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On some Turonian and Coniacian ammonites from central Colombia

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ABSTRACT:

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The rich collections of Turonian and Coniacian ammonites from Colombia, housed in the University of California Museum of Paleontology, Berkeley, are described, with 20 species recognized, referred to the genera *Reymenticoceras* Kennedy, 2018, *Vascoceras* Choffat, 1898, *Fagesia* Pervinquière, 1907, *Wrightoceras* Reyment, 1954a, *Subprionocyclus* Shimizu, 1932, *Subprionotropis* Basse, 1951, *Prionocycloceras* Spath, 1926, *Barroisiceras* de Grossouvre, 1894, *Forresteria* Reeside, 1932, *Niceforoceras* Basse, 1948, *Peroniceras* de Grossouvre, 1894, *Gauthiericeras* de Grossouvre, 1894, *Protexanites* Matsumoto, 1955, and *Metaptychoceras* Spath, 1926. One species, *Reymenticoceras ornatum*, is new. Most of the species described can be assigned to the substages and ammonite zones recognized in Western Europe.

Key words: Ammonites; Turonian; Coniacian; Colombia.

INTRODUCTION

"Published accounts of the palaeontology of the mid-Cretaceous of Colombia, despite their disclosures of rich and interesting associations, hardly do justice to the almost unbelievable wealth of fossil associations, not least of which are the ammonites. In a country where ammonites can be bought in heaps from vendors plying their trade in the streets, one may conclude that our knowledge of the paleontology of the Cretaceous is still in its infancy…" So wrote Richard Reyment in 1981 (p. 175), and the same sentiment applies 40 years later. The position is not improved by the fact that the large collections in Western Europe and the United States commonly lack precise details as to provenance. This is the case with the outstanding collections in Grenoble, described by Kakabadze and Thieuloy (1991) and the present material, in the collections of the University of California Museum of Paleontology (UCMP), Berkeley. It forms a part of extensive collections from Colombia, made by field geologists of a number of now defunct organizations, including the California Exploration Company, in the middle decades of the last century. There is no further information with many of the collections, only locality numbers, which allow in some cases the recognition of faunal associations; in other cases the collections from individual localities are monospecific. Dr. Fernando Etayo-Serna (Bogota) examined the material some years ago, confirmed the provenance, and indicated that the material was from the equivalents of the La Frontera Formation (Etayo-Serna 1979, p. 11).

As noted elsewhere (Kennedy 2018, p. 384) the ammonites described in this account note were loaned, in the 1950's, to the late C.W. Wright (1917–2010), author of the Cretaceous Ammonoidea sections of the 1957 and 1996 Treatise volumes. The material was left to the present author to describe. In dealing with this material, I find myself like many a nine-

teenth century worker describing material brought back from remote parts with little information, but this does not reduce the value of the information the present collections hold.

AGE OF THE FAUNAS

The ammonites described below are of Turonian and Coniacian age based on occurrences of the same taxa in well-dated sections elsewhere in the world, although the dating of some endemic taxa is challenging. It is therefore fortunate that Patarroyo and Bengtson (2018) have recognized many of the species described below in the Loma Gorda Formation of Bambucá Creek in the Department of Huila in Colombia in a well-constrained stratigraphic context. Text-fig. 1 sets out the generally accepted Turonian and Coniacian ammonite zonal sequences developed in Western Europe. Substage assignation of the Coniacian zonal sequence varies between authors; that used here is based on that developed in the type area of the stage in the Aquitaine basin of Western France (Kennedy 1984). It is against this sequence that the present material is calibrated.

It should be noted that there is as yet no agreed Global Boundary Stratotype Section and Point for the base of the Coniacian Stage. The preferred choice of the Second International Symposium on Cretaceous Stage Boundaries, as set out by Kauffman *et al.* (1996) was the first occurrence of the inoceramid bivalve *Cremnoceramus rotundatus* (*sensu* Tröger, 1967, *non* Fiege 1930), subsequently shown to be a junior synonym of *Cremnoceramus deformis erectus* (Meek, 1877) (Walaszczyk and Wood 1998; Walaszczyk and Cobban 2000). The discovery of a specimen of *Forresteria* (*Harleites*) *petrocoriensis* (Coquand, 1859), index species of the lowest Coniacian ammonite zone, in the Upper Turonian *Mytiloides scupini* Zone in the Vistula valley (Poland) (Kennedy and Walaszczyk 2004), 3.1 m below the first occurrence of *Cremnoceramus deformis erectus* means that if the first occurrence of the latter species is adopted as the marker for the base of the Coniacian Stage, there will be no ammonite marker for the boundary (see Walaszczyk and Cobban 2000, p. 4 for further discussion).

Patarroyo and Bengtson (2018) recognized *Mytiloides scupini* (Heinz, 1930) in the Bambucá Creek section, allowing dating of many of the taxa described below as Turonian versus Coniacian. Their faunas are neither described nor illustrated (*Codazziceras ospinae* Karsten, 1858 apart), and some anomalies remain.

STAGE	SUBSTAGE	ZONE
Coniacian	Upper	*Paratexanites serratomarginatus* *Gauthiericeras margae*
	Middle	*Peroniceras tridorsatum*
	Lower	*Forresteria petrocoriensis*
Turonian	Upper	*Prionocyclus germari* *Subprionocyclus neptuni*
	Middle	*Collignoniceras woollgari*
	Lower	*Mammites nodosoides* *Fagesia catinus* *Watinoceras devonense*

Text-fig. 1. Turonian and Coniacian substages and ammonite zones recognized in Western Europe. The base of the Coniacian is drawn above the base of the *petrocoriensis* Zone on the basis of the occurrence of the index species below the first occurrence of *Cremnoceramus deformis erectus* (Meek, 1877), the proposed inoceramid marker for the base of the stage in the Vistula Valley, Poland (see text for further discussion).

Repositories of specimens:

MNHN: Muséum National d'Histoire Naturelle, Paris.
UCMP: University of California Museum of Paleontology, Berkley, USA.

CONVENTIONS

The suture terminology is that of Korn *et al.* (2003): E = external lobe; A = adventive lobe (= lateral lobe, L, of Kullmann and Wiedmann 1970); U = umbilical lobe; I = internal lobe.

The taxonomy of Wright (1996) is followed here. A number of the species described below have received detailed discussion in recent publications, and these are referred to rather than repeating them.

SYSTEMATIC PALAEONTOLOGY

Order Ammonoidea Zittel, 1884
Suborder Ammonitina Hyatt, 1889
Superfamily Acanthoceratoidea de Grossouvre, 1894
Family Acanthoceratidae de Grossouvre, 1894
Subfamily Mammitinae Hyatt, 1900

Genus *Reymenticoceras* Kennedy, 2018

TYPE SPECIES: *Mammites nodosoidesappelatus* Etayo-Serna, 1979, p. 85, pl. 13, fig. 1, by the original designation of Kennedy (2018, p. 386).

Reymenticoceras ornatum sp. nov.
(Pl. 1, Figs 4–9)

DIAGNOSIS: A species of *Reymenticoceras* in which a growth stage with primary and intercalated ribs that have inner and outer ventrolateral tubercles is succeeded by one in which the intercalated ribs have outer ventrolateral tubercles only; the adult body chamber develops inner ventrolateral horns, and the intercalated ribs are lost, leaving only outer ventrolateral tubercles between successive widely separated primaries.

TYPE SPECIMENS: The holotype is UCMP C1721-18 (Pl. 1, Figs 4, 5), paratypes are UCMP C1721-19 (Pl. 1, Figs 6, 7) and UCMP C1721-20 (Pl. 1, Figs 8, 9).

TYPE STRATUM: From the equivalents of the La Frontera Formation (see above).

DERIVATION OF NAME: Ornate (English): ornamented.

DESCRIPTION: The holotype (Pl. 1, Figs 4, 5) is a 180º sector of three successive whorls; the maximum preserved diameter is 79 mm. Coiling is moderately involute, with 67% of the previous whorl covered, the deep umbilicus comprising 23% of the diameter. The umbilical wall is very feebly convex and outward-inclined, the umbilical shoulder broadly rounded. The intercostal whorl section is slightly compressed, with flattened convergent flanks, the ventrolateral shoulders broadly rounded, the venter flattened. The costal whorl section is trapezoidal-polygonal, with the greatest breadth at the umbilical bullae, the costal whorl breadth to height ratio 0.95. Six coarse blunt bullae perch on the umbilical shoulder. They give rise to a single low prorsiradiate rib that links to a strong inner ventrolateral clavus. This is linked by a broad prorsiradiate rib to a smaller outer ventrolateral clavus. Single intercalated ribs arise both low and high on the flank and have a ventrolateral development comparable to that of the primaries. The fifth and sixth ribs from the adapical end of the fragment are separated by a very weak rib with a small transversely elongated outer ventrolateral clavus. On the adapertural 90º sector the primary ribs are separated by single intercalated ribs with an outer ventrolateral clavus only.

Paratype UCMP C1721-19 (Pl. 1, Figs 6, 7) is a 60º whorl sector of body chamber with a maximum preserved whorl height of 35 mm. Three widely separated primary ribs are present on the fragment. They are strong and narrow, arising on the umbilical shoulder without developing into a bulla, and are straight and prorsiradiate on the flanks, linking to an oblique, laterally compressed inner ventrolateral horn, from which a broad rib sweeps forwards to a rounded outer ventrolateral tubercle, the venter smooth between the outer ventrolateral tubercles. A pair of well-developed, rounded tubercles separates the adapical primary ribs.

Paratype UCMP C1721-20 (Pl. 1, Figs 8, 9) is a 120º whorl sector of body chamber, lacking the inner flank region. Tuberculation on the adapical part is as in the previous specimen, but the flank ribbing is very weak. This is succeeded by a wide unornamented sector, with an inner ventrolateral horn and conical outer ventrolateral tubercle but no flank rib at the adapertural end.

DISCUSSION: *Reymenticoceras ornatum* sp. nov. differs from the type species, *R. nodosoidesappelatus* (Kennedy 2018, p. 387; text-figs 2f–j, 3a–d, 4a, b (pars), 5e (pars)) in having a late growth stage in which primary and secondary ribs with inner and outer ventrolateral tubercles is succeeded by one in which intercalated ribs are lost, leaving only outer ventrolateral tubercles between successive very widely separated primaries on the late phragmocone and body chamber. The adapertural part of the adult body chamber of *R. nodosoideoappelatus* has crowded delicate flank ribs, with inner and outer ventrolateral tubercles.

OCCURRENCE: Upper Turonian, based on the association with *Prionocycloceras guayabanum* (Gerhardt, 1897b), central Colombia.

Reymenticoceras sp.
(Pl. 1, Figs 1–3)

MATERIAL: UCMP C1510-16.

DESCRIPTION: The specimen is an adult, with a maximum preserved diameter of 42.3 mm. The adapical part of the incomplete outer whorl (most of which is interpreted as body chamber) has a rectangular intercostal section, with flattened, subparallel flanks and broadly rounded umbilical shoulders. The adapicalmost of the primary ribs arises from a strong umbilical bulla, and is narrow, straight and prorsiradiate; the umbilical region of the succeeding ribs is damaged. They are narrow, straight and feebly prorsiradiate, linking to conical inner ventrolateral tubercles in turn linked by a prorsiradiate rib to an outer ventrolateral clavus, the clavi linked across the venter by a very low, near-effaced rib. There are five ribs in this style. The succeeding section is characterized by the appearance of much weaker and narrower intercalated ribs with barely developed inner and outer ventrolateral tubercles between successive primaries. The adapertural section is characterized by the disappearance of strong primary ribs, and an ornament of crowded weak primary and intercalated ribs, prorsiradiate and straight on the inner flank, flexed back at mid-flank, feebly concave on the outer flank, and very feebly convex over the venter, where they bear the feeblest of transversely elongated ventrolateral clavi.

DISCUSSION: The ontogenetic stages of this distinctive specimen parallel those of *Reymenticoceras nodosoidesappelatus*, from which it differs in its diminutive adult size. It might be a microconch, or perhaps a paedomorphic dwarf offshoot. The material is too slight to comment further.

OCCURRENCE: Upper Turonian, on the basis of the association with *Subprionocyclus branneri* (Anderson, 1902), central Colombia.

Family Vascoceratidae H. Douvillé, 1912

Genus *Vascoceras* Choffat, 1898

TYPE SPECIES: *Vascoceras gamai* Choffat, 1898, p. 54, pl. 7, figs 1–4; pl. 8, fig. 1; pl. 10, fig. 2; pl. 31, figs 1–5, by the subsequent designation of Diener (1925, p. 182).

Vascoceras venezolanum Renz, 1982
(Pl. 2, Figs 1–10; Text-fig. 2C, D)

1982. *Vascoceras venezolanum* Renz, p. 80, pl. 23, figs 5–7; text-fig. 61i.
1982. *Vascoceras venezolanum* Renz, 1982, forma a; Renz, p. 80, pl. 23, figs 8–11, text-fig. 61a, b, f, l.
1982. *Vascoceras venezolanum* Renz, 1982, forma b; Renz, p. 81, pl. 24, figs 1–3, text-fig. 61k.
1982. *Vascoceras venezolanum* Renz, 1982, forma c; Renz, p. 82, pl. 24, figs 4–7; text-fig. 61d, g.
1982. *Vascoceras venezolanum* Renz, 1982, forma d; Renz, p. 82, pl. 24, figs 8–10; pl. 25, figs 1, 2; text-fig. 61c.
1982. *Vascoceras venezolanum* Renz, 1982, forma e; Renz, p. 84, pl. 25, figs 3–8; text-fig. 61c, h.
?2016. *Vascoceras* cf. *venezolanum* Renz, 1982; Patarroyo, p. 46, pl. 1, figs 8–11.

TYPE: The holotype, by original designation is no. Re 6799-20, in the collections of Maravan S.A., Caracas, and from the Lower Turonian Chejendé Member of the La Luna Formation, la Morita, Venezuela.

MATERIAL: UCMP C1692-1 to 8, plus 40 additional specimens.

DESCRIPTION: Specimens are up to 48 mm in diameter. Most are worn and poorly preserved. Coiling is involute, the umbilicus comprising 20% approximately of the diameter. The whorl section is depressed reniform with whorl breadth to height ratios of around 1.2. Up to five umbilical bullae per half whorl give rise to pairs of ribs, with additional long and short ribs of variable strength intercalating to give a total of up to 18 ribs per half whorl, the ribs straight and prorsiradiate on the flanks, and crossing the venter in a broad convexity. There is wide intraspecific variation. UCMP C1692-1 (Pl. 2, Figs 1, 2) has even, relatively coarse ribbing. UCMP C1692-2 (Pl. 2, Figs 3, 4) has a wide near-smooth whorl sector, succeeded by a constriction and flared collar-rib. UCMP C1692-3 (Pl. 2, Figs 7, 8) has strong bullate primary ribs separated by several finer ribs of variable strength, with stronger ribs succeeded by deeper interspaces. The differentiation of ornament is even more strongly expressed in UCMP C1692-6 (Pl. 2, Figs 5, 6). The largest specimen, UCMP C1692-8, has ornament of this type to a whorl height of 15 mm. Beyond this, umbilical bullae strengthen, but flank and venter ornament weakens and effaces, as in forma d of Renz (1982, pl. 25, fig. 1). None of the specimens show the sutures.

DISCUSSION: See Renz (1982, p. 80).

OCCURRENCE: Upper Lower Turonian, based on the occurrence in association with *Mammites nodosoides* (Schlüter, 1871), in the Chejendé Member of

the La Luna Formation near La Morita (Renz 1982, p. 73), Venezuela, and central Colombia.

Genus *Fagesia* Pervinquière, 1907

TYPE SPECIES: *Olcostephanus superstes* Kossmat, 1897, p. 26 (133), pl. 6 (17), fig. 1 only, by the original designation of Pervinquière (1907, p. 322).

Fagesia tevesthensis (Peron, 1896)
(Text-fig. 2A, B, E–G)

1896. *Mammites*? *tevesthensis* Peron, p. 23, pl. 1(7), figs 2, 3.
1994. *Fagesia tevesthensis* (Peron, 1986); Chancellor *et al*., p. 62, pl. 15, figs 1–3, 10, 11 (with synonymy).
2009. *Fagesia tevesthensis* (Peron, 1896); Barroso-Barcenilla and Goy, p. 25, text-figs 4.4, 5.1 (with additional synonymy).

TYPE: The holotype, by monotypy, is MNHN F. J04308, the original of Peron (1896, pl. 1 (7), figs 2, 3), from Tebessa, Algeria. It was refigured by Chancellor *et al.* (1994, pl. 15, figs 10, 11).

MATERIAL: UCMP C1476-1; UCMP C1247-1.

DESCRIPTION: UCMP C1247-1 (Text-fig. 2E–G) is partially embedded in matrix, and preserved to an estimated diameter of 40 mm. Coiling appears to have been involute, the whorl section depressed-reniform, Coarse straight prorsiradiate ribs arise in pairs from coarse umbilical bullae, with additional ribs intercalating. All ribs strengthen across the flanks and ventrolateral shoulders, crossing the venter in a feeble convexity. UCMP C1476-1 (Text-fig. 2A, B) is preserved to a maximum diameter of 51 mm (only the well-preserved part of the specimen is figured here). Coiling is very involute, the deep umbilicus comprising 20% of the diameter. The whorl section is very depressed reniform, with a whorl breadth to height ratio of 2.1, the greatest breadth at the umbilical shoulder. Ribs arise in groups of two or three from umbilical bullae, and cross flanks and venter in a very feeble convexity. This ornament is interrupted by a single very wide interspace succeeded by a flared rib.

DISCUSSION: See Chancellor *et al*. (1994, p. 64).

OCCURRENCE: Upper Lower Turonian, based on the co-occurrence with *Mammites nodosoides* in the Iberian Trough, Spain (Barosso-Barcenilla and Goy 2009, p. 31), Central Tunisia, Algeria, Egypt, Israel, Portugal, Spain, France, and central Colombia.

Family Pseudotissotinae Hyatt, 1903

Genus *Wrightoceras* Reyment, 1954a

TYPE SPECIES: *Bauchioceras* (*Wrightoceras*) *wallsi* Reyment, 1954a, p. 160, pl. 2, fig. 4; pl. 3, fig. 3, by the original designation of Reyment (1954a, p. 159).

Wrightoceras munieri (Pervinquière, 1907)
(Pl. 3, Figs 3–7; Pl. 4, Figs 8, 9)

1907. *Hoplitoides Munieri* Pervinquière, p. 217, pl. 10, figs 1, 2; text-fig. 83.
1994. *Wrightoceras munieri* (Pervinquière, 1907); Chancellor *et al*., p. 96, pl. 26, figs 1, 5, 8; pl. 28, figs 1–4; pl. 29, figs 3–8; pl. 36, figs 1, 2; text-figs 18g–h; 19h–i (with synonymy).
2007. *Wrightoceras munieri* (Pervinquière, 1907); Barroso-Barcenilla and Goy, p. 480, text-fig. 10.3, 4 (with additional synonymy).
2016. *Wrightoceras munieri* (Pervinquière, 1907); Patarroyo, p. 44, pl. 1, figs 1–7.

