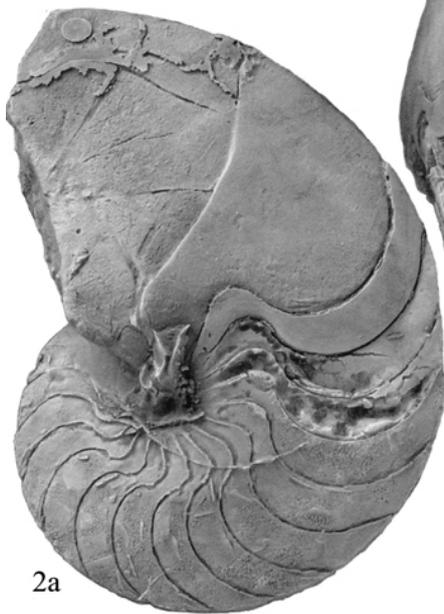


Plate XVII

Fig. 1a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. EM700, Early Aptian?, Bir Lagama, Gabal Maghara (Egypt).

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. A-127, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PMBb2, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

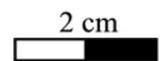
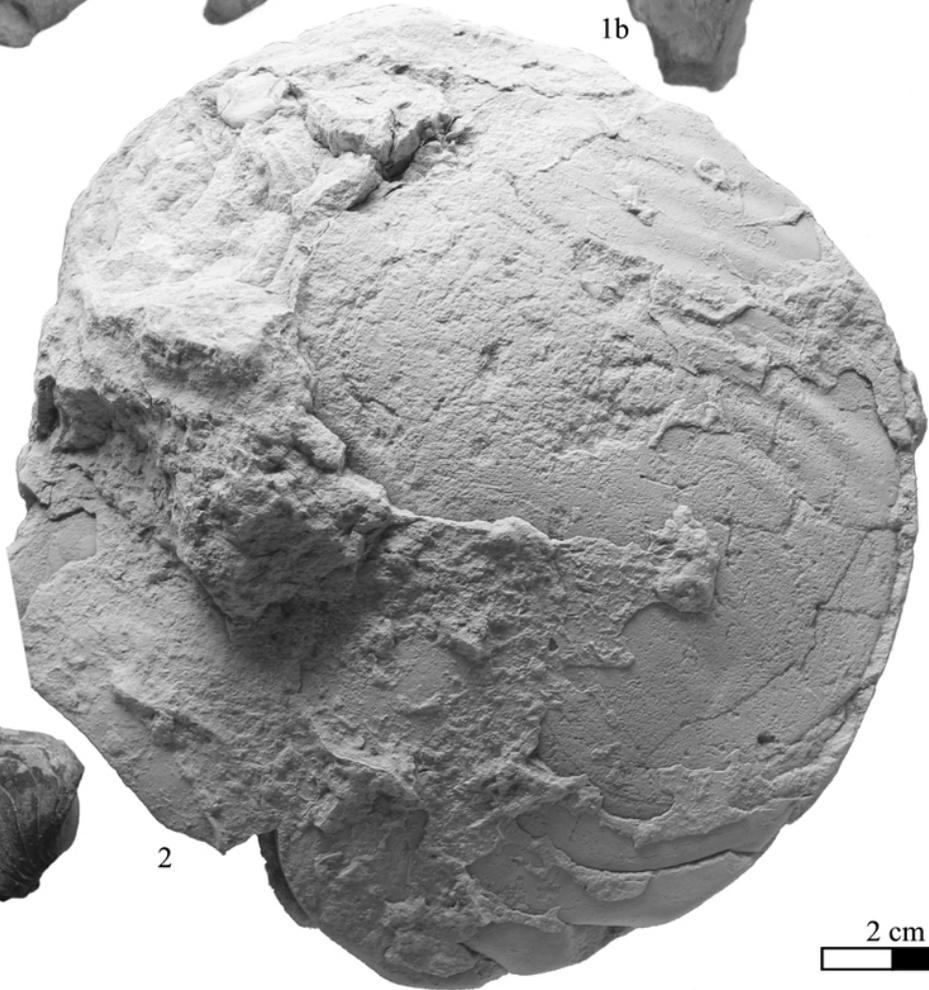
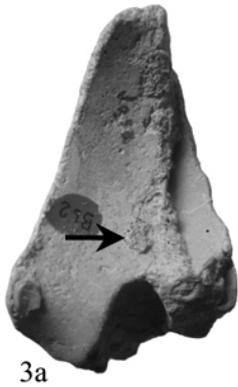
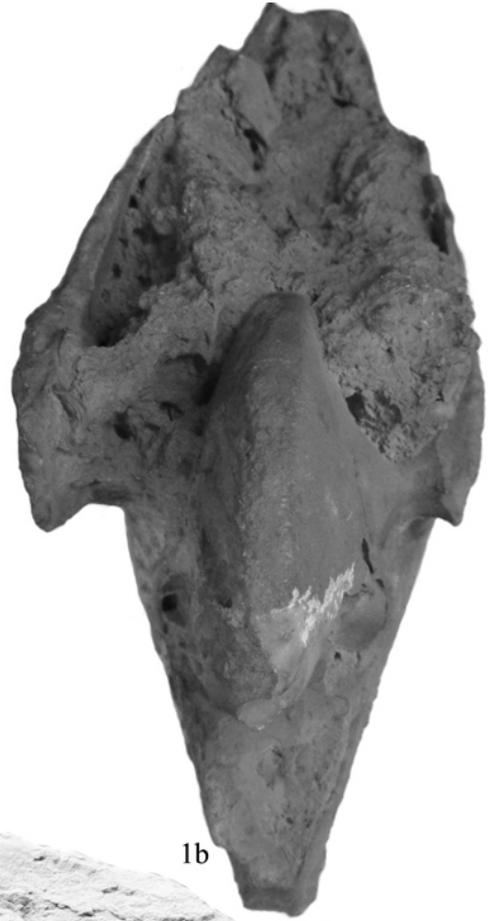


Plate XVIII

Fig. 1: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. A-144, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. A-145, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 88767, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Tolodella, Maestrat Basin (Spain).

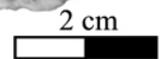
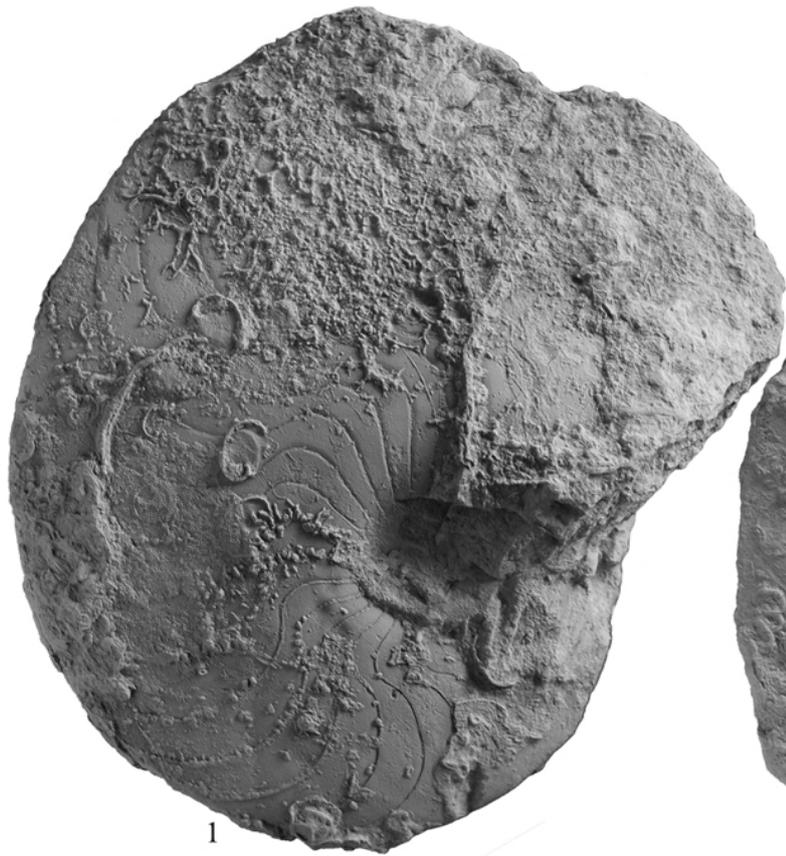


Plate XIX

Fig. 1: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. MV 428.3, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mola Murada, Maestrat Basin (Spain).

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 88762, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Lo Pui, Organyà Basin (Spain).

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. JM-34, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.

