

Heteromorphic ammonites from the Barremian and Aptian strata of Colombia

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Key words – heteromorphic ammonites, Barremian, Aptian, Colombia.

Thirty seven species and subspecies of ammonites of the families Ancyloceratidae Gill, 1871, and Heteroceratidae Spath, 1922, are described. The following new taxa are described; *Crioceratites* (*Paracrioceras*) *leyvaensis*, *C. (P.) royogomezi*, *C. (P.) cabraensis*, *Pedioceras multicostatum*, *Pseudocrioceras guanense*, *Kutatissites creutzbergi*, *K. densecostatus compactus*, *K. etayosernai*, *K. grandis*, *K.? galanensis*, *Ammonitoceras galanense*, *A. giganteum*, *Hamiticeras ventrotuberculatum*, *H. longum*, *Hemihoplites* (*Matheronites*) *ridzewskiji sachicaensis*, *Colchidites riosuarezi*, *C. pseudovulanensis*, *C. guanensis* and *C. striatosulcatus*. Moreover, one new genus, *Laqueoceras* gen. nov., with the type species *L. laqueus* sp. nov., is proposed.

Contents

Systematic palaeontology	39
References	93

Systematic palaeontology

All specimens described below are kept in the Nationaal Natuurhistorisch Museum (prefixed RGM, referring to the former Rijksmuseum van Geologie en Mineralogie).

Class Cephalopoda Zittel, 1884

Order Ammonitida Zittel, 1884

Suborder Ancyloceratina Wiedmann, 1966

Superfamily Ancyloceratoidea Gill, 1871

Family Ancyloceratidae Gill, 1871

Genus *Crioceratites* Léveillé, 1837

Subgenus *Crioceratites* (*Paracrioceras*) Spath, 1924

- pars* 1924 *Paracrioceras* Spath, p. 84.
- pars* 1954 *Emericiceras* Sarkar, p. 97.
- pars* 1955 *Emericiceras* Sarkar, p. 74.
- 1957 *Paracrioceras* Wright, p. L208.
- pars* 1962 *Crioceratites* Wiedmann, p. 112.
- pars* 1964 *Crioceratites* (*Emericiceras*) Thamel, p. 30.
- 1967 *Paracrioceras* Dimitrova, p. 52.
- pars* 1975a *Paracrioceras* Rawson, p. 279.
- pars* 1977 *Emericiceras* Sarkar, p. 260.

- pars* 1978 *Crioceratites* Immel, p. 28.
1981 *Paracrioceras* Kakabadze, p. 87.
1981 *Cryptocrioceras* Aguirre Urreta & Ramos, p. 114.
pars 1983 *Crioceratites* (*Paracrioceras*) Rawson, p. 498.
pars 1983 *Crioceratites* (*Paracrioceras*) Rawson & Mutterlose, p. 138.
1992 *Emericiceras* Delanoy, p. 52.
pars 1992 *Crioceratites* Klinger & Kennedy, p. 74.
pars 1996 *Crioceratites* (*Paracrioceras*) Wright *et al.*, p. L211.

Type species – *Paracrioceras occultum* (Seeley, 1865), England, Speeton, upper Barremian.

Diagnosis – The early whorls have a more or less close crioconic coiling; the coiling becomes closer in the outer whorls and in some cases the last whorls may be contiguous. The sculpture is more or less coarse. On the early whorls it consists of simple non-tuberculate ribs, and with growth ventral, lateral and umbilical spines appear. Generally, the ventral tubercles are stronger than the lateral and umbilical ones. The number of intermediate ribs between the main ones is generally one to two, rarely more, whilst in some species they may be absent. Intermediate ribs may rarely bear weak ventral tubercles. Looped ribs between the upper lateral and umbilical tubercles may also occur. In the gerontic stage trituberculation disappears and only strong, distant simple ribs remain. The suture line is of the ancyloceratid type.

Comparison – *Crioceratites* (*Paracrioceras*) differs from *Crioceratites* (*Crioceratites*) in having its crioconic whorls closer together or even in contact with each other in the adult stage, in having stronger ribs with stronger spines, and in the smaller number or absence of intermediate ribs.

Remarks – Spath (1924) did not give detailed characteristics of *Paracrioceras*. He merely pointed out that *Paracrioceras* has a strong trituberculate sculpture and that apart from the type species, *Ammonites* (*Crioceras*) *occultum* Seeley, 1865, also *Crioceratites roeveri* Koenen, 1902, *C. elegans* Koenen, 1902, *C. robustum* Koenen, 1902, and the Mediterranean species *C. emerici* Léveillé, 1837, belong to this genus.

Sarkar (1954, 1955) chose *Crioceratites emerici* as type species of *Emericiceras*. He united five groups of species in *Emericiceras*: 1. Group of *E. emerici* with a very open crioconic spire of which the whorls slowly increase in height. The sculpture consists of trituberculate main ribs separated by usually four to five thin, non-tuberculate intermediate ribs. 2. Group of *Emericiceras barremense* (Kilian) of which the shell consists of closely coiled crioconic early whorls; the whorls become almost contiguous or even truly contiguous in a late ontogenetic stage. The tuberculate main ribs are dominant, whereas the number of intermediate ribs is small or zero. 3. Group of *Emericiceras lardyi* (Ooster), which is characterized by simple trituberculate ribs on the early whorls, but in the mature stage by an alternation of tuberculate main ribs and one to three non-tuberculate intermediate ribs between them. 4. Group of *Emericiceras clausum* (Sarasin & Schöndelmayer), which is characterized by closely coiled crioconic whorls with coarse ribbing. The main trituberculate ribs are hardly stronger than the intermediate ones. 5. Group of *Emericiceras thiollierei* (Astier), which has very large shells, with typical open

crioconic coiling. The sculpture is very similar to *E. emerici*, but differs from it in having looped ribs. According to Thomel (1964) a sixth group of *E. tenuicostatum* Thomel also has to be included. This group is characterized by thin main trituberculate ribs and four to six still thinner, non-tuberculate intermediate ribs between them.

There are rather different points of view in relation to the validity of *Emericiceras*. Wright (1957) included *Emericiceras* with a question mark in *Crioceratites*. According to Wiedmann (1962, 1966), *Emericiceras* and *Paracrioceras* are junior synonyms of *Crioceratites*. Thomel (1964) and Delanoy (1992) considered *Emericiceras* a subgenus of *Crioceratites*. Rawson (1975a) considered *Emericiceras* a junior synonym of *Paracrioceras*. Lately it was suggested (Rawson, 1983; Rawson & Mutterlose, 1983; Wright *et al.*, 1996) that *Paracrioceras* should be regarded as a subgenus of *Crioceratites*, indicating that *Emericiceras* is the junior synonym of *Crioceratites* (*Paracrioceras*).

We consider *Emericiceras* an invalid taxon (see also Kakabadze, 1981, p. 88); a part of the species groups, united by Sarkar (1955) and Thomel (1964) into *Emericiceras*, should be included in *Crioceratites* (*Paracrioceras*) and another part in *Crioceratites* (*Crioceratites*). The groups of "*Emericiceras*" *emerici*, of "*E.*" *thiollierei* and of "*E.*" *tenuicostatum* are characterized by morphological features that typify the subgenus *Crioceratites* (*Crioceratites*), and they were included in this subgenus.

Distribution – Barremian. England, Germany, France, Bulgaria, Romania, Italy, North Caucasus, Georgia, Turkey, Marocco, South Africa, Colombia.

***Crioceratites* (*Paracrioceras*) *leyvaensis* sp. nov.**

Pl. 1; Pl. 2, figs. 1-2.

1997 *Paracrioceras* sp. ex gr. *barremense* (Kilian & Leenhardt): Kakabadze & Hoedemaeker, p. 66, pl. 4, fig. 1.

Holotype – RGM 352 596.

Paratype – RGM 345 115.

Type locality – Villa de Leyva, Monastery of Santo Ecce Homo.

Type horizon – Lower? Barremian.

Derivatio nominis – Named after municipal of Villa de Leyva in which the monastery is situated.

Diagnosis – Crioconic whorls, which moderately increase in height. The sculpture consists of an alternation of trituberculate main and thin, non-tuberculate intermediate ribs. All ribs cross the venter without interruption. On the dorsum the main and intermediate ribs are equally thin and curved forward.

Description – The crioconic whorls are moderately increasing in height. Up to D = 25-30 mm the flanks are slightly convex, but later they become almost flattened. The venter is rounded, whereas the dorsum is almost flattened. Up to D = 28-30 mm the

whorl section is subcircular, but at greater diameters it becomes sub-ellipsoidal (higher than wide). The costal section (= along the main tuberculate ribs) has a sub-rectangular shape. The ornamentation on the earliest part of the preserved whorl of the holotype consists of radial, straight tuberculate ribs of which every two are separated by one thin, non-tuberculate rib. The ventral spines appear first, lateral tubercles develop slightly later. In the holotype two thin ribs arise from one lateral tubercle. The umbilical tubercles appear still later. On the earliest preserved part of the whorl of the holotype the ventral spines are rather prominent, very long (as long as the whorl height) and thin. After $D = 20\text{--}25$ mm the ornamentation characteristic for the species is rapidly formed. It consists of an one to one alternation of the trituberculate main ribs and thin, non-tuberculate intermediate ribs. In a few cases the main ribs lack umbilical tubercles. In RGM 345 115 one of the intermediate ribs bears a weak ventral tubercle. On the venter between the ventral tubercles the ribs are somewhat flattened. The ventral spines are much stronger than the lateral and umbilical ones. On the first whorl the ribs are radial, but occasionally they are slightly inclined backward on later whorls. The intermediate ribs cross the venter in a straight line, without interruption and without broadening. On the dorsum all ribs are equally thin and pass with a convex curve.

Measurements – Key: d = diameter of the last helicoidal whorl; h_1 = whorl height of the helicoidal spiral; D = diameter of the plane spiral; H = whorl height of the plane spiral; W = whorl thickness of the plane spiral; U = umbilical width; h = whorl height at 180° ; H_1 = height of the shaft section; W_1 = whorl thickness of the shaft; H_2 = height of the hook section; W_2 = whorl thickness of the hook; D_1 = transverse diameter of uncoiled shell (shaft with hook); L = length of the shaft; L_1 = length of the whole shell; - = not measured. Similar abbreviations used below. All measurements given here and below are in mm unless stated otherwise. RGM 352 596: $D = 100.0$ (63.0); $H = 29.8$ (20.0); $W = 29.0$ (19.0); $U = 52.3$ (33.5). RGM 345 115: $D = 66.8$; $H = 21.2$; $W = 18.5$; $U = 35.4$.

Remarks – The described species resembles *Paracrioceras barremense* (Kilian) in the regular alternation of one main and one intermediate rib, and in the rather tightly coiled crioconic whorls, but clearly differs from it in the main and intermediate ribs crossing the venter without interruption and in the smaller number of intermediate ribs between the main ones. In Kakabadze & Hoedemaeker (1997, p. 66) the holotype of this new species was described as *Paracrioceras* sp. ex gr. *barremense* (Kilian & Leenhardt, 1895) and in the synonymy was listed *Emericeras* sp. gr. *barremense* (forme 1) described by Delanoy (1992, p. 54, pl. 19, fig. 3). However, careful examination of additional material showed that *P. leyvaensis* clearly differs from Delanoy's specimen in the more open crioconic coiling and in the ribs not being interrupted on the venter.

Occurrences – Villa de Leyva, Santo Ecce Homo; lower? Barremian.

***Crioceratites (Paracrioceras) royogomezi* sp. nov.**

Pl. 2, fig. 3.

Holotype – RGM 352 542. The earliest ontogenic stage (embryonal camera) is not preserved, but a portion of the second whorl and the third whorl are very well preserved, so that the whole development of the sculpture can be studied.

Type locality – Villa de Leyva, Monastery of Santo Ecce Homo.

Type horizon – Barremian.

Derivatio nominis – In honour of the famous Colombian geologist and palaeontologist J. Royo y Gomez.

Diagnosis – The second whorl consists of a very open, rapidly expanding crioconic spire with a very wide “umbilical hiatus”. The ornamentation of the early whorls consists of dense, tuberculate main ribs regularly alternating with one non-tuberculate intermediate rib. The ribs cross venter and dorsum without interruption.

Description – The earliest whorl is slender and thread-like. At the beginning it is rapidly increasing in height ($H:h = 1.7$), but after $D = 25$ mm the whorls only moderately increase in height ($H:h = 1.4$). The flanks and venter are slightly convex. At the outset the dorsum is rounded, but later it becomes slightly flattened. The cross section is circular. The ornamentation is already formed when the whorl height is 2.0-2.5 mm.

Thin, dense ribs are slightly inclined forward. The main ribs bear thin ventral tubercles with a rounded basis. Between every two main ribs is one non-tuberculate intermediate rib. From $D = 15$ mm lateral tubercles appear and, at $D = 23-25$ mm, also umbilical tubercles. All ribs cross the venter without interruption. On the venter between the ventral tubercles the ribs are slightly flattened. In the early stage the ribs cross the dorsum in a straight line, but from $D = 14-15$ mm all ribs cross the dorsum with an adorally convex curve.

Measurements – $D = 32.8$; $H = 10.0$; $W = 10.0$; $U = 17.8$. At a lower diameter the measurements are: $D = 21.2$; $H = 5.8$; $W = 5.4$; $U = 13.6$.

Comparison – The described specimen resembles *P. leyvaense* in the way in which every main rib alternates with one intermediate rib, but clearly differs in having denser ribbing and very loosely coiled, crioconic, early whorls, which rapidly increase in height. From those species of the *P. barremense* group that have a similarly open early crioconic spire, *P. royogomezii* differs in the rapidly increasing height of the early whorls and in the ribs crossing the venter without interruption.

Occurrence – Villa de Leyva (Monastery of Santo Ecce Homo). Barremian.

***Crioceratites (Paracrioceras) cabreraensis* sp. nov.**

Pl. 2, fig. 4; Pl. 67, fig. 3.

1991 *Crioceratites thiollieri* (Astier): Kakabadze & Thieuloy, p. 83, pl. 1, fig. 3-6, text-fig. 2.

Holotype – RGM 352 547.

Paratype – RGM 353 607.

Type locality – Loma Cabrera near Villa de Leyva.

Type horizon – Lower Barremian (together with *Nicklesia*, after Creutzberg).

Derivatio nominis – The subspecies is named after the type locality.

Diagnosis – Typical rather tightly coiled, crioconic shells, with low, inflated whorls. The sculpture consists of an one to one alternation of main and intermediate ribs. There are rarely two intermediate ribs between two main ones. Looped ribs are present between the upper lateral and umbilical tubercles.

Description – The shell consists of rather tightly coiled crioconic whorls. Until $D = 5$ mm the whorls are rapidly increasing in height ($H:h = 1.8$), but later they only moderately increase in height. The whorls are low, with convex flanks. The venter is rounded; in the beginning the dorsum is rounded also, but later it gradually flattens. The whorl section is low ellipsoidal, i.e., wider than high. The whorl section of the last whorl of the holotype is almost round. The origin and development of the sculpture can be followed on the holotype; up to $D = 3.5$ mm the ornamentation consists of rather weak, simple ribs. From that diameter the ribs are differentiated into main and intermediate ribs. The main ribs become stronger, and one can follow the development of the ventral and lateral tubercles (with a circular basis) on them. The umbilical tubercles (also with a circular basis) appear later (after $D = 7$ mm). The number of the non-tuberculate intermediate ribs between every two main ones is one, rarely two in a late ontogenetic stage (on the holotype after $D = 18$ mm). The looped ribs between the lateral and umbilical tubercles are only present in a late stage (on the last part of the last whorl of the holotype). Between the ventral tubercles the ribs are slightly flattened. The intermediate ribs cross the venter in a straight line without interruption or broadening. On the dorsum all ribs are equally thin and describe a forward curve. The suture line is only fragmentarily seen on RGM 353 607.

Measurements – RGM 352 547: $D = 24.0$; $H = 8.5$; $W = 9.3$; $U = 10.6$. RGM 353 607: $D = 18.0$; $H = 6.5$; $U = 7.8$.

Remarks – Besides the two specimens described here we include in this new species the two specimens described in Kakabadze & Thieuloy (1991) under the name *C. thiollierei* (Astier, 1851). The holotype of this new species is represented by the early ontogenetic stage, but the two specimens from the Institute Dolomieu in Grenoble represent an early and a mature ontogenetic stage. The morphological analysis of all four specimens shows that they belong to the same species. They differ from *C. thiollierei* in the mode of coiling; the holotype of *C. thiollierei* has a very loosely coiled spire. Its early whorls are higher than thick; they become slightly thicker than high only in the mature stage. RGM 352 547 and 353 607 have more tightly coiled, crioconic whorls. Moreover, the new species has a much smaller number of intermediate ribs between every two main ones. By the more tightly coiled whorls, which are wider than high, *Paracrioceras cabreraensis* sp. nov. approaches *P. spathi* Kemper et al., 1981, but differs from it in the smaller number (one, rarely two, instead of three to four, rarely two) of intermediate ribs between every two main ones on the early whorls. Moreover, in *P. spathi*, some of the finer ribs loop to the major ones especially over the venter, whereas in *P. cabreraensis* both sides of the loops are equal.

Occurrence – Loma Cabrera near Villa de Leyva, lower Barremian.

Genus *Pedioceras* Gerhardt, 1897

- 1897 *Pedioceras* Gerhardt, p. 172.
1938 *Pedioceras* Roman, p. 395.
1949 *Pedioceras* Basse, p. 691.
pars 1957 *Pedioceras* Wright, p. L208.
pars 1996 *Pedioceras* Wright *et al.*, p. L214.
1997 *Pedioceras* Kakabadze & Hoedemaeker, p. 63.

Type species – *Ammonites Caquesensis* Karsten, 1858, lower Barremian, Colombia.

Diagnosis – Early whorls are crioconic and may be slightly asymmetric; the later whorls are in contact and have a subcircular or subquadrate cross section, which is thicker than high. The inner whorls are ornamented with simple uniform ribs. Ventral and ventrolateral tubercles appear a little later. On later whorls also umbilical tubercles appear and many non-tuberculate intermediate ribs separate every two trituberculate main ribs.

Remarks – We do not agree on the solution of Wright (1957) and Wright *et al.* (1996) to consider *Pseudocrioceras* Spath, 1924, a junior synonym of *Pedioceras* Gerhardt, 1897. This question was discussed in Kakabadze & Hoedemaeker (1997, p. 63) and Kakabadze (1978, 1981), who advocated the independence of both genera.

Distribution – Lower Barremian. Colombia, Mexico, California.

***Pedioceras multicostratum* sp. nov.**

Pl. 6, fig. 1; Fig. 1.

Holotype – RGM 353 635.

Type locality – Villa de Leyva.

Type horizon – Lower Barremian.

Derivatio nominis – *Multi* (Latin) = many, *costa* (Latin) = rib; because of its numerous ribs.

Diagnosis – Evolute planispiral shell with whorls that moderately increase in height. The whorl section is subellipsoidal and much higher than wide. The ornamentation consists of dense, thin, radial ribs. Up to D = 50 mm intermediate ribs are very rare, but later they become rather frequent. On the last half whorl 43-44 ribs were counted. The ventral tubercles are stronger than the lateral ones. The latter become very weak in the adult stage.

Description – The shell consists of contiguous planispiral whorls, which moderately increase in height (H:h varies from 1.45 to 1.62). The umbilicus is wide (U:D = 0.39)

with a steep wall. Up to $D = 35$ mm the whorl section is oval with the maximal thickness on the umbilical wall; at greater diameters it becomes subellipsoidal and is much higher than thick. The ornamentation consists of thin, dense, radial ribs. On the first planispiral whorl the ribs are separated by interspaces, which are equal to their breadth. On the next whorl the breadth of ribs does not change, but the interspaces exceed their thickness almost twice. On the flanks the ribs are slightly flexuous and above the lateral tubercles they slightly bent forward; on the dorsum they make a conspicuous, adorally convex curve. Each main rib bears rather small ventral and lateral tubercles. The lateral tubercles are smaller than the ventral ones. On the last whorl the lateral tubercles become much weaker and finally disappear. In the space between the ventral tubercles the ribs are slightly weakened and this part of the venter is almost flat. On the last whorl there are one or two intermediate ribs between every two main ribs; some of them also bear ventral tubercles. Also, a few bifurcating ribs were found. The branches and the intercalatory ribs arise from the umbilical area.

Measurements – $D = 106.5$; $H = 39.0$; $W = 33.0$; $U = 41.6$.

Comparison – The shape of the whorls and the sculpture on the early growth stage of *P. multicostratum* is similar to that of *P. caquesense*, but in the adult stage the latter is characterized by stronger trituberculate main ribs, with two to four (rarely one) intermediate ribs between them, whereas the adult of the new species is characterized by radial, slightly flexuous, thin and dense ribs with only ventral and lateral tubercles (umbilical tubercles absent).

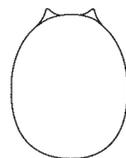


Fig. 1. Whorl section of the *P. multicostratum* sp. nov. on the last planispiral whorl (holotype), $\times 1$.

Occurrence – Villa de Leyva, lower Barremian.

Pedioceras caquesense (Karsten, 1858)

Pl. 5.

1997 *Pedioceras caquesense* (Karsten): Kakabadze & Hoedemaeker, p. 63, figs. 1-4, pl. 7, figs. 1-2 (see synonymy).

Type species – The specimen figured by Karsten (1858, pl. 1, fig. 7a, b), lower Barremian of Caquesa, Cundinamarca, Colombia.

Material – RGM 353 639.

Remarks – Colombian specimens of *P. caquesense* were described in detail by Kakabadze & Hoedemaeker (1997). The specimen figured here is more mature and the sculpture of this mature stage is shown for the first time. It consists of trituberculate main ribs and three to four intermediate non-tuberculate ribs between every two of them.

Occurrence – Loma Cabrera, lower Barremian.

Distribution – Lower Barremian of Colombia, Mexico?

Genus *Ancyloceras* d'Orbigny, 1842

- pars* 1842 *Ancyloceras* d'Orbigny, p. 447.
pars 1889 *Ancyloceras* Haug, p. 212.
pars 1913 *Ancyloceras* Kilian, p. 351.
pars 1952 *Ancyloceras* Luppov, p. 228.
 1957 *Ancyloceras* Wright, p. L211.
 1958 *Ancyloceras* Drushchits & Eristavi, p. 104.
 1960 *Ancyloceras* Casey, p. 19.
 1964 *Ancyloceras* Thomel, p. 52.
pars 1967 *Ancyloceras* Dimitrova, p. 56.
 1981 *Ancyloceras* Kakabadze, p. 100.
pars 1996 *Ancyloceras* Wright *et al.*, p. 216.

Type species – Designated by Haug, 1889, p. 212: *Ancyloceras matheronianum* d'Orbigny, 1842, France, lower Aptian.

Diagnosis – The early whorls are cryptoconic, which are followed by a rather long shaft and a final hook. The ornamentation of the early whorls and the shaft consists of trituberculate main ribs and one to five fine, non-tuberculate intermediate ribs between them. The tubercles are the bases of hollow spines. On the hook the intermediate ribs disappear, and the tuberculate main ribs become stronger and more distant. At the end of the hook the tuberculation ceases and in some cases tubercles totally disappear.

The suture line consists of a bifid ventral (E) and trifid lateral (L), umbilical (U) and dorsal (I) lobes. The lateral lobe is characterized by a very long middle branch. The umbilical lobe is generally asymmetric and markedly shorter than the lateral and dorsal lobes.

Remarks – *Ancyloceras* generally differs from other related genera (*Australiceras* Whitehouse, *Pseudocrioceras* Spath, *etc.*) in having an ancyloceratid type of sculpture, i.e., an alternation of trituberculate main ribs and non-tuberculate intermediate ribs in almost all ontogenetic stages.

Distribution – Barremian-lower Aptian. France, Bulgaria, England, Spain, Italy, Georgia, Azerbaijan, Volga region, Turkmenistan, Japan, California, Colombia.

***Ancyloceras* cf. *matheronianum* d'Orbigny, 1842**

Pl. 8; Pl. 9, fig. 1; Pls. 12-15, Fig. 2.

Material – Four specimens; three (RGM 354 119, RGM 353 620, RGM 345 125) preserved with a shaft and a hook, the fourth (RGM 353 619) only by the shaft.

Description – The long pipe-like shaft has a slight dorsal bulge in the middle. The hook is not broadly arched and its straight last portion is subparallel to the shaft. The

cross section from the end of the planispiral whorls up to the middle of the shaft is subcircular, but in the upper portion of the shaft and on the first portion of the hook it is ellipsoidal, and significantly wider than high. Still later the cross section becomes subtrapezoidal and is only slightly wider than high.

The ornamentation of the last part of the planispiral whorl and on shaft of RGM 354 119 consists of strong trituberculate main ribs generally separated by four to five (rarely three, but in one place even six), thin, non-tuberculate intercalated ribs, which cross the venter without interruption, and without becoming broader. All ribs are straight, slightly inclined forward on the upper part of the shaft. RGM 354 125 is very similar to the holotype, i.e., there are three, later two intermediate ribs between every two trituberculate main ribs on the first part of the shaft and at the beginning of the hook only one. Three (rarely four) thin branches originate from the umbilical spines, which are thin like the intermediate ribs and cross the dorsum in a straight line. On the straight portion of the hook (RGM 354 119, 354 125) only trituberculate main ribs are present. The ventral spines have a circular basis, whereas the bases of the lateral and umbilical spines are elongated in the direction of ribbing. The lateral spines are longer than the ventral and umbilical ones. On the hook the main ribs become very prominent, and the lateral and umbilical spines are longer than the ventral ones.

Measurements – RGM 354 119: $H_1 = 49.0$; $W_1 = 49.5$; $H_2 = 55.5$; $W_2 = 56.5$; $D_1 = 120.5$.
RGM 354 125: $H_1 = 62.5$; $W_1 = 59.0$; $H_2 = 61.0$; $W_2 = 75.2$; $D_1 = 155.0$.

Comparison and remarks – The described specimens (except RGM 354 125) differ from the holotype in having a slightly smaller shell, but it has to be regarded as an example of intraspecific variation in shell size. On the shaft of RGM 353 620 there is a clear example of an injury received when the animal was still alive (see Pl. 15, fig. 1a, b).

Occurrences – Guane, Vereda Chaguete, (RGM 354 119, RGM 354 125); Guane, Vereda Chaguete, along the road (RGM 353 619), Barichara; lowermost? Aptian.

Distribution – Upper? Barremian-lower Aptian of France, North Caucasus (Russia), Crimea?, Colombia.

Ancyloceras cf. mantelli Casey, 1960

Pl. 77; Fig. 3.

Material – RGM 353 621, represented by the upper part of the shaft and an incomplete hook.

Description – The shell is rather large. The shaft is almost straight, with a slight dorsal bulge. The straight part of the dorsal side of the hook is parallel to the shaft. On the transit portion between the shaft and hook the flanks, dorsum, and venter are rounded. The cross section on the shaft is ellipsoidal (higher than wide). On the hook it is still ellipsoidal, but markedly greater in width.

The ornamentation on the shaft consists of trituberculate main and non-tuberculate intermediate ribs. The main ribs are straight, slightly inclined forward. On the

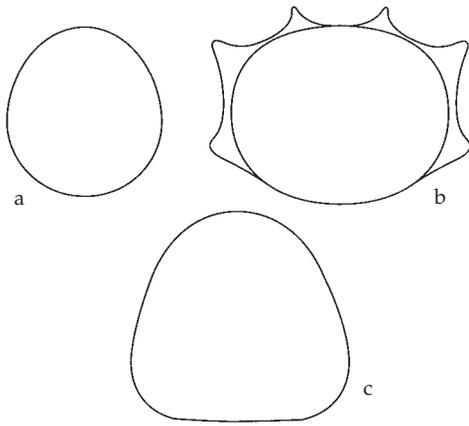


Fig. 2. Cross sections of *A. cf. matheronianum* d'Orbigny, on the shaft (a, b); on the hook (c); RGM 354 119, $\times 1$

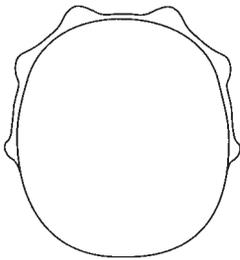


Fig. 3. Cross section of *Ancyloceras cf. mantelli* Casey on the shaft (RGM 353 621), $\times 1$.

venter between the ventral tubercles the ribs are flattened. The bases of the ventral and lateral tubercles are rounded, whereas the bases of the umbilical tubercles are slightly stretched in the direction of the ribs. On the shaft the umbilical tubercles are situated just below the middle of the whorl height, but on the hook, they migrate to a mid-lateral position. The lateral tubercles are situated at four fifths of the whorl height. The intermediate ribs are rather thin; they cross venter in a straight line without interruption. On the shaft and hook the number of intermediate ribs between every two main ribs is generally two, in one occasion one, viz. on the shaft-hook transition. On the shaft there is conspicuous damage of the shell, which has occurred when the animal was alive, and which caused the ribs to be irregularly oriented. From the umbilical tubercles originate two or three thin ribs, which on the dorsum have the same thickness as the intercalated ribs. They cross the dorsum of the shaft with a slight adapically convex curvature, but cross the dorsum of the hook with an adorally convex curvature.

Remarks – The described specimen resembles *A. mantelli* (Fig. 3) in the morphology of the uncoiled part (shaft and hook) and in its sculpture, but differs in having the umbilical tubercles placed higher on the flank, and in having fewer intermediate and intercalatory dorsal ribs. As it was mentioned by Casey (1960, p. 23), “There is no other species of *Ancyloceras* that calls for critical comparison.”

