

# The ammonite genera *Dipoloceras*, *Diplasioceras*, *Euspectroceras*, and *Rhytidoceras* from the Upper Albian of KwaZulu-Natal, South Africa

WILLIAM JAMES KENNEDY<sup>1</sup> and HERBERT CHRISTIAN KLINGER<sup>2</sup>

<sup>1</sup> Oxford University Museum of Natural History, Parks Road, Oxford OX1 3PW, UK and Department of Earth Sciences, South Parks Road, Oxford OX1 3AN, UK; e-mail: jim.kennedy@oum.ox.ac.uk

<sup>2</sup> Natural History Collections Department, Iziko South African Museum, P.O. Box 61, Cape Town, 8000 South Africa; e-mail: ingrid45.hk@gmail.com

## ABSTRACT:

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The lower Upper Albian ammonite genus *Dipoloceras* Hyatt, 1900 (subfamily Mojsisovicsiinae Hyatt, 1903) is represented in KwaZulu-Natal by the type species, *D. cristatum* (Brongniart, 1822), marker species for the base of the Upper Albian Substage. *Rhytidoceras* van Hoepen, 1931 (of which *Drepanoceras* van Hoepen, 1931, *non* Stein 1878 and *Ricnoceras* van Hoepen, 1941, are synonyms), previously regarded as subgenera of *Dipoloceras*, are afforded generic status as are its supposed synonyms *Diplasioceras* van Hoepen, 1946a, and *Euspectroceras* van Hoepen, 1946a. The type species of these genera are revised, and assigned to the subfamily Pervinquierinae Spath, 1926.

**Key words:** Lower Cretaceous; Albian; Ammonites; KwaZulu-Natal; South Africa.

## INTRODUCTION

In this contribution we continue our revision (Kennedy and Klinger 2011, 2012) of the Albian ammonites of the Family Brancoceratidae Spath, 1934, from KwaZulu-Natal, including those described by van Hoepen (1931–1955b), describing the following below: *Dipoloceras cristatum* (Brongniart, 1822) of the Mojsisovicsiinae Hyatt, 1903, and *Diplasioceras fallax* van Hoepen, 1946a, *Euspectroceras newtoni* (Spath, 1925), and *Rhytidoceras elegans* van Hoepen, 1931, which we assign to the Pervinquierinae Spath, 1926.

The most widely used division of the Brancoceratidae is that of Wright (1957, p. 402; 1996, p. L134), who recognised the following subfamilies and their synonyms: Subfamily Brancoceratinae Spath, 1934 (=

Erioliceratidae van Hoepen, 1955b); Subfamily Mojsisovicsiinae Hyatt, 1903 (= Dipoloceratidae Spath, 1921, p. 277; Cechenoceratidae van Hoepen, 1941, p. 61; Drepanoceratidae van Hoepen, 1941, p. 89); and Subfamily Mortoniceratinae Douvillé, 1912 (= Inflaticeratidae Spath, 1925, p. 181; Pervinquieridae Spath, 1926, p. 79; Arestoceratidae van Hoepen, 1942, p. 117; Cainoceratidae van Hoepen, 1942, p. 127).

Wright noted (1996, p. L137) that “Apparently there are two main stocks (both derived from *Moj-sisovicsia* or one from the other): one compressed and high-whorled, which left no descendants, and the other more evolute which by acquisition of tubercles led to Mortoniceratinae. The boundary between subfamilies is arbitrarily taken at the point when large umbilical and ventrolateral tubercles are stabilized in the adult.” He later noted (p. L141) “As the synon-

ymies of subfamily and genera [of *Mortoniceratinae*] show, both the nomenclature and scale of classification of the group have been in doubt. A large number of species with many of the same basic characters vary in detail and in combination of whorl section, number and shape of tubercles at different growth stages, and in strength and direction of the ribs. An attempt is made here to classify them in accord with the scale accepted in allied groups. The subfamily is derived from *Mojsisovicsiinae* along one or several closely allied lines and remains very uniform.”

The revision of the type species of *Mortoniceras* Meek, 1876 and other ammonites from the Kiamichi, Duck Creek, and Fort Worth Formations of Texas (Kennedy in Gale and Kennedy 2020), combined with the present revision of lower Upper Albian ammonites from the Mzinene Formation of northern KwaZulu-Natal in South Africa leads to a rather different conclusion from that of Wright (1996), and also to that of Cooper (2018a), with the recognition of separate subfamilies *Mortoniceratinae* and *Pervinquierinae*.

## REPOSITORIES OF SPECIMENS

The following abbreviations are used to indicate the repositories of specimens cited in the text: BMNH, The Natural History Museum, London, UK; EMP – École des Mines Collections, currently housed in the collections of Faculté des Sciences of the Université Claude Bernard, Lyon 1, Villeurbanne, France; MNHN – Muséum National d’Histoire Naturelle, Paris, France; OUMNH – Oxford University Museum of Natural History, Oxford, UK; SAM – Natural History Collections Department, Iziko, South African Museum, Cape Town, South Africa.

## FIELD LOCALITIES

Details of field localities are given by Kennedy and Klinger (1975); further descriptions of these localities are deposited in the Earth Collections, Oxford University Museum of Natural History, The Natural History Museum, London, and the Natural History Collections Division, Iziko, South African Museum, Cape Town. The relationship of these localities to those of van Hoepen (1931–1955b) are set out below, and those on the Mzinene (formerly Umsinene) River and its tributary, the Munywana (formerly Manuan) are shown in Text-fig. 1.

Locality 51 of Kennedy and Klinger (1975, p. 288,

text-fig. 4) is an 18 m section in the river bed and banks over a 500 m interval around the eastern limb of the broad meander ENE of the sisal factory north of Hluhluwe, around 27°53’43’’ S, 32°19’22’’ E. The sequence is made up of a series of cycles: thick, poorly exposed bioturbated glauconitic silts and thirteen thin, richly fossiliferous storm-generated concretionary shell beds. This locality corresponds to van Hoepen’s (1931, p. 45) “Oemsinene rivier oos van der drift”. The 13 concretionary shell beds we recognised are the ‘banks’ of van Hoepen, but we were unable to exactly correlate our beds with van Hoepen’s banks.

The Manuan Creek is a term used by Spath (1921) and others for what is now the Munywana, a tributary of the Mzinene (Text-fig. 1), and includes localities 64–70 of Kennedy and Klinger (1975, p. 289).

Beacon 624 – this locality of van Hoepen (1931) is problematic, as the beacon has disappeared. It appears to correspond to locality 54 of Kennedy and Klinger (1975, p. 288), 200–300 m west of the south trending gully which joins the Mzinene in the section Munywana 13161, close to where the river turns sharply eastwards, 27°52’46’’ S, 32°19’40’’ E. Van Hoepen (1931) used it as the reference point for the following successively younger localities: Ridge west of ridge that is west of Beacon 624; Ridge west of Beacon 624; and Beacon 624.

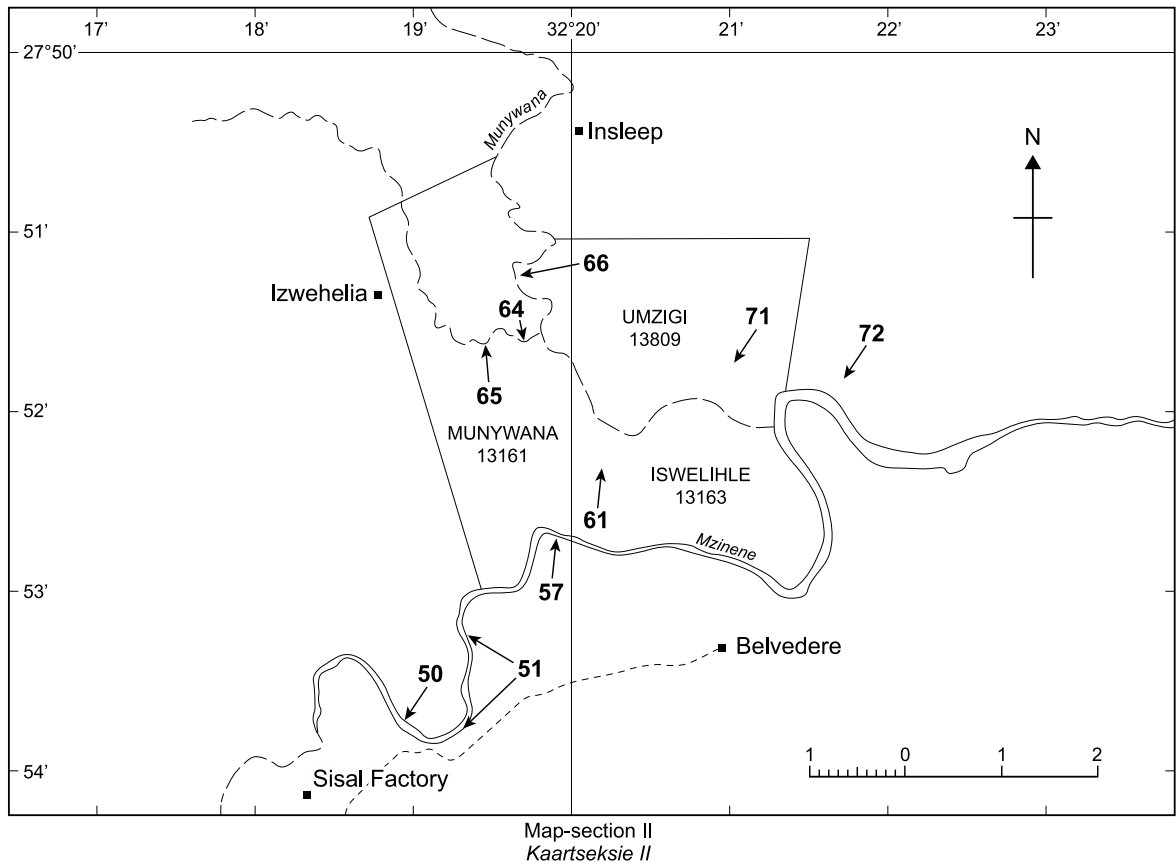
Locality 177 of Kennedy and Klinger (1975, p. 302) is fields along the north side of the Msunduzi Pan in Wisteria 18122 location, 2 km south-west of the Ndumu Store, 26°56’08’’ S, 32°13’57’’ E.

Locality 178 of Kennedy and Klinger (1975, p. 304) is a sisal field north of the Msunduzi Pan on Ndumu A location, 1400 m south-west of Ndumu Store, 26°56’14’’ S, 32°14’25’’ E.

## CONVENTIONS

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

Where specimens have been re-catalogued with SAM PCZ numbers, the numbers in the original publications by Spath (1921–1934) and van Hoepen (1931–1955b), the latter D numbers, are given in parentheses.



Text-fig. 1. Localities in the lower reaches of the Mzinene River north-north-east of Hluhluwe in northern KwaZulu-Natal, South Africa (after Klingler 1976, map 11).

#### A NOTE ON DATES OF PUBLICATION

Egbert C.N. van Hoepen's "Die Kryt fauna van Soeloland. 2. Voorlopige beskrywing van enige soelolandse ammoniete. 1. *Lophoceras*, *Rhytidoceras*, *Drepanoceras* en *Deiradoceras*" was published in *Paleontologiese Navorsing* on May 4<sup>th</sup>, 1931. Part 8 of L.F. Spath's Monograph of the Ammonoidea of the Gault, pp. 313–378, pls 31–36 was published in December 1931. Accordingly, van Hoepen's names have priority of those of Spath in cases where we regard them as synonyms.

#### SYSTEMATIC PALAEOLOGY

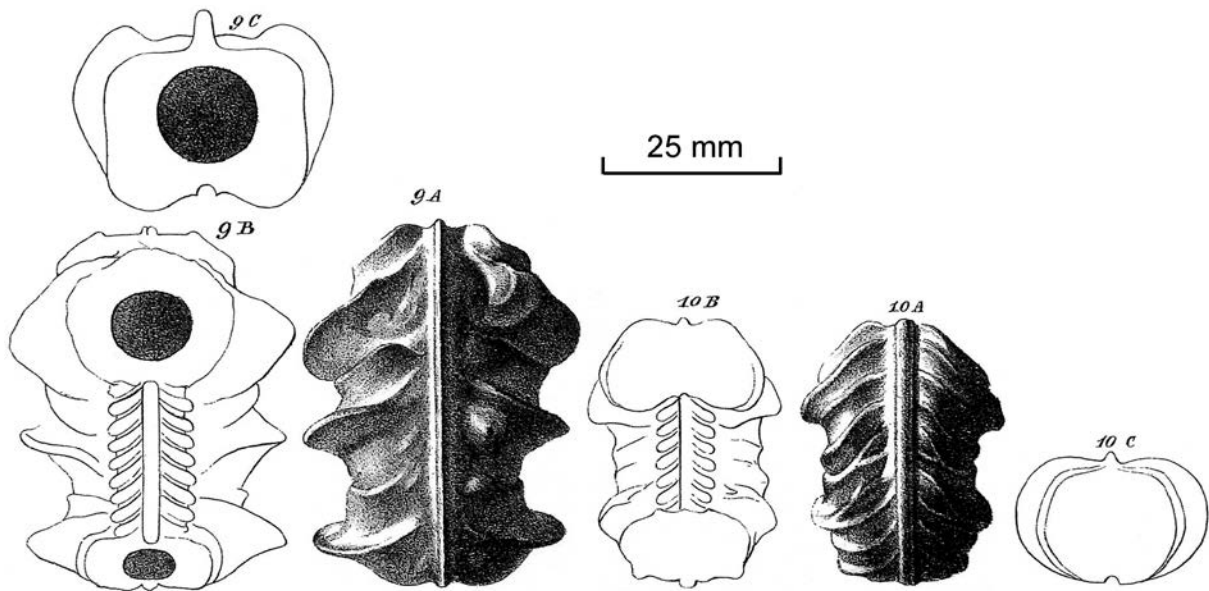
Order Ammonoidea von Zittel, 1884  
 Suborder Ammonitina Hyatt, 1889  
 Superfamily Acanthoceratoidea von Zittel, 1884  
 Family Brancoceratidae Spath, 1934  
 Subfamily Mojsisovicsiinae Hyatt, 1903  
 (= Dipoloceratidae Spath, 1921)

REMARKS: Wright (1996, p. L137) regarded *Cechenoceratidae* van Hoepen, 1941 and *Drepanoceratidae* van Hoepen, 1941 as synonyms of *Mojsisovicsiinae*. The taxa included in these families by van Hoepen are either *Deiradoceras* van Hoepen, 1931, or *Rhytidoceras* van Hoepen, 1931 in our view, and these families are synonyms of *Pervinquierinae* Spath, 1926.

Genus *Dipoloceras* Hyatt, 1900

TYPE SPECIES: *Ammonites cristatus* Brongniart, 1822 (pp. 95, 395, pl. 7, fig. 9), by the original designation of Hyatt (1900, p. 589).

DIAGNOSIS: Moderately evolute, with a strong siphonal keel. Ornament of early phragmocone whorls comprises single ribs or pairs of flexuous ribs that arise at the umbilical shoulder with a feeble bulla or not. Later phragmocone whorls and adapical part of adult body chamber with periodic flared ribs that may branch once or twice, and rise above the siphon.



Text-fig. 2. Copies of Brongniart's (1822) pl. 7, fig. 9A–C, the holotype of his *Ammonites cristatus* and fig. 10A–C, the holotype of his *Ammonites subcristatus*.

nal keel, producing a trapezoidal costal whorl section. The ribs develop into massive ventrolateral horns in some. Apertural part of body chamber with widely spaced equal single ribs that lack flares. Suture with moderately incised bifid elements.

DISCUSSION: Wright (1996, p. L140) divided *Diploceras* into two subgenera, *Diploceras* (*Diploceras*) with *Cechenoceras* van Hoepen, 1941 as a synonym, and *Diploceras* (*Rhytidoceras*) van Hoepen, 1931, of which he regarded *Ricnoceras* van Hoepen, 1941, *Euspectroceras* van Hoepen, 1946a, and *Diplasioceras* van Hoepen, 1946a as synonyms, and *Mortoniceratoides* Cooper, 1982, as a possible synonym. We have reached very different conclusions. The genera introduced by van Hoepen (1931, 1941, 1946a) and placed in synonymy by Wright are characterised by the development of spiral ridges, a feature developed in *Ammonites inflatus* J. Sowerby, 1817 (p. 170, pl. 178; see detailed description in Kennedy in Gale and Kennedy 2020, p. 40, pl. 11, figs 4–6), the type species of *Pervinquieria* Böhm, 1910, of the Subfamily Pervinquieridae Spath, 1926. As discussed below, we regard *Ricnoceras* as a junior synonym of *Rhytidoceras*, afford *Diplasioceras* and *Euspectroceras* full generic status, and refer them to the Pervinquieridae. In contrast, the flank ornament of juvenile *Mortoniceratoides* corresponds to that of the early growth stage of *Diploceras cristatum*, but rather than developing flared ribs, this pattern

extends to the greatest diameter known in the type species, *Mortoniceratoides rigidum* (Spath, 1931), and there are well-developed spiral ridges.

The holotype of *Cechenoceras reversum* van Hoepen, 1941 (p. 62, text-figs 9, 10) is SAM PCZ 19103 (ex D.2362), a juvenile with well-developed spiral ridges and small ventral tubercles. The second specimen of the species figured by van Hoepen (1941, text-fig. 12) is an adult, with well-developed umbilical and ventrolateral tubercles. *Cechenoceras* is interpreted as synonym of *Pervinquieria* (*Deiradoceras*) van Hoepen, 1931.

*Diploceras cristatum* (Brongniart, 1822)

(Text-figs 2; 3A–K; 4A, B; 5A–D; 6A–D;  
7; 8E–I; 9A, C, D; 10A–K; 11A–D)

1822. *Ammonites cristatus* Brongniart, pp. 95, 395, pl. 7, fig. 9.  
1822. *Ammonites subcristatus* Brongniart, pp. 95, 396, pl. 7, fig. 10.  
1921. *Diploceras quadratum* Spath, p. 278, pl. 25, fig. 3.  
1928. *Diploceras fredricksburgense* Scott, p. 115, pl. 15, figs 1–4.  
1963. *Diploceras cristatum andranofotsyense* Collignon, p. 144, pl. 298, fig. 1290.  
1963. *Diploceras cristatum umbilicata* Collignon, p. 146, pl. 299, fig. 1292.  
1999. *Diploceras* (*Diploceras*) *cristatum* (Brongniart, 1822); Kennedy in Kennedy *et al.*, p. 1105, text-figs

- 4.9, 5.1–5.11, 6.7–6.12, 7.8, 7.9, 10.5 (with synonymy).
2018. *Dipoloceras (Dipoloceras) cristatum cristatum* (Brongniart, 1822); Klein, pp. 85, 88 (with synonymy).
2018. *Dipoloceras cristatum andranofotsyense* Collignon, 1963; Klein, pp. 85, 88.
2018. *Dipoloceras cristatum umbilicatum* Collignon, 1963; Klein, pp. 85, 92.
2018. *Dipoloceras (Dipoloceras) quadratum* Spath, 1921; Klein, pp. 86, 94 (with synonymy).
- 2018b. *Dipoloceras cristatum* (Deluc); Cooper, pl. 21, fig. f.

TYPE: The holotype, by monotypy, is the original of Brongniart (1822, pp. 95, 395; pl. 7, fig. 9; Text-figs 2, 9 herein), from Folkestone, Kent; it has not been traced.

MATERIAL: SAM PCZ 22513 (ex E. Meyer collection 75) from the environs of Ndumu. SAM PCZ 22514 (ex Z17/7) and SAM PCZ 22515 (ex Z17/22), both from locality Z17 of Haughton (1936, p. 289, text-fig. 3), on the Pongola River north of the Mfongosi Spruit. SAM PCZ 22516 (ex D.2359) from locality 51, bank 7 of van Hoepen (1931). SAM PCZ 22517-8, from locality 51, bed 7 of Kennedy and Klinger (1975). SAM PCZ 19478 (ex 2727), the original of Spath (1921, p. 277), and SAM PCZ 19481 (ex 2728), the original of Spath (1921, p. 277, pl. 25, fig. 2, pl. 26, fig. 6), both from the “Manuan Creek”. SAM PCZ 19105 (ex 836), the original of van Hoepen (1941, p. 58), from the environs of locality 51. SAM PCZ 19106 (ex D.1259), the original of van Hoepen (1941, pp. 56, 57, text-figs 1, 2), from his bank 11 at locality 51. SAM PCZ 19475 (ex 4955), the holotype of *Dipoloceras quadratum* Spath, 1921 (p. 278, pl. 25, fig. 3), from the “Middle branch, Manuan Creek”. OUMNH KX.11736–7, from bed 3 at locality 51. OUMNH KX.10214, from locality 177.

