

The ammonite subgenus *Pervinquieria* (*Deiradoceras*) van Hoepen, 1931 from the Upper Albian of KwaZulu-Natal, South Africa. Part I

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ABSTRACT:

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The cosmopolitan Late Albian ammonite subgenus *Pervinquieria* (*Deiradoceras*) van Hoepen, 1931, and its synonyms *Cechenoceras* van Hoepen, 1941 and *Mimeloceras* van Hoepen, 1944, originally based on material from northern KwaZulu-Natal, are reviewed. The type material of the type species, *Subschloenbachia pre-rostrata* Spath, 1921, is revised and reillustrated, as are its numerous synonyms.

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

INTRODUCTION

In this contribution we continue our revision of the ammonites described in E.C.N. van Hoepen's 'Die gekielde ammoniete van die Suid-Afrikaanse Gault' (1931–1951), dealing specifically with those that he assigned to *Deiradoceras* van Hoepen, 1931, which we treat as a subgenus of *Pervinquieria* Böhm, 1910. We regard *Cechenoceras* van Hoepen, 1941 (p. 61) and *Mimeloceras* van Hoepen, 1944 (p. 196; introduced as a *nomen novum* for *Mimoceras* van Hoepen, 1941, p. 85, *non* Hyatt, 1884) as synonyms of *Deiradoceras*, and will describe the species assigned to these genera by van Hoepen in a subsequent publication (Kennedy and Klinger 2023b)

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.
SAM: Natural History Collections Department, Iziko, South African Museum, Cape Town, South Africa.

FIELD LOCALITIES

Details of field localities can be found in Kennedy and Klinger (1975, 2023a).

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. 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 (1931–1951b), the latter being D numbers, are given in parentheses.

SYSTEMATIC PALAEOLOGY

Order Ammonoidea von Zittel, 1884

Suborder Ammonitina Hyatt, 1889

Superfamily Acanthoceratoidea von Zittel, 1884

Family Brancoceratidae Spath, 1934

Subfamily Pervinquieriinae Spath, 1926

Genus *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; *Styphloceras* van Hoepen, 1951b, p. 300; *Omocrateceras* van Hoepen, 1951b, p. 313; *Subpervinquieria* Mirzoyev, 1969, p. 46).

TYPE SPECIES: *Ammonites inflatus* J. Sowerby, 1817 (p. 170, pl. 178), by the original designation of Böhm (1910, p. 152).

DIAGNOSIS: Umbilical bullae give rise to single ribs or pairs of ribs; additional ribs intercalate. The ribs strengthen across the ventrolateral shoulder into a coarse, blunt, spatulate termination. There is a strong siphonal keel. The umbilical bullae may be accompanied by a single row of ventrolateral tubercles, a lateral row and a single row of ventrolateral tubercles, or a lateral, inner and outer ventrolateral row. Rows of spiral ridges are present on the flanks and ventrolateral shoulders. Adult apertures develop a rostrum, which may be recurved in a dorsal or ventral direction.

DISCUSSION: The subgenus *Pervinquieria* (*Pervinquieria*) is characterised by the presence of three rows of tubercles, umbilical, lateral and ventrolateral, in part or all of the ontogeny. It differs from the subgenus *Deiradoceras* and its synonyms (discussed further below), which are characterised by the presence of umbilical and ventrolateral rows of tubercles that are strongly developed in the later growth stages. The subgenus *Subschloenbachia* Spath, 1921 (type species: *Ammonites rostratus* J. Sowerby, 1817, p. 163, pl. 173, by original designation), of which

Durnovarites Spath, 1932 (p. 380) and *Reyericeras* Collignon, 1979 (p. 34) are synonyms, has four rows of tubercles in part or all of the ontogeny: umbilical, lateral, inner and outer ventrolateral (see discussion in Kennedy *et al.* 1998, p. 15).

OCCURRENCE: The genus first appears some way above the base of the Upper Albian, and extends to the top of the *Pervinquieria* (*Subschloenbachia*) *perinflata* Zone, i.e., upper Upper, but not uppermost, Albian. The geographical distribution extends from western Europe to Kazakhstan, Iran, north, east and west Africa, Madagascar, south India, Pakistan, Japan, the southern part of the United States Western Interior, Texas, Mexico and Venezuela.

Subgenus *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, p. 85, *non* Hyatt, 1884, p. 309)

TYPE SPECIES: *Subschloenbachia prerostrata* Spath, 1921 (p. 284, pl. 24, fig. 10), by the original designation of van Hoepen (1931, p. 52).

DIAGNOSIS: With umbilical and a single row of ventrolateral tubercles on the adult whorls.

DISCUSSION: A translation of van Hoepen's original diagnosis of *Deiradoceras* is as follows:

“Evolute ammonites with a square whorl section. Keel free, high. Umbilical wall oblique and high. Ribs already on early whorls coarse and forked. On later whorls they form coarse tubercles along the edge of the umbilical wall. Then the thickened parts of the ventral ends of the ribs also give rise to tubercles, and finally the tubercles of both rows acquire large dimensions. The early whorls are strongly convex; later the flanks become flatter. The ribs are initially convex, but after the appearance of the tubercles, they become concave edges that connect the tubercles or which run from a ventral tubercle and terminate at the umbilical edge. The ribs are often single on the body chambers of large individuals. The shell is ornamented spirally.

Differs from the former genera [= *Rhytidoceras* van Hoepen, 1931; *Drepanoceras* van Hoepen, 1931] and from *Inflatoceras* Stieler by its enormous formation of tubercles and from the former also by its whorl section and concave ribs.

Type: *Deiradoceras prerostratum* Spath sp.”

Wright (1996, p. L142) regarded *Drepanoceras* as a synonym of *Durnovarites*; we disagree and consider it as a separate and distinct genus, as discussed previously (Kennedy and Klinger 2023a). Wright also regarded *Mimoceras* van Hoepen, 1944 (p. 196, type species *Mimoceras binodosum* van Hoepen, 1941, p. 86, pl. 18, text-figs 51–53), introduced as a *nomen novum* for *Mimoceras* van Hoepen, 1941 (p. 85, *non* Hyatt, 1884, p. 309) as a synonym of *Deiradoceras*, a conclusion with which we agree. A translation of van Hoepen's original diagnosis of *Mimoceras* is as follows:

“Genus *Mimoceras* n. g.

Characteristics of the family [Drepanoceratidae]. Ribs rounded, and in the juvenile stages sickle-shaped curved; on the last whorl the ribs have a ventral tubercle on the [ventral] edge, which, with the umbilical tubercle, can become very large. The ribs then are concave on the flanks.

Type: *Mimoceras binodosum* n. sp.

Differs from *Deiradoceras* by its flat early whorls with umbilical tubercles on the edge of the vertical umbilical wall.”

The ontogenetic changes shown by adult *binodosum* correspond to those shown by the type species of *Deiradoceras*, with a sequence from ribs arising in pairs to single ribs, with strong umbilical and ventrolateral tubercles at both growth stages. The inner whorls of the type species of the two genera differ, but there are transitions between the two in species assigned to *Deiradoceras* by van Hoepen (1931), as with the inner whorls of *Deiradoceras varicostatum* van Hoepen, 1931 (p. 54, text-fig. 14; 1941, p. 77, pl. 13).

We also regard *Cechenoceras* van Hoepen, 1941 (p. 61; type species *Cechenoceras reversum* van Hoepen, 1941, p. 62, figs 9–12) as a synonym of *Deiradoceras*. A translation of van Hoepen's original diagnosis is as follows:

“Family Cechenoceratidae n. fam.

Keeled ammonites of the Gault of which the juvenile forms have inflated, rounded flanks and bear old apertures which, especially at mid-flank overlap on the preceding ribs. The flanks of very early stages can exhibit a slight flattening between the apertures.

Type: *Cechenoceras* n. g.

Also belonging to this group: *Rhytidoceras* v. Hp. and *Deiradoceras* v. Hp.

Genus: *Cechenoceras* n. g.

Characteristics of the family: The ribs of the juvenile and adult forms are sharp [acute], but they can exhibit a tendency towards rounding at the extreme ventral end. Flanks with spiral ornament.

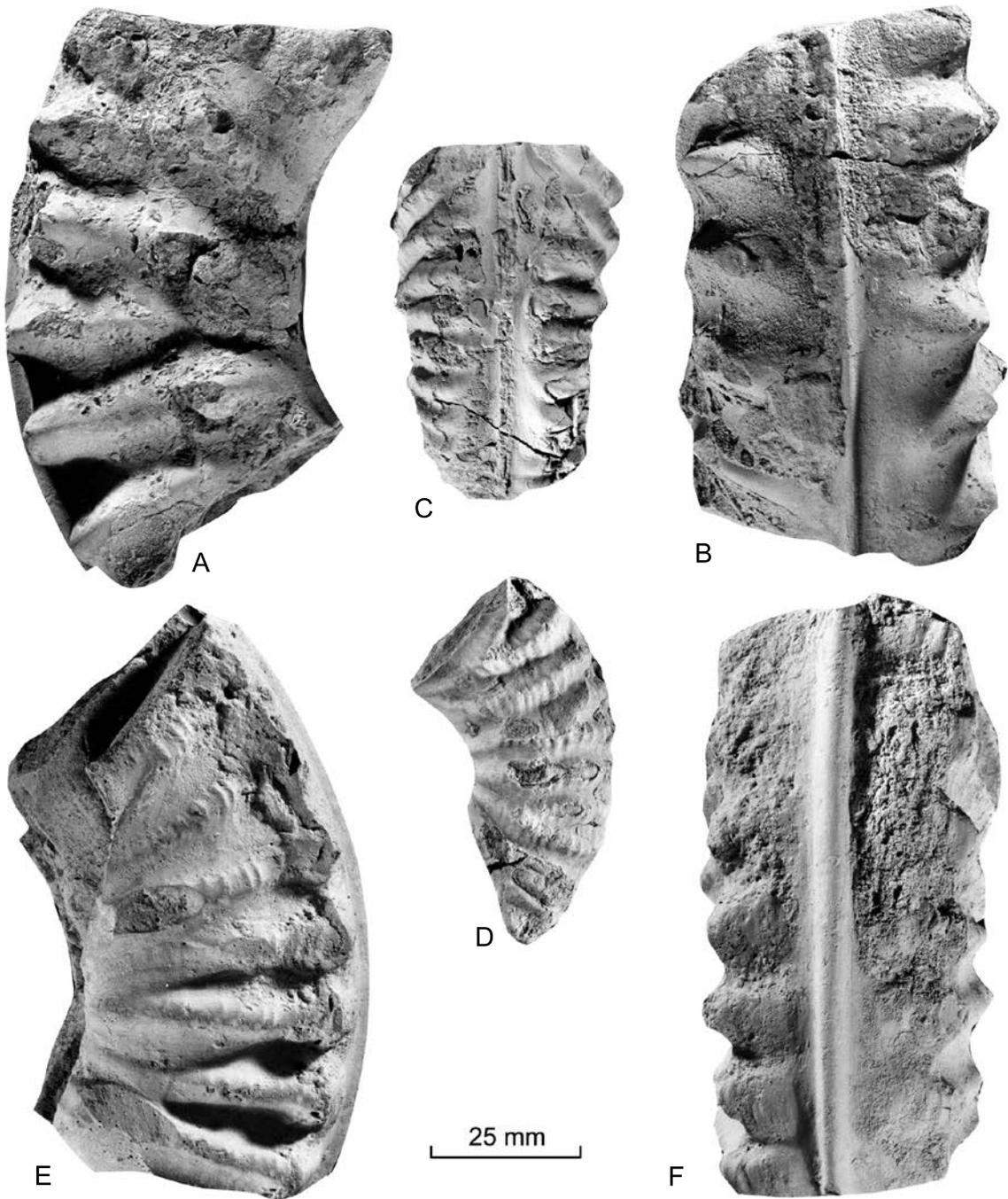
Type: *Cechenoceras reversum* n. sp.”