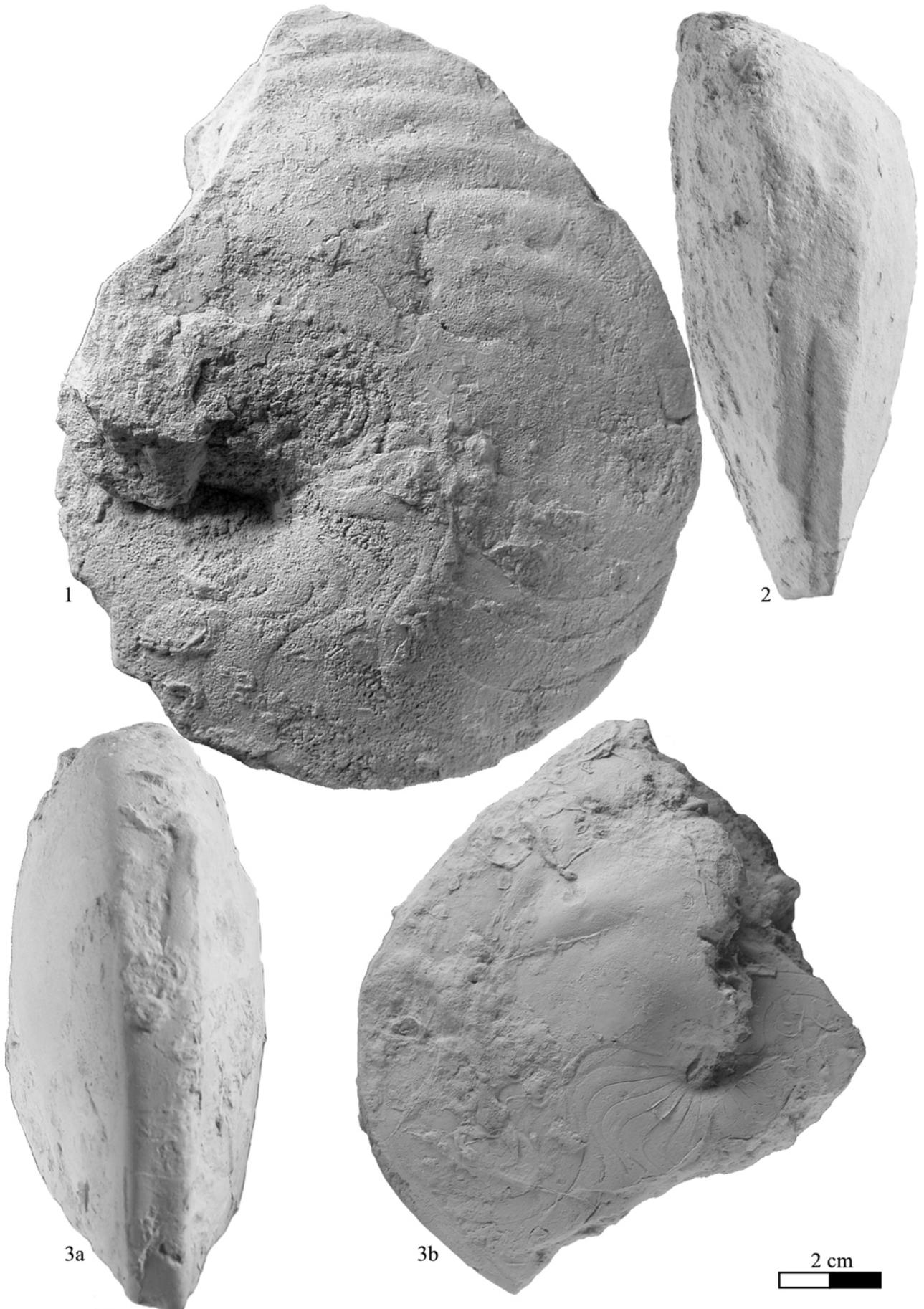


Plate XX

Fig. 1a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PNRL 1189, Early Aptian, *Deshayesites forbesi* Zone, Murs (Vaucluse, France). Coll. A. PICTET.

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 89788, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Galve, Province of Teruel (Spain).

Fig. 3: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. AG-3, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.

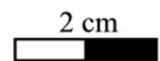
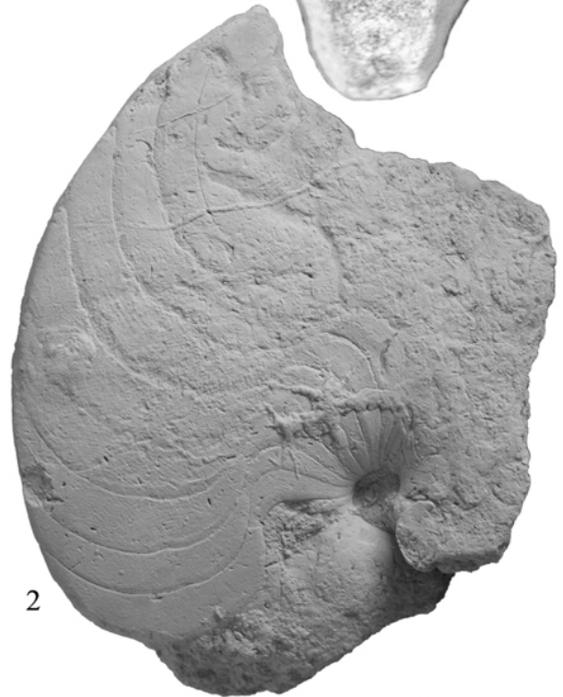
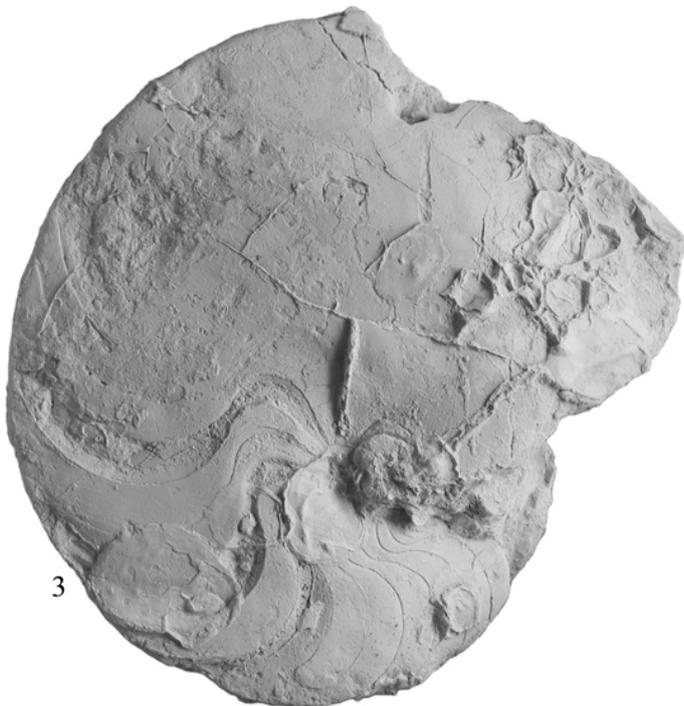


Plate XXI

Fig. 1: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. MV 428.2, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mola Murada, Maestrat Basin (Spain).

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PM3N11, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

Fig. 3: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PM1, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

Fig. 4: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 89788, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Galve, Province of Teruel (Spain).

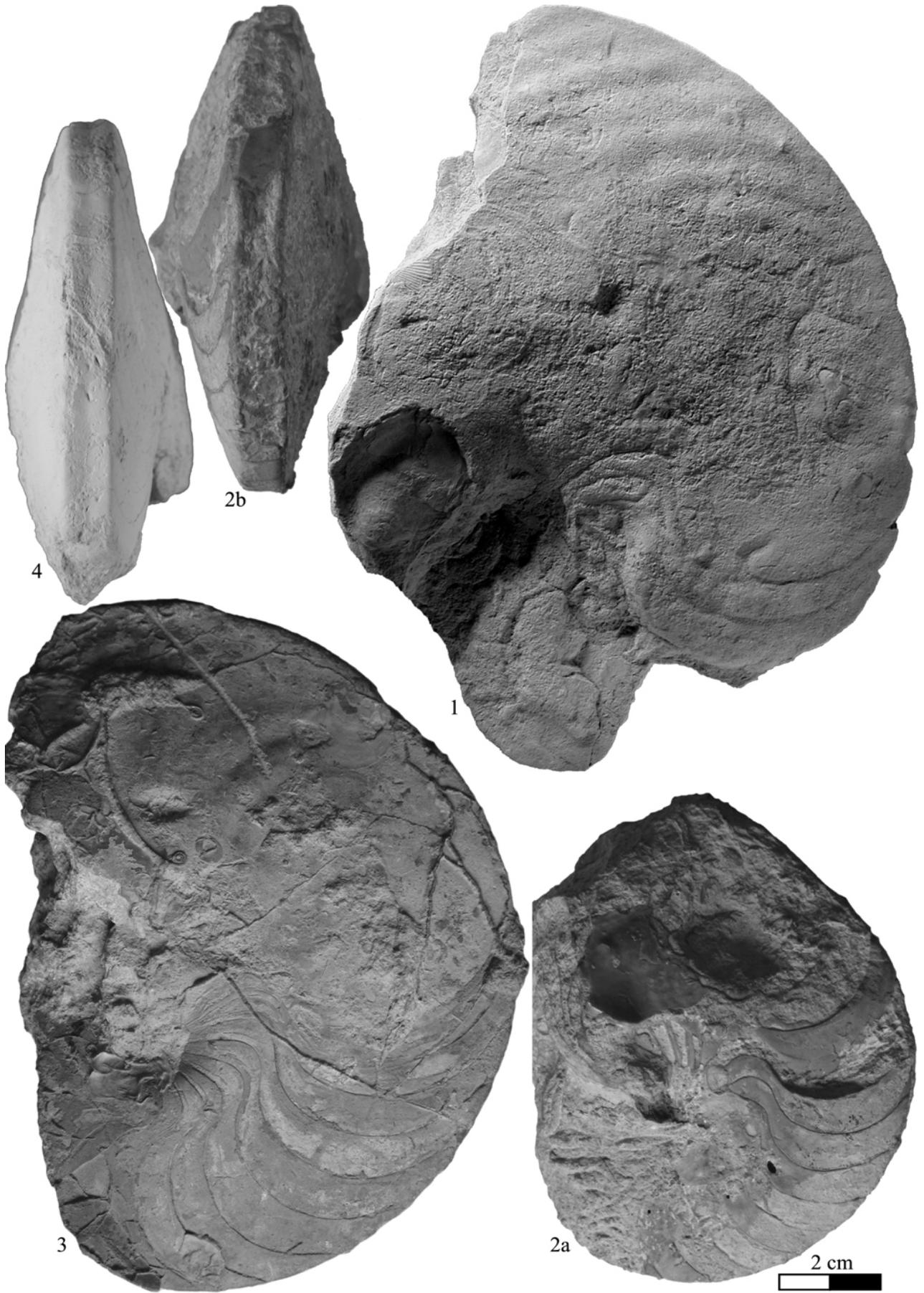


Plate XXI

Fig. 1a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PM13, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48013, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 3: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PM1, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

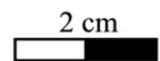


Plate XXIII

Fig. 1a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48042, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48013, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 3: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48158, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 4a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48255, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).



