

Lower Cenomanian ammonites from la Bédoule, Bouches-du-Rhône, France

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Abstract

A 0.10-0.50 metre thick lens of sandstone in the abandoned Comte quarry (La Bédoule, Bouches-du-Rhône France), has yielded an abundant ammonite fauna, including the index species of the upper Lower Cenomanian *Mantelliceras dixoni* Zone, previously unknown in the area. The fauna is dominated by the genus *Mantelliceras* (50% of the assemblage) together with diverse Tethyan and cosmopolitan species, and common *Hyphoplites* (18% of the assemblage), a typically (but not exclusively) Boreal genus; in contrast, *Schloenbachia*, the dominant Boreal Lower Cenomanian genus is absent, as elsewhere in the Basse Provence Gulf, in contrast to its common occurrence in the Vocontian Basin, north of the Durancian Isthmus.

One new species, *Stoliczkaia (Lamnayella) duboisi* sp. nov., is described.

Keywords

Ammonites, Cretaceous, Cenomanian, south-east France.

1. INTRODUCTION

Lower Cenomanian outcrops and ammonites are well-known in the la Bédoule-Cassis area of Bouches-du-Rhône, France (Coquand, 1842; Hébert, 1872; Kilian & Reboul, 1914; Breistroffer, 1937; Fabre, 1937, 1940; Kennedy, 1994). In the 1980's, an amateur collector, Jean Dubois (Gardanne, Bouches-du-Rhône, France), discovered a lens of sandstone with a rich Lower Cenomanian fauna overlying Aptian marls, in the upper part of the abandoned Comte quarry (La Bédoule, Bouches-du-Rhône, France), east of the road D1 from Cassis to la Bédoule (coordinates 43°14'12"N; 5°33'51"E: Fig. 1). A thick series of basal upper Aptian alternating black marls and argillaceous limestones are overlain by 0.2 to 5 metres of grey to green marls, containing small nodules of argillaceous limestone and phosphatised concretions. This latter interval contains spicules of sponges, ostracods and foraminifera. The latter fauna has been examined by G. Tronchetti (University of Marseille) who identified both benthic (Nodosariidae, *Patellina subactacea*, *Spirillina minima*, *Gavelinella flandrini*, *Tritaxia pyramidata*, *Falsogaudryinella alta*, *Ammobaculites* sp., *Ammodiscus gaultinus*) and planktonic forms (*Hedbergella* gr. *infracretacea*, *Globigerinelloides ferreolensis*, *Globigerinelloides algerianus*), indicating the upper Aptian (upper Gargasian sensu Tronchetti).

Above these marls, there is a stratigraphic gap that spans the upper part of the upper Aptian, the whole Albian and the basal Cenomanian (see below). The overlying transgressive unit, with Lower Cenomanian ammonites, including those indicative of the upper Lower Cenomanian *Mantelliceras dixoni* Zone is a 0.10-0.50 metre thick lenticular thick unit of fine-grained sandstone, crowded with large quartz grains with ferruginous crust. This unit locally contains an abundant macrofauna, preserved as pyritised internal moulds. This fauna is dominated by echinoids (173 specimens) and ammonites (107 specimens). Rare gastropods, bivalves and fish teeth are also present. The echinoid fauna, largely dominated by *Oolopygus bargesii*, also includes *Discoides* cf. *subuculus*, *Crassiholaster subglobosus*, *Hemaster bufo* and *Labrotaxis* sp., identified by D. Néraudeau (Rennes) (Fig. 1). This association indicates deposition on a distal circalittoral platform. This fossiliferous interval may be equivalent to level 3 of the Pas d'Ouiller section described by Hébert (1872), a few kilometers north-east of the Comte quarry, about 10 metres of: "grès gris en lits minces à graviers siliceux alternant avec lits argileux et sableux (Orbitolines, Echinides, Nautilus, *Amm. Mantelli* et *subplanatus*)".

Above the fossiliferous level, both fauna and terrigenous detritus are rare. A 20 m sequence of calcareous sandstones yield poorly preserved echinoids and scarce,

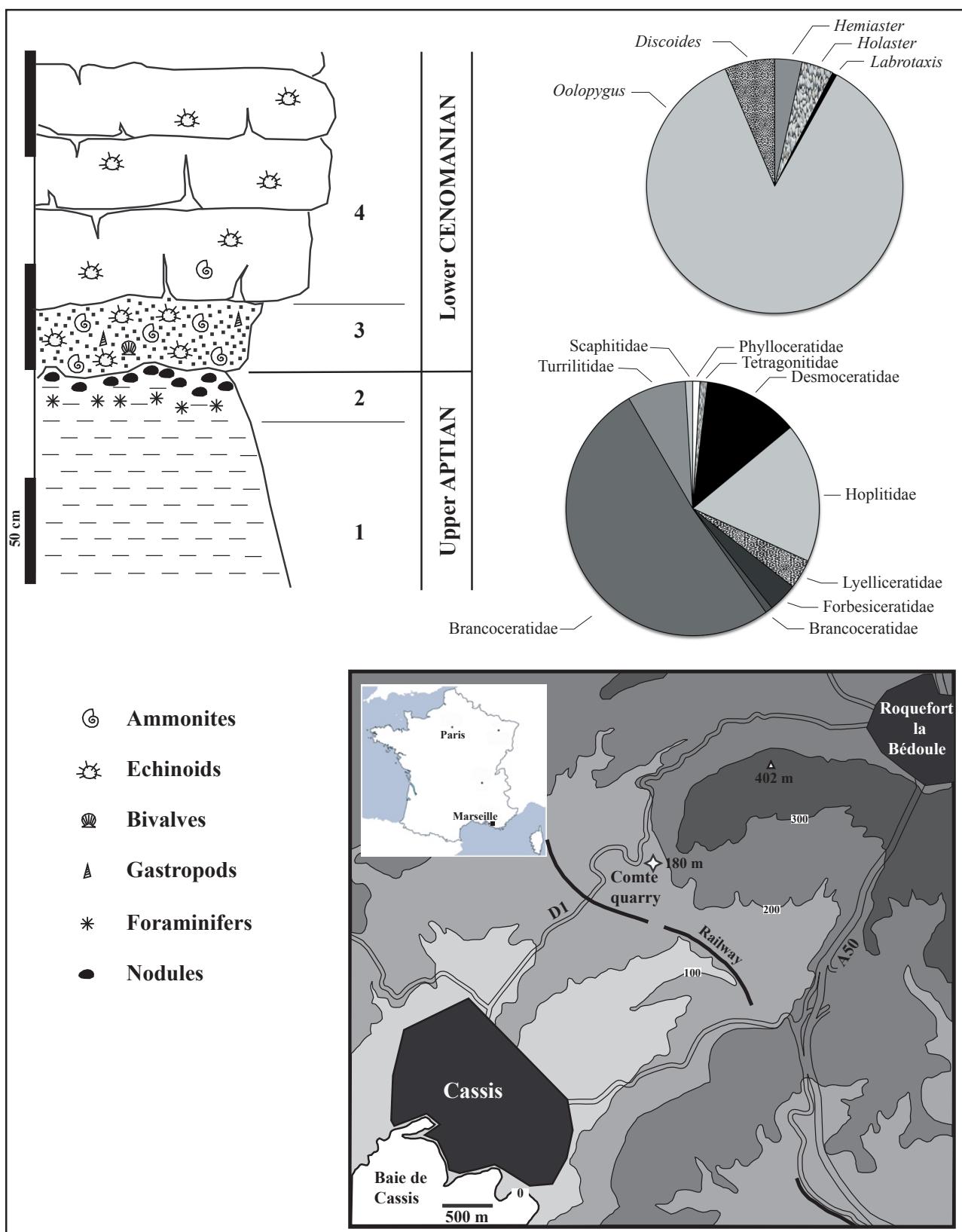


Fig. 1: The la Bédoule section: map of the area, lithological sequence, pie charts showing the percentage distribution of echinoid genera and ammonite families.

large fragments of unidentified desmoceratid ammonites. It should be noted that a small outcrop of the fossiliferous sandstone is present south of the Comte quarry, at the west entrance of the railroad tunnel, but no ammonites have been found.

2. AGE OF FAUNA

The standard Lower Cenomanian zonal and subzonal sequence for north-west Europe (Kennedy & Gale, 2017) is:

<i>Mantelliceras dixoni</i> Zone	
<i>Mantelliceras mantelli</i> Zone	<i>Mantelliceras saxbii</i> Subzone <i>Sharpeiceras schlueteri</i> Subzone <i>Neostlingoceras carcinanense</i> Subzone
<i>Pleurohoplites briacensis</i> Zone (part)	

The la Bédoule fauna is: *Phylloceras (Hypophylloceras) seresitense* Pervinquier, 1907, *Tetragonites* sp., *Desmoceras latidorsatum* (Michelin, 1838), *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841), *Hyphoplites falcatus falcatus* (Mantell, 1822), *Hyphoplites campichei* Spath, 1925, *Hyphoplites curvatus curvatus* (Mantell, 1822), *Euhystrichoceras nicasei* (Coquand, 1862), *Stoliczkaia (Lamnayella) duboisi* sp. nov., *Forbesiceras largilliertianum* (d'Orbigny, 1841), *Forbesiceras* cf.

beaumontianum (d'Orbigny, 1841), *Mantelliceras mantelli* (J. Sowerby, 1814), *Mantelliceras picteti* Hyatt, 1903, *Mantelliceras lymense* (Spath, 1926), *Mantelliceras dixoni* (Spath, 1926), *Sharpeiceras schlueteri* Hyatt, 1903, *Sharpeiceras* sp. juv., *Hypoturrilites gravesianus* (d'Orbigny, 1842), *Ostlingoceras (Ostlingoceras)* sp., *Mesoturrilites serpuliforme* (Coquand, 1862), and *Scaphites equalis* J. Sowerby, 1813.

The distribution of well-documented species in the subzones of the *mantelli* Zone and in the *dixoni* Zone is set out in Table 1

The presence of *Mantelliceras dixoni* indicates the uppermost zone of the standard north-west European sequence, while 13, possibly 14 of the well-dated species present are also known from the zone. That some material may be from lower horizons in the Lower Cenomanian is suggested by a single specimen of *Forbesiceras* cf. *beaumontianum*, a *carcitanense* and *saxbii* Subzone species, and a single fragment of *Sharpeiceras schlueteri*, index of the eponymous Subzone. These are the exceptions; 105 of the 107 ammonites (98%) are species that have a range that includes the *dixoni* Zone elsewhere.

3. COMPOSITION AND BIOGEOGRAPHIC AFFINITIES OF THE AMMONITE FAUNA

Owen (1971) recognised a Boreal hoplitinid faunal province in the Middle Albian, and Juignet & Kennedy (1976, p. 136, fig. 20) described its persistence into

Table 1: Stratigraphic distribution of well-documented elements of the la Bédoule fauna.

species	<i>carcitanense</i>	<i>schlueteri</i>	<i>saxbii</i>	<i>dixoni</i>
<i>P. (H.) seresitense</i>	*	*	*	*
<i>Tetragonites</i> sp.	*	*	*	*
<i>P. (P.) mayoriana</i>	*	*	*	*
<i>H. falcatus falcatus</i>	*	*	*	*
<i>H. campichei</i>	*	*	*	*
<i>H. curvatus curvatus</i>	*	*	*	*
<i>E. nicasei</i>	*			*
<i>F. largilliertianum</i>	*	*	*	*
<i>F. cf. beaumontianum</i>	*	*		
<i>M. mantelli</i>	*	*	*	*
<i>M. picteti</i>	*	*	*	*
<i>M. lymense</i>	*	*	*	*
<i>M. dixoni</i>				*
<i>S. schlueteri</i>		*		
<i>H. gravesianus</i>	*	*	*	*
<i>M. serpuliforme</i>	*		?	?
<i>S. equalis</i>	*	*	*	*

the Cenomanian, characterised by the occurrence of *Schloenbachia* and *Hyphoplites* (Fig. 2). In the Lower Cenomanian of northwest Europe, the genus *Schloenbachia* makes up over 99% of assemblages at some localities in southern England, and dominates assemblages in the Boulonnais, Haute-Normandie, Aube, and Maine in France, Germany, Poland and eastwards to the Mangyschlak Mountains in Western Kazakhstan, the Kopet-Dag in Turkmenistan and northern Iran, and Iran north of the Zagros (Fig. 2). It should be noted that to the east, *Schloenbachia* is abundant in glauconitic limestones in Central Iran (Kennedy *et al.*, 1979; Immel & Seyed-Emami, 1985), whereas Wilmsen *et al.* (2013, p. 495, text-fig. 4c, d) recorded only a single specimen, identified as *S. cf. varians*, from the Lower Cenomanian of the Yazd block, 260 km to the east-south-east, on the eastern side of the Sabzevar Ocean. Only in Provence is there the opportunity to examine the nature of the southern boundary of the *Schloenbachia* dominated faunal province. Figure 3 shows the lower Cenomanian distribution of *Schloenbachia* in southeastern France. The genus is abundant in the slopes of the continental margin of the alpine sea (the Vocontian Basin), north of the Durancian Isthmus, but is very rare on the continental shelf (Thomel, 1992). We suggest that the absence of *Schloenbachia* at la Bédoule and Cassis in the Basse Provence Gulf (Kennedy, 1994) is related to the presence of the Durancian Isthmus, which separated the alpine sea from the Basse Provence Gulf.

We have 107 ammonites from the la Bédoule section, and *Schloenbachia* is absent. The numbers and percentage composition of the assemblage is:

Phylloceras (Hypophylloceras) 1 (0.9%)
Tetragonites sp. 1 (0.9%)
Desmoceras 11 (10.3%)
Puzosia 2 (1.9%)
Hyphoplites 19 (17.8%)
Stoliczkaia (Lamnayella) 4 (3.7%)
Forbesiceras 4 (3.7%)
Euhystrichoceras 1 (0.9%)
Mantelliceras 53 (49.5%)
Sharpeiceras 2 (1.9%)
Ostlingoceras 1 (0.9%)
Mesoturrilites 3 (2.8%)
Hypoturrilites 4 (3.7%)
Scaphites 1 (0.9%)

It will be seen that *Hyphoplites* (17.8%) and *Mantelliceras* (49.5%) together make up 67.3% of the assemblage, and that classic Tethyan genera: *Phylloceras*, *Tetragonites*, and *Desmoceras*, make up only 14% of the assemblage. *Schloenbachia* may be absent, but what is remarkable is the abundance of *Hyphoplites*, the last surviving genus of the typically Boreal Hoplitidae. This atypical abundance at la Bédoule is matched elsewhere in terms of occurrence (if not abundance) with records from the condensed Cenomanian succession at Cassis, 4 km south-west of la Bédoule (Fabre, 1940; Kennedy, 1994), and records from Israel (Avnimelech, 1965) and Central Tunisia (Kennedy



Fig. 2: Geographic distribution of the genus *Schloenbachia* (after Juignet & Kennedy 1976).

& Gale, 2015). Ancestral *Discohoplites* occurs in the upper Upper Albian of north-eastern Algeria (Kennedy, 2020).

4. CONVENTIONS AND REPOSITORIES OF SPECIMENS

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus; c = costal dimension; ic = intercostal dimension. Figures in parentheses are dimensions as a percentage of the diameter. The suture terminology is that of Korn *et al.* (2003). E = external lobe; A = adventive lobe (the lateral lobe, L, of Kullmann & Wiedmann, 1970); U = umbilical lobe; I = internal lobe.

The following abbreviations are used to indicate the repositories of specimens.

BMNH: The Natural History Museum, London.

MNHP: The Laboratoire de Paléontologie of the Muséum National d'Histoire Naturelle, Paris.
UJF-ID: Université Joseph Fourier, Grenoble.

5. SYSTEMATIC PALAEONTOLOGY

Order Ammonoidea Zittel, 1884
Suborder Phylloceratina Arkell, 1950
Superfamily Phylloceratoidea Zittel, 1884
Family Phylloceratidae Zittel, 1884
Subfamily Phylloceratinæ Zittel, 1884
Genus *Phylloceras* Suess, 1866
Type species: *Ammonites heterophyllus* J. Sowerby, 1820, p. 119, pl. 226, by monotypy.

Subgenus *Hypophylloceras* Salfeld, 1924
Type species: *Phylloceras onoense* Stanton, 1895, p. 74, by monotypy.