The holotype of the type species (van Hoepen 1941, p. 62, text-figs 9, 10; see also below), is a juvenile which differs from the inner whorls of *Pervinquieria* (*Deiradoceras*) *prerostrata* in having better-differentiated ventral tubercles. The adult assigned to *reversum* by van Hoepen (1941, text-fig. 12) shows a comparable adult ornament to adults he referred to *prerostrata*, with bituberculate ribs arising in pairs from umbilical bullae succeeded by single bituberculate ribs. Wright (1996, p. L140) regarded *Cechenoceras* as a synonym of *Dipoloceras sensu stricto*. The presence of spiral ridges and strong tubercles in adult *Cechenoceras* distinguishes the two and they belong to different subfamilies, as discussed previously (Kennedy and Klinger 2023a). What is of interest is the presence of flared flank ribs in juveniles of *Pervinquieria* (*Deiradoceras*) *prerostrata* and ‘*Dechenoceras*’ *reversum*, recalling ancestral *Rhytidoceras* (Kennedy and Klinger 2023a, text-fig. 21A–H).

OCCURRENCE: The subgenus first appears some way above the base of the Upper Albian, and extends to the middle of the substage. The geographical distribution extends from northern KwaZulu-Natal to Mozambique, Madagascar, Venezuela, Texas in the United States, Western Europe, Bulgaria, the Russian platform, North Africa, Egypt, Iran and Japan.

Pervinquieria (*Deiradoceras*) *prerostrata*
 (Spath, 1921)
 (Text-figs 1–14)

- 1921. *Subschloenbachia prerostrata* Spath, p. 284, pl. 24, fig. 10.
- 1921. *Subschloenbachia bispinosa* Spath, p. 285, pl. 24, fig. 9.
- 1921. *Subschloenbachia* cf. *trinodosa* Böse sp.; Spath, p. 285, pl. 25, fig. 4.
- 1931. *Deiradoceras bispinosum* Spath; van Hoepen, p. 54, text-fig. 12.
- 1931. *Deiradoceras varinodosum* van Hoepen, p. 54, text-fig. 13.
- 1931. *Deiradoceras varicostatum* van Hoepen, p. 54, text-fig. 14.
- 1936. *Mortoniceras* (*Deiradoceras*) *devonense* Spath; Venzo, p. 93 (35), pl. 9 (5), fig. 4; pl. 11 (7), fig. 14.
- 1941. *Deiradoceras bispinosum* Spath; van Hoepen, p. 75, pl. 12, text-figs 33–35.
- 1941. *Deiradoceras varinodosum* van Hoepen; van Hoepen, p. 76, figs 36, 37.
- 1941. *Deiradoceras varicostatum* van Hoepen; van Hoepen, p. 77, pl. 13, text-figs 38, 39.



Text-fig. 1. *Pervinqueria* (*Deiradoceras*) *prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa. A–D – SAM PCZ 4970, the holotype, the original of Spath (1921, p. 284, pl. 24, fig. 10), from the “Middle branch, Manuan Creek.” E, F – SAM PCZ 4972, the original of *Subschoenbachia trinodosa* Böse sp. of Spath (1921, p. 285, pl. 25, fig. 4), from the “South side of Manuan Creek Valley.”

1941. *Deiradoceras exilis* van Hoepen, p. 78, pl. 14; text-figs 40, 41.
 ?1941. *Deiradoceras linguatum* van Hoepen, p. 79, text-figs 42, 43.
 1950. *Deiradoceras besairiei* Collignon, p. 75, pl. 12 (3), figs 3, 4.

1950. *Deiradoceras* (*Mimoceras*?) *mokarahaense* Collignon, p. 77, pl. 12 (4), fig. 3; text-fig. 8.
 1963. *Mortoniceras* (*Deiradoceras*) *mokarahaense* Collignon; Collignon, p. 172, pl. 312, fig. 1319.
 1963. *Mortoniceras* (*Deiradoceras*) *besairiei* Collignon; Collignon, p. 172, pl. 312, fig. 1321.

2018. *Mortoniceras (Deiradoceras) besairiei* Collignon, 1963; Klein, pp. 129, 131 (with additional synonymy).
2018. *Mortoniceras (Deiradoceras) bispinosum* Spath, 1921; Klein, pp. 129, 132 (with additional synonymy).
2018. *Mortoniceras (Deiradoceras) exilis* van Hoepen, 1941; Klein, pp. 130, 134 (with additional synonymy).
- ?2018. *Mortoniceras (Deiradoceras) linguatum* van Hoepen, 1941; Klein, pp. 130, 134.
2018. *Mortoniceras (Deiradoceras) mokarahaense* Collignon, 1950; Klein, pp. 130, 135 (with additional synonymy).
2018. *Mortoniceras (Deiradoceras) prerostratum* (Spath, 1921); Klein, pp. 130, 135 (with synonymy).
2018. *Deiradoceras varinodosum* van Hoepen, 1931; Klein, pp. 130, 136 (with additional synonymy).
2018. *Deiradoceras varicostatum* van Hoepen, 1931; Klein, pp. 130, 136.
2018. *Deiradoceras prerostratum* (Spath); Cooper, p. 103, pl. 26e.

NAME OF THE SPECIES: We believe *Subschloenbachia prerostrata* Spath, 1921 (p. 284, pl. 24, fig. 10) and *Subschloenbachia bispinosa* Spath, 1921 (p. 285,

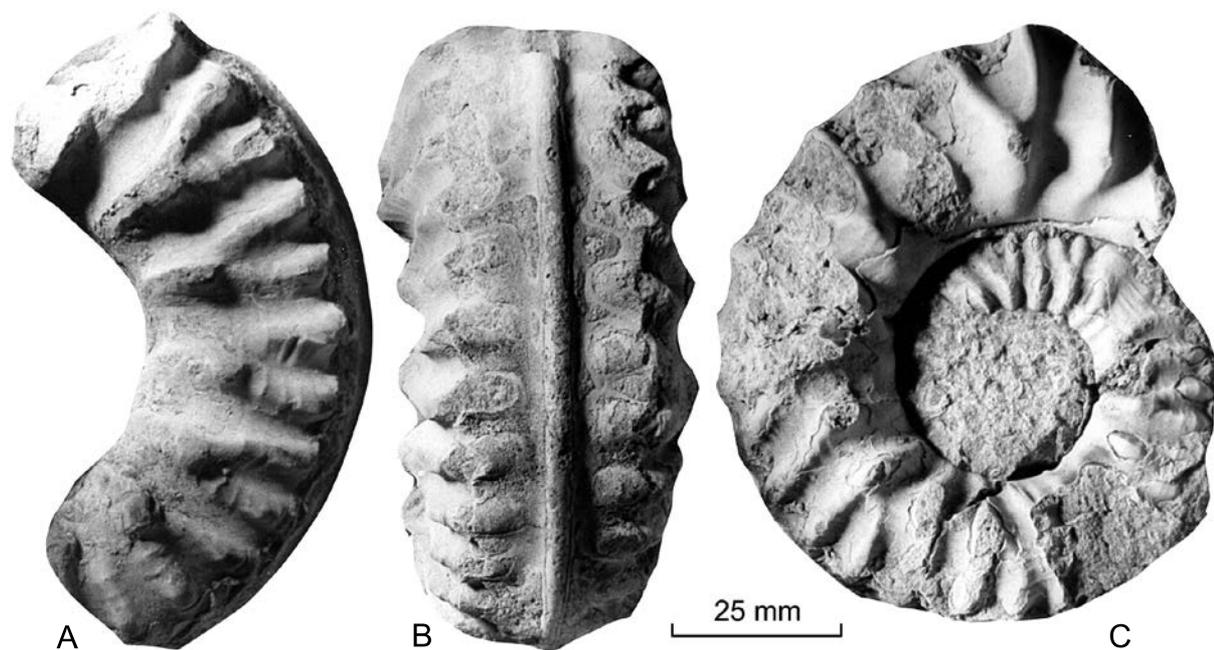
pl. 24, fig. 9) to be conspecific, and as first revising authors select the name *prerostrata* for the species.

TYPE: The holotype, by monotypy, is SAM PCZ 4970 (Text-fig. 1A–D), the original of Spath 1921 (p. 284, pl. 24, fig. 10), from the middle branch of the Manuan (Munywana) Creek in KwaZulu-Natal, South Africa.

