



**Adult morphologies of *Puzosia quenstedti* (PARONA & BONARELLI, 1897)
(Ammonoidea, Desmoceratidae)
in the Albian of the South-East of France.
Taxonomic implications**

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Abstract: Several adult specimens belonging to the genus *Puzosia* BAYLE, 1878, were collected in the Albian of Lieuche (Alpes-Maritimes, France). Comparison with material from the condensed Albian levels of La Balme de Rencurel (Isère, France), in particular those described and figured by JACOB (1908), has highlighted a morphological link between the adult forms from Lieuche and the incomplete specimens from the condensed levels of the Lower-Middle Albian of south-eastern France and to identify them as *Puzosia quenstedti* (PARONA & BONARELLI, 1897). These new details on the ontogenetic development of this species also allow new perspectives in the taxonomic treatment of Albian *Puzosia* species. A modified diagnosis of *Puzosia quenstedti* is proposed.

The presence of *Douvilleiceras* sp. juv. aff. *D. mammillatum* (SCHLOTHEIM, 1813) in superimposed overlying levels allows assignation of a Lower Albian (*Douvilleiceras mammillatum* Superzone) to a basal Middle Albian age (*Hoplites dentatus* Zone).

Key-words:

- Vocontian basin;
- South-East France;
- ammonites;
- Albian;
- *Puzosia*;
- *Douvilleiceras*

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Résumé : Morphologies adultes de *Puzosia quenstedti* (PARONA & BONARELLI, 1897) (Ammonoidea, Desmoceratidae) dans l'Albian du Sud-Est de la France. Implications taxonomiques.-

Plusieurs spécimens adultes appartenant au genre *Puzosia* BAYLE, 1878, ont été collectés dans l'Albian de Lieuche (Alpes-Maritimes, France). La comparaison avec le matériel des niveaux albiens condensés de La Balme de Rencurel (Isère, France), notamment celui décrit et figuré par JACOB (1908), a permis de mettre en évidence un lien morphologique entre les formes adultes de Lieuche et les spécimens incomplets des niveaux condensés de l'Albian inférieur-moyen du Sud-Est de la France et de les identifier comme *Puzosia quenstedti* (PARONA & BONARELLI, 1897). Ces précisions inédites sur le développement ontogénétique de cette espèce autorise également de nouvelles perspectives dans le traitement taxonomique des espèces albiennes de *Puzosia*. Une diagnose modifiée de *Puzosia quenstedti* est proposée.

La présence de *Douvilleiceras* sp. juv. aff. *D. mammillatum* (SCHLOTHEIM, 1813) dans des niveaux sus-jacents permet de donner un âge Albian inférieur (Superzone à *Douvilleiceras mammillatum*) à Albian moyen (*Hoplites dentatus* Zone).

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**Mots-clefs :**

- bassin vocontien ;
- Sud-Est de la France ;
- ammonites ;
- Albian ;
- *Puzosia* ;
- *Douvilleiceras*

1. Introduction - Geographical and geological settings

In the North-West of the Alpes-Maritimes department (SE France), the Dôme de Barrot, which culminates at 2137 m, corresponds to a rise in the Palaeozoic basement, bringing out a thick Permian series within the Mesozoic formations. They form a sedimentary aureole of which the Cretaceous grounds are particularly well exposed on the southern side of the dome. The area is deeply cut by two spectacular gorges, the Daluis gorge to the west and the Cians gorge to the east. The village of Lieuche, located on the south side of the Dôme de Barrot, is on the left bank of the Cians, in the lower part of the gorges, facing the village of Rigaud on the right bank. The two villages are established on the Cretaceous strata of the Dôme de Barrot sedimentary aureole (Fig. 1).

In 1896, BERTRAND mentioned the presence of the Aptian following the discovery of *Belemnites minimus* in a ravine south of Rigaud.

GOGUEL (1944, p. 19) described a Cretaceous section located near the same village. In his description, the Aptian marls "supportent un niveau de grès glauconieux très durs qui doit représenter l'Albian". According to BORDET (1950, p. 15), the Lower Cretaceous ("Neocomian") of the Barrot sedimentary aureole is replaced by a series of black marls comprising non-fossiliferous, dark limestone beds, representing by analogy the Aptian and possibly the base of the Albian. This series is topped by a hard, limonitic or glauconitic, limestone bed, jutting out into the topography and which would have provided "*Tetragonites jurinianum* PICTET and *Latidorsella latidorsata* MICH.", indicating an Albian age. The author (BORDET, 1950) points out that in the Lieuche area, a second bed appears a little higher, and that the overlying series, consisting of an alternation of lighter marls and yellowish limestone beds would represent the Cenomanian *sensu lato*.

FAURE-MURET (1953, p. 275) refined the data presented by GOGUEL (1944) and BORDET (1950), underlining that in the Lieuche region, there is a second glauconitic intercalation continuing towards the east, and which would constitute the

equivalent of the glauconitic marly limestone level located to the south-east of Ilonse, where "*Paraturrilites bergeri* BRONGN., *Anisoceras perarmatum* PICT. et CAMP., *Stoliczkaia* sp." were collected, indicating an uppermost Albian age (FAURE-MURET, 1953, p. 275).

In 1965, COTILLON described the Lower Cretaceous in the regions of Daluis and Entrevaux. He recognized the monotonous character of the poorly fossiliferous, thick cretaceous series of the sedimentary aureole of the Dôme de Barrot. The study of numerous sections, mainly on the basis of micropaleontological observations, allowed him to refine Lower Cretaceous stratigraphy. He therefore separated a Lower-Middle Albian unit from the Upper Albian.

Another contribution to the study of the Albian of the region was offered by THOMEL (1960), who studied the so-called Aptian complex of black marls in the vicinity of Puget-Theniers. These marls gave him upper Aptian ("Gargasian") and uppermost Albian ("Vraconian") faunas, respectively at the base and at the top of the series. He admitted that the marls between the fossiliferous Aptian and the uppermost Albian represent the "Albian *sticto sensu*".

COTILLON (1971, p. 135-138) recognized that the Albian of the southern reverse of the Dôme de Barrot thickens from Daluis to the Gorge du Cians. Sedimentological and micropaleontological observations of the Albian of the northern flank of the Tonon ravine at Rigaud show the presence of two thick sandy-glaucous limestone beds: A lower one of Middle Albian age, and an upper unit, beginning in the Middle Albian and ending in the uppermost Albian.

In 1982, RAGAZZI provided a detailed study of the Aptian levels in the immediate vicinity of the village of Lieuche, at a place called Les Laubes. In the absence of macrofauna, the micropaleontological study allowed him to recognize the presence of the middle part of upper Aptian ("upper Gargasian"), which passes directly to the Albian marls, the uppermost Aptian ("Clansayesian") being absent.

BRÉHÉRET (1997) recognized a hiatus comprising the uppermost Aptian and the basal Albian, and the presence of Lower (non-basal), Middle and Upper Albian in the area south of the Dôme du Barrot.

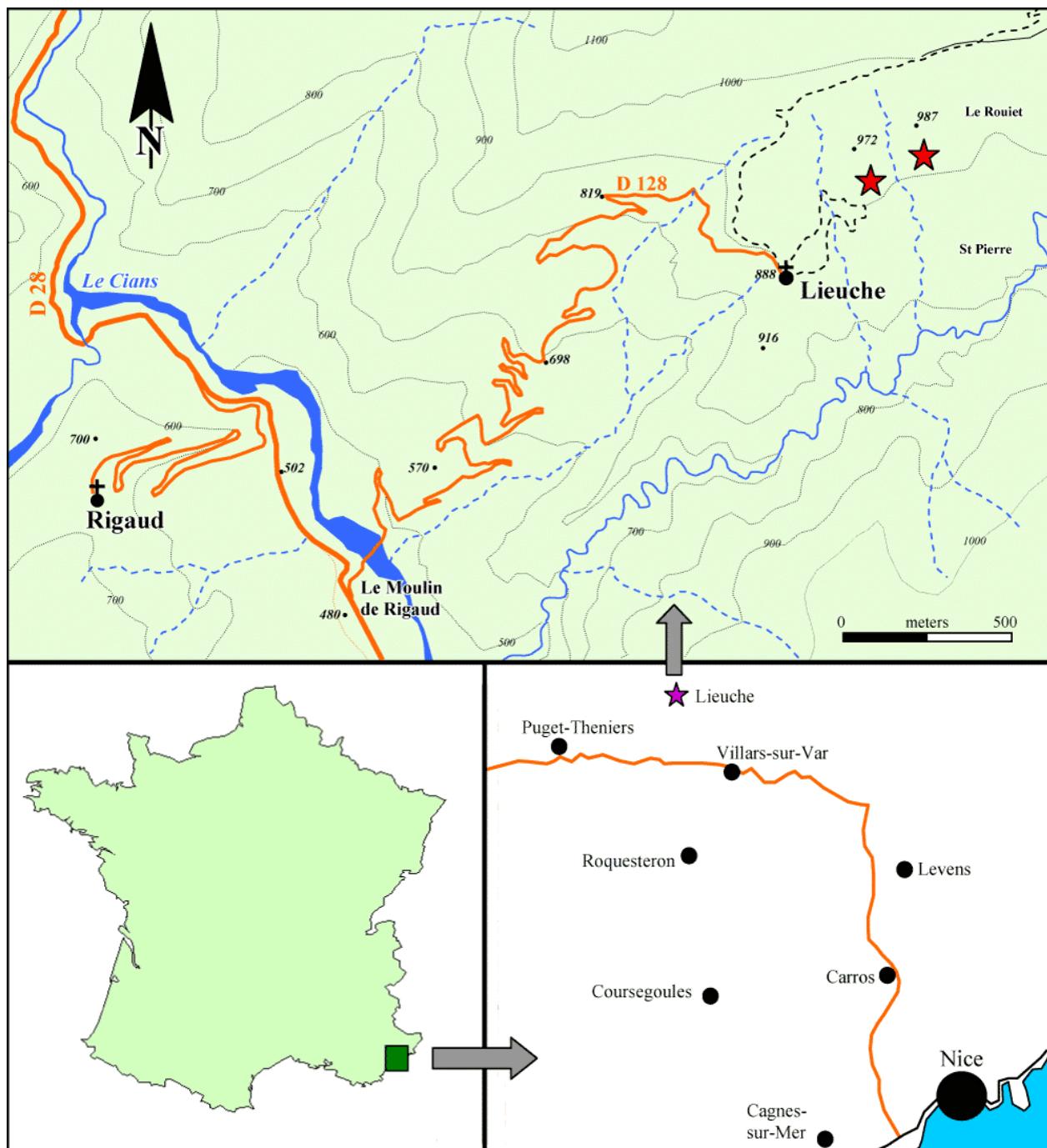


Figure 1: Geographical location of the village of Lieuche. The red stars indicate the source at outcrop where ammonites studied in this work were collected.