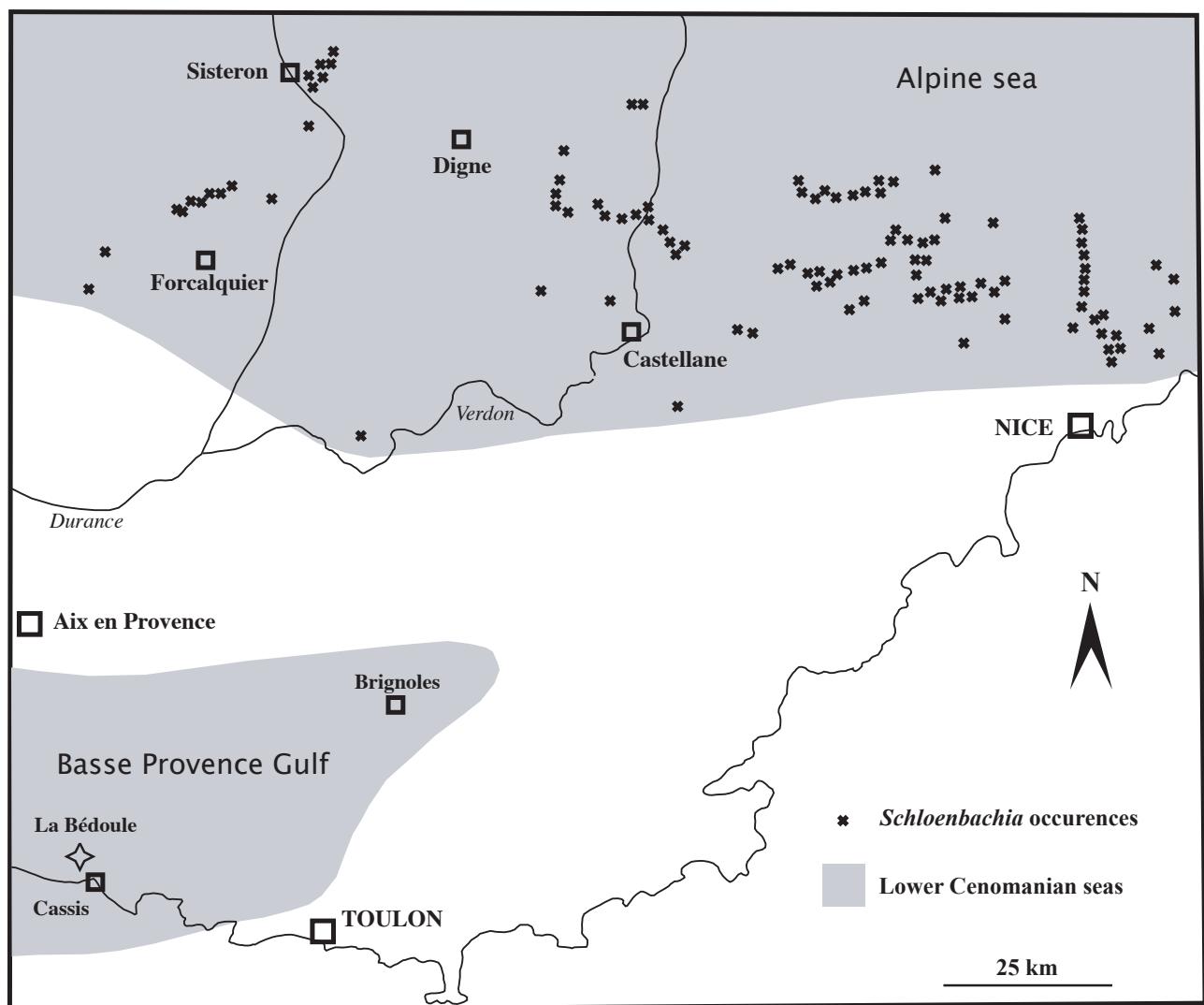


Fig. 3: Distribution of the genus *Schloenbachia* in the Lower Cenomanian of the south-east of France (after Thomel, 1992)

Phylloceras (Hypophylloceras) cf. seresitense
Pervinquier, 1907
Fig. 4G, H

1907. *Phylloceras velledae* var. *Seresitensis* Pervinquier, p. 52.
2009. *Hyporbulites seresitensis seresitensis* (Pervinquier).—Klein *et al.*, pp. 90, 93 (with full synonymy).
2019. *Phylloceras (Hypophylloceras) seresitense seresitense* (Pervinquier).—Kennedy in Gale *et al.*, p. 189, pl. 1, figs 11–18; pl. 2, figs 13, 14, 21, 22; text-fig. 13B.
2020. *Phylloceras (Hypophylloceras) seresitense seresitense* (Pervinquier).—Kennedy, p. 154, pl. 2, figs 14–18; pl. 3, figs 21, 22.

Types: These have not been traced. See discussion in Kennedy in Gale *et al.*, 2019, p. 190.

Material: UJF-ID10889.

Dimensions: See Table 2.

Description and Discussion: The specimen is a somewhat worn internal mould of a phragmocone. Coiling is very involute, the umbilicus blocked by sediment, and not measurable. The umbilical wall is convex and outward-inclined. The whorl section is compressed, with a whorl breadth to height ratio of 0.71, the greatest breadth around mid-flank, the flanks subparallel, very feebly convex, the ventrolateral shoulders and venter broadly and evenly rounded. The surface of the mould is smooth. The suture has a deeply incised E/A, A/U2 only slightly smaller than E/A, with A deeply incised and trifid.

Occurrence: The species ranges from Upper Aptian to Cenomanian. The geographic range extends from southern France to northern Spain, Germany, Hungary, Algeria, Tunisia, the Balearic Islands, Angola, KwaZulu-Natal in South Africa, Madagascar, south India, Japan, Alaska, and California.

Suborder Lytoceratina Hyatt, 1889
Superfamily Tetragonitoidea Hyatt, 1900
Family Tetragonitidae Hyatt, 1900
Subfamily Tetragonitinae Hyatt, 1900
Genus *Tetragonites* Kossmat, 1895

Type species: *Ammonites Timotheanus* Pictet, 1847, p. 295, pl. 2, fig. 6; pl. 3, figs 1, 2, by the original designation of Kossmat, 1895, p. 131 (35).

***Tetragonites* sp.**
Fig. 4C, D

Material: UJF-ID10890.

Description and Discussion: The specimen is a phosphatic internal mould of a juvenile with a 90° sector

of body chamber, complete to a diameter of 17.2 mm, beyond which the ventral part of the mould is damaged. Coiling is quite evolute, with 50% of the previous whorl covered. The umbilicus comprises 38% approximately of the diameter, quite shallow, with a flattened, outward-inclined wall, and narrowly rounded umbilical shoulder. The whorl section is slightly depressed, with feebly convex subparallel inner flanks, flattened outer flanks, broadly rounded ventrolateral shoulders, and a broad, very feebly convex venter. A single prominent prorsiradiate constriction is present towards the adapertural end of the outer whorl. A second, very weak transverse constriction is present on the venter 90° adaperturally of this. The well-preserved suture is moderately incised, with a trifid A. The specimen is specifically indeterminate.

Occurrence: Lower Cenomanian, la Bédoule.

Superfamily Desmoceratoidea Zittel, 1895

Family Desmoceratidae Zittel, 1895

Subfamily Desmoceratiniae Zittel, 1895

Genus and Subgenus *Desmoceras* Zittel, 1884

Type species: *Ammonites latidorsatus* Michelin, 1838, p. 101, pl. 12, fig. 9, by the subsequent designation of Böhm, 1895, p. 364.

Desmoceras (Desmoceras) latidorsatum
(Michelin, 1838)
Fig. 4E-F, I-N, 7A, B

1838. *Ammonites latidorsatus* Michelin, p. 101, pl. 12, fig. 9.
2011. *Desmoceras (Desmoceras) latidorsatum* (Michelin).—Klein & Vašíček, pp. 141, 144 (with full synonymy).
2020. *Desmoceras (Desmoceras) latidorsatum* (Michelin).—Kennedy, p. 168, pl. 7, figs 16–18; pl. 8, figs 14–19 (with additional synonymy).

Type: The holotype by monotypy, and now lost, is the original of Michelin, 1838, p. 101, pl. 12, fig. 9, from the Albian Gault Clay of Aube, France. Joly in Gauthier (2006, p. 97, pl. 3, fig. 1) designated MNHP F. B46095, *ex d'Orbigny Collection 5773-B1*, neotype. It is from the condensed Albian of Escragnolles, Var, France.

Material: UJF-ID10891-94, 10896-97, 10983-86 (Dubois collection); 10895 (Latil collection).

Dimensions: See Table 3.

Discussion: All of the specimens are phosphatic internal moulds of phragmocones, varying from slightly depressed to equidimensional in whorl cross section. Most of the specimens lack constrictions, but UJF-ID10893 (Fig. 4K, L) has three very faint constrictions on a half whorl. They are straight and prorsiradiate on the inner flank, flexed

Table 2: Dimensions of *Phylloceras (Hypophylloceras) cf. seresitense* Pervinquier, 1907.

	D	Wb	Wh	Wb:Wh	U
ID10889	33.7(100)	13.2(39.2)	18.6(55.2)	0.71	- (-)

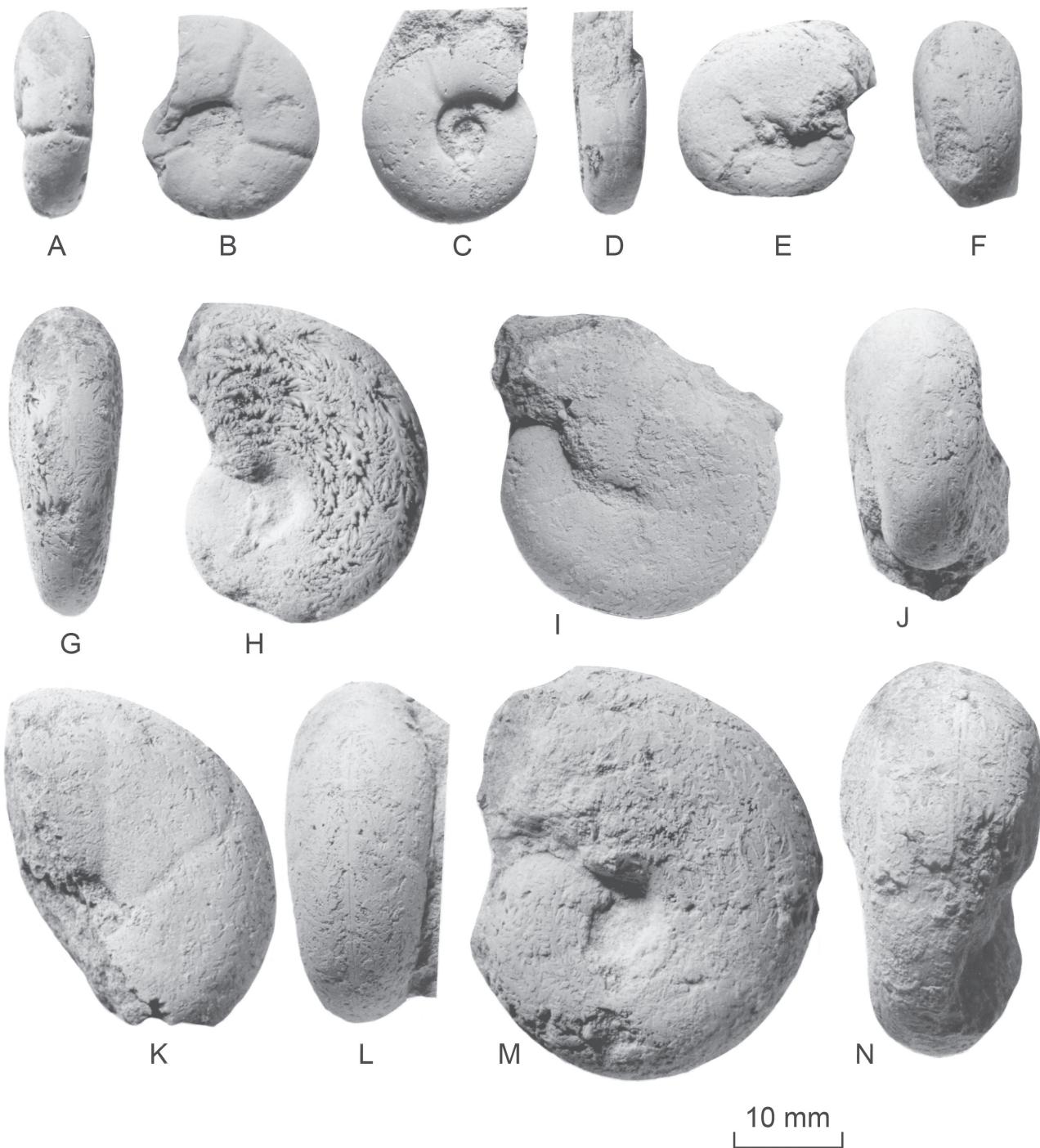


Fig. 4. A, B, *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841), UJF-ID10898. C, D, *Tetragonites* sp., UJF-ID10890. E, F, I-N, *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838). E, F, UJF-ID10891; I, J, UJF-ID10892; K, L, UJF-ID10893; M-N, UJF-ID10894. G, H, *Phylloceras (Hypophylloceras) cf. seresitense* Pervinquière, 1907. UJF-ID10889.

Table 3: Dimensions of *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838).

	D	Wb	Wh	Wb:Wh	U
ID10896	35.2 (100)	16.2 (46.0)	19.4 (55.1)	0.84	4.1 (11.6)
ID10897	35.2 (100)	16.9 (48.0)	16.7 (47.4)	1.0	-(-)
ID10894	40.2 (100)	21.3 (53.0)	20.4 (50.7)	1.0	6.2 (15.4)
ID10895	54.0 (100)	24.2 (44.8)	29.1 (53.9)	0.83	6.7 (12.4)

back and concave on the outer flank, projecting forwards over the ventrolateral shoulder, to cross the venter in an obtuse chevron with a narrow, rounded peak.

Juveniles of *D. (D.) latidorsatum* show wide intraspecific variation, and a number of subspecies/varieties have been introduced in addition to the typical form. Four morphotypes are recognised, based on variations in whorl section and the presence/absence of constrictions: *forma complanata* Jacob, 1907 (p. 38, pl. 14 (4), fig. 10; pl. 15 (5), fig. 2); *forma media* Jacob, 1907 (p. 37, pl. 16 (4), fig. 14); *forma inflata* Breistroffer, 1933, p. 193 (as *nomen novum* for var. *a* Kossmat as emended by Jacob, 1907, p. 35, pl. 14 (4), fig. 13); *forma perinflata* Cooper & Kennedy, 1979 (p. 237, figs 37-38, 39d-f).

The present specimens correspond most closely to *forma complanata* of Jacob.

Occurrence: Middle Albian to Upper Cenomanian, southern England, southern France, northern Spain, southern Germany, Switzerland, Hungary, Romania, Serbia, Poland, Sardinia, Ukraine (Crimea), northern Algeria, Central Tunisia Mozambique, Angola, KwaZulu-Natal in South Africa, Madagascar, south India, Pakistan, Japan, New Zealand, Mexico, and Venezuela.

Subfamily Puzosiinae Spath, 1922a

Genus and Subgenus *Puzosia* Bayle, 1878

Type species: *Ammonites planulatus* J. de C. Sowerby, 1827, p. 134, pl. 570, fig. 5, *non* Schlotheim, 1820, p. 59; = *Ammonites mayoriana* d'Orbigny, 1841, p. 267, pl. 79, figs 1-3, by subsequent designation by H. Douvillé, 1879, p. 91.

Puzosia (Puzosia) mayoriana (d'Orbigny, 1841)

Figs 4A, B; 7H, I, M

- 1827. *Ammonites planulatus* J. de C. Sowerby, p. 597, pl. 570, fig. 5 (*non* Schlotheim, 1820, p. 59).
- 1841. *Ammonites Mayoriana* d'Orbigny, p. 267, pl. 79, figs 1-3.
- 2020. *Puzosia (Puzosia) mayoriana* (d'Orbigny).—Kennedy, p. 165, pl. 6, figs 1-4, 7-10; pl. 7, figs 1, 2, 7-9, 15; text-fig. 9d (with full synonymy).

