

# Cretaceous faunas from Zululand and Natal, South Africa.

## The ammonite subfamily Lyelliceratinae Spath, 1921

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The Lower and basal Middle Albian ammonite Subfamily Lyelliceratinae Spath, 1921 is reviewed, and restricted to the genera *Tegoceras* Hyatt, 1903, *Lyelliceras* Spath, 1921, and *Pseudobrancoceras* Kennedy, 2004. An evolutionary origin in Brancoceratinae Spath, 1934 is proposed. The South American taxa from Colombia and Peru referred to *Tegoceras*, *Lyelliceras*, *Prollyelliceras* Spath, 1930b, and its synonym *Ralphimlayites* Etayo-Serna, 1979, are lyelliceratine homoeomorphs, derived independently from Brancoceratinae. The North African '*Prionotropis*' *radenaci* Pervinquière, 1907 is tentatively referred to *Prollyelliceras*, while '*Lyelliceras*' *flandrini* Dubourdiou, 1953 is a further lyelliceratine homoeomorph subgenerically or generically distinct from *Prollyelliceras*. The following are described from KwaZulu: *Tegoceras mosense* (d'Orbigny, 1841), *T. collignoni* (Breistroffer, 1953), *T. camatteanum* (d'Orbigny, 1841), *Lyelliceras lyelli* (d'Orbigny, 1841), *L. pseudolyelli* (Parona & Bonarelli, 1897), *L. latili* sp. nov., and *Pseudobrancoceras versicostatum* (Michelin, 1838). On the basis of this revision, a sequence of four faunas are recognized, characterized, successively, by the presence of 1: *Tegoceras gladiator* and *Aioloceras*, 2: *Tegoceras camatteanum*; 3: *Lyelliceras pseudolyelli*, and 4: *Lyelliceras lyelli*, the appearance of the last-named marking the base of the Middle Albian Substage.

**Key words:** Ammonites, Lyelliceratinae, Cretaceous, KwaZulu, South Africa.

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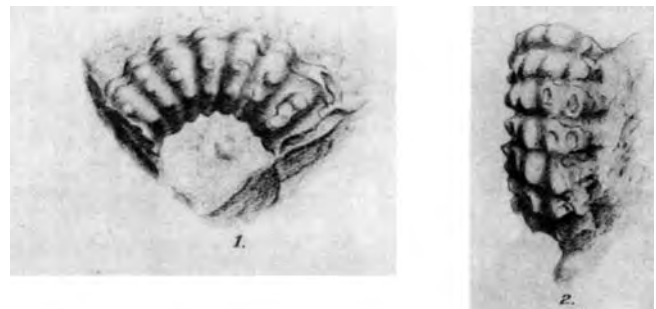
### INTRODUCTION

Members of the ammonite subfamily Lyelliceratinae Spath, 1921 are key stratigraphic indicators for the recognition of the Lower–Middle Albian boundary, currently defined on the basis of the first appearance of *Lyelliceras lyelli* (d'Orbigny, 1841) (Hart *et al.* 1996). Lyelliceratines are known from scattered localities in KwaZulu-Natal, north of the Mzinene River, in the Mkuze Game Reserve, and in the Ndumu area. Among the early accounts of ammonites from KwaZulu, *Douvilleiceras* (?) *nodosa* Etheridge, 1907 (p. 87, pl. 4, figs 1, 2), from a locality on the Mzinene [Umsinene] River is a fragment of a *Lyelliceras lyelli* (Fig. 1).

### COMPOSITION AND TAXONOMIC POSITION OF THE LYELLICERATINAE

Figure 2 shows the known distribution of genera and species relevant to the present discussion, based on records in

western Europe and the southern United States. The distribution of species of *Tegoceras*, *Lyelliceras* and *Pseudobrancoceras* in western Europe was clarified in the careful



**Fig. 1.** The holotype of *Douvilleiceras* (?) *nodosa* Etheridge, 1907, a *Lyelliceras lyelli* (d'Orbigny, 1841), from an outcrop along the Mzinene River in KwaZulu.

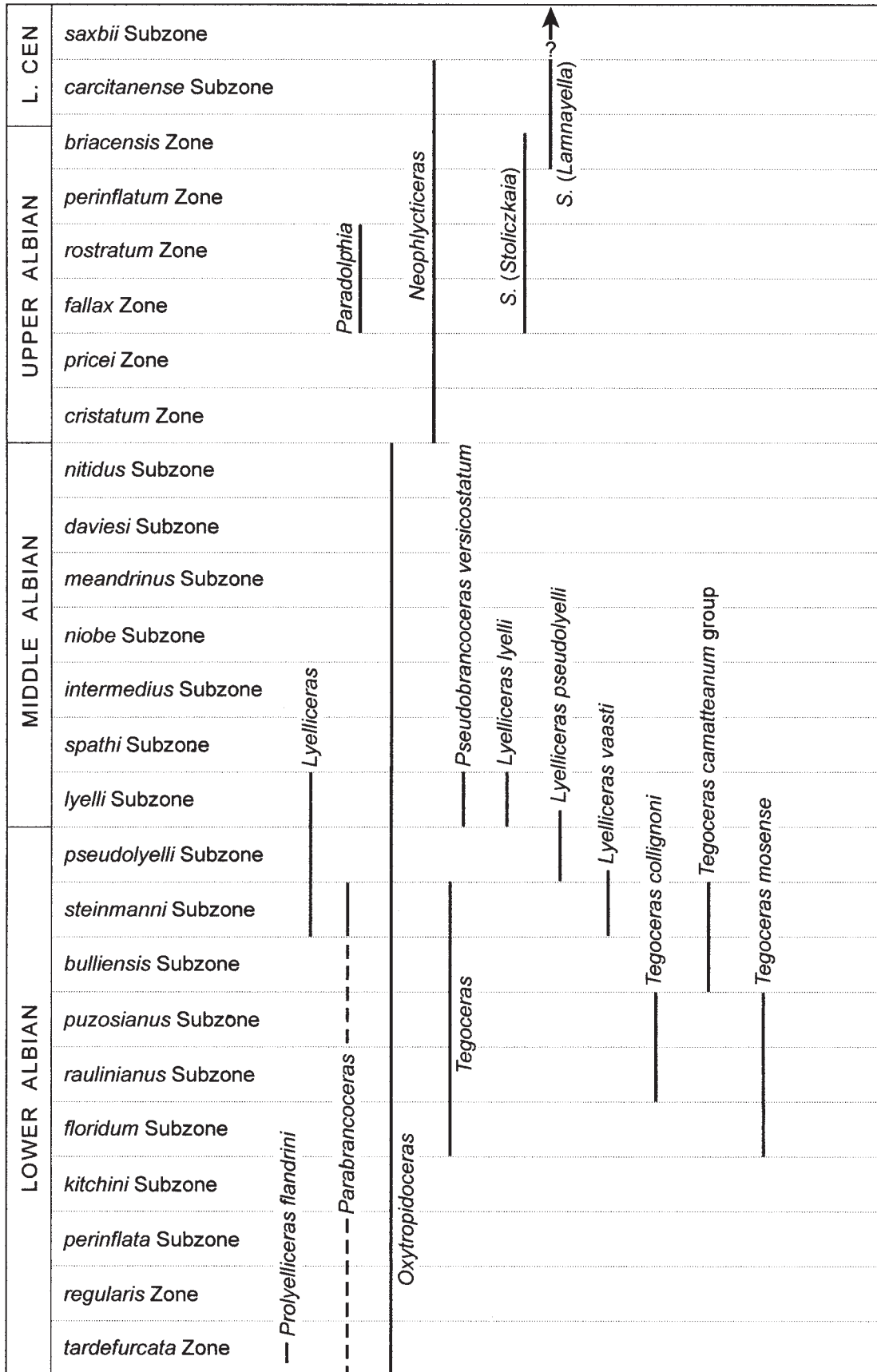


Fig. 2. Known stratigraphic ranges of genera and species of Lyelliceratinae, Stoliczkaia, and other key taxa in northwest Europe, plotted against the standard zonal/subzonal sequence.

studies by Destombes *et al.* (1973), Destombes (1977a,b; 1979), Amédéo (1992), Latil (1995) and Latil & Dommergues (1997). Later studies by Kennedy (*in* Kennedy *et al.* 2000) in southeast France revealed the first occurrences of three key genera, *Brancoceras*, '*Prollyelliceras*', and *Oxytropidoceras* at a much lower level than previously known: in the *Leymeriella tardefurcata* Zone (Fig. 2). The distribution of representatives of the Stoliczkaiinae shown in Fig. 2 is based on Wright & Kennedy (1994), Kennedy & Delamette (1994), and ongoing work in southeast France.

Cooper (1992) presented what he termed a phylogenetic analysis of this group, based on a cladistic approach. He concluded that the families Lyelliceratinae, Forbesiceratinae and Flickiidae formed a monophyletic group, for which he introduced the superfamily Lyelliceratoidea [as Lyellicerataceae]. Cooper further subdivided the Forbesiceratinae into Forbesiceratinae and Neophlycticeratinae Cooper, 1992, and included Stoliczkaiinae in the family because 'they are morphologically closer to Neophlycticeratinae'. He stated that the Lyelliceratoidea [Lyellicerataceae] was ancestral to the Acanthoceratoidea [Acanthocerataceae], leaving the Leymeriellidae and Brancoceratidae as the Superfamily Brancoceratoidea [Brancocerataceae] Cooper, 1992. In his detailed discussion, Cooper (1992) stated that *Prollyelliceras* was closer to *Brancoceras* than to *Leymeriella*, and noted that Casey had figured a specimen (from the condensed Albian of Peille in Alpes-Maritimes, France) as *Prollyelliceras* sp. (1957, pl. 7, fig. 6), transitional to *Brancoceras*. Cooper then derived the sequence *Prollyelliceras* → *Ralphimlayites* → *Lyelliceras* → *Tegoceras* as the evolutionary line within the group. He described *Lyelliceras* as having siphonal clavi that outnumber ventrolateral clavi, ribs that frequently zigzag across the venter, and noted that some may have an additional lateral tubercle (he did not, unfortunately, indicate which species he regarded as assignable to *Lyelliceras*). *Tegoceras* was derived from *Lyelliceras* by flattening of the whorl sides and venter, accompanied by strengthening of the ventrolateral clavi and virtual effacement of the siphonal clavi. *Neophlycticeratas* (placed by Cooper in a subfamily Neophlycticeratinae Cooper, 1992, of the Forbesiceratinae) of the basal Upper Albian was then presumed to be the link between Middle Albian Lyelliceratinae and uppermost Albian to Lower Cenomanian Stoliczkaiinae.

Latil (1995) and Latil & Dommergues (1997) presented a detailed analysis of the French representatives of the Lyelliceratinae. This work provides a sound stratigraphy-based analysis that is the basis for the present account. It reveals, however, the problem associated with an analysis of the group in this region: much of the material available for study comes from highly condensed phosphatic units at classic localities such as Escragnoles, Gourdon, and Les Rimets in southeast France (Collignon 1949; Gebhard 1979, 1982), and the condensed successions of Haute Savoie in France and adjacent parts of Switzerland, as documented by Delamette (1988, 1989; Delamette *et al.* 1997). Only in Aube (Destombes 1979; Latil 1995) and Haute Normandie (Destombes 1977a,b, 1983; Destombes *et al.* 1973) are there expanded sequences, in clay facies, often seen only in short-lived excavations.

Latil (1995) rejected Cooper's (1992) views. He concluded that the Lyelliceratinae are a direct offshoot of Leymeriellinae;

Flickiidae and Acanthoceratinae are direct offshoots of Stoliczkaiinae, and that there is no evidence of close relationship between Lyelliceratinae and Stoliczkaiinae. Latil recognized the following species in the *Tegoceras* – *Lyelliceras* lineage in the uppermost Lower and basal Middle Albian:

*Tegoceras mosense* → *Tegoceras camatteanum* → *Lyelliceras vaasti* → *Lyelliceras pseudolyelli* → *Lyelliceras lyelli*.

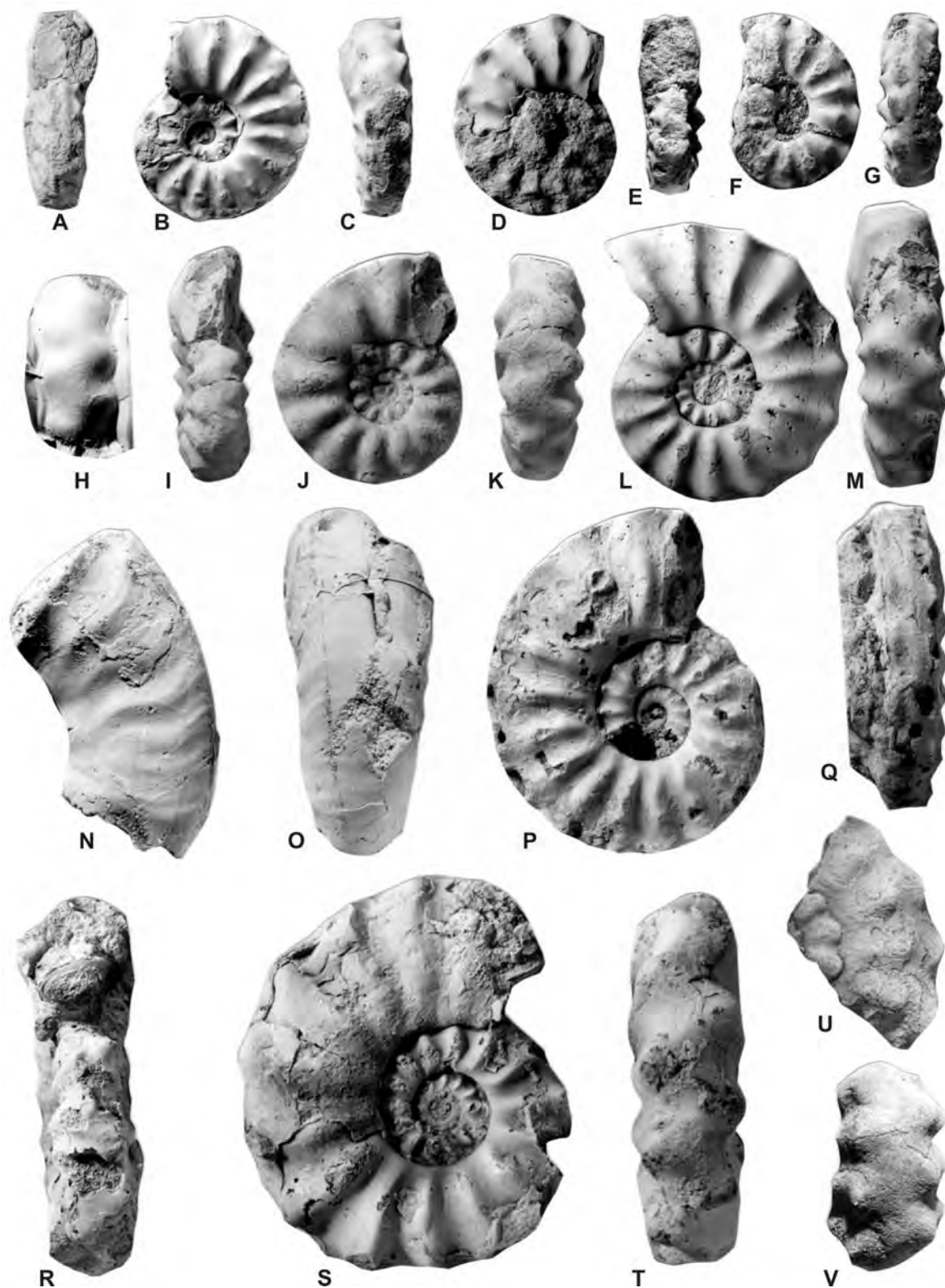
*Tegoceras mosense* (d'Orbigny, 1841) (Figs 3H–O, R–T), with *gladiator* (Bayle, 1878) (Fig. 3R–T) as a junior synonym, was recognized as the earliest representative of the genus, ranging from the *Cleoniceras floridum* Subzone of the *Sonneratia chalensis* Zone to the *Protohoplites* (*Hemissonneratia*) *puzosianus* Subzone of the upper Lower Albian *Otohoplites auritifformis* Zone (Fig. 2). This species was characterized by the coarse ribbing, the ribs alternating in position across the venter, and linked by a zigzag rib, lack of umbilical tubercles, transient lateral tubercles, and ventrolateral, but no ventral tubercles. Coiling is subinvolute, with little overlap between successive whorls. Adult size is in excess of 100 mm.

*Tegoceras gladiator* was succeeded by *Tegoceras camatteanum* (d'Orbigny, 1841) (Figs 3A–G, P, Q; 7C–F) (of which Latil regarded *senebrianum* (Pictet, 1847) (Fig. 4 T–V), *seunesi* (Parona & Bonarelli, 1897) (Figs 4A,B,J,K,S; 5), *collignoni* Breistroffer, 1953 (*in* Breistroffer & de Villoutreys 1953) (Fig. 6/6) and *quadratum* Destombes, 1977b, to be synonyms).

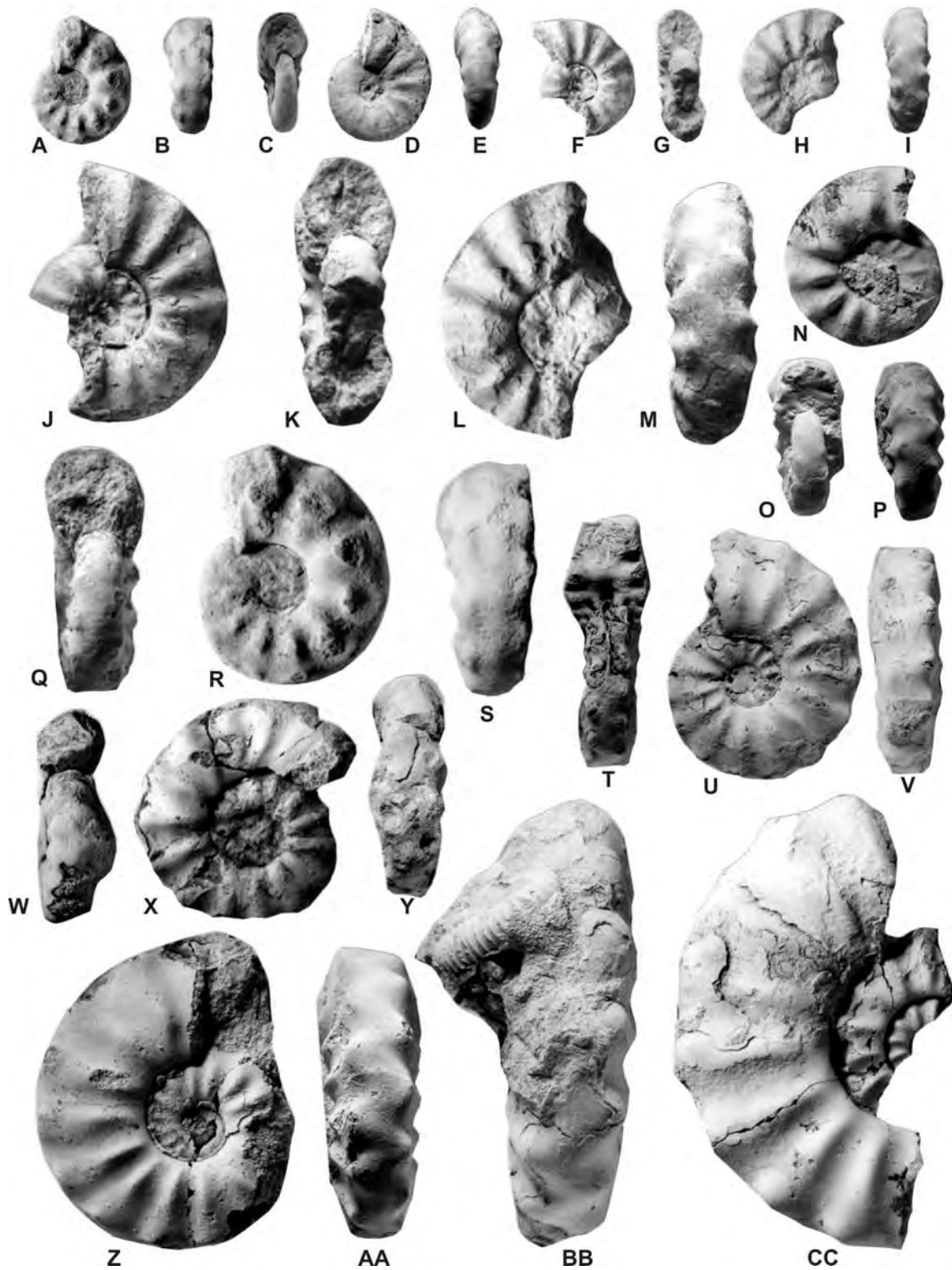
By his interpretation, the species ranges through the *Otohoplites bulliensis* and *Pseudosonneratia* (*Isohoplites*) *steinmanni* subzones of the upper Lower Albian *auritifformis* Zone. The characteristic features recognized were the absence of umbilical tubercles, presence of lateral tubercles elongated in the sense of the rib (= bullate herein) on the inner to mid-flank, presence of ventrolateral tubercles elongated in the sense of the coiling (= clavate herein), absence of ventral (= siphonal herein) tubercles, well-developed flank ribs, and a zigzag rib linking the ventral clavi. Coiling is subinvolute to subevolute, with little overlap between whorls. The adult size is in excess of 70 mm.

Latil regarded *Prollyelliceras* Spath, 1930b and *Ralphimlayites* Etayo-Serna, 1979 as synonyms of *Lyelliceras*, and recognized *Lyelliceras vaasti* Destombes *et al.*, 1973, from the *steinmanni* Subzone and the base of the succeeding *Lyelliceras pseudolyelli* Subzone of the upper Lower Albian *auritifformis* Zone. He characterized this species, regarded as a passage form between *Tegoceras* and *Lyelliceras*, by the presence of weak umbilical bullae, lateral tubercles elongated in the sense of the ribs, and situated on the outer part of the flanks, ventrolateral tubercles elongated in the sense of the enrollment of the shell, the presence of ventral tubercles in juveniles, weak ribs that were flexuous, did not cross the venter in the early growth stages, but tended to develop in a zigzag pattern across the venter in the adult.

*Lyelliceras huberianum* (Pictet, 1847) (Fig. 7A,B), was characterized by variable umbilical tubercles that probably appeared at a late ontogenetic stage, strong, rounded lateral tubercles on the outer flank that also appeared at a relatively late ontogenetic stage, very strong ventrolateral tubercles elongated in the sense of enrollment of the shell, numerous



**Fig. 3.** A–G, P, Q, *Tegoceras camatteanum* (d'Orbigny, 1841). A–D, the lectotype, BMNH 37629, ex Astier Collection, from the condensed Albian of Escragnoles, Alpes-Maritimes, France. E–G, EMP A.830, from the condensed Albian of Clars, Alpes-Maritimes, France. P, Q, a specimen in the EMP Collections, from the condensed Albian of Les Ravix, Balme-de-Rencurel, Isère, France. H–O, R, T, *Tegoceras mosense* (d'Orbigny, 1841). H, N, O, the holotype, EMP A.1369, from Varennes, Meuse, France. H is an artificial mould taken from the dorsum of the holotype. I–K, OUM KX4925–6 (parts of one specimen), from the Mzinene Formation, Lower Albian, Albian III, of locality 53. L, M, EMP. A452, the original of R. Douvillé (1911, fig. 2) from the condensed Albian of Machéroménil, Ardennes, France. R–T, the holotype of *Tegoceras gladiator* (Bayle, 1878), EMP Collections, the original of Bayle (1878, pl. 45, figs 1, 2) from the condensed Albian of Machéroménil, Ardennes, France. U, V, the original of *Tegoceras (Raulinicerias) seunesi* Parona & Bonarelli of Collignon (1963, pl. 317, fig. 1346) from the 'Albien Supérieur (*sensu lato*). Gisement 435. Pied est du Vohimaranitra, Madagascar'. All figures are x1.



**Fig. 4.** **A, B, J, K, S,** *Tegoceras seunesi* (Parona & Bonarelli, 1897). MNHP d'Orbigny Collection 5768a-1, catalogued as *Ammonites camatteanus* d'Orbigny, from 'Clar[s]', near Escragnolles, Alpes-Maritimes, France. **C–P, W–CC,** *Tegoceras mosense* (d'Orbigny, 1841). **C–E, F–G,** Sorbonne Collections, the original of *Acanthoceras camatteanum* d'Orbigny of Pervinrière (1910, p. 40, pl. 13 (4), figs 38, 39) from the Albian of Pont des Gorges, Aumale, Algeria. **N–P,** MNHP 52886a; **Z–AA,** MNHP R52886b, both Peron Collection, 1908–36, from the condensed Albian of Clar[s], Alpes-Maritimes, France. **W–Y,** MNHP d'Orbigny Collection 5768a, catalogued as *Ammonites camatteanus* d'Orbigny, from Escragnolles, Alpes-Maritimes, France. **BB, CC,** EMP Collections, from the condensed Albian of Machéroménil, Ardennes, France, currently housed in the collections of the Institut Dolomieu, Grenoble. **T–V,** *Tegoceras senebrianum* (Pictet, 1847), from the condensed Albian of Machéroménil, Ardennes, France, currently housed in the collections of the Institut Dolomieu, Grenoble. Figures A, B, F–I, T–Y, BB–CC are x1; C–E, N–P, Q–S, Z–AA are x2.



**Fig. 5.** *Tegoceras seunesi* (Parona & Bonarelli, 1897), copy of Parona & Bonarelli (1897, pl. 14, fig. 9), the figured syntype from Escragnoles, Alpes-Maritimes, France. Figures are reproduced at original size, presumed to be  $\times 1$ .

ventral tubercles that were present from an early stage of development, strong, straight, widely separated ribs, that did not cross the venter in the juvenile growth stages, and subinvolute coiling. The adult size is unknown. Known with certainty only from condensed sequences, Latil regarded *huberianum* as a primitive species of *Lyelliceras*, perhaps a contemporary of *Lyelliceras vaasti*.

*Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897) (Figs 6/1a,b; 8/1, 2; 9/1, 2, 3 (*pars*); 11H–K; 12A–F, J–O, S–U; 24A–O; 25D–H, J–O, R–T; 27A,B; 28), of which *hirsutum* (Parona & Bonarelli, 1897) (Fig. 6/2a,b; 8/4–6) was regarded as a synonym), was characterized by the presence of umbilical bullae, lateral tubercles that were rounded, or elongated in the sense of the ribs on the outer third of the flanks, ventrolateral tubercles elongated in the sense of the coiling, alternating in position on either side of the siphonal line, numerous ventral tubercles, both rounded and elongated in the sense of the coiling, radial ribs that do not cross the venter, a variable whorl section, and subserpentine coiling. The adult size is in excess of 80 mm. The species ranges throughout the *pseudolyelli* Subzone of the *Otohoplites auritifformis* Zone and occurs as rare examples in the succeeding *lyelli* Subzone of the *Hoplites dentatus* Zone.

*Lyelliceras lyelli* (d'Orbigny, 1841) (Figs 9/3 (*pars*), 4; 10, 11A–G; 12P–R; 24P–Y; BB–GG; 25A–C, I, P, Q, U; 26), of which *gevreyi* Jacob, 1907 (Fig. 6/7a,b), var. *ornatissima* (Ciry, 1927), and *cotteri* Spath, 1930b, were regarded as synonyms, was characterized by the general (but not invariable) presence of umbilical tubercles, lateral tubercles on the outer third of the flank that were rounded, or elongated in the sense of the coiling of the shell, ventrolateral tubercles elongated in the sense of the coiling of the shell, ventral tubercles that are rounded or elongated in the sense of the coiling of the shell, and aligned with the ventrolateral tubercles. In some cases there are more ventral than ventrolateral tubercles in juveniles. The ribs are radial, and weaken across the venter; the whorl section is variable, rectangular, compressed to depressed. The coiling is subserpentine. Adult size is in excess of 80 mm. The species is restricted to the basal Middle Albian *lyelli* Subzone of the *Hoplites dentatus* Zone.

Latil also recognized a distinctive *Lyelliceras* sp. nov., a diminutive species from the condensed Albian of Escragnoles (Alpes-Maritimes), and *L. versicostatum* (Michelin, 1838); the last-named is restricted to the basal Middle Albian *lyelli*

Subzone of the *Hoplites dentatus* Zone.

*Lyelliceras flandrini* Dubourdieu, 1953, and its varieties (p. 27, pl. 3, figs 6–22), from the lower Lower Albian of the Monts du Mellègue in Algeria (Fig. 13H–GG) were regarded as a homoeomorph of *Lyelliceras*. *Prionotropis radenaci* Pervinquièrre, 1907 (p. 251, pl. 12, fig. 4; Fig. 13A–G) from the Lower Albian of Tunisia, was regarded as an ally of *flandrini*.

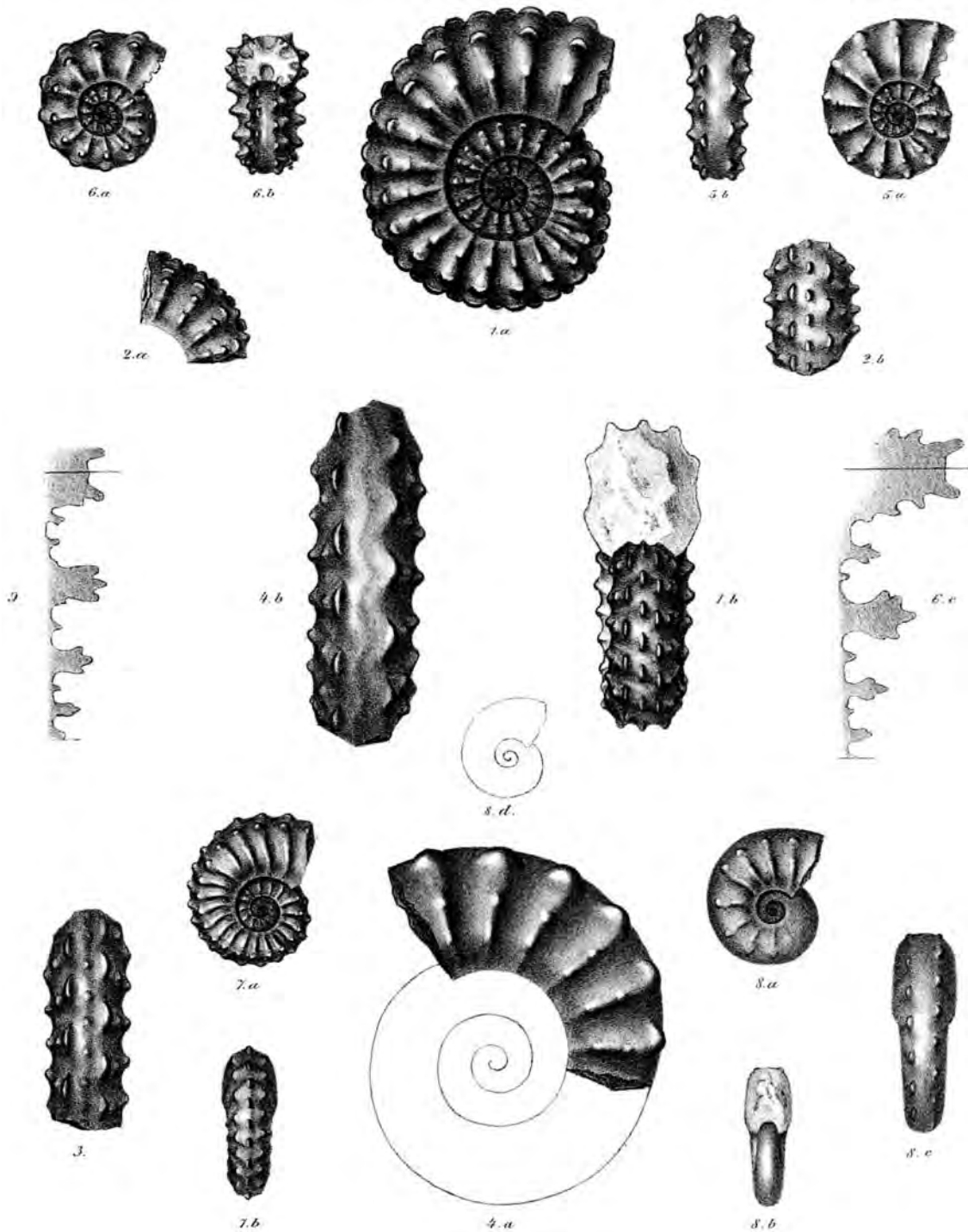
Latil (1995, p. 345) noted the presence of the European *Tegoceras*–*Lyelliceras* lineage in Venezuela (Renz 1982) and Madagascar (Collignon 1963). He pointed out the presence of what he believed to be *L. lyelli* and *pseudolyelli* in the Andes (Peru and Colombia: Benavides-Cáceres 1956), and drew attention to the apparently different history of the group in this region.

Robert (2002) provided, for the first time, a stratigraphic framework for the supposed lyelliceratids of Peru. This is reproduced as Fig. 14 herein. This phylogeny, confirmed subsequently by Latil *et al.* (in press), demonstrates that these ammonites are heterochronous/synchronous homoeomorphs of true *Lyelliceras*, that are derived from *Tegoceras*. The Colombian taxa derived from what Robert referred to *Prollyelliceras* Spath, 1930b. We further doubt that the *Lyelliceras lyelli* and *pseudolyelli* of Robert (2002) and Robert *et al.* (2002) actually belong to these Old World taxa.

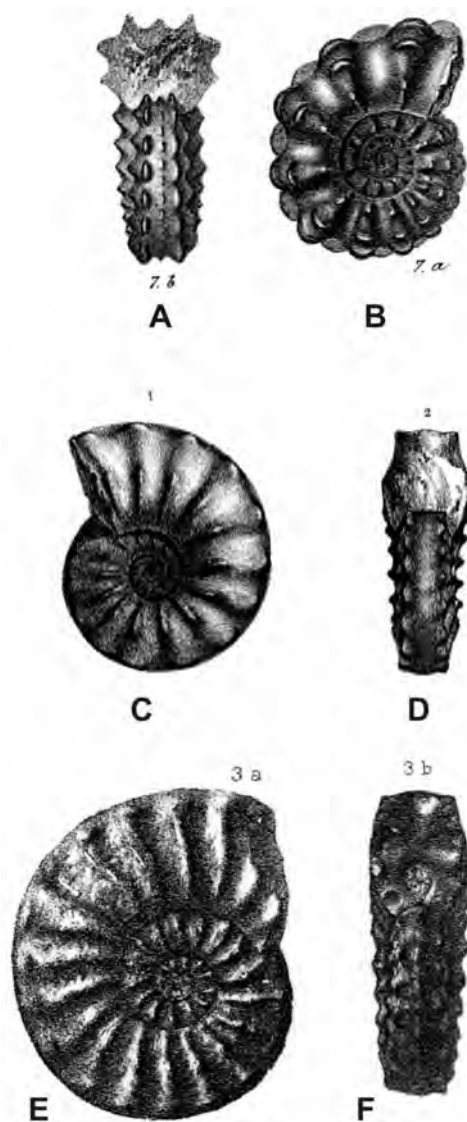
Kennedy (2004) revised the representatives of the genus *Branco-ceras* from the Albian of France, and recognized that *Ammonites versicostatus* Michelin, 1838 (Fig. 29A–P) was neither a *Branco-ceras* nor a *Lyelliceras*, but a pedomorphic offshoot of the latter: *Pseudobranco-ceras* Kennedy, 2004, to which a second species, *Pseudobranco-ceras transiens* Kennedy, 2004 (p. 254, pl. 2, figs 9, 10, 14, 20; text-figs 2a–e; 3a–f; Fig. 31E–L) was also referred.

Accordingly, we refer only *Tegoceras* Hyatt, 1903, *Lyelliceras* Spath, 1921 and *Pseudobranco-ceras* Kennedy, 2004, to the Lyelliceratinae. In his account of the French material of *Lyelliceras pseudolyelli* and *lyelli*, Latil referred to 'Prollyelliceras' morphotypes of these species with a trituberculate venter (Latil 1995, text-figs 23–25; pl. 3, figs 15–17). These morphotypes are absent from the KwaZulu collections of these species, and our own researches indicate the possible presence of additional lyelliceratine taxa in the French Albian, a typical example of which is associated with the types of *Lyelliceras lyelli* (Fig. 31A–D).

The origins of *Tegoceras* and the Lyelliceratinae are problematic. Casey (1957, text-fig. 5) appears to suggest an origin in Desmocerataceae [Desmoceratoidea], yet figures what he refers to as a *Prollyelliceras* transitional to *Branco-ceras* from 'Pelle' (1957, pl. 7, fig. 7; presumably Peille) in Alpes-Maritimes, France. An examination of this specimen reveals that it is simply a juvenile *Branco-ceras*. Latil (1995, p. 347; text-fig. 16) suggested an origin of Lyelliceratinae in either Leymeriellinae or Desmoceratinae. The recognition of Branco-ceratidae from the *Leymeriella tardefurcata* Zone in southeast France (*Parabranco-ceras dromense* Kennedy, in Kennedy *et al.* 2000, p. 675, figs 44b, 47c,e), suggests an alternative origin for the earliest lyelliceratines. *Branco-ceras* from the condensed Lower to lower Upper Albian of southeast France include forms with ribs that are both opposite across the venter, and those in which they alternate (Kennedy 2004). The latter condition (*Branco-ceras*



**Fig. 6.** Copy of pl. 24 of Pictet & Campiche (1860), described originally as varieties of *Ammonites lyelli* Leymerie. **1a,b** are referred to *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897) from the 'Gault du Saxonet'. **2a,b**, is the holotype, by monotypy, of *Lyelliceras hirsutum* (Parona & Bonarelli, 1897) interpreted here as a fragment of *Lyelliceras pseudolyelli*, from the 'Gault moyen de Sainte-Croix'. **3** was referred to their 'troisième variété' by Pictet & Campiche; it appears to be a *Lyelliceras* allied to *pseudolyelli*. The original was from the 'Gault moyen de Sainte-Croix'. **4** was also referred to their 'troisième variété', and is interpreted here as a *Tegoceras camatteanum* (d'Orbigny, 1841). Destombes (1977b) referred it to his new species *Tegoceras quadratum*. The original was from the 'Gault moyen de Sainte-Croix'. **5** was attributed to their 'quatrième variété ou *Ammonites camatteanum*' by Pictet & Campiche, and is a *Tegoceras* sp. juv. The original was from the 'Gault moyen de Sainte-Croix'. **6** was referred to their 'cinquième variété' by Pictet & Campiche, and is the holotype, by monotypy, of *Tegoceras* [*Raulinicer* (*Seunesiceras*)] *collignoni* (Breistroffer, 1953). The original was from the 'Gault moyen de Sainte-Croix'. **7** was referred to their 'deuxième variété' by Pictet & Campiche, and is the holotype, by monotypy, of '*Prollyelliceras*' [*Acanthoceras*] *gevreyi* (Jacob, 1907). The original was from the 'Gault des Gorges, près Bellegard'. **8** was regarded as a juvenile of their 'cinquième variété' by Pictet & Campiche, and is a *Tegoceras* sp. juv., from the the 'Gault moyen de Sainte-Croix'. **9** is described as being the suture line of the 'type normal'. Figures are reproduced at their original size, presumed to be x1.