2. The Aptian-Albian of Lieuche

To the north-east of the village, the Aptian-Albian series is cut by gullies which allows observation of the stratigraphic succession. The series is particularly well exposed near hillsides 972 and 987 (Les Lauves in RAGAZZI, 1982) (Fig. 1). The Aptian marls ("Upper Gargasian" of RAGAZZI, 1982), about thirty meters thick, are characterized by the appearance at their summit of yellowish sandy calcareous beds with marly interbeds, of variable thickness, probably corresponding to the upper Aptian "faisceau FROMAGET" of BRÉHÉRET (1997). This marl-lime-

stone alternation is capped by a bar, 2-3 metres thick, composed of sandy limestone beds (Fig. 2.A). This bar is interpreted here as the Lower Albian "barre inférieure" of COTILLON (1971). Next come schistose marls (Fig. 2.B), the base of which shows several decimetric sandy limestone beds. The roof of the limestones and the base of the marly series yield large, calcareous or marly, internal moulds of Puzosiiinae, herein identified as *Puzosia quenstedti* (PARONA & BONARELLI, 1897) (Fig. 3.A-B). No other ammonites have been found in these levels; an indeterminable internal mould of a nautiolid genus was also recovered by one of us (G.D.).

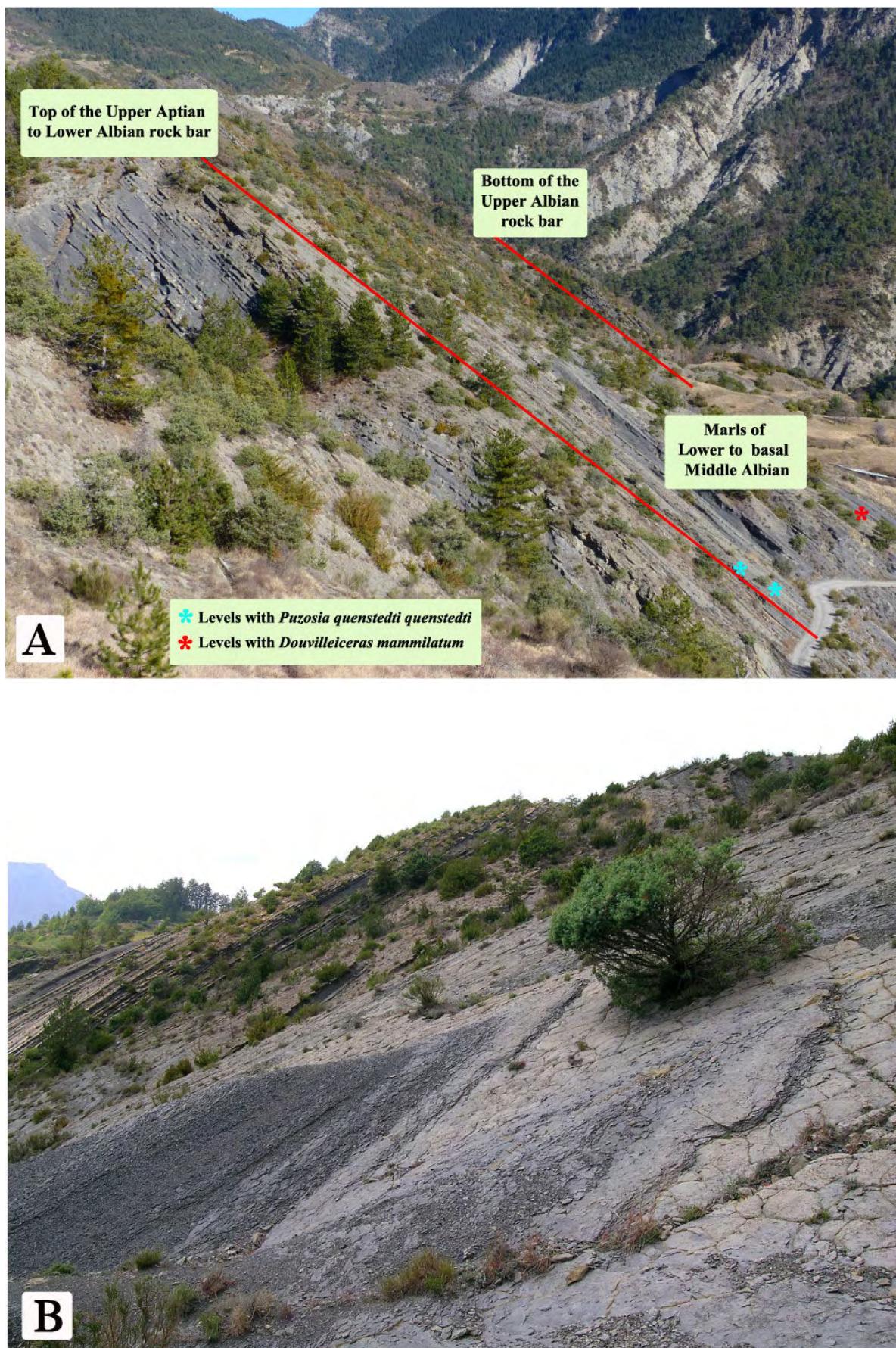


Figure 2: **A** - view of the Lieueche Albian exposures showing the lithological and stratigraphical subdivisions and the positions of the collected ammonite faunas. **B** - base of the Lower to Middle Albian shales.



Douvilleiceras sp. juv. aff. *D. mammillatum* (SCHLOTHEIM, 1813) and *Desmoceras latidorsatum* (MICHELIN, 1838) were also collected at 4-5 metres above the *Puzosia* levels. The thickness of these marls is estimated with difficulty because they disappear very quickly under the effect of tectonics beneath the grassy terraces of the St Pierre area. They are, however, observable, despite the vegetation, a little further to the east, at Le Rouiet, where their thickness is estimated at 10-15 metres. They are crowned by the base of the Middle Albian "barre supérieure" of COTILLON (1971), which then disappears into the vegetation that covers the slope above the Chaudanne valley (Fig. 2.A).

The age of the *Puzosia* levels of Lieuche is very probably Lower Albian, *Douvilleiceras mammillatum* Superzone of OWEN (1988), even if a basal Middle Albian age cannot be excluded.

3. Systematic palaeontology

Dimensions are given in millimetres: D = diameter; Wb = whorl breadth; Wh = whorl height; U = umbilicus. Figures in parentheses are dimensions as a percentage of the diameter. The repositories of specimens are: UJF-ID: ISTerre, OSUG, Université de Grenoble Alpes, ex Institut Dolomieu collections; PU: Museo Regionale di Scienze Naturali, Torino (Italy).

Order Ammonoidea ZITTEL, 1895

Suborder Ammonitina HYATT, 1889

Superfamily Desmoceratoidea ZITTEL, 1895

Family Desmoceratidae ZITTEL, 1895

Subfamily Puzosiinae SPATH, 1922

Genus *Puzosia* BAYLE, 1878

Type species. *Ammonites planulatus* J. de C. SOWERBY, 1827, p. 136, Pl. 520, fig. 5; by the subsequent designation of DOUILLÉ, 1879, p. 91.

= *Pleuropachydiscus* HYATT, 1900, p. 571

Type species. *Ammonites Hoffmannii* GABB, 1864, p. 65 (MURPHY & RODDA, 1978, p. 79, Figs. 1-2) (OD).

= *Matsumotoceras* HOEPEN, 1968, p. 158

Type species. *Matsumotoceras donlisteri* HOEPEN, 1968, p. 158, Fig. 1a, Pl. I (OD).

= ? *Puzosiella* EGOIAN, 1969, p. 174

Type species. *Puzosiella minuta* EGOIAN, 1969, p. 174, Pl. XVI, fig. 8; Pl. 26, fig. 72 (OD).

= ? *Hyperpuzosia* MATSUMOTO, 1988, p. 26

Type species. *Hyperpuzosia tamon* MATSUMOTO, 1988, p. 147, Figs. 69A-C, 70A (OD).

Discussion. The subgenus *Anapuzosia* (type species: *Puzosia buenaventura* ANDERSON, 1938, p. 185) was proposed by MATSUMOTO (1954, p. 71) for puzosids showing vigorous body chamber ornamentation comprising strong, rather rectiradiate major ribs and more or less wide intervals without minor ribs. MATSUMOTO (1988, p. 16) emended the original diagnosis as follow: "from fairly early middle growth stage onward numerous long ribs develop, which arise at or near the umbilical rim, more or less sigmoidal on flank with branched and also intercalated shorter ribs on the outer part; also periodic constrictions well marked and associated flares distinct", and proposed *Anapuzosia* as a distinct genus. *Anapuzosia* differs mainly from *Puzosia* by its young stages showing long riblets arising on the lower third of the flanks with branched and also intercalated shorter ribs. Pending a revision of this group, we herein maintain *Anapuzosia* as a distinct genus.

The taxonomy of the Albian *Puzosia* is unresolved. Very different approaches are found in the literature, mainly on the basis of the study of juvenile specimens.

WIEDMANN and DIENI (1968) separate two different groups within the genus *Puzosia*:

1. the group of *Puzosia mayoriana* (ORBIGNY, 1841), characterized by 4-6 deep and wide sigmoidal constrictions per whorl, strongly convex on the venter, sub-parallel, rarely rounded flanks, a widely rounded venter and a rather wide umbilicus. This group includes *Puzosia mayoriana* (ORBIGNY, 1841), *Puzosia provincialis* (PARONA & BONARELLI, 1897), *Puzosia subplanata* (SCHLÜTER, 1871), *Puzosia lata* SEITZ, 1932, and *Puzosia seitzi* WIEDMANN & DIENI, 1968;

2. the group of *Puzosia quenstedti* (PARONA & BONARELLI, 1897), which differs from the group of *Puzosia mayoriana* by its 6-7 more radial and less flexuous constrictions per whorl, passing across the venter with a convex sinus, flanks converging to a narrowly rounded venter and a wider umbilicus. The authors include in this group:

- *P. communis* SPATH, 1923: whorl section much higher than wide, flanks strongly convergent, narrow umbilicus (uppermost Albian-Lower Cenomanian);
- *P. furnitana* PERVINQUIÈRE, 1907: whorl section much higher than wide, suboval whorl section with a maximum of width at about mid-flanks, rather narrow umbilicus (Upper Albian);
- *P. quenstedti* (PARONA & BONARELLI, 1897): whorl section higher than wide, narrow umbilicus (Middle and Upper Albian);
- *P. media* SEITZ, 1932: whorl section as large as wide, narrow umbilicus (Middle and Upper Albian);
- *P. petkovici* WIEDMANN & DIENI, 1968: whorl section depressed, wide umbilicus, Upper Albian.