Type: The lectotype, by the subsequent designation of Wright & Wright, 1951, p. 35, is BMNH 9381, the original of J. de C. Sowerby, 1827, pl. 570, fig. 5, from the Cenomanian Lower Chalk of Hamsey, near Lewes, Sussex.

Material: UJF-ID10898, 99.

Dimensions: See Table 4.

Description and Discussion: UJF-ID10898 (Fig. 4A, B) retains a short sector of body chamber. The well-preserved phosphatic internal mould lacks all trace of ribs. There are five prominent constrictions on the outer whorl. They are deeply incised into the umbilical shoulder, straight and prorsiradiate on the inner and middle flank, sweeping forwards and concave on the outer flank and ventrolateral shoulder to form an obtuse chevron on the venter. UJF-ID10899 (Fig. 7H, I, M) is wholly septate, the surface of the phosphatic internal mould again lacks all trace of ribbing. There are five constrictions that trace the same course as in the previous specimen. They are near-effaced at mid-venter, where the siphuncle is clearly visible. Absence of ribs is attributed to preservation, as is also shown by phosphatised specimens from southern England (Wright & Kennedy, 1984, pl. 3, fig. 11).

Occurrence: Upper Albian to Upper Cenomanian, southern England, France, Spain, Switzerland, Germany, Poland, Romania, Bulgaria, Ukraine (Crimea), Georgia, Kazakhstan, northern Algeria, Central Tunisia, Egypt, Madagascar, and, possibly, Japan.

Superfamily Hoplitoidea H. Douvillé, 1890

Family Hoplitidae H. Douvillé, 1890

Subfamily Hoplitinae H. Douvillé, 1890

Genus *Hyphoplites* Spath, 1922b

Type species: *Ammonites falcatus* Mantell, 1822, p. 117, pl. 21, figs 6, 12; by original designation by Spath, 1922b, p. 110.

Hyphoplites falcatus falcatus (Mantell, 1822)

Fig. 5A, G, H

- 1822. *Ammonites falcatus* Mantell, p. 117 (*pars*), pl. 21, fig. 12, non 6 (= *H. falcatus aurora* Wright & Wright, 1949).
- 2014. *Hyphoplites falcatus falcatus* (Mantell).—Klein, pp. 81, 88 (with full synonymy).

Type: The lectotype, by the subsequent designation of Wright & Wright, 1949, p. 484, is BMNH 33546, the original of Mantell, 1822, pl. 21, fig. 12, refigured by Wright & Kennedy, 1984, pl. 6, fig. 11, from the Lower Cenomanian Chalk Marl of Stoneham, Sussex, England.

Material: UJF-ID10900 (Dubois collection); 10901 (Latil collection).

Description and Discussion: UJF-ID10901 (Fig. 5A) is a phragmocone 20 mm in diameter. Five well-developed

Table 4: Dimensions of *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841).

	D	Wb	Wh	Wb:Wh	U
ID10898	20.0 (100)	7.9 (39.5)	9.7 (48.5)	0.81	5.3 (26.5)
ID10899	58.9 (100)	18.9 (32.1)	25.1 (42.6)	0.75	16.8 (28.5)

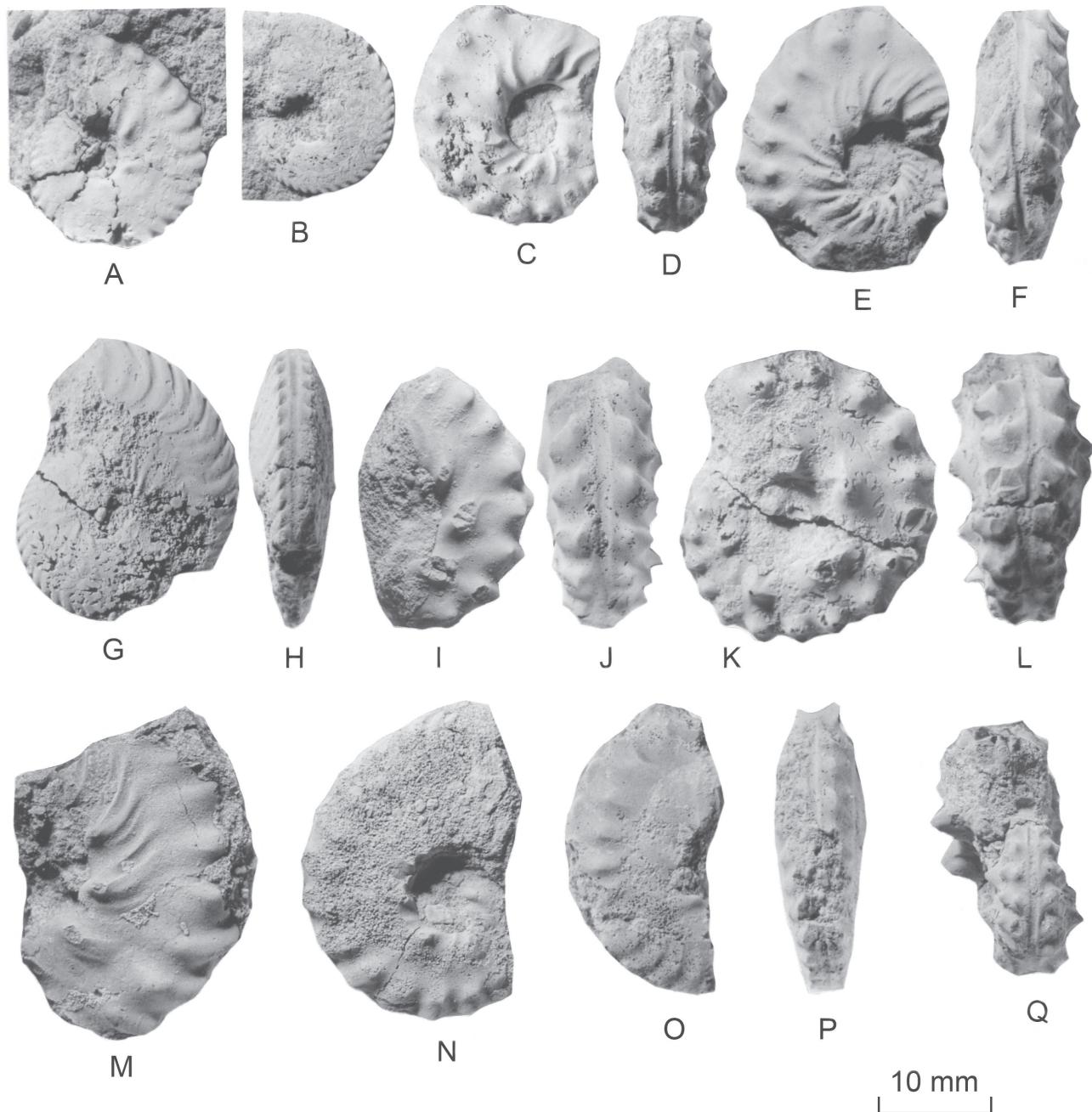


Fig. 5: A, G, H, *Hyphopites falcatus falcatus* (Mantell, 1822). A, UJF-ID10901; G, H, UJF-ID10900. B, *Hyphopites campichei* Spath, 1925, UJF-ID10902. C-F, I-Q, *Hyphopites curvatus curvatus* (Hébert & Munier-Chalmas, 1875). C, D, UJF-ID10908; E, F, UJF-ID10906; I, J, UJF-ID10909; K, L, Q, UJF-ID10907; M, UJF-ID10905; N, UJF-ID10910; O, P, UJF-ID10911.

bullae perch on the umbilical shoulder, and give rise to pairs of low, broad falcoïd ribs that have a narrow prorsiradiate straight ‘haft’ section, the concave ‘blade’ terminating in an elongated ventral clavus. There are occasional short intercalated ‘blades’. UJF-ID10900 (Fig. 5G, H) is 25.6 mm in diameter, with a 120° sector of body chamber, and similar ornament. The ribs are single in *H. falcatus falcatus* (see revision in Wright & Kennedy, 1984, p. 66, pl. 6, figs 11, 13; pl. 7, fig. 2; text-figs 7e-g; 9c); in *H. falcatus aurora* Wright & Wright,

1949 (see revision in Wright & Kennedy, p. 67, pl. 6, figs 10, 12, 15; text-figs 7k, 9b) the ribs are mostly dichotomous, branching at various levels; in *H. falcatus interpolatus* Wright & Wright, 1949 (see revision in Wright & Kennedy, 1984, p. 68, pl. 6, fig. 14; pl. 7, fig. 3; text-figs 8e, 9d) has the ribs split for most of their length, such that sickle ‘blades’ have more than one haft or the blades may even be split for part of their length.

Occurrence: *Hyphopites falcatus falcatus* ranges throughout the Lower Cenomanian *Mantelliceras mantelli*

and *M. dixoni* Zones. The geographic distribution extends from southern England to Argyll, western Scotland, across France to the present occurrence at la Bédoule, Switzerland, Germany, the Mangyschlak Mountains of western Kazakhstan, the Kopet Dag in Turkmenistan, Iran north of the Zagros, and Israel.

***Hypoplites campichei* Spath, 1925**

Fig. 5B

- 1859. *Ammonites falcatus* Mantell.— Pictet & Campiche, p. 210 (*parts*), pl. 27, fig. 1.
- 1925. *Hypoplites campichei* Spath, p. 83.
- 2014. *Hypoplites campichei* Spath.— Klein, p. 81 (with synonymy).

Type: The holotype, by monotypy is no. 39845 in the collections of the Naturhistorisches Museum, Basel, Switzerland, figured by Pictet & Campiche, 1859, pl. 27, fig. 1, and Renz, 1968, pl. 2, fig. 7, from the upper Upper Albian *perinflata* Zone of Sainte-Croix, Kanton Waadt, Switzerland.

Material: UJF-ID10902-4 (Latil collection).

Description and Discussion: The present specimens are phragmocones, 18.6–20 mm in diameter. Coiling is very involute, the whorl section very compressed and the ornament subdued. Very feeble to obsolete umbilical bullae are strongly prorsiradiate, and give rise to fine, delicate falcoid ribs that bifurcate twice on the outer flank, and terminate in tiny outer ventrolateral clavi, so that there are many more ribs at the ventrolateral shoulder than the umbilical shoulder. *Hypoplites costosus* Wright & Wright, 1949 (p. 484, pl. 29, fig. 7; see revision in Wright & Kennedy, 1984, p. 70, pl. 7, fig. 12) has single ribs and lacks ventrolateral clavi. *Hypoplites falcatus aurora* Wright & Wright, 1949 (p. 458, pl. 29, figs 3, 9; pl. 30, fig. 5; see revision in Wright & Kennedy, 1984, p. 67, pl. 6, figs 10, 12, 15; text-figs 7k, 9b) has predominantly dichotomous, rather than bidichotomous ribs. *H. campichei* and *H. falcatus aurora* are linked by passage forms in the Upper Albian.

Occurrence: The species ranges from the upper Upper Albian *perinflata* Zone to the *carcitanense* Subzone of the lower Lower Cenomanian *mantelli* Zone. There are records from the Upper Albian of southern England, south-east France, northern Spain and Switzerland, and the Lower Cenomanian of southern England, Normandie, Sarthe and Provence in France, northern Spain, Germany, Poland, the Mangyschlak Mountains of western Kazakhstan, and the Kopet Dag in Turkmenistan.

***Hypoplites curvatus* (Mantell, 1822) *arausionensis*
(Hébert & Munier-Chalmas, 1875)**

Fig. 5C-F, I-Q

- 1875. *Ammonites arausionensis* Hébert & Munier-Chalmas, p. 115 (*parts*), pl. 4, fig. 5 only.

- 2014. *Hypoplites curvatus arausionensis* (Hébert & Munier-Chalmas).— Klein, pp. 81, 83 (with synonymy).
- 2015. *Hypoplites curvatus arausionensis* (Hébert & Munier-Chalmas).— Kennedy in Morel, p. 134, text-fig. 128a, b.

Type: The lectotype is MNHP. F. J07816, original of Hébert & Munier-Chalmas, 1875, pl. 4, fig. 5, by the subsequent designation of Wright & Wright, 1949, p. 491. It is from Gacé, Orne, France.

Material: UJF-ID10909-15 (Dubois collection); 10905-8; 10916-18 (Latil collection).

Description and Discussion: Specimens range from 13.7 to 30 mm in diameter, with a fragment with a whorl height of 12.4 mm (Fig. 5M). There is wide intraspecific variation, from specimens with a depressed whorl section and seven massive conical umbilical tubercles and twice as many strong conical inner ventrolateral tubercles and strong outer ventrolateral clavi per whorl to compressed individuals with much more subdued tuberculation (Figs 5O, P). The diagnostic features of subspecies *arausionensis* are the presence, on the phragmocone, of bullate to spinate umbilical tubercles that give rise to pairs of ribs, with occasional short intercalaries, all ribs bearing strong inner and outer ventrolateral tubercles. This ornament persists onto the adapical end of the adult body chamber; on the adapertural part the ornament weakens, inner and outer ventrolateral tubercles merge and eventually disappear, with associated rounding of the venter, while delicate flank ribs, resembling those of the nominate subspecies, may appear on the flanks of the body chamber, well-shown by the present material (Fig. 5C, E, M). *H. curvatus curvatus* (Mantell, 1822) (p. 118, pl. 21, fig. 18; see revision in Wright & Kennedy, 1984, p. 71, pl. 7, figs 1, 5, 6, 8–10; pl. 8, figs 2, 4, 8, 10, 12, 14; text-figs 6f-l, 9f-h) is characterised by strong umbilical, inner and outer ventrolateral tubercles, the umbilical and inner ventrolateral tubercles linked by numerous fine ribs. *H. curvatus pseudofalcatus* (Semenov, 1899) (p. 129; see revision in Wright & Kennedy, 1984, p. 72, pl. 6, fig. 7; pl. 7, figs 4, 7, 11, 13; pl. 8, figs 3, 5, 9; text-figs. 6a-e, 7a-d, 8c, 9k) is a compressed subspecies that lacks prominent umbilical bullae, and has weak or no inner ventrolateral tubercles.

Occurrence: *Hypoplites curvatus arausionensis* ranges throughout the Lower Cenomanian *mantelli* and *dixoni* Zones. There are records from southern England, France, northern Spain, Germany, the Mangyschlak Mountains of Kazakhstan, Turkmenistan, and Iran north of the Zagros.

Superfamily Acanthoceratoidea de Grossouvre, 1894

Family Brancoceratidae Spath, 1934 (1900)

Subfamily Mortoniceratiniae H. Douville, 1912

Genus and Subgenus *Euhystrichoceras* Spath, 1923

Type species: *Ammonites nicei* Coquand, 1862, p. 323, pl. 35, figs 3, 4, by the original designation of Spath, 1923, p. 143.

Euhystrichoceras (Euhystrichoceras) nicesei

(Coquand, 1862)

Fig. 6G-I

1862. *Ammonites nicesei* Coquand, p. 323, pl. 35, figs 3, 4.
 2020. *Euhystrichoceras (Euhystrichoceras) nicesei* (Coquand).— Kennedy, p. 180, pl. 11, figs 16-24; pl. 12, figs 16-30, 34-36 (with synonymy).

Lectotype: By the subsequent designation of Kennedy & Wright, 1981, p. 420, the Coquand specimen figured by Pervinquier, 1910, pl. 17 (6), fig. 7, and refigured by Kennedy & Wright, 1981, pl. 59, figs 8-10 and Kennedy 2020, pl. 12, figs 34-36, from west of Boghar, Algeria, in the collections of the Geological Institute, Budapest. There are four paralectotypes.

Material: UJF-ID10919 (Dubois collection).

Description and Discussion: The present specimen is 11.9 mm in diameter, and retains half a whorl of body chamber. Coiling is moderately evolute, the umbilicus comprising 35% of the diameter, quite deep, with a high convex outward-inclined wall and broadly rounded umbilical shoulder. The intercostal whorl section is depressed, reniform, with the greatest breadth below mid-flank. The greatest breadth is at the umbilicolateral bullae in costal section. Eleven broad primary ribs arise at the umbilical seam, and strengthens across the umbilical wall and shoulder, developing into massive conical umbilicolateral bullae. These give rise to one or two coarse straight prorsiradiate ribs, while additional ribs intercalate, to give a total of 11 ribs on the ventrolateral shoulder of the adapertural half whorl of the specimen.