**Fig. 7.** A, B, The figured syntype of *Ammonites huberianum* Pictet, 1847, copy of Pictet (1847, pl. 7, fig. 7). The original was from the condensed Albian of 'Mont Saxonnet' (=Bourgets of Delamette *et al.* 1977, p. 291). C–F, *Tegoceras camatteanum* (d'Orbigny, 1841). C, D, the lectotype, copy of d'Orbigny (1841, pl. 69, figs 1–2). The original, shown in Fig. 3A–D, is from Escragnoles, Alpes-Maritimes, France. E, F, copy of Seunes (1887, pl. 13, fig. 3) of a specimen in the École des Mines Collections, from Clars, Alpes-Maritimes, France. Figures are reproduced at original size, presumed to be  $\times 1$ .

*alternatum* Kennedy, 2004 (p. 267, pl. 8, figs 1–5; text-fig. 6a) suggests to us an origin for *Tegoceras*, and hence the Lyelliceratinae, in Brancoceratinae. Pervinquière (1910, p. 40, pl. 13 (4), figs 38, 39) figured two juvenile *Tegoceras* from the Albian of Aumale, Algeria, refigured here as Fig. 4C–G. The smaller specimen (Fig. 4C–E), only 13.3mm in diameter, has an initial smooth stage with a distinctly fastigiate venter, followed by the appearance of ribs that alternate in position, and bear umbilicolateral bullae alone, in turn followed by the appearance of ventrolateral thickenings on the ribs. The larger specimen, 26.6 mm in diameter (Fig. 4F–G) develops into a typical *Tegoceras mosense*. The ornament of the smaller of these specimens again suggests, in our view, derivation from Brancoceratinae.

The relationship between Lyelliceratinae and Stoliczkaiinae was reviewed by Latil (2005, p. 347). As he noted, the conventional view has been to derive Stoliczkaiinae from Lyelliceratinae. However, he noted that 'les caractères ornementaux sont presque tous différentes (enroulement, costulation, forme de la section, tuberculation). – La ligne suturale très découpée des premiers Stoliczkaiinae (genre *Neophlycticer*) suggère un enrancement plus 'direct' au sein des Desmocerataceae...'. He also noted the gap in the record between the last lyelliceratine and the first stoliczkaiine (all but the *lyelli* Subzone of the Middle Albian: Fig. 2). In fact, there is a very limited record of Acanthoceratoidea in this interval, other than Brancoceratidae. We note, however, the presence of what are morphological intermediates between *Lyellicer* and *Neophlycticer* in the condensed Albian (Lower to basal Upper Albian) of Clars/Escragnoles in Alpes-Maritimes, France, and the expanded facies of the basal Middle Albian *lyelli* Subzone in southern England. We will return to this material in our forthcoming account of the KwaZulu Stoliczkaiinae.

If the Lyelliceratinae are not the origin of the Stoliczkaiinae, the latter are best associated with the Acanthoceratidae, and the subfamily Lyelliceratinae placed within Brancoceratidae. There is no definitive evidence, and the Lyelliceratinae and Stoliczkaiinae are accordingly treated as subfamilies of the family Lyelliceratidae within the Acanthoceratoidea.

#### The lyelliceratine homoeomorphs: *Prollyellicer*, *Ralphimlayites* and related taxa

As noted above, the phylogenetic relationships established by Robert *et al.* (2002), Robert *et al.* (2002), and Latil *et al.* (in press) indicated that the 'lyelliceratines' of Peru and adjacent areas are not related to the *Tegoceras-Lyellicer* lineage, and are thus lyelliceratine homoeomorphs. We understand that Dr Latil and his colleagues are to revise this group. We present here our independent observations and views on some of these taxa, leaving the definitive account to our French colleagues.

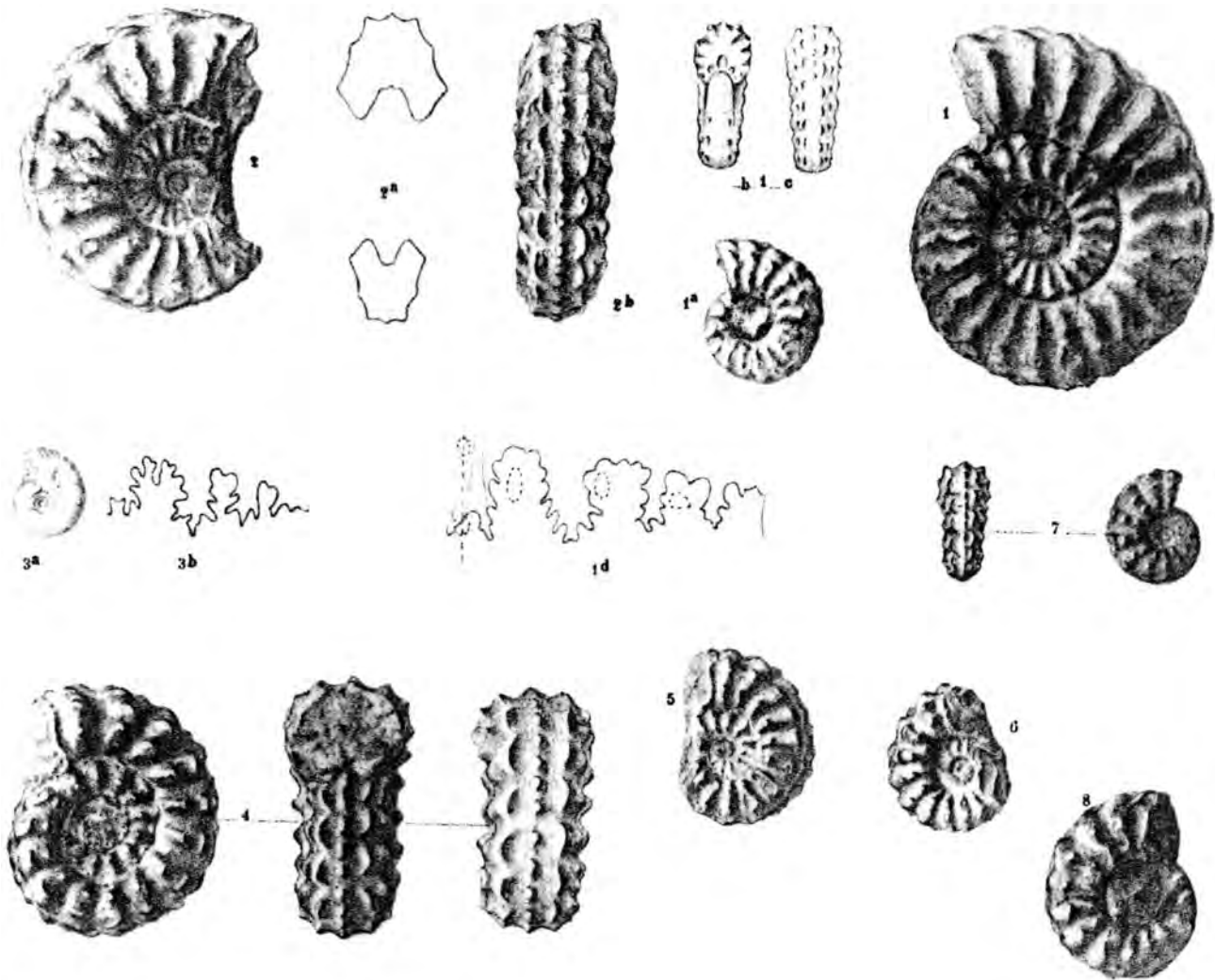
#### Genus *Prollyellicer* Spath, 1930b

*Prollyellicer* Spath, 1930b is one of the less fortunate of the genera introduced in characteristic perfunctory style by that author in a footnote: '*Prollyellicer* (gen. nov.)<sup>8</sup> Proposed for *Prollyellicer peruvianum*, nom. nov. = *prorsocurvatum* (non Gerhardt) R. Douvillé, *loc. cit.*, 1907, p. 144, pl. ii, figs 1, 1a. To this genus also belongs Sommermeier's (*loc. cit.*, p. 380, pl. xv, fig. 3) *Prionotropis radenaci*, (non Pervinquière) and less certainly the Tunisian species previously discussed (Spath 1922, Angola, p. 108) *Prollyellicer* without lateral tubercles, connects *Lyellicer* morphologically with the parahoplitids (*Colombicer*), but may be an independent Puzosid offshoot' (Spath 1930b, p. 65, footnote 8).

In our interpretation, *Prollyellicer* is understood to have umbilical, inner and outer ventrolateral and siphonal tubercles. The holotype of *peruvianum*, the type species, is thus the original of R. Douvillé (1907, p. 144, pl. ii, figs 1, 1a, reproduced here as Fig. 15).

The specimen was illustrated in a paper describing ammonites sent to H. Douvillé by a former student, Pinillos





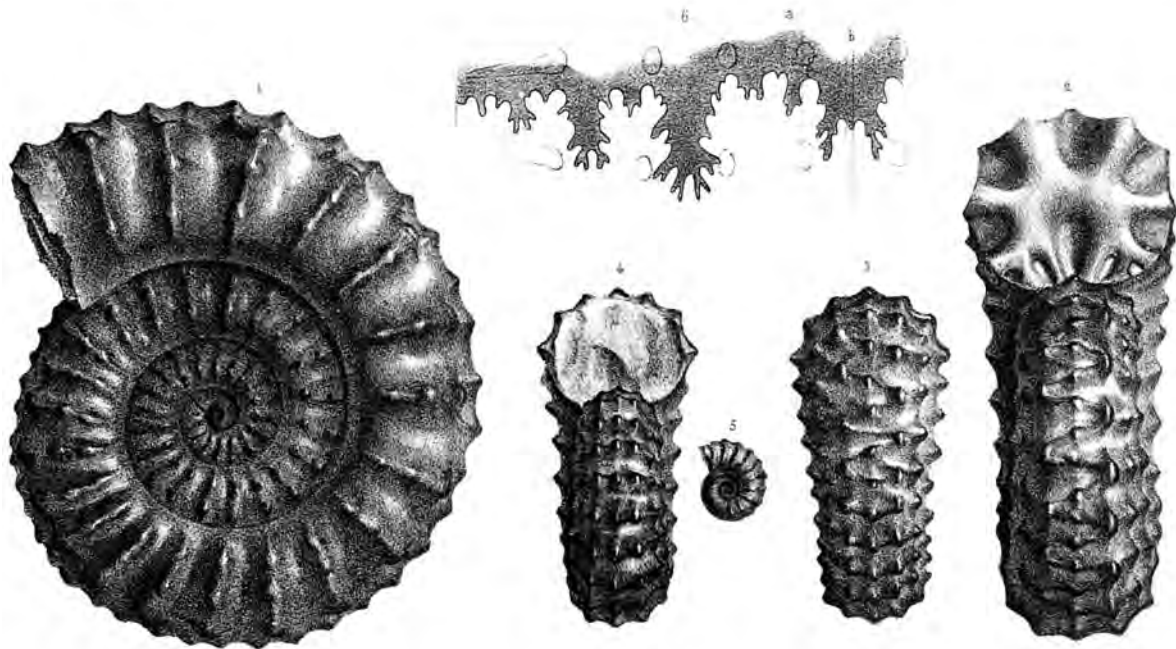
**Fig. 8.** Copy of part of plate 14 (5) of Parona & Bonarelli (1897). 1 is a paralectotype of *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897); Fig. 2 is the lectotype. Fig. 3 is a *Hoplites dentatus* (J. Sowerby, 1821). 4–6 were referred to their *Lyelliceras* [*Acanthoceras*] *hirsutum* by Parona & Bonarelli, here regarded as a synonym of *Lyelliceras pseudolyelli*. 7 and 8 were referred to *Lyelliceras*? [*Acanthoceras*] *huberianum* (Pictet, 1847) by Parona & Bonarelli. The originals were all from the condensed Albian of Escragnolles, Alpes-Maritimes, France, and in the Collections of the Museo Geologico, Turin. All figures are reproduced at their original size, which is presumed to be  $\times 1$ .

Mártin, from the environs of Truxillo, Peru. The material described by Douvillé is housed in the collections of the École National supérieur des Mines, now in the Université de Lyon-Villeurbanne. One of us (WJK) has sought in vain for this specimen, although the other specimens figured in the paper survive; it is presumed lost. The original account of this specimen is unhelpful: 'Ce fragment de tour parait avoir appartenu à une Ammonite extrêmement voisine de celle figurée par Gerhardt. Cependant notre espèce a un enroulement un peu moins rapide et des côtes moins flexueuses.' The original figure is reproduced here (Fig. 15). It appears to be a body chamber, a  $120^\circ$  sector of whorl. From the illustrations it is 62 mm long approximately, with a maximum preserved whorl height of 25.2 mm, and a costal whorl breadth to height ratio of 0.84. The greatest breadth in costal section appears to be low on the flanks, possibly at a feeble umbilicolateral bulla. The ribs are narrower than the interspaces, prorsiradiate, feebly concave on the outer flank, strong and transverse on the venter, where they bear a single row of ventrolateral tubercles, no wider than the ribs,

and a similar siphonal row. Robert (2002) gave an extensive synonymy for this species, and illustrated a number of specimens. Far better-preserved material attributed to this species was described and figured by Benavides-Cáceres (1956, p. 462, pl. 50, figs 1–4, reproduced here as Fig. 16), including an adult body chamber with strikingly fastigiata venter (Fig. 16/1, 2, herein). Robert (2002, p. 141) excluded this specimen from *peruvianum*, referring it (p. 143) to *Prollyelliceras lobatum* (Riedel, 1938), a view with which we agree. According to Benavides-Cáceres the phragmocones of his specimens of *peruvianum* are trituberculate across the venter. But are these phragmocones the same species as the lost holotype of *peruvianum*? We think not. Instead, an examination of specimens of *Prollyelliceras* from between Viola and Portillo, Cundinamarca, Colombia (Fig. 17C–I), described below, have convinced us that Robert (2002) was correct. The missing holotype of *peruvianum* Spath, 1930a is the body chamber of a microconch; the holotype of *prorsocurvatum* Gerhardt, 1897, is an incomplete macroconch of the same species. *Prollyelliceras peruvianum* of

T. Crétacés.

Pl. 74

*J. Dolarus del.**A. Lyelli. Leymerie (i)*

**Fig. 9.** Copy of plate 74 of d'Orbigny (1841). The original plate description is as follows:

'Fig. 1. Individu de grandeur naturelle, vue de côté. De ma collection.

Fig. 2. Le même, vu du côté de la bouche.

Fig. 3. Un individu plus jeune, vu sur le dos, montrant le passage des côtes entières aux côtes alternes.

Fig. 4. Un autre individu, vu du côté de la bouche. C'est le jeune à côtes continues.

Fig. 5. Très-jeune individu, a l'instant où, de lisse qu'il est, il commence à prendre les côtes.

Fig. 6. Une cloison grossie, pour montrer que la ligne médiane étant à, le lobe dorsal passé à droite à, au lieu de passer au milieu. Les tubercles sont indiqués par rapport à la position respective des lobes et selles. Dessinée par moi.'

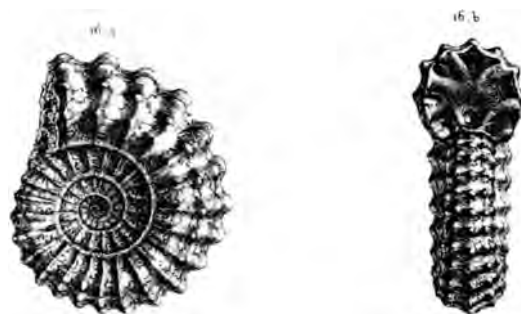
Several of these figures are composites, based on more than one individual, and reconstructed from fragments. From his description and figure explanation it is clear that d'Orbigny envisaged his *Ammonites lyelli* as a species in which the ribs were regular, opposite across the venter, and linked by a simple transverse rib in juveniles, as in his fig. 4. In his interpretation, the ribs alternate in position in adults, and zigzag across the venter, as in his fig. 2, with the passage between what he believed to be juvenile and adult ornament shown in his fig. 3. Figs 1 and 2 are probably a restoration based on the specimen shown in Fig. 25R–T herein, even though this specimen is a body chamber and the figures shown a wholly septate individual. It is a *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). Fig. 3 does not correspond to any of his specimens, and is a chimaera, combining the ornament of *Lyelliceras lyelli* on the adapical part and that of *Lyelliceras pseudolyelli* on the adapertural part. Fig 4 does not correspond to any of his surviving specimens, and is interpreted as being based on a specimen or specimens of *Lyelliceras lyelli*. Fig. 5 may be based on one of the juvenile ammonites shown in Fig. 25V herein. The original of fig. 6 has not been recognized. Figures are reproduced at the original size, which is presumed to be  $\times 1$ .

Spath is thus a juvenile synonym of *prorsocurvatum* of Gerhardt, and *peruvianum* of Benavides-Cáceres (1956) should be referred to *lobatum* of Riedel. If this last-named species indeed lacks inner ventrolateral tubercles throughout ontogeny, as Benavides-Cáceres states, it requires generic or subgeneric separation from *Prolyelliceras*.

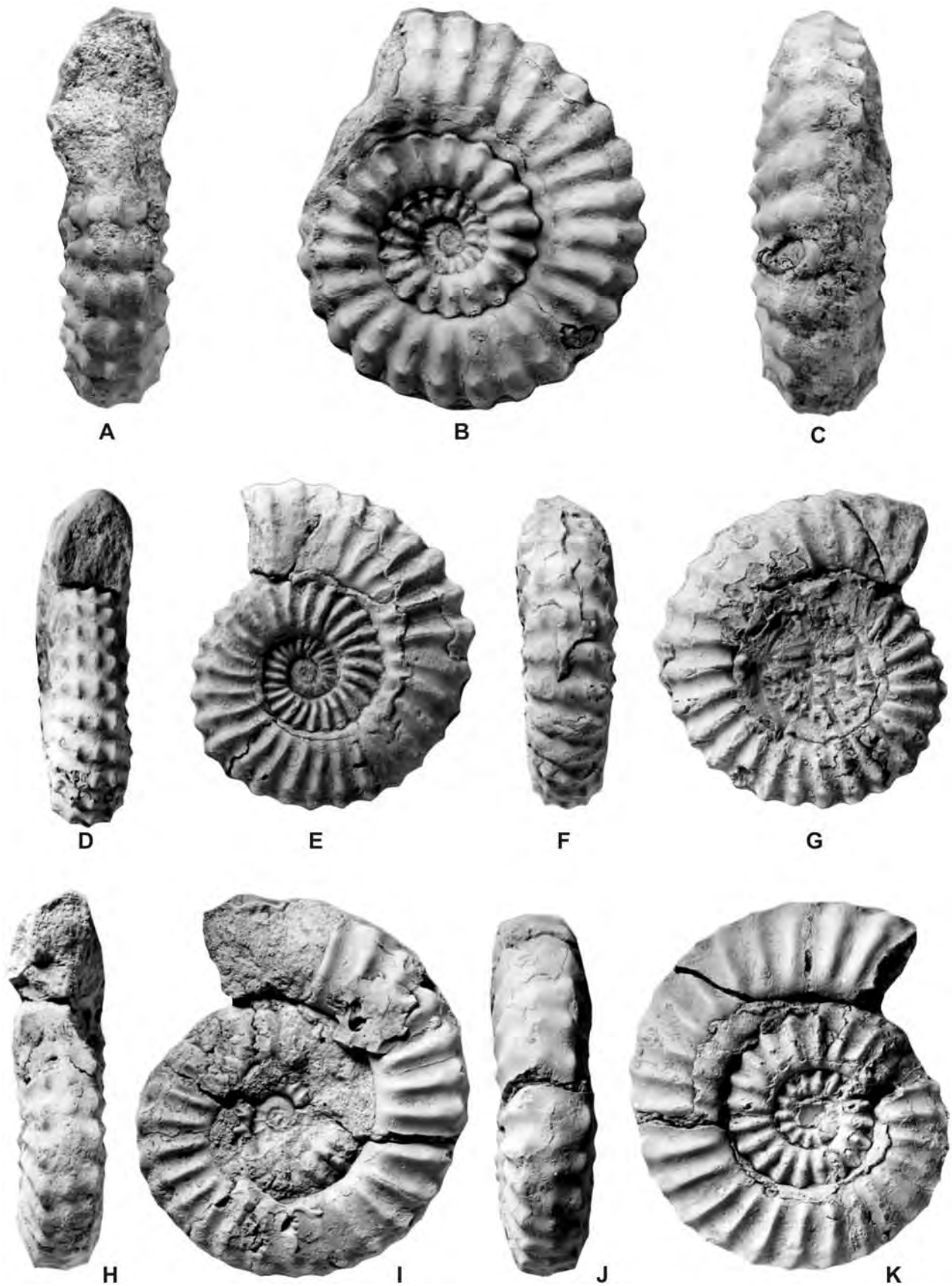
Whatever the status of the material figured by Benavides-Cáceres, it is clear that this material is quite separate from Old World *Lyelliceras* on the basis of whorl section, form of ribs, and tuberculation.

#### Genus *Ralphimlayites* Etayo-Serna, 1979

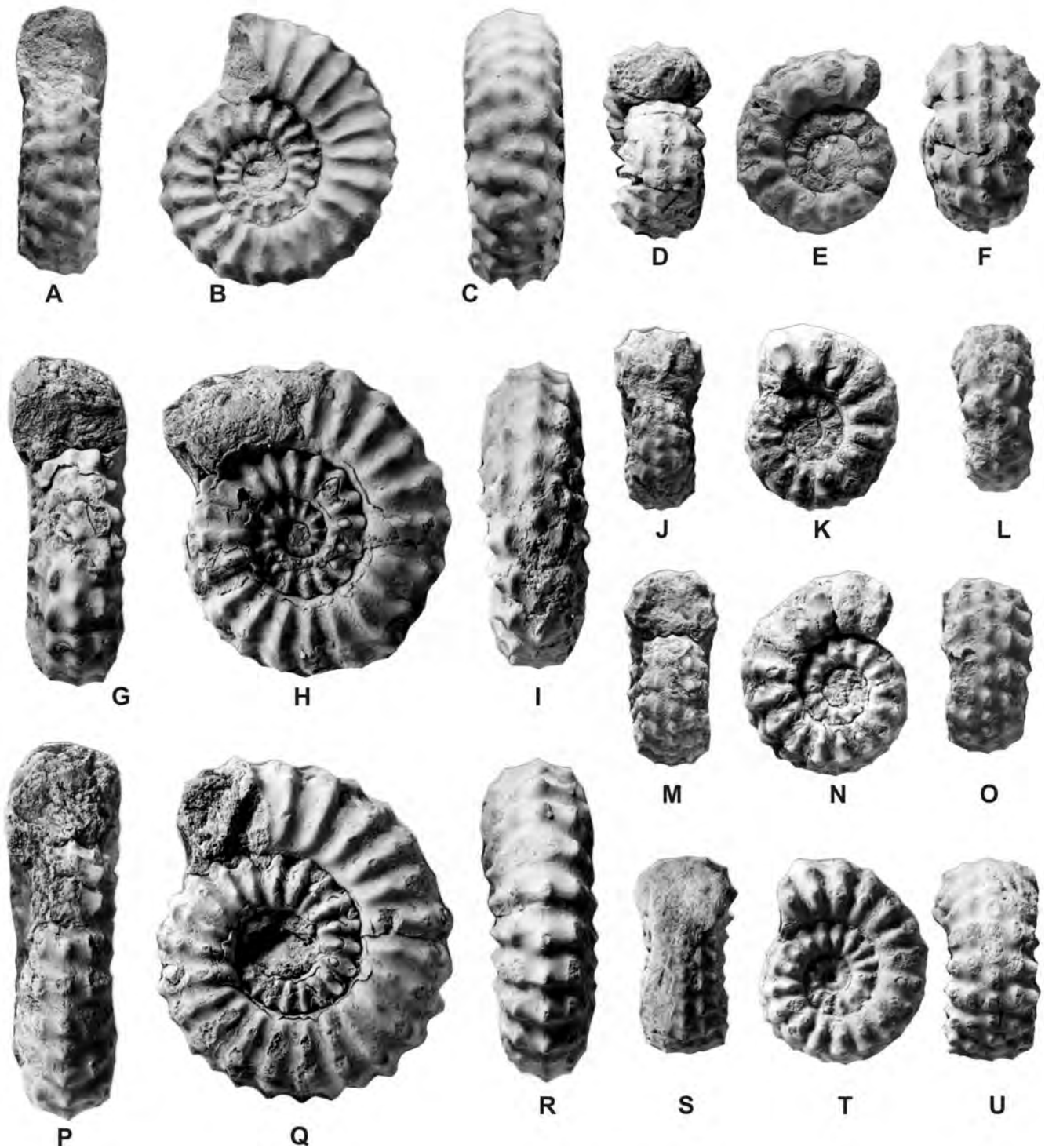
As noted above, we regard the type species of *Prolyelliceras* and *Ralphimlayites* as conspecific, the generic name *Prolyelliceras* thus having priority. The type species of



**Fig. 10.** *Lyelliceras lyelli* (d'Orbigny, 1841). Copy of *Ammonites lyelli* in Leymerie (1842, pl. 17, fig. 16), based on a specimen from the Gault of Le Gaty, Aube, France. The original specimen has not been traced. Figures are reproduced at the original size, which is presumed to be  $\times 1$ .



**Fig. 11.** A–G, *Lyellicerias lyelli* (d'Orbigny, 1841). A–C, EMP Collections, the original of Bayle (1878, pl. 75, fig. 4) from the Gault of Saint-Florentin, Yonne, France. D–G, EMP A210; H–K, *Lyellicerias pseudolyelli* (Parona & Bonarelli, 1897), EMP A233, both from Clars, Escragnolles, Alpes-Maritimes, France. All figures are  $\times 1$ .

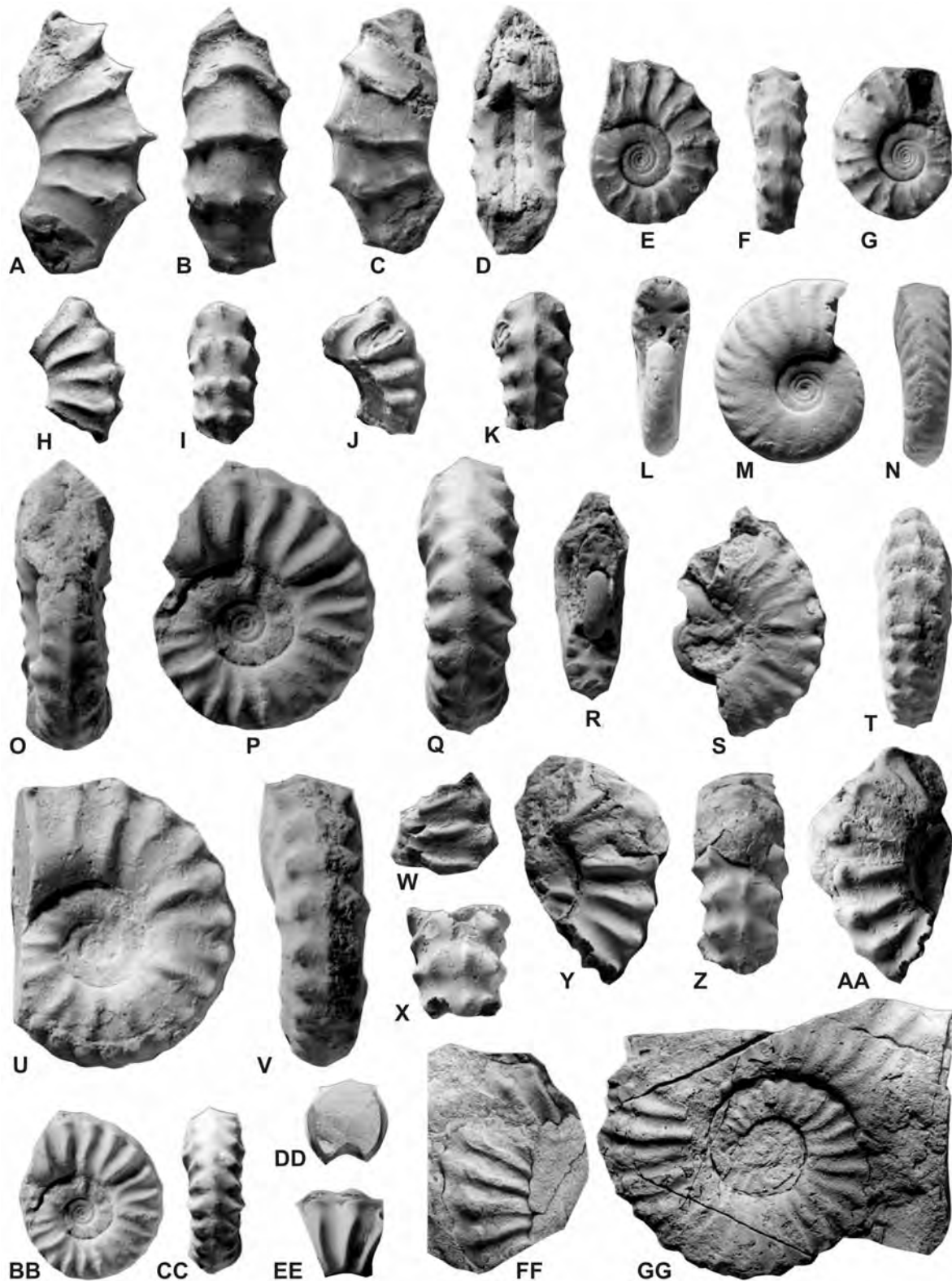


**Fig. 12.** A–F, J–O, S–U, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). A–C, EMP Collections, the original of Bayle (1878, pl. 75, figs 5, 6) from the condensed Albian of Clars, near Escagnolles, Alpes-Maritimes, France. D–F, EMP A228, locality and horizon as A–C. J–L, ID2014; M–O, ID2012, from the condensed Albian of Gourdon, Alpes-Maritimes, France. S–U, EMP A223, from the condensed Albian of Les Rimets, near La Balme-de-Rencurel, Isère, France. G–I, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897), transitional to *Lyelliceras lyelli* (d'Orbigny, 1841), EMP A218a, ex Puzos Collection, locality and horizon as A–C. P–R, *Lyelliceras lyelli* (d'Orbigny, 1841), EMP A218b, ex Puzos Collection, locality and horizon as A–C. All figures are  $\times 1$ .

*Ralphimlayites*, by original designation by Etayo-Serna (1979, p. 81), is *Acanthoceras prorsocurvatum* Gerhardt, 1897 (p. 168, pl. 4, fig. 8) (reproduced here as Fig. 17A,B). The original diagnosis is as follows: 'Evolute conchs with subquadrangular whorl section from early in the ontogeny;

three rows of tubercles on the flanks; periumbilical bullae, subclavate tubercles abventral to prominent ventral clavi; ventral median clavi corresponding to the ventrolateral ones.'

At first sight, the presence of inner ventrolateral tubercles



**Fig. 13.** A–G, the lectotype of *Prionotropis radenaci* Pervinquière, 1907, pl. 12, fig. 4, text-fig. 10, SP unregistered, from the Lower Albian of Djebel Hamaima, western Tunisia. H–GG, *Lyellicerias flandrini* Dubourdiou, 1953, representative examples of the forms recognized by Dubourdiou, and illustrated in his pl. 3: H, I, 'forme typique' (pl. 3, figs 13,14); J, K, 'forme typique' (pl. 3, figs 16, 17); L–N, 'var. *crenulata*' (pl. 3, figs 25–28); O–Q, BB, CC, 'forme typique' (pl. 3, figs 10–12); R–T, 'var. *crenulata*' (pl. 3, figs 32–35); U, V, 'var. *media*' (pl. 3, figs 39–41); W, X, '*L. aff. flandrini*' (pl. 3, figs 42–45); Y, Z, AA, 'forme typique' (pl. 3, figs 6–9); DD–EE, 'forme typique' (pl. 3, figs 18–20); FF, '*L. flandrini sensu lato*' (pl. 3, fig. 24); GG, '*L. flandrini sensu lato*' (pl. 3, fig. 23). The specimens were originally housed in the collections of the Collège de France, Paris, and transferred to the collections of the Université de Lyon-Villeurbanne in 1995. The specimens are from the Lower Albian of the Monts du Mellègue in western Algeria. Figures A–G, J, K, W–GG are x1; H, I, L–V are x3.

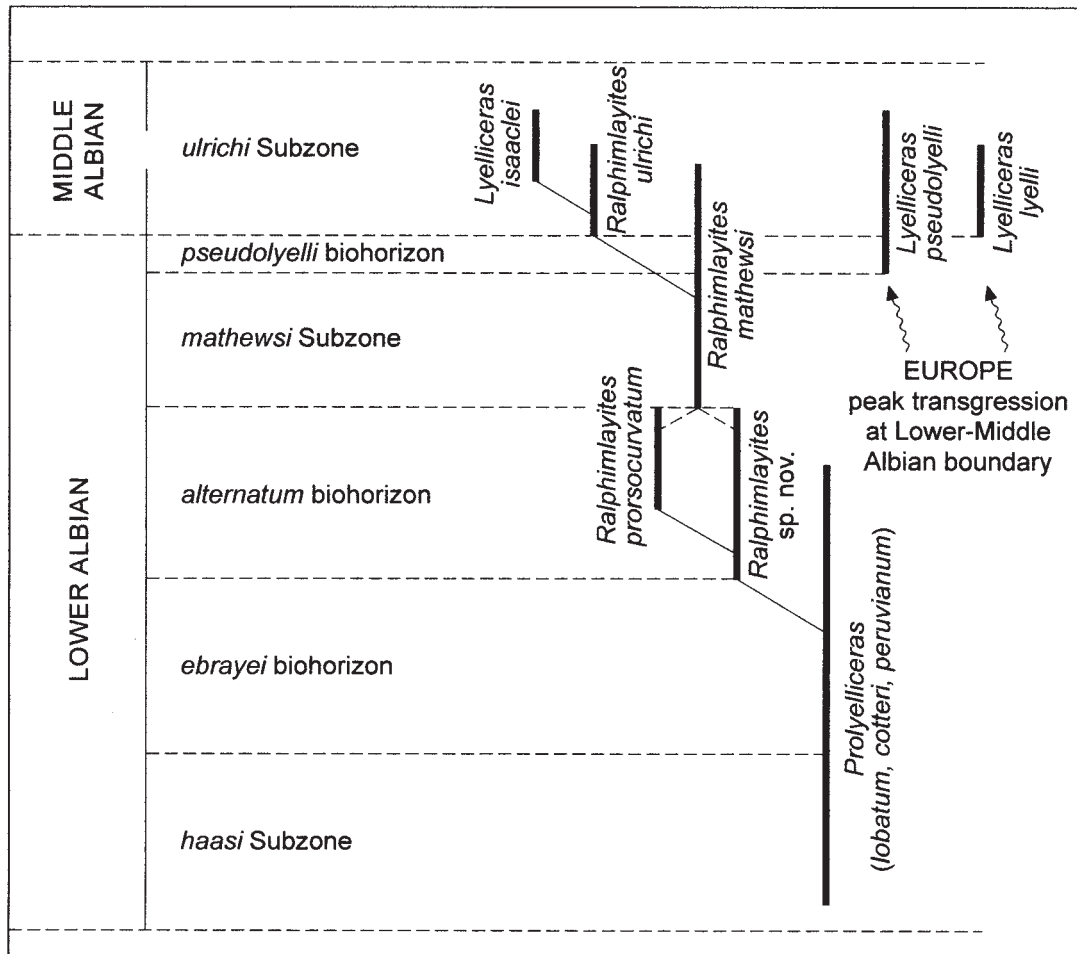


Fig. 14. Evolutionary relationships between the Peruvian taxa referred to the Lyelliceratidae according to Robert (modified after Robert 2002, fig. 56).

in *Ralphimlayites* and their apparent absence in *Prolyelliceras* seems distinctive enough. However, Gerhardt's figure shows the inner ventrolateral row effacing on the outer whorl, and absent from the adapertural 10 ribs, from which point the holotype of *prorsocurvatum* differs in no significant respects from the lost holotype of *peruvianum*.

Robert (2002, p. 141) regarded *prorsocurvatum* of Gerhardt as a possible synonym of *peruvianum* of Spath, although, inexplicably, he continued to use *Ralphimlayites* as a genus separate from *Prolyelliceras*. He further stated, in his discussion of *Ralphimlayites* (p. 146) that 'L'espèce-typique *Acanthoceras prorsocurvatum* Gerhardt (1897, p. 168, pl. 4, fig. 8a,b, text-fig. 16), choisie par Etayo-Serna perd les tubercules latéraux inférieurs sur le dernier demi-tour de la coquille. La chambre d'habitation supposée (non indiquée par son auteur) ne porte que deux rangées de tubercules. Du point de vue nomenclatorial, l'espèce figurée par Gerhardt est ici placée dans le genre *Prolyelliceras*. Une nouvelle espèce type doit être désignée.'

Changing the type species of a genus is not a valid concept or procedure.

In spite of concluding that the type species of *Ralphimlayites* may be a synonym of the type species of *Prolyelliceras*, and that it is a *Prolyelliceras* (with the consequence that *Ralphimlayites* becomes a junior synonym of *Prolyelliceras*),

Robert continued to use *Ralphimlayites*, and referred the following to the genus: *Lyelliceras ulrichi* Knechtel, 1947 (p. 99, pl. 23, fig. 1, text-fig. 5: Fig. 18C,D herein); *Lyelliceras mathewsi* Knechtel, 1947 (p. 101, pl. 21, fig. 3,



Fig. 15. The holotype of *Prolyelliceras peruvianum* Spath, 1930b. Copy of R. Douvillé (1907, pl. 2, fig. 1, 1a). This is the type specimen of the type species of *Prolyelliceras*, and is from Truxillo, Peru. It appears to be lost. Figures are reproduced at original size, and presumed to be x1.



