

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

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ABSTRACT:

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 (2), 251-271. Warszawa.

A re-examination of the type material of *Ammonites senequieri* D'ORBIGNY, 1841, the type species of *Brancoceras* STEINMANN, 1881, shows D'ORBIGNY's original figures to be a chimaera, based on specimens of two species, while the other specimens in his collection belong to several other species, many of them named by COLLIGNON (1949), all of which are revised. The following species are described: *Brancoceras senequieri* (D'ORBIGNY, 1841), *B. magneti* COLLIGNON, 1949, *B. helcion* (REYNÈS, 1876), *B. subcompressum* COLLIGNON, 1949, *B. paronai* COLLIGNON, 1949, *B. retrorsum* COLLIGNON, 1949, *B. alternatum* sp. nov., *B. flexuosum* sp. nov., and *B. multicoatum* sp. nov. *Ammonites versicostatus* MICHELIN, 1838, referred to *Brancoceras* by some authors, belongs to Lyelliceratinae, as proposed most recently by LATIL (1995), and is a brancoceratid homeomorph referred to *Pseudobrancoceras* gen. nov., of which it is the type species, and to which a second species, *P. transiens* sp. nov., is also referred.

**Key words:** Cretaceous, Albian, Ammonites, France.

INTRODUCTION

This contribution arises from an examination of the type material of *Ammonites senequieri* D'ORBIGNY, 1841 (p. 292, pl. 86, figs 3-5) as a contribution to the forthcoming revision of D'ORBIGNY's *Paléontologie française; Terrains crétacés. 1, Cephalopodes* (1840-1842). This suggested that the original figures of this species were a chimaera, based on specimens of two different species, while the other material in the D'ORBIGNY Collection assigned to *senequieri* also belonged to several species. A search through the collections of the Institut Dolomieu

(Grenoble), and the École des Mines, Paris (now housed in the Université Claud Bernard, Lyon) revealed a wealth of specimens that could be assigned to *Brancoceras*. Many of these specimens could be referred to species introduced by COLLIGNON (1949) that were well (if briefly) described, but very poorly illustrated; others represented new forms. An examination of abundant specimens of *Ammonites versicostatus* MICHELIN, 1838 (p. 101, pl. 12, fig. 10), a species referred to both *Brancoceras* and *Lyelliceras* by recent authors, revealed it as a homoeomorphic contemporary of *Brancoceras*, and probably a paedomorphic offshoot of *Lyelliceras* SPATH, 1922.

## CONVENTIONS

Repositories of specimens are abbreviated as follows:

BMNH: The Natural History Museum, London

EMP: Collections of the École des Mines, Paris, now housed in the Université Claude Bernard, Lyon

ID: Institut Dolomieu, Grenoble

OUM: Oxford University Museum of Natural History

MNHP: Muséum National d'Histoire Naturelle, Paris

USNM: U.S. National Museum of Natural History, Washington D.C.

All dimensions of specimens are given in millimetres: D = diameter, Wb = whorl breadth, Wh = whorl height, U = umbilical diameter. Figures in parentheses are dimensions as a percentage of the diameter at the point of measurement.

Suture terminology is that of WEDEKIND (1916), as applied by KULLMAN & WIEDMANN (1970).

## SYSTEMATIC PALAEOLOGY

Order Ammonoidea ZITTEL, 1884

Suborder Ammonitina HYATT, 1889

Superfamily Acanthocerataceae DE GROSSOUVRE, 1894

Family Lyelliceratidae SPATH, 1921

Subfamily Lyelliceratinae SPATH, 1921

Genus *Pseudobranco-ceras* gen. nov.

TYPE SPECIES: *Ammonites versicostatus* MICHELIN, 1838, p. 101, Pl. 12, Fig. 10, from the lower Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli* Subzone Argiles Tegulines 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 and L<sub>2</sub>, U<sub>2</sub>/U<sub>3</sub> and auxiliary saddles bifid, with minor incisions.

DISCUSSION: *Ammonites versicostatus* of MICHELIN has been variously referred to *Branco-ceras* (*Eubranco-*

*ceras*) (GEBHARD, 1979; MARCINOWSKI & WIEDMANN, 1990), *Raulinicer* [= *Tegoceras*] (SPATH, 1931; DESTOMBES, 1979), and *Lyelliceras* (LATIL, 1995). It is here interpreted as a homoeomorph of *Branco-ceras*, 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 *Branco-ceras*, while the zig-zag 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) (Text-fig. 3G-I), 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. *Pseudobranco-ceras transiens* sp. nov., described below, links the two genera.

OCCURRENCE: Lower Middle Albian, France.

*Pseudobranco-ceras versicostatum* (MICHELIN, 1838)

(Pl. 1, Figs 1-24; Pl. 2, Figs 3-8, 11-13; Pl. 3, Figs 1-9, 13-17; Text-Figs 1, 8D, E, F)

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

1841. *Ammonites versicostatus* MICHELIN; D'ORBIGNY, p. 273, pl. 81, figs 1-3.

1911. *Ammonites versicostatus* MICHELIN; DOUVILLÉ; figs P<sup>2</sup>, P<sup>2a</sup>, 3.

1934. *Raulinicer* *versicostatum* (MICHELIN); SPATH, text-fig. 161m.

1979. "*Raulinicer*" *versicostatum* (MICHELIN); DESTOMBES, p. 109.

?non 1990. *Branco-ceras* (*Eubranco-ceras*) *versicostatum* (MICHELIN); MARCINOWSKI & WIEDMANN, p. 81, pl. 8, fig. 2.

1995. *Lyelliceras versicostatum* (MICHELIN, 1838); LATIL, p. 367, pl. 3, figs 21-24; text-figs 29, 30.

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, *Lyelliceras lyelli* Subzone, Argiles Tegulines of Le Gaty, Aube, France. DOUVILLÉ (1911) figured what he claimed 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.

MATERIAL: MNHP R52292/1-5, 7-11 (ex PERON Collection, 1908-26), from the lower Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli* Subzone Argiles Tegulines of Le Gaty, Aube, France. EMP A.246/1-2,

from the same biostratigraphic horizon at St Florentin, Yonne, France. ID 2010/1 – 2010/22, from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
MNHP R52292/1	15.0 (100)	6.2 (41.3)	5.8 (38.7)	1.07	5.4 (36)
MNHP R52292/2	14.7 (100)	7.2 (49.0)	6.2 (42.2)	1.2	4.9 (33)
MNHP R52292/3	15.9 (100)	6.9 (43.4)	6.4 (40.3)	1.08	6.2 (39)
MNHP R52292/4	16.2 (100)	7.4 (45.7)	6.2 (38.3)	1.2	6.4 (39.5)
MNHP R52292/5	16.5 (100)	6.9 (41.8)	6.6 (40)	1.05	6.4 (38.7)
MNHP R52292/11	19.2 (100)	7.6 (39.6)	7.4 (38.5)	1.02	7.4 (38.5)
MNHP R52292/7	21.9 (100)	9.7 (44.3)	8.5 (38.8)	1.14	8.2 (37.4)
MNHP R52292/8	21.9 (100)	8.1 (37.0)	8.6 (39.3)	0.94	7.7 (35.1)
MNHP R52292/10	21.0 (100)	8.2 (39.0)	8.8 (41.9)	0.93	7.2 (34.2)
EMP A246/4	22.4 (100)	10.1 (45.0)	8.1 (36.1)	1.24	8.9 ( )
EMP A246/3	23.5 (100)	8.9 (37.9)	9.5 (40.4)	0.94	7.3 (31.0)
ID 2010/2	25.6 (100)	10.0 (39.1)	9.7 (37.9)	1.03	10.3 (40.2)

**DESCRIPTION:** Specimens from Le Gaty are limonitic or pyritic phragmocones, up to 22 mm diameter, at which growth stage sutures are approximated, showing the largest specimens to be adult phragmocones. Coiling very evolute, whorl section varies from compressed to depressed, with whorl breadth to height ratios of 0.93–1.2, the whorl section compressed to depressed reniform, with the greatest breadth just outside the umbilical shoulder. The umbilicus varies from 33–39.5% of the diameter with a convex wall. The umbilical shoulder is broadly rounded, the flanks, ventrolateral shoulders and venter broadly convex. Coarse, distant primary ribs, 15–24 per whorl, arise on the umbilical shoulder and strengthen across the flanks, where they may be incipiently bullate. The ribs are straight and prorsiradiate to feebly convex, and reach their maximum development on the ventrolateral shoulders, where they are straight

and transverse. The primary ribs on one flank commonly terminate on the ventrolateral shoulder of the opposite flank. Less commonly, they link to a primary rib on the opposite flank, as a secondary rib; even less commonly, opposed primary ribs on the two flanks are linked by a pair of looped secondary ribs. The net result is that there are 24–32 ribs at the ventrolateral shoulder, while the pattern of ventral ribbing is typically looped or irregularly zig-zag.

Compressed, densely ribbed variants (MNHP R52292/10: Pl. 3, Figs 7–9) lack any indication of tuberculation, but sparsely and coarsely ribbed individuals with depressed whorl sections show a ventrolateral, and, rarely, a siphonal angulation on the ribs, that may develop into an incipient tubercle on the outer whorl (MNHP R52292/5: Pl. 1, Figs 10–12).

EMP A.246/c and d are exquisitely preserved specimens with recrystallised shell preserved, retaining parts of the adult body chamber. A.246/d (Pl. 3, Figs 15–17) is a robust, coarse ribbed variant, preserving the characteristic ventral ribbing pattern throughout. A.246/c (Pl. 3, Figs 13, 14) is an adult of the slender variant with excentric coiling, the last two ribs simple and annular.

The abundant material from Gourdon (Pl. 1, Figs 13–24) includes adult specimens (Pl. 1, Figs 19–21) up to 25.6 mm in diameter, with half a whorl of incomplete body chamber preserved, with characteristic ventral ribbing throughout.

Suture with plump, moderately incised bifid saddles, and smaller, narrower lobes (Text-fig. 1).

**DISCUSSION:** The specimen from the Tatra Mountains figured by MARCINOWSKI & WIEDMANN (1990, pl. 8, fig. 2) shows coarse, simple ribbing on the venter, rather than the characteristic zig-zag ornament of the present material, and belongs to some other species.

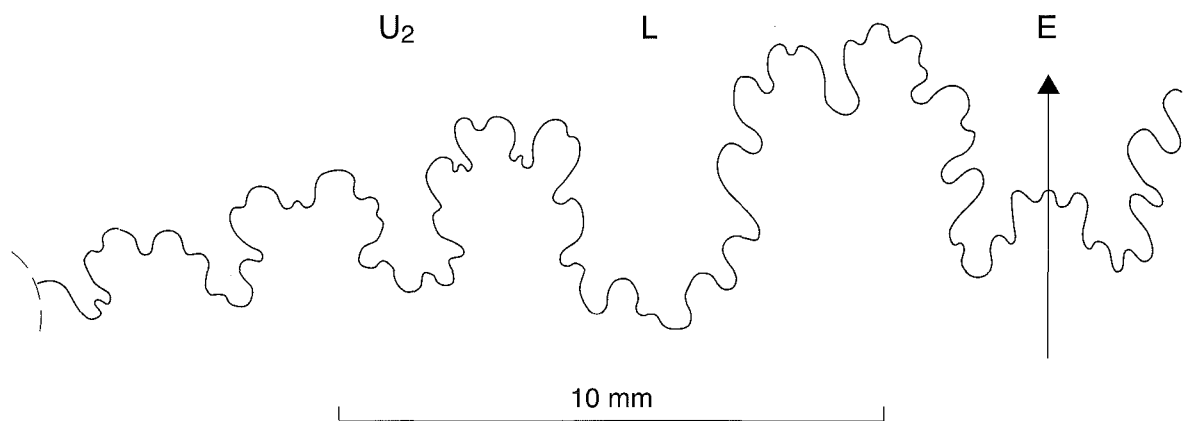


Fig. 1. External suture of *Pseudobrancocheras versicostatum* (MICHELIN, 1838), MNHP R52292/8

OCCURRENCE: Lower Middle Albian *H. dentatus* Zone, *L. lyelli* Subzone in Aube and Yonne, France. Condensed Lower to lower Upper Albian of Clars/Escragnoles and Gourdon, Alpes-Maritimes, France.

*Pseudobranco-ceras transiens* sp. nov.

(Pl. 2, Figs 9-10, 14-20; Text-Figs 2A-F)

TYPES: The holotype is MNHP 5792A-1, D'ORBIGNY Collection, from the Lower Middle Albian of Maurepaire, as is paratype MNHP 5792A-2. Paratypes ID 2061-2068 are from the condensed Albian of Le Rimet, Isère, France. Paratype BMNH 37630 is from Clars/Escragnoles, Alpes-Maritimes, France.

DIAGNOSIS: A compressed species of *Pseudobranco-ceras*, adult at 25-32 mm diameter, with 21-25 ribs per

whorl bearing outer ventrolateral clavi, siphonal tubercles more numerous than ventral clavi, to which they are linked by irregular transverse and zig-zag ribs, or not; all tubercles lost on adapical part of adult body chamber, where venter rounds. Suture little-incised, with broad bifid E/L.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
Paratype					
BMNH 37630	25.7(100)	8.9(34.6)	10.4(40.5)	0.86	9.3(36.2)
Paratype					
MNHP 5792A-2	26.7(100)	8.8(33.0)	10.1(37.8)	0.87	9.7(36.3)
Holotype					
MNHP 4972A-1	27.5(100)	7.9(28.7)	10.8(39.3)	0.73	9.4(34.2)
Paratype					
ID 2067	28.7(100)	9.5(33.1)	10.9(38.0)	0.87	10.4(36.2)
Paratype					
ID 2068	32.6(100)	10.4(31.9)	12.2(37.4)	0.85	12.5(38.3)

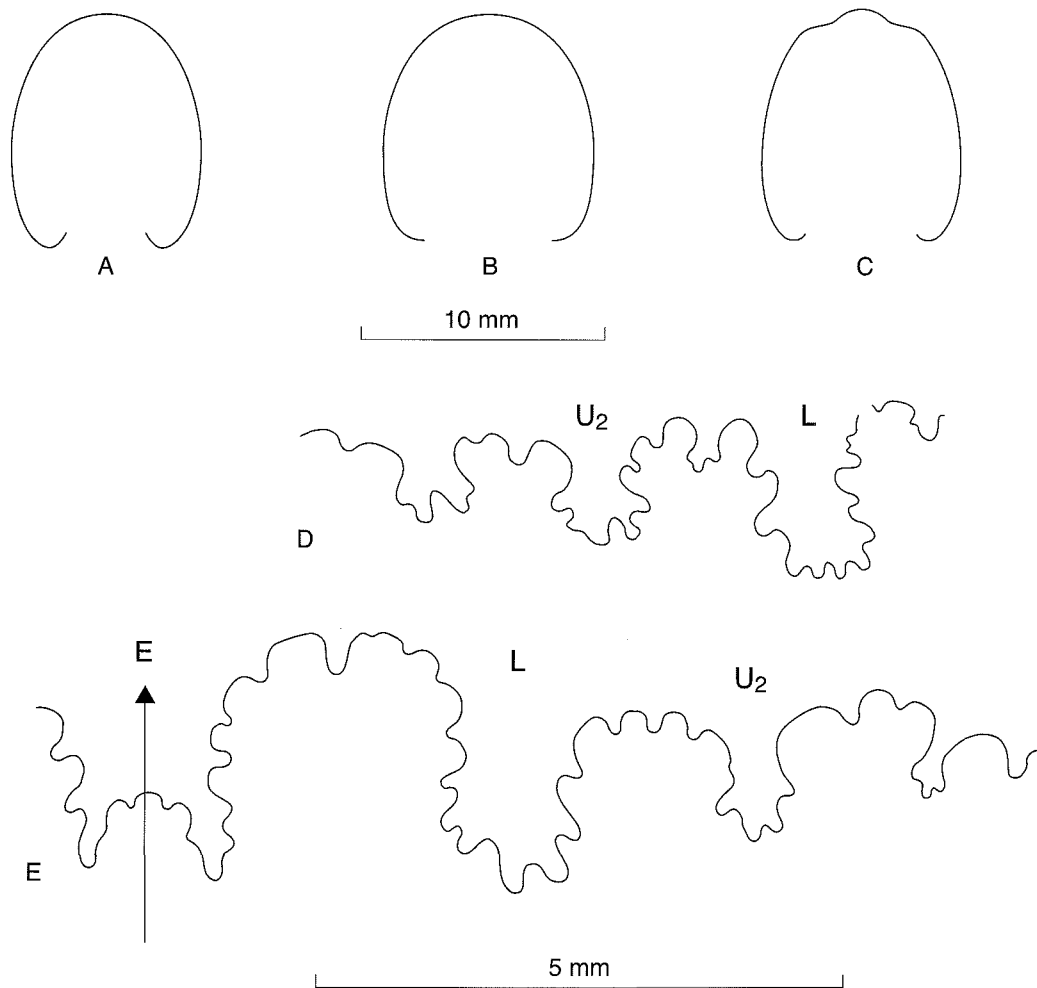


Fig. 2. Whorl sections and external suture lines of *Pseudobranco-ceras transiens* sp. nov. a, holotype, MNHP 5792a-1; B, E, paratype BMNH 37630; C, paratype EMP 5922a-2; D, ID 2061

**DESCRIPTION:** The holotype (Pl. 2, Figs 17-20) is a phosphatic internal mould 27.5 mm in diameter, a small complete adult individual with approximated sutures and just over half a whorl of body chamber preserved. Coiling is evolute, the broad, shallow umbilicus comprising 34% of the diameter, with a low, feebly convex umbilical wall. The whorl section is compressed trapezoidal, with feebly convex convergent flanks on the phragmocone and adapical part of the body chamber, and fastigate venter in costal section. There are 24 primary ribs on the outer whorl; they arise at the umbilical seam and strengthen across the umbilical wall and shoulder, without developing into a bulla. They are straight, prorsiradiate and feebly flexuous, strengthening and coarsening on the ventrolateral shoulder, where they bear small ventral clavi. The siphonal tubercles are more numerous than the ventrolateral, to which they may be linked by irregular transverse or oblique zig-zag ribs, or may be elongated into a short transverse rib. On the adapical section of the body chamber, the ventrolateral and siphonal tubercles are lost, and the last 2-3 ribs are simple, annular, and transverse on the broadly rounded venter. The adult suture (Text-fig. 2E) is little incised, with broad, plump saddles and narrower lobes. Paratype MNHP 5792A-2 (Pl. 2, Figs 9, 10) has twelve ribs on the outer half whorl, and is incomplete. BMNH C37630 (Pl. 2, Figs 14-16) is an adult individual 25.7 mm in diameter with approximate sutures and 23 ribs per whorl, lacking only the final few adapertural ribs. ID2067-8 (Text-fig. 3A-C, E-F) are also adults,

showing weakening and loss of tubercles and a rounding of the venter on the final few ribs.