Occurrence – Santa Sofia, lower Aptian.

Distribution – Lower Aptian of England and Colombia.

***Ancyloceras* sp. (Forme 1)**
Pl. 9, fig. 2; Pl. 10; Pl. 16, fig. 1.

Material – Three incomplete specimens. RGM 353 625 is represented by a slightly deformed shaft and hook, but RGM 353 624 and 353 623 are fragments of the shaft.

Description – The morphology of the planispiral whorls is unknown. The shaft is rather long, moderately increasing in height and slightly bent like a horn. The passage from shaft to the hook is rather sharp and accordingly the transverse diameter (D_1) of the shaft-hook is small in comparison to the length of the shaft. The dorsal sides of the shaft and final part of the hook are sub-parallel. The cross section (RGM 353 624) at the early portion of the shaft is subcircular, but after that it becomes subellipsoidal (higher than wide).

The ornamentation of the shaft consists of strong, trituberculate main ribs and three (rarely two) thin, non-tuberculate intermediate ribs between every pair. On the flanks the ribs are straight, and on the first portion of the shaft they are oriented perpendicularly to the attitude of the ventral and dorsal sides, but later they become inclined forward and pass the venter with a gently forward curve. The bases of the ventral spines are circular, whereas the bases of the lateral and umbilical spines are stretched in the direction of the ribs. From each umbilical tubercle three (rarely two) thin dorsal branches originate. All ribs cross the dorsum without interruption; on this side they are equally thin and slightly flexuous. The intermediate ribs cross the venter without interruption with a weak, forward curve. On the hook the main spiny ribs become very strong. Meanwhile, the number of intermediate ribs between every two main ones diminishes to one and on the last straight portion of the hook there are only simple trituberculate main ribs. On this part each umbilical tubercle gives rise to two branches, which cross the dorsum without interruption. Fragments of the suture line are visible on RGM 353 623; it is of the ancyloceratid type.

Measurements –

	H_1	W_1	H_2	D_1
RGM 353 625	39.0	-	61.2	120.0
RGM 353 624	40.0	46.2	-	-
RGM 353 623	40.0	44.5	-	-

Remarks – By the morphology of the shaft and hook, and by the type of sculpture the described specimens should be included in the genus *Ancyloceras*, but because of the lack of sufficient material it is impossible to carry out further specific identification.

Occurrence – Guane, lower Aptian.

***Ancyloceras* sp. (Forme 2)**

Pl. 11.

Material – RGM 353 626, represented by a fragment of the shaft.

Description – The fragment is straight, very slowly increasing in height and width. Its cross section is subellipsoidal and slightly convex on the umbilical area. The ornamentation consists of strong, straight, trituberculate main ribs, and between every pair one thin, straight, non-tuberculate intermediate rib, which cross the venter in a straight line without interruption. On the dorsum all ribs are rather thin

and straight. The bases of the spines are circular. Sometimes two branches arise from the umbilical tubercles; on the dorsum these branches have the same thickness as the short intercalated ribs. When there is no bifurcation from the umbilical spines, the simple ribs on the dorsum are thin, but still thicker than the bifurcating and intercalated ribs.

Remarks – In the style of ribbing (regular alternation of one thick main and one thin intermediate rib) the described fragment is similar to *Ancyloceras vandenheckii* Astier. But, as we do not know the morphology of the earlier and later ontogenetic stages it is identified as *Ancyloceras* sp.

Occurrence – Villa de Leyva, Santa Sofia; upper? Barremian.

Genus *Pseudocrioceras* Spath, 1924

- 1924 *Pseudocrioceras* Spath, p. 72.
pars 1933 *Ancyloceras* Rouchadzé, p. 212.
 1938 *Pseudocrioceras* Anderson, p. 205.
 1938 *Pseudocrioceras* Roman, p. 353.
pars 1949 *Crioceras* (*Pseudocrioceras*) Jenne, p. 623.
pars 1957 *Pedioceras* Wright, p. L208.
 1958 *Pseudocrioceras* Drushtchits & Eristavi, p. 104.
 1978 *Pseudocrioceras* Kakabadze, p. 34.1.
 1981 *Pseudocrioceras* Kakabadze, p. 101.
 1990 *Pseudocrioceras* Delanoy & Bulot, p. 15.
pars 1996 *Pedioceras* Wright *et al.*, p. L214.
 1997 *Pseudocrioceras* Kakabadze & Hoedemaeker, p. 68.
 1999 *Pseudocrioceras* Ropolo & Gonnet, p. 122.
 1999 *Pseudocrioceras* Ropolo *et al.*, p. 168.
 2000 *Pseudocrioceras* Ropolo *et al.*, p. 91.

Type species – *Scaphites abichi* Bacevich & Simonovich, 1873, West Georgia, uppermost? Barremian.

Diagnosis – The initial whorls are crioconic; the last two whorls of the spire become contiguous or very close to each other. After the planispiral coiling follows a straight or slightly curved shaft of various lengths; the shaft is terminated by a variably curved hook, which maintains the same plane of symmetry as the shaft and the spiral. In some cases the shaft is very short and curved, so that the last part of the hook is in touch or very close to the last planispiral whorl. The ornamentation of the inner whorls consists of equal, fine, flexuous or straight simple ribs. Then appear the ventrolateral tubercles, and a little later the umbilical and lateral ones. On the later whorls there are bituberculate or trituberculate main ribs, with one to two non-tuberculate intermediate ribs between every two of them. In some cases the ribs split into two branches, which originate from the umbilical or lateral tubercles. On the venter between the ventrolateral tubercles the ribs may be interrupted, whereas on the dorsum they are not interrupted. On the shaft the sculpture becomes

stronger. The ventrolateral and lateral tubercles become more prominent than the umbilical ones. The latter may disappear earlier. Between the main ribs are one to five non-tuberculate intermediate ribs. On the shaft the ornamentation consists of strong, distant main ribs with or without tuberculation. The suture line is of the ancyloceratid type.

Remarks – On the basis of the peculiarities of the sculpture on the planispiral whorls (in fact on the last two planispiral whorls), Ropolo & Gonnet (1999, p. 122) separated four morphological groups in genus *Pseudocrioceras*.

1. The group of *P. kutatysiense* is characterized by the presence of strong, equal ribs on the spire; these ribs originate in two from umbilical tubercles or bullae. (Consists of *P. kutatysiense* (Rouchadze), *P. kutatysiense* morphe *tuberculata* Ropolo & Gonnet, *P. breve* (d'Orbigny)).
2. The group of *P. waageni* is characterized by bituberculate or trituberculate ribs on the spire; between them a variable number of the intermediate ribs is intercalated. (Consists of *P. waageni waageni* (Anthula), *P. waageni rouchadzei* Dimitrova, *P. waageni sapitshkiensis* (Rouchadzé), *P. waagenoides* (Rouchadzé), *P. abichi* (Anthula), *P. sahariense* (Rouchadzé), *P. steinmanni* (Simonovich & Bacevich), *P. imericum* (Rouchadzé), *P. orbignyianum* (Matheron), *P. kornebaense* Kakabadze, *P. phasiense* (Rouchadzé)).
3. The group of *P. fasciculare* is characterized by bundles of three or four ribs originating from umbilical tubercles or bullae, sometimes also from the lateral tubercles. (Consists of *P. fasciculare fasciculare* (d'Orbigny) and *P. fasciculare bituberculatum* (Ropolo et al.)).
4. The group of *P. coquandi* is characterized by having fine ribs on the spire; these ribs are either parallel or bifurcate from small umbilical tubercles or bullae. (Consists of *P. coquandi* (Matheron), *P. provinciale* (Matheron), *P. duvalianum* (d'Orbigny), *P. anthulai* (Eristavi), *P. densecostatum* Kakabadze, *P. massei* Ropolo & Gonnet, *P. rawsoni* Ropolo & Gonnet, *P. mickali* Ropolo & Gonnet).

Analysis of existing and new additional material reveals that the *P. kutatysiense* and *P. coquandi* groups had better be united, because there is no principal difference in ornamentation between them. Thus, we distinguish only three groups in the genus *Pseudocrioceras*, *P. kutatysiense*, *P. fasciculare* and *P. waageni*.

Distribution – Upper Barremian-lower Aptian. Caucasus, western Europe, Morocco, Colombia, California.

***Pseudocrioceras guanense* sp. nov.**

Pl. 6, fig. 2; Pl. 60, fig. 2; Fig. 4.

Holotype – RGM 353 633.

Paratype – RGM 353 634 is only a fragment of half a whorl.

Type locality – Guane.

Type horizon – Uppermost? Barremian.

Derivatio nominis – The species is named after the type locality Guane.

Diagnosis – The shell consists of almost contiguous whorls, which rapidly increase in height. The morphology of the shaft and the hook is not known. The whorl section is subtrapezoidal in the adult ontogenetic stage. During ontogeny the ventrolateral tubercles appear earlier than the lateral ones, while the umbilical tubercles appear much later (at $D = 45$ mm). Up to $D = 40$ mm the ribbing is fine and dense, but at greater diameters it becomes coarse. In a few cases two branches arise from the ventrolateral tubercles crossing the dorsum without interruption.

Description – The shell consists of nearly contiguous whorls, which rapidly increase in height ($H:h = 1.88$ or 1.78). The umbilicus is wide ($U:D = 0.40$) with a steep wall. The earliest whorls are absent, but with respect to the ratio between the diameter of the cryptoconic shell and the height of the whorl it is possible to conclude that the umbilical hiatus was rather wide. The flanks are slightly convex. On the venter the space between the ventrolateral tubercles is flattened. The dorsum is rather wide and flat. The early whorls (until $D = 40$ mm) are ornamented with straight dense ribs, which bear small ventral tubercles. In a few cases two equal branches spring from the ventrolateral tubercles and cross the dorsum. In this early stage all ribs are equally thin, straight and cross the venter with a forward curve, whereas on the dorsum the ribs pass in a straight line. At $D = 40$ mm the sculpture changes abruptly; it generally consists of straight main ribs, becoming very thin passing the dorsum with a forward curve. From the umbilical margin they gradually become stronger, and on the venter they are very thick. The ventrolateral tubercles are large, and the space on the venter between them is flattened. At this stage the lateral tubercles are weak, but the umbilical ones are still weaker. The ontogenetic development of the whorl section can be traced from $D = 20$ mm. As it is shown on the Figure 4, it changes from ellipsoidal to subtrapezoidal.

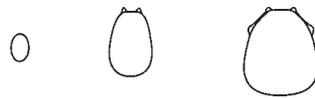


Fig. 4. Whorl section of the cryptoconic whorl of *P. guanense* sp. nov. (holotype), $\times 1$.

Measurements – The holotype measures: $D = 64.2$; $H = 25.3$; $W = 23.2$; $U = 26.4$.

Comparison – The new species resembles *P. anthulai* (Eristavi) in the rapid increase in whorl height and the type of whorl section (ellipsoidal-subtrapezoidal), but clearly differs from it in having coarser ribbing on the late planispiral whorl, weaker umbilical and stronger ventrolateral tubercles, and in the occasional presence of forking ribs (two equal branches may arise from the ventral tubercles and cross the dorsum with a forward curve).

Occurrence – Guane uppermost? Barremian.

Pseudocrioceras anthulai (Eristavi, 1955)

Pl. 3, fig. 1; Pl. 4.

- 1899 *Crioceras Orbigny* (Matheron): Anthula, p. 125, pl. 12, fig. 2a-c.
 1938 *Ancyloceras Anthulai*: Rouchadzé (in coll.).
 1955 *Ancyloceras anthulai*: Eristavi, p. 113.
non 1981 *Pseudocrioceras anthulai* (Eristavi): Kakabadze, pl. 18, fig. 1.
 1991 *Pseudocrioceras anthulai* (Eristavi): Kakabadze & Thieuloy, p. 89, pl. 3, fig. 2-4; text fig. 9.

Holotype – The specimen figured by Anthula (1899, pl. 12, fig. 2a-c). Institute of Palaeontology of the Vienna University. Lowermost? Aptian, Akusha (Daghestan).

Material – RGM 353 851, 353 632, 353 631.

Description – The planispiral part consists of almost contiguous whorls, which rapidly increase in height (H:h varies from 1.70 to 2.00); the earliest whorls are not preserved. The cross section is subtrapezoidal (higher than wide). The umbilicus is wide, moderately deep with a steep wall. The transition from flanks to dorsum is abrupt. The latter is broad, with a slight depression in the middle. The uncoiled part of the shell is represented only by an imprint, which shows that the shaft is short and that the dorsal part of the hook near the aperture touches the ventral side of the last planispiral whorl. In all three specimens only the ornamentation of the planispiral whorls is visible. It consists of simple, radial trituberculate ribs, which are slightly bent forward above the lateral tubercles. The ventrolateral tubercles are larger than the lateral and umbilical ones. Some ribs do not have umbilical tubercles.

Measurements –

	D	H	U
RGM 353 851	103.0	43.5	33.5
RGM 353 632	95.2	48.6	34.5
RGM 353 631	93.0	42.5	35.2

Remarks – Complete specimens of this species were described from Colombia (Kakabadze & Thieuloy, 1991). When these specimens are compared with those described here, a very interesting variation in the shape of the uncoiled part came to light. On specimen RGM 353 851 the shaft is very short and the dorsum of the last part of the hook is in touch with the ventral side of the last planispiral whorl. RGM 353 631 has a similar shape of its uncoiled part. On the other hand, in Kakabadze & Thieuloy (1991, p. 89, pl. 3, figs. 2-4, pl. 4, figs. 1-3), the uncoiled parts of the two figured specimens are not equal in morphology and size, but are longer than Creutzberg's specimens. Nevertheless, the dorsal sides of the last part of the hook (apertural area) of both specimens are also in touch with the ventral side of the last planispiral whorl. We conclude that the different shapes of the uncoiled parts should be regarded as an example of intraspecific variation in *P. anthulai*.

Comparison – The described species resembles *P. densecostatum* Kakabadze in the subtrapezoidal cross section of the last planispiral whorl and by the equal, simple

trituberculate ribs on the planispiral whorls, but differs from it in the thinner, denser ribbing and the smaller tubercles. Moreover, the last part of the hook of *P. densecostatum* is sharply bent, so that its dorsal side cannot touch the venter of the planispiral whorl (the latter is the characteristic feature of *P. anthulai*).

Occurrence – Guane, along the road near the estate of Family Rivera (RGM 353 851); Guane (Quebrada Barichara) (RGM 353 631); Villa de Leyva (RGM 353 632); uppermost? Barremian.

Distribution – Uppermost Barremian? - lower Aptian of Daghestan, Georgia, Colombia.

Genus *Kutatissites* Kakabadze, 1970

- pars* 1955 *Ancyloceras* Eristavi, p. 116.
 1970 *Kutatissites* Kakabadze, p. 734.
 1976 *Simionescites* Avram, p. 77.
 1978 *Kutatissites* Kakabadze, p. 34.4.
 1981 *Kutatissites* Kakabadze, p. 125.
 1983 *Kutatissites* Etayo Serna, p. 4.
 1992 *Kutatissites* Stoykova, p. 253.
 1996 *Kutatissites* Wright *et al.*, p. 228.
 1997 *Kutatissites* Delanoy & Ebbo, p. 4.

Type species – *Kutatissites bifurcatus* Kakabadze, 1970, western Georgia, lowermost? Aptian.

Diagnosis – Very large to medium-sized shells. Early whorls are helicoidal, which are just, or just not, touching. The helicoidal part is followed by planispiral coiling. In some species planispiral coiling is poorly developed (less than one whorl), but most have a well developed plane spire with one to two (sometimes more) contiguous or non-touching whorls. In some cases the morphology of the adult shell consists only of the combination of helicoidal and planispiral coiling, but in others the planispiral whorls are followed by a straight or curved shaft, which ends in a final hook. The cross section of the last helicoidal whorl is asymmetric subcircular or wide-oval; in the planispiral whorl it becomes symmetric subquadrate or wide-oval (wider than high); in the shaft and hook the cross section may be wide-oval, subellipsoidal. The ornamentation of the early helicoidal whorls consists of simple trituberculate asymmetric ribs. On the last helicoidal whorl intermediate ribs may appear, which may bear ventral tubercles. Moreover, there may be bifurcating ribs. Generally the bifurcation point is at the umbilical tubercles. On the planispiral whorls the umbilical tubercles become strong, whereas in some cases the ventral and lateral tubercles decrease, or even disappear, but reappear later. In the species without shaft and hook, the intermediate and bifurcating ribs gradually disappear in the gerontic stage; on the living chamber there are only strong, distant main ribs. The uncoiled species, however, have on the shaft and hook an ancyloceratitid type of sculpture. On the shaft the main ribs generally bear rather strong ventral, lateral, and umbilical tubercles, and

there are one to four (possibly more) thin, non-tuberculate intermediate ribs between every two main ones. On the last part of the hook the number of intermediate ribs between two main ones reduces; they may be absent. The suture line is of the ancyloceratid type; bifid ventral (*E*), and trifid lateral (*L*), umbilical (*U*) and dorsal (*I*) lobes. The lateral lobe is very long.

Remarks – Kakabadze (1981) united uncoiled (= with shaft and hook) and not uncoiled (= without shaft and hook) species in *Kutatissites*. Stoykova (1992) proposed a new genus for the uncoiled (= with shaft and hook) species of *Kutatissites*, but did not give a name to this group. Delanoy & Ebbo (1997) discussed this question carefully and gave the following possible explanations for the existence of uncoiled and not-uncoiled groups in *Kutatissites*; it could be the expression either of strong polymorphism (not related to sexual dimorphism), sexual dimorphism or phylogenetic evolution.

The analysis of all existing and new material from Colombia shows that the type of sculpture, whorl section and suture line are similar in all species of these two groups, and we suppose that there is no fundamental ground to split *Kutatissites* into new genera (or subgenera). It is remarkable to note that among the uncoiled *Kutatissites* there are species, e.g., *K. creutzbergi*, that are characterized by a poorly developed planispiral coiling, viz. after the last helicoidal whorl follows only half a planispiral whorl, which passes into a shaft and ends in a hook. The sculpture and whorl section of this species is typical for *Kutatissites*. It is remarkable that in Colombia this species occurs together with not-uncoiled species of *Kutatissites*. It should be noted that uncoiled and not uncoiled species of *Kutatissites* are also found together in the uppermost Barremian of France (Delanoy & Ebbo, 1997) and in the lowermost? Aptian of Georgia (Kakabadze, 1981). These data make it difficult to accept the assumption of a phylogenetic trend in the mode of coiling of *Kutatissites* during the latest Barremian and earliest Aptian. Such a morphological variability is supposed to be a phenomenon of intrageneric variation.

Distribution – Upper Barremian-lower? Aptian. Georgia, north Caucasus, Daghستان, Turkey, Bulgaria, Romania, France, Spain, Colombia.

***Kutatissites creutzbergi* sp. nov.**

Pls. 18-22; Pl. 45, Fig. 5.

Holotype – RGM 345 790.

Paratype – RGM 353 844.

Type locality – Galan, left bank of Río Suarez.

Type horizon – Uppermost? Barremian.

Derivatio nominis – In honour of Peter Hans Creutzberg (Bogotá, Colombia).

Diagnosis – Very large shell. After the helicoidal spire follows half a planispirally coiled whorl, which passes into a relatively short, U-shaped shaft and hook. The plane of symmetry of the planispiral whorl does not coincide with that of shaft and hook. The

ornamentation of the penultimate helicoidal whorl consists of rather strong, asymmetric, trituberculate, simple main ribs. However, between every two trituberculate ribs on the last helicoidal whorl there is one thin intermediate rib, which bears only a ventral tubercle. On the last part of the planispiral whorl the number of intermediate ribs increases to two and most of them do not bear any tubercles. On the shaft there are three, rarely four, intermediate ribs between every two main ones. On the first part of the hook the number of intermediate ribs between every two main ones diminishes to two, then to one, and on the last part only strong, distant simple ribs are present. The intermediate ribs cross the venter without interruption. The mid ventral space between two opposite ventrolateral tubercles is strongly flattened.

Description – The helix of the holotype is incomplete; only its last two contiguous whorls are preserved and the early helicoidal whorls (visible on Pl. 18, fig 1) are a plastercast made by P. Creutzberg. The axes of coiling of the helix makes an angle with the plane of symmetry of the planispirally half whorl. This planispiral whorl passes into a relatively short U-shaped shaft and hook, of which the plane of symmetry does not coincide with the plane of symmetry of the planispiral half whorl. The cross section of penultimate helicoidal whorl is asymmetrically subcircular, and of the last helicoidal whorl plane spiral, and of the shaft-hook it is suboval (wider than high). Beginning from the last part of helicoidal whorl the dorsum is flat; the venter, however, is slightly rounded.

The ornamentation of the penultimate helicoidal whorl consists of asymmetrical, strongly tuberculate, simple ribs. The thickness of the ribs exceeds the space between them. On the last helicoidal whorl and on the planispiral whorl there is one thin intermediate rib between every two trituberculate main ribs; the intermediate ribs generally do not have tubercles. Only on the last helicoidal whorl some of the intermediate ribs bear ventral tubercles. In later ontogenic stages the presence of tubercles on intermediate ribs is very rare. On the shaft there are three or four intermediate ribs between every two main ones, but on the hook their number decreases to one and on the last part of the hook there are only strong, distant, trituberculate main ribs. On the shaft and hook the main ribs bear very strong umbilical, lateral and ventral tubercles, the bases of which are stretched in the direction of the ribs. The intermediate ribs straightly cross the venter without interruption and without thickening. On the dorsum all ribs are thinning out and pass it with a forward curve.

Measurements – The holotype measures $L_1 = 240.0$; $H_1 = 72.0$; $W_1 = 94.0$; $H_2 = 78.0$; $W_2 = 95.0$.

Remarks – On account of the helicoidal coiling, the mode of transition from helicoidal to planispiral coiling, the presence of a shaft and hook, and the ontogenetic development of the sculpture, the described species belongs to *Kutatissites*. However, it differs from all hitherto known species of this genus in the mode of transition from planispiral whorl into shaft, *viz.* the plane of symmetry of the planispiral whorl does not coincide with the plane symmetry of the shaft and hook. Such differences in coiling should be regarded as intrageneric variation within the genus *Kutatissites*.

Occurrence – Galan, left bank of the Rio Suarez, uppermost? Barremian.

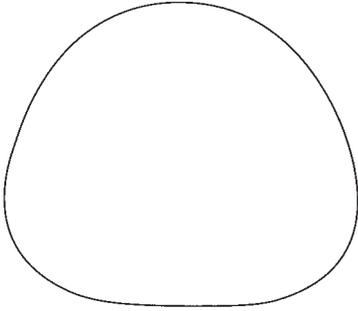


Fig. 5. Whorl section of *Kutatissites creutzbergi* sp. nov. on the hook (holotype), $\times 1$.

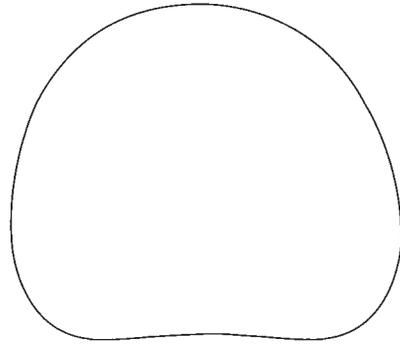


Fig. 6. Cross section of *Kutatissites densecostatus compactus* subsp. nov. at the end of the living chamber (D = 300 mm) (holotype), $\times 1$.

***Kutatissites densecostatus* Kakabadze, 1981**
***Kutatissites densecostatus compactus* subsp. nov.**
 Pls. 23-26; Fig. 6

Holotype – RGM 353 840.

Type locality – Galan, left bank of Río Suarez.

Type horizon – Uppermost? Barremian.

Derivatio nominis – *Compactus* (Latin) = closely and firmly packed, referring to the compactly coiled whorls.

Diagnosis – The rather small helix is surrounded by two and a half contiguous whorls. The first planispiral whorl is rapidly increasing in height, in later whorls the increment in height slows down; the whorl height of the living chamber is strongly decreasing and its oval cross section becomes wider than high. The sculpture of the first planispiral whorl consists of simple and bifurcating ribs. The bifurcation point is in the umbilical tubercles. In a late ontogenetic stage, especially on the living chamber, there are very strong trituberculate main ribs of which every two are separated by one-three intermediate ribs.

Description – The shell is very large (D = 300 mm) and consists of contiguous helicoidal and planispiral whorls. From the helicoidal part only the last whorl is preserved and on account of its diameter (d = 30 mm) one may conclude that the helix is rather small compared to the size of the whole shell. The transition of the last helicoidal whorl into the planispiral one is rapid. The first planispiral whorl is rapidly increasing in height, but after 1.5 whorls the increment in height is moderate, and at the end of the living chamber the whorl height is smaller than at the beginning of the living chamber. The venter of the planispiral whorl is rounded as is the transition to

flanks. On the living chamber the flanks are flat, but the venter and its junction to the flanks remain rounded. The dorsum is broad and flat. The umbilicus is wide ($U:D = 0.41$) with a steep wall.

The cross section of the last helicoidal whorl cannot be observed. At the beginning of the planispiral coiling the cross section is suboval (slightly wider than high). The cross section of the first part of the beginning of the living chamber is wide suboval (slightly higher than wide), but at the end it has a low oval form (slightly wider than high) (Fig. 6).

The ornamentation of the last helicoidal whorl consists of rather strong, dense, slightly flexuous trituberculate ribs. On the first planispiral whorl there are simple trituberculate main ribs, simple non-tuberculate intermediate ribs and bifurcating tuberculate ribs. The bifurcation point is situated at the umbilical tubercles. This type of ribbing is characteristic for the last planispiral whorl of this species. The penultimate whorl is not well preserved, but its first half is ornamented by dense straight ribs of which the thickness exceeds the space between them. The main ribs bear umbilical and lateral tubercles. The ventral tubercles are not represented over the entire second planispiral whorl. On the third whorl the type of sculpture changes; there reappear the straight trituberculate main ribs, which cross the venter straightly without interruption. There are simple intermediate ribs and rarely bifurcating ribs between the main ones. The point of forking is at the umbilical tubercles. In a few cases two or more thin branches appear from the lateral tubercle of the main ribs; they cross the venter without interruption. On the living chamber the number of the intermediate ribs between every two main ones decreases from four to two. All ribs pass the dorsal side with a forward curve.

The suture line is fragmentarily preserved on the second planispiral whorl. It is characterized by rather intense frilling. The lateral (L) and umbilical (U_1) lobes are rather narrow and trifid, but the L/U_1 saddle is broad and rather high, and divided into two branches by narrow secondary lobe. The umbilical lobe is situated on the umbilical wall, near the umbilical rim.

Measurements – RGM 353 840: d (helix) = 30.0; D = 300.0; H = 89.8; E = 103.0; U = 125.0.

Remarks – The described specimen resembles *K. densecostatus* in the general shell form, the rather small helix, the density of the ribs and in the type of bifurcation (i.e., branching from the umbilical tubercles) on the first planispiral whorl, but differs from it in the smaller number of intermediate ribs (between every two main ones) and in the higher cross section of the last planispiral whorl. The Colombian specimen is more complete than the holotype of *K. densecostatus*, because it includes the gerontic stage.

Comparison – The described subspecies resembles *K. ostricensis* Stoyakova, 1992, in the density of the ribs on the helix and on the first planispiral whorl, and by the type of bifurcation (branches arise from the umbilical tubercles) on the first planispiral whorl, but differs in the lower suboval cross section of the planispiral whorls, and the coarser ribbing on the last helicoidal and first planispiral whorls. *Kutatissites densecostatus compactus* resembles *K. princeps* (Avram) by the type of ornamentation, but the

latter is characterized by the greater diameter of the helix and the rapidly increase in height of the first planispiral whorl.

Occurrence – Galan, left bank of Río Suarez. Uppermost? Barremian.

***Kutatissites simionescui* (Avram, 1976)**

Pl. 3, fig. 3; Pls. 27-34; Fig. 7.

1976 *Simionescites simionescui* Avram, p. 80, text-fig. 4, pl. 2, fig. 1, pl. 5, fig. 1, pl. 6, fig. 1.

1992 *Kutatissites simionescui* (Avram): Stoykova, p. 255, figs. 2, 3.

Holotype – The specimen figured by Avram (1976, pl. 5, fig. 1), Roumania, v. Muieri, Couloir of Dimbovicioara. Lowermost Aptian? or uppermost Barremian.

Material – Three specimens, RGM 353 854, 353 837 and 353 839.

Description – The transition from helicoidal to planispiral coiling occurs at $h_1 = 28$ mm. The plane spiral consists of very low, nearly contiguous whorls, which moderately increase in height. The venter is rather broad and flattened; the dorsum is broader, also flattened, and has a shallow depression in the adult growth stage. The flanks are convex with the point of maximum thickness in the umbilical area. The cross section of the last helicoidal whorl has an asymmetric wide-oval (slightly broader than high) shape, but the planispiral whorls have a symmetric wide-oval (significantly broader than high) cross section. The umbilicus is wide ($U:D = 0.39$) with a steep, almost vertical wall.