**Fig. 16.** Copy of pl. 50, figs 1–4 of Benavides-Cáceres, 1956, referred by him to *Prollyelliceras peruvianum* Spath, 1930b. **1, 2**, AMNH 27867:1; **3**, AMNH 27867:3; **4**, AMNH 27867:2. All specimens are from the Chulec Formation of the Cajamarca section, northern Peru. Robert (2002) refers the original of figs 1 and 2 to *Prollyelliceras lobatum* Riedel, 1938, regarded as a synonym of *peruvianum* by Benavides-Cáceres. All figures are  $\times 1$ .

text-fig. 6: Fig. 18A,B herein); *Ralphimlayites apuloense* Etayo-Serna, 1979 (p. 81, pl. 9, fig. 6), *Lyelliceras cotteri* Spath, 1930b (p. 65, pl. 9, figs 1, 8), *Ralphimlayites alternatum* Robert, 2002 (p. 154, pl. 21, figs 7–9; pl. 22, figs 1–3) and *Ralphimlayites* sp. juv. (Robert 2002, p. 155, pl. 22, figs 4, 5). In this interpretation, *Ralphimlayites* includes species with a single row of ventrolateral tubercles in addition to the siphonal (*cotteri*), and inner and outer ventrolateral tubercles in addition to the siphonal (*mathewsi*).

#### Observations on some *Prollyelliceras* and other false lyelliceratinines

##### *Prollyelliceras prorsocurvatum* (Gerhardt, 1897)

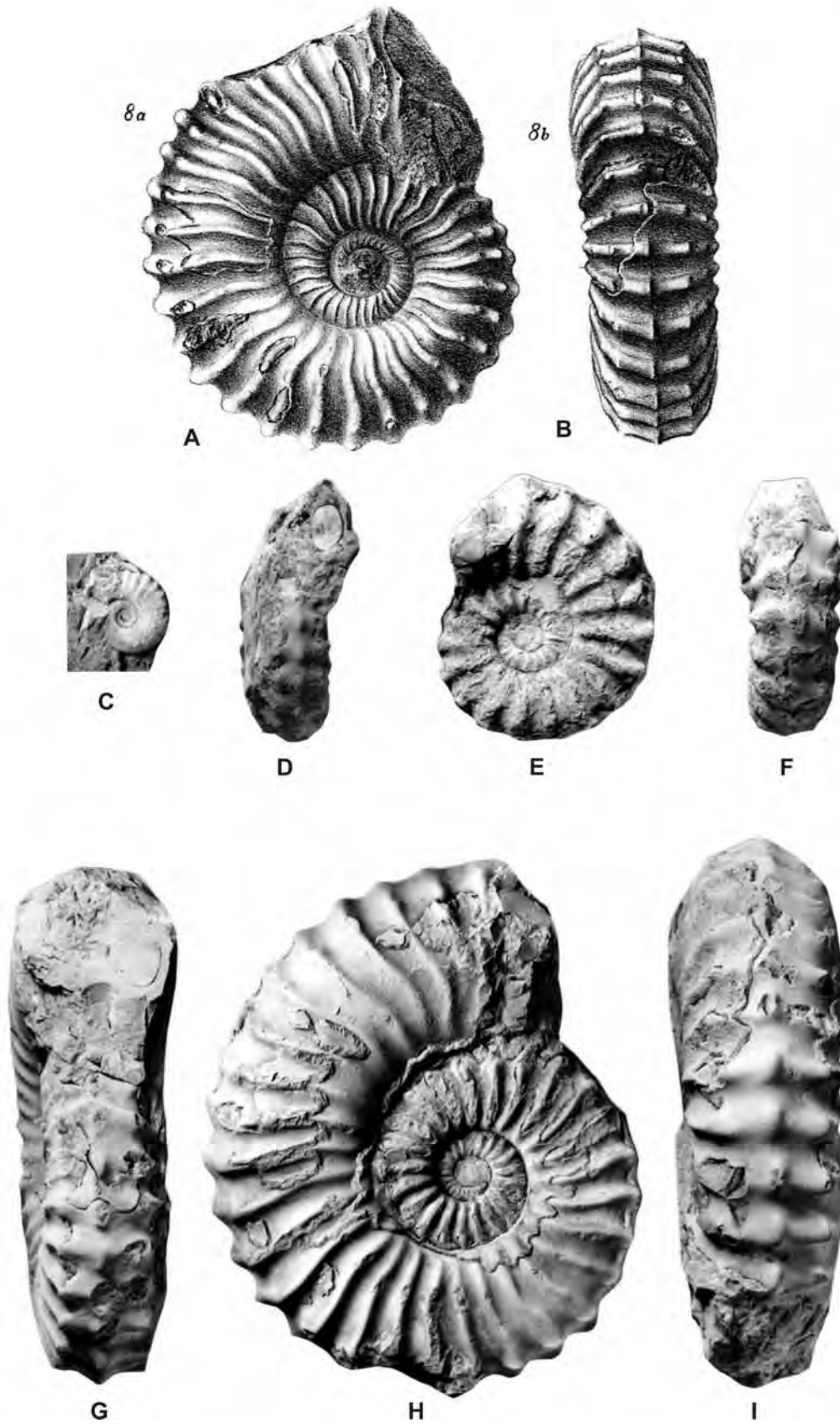
The original illustration of the holotype, from Ubaque, Cundinamarca, Colombia (Gerhardt 1897, pl. 4, fig. 8) is reproduced here as Fig. 17A,B.

Specimens BMNH C74786–74788 are shown in Fig. 17C–I. They were collected by J. V. Harrison on the road between Viola and Portillo, Cundinamarca, Colombia. Owen (1971, p. 135) drew attention to these specimens, and commented as follows: ‘From specimens in the British Museum (Nat. Hist.) e. g. BMNH C74786 [Fig. 17D–F herein]... It is apparent that these so-called ‘*Prollyelliceras*’ are in fact large specimens of *Lyelliceras* of *lyelli-ulrichi* type, the ornament of which modifies at diameters which are as yet unknown in the old world. *Prollyelliceras* is considered here to be a junior subjective synonym of *Lyelliceras*...’.

A comparison of Figs 17A–B and 17G–I, leaves no doubt that the largest of these specimens is conspecific with

*prorsocurvatum* of Gerhardt, as are the smaller specimens. The smallest of these, BMNH C74788 (Fig. 17C) is a juvenile 10 mm in diameter. Coiling is very evolute, the umbilicus comprising 25% approximately of the diameter. The whorls expand slowly, and are initially smooth. Ornament at the beginning of the adapertural half of the outer whorl consists of relatively coarse concave ribs on the ventrolateral shoulder that sweep forwards on the venter, forming an obtuse ventral chevron with a pronounced siphonal ridge at the apex. As size increases, these ribs extend down to the umbilical shoulder, and are relatively strong, prorsiradiate, flexuous, and bear a small outer ventrolateral tubercle.

BMNH C74787 (Fig. 17D–F) has a maximum preserved diameter of 55 mm, the adapertural end of the outer whorl damaged. Where complete, the costal dimensions are: D = 47.9 (100); Wb = 18.6 (38.8); Wh = 19.1 (39.9); Wb:Wh = U = 19.3 (40.3). Coiling is very evolute, the umbilicus broad and shallow, with a low, convex wall and broadly rounded shoulder. The intercostal whorl section is compressed; the costal whorl section is slightly compressed, with the greatest breadth at the inner ventrolateral tubercles, and the venter markedly fastigiate. There are 19–20 exclusively primary ribs on the outer whorl. They arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and are coarse and recti- to incipiently rursiradiate on the inner and middle flank. They bear an inner ventrolateral bulla, connected by a coarse prorsiradiate rib to a strong outer ventrolateral clavus, these clavi linked across the markedly fastigiate venter by a broad, coarse transverse rib that bears a strong siphonal clavus.



**Fig. 17.** A–G, *Prollyliceras prorsocurvatum* (Gerhardt, 1898). A, B, Copy of Gerhardt (1898, pl. 4, fig. 8), the holotype of *Acanthoceras prorsocurvatum* Gerhardt, 1898, the type species of *Raphimlayites* Etayo-Serna, 1979; the original is from Ubaque, Cundinamarca, Colombia. C, BMNH C74788; D–F, BMNH C74787; G–I, BMNH C74786, all from the road between Viola and Portillo, Cundinamarca, Colombia. Figures A and B are  $\times 0.84$ , originally presumed to be  $\times 1$ . Figure C is  $\times 1.5$ ; D–I are  $\times 0.75$ .



BMNH C74786 (Fig. 17G–I) is a complete, or near-complete, adult with a 180° sector of body chamber. The costal dimensions are: D = 118.7 (100); Wb = 34.2 (28.8); Wh = 42.1 (35.5); Wb:Wh = 0.81; U = 46.3 (39.0). Coiling is very evolute, the umbilicus broad and shallow, the umbilical wall low, subvertical and convex, the umbilical shoulder broadly rounded on the phragmocone and adapical part of the body chamber, but flattening and inclining outwards to merge imperceptibly with the flanks on the adapertural part of the body chamber. There are 22 ribs on the penultimate whorl. They arise at the umbilical seam, and strengthen without developing into an umbilical bulla. They are straight and recti- to feebly prorsiradiate on the innermost flank, flexing back and slightly rursiradiate on the exposed mid-flank region. The outer whorls are compressed, with the greatest breadth below mid flank, the costal whorl section with broadly convex flanks, the venter concave on either side of the siphonal clavi. There are 31 narrow, distant primary ribs on the outer whorl. At the adapical end of the outer whorl they are feebly prorsiradiate on the umbilical wall, shoulder, and innermost flank, flexing back and rursiradiate on the outer flank, where they bear a weak inner ventrolateral bulla, from which the ribs flex forwards, strengthen, and are feebly concave, linking to a strong, feebly clavate outer ventrolateral tubercle, linked to a strong, siphonal clavus by a strong, transverse rib. The siphonal clavi are linked by a weak siphonal ridge. As size increases, the inner ventrolateral bullae weaken rapidly, becoming a mere angulation in the rib profile, and even this is lost on the adapertural 120° sector of the body chamber. The ribs become increasingly prorsiradiate on the umbilical wall, shoulder, and innermost flank, flex back and are convex on the inner flank, and markedly rursiradiate on the outer flank. The outer ventrolateral tubercle round and weaken progressively as size increases, but persist to the largest preserved diameter, as do the progressively weakening siphonal clavi.

The body chamber ribs of this specimen and the holotype (Fig. 17A,B) are more markedly flexuous than those of the holotype of *Prolyelliceras peruvianum* (Fig. 15), whereas those on the penultimate whorl of the present specimen follow a more similar course.

#### *Prolyelliceras ulrichi* (Knechtel, 1947)

The lectotype, by the subsequent designation of Robert (2002, p. 149), is USNM 152942, the original of Knechtel (1947, pl. 32, fig. 1, figured here as Fig. 18C,D), and from Pongo de Manseriche in northern Peru. The holotype is a complete, or near-complete adult 115 mm in diameter, with at least half a whorl of body chamber preserved. Coiling is very evolute. The ribs are straight, narrow, and prorsiradiate, arising at the umbilical seam. They lack umbilical bullae, and pass straight across the venter, bearing inner and outer ventrolateral and siphonal tubercles to the end of the body chamber. In his description, Knechtel referred to a specimen in which the full complement of tubercles was present at a diameter of 18 mm. Benavides-Cáceres (1956, p. 464, pl. 51, figs 4–7, reproduced here as Fig. 19/4–7) illustrated two beautifully preserved specimens. The smaller, figured  $\times 2.2$  (Fig 19/6,7) would, if found in isolation, be taken for a juvenile *Brancocheras*.

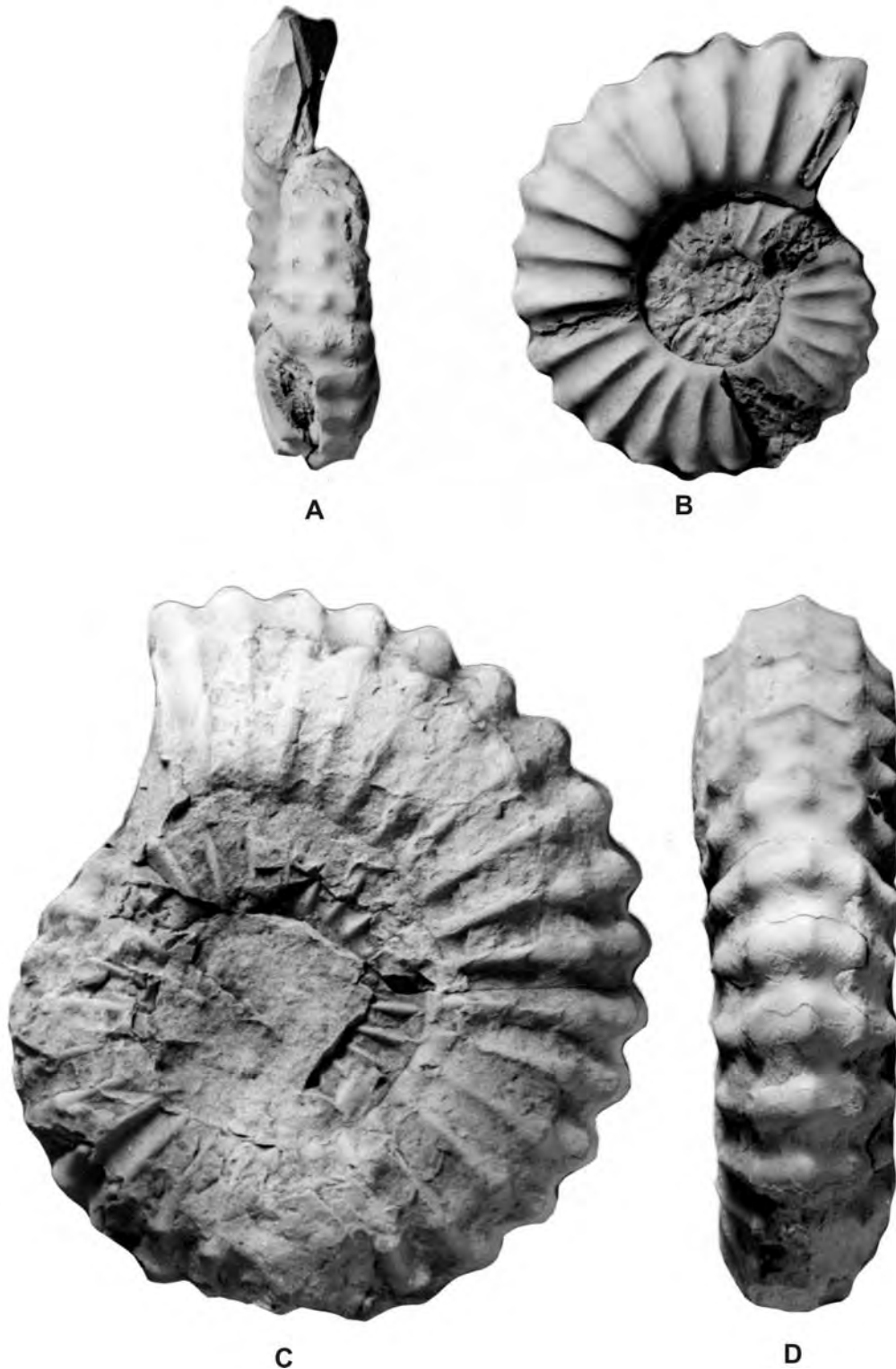
*Prolyelliceras ulrichi* is the closest member of this South American group to *Lyelliceras lyelli*. They differ in the absence of the early ‘*Brancocheras*’-like growth stage in *lyelli*, the presence of umbilical bullae, the notching of the umbilical seam to accommodate the inner ventrolateral tubercles of the preceding whorl, and the much smaller adult size of *lyelli* (compare Figs 11A–G and 18C,D).

#### *Prolyelliceras mathewsi* (Knechtel, 1947)

The lectotype of *Prolyelliceras mathewsi* (Knechtel, 1947) (p. 101, pl. 21, fig.3, text-fig. 6), by the subsequent designation of Robert (2002, p. 151), is USNM 152906. It is illustrated here as Fig. 18A,B. The lectotype is more compressed and higher-whorled than specimens of *ulrichi*, with fewer ribs, 24–25 per whorl versus an estimated 32, and is trituberculate, with only siphonal and a single row of ventrolateral tubercles to a diameter of 60 mm, at which size the inner ventrolateral row appears. *Prolyelliceras ulrichi* has a full complement of five rows of tubercles from a diameter of 18 mm according to Knechtel.

We have studied an extensive suite of ammonites from the Pariatambo Formation of Huanzola, Huanunco, Peru (OUM KU405–448). They occur in black bituminous limestone, and correspond to the assemblage described by Steinmann (1881, p. 133, ‘in einem schwarzen, bituminösen Kalkstein’) and Obata *et al.* (1975). The assemblage comprises rare *Oxytropidoceras*, rare *Prolyelliceras ulrichi* (Fig. 21F (*pars*), P–R), common *Eubrancocheras aegoceratoides* (Steinmann, 1881) (Fig. 21F (*pars*); see also Kennedy 2004, fig. 5 a–t, z), and *Prolyelliceras mathewsi* (Fig. 20A–M, 21A–D, G–I, M–V). Steinmann’s *Acanthoceras lyelli* (1881, pl. 7, fig. 3) is a *Prolyelliceras mathewsi* in our view. At small diameters, specimens referred to *mathewsi* have prorsiradiate feebly flexuous ribs that strengthen across the flanks, and terminate in thickened endings on either side of the venter, which is arched and smooth between (Fig. 20I,J), thereafter at diameters of around 10–12 mm, the rib endings strengthen into weak ventrolateral clavi, a low rounded mid-ventral ridge appears (Fig. 20E–F, L–M), producing an obtusely fastigate venter. A progressively better differentiated siphonal clavus appears, opposite the ventrolateral clavi, at variable diameters, from as little as 15 mm in some specimens (Fig. 20F,G,K,M). A row of inner ventrolateral clavi appear much later in ontogeny. OUM KU445 (Fig. 21D,E), lacks well-differentiated inner ventrolateral clavi to the maximum preserved diameter of 43 mm. In OUM KU447 (Fig. 21M–O), they appear abruptly at a diameter of 55 mm, in an individual with a distinctive fastigate venter and relatively feeble siphonal tubercles. In OUM KU 441 (Fig. 21S,T), they begin to develop, initially as mere angulations on the rib, at around 40 mm diameter.

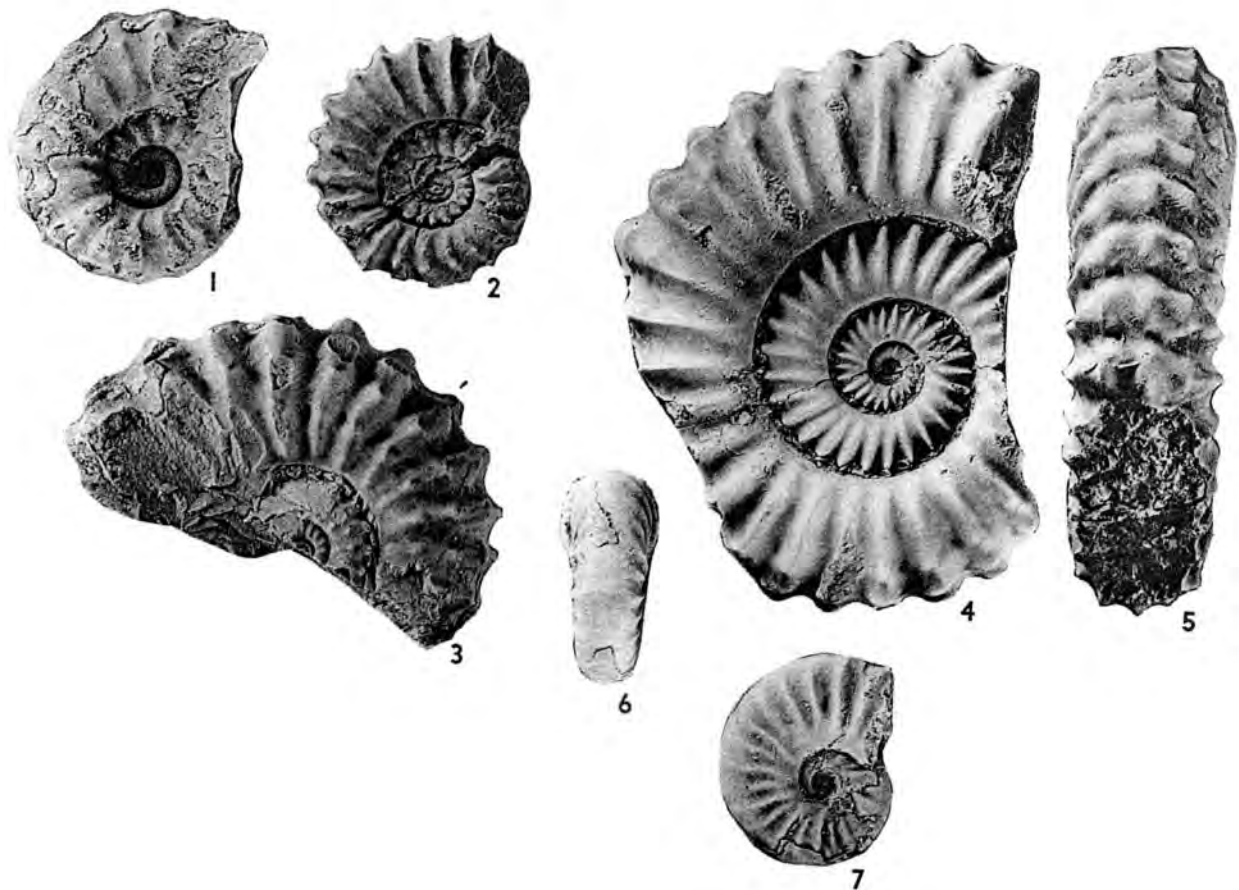
Interpretation of this assemblage is problematic. The range chart in Robert (2002, fig. 50) shows *Prolyelliceras* [‘*Ralphimlayites*’] *mathewsi* preceding both *P.* [‘*R.*’] *ulrichi* and *Eubrancocheras aegoceratoides*, without overlap, and this is confirmed in the text. However, his figure 56 (redrawn here as Fig. 14) shows *P.* [‘*R.*’] *mathewsi* and *ulrichi* co-occurring in his *ulrichi* Subzone, where *E. aegoceratoides* first occurs. On the basis of ranges in Robert’s figure 50, the



**Fig. 18. A, B**, the lectotype of *Prolyelliceras mathewsi* (Knechtel, 1947), the original of Knechtel (1947, pl. 21, fig. 3), from the Albian of Pongo de Manseriche in northern Peru, USNM152906. **C, D**, the lectotype of *Prolyelliceras ulrichi* (Knechtel, 1947), the original of Knechtel (1947, pl. 23, fig. 1), from the Albian of Pongo de Manseriche in northern Peru, USNM152942. All figures are  $\times 1$ .

assemblage discussed here is condensed. On the basis of his figure 56, it is not. The early ontogeny of our specimens of *Prolyelliceras mathewsi* are very brancoceratid-like, as with the early whorls of *P. ulrichi* as figured by Benavides-Cáceres (1956, pl. pl. 51, figs 6, 7; Fig. 19/6,7, herein), con-

firmed, in our view, the origin of the South American lyelliceratine homoeomorphs in the Brancoceratinae, presumably *Parabrancoceras* Breistroffer, 1951. There are juveniles in the material we have studied that are difficult to refer to *P. mathewsi* versus *Eubrancoceras aegoceratoides*:



**Fig. 19.** Copy of Benavides-Cáceres (1956, pl. 51, figs 1–7). Figs 1–3 were referred to *Lyelliceras lyelli* (d'Orbigny, 1841); 1 is AMNH 27868:6; 2 is AMNH 27868:4; 3 is AMNH 27868:2, from the Pariahuanca Formation of the Pomachacha section in northern Peru. Figs 4–7 were referred to *Lyelliceras ulrichi* Knechtel, 1947; 4, 5 are AMNH 27870:3; 6, 7 are AMNH 27870:1, from the Pariatambo Formation in northern Peru. No locality is given. Figures 1–5 are  $\times 1$ ; 6, 7  $\times 2.2$ .

*Eubrancoceras* may thus be a paedomorphic dwarf offshoot of *Prollyelliceras mathewsi*, which precedes it in the South American sequence.

#### *Prollyelliceras alternatum* (Robert, 2002)

The holotype of '*Ralphimlayites*' *alternatum* Robert, 2002\* (p. 154, pl. 21, figs 7–7; pl. 22, figs 1–3) is the original of Robert's pl. 21, figs 7–9, 99-RB114B-37, from the Chulec Formation of Pongo de Rentema, Peru. Robert described this species as having ribs that alternate in position on the opposite flanks as the diagnostic character, which it shares with *Lyelliceras pseudolyelli*. He described the tuberculation as consisting of lateral tubercles on the inner third of the flanks that are reduced to mere points, ventrolateral and ventral clavi that alternate. However, the side view of the holotype (Robert 2002, pl. 21, fig. 7) appears to show an inner ventrolateral row.

We have seen two specimens in the collections of the University of Berkeley that may be *Prollyelliceras alternatum*. UBC C-1687 (Fig. 22A,B) has a nucleus an estimated 54 mm in diameter. There are 11 coarse distant straight prorsiradiate ribs, with strong umbilicolateral bullae, and strong, clavate inner ventrolateral clavi.

The outer whorl includes a 120° sector of body chamber.

\*In his thesis, dated 2001, Robert gave the name as '*alternum*', but in the subsequent (2002) published copy the name is given as '*alternatum*'.

The intercostal whorl section is compressed oval, with a whorl breadth to height ratio of 0.92. The costal section is trapezoidal-polygonal, with a feebly fastigiata venter. A 120° sector of body chamber bears 10 ribs. At the adapical end, there are feeble umbilical bullae, effacing inner ventrolateral bullae, strong outer ventrolateral clavi, and feeble, low siphonal clavi. The ribs alternate in position on the opposite sides of the venter, and are linked by a low, broad, effacing rib. The inner ventrolateral tubercles efface progressively, but the outer ventrolateral clavi persist to the largest preserved diameter. UBC-C1693 (Fig. 22C,D) is a well-preserved complete adult, 100 mm in diameter. Coiling is very evolute, the umbilicus comprising 41% of the diameter, broad and shallow, with a feebly convex, outward-inclined umbilical wall. There are 19–20 primary ribs on the outer whorl. On the phragmocone and adapical part of the body chamber the strong ribs bear coarse umbilical bullae, coarse conical inner ventrolateral and coarse outer ventrolateral clavi. The subdued ventral clavi are more numerous than the outer ventrolateral. The latter alternate in position, and outer ventrolateral and siphonal clavi are linked by a low, subdued zigzag rib. Umbilical bullae and inner ventrolateral tubercles efface on the adapertural part of the body chamber, and the outer ventrolateral clavi decline markedly. These specimens are a South American analogue of *Lyelliceras pseudolyelli*. They differ in the apparent smaller

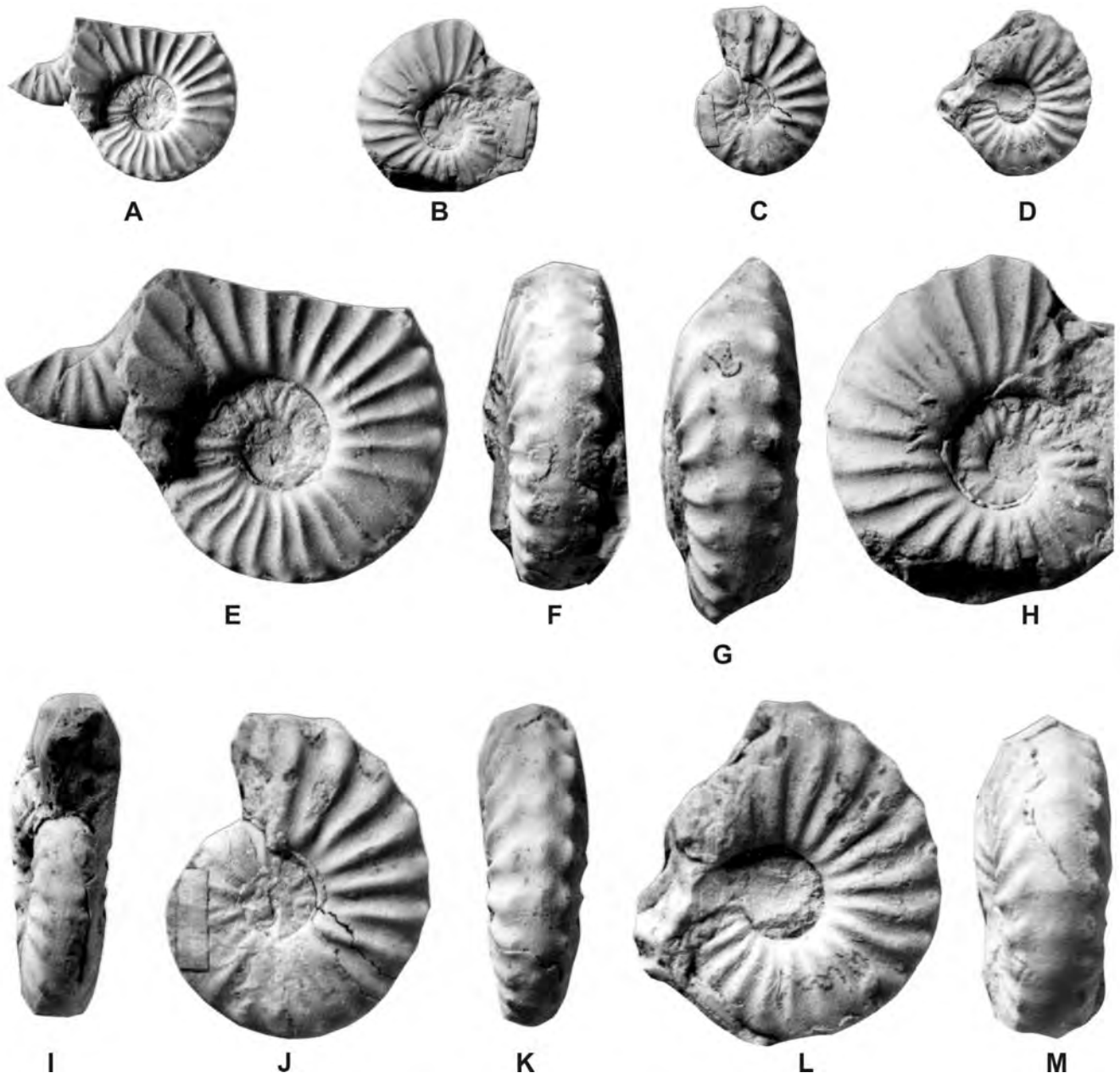


Fig. 20. A–M, *Prollyliceras mathewsi* (Knechtel, 1947). A, E, F, OUM KU422; B, G, H, OUM KU420; C, I, J, K, OUM KU625; D, L, M, OUM KU426. All specimens are from the Pariatambo Formation of Huaraz, Huánuco, Peru. Figures A–D are  $\times 1$ ; E–M are  $\times 2$ .

size of adult *pseudolyelli*, persistent ventrolateral tubercles, and more numerous, stronger, and persistent siphonal tubercles (compare Fig. 22A–D and Figs 11H–K, 28).

#### '*Lyelliceras*' *flandrini* Dubourdieu, 1953

The type material of *Lyelliceras flandrini* and its varieties (Dubourdieu 1953, p. 27, p. 3, figs 6–22) are illustrated here as Fig. 13H–GG. The material, originally in the collections of the Collège de France, Paris, is currently housed in the collections of the Université de Lyon-Villeurbanne, and is from the Lower Albian of the Monts du Mellègue in western Algeria. The species has been recognized subsequently in the lower Lower Albian *Leymeriella tardefurcata* Zone of southeast France and Austria (Kennedy in Kennedy *et al.* 2000, p. 681, figs 44a,c,d; 47g,i,k,m). The wide stratigraphic sepa-

ration between this species and the earliest members of the *Tegoceras-Lyelliceras* lineage (Fig. 2) suggests that, like the South American taxa discussed above, *flandrini* is a distinct taxon, unrelated to later *Lyelliceras*, from which it is distinguished by the smooth, compressed innermost whorls followed by a growth stage with delicate flank ornament of flexuous primary and intercalated ribs (Fig. 13L–N, R–T), and adult ornament of coarse flexuous bullate and non-bullate primaries and intercalated ribs with ventral clavi, linked by a coarse rib to coarse siphonal clavi, the ventrolateral clavi near-opposite to slightly offset across the venter (Fig. 13O–Q, U–V, BB–FF). The early growth stages of '*Lyelliceras flandrini*' differ in no significant respects from those of *Prollyliceras prorsocurvatum* described above (compare Fig. 13L–N and Fig. 17C,D), suggesting affinity.

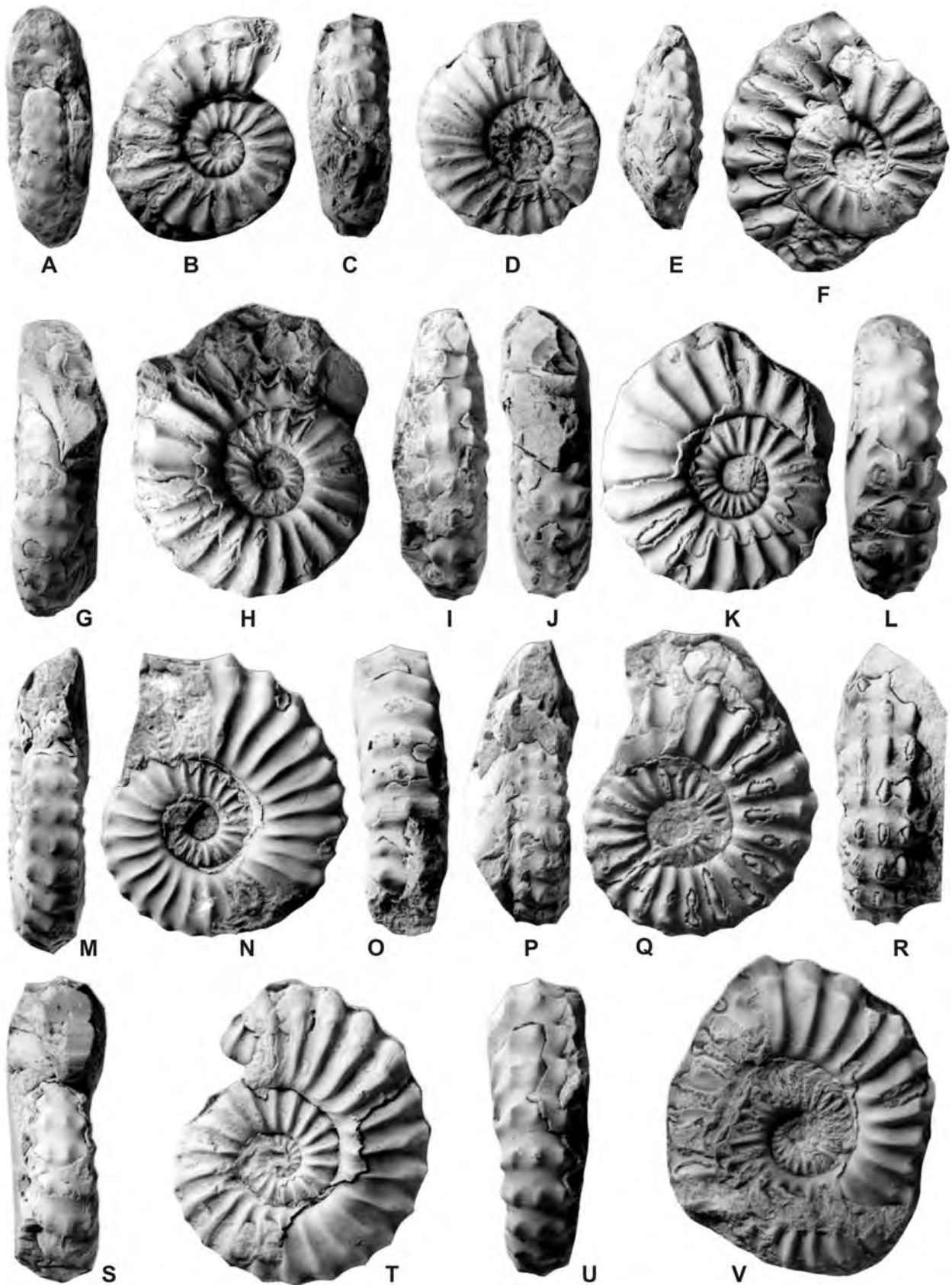
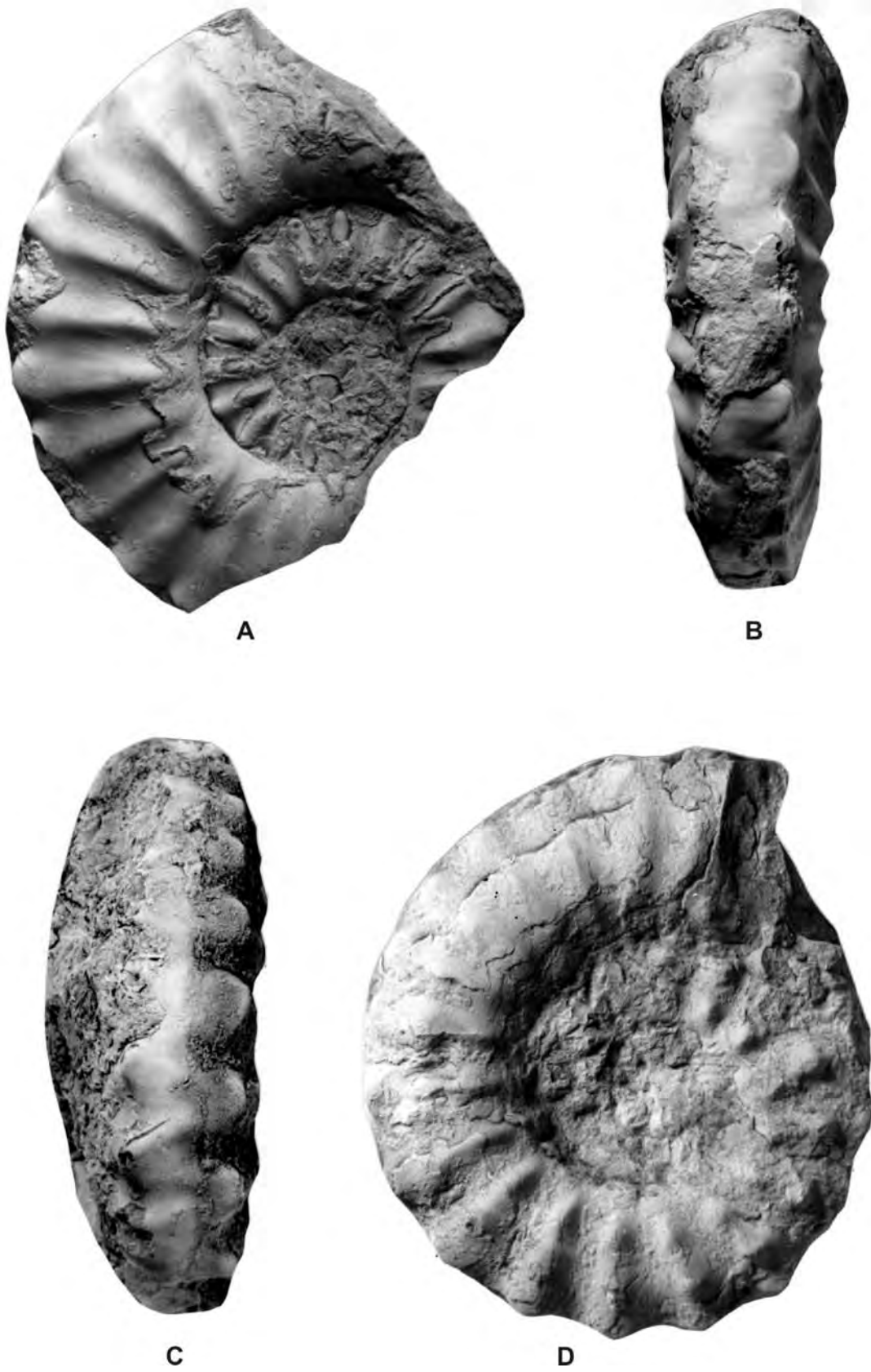


Fig. 21. A–E, G–I, M–V, *Polyelliceras mathewsi* (Knechtel, 1947). A–C, OUM KU444; D–E, OUM KU445; G–I, OUM KU443; J–L, OUM KU448; M–O, OUM KU447; S, T, OUM KU441; U, V, OUM KU440. F, *Eubrancoceras aegoceratoides* (Steinmann, 1881) and *Polyelliceras ulrichii* (Knechtel, 1947), OUM KU438. P–R, *Polyelliceras ulrichi* (Knechtel, 1947), OUM KU442. All specimens are from the Pariatambo Formation of Huaraz, Huánuco, Peru. All figures are x1.



