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The Cretaceous nautiloid genus Anglonautilus SPATH, 1927, in France

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Abstract: The occurrence of the nautiloid genus *Anglonautilus* SPATH in France was limited to the report of *Anglonautilus dorsoplicatus* (WIEDMANN) from the Albian of Escragnolles (Alpes-Maritimes) and *Anglonautilus* sp. from the Aptian of Les Ferres (Alpes-Maritimes). Here we document the presence of the successive species *Anglonautilus praeundulatus* LEHMANN *et al.*, *Anglonautilus undulatus* (SOWERBY) and *Anglonautilus dorsoplicatus* (WIEDMANN) from the Cretaceous of France. The stratigraphic range of *Anglonautilus* SPATH, hitherto unknown before Aptian times is extended downward to the Hauterivian. The Hauterivian species *Nautilus begudensis* KILIAN & REBOUL, sometimes assigned to the genus *Anglonautilus* SPATH, is revised and re-assigned to the genus *Cymatoceras* HYATT.

Key-words:

- Nautiloidea;
- Nautilidae;
- Anglonautilus;
- Cymatoceras;
- Lower Cretaceous

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Résumé : *Les nautiloïdes crétacés du genre* **Anglonautilus** *SPATH,* **1927, en** *France.-* La répartition du genre *Anglonautilus* SPATH en France était jusqu'à présent limitée à la présence d'*Anglonautilus dorsoplicatus* (WIEDMANN) dans l'Albien d'Escragnolles (Alpes-Maritimes) et d'*Anglonautilus* sp. dans l'Aptien de Les Ferres (Alpes-Maritimes). Nous rapportons ici la présence des espèces successives *Anglonautilus* praeundulatus LEHMANN *et al., Anglonautilus undulatus* (SOWERBY) et *Anglonautilus dorsoplicatus* (WIEDMANN) dans le Crétacé de France. Le genre *Anglonautilus* SPATH, connu jusqu'alors uniquement à partir de l'Aptien, est présent dès l'Hauterivien. L'espèce hauterivienne *Nautilus begudensis* KILIAN & REBOUL, parfois attribuée au genre *Anglonautilus* SPATH, est révisée et transférée au genre *Cymatoceras* HYATT.

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Mots-clefs :

- Nautiloidea ;
- Nautilidae ;
- Anglonautilus ;
- Cymatoceras ;
- Crétacé inférieur

1. Introduction

The extinct genus Anglonautilus SPATH, 1927, remains a rather neglected nautiloid taxon from the Lower Cretaceous of both, the Tethys and the Boreal realms. Its first occurrence is probably in the upper Valanginian, and it certainly ranges through the Hauterivian into the Albian, with the species Anglonautilus praeundulatus LEHMANN et al., 2017, A. karpinskyi (Karakasch, 1907), A. undulatus (Sowerby, 1813), A. farringdonensis (SHARPE, 1854), and A. dorsoplicatus (WIEDMANN, 1960). Its presence in the Upper Cretaceous is based on the species A. dorsoplicatus (WIED-MANN), with an occurrence in the Middle Cenomanian of France and possibly in the Lower Cenomanian of Spain, England and Iran, and ? A. catarinae SUNDBERG, 1984, from the Maastrichtian of Baja California (Mexico). There are also doubtful records in the basal Paleocene [A. somovitensis (TZANKOV, 1941)] and the Eocene (JIBULEAC & AJDANLIJSKY, 2017, p. 59) of Bulgaria, but their generic affiliation is in need of revision.

LEHMANN *et al.* (2017) recently attempted to reconstruct the evolutionary history of the genus, and also introduced the new species *Anglonautilus praeundulatus* LEHMANN *et al.* It is worth noting that the Upper Cretaceous species *Anglonautilus japonicus* MATSUMOTO & TAKAHASHI, 1982, *Anglonautilus mamiyai* MATSUMOTO & MIYAUCHI, 1983, and *Anglonautilus suciensis* (WHITEAVES, 1879) have been excluded from that genus by LEHMANN *et al.* (2017) since they share only superficial similarities with the type species *A. undulatus* (SOWERBY).

The collection of new specimens from the Cretaceous of France improves our understanding of the genus *Anglonautilus* SPATH, especially regarding its earliest members.

2. Methodology and conventions

The measurements are given in millimeters; measurements of height (WH), width of the whorls (WB) and diameter of the umbilicus (U) were made at the largest diameter (D); Wh is taken at a position diametrically opposed to that of WH (Fig. 1) and a is the angle of that part of whorl where the undulations typical of Anglonautilus SPATH, 1927, are present.



Figure 1: Explanatory scheme for the measurements made on the studied specimens (illustration from ORBI-GNY, 1840-1842, modified).

The biostratigraphic scheme of the Lower Cretaceous followed herein (Fig. 2) is that developed by the IUGS Lower Cretaceous Ammonite Working Group (REBOULET *et al.*, 2018) for the northern and western Tethys.

Table 1: List of abbreviations used in the text.

CF	Camille FRAU coll., Muséum d'Histoire Naturelle d'Aix-en- Provence (France)												
GACO	ESPARRAC coll., Musée de Paléontologie de Provence, Aix- Marseille University (France)												
GD	Gérard DELANOY coll.												
GSC, GSM	British Geological Survey, Nottingham (UK)												
GSUB	Geowissenschaftliche Sammlung, Bremen University (Germany)												
PMAL	Pierre MARTEL coll., Réserve Naturelle Géologique du Luberon, Apt (France)												
PU	Museo Regionale di Scienze Naturali, Turin (Italy)												
RG	Roland GONNET coll.												
UJF-ID	Observatoire des Sciences de l'Univers de Grenoble, Saint-Martin d'Hères, Isère (France)												
ULP	Cyril BAUDOUIN coll.												

The suprageneric classification follows that of LEHMANN *et al.* (2017), who have confirmed that the genus *Anglonautilus* SPATH is closely related to *Cymatoceras* HYATT, 1884, and is probably derived from it, which leads its classification within the Nautilidae BLAINVILLE, 1825 (SHIMANSKY, 1975; TINTANT & KABAMBA, 1983; TINTANT, 1993).

C	ronosti	ratigra	my	North Tathus Domain	(REDOULTET at al. 2018)			
	1	2	3	North-Tethys Domain	(REBOULET <i>et al.</i> , 2018)			
				Zones	Subzones			
				Arrhaphoceras briacense				
Albian	1400			Mortoniceras perinflatum				
	per			Mortoniceras rostratum	8			
	Cb			Mortoniceras fallax				
				Mortoniceras inflatum				
				Mortoniceras pricei				
				Dipoloceras cristatum				
	63			Euhoplites lautus				
	Ipt			Euhoplites loricatus				
	Mic			Harditan dantatun	Hoplites spathi			
	~			Hopmes demanas	Lyelliceras lyelli			
	La C			D	Lyelliceras pseudolyelli			
	MO			Douvilleiceras mammiliatum				
	L			Levmeriella tardefurcata				
	1			Hypacanthoplites jacobi				
				4				
	H			Acanthonopilles notani	Diadochoceras nodosocostatum			
	bbe	Ħ	5.5	Parahoplites melchioris				
	n	bbe	ian		Epicheloniceras buxtorfi			
1.1		=	Apt	Epicheloniceras martini	Epicheloniceras gracile			
an					Epicheloniceras debile			
j.	1 P			D. C	Dufrenovia dufrenovi			
Aptian				Dufrenoyia furcala	Dufrenovia furcata			
					Deshayesites grandis			
	ver	100000	E	Desnayesites desnayesi				
	low	ver	ulia	Del marine Calenti	Roloboceras hambrovi			
		lov	opo	Desnayesiles forbesi				
			ň	Dashmasitas oglanlansia	Deshayesites luppovi			
				Desnayesties Ogianiensis				



1: REBOULET et al., 2018

2: International Commission on Stratigraphy

3: MOULLADE et al., 2011

Figure 2: Biozonation of the Lower Cretaceous used in this work, adopted from REBOULET et al. (2018).