**DISCUSSION:** *Pseudobrancoceras transiens* sp. nov. has its evolutionary origins in *Lyelliceras pseudolyelli* (PARONA & BONARELLI, 1897) (p. 138, pl. 10, fig. 3; see Text-fig. 3G-I) which has a similar irregular style of ventral ornament; they differ in that the latter reaches a much larger adult size (in excess of 80 mm) and has umbilical and inner ventrolateral tubercles, absent in *P. transiens* sp. nov. Small adult size, and simple suture suggests that *P. transiens* sp. nov. is a paedomorphic dwarf offshoot of *L. pseudolyelli*; it provides a morphological link to the even smaller, paedomorphic *P. versicostatum*, where the same style of irregular ventral ornament is present, but tuberculation weak or absent, with coarse nontuberculate ribs on the adult body chamber.

**OCCURRENCE:** Lower Middle Albian of Aube, and condensed Albian of Escragnoles, Var, and Le Rimet, Isère, France.

Family Brancoceratidae SPATH, 1934

Subfamily Brancoceratinae SPATH, 1934

**DISCUSSION:** There is a measure of agreement (WIEDMANN, 1966, p. 73; OWEN, 1988, p. 225; WRIGHT, 1996, p. 133) that the origins of the Acanthoceratoidea

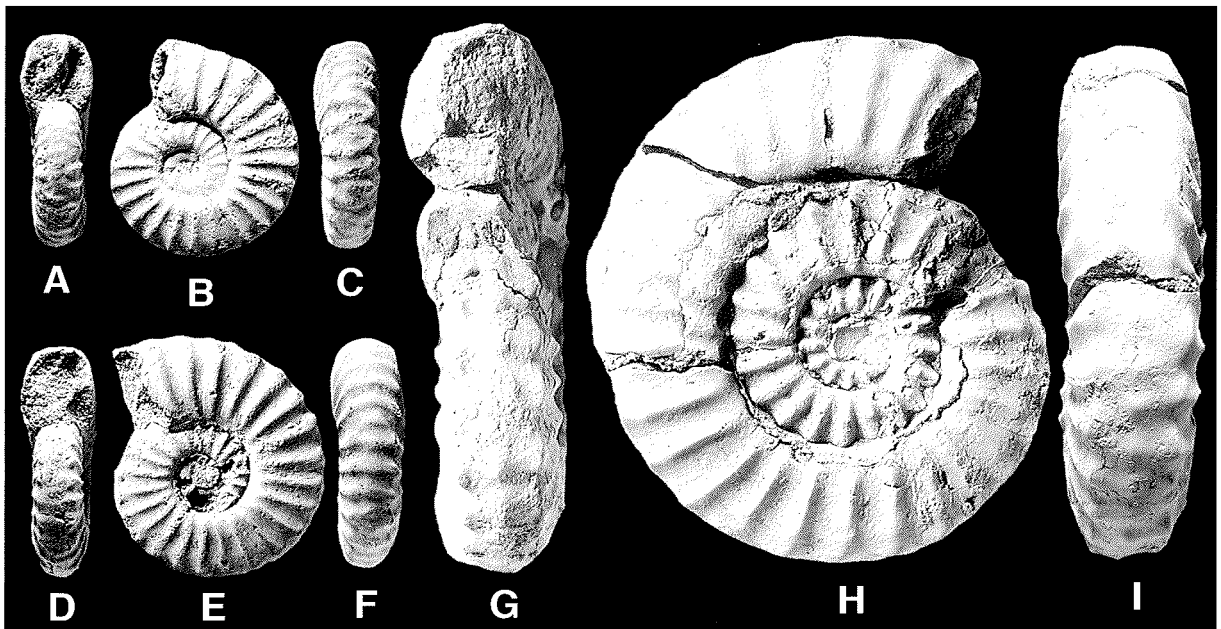


Fig. 3. A-F – *Pseudobrancoceras transiens* sp. nov. A-C, paratype ID 2067; D-E, paratype ID 2068, from the condensed Albian of Le Rimet, Rencurel, Isère, France. G-I, *Lyelliceras pseudolyelli* (PARONA & BONARELLI, 1897), EMP A233, ex PUZOS Collection, from Clars, Alpes-Maritimes, France.

All figures are natural size

lies in Desmoceratoidea, but as WRIGHT (1996) pointed out, not enough is known of the relative timing of initial appearance and phylogeny of the constituent families in the early Albian. This gap in our knowledge of first occurrences of families has been clarified by the accounts of the lower Lower Albian ammonite faunas of the *Leymeriella tardefurcata* Zone of Austria (KENNEDY & KOLLMANN, 1979), and southern France (KENNEDY & *al.* 2000); *Parabrancoeras* of the Brancoceratinae and *Oxytropidoceras* of the Mojsisoviciinae both appear at this level, as does what appears to be the earliest representative of the Lyelliceratinae. These extended ranges do not, however, clarify the ancestry of these groups. The general view has been that Brancoceratinae arose from *Silesitoides* of the Subfamily Silesitoidinae BREISTROFFER, 1953, which gave rise to *Parabrancoeras* of the Brancoceratinae. The type species of *Parabrancoeras* BREISTROFFER, 1951, is *Brancoceras besairiei* COLLIGNON, 1949 (p. 89, pl. 19, figs 1-4; text-figs 25-27) from the upper Lower Albian of Madagascar. This has smooth inner whorls with marked constrictions as a record of desmoceratid origins.

Genus *Brancoceras* STEINMANN, 1881

TYPE SPECIES: *Ammonites senequieri* D'ORBIGNY (1841, p. 292, pl. 86, figs 3-5), by the subsequent designation of HYATT, 1900, p. 590.

DIAGNOSIS: Small, evolute to moderately involute, ribbed from an early growth stage, or with a prolonged, commonly compressed and involute feebly ornamented or near-smooth in early to middle growth. Primary ribs arise singly or in pairs, with or without bullae in early and middle growth stages, all ribs primary in later growth stages. Interspaces may be deepened and constricted. Venter with weak to strong siphonal keel or not. Suture line simple, with minor incisions in saddles and lobes or saddles may be entire.

DISCUSSION: A re-examination of the lectotype of the type species, *Brancoceras senequieri*, shows it to be ribbed from an early stage, with a weak transient siphonal ridge (Pl. 4, Figs 1-3). It differs from the type species of *Eubrancoeras* in the presence of this ridge. The suture of *B. senequieri* is simplified, with entire L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> (Text-fig. 7F), that of *B. aegoceratoides* has lobes and saddles with minor incisions.

*Parabrancoeras* differs from *Brancoceras* in the presence of marked, regularly spaced constrictions on the involute early growth stage. A number of species described below have smooth or near-smooth early to middle growth

stages, but these lack regular constrictions (although these may appear in the later growth stages of species such as *Brancoceras magneti* COLLIGNON, 1949 (pl. 5, figs 8-10, 17-19)), and have a marked siphonal ridge or keel.

The smooth to near-smooth, involute and carinate early growth stages of species such as *Brancoceras magneti* recall those of contemporary *Oxytropidoceras* (e.g. *Oxytropidoceras roissyanum* (D'ORBIGNY, 1841). Indeed, KENNEDY & COOPER (1977) misidentified *B. magneti* nuclei as juvenile *Oxytropidoceras*. The similarity may indicate common ancestry, and suggest that Brancoceratinae and Mojsisoviciinae are closely allied.

Most of the species described below come from condensed Lower to lower Upper Albian phosphatic deposits at Clars/Escragnoles and Gourdon in Alpes-Maritimes, France. From the careful studies of GEBHARD (1979, 1992) it is inferred that they are from the lower Middle Albian. The following species are described below:

*Brancoceras senequieri* (D'ORBIGNY, 1841) [lower Middle Albian]

*Brancoceras magneti* COLLIGNON, 1949 [lower Middle Albian]

*Brancoceras helcion* (REYNÈS, 1876) [lower Middle Albian]

*Brancoceras subcompressum* COLLIGNON, 1949 [lower Middle Albian]

*Brancoceras paronai* COLLIGNON, 1949 [lower Middle Albian]

*Brancoceras retrorsum* COLLIGNON, 1949 [lower Middle Albian]

*Brancoceras alternatum* sp. nov. [lower Middle Albian]

*Brancoceras flexuosum* sp. nov. lower Middle Albian, *Hoplites dentatus* Zone, *Lyelliceras lyelli* Subzone

*Brancoceras multicostratum* sp. nov. lower Middle Albian, *Hoplites dentatus* Zone, *Lyelliceras lyelli* Subzone

OCCURRENCE: *Brancoceras* ranges from the lower Middle Albian, and may occur in the basal Upper Albian. The geographic range is: southern England, France, Poland, India, Madagascar, Colombia, Peru, Venezuela and Texas.

*Brancoceras senequieri* (D'ORBIGNY, 1841)

(Pl. 4, Figs 1-3, 14-15; Pl. 5, Figs 20-28; Pl. 6, Figs 1-12; Text-Figs 6E, J, 7F)

1841. *Ammonites senequieri* D'ORBIGNY, p. 292 (*pars*), pl. 86, figs 3-5 (*pars*).

1849. *Ammonites senequieri* D'ORBIGNY; QUENSTEDT, p. 212, pl. 17, fig. 3.

1850. *Ceratites senequieri* D'ORB.; D'ORBIGNY, p. 122.  
 non 1887. *Schloenbachia Senequieri* D'ORB. sp.; SUENES, p. 561, pl. 13, fig. 2 (= *Branco ceras paronai* COLLIGNON, 1949).  
 non 1897. *Schloenbachia Senequieri* D'ORB. f.; PARONA & BONARELLI, p. 89, pl. 12, fig. 11 (= *Branco ceras subcompressum* COLLIGNON, 1949), fig. 12 (= *Branco ceras paronai* COLLIGNON, 1949).  
 1938. *Branco ceras senequieri* D'ORB.; ROMAN, p. 375, pl. 37, fig. 358, 358a (pars; copy of D'ORBIGNY, 1841).  
 1957. *Branco ceras senequieri* (D'ORBIGNY); WRIGHT, p. L403, fig. 521:2.  
 1979. *Branco ceras (Eubranco ceras) versicostatum* (MICHELIN); GEBHARD, p. 94, pl. 6, fig. 9; pl. 7, fig. 1; text-figs 59, 60.  
 1979. *Branco ceras (Eubranco ceras) aff. versicostatum* (MICHELIN); GEBHARD, p. 95, pl. 7, fig. 2; text-figs 61, 62.  
 1996. *Branco ceras (Branco ceras) senequieri* (D'ORBIGNY); WRIGHT, p. 135, text-fig. 104.4

TYPES: D'ORBIGNY indicated (1841, p. 294) that ... 'MM. Émeric et Astier ont recueilli cette jolie espèce à Escragnolle (Var), dans le gault on grès vert inférieur. In the explanation of his figures (reproduced here as Text-fig. 4), he stated ... 'pl. 86, fig. 3. Individu adulte, vu de côté. De ma collection. fig. 4. Le même, vu du côté de la bouche, montrant le dessus d'une cloison'.

The catalogue of the D'ORBIGNY Collection lists the following:

'5799 *A. senequieri* D'ORB., Ervy, Aube, 1'.

The original tablet on which this specimen was mounted survives, but the specimen has been separated from it. The back of the table has been annotated by M. BREISTROFFER '*Acanthoplites* sp. du Gargas'. It was not part of the original type series, as Ervy was not a locality mentioned by D'ORBIGNY.

'5803 T. [*Ceratites*] *Senequieri* D'ORB. Escragnolles, Var, 10' and '[5803] a id. Clars id. 6'.

What survive are the following: A tray of three specimens mounted on a card, labelled 'Clars (Var) 5803'. A

tablet to which six specimens were attached labelled 'Clars (Var) Coll. D'ORBIGNY, but without a contemporary number; the back of the tablet bears a small octagonal label with blue border '*Ceratites Senequieri* D'ORB.', a further label 'Clars' (in pencil) and 'M. Mouton' (in ink), plus 'Coll. D'ORBIGNY Albiens 5803' written in BREISTROFFER's hand. The tablet has been snapped in half, and is now in a tray associated with 8 specimens. It is not possible to convincingly match specimens to tablet.

A further tablet is associated with 2 specimens, and is labelled:

*Ceratites Senequieri* 5803 Escragnolles [... illegible] Albiens'. The reverse bears a circular blue label with blue border '5803'.

A further tablet is labelled:

'*Schloenbachia Senequieri* Albiens Escragnolles (Alpes-Maritimes)' [illegible].

It has been split, so that any information on the back of the tablet has been lost, but the front has been labelled 'Orb. 5803A' by J. SORNAY.

Two additional specimens that lack any original labels, have a label written by J. SORNAY, probably in the 1950's or 1960's, which I first noted in 1967: '*Branco ceras senequieri* (D'ORB.) Albiens Escragnolles, Clars (Alpes M<sup>m</sup>) Coll. D'ORB. 5803 et 5803A 5803 (le petit) = type'.

It will be seen that no specimens have the original number 5803A associated with them, but that specimens on tablets to which original small blue-edged labels bearing the number 5803 are from Escragnolles (2) and Clars (9), plus a further two that have a damaged tablet labelled 'Escragnolles', plus 3 other specimens that lack original labels, and may be from either Escragnolles or Clars.

All may be reasonably assumed to be syntypes, but it is no longer possible to assign all of them to Escragnolles versus Clars. The latter is sometimes referred to as 'au quartier de Clars, près Escragnolles' (PARONA & BONARELLI, 1897, p. 53), all specimens are in the same phosphatic preservation, and the lack of details of locali-

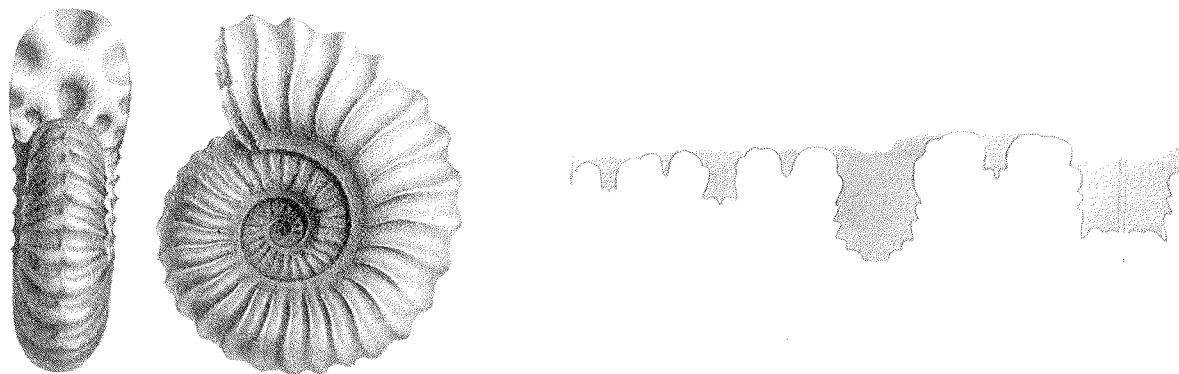


Fig. 4. Copy of D'ORBIGNY original figures of *Ammonites senequieri* (1841, pl. 86, figs 3-5). Figures are reproduced at original size

ty, Escragnolles versus Clars, is probably of no great significance. For convenience, these specimens are here referred to as MNHP 5803-1 to 5803-17 (Pl. 4, Figs 1-25; Pl. 5, Figs 1-19).