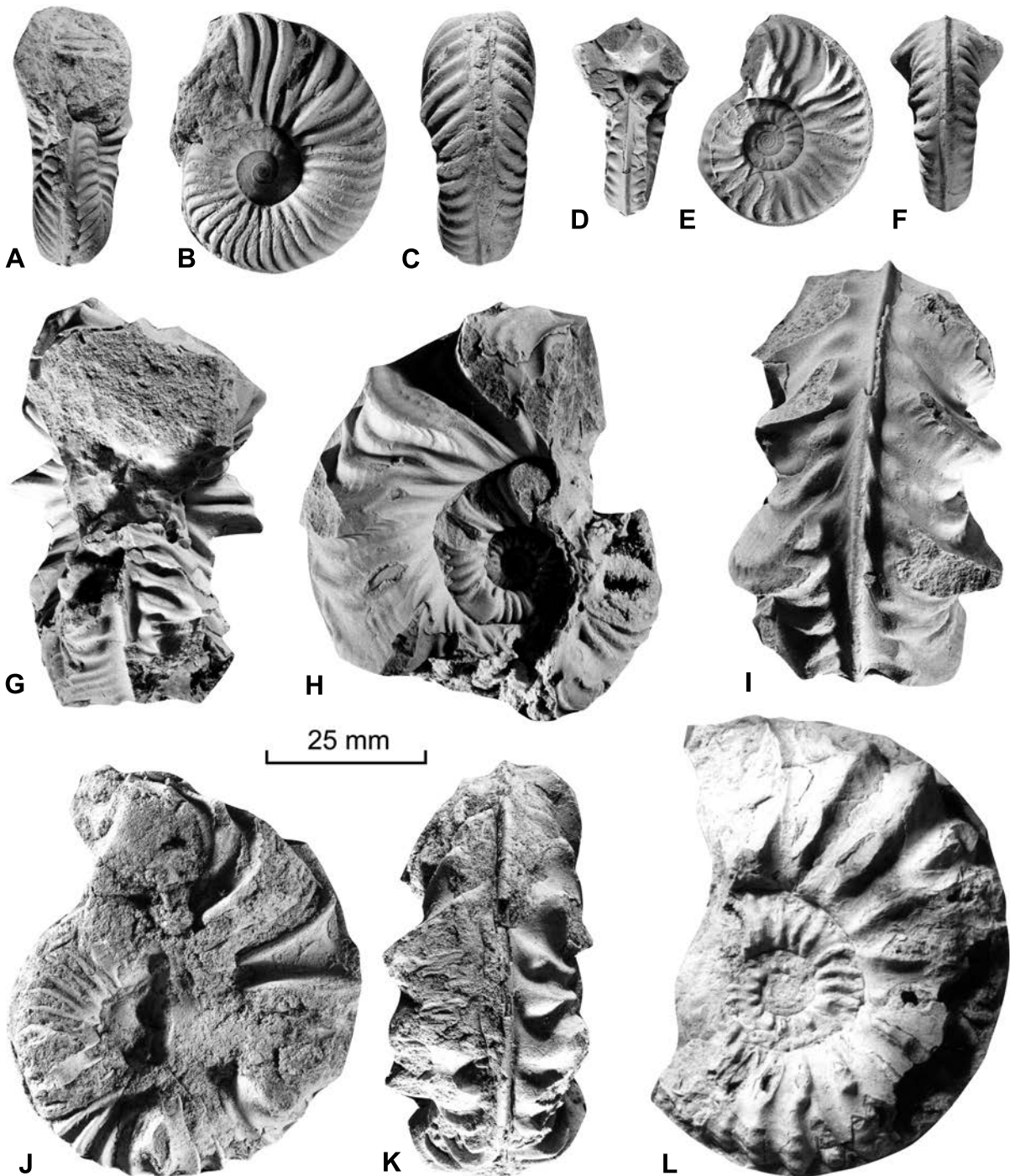
#### DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19475 costal	40.4 (100)	17.8 (44.1)	18.6 (46.0)	0.96	13.3 (32.9)
SAM PCZ 22517	32.5 (100)	18.1 (55.7)	12.5 (38.5)	1.5	10.4 (32.0)
SAM PCZ 22515 (m)	95.0 (100)	32.0 (33.7)	32.0 (33.7)	1.0	37.0 (38.9)
SAM PCZ 19481 (M)	135.0 (100)	43.5 (32.2)	49.5 (36.7)	0.89	56.0 (41.5)

DESCRIPTION: SAM PCZ 22517 (Text-fig. 3D–F), SAM PCZ 19105 (ex D.836) (Text-fig. 4A, B), SAM PCZ 19106 (ex D.1259) (Text-fig. 5) and OUMNH KX.11737 show the inner whorls well. In the first

growth stage, which extends to up to 25 mm in diameter, the coiling is very evolute, with a broad, shallow umbilicus, convex, outward-inclined umbilical wall and narrowly rounded umbilical shoulder. The whorl section is compressed, with flattened, convergent flanks, broadly rounded ventrolateral shoulders and a convex venter with a strong, sharp siphonal keel. There are 28–30 ribs per whorl, most of which arise at the umbilical seam. They strengthen across the umbilical wall, and may develop into feeble umbilical bullae or not. A few bifurcate at this point, and there are occasional intercalated ribs. The ribs flex back at the umbilical shoulder, and are recti- to feebly rursiradiate, feebly convex on the inner flank, feebly concave at mid-flank, and projected forwards on the ventrolateral shoulder, where they form an obtuse chevron. Beyond 25 mm diameter, the ribs begin to differentiate markedly in strength, a feature scarcely detectable below this diameter. Initially, the strongest ribs are separated by one to three weaker ribs of variable strength. As diameter increases, the strongest ribs develop a flared inner portion and bifurcate, the position of maximum development migrating outwards to a mid-flank position, leading to a very depressed, diamond-shaped costal whorl section. The flares give rise to two, sometimes three ribs that form an obtuse chevron on the venter, the rib terminations separated from the siphonal keel by a narrow smooth zone. This style of ornament persists on the inner whorls of SAM PCZ 19106 (ex D.1259) (Text-fig. 5), the original of van Hoepen (1941, text-figs 1, 2), interpreted as a microconch. At a diameter of 41 mm, this specimen has a costal whorl breadth to height ratio of 1.78. Up to four ribs are linked in varying degrees to a single flared rib, projecting high above the venter. Up to four minor ribs separate successive flared ribs on the adapical part of the body chamber. At the adapertural end, ornament is of single unbranched ribs without flares. SAM PCZ 22515 (Text-fig. 6A, B), 95 mm in diameter, is a further near-complete microconch with ornament of this type, as are SAM PCZ 22516 (ex D.2359), SAM PCZ 22518, and OUMNH KX.11736 (Text-fig. 9C, D). SAM PCZ 22521 (Text-fig. 3G–I) is a very coarsely and grossly ornamented variant with an estimated maximum preserved diameter of 68 mm. It has much stronger flares than the other individuals in the collection, and irregular ridges of variable orientation on the adapical face of some of the ribs.

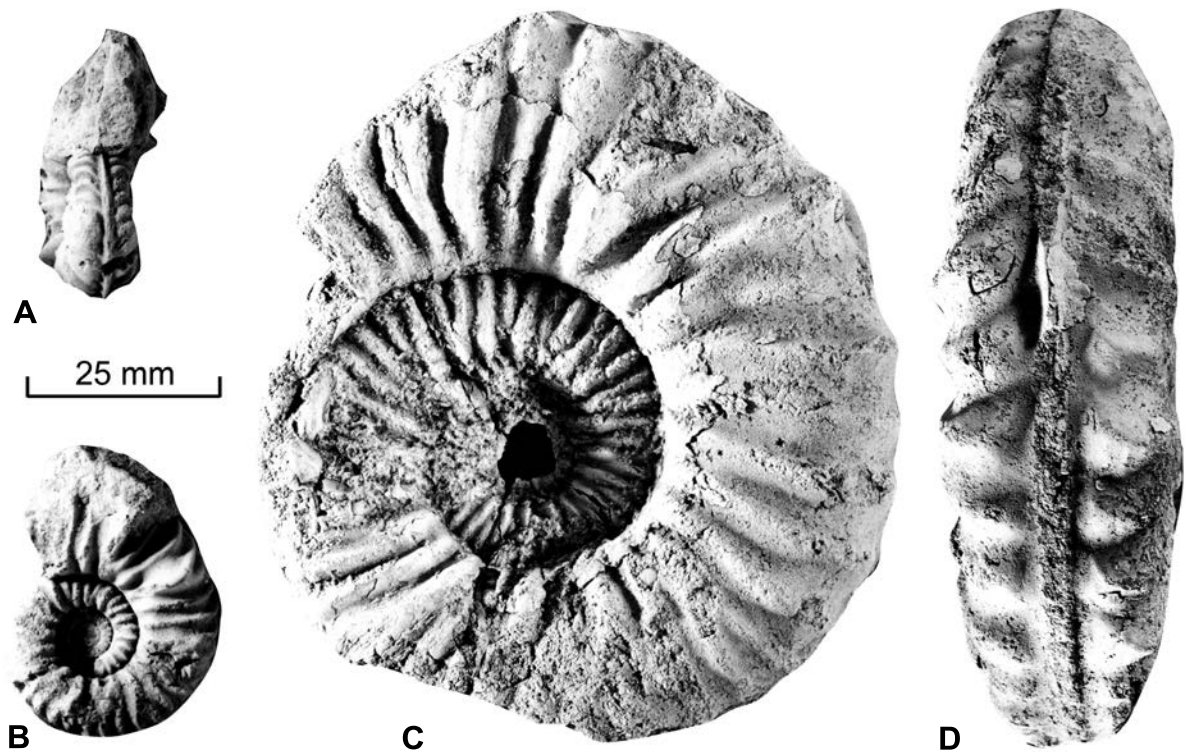
We regard *Dipoloceras quadratum* Spath, 1921 (p. 278, pl. 25, fig. 3), the holotype of which is SAM PCZ 19475 (ex 4955; Text-fig. 3A–C), a juvenile, from the “Middle branch of the Manuan Creek”, as a synonym



Text-fig. 3. Selected representatives of the Mojsisovicsiinae Hyatt, 1903 and Pervinquierinae Spath, 1926 from KwaZulu-Natal, South Africa. A–K – *Dipoloceras cristatum* (Brongniart, 1822). A–C – SAM PCZ 19475 (ex D.4955), the holotype of *Dipoloceras quadratum* Spath, 1921 (p. 278, p. 23, fig. 3), from the “Middle Branch of the Manuan Creek”; D–F – SAM PCZ 22517, from locality 51, bed 7; G–I – SAM PCZ 22521, from locality 51, bed 7; J, K – SAM PCZ 19478 (ex D.2727), the original of Spath (1921, p. 277). L – *Euspectroceras newtoni* (Spath, 1925), OUMNH KX.10212, from locality 177.

of *cristatum*. It retains limonitised shell. Coiling is moderately involute, the deep umbilicus comprising 33% of the diameter, with a convex umbilical wall.

The intercostal whorl section is rounded-quadrate, and slightly compressed. Twenty four strong, narrow, rounded primary ribs arise at the umbilical seam of



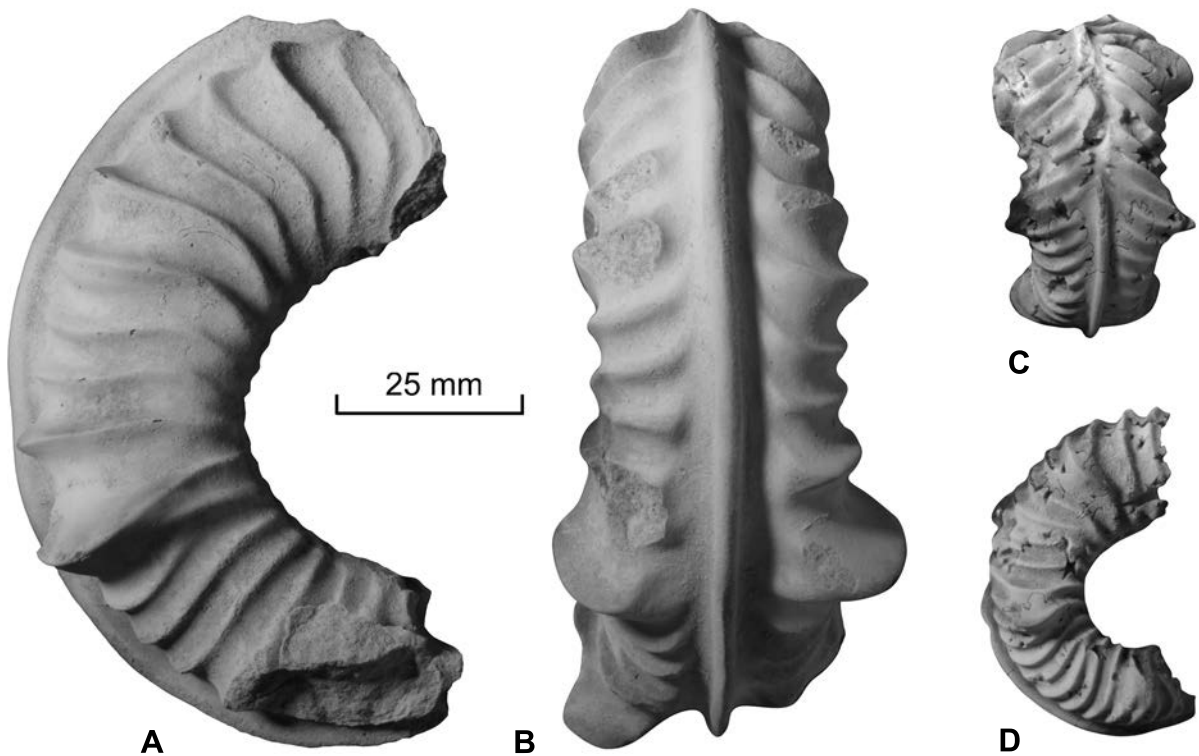
Text-fig. 4. Selected representatives of the Mojsisovicsiinae Hyatt, 1903 and Pervinquierinae Spath, 1926 from KwaZulu-Natal, South Africa. A, B – *Dipoloceras cristatum* (Brongniart, 1822); SAM PCZ 19105 (ex D.836), mentioned by van Hoepen (1941, p. 58), from the environs of locality 51. C, D – *Diplasioceras fallax* van Hoepen, 1946a, the holotype, SAM PCZ 19457 (ex D.368), from locality 51, bank 7.

the outer whorl and are straight and prorsiradiate on the umbilical wall. They are crowded, prorsiradiate, and feebly flexuous on the flanks, feebly convex on the umbilical shoulder and innermost flanks, feebly concave on the outer flank and ventrolateral shoulder, projected strongly forwards on the venter, and separated from the strong siphonal keel by a delicate groove. There are occasional intercalated ribs, and occasional primary ribs bifurcate low on the flanks or just outside the umbilical shoulder. All ribs are of equal development on the outer flanks, ventrolateral shoulders and venter to a diameter of 38 mm, where the adapertural of a pair of secondary ribs is expanded into a flare of moderate strength.

The macroconch is represented by SAM PCZ 19481 (ex 2728) (Text-fig. 7), the original of Spath (1921, pl. 25, fig. 2; pl. 26, fig. 6). The ornament of such as is visible of the inner whorls is as in the microconchs described above. The change from periodic flared ribs to even ribbing, characteristic of the adapertural part of the body chamber of adult microconchs, is delayed to a much greater diameter; the adult microconch to macroconch size ratio is 1:1.35 approximately.

The suture of SAM PCZ 19481 (ex 2728) was illustrated by Spath (1921, pl. 26, fig. 6), and that of SAM PCZ 19106 (ex D.1259) by van Hoepen (1941; Text-fig. 5 herein). They are moderately incised, with bifid E/A, A and A/U2.

DISCUSSION: Brongniart based his species on a fragment in the Deluc collection; it has not been traced. The original figures are reproduced here as Text-figs 1, 9A–C (Brongniart's original figure numbers are retained). Described as being from the "craie inférieure" of Folkestone, it is actually from the Gault Clay, specifically the *cristatum* nodule bed, bed viii of authors (see section in fig. 1.5, D in Young *et al.* 2010). *Ammonites subcristatus* Brongniart, 1822 (pp. 95, 396, pl. 7, fig. 9; Text-figs 2, 10A–C; again, the original figure numbers are retained) is based on a fragment from the same horizon and locality, and is a clear synonym. The original specimen has not been traced. The most widely used illustration of the species is that of d'Orbigny (1841, pl. 88, figs 1–5; Text-fig. 8I). D'Orbigny (1841) mentions specimens collected by Deluc, Brongniart, and Mayor at Perte du Rhône, Ain; by d'Archiac and himself at Saint Pot



Text-fig. 5. *Dipoloceras cristatum* (Brongniart, 1822) from KwaZulu-Natal, South Africa. SAM PCZ 19106 (ex D.1259), the original of van Hoepen (1941, text-figs 1, 2), from locality 51, bank 11.

near Boulogne, Pas-de-Calais, and by Weyman at the Montagne de Fis, Savoie, and stated that the figures were based on a specimen in his own collection. The catalogue of the d'Orbigny Collection lists the following:

- ‘5762 *A. cristatus* Wissant Pas de Calais’; there are five specimens under this number, one of which is, from its preservation, from south-east France, and clearly the basis of d'Orbigny's figure;
- ‘5762a Perte du Rhône Ain 4’. All survive; three are poorly preserved *Rhytidoceras pseudoaon* (Spath, 1931), one a *D. cf. cristatum*, and a further poorly preserved specimen which is a douvilleiceratid.

The basis of d'Orbigny's figure (Fig. 8E–H) now bears the number MNHN F. R04278, and has the following dimensions:

	D	Wb	Wh	Wb:Wh	U
intercostal	51.0 (100)	22.5 (44.1)	20.0 (39.2)	1.1	18.5 (36.3)
costal		28.0 (54.9)	20.0 (39.2)	1.4	

Coiling is evolute, the broad umbilicus comprising 36.3% of the diameter, quite deep, with a broadly

rounded umbilical wall and more narrowly rounded umbilical shoulder. The intercostal whorl section is oval and slightly depressed, the costal section depressed, with a whorl breadth to height ratio of 1.4, trapezoidal, becoming more depressed and inverted reniform when taken through the flared ribs. There are 32 ribs on the outer whorl. They arise at the umbilical seam, and strengthen across the umbilical wall and shoulder. On the flanks, most ribs are simple, high, much narrower than the interspaces, prorsiradiate and feebly flexuous, concave across the umbilical shoulder, straight across the middle of the flanks, then strengthened, projected forwards and concave on the outer flank and ventrolateral shoulder, and separated from a high siphonal keel by a smooth zone. On the outer whorl, six ribs are much stronger than the remainder throughout their length, and develop into high flares on the umbilical shoulder and flank at the smallest diameter visible. These flares give rise to up to three ribs. At the largest diameter preserved, the flare extends across the middle and outer flank, and gives rise to a pair of ribs. The specimen finds a match in the inner whorls of SAM PCZ 19106 (ex D.1259) (Text-fig. 5).



The lectotype of *Dipoloceras bouchardianum* (d'Orbigny, 1841) (p. 300, pl. 88, figs 6–8; the original figures are reproduced here as Text-fig. 8D), designated by Spath (1931, p. 374, as 'type') is d'Orbigny's figured specimen, MNHN. F. R04279 (ex d'Orbigny Collection 5759) from Wissant in the Pas-de-Calais, France (Text-fig. 8A–C). It is a pyritic phragmocone with traces of aragonitic shell. The dimensions are as follows:

D	Wb	Wh	Wb:Wh	U
40.0 (100)	18.2 (45.5)	16.2 (40.5)	1.12	12.9 (32.3)

Coiling is evolute, the umbilicus of moderate depth, the umbilical wall broadly rounded and inclined outwards; the ventrolateral shoulders merge with the broadly rounded flanks. The intercostal whorl section is compressed oval, with broadly rounded ventrolateral shoulders and a flattened venter. The costal whorl section is compressed oval, with a whorl breadth to height ratio of 1.12. An estimated 24 ribs arise at the umbilical seam. They are strong, wider than the interspaces on the umbilical wall and shoulder, straight and prorsiradiate on the innermost flanks, bifurcating low on the flanks, flexed back and markedly convex on the middle and outer flank, where occasional intercalated ribs arise. All ribs strengthen across the ventrolateral shoulders, and sweep forwards across the venter, declining in strength and forming an obtuse chevron with a high siphonal keel at the apex. There 44 to 46 ribs on the outer whorl at the ventrolateral shoulder. BMNH 37585 (Spath 1931, pl. 33, fig. 5) is a much larger individual with comparable ribbing; the delicate even ribs and lack of strong flares distinguish the species from *cristatum*. *Dipoloceras bouchardianum* var. *moniliformis* Spath, 1931 (p. 373, pl. 32, fig. 10: Text-fig. 28H) is a *Rhytidoceras*, discussed further below.

*Dipoloceras bouchardianum* var. *rectangularis* Spath, 1931 (p. 376, pl. 32, fig. 19) was based on a nucleus figured by Spath, and at least one other specimen, BMNH C.35107 (Text-fig. 9B), cited by Spath on p. 378, which has a distinctive undulose keel (see also Text-fig. 9E); the latter is here designated lectotype, and this character distinguishes it from all other *Dipoloceras*; it is, accordingly, afforded specific status.

*Dipoloceras fredricksbergense* Scott, 1928 (p. 115, pl. 15, figs 1–4) is a synonym of *cristatum*, as discussed by Kennedy in Kennedy *et al.* (1999, p. 1107). OUMNH KX.11736 (Text-fig. 9C, D) is comparable to the holotype, and the Folkestone example assigned to *fredricksbergense* by Spath (1931, pl. 34, fig. 14; see Text-fig. 10J). *Dipoloceras tarrantense* Scott, 1928 (p.

112, pl. 16, figs 1, 2; text-fig. A3) is distinguished by the massive outward-directed horns that occupy all of the flanks in early and middle growth, strikingly developed in the adult individual from Ecuador described by Bulot *et al.* (2005, p. 453, text-figs 3, 4).

Nuclei corresponding to *Dipoloceras cristatum alata* Spath, 1931 (p. 368, pl. 35, figs 11–15), with strong flares, are the inner whorls of SAM PCZ 19106 (ex D.1259), the original of van Hoepen (1941, p. 57, figs 1, 2; Text-fig. 5), and the nucleus figured by Kennedy (1978, pl. 1, fig. 4).

*Dipoloceras cristatum umbilicata* Collignon, 1963 (p. 146, pl. 299, fig. 1292; Text-fig. 10A, B) is based on a worn adult of the species; *Dipoloceras cristatum andranofotsyensis* Collignon, 1963 (p. 144, pl. 298, fig. 1290; Text-fig. 11C, D) appears to be a slender, densely ribbed variant. Both are from Andranofotsty, Madagascar,

OCCURRENCE: Lower Upper Albian, index of the *cristatum* Zone, the base of which defines the base of the Upper Albian substage in ammonite terms (Hart *et al.* 1996). There are records from southern England, France, Spain, Germany, Switzerland, Poland, Slovakia, Bulgaria, the Northern Caucasus in the Russian Federation, Morocco, Tunisia, India, KwaZulu-Natal in South Africa, Mozambique, Madagascar, Japan, Texas and Patagonia.

#### Subfamily Pervinquierinae Spath, 1926

DIAGNOSIS: Keeled derivatives of the Mojsisoviicsiinae with up to four rows of tubercles: umbilical, lateral, inner and outer ventrolateral, and well-developed spiral ridges.

DISCUSSION: Spath (1926, p. 79) introduced his Family Pervinquieridae within a discussion of the Upper Campanian *Submortoniceratidae* Spath, 1926, as follows: "The still earlier so-called *Mortoniceratidae* of the Upper Albian (*Pervinquieria* J. Böhm, 1910 = *Inflaticeratidae* Stieler, 1920) are somewhat homoeomorphic, but unrelated (family Pervinquieridae n. n. to replace *Inflaticeratidae* Spath)" but later (1932, p. 379) abandoned it and treated it as a junior synonym of *Mortoniceratidae* Spath, 1925 (p. 199). As discussed elsewhere (Kennedy in Gale and Kennedy 2020, p. 30, pl. 11, figs 7–9; text-figs 18–24), *Mortoniceratidae* (type species *Ammonites vespertinus* Morton, 1834, p. 40, pl. 17, fig. 1, by original designation) has a distinctive ontogeny, with strong inner and feeble outer ventrolateral clavi in the earliest growth stage

of the type species, after which the outer ventrolateral row efface and a lateral row appears, the ribs trituberculate thereafter. It also does not develop the spiral ridges that are such a distinctive feature of the type species of *Pervinquieria* (*Ammonites inflatus* J. Sowerby, 1817, p. 170, pl. 178, by original designation) and its subgenera. We include the following in the subfamily:

- *Pervinquieria* (*Pervinquieria*) Böhm, 1910 (= *Inflatoceras* Stieler, 1920, p. 346; *Ophryoceras* van Hoepen, 1942, p. 91; *Ameleceras* van Hoepen, 1942, p. 115; *Rusoceras* van Hoepen, 1946a, p. 238; *Collignonia* van Hoepen, 1951b, p. 295; *Omostrateceras* van Hoepen, 1951b, p. 313; non *Subpervinquieria* Mirzoyev, 1969, p. 46);
- *Pervinquieria* (*Deiradoceras*) van Hoepen, 1931 [= *Cechenoceras* van Hoepen, 1941, p. 61; *Mimeloceras* van Hoepen, 1944, p. 196 (introduced as *nomen novum* for *Mimoceras* van Hoepen, 1941, 85, non Hyatt 1884, p. 309)];
- *Pervinquieria* (*Subschloenbachia*) Spath, 1921 (= *Durnovarites* Spath, 1932, p. 380);
- *Prohysteroceceras* Spath, 1921;
- *Elobiceras* (*Elobiceras*) Spath, 1921;
- *Elobiceras* (*Craginites*) Young, 1957;
- *Rhytidoceras* van Hoepen, 1931 (= *Drepanoceras* van Hoepen, 1931, p. 46, non Stein, 1878, p. 25; *Ricnoceras* van Hoepen, 1941, 59);
- *Euspectroceras* van Hoepen, 1946a;
- *Diplasioceras* van Hoepen, 1946a.