On the helix and the first half of the first planispiral whorls the ornamentation (which is well preserved on RGM 353 854) is asymmetric. On one flank the ribs bear thick umbilical and lateral tubercles; from the lateral tubercles they fork into two or three branches, which bear very weak ventral tubercles. On the other flank, however, the ornamentation is weaker and neither ventral nor lateral tubercles are developed. Only comparatively weak umbilical tubercles are present on the main ribs. From some of the umbilical tubercles two ribs may arise, which, like the simple main ribs, are asymmetric on the venter. On the second part of the first planispiral whorl the ornamentation becomes symmetric. On the last part of the first planispiral whorl and on the first part of the second planispiral whorl the ribs are slightly inclined backward. Between every two main ribs one to two, in some cases (at the end of the first whorl and at the beginning of the second whorl) three to four weak, non-tuberculate intermediate ribs are present. On the second planispiral whorl, besides the umbilical and upper lateral tubercles, ventral tubercles appear again. The ribs bifurcate from the umbilical tubercles, rarely from the lateral tubercles. The suture line is fragmentarily preserved.

Measurements – RGM 353 854: $D = 190.0$; $H = 74.0$; $W = 90.0$; $U = 75.0$ (on the other side of the shell $U = 67.0$); RGM 353 839: $D = 181.0$; $H = 69.0$; $W = 82.0$; $U = 75.0$ (on the other side of the shell $U = 58.0$).

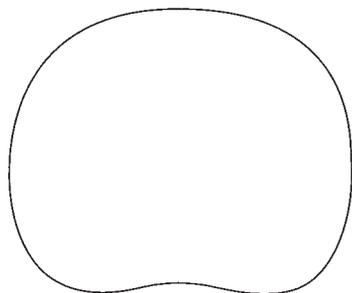


Fig. 7. Whorl section of *K. simionescui* (Avram) at the beginning of the second planispiral whorl (RGM 353 854), $\times 1$.

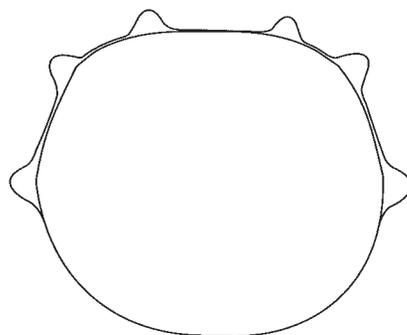


Fig. 8. Cross section of *K. aff. simionescui* (Avram) at the end of the first planispiral whorl (RGM 353 835), $\times 1$.

Remarks – The described Colombian specimens resemble the holotype of *K. simionescui* in the large area of the basis of the helix, the morphology of the planispiral whorls (which are almost contiguous with low and wide-oval cross section), the bifurcation of the ribs from the umbilical tubercles and rarely from the upper lateral ones, and the rarity of ventral tubercles on the first planispiral whorl. There is also a great resemblance between Colombian and Bulgarian specimens (Stoykova, 1992) of this species.

Comparison – The described species resembles *K. densecostatus* Kakabadze in the general shape of the shell, in the wide-oval cross section of the last helicoidal and the first planispiral whorls, and in the frequency of bifurcation of the ribs from umbilical tubercles, but clearly differs from it in having a lower and wider cross section of the planispiral whorls, and in the rarity of the ventral tubercles on the first planispiral whorl.

Occurrence – Galan, left bank of the Río Suarez (RGM 353 854); Guane (Quebrada Barichara), right bank of the Río Suarez (RGM 353 839); Guane (Vereda Chagueta) (RGM 353 837); uppermost? Barremian.

Distribution – Roumania, Couloir of Dimbovicioara, probably lower Bedoulian; Bulgaria, immediately below the beds containing *Deshayesites* (probably uppermost Barremian); Colombia; uppermost? Barremian.

***Kutatissites aff. simionescui* (Avram, 1976)**

Pls. 35-42; Fig. 8.

Material – RGM 353 835, 353 836 and 353 838.

Description – The helix is large; due to the morphology of the preserved three last, almost contiguous whorls, it can be concluded that it consists of five or six whorls. The diameter of the base of the helix (RGM 353 835) is 75 mm. The angle between the axes of

coiling of the helix and plane of coiling of the planispiral whorl is almost 85°. The transition from helicoidal to planispiral coiling comes about at $h_1 = 30\text{--}34$ mm. The plane spiral consists of whorls that only moderately increase in height ($H:h = 1.39$). The umbilicus is wide, deep and has a steep wall. The cross section of the helicoidal whorls is asymmetrical subcircular, but the cross section of the first planispiral whorl is low and wide-oval (much wider than high). From the end of the first planispiral whorl onwards the cross section (especially its costal section) is suboctagonal.

The ornamentation of the helix is asymmetrical and consists of flexuous trituberculate ribs. The asymmetry is also expressed by development of the tubercles: on the one flank the ventral, lateral and umbilical tubercles are rather strong, whereas on the other flank they are very weak. The asymmetry of the sculpture continues on the first part of the first planispiral whorl (RGM 353 835); on the one flank the ornamentation consists of an alternation of trituberculate main ribs with thin, non-tuberculate intermediate ribs. Moreover, from the umbilical or lateral tubercles of some main ribs originate thin non-tuberculate branches, which, like the intermediate ribs, cross the venter in a straight manner without interruption; very weak ventral tubercles are present. On the other flank of this first part of the first planispiral whorl the sculpture is different, *viz.* only weak umbilical tubercles are present from which sometimes thin ribs may arise.

On the second half of the first planispiral whorl the ornamentation becomes symmetrical and consists of rather strong, slightly rursiradiate, trituberculate main ribs, with two, rarely one or three, non-tuberculate secondary ribs. Rarely (RGM 353 838), bifurcating intermediate ribs are present of which the bifurcation point is situated in the middle of the flank. However, on the opposite flank these branches continue as simple intermediate ribs. The branches may very rarely arise from the umbilical tubercles. The siphonal band between the ventral tubercles is depressed and the ribs are flattened (in some cases they are even not visible), but the intermediate ribs cross the venter in a straight line without interruption. On the dorsum the ribs are thinner and bent forward.

Measurements –

	D	H	W	U
RGM 353 835	236.0	80.0	95.0	102.0
RGM 253 838	164.0	61.5	82.5	73.0
RGM 353 836	-	58.0	77.5	-

Remarks – The described specimens approaches *K. simionescui* in the contiguous planispiral whorls, which moderately increase in height, and in the slightly backwardly inclined ribbing, but differ from it in the low wide-oval cross section of the planispiral whorls and in the absence of a depression on the dorsum. Moreover, the first planispiral whorl bears only umbilical and lateral tubercles, whereas *K. simionescui* has in addition weak ventral tubercles on the first half of the first planispiral whorl. The Colombian specimens differ from *K. aff. simionescui* (Avram), described by Delanoy & Ebbo (1997), in having significantly coarser ribbing on the helix and on the first planispiral whorl, in having slightly retroradiate ribs, and in the orientation of axis of the helix in relation to the symmetry plane of the planispiral whorls.

Occurrence – Galan, left bank of Río Suarez (RGM 353 835); Guane (Vereda Chaguetá, exact location unknown) (RGM 353 836); Guane (Quebrada Barichara, (RGM 252 838); uppermost? Barremian.

***Kutatissites etayosernai* sp. nov.**

Pls. 43-44, 46-49.

Holotype – RGM 353 841.

Paratype – RGM 353 842.

Type locality – Galan, left bank of Río Suarez.

Type horizon – Uppermost? Barremian.

Derivatio nominis – Named in honour of Professor Dr. F. Etayo-Serna (Bogotá, Colombia).

Diagnosis – The very large shell consists of helicoidal and planispiral whorls, which are contiguous. The third, uncoiled stage (shaft, hook) is not developed. The planispiral whorls are low and broad. On the first half of the first planispiral whorl, strong, trituberculate main ribs are present, usually with two to four non-tuberculate intermediate ribs between every two main ones, but on the second half of the same whorl the number of intermediate ribs reduces to one, and still later they totally disappear. On this part of the shell there are only very strong and dense main ribs.

Description – The coiling of the helix is sinistral; the helix is rather large and consists of more than four contiguous whorls. The last helicoidal whorl is sharply bent, so that it partly covers the earlier whorls, and then passes into the planispiral coiling. The flanks of the planispiral whorls are convex. The venter is broadly arched, whereas the dorsum is flattened. The cross section of the planispiral whorl changes from oval to subtrapezoidal (wider than high). The ornamentation of the last helicoidal whorl is asymmetric, and consists of trituberculate main ribs and non-tuberculate intermediate ribs. At the beginning of the planispiral coiling the sculpture becomes symmetrical. On the first half of the first planispiral whorl the number of intermediate ribs between every two main ones is two to four, rarely five, but later it reduces to two. From some umbilical tubercles two thin ribs arise, which bear weak lateral and stronger ventral tubercles. On the second half of the first planispiral whorl the number of intermediate ribs between two main ribs reduces to one, and after that there are only widely spaced main ribs. All ribs are slightly inclined backward, but they cross the venter in a straight line without interruption, whereas on the dorsum they are thin and curved forward. The elaborately frilled suture line is fragmentarily preserved on RGM 353 842.

Measurements – RGM 353 841: D = 200.0; H = 71.5; W = 90.0; U = 71.0. RGM 353 842: D = 190.0; H = 61.0; W = 80.2; U = 78.3.

Comparison – The described species differs from the other species of *Kutatissites* in having the ‘gerontic’ type of sculpture already on the second half of the first planispiral whorl. The gerontic sculpture consists of very strong, distant trituberculate main ribs, between which only one intermediate rib is intercalated; finally only very strong, distant trituberculate main ribs are present.

Occurrence – Galan (left bank of Río Suarez); uppermost? Barremian.

***Kutatissites grandis* sp. nov.**

Pls. 50-52; Fig. 9.

Holotype – RGM 353 847.

Paratype – RGM 353 846.

Type locality – Guane (Quabrada Barichara, right bank of Río Suarez).

Type horizon – Uppermost? Barremian.

Derivatio nominis – *Grandis* (Latin) = large referring to its large shell.

Diagnosis – The shell is large. The transition from helicoidal to planispiral coiling is rather abrupt. The planispiral whorl is very low and broad. It is ornamented with bituberculate (umbilical and lateral tubercles) main ribs, separated by non-tuberculate intermediate ribs. Ventral tubercles are visible only at the transition between the helicoidal and planispiral coiling.

Description – The coiling of the helix is sinistral. Only the last three contiguous whorls are preserved on the holotype, but on account of the space left open one may assess the total number of whorls to be five or six. The transition from helicoidal into planispiral coiling comes about in two steps. At the beginning the change in coiling is gradual, but approximately after a quarter of the whorl an abrupt change in the orientation of coiling sets in, i.e., the plane of symmetry turns 90° and the whorl abruptly turns with it passing into the second step. The part of the whorl that is transitional between helicoidal and planispiral coiling covers the helix (protecting it against damage) and after that the planispiral whorl becomes oriented in a new plane, winding around the remainder of shell. This planispiral coiling is preserved only over an interval of three quarters of a whorl; later stages are not preserved.

The cross section of the last helicoidal whorl is asymmetric subcoronate-oval (wider than high). On the part of the whorl that is transitional

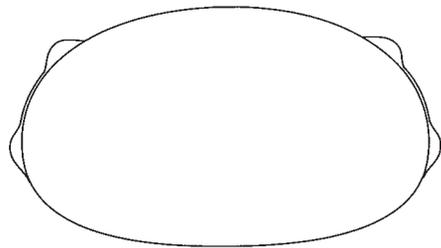


Fig. 9. Cross section of *K. grandis* sp. nov. in the planispiral stage (holotype), $\times 1$.

from helicoidal to planispiral coiling, the cross section is still asymmetric and has a low-oval to coronate-oval form. In the planispiral part the cross section becomes symmetric and obtains a very low and wide-oval shape. The ribbing of the helicoidal whorls is asymmetrically flexuous. The last helicoidal whorl is ornamented with simple and bifurcating ribs. The point of bifurcation is in the umbilical area. Unfortunately, the tuberculation is not visible because of bad preservation of the last helicoidal whorl. On the first part of the planispiral whorl the sculpture consists of tuberculate main ribs, in a few cases separated by only one non-tuberculate intermediate rib. The main ribs bear very strong umbilical and lateral tubercles. The ventral tubercles are very weak (rudimentary thickenings) and only present on the first part of the planispiral whorl. On the siphonal band between the ventral thickenings the ribs are flattened. Later, the ventral thickenings disappear and the main ribs bear only umbilical and lateral tubercles, which are rather strong. From some umbilical tubercles arise two ribs, which do not bear lateral tubercles. On the second part of the planispiral whorl the bituberculate main ribs become stronger, and the number of the non-tuberculate intermediate ribs between every two main ones varies from one to six. From some of the umbilical tubercles on the main ribs a thin branch may originate. All ribs cross the venter in a straight line without interruption. On the dorsum they are weak, but the difference between main and intermediate ribs remains visible. It is remarkable that they cross the dorsum rectilinearly.

Remarks – The described species differs from the other species of *Kutatissites* in the last helicoidal and first planispiral whorl having a very low and wide-coronate cross section, in bearing strong umbilical and lateral tubercles, and in the straight crossing of the ribs over the dorsum. Since a complete adult specimen of this species is not available, the morphology of the gerontic stage of the shell is unknown. However, on account of the morphology of the planispiral whorl, which significantly decreases in height, one may assume that *K. grandis* is characterized by not having a third uncoiled (shaft and hook) ontogenetic stage.

Occurrence – Guane, Quebrada Barichara, (RGM 353 847); Galan (left bank of Río Suarez) (RGM 353 846); uppermost? Barremian.

***Kutatissites? galanensis* sp. nov.**

Pl. 53; Pl. 54, fig. 1; Pl. 55.

Holotype – RGM 353 843.

Type locality – Galan (left bank of Río Suarez).

Type horizon – Uppermost? Barremian.

Derivatio nominis – The species is named after the type locality Galan (Colombia).

Diagnosis – The planispiral whorls are almost contiguous. The umbilicus is wide and has a steep umbilical wall. The ornamentation of the first planispiral whorl consists

of simple, thin, trituberculate main ribs. Bifurcating and simple intermediate ribs appear later; the branches arise from the umbilical tubercles.

Description – The morphology of the early whorls (up to $h_1 = 11$ mm) is unknown. The plane spiral consists of 2.3 almost contiguous whorls, which at first increase rapidly in height, but on the last whorl only moderately increase in height. The umbilicus is wide ($U:D = 0.38$) and has a steep wall. The venter is broadly rounded, the flanks are slightly convex, the transition to the dorsum is rather sharp, the dorsum is wide and flattened, and the whorl section is low-suboval (significantly wider than high). It is remarkable that the preserved beginning of the whorl is not in the same plane of symmetry as the following planispiral whorls. Up to $D = 65$ mm the ornamentation consists of simple, trituberculate, rather thin, widely spaced ribs; the intercostal space exceeds twice the thickness of the ribs. After $D = 65$ mm, in addition, bifurcating and non-tuberculate intermediate ribs appear. As a rule the branches arise from the umbilical tubercles. After $D = 160$ mm a typically ancyloceratic sculpture develops, i.e., between every two trituberculate main ribs, two to three (rarely more) thin intermediate ribs are intercalated. On the flanks the ribs are straight and pass without interruption straight over the venter. On the siphonal band between the ventral tubercles the ribs are very flattened. On the dorsum all ribs are thinning out and curved forward.

Measurements – $D = 227.0$; $H = 80.2$; $W = 98.0$; $U = 87.0$.

Remarks – Although the earlier whorls of the holotype are missing, it is clear that the plane of symmetry of the preserved earliest part of the planispiral whorls deviates from the plane of coiling of the other planispiral whorls. Therefore, this earliest part of the whorl is supposed to belong to the transitional part between helicoidal and planispiral coiling. Moreover, the type of the sculpture and whorl section is similar of those of *Kutatissites*. However, the described specimen also resembles the genus *Pseudocrioceras* by its type of sculpture in the planispiral stage. However, the cross section of the planispiral whorls of *Pseudocrioceras* is generally higher than wide. On account of these data we concluded that the described species should be considered, tentatively, to belong to *Kutatissites*.

The described species is very similar to *K. heliceroides* (Rouchadze) in its rapid increase in height of the planispiral whorls and in the general morphology of the whorl section and sculpture, but differs in the ornamentation of the first planispiral whorl, which shows only simple, thin trituberculate ribs (i.e., on the first planispiral whorl bifurcating and intermediate ribs are absent).

Occurrence – Galan (left bank of Río Suarez); uppermost? Barremian.

Genus *Ammonitoceras* Dumas, 1876

1876 *Ammonitoceras* Dumas, p. 405.

1910 *Ammonitoceras* Kilian, p. 353.

1957 *Ammonitoceras* Wright, p. L211.

1961 *Ammonitoceras* Casey, p. 6.

pars 1981 *Ammonitoceras* Kakabadze, p. 118.
1996 *Ammonitoceras* Wright *et al.*, p. 221.

Type species – *Ammonitoceras ucetiae* Dumas, 1876, lower Aptian, France.

Diagnosis – The whorls are contiguous except for the crioconic initial whorls. In some cases the last whorl (the last part of the living chamber) may be crioconically uncoiled again. The whorl section may be ellipsoidal or oval, but always is wider than high. The ornamentation of the inner whorls consists of simple trituberculate ribs. The ventrolateral tubercles disappear in an early stage; after their disappearance the sculpture consists of strong, bituberculate main ribs, of which every two are separated by one to three (possible more) thin, non-tuberculate intermediate ribs. On the early whorls most main ribs bifurcate at the lateral tubercles, and on the venter all ribs are equal and not interrupted. In the gerontic stage, i.e., the living chamber, tubercles may be absent and the sculpture consists of very distant, strong, simple main ribs. The suture line is characterized by a narrow bifid ventral lobe (*E*), a long, asymmetric trifid lateral lobe (*L*), and a very narrow first lateral saddle (*E/L*).

Comparison – The character of ornamentation (bituberculate main ribs, separated by one to three thin non-tuberculate intermediate ribs) in the middle growth stage of *Ammonitoceras* is similar to *Epancyloceras* Spath, but *Ammonitoceras* differs from the latter in the absence of a shaft and hook. The comparison with the other similar genus, *Laqueoceras*, is given below.

Distribution – Lower Aptian-upper Aptian. France, England, Germany, Mangyshlak (Kazakhstan), Turkmenistan, north Caucasus, Georgia, Turkey, Bulgaria, Zululand, Mozambique, Mexico, Colombia.

***Ammonitoceras galanense* sp. nov.**

Pl. 57, fig. 1; Pl. 59; Fig. 10.

Holotype – RGM 353 736, consisting of three planispirally coiled whorls.

Type locality – Galan (left bank of Río Suarez).

Type horizon – Middle? Aptian.

Derivatio nominis – Named after the type locality.

Diagnosis – Early whorls are crioconic, later whorls become contiguous. The planispiral whorls moderately increase in height, and have convex flanks. The umbilicus is wide and has a steep wall. The whorl section is suboval (wider than high). The ornamentation

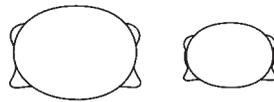


Fig. 10. Whorl section of *Ammonitoceras galanense* sp. nov. (holotype), $\times 1$.

of the last whorls consists of bituberculated main ribs and non-tuberculate intermediate ribs. The lateral spines are larger than the umbilical ones and their bases are slightly elongated in the direction of coiling, whereas the umbilical tubercles have circular bases. From the umbilical tubercles originate two, rarely three thin ribs, which on the dorsum are fine and curved forward. From the lateral spines spring three, rarely four branches, which cross the venter without interruption with a slightly forward curve. Between every two bituberculate main ribs are one to two non-tuberculate intermediate ribs. On the venter all ribs are equal.

Description – The early whorls are only fragmentarily preserved; they are conic with an umbilical 'hiatus'. The following whorls are moderately increasing in height ($H:h = 1.5$). The whorls are mainly depressed coronatiform with a broadly rounded venter and slightly concave flanks. The dorsum is flattened and has a depression on the last whorl. The cross section is suboval (wider than high). The umbilicus is wide ($U:D = 0.46$), deep and has a steep wall.

The ornamentation is well visible on the adult stage, approximately from $D = 45$ mm. It consists of bituberculate main ribs and non-tuberculate intermediate ribs. The number of intermediate ribs between every two main ones is one or two. The lateral spines are larger than the umbilical tubercles and their bases are slightly elongated in the direction of coiling. The umbilical tubercles are small and have rounded bases. Moreover, with increasing shell size the umbilical tubercles move to a higher position on the flanks. Some non-tuberculate intermediate ribs pass over to the other flank and become united with the lateral tubercles there. In a few cases looped ribs have developed between the lateral and umbilical tubercles. On the dorsum the intermediate ribs are equally thin as the ribs that originate in pairs (rarely in threes) from the umbilical tubercles and slightly curved forward. It is remarkable that the last tiny ventral tubercle is observed at the $D = 51$ mm; on larger diameters no ventral tubercles are present. The ventral side of the early whorls is not visible.

Measurements – $D = 103.5$; $H = 40.0$; $W = 45.0$; $U = 47.5$.

Comparison – The new species approaches *Ammonitoceras sowerbyi* Casey, 1961, in the type of coiling and the oval whorl section, but differs in the finer bunch-like ribs that arise from the lateral tubercles and in the bases of the lateral tubercles being slightly elongated in the direction of coiling.

Occurrence – Galan (left bank of Río Suarez); middle? Aptian.

Ammonitoceras giganteum sp. nov.

Pl. 58.

Holotype – RGM 353 845.

Type locality – Guane.

Type horizon – Middle? Aptian.

Derivatio nominis – *Gigas* (Latin) = giant; from its giant size.

Diagnosis – Very large shell of discoidal shape with contiguous planispiral whorls, which rapidly increase in height. Up to $D = 70$ mm the cross section of the early whorls is subcircular (slightly wider than high), after that diameter it is oval (higher than wide). Until $D = 110$ mm the ornamentation consists of simple, straight, non-tuberculate ribs. From that diameter onward umbilical and lateral tubercles appear. Bifurcation often occurs, especially at the umbilical tubercles, but rarely also at the lateral tubercles. The lateral tubercles are situated slightly above the middle of the flank. The tubercles disappear after $D = 310$ mm and up to $D = 480$ mm the ornamentation consists of dense, slightly backwardly inclined simple ribs. A very few ribs bifurcate. After $D = 480$ mm the ornamentation consists only of coarse, very distant, straight simple ribs.

Description – Very large shell of discoidal shape ($D > 500$ mm) composed of contiguous planispiral whorls which rapidly increase in height. The early whorls (up to $D = 70$ mm) are rounded and low, but later the convexity of the flanks diminishes and the whorls increase more rapidly in height. The venter is rounded, the dorsum is flattened. Up to $D = 70$ mm the whorl section is subcircular (slightly wider than high), but after that diameter it becomes oval (higher than wide) with the point of maximum thickness in the umbilical area. Up to $D = 105-110$ mm the ornamentation consists of simple, straight, coarse, closely spaced ribs, which cross the venter in a straight line while becoming slightly thicker. The space between the ribs is equal to their thickness. After $D = 110$ mm umbilical tubercles appear on some ribs and a little later also lateral tubercles appear. The latter are situated a little above the middle of the flank. Frequently the umbilical tubercles give rise to two equal ribs of which generally one bears a lateral tubercle. Rarely, bifurcation occurs at the lateral tubercles. Between the main tuberculate ribs thin, simple, non-tuberculate intermediate ribs occur, which are irregularly distributed. Tuberculation is present only on one whorl and the lateral tubercles disappear earlier than the umbilical ones. Approximately from $D = 310$ mm the sculpture consists of rather dense, simple ribs, which are slightly inclined backwards. Only a few of them bifurcate at mid flank. On the venter the ribs are slightly curved forward without becoming broader. After $D = 480$ mm the ornamentation abruptly changes; the ribs become very strong and substantially distant. This should be the beginning of the living chamber. The later part of the living chamber is not preserved.

Measurements – $D = 530.0$; $H = 190.2$; $W = 135.3$; $U = 210.0$.

Remarks – The described species exhibits the characteristic features of the genus *Ammonitoceras* Dumas, viz. the early whorls are contiguous and low, with convex flanks (cross section is wider than high). Umbilical and lateral tubercles are present in a specific stage of the ontogeny; they disappear in a later stage. Also the manner in which the ribs bifurcate is similar to *Ammonitoceras*. The manner of bifurcation is reminiscent of *Ammonitoceras lahuseni* (Sinzow), but in the latter species bifurcation from lateral tubercles occurs more frequently and the cross section of the whorls in late ontogenetic stages is low and broad.

Occurrence – Guane; middle? Aptian.

Genus *Laqueoceras* gen. nov.

Type species – *Laqueoceras laqueus* sp. nov.

Derivatio nominis – The genus is named after its peculiar lasso-like mode of coiling: *Laqueus* (Latin) = snare, noose, lasso; and *ceras* = horn.

Diagnosis – Lasso-like curved shell in the adult growth stage. The morphology of the early whorls is not known. The cross section of the lasso changes from subcircular via subquadrate to subtrapezoidal. On the first half of the noose-shaped whorl the sculpture consists of distant main ribs with umbilical and lateral tubercles. From the latter the ribs bifurcate into two branches. Occasionally one thin, non-tuberculate intermediate rib is intercalated between two main ribs. On the second half of the noose-shaped whorl only bifurcating, bituberculate, distantly spaced main ribs occur.

Remarks – Heteromorphic ammonites with a lasso-like coiling ornamented with bituberculate, bifurcating main ribs and non-tuberculate simple intermediate ribs have not been described before. We believe that they belong to a new genus, though we must acknowledge that we had only two incomplete specimens at our disposal. The suture line is of the ancyloceratid type.

Comparison – The ornamentation of the new genus is reminiscent of a specific ontogenetic stage of *Ammonitoceras* Dumas. However, the new genus differs from *Ammonitoceras* in having a noose-like uncoiled shell shape and in exhibiting the peculiar development of the whorl section (subcircular – subquadrate – subtrapezoidal) in the mature ontogenetic stage.

Distribution – Middle? Aptian of Colombia.

***Laqueoceras laqueus* sp. nov.**

Pl. 60, fig. 1; Pls. 61-63; Fig. 11.

Holotype – RGM 353 735.

Paratype – RGM 353 734.

Type locality – Villa de Leyva (Loma Gonzalez).

Type horizon – Middle? Aptian.

Derivatio nominis – *Laqueus* (Latin) = snare, noose, lasso; from its peculiar lasso-like mode of coiling.

Diagnosis – In the adult stage the shell consists of lasso-like coiled whorl. The cross

section changes from subcircular via subquadrate to subtrapezoidal. The ornamentation on the first half of the lasso-like whorl consists of distant, bituberculated ribs, which bifurcate from the lateral tubercles. Occasionally one thin, non-tuberculate intermediate rib is intercalated between two main ribs. On the second half of the lasso-like whorl only bifurcating, bituberculate, distant main ribs are present.

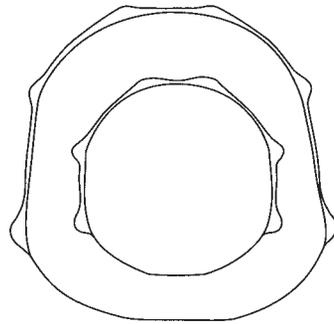


Fig. 11. Cross section of *Laqueoceras laqueus* sp. nov. at the beginning of the first stretch of the lasso-like whorl and at the end of the second stretch of the lasso (holotype), $\times 1$.

Description – Both specimens consist only of a lasso-like coiled whorl. The morphology of the early whorls is not known. The first half of the lasso-like whorl is curved like a horn. It slowly increases in height and in breadth, but in the arched transition to the second half of the lasso-like bow, the whorl rapidly increases in height and breadth. In the second half of the lasso-like whorl the increment in height and breadth slows down again. It is remarkable that the plane of symmetry of the first arm of the lasso deviates from the plane symmetry of the second lasso arm. The whorl section changes from subcircular to suboctagonal (higher than wide). The costal section changes from subquadrate via suboctagonal to subtrapezoidal (higher than wide).

The ornamentation on first half of the lasso-like whorl consists of strong, distant, bituberculate ribs, which bifurcate from lateral tubercles. Only one trituberculate rib was found. Occasionally one rather thin, non-tuberculate secondary rib is intercalated between two tuberculate main ribs. The main ribs and the intermediate ribs are equal on the venter. Only the anterior branches of the main bifurcating ribs are slightly curved forward, whereas the posterior branches and the secondary ribs cross the venter in a straight line. In the siphonal band the ribs are depressed. On the venter of the transitional part between the two arms of the lasso the ribs are curved forward. On the second lasso-like whorl the sculpture consists of only bifurcating, bituberculated, distant main ribs. As a rule bifurcation occurs at the upper lateral tubercles; only in one case the branches arise from the umbilical tubercles. The ribs cross the venter in a straight line without thickening. The thin ribs of the dorsal side arise by two or three from the umbilical tubercles and are curved forward. Fragments of the elaborately frilled suture line are visible on both lasso-like whorls.

Measurements – RGM 353 734: $D_1 = 240.0$; $H_1 = 59.2$; $W_1 = 55.2$; $H_2 = 86.0$; $W_2 = 79.0$.
RGM 353 735: $D_1 = 220.0$; $H_1 = 55.2$; $W_1 = 55.2$; $H_2 = 77.0$; $W_2 = 75.3$.

Remarks – Both described specimens have similar ornamentation and cross section; they differ from each other only by the quality of the lasso-like bending, viz. RGM 353 735 has longer and less curved lasso arms than RGM 353 734. Although both specimens are incomplete and the shape of their total shells is unknown, we

assume that such small differences in coiling should be regarded as variations within one species.

Occurrence – Villa de Leyva (Loma Gonzalez); middle? Aptian.