3. Paleontological study Order Nautilida AGASSIZ, 1847 Superfamily Nautiloidea BLAINVILLE, 1825

Family Nautilidae BLAINVILLE, 1825 Genus Anglonautilus SPATH, 1927 (=Palelialia SHIMANSKY, 1955)

Type species: *Nautilus undulatus* SOWERBY, 1813, by original designation of SPATH (1927, p. 21).

Diagnosis: The genus *Anglonautilus* SPATH, 1927, is characterised by an involute coiling and a subtrapezoidal to suboval whorl section, compressed to moderately depressed. The ornamentation consists of broad undulations present at the top of the flanks and especially on the ventral region, on a part of the shell ranging from $a = 60^{\circ}$ to 200°, generally at the end of the phragmocone and/or at the beginning of the body chamber. Their strength is highly variable, ranging from discrete to very marked. These undulations are sometimes followed by cymatoceratid ribs towards the end of the body chamber.

The suture line is generally slightly sinuous, with a more or less marked lateral lobe and sometimes a weak ventral lobe. If exposed, the siphuncle is seen to be located close to the middle of the section, slightly shifted dorsally.

Geographical and stratigraphical distribution: The genus *Anglonautilus* SPATH, 1927, appears in the Early Hauterivian (Fig. 3) and probably even in the Late Valanginian in Germany (LEHMANN, unpublished data). However, it is rare



Figure 3: Stratigraphic position and suture line of the different species of the genus *Anglonautilus* SPATH, 1927.





Figure 4: Paleogeographical distribution of the different species of the genus *Anglonautilus* SPATH, 1927. Paleogeographical map of the Early Albian from SCOTESE, 2013, used here as an approximation of the Hauterivian-Cenomanian paleogeography. Data from KARAKASCH, 1907; SHIMANSKY, 1975; KENNEDY *et al.*, 1979; MUTTERLOSE, 1996; WEBER, 1996; WILMSEN, 2000; KENNEDY, 2002, and LEHMANN *et al.*, 2017.

in the Hauterivian and Barremian. At the current state of knowledge, only two specimens are known in the Hauterivian: the specimen figured by KARAKASCH (1907, Pl. II, fig. 9) as *Nautilus pseudoelegans* ORBIGNY, 1840, from the "Hauterivian sandstone of Biasala" (Crimea), which can be attributed to the Lower Hauterivian, and a recently discovered specimen of *Anglonautilus praeundulatus* LEHMANN *et al.*, 2017, from the Lower Hauterivian (*Lyticoceras nodosoplicatum* Zone) of Curnier (Drôme, France) (RG2007, figured here on Pl. I, fig. 1.a-b; Pl. II, fig. 1.a-b).

The genus occurs in Europe (England, France, Germany, Spain, Bulgaria?) and Asia (Crimea, Russia (northern Caucasus), Kazakhstan (Mangyshlak), Iran, Turkmenistan?), as well as possibly in Baja California, Mexico (KARAKASCH, 1907; TZANKOV, 1941; SHIMANSKY, 1975; KENNEDY *et al.*, 1979; SUNDBERG, 1984; MUTTERLOSE, 1996; WEBER, 1996; WILMSEN, 2000; KENNEDY, 2002; LEHMANN *et al.*, 2017) (Fig. 4).

Discussion: As currently defined, the genus *Anglonautilus* SPATH, 1927, includes the following species:

- A. dorsoplicatus (WIEDMANN, 1960)
- A. farringdonensis (SHARPE, 1854)
- A. karpinskyi (Karakasch, 1907)
- A. praeundulatus LEHMANN et al., 2017
- A. subalbensis (SINZOW, 1913)
- *A. undulatus* (Sowerby, 1813) Doubtful are:
- A.? catarinae Sundberg, 1984,
- A.? somovitensis (TZANKOV, 1941).

The lower Barremian taxon *Nautilus karpinskyi* KARAKASCH, 1907, type-species of the genus *Pale-lialia* SHIMANSKY, 1955, has been revised by SHI-MANSKY (1975), who, in the same publication, designated specimen no. 103/107 (p. 130, figured by KARAKASCH, 1907, Pl. VIII, fig. 10) as well as specimen no. 103/106 as lectotype (p. 200, caption in Pl. XXIX, fig. 1; specimen figured by KARA-KASCH, 1907, Pl. II, fig. 2, and refigured by SHI-MANSKY, 1975). Therefore, it is unclear which specimen SHIMANSKY intended as lectotype and this designation is therefore invalid (ICZN art. 74.5). Subsequently, TINTANT (1980, p. 64) designated specimen no. 103/106 as lectotype.

An understanding of the taxon Nautilus karpinskyi KARAKASCH and thus the genus Palelialia SHIMANSKY is therefore based on the lectotype no. 103/106 (KARAKASCH, 1907, Pl. II, fig. 2). This specimen develops an ornamentation composed of distinct undulations, followed by cymatoceratid ribbing, which is typical of the genus Anglonautilus SPATH. Furthermore, the suture line of this species, rather sinuous with a distinctive lateral lobe, has also been observed in other representatives of the genus Anglonautilus SPATH (this work, Pl. IV, fig. 2; Pl. XII, fig. 1.a-b) and does not in itself justify a generic distinction. We therefore consider the genus Palelialia SHIMANSKY as a junior synonym of Anglonautilus SPATH. Pending re-examination, the species P. alpanensis (ROUCHADZÉ, 1938) and P. imerica (ROUCHADZÉ, 1938) are kept separate from Anglonautilus SPATH as they lack of ornamentation and their suture lines differ from that of the genus. Their generic affinities remain to be investigated.



Interpretation of the species A. farringdonensis (SHARPE) was thus far based on the original hand-drawing and description of SHARPE (1854). Three specimens assigned to this species from the Faringdon Sponge Gravels (upper Aptian, Parahoplites nutfieldiensis Zone) of Faringdon (Berkshire, England) are kept in the collections of the British Geological Survey (Nottingham, England). They are here figured on Plates XII, XIII and XIV. Specimen no. GSC7552 (Pl. XII, fig. 2.a-b; Pl. XIII, fig. 2) corresponds to the specimen depicted by SHARPE (British Geological Survey comm.). It is herein designated as lectotype. The species is characterised by weak ornamentation, with only slight ventral undulations, and by a slightly sinuous suture line.

The species *A. catarinae* SUNDBERG, from the Lower Maastrichtian of Baja California (Mexico), bears low undulations on the venter in later growth stages, present on only a few specimens (SUNDBERG, 1984, p. 46). Its suture line is slightly sinuous, with a broad and weak lateral lobe. Its indistinct undulations question its generic attribution.

The species *A. somovitensis* (TZANKOV) is based on two specimens from the Lower Paleocene (Danian/Montian) of Somovit (Bulgaria). The poor quality illustration does not permit recognition of its main features. The species likely develops a few irregular undulations at the beginning of the body chamber. A re-examination of the material is needed to confirm its generic assignment.

The Upper Cretaceous taxa *A. hewaidyi* Mo-NEER *et al.*, 2021, *A. japonicus* MATSUMOTO & TAKA-HASHI, 1982, *A. mamiyai* MATSUMOTO & MIYAUCHI, 1983, and *A. suciensis* (WHITEAVES, 1879) develop a peculiar ornamentation, composed of undulations arising from cymatoceratid ribbing (CHIRAT & BUCHER, 2006, p. 62) and not independently as in the Lower Cretaceous forms. These taxa should be excluded from *Anglonautilus* SPATH (LEHMANN *et al.*, 2017, p. 74).

The taxon *Nautilus begudensis* KILIAN & RE-BOUL, 1915, from the Lower Hauterivian of the Alpes-de-Haute-Provence (France), has been assigned to the genus *Anglonautilus* SPATH by KUM-MEL (1956) and SHIMANSKY (1975); it is revised in this work and re-assigned into the genus *Cymatoceras* HYATT, 1884, in agreement with THIEULOY (1972) and LEHMANN *et al.* (2017).