OCCURRENCE: Upper Albian, cosmopolitan.

#### Genus *Diplasioceras* van Hoepen, 1946a

TYPE SPECIES: *Diplasioceras fallax* van Hoepen, 1946a (p. 203, text-figs 178–181), by original designation.

DIAGNOSIS: Evolute, whorl section rectangular, flanks subparallel. On the phragmocone, rursiradiate ribs arise singly or in pairs from small bullae and terminate in small ventrolateral tubercles. On the body chamber ribs are predominantly rursiradiate primaries that strengthen into bullae on the ventrolateral shoulder.

DISCUSSION: Van Hoepen's original diagnosis (1946a, p. 203) is as follows: "Keel-ed ammonites of the Gault. Young forms with rectangular section and with flat flanks. The young forms have no old mouth-edges. There are umbilical tubercles from where ribs

are visible. Older whorls with spiral ornament. Ribs on younger whorls round and nearly straight. There is no ventral tubercle on young whorls, but the ventral ends of the ribs are broadened. The ribs of later whorls are sharp and they project ventrally."

*Diplasioceras* differs from *Dipoloceras* in lacking flared ribs, the presence of umbilical bullae, strengthening of the rib terminations into ventrolateral bullae, and the presence of spiral ridges on the surface of the shell. Van Hoepen (1946a, p. 205) in his account of the holotype of the type species stated that "The ventral half of the cast shows traces of spiral ornament; this is not present on the piece of shell of the dorsal part of the end of the whorl." In fact, delicate spiral ridges are also present on the inner flank region of the surface of the shell (Text-fig. 4C).

OCCURRENCE: Lower Upper Albian of northern KwaZulu-Natal and Madagascar.

#### *Diplasioceras fallax* van Hoepen, 1946a (Text-fig. 4C, D)

1946a. *Diplasioceras fallax* van Hoepen, p. 203, text-figs 178–181.

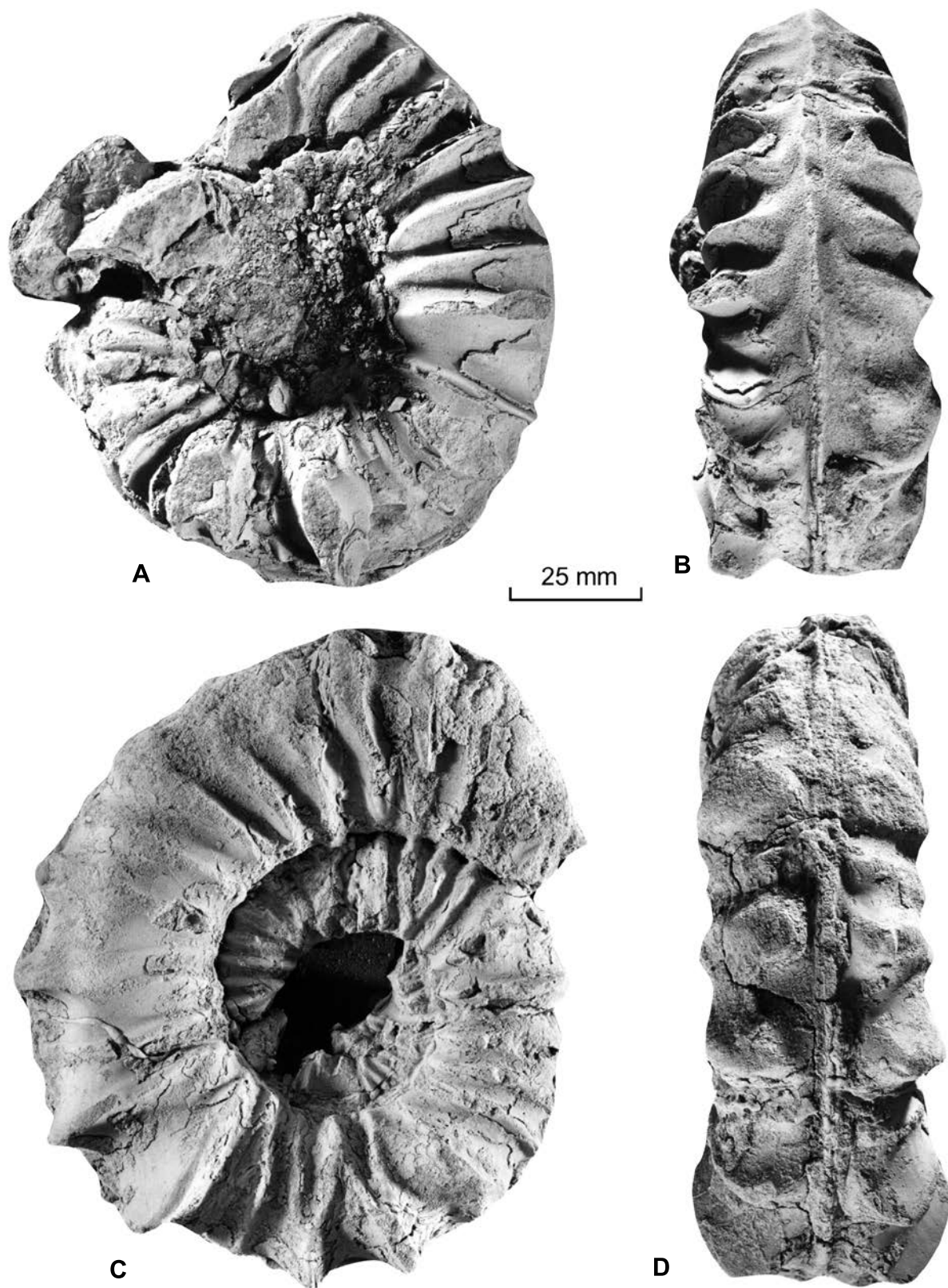
2018. *Dipoloceras* (*Rhytidoceras*) *fallax* (van Hoepen, 1946); Klein, pp. 95, 96 (with synonymy).

TYPE: The holotype, by original designation, is SAM PCZ 19457 (ex D.368), the original of van Hoepen (1946a, p. 203, text-figs 178–181), from his bank 7 at locality 51.

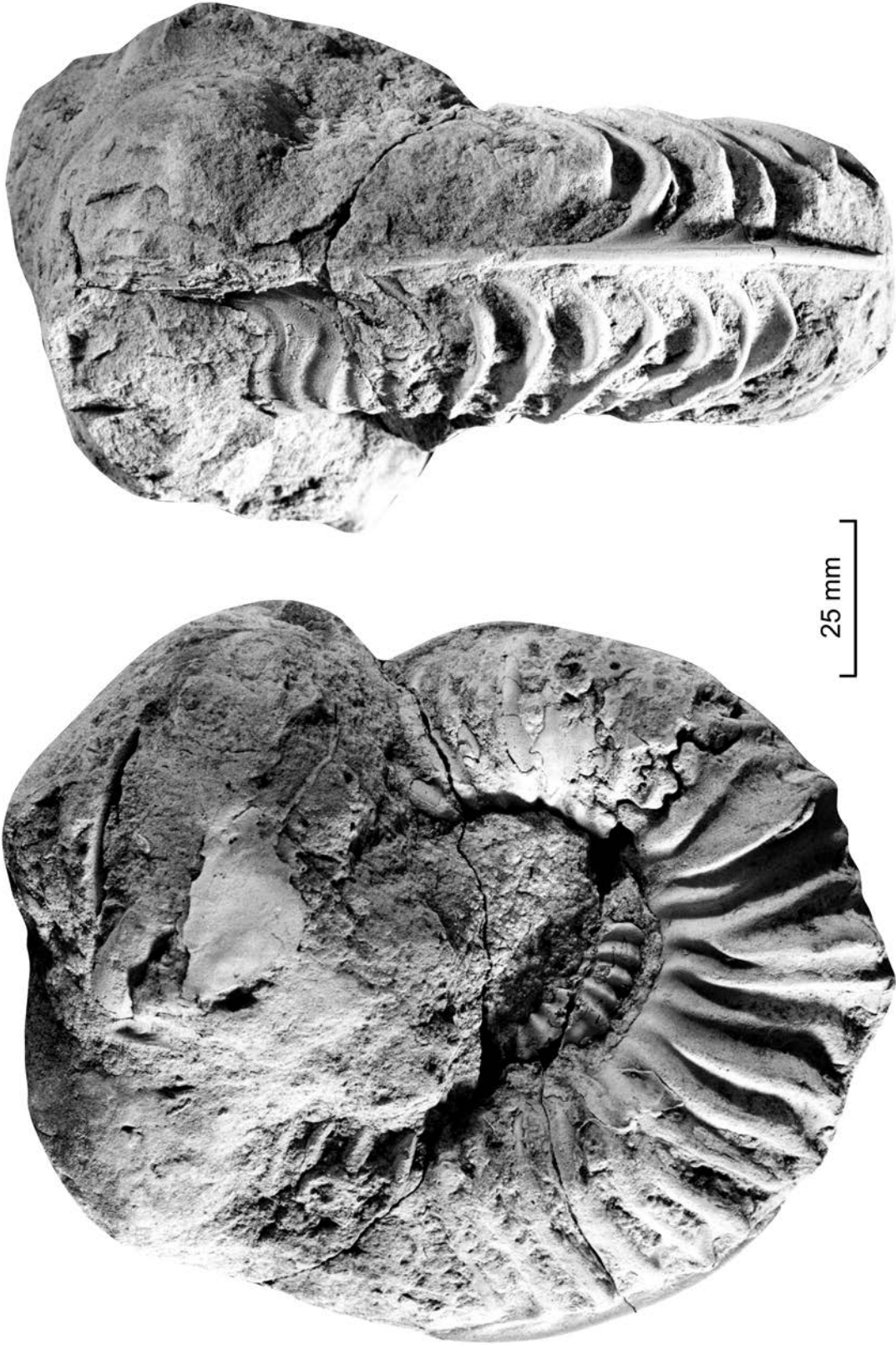
#### DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19457 c at	89.1 (100)	– (–)	34.7 (38.9)	– (–)	36.6 (41.1)

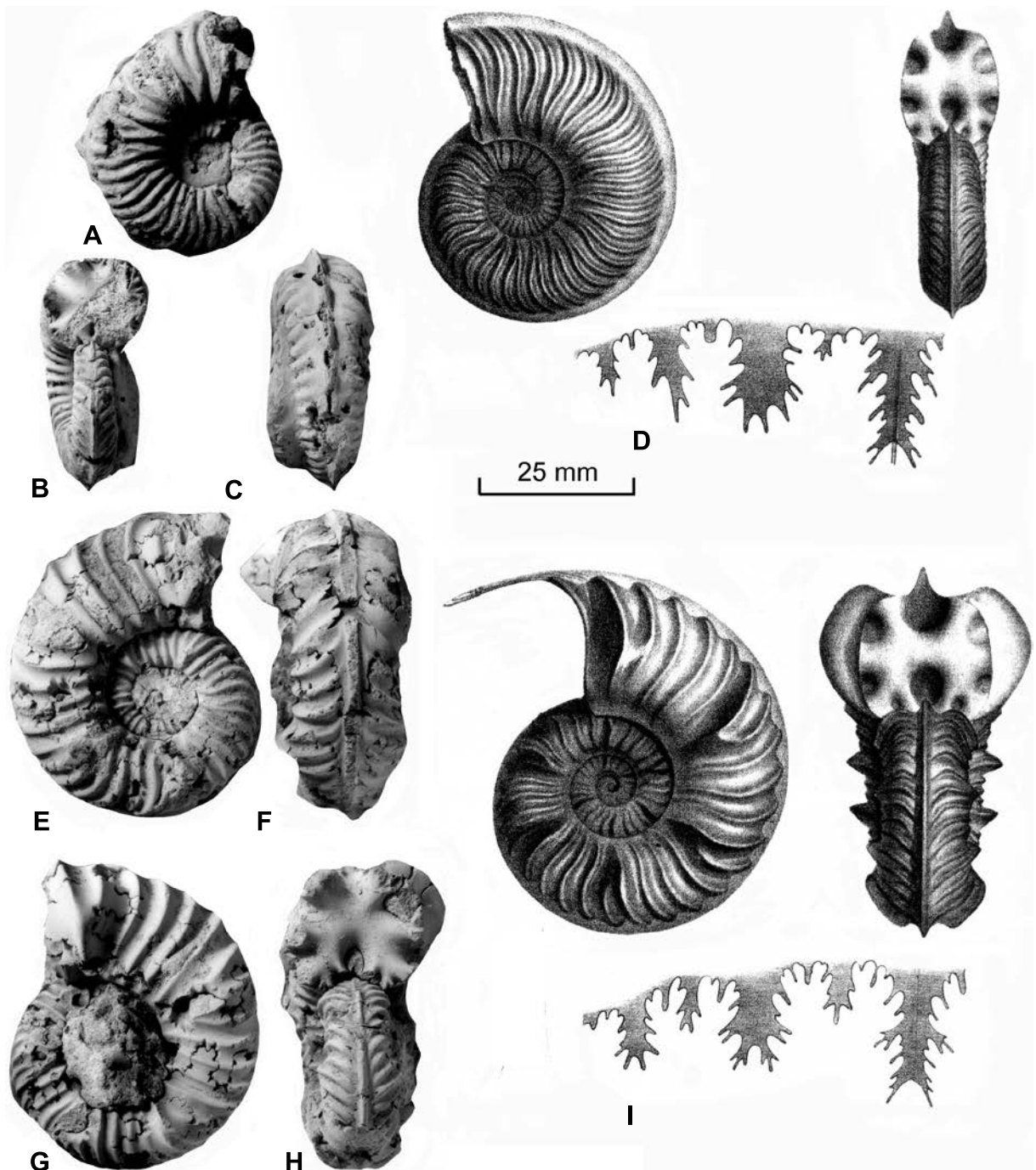
DESCRIPTION: The holotype (Text-fig. 4C, D) is worn and broken, with a maximum preserved diameter of 94 mm, and retains a 240° sector of body chamber. Coiling is very evolute, the umbilicus comprising 41.1% of the diameter, broad and shallow, with a low, convex, outwardly-inclined wall and broadly rounded umbilical shoulder. The whorl section is rectangular, with subparallel flanks in both costal and intercostal section, broadly rounded ventrolateral shoulders and a flattened venter with a strong siphonal keel. The phragmocone retains much of the original shell, most of which is lost on the body chamber. On the phragmocone, 26 primary ribs arise at the umbilical seam and strengthen into small bullae, perched on the umbilical shoulder. These give rise to a single rib or a pair of ribs,



Text-fig. 6. *Dipoloceras cristatum* (Brongniart, 1822) from KwaZulu-Natal, South Africa; A, B – SAM PCZ 22515; C, D – SAM PCZ 22514, both from locality 17 of Haughton (1936, p. 289, text-fig. 3), east of the Mfongosi Spruit.



Text-fig. 7. *Dipoloceras cristatum* (Brongniart, 1822) from KwaZulu-Natal, South Africa: SAM PCZ 19481 (D.2728), the original of Spath (1921, p. 277, pl. 25, fig. 2; pl. 26, fig. 6), from "the Mantuan Creek".

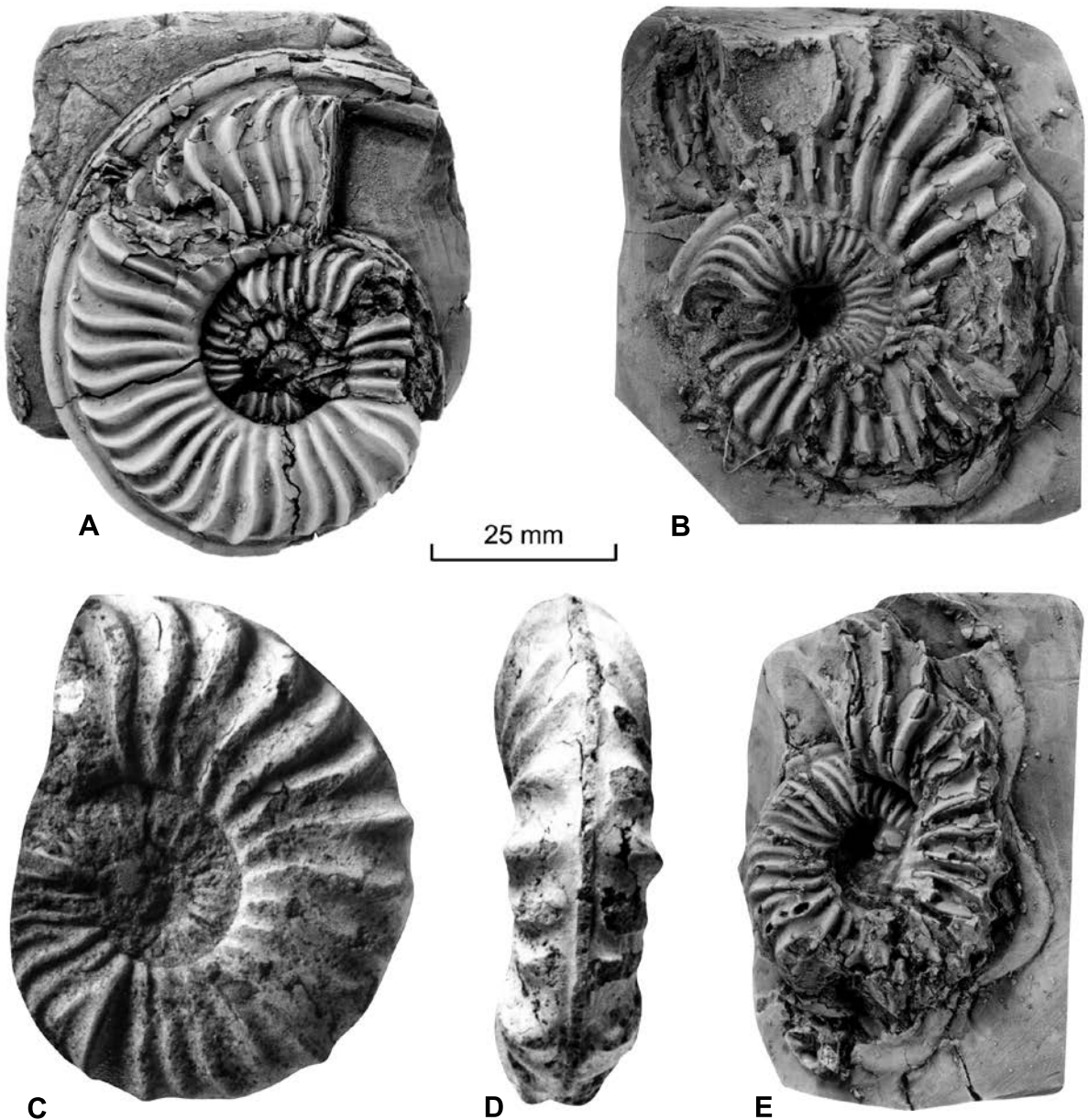


Text-fig. 8. Selected representatives of the Mojsisovicsiinae Hyatt, 1903 and Pervinquierinae Spath, 1926 from France. **A–D** – *Dipoloceras bouchardianum* (d’Orbigny, 1841). A–C, the lectotype, MNHN F. R04279, ex d’Orbigny Collection 5759, from Wissant, Pas-de-Calais, France; D – the figures based on this specimen (d’Orbigny 1841, pl. 88, figs 6–8). **E–I** – *Dipoloceras cristatum* (Brongniart, 1822). E–H – MNHN F. R04278, ex d’Orbigny Collection 5762, recorded as being from Wissant, Pas-de-Calais, France, but by its preservation from south-east France.

It is the basis of d’Orbigny’s figures (1841, pl. 88, figs 1–5), in part reproduced here as I.

while there are additional long intercalated ribs. The ribs are feebly rursiradiate, rounded, crowded, straight on the flanks, and projected forwards and very feebly

convex on the ventrolateral shoulder. Preservation is deficient, but they appear to terminate in small ventrolateral tubercles. The 240° sector of body chamber

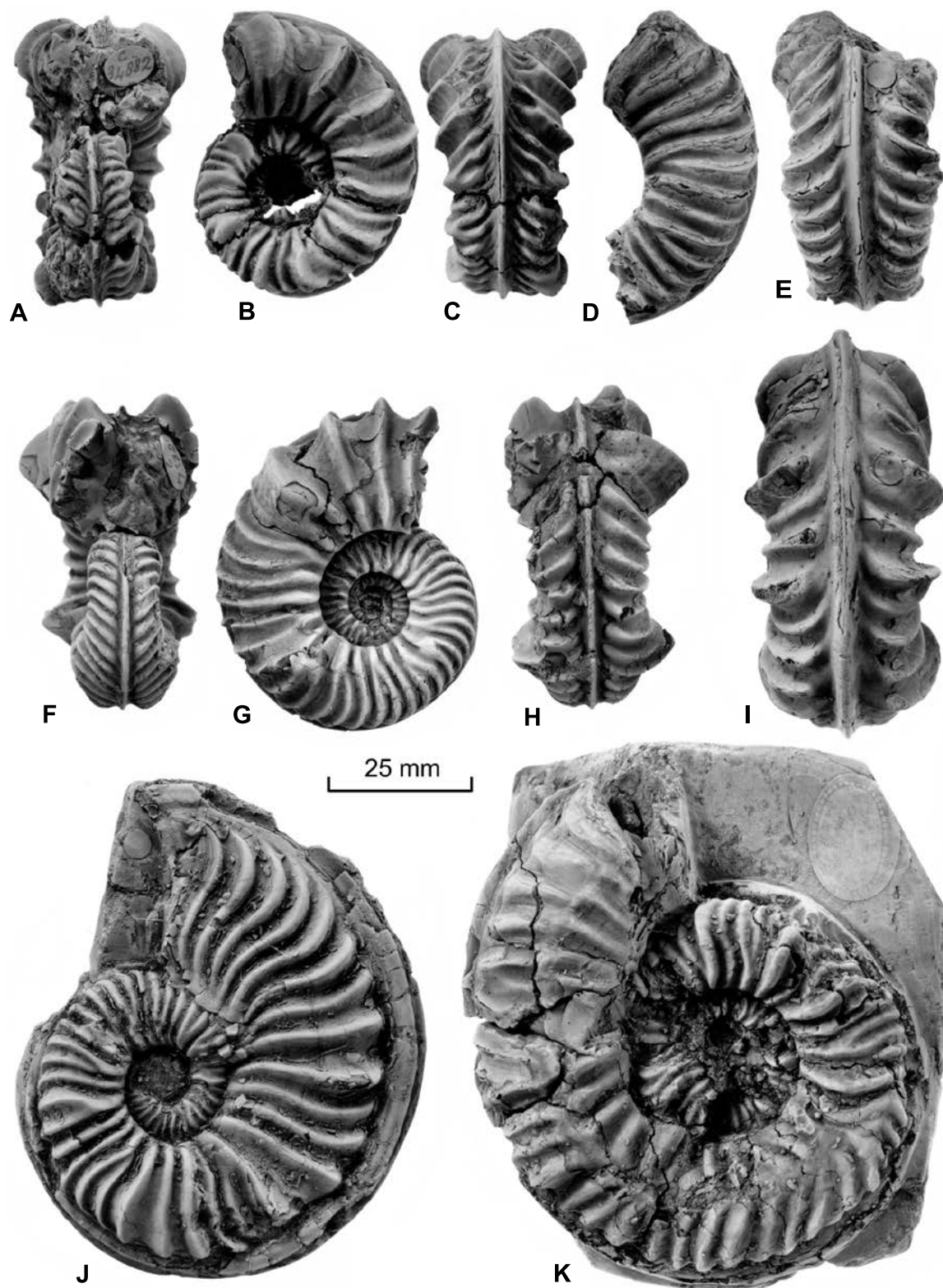


Text-fig. 9. Selected representatives of the Mojsisovicsiinae Hyatt, 1903 from the UK and South Africa. **A, C, D** – *Dipoloceras cristatum* (Brongniart, 1822). **A** – BMNH C.35112, from the Gault Clay of Folkestone, Kent, UK; **C, D** – OUMNH KX.11736, from bed 3 at locality 51, KwaZulu-Natal, South Africa. **B, E** – *Dipoloceras rectangularis* Spath, 1931. **B** – the lectotype, BMNH C.35107; **E** – BMNH C.789, both from the Upper Albian Gault Clay at Folkestone, Kent, UK.

