

New insights on the genus *Prolyelliceras* SPATH, 1930 and the identity of *Acanthoceras gevreyi* JACOB, 1907 (Cephalopoda, Ammonitina)

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With 3 figures

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Abstract: *Acanthoceras gevreyi* JACOB, 1907 originates from a condensed Albian horizon at La Perte du Rhône, Bellegarde (Ain, France). This species is still very poorly known and its taxonomic interpretation in the literature is most often erroneous. New and abundant material from SE France, North Africa and South America allows the revision of this taxon and shows that *Lyelliceras flandrini* DUBOURDIEU, 1953, is one of its minor subjective synonyms. As a consequence the systematic position, stratigraphic range and palaeobiogeographic distribution of *Acanthoceras gevreyi* JACOB are discussed. *Prolyelliceratidae* fam. nov. is proposed.

Key words: Ammonoidea, Cretaceous, Albian, taxonomy, revision.

1. Introduction

This contribution originates from the examination of the type material of *Acanthoceras gevreyi* JACOB, 1907 (p. 37) as a contribution of the forthcoming revision of the genus *Prolyelliceras* SPATH, 1930. A search through the collections of the Institut Dolomieu (Grenoble), the Museum of Natural History (Geneva) and the University Claude Bernard (Lyon) revealed a series of ammonites from the south-east of France that is clearly referable to the poorly known *Prolyelliceras gevreyi* (JACOB, 1907).

Recent investigations in central Tunisia (JAILLARD et al. 2005; LATIL 2005), allow a revision of both *Acanthoceras gevreyi* JACOB, 1907 and *Lyelliceras flandrini* DUBOURDIEU, 1953, on the basis of new and abundant material. The study of these ammonites, which were commonly referred by authors to the

genus *Lyelliceras* SPATH, 1922, confirms the hypothesis of homoeomorphy of the genera *Lyelliceras* and *Prolyelliceras* (LATIL 1995; LATIL & DOMMERGUES 1997).

Moreover, recent field data (KENNEDY et al. 2000; LATIL 2005) allow to precise the age of these faunas. New material from Peru described by ROBERT (2002) allows a better understanding of the genus *Prolyelliceras*.

2. Origin and age of the material studied

South Eastern France and Austria. – The material from SE France originates mainly from historic collections now stored at the Institut Dolomieu of the University of Grenoble. The best preserved specimens are from the Lower Albian condensed levels of the Vercors Plateau (BREI-

STROFFER, 1931), Jurassic and North Provencal Platform (COTILLON 1971; DELAMETTE 1988). Additional, but rare, specimens were collected from the Paquier Level (Lower Albian, *Leymeriella tardefurcata* Zone) of the Marnes Bleues Formation of the Vocontian Basin (KENNEDY 2000). The same assemblages were also described from a similar level in Austria (KENNEDY & KOLLMANN 1979). Most specimens from South-East France are from the Early Albian condensed level of Les Prés de Rencurel (Isère).

Algeria and Tunisia. – *Lyelliceras flandrini* DUBOURDIEU, 1953 (herein considered as a minor subjective synonym of *Prollyelliceras gevreyi*) was originally described from the Lower Albian of the Monts de Mellègue (Algeria). The studied material includes sixteen specimens from Algeria (including the originals from DUBOURDIEU 1953) and seventy-two specimens from Tunisia, mostly preserved as crushed, calcareous, adult internal moulds. The Albian age has been disputed in the literature (DUBOURDIEU 1953, 1956; MEMMI 1999). As already pointed out by LATIL (2005), the *Prollyelliceras* fauna was not collected from a condensed level, as suggested by DUBOURDIEU (1953) and KENNEDY (2000), but in an expanded section of several tens of meters.

An equivalent fauna was most recently collected by one of us (J.L.L.) in the nearby outcrops of northern Tunisia (Djebel Hameima) (JAILLARD et al. 2005). In this section, *Prollyelliceras gevreyi* ranges from bed HMA-52 to bed HMA-68, which represents a total thickness of about 80 m. A thin limestone bed (HMA-63), marked by an erosional surface at its base and containing phosphatic pebbles, occurs about 65 meters above the base of this interval. This erosional surface is interpreted as sequence boundary (JAILLARD et al. 2005). HMA-63 is correlated with level 3 of Djebel Def and the SW Ouenza sections, and probably with the base of level 3 of the Bou Khadra section (DUBOURDIEU 1956). At Djebel Def (Algeria), *Prollyelliceras gevreyi* was collected from a thin

phosphatized bed (0.50 m), but at SW Ouenza, Djebel Def and Bou Khadra, the main fauna comes from the marls that cap the phosphatized bed.

In the Hameima section, *Prollyelliceras gevreyi* (Fig. 2j, m) co-occurs with *Mirapelia advena* KENNEDY, 2000 in bed HMA-57, and with *Mirapelia* cf. *alticarinata* (SPATH, 1922) in bed HMA-67-68. It should also be noted that at the base of its range (bed HMA-52), *Prollyelliceras gevreyi* co-occurs with the last Acanthohoplitinae. *Mirapelia advena* is known from the *Leymeriella tardefurcata* Zone of the South-East of France and Austria; and *Mirapelia alticarinata* is known from the *Cleonicerias floridum-Otohoplites raulinianus* subzones of England. Therefore, we can reasonably assume that the interval from bed HMA-52 to bed HMA-68 can be correlated with upper part of the *Leymeriella tardefurcata* Zone and lower part of the *Douvilleicerias mammillatum* Zone of the Mediterranean Province (*Sonneratia chalcensis* Zone of the Anglo-Paris Basin).