In his account of *Ammonites senequieri* D'ORBIGNY gives a diameter of 26 mm for a specimen, while his figures (1841, pl. 83, figs 3-4; and Text-fig. 4 herein) show a specimen 51 mm in diameter. None of the specimens in the D'ORBIGNY Collection correspond to his Figs 4 and 5; all specimens that approach the size of the figure are body chamber, and in consequence do not show a terminal septal face, as is shown in his pl. 83, fig. 4. Only one specimen from Escragnolles, MNHP 5803-1 (Pl. 4, Figs 1-3) corresponds to the dimensions given by D'ORBIGNY, and is 26.2 mm in diameter. It is clearly the basis for the inner whorls of his fig. 3, and is here designated lectotype of the species. The outer whorl of the figure appears to be based on MNHP 5803-2 (Pl. 4, Figs 4, 5), a 46.5 mm long body chamber fragment with a maximum preserved whorl height of 17.1 mm. It shows the distinctive thickening of the ventral rib, projected adaperturally into a siphonal keel (not adapically as shown in D'ORBIGNY's fig. 4). D'ORBIGNY's figs 3 and 4 are a composite based on these two specimens; the reconstruction is erroneous with respect to the ventral ornament, while the two specimens used in the reconstruction belong to different species: the larger paralectotype fragment is the body chamber of a *Brancocheras magneti* COLLIGNON, 1949.

The syntypes in the D'ORBIGNY collection can be assigned as follows:

MNHP 5803-1 (Pl. 4, Fig 1-3): lectotype of *Brancocheras senequieri*. Of the paralectotypes, MNHP 5803-2 (Pl. 4, Fig 4, 5), 5803-4 (Pl. 4, Figs 8-10), 5803-8 (Pl. 4, Figs 20-22), 5803-9 (Pl. 4, Figs 23-25), 5803-10 (Pl. 5, Figs 1-2), 5803-11 (Pl. 5, Figs 3-5), 5803-12 (Pl. 5, Figs 8-10), 5803-13 (Pl. 5, Figs 17-19), are all *Brancocheras magneti* COLLIGNON, 1949.

MNHP 5803-3 (Pl. 4, Figs 6, 7), and 5803-14 (Pl. 5, Figs 14-16), are *Brancocheras paronai* COLLIGNON, 1949.

MNHP 5803-5 (Pl. 4, Figs 11-13), and 5803-7 (Pl. 4, Figs 16-19) are *Brancocheras subcompressum* COLLIGNON, 1949.

MNHP 5803-15 (Pl. 5, Fig. 11) is *Brancocheras* sp.

MNHP 5803-6 (Pl. 4, Figs 14, 15), MNHP 5803-16 (Pl. 5, Figs 12, 13), and 5803-17 (Pl. 5, Figs 6, 7) are *Brancocheras senequieri*.

**MATERIAL:** Paralectotypes MNHP 5803-6, 16, 17; EMPA-321 (ex DE VERNEUIL Collection, 1873), from Escragnolles; MNHP 5803-16, 17; EMP A.240a, from Clars; ID 1985, 1992, 1994-1997, 1999, from Gourdon, all from condensed Lower to lower Upper Albian phosphates.

	DIMENSIONS: D	Wb	Wh	Wb:Wh	U
Lectotype					
MNHP 5803-1	26.2(100)	9.28(35.4)	8.97(34.2)	0.7	9.8(37.4)
EMP A.240a	29.1(100)	12.2(41.9)	10.0(34.4)	1.2	12.2(41.9)
ID 1992	33.2(100)	11.5(28.9)	13.1(39.5)	0.88	11.3(34.0)
ID 1995	34.3(100)	13.5(39.4)	12.7(37.0)	1.06	12.5(36.4)
ID 1985	34.5(100)	-(-)	12.5(36.2)	-	13.3(38.6)
ID 1999	42.3(100)	14.1(33.3)	14.9(35.2)	0.95	15.7(37.1)
MNHP 5803-6	-(-)	16.4(-)	15.0(-)	1.09	-(-)
ID 1996	50.1(100)	15.0(29.9)	16.1(32.1)	0.93	22.0(43.9)
EMP A.321	57.9(100)	17.6(30.4)	19.1(33.0)	0.92	23.2(40.1)

**DESCRIPTION:** The lectotype (Pl. 4, Figs 1-3) is a phosphatic internal mould with traces of phosphatic shell preserved. The specimen is a juvenile, with half a whorl of body chamber preserved. Coiling is evolute, serpenticone, the relatively wide umbilicus comprising 37.4% of the diameter. The umbilicus is very shallow, with a low wall. The whorls expand slowly, the whorl section is slightly compressed, with a whorl breadth to height ratio of 0.96, the intercostal whorl section oval, the costal section with flattened flanks, broadly rounded ventrolateral shoulders, and a broad, feebly convex venter. The flanks of the earliest whorls appear to be very feebly ribbed or smooth. The first clearly differentiated rib appears at the beginning of the outer half of the penultimate whorl, which bears 10 coarse ribs; umbilical bullae give rise to one or two coarse ribs, with long non-bullate ribs and shorter intercalated ribs. There are approximately 22 ribs at the umbilical shoulder on the outer whorl. Pairs of primary ribs arise from six coarse umbilical bullae; the adapical rib of the pair is straight and feebly prorsiradiate; the adapertural rib of the pair is projected strongly forwards at an acute angle to the umbilical seam on the innermost flank before flexing back and passing straight across the flank. There are non-bullate primary ribs that may be strongly projected forward on the inner flank between the bullate pairs, as well as very long intercalated ribs that extend to the inner flank. The ribs thicken and flex back across the ventrolateral shoulder, and are coarse, rounded and transverse across the venter. A very delicate siphonal ridge is visible under low angle oblique light.

The partially exposed suture line is imperfectly exposed, with broad, little-incised saddles and narrower lobes.

ID 1985 (Pl. 6, Figs 4, 5) overlaps in size with the lectotype. It is a somewhat robust individual, with a whorl breadth to height ratio of 1.0 at the largest preserved diameter of 34.5 mm. The last half whorl, the body chamber of a juvenile, has a subquadrate whorl section, with flattened, parallel flanks, broadly rounded ventrolateral shoulders, and a feebly convex venter.



There are 12 coarse primary ribs, eight single, the remainder arising in pairs from the umbilical shoulder. The ribs are of variable strength at the umbilical shoulder; one single rib, and one pair of ribs arise at a bulla. The ribs are coarse, straight, distant and prorsiradiate on the flanks, coarsen and strengthen across the ventrolateral shoulders and are strong, coarse and transverse on the venter. ID 1999 (Pl. 5, Figs 27, 28), a body chamber 42 mm in diameter, has a whorl breadth to height ratio of 0.95. There are 12 ribs per half whorl, all of them coarse, feebly prorsiradiate primaries, coarse and transverse on ventrolateral shoulders and venter. The rounded-quadrate whorl section is distinctive, as it is in comparable individuals such as ID1997 (Pl. 6, Figs 6, 7).

The adult of the species is represented by ID 1996 (Pl. 6, Figs 8-10), 50 mm in diameter, with approximated sutures, and 180° of body chamber preserved. There are 25 ribs on the penultimate whorl, so that this specimen is a little more densely ribbed than the lectotype. The ribs are both single and paired primaries. There are 26 ribs on the outer whorl, which has the distinctive quadrate whorl section described above. The ribs are all primaries on the body chamber; they progressively lose the ventrolateral and ventral thickening that characterises the early whorls, becoming sharp, narrow, and rectiradiate.

Also referred to the species are individuals with the characteristic bullae and paired ribs in early growth and quadrate whorl section in middle growth combined with thickened ventrolateral and ventral ribbing that develop a transient coarse ventral ridge in middle growth, most conspicuous in the interspaces between ribs (ID 1993, Pl. 6, Figs 1-3; EMP A.321: Pl. 5, Figs 24-26), as in *Branco CERAS paronai* COLLIGNON, 1949, described below, but with the ribs transverse, rather than projected forwards into a chevron.

Suture (Text-fig. 7F) pseudoceratitic, with broad, asymmetrically bifid E/L, with minor incisions on external side; L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> entire; lobes narrow, bifid, with minor incisions.

**DISCUSSION:** Presence of ribbing from an early ontogenetic stage, ribs that arise either singly or in pairs, and presence of bullae in middle growth, together with the distinctive quadrate whorl section characterise *Branco CERAS senequieri* as interpreted here, and separate it from other French species of the genus. The species most closely resembles *Eubranco CERAS aegoceratoides* (STEINMANN, 1881) (p. 133, pl. 7, fig. 2; Text-fig. 5Y herein; for synonymy see RENZ, 1982, p. 40, pl. 5, fig. 11; text-fig. 25b). Comparison with a large collection (70 specimens) from the lower Middle Albian of

Huarou, Peru (OUM KU 406-410, Text-fig. 5A-T, Z) shows both species to develop ribs from an early ontogenetic stage, but the ribs are all single primaries in *aegoceratoides*, the whorl section higher, and the ribs more markedly prorsiradiate, the whorl section trapezoidal rather than quadrate, but with the same coarsening and thickening of the ventrolateral and ventral ribs in both species.

The sutures are not well-shown by the Huarou collection; that illustrated by STEINMANN (1881, pl. 7, fig. 2b; see Text-fig. 5Y herein) is ammonitic, with incisions in E/L, L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub>, whereas the suture of *B. senequieri* is pseudoceratitic, with E/L much less incised, and L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> entire.

The Huarou collection also includes individuals that correspond to *Branco CERAS quenstedti* KNETCHEL, 1947 (p. 103, pl. 21, fig. 5; text-fig. 7; see Text-fig. 5U, V herein). These are very sparsely ribbed, with a compressed, high whorl section, immediately separable from *B. senequieri*, and possibly no more than extreme variants of *B. aegoceratoides* (Text-fig. 5J-L, P-T).

**OCCURRENCE:** Condensed Lower to lower Upper Albian, Clars/Escagnolles and Gourdon, Alpes-Maritimes, France.

*Branco CERAS magneti* COLLIGNON, 1949

(Pl. 4, Figs 8-10, 20-25; Pl. 5, Figs 1-19; Pl. 6, Figs 13-31; Pl. 7, Figs 1-20, 26-28; Text-figs 6F, H, K, 7A, B)

1841. *Ammonites senequieri* D'ORBIGNY, p. 292, pl. 86, figs 3, 4 (*pars*), ?5.

1949. *Branco CERAS magneti* COLLIGNON, 1949, p. 98, pl. 22, fig. 5.

1977. *Oxytropidoceras* sp. juv. KENNEDY & COOPER, p. 794, pl. 105, figs 8, 9; text-fig. 2 (*pars*).

**TYPES:** COLLIGNON (1949, p. 98) mentioned specimens from both Escagnolles and Gourdon in his brief account of this species, and figured an example from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France, which is here designated lectotype of this species. The present whereabouts of the specimen is not known.

**MATERIAL:** MNHP 5803-2, 4, 9, 10, 13, from the condensed upper Lower to lower Upper Albian of Escagnolles/Clars, Alpes-Maritimes, France; EMP unregistered (2 specimens, a and b), EMP A.240b (*ex* PUZOS Collection, 1848), from Escagnolles; EMP A.241a-b (*ex* PUZOS Collection), from Clars; ID 1983, 1984, 2004-2009 from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France.

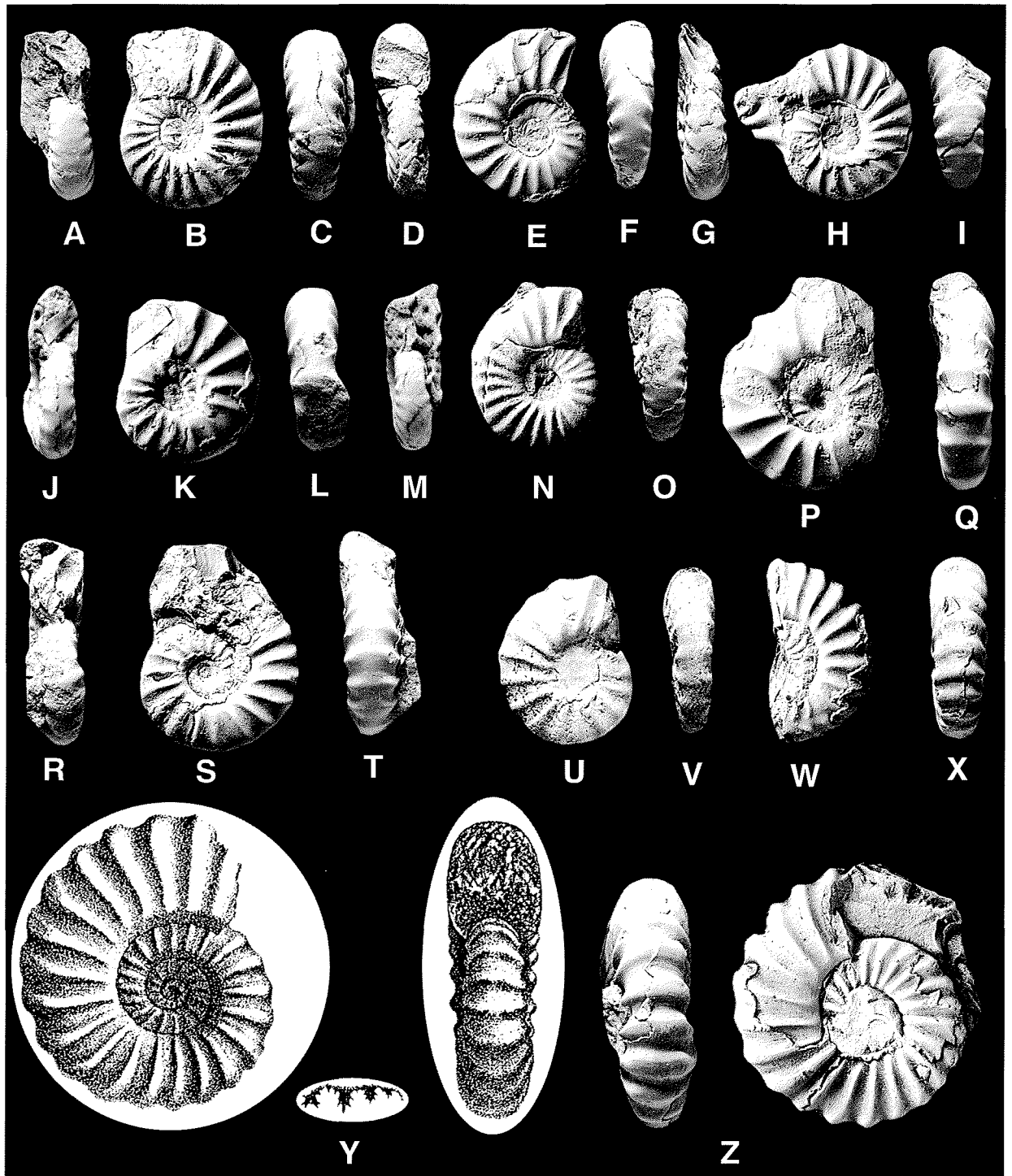


Fig. 5. A-O, R-T, W-Z, *Eubrancoceras* from the Middle Albian Pariatambo Formation of Huarouzu, Peru. A-C, OUM KU410/1; D-F, OUM KU410/2; G-I, OUM KU410/3; J-L, OUM KU408; M-O, OUM KU410/4; R-T, OUM KU 407; Z, OUM KT439, specimens corresponding to *Eubrancoceras aegoceratoides* (STEINMANN, 1881). U-V, the holotype of *Eubrancoceras quenstedtii* (KNETCHEL, 1947), USNM 1134, from Pongo de Manseriche on the Rio Marañon, Peru (original of KNETCHEL, 1947, pl. 21, fig. 5). W, X, *Eubrancoceras aegoceratoides* (STEINMANN, 1881), original of KNETCHEL (1947, pl. 21, fig. 4). Y, *Eubrancoceras aegoceratoides* (STEINMANN, 1881), copy of STEINMANN (1881, pl. 7, fig. 2), from Huallanca, Peru.