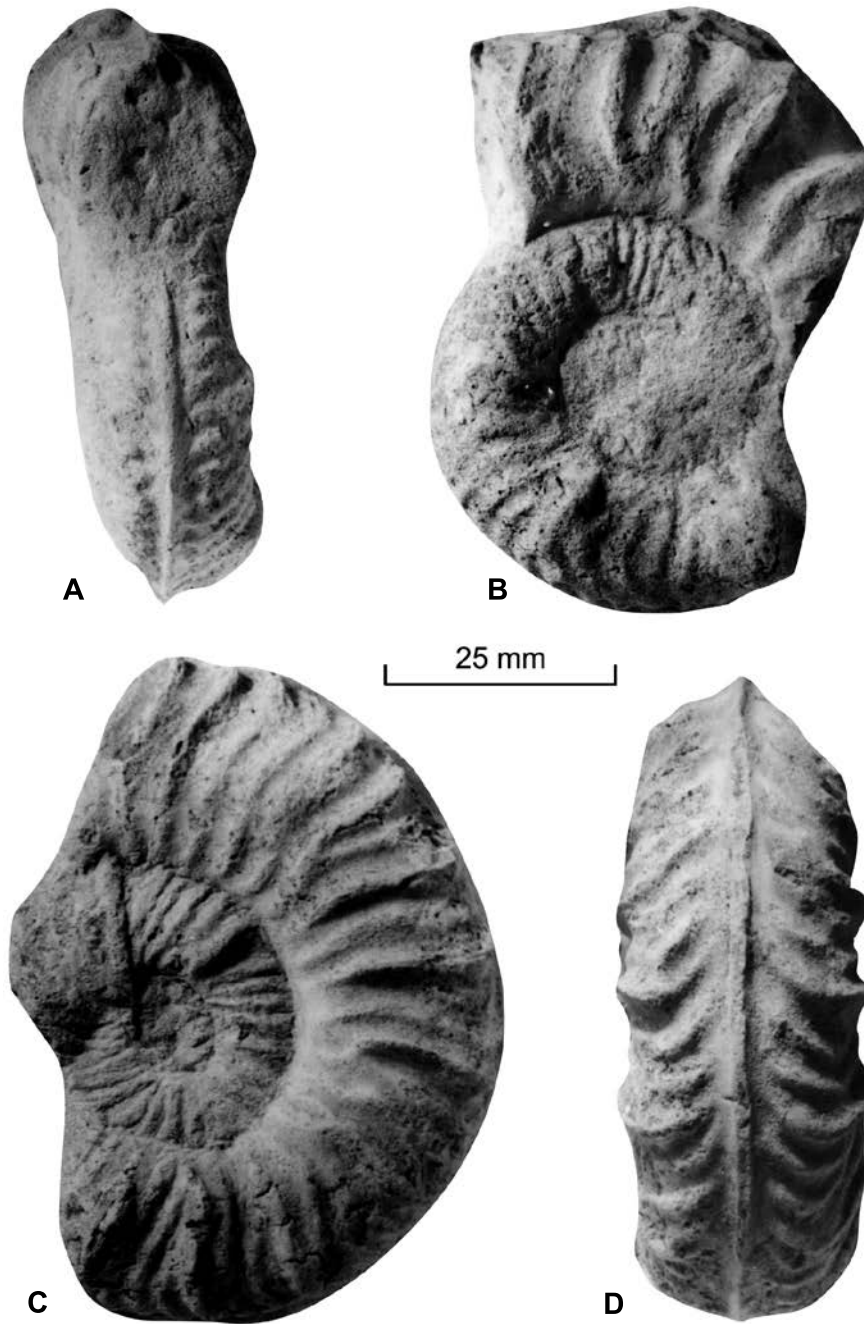
bears 20 primary ribs that arise at the umbilical seam and strengthen across the umbilical wall. Some develop into a small umbilical bulla that gives rise to a pair of ribs; the majority of ribs are single, non- or incipiently bullate; there are thus slightly more ribs at the ventrolateral shoulder than at the umbilical shoulder. The ribs are markedly rursiradiate, straight on the flanks, strengthen progressively and terminate

in prominent ventrolateral bullae. These give rise to a broad, progressively effacing rib leaving a smooth zone on either side of the siphonal keel.

**DISCUSSION:** The holotype is the only specimen of the species known to us. Collignon (1951, 1963) described three further species from the lower Upper Albian of Andranofotsy, Madagascar. *Diplasioceras*



Text-fig. 10. *Dipoloceras cristatum* (Brongniart, 1822) from the Upper Albian Gault Clay at Folkestone, Kent, UK. A–C – BMNH C.34882, the original of Spath (1931, pl. 33, fig. 4); D, E – BMNH C.73328, the original of Spath (1931, pl. 35, fig. 7); F–H – BMNH C.73327, the original of Spath (1931, pl. 32, fig. 2); I – BMNH C.77727, the original of Spath (1931, pl. 35, fig. 8); J – BMNH C.77789 (ex 39672a), the original of *Dipoloceras fredricksburgense* Scott, 1928, of Spath (1931, p. 371, pl. 34, fig. 14); K – BMNH C. 12487.

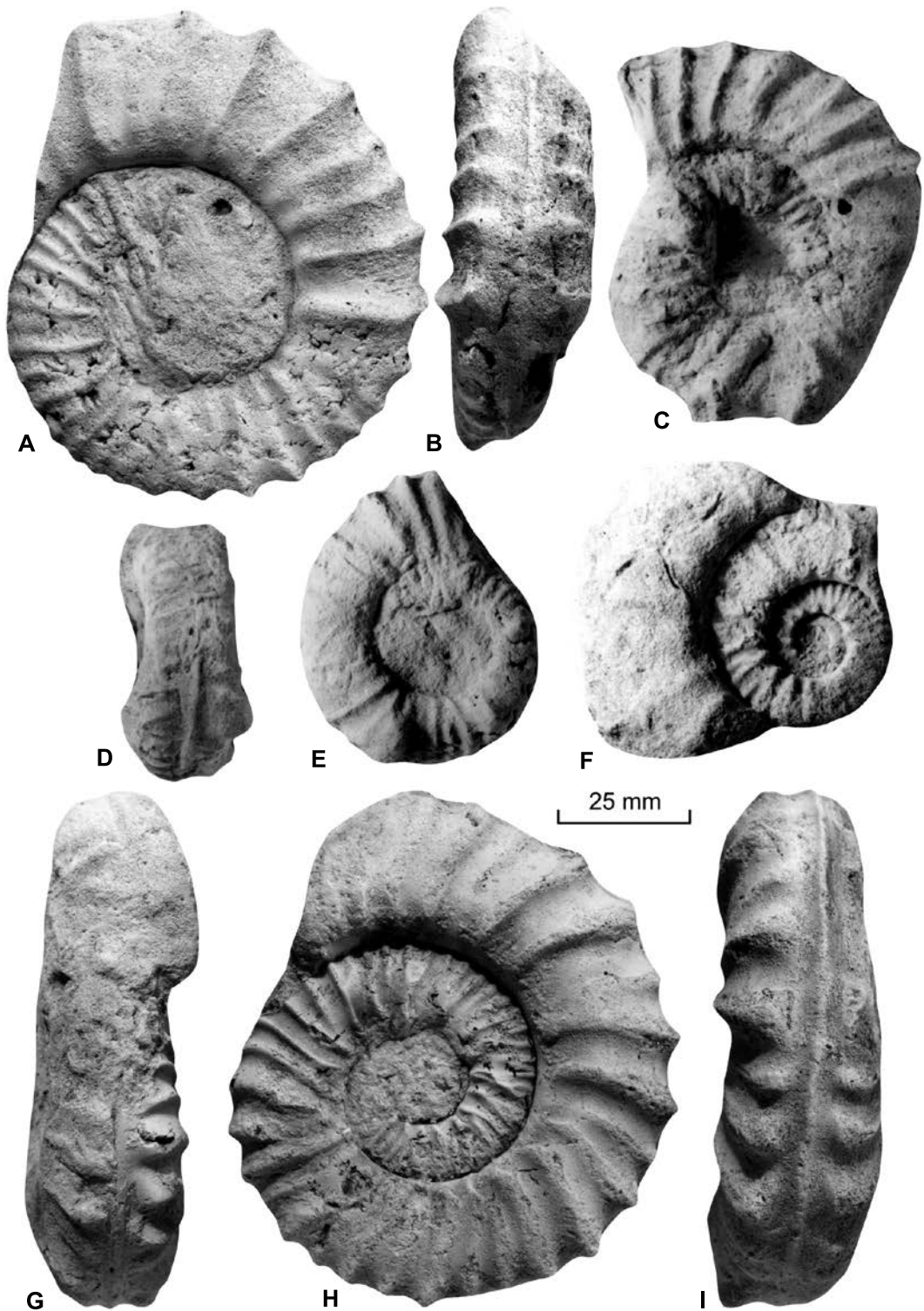


Text-fig. 11. *Dipoloceras cristatum* (Brongniart, 1822) from the Upper Albian of Collignon's Gisement 364, Andranofotsy (Manja), Madagascar. A, B – the original of *Dipoloceras cristatum evolutum* Collignon, 1963 (p. 146, pl. 299, fig. 1292); C, D – the original of *Dipoloceras cristatum andranofotsyensis* Collignon, 1963 (p. 144, pl. 298, fig. 1290). Both specimens are housed in the collections of the Université de Bourgogne, Dijon, France.

*besairiei* (Collignon, 1951) (p. 25, pl. 3, fig. 4; text-fig. 8; 1963, p. 148, pl. 300, fig. 1296; Text-fig. 12G–I) has inner whorls like those of *fallax*, but the body chamber ornament differs markedly, with widely separated convex, strongly rursiradiate ribs. *Diplasioceras*

*hirtzi* (Collignon, 1951) (p. 24, pl. 3, figs 2, 3; text-fig. 7; 1963, p. 148, pl. 300, fig. 1297; Text-fig. 12A, B, F) also differs in the widely spaced, rather than crowded ribs of the adult body chamber, but they are straight rather than convex, and only feebly rursirdi-





Text-fig. 12. Selected representatives of Pervinquierinae Spath, 1926 from the Upper Albian of Andranofotsy (Manja), Madagascar. **A, B, F** – *Diplasioceras hirtzi* Collignon, 1951. A, B – the holotype, EMP 1529, the original of Collignon (1951, p. 24, pl. 3, fig. 3); F – the original of Collignon (1963, pl. 300, fig. 1297), housed in the collections of the Université de Bourgogne, Dijon. **C–E** – *Diplasioceras horridum* Collignon, 1963; C – the original of Collignon (1963, pl. 300, fig. 1299); D, E – the holotype, the original of Collignon (1963, pl. 300, fig. 1298), both in the collections of the Université de Bourgogne, Dijon. **G–I** – *Diplasioceras besairiei* Collignon, 1951, the holotype, EMP 1514, the original of Collignon (1951, p. 25, pl. 3, fig. 4).

ate. *Diplasioceras horridum* (Collignon, 1963) (p. 148, pl. 300, figs 1298, 1299; Text-fig. 12C–E) is highly distinctive. It is based on two specimens, the holotype 54 mm in diameter (Collignon 1963, pl. 300, fig. 1298; Text-fig. 12D, E), the second specimen 70 mm in diameter (Text-fig. 12C). Coiling is very evolute. The ribbing on the body chamber is distant and strongly rursiradiate, whilst there are sparse swollen flares on the outermost flanks and ventrolateral shoulders, like those developed in *Dipolocerooides* Breistroffer, 1947 (Kennedy and Klinger 2012, text-figs 5, 6).

*Dipoloceras* (*Diplasioceras*) *tosaense* Matsumoto and Hirata, 1969 (p. 179, pl. 20, fig. 1) from the Upper Albian of Shikoku, Japan, is immediately distinguished from the present species on the basis of the sinuous, rather than straight ribs.

*Diplasioceras douiraense* Collignon, 1968 (p. 21, pl. 1, fig. 3), from the Upper Albian of Morocco, is based on a 180° whorl fragment 67 mm in diameter, with a maximum preserved whorl height of 34 mm. Coiling is very evolute, with a low expansion rate. Ornament is of coarse umbilical bullae that give rise to single ribs or a pair of ribs that are very strongly rursiradiate, all of which immediately distinguish it from the present species.

OCCURRENCE: As for type.

#### Genus *Euspectroceras* van Hoepen, 1946a

TYPE SPECIES: *Euspectroceras strigilis* van Hoepen, 1946a (p. 202, text-figs 175–177), by original designation; = *Elobiceras newtoni* Spath, 1925 (p. 186, pl. 29, fig. 3; pl. 30, fig. 1).

DIAGNOSIS: Evolute, whorl section rounded. On the phragmocone and adapical part of body chamber strong primary ribs are flared on the inner flanks, and bear inner lateral bullae that give rise to one or two ribs; they alternate with ribs that are weak on the inner flank, without inner lateral bullae. All ribs flared on ventrolateral shoulder. Spiral ridges strongly developed. Ribs weaken and crowd before an adult aperture with a long rostrum.

DISCUSSION: Van Hoepen's (1946a, p. 202) original diagnosis was as follows: "Strongly keeled evolute ammonites with sharp and high ribs, which are steeper in front than behind. Flanks of old whorls convex and of young whorls flat. From extremely young whorls onwards there are umbilical tubercles. There are sudden thickening of the whorls, but no old mouth edges".

This diagnosis fails to capture what are for us the distinctive features of the genus: the alternation of ribs that are markedly flared on the inner flanks and develop an inner lateral bulla alternating with ribs that are weak on the inner flank, with all ribs flared on the ventrolateral shoulders, and the strong spiral ridges.

Wright (1957, p. 404) regarded *Euspectroceras* as a synonym of *Dipoloceras*. The presence of spiral ridges and development of inner lateral tubercles in the former distinguish the two. In 1996 (p. L140) he regarded it as a synonym of *Rhytidoceras* van Hoepen, 1931, described below. They differ markedly, in both the distinctive flank ribbing and tuberculation of *Euspectroceras*.

Klein (2018, p. 175) regarded *Euspectroceras* as a synonym of *Craginites* Young, 1957, type species *Schloenbachia leonensis* var. *serratescens* Cragin, 1893 (p. 24). However, *Euspectroceras* has priority (1946 vs. 1957). *Craginites* was revised by Kennedy (in Gale and Kennedy 2020, p. 16), who regarded it as a subgenus of *Elobiceras* Spath, 1921. *Craginites* species are compressed, may have small umbilical, inner and outer ventrolateral tubercles, lack the strongly differentiated ribbing, flared inner flank ribs and inner lateral bullae of the stronger ribs, and flared ventrolateral ribbing of *Euspectroceras*.

OCCURRENCE: Lower Upper Albian of northern KwaZulu-Natal, south-eastern Mozambique, and south-east France.

#### *Euspectroceras newtoni* (Spath, 1925) (Text-figs 3L; 13; 14A–E)

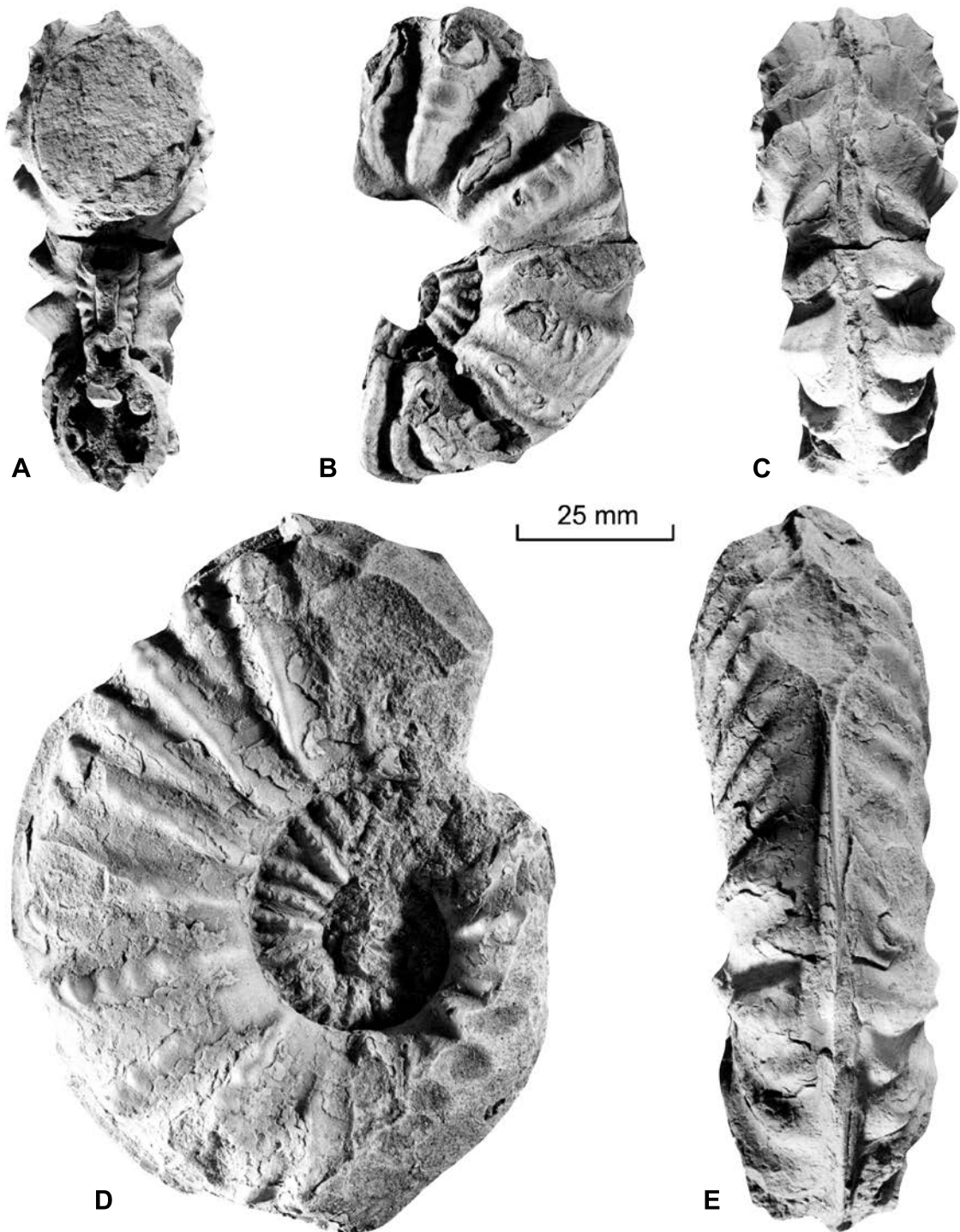
1922. *Mortoniceras* cf. *lenzi* Crick ms. Spath, p. 103.  
1925. *Elobiceras newtoni* Spath, p. 186, pl. 29, fig. 3; pl. 30, fig. 1.  
1946a. *Euspectroceras strigilis* van Hoepen, p. 202, text-figs 175–177.  
2011. *Elobiceras* (*Craginites*) *newtoni* Spath, 1925; Kennedy in Gale *et al.*, p. 79, text-figs 21b–e; 22a–j; 25f; 31g; 32d; 34j; 37k.  
2018. *Craginites newtoni* Spath, 1925; Klein, pp. 175, 176 (with additional synonymy).  
2018b. *Euspectroceras strigile*; Cooper, pl. 24, fig. f.

TYPE: The holotype, by monotypy, is the original of Spath (1925, p. 186, pl. 29, fig. 3; pl. 30, fig. 1), no. 1314 in the collections of the Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, from Catuane, Mozambique.

MATERIAL: SAM PCZ 19126 (*ex* D.2579), the ho-



Text-fig. 13. *Euspectroceras newtoni* (Spath, 1925) from KwaZulu-Natal, South Africa. SAM PCZ 19126 (ex D.2579), the holotype of *Euspectroceras strigilis* van Hoepen, 1946a (p. 202, text-figs 175–177), from the “Ridge West of Ridge which is West of Beacon 624” (van Hoepen 1946a, p. 202).



Text-fig. 14. *Euspectroceras newtoni* (Spath, 1925) from KwaZulu-Natal, South Africa. A–C – SAM PCZ 22519; D, E – SAM PCZ 22920, both from the environs of Ndumu.

lotype, by monotypy, of *Euspectroceras strigilis* van Hoepen, 1946a (p. 202, text-figs 175–177), from the “Ridge West of Ridge which is West of Beacon 624”

(van Hoepen 1946a, p. 202). SAM PCZ 22519 (ex E. Meyer Collection 179) and SAM PCZ 22520 (ex E. Meyer Collection 78), both from the environs of

Ndumu. OUMNH KX.6997–6999, from west of locality 178, SSW of the store at Ndumu. OUMNH KX.10211–2, from locality 177, SW of the store at Ndumu.

#### DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 22520	110.5 (100)	35.9 (32.5)	42.3 (38.2)	0.85	40.0 (36.2)
SAM PCZ 22519	75.0 (100)	33.5 (44.7)	34.7 (46.3)	0.97	26.0 (34.7)
SAM PCZ 19126 c	137.0 (100)	42.9 (31.3)	50.3 (36.7)	0.85	51.3 (37.4)
ic		37.5	50.3	0.74	
at c		52.0	48.5		
	125.5 (100)	(41.4)	(38.6)	1.1	46.8 (37.3)
		39.2	48.5	0.82	

DESCRIPTION: The earliest growth stages seen are OUMNH KX.6997–99, fragments with whorl heights of 20–22 mm that retain limonitised shell (Text-fig. 3L). The whorl section is compressed in intercostal section, the umbilical wall flattened, the umbilical shoulder broadly rounded, the flanks subparallel, the ventrolateral shoulders broadly rounded, the venter feebly convex, with a strong siphonal keel. Coarse primary ribs arise at the umbilical seam, strengthen across the umbilical wall and shoulder and develop into a straight, narrow prorsiradiate primary rib that strengthens markedly into an umbilicolateral flare bearing coarse spiral ridges, the ventralward one strengthened into an inner lateral bulla. The rib elevation declines beyond this before strengthening into a ventrolateral flare bearing coarse spiral ridges. The ribs sweep forwards and decline, forming an obtuse ventral chevron, the ribs extending to the siphonal keel. Much weaker primary ribs separate successive strong primaries, lack an umbilical flared sector, and have a weaker ventrolateral development.