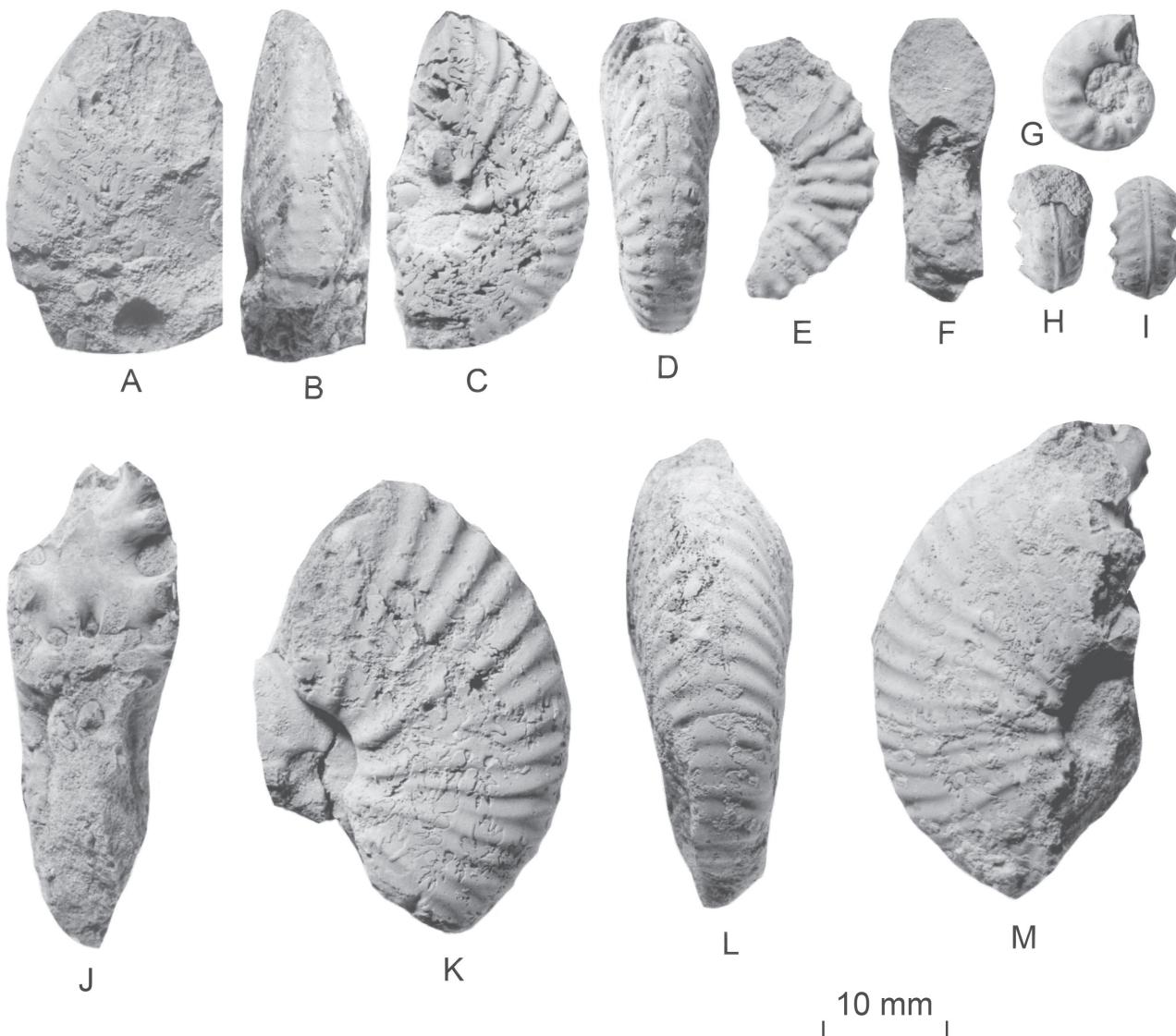


Fig. 6: A, B, *Forbesiceras cf. beaumontianum* (d'Orbigny, 1841), UJF-ID10926. C, D, J-M, *Stoliczkaia (Lamnayella) duboisi* sp. nov. C, D, paratype UJF-ID10922; J, K, paratype UJF-ID10923; L, M, paratype UJF-ID10921. E, F, *Mantelliceras picteti* Hyatt, 1903, UJF-ID10941. G-I, *Euhystrichoceras nicesei* (Coquand, 1862), UJF-ID10919.

The ribs sweep forwards across the ventrolateral shoulder and develop into an oblique ventrolateral clavus from which a progressively declining rib sweeps forwards and declines before reaching the strong siphonal keel, which is flanked by feeble grooves.

The specimen differs in no significant respects from the inner whorls of North African material at the same diameter [Pervinquier, 1910, pl. 17 (6), figs 1-10; Kennedy & Wright, 1981, pl. 59, figs 9, 12, 13, 15; Kennedy 2020, pl. 11, figs 16-24; pl. 12, figs 16-24, 34-36]. See Kennedy & Wright (1981) and Kennedy (2020) for comprehensive discussions of the species.

Occurrence: Lower Cenomanian, Haute-Normandie, Sarthe, and Bouches-du-Rhône, France, Algeria, Tunisia, and Madagascar.

Family Lyelliceratidae Spath, 1921
Subfamily Stoliczkaiinae Breistroffer, 1953
Genus *Stoliczkaia* Neumayr, 1875

Type species: *Ammonites dispar* d'Orbigny, 1841, p. 142, pl. 45, figs 1, 2, by the subsequent designation of Diener, 1925, p. 179.

Subgenus *Lamnayella* Wright & Kennedy, 1978

Type species: *Stoliczkaia (Lamnayella) juigneti* Wright & Kennedy, 1978, p. 398, pl. 37, figs 1-10; pl. 38, figs 1-12, by original designation.

Stoliczkaia (Lamnayella) duboisi sp. nov.
Figs 6C, D, J-M; 7C-E; 8E, F

Derivation of name: For Jean Dubois of Gardanne, who discovered the la Bédoule fauna.

Types: The holotype is UJF-ID10920 (Fig. 7C-E), paratypes are UJF-ID10923 (Figs 6J, K; 8E, F), UJF-ID10921 (Fig. 6L, M) and UJF-ID10922 (Fig. 6C, D), all from the Lower Cenomanian of la Bédoule.

Diagnosis: A compressed *Lamnayella* with well-developed outer ventrolateral tubercles and fastigiate venter on penultimate whorl of phragmocone. Bullate primary ribs separated by three or four long and short intercalated ribs, ventrolateral shoulders angular with feeble outer ventrolateral clavi on adapertural part of phragmocone and adapical part of body chamber, connected over venter by coarse flat-topped rib.

Dimensions: See Table 5.

Description: The fragmentarily preserved adapical end of the outer whorl of UJF-ID10923 (Fig. 8E-F) has a

whorl height of 10.8 mm and a whorl breadth to height ratio of 0.73, the flanks subparallel and feebly convex, the greatest breadth around mid-flank, the ventrolateral shoulders broadly rounded in intercostal section and angular in costal section, the venter very obtusely fastigiate. Narrow primary ribs arise from delicate umbilical bullae, and are straight and prorsiradiate on the inner flank, flexing forwards, broadening, and concave on the outer flank. Four long and short ribs intercalate between successive bullate primaries. All ribs develop tiny ventrolateral clavi, linked across the fastigiate venter by a progressively broadening rib that forms a very obtuse chevron. The outer 120° whorl sector of the phragmocone of this specimen has a maximum preserved whorl height of 21 mm, and a whorl breadth to height ratio of 0.76. There are five bullate primary ribs, and a total of 16 ribs at the ventrolateral shoulder. The outer ventrolateral clavi are barely detectable, and the venter has rounded. UJF-ID10922 (Fig. 6C, D) is a 180° sector of phragmocone with a maximum preserved whorl height of 29 mm and a whorl breadth to height ratio of 0.76, five bullate primary ribs and 20 ribs at the ventrolateral shoulder, all ribs with well-differentiated outer ventrolateral clavi linked over the fastigiate venter by a broad rib forming a very obtuse chevron. UJF-ID10921 (Fig. 6L, M) consists of just under half a whorl of phragmocone, with a maximum preserved whorl height of 20 mm. The bullate primaries and long intercalated ribs are less obviously differentiated than in the other specimens. The holotype, UJF-ID10920 (Fig. 7C-E) has a maximum preserved diameter of 49 mm, and retains a 120° sector of body chamber; it appears to be an incomplete adult. There are an estimated six bullate primaries and a total of 24 ribs at the ventrolateral shoulder. The phragmocone ornament is as in the paratypes. On the body chamber, the primary ribs coarsen progressively, and become more markedly differentiated from the intercalated ribs. The outer ventrolateral clavi weaken progressively, and have effaced on the last rib, their site marked by a weak angulation. The ribs are coarse, narrow and flat-topped, and separated by slightly wider interspaces. The suture is moderately incised, with an asymmetrically bifid E/A, narrow A and U2.

Discussion: *Stoliczkaia (Lamnayella) duboisi* differs from both *S. (L.) sanctaecatherinae* Wright & Kennedy, 1978 (p. 402, pl. 38, figs 13-16, 22, 23; pl. 39, figs 9-11; text-fig. 4a-c) and *S. (L.) chancellorii* Wright & Kennedy, 1984 (p. 78, pl. 10, fig. 11; text-fig. 11e), which are coarsely ornamented species, with stout whorl sections. The type species, *S. (L.) juigneti* (Wright & Kennedy,

Table 5: Dimensions of *Stoliczkaia (Lamnayella) duboisi* sp. nov.

	D	Wb	Wh	Wb:Wh	U
ID10922	29.0 (100)	11.1(38.3)	14.6 (50.3)	0.76	5.9(20.3)
ID10920	48.1 (100)	-(-)	23.1(48.0)	-	10.6(22.0)

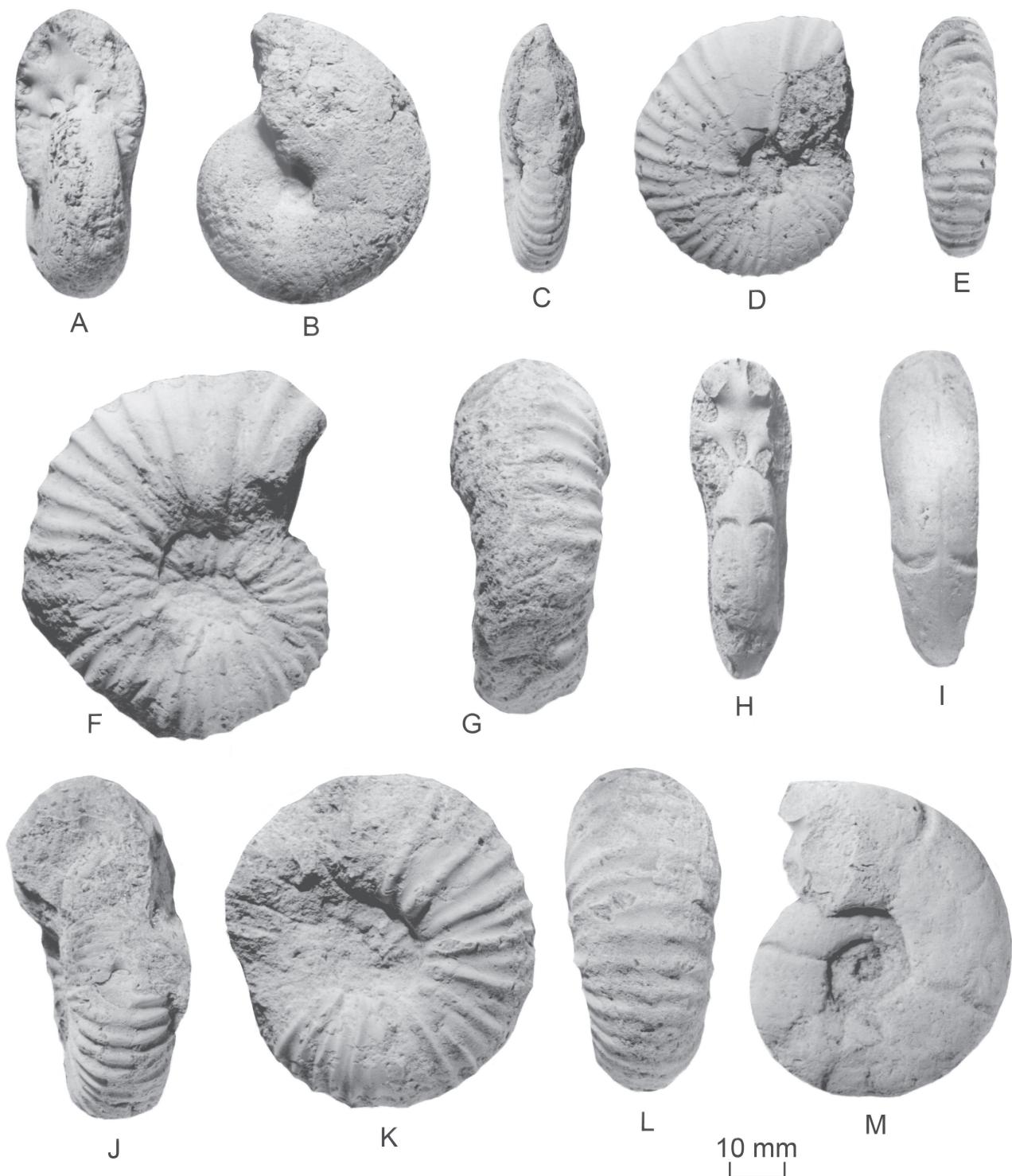


Fig. 7: A, B, *Desmoceras (Desmoceras) latidorsatum* (Michelin, 1838), UJF-ID10895; C-E, *Stoliczkaia (Lamnayella) duboisi* sp. nov., the holotype, UJF-ID10920. F, G, J-L, *Mantelliceras dixoni* Spath, 1926. F, G, UJF-ID10956; J-L, UJF-ID10955. H, I, M, *Puzosia (Puzosia) mayoriana* (d'Orbigny, 1841), UJF-ID10899.

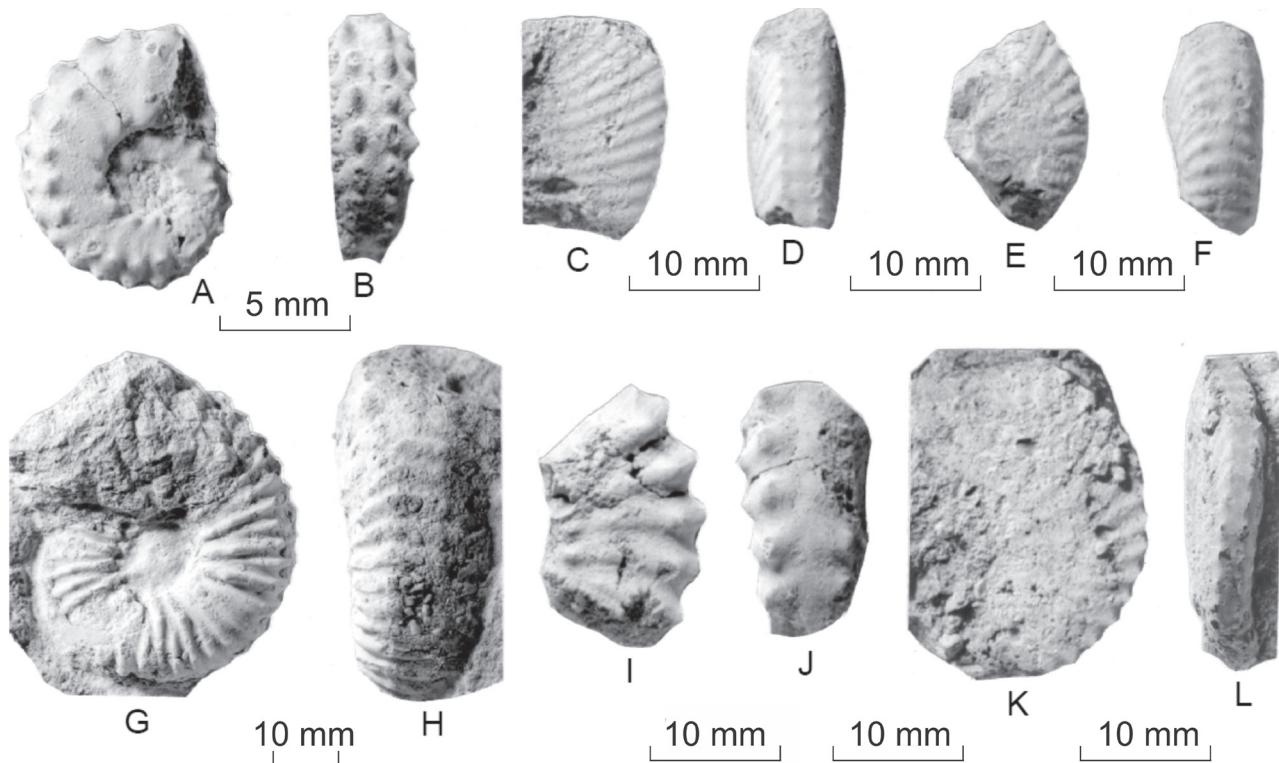


Fig. 8: A, B, *Sharpeiceras* sp. juv., UJF-ID10973. C, D, K, L, *Forbesiceras largilliertianum* (d'Orbigny, 1841). C, D, UJF-ID10924; K, L, UJF-ID10925. E, F, *Stoliczkaia (Lamnayella) duboisi* sp. nov., paratype UJF-ID10923. G, H, *Mantelliceras mantelli* (J. Sowerby, 1814), UJF-ID10927. I, J, *Sharpeiceras schlueteri* Hyatt, 1903, UJF-ID10972.