All figures are natural size

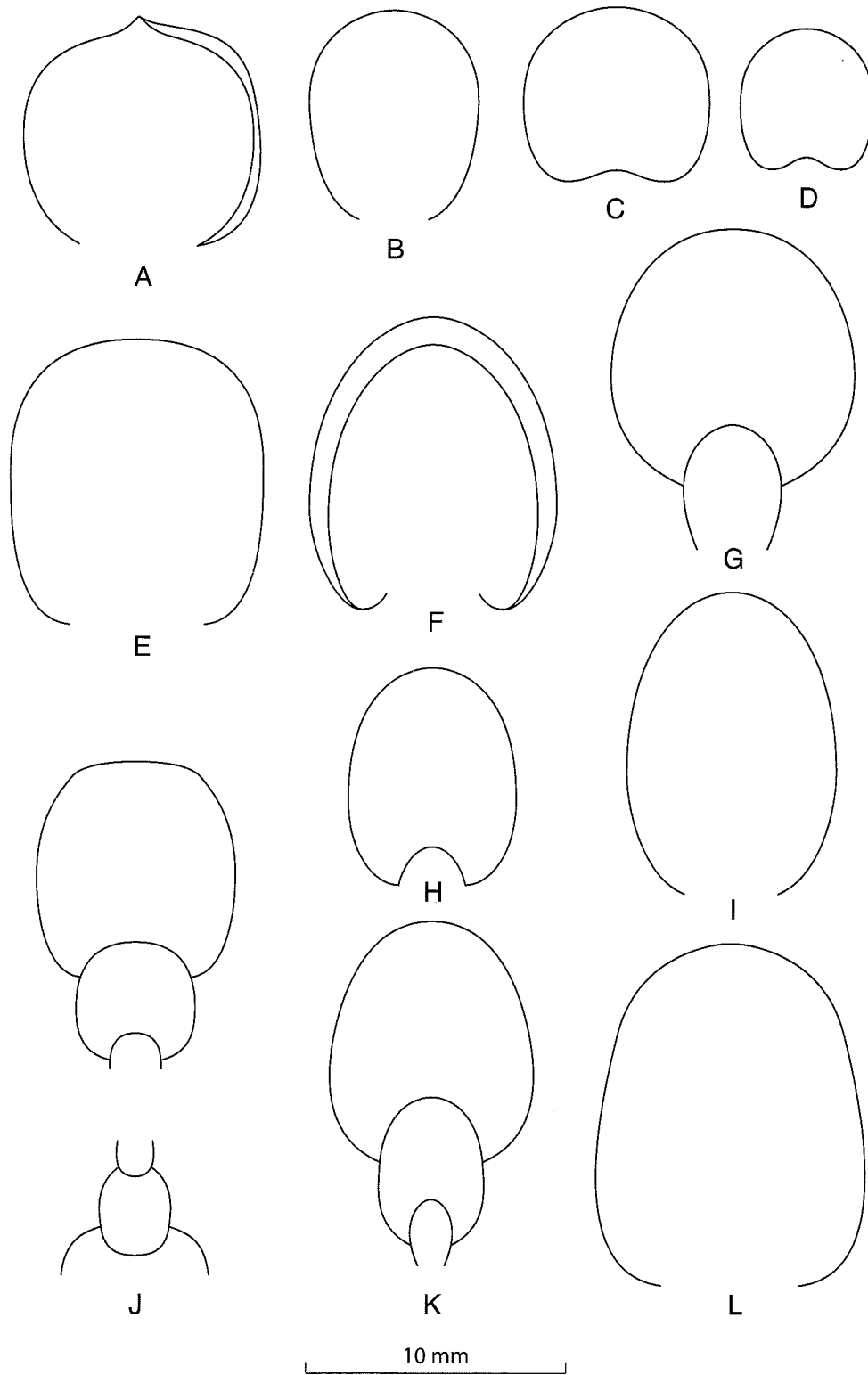


Fig. 6. Whorl sections of A: *Brancoceras alternatum* sp. nov.; EMP A243; B, D, *Brancoceras retrorsum* COLLIGNON, 1949, B is ID 2075, D is ID 2075; C, *Brancoceras helcion* (REYNÈS, 1876), ID 2011/3; E, J, *Brancoceras senequieri* (D'ORBIGNY, 1841), E is ID 1996, J is ID 1994; F, H, K, *Brancoceras magneti* COLLIGNON, 1949, F is ID 2007, H is ID 5803/10, K is ID 2005; G, *Brancoceras paronai* COLLIGNON, 1949, ID 2072; I, L, *Brancoceras subcompressum* COLLIGNON, 1949, I is ID 2073, L is EMP A239

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
MNHP 5803-10	29.2(100)	8.8(30.1)	12.0(41.0)	0.73	9.7(33.2)
EMP unreg. a	30.3(100)	10.9(35.9)	12.8(42.2)	0.85	10.8(35.0)
MNHP 5803-9	30.9(100)	11.8(38.2)	12.1(39.1)	0.97	11.5(37.2)
MNHP 5809-11	35.9(100)	11.8(32.9)	13.1(36.5)	0.90	14.2(39.6)
EMP A.240b	37.4(100)	13.1(35.0)	16.0(42.8)	0.82	13.4(35.8)
ID 2006	37.5(100)	12.2(34.4)	14.3(38.1)	0.85	12.6(33.6)
EMP unreg. b	41.1(100)	-(-)	14.7(35.8)	-	15.2(37.0)
MNHP 5803-13	46.7(100)	15.4(33.0)	18.4(39.4)	0.84	17.1(36.6)
MNHP 5803-12	51.2(100)	-(-)	18.9(36.9)	-	19.6(38.3)

**DESCRIPTION:** There are three distinctive ontogenetic stages. The first stage extends to as much as 15 mm diameter. Coiling is very involute, the umbilicus comprising around 20% of the diameter, the whorls high and compressed, with a whorl breadth to height ratio of around 0.6-0.7, the flanks feebly convex, subparallel, the ventro-

lateral shoulders converging to a fastigate venter with a delicate median keel. Initially smooth, the transition to the second growth stage is marked by the appearance of delicate, blunt, crowded, prorsiradiate flank ribs. The second ontogenetic stage extends through the rest of the phragmocone, and onto the adapical part of the adult body chamber. Coiling becomes progressively more evolute, the umbilicus comprising 33-39% of the diameter, the whorl section less compressed, with whorl breadth to height ratios of 0.7-0.9, the flanks broadly convex, the ventrolateral shoulders broadly rounded, the venter convex to feebly fastigate. There are two distinctive rib types, and constrictions. Sharp, narrow ribs arise at the umbilical seam, strengthen across the umbilical shoulder and are straight to feebly concave and prorsiradiate on the flanks, and cross the venter in the shallowest of convexities. They are flanked by wide interspaces that are com-

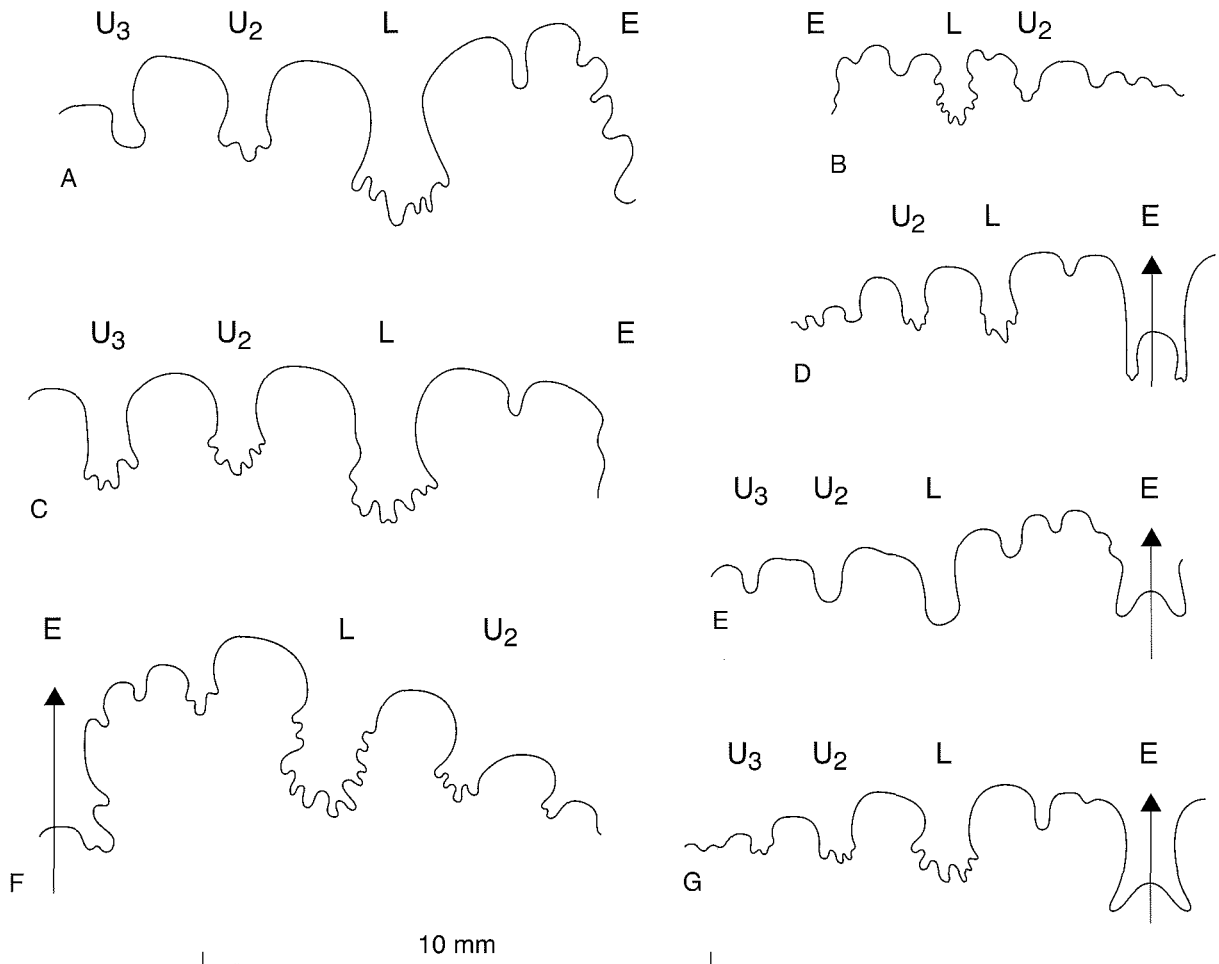


Fig. 7. External sutures of: A, B: *Brancoceras magneti* COLLIGNON, 1949, A, ID 2005; B, ID 2081; C: *Brancoceras subcompressum* COLLIGNON, 1949, MNHP 5803/7; D: *Brancoceras helcion* (REYNÈS, 1876), ID 2011/3; E: *Brancoceras retrorsum* COLLIGNON, 1949, ID 2075; F: *Brancoceras senequieri* (D'ORBIGNY, 1841), ID 1987; G: *Brancoceras retrorsum* COLLIGNON, 1949, ID 2076

monly accentuated into constrictions, especially the adapical interspace. These interspaces and constrictions define the second rib type, triangular wedges that are narrow at the umbilical shoulder, but broaden across the flanks, with a markedly asymmetric profile: gently sloping adapically (where terminated by an interspace), and steeply sloping adaperturally (where terminated by a constriction). There are up to 8-9 such wedge-shaped ribs per whorl, with, typically, a single normal rib between, to give a total of up to 18 ribs per whorl on the late phragmocone and adapical body chamber. The venter may be weakly fastigiate, with a suggestion of a keel, or not at this ontogenetic stage. The change to the third ontogenetic stage, which extends for the final 90° sector of the adult body chamber, is characterised by the abrupt disappearance of wedge-shaped ribs. The last part of body chamber is ornamented by narrow sharp ribs, separated by wide interspaces. The ribs arise at the umbilical seam and strengthen across the umbilical wall. They are straight and prorsiradiate across the flanks, and transverse and near-straight over the venter. In the transition between the second and third ontogenetic stages of some specimens, the ribs may thicken ventrally, and a blunt mid-ventral ridge may develop, projecting forwards and declining across the interspaces to form a keel of variable strength.

The largest adult seen is 52 mm in diameter, with the second ontogenetic stage occupying a complete whorl (Pl. 5, Figs 8-10). In MNHP 5803-8 (Pl. 4, Figs 20-22) the second ontogenetic stage occupies only half a whorl, the specimen retaining 120° of body chamber at a diameter of 35 mm.

The suture line (Text-fig. 7A) is pseudoceratitic. E/L is broad, asymmetric, with a small median incision and further minor incisions on the ventral side; the dorsal side is entire, as are  $L/U_2$  and  $U_2/U_3$ . The intervening saddles are narrow, with minor incisions.

**DISCUSSION:** The three distinctive ontogenetic stages, in particular the wedge-shaped ribs of the middle stage, immediately distinguish *B. magneti* from all other described *Brancoceras*. As noted above, D'ORBIGNY'S pl. 86, figs 3 and 4 is in part based on a fragment of *B. magneti*, MNHP 5803-2 (Pl. 4, Figs 4,5).

The lectotype, here designated of *Brancoceras gignouxi*, is the original of COLLIGNON (1949, pl. 22, fig. 4); it, and a paralectotype are from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France. Their present whereabouts is not known, while the original figures are poor. The original description of the species is as follows (COLLIGNON, 1949, p. 96): 'deux exemplaires de l'Albien de Gourdon (ma collection) que je désigne sous le nom de *Brancoceras Gignouxi* nov. sp. (pl. 22, fig. 4, 4a, 4b). D = 0.038 m, H = 0.013 m (0,39),

E = 0,010 m (0,30), O = 0,009 m (0,27), H/E = 1,30. C'est une ammonite plate, de section subrectangulaire, d'allure générale semblable à celle de *B. aenigmaticum* nov. sp., à tours internes lisses, et dont l'ornementation du demi-tour visible est constituée de larges plages lisses, déprimées, encadrant des côtes fines saillantes, s'épaississant à la périphérie et sur la région externe qu'elles traversent en décrivant un chevron assez aigu. Très légère et très fine carène au début du dernier tour'.

There are four specimens in the collections of the Institut Dolomieu (ID 2078-2081) identified by BREISTROFFER (who one assumes had seen the types) as *Brancoceras gignouxi*. Their dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
ID 2081	23.7(100)	8.2(34.6)	9.9(41.7)	0.83	7.4(30.6)
ID 2080	24.2(100)	7.4(30.6)	10.9(49.5)	0.68	6.2(25.6)
ID 2078	30.6(100)	9.6(31.3)	11.8(38.6)	0.81	10.6(34.6)
ID 2079	30.3(100)	10.8(35.6)	11.9(39.3)	0.91	9.6(31.7)

ID 2080 and 2081 (Pl. 7, Figs 7-9, 15-17) are 23-24 mm diameter nuclei. Coiling is only moderately evolute, the umbilicus comprising 25.6-30.6% of the diameter, shallow, with a low, convex wall. Whorl section compressed, with whorl breadth to height ratio 0.68-0.83, the flanks feebly convex, subparallel, the ventrolateral shoulders and venter broadly and evenly rounded. ID 2080 has delicate ribs extending around all of the outer whorl. In ID 2081, they are present but very weak on the adapical 270° sector of the outer whorl, but strengthen on the adapertural 90° sector, where they are narrow, delicate, straight and prorsiradiate on the flanks, project forwards and efface across the ventrolateral shoulders to form an incomplete ventral chevron. ID 2080 has a delicate siphonal keel throughout; in ID 2081 it extends around the adapical 270° sector of the outer whorl but is absent on the last 90° sector, possibly due to abrasion of the mould. ID 2079 (Pl. 7, Figs 18-20) is a wholly septate half whorl 30.3 mm in diameter. The adapical 120° sector bears delicate flexuous prorsiradiate striae and riblets, which strengthen into narrow ribs, with the final interspace deepened and constriction-like. There is a delicate siphonal keel throughout. ID 2078 (Pl. 7, Figs 10-12) has feebly ornamented early whorls to an estimated diameter of 19 mm, the last 120° sector bearing 12 narrow, flexuous prorsiradiate ribs that arise either singly or in pairs from the umbilical seam, are feebly convex on the inner flank, feebly concave on the outer flank, and project forwards and strengthen across the ventrolateral shoulder to form a pronounced ventral chevron. There is a delicate siphonal keel throughout. The sutures are incompletely preserved on most of the specimens. The juvenile

suture of ID 2081 includes a broad, bifid, little-incised E/L, little incised L/U<sub>2</sub> and entire U<sub>2</sub>/U<sub>3</sub>. The lobes are narrow and little incised.