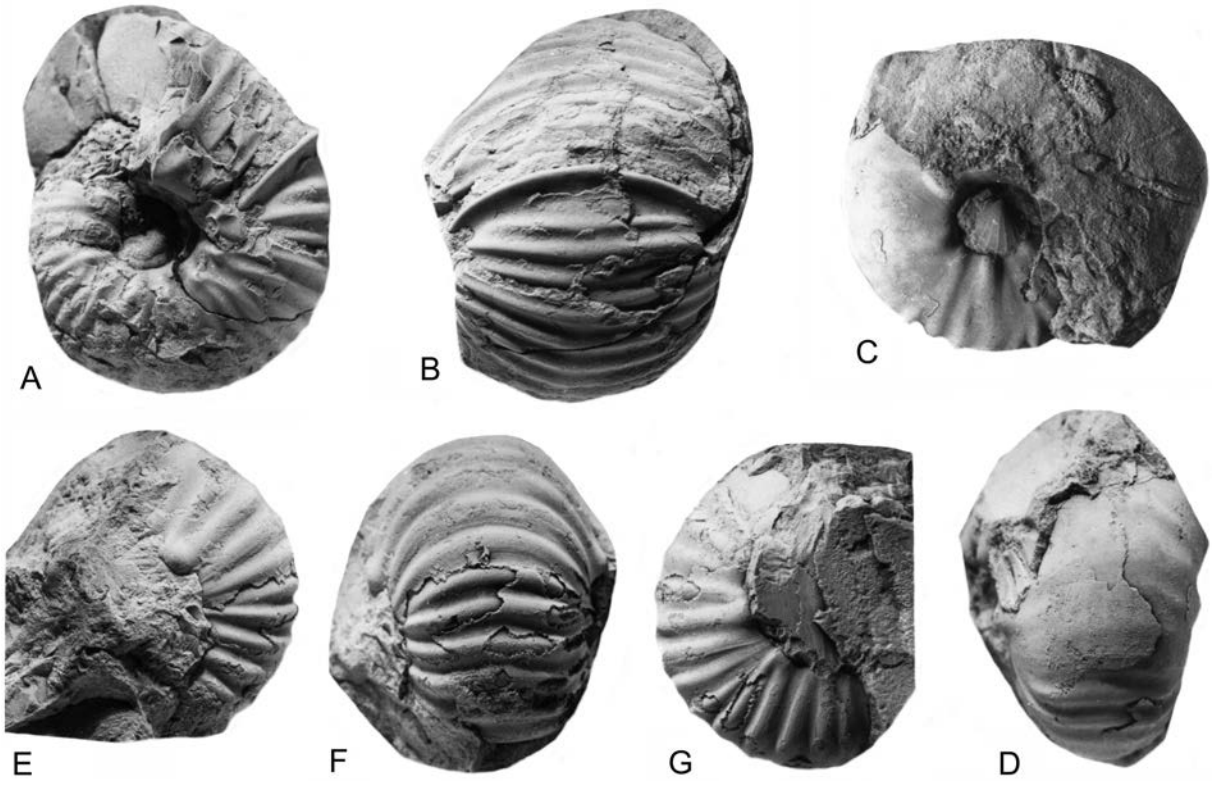
TYPE: The holotype, by the original designation of Pervinquière (1907, explanation of plate 10), is MNHN. F. J04262, the original of Pervinquière (1907, pl. 10, fig. 2), refigured by Chancellor *et al*. (1994, pl. 29, figs 6–8), from the Lower Turonian of Draa el Miaad, Central Tunisia.

MATERIAL: UCMP C1610-1, UCMP C9769-1 and 2.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C9769-1 at	72.8 (100	19.1 (26.2)	43.8 (60.2)	0.43	5.9 (8.1)
UCMP C9769-2 at	79.3 (100	20.8 (26.2)	45.3 (57.1)	0.46	– (–)

DESCRIPTION: Specimens range from 45 mm to an estimated 105 mm in diameter. Coiling is very involute, the tiny umbilicus shallow, with a flattened wall and quite narrowly rounded umbilical shoulder. The whorl section is very compressed, with a whorl breadth to height ratio of 0.43 to 0.46, the greatest breadth well below mid-flank, the inner flanks very feebly convex, the outer flanks flattened and converging to sharp ventrolateral shoulders, the narrow venter flat between. Ornament on the surface of the



Text-fig. 2**A**, **B**, **E-G** – *Fagesia tevesthensis* (Peron, 1896). A, B – UCMP 1476-1; E–G – UCMP C12247-1. **C**, **D** – *Vascoceras venezolanum* Renz, 1982, C1692-8. The figures are ×1.

recrystallized shell consists of delicate crowded riblets and lirae that arise in groups at the umbilical shoulder and increase by branching and intercalation on the flanks. They are feebly concave across the umbilical wall and shoulder, sweep forwards and are prorsiradiate on the inner flank, flex back and are very feebly convex at mid-flank then flexing forwards and feebly concave on the outermost flank. The sutures are not seen.

DISCUSSION: See Chancellor *et al.* (1994, p. 100) and Barroso-Barcenilla and Goy (2007, p. 480).

OCCURRENCE: Upper Lower Turonian, based on co-occurrence with *Mammites nodosoides*, as for example in Central Tunisia and Morocco (Kennedy *et al.* 2008, p. 152), Central Tunisia, Algeria, Morocco, Trans-Pecos Texas in the United States, Spain, Venezuela, central Colombia, Peru, Niger, and, possibly, Nigeria, Gabon, and Coahuila, Mexico. Wiese (1997) recorded the species from the Middle Turonian of northern Spain.

Wrightoceras lagiraldae (Etayo-Serna, 1979)
(Pl. 3, Figs 1, 2; Pl. 4, Figs 1–7, 10, 11; Pl. 6, Fig. 5)

1979. *Hoplitoides lagiraldae* Etayo-Serna, 1979, p. 92, pl. 13, fig. 14.

?non 2011. *Hoplitoides* cf. *lagiraldae* Etayo-Serna; Patarroyo, p. 77, pl. 2, figs 5–8.

TYPE: The holotype is the original of Etayo-Serna (1979, pl. 13, fig. 14), from the Lower Turonian La Frontera Formation at La Cabaña on the Cumaca–Viotá road in Central Colombia.

MATERIAL: UCMP C1510-17–22; C1513-1; C1998-1 and 2.

DESCRIPTION: Specimens range from 33 mm to an estimated 110 mm in diameter. Coiling is very involute, the tiny umbilicus comprising around 6% of the diameter, with a feebly convex wall and broadly rounded umbilical shoulder. The whorl section is

very compressed, the whorl breadth to height ratio 0.4, the inner to mid flank very feebly convex, the outer flanks flattened and convergent, the ventrolateral shoulders sharp, the narrow venter markedly concave between through most of the ontogeny, but broadening and becoming very feebly convex with faint ridges that are the traces of the sharp ventrolateral shoulders. The smallest individual seen, UCMP C1510-19, is 33 mm in diameter. The innermost part of the primary ribs is strengthened into barely differentiated bullae in some cases, the ribs feebly convex and prorsiradiate on the inner flank, flexing back at mid-flank, where they increase by branching and intercalation, then sweeping forwards and strengthening markedly into coarse crescents, 11 per half whorl, thereafter declining and effacing before reaching the ventrolateral shoulder. Ornament of this type extends to a diameter of 63 mm in UCMP C1510-20 (Pl. 6, Figs 2, 3), the ribs distinctly falcoid, the outer, concave part less distinct from the inner part than in smaller individuals. UCMP C1510-17 (Pl. 3, Figs 1, 2) shows the transition to what is interpreted as the adult ornament of delicate falcoid riblets and lirae, straight and prorsiradiate on the inner two-thirds of the flanks and concave on the outer third. At this growth stage, the venter becomes less markedly concave.

DISCUSSION: The present species is referred to *Wrightoceras* rather than *Hoplitoides* on the basis of the shape of the venter. Although the holotype was figured in side view only, Etayo-Serna (1969, p. 92) described it as "pulley-like, forming an open V, paralleling on both margins with an acute carina". *Wrightoceras lagiraldae* differs from *Wrightoceras munieri* in the greater whorl compression, more markedly concave venter and the strong crescentic outer flank ribs of early and middle growth stages

OCCURRENCE: Lower Turonian of central Colombia.

Family Collignoniceratidae Wright and Wright, 1951

Subfamily Collignoniceratinae Wright and Wright, 1951

Genus *Subprionocyclus* Shimizu, 1932

TYPE SPECIES: *Prionocyclus hitchinensis* Billinghurst, 1927, p. 516, pl. 16, figs 1, 2, by the original designation of Shimizu (1932, p. 2).

Subprionocyclus loboi (Etayo-Serna, 1979)
(Pl. 9, Figs 5–8)

1979. *Buenoceras loboi* Etayo-Serna, p. 102, pl. 14, fig. 2; text-fig. 9r, u.

TYPE: The holotype, by original designation, is the original of Etayo-Serna (1979, pl. 14, fig. 2), from, the 'Lower Coniacian' Cucita Member of central Colombia.

MATERIAL: UCMP C1618-1 and 2.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1618-7	44.7 (100)	12.3 (27.5)	23.7 (53.0)	0.52	7.7 (17.2)

DESCRIPTION: UCMP C1618-7 (Pl. 9, Figs 5–8) is a well-preserved adult 44.7 mm in diameter, retaining extensive areas of recrystallized shell. The adapical 240º sector of the outer whorl is body chamber. Coiling is very involute, the umbilicus comprising 17.2% of the diameter, with a low, flattened wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breath to height ratio of 0.52, the greatest breadth just outside the umbilical shoulder. The flanks are flattened, converging to rounded ventrolateral shoulders and a fastigiate venter. Tiny bullae perch on the umbilical shoulder and give rise to primary ribs, either singly or in pairs, the ribs narrow, straight and prorsiradiate on the flanks, where they increase by branching and intercalation to give a total of 18–20 ribs per half whorl at the ventrolateral shoulder, where they link to oblique ventrolateral clavi. These give rise to a prorsiradiate rib that forms an obtuse ventral chevron with the siphonal keel at the apex. The keel bears delicate siphonal clavi, corresponding to, but displaced adaperturally of, the ventrolateral clavi. The aperture is marked by a broad, shallow depression and flared margin. The suture is moderately incised, with a broad, asymmetrically bifid E/A.

DISCUSSION: *Subprionocyclus loboi* is separated from *S. branneri*, described below, and the second *Subprionocyclus* species recognized in the present faunas, on the basis of the much coarser ribbing and strong inner and outer ventrolateral tubercles of the latter.

OCCURRENCE: Upper Turonian, based on co-oc-

currence with *Prionocycloceras guayabanum* and *Barroisicers haberfellneri* (Hauer, 1866), central Colombia.

Subprionocyclus branneri (Anderson, 1902)
(Pl. 10, Figs 8–10; Pl. 12, Fig. 14)

1902. *Prionocyclus branneri* Anderson, p. 125, pl. 1, figs 11–16.
2019. *Subprionocyclus branneri* (Anderson, 1902); Kennedy and Kaplan, p. 74, pl. 1, fig. 8; pl. 38, figs 1, 5, 6, 10; pl. 39, figs 6–13, 16, 17; text-figs 26a, 27a–d, i, j.
2019. *Subprionocyclus branneri* (Anderson, 1902); Kennedy, p. 104, pl. 35, figs 1–6, 12–27; pl. 36, figs 5–9, 14–19, 22, 23; text-figs 57a, e, 55a, c, 58a–d, i, j (with full synonymy).

TYPE: The lectotype, by the subsequent designation of Matsumoto (1959, p. 110) is no. 445A in the collections of the California Academy of Sciences from near Phoenix, Oregon, the original of Anderson (1902, pl. 1, figs 11, 12).

MATERIAL: UCMP C1510-8a–d.

DESCRIPTION: UCMP C1510-8a–d are preserved on a single slab of matrix (Pl. 10, Figs 8–10; Pl. 12, Fig. 14). UCMP C1510-8a is 20.8 mm in diameter, UCMP C1510-8b 24 mm in diameter, and UCMP C1510-8c 29.2 mm in diameter. Coiling is involute, comprising 15% of the diameter in UCMP C1510-8c, shallow, with a convex wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with flattened, subparallel flanks, rounded ventrolateral shoulders, and a feebly convex venter in intercostal section. Seven primary ribs per half whorl arise at the umbilical seam and strengthen across the umbilical wall and shoulder. Some develop into small umbilical bullae that give rise to one or two ribs; other ribs arise at the umbilical shoulder without developing a bulla, or intercalate to give a total of 11–12 ribs per whorl at the ventrolateral shoulder. The ribs are relatively coarse, straight and prorsiradiate, and link to well-developed conical inner ventrolateral tubercles. These give rise to a stronger straight, slightly more prorsiradiate rib that links to a well-developed outer ventrolateral clavus from which a prorsiradiate rib links to an adaperturally displaced siphonal clavus at the apex of an obtuse ventral chevron. UCMP C1510-8d (Pl. 8, Fig. 10) is part of the internal mould of the flank and venter of a much larger fragment of what is interpreted as body chamber. The maximum preserved whorl height is 26.4 mm. The flanks are flattened and subparallel. Four relatively weak umbilical bullae are preserved on the fragment. They give rise to one or two feeble prorsiradiate ribs, with additional ribs intercalating, to give a total of nine ribs at the ventrolateral shoulder of the fragment, where they link to conical to feebly bullate tubercles, linked by a broad rib to slightly weaker outer ventrolateral clavi. A very low, barely differentiated prorsiradiate rib sweeps forwards on the venter, with a stronger, adaperturally displaced siphonal clavus at the apex.

DISCUSSION: See above.

OCCURRENCE: Upper Turonian, *Subprionocyclus nepuni* Zone and correlatives. The geographic distribution is southern England, northern and southern France, Germany, Japan, Oregon in the United States, and central Colombia.

Genus *Subprionotropis* Basse, 1951

TYPE SPECIES: *Subprionotropis colombianus* Basse, 1951, p. 250, pl. 11, figs 8–10, by the original designation of Basse (1951, p. 250).

Subprionotropis colombianus Basse, 1951
(Pl. 10, Figs 13, 14; Pl. 11, Figs 1–20; Pl. 12, Fig. 11)

1951. *Subprionotropis colombianus* Basse, p. 250, pl. 11, figs 8–10.
1957. *Subprionotropis columbianus* Basse, 1950 (*sic*); Wright, p. 427, text-fig. 547.7.
1981. *Subprionotropis* aff. *colombianus* Basse; Reyment, pl. 1, fig. 3.
1981. ?*Subprionotropis colombianus* Basse; Reyment, pl. 1, fig. 4.
1981. *Subprionotropis* sp. nov. Reyment, pl. 1, fig. 5.
1982. *Subprionotropis columbianus* Basse (*sic*); Renz, p. 106, pl. 35, figs 5–10; text-fig. 82a.
1996. *Subprionotropis colombianus* Basse, 1951; Wright, p. 186, text-fig. 141.2a, b.
2011. *Subprionotropis colombianus* Basse; Patarroyo, p. 80, pl. 3, figs 14–18.

TYPE: The holotype, by original designation, is MNHN. F. J14214, the original of Basse (1951, p. 250, pl. 11, fig. 8), from the Mutsicua region, Cucuta, Norte de Santandar Province, Colombia.

MATERIAL: UCMP C1721-1–10 and 24 additional

specimens. UCMP C14958, 11 specimens. UCMP C14596, one specimen. UCMP C1929, two specimens.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1721-3 c	35.8 (100)	11.6 (32.4)	18.0 (50.3)	0.64	7.0 (19.6)
UCMP C1721-5 c	48.7 (100)	14.8 (30.4)	23.3 (47.8)	0.63	9.5 (19.5)
UCMP C1721-1 c	50.0 (100)	(–)	25.7 (51.4)	–	9.6 (19.2)
UCMP C1721-7 ic	59.2 (100)	17.3 (29.2)	29.8 (50.3)	0.58	11.6 (19.6)

DESCRIPTION: Coiling is involute, the umbilicus small, comprising around 20% of the diameter, of moderate depth, with a flattened wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with intercostal whorl breadth to height ratios of 0.6 or less. The flanks are flattened and subparallel, the ventrolateral shoulders broadly rounded, the venter obtusely fastigiate. On phragmocones, between eight and ten primary ribs arise at the umbilical seam, strengthen across the umbilical wall, and develop into coarse umbilical bullae. These give rise to coarse ribs either singly or in pairs, straight and prorsiradiate to mid-flank, then flexing back and rectiradiate; additional single ribs intercalate to give a total of 10–12 ribs per half whorl at the ventrolateral shoulder, where all link to a coarse oblique ventrolateral clavus, linked in turn by a prorsiradiate rib to a strong siphonal clavus, the siphonal clavi linked by a siphonal ridge. Ornament of this type extends to the adapical part of the adult body chamber. Beyond this, the umbilical bullae are abruptly lost, as are the ventrolateral clavi. Flank ribs weaken (Pl. 11, Figs 12–20; Pl. 12, Fig. 11), to be replaced by flexuous prorsiradiate growth lines, lirae and riblets. A siphonal ridge persists in some, with minute clavi associated with the riblets. The whorl height of adult body chambers varies from 15 to over 30 mm, and one adult phragmocone (UCMP C1721-1, Pl. 10, Figs 13, 14) is septate to 50 mm diameter. This wide range of adult diameters may indicate size dimorphism, but there are too few adults to confirm this. The suture is moderately incised, with a broad, asymmetrically bifid E/A and incipiently trifid, narrow A.

DISCUSSION: Small adult size and the loss of all but the feeblest ornament on the adapertural parts of the adult body chamber distinguish *Subprionotropis colombianus* from all other Collignoniceratine and Barroisiceratinae in the present faunas.

OCCURRENCE: Upper Turonian, based on co-occurrence with *Prionocycloceras guayabanum* in the present collections, central Colombia and Venezuela.

Genus *Prionocycloceras* Spath, 1926
(= *Donjuaniceras* Basse, 1951)

TYPE SPECIES: *Prionocyclus guayabanus* Gerhardt, 1897b, p. 197, pl. 5, fig. 22, text-fig. 19, by the original designation of Spath (1926, p. 80).