When the shell is not preserved, the study of nautiloids with rib ornamentation can also be

complicated by the different types of mould preservation, as noted by MALCHYK et al. (2017). The thickness and structure of nautiloid shells, with different internal and external ornament, induces different types of mould preservation (composite moulds; CRAMPTON, 2004; WILMSEN, 2016). Therefore, the preserved ornamentation might represent a mixture of external and internal shell features. However, a study of a sufficient number of representatives of the genus Anglonautilus SPATH allows us to confirm that, in this genus, one never observes ornamentation of the Cymatoceras type in association with the typical undulations of Anglonautilus SPATH in that stage and that the two genera are indeed distinct, although certainly phyletically closely related.

Anglonautilus praeundulatus LEHMANN et al., 2017

(Pl. I, fig. 1.a-b; Pl. II, fig. 1.a-b; Pl. III, fig. 1.a-c; Pl. IV, figs. 1.a-b, 2; Pl. V, figs. 1, 2.a-b; Pl. VI, fig. 1)

2017. Anglonautilus praeundulatus sp. nov. - LEHMANN et al., p. 69, Fig. 2.

2019. Anglonautilus sp. - BERSAC & BERT, Pl. 3, figs. 7-8.

Material (n = 6): Specimen no. RG2007, Lower Hauterivian, *Lyticoceras nodosoplicatum* Zone, Curnier (Drôme, France); no. RG2004, lower Barremian, *Kotetishvilia compressissima* Zone ("Combe-Petite" Horizon), Lure Mountain (Alpes-de-Haute-Provence, France); no. RG2005, upper Barremian, Lure Mountain (Alpes-de-Haute-Provence, France); no. CF-B-EM.5, lower Aptian, lower part of the *Deshayesites deshayesi* Zone, bed 160, Conte Quarry, Cassis (Bouchesdu-Rhône, France); specimens no. GD28800, GD28801, lower Aptian, *Deshayesites deshayesi* Zone, *Deshayesites grandis* Subzone, bed 107, Les Graoux, Les Ferres (Alpes-Maritimes, France).

Type: Holotype is specimen no. GSUB C7505, deposited at the Geowissenschaftliche Sammlung, University of Bremen, Germany. It originates from the Forcall Formation, *Deshayesites deshayesi* Zone, lower Aptian, Castellote (Teruel, Spain).

Geographical and stratigraphical distribution: Based on our new data, *Anglonautilus praeundulatus* LEHMANN *et al.*, 2017, ranges from the Lower Hauterivian (*Lyticoceras nodosoplicatum* Zone) to the lower Aptian (*Deshayesites deshayesi* Zone) and is known from eastern Spain and southeastern France.

Dimensions (in mm)

Table 2: Measurements of Anglonautilus praeundulatus LEHMANN et al., 2017.

no.	D	U	WH	Wh	WB	a	U/D	WH/D	WH/Wh	WB/D	WB/WH
RG2004	100.1	10.3	58.2	33.7	55.1	150	0.10	0.58	1.73	0.55	0.95
RG2005	119.8	9.1	63.3	47.2	-	110	0.08	0.53	1.34	-	-
	96.2	7	57.1	30.4	46.6		0.07	0.59	1.88	0.48	0.82
RG2007	145.6	4.2	84.6	51.6	65.8	150	0.03	0.58	1.64	0.45	0.78
CF-B-EM.5	129.4	17.9	68.4	41.9	-	c120	0.14	0.53	1.63	-	-
GSUB C7505	112.5	15	55	35	48	90	0.13	0.49	1.57	0.43	0.87
GD28800	149	16.5	87	46.5	-	-	0.11	0.58	1.87	-	-
GD28801	c114	-	-	-	-	-	-	-	-	-	-



Description: The six specimens at our disposal show an involute coiling, with a *U/D* ratio between 0.03 and 0.14, the earlier specimens appearing to be more involute. Most specimens are affected by sediment compaction; the best-preserved specimens RG2004, RG2005 and RG2007 show a subtrapezoidal and moderately compressed whorl section. The flanks, which are slightly rounded in the inner whorls, become convex during growth to give the section a suboval shape beyond a diameter of about 100 mm. The venter is moderately broad and rounded. The peristome, preserved in specimens RG2004, RG2007 and CF-B-EM.5, is slightly sinuous, with a rounded indentation on the ventral region.

The suture line is slightly sinuous, with a shallow ventral lobe, slightly deeper on specimen CF-B-EM.5. The position of the siphuncle is unknown.

The ornamentation is composed of undulations on the ventral region, appearing at about D = 70-80 mm, on the last half or quarter whorl of the phragmocone. These undulations occur throughout an interval of between $a = 90^{\circ}$ and $a = 150^{\circ}$ and, on the largest specimens, disappear at about D = 90-100 mm to give way to an ornamentation of cymatoceratid ribs. As observed on specimens RG2005 and RG2007, the change from undulations to ribs is quite progressive, since undulations gradually lose their width and increase in density. The ribs are weak and mainly visible on the ventral region, but also on the flanks of specimens RG2007 and CF-B-EM.5 at the end of the body chamber. On specimen CF-B-EM.5, this change is more abrupt and the cymatoceratid ribbing appears as soon as the undulations disappear at the end of the phragmocone; they are thin on the main part of the body chamber and progressively strengthen when approaching the peristome.

Discussion and comparisons: Anglonautilus praeundulatus LEHMANN et al., 2017, is the earliest species of the genus Anglonautilus SPATH, 1927.

The species is closely allied to *Anglonautilus undulatus* (SOWERBY, 1813). It can be distinguished by a much narrower ventral region and a more compressed section, with a *WB/WH* ratio between 0.87 and 0.95 in *A. praeundulatus* LEH-MANN *et al.* and about 1.23 in the neotype of *A. undulatus* (SOWERBY). In addition, in *A. praeundu-*

latus LEHMANN *et al.* the undulations are less pronounced and occupy a smaller portion of the shell [between $a = 90^{\circ}$ and $a = 150^{\circ}$ in *A. praeundulatus* LEHMANN *et al.* versus $a = 180^{\circ}$ in *A. undulatus* (SOWERBY)].

The earlier species, *A. praeundulatus* LEHMANN et al. is from the lower Aptian, *Deshayesites deshayesi* Zone and probably ranges into the *Dufrenoyia furcata* Zone (*Anglonautilus* aff. *praeundulatus* LEHMANN et al., *infra*), whereas it was succeeded by *A. undulatus* (SOWERBY) in the upper Aptian, *Epicheloniceras martini* Zone.

Anglonautilus praeundulatus LEHMANN et al. can be easily distinguished from the Barremian species Anglonautilus karpinskyi (KARAKASCH, 1907) by its compressed whorl section [*WB/WH* about 1.19 in the lectotype of *A. karpinskyi* (KARA-KASCH)] and by its much less sinuous suture line, with a shallower lateral lobe.

Anglonautilus praeundulatus LEHMANN et al. differs from Anglonautilus farringdonensis (SHARPE, 1854) by a more compressed section and a stronger ornamentation, the undulations being very attenuated in *A. farringdonensis* (SHARPE).

Finally, Anglonautilus praeundulatus LEHMANN et al. can be distinguished from Anglonautilus dorsoplicatus (WIEDMANN, 1960) by a longer stage with undulations [$a = 60^{\circ}$ to 70° in A. dorsoplicatus (WIEDMANN)]. It also occupies a different stratigraphic position since A. dorsoplicatus (WIED-MANN) is only known from the Middle Albian to the Middle Cenomanian.

Anglonautilus aff. praeundulatus LEHMANN et al., 2017

(Pl. VII, fig. 1.a-b; Pl. VIII, fig. 1.a-b) 2018. *Anglonautilus* sp. - DELANOY *et al.*, Fig. 17.B-C.