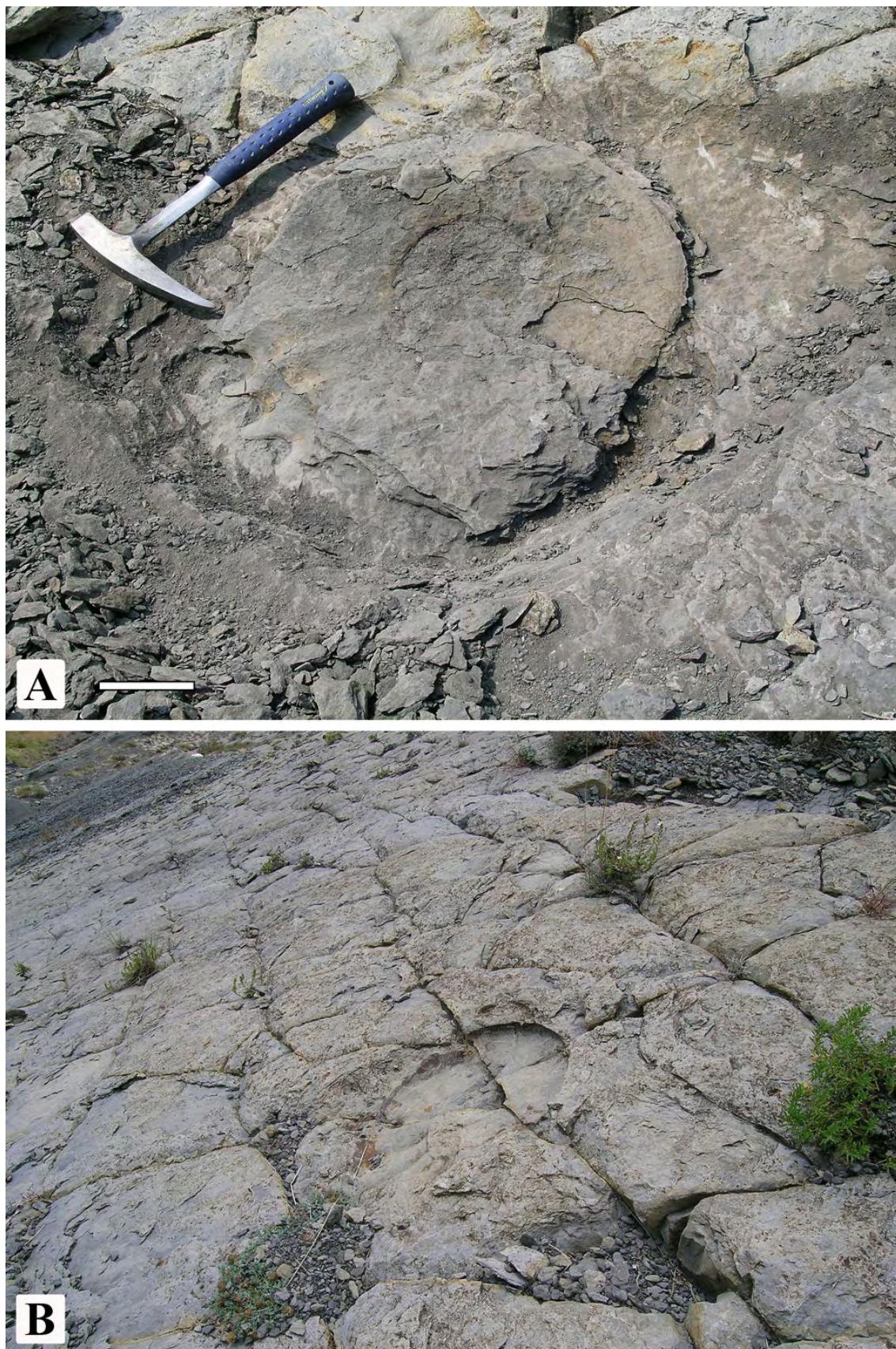


Figure 3: **A** - *Puzosia quenstedti* (PARONA & BONARELLI, 1897), specimen ID-UJF.10991 (Pl. 6, fig. 1) *in situ* at the base of the Lower to basal Middle Albian shales. The last tooth-shaped spine has been destroyed during the extraction of the specimen (scale bar: 10 cm). **B** - Top of the Lower-Middle Albian limestone with a print of a large specimen of *Puzosia quenstedti* (PARONA & BONARELLI, 1897).



WRIGHT and KENNEDY (1984), following SCHOLZ (1979), have suggested that "there is probably a single widespread Albian and Cenomanian (and perhaps Turonian) species of *Puzosia*, perhaps with a few more localized separate species". In 1987, COOPER and KENNEDY have also suggested that the *Puzosia majoriana* "plexus" sensu WIEDMANN and DIENI (1968) comprises mainly macroconch "species" whose microconch correspondents are to be found in the gr. of *Puzosia quenstedti*.

This point of view is not followed by MARCINOWSKI and WIEDMANN (1990) who consider that the two groups defined by WIEDMANN and DIENI (1968) correspond to two different species: *Puzosia quenstedti* and *Puzosia majoriana*.

***Puzosia quenstedti* (PARONA & BONARELLI, 1897)**

- (Figs. 3-4; Pl. 1, figs. 1-2; Pl. 2, figs. 1-3;
Pl. 3, figs. 1-2; Pl. 4, figs. 1-2;
Pl. 5, figs. 1-2; Pl. 6, figs. 1-2)
- 1847 *Ammonites planulatus* QUENSTEDT, p. 221, Pl. 17, fig. 13b only.
- 1897 *Desmoceras Quenstedti* PARONA & BONARELLI; p. 81(29), Pl. 11(2), fig. 3.
- 1908 *Desmoceras (Puzosia) Majorianum* d'ORBIGNY sp. pars.; JACOB, Figs. 23-24, Pl. 16(6), figs. 1-3 (non fig. 4).
- ?1929 *Puzosia quenstedti* SCHINDEWOLF, p. 58, Fig. 31a-e.
- ?non 1930 *Puzosia Majoriana* (d'ORBIGNY); PASSENDORFER, Pl. 3, figs. 57-58.
- 1931 *Puzosia Quenstedti* PAR. et BON. sp.; BREISTROFFER, p. 194.
- 1932 *Puzosia quenstedti* (PAR. et BON.); SEITZ, p. 401, Pl. 16, figs. 3-4.
- 1933 *Puzosia Quenstedti* PAR. et BON. sp. id. var. nov.; BREISTROFFER, p. 8.
- 1936 *Puzosia quenstedti* var. *bonarellii*, BREISTROFFER, p. 171, Fig. 10.e-f.
- non 1936 *Puzosia jacobi* COLLIGNON, p. 193.
- ?non 1942 *Puzosia quenstedti* var. *angolana* HAAS, p. 149, Fig. 20a-g, Pl. 37, figs. 2-9, Pl. 41, figs. 1-6.
- ?non 1942 *Puzosia quenstedti* var. *applanata* HAAS, p. 151, Fig. 20h-j, Pl. 37, figs. 10-11; Pl. 41, figs. 7-8.
- 1947 *Puzosia Quenstedti* PAR. et BON. sp. id. var. nov.; BREISTROFFER, p. 26.
- ?1949 *Puzosia quenstedti* PAR. et BONAR.; LUPPOV et al., p. 215, Pl. 62, fig. 1.
- 1950 *Puzosia Quenstedti* PAR. ET BON.; COLLIGNON, p. 44, Pl. 9(7), fig. 1.
- 1953 *Puzosia quenstedti* PAR. et BON. sp., BREISTROFFER in BREISTROFFER & VILLOUTREYS, p. 70.
- ?1953 *Puzosia bonarellii* BREISTR. (prius pro var.), BREISTROFFER in BREISTROFFER & VILLOUTREYS, p. 70.
- non 1958 *Puzosia hopkinsi* (FORBES); BÜRGL, p. 136, Pl. 10, fig. 1.
- non 1958 *Puzosia* nov. sp. aff. *majoriana* (d'ORBIGNY); BÜRGL, p. 136, Pl. 11, fig. 4.
- 1960 *Puzosia quenstedti* (PARONA et BONARELLI); PAUCA & PATRULIUS, p. 95(11), Fig. 3, Pl. 3, fig. 24.
- ? 1966 *Puzosia cf. quenstedti* (PAR. & BONAR.); SCHINDEWOLF, Fig. 373.
- 1966 *Puzosia quenstedti* (PAR. & BONAR.);

SCHINDEWOLF, Figs. 374, 396.

- 1968 *Puzosia quenstedti* (PARONA & BONARELLI); WIEDMANN & DIENI, p. 114, Figs. 72, 73 (= PARONA & BONARELLI, 1897, Pl. 11(2), fig. 3), Pl. 10, fig. 11, Pl. 12, fig. 3.
- non 1975 *Puzosia quenstedti* (PARONA & BONARELLI); LILLO BEVIÁ, p. 685, Pl. 4, figs. 1-2, Pl. 8, fig. 4.
- ? 1976 *Puzosia* gr. *quenstedti* (PARONA & BONARELLI); MARTÍNEZ, p. 45, Pl. 9, fig. 1.
- ? 1978 *Puzosia quenstedti* (PARONA & BONARELLI); WIEDMANN & NEUGEBAUER, p. 711, Pl. 2, fig. 1.
- ? 1979 *Puzosia* sp., group of *P. quenstedti* (PARONA & BONARELLI); KENNEDY & KOLLMANN, p. 6, Pl. 1, figs. 2-3; Pl. 4, figs. 1-5.
- 1979 *Puzosia (Puzosia) planulata quenstedti* (PARONA & BONARELLI); SCHOLZ, p. 66.
- ? 1979 *Puzosia* gr. *quenstedti* (PARONA & BONARELLI); MARTÍNEZ, p. 347, Fig. 7 (= MARTÍNEZ, 1976, Pl. 9, fig. 1), Pl. 1, fig. 7.
- 1980 *Puzosia quenstedti* PARONA & BONARELLI; THOMEL, p. 122, Fig. 244.
- non 1981 *Puzosia quenstedti* (PARONA & BONARELLI); CHIRIAC, p. 76, Fig. 27, Pl. 8, fig. 1a-b.
- ? 1982 *Puzosia* ? sp. aff. *Puzosia gr. quenstedti* (PARONA & BONARELLI); MARTÍNEZ, p. 70, Fig. 12 (= MARTÍNEZ, 1976, Pl. 9, fig. 1d), Pl. 4, fig. 12.
- 1982 *Puzosia quenstedti* (PARONA & BONARELLI); RENZ, p. 34, Pl. 4, fig. 8.
- ? 1982 *Puzosia* aff. *quenstedti*; COLLETÉ et al., Pl. 14, fig. 1.
- ?non 1984 *Puzosia majoriana* (d'ORBIGNY); LEFELD, p. 115, Pl. 42, fig. 1 (= PASSENDORFER, 1930, Pl. 3, figs. 57-58).
- ? 1986 *Puzosia* gr. *quenstedti* PARONA et BONARELLI; BRÉHÉRET et al., Pl. 8, fig. 1.
- non 1988 *Puzosia* sp. aff. *quenstedti* (PARONA & BONARELLI); DELANOY & LATIL, p. 752, Pl. 1, fig. 7.
- ? 1988 *Puzosia quenstedti* PARONA & BONARELLI; KHALILOV, p. 358, Pl. 14, fig. 1.
- ? 1989 *Puzosia (Puzosia) quenstedti* (PARONA & BONARELLI); FÖLLMI, p. 136, Pl. 9, figs. 4-7.
- ?non 1989 *Puzosia majoriana octosulcata* (SHARPE); MARKEK et al., p. 88, Pl. 43, fig. 1 (= PASSENDORFER, 1930, Pl. 3, figs. 57-58).
- ?non 1990 *Puzosia quenstedti quenstedti* (PARONA & BONARELLI); MARCINOWSKI & WIEDMANN, p. 54, Pl. 5, fig. 7 (= PASSENDORFER, 1930, Pl. 3, fig. 57-58).
- ?non 1992 *Puzosia* cf. *quenstedti* (PARONA & BONARELLI); AGIRREZABALA et al., p. 154, Pl. 1, fig. 3.
- ? 1996 *Puzosia quenstedti* (PARONA & BONARELLI); SEYDEMAMI & IMMEL, p. 10, Pl. 5, figs. 1-2.
- ? 1997 *Puzosia (Puzosia)* sp. group of *quenstedti* (PARONA & BONARELLI); KENNEDY et al., p. 464, Pl. 1, fig. 11; Pl. 7, fig. 1, 8, 10, 12; Pl. 9, fig. 1-3.
- 2000 *Puzosia (Puzosia) quenstedti* (PARONA & BONARELLI); KENNEDY, p. 663, Fig. 43n (= JACOB, 1908, Pl. 16(6), fig. 1a).
- ? 2000 *Puzosia (Puzosia) quenstedti* (PARONA & BONARELLI); KENNEDY, p. 663, Figs. 47j, n-o, 48b, d, 49a, d, 51i.
- ? 2002 *Puzosia* cf. *quenstedti* (PARONA & BONARELLI); ROBERT, p. 173, Pl. 28, figs. 1-3.
- non 2004 *Puzosia quenstedti* (PARONA & BONARELLI); BOGDANOVA & HOEDEMAEKER, p. 240, Pl. 40, fig. 1; Pl. 43, fig. 2; Pl. 44.
- ? 2005 *Puzosia (Puzosia) quenstedti* - PRINS, p. 33, Pl. 4.
- ? 2011 *Puzosia (Puzosia)* aff. *quenstedti* (PARONA & BONARELLI); LATIL, p. 340, Pl. 1, figs. 11-13.
- 2011 *Puzosia (Puzosia) quenstedti quenstedti* (PARONA & BONARELLI); KLEIN & VASICEK, p. 86 pars.
- 2011 *Puzosia (Puzosia) quenstedti bonarellii* BREISTROFFER; KLEIN & VASICEK, p. 86.