Prionocycloceras guayabanum (Gerhardt, 1897b)
(Pl. 7, Figs 1–10; Pl. 8, Figs 1–10; Pl. 9, Figs 1–4, 9–13; Pl. 10, Figs 1–5; Text-figs 3, 4)

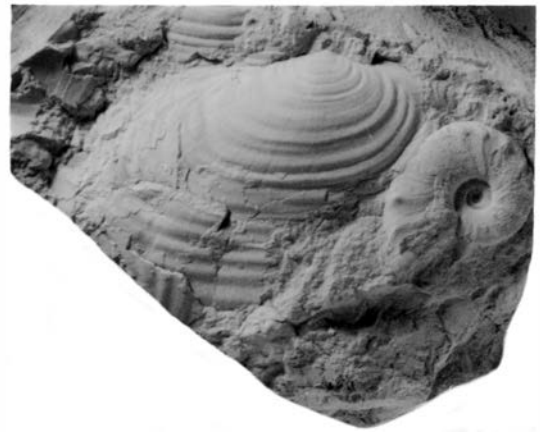
1897b. *Prionocyclus guayabanus* Gerhardt, p. 197, pl. 5, fig. 22; text-fig. 19.
1897b. *Prionocyclus mediotuberculatum* Gerhardt, p. 198, pl. 5, fig. 23.
1925. *Prionocyclus guayabanus* Gerhardt; Diener, p. 155.
1925. *Prionocycloceras mediotuberculatus* Gerhardt; Diener, p. 155.
1926. *Prionocycloceras guayabanum* (Gerhardt); Spath, p. 80.
1936. *Prionocycloceras* aff. *guyabanus* Steinmann; Besairie, p. 203, pl. 24, figs 19, 20.
1938. *Neophlycticeras* (?) *subtuberculatum* Gerh.; Riedel, p. 61, pl. 10, figs 1–3.
1951. *Donjuaniceras longispinata* Basse, p. 247, pl. 11, figs 1–4.
1951. *Donjuaniceras acutospinata* Basse, p. 247, pl. 11, figs 5, 6.
1952. *Prionocycloceras guayabanum* (Gerhardt); Basse, p. 664, pl. 24, fig. 12.
1957. *Prionocycloceras guyabanum* (Steinmann); Wright, p. *L*429, text-fig. 548.2.
1957. *Prionocycloceras* aff. *mediotuberculatum* (Gerhardt); Bürgl, p. 138, pl. 14, fig. 2.
1957. *Prionocycloceras* spec. nov.; Bürgl, p. 138, pl. 14, figs 3, 5.
1957. *Prionocycloceras mediotuberculatum* (Gerhardt); Bürgl, p. 138, pl. 14, fig. 4.
1963. *Prionocycloceras guayabanum* (Steinmann in Gerhardt, 1897); Young, p. 67, pl. 23, figs 5, 6; pl. 27, figs 2, 3; text-figs 12a, 14d, 33d.
1965. *Prionocycloceras* sp. aff. *P. guayabanum* (Steinmann); Matsumoto, p. 43, pl. 11, fig. 4; text-figs 19, 20.
1967. *Prionocycloceras guayabanum* Steinmann; Collignon, p. 48, pl. 29, figs 1–6.

non 1972. *Prionocycloceras guayabanum* (Steinmann in Gerhardt, 1897); Atabekian and Akopian, p. 4, pl. 1, figs 1–3.
1979. *Prionocycloceras longispinatum* (Basse); Etayo-Serna, p. 94, pl. 13, fig. 16; text-fig. 9s, t (with additional synonymy).
1979. *Prionoocycloceras portarum* Etayo-Serna, p. 95, pl. 13, fig. 12; pl. 14, fig. 4; text-fig. 9n.
1981. *Prionocycloceras guayabanum* (Steinmann); Reyment, pl. 1, fig. 6.
1981. *Prionocycloceras* cf. *mediotuberculatum* Gerhardt); Reyment, pl. 1, fig. 7.
1981. *Prionocycloceras* aff. *mediotuberculatum* (Gerhardt); Reyment, pl. 1, fig. 8.
1982. *Prionocycloceras guayabanum* (Steinmann); Renz, p. 107, pl. 35, figs 11–14.
1982. *Prionocycloceras mediotuberculatum* (Gerhardt); Renz, p. 108, pl. 40, figs 2, 7.
1982. *Prionocycloceras* sp. indet. Renz, p. 108, pl. 34, fig. 7.
1996. *Prionocyclus guayabanum* (Gerhardt); Wright, p. 187, text-fig. 142.2.
2011. *Prionocycloceras guayabanum* (Steinmann in Gerhardt); Patarroyo, p. 79, pl. 3, figs 3–7.
2011. *Prionocycloceras* sp.; Patarroyo, p. 79, pl. 3, figs 1, 2.

NAME Of THE SPECIES: *Prionocyclus guayabanus* and *Prionocyclus mediotuberculatus* of Gerhardt (1897b) are conspecific in my view, and as first revising author I select *guayabanus* as the name of the species.

TYPES: The lectotype of *Prionocyclus guayabanus*, by the subsequent designation of Matsumoto (1965, p. 43), is the original of Gerhardt (1897b, pl. 5, fig. 22), from the Rio Guayabo on the south-west side of the Cerro Pelado, Colombia. There are six paralectotypes; neither they nor the lectotype have been traced. The holotype, by monotypy of *Prionocyclus mediotuberculatu*s Gerhardt, 1897b, is the original of his pl. 5, fig. 23, from the same locality as the types of *guayabanus*. The holotype, by original designation, of *Donjuaniceras longispinata* Basse, 1951, p. 247, pl. 11, fig. 1, is MNHN. F. J14208, from la Donjuana in the Department of Norte de Santander, Colombia. The holotype, by original designation, of *Donjuaniceras acutospinata* Basse, 1951, p. 247, pl. 11, fig. 5, is MNHN. F. J14212, from Mutsicua in the Department of Norte de Santander, Colombia

MATERIAL: There are numerous specimens: UCMP C151; C1510-1–8, plus 24 additional specimens; C1618; C1618-3 to 6, plus 11 additional specimens; C2007-1–9 plus 20 additional specimens.



Text-fig. 3. *Prionocyclus guayabanum* (Gerhardt, 1897b) and *Didymotis* sp. UCMP C 2007-8. The figure is ×1.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1721-1 c	51.6 (100)	19.9 (38.6)	23.4 (45.3)	0.85	14.0 (27.1)
UCMP C1510-8 c	53.0 (100)	18.8 (35.5)	22.1 (41.7)	0.85	15.4 (29.0)
UCMP C2007-1 ic	67.8 (100)	– (–)	25.1 (37.0)	–	27.0 (39.8)
UCMP C2007-4 ic	78.2 (100)	25.0 (31.9)	33.0 (42.1)	0.76	24.0 (30.7)
UCMP C1618-5 ic	85.4 (100)	27.9 (32.7)	36.0 (42.2)	0.77	24.0 (28.1)

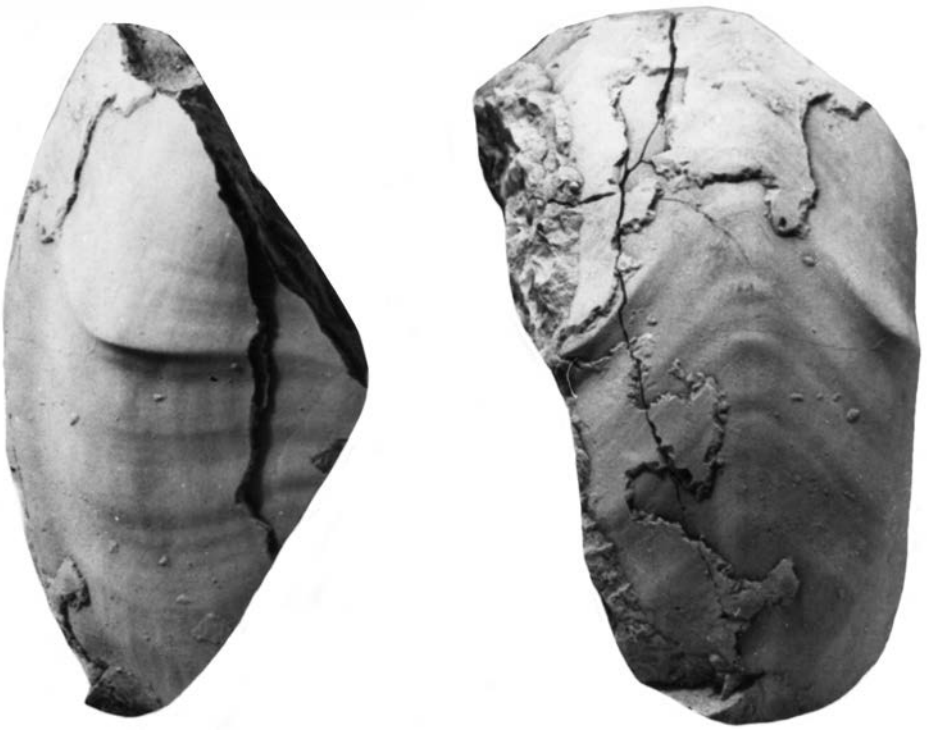
DESCRIPTION: There are both gracile and robust individuals. Juveniles such as UCMP C1510-2 and 3 (Pl. 7, Figs 3–6) are 27.6 and 25.2 mm in diameter, respectively. Costal whorl breadth to height ratios are as little as 0.7. There are eight primary ribs per half whorl. They arise at the umbilical seam, and are concave on the umbilical wall and shoulder, across which they strengthen, developing into the feeblest of concave bullae, or not. They are prorsiradiate on the inner flank, flexing back and convex at mid-flank, straight on the outer flank, where they link to delicate oblique ventrolateral clavi, from which a progressively weakening rib projects forwards to form an obtuse ventral chevron. There is a well-developed crenulate siphonal keel, the crenulations far more numerous than the ventrolateral tubercles. The surface of the replaced shell, where well-preserved

(Pl. 7, Fig. 5), is covered in delicate growth lines and ridges that parallel the ribs. The ontogeny is continued by specimens such as UCMP C1510-7 (Pl. 7, Figs 9, 10) and UCMP C1618-4 (Pl. 9, Fig. 10), 81 mm in diameter. The ribs are very widely spaced, with five in the adapertural 90º whorl sector. Umbilical bullae are small, but clearly differentiated. The ribs are low and broad, barely flexed compared with the previous specimens, broadening across the flanks and strengthened into a low outer flank bulla, and a strong outer ventrolateral clavus. UCMP C1510-1, 25 mm in diameter, is a juvenile of a more robust variant (Pl. 7, Figs 1, 2) with well-developed umbilical bullae. UCMP C2007-3 (Pl. 8, Fig. 5), 54 mm in diameter, continues the ontogeny. There are an estimated 14–15 primary ribs on the outer whorl that arise from well-developed umbilical bullae. UCMP C2007-1 (Pl. 8, Figs 1, 2) is a very evolute individual. On most of the outer whorl ribbing is as in the previous specimen, with well-developed umbilical bullae and ventrolateral clavi. In contrast, the penultimate whorl shows the ventrolateral tubercles to be in the form of long spines, a feature better shown by UCMP C792-1 (Pl. 10, Figs 4, 5). The adapertural 60º sector of the outer whorl shows an abrupt loss of flank ornament, with barely trace of the ventrolateral tuberculation, but a persistent crenulate siphonal keel. Taken together with the very evolute coiling, these features suggest the specimen to be adult. UCMP C1618-5 (Pl. 9, Figs 11–13) is the largest individual of this type, 106 mm in maximum preserved diameter. Ornament of the phragmocone and adapical 240º sector of the outer whorl is comparable to the previous specimens, but the adapical 120º sector, interpreted as body chamber, has three very widely space primary ribs, with massive ventrolateral horns.

UCMP C1510-6 (Pl. 7, Figs 12, 13), UCMP C2007-2 (Pl. 8, Figs 3, 4) and UCMP C2007-1 (Pl. 8, Figs 1, 2) are the most robust juveniles, with costal whorl breadth to height ratios of up to 1.2. There are eight coarse umbilical bullae per half whorl that give rise to coarse straight prorsiradiate ribs that link to coarse conical ventrolateral tubercles. UCMP C2007-2 (Pl. 8, Figs 3, 4) has short ventrolateral spines preserved on the penultimate whorl, housed in grooves in the umbilical wall of the succeeding whorl.

The development of adult features in the present material is distinctive. UCMP C2007-1 (Pl. 8, Figs 1, 2) shows an abrupt weakening and loss of flank ornament at 65 mm diameter, and UCMP C2007-4 (Pl. 8, Figs 6, 7) at 77 mm diameter. I take UCMP C1618-3 and C1510-4 to be incomplete body chamber fragments of this type. UCMP C1618-3 (Pl. 9, Figs 3, 4) is the better-preserved, an internal mould of a 120º sector with a maximum preserved whorl height of 32 mm and a whorl breadth to height ratio of 0.72. The umbilical wall is low, feebly convex, and outward-inclined. The umbilical shoulder is broadly rounded, the flanks very feebly convex, and subparallel. The ventrolateral shoulders are broadly rounded, and the venter very feebly convex, with a feeble siphonal ridge. At the adapical end of the fragment there is a feeble prorsiradiate flank rib that links to a weak ventrolateral tubercle. The flanks and ventrolateral shoulders of the remainder of the fragment are ornamented by feeble flexuous prorsiradiate growth lines and ridges, with a single minute ventrolateral bulla towards the adapertural end. The siphonal ridge bears feeble corrugations. There is a low, flexuous, prorsiradiate rib succeeded by a constriction at the adapertutral end of the fragment, possibly marking the adult aperture. UCMP C1510-4 (Pl. 7, Figs 7, 8) is worn, but preserves traces of two ventrolateral clavi. These specimens are interpreted as possible adult microconchs. UCMP C1618-5 (Pl. 9, Figs 10–12) is interpreted as a possible macroconch, with part of the adapical end of the body chamber. UCMP C1510-5 (Pl. 7, Fig. 11) is a 120º whorl sector of phragmocone with only one flank preserved and a maximum preserved whorl height of 45 mm, showing the same very widely separated ribs, with massive ventrolateral clavi. The largest body chamber fragments seen are very incomplete (UCMP C2004-7, Text-fig. 4; UCMP C1618-6), with whorl heights of up to 46 mm. Ornament on these short fragments is reduced, as with the presumed adult microconchs, the flank ornament weakened, and the ventrolateral tubercles transformed into concave crescentic ridges, the siphonal keel low and broad, with feeble undulations.

DISCUSSION: The variation seen in the large assemblages from single localities described here form the basis for most *Prionocycloceras* described from Colombia and Venezuela being regarded as synonyms of a variable *P. guayabanum*. Young (1963, pl. 23, figs 5, 6; pl. 27, figs 2, 3; text-figs 12a, 14a, 33d) illustrated even larger individuals than those in the present collections, with diameters of up to 220 mm, with widely separate ventrolateral horns as in UCMP C1618-5 (Pl. 9, Figs 10–12) and a final adapertural sector of body chamber with effaced ornament (Young 1963, pl. 27, fig. 3). Collignon (1967, pl. 29, figs 5, 6) described and illustrated material from the Tarfaya Basin (Morocco) that retained silicified shell, preserving massive ventrolateral spines.



Text-fig. 4. *Prionocyclus guayabanum* (Gerhardt, 1897b). UCMP C2004-7. The figures are ×1.

There are several species referred *Prionocycloceras* with comparable styles of ornament. *Prionocycloceras gaudryi* (Boule, Lemoine and Thévenin, 1907) (Boule *et al*., p. 16 (36), pl. 3 (10)), from the Montagne des Française, Madagascar has strong umbilical bullae on the penultimate whorl, and develops numerous strong ribs on the body chamber that are markedly concave on the outermost flank and ventrolateral shoulder, and periodically develop long ventrolateral spines. *Prionocycloceras keithyoungi* Collignon, 1967 (p. 49, pl. 30, figs 1–5) was differentiated on the basis of the presence of well-developed umbilical bullae on the early whorls that migrate out to a mid-flank position. *Prionocycloceras sigmoidale* Matsumoto, 1965 (p. 41, pl. 9, fig. 1; pl. 10, figs 1, 2; text-figs 17, 18) from Hokkaido, Japan, is based on rather slight material, with strong umbilical bullae, the flank ribs flexuous. *Prionocycloceras wrighti* Matsumoto, 1971 (p. 134, pl. 22, fig. 2; text-fig. 4) was differentiated from *P. guayabanum* on the basis of the presence of a feeble outer ventrolateral tubercle in addition to a strong inner ventrolateral spine.

The affinities of some of the other species referred to the genus is doubtful. *Prionocyclus carvaholi* Howarth, 1966 (p. 224, pl. 1, figs 8–11; pl. 2, figs 3–6) is a synonym of *Prionocyclus germari* (Reuss, 1845) according to Kennedy *et al.* (2001, p. 127). Matsumoto (1965, p. 41) thought the Texas species *Prionocycloceras hazzardi* (Young, 1963) (p. 71, pl. 24, fig. 4; pl. 25, figs 2, 3; pl. 26, figs 1, 2; pl. 27, fig. 4; pl. 34, fig. 2; pl. 39, fig. 3; text-figs 12f, 13b, d, 14g, 20h) and *P. gabrielense* Young, 1963 (p. 69, pl. 24, figs 1–3; pl. 29, fig. 5; pl. 67, fig. 1; text-fig. 21c) might be *Protexanites* Matsumoto, 1955. The type specimens of *Prionocycloceras maarfiaense* Sornay, 1957 (p. 191, pl. 16, figs 8, 11; text-fig. 1c) and *P.* (?) *recticostatum* Sornay, 1957 (p. 193, pl. 16, fig. 7; text-fig. 1d) are minute nuclei from Haute Medjerda, Constantine, Algeria, too small to make meaningful comparisons with the present material.

OCCURRENCE: Upper Turonian, based on co-occurrence with *Subprionocyclus branneri* in the present collection, together with *Didymotis* (Text-fig. 3) suggesting correlation with the *Didymotis* event in the *scupini* inoceramid zone of the United States Western Interior (Walaszczyk and Cobban 2000). An Upper Turonian horizon is supported by data in Patarroyo and Bengtson (2018, text-fig. 4), which

shows the species range to be below the occurrence of the Upper Turonian inoceramid *Mytiloides scupini.* The geographic distribution is central Colombia, Venezuela, Morocco, and Madagascar.

Subfamily Barroisiceratinae Basse, 1947

Genus *Barroisiceras* de Grossouvre, 1894

TYPE SPECIES: *Ammonites haberfellneri* Hauer, 1866, p. 2, pl. 1, figs 1–5, by the subsequent designation of Solger (1904, p. 163).

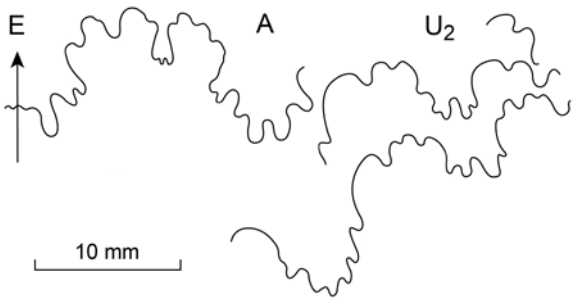
Barroisiceras habefellneri (Hauer, 1866)
(Pl. 13, Figs 3, 4; Text-fig. 5)

1866. *Ammonites Haberfellneri* Hauer, p. 2, pl. 1, figs 1–5.
1996. *Barroisiceras* (*Barroisiceras*) *haberfellneri* (Hauer, 1866); Summesberger and Kennedy, p. 121, pl. 3, figs 6, 7; pl. 5, figs 1–10, pl. 6, figs 1–5; pl. 7, figs 4–6; pl. 8, figs 1–8; pl. 9, figs 1–8; pl. 10, figs 1–11; pl. 11, figs 1–15; pl. 12, figs 1–6; pl. 13, figs 1–4; pl. 16, figs 1–16; text-figs 17, 18a–d, 19a–g, 20a–c, 21a–c, 22 (with full synonymy).
2012. *Barroisiceras* (*Barroisiceras*) *haberfellneri* (Hauer, 1866); Summesberger and Zorn, p. 103, pl. 4, fig. 3.

TYPE: The lectotype, by the subsequent designation of Reyment (1958, p. 46), is no. 3464 in the collections of the Geologischen Bundesanstalt, Vienna, and from the Upper Turonian of Gams, Austria. It has been frequently refigured, most recently by Summesberger and Zorn (2012, pl. 4, fig. 2). Summesberger and Kennedy (1996, p. 122) list previous depictions of the specimen.

MATERIAL: UCMP C1618-1 and 2.

DESCRIPTION: UCMP C1618-1 (Pl. 13, Figs 3, 4) is the better preserved of the two specimens, and consists of an internal mould of a 180º whorl sector 78 mm in diameter, the adapertural 60º body chamber. Approximation of the last few septa suggests the specimen to be part of an adult. Coiling is involute, the umbilicus comprising an estimated 16% of the diameter. The whorl section is compressed, with an estimated whorl breadth to height ratio of 0.6 to 0.7, the flanks feebly convex, convergent, the ventrolateral shoulders broadly rounded, the venter obtusely fastigiate. Six large blunt bullae perch on the umbilical shoulder, and give rise to pairs of ribs, with additional ribs intercalating. The ribs are low, and broaden progressively across the flanks, straight and prorsiradiate to mid-flank, then flexed back and linking to well-developed ventrolateral clavi. There are strong siphonal clavi, displaced adaperturally of the outer ventrolateral. The ribs efface on the short sector of body chamber that is preserved. The sutures are moderately incised, with a broad, bifid E/A, subtrifid A and broad, bifid A/U2 (Text-fig. 5).



Text-fig. 5. External sutures of *Barroisiceras haberfellneri* (Hauer, 1866). UCMP C1618-1.

DISCUSSION: See Summesberger and Kennedy (1996, p. 123 *et seq*.)