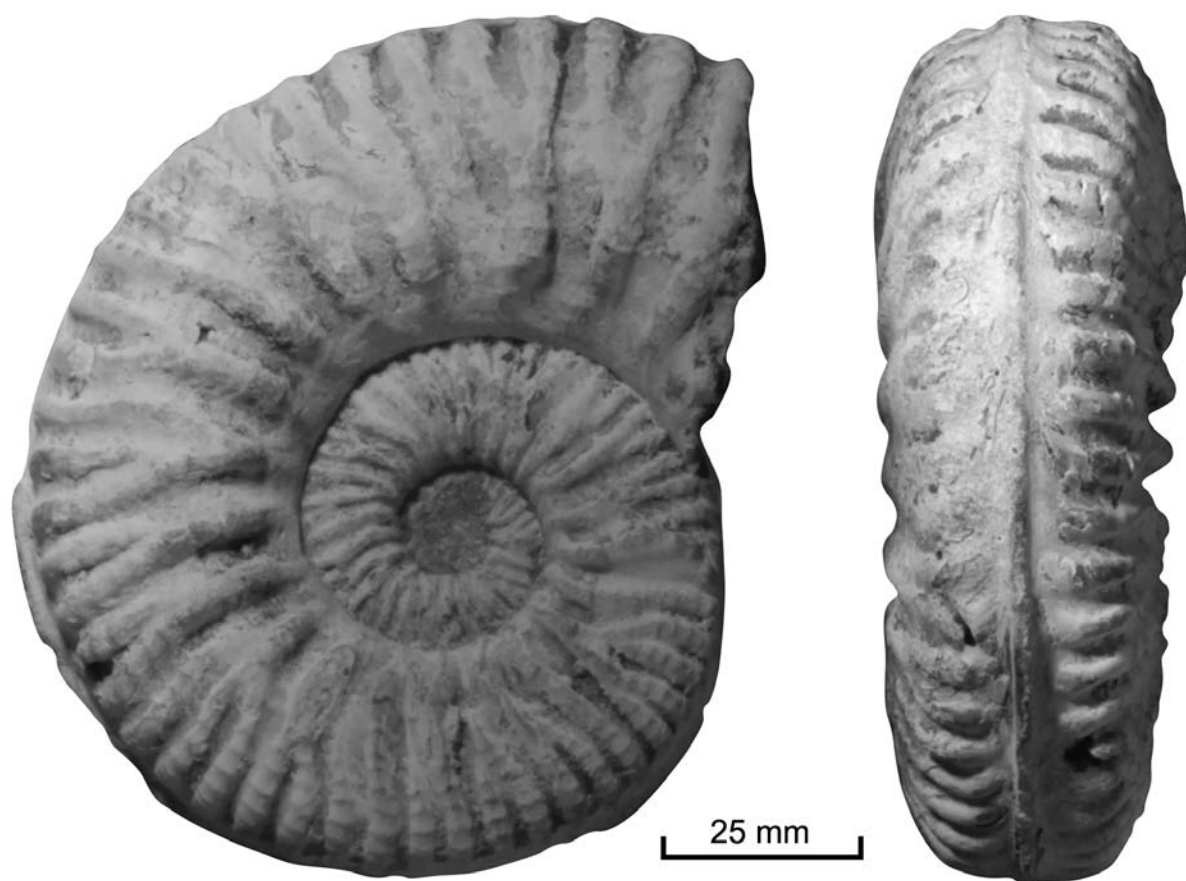
SAM PCZ 22520 (Text-fig. 14D, E) retains traces of shell and is septate to 78 mm diameter. Coiling is evolute, with a broad, shallow umbilicus that comprises 36.2% of the diameter. The whorl section is compressed, with the greatest breadth below mid-flank intercostally and at the umbilical bullae in costal section. The umbilical wall is convex, the umbilical shoulder broadly rounded, the intercostal section ovoid, with a strong siphonal keel. The ornament of the inner whorls is poorly visible, but consists of strong, narrow, rounded prorsiradiate ribs that arise singly or in pairs from weak umbilical bullae. The exposed parts of the ribs bear five rows of coarse spirally elongated ridges. The outer whorl, of which the adapertural 180° sector is body chamber, shows

marked morphological changes, indicating the specimen to be an adult. There are 13 ribs on the adapical half of the outer whorl. Most are primaries, arising at the umbilical seam, and most develop into strong umbilical bullae; these are lost on the adapertural half of the outer whorl. The ribs are strong, straight, and rounded. They decline somewhat at mid-flank, then strengthen and link to strong, blunt tubercles on the ventrolateral shoulder. These decline and efface before reaching the siphonal keel. Three short intercalated ribs are also present. There are eight rows of coarse spirally elongate ridges on the primary ribs, four of the rows on all ribs are borne on the ventrolateral tubercles. SAM PCZ 22519 (Text-fig. 14A–C) is a whorl of a fragmentary adult, from the adapical end of the adult body chamber. The maximum preserved diameter is 75 mm. The intercostal whorl breadth to height ratio is 0.69, the costal whorl breadth to height ratio 0.97. There are 11–12 ribs per half whorl. They are predominantly very coarse primaries with umbilical bullae of variable strength, and strong ventrolateral tubercles. There are well-developed spiral ridges, particularly well-developed on the tubercles.

The holotype of *Euspectroceras strigilis* (Text-fig. 13) is a complete adult, septate to a diameter of 90mm, with a 180° sector of body chamber, the adult aperture and rostrum preserved, retaining recrystallized shell. Coiling is very evolute, the umbilicus comprising 37.4% of the diameter. The umbilical wall is low and convex, the umbilical shoulder broadly rounded. The intercostal whorl section is compressed oval, with a whorl breadth to height ratio of 0.82–0.85, the greatest breadth outside the umbilical shoulder. The costal section is trapezoidal, and varies from slightly compressed to slightly depressed, with the greatest breadth at the umbilical bullae. There is a strong siphonal keel. On the phragmocone, 20 primary ribs arise at the umbilical seam, strengthen across the umbilical wall and shoulder, and bear strong spiral ridges. The ventralmost of these becomes bullate, and may give rise to a pair of ribs in some cases. The ribs strengthen markedly on the ventrolateral shoulders and are flared, bearing strong spiral ridges. Additional ribs arise on the umbilical shoulder and are initially weak; others intercalate on the inner to mid-flank, and strengthen to match the primary ribs at the ventrolateral shoulder. There are 23 ribs at the ventrolateral shoulder at a diameter of 125 mm, and 24–25 at a diameter of 137 mm. Where the surface of the recrystallized shell is preserved, spiral ridges are well-developed, strong on the ribs and tubercles, and weak on the interspaces. The ribs bear up to ten rows of spiral ridges; they are strongest on the umbilical



Text-fig. 15. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19129 (ex D.2363), the holotype, the original of van Hoepen (1931, p. 43, text-fig. 4 and 1941, p. 64, text-figs 14, 15, and 17), from his bank 9 at locality 51.



Text-fig. 16. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19088 (ex D.2361), the original of van Hoepen (1931, text-fig. 7, referred to as a paratype of *Rhytidoceras elegans*; 1941, p. 64, text-fig. 19, referred to *Rhytidoceras crassicostatum*), from his bank 8 at locality 51.

and ventrolateral bullae. Ribbing coarsens markedly on the body chamber, ribs that are strong on the inner flank alternating with weaker ones. Bullae and ribs weaken markedly towards the adult aperture, and the final two ribs are very weak and approximated. The apertural margin is preceded by a short tubular section, ornamented by flexuous riblets and striae. The aperture is perfectly preserved, and follows a feebly flexuous course, concave on the umbilical shoulder, broadly convex across the flanks, feebly concave on the ventrolateral shoulders and projected forwards into a long ventral rostrum that follows the logarithmic curve of the venter; the terminal part is missing. OUMNH KX.10211 is a fragment from the adapertural end of the body chamber with a comparable change of ornament, indicating that it too is adult with a maximum preserved whorl height of 41 mm.

DISCUSSION: See above.

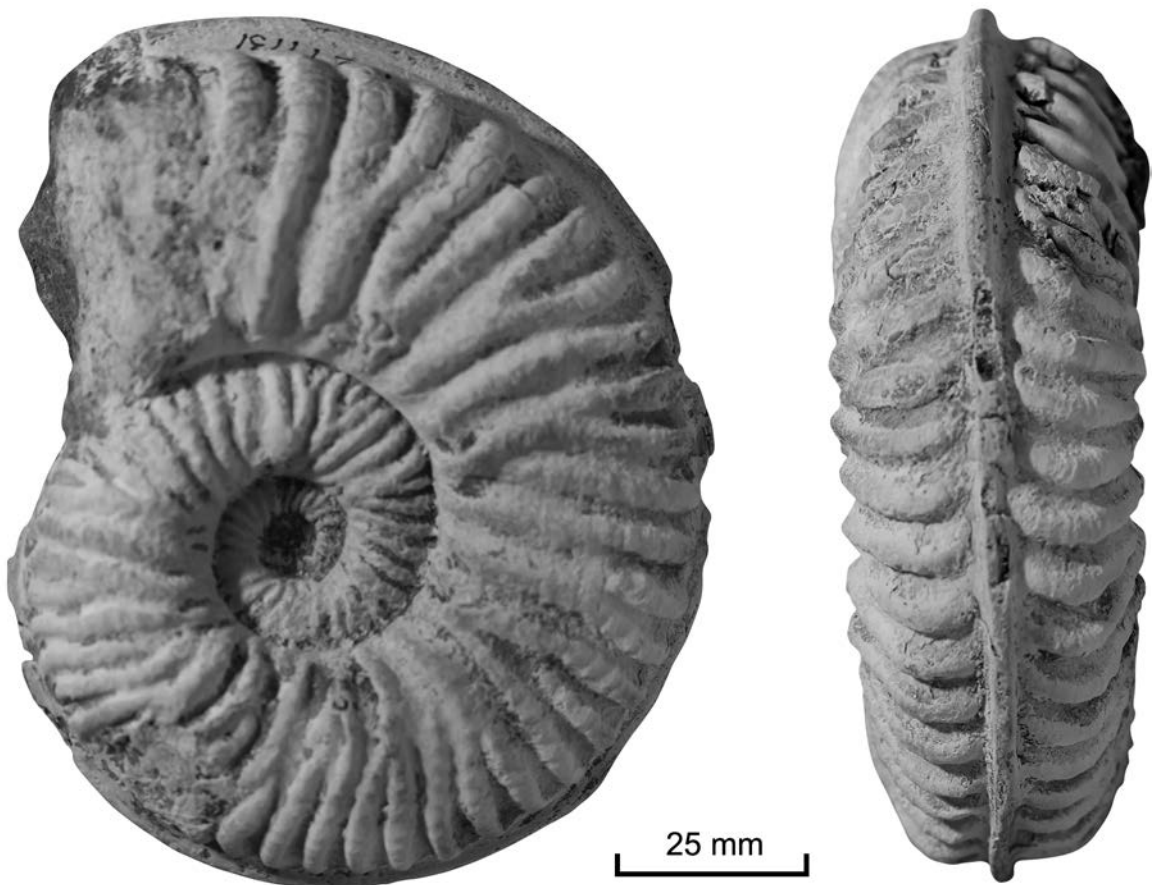
OCCURRENCE: Lower Upper Albian of northern KwaZulu-Natal, south-eastern Mozambique, and southeast France.

#### Genus *Rhytidoceras* van Hoepen, 1931

(= *Drepanoceras* van Hoepen, 1931, p. 46, non Stein, 1878, p. 25, type species *Drepanoceras undatum* van Hoepen, 1931, p. 47, text-fig. 9; *Ricnoceras* van Hoepen, 1941, p. 59, type species *Ricnoceras pandai* van Hoepen, 1941, p. 59, text-figs 4, 5)

TYPE SPECIES: *Rhytidoceras elegans* van Hoepen, 1931 (p. 43, text-fig. 4), by the original designation of van Hoepen (1931, p. 43).

DIAGNOSIS: Coiling very evolute, expansion rate low, ribs crowded, recti- to feebly rursiradiate, flex-



Text-fig. 17. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19131 (ex D.2365), the holotype of *Rhytidoceras rotundum* van Hoepen, 1931, the original of van Hoepen (1931, p. 45, text-fig. 8; 1941, p. 68, text-fig. 23), from his bank 9 at locality 51.

uous, single, bifurcating on umbilical shoulder or inner flank, with or without developing a feeble umbilical bulla, some ribs expanded into umbilical bulges or flares, and bifurcating a second time, projecting forwards on ventrolateral shoulder and strengthening into a blunt bulla, ribs transverse on venter or forming a feebly obtuse ventral chevron, separated from the strong siphonal keel by a smooth zone. On the adapertural part of adult body chamber ribs single, weakened on the inner flank, less markedly flexuous, and effacing immediately before the adult aperture. Prominent spiral ridges present throughout and prominent on ribs and tubercles. Adult aperture biconcave, with a rostrum that curves up and terminates close to the venter of the adapical part of the outer whorl. Suture moderately incised, with bifid E/A, A and U2.

DISCUSSION: A translation of van Hoepen's original diagnosis is as follows: "Evolute ammonites with a

whorl section that sometimes is wider than high and sometimes higher than wide. Flanks of later whorls more or less flattened, those of earlier whorls convex. Keel high, ribs numerous, closely spaced, sickle-shaped. They originate weakly at the umbilical suture; in the early stages they simply cross the high umbilical wall and the convex flanks towards the keel. At this stage there occur at regular intervals thicker ribs, that apparently are situated behind old apertures, and which bi- or trifurcate, resulting in three or four ends at the keel. There are no umbilical or other tubercles. Only the apertures result in irregular formation of tubercles. On later whorls, the ribs have an elongated tubercle on top of the umbilical wall, and are mostly split once or twice. Also, the tubercles are irregular; the larger ones usually indicate the presence of old apertures. The whole of the flank is ornamented with spiral ornament. Differs from *Dipoloceras* by the absence of ventral grooves, rounding of the venter in the young stage and by the round ribs."





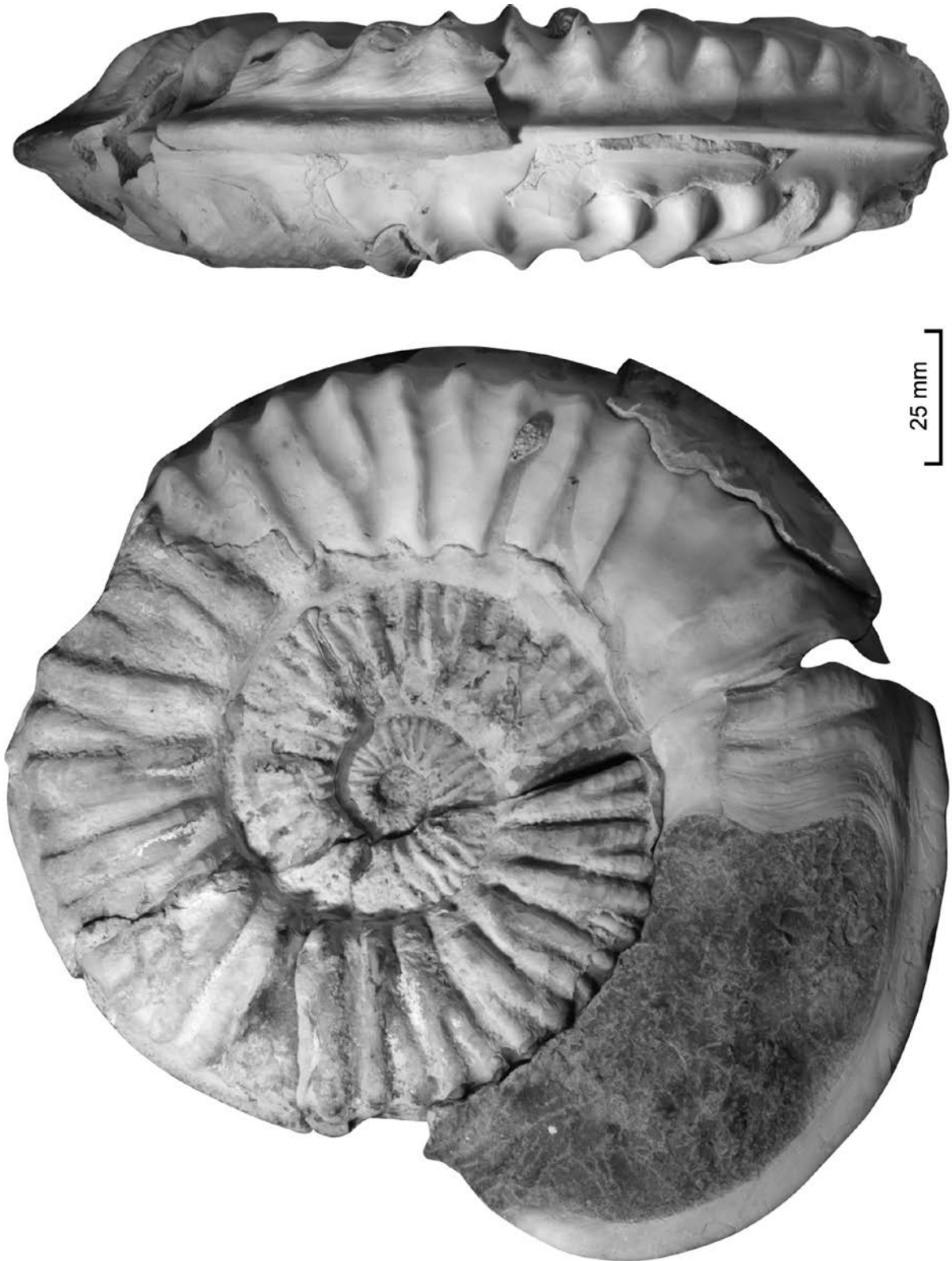
Text-fig. 18. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19128 (ex D.2366), assigned to *Rhytidoceras rotundum* by van Hoepen (1941, p. 69), from his bank 9 at locality 51.

Wright (1957, p. 404; 1996, p. L140) regarded *Rhytidoceras* as a subgenus of *Dipoloceras*. As discussed above, they are, in our view generically distinct, and indeed belong to different subfamilies of Brancoceratidae, the distinguishing features of *Rhytidoceras* being the evolute coiling, low expansion rate, flexuous ribs, absence of flared ribs and presence of spiral ridges (spiral ridges are not developed in the type species of *Dipoloceras*). The type species of *Rhytidoceras* shares these features with the type species of *Drepanoceras* van Hoepen, 1931 (p. 46, non Stein, 1878, p. 25, type species *Drepanoceras undatum* van Hoepen, 1931, p. 47, text-fig. 9). A translation of van Hoepen's original diagnosis is as follows: "Evolute ammonites with a whorl section higher than wide. Flanks of early whorls flattened. Ribs abundant, closely spaced, sickle-shaped curved. The ribs gradually become thicker towards their ventral end; they originate on the umbilical wall and at the upper margin

thereof give rise to a protruding tubercle; from here they fork, often in pairs, while at the middle of the flanks they fork again. Sometimes the ribs are single at the tubercle, and then fork at mid-flank. Umbilical wall oblique. Flanks ornamented spirally. Differs from *Elobiceras* by the double row of tubercles at the umbilical edge and by the high keel. from *Rhytidoceras* by its flat early whorls and the row of tubercles close to the umbilical edge."

*Ricnoceras* van Hoepen, 1941, type species *Ricnoceras pandai* van Hoepen, 1941 (p. 59, text-figs 4, 5), is a further synonym of *Rhytidoceras*. A translation of the original diagnosis is as follows: "Strongly keeled evolute ammonites. Early whorls with strong convex flanks. Older whorls with flattened or weakly convex flanks. This area ornamented by well-formed umbilical tubercles. Numerous thin, closely-spaced ribs. Transversely protruding old apertures."

Van Hoepen further notes: "To this genus possi-



Text-fig. 19. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19130 (ex D.500 in van Hoepen 1931, p. 44, text-figs 5, 6, but referred to as D.2360 in 1941 p. 67, pl. 9), the holotype of *Rhytidoceras crassicosatum* van Hoepen, 1931 (p. 4, text-figs 5, 6; as *Rhytidoceras elegans* var. *crassicosatum*, refigured in 1941, pl. 9), from his bank 9 at locality 51.

bly also should be referred *Dipoloceras quadratum* Spath, which is small, but which, after the end of the last whorl exhibits the formation of tubercles. Also, *Dipoloceras bouchardianum* d'Orb. sp., varieties of which, according to Spath also have umbilical tubercles."

Specimens assigned to species of *Rhytidoceras*, *Ricnoceras*, and *Drepanoceras sensu* van Hoepen and related taxa, are meticulously documented by van Hoepen and assigned to his "banks" at our locality 51, his classic locality east of the drift on the Mzinene (Umsinene) River as set out in Table 1.

The species assigned to *Rhytidoceras*, *Drepanoceras*, and *Ricnoceras* by van Hoepen have overlapping ranges, and we regard them as a single variable species. Van Hoepen himself referred one specimen [SAM PCZ 19088, ex D.584 (1941); D.2580 (1946a): Text-fig. 16] to '*Drepanoceras*' *undatum* in 1941 (p. 83), re-identifying it as *Rhytidoceras elegans* in 1946a (p. 201).

As first revising authors we select the name *elegans* for the species, and regard the following species described by van Hoepen as synonyms:

- *Rhytidoceras elegans* van Hoepen, 1931 (p. 43, text-figs 4, 7);
- *Rhytidoceras* [*elegans* var.] *crassicostatum* van Hoepen, 1931 (p. 43, figs 5, 6);
- *Rhytidoceras rotundum* van Hoepen, 1931 (p. 45, text-fig. 8; 1941, p. 68, text-figs 21–23);
- *Rhytidoceras megaera* van Hoepen, 1941 (p. 69, text-figs 24–28; 1951a, p. 276, text-fig. 279);
- '*Drepanoceras*' *undatum* van Hoepen, 1931 (p. 47, text-fig. 9; 1941, p. 77, pl. 13; text-figs 38, 39);
- '*Drepanoceras*' *rudis* van Hoepen, 1931 (p. 47, text-fig. 10; 1941, pl. 17, text-figs 49, 50);
- '*Drepanoceras*' *crassicostatum* van Hoepen, 1941 (p. 83, text-figs 46–48);
- *Ricnoceras pandai* van Hoepen, 1941 (p. 59, text-figs 4, 5).