Genus *Pseudoaustraliceras* Kakabadze, 1981

1981 *Pseudoaustraliceras* Kakabadze, p. 114.

1983 *Pseudoaustraliceras* Etayo Serna, p. 7.

1996 *Pseudoaustraliceras* Wright *et al.*, p. L216.

Type species – *Crioceras ramososeptatum* Anthula, 1899, Daghestan, village Ashilta, middle Aptian.

Diagnosis – Very large shell with crioconic early whorls followed by contiguous whorls in a late ontogenetic stage. The cross section of the early whorls is circular and later in the ontogeny subellipsoidal, subrectangular or suboval (wider than high); in the adult stage it generally becomes higher than wide. The ornamentation of the earliest whorls consists of fine, simple, equal, non-tuberculate ribs. Then appear the lateral tubercles. The umbilical and ventrolateral tubercles appear still later. Simultaneously appear the intermediate non-tuberculate ribs. The umbilical tubercles are smaller than the lateral and ventrolateral ones. In a few cases looped ribs may develop between the lateral and ventrolateral tubercles. The thin intercalatory ribs and the equally thin ribs that arise in two to four branches from the umbilical tubercles uninterruptedly cross the dorsum with a forward curve. In the mature stage the tubercles have disappeared, and the ornamentation consists of simple, strong, distant main ribs, which in rare occasions may bifurcate, and of intermediate ribs between them. On the living chamber the sculpture consists only of simple, thick, non-tuberculate distant ribs. The suture line is of the ancylocertatid type. In the mature stage it is characterized by narrow and elaborately frilled lobes and saddles.

Remarks – *Pseudoaustraliceras* resembles middle Aptian planispiral *Australiceras* (*Australiceras*) Whitehouse in the general type of coiling, and the type of sculpture in the mature and gerontic stages, but clearly differs from it in the type of tuberculation; in *Pseudoaustraliceras* the lateral tubercles appear earlier, and are markedly larger than the ventrolateral and umbilical ones. Moreover, *Pseudoaustraliceras* is characterized by a smaller number (one, rarely two) of intermediate ribs between the main ones, and by the existence of the thin ribs arising from the umbilical tubercles and crossing the dorsum. Finally, *Pseudoaustraliceras* has no tubercles on the living chamber, whereas *Australiceras* is characterized by coarse trituberculate ribbing in the gerontic stage.

Distribution – Middle and upper Aptian. Mangyshlak (Kazakhstan), Kopetdag, Bolshoy Balchan and Tuarkyr (Turkmenistan), Georgia, Armenia, Azerbaijan, north Caucasus, Volga region (Russia), Bulgaria, Hungary, Switzerland, Germany, Madagascar, Angola, India, Colombia.

***Pseudoaustraliceras columbiae* (Basse, 1928)**

Pl. 64, fig. 1; Pl. 66, fig. 2; Pl. 67, fig. 1.

1928 *Ancyloceras Columbiae* Basse, p. 142, text fig. 20, pl. 8, fig. 6, 7a-b.1983 *Pseudoaustraliceras columbiae* (Basse): Etayo Serna, p. 7, text figs. 3a-d, 4a-d, pls. 1, 2.1991 *Pseudoaustraliceras columbiae* (Basse): Kakabadze & Thieuloy, p. 92, text fig. 11, pl. 4, figs. 7-8, pl. 5 figs. 1-5.1997 *Pseudoaustraliceras columbiae* (Basse): Kakabadze & Hoedemaeker, pl. 8, fig. 1, pl. 9, fig. 1, pl. 10, fig. 1, pl. 11, fig. 1, pl. 12, figs. 1, 2.

Lectotype – The specimen figured by Basse (1928, pl. 8, fig. 7a-b) and described by Etayo Serna (1983, fig. 3b-c); middle? Aptian of Villa de Leyva, Boyoca, Colombia.

Material – RGM 353 609, 353 610, 353 737.

Diagnosis – The shell is very large ($D > 400$ mm) and consists of crioconic whorls. Only the last whorl (i.e., portion of the living chamber) almost touches the previous whorl. The whorl section is oval; on the early whorls the oval is wider than high, but later it becomes higher than wide. The ornamentation of the early whorls consists of simple non-tuberculate ribs. This ornamentation is followed by the appearance of ventral and lateral tubercles, and a little later also of umbilical tubercles. Between every two trituberculate main ribs there is normally one simple, non-tuberculate intermediate rib. All ribs are straight on the flanks and cross the venter in a straight way. The intermediate ribs cross the venter without interruption, whereas the siphonal parts of the main ribs are so weak that, on the steinkern, it looks as if they are interrupted. From the umbilical tubercles originate two, rarely three ribs, which are as thin as the intermediate ribs and which together with the intermediate ribs cross the dorsum with a forward curve. From approximately $D = 150$ mm a peculiar sculpture develops, viz. from each lateral tubercle spring two equal branches which on the venter have the same thickness as the intermediate ribs. This bifurcating sculpture continues up to $D = 250$ mm (RGM 353 609). Later the tubercles gradually disappear and the ornamentation consists only of non-tuberculate ribs. On the latest stage (RGM 353 737) the ornamentation consists of straight, closely spaced (the intercostal space is equal to the thickness of the ribs), non-tuberculate, simple ribs, which cross the venter in a straight line, but cross the dorsum with a forward curve and slightly thinned. The suture line is of the ancyloceratid type and elaborately frilled.

Measurements – RGM 353 609: $D = 300.0$ (165.0); $H = 90.0$ (56.0); $W = (53.0)$; $U = 144.2$ (86.0). RGM 353 610: $D = 77.0$ (63.0); $H = 25.0$; $W = (23.5)$; $U = 37.5$ (29.8). RGM 353 737: $D = 350.0$; $H = 111.3$; $W = 90.2$; $U = 165.0$.

Comparison – The described species resembles *P. ramososeptatum* in the shape of the shell, the moderate increase in whorl height, and in the type of sculpture up to $D = 60$ – 70 mm and on the living chamber, but differs from it in having ribs that bifurcate from the lateral tubercles in the mature stage and an oval whorl section instead of suboctagonal one. Moreover, in *P. ramososeptatum* the tubercles disappear much earlier in the ontogeny than in *P. columbiae*.

Occurrence – Guane, Quebrada “la Azofcada” (RGM 353 737); Villa de Leyva (Loma Blanca) (RGM 353 609, RGM 353 610); middle? Aptian.

Distribution – Middle? Aptian of Colombia.

***Pseudoaustraliceras pavlowi* (Wassiliewskyi, 1908)**

Pl. 66, fig. 1.

1908 *Crioceras pavlowi* Wassiliewskyi, p. 46, pl. 3, fig. 1a-c.

1949 *Ammonitoceras pavlowi* Luppov, in Luppov *et al.*, p. 251, pl. 77, fig. 4a-c, text fig. 81.

1960 *Ammonitoceras pavlowi* Drushchits, p. 294, pl. 28, fig. 2a-b; pl. 39, fig. 2.

1967 *Ammonitoceras pavlowi* Dimitrova, p. 63, pl. 30, fig. 2.

1981 *Pseudoaustraliceras pavlowi* Kakabadze, pl. 8, fig. 4a-c.

1997 *Pseudoaustraliceras pavlowi* Kakabadze & Hoedemaeker, p. 69, pl. 9, figs. 2a-c.

Holotype – The specimen figured by Wassiliewskyi (1908, pl. 3, fig. 1a-c), Saratow region, middle Aptian.

Material – RGM 353 630.

Remarks – One specimen of *P. pavlowi* from Colombia was described recently in detail (Kakabadze & Hoedemaeker, 1997). This is the second specimen of *P. pavlowi* known from Colombia.

Measurements – D = 98.5; H = 31.0; W = 31.5; U = 49.5.

Occurrence – Villa de Leyva, Aptian (probably middle Aptian).

Distribution – Middle Aptian of north Caucasus (Russia), Mangyshlak (Kazakhstan), Bolshoi Balkhan (Turkmenistan), western Europe, Colombia.

Genus *Toxoceratoides* Spath, 1924

1924 *Toxoceratoides* Spath, p. 78.

1958 *Toxoceratoides* Drushchits & Eristavi, p. 105.

1961 *Toxoceratoides* Casey, p. 77.

1977 *Toxoceratoides* Klinger & Kennedy, p. 305.

1981 *Toxoceratoides* Kakabadze, p. 129.

1986 *Toxoceratoides* Aguirre Urreta, p. 295.

1988 *Toxoceratoides* Khalilov, p. 355.

1996 *Toxoceratoides* Wright *et al.*, p. L223.

Type species – *Toxoceras royerianum* d’Orbigny, 1842, lower Aptian of southeast France.

Diagnosis – The shell consists of an open initial spire (the morphology of the earliest whorls is unknown) followed by a more or less arcuate shaft and a short, strongly curved, terminal hook. The ornamentation on the shaft consists of an alternation of

trituberculate main ribs and non-tuberculate intermediate ribs. On the strongly curved part of the hook, the ribs bifurcate or trifurcate from umbilical tubercles. On the last straight part of the hook the tubercles disappear and only simple, straight ribs remain. The suture line is of the ancyloceratid type.

Comparison – It differs from the genus *Hamiticeras* Anderson, 1938, which it closely resembles, in the sharp ribs springing in bundels from umbilical tubercles on the strongly curved part of the hook and in the markedly open hook; in *Hamiticeras* the shaft and hook are very close to each other, and in some cases may touch each other.

Distribution – Lower Barremian-Upper Aptian. France, Spain, England, Germany, Roumania, The Crimea, Caucasus, Australia?, Mozambique, Zululand, Patagonia, Antarctica, Colombia, California, Canada.

***Toxoceratoides aff. nagerai* (Leanza, 1970)**

Pl. 66, fig. 3.

Material – RGM 353 673.

Description – The shaft and hook exhibit a typical toxoceratoid uncoiling. The mode of coiling of the earlier ontogenetic stages is unknown. The flanks, the venter and the dorsum of the shaft are rounded, but on the hook the dorsum gradually becomes flattened. The cross section at the beginning of the shaft is subcircular, but gradually becomes ellipsoidal (higher than wide). On the hook the cross section is subtrapezoidal. The ornamentation on the shaft consists of an alternation of trituberculate, rather strong main ribs and non-tuberculate, thinner intermediate ribs. Up to the middle of the length of the shaft the main and intermediate ribs alternate one to one, but on the second half of the shaft the intermediate ribs are rare. The ventral tubercles are stronger than the lateral and umbilical ones. On the shaft the ribs are straight and slightly inclined forward. They pass over the venter and dorsum in a straight line, becoming rather thin on the dorsum. On the U-like curve of the hook is one bifurcating rib; its equal branches arise from the umbilical tubercle. On the straight last part of the hook there are no tuberculate ribs, but only more distant, straight, simple non-tuberculate ribs.

Measurements – $H_1 = 11.8$; $H_2 = 16.5$; $D_1 = 37.5$.

Remarks – The described specimen approaches *Toxoceratoides nagerai* by the morphology of the shaft and hook, and by the general features of the ornamentation. *Toxoceratoides nagerai* was studied by Aguirre-Urreta (1986), who showed on the basis of rich palaeontological material the rather wide range of intraspecific variation of this species. The intraspecific variation manifests itself by the differences in shell size, and by the distribution of main and intermediate ribs. Our specimen most closely approaches the specimen figured by Aguirre-Urreta (1986, fig. 17 A-B), but differs from it in the peculiar distribution of main and intermediate ribs on the shaft. *Toxoceratoides nagerai* has three to four, sometimes five intermediate ribs between each two main ribs on the shaft, whereas our specimen has no more than one inter-

mediate rib between each two main ribs. On the basis of these differences our specimen was determined as *T. aff. nagerai*.

Occurrence – Guane, near the house of the Rivera family; Barremian?/ Aptian boundary strata.

Genus *Helicancylus* Gabb, 1869, emend. Aguirre-Urreta, 1986

- pars* 1869 *Helicancylus* Gabb, p. 140.
non 1938 *Helicancylus* Anderson, p. 222.
pars 1938 *Hamiticerias* Anderson, p. 222.
non 1957 *Helicancylus* Wright, p. L212.
non 1957 *Hamiticerias* Wright, p. L212.
pars 1961 *Helicancylus* Casey, p. 70.
non 1981 *Helicancylus* Kakabadze, p. 123.
pars 1986 *Helicancylus* Aguirre-Urreta, p. 283.
pars 1996 *Helicancylus* Wright *et al.*, p. L224.
pars 1999 *Hamiticerias* Vermeulen *et al.*, p. 79.

Type species – *Ptychoceras aequicostatus* Gabb, 1864, from the Aptian of California.

Diagnosis – The early whorls have the shape of a conical open spire; this spire is followed by a straight or curved shaft, which passes into a hook with an U-shaped bend. In some cases the shaft and hook are rather close to each other. The ornamentation of the upper part of the shaft and the hook of the type species consists of equal, simple ribs, each with a pair of ventral tubercles; the ventral tubercles disappear on the hook. The terminal straight part of the hook is ornamented only with non-tuberculate, simple, distant ribs. On the early part of the shaft the ribs may bear one to three rows of tubercles. The suture line has an asymmetrically trifid lateral lobe and a symmetric trifid umbilical lobe.

Remarks – The nomenclatorial problems of *Helicancylus* Gabb, 1869, and *Hamiticerias* Anderson, 1938, have been discussed by many authors, but because of the absence of well preserved palaeontological material there is no consensus on these problems. When Gabb (1869) described his genus *Helicancylus*, he figured three incomplete specimens. One of them is helicoidally coiled, whereas the others are fragments of uncoiled parts (shaft, hook). He believed that the helicoidal whorl fragment probably was the early part of the figured shaft and hook. The latter was described and figured earlier by Gabb (1864, p. 74, pl. 13, fig. 20) as *Ptychoceras aequicostatus*.

Anderson (1938, p. 215) described the same three specimens and restricted the genus name *Helicancylus* to the specimen with the helicoidal coiling, redescribing it as *Helicancylus gabbii* Anderson. He chose it as the type species of *Helicancylus*. The two other specimens of Gabb were included in the new genus *Hamiticerias*. The specimen figured by Gabb (1869, pl. 25, figs. C-F) was described as *Hamiticerias pilsbryi* Anderson, 1938, and chosen as type species of *Hamiticerias*. The other specimen received the name *Hamiticerias aequicostatum* (Gabb, 1864).

Casey (1961; see also Wright *et al.*, 1996) noted that the type species of *Helicancylus*

Gabb, 1869, should be *Ptychoceras aequicostatus* Gabb, 1864, and he supposed that this species was congeneric with *Hamiticeras pilsbryi* Anderson, 1938. Thus, according to Casey (1961), *Hamiticeras* Anderson, 1938, should be considered a junior synonym of *Helicancylus* Gabb, 1869.

Aguirre-Urreta (1986) was of the opinion that the three specimens of Gabb mentioned above belong to three different valid genera. She considered, in accordance with Casey (1961), but in contrast to Anderson (1938), the type species of *Helicancylus* to be *Ptychoceras aequicostatus*. She considered, in contrast to Anderson (1938), the species *aequicostatus* and *pilsbryi* not to be congeneric, because of the marked difference in ornamentation. In accordance with Anderson (1938) she considered the type species of *Hamiticeras* to be *Hamiticeras pilsbryi*. Finally, she considered Gabb's helical fragment (*'Helicancylus' gabbi* of Anderson, 1938) a representative either of *Helicancylus* Klingler & Kennedy or *Kutatissites* Kakabadze.

Our study of the Colombian material, which comprises species of both *Helicancylus* and *Hamiticeras*, reveals that Aguirre-Urreta's point of view is acceptable, but we do not agree with all the species she includes in the genus *Helicancylus*. For instance, she tentatively included "*Acrioceras*" *bonarellii* Leanza (1970, p. 209, fig. 8) (Aguirre-Urreta, 1986, p. 292, fig. 13A-F), "*Toxoceratoides?*" *elatum* Koenen (1902, p. 375, pl. 38, fig. 8a-c; Kemper, 1976, pl. 38, fig. 1) and "*Ancyloceras fusciforme* Koenen (1902, p. 384, pl. 49, figs. 4-5, 7, 9, pl. 53, figs. 8-9). These species should be excluded from *Helicancylus* because none of them have the clearly distinct sculpture on the shaft and hook that is so characteristic for this genus.

Distribution – The earliest species is *Helicancylus crevolai* (Vermeulen *et al.*, 1999), which was described recently from the upper Hauterivian of southeast France. Other species are known from the Aptian of California, Oregon, Colombia, Argentina (Patagonia), Switzerland, Roumania, Caucasus.

***Helicancylus* cf. *philadelphium* Anderson, 1938**

Pl. 64, fig. 2.

Holotype – The specimen figured by Anderson (1938, pl. 79, fig. 2, 3, specimen No 4797, Academy of Natural Sciences of Philadelphia), from the middle Aptian of the north fork of Cottonwood Creek, Shasta Country.

Material – RGM 344 981, 344 986.

Description – The shaft is nearly parallel to the straight part of the hook. The cross section of the shaft is subcircular becoming subellipsoidal (higher than wide) on the hook. The ornamentation of the shaft consists of straight simple ribs, which are inclined forward, and bear very weak lateral tubercles and ventral tubercles. The former disappear on the upper part of the shaft. The bases of the tubercles are circular. The ribs pass straight over the venter and the siphonal band between the ventral tubercles is depressed. On the curved part of the hook the straight ribs still bear ventral tubercles, but later, on the straight part of the hook, the ventral tubercles disappear and the straight ribs become appreciably distant; they pass straight over the

venter without thickening. On the dorsum all ribs are thin; on the dorsum of the shaft they are curved backward, whereas on the dorsum of the hook they are slightly curved forward.

Measurements – RGM 344 981: $H_1 = 11.5$; $W_1 = 12.8$; $H_2 = 22.0$; $W_2 = 18.0$; $D_1 = 39.5$.

Comparison – The described species differs markedly from the other species of the genus *Hamiticeras* in the early disappearance of the lateral tubercles on the shaft and in the absence of intermediate ribs on the upper part of the shaft.

Occurrence – Villa de Leyva, middle Aptian.

Distribution – Middle Aptian of California, Oregon and Colombia.

Genus *Hamiticeras* Anderson, 1938

- pars* 1869 *Helicancylus* Gabb, p. 140.
- 1938 *Hamiticeras* Anderson, p. 222.
- pars* 1957 *Hamiticeras* Wright, p. L212.
- pars* 1960 *Helicancylus* Casey, p. 70.
- pars* 1986 *Hamiticeras* Aguirre-Urreta, p. 281.
- 1997 *Hamiticeras* Kakabadze & Hoedemaeker, p. 75.

Type species – *Hamiticeras pilsbryi* Anderson, 1938, upper Aptian (argonauta Zone) of California (Pl. 54, fig. 2).

Revised diagnosis – After the initial whorl (presumably a planispiral, crioconic spire) follows a straight or slightly curved shaft and a long terminal hook. The shaft and hook are subparallel and may be attached to each other by a hairpin-shaped bend. The ornamentation of the earliest part of the shaft consists of simple, non-tuberculate ribs followed by an ancyloceratid type of sculpture, *viz.* an alternation of trituberculate main ribs and thin, non-tuberculate intermediate ribs. In some cases the latter may bear ventral tubercles. The umbilical and lateral tubercles are weaker than the ventral ones; the umbilical and lateral tubercles disappear at the end of the shaft, whereas the ventral tubercles may still be present on the hairpin shaped bend or sometimes even on the beginning of the straight part of the hook. On the remainder of the hook there are only simple, non-tuberculate ribs. The suture line is of the ancyloceratid type.

Remarks – The discussion about the nomenclatorial problems and the validity of the genus *Hamiticeras* is given in the remarks on the genus *Helicancylus* Gabb, 1869. Perhaps *Helicancylus* and *Hamiticeras* may be regarded as subgenera of one and the same genus; *Helicancylus* might consist of *Helicancylus (Helicancylus)* Gabb and *Helicancylus (Hamiticeras)* Anderson.

Distribution – Aptian. California, Oregon, Colombia, Caucasus, Roumania.

***Hamiticeras ventrotuberculatum* sp. nov.**

Pl. 16, fig. 2.

Holotype – RGM 353 629. The only specimen known.

Type locality – Villa de Leyva, Santo Ecce Homo.

Type horizon – Middle? Aptian.

Derivatio nominis – *Venter* (Latin) = belly; *tuberculus* (Latin) = a small swelling; named after the peculiar ribbing with only ventral tubercles.

Diagnosis – *Hamiticeras*-like shell, i.e., the shaft and the straight part of the hook are subparallel, and the aperture is nearer to the shaft than at the beginning of the hook. On the shaft the ornamentation consists of an alternation of the thick, simple main ribs with ventral tubercles and thinner non-tuberculate intermediate ribs. On the hook the ribs are thick, straight, and non-tuberculate.

Description – The length of the incompletely preserved shaft is 57 mm. The transition to the hook is geniculate. The last straight part of the hook is more than 70 mm long and nearly parallel to the shaft. The flanks and the venter are rounded, whereas the dorsum is slightly flattened. The cross section of the shaft is circular becoming subcircular (wider than high) on the hook. The ornamentation of the shaft consists of an alternation of the strong, thick main and thinner intermediate ribs. On the flanks all ribs exhibit a slight forward inclination. The main ribs bear rather strong ventral tubercles with a circular basis. Near the end of the shaft the ventral tubercles disappear, and on this last part of the shaft and on the hook only strong, straight, distant, simple non-tuberculate ribs are present, which pass straight over the venter without broadening. They also pass straight over the dorsum, but there they become thin.

Measurements – $H_1 = 11.4$; $W_1 = 11.4$; $H_2 = 19.5$; $W_2 = 22.0$; $D_1 = 34.0$.

Comparison – The described specimen approaches *H. pilsbryi* Anderson, by the shape of its shaft and hook, by the shape of its cross section, and by its ornamentation, but it clearly differs in the absence of umbilical and lateral tubercles, and in having only ventral tubercles on the shaft.

Occurrences – Villa de Leyva, Santa Ecce Homo, middle? Aptian.

***Hamiticeras longum* sp. nov.**

Pl. 3, fig. 2.

Holotype – RGM 345 180.

Paratype – RGM 345 181.

Type locality – Sáchica.

Type horizon – Middle? Aptian.

Derivatio nominis – *Longus* (Latin) = long. It is named after the long shaft.

Diagnosis – Long, slightly curved shaft, which slowly increases in whorl height, and is ornamented by an alternation of thick, straight, simple, closely spaced main ribs and thin intermediate ribs. On the lower portion of the shaft the ornamentation consists of equal, dense, non-tuberculate ribs. The ventral tubercles are the first to appear on the main ribs, followed by the lateral tubercles. Only on the upper part of the shaft is there one trituberculate rib with an umbilical, a lateral, and a ventral tubercle. Only some of the intermediate ribs bear ventral tubercles; the majority do not bear tubercles. The ribs pass straight over the venter, while on the dorsum they become thin and slightly curved backwards. On the transitional part of the hook there are no tubercles and when the ribs cross the venter they are strongly thickened.

Description – The incompletely preserved shaft is 107 mm long, slowly increasing in height and has the approximate shape of a slightly bent pipe. The whorl height in the U-shaped bend of the hook is 11.0-11.5 mm. The costal cross section on the early part of the shaft is circular, but later it becomes subellipsoidal (slightly higher than wide). On the earliest part of the shaft the ornamentation consists of thin, straight, equal ribs. The differentiation into thick main and thin intermediate ribs occurs later. Between every two main ribs there are one or two intermediate ribs. At first the ventral tubercles appear on the main ribs, then the lateral ones. Both types of tubercles are spines with circular bases and sharp tops. Only on the upper part of the shaft is there one rib which, in addition, bears an umbilical tubercle. Some of the main ribs have only ventral tubercles, but the majority of them bear both ventral and lateral tubercles. The majority of the intermediate ribs are non-tuberculate and pass straight over the venter without interruption, but some of them bear weak ventral tubercles. The ribs on the siphonal band between the ventral tubercles are weak and slightly curved backwards. On the U-shaped curve of the hook there are no tubercles, and the ribs are markedly broader and flattened on the venter.

Remarks – The morphology of the described specimens is close to *Hamiticeras chipatai* Kakabadze & Hoedemaeker, 1997. Both species have a shaft that has the shape of a slightly curved pipe that slowly increases in height and have dense, equally thin ribs on the early part of the shaft. However, *H. longum* differs in having a longer shaft, and main ribs with only ventral and lateral tubercles, whereas *H. chipatai* has trituberculate main ribs on the shaft.

Occurrence – Sáchica; middle? Aptian.

Hamiticeras? sp.

Pl. 65.

Material – RGM 353 650, 353 651 and 353 652.

Description – The shaft is straight and passes into the hook with a very sharp U-shaped bend. The dorsum of the straight part of the hook is very close to the shaft. The flanks of the shaft and venter are rounded, but the dorsum is flattened. On the hook the dorsum is appreciably broad and flat. The cross section on the shaft is sub-oval; at the beginning of the preserved upper part of the shaft it is higher than wide, but higher in the shaft it becomes subcircular and even becomes wider than high in the U-shaped bend. The cross section of the straight part of the hook is not visible because it is not preserved. The ornamentation on the shaft consists of simple, prominent, straight, rather thick ribs, which are equal and inclined forward. On the margins of the venter the ribs become more prominent. Tubercle-like thickenings occur only on the earliest preserved rib of the preserved upper part of the shaft, and because of this it is supposed that in the early ontogenetic stage the ribs were furnished with ventral tubercles and possibly even lateral and umbilical ones. On the preserved upper part of the shaft the tubercle-like thickenings have already disappeared. On the U-shaped part of the hook bifurcated ribs appear. Branching occurs in the middle or at one third flank height. On the venter of the U-shaped bend there are again tubercle-like thickenings between which the ribs are weak. On the straight part of the hook are only simple ribs.

Remarks – The described specimens belong to *Hamiticeras* on account of the morphology of the shaft and hook, but as there are no clearly distinguishable tuberculate ribs, we are not confident of this assignment. On the other hand, there are arguments to assume that the first part of the shaft was ornamented by tuberculate ribs because of the presence of tubercle-like thickenings on the earliest rib of the shaft and on the U-shaped bend.

The described specimens resemble that identified by Avram (1976, pl. 2, fig. 1; upper Gargasian) as *Hamiticeras* sp. on account of the morphology of the shaft and hook. It is ornamented by simple, equal ribs, which sometimes bifurcate on the U-shaped part of the hook. On the shaft the ribs are inclined forward. Avram had the opinion that this feature is not significant for species identification and he mentioned similarities either to *Hamiticeras pilsbryi* (Anderson) or *H. aequicostatum* (Gabb). Unfortunately, Avram did not mention whether his specimen has tuberculate ribs or not.

Occurrence – Villa de Leyva (southern flank of Loma Blanca) (RGM 353 650); Galan (left bank of Río Suarez) (RGM 353 651, 353 652); middle? Aptian.

Genus *Hemihoplites* Spath, 1924

- 1924 *Hemihoplites* Spath, p. 84.
- 1926 *Matheronites* Renngarten, p. 27.
- 1936 *Matheronites* Luppov, p. 122.
- 1957 *Hemihoplites* Wright, p. L212.
- 1960 *Matheronites* Drushchits, p. 287.
- 1962 *Hemihoplites* Wiedmann, p. 81.
- 1967 *Matheronites* Dimitrova, p. 66.
- 1971 *Matheronites* Bogdanova, p. 62.
- 1981 *Hemihoplites* (*Matheronites*) Kakabadze, p. 93.

pars 1989 *Hemihoplites* Riccardi & Aguirre-Urreta.
1996 *Hemihoplites* Wright *et al.*, p. L228.

Type species – *Ammonites ferraudianus* d’Orbigny, 1841, Barremian of southeast France.

Diagnosis – [The morphology of the earliest whorls were studied in *H. (Matheronites) ridzewskyi* (Sharikadze *et al.*, 1989) and in *H. (Hemihoplites) brevicostatus* (Bogdanova, 1971).] After the first embryonal whorl, the second whorl is uncoiled arc-like, but the third whorl is in contact again with the second whorl. Thus, between the first embryonal whorl and the second whorl is a perforation. The whorls are semi-evolute in a later ontogenetic stage and may become slightly involute in a still later stage. The whorl section varies from circular-octagonal (generally in the early ontogenetic stage) to ellipsoidal, suboctagonal or subtrapezoidal (higher than wide). The ornamentation consists of straight or slightly curved main ribs, bearing one to three rows of tubercles. The presence of ventral tubercles is characteristic for all species of *Hemihoplites*, while some species lack lateral or umbilical tubercles, or both. Besides simple ribs, there are also bifurcating or intercalatory (short or long) ribs in the mature stage of some species. The suture line is of the ancyloceratid type, with a long bifid ventral (*E*) lobe, a trifid long lateral lobe (*L*), a short umbilical lobe (*U*) and a medium long dorsal (*I*) lobe.

Remarks – There is no consensus as to the validity of the family Hemihoplitidae, erected by Spath (1924), who included three genera in it; *Hemihoplites*, *Pseudothurmannia* and, with a question mark, *Metahoplites?* (now included in Holcodiscidae Spath, 1923). According to Wright (1957), Hemihoplitidae consists of *Pseudothurmannia*, *Hemihoplites* and *Balearites*. Wiedmann (1962, 1966) did not acknowledge the validity of the family Hemihoplitidae and included all noted genera in Crioceratitinae (family Ancyloceratidae). In later publications some authors (Dimitrova, 1967; Bogdanova, 1971; Riccardi & Aguirre Urreta, 1989) did acknowledge the Hemihoplitidae, while others (Immel, 1978; Rawson, 1975a, b; Kakabadze, 1981) did not.