Material (n = 1): Specimen no. GD28773, lower Aptian, *Dufrenoyia furcata* Zone, *Dufrenoyia dufrenoyi* Subzone, bed 110, Les Graoux, Les Ferres (Alpes-Maritimes, France).

Geographical and stratigraphical distribution: Anglonautilus aff. praeundulatus LEHMANN et al., 2017, is only known from bed 110 of Les Graoux, Les Ferres (Alpes-Maritimes, France), assigned to the lower Aptian, Dufrenoyia furcata Zone, Dufrenoyia dufrenoyi Subzone.

Dimensions (in mm)

 D
 U
 WH
 WB
 a
 U/D
 WH/D
 WH/Wh
 WB/D
 WB/WH

 GD28773
 170
 110

Description: Specimen GD28773 is strongly distorted, and its whorl section is difficult to characterise; it is seemingly moderately compressed, suboval on the body chamber. The flanks are relatively flat on the phragmocone and become rounded on the body chamber. The ventral region is narrow and rounded. The suture line is rather sinuous and shows a distinctive lateral lobe. The position of the siphuncle is not known.

The ornamentation appears on the phragmocone at D = 50-60 mm. It is first composed of well-marked, distant undulations, visible only on the ventral region where they form a chevron. At the transition between the phragmocone and the body chamber, at D = 85 mm, the undulations disappear and give way to a dense and strong cymatoceratid ribbing, present on both flanks and venter of the body chamber. These ribs follow a convex path on the flanks and cross the ventral region strongly curved backwards, forming a chevron of the same shape as the undulations on the phragmocone.



Discussion and comparisons: Anglonautilus aff. praeundulatus LEHMANN et al., 2017, is close to A. praeundulatus LEHMANN et al.; it mainly differs by the presence of strong cymatoceratid ribs on the body chamber. This ribbing can be observed, although much less developed, on specimens CF-B-EM.5 and GD28800 of A. praeundulatus LEHMANN et al. A. aff. praeundulatus LEHMANN et al. can therefore be interpreted as a form showing strongly developed cymatoceratid ribbing of the type seen in A. praeundulatus LEHMANN et al. However, given the uniqueness of this specimen, its rather poor preservation and its slightly later stratigraphic position, it seems preferable to leave its true affinities open to questions.

Anglonautilus undulatus (SOWERBY, 1813)

(Pl. IX, figs. 1.a-b, 2; Pl. X, figs. 1-2, 3.a-b; Pl. XI, fig. 1.a-b)

- 1813. *Nautilus undulatus* sp. nov. SOWERBY, p. 87, Pl. XL, upper figure.
- non 1853. Nautilus undulatus Sowerby Sharpe, p. 15, Pl. V, fig. 4.a-c [? = Anglonautilus dorsoplicatus (WIEDMANN, 1960)].
- 1913. Nautilus subalbensis sp. nov. SINZOW, p. 113, Pl. VI, fig. 7, 7a.
- non 1951. Anglonautilus undulatus (SOWERBY) C.W. WRIGHT & E.V. WRIGHT, p. 12, Pl. V, fig. 4 [? = Anglonautilus dorsoplicatus (WIEDMANN, 1960)].
- 1956. Anglonautilus undulatus (SOWERBY) KUMMEL, p. 430, Fig. 26, Pl. 20, figs. 1-2.
- 1960. Anglonautilus undulatus (SOWERBY) SHIMANSKY, p. 244, Pl. VII, fig. 1.а-в.
- 1960. Angulithes (Pseudocenoceras) undulatus (SOWER-BY) - WIEDMANN, p. 176.
- 1964. Anglonautilus undulatus (SOWERBY) KUMMEL, p. K453, Fig. 334, 3.a-b.
- 1975. Anglonautilus subalbensis (SINZOW) SHIMANSKY, p. 120, Pl. XXVII, fig. 2.a- 6.
- 1975. Anglonautilus undulatus (SOWERBY) SHIMANSKY, p. 119, Pl. XXVII, fig. 1.a-6.
- non 1979. Anglonautilus undulatus (SOWERBY) KENNEDY et al., p. 7, Pl. 1, fig. 1 [? = Anglonautilus dorsoplicatus (WIEDMANN, 1960)].
- 1983. Anglonautilus undulatus (SOWERBY) KABAMBA, Pl. IV, fig. 3.a-b.
- ? 1983. Anglonautilus ou Cymatoceras KABAMBA, p. 59, Pl. IV, fig. 4.
- 1996. Anglonautilus undulatus (SOWERBY) MUTTERLOSE, Pl. 6, fig. 2.
- 1996. Anglonautilus undulatus (SOWERBY) WEBER, Pl. 9, fig. 3.
- non 2002. Anglonautilus undulatus (SOWERBY) KENNE-DY, p. 231, Fig. 10.1I [? = Anglonautilus dorsoplicatus (WIEDMANN, 1960)].
- ? 2016. Anglonautilus ? sp. LEHMANN et al., Pl. 5, fig. 2; Pl. 10, fig. 3.

Material (n = 5): Specimen no. CF-B-PM.4.13, upper Aptian, lower part of the *Epicheloniceras martini* Zone, bed 191?, La Marcouline gate, Cassis (Bouches-du-Rhône, France); no. CF-B-LM.12, upper Aptian, upper part of the *Epicheloniceras martini* Zone, bed M52, La Marcouline quarry, Cassis (Bouches-du-Rhône, France); no. CF-FcFb.65, CF-FcFb.106, CF-CUG.1, upper Aptian, upper part of the *Epicheloniceras martini* Zone (equivalent to bed M52), Fontblanche Forest, Roquefort-la-Bédoule (Bouches-du-Rhône, France).

Type: According to KUMMEL (1956, p. 431), the type specimen of Sowerby is lost. The original illustration is idealised and makes it difficult to appreciate its diagnostic features. Indeed, the ventral undulations described by SOWERBY are not illustrated in his drawing. Interpretation of this species was subsequently based on the topotype B.M.N.H. 66336, illustrated by KUMMEL (1956, Pl. 20). In order to define Sowerby's species much more comprehensively than the original illustration allows, we herein retain specimen no. B.M.N.H. 66336 as neotype of A. undulatus (SOWERBY, 1813). It originates from the type locality (Nutfield, Surrey, England) and is assigned to the upper Aptian, Parahoplites nutfieldiensis Zone; it is stored in the collections of the Natural History Museum in London.

Geographical and stratigraphical distribution: The species is recorded from the upper Aptian of England, southeastern France, Germany, Russia (northern Caucasus) and Kazakhstan (Mangyshlak). Anglonautilus subalbensis (SINZOW, 1913) [= Anglonautilus undulatus (SOWERBY, 1813)] is also recorded in Turkmenistan (Tuarkyr mountains) according to SHIMANSKY (1975), but the corresponding specimen lacks illustration. This species would extend up into the Lower Albian according to SHIMANSKY (1975); the Albian specimen from Hunstanton (England) figured by KABAMBA (1983, Pl. IV, fig. 4) as "Anglonautilus or Cymatoceras" could also be a representative of Anglonautilus undulatus (SOWERBY). Specimens attributed to Anglonautilus undulatus (SOWERBY) by Sharpe (1853), C.W. WRIGHT & E.V. WRIGHT (1951) and KENNEDY et al. (1979) from the Lower Cenomanian of England and Iran are here tentatively re-assigned to Anglonautilus dorsoplicatus (WIEDMANN, 1960).