DESCRIPTION: The early whorls are ornamented by crowded recti- to rursiradiate ribs that arise singly or in pairs from well-developed umbilicolateral bullae and may bifurcate on the outer flanks and ventrolateral shoulders, where poorly differentiated ventrolateral tubercles may develop. The second growth stage is characterised by ribs that strengthen into umbilicolateral bullae that give rise to pairs of ribs, the adapical of each pair strongly rursiradiate, the adapertural one less so or even feebly prorsiradiate; there are occasional single ribs. The third growth stage, which extends over most of the adult body chamber, is ornamented by predominantly single rursiradiate primary ribs with progressively weakening umbilical and ventrolateral tubercles in the proximity of the adult aperture, while there may be occasional short intercalated ribs.

Species	10	11	12	13	14	15	WW	ERW	W	624
<i>Deiradoceras prerostratum</i>			*	*	*					
<i>Deiradoceras bispinosum</i>	*									
<i>Deiradoceras varinodosum</i>	*			*	*					
<i>Deiradoceras varicostatum</i>	*		*							
<i>Deiradoceras linguatum</i>					*					
<i>Mimoceras binodosum</i>	*									
<i>Mimoceras obesum</i>			*?	*?			*			
<i>Mimeloceras modestinodosum</i>						*				
<i>Mimeloceras macrondosum</i>							*			
<i>Mimeloceras strigosum</i>							*			
<i>Mimeloceras latiumblicatum</i>							*			
<i>Mimeloceras agrestis</i>								*		
<i>Mimeloceras auctum</i>								*		
<i>Ophryoceras jugosum</i>									*	
<i>Ophryoceras costatum</i>					*			*		
<i>Ophryoceras tenuicostatum</i>									*	
<i>Ophryoceras crassum</i>									*	
<i>Ophryoceras spinosum</i>									*	
<i>Ophryoceras annalida</i>									*	
<i>Ophryoceras liberta</i>									*	
<i>Ophryoceras opimum</i>									*	
<i>Ophryoceras tereticostatum</i>									*	
<i>Ophryoceras obsoletum</i>									*	
<i>Ophryoceras undosum</i>										

Table 1. Distribution of species of *Pervinqueria (Deiradoceras)* described by van Hoepen (1931) from his banks at locality 51 of Kennedy and Klinger (1975).



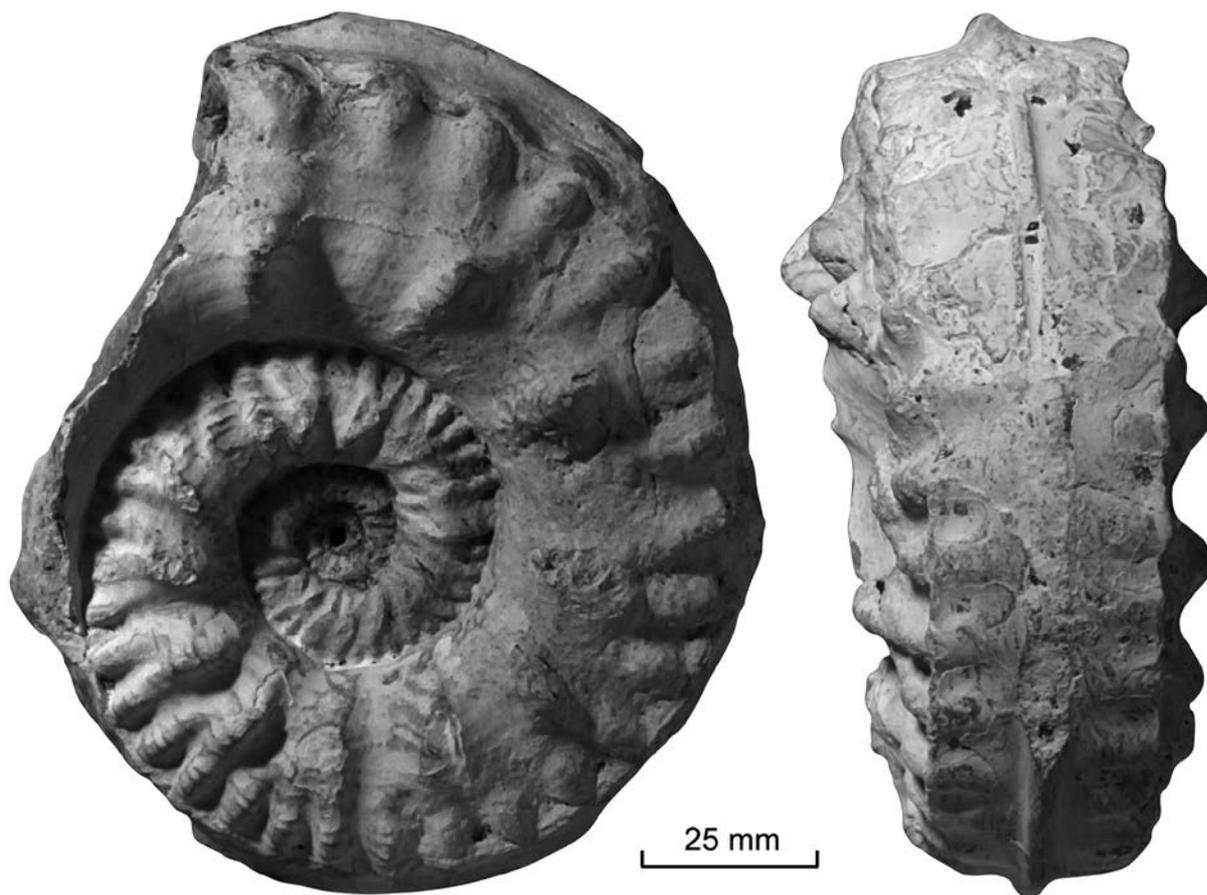
Text-fig. 2. *Pervinquieria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa. A, B – SAM PCZ 19194 (ex D.2371), mentioned by van Hoepen (1942, p. 75), from what translates as “the hill that is west of the cliff, which (in turn) is again west of beacon no. 624.” C – SAM PCZ 19193 (ex D.2370), from his bank 14 at locality 51.

Both coarsely and more delicately ornamented co-occurring variants are recognised at locality 51, and were assigned to five species by van Hoepen (see Table 1).

The holotype of *prerostrata* is a coarsely ornamented individual, as is the holotype of *bispinosa*. The holotype of *linguata* is a very coarsely ornamented nucleus. The holotypes of *Pervinquieria (Deiradoceras) varicostata*, and *varinodosa* are interpreted as more delicately ribbed individuals. They are described below.

The holotype of *Pervinquieria (Deiradoceras) prerostrata* (Text-fig. 1A–D) consists of fragments of two successive phragmocone whorls, the larger interpreted as part of the outer whorl of an adult. Coiling is very evolute. The smaller fragment (Text-fig. 1C, D) has a maximum preserved length of 62.1 mm. The intercostal whorl section is depressed, with a whorl breadth to height ratio of 1.3, with convex flanks and a broad, flattened venter with a strong siphonal keel. The costal whorl section is polygonal and very depressed, with the greatest breadth at a strong umbilicolateral tubercle, and a whorl breadth to height ratio of 1.47. The umbilicus is deep, with a strongly convex wall. Coarse ribs arise on the umbilical wall, and strengthen across the umbilical shoulder, developing into a weak to strong umbilicolateral tubercle. These

give rise to a single rib or a pair of coarse, straight ribs. The ribs strengthen across the ventrolateral shoulder, and bear feebly differentiated ventrolateral tubercles. One single rib bifurcates at the level of the feebly differentiated ventrolateral tubercles. Both the internal mould and areas of recrystallised shell bear well-developed spiral ridges. The larger fragment (Text-fig. 1A, B) is septate and has a maximum preserved length of 95 mm and a maximum preserved whorl height of 51 mm. The intercostal whorl section is rounded-trapezoidal and slightly depressed. The costal whorl section is depressed, quadrate, with the greatest breadth at the umbilical tubercles; the whorl breadth to height ratio is 1.2 approximately. Parts of six ribs are preserved at the ventrolateral shoulder. Four low, broad ribs arise at the umbilical seam, strengthen across the umbilical wall and shoulder, developing into strong, subspinose umbilical tubercles. These give rise to one or two strong, coarse, recti- to feebly prorsiradiate ribs that weaken at mid-flank, then strengthen on the outer flank and develop into a strong inner ventrolateral tubercle that extends near-transverse across the ventrolateral shoulder, declines on the venter, leaving a smooth zone on either side of the strong siphonal keel. The outer whorl fragment retains traces of recrystallised shell; there are faint traces of spiral ridges.



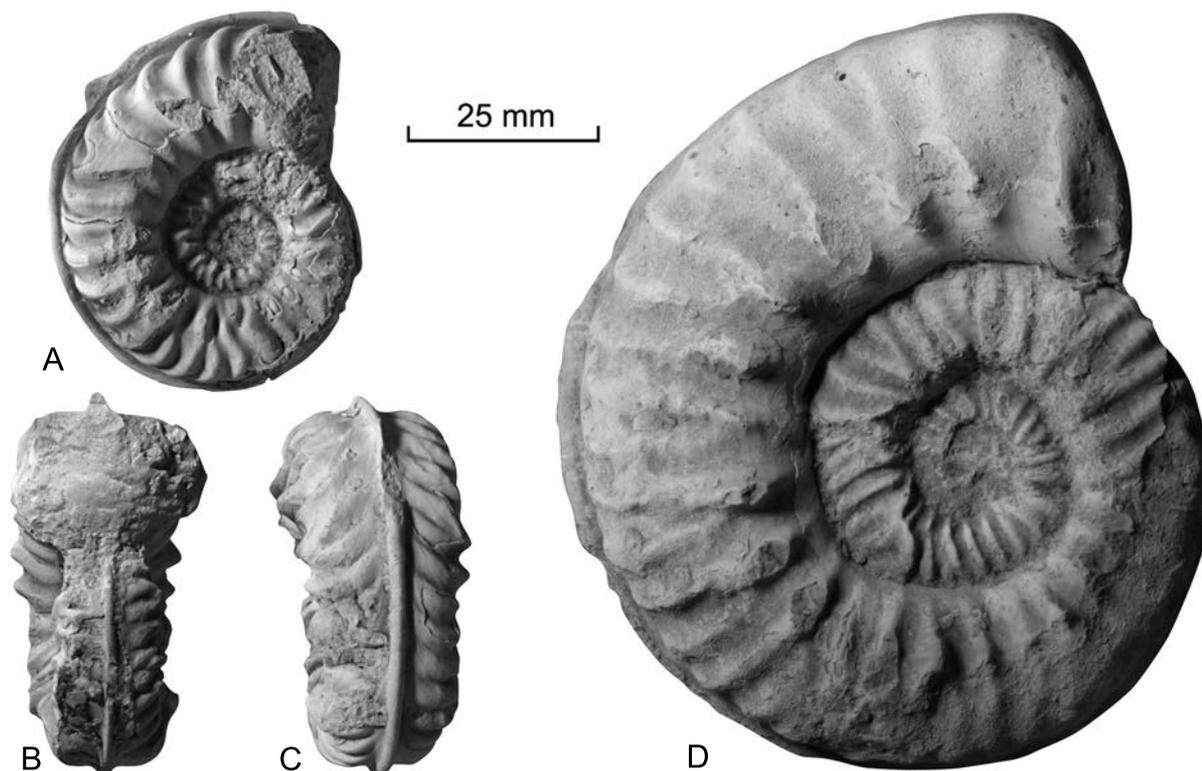
Text-fig. 3. *Pervinqueria* (*Deiradoceras*) *prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19111 (ex D.1265), the original of van Hoepen (1941, p. 73, text-figs 29–32), from his bank 14 at locality 51.