Wright *et al.* (1996, p. L228) noted that “Hemihoplitidae are separated from Crioceratitinae only because ammonitic coiling is fully realized and the last trace of crioceratine ribbing have disappeared.” However, analysis of the existing material shows that the shell of *Hemihoplites* has an uncoiled second whorl leaving a so-called umbilical hiatus, and only the following whorls are contiguous or slightly involute (such coiling is common in Ancyloceratidae); the type of ribbing, *viz.* tuberculate main ribs with, in rare occasions, intermediate ribs, is not an uncommon feature of some genera of Ancyloceratidae as well (e.g., in *Tropaeum*, in some *Paracrioceras*); and the suture line is typically ancyloceratid. Taking all these data into account, we consider Hemihoplitidae Spath, 1924, invalid (i.e., it is considered a junior synonym of Ancyloceratidae Gill, 1871).

We do not accept the identification by Klinger & Kennedy (1992, pp. 123-129, fig. 36A-E) of specimens from the lower Barremian of Zululand as *Hemihoplites cf. varicostatus* Riccardi & Aguirre-Urreta, 1989, because they have very narrow umbilicuses, are very involute, exhibit rapidly increasing whorl heights and have blunt ventral developments of the ribs. All these features are not characteristic for the genus

Hemihoplites, and, therefore, above mentioned Patagonian and South African species can not be included in the genus *Hemihoplites* Spath, 1922.

Distribution – Upper Barremian of France, Mallorca, Balearic Islands, north Germany, Bulgaria, Yugoslavia, north Caucasus, Daghestan, Georgia, Turkmenistan, Mangyshlak (Kasakhstan), Colombia, Mexico?, Canada? The reported presence of this genus in Indonesia?, Patagonia? and Zululand rest on erroneous identifications.

Subgenus *Hemihoplites* (*Matheronites*) Renngarten, 1926, emend. Kakabadze, 1981
***Hemihoplites* (*Matheronites*) *ridzewskyi* (Karakasch) *sachicaensis* subsp. nov.**
 Pl. 67, fig. 2.

pars 1960 *Matheronites ridzewskyi* Karakasch; Drushchits, p. 287, pl. 30, fig. 2.

Holotype – RGM 352 534. The only specimen known.

Type horizon – Upper Barremian?

Derivatio nominis – The subspecies is named after the type locality, SÁCHICA (Boyacá, Colombia).

Diagnosis – Moderately expanding, semi-evolute whorls, with umbilical hiatus between the first embrional whorl and the second whorl. The umbilicus is wide and saucer-like with a moderately steep wall. The ornamentation on the early whorls consists of dense, simple ribs, which are slightly inclined forward, but later the ribs become significantly distant. Each rib bears two pairs of tubercles, ventral and lateral.

Description – The first embryonal whorl is not preserved. The second whorl is well preserved and is uncoiled as an open-arc, whereas the following whorls are contiguous, so that the shell is characterized by an umbilical hiatus inside the second whorl. The whorls increase in height moderately. The umbilicus is wide, shallow, saucer-like, with a moderately steep wall and a rounded umbilical rim.

The ornamentation consists of simple ribs, which on the penultimate whorl are slightly prorsiradiate. On the last whorl the ribs are straight and markedly distant (the interspaces between the ribs exceed their thickness three times). All ribs bear ventral and lateral tubercles. Between the ventral tubercles of the penultimate whorl the ribs are flattened, but on the last whorl they have almost disappeared. The suture line is not observed.

Measurements – D = 25.5; H = 9.8; W = 10.3; U = 9.0; H:D = 0.37; W:D = 0.40; U:D = 0.35; H:h = 1.43.

Remarks – RGM 352 534 closely resembles the specimen, described as *Matheronites ridzewskyi* Karakasch by Drushchits (1960, pl. 30, fig. 2a-c), in its shell shape, umbilical hiatus, slightly prorsiradiate ribs on the early whorls and distant, strong straight ribs on the last whorl, which bear rather strong ventral and lateral tubercles. These two

specimens clearly differ from the type of *Hemihoplites* (*Matheronites*) *ridzewskyi* in having stronger and more distant ribs, but also in not having umbilical tubercles or even tubercle-like thickenings during the whole ontogeny. Therefore, we suppose these specimens to be a subspecies of *H. (M.) ridzewskyi*.

Distribution – Uppermost? Barremian of Daghestan and Colombia.

Occurrence – Sáchica, uppermost? Barremian.

Family Heteroceratidae Spath, 1922
Genus *Heteroceras* d'Orbigny, 1849
Subgenus *Heteroceras* (*Argvethites*) Rouchadzé, 1933

1933 *Heteroceras* (*Argvethites*) Rouchadzé, p. 233.

1955 *Heteroceras* (*Argvethites*) Eristavi, p. 119.

1975 *Argvethites* Kakabadze, p. 93.

1992 *Argvethites* Delanoy, p. 116.

Type species – *Heteroceras* (*Argvethites*) *minor* Rouchadzé, 1933, upper Barremian, Ghoresha, Western Georgia.

Diagnosis – The shape of the shell is similar to that of *Heteroceras* (*Heteroceras*); the early whorls are helically coiled, and followed by a shaft and a terminal hook. On the helicoidal whorls the ribs are asymmetric-sinusoid, but on the uncoiled part (shaft, hook) they become symmetric, slightly bent or straight. Besides the simple main ribs there may be intercalatory ribs and bifurcating or trifurcating ribs, which cross the venter without interruption. *Heteroceras* (*Argvethites*) is characterized by one pair of ventral tubercles, which in most cases only appear on the last helicoidal whorl (sometimes earlier) or on the earliest part of the shaft. They become stronger on the shaft, but on the hook they gradually weaken and in most cases disappear. In some cases the ribs may fork at the ventral tubercles; in those cases the branches cross the dorsum without interruption. On the venter of the transition between shaft and hook a syphonal furrow is generally developed.

Distribution – Upper Barremian. Georgia, Armenia, north Caucasus (Russia), Bolshoi Balkhan and Kopetdag (Turkmenistan), southeast France, England, South Africa, Colombia, California?

***Heteroceras?* (*Argvethites*) sp.**

Pl. 56, figs. 3-4.

Material – Two incomplete specimens, RGM 353 655a, 353 655b.

Description – The upper part of the shaft, which very slowly increases in height, is almost parallel to the last straight part of the hook. The transition to the hook is rather abrupt, though the first part has the shape of a wide arch. The cross section of the shaft

is subellipsoidal (higher than wide), on the hook it becomes subcircular (slightly wider than high). The ornamentation on the shaft consists of dense, rather strong, straight, simple ribs, which are slightly inclined forward. On the geniculate curve of the hook bifurcating ribs appear among the simple ones. At first, forking takes place at lower third flank height, but later at mid-flank or in the upper part of the flank. Only simple ribs are present on the last straight portion of the hook. The ribs pass straight over the venter without broadening. On the ventral part of the bend of the hook there is a shallow forrow and on its two margins the ribs bear fine tubercle-like thickenings (best seen on RGM 353 655b).

Measurements – RGM 353 655a: $D_1 = 32.5$; $H_1 = 9.7$; $H_2 = 14.0$; $W_2 = 14.2$.

Remarks – The described specimens resemble the species of *Heteroceras* (*Argoethites*) in the morphology of the shaft and hook, and by the type of ornamentation. As we have no information about the morphology of the early ontogenetic stages, we are not sure whether these specimens have the characteristics of the early helicoidal stage of *Heteroceras* (*Argoethites*).

Occurrence – Guane, along the road, upper Barremian.

Genus *Colchidites* Djanelidzé, 1926

- 1926 *Colchidites* Djanelidzé, p. 261.
- 1933 *Colchidites* Rouchadzé, p. 237.
- 1945 *Heteroceras* (*Santandericeras*) Royo & Gomez, p. 468.
- 1955 *Colchidites* Eristavi, p. 119.
- 1957 *Colchidites* Wright, p. L212.
- 1958 *Colchidites* Drushchits & Eristavi, p. 105.
- 1960 *Colchidites* Drushchits, p. 296.
- 1971 *Colchidites* Kakabadze, p. 47.
- 1984 *Colchidites* Klinger *et al.*, p. 45.
- 1986 *Colchidites* Aguirre-Urreta & Klinger, p. 325.
- 1989 *Martelites* Conte, p. 43.
- 1994 *Martelites* Delanoy, p. 545.
- pars* 1996 *Colchidites* Wright *et al.*, p. L22.
- 1997 *Martelites* Delanoy, p. 125.

Type species – *Colchidites colchicus* Djanelidze, 1926; upper Barremian, Georgia.

Diagnosis – Small to very large shells. The early whorls (two to eight whorls, possibly more) are helicoidal (helicoidal stage) and are followed by planispiral whorls (planispiral stage). The number of planispiral whorls in some species may reach three (possibly more), but in others does not even attain one. The whorl height may increase very slowly, or moderately, or rather rapidly. The ontogeny of some species ends with the planispiral stage, but in some species the planispiral coiling is followed by an uncoiled stage consisting of a straight or more or less curved shaft ending in a hook. Some species show a considerable variation in the mode of coiling and uncoiling after the helicoidal stage, for instance, a (several times) repeated uncoiling and recoiling in

the planispiral stage (e.g., *C. breistrofferi*). The plane of symmetry of the planispiral whorls and the shaft and hook of the uncoiled stage is the same, whereas the axes of coiling of the helix makes an angle with this symmetry plane; this angle is different for each species, but also, though rarely, may coincide with it. The sculpture of the helicoidal whorls consists of asymmetric-sinusoid ribbing. On the planispiral whorls and on the shaft and hook the ornamentation is symmetrical or almost symmetrical. Besides simple ribs there may be forked ribs and intercalatory ribs. All these ribs pass the venter without interruption. The short, thin intercalatory ribs may also be present on the dorsum of the shaft and hook, and sometimes also on the last planispiral whorl. In the gerontic stage the sculpture consists of strong, distant simple ribs. The suture line is of the heteroceratid type and consists of trifid lateral (*L*), umbilical (*U*) and dorsal (*I*) lobes, and bifid ventral (*E*) lobes. The lateral lobe has the same length or is slightly longer than the ventral one.

Remarks – On the basis of whorl coiling three morphological groups can be distinguished in *Colchidites*:

1. Group of *C. intermedius* Djanelidze, characterized by a well developed helical spire (whorl number five to eight, possibly more), a poorly developed plane spiral (not exceeding one whorl), and a well developed shaft and hook.
2. Group of *C. colchicus* Djanelidze with well-developed helicoidal whorls (number of whorls four to seven, possibly more), planispiral whorls (number of whorls one to two, possibly more), and a more or less well developed shaft and hook.
3. Group of *C. shaoriensis* Djanelidze; this group is characterized by the presence of helicoidal whorls (number of whorls two to seven, possibly more) and planispiral whorls (whorl number one to three, possibly more).

Each of these three groups contain species with different shell size (small, medium, or large), and such variation in size has also been observed among the individuals of one and the same species.

Comparison – *Colchidites* differs from *Heteroceras* in the presence of planispiral whorls after the initial helicoidal whorls.

Distribution – Upper Barremian. North Caucasus, Transcaucasus (Georgia, Armenia), Turkey, Turkmenistan, Iran, France, South Africa (Zululand), Patagonia, Cuba, Colombia.

***Colchidites apolinari* (Royo y Gomez, 1945)**

Pls. 69, 75; Pl. 76, fig. 2.

1945 *Heteroceras* (*Santandericeras*) *apolinari* Royo y Gomez, p. 468, pl. 74, fig. 1a-b, pl. 75, fig. 1.

1968 *Colchidites* (*Colchidites*) *apolinari* (Royo y Gomez): Etayo-Serna, p. 59, pl. 1, fig. 4-6, pl. 2, fig. 1-2, text fig. 3b, 4 (4).

1991 *Colchidites apolinari* (Royo y Gomez): Kakabadze & Thieuloy, p. 96, pl. 5, fig. 6, fig. 10-11; text fig. 12.

Holotype – The specimen figured by Royo y Gomez (1945, pl. 74, fig. a-b), which is lost (see Etayo Serna, 1968).

Neotype – Specimen ID 3044, figured by Kakabadze & Thieuloy (1991, pl. 5, fig. 6, text fig. 12), Institute Dolomieu, Joseph Fournier University of Grenoble.

Material – Six specimens, RGM 353 691-353 696.

Description – The helix is small and consists of four or five whorls only. The planispiral part consists of 1.6 contiguous whorls, which rapidly increase in height ($H:h = 1.68$). The transition from helicoidal to planispiral coiling takes place at $h_1 = 37$ mm (RGM 353 692). The shaft is rather short, slightly curved. Shaft and hook together display an aspinoceratid type of uncoiling. It appears that the dorsal side of the hook, i.e., the adult living chamber, was in touch with the ventral side of the last planispiral whorl. The first planispiral whorl has convex flanks; the later planispiral whorls, the shaft and the hook have flattened flanks. The ventral side is broad and rounded, whereas the dorsal side of the early planispiral whorl is flattened and in a later stage even becomes depressed. The whorl section of the first planispiral whorl is subellipsoidal (higher than wide), on the second whorl and on the shaft it is subrectangular. The last part of the hook has a subtrapezoidal cross section. It is not possible to measure the breadth of the hook, but it is probably slightly wider than high. The ornamentation is visible from the very beginning of the first planispiral whorl and consists of very thin, dense, slightly flexuous ribs, which are slightly inclined backwards at the end of the second planispiral whorl. Besides, the main ribs may be simple or bifurcated and are rarely separated by intercalatory ribs. The point of bifurcation and the point of origination of the intercalatory ribs are at mid-flank, rarely higher. All ribs pass straight over the venter and become slightly broader. The ribs become thinner from the umbilical margin downwards and pass the dorsum with a forward curved. The shaft is ornamented with simple, straight, rather distant ribs. At the beginning of the shaft the ribs are slightly inclined backwards, but later they are inclined forward. On the hook the ribs are more distant. The ribs pass straight over the venter of the shaft and hook.

Measurements – RGM 353 692: L = 185.1. RGM 353 693: D = 48.0; H = 22.3; U = 17.0. RGM 353 694: D = 81.2 (56.6); H = 32.5 (22.5); W = (20.0).

Remarks – Some of the described specimens (e.g., RGM 353 692) differ from the holotype and neotype in having more prominent and less dense ribbing. In one specimen (RGM 353 696) there is one intercalatory rib on the planispiral stage. These differences are probably due to intraspecific variation.

Comparison – The described species is most similar to *C. riosuarez*, sp. nov. (see below).

Occurrence – Upper Barremian of Galan (in concretions in the left bank of Río Suarez).

Distribution – Upper Barremian of Colombia.

Colchidites riosuarezi sp. nov.

Pl. 56, fig. 2; Pl. 68; Pl. 70.

Holotype – RGM 353 682.*Paratype* – RGM 353 681.*Type locality* – Galan (left bank of Río Suarez) (Colombia).*Type horizon* – Upper Barremian.*Derivatio nominis* – Named after the Río Suarez (Colombia).

Diagnosis – Colchiconic shell, with a helicoidal part, a planispiral part (two contiguous whorls) and a compact uncoiled part. The cross section of the last helicoidal whorl is subcircular, of the planispiral whorls and shaft ellipsoidal, and on the hook it is trapezoidal. The ornamentation of the planispiral and uncoiled whorls consists only of simple, straight ribs. On the shaft and especially the hook the ribs are rather distant.

Description – The coiling of the rather small helix is sinistral. As only the last two whorls are preserved, the full number of helicoidal whorls is not known. The transition from helicoidal to planispiral coiling occurs at $h_1 = 7$ mm. The planispiral part consists of two contiguous whorls, of which the first whorl moderately increases in height ($H:h = 1.6$), whereas the increment in height of the second one is rather rapid ($H:h = 1.8$). The shaft is rather short and slightly curved. The transition to the hook is gradual and forms a rather wide arch; it therefore becomes clear that the dorsal side of the aperture should have been in touch with the ventral side of the last planispiral whorl. The cross section of the last helicoidal whorl is subcircular, but the cross section of the planispiral whorls and shaft becomes ellipsoidal (higher than wide). The cross section (especially costal section) of the hook is subtrapezoidal (higher than wide). The ornamentation of the last helicoidal whorl consists of thin, dense, flexuous ribs. From the beginning of the planispiral coiling the ribs are straight; on the first planispiral whorl 40 moderately distant, straight, simple, ribs were counted, which pass straight over the venter while becoming slightly broader. On the second whorl the ribs are generally straight; only two ribs are slightly flexuous, which is apparently due to healed injuries received when the animal was alive. The space between the ribs is two times broader than the thickness of the ribs. The ribs on the dorsum are thin and curved forward. The ribs on the shaft are straight and are slightly inclined forward. The spaces between the ribs are twice as wide as the breadth of the ribs, on the last part of the shaft even three times wider. On the hook the ribs become stronger and still more distant; they pass straight over the venter, becoming slightly broader. On the dorsum of the shaft and hook all ribs are thin and curved forward. The suture line has the typical features of the genus *Colchidites*.

Measurements – RGM 353 682: $L_1 = 182.0$. $D = 94.0$; $H = 39.0$; $U = 33.5$; $L = 92.0$; $D_1 = 162.0$; $H_1 = 55.5$; $H_2 = 66.0$. RGM 353 681: $D = 90.0$; $H = 37.5$; $U = 32.0$.

Comparison – *Colchidites riosuarezi* approaches *C. apolinari* in its mode of coiling, but differs in having only simple ribs, and in the smaller density of the ribs on the planispiral whorls and especially on the shaft. Moreover, *C. riosuarezi* has a more compact uncoiled part (shaft, hook) and two planispiral whorls instead of one and a half in *C. apolinari*.

Occurrences – Upper Barremian: Galan (left bank of Río Suarez) (holotype); Guane, along the road near the finca of the family Rivera (RGM 353 681).

***Colchidites breistrofferi* Kakabadze & Thieuloy, 1991**

Pls. 7, 71.

1991 *Colchidites breistrofferi* Kakabadze & Thieuloy, p. 97, text fig. 13, pl. 5, fig. 7, pl. 6, fig. 1-9.
pars 1997 *Colchidites breistrofferi* Kakabadze & Thieuloy: Kakabadze & Hoedemaeker, p. 81, pl. 14, fig. 5a, b (*non?* pl. 15, fig. 2a, b).

Holotype – ID 3046 (Institute Dolomieu, Grenoble), uppermost Barremian of Simiti (Colombia).

Material – Three well preserved specimens, RGM 353 698, 353 700, 353 701.

Remarks – The Colombian specimens of *Colchidites breistrofferi* (including the holotype) were described by Kakabadze & Thieuloy (1991). *Colchidites breistrofferi* is distinguished from the other species of *Colchidites* in exhibiting periodical crioconic uncoiling during ontogeny. The morphology of the living chamber of this species was not known when the holotype was described. In the Creutzberg collection there is RGM 353 698, in which a part of the living chamber is preserved. It appears that a part of the living chamber becomes uncoiled, but shortly afterwards becomes contiguous again (Pl. 7). The ornamentation on the living chamber consists of simple ribs, which are slightly inclined backwards, but later becoming more distant and straight.

The type of coiling and sculpture on the helicoidal part and on the first planispiral whorl of *C. breistrofferi* is virtually identical to those of *C. riosuarezi* and *C. pseudovulanensis*. However, *C. riosuarezi* is characterized by the presence of helicoidal, planispiral and uncoiled stages, whereas *C. pseudovulanensis* has only helicoidal and planispiral stages. The resemblance is so close that it is practically impossible to identify (down to the species level) incomplete specimens that consist only of a helix and the first planispiral whorl. Therefore, the synonymy published by Kakabadze & Hoedemaeker (1997) can only partly be accepted.

The differences in the size of the helix were assigned to sexual dimorphism; on account of this feature microconchs and macroconchs of this species have been distinguished (Kakabadze & Thieuloy, 1991, p. 98; Kakabadze & Hoedemaeker, 1997, p. 81). However, the analysis of all existing material revealed that there are intermediate forms between the groups with a micro and macro helix. Therefore, we conclude that these differences should be regarded as intraspecific variation and possibly have no direct connection with sexual dimorphism.

Occurrences – Chipatá (RGM 353 701, 353 699); Guane (along the road near the finca of the family Rivera) (RGM 353 700); Guane (Vereda Chagueta) (RGM 353698); upper Barremian.

Distribution – Upper Barremian of Colombia.

***Colchidites pseudovulanensis* sp. nov.**

Pl. 76, fig. 1.

Holotype – RGM 353 680. The only specimen known.

Type locality – Galan (left bank of Río Suarez).

Type horizon – Upper Barremian.

Derivatio nominis – The species is so named because it has a certain resemblance to *Colchidites vulanensis* Egoian, 1965.

Diagnosis – The shell consists of helicoidal and planispiral whorls. The uncoiled part (shaft and hook) is not developed. The plane spiral consists of moderately increasing (in height) ($H:h = 1.63$) contiguous whorls, with ellipsoidal whorl section (higher than wide). The sculpture of the plane spiral consists of radial, straight, strong, wedge-like, simple ribs, which become broader on the venter.

Description – The helicoidal whorls are not preserved, but the left-open part in the centre of the holotype indicates that the helix was small. The plane spiral consists of contiguous whorls, which moderately increase in height ($H:h = 1.63$). The umbilicus is wide ($U:D = 0.36$). The cross section of the early planispiral whorls is ellipsoidal (higher than wide), but then it becomes oval with the point of maximum thickness at the umbilical margin. The ornamentation consists of straight, wedge-like, strong simple ribs, broadening on the venter. With growth the ribs become considerably stronger and distant. On the dorsum all ribs are equally thin and curved forward.

Measurements – $D = 90.0$; $H = 36.0$; $U = 33.0$.

Comparison – The new species resembles *C. vulanensis* in the type of coiling (contiguous whorls), the shape of the cross section of the planispiral whorls, the broadening of the ribs on the venter and the density of the ribs, but differs in the absence of intercalatory and bifurcating ribs, and in the less rapid increment in the height of the planispiral whorls.

Occurrence – Galan, left bank of Río Suarez; upper Barremian.

***Colchidites guanensis* sp. nov.**

Pl. 17; Pl. 56, fig. 1; Pl. 57, fig. 2; Pl. 72; Pl. 73, fig. 1; Pl. 74; Fig. 12.

Holotype – RGM 353 683.

Paratype – RGM 353 679, 353 684, 353 689.

Type locality – Guane (Vereda Chagueta), Colombia.

Type horizon – Upper Barremian.

Derivatio nominis – The species is named after the village of Guane (Colombia).

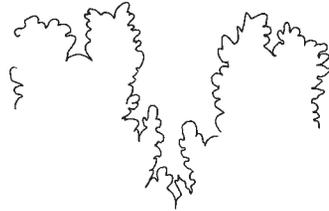


Fig. 12. Suture line of *Colchidites guanense* sp. nov., RGM 353 679, $\times 1$ ($h = 60$ mm).

Diagnosis – The very large shell consists of a very small helix and contiguous planispiral whorls, which moderately increase in height. An uncoiled part (shaft and hook) is not developed. On the helicoidal whorls the ribs are thin, dense and flexuous. On the first planispiral whorl the ribs become straight, but they still are thin and dense. Beginning from the second planispiral whorl the ribs become stronger and more distant, and they pass straight over the venter. There are only simple ribs on the planispiral whorls.

Description – The coiling of the helix is sinistral or dextral. On the holotype the last three helicoidal whorls are preserved and, on account of the space left by the broken-off part of the early helicoidal whorls, it is possible to conclude that the full number does not exceed five. The transition from the helicoidal to the planispiral mode of coiling comes about at $h_1 = 3-4$ mm. The axis of coiling of the helix coincides with the plane of coiling of the planispiral section. The planispiral part of the holotype is incomplete and consists only of two and a half contiguous whorls, which moderately increase in height ($H:h = 1.54$). On RGM 353 684 the number of planispiral whorls is three, but as the living chamber is not complete, we can only conclude that the full number of planispiral whorls is more than three. The umbilicus is wide ($U:D = 0.35-0.37$) and has a steep wall. The cross section of the last helicoidal whorl is subcircular and becomes suboval (higher than wide) in the planispiral whorls, so that the planispiral whorls create a flat-discoidal shell. The ornamentation of the last helicoidal whorl is well preserved on the holotype and on RGM 353 686; it consists of thin, dense, asymmetric flexuous ribbing. On the first whorl of the plane spiral the ribs are straight, thin and dense; the thickness of ribs is equal to the space between the ribs. All ribs pass straight over the venter without broadening, but on the dorsum they are thin and curved forward. With age the ribs become stronger and more distant, so that the space between the ribs becomes two times wider than the breadth of the ribs, and in some cases even three times. In general there are only simple ribs, and between them there are a few very thin, simple intermediate ones, for instance, three on the first planispiral whorl, none on the second whorl and two on the third whorl. It should be noted that some of the specimens have no intermediate ribs at all. The living chamber is ornamented with straight, strong ribs, which are wide apart. They pass straight over the venter without broadening. On the dorsum all ribs are very thin and curved forward.

The suture line is visible at H = 60-65 mm on RGM 353 679; the lateral lobe (*L*) is large and asymmetrically trifid; the umbilical lobe (*U*) is smaller than the lateral one and is also asymmetrically trifid. The first and second lateral saddles (*E/L*, *L/U*₁) have approximately the same height, and are asymmetrically bifid.

Measurements –

	D	H	W	U
RGM 353 683	102.0	38.5	-	36.5
RGM 353 684	190.0	70.0	-	78.0
RGM 353 679	121.0	49.0	-	41.0
RGM 353 686	65.5	25.7	23.0	24.0

Comparison – See description of *Colchidites striatocostatus* below.

Occurrence – Guane (Vereda Chagueta) (RGM 252 683, 252 684); Guane (along the road near the finca of Fam. Rivera) (RGM 353 679, 353 686-353 689); upper Barremian.

***Colchidites striatocostatus* sp. nov.**

Pl. 73, fig. 2.

Holotype – RGM 353 697. The only specimen known.

Type locality – Guane, along the road near the finca of the family Rivera.

Type horizon – Upper Barremian.

Derivatio nominis – *Striatus* (Latin) = striated and *costatum* (Latin) = ribbed; from its thin ribbing.

Diagnosis – The helix is very small. The planispiral whorls increase rapidly in height. The ornamentation of the helicoidal and first planispiral whorls consists of very thin, numerous, dense, simple ribs, which are curved forward on the venter.

Description – The helix is very small, and its coiling sinistral. On the holotype only the last helicoidal whorl is preserved, but it is possible to conclude that the helix had no more than four whorls. The transition from helicoidal to planispiral coiling comes about at $h_1 = 3$ mm. The plane spiral consists of 1.4 contiguous whorls, which rapidly ($H:h = 1.90 - 1.66$) increase in height. The morphology of the later whorls is unknown. The umbilicus is wide ($U:D = 0.34$). The cross section of the last helicoidal whorl is subcircular, but on the plane spiral the cross section is oval (slightly higher than wide). Very thin, asymmetrically flexuous ribs adorn the last helicoidal whorl. The space between the ribs slightly exceeds the breadth of the ribs. On the planispiral whorl the ornamentation consists of thin, numerous, dense, simple ribs, which on the venter are curved forward (without broadening). On the flanks the ribs are straight; on the umbilical wall they become thin and they cross the dorsum with a slight forward curve. The number of ribs on the first planispiral whorl is 32, and there are 24 on the first half of the second planispiral whorl.

Measurements – D = 36.8; H = 15.5; W = 15.1; U = 12.5.

Comparison – *Colchidites striatocostatus* resembles *C. tenuicostatus* Kakabadze in the very small size of helix, and the very dense and thin ribbing in both helicoidal and planispiral stages, but it differs from the latter in the more rapid increment in height of the planispiral whorls, and in the absence of intercalatory and bifurcating ribs. Moreover, *C. striatocostatus* has no depressed dorsum, which is a characteristic feature of *C. tenuicostatus*. The described new species resembles *C. veurensis* in the small helix, the evolute planispiral whorls and the morphology of ribbing, but strongly differs in the rapid increment in the height of the planispiral whorls and the narrower umbilicus. Moreover, beginning from the second planispiral whorl, the ornamentation of the *C. veurensis* comprises, besides simple ribs, short intercalatory ribs and a few bifurcating ribs, whereas *C. striatocostatus* is ornamented only with simple ribs. *Colchidites striatocostatus* also resembles *C. guanensis* in the smallness of the helix, and the density of the fine ribbing on the helicoidal whorls and the first planispiral whorl, but differs from the latter in the much more rapid increase in height of the planispiral whorls and in having the ribs curved forward on the venter.

Remarks – The gerontic stage of this species is unknown, for the holotype has only one and a half planispiral whorls preserved; therefore, we neither know the full number of planispiral whorls, nor whether this species has an uncoiled part (shaft, hook). Most likely this species was characterized by having only helicoidal and planispiral stages, but this preliminarily conclusion has to be proved with additional palaeontological material.

Occurrence – Guane, along the road near the finca of the family Rivera; upper Barremian.

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Explanations of plates

Plate 1

Figs. 1-2. *Crioceratites (Paracrioceras) leyvaensis* sp. nov., lower? Barremian, Villa de Leyva (Santo Ecce Homo).

Fig. 1. RGM 352 596, holotype. a, right-lateral view. b, apertural view

Fig. 2. RGM 345 115. a, left-lateral view. b, apertural view. c, ventral view.