1978, p. 398, pl. 37, figs 1-10; pl. 38, figs 1-12) develops distant feebly flexuous high narrow primary ribs only on the adult body chamber.

Occurrence: Lower Cenomanian of la Bédoule.

Family *Forbesiceratidae* Wright, 1952
Genus *Forbesiceras* Kossmat, 1897

Type species: *Ammonites largilliertianus* d'Orbigny, 1841, p. 320, pl. 95, by the subsequent designation of Diener, 1925, p. 180.

***Forbesiceras cf. largilliertianum* (d'Orbigny, 1841)**
Fig. 8C, D, K, L

Compare:

- 1841. *Ammonites Largilliertianus* d'Orbigny, p. 320, pl. 95.
- 2018. *Forbesiceras largilliertianum* (d'Orbigny).— Klein, pp. 256, 261 (with synonymy).
- 2020. *Forbesiceras largilliertianum* (d'Orbigny).— Kennedy, p. 193, pl. 19, figs 1, 2, 4, 5, 9, 12, 13; pl. 24, figs 13, 14, 17, 18; text-fig. 10h (with additional synonymy).

Lectotype: MNHP B46129 (d'Orbigny Collection 6120 A-1) figured by Wright & Kennedy, 1984, text-fig. 12d, e, from the Middle Cenomanian Rouen Fossil Bed of Côte Ste Catherine, Rouen, Seine-Maritime, France.

Material: UJF-ID10924-25 (Latil collection).

Description and Discussion: The material comprises

phragmocone fragments with whorl heights of up to 12 mm. Ornament consists of delicate crowded ribs that increase by branching and intercalation, strengthening on the outer flanks, where they link to small clavi perched on the sharp ventrolateral shoulders. Although fragmentary, the material recalls relatively coarsely ribbed individuals of comparable size from southern England (Wright & Kennedy, 1984, pl. 11, fig. 5). The fragments differ from the fragment compared with *Forbesiceras beaumontianum* (d'Orbigny, 1841) below (Fig. 3A, B) in having ribs that are even on the outer flank, rather than being differentiated into primaries and short intercalaries.

Occurrence: *Forbesiceras largilliertianum* ranges throughout the Lower and Middle Cenomanian. The geographic distribution extends from southern England to France, Switzerland, northern Spain, Algeria, Tunisia, KwaZulu-Natal in South Africa, Madagascar, South India, and Japan.

***Forbesiceras cf. beaumontianum* (d'Orbigny, 1841)**
Fig. 6A, B

Compare:

- 1841. *Ammonites Beaumontianus* d'Orbigny, p. 328, pl. 98, figs 1, 2.
- 2018. *Forbesiceras beaumontianum* (d'Orbigny).— Klein, pp. 256, 257 (with synonymy).

Type: The lectotype, designated by Wright & Kennedy, 1984, p. 92, is no. 5523 in the collections of the Ecole des Mines, Paris, housed in the collections of the Université de Lyon-Villeurbanne, and figured by Wright & Kennedy, 1984, text-fig. 16a, b, from Lamnay, Sarthe, France.

Material: UJF-ID10926 (Latil collection).

Description and Discussion: The specimen is a fragment of phragmocone with a maximum preserved whorl height of 24 mm. When compared with fragments referred to *Forbesiceras largilliertianum*, above, the venter is broader, with some ribs bifurcating on the outermost flank, and very short intercalated ribs, the ventral tubercles weaker, and connected across the obtusely fastigiate venter by a weak but distinct transverse rib. These features find a match in fragments from southern England (Wright & Kennedy, 1984, pl. 12, fig. 7).

Occurrence: Lower Cenomanian *Mantelliceras mantelli* Zone, southern England, Sarthe, Var, and Bouches-du-Rhône in France, Central Tunisia, KwaZulu-Natal, South Africa, and Texas.

Family Acanthoceratidae de Grossouvre, 1894
Subfamily Mantelliceratiniae Hyatt, 1903

Genus *Mantelliceras* Hyatt, 1903

Type species: *Ammonites mantelli* J. Sowerby, 1814, p. 119 (ICZN Specific Name no. 1634).

Discussion: With 53 specimens, *Mantelliceras* makes up 49.5% of the fauna. Of these, all but three (Figs 4F, G, J-L; 5G, H) are nuclei 15-30 mm in diameter. Not all are identifiable to specific level, but those that are, fall into four groups:

1. Whorl section polygonal, with umbilical, lateral, inner and outer ventrolateral tubercles on primary ribs, intercalated ribs with inner and outer ventrolateral tubercles: *Mantelliceras mantelli* (J. Sowerby, 1814).
2. Whorl section compressed, primary ribs with umbilical bullae, stronger lateral tubercles, conical inner ventrolateral tubercles, and stronger outer ventrolateral clavi. Intercalated ribs with inner and outer ventrolateral tubercles only: *Mantelliceras picteti* Hyatt, 1903.
3. Whorl section rounded, primary ribs with umbilical bullae and outer ventrolateral clavi, intercalated ribs with outer ventrolateral clavi. In some individuals the outer ventrolateral clavi are lost. Others have a weak

indication of an inner ventrolateral tubercle, but these are soon lost: *Mantelliceras lymense* (Spath, 1926).

4. Whorl section rounded. Primary ribs with umbilical and inner lateral tubercles linked by a strong rib and an outer ventrolateral clavus. Inner ventrolateral tubercles weak, and lost at an early stage: *Mantelliceras dixoni* Spath, 1926.

Mantelliceras mantelli (J. Sowerby, 1814)

Fig. 8G, H, 9G-K

1814. *Ammonites mantelli* J. Sowerby, p. 119, pl. 55, lower figure only.
 1884. *Mantelliceras mantelli* (J. Sowerby).— Wright & Kennedy, p. 99, pl. 16, fig. 5; pl. 17, figs 1, 3; pl. 18, figs 1-3; pl. 19, figs 1-6; pl. 21, figs 1, 2, 4; pl. 24, fig. 3; pl. 36, fig. 1; text-figs 20a-d, 26a, c, e (with full synonymy).
 2019. *Mantelliceras mantelli* (J. Sowerby).— Kennedy in Gale et al., p. 221, pl. 20, figs 5, 6; pl. 21, figs 4, 5 (with additional synonymy).
 2020. *Mantelliceras mantelli* (J. Sowerby).— Kennedy, p. 197, pl. 21, figs 14-16; pl. 23, figs 29-33.

Type: The lectotype, by the subsequent designation of Kennedy 1971, p. 52, is BMNH 43940a from the Lower Cenomanian Chalk Marl of Ringmer near Lewes, Sussex, the original of J. Sowerby (1814, pl. 55, lower figure only, refigured by Wright & Kennedy 1984, pl. 18, fig. 3a-c).

Material: UJF-ID10929-31; 10940 (Dubois collection); UJF-ID10927, 28, 30 (Latil collection).

Dimensions: See Table 6.

Description: Nuclei range from 15-30 mm in diameter. Coiling is moderately evolute, the umbilicus comprising 25.7-27.5% of the diameter, with a convex wall and broadly rounded umbilical shoulder. The whorl section is depressed trapezoidal in intercostal section and depressed polygonal in costal section, with the greatest breadth at the lateral tubercle. In coarsely ornamented specimens, there are 12 primary ribs with coarse umbilical, lateral, inner and outer ventrolateral tubercles, separated by one or two intercalated ribs with inner and outer ventrolateral tubercles, to give a total of 26 ribs at the ventrolateral shoulder. In others, the ribbing and tuberculation are weaker, with up to 28 ribs at the ventrolateral shoulder. UJF-ID10927 (Fig. 8G, H) is a finely ornamented variant

Table 6: Dimensions of *Mantelliceras mantelli* (J. Sowerby, 1814).

	D	Wb	Wh	Wb:Wh	U
ID10930	18.9 (100)	11.1 (58.7)	9.0 (47.6)	1.23	5.2 (27.5)
ID10928	23.7 (100)	13.5 (57.0)	10.6 (44.7)	1.27	6.5 (27.4)
ID10931	23.2 (100)	12.9 (55.6)	10.8 (47.0)	1.19	6.1 (26.3)
ID10932	23.7 (100)	13.1 (55.3)	11.7 (49.3)	1.12	6.1 (25.7)

42 mm in diameter, with a 90° sector of body chamber, and is close to the lectotype.

Occurrence: Commonest in the *Mantelliceras mantelli* Zone of the Lower Cenomanian, but extending into the succeeding *Mantelliceras dixoni* Zone. The species ranges from England to Northern Ireland, France, Germany, Russia, Iran, North Africa, KwaZulu-Natal South Africa, Madagascar, southern India, and Japan.

Mantelliceras picteti Hyatt, 1903

Fig 6E, F

- 1859. *Ammonites Mantelli* Sowerby.— Pictet & Campiche, p. 200, pl. 26, fig. 3, ?figs 1, 2.
- 1903. *Mantelliceras picteti* Hyatt, p. 114 (*paris*).
- 1984. *Mantelliceras picteti* Hyatt.— Wright & Kennedy, p. 117, pl. 27, figs 1-5; pl. 28, figs 1-3; text-figs 25g, 27i, n-q (with full synonymy).
- 1998. *Mantelliceras picteti* Hyatt.— Kaplan, Kennedy, Lehmann & Marcinowski, p. 120, pl. 17, figs 14-17 (with additional synonymy).
- 2013. *Mantelliceras picteti* Hyatt.— Kennedy, Walaszczuk, Gale, Dembicz & Praskier, p. 638, pl. 7, figs 5, 6, 7; text-fig. 4a, b.
- 2015. *Mantelliceras picteti* Hyatt.— Kennedy in Morel, p. 135, text-fig. 131c-e.

Lectotype: The lectotype, designed by Wright & Kennedy, 1984, p. 118, is the original of Pictet & Campiche, 1859, pl. 26, fig. 3, from the Cenomanian of Sainte Croix, Switzerland; this is the holotype by original designation of *Mantelliceras tenue* Spath, 1926, which thus becomes an objective synonym of *M. picteti*.

Material: UJF-ID10941 (Dubois collection).

Description: The specimen consists of just under half a whorl of phragmocone with an estimated diameter of 22.7 mm and a maximum preserved whorl height of 10 mm approximately. The coiling is moderately evolute, the umbilicus of moderate depth, with a convex outward-inclined umbilical wall and broadly rounded umbilical shoulder. The intercostal whorl section is compressed rectangular, with broadly rounded ventrolateral shoulders and a flattened venter. There are seven primary ribs on the fragment. They arise at the umbilical seam, strengthen across the umbilical wall and develop into well-developed bullae, perched on the umbilical shoulder. The ribs are coarse and prorsiradiate across the flanks, with a stronger inner lateral tubercle, a strong, rounded inner ventrolateral tubercle and a strong, high outer

ventrolateral clavus. There are occasional intercalated ribs with inner and outer ventrolateral tubercles only. The venter is deeply concave between the clavi in costal section.

Occurrence: *Mantelliceras picteti* ranges throughout the lower Lower Cenomanian *M. mantelli* Zone, and also occurs in the succeeding *M. dixoni* Zone. There are records from southern England, France from the Boulonnais to Sarthe, Argonne, Isère and Provence, Germany, northern Spain, Switzerland, Podolia, Ukraine (Crimea), Iran, and Madagascar.

Mantelliceras lymense (Spath, 1926)

Fig. 9A, B

- 1926. *Eucalycoceras lymense* Spath, pp. 427, 431.
- 1984. *Mantelliceras lymense* (Spath).— Wright & Kennedy, p. 102, pl. 10, fig. 9; pl. 22, figs 1-6; pl. 23, figs 1-3; pl. 31, figs 1, 2; pl. 36, fig. 4; text-figs 19, 24a, b, 26d, 28f-j (with full synonymy).
- 2011. *Mantelliceras lymense* (Spath).— Mosavina & Wilmsen, p. 182, text-figs 4d, e (with additional synonymy).
- 2015. *Mantelliceras lymense* (Spath).— Kennedy in Kennedy & Gale, p. 265, pl. 10, fig. 8 (with synonymy).
- 2020. *Mantelliceras lymense* (Spath).— Kennedy, p. 200, text-fig. 18c, d.

Type: The lectotype, by the subsequent designation of Wright & Kennedy, 1984, p. 102, is the original of Pervinquier, 1907, pl. 16, fig. 16, refigured by Wright & Kennedy, 1984, text-fig. 24a, b, and Kennedy, 2020, text-fig. 18c, d, from south of Bargou, Tunisia, an unregistered specimen in the collections of the Ecole des Mines, Paris, currently housed in the collections of the Université de Lyon-Villeurbanne.

Material: UJF-ID10942-51 (Dubois collection); 10952-54 (Latil collection).

Dimensions: See Table 7.

Description: The specimens range from 15 to 31.5 mm in diameter. Coiling is moderately involute, the umbilical wall convex, the umbilical shoulder broadly rounded. There are an estimated 14 bullae perched on the umbilical shoulder. They give rise to primary ribs either singly or in pairs, with long and short intercalated ribs to give a total of 34-36 ribs per whorl at the ventrolateral shoulder. The ribs are straight and prorsiradiate, and cross the venter in the feeblest of convexities. There are feeble outer ventrolateral clavi in most specimens, although some, such as UJF-ID10942 (Fig. 9A, B) have lost the tubercle,

Table 7: Dimensions of *Mantelliceras lymense* (Spath, 1926).