Plate XXIV

Fig. 1: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. 12576, Early Aptian, "Provence" (France). Coll. FSM.

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 88373, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Cuchía, Basque Cantabrian Basin (Spain).

Fig. 3a-b: ? *Heminautilus saxbii* (MORRIS, 1848). Specimen no. MB RE1962A, Early Aptian, Tibú Formation, Seboruco section, east of Mérida (Venezuela).

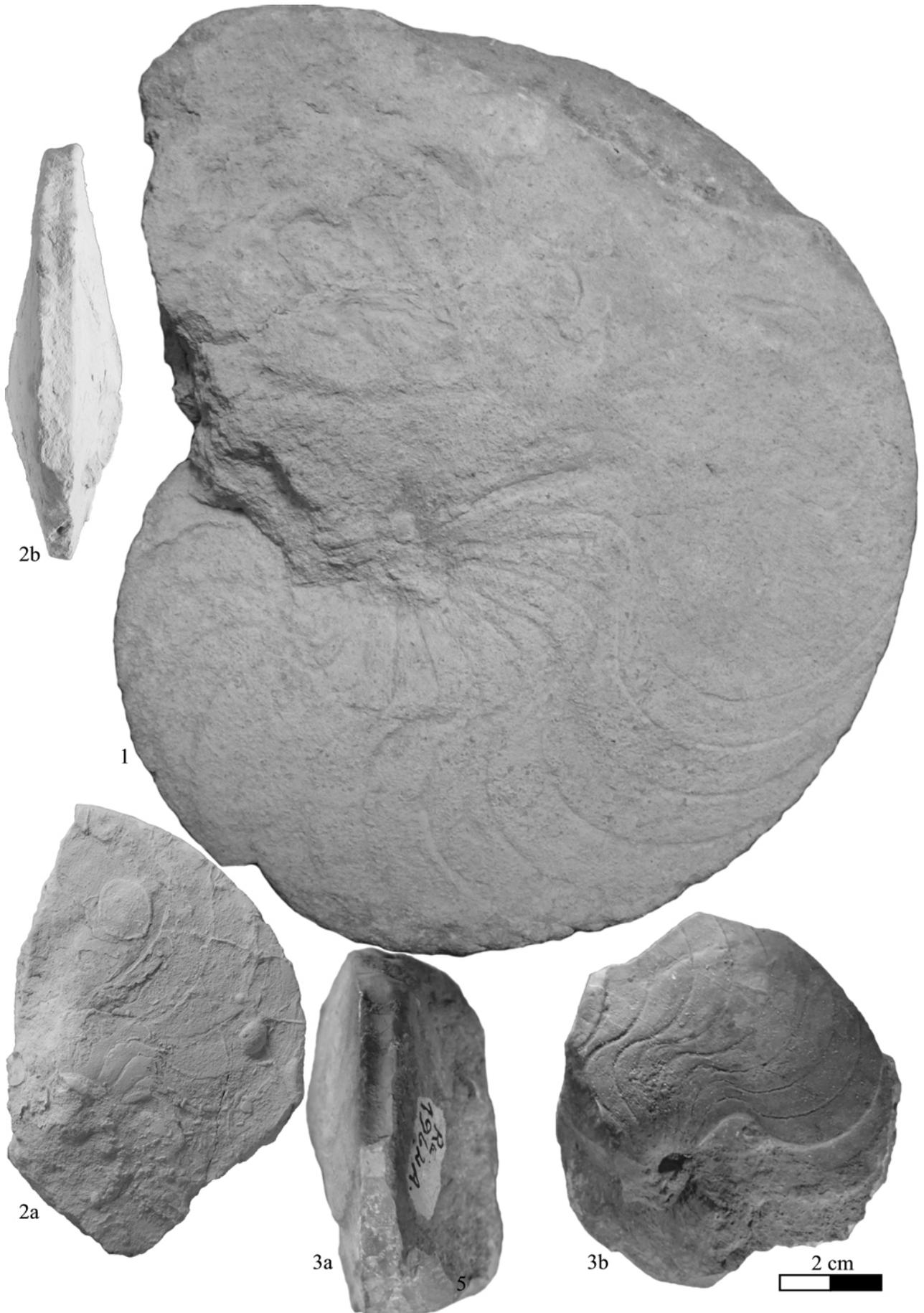


Plate XXV

Fig. 1: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. 12576, Early Aptian, "Provence" (France). Coll. FSM.

Fig. 2a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 88372, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Cuchía, Basque Cantabrian Basin (Spain).

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48261, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 4: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48044 (paratype of *Heminautilus tejeriense* MARTÍNEZ & GRAUGES, 2006), Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

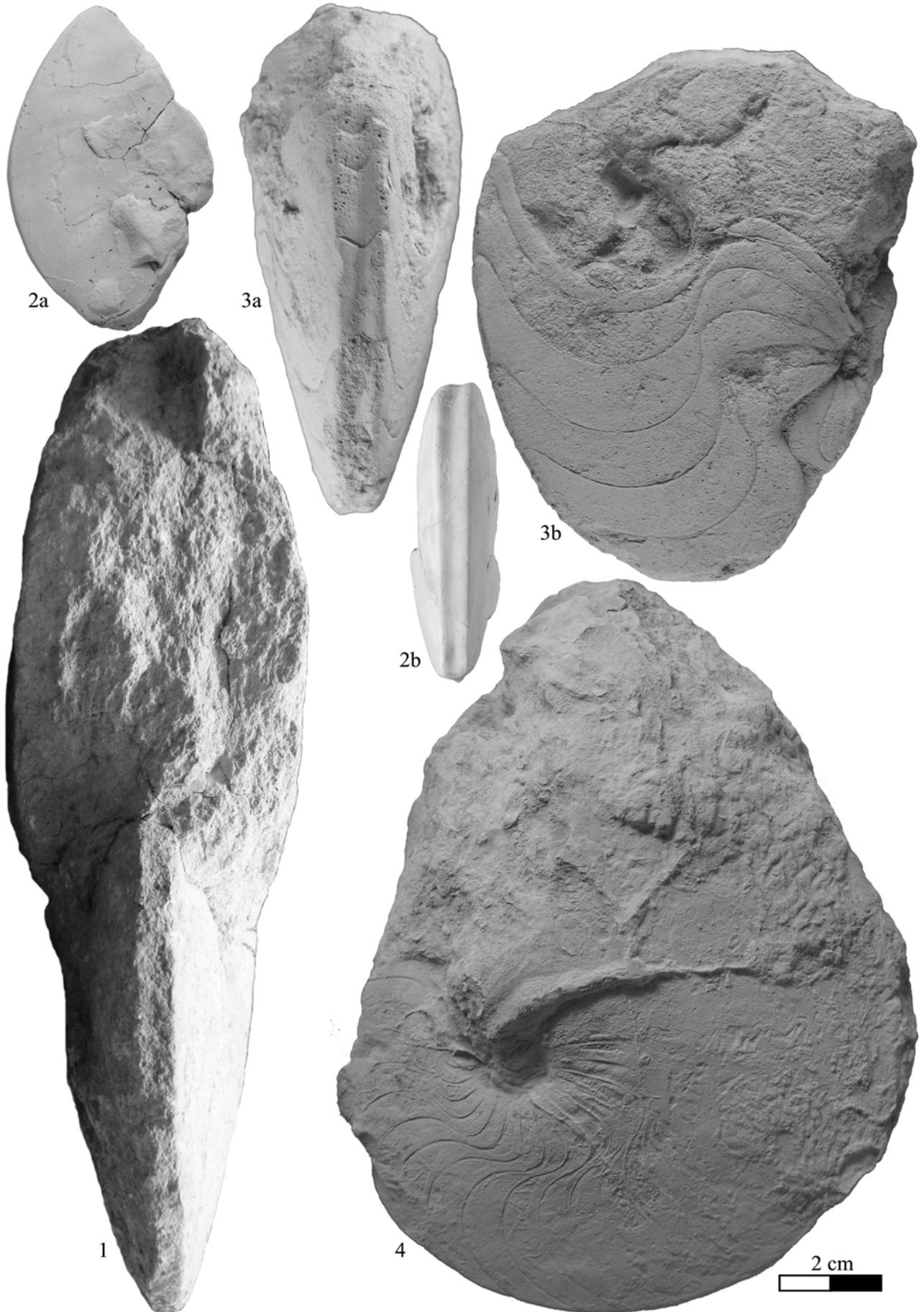


Plate XXVI

Fig. 1a-b: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48292 (holotype of *Heminautilus tejeriensis* MARTÍNEZ & GRAUGES, 2006), Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 2: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48044 (paratype of *Heminautilus tejeriensis* MARTÍNEZ & GRAUGES, 2006), Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 3a-b: *Heminautilus saxbii* (MORRIS, 1848). Early Aptian, Josa, Province of Teruel (Spain). Holotype of *Heminautilus verneuilli* VILANOVA, 1870, reproduction of the original illustration.