All figures $\times 1$.

Plate 2

Figs. 1-2. *Crioceratites (Paracrioceras) leyvaensis* sp. nov., lower? Barremian, Villa de Leyva (Santo Ecce Homo)

Fig. 1. RGM 352 596 (holotype). a, left-lateral view. b, ventral view

Fig. 2. RGM 345 115. Right-lateral view.

Fig. 3. *Crioceratites (Paracrioceras) royogomezzi* sp. nov., Barremian, Villa de Leyva (Santo Ecce Homo). RGM 352 542, holotype. a, right lateral view. b, ventral view.

Fig. 4. *Crioceratites (Paracrioceras) cabreraensis* sp. nov., lower Barremian, Loma Cabrera. RGM 352 547, holotype. a, left-lateral view. b, ventral view.

All figures $\times 1$.

Plate 3

Fig. 1. *Pseudocrioceras anthulai* (Eristavi, 1955), uppermost? Barremian, Guane (along the road near the finca of the Family Rivera). RGM 353 951. Left-lateral view. $\times 1$.

Fig. 2. *Hamiticeras longus* sp. nov., middle? Aptian, Sáchica. RGM 345 180, holotype. a, ventral view. b, right-lateral view. $\times 1$.

Fig. 3. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Guane (Vereda Chagueta). RGM 353 837. Left-lateral view. $\times 0.86$.

Plate 4

Fig. 1. *Pseudocrioceras anthulai* (Eristavi, 1955), uppermost? Barremian, Guane (Quebrada Barichara). RGM 353 631. Right-lateral view. $\times 0.88$.

Plate 5

Fig. 1. *Pedioceras caquesense* (Karsten, 1858), lower Barremian, Loma Cabrera. RGM 353 639. a, left-lateral view. b, ventral view. $\times 1$.

Plate 6

Fig. 1. *Pedioceras multicoatum* sp. nov., lower Barremian, Villa de Leyva. RGM 353 635, holotype. a, left lateral view. $\times 1$. b, apertural view. $\times 1$. c, ventral view. $\times 1$.

Fig. 2. *Pseudocrioceras guanense* sp. nov., uppermost? Barremian, Guane. RGM 353 633, holotype. a, right lateral view. b, ventral view. $\times 1$.

Plate 7

Fig. 1. *Colchidites* cf. *breistrofferi* Kakabadze & Thieuloy, 1991; upper Barremian, Guane (Vereda Chagueta).

RGM 353 698. Left-lateral view. $\times 0.83$.

Plate 8

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Vereda Chaguete). RGM 354 119. Right-lateral view. $\times 0.6$.

Plate 9

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Vereda Chaguete). RGM 354 119. Ventral view. $\times 0.6$.

Fig. 2. *Ancyloceras* sp. (Forme 1), lower Aptian, Guane. RGM 353 625. Ventral view. $\times 0.67$.

Plate 10

Fig. 1. *Ancyloceras* sp. (Forme 1), lower Aptian, Guane. RGM 353 624. a, right-lateral view. b, ventral view, $\times 0.6$.

Plate 11

Fig. 1. *Ancyloceras* sp. (Forme 2), upper? Barremian, Villa de Leyva (Santa Sofia). RGM 353 626. a, left-lateral view. b, ventral view. $\times 1$.

Plate 12

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Vereda Chaguete). RGM 354 125. Left-lateral view. $\times 0.8$.

Plate 13

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Vereda Chaguete). RGM 354 125. a, apertural view. b, ventral view. $\times 0.8$.

Plate 14

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Vereda Chaguete, along the road). RGM 353 619. a, right-lateral view. b, ventral view. $\times 0.6$.

Plate 15

Fig. 1. *Ancyloceras* cf. *matheronianum* d'Orbigny, 1842, lowermost? Aptian, Guane (Guabrada Barichara). RGM 353 620. a, left-lateral view. b, ventral view. $\times 1$.

Plate 16

Fig. 1. *Ancyloceras* sp. (Forme 1), lower Aptian, Guane. RGM 353 625. left-lateral view. $\times 0.6$.

Fig. 2. *Hamiticeras ventrotuberculatum* sp. nov., middle? Aptian, Villa de Leyva, Santo Ecce Homo. RGM 353 629, holotype. a, right-lateral view. b, ventral view. $\times 1$.

Plate 17

Fig. 1. *Colchidites guanensis* sp. nov., upper Barremian, Guane (Vereda Chaguete). RGM 353 685. a, right-lateral view. b, ventral view. $\times 0.67$.

Plate 18

Fig. 1. *Kutatissites creutzbergi* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 345 790, holotype. Right-lateral view. $\times 0.6$.

Plate 19

Fig. 1. *Kutatissites creutzbergi* sp. nov., RGM 345 790, holotype.? uppermost Barremian, Galan (left bank of Río Suarez). Left-lateral view. $\times 0.6$.

Plate 20

Fig. 1. *Kutatissites creutzbergi* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 345 790, holotype. Ventrolateral view. $\times 0.6$.

Plate 21

Fig. 1. *Kutatissites creutzbergi* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 345 790, holotype. Ventral view. $\times 0.6$.

Plate 22

Fig. 1. *Kutatissites creutzbergi* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 345 790, holotype. Apertural view. $\times 0.6$.

Plate 23

Fig. 1. *Kutatissites densecostatus compactus* subsp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 840 (holotype). Left-lateral view. $\times 0.5$.

Plate 24

Fig. 1. *Kutatissites densecostatus compactus* subsp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 840, holotype. Apertural view. $\times 0.5$.

Plate 25

Fig. 1. *Kutatissites densecostatus compactus* subsp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 840, holotype. Right-lateral view. $\times 0.5$.

Plate 26

Fig. 1. *Kutatissites densecostatus compactus* subsp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 840, holotype. Ventral view. $\times 0.5$.

Plate 27

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 854. Left-lateral view. $\times 0.86$.

Plate 28

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 854. Ventral view. $\times 0.86$.

Plate 29

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 854. Right-lateral view. $\times 0.86$.

Plate 30

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 854. Apertural view. $\times 0.86$.

Plate 31

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 839. Right-lateral view. $\times 0.88$.

Plate 32

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 839. Left-lateral view. $\times 0.88$.

Plate 33

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank).

RGM 353 839. Ventral view. $\times 0.88$.

Plate 34

Fig. 1. *Kutatissites simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank).

RGM 353 839. Apertural view. $\times 0.88$.

Plate 35

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 838. Right-lateral view. $\times 1$.

Plate 36

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 838. Apertural view. $\times 1$.

Plate 37

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 838. Left-lateral view. $\times 1$.

Plate 38

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 838. Ventral view. $\times 1$.

Plate 39

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 835. Left-lateral view. $\times 0.71$.

Plate 40

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 835. Right-lateral view. $\times 0.71$.

Plate 41

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 835. Ventral view. $\times 0.71$.

Plate 42

Fig. 1. *Kutatissites* aff. *simionescui* (Avram, 1976), uppermost? Barremian Galan (left bank of Río Suarez). RGM 353 835. Apertural view. $\times 0.71$.

Plate 43

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 842.

Left-lateral view. $\times 0.88$.

Plate 44

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 842.

Ventral view. $\times 0.88$.

Plate 45

Fig. 1. *Kutatissites creutzbergi* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 844. Right-lateral view. $\times 0.86$.

Plate 46

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 842. Apertural view. $\times 0.88$.

Plate 47

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 841, holotype. Right-lateral view. $\times 0.67$.

Plate 48

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 841, holotype. Left-lateral view. $\times 0.67$.

Plate 49

Fig. 1. *Kutatissites etayosernai* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 841, holotype. a, Apertural view. b, ventral view. $\times 0.67$.

Plate 50

Fig. 1. *Kutatissites grandis* sp. nov., uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 847, holotype. Left-lateral view. $\times 0.6$.

Plate 51

Fig. 1. *Kutatissites grandis* sp. nov., uppermost? Barremian, Guane (Quebrada Barichaea, left bank). RGM 353 847, holotype. Right-lateral view. $\times 0.6$.

Plate 52

Fig. 1. *Kutatissites grandis* sp. nov., uppermost? Barremian, Guane (Quebrada Barichara, left bank). RGM 353 847, holotype. Apertural view. $\times 0.6$.

Plate 53

Fig. 1. *Kutatissites? galanensis* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 843, holotype. Left-lateral view. $\times 0.67$.

Plate 54

Fig. 1. *Kutatissites? galanensis* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 843, holotype. Ventral view. $\times 0.67$.

Fig. 2. *Hamiticeras pilsbryi* Anderson, 1938, middle? Aptian, Villa de Leyva. RGM 354 122. a, right-lateral view. b, apertural view. $\times 1$.

Plate 55

Fig. 1. *Kutatissites? galanensis* sp. nov., uppermost? Barremian, Galan (left bank of Río Suarez). RGM 353 843, holotype. Right-lateral view. $\times 0.67$.

Plate 56

Fig. 1. *Colchidites guanensis* sp. nov., upper Barremian, Guane (by Fam. Rivera, along the road). RGM 353 687. Right-lateral view. $\times 1$.

Fig. 2. *Colchidites riosuarezi* sp. nov., upper Barremian, Guane (by Fam. Rivera, along the road). RGM 353 681, cast. Right-lateral view. $\times 0.9$.

Fig. 3. *Heteroceras? (Argvethites)* sp., upper Barremian, Guane (along the road). RGM 353 655a. a, left-lateral view. b, right-lateral view. c, apertural view. $\times 1$.

Fig. 4. *Heteroceras? (Argvethites) sp.*, upper Barremian, Guane (along the road). RGM 353 655b. Ventral view. $\times 1$.

Plate 57

Fig. 1. *Ammonitoceras galanense sp. nov.*, middle? Aptian, Galan (left bank of Río Suarez). RGM 353 736, holotype. Left-lateral view.

Fig. 2. *Colchidites guanensis sp. nov.*, upper Barremian, Guane (by Fam. Rivera, along the road). RGM 353 686. a, right-lateral view. b, apertural view. c, ventral view.

All figures $\times 1$.

Plate 58

Fig. 1. *Ammonitoceras giganteum sp. nov.*, middle? Aptian, Guane. RGM 353 845, holotype. Right-lateral view. $\times 0.33$.

Plate 59

Fig. 1. *Ammonitoceras galanense sp. nov.*, middle? Aptian, Galan (left bank of Río Suarez). RGM 353 736, holotype. a, right-lateral view. b, apertural view. $\times 1$.

Plate 60

Fig. 1. *Laqueoceras cf. laqueus sp. nov.*, middle? Aptian, Villa de Leyva (Loma Gonzalez). RGM 353 734. Right-lateral view. $\times 0.4$.

Fig. 2. *Pseudocrioceras guanense sp. nov.*, lowermost? Aptian, Guane. RGM 353 634. a, right-lateral view. b, left-lateral view. c, ventral view. $\times 1$.

Plate 61

Fig. 1. *Laqueoceras laqueus sp. nov.*, middle? Aptian, Villa de Leyva (loma Gonzalez). RGM 353 735, holotype. Right-lateral view. $\times 0.5$.

Plate 62

Fig. 1. *Laqueoceras laqueus sp. nov.*, middle? Aptian, Villa de Leyva (loma Gonzalez). RGM 353 735, holotype. Left-lateral view. $\times 0.5$.

Plate 63

1. *Laqueoceras laqueus sp. nov.*, middle? Aptian, Villa de Leyva (loma Gonzalez). RGM 353 735, holotype. a, apertural-ventral view. b, ventral view $\times 0.5$.

Plate 64

Fig. 1. *Pseudoaustraliceras columbiae* (Basse, 1928), middle? Aptian, Guane, Quebrada "la Azofcada". RGM 353 737. Right-lateral view. $\times 0.33$.

Fig. 2. *Helicancyclus cf. philadelphium* Anderson, 1938, middle? Aptian, Villa de Leyva. RGM 344 981. a, left-lateral view. b, apertural-ventral view. c, ventral view. $\times 1$.

Plate 65

Fig. 1. *Hamiticeras? sp.*, middle? Aptian, Villa de Leyva, Loma Blanca. RGM 353 650. a, left-lateral view. b, ventral view. $\times 1$.

Plate 66

Fig. 1. *Pseudoaustraliceras pavlowi* (Wassiliewskyi, 1908), middle? Aptian, Villa de Leyva. RGM 353 630. a, left-lateral view. b, apertural view.

Fig. 2. *Pseudoaustraliceras columbiae* (Basse, 1928), middle? Aptian, Villa de Leyva. RGM 353 610. Left-lateral view.

Fig. 3. *Toxoceratoides* aff. *nagerai* (Leanza, 1970), Barremian/Aptian boundary strata?, Guane (by Fam. Riviera). RGM 353 673, cast. Left-lateral view.

All figures $\times 1$.

Plate 67

Fig. 1. *Pseudoaustraliceras columbiae* (Basse, 1928), middle? Aptian, Villa de Leyva (Loma Blanca). RGM 353 609. Right-lateral view. $\times 0.5$.

Fig. 2. *Hemihoplites* (*Matheronites*) *ridzewskyi sáchicaensis* subsp. nov., upper? Barremian, Sáchica. RGM 352 534. a, left-lateral view. b, ventral view. $\times 1$.

Fig. 3. *Crioceratites* (*Paracrioceratites*) *cabreraensis* sp. nov., lower Barremian, Villa de Leyva (Loma Cabrera). RGM 352 547, holotype. a, right-lateral view. b, left-lateral view. c, ventral view. $\times 1$.

Plate 68

Fig. 1. *Colchidites riosuarezi* sp. nov., upper Barremian, Galan (left bank of Río Suarez). RGM 353 682, holotype. Right-lateral view. $\times 0.88$.

Plate 69

Fig. 1. *Colchidites apolinari* (Royo y Gomez, 1945), upper Barremian, Galan (left bank of Río Suarez). RGM 353 692. Left-lateral view. $\times 0.88$.

Plate 70

Fig. 1. *Colchidites riosuarezi* sp. nov., upper Barremian, Guane (along the road near Fam. Riviera). RGM 353 681. Left-lateral view. $\times 0.9$.

Plate 71

Figs. 1-2. *Colchidites breistrofferi* Kakabadze & Thieuloy, 1991, upper Barremian, Chipatá.

Fig. 1. RGM 353 699. a, left-lateral view. b, ventral view.

Fig. 2. RGM 353 701. Right-lateral view.

All figures $\times 1$.

Plate 72

Fig. 1. *Colchidites guanensis* sp. nov., upper Barremian, Guane (along the road by Fam. Riviera). RGM 353 679.

Right lateral view. $\times 0.88$.

Plate 73

Fig. 1. *Colchidites guanensis* sp. nov., upper Barremian, Guane (Vereda Chagueta). RGM 353 683, holotype, cast. Left-lateral view.

Fig. 2. *Colchidites striatosulcatus* sp. nov., upper Barremian, Guane (along the road by Fam. Riviera). RGM 353 697, holotype. a, left lateral view. b, apertural view. c, ventral view.

All figures $\times 1$.

Plate 74

Fig. 1. *Colchidites guanensis* sp. nov., upper Barremian, Guane (Vereda Chagueta). RGM 353 684, cast. Right-lateral view. $\times 0.88$.

Plate 75

Fig. 1. *Colchidites apolinari* (Royo y Gomez, 1945), upper Barremian, Guane (Vereda Chagueta). RGM 353 696, cast. Left-lateral view. $\times 0.67$.

Plate 76

Fig. 1. *Colchidites pseudovulanensis* sp. nov., upper Barremian, Galan (left bank of Río Suarez). RGM 353 680, holotype, cast. Left-lateral view.

Fig. 2. *Colchidites apolinari* (Royo y Gomez, 1945), upper Barremian, Sáchica. RGM 353 700. a, right-lateral view. b, ventral view. c, apertural view.

All figures $\times 1$.

Plate 77

Fig. 1. *Ancyloceras* cf. *mantelli* Casey, 1960, lower Aptian, Santa Sofia. RGM 353 621. Right-lateral view. $\times 0.75$.