OCCURRENCE: Upper Turonian where well-dated (Summesberger and Kennedy 1996). The geographic distribution extends from Austria, to southern England, Armenia and central Colombia.

Barroisiceras sp.
(Pl. 14, Figs 4, 9)

MATERIAL: UCMP C2005-1.

DESCRIPTION: The specimen appears to be a body chamber that retains recrystallized shell on the figured side; the other side is worn away. The maximum preserved diameter is 87 mm. Coiling is involute, the umbilicus comprising an estimated 22% of the diameter approximately, deep, with a broadly rounded umbilical shoulder. The whorl section is compressed trapezoidal, with convergent, very feebly convex flanks, broadly rounded ventrolateral shoulders and a very feebly convex venter. Four massive umbilical bullae are present on the 240º well-preserved whorl sector. Very low, broad, straight ribs arise in pairs, and there is a single shorter, intercalated rib. All ribs link to well-developed ventrolateral clavi, elongated parallel to the mid-line of the venter, which is smooth.

DISCUSSION: The specimen is interpreted as an adult of an inflated *Barroisiceras*, of the group referred to *Basseoceras* Collignon, 1965, and comprehensively discussed by Matsumoto (1969, p. 303). It most closely resembles *Barroisiceras* [*Solgerites*] *tuberculatum* (Reyment, 1954b) (p. 267, pl. 2, text-fig. 11; 1955, p. 67, pl. 17, fig. 5), from the Coniacian of Nigeria.

OCCURRENCE: Central Colombia; Coniacian?.

Genus and subgenus *Forresteria* Reeside, 1932

TYPE SPECIES: *Barroisiceras* (*Forresteria*) *forresti* Reeside, 1932, p. 17, pl. 5, figs 2–7, by the subsequent designation of Wright (1957, p. *L*432) = *Acanthoceras* (*Prionotropis*) *alluaudi* Boule, Lemoine and Thévenin, 1907, p. 12 (32), pl. 1 (8), figs 6, 7; text-fig. 17.

Forresteria (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907)
(Pl. 14, Figs 1–3, 6, 7; Text-fig. 6)

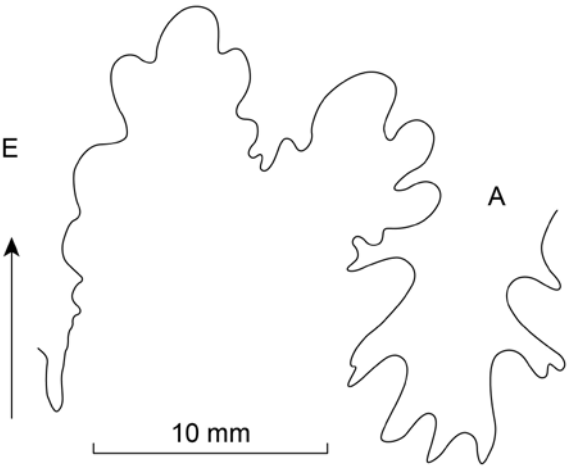
1907. *Acanthoceras* (*Prionotropis*) *alluaudi* Boule, Lemoine and Thévenin, p. 12 (32), pl. 1 (8), figs 6, 7; text-fig. 17.
1983. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907); Kennedy *et al*., p. 267, text-figs 5–9; 10a, b, e, f ; 11–14; 15a, b; 16–31; 33–34; 35c–e; 40d–e (with synonymy).
1984. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907); Kennedy, p. 46, pl. 8, figs 4–9.
1996. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907); Wright, p. 187, text-fig. 145.2.
2019. *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907); Ifrim *et al*., p. 178, text-figs 8a–h, 9 (with additional synonymy).

TYPE: The lectotype, by the subsequent designation of Kennedy *et al*. (1983, p. 268), is the original of Boule *et al*. (1907, p. 12 (32), pl. 1 (8), fig. 7; text-fig. 17), from the Sénonien supérieur of Mont-Carré, Madgascar.

MATERIAL: UCMP C1982-1, C2004-2.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C2004-2 c	45.9 (100)	18.2 (39.7)	19.0 (41.4)	0.96	15.6 (34.0)
UCMP C192-1 c at	75.3 (100)	34.4 (45.7)	34.0 (45.2)	1.0	19.3 (25.6)



Text-fig. 6. External suture of *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907). UCMP C192-4.

DESCRIPTION: UCMP C2004-4 (Pl. 14, Figs 6, 7) has a maximum preserved diameter of 44.6 mm. The umbilicus comprises 34% of the diameter, and is of moderate depth, the umbilical wall convex, the umbilical shoulder broadly rounded. The intercostal whorl section is compressed, with feebly convex inner flanks, flattened, convergent outer flanks, broadly rounded ventrolateral shoulders and a feebly convex venter with a marked siphonal ridge. The costal whorl section is only slightly compressed, the greatest breadth at the lateral tubercles, the cross section concave between the tubercles. Fifteen primary ribs arise at the umbilical seam, and strengthen into predominantly strong conical, subspinose umbilical tubercles, with a few much weaker. The bullae give rise to strong, coarse, prorsiradiate ribs that link to strong, conical, subspinose lateral tubercles. These give rise to a single rib or a pair of ribs, while additional ribs, lacking a lateral tubercle, intercalate to give a total of an estimated 24 ribs per whorl at the ventrolateral shoulder. All ribs bear coarse subspinose ventral clavi, from which a progressively weakening rib sweeps forwards to form an obtuse chevron with a strong siphonal clavus at the apex. UCMP C192–4 (Pl. 14, Figs 1–3) has a maximum preserved diameter of 84 mm, and is more involute than the previous specimen, with a costal whorl section that is as wide as high. Ornament is comparable, with 12 bullae at the umbilical shoulder and 21–22 ribs at the ventrolateral shoulder. The suture of this specimen is well-preserved (Text-fig. 6), with moderately incised

Text-fig. 7. *Forresteria* (*Forresteria*) *peruanum* (Brüggen, 1910). UCMP C2006-1. The figures are ×1.

elements; E/A is broad and bifid, as is A/U2, with A narrower and bifid.

DISCUSSION: See Kennedy *et al.* (1983, p. 75).

OCCURRENCE: Middle Coniacian *tridorsatum* Zone where well-dated. The geographic distribution extends from of Madagascar to northern KwaZulu–Natal in South Africa, Japan, the Unites States Western Interior, Mexico, Colombia, Peru, south-east France, northern Spain, the Czech Republic and, possibly, Israel.

Forresteria (*Forresteria*) *peruana* (Brüggen, 1910)
(Pl. 13, Figs 1, 2, 5–8; Pl. 14, Figs 5, 8; Text-fig. 7)

1910. *Gauthiericeras margae* var. *peruanum* Brüggen, p. 720, pl. 27, fig. 3.
1910. *Barroisiceras haberfellneri* v. Hauer; Brüggen, p. 730, text-fig. 10.

1918. *Schloenbachia* (*Gauthiericeras*) *margae* var. *peruana* Lüthy, p. 41, pl. 1, fig. 2.
1930. *Barroisiceras haberfellneri* Hauer; Steinmann, text-fig. 195a–c.
1956. *Barroisiceras* (*Forresteria*) *bassae* Benavides-Cáceres, p. 477, pl. 58, fig. 5.
1983. *Forresteria* (*Forresteria*) *peruanua* (Brüggen); Kennedy *et al*., p. 279.
1989. *Forresteria peruana* (Brüggen); Cobban and Hook, p. 254, text-fig. 10r, s.
1991. *Forresteria* (*Forresteria*) *peruana* (Brüggen, 1910); Kennedy and Cobban, p. 26, pl. 2, figs 1, 15–17; pl. 5, figs 1–11; text-fig. 4c, 6, 7.

TYPES: The lectotype, here designated, is the original of Brüggen (1910, p. 720, pl. 27, fig. 10), from Otuzco [Otusco], Otuzco Province, Peru. There are nine paralectotypes.

MATERIAL: UCMP 2004-1, 3, 4, and UCMP 2006-1.

DESCRIPTION: UCMP C2004-1 (Pl. 14, Fig. 5) is a compressed juvenile 29 mm in diameter. Eight closely spaced bullae per half whorl perch on the umbilical shoulder and give rise to straight prorsiradiate ribs that bear small lateral bullae. Additional ribs intercalate on the outer flank, and all ribs link to strong ventrolateral clavi from which a prorsiradiate rib sweeps forwards to form an obtuse chevron with a strong siphonal clavus at the apex. UCMP C2004-2 (Pl. 13, Figs 5, 6) is a larger individual, complete to a diameter of 58 mm, with part of a further 90º whorl sector. Coiling is involute, the shallow umbilicus comprising 20% approximately of the diameter. The umbilical wall is low, with a narrowly rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.68, the greatest breadth around mid-flank. The flanks are subparallel, the ventrolateral shoulders broadly rounded, the venter very feebly convex in intercostal section. Tiny bullae, 7–8 per half whorl, perch on the umbilical shoulder. They give rise to delicate straight prorsiradiate ribs, either singly or in pairs, with additional ribs intercalating. All ribs link to small oblique ventrolateral clavi that give rise to progressively weakening prorsiradiate ribs that form an obtuse ventral chevron, with a well-developed siphonal clavus at the apex. Lateral bullae only appear on the adapertural fragmentary part of the outer whorl. The specimen corresponds in this respect with the original of Kennedy and Cobban (1991, pl. 5, figs 5 and 6). UCMP C2005-2 (Pl. 13, Figs 7, 8) is 63 mm in diameter, with tiny umbilical bullae and well-developed ventrolateral and siphonal clavi; the worn flanks are near-smooth. UCMP C2004-3 is a comparable worn individual 101 mm in diameter. UCMP C2004-1 (Pl. 14, Fig. 8) is a phragmocone 125 mm in diameter, with all of one flank worn away. The whorl section is compressed, with an estimated whorl breadth to height ratio of 0.8 approximately, the inner to mid-flank region feebly convex, the outer flank flattened and convergent, the ventrolateral shoulder broadly rounded. Eight blunt bullae of variable strength perch on the umbilical shoulder of the adapertural half whorl and give rise to low ribs that broaden and strengthen across the flanks, while additional short ribs intercalate to give 10 ribs on the ventrolateral shoulder of the adapertural half whorl. The primary ribs bear large low, blunt, rounded mid-lateral bullae, and all ribs bear coarse ventrolateral clavi. UCMP C2006-1 (Text-fig. 7) is a 120º sector of body chamber derived from a much larger individual with a maximum preserved whorl height of 93 mm. The umbilical bullae weaken progressively, as does the flank ornament, the lateral bullae are lost, but coarse ventrolateral and siphonal clavi persist.

DISCUSSION: See Kennedy *et al.* (1983, p. 279) and Kennedy and Cobban (1991, p. 28).

OCCURRENCE: Upper Upper Turonian. The species is only well dated in the United States Western Interior, where it occurs in the *M. scupini* inoceramid zone, below the first occurrence of *Cremnoceramus deformis erectus* (see discussion in Walaszczyk and Cobban 2000, p. 5). The geographic distribution extends from Peru to central Colombia, Colorado, Wyoming and New Mexico in the United States.

Genus *Niceforoceras* Basse, 1948

TYPE SPECIES: *Nicephoroceras columbianus* Basse, 1948, p. 694, pl. 25, fig. 2, by the original designation of Basse (1948, p. 694).

Niceforoceras columbianus Basse, 1948
(Pl. 10, Figs 6, 7, 11, 12; Pl. 11, Figs 21, 22; Pl. 12, Figs 9, 10, 12, 13)

1948. *Niceforoceras columbianus* Basse, 1948, p. 694, pl. 25, fig. 2.
1948. *Niceforoceras umbulaziforme* and var. *spathi* Basse, p. 695, pl. 25, figs 3–5.
1957. *Niceforoceras umbulaziforme* Basse; Wright, p. *L*427, text-fig. 547.4.

1979. *Niceforoceras bayacaense* Etayo-Serna, p. 92, pl. 14, fig. 7.
?1981. *Niceforoceras* aff. *umbulaziforme* Basse; Reyment, pl. 1, fig. 3.
1982. *Niceforoceras umbulaziforme* Basse; Renz, p. 68, pl. 21, fig. 2.
1996. *Niceforoceras umbulaziforme* Basse; Wright, p. 187, text-fig. 143.3.

NAME OF THE SPECIES: I regard *Niceforoceras columbianus* and *Niceforoceras umbulaziforme* of Basse (1948), published simultaneously, as conspecific, and as first revising author, select *columbianus* as the name of the species.

TYPE: The holotype, by monotypy, is the original of Basse (1948, pl. 25, fig. 2), from Mustica, 70 km SSW of Cucuta, Department of Norte de Santander, Colombia.

MATERIAL: UCMP C1721-1 to 17.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1721-16	39.9 (100)	9.8 (24.6)	22.8 (58.8)	0.43	6.3 (15.8)
UCMP C1721-17	44.9 (100)	9.4 (20.9)	23.4 (52.1)	0.40	6.4 (14.2)
UCMP C1721-12	61.6 (100)	13.2 (21.4)	31.0 (50.3)	0.43	11.0 (19.9).

DESCRIPTION: Coiling is very involute, the umbilicus comprising around 14–15% of the diameter on phragmocones, shallow, with a low wall and narrowly rounded umbilical shoulder. The whorl section is very compressed, with whorl breadth to height ratios varying around 40–43% of the diameter. The flanks are flattened and subparallel, the venter narrowly fastigiate, and concave between the ventrolateral tubercles and the line of the mid-venter. Ornament consists of crowded ribs, up to 24 per half whorl. They arise from tiny umbilical bullae, either singly or in pairs, with some bifurcating and additional ribs intercalating. The ribs are straight and prorsiradiate on the inner flank, flexing back at mid-flank, and feebly concave on the outer flank. All link to small conical to obliquely clavate ventrolateral tubercles, from which a low rib sweeps forwards towards the crenulate siphonal keel. Where the shell surface is well-preserved (Pl. 12, Figs 9, 11, 13), the surface is seen to be covered in delicate lirae, growth lines and striae that parallel the ribs. UCMP C1721-11 (Pl. 10, Figs 6, 7) and UCMP C1721-12 (Pl. 10, Figs 11, 12) are adults. The umbilical diameter increases to 20% in the latter. Flank ornament weakens progressively, and in UCMP C1721-11, the final 60% sector has lost the ventrolateral tubercles, the flanks ornamented by crowded flexuous delicate riblets, convex at mid-flank, concave on the outer flank, and projected strongly forwards on the ventrolateral shoulder. The siphonal ridge is minutely crenulate. The suture is little incised, with a broad, bifid E/A and narrow, subtrifid A.

DISCUSSION: The present material, from a single locality, spans the range of morphologies represented by all species previously assigned to *Niceforoceras*. Renz (1984, p. 68) assigned the genus to the family Schloenbachiidae, and regarded it as Cenomanian in age. Basse (1948, p. 695) noted that the type specimen came from a locality with outcrops dated as Barremian to Cenomanian and Coniacian, and that the same locality had yielded two specimens of *Paralenticeras sieversi* (Gerhardt, 1897a). Etayo-Serna (1979) and Wright (1996) regard the genus as Coniacian.

Niceforoceras (?) *japonicum* Matsumoto, 1955 (p. 71, pl. 11, fig. 1; text-fig. 40) appears to belong to some different genus; it has well-developed umbilical bullae, lacks ventrolateral tubercles, and has an entire siphonal keel, without crenulations. *Niceforoceras* sp., described below, has smooth inner flanks on the early phragmocone whorls, the later phragmocone whorls with well-developed umbilical bullae in some individuals and falcoid ribs that arise singly or in pairs from the bullae and intercalate, strengthen markedly on the outer flank, where they link to weak ventrolateral clavi, the keel bearing stronger clavi.

OCCURRENCE: Upper Upper Turonian, based on co-occurrence with *Prionocycloceras guayabanum*, central Colombia and Venezuela.

Niceforoceras sp.
(Pl. 12, Figs 1–8)

MATERIAL: UCMP C1510-10 to 15, plus 24 further specimens.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1510-11	16.0 (100)	4.7 (29.4)	7.8 (48.8)	0.6	3.9 (24.4)
UCMP C1510-14	17.4 (100)	– (–)	7.5 (43.1)	–	4.6 (26.4)
UCMP C1510-13	18.7 (100)	5.4 (28.9)	9.5 (48.1)	0.57	5.2 (27.8)

DESCRIPTION: Coiling is very involute, the umbilicus shallow, with a low, flattened wall and broadly rounded umbilical shoulder on the phragmocone. The whorl section is compressed, with flattened subparallel flanks, broadly rounded ventrolateral shoulders, the venter fastigiate, with a siphonal keel. The flanks of the inner whorls and the adapical part of the outer phragmocone whorl are near-smooth, but for traces of delicate riblets; these strengthen on the outermost flank and ventrolateral shoulder, flex forwards, and strengthen further into prorsiradiate ventrolateral clavi, linked by a prorsiradiate rib to an adaperturally displaced siphonal clavus, borne on the siphonal keel. On the adapertural part of the phragmocone and adapical part of the body chamber, primary ribs arise at the umbilical seam and strengthen across the wall and shoulder, where small bullae develop in some specimens (Pl. 12, Fig. 3). Ribs arise singly or in pairs at the umbilical shoulder or bulla, with additional ribs intercalating. The ribs strengthen and broaden across the flanks. They are straight and prorsiradiate on the inner flank, flex back at mid-flank, coarsen, are feebly concave on the outer flank, and link to small ventrolateral clavi, linked by a prorsiradiate rib to stronger siphonal clavi. UCMP C1510-11 to 15 all retain body chamber, and some, such as UCMP C1510-14 (Pl. 12, Fig. 7) show a weakening of flank ornament, perhaps indicating maturity and proximity to the adult aperture. The very poorly preserved sutures appear to have been relatively simple.

DISCUSSION: Differences from *Niceforoceras columbianus* are discussed above under that species.

OCCURRENCE: Upper Upper Turonian, based on co-occurrence with *Prionocycloceras guayabanum*, central Colombia

Subfamily Peroniceratinae Hyatt, 1900

Genus and subgenus *Peroniceras* de Grossouvre, 1894

TYPE SPECIES: *Peroniceras moureti* de Grossouvre, 1894, p. 100, pl. 11, fig. 4, by original designation (= *Ammonites tridorsatus* Schlüter, 1867, p. 26, pl. 5, fig. 1).

Peroniceras (*Peroniceras*) *tridorsatum* (Schlüter, 1867)

(Pl. 15, Figs 1–5; Pl. 16, Fig. 4; Text-fig. 8)

1867. *Ammonites tridorsatus* Schlüter, 1867, p. 26, pl. 5, fig. 1.

1984. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867); Klinger and Kennedy, p. 139, figs 3–15, 16d, e (with full synonymy).

1994. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867); Kaplan and Kennedy, p. 45, pl. 14, figs 4, 5; pl. 5, figs 18, 19; pl. 20, figs 2, 3, 6, 8; pl. 21, figs 1–5; pl. 22, figs 2, 3; pl. 28, figs 1, 3, 4 (with additional synonymy).

2011. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867); Ifrim *et al*., p. 526, text-fig. 4.1–4.3.

2019. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867); Ifrim *et al*., p. 172, text-fig. 5a.

TYPE: The holotype, the original of Schlüter (1867, p. 26, pl. 5, fig. 1), from the Coniacian of Westphalia, is lost.

MATERIAL: UCMP C192-1 and 2 and 8 fragments that may belong here; UCMP C363-1 and 2; UCMP C739-1.