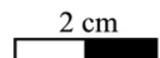


Plate XXVII

Fig. 1a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. PUAB 89780, Early Aptian, probably *Deshayesites forbesi* Zone, El Vendrell, Garraf (Spain).

Fig. 2a-c: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. 85-3, Early Aptian, upper part of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France). Coll. MHNA.



1a

2a

2b

2c

1b

2 cm

Plate XXVIII

Fig. 1a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. PM95, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. MARIN.

Fig. 2a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. MGB 22607, Early Aptian, Garraf (Spain).

Fig. 3a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. MPP.B-EM.69, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, banc no. 148, La Bédoule (Bouches du Rhône, France). Coll. Frau, FSM.

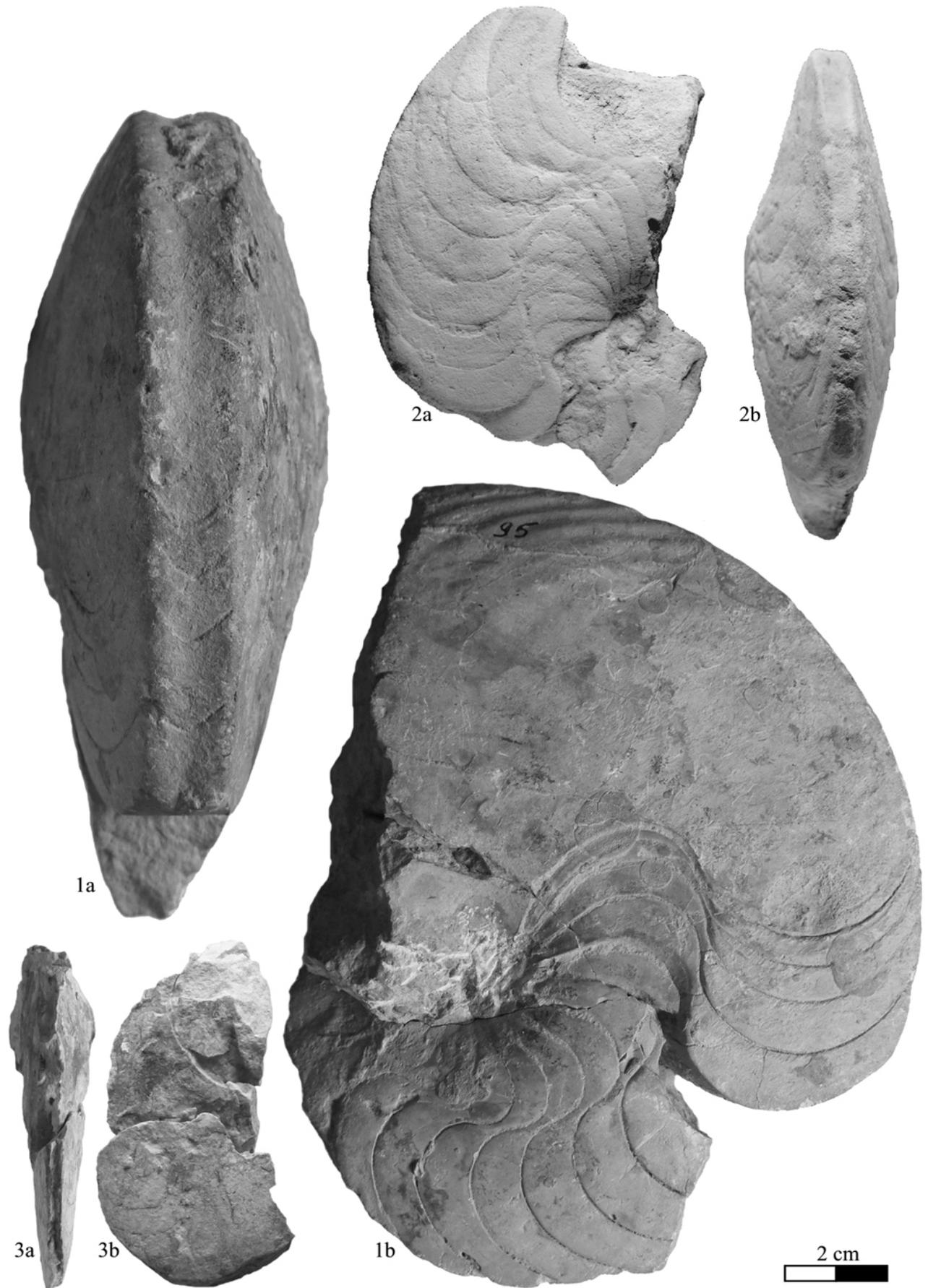


Plate XXIX

Fig. 1a-c: *Heminautilus lallierianus* (ORBIGNY, 1841). Lectotype no. MNHN.F.A32800, coll d'Orbigny (no. 5573), Early Aptian, upper part of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France). Coll. d'Orbigny.

Fig. 2: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. 77-543, Early Aptian, upper part of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France). Coll. MHNA.

Fig. 3a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1028, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

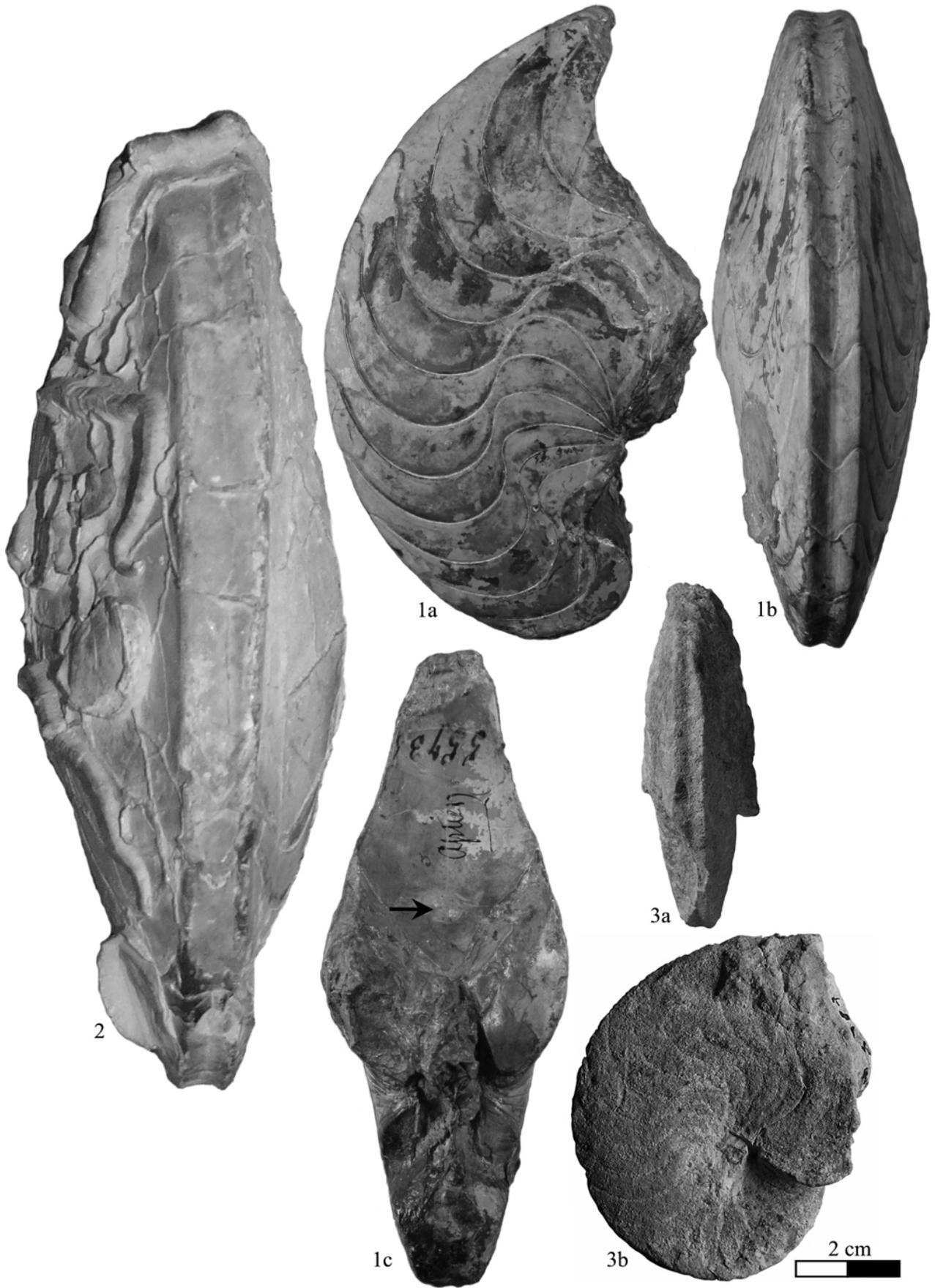


Plate XXX

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. 77-543, Early Aptian, upper part of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France). Coll. MHNA.