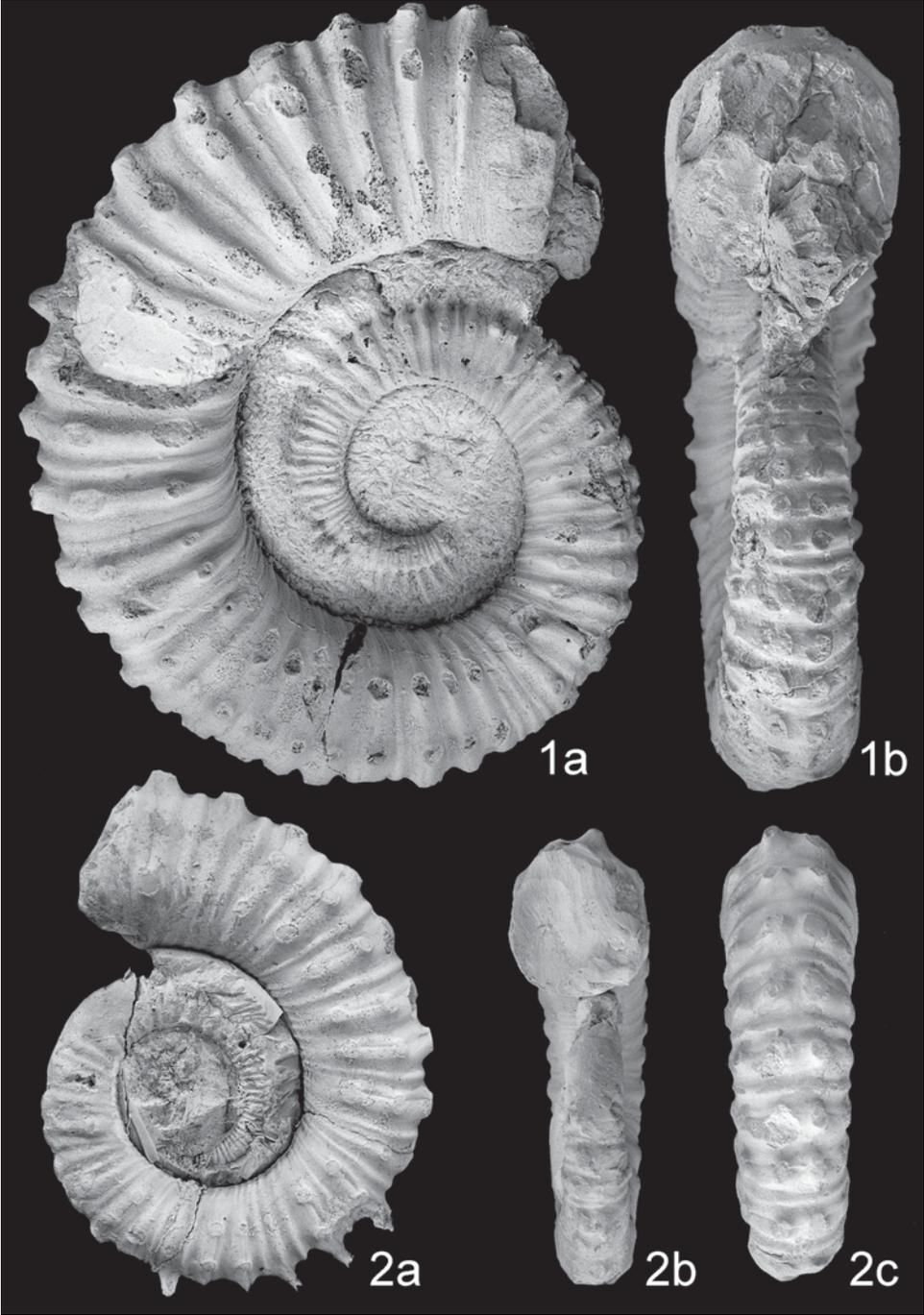


Plate 1

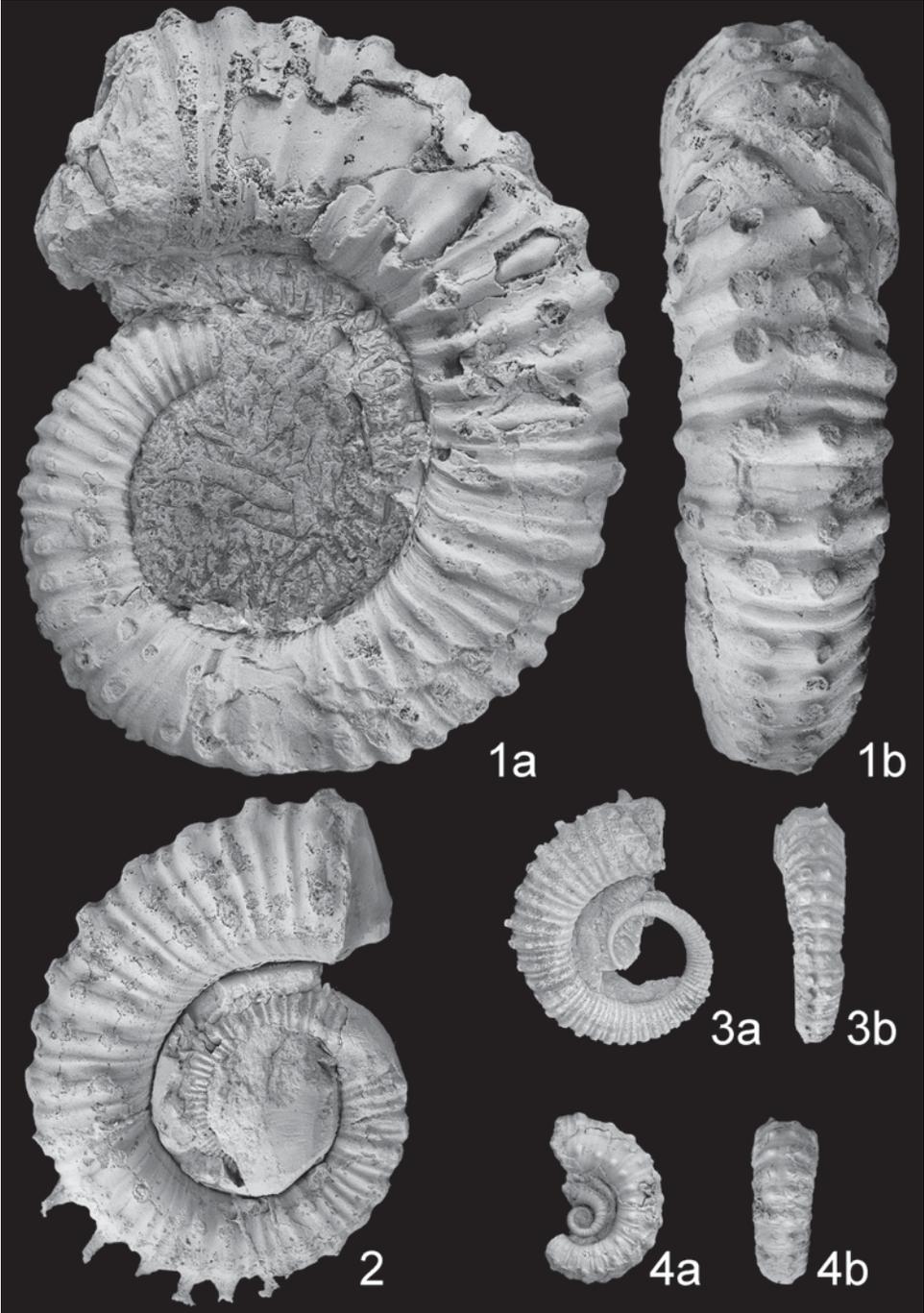


Plate 2

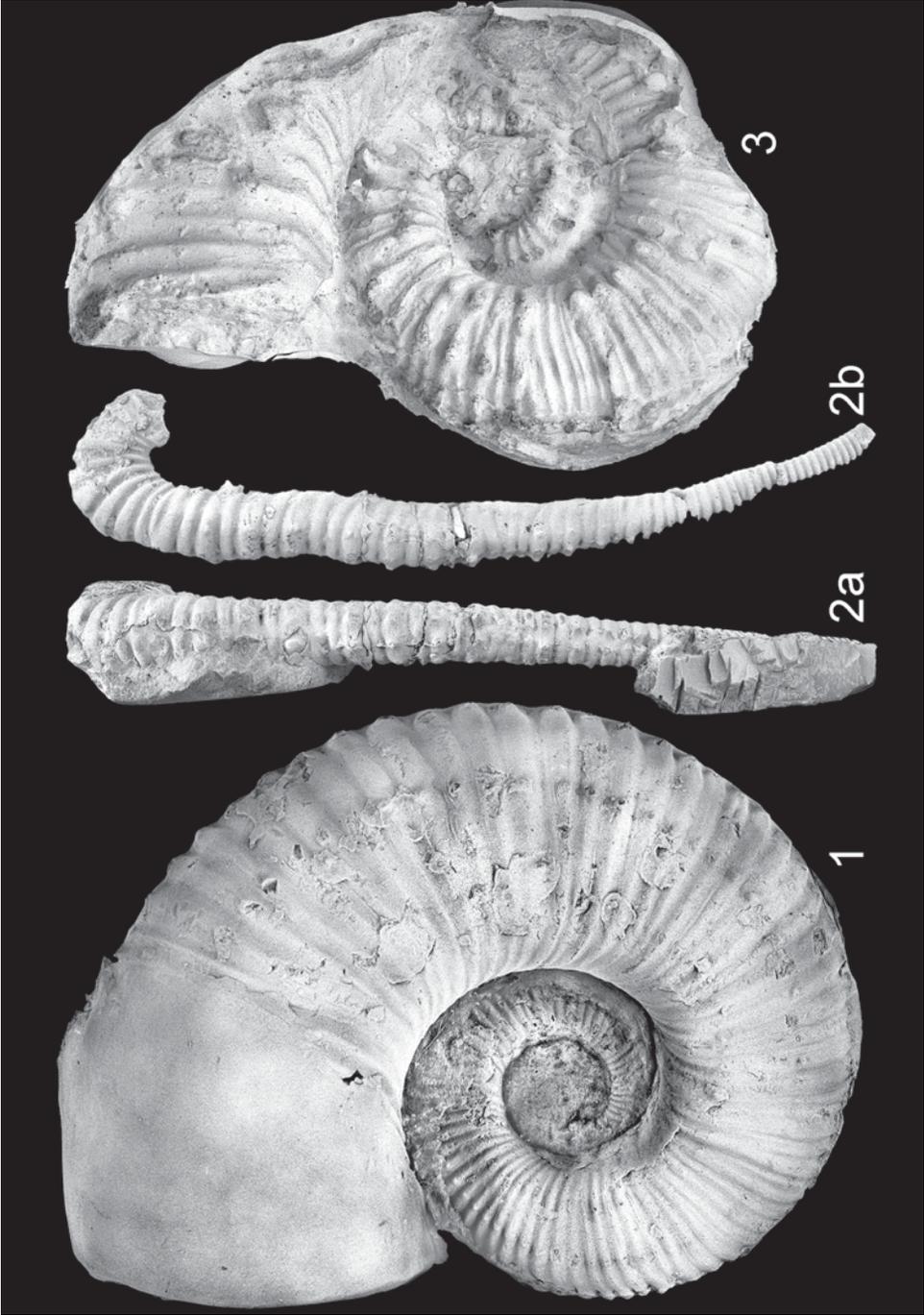


Plate 3

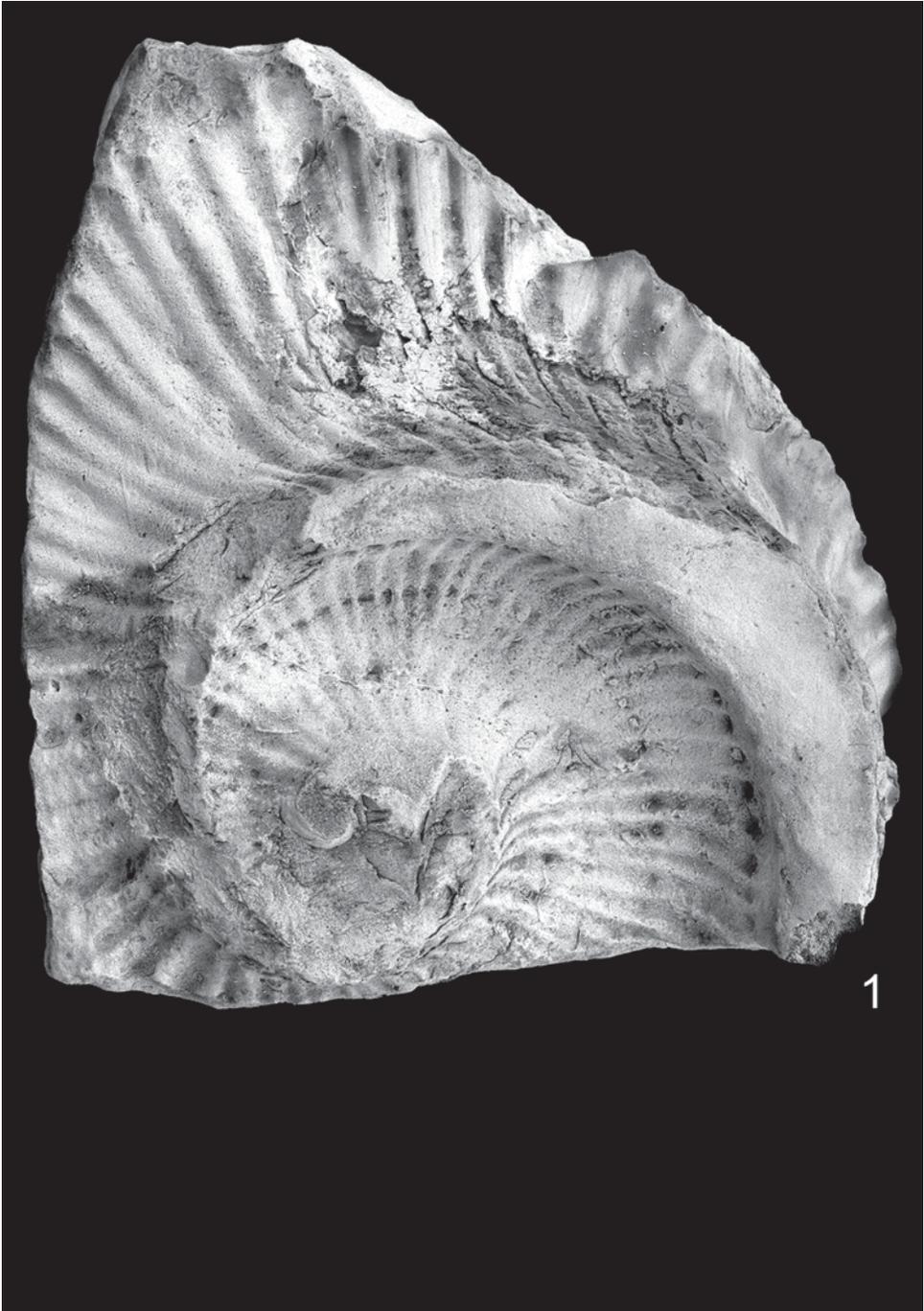


Plate 4

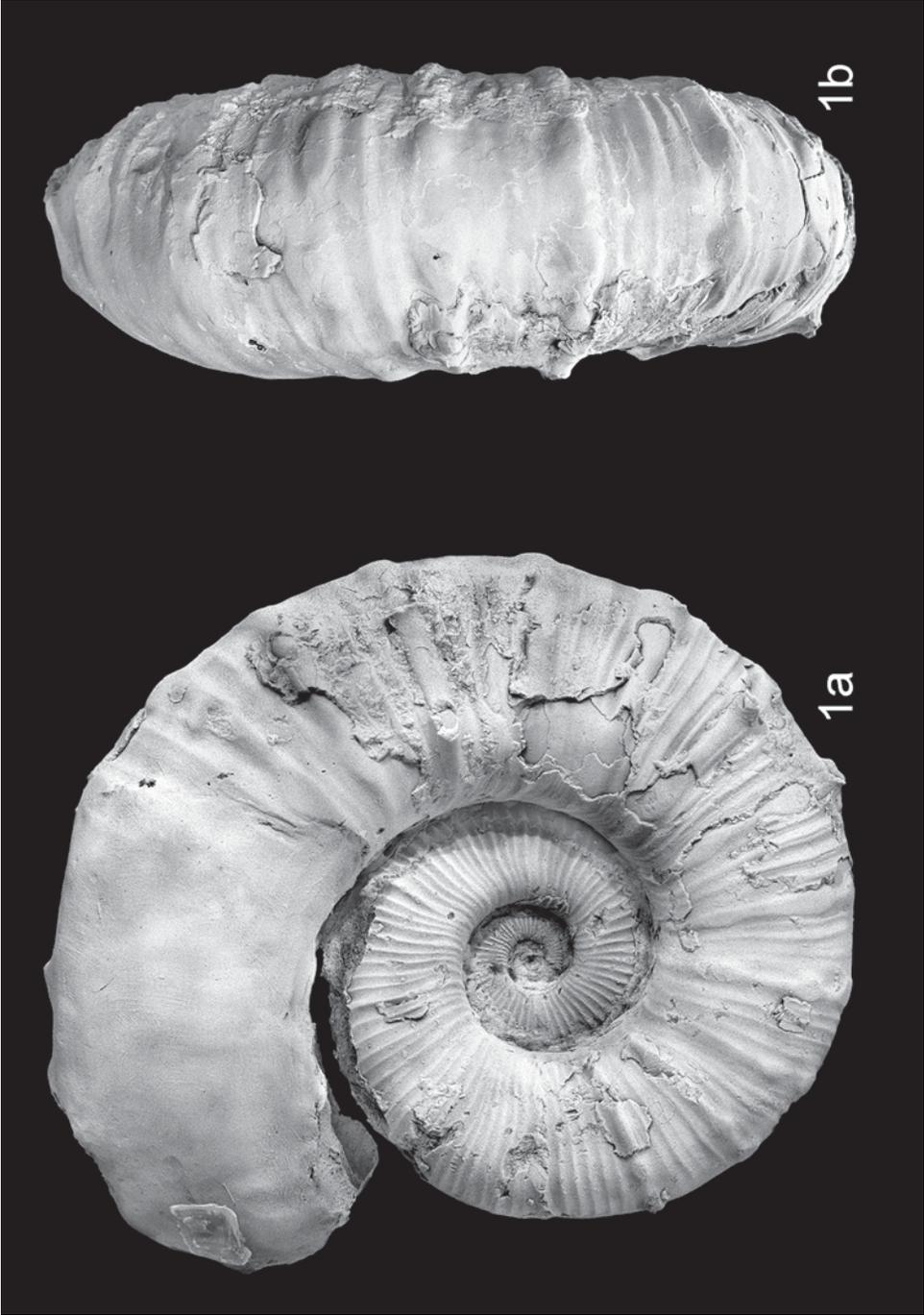


Plate 5

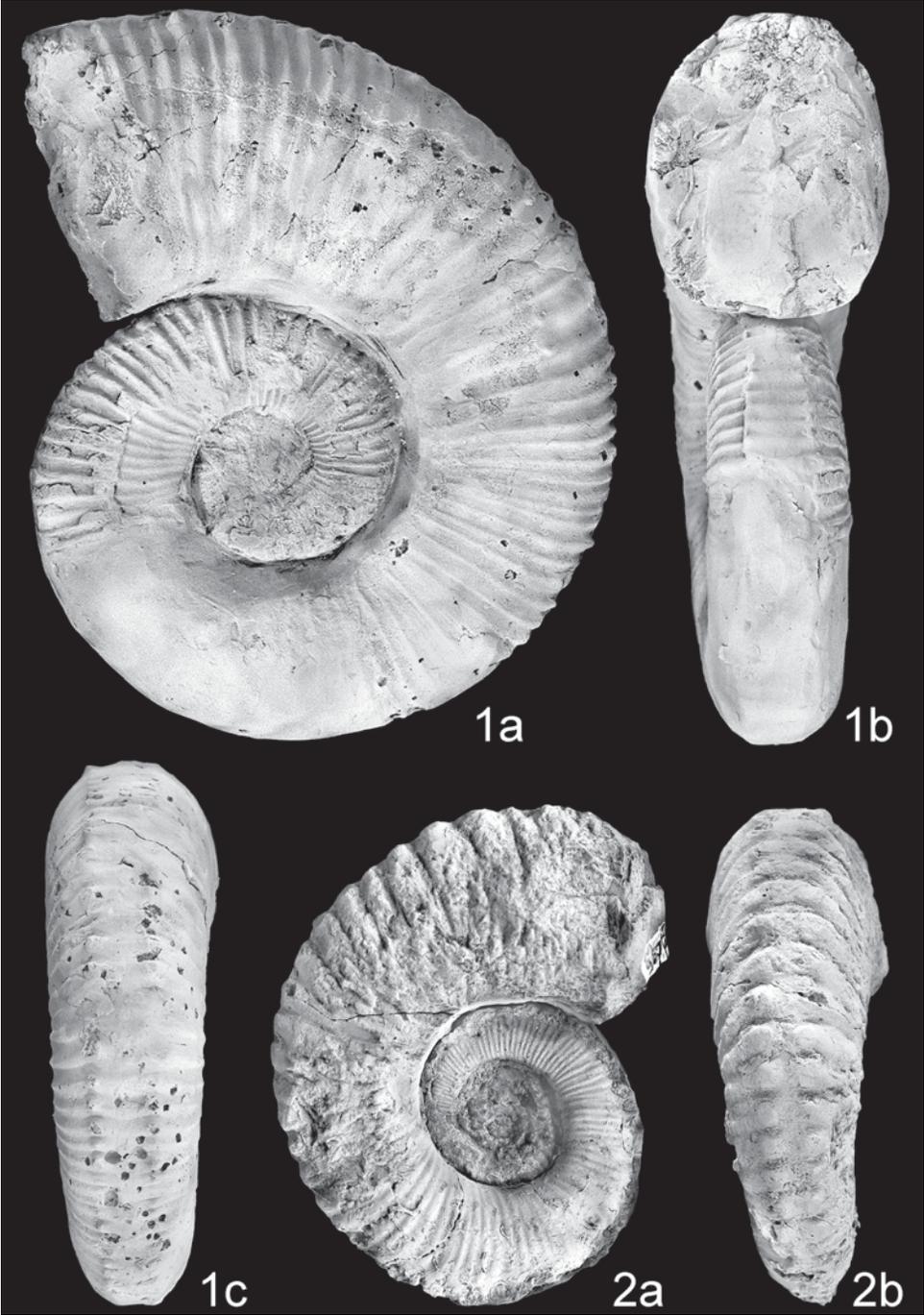


Plate 6



Plate 7



Plate 8



Plate 9



Plate 10



Plate 11

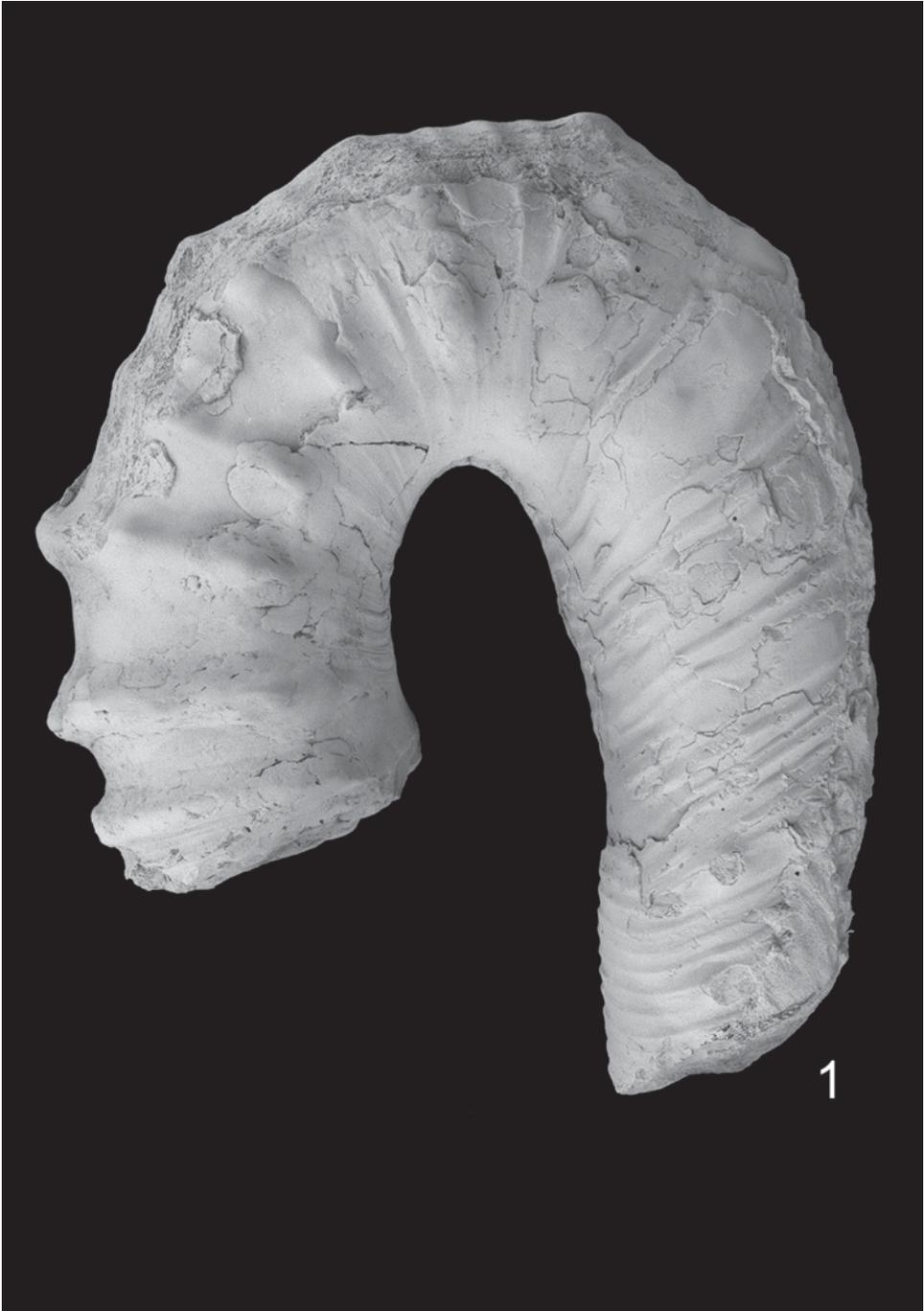


Plate 12



Plate 13



Plate 14



Plate 15



Plate 16

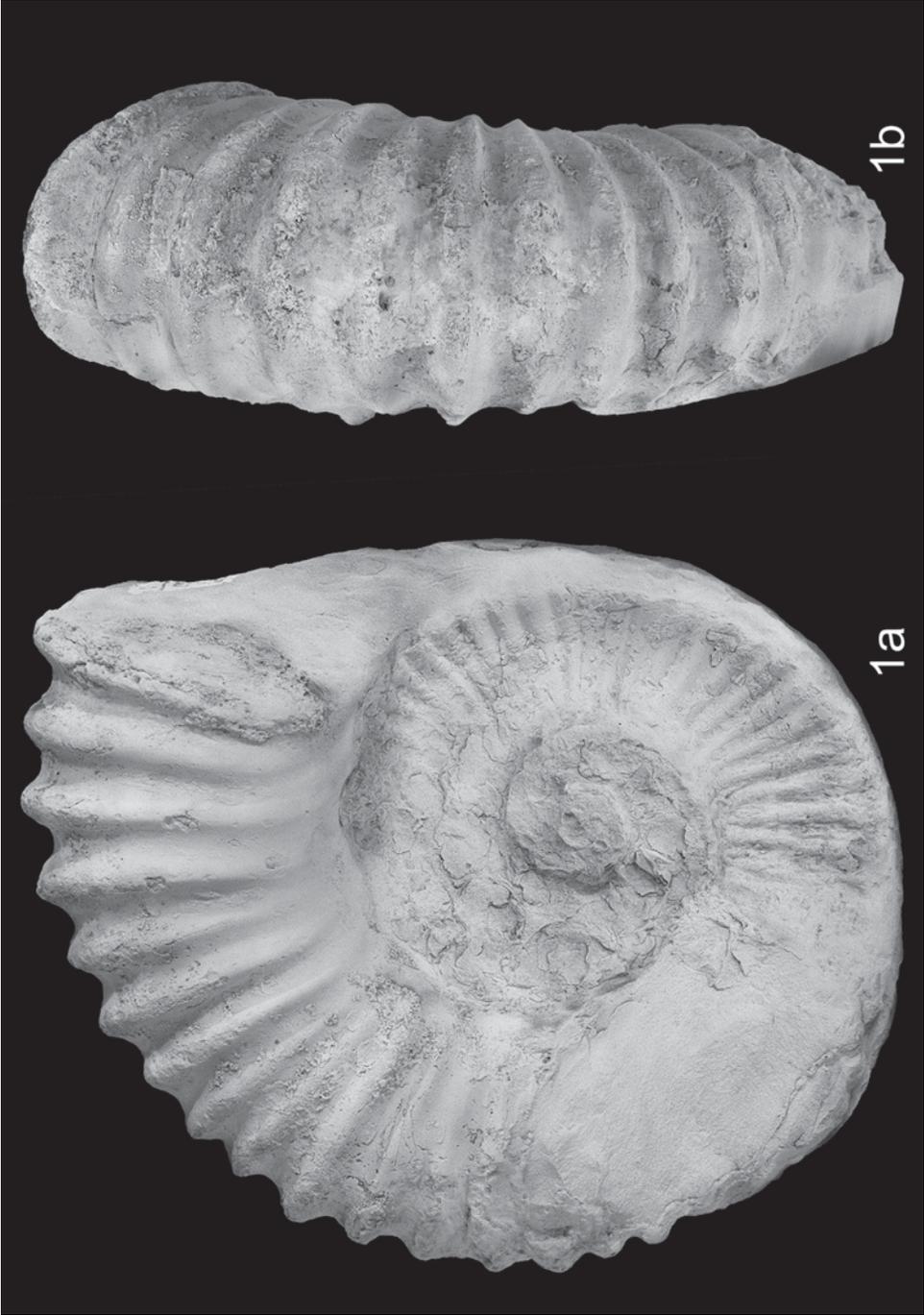


Plate 17



Plate 18



Plate 19



Plate 20



Plate 21



Plate 22



Plate 23



Plate 24



Plate 25



Plate 26



Plate 27



Plate 28



Plate 29



Plate 30



Plate 31



Plate 32



Plate 33



Plate 34



Plate 35



Plate 36



Plate 37



Plate 38



Plate 39



Plate 40



Plate 41



Plate 42



Plate 43



Plate 44