- ? 2012 *Puzosia quenstedti* (PARONA & BONARELLI); BERT, p. 12, Pl. C, figs. 1-3.
- ? 2014 *Puzosia* (*Puzosia*) sp., group of *quenstedti* (PARONA & BONARELLI); KENNEDY & FATMI, p. 56, Fig. 9J-L.
- non 2017 *Puzosia* (*Puzosia*) *quenstedti quenstedti* (PARONA & BONARELLI); TAIKA et al., p. 28, Fig. 6 Z-AC.
- ? 2018 *Puzosia quenstedti* (PARONA & BONARELLI); AYOUB-HANNA et al., p. 291, Figs. 10 G-J, 12 A-C.

Emended diagnosis. Juvenile with moderately involute coiling (U/D between .30 and .35), slightly higher than wide, whorl section, 5-7 constrictions by whorl that are very slightly flexuous on the flanks, concave on the ventrolateral shoulders and slightly convex on the venter. The number of constrictions per whorl increases with age numbering 9-10 on the adult phragmocone, at a diameter of about 300 mm. There is no discernible ornamental change on the first half of the body chamber. The outer part of the adult body chamber is characterized by the presence of three strong ribs on the flanks, the first one ending with an outer lateral tubercle, the second and the third ones terminating with huge ventrolateral tubercles, the third one developing a ventral swelling. Two to three ribs close to the aperture, without ventrolateral tubercles, develops huge ventral spines. Largest known size at about 450 mm of diameter.

Material. 8 adult specimens and a fragment of a juvenile (UJF-ID10989-10997), preserved as crushed and distorted internal moulds, from Lieuche (Alpes-Maritimes, France), *Douvilleiceras mammillatum* Superzone or *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian); 7 phosphatized specimens from La Balme de Rencurel (Isère, France), condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian): UJF-ID.1036, 1068, 1066 [= *Desmoceras* (*Puzosia*) *Mayorianum* ORB. in JACOB, 1908, Pl. 16(6), figs. 1-3 only], UJF-ID.10987 and 10988 and two additional unnumbered juveniles; a single loose fragment from the Albian of Châteauneuf-Val-Saint-Donat (Alpes-de-Haute-Provence, France) (UJF-ID. 10998), an inconclusively dated series, which, however, was assigned to the Middle Albian by FRIÈS (1987).

Holotype. *Desmoceras Quenstedti* PARONA & BONARELLI, 1897, p. 81, Pl. 11(2), fig. 3, refigured by WIEDMANN and DIENI (1968, p. 114, Pl. 12, fig. 3), and herein refigured Pl. 2, fig. 3, housed in the paleontological collections of the Museo Regionale di Scienze Naturali, Torino (Italy) under the no. PU20453.

The type specimen is a juvenile phragmocone, 38 mm in diameter, preserved as a phosphatized internal mould with some remains of

the shell, from Escragnolles (Alpes-Maritimes, France). The umbilicus is rather narrow ($U/D = 0.32$). There are 6-7, radial to feebly proverse, slightly flexuous, shallow and narrow constrictions on the last preserved whorl. The constrictions are only feebly curved forward on the rounded venter. The section is moderately elevated ($Wh/D = 0.42$) and is described by the authors as sub-circular and slightly compressed ($Wb/Wh = 0.90$). Between the constrictions, there are numerous fine, slightly flexuous riblets on the outer half of the flanks and the venter. These riblets are mainly visible when the shell is preserved.

The age of the holotype. The type of *Puzosia quenstedti* is quoted in the literature from the Lower-Middle Albian. GEBHARD (1983) described a detailed Escragnolles succession, showing the presence of three successive condensed levels with ammonites: A lower one, about 50 cm above the base of the Albian, with Lower Albian ammonites of the *Douvilleiceras mammillatum* Superzone; a second one, about one metre higher (approximately 1.5 m above base), with Lower Albian and basal Middle Albian ammonites; and a third, one metre higher (about 2.5 m above basal Albian), with Middle and basal Upper Albian ammonites. Since the stratigraphic position of the type of *P. quenstedti* is uncertain within the section, its age remains unclear, between the base of the *Douvilleiceras mammillatum* Superzone (Lower Albian) and the *Dipoloceras cristatum* Zone (base of the Upper Albian).

Table 1 : Measurements of *Puzosia quenstedti* (in mm). Lieuche specimens are not included in the table because of their *post-mortem* deformation.

Specimen no.	D	Wh	Wb	U	Wb/Wh
PU20453 ⁽¹⁾ (holotype)	38.0	16 (0.42)	14.5 (0.38)	12.3 (0.32)	0.90
UJF-ID.1036	46.0	17.0 (0.37)	16.0 (0.35)	15.5 (0.34)	0.94
UJF-ID.10987	61.8	25.0 (0.40)	23.5 (0.38)	19.6 (0.32)	0.94
UJF-ID.10988	104.0	44.0 (0.42)	ca 47.0 (0.45)	?	1.07
UJF-ID.1068	285.0	?	?	87.0 (0.30)	?
C 370.0	122.0 (0.34)	?	127.0 (0.35)	?	

⁽¹⁾ after WIEDMANN and DIENI, 1968, p. 115.

The specimen UJF-ID.1036 (JACOB, 1908, p. 38, Pl. 6, fig. 1) is an incomplete phragmocone preserved as a phosphatized internal mould, with some remains of the shell, with a total preserved diameter of 46 mm. The umbilical wall is low and convex, the flanks are feebly convex, converging to a narrowly rounded venter. The whorl section is suboval, slightly higher than wide. There are 6-7, radial to slightly prosiradiate constrictions on the last preserved whorl, which are projected forward on the ventrolateral area and feebly curved on the venter. A feeble rib on the adapical edge of the constriction is visible only on the inner flanks of the internal mould. The shell shows numerous flexuous



riblets that are slightly rursiradiate on the inner half of the flanks and are strongly projected forward on the ventral area. The ornament on the internal mould between constrictions is inconspicuous on juveniles, and feeble beyond a diameter of 40 mm.

Beyond a diameter of 50 mm (UJF-ID.10987: Pl. 1, fig. 1), the umbilical wall steepens to subvertical and the umbilical shoulder is narrowly rounded. The whorl section becomes slightly less compressed with a maximum width at the inner third of the flank. UJF-ID.10988 (Pl. 2, fig. 2), 104 mm in diameter, on which some parts of the shell are preserved, has six feeble constrictions on the last preserved whorl that are slightly flexuous and feebly convex on the venter. There are about eighteen to twenty small ribs between each constriction, almost inconspicuous when the shell is not preserved, straight and prorsiradiate on the outer part of the flanks, slightly projected forward on the ventrolateral shoulders and very feebly convex on the venter.

The specimen UJF-ID.1068 (JACOB, 1908, p. 38, Pl. 6, fig. 2), herein refigured (Pl. 1, fig. 1; Pl. 2, fig. 1), is a large incomplete adult specimen, about 370 mm in diameter, including a 90° sector of body chamber, preserved as an internal mould with remains of calcified shell. One side is strongly weathered.

The phragmocone is about 300 mm in diameter. The inner whorls, prior to a diameter of about 70 mm, are not preserved. The umbilical wall is low and vertical. The umbilical shoulder is narrowly convex. The flanks are feebly convex, the venter is rather broadly rounded. The ornament is poorly preserved, especially on the internal mould where only some radial straight constrictions can be observed. There are nine constrictions on the last preserved whorl. When the shell is preserved, numerous feeble, radial riblets can be observed between two straight primary ribs (constrictions on the internal mould). On the beginning of the body chamber, the coiling is more evolute, the umbilical wall is vertical when the shell is preserved, slightly oblique on the internal mould. The shell is about 5 mm thick. At about 340 mm in diameter, a radial, coarse rib appears on the inner part of the flanks, ending with a strong outer lateral tubercle. The next rib is stronger and arises at the umbilical shoulder, ending with a huge ventrolateral horn.

A large fragment of an adult body chamber (UJF-ID.1066, JACOB, 1908, p. 38, Pl. 6, fig. 3) preserved as an internal mould with remains of calcified shell, has a maximum whorl height of 130 mm (Pl. 5, fig. 2) (a juvenile *Douvilleiceras* is preserved inside the body chamber). There are three strong, coarse, radial ribs. The first one bears a strong ventrolateral horn and a spirally elongated swelling. The next one bears a

small ventrolateral tubercle and a huge spirally elongated ventral spine.

Material from Lieueche (Pl. 3, figs. 1, 2a-b; Pl. 4, figs. 1-2; Pl. 5, fig. 1a-b; Pl. 6, fig. 1). The best-preserved specimen (UJF-ID.10989: Pl. 3, fig. 1; Pl. 4, fig. 1), an almost complete adult, about 400 mm in diameter, shows the end of the phragmocone and a 180° sector of body chamber. The inner whorls are not preserved, the end of the phragmocone is crushed and poorly preserved. The first part of the body chamber shows three rather prorsiradiate ribs, tending to be projected forward on the ventrolateral area with numerous, almost inconspicuous riblets in between, on the outer part of the flanks. The riblets disappear on the outer half of the body chamber. A strong outer lateral tubercle appears at a diameter of 350 mm, followed by two coarse, strong, radial to slightly prorsiradiate ribs ending with a huge ventrolateral tubercle (Pl. 3, fig. 1; Pl. 4, figs. 1-2; Pl. 5, fig. 1), the last one developing a spirally elongated ventral swelling (Pl. 3, fig. 1). The two last preserved ribs lose their ventrolateral tubercles to develop huge spirally elongated siphonal spines (Pl. 3, figs. 1-2; Pl. 4, figs. 1-2; Pl. 6, fig. 1). The most complete specimen (UJF-ID.10991: Pl. 6, fig. 1), 450 mm in diameter, shows three ribs with ventral spines on the outer part of the body chamber. It would appear that the last rib and its ventral spine, close to the aperture, are attenuated. The whorl height (Wh/D) diminishes on the adapical half of the body chamber. All the specimens have an estimated adult diameter of 450 mm. The evolution of the ornamentation is summarized on Figure 4.