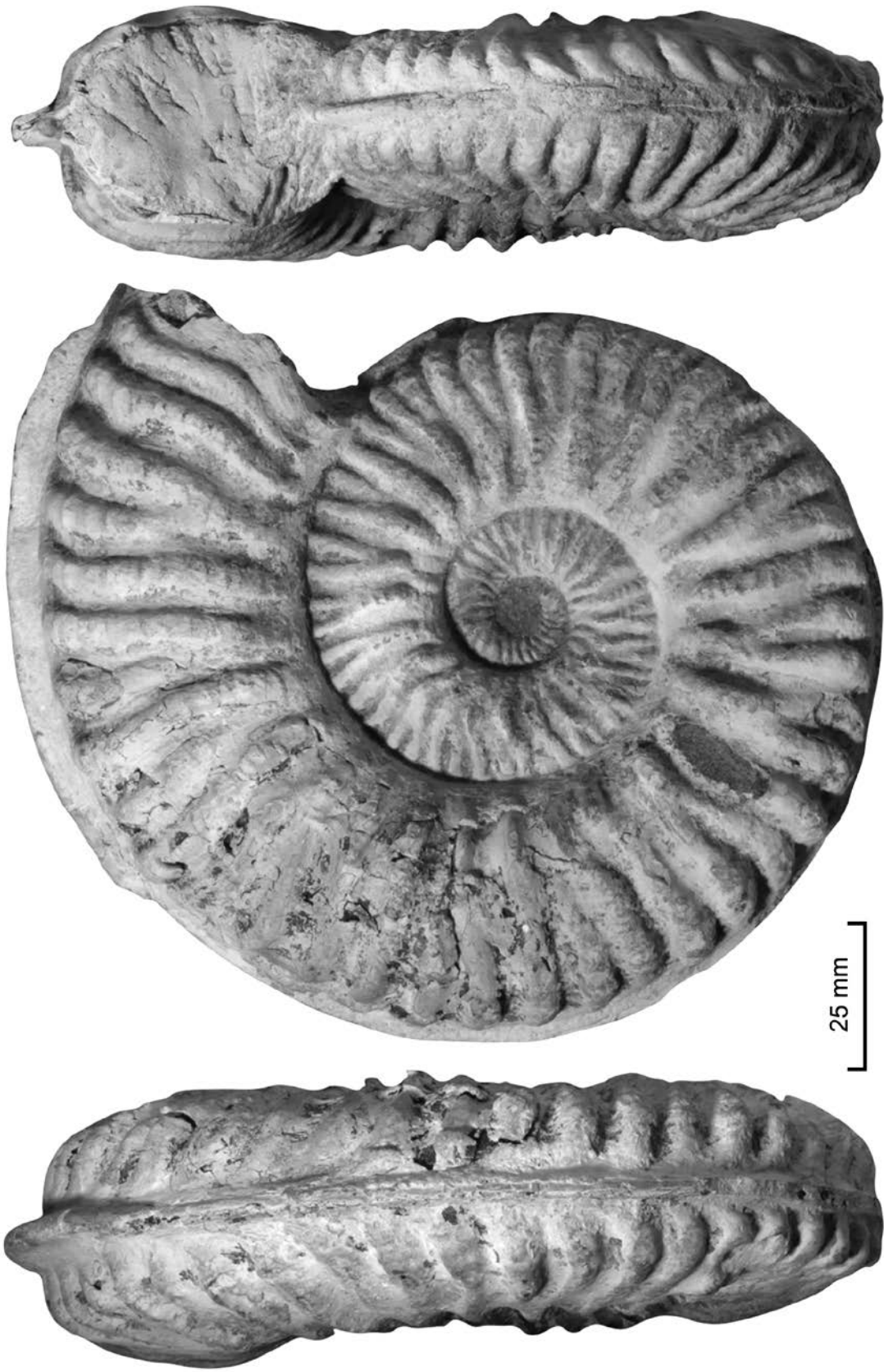
OCCURRENCE: Lower Upper Albian, KwaZulu-Natal, Madagascar, Angola, Ecuador, southern England, France, Switzerland, northern Pakistan, and Japan. We are unable to confirm the records from Algeria in Lafitte (1939).

*Rhytidoceras elegans* van Hoepen, 1931  
(Text-figs 15–26; 27A–E; 28A–M; 29)

- 1931. *Rhytidoceras elegans* van Hoepen, p. 43, text-figs 4, 7.
- 1931. *Rhytidoceras elegans* var. *crassicostatum* van Hoepen, p. 43, text-figs 5, 6.

- 1931. *Rhytidoceras rotundum* van Hoepen, p. 45, text-fig. 8.
- 1931. *Drepanoceras undatum* van Hoepen, p. 47, text-fig. 9.
- 1931. *Drepanoceras rudis* van Hoepen, p. 47, text-fig. 10.
- 1931. *Dipoloceras pseudaoon* Spath, p. 373, pl. 32, fig. 10.
- 1931. *Dipoloceras pseudaoon* passage form to *D. cristatum* var. *subcristata* Spath, p. 373, pl. 34, fig. 2.
- 1931. *Dipoloceras pseudaoon* var. *moniliformis* Spath, p. 373, pl. 32, fig. 10.
- 1941. *Ricnoceras pandai* van Hoepen, p. 59, text-figs 4, 5.
- 1941. *Rhytidoceras elegans* v. Hoepen; van Hoepen, p. 64, text-figs 14–18.
- 1941. *Rhytidoceras crassicostatum* v. Hoepen; van Hoepen, p. 67, text-figs 19, 20; pls 9, 10.
- 1941. *Rhytidoceras rotundum* van Hoepen, p. 68, text-figs 21–23.
- 1941. *Rhytidoceras megaera* van Hoepen, p. 69, figs 24–28.
- 1946a. *Rhytidoceras elegans* v. Hp.; van Hoepen, p. 201.
- 1946a. *Rhytidoceras* sp. van Hoepen, p. 202.
- 1951. *Dipoloceras* (?*Rhytidoceras*) *trifurcatum* Collignon, p. 27, pl. 4, figs 2–4; text-figs 10, 11.
- 1979. *Mortoniceras* (*Drepanoceras*) *undatum* van Hoepen; Collignon, p. 28, pl. 11, fig. 3.
- 1999. *Dipoloceras* (*Rhytidoceras*) sp.; Kennedy and Fatmi, p. 73, text-fig. 18a.
- 2005. *Dipoloceras* (*Rhytidoceras*) aff. *elegans* van Hoepen, 1931; Bulot *et al.*, p. 454, text-fig. 5.
- 2018. *Dipoloceras* (*Dipoloceras*) *pseudaoon* Spath, 1931; Klein, pp. 86, 93 (with synonymy).
- 2018. *Dipoloceras* (*Rhytidoceras*) *elegans* (van Hoepen, 1931); Klein, p. 95 (with additional synonymy).
- 2018. *Dipoloceras* (*Rhytidoceras*) *megaera* (van Hoepen, 1941); Klein, pp. 95, 96.
- 2018. *Dipoloceras* (*Rhytidoceras*) *pandai* (van Hoepen, 1941); Klein, pp. 95, 96.
- 2018. *Dipoloceras* (*Rhytidoceras*) *rotundum* (van Hoepen, 1931); Klein, pp. 95, 96.
- 2018. *Dipoloceras* (?*Rhytidoceras*) *trifurcatum* Collignon, 1951; Klein, pp. 95, 96.
- 2018. *Mortoniceras* (*Deiradoceras*) *undatum* (van Hoepen, 1931); Klein, pp. 130, 136.
- 2018. *Mortoniceras* (*Drepanoceras*) *rudis* (van Hoepen, 1931); Klein, pp. 130, 136.
- 2018. *Mortoniceras* (*Deiradoceras*) *crassicostatum* (van Hoepen, 1941); Klein, pp. 129, 132.
- 2018b. *Ricnoceras pandai*; Cooper, pl. 26, fig. a.

TYPES: The holotype of *Rhytidoceras elegans* van Hoepen, 1931 is SAM PCZ 19129 (ex D.2363), the original of van Hoepen (1931, p. 43, text-fig. 4) and van Hoepen (1941, p. 64, text-figs 14, 15, and 17), from bank 9 at locality 51. Van Hoepen referred to the original of his 1931 text-fig. 7 as a paratype of *Rhytidoceras elegans*. This specimen is SAM PCZ



Text-fig. 20. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa. SAM PCZ 19091 (ex D.2361), referred to *Rhytidoceras crassicoostatum* by van Hoepen (1931), from his bank 9 at locality 51.

19088 (ex D.2361). In 1941 (p. 64, fig. 19) he referred it to *Rhytidoceras crassicosatum* van Hoepen, 1931. It is from bank 8 at locality 51.

**MATERIAL:** Specimens referred to *Rhytidoceras elegans* by van Hoepen: SAM PCZ 19084 (formerly D.2357), the original of van Hoepen (1931, p. 44; 1941, p. 66); SAM PCZ 19127 (formerly D.2357), the original of van Hoepen (1931, p. 44, 1941, p. 66); SAM PCZ 19461 (formerly D.2580, previously D.584); the original of van Hoepen (1941, p. 83, as *Drepanoceras undatum*; 1946a, p. 201 as *Rhytidoceras elegans*), from bank 10 at locality 51.

Specimens assigned to *Rhytidoceras rotundum* by van Hoepen: SAM PCZ 19131 (ex D.2365) – the holotype of *Rhytidoceras rotundum*, the original of van Hoepen (1931, p. 45, text-fig. 8; refigured in 1941 as text-fig. 22); SAM PCZ 19092 (ex D.2366), the original of van Hoepen (1941, text-fig. 21); SAM PCZ 19128 (ex D. 2366), the original of van Hoepen (1941, p. 69), all from bank 9 at locality 51.

Specimens assigned to *Rhytidoceras elegans* var. *crassicosatum* van Hoepen, 1931 = *Rhytidoceras crassicosatum* van Hoepen, 1941: the holotype of *Rhytidoceras crassicosatum* – SAM PCZ 19130 (ex D.500 in van Hoepen 1931, p. 44, text-figs 5, 6, but referred to as D.2360 in 1941 p. 67, pl. 9), from bank 9; SAM PCZ 19086 (ex D.573), mentioned by van Hoepen (1941, p. 67), from bank 10; SAM PCZ 19087 (ex D.2364), mentioned by van Hoepen (1941, p. 67), from bank 10; SAM PCZ 19088 (ex D.2361), mentioned by van Hoepen (1941, p. 67); SAM PCZ 19089 (ex D.2361), mentioned by van Hoepen (1941, p. 67); SAM PCZ 19090 (ex D.2361), mentioned by van Hoepen (1941, p. 67, pl. 10); SAM PCZ 19091 (ex D.2361), mentioned by van Hoepen (1941, p. 67), all from bank 9.

Specimens assigned to *Rhytidoceras megara* by van Hoepen: the holotype of *Rhytidoceras megara* is D.2368, the original of van Hoepen (1941, text-figs 24 and 27); it has not been traced; a second specimen, SAM PCZ 21624 (ex D.2369) 23 mm in diameter was illustrated as his text-figs 25 and 26; his text-fig. 28 is based on an unspecified individual. Four further specimens are from bank 9: SAM PCZ 21624, 19093, 190954, 190955 (all ex D.2369).

Specimens assigned to '*Drepanoceras undatum*' by van Hoepen: the holotype is SAM PCZ 19135 (ex D.2382), the original of van Hoepen (1931, p. 14, text-fig. 9; 1941, p. 82, pl. 16), from bed 9; the paratype 245 mm in diameter referred to by van Hoepen (1931, p. 47) is SAM PCZ 19110 (ex D.2383), from bed 9; SAM PCZ 19482 (ex D.584), from bed 10.

Specimens assigned to '*Drepanoceras rudis*' by van Hoepen: the holotype of '*Drepanoceras rudis*', by original designation, is SAM PCZ 19134 (ex D.2386), the original of van Hoepen (1931, p. 47, text-fig. 10; 1941, p. 84, text-fig. 49), from bed 9; SAM PCZ 19101 (ex D.2387) is the paratype; SAM PCZ 19187 (ex D. 2387), SAM PCZ 19096 (ex D.2387), SAM PCZ 19097 (ex D.2387) and SAM PCZ 19108 (ex D.2387), all from bed 9.

Specimens assigned to '*Drepanoceras crassicosatum*' by van Hoepen: the holotype is SAM PCZ 19133 (ex D.2384), the original of van Hoepen (1941, p. 83, text-figs 46 and 48), from bed 10; SAM PCZ 19098 (ex D.2385) is the original of van Hoepen (1941, text-fig. 47), from bed 10.

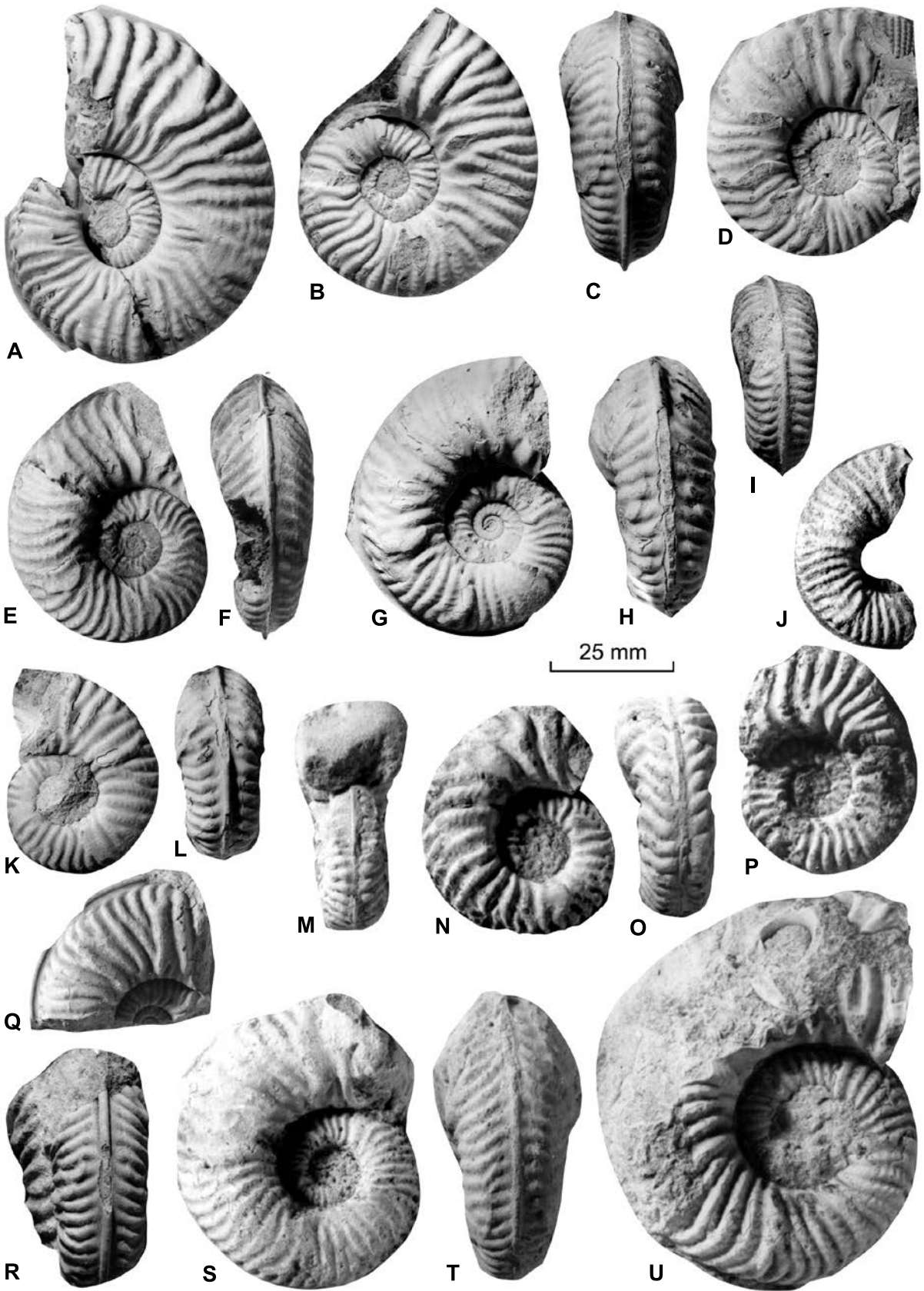
Specimens assigned to *Ricnoceras pandai* by van Hoepen: the holotype is SAM PCZ 19189 (ex D.500), the original of van Hoepen (1941, p. 59, text-figs 4, 5), from bed 9.

From locality 51 of Kennedy and Klinger (1975): OUMNH KX.11741 from bed 5; OUMNH KX.11753, from bed 5 or 6; OUMNH KX.11774, 11777a, 11784, 11789, and 11792, from bed 6; OUMNH KX.11850, from bed 7; OUMNH KX.11888, from bed 11; OUMNH KX.11913, from bed 11 or 12; OUMNH KX.10215 and 10216 from locality 177; OUMNH KX.10022, from between localities 176 and 177.

**DESCRIPTION:** The holotype of *Rhytidoceras elegans*, SAM PCZ 19129 (ex D.2363) (Text-fig. 15), has the following dimensions:

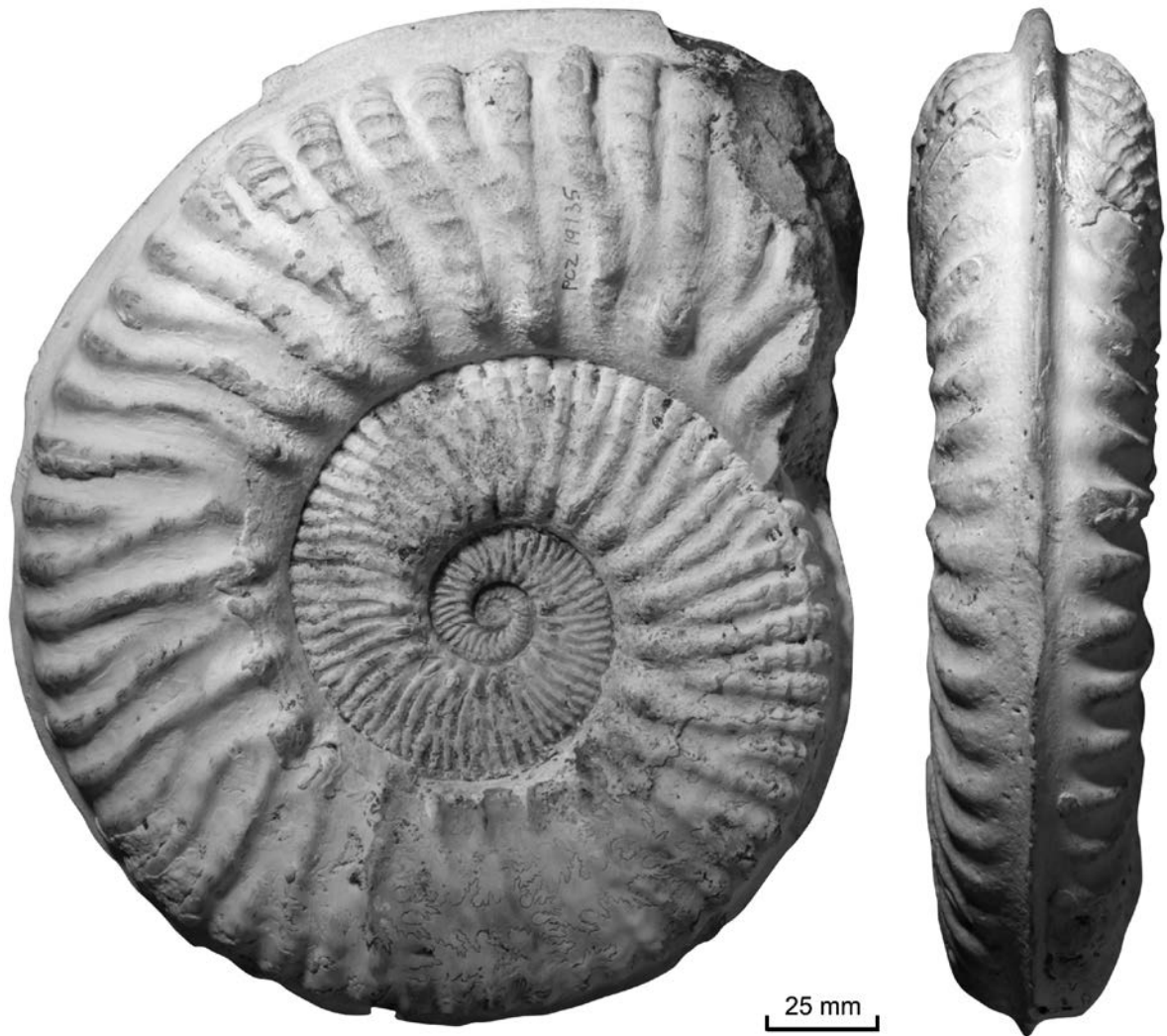
	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19129	154.0 (100)	43.4 (28.2)	55.3 (35.9)	0.78	58.2 (37.8)

It is a well-preserved internal mould 154 mm in diameter, with a 270° sector of body chamber preserved, the last few septa approximated, whilst modification of the last few ribs suggest the specimen is a near-complete adult. Coiling is very evolute, with 30% of the previous whorl covered, the wide, shallow umbilicus comprising 37.8% of the diameter, the umbilical wall feebly convex and outward-inclined, merging with the broadly rounded umbilical shoulder. On the penultimate whorl, 30 primary ribs arise at the umbilical seam and are straight and prorsiradiate on the umbilical wall, flex back and are convex across the umbilical shoulder, straight on the inner flank and feebly concave before disappearing below the umbilical seam of the succeeding whorl. The ribs are either single, or bifurcate at the umbilical shoulder or low on the flank, to give a total of an estimated 48 on the outer flank. A few ribs branch high on the flank.



