Adult morphologies of Puzosia quenstedti (PARONA & BONARELLI, 1897) (Ammonoidea, Desmoceratidae) in the Albion 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 Albion of Lieuche (Alpes-Maritimes, France). Comparison with material from the condensed Albion 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 Albion 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 Albion 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 Albion (Douvilleiceras mammillatum Superzone) to a basal Middle Albion age (Hoplitites dentatus Zone).

Key-words:
• Vocontian basin;
• South-East France;
• ammonites;
• Albion;
• Puzosia;
• Douvilleiceras

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Résumé : Morphologies adultes de Puzosia quenstedti (PARONA & BONARELLI, 1897) (Ammonoidea, Desmoceratidae) dans l’Albien du Sud-Est de la France. Implications taxonomiques.- Plusieurs spécimens adultes appartenant au genre Puzosia BAYLE, 1878, ont été collectés dans l’Albien 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’Albien 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 Albien inférieur (Superzone à Douvilleiceras mammillatum) à Albien moyen basal (Hoplitites dentatus Zone).

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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’Albien". 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 the Aptian marls "supportent un niveau de grès glauconieux très durs qui doit représenter l’Albien". 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 Illons, where "Par- raturritites bergeri BRONGN., Anisoceras perarma- tum PICT. et CAMP., Stoliczkaia sp." were collected, indicating an uppermost Albian age (FAURE-MURET, 1953, p. 275).

In 1965, COTILLON described the Lower Creta- ceous in the regions of Daluis and Entrevaux. He recognized the monotonous character of the poorly fossiliferous, thick cretaceous series of the sedi- mental aureole of the Dôme de Barrot. The study of numerous sections, mainly on the basis of mi- cropaleaeontological 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 "Albien sticto sensu".

COTILLON (1971, p. 135-138) recognized that the Albian of the southern reverse of the Dôme of Barrot thickens from Daluis to the Gorge du Cians. Sedimentological and micropaleontological observations of the Albian of the northern flank of the To- ron ravine at Rigaud show the presence of two thick sandy-glauconitic limestone beds: A lower one of Middle Albian age, and an upper unit, begin- ning in the Middle Albian and ending in the upper- most 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 Lauves. 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 up- permost 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.

Mots-clefs :
- bassin vocontien ;
- Sud-Est de la France ;
- ammonites ;
- Albian ;
- Puzosia ;
- Douvilleiceras
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-limestone 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 nautiloid genus was also recovered by one of us (G.D.).
Figure 2: A - View of the Lieuche 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 between 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 of 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 Desmocerotidae 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 Douvillé, 1879, p. 91.

= *Pleuropachydiscus hyatt*, 1900, p. 571


= *Matsumotoceras hoepen*, 1968, p. 158

*Type species.* *Matsumotoceras donilisteri hoepen*, 1968, p. 158, fig. 1a, Pl. I (OD).

= *Puzosiella egian*, 1969, p. 174

*Type species.* *Puzosiella minuta egian*, 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 unresol

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* Perpinquière, 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);
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).
null
? 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. 93-L.
non 2017 *Puzosia* (Puzosia) quenstedti quenstedti (PARONA & BONARELLI); TAJIKA et al., p. 28, Fig. 6 Z-AC.
? 2018 *Puzosia quenstedti* (PARONA & BONARELLI); AYOVOS-HANNA et al., p. 291, Figs. 10 G-J, 12 A-C.

**Emended diagnosis.** Juvenile with modera-
tedly involute coiling (U/D between .30 and .35), slightly higher than wide, whor section, 5-7 constrictions by whor that are very slightly flexuous on the flanks, concave on the ventro-
terolateral shoulders and slightly convex on the ven-
ter. The number of constrictions per whor in-
creases with age numberings 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 termin-
ating with huge ventrolateral tubercles, the third one developing a ventral swelling. Two to three ribs close to the aperture, without ventro-
terolateral tubercles, develops huge ventral spines. Largest known size at about 450 mm of diame-
ter.

**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 den-
tatus* Zone (Lyelliceras lyelli Subzone) (Lower Albian or basal Middle Albian); 7 phosphatized specimens from La Balme de Rencurel (Isère, Albian or basal Middle Albian); *Puzosia* (Puzosia) sp., group of quenstedti (PARONA & BONARELLI); speci-
mens from La Balme de Rencurel (Isère, Albian or bas-
al Middle Albian); 7 phosphatized specimens from Lieuche (Alpes-Maritimes, France), as crushed and distorted internal moulds, from

**Largest known size at about 450 mm of diameter.**

**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 sec-
ond 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 Mid-

dle and basal Upper Albian ammonites. Since the stratigraphic position of the type of *P. quenstedti* is uncertain within the section, its age remains un-
clear, between the base of the *Douvilleiceras mam-
millatum* Superzone (Lower Albian) and the *Diplo-
ceras cristatum* Zone (base of the Upper Albian).

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

<table>
<thead>
<tr>
<th>Specimen no.</th>
<th>D (mm)</th>
<th>Wh (mm)</th>
<th>Wb (mm)</th>
<th>U (mm)</th>
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<td>14.0</td>
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<td>1.07</td>
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<tr>
<td>UJF-ID.1068</td>
<td>285.0</td>
<td>?</td>
<td>?</td>
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</tbody>
</table>

(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 pre-
served 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 prorosiradiate constrictions on the last preserved whor. 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.