Dimensions (in mm)

Table 4: Measurements	of Anglonautilus undulatus (SOWERBY, 18	13)
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no.	D	U	WH	Wh	WB	a	U/D	WH/D	WH/Wh	WB/D	WB/WH
CF-B-LM.12	c134.7	15.8	69	c48.2	-	180	0.12	0.51	1.43	-	-
CF-B-PM.4.13	94.5	-	-	-	-	200	-	-	-	-	-
CF-FcFb.65	-	-	46.3	-	-	-	-	-	-	-	-
CF-FcFb.106	145.8	18.5	75.1	56.4	66.9	c170	0.13	0.52	1.33	0.46	0.89
CF-CUG.1	c146.2	c13.8	95	-	-	-	0.09	0.65	-	-	-

Description: The five specimens at our disposal are distorted by sedimentary compaction, and only specimen no. CF-FcFb.106 shows a whorl section suitable for measurement. The coil-

ing is moderately involute, with a relatively open umbilicus (U/D ratio greater than 0.10). The section is suboval, inflated, with increasingly rounded flanks during growth and a relatively wide,



rounded ventral region. The peristome, preserved on specimens no. CF-FcFb.106 and CF-CUG.1, is sinuous, with a ventral indentation, following the same shape as the ribs. The suture line, as those seen in specimen no. CF-B-LM.12, is not very sinuous, with a wide and shallow lateral lobe. The position of the siphuncle remains unknown.

The ornamentation is first composed of relatively strong undulations, widely spaced, visible over about $a = 180^{\circ}$, present on the ventral region and the top of the flanks of the last part of the phragmocone; they are also present on the first part of the body chamber of specimen no. CF-CUG.1. Specimen no. CF-FcFB.106 develops a few thin and very attenuated riblets, overlapping the undulations. These undulations are followed, on the body chamber of specimens no. CF-FcFb.106, CF-B-LM.12 and CF-CUG.1, by an ornamentation of relatively weak cymatoceratid ribs, attenuated on the lower half of the flanks; they are more clearly marked on the umbilical wall and the upper part of the flanks, especially near the peristome. They are convex on the flanks and then curve backwards on the upper third of the flanks. In specimen CF-FcFb.106, they cross the venter where they are attenuated, forming a rounded chevron. On specimen no. CF-B-LM.12 there are also fine growth striae superimposed on the ribs and of the same pattern, visible on the upper half of the flanks of the last half of the body chamber.

Discussion and comparisons: The species *Anglonautilus subalbensis* (SINZOW, 1913), from the upper Aptian of Kazakhstan (Mangyshlak), is similar to *Anglonautilus undulatus* (SOWERBY, 1813), both regarding general morphology and ornamentation. SHIMANSKY (1975) indicates that *A. subalbensis* (SINZOW) has a more trapezoidal whorl section and that the undulations of this species are only present on the ventral region.

However, the section, which is obviously very close to that of *A. undulatus* (SOWERBY), is only partially visible on the original figure of *A. subalbensis* (SINZOW), and the undulations seem to be present at the top of the flanks of the type-specimen. These differences do not seem to justify a specific distinction and *A. subalbensis* (SINZOW) is thus regarded as a junior synonym of *A. undulatus* (SOWERBY).

Anglonautilus undulatus (SOWERBY) closely resembles Anglonautilus praeundulatus LEHMANN *et al.*, 2017. Differences between the two species have been discussed above.

Anglonautilus undulatus (SOWERBY) differs from Anglonautilus farringdonensis (SHARPE, 1854) by its distinct undulations, present over about half a whorl, whereas these are discrete in *A. farringdonensis* (SHARPE).

Anglonautilus undulatus (SOWERBY) is also closely related to Anglonautilus dorsoplicatus (WIEDMANN, 1960). A. undulatus (SOWERBY) differs from it in having a much wider section, a slightly less sinuous suture line and, above all, much more developed undulations, present for a range of about $a = 180^{\circ}$, whereas they are present for only about $a = 60^{\circ}$ -70° in A. dorsoplicatus (WIED-MANN).

Anglonautilus aff. undulatus (Sowerby, 1813)

(Pl. I, fig. 2.a-b; Pl. II, fig. 2.a-b)

Material (n = 1): Specimen no. RG2006, upper Barremian, Lure Mountain (Alpes-de-Haute-Provence, France).

Geographical and stratigraphical distribution: Anglonautilus aff. undulatus (SOWERBY, 1813) is only known in the upper Barremian of the Lure Mountain (Alpes-de-Haute-Provence, France).

Dimensions (in mm)

 D
 U
 WH
 WB
 a
 U/D
 WH/Wh
 WB/D
 WB/WH

 RG2006
 83.7
 9.1
 50.4
 26.2
 50.5
 170
 0.11
 0.60
 1.92
 0.60
 1.00

Description: Specimen no. RG2006 is smallsized, well preserved, complete with its body chamber and peristome. The coiling is involute and the section is subtrapezoidal, with slightly rounded flanks converging to a broadly rounded ventral region. The peristome is sinuous, with a slight ventral indentation. Neither the suture line nor the position of the siphuncle are discernable.

Ornamentation, absent on the phragmocone, appears at the beginning of the body chamber, formed by widely spaced undulations on the ventral region well-marked and of irregular strength. The undulations are slightly rursiradiate and cross the ventral region forming a weak adapical sinus. In the last half of the body chamber, feebly convex, slightly marked and irregularly shaped cymatoceratid ribs appear on the flanks, becoming somewhat more pronounced towards the peristome.

Discussion and comparisons: Specimen no. RG2006 shows great affinities to Anglonautilus undulatus (SOWERBY, 1813) by its wide whorl section and distinctive undulations, present over about $a = 170^{\circ}$. However, it differs from it by the irregularity of these undulations and their presence on the body chamber only, whereas in A. undulatus (SOWERBY) they are mainly present on the last 180° of the phragmocone, sometimes at the beginning of the body chamber. It also occupies a much earlier stratigraphic position, in the upper Barremian, whereas A. undulatus (Sower-BY) is only known from the upper Aptian. The peculiarities and uniqueness of specimen no. RG2006 do not allow us to integrate it into the Sowerby's species; it may either represent an atypical form because of its lower stratigraphic position, which needs to be supported by more material, or it may represent an undescribed species.

Specimen no. RG2006 shares some similarities with the lower Barremian species *Anglonautilus karpinskyi* (KARAKASCH, 1907) by the shape of its whorl section. However, the lectotype of *A. karpinskyi* (KARAKASCH) can be easily distinguished by the undulations present on its phragmocone and the early appearance of a distinctive cymatoceratid ribbing. The lack of the body chamber in the lectotype of *A. karpinskyi* (KARAKASCH) and the impossibility to observe the suture line on specimen no. RG2006 prevent further comparison.

Specimen no. RG2006 can be distinguished from *Anglonautilus praeundulatus* LEHMANN *et al.*, 2017, by its distinctly wider whorl section and by the well-marked undulations, present only on the body chamber, being more persistent ($a = 170^{\circ}$ instead of $a = 90^{\circ}$ to 150° in *A. praeundulatus* LEHMANN *et al.*).

Anglonautilus dorsoplicatus (WIEDMANN, 1960)

(Pl. VI, fig. 2.a-c; Pl. XI, fig. 2.a-c; Pl. XIV, fig. 2.a-c)

- pars 1853. Nautilus largilliertianus d'ORBIGNY SHARPE, p. 16, Pl. VI, fig. 2 ?; non Pl. VI, fig. 1 [= Pseudocenoceras largilliertianum (ORBIGNY)].
- ? 1853. Nautilus undulatus SOWERBY SHARPE, p. 15, Pl. V, fig. 4.a-c.
- 1897. Nautilus largilliertianus ? d'ORBIGNY PARONA & BONARELLI, p. 76, Pl. 10, fig. 6.
- ? 1951. Anglonautilus undulatus (Sowerby) C.W. WRIGHT & E.V. WRIGHT, p. 12, Pl. V, fig. 4.
- 1960. Angulithes (Pseudocenoceras) dorsoplicatus nov. sp. - WIEDMANN, p. 176.
- ? 1979. Anglonautilus undulatus (SOWERBY) KENNEDY et al., p. 7, Pl. 1, fig. 1.
- pars 1999. Pseudocenoceras cf. fittoni (SHARPE) WIT-TLER et al., p. 25, Fig. 32.a-b, non Fig. 30a, b [= Pseudocenoceras fittoni (SHARPE)], 31.a-b (= ? Eutrephoceras sp.).
- ? 2000. Pseudocenoceras dorsoplicatus (WIEDMANN) -WILMSEN, p. 41, Pl. 5, figs. 13, 26.
- ? 2002. Pseudocenoceras dorsoplicatus (WIEDMANN) -

KENNEDY, p. 223, Fig. 10.1F.