DESCRIPTION: UCMP C192-2 (Pl. 15, Figs 3, 4) is an internal mould of a 90º sector of three successive whorls, the outermost body chamber, with a maximum preserved whorl height of 39 mm. Coiling is very evolute, the umbilicus broad and shallow, with a feebly convex, outward-inclined umbilical wall, the umbilical shoulder broadly rounded. The whorl section is as wide as high, the flanks feebly convex, subparallel, the ventrolateral shoulders broadly rounded, the venter with three strong, narrow keels separated by slightly wider grooves. The inner two whorls are ornamented by crowded coarse, straight, prorsiradiate primary ribs that arise at the umbilical seam. On the outer whorl, the ribs coarsen, and are more widely spaced. The umbilical wall is smooth. Feeble bullae develop on the umbilical shoulder, and give rise to single prorsiradiate ribs that link to well-developed ventrolateral clavi, from which a rib sweeps forwards, weakens, and effaces before reaching the outer of the siphonal keels. There are faint traces of delicate spiral ridges There are nine ribs on the outer whorl fragment, and 13–14 on the corresponding sector of the penultimate whorl. UCMP C192-1 (Pl. 16, Fig. 4) is an external mould of parts of five successive whorls and has even ribbing throughout. UCMP C363-1 (Pl. 15, Figs 1, 2) is a partially crushed fragment of two successive whorls. The outer has a maximum preserved whorl height of 39 mm and retains recrystallized shell with well-preserved, strong growth lines. The ventrolateral clavi are relatively

Text-fig. 8. *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867). UCMP C739-1. The figures are ×1.

sharp in some cases. The ribbing on the penultimate whorl is coarser, and that on the outer whorl finer than in the previous specimen. UCMP C363-2 (Pl. 15, Fig. 5) a fragment of comparable size, is very crushed, and has a rib density intermediate between that of the previous specimens. UCMP C739-1 (Text-fig. 8) is a much larger body chamber fragment, with a maximum preserved whorl height of 68 mm. The ribs are narrow, widely separated, and prorsiradiate. The ventral keels are weakened and effacing. It is interpreted as part of an adult shell.

DISCUSSION: See Klinger and Kennedy (1984, p. 145) and Kaplan and Kennedy (1994, p. 46).

OCCURRENCE: Middle Coniacian, index of the eponymous zone. The geographic distribution extends from Germany to south-eastern France, northern

Spain, Italy, Poland, Romania, North Africa, northern KwaZulu–Natal in South Africa, Madagascar, Texas and New Mexico in the United States, northern Coahuila, Mexico, and central Colombia.

Peroniceras (*Peroniceras*) sp. juv. cf. *tridorsatum* (Schlüter, 1867)
(Pl. 13, Figs 9, 10)

MATERIAL: UCMP C1911-1.

DESCRIPTION: UCMP C1911-1 (Pl. 13, Figs 9, 10; figured × 2) is a whorl fragment with a maximum preserved whorl height of 11 mm. The whorl section is compressed, with a whorl breadth to height ratio of 0.8. The flanks are flattened and subparallel, with broadly rounded ventrolateral shoulders and a tricarinate venter. There are parts of five ribs preserved on the figured side. They arise singly or in one case in a pair from small umbilical bullae, are straight and prorsiradiate, apart from the adapical of the paired ribs, which is feebly rursiradiate. All ribs link to conical ventrolateral tubercles that give rise to a rapidly effacing prorsiradiate rib.

DISCUSSION: Although only a fragment, the presence of a paired rib recalls the distinctive ornament of *P.* (*P.*) *tridorsatum*.

OCCURRENCE: As for material.

Peroniceras (*Peroniceras*) *diabloi* Etayo-Serna, 1979
(Pl. 13, Figs 11, 12)

1979. *Peroniceras diabloi* Etayo-Serna, p. 93, pl. 14, fig. 1; text-fig. 9e, f, g.

TYPE: The holotype, by original designation, is the original of Etayo-Serna (1979, p. 93, pl. 14, fig. 1; text-fig. 9e, f, g), from the Coniacian Cucaita Member of the Coineja Formation at the type locality, the Alto del Conejo on the Oicatá-Chivata road, 9 km northeast of Tunja in the Province of Boyacá.

MATERIAL: UCMP C1999-1.

DESCRIPTION: The specimen (Pl. 13, Figs 11, 12) is a fragment with a maximum preserved whorl height of 28 mm. The whorl section appears to have been rectangular, with flattened, subparallel flanks, and broadly rounded ventrolateral shoulders. The venter is damaged. There are parts of nine ribs on the fragment. Most are very coarse primaries that arise singly at the umbilical seam, sweep back and strengthen across the umbilical wall, and strengthen into coarse umbilical bullae. These give rise to coarse, low, feebly prorsiradiate, crowded primary ribs that are concave on the outer flank, and link to coarse ventrolateral clavi that give rise to coarse prorsiradiate ribs on the ventrolateral shoulder. Towards the adapertural end of the fragment, a pair of ribs arise from a single umbilical bulla.

DISCUSSION: The fragment has the same coarse ornament as that of the much smaller holotype of *P.* (*P.*) *diaboloi*, and this coarseness distinguishes the specimen from those assigned to *P.* (*P.*) *tridorsatum* in the present collection.

OCCURRENCE: Coniacian of Central Colombia.

Genus *Gauthiericera*s de Grossouvre, 1894

TYPE SPECIES: *Ammonites margae* Schlüter, 1867, p. 29, pl. 25, fig. 2, by the original designation of de Grossouvre (1894, p. 87).

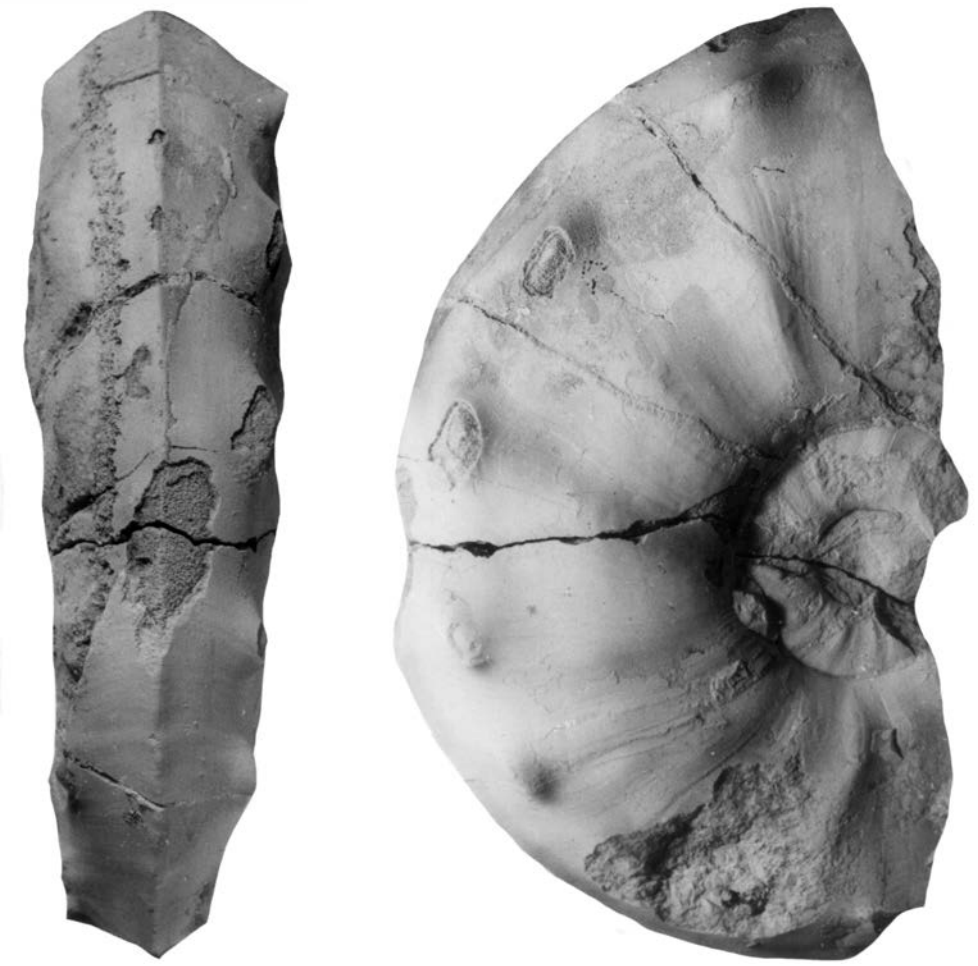
Gauthiericeras margae (Schlüter, 1867)
(Text-fig. 9)

1867. *Ammonites margae* Schlüter, p. 29, pl. 5, fig. 2.
1984. *Gauthiericeras margae* (Schlüter, 1867); Kennedy, p. 88, pl. 18; pl. 20, figs 3, 4, 8–10; pl. 21, figs 1, 5; pl. 22, figs 13–17; text-figs 27, 28, 29a, b, 31 (with full synonymy).
1994. *Gauthiericeras margae* (Schlüter, 1867); Kaplan and Kennedy, p. 44, pls 10–13, pl. 14, figs 1, 6, ?2, 3; pls 15–17; pl. 28, fig. 2 (with additional synonymy).
1996. *Gauthiericeras margae* (Schlüter, 1867); Wright, p. 191, text-fig. 147. 2a–c.
2000. *Gauthiericeras margae* (Schlüter); Wiese, pl. 4, fig. 2.

TYPE: The holotype, by monotypy, is no. 25 in the Schlüter collection, housed in the Paläontologisches Institut der Rheinischen Friedrich-Wilhelms-Universität, Bonn, Germany, the original of Schlüter (1867, p. 29, pl. 5, fig. 2), from the Emscher-Mergel of the Schacht von der Heydt, Herne, Westphalia, Germany. It was refigured by Kennedy (1984, text-fig. 28) and Kaplan and Kennedy (1994, pls 11, 12).

MATERIAL: UCMP C192-3 and UCMP C363-3.

DESCRIPTION: UCMP C 192-3 (Text-fig. 9) is an incomplete individual, a 300º outer whorl fragment,



Text-fig. 9. *Gauthiericeras margae* (Schlüter, 1867). UCMP C192-3. The figures are ×1.

with part only of the preceding whorls. Only the better-preserved adapical 180º whorl sector is figured. It retains extensive areas of recrystallized shell. The sutures are not visible, but the adapertural 240º appears to be body chamber. The maximum preserved diameter is 160 mm. Coiling is evolute, the umbilicus comprising 27% of the diameter, shallow, with a low wall, the umbilical shoulder very feebly convex. The intercostal whorl section is compressed oval, the flanks feebly convex, the ventrolateral shoulders broadly rounded, the venter fastigiate, with a sharp siphonal keel. The greatest breadth is around mid-flank, the whorl breadth to height ratio 0.63. There are nine ribs per half whorl. All but one are primaries, arising on the umbilical wall, and strengthening across the umbilical shoulder without developing into a bulla. They are low, broad, straight and prorsiradiate across the flanks, and strengthen into a low, broad, feeble mid-lateral bulla, from which a broad rib links to strong, spirally elongated ventrolateral bullae. There are shallow depressions on either side of the siphonal keel. This shows traces of minute crenulations in places. The surface of the replaced shell is ornamented by crowded growth lines. UCMP C363-3 (not figured) is a comparable, if worn 90° whorl fragment with a maximum preserved whorl height of 56 mm.

DISCUSSION: The ornament of UCMP C192-3 is identical to that of the holotype at the same diameter. See Kennedy (1984, p. 93) for a review of differences from other species referred to the genus.

OCCURRENCE: Index of the lower Upper Coniacian

margae Zone of Western Europe, with records from France, Germany, Austria, the Czech Republic, Spain, Romania, Colombia, Montana in the United States Western Interior and, possibly, Tunisia.

Subfamily Texanitinae Collignon, 1948

Genus and subgenus *Protexanites* Matsumoto, 1955

TYPE SPECIES: *Ammonites bourgeoisianus* d'Orbigny, 1850, p. 212, by the original designation of Matsumoto (1955, p. 38).

Protexanites (*Protexanites*) cf. *canaense*
(Gerhardt, 1897a)
(Pl. 16, Figs 1–3)

1897a. *Mortoniceras canaense* Gerhardt, p. 73, pl. 1, fig. 2; text-fig. 4.
1897a. *Mortoniceras canaense* var. *oblique-costata* Gerhardt, p. 76, text-fig. 2a.
1925. *Mortoniceras canaense* Gerhardt; Diener, p. 145.

TYPE: The lectotype, here designated, is the original of Gerhardt (1897a, p. 73, pl. 1, fig. 2), from Táchira, between Caña and Amarillo, near Rubio in Táchira State, Venezuela. It has not been traced.

MATERIAL: UCMP C772-1.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C772-1 at	76.9 (100)	27.7 (36.0)	30.9 (40.2)	0.9	29.6 (38.5)

DESCRIPTION: The specimen has an estimated maximum preserved diameter of 103 mm and there are indications of a further 120º whorl sector, now lost. Coiling is evolute, the umbilicus comprising 29.6% of the diameter, shallow, with a feebly convex outward inclined wall and rounded umbilical shoulder. The whorl section is compressed, with a whorl breadth to height ratio of 0.9. The flanks are flattened and subparallel, the ventrolateral shoulders broadly rounded, the venter tricarinate. The ornament is well-preserved to a diameter of 77 mm on one flank (Pl. 16, Fig. 3). Twenty four primary ribs per whorl arise at the umbilical seam, strengthen across the umbilical wall and shoulder and develop into small umbilical bullae, sharp where shell material is preserved. These give rise to single straight, feebly prorsiradiate relatively weak ribs that link to small, sharp, conical ventrolateral tubercles, from which a wedge-shaped rib extends to the outer ventral keel. This is markedly undulose, the undulations more numerous than the ventrolateral tubercles. The median keel is also undulose, but less markedly so than the lateral. The opposite, less well-preserved side (Pl. 16, Fig. 1) of the specimen shows a coarsening of the ribs, which become more widely separated. In some cases, the ribs develop a median groove, such that a pair of riblets loop between umbilical and ventral tubercles.

DISCUSSION: Rib density, style and tuberculation match that of the lectotype, as does the development of undulations on the keels. *Peroniceras* aff. *canaense* (Gerhardt) of Renz (1982, p. 109, pl. 35, figs 16, 17) is indeed a *Peroniceras*, and does not have undulose keels. In contrast, his *Andersonites* cf. *listeri* van Hoepen (Renz 1982, p. 108, text-fig. 83) has looped ribs and undulose lateral keels and may be an ally of the present species.

OCCURRENCE: Upper Coniacian? of Central Colombia. There is no dateable associated fauna with the present specimen.

Family Coilopoceratidae Hyatt, 1903

Genus *Hoplitoides* von Koenen, 1898

TYPE SPECIES: *Hoplitoides latesellatus* von Koenen, 1898, p. 56, pl. 6, figs 1–3, by original designation (= *Neoptychites*? *ingens* von Koenen, 1897, p. 12, pl. 1, fig. 4; pl. 2, figs 5, 8).

Hoplitoides ingens (von Koenen, 1897)
(Pl. 4, Figs 12, 13; Pl. 5, Figs 1–5; Pl. 6, Figs 1, 4)

1897. *Neoptychites* ? *ingens* von Koenen, p. 12, pl. 1, fig. 4; pl. 2, figs 5, 8.
1898. *Hoplitoides latesellatus* von Koenen, p. 56, pl. 6, figs 1–3.
1955. *Hoplitoides ingens* (von Koenen) and subspecies; Reyment, p. 79, pl. 18, figs 2, 4; pl. 19, fig. 2; pl. 20, figs 1–3; text-fig. 38 (with synonymy).
1981. *Hoplitoides ingens* (von Koenen)?; Reyment, pl. 2, fig. 3.
1987. *Hoplitoides ingens* (von Koenen); Zaborski, pp. 53, 54, 59.
1990. *Hoplitoides ingens* (von Koenen); Zaborski, text-figs 26, 27.

1994. *Hoplitoides ingens* (von Koenen, 1897); Chancellor *et al*., p. 106, pl. 30, figs 3–6.
?2005. *Hoplitoides* aff. *ingens* (von Koenen, 1897); Meister and Abdallah, p. 141.
2011. *Hoplitoides ingens* (von Koenen); Patarroyo, p. 76, pl. 2, fig. 9.

TYPES: Von Koenen (1897, p. 12) based the present species on three syntypes from Cameroon.

MATERIAL: UCMP C1998-3, 4, 5, 6, 7; UCMP C1223-1.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
UCMP C1998-4 at	75.0 (100)	17.7 (23.6)	43.9 (58.5)	0.40	4.0 (5.3)
UCMP C1998-3	92.0 (100)	– (–)	52.7 (57.3)	–	5.0 (5.4)

DESCRIPTION: Specimens range from 29 to 92 mm in diameter, with a body chamber fragment with a whorl height of 80 mm (Pl. 5, Figs 5, 6). Coiling is oxycone, with a minute umbilicus comprising around 5% of the diameter. The whorl breadth to heigh ratio is around 0.4, the greatest breadth well below mid-flank, the inner and mid-flank region convex, the outer flanks concave. The smallest specimen (Pl. 6, Fig. 4) has ornament only partially preserved at a whorl height of 10–12 mm. Primary ribs arise at the umbilical seam and are concave across the umbilical shoulder and innermost flank, sweeping forwards and bifurcating, convex at mid-flank and concave on the outer flank, where they strengthen into a distinctive crescentic element that projects forwards and declines towards the sharp venter. UCMP C1998-4 (Pl. 4, Figs 12, 13; Pl. 5, Fig. 2) has a maximum preserved diameter of 75 mm. Delicate primary ribs arise at the umbilical seam, and are feebly concave on the umbilical shoulder, straight and prorsiradiate to mid-flank, broadening progressively, flexing back and convex at mid-flank, then strengthening markedly before flexing forwards, broadening further, and concave on the outer flank. Additional ribs intercalate both low and high on the flank. The shell surface is covered in delicate growth lines and ridges that parallel the ribs. UCMP C1998-3 (Pl. 5, Fig. 1) has a comparable style of ornament, with delicate crowded flexuous ribs that are strengthened on the outer flank. UCMP C1998-6 (Pl. 5, Fig. 4) has in contrast, broader, coarser ribs. The largest fragment of body chamber, UCMP C1998-5 (Pl. 5, Figs 5, 6) shows the progressive decline of ribbing, presumably an indication of maturity, leaving the adapertural part of the fragment ornamented by growth lines and ridges only.

None of the specimens shows the sutures.

DISCUSSION: Reyment (1955 p. 79, pl. 18, figs 2, 4; pl. 19, fig. 2; pl. 20, figs 1–3; text-fig. 38) recognized three subspecies within *koeneni*, which are regarded here as intraspecific variants. Among the present specimens are individuals corresponding to *ingens costatus* Solger, 1904 (pl. 5, fig. 9; Reyment 1955, pl. 20, fig. 2; text-fig. 38d, e, g, i): Pl. 5, Fig. 4 herein; *ingens laevis* Solger, 1904 (pl. 5, fig. 10; Reyment 1955, pl. 18, fig. 2; pl. 19, fig. 2; pl. 20, fig. 3; text-figs 38f, h): Pl. 5, Fig. 1 herein, as well as what Reyment referred to as *ingens ingens* .

OCCURRENCE: Upper Lower or Lower Middle Turonian on the basis of records from the Dukul Formation in Nigeria (Zaborski 1990, p. 11); the species also occurs in Cameroon, Algeria, Tunisia, and central Colombia.

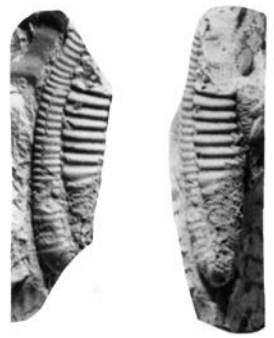
Suborder Ancyloceratina Wiedmann, 1966
Superfamily Turrilitoidea Gill, 1871
Family Hamitidae Gill, 1871

Genus *Metaptychoceras* Spath, 1926

TYPE SPECIES: *Ptychoceras smithi* Woods, 1896, p. 74, pl. 2, fig 1, by the original designation of Spath (1926, p. 80).