**Fig. 22. A–D, *Prolyellicerus alternatum*** (Robert, 2002). **A, B**, UBC C-1687; **C, D**, UBC-1693, from the Sierra Orientale of Colombia. All figures are x1.

However, *flandrini* never develops an inner ventrolateral tubercle and has intercalated ribs, suggesting it merits sub-generic or generic separation from *Prolyellicerias*.

#### '*Prionotropis*' *radenaci* Pervinquieré, 1907

The lectotype, here designated, of '*Prionotropis*' *radenaci* Pervinquieré, 1907 (p. 251) is the original of his pl. 12, fig. 4; text-fig. 10, illustrated here in Fig. 13A–G. It is from the Lower Albian of Djebel Hamaima, in western Tunisia. The paralectotype is a fragment consisting of a single chamber and the adapical end of the body chamber; the maximum preserved whorl height is 5.7 mm. The species was meticulously described by Pervinquieré. The first five whorls are smooth (Fig. 13E,G). The outer whorl of the nucleus of the holotype is 15.8 mm in diameter. There are sixteen ribs at the ventrolateral shoulder. The ribs are predominantly feebly flexuous prorsiradate primaries with weak to strong umbilical bullae, tiny conical inner ventrolateral tubercles, and stronger outer ventrolateral clavi linked to strong siphonal clavi by low, broad, triangular ribs. The siphonal clavi are linked by a low siphonal ridge. The outer 120° whorl fragment of the lectotype is body chamber (Fig. 13A–D), possibly of an adult. The maximum preserved costal whorl height is 11 mm. Parts of six feebly flexuous prorsiradate primary ribs are preserved. They are very narrow, and separated by very wide interspaces. They arise at the umbilical seam, and strengthen into tiny, sharp bullae that weaken progressively towards the adapertural end of the fragment. The umbilical bullae are connected by a narrow rib to a tiny inner, and larger outer ventrolateral bulla. A strong high rib links to tiny conical siphonal tubercles that are linked by a feeble siphonal ridge.

The early ontogeny of *radenaci* is comparable to that of *Prolyellicerias prorsocurvatum*, and the presence of inner and outer ventrolateral and siphonal tubercles in the succeeding growth stage indicate it to be further probable *Prolyellicerias* species.

### STRATIGRAPHIC IMPLICATIONS OF THE PRESENT STUDY

The recognition of members of the European *Tegoceras*-*Lyellicerias*-*Pseudobrancoceras* lineage in KwaZulu allows the precise dating of the faunas of the Lower and basal Middle Albian of the area, and a reassessment of the relative positions of the scattered localities where they occur. In 1975, we recognized the presence of an unconformity between the uppermost Aptian and lowest Albian in KwaZulu. Above the unconformity, which encompasses an unquantified interval we termed Albian I, we recognized the following:

#### Albian II

Abundant *Douvilleiceras*, including forms close to *D. orbignyi* Spath, *D. mammillatum* (von Schlotheim) and varieties. Other ammonites are scarce, but include poorly preserved desmoceratids and lycoceratids.

#### Albian III

*Douvilleiceras* is abundant, but in contrast to Albian II, diverse other ammonites occur. A *Damesites?* sp. nov. is common [= *Carinophylloceras collignoni* Klinger *et al.*, 1975], whilst *Lyellicerias* species, including *L. lyelli*

(d'Orbigny) and *L. pseudolyelli* (Parona & Bonarelli) are frequent, together with '*Neosilesites*' [= *Umsinenoceras linguatuberculatum* Kennedy, *et al.*, 1979], *Phylloceras* (*Hypophylloceras*), '*Beudanticeras*', '*Cleonicerias*', and '*Sonneratia*' species, *Rossalites*, *Ammonoceratites*, abundant *Angaudryceras sacya* (Forbes), *Eubrancoceras* aff. *aegoceratoides* (Steinmann) [= *Pseudobrancoceras versicostatum* (Michelin, 1838)], and *Oxytropidoceras* species.'

Albian II and part of Albian III can be assigned to the Lower Albian *Douvilleiceras mammillatum* Zone of Owen (1988). The presence of *Lyellicerias lyelli* at localities previously referred to Albian II indicates the presence of the basal *lyelli* Subzone of the Middle Albian, the substage being defined by the first appearance of the species (Hart *et al.* 1996).

Within Albian III four successive faunas can now be distinguished. These are, from oldest to youngest, as follows:

The *Tegoceras mosense*/*Aioloceras* fauna (localities 35, 36, 53, 142, and 175). The assemblage is *Phylloceras* (*Hypophylloceras*) *velledae* (Michelin, 1838) *Carinophylloceras collignoni* Klinger *et al.*, 1975, *Ammonoceratites* (*Ammonoceratites*) *mahadeva* (Stoliczka, 1865), *Anagaudryceras sacya* (Forbes, 1846), *Umsinenoceras linguatuberculatum* Kennedy *et al.*, 1979, *Puzosia saintoursi* Collignon, 1963, *Bhimaites* sp., *Alopecoceras ankeritterae* Kennedy & Klinger, 1978, *Aioloceras* sp., *Tegoceras mosense*, *Protanisoceras* (*Rossalites*) aff. *superbus* (Collignon, 1949), *Douvilleiceras mammillatum* (von Schlotheim, 1813), *D. scabrosum* Casey, 1962, and *D. orbignyi* Hyatt, 1903. On the basis of the occurrence of *T. gladiator* in western Europe, this fauna corresponds to the interval comprising the *Cleonicerias floridum* Subzone of the *Sonneratia chalcensis* Zone to the *Protohoplites puzosianus* Subzone of the *Otohoplites auritifformis* Zone of western Europe, the mid-*mammillatum* Zone of authors (Fig. 2).

The *Tegoceras camatteanum* fauna (locality 175). The assemblage is *Tegoceras camatteanum*, *Douvilleiceras inaequinodum* (Quenstedt, 1849), and *D. mammillatum*, together with the bivalve *Actinoceramus salomoni salomoni* (d'Orbigny, 1850). This corresponds to the *Otohoplites bulliensis* and *Hoplites steinmanni* subzones of the *Otohoplites auritifformis* Zone of western Europe: upper *mammillatum* Zone.

The *Lyellicerias pseudolyelli* fauna occurs in the area southwest of Ndumu, and comprises *L. pseudolyelli* and *Douvilleiceras* spp. This corresponds to the *pseudolyelli* Subzone of the *Otohoplites auritifformis* Zone of Western Europe: uppermost Lower Albian.

The *Lyellicerias lyelli* fauna (localities 154 and 176). The assemblage is: *Oxytropidoceras alticarinatum* Spath, 1922, *Lyellicerias lyelli*, *L. pseudolyelli*, *Pseudobrancoceras versicostatum*, *Mkuzeiella andersoni* Klinger & Kennedy, 2008, *Douvilleiceras clementianum* (d'Orbigny, 1841), *D. inaequinodum*, and the bivalve *Actinoceramus concentricus sensu lato* of Crampton (1996) This corresponds to the *lyelli* Subzone of the *Hoplites dentatus* Zone of western Europe: basal Middle Albian.

### REPOSITORIES OF SPECIMENS

The following abbreviations are used to indicate the repositories of specimens cited in the text:

AMNH: American Museum of Natural History, New York.

BMNH: The Natural History Museum, London.  
 EMP: École national Supérieur des Mines, Paris, now housed in the Université de Lyon-Villeurbanne.  
 ID: Institut Dolomieu, Grenoble.  
 FSL: Université de Lyon, Villeurbanne.  
 MMNP: Laboratoire de Paléontologie, Muséum National d'Histoire Naturelle, Paris.  
 OUM: Oxford University Museum of Natural History.  
 SAM: Natural History Collections Department, Iziko South African Museum, Cape Town.  
 UBC: University of Berkley, California.  
 UBGD: UFR Sciences de la Terre, Université de Bourgogne, Dijon (Collignon Collection).  
 USNM: U.S. National Museum of Natural History, Washington D. C.

### FIELD LOCALITIES

Details of field localities are given by Kennedy & Klinger (1975); further descriptions of these localities are deposited in the Geological Collections, Oxford University Museum of Natural History, The Natural History Museum, London, and the Natural History Collections Department, Iziko South African Museum, Cape Town.

### CONVENTIONS

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

### SYSTEMATIC PALAEONTOLOGY

Family **LYELLICERATIDAE** Spath, 1921

Genus ***Tegoceras*** Hyatt, 1903

Type species

*Ammonites mosensis* d'Orbigny, 1841, p. 237, pl. 67, figs 5–7, by the original designation of Hyatt (1903, p. 84).

Diagnosis

Small to medium-sized, moderately involute to evolute, whorl section compressed to depressed. Ribs alternate in position across the venter, and may be linked by a zigzag ventral rib. Tuberculation variable: feeble to incipient umbilical bullae and poorly developed ventrolateral clavi, or well-developed umbilical bullae and ventrolateral clavi, accompanied by lateral tubercles in some species. A siphonal ridge may show incipient development of siphonal clavi in species transitional to *Lyelliceratas*. Ornament may efface on adult body chamber.

Discussion

*Rauliniceratas* H. Douvillé, 1911 (p. 85) was originally proposed with *Hoplites gladiator* Bayle, 1878 (pl. 45, figs 1, 2) as type species, and is a junior synonym, *gladiator* of Bayle being a junior synonym of *mosense* of d'Orbigny (the subsequent change of the type species of *Tegoceras* to *Ammonites*

*cammateanus* d'Orbigny, 1841, by H. Douvillé in 1912 (p. 298) is invalid). *Seunesiceratas* Breistroffer, 1953 (p. 74), introduced as a subgenus of *Rauliniceratas*, is a *nomen nudum*.

The following species are referred to the genus:

- Tegoceras mosense* (d'Orbigny, 1841), p. 237, pl. 67, figs 5–7, revised below.  
*Tegoceras camatteanum* (d'Orbigny, 1841), p. 241, pl. 69, figs 1, 2, revised below.  
*Tegoceras senebrianum* (Pictet, 1852) in Pictet & Roux, p. 73, pl. 6, fig. 7.  
*Tegoceras gladiator* (Bayle, 1878), pl. 45, figs 1, 2, revised below, a synonym of *T. mosense*.  
*Tegoceras seunesi* (Parona & Bonarelli, 1897), p. 48, pl. 14, fig. 9.  
*Tegoceras collignoni* (Breistroffer, 1953), in Breistroffer & Villoutreys, p. 74, as *nomen novum* for *Ammonites lyelli cinquième variété* of Pictet & Campiche, 1860, p. 198, pl. 24, fig. 6; see below.  
*Tegoceras quadratum* Destombes, 1977b, p. 39, pl. 1, fig. 2; a synonym of *T. collignoni*: see below  
*Tegoceras miles* Casey, 1978, p. 627, pl. 100, figs 3–4; a synonym of *T. mosense*.  
*Tegoceras* sp. Casey, 1978, p. 629, pl. 100, fig. 6; a synonym of *T. mosense*  
*Tegoceras gladiator evoluta* Destombes, 1979, p. 107, pl. 4–23, fig. 3; a synonym of *T. mosense*.  
*Tegoceras gladiator attenuata* Destombes, 1979, p. 107, pl. 4–23, fig. 3; a synonym of *T. mosense*.  
? *Tegoceras benavidescaceresi* Etayo-Serna, 1979, p. 82, pl. 11, fig. 8; text-figs 8z, 8z'; Robert, 2002, p. 137, pl. 17, figs 1–3; perhaps a lyelliceratine homoeomorph.  
*Tegoceras armatum* Destombes, 1983, p. 50, pl. 1, fig. 2; a synonym of *T. collignoni*; see below.  
*Tegoceras* n. sp. aff. *gladiator* (Bayle, 1878), Young, 1993, p. 172, figs 2: 24, 28, 29; 3: 3, 4.  
*Tegoceras* sp. 1, Young, 1993, p. 173, figs 2: 12, 13, 19–21; 3: 12–13.  
*Tegoceras maderoense* Young, 1993, p. 174, figs 2: 22–23, 25–27, 30–43; 3: 6, 8–11.

Occurrence

Upper Lower Albian, southern England, France, Switzerland, northern Spain, northern Mexico, Venezuela, northern Pakistan, Madagascar, and KwaZulu, South Africa.

***Tegoceras mosense*** (d'Orbigny, 1841)

Pl. 1, figs 10–13; Figs 3H–O, R–T

1841 *Ammonites Mosensis* d'Orbigny, p. 237, pl. 67, figs 5–7.

1850 *Ammonites Mosensis* d'Orbigny, p. 123.

1878 *Hoplites gladiator* Bayle, pl. 45, figs 1, 2.

1903 *Tegoceras mosense* (d'Orbigny); Hyatt, p. 84.

1907 *Acanthoceras gladiator* (Bayle); Jacob, p. 102.

1910 *Acanthoceras camatteanum* d'Orbigny; Pervinquier, p. 40, pl. 42, figs 38, 39.

1911 *Ammonites mosensis* d'Orbigny; R. Douvillé, fiche 219, figs 1, 5–7. H<sup>1</sup>–H<sup>1b</sup>.

1911 *Ammonites gladiator* Bayle; R. Douvillé, fiche 219, figs P<sup>1</sup>–P<sup>1a</sup>, fig. 2.

1911 *Rauliniceratas gladiator* (Bayle); H. Douvillé, p. 85.



- 1912 *Raulinicerias gladiator* (Bayle); H. Douvillé, p. 298, fig. 13. (Dated 1911, but published May 1912.)
- 1912 *Raulinicerias mosense* (d'Orbigny); H. Douvillé, fig. 14. (Dated 1911, but published May 1912.)
- 1925 *Raulinicerias gladiator* (Bayle); Spath, p. 78.
- 1931 *Raulinicerias gladiator* (Bayle); Spath, p. 313.
- 1932 *Acanthoceras gladiator* (Bayle); Larcher, p. 42.
- 1938 *Raulinicerias gladiator* Bayle; Roman, p. 431.
- 1947 *Raulinicerias gladiator* Bayle sp.; Breistroffer, p. 24.
- 1953 *Raulinicerias gladiator* Bayle; Breistroffer & de Villoutreys, p. 70.
- 1957 *Tegoceras gladiator* (Bayle); Casey, p. 32, pl. 7, fig. 8; text-fig. 1a.
- 1961 *Tegoceras gladiator* (Bayle); Casey, pp. 546, 610.
- 1966 *Tegoceras gladiator* (Bayle); Schindewolf, p. 713.
- 1977b *Tegoceras mosense* (d'Orbigny); Destombes, p. 40.
- 1978 *Tegoceras gladiator* (Bayle); Casey, p. 624, pl. 100, figs 1, 2; text-fig. 283a–f.
- 1978 *Tegoceras miles* Casey, p. 627, pl. 100, figs 3, 4; text-fig. 238g.
- 1978 *Tegoceras mosense* (d'Orbigny); Casey, p. 100, fig. 5; text-fig. 239.
- ?1978 *Tegoceras* sp. Casey, p. 629, pl. 100, fig. 6.
- 1979 *Tegoceras gladiator* (Bayle), 1878, including varieties *evoluta* and *attenuata*; Destombes, p. 105, pl. 4–19, figs 2,3; pl. 4–23; figs 1–3.
- 1979 *Tegoceras mosense* (d'Orbigny), 1841; Destombes, p. 107, text-fig. 4–13.
- ?1982 *Tegoceras gladiator* (Bayle); Renz, p. 39, pl. 5, fig. 16; text-fig. 26a,b.
- 1995 *Tegoceras mosense* (d'Orbigny, 1841); Latil, p. 352, pl. 1, figs 1–5; text-fig. 18.
- 1996 *Tegoceras mosense* (Orbigny); Wright, p. 147, fig. 113. 1a–d,
- 2006 *Tegoceras mosense* (d'Orbigny, 1841); Kennedy & Juignet *in* Gauthier, p. 87, pl. 35, fig. 2.

### Type

The holotype, by monotypy, is EMP A.1396, the original of d'Orbigny (1841, p. 237, pl. 67, figs 5–7) from Varennes, Meuse, France, refigured here as Fig. 3H,N,O.

### Material

SAM-PCZ22182, from the Lower Albian, Albian III, Mzinene Formation, locality 175, SW of Ndumu. OUM KX 4925–6 (parts of one specimen), from the Lower Albian, Albian III, Mzinene Formation, locality 53, north of Hluhluwe.

### Dimensions

	D	Wb	W	Wb:Wh	U
KX4925–6	45.0 (100)	–(–)	17.3 (38.4)	–	15.7 (34.9)
PCZ22182	66.6 (100)	–(–)	24.1 (36.2)	–	27.7 (41.6)
EMP 1275c	74.5 (100)	19.9 (26.7)	28.8 (38.7)	0.69	24.8 (33.2)

### Description

OUM KX4925–6 (Fig. 3I–K) is a very well-preserved, almost wholly septate juvenile with a maximum preserved

diameter of 45 mm. Coiling is very evolute, the umbilical seam notched to accommodate the ventrolateral tubercles of the preceding whorl. The umbilicus is broad (34.9% of the diameter), shallow, with a low, convex, outward-inclined wall that merges with the broadly rounded umbilical shoulder. The whorl section is rounded-trapezoidal in intercostal section, and each flank defines a half trapezium in costal section (a consequence of the alternation of the ribs), the greatest breadth at the umbilicolateral bulla. There are 13 ribs on the outer whorl, which alternate on the opposing flanks. They arise at the umbilical seam, and are very coarse, straight and prorsiradiate, strengthening into coarse umbilicolateral bullae that link to a blunt, thickened ventrolateral node. The ribs are connected by a low, broad zigzag ventral rib.

SAM-PCZ22182 (Pl. 1, figs 10–13) is a somewhat battered individual with a maximum preserved diameter of 66 mm approximately. Much of the outer whorl appears to be body chamber, but the position of the final septum cannot be established. Coiling is very evolute, the broad umbilicus comprising 41.6% of the diameter. The umbilical wall is feebly convex, outward-inclined, and merges imperceptibly with the umbilical shoulder. The intercostal whorl section is compressed oval, with the greatest breadth below mid-flank. The inner to middle flanks are broadly rounded, the outer flanks convergent, the ventrolateral shoulders broadly rounded, the broad venter feebly convex. The costal whorl section is slightly depressed, rounded-trapezoidal, with a whorl breadth to height ratio of 1, the greatest breadth around mid-flank. The flanks are broadly rounded, converging to more narrowly rounded ventrolateral shoulders and a broad, feebly convex venter. The ornament is partially visible on the inner whorls at a diameter of 22–23 mm approximately. Thirteen to fourteen coarse crowded primary ribs arise at the umbilical seam, and strengthen across the umbilical shoulder. They are straight and prorsiradiate, coarse and very crowded, broadening and strengthening across the flanks. They strengthen further on the ventrolateral shoulder, and develop into poorly differentiated ventrolateral tubercles that are little more than an angulation in the rib profile. This style of very coarse ornament is also present on the adapical part of the outer whorl. The venter is exposed, and a broad swelling zigzags between the ribs, which alternate in position on either side of the venter. There are eight ribs on the adapertural half of the outer whorl. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, without developing into a bulla. They are broad, straight, and prorsiradiate on the flanks, and strengthen progressively towards the ventrolateral shoulder. They are less crowded than on the inner whorls. The ribs reach their maximum strength on the ventrolateral shoulder, where there is a marked angulation in the rib profile, but no clearly differentiated ventrolateral tubercle. A broad rib zigzags between the tubercles.

### Discussion

The holotype of *Tegoceras mosense* is shown in Fig. 3H,N,O. The specimen is a phosphatic internal mould of a 90° sector of internal mould from the adapical end of the body chamber, 59 mm long, crushed and deformed, with an esti-

mated maximum whorl height of 29.5 mm, and a whorl breadth to height ratio of 0.81. The umbilical wall of the fragment merges imperceptibly with the broad rounded umbilical shoulder. The inner flanks are broadly rounded, the outer flanks flattened and convergent. The ventrolateral shoulders are broadly rounded, the venter feebly convex. Five primary ribs arise at the umbilical seam. They are feeble, low, straight and prorsiradiate to the umbilical shoulder, where they strengthen markedly, flex back, and are coarse, blunt, prorsiradiate and concave on the flanks, where they are accompanied by riblets and striae. The ribs weaken over the venter, which is crossed by delicate feebly convex riblets and striae. There are traces of spiral ridges on the flanks.

The dorsum (Fig. 3H) shows the inner whorls to have borne coarse ribs that alternate in position on either side of the venter, across which they are connected by a blunt rib that zigzags between the ends of the ribs.

The ornament preserved in the dorsum of the holotype fragment led authors from R. Douvillé (1912) onwards to regard *mosensis* of d'Orbigny and *gladiator* of Bayle as congeneric, or conspecific. The latter position is favoured here. The holotype of *T. gladiator* is shown in Fig. 3R–T. It agrees closely with the larger KwaZulu specimen. It consists of phosphatized phragmocone with half a whorl of body chamber preserved, and retains traces of phosphatized shell in places. Coiling is very evolute, the umbilicus broad and shallow, comprising up to 35.5% of the diameter on the phragmocone. The umbilical shoulder is low, and broadly rounded. The whorl section is compressed, with a costal whorl breadth to height ratio of 0.69. The flanks are broadly rounded in intercostal section, and trapezoidal in costal section. Sixteen primary ribs arise at the umbilical seam on the outer whorl, and are alternate in position on opposing flanks. They strengthen into strong umbilical bullae on the phragmocone and adapical part of the body chamber. These bullae give rise to single coarse, distant, prorsiradiate primary ribs that flex back, and terminate in a coarse, rounded ventrolateral tubercle. A coarse rib zigzags across the venter between these tubercles. The bullae weaken somewhat on the last few ribs of the phragmocone, and become feebly concave. The umbilical seam egresses, suggesting the approach of maturity, as does the crowding of the last few sutures. When the ventral ornament is compared with that of the holotype of *mosense*, the principal differences are the greater differentiation of the ventrolateral tubercles of the holotype of *gladiator* at the same diameter.

*Tegoceras* was comprehensively revised by Casey (1978, p. 623) who recognized *mosense* of d'Orbigny and *gladiator* of Bayle as separate species. He described the latter as 'much more compressed ... with early degeneration of sculpture, the whorls from 40–45 mm diameter becoming smooth, with subelliptical section, rounded venter, and high, flat umbilical slope'. These apparent differences are explained by the fact that Casey based them on what is clearly a microconch (Casey 1978, pl. 100, fig. 5). The holotype of *mosense* is, in contrast, the adapical end of the body chamber of a macroconch. *Tegoceras miles* Casey, 1978 (p. 627, pl. 100, figs 3, 4) was separated from *T. gladiator* on the basis of 'its much greater evolution, more inflated whorls, and its much

more tumid and bulging ribs'. He also recognized a further species, that he did not name, 'a compressed ... form with flexuous ribbing' (1978, p. 629, pl. 100, fig. 6). These differences are those of individuals, rather than species, in our view.

Destombes (1979) described *Tegoceras* from the Albian of Aube, France, and recognized dimorphism, illustrating a body chamber he referred to *mosense* as a microconch, and recognizing the holotype of the species as a fragment of a macroconch. He also described 34 individuals from two successive horizons that he referred to *Tegoceras gladiator*. He noted that individuals from his lower, *floridum* Subzone, had a 'nodosité ventro-latérale arrondie', whereas in those from the succeeding *larcheri* Subzone (= *raulinianus* Subzone herein), the tubercle tended to 'soit à se pincer, soit à disparaître.' He recognized two varieties. *Tegoceras gladiator* var. *evoluta* (Destombes, 1979, p. 107, pl. 4–23, fig. 3) was characterized by the early loss of the umbilical bullae, and var. *attenuata* (1979, p. 107, pl. 4–23, figs 1, 2), was characterized by weakening of the ribs. This latter group comprised 14 individuals, in which Destombes recognized clear size dimorphism, with adult macroconchs 61–65 mm in diameter, and adult macroconchs 90–100 mm in diameter.

In the latest revision of *Tegoceras*, Latil (1995, p. 351, pl. 67, figs 5–7) treated *gladiator* and *mosense* as synonyms, a view with which we concur, from our own examination of the types and other available French material in the BMNH, ID, MNHP, UBGD, and FSL Collections.

With only two KwaZulu specimens, it is not possible to speculate on the exact age of the individuals in terms of the early and late forms recognized by Destombes.

The *Acanthoceras camatteanum* of Pervinquier (1910, p. 40, pl. 42, figs 38, 39; Fig. 4C–M herein), comes from the the Albian of Pont des Gorges, Aumale, Algeria. The larger of Pervinquier's specimens (Fig. 4C–E, F–G) is 27.2 mm in diameter, and has poorly differentiated umbilical and ventrolateral tubercles associated with a relatively stout whorl section; it appears to be *T. mosense*.

*Tegoceras gladiator* (Bayle) of Renz (1982, p. 39, pl. 5, fig. 16; text-fig. 26a,b) has a distinct mid-flank tubercle, and appears more closely allied to later *Tegoceras*, such as *T. camatteanum* (see below).

#### Occurrence

*Tegoceras gladiator* is only well dated in the Boreal Hoplitid Faunal province, where it occurs mainly in condensed phosphatic units. The record in more expanded sequences indicates a range from the *Cleonicerias floridum* Subzone of the *Sonneratia chalensis* Zone to the *Protohoplites puzosianus* Subzone of the *Otohoplites auritifformis* Zone, the mid-*Douvilleicerias mammillatum* Zone of authors (Fig. 2). The geographic distribution extends from southern England to France, Venezuela, and KwaZulu in South Africa.

#### *Tegoceras camatteanum* (d'Orbigny, 1841)

Pl. 1, figs 7–9, 14, 15; Pl. 2, figs 1–25; Figs 3A–G, P, Q; 6/4a, b; 7C–F

1841 *Ammonites camatteanus* d'Orbigny, p. 241, pl. 69, figs 1, 2.

- 1850 *Ammonites camatteanus* d'Orbigny; d'Orbigny, p. 123.
- 1860 *Ammonites lyelli* d'Orbigny; Pictet & Campiche, troisième variété, p. 198 (*pars*), pl. 24, fig. 4 only.
- 1860 *Ammonites lyelli* d'Orbigny; Pictet & Campiche, cinquième variété, p. 198 (*pars*), pl. 24, fig. 8 only.
- 1887 *Acanthoceras camattei* d'Orb. Sp.; Seunes, p. 562, pl. 13, fig. 3.
- 1897 *Acanthoceras camatteanum* (d'Orbigny); Parona & Bonarelli, p. 100.
- non 1910 *Acanthoceras camatteanum* d'Orbigny; Pervinquière, p. 40, pl. 42, figs 38, 39.
- 1931 *Raulinicerias camatteanum* (d'Orbigny); Spath, p. 313.
- 1949 *Raulinicerias camattei* (d'Orbigny); Collignon, p. 121.
- ?1957 *Tegoceras camatteanum* d'Orbigny; Almela & de la Revilla, p. 32, pl. 8, fig. 2.
- 1978 *Tegoceras camatteanum* (d'Orbigny); Casey, p. 624.
- 1979 *Tegoceras camatteanum* (d'Orbigny), 1841; Destombes, p. 108.
- ?1979 *Tegoceras* aff. *camatteanum* (d'Orbigny), 1841; Destombes, p. 109, pl. 4–13, fig. 3.
- ?1982 *Tegoceras gladiator* (Bayle); Renz, p. 39, pl. 5, fig. 6; text-figs 26a,b.
- 1992 *Tegoceras seunesi* (Parona & Bonarelli); Cooper, fig. 2.
- 1995 *Tegoceras camatteanum* (d'Orbigny, 1841); Latil, p. 352 (*pars*); pl. 1, fig. 13 only; text-fig. 19c, l only.
- 1995 *Lyelliceras* sp. cf. *pseudolyelli* (Parona & Bonarelli, 1897); Latil, pl. 2, fig. 6.
- 1997 *Tegoceras* cf. *camatteanum* (d'Orbigny); Delamette *et al.*, pl. 21, fig. 4.
- 2006 *Tegoceras camatteanum* (d'Orbigny, 1841); Kennedy & Juignet *in* Gauthier, p. 88, pl. 35, fig. 1.

### Types

The lectotype, by the subsequent designation of Kennedy & Juignet *in* Gauthier (2006, p. 88, pl. 35, fig. 1) is BMNH 37629, (*ex* Astier Collection), from the condensed Albian of Escragnolles, Apes-Maritimes, France, illustrated here as Fig. 3A–D. Previous authors have referred to pl. 69, figs 1, 2, in d'Orbigny (1841) as being the 'type' (Latil 1995, p. 354), but as pointed out by Kennedy & Juignet, the matter is more complex, as with so many of d'Orbigny's illustrations, which are clearly composites. D'Orbigny stated that his species was based on material from Causelles, near Grasse (Var), sent by Duval on behalf of a Monsieur Camatte, after whom he named the species, and a second example from Escragnolles (Var), collected by Astier. The illustrations are said to be based on a specimen in the 'collection de M. Camatte à Grasse, et de la mienne' – in other words, a composite. The catalogue of the d'Orbigny Collection lists the following: '5768 T Escragnolles 1'. The specimen survives, and is a *Tegoceras mosense* 51.5 mm in diameter. It bears no resemblance whatsoever to d'Orbigny's figures. The catalogue also records '5678 Clar 3'; there are actually four specimens; three are *Tegoceras mosense* (one illustrated here as Fig. 4W–Y; one is a *Tegoceras seunesi* (Parona & Bonarelli, 1897) (Fig. 4A,B,Q, R). The specimen sent to d'Orbigny by Camatte has not been traced, leaving the Astier specimen as the only surviving syntype, now lectotype of the species. It was figured

previously by Latil (1995, pl. 2, fig. 6) as *Lyelliceras* sp. cf. *pseudolyelli* (Parona & Bonarelli, 1897).

### Material

OUM KX9954–9958, 9959a–c, 9960, and SAM PCZ22191 from locality 175, SW of Ndumu, Mzinene Formation, Lower Albian, Albian III. SAM A2126 and SAM-PCZ22187, without locality data. Preservation suggests the Ndumu area.

### Dimensions

	D	Wb	W	Wb: Wh	U
KX9959b	33.0 (100)	10.1 (30.6)	14.9 (45.2)	0.68	8.6 (26.1)
KX9955c	34.5 (100)	11.2 (32.5)	15.8 (45.8)	0.71	10.2 (29.6)
BMNHC37629	39.8 (100)	13.4 (33.4)	15.4 (38.7)	0.87	13.7 (34.4)
KX9958c	43.2 (100)	15.5 (35.8)	17.4 (40.3)	0.89	14.4 (33.3)
PCZ22187	66.5 (100)	–(–)	24.9 (37.4)	–(–)	23.6 (35.5)

### Description

OUM KX9959b (Pl. 2, figs 8–13) shows the inner whorls of the weakly ornamented variant of the species, visible at a diameter of 19 mm approximately. Coiling is moderately evolute; the umbilicus is very shallow, with a very low, feebly convex, outward-inclined wall and broadly rounded shoulder. The whorl section is compressed, with a costal whorl breadth to height ratio of 0.78, the inner flanks feebly convex in intercostal section, the outer flanks flattened and convergent, the ventrolateral shoulders broadly rounded, the venter obtusely fastigate. At the smallest diameter visible, ornament consists of low, prorsiradiate ribs, with incipient umbilical bullae. OUM KX9959a (Pl. 2, figs 1, 2) is a fragment of a comparably weakly ornamented individual, a 120° sector of whorl with a minimum whorl height of 10.8 mm. Eight ribs are preserved. They arise at the umbilical seam, and are markedly prorsiradiate, strengthening across the umbilical wall, and developing into delicate, elongated umbilical bullae that give rise to widely separated narrow primary ribs that strengthen across the flanks, with a mid-lateral bulla that strengthens progressively as size increases. All ribs terminate in a large ventrolateral clavus. OUM KX9959b (Pl. 2, figs 8–13) continues the ontogeny, and appears to be an adult microconch, with a maximum preserved diameter of 33.5 mm, and a 240° sector of body chamber preserved. The shallow umbilicus comprises 26.1% of the diameter and is very shallow, the feebly convex umbilical wall sloping outwards, the umbilical shoulder broadly rounded. The inner to mid-flank region is very feebly convex in intercostal section, the outer flanks are flattened and convergent, the ventrolateral shoulders quite narrowly rounded, the venter broadly fastigate. There are 18 primary ribs on the outer whorl. They arise at the umbilical seam, strengthen across the umbilical wall and shoulder, where they are feebly prorsiradiate, and develop into a delicate umbilical bulla that strengthens progressively as size increases. The ribs are narrow, rounded and prorsiradiate, and strengthen progressively across the flanks. All bear a

stronger rounded to weakly bullate lateral tubercle, and terminate in a stronger ventrolateral clavus. The ribs and clavi alternate in position on either side of the venter, and are linked by a barely perceptible low, rounded ridge that zigzags between the clavi. The last few ribs weaken and crowd, the umbilical and lateral bullae decline, indicating proximity to the adult aperture.

OUM KX9955 (Pl. 2, figs 22–25) is a strongly ornamented variant of the species, of the same diameter approximately as the previous specimen. There are 14 coarse, narrow prorsiradiate ribs on the outer whorl. Umbilical bullae strengthen progressively, and move out to an inner lateral position at the greatest preserved diameter, where they are close to the stronger, progressively coarsening outer lateral bullae. The outer ventrolateral clavi are strong, pinched, and rise high above the venter, across which they are linked by a low, broad, rounded ridge that zigzags between them.

OUM KX9958 (Pl. 2, figs 3–7) is an even more strongly ornamented individual, 42.6 mm in diameter, with eight strong ribs on the outer half whorl. The umbilical bullae are only slightly weaker than the lateral bullae in this specimen, and have migrated out to an inner lateral position.

SAM-PCZ22187 (ex A2126) (Pl. 2, figs 14, 15, 19–21) is interpreted as an adult macroconch. It is 66.4 mm in maximum preserved diameter, with just over half a whorl of body chamber preserved. There are nine coarse, distant primary ribs on the outer whorl, with the same pattern of tuberculation as in the previous specimens at the adapical end. Towards the adapertural end of the body chamber the umbilical bullae decline, indicating the proximity to the adult aperture. The venter lacks the low ridge that zigzags between the ventral clavi of juveniles; there is an obscure siphonal ridge.

#### Discussion

The lectotype of *Tegoceras camatteanum* (Fig. 3A–D) is a phosphatic internal mould with a 240° sector of body chamber preserved. Coiling is fairly evolute, the umbilicus comprising 34.4% of the diameter, shallow, with a low, outward-inclined umbilical wall. The whorl section is compressed, oval in intercostal section, and polygonal in costal section, with the greatest breadth at the lateral tubercle. There are 16 distant primary ribs on the outer whorl. They arise at the umbilical seam and strengthen into weak umbilical bullae. Straight and prorsiradiate on the flanks, they bear an outer lateral tubercle, connected by a broad rib to stronger ventral clavi that alternate in position across the markedly convex venter. An ill-defined low, broad, rounded ridge zigzags between them. This specimen finds a close match in the feebly ornamented KwaZulu specimens, as does a further French specimen from Escragnoles (Pl. 2, figs 16–18).

A macroconch from the condensed Albian of Les Ravix, Isère, France (EMP, ex Stuer Collection) is shown in Fig. 3P, Q. It is 58.7 mm in diameter and retains phosphatized shell. As a result, the position of the final septum cannot be established. Coiling is very evolute, the umbilicus broad and shallow, comprising 34.6% of the diameter. Forty-four per cent of the previous whorl is covered. The umbilical wall inclines outwards, merging with the feebly convex umbilical shoulder. The whorl section is compressed subtrapezoidal in intercostal section. The costal section is polygonal, convex

on the inner to mid flank, and concave on the outer flank; the greatest breadth is around mid-flank. The venter is convex between the ribs and concave costally. There are 18 primary ribs on the outer whorl. They arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and are straight and prorsiradiate across the flanks. There are small but clearly differentiated umbilical bullae, stronger outer lateral bullae, and strong ventrolateral clavi. The ribs alternate across the venter. There is also a low siphonal ridge.