Additional material. UJF-ID.10998 (Pl. 6, Fig. 2), a single loose fragment from the Middle-basal Upper Albian of Châteauneuf-Val-Saint-Donat (Alpes-de-Haute-Provence, France), with an estimated diameter of 400 mm, comprises an incomplete body chamber. The first outer lateral tubercle appears at a whorl height of 150 mm (estimated diameter of 350 mm). Two ventrolateral tubercles are also visible. This strongly weathered specimen is closely related to the Lieueche material.

Discussion. According to MATSUMOTO (1988, p. 27): "The large specimens illustrated by JACOB (1908, p. 38, Pl. 16, figs. 2-4) under *Desmoceras* (*Puzosia*) *Mayorianum* are not referred to *Puzosia* nor to *P. mayoriana* (d'ORBIGNY) and probably a species of *Hyperpuzosia*". MATSUMOTO (1988, p. 34) mentions that he previously referred the specimen figured by JACOB (1908, Pl. 16, fig. 2) to *Anapuzosia*, adding: "but this was probably wrong because its phragmocone has fine ribs on the outer part of the whorl as in typical *Puzosia* and is different from the more strongly ribbed phragmocone of *P. buenaventura* ANDERSON, the type species of *Anapuzosia*". We herein consider that the juvenile of *Puzosia quenstedti* is characteristic of the genus *Puzosia* and that the poorly known genus *Hyperpuzosia* is not clearly distinct from *Puzosia*.

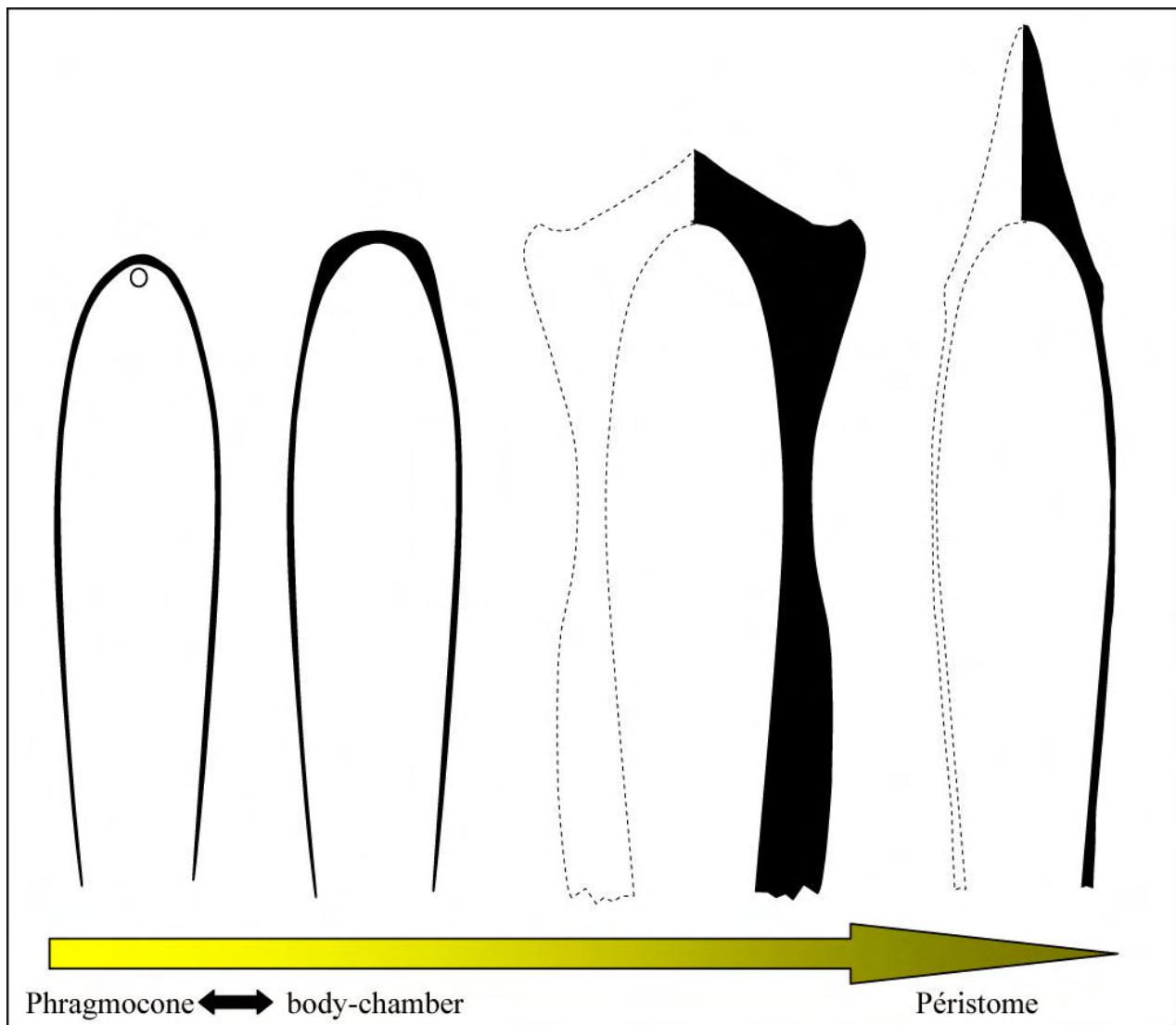


Figure 4: Evolution of the ornamentation from the end of the phragmocone to the peristomal region from Lieue specimens (the shape of the whorl section as herein figured is a result of compaction of these specimens).

The specimen UJF-ID.1067, figured as *Desmoceras (Puzosia) Mayorianum*, by JACOB (1908, p. 38, Pl. 6, fig. 4), from the basal to Lower part of the Middle Albian at La Balme de Rencurel, is a large fragment of an adult body chamber, preserved as an internal mould, with a maximum whorl height of 125 mm. It shows narrow, high, sharp, prorsiradiate ribs arising on the perumbilical edge that appear to cross the ventral area without interruption. This unidentified specimen is herein excluded from the synonymy.

Puzosia quenstedti differs from *Puzosia mayoriana* (ORBIGNY, 1841) by its different stratigraphical level (uppermost Albian-Lower Cenomanian), its smaller size (more than 800 mm in diameter for *P. mayoriana*), the lack of a ventral chevron on juveniles, the presence of tubercles and spines on the adult body chamber. A fragment of an adult phragmocone of *P. mayoriana* (UJF-ID.10999), from bed 96 of the Montlaux section (uppermost Albian, Mortonice-

ras (*Subschloenbachia*) *perinflatum* Zone), with a whorl height of 180 mm, is herein figured (Pl. 4, fig. 3) (see also KENNEDY & LATIL, 2007).

Achilleoceras erasmii HOEPEN, 1951, holotype, is an adult of 800 mm in diameter from the uppermost Albian of Zululand (South Africa), that bears similar ventral spines but differs from *P. quenstedti* by its size, its higher stratigraphical level, juvenile ornamentation, the presence of lateral and inner lateral spines, the lack of ventrolateral tubercles and a greater number of ventral spirally elongated spines.

According to KENNEDY (2000, p. 664), *Puzosia provincialis* (PARONA & BONARELLI, 1897) comprises microconchs of *P. quenstedti*. This view is not supported by the facts presented herein. The holotype of *Puzosia provincialis* is a juvenile, comprising the phragmocone and a sector of about 180° of body chamber, 22.5 mm in diameter, preserved as a phosphatized internal mould with some remains of the shell, from the upper Lower Albian-Middle Albian of Escragnolles (Alpes-Maritimes, France). The umbilicus is rather narrow ($U/D = 0.31$). There are



5, radial, strongly flexuous, shallow and narrow constrictions on the last preserved whorl. They are slightly curved forward on the venter. The section is moderately elevated ($Wh/D = 0.40$), as high as wide. *Puzosia provincialis* is unknown, neither at La Balme de Rencurel, nor at Lieuche. *P. provincialis* is a poorly known species of the group of *Puzosia majoriana* as defined by WIEDMANN and DIENI (1968).

Puzosia quenstedti var. *bonarellii* BREISTROFFER, 1936 (p. 171, Fig. 10.e-f), from the Middle Albian of Berambo (Madagascar) is noted to differ from the present species only from its oval whorl section, higher than wide, and by its slightly deeper constrictions. At the same size, the ratio Wb/Wh is the same for the La Balme de Rencurel material and for the smallest Malagasy specimen (0.94). This material is herein assigned to the present species. It should be noted that BREISTROFFER (1947, p. 77) considers *Puzosia jacobi* COLLIGNON, 1936, p. 193, from the Upper Albian of Maniamba-amba (Madagascar) as a synonym of *Puzosia quenstedti* var. *Bonarellii* BREISTROFFER ["*Puzosia Quenstedti* PAR. et Bon. sp. (inclus. var. *Bonarellii* BREISTR. ... = *P. jacobi* COLLIGN.) ... : tours un peu plus hauts que larges, comme dans le métatype de QUENSTEDT (Pl. 17, fig. 13 b-d et ap. O. SEITZ 1932, Pl. 16, fig. 3 a-c) mais les constrictions sont moins superficielles et un peu plus courbées vers l'avant sur le pourtour externe, caractère annonçant la var. *media* SEITZ 1932 (Pl. 16, fig. 5a-b = *Desmoceras* "cf. *Emerici*" PAR. et Bon. 1897, Pl. 11, fig. 1a-c), à section subcirculaire"]. The non-figured species of COLLIGNON is characterized by the presence of 5-6 constrictions on the last preserved whorl that are strongly projected forward on the venter where they form a deep sinus. This feature does not fit the definition of *Puzosia quenstedti bonarellii* and so, *Puzosia jacobi* is removed from synonymy with *P. quenstedti bonarellii*.

Puzosia media SEITZ, 1932 (p. 402, Pl. 16, fig. 5a-b), is named from *Desmoceras* cf. *Emerici* in PARONA and BONARELLI (1897, p. 80(28), Pl. 11(23), fig. 1a-c), from the condensed Albian of Escragnolles. This specimen, about 35 mm in diameter, is characterized by a whorl section almost as wide as high, with rather convex flanks and a maximum width at about the inner third of the flanks, and the presence of 6 constrictions on the last preserved whorl that are slightly flexuous on the flanks, projected forward on the ventrolateral shoulders and that are concave on the venter. The specimen figured by SEITZ (1932, Pl. 16, fig. 5) shows only five constrictions which are not concave on the venter. In the collections of the University of Grenoble, *P. media*, known only by one specimen from Gourdon (Alpes-Maritimes) and another from Escragnolles, remains a poorly known taxon that we herein provisionally consider as a separate morphospecies. More investi-

gations are needed to establish whether or not it could represent an inflated variant of *P. quenstedti*.

The specimen identified as *Puzosia Majoriana* by PASSENDORFER (1930, Pl. III, figs. 57-58) re-identified as *Puzosia majoriana* by LEFELD (1984, p. 115, Pl. 42, fig. 1), as *Puzosia majoriana octosulcata* (SHARPE, 1857) by MAREK et al. (1989, p. 88, Pl. 43, fig. 1), and as *Puzosia quenstedti quenstedti* by MARCINOWSKI and WIEDMANN (1990, p. 54, Pl. 5, fig. 7), from the condensed Albian of Poland, is doubtfully referred to the present species.

Juvenile specimens from the Upper Albian of Angola, described as *Puzosia quenstedti* var. *angolana* HAAS, 1942 (p. 149, Fig. 20a-g, Pl. 37, figs. 2-9; Pl. 41, figs. 1-6), and *Puzosia quenstedti* var. *applanata* HAAS, 1942 (p. 151, Fig. 20h-j, Pl. 37, figs. 10-11; Pl. 41, figs. 7-8), are characterized by the presence of few, faint intercostae and rather involute coiling. The material described by HAAS requires revision following further analysis.