Metaptychoceras crassum Kennedy, 1988
(Text-fig. 10)

1988. *Metaptychoceras crassum* Kennedy, p. 98, pl. 21, figs 11, 12, 16–18, 21–24 (with synonymy).



Text-fig. 10. *Metaptychoceras crassum* Kennedy, 1988. UCMP C1721-2. The figures are ×2.

MATERIAL: UCMP C1721-22.

DESCRIPTION: The specimen consists of two closely adpressed shafts; the maximum preserved length is 17 mm. The penultimate shaft is slightly curved, and ornamented by regular, close-spaced transverse ribs. The final shaft is straight, the rounded ribs coarse and transverse, with a rib index of four. They pass straight across the venter.

DISCUSSION: See Kennedy (1988, p. 98).

OCCURRENCE: Upper Turonian *Prionocyclus hyatti* Zone, Texas; central Colombia.

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PLATE 1

1-3 – *Reymenticoceras* sp., UCMP C1510-16.

4-9 – *Reymenticoceras ornatum* sp. nov. 4, 5 – UCMP C1721-18, the holotype; 6, 7 – paratype UCMP C1721-19; 8, 9 – paratype UCMP C1727-20.

Figures are × 1

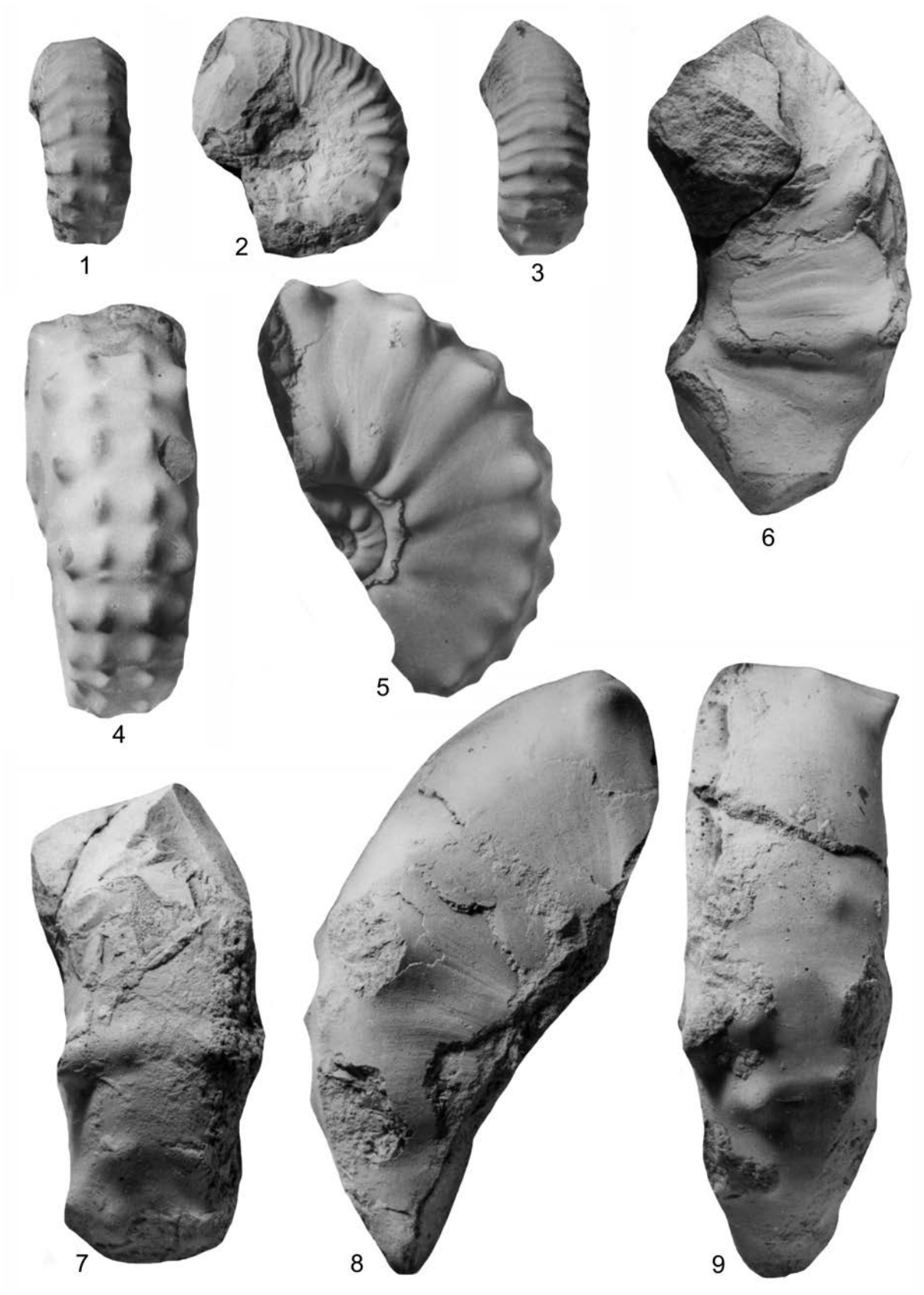
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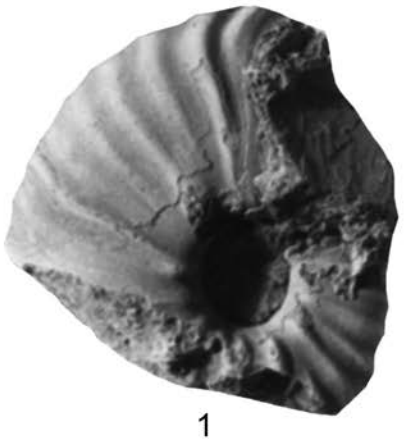
PLATE 2

Vascoceras venezolanum Renz, 1982

1, 2 – UCMP C1692-1; 3, 4 – UCMP C1692-2; 5, 6 – UCMP C1692-6; 7, 8 – UCMP C1692-3; 9, 10, UCMP CC1692-7.

Figures are × 2



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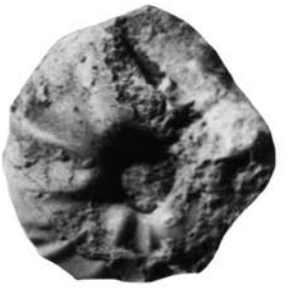

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PLATE 3

1, **2** – *Wrightoceras lagiraldae* (Etayo-Serna, 1979), UCMP C1510-17.

3-7 – *Wrightoceras munieri* (Pervinquière, 1907). 3, 4 – UCMP C9769-1; 5-7 – UCMP C9769-2.

Figures are × 1

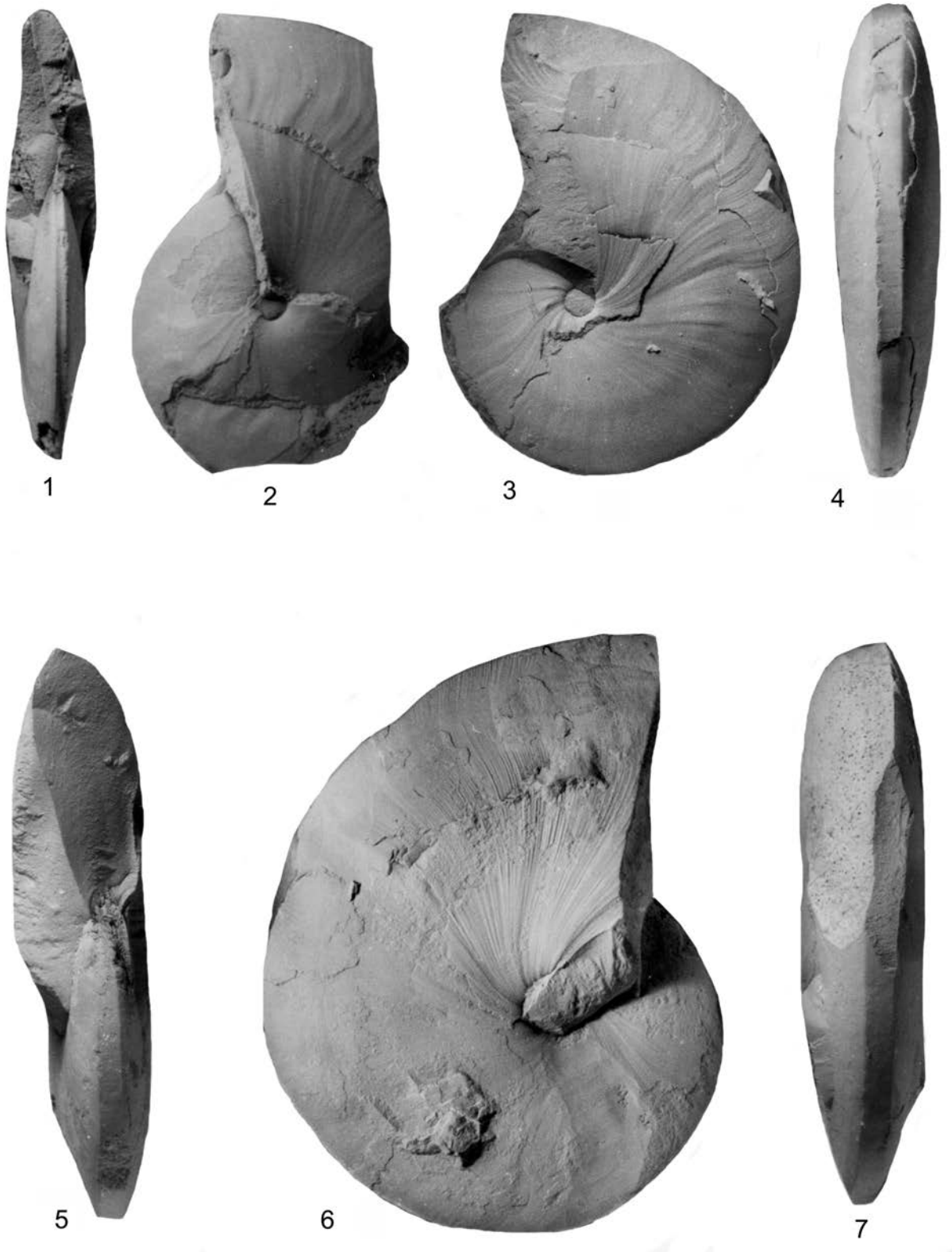
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PLATE 4

1–**7**, **10**, **11** – *Wrightocereas lagiraldae* (Etayo-Serna, 1979). 1–3 – UCMP C1998-1; 4, 5 – UCMP C1510-18; 6, 7 – UCMP C1510-19; 10, 11 – UCMP C1513-1.

8, **9** – *Wrightoceras munieri* (Pervinquière, 1907), UCMP C1610-1.

12, **13** – *Hoplitoides ingens* (von Koenen, 1897), UCMP C1998-4.

Figures 1-5, 10-13 are ×l; figures 6 and 7 are × 2

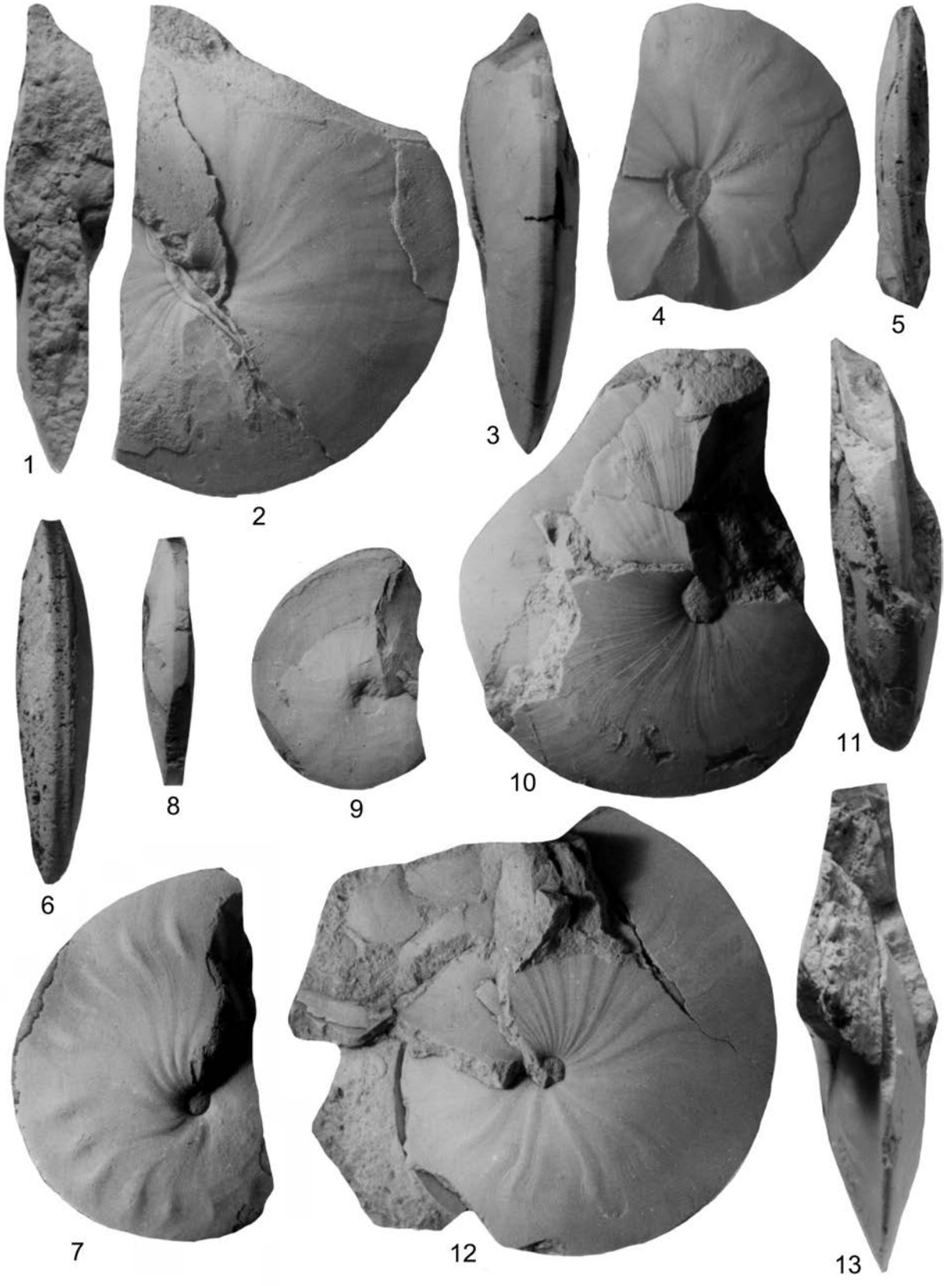
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PLATE 5

Hoplitoides ingens (von Koenen, 1897)

1 – UCMP C1998-3; 2, 3 – UCMP C1998-4; 4 – UCMP C1998-6; 5, 6 – UCMP 1998-5.

Figures are × 1

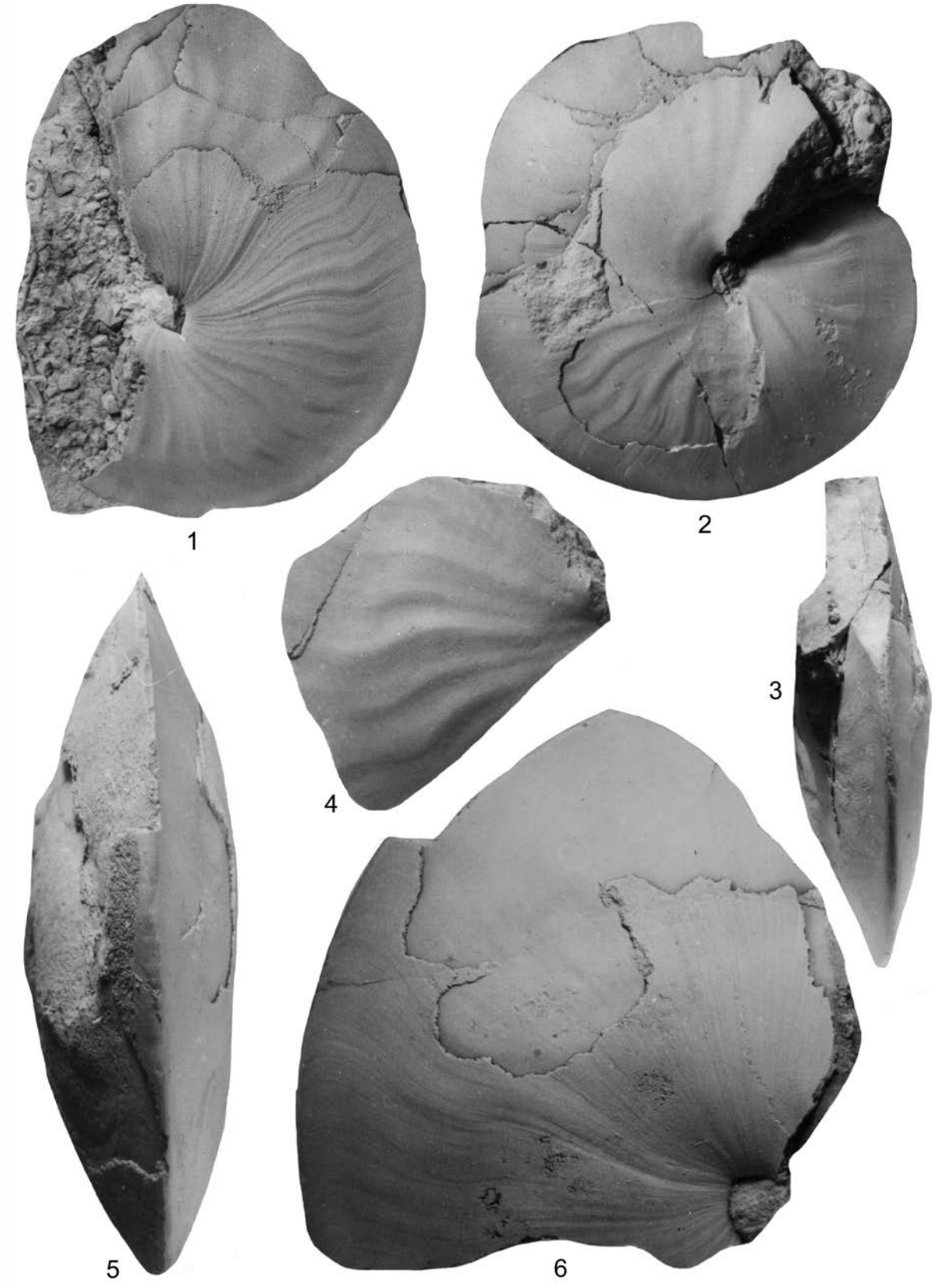
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PLATE 6

1-4 – *Hoplitoides ingens* (von Koenen, 1897). 1 – UCMP C1223-1; 2, 3 – UCMP C1510-20; 4 – UCMP C1998-7.

5 – *Wrightoceras lagiraldae* (Etayo-Serna, 1979). UCMP C1998-2.