**Holotype.** *Desmoceras Quenstedti* PARONA & BONARELLI, 1897, p. 81, Pl. 11(2), fig. 3, refig-
ured 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. UPU20453.

The type specimen is a juvenile phragmo-
cone, 38 mm in diameter, preserved as a phos-
phatized internal mould with some remains of

**Table 1 :** Measurements of *Puzosia quenstedti* (in mm). Lievece specimens are not included in the table because of their post-mortem deformation.
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 ventral 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 ribs 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 spiral elongated swelling. The next one bears a small ventrolateral tubercle and a huge spirally elongated ventral spine.

**Material from Lieuche** (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 Lieuche 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 Ana puzosia, 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 Ana puzosia". 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.
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 periumbilical 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 erasmusi Hoeven, 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/Wh = 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 mayoriana as defined by WIEDMANN and DIENI (1968).

Puzosia quenstedti var. bonarellii BREITROFFER, 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 BREITROFFER (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 BREITROFFER ["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 PARONAND BONAREL (1897, p. 80(28), Pl. 11(23), fig. 1a-c), from the condensed Albian of Escargolles. 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 Escargolles, remains a poorly known taxon that we herein provisionally consider as a separate separate morphospecies. More investigations are needed to establish whether or not it could represent an inflated variant of P. quenstedti.

The specimen identified as Puzosia Mayoriana by PASSENDORFER (1930, Pl. III, figs. 57-58) re-identified as Puzosia mayoriana by LEFELD (1984, p. 115, Pl. 42, fig. 1), as Puzosia mayoriana octosulcata (SHARPE, 1857) by MAREK et al. (1989, p. 88, Pl. 43, fig. 1), and as Puzosia quenstedti quenstedti by ARCINOWSKI 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 BEVIA (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 MARTINEZ (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 constrictions that makes a deep chevron on the venter, probably belongs to an unidentified species of the Puzosia maioriana group sensu WIEDMANN and DIENI, 1968.

KHÀLÌLOV (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 DELANDY and LATIL (1988, p. 752, Pl. 1, fig. 7) is probably a fragment of a juvenile Puzosia mayoriana.

The small specimens depicted by FÖLMLI (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-EMAMIAND IM-MEL (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 ribs 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 BODANANOVA and HOSEMMAKER (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 middle flanks, their more compressed section and more involute coiling.

TAJIK et al. (2017, p. 28, Fig. 6 2-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 AYOOBHANNA 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 possibly fewer constrictions. An Upper Albian to basal Cenomanian age for this condensed level is given by the presence of mortoniceratids.

According to BREISTRÖFFER (1947, p. 77): "Le véritable lectogénotype de Pleurophadysdiscus est l’Ammonites Hoffmanni GABB 1864 (p. 65, PL XI, fig. 13 : composite) = Desmoceras Hoffmanni SART 1894, ANDERS. 1902 pars (p. 94, PL IV, 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 omniblic un plus ouvert que dans la var. Bonarellia BREISTR ap. BEI. 1936, qui a des constrictions moins larges, limitées en arrière sur le pourtour externe par un bourrelet moins épais". MURPHY HDODA (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. hoffmani, 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 WIEMMANN 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 (WIEMMANN & 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 hulinense 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 southeast 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 Diploceras cristatum 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 southeast 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 & Patru, 1959), Middle Albian (Hoplites dentatus Zone) of Venezuela (Renz, 1982), the Lower Albian of Comie-vitra, Madagascar (Collignon, 1950), the Middle Albian of Beramag, 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 Wiemmann, 1966
Superfamily Douvilleiceratoidea
Parona & Bonarelli, 1897
Family Douvilleiceratidae
Parona & Bonarelli, 1897
Subfamily Douvilleiceratinae
Parona & Bonarelli, 1897
Genus Douvilleiceras Grossouvre, 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 (Lyellliceris iyelli 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 ontogenic 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 latero-ventral 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 tardiurata 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 nominated 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 it. 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 *Dipoloceras cristatum* Zone (base of the Upper Albian). Scale bar = 1 cm.
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), Lieuche (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 (*Lyellliceras 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 (*Lyellliceras 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 iyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 5 cm.

The arrow indicates the end of the phragmocône.

**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 iyelli* Subzone (upper part of Lower Albian and base of Middle Albian), La Balme de Rencurel (Isère). Scale bar = 5 cm.

**Fig. 3:** *Douvilleiceras mammillatum* (SCHLOTHEIM, 1813): UJF-ID.11000, coll. DELANOY & DELATTRE, *Douvilleiceras mammillatum* Superzone- *Hoplites dentatus* Zone (*Lyelliceras iyelli* Subzone) (Lower Albian or basal Middle Albian), Lieuche (Alpes-Maritimes). Scale bar = 1 cm.
Plate 6:

**Fig. 1:** *Puzosia quenstedti* (PARONA & BONARELLI, 1897): UJF-ID.10991, coll. DELANOV & DELATRE, *Douvilléiceras 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 Châ- teauneuf-Val-Saint-Donat (Alpes-de-Haute-Provence, France). Scale bar = 5 cm.

The arrow indicates the end of the phragmocône.