LUPPOV et al. (1949, p. 215, Pl. 62, fig. 1) figured a specimen from the Albian of Crimea that shows differences in ornamentation when the shell is preserved, including strong flexuous ribs, which are visible even on the inner half of the flanks rather than inconspicuous intermediate ribs on internal moulds, when shell is absent.

The undescribed, juvenile limonitic specimen, from the uppermost Albian of Aguas de busot (Spain), figured by LILLO BEVIÁ (1975, p. 685, Pl. 4, figs. 1-2, Pl. 8, fig. 4), with rather involute coiling (U/D at about 0.26), and depressed whorl section (Wb/Wh at about 0.33: measurements obtained from illustrative material), looks more like a *Desmoceras* sp. than a *Puzosia*, but ornamental detail cannot be discerned from the figuration.

Small juvenile, limonitic specimens briefly described by MARTÍNEZ (1976, p. 45, Pl. IX, fig. 1; 1979, p. 347, Fig. 7, Pl. I, fig. 7; 1982, Fig. 12, Pl. 4, fig. 12), from the Margas de Lluçà Formation, Serie Rio Flamisell, NE Spain (Middle Albian to Lower Cenomanian), cannot be identified at a species level and are herein provisionally excluded from the synonymy.

WIEDMANN and NEUGEBAUER (1978, p. 711, Pl. 2, fig. 1) figured as *Puzosia quenstedti* from the Upper Albian of the Angola Basin (DSDP Leg 40), a small complete specimen, about 28 mm in diameter: it is too small to be identified at species level.

The fragment figured by CHIRIAC (1981, p. 76, Fig. 27, Pl. 8, fig. 1a-b) from the Upper Albian of Seimeni, Romania, showing a strongly flexuous constriction that makes a deep chevron on the venter, probably belongs to an unidentified species of the *Puzosia majoriana* group *sensu* WIEDMANN and DIENI, 1968.

KHALILOV (1988, p. 358, Pl. 14, fig. 1) figured a poorly preserved specimen from the Middle Albian of Azerbaijan, with numerous flexuous constrictions and strong intermediate ribs, which cannot be assigned to species level.



The fragment from the uppermost Albian of Pont-de-Peille (Alpes-Maritimes) figured as *Puzosia* sp. aff. *quenstedti* (PARONA & BONARELLI) by DELANOY and LATIL (1988, p. 752, Pl. 1, fig. 7) is probably a fragment of a juvenile *Puzosia mayoriana*.

The small specimens depicted by FÖLLMI (1989, p. 136, Pl. 9, figs. 4-7) from the condensed Albian of Austria (Voralberger Garschella Formation) cannot be identified at species level.

A poorly preserved fragment figured as *Puzosia* cf. *quenstedti* by AGIRREZABALA et al. (1992, p. 154, Pl. 1, fig. 3), from the Upper Albian of NW Spain, with a reduced number of constrictions which seem to be flexuous on the flanks cannot be identified to species level and is herein excluded from the synonymy.

The two specimens from the Albian of Shapur (central Iran) figured by SEYED-EMAMI and IMMEL (1996, p. 10, Pl. 5, figs. 1-2) cannot be assigned to *P. quenstedti* with certainty. The ammonite figured Pl. 5, fig. 1, has only 5 constrictions at a diameter of 64 mm, and the specimen figured on Pl. 5, fig. 2, with its compressed section and more involute coiling appears closer to *Puzosia communis* SPATH, 1923.

The crushed specimens identified a *Puzosia* gr. *quenstedti* PARONA et BONARELLI by BRÉHÉRET et al. (1986, Pl. 8, fig. 1), and as *Puzosia quenstedti* by KENNEDY (2000) and BERT (2012) from the PAQUIER Level of southeastern France (Lower Albian, *Leymeriella tardefurcata* Zone), with well-marked riblets on the inner part of the flanks are in need of further investigations to confirm their taxonomic position. They are doubtfully assigned to the present species.

The material figured by BOGDANOVA and HOEDEMAEKER (2004, p. 240, Pl. 40, fig. 1; Pl. 43, fig. 2; Pl. 44) from the ?Albian of Anapoima-Apulo (Colombia), has measurements that do not fit the description of *Puzosia quenstedti*, with a narrower umbilicus (U/D between 0.23 and 0.25 cf. between 0.30 and 0.35 in *P. quenstedti*). These specimens, just like the specimen figured as *Puzosia hopkinsi* (FORBES) by BÜRGL (1958, p. 136, Pl. 10, fig. 1) should not even be assigned to the genus *Puzosia*.

The specimens identified and figured as *Puzosia* sp. group of *quenstedti* PARONA & BONARELLI by KENNEDY and KLINGER (2014, p. 6, Fig. 5) from the Upper Albian of South Africa, clearly differ from *P. quenstedti* by their oval whorl section with a maximal width at about the mid-flanks, their more compressed section and more involute coiling.

TAJKA et al. (2017, p. 28, Fig. 6 Z-AC) figured two juvenile specimens from the condensed Albian of In Ränken, Plona, Garschella

Formation; and Stütze 2 Säntisbahn S. (Switzerland) have a compressed whorl section (Wb/Wh at about 0.80) and constrictions that are too strongly projected forward on the venter, forming a deep sinus, features that are rather typical of the Upper Albian morphologies.

The fragment from the condensed Albian of the Kosmaj Mountain, central Serbia, figured by AYOUB-HANNA et al. (2018, p. 291, Figs. 10 G-J, 12 A-C), is very similar to *P. quenstedti*, from which it differs by a little more involute coiling and by probably fewer constrictions. An Upper Albian to basal Cenomanian age for this condensed level is given by the presence of mortoniceratids.

According to BREISTROFFER (1947, p. 77): "Le véritable lectogénotype de *Pleuropachydiscus* est l'*Ammonites Hoffmanni* GABB 1864 (p. 65, Pl. XI, fig. 13 : composite) = *Desmoceras Hoffmanni* STANT. 1894, ANDERS. 1902 pars (p. 94, Pl. X, fig. 203) = *Puzosia Hoffmanni* ANDERS. 1938 (p. 186, Pl. XLV, figs. 1-2). Très voisine de *P. Quenstedti* PAR. et BON. sp., cette espèce a un ombilic un peu plus ouvert que dans la var. *Bonarellii* BREISTR. ap. BE-SAIR. 1936, qui a des constrictions moins larges, limitées en arrière sur le pourtour externe par un bourrelet moins épais". MURPHY and RODDA (1978), revising the type material of *Puzosia hoffmanni*, designated a new lectotype and excluded the material figured by ANDERSON (1938, Pl. 45, figs. 1-2) from the synonymy of *P. hoffmanni*, claiming that this material belongs to an undescribed taxon. In any case, these two specimens from the upper beds of the Horsetown Group of ANDERSON (?Lower Albian), seem to differ from *P. quenstedti* only by their wider and deeper constrictions.

The presence of specimens belonging to the genus *Puzosia*, and bearing lateral lappets and/or a short siphonal rostrum, have been occasionally reported from the Lower-Middle Albian (ANDERSON, 1938; BERT, 2012). Such ammonites have been interpreted as microconchs (see also MARCINOWSKI, 1980). On the basis of the abundant material at our disposal, we have no evidence to confirm this hypothesis. The presence of a short rostrum would appear associated with morphologies showing constrictions forming ventral chevrons, that is, on the ammonites of the *Puzosia mayoriana* group of WIEDMANN and DIENI (MARCINOWSKI, 1980). In the genus *Puzosia*, the lateral lappets are known at various sizes and not always on adult body chambers: they can be observed as ghosts on the shell of several specimens of *Puzosia provincialis* PARONA & BONARELLI, 1897 (WIEDMANN & DIENI, 1968, Pl. 11, figs. 2, 4-5). To our knowledge, the only documented case of the presence of small lateral lappets on an Lower-Middle Albian adult morphology is on *Puzosia Buenaventura* ANDERSON, 1938 (Pl. 41, fig. 2), from the Lower Albian (upper *Leconteites lecontei* Zone to lowest *Brewericeras hulenense* Zone) of northern California.



Stratigraphic distribution. BREISTROFFER (1931, 1937, 1947; *in* BREISTROFFER & VILLOUTREYS, 1953) made several references to the presence of *Puzosia quenstedti* in the south-east of France within an interval from the uppermost Aptian to the Lower and Middle Albian. According to this study, *Puzosia quenstedti* is known with certainty from south-eastern France from an unknown stratigraphic level, between the Lower Albian and the basal Middle Albian of La Balme-de-Rencurel (Isère); from the *Douvilleiceras mammillatum* Superzone (Lower Albian) or the base of Middle Albian of Lieuche and from an unknown stratigraphic level, between the top of Lower Albian and the basal Upper Albian of Châteauneuf-Val-Saint-Donat (Alpes-de-Haute-Provence). *P. quenstedti* is also present at Escragnolles and Gourdon (Alpes-Maritimes), in an unknown stratigraphic level between the base of the *Douvilleiceras mammillatum* Superzone (Lower Albian) and the *Dipoloceras crista* statum Zone (base of the Upper Albian). The species is also known from the Lower Albian of la Frassette (Savoie) and Les Prés de Rencurel (Isère), from the Lower/Middle Albian of Peille (Alpes-Maritimes), and the Middle Albian of la Perte-du-Rhône (Ain).

Among the hundreds of specimens assigned to the genus *Puzosia* in collections, which were collected from the Upper Albian of the south-east of France, there is not a single specimen from the *quenstedti/bonarelli/media* complex.

The species is also known from the Middle Albian of Romania (PAUCA & PATRULIU, 1959), Middle Albian (*Hoplites dentatus* Zone) of Venezuela (RENZ, 1982), the Lower Albian of Komievitra, Madagascar (COLLIGNON, 1950), the Middle Albian of Berambo, Madagascar (BREISTROFFER, 1936), and the Lower Albian of Tunisia (LATIL, 2011). One of us (J.-L.L.) and Emmanuel ROBERT have seen the same morphologies within the *Douvilleiceras mammillatum* Superzone (Lower Albian) of Morocco.

Suborder Ancyloceratina WIEDMANN, 1966

Superfamily Douvilleiceratoidea

PARONA & BONARELLI, 1897

Family Douvilleiceratidae

PARONA & BONARELLI, 1897

Subfamily Douvilleiceratinae

PARONA & BONARELLI, 1897

Genus *Douvilleiceras* GROSSEVOIRE, 1894

Type species. *Ammonites mammillatus* SCHLOTHEIM, 1813, p. 111, ICZN specific name No. 764.

***Douvilleiceras* sp. juv. aff. *D. mammillatum* (SCHLOTHEIM, 1813)**

(Pl. 5, fig. 3)

Material. A crushed fragment of a pyritized juvenile specimen (UJF-ID.11000) with a length of 22 mm (Pl. 5, fig. 3).

Description. The whorl section is depressed. The ornament on the flanks is poorly preserved. The ventrolateral tubercle is divided into three to four spirally elongated clavi. The ventral sulcus is low. This juvenile specimen cannot be identified to species level. It gives a Lower Albian (*Douvilleiceras mammillatum* Superzone) to basal Middle Albian (*Leyeliceras lyelli* Subzone of the *Hoplites dentatus* Zone) age.