Venezuela. – A single specimen (NHMB.J29129, Fig. 1i, j) from the Lower Albian Machiques Formation of the Perija foothills, Quebrada Santa Rosita, Venezuela (= *Prollyelliceras flandrini* (DUBOURDIEU) in RENZ 1982: 32, text-fig. 20, pl. 4, fig. 3) has been collected with a primitive member of *Parengonoceras* SPATH, 1924. This association probably belongs to the lower part of *Douvilleicerias mammillatum* Zone of the Mediterranean Province.

Peru. – A single specimen (UJF-ID.12149) from Baños del Inca (Dept. Cajamarca, Peru) (ROBERT 2002: 142, pl. 19, figs. 3-5) (Fig. 1k, l), was collected in association with engonoceratids and prolyelliceratids from the lowermost part of the *Glottoceras raimondi* Zone (bed 7 of the Banos del Inca section in Robert 2002, fig. 40), above *Neodeshayesites* beds and below a level with primitive *Mirapelia*. It should be noted that a similar association of primitive representatives of *Prollyelliceras*, *Mirapelia* and engonoceratids was found in Algeria (DUBOURDIEU 1953) and Tunisia (LATIL 2005). These biostratigraphic data

Fig. 1. *Prollyelliceras gevreyi* (JACOB, 1907), from the Lower Albian of South America. a, b, UJF-ID.10714, from Portillo, (Apulo-Viota area, Cundinamarca, Colombia); c, d, UJF-ID.10600, same locality as above; e, f, UJF-ID.10602 same locality as above; g, h, UJF-ID.10601, from Sierra del Capote (Apulo-Viota area, Cundinamarca, Colombia); i, j, NHMB.J29129, from the Quebrada Santa Rosita (Perija foothills, Venezuela); k, l, UJF-ID.12149 from Banos del Inca (Dpt. Cajamarca, Peru); m-p, *P. peruvianum* SPATH, 1930, neotype, AMNH 35364 from level 8 of Sihuas section, SE of Trujillo, Peru. – All figures x 1.

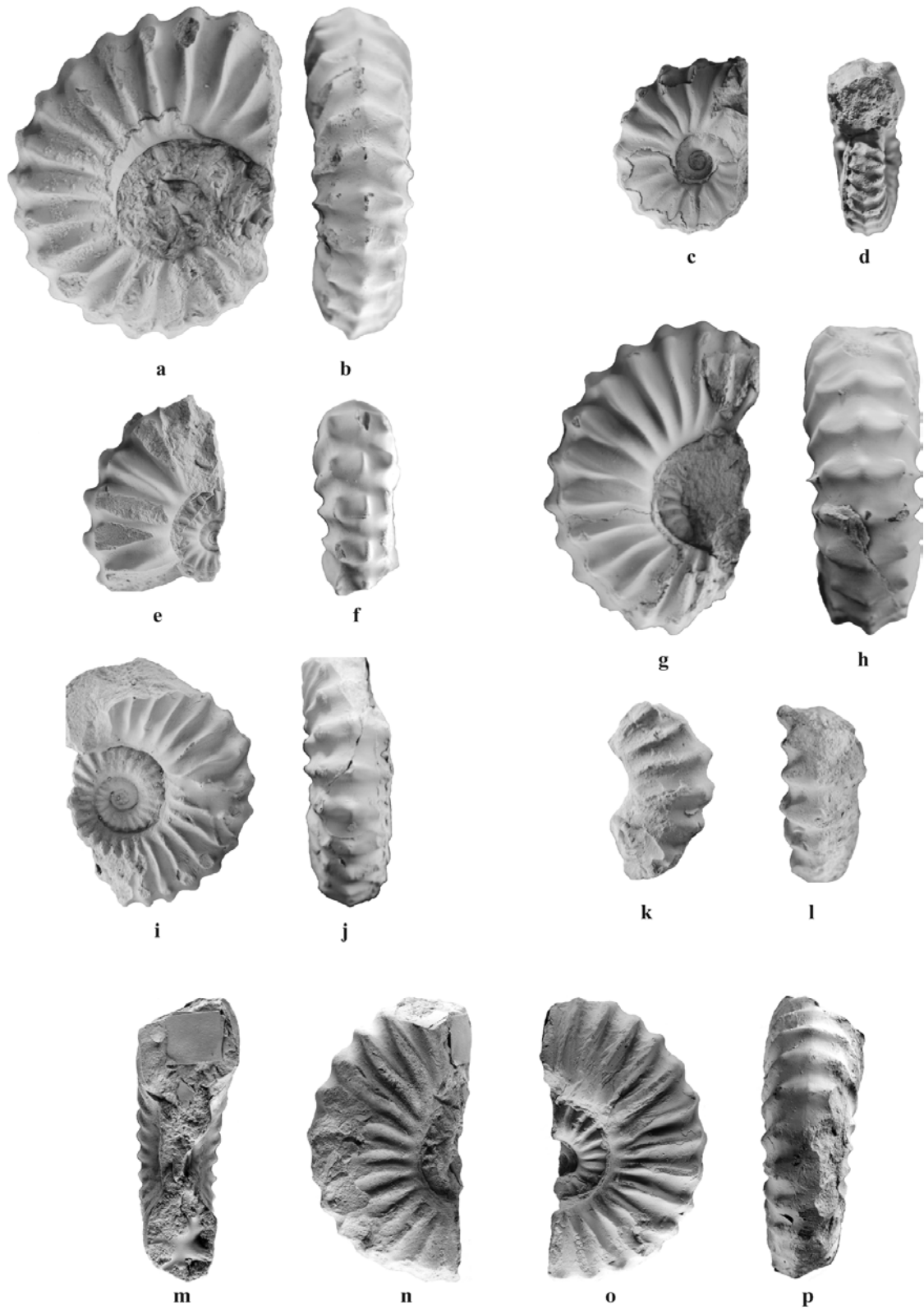


Fig. 1 (Legend see p. 338)