	D	Wb	Wh	Wb:Wh	U
ID10953	20.4 (100)	10.8 (52.9)	10.2 (50.0)	1.1	4.9 (24.0)
ID10954	21.8 (100)	- (-)	10.7 (49.1)	-	4.7 (21.6)
ID10942	24.5	- (-)	12.3 (50.2)	-	6.3 (25.7)

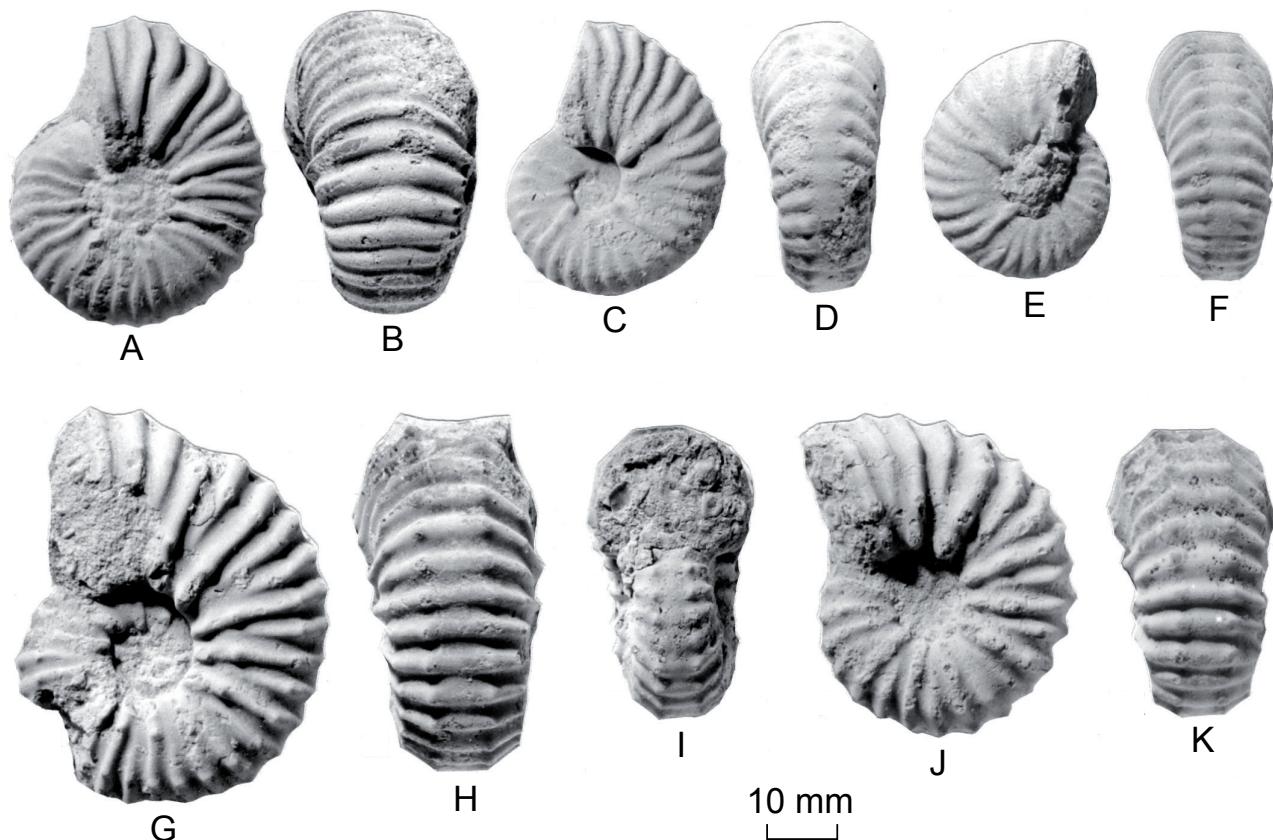


Fig. 9: A, B, *Mantelliceras lymense* (Spath, 1926), UJF-ID10942. C-F, *Mantelliceras dixoni* Spath, 1926. C, D, UJF-ID10958; E, F, UJF-ID10959. G-K, *Mantelliceras mantelli* (J. Sowerby, 1814). G, H, UJF-ID10929; I-K, UJF-ID10928.

with only a faint angulation beyond a whorl height of 6–7 mm.

Occurrence: Lower Cenomanian, *Mantelliceras mantelli* and *Mantelliceras dixoni* Zones, southern England, Northern Ireland, France from the Boulonnais south to Bouches-du-Rhône, Algeria, Tunisia, Madagascar, and possibly Germany and Iran.

Mantelliceras dixoni Spath, 1926

Fig. 7F, G, J-L; 9C-F

- 1850. *Ammonites Milletianus*? d'Orbig. – J. de C. Sowerby in Dixon, p. 359, pl. 29, fig. 15.
- 1926. *Mantelliceras dixoni* Spath, pp. 427, 430.
- 1984. *Mantelliceras dixoni* Spath. – Wright & Kennedy, p. 124, pl. 37, figs 1-6; pl. 38, figs 2-5; pl. 39, figs 2-5; pl. 40, figs 1-5; text-figs 21d-f, 22a-g, 23, 25e, j, 27m, r, s (with full synonymy).
- 1998. *Mantelliceras dixoni* Spath. – Kaplan, Kennedy, Lehmann & Marcinowski, p. 122, pl. 20, figs 4, 5; pl. 23, figs 1-7; pl. 24, figs 7-9; pl. 54, fig. 2 (with additional synonymy).
- 2013. *Mantelliceras dixoni* Spath. – Kennedy, Walaszczyk, Gale, Dembicz & Praskier, p. 639, pl. 4, figs 1, 2; text-fig. 5.
- 2015. *Mantelliceras dixoni* Spath. – Kennedy in Morel, p. 138, text-figs 106, 130b, c.

Type: The holotype by original designation is BMNH C33630, from the Lower Chalk of Sussex, the original of J. de C. Sowerby in Dixon, 1850, pl. 29, fig. 12. It was figured by Wright & Kennedy, 1984, pl. 37, fig. 6.

Material: UJF-ID10956-71 (Dubois collection); 10955 (Latil collection).

Dimensions: See Table 8.

Description: Nuclei range from 14.4-28.6 mm in diameter. Coiling is moderately evolute; the whorl section varies from slightly compressed to slightly depressed, with feebly convex subparallel flanks, broadly rounded ventrolateral shoulders and a broadly convex venter. The ribs arise at the umbilical seam and strengthen into small bullae, 12-16 per whorl, perched on the umbilical shoulder. A strong prorsiradiate rib connects to a strong inner lateral bulla, from which a strong rib flexes forwards and is feebly convex over the ventrolateral shoulder, crossing the venter near-transverse. Weak inner ventrolateral tubercles are present at the smallest diameters seen, but are soon lost, whereas outer ventrolateral clavi persist. Long intercalated ribs have inner and outer ventrolateral clavi at the smallest diameters seen; short intercalated ribs have outer ventrolateral tubercles only. There are 28-36 ribs at the ventrolateral shoulder in these specimens. The largest individuals UJF-ID10955

Table 8: Dimensions of *Mantelliceras dixoni* Spath, 1926.

	D	Wb	Wh	Wb:Wh	U
ID10957	16.6 (100)	8.8 (53.0)	8.3 (49.7)	1.06	3.4 (20.5)
ID10966	17.8 (100)	9.8 (55.1)	8.6 (48.3)	1.14	4.5 (25.3)
ID10958	21.2 (100)	11.0 (51.9)	9.8 (46.2)	1.12	5.0 (23.6)
ID10960	25.4 (100)	13.7 (53.9)	12.2 (48.0)	1.12	6.1 (24.0)
ID10955	60.4 (100)	30.1 (49.8)	26.7 (44.2)	1.13	16.8 (27.8)

(Fig. 7J-L) and 10956 (Fig. 7F, G) are 61 and 71 mm in diameter respectively. The former has eight bullae on the adapertural half whorl. Most give rise to a strong, bar-like rib that links to a strong inner lateral tubercle. There are long and short intercalated ribs to give a total of 20 ribs at the ventrolateral shoulder on the half whorl. The ribs are straight and pro-spiral, and near transverse over the venter. All bear small outer ventrolateral clavi. UJF-ID10956 (Fig. 7F, G) has densely and finely ribbed inner whorls, and is in this respect atypical; the outer half whorl is body chamber, with typical *dixoni* flank ornament at the largest preserved diameter.

Occurrence: The species is restricted to the upper Lower Cenomanian *Mantelliceras dixoni* Zone. There are records from southern England, the Boulonnais, Haute-Normandie, Sarthe, Jura, Basses-Alpes, and Bouches-du-Rhône in France, Germany, Switzerland, Romania, Iran north of the Zagros (?), northern Mexico, El Salvador and Madagascar.

Genus *Sharpeiceras* Hyatt, 1903

Type species: *Ammonites laticlavius* Sharpe, 1855, p. 31, pl. 14, fig. 1, by the original designation of Hyatt, 1903, p. 111.

Sharpeiceras schlueteri Hyatt, 1903

Fig. 8I, J

- 1871. *Ammonites laticlavius* Sharpe.— Schlüter, p. 18 (*paris*), pl. 7, figs 4-8.
- 2015. *Sharpeiceras schlueteri* Hyatt.— Kennedy in Kennedy & Gale, p. 274, pl. 10, figs 2, 5, 10; pl. 11, figs 1, 2; text-fig. 18 (with synonymy).
- 2020. *Sharpeiceras schlueteri* Hyatt.— Kennedy, p. 200, pl. 23, figs 22, 23.

Type: The lectotype, by the subsequent designation of Wright & Kennedy (1987, p. 130) is the original of Schlüter, 1871, pl. 7, figs 4, 5, from a mine shaft near Altenessen, Germany. The specimen has not been traced.

Material: UJF-ID10972 (Latil collection).

Description: The specimen is a 60° whorl sector of a phragmocone with a maximum preserved whorl height of 11.5 mm, and a whorl breadth to height ratio

of 0.8 approximately. The intercostal whorl section is compressed rectangular, with flattened subparallel flanks, quite narrowly rounded ventrolateral shoulders, and a flattened venter. There are five primary ribs on the fragment. They are straight and pro-spiral, broadening and strengthening across the flanks, and all bear a small umbilical bulla, a much weaker lateral bulla, a much stronger, rounded inner ventrolateral tubercle, linked by a strong coarse rib to a strong outer ventrolateral clavus. The clavi are linked over the venter by a low, broad rib.

Discussion: The coarse distant ribbing of this fragment corresponds to that of the Sarthe individual figured by Kennedy *et al.* (1986, text-fig. 23g-m). *Sharpeiceras laticlavium* (Sharpe, 1855, p. 32, pl. 14, fig. 1) (see revision in Wright & Kennedy, 1987, p. 127, pl. 41, fig. 4; text-figs 29, 30, 34a), although known only from much larger specimens, has much more involute coiling, a higher whorl, higher expansion rate, dense, crowded ribs, and weaker ventrolateral tuberculation.

Occurrence: *Sharpeiceras schlueteri* is the index fossil of the middle Subzone of the *Mantelliceras mantelli* Zone, and ranges into the *Mantelliceras dixoni* in southern England. The geographic distribution extends from southern England to France, Switzerland, Central Tunisia, Angola, Mozambique, and Madagascar.

Sharpeiceras sp. juv.

Fig. 8A, B

Compare:

- 1931. *Acanthoceras (Mantelliceras) falloti* Collignon, p. 81 (*paris*), pl. 8 (4), fig. 9 only.
- 1987. *Sharpeiceras falloti* (Collignon).— Wright & Kennedy, p. 129.
- non 2013. *Sharpeiceras falloti* (Collignon).— Kennedy *et al.*, p. 642, pl. 5, figs 1-14 (= *Sharpeiceras australe* Kennedy, 2014).
- 2015. *Sharpeiceras falloti* (Collignon).— Kennedy, Klinger & Lehmann, p. 12, text-figs 13a-e, I, 14a-v.

Material: UJF-ID10973 (Dubois collection).

Description: The specimen is a well-preserved nucleus 11.3 mm in diameter. Coiling is moderately evolute, the umbilicus comprising around 30% of the diameter, the umbilical wall flattened and subvertical, the intercostal

whorl section rectangular, with broadly rounded ventrolateral shoulders and a flattened venter. There are an estimated 14 well-developed strongly prorsiradiate bullae at the umbilical shoulder, separated by deep interspaces. They give rise to one or two ribs that are coarse, straight and prorsiradiate across the flanks. There are 24 ribs at the ventrolateral shoulder, with strong inner, and stronger outer ventrolateral clavi on either side of a venter that is markedly concave in costal section.

Discussion: The present specimen differs in no significant respects from one of the paralectotypes of *Acanthoceras (Mantelliceras) falloti* Collignon, 1931, p. 81, pl. 8 (4), fig. 9. This specimen has the same distinctive prorsiradiate umbilical bullae and interspaces, ribs and tubercles, and represents the early ontogenetic growth stage of a *Sharpeiceras* prior to the appearance of the lateral tubercle.

Occurrence: Lower Cenomanian of Madagascar, and la Bédoule, Bouches-du-Rhône.

Suborder Ancyloceratina Wiedmann, 1966
 Superfamily Turrilitoidea Gill, 1871
 Family Turrilitidae Gill, 1871
 Genus *Hypoturrilites* Dubourdieu, 1953

Type species: *Turrilites gravesianus* d'Orbigny, 1842, p. 596, pl. 144, figs 3-5, by the original designation of Dubourdieu, 1953, p. 44.

***Hypoturrilites gravesianus* (d'Orbigny, 1842)**
 Fig. 10F, G, K, L

- 1842. *Turrilites gravesianus* d'Orbigny, p. 596, pl. 144, figs 3-5.
- 2015. *Hypoturrilites gravesianus* (d'Orbigny).— Klein, pp. 156, 159 (with synonymy).
- 2019. *Hypoturrilites gravesianus* (d'Orbigny).— Kennedy in Gale *et al.*, p. 289, pl. 58, figs 8, 9, 12 (with additional synonymy).

Type: The lectotype (International Commission on Zoological Nomenclature Opinion, 1925, 1999) is BMNH C5762b, the original of Mantell, 1822, pl. 24, fig. 6, from the Lower Chalk of Middleham, near Ringmer, Sussex.

Material: UJF-ID10974-76 (Dubois collection).

Description and Discussion: UJF-ID10976 (Fig. 10F, G) is a 90° whorl sector with a maximum preserved whorl height of 7 mm. The junction of the concave upper and convex outer whorl face is deeply notched. Three large rounded tubercles are situated above the middle of the outer whorl face, and there is a second row of six spirally elongated tubercles towards the base of the face. A third and fourth row of tubercles are borne on a single swelling that gives rise to a coarse radial rib that declines across the lower whorl face. UJF-ID10975 (Fig. 10K, L) is a 240° whorl sector with a maximum preserved whorl height of 13.8 mm; UJF-ID10974 (Fig. 10J) is further

fragment, with a maximum preserved whorl height of 12 mm. As with the previous specimen, there are two large, and four small tubercles in a distance equivalent to the exposed whorl height, but here, the tubercles in the third and fourth rows are clearly separated. Fragments of *Hypoturrilites gravesianus* have two large and four small tubercles in a distance equal to the exposed whorl height, as in the present specimens, whereas the closely related *Hypoturrilites tuberculatus* (Bosc, 1801) (see revision in Wright & Kennedy, 1996, p. 364, pl. 102, fig. 10; pl. 109, figs 1-6; pl. 110, figs 2, 8, 9; pl. 111, fig. 6; pl. 112, figs 1, 3; pl. 113, figs 1, 2, 5, 7, 10-12; text-figs 134r, 140j, k, 141e, 145f, 147e, g) has three large and five to six small tubercles in a distance equal to the exposed whorl height

Occurrence: The species ranges throughout the Lower Cenomanian. The geographic distribution extends from southern England across Europe from France and Spain to Germany, and eastwards to Turkmenistan and Kazakhstan in Central Asia; North Africa, KwaZulu-Natal in South Africa, Madagascar, Northern Australia, the United States Gulf Coast region, and Argentina. There are rare individuals in the Middle Cenomanian basement beds of the Chalk in south-west England, but these may be reworked.

***Hypoturrilites tuberculatoplicatus* (Seguenza, 1882)**

Fig. 10H, I

- 1883. *Turrilites tuberculatoplicatus* Seguenza, p. 53, pl. 5, fig. 3.
- 1996. *Hypoturrilites tuberculatoplicatus* (Seguenza).— Wright & Kennedy, p. 374, pl. 108, fig. 7; pl. 113, figs 3, 4, 6, 8, 9 (with full synonymy).
- 2015. *Hypoturrilites tuberculatoplicatus* (Seguenza).— Klein, pp. 157, 166 (with additional synonymy).
- 2019. *Hypoturrilites tuberculatoplicatus* (Seguenza).— Kennedy in Gale *et al.*, p. 289, pl. 56, figs 1-3, 5-7; pl. 58, fig. 1; text-fig. 39.

Type: The holotype, by monotypy, is the original of Seguenza, 1883, pl. 5, fig. 3, from San Giorgio, near Brancaleone, Italy.

Material: UJF-ID10977 (Dubois collection).

Description: The specimen is a 120° whorl sector with a maximum preserved whorl height of 9.6 mm. The junction of the concave upper and convex outer whorl face is narrowly rounded, and notched to accommodate the lowest row of tubercles on the preceding whorl. There are four large circular flat-topped tubercles at mid-flank. Below, there are two close-spaced, discontinuous spiral ridges that bear an estimated 12-14 delicate spirally elongated tubercles. A fourth row of tiny radially elongated tubercles lie at the junction of the outer and lower whorl faces, and give rise to narrow ribs that extend across the lower whorl face. There are up to four delicate prorsiradiate ribs between the tubercles on the outer whorl face.