4. Conclusion

The study of *Puzosia quenstedti* carried out on the faunas from the Albian of Lieuche (Alpes-Maritimes) and from various deposits in SE France allows us to give a complete description of the ontogenetic development of this species, for which the maximum size is estimated to 450 mm in diameter. For the first time the adult stage of this species is described: which shows the appearance on the outer part of the body chamber of strong lateroventral tubercles and then strong ventral tooth-shaped spines. This study does not support the previous theory for sexual dimorphism within *Puzosia*.

Puzosia quenstedti, as herein understood, is a Lower Albian (*Douvilleiceras mammillatum* Superzone) to basal Middle Albian (*Hoplites dentatus* Zone) species. Faunas from the lower part of the Lower Albian (*Leymeriella tardefurcata* Zone), and the upper part of the Middle Albian are still to be investigated.

It is now clear that the proposition of SCHOLZ (1979) and WRIGHT and KENNEDY (1984), who nominate only one biospecies for *Puzosia*, cannot be accepted: to believe that an ammonite species can live for several tens of millions of years would be tantamount to admitting our inability to characterize its evolution. The taxonomy of the Albian species of *Puzosia* still remains unclear, mainly because the available material comprises juvenile, incomplete specimens.

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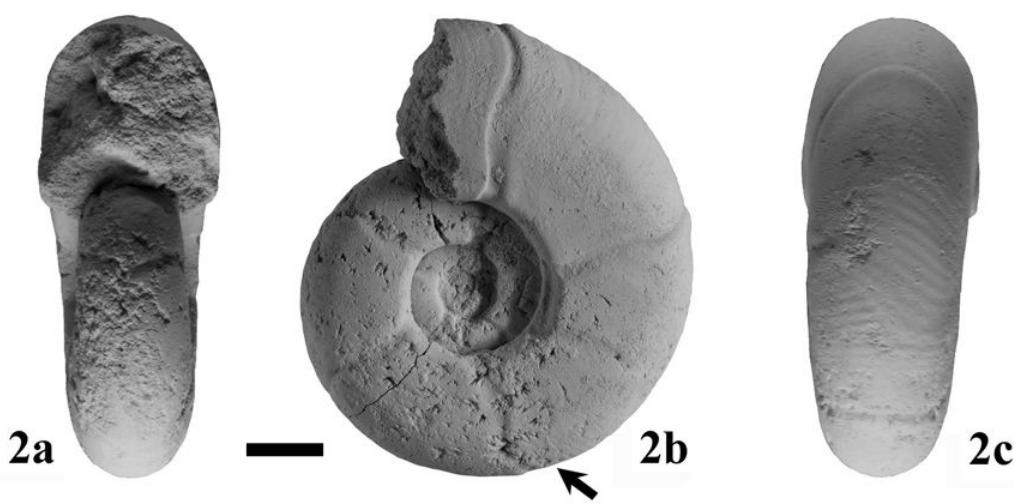
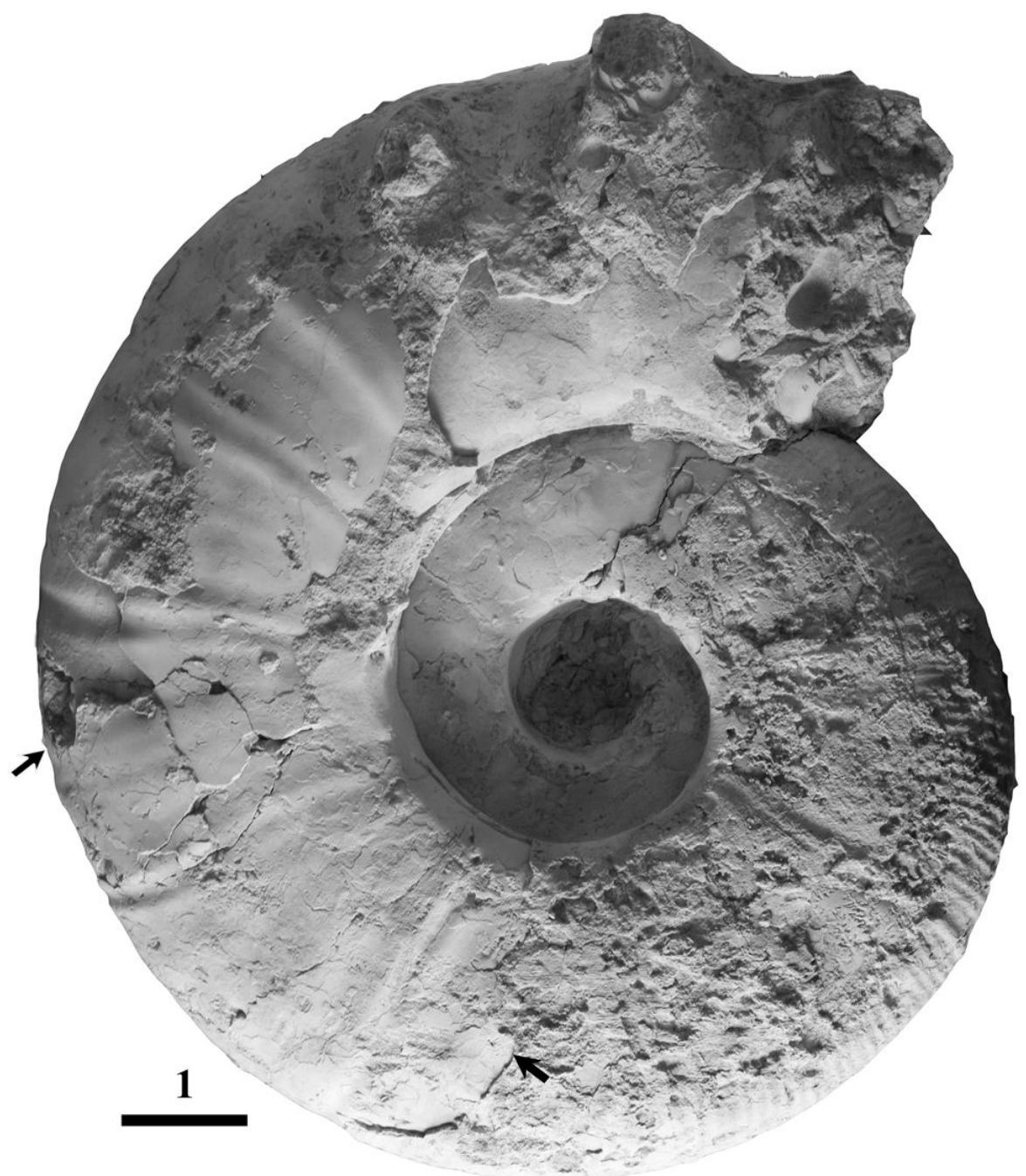
Plates

Plate 1:

Fig. 1: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.1068, coll. JACOB, condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère) (figured in JACOB, 1908, Pl. 6, fig. 2). Scale bar = 5 cm.

Fig. 2a-c: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10987, collector unknown, condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère). Scale bar = 1 cm.

The arrow indicates the end of the phragmocône.



**Plate 2:**

Fig. 1: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.1068, coll. JACOB, condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère) (ventral view of the specimen figured Pl. 1, fig. 1). Scale bar = 5 cm.

Fig. 2a-b: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10988, condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère). Scale bar = 1 cm.

Fig. 3a-b: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): holotype, PU20453, coll. Ist. Geol. Torino, from an unknown stratigraphic level between the base of the *Douvilleiceras mammillatum* Superzone (Lower Albian) and the *Diploceras cristatum* Zone (base of the Upper Albian). Scale bar = 1 cm.



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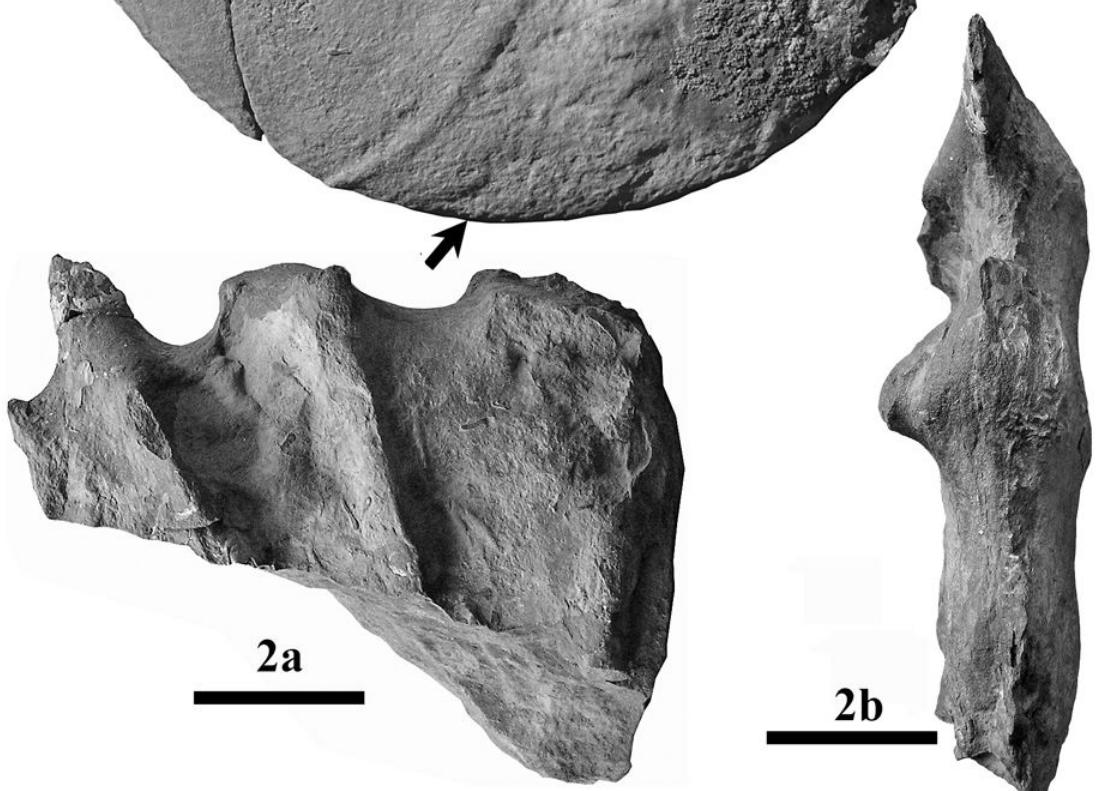


Plate 3:

Fig. 1: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10989, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieu-che (Alpes-Maritimes). Scale bar = 5 cm.

The arrow indicates the end of the phragmocône.

Fig. 2a-b: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): lateral and ventral view of the end of body chamber of specimen UJF-ID.10996, coll DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 5 cm.