It will be seen from the description of the present material that we interpret *Tegoceras camatteanum* as a compressed species with distant ribs that bear umbilical bullae that migrate out to an inner flank position in later ontogeny, stronger lateral bullae, and even stronger ventrolateral clavi, linked by a low zigzag ridge in early and middle growth. The lectotype and other French specimens (Fig. 3A–G, P, Q; Pl. 2, figs 16–18) fall within the range of variation of the KwaZulu material. On this basis, *Tegoceras senebrianum* (Pictet, 1847) (*in* Pictet & Roux, p. 73, pl. 6, fig. 7; holotype, by monotypy, refigured by Delamette *et al.* 1997, pl. 21, fig. 2; Fig. 4T–V) is maintained as a separate species, distinguished from the present species on the basis of the absence of umbilical and lateral tubercles. The holotype is no. 19089 in the collections of the Muséum d'Histoire naturelle de Genève, ex Pictet Collection, and comes from the condensed Albian of Sommier d'Aval [Reposoir of Pictet]. The characters of the species are very clearly set out by Pictet (*in* Pictet & Roux 1860, p. 73): 'Coquille discoïdale, comprimée, ornée par tours de seize côtes saillantes, régulières simples et égales; chacun d'elles commence à l'ombilic, sans former des tubercles, puis se déprime en avant vers le dos pour se relever en un fort tubercle comprimé; ses tubercles sont alternes en le dos à peu près plat.'

The holotype of *Tegoceras seunesi* (Parona & Bonarelli, 1897) (p. 100 (48), pl. 14 (4), fig. 9) is the original of Pictet & Campiche (1860, pl. 24, fig. 5 (Fig. 6/5a,b, herein)), from the 'Gault Moyen' of Sainte-Croix, Switzerland ('Consideriamo come tipo di questa forma la figura di PICTET et CAMPICHE, che abbiamo citato in sinonima': Parona & Bonarelli, p. 100 (48)); they also referred the original of Seunes (1887, pl. 13, fig. 3 (Fig. 7E,F)), and of their own pl. 14 (5), fig. 9 (Fig. 5), in the collections of the Museo Geologico, Turin, to their new species. *Tegoceras seunesi* differs from *T. camatteanum* in lacking umbilical bullae, while the specimen figured by Parona & Bonarelli (Fig. 5) has a straight mid-ventral ridge, rather than the low zigzag ridge of the present species.

*Tegoceras collignoni* (Breistroffer, 1953) (*in* Breistroffer & de Villoutreys, p. 74, introduced as *nomen novum* for *Ammonites lyelli cinquième variété* of Pictet & Campiche 1860, p. 198, pl. 24, fig. 6; Fig. 6/6a,b, herein) and its synonyms differs from the present species in lacking umbilical bullae and having a whorl section that may be very depressed.

*Tegoceras benavidescaceresi* Etayo-Serna, 1979 (p. 82, pl. 11, fig. 8; text-figs 8z, 8z') is a giant species: Etayo-Serna's figure is 90 mm in diameter, and said to be at a magnification of 1.06. Robert (2002, p. 137, pl. 17, figs 1–3) illustrated a specimen 160 mm in diameter. The holotype has weak umbilical and lateral bullae, stronger ventrolateral

clavi, and a row of siphonal clavi, which distinguish it from the present species, and, indeed, would exclude it from *Tegoceras*, as Robert (2002, p. 137) noted. No such tubercles are present in his Peruvian specimen. *Tegoceras benavidescaceresi* may well be a further South American lyelliceratinae homoeomorph.

The tiny *Tegoceras* from northern Mexico described by Young (1993) differ from the present species in their flexuous ribbing, and lack of umbilical and lateral tubercles.

#### Occurrence

The material from southeast France comes from condensed phosphatic units at localities such as Escragnoles, and can be dated no more precisely than upper Lower to lower Middle Albian (Gebhard 1979, 1982). Material from Reposoir in Haute-Savoie, France (Delamette *et al.* 1997, pl. 21, fig. 4) come from the even more condensed Horizon de Romme. There is no modern account of the context of the Sainte-Croix material. The doubtful juvenile from the Sierra de Ricote, Murcia, Spain, is imprecisely dated.

#### *Tegoceras collignoni* (Breistroffer, 1953)

Pl. 1, figs 1–6; Fig. 6/6a,b

1860 *Ammonites lyelli* Leymerie, *cinquième variété* Pictet & Campiche, p. 198, pl. 24, fig. 6.

1953 *Raulinicerias* (*Seunesicerias*) *collignoni* Breistroffer in Breistroffer & de Villoutreys, p. 74.

1977b *Tegoceras quadratum* Destombes, p. 39, pl. 1, fig. 2.

1979 *Tegoceras* sp. Destombes, text-fig. 4–12.

1983 *Tegoceras armatum* Destombes, p. 50, pl. 1, fig. 2.

#### Types

The holotype, by monotypy, of *Raulinicerias* (*Seunesicerias*) *collignoni* Breistroffer in Breistroffer & de Villoutreys, 1953, p. 74, introduced as *nomen novum* for *Ammonites lyelli* Leymerie, *cinquième variété* Pictet & Campiche, p. 198, pl. 24, fig. 6, reproduced here as Fig. 6/6a,b, is the original of that specimen, from the ‘Gault Moyen’ of Sainte-Croix, Canton Vaud, Switzerland.

The holotype of *Tegoceras quadratum* Destombes, 1977b, is the original of Destombes (1977b, p. 40, pl. 1, fig. 2) from the upper part of the *Otohoplites raulinianus* Subzone of the *Otohoplites auritifomis* Zone of Bully-Saint-Martin l’Hortier, Normandy, France. The holotype of *Tegoceras armatum* is the original of Destombes (1983, p. 50, pl. 1, fig. 2) a specimen in the G. Ermiger Collection; there are three paratypes, from the upper Lower Albian *Otohoplites bulliensis* Subzone of the *Otohoplites auritifomis* Zone of Bully-Saint-Martin l’Hortier, Normandy, France.

#### Material

SAM-PCZ22186, in a preservation indicating it to be from Albian III of the Ndumu area.

#### Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ22186	32.8 (100)	13.6 (41.50)	13.7 (42.0)	0.99	10.4 (31.7)

#### Description

SAM-PCZ22186 is a well-preserved phragmocone with recrystallized shell preserved. Coiling is very evolute, the

umbilicus comprising 31.7% of the diameter, of moderate depth, with a convex, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The intercostal whorl section is oval, with the greatest breadth around mid-flank. The costal whorl section is polygonal, with the greatest breadth at the inner ventrolateral tubercle. Fifteen to sixteen primary ribs arise at the umbilical seam on the outer whorl, and strengthen across the umbilical wall and shoulder. There are no umbilical bullae. The ribs are rounded, coarse, straight and prorsiradiate across the flanks. All develop a conical inner ventrolateral tubercle that is connected by a broad rib to a coarse outer ventrolateral clavus. The ribs and clavi alternate in position on either side of the venter, and are connected by a subdued swelling that zigzags between the clavi. There is a low, rounded, coarse siphonal ridge that is feebly undulose, with incipient clavi that are more numerous than the outer ventrolateral.

#### Discussion

The holotype (Fig. 6/6a,b) is more depressed than the present specimen, with 13 ribs per whorl, but shows the same rib and tubercle development. Both also possess a mid-ventral ridge, the incipient development of clavi more obvious in the present specimen.

#### Occurrence

Upper Lower Albian, *Otohoplites bulliensis* Subzone of the *Otohoplites auritifomis* Zone of Bully-Saint-Martin l’Hortier, Normandy, France; Lower Albian of Switzerland. Albian III of the Ndumu area.

#### Genus *Lyelliceras* Spath, 1921

##### Type species

*Ammonites lyelli* d’Orbigny, 1841, p. 255, pl. 74, figs 1, 2, by the original designation of Spath (1921, p. 222, footnote).

##### Diagnosis

Small to medium-sized, evolute to very evolute, whorl section compressed to depressed, slowly expanding. Umbilical, inner and outer ventrolateral tubercles appear at an early developmental stage. In middle and later growth there are umbilical bullae, inner and outer ventrolateral and siphonal clavi. Ribs and ventrolateral clavi are opposite, or alternate across the venter. Siphonal clavi are more numerous than, or equal in number to the ventrolateral clavi. In the former, an irregular zigzag ventral rib links outer ventrolateral and siphonal clavi. In the latter, ventral ribs are regular and transverse.

##### Discussion

The differences between *Lyelliceras* and the various homoeomorphous developments referred to ‘*Prolyelliceras*’ and ‘*Ralphimlayites*’ are discussed above. In the present interpretation, the following species are referred to *Lyelliceras*:

*Lyelliceras lyelli* (d’Orbigny, 1841), p. 255 (*pars*), pl. 74, figs 3 (*pars*) 4, ?fig. 5, *non* figs 1, 2, 3 (*pars*) (= *L. pseudolyelli* (Parona & Bonarelli, 1897).

*Lyelliceras? huberianum* (Pictet, 1847), p. 82, pl. 7, fig. 7.

*Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897), p. 99 (47), pl. 14 (5), figs 1, 2.

- Lyelliceras hirsutum* (Parona & Bonarelli, 1897), p. 99 (47), pl. 14 (5), figs 4–6 (synonym of *L. pseudolyelli*).
- Lyelliceras nodosa* (Etheridge, 1907), p. 87, pl. 4, figs 1, 2 (synonym of *L. lyelli*).
- 1927 *Lyelliceras lyelli* (d'Orbigny) var. *ornatissima* Ciry, 1927 p. 562, pl. 6, fig. 4 (synonym of *L. lyelli*).
- Lyelliceras gratum* (van Hoepen, 1968), p. 161, pl. 5 (synonym of *L. lyelli*).
- Lyelliceras vaasti* Destombes *et al.*, 1973 (p. 90, pl. 3, fig. 9; text-fig. 9.3).
- Lyelliceras latili* sp. nov., described below.

#### Occurrence

Uppermost Lower Albian to lower Middle Albian. Southern England, France, Switzerland, northern Spain, central Iran, Venezuela, Madagascar, and KwaZulu, South Africa.

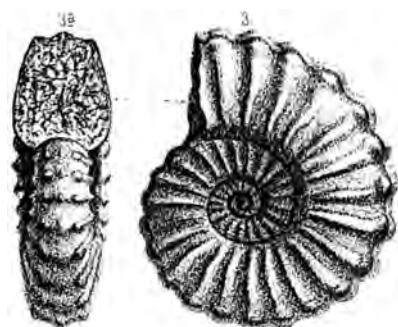
#### *Lyelliceras lyelli* (d'Orbigny, 1841)

- Pl. 3, figs 1–11, 17–21; Pl. 4, figs 1–5, 7–9, 11–14, 17, 18; Pl. 5, figs 1–11, 14–20; Pl. 6, figs 1–16, 19, 20; Pl. 7, figs 1, 2, 5, 9; Pl. 8, figs 1–13, 16–20; Figs 9/3 (*pars*), 4; 10, 11A–G; 12P–R; 24P–Y; BB–GG; 25A–C, I, 'P, Q, U; 26A–D.
- 1841 *Ammonites Lyelli* Leymerie; d'Orbigny, p. 255 (*pars*), pl. 74, fig. 3 (*pars*), fig. 4, ?fig. 5, *non* figs 1, 2, 3 (*pars*) (= *L. pseudolyelli* (Parona & Bonarelli, 1897)).
- 1842 *Ammonites Lyelli* Leymerie, p. 15, 22, pl. 17, fig. 16.
- 1846 *Ammonites Lyelli* Leymerie; Leymerie, pl. 5, fig. 2.
- 1846 *Ammonites Lyelli* Leymerie; Quenstedt, p. 138, pl. 10, fig. 3.
- non* 1847 *Ammonites Lyelli* d'Orbigny; Pictet, p. 80, pl. 7, fig. 6 (= *Lyelliceras pseudolyelli*).
- 1850 *Ammonites Lyelli* Leymerie; d'Orbigny, p. 123 (*pars*).
- non* 1860 *Ammonites Lyelli* Pictet & Campiche, p. 197, pl. 24, figs 1–8 (= *Lyelliceras* and *Tegoceras*, div. spec.).
- 1878 *Acanthoceras Lyelli* Leymerie; Bayle, pl. 74, figs 5, 6, *non* 4 (= *L. pseudolyelli*).
- 1897 *Acanthoceras lyelli* Leymerie; Parona & Bonarelli, p. 96, pl. 13(4), figs 6–12.
- 1907 *Douvilleiceras nodosa* Etheridge, p. 87, pl. 4, figs 1, 2.
- ?1923 *Acanthoceras* del grupo de *A. Lyelli* Leymerie; Böse, p. 160, pl. 11, fig. 3 (indeterminate).
- 1927 *Acanthoceras lyelli* Desh. In Leym.; Ciry, p. 561, pl. 6, figs 2, 3.
- 1927 *Lyelliceras lyelli* (d'Orbigny) var. *ornatissima* Ciry, p. 562, pl. 6, fig. 4.
- 1930b *Lyelliceras lyelli* (d'Orbigny); Spath, p. 61, pl. pl. 9, figs 7, 9, 11.
- 1931 *Lyelliceras lyelli* (Leymerie MS.), *A. D'Orbigny* sp.; Spath, p. 316, pl. 23, fig. 9, 12, 13; text-fig. 103d (with additional synonymy).
- 1949 *Lyelliceras lyelli* (Leymerie); Collignon, p. 121.
- 1956 *Lyelliceras lyelli* (Leymerie) d'Orbigny; Benavides-Cáceres, p. 463, pl. 51, figs 1–3.
- 1957 *Lyelliceras lyelli* (Leymerie); Wright, p. L409, *non* fig. 503, 1a,b (= *L. pseudolyelli*) ?1c.
- 1957 *Lyelliceras lyelli* Leym.; Almela & de la Revilla, p. 31, pl. 8, fig. 1.
- 1963 *Lyelliceras lyelli* Leym; Collignon, p. 315, fig. 1333.
- 1963 *Lyelliceras hirsutum* Par. et Bon.; Collignon, p. 179, pl. 315, fig. 1335.
- 1966 *Lyelliceras lyelli* (d'Orb.); Schindewolf, p. 789, fig. 435.

- 1968 *Collignoniceras* (*Selwynoceras*) *gratum* van Hoepen, p. 161, pl. 5.
- 1971 *Lyelliceras lyelli* (d'Orbigny); Owen, pl. 2, fig. 2.
- 1973 *Lyelliceras lyelli* (d'Orbigny) var. *ornatissima* Ciry; Destombes *et al.*, p. 90, pl. 5, fig. 5; text-fig. 5a,b.
- 1979 *Lyelliceras lyelli* (Leymerie); Gebhard, p. 112, pl. 8, figs 4–7; text-figs 79, 80.
- 1979 *Lyelliceras lyelli* (Leymerie in d'Orbigny); Destombes, p. 110, pl. 4–24, fig. 2.
- 1979 *Lyelliceras lyelli* var. *ornatissima* Ciry; Destombes, p. 110, pl. 4–24, fig. 3.
- 1979 *Lyelliceras lyelli* (d'Orbigny); Renz, p. 364, pl. 2, fig. 5.
- 1982 *Lyelliceras lyelli* (Leymerie); Renz, p. 38, pl. 5, fig. 14.
- ?1982 *Prollyelliceras gevreyi* (Jacob); Renz, p. 38, pl. 5, fig. 13.
- 1988 *Lyelliceras lyelli* (d'Orbigny); Delamette, pl. 13, fig. 4.
- 1989 *Lyelliceras lyelli* (d'Orbigny); Delamette, pl. 2, fig. 6.
- 1995 *Lyelliceras lyelli* (Leymerie in d'Orbigny); Latil, p. 361 (*pars*), pl. 2, figs 12, 13 pl. 3 (given as 73, in error), figs 1–14, *non* 15–17; text-fig. 24 (*pars*); text-fig. 23 (*pars*); text-fig. 26 (*pars*); fig. 27 (?*pars*).
- 1995 *Lyelliceras* sp., ex gr. *lyelli* (Orbigny); Seyed-Emami, p. 436, figs 14–20.
- 1996 *Lyelliceras lyelli* (d'Orbigny); Wright, p. 14 (*pars non* fig. 148, 2a,b (= *L. pseudolyelli*)); ?3.
- 1997 *Lyelliceras lyelli* (d'Orbigny, 1841); Latil & Dommergues, p. 105, fig. 3; fig. 5 (*pars*).
- 1997 *Lyelliceras lyelli* (d'Orbigny, 1841); Delamette *et al.*, pl. 21, fig. 3.
- 2002 *Lyelliceras lyelli* (d'Orbigny, 1841); Robert, *non* p. 158, *non* pl. 22, figs 6–10, *non* pl. 23, figs 1–3 (*pars*); text-fig. 59, 4 (copy of d'Orbigny) only.
- 2005 *Lyelliceras lyelli* (d'Orbigny, 1841); Amédéo & Robaszynski, p. 603, fig. 12(2).
- 2006 *Lyelliceras lyelli* (d'Orbigny, 1841); Guérin-Franiatte in Gauthier, p. 92, pl. 39, fig. 3.

#### Types

Lectotype designation of the original of d'Orbigny (1841, pl. 74, fig. 4) is generally attributed to Parona & Bonarelli (see for example Spath 1931, p. 316), who, in their synonymy, restrict the species to this figure only. The illustration is idealized, and does not correspond to any of the surviving syntypes; it may even be a composite, as is common with d'Orbigny's figures. Guérin-Franiatte (*in* Gauthier 2006, p. 92) stated that, ' Parmi les exemplaires conservés dans la coll. D'Orbigny, 7 petites échantillons correspondent à *A. Lyelli*. Le spécimen n° 5792 de Clar, à Escragnolles (Alpes-Maritimes) à une taille proche de la fig. 4 de d'Orbigny, et peut être considéré comme l'original. Sa localité d'origine est citée dans le text.... Lectotype, Clar, commune d'Escragnolles (Alpes-Maritimes) n° LPMP-R4308 (Coll. d'Orbigny) n° 5792-D-1' clarified the situation. The lectotype is reillustrated here as Fig. 24BB-DD. The actual status of d'Orbigny's type series is oversimplified by Guérin-Franiatte. D'Orbigny referred to a considerable range of specimens, all of which are in fact syntypes (1841, p. 257: 'cette espèce caractérise bien tout le gault ou grès vert inférieur, du nord, de l'est et du midi de la France. Elle a été trouvée par MM. Clément Mullet, Dufrenoy, de Vibraye, Leymerie, Dupin, Michelin et moi, à Larrivour, à Belle-Épine, à Maurepaire, aux Gasty, commune de Girodot; à



**Fig. 23.** Copy of '*Acanthoceras lyelli*,' of Steinmann (1881, pl. 7, fig.3) from the Albian of Pariatambo, Peru, where Steinmann recorded it in association with *Eubranconoceras* [*Branconoceras*] *aegoceratoides*, the latter occurring 'in einem schwarzen, bituminösen Kalkstein' (1881, p. 133). It is interpreted here as a specimen of *Prolyelliceras mathewsi* (Knechtel, 1947). Figures are reproduced at original size, which is presumed to be  $\times 1$ .

Courcelle et près d'Ervy (Aube). MM. Émeric, Astier, Duval et moi, l'avons également rencontrée au quartier de Clar, près d' Escragnolle, sur le chemin de Grasse à Castellanne. (Var); M. Raulin, à Maufaucou, près de Varennes (Meuse); M. Carteron, aux environs de Morteau (Doubs); M. Dudressier, à Bucey-les-Gy (Haute-Saône); M. Hugard, à la Montagne des Fis (Savoie); M. Deluc, au Reposoir. Elle est tantôt à l'état de fer sulfuré, de fer hydraté dans l'est de la France, et à l'état calcaire, dans le midi et le nord.'

The catalogue of the d'Orbigny Collection lists the following:

'5792 A. *Lyellii* Leym. St. Dizier h<sup>te</sup>. Marne 4'

Three of these specimens survive, attached to their original tablet (Fig. 25V); one of these may be the basis for d'Orbigny's pl. 74, fig. 5: 'Très jeune individu, à l'instant où, de lisse, qu'il est, il commence à prendre les côtes.'

[5792] 'a id. *Maurepaire* 4'

All four decomposing specimens survive on their original tablet (Fig. 25U), and are *Lyelliceras lyelli*.

[5792] 'b id. *Epothlemont* 3'

The specimens have all decomposed.

[5792] 'c id. *Wissant Pas de Calais* 4'

These specimens survive (Fig. 24E–F, I–J; 25D–E, R–T). One of them, a body chamber (Fig. 25R–T) appears to be the basis, in whole or in part, of d'Orbigny's pl. 74, figs 1, 2, and is a fine example of *Lyelliceras pseudolyelli*.

[5792] 'd id. *Claré Var* 10'

There are actually 11 surviving specimens, some associated with tablets labelled 'Clar' or 'Escragnolle'. It is one of these (Fig. 24BB–DD) that has been designated lectotype. The other specimens include a fine *Lyelliceras hirsutum* of authors (Fig. 25M–O), that is to say a juvenile *L. pseudolyelli*, with multiple siphonal tubercles, and a more compressed form (Fig. 25P,Q). This last individual retains aragonitic shell and is pyritized, a preservation indicating that it is not from Escragnolle, but more probably from the eastern Paris Basin. The distinctive whorl section is the result of *post-mortem* crushing of the body chamber.

[5792] 'e id. *Varennes Meuse* 1'

The specimen survives (Fig. 25 J–L).

Also present in the collection is a tablet labelled '5792D, *Maurepaire*' on the front, and '5792A' on the back.

*Maurepaire* lies to the west of the Lac d'Orient in Aube, in the same region as the localities described by Destombes (1979) and Latil (1995), 5792D-1 and 2 are *Parabranconoceras transiens* Kennedy, 2004 (Fig. 31E–L); the third (Fig. 31 A–D) is an undescribed species of *Lyelliceras*.

#### Material

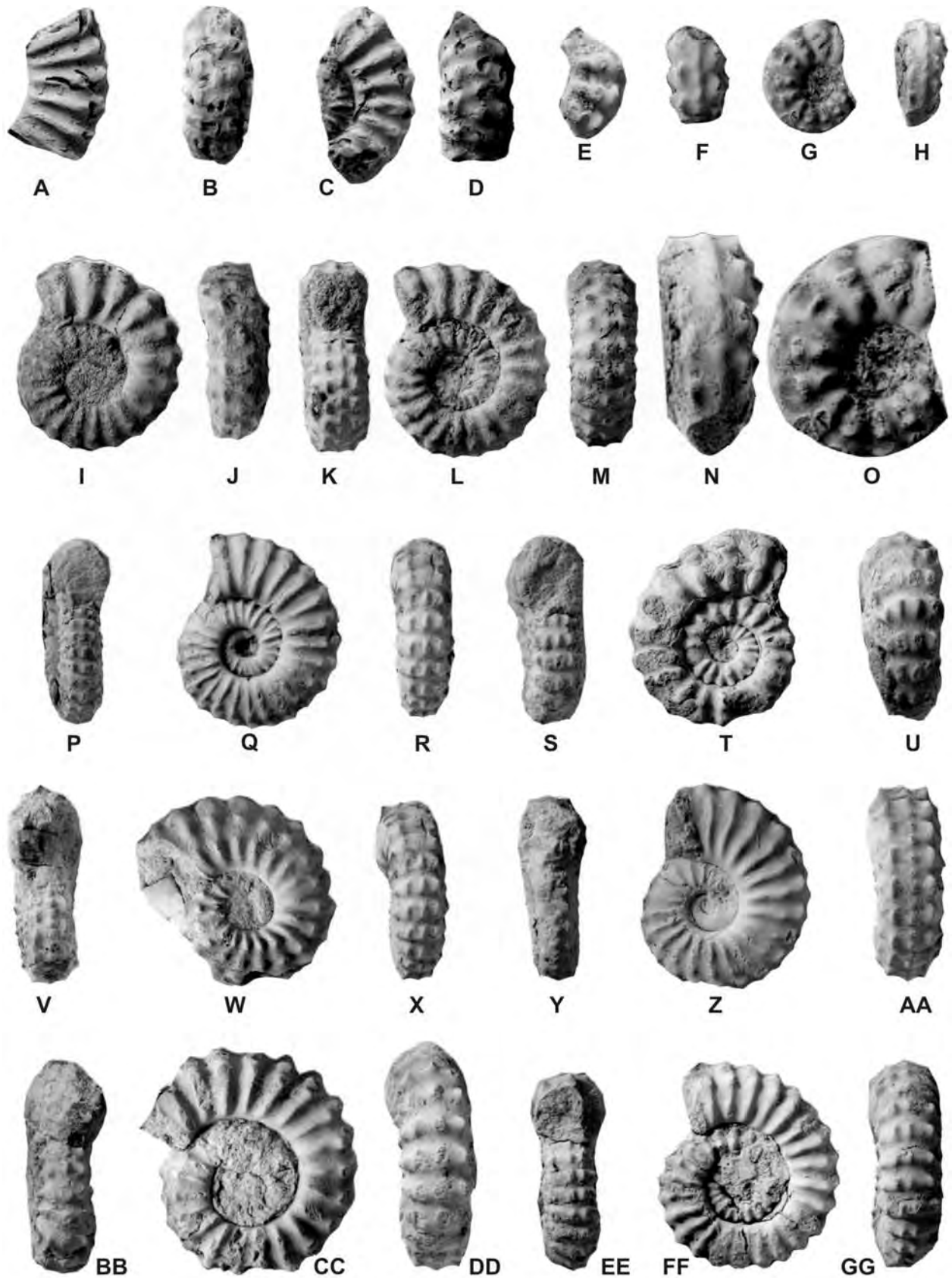
OUM KX9267–9270, 9276, 9277, 9284, 9286, 9387, 9876, SAM-PCZ22219, 22222–22236, SAM L54 from locality 154 in the southern part of the Mkuze Game Reserve, Mzinene Formation, Albian III, basal Middle Albian. OUM KX9998–10002, 10004a–c, SAM-PCZ22221, from locality 176, Mzinene Formation, Albian III, basal Middle Albian, near Ndumu. PCZ EM67 is presumably from the same locality. SAM Z1092, the holotype of *Collignonoceras* (*Selwynoceras*) *gratum* van Hoepen, 1968, from the Mkuze Game Reserve. SAM EM176, presumably from Ndumu.. Where no horizon is given, the specimens are inferred, from their preservation, to be from the Mzinene Formation, Albian III, basal Middle Albian.

#### Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ22228c	24.6 (100)	11.1 (45.1)	10.3 (41.8)	1.1	7.8 (31.7)
PCZ22224c	2.8 (100)	13.8 (42.1)	12.1 (36.9)	1.1	12.4 (37.8)
PCZ22222c	34.5(100)	14.3 (41.4)	13.0 (37.7)	1.1	13.7 (39.7)
KX9998c	36.4(100)	17.0 (46.7)	13.0 (35.7)	1.3	14.2 (39.0)
KX10001c	37.4(100)	16.2 (43.3)	13.5 (37.4)	1.2	14.2 (38.0)
PCZ22227c	37.9(100)	–(–)	13.7 (36.1)	–	15.0 (39.6)
PCZ22225c	44.9(100)	17.0 (37.9)	16.9 (37.6)	1.0	16.2 (36.1)
Z1092c	45.1(100)	15.9 (35.3)	17.3 (38.4)	0.9	17.4 (38.6)

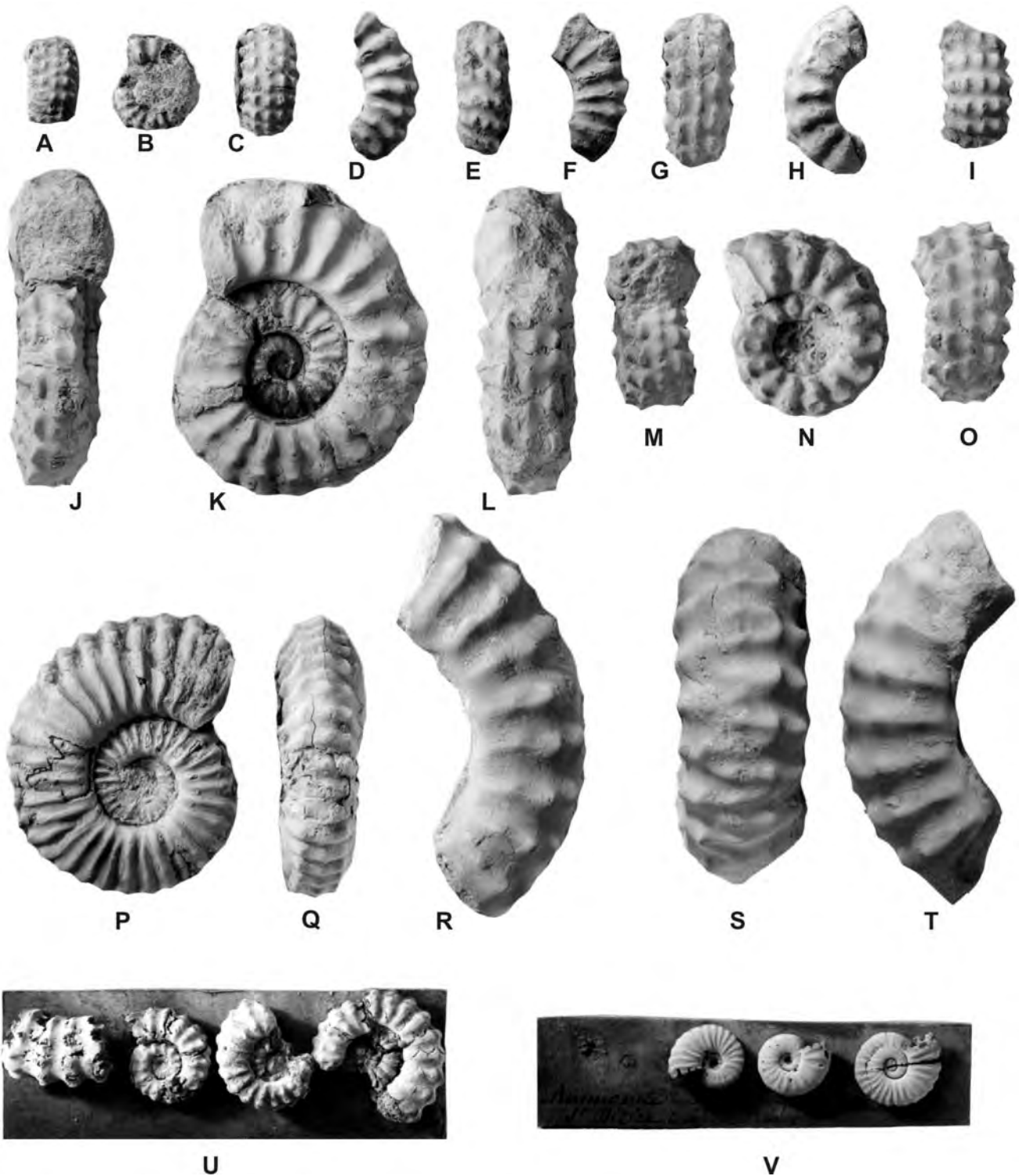
#### Description

SAM-PCZ22230 (Pl. 4, figs 1–4) preserves a nucleus 14 mm in diameter, and part of the succeeding whorl, with a maximum preserved whorl height of 9.2 mm. This specimen has 10 primary ribs on the 120° sector of outer whorl preserved, the ribs and outer ventrolateral clavi opposite across the venter, and linked by a transverse rib bearing a large ventrolateral clavus. The ventrolateral and siphonal clavi are equal in number, indicating the specimen to be a *Lyelliceras lyelli*. The nucleus bears six delicate, straight, prorsiradiate ribs on the adapertural half whorl, each bearing a conical inner and feebly clavate outer ventrolateral tubercle. The ribs and ventrolateral clavi are opposite across the venter, which is fastigiate, with a siphonal ridge bearing siphonal clavi that are more numerous than the ventrolateral. The adapertural half on the nucleus shows the rapid acquisition of eight umbilical bullae and strong ribs. We have several nuclei of this type, associated with typical *lyelli* outer whorls. All show this pattern of development, as with OUM KX9286a (Pl. 4, figs 11, 12), a well-preserved nucleus 11.8 mm in diameter.



**Fig. 24.** A–GG, Lectotype (BB–DD), and paralectotypes of *Lyelliceras lyelli* (d'Orbigny, 1841). A–O, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1896). P–Y, BB–GG, *Lyelliceras lyelli* (d'Orbigny, 1841). Y–AA, *Lyelliceras* sp. Specimen with opposite ventrolateral clavi, and more siphonal than ventrolateral clavi. MNHP d'Orbigny Collection 5792d. A–D, G, H, K–GG, from the condensed Albian of 'Claré' (presumably Clars, Escragnolles, Alpes-Maritimes, France). E, F, I, J are said to be from Wissant, Pas de Calais. Figures A–M, P–GG are x1; N, O are x2.





**Fig. 25.** A–V, paralectotypes of *Lyelliceras lyelli* (d'Orbigny, 1841). A–C, I, P, Q, U, *Lyelliceras lyelli* (d'Orbigny, 1841). D–H, J–O, R–T, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). V, juvenile ammonites. A–C, G–I, M–Q, MNHP d'Orbigny Collection 5792d from 'Claré' (presumably Clars, Escragnoles, Alpes-Maritimes); D, E, R–T, 5792c from Wissant, Pas de Calais; J–L, 5792e, from Varennes, Meuse, France; U, 5792a, from Maurepaire, Aube, France; V, 5792, from St Dizier, Haute Marne, France. All figures are  $\times 1$ .

Opposite ribs and ventrolateral clavi with siphonal clavi more numerous than ventrolateral is a characteristic feature of the early growth stages of many of our specimens (Pl. 3, figs 17–21; Pl. 4, figs 5, 7–9, 13, 14; Pl. 5, figs 4–11, 14–20). The feature is well shown by SAM-PCZ22232 (Pl. 4,

figs 13, 14), a fragment with a diameter of 15.4 mm: nine ribs and ventrolateral clavi correspond to 14 siphonal clavi. OUM KX9284 (Pl. 3, figs 17–21) is a robust individual, an estimated 40 mm in diameter. Coiling is very evolute, the umbilicus comprising 32% of the diameter, shallow, with a

feebly convex, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The intercostal whorl section is slightly compressed, oval, with the greatest breadth below mid-flank. The costal whorl section is polygonal, with a whorl breadth to height ratio of 1, the greatest breadth at the umbilical bullae. There are 21–22 ribs on the outer whorl. They arise at the umbilical seam, and strengthen into feeble umbilical bullae at the adapical end of the outer whorl. These strengthen progressively, and migrate outwards to an umbilicolateral position at the greatest preserved diameter. The ribs are straight, and recti-to feebly prorsiradiate, strengthening progressively across the flanks. All bear a well-developed inner ventrolateral clavus, connected to a larger outer ventrolateral clavus by a broad, wedge-shaped rib. On the adapical half whorl, the siphonal clavi are smaller than the outer ventrolateral, and linked to them by low, broad ribs, either transverse and simple, or a pair of ribs link a single outer ventrolateral clavus to two siphonal clavi in a diamond-shaped pattern (Pl. 3, fig. 18; see also Pl. 8, figs 3, 5, 19; Fig. 26). On the adapertural half whorl (Pl. 3, fig. 20), ribs, and subequal outer ventrolateral and siphonal clavi correspond, and are linked by a simple, transverse rib.

SAM Z1092 (Pl. 8, figs 10–12) is a compressed variant, the holotype of *Collignonicerias* (*Selwynoceras*) *gratum* (Van Hoepen, 1968) (p. 161, pl. 5). It is 45 mm in diameter, and retains recrystallized shell. A part of the outer whorl is body chamber. Coiling is very evolute: the broad, shallow umbilicus comprises 38.6% of the diameter. The umbilical wall is low, the whorl section compressed, with a costal whorl breadth to height ratio of 0.92, the greatest breadth below mid-flank. Twenty-four ribs arise at the umbilical seam on the outer whorl, and strengthen across the umbilical wall and shoulder, developing into a tiny umbilical bulla, present on the adapical half of the outer whorl, but lost thereafter. The ribs are straight and prorsiradiate, strengthening across the flanks, and linking to conical inner ventrolateral tubercles. These give rise to a strong transverse rib that bears subequal outer ventrolateral and siphonal clavi. There are a few additional intercalated siphonal clavi at the adapical end of the outer whorl.

A second group of specimens have equal numbers of outer ventrolateral and siphonal clavi, linked across the venter by a simple transverse rib. SAM-PCZ22221 (Pl. 6, figs 1–4) is typical. It is 26.6 mm in maximum preserved diameter, with a 180° sector of body chamber preserved. Coiling is very evolute, the umbilicus comprising 42% of the diameter, shallow, with a flattened and outward-inclined umbilical wall and broadly rounded umbilical shoulder. The costal whorl section is polygonal, depressed, with a whorl breadth to height ratio of 1.26, the maximum whorl breadth at the umbilicolateral bullae. There are 20 ribs on the outer whorl. They arise at the umbilical seam, and are strong and coarse on the umbilical wall. They strengthen into strong, subspinose umbilical bullae that migrate out to an umbilicolateral position as size increases. Coarse, straight, prorsiradiate ribs link to conical inner ventrolateral tubercles, linked across ventrolateral shoulders and venter by a low, broad, transverse rib bearing strong outer ventrolateral and siphonal clavi. SAM EM-176 is a coarsely ribbed variant of this type, 47.6 mm in diameter (Pl. 8, fig. 16). SAM-PCZ22224 (Pl. 3, figs 1–6), a densely ribbed variant

with 26 ribs on the outer whorl at a diameter of 32 mm, has equal ventrolateral and siphonal tubercles linked by a simple rib. The tubercles are relatively weak in this individual.

None of the specimens shows the sutures.

#### Discussion

*Lyelliceras? huberianum* (Pictet, 1847) (p. 82, pl. 7, fig. 7) is an enigmatic species. It is based on two specimens, one in the Mayor Collection, and one in the Favre Collection, both from the condensed Albian of 'Mont Saxonnet' (=Bourgetts; Delamette *et al.* 1997, p. 291). These specimens have not been traced (Latil 1995, p. 356). Pictet's original figure of a syntype is reproduced here as Fig. 7A,B. Pictet (1847, p. 83) distinguished his *Ammonites huberianus* from *Ammonites lyelli* on the basis of '1° par son enroulement beaucoup plus rapide et son ombilic plus petit; 2° par le nombre plus petit des côtes; 3° par le nombre relativement plus grand des tubercles dorsaux; 4° par la forme des tubercles lateraux plus grand et plus comprimés (ce caractère n'est peut-être pas constant); 5° par ses cloisons, dont les lobe latéraux sont formés de parties impaires et dont le lobe dorsale est plus grand et moins dévié.' Latil (1995, p. 356, pl. 2, figs 4, 5; text-fig. 21) regarded this species as related to the *Tegoceras camatteanum*–*Lyelliceras vaasti*–*L. pseudolyelli* group, and referred a number of specimens from the condensed Albian of southeast France to the species. Delamette *et al.* (1997, pl. 13, figs 2, 3; pl. 30, figs 1, 2) figured, as *Lyelliceras huberianum* (Pictet) forme *hirsutum* (Parona & Bonarelli) four specimens of rather different appearance. We are uncertain of the affinities of this species. The original figure shows an individual with the ventrolateral clavi opposite rather than alternate, and thus distinct from the *Tegoceras camatteanum*–*Lyelliceras vaasti*–*L. pseudolyelli* group. The pattern of tuberculation, notably the very large inner and outer ventrolateral tubercles and numerous, tiny siphonal clavi are immediately distinctive, but to what extent the figure accurately represents the specimen is unclear.