Fig. 2: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1056, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 3a-c: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. 35733, upper part of the Early Aptian, locality A (DURHAM, 1946), Tolima department (Colombia). Coll. MPUC.

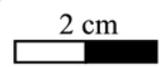
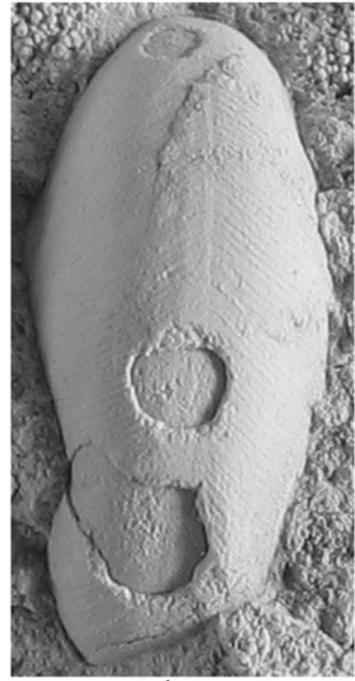


Plate XXXI

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. tl056, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

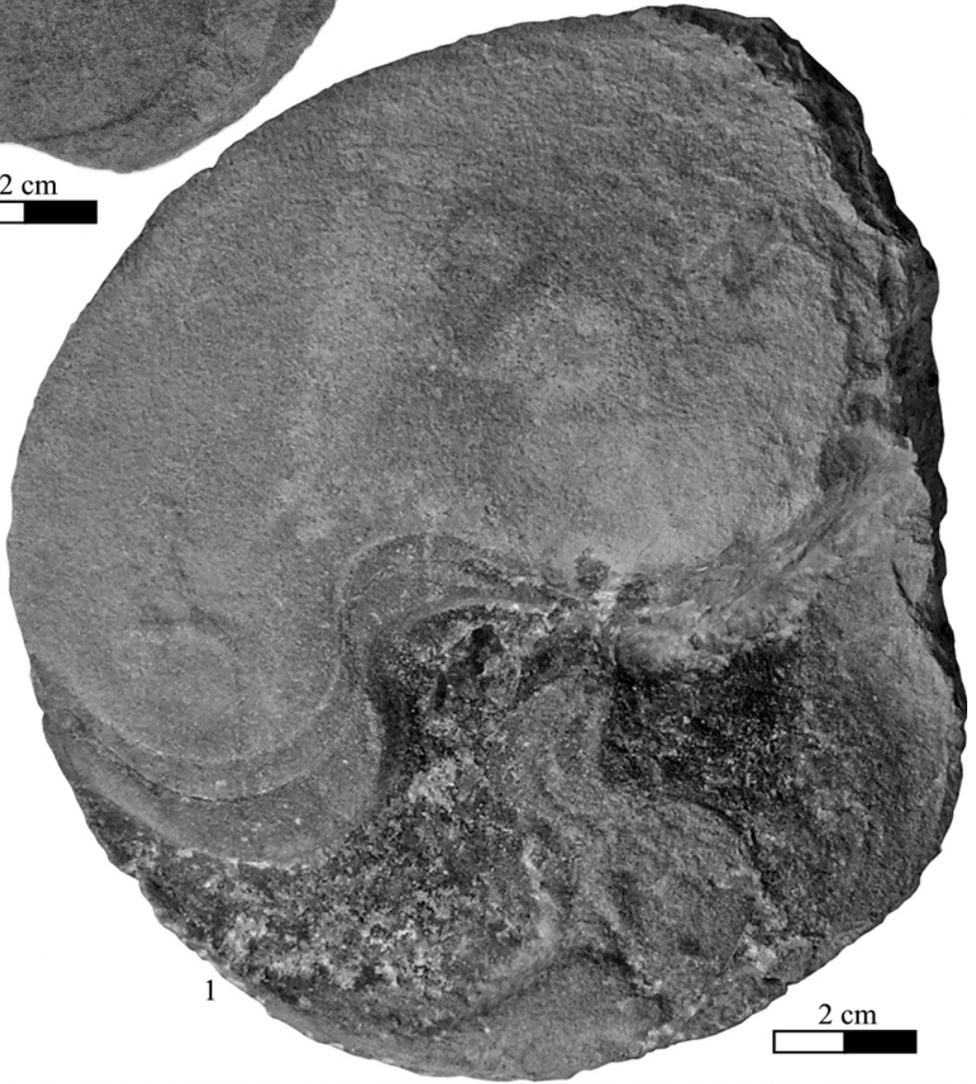
Fig. 2a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. BRG103, upper part of the *Deshayesites forbesi* Zone, bed no. 12, Pierrelatte section (Drôme, France). Coll. BAUDOUIN.

Fig. 3: *Heminautilus saxbii* (MORRIS, 1848). Specimen no. PUAB 48158, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).



1 cm

2 cm



2 cm

Plate XXXII

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. VI009, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.

Fig. 2a-b: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. MB RE1962a, Early Aptian, Tibú Formation, Seboruco section, east of Mérida (Venezuela).



2a

2b

1

2 cm

Plate XXXIII

Fig. 1a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1069, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 2a-c: *Heminautilus* ? *tyosiensis* (YABE & OSAKI, 1953). Holotype no. NMNS P1-4200, upper part of the Early Aptian (= *Dufrenoyia furcata* Zone), Tokawa quarry, Tyōsi Peninsula, Tiba Prefecture (Japan).



Plate XXXIV

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1078, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 2a-b: *Heminautilus* ? *tyosiensis* (YABE & OSAKI, 1953). Specimen no. NMNS PM6858, upper part of the Early Aptian (= *Dufrenoyia furcata* Zone), Tyōsi Peninsula, Tiba Prefecture (Japan).

Fig. 3a-c: *Heminautilus* ? *tyosiensis* (YABE & OSAKI, 1953). Specimen no. NMNS PM6859, upper part of the Early Aptian (= *Dufrenoyia furcata* Zone), Tyōsi Peninsula, Tiba Prefecture (Japan).