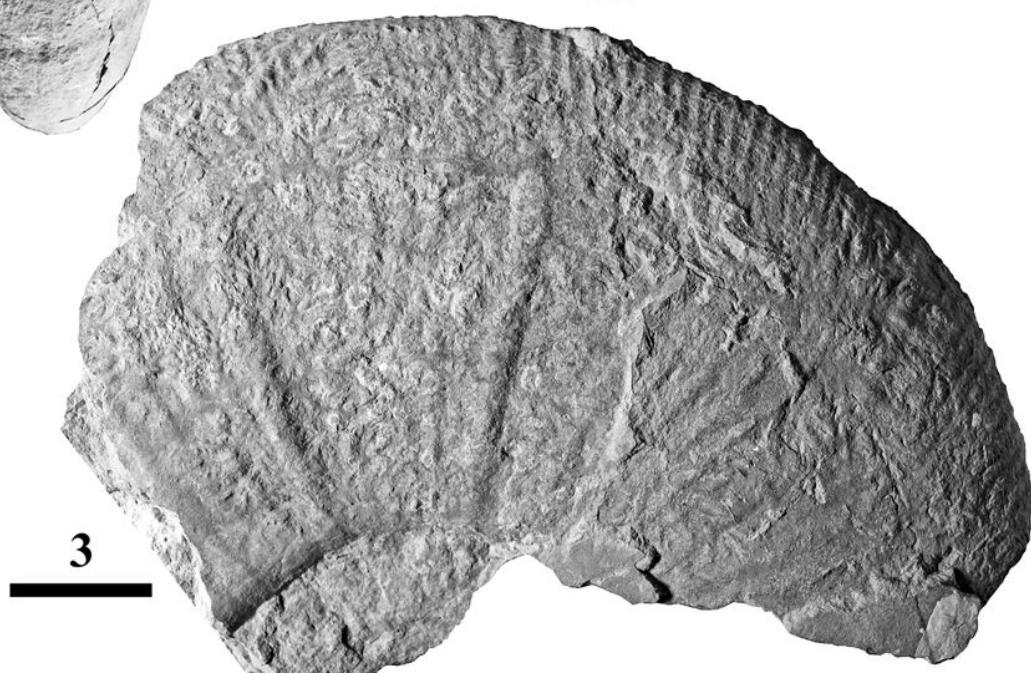


**Plate 4:**

Fig. 1: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): ventral view of the body chamber of specimen UJF-ID.10989 figured Pl. 3, fig. 1, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 5 cm.

Fig. 2: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10994, coll DELANOY & DELATTRE *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 5 cm.

Fig. 3: *Puzosia mayoriana* (ORBIGNY, 1841): UJF-ID.10999, coll. LATIL, Upper Albian, Montlaux (Alpes de Haute-Provence). Scale bar = 5 cm.



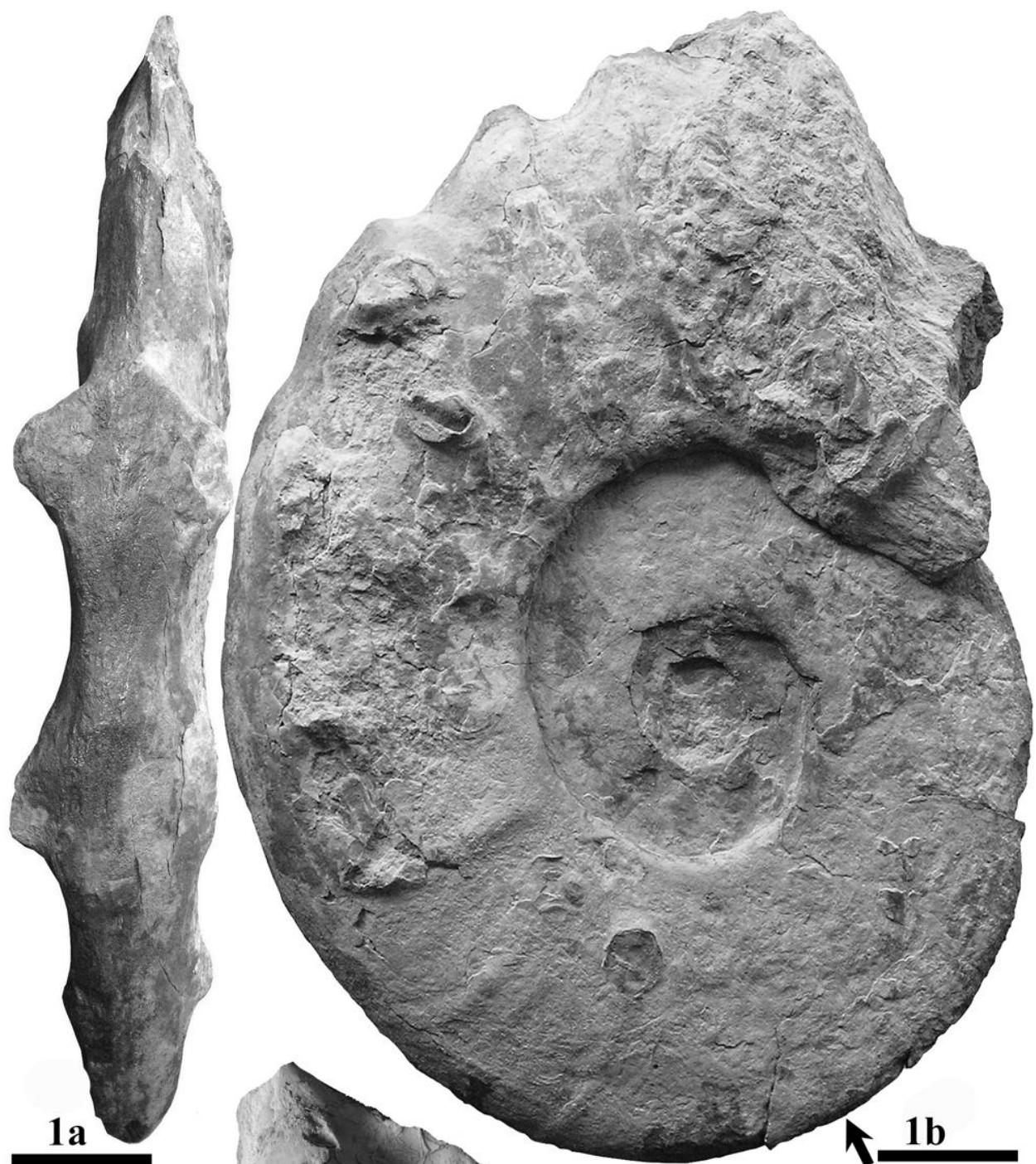
**Plate 5:**

Fig. 1a-b: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10995, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 5 cm.

Fig. 2: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): fragment of the end of the body chamber of the specimen UJF-ID.1066, coll. JACOB, condensed level comprising the *Douvilleiceras mammillatum* Superzone and the *Lyelliceras lyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère). Scale bar = 5 cm.

The arrow indicates the end of the phragmocône.

Fig. 3: *Douvilleiceras mammillatum* (SCHLOTHEIM, 1813): UJF-ID.11000, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 1 cm.



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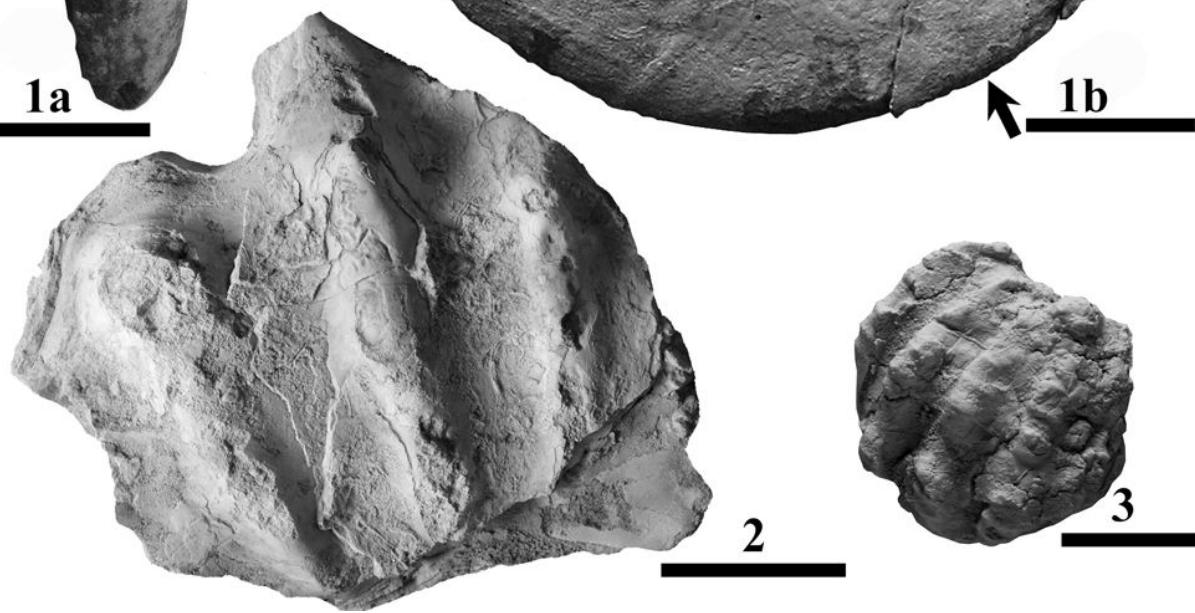




Plate 6:

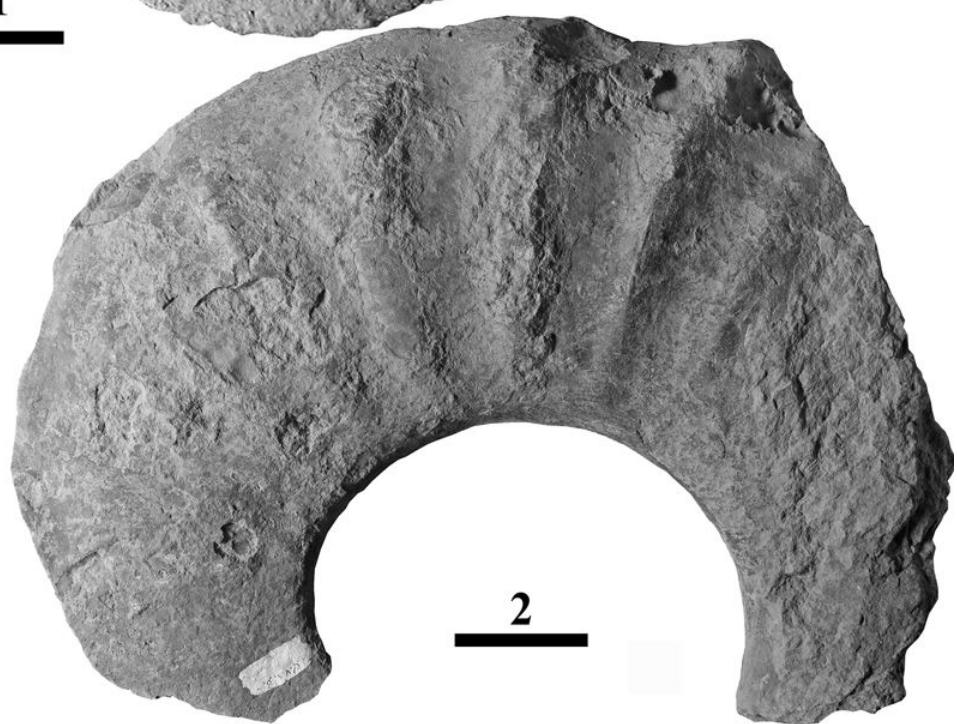
Fig. 1: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10991, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras lyelli* Subzone) (Lower Albian or basal Middle Albian), Lieu-che (Alpes-Maritimes). Scale bar = 5 cm.

Fig. 2: *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10998, coll. LATIL, Middle-basal Upper Albian of Châteauneuf-Val-Saint-Donat (Alpes-de-Haute-Provence, France). Scale bar = 5 cm.

The arrow indicates the end of the phragmocône.



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