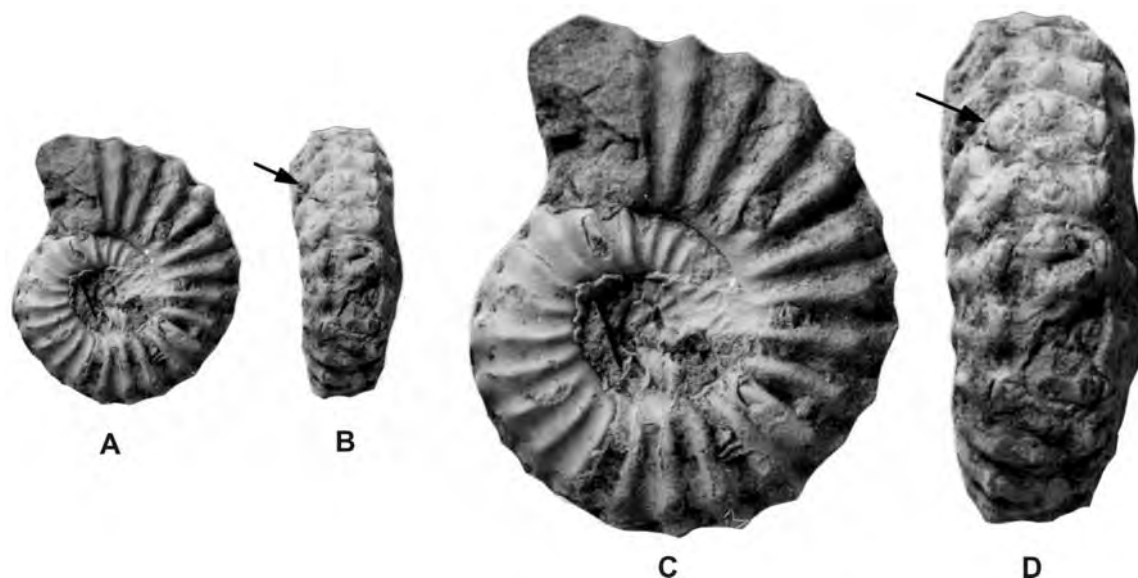
*Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897) (p. 99 (47), pl. 14 (5), figs 1, 2; Fig. 8/1, 2) and its synonym *Lyelliceras hirsutum* (Parona & Bonarelli, 1897) (p. 99 (47), pl. 14 (5), figs 4–6) are described below. They differ in that the ribs and ventrolateral clavi are alternate rather than opposite over the venter, with siphonal clavi more numerous than ventrolateral, and linked by an irregular zigzag rib throughout ontogeny.

*Lyelliceras nodosa* (Etheridge, 1907) (p. 87, pl. 4, figs 1, 2) (Fig. 1) is a subjective synonym of *L. lyelli*. The holotype is a short whorl fragment 42 mm long, with parts of seven ribs preserved, with small umbilical bullae, stronger conical inner ventrolateral tubercles and strong, subequal outer ventrolateral and siphonal clavi borne on simple transverse ribs.

*Lyelliceras lyelli* (d'Orbigny) var. *ornatissima* Ciry, 1927 (p. 562, pl. 6, fig. 4) is a further synonym of *L. lyelli*, and is interpreted as nothing more than a coarsely ornamented variant. A comparable individual is shown in Pl. 8, fig. 16.

*Lyelliceras gratum* (van Hoepen, 1968) (p. 161, pl. 5), described above, is interpreted as a compressed variant of the present species.

*Lyelliceras vaasti* Destombes *et al.*, 1973 (p. 90, pl. 3, fig. 9;



**Fig. 26. A–D.** *Lyelliceras lyelli* (d'Orbigny, 1841). OUM KX9279, from the Mzinene Formation, Middle Albian, Albian III, of locality 154, in the Mkuze Game Reserve. This specimen has opposite ventrolateral clavi, with siphonal clavi more numerous than the ventrolateral, and linked to them either singly, by a transverse rib, or in pairs, producing an intermittent diamond-shaped ventral rib pattern (arrowed). Figures A, B are  $\times 1$ ; C, D are  $\times 2$ .

text-fig. 9.3; see revision in Latil 1995, p. 356, pl. 2, figs 1–3; text-fig. 20) has the ribs and outer ventrolateral clavi alternate in position on the two flanks, siphonal clavi more numerous than the ventrolateral, with an irregular zigzag rib linking outer ventrolateral and siphonal clavi.

*Lyelliceras latili* sp. nov., described below, differs from *Lyelliceras lyelli* in the irregular strength and development of phragmocone ornament, and the distinctive polygonal umbilical seam.

#### Occurrence

The first occurrence of *Lyelliceras lyelli* defines the base of the Middle Albian, where it defines a distinct Zone/Subzone. The geographic distribution extends from southern England to France, Switzerland, northern Spain, offshore Spain at 40°57.6'N, 10°43.1'W, south of Vigo Seamount, central Iran, Madagascar, KwaZulu, Pakistan, California and Venezuela.

#### *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897)

Pl. 3, figs 12–16; Pl. 4, figs 6, 10, 15, 16; Pl. 5, figs 12, 13; Pl. 6, figs 5, 8–10; Pl. 7, figs 3, 4, 6–8, 10–17; Pl. 8, figs 14–15; Figs 6/1a,b; 8/1, 2; 9/1, 2, 3 (*pars*); 11H–K; 12A–F, J–O, S–U; 24A–GG; 25D–H, J–O, R–T; 27A,B; 28.

1841 *Ammonites Lyelli* Leymerie; d'Orbigny, p. 255 (*pars*), pl. 74, figs 1, 2, 3 (*pars*) only.

1847 *Ammonites Lyelli* d'Orbigny; Pictet, p. 80, pl. 7, fig. 6.

1846 *Ammonites Lyelli* Leymerie; Quenstedt, p. 138, pl. 10, fig. 3.

1850 *Ammonites Lyelli* Leymerie; d'Orbigny, p. 123 (*pars*).

1860 *Ammonites Lyelli* Leymerie; Pictet & Campiche, p. 196 (*pars*), pl. 24, figs 1, 2, only.

1897 *Acanthoceras pseudolyelli* Parona & Bonarelli, p. 99 (47), pl. 14 (5), figs 1, 2.

1897 *Acanthoceras hirsutum* Parona & Bonarelli, p. 99 (47), pl. 14 (5), figs 4–6.

1930b *Lyelliceras pseudolyelli* (Parona & Bonarelli); Spath, p. 62.

1931 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Spath, p. 319, pl. 32, figs 14, 15; text-fig. 103a–c.

non 1938 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Riedel, p. 54, pl. 9, figs 5, 6; pl. 13, fig. 16.

1949 *Lyelliceras pseudolyelli* (Par. et Bon.); Collignon, p. 121.

non 1956 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Benavides-Cáceres, p. 463, pl. 52, fig. 3.

1957 *Lyelliceras lyelli* (Leymerie); Wright, p. L409, fig. 503, 1a,b, ?1c.

1963 *Lyelliceras pseudo-lyelli* Par. et Bon.; Collignon, p. 179, pl. 315, fig. 1334.

non 1963 *Lyelliceras hirsutum* Par. et Bon.; Collignon, p. 315, fig. 1335.

1966 *Lyelliceras pseudolyelli* (d'Orb.); Schindewolf, p. 789, fig. 436.

1979 *Lyelliceras lyelli* (d'Orbigny). 1841; Destombes, p. 110, pl. 4.24, fig. 2.

1979 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Gebhard, p. 114, pl. 8, figs 8–11; text-figs 81, 82.

1982 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Renz, p. 39, pl. 5, fig. 15; text-fig. 26c,d.

1988 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Delamette, pl. 8, fig. 16.

1989 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Delamette, pl. 1, fig. 2.

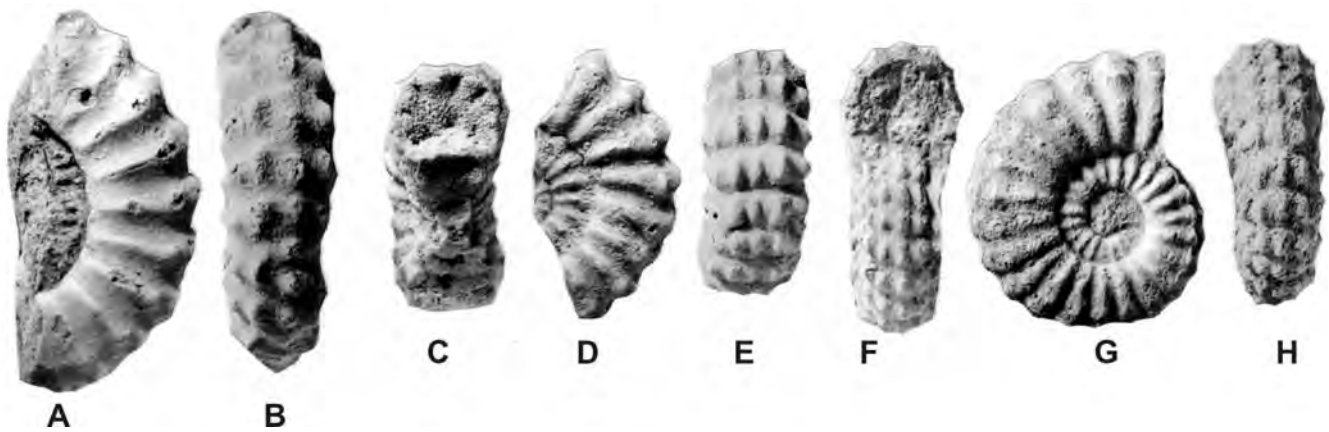
1995 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Latil, p. 358, pl. 2, figs 5–11 (non 6; = lectotype of *Tegoceras camatteanum*); text-figs 22, 23.

1996 *Lyelliceras lyelli* (d'Orbigny); Wright, p. 14 (*pars*), fig. 148, 2a,b; ?3.

1997 *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897); Latil & Dommergues, p. 102, text-fig. 2.

1997 *Lyelliceras* groupe *huberianum* (Pictet), forme *hirsutum* (Parona & Bonarelli); Delamette *et al.*, pl. 13, figs 2, 3; pl. 14, fig. 1; pl. 30, figs 1, 2.

?non 2002 *Lyelliceras pseudolyelli* Parona & Bonarelli (1897); Robert, p. 161, pl. 23, figs 4–9; pl. 24, figs 1–3.



**Fig. 27.** Lyelliceratinae from Madagascar. **A, B**, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). Original of Collignon (1963, pl. 315, fig. 1334) from the 'Albien Moyen, Zone à *Lyelliceras lyelli*' of gisement 760, Rive Est du Lac Hima, 4km Est d'Ankaboka (Belo sur Tsiribihina). **C–H**, *Lyelliceras lyelli* (d'Orbigny, 1841). **C–E**, original of *Lyelliceras hirsutum* (Parona & Bonarelli) of Collignon (1963, pl. 315, fig. 1335) from the 'Albien Moyen, Zone à *Lyelliceras lyelli*' of gisement 421, Aontzy-Ampabako (Betioky). **F–H**, original of *Lyelliceras lyelli* (d'Orbigny, 1841) of Collignon (1963, pl. 315, fig. 1333) from the same horizon and locality as C–E. All specimens are in the Collignon Collection, housed in the Université de Bourgogne, Dijon. All figures are x1.

?non 2002 *Lyelliceras pseudolyelli* (Parona & Bonarelli); Robert *et al.*, fig. 4.8.

2006 *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897); Guérin-Franjat, *in* Gauthier, p. 92, pl. 38, fig. 5.

#### Name of the species

As first revising authors, we select the name *pseudolyelli* Parona & Bonarelli, 1897, p. 99 (47), pl. 14 (5), figs 1, 2 for the species, for those who regard *hirsutum* Parona & Bonarelli, 1897, p. 99 (47), pl. 14 (5), figs 4–6, and *pseudolyelli* as conspecific.

#### Types

The lectotype, by the subsequent designation of Spath

(1931, p. 320), is the original of Parona & Bonarelli (1897, p. 99 (47), pl. 14 (5), fig. 2 (Fig. 8/2)) from the condensed Albien of Escragnoles, Var, France. The specimen is said to be housed in the collections of the Museo Geologico, Turin. There are three paralectotypes from Escragnoles, including the original of Parona & Bonarelli (1897, pl. 14(4), fig. 1 (Fig. 8/1)), and four from Eza, Var, France.

#### Material

OUM KX9271, 9276, 9279, 9280, 9281, 9876, SAM-PCZ 22188, 22189, 22190, 22231, 22237, SAM-L44 from locality 154 of Kennedy & Klinger (1975), Mzinene Formation, Albien III, Middle Albien, in the Mkuze Game Reserve. OUM KX 9997, SAM-PCZ 22220, from locality 176,



**Fig. 28.** *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). SP 62–916, ex Lazarette Collection, from the condensed Albien of Escragnoles, Alpes-Maritimes, France. The specimen is interpreted as an adult macroconch; all of the surviving outer half whorl is body chamber. Figures are x1.

Albian III, near Ndumu; SAM-EM124, SAM-EM174, SAM-PCZ5872 from Ndumu.

#### Dimensions

	D	Wb	Wh	Wb:Wh	U
PCZ5872c	17.6 (100)	8.0 (45.5)	8.5 (48.3)	0.94	4.8 (27.3)
KX9271c	37.0 (100)	15.0 (40.5)	15.7 (42.4)	0.96	13.5(36.5)
PCZ22190c	38.4 (100)	14.2 (36.9)	12.9 (31.0)	1.1	17.6 (45.8)
KX9279	40.9 (100)	14.5(35.5)	15.7(38.4)	0.92	14.7 (35.9)
KX9997	58.3 (100)	–(–)	20.9 (35.8)	–	27.3(46.8)
SAM L44	64.3 (100)	21.0 (32.7)	19.4 (30.2)	1.1	31.7 (49.0)

#### Description

As here conceived, the diagnostic characters of *Lyelliceras pseudolyelli* are the presence to middle and late growth stages of: (i) the alternation in position of outer ventrolateral clavi across the venter; (ii) siphonal clavi that are more numerous than the ventrolateral, and (iii) ribs that zigzag irregularly between the ventrolateral and siphonal clavi. These characters may all occur in the same individual. Character (i) or character (ii) or both of these characters may be absent for part or all of the ontogeny of some individuals. There are also individuals in which character (i) is poorly expressed. As noted above, in the discussion of *L. lyelli*, there are individuals of that species in which some or all of these features are expressed during early ontogeny, to be succeeded in middle and later growth by an ornament of opposite outer ventrolateral clavi and an equal number of siphonal clavi, or opposite outer ventrolateral clavi and slightly more numerous siphonal clavi. This retention of ancestral *pseudolyelli* morphology means that some juveniles cannot always be referred to *lyelli* versus *pseudolyelli* with complete confidence.

Three forms of *Lyelliceras pseudolyelli* are recognized amongst the present material.

**Form 1.** SAM-PCZ22190 (Pl. 7, figs 3, 4, 8, 13, 14) has a diameter of 38.4 mm, and retains a 180° sector of body chamber. The penultimate whorl, at an estimated 12.2 mm diameter bears 16 coarse prorsiradiate primary ribs that arise at the umbilical seam and strengthen progressively across ventrolateral shoulders and venter. All bear a coarse umbilical bulla, and a coarse, feebly bullate inner ventrolateral tubercle. The ventral region is well preserved (Pl. 7, fig. 3). A broad, strong, coarse rib connects the inner ventrolateral tubercle to a strong outer ventrolateral clavus. The ribs and clavi alternate in position across the venter. There is a low, broad siphonal ridge that bears small siphonal clavi, eight corresponding to five ventrolateral clavi. On the outer whorl, the umbilicus comprises 45.8% of the diameter, and is shallow, with a low, feebly convex wall, notched to accommodate the inner ventrolateral tubercles of the preceding whorl. The intercostal whorl section is depressed, with the greatest breadth below mid-flank, the inner flanks markedly convex, the outer flanks feebly

convex, converging to the markedly convex venter. The costal whorl section is polygonal, with the greatest breadth at the umbilical bullae. There are 12 primary ribs on the outer half whorl. They arise at the umbilical seam, strengthen across the umbilical wall, and are strong, straight and prorsiradiate across the flanks, and narrower than the interspaces. At the adapical end of the outer whorl, the ribs bear strong umbilical bullae, and weaker inner ventrolateral tubercles. The latter are connected to narrow outer ventrolateral clavi by a broad triangular rib. The ribs and ventrolateral tubercles alternate in position across the venter. Eighteen small ventrolateral tubercles, the adapical ones alternately feebly clavate and conical, the adapertural ones all conical, correspond to the 12 ribs. The outer ventrolateral and siphonal clavi are linked by an irregular, low rib that zigzags between the tubercles, with occasional interruptions.

Towards the adapertural end of the fragment, the umbilical and inner ventrolateral tubercles weaken, suggesting the specimen may be an incomplete adult microconch.

The following three specimens are interpreted as macroconchs. SAM-EM174 (Pl. 7, figs 10–12) is a fragment of a larger individual of this type. It has a maximum preserved whorl height of 15.9 mm. The costal whorl breadth to height ratio is 1.0. The greatest breadth is at the inner ventrolateral tubercles. Parts of five ribs are preserved on the fragment, alternating in position on the two flanks. The ribs are very coarse, even on the umbilical wall, and straight and prorsiradiate on the flanks. There are coarse conical umbilical tubercles, subequal inner ventrolateral clavi, and much stronger coarse outer ventrolateral clavi, the ventrolateral tubercles linked by a strong, broad rib. Six coarse siphonal clavi correspond to 4 outer ventrolateral clavi to which they are linked by an obscure zigzag rib. OUM KX9997 (Pl. 7, figs 6, 7) preserves parts of three successive whorls; the outermost is a 180° sector of whorl that is mostly body chamber, with an original estimated maximum diameter of 60 mm. Coiling is very evolute, the umbilicus comprising 46.8% of the diameter, shallow, with a broadly rounded, outward-inclined umbilical wall that is notched to accommodate the outer ventrolateral clavi of the preceding whorl. Coarse radial to feebly prorsiradiate ribs are present on the inner whorls. A total of 11 primary ribs are present on the outermost half whorl. They arise at the umbilical seam, between the notches to accommodate the outer ventrolateral clavi of the preceding whorl. They are strong, straight and recti- to feebly prorsiradiate on the flanks, across which they strengthen markedly. All bear strong conical to feebly bullate umbilical tubercles, inner ventrolateral clavi of subequal strength, and stronger outer ventrolateral clavi. The ventrolateral clavi alternate in position across the venter. Eleven siphonal clavi correspond to seven ventrolateral clavi on the best-preserved part of the fragment. Outer ventrolateral and siphonal clavi are linked by a low, broad, coarse zigzag ridge. SAM L44 (Pl. 7, figs 15–17) is an internal mould with just over 180° of body chamber preserved. Coiling is very evolute, the umbilicus comprising 49% of the diameter, the umbilical seam notched to accommodate the outer ventrolateral clavi of the previous whorl. The umbilical wall is broadly rounded, the costal section depressed oval, the costal whorl section depressed

polygonal, with a whorl breadth to height ratio of 1.1, the greatest breadth at the umbilical bulla. The inner whorls (Pl. 7, fig. 17) show exceptionally coarse, crowded ribs, 13–14 per whorl, with coarse umbilical bullae and somewhat weaker inner ventrolateral clavi. There are 12–13 primary ribs on the adapertural half of the outer whorl; they show progressive modification, indicating the specimen to be a complete, or near-complete, adult. At the adapical end of the outer whorl, the ribs are coarse, narrow, prorsiradiate, and very widely separated. They bear relatively weak bullae compared with those on the penultimate whorl. The specimen has suffered non-lethal damage that briefly affects the ornament of the adapertural 120° of the outer whorl. Beyond this, the normal ornament resumes. The ribs crowd progressively, and the adapertural few are feebly flexuous. The umbilical bullae weaken and disappear, and the inner ventrolateral tubercles decline markedly. The outer ventrolateral clavi alternate in position across the venter, and are very elongate. The siphonal clavi are smaller and more numerous than the outer ventrolateral, to which they are linked by a low, broad, irregularly developed zigzag ridge.

**Form 2.** The somewhat different early growth stages of this form are shown by SAM-PCZ5872 (Pl. 4, figs 15, 16). There are 10–11 ribs per half whorl at a diameter of 17.6 mm. They arise at the umbilical seam, and strengthen across the relatively high umbilical wall, developing into poorly differentiated bullae, perched on the umbilical shoulder. The ribs are relatively coarse, crowded, straight and feebly prorsiradiate, and strengthen progressively across the flanks. They bear small feebly clavate to conical inner ventrolateral tubercles and outer ventrolateral clavi that alternate in position on either side of the venter. There are 14 siphonal clavi corresponding to the 11–12 outer ventrolateral clavi, to which they are linked by a low, broad, zigzag ridge. This same pattern of relatively dense ornament is seen on SAM-PCZ22237 and SAM-EM 124 (Pl. 6, figs 5, 8–10), with 12 ribs on the outer half whorl at a diameter of 15 mm.

**Form 3.** Individuals of this group (Pl. 3, figs 12–16; Pl. 4, figs 6, 10; Pl. 5, figs 12, 13; pl. 8, figs 14–15) are transitional to *L. lyelli* in overall coiling and whorl section, while retaining ornament typical of *pseudolyelli* to maturity. The early growth stages are represented by SAM-PCZ22189 (Pl. 4, figs 6, 10), an individual 19.2 mm in diameter. Coiling is evolute, the umbilicus comprising 35% of the diameter, of moderate depth, with a feebly convex wall. The whorl section is rounded-rectangular in intercostal section and slightly depressed polygonal in costal section, with the greatest breadth at the inner ventrolateral tubercle. There are 20 ribs on the outer whorl. They bear feeble umbilical bullae, stronger, bullate to feebly clavate inner ventrolateral tubercles, and much stronger elongate outer ventrolateral clavi that alternate in position on either side of the venter. The siphonal clavi are slightly more numerous than the outer ventrolateral. OUM KX9271 (Pl. 3, figs 12–16) is an individual 37 mm in diameter with 20–21 ribs on the outer whorl, with weak umbilical bullae, strong inner and stronger outer ventrolateral clavi, alternating in position on either side of the venter. The siphonal clavi are the same size as the outer ventrolateral, and slightly more numerous: 26–27 versus 20–21. The zigzag ribbing so conspicuous in form 1 is not

developed. In SAM-PCZ22188 (Pl. 5, figs 12, 13), the outer ventrolateral clavi alternate in position to the adapertural end of the specimen at an estimated diameter of over 40 mm, but there is only one more siphonal than outer ventrolateral clavi on the fragment, which could equally be referred to *L. lyelli*. SAM-PCZ22220 (Pl. 8, figs 14–15) preserves parts of three whorls, the outer a 120° sector of body chamber, with a maximum preserved whorl height of 21.3 mm. The whorl breadth to height ratio is 1.0, the greatest breadth at the umbilical bullae in costal section. Ten ribs are preserved on the fragment. They are relatively coarse, arise at the umbilical seam, sweep back across the umbilical wall, and strengthen into feeble umbilical bullae. The ribs are straight and prorsiradiate on the flanks, across which they strengthen, and link to strong inner, and stronger outer ventrolateral clavi. The outer ventrolateral clavi alternate irregularly on the two sides of the venter, and are sometimes almost opposite. Eleven siphonal clavi, equal in strength to the outer ventrolateral, correspond to 10 outer ventrolateral clavi, to which they are linked by a low, ill-defined to effaced zigzag ridge.

OUM KX9876 (Pl. 6, figs 19, 20) is a fragmentary macroconch with a maximum preserved whorl height of 24 mm approximately. There are 23 ribs on the penultimate whorl. The damaged venter shows typical zigzag ribbing and alternate ventrolateral clavi to the greatest preserved diameter.

None of the specimens shows the suture.

#### Discussion

Individuals referred to form 1, above, find a close match in French specimens such as those figured by d'Orbigny (1841, pl. 74, figs 1, 2; Fig. 25R–T), and Bayle (1878, pl. 74, fig. 6: Fig. 12A–C).

Latil (1995, p. 358) placed *Lyelliceras hirsutum* (Parona & Bonarelli, 1897) (p. 99 (47), pl. 14 (4), figs 4–6; Fig. 8/4–6) into the synonymy of *L. pseudolyelli* without discussion. The holotype ('Considieramo come tipo di questa forma': Parona & Bonarelli 1897, p. 100 (48)) is the original of Pictet & Campiche 1860, pl. 24, fig. 2)); the original figure is reproduced here as Fig. 6/2a–b. The holotype fragment matches closely the inner whorls of SAM-PCZ22190 (Pl. 7, fig. 3), and we too regard *hirsutum* as a synonym of *pseudolyelli*. The original figures of Parona & Bonarelli (1897, pl. 14 (5), figs 4–6) are reproduced here (Fig. 8/4–6), as are a series of French specimens corresponding to their largest specimen (Figs 12D–F, J–L, M–O, S–U). The more slender of these (Fig. 12J–L) resembles the inner whorls of the KwaZulu specimens. The more depressed French individuals (Fig. 12D–F, M–O, S–U) do not find a match in our material. The specimens of *L. pseudolyelli* figured by Parona & Bonarelli (1897, pl. 14 (5) figs 1–4) correspond most closely to form 2 of the present material. The larger of the specimens figured by Parona & Bonarelli (1897, pl. 14 (5), fig. 1) has 23 ribs on the outer whorl at a diameter of 52.6 mm. Their pl. 14(5), fig. 2 (Fig. 8/2) has 11 ribs on the outer half whorl at a diameter of 41 mm. The ventral view of the lectotype shows 15–16 siphonal clavi corresponding to nine outer ventrolateral clavi, the outer ventrolateral clavi very elongate when compared with the siphonal, a feature not shown by our material, nor by French material we have examined.

Latil (1995, figs 8, 23) and Latil & Dommergues (1997, fig. 2) analysed the morphotypes present in this species on the basis of material from successive horizons in the uppermost *pseudolyelli* Subzone of the *Otohoplites auritus* Zone of Mesnil-St-Père (Aube, France). They recognized three morphologies: i, 'tegoceratoides' without siphonal clavi, the outer ventrolateral clavi alternating on either side of the venter, and linked by a zigzag ridge; ii, 'subcarénées' with a siphonal ridge, with or without siphonal clavi that are more numerous than the ventrolateral, and iii, 'pseudolyelli' with large outer ventrolateral clavi, smaller, more numerous siphonal clavi, and no zigzag ridge linking the clavi. Only the morphotype 'pseudolyelli' is recognized amongst the KwaZulu material. Our largest collection, from Locality 154, is associated with *L. lyelli* of the basal Middle Albian, and the absence of 'tegoceratoides', and 'subcarénées' morphotypes, together with the presence of other variants is presumed to be a result of this age difference.

The *Lyelliceras pseudolyelli* of Riedel (1938, pl. 9, figs 5, 6) does not show a venter with siphonal clavi more numerous than the outer ventrolateral clavi, and does not belong here, and instead is assigned to the *Ralphimlayites* group. The Peruvian *L. pseudolyelli* of Benavides-Cáceres (1956, p. 463, pl. 52, fig. 3; Fig. 19/3 herein) and other large South American 'pseudolyelli' (for example Robert 2002, p. 23, figs c4–9; pl. 24, figs 1–3) are a homeomorphous development of the *Ralphimlayites* group.

Differences from *Lyelliceras lyelli* are discussed above.

#### Occurrence

*Lyelliceras pseudolyelli* is best known from condensed units in southeast France such as Escragnolles (Alpes-Maritimes), Les Rimets (Isère), and Sainte-Croix in Switzerland. In expanded sections as in Aube, France, it is the index of the highest, *pseudolyelli* Subzone of the uppermost Lower Albian *Otohoplites auritifomis* Zone and survives as a rarity into the base of the succeeding *Lyelliceras lyelli* Subzone of the lower Middle Albian *Hoplites dentatus* Zone of the north-west European standard sequence. There are also records from southern England (Owen 1971, p. 154), Venezuela, and Madagascar (Fig. 27A,B).

The scattered, well-characterized individuals from the Ndumu area, including Locality 176, indicate the presence of the uppermost Lower Albian. The assemblage from locality 154 in the Mkuze Game Reserve, associated with *L. lyelli* and transitional forms, together with *Pseudobrancoceras versicostatum* are basal Middle Albian.

#### *Lyelliceras latili* sp. nov.

Pl. 6, figs 17, 18, 21–23; Fig. 30A–E

#### Derivation of name

For Dr J.–L. Latil of Lazer, Hautes-Alpes, France.

#### Types

The holotype is BMNH C37265c (Latil 1995, pl. 3, fig. 19; Fig. 30A–E herein), from the condensed Albian of Escragnolles, Alpes-Maritimes, France, as are paratype MNHP 1986–69 (Latil 1995, pl. 3, fig. 20, text-fig. 28b) and Paratype FSL341505 (Latil, text-fig. 28a; pl. 3, fig. 18). Paratype OUM KX11038 (Pl. 6, figs 17, 18, 21–23) is from

the Mzinene Formation, Lower Albian, Albian III, *Tegoceras mosense-Aioloceras* fauna, of locality 35 of Kennedy & Klinger (1975) on the Mzinene River, north of Hluhluwe.

	D	Wb	Wh	Wb:Wh	U
C37265c	22.5 (100)	9.4 (41.8)	8.3 (36.9)	1.13	9.5 (42.2)

#### Diagnosis

Very evolute; umbilical seam traces a polygonal course as a result of notches in umbilical wall to accommodate inner ventrolateral tubercles of preceding whorl. On phragmocone, strong primary ribs with strong umbilical bullae, massive inner ventrolateral horns and smaller outer ventrolateral clavi are separated by one or two weaker primary ribs with no or weak inner ventrolateral tubercles. Body chamber with more regular coarse, distant primary ribs with coarse umbilical bullae, subspinose inner ventrolateral tubercles and outer ventrolateral and siphonal clavi, borne on a coarse, transverse rib. Ribs opposite throughout ontogeny.

#### Description

The holotype (Fig. 30A–E) is a phosphatic internal mould of a phragmocone 22.5 mm in diameter. Coiling is very evolute, the umbilicus comprising 42.2% of the diameter. The feebly convex umbilical wall is notched to accommodate the massive inner ventrolateral horns of the previous whorl. As a consequence, the umbilical seam follows a distinctive polygonal course. The expansion rate is low. The whorl section is slightly depressed oval in intercostal section, and rectangular in costal section, with the greatest breadth at the inner ventrolateral horns. There are 19 primary ribs on the outer whorl, all primaries, divided into two orders. Seven major primaries arise at the umbilical seam and are coarse, straight and prorsiradiate across the flanks. They bear strong subspinose umbilical bullae, and massive clavate ventrolateral horns. These are linked across the venter by a broad, coarse transverse rib that bears relatively feeble outer ventrolateral and siphonal clavi. The major primaries are separated by one or two minor primaries. These are as broad as the major primaries, but bear very weak umbilical bullae and very weak or no inner ventrolateral tubercles. They are connected across the venter by a narrower transverse rib than that of the major primaries, with outer ventrolateral and siphonal clavi equal to or very slightly weaker than those on the major ribs.

Paratype OUM KX11038 (Pl. 6, figs 17, 18, 21–23) consists of fragments of the inner whorls of the phragmocone and a body chamber of an individual estimated at 36 mm in diameter, with a maximum preserved whorl height of 12.5 mm. The inner whorl fragments already show the ornament typical of the species at a whorl height of 4.7 mm. The intercostal whorl section is depressed oval, with the greatest breadth below mid-flank. The costal whorl section is depressed polygonal, with a whorl breadth to height ratio of 1.3, the greatest breadth at the inner ventrolateral tubercles. Most of the broad, coarse primary ribs bear coarse conical umbilical bullae, stronger, feebly clavate subspinose inner ventrolateral tubercles, strong outer ventrolateral clavi, and weaker siphonal clavi. One rib on the fragment is much

weaker than the others, lacks an umbilical bulla, and has weaker ventrolateral and siphonal tubercles. The body chamber has a comparable whorl section, with a costal whorl breadth to height ratio of 1.14, the greatest breadth at the umbilical bullae. Coiling is very evolute, the umbilicus comprising an estimated 46% of the diameter. The umbilical seam is notched to accommodate the inner ventrolateral tubercles of the previous whorl; as a result, it follows a distinctive polygonal course rather than a smooth logarithmic curve. The umbilical wall is very feebly convex, and outward-inclined, the umbilical shoulder very broadly rounded. There are 10 primary ribs on the 120° body chamber fragment. They arise at the umbilical seam, and are straight, and prorsiradiate, strengthening progressively across the flanks. Nine of them bear sharp, subspinose bullae perched on the umbilical shoulder. There are strong, subspinose inner ventrolateral clavi, and strong outer ventrolateral and siphonal clavi, linked across the venter by a coarse, transverse rib. The second rib from the adapical end of the fragment differs from the others in being weaker, with weaker tuberculation. The dorsum preserves traces of the ventrolateral ornament of the penultimate whorl, with indications of the irregular rib and tubercle development of the holotype.

#### Discussion

The distinctive features of *Lyelliceras latili* sp. nov. are the irregular rib and tubercle strength of the phragmocone ornament, present from an early growth stage, depressed whorl section, and distant, coarse, strongly tuberculate ornament throughout. The opposite flank ribs, linked across the venter by a transverse rib, distinguish the species from *Lyelliceras pseudolyelli*, in which the ribs and ventrolateral clavi alternate in position across the venter, and the siphonal clavi are more numerous than the ventrolateral, to which they are linked by an irregular zigzag rib. The species differs from *Lyelliceras lyelli* in the irregular strength and development of phragmocone ornament, and the distinctive polygonal umbilical seam.

The KwaZulu paratype comes from the Lower Albian *Tegoceras mosense-Aioloceras* fauna of locality 35 north of Hluhluwe; *L. latili* is thus the oldest species of the genus in KwaZulu, and is a problematic form, seemingly distinct from the main *pseudolyelli-lyelli* lineage. The holotype and other paratypes are imprecisely dated, coming from the condensed Albian of Escagnolles, Alpes-Maritimes, France.

#### Occurrence

As for types.

Genus *Pseudobrancoceras* Kennedy, 2004

#### Type species

*Ammonites versicostatus* Michelin, 1838, p. 101, pl. 12, fig. 10, from the lower Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli* subzone Argiles Tégulines of Le Gaty, Aube, France.

#### Diagnosis

'Small; phragmocone evolute with slightly depressed to slightly compressed reniform whorl section. Flank ribbing

variable. Coarse, even prorsiradiate primaries extend from umbilicus across flank and venter, but commonly do not extend across the opposite flank, or link to the adapical primary on the opposite flank as a secondary rib, such that ventral ribbing has an irregular zig-zag pattern, or primary ribs may bifurcate on the outer flank and loop across the venter. Relatively weak, feeble or incipient tubercles, often reduced to a mere angulation variably present in ventrolateral and siphonal positions, notably in depressed variants. Suture moderately incised with broad, bifid E/L (=A) and L<sub>2</sub>, U<sub>2</sub>/U<sub>3</sub> and auxiliary saddles bifid, with minor incisions' (after Kennedy 2004)

#### Discussion

*Ammonites versicostatus* of Michelin has been variously referred to *Brancoceras* (*Eubrancoceras*) (Gebhard 1979; Marcinowski & Wiedmann 1990), *Raulinicer* [= *Tegoceras*] (Spath 1931; Casey 1978; Destombes 1979), and *Lyelliceras* (Latil 1995). It is here interpreted as a homoeomorph of *Brancoceras*, which it resembles in coiling and flank ribbing, its true affinities lying with *Lyelliceras*, as proposed by Latil (1995). The suture line is moderately complex, unlike the simplified suture of many *Brancoceras*, while the zigzag and looped ventral ribbing, with some primary ribs either effacing or becoming secondary ribs on the opposite flank, is a characteristic of *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897) of which it is interpreted as a pedomorphic offshoot. Links with *Lyelliceratinae* are further supported by the presence of incipient to feeble ventrolateral and siphonal tubercles in robustly ornamented individuals' (Kennedy 2004, p. 252). As Kennedy (2004) noted, *Pseudobrancoceras transiens* Kennedy, 2004, (fig. 31E–L) links the two genera.

#### Occurrence

Lower Middle Albian, southern England, France, central Iran. KwaZulu, South Africa.

#### *Pseudobrancoceras versicostatum* (Michelin, 1838)

Pl. 9, figs 1–35; Figs 29A–P

1838 *Ammonites versicostatus* Michelin, p. 101, pl. 12, fig. 10.

1841 *Ammonites versicostatus* Michelin; d'Orbigny, p. 273, pl. 81, figs 1–3.

1847 *Ammonites versicostatus* Michelin; Quenstedt, p. 212.

1850 *Ammonites versicostatus* Michelin; d'Orbigny, p. 124.

1860 *Ammonites versicostatus* Michelin; Pictet & Campiche, p. 340.

1911 *Ammonites versicostatus* Mich.; R. Douvillé, figs P<sup>2</sup>, P<sup>2a</sup>, 3.

1931 *Raulinicer* (?) *versicostatum* (Michelin); Spath, p. 313.