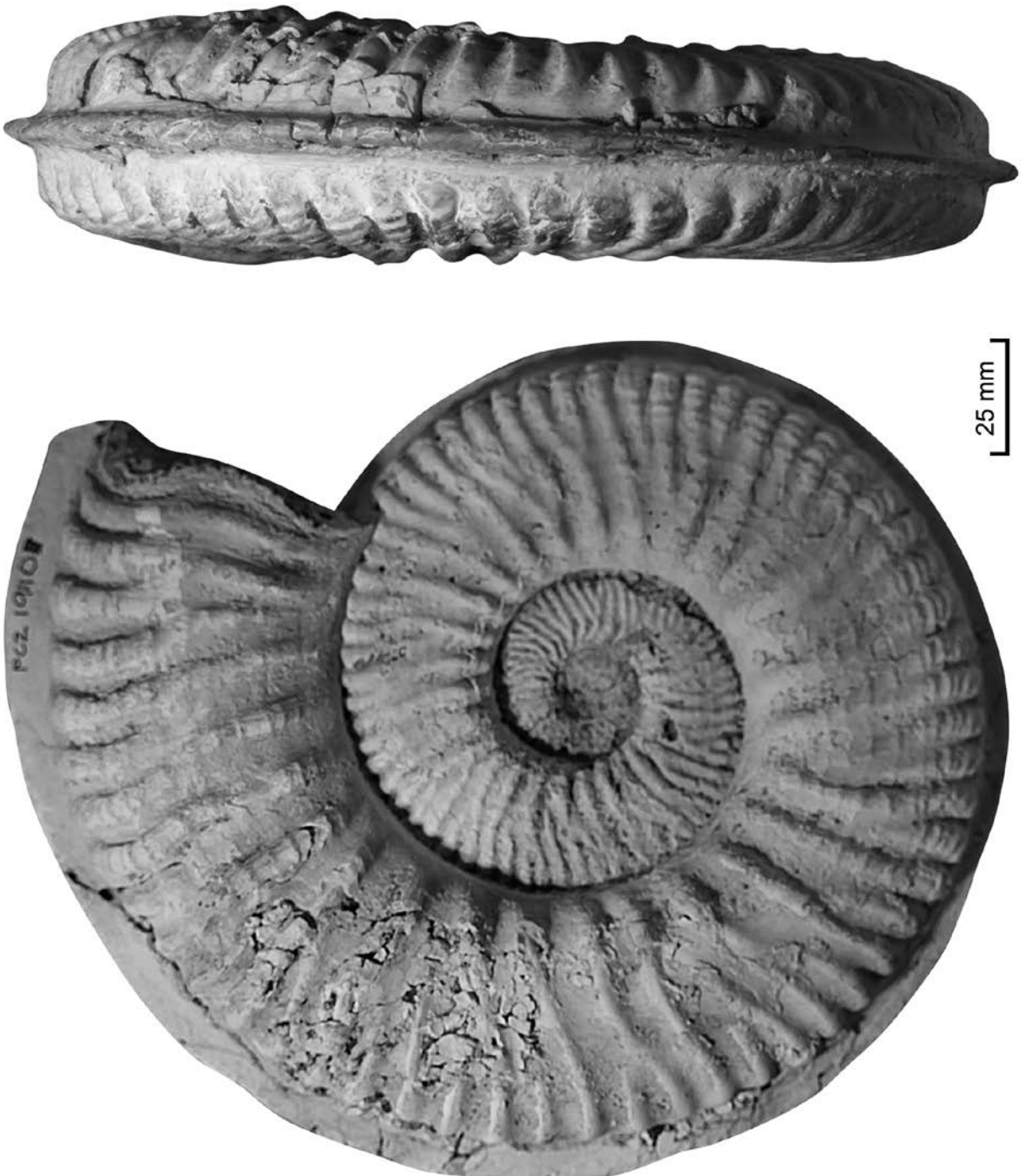
Some ribs are incipiently bullate at the umbilical shoulder, and occasional ribs are borne on an incipient umbilical bulge, albeit weak. There are 28 ribs on the umbilical wall of the outer whorl, and a total of 47 at the ventrolateral shoulder. The ribs sweep forwards on the umbilical wall, and strengthen into long, sharp bullae on the umbilical shoulder. The bullae give rise to a single rib or a pair of ribs on the phragmocone

and adapical part of the body chamber. Some ribs branch low on the flank or at mid-flank. The ribs are rectiradiate to feebly rursiradiate, narrow, crowded, straight on the inner flank, flexing forwards and feebly concave on the outer flank, where they strengthen and sweep forwards across the ventrolateral shoulder to form an obtuse chevron, interrupted by a smooth zone on either side of the siphonal keel. The last three



Text-fig. 22. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19135 (ex D.2382), the holotype of *Drepanoceras undatum* van Hoepen, 1931, the original of van Hoepen (1931, p. 14, text-fig. 9; 1941, p. 82, pl. 16), from his bed 9 at locality 51.

- ← Text-fig. 21. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa. A – OUMNH KX.11888, from bed 11 at locality 51; B – OUMNH KX.11774, from bed 6 at locality 51; C, D – OUMNH KX.11913 at locality 51, beds 12–13; E, F – OUMNH KX.10215, from locality 177; G, H – OUMNH KX.11784, from bed 6 at locality 51; I, J – SAM PCZ 21624 (ex D.2369), referred to *Rhytidoceras megara* by van Hoepen (1941, p. 69), from his bank 9 at locality 51; K, L – OUMNH KX.11792, from bed 6 at locality 51; M–O – SAM PCZ 19087 (ex D.2364), referred to *Rhytidoceras crassicostatum* by van Hoepen (1941, p. 67, text-fig. 20), from his bank 10 at locality 51; P – SAM PCZ 19098 (ex D.2385), referred to *Drepanoceras crassicostatum* by van Hoepen (1941, p. 83, text-fig. 47); Q, R – SAM PCZ 19095 (ex D.2369), assigned to *Rhytidoceras megara* by van Hoepen (1941, p. 69), from his bank 9 at locality 51; S, T – SAM PCZ 21624 (ex D.2369), a paratype of *Rhytidoceras megara* van Hoepen, 1941 (p. 69), from his bank 9 at locality 51; U – SAM PCZ 19092 (ex D.2366), assigned to *Rhytidoceras rotundum* by van Hoepen (1941, p. 68, text-fig. 21).



Text-fig. 23. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19110 (ex D.2383), the paratype of *Drepanoceras undatum* mentioned by van Hoepen (1931, p. 47, 1941, p. 82), from his bank 9 at locality 51.

ribs on the body chamber are weaker than those that precede them; one is single, lacks an umbilical bulla and is straight and prorsiradiate on the flanks.

The paratype of *elegans*, SAM PCZ 19088 (ex

D.2361) (Text-fig. 16), is the original of van Hoepen (1931, text-fig. 7). It is an individual lacking the early whorls and is in part body chamber. It retains traces of aragonitic shell. The dimensions are:





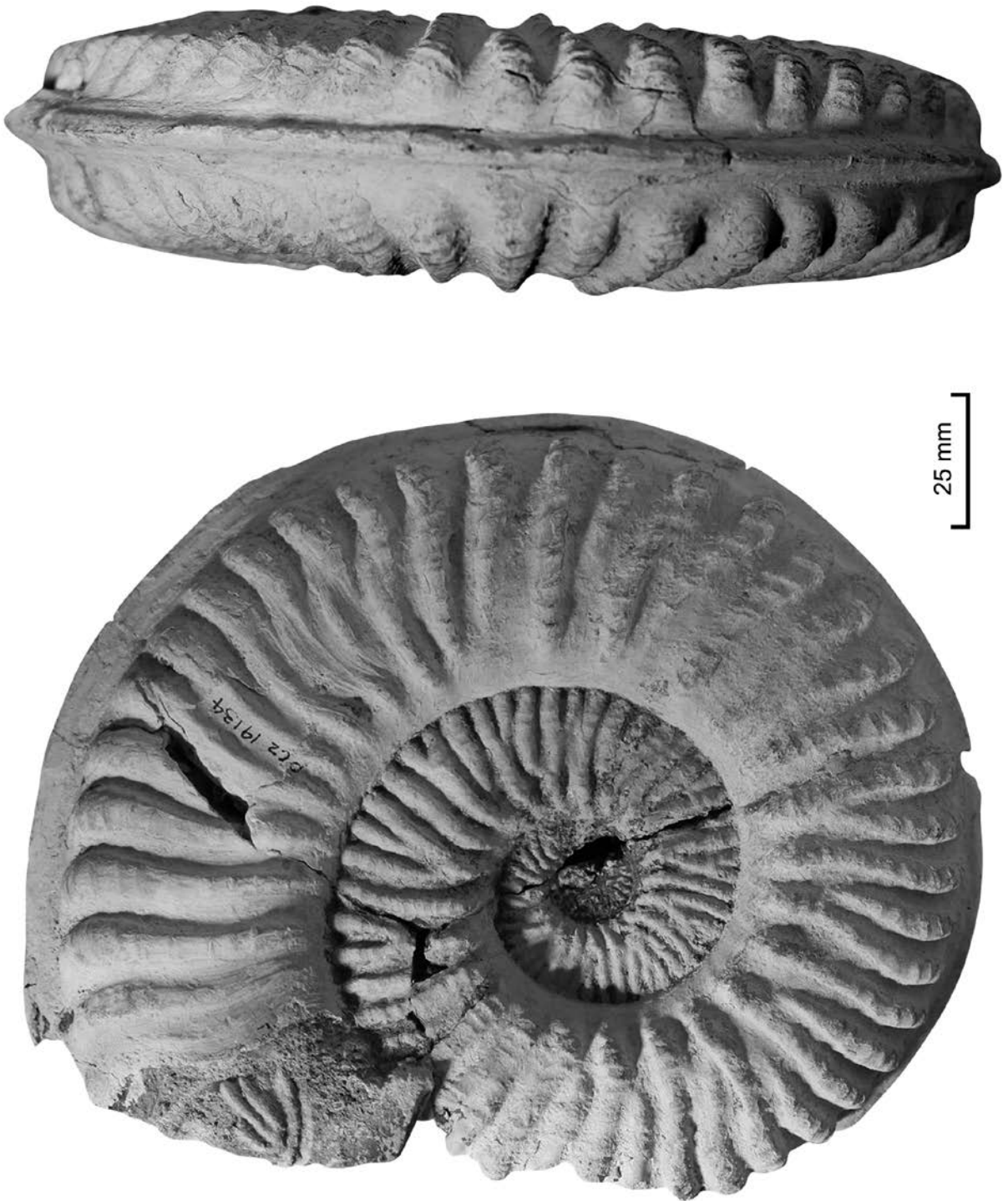
Text-fig. 24. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19482 (ex D.584), assigned to *Drepanoceras undatum* by van Hoepen (1931, p. 47; 1941, p. 82), from his bed 10 at locality 51.

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19088 costal	122.0 (100)	39.4 (32.3)	44.1 (36.1)	0.89	44.0 (36.1)

Umbilical bulges are much more conspicuous than in the holotype, with three present on the adapertural half of the penultimate whorl. There are 24 primary ribs on the umbilical wall of the outer whorl, and an estimated 48 at the umbilical shoulder.

SAM PCZ 19461 (ex D.2580) is a water-worn internal mould with 44 ribs at the ventrolateral shoulder of the outer whorl. It appears to be an incomplete macroconch, septate to 180 mm in diameter. The better-preserved inner whorls have a few weak umbilical bulges. The dimensions are:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19461 costal	161.0 (100)	– (–)	56.4 (35.0)	–	63.2 (39.3)



Text-fig. 25. *Rhytidoceras elegans* van Hoepen, 1931 from KwaZulu-Natal, South Africa; SAM PCZ 19134 (ex D.2386), the holotype of *Drepanoceras rudis* van Hoepen, 1931 (p. 47, text-fig. 10; 1941, p. 84, text-fig. 49, pl. 17), from his bank 9 at locality 51.

The holotype of *Rhytidoceras rotundum*, SAM PCZ 19131 (ex D.2365) (Text-fig. 17), has the following dimensions:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19131	134.0 (100)	48.6 (36.2)	53.5 (39.9)	0.91	47.2 (35.2)



Text-fig. 26. *Rhytidoceras elegans* van Hoepen, 1931 from Kwa-Zulu-Natal, South Africa; SAM PCZ 19133 (ex D.2384), the holotype of *Drepanoceras crassicosatum* van Hoepen, 1941 (p. 83, text-fig. 46, 48), from his bank 10 at locality 51.

Coiling is very evolute, the umbilicus of moderate depth, comprising 35.2% of the diameter, the umbilical wall broadly rounded and outward-inclined, merging with the broadly rounded umbilical shoulder. The whorl section is slightly compressed, with the greatest breadth below mid-flank, the flanks feebly convex, converging to broadly rounded ventrolateral shoulders and a broad venter with a strong siphonal keel. The ornament of the inner whorls is damaged, but coarse crowded primary ribs arise at the umbilical seam and strengthen into umbilical bullae that give rise to pairs of ribs, while additional ribs intercalate low on the flank or arise at the umbilical seam without developing into a clearly differentiated bulla. Some ribs bifurcate a second time on the flanks, producing a complex pattern of crowded recti- to rursiradiate ribs, with two umbilical swellings. Twenty six to twenty seven ribs arise at the umbilical seam of the outer whorl, and sweep forwards across the umbilical wall. Some but not all develop umbilical bullae. The bullae generally give rise to a pair of ribs, or a single rib. The ribs may bifurcate low on the flanks, or on the mid-to outer flank to give a total of 48 crowded ribs at the ventrolateral shoulder. The ribs are straight and recti- to rursiradiate on the flanks, and flex forwards to become feebly concave

on the outer flanks and ventrolateral shoulders. They project forwards and decline across the venter, forming an obtuse chevron, separated from the strong siphonal keel by a smooth zone. There are at least 12 rows of spiral grooves and ridges on the flanks and ventrolateral shoulders.

SAM PCZ 19092 (ex D.2366) (Text-fig. 21U) is the original of van Hoepen (1941, text-fig. 21), a very damaged individual with the inner whorls well-preserved to a diameter 57.3 mm. The crowded ribbing is as in the holotype, with five umbilical swellings per whorl.

SAM PCZ 19128 (ex D.2366) (Text-fig. 18) from bed 9, was mentioned by van Hoepen (1931, p. 46; 1941, p. 69) as the paratype 217 mm in diameter. The dimensions are:

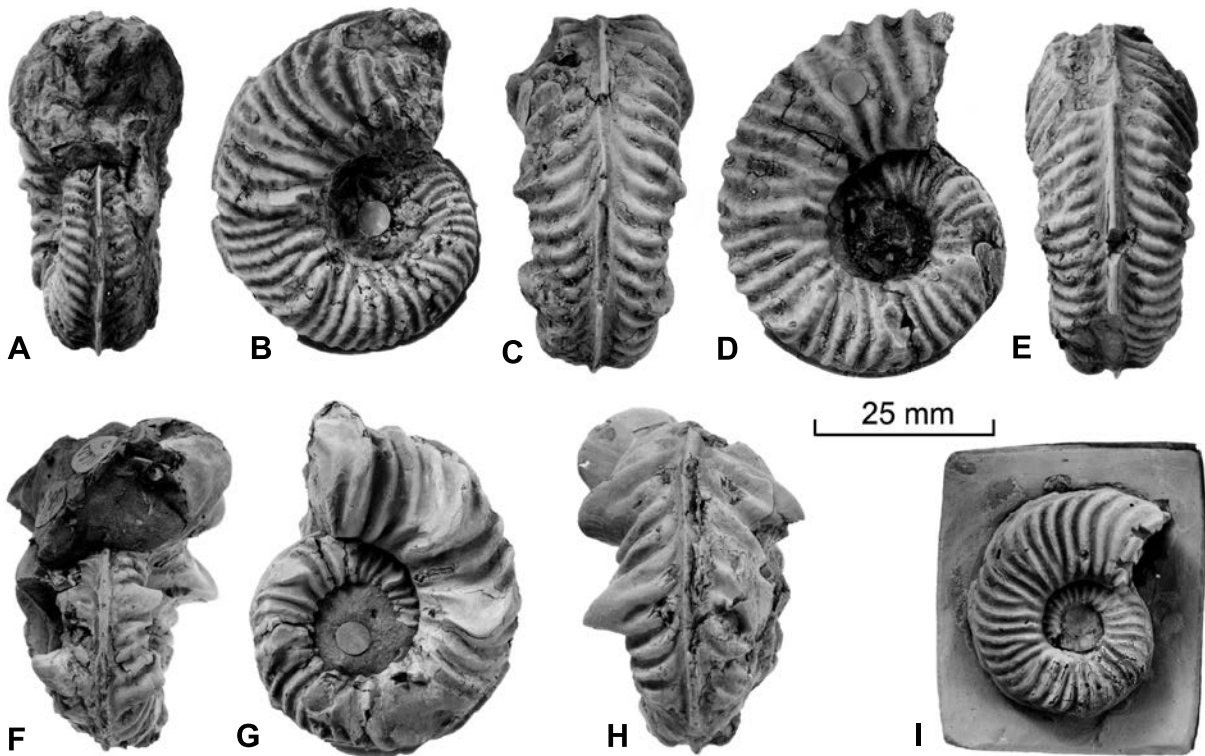
	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19128	217.0 (100)	53.5 (24.7)	70.0 (32.3)	0.76	97.0 (44.7)

The specimen is interpreted as a near-complete adult macroconch; it retains original shell, and the position of the last septum cannot be established. There are 18 ribs on the umbilical wall of the adapertural half of the outer whorl. Initially they give rise bullae from which pairs of ribs arise, but over the adapertural 90° sector, there is a transition to progressively weakening single ribs, the bullae crowding.

The holotype of *Rhytidoceras crassicosatum*, SAM PCZ 19130 (ex D.500) (Text-fig. 19) is a macroconch. The dimensions at the end of the body chamber, excluding the rostrum, are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19130 costal	195.0 (100)	51.5 (26.4)	62.4 (32.0)	0.83	93.8 (48.1)
at	170.0 (100)	52.1 (30.6)	54.3 ()	0.96	73.7 (43.4)

Coiling is very evolute, with a low expansion rate, the broad, shallow umbilicus comprising 48.1% of the diameter at the apertural margin. The low umbilical wall is flattened, the umbilical shoulder broadly rounded. There are an estimated 26 ribs on the umbilical wall of the penultimate whorl. They pass straight up the wall and strengthen into bullae, perched on the umbilical shoulder. These give rise to pairs of ribs, recti- to feebly rursiradiate, and passing straight across the flanks, where they are coarse and crowded, numbering an estimated 52 at the point where they disappear below the umbilical seam of the outer whorl. Ornament is comparable on the outer whorl, with 12 ribs on the umbilical wall of the adapical half whorl. They strengthen into well-developed umbilical bullae that give rise to pairs of coarse



Text-fig. 27. Selected representatives of the Mojsisovicsiinae Hyatt, 1903 and Pervinquierinae Spath, 1926 from the Upper Albian Gault Clay of Folkestone, Kent, UK. A–E – *Rhytidoceras elegans* van Hoepen, 1931. A–C – BMNH C.37893, the holotype of *Dipoloceras pseudaoon* Spath, 1931 (p. 373, pl. 34, fig. 3); D, E – BMNH C.37134, the original of Spath (1931, p. 368, pl. 35, fig. 6), described by as a passage form to *Dipoloceras pseudaoon*. F–H – *Dipoloceras cristatum* (Brongniart, 1822), BMNH C.77788 (ex 37891c), the original of Spath (1931, pl. 32, fig. 1). I – *Dipoloceras rectangularis* Spath, 1931, the paralectotype BMNH C.7726 (ex C.793 m), the original of Spath (1931, pl. 32, fig. 19).

straight recti- to feebly rursiradiate ribs that develop into incipient ventral bullae and pass straight across the venter, the rib terminations separated from the coarse siphonal keel by a narrow smooth zone. There are occasional short intercalatories and single long bullate ribs. Spiral ridges are well-developed. The body chamber extends to 120°, and shows a change in ornament from ribs that arise in pairs from umbilical bullae to alternating long and short ribs, the last six ribs crowding and weakening. The final sector of the shell, immediately preceding the apertural margin, is ornamented by crowded biconcave growth lines and striae on the flanks that parallel the apertural margin. The ventral part of the apertural margin is projected forwards as a long rostrum that extends for a further 80°, the final part curving back to within 8 mm of the venter of the adapertural part of the outer whorl.

SAM PCZ 19088 (ex D.2361) (Text-fig. 16) is a paratype of *Rhytidoceras elegans*, the original of van Hoepen (1931, text-fig. 7); it was assigned to *Rhytidoceras crassicoatum* by van Hoepen in 1941 (p. 67); see below.

Of specimens referred to *Rhytidoceras crassicoatum* by van Hoepen in 1941, SAM PCZ 19090 (ex D.2361) is a near complete macroconch 235 mm in diameter; SAM PCZ 19088 (ex D.2361) (Text-fig. 16) is 118.7 mm in diameter, with 22 umbilical bullae and 48 ribs at the ventrolateral shoulder; there are prominent umbilical bulges at the adapertural end of the penultimate whorl; and SAM PCZ 19086 (ex D.573) is a fragment lacking umbilical bullae.

The holotype of *Rhytidoceras megara* originally catalogued by van Hoepen (1941, p. 72, text-figs 24, 27) as D.2368, has not been traced; it is a densely ribbed variant, a nucleus 59 mm in diameter, from bank 9. A second specimen 45 mm in diameter was illustrated as his text-figs 25, 26. His text-fig. 28 is based on an unspecified individual. SAM PCZ 21624 (ex D.2369) (Text-fig. 21Q, R) consists of two fragments with relatively coarse ribbing and a well-developed lateral bulge in each fragment.