- ? 2002. Anglonautilus undulatus (Sowerby) KENNEDY, p. 231, Fig. 10.1I.
- 2017. Anglonautilus dorsoplicatus (WIEDMANN) LEH-MANN et al., Fig. 3.

Material (n = 3): Cast of the holotype no. GSUB C7523, Middle Albian, Escragnolles (Alpes-Maritimes, France); specimen no. PMAL 340, Upper Albian, Saint-Etienne-les-Orgues (Alpes-de-Haute-Provence, France); no. ULP01, Middle Cenomanian, Acanthoceras rhotomagense Zone, Turrilites costatus Subzone, Saint-Ulphace (Sarthe, France).

Type: The holotype is the specimen no. PU20409 figured by PARONA & BONARELLI (1897, Pl. 10, fig. 6) and refigured here Pl. XI, fig. 2.a-c; it is housed at the Museo Regionale di Scienze Naturali in Turin (Italy) and comes from the Middle Albian of Escragnolles (Alpes-Maritimes, France); it originates from beds having a condensed fauna including ammonites indicative of the *Lyelliceras lyelli, Hoplites spathi* and *Anahoplites intermedius* subzones (LEHMANN *et al.*, 2017, p. 68). We have access to a cast, stored as no. GSUB C7523 in the Geowissenschaftliche Sammlung of the University of Bremen (Germany) that was already figured by LEHMANN *et al.* (2017, Fig. 3).

Geographical and stratigraphical distribution: The species ranges from the Middle Albian to the Middle Cenomanian of France and Germany and is possibly present in the Lower Cenomanian of northern Cantabria, Spain. The Lower Cenomanian specimens from England and Iran figured by SHARPE (1853, Pl. VI, fig. 2 only) as *Pseudocenoceras largilliertianum* (ORBIGNY, 1840) and by SHARPE (1853), C.W. WRIGHT & E.V. WRIGHT (1951) and KENNEDY *et al.* (1979) as *Anglonautilus undulatus* (SOWERBY, 1813) probably belong to *Anglonautilus dorsoplicatus* (WIEDMANN, 1960).

Dimensions (in mm)

Table 6: Measurements of Anglonautilus dorsoplicatus (WIEDMANN, 1960).

no.	D	U	₩Н	Wh	WB	a	U/D	WH/D	WH/Wh	WB/D	WB/WH
GSUB C7523	60.5	6.8	37.3	22.6	32.9	60	0.11	0.62	1.65	0.54	0.88
PMAL 340	69.6	-	39.2	25.9	-	70	-	0.56	1.51	-	-
ULP01	63	6.8	34.6	22	26.8	-	0.11	0.55	1.57	0.43	0.77

Description: The three specimens show a fairly involute coiling and a compressed subtrapezoidal section, with slightly rounded flanks and a relatively narrow, rounded ventral region. On the holotype and specimen no. PMAL 340, only the very beginning of the body chamber is preserved; specimen no. ULP01 is entirely septate. The suture line is weakly sinuous on the holotype and specimen no. ULP01, with a broad, shallow lateral lobe and the absence of a ventral lobe. The lateral lobe is less marked on specimen no. PMAL 340. According to PARONA & BONARELLI (1897, p. 76), the siphuncle is located on the inner quarter of the septal surface in the holotype; it is not visible on cast no. GSUB C7523. However, it is also visible on the inner quarter of the septal surface of specimen no. ULP01 (Pl. XIV, fig. 2c).

Ornamentation, comprising a few undulations, is present only during a short stage (about $a = 60^{\circ}-70^{\circ}$) at the end of the phragmocone, appearing at the top of the flanks and especially visible on the ventral region. They are distinctly rursiradiate and form a more or less angular sinus in the ventral region.

Discussion and comparisons: The Lower Cenomanian specimens figured by SHARPE (1853), C.W. WRIGHT & E.V. WRIGHT (1951) and KENNEDY *et al.* (1979) are doubtfully re-assigned here to *Anglonautilus dorsoplicatus* (WIEDMANN, 1960) since they show some differences to the holotype. The position of the siphuncle in the very fragmentary specimen of SHARPE (1853, Pl. VI, Fig. 2), referred to as *Nautilus largilliertianus* ORBIGNY, 1840, shown at the base of the septal surface, differs markedly from that of the holotype, where it is



situated in the lower quarter of that surface. However, the position of the siphuncle as shown in SHARPE's drawing is questioned by PARONA & BO-NARELLI (1897, p. 76). On the specimen figured by SHARPE (1853) and C.W. WRIGHT & E.V. WRIGHT (1951) as *Anglonautilus undulatus* (SOWERBY, 1813), the undulations show a similar development to those of *A. dorsoplicatus* (WIEDMANN) but are located on the last part of the body chamber, whereas they are present on the phragmocone of the holotype of *A. dorsoplicatus* (WIEDMANN). Finally, on the specimen figured by KENNEDY *et al.* (1979) as *A. undulatus* (SOWERBY), the section appears distinctly different, wider and subcircular.

Anglonautilus dorsoplicatus (WIEDMANN) differs from Anglonautilus undulatus (SOWERBY) by its much more compressed section and by its undulations being present for a much shorter stage, about $a = 60-70^{\circ}$ instead of $a = 180^{\circ}$.

Anglonautilus dorsoplicatus (WIEDMANN) is also close to Anglonautilus praeundulatus LEHMANN et al., 2017, but is essentially different by its less developed undulations, present over about a =60°-70° instead of a = 90°-150° in A. praeundulatus LEHMANN et al. It also occupies a different stratigraphic position.

Anglonautilus dorsoplicatus (WIEDMANN) differs from Anglonautilus farringdonensis (SHARPE, 1854) by a much more compressed section and by its more pronounced undulations, which are barely perceptible in *A. farringdonensis* (SHARPE).

Anglonautilus dorsoplicatus (WIEDMANN) is also close to the Cenomanian species *Pseudocenoceras largilliertianum* (ORBIGNY), from which it differs only by the presence of weak undulations on the ventral region. Affinities between the genus *Anglonautilus* SPATH, 1927, and *P. largilliertianum* (ORBIGNY) have already been noted by TINTANT (1993, p. 365), and *A. dorsoplicatus* (WIEDMANN) has frequently been attributed to the genus *Pseudocenoceras* SPATH, 1927 (WIEDMANN, 1960; WILM-SEN, 2000; KENNEDY, 2002). The phyletic relationships between *A. dorsoplicatus* (WIEDMANN) and *P. largilliertianum* (ORBIGNY) need to be clarified.

Anglonautilus sp.

(Pl. XII, fig. 1.a-b)

Material (n = 1): Specimen no. GACO.033, upper Aptian, base of the *Epicheloniceras martini* Zone, La Marcouline quarry, Cassis (Bouches-du-Rhône, France).

Geographical and stratigraphical distribution: *Anglonautilus* sp. is based on specimen no. GACO.033, from the upper Aptian (base of the *Epicheloniceras martini* Zone) of Roquefort-la-Bédoule (Bouches-du-Rhône, France).

Dimensions (in mm)

 Table 7: Measurements of Anglonautilus sp.

no.	D	U	WH	Wh	WB	a	U/D	WH/D	WH/Wh	WB/D	WB/WH
GACO.033	137.2	19	73.6	55.6	41.6	c110	0.14	0.54	1.32	0.30	0.57

Description: Specimen no. GACO.033 is complete with its body chamber. It shows an involute coiling and a compressed section, with slightly rounded flanks and a narrow, rounded ventral region. The very sinuous suture line shows a very wide and deep lateral lobe. The position of the siphuncle is unknown.