The original of *Subschloenbachia* cf. *trinodosa* Böse sp. of Spath (1921, p. 285) is SAM PCZ 4972 (Text-fig. 1E, F), from the “south side of the Manuan Creek Valley,” interpreted as a fragment of *prerostrata* body chamber. It is a well-preserved fragment, 95 mm long, with a maximum preserved whorl height of 49 mm and a costal whorl breadth to height ratio of 1. Coiling appears to have been very evolute, the whorls expanding slowly, with an umbilicus of moderate depth. The intercostal whorl section is polygonal, with the greatest breadth at mid-flank and a whorl breadth to height ratio of 0.9, with the greatest breadth just outside the umbilical shoulder, the flanks broadly rounded, the outer flanks converging, the venter feebly convex, with a strong siphonal keel. Six ribs are preserved on the fragment, and are straight, recti- to feebly prorsiradiate, coarse and strong, and alternately long and short. The long, primary ribs arise on the umbilical wall, strengthen across the umbilical shoulder and develop into a strong um-

bicolateral bulla on the lower third of the flanks. The intercalated ribs arise low on the flank. All ribs strengthen on the outer third of the flank. They strengthen further, and develop into a coarse, blunt ventrolateral tubercle that extends across the venter as a broad, transverse rib that effaces before reaching the siphonal keel. Spiral ridges are present on all of the ribs, and are weak on the inner flank, strengthening on the tubercles and venter.

Descriptions of specimens referred to *Pervinqueria* (*Deiradoceras*) *prerostrata* by van Hoepen are as follows.

SAM PCZ 19194 (ex D.2371) (Text-fig. 2A, B), the original of van Hoepen (1941, p. 75), from a locality that translates as, “on the hill that is west of the cliff, which (in turn) is again west of Beacon no. 624”. It is a 120° sector of phragmocone of a coarsely ornamented individual with a massive depressed trapezoidal-polygonal whorl section with a costal whorl breadth to height ratio of 1.23 and a maximum preserved whorl



Text-fig. 4. *Pervinquieria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa. A–C – SAM PCZ 19470 (ex D.2567), mentioned by van Hoepen (1946a, p. 199), from his banks 11–12 at locality 51; D – SAM PCZ 19468 (ex D.2571), mentioned by van Hoepen (1946a, p. 199; “another fairly good small specimen”), from the “Ridge West of the Ridge which is West of Beacon 624.”

height of 39.5 mm. There are seven primary ribs on the fragment which strengthen into massive subspinose umbilical bullae that give rise to pairs of ribs, the adapical one rursiradiate, the adapertural one rectiradiate. There are strong spiral ridges.

SAM PCZ 19112 (ex D.2370), mentioned by van Hoepen (1941, p. 75), from his bank 13 at locality 51, is a 120° sector of the penultimate whorl and body chamber, from close to the aperture of a macroconch. The maximum preserved whorl height is 78.5 mm.

SAM PCZ 19111 (ex D.1265), from bank 14 at locality 51, is the original of van Hoepen (1941, p. 72, text-figs 29, 31). The costal dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19111	124.3 (100)	58.6 (47.1)	46.6 (37.5)	1.26	47.3 (38.1)

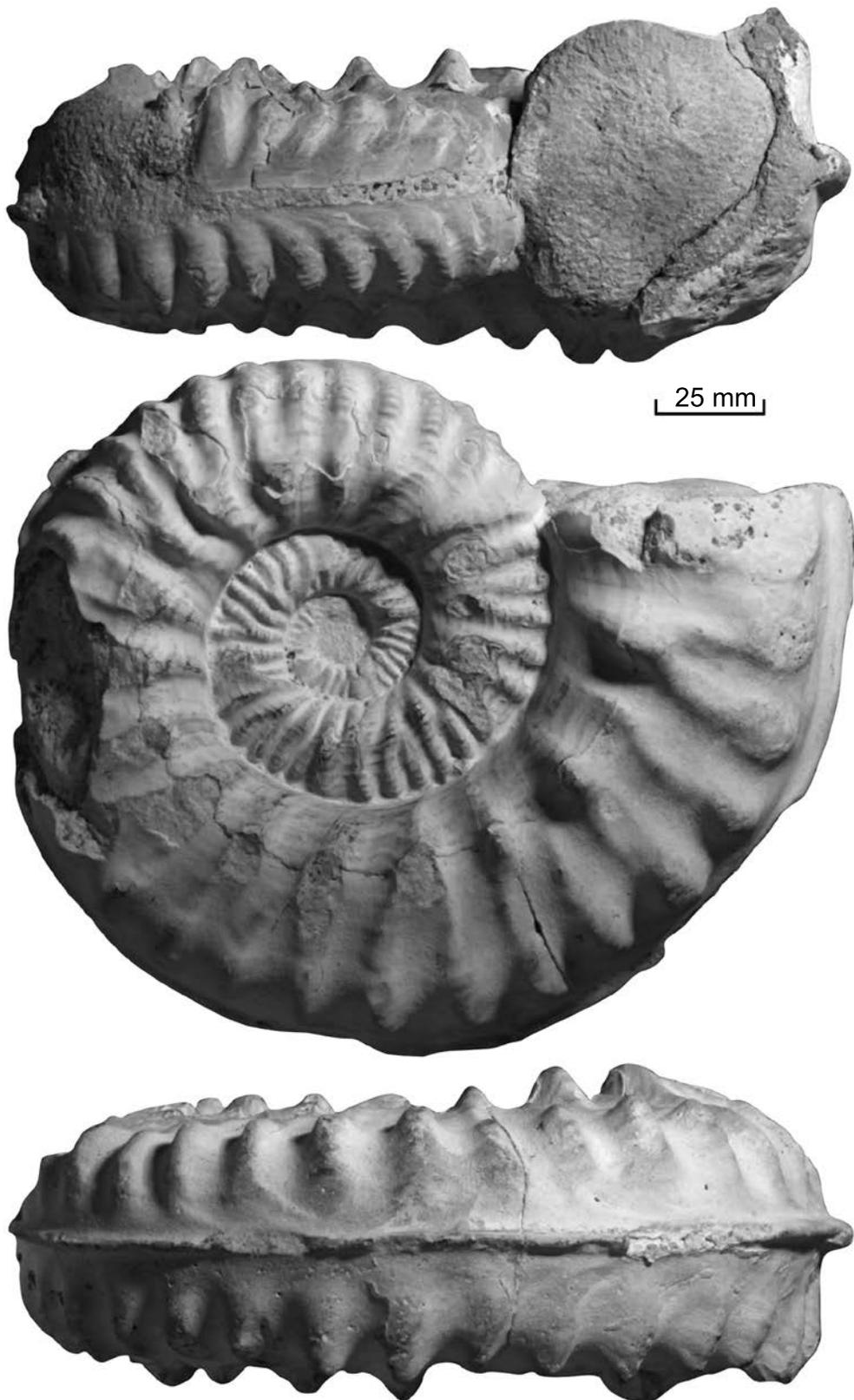
This specimen (Text-fig. 3) is a phragmocone, the inner whorls with strong umbilical bullae and crowded bifurcating ribs. On the outer whorl, twelve subspinose umbilical bullae increase rapidly in size, and are massive at the greatest preserved diameter. They give rise to pairs of ribs in a distinctive

Y-shaped branching pattern, the adapical rib rursiradiate, the adapertural one recti- to feebly rursiradiate. There are also occasional intercalated ribs, to give a total of 30–32 at the ventrolateral shoulder, where they link to progressively strengthening ventrolateral tubercles. Spiral ridges are well-developed.

SAM PCZ 19468 (ex D.2571; Text-fig. 4D), mentioned by van Hoepen (1946a, p. 199), is from the “Ridge west of the ridge which is West of Beacon 624”. It is a worn juvenile, 85.4 mm in diameter, a densely ribbed variant with 25 umbilical bullae on the outer whorl and an estimated 40+ ribs at the ventrolateral shoulder. The ornament of the inner whorls is transitional to that developed in the holotype of *Pervinquieria (Deiradoceras) varinodosa*.

SAM PCZ 19469 (ex D.2571) was mentioned by van Hoepen (1946a, p. 199); it is from his Beacon 624/locality 54. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
costal	146.5 (100)	(–)	54.2 (37.0)	–	56.3 (38.4)
intercostal		46.2 (31.5)	54.2 (37.0)	0.85	



Text-fig. 5. *Pervinquieria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19471 (ex D.2567), mentioned by van Hoepen (1946a, p. 199, “a rather large specimen”), from the “Ridge West of the Ridge which is West of Beacon 624.”



Text-fig. 6. *Pervinqueria* (*Deiradoceras*) *prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19477 (formerly 4993), the holotype of *Subschloenbachia bispinosa* Spath, 1921 (p. 285, pl. 24, fig. 9), from the “Middle Branch of the Manuan Creek.”