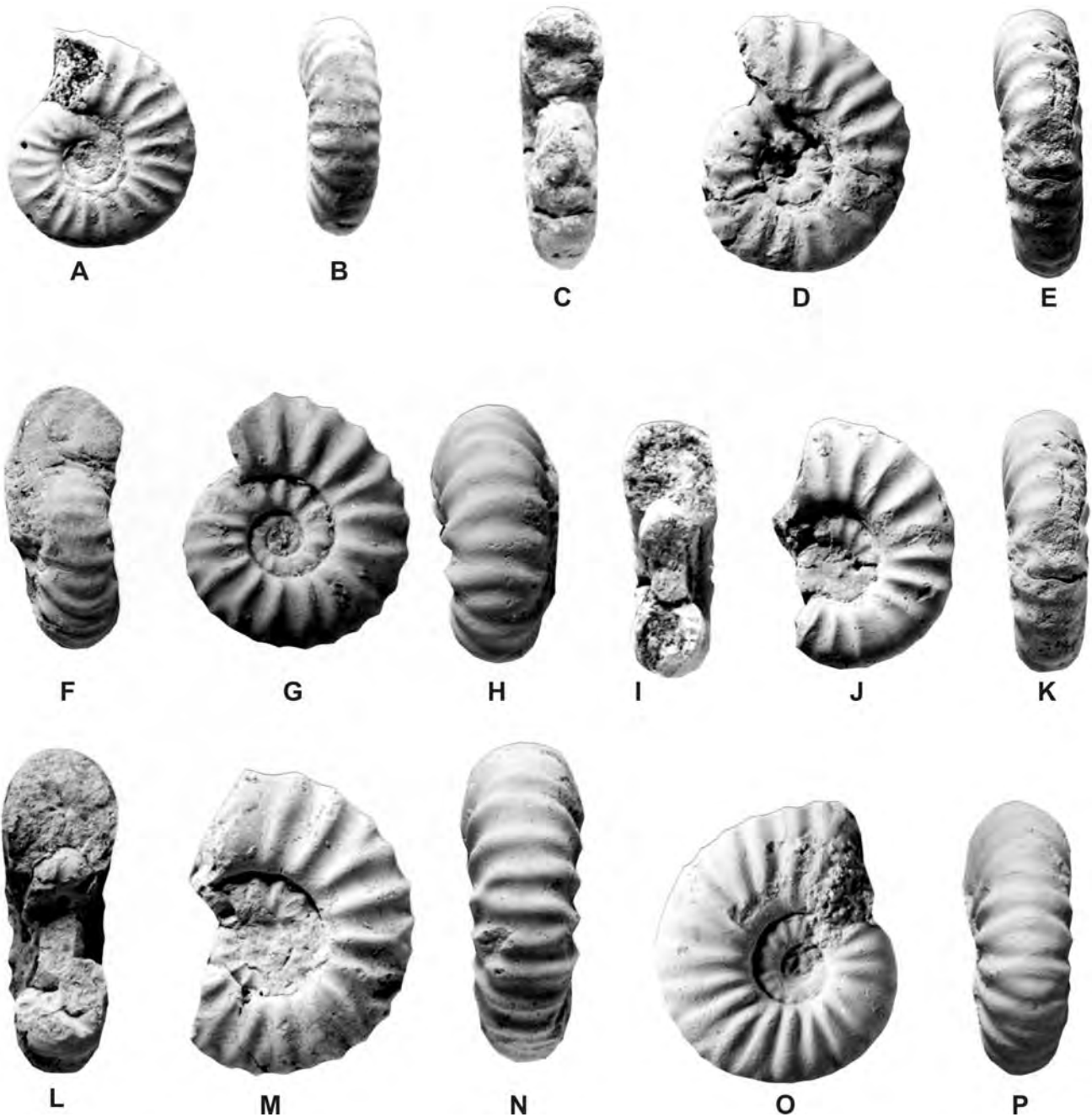
1934 *Raulinicer* *versicostatum* (Michelin); Spath, text-fig. 161m.

1949 *Raulinicer* *versicostatum* (Michelin); Collignon, p. 121.

1978 *Ammonites versicostatus* Michelin; Casey, p. 626.

1979 '*Raulinicer*' *versicostatum* (Michelin); Destombes, p. 109.





**Fig. 29 A–P**, *Pseudobrancoceras versicostatum* (Michelin, 1838). **A, B**, ID 2010/5; **C–E**, ID 2010/11; **I–K**, ID 2010/4; **L–N**, ID 2010/2, all from the condensed Albian of Gourdon, Alpes-Maritimes, France. **F–H**, EMP A246d; **O, P**, EMP A246c, both from the lower Middle Albian of St Florentin, Aube, France. All figures are  $\times 2$ .

1979 *B. (Eubrancoceras) versicostatum* (Michelin); Gebhard, p. 94, pl. 6, fig. 9; pl. 7, fig. 1; text-figs 59, 60.

?non 1990 *Brancoceras (Eubrancoceras) versicostatum* (Michelin); Marcinowski & Wiedmann, p. 81, pl. 8, fig. 2.

1995 *Lyellicerus versicostatum* (Michelin, 1838); Latil, p. 367, pl. 3, figs 21–24; text-figs 29, 30.

1995 *Brancoceras (Eubrancoceras) versicostatum* (Michelin, 1838); Seyed-Emami, p. 432, figs 3, 5.

1997 *Lyellicerus versicostatum* (Michelin, 1838); Latil & Dommergues, p. 105, text-fig. 4.

2004 *Pseudobrancoceras versicostatum* (Michelin, 1838); Kennedy, p. 252, pl. 1, figs 1–24; pl. 2, figs 3–8; pl. 3, figs 1–9, 13–17; text-figs 1, d, e, f.

#### Type

The holotype, by monotypy, is the original of Michelin (1838, p. 101, pl. 12, fig. 10) from the lower Middle Albian *Hoplites dentatus* Zone, *Lyellicerus lyelli* Subzone, Argiles Tégulines of Le Gaty, Aube, France. Douvillé (1912) illustrated what he believed to be Michelin's type as his figure P<sup>2</sup>, P<sup>2a</sup>, and indicated the specimen to be in the École des Mines Collections. It has not been traced.

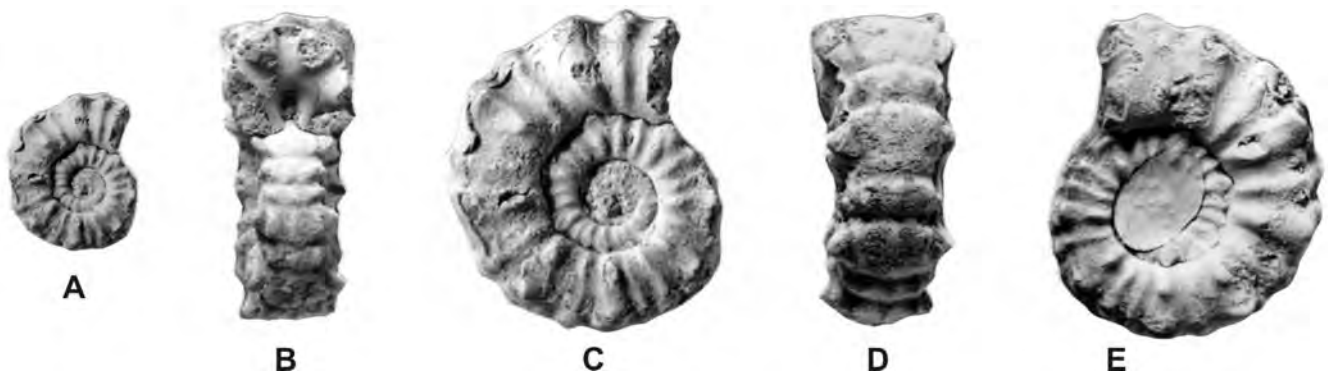


FIG. 30. A–E, *Lyelliceras latili* sp. nov., the holotype, BMNH 37265c, from the condensed Albian of Escagnolles, Alpes-Maritimes, France. Figure A is  $\times 1$ ; B–E are  $\times 2$ .

#### Material

OUM KX9272, 9278, 9285a–f, 9287–9295, 9296a–l, SAM-PCZ22183–5, from locality 154, near Mantuma Rest Camp in the Mkuze Game Reserve. OUM KX9994, 9995, and 9996 a–i, from locality 176, SW of Ndumu.

#### Dimensions

	D	Wb	Wh	Wb:Wh	U
KX9296a	15.0 (100)	6.3 (42.0)	6.6 (44.0)	0.95	5.5 (36.7)
KX9272	20.2 (100)	7.4 (36.6)	9.2 (45.5)	0.8	6.8 (33.7)
KX9944	21.4 (100)	8.7 (40.6)	8.6 (40.2)	1.0	8.1 (37.9)
PCZ22183	24.0 (100)	9.1 (37.9)	9.5 (37.9)		9.6 (40.0)
KX9289	27.8 (100)	10.0 (36.0)	10.2 (36.7)	0.98	11.1 (39.9)
KX9290	29.7 (100)	– (–)	11.6 (39.1)	–	10.9 (36.7)
KX9995	30.9 (100)	8.6 (27.8)	10.5 (26.9)	0.82	12.0 (38.8)

#### Description

The early whorls to a diameter of around 8 mm are moderately evolute, the umbilicus of moderate depth, with a low, rounded umbilical wall. The inner to middle flanks are feebly convex. The outer flanks converge to an evenly rounded venter. There is no ornament at this stage. The first ornament to appear is the ribs. These arise at the umbilical seam, and strengthen across the umbilical wall and shoulder. They are coarse, distant and prorsiradiate on the inner flank, flex back and may develop an incipient bulla on the outer flank, thereafter effacing, leaving the ventrolateral shoulders and venter smooth. After six or seven such ribs the mature ornament develops. At this growth stage, coiling is very evolute, the umbilicus comprising 36–40% of the diameter, the umbilical shoulder convex. The whorl section varies from slightly compressed to slightly depressed, with broadly convex flanks, ventrolateral shoulders and venter. Around 20 primary ribs per whorl arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and may develop into an incipient bulla. They are coarse,

straight and prorsiradiate on the flanks, and bifurcate irregularly at the ventrolateral shoulder, as a result of which there are more ribs on the ventrolateral shoulders and venter than at the umbilical margin. A primary rib on one flank may terminate as an intercalated rib on the opposite flank, or become a secondary rib. As a result, the ventral profile shows a distinctive looped and zigzag pattern to the coarse ventral ribbing (Pl. 9, figs 23, 31, 33). Some individuals lack all trace of tubercles in middle and late growth; others show a ventrolateral and mid-ventral angulation; yet others develop incipient to tiny well-differentiated ventrolateral and siphonal tubercles (Pl. 9, figs 16, 17, 32–34). OUM KX 9290 (Pl. 9, figs 7, 35) is interpreted as an adult macroconch, 29.7 mm in diameter. The final rib is much weakened, and the adult aperture is slightly flared, the margin feebly prorsiradiate, convex on the inner flank region, and feebly concave on the outer flank. OUM KX 9272 (Pl. 9, figs 15, 30, 31) is interpreted as an adult microconch, and shows crowding and approximation of the sutures at a diameter of 15.3 mm. The maximum preserved diameter is 20.2 mm, the adapertural half of the outer whorl is body chamber, and the final few ribs are attenuated. The suture is made up of plump, moderately incised bifid saddles and narrower lobes.

#### Discussion

*Pseudobrancoceras versicostatum* is interpreted as a pedomorphic offshoot of *Lyelliceras pseudolyelli* type. The only other species referred to the genus is *P. transiens* Kennedy, 2004 (p. 254, pl. 2, figs 9, 10, 14–20; text-figs 2a–e, 3a–f; Fig. 31E–L, herein), which has the same style of irregular ventral ornament, but is more compressed, higher-whorled, with well-developed ventrolateral and siphonal clavi on all but the adapertural part of the adult body chamber.

#### Occurrence

Lower Middle Albian, *Lyelliceras lyelli* Subzone of the *Hoplites dentatus* Zone in Aube and Yonne, France. Condensed Lower to lower Upper Albian of Clars/Escagnolles and Gourdon, Alpes-Maritimes, France. Lower Middle Albian of central Iran. The KwaZulu material is associated with *Lyelliceras lyelli*, indicating the lower Middle Albian.

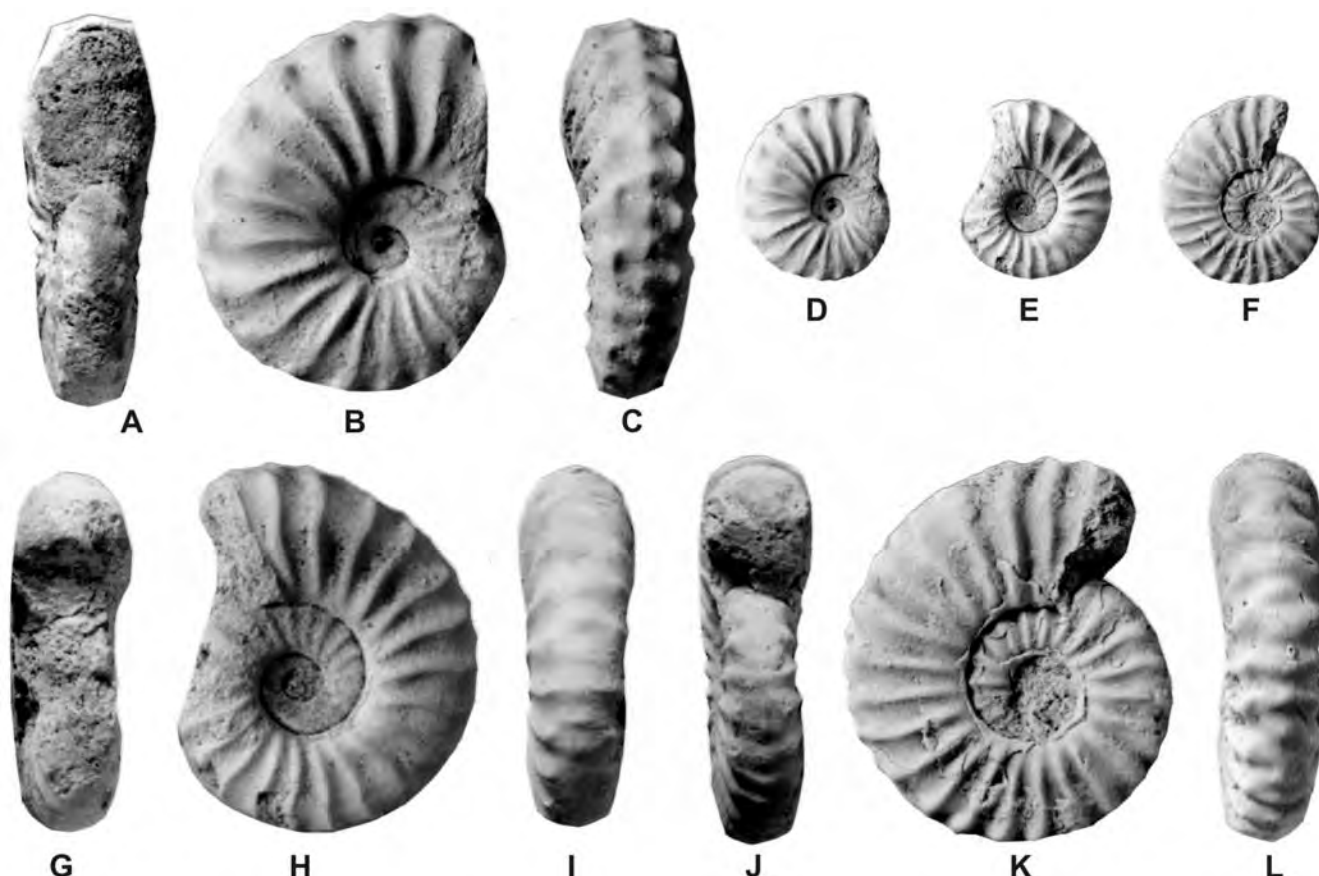


Fig. 31. A–D, *Lyellicerat*? sp. nov. MNHP, d'Orbigny Collection 5792a-3. E–L, *Pseudobrancoceras transiens* Kennedy, 2004. E, G–I, paratype, MNHP d'Orbigny Collection 5792a-2; F, J–L, holotype, MNHP d'Orbigny Collection 5792a-1. All specimens are from the upper Lower or lower Upper Albian of Maurepaire, Aube, France. Figures A–C, G–L are  $\times 2$ , D–F are  $\times 1$ .

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#### REFERENCES

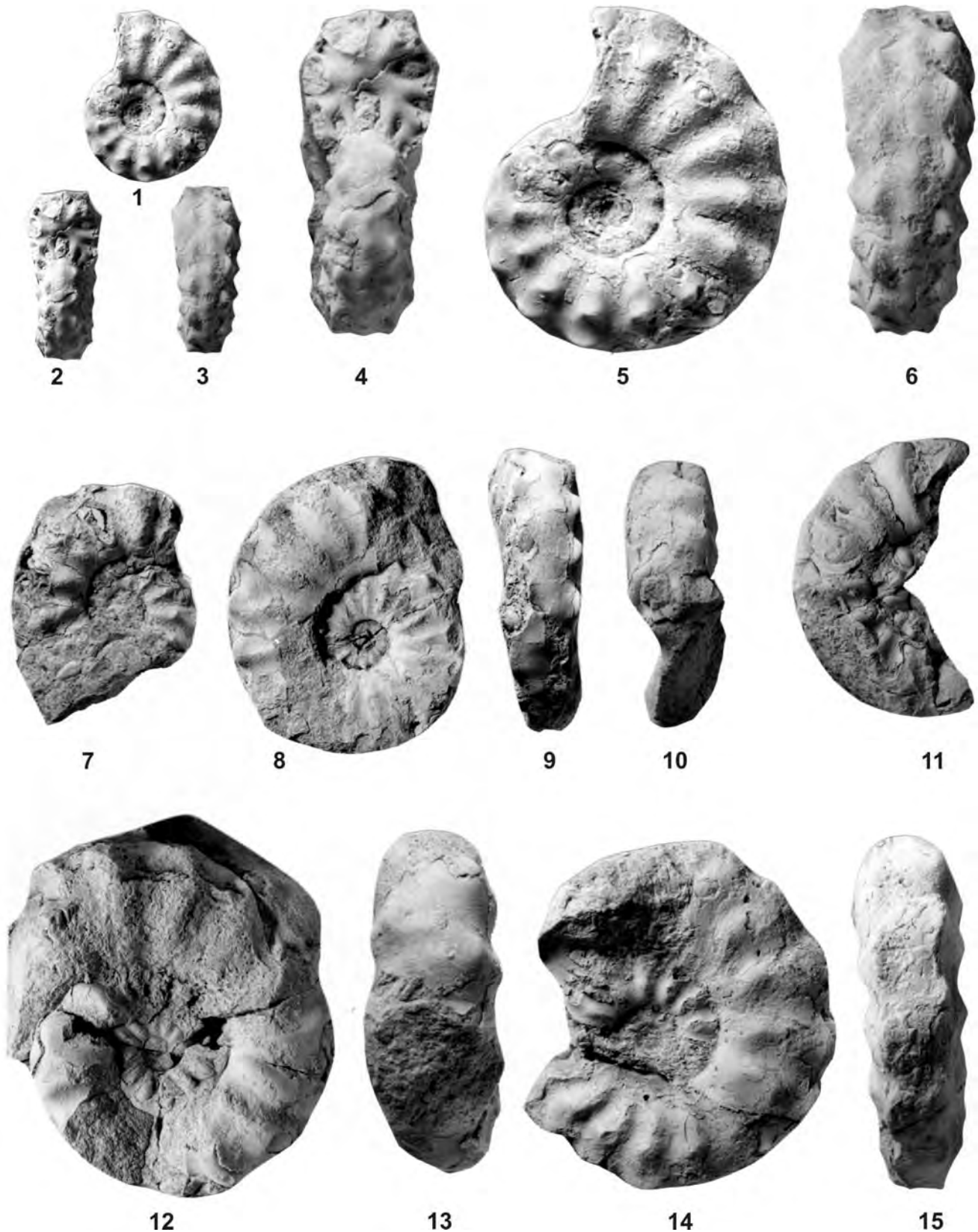
ALMELA, A. & REVILLA, J.D. de la 1957. Fósiles piritosos del Cretáceo de la Sierra de Ricote (Murcia). *Boletín del Instituto Geológico y Minero de España* **68**: 45–83.  
 AMÉDRO, F. 1992. L'Albien du Bassin Anglo-Parisien: ammonites, zonation phylétique, séquences. *Bulletin des Centres de Recherches Exploration-Production Elf-Aquitaine* **16**: 187–233.

BAYLE, É. 1878. Fossiles principaux des terrains de la France. *Explication de la Carte Géologique de France*, 4(1), (Atlas), 158 pls. Paris: Imprimerie nationale.  
 BENAVIDES-CÁCERES, V.E. 1956. Cretaceous system in northern Peru. *Bulletin of the American Museum of Natural History* **108**: 353–494.  
 BÖSE, E. 1923. Algunas faunas Cretácicas de Zacatecas, Durango y Guerrero. *Boletín del Instituto Geológico de México* **42**: iv + 1–219.  
 BREISTROFFER, M., 1947. Sur les zones d'ammonites dans l'Albien de France et d'Angleterre. *Travaux du Laboratoire de Géologie de l'Université Grenoble* **26**: 17–104 (1–88 in separates).  
 BREISTROFFER, M. 1951. Sur quelques ammonites de l'Albien inférieur de Madagascar. *Comptes Rendus Sommaires des Séances de la Société Géologique de France* **15**: 266–268.  
 BREISTROFFER, M. 1953. Commentaires taxonomiques. In BREISTROFFER, M. & VILLOUTREYS, O. DE. Les ammonites albiennes de Peille (Alpes-Maritimes). *Travaux du Laboratoire de Géologie de l'Université de Grenoble* **30** (for 1952): 69–74.  
 CASEY, R. 1957. The Cretaceous ammonite genus *Leymeriella*, with a systematic account of its British occurrences. *Palaeontology* **1**: 28–59.  
 CASEY, R. 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology* **3**: 487–621.  
 CASEY, R. 1962. A monograph of the Ammonoidea of the Lower Greensand. Part 4. *Palaeontographical Society Monograph*: 217–288.  
 CASEY, R. 1978. A Monograph of the Ammonoidea of the Lower Greensand. Part 8. *Palaeontographical Society Monograph*: 583–632.

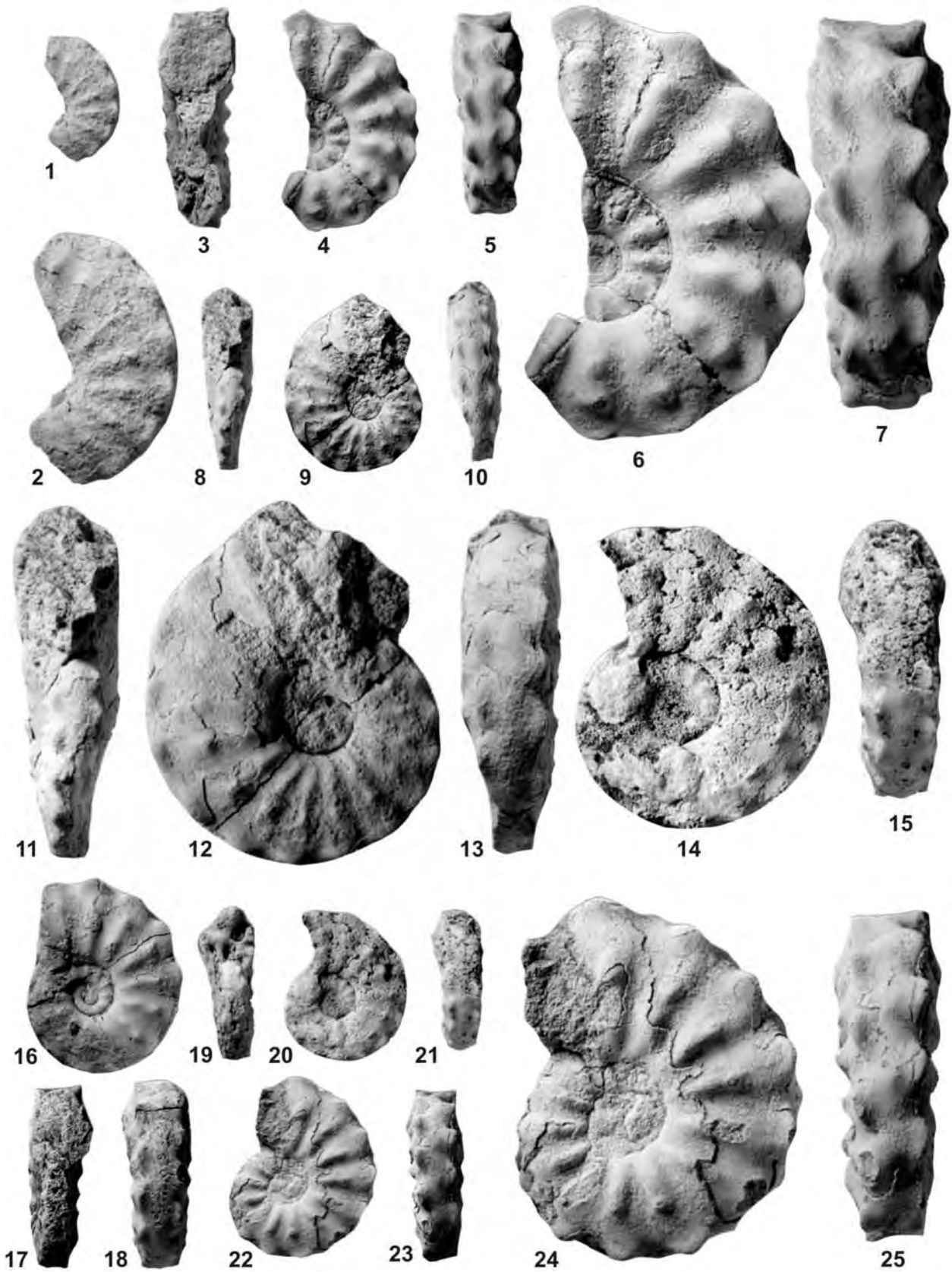
- CIRY, R. 1927. Révision de la faune albiennaise du Département de la Côte d'Or. *Bulletin de la Société d'Histoire Naturelle de Toulouse* **56**: 549–575.
- COLLIGNON, M. 1949. Recherches sur les faunes albiennes de Madagascar. I. L'Albien d'Ambarimaninga. *Annales Géologiques du Service des Mines de Madagascar* **16**: 1–128.
- COLLIGNON, M. 1963. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*. X. Albien. xv + 1–184. Tananarive: Service Géologique.
- COOPER, M.R. 1992. Towards a phylogenetic classification of the Cretaceous ammonites: II Lyelliceratinae. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **185**: 21–38.
- CRAMPTON, J.S. 1996. Biometric analysis, systematics and evolution of Albian *Actinoceramus* (Cretaceous Bivalvia, Inoceramidae). *Institute of Geological and Nuclear Science Monograph* **15** (New Zealand Geological Survey Paleontological Bulletin **71**): 1–73.
- DELAMETTE, M. 1988. L'Évolution du Domaine Helvétique (entre Bauges et Morcles) de l'Aptien Supérieur au Turonien: séries condensées, phosphorites et circulations océaniques. *Publications du Département de Géologie et de Paléontologie de l'Université de Genève* **5**: 1–316.
- DELAMETTE, M. 1989. L'origine des mélanges de faunes dans les conglomérats phosphatés albiens et cénomaniens de la plate-forme helvétique (Alpes occidentales). *Revue de Paléobiologie* **3**: 19–37.
- DELAMETTE, M., CHARROLAIS, J., DECROUEZ, D. & CARON, M. 1997. Les Grès Verts Helvétiques (Aptien Moyen-Albien Supérieur) de Haute-Savoie, Valais et Vaud (Alpes Occidentales Franco-Suisse). Analyse stratigraphique et inventaire paléontologique. *Université de Genève, Publications du Département de Géologie et Paléontologie* **23**: 1–400.
- DESTOMBES, P. 1977a. The Gault at Bully. *Proceedings of the Geologists' Association* **88**: 25–27.
- DESTOMBES, P. 1977b. Some new ammonites from the Gault at Bully. *Proceedings of the Geologists' Association* **88**: 39–43.
- DESTOMBES, P. 1979. Les Ammonites de l'Albien inférieur et moyen dans le stratotype de l'Albien: Gisements, paléontologie, biozonation. pp. 51–194 *In*: RAT, P. *et al.*, *Les Stratotypes Française*, **5**, L'Albien de l'Aube: 1–448. Paris: CNRS.
- DESTOMBES, P. 1983. Recherches sur la mésofaune de l'Albien Inférieur de Bully-Saint-Martin l'Hortier (Pays de Bray). *Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre* **70**: 43–57.
- DESTOMBES, P., JUIGNET, P. & RIOULT, M. 1973. Ammonites de l'Aptien-Albien du Bec de Caux, Normandie (NW France). *Bulletin Trimestriel de la Société Géologique de Normandie et des Amis du Muséum du Havre* **61**: 49–106.
- DOUVILLÉ, H. 1911. Évolution et classification des Pulchellidés. *Compte Rendu Sommaire des Séances de la Société Géologique de France*. Séance du 24 Avril 1911: 85–86.
- DOUVILLÉ, H. 1912. Sur la classification des Pulchellidés. *Bulletin de la Société Géologique de France* (4) **11**: 285–320 (for 1911).
- DOUVILLÉ, R. 1907. Sur les Ammonites du Crétacé sud-américain. *Annales de la Société Royal Zoologique et malacologique de Belgique* **41**: 142–155.
- DOUVILLÉ, R. 1911. *Ammonites Mosensis* d'Orbigny, 1840. *Palaeontologia Universalis*, n.s., Fiche 219.
- DUBOURDIEU, G. 1953. Ammonites nouvelles des Monts du Mellègue. *Bulletin du Service de la Carte Géologique de l'Algérie. 1e série, Paléontologie* **16**: 1–76.
- ETAYO-SERNA, F. 1979. Zonation of the Cretaceous of central Colombia by Ammonites. *Publicaciones Geológicas Especiales del Ingeominas, Bogota* **2**: 1–186.
- ETHERIDGE, R. 1907. Cretaceous fossils of Natal. II. The Umsinene River Deposit. *Report of the Geological Survey of Natal and Zululand* **3**: 367–390.
- FORBES, E. 1846. Report on the Fossil Invertebrata from southern India, collected by Mr. Kaye and Mr. Cunliffe. *Transactions of the Geological Society of London* (2) **7**: 97–174.
- GAUTHIER, H. 2006. *Révision Critique de la Paléontologie Française d'Alcide d'Orbigny*, **6**, Céphalopodes Crétacés. 1–292 + 1–662. Leiden: Backhuys.
- GEBHARD, G. 1979. *Glaukonitische Kondensation im Alb der sub-alpinen Ketten (Clars, Escragnolles, SE-Frankreich), deren Ammonitenfauna und Kartierung in der Umgebung von Escragnolles*. Unpublished thesis, University of Tübingen.
- GEBHARD, G. 1982. Glauconitic condensation through high energy events in the Albian near Clars (Escragnolles, Var, SE France). *In*: EINSELE, G. & SEILACHER, A. *Cyclic and Event Stratification*, pp. 286–298. New York: Springer.
- GERHARDT, K. 1897. Beiträge zur Kenntniss der Kreideformation in Columbien. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie Beilage-Band* **11**: 118–208.
- GUÉRIN-FRANIATTE, S. 2006. *Lyelliceras lyelli*, p. 92. *In*: GAUTHIER, H. *Révision Critique de la Paléontologie Française d'Alcide d'Orbigny*, **6**, Céphalopodes Crétacés. 1–292 + 1–662. Leiden: Backhuys.
- HART, M.B., AMEDRO, F. & OWEN, H.G. 1996. The Albian stage and substage boundaries. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre* **66** (Supplément): 45–56.
- HOEPEN, E.C.N. VAN 1968. New and little known Zululand and Pondoland ammonites. *Annals of the Geological Survey of South Africa* **4**(1965): 157–181(1965).
- HYATT, A. 1903. Pseudoceratites of the Cretaceous. *United States Geological Survey Monograph* **44**: 1–351.
- JACOB, C. 1907. Études paléontologiques et stratigraphiques sur la partie moyenne des terrains crétaqués dans les Alpes françaises et les régions voisines. *Annales de l'Université de Grenoble* **19** (2): 221–534 (published also in 1908 in *Travaux du Laboratoire de Géologie de l'Université de Grenoble* **8**(2): 280–590 and later in 1908 in *Bulletin de la Société de Statistique des Sciences Naturelles et des Arts Industriels du Département d'Isère (Grenoble)* (4) **10**: 201–514).
- KENNEDY, W.J. *In*: KENNEDY, W.J., GALE, A.S., BOWN, P.R., CARON, M., DAVEY, R.J., GRÖCKE, D. & WRAY, D.S. 2000. Integrated stratigraphy across the Aptian-Albian boundary in the Marnes Bleues, at the Col de Pré-Guittard Arnyon (Drôme), and at Tartonne (Alpes-de-Haute-Provence), France: a candidate Global Boundary Stratotype Section and Boundary Point for the base of the Albian Stage. *Cretaceous Research* **21**: 591–720.
- KENNEDY, W.J. 2004. On *Brancoceras* Steinmann, 1881 (Brancoceratidae) and *Pseudobrancoceras* gen. nov. (type species *Ammonites versicostatus* Michelin, 1838: Lyelliceratinae) from the Albian (Cretaceous) of the western Paris Basin and Provence, France. *Acta Geologica Polonica* **54**: 251–272.
- KENNEDY, W.J. & DELAMETTE, M. 1994. *Neophlycticeras* Spath, 1922 (Ammonoidea) from the Upper Albian of Ain, France. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **191**: 1–24.
- KENNEDY, W.J. & JUIGNET, P. *In*: GAUTHIER, H. 2006. *Révision Critique de la Paléontologie Française d'Alcide d'Orbigny*, **6**, Céphalopodes Crétacés. 1–292 + 1–662. Leiden: Backhuys.
- KENNEDY, W.J. & KLINGER, H.C. 1975. Cretaceous faunas from Zululand and Natal, South Africa. Introduction, Stratigraphy. *Bulletin of the British Museum of Natural History (Geology)* **25**: 263–315.
- KENNEDY, W.J. & KLINGER, H.C. 1978. Cretaceous faunas from Zululand and Natal, South Africa. A new genus and species of Gastroplitinae from the Mzinene Formation (Albian). *Annals of the South African Museum* **77**: 57–69.
- KENNEDY, W.J., WRIGHT, C.W. & KLINGER, H.C. 1979. Cretaceous faunas from Zululand and Natal, South Africa. A new genus and species of tuberculate desmoceratacean from the Mzinene

- Formation (Albian). *Annals of the South African Museum* **78**: 29–38.
- KLINGER, H.C. & KENNEDY, W.J. 2008. *Mkuzeiella andersoni* gen. et sp. nov. (Cephalopoda, Ammonoidea) from the Albian Mzinene Formation of KwaZulu Natal, South Africa. In: STEURBAUT, E., JAGT, J.W.M. & JAGT-YAZYKOVA, E.E. (Eds) Annie V. Dhondt Memorial Volume. *Bulletin de l'Institut royal des Sciences Naturelles de Belgique, Sciences de la Terre* **78**: 179–191.
- KLINGER, H.C., WIEDMANN, J. & KENNEDY, W.J. 1975. A new carinate phylloceratid ammonite from the early Albian (Cretaceous) of Zululand, South Africa. *Palaeontology* **18**: 657–664.
- KNECHTEL, M.M. 1947. In: KNECHTEL, M.M., RICHARDS, E.F. & RATHBUN, M.V. Mesozoic fossils of the Peruvian Andes. *Johns Hopkins University Studies in Geology* **15**: 1–150.
- KORN, D., EBBINGHAUSEN, V., BOCKWINKEL, J. & KLUG, C. 2003. The A-mode sutural ontogeny in prolecanitid ammonoids. *Palaeontology* **46**: 1123–1132.
- KULLMANN, J. & WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *University of Kansas, Paleontological Contributions* **42**: 1–32.
- LARCHER, C. 1936. Contribution à l'étude de l'Albien du département de l'Aube. *Bulletin Scientifique de Bourgogne* **6**: 37–44.
- LATIL, J.L. 1995. Les Lyelliceratinae Spath, 1921 (Ammonitina, Ammonoidea) de l'Albien inférieur et moyen dans le bassin de Paris et sur les bordures du basin vocontienne: stratigraphie, paléobiogéographie et taxonomie. *Géologie Alpine Mémoires, Hors Série* **20**: 327–381.
- LATIL, J.L. & DOMMERGUES, J.L. 1997. Variabilité, ontogénèse et phylogénie des Lyelliceratinae (Ammonites de l'Albien). *Revue de Paléobiologie* **16**: 101–113.
- LATIL, J.L., ROBERT, E., & BULOT, L.G. In press. New insights on the genus *Prolyellicerias* Spath, 1930, and the identity of *Acanthoceras gevreyi* Jacob, 1907 (Cephalopoda, Ammonoidea). *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen*.
- LEYMERIE, A. 1841–1842. Mémoire sur le Terrain Crétacé du Département de l'Aube, contenant des considerations générales sur le Terrain Néocomien. *Mémoires de la Société Géologique de France* (1) **4** (1841): 291–364; **5** (1842): 1–34.
- LEYMERIE, A. 1846. *Statistique géologique et minéralogique du département de l'Aube*. Xvi + 676 pp. Troyes: Laloy.
- MARCINOWSKI, R. & WIEDMANN, J. 1990. The Albian ammonites of Poland. *Palaeontologica Polonica* **50**: 1–94.
- MICHELIN, H. 1838. Note sur une argile dépendant du Gault, observée au Gaty, commune de Gérodot, département de l'Aube. *Mémoires de la Société Géologique de France* (1) **3**: 97–103.
- OBATA, I., SHIBATA, K. & OGAWA, Y. 1975. Albian ammonites from the central Andes. *Bulletin of the National Science Museum, Series C, Geology* **1**: 69–82 (in Japanese).
- ORBIGNY, A. d'. 1840–1842. *Paléontologie française: Terrains crétacés*. **1**. *Céphalopodes*. 1–120 (1840); 121–430 (1841); 431–662 (1842). Paris: Masson.
- ORBIGNY, A. d'. 1850. *Prodrome de paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au cours élémentaire de paléontologie et de géologie stratigraphiques*. **2**: 1–427. Paris: Masson.
- OWEN, H.G. 1971. Middle Albian stratigraphy in the Anglo-Paris Basin. *Bulletin of the British Museum of Natural History (Geology)*, supplement **8**: 1–164.
- OWEN, H.G. 1988. The ammonite zonal sequence and ammonite taxonomy in the *Douvilleiceras mammillatum* Superzone (Lower Albian) in Europe. *Bulletin of the British Museum of Natural History (Geology)* **44**: 177–231.
- PARONA, C.F. & BONARELLI, G. 1897. Fossili Albiani d'Escragnoles, del Nizzardo e della Liguria occidentale. *Palaeontographia Italica* **2**: 53–107 (1–55).
- PERVINQUIÈRE, L. 1907. Études de paléontologie tunisienne. 1. Céphalopodes des terrains secondaires. *Carte Géologique de la Tunisie*, v + 1–438. Paris: de Rudeval.
- PERVINQUIÈRE, L. 1910. Sur quelques ammonites du Crétacé algérien. *Mémoires de la Société Géologique de France. Paléontologie* **17**: 1–86.
- PICTET, F.J. 1847. In: PICTET, F.J. & ROUX, W. 1847–1854. Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* **11**(1847): 257–412; **12**(1849): 21–151; **13**(1852): 73–173; **14**(1854): 279–341. Geneva: Kessmann & Georg.
- PICTET, F.J. & CAMPICHE, G. 1858–1864. Description des fossiles du terrain crétacé des environs de Sainte-Croix part 2 (1). Description des fossiles. *Matériaux pour la Paléontologie Suisse* (2) part 1, 1–380; part 2, 1–752.
- PICTET, F.J. & ROUX, W. 1847–1854. Description des mollusques fossiles qui se trouvent dans les Grès Verts des environs de Genève. *Mémoires de la Société de Physique et d'Histoire Naturelle de Genève* **11**(1847): 257–412; **12**(1849): 21–151; **13**(1852): 73–173; **14**(1854): 279–341. Geneva: Kessmann & Georg.
- QUENSTEDT, F.A. 1845–1849. *Petrefactenkunde Deutschlands*. **1**, *Cephalopoden*. i, 1–104 (1845); ii, 105–184 (1846); iii, 185–264 (1847); iv, v, 265–472 (1848); vi, 473–580 (1849). Tübingen: H. Laupp.
- RENZ, O. 1979. Lower Cretaceous Ammonoidea from the northern Atlantic, leg 47B. Hole 398D. *Initial Reports of the Deep Sea Drilling Project* **47/2**: 361–369.
- RENZ, O. 1982. *The Cretaceous Ammonites of Venezuela*. 1–132. Basel: Maraven.
- RIEDEL, L. 1938. Ammonites del Cretácico inferior de la Cordillera Oriental. In *Estudios geológicos y paleontológicos sobre la Cordillera Oriental de Colombia* **2**, 7–78. Bogota: Departamento de Minas y Petroleos, Ministerio de Industrias y Trabajo.
- ROBERT, E. 2001. La transgression albienne dans le bassin andin (Pérou). Biostratigraphie, paléontologie (ammonites) et stratigraphie séquentielle. Thèse pour obtenir le grade de docteur de l'université Toulouse III.
- ROBERT, E. 2002. La transgression albienne dans le Bassin Andin (Pérou): Biostratigraphie, Paléontologie (ammonites) et stratigraphie séquentielle. *Strata* **38**: 1–380.
- ROBERT, E., BULOT, L.G., JAILLARD, É. & PEYBERNÈS, B. 2002. Proposition d'une nouvelle biozonation par ammonites de l'Albien du bassin andin (Pérou). *Comptes Rendu Palevol* **1**, 1–9.
- ROMAN, F. 1938. *Les ammonites jurassiques et crétacées. Essai de genera*. 1–554. Paris: Masson.
- SCHINDEWOLF, O.H. 1966. Studien zur Stammesgeschichte der Ammoniten: **VI**. *Akademie der Wissenschaften und der Literatur, Abhandlungen der Mathematisch-Naturwissenschaftlichen Klasse* **1966**(8): 723–808.
- SCHLOTHEIM, E.F. VON 1813. Beiträge zur Naturgeschichte der Versteinerungen in geognostischer Hinsicht. *Leonard's Taschenbuch für die gesammte Mineralogie* **7**: 3–134.
- SEUNES J. 1887. Sur quelques ammonites du Gault. *Bulletin de la Société Géologique de France* (3), **15**: 557–571.
- SEYED-EMAMI, K. 1995. Lyelliceratidae und Brancoceratidae (Ammonoidea) aus dem tieferen Mittelalb (Kreide) bei Soh, Zentraliran. *Neues Jahrbuch für Geologie und Paläontologie Monatshefte* **1995**: 430–440.
- SPATH, L.F. 1921. On Cretaceous Cephalopoda from Zululand. *Annals of the South African Museum* **12**: 217–321.
- SPATH, L.F. 1922. On Cretaceous Ammonoidea from Angola, collected by Professor J.W. Gregory, D.Sc., F.R.S. *Transactions of the Royal Society of South Africa* **53**: 91–160.
- SPATH, L.F. 1923–1943. A monograph of the Ammonoidea of the Gault. *Palaeontographical Society Monographs*, 1–787. 1–72 (1923); 73–110 (1925); 111–146 (1925); 147–186 (1926); 187–206 (1927); 207–266 (1928); 267–311 (1930a); 313–378 (1931);