Discussion: The presence of delicate ribs on the

outer whorl face together with four rows of tubercles characterise this species and separate it from *Hypoturrilites laevigatus* (Coquand, 1862) (see revision in Wright & Kennedy, 1996, p. 373, pl. 102, fig. 2; text-fig. 146k-m, p, q; Kennedy in Kennedy & Gale, 2015, p. 312, pl. 24, fig. 18; text-fig. 34a-d) and *Hypoturrilites nodiferus* (Crick, 1907) (p. 177, pl. 11, fig. 5; see revision in Klinger & Kennedy, 1978, p. 4, fig. 1), which have only three rows of tubercles.

Occurrence: Lower Cenomanian of Sicily, la Bédoule, Bouches-du-Rhône, southern England and, possibly, Ukraine (Crimea).

Genus and Subgenus *Ostlingoceras* Hyatt, 1900

Type species: *Turrilites puzosianus* d'Orbigny, 1842, p. 587, pl. 143, figs 1, 3, by the original designation of Hyatt, 1900, p. 587.

Ostlingoceras (Ostlingoceras) sp.

Fig. 10E

Material: UJF-ID10978 (Dubois collection).

Description and Discussion: The specimen is a near-complete whorl with a maximum preserved whorl height of 6.5 mm. The outer whorl face is strongly convex. There are six to seven delicate prossiradiate ribs in a distance equal to the whorl height. They develop a tiny transversely elongate tubercle around mid-flank, and then link, either singly or in pairs, at a second row of spirally elongated tubercles low on the whorl face. These are separated by a smooth zone from a third row of spirally elongated tubercles at the junction of outer and lower whorl faces. The tubercles of the third row give rise to single straight ribs that weaken progressively across the lower whorl face.

The specimen most closely resembles *O. (O.) bechei* (Sharpe, 1857, p. 66, pl. 26, fig. 13) (see revision in Wright & Kennedy, 1996, p. 321, pl. 98, figs 6, 14-16, 18, 23), from which it differs in having only three, rather than four rows of tubercles.

Occurrence: Lower Cenomanian of la Bédoule, Bouches-du-Rhône.

Genus *Mesoturrilites* Breistroffer, 1953

Type species: *Turrilites aumalensis* Coquand, 1862, p. 323, pl. 35, fig. 5, by the original designation of Breistroffer, 1953, p. 1351.

Mesoturrilites serpuliforme (Coquand, 1862)

Fig. 10A-D

- 1862. *Heteroceras serpuliforme* Coquand, p. 175, pl. 2, fig. 7.
- 1910. *Turrilites Peroni* Pervinquière, p. 60, pl. 14(5), figs 27-30.
- 1996. *Mesoturrilites serpuliforme* (Coquand).— Wright & Kennedy, p. 348, pl. 98, fig. 10, pl. 102, fig. 5; text-figs 138p, q, r, x, 146h, i, j (with synonymy).

- 1998. *Mesoturrilites serpuliforme* (Coquand).— Kaplan, Kennedy, Lehmann & Marcinowski, p. 211, pl. 63, fig. 9.
- 2015. *Mesoturrilites (Klingerella) serpuliforme* (Coquand).— Klein, pp. 174, 175 (with additional synonymy).
- 2020. *Mesoturrilites serpuliforme* (Coquand).— Kennedy, p. 98, pl. 37, figs 16-18, 21, 25; text-fig. 27h-j.

Types: The lectotype, by the subsequent designation of Wright & Kennedy, 1996, p. 348 is K8456, the smaller of the two specimens in the Coquand collection, currently housed in the collections of the Department of Palaeontology and Geology of the Hungarian Geological Museum, Budapest, figured by Wright & Kennedy, 1996, text-fig. 146h, and Kennedy, 2020, text-fig. 27h. Paralectotype K8822 is a larger individual, figured by Wright & Kennedy, 1996, text-fig. 146i-j, and Kennedy, 2020, text-fig. 27i, j. Both are from Sour-El-Ghozlane (formerly Aumale), northern Algeria.

Material: UJF-ID10979, 80 (Dubois collection); 10981 (Latil collection).

Description and Discussion: These fragments have whorl heights of between 6.7 and 9.4 mm. The outer whorl face is very feebly convex, the junction between the outer and lower whorl faces quite narrowly rounded. There are five ribs in a distance equal to the whorl height on the outer, exposed whorl face. They are narrow, markedly prossiradiate, straight on the upper and middle part of the whorl face, projecting forwards on the lower third, where they strengthen into an incipient tubercle in some individuals. Below, there are two rows of tiny elongated clavi, borne on delicate spiral ridges. The specimens are close to the Algerian types.

Occurrence: Lower Cenomanian, southern England, la Bédoule, Bouches-du-Rhône, the Münster Basin, Germany, Algeria and Tunisia.

Superfamily Scaphitoidea Gill, 1871

Family Scaphitidae Gill, 1871

Subfamily Scaphitinae Gill, 1871

Genus *Scaphites* Parkinson, 1811

Type species: *Scaphites equalis* J. Sowerby, 1813, p. 53, pl. 18, figs 1-3, by the subsequent designation of Meek, 1876, p. 413.

Scaphites equalis J. Sowerby, 1813

Fig. 9M

- 1813. *Scaphites equalis* J. Sowerby, p. 53, pl. 18, figs 1-3.
- 1996. *Scaphites equalis* J. Sowerby.— Wright & Kennedy, p. 394, pl. 116, figs 1-5, 7-11; pl. 117, figs 1-11; pl. 118, figs 1-13; text-fig. 128b, c.
- 2016. *Scaphites equalis equalis* J. Sowerby.— Klein, pp. 53, 63 (with synonymy).

Type: The lectotype is BMNH 43987a from the Lower Chalk of Hamsey (Sussex, England), the original of J. Sowerby 1813, p. 54, pl. 18, figs 4-6, designated by

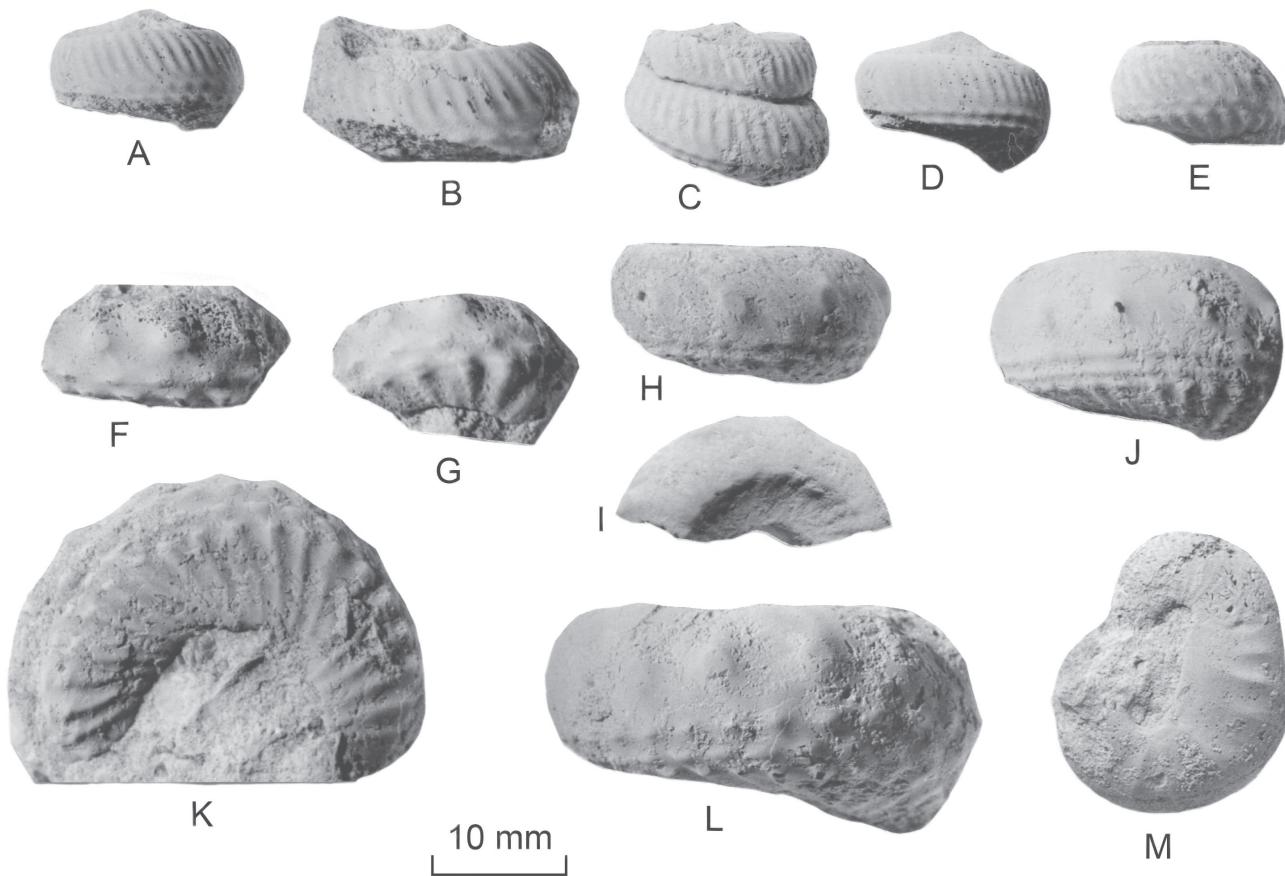


Fig. 10: A-D, *Mesoturrilites serpuliforme* (Coquand, 1862). A, D, UJF-ID10979; B, UJF-ID10980; C, UJF-ID10981. E, *Ostlingoceras* (*Ostlingoceras*) sp., UJF-ID10978. F, G, J- L, *Hypoturrilites gravesianus* (d'Orbigny, 1841). F, G, UJF-ID10976 J, UJF-ID10974; K, L, UJF-ID10975. H, I, *Hypoturrilites tuberculatoplicatus* (Seguenza, 1883), UJF-ID10977. M, *Scaphites equalis* J. Sowerby, 1813, UJF-ID10982.

Kennedy, 1971, p. 33, and reillustrated by Wright & Kennedy, 1996, pl. 114, fig. 18.

Material: UJF-ID10982 (Latil collection).

Description and Discussion: The specimen is a complete adult 22 mm long. The distinctive feature is the presence of coarse distant primary ribs on the shaft and final recurved sector of the body chamber. *Scaphites obliquus* J. Sowerby, 1813 (see revision in Wright & Kennedy, 1996, p. 394, pl. 116, figs 1-5, 7-11; pl. 117, figs 1-11; pl. 18, figs 1-13; text-fig. 129b, c) has a much shorter shell, with fine dense prossiradiate ribs on the body chamber.

Occurrence: *Scaphites equalis* ranges from the base of the *Neostlingoceras carcitanese* Subzone of the Lower Cenomanian *Mantelliceras mantelli* Zone to the Upper Cenomanian *Metoicoceras geslinianum* Zone. The geographic distribution extends from southern England to France, Germany, Poland, the Czech Republic, Bulgaria, Ukraine, the Caucasus, the Mangyschlak Mountains, western Kazakhstan, Turkmenia, Iran, Algeria, Tunisia, and South India.

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REFERENCES

- Arkell W.J. 1950. A classification of the Jurassic ammonites. *Journal of Paleontology*, 24: 354-364.

- Avnimelech M.A. 1965. Sur la présence de *Hyphoplites falcatus* (Mantell) (Ammonoidea: Hoplitidae) dans le Cénomanien inférieur du Carmel (Israël). *Comptes Rendus Sommaires des Séances de la Société géologique de France*, (1965): 160-162.
- Bayle E. 1878. *Fossiles principaux des terrains*. Explication de la Carte géologique de France 4, (1), (Atlas). Service de la Carte géologique détaillée, Paris, 158 pls.
- Böhm J. 1895. [Review of A. de Grossouvre: Recherches sur la craie supérieure. 2nd part]. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie*, 2: 360-366.
- Bosc L.A.G. 1801. (An. 13). In: Roissy, F. *Histoire Naturelle générale et particulière, des Mollusques, Animaux sans vertèbres et à sang blanc. Ouvrage faisant suite aux Œuvres de Leclerc de Buffon, et partie du cours complet d'Histoire naturelle, rédigé par C.S. Sonnini, membre de plusieurs Sociétés savantes. Continué par F. de Roissy*. Imprimerie de F. Dufort, Paris.
- Breistroffer M. 1933. Etude sur l'étage Albien dans le massif de la Chartreuse (Isère et Savoie). *Travaux du laboratoire de Géologie de l'Université de Grenoble*, 17: 187-236.
- Breistroffer M. 1937. Sur l'âge exact du « Banc des Lombards » près Cassis (Bouches-du-Rhône). *Comptes Rendus sommaires de la Société géologique de France*, 16: 936-937.
- Breistroffer M. 1953. Commentaires taxonomiques. In: Breistroffer M. & Villoutreys O. de. Les ammonites albiennes de Peille (Alpes-Maritimes). *Travaux du Département du Laboratoire de Géologie de l'Université de Grenoble*, 30: 69-74.
- Collignon M. 1931. Paléontologie de Madagascar, XVI. La faune du Cénomanien à fossiles pyriteux du nord de Madagascar. *Annales de Paléontologie*, 20: 43-104 (1-64).
- Cooper M.R. & Kennedy W.J. 1979. Uppermost Albian (*Stoliczkaia dispar* Zone) ammonites from the Angolan littoral. *Annals of the South African Museum*, 77: 175-308.
- Coquand H. 1842. In: Réunion extraordinaire de la Société géologique de France à Aix, du 4 au 17 septembre 1842, excursion à Cassis. *Bulletin de la Société géologique de France*, (1)13: 509-532.
- Coquand H. 1862. Géologie et paléontologie de la région de la Province de Constantine. *Mémoires de la Société d'Emulation de la Provence*, 2: 1-341.
- Crick G.C. 1907. Cretaceous fossils of Natal. In: Anderson, W. *Third and final report of the Geological Survey of Natal and Zululand*. West, Newman & Co., London, pp. 161-250.
- Diener C. 1925. Ammonoidea neocretacea. *Fossilium Catalogus* (1: Animalia), 29: 244 pp.
- Dixon F. 1850. *The Geology and Fossils of the Tertiary and Cretaceous Formations of Sussex*. W.J. Smith, Brighton. XVI+423 pp.
- Douvillé H. 1879. (Note accompagnant la présentation de l'Atlas du t.iv de l'explication de la carte géologique de France de E. Bayle & R. Zeiller). *Bulletin de la Société géologique de France*, (3)7: 91-92.
- Douvillé H. 1890. Sur la classification des Cératites de la Craie. *Bulletin de la Société géologique de France*, (3)18: 275-292.
- Douvillé H. 1912. Evolution et classification des Pulchelliidés. *Bulletin de la Société géologique de France*, (4)11: 285-320.
- Dubourdieu G. 1953. Ammonites nouvelles des Monts du Mellègue. *Bulletin du Service de la Carte géologique de l'Algérie*. 1^e série, Paléontologie, 16: 1-76.
- Fabre S. 1937. Le « Banc des Lombards » près de Cassis-sur-Mer (Bouches-du-Rhône). *Comptes Rendus Sommaires de la Société géologique de France*, 12: 204-205.
- Fabre S. 1940. Le Crétacé supérieur de la Basse - Provence Occidentale; 1 Cénomanien et Turonien. *Annales de la Faculté des Sciences de Marseille*, (2)14: 1-355.
- Gale A. S., Kennedy W. J. & Walaszczyk I. 2019. Upper Albian, Cenomanian and Lower Turonian stratigraphy, ammonite and inoceramid bivalve faunas from the Cauvery Basin, Tamil Nadu, South India. *Acta Palaeontologica Polonica*, 69: 161-338.
- Gauthier H. 2006. *Révision Critique de la Paléontologie Française d'Alcide d'Orbigny*, 6, *Céphalopodes Crétacés*. Backhuys, Leiden. 292 + 662 + 28 pp.
- Gill T. 1871. Arrangement of the Families of Mollusks. *Smithsonian Miscellaneous Collections*, 227: xvi + 1-49.
- Grossouvre A. de 1894. Recherches sur la craie supérieure, 2, Paléontologie. Les ammonites de la craie supérieure. *Mémoires du Service de la Carte géologique détaillée de la France*, 264 pp. (misdated 1893).
- Hébert E. 1872. Documents relatifs au terrain crétacé du midi de la France. 2^e partie. *Bulletin de la Société géologique de France*, (2) 21: 398-415.
- Hébert E. & Munier-Chalmas E.P.A. 1875. Fossiles du Bassin d'Uchaux. *Annales des Sciences géologiques*, Paris, 6: 113-132.
- Hyatt A. 1889. Genesis of the Arietidae. *Smithsonian Contributions to Knowledge*, 673: xi + 1-239.
- Hyatt A. 1900. Cephalopoda [pp. 502-604]. In: Zittel K.A. Von, 1896-1900, *Textbook of Palaeontology*, transl. Eastman, C.R. Macmillan, London and New York. VIII + 706 pp.
- Hyatt A. 1903. Pseudoceratites of the Cretaceous. *United States Geological Survey Monograph*, 4: 1-351.
- Immel H. & Seyed-Emami K. 1985. Die Kreideammoniten des Glaukonitkalkes (0. Alb- 0. Cenoman) des Kolah - Qazi - Gebirges südöstlich von Esfahan (Zentral Iran). *Zitteliana*, 12: 87-137.
- International Commission on Zoological Nomenclature. 1999. Opinion 1925. *Turrilites gravisianus* d'Orbigny, 1842 (currently *Hypoturrilites gravisianus*; Mollusca, Ammonoidea): specific name conserved and replacement lectotype designated; *Turrilites tuberculatus* Bosc, [1842] (currently *Hypoturrilites gravisianus*) placed on the Official List. *Bulletin of Zoological Nomenclature*, 56: 154-155.
- Jacob C. 1907. Etudes paléontologiques et stratigraphiques sur la partie moyenne des terrains crétacés dans les Alpes françaises et les régions voisines. *Annales de l'Université de Grenoble*, 19: 221-534 [published also in 1908 in *Travaux du Laboratoire de Géologie de l'Université de Grenoble*, 8 (2): 280-590, and later in 1908 in *Bulletin de la Société de Statistique des Sciences Naturelles et des Arts Industriels du Département d'Isère* (Grenoble), (4)10: 201-514].
- Juignet P. & Kennedy W.J. 1976. Faunes d'ammonites et biostratigraphie comparée du Cénomanien du nord-ouest de la France (Normandie) et du sud d'Angleterre. *Bulletin Trimestriel de la Société géologique de Normandie et des Amis du Muséum du Havre*, 63: 1-193.
- Kaplan U., Kennedy W.J., Lehmann J. & Marcinowski R. 1998. Stratigraphie und Ammonitenfaunen des westfälischen Cenoman. *Geologie und Paläontologie in Westfalen*, 51: 1-236.
- Kennedy W.J. 1971. Cénomanian ammonites from southern England. *Special Papers in Palaeontology*, 8: v + 1-133.