There are 19 primary ribs on the penultimate whorl, twelve of which have well-developed umbilical bullae, 10 ribs at the umbilical shoulder of the adapical half of the outer whorl, and 15 at the ventrolateral shoulder.

SAM PCZ 19470 (*ex* D.2567; Text-fig. 4A–C) was mentioned by van Hoepen (1946a, p. 199), and is from banks 11–12 at locality 51. It is a very well-preserved juvenile retaining original shell material. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19470	44.0 (100)	(–)	17.0 (38.6)		17.5 (39.8)

Coiling is very evolute, the umbilicus of moderate depth, with a feebly convex, outward-inclined umbilical wall and broadly rounded umbilical shoulder. The whorl section is depressed, with the greatest breadth at the umbilical bullae. Twenty-two to twenty-four low, broad ribs arise at the umbilical seam

and strengthen across the umbilical wall, the majority developing into coarse umbilical bullae. These give rise to pairs of ribs or a single rib. Of the paired ribs, the adapical one is rursiradiate, the adapertural one rectiradiate. The ribs are distinctly concave on the ventrolateral shoulders and venter, and form a very obtuse chevron, with a feebly differentiated ventrolateral tubercle. Spiral ridges are feebly developed.

The holotype of *Subschloenbachia bispinosa* Spath, 1921 (p. 285, pl. 24, fig. 9; Text-fig. 6) is SAM PCZ 19477 (formerly 4993), from the “Middle Branch, Manuan [Munywana] Creek.” As noted by Spath, the specimen is embedded in a calcareous sandstone concretion, planed off by erosion to expose a median section. A detached fragment of the phragmocone is 148 mm in diameter. The umbilicus is broad and shallow, comprising 48% of the diameter, the low umbilical wall outwardly inclined. The intercostal whorl breadth to height ratio is an estimated 1.1; the costal ratio an estimated 1.2. The greatest breadth is low on the flanks, the inner flanks being broadly convex, the outer flanks flattened and convergent, the ventrolateral shoulders broadly rounded. The ornament of the penultimate whorl is badly damaged. That of the antepenultimate whorl consists of coarse bullae that give rise to pairs of coarse, straight, prorsiradiate ribs, with a single rib intercalated between successive pairs. The outer half whorl bears ten ribs, the adapical part being damaged; there were an estimated 12–14 ribs per half whorl. Primary ribs arise at the umbilical seam and are broad, coarse and straight, strengthening into well-developed umbilical bullae from which low, broad, recti- to feebly rursiradiate ribs arise, either singly or in pairs, extending across the flanks and linking to a strong subspinose ventrolateral tubercle; the costal whorl section is concave between the tubercles. The ventrolateral tubercles give rise to strong, broad, transverse ribs with a distinctive triangular shape in ventral view, weakening and effacing across the venter to leave a smooth zone on either side of the coarse siphonal keel. Intercalated ribs arise around mid-flank, and strengthen to match the primaries in their ventral development. There are feeble indications of spiral grooves and ridges on the adapical part of the outer whorl fragment.

SAM PCZ 19480 (formerly 4971) is a worn fragment of body chamber 145 mm long that may belong here.

The original of van Hoepen (1931, p. 54, text-fig. 12; 1941, p. 75, pl. 12) was not seen. It is an adult 207 mm in diameter, with coarse ribs predominantly arising in pairs on the penultimate whorl and adapical



Text-fig. 7. *Pervinqueria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19115 (ex D.2374), from van Hoepen's bank 12 at locality 51.

part of the outer whorl, succeeded by an ornament of predominantly single primary ribs that weaken markedly prior to what is interpreted as the sinuous apertural margin, which retains a part of a ventral rostrum.

The following specimens from locality 51 were assigned to *Deiradoceras bispinosum* by van Hoepen:

- SAM PCZ 19195 (ex D.2372), SAM PCZ 19113 (ex D.2372), SAM PCZ 19198 (ex D.2372), in 1941 (possibly the original of text-fig. 33, a whorl section), and SAM PCZ 19473 (ex D.2372), in 1941, all mentioned in 1941 (p. 75), from bank 10.
- SAM PCZ 19196 (ex D.2372) and SAM PCZ 19472

(ex D.2373), mentioned in 1941 (p. 75), from banks 11–12;

- SAM PCZ 19115 (ex D.2374) and SAM PCZ 19382 (ex D.2373) mentioned in 1941 (p. 75), from bank 12;
- SAM PCZ 19114 (ex D.2375), mentioned in 1941 (p. 7), from bank 14.

Amongst these, the inner whorls are well represented by SAM PCZ 19115 (Text-fig. 7), a phragmocone 90 mm in diameter and a 120° sector of body chamber. Coiling is evolute, the umbilicus comprising 43.3% of the diameter, of moderate depth, with a feebly convex subvertical umbilical wall, the umbilical shoulder broadly rounded. On the adapertural half



Text-fig. 8. *Pervinqueria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19198 (ex D.2372), from van Hoepen's bank 10 at locality 51. The specimen may be the original of van Hoepen (1941, text-fig. 43; a whorl section), assigned by him to *Deiradoceras bispinosum*.

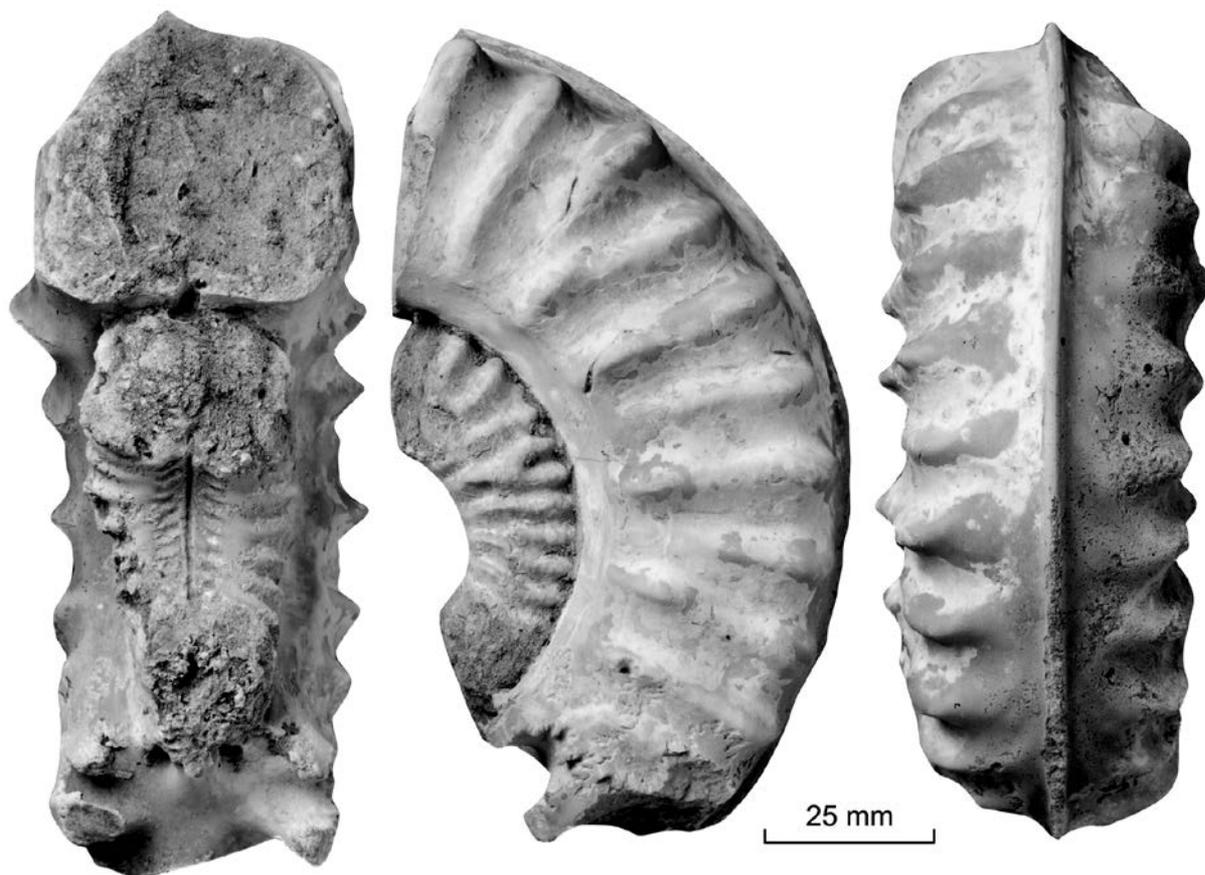
whorl, eight low, broad primary ribs arise at the umbilical seam, sweep back across the umbilical wall, and develop into very strong bullae, perched on the umbilical shoulder. These give rise to coarse, straight recti- to feebly rursiradiate ribs, with occasional intercalated ribs arising low on the flanks to give a total of 17 ribs at the ventrolateral shoulder per half whorl. All of the ribs bear strong feebly clavate ventrolateral tubercles. Spiral ridges are well developed, and most conspicuous on the outermost flanks and ventrolateral shoulders. The 120° sector of body chamber appears to be that of a microconch. It has a rectangular to feebly trapezoidal whorl section with an intercostal whorl breadth to height ratio of 0.83 and a costal whorl breadth to height ratio of 0.96. The greatest breadth is at the umbilical bullae, the costal whorl section concave between umbilical and ventrolateral tubercles. There are 11 ribs on the fragment: six arise from

coarse subspinose umbilical bullae and are broad and coarse, recti- to feebly rursiradiate, and linking to strong conical to feebly clavate ventrolateral tubercles. Other ribs arise at the umbilical shoulder without developing a bulla, or low on the flanks, strengthening to match the bullate ribs on outer flanks and ventrolateral shoulders. The ventrolateral clavi give rise to a broad rib that expands, declines, and effaces before reaching the strong siphonal keel. The body chamber has spiral ridges well-developed on the outer flank and ventrolateral shoulder, notably on the adapical face of the ribs and ventrolateral clavi.

SAM PCZ 19113 consists of a 90° sector of body chamber and the adapertural three camerae. An internal mould, there are 11 ribs, coarse, distant, and alternately coarsely and weakly bullate. The tuberculation weakens at the adapertural end of the fragment, which is interpreted to be that of microconch.