Plate 45



Plate 46



Plate 47

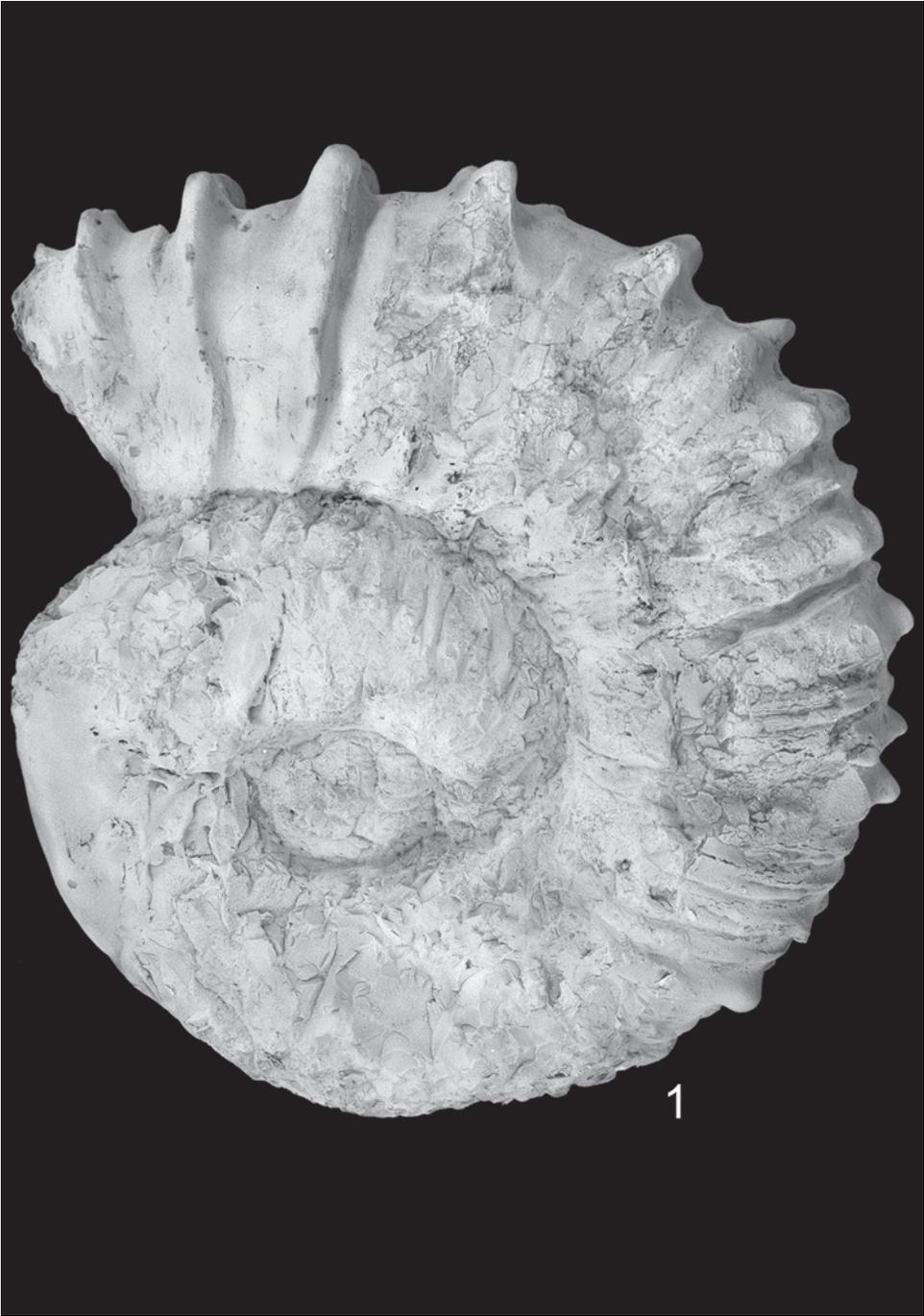


Plate 48

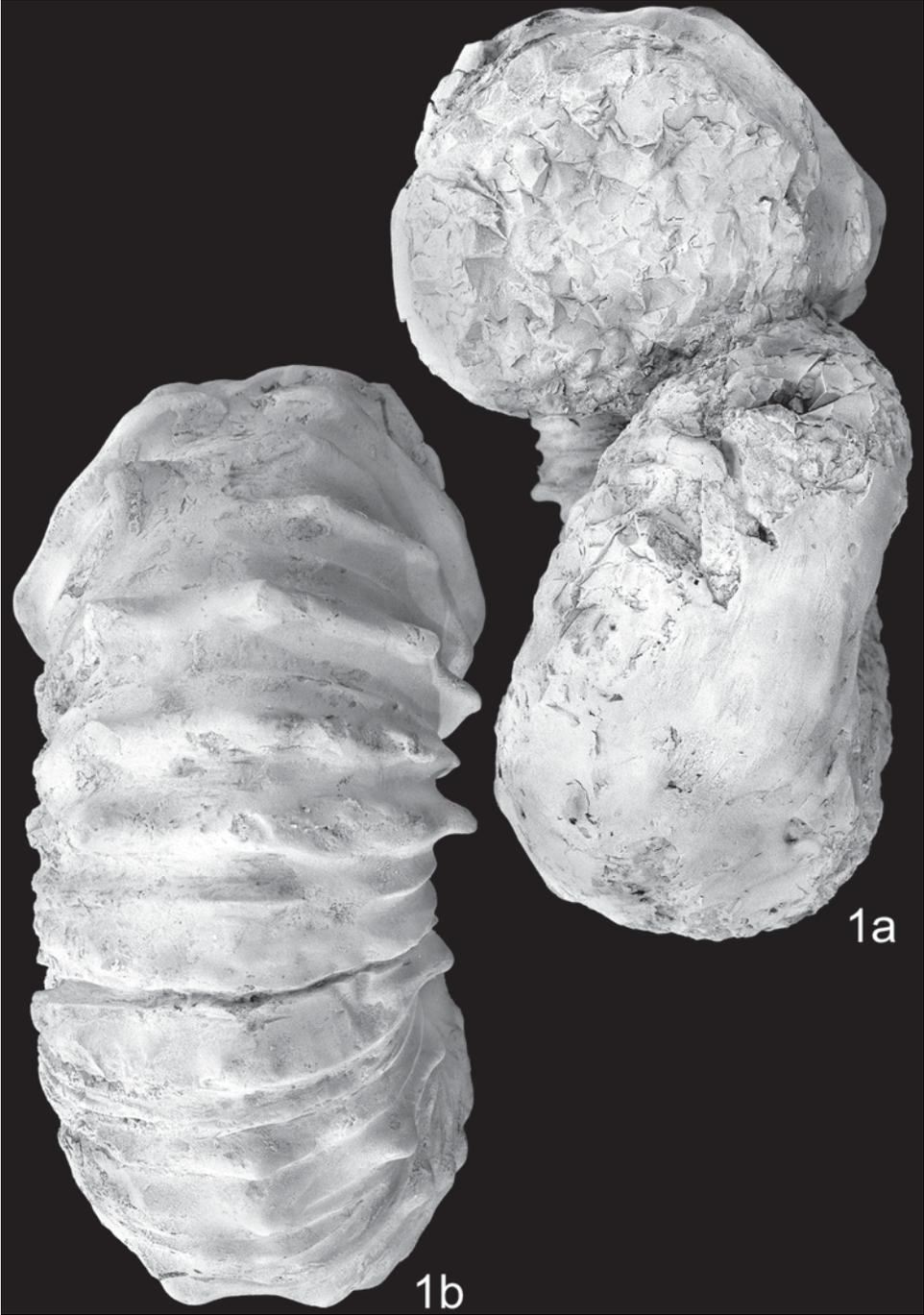


Plate 49



Plate 50

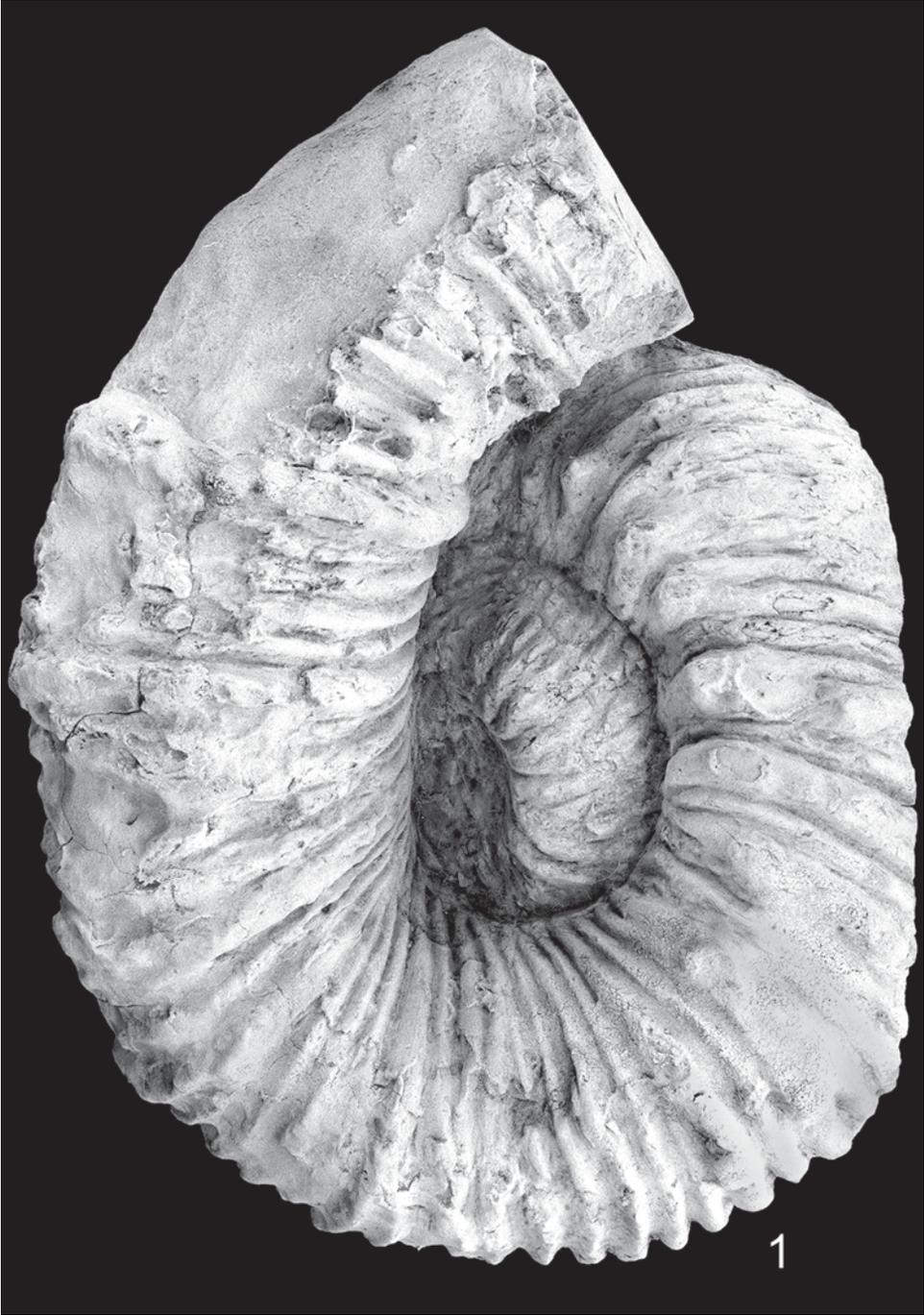


Plate 51



Plate 52



Plate 53

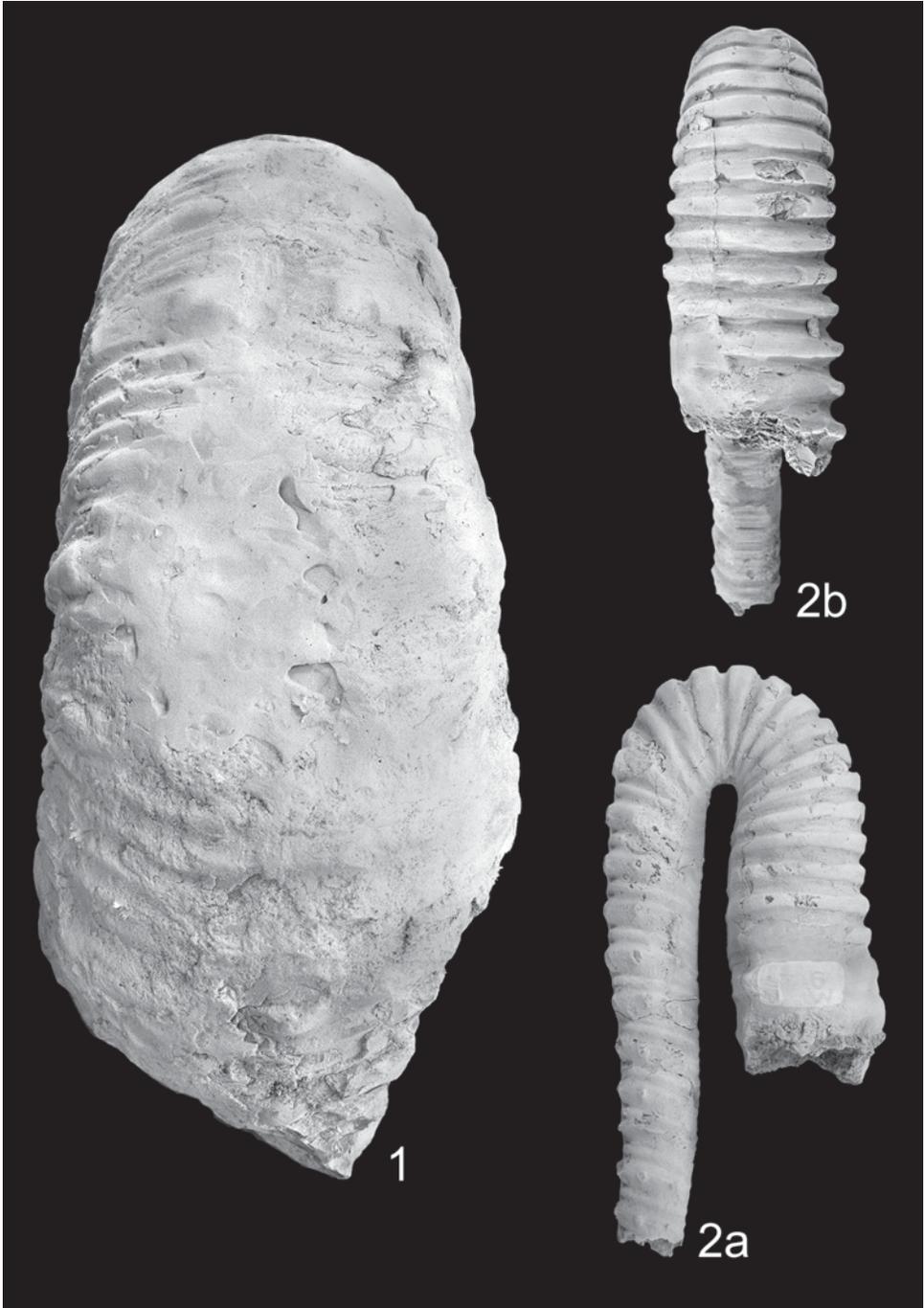


Plate 54



Plate 55

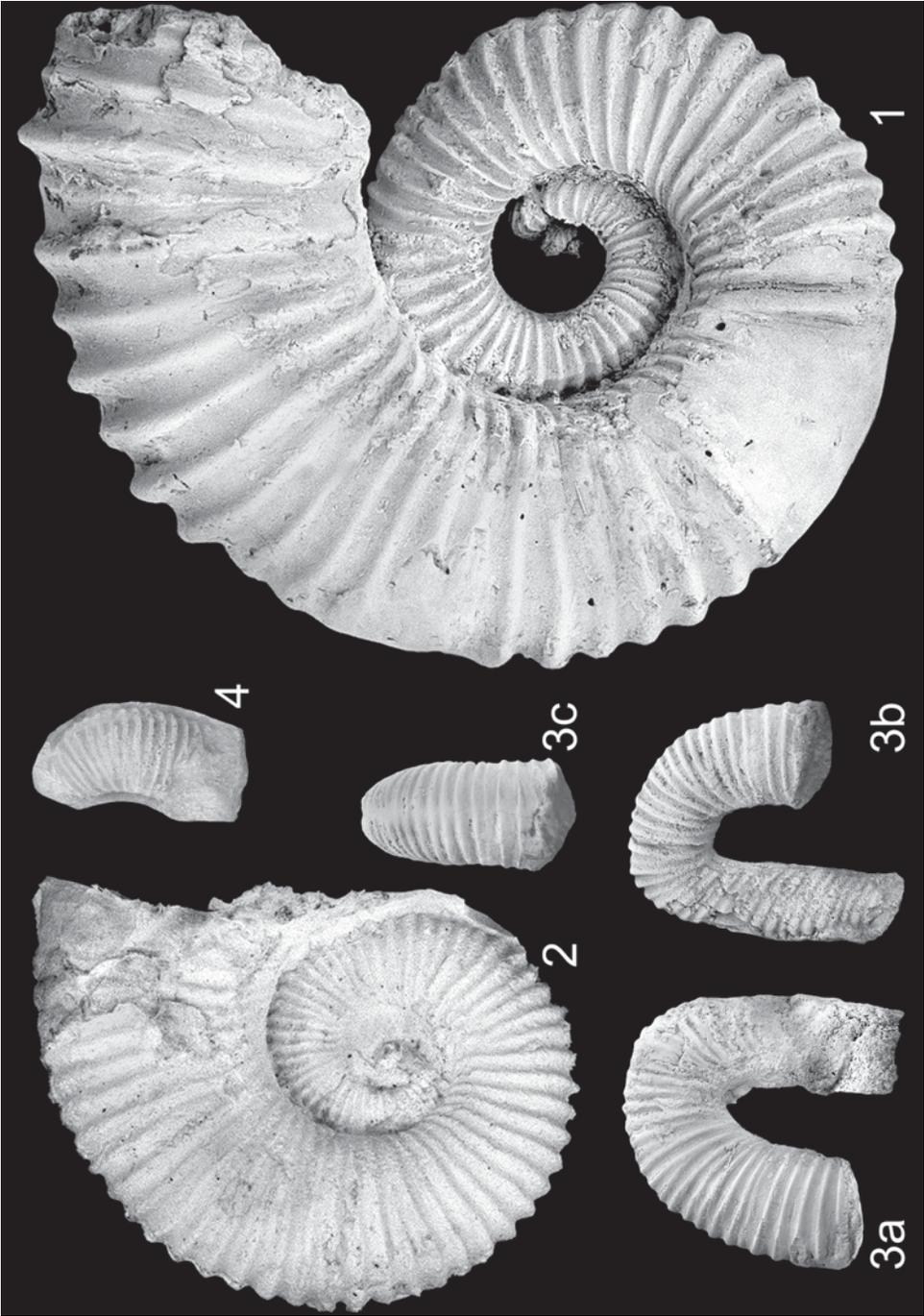


Plate 56

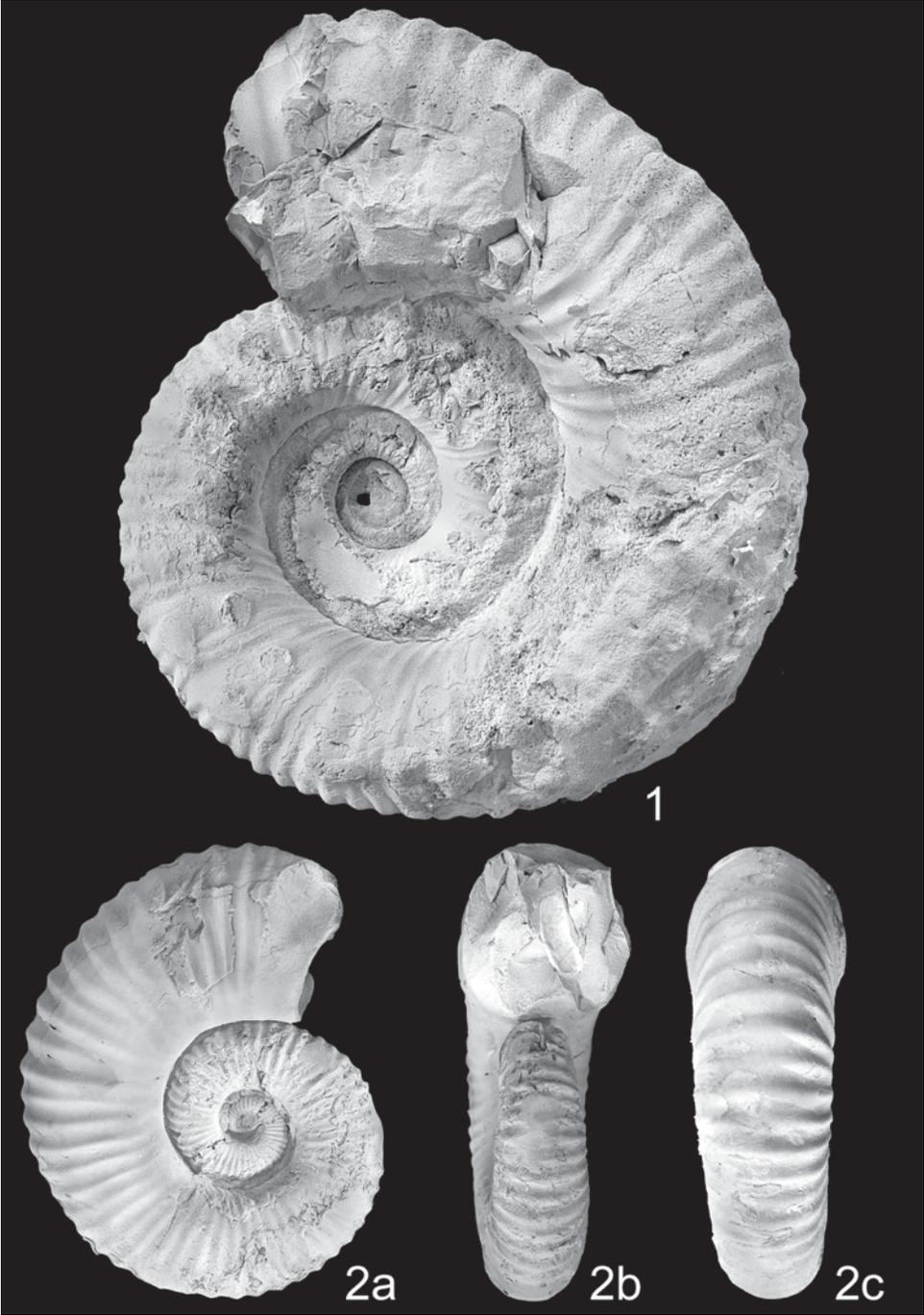


Plate 57



Plate 58

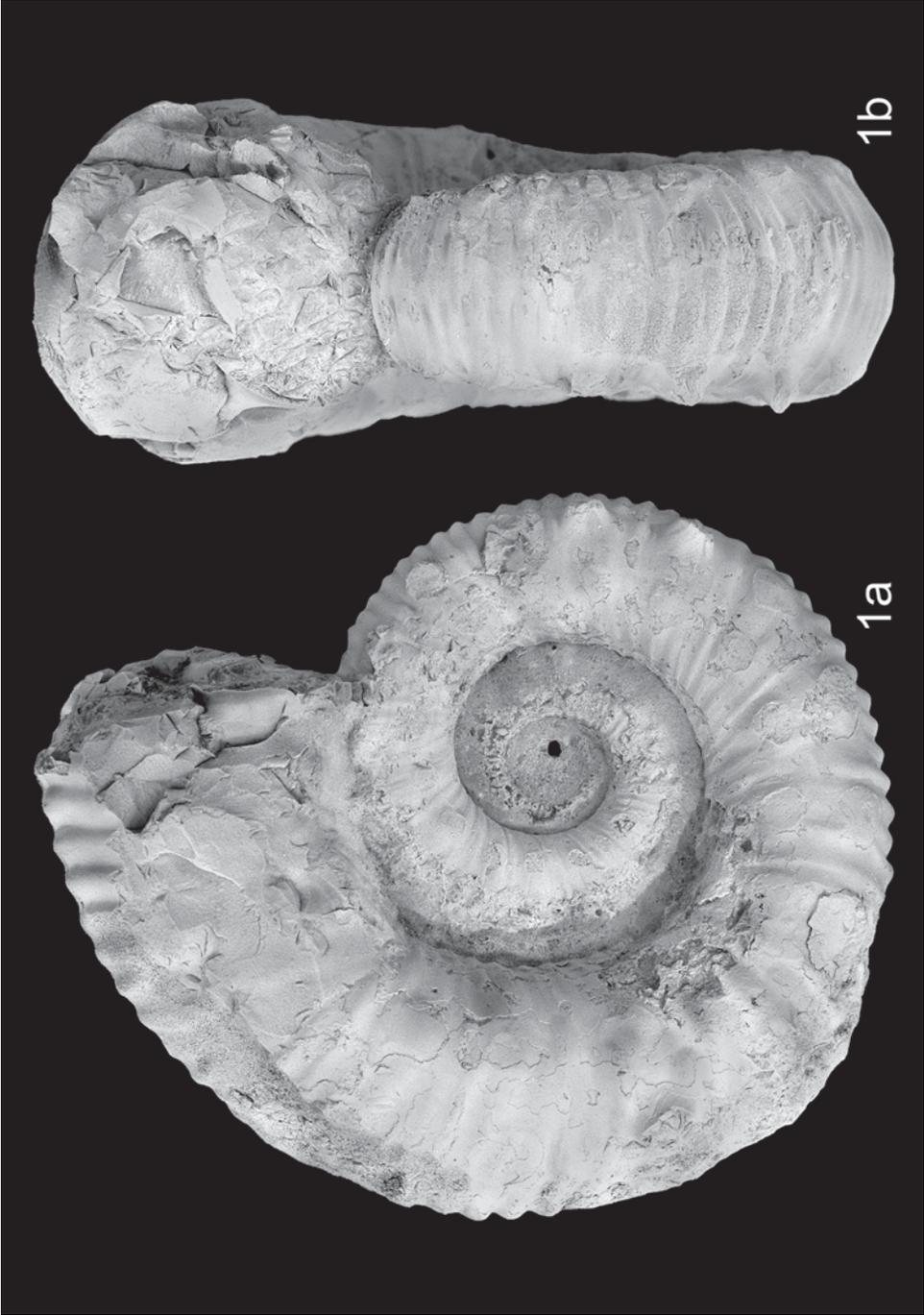


Plate 59



Plate 60



Plate 61



Plate 62

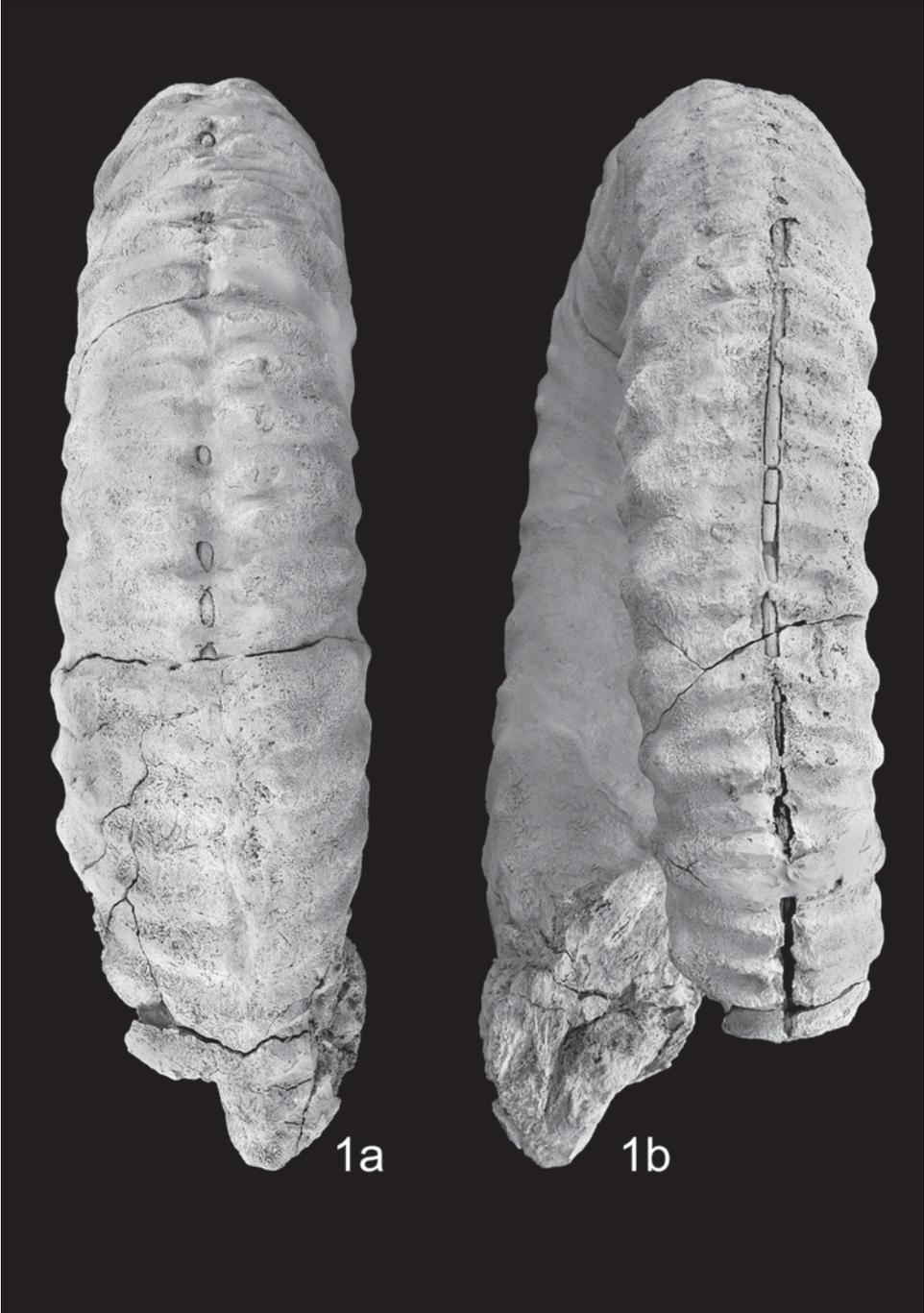


Plate 63



Plate 64

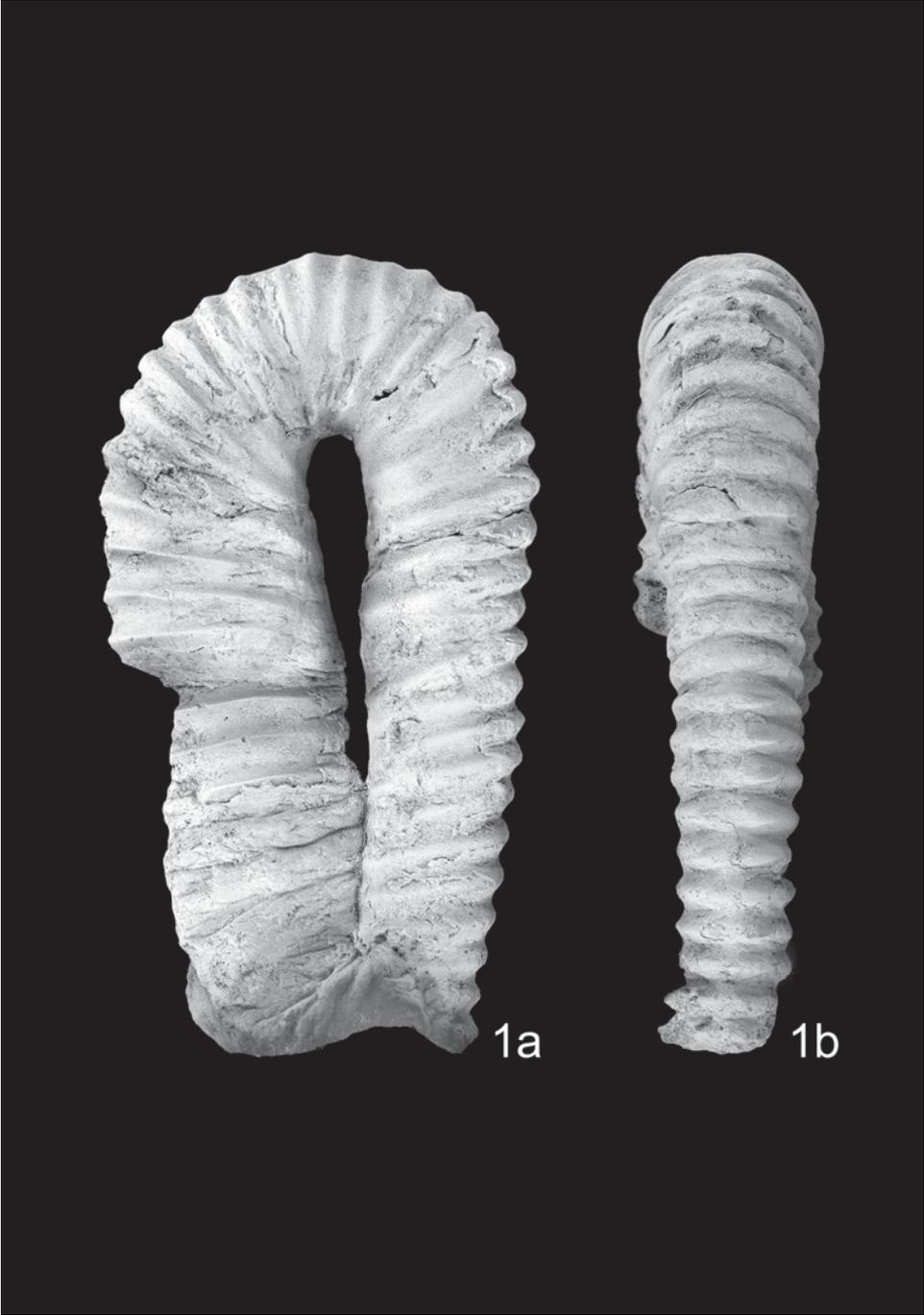


Plate 65

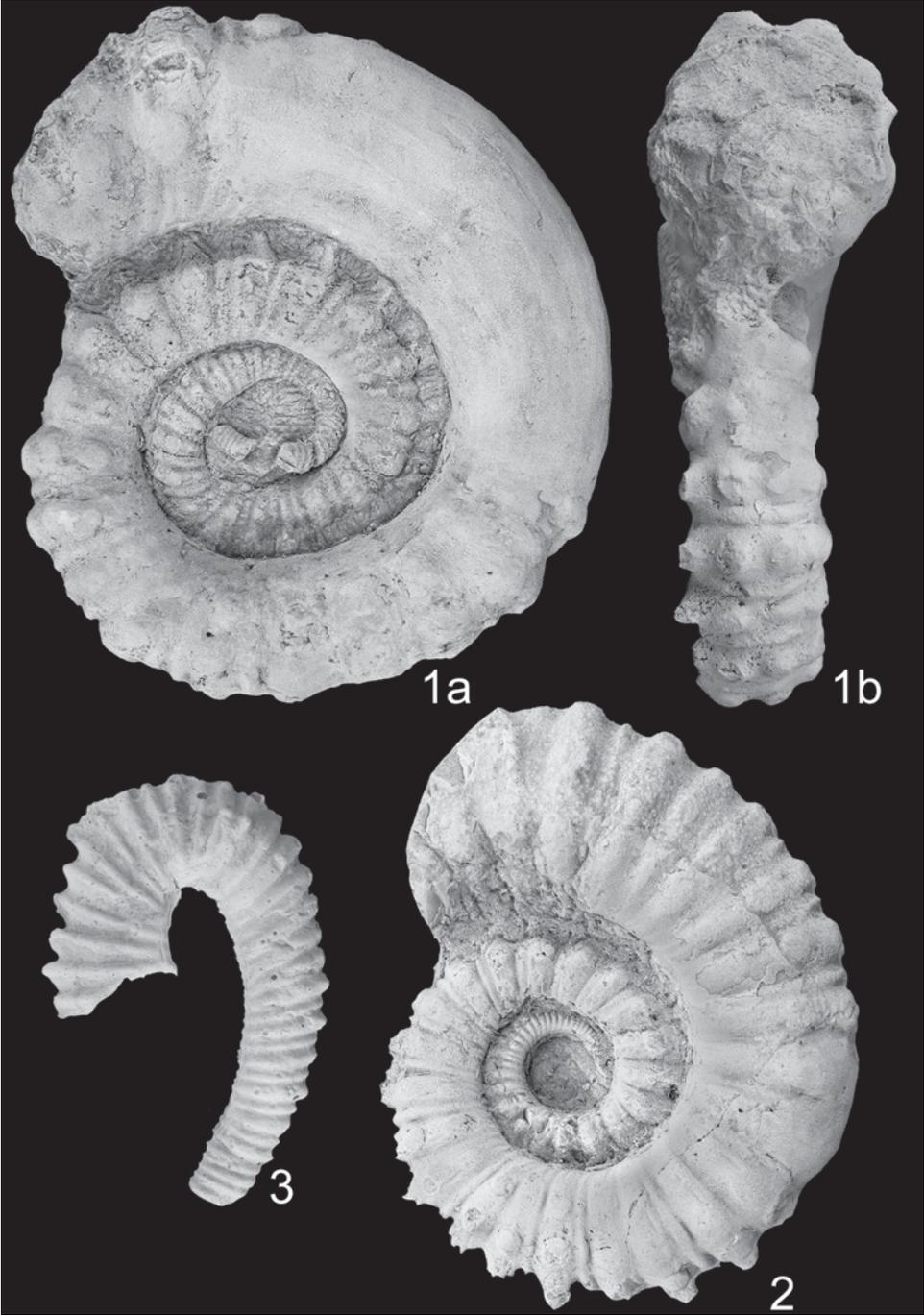


Plate 66



Plate 67



Plate 68



Plate 69



Plate 70

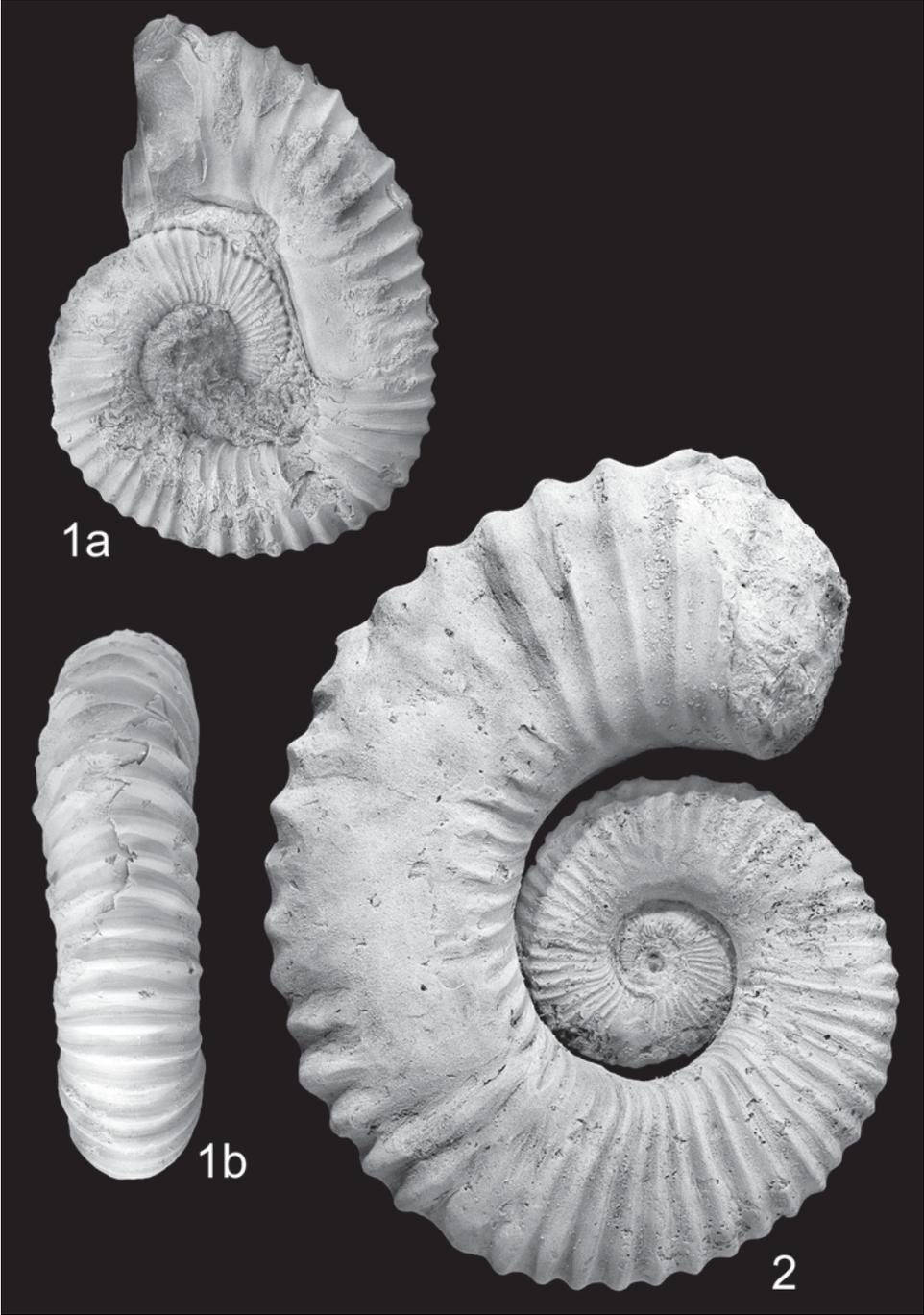


Plate 71



Plate 72



Plate 73



Plate 74



Plate 75



Plate 76



Plate 77