Selected specimens assigned to '*Drepanoceras undatum*' by van Hoepen have the following dimensions:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19135 costal	228.0 (100)	55.0 (24.1)	77.8 (34.1)	0.71	95.0 (41.7)
SAM PCZ 19110 costal	245.0 (100)	59.7 (24.4)	82.8 (33.8)	0.72	101.9 (41.6)
costal at	215.0 (100)	51.6 (25.7)	72.5 (33.7)	0.71	90.0 (41.9)

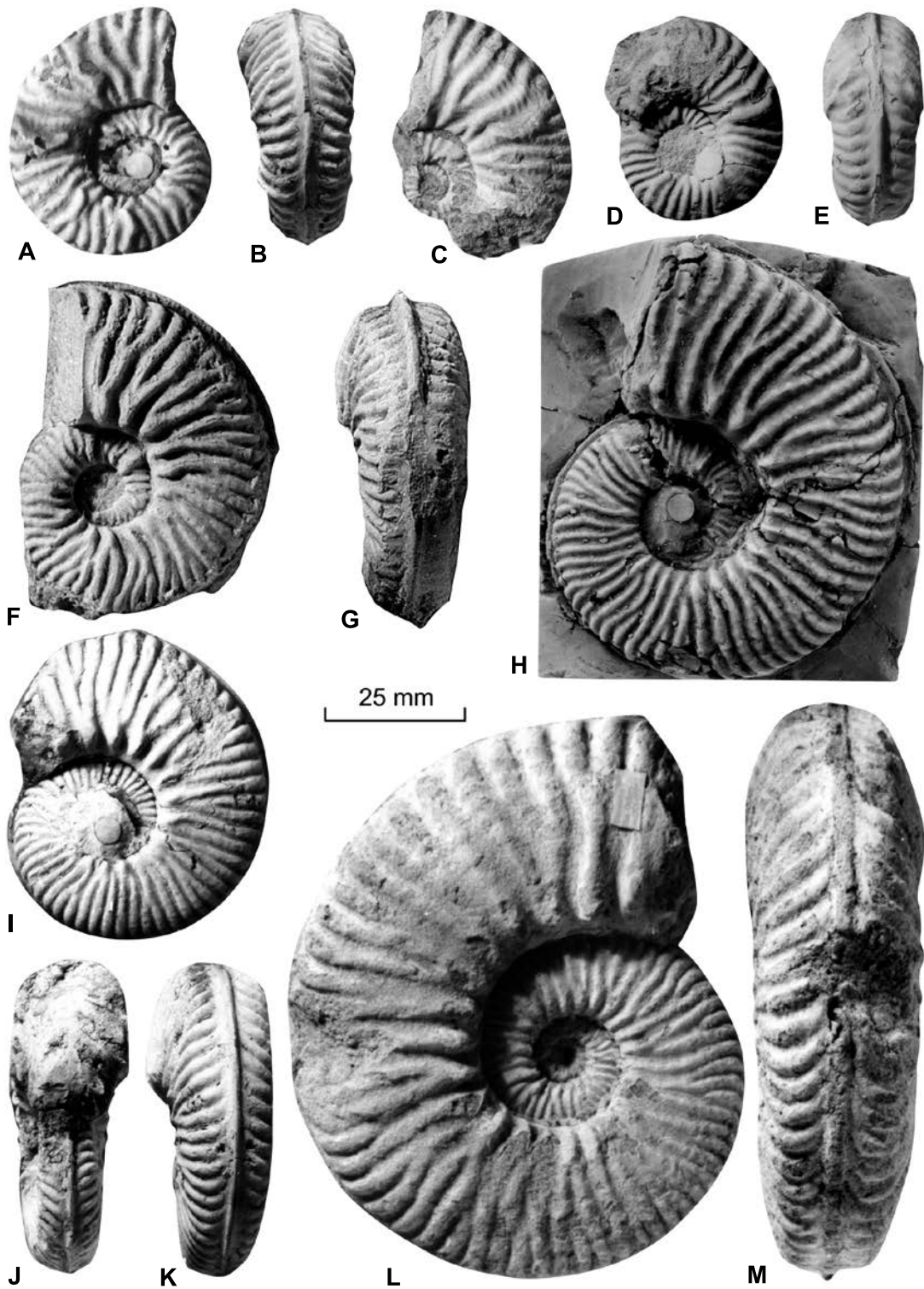
The holotype of *Rhytidoceras undatum*, SAM PCZ 19135 (ex D.2382) (Text-fig. 22), is an internal mould of an incomplete macroconch with a 120° sector of body chamber, retaining traces of original shell material. Coiling is very evolute, with 29% of the previous whorl covered, the broad, shallow umbilicus comprising 41.7% of the diameter, the low umbilical wall feebly convex and merging with the broadly rounded umbilical shoulder. The intercostal whorl section is compressed trapezoidal, with the greatest breadth low on the flanks, the flanks flattened and convergent, the ventrolateral shoulders broadly rounded, the venter broad and flat, with a strong siphonal keel. There are 24 crowded narrow prorsiradiate primary ribs on the umbilical wall of the penultimate whorl that develop into sharp elongated bullae on the umbilical shoulder. These give rise to pairs of ribs or, occasionally, a single rib; some ribs bifurcate on the outer flank to give a total of 64 ribs at the point where the flanks are concealed by the umbilical seam of the outer whorl. The ribs are straight and recti- to feebly prorsiradiate on the inner flank, flexing back and concave on the outer flank. There are 26 ribs on the umbilical wall of the outer whorl and 52 at the ventrolateral shoulder. The ribs are weak on the umbilical wall, but strengthen into elongate umbilical bullae. These give rise to predominantly pairs of ribs, some of which bifurcate on the outer flank, where additional ribs intercalate. The ribs are rectiradiate on the phragmocone, but become progressively more markedly rursiradiate on the body chamber. They are straight on the inner flank and feebly concave on the outer flank and ventrolateral shoulder, the concavity becoming more marked on the adapical part of the body chamber. The ribs form an obtuse chevron on the venter, with a smooth zone separating the rib terminations from the strong siphonal keel. Spiral ridges, inconspicuous on the inner whorls, become increasingly conspicuous on the outer whorl; 10 or 11 in number, they strengthen progressively from the umbilical shoulder to the ventrolateral shoulder. Those on the venter are weaker and more closely spaced than those on the flanks. SAM PCZ 19482 (ex D.584) (Text-fig. 24) is a complete micrococh 152 mm in diameter. Very water-worn, the last seven ribs are all single primaries that are weaker and crowded

with weakened umbilical bullae compared to those on the earlier parts of the body chamber, and much more markedly projected forwards, suggesting the presence of a long apertural rostrum. SAM PCZ 19110 (ex D.2383) (Text-fig. 23) is one of the specimens mentioned by van Hoepen in 1941 (p. 83), an incomplete macroconch 245 mm in diameter, retaining a 180° sector of body chamber; there are 28 primary ribs on the umbilical wall and 59 at the ventrolateral shoulder of the outer whorl.

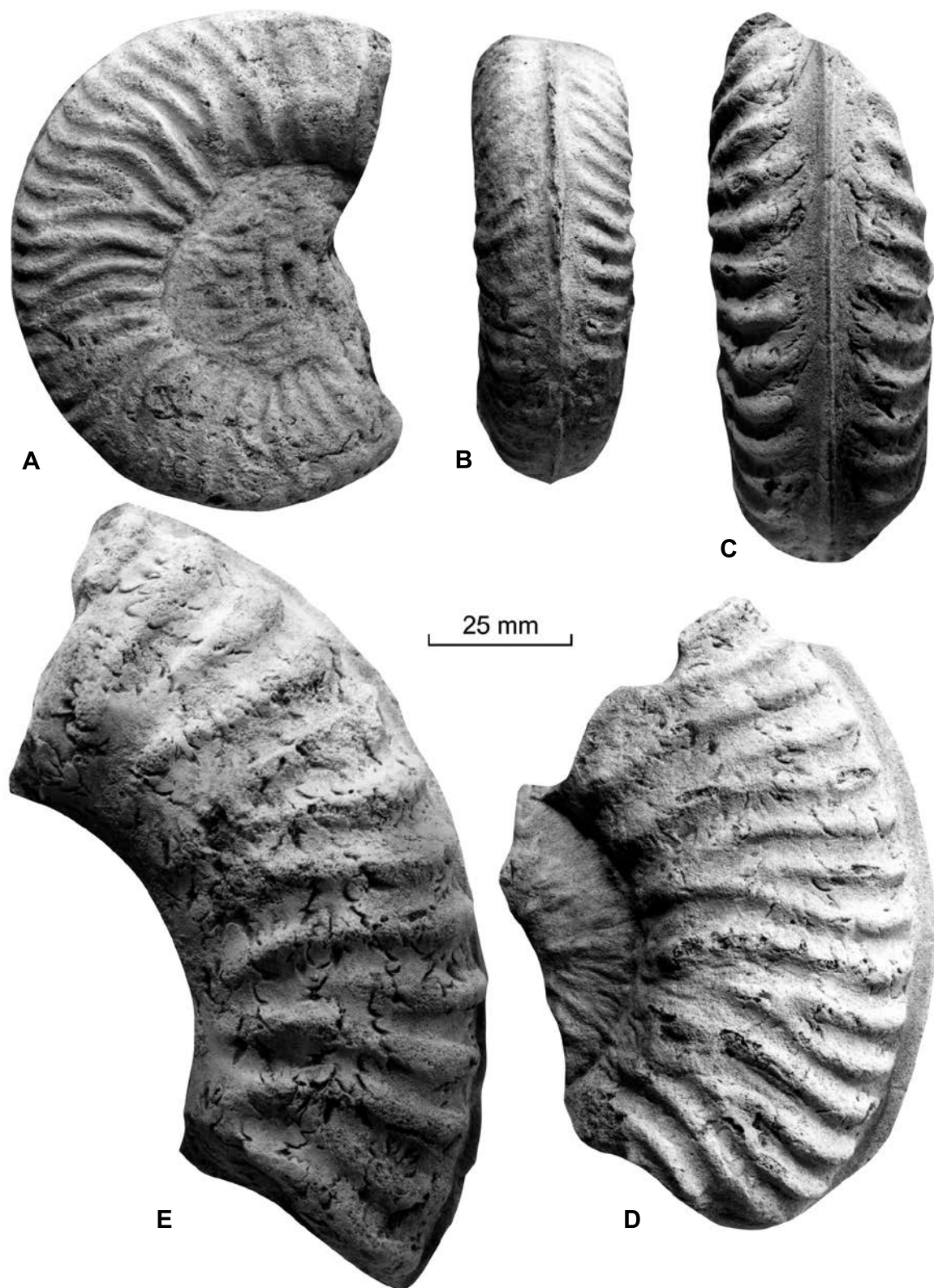
The holotype of *Drepanoceras rudis*, SAM PCZ 19134 (ex D.2386) (Text-fig. 25) has the following dimensions:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19134 costal	185.0 (100)	— (—)	61.2 (33.1)	— (—)	79.4 (42.9)
at	165.0 (100)	46.8 (28.4)	56.8 (34.4)	0.82	67.4 (40.8)

It is a microconch, septate to a diameter of 120 mm, and retaining extensive traces of shell material. The style of ornament is as in specimens van Hoepen assigned to *Drepanoceras undatum*, but coarser. There are 23 primary ribs on the umbilical wall of the penultimate whorl that develop into strong bullae, perched on the umbilical shoulder. These give rise to single ribs or pairs of ribs, with some ribs branching on the flanks, and occasional intercalated ribs to give a total of 47 crowded ribs at the umbilical seam of the succeeding whorl. The ribs are straight and recti- to rursiradiate on the inner flanks. There are 29 primary ribs on the umbilical wall of the outer whorl that strengthen into strong umbilical bullae; the pattern of ribbing on the phragmocone and adapical part of the body chamber are as on the penultimate whorl; there are well-developed spiral ridges. The last few ribs are all single primaries, weakening progressively towards the adult aperture, part of which is preserved; it is preceded by a short sector of shell that is ornamented by growth lines and striae only. Paratype SAM PCZ 19109 (ex D.2387) is the 247 mm diameter specimen mentioned by van Hoepen (1931, p. 49; 1941, p. 84, text-fig. 50). It is a complete macroconch with 27 umbilical bullae on the penultimate whorl and 47 ribs at the umbilical seam of the succeeding whorl. There are 32 umbilical bullae and 47 ribs at the ventrolateral shoulder of the outer whorl. The last 11 ribs of the body chamber are all primaries on which the umbilical bullae weaken progressively and are lost. The ventrolateral rib strength diminishes, the growth lines projecting strongly forwards, indicating the development of a long ventral rostrum. The surface of the shell immediately preceding the aperture



Text-fig. 28. *Rhytidoceras elegans* van Hoepen, 1931 from the Gault Clay at Folkestone, Kent, UK (A–C, H–K) and the Mzinene Formation of KwaZulu-Natal, South Africa (D–G, L, M). A, B – BMNH C.77786 (ex 37875b), the original of *Dipoloceras pseudoaon* of Spath (1931, pl. 34, fig. 2); C – OUMNH KX.11777a; D, E – OUMNH KX.11789, both from bed 6 at locality 51; F, G – SAM PCZ 19189 (ex D.500), the holotype of *Ricnoceras pandai* van Hoepen, 1941 (p. 59, text-figs 4, 5), from his bank 9 at locality 51; H – BMNH C.12486, the original of *Dipoloceras pseudoaon* var. *moniliformis* of Spath (1931, p. 373, pl. 32, fig. 10); I–K – BMNH 39666, the original of *Dipoloceras pseudoaon* of Spath (1931, pl. 32, fig. 10); L, M – OUMNH KX.11850, from bed 7 at locality 51.



Text-fig. 29. *Rhytidoceras elegans* van Hoepen, 1931 from the lower Upper Albian of Andranofotsy, Madagascar. A–E – *Dipoloceras* (?*Rhytidoceras*) *trifurcatum* Collignon, 1951; A, B – the holotype, EMP 1530, the original of Collignon (1951, pl. 4, fig. 2); C, D – EMP 1524, the original of Collignon (1951, pl. 4, fig. 3); E – EMP 1512, the original of Collignon (1951, pl. 4, fig. 4).

is ornamented by prominent growth lines and striae. Of the other examples referred to *undatum* by van Hoepen (1941, p. 85), SAM PCZ 19096 (ex D.2387) is a worn juvenile 140 mm in diameter. SAM PCZ 19097 (ex D.2387) is a 120° fragment of phragmocone with a maximum preserved whorl height of 53 mm and 14 rows of prominent spiral ridges. SAM PCZ 19187 (ex D.2387) is a worn, incomplete individual 125 mm in diameter. SAM PCZ 19108 (ex D.2387) is a 120° sector of body chamber with apertural modifications; the maximum preserved whorl height is 64 mm.

Dimensions of specimens assigned to *Drepanoceras crassicostatum* by van Hoepen are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19098 costal	44.2 (100)	17.5 (39.6)	18.7 (42.3)	0.94	15.6 (35.3)
SAM PCZ 19133 costal	103.6 (100)	34.7 (33.5)	41.2 (39.8)	0.84	36.5 (35.2)

SAM PCZ 19098 (van Hoepen 1941, text-fig. 47; Text-fig. 21P) is a damaged juvenile retaining extensive traces of recrystallized shell. The costal whorl section is slightly compressed rectangular to feebly trapezoidal, with the greatest breadth at the umbilical bullae. Primary ribs arise at the umbilical seam, sweep forwards across the umbilical wall and develop into small, sharp bullae, approximately 20 per whorl, perched on the umbilical shoulder. The bullae give rise to a pair of ribs or a single rib, and ribs may branch low on the flanks or intercalate. The ribs are crowded, straight, recti- to feebly rursiradiate on the inner to middle flanks, flexing forwards, strengthening, and concave on the outer flanks and venter, where they form an obtuse chevron, the rib terminations separated from the strong siphonal keel by a narrow smooth zone. The holotype, SAM PCZ 19133 (ex D.2384) (Text-fig. 26) is a phragmocone with traces of original shell material, preserved complete to a diameter of 103.6 mm, with parts of a further 60° whorl sector. Coiling is very evolute, with 28% of the previous whorl covered, the umbilicus broad and shallow, the low umbilical wall feebly convex and outward-inclined, the umbilical shoulder broadly rounded. The whorl section is slightly compressed trapezoidal, with the greatest breadth at the umbilical bullae in costal section. There are 21 ribs on the umbilical wall of the penultimate whorl. They sweep forwards and strengthen into small sharp bullae, perched on the umbilical shoulder. These give rise to pairs of ribs that are straight and recti- to feebly rursiradiate to the point where they disappear below the umbilical seam of the outer whorl. There are 21–22 ribs on the umbilical wall of the outer whorl. They

strengthen into sharp bullae, perched on the umbilical shoulder to inner flank region, and strengthen markedly over the apertural 90° whorl sector. The bullae give rise to pairs of ribs; there are occasional single or non-bullate primary ribs plus intercalated ribs to give a total of 44 ribs approximately at the ventrolateral shoulder. The ribs are recti- to feebly rursiradiate, straight on the inner flanks, then flexing forwards, strengthening and slightly concave on the ventrolateral shoulders and venter, where they form an obtuse chevron, the rib terminations separated from the strong siphonal keel by a narrow smooth zone. There are at least nine rows of spiral ridges on the flanks and ventrolateral shoulders.

The holotype of *Ricnoceras pandai*, SAM PCZ 19189 (ex D.500) (Text-fig. 28F, G) is a wholly septate juvenile retaining traces of shell material. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19189	58.9 (100)	23.9 (40.6)	26.3 (44.7)	0.91	16.8 (28.5)

Coiling is evolute, the umbilicus small, comprising 28.5% of the diameter, of moderate depth, with a subvertical umbilical wall and broadly rounded umbilical shoulder. The whorl section is compressed-rectangular to feebly trapezoidal, with the greatest breadth close to mid-flank. Twenty primary ribs arise at the umbilical seam, pass straight up the umbilical wall and strengthen into small bullae, perched on the umbilical shoulder. These give rise to a pair of ribs or a single rib that bifurcates low on the flank, while additional ribs may bifurcate at mid-flank. There are single long intercalated ribs, to give a total of 50 ribs at the ventrolateral shoulder. The ribs are straight and recti- to feebly rursiradiate on the innermost flank, convex on the outer flank on the adapical part of the outer whorl then convex, before reverting to feebly concave on the apertural 60° sector. There is a strong siphonal keel. Growth lines sweep forwards, indicating the presence of a long ventral rostrum at the aperture. There is a prominent umbilical bulge on the apertural part of the penultimate whorl. Delicate spiral ridges are present on the outer flanks and ventrolateral shoulders.

DISCUSSION: The occurrence of all of van Hoepen's taxa described above in a narrow interval at a single locality (Table 1), plus the presence of passage forms leads us to conclude that only a single variable species is present, the variation no greater than in other Cretaceous ammonites.

The holotype of *Dipoloceras pseudoaon* Spath, 1931 (p. 373, pl. 34, fig. 3), BMNH C.34881 (Text-



fig. 27A–C) has well-developed spiral ridges, and is a *Rhytidoceras*, differing in no significant respects from juveniles in the present collection such as OUMNH KX.11774, 11784, and 11913 (Text-fig. 21B–D, G, H). *Dipoloceras pseudodaon moniliformis* Spath, 1931, (p. 373, pl. 32, fig. 10; Text-fig. 28H) finds a close match in the inner whorls of the holotype of *Drepanoceras undatum*, SAM PCZ 19135 (ex D.584) (Text-fig. 24), and OUMNH KX.11850 (Text-fig. 28L, M).

*Dipoloceras* (?*Rhytidoceras*) *trifurcatum* Collignon, 1951 (p. 27, pl. 4, figs 2–4; text-figs 10, 11; 1963, p. 147, pl. 300, fig. 1300; Text-fig. 29A–E) was compared to *Rhytidoceras elegans*. “Pour trouver un style de côtes absolument semblable, il faut comparer ces ammonites à *Rhytidoceras elegans*...qui m’en paraît extrêmement voisine, avec cette différence que cette dernière espèce ne comporte pas des côtes trifurquées, que les côtes ne se projetant pas en avant au voisinage de la carène et que l’ombilic est sensiblement plus étroit.” Occasional trifurcating ribs are seen in some of the present material, as with the penultimate whorl of SAM PCZ 19131 (ex D.2365; Text-fig. 17), an individual with a comparable ventral ornament to the original of Collignon’s (1951, pl. 4, fig. 3; Text-fig. 29A, B). We regard it as a synonym.

OCCURRENCE: As for genus.

## DISCUSSION

Determining the order of appearance of relevant Mojsisovicsiinae and Pervinquierinae across the Lower/Middle Albian boundary in KwaZulu-Natal depends almost entirely on the interpretation of the section described by van Hoepen (1941) as east of the drift on the Umsinene, where he meticulously recorded his material from a series of sixteen banks, summarised in his text-fig. 55, and set out here in Table 1. As noted above, this locality corresponds to locality 51 of Kennedy and Klinger (1975, p. 288, text-fig. 4), where we logged an 18 m section in the river bed. Our bed 1 yielded an upper Lower Albian fauna with *Mojsisovicsia ventanillensis* (Gabb, 1877) (Kennedy and Klinger 2012, p. 3, text-figs 1–3), *Dipoloceroïdes semicornutum* (Spath, 1931) (Kennedy and Klinger 2012, text-fig. 5), *Falloticerias proteus* (d’Orbigny, 1842) (Kennedy and Klinger 2012, text-fig. 8), and *Oxytropidoceras* (*Manuaniceras*) *manuanense* (Spath, 1921) (Kennedy and Klinger 2011, p. 72, text-figs 1m, n; 4a–e; 5a, c–e; 6–9; 10a, b, 11). This is an upper Lower Albian association on the basis of the presence of *Dipoloceroïdes* and *Falloticerias* species. Three metres higher in the

section, bed 3 yielded the first *Dipoloceras cristatum*, which extends to bed 7. *Rhytidoceras* first appears in numbers in bed 5. This sequence of first occurrences corresponds to that documented by van Hoepen (1941, text-fig. 55), with the notable exception of his record of *Dipoloceras* from his bank 11. The holotype and only known specimen of *Diplasioceras fallax* came from van Hoepen’s bank 7, the lowest bank he recognised, suggesting it to be from low in the Middle Albian sequence. *Euspectroceras newtoni* was originally described from Catuane in southern Mozambique. In KwaZulu-Natal, the holotype of *Euspectroceras strigilis* came from the “Ridge West of Ridge which is West of Beacon 624.” This locality is at a horizon higher than anything exposed on the Mzinene at locality 51, but still within the range of *Hysterocheras*, whilst *Euspectroceras newtoni* co-occurs with *Hysterocheras* at sections near Ndumu. The common features of *Rhytidoceras*, *Diplasioceras* and *Euspectroceras*, described above, notably spiral ridges, are shared with the well-established *Pervinquieria* (*Deiradoceras*) – *P. (Pervinquieria)* – *P. (Subschloenbachia)* lineage (Latil 1995; Kennedy and Latil 2007), and we accordingly refer these genera to the Subfamily Pervinquierinae. We also refer to the Pervinquierinae four taxa not present in KwaZulu-Natal: *Elobiceras* (*Elobiceras*), *Elobiceras* (*Craginites*), *Prohysterocheras*, and *Mortoniceratoides*. *Elobiceras* is known from Angola, Nigeria, Gabon, Brazil and Texas. The diverse *E. (Elobiceras)* species described from near Hahna in Angola by Haas (1942) came from what he interpreted to have been a single block (Haas 1942, p. 3), associated with both *Dipoloceras*, *Hysterocheras*, and *Prohysterocheras* species, indicating a lower Upper Albian horizon (the association of *Elobiceras* and *Hysterocheras* is also noted by Tavares *et al.* 2007, p. 148). *Elobiceras* (*Craginites*) is known only from Texas, where it occurs at the base of the Duck Creek Limestone, also in association with *Hysterocheras*, and is, again, lower Upper Albian (Gale and Kennedy 2020). *Prohysterocheras* species are known from Angola, southern England and Texas. The genus first appears in the lower Upper Albian, but appears to range higher than the other taxa discussed here according to Tavares *et al.* (2007, p. 147). *Mortoniceratoides* is known from the lower Middle Albian of southern England and Ecuador (Bulot *et al.* 2005).

Cooper (2018a) placed *Elobiceras*, *Craginites*, and *Prohysterocheras* in the Subfamily Arestoceratinae van Hoepen, 1942, expanding van Hoepen’s (1942, p. 117) original diagnosis of the subfamily to include “spiral ornament variably developed, generally weak or absent” (Cooper 2018a, p. 304). However, spiral ornament is at

Species	7	8	9	10	11	12	13	14	15	16
<i>Rhytidoceras elegans</i>		*	*	*						
<i>Rhytidoceras rotundum</i>			*	*						
<i>Rhytidoceras crassicosatum</i>			*	*						
<i>Rhytidoceras megara</i>			*	*						
<i>Drepanoceras undatum</i>			*	*						
<i>Drepanoceras rudis</i>			*							
<i>Drepanoceras crassicosatum</i>				*						
<i>Cechenoceras reversum</i>		*								
<i>Cechenoceras magnum</i>			*							
<i>Dipoloceras cristatum</i>					*					
<i>Ricnoceras pandai</i>			*							
<i>Deiradoceras preostratum</i>						*	*	*		
<i>Deiradoceras bispinosum</i>				*		*		*		
<i>Deiradoceras varinodosum</i>				*			*	*		
<i>Deiradoceras varicosatum</i>				*		*				
<i>Deiradoceras linguatum</i>								*		
<i>Mimoceras binodosum</i>				*						
<i>Mimoceras? obesum</i>							*			
<i>Pervinquieria fluctuato-costata</i>								*		
<i>Diplasioceras fallax</i>	*									
<i>Mimeloceras modestinodosum</i>									*	
	7	8	9	10	11	12	13	14	15	16

Table 1. Distribution of selected ammonites, based on his records, in van Hoepen's (1931, p. 45) banks at his "Oemsinene rivier oos van der drift" locality, corresponding to locality 51 of Kennedy and Klinger (1975, p. 288).

its maximum development within the Brancoceratidae in *Elobiceras* and *Craginites*. There are two possibilities: the spiral ridges in Brancoceratidae evolved only once, and characterise the Pervinquierinae only, in which case the Arestoceratinae as conceived by Cooper is polyphyletic. Alternatively, spiral ridges evolved at least twice in Brancoceratidae, and the Pervinquierinae as here conceived is polyphyletic.

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