Figures 1-3, 5 are ×1; figure 4 is × 2

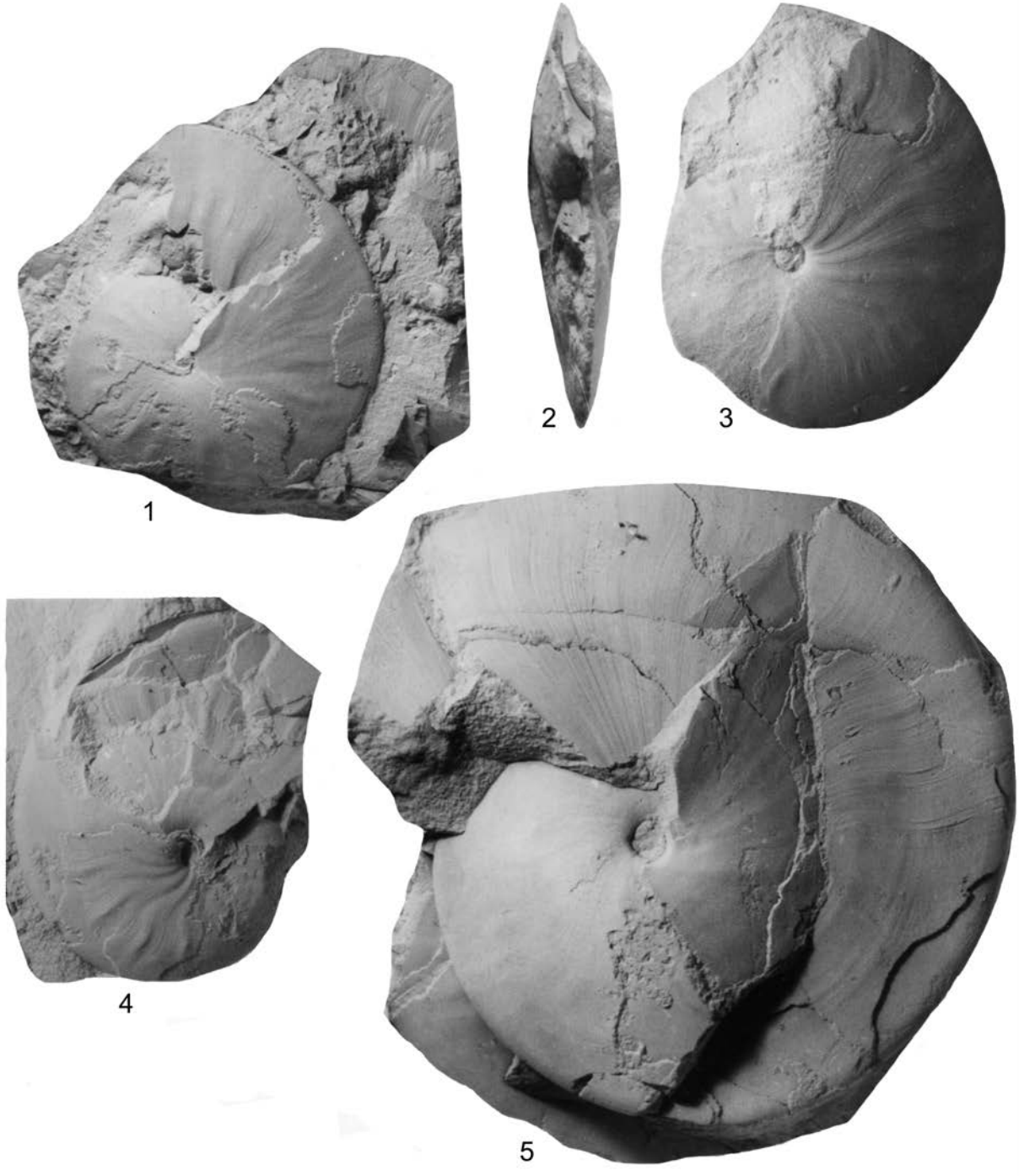
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PLATE 7

Prionocycloceras guayabanum (Gerhardt, 1897b).

1, 2 – UCMP C1510-1; 3, 4 – UCMP C1510-2; 5, 6 – UCMP C1510-3; 7, 8 – UCMP C1510-4; 9, 10 – UCMP C1510-7; 11 – UCMP C1501-5; 12, 13 – UCMP C1510-6.

Figures 1-6 are ×2; figures 7-13 are × 1

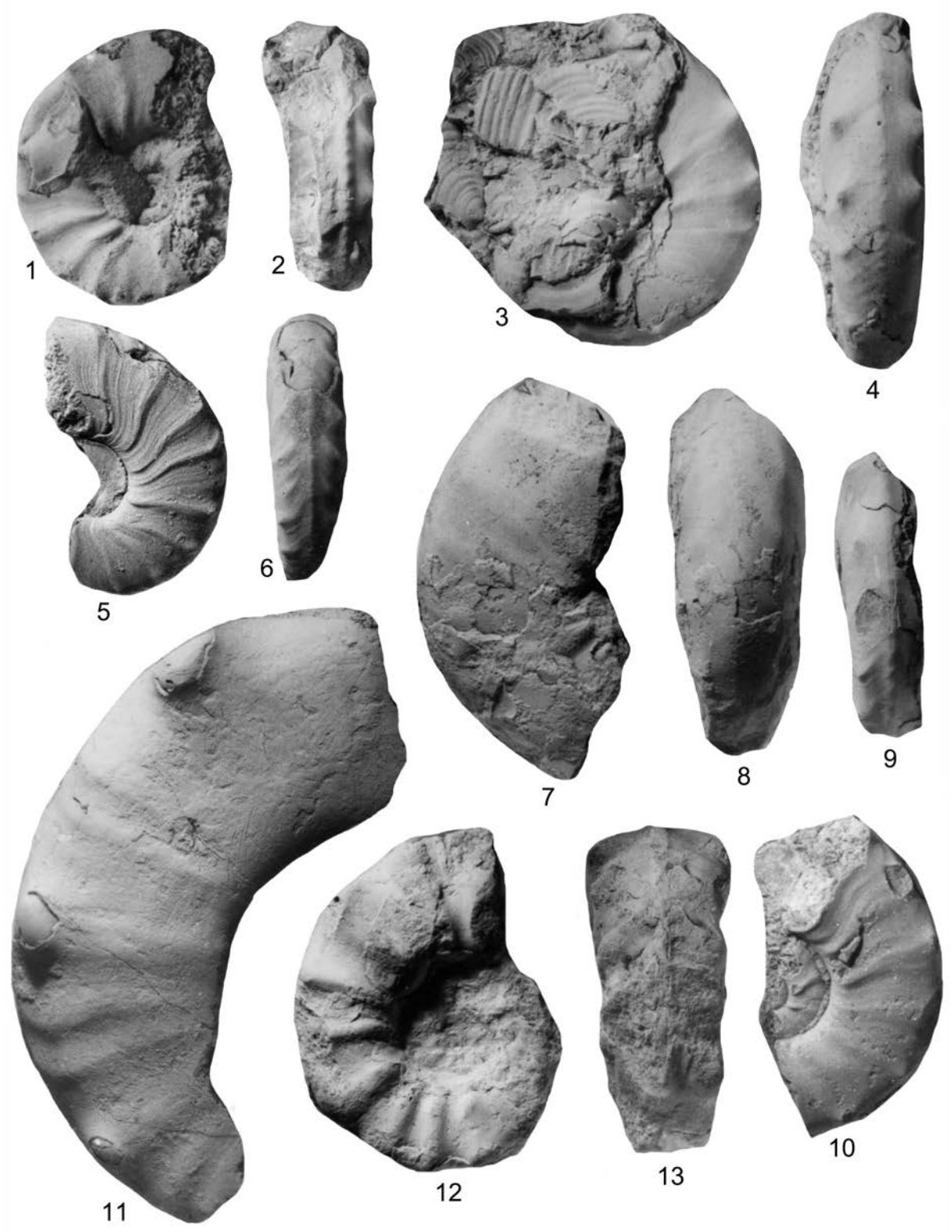
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PLATE 8

Prionocycloceras guayabanum (Gerhardt, 1897b).

1, 2 – UCMP C2007-1; 3, 4 – UCMP C2007-2; 5 – UCMP C2007-3; 6, 7 – UCMP C2007-4; 8 – UCMP C2007-5; 9, 10 – UCMP C2007-6.

All figures are × 1

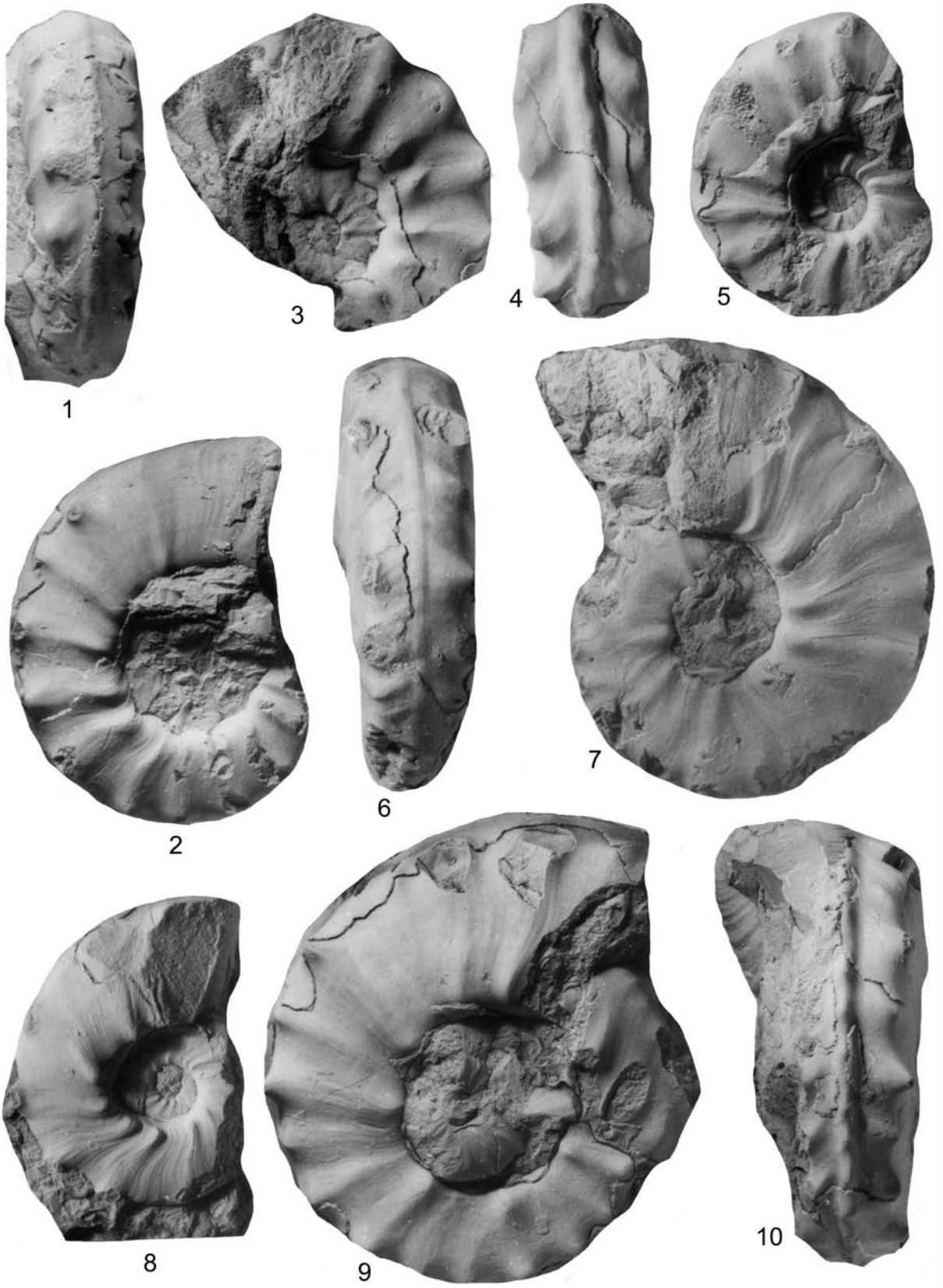
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PLATE 9

1-4, **9-12** – *Prionocycloceras guayabanum* (Gerhardt, 1897b). 1, 2 – UCMP C2007-9; 3, 4 – UCMP C1618-3; 9 – UCMP C1618-4; 10-12 – UCMP C1618-5.

5-8 – *Subprionocyclus loboi* (Etayo-Serna, 1979), UCMP C1618-7.

All figures are × 1

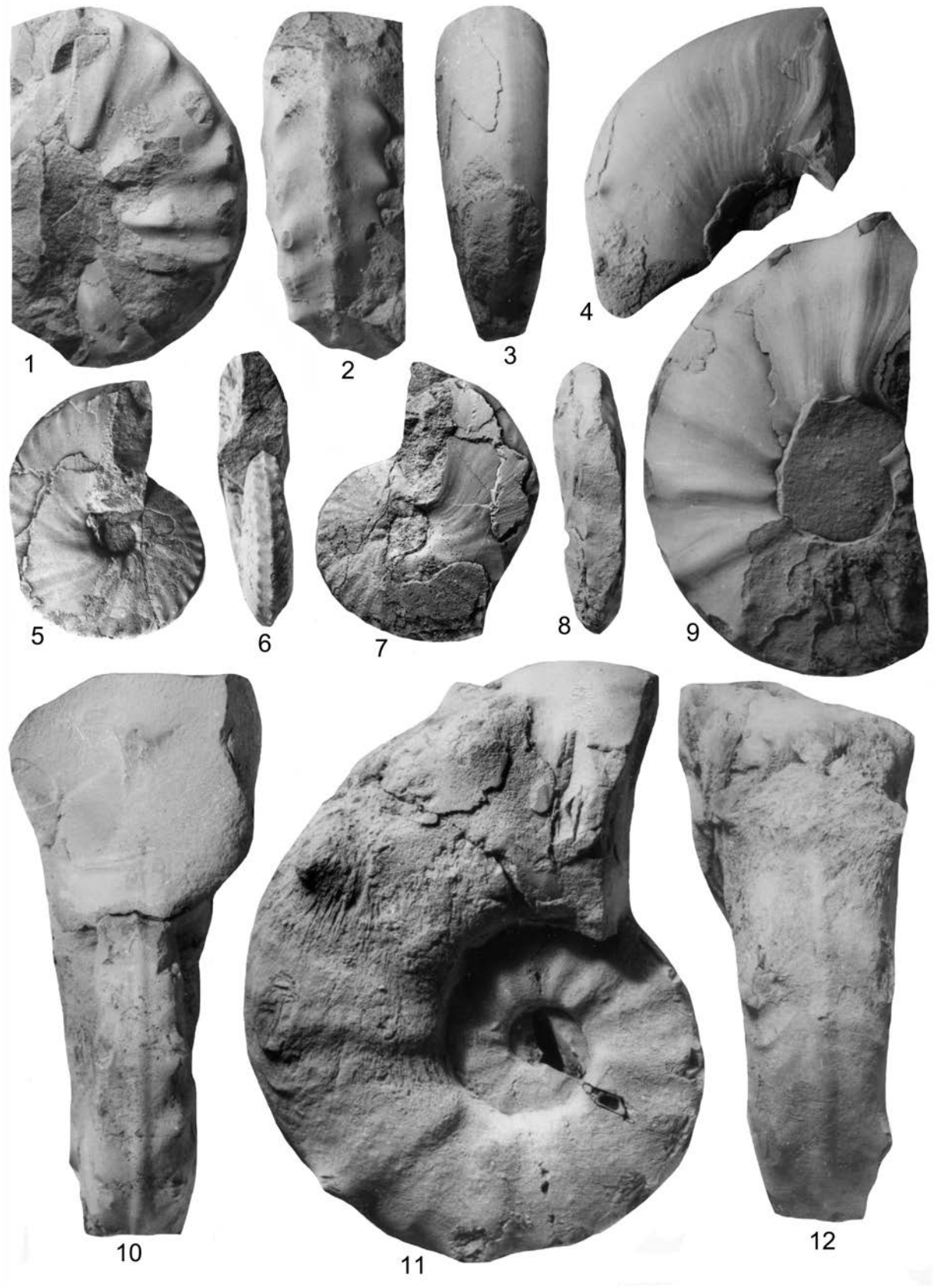
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PLATE 10

1-5 – *Prionocycloceras guayabanum* (Gerhardt, 1897b). 1, 2 – UCMP C1721-1; 3 – UCMP C1510-8; 4, 5 – UCMP C792-1.

6, **7**, **11**, **12** – *Niceforoceras columbianus* Basse, 1948. 6, 7 – UCMP C1721-11; 11, 12 – UCMP C1721-12.

8-10 – *Subprionocyclus branneri* (Anderson, 1902), UCMP C1510-8, a body chamber fragment, C1510-8d, containing three juveniles, C1510-8a–c; see also Pl. 12, Fig. 14.

13, **14** – *Subprionotropis colombianus* Basse, 1950, UCMP C1721-1.

All figures are × 1

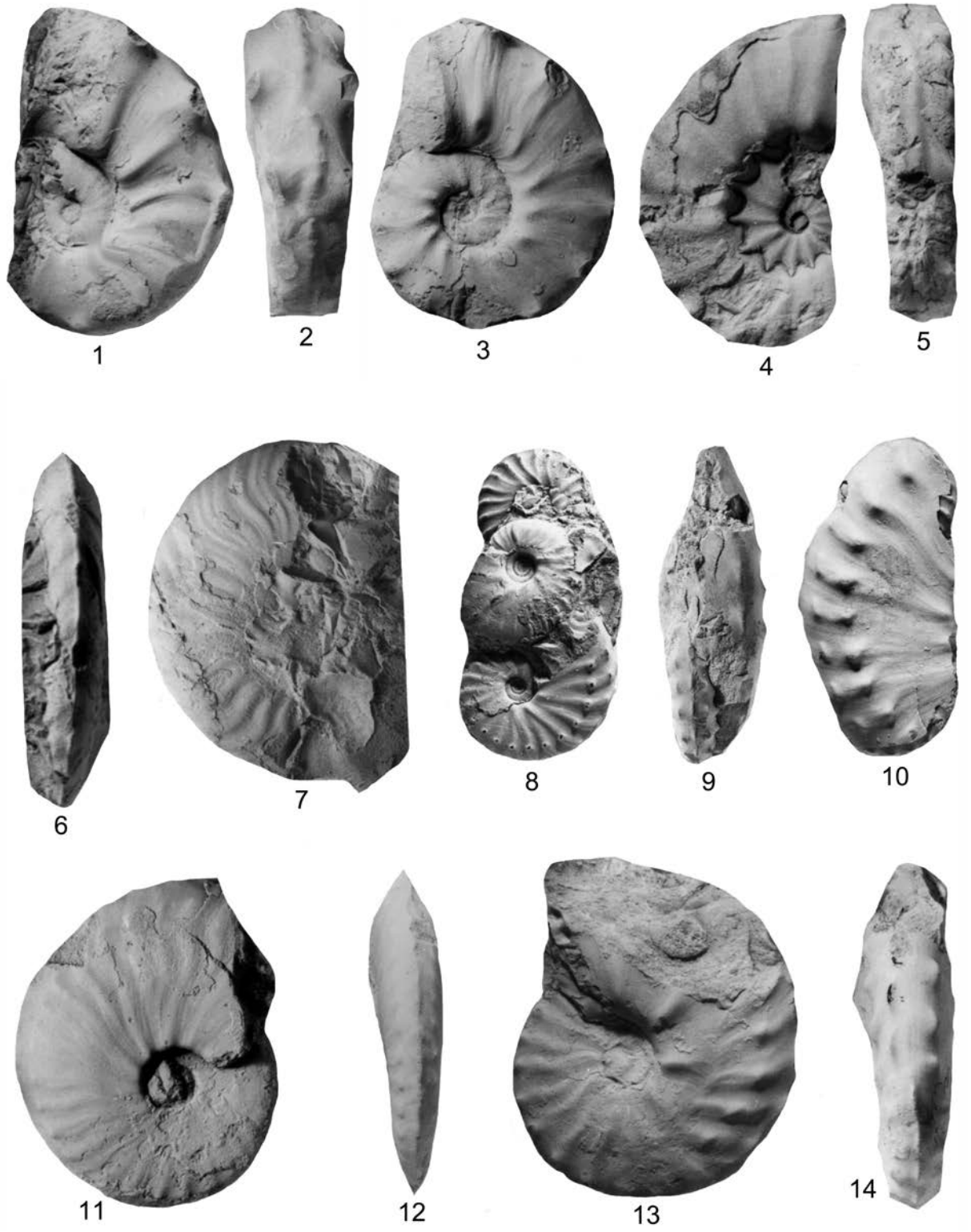
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PLATE 11

1-20 – *Subprionotropis colombianus* Basse, 1950. 1-3 – UCMP C1721-2; 4 – UCMP C1721-3; 5, 6 – UCMP C1721-4; 7-9 – UCMP C1721-5; 10, 11– UCMP C1721-6; 12, 13 – UCMP C1721-7; 14, 15 – UCMP C1721-8; 16, 17 – UCMP C1721-9; 18-20 – UCMP C1721-10.