From COLLIGNON's description, *Brancocheras gignouxi* is a species with a prolonged smooth stage with a delicate siphonal keel, followed by half a whorl ornamented by narrow prominent ribs separated by wide interspaces, broadening on the ventrolateral shoulders and forming a pronounced ventral chevron. As such the species is clearly allied to *Brancocheras magneti*, from which it differs in developing neither the prominent wedge-shaped ribs, nor the constrictions of the second.

Of the specimens attributed to *B. gignouxi* by BREISTROFFER, and described above, the two smooth nuclei ID 2080 and 2081, cannot be separated from inner whorls of *B. magneti* of the same diameter (Pl. 5, Figs 9, 14). ID 2079 (Pl. 7, Figs 18-20) matches the inner whorl of an unregistered EMP specimen (Pl. 7, Figs 13, 14) at the same diameter. ID 2078 (Pl. 7, Figs 10-12) which matches exactly with COLLIGNON's description of *B. gignouxi* is a juvenile (the sutures are not approximated) which differs from specimens of *B. magneti* of the same size and at the same ontogenetic stage only in being compressed, with a delicate keel, and lacking prominent wedge-shaped ribs. It appears likely that it is no more than a juvenile *magneti* in which wedge-shaped ribs appear at a relatively late stage (compare the EMP specimen, Pl. 7, Figs 13, 14). If the lectotype of *B. gignouxi* is also a juvenile (the state of maturity of the specimen is not indicated by COLLIGNON) then *gignouxi* and *magneti* may be conspecific, in which case, I select the name *magneti* for the species, as first revising author. If, however, the lectotype of *gignouxi* is an adult, there is a case for retaining the name for the species, and separating it from *magneti* on the basis of absence of constrictions and wedge-shaped ribs. This can only be resolved when the lectotype is located, described and illustrated. At this time, ID 2078-2081 are all assigned to *B. magneti*.

**OCCURRENCE:** Condensed Lower to lower Upper Albian, Clars/Escragnoles and Gourdon, Alpes-Maritimes, France.

*Brancocheras helcion* REYNÈS, 1876  
(Pl. 7, figs 21-25; Text-figs 6C, 7D)

1876. *Ammonites helcion* REYNÈS, p. 92.

1925. *Ammonites helcion* REYNÈS; SPATH, p. 98, pl. 4, fig. 1.

1949. *Brancocheras helcion* REYNÈS; COLLIGNON, p. 91.

1977. *Brancocheras helcion* KENNEDY, fig. 24, 1-2.

1989. *Brancocheras* sp.; KENNEDY, fig. 13g, h.

**TYPE:** The holotype is the original of SEUNES (1876, p. 92), refigured by SPATH (1925, pl. 4, fig. 1), from the condensed Albian of Escragnoles, Var, France, in the Collections of the Musée d'Histoire Naturelle de Marseille, although I was unable to locate the specimen during a visit some years ago.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
ID 2011/3	24.9(100)	8.6(34.5)	9.1(36.5)	0.95	11.1(44.6)
BMNH C82480	51.6(100)	15.5(30.0)	17.3(33.5)	0.90	23.4(45.3)

**DESCRIPTION:** The middle growth stages are represented by ID 2011/3 (Pl. 7, Figs 21-23). Coiling is very evolute, serpenticonic, with a broad shallow umbilicus comprising 44.6% of the diameter, the umbilical wall feebly convex, and outward-inclined. The whorl section is rectangular, slightly compressed, with a narrowly rounded umbilical shoulder, feebly convex parallel flanks, narrowly rounded ventrolateral shoulders and a broad, feebly convex venter. Only a short section of the penultimate whorl is preserved; the ribs are alternately long and short. There are 22-23 ribs on the outer whorl, all primaries, that are of variable strength on umbilical wall and shoulder, straight, and recti- to feebly rursiradiate on the flanks, coarsening markedly on ventrolateral shoulders and venter, where they are even, blunt, and transverse. The specimen retains half a whorl of body chamber. The juvenile suture (Text-fig. 7D) is pseudoceratitic; E/L has a minor incision and is bifid; L/U<sub>2</sub>, U<sub>2</sub>/U<sub>3</sub> and the auxiliary lobes are entire. The narrow lobes have only minor incisions.

BMNH C2480 (Pl. 7, Figs 24, 25) is an adult, a phosphatic internal mould with 240° of body chamber preserved. Coiling very evolute, the umbilicus broad and shallow. Whorl section slightly compressed (whorl breadth to height ratio 0.90), the umbilical wall low, feebly convex, and inclined outwards. Flanks feebly convex in costal section, subparallel, ventrolateral shoulders broadly rounded, venter very feebly convex. Ornament is preserved on the greater part of the penultimate whorl and on the outer whorl, which bears 22 ribs. The ribs arise at the umbilical seam on the umbilical shoulder, and are of slightly varying strength across the umbilical wall and shoulder. They are straight, and markedly rursiradiate across the flanks, strong, narrow, and widely separated, they strengthen markedly across the ventrolateral shoulders, and are convex and transverse across the venter.

**DISCUSSION:** *Brancocheras helcion* is characterised by its very coarse, distant ribs that become markedly rursiradiate in middle and later growth, a feature which readily distinguishes it from both *B. retrorsum*, and *B. compressum*.

OCCURRENCE: Condensed Lower to low Upper Albian, Escagnolles and Gourdon, Alpes-Maritimes, France.

*Branco ceras subcompressum* COLLIGNON, 1949  
(Pl. 4, Figs 11-13; 16-19; Pl. 7, Figs 29-34; Pl. 8, Figs 13-23; Text-figs 6I, L, 7C)

1897. *Schloenbachia senequieri* D'ORB. f.; PARONA & BONARELLI, p. 89 (*pars*), pl. 11, fig. 11 only.

1934. *Branco ceras* aff. *senequieri* (D'ORBIGNY); SPATH, text-fig. 160d.

1949. *Branco ceras subcompressum* COLLIGNON, p. 93, pl. 22, fig. 1.

TYPES: COLLIGNON (1949, p. 93) mentioned four specimens in his collection, and figured one (pl. 22, fig. 1), which is here designated lectotype of the species. It and the paralectotypes were from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France. The present whereabouts of these specimens is not known.

MATERIAL: MNHP 5803-5 and 5803-7, two of the paralectotypes of *Ammonites senequieri*, from the condensed Lower to lower Upper Albian of Clars/Escagnolles, Var, France; EMP A239 (*ex* Puzos Collection, 1848) is from the same horizon and locality. ID 2073-4 (*ex* BREISTROFFER & DE VILLOUTREYES Collection). ID 1987-1990, from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
ID 2074	30.3(100)	9.5(31.4)	10.8(35.6)	0.88	11.8(38.9)
ID 2073	35.6(100)	11.0(30.9)	14.3(40.2)	0.77	11.6(32.5)
MNHP 5803-7	34.3(100)	10.2(29.7)	13.8(40.2)	0.74	11.6(33.8)
EMP A.239	49.7(100)	13.2(26.6)	17.7(35.6)	0.75	19.4(39.0)

DESCRIPTION: Coiling very evolute, with less than a third of the previous whorl covered. Umbilicus broad (32.5-39% of diameter), becoming increasingly so at maturity; shallow, with a low, convex wall. Whorl section compressed (whorl breadth to height ratio 0.75-0.88), with greatest breadth just outside umbilical shoulder in costal section, flanks flattened, convergent, ventrolateral shoulders and venter broadly rounded. The early growth stages, only partially visible in the umbilicus of adult/subadult specimens, appears to have been much more involute than the later growth stages, and smooth for at least the two earliest whorls, and perhaps more (the earliest post-ammonitelle stage is not visible). Ornament first appears on the outer half of the penultimate whorl as crowded, low, broad convex, prorsiradiate ribs on the middle to outer flank region. There are 29

ribs on the outer whorl of MNHP 5803-7 (Pl. 4, Figs 16-19) at an estimated diameter of 36.5 mm, the specimen preserving less than 90° of body chamber. EMP A.239 (Pl. 7, Figs 29-31) retains half a whorl of body chamber, and has 27-28 ribs on the outer whorl at a diameter of 49.7 mm. In these specimens, and MNHP 5803-5 (Pl. 7, Figs 29-31), a half whorl of body chamber with a maximum preserved diameter of 42.5 mm, all of the ribs are primaries. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder, where they vary from straight to feebly convex. They are straight to very feebly flexuous, narrow and rectiradiate on the flanks but strengthen and broaden markedly on the ventrolateral shoulders, and are strong, coarse and transverse over the venter. Viewed in strong oblique light there is a faint siphonal ridge on the outer whorl, most conspicuous in ID 2073 (Pl. 8, Figs 15, 16).

Suture (Text-fig. 7C) pseudoceratitic; E/L with a single median incision, L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> entire.

DISCUSSION: The prolonged early unornamented stage, followed by a strongly ribbed subadult to adult growth stage, the ribs all primaries that strengthen markedly on the ventrolateral shoulders, combined with a compressed whorl section, characterise this species. The prolonged smooth stage recalls *Branco ceras gignouxi* COLLIGNON, 1949 (p. 96, pl. 22, fig. 4; see above), but this has sinuous ribs in later growth, the interspaces sometimes deepened into constrictions, with the ribs projected into a marked chevron over the venter, without the prominent ventrolateral and ventral thickening shown by the present species, where the ribs are transverse across the venter.

OCCURRENCE: Condensed Lower to lower Upper Albian of Escagnolles/Clars and Gourdon, Alpes-Maritimes, France.

*Branco ceras paronai* COLLIGNON, 1949  
(Pl. 5, Figs 14-16; Pl. 8, Figs 24-34; Text-fig. 6G)

1887. *Schloenbachia* [*sic*] *Senequieri* D'ORB. sp.; SEUNES, p. 561, pl. 13, fig. 2.

1897. *Schloenbachia senequieri* D'ORB. f. PARONA & BONARELLI, p. 89 (*pars*), pl. 11, fig. 12 only.

1949. *Branco ceras paronai* COLLIGNON, p. 97.

1934. *Branco ceras* aff. *senequieri* (D'ORBIGNY); SPATH, text-fig. 160e.

1979. *B. (Branco ceras) paronai* COLLIGNON; GEBHARD, p. 90, pl. 6, fig. 6; text-figs 54, 55.

TYPE: The holotype, by monotypy, is the original of PARONA & BONARELLI (1897, pl. 11, fig. 12), from the

Lower to lower Upper Albian of Escragnolles, Alpes-Maritimes, France.

MATERIAL: MNHP 5803-3 and 14, and ID 2070-2072, from Escragnolles, EMP A.242 (ex PUZOS Collection, 1848), from Clars and ID 2069 from Gourdon, Alpes-Maritimes, condensed Lower to lower Upper Albian.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
MNHP 5803-14	23.8(100)	92.(38.7)	10.0(42.0)	0.92	8.3(34.9)
EMP A.242	26.0(100)	9.8(37.7)	10.4(40.0)	0.94	8.6(33.1)
ID 1971	27.2(100)	10.8(39.7)	11.1(40.8)	0.97	9.8(36.0)
ID 2069	28.5(100)	11.5(40.3)	11.5(40.4)	1.0	10.7(37.5)
IDD 2072	34.7(100)	13.6(39.2)	13.5(38.9)	1.0	11.5(33.1)
ID 2070	41.0(100)	14.8(36.1)	16.5(40.2)	0.90	15.1(36.8)

DESCRIPTION: Coiling evolute, umbilicus comprises 33-37.5% of the diameter, shallow, with a low, convex, outwards-inclined wall. Whorl section slightly compressed to equidimensional, with greatest breadth below mid-flank. Flanks convex, ventrolateral shoulders broadly rounded, venter feebly convex. The inner whorls, visible in the umbilicus of MNHP 5803-14 (Pl. 5, Figs 14-16) and ID 2070 (Pl. 8, Figs 32-34) are ornamented from a very early stage, the inner to mid-flank region bearing blunt, crowded, prorsiradiate ribs. Adult and subadult specimens have 22-25 single primary ribs per whorl. The ribs arise at the umbilical seam and are well-developed on the umbilical wall. They are feebly prorsiradiate and feebly sinuous on the flanks, narrow on the umbilical shoulder, but strengthen and broaden markedly on the ventrolateral shoulders and venter where they form an obtuse chevron, the apex marked by a coarse, blunt, continuous siphonal keel. Occasional interspaces may be deepened into incipient constrictions.

Suture with broad, little-incised, bifid E/L; L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> bifid, with few incisions; L and U<sub>2</sub> narrow.

DISCUSSION. The distinctive features of *Brancocheras paronai* are the presence of ornament from a very early ontogenetic stage, the numerous primary ribs, with their marked ventrolateral and ventral thickening, together with the coarse, prominent siphonal keel. The species most closely resembles *B. senequieri*, where ornament also appears at an early stage, but the latter has a more rectangular whorl section, with primary ribs that are transverse on the venter, not forming a chevron. COLLIGNON (1949, p. 97, pl. 22, fig. 2) described a second markedly carinate *Brancocheras* from Gourdon, which he named *B. subcarinatum*. His brief description is as follows: 'Ammonite épaisse à tours aussi élevés que hauts, de section subcarrée, à flancs convexes et portant une légère carène. Paroi ombilicale élevée et verticale à la fin du dernier tour. Omphaloc moyen.

Ornementation de côtes légèrement sigmoïdales, simples, naissant au sommet de la paroi ombilicale, puis s'épaississant et prenant des versants dissymétriques à la façon de beaucoup d'*Oxytropidoceras*. Légèrement projetées en avant à la périphérie, elles se rejoignent en dessinant une carène subaiguë.

A la différence de l'exemplaire figuré par PARONA & BONARELLI, les tours internes sont absolument lisses, et l'ornementation ci-dessus décrite ne commence qu'au début de la deuxième moitié du dernier tour qui est la chambre d'habitation.

Cloison: n'a pu être décelée, sauf sur les tours internes, où les éléments visibles, à selles arrondies non découpées, sont du type *Brancocheras*'.

COLLIGNON's figures are very poor indeed, but show *B. subcarinatum* to differ from *B. paronai* in having a prolonged involute growth stage of development, with the last half whorl of the specimen only ribbed, the ribs not apparently thickened on the ventrolateral shoulders and venter. None of the *Brancocheras* from Gourdon examined in connection with the present investigation can be referred to *B. subcarinatum* with confidence. A single specimen, ID 1982, is regarded as in some respects transitional between the two species. It is a phragmocone 21.7 mm in diameter, with involute compressed inner whorls, as in *B. subcarinatum* but with low, broad, crowded ribs, rather than being smooth, while the umbilicus at the largest preserved diameter equals 27%, narrower than in *B. paronai*, although the ribs thicken on the ventrolateral shoulder, as in that species. *Schloenbachia* [sic] *senequieri* of SEUNES (1887, p. 561, pl. 13, fig. 2) is based on a specimen 42 mm in diameter, with 22 single primary ribs on the outer whorl, a persistent siphonal keel, and ornament from an early ontogenetic stage; it is interpreted as a coarsely ornamented variant of *B. paronai*.

OCCURRENCE: Condensed Lower to lower Upper Albian of Escragnolles/Clars, and Gourdon, Alpes-Maritimes, France. GEBHARD (1979) found this species in his unit II, which yielded lower Middle to lower Upper Albian ammonites.

*Brancocheras retrorsum* COLLIGNON, 1949  
(Pl. 8, Figs 6-12; Text-figs 6B, D, 7E, G)

1949. *Brancocheras retrorsum* COLLIGNON, p. 94, pl. 22, fig. 3.

TYPE: The holotype, by monotypy, is the original of COLLIGNON, 1949, pl. 22, fig. 3, from the condensed Lower to lower Middle Albian of Escragnolles, Alpes-Maritimes, France. The specimen has not been traced.



**MATERIAL:** MNHP R52291b (ex DE GROSSOUVRE Collection) from the condensed Lower to lower Upper Albian of Clars, Escragnolles, Alpes-Maritimes, France. ID 2075-6, from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes, France.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
ID 2076	21.2(100)	6.8(32.0)	7.4(35.0)	0.92	8.8(41.5)
ID 2075	26.9(100)	8.3(36.7)	9.7(36.1)	0.86	11.1(41.3)
MNHP R52291b	30.9(100)	9.9(32.0)	10.1(32.7)	0.98	14.3(46.2)

**DESCRIPTION:** Coiling is very evolute, the wide, shallow umbilicus comprising 41.5-46.2% of the diameter. The umbilical wall is low and convex. The whorls expand very slowly: coiling is serpentine. The whorl section is slightly compressed, oval, with feebly convex flanks and a broadly rounded venter. An initial near-smooth stage, visible in the umbilicus of ID 2075 (Pl. 8, Figs 10-12) is succeeded by the appearance of blunt umbilical bullae that give rise to pairs of ribs, visible in the umbilicus of ID 2075-6. Ornament at a diameter of 21 mm is shown by ID 2076 (Pl. 8, Figs 7-9). At the beginning of the outer whorl, pairs of ribs arise at relatively coarse umbilical bullae, with single bullate primary ribs and short intercalated ribs between the paired ribs. As size increases, the bullate primary and intercalated ribs predominate, with few ribs arising in pairs. The ribs are straight and rursiradiate on the flank, thickening and projecting slightly forwards or not across the ventrolateral shoulder, thickening further, and near-transverse over the venter. There are 32 ribs at the ventrolateral shoulder on the outer whorl. ID 2075 (Pl. 8, Figs 10-12) has half a whorl of body chamber preserved, but does not show sutural crowding, and is presumed to be subadult. There are approximately 30 ribs on the outer whorl; pairs of ribs, arising from the umbilical shoulder, persist to 23 mm; beyond this diameter, all of the ribs are single.