The ornamentation consists of well-marked undulations, present over at least $a = 110^{\circ}$, on the entire visible part of the phragmocone. The undulations appear at the top of the flanks and are mainly visible on the ventral region where they are strong, widely spaced and clearly rursiradiate, forming a rounded adapical sinus. On the body chamber, the undulations disappear and the ornamentation is composed only of faint growth striae visible on the flanks. The peristome is preserved on one flank; it is sinuous, with a lappet in the upper third of the flank and then strongly retroverse as it approaches the ventral region.

Discussion and comparisons: Specimen no. GACO.033 shows some affinities to *Anglonautilus undulatus* (SowERBY, 1813), notably by the strong development of its undulations, present over at least $a = 110^{\circ}$. However, it differs from that species by its much narrower section and especially by its very sinuous suture line with a well-developed lateral lobe, very different from the suture line of most other species of the genus *Anglonautilus* SPATH, 1927.

The suture line of specimen GACO.033 is however similar to that of the lectotype of *Anglonautilus karpinskyi* (KARAKASCH, 1907), which also shows a very wide and deep lateral lobe. However, the shell morphology of *A. karpinskyi* (KARA-KASCH) differs by its much wider section, undulations present for a much shorter stage, and the appearance of strongly developed cymatoceratid ribs on the phragmocone.

The unusual features of specimen no. GACO.033 do not allow attribution to any *Anglonautilus* species. It could represent a new species, but this could only be confirmed by additional material.

Genus Cymatoceras HYATT, 1884

Type species: Nautilus pseudoelegans ORBI-GNY, 1840, by original designation of HYATT (1884, p. 301).

Cymatoceras begudensis (KILIAN & REBOUL, 1915)

- (Pl. XV, fig. 1.a-c; Pl. XVI, figs. 1.a-c, 2.a-b)
- 1915. Nautilus begudensis sp. nov. KILIAN & REBOUL, p. 227, Pl. X, fig. 1.
- 1956. Anglonautilus begudensis (KILIAN & REBOUL) -KUMMEL, p. 431.
- 1972. Anglonautilus ? begudensis (KILIAN & REBOUL) -THIEULOY, p. 22.
- 1975. Anglonautilus begudensis (KILIAN & REBOUL) SHI-MANSKY, p. 119.



2017. "Anglonautilus" begudensis (KILIAN & REBOUL) -LEHMANN et al., p. 72.

Material (n = 3): Specimens no. UJF-ID 434, UJF-ID 435, UJF-ID 25328, Lower Hauterivian, *Lyticoceras nodosoplicatum* Zone, La Bégude, La-Palud-sur-Verdon (Alpes-de-Haute-Provence, France).

Type: The lectotype, designated by THIEULOY (1972), is specimen no. UJF-ID 434 (lectotype designation before 2000, CINZ art. 74.5), figured on Pl. XVI, fig. 1.a-c.

Geographical and stratigraphical distribution: *Cymatoceras begudensis* (KILIAN & REBOUL, 1915) only occurs in the Lower Hauterivian, *Lyticoceras nodosoplicatum* Zone of La-Palud-sur-Verdon (Alpes-de-Haute-Provence, France). The species is also reported (without illustration) from the Lower Hauterivian, *Crioceratites loryi* Zone, *Olcostephanus jeannoti* Subzone of Rottier (Drôme) and from Rougon (Alpes-de-Haute-Provence) by THIEULOY (1972), but these unnumbered specimens have not been found in the collections of the Observatoire des Sciences de l'Univers de Grenoble.

Dimensions (in mm)

Table 8: Measurements of Cymatoceras begudensis (KILIAN & REBOUL, 1915).

no.	D	U	WH	Wh	WB	U/D	WH/D	WH/Wh	WB/D	WB/WH
UJF-ID 434	95.3	10	56.7	-	43.8	0.10	0.59	-	0.46	0.77
UJF-ID 435	87.8	-	49.2	-	42.9	-	0.56	-	0.49	0.87
UJF-ID 25328	124.9	16.9	64.1	-	59	0.14	0.51	-	0.47	0.92

Description: The three specimens studied here show a compressed (*WB/WH* close to 0.80-090) and relatively evolute shell (*U/D* between 0.10 and 0.14). The section is oval, with slightly rounded flanks. The suture line, visible on specimen no. UJF-ID 435 (Pl. XVI, fig. 2.a-b), is only slightly sinuous. The position of the siphuncle is unknown.

The ornamentation is only visible from about D = 55 mm. It is first composed of sinuous and slightly concave ribs. They are weak on the flanks, then become stronger in the upper third and bend abruptly backwards to cross the ventral region forming a clear concave sinus.

From about D = 70-80 mm, there is a short stage where some ribs (about one in two) strengthen very strongly as they pass through the ventral region while conversely, the remaining ribs weaken.

Beyond about D = 100 mm, the ornamentation becomes regular again. The ribs are well marked on the flanks where they are straight to slightly concave, then bend backwards to cross the ventral region in equal strength.

Discussion and comparisons: The ornamentation of Cymatoceras begudensis (KILIAN & REBOUL, 1915), with a short stage showing strengthened ribs on the ventral region, led KUM-MEL (1956) to assign the species to Anglonautilus SPATH, 1927. However, as noted by THIEULOY (1972) and LEHMANN et al. (2017), these ribs are superimposed on a typical cymatoceratid ribbing as defined by CHIRAT & BUCHER (2006) and do not conform to the stage with independent undulations as observed in Anglonautilus SPATH. These strengthened ribs are also very different from the undulations observed in typical representatives of the genus Anglonautilus SPATH, with a much higher, narrow and angular shape. As such, the species of KILIAN & REBOUL compares better with typical Cymatoceras HYATT, 1884.

THIEULOY (1972) suggested that *Cymatoceras* begudensis (KILIAN & REBOUL) may correspond to a peculiar morphotype of *Cymatoceras bifurcatus* (OOSTER, 1858). This species remains little studied. Note that the type specimens of OOSTER come from the Albian and the "Neocomian" of Switzerland and are probably not conspecific. As a consequence, THIEULOY's hypothesis remains unclear and a revision of the taxonomy and age of *C. bifurcatus* (OOSTER) is needed. However, the particular ornamental characters and the restricted stratigraphic position of *C. begudensis* (KILIAN & REBOUL) suggest that this may be a distinct species.

Cymatoceras begudensis (KILIAN & REBOUL) is also closely allied to *Cymatoceras neocomiense* (ORBIGNY, 1840), a species present in the Hauterivian and Barremian. It is distinguished by its much more compressed section and its short stage with strengthened ribs in the ventral region, by contrast to the regular cymatoceratid ribbing of *C. neocomiense* (ORBIGNY).

4. Conclusions

The study of new material of the genus Anglonautilus SPATH, 1927, from southeastern France has allowed us to identify the stratigraphic succession of the species A. praeundulatus LEHMANN et al., 2017, A. undulatus (SOWERBY, 1813) and A. dorsoplicatus (WIEDMANN, 1960) in the Lower Cretaceous and base of the Upper Cretaceous and also to define their specific characteristics. In addition, we have been able to show that the genus Anglonautilus SPATH, present in the Early Hauterivian, was most certainly derived from the genus Cymatoceras HYATT, 1884. The illustration of the lectotype and two other topotypes of Nautilus farringdonensis SHARPE, 1854, allowed us to confirm that this species also belongs to the genus Anglonautilus SPATH. However, a study of typical specimens of Nautilus begudensis KILIAN & REBOUL, 1915, led us to exclude this species from the genus Anglonautilus SPATH and to attribute it to the genus Cymatoceras HYATT instead.



The genus Anglonautilus SPATH is still present in the Upper Cretaceous but remains poorly known, especially regarding the post-Cenomanian taxa. In particular, the phyletic links of Early Cretaceous species with the latest Cretaceous (Maastrichtian) species ? *A. catarinae* SUNDBERG, 1984, and Paleocene (Danian/Montian) ? *A. somovitensis* (TZANKOV, 1941) remain to be clarified. The generic assignment of these two species to the genus Anglonautilus SPATH still has to be confirmed.