SAM PCZ 19198 (ex D.2372; Text-fig. 8) may be the original of van Hoepen (1941, text-fig. 43), a whorl section. It has a maximum preserved diameter of 245 mm and is interpreted as a near-complete macroconch. The very wide umbilicus comprises 43.7% of the diameter, and is of moderate depth, the umbilical wall convex and inclined outwards, the umbilical shoulder broadly rounded. The penultimate half whorl bears very strong subspinose umbilical bullae that give rise to pairs of coarse radial recti- to feebly rursiradiate ribs, with occasional single non-bullate, long ribs to give a total of 16 ribs at the umbilical seam of the outer whorl. All ribs bear strong conical to feebly clavate ventrolateral tubercles, housed in notches in the umbilical wall of the body chamber. The body chamber has a maximum preserved whorl height of 79.2 mm, the intercostal whorl breadth to height ratio 0.72, rounded-trapezoidal, with broadly rounded inner flanks, flattened convergent outer flanks, broadly rounded ventrolateral shoulders and a broad, feebly convex venter. The costal whorl breadth to height ratio is 0.98, the greatest breadth at the umbilical bullae. Eighteen ribs are preserved on the body chamber. Primary ribs with strong subspinose umbilical bullae alternate regularly with non-bullate ribs that arise on the umbilical wall or low on the flank. They efface markedly at mid-flank, then strengthen into conical ventrolateral tubercles. Rectiradiate over most of the body chamber, the last few ribs show a weakening of the tubercles, crowd and become feebly flexuous and feebly rursiradiate, suggesting the proximity of the adult body chamber. Being an internal mould, there is no trace of spiral ridges.

BMNH C. 52980 (ex L.F. Spath Collection; Text-fig. 9) from the Mzinene River is a particularly



Text-fig. 9. *Pervinquieria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; BMNH C.52980 (ex L.F. Spath Collection) from the lower reaches of the Mzinene River; the preservation suggests locality 51.

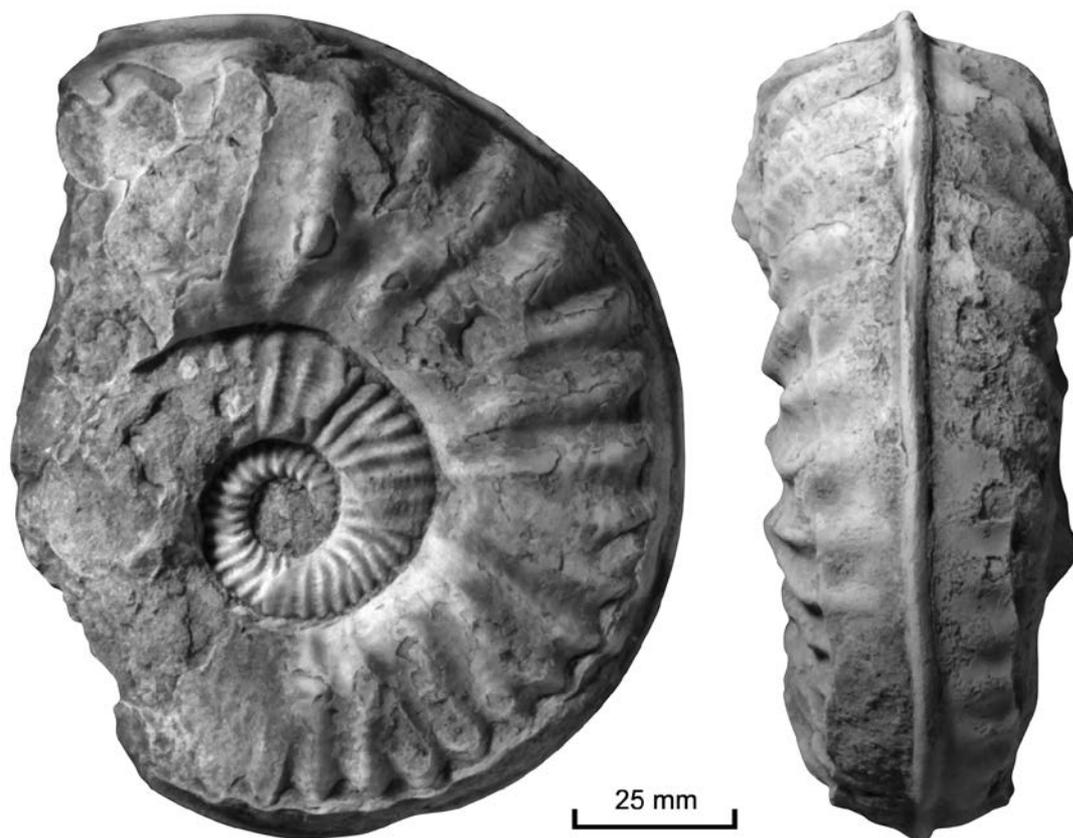
well-preserved internal mould of a 120° sector of the penultimate whorl and the adapical part of what is interpreted as the body chamber of an adult micro-conch, with a maximum preserved whorl height of 47 mm.

The holotype of *Pervinquieria (Deiradoceras) varinodosa* is SAM PCZ 19132 (ex D.1264), the original of van Hoepen (1931, text-fig. 13, refigured in 1941 as his text-figs 36, 37). It is from bed 14 at locality 51. Van Hoepen (1931) mentioned four further examples, from banks 10, 13 and 14 at locality 51. The holotype (Text-fig. 10) is a damaged phragmocone with a maximum preserved diameter of 132 mm. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19132	132.0 (100)	47.0 (35.6)	51.1 (38.7)	0.92	48.6 (36.8)

It retains some original shell material, and there are indications of the former presence of a further whorl. Coiling is very evolute, with 28% of the previ-

ous whorl covered, the umbilicus broad, of moderate depth, with a convex, outwardly inclined wall and broadly rounded umbilical shoulder. The intercostal whorl breadth to height ratio is 0.97, the whorl section rounded-hexagonal with the greatest breadth at the umbilical shoulder. The costal whorl section is depressed hexagonal, with the greatest breadth at the umbilical bullae. On the penultimate whorl, 26 coarse, crowded, rounded ribs arise at the umbilical seam and are feebly rursiradiate to rectiradiate on the umbilical wall. They strengthen into feeble umbilical bullae which give rise to pairs of straight, rectiradiate ribs. There are also occasional non-bullate primaries and short intercalated ribs to give a total of 36 ribs at the umbilical seam of the succeeding whorl. There are two flat-topped lateral swellings that disrupt the rib. Eleven low, broad, weak ribs arise at the umbilical seam of the outer whorl and develop into coarse umbilical bullae that strengthen progressively as size increases. The bullae give rise to a pair of ribs, the adapical one rursiradiate, the adapertural one rectira-



Text-fig. 10. *Pervinqueria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19132 (ex D.1264), the holotype of *Deiradoceras varinodatum* van Hoepen, 1931, the original of van Hoepen (1931, p. 54, text-fig. 13, refigured in 1941 as his text-figs 36, 37), from his bank 14 at locality 51.

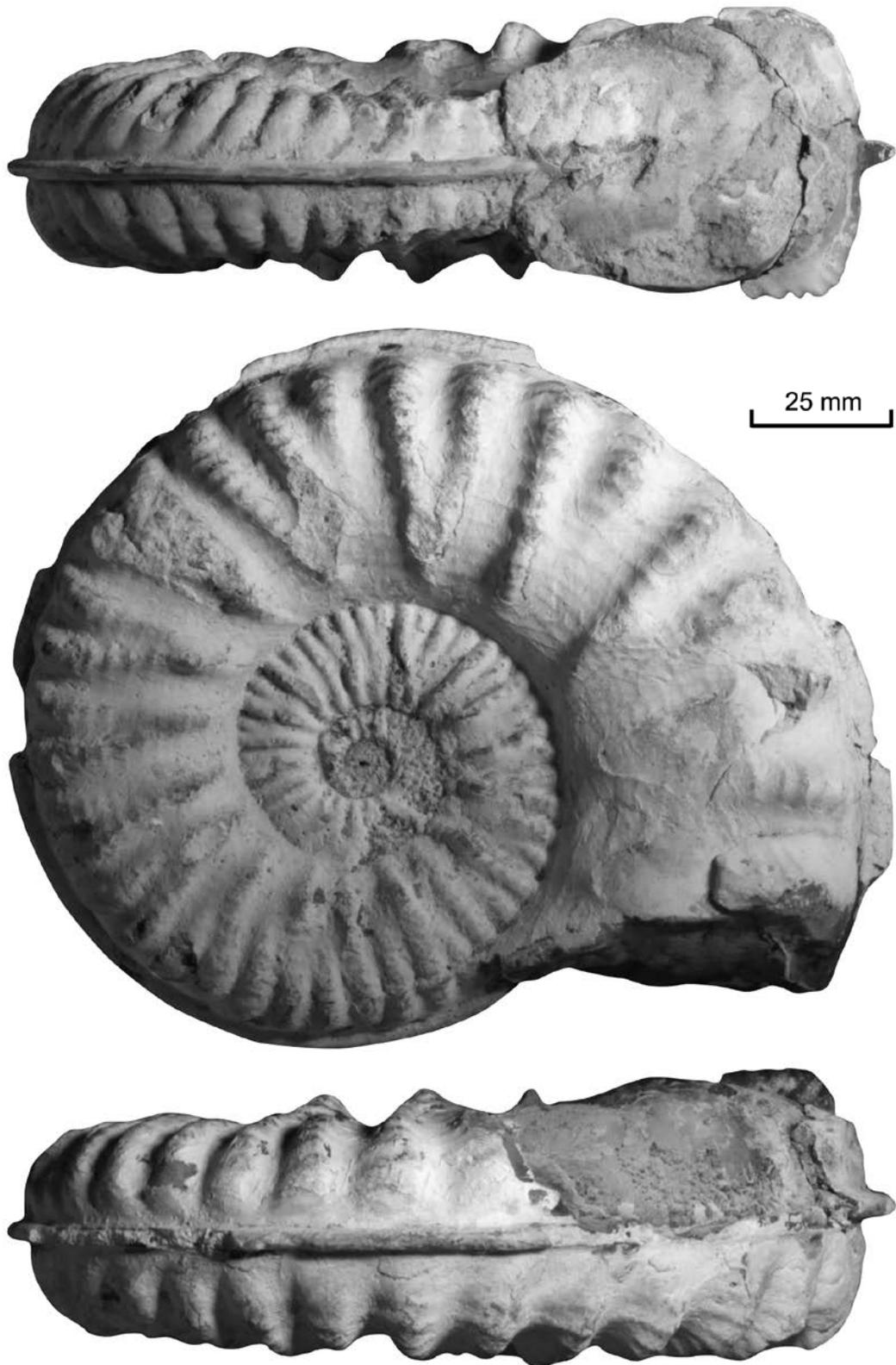
diate, while there are also rectiradiate single primary ribs, to give a total of 19 ribs per half whorl at the ventrolateral shoulder. The ribs strengthen markedly on the ventrolateral shoulder, developing into an incipient and not clearly differentiated bulla, then declining and effacing, leaving a smooth zone on either side of the siphonal keel. Spiral ridges are present over all of the surface of the shell, and are most conspicuous on the ventrolateral shoulders. It is interpreted as a compressed variant of *prerostrata* with a high density of crowded ribs on the inner whorls. None of van Hoepen's other cited specimens have been traced.