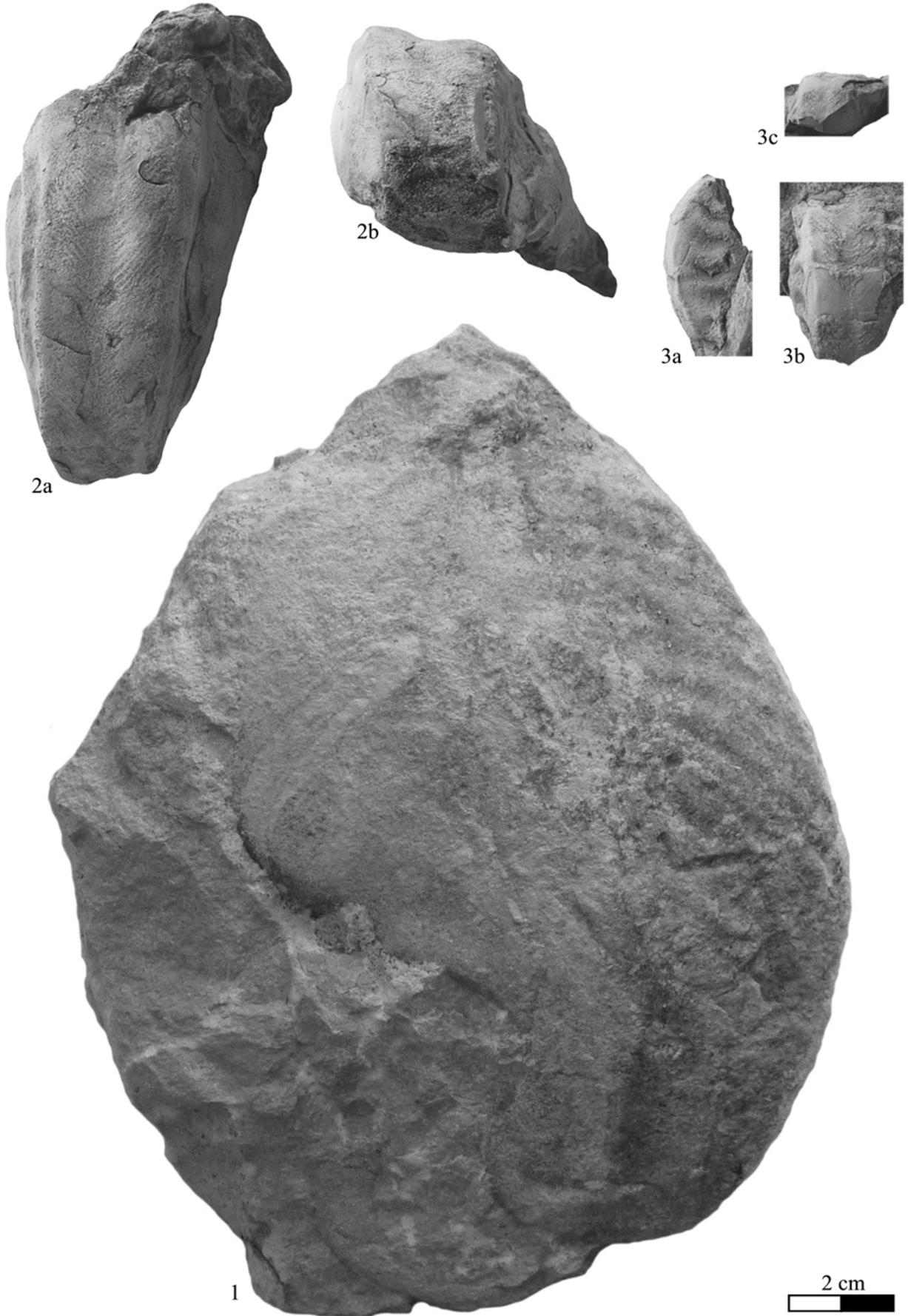


Plate XXXV

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1029, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 2: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1078, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 3a-b: *Heminautilus* ? *tyosiensis* (YABE & OSAKI, 1953). Specimen no. NMNS PM6858, upper part of the Early Aptian (= *Dufrenoyia furcata* Zone), Tyōsi Peninsula, Tiba Prefecture (Japan).

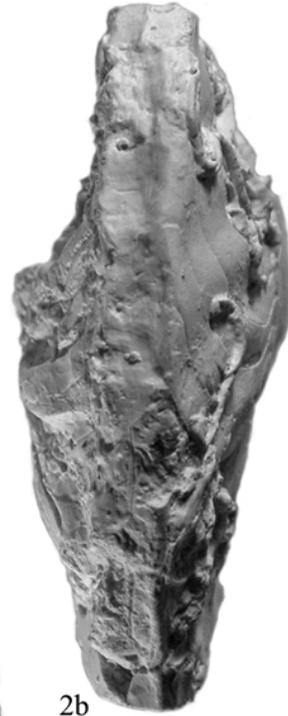
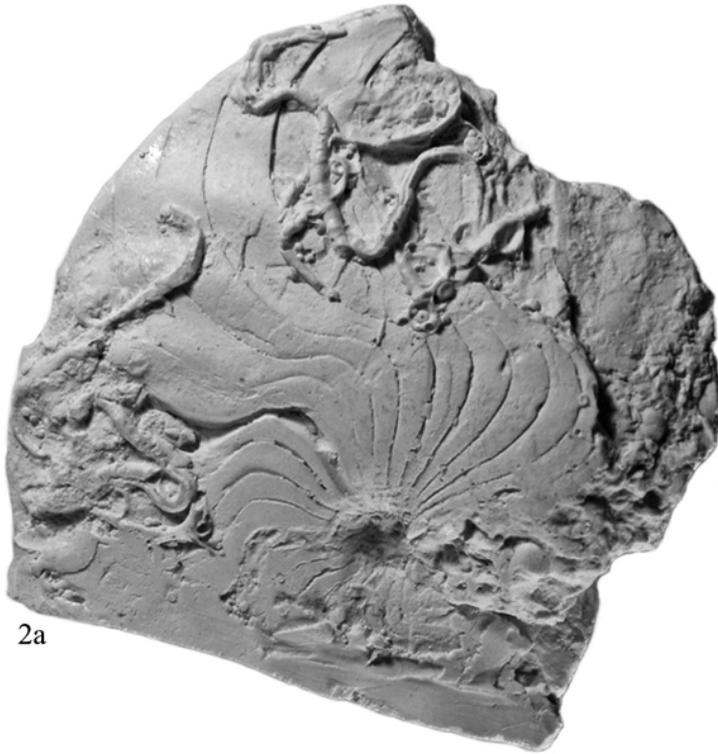


Plate XXXVI

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. t1029, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 2a-b: *Heminautilus stantoni* (SCOTT, 1940). Plastotype no. 35688, uppermost part of the Early Aptian, probably *Dufrenoyia justinae* Zone, locality M15, near Murfreesboro (Arkansas, USA). Coll. BEG.

Fig. 3: *Heminautilus stantoni* (SCOTT, 1940). Holotype no. USNM103260, uppermost part of the Early Aptian, probably *Dufrenoyia justinae* Zone, locality M15, near Murfreesboro (Arkansas, USA).



2 cm

Plate XXXVII

Fig. 1a-c: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. 12573, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, La Bédoule (Bouches du Rhône, France). Coll. FSM.



1c

1b

1a

2 cm

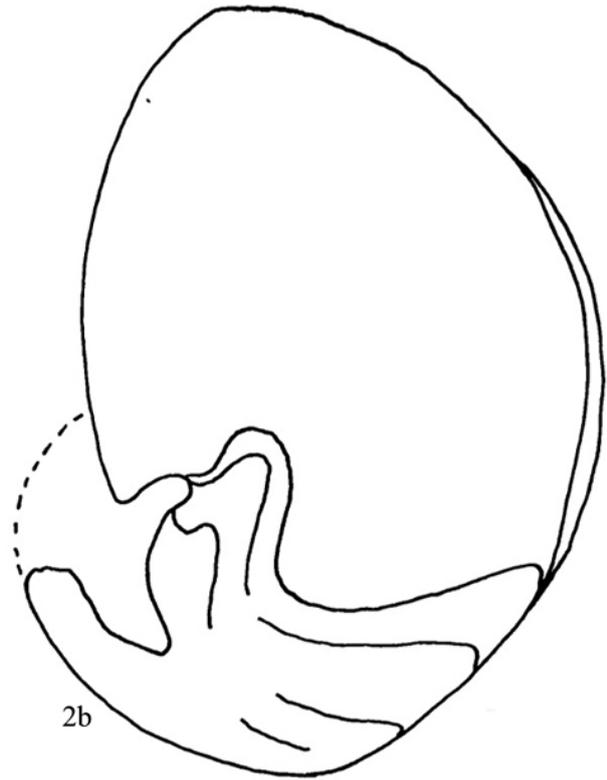
Plate XXXVIII

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. 12572, Early Aptian, Hameau of Les Roux, Cuges-les-Pins (Bouches du Rhône, France). Coll. FSM.

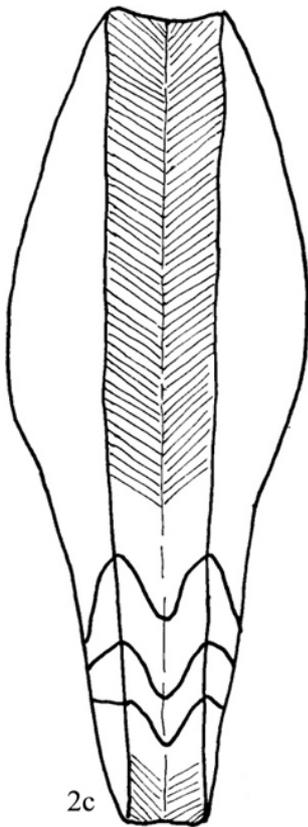
Fig. 2a-c: *Heminautilus ? japonicus* sp. nov. Unregistered specimen, Late Barremian (= *Imerites giraudi* Zone?), north of Yuasa-machi, Wakayama Prefecture (Japan). Reproduction of the illustration of OBATA & OGAWA (1976).



2a



2b



2c



1

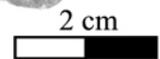


Plate XXXIX

Fig. 1: *Heminautilus* aff. *lallierianus* (ORBIGNY, 1841). Specimen no. IGM 10050, Early Aptian, *Dufrenoyia justinae* Zone, bed no. 15, Mina Texali, Santa Isabel Atenayuca, Puebla State (Mexico).

Fig. 2: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. PUAB 48057, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 3a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. PUAB 48276, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).



1a



1b



2



3a



3b

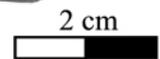


Plate XL

Fig. 1a-b: *Heminautilus* aff. *lallierianus* (ORBIGNY, 1841). Specimen no. MPL1, Early Aptian, *Dufrenoyia justinae* Zone, Sierra del Rosario, Durango State (Mexico).

Fig. 2a-b: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. UPMC-250, Early Aptian, upper part of the *Deshayesites forbesi* Zone?, Gurgy (Yonne, France). Coll. TOMBECK.



1a



1b



2a



2b



2c

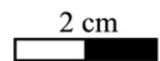


Plate XLI

Fig. 1: *Heminautilus lallierianus* (ORBIGNY, 1841). Specimen no. AMNH 25455, median part of the Early Aptian, Harrar region (Ethiopia). Reproduction of the illustration of SCOTT (1943).

Fig. 2: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. PUAB 48222, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).

Fig. 3a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. PUAB 48302, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).



1a



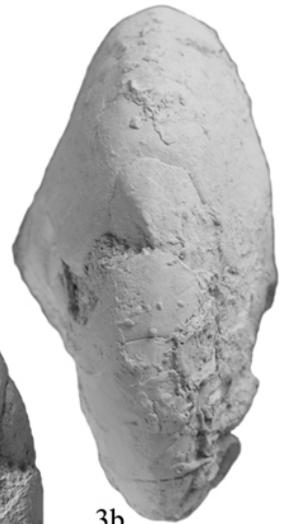
1b



2



3a



3b

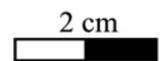


Plate XLII

Fig. 1: *Heminautilus etheringtoni* DURHAM, 1946. Holotype no. 35731, upper part of the Early Aptian, locality A (DURHAM, 1946), Tolima department (Colombia). Coll. MPUC.