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Plate I:

Fig. 1.a-b: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. RG2007, Lower Hauterivian, Lyticoceras nodosoplicatum Zone, Curnier (Drôme, France). Fig. 2.a-b: Anglonautilus aff. undulatus (SOWERBY, 1813). Specimen no. RG2006, upper Barremian, Lure Mountain (Alpes-de-Haute-Provence, France).



Plate II:

Fig. 1.a-b: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. RG2007, Lower Hauterivian, Lyticoceras nodosoplicatum Zone, Curnier (Drôme, France). Fig. 2.a-b: Anglonautilus aff. undulatus (SOWERBY, 1813). Specimen no. RG2006, upper Barremian, Lure Mountain

(Alpes-de-Haute-Provence, France).



Plate III: Fig. 1.a-c: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. RG2005, upper Barremian, Lure Moun-tain (Alpes-de-Haute-Provence, France).



Plate IV:

Fig. 1.a-b: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. RG2004, lower Barremian, Kotetishvilia compressissima Zone ("Combe-Petite" Horizon), Lure Mountain (Alpes-de-Haute-Provence, France). Fig. 2: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. CF-B-EM.5, lower Aptian, lower part of the

Deshayesites deshayesi Zone, bed 160, Conte Quarry, Cassis (Bouches-du-Rhône, France).





Plate V:

Fig. 1: Anglonautilus praeundulatus LEHMANN *et al.*, 2017. Specimen no. GD28800, lower Aptian, *Deshayesites deshayesi* Zone, *Deshayesites grandis* Subzone, bed 107, Les Graoux, Les Ferres (Alpes-Maritimes, France). **Fig. 2.a-b:** Anglonautilus praeundulatus LEHMANN *et al.*, 2017. Specimen no. GD28801, lower Aptian, *Deshayesites deshayesi* Zone, *Deshayesites grandis* Subzone, bed 107, Les Graoux, Les Ferres (Alpes-Maritimes, France).





Plate VI:

Fig. 1: Anglonautilus praeundulatus LEHMANN et al., 2017. Specimen no. GD28800, lower Aptian, Deshayesites deshayesi Zone, Deshayesites grandis Subzone, bed 107, Les Graoux, Les Ferres (Alpes-Maritimes, France). **Fig. 2.a-c:** Anglonautilus dorsoplicatus (WIEDMANN, 1960). Specimen no. PMAL 340, Upper Albian, Saint-Etienne-les-Orgues (Alpes-de-Haute-Provence, France).





Plate VII: Fig. 1.a-b: Anglonautilus aff. praeundulatus LEHMANN et al., 2017. Specimen no. GD28773, lower Aptian, Dufrenoyia furcata Zone, Dufrenoyia dufrenoyi Subzone, bed 110, Les Graoux, Les Ferres (Alpes-Maritimes, France).





Plate VIII: Fig. 1.a-b: Anglonautilus aff. praeundulatus LEHMANN et al., 2017. Specimen no. GD28773, lower Aptian, Dufrenoyia furcata Zone, Dufrenoyia dufrenoyi Subzone, bed 110, Les Graoux, Les Ferres (Alpes-Maritimes, France).



Plate IX:

Fig. 1.a-b: Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-FcFb.106, upper Aptian, upper part of the *Epicheloniceras martini* Zone (equivalent to bed M52 of La Marcouline quarry), Fontblanche Forest, Roquefort-la-Bédoule (Bouches-du-Rhône, France).

Fig. 2: Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-FcFb.65, upper Aptian, upper part of the *Epiche-*loniceras martini Zone (equivalent to bed M52 of La Marcouline quarry), Fontblanche Forest, Roquefort-la-Bédoule (Bouches-du-Rhône, France).



Plate X:

Fig. 1: Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-FcFb.106, upper Aptian, upper part of the Epi*cheloniceras martini* Zone (equivalent to bed M52 of La Marcouline quarry), Fontblanche Forest, Roquefort-la-Bé-doule (Bouches-du-Rhône, France).

Fig. 2: Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-B-LM.12, upper Aptian, lower part of the *Epicheloniceras martini* Zone, bed M52, La Marcouline quarry, Cassis (Bouches-du-Rhône, France). **Fig. 3.a-b:** Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-B-PM.4.13, upper Aptian, lower part of the *Epicheloniceras martini* Zone, bed 191?, La Marcouline gate, Cassis (Bouches-du-Rhône, France).



Plate XI:

Fig. 1.a-b: Anglonautilus undulatus (SOWERBY, 1813). Specimen no. CF-CUG.1, upper Aptian, upper part of the *Epi-cheloniceras martini* Zone (equivalent to bed M52 of La Marcouline quarry), Fontblanche Forest, Roquefort-la-Bé-doule (Bouches-du-Rhône, France).

Fig. 2.a-c: Anglonautilus dorsoplicatus (WIEDMANN, 1960). Holotype no. PU20409, Middle Albian, Escragnolles (Alpes-Maritimes, France).



Plate XII:

Fig. 1.a-b: Anglonautilus sp. Specimen no. GACO.033, upper Aptian, base of the Epicheloniceras martini Zone, La

Fig. 2.a-b: Anglonautilus spi: Specificit No. GRE0.055, upper Aptian, base of the Epichelonicerus martim Zone, ta Marcouline quarry, Cassis (Bouches-du-Rhône, France). **Fig. 2.a-b:** Anglonautilus farringdonensis (SHARPE, 1854). Lectotype no. GSC7552, upper Aptian, Parahoplites nut-fieldiensis Zone (Faringdon Sponge Gravels), Faringdon (Berkshire, England). Reproduced with the permission of the British Geological Survey ©UKRI. All rights Reserved.

Plate XIII:

Fig. 1.a-c: Anglonautilus farringdonensis (SHARPE, 1854). Specimen no. GSC2779, upper Aptian, Parahoplites nutfieldiensis Zone (Faringdon Sponge Gravels), Faringdon (Berkshire, England). Reproduced with the permission of the British Geological Survey ©UKRI. All rights Reserved.

Fig. 2: Anglonautilus farringdonensis (SHARPE, 1854). Lectotype no. GSC7552, upper Aptian, Parahoplites nutfieldiensis Zone (Faringdon Sponge Gravels), Faringdon (Berkshire, England). Reproduced with the permission of the British Geological Survey ©UKRI. All rights Reserved.

Plate XIV:

Fig. 1.a-c: Anglonautilus farringdonensis (SHARPE, 1854). Specimen no. GSM52386, upper Aptian, Parahoplites nut-fieldiensis Zone (Faringdon Sponge Gravels), Faringdon (Berkshire, England). Reproduced with the permission of the British Geological Survey ©UKRI. All rights reserved. **Fig. 2.a-c:** Anglonautilus dorsoplicatus (WIEDMANN, 1960). Specimen no. ULP01, Middle Cenomanian, Acanthoceras rhotomagense Zone, Turrilites costatus Subzone, Saint-Ulphace (Sarthe, France).

Plate XV: Fig. 1.a-c: Cymatoceras begudensis (KILIAN & REBOUL, 1915). Specimen no. UJF-ID 25328, Lower Hauterivian, Lyti-coceras nodosoplicatum Zone, La Bégude, La-Palud-sur-Verdon (Alpes-de-Haute-Provence, France).

Plate XVI:

Fig. 1.a-c: *Cymatoceras begudensis* (KILIAN & REBOUL, 1915). Lectotype no. UJF-ID 434, Lower Hauterivian, Lyticoceras nodosoplicatum Zone, La Bégude, La-Palud-sur-Verdon (Alpes-de-Haute-Provence, France). **Fig. 2.a-b:** *Cymatoceras begudensis* (KILIAN & REBOUL, 1915). Specimen no. UJF-ID 435, Lower Hauterivian, Lyticoceras nodosoplicatum Zone, La Bégude, La-Palud-sur-Verdon (Alpes-de-Haute-Provence, France).