The holotype of *Pervinqueria (Deiradoceras) varicostatum* van Hoepen, 1931 is SAM PCZ 19119 (ex D.2567), the original of van Hoepen (1931, p. 54, text-fig. 14; 1941, p. 78, figs 38, 39), from bank 10 at locality 51. Van Hoepen (1931) mentioned a total of five specimens from banks 10 and 12 at locality 51.

The holotype (Text-fig. 11) is almost wholly septate, and retains some shell material. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19119 c	155.0	46.9 (30.3)	59.9 (38.6)	00.78	61.4
intercostal	(100)	42.5 (27.4)	59.9 (38.6)	00.71	(39.6)

Coiling is very evolute, with 37% of the previous whorl covered. The whorl section is compressed trapezoidal, with the greatest breadth low on the flanks in intercostal section and at the umbilical bullae in costal section, the ventrolateral shoulders broadly rounded, the venter feebly convex, with a strong siphonal keel. The umbilicus is shallow, and comprises 39.6% of the diameter, the feebly convex umbilical wall outwardly inclined, the umbilical shoulder broadly rounded. On the penultimate whorl, 20–22 ribs per whorl arise at the umbilical seam and strengthen into small elongate bullae, perched on the umbilical shoulder. These give rise to pairs of coarse, rounded, straight ribs, the adapical rib of each pair rursiradiate, the adapertural rib recti- to feebly rursiradiate. There are a few non-bullate primaries, to give a total of 39–40 ribs on the outer flank. There are 16 umbilical bullae



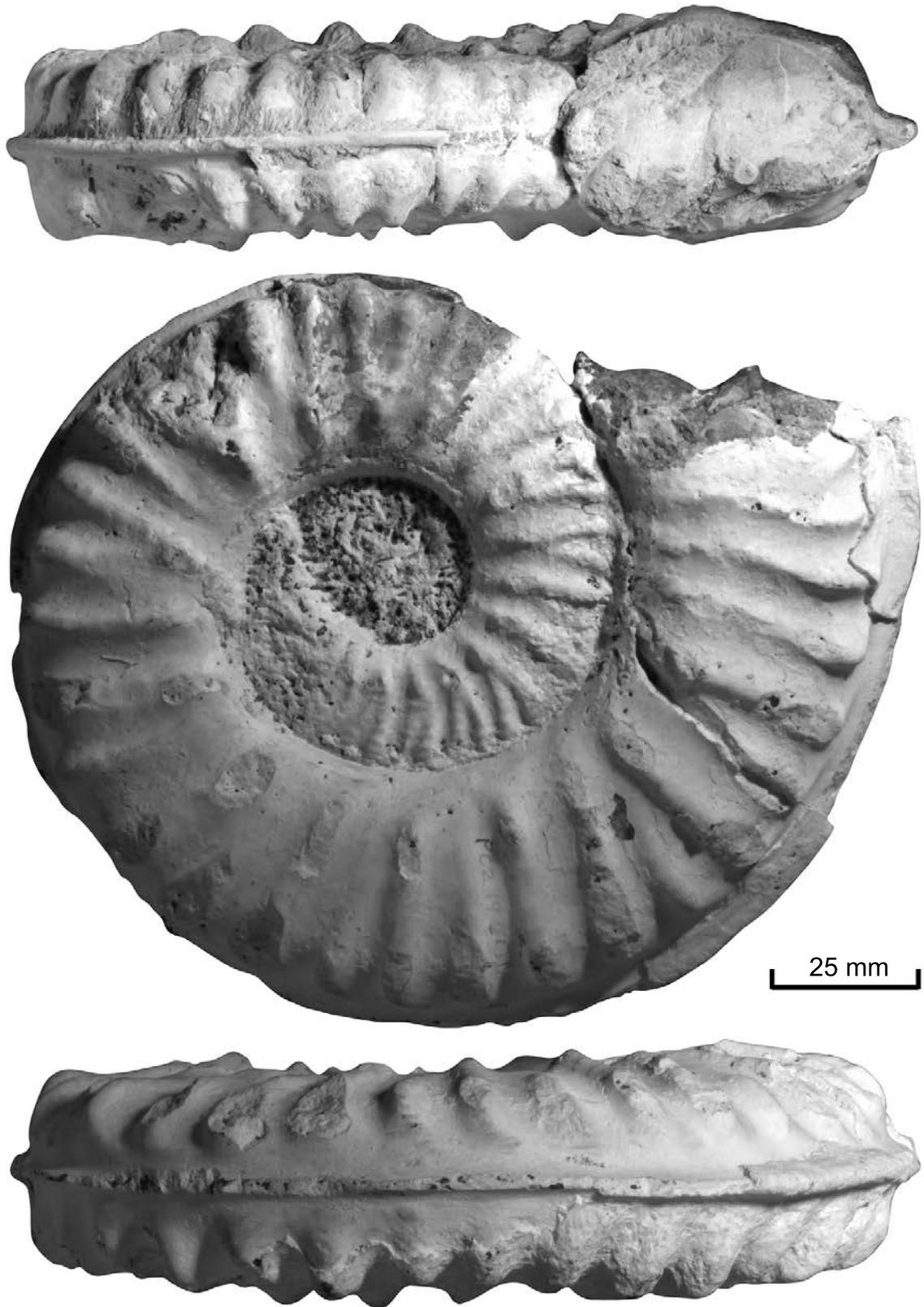
Text-fig. 11. *Pervinqueria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19199 (ex D.2567), the holotype of *Deiradoceras varicostatum* van Hoepen, 1931, the original of van Hoepen (1931, p. 54, text-fig. 14; 1941, p. 78, text-figs 38, 39), from his bank 10 at locality 51.



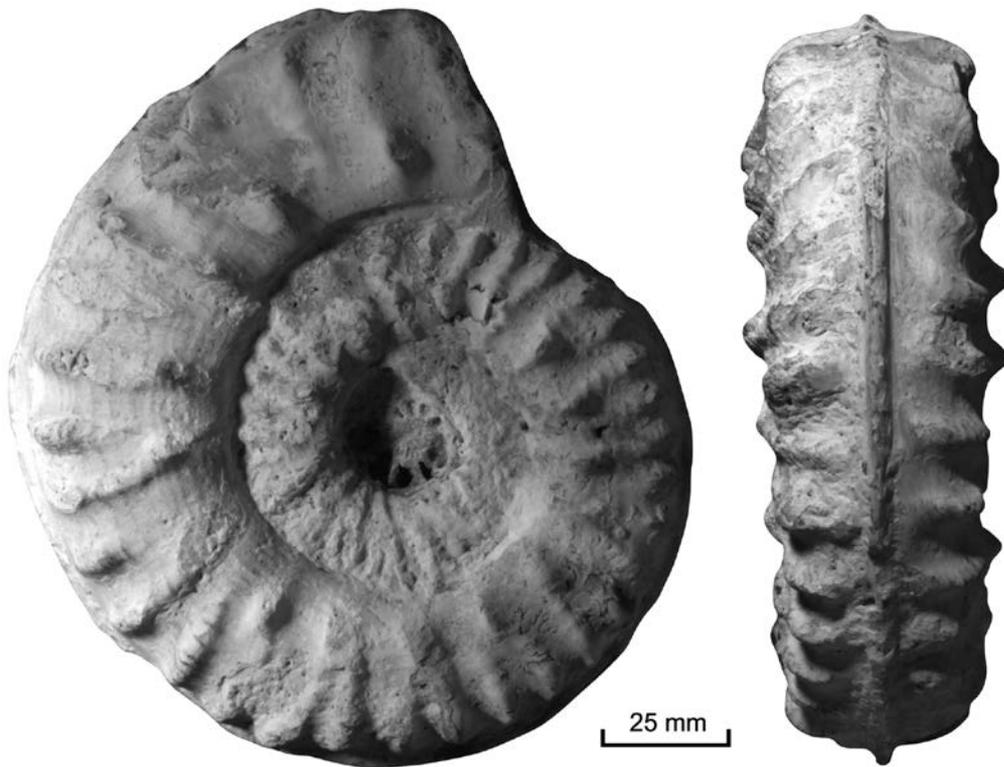
Text-fig. 12. *Pervinquieria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa, SAM PCZ 19202 (ex D.2378), the original of *Deiradoceras varicostatum* van Hoepen, 1931 (p. 54; 1941, p. 77, pl. 13), from his bank 10 at locality 51.

on the outer whorl that become increasingly widely spaced as size increases. They give rise to pairs of coarse ribs at the adapical end of the outer whorl. The ribs broaden and coarsen across the flanks and ventrolateral shoulders, without developing a clearly