Fig. 2a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Holotype no. MNCN I-14855, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Reproduction of the illustration of MARTÍNEZ & GRAUGES (2006).



1

2a

2b

2 cm

Plate XLIII

Fig. 1a-b: *Heminautilus etheringtoni* DURHAM, 1946. Holotype no. 35731, upper part of the Early Aptian, locality A (DURHAM, 1946), Tolima department (Colombia). Coll. MPUC.

Fig. 2a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. PUAB 48178, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain).



Plate XLIV

Fig. 1: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. UN-DG-NT-001, Early Aptian, Firavitoba, Boyacá department (Colombia). Coll. UNCB.

Fig. 2a-c: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. M3, Early Aptian, Quebrada el Cobre, Payandé, Tolima department (Colombia). Coll. UNCB.

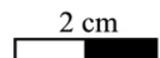


Plate XLV

Fig. 1: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. UN-DG-NT-001, Early Aptian, Firavitoba, Boyacá department (Colombia). Coll. UNCB.

Fig. 2a-b: *Heminautilus etheringtoni* DURHAM, 1946. Specimen no. 124, Early Aptian, Quebrada el Cobre, Payandé, Tolima department (Colombia). Coll. UNCB.



Plate XLVI

Fig. 1: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. VI011, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.

Fig. 2: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. Se-11.1, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mas Segura, Maestrat Basin (Spain). Coll. MV.

Fig. 3: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. A-148, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Josa, Province of Teruel (Spain). Coll. PUAB.



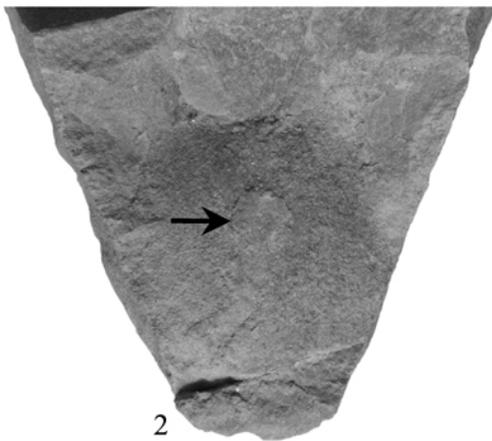
Plate XLVII

Fig. 1a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. VI011, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.

Fig. 2: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. CH01, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BAUDOUIN.



1a



2



1b

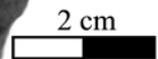


Plate XLVIII

Fig. 1: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. VI011, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.

Fig. 2: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. CH01, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BAUDOUIN.

Fig. 3: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. Se-11.1, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Mas Segura, Maestrat Basin (Spain). Coll. MV.



Plate XLIX

Fig. 1a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. tl074, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Le Teil (Ardèche, France). Coll. BAUDOUIN.

Fig. 2a-b: *Heminautilus ? japonicus* sp. nov. Holotype no. SH-1, Late Barremian (= *Imerites giraudi* Zone?), locality 203, sector of Sanchu, Kwanto Moutains, Gunma Prefecture (Japan). Coll. E. SHIMIZU. Reproduction of the illustration of OBATA *et al.* (1984).

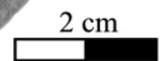
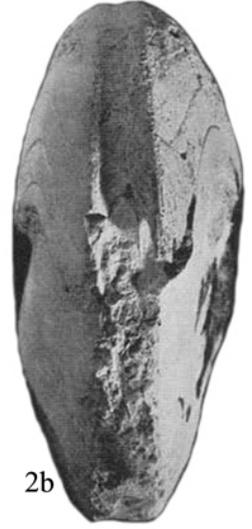


Plate L

Fig. 1a-b: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. MHNG GEPI 83570, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Groumaud section, Bourg-Saint-Andéol (Ardèche, France). Coll. A. PICTET.

Fig. 2: *Josanautilus* aff. *lacerdae* (VILANOVA, 1870). Specimen no. VI010, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.

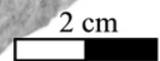
Fig. 3: *Heminautilus ? japonicus* sp. nov. Holotype no. SH-1, Late Barremian (= *Imerites giraudi* Zone?), locality 203, sector of Sanchu, Kwanto Moutains, Gunma Prefecture (Japan). Coll. E. Shimizu. Reproduction of the illustration of OBATA *et al.* (1984).



1



2



3

Plate LI

Fig. 1: *Josanautilus lacerdae* (VILANOVA, 1870). Specimen no. MHNG GEPI 83570, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Groumaud section, Bourg-Saint-Andéol (Ardèche, France). Coll. A. PICTET.

Fig. 2a-b: *Josanautilus* aff. *lacerdae* (VILANOVA, 1870). Specimen no. VI010, Early Aptian, *Deshayesites forbesi* Zone, *Roloboceras hambrovi* Subzone, Viviers (Ardèche, France). Coll. BOSELLI.



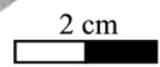
1



2a



2b



Appendix

Appended table: List of and information on the specimens of Nautiloidea BLAINVILLE, 1825, studied, referred to or depicted.

Number	Identification	Collection	Repositories	Figured by
103/101	<i>Xenochellus ulixis</i> SHIMANSKY & ERLANGER, 1955			KARAKASCH (1907)
Unregistered	<i>Pseudocenoceras campichei</i> (KARAKASCH, 1907)			KARAKASCH (1907)
MHNG GEPI 15856	<i>Aulaconautilus sexcarinatus</i> (F.-J. PICTET, 1867)	F.-J. PICTET	Natural History Museum of Geneva, Switzerland	F.-J. PICTET (1867)
GK. H6909	" <i>Heminautilus</i> " <i>akatsui</i> MATSUMOTO, 1980		Kyushu University, Japon	MATSUMOTO <i>et al.</i> (1980)
MNH.N.F.A52065	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	FRAU	Muséum National d'Histoire Naturelle of Paris, France	DELANOY <i>et al.</i> (2012)
LUS01, LUS02	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	Boselli		
Mej01 (holotype)	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	BAUDOUIN	Muséum National d'Histoire Naturelle of Paris, France (cast)	DELANOY <i>et al.</i> (2012)
Mej02, Mej03	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	BAUDOUIN		DELANOY <i>et al.</i> (2012)
Mej11	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	BAUDOUIN		
RG2000, RG2001, RG2002a, RG2002b	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	GONNET		DELANOY <i>et al.</i> (2012)
MHNG GEPI 15935	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	F.-J. PICTET	Natural History Museum of Geneva, Switzerland	
415950	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012	VERMEULEN		Quoted by VERMEULEN (2002, p. 37)
M 2002.554	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012		Hungarian Natural history Museum	FOZY & SZENTE (2013)
K1 1693, K1 1694	<i>H. boselliorum</i> DELANOY <i>et al.</i> , 2012		Museum of Paleontology, Sofia University, Bulgaria	
EM696, EM697, EM698, EM699 (neotype)	<i>H. rangei</i> (HOPPE, 1922)	École des Mines	Claude Bernard University, Lyon, France	DOUVILLÉ (1916)
TK25-15	<i>H. rangei</i> (HOPPE, 1922)		Geological Museum of Mansoura University, Egypt	ABU-ZIED (2008)
Unregistered (2 specimens)	<i>H. rangei</i> (HOPPE, 1922)	RANGE	Geologisch- paläontologischen Institut der Universität Leipzig, Germany (lost)	HOPPE (1922)