support the long-range correlations between North Africa and South America based on depositional sequences (JAILLARD et al. 2005).

Colombia. – The collections of the Institut Dolomieu (Grenoble) revealed several specimens, from the many collected by Maurice BREISTROFFER in the late 40's and early 50's in the Cundinamarca region of Central Colombia, that have remained mostly undescribed until now. The material is perfectly preserved, but lacks detailed stratigraphic data. The stratigraphic distribution of the Colombian specimens can only be deduced by comparison with the Peruvian material mentioned above, and the specimen figured by BÜRGL (1955, see discussion below).

Abbreviations: All dimensions of specimens are given in millimetres: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter, dc = distance between two ribs at ventro-lateral edge. Figures in parentheses are dimensions as a percentage of the diameter at the point of measurement. The suture terminology is that of KORN et al. (2003): E = external lobe; A = adventive lobe; U = umbilical lobe, I = internal lobe.

The following acronyms are used to indicate the repositories of specimens mentioned in the text: UJF-ID: Université Joseph Fourier, Institut Dolomieu, Grenoble; FSL: Université Claude Bernard, Lyon; NHMB: Naturhistorisches Museum Basel, Switzerland; MHNG, Muséum d'Histoire Naturelle de Genève, Switzerland, ENSM: Ecole Nationale Supérieure des Mines; AMHN: American Museum of Natural History, New York.

3. Systematic palaeontology

Order Ammonoidea ZITTEL, 1884

Suborder Ammonitina HYATT, 1889

Superfamily Acanthoceratoidea DE GROSSOUVRE,
1894

Family *Prolyelliceras* fam. nov.

Discussion: WRIGHT et al. (1996) consider *Prolyelliceras* (including *Ralphimlayites*) as Lyelliceratinae. The taxonomic analysis discussed below shows that all Andean species previously referred to *Prolyelliceras* SPATH, 1930

and *Ralphimlayites* ETAYO SERNA, 1979 do not have any phylogenetic relationship with Lyelliceratinae, e.g. the *Tegoceras* – *Lyelliceras* lineage established by LATIL (1995) and LATIL & DOMMERGUES (1997).

It is now clearly established that the earliest members of *Prolyelliceras* occur in the *Leymeriella tardefurcata* Zone of SE France and Austria (KENNEDY 2000). As already pointed out by LATIL (1995) a common origin of the “*Prolyelliceras* complex” with the Lyelliceratinae must be dismissed. As a consequence, *Prolyelliceras* has to be excluded from Lyelliceratinae. Pending a better understanding of the phylogenetic relationships between *Prolyelliceras* and other Acanthoceratoidea from the lowermost Albian, such as the earliest Brancoceratidae, we propose to introduce the new family *Prolyelliceratinae*. As herein understood, *Prolyelliceratinae* is monogeneric and retains the species listed below.

Genus *Prolyelliceras* SPATH 1930

(= *Ralphimlayites* ETAYO SERNA, 1979: 81, type species *R. prorsocurvatum* (GERHARDT, 1897) by original designation).

Type species: *P. peruvianum* SPATH, 1930, by original designation of SPATH 1930: 65 (= *Acanthoceras prorsocurvatum* (non GERHARDT) R. DOUVILLÉ, 1906: 144, pl. 2, fig. 1. The type specimen is supposed to be preserved in the former ENSM collections, now at Lyon University (FSL). Despite a careful examination of the DOUVILLÉ collection from South America, we have been unable to locate the specimen and it is believed to be lost. Since *Prolyelliceras peruvianum* SPATH was never described by DOUVILLÉ (1906) nor by SPATH (1930), *Prolyelliceras* could be regarded as a *nomen dubium* and we therefore designate the specimen AMNH 35364 in BENAVIDES CACERES 1956, pl. 50 fig. 4 (from level 8 of Sihuas section, SE of Trujillo, Peru) as the neotype (Fig. 1m-p).

Diagnosis: Slightly compressed and high whorled with radiate to prorsiradiate, straight to flexuous ribs, with ribs continuous across venter or in some flattened on it at early growth stages. Ventrolateral and siphonal clavi subordinate to ribs. No lateral tubercles on primitive morphologies. Outer lateral punctiform to clavate tubercles in evolute species during middle growth, perhaps not disappearing completely on body chamber. Inner lateral punctiform tubercles in most evolute species restricted to young and middle growth stages.

Fig. 2. *Prolyelliceras gevreyi* (JACOB, 1907), from the Lower Albian of type locality and North-Africa. a, b, MHNG.54405 from Bellegarde (Ain, France); c, d, MHNG AV-38-19053, the holotype from the same locality; e, f, FSL.596674 from Bou Khadra (Algeria); g, h, FSL.596652 from the same locality; i, FSL 596651, from Djebel Def (Algeria); j, UJF-ID.10712 from the Lower Albian, bed RR.59, Hameima, Tunisia; k, FSL 596639, from Djebel Def (Algeria); l, FSL 596638, from Djebel Def (Algeria); m, UJF-ID.10713 from the Lower Albian, bed RR.59, Hameima, Tunisia; n, *Prolyelliceras gevreyi* (JACOB, 1907), suture after DUBOURDIEU 1953, fig. 9. x 10. – Fig. 2a, b, e-h, j, m: x 1; Figs. 2c, d, i, k, l: x 2.

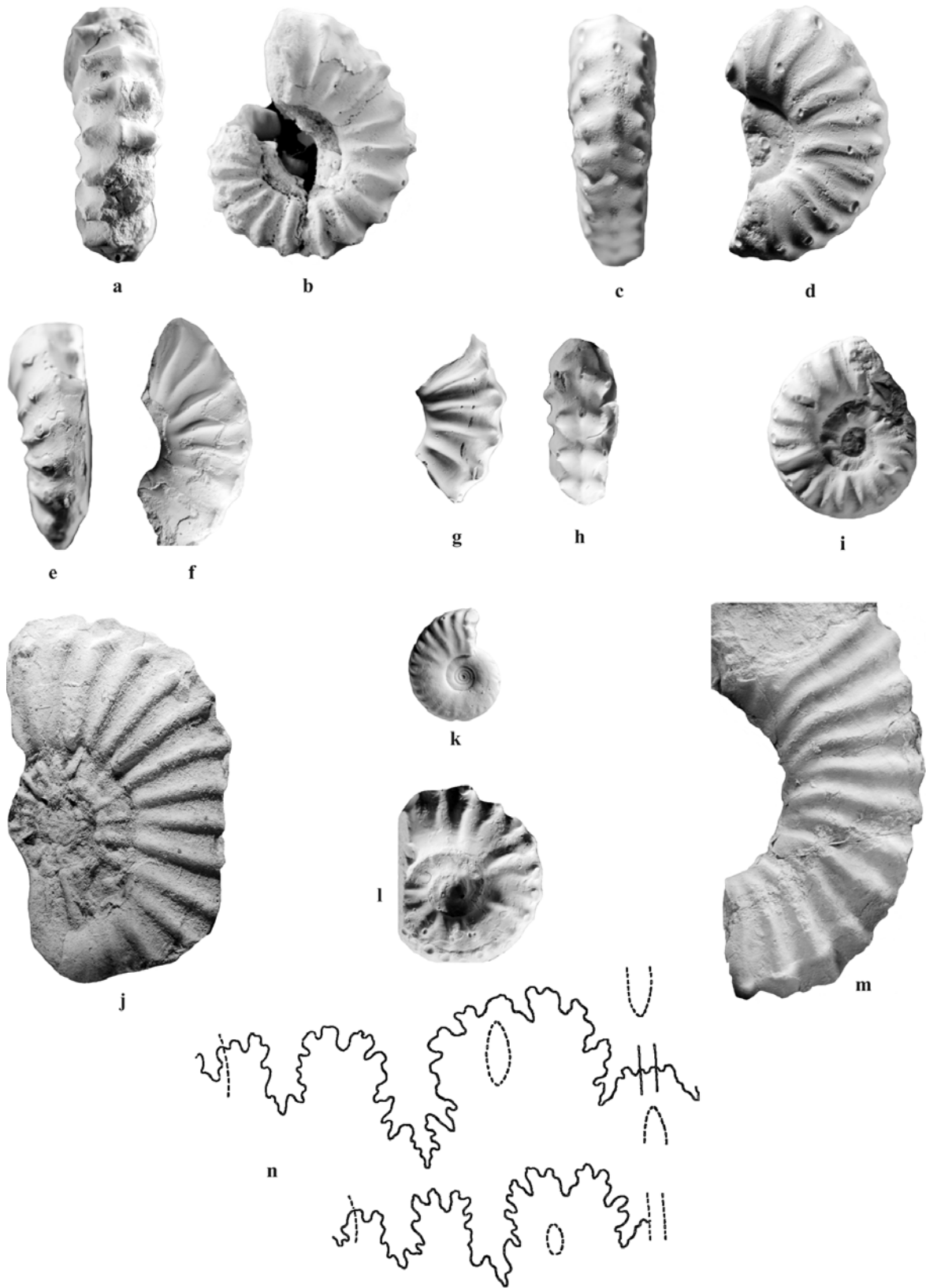


Fig. 2 (Legend see p. 340)

Discussion: The occurrence of *Polyelliceras* was already suspected in the early Lower Albian of SE France and Algeria (LATIL 1995; KENNEDY 2000), but its relationship with the Andean species of the *Polyelliceras peruvianum* group was never investigated.

As herein accepted, *Polyelliceras* includes the following species from the literature: *P. peruvianum* SPATH, 1930: 65; *P. prorsocurvatum* (GERHARDT, 1897: 168, text-fig. 16, pl. 4, fig. 8a-b); *P. gevreyi* (JACOB, 1907: 37); *P. radenaci* (PERVINQUIÈRE, 1907: 251, pl. 12, fig. 4); *P. lobatum* (RIEDEL, 1938: 57-59, pl. 9, figs. 9-11); *P. mathewsi* (KNECHTEL, 1947: 101, pl. 21, fig. 3); *P. ulrichi* (KNECHTEL, 1947: 99, pl. 23, fig. 1); *P. flandrini* (DUBOURDIEU, 1953: 32, pl. 3, figs. 6-50); *P. apuloense* (ETAYO SERNA, 1979: 81, pl. 9, fig. 6); *P. isaacleai* (ETAYO SERNA, 1979, p. 80-81, pl. 11, fig. 1); *P. carvajalorum* (ETAYO SERNA, 1979: 79-80, text-fig. 8h-i, pl. 11, fig. 5); *P. pseudolyelliforme* (ETAYO SERNA, 1979: 80, pl. 9, fig. 5, text-fig. 8E) and *P. alternum* (ROBERT, 2002: 152-153, pl. 21, figs. 7-9, pl. 22, figs. 1-3). This complex has yet to be revised.

Stratigraphic and geographic distribution: Lower Albian of North Africa (Algeria, Tunisia), and Europe (France, Austria). Lower to early Middle Albian of South America (Venezuela, Colombia, Peru).

Polyelliceras gevreyi (JACOB, 1907)

Figs. 1-3

- 1860 *Ammonites Lyelli* LEYMERIE. – PICTET & CAMPICHE, p.198, pl. 24, fig. 7 only.
- 1907 *Acanthoceras gevreyi*. – JACOB, p. 37.
- 1953 *Lyelliceras flandrini*. – DUBOURDIEU, p. 27, text-fig. 9, pl. 3, figs. 6-22.
- 1953 *Lyelliceras flandrini* var. *crenulata*. – DUBOURDIEU, p. 32, pl. 3, figs. 23-35.
- 1953 *Lyelliceras flandrini* var. *media*. – DUBOURDIEU, p. 32, pl. 3, figs. 36-41.
- 1953 *Lyelliceras* aff. *flandrini*. – DUBOURDIEU, p. 32, pl. 3, figs. 42-45.
- 1953 *Lyelliceras* aff. *flandrini* var. *media*. – DUBOURDIEU, pl. 3, figs. 46-50.
- 1955 *Lyelliceras prorsocurvatum* GERHARDT. – BÜRGL, p. 15, pl. 4, fig. 3.
- 1979 *Leymeriella* (*Leymeriella*) *pseudoregularis* SEITZ. – KENNEDY & KOLLMANN, p. 8 (*pars*), pl. 5, figs. 3, 5, 7, 10 only.
- 1986 (?) *Leymeriella* (*Leymeriella*) *pseudoregularis* SEITZ. – BRÉHERET et al., pl. 8, fig. 3.
- 1982 *Polyelliceras flandrini* (DUBOURDIEU). – RENZ, p. 32, text-fig. 20, pl. 4, fig. 3.
- non 1982 *Polyelliceras gevreyi* (JACOB). – RENZ, p. 38, pl. 5, fig. 13.
- 1995 *Lyelliceras flandrini* DUBOURDIEU, 1953. – LATIL, p. 367, text-figs. 32-33.
- 1995 Gen. indet. – LATIL, fig. 31, pl. 3, fig. 25.
- 2000 '*Polyelliceras*' *flandrini* (DUBOURDIEU). – KENNEDY, p. 681, figs. 44a, c, d, 47g, i, k, m.
- 2002 *Polyelliceras* sp. – ROBERT, p. 144-145, pl. 19, figs. 3-5.

Holotype: JACOB (1907: 37) has presented *Acanthoceras gevreyi* as *nomen novum* for PICTET & CAMPICHE 1860, fig. 7, pl. 24. The original was identified as specimen MNHG AV-38-19053b and is the holotype by monotypy (PICTET Collection from La Perte du Rhône, Bellegarde (Ain, SE France), a condensed level of Albian age) (Fig. 2c, d).

Diagnosis: A species of *Polyelliceras* of rather small adult size (D of about 80mm in larger specimens). Rounded ventral area. Ribs rising at umbilical edge, tending to become coarser and wider on outer third of flank toward the venter. Strong, spirally elongated ventro-lateral and siphonal tubercles throughout ontogeny. Simplified suture line EAU2U11, moderately incised, with exceptionally broad, massive, somewhat bifid E/A, wide A/U2 and U2/U1.

Material examined: The holotype (MHNG AV-38-19053) from Bellegarde (Ain, France) (Fig. 2c, d), MHNG. 54405 from the same locality (Fig. 2a, b), 1 specimen from Saint-André-les-Alpes (Alpes de Haute-Provence, France), ID 10603 from Les Combettes (Isère, France) (Fig. 3c, d), ID 10604 from Peille (Alpes Maritimes, France) (Fig. 3a, b), ID 10605 from La Frasette (Isère, France) (Fig. 3o, p), FSL 13931 from Les Rimets (Rencurel, Isère), 28 specimens (ID) from Les Près (Rencurel, Isère, France) including ID 10606-611, 10711 (Fig. 3e-n, q-u), UJF-ID. 12149 from Banos del Inca (Dept. Cajamarca, Peru) (Fig. 1k, l), 5 specimens (ID) from San Luis (Apulo-Viota area, Cundinamarca, Colombia) including ID 10600 and ID 10602, ID 10714 from Portillo, (Apulo-Viota area, Cundinamarca, Colombia) (Fig. 1a-f), one specimen (ID.10601) from Sierra del Capote (Apulo-Viota area, Cundinamarca, Colombia) (Fig. 1g, h); NHMB.J29129, from the Quebrada Santa Rosita (Perija foothills, Venezuela) (Figs. 1i, j); FSL 596636-41, 44, 49, 51, from Djebel Def (Algeria) (Fig. 2i, k, l), FSL.596652, 56, 74, from Bou Khadra (Algeria) (Fig. 2e-h), FSL.596658, 59, 61, 63 from Djebel Ouenza (Algeria), UJF-ID.10712-13 and 68 still unregistered specimens from Djebel Hameima (Tunisia) (Fig. 2j, m).

Description: 33 specimens from the south-east of France preserved as phosphatized, juvenile or pre-adult internal moulds, 16 specimens from Algeria, preserved as juvenile and pre-adult pyritized internal moulds, and about 70 specimens from Tunisia, mostly preserved as crushed, calcareous, adult internal moulds. They range in diameter from 5 mm to an estimated 75 mm. Coiling is moderately evolute, tending to become evolute with age, U/D comprising between 0.28 (for the holotype) to 0.41. Umbilical wall rounded and low. Moderately compressed to slightly depressed oval to sub-ogival whorl section, Wb/Wh ranging from 0.78 to 1.07. Whorl section shows high level of variability, Wb/D ranging from 0.27 to 0.42, Wh/D from 0.31 to 0.42. It should be noted that the holotype represents an extreme morphology, with a high-whorled section (Wh/D = 0.41) and a narrow umbilicus (U/D = 0.28).

Innermost whorls, to about 5 mm in diameter, are nearly smooth, occasionally showing a faint siphonal keel. At 5-10 mm in diameter (Fig. 2k), prorsiradiate, slightly flexuous, irregular ribs appear on flanks, ending with feeble,

Dimensions:	D	Wb	Wh	U	dc/Wh	Wb/Wh
S.E. France:						
Holotype	23 (100)	8 (0.35)	9.5 (0.41)	6.5 (0.28)	0.35	0.84
MHNG.54405	38 (100)	13.5 (0.36)	13.5 (0.36)	15.5 (0.41)	0.35	1.00
FSL.13931	33 (100)	10.5 (0.32)	13 (0.40)	10.5 (0.32)	0.38	0.81
UJF-ID.10605	22.5 (100)	7 (0.31)	8.3 (0.37)	7.9 (0.35)	0.43	0.84
ID.10604	32 (100)	10.5 (0.33)	12.3 (0.38)	11.5 (0.36)	0.57	0.85
ID.10603	29 (100)	11.5 (0.40)	11 (0.38)	9.5 (0.33)	0.47	1.05
ID.10606	17 (100)	7.2 (0.42)	6.7 (0.39)	5.8 (0.34)	0.54	1.07
ID.10607	20 (100)	6.5 (0.32)	8.3 (0.42)	6 (0.30)	0.39	0.78
ID.10609	22 (100)	7.5 (0.34)	8.8 (0.40)	7.2 (0.33)	0.57	0.85
ID.10610	16.5 (100)	5.4 (0.33)	6 (0.36)	5.8 (0.35)	0.37	0.90
ID.10611	34 (100)	11 (0.32)	10.5 (0.31)	14 (0.41)	0.57	1.05
Algeria:						
FSL. 596651	15 (100)	4 (0.27)	5.3 (0.35)	6 (0.40)	0.42	0.75
FSL.596639	10.5 (100)	3.2 (0.30)	4.4 (0.42)	3 (0.29)	0.30	0.72
FSL.596638	16 (100)	5 (0.31)	6.5 (0.41)	6.2 (0.39)	0.46	0.77
Venezuela:						
NHMB.J29129	41 (100)	14.5 (0.35)	15 (0.36)	15.5 (0.38)	0.40	0.97
Colombia:						
UJF-ID unreg.	56 (100)	17 (0.30)	19.4 (0.35)	21.5 (0.38)	0.41	0.88
UJF-ID.10600	30 (100)		12 (0.40)	8.3 (0.28)	0.48	
UJF-ID.10601	54 (100)	17.5 (0.32)	20 (0.37)	19 (0.35)	0.29	0.88

spirally elongated clavi, sometimes crossing the ventral area with a tendency to be projected forward. The ventral area shows a crenulate keel, which tends to be rapidly replaced by a row of spirally elongated clavi, displaced adaperturally, or not, of the ventro-lateral clavi.

Beyond 10 mm in diameter, irregular ribbing is progressively replaced by the more typical adult ornament, made with sharp, single, straight or slightly flexuous, radial to prorsiradiate ribs, rising at the umbilical edge, tending to become coarser and wider on the outer third of the flank. Ribs develop strong, spirally elongated, ventro-lateral clavi, and generally cross over the ventral area, tending to become wider, shallower and coarser.

Rib density is highly variable on juveniles, dc/D ranging from 0.11 to 0.23, and increases suddenly on adult stages (dc/D = 0.08-0.11 beyond 40 mm in diameter) (Fig. 2j, m).

Suture EAU2U1I, moderately incised, with exceptionally broad, massive, somewhat bifid E/A, wide A/U2 and U2/U1 and no visible auxiliary saddle. Suture of the present species differs from those of *Lyelliceras* by having a reduced number of saddles and much wider E/L (Fig. 2n).

Discussion: DUBOURDIEU (1953) pointed out the affinities of *L. flandrini* and *L. gevreyi*. *L. flandrini* was said to differ to *L. gevreyi* by a more depressed whorl section, stronger ventro-lateral tubercles, higher ribs and innermost whorls with irregular ribbing. The Algerian sample, characterized by high level of variability in shape and ornament, was compared to a single poorly figured specimen. Our material clearly shows that both French and Algero-Tunisian material show enhanced plasticity, especially at early ontogenetic stages.

Juvenile morphologies range from compressed, feebly ornamented shells (UJF-ID.10711, Fig. 3n) to depressed, strongly ribbed forms (UJF-ID.10606, Fig. 3t, u).

UJF-ID.10605 (Fig. 3o, p), from the Late Aptian – Early Lower Albian condensed bed of La Frassette (Isère), is characterized by a compressed section and lack of ornamentation on the flanks at a rather large diameter (about 10 mm).

MHNG.54405 (Fig. 2a, b) represents another extreme morphology – with strong tuberculation, elevated, coarse, wide ribs that cross over the ventral area without attenuation. Irregular ribbing and attenuated tuberculation at the end of the last whorl is teratological.

This revision shows that the type specimen of *P. gevreyi* represents the compressed variant, whereas *L. flandrini* morphologies are dominant in the populations studied. The “*Prollyliceras*”-like morphologies of *Lyelliceras pseudo-lyelli* (PARONA & BONARELLI, 1897) and *Lyelliceras lyelli* (D’ORBIGNY, 1841) described by LATIL (1995) and LATIL & DOMMERGUES (1997) are homoeomorphs of *Prollylicera gevreyi*. They differ from *Prollyliceras gevreyi* in having punctiform siphonal tubercles and ribs that do not cross the ventral area.

Andean specimens differ mainly by showing attenuated ornament on juveniles, increase of rib density at smaller diameters and rather punctiform ventro-lateral and ventral clavi. These differences may be of taxonomic significance, but since intermediate forms with elongated tubercles seems to occur (UJF-ID.10602, Fig. 1e, f), we prefer to place the Andean samples within *Prollyliceras gevreyi*.

Prollyliceras gevreyi (JACOB) (RENZ 1982: 38, pl. 5, fig. 13) from the Middle Albian of Venezuela represents a

morphology of *Lyelliceras lyelli* (LEYMERIE in D'ORBIGNY, 1841) that lacks tuberculation on flanks (LATIL 1995).

The most closely related Andean species are *Prolyelliceras peruvianum* and *Prolyelliceras lobatum*, most probably representing two different growth stages of the same species (compare the specimen illustrated by BENAVIDES CACERES (1956 pl. 50, fig. 4) with the early whorls of the holotype of *Prolyelliceras lobatum* figured by RIEDEL 1938, pl. 9, fig. 9-11). *Prolyelliceras gevreyi* differs from the *Prolyelliceras* of the *peruvianum* – *lobatum* plexus by its smaller adult size, persistence of ventrolateral tubercles on the body chamber, subquadratic whorl section and less complex suture line. All other species of *Prolyelliceras* show one or two lateral rows of tubercles including *Prolyelliceras radenaci* (PERVINQUIÈRE, 1907) from the Lower Albian of Tunisia.

Occurrence: *Prolyelliceras gevreyi*, as understood herein, has a widespread geographical distribution that covers Western Europe (SE France, Austria), North Africa (Algeria, Tunisia) and South America (Colombia, Peru and Venezuela). This species is of Lower Albian age. Specimens from SE France are known from the lowermost Albian (*Leymeriella tardefurcata* Zone of the Mediterranean Province). Specimens from Tunisia are known from above the Acanthoplitinid beds (lower part of *Douvilleiceras mammillatum* Zone Mediterranean Province). The Peruvian specimen occurs above the *Neodeshayesites* beds (*Neodeshayesites nicholsoni* Zone) in the lower part of the *Glottoceras raimondii* Zone (*Parengonoceras ebrayi* biohorizon). This level correlates with the *Douvilleiceras mammillatum* Zone of the Mediterranean Province. The species is herein reported from Colombia for the first time, but has already been illustrated by BÜRGL (1955, pl. 4, fig. 4) as *Lyelliceras prorsocurvatum*. Most specimens before us do not have any stratigraphic data, but BÜRGL's individuals were collected with *Neodeshayesites* of the *karsteni* group.

4. Conclusions

On the northern margins of Tethys, *Prolyelliceras gevreyi* is known from the lowermost Albian (*Leymeriella tardefurcata* Zone) in Austria and South East France, where it co-occurs with *Leymeriella tardefurcata* (D'ORBIGNY, 1841) and the genus *Hypacanthoplitites* SPATH, 1923. In the candidate GSSP sections in SE France (KENNEDY 2000), the first

occurrence of *P. gevreyi* is close to the first occurrence of *Leymeriella tardefurcata*, and it could therefore be regarded as a secondary marker for the first occurrence of *L. tardefurcata*, but this species remains scarce and its range is unknown.

In Tunisia, the first-known occurrence of *Prolyelliceras gevreyi* strictly corresponds with the last occurrence of Acanthoplitinae (bed 52 at Hameima). The last-known occurrence of *Prolyelliceras gevreyi* is slightly above the first occurrence of *Mirapelia* cf. *alticarinata* (SPATH, 1922) (bed 67 at Hameima). In Tunisia, the range of *P. gevreyi* (about 90 m) starts in the upper part of the *Leymeriella tardefurcata* Zone, and ends in the lower part of the *Douvilleiceras mammillatum* Superzone (*Sonneratia chalcensis* Zone).

If the ammonite zonation proposed by KENNEDY (2000) is accepted, the co-occurrence of *P. gevreyi* and Acanthoplitinae characterizes the base of the Albian Stage. In contrast, if the ammonite zonation proposed by OWEN (2002) is retained, the *P. gevreyi*-Acanthoplitinae association characterizes the uppermost part of the *Leymeriella tadefurcata* Zone, and the association *Douvilleiceras*-Acanthoplitinae can be used to characterize the earliest Lower Albian. In any case, *P. gevreyi* alone cannot be used as a marker for the base of the Albian Stage in Tunisia and South America.

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Fig. 3. *Prolyelliceras gevreyi* (JACOB, 1907), from the condensed Lower Albian SE France. a, b, UJF-ID.10604 from Peille (Alpes Maritimes, France); c, d, UJF-ID. 10603 from Les Combettes (Isère, France); e, f, UJF-ID. 10611 from Les Près (Rencurel, Isère, France); g-i, UJF-ID.10607 from the same locality; j-l, UJF-ID.10609 from the same locality; m, UJF-ID.10608 from the same locality; n, UJF-ID.10711 from the same locality; o, p, UJF-ID.10605 from La Frasette (Isère, France); q-s, UJF-ID. 10610 from Les Près (Rencurel, Isère, France); t, u, UJF-ID. 10606 from the same locality. – All figures x 2.

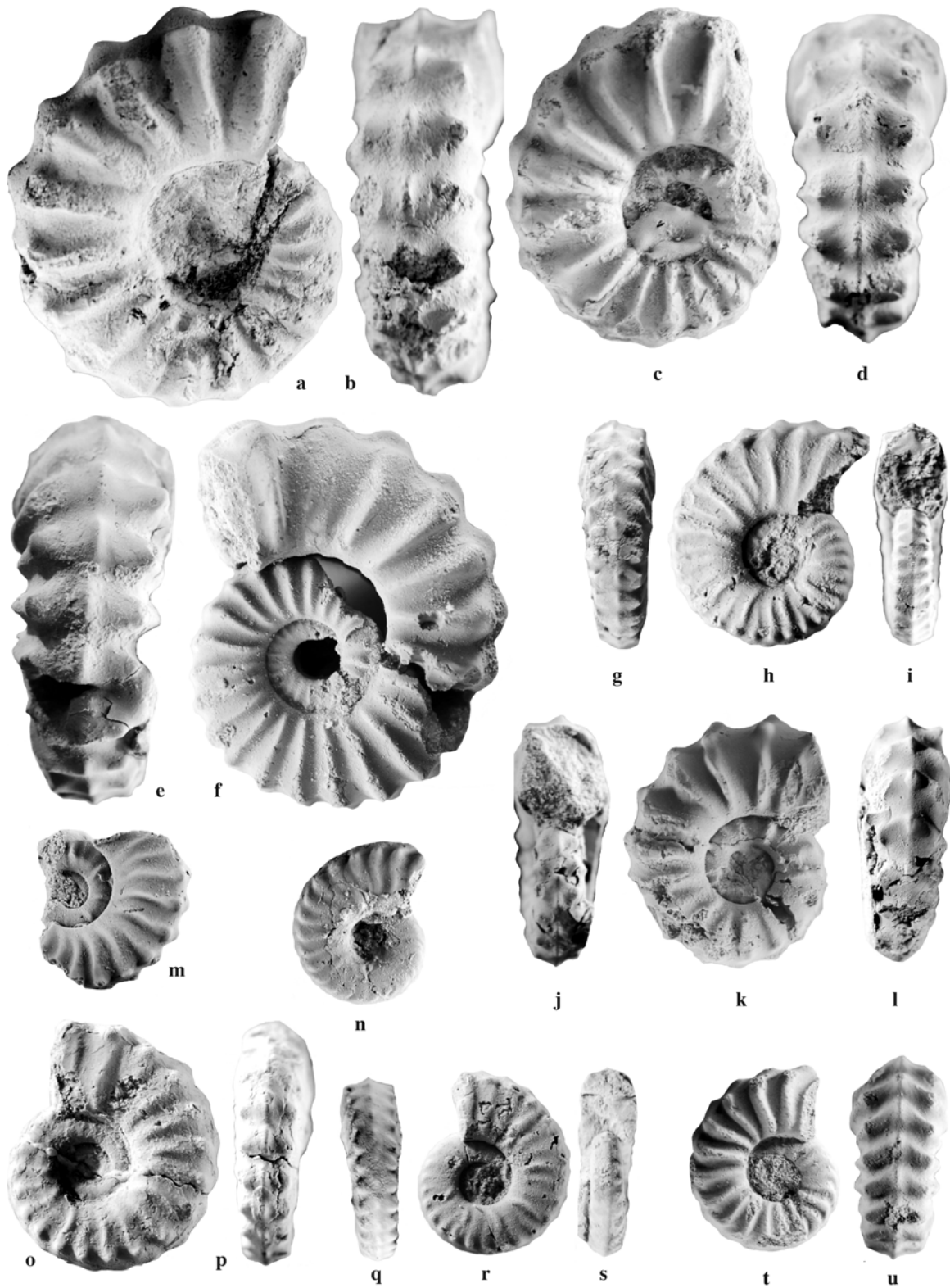


Fig. 3 (Legend see p. 344)

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