MNHP R52291b (Pl. 8, Fig. 6) is 30.9 mm in diameter, with half a whorl of body chamber preserved, the sutures not approximated. Coiling is very evolute, serpentine, the umbilicus broad, shallow with a low, feebly convex wall. The whorls expand slowly, and are slightly compressed, with a broadly rounded umbilical shoulder, feebly convex flanks, broadly rounded ventrolateral shoulder, and broad, feebly convex venter. There are 32-34 ribs per whorl at the ventrolateral shoulder on the outer whorl. Pairs of primaries arise at umbilical bullae, with one or more single non-bullate primaries, long or short intercalated ribs between. The ribs are straight and very strongly rursiradiate on the flanks, broadening and thickening across ventrolateral shoulders and venter, where they are straight and transverse. Paired ribs extend to the largest preserved diameter.

Suture line (Text-fig. 7E, G) pseudoceratitic, E/L large, bifid, with minor median incision and small incisions on external side; L/U<sub>2</sub> and U<sub>2</sub>/U<sub>3</sub> entire, or with slightly indented outline. Saddles narrow, with minor incisions in juveniles, tending to become entire at maturity.

**DISCUSSION:** The distinctive features of *Brancoeras retrorsum* are the relatively short smooth stage, the presence of bullae that give rise to pairs of ribs, and the rursiradiate direction of the numerous ribs, which distinguish it from all others referred to the genus.

**OCCURRENCE:** Condensed Lower to lower Upper Albian of Clars/Escragnolles and Gourdon, Alpes-Maritimes, France.

*Brancoeras alternatum* sp. nov.  
(Pl. 8, figs 1-5; Text-fig. 6A)

**TYPES:** The holotype is EMP A.243 (ex PUZOS Collection, 1848) (Pl. 8, Figs 1-3), from the condensed Lower to lower Upper Albian of Clars, Escragnolles, Alpes-Maritimes, France. Paratype ID 2077 (ex JACOB & GUEBHARD Collection), from the condensed Lower to lower Upper Albian of Gourdon, Alpes-Maritimes (Pl. 8, Figs 4, 5).

**DIAGNOSIS:** A *Brancoeras* with ribs from an early developmental stage, initially transverse and opposite on either side of the coarse siphonal keel, becoming alternate and transverse on the adult body chamber.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
Holotype					
EMP A.243	30.4(100)	11.3(37.2)	12.0(39.5)	0.94	10.7(35.2)
Paratype					
ID 2077	(-)	13.8(-)	13.8(-)	1.0	(-)

**DESCRIPTION:** The holotype is an internal mould 30.4 mm in diameter, with the adapical end of the body chamber preserved. Coiling is very evolute, the umbilicus comprising 35% of the diameter, of moderate depth, with an outward-inclined, convex wall. The whorl section varies from very slightly depressed to equidimensional, rounded-rectangular, with feebly convex subparallel flanks, more narrowly rounded ventrolateral shoulders, and a broad, flat venter. There are 21 ribs on the outer whorl. They arise at the umbilical seam, and are straight and prorsiradiate on the flanks, narrow on the umbilical shoulder, but broadening and coarsening into spatulate terminations on the ventrolateral shoulders and venter. At the beginning of the outer whorl, these rib terminations are transverse and

opposite across the venter, interrupted by the coarse siphonal keel. Traced around the outer whorl, the keel persists, and the ribs remain transverse but change from opposite to alternate, a distinctive feature shown well by the paratype, a body chamber fragment (Pl. 8, Figs 4, 5). The poorly preserved sutures show little incised, broad saddles, and narrower lobes.

**DISCUSSION:** Subadults, with opposite ribs most closely resemble the strongly keeled *Brancocheras paronai* COLLIGNON, 1949 (Pl. 8, Figs 24-34) but can be distinguished by their rounded-quadrate whorl section, and transverse ventral ribs, not projected into a chevron.

When adult, the alternate ribs distinguish the species from all other *Brancocheras*.

**OCCURRENCE:** Condensed Lower to lower Upper Albian of Clars and Gourdon, Alpes-Maritimes, France.

*Brancocheras flexuosum* sp. nov.

(Pl. 3, Figs 10-12, 20-22; Text-figs 8c, 9A)

**TYPE:** The holotype (Pl. 3, Figs 10-12) is MNHP R52292/9 (ex PERON Collection, 1908-26), from the lower Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli*

Argiles Tégulines of Le Gaty, Aube, France. Paratype EMP A246a (Pl. 3, Figs 20-22) is from the lower Middle Albian of St Florentin, Yonne, France.

**DIAGNOSIS:** A compressed *Brancocheras* with 20 flexuous prorsiradiate ribs per whorl, strengthened and projected forwards on the ventrolateral shoulders, and weakened across the venter.

**DIMENSIONS:** D Wb Wh Wb:Wh U  
MNHP R52292/9 19.0(100) 7.0(36.8) 7.9(41.5) 0.88 5.8(30.5)

**DESCRIPTION:** The holotype is a limonitic phragmocone 19 mm in diameter. Coiling is moderately evolute, with 45% of the previous whorl covered. The umbilicus is shallow and comprises 30% of the diameter. The whorls expand slowly, the whorl section is compressed, with a whorl breadth to height ration of 0.88, the umbilical wall low, convex, and inclined outwards. The flanks are feebly convex, with greatest breadth below mid-flank, the ventrolateral shoulders broadly rounded, the venter flattened. The penultimate whorl is smooth. There are 20 ribs on the outer whorl, all primaries. They arise at the umbilical seam and strengthen across umbilical wall and shoulder, where they vary from weak to strong. The ribs are sharp, narrow, distant and prorsiradiate on the flanks,

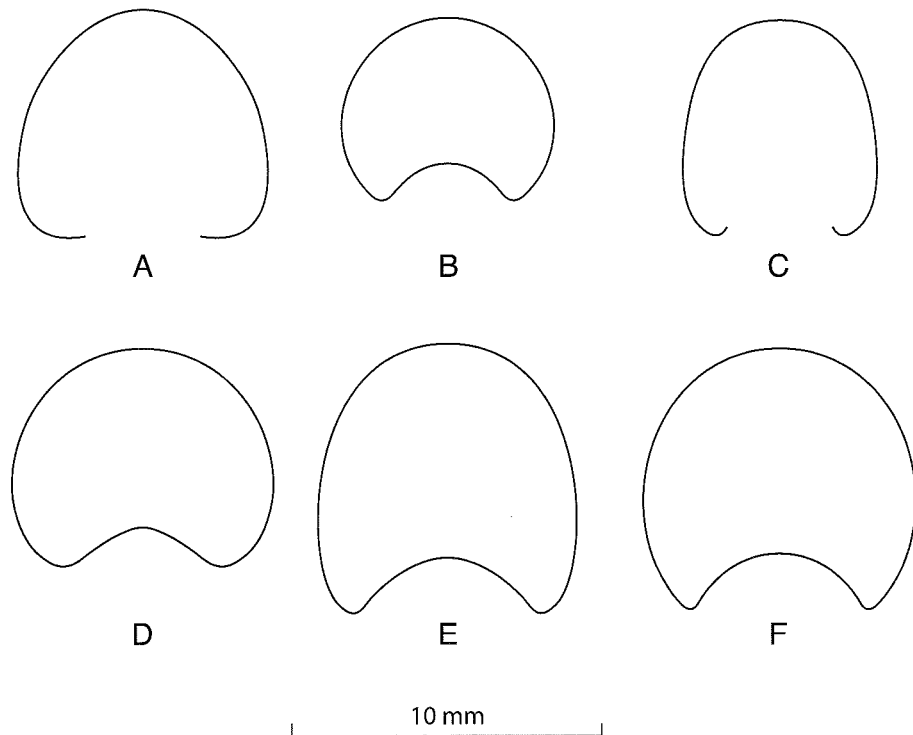


Fig. 8. Whorl sections of A: *Brancocheras multicostatum* sp. nov.; MNHP R52292/6; B, D, E, F: *Pseudobrancocheras versicostatum* (MICHELIN, 1838), B is MNHP R52292/6, D is MNHP R52292/11, E is MNHP R52292/8, F is MNHP R52292/10; C: *Brancocheras flexuosum* sp. nov., MNHP R52292/9

across which they strengthen. They are feebly convex on the inner flank, flex forwards and are feebly concave on the outer flank where they strengthen and project forwards on the ventrolateral shoulder. The ribs weaken over the venter, which they cross in a shallow convexity.

Suture (Text-fig. 9A) with broad, little-incised saddles and narrow lobes.

DISCUSSION: Whorl section and distant flexuous ribs, projected on the ventrolateral shoulder, and effacing on the venter characterise *Brancoeras flexuosum*. It most closely resembles *Brancoeras cricki* SPATH, 1934 (p. 469, pl. 56, figs 12-14; text-fig. 160a), from which it differs in that the latter has blunt alternately long and short or bifurcating ribs on the inner whorls.

OCCURRENCE: As for types.

*Brancoeras multicostatum* sp. nov.

(Pl. 2, Figs 1, 2; Pl. 3, Figs 18, 19; Text-figs 8A, 9B)

TYPES: The holotype (Pl. 3, Figs 18, 19) is EMP A246.1, from the lower Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli* Subzone of St. Florentin, Yonne, France. Paratype MNHP R52292/6 (Pl. 2, Figs 1, 2) is from the Middle Albian *Hoplites dentatus* Zone, *Lyelliceras lyelli* Zone Argiles Tégulines of Le Gaty, Aube, France.

DIAGNOSIS: *Brancoeras* with depressed, reniform whorl section with 26 crowded rursiradiate primary ribs per whorl in the juvenile, and 16 ribs per half whorl in the adult.

DIMENSIONS:	D	Wb	Wh	Wb:Wh	U
Paratype,					
MNHP R52292/6	16.9(100)	8.4(49.7)	7.7(45.6)	1.09	6.1(36.1)
Holotype,					
EMP A.246/1	32.4(100)	12.6(38.9)	11.5(35.5)	1.1	12.5(38.6)

DESCRIPTION: The paratype (Pl. 2, Figs 1-2) is a limonitic internal mould 16.9 mm in diameter, septate

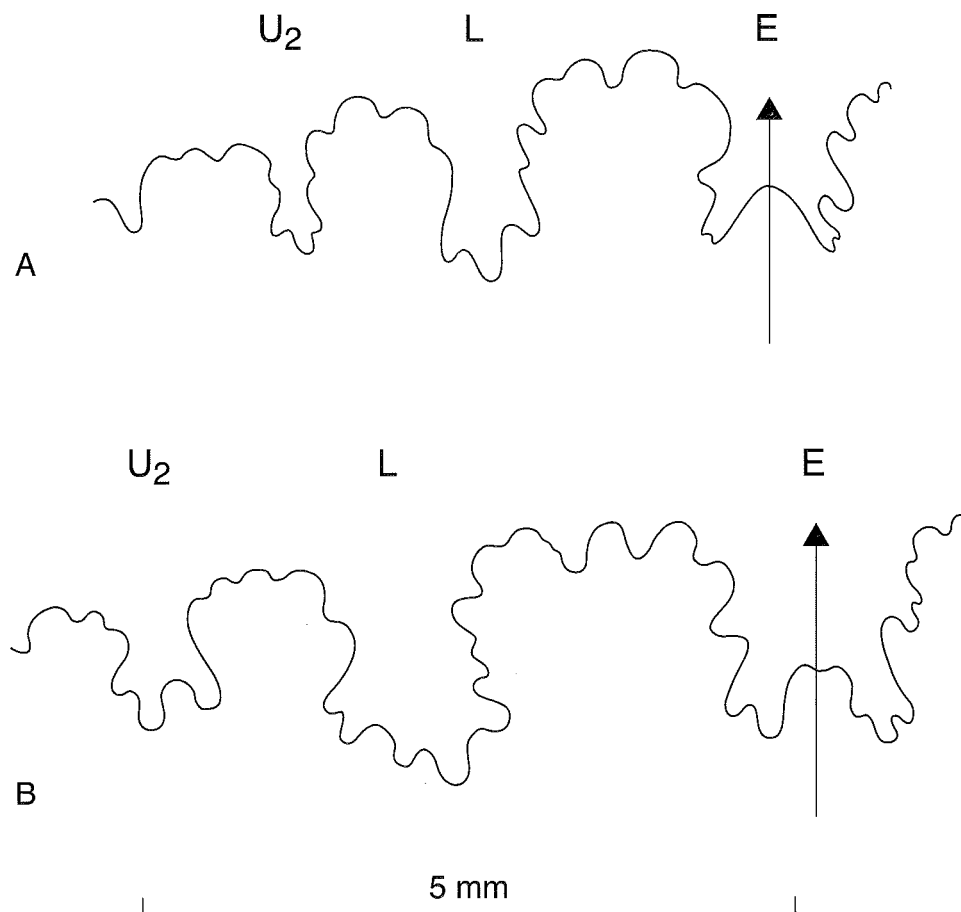


Fig. 9. External suture lines of A: *Brancoeras flexuosum* sp. nov. MNHP R52292/9; B: *Brancoeras multicostatum* sp. nov. MNHP R52292/6

but for a short section corresponding to the last 5 ribs. Coiling evolute, whorl section depressed reniform, with whorl breadth to height ratio 1.09, the greatest breadth below mid-flank. The umbilical wall is convex, the flanks, ventrolateral shoulders and venter broadly rounded. The inner whorls are strongly ribbed at the smallest diameter visible. There are 21 primary ribs on the outer whorl that arise at the umbilical seam or on the umbilical shoulder. The ribs strengthen across the umbilical shoulder, and are of variable strength and development on the inner flank, narrow, strong and crowded. They strengthen across the middle and outer flanks, and are at their maximum development on ventrolateral shoulders and venter. The ribs are feebly convex on the inner flank, flex back and are rursiradiate on the outer flank, and are straight and transverse over the venter.

The holotype (Pl. 3, Figs 18, 19) is a well-preserved near-complete adult retaining recrystallised shell, 32.4 mm in diameter. Coiling is very evolute, the umbilicus comprising 38.6% of the diameter, and of moderate depth, with a convex wall. The whorl section is slightly depressed, reniform, with the greatest breadth below mid-flank. There are an estimated 25-26 ribs on the penultimate whorl, all primaries that arise at the umbilical seam, and are both weak and strong on umbilical shoulder and inner flank. There are 16 ribs on the outer half whorl. All are primaries and arise at the umbilical seam. They are straight, and feebly rursiradiate, becoming recti-, and then feebly prorsiradiate at the largest preserved diameter. They coarsen and thicken markedly on the ventrolateral shoulders and venter, where they are straight and transverse.

Suture with broad, little-incised bifid lobes, and narrow saddles (Text-fig. 9B).

**DISCUSSION:** *Eubrancoeras multicostatum* most closely resembles *E. cricki* SPATH, 1934 (p. 469, pl. 56, figs 12-14; text-fig. 160a), from which it differs in having more numerous and curved, rursiradiate, ribs.