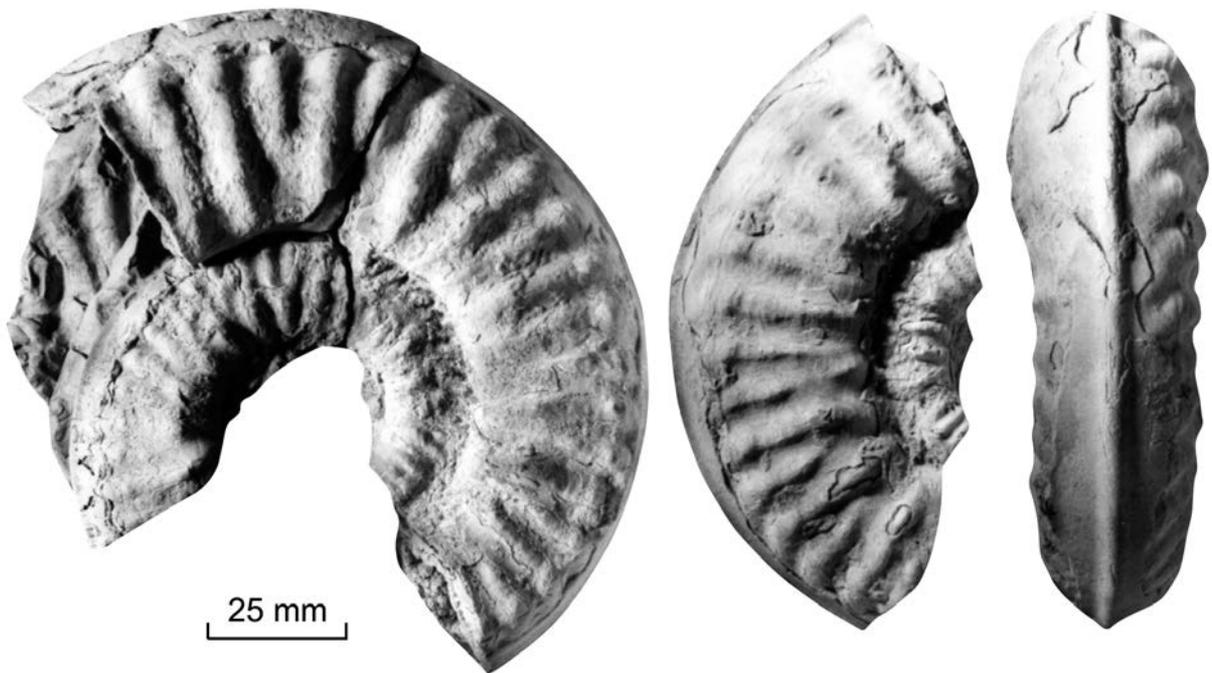
differentiated ventrolateral tubercle, broaden and decline before reaching the strong siphonal keel. Spiral ridges are well developed over all of the surface of the shell. The style of ornament and the change from penultimate to outer whorl matches that of specimens



Text-fig. 13. *Pervinqueria (Deiradoceras) preostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19201 (ex D.2378), the original of *Deiradoceras varicostatum* van Hoepen, 1931 (p. 54; 1941, p. 77), from his bank 10 at locality 51.



Text-fig. 14. *Pervinqueria (Deiradoceras) prerostrata* (Spath, 1921) from KwaZulu-Natal, South Africa; SAM PCZ 19230 (ex D.2380), the holotype of *Deiradoceras exilis* van Hoepen, 1941 (p. 78, text-figs 40, 41, pl. 14), from near Beacon 624, corresponding to locality 54 of Kennedy and Klinger (1975).



Text-fig. 15. *Pervinqueria (Deiradoceras) recurvicostata* (van Hoepen, 1941) from KwaZulu-Natal, South Africa; SAM PCZ 19204 (ex D. 2381), the holotype, the original of van Hoepen (1941, p. 80, pl. 15), from 300–400 m west of Beacon 624, locality 54 of Kennedy and Klinger (1975).

referred to *prerostrata* by van Hoepen, the only obvious difference being the compressed whorls and more subdued ribbing of *varicostata*, most obvious on the inner whorls. It is regarded as an intraspecific variant.

SAM PCZ 19202 (*ex* D.2378) (Text-fig. 12) is the original of van Hoepen (1931, p. 54; 1941, p. 77, pl. 13), from bank 10 at locality 51. The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19202 c	180 (100)	46.3 (25.7)	66.3 (36.8)	0.7	81.9 (45.5)

It is a near-complete adult; the ribs arise from bullae, predominantly in pairs on the adapical half of the outer whorl, on the adapertural half the bullae decline in strength, and single rursiradiate primary ribs alternate with long or short intercalated ribs. The last few ribs lack umbilical bullae and weaken.

SAM PCZ 19201 (*ex* D.2378; Text-fig. 13) is the original of van Hoepen (1931, p. 54; 1941, p. 77), from bank 10 at locality 51. It is a complete adult with an estimated maximum diameter of 190–200 mm; loss of umbilical bullae and weakening of the last few ribs indicate maturity.

The holotype of *Deiradoceras exilis* is SAM PCZ 19230 (*ex* D.2380), the original of van Hoepen (1941, p. 78, text-figs 40, 41; pl. 14), from near Beacon 624, corresponding to locality 54 of Kennedy and Klinger (1975). The dimensions are as follows:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19230	160.0 (100)	– (–)	48.5 (30.3)	–	76.6 (47.90)

The poorly preserved penultimate whorl of the holotype (Text-fig. 14) is more finely and densely ribbed than in the holotype of *prerostrata*, and closer to that of specimens referred to *varicostata* by van Hoepen (Text-fig. 11 herein), while the whorl proportions are intermediate between those of specimens referred to *prerostrata* and *varicostata* by van Hoepen. There are 17 coarse umbilical bullae on the outer whorl, corresponding to 34 ribs at the ventrolateral shoulder.

We have not seen the holotype of *Deiradoceras linguatum* van Hoepen, 1941 (p. 80, text-figs 42, 43, his D.647), from bank 14 at locality 51. It is a nucleus 38 mm in diameter, and very coarsely ribbed and tuberculate, as in SAM PCZ 19193 (Text-fig. 2C), although this is a much larger individual. Its position in relation to other specimens referred to *prerostrata* is uncertain.

The suture of *Pervinquieria* (*Deiradoceras*) *prerostrata* is quite deeply incised, with bifid E/A and A/U2 and narrow A.

DISCUSSION: Differences between the present species and *P. (D.) recurvicostata* are discussed below, and differences from species assigned to *Cechenoceras* and *Mimeloceras* by van Hoepen will be discussed in a subsequent publication (Kennedy and Klinger 2023b).

Mortoniceras (*Deiradoceras*) *devonense* Spath of Venzo (1936, p. 93 (35), pl. 9 (5), fig. 4), from “Ndabana-Umsinene” is interpreted as a body chamber fragment and part of the penultimate whorl of the present species. *Deiradoceras besairiei* Collignon, 1950 (p. 75, text-fig. 5; pl. 12 (3), figs 3, 4), from the lower Upper Albian of Mokaraha, Madagascar, is no more than an intraspecific variant. Collignon (1950, p. 76) noted that, “Elle est plus voisine de *Deiradoceras bispinosum* van Hoepen... qui comporte une ornementation presque identique. Mais *D. bispinosum* a des tours bien moins élevés, plus étroits et un ombilic beaucoup plus large.” There are in fact no significant differences in proportions between his specimens and the present material. *Deiradoceras* (*Mimoceras*?) *mokarahaense* Collignon, 1950 (p. 77, text-fig. 8, pl. 13 (4), fig. 3) is based on a worn 120° sector of body chamber and penultimate whorl that corresponds to the body chamber of SAM PCZ 19115 (Text-fig. 7). The larger fragment assigned to *mokarahaense* by Collignon in 1963 (pl. 312, fig. 1319) is close to the holotype of *Subschloenbachia bispinosa* (Text-fig. 6). *Deiradoceras fibulatum* Collignon, 1950 (p. 76, pl. 13(4), fig. 2), also from Mokaraha, is a curiosity. Based on a 90° whorl fragment of phragmocone, it has the umbilical and ventral tubercles linked by pairs of ribs, a unique condition in the Pervinquieriinae. The condition is less obvious in the fragment figured by Collignon in 1963 (pl. 312, fig. 1320).

OCCURRENCE: Lower Upper Albian, northern KwaZulu-Natal, Mozambique, Angola, Venezuela, Texas, Bulgaria and northern Spain. There are also possible records from Algeria and Japan.

Pervinquieria (*Deiradoceras*) *recurvicostata*
(van Hoepen, 1941)
(Text-fig. 15)

1941. *Deiradoceras recurvicostatum* van Hoepen, p. 80, pl. 15.

2018. *Mortoniceras* (*Deiradoceras*) *recurvicostatum* van Hoepen 1941; Klein, pp. 130, 136.

TYPE: The holotype, by original designation, is SAM PCZ 19204 (*ex* D.2381), the original of van Hoepen (1941, p. 80, pl. 15), from 300–400 m west of Beacon 624/locality 54.

DIMENSIONS:

	D	Wb	Wh	Wb:Wh	U
SAM PCZ 19204 costal	139.3 (100)	39.6 (28.4)	44.7 (32.1)	0.89	62.3 (44.7)

DESCRIPTION: Only the fragmentary inner whorls of the holotype survive (Text-fig. 15); the fragment of body chamber figured by van Hoepen (1941) has not been traced. Coiling is very evolute, the broad, shallow umbilicus comprising 44.7% of the diameter, the umbilical wall convex and subvertical, the umbilical shoulder broadly rounded. The whorl section is compressed, rounded-polygonal in intercostal section, with the greatest breadth low on the flanks, the inner flanks feebly convex, the outer flanks convergent, the venter obtusely fastigiate. The greatest breadth is at the umbilical bullae in costal section. There are 13–14 coarse transverse ribs on the umbilical wall per half whorl that strengthen into coarse, blunt umbilicolateral bullae. These give rise to pairs of strong, coarse, rursiradiate ribs on the smaller whorl fragment, with occasional shorter intercalated ribs. There is a transition from coarse bullae giving rise to pairs of ribs to alternating coarse bullate ribs and shorter intercalated ribs. All ribs bear a conical ventrolateral tubercle from which the ribs sweep back to form an acute adapically directed ventral chevron, the ribs declining and effacing, leaving a smooth zone on either side of the coarse siphonal keel. There are traces of spiral ridges, most obvious on the outer flanks and ventrolateral shoulders.

DISCUSSION: This is a very distinctive species, differing from other *Deiradoceras* from KwaZulu-Natal in the evolute coiling, compressed whorl section, umbilicolateral rather than umbilical bullae, and a ventral chevron directed adapically rather than adaperturally.

OCCURRENCE: As for type.

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