- Kennedy W.J. 1994. Cenomanian ammonites from Cassis, Bouches-du-Rhône, France. *Palaeopelagos*, Special Volume 1: 209-254.
- Kennedy W.J. 2014. *Sharpeiceras australe* sp. nov., replacement name for *Sharpeiceras falloti* Kennedy, 2013, non Collignon, 1931. *Acta Geologica Polonica*, 64: 109-111.
- Kennedy W.J. 2020. Upper Albian, Cenomanian and Turonian ammonites from the Fahdène Formation in central Tunisia and correlatives in northern Algeria. *Acta Geologica Polonica*, 38: 147-272.
- Kennedy W.J. & Gale A.S. 2015. Upper Albian and Cenomanian ammonites from Djebel Mrhila, Central Tunisia. *Revue de Paléobiologie*, 34: 235-361.
- Kennedy W.J. & Gale A. S. 2017. The Ammonoidea of the Lower Chalk, part 7. *Palaeontographical Society Monographs*, 461-561.
- Kennedy W.J. & Wright C.W. 1981. *Euhystrochoceras* and *Algericeras*, the last mortoniceratine ammonites. *Palaeontology*, 24: 417-435.
- Kennedy W.J., Chahida M. R. & Djafarian M. A. 1979. Cenomanian cephalopods from the Glauconitic Limestone southeast of Isfahan. *Acta Palaeontologica Polonica*, 24: 3-50.
- Kennedy W.J., Juignet P. & Wright C.W. 1986. A revision of the ammonite faunas of the type Cenomanian. 3. Mantelliceratinae. *Cretaceous Research*, 7: 19-62.
- Kennedy W.J., Walaszczyk I., Gale A. S., Dembicz K. & Praskier T. 2013. Lower and Middle Cenomanian ammonites from the Morondava Basin, Madagascar. *Acta Geologica Polonica*, 63: 625-655.
- Kennedy W.J., Klinger H.C. & Lehmann J. 2015. Cretaceous faunas from Zululand and Natal, South Africa. The ammonite Subfamily Mantelliceratinae Hyatt, 1903. *African Natural History*, 11: 1-42.
- Kilian W. & Reboul P. 1914. Sur la présence de céphalopodes à affinités indo-africaines dans le Crétacé moyen de Cassis (Bouches-du-Rhône). *Travaux du Laboratoire de Géologie de Grenoble*, 11: 55-56.
- Klein J. 2014. Lower Cretaceous Ammonites VII Hoplitoidea & Engonoceratoidea. *Fossilium Catalogus* I: Animalia, Pars 152: 280 pp.
- Klein J. 2015. Lower Cretaceous Ammonites VIII Turrilitoidea – Anisoceratidae, Hamitidae, Turrilitidae, including representatives of the Upper Cretaceous species. *Fossilium Catalogus* I: Animalia, Pars 154: 265 pp.
- Klein J. 2016. Lower Cretaceous Ammonites X Scaphitoidea, including Upper Cretaceous representatives. *Fossilium Catalogus* I: Animalia, Pars 157: 203 pp.
- Klein J. 2018. Lower Cretaceous Ammonites XI Acanthoceratoidea: Leymeriellidae, Brancoceratidae, Lyelliceratidae, Flickiidae, Forbesiceratidae, including Upper Cretaceous representatives. *Fossilium Catalogus* (I: Animalia), Pars 158: 333 pp.
- Klein J. & Vašček Z. 2011. Lower Cretaceous Ammonites V Desmoceratoidea. *Fossilium Catalogus* 1: Animalia, Pars 148: 311 pp.
- Klein J., Hoffmann R., Joly B., Shigeta Y. & Vašček Z. 2009. Lower Cretaceous Ammonites IV Boreophylloceratoidea, Phylloceratoidea, Lytoceratoidea, Tetragonitoidea, Haploceratoidea including Upper Cretaceous representatives. *Fossilium Catalogus* (1: Animalia), Pars 146: 416 pp.
- Klinger H.C. & Kennedy W.J. 1978. Turrilitidae (Cretaceous Ammonoidea) from South Africa, with a discussion of the evolution and limits of the family. *Journal of Molluscan Studies*, 44: 1-48.
- Korn D., Ebbighausen V., Bockwinkel J. & Klug C. 2003. The A-mode ontogeny in prolecanitid ammonites. *Palaeontology*, 46: 1123-1132.
- Kossmat F. 1895-1898. Untersuchungen über die Südindische Kreideformation. *Beiträge zur Paläontologie Österreich-Ungarns und des Orients*, 9 (1895): 97-203 (1-107); 11 (1897), 1-46 (108-153); 11 (1898): 89-152 (154-217).
- Kullmann J. & Wiedmann J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas, Paleontological Contributions*, 42: 1-32.
- Mantell G.A. 1822. *The fossils of the South Downs; or illustrations of the geology of Sussex*. Lupton Relfe, London. XVI + 327 pp.
- Meek F.B. 1876. A report on the invertebrate Cretaceous and Tertiary fossils of the upper Missouri country. In: Hayden F.V., *Report of the United States Geological Survey of the Territories*, 9: lxiv + 1-629.
- Michelin H. 1838. Note sur une argile dépendant du Gault, observée au Gaty, commune de Gérotot, département de l'Aube. *Mémoires de la Société géologique de France*, (1)3: 97-103.
- Morel N. (coordinator) 2015. *Stratotype Cénomanien*. Muséum National d'Histoire Naturelle; Paris and Biotope; Mèze. 383 pp.
- Mosavina A. & Wilmsen M. 2011. Cenomanian Acanthoceratoidea from the Kopbeh Dagh, NE Iran: taxonomy and stratigraphic implications. *Acta Geologica Polonica*, 61: 175-192.
- Neumayr M. 1875. Die Ammoniten der Kreide und die Systematik der Ammonitiden. *Zeitschrift der Deutschen Geologischen Gesellschaft*, 27: 854-942.
- Orbigny A. d'. 1840-1842. *Paléontologie française: Terrains crétacés*. 1. *Céphalopodes*. Masson, Paris. 1-120 (1840); 121-430 (1841); 431-662 (1842).
- Owen H.G. 1971. Middle Albian stratigraphy in the Anglo-Paris Basin. *Bulletin of the British Museum (Natural History) Geology*, Supplement 8: 1-164.
- Parkinson J. 1811. *Organic remains of a former world*, 3. J. Robson, London, 479 pp.
- Pervinquier L. 1907. Etudes de paléontologie tunisienne. 1. Céphalopodes des terrains secondaires. *Carte géologique de Tunisie*. de Rudeval, Paris. v + 438 pp.
- Pervinquier L. 1910. Sur quelques ammonites du Crétacé algérien. *Mémoires de la Société géologique de France. Paléontologie*, 17 (2-3): 1-86.
- Pictet F.J. 1847. In: Pictet F.J. & Roux W. 1847-1854. Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève. *Mémoire de la Société de Physique et d'Histoire Naturelle de Genève*, 11: (1847), 257-412; 12 (1849), 21-151; 13 (1852), 73-173; 14 (1854), 279-341.
- Pictet F.J. & Campiche G. 1858-1860. Description des fossiles du terrain crétacé des environs de Sainte-Croix, part 2(1). Description des fossiles. *Matériaux pour la Paléontologie Suisse*, (2) part 1: 29-380.
- Renz O. 1968. Die Ammonoidea im Stratotyp des Vraonnien bei Sainte-Croix (Kanton Waadt). *Schweizerische Paläontologische Abhandlungen*, 87: 1-99.
- Salfeld H. [J.C.A.] 1924. *Die Bedeutung der Konservativstämme für die Stammesentwicklung der Ammonoideen*. Max Weg, Leipzig, 16 pp.

- Schlotheim E.F. Von. 1820. *Die Petrefaktenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier- und Pflanzenreiches der Vorwelt erläutert.* Becker, Gotha. LXII + 437 pp.
- Schlüter C. 1871-1876. Cephalopoden der oberen deutschen Kreide. *Palaeontographica*, 21: 1-24 (1871); 21, 25-120 (1872); 24, 1-144 (121-264) + x (1876).
- Seguenza G. 1881-1882. Studii geologici e paleontologici sul cretaceo medio dell'Italia meridionale. *Memorie Atti della Real Academia dei Lincei*, 12 (for 1879): 65-214 (1-152).
- Semenov W.P. 1899. [The fauna of the Cretaceous deposits of Mangychlak and some other localities in the Transcaspian province]. *Travaux de la Société Impériale des Naturalistes de St. Pétersbourg*, 28 (5), Section Géologie et Minéralogie: 1-178 (in Russian).
- Sharpe D. 1853-57. Description of the fossil remains of Mollusca found in the Chalk of England. I, Cephalopoda. *Palaeontographical Society Monographs*: 1-68. 1-26 (1853); 27-36 (1855); 37-68 (1857).
- Sowerby J. 1812-1822. *The Mineral Conchology of Great Britain*. 1, pls 1-9 (1812), pls 10-44 (1813), pls 45-78 (1814), pls 79-102 (1815); 2, pls 103-14 (1815), pls 115-50 (1816), pls 151-86 (1817), pls 187-203 (1818); 3, pls 204-21 (1818), pls 222-53 (1819), pls 254-71 (1820), pls 272-306 (1821); 4, pls 307-18 (1821), pls 319-83 (1822). The author, London.
- Sowerby J. de C. 1823-1846. *The Mineral Conchology of Great Britain* (continued): 4, pls 384-407 (1823); 5, pls 408-443 (1823), pls 444-485 (1824), pls 486-603 (1825); 6, pls 504-544 (1826), pls 545-580 (1827), pls 581-597 (1828), pls 598-609 (1829); 7, pls 610-618 (1840), pls 619-623 (1841), pls 624-628 (1843), pls 629-643 (1844), pls 644-648 (1846), The author, London.
- Spath L.F. 1921. On Cretaceous Cephalopoda from Zululand. *Annals of the South African Museum*, 12: 217-321.
- Spath L.F. 1922a. On the Senonian ammonite fauna of Pondoland. *Transactions of the Royal Society of South Africa*, 10: 113-147.
- Spath L.F. 1922b. On Cretaceous Ammonoidea from Angola, collected by Professor J.W. Gregory, D. Sc., F.R.S. *Transactions of the Royal Society of South Africa*, 53: 91-160.
- Spath L. F. 1923. On the ammonite horizons of the Gault and contiguous deposits. *Summary of Progress of the Geological Survey of Great Britain for 1922*: 139-149.
- Spath L.F. 1925. A monograph of the Ammonoidea of the Gault. Part 2. *Palaeontographical Society Monographs*: 73-110.
- Spath L.F. 1926. On the zones of the Cenomanian and the uppermost Albian. *Proceedings of the Geologists' Association*, 37: 420-432.
- Spath L.F. 1934. A monograph of the Ammonoidea of the Gault. Part 11: *Palaeontographical Society Monographs*: 443-496.
- Stanton T.W. 1895. Contributions to the Cretaceous Palaeontology of the Pacific Coast. The fauna of the Knoxville Beds. *Bulletin of the United States, Geological Survey*, 133: 1-132.
- Suess E. 1866. Über Ammoniten. *Sitzungsberichte der Akademie der Wissenschaften, Mathematische-Naturwissenschaftliche Classe, Wien*, 52 (for 1865), Abteilung 1: 71-89.
- Thomel G. 1992. *Ammonites du Cénomanien et du Turonien du Sud-Est de la France*. Editions Serre, Nice. 1: 1-422; 2: 1-383.
- Wiedmann J. 1966. Stammesgeschichte und System der post-triatischen Ammonoideen; ein Überblick. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*, 125: 49-79; 127: 13-81.
- Wilmsen M., Storm M., Fürsich F. T. & Majidifard M. R. 2013. Upper Albian and Cenomanian (Cretaceous) ammonites from the Debarsu Formation (Yazd Block, Central Iran). *Acta Geologica Polonica*, 63: 489-513.
- Wright C.W. 1952. A classification of the Cretaceous Ammonites. *Journal of Paleontology*, 26: 213-222.
- Wright C.W. & Kennedy W.J. 1978. The Ammonite *Stoliczkaia* from the Cenomanian of England and northern France. *Palaeontology*, 21: 393-409.
- Wright C.W. & Kennedy W.J. 1984. The Ammonoidea of the Lower Chalk. Part 1. *Palaeontographical Society Monographs*: 1-126.
- Wright C.W. & Kennedy W.J. 1987. The Ammonoidea of the Lower Chalk. Part 2. *Palaeontographical Society Monographs*: 127-218.
- Wright C.W. & Kennedy W.J. 1996. The Ammonoidea of the Lower Chalk. Part 3. *Palaeontographical Society Monographs*: 320-423.
- Wright C.W. & Wright E.V. 1949. The Cretaceous ammonite genera *Discohoplites* Spath and *Hyphoplites* Spath. *Quarterly Journal of the Geological Society of London*, 104: 477-497.
- Wright C.W. & Wright E.V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. *Palaeontographical Society Monographs*: 1-40.
- Zittel K.A. Von. 1884. In: *Handbuch der Palaeontologie*. Band 1, Abt. 2; (Lief 3), Cephalopoda. R. Oldenbourg, Munich & Leipzig, pp. 329-522.
- Zittel K.A. Von. 1895. *Grundzüge der Palaeontologie (Palaeozoologie)*. R. Oldenbourg, Munich & Leipzig VII + 972 pp.