**OCCURRENCE:** As for types.

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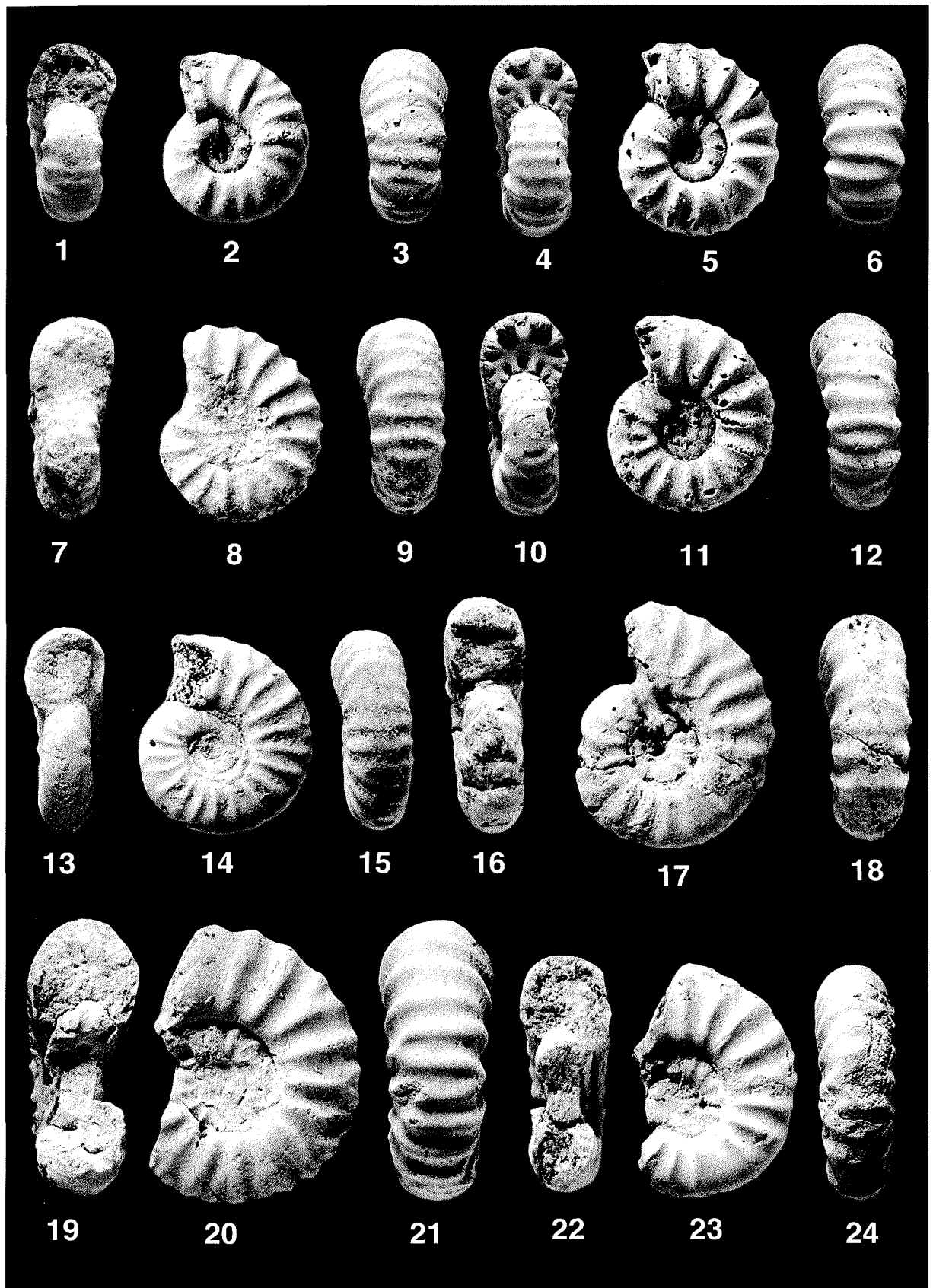
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## PLATE 1

**1-24** – *Pseudobrancocheras versicostatum* (MICHELIN, 1838). 1-3 – MNHP R52292/2; 4-6 – MNHP R52292/4; 10-12 – MNHP R52292/5; from the lower Middle Albian of Le Gaty, Aube, France. 7-9 – ID 2010/3; 13-15 – ID 2010/5; 16-18 – ID 2010/1; 19-21 – ID 2010/2; 22-24 – ID 2010/4, from the condensed Albian of Gourdon, Alpes-Maritimes, France.

All figures are x 2.

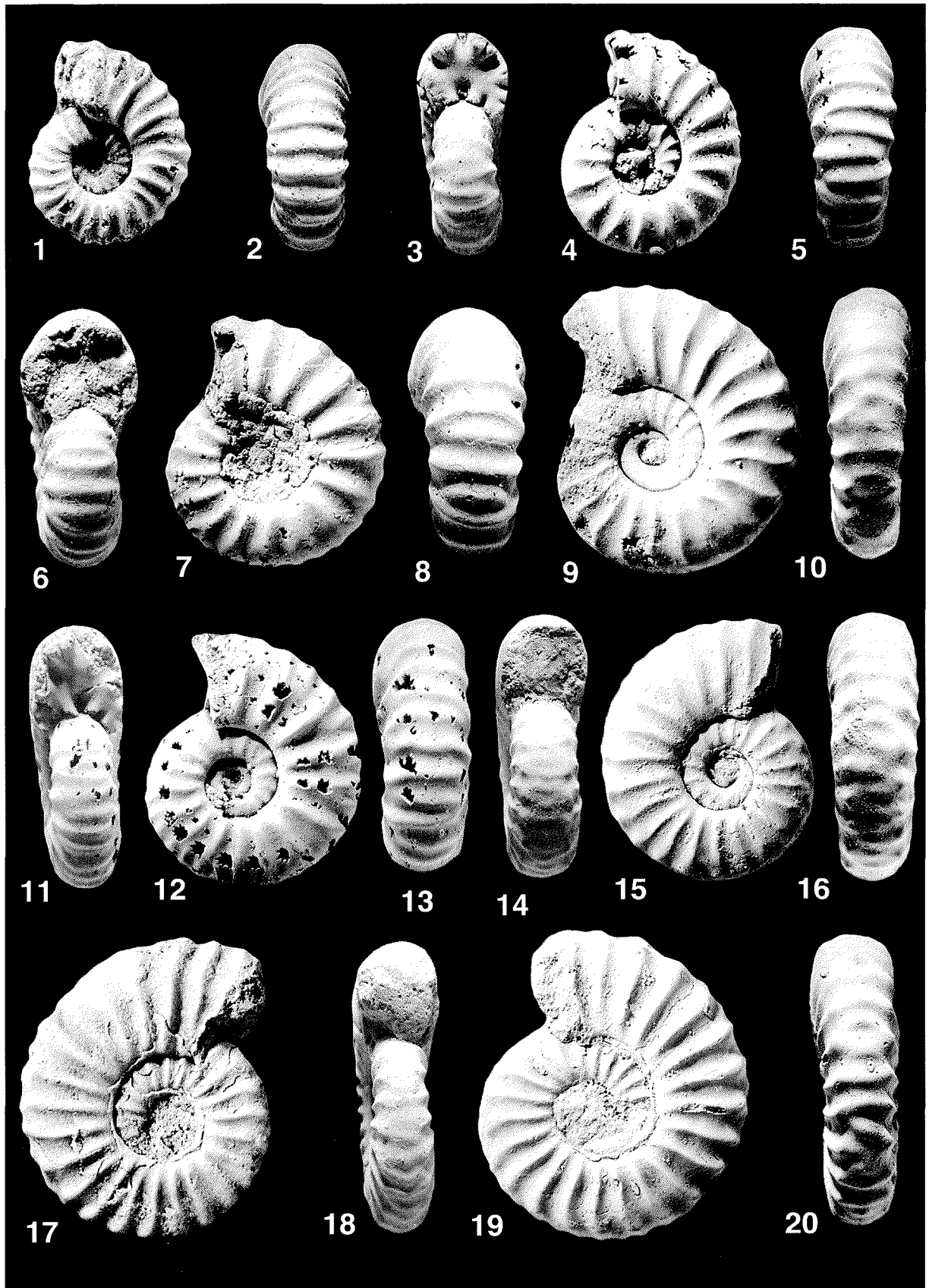


## PLATE 2

- 1-2** – *Brancoceras multicostratum* sp. nov., paratype MNHP 52292/6, from the lower Middle Albian of Le Gaty, Aube, France.
- 3-8, 11-13** – *Pseudobrancoceras versicostatum* (MICHELIN, 1838). 3-5 – MNHP 52292/11; 6-8 – MNHP 52292/7; 11-13 – MNHP 52292/8, all from the lower Middle Albian of le Gaty, Aube, France.
- 8-10, 14-20** – *Pseudobrancoceras transiens* sp. nov. 9-10 – paratype MNHP 5972A-2; 17-20 – holotype, MNHP 5972A-1, both from the lower Middle Albian of Maurepaire, Aube, France. 14-16 – paratype BMNH 37630, from the condensed Albian of Escragnolles, Alpes-Maritimes, France.

All figures are  $\times 2$

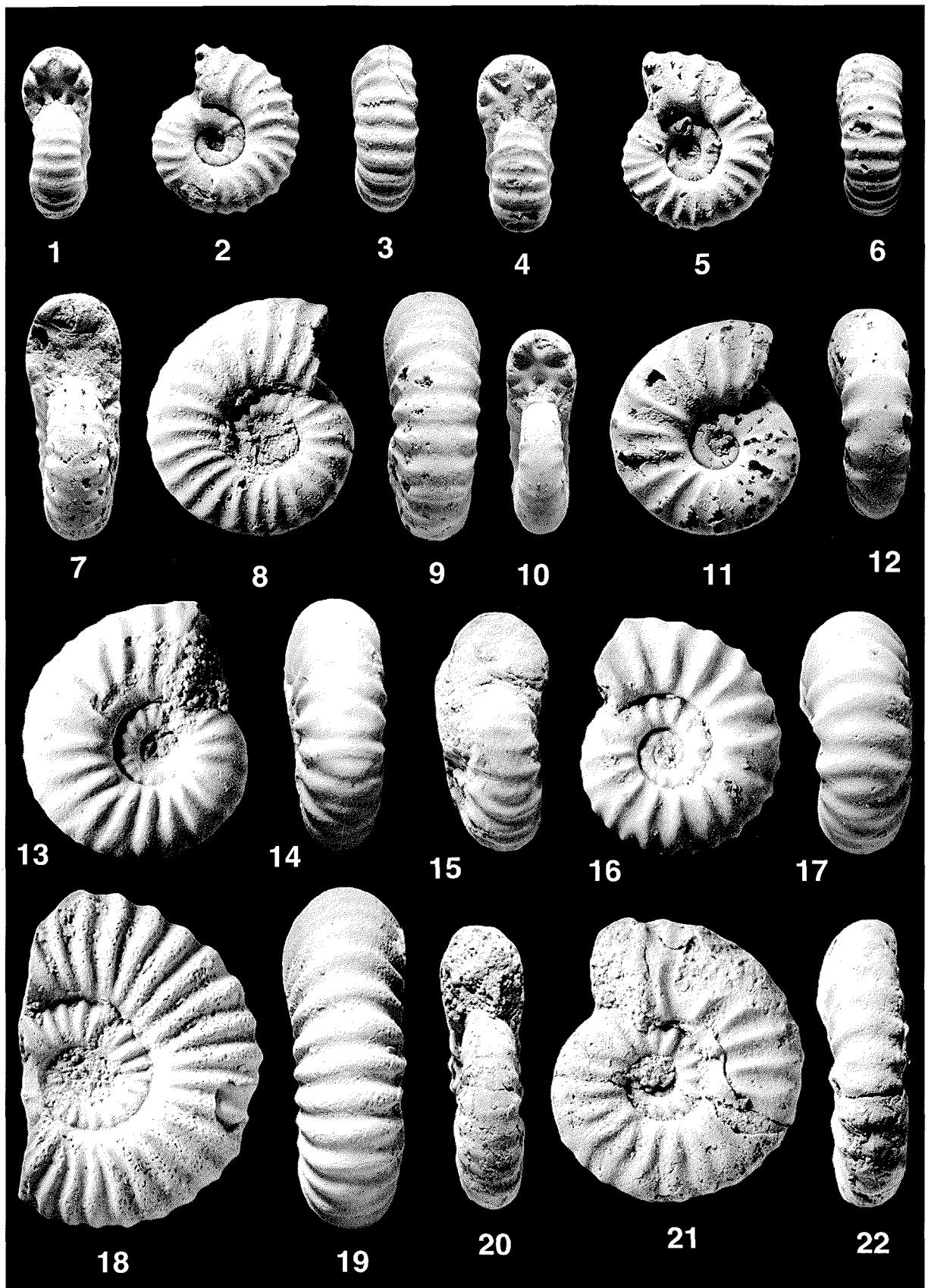




## PLATE 3

- 1-9, 13-17** – *Pseudobrancoceras versicostatum* (MICHELIN, 1838). 1-3 – MNHP 52292/1; 4-6 – MNHP 52292/3, from the lower Middle Albian of le Gaty, Aube, France. 13-14 – EMP A246c; 15-17 – EMP A246d, from the lower Middle Albian of St Florentin, Yonne, France.
- 10-12, 20-22** – *Brancoceras flexuosum* sp. nov.; 10-12 – holotype, MNHP 52292/9, from the lower Middle Albian of Le Gaty, Aube, France. 20-22 – EMP A246a, paratype from the lower Middle Albian of St Florentin, Yonne, France.
- 18-19** – *Brancoceras multicosatum* sp. nov.; holotype EMP A246b, from the lower Middle Albian of Le Gaty, Aube, France.

All figures are  $\times 2$



## PLATE 4

Syntypes of *Ammonites senequieri* D'ORBIGNY, 1841

**1-3, 14-15** – *Brancocheras senequieri* (D'ORBIGNY, 1841); 1-3 – lectotype, MNHP 5803-1;  
14-15 – MNHP 5803-6.

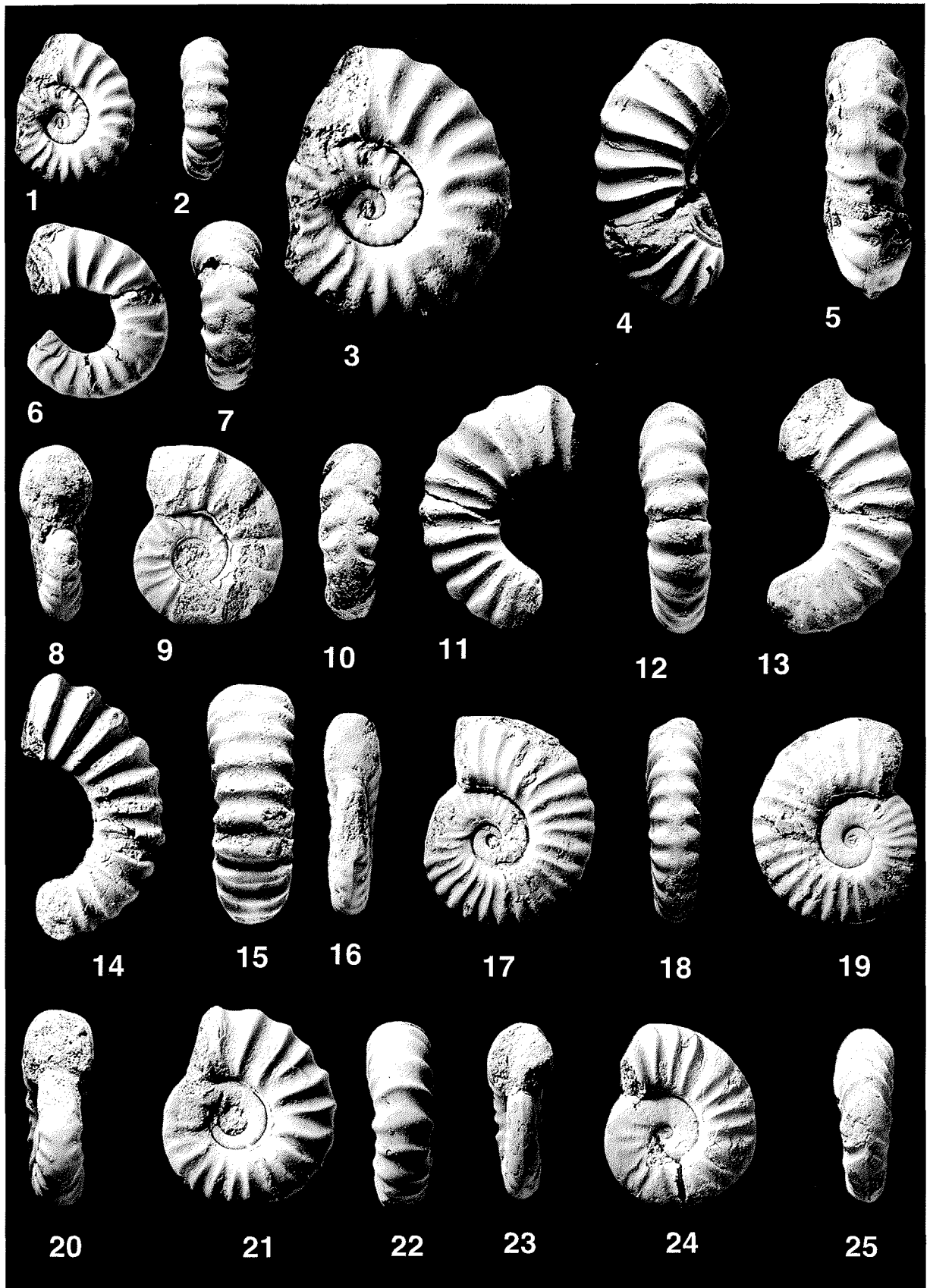
**6-7** – *Brancocheras paronai* COLLIGNON, 1949; MNHP 5803-4.

**4-5, 8-10, 20-25** – *Brancocheras magneti* COLLIGNON, 1949; 4-5 – MNHP 5803-2; 8-10 – MNHP  
5803-4; 20-22 – MNHP 5803-8; 23-25 – MNHP 5803-9.

**11-13, 16-19** – *Brancocheras subcompressum* COLLIGNON, 1949; 11-13 – MNHP 5803-5;  
6-19 – MNHP 4803-7.

All specimens are from the condensed Albian of Escragnolles, Clars, Alpes-Maritimes, France.

All figures are natural size with the exception of 3, which is  $\times 2$



## PLATE 5

- 1-19** – Syntypes of *Ammonites senequieri* D'ORBIGNY, 1841.
- 1-5, 8-10, 17-19** – *Brancocheras magneti* COLLIGNON, 1949; 1-2 – MNHP 5803-10; 3-5 – MNHP 5803-11; 8-10 – MNHP 5803-12; 17-19 – MNHP 5803-13.
- 6-7, 12-13** – *Brancocheras senequieri* (D'ORBIGNY, 1841); 6-7 – MNHP 5803-17; 12-13 – MNHP 5803-16.
- 11** – *Brancocheras* sp.; MNHP 5803-15.
- 14-16** – *Brancocheras paronai* COLLIGNON, 1949; MNHP 5803-14, all specimens are from the condensed Albian of Escragnolles/Clars, Alpes-Maritimes, France.
- 20-28** – *Brancocheras senequieri* (D'ORBIGNY, 1841); 20-21 – ID 1998; 22-23 – ID 2003; 27-28 – ID 1999, from the condensed Albian of Gourdon, Alpes-Maritimes, France. 24-26 – EMP A321, ex DE VERNEUIL Collection, 1873, from the condensed Albian of Clars, Alpes-Maritimes, France.

All figures are natural size

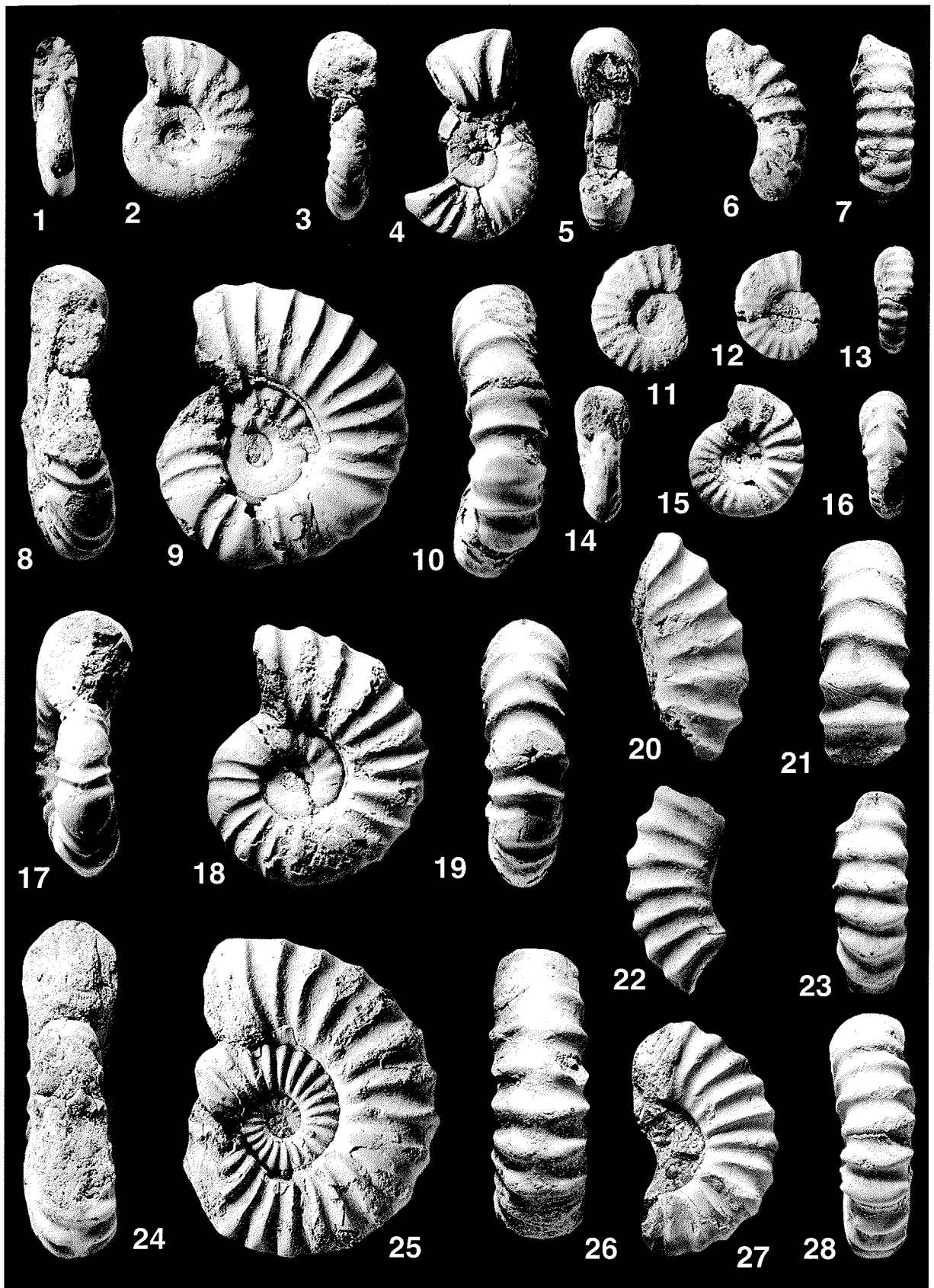
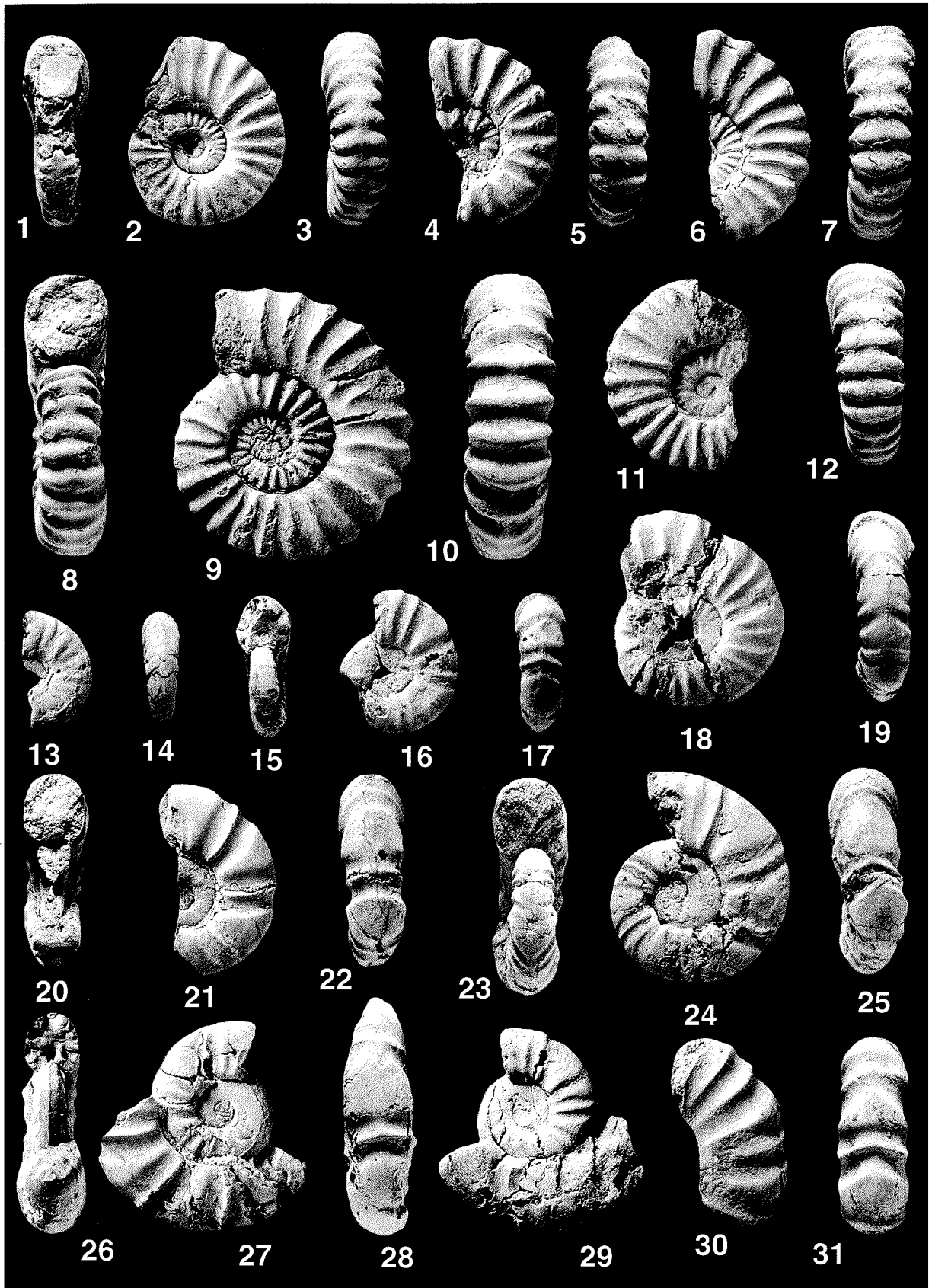


PLATE 6

- 1-12** – *Brancocheras senequieri* (D'ORBIGNY, 1841); 1-3 – ID 1993; 4, 5 – ID 1985;  
6, 7 – ID 1997; 8-10 – ID 1996; 11, 12 – ID 1995.
- 13-31** – *Brancocheras magneti* COLLIGNON, 1949; 13, 14 – ID 2008; 15-17 – ID 2009;  
18, 19 – ID 1984; 20-22 – ID 2005; 23-25 – ID 2006; 26-29 – ID 2004; 30, 31 – ID 2007.
- All specimens are from the condensed Albian of Gourdon, Alpes-Maritimes, France.

All figures are natural size

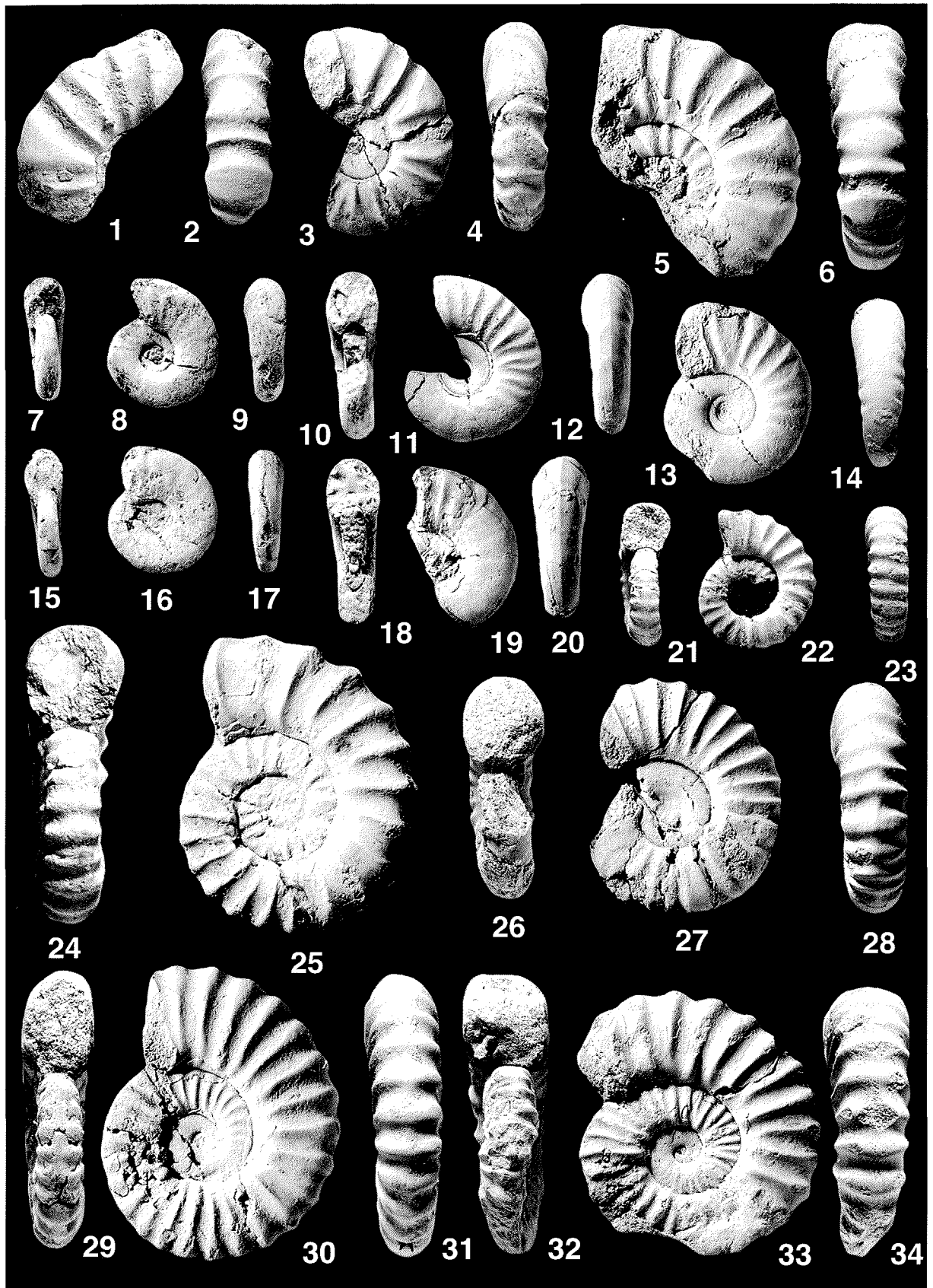




## PLATE 7

- 1-20, 26-28** – *Brancocheras magneti* COLLIGNON, 1949; 1-2 – EMP A241a; 3-4 – EMP A240b; 5-6 – EMP A241b, all ex PUZOS Collection, 1848, from the condensed Albian of Clars, Alpes-Maritimes, France. 7-9 – ID 2080; 10-12 – ID 2078; 15-17 – ID 2081; 18-20 – ID 2079, all from the condensed Albian of Gourdon, Alpes-Maritimes, France. 13-14, 26-28 – EMP unregistered, from the condensed Albian of Escragnolles, Alpes-Maritimes, France.
- 21-25** – *Brancocheras helcion* (REYNÈS, 1876); 21-23 – ID 2011/3, from the condensed Albian of Gourdon, Alpes-Maritimes, France. 24-25 – BMNH 37632, ex ASTIER collection, from the condensed Albian of Escragnolles, Alpes-Maritimes, France, mentioned by SPATH (1934, p. 491).
- 29-34** – *Brancocheras subcompressum* COLLIGNON, 1949; 29-31 – EMP A239, ex PUZOS Collection, 1848, from the condensed Albian of Clars, Alpes-Maritimes, France. 32-34 – ID 1987, from the condensed Albian of Gourdon, Alpes-Maritimes, France.

All figures are natural size



## PLATE 8

- 1-5** – *Brancocheras alternatum* sp. nov.; 1-3 – holotype, EMP A243, ex PUZOS Collection, 1848, from the condensed Albian of Clars, Escragnolles, Alpes-Maritimes, France. 4-5 – paratype ID 2077, from the condensed Albian of Gourdon, Alpes-Maritimes, France.
- 6-12** – *Brancocheras retrorsum* COLLIGNON, 1949; 6, MNHP R52291b, ex DE GROSSOUVRE Collection, from the condensed Albian of Clars, Alpes-Maritimes, France. 7-9 – ID 2076; 10-12 – ID 2075, from the condensed Albian of Gourdon, Alpes-Maritimes, France.
- 13-23** – *Brancocheras subcompressum* COLLIGNON, 1949. 13-14 – ID 2074; 15-16 – ID 2073; 17-18 – ID 1986; 19-21 – ID 1988; 22-23 – ID 1989, all from the condensed Albian of Gourdon, Alpes-Maritimes, France.
- 24-34** – *Brancocheras paronai* COLLIGNON, 1949; 24-26 – ID 2071; 27-28 – ID 2072; 29-31 – ID 2069; 32-34 – ID 2070, from the condensed Albian of Gourdon, Alpes-Maritimes, France.

All figures are natural size