21, **22** – *Niceforoceras columbianus* Basse, 1950, UCMP C1721-16.

All figures are × 1

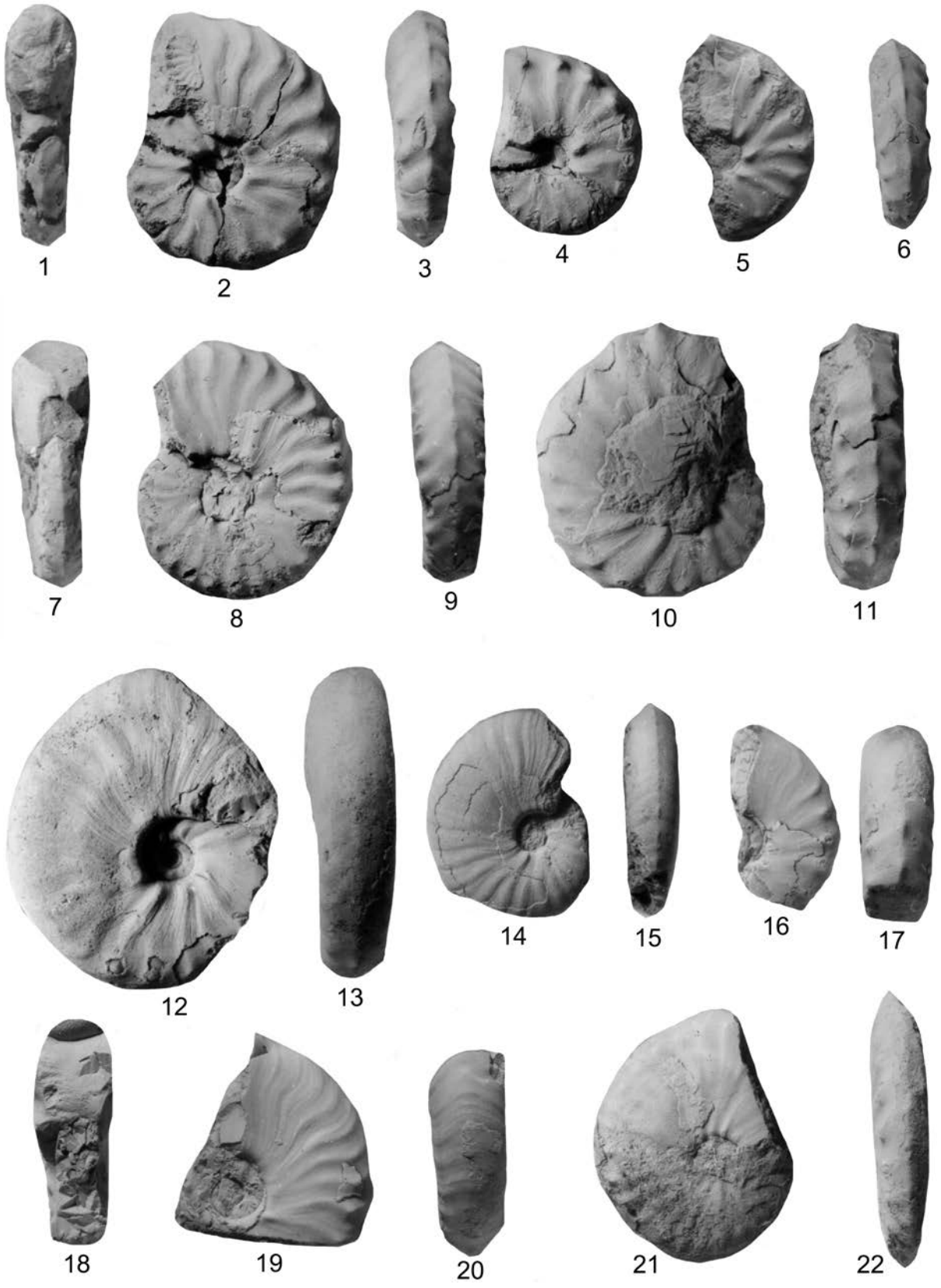
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PLATE 12

1-8 – *Niceforoceras* sp. 1 – UCMP C1510-10; 2 – UCMP C1510-11; 3, 4 – UCMP C1510-12; 5, 6 – UCMP C1510-13; 7 – UCMP C1510-14; 8 – UCMP C1510-15.

9, **10**, **12**, **13** – *Niceforoceras columbianus* Basse, 1950. 9, 10 – UCMP C1721-13; 12, 13 – UCMP C1721-15.

11 – *Subprionotropis colombianus* Basse, 1948, UCMP C1721-10.

14 – *Subprionocyclus branneri* (Anderson, 1902), UCMP C1510-8a–c; see also Pl. 10, Fig. 8.

All figures are × 2

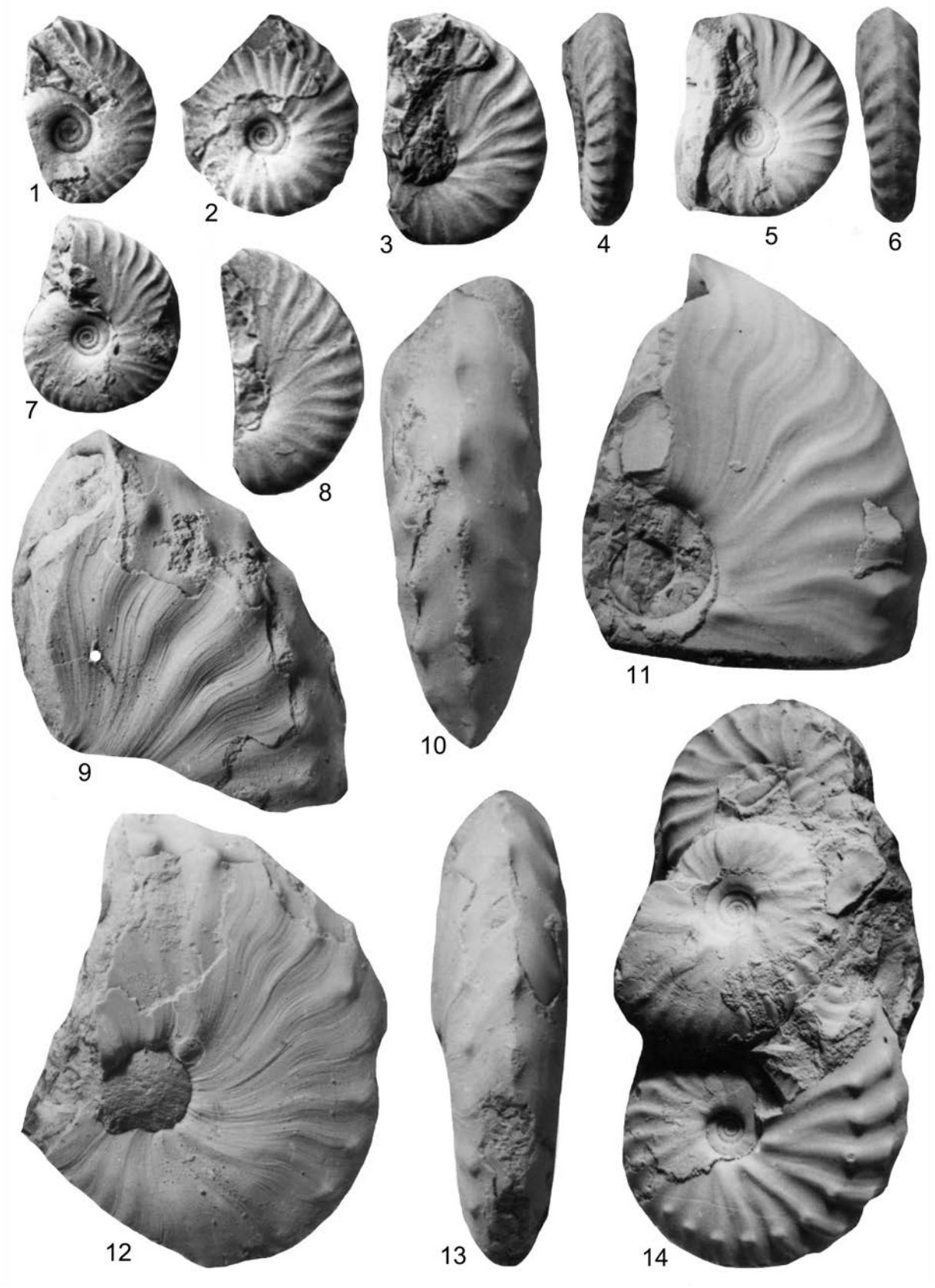
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PLATE 13

1, **2**, **5**-**8** – *Forresteria* (*Forresteria*) *peruana* (Brüggen, 1910). 1, 2 – UCMP C2004-3; 5, 6 – UCMP C2004-2; 7, 8 – UCMP C2005-2.

3, **4** – *Barroisiceras haberfellneri* (Hauer, 1866), UCMP C1618-1.

9, **10** – *Peroniceras* (*Peroniceras*) cf. *subtricarinatum* (d'Orbigny, 1850), UCMP C1911-1.

11, **12** – *Peroniceras* (*Peroniceras*) cf. *diaboloi* Etayo-Serna, 1979, UCMP C1999-1.

Figures 1-8, 11-12 are ×1; figures 9 and 10 are × 2

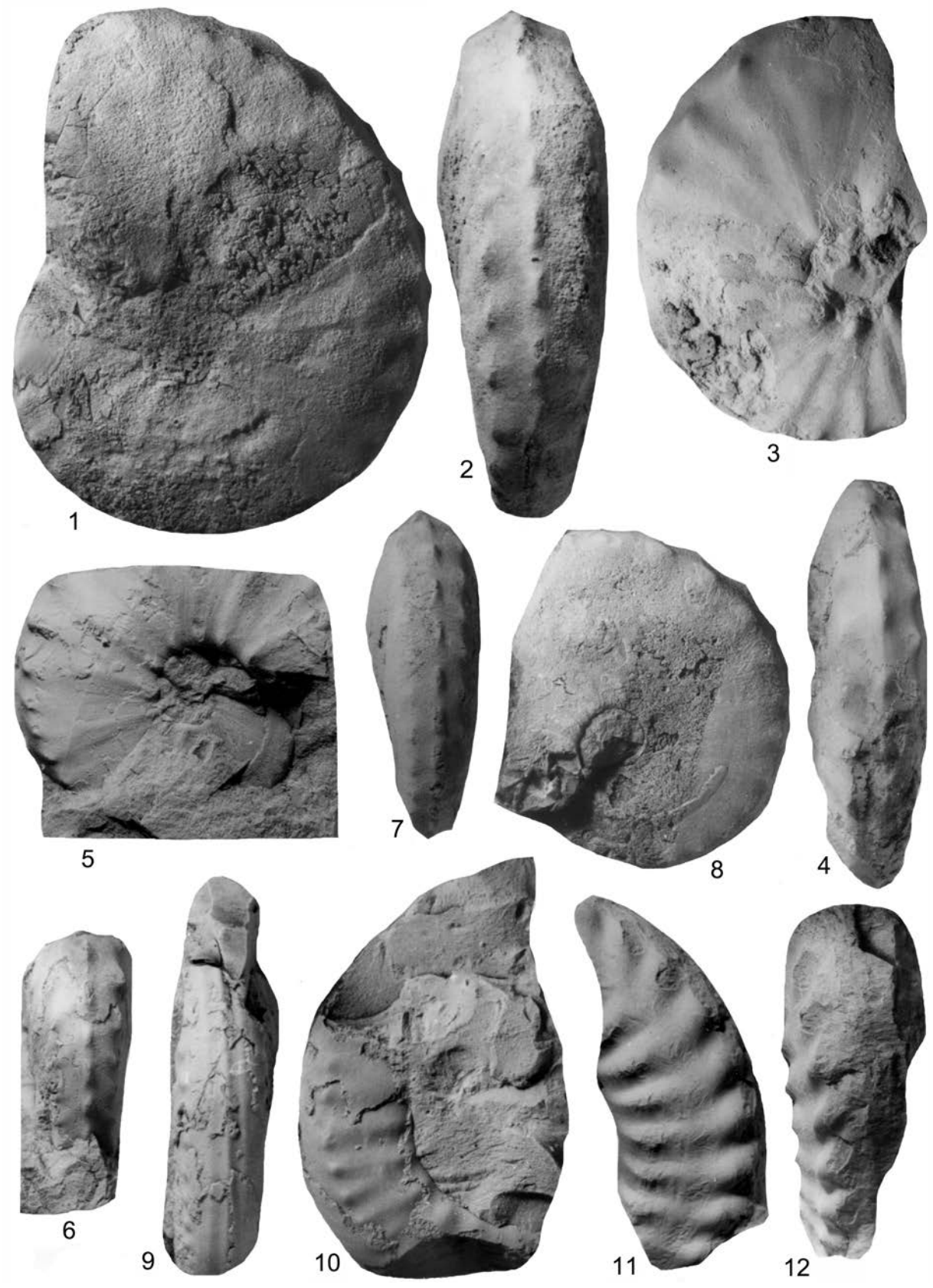
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PLATE 14

1-3, **6**, **7** – *Forresteria* (*Forresteria*) *alluaudi* (Boule, Lemoine and Thévenin, 1907). 1-3 – UCMP C192-4; 6, 7 – UCMP C2004-4.

4, **9** – *Barroisiceras* sp., UCMP C2005-1.

5, **8** – *Forresteria* (*Forresteria*) *peruana* (Brüggen, 1910). 5 – UCMP C2004-1; 8 – UCMP C2004-1.

All figures are × 1

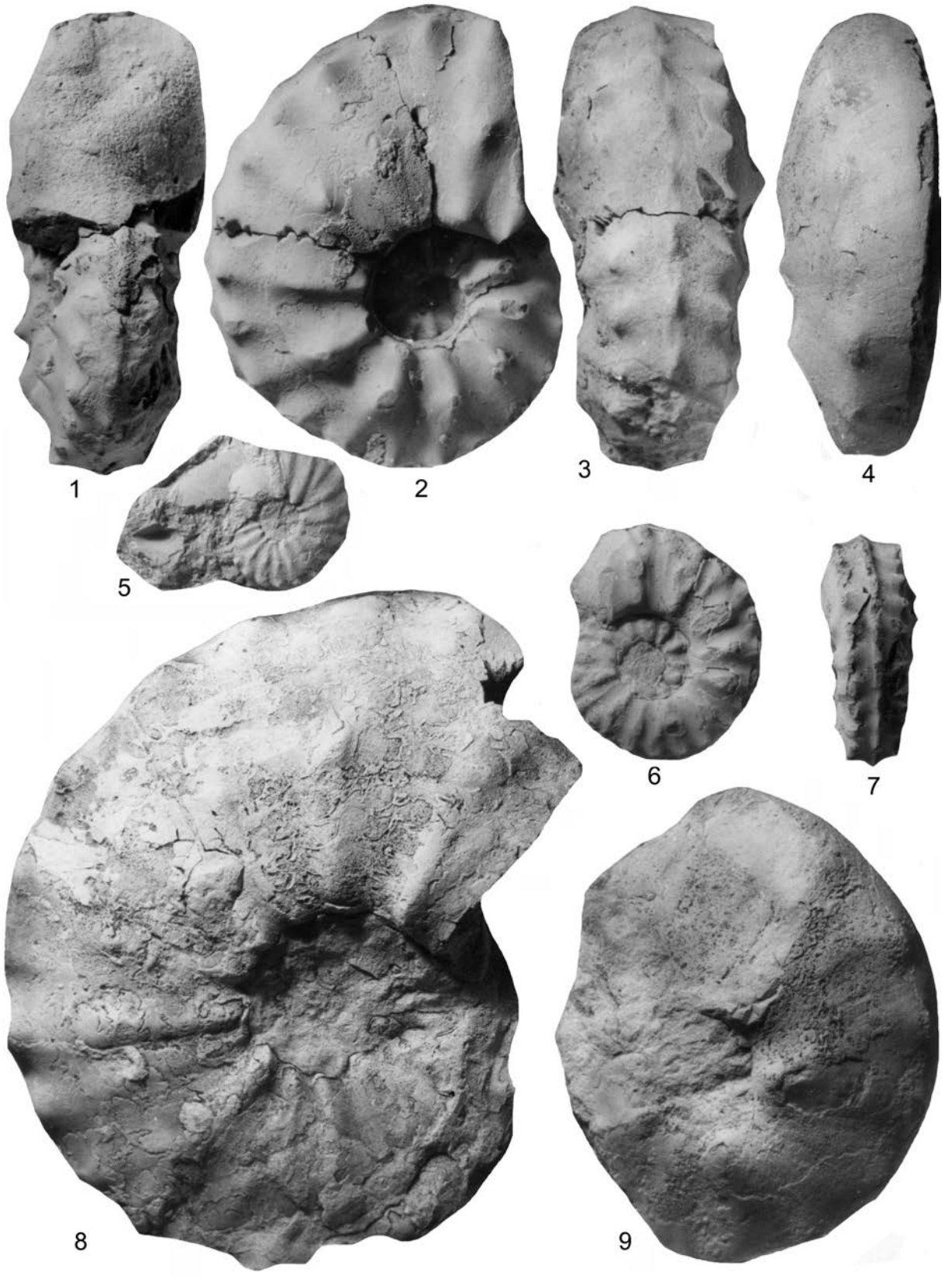
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PLATE 15

Peroniceras (*Peroniceras*) *tridorsatum* (Schlüter, 1867).

1, 2 – UCMP C363-1; 3, 4 – UCMP C192-2; 5 – UCMP C363-2.

All figures are × 1

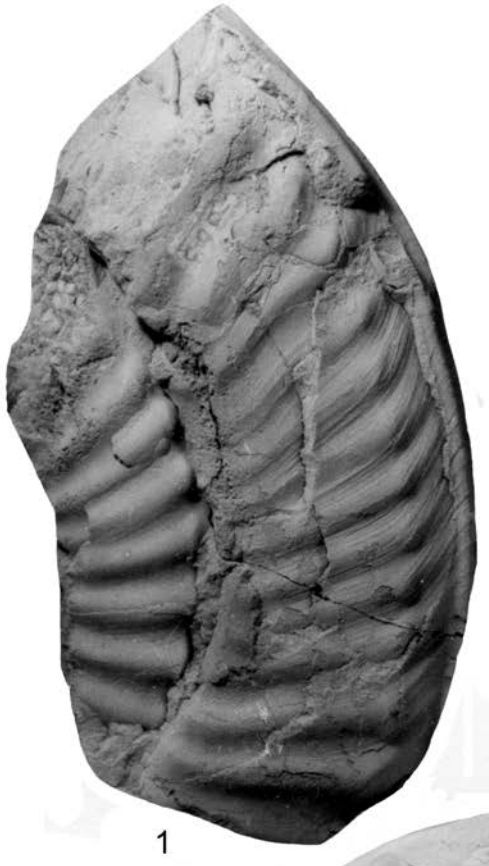
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PLATE 16

1-3 – *Protexanites* cf. *canaense* (Gerhardt, 1897a), UCMP C772-1.

4 – *Peroniceras* (*Peroniceras*) *tridorsatum* (Schlüter, 1867), UCMP C192-1.

All figures are × 1

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