K1 1692	<i>H. sanctaerucis</i> CONTE, 1980		Museum of Paleontology, Sofia University, Bulgaria	DIMITROVA (1967)
K1 6001, K1 6002, K1 6003, K1 6004, K1 6005	<i>H. sanctaerucis</i> CONTE, 1980		Museum of Paleontology, Sofia University, Bulgaria	NIKOLOV & PARASHKEVANOV (1995)
MCGL 20747 (holotype)	<i>H. sanctaerucis</i> CONTE, 1980	F.-J. PICTET	Muséum Géologique Cantonal of Lausanne, Switzerland	F.-J. PICTET & CAMPICHE (1858); CONTE (1980)
MHNG GEPI 15936	<i>H. sanctaerucis</i> CONTE, 1980	F.-J. PICTET	Natural History Museum of Geneva, Switzerland	
MHNN 26904	<i>H. sanctaerucis</i> CONTE, 1980	JACQUART	Natural History Museum of Neuchâtel, Switzerland	
Unregistered	<i>H. sanctaerucis</i> CONTE, 1980	FRASALI		CONTE (2010)
131H	<i>H. sanctaerucis</i> CONTE, 1980	GESBERT		
Bw599	<i>H. sanctaerucis</i> CONTE, 1980	GONNET	Faculté des Sciences of Marseille, France	
GSUB C4035	<i>H. sanctaerucis</i> CONTE, 1980		Geosciences Collection of the University of Bremen, Germany	LEHMAN <i>et al.</i> (2009)
415951	<i>H. aff.</i> <i>sanctaerucis</i> CONTE, 1980	BAUDOIN (donated by VERMEULEN)		
EM700	<i>H. saxbii</i> (MORRIS, 1848)		Claude Bernard University, Lyon, France	DOUVILLÉ (1916)
BMNH 47019 (holotype)	<i>H. saxbii</i> (MORRIS, 1848)	SAXBY	British Museum of Natural History, England	MORRIS (1847); KUMMEL (1956); DONOVAN & BAKER (2003); CONTE (2010)
PNRL 1189	<i>H. saxbii</i> (MORRIS, 1848)	A. PICTET	Parc Naturel Régional du Lubéron, France	
12576	<i>H. saxbii</i> (MORRIS, 1848)		Faculté des Sciences of Marseille, France	
PM1, PM2, PM3, PM3N1, PM3N2, PM3N11, PM4, PM5, PM6, PM13, PMBb2	<i>H. saxbii</i> (MORRIS, 1848)	MARIN	Muséum National d'Histoire Naturelle of Paris, France	
PUAB 48042	<i>H. saxbii</i> (MORRIS, 1848)		Universitat Autònoma de Barcelona, Spain	MARTINEZ & GRAUGES (2006); MORENO (2007)
PUAB 48013, PUAB 48044, PUAB 48046, PUAB 48168, PUAB 48292	<i>H. saxbii</i> (MORRIS, 1848)		Universitat Autònoma de Barcelona, Spain	MARTINEZ & GRAUGES (2006)
PUAB 88372, PUAB 88373	<i>H. saxbii</i> (MORRIS, 1848)		Universitat Autònoma de Barcelona, Spain	Quoted by NAJARRO <i>et al.</i> (2011, fig. 7)

A-114, A-117, A-119, A-122, A-127, A-131, A-142, A-140, A-145, A-146, AG-3, AG-13, JM-26, JM-34, JM-36, JM-37, JM-38, M-8, PUAB 5905, PUAB 48009, PUAB 48011, PUAB 48018, PUAB 48027, PUAB 48035, PUAB 48037, PUAB 48040, PUAB 48043, PUAB 48064, PUAB 48074, PUAB 48092, PUAB 48093, PUAB 48095, PUAB 48098, PUAB 48106, PUAB 48125, PUAB 48127, PUAB 48128, PUAB 48133, PUAB 48143, PUAB 48158, PUAB 48163, PUAB 48164, PUAB 48165, PUAB 48169, PUAB 48177, PUAB 48202, PUAB 48205, PUAB 48215, PUAB 48223, PUAB 48232, PUAB 48242, PUAB 48246, PUAB 48254, PUAB 48255, PUAB 48256, PUAB 48261, PUAB 48275, PUAB 48277, PUAB 48278, PUAB 48080, PUAB 48282, PUAB 48288, PUAB 48295, PUAB 48304, PUAB 48314, PUAB 48316, PUAB 48318, PUAB 48321, PUAB 48322, PUAB 48328, PUAB 48366, PUAB 88762, PUAB 88763, PUAB 88767, PUAB 88770, PUAB 89786, PUAB 89787, PUAB 89788, PUAB 89790, PUAB 89791	<i>H. saxbii</i> (MORRIS, 1848)		Universitat Autònoma de Barcelona, Spain	
MV 423.1, MV 428.2, MV 428.3	<i>H. saxbii</i> (MORRIS, 1848)		Valltorta Museum, Spain	
Unregistered	<i>H. saxbii</i> (MORRIS, 1848)			CONTE (2007, photo 11)
Unregistered	<i>H. saxbii</i> (MORRIS, 1848)			PEROPADRE MEDINA (2011, fig. 3.12)
<i>Nautilus verneuilli</i> VILANOVA, 1870 (holotype)	<i>H. saxbii</i> (MORRIS, 1848)		Museo Nacional de Ciencias Naturales, Madrid, Spain	VILANOVA (1870)
MB RE1962A	<i>H. saxbii</i> (MORRIS, 1848)	RENZ	Natural History Museum of Bâle, Switzerland	
MNHN.F.A32800 (lectotype)	<i>H. lallierianus</i> (ORBIGNY, 1841)	ORBIGNY	Muséum National d'Histoire Naturelle of Paris, France	CONTE (1980, 2007)
77-543	<i>H. lallierianus</i> (ORBIGNY, 1841)		Muséum d'Histoire Naturelle of Auxerre, France	CONTE (2007)
85-3	<i>H. lallierianus</i> (ORBIGNY, 1841)		Muséum d'Histoire Naturelle of Auxerre, France	
UPMC-250	<i>H. lallierianus</i> (ORBIGNY, 1841)	TOMBECK	Pierre et Marie Curie University collections, Paris, France	
12572, 12573	<i>H. lallierianus</i> (ORBIGNY, 1841)		Faculté des Sciences of Marseille, France	CONTE (1985, no. 1 and 2)
MGB 22607	<i>H. lallierianus</i> (ORBIGNY, 1841)		Museu de Geologia de Barcelona, Spain	MORENO <i>et al.</i> (2008)
PM95	<i>H. lallierianus</i> (ORBIGNY, 1841)	MARIN	Muséum National d'Histoire Naturelle of Paris, France	CONTE (2007)
BRG098, BRG103, tI028, tI029, tI056, tI069, tI078, tI079	<i>H. lallierianus</i> (ORBIGNY, 1841)	BAUDOIN		
MPP.B-EM.69	<i>H. lallierianus</i> (ORBIGNY, 1841)	FRAU	Faculté des Sciences of Marseille, France	

VI009, VI012	<i>H. lallierianus</i> (ORBIGNY, 1841)	BOSELLI		
PUAB 89780	<i>H. lallierianus</i> (ORBIGNY, 1841)		Universitat Autònoma de Barcelona, Spain	
AMNH 25455	<i>H. lallierianus</i> (ORBIGNY, 1841)		American Museum of Natural History, New York, United States	SCOTT (1943)
Unregistered (1 specimen)	<i>H. lallierianus</i> (ORBIGNY, 1841)			CONTE (2007, no. 7)
IGM 10050	<i>H. aff. lallierianus</i> (ORBIGNY, 1841)		Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México	
MPL1	<i>H. aff. lallierianus</i> (ORBIGNY, 1841)		Museo Paleontológico Laguna, Torreón, Coahuila State, Mexico	
35731 (holotype)	<i>H. etheringtoni</i> DURHAM, 1946		Museum of Paleontology, California University, United States	DURHAM (1946)
35733, 35735	<i>H. etheringtoni</i> DURHAM, 1946		Museum of Paleontology, California University, United States	DURHAM (1946)
M3, 124, UN-DG-NT-001	<i>H. etheringtoni</i> DURHAM, 1946		Colecciones Paleontológicas, Departamento de Geociencias, Universidad Nacional de Colombia, Bogotá	
F-15	<i>H. etheringtoni</i> DURHAM, 1946		Museo de Historia Natural of the Universidad Nacional de Colombia, Bogota	ETAYO-SERNA (1979)
MB RE1962a	<i>H. etheringtoni</i> DURHAM, 1946	RENZ	Natural History Museum of Bâle, Switzerland	
USNM103260 (holotype)	<i>H. stantoni</i> (SCOTT, 1940)		United States National Museum, Washington, United States	SCOTT (1940)
SH-1 (holotype)	<i>H.? japonicus</i> sp. nov.	E. SHIMIZU	National Science Museum, Tokyo, Japan (cast no. NSM-PM 9381)	OBATA <i>et al.</i> (1984)
Unregistered	<i>H.? Japonicus</i> sp. nov.			OBATA & OGAWA (1976)
NMNS P1-4200 (holotype)	<i>H.? tyosiensis</i> (YABE & OSAKI, 1953)		National Science Museum, Tokyo, Japan	YABE & OSAKI (1953)
NMNS PM6858, NMNS PM6859	<i>H.? tyosiensis</i> (YABE & OSAKI, 1953)		National Science Museum, Tokyo, Japan	Obata <i>et al.</i> (1975)
MNCN I-14855 (holotype)	<i>J. lacerdae</i> (VILANOVA, 1870)		Museo Nacional de Ciencias Naturales, Madrid, Spain	VILANOVA (1870); BATALLER (1950); WIEDMANN (1960); MARTINEZ & GRAUGES (2006)
tl074, CH01	<i>J. lacerdae</i> (VILANOVA, 1870)	BAUDOQUIN		

MHNG GEPI 83570	<i>J. lacerdae</i> (VILANOVA, 1870)	A. PICTET	Natural History Museum of Geneva, Switzerland	
VI011	<i>J. lacerdae</i> (VILANOVA, 1870)	BOSELLI		
PUAB 48003, PUAB 48057, PUAB 48082, PUAB 48302	<i>J. lacerdae</i> (VILANOVA, 1870)		Universitat Autònoma de Barcelona, Spain	MARTINEZ & GRAUGES (2006)
A-148, JM-35, PUAB 48086, PUAB 48178, PUAB 48222, PUAB 48276	<i>J. lacerdae</i> (VILANOVA, 1870)		Universitat Autònoma de Barcelona, Spain	
Se-11.1	<i>J. lacerdae</i> (VILANOVA, 1870)		Valltorta Museum, Spain	
VI010	<i>J. aff. lacerdae</i> (VILANOVA, 1870)	BOSELLI		