- 379–410 (1932); 411–442 (1933); 443–496 (1934); 497–540 (1937); 541–608 (1939); 609–668 (1941); 669–720 (1942); 721–287, i–x (1943).
- SPATH, L.F. 1930*b*. The fossil fauna of the Samana Range and some neighbouring areas. v. The Lower Cretaceous Ammonoidea with notes on Albian Cephalopods from Hazara. *Palaeontologica Indica* N.S. **15**(5): 51–66.
- STEINMANN, G. 1881. Über Tithon und Kreide in den Peruanischen Anden. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* **2**: 130–153.
- STOLICZKA, F. 1863–1866. The fossil Cephalopoda of the Cretaceous rocks of southern India. Ammonitidae with revision of the Nautilidae etc. *Memoirs of the Geological Survey of India*. (1), *Palaeontologica Indica* (3) **1**: 41–56(1863); **2–5**: 57–106(1864); **6–9**: 107–154(1865); **10–13**: 155–216(1866).
- WRIGHT, C.W. 1957. [*Cretaceous Ammonoidea*]. In: MOORE, R.C. (ed.), *Treatise on Invertebrate Paleontology. Part L, Mollusca 4, Revised Cephalopoda Ammonoidea*. xxii + 1–490. New York and Lawrence: Geological Society of America and University of Kansas Press.
- WRIGHT, C.W. 1996. In: *Treatise on Invertebrate Paleontology. Part L, Mollusca 4: Cretaceous Ammonoidea*. xx + 1–362 (with contributions by J.H. Calloman (sic) and M.K. Howarth). Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.
- WRIGHT, C.W. & KENNEDY, W. J. 1994. Evolutionary relationships among Stoliczkaianae (Cretaceous ammonites) with an account of some species from the English *Stoliczkaia dispar* Zone. *Cretaceous Research* **15**: 547–582.
- YOUNG, K. 1993. Middle Albian ammonites from El Madero, west-central Chihuahua. *Texas Journal of Science*: **45**: 165–176.

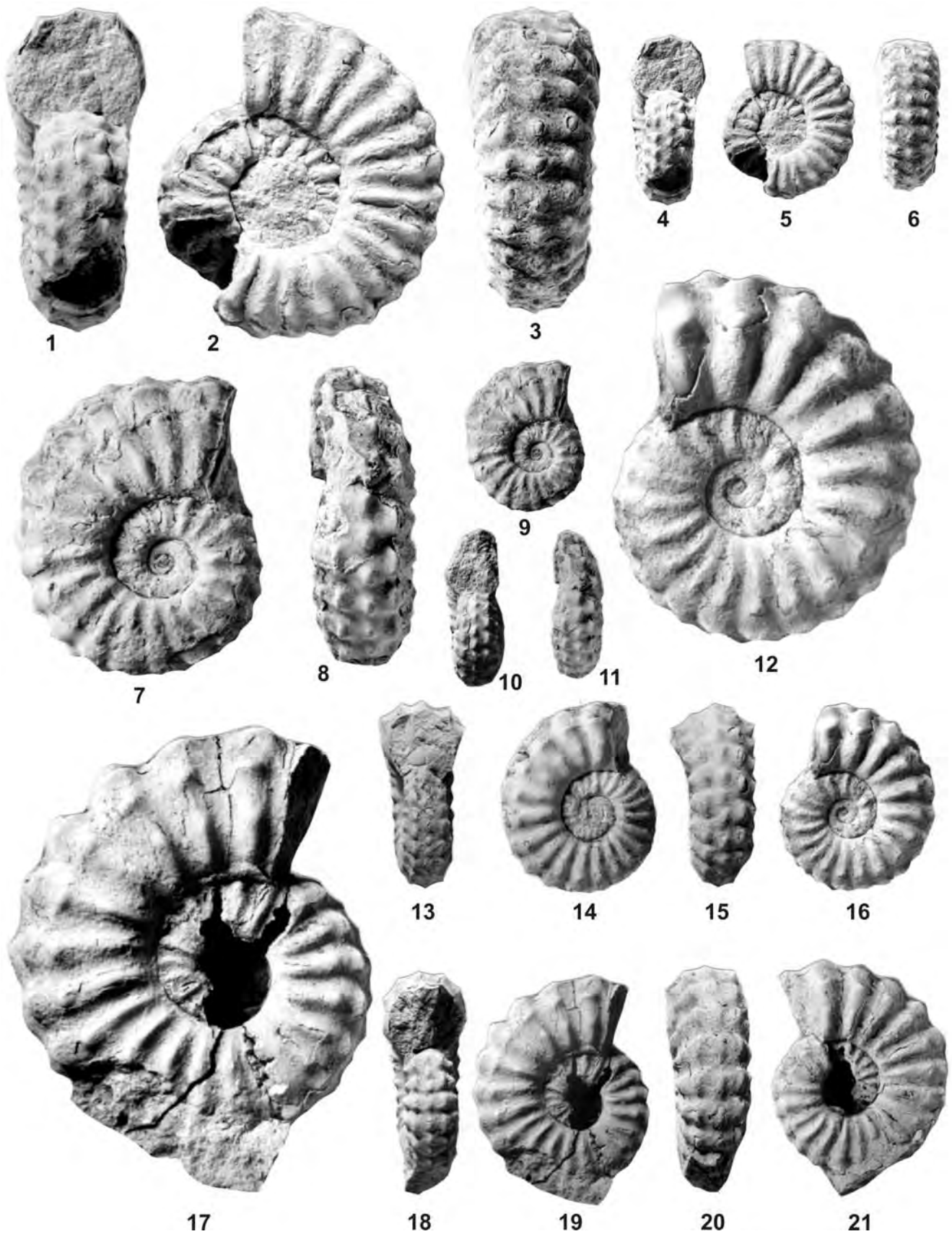


**Plate 1.** Figs 1–6, *Tegoceras collignoni* (Breistroffer, 1953), SAM-PCZ22186, by its preservation from the Mzinene Formation Albian III of the Ndumu area of northern KwaZulu. 7–9, 14, 15, *Tegoceras camatteanum* (d'Orbigny, 1841). 7, OUM KX9957, from the Mzinene Formation, Albian III of locality 175; 8, 9, SAM PCZ22191, from the Mzinene Formation, Albian III of locality 176; 14, 15, SAM-PCZ22187, by its preservation from the Mzinene Formation Albian III of the Ndumu area of northern KwaZulu. 10–13, *Tegoceras mosense* (d'Orbigny, 1841), SAM-PCZ22182, from the Mzinene Formation, Albian III of locality 175. Figures 1–3, 7–15 are x1; 4–6 are x2.

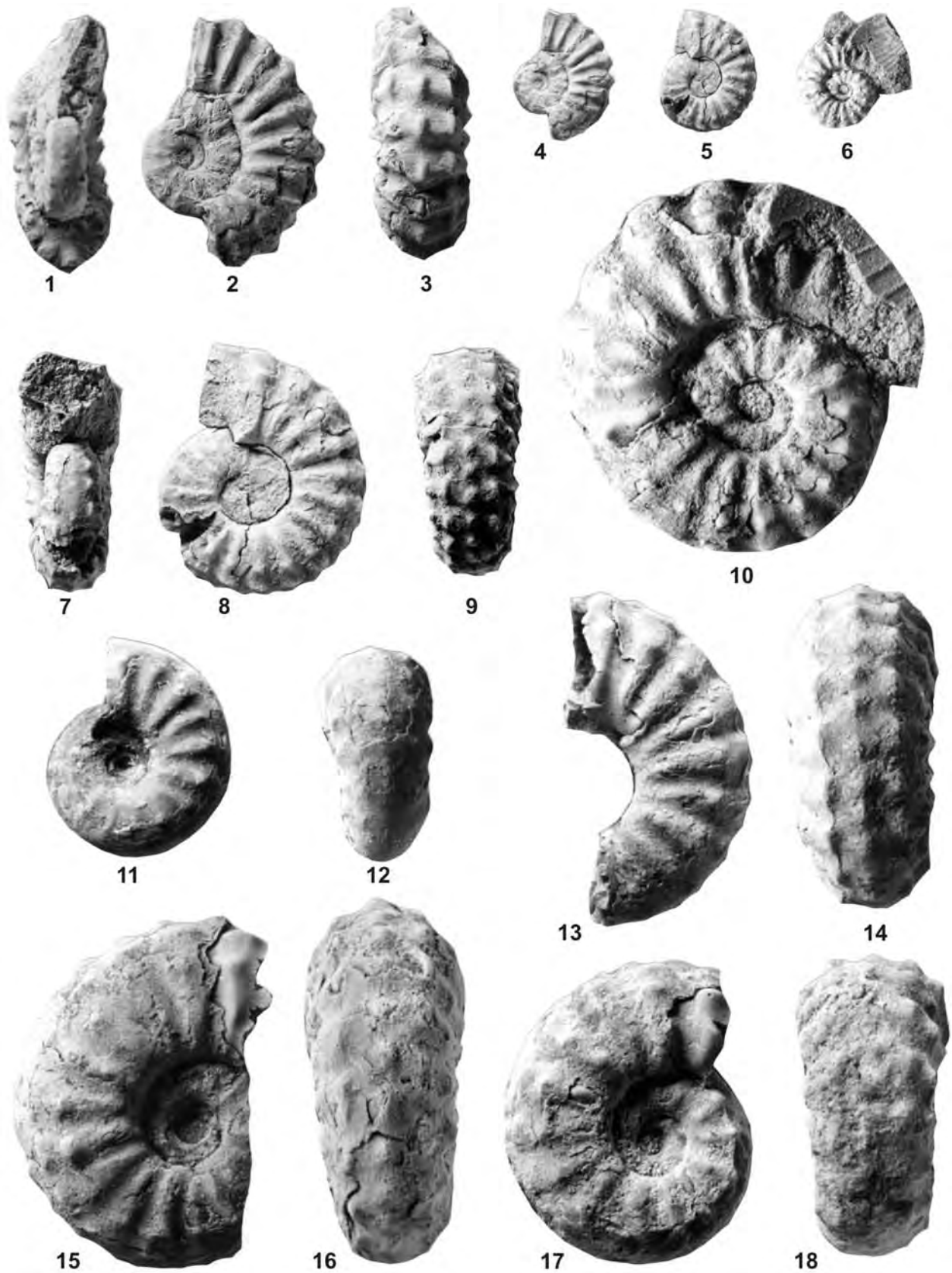


**Plate 2. Figs 1–25, *Tegoceras camatteanum* (d’Orbigny, 1841).** 1, 2, OUM KX9959a; 3–7, OUM KX9958; 8–13, OUM KX9959b, from the Mzinene Formation, Albian III of locality 175. 14, 15, 19–21, SAM-PCZ22187 (ex SAM A2126), from the Mzinene Formation probably also from locality 175. 16–18, EMP Collections, from the condensed Albian of Escragnoles, Alpes-Maritimes, France. 22–25, OUM KX9955, from the same horizon and locality as the originals of Figs 1, 2, 3–13. Figures 1, 3–4, 8–10, 16–23 are x1; 6, 7, 11–15, 24, 25 are x2.

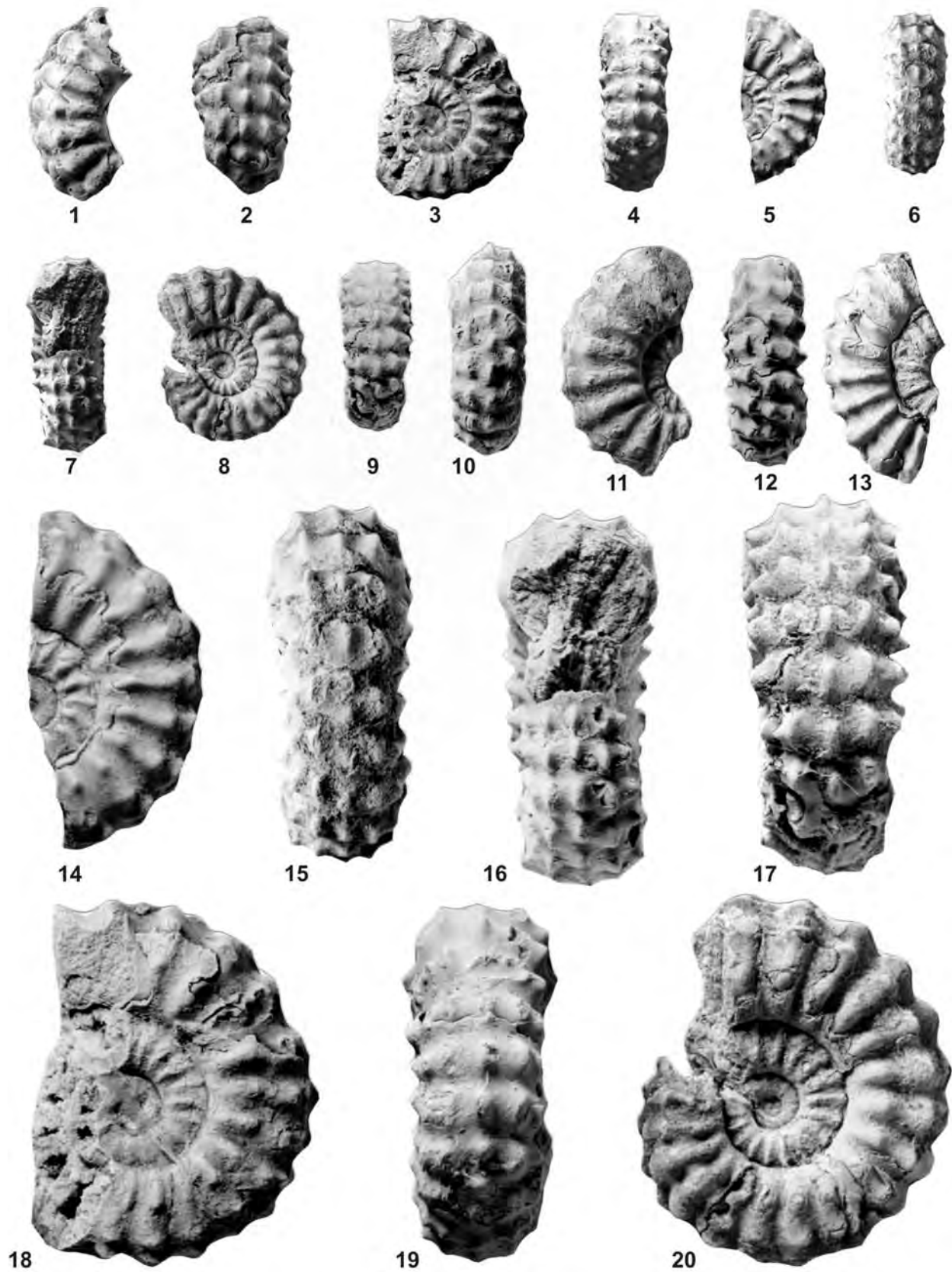




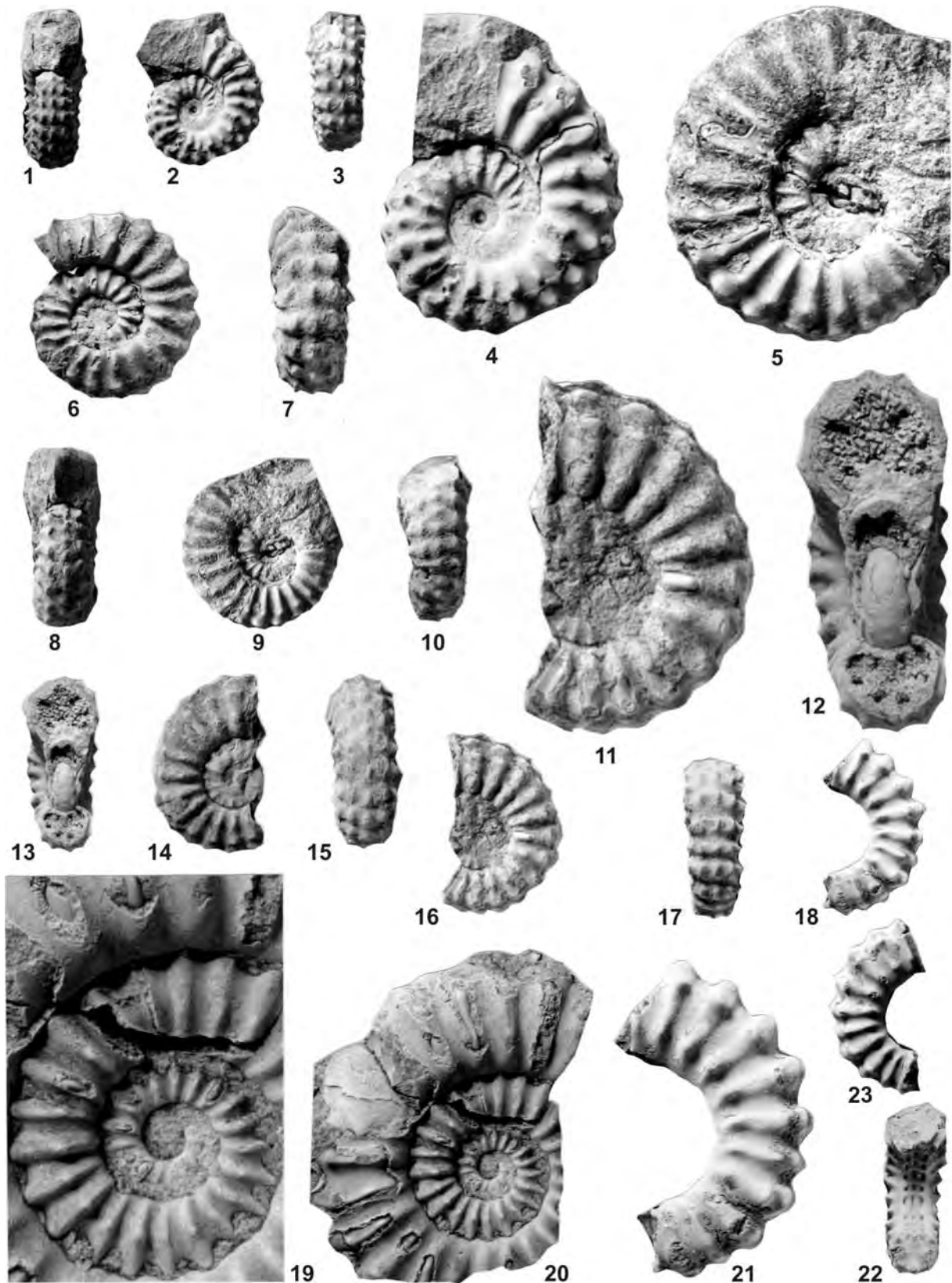
**Plate 3.** Figs 1–11, 17–21, *Lyellicerus lyelli* (d'Orbigny, 1841). 1–6, SAM-PCZ22224; 7–11, SAM-PCZ154; 17–21, OUM KX9284. 12–16, *Lyellicerus pseudolyelli* (Parona & Bonarelli, 1897). OUM KX9271. All specimens are from the Mzinene Formation, Albian III, of locality 154. Figures 4–6, 9–11, 13–16, 18–21 are x1; 1–3, 7, 8, 12, 17 are x2.



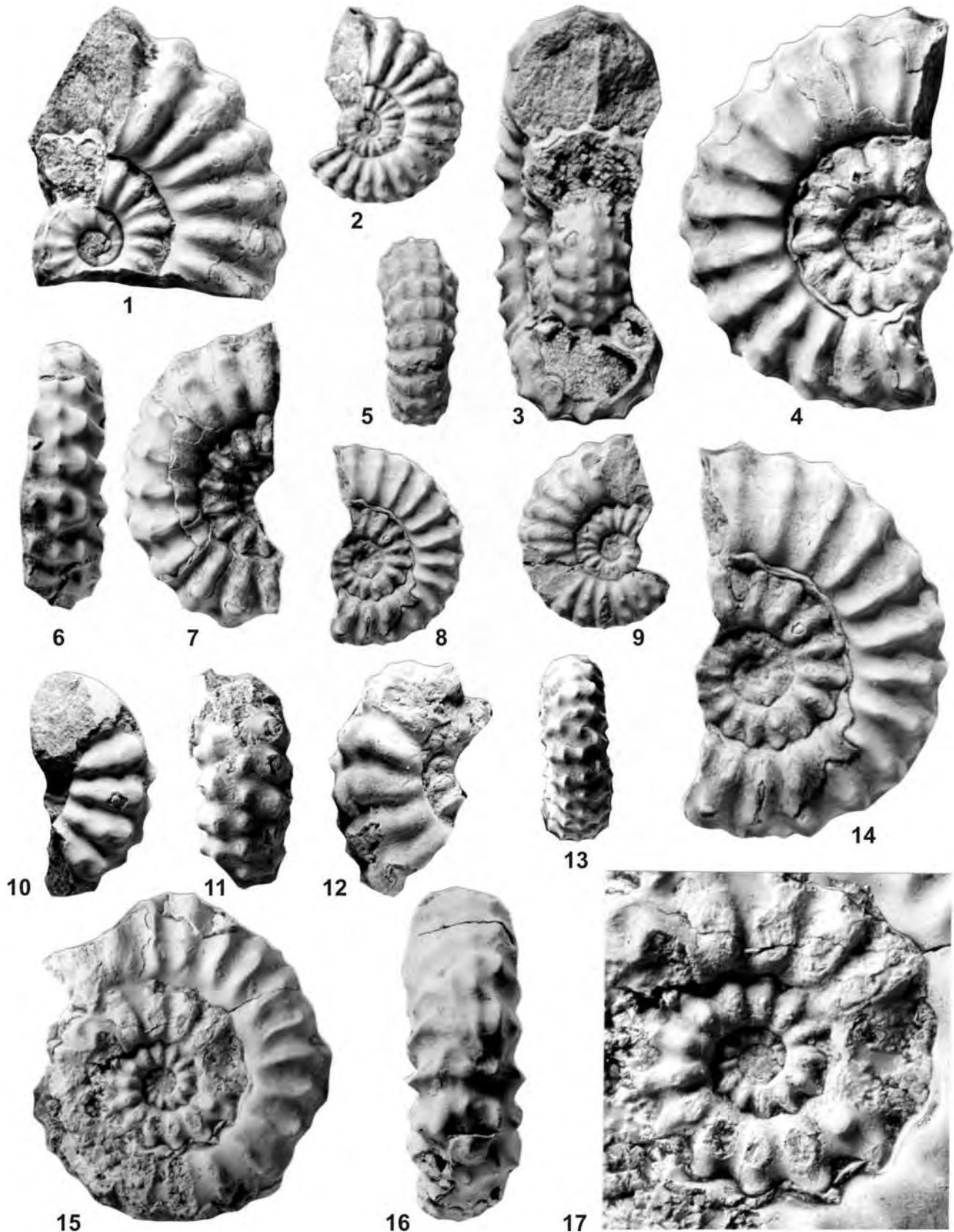
**Plate 4.** Figs 1–5, 7–9, 11–14, 17, 18, *Lyelliceras lyelli* (d'Orbigny, 1841). 1–4, SAM-PCZ22230; 5, 7–9, SAM-PCZ22228; 11, 12, OUM K9286a; 13, 14, SAM-PCZ22232; 17, 18, SAM-PCZ22229. 6, 10, 15, 16, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). 6, 10, SAM-PCZ22189; 15, 16, SAM-PCZ5872. All specimens are from the Mzinene Formation, Albian III, of locality 154. Figures 1–3, 7–9 are x2; 4–6 are x1; 10–18 are x4.



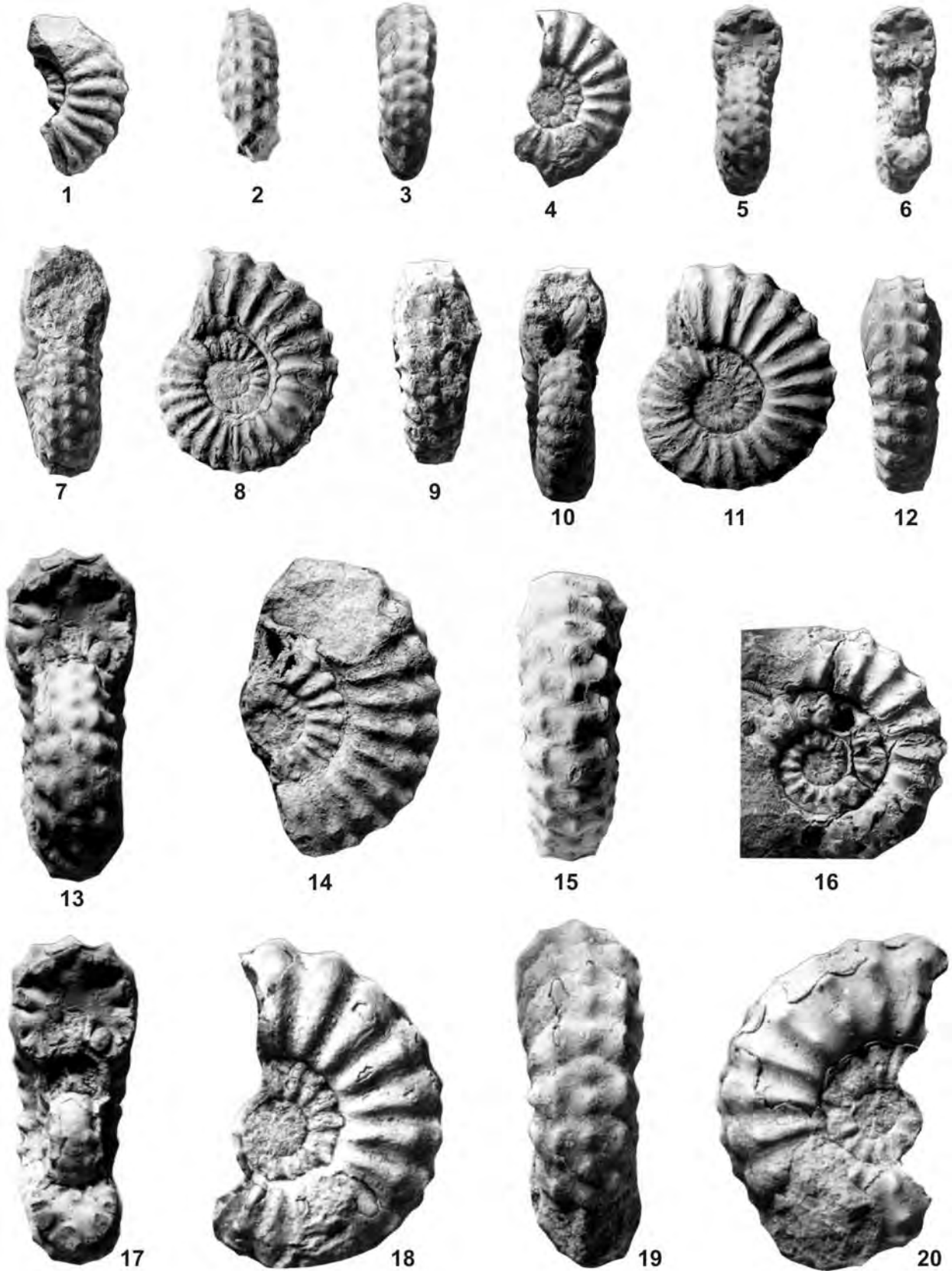
**Plate 5.** Figs 1–11, 14–20, *Lyellicereras lyelli* (d'Orbigny, 1841). 1, 2, SAM-PCZ222193, 4, 18, 19, SAMPCZ22227; 5, 6, 14, 15, SAM-PCZ22226; 7–9, 16, 17, 20; OUM KY9998; 10, 11, OUM KX10002. 12, 13, *Lyellicereras pseudolyelli* (Parona & Bonarelli, 1897). SAM-PCZ22188. All specimens are from the Mzinene Formation, Albian III. The originals of 1–6, 12, 13, 14, 15, 18, 19 are from locality 154. The original of 7–11, 16, 17, 20 are from locality 176. Figures 1–13 are x1; 14–20 are x2.



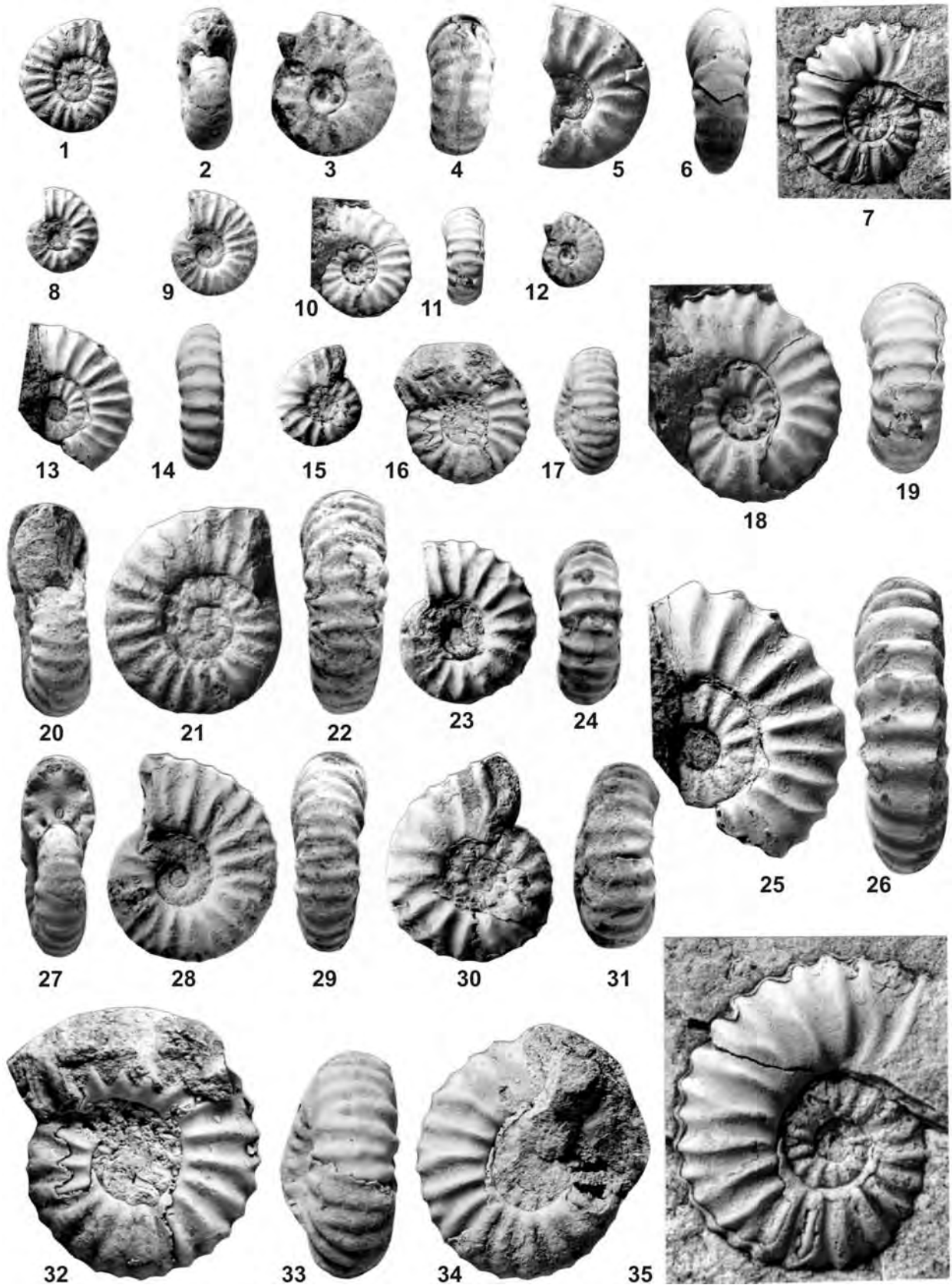
**Plate 6.** Figs 1–16, 19–20, *Lyelliceras lyelli* (d'Orbigny, 1841). 1–4, SAM-PCZ22221, from the Mzinene Formation, Albian III of the Ndumu area; 6, 7, SAMEM167, from the same area. 11–16, SAM-PCZ22222, from the Mzinene Formation, Albian III, of locality 154; 19–20, OUM KX9876 from locality 176, Ndumu, Albian III. 5, 8–10, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). SAM EM124, from the Ndumu area. 19, 20, OUM KX9876, from the Mzinene Formation, Albian III, of locality 154. 17, 18, 21–23, *Lyelliceras latili* sp. nov., paratype, OUM KX11038, from the Mzinene Formation, Albian III, at locality 35. Figures 1–3, 6–10, 13–18, 20, 22, 23 are x1; 4, 5, 11, 12, 19, 21 are x2.



**Plate 7.** Figs 1, 2, 5, 9, *Lyelliceratid lyelli* (d'Orbigny, 1841). OUM KX10001, From the Mzinene Formation, Albian III, at locality 176. 3, 4, 6–8, 10–17, *Lyelliceratid pseudolyelli* (Parona & Bonarelli, 1897). 3, 4, 8, 13, 14, SAM-PCZ22190, 15–17, SAM L44 from the Mzinene Formation, Albian III, of locality 154; 6, 7, OUM KX9997, from the Mzinene Formation, Albian III, at locality 176; 10–12, SAM EM174 probably from the same locality. Figures 1, 3, 4, 14, 17 are x2; 2, 5–13, 15, 16 are x1.



**Plate 8. Figs 1–13, 16–20, *Lyelliceras lyelli* (d'Orbigny, 1841). 1, 2, SAM-PCZ22223; 3–6, 13, 16–20, SAM-PCZ22236; 7–9, SAM-PCZ22225, all from the Mzinene Formation, Albian III, of locality 154; 10–12, SAM Z1092, the holotype of *Collignoniceras (Selwynoceras) gratum* Van Hoepen, 1968, from the Mzinene Formation of the Mkuze Game Reserve; 16, SAM EM176, from the Ndumu area. 14, 15, *Lyelliceras pseudolyelli* (Parona & Bonarelli, 1897). SAM-PCZ22220, from the Mzinene Formation of the Ndumu area. Figures 1–12, 14–16 are x1; 13, 17–20 are x2.**



**Plate 9. Figs 1–35.** *Pseudobrancoceras versicostatum* (Michelin, 1838). 1, 20–22, OUM KX9996b; 2–4, 12, OUM KX9296a; 5, 6, OUM KX9296b; 7, 35, OUM KX9290; 8, 23, 24, OUM KX9996b; 9, 27–29, OUM KX9994; 10, 11, 18, 19, SAM-PCZ22184; 13, 14, 25, 26, OUM KX9995; 15, 30, 31, OUM KX9272; 16, 17, 32–35, SAM-PCZ22183. The original of Figs 1–6, 8, 9, 12, 13, 14, 20–29 are from the Mzinene Formation of locality 176; the originals of Figs 7, 10, 11, 16–19, 30, 31, 32–35 are from locality 154. Figures 1, 7, 8–17 are  $\times 1$ ; 3–6, 18–35 